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STABILITY OF SOLUTIONS OF LOTKA—VOLTERRA DIFFERENTIAL EQUATIONS

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Asymptotic behavior of the Lotka—Volterra system of differential equations is analyzed [1, 2]. The following aspects are considered: behavior of the Lotka-Volterra system for interactions of the predator—prey type with partial limitation, and the over-all stability in a model of competitive type with symmetric matrix of interactions.

1. Introduction. In considering the kinetics of chemical reactions Lotka [1] and, then independently of him, Volterra [2] for describing the dynamics of group numbers that constitute a biological association, had proposed the following system of ordinary differential equations:

$$x_i' = x_i\left(b_i + \sum_{j=1}^{n} a_{ij}x_j\right) \quad (i = 1, \ldots, n) \tag{1.1}$$

where $x_i(t)$ is the count (or mass) of the i-th group of the association (or of the substance taking part in a chemical reaction) at instant t, the constants b_i and a_{ii} define the rate of increase of the i-th group in the absence of any other, the constants a_{ij} define the effect of interaction between groups on the rate of increase, and the prime denotes derivatives with respect to time t.

Recently Volterra obtained some results of a qualitative character on the behavior of solutions $\mathbf{x}(t) = (x_1(t), \ldots, x_n(t))$ of system (1.1) on various assumptions about vector $\mathbf{b} = (b_1, \ldots, b_n)$ and matrix $A = (a_{ij})_{n\times n}$. These results were consolidated and systematized in [3] to which we shall subsequently refer. An exhaustive information on Volterra's mathematical investigations in the field of ecology can be found in [4].

The admissibility of describing the evolution of biological associations by equations of the kind (1.1) was the subject of numerous publications [5]. Some authors of these had noted the insufficient substantiation of two of Volterra's basic assumptions used by him in the derivation of system (1.1). We mean here the principle of collision (in other words conjugate interactions) which makes it possible to limit the right-hand sides of systems (1.1) to quadratic terms, which in turn gave rise to particular complaints about the principle of equivalence [3]. The latter results in the requirement for matrix A to be skew-symmetric and makes system (1.1) conservative, which cannot be substantiated experimentally. It should be pointed out that Volterra himself saw the shortcomings of the indicated principles, and had clearly defined the limits of their applicability [3]. He also obtained various modifications of system (1.1) with arguments for and against the consideration of these, and indicated cases in which theoretical results of investigation of that system and its modifications are well supported by experimental data [3]. The necessity of a detailed analysis of system (1.1) and its possible modifications are stressed in the recent reprint of Kolmogorov s work [6] in which the importance of obtaining "qualitative results on qualitative premises" is indicated. It can be stated at present that the Lotka—Volterra equations represent one of the fundamental concepts of that branch of applied mathematics generated by problems of theoretical ecology [7].

The attention of investigators to system (1. 1) is drawn by its universality that was noted by Lotka [8] who based it on the following general proposition. Let the dynamics of some interacting objects be defined by the system of ordinary differential equations

$$x_i' = X_i(x_1, \ldots, x_n) \quad (i = 1, \ldots, n)$$

If that system is isolated, then the equality $x_i = 0$ implies that $X_i(x_1, \ldots, x_{i-1}, 0, x_{i+1}, \ldots, x_n) = 0$. Using this relationship Lotka concluded that

$$X_i(x_1, \ldots, x_n) = x_i G(x_1, \ldots, x_n) \quad (i = 1, \ldots, n)$$

Function G_i represents in this case the generalized coefficients of relative growth. The simplest expression for such functions is, evidently, linear, i.e.

$$G_i(x_1, \ldots, x_n) = b_i + \sum_{j=1}^{n} a_{ij} x_j \quad (i = 1, \ldots, n)$$

which leads to Eqs. (1. 1).

The above imples that equations of the type (1. 1) are in a certain sense "follow-up" equations after the linear ones, as regards their complexity, in defining the evolution of various interacting objects. Equations of that kind occur in investigations of chemical reaction kinetics [1, 9, 10], of the activity of neutrons [11], in mathematical economics [12, 13], and in sociology [14, 15].

The American mathematician Kerner had constructed statistical mechanics of biological systems [16—18] based on the Lotka—Volterra equations. Some of the gaps in Kerner's works were later filled in [19].

Numerical analysis of Eqs. (1. 1) and comparison of theoretical and experimental data were the subject of numerous papers [20—22]. A graphic method was proposed in [23] for analyzing stability for $n \leqslant 3$ by investigating isoclines. The conditions of stability of the equilibrium position $x^* > 0$ of system (1. 1) in the "small" are presented in [24].

From among Soviet authors we select those who had considered the possible generalizations of Volterra's method [25 — 28].

In concluding this brief survey we draw the attention to two recent publications [29, 30] which provide a detailed exposition of the present state of the problem.

In spite of the considerable number of publications devoted to the analysis of system (1. 1), several problems of qualitative character remain open. Among these the problem of stability is of the greatest interest [31, 32]. In particular, the problem of over-all stability of the equilibrium position of system (1. 1) has not been fully investigated in the case of interaction of the "predator - prey" type with partial limitations, which formally corresponds to the presence in the diagonal of the skew-symmetric matrix A of nonzero elements. This question was considered in [33], however, the proof of the result derived there contains a substantial gap which casts doubt on its validity. The present work is devoted to the solution of this problem and to the consideration of conditions of stability of points of quiescence of system (1. 1) in the case of interactions of the competing type, i.e. when $a_{ij} \leqslant 0$ $(i, j = 1, \ldots, n)$.

2. Preliminary remarks. The statement of the considered problem implies that only nonnegative solutions of system (1. 1) have a physical meaning. We denote by R_+^n the nonnegative orthant of the n-dimensional Euclidean space R^n. The form of system

(1.1) clearly shows that when $\mathbf{x}(0) \in R_+^n$, then $\mathbf{x}(t) \in R_+^n$ for all $|t| < \infty$, i.e. that R_+^n is an invariant set of system (1.1). This property makes it possible to consider R_+^n as the phase space of the investigated system.

The coordinates of the equilibrium position are determined by the system of equations

$$x_i\left(b_i + \sum_{j=1}^{n} a_{ij}x_j\right) = 0 \quad (i = 1, \ldots, n) \tag{2.1}$$

It can be shown that this system has not more than 2^n isolated solutions. The greatest interest is attached to the analysis of the nontrivial equilibrium position, i.e. such that all components of vector $\mathbf{x}^*$ which is the solution of system (2.1) are positive.

Let us assume that such equilibrium position exists. In this case it is convenient to analyze system (1.1) by first reducing it to the form

$$x_i' = x_i \sum_{j=1}^{n} a_{ij}(x_j - x_j^*) \quad (i = 1, \ldots, n) \tag{2.2}$$

In the case of skew-symmetric matrix A this form makes it possible to obtain without too much trouble the expression for the first integral of system (2.2). In fact, if $A = -A^T$, the quadratic form

$$\sum_{i,j=1}^{n} a_{ij}x_ix_j \equiv 0, \quad \forall \mathbf{x} \in R^n$$

Let us try to find such function $V: R_+^n \to R^1$ that its derivative along the trajectory of system (2.2) would be expressed as follows:

$$V^\cdot(\mathbf{x}) = \sum_{i=1}^{n} \frac{\partial V(\mathbf{x})}{\partial x_i} x_i' \equiv \sum_{i,j=1}^{n} a_{ij}(x_j - x_j^*)(x_i - x_i^*) \equiv 0 \tag{2.3}$$

It will be seen that the partial derivatives of function V must satisfy relationships

$$\frac{\partial V(\mathbf{x})}{\partial x_i} = \frac{x_i - x_i^*}{x_i} \quad (i = 1, \ldots, n)$$

whose integration yields

$$V(\mathbf{x}) = \sum_{i=1}^{n} (x_i - x_i^* \ln x_i) \tag{2.4}$$

It is exactly in this way that function V was introduced by Volterra [3]. It is obvious that function V is for all $\mathbf{x} > 0$ convex downward and reaches its minimum $V(\mathbf{x}^*) = 0$ at point $\mathbf{x} = \mathbf{x}^*$. Hence if $A = -A^T$, $\mathbf{x}^*$ is a singular point of the kind of a generalized center.

It is shown in [34] that a construction similar to (2.4) may be useful in investigations of stability not only of system (1.1), but also of equations of another kind.

It is sometimes advantageous to consider besides function (2.4) as the Liapunov function for system (1.1) also function

$$U(\mathbf{x}) = \sum_{i=1}^{n} \alpha_i(x_i - x_i^* \ln x_i) \tag{2.5}$$

which was also introduced by Volterra [3]. The use of function (2.5) is expedient if the structure of matrix A is $A = \operatorname{diag}(\beta_i)D$, where $\beta_i \neq 0$ $(i = 1, \ldots, n)$, and matrix D is skew-symmetric. Then, setting $\alpha_i = 1/\beta_i$ we obtain $U^\cdot(\mathbf{x}) \equiv 0$.

If system (1.1) in addition to the principle of equivalence which determines the previously defined form of matrix A, is subjected to limitation, negative terms $a_{ii} < 0$ appear at the matrix diagonal. In that case the derivative of function V along the system trajectory is

$$V^{\cdot}(\mathbf{x}) = \sum_{i=1}^{n} a_{ii}(x_i - x_i^*)^2 \qquad (2.6)$$

If $a_{ii} < 0$ for all $i = 1, \ldots, n$, $V^{\cdot}(\mathbf{x}) < 0$ for $\mathbf{x} \neq 0$ and, consequently, the equilibrium position $\mathbf{x}^*$ is asymptotically stable in the large [3]. We remind that here and in what follows we consider only solutions that begin in R_+^n. If, however, the limitation is partial, i.e. $a_{ii} < 0$ for $i = 1, \ldots, r$ and $a_{ii} = 0$ for $i = r + 1, \ldots, n$, which is closer ro actual situations, it is not possible to guarantee asymptotic stability without additional limitations. The corresponding sufficient conditions that guarantee asymptotic stability in the large are formulated below.

3. Interactions of the predator-prey type with partial limitation.

Theorem 1. Let elements of matrix A satisfy the following conditions: $a_{ij} = -a_{ji}$ when $i \neq j$; $a_{ii} < 0$ when $i = 1, \ldots, r$; $a_{ii} = 0$ when $i = r + 1, \ldots, n$, and let system (1.1) have an isolated equilibrium position $\mathbf{x}^* > 0$.. Finally, let the system of $(2r + 1)$ equations in $(n - r)$ variables

$$\text{a)} \quad \sum_{j=r+1}^{n} a_{ij}(x_j - x_j^*) = 0 \quad (i = 1, \ldots, r) \qquad (3.1)$$

$$\text{b)} \quad \sum_{j=r+1}^{n} a_{ij}x_j \sum_{k=r+1}^{n} a_{jk}(x_k - x_k^*) = 0 \quad (i = 1, \ldots, r)$$

$$\text{c)} \quad \sum_{i=1}^{n} (x_i - x_i^* \ln x_i) = c$$

have no nonisolated solutions. Then any solution $\mathbf{x}(t)$ of system (1.1) with initial conditions $\mathbf{x}(0) > 0$ is bounded, and indefinitely tends to point $\mathbf{x}^*$ when $t \to \infty$

Proof. Let us prove that function (2.4) satisfies conditions of the Barbashin-Krasovskii theorem [35].

It was already indicated that $V(\mathbf{x}) > 0$ when $\mathbf{x} > 0$ and $\mathbf{x} \neq 0$. It follows from (2.6) that $V^{\cdot}(\mathbf{x}) \leqslant 0$ for all $\mathbf{x} \in R^n$. It is thus necessary to show that surfaces of level $V(\mathbf{x}) = c$ are bounded for $\mathbf{x} > 0$ and $c > V(\mathbf{x}^*)$, and that the set $V^* = \{\mathbf{x}\colon \mathbf{x} > 0,\ V^{\cdot}(\mathbf{x}) = 0\}$ does not contain integral trajectories, except the quiescent point $\mathbf{x}^*$. The boundedness of the surface of level $V(\mathbf{x}) = c$ is almost obvious. It is sufficient to note that for considerable c it is possible to find λ that is independent of c and such that the surface $V(\mathbf{x}) = c$ lies entirely inside the hypercube $0 \leqslant x_i \leqslant \lambda c$ $(i = 1, \ldots, n)$. This problem was considered in detail in [19].

Let us write the explicit expression for the set V^*. From the relationship

$$\sum_{i=1}^{r} a_{ii}(x_i - x_i^*)^2 = 0$$

we obtain

$$V^* = \{\mathbf{x}\colon x_i = x_i^* \text{ for } (i = 1, \ldots, r),\ \mathbf{x} > 0\}.$$

If we assume that $\mathbf{y}(t) \equiv (y_1(t), \ldots, y_n(t)) > 0$ is the solution of system (1.1) such that $\mathbf{y}(t) \in V^*$ when $|t| < \infty$, we obtain

$$\text{a)} \quad y_i'(t) = x_i^* \sum_{j=r+1}^{n} a_{ij}(y_j(t) - x_j^*) \equiv 0 \quad (i = 1, \ldots, r)$$

b) $$\sum_{j=r+1}^{n} a_{ij}y_j'(t) \equiv 0 \Rightarrow$$

$$\sum_{j=r+1}^{n} a_{ij}y_j(t) \sum_{k=r+1}^{n} a_{jk}(y_k(t) - x_k^*) \equiv 0 \quad (i = 1, \ldots, r)$$

c) $$\sum_{i=r+1}^{n} (y_i(t) - x_i^* \ln y_i(t)) = c$$

Thus if system (3.1) has only isolated solutions, then owing to the uniqueness of the quiescent point $\mathbf{x}^*$, the set V^* does not contain integral trajectories. The theorem is proved.

In the majority of cases of investigations of specific objects, of interest are systems that by Andronov-Pontriagin definition are "coarse", i.e. systems whose topological structure does not change for small variations of the right-hand sides of equations. In the considered case it is necessary to see that perturbations of the right-hand sides do not impair the structures of vector $\mathbf{b}$ and matrix A, when formulating the conditions of coarseness. Taking this into account we call system (1.1) coarse, if for fairly small ε_{ij} and η_j $(i, j = 1, \ldots, n)$, such that $(a_{ij} + \varepsilon_{ij}) = -(a_{ji} + \varepsilon_{ji})$ and sign $(a_{ij} + \varepsilon_{ij}) =$ sign (a_{ij}) when $i, j = 1, \ldots, n$, and sign $(b_i + \eta_i) =$ sign (b_i) when $i = 1, \ldots, n$, the system of equations

$$x_i' = x_i\left[(b_i + \eta_i) + \sum_{j=1}^{n} (a_{ij} + \varepsilon_{ij}) x_j\right] \quad (i = 1, \ldots, n) \tag{3.2}$$

and system (1.1) have the same topological structure.

Corollary. If system (1.1) is coarse, the elements of matrix A satisfy the conditions of Theorem 1, and $r \geqslant (n - 1) / 3$ then each solution $\mathbf{x}(t)$ of system (1.1) with initial conditions $\mathbf{x}(0) > 0$ is bounded and indefinitely tends to point $\mathbf{x}^*$ when $t \to \infty$.

Proof. By assumption $r \geqslant (n - 1)/3$, i.e. the number of unknowns in system (3.1) is not greater than the number of equations. If system (3.1) has only isolated solutions, the proof of this corollary follows from Theorem 1. Let us assume that system (3.1) has nonisolated solutions and consider besides (1.1) its perturbed variant, i.e. system (3.2). Taking advantage of the freedom of perturbation selection, we chose these so that system (3.1) has only isolated solutions. For this it is sufficient to choose, for instance, the perturbations so that the rank of matrix composed of the first derivative functions appearing in the perturbed system (3.1) and computed for the considered point is equal $n - r$. Since by Theorem 1 all solutions of system (3.2) with initial conditions $\mathbf{x}_\varepsilon(0) > 0$ are bounded and tend to the quiescent point $\mathbf{x}_\varepsilon^*$, the same statement is valid also for the input system.

However in certain cases it is better to substitute a specific consideration of the structure of set V^* for the above results.

Let us consider a biological association consisting of populations of n species in which each following species is a consumer of the preceding, i.e. the number i species consumes the $i - 1$ species and only the latter, with no natural limitation for all species, except the first whose growth is limited [26]. In that case system (1.1) is of the form

$$\begin{aligned} x_1' &= x_1(b_1 - a_{11}x_1 - a_{12}x_2) \\ x_i' &= x_i(b_i + a_{i,\,i-1}x_{i-1} - a_{i,\,i+1}x_{i+1}) \\ a_{n,\,n+1} &= 0 \quad (i = 2, \ldots, n) \end{aligned} \tag{3.3}$$

Coordinates of the equilibrium position of system (3.3) can be explicitly defined (we omit here the procedure, since it does not present any difficulties).

We define coefficients α_i $(i = 1, \ldots, n)$ of function U (see (2.5)) as follows:

$$\alpha_1 = 1, \quad \alpha_{i+1} = \alpha_i \frac{a_{i,\,i+1}}{a_{i+1,\,i}} \quad (i = 1, \ldots, n-1)$$

For these values of α_i we have $U^{\cdot}(\mathrm{x}) = -a_{11}(x_1 - x_1^*)^2$. We shall show that the set $U^* = \{\mathrm{x}\colon x_1 = x_1^*, \mathrm{x} > 0\}$ does not contain integral trajectories, except the quiescence point $\mathrm{x} = \mathrm{x}^*$. In fact the structure of Eqs. (3.3) is such that the following inferences are justified:

$$\begin{aligned} x_1'(t) &= 0 \Rightarrow x_2(t) = x_2^* \\ x_2'(t) &= 0 \Rightarrow x_3(t) = x_3^* \\ &\cdots\cdots\cdots\cdots \\ x_{n-1}'(t) &= 0 \Rightarrow x_n(t) = x_n^* \end{aligned}$$

which proves the absence of integral trajectories in the set U^*, except the point x^* and, consequently, also the following theorem.

Theorem 2. Let some association consist of species that interact as "predator — prey". Let each following species be a consumer of only the preceding one, and let the growth of the first species be limited. Then, if the association has an equilibrium state $\mathrm{x}^* > 0$, the association evolution is such that for any initial conditions $\mathrm{x}(0) > 0$ $\mathrm{x}(t) \to \mathrm{x}^*$ when $t \to \infty$.

4. Interactions of the competing kind. For this kind of interaction the elements of matrix A are nonpositive and vector $\mathbf{b} > 0$. With certain additional limitations imposed on the interaction mechanism (these limitations were considered in detail in [38]) matrix A proves to be symmetric. It was proposed in (39) to investigate the solutions of system (1.1) with symmetric matrix A by using functions

$$F(\mathrm{x}) = \sum_{i=1}^{n} b_i x_i + \frac{1}{2} \sum_{i,\,j=1}^{n} a_{ij} x_i x_j \tag{4.1}$$

whose derivative along solutions of system (1.1) is of the form

$$F^{\cdot}(\mathrm{x}) = \sum_{i=1}^{n} x_i \left(\frac{\partial F}{\partial x_i}\right)^2 \geqslant 0 \quad \text{for} \quad \mathrm{x} > 0 \tag{4.2}$$

The last inequality with some additional notation will be used for formulating another theorem.

Let $M \subset R_+^n$ be an invariant set of system (1.1) consisting of points of quiescence. Set M consists in the general case of several components of connectedness. We denote by M_+ that of its connectedness components which contains points at positive coordinates, i.e. $M_+ \cap \mathrm{Int}\, R_+^n \neq \varnothing$ ($\varnothing$ denotes an empty set and $\mathrm{Int}\, R_+^n$ the interior of set R_+^n). It is evidently possible to speak of a single component of M_+, since the coordinates of points of quiescence with positive coordinates are determined by the linear system of Eqs. (2.1). Note that when $\det A \neq 0$, then M_+ either consists of a single point $\mathrm{x}^* > 0$ or $M_+ = \varnothing$.

Theorem 3. If matrix $A \leqslant 0$ and vector $\mathbf{b} > 0$, then:

1) the limit set of any bounded solution $\mathrm{x}(t)$ of system (1.1) with initial conditions $\mathrm{x}(0) \geqslant 0$ consists of two quiescence points;

2) the set M_+ is asymptotically stable, if and only if function F reaches its maximum (proper or improper) in it, and

3) all components of set $M \setminus M_+$ are unstable.

Proof. Formulas (4.1) and (4.2) clearly imply that

$$\{\mathbf{x}\colon F(\mathbf{x}) = 0,\ \mathbf{x} \geqslant 0\} = \{\mathbf{x}\colon F^{\cdot}(\mathbf{x}) = 0,\ \mathbf{x} \geqslant 0\} = M$$

and, consequently, the first two statements of the theorem directly follow from the related LaSalle and Chetaev theorems (see [40], pp. 75 and 52, respectively). Validity of the third statement is proved by noting that owing to the inequality $\mathbf{b} > 0$ function F does not reach its local maximum at any of the quiescence points $\mathbf{x}^* \in \mathrm{Fr}\, R_+^n$ ($\mathrm{Fr}\ R_+^n$ is the boundary of set R_+^n).

Corollary. Let $M_+ \neq \varnothing$ and matrix A not have positive characteristic numbers. Then any solution $\mathbf{x}(t)$ of system (1.1) with initial conditions $\mathbf{x}(0) > 0$ tends indefinitely to set M_+ when $t \to \infty$.

Proof. Assuming that $\mathbf{x}^* \in M_+$ and $\mathbf{y} = \mathbf{x} - \mathbf{x}^*$, we obtain for function F the following expression:

$$F(\mathbf{y}) = \frac{1}{2} \sum_{i,j=1}^{n} a_{ij} y_i y_j$$

Thus for function F to reach its maximum at point $\mathbf{x}^*$ it is necessary and sufficient that the matrix does not have positive characteristic numbers.

We stress that in accordance with the corollary formulated above, the stability of set M_+ is determined only by the properties of matrix A and is independent of the linear growth coefficients b_i $(i = 1, \ldots, n)$.

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