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# A General Cooperation Theorem for Hypercycles

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**Abstract.** We derive a condition for a closed invariant subset of a compact dynamical system to be an attractor (resp. repellor) combining the usual Ljapunov function methods with time averages. Applications are given to concrete systems endowed with some cyclic symmetry. In particular, cooperation of the inhomogeneous hypercycle is shown.

## 1. The General Theorem

We consider a dynamical system on the simplex

$$S_n = \{x = (x_1, \ldots, x_n) \in \mathbb{R}^n \colon \forall\, i \colon x_i \geqslant 0, \textstyle\sum x_i = 1\}$$

which leaves the boundary and all faces of $S_n$ invariant. Such a system is given by the differential equation

$$\dot{x}_i = x_i [G_i (x_1, \ldots, x_n) - \Phi], \quad i = 1, \ldots, n \tag{1.1}$$

with $\Phi = \sum_{i=1}^{n} x_i G_i(x)$.

This type of equation was introduced by EIGEN and SCHUSTER [1], who called it a *dynamical system under constant organization.* Equation (1.1) and in particular the special case where the functions $G_i$ are linear, plays an important role in such different fields as prebiotic evolution [1], population genetics and animal behaviour [3].

Such a dynamical system on $S_n$ is called *cooperative*, if the boundary $\operatorname{bd} S_n$ is a repellor, i. e. there exists a constant $\varrho > 0$ such that if $x_i(0) > 0$ for all $i$ then $x_i(t) > \varrho$ for all sufficiently large $t$ and all $i = 1, \ldots, n$.

Let $x(t)$ be the orbit of (1.1) with $x(0) = x$. Let $P$ be a (differentiable) function on $S_n$ which satisfies

$$P(x) = 0 \quad x \in \operatorname{bd} S_n, \qquad P(x) > 0 \quad x \in \operatorname{int} S_n \tag{1.2}$$

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and assume further that (1.1) implies

$$\dot{P} = P \cdot \psi(x) \text{ where } \psi \text{ is continuous on } S_n. \tag{1.3}$$

**Theorem 1:** *If for some function P which satisfies* (1.2) *and* (1.3) *the condition*

$$\forall x \in \operatorname{bd} S_n \ \exists T > 1 \text{ such that } \int_0^T \psi(x(t))\,dt > 0 \tag{1.4}$$

*is fulfilled, then the system* (1.1) *is cooperative.*

*Remark:* Condition (1.4) implies that for every fixed point $x \in \operatorname{bd} S_n$ we have $\psi(x) > 0$. Conversely, if $\psi$ is strictly positive on the whole $\omega$-limit of the orbits on the boundary, (1.4) is satisfied and the theorem applies.

**Corollary:** *If P satisfies* (1.2) *and* (1.3) *and every orbit on the boundary of* $S_n$ *converges to a fixed point, then*

$$\psi(x) > 0 \text{ for all fixed points on the boundary}$$

*implies cooperation.*

This corollary was proved by SIGMUND in [4] — although it was not explicitly stated in this form.

*Proof:* Let $h > 0$ and

$$U_h = \left\{x \in S_n \colon \exists T > 1 \text{ with } \frac{1}{T}\int_0^T \psi(x(t))\,dt > h > 0\right\}.$$

For $x \in U_h$ we can define the function

$$T_h(x) = \inf\left\{T > 1 \colon \frac{1}{T}\int_0^T \psi(x(t))\,dt > h\right\}.$$

(1) For every $x \in U_h$ and $\alpha > 0$ there exists a $\delta > 0$ such that if $y \in S_n$ with $d(x, y) < \delta$ then $y \in U_h$ and $T_h(y) \leqslant T_h(x) + \alpha$. This means that $U_h$ is open and $T_h$ is upper semicontinuous on $U_h$. Indeed, for any $\alpha > 0$ there exists a time $T \in (1, T_h(x) + \alpha)$ such that

$$\varepsilon := \frac{1}{T}\int_0^T \psi(x(t))\,dt - h > 0.$$

Since $\psi$ is uniformly continuous on $S_n$ there exists a $\delta_1 > 0$ such that $d(y, \bar{y}) < \delta_1$ implies

$$|\psi(y) - \psi(\bar{y})| < \varepsilon. \tag{1.5}$$

Since the solutions of an ordinary differential equation depend continuously on the initial conditions, there exists a $\delta > 0$ such that $d(x, y) < \delta$ implies $d(x(t), y(t)) < \delta_1$ for all $t \in [0, T]$. Together with (1.5) we obtain

$$\left|\frac{1}{T}\int_0^T \psi(x(t))\,dt - \frac{1}{T}\int_0^T \psi(y(t))\,dt\right| \leqslant \frac{1}{T}\int_0^T |\psi(x(t)) - \psi(y(t))|\,dt < \varepsilon$$

and therefore

$$\frac{1}{T}\int_0^T \psi(y(t))\,dt > \frac{1}{T}\int_0^T \psi(x(t))\,dt - \varepsilon = h.$$

Hence $y \in U_h$ and $T_h(y) \leqslant T < T_h(x) + \alpha$ for all $y$ with $d(x, y) < \delta$.

(2) Condition (1.4) says that for each $x \in \operatorname{bd} S_n$ there exists a $h > 0$ with $x \in U_h$, in other words: $\{U_h, h > 0\}$ is an open covering of $\operatorname{bd} S_n$. The compactness of $\operatorname{bd} S_n$ then implies that for some $h > 0$ we have $\operatorname{bd} S_n \subseteq U_h$, and that there exists a $p > 0$ such that

$$I(p) := \{x \in S_n \colon 0 < P(x) \leqslant p\} \subseteq U_h.$$

(3) If $x \in U_h \cap \operatorname{int} S_n$, then $x(t) \notin U_h$ for some $t > 0$.

Indeed, otherwise we would have $x(t) \in U_h$ for all $t > 0$. This means that to each point $x(t)$ of the orbit there exists a length of time $T > 1$ such that

$$Th < \int_t^{t+T} \psi(x(s))\,ds = \int_t^{t+T} \frac{\dot{P}(x(s))}{P(x(s))}\,ds = \log P(x(t+T)) - \log P(x(t))$$

that is

$$P(x(t+T)) > P(x(t))\,e^{Th} > P(x(t))\,e^{h}. \tag{1.6}$$

Proceeding inductively one would obtain a sequence

$$0 = t_0 < t_1 < t_2 < \ldots \text{ with } P(x(t_{n+1})) > P(x(t_n))\,e^{h},$$

i. e. $P(x(t_n))$ would tend to infinity which is not possible.

(4) There exists a $q \in (0, p)$ such that $x \notin U_h$ implies $x(t) \notin I(q)$ for all $t \geqslant 0$.

Indeed, since $T_h$ is upper semicontinuous there exists an upper bound $T_h(x) < \bar{T}$ for $x \in \overline{I(p)}$. Let $t_0'$ be the first time when the orbit of $x$ enters the layer $I(p)$, i. e.

$$t_0' = \min\{t \geqslant 0,\ x(t) \in I(p)\}.$$

Let $y = x(t_0')$. Then $P(y) = p$. Now define $m = \min\{\psi(x): x \in S_n\}$, which is a negative number in general and $q = pe^{-|m|\bar{T}}$. For all $t \in [0, \bar{T})$ we have

$$\frac{1}{t}\int_0^t \psi(y(s))\,ds \geqslant m$$

and hence $P(y(t)) \geqslant P(y(0))e^{mt} > pe^{-|m|\bar{T}} = q$ and for at least one point of time $T \in [T_h(y), \bar{T}]$ we obtain from (1.6)

$$P(y(T)) \geqslant P(y(0))e^h > p.$$

This shows that $y(t)$ does not reach $I(q)$ for $0 \leqslant t \leqslant T$ and $y(T) = x(t_0' + T) \notin I(p)$, so that at time $t_0' + T$ we are in the same situation as at time 0. Repeating this argument we see that $x(t)$ never reaches $I(q)$.

*Remark:* It is obvious that it is not essential for the dynamical system to be defined on the simplex $S_n$: $S_n$ may be replaced by any compact space $X$ and bd $S_n$ by any closed invariant subset $Y$ of $X$. Our theorem then gives a rather general condition which implies that the set $Y$ is a repellor. A similar condition

$$\left(\forall x \in Y\ \exists\, T > 1 \text{ such that } \frac{1}{T}\int_0^T \psi(x(t))\,dt < 0\right)$$

forces $Y$ to be an attractor. In this sense the function $P$ of Theorem 1 may be considered as a generalization of the concept of a Ljapunov function.

## 2. Applications

### 2.1 The Inhomogeneous Hypercycle

$$\dot{x}_i = x_i(q_i + k_i x_{i-1} - \Phi), \quad k_i > 0,\ i = 1, \ldots, n. \tag{2.1}$$

This equation was studied in [5]. The following results were obtained there: The system is cooperative if the selfreplication terms $q_i$ are sufficiently small, i. e. if it is only a slight perturbation of the homogeneous hypercycle (all $q_i = 0$), for which cooperation was shown in [4]. On the other side, (2.1) and more general systems can only be cooperative if there exists a unique inner equilibrium (see Theorem 4 or [5]). The converse of this statement is left there as an open problem.

**Theorem 2:** *The inhomogeneous hypercycle* (2.1) *is cooperative iff there exists a fixed point in* int $S_n$.

*Proof:* Let $p = (p_1, \ldots, p_n)$ be the fixed point in int $S_n$. Then the following equations are satisfied:

$$q_i + k_i p_{i-1} = \Phi(p), \quad i = 1, \ldots, n. \tag{2.2}$$

Since all coordinates $p_i$ are positive we have

$$\Phi(p) > \max_{1 \leqslant i \leqslant n} q_i. \tag{2.3}$$

Using (2.2), the differential equation (2.1) takes the form

$$\dot{x}_i = x_i [k_i (x_{i-1} - p_{i-1}) + \Phi(p) - \Phi].$$

For $P = \prod_{i=1}^{n} x_i^{1/k_i}$ we obtain

$$\dot{P}/P = \psi(x) = \sum \frac{1}{k_i} [k_i (x_{i-1} - p_{i-1}) + \Phi(p) - \Phi] =$$

$$= \left(\sum \frac{1}{k_i}\right) [\Phi(p) - \Phi] > \left(\sum \frac{1}{k_i}\right) (\max q_i - \Phi).$$

In order to satisfy condition (1.4) of Theorem 1 and because of (2.3) it remains to prove the following statement: For every $x \in \text{bd}\, S_n$ and every $\varepsilon > 0$ there exists a time $T > 1$ such that

$$\frac{1}{T} \int_0^T \Phi(x(t))\, dt < \max q_i + \varepsilon.$$

We proceed indirectly and show inductively that otherwise all coordinates $x_i(t)$ would tend to 0 with $t \to \infty$, which contradicts $\sum x_i = 1$. Assume $x_{i-1}(t) \to 0$ (since $x \in \text{bd}\, S_n$, at least one coordinate is equal to 0). Then $\dot{x}_i / x_i = q_i + k_i x_{i-1} - \Phi$ implies

$$\frac{1}{T} \int_0^T \frac{\dot{x}_i}{x_i} = \frac{\log x_i(T) - \log x_i(0)}{T} =$$

$$= q_i + k_i \frac{1}{T} \int_0^T x_{i-1}(t)\, dt - \frac{1}{T} \int_0^T \Phi(x(t))\, dt$$

and for sufficiently large $T$

$$\frac{1}{T} \log x_i(T) \leqslant q_i - \max q_j - \varepsilon \leqslant -\varepsilon.$$

Hence $x_i(T) \leqslant e^{-\varepsilon T}$ and $x_i(T) \to 0$, and the proof is finished.

### 2.2 The Generalized Hypercycle

$$\dot{x}_i = x_i[x_{i-1} F_i(x) - \Phi], \quad i = 1, \ldots, n \tag{2.4}$$

where the $F_i$ are continuous and strictly positive functions on $S_n$. That these rather general assumptions already guarantee cooperation has been proved in [2]. This result follows also in an easy way from Theorem 1: We choose $P = \prod_{i=1}^{n} x_i$. Then

$$\dot{P}/P = \psi(x) = \sum x_{i-1} F_i(x) - n\Phi.$$

Since $\sum x_{i-1} F_i(x) \geqslant m > 0$ holds on $S_n$ for some $m$ it remains to show the following assertion: For every $x \in \operatorname{bd} S_n$ and every $\varepsilon > 0$ there exists a $T > 1$ such that

$$\frac{1}{T}\int_0^T \Phi(x(t))\,dt < \varepsilon.$$

Indeed, otherwise $\frac{1}{T}\int_0^T \Phi(x(t))\,dt \geqslant \varepsilon$ would hold for all $T \geqslant 1$ and integrating $\dot{x}_i/x_i = x_{i-1} F_i(x) - \Phi$ would under the assumption $x_{i-1} \to 0$ again imply $x_i(T) \leqslant e^{-T\varepsilon}$ for large $T$. This leads to the same contradiction as in 2.1, namely that all coordinates would tend to 0.

### 2.3 Stability of a Polygon with Cyclic Flow

Let us consider a $C^1$-flow on a two-dimensional orientable manifold $M$ which exhibits a finite number of cyclically connected saddles. Of course the flow is then not structurally stable, but such situations often occur in concrete dynamical systems (defined on compact subsets of $\mathbb{R}^n$ where the boundary is invariant).

Let $L$ be this connected invariant set consisting of $n$ saddles $F_1, \ldots, F_n$ and $n$ connecting orbits. Since the manifold is orientable, a certain neighbourhood $U$ of $L$ may be embedded diffeomorphically in the plane. Let $V$ be the component of $U \setminus L$ which lies "inside" the polygon $L$. An orbit starting in $V$ (close to $L$) which is not closed may have $L$ as $\alpha$- or as $\omega$-limit. Our aim is to derive a criterion which of these cases occurs.

One can choose "coordinates" $x_i: M \to \mathbb{R}$ such that $x_i > 0$ in $V$, $x_i = 0$ along the orbit connecting $F_{i-1}$ with $F_i$ and finally $x_i \times x_{i+1}$ is a diffeomorphism of a neighbourhood of $F_i$ onto a neighbourhood of the origin in $\mathbb{R}^2$. Then consider the vectorfield near the saddle $F_i$: Along the orbit $x_i = 0$ we have $\frac{d}{dt} x_{i+1}(x(t)) \sim \mu_i x_{i+1}(x(t))$ near $x_{i+1} = 0$ and along $x_{i+1} = 0$ we have $\frac{d}{dt} x_i(x(t)) \sim \lambda_i x_i(x(t))$ near $x_i = 0$, where $\lambda_i > 0$ and $\mu_i < 0$ are the eigenvalues at the saddle point $F_i$.

**Theorem 3:** *Let L be the above polygon, $\lambda_i > 0$, $\mu_i < 0$ the eigenvalues of the saddles and let*

$$\nu = \prod_{i=1}^{n} \left( -\frac{\lambda_i}{\mu_i} \right).$$

*Then L is an attractor (for orbits in V close to L) if $\nu < 1$, and a repellor if $\nu > 1$.*

*Hence $\nu$ may be interpreted as something like the eigenvalue of a certain Poincare section map.*

*Proof:* Consider the function $P = \prod_{i=1}^{n} x_i^{p_i}$ (where $p_i > 0$ will be specified later), which is positive on $V$ and equal to 0 on $L$. Then

$$\psi(x) = \frac{\dot{P}}{P} = \sum_{j=1}^{n} p_j \frac{\dot{x}_j}{x_j} \tag{2.5}$$

is continuous since $\dot{x}_j = 0$ for $x_j = 0$ and the vectorfield $(\dot{x}_i)$ is $C^1$. In view of the above remarks, (2.5) reduces at the $i$-th corner to

$$\psi(F_i) = p_i \lambda_i + p_{i+1} \mu_i$$

which is positive iff $\frac{p_{i+1}}{p_i} < -\frac{\lambda_i}{\mu_i}$.

Multiplying over all $i = 1, \ldots, n$, we see that this is possible for all $i$ iff $\nu = \prod_{i=1}^{n} \left( -\frac{\lambda_i}{\mu_i} \right) > 1$ $\left( \text{define e. g. } \frac{p_{i+1}}{p_i} = -\frac{\lambda_i}{\mu_i} \nu^{-1/n} \right)$. Hence the corollary of Theorem 1 applies and $L$ is a repellor for $\nu > 1$, and an attractor if $\nu < 1$.

*Remark:* A special case of this situation was treated in [3] and applied to prove the existence of limit cycles inside the polygon.

## 3. An Exclusion Principle

The following theorem strengthens a result obtained in [5] for equations (1.1) with linear growth functions $G_i$.

**Theorem 4.** *If the system*

$$\dot{x}_i = x_i\left[\sum_{j=1}^{n} a_{ij}x_j - \Phi\right] \quad \textit{with} \quad \Phi = \sum_{i,j=1}^{n} x_i a_{ij} x_j$$

*defined on $S_n$ has no fixed point in* int $S_n$ *then the nonwandering set and hence the $\omega$-limit of every orbit is contained in the boundary of $S_n$.*

*Proof:* If there is no interior equilibrium then the convex set

$$\{Ax = (\sum_j a_{ij}x_j)_i \colon x \in \operatorname{int} S_n\} \subseteq \mathbb{R}^n$$

is disjoint from the line $M := \{y \in \mathbb{R}^n : y_1 = \ldots = y_n\}$. Hence there exists a linear functional $c = (c_1, \ldots, c_n)$ such that

$$cAx = \sum_{i,j=1}^{n} c_i a_{ij} x_j < \sum_{i=1}^{n} c_i y_i = (\sum_{i=1}^{n} c_i)\, y_1$$

holds for $x \in \operatorname{int} S_n$ and $y \in M$. Since we may choose an arbitrary $y_1 \in \mathbb{R}$, $\sum_{i=1}^{n} c_i$ has to vanish. But then the function $P = \prod_{i=1}^{n} x_i^{c_i}$, defined on $\operatorname{int} S_n$, satisfies $\dot{P} = P \cdot \sum_{i,j=1}^{n} c_i a_{ij} x_j < 0$ on $\operatorname{int} S_n$. Therefore every point in the interior of $S_n$ is wandering which proves the theorem.

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