Competitive and Cooperative Systems: a mini-review

Morris W. Hirsch[1] and Hal L. Smith[2]

[1] Department of Mathematics, University of California, Berkeley, CA, 94720,
   `hirsch@math.berkeley.edu`
[2] Department of Mathematics, Arizona State University, Tempe, AZ 85287, USA
   Institute 2, `halsmith@asu.edu`

Abstract. The theory of competitive and cooperative dynamical systems has had some remarkable applications to the biological sciences. The interested reader may consult the monograph [28] and lecture notes [29] of Smith, and to a forthcoming review by the authors [11] for a more in-depth treatment.

1 Strong Monotonicity for ODEs

In this brief review we give some of the main results in the theory of competitive and cooperative systems. But first, we give some new strong monotonicity results for odes. Let J be a nontrivial open interval, $D \subset \mathbb{R}^n$ be an open set, $f : J \times D \to \mathbb{R}^n$ be a locally Lipschitz function, and consider the ordinary differential equation

$$x' = f(t, x) \tag{1}$$

Denote by $x(t, t_0, x_0)$ the non-continuable solution of the initial value problem $x(t_0) = x_0$ for $t_0 \in J$.

A cone K in $\mathbb{R}^n$ is a non-empty, closed subset of $\mathbb{R}^n$ satisfying $K + K \subset K$, $\mathbb{R} \cdot K \subset K$ and $K \cap (-K) = \{0\}$. We hereafter assume K nonempty interior in $\mathbb{R}^n$. The order relations $\leq, <, \ll$ are induced by K as follows: $x \leq y$ if and only if $y - x \in K$; $x < y$ if $x \leq y$ and $x \neq y$, and $x \ll y$ whenever $y - x \in \mathrm{Int}K$. A cone is a *polyhedral cone* if it is the intersection of a finite family of half spaces. The standard cone $\mathbb{R}^n_+ = \cap_{i=1}^n \{x : \langle e_i, x \rangle \geq 0\}$ is polyhedral (e_i is the unit vector in the x_i-direction) while the ice cream cone $K = \{x \in \mathbb{R}^n : x_1^2 + x_2^2 + \cdots + x_{n-1}^2 \leq x_n^2, x_n \geq 0\}$ is not. The dual cone K^* is the set positive linear functionals, i.e., linear functionals $\lambda \in (\mathbb{R}^n)^*$, the dual space of $\mathbb{R}^n$, such that $\lambda(K) \geq 0$. If we adopt the standard inner product $\langle , \rangle$ on $\mathbb{R}^n$ then we can identify $(\mathbb{R}^n)^*$ with $\mathbb{R}^n$ since for each $\lambda \in K^*$ we can find $a \in \mathbb{R}^n$ such that $\lambda(x) = \langle a, x \rangle$ for all x. We use the following easy result; see e.g. Walcher [35].

Lemma 1. *Let $x \in K$. Then $x \in IntK$ if and only if $\lambda(x) > 0$ for all $\lambda \in K^* \setminus \{0\}$.*

We say that (1) is *monotone*, or order-preserving, if whenever $x_0, x_1 \in D$ satisfy $x_0 \leq x_1$ and the solutions $x(t, t_0, x_0)$ and $x(t, t_0, x_1)$ are defined on $[t_0, t_1]$, $t_1 > t_0$, then $x(t, t_0, x_0) \leq x(t, t_0, x_1)$ holds for $t \in [t_0, t_1]$.

The vector field $f : J \times D \to \mathbb{R}^n$ is said to satisfy the *quasimonotone condition* in D if for every $(t, x), (t, y) \in J \times D$ we have

(Q) $x \leq y$ and $\phi(x) = \phi(y)$ for some $\phi \in K^*$ implies $\phi(f(t, x)) \leq \phi(f(t, y))$.

The quasimonotone condition was introduced by Schneider and Vidyasagar [25] for finite dimensional, autonomous linear systems and used later by Volkmann [34] for nonlinear infinite dimensional systems. The following result is certainly inspired by a result of Volkmann [34] and work of W. Walter [**?**]. See also Uhl [33] and Walcher [35]. The proof appears in [11].

Theorem 1.1 *Let f satisfies (Q) in D, $t_0 \in J$, and $x_0, x_1 \in D$. Let $<_r$ denote any one of the relations $\leq, <, \ll$. If $x_0 <_r x_1$ and $t > t_0$ are such that both $x(t, t_0, x_i)$, $i = 0, 1$ are defined, then $x(t, t_0, x_0) <_r x(t, t_0, x_1)$. Conversely, if (1) is monotone, then f satisfies (Q).*

It will be useful to specialize to linear systems since it is convenient in the applications to verify (Q), as well as other monotonicity hypotheses, using derivatives. Let $A(t)$ be a continuous matrix-valued function defined on the interval J containing t_0 and consider the linear initial value problem for the matrix solution X:

$$X' = A(t)X, \quad X(t_0) = I. \tag{2}$$

For linear systems, (Q) is equivalent to the following:

(M) for all $x \in \partial K$ and $\lambda \in K^*$ such that $\lambda(x) = 0$, $\lambda(A(t)x) \geq 0$.

Therefore, we have the following Corollary of Theorem 1.4.

Corollary 1.1 *The matrix solution $X(t)$ satisfies $X(t)K \subset K$ for $t \geq t_0$ for each $t_0 \in J$ if and only if for all $t \in J$, (M) holds for the function $x \to A(t)x$. In fact, (M) implies that $X(t)(K \setminus \{0\}) \subset (K \setminus \{0\})$ and $X(t)IntK \subset IntK$ for $t > t_0$.*

A matrix A is *K-nonnegative* if $A(K) \subset K$. Corollary 1.1 says that $X(t)$ is K-nonnegative for $t \geq t_0$ if (M) holds.

The domain D is *p-convex* if for every $x, y \in D$ satisfying $x \leq y$ the line segment joining them also belongs to D. Let $\frac{\partial f}{\partial x}(t, x)$ be continuous on $J \times D$. We say that f (or (1)) is *K-cooperative* if for all $t \in J$, $y \in D$, (M) holds for the function $x \to \frac{\partial f}{\partial x}(t, y)x$. By Corollary 1.1 applied to the variational equation

$$X'(t) = \frac{\partial f}{\partial x}(t, x(t, t_0, x_0))X, \quad X(t_0) = I$$

we conclude that if f is K-cooperative then $X(t) = \frac{\partial x}{\partial x_0}(t, t_0, x_0)$ is K-positive. Straightforward arguments lead to the following result.

Theorem 1.2 *Let $\frac{\partial f}{\partial x}(t, x)$ be continuous on $J \times D$. Then (Q) implies that f is K-cooperative. Conversely, if D is p-convex and f is K-cooperative, then (Q) holds.*

If $K = \mathbb{R}^n_+$, then it is easy to see by using the standard inner product that we may identify K^* with K. The quasimonotone hypothesis reduces to the Kamke condition [22, 14]: $x \leq y$ and $x_i = y_i$ implies that $f_i(t, x) \leq f_i(t, y)$. This holds by taking $\phi(x) = \langle e_i, x \rangle$ and noting that every $\phi \in K^*$ can be represented as a positive linear combination of these functionals. If f is differentiable, the Kamke condition implies

$$\frac{\partial f_i}{\partial x_j}(t, x) \geq 0, \ i \neq j. \tag{3}$$

Conversely, if $\frac{\partial f}{\partial x}(t, x)$ is continuous on $J \times D$ and satisfies (3) and if D is p-convex, then the Kamke condition holds.

Stern and Wolkowicz [32] give necessary and sufficient conditions for (M) to hold for matrix A relative to the ice cream cone $K = \{x \in \mathbb{R}^n : x_1^2 + x_2^2 + \cdots + x_{n-1}^2 \leq x_n^2, \ x_n \geq 0\}$. Let Q denote the $n \times n$ diagonal matrix with first $n - 1$ entries 1 and last entry -1. Then (M) holds for A if and only if $QA + A^T Q + \alpha Q$ is negative semidefinite for some $\alpha \in \mathbb{R}$. Their characterization extends to other ellipsoidal cones.

Additional hypotheses are required for establishing the strong order preserving property and here we provide full details following [11]. Recall that the matrix A is *strongly positive* if $A(K \setminus \{0\}) \subset \text{Int}K$. The following hypothesis for the matrix A follows Schneider and Vidyasagar [25].

(T) for all $x \neq 0$, $x \in \partial K$, there exists $\nu \in K^*$ such that $\nu(x) = 0$ and $\nu(Ax) > 0$.

Our next result was proved by Elsner [3] for the case of constant matrices, answering a question in [25]. Our proof follows that of Theorem 4.3.26 of Berman et al [1].

Proposition 1.1 *Let the linear system (2) satisfy (M). Then the fundamental matrix $X(t_1)$ is strongly positive for $t_1 > t_0$ if there exists s satisfying $t_0 < s \leq t_1$ such that (T) holds for $A(s)$.*

Proof: If not, there exists $x > 0$ such that the solution of (2) given by $y(t) = X(t)x$ satisfies $y(t_1) \in \partial K \setminus \{0\}$. By Corollary 1.1, $y(t) > 0$ for $t \geq t_0$ and $y(t) \in \partial K$ for $t_0 \leq t \leq t_1$. Let $s \in (t_0, t_1]$ be such that (T) holds for $A(s)$. Then there exists $\nu \in K^*$ such that $\nu(y(s)) = 0$ and $\nu(A(s)y(s)) > 0$. As $\nu \in K^*$ and $y(t) \in K$, $h(t) := \nu(y(t)) \geq 0$ for $t_0 \leq t \leq t_1$. But $h(s) = 0$ and $\frac{d}{dt}|_{t=s}h(t) = \nu(A(s)y(s)) > 0$ which, taken together, imply that $h(s - \delta) < 0$ for small positive δ, giving the desired contradiction. ∎

Proposition 1.2 leads immediately to a result on strong monotonicity for the nonlinear system (1).

Theorem 1.3 *Let D be p-convex, $\frac{\partial f}{\partial x}(t, x)$ be continuous on $J \times D$, and f be K-cooperative. Let $B = \{(t, x) \in J \times D : (T)$ does not hold for $\frac{\partial f}{\partial x}(t, x)\}$. Suppose that for all $(t_0, x_0) \in J \times D$, the set $\{t > t_0 : (t, x(t, t_0, x_0)) \in B\}$ is nowhere dense. Then $x(t, t_0, x_0) \ll x(t, t_0, x_1)$ for $t > t_0$ for which both solutions are defined provided $x_0, x_1 \in D$ satisfy $x_0 < x_1$. In particular, this holds if B is empty.*

Proof: We apply the formula

$$x(t, t_0, x_1) - x(t, t_0, x_0) = \int_0^1 \frac{\partial x}{\partial x_0}(t, t_0, sx_1 + (1 - s)x_0)(x_1 - x_0)ds$$

where $X(t) = \frac{\partial x}{\partial x_0}(t, t_0, y_0)$ is the fundamental matrix for (2) corresponding to the matrix $A(t) = \frac{\partial f}{\partial x}(t, x(t, t_0, y_0))$. The left hand side belongs to $K \setminus \{0\}$ if $x_0 < x_1$ by Theorem 1.5 and Theorem 1.4 but we must show it belongs to $\text{Int} K$. For this to be true, it suffices that for each $t > t_0$ there exists $s \in [0, 1]$ such that the matrix derivative in the integrand is strongly positive. In fact, it is K-positive by Corollary 1.1 for all values of the arguments with $t \geq t_0$ so application of any nontrivial $\phi \in K^*$ to the integral gives a nonnegative numerical result. If the condition mentioned above holds then the application of ϕ to the integrand gives a positive numerical result for all s' near s by continuity and Lemma 1.1 and hence the integral belongs to $\text{Int} K$ by Lemma 1.1. By Proposition 1.2, $\frac{\partial x}{\partial x_0}(t, t_0, y_0)$ is strongly positive for $t > t_0$ if (T) holds for $A(r) = \frac{\partial f}{\partial x}(r, x(r, t_0, y_0))$ for some $r \in (t_0, t]$. But this is guaranteed by our hypotheses. $\blacksquare$

The somewhat stronger condition of irreducibility may be more useful in applications because there is a large body of theory related to it [2, 1]. A closed subset F of K that is itself a cone is called *a face* of K if $x \in F$ and $0 \leq y \leq x$ (inequalities induced by K) implies that $y \in F$. For example, the faces of $K = \mathbb{R}^n_+$ are of the form $\{x \in \mathbb{R}^n_+ : x_i = 0, \ i \in I\}$ where $I \subset \{1, 2, \cdots n\}$. For the ice-cream cone $K = \{x \in \mathbb{R}^n : x_1^2 + x_2^2 + \cdots + x_{n-1}^2 \leq x_n^2, x_n \geq 0\}$, the faces are the rays issuing from the origin and passing through its boundary vectors. A K-positive matrix A is *K-irreducible* if the only faces F of K for which $A(F) \subset F$ are $\{0\}$ and K. The famous Perron-Frobenius Theory is developed for K-positive and K-irreducible matrices in Berman and Plemmons [2]. In particular, the spectral radius of A is a simple eigenvalue of A with corresponding eigenvector in $\text{Int} K$. The next result is adapted from Theorem 4.3.17 of Berman et al. [1].

Proposition 1.2 *Let A be a matrix such that $B := A + \alpha I$ is K-positive for some $\alpha \in \mathbb{R}$. Then B is K-irreducible if and only if (T) holds for A.*

Motivated by Proposition 1.3, we introduce the following hypothesis for matrix A.

(I) There exists $\alpha \in \mathbb{R}$ such that $A + \alpha I$ is K-positive and K-irreducible.

In the special case that $K = \mathbb{R}_+^n$, $n \geq 2$, matrix A satisfies (I) if and only if $a_{ij} \geq 0$ for $i \neq j$ and for every non-empty, proper subset I of $N := \{1, 2, \cdots, n\}$, there is an $i \in I$ and $j \in N \setminus I$ such that $a_{ij} \neq 0$. This is equivalent to the assertion that the incidence graph of A is strongly connected. See Berman and Plemmons [2].

The following is a direct corollary of Theorem 1.6.

Corollary 1.2 *Let D be p-convex, $\frac{\partial f}{\partial x}(t, x)$ be continuous on $J \times D$ and f be K-cooperative. Let $\tilde{B} = \{(t, x) \in J \times D : $ (I) does not hold for $\frac{\partial f}{\partial x}(t, x)\}$. Suppose that for all $(t_0, x_0) \in J \times D$, the set $\{t > t_0 : (t, x(t, t_0, x_0)) \in \tilde{B}\}$ is nowhere dense. Then $x(t, t_0, x_0) \ll x(t, t_0, x_0)$ for $t > t_0$ for which both solutions are defined provided $x_0, x_1 \in D$ satisfy $x_0 < x_1$. In particular, this holds if $\tilde{B}$ is empty.*

Corollary 1.2 is an improvement of the restriction of Theorem 10 of Kunze and Siegel [15] to the case that K has nonempty interior. Their results also treat the case that K has empty interior in $\mathbb{R}^n$ but nonempty interior in some subspace of $\mathbb{R}^n$.

Theorem 4.3.40 of Berman et al. [1] implies that for polyhedral cones a matrix A satisfies (M) and (T) if and only if there exists $\alpha \in \mathbb{R}$ such that $A + \alpha I$ is K-positive and K-irreducible. Therefore, for polyhedral cones like $\mathbb{R}_+^n$, Corollary 1.2 and Theorem 1.6 are equivalent.

2 Competitive and Cooperative Systems

We now focus on the autonomous system of ordinary differential equations

$$x' = f(x) \tag{4}$$

where f is continuously differentiable on an open subset $D \subset \mathbb{R}^n$. Let $\phi_t(x)$ denote the solution of (4) that starts at the point x at $t = 0$. ϕ_t will be referred to as the *flow* corresponding to (4). We sometimes refer to f as the *vector field* generating the flow ϕ_t. We introduce following mild dissipativity condition for our next result.

(A) For each $x \in D$, $\phi_t(x)$ is defined for all $t \geq 0$ and $\phi_t(x) \in D$. Moreover, for each bounded subset A of D, there exists a compact subset $B = B(A)$ of D such that for each $x \in A$, $\phi_t(x) \in B$ for all large t.

The following result should be viewed as prototypical of the generic convergence result that may be proved using general results in [30, 28].

Theorem 2.1 *Let the hypotheses of Theorem 1.6 hold for (4), assume $D = \mathbb{R}^n$ or $D = \mathbb{R}_+^n$, and assume that (A) holds. Then the set C of convergent points contains an open and dense subset of D.*

We say that (4) is *K-competitive* in D if the time-reversed system $x' = -f(x)$ is *K-cooperative*. Observe that if (4) is a *K*-competitive system with flow ϕ_t then the time reversed system above is a *K*-cooperative system with flow ψ_t where $\psi_t(x) = \phi_{-t}(x)$, and conversely. Therefore, by time reversal, a competitive system becomes a cooperative system and vice-versa. We will sometimes drop the K from K-cooperative (competitive) when no confusion may result.

Let A be an invariant set for (4) with flow ϕ_t (i.e. $\phi_t(A) = A$ for all t) and let B be an invariant set for the system $y' = F(y)$ with flow ψ_t. We say that the flow ϕ_t on A is *topologically equivalent* to the flow ψ_t on B if there is a homeomorphism $Q : A \to B$ such that $Q(\phi_t(x)) = \psi_t(Q(x))$ for all $x \in A$ and all $t \in \mathbb{R}$. The relationship of topological equivalence says, roughly, that the qualitative dynamics of the two flows are the same. With these definitions, we can state a result of Hirsch [4].

Theorem 2.2 *The flow on a compact limit set of a competitive or cooperative system in $\mathbb{R}^n$ is topologically equivalent to a flow on a compact invariant set of a Lipschitz system of differential equations in $\mathbb{R}^{n-1}$.*

The Poincaré-Bendixson Theorem for three dimensional cooperative and competitive systems is the most notable consequence of Theorem 1.9. It was proved by Hirsch [10] who improved earlier partial results [4, 26].

Theorem 2.3 *(Poincaré-Bendixson Theorem for* 3*-Dimensional Competitive and Cooperative Systems) A compact limit set of a competitive or cooperative system in $\mathbb{R}^3$ that contains no equilibrium points is a periodic orbit.*

The following result of Smith [28] is useful for verifying that an omega limit set is a periodic orbit.

Theorem 2.4 *Suppose that $D \subset \mathbb{R}^3$ contains a unique equilibrium p for the competitive system (4) and it is hyperbolic. Suppose further that its stable manifold $W^s(p)$ is one-dimensional and tangent at p to a vector $v \gg 0$. If the orbit of $q \in D \setminus W^s(p)$ has compact closure in D, then $\omega(q)$ is a nontrivial periodic orbit.*

The existence of $v \gg 0$ usually follows from the Perron-Frobenius Theorem. Zhu and Smith [37] establish the existence of an orbitally asymptotically stable periodic orbit if (4) is dissipative and f is analytic. Ortega and Sánchez [?] observed that the above results hold for general cones.

Competitive systems arise naturally from models in the biological sciences, not just in population biology. The following, taken from de Leenheer and Smith [12], illustrates this point. Consider an individual infected with a virus V which attacks target cells T producing infected cells T^* which in turn each produce on average N virus particles during their lifetimes. Following Perelson et al. [24], who focus on HIV, we obtain the following system for the dynamics of the vector of blood-concentrations $(T, T^*, V) \in \mathbb{R}^3_+$.

$$\dot{T} = f(T) - kVT$$
$$\dot{T}^* = -\beta T^* + kVT \qquad\qquad (5)$$
$$\dot{V} = -\gamma V + N\beta T^* - kVT.$$

Perelson et al. [24] take $f(T) \equiv \delta - \alpha T + pT(1 - \frac{T}{T_{max}})$ with $\delta, \alpha, p, T_{max}$ positive and denote by $\bar{T}$ the positive root of $f(T) = 0$. The basic reproductive number for the model, $R_0 = k\bar{T}(N-1)/\gamma$, gives the number of infected T cells produced by a single infected T cell in a healthy individual.

Among other results, de Leenheer and Smith [12] prove the following.

Theorem 2.5 *If $R_0 > 1$, in addition to the unstable virus-free state $E_0 \equiv (\bar{T}, 0, 0)$, there is a "chronic disease" steady state $E_e \equiv (T_e, T_e^*, V_e)$ given by*

$$T_e = \bar{T}/R_0, \quad T_e^* = \gamma V_e/(N-1)\beta, \quad V_e = f(T_e)/kT_e.$$

which is locally attracting if $f'(T_e) \leq 0$. The omega limit set of every solution with initial conditions satisfying $T^*(0) + V(0) > 0$ either contains E_e or is a nontrivial periodic orbit. There exist parameter values for which E_e is unstable with a two dimensional unstable manifold. In this case, there exists an orbitally asymptotically stable periodic orbit; every solution except those with initial data on the one-dimensional stable manifold of E_e or on the T axis converges to a non-trivial periodic orbit.

System (5) is competitive with respect to the cone $K := \{T, V \geq 0, T^* \leq 0\}$. The change of variables $T^* \rightarrow -T^*$ results in a system the Jacobian for which has non-positive off-diagonal terms on the relevant domain and hence is competitive in the $\mathbb{R}^3_+$-sense. In [12], it is shown that E_e is unstable with a two-dimensional unstable manifold when $kT_{max} > \beta + \gamma + \frac{2\gamma}{N-1}$ and p is sufficiently large. The final assertion of Theorem 1.12 follows from Theorem 1.11; domain D is chosen to exclude E_0. The existence of an orbitally asymptotically stable periodic orbit uses the analyticity of the system and results of [37].

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