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Dynamics of a class of 3–dimensional Lotka–Volterra systems

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Abstract: We provide the complete dynamics of the Lotka–Volterra differential system

$$\dot{x} = x(ay - cz), \quad \dot{y} = y(bz - ax), \quad \dot{z} = z(cx - by),$$

where a, b, c are positive parameters and x, y, z are in the positive octant of $\mathbb{R}^3$. In particular we show that this system is completely integrable, i.e. it has two independent first integrals. Fixing one of these first integrals we obtain invariant triangles in the positive octant of $\mathbb{R}^3$. The dynamics of the system on each one of these invariant triangles is given by an equilibrium point surrounded by periodic orbits, i.e. by a center. In short all the orbits of these system are either equilibrium points, or periodic orbits.

This nonlinear differential system models, under the conservation of mass, a cycle of irreversible autocatalytic reactions between the different states of three macromolecules and allows to describe stable chemical oscillations.

1. Introduction and statement of the main results

In 1910 in the work [16] of A.J. Lotka's appeared for the first time the now called Lotka-Volterra systems, and also Lotka in 1920 considered the system

$$\frac{dx}{dt} = x(\alpha - \beta y), \quad \frac{dy}{dt} = y(-\gamma + \delta x),$$

to model the interectation between an herbivorous animal and a plant (see [17]). Here the number of preys and predators are denoted by x and y, while the interaction between the two species is given by the real parameters α, β, γ and δ, which are positive. Later on in 1926 Volterra [21] developed the model of Lotka for explaining the relationship

between fish and predatory fish. In 1936 Kolmogorov [8] extended these systems to degree greater than two.

Lotka–Volterra as well as Kolmogorov systems have been generalized for analyzing the dynamics of the interaction among several species, and to model the dynamics in many distinct areas, see for instance [1, 2, 3, 7, 9, 10, 12, 13, 14, 19, 22] and the references therein).

In biochemistry the pioneering work of Wyman [23] models the autocatalytic chemical reactions. When the law of mass conservation is considered it was proved in [5] that the autocatalytic chemical reactions between x_i, $i = 1, \ldots, n$ are governed by the differential system

$$\begin{aligned} \dot{x}_1 &= x_1(k_1x_2 - k_nx_n), \\ \dot{x}_2 &= x_2(k_2x_3 - k_1x_1), \\ &\cdots \\ \dot{x}_n &= x_n(k_nx_1 - k_{n-1}x_{n-1}), \end{aligned} \tag{1}$$

where the parameters satisfy $k_i \in \mathbb{R}^+ \setminus \{0\}$.

When $n = 3$ system (1) can be written as

$$\dot{x} = x(ay - cz), \quad \dot{y} = y(bz - ax), \quad \dot{z} = z(cx - by), \tag{2}$$

where a, b, c are positive parameters. As far as we know system (1) appeared by the first time in the paper of Di Cera et al. [5]. These authors obtained numerically some information about the dynamics of system (1).

The polynomial vector field associated to the differential system (2) is

$$X = x(ay - cz)\frac{\partial}{\partial x} + y(bz - ax)\frac{\partial}{\partial y} + z(cx - by)\frac{\partial}{\partial z}.$$

Let U be an open and dense subset of $\mathbb{R}^3$. If there exists a non-locally constant analytic function $H\colon U \to \mathbb{R}$ such that H is constant on all orbits $(x(t), y(t), z(t))$ of system (2) contained in U, then the function H is called a *first integral* of system (2) on U. Hence H is a first integral on U if and only if $XH = 0$. We say that two first integrals H_1 and H_2 defined in U are *independent* if their gradients are independent in all the points of U except perhaps in a zero Lebesgue measure set. If system (2) has two independent first integrals, then we say that it is *completely integrable*, and the trajectories of system (2) in U are contained in the curves $\{H_1(x, y, x) = constant\} \cup \{H_2(x, y, x) = constant\}$.

Our main result characterizes the global dynamics of system (2) in the positive octant of $\mathbb{R}^3$.

Theorem 1. *For system* (2) *the following statements hold.*

(*a*) *System* (2) *is completely integrable with the two independent first integrals*

$$H_1 = x + y + z \quad \textit{and} \quad H_2 = x^b y^c z^a.$$

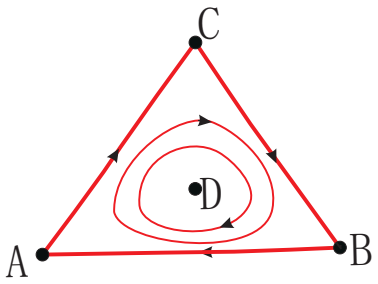

FIGURE 1. Phase portrait of system (2) in the triangle L_h. Here $A = P_h^x$, $B = P_h^y$, $C = P_h^z$ and $D = P_h^+$.

(*b*) *The phase portrait of system* (2) *on the invariant triangle*

$$T_\kappa = \{(x, y, z) |\ x + y + z = \kappa, x \geq 0, y \geq 0, z \geq 0\}$$

with $\kappa > 0$ *is topologically equivalent to the one of Figure* 1.

We note that statement (a) of Theorem 1 is already well known, see for instance Theorem 1 of [11, 15].

The proof of Theorem 1 is given in section 2.

2. Proof of Theorem 1

Since the proof of statement (a) is very short we provide it.

Proof of statement (*a*) *of Theorem 1.* It follows by direct calculations showing that

$$XH_i = x(ay - cz)\frac{\partial H_i}{\partial x} + y(bz - ax)\frac{\partial H_i}{\partial y} + z(cx - by)\frac{\partial H_i}{\partial z} = 0,$$

for $i = 1, 2$. □

Proof of statement (*b*) *of Theorem 1.* Since H_1 is a first integral, the planes $x+y+z =$ *constant* are *invariant* for the flow of system (2), i.e. if an orbit has a point on one of such planes the whole orbit is contained in that plane. Then for studying the dynamics of system (2) in the positive octant it is sufficient to study the dynamics of system (2) in each plane $x + y + z = \kappa$ for all $\kappa > 0$.

We note that the plane $x = 0$ is invariant for the flow of system (2), because $\dot{x}|_{x=0} = 0$. For the same reason also the planes $y = 0$ and $z = 0$ are invariant.

We denote by T_κ the restriction of the plane $x + y + z = \kappa$ to the positive octant of $\mathbb{R}^3$. So we must have $\kappa \geq 0$. If $\kappa = 0$ then T_κ is just the origin. If $\kappa > 0$ then T_κ is a triangle being their boundaries denoted as T_κ^x, T_κ^y and T_κ^z. Note that T_κ^x, T_κ^y and T_κ^z are invariant and are located on the yz, xz and xy planes, respectively. Indeed, this follows from the invariance of the three coordinate planes and of the plane T_κ. The

three vertices of T_κ are denoted by $p_\kappa^x = (h, 0, 0)$, $p_\kappa^y = (0, h, 0)$ and $p_\kappa^z = (0, 0, h)$. They are equilibrium points of system (2) and are located on the x, y and z axes, respectively.

In view of the above explanation we only need to study the global dynamics of system (2) on the triangle T_κ. Restricting system (2) to the invariant set T_κ we obtain

$$\begin{aligned} \dot{x} &= x(-c\kappa + cx + (a+c)y), \\ \dot{y} &= y - y(-b\kappa + (a+b)x + by). \end{aligned} \tag{3}$$

System (3) additional to the equilibrium points p_κ^x, p_κ^y and p_κ^z (i.e. to the equilibria ($P_\kappa^x = (\kappa, 0)$, $P_\kappa^y = (0, \kappa)$, and $P_\kappa^0 = (0, 0)$ of system (3) once we restrict them to the triangle T_κ), it has the fourth equilibrium point

$$D = \left(\frac{b\kappa}{a+b+c}, \frac{c\kappa}{a+b+c} \right),$$

in T_κ because $a + b + c > 0$. The Jacobian matrix of system (3) is

$$\begin{pmatrix} -ch + 2cx + (a+c)y & (a+c)x \\ -(a+b)y & bh - (a+b)x - 2by \end{pmatrix}.$$

It is easy to show that the equilibria P_κ^x, P_κ^y and P_κ^z of system (3) at the vertices of the triangle T_κ have the eigenvalues $(-a\kappa, c\kappa)$, $(a\kappa, -b\kappa)$ and $(b\kappa, -c\kappa)$, respectively. So these three equilibria are saddles (for more details see for instance Theorem 2.15 of [6]). The equilibrium point D in the interior of the triangle T_κ, has the pair of pure imaginary eigenvalues

$$\pm\sqrt{\frac{abc}{a+b+c}}\, hi, \quad i = \sqrt{-1}.$$

This equilibrium point is a center, because in the triangle T_κ we have defined the first integral

$$H_\kappa(x, y, z) = x^b y^c (\kappa - x - y)^a, \tag{4}$$

of system (3), due to the existence of the first integral H_2 (see statement (a) of Theorem 1). Indeed, by the classical Poincaré–Lyapunov theorem (see [18, 20]), we have that an elementary monodromy equilibrium point (i.e. a focus or a center) of a planar analytic differential system is a center if and only if it has an analytic first integral defined in a neighborhood of it. Using this result and the first integral in (4) we get that the equilibrium point D is a center.

Moreover, using the first integral H_κ we can prove that the periodic orbits of system (3) fill up the interior of L_κ except the equilibria p_κ. So system (2) has the phase portrait in T_κ given in Figure 1 and the proof of statement (b) of Theorem 1 is done. □

3. Conclusions

We analyze the nonlinear differential system proposed by Di Cera et al. [5] which modelizes the autocatalytic chemical reactions between three macromolecules. We provide the complete dynamics of this model in the open positive octant of $\mathbb{R}^3$. First

we prove that this system is completely integrable, showing the existence of two independent first integrals. Moreover, we prove that all their orbits either are equilibrium points or periodic orbits which live on invariant triangles obtained fixing one of the two independent first integrals of the system, see Theorem 1.

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