STABILITY FOR SOME EQUATIONS OF
MATHEMATICAL BIOLOGY AND MONOTONE FLOWS

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The theory of monotone flows and operators is applied to study stable equilibria
of autonomous cooperative systems and stable periodic solutions of periodic per-
turbations of these systems. The connection between analyticity and the property
of asymptotic stability is established.

The purpose of this paper is to apply the theory of monotone flows and operators
recently developed in [5, 9, 2] to some systems of mathematical biology. We shall study
the existence of (asymptotically) stable equilibria for cooperative autonomous systems
and the existence of (asymptotically) stable periodic solutions for their perturbations.

Before describing these systems we present one result for strongly monotone flows,
which gives an answer to the following question.

On the one hand, it is well known [9, 2] that the result on the existence of a stable
fixed point of a strongly monotone operator in an order interval may be extended to
the existence of an asymptotically stable fixed point under the additional assumption
of analyticity of this operator. On the other hand, the existence of stable equilibria in
attractors of strongly monotone flows was obtained in [5]. What is the connection of
existence of an asymptotically stable equilibrium and analyticity for strongly monotone
flows?

1. ASYMPTOTICALLY STABLE EQUILIBRIA IN STRONGLY MONOTONE FLOWS

We use notations and definitions of [5]. Let ϕ be a strongly monotone flow in
$\Omega \subset \mathbb{R}^n$. The set Ω is open and if $p_1, p_2 \subset \Omega$, $p_1 \ll p_2$ then

$$[p_1, p_2] = \{z \in \mathbb{R}^n \mid p_1 \leqslant z \leqslant p_2\} \subset \Omega.$$

It follows from [5] that every attractor K for this flow contains a stable equilibrium.

THEOREM 1. *Let the flow ϕ be analytic. If there exists an attractor K then the
flow ϕ has at least one asymptotically stable equilibrium.*

2. MODELS

Many mathematical models in the biological sciences lead to the study of systems of differential equations

$$(1) \qquad \frac{dx_i}{dt} = x_i F_i(x), \ \big(x = (x_1, \dots, x_n) \in \mathbb{R}_+^n, \ F_i(x) \in C_1(\mathbb{R}^n) \, (1 \leqslant i \leqslant n)\big)$$

which have special properties.

We consider the following hypotheses.

H1.   System (1) is dissipative (see [3]).

H2.   System (1) is cooperative. This means

$$\frac{\partial F_i}{\partial x_j} \geqslant 0 \quad (i \neq j; \, i,j = 1, \dots, n) \, \big(x \in \text{ int } \mathbb{R}_+^n\big).$$

We also require that the Jacobian matrix $[(\partial F_i)/(\partial x_j)]$ is irreducible for $x \in \text{ int } \mathbb{R}_+^n$ (see [5]).

H3.   System (1) is a uniformly persistent system (see [1]).

H4.   The functions F_i are analytic in int $\mathbb{R}_+^n$.

THEOREM 2. *Suppose (H1)-(H3) hold. Then system (1) has at least one stable equilibrium in int $\mathbb{R}_+^n$. If in addition the assumption H4 holds then system (1) has at least one asymptotically stable equilibrium $x_* \in$ int $\mathbb{R}_+^n$.*

Let

$$(2) \qquad\qquad \frac{dx_i}{dt} = x_i(F_i(x) + \varepsilon\varphi_i(t,x)), \quad \big(x \in \mathbb{R}_+^n\big)$$

be the periodic perturbed system for the system (1).

H5.   The vector-function $\varphi(t,x) = (\varphi_1(t,x), \varphi_2(t,x), \dots, \varphi_n(t,x))$ is smooth, periodic in t of period ω

$$\varphi(t + \omega, x) \equiv \varphi(t,x).$$

Instead of hypothesis H2 we consider a stronger condition.

H6. $\qquad \dfrac{\partial F_i}{\partial x_j} > 0 \quad (i \neq j; \, i,j = 1, \dots, n) \, \big(x \in \text{ int } \mathbb{R}_+^n\big).$

We also consider

H7.   The vector-function $\varphi(t,x)$ is analytic.

THEOREM 3. *Suppose H1, H3, H5, H6. Then there exists $\varepsilon_0 > 0$ such that for $\varepsilon \in (0, \varepsilon_0]$ system (2) has at least one stable ω-periodic solution $x(t, \varepsilon) \in$ int $\mathbb{R}_+^n$.*

THEOREM 4. *Suppose H1, (H3)–(H6) hold. Let $x_* \in$ int $\mathbb{R}_+^n$ be an asymptotically stable equilibrum of system (1), which exists by Theorem 1. Then for each $\delta > 0$*

there exists $\varepsilon(\delta) > 0$ such that for each $\varepsilon \in (0, \varepsilon(\delta)]$ system (2) has a stable ω-periodic solution $x(t, \varepsilon)$ and the inequality

$$(3) \qquad\qquad\qquad \|x(t, \varepsilon) - x_*\| < \delta$$

holds.

THEOREM 5. *Let the conditions of Theorem 4 and H7 hold. Then for each $\delta > 0$ there exists $\varepsilon(\delta) > 0$ such that for each $\varepsilon \in (0, \varepsilon(\delta)]$ system (2) has an asymptotically stable ω-periodic solution $x(t, \varepsilon)$ and the inequality (3) holds.*

3. PROOFS

We consider $\mathbb{R}^n$ as the semiordered space with cone $\mathbb{R}^n_+$ (see [7]). We use the terminology of semiordered spaces

$$x \geqslant y \Leftrightarrow x - y \in \mathbb{R}^n_+, \ x \gg y \Leftrightarrow x - y \in \text{int } \mathbb{R}^n_+.$$

For points $x_- \ll x_+$ the set

$$[x_-, x_+] = \{p \mid x_- \leqslant p \leqslant x_+\}$$

is called the order interval.

The operator A is a strongly monotone operator if for every two points $x_1 \neq x_2$ belonging to its domain the inequality

$$x_1 \geqslant x_2$$

implies $$Ax_1 \gg Ax_2.$$

DEFINITION: Let x_* be a fixed point of the operator A. Let the operator A be defined in some neighbourhood of the point x_*. The point x_* is called a stable fixed point of the operator A if for each $\varepsilon > 0$ there exists a $\delta > 0$ such that the inequality $|x - x_*| < \delta$ implies the inequality $\|A^n x - x_*\| < \varepsilon$ $(n = 1, 2, \dots)$. If in addition

$$\|A^n x - x_*\| \to 0 \quad (n \to +\infty)$$

for points x from some neighbourhood of the point x_* then the point x_* is called an asymptotically stable fixed point.

Proofs of Theorems 1–5 are based on the following statements, which are simple corollaries of results in [9, 2].

THEOREM **6.** *Let the strongly monotone operator* A *be defined in the order interval* $[x_-, x_+]$. *Let the inequalities*

$$Ax_- \gg x_-, \quad Ax_+ \ll x_+$$

hold. Then the operator A *has at least one stable fixed point* $x_* \in [x_-, x_+]$.

THEOREM **7.** *Let the conditions of Theorem 6 hold. Let the operator* A *be analytic in some neighbourhood of all its fixed points. Then there exists at least one asymptotically stable fixed point* $x_* \in [x_-, x_+]$.

PROOF OF THEOREM 1: Let the conditions of Theorem 1 hold. Let K_0 be the set of non-wandering points which belong to K. The set K_0 is nonempty. Fix $z \in K_0$. There exists a maximal element $p_1 \in K_0$, a minimal element $p_2 \in K_0$, $p_1 \geqslant p_2$. It follows from [5] that the point p_1 is an asymptotically upper stable equilibrium and the point p_2 is an asymptotically lower stable equilibrium. If $p_1 = p_2$ then the point p_1 is an asymptotically stable equilibrium. Suppose $p_1 \neq p_2$. Then $p_1 \ll p_2$ because the flow ϕ is strongly monotone. By [5], there exist $y_2 \ll p_2$, $p_1 \ll y_1$ $(y_1, y_2 \in \Omega)$ such that $y_1(t) \to p_1$, $y_2(t) \to p_2$. So there exists $T > 0$ such that the following inequalities hold

$$y_1 \ll \phi(T)y_1 \ll p_1 \ll p_2 \ll \phi(T)y_2 \ll y_2.$$

Since the operator $A = \phi(T)$ is analytic [8], by Theorem 7, it has an asymptotically stable fixed point $x_* \in [y_1, y_2]$. Hence the point x_* belongs to the asymptotically stable periodic solution of system (1). But it is well known [4] that this solution has to be an equilibrium. Theorem 1 has been proved.   ◻

PROOF OF THEOREM 2: Theorem 2 follows from [5, Theorem 4.1] and Theorem 1 for the attractor

$$(4) \qquad\qquad K = \overline{\bigcup_{x \in \text{int } \mathbb{R}^n_+} \Lambda^+(x)},$$

where $\Lambda^+(x)$ is the omega limit set of the orbit through x.   ◻

PROOF OF THEOREM 3: Let the maximal element $p_1 \in K_0$ and the minimal element $p_2 \in K_0$, $p_2 \leqslant p_1$ be as in the proof of the Theorem 3. The points p_1 and p_2 are asymptotically upper and lower stable equilibria, respectively.

LEMMA **1.** *There exist two points* $x_-, x_+ \in \text{int } \mathbb{R}^n_+$ *such that the inequality*

$$(5) \qquad\qquad x_- \ll \phi(\omega)x_- \ll p_2 < p_1 \ll \phi(\omega)x_+ \ll x_+$$

holds.

PROOF OF LEMMA 1: We prove the existence of an element x_+ such that the inequality

(6) $$p_1 \ll \phi(\omega)x_+ \ll x_+$$

holds.

Let $O(\delta_0, p_1) = \{p \mid \|p - p_1\| < \delta_0\}$ for some $\delta_0 > 0$ be a neighbourhood of the point p_1 such that for each $x \in O(\delta_0, p_1)$ the condition

(7) $$\phi(t)x \to p_1$$

holds. Krasnoselskii's Theorem about eigenvectors [7] implies the existence of the point $x_+ \in O(\delta_0, p_1) \cap (p_1 + \operatorname{int} \mathbb{R}^n_+)$ such that

$$\phi(\omega)x_+ = \lambda(x_+ - p_1) + p_1,$$

where $\lambda > 0$.

Suppose $\lambda \geqslant 1$. Then $\phi(\omega)x_+ \geqslant x_+$. Since $\phi(\omega)$ is a strongly monotone operator we have $\phi(n\omega)x_+ \geqslant x_+$ $(n = 1, 2, \dots)$. This inequality contradicts the condition (7). Hence the inequality (6) holds.

By the same reasoning the existence of the element x_- may be obtained.   □

Let

$$G = \{\phi(t)x \mid x \in [x_-, x_+],\ t \in [0, \omega]\}.$$

The set G is compact and $G \subset \operatorname{int} \mathbb{R}^n_+$. Choose a compact set $G_0 \subset \operatorname{int} \mathbb{R}^n_+$ such that $G \subset G_0$. Choose $\varepsilon_1 > 0$ such that inequalities

$$x_i\left(\frac{\partial F_i}{\partial x_j} + \varepsilon\frac{\partial \varphi_i(t, x)}{\partial x_j}\right) > 0 \quad (0 < \varepsilon \leqslant \varepsilon_1,\ x \in G,\ t \in [0, \omega],\ i = 1, \dots, n)$$

hold. Such an $\varepsilon_1 > 0$ exists due to H6.

By the theorem of continuation of solutions [4], there exists $\varepsilon_2 \in (0, \varepsilon_1]$ such that

$$p(t, x, \varepsilon) \in G_0\ (x \in [x_-, x_+],\ \varepsilon \in (0, \varepsilon_2],\ t \in [0, \omega]),$$

where $p(t, x, \varepsilon)$ is the solution of system (2), $p(0, x, \varepsilon) = x$. Let $U(\omega, \varepsilon)$ be the operator of translation along trajectories of system (2)

$$U(\omega, \varepsilon)x = p(\omega, x, \varepsilon) \quad (x \in [x_-, x_+],\ \varepsilon \in (0, \varepsilon_2],\ t \in [0, \omega]).$$

The operator $U(\omega, \varepsilon)$ is a strongly monotone operator in $[x_-, x_+]$ (see [6]). It follows from (5) and the theorem of continuation of solutions [4] that there exists an $\varepsilon_0 \in (0, \varepsilon_2]$ for which the inequality

$$x_- \ll U(\omega, \varepsilon)x_- \ll p_2 \ll U(\omega, \varepsilon)x_+ \ll x_+ \quad (\varepsilon \in (0, \varepsilon_0])$$

holds. Applying Theorem 6 to $[x_-, x_+]$ and $A = U(\omega, \varepsilon)$ $(\varepsilon \in (0, \varepsilon_0])$ we obtain the existence of a stable fixed point for the operator $U(\omega, \varepsilon)$ $(\varepsilon \in (0, \varepsilon_0])$ in $[x_-, x_+]$. This proves Theorem 3.   ▯

PROOF OF THEOREMS 4, 5: Let the conditions of Theorem 4 hold. Let x_* be an asymptotically stable equilibrium of system (1), which exists by Theorem 2.

LEMMA 2. *For each $\delta-$neighbourhood $O(\delta, x_*) = \{p \mid \|p - x_*\| < \delta\}$ $(\delta > 0)$ there exist points $p_-, p_+ \in O(\delta, x_*)$ such that the inequality*

$$(8) \qquad\qquad p_- \ll \phi(\omega)p_- \ll x_* \ll \phi(\omega)p_+ \ll p_+$$

holds.

PROOF OF LEMMA 2: The reasoning is the same as in the proof of Lemma 1.   ▯

Due to H6 we may choose $\varepsilon_1 > 0$, $\delta > 0$ such that for $\varepsilon \in (0, \varepsilon_1]$ and for the functions

$$\Phi_i(x, t) = x_i(F_i(x_1, \dots, x_n) + \varepsilon\varphi_i(t, x)), \quad (i = 1, \dots, n)$$

the inequalities

$$\frac{\partial \Phi_i}{\partial x_j} > 0 \quad (x \in O(\delta_1, x_*), \ i \neq j, \ i, j = 1, \dots, n)$$

hold.

LEMMA 3. *There exist $\varepsilon_2 \in (0, \varepsilon_1]$, $\delta_2 \in (0, \delta_1]$ such that the solution $p(t, x, \varepsilon)$ of system (2) $(p(0, x, \varepsilon) = x, \ \varepsilon \in (0, \varepsilon_2], \ x \in O(\delta_2, x_*))$ is defined for all $t \in [0, \omega]$ and*

$$p(t, x, \varepsilon) \in O(\delta_1, x_*) \quad (x \in O(\delta_2, x_*)).$$

PROOF OF LEMMA 3: Since the point x_* is an equilibrium of system (1), this statement follows from the Theorem of continuation of solutions [4].   ▯

Now consider the operator $U(\omega, \varepsilon)$, which is defined by the formula

$$U(\omega, \varepsilon)x = p(\omega, x, \varepsilon) \quad (x \in O(\delta_2, x_*)).$$

It follows from [6] that this operator is a strongly monotone operator in $O(\delta_2, x_*)$.

LEMMA 4. *Let the numbers $\varepsilon_2 > 0$, $\delta_2 > 0$ be choosen according to Lemma 3. For each $\delta \in (0, \delta_2)$ we may choose $\varepsilon(\delta) \in (0, \varepsilon_2]$ such that in the neighbourhood $O(\delta, x_*)$ there exist two points x_-, x_+ for which the following condition*

$$x_- \ll U(\omega, \varepsilon)x_- \ll x_+ \ll U(\omega, \varepsilon)x_+ \ll x_+$$

holds.

PROOF OF LEMMA 4: For each $\delta \in (0, \delta_2)$ we choose points p_-, p_+ such that (8) holds. Let $x_- = p_-$, $x_+ = p_+$. Lemma 4 follows from the inequality (8) and the theorem of continuation of solutions [4].

Theorem 4 follows from Lemma 4 and Theorem 6. If H7 holds then the operator $U(\omega, \epsilon)$ is analytic [8]. So Theorem 5 follows from Lemma 4 and Theorem 7. ▯

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