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THE RATE OF SATIATION IN A COOPERATIVE SYSTEM

BY
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1. Introduction

An extensive literature in population ecology on deterministic models is devoted to the study of models of the form

$$\dot{x}_i = x_i f_i(x_1, x_2, ..., x_n), \quad i = 1,2,...,n, \tag{1.1}$$

where x_i stands for the population density of the i^{th} species and f_i for the per capita growht rate of the i^{th} species.

One important situation described by (1.1) is in the case where a cooperation between the various species can be observed. Following Hirsch [3,4] the system (1.1) is called cooperative if $\frac{\partial f_i}{\partial x_j} \geqslant 0$, $i \neq j$, namely if an increase to any one species' density results increase to the others. The global behavior of solutions of (1.1) has been discussed by many authors. For instance, Huston and Law [5] examine asymptotic stability under the assumption that there exists a compact set which attracts all (positive) orbits. Also periodic orbits of (1.1) are studied by Smith [7], where a Poincaré-Bendixson like result is given improving a previous result due to Hirsch [3]. Smith also motivated from the behavior of the Lotka-Volterra system

$$\dot{x}_i = x_i \left(r_i + \sum_{j=1}^{n} a_{ij} x_j \right), \quad i = 1,2,...,n \tag{1.2}$$

studied by many authors and expecially by Goh [2] and impossing a monotonicity condition on the derivative Df discuses the global bejavior of (1.1) [8]. Among his results he shows that if (1.1) has no positive equilibrium point, then any solution with positive initial conditions tends to $+\infty$.

In [6] we called (1.1) a job sustem if it is cooperative and furthermore $\frac{\partial f_i}{\partial x_i} < 0$, $i = 1,2,...,n$. There was used the assumption that each f_i is linear

and $r_i = 0$, namely we considered the system

$$\dot{x}_i = x_i \sum_{j=1}^{n} a_{ij} x_j, \quad i = 1,2,...,n. \tag{1.3}$$

In this case the origin is an equilibrium which might be unique. Here we have three possible situations for the behavior of the solutions: Either each solution tends to the origin if $t \to +\infty$, or it tends to a positive state, which depends on the initial value, or it tends to $+\infty$ if the time approaches a finite value (and not $+\infty$). In this last case we have a satiation of the system.

In this paper we want to find the relative rate of this satiation as the time tends to its (finite) limiting value. This will be succeeded by giving a first integral curve for (1.3) and proving that this curve attracts any solution with positive initial condition. More precisely we obtain a first integral curve which is a straight line ℓ with the property that $\mathrm{dist}(x(t), \ell) \to 0$, as t tends to a finite moment T_x for all those solutions x with $x_i(0) > 0$ and $x_i(t) \to +\infty$, as $t \to T_x$. Conditions which guarantee such a convergence to $+\infty$ are also provided.

2. Preliminaries

Let $A = (a_{ij})$ be an $n \times n$ matrix with real elements such that

$$a_{ii} < 0 \text{ and } a_{ij} > 0 \text{ if } i \neq j. \tag{2.1}$$

Then clearly A can be written in the form

$$A = B - sI_{n \times n}, \tag{2.2}$$

where B is a positive $n \times n$ matrix and $s > 0$. $I_{n \times n}$ stands for the $n \times n$ identity matrix. From Perron-Frobenius theory on nonnegative matrices [1] we know that the spectral radius $\rho(B)$ of the matrix B is a positive eigenvalue of B and there exists an eigenvector $z \in R^n$ such that $z_i > 0$, $i = 1,2,...,n$ which corresponds to $\rho(B)$. Any other positive eigenvector of B is a multiple of z. Taking into account these observations we can easily see that if A has another representation $A = B_1 - s_1 I_{n \times n}$, where B_1 is a positive matrix and $s_1 > 0$, then

$$\rho(B_1) - s_1 = \rho(B) - s$$

Our basic assumption on the matrix A is the following:

(H) There exists a vector $u \in R^n$ such that $u_i > 0$, $i = 1,2,...,$ with

$$Au = (1,1,...,1)^T \tag{1}$$

$$AU = UA^T \tag{2}$$

and

$$a_{ij}u_j > 1, \text{ for each } i \neq j, \tag{3}$$

where U is the diagonal matrix diag $[u_1, u_2, ..., u_n]$. Notice that for any matrix K we write K^T to denote its transpose.

Under the assumption (H1) we can prove the following simple but important result:

Lemma 1. Assume that A is an $n \times n$ matrix satisfying (2.1). If the assumption (H1) holds, then for each representation (2.2) of A we have

$$\rho(B) > s \tag{2.3}$$

Proof. Assume that inequality (2.3) does not hold, namely we have $\rho(B) < s$. Then the matrix $-A = sI_{n\times n} - B$ would be an M-matrix, see [1]. Clearly the same happens for the matrix $-A^T = sI_{n\times n} - B^T$. From the theory of M-matrices we know that for each $x \neq 0$ there exists a nonnegative diagonal matrix D_x such that

$$x^T D_x x \neq 0 \text{ and } x^T(-A^T)D_x x \geqslant 0, \tag{2.4}$$

see [1, p. 149, A_4]. Thus for $x = u$ and $D_u = \text{diag}[d_1, d_2, ..., d_n]$ we get on one hand

$$\sum d_i u_i^2 \neq 0$$

and therefore $d_i \geqslant 0$ and $d_{i_o} > 0$, for at least one index i_o, and on the other hand

$$u^T(-A^T)D_u u = -(Au)^T D_u u = -\sum d_i u_i < 0,$$

which contradicts the second inequality in (2.4). This proves the lemma.

Consider now the condition (H2). This means that

$$a_{ij}u_j = a_{ji}u_i, \text{ for all } i,j \tag{2.5}$$

and therefore taking into account (H1) we get that

$$u_i = \left(\sum_l a_{ji}\right)^{-1}, \quad i = 1,2,...,n,$$

which is the solution of the system of equations (H1), (H2). Clearly (H2) (or (2.5)) means that the matrix $\bar{A} = AU$ is a symmetric $n \times n$ matrix.

3. The main results

As we said in the introduction, our subject of study in this paper is the system of differential equations

$$\dot{x}_i = x_i \sum_{j=1}^{n} a_{ij} x_j. \tag{3.1}$$

Here assume that the numbers a_{ij} satisfy (2.1) and let $A = (a_{ij})$. Also assume for a moment that A satisfies (H1) and consider the convex cone

$$C = \{ x \in R^n : \sum_i a_{ij} x_j \geqslant 0 \}.$$

The straight line

$$\ell : x = su, \quad s \geqslant 0 \tag{3.2}$$

is a path into the cone C and we shall show the following:

Theorem 1. The straight line $\ell : x = su$, $s \geqslant 0$ is an integral curve for system (3.1), which remains into the cone C.

Proof. Setting $x_i(t) = s(t)u_i$, substituting into (3.1) and taking into account (H1) we get

$$\dot{s}(t)u_i = s(t)u_i \sum_j a_{ij} s(t) u_j = s^2(t) u_i,$$

and so

$$\dot{s}(t) = s^2(t),$$

which does not depend on i. This proves the result.

Theorem 1 shows also that the solution x of (3.1) which starts from a point $s_o u$ of the line (3.2) will remain on it for all time $t \in [0, s_0^{-1})$. This time interval is the maximal right interval of existence of the solution x and it is such that

$$\lim_{t \to \frac{1}{s_0}} x_i(t) = +\infty,$$

for all $i = 1, 2, \ldots, n$.

Moreover this result holds not only for this particular solution, but also for all solutions starting from a point x_0 with positive components. Indeed we have the following result:

Theorem 2. Let A satisfies (2.1) and (H1). Then each solution x of system (3.1) with positive initial value remains positive for all time of its existence and for some T_x with $0<T_x<+\infty$ we have

$$\lim_{t\to T_x^-} x_i(t)=+\infty,$$

for all indices $i=1,2,...,n$.

Proof. From Lemma 1 we have that $\rho(B)>s$, where B is any positive matrix and $s>0$ being such that $A=B-sI_{n\times n}$. Now the result follows from [6].

We are now ready to state and prove our main result of this paper.

Theorem 3. Consider the system of differential equations (3.1), where assume that the matrix A satisfies (2.1) and condition (H). If x is any solution of (3.1) with positive initial state and maximal interval of existence $[0,T_x)$ then

$$\lim \operatorname{dist}(x(t),\mathfrak{L})=0, \tag{3.3}$$

and $\mathfrak{L}$ is an asymptote for all solutions. Thus $\mathfrak{L}$ is an integral surve for (3.1) and also an attractor for (3.1) having the positive orthant R_+ as its region of attraction.

Proof. Let x(t) be a solution of (3.1) such that $x_i(0)>0$, $i=1,2,...,n$ and let $[0,T_x)$ be its (bounded) maximal existence interval. From Theorem 1 we can assume that $x(0)\notin\mathfrak{L}$.

Let $y_i=\dfrac{x_i}{u_i}$, $i=1,2,...,n$ and let $\bar{a}_{ij}=a_{ij}u_j$, for all i,j. Then clearly $y=(y_1,y_2,...,y_n)^T$ is a solution of the system

$$\dot{y}_i=y_i\sum_j \bar{a}_{ij}y_j \tag{3.4}$$

such that $y_i(0)>0$, for all indices $i=1,2,...,n$. Under this transformation the straight line $\mathfrak{L}$ is transformed into $\mathfrak{L}_1$, where

$$\mathfrak{L}_1: y=sl=(s,s,...,s)^T,\quad s\geqslant 0.$$

So, in order to prove (3.3) it is enough to show that for each i,j

$$\lim_{t\to T_x} |y_i(t)-y_j(t)| = 0.$$

Indeed, let t be fixed. The ith component of the orthogonal projection of the point $x(t)$ to the line ℓ is the point

$$p_i x(t) = \frac{1}{|u|^2}\sum_j x_j(t)u_j\cdot u_i$$

and therefore for some i_o, j_o we have

$$\operatorname{dist}(x(t),\ell) = \left(\sum [x_i(t)-p_i x(t)]^2\right)^{\frac{1}{2}} \leqslant$$

$$\leqslant n^{1/2}\left|x_{i_o}(t) - \frac{1}{|u|^2}\sum_k x_k(t)u_k u_{i_o}\right|$$

$$= n^{1/2}\left|y_{i_o}(t)u_{i_o} - \frac{1}{|u|^2}\sum y_k(t)u_k\, u_{i_o}\right|$$

$$= n^{1/2}\left||u|^2 y_{i_o}(t) - \sum_k y_k(t)u_k^2\right|\cdot\frac{u_{i_o}}{|u|^2}$$

$$\leqslant n^{1/2}\sum_k u_k^2|y_{i_o}(t)-y_k(t)| \leqslant n^{1/2}|u|^2|y_{i_o}(t)-y_{j_o}(t)|.$$

Now, to prove (3.5) we set

$$V(t) = \max_{i,j}|y_i(t)-y_j(t)| = y_{i_o}(t)-y_{j_o}(t), \quad t\in[0,T_x).$$

This is a nonnegative continuous function having a lower left Dini derivative $D_-V(t)$ such that

$$D_-V(t) = \liminf_{h\to 0_+}\frac{V(t)-V(t-h)}{h} \leqslant \lim_{h\to 0_+}\frac{y_{i_o}(t)-y_{j_o}(t)-y_{i_o}(t-h)+y_{j_o}(t-h)}{h}$$

$$= \dot{y}_{i_o}(t)-\dot{y}_{j_o}(t).$$

Since y satisfies (3.4) we have

$$D_-V(t) \leqslant y_{i_o}(t)\sum_i \bar{a}_{i_o i}y_i(t) - y_{j_o}(t)\sum_i \bar{a}_{j_o i}y_i(t) =$$

$$= \bar{a}_{i_o i_o}y_{i_o}^2(t) + \bar{a}_{i_o j_o}y_{i_o}(t)y_{j_o}(t) + y_{i_o}(t)\sum_{j\neq i_o, j_o}\bar{a}_{i_o j}y_j(t) -$$

$$-\bar{a}_{j_0i_0}y_{j_0}^2(t)-\bar{a}_{j_0i_0}y_{j_0}(t)y_{i_0}(t)-y_{j_0}(t)\sum_{i\neq i_0,i_0}\bar{a}_{j_0i}y_i(t).$$

Since the matrix (a_{ij}) is symmetric and such that

$$\sum_i \bar{a}_{ij}=\sum a_{ij}u_j=1,$$

we will have

$$\begin{aligned}D_V(t)&\leqslant \bar{a}_{i_0i_0}y_{i_0}^2(t)+y_{i_0}^2(t)(1-\bar{a}_{i_0,i_0}-\bar{a}_{i_0,j_0})-\\&-\bar{a}_{j_0,j_0}y_{j_0}^2(t)-y_{j_0}^2(t)(1-\bar{a}_{j_0,j_0}-\bar{a}_{j_0,i_0})=\\&=-(\bar{a}_{i_0j_0}-1)(y_{i_0}(t)-y_{j_0}(t))(y_{i_0}(t)+y_{j_0}(t)).\end{aligned}$$

Thus, because of (H3) and the fact that $y(t)\in\mathfrak{L}_1$, for all t we get

$$D_V(t)<-M(t)V(t), \tag{3.6}$$

where $M(t)=(\bar{a}_{i_0j_0}-1)(\max_i y_i(t)+\min_i y_i(t))>0$. This means that the limit $\lim_{t\to T_x} V(t)$ exists. Let

$$\lim_{t\to T_x} V(t)=m.$$

Then $m\geqslant 0$ and we claim that $m=0$. To prove this fact we shall show first that

$$\int_0^{T_x} M(t)\,dt=+\infty. \tag{3.7}$$

Indeed, let us assume that this integral is finite. Then for some $k>0$ we should have

$$\int_0^{T_x} y_i(t)\,dt\leqslant k, \text{ for each } i=1,2,\ldots,n. \tag{3.8}$$

Take any index i and observe that

$$\dot{y}_i(t)=y_i(t)\sum_j \bar{a}_{ij}y_j(t)<y_i(t)\sum_{j\neq i}\bar{a}_{ij}y_j(t)$$

and therefore

$$\frac{\dot{y}_i(t)}{y_i(t)}<\sum_{j\neq i}a_{ij}y_j(t).$$

By integration from 0 to t we get

$$y_i(t) \leqslant y_i(0) \exp \sum_{j \neq i} \bar{a}_{ij} \int_0^t y_j(s)\, ds$$

and from (3.8)

$$y_i(t) \leqslant y_i(0) \exp[k(1-\bar{a}_{ii})], \quad t \in [0, T_x)$$

which contradicts the fact that y_i is not bounded. Therefore (3.7) holds.

Consider now the initial value problem

$$\dot{w} = -M(t)w, \quad w(0) = V(0) > 0.$$

Then $w(t) = V(0) \exp\left(-\int_0^t M(s)\, ds\right) \to 0$, as $t \to T_x$, because of (3.7). But from (3.6) we have $m \leqslant V(t) \leqslant w(t)$ and so $\lim_{t \to T_x} V(t) = 0$. The proof of the theorem is complete.

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