Title

Systems of Differential Equations that are Competitive or Cooperative I: Limit Sets

Journal

Siam J. Math. Anal, 13(2)

Author

Hirsch, Morris W

Publication Date

1982

Peer reviewed

SIAM J. MATH. ANAL.
Vol. 13, No. 2, March 1982

0036-1410/82/1302-0001 $01.00/0

SYSTEMS OF DIFFERENTIAL EQUATIONS WHICH ARE COMPETITIVE OR COOPERATIVE. I: LIMIT SETS*

MORRIS W. HIRSCH†

Abstract. A vector field in n-space determines a competitive (or cooperative) system of differential equations provided all the off-diagonal terms of its Jacobian matrix are nonpositive (or nonnegative). The principal result is that limit sets of such systems cannot be more complicated than invariant sets of systems of one lower dimension. In fact orthogonal projection along any positive direction maps a limit set homeomorphically and equivariantly onto an invariant set of a Lipschitz vector field in a hyperplane. Limit sets are nowhere dense, unknotted and unlinked. In dimension 2 every trajectory is eventually monotone. In dimension 3 a compact limit set which does not contain an equilibrium is a closed orbit or a cylinder of closed orbits.

Introduction. One of the most interesting questions to ask about a dynamical system is: what is the long-run behavior of its trajectories? In many systems it is natural to expect, or at least hope, that almost all trajectories either converge to an equilibrium or asymptotically approach a closed orbit (= periodic trajectory). Unfortunately there are many systems that not only lack this convenient property, but cannot even be approximated by systems that have it. Such systems are often said to be "chaotic" or to possess "strange attractors".

To make matters worse, it is very hard to discover the long-run behavior of any but the simplest systems. Research on this problem has bifurcated into two quite different methodologies. A great deal of recent work has gone toward exploring the consequences of various assumptions about the large scale structure of the system, e.g., hyperbolicity of the nonwandering set, structural stability, ergodicity, and so forth. The basic examples come from geometry and physics; the mathematical techniques tend to be topological. For a recent overview of this work see Smale [15, Chapt. I].

This structural approach is very useful for the conceptual understanding of dynamical systems, but usually it is of little direct help to the researcher who wants to understand a particular system. Not only is it extremely difficult to decide whether a particular system has a given structural feature, but many systems do not satisfy any of the axiom systems commonly used in the structural approach. In consequence much research has gone into determining the long-run behavior of special systems (or classes of systems) that arise as models in biology, chemistry, economics and so forth. Algebraic techniques play a prominent role, but owing to the diversity of systems studied very few general principles have been developed.

In this and subsequent articles I hope to make a start at bridging the gap between these two approaches by using structural ideas to analyze a fairly broad class of systems, namely those which are competitive or cooperative (defined below). Such systems are sometimes associated with the concept of negative or positive feedback. They have been used to model a variety of biological, chemical and economic systems; see, e.g., [1], [5], [8], [9], [11], [12], [13], [14].

A general principle emerging from this analysis is that in such systems, especially cooperative ones, there is a strong tendency for bounded trajectories to converge to

* Received by the editors November 12, 1980, and in revised form May 12, 1981. This research was supported in part by the National Science Foundation under grant MCS 77-04242.
† Department of Mathematics, University of California, Berkeley, California 94720.

equilibria or to periodic trajectories. This will be made more precise in later articles, but Theorem C below can be viewed as an instance of this phenomenon.

An efficient way of investigating the long-term behavior of a trajectory $x(t)$ defined for all $t \geqq 0$ is to study its *ω-limit set* $\omega(x)$; the set of points which are limits of sequences $x(t_k)$ where $t_k \to +\infty$. Thus, to say that $\omega(x)$ consists of a single point p means that $x(t)$ converges to p; such a p is necessarily an equilibrium. On the other hand, if $\omega(x)$ is a closed orbit of period T then $x(t)$ will eventually oscillate with period approaching T.

In addition to ω-limit sets there are α-limit sets, defined similarly by letting $t_k \to -\infty$. These are less important in applications but are useful for technical reasons.

The basic theme of this paper is that there are strong geometrical and topological restrictions on the way limit sets are placed in Euclidean n-space. Section 1 contains the basic definition and states the main theorems. Basic technical results about limit sets are proved in § 2. The remaining sections contain the proofs of the main theorems.

1. The main results. Consider a C^1 system of differential equations in $\mathbb{R}^n$,

$$\frac{dx_i}{dt} = F_i(x_1, \cdots, x_n) = F_i(x), \qquad i = 1, \cdots, n. \tag{1.1}$$

The system is called

competitive if $\partial F_i/\partial x_j \leqq 0$ for $j \neq i$,

cooperative if $\partial F_i/\partial x_j \geqq 0$ for $j \neq i$.

A well-known type of competitive system is the model of *competing species*,

$$\frac{dx_i}{dt} = F_i(x) = x_i M_i(x), \tag{1.2}$$

where

$$\frac{\partial M_i}{\partial x_j} < 0 \quad \text{for } j \neq i \tag{1.3}$$

and x is restricted to the nonnegative orthant

$$\mathbb{R}^n_+ = \{x \in \mathbb{R}^n : x_i \geqq 0, i = 1, \cdots, n\}.$$

It is known that, for $n = 2$, *every bounded solution defined on* $[0, \infty)$ *or on* $(-\infty, 0]$ *converges.* (Compare [5], [6], [11], [13]. A stronger result is proved in Theorem 2.3 below.) In contrast to this, Leonard and May [9] give examples of 3 competing species having oscillatory solutions.

Smale [14] has proved the general result that any dynamical system in $\mathbb{R}^{n-1}$ can be embedded in a system of n competing species. Let $\Delta^{n-1} \subset \mathbb{R}^n$ be the simplex spanned by the unit vectors e_i, $i = 1, \cdots, n$, where the kth component of e_i is δ_{ik}.

THEOREM (Smale). *Let X be any C^1 vector field in Δ^{n-1}. Then there exists a C^1 vector field $F = (F_1, \cdots, F_n)$ in $\mathbb{R}^n$ satisfying* (1.2) *and* (1.3), *such that $F|\Delta^{n-1} = X$ and Δ^{n-1} is an attractor.*

This result means that for $n > 2$ there is no hope of proving an analogous convergence theorem. It seems to imply that the limiting behavior of competitive systems can be arbitrarily complicated. For example one can start with a strange attractor in Δ^3 and extend it to a structurally stable competitive system in $\mathbb{R}^4$. On the other hand the results below show that there are in fact important restrictions on the limit set structure of competitive systems.

Briefly put, our main result is that *compact limit sets in a competitive or cooperative system are unknotted and unlinked.* In a kind of converse to Smale's theorem, Theorem A shows that a limit set of such a system can be deformed isotopically and equivariantly into an invariant set of some Lipschitz system in one dimension lower; moreover, the deformation is very simple geometrically. (Theorem A also implies that Smale's choice of the simplex Δ^{n-1} is not entirely arbitrary; for example the conclusion is not true for any simplex containing 0 and a positive vector.)

Theorem B says that a finite family of disjoint compact limit sets can be isotoped into disjoint convex sets.

Theorem C concerns 3-dimensional systems; it says that a compact limit set which contains no equilibrium is either a closed orbit or a ribbon of closed orbits. Thus generically it is a closed orbit.

We now explain the main results in more detail.

By a *limit set* we mean either an α-limit set or an ω-limit set (full definitions are given in § 2).

In the rest of this section we assume that (1.1) is cooperative or competitive and is defined in $\mathbb{R}^n$ or $\mathbb{R}^n_+$. More general domains are described in § 2.

Let $L \subset \mathbb{R}^n_+$ be a set. Let $E^{n-1} \subset \mathbb{R}^n$ be a hyperplane orthogonal to a vector v. Define $\pi: \mathbb{R}^n \to E^{n-1}$ to be an orthogonal projection. We say L is *compressible along* v if $\pi|L$ is a homeomorphism with Lipschitz inverse, and π maps L equivariantly respecting the flow of some locally Lipschitz vector field Y in E^{n-1}. (*Equivariant* means π takes trajectories of (1.1) in L to trajectories of Y, respecting parameterization.)

A vector v is *positive* if $v_i > 0$, $i = 1, \cdots, n$.

THEOREM A. *Let L be a limit set* (*of a system* (1.1) *as above*). *Then L is compressible along any positive vector.*

This has the corollary that every trajectory is nowhere dense. Moreover, the Lipschitzian nature of $(\pi|L)^{-1}$ implies that the dimension, and even the Hausdorff dimension, of L is $\leqq n-1$.

The proof of Theorem A is given in § 3.

A collection $L_1, \cdots, L_r$ of disjoint subsets of $\mathbb{R}^n$ is *unlinked* if there is a diffeotopy of $\mathbb{R}^n$ carrying them into disjoint convex sets. In § 6 we prove:

THEOREM B. *Every finite collection of disjoint compact limit sets is unlinked.*

In dimension 3 Theorems A and B imply that closed orbits are unknotted and unlinked. Theorem A allows us to bring into play the Poincaré–Bendixson theorem in studying 3-dimensional competitive or cooperative systems. In § 4 we prove:

THEOREM C. *Suppose $n = 3$. Let L be a compact limit set which contains no equilibrium. Then*:

(a) *L is either a closed orbit or a cylinder of closed orbits.*

(b) *L is a closed orbit if the system is cooperative and L is an ω-limit set.*

(c) *L is a closed orbit if all closed orbits are hyperbolic.*

Theorem C has interesting implications about the *observed* long-term behavior of a bounded solution $x(t)$ of a 3-dimensional competitive or cooperative system.

First consider the case when the ω-limit set L contains an equilibrium p. Then $x(t)$ gets arbitrarily near p; moreover, it stays within any given neighborhood of p for arbitrarily long periods of time. An observer would be hard put not to conclude that $x(t)$ has stabilized at p.

Consider next the case when L does not contain any equilibrium. Then according to Theorem C $x(t)$ will either converge to a limit cycle, or it will oscillate with slowly varying period, the rate of variation tending to zero.

Section 5 also contains a proof that if a cooperative system has a certain generic behavior then the only compact ω-limit sets are closed orbits.

The proofs of Theorems A, B and C are based on a famous comparison principle of Kamke which implies that *the flow of a cooperative system preserves the vector ordering* (Kamke [7]; see also Coppel [2]). Recall that this ordering is defined by

$$x < y \quad \text{if } x_i < y_i \quad \text{for all } i.$$

We also write

$$x \leqq y \quad \text{if } x_i \leqq y_i \quad \text{for all } i.$$

This result can also be used to study competitive systems since these correspond to cooperative ones through *time-reversal*: changing the independent variable from t to $-t$.

Define vectors x, y to be *related* if $x < y$ or $y > x$, and to be *unrelated* otherwise, i.e., when there exist i, j with $x_i \leqq y_i$ and $x_j \geqq y_j$.

The form of Kamke's result we shall use is:

THEOREM D. *Let $x(t)$, $y(t)$ be solutions defined for $a \leqq t \leqq b$.*

(a) *Suppose the system is cooperative. If $x(a) < y(a)$ then $x(b) < y(b)$.*

(b) *Suppose the system is competitive. If $x(a)$ and $y(a)$ are unrelated then so are $x(b)$ and $y(b)$.*

This result is valid for systems defined in $\mathbb{R}^n$ or $\mathbb{R}^n_+$, and also for systems defined in sets Γ described in § 2.

2. Limit sets. In this section we consider a cooperative or competitive system

$$\frac{dx_i}{dt} = F_i(x_1, \cdots, x_n), \qquad i = 1, \cdots, n \tag{2.1}$$

defined by a C^1 vector field $F: \Gamma \to \mathbb{R}^n$. The precise assumptions on the domain $\Gamma \subset \mathbb{R}^n$ are given below following the statement of the main results of this section. They are satisfied if $\Gamma = \mathbb{R}^n_+$ or $\mathbb{R}^n$.

The first result is a useful criterion for a solution to converge. It can also be viewed as an existence criterion for certain kinds of equilibrium points.

A point $p \in \Gamma$ is an *equilibrium* if $F(p) = 0$.

THEOREM 2.1. *Assume* (2.1) *is cooperative. Let $x: [0, \infty) \to \Gamma$ be a solution whose image has compact closure in Γ. If $x(T)$ is related to $x(0)$ for some $T > 0$, then $x(t)$ converges to an equilibrium as $t \to \infty$.*

This implies that no two points of a closed orbit of a cooperative system can be related, and the same holds for competitive systems by time reversal. It follows easily that in dimension 3 a closed orbit cannot be knotted.

The following result expresses important limitations on the geometry of limit sets.

THEOREM 2.2. *Suppose* (2.1) *is cooperative or competitive. Then no two points of a limit set can be related. Moreover, if y is a limit point then the vector $F(y)$ is unrelated to the zero vector.*

The following result shows that 2-dimensional cooperative or competitive systems have trivial dynamics.

THEOREM 2.3. *Assume* (2.1) *is cooperative or competitive and $n = 2$. Let $y: [0, \tau) \to \Gamma$ be the solution through $y(0)$, $\tau = t_+(y)$. Then either $|y(t)| \to \infty$ as $t \to \tau$, or else $y(t)$ converges to some point of $\bar{\Gamma}$ as $t \to \tau$. In fact $[0, \tau)$ is the union of two intervals, in each of which both $y_1(t)$ and $y_2(t)$ are monotone.*

Before proving these results we describe the assumption on the domain Γ. We wish to cover the cases where $\Gamma = \mathbb{R}^n$ or $\mathbb{R}^n_+$. But there are interesting systems which are cooperative in some regions and competitive in others. Consider for example the following system in $\mathbb{R}^n_+$:

$$\frac{dx_i}{dt} = a_i(x_i)[b_i(x_i) + g(s)], \tag{2.2}$$

where $a_i \geqq 0$ and $s = x_1 + \cdots + x_n$. Evidently (2.2) is competitive where $g'(s) \leqq 0$ and cooperative where $g'(s) \geqq 0$. (Such systems are suggested by Grossberg's models of adaptive networks [5]. They also arise in models of economic competition.)

From now on Γ is a locally closed subset of $\mathbb{R}^n$ whose interior $\operatorname{Int}\Gamma$ is dense in Γ. This means that Γ is the intersection of an open set with the closure of an open set. The vector field $F: \Gamma \to \mathbb{R}^n$ is assumed to extend to a C^1 map on an open set in $\mathbb{R}^n$.

The final assumption is that Γ is *p-convex*: if $a, b \in \Gamma$ and $a \geqq b$ then Γ contains the line segment between a and b. Kamke's comparison principle (Theorem D above) is then valid. (But Theorem 2.3 is valid without p-convexity.)

The following statements on domains of solutions and limit sets are easily proved using standard theorems in differential equations and the assumptions about Γ.

Let $W \subset \mathbb{R}^n$ be an open set containing Γ and $G: W \to \mathbb{R}^n$ a C^1 vector field extending F. For any $y \in \Gamma$ there is a unique nonextendible solution $\xi(t)$, $\alpha < t < \beta$ to the initial value problem

$$\frac{d\xi}{dt} = G(\xi), \qquad \xi(0) = y.$$

Let $I(y) \subset \mathbb{R}$ be the connected component of 0 in the set

$$\{t: \alpha < t < \beta \text{ and } \xi(t) \in \Gamma\}.$$

The restriction of ξ to $I(y)$ is the solution (in Γ) to (2.1) passing through y at time $t = 0$. It is denoted by $y(t)$ or $\phi_t(y)$. Since the interior of Γ is dense this solution is independent of the choice of W and G.

Set

$$t_+(y) = \sup\{t: t \in I(y)\}, \qquad t_-(y) = \inf\{t: t \in I(y)\},$$

so that $-\infty \leqq t_-(y) \leqq 0 \leqq t_+(y) \leqq \infty$. We say the solution through y *terminates* if $t_+(y) \in I(y)$; otherwise it is *nonterminating*. In the nonterminating case if $t_+(y) < \infty$, then either $|y(t)| \to \infty$ or $y(t)$ approaches the boundary $\partial\Gamma$ of Γ as $t \to t_+(y)$. If $y(t)$ is nonterminating and the *forward orbit*

$$O_+(y) = \{y(t): 0 \leqq t < t_+(y)\}$$

has compact closure in Γ, then $t_+(y) = \infty$.

Suppose $y(t)$ is nonterminating. Its *ω-limit set* $\omega(y) = \omega(y(0))$ is defined to be the set of points $p \in \Gamma$ such that

$$p = \lim_{k \to \infty} y(t_k)$$

for some sequence t_k in $I(y)$ converging to $t_+(y)$. It is easy to prove that if p is an ω-limit point of y (i.e., $p \in \omega(y)$) then the solution through p is nonterminating. It is also noninitiating, i.e., $t_-(p) \notin I(p)$. Moreover, $\omega(y)$ is *invariant*: if $p \in \omega(y)$ then $\phi_t(p) \in \omega(y)$ for all $t \in I(p)$. It is well known that $O_+(y)$ has compact closure in Γ if and only if $\omega(y)$ is a nonempty compact connected set. In this case $t_+(y) = \infty$.

If $y(t)$ terminates then $\omega(y)$ is defined as the empty set.

The α-limit set $\alpha(y)$ is defined similarly, replacing $t_+(y)$ with $t_-(y)$; it has analogous properties.

A *closed orbit* γ of *period* $T \neq 0$ is the image of a solution $u:\mathbb{R} \to \Gamma$ such that $u(t+T) = u(t)$ for all t. Notice the set of periods of γ, together with 0, is a closed subgroup of $\mathbb{R}$.

PROPOSITION 2.4. *Assume* (2.1) *is cooperative and* $x:[0,\infty) \to \Gamma$ *is a solution. Let* $T > 0$ *be such that* $x(T) \geqq x(0)$ *or* $x(T) \leqq x(0)$. *Let* $p \in \Gamma$ *be a limit point of* $\{x(kT): k \in \mathbb{Z}_+\}$ *with* $T \in I(p)$. *Then* p *lies on a closed orbit* γ *of period* T *and* $\omega(x) = \gamma$.

Proof. We suppose $x(T) \geqq x(0)$, the other case being similar. Then

$$x(t+T) \geqq x(t) \quad \text{for all } t > 0.$$

In particular,

$$x((k+1)T) \geqq x(kT) \quad \text{for all } k \in \mathbb{Z}_+.$$

It follows easily that

$$p = \lim_{k\to\infty} x(kT) = \lim_{k\to\infty} x((k+1)T), \qquad k \in \mathbb{Z}_+. \tag{2.3}$$

Therefore $p(T) = p$, so p lies on a closed orbit γ of period T. From (2.3) and the continuity of solutions it follows that $\gamma = \omega(x)$. Q.E.D.

Proof of Theorem 2.1. Let $x:[0,\infty) \to \Gamma$ be as in Theorem 2.1. There is an open set $S \subset \mathbb{R}$ containing T such that $x(s) > x(0)$ [or $< x(0)$] for all $s \in S$. By Proposition 2.4, $\omega(x)$ is a closed orbit γ and γ has period s for all $s \in S$. It follows that γ consists of a single equilibrium p. Q.E.D.

The proof of Theorem 2.2 requires the following result, Proposition 2.5, which has some independent interest: it shows that solutions to (2.1) cannot oscillate with respect to the partial ordering $<$.

Let $y(t)$ be a curve in $\mathbb{R}^n$ defined on some interval $I \subset \mathbb{R}$. A subinterval $J = [a, b] \subset I$ is called an *up-interval* if $y(a) < y(b)$, and a *down-interval* if $y(a) > y(b)$.

The following result is due to L. Ito.

PROPOSITION 2.5. *Assume* (2.1) *is cooperative or competitive. Then a solution* $y: I \to \Gamma$ *cannot have an up-interval and a down-interval which are disjoint.*

Proof. We prove the cooperative case; the competitive case follows by time-reversal.

Suppose there are an up-interval K and a down-interval J with $J \cup K \subset I$, $J \cap K = \varnothing$. We assume $J < K$ (i.e., $u < v$ for all $u \in J$, $v \in K$), the other case being similar. Put

$$J = [a, r], \qquad K = [s, b], \qquad a < r < s < b.$$

Let $s' \in K$ be the smallest number such that $y(s') \leqq y(t)$ for all $t \in K$; we denote this by $y(s') = \inf y(K)$. Then $[s', b]$ is an up-interval disjoint from J, so we may replace K by $[s', b]$. Thus we may assume that $y(s) = \inf y(K)$.

We prove the proposition by showing that neither $r - a \leqq b - s$ nor $r - a > b - s$ can hold.

Assume $r - a \leqq b - s$. Then $s < s + r - a \leqq b$. Since $[s, s+r-a]$ is a translate to the right of $[a, r]$ it follows that $[s, s+r-a]$ is a down-interval. But then

$$y(s+r-a) < y(s) \quad \text{and} \quad s+r-a \in K,$$

contradicting $y(s) = \inf y(K)$.

Assume $r-a>b-s$. Then $a<a+b-r<s<b$. Since $[a+b-r, b]$ is a translate of $[a, r]$ to the right it follows that $[a+b-r, b]$ is a down-interval. Thus

$$y(a+b-r)>y(b)>y(s).$$

Define $c\in[a+b-r, s]$ to be the largest number such that $y(c)\geqq y(b)$, so that $c<s<b$. Then $y(c)>y(s)$, i.e., $[c, s]$ is a down-interval.

Suppose $s-c\leqq b-s$. Then translating $[c, s]$ by $s-c$ provides a down-interval $[s, 2s-c]\subset[s, b]$, contradicting $y(s)=\inf y(K)$.

Finally, suppose $s-c>b-s$. Then $c<c+b-s$; since $[c+b-s, b]$ is a right-translate of the down-interval $[c, s]$ we have

$$y(c+b-s)>y(b).$$

But this contradicts the definition of c. The proof of Proposition 2.5 is complete. Q.E.D.

In the cooperative case the following result also holds: *if $z(t)$ is a solution defined for all $t\geqq 0$ then it cannot have both an up-interval and a down-interval.* For one of the intervals could be translated to the right until it is disjoint from the other interval, in contradiction to Proposition 2.5. A similar (but less interesting) conclusion holds for a solution to a competitive system defined for all $t\leqq 0$.

Proof of Theorem 2.2. Suppose $p<q$. From the definition of limit set there must exist $t_1<t_2<t_3<t_4$ with $z(t_1)$, $z(t_4)$ so close to p, and $z(t_2)$, $z(t_3)$ so close to q, that $z(t_1)<z(t_2)$ and $z(t_4)<z(t_3)$. Therefore $[t_1, t_2]$ is an up-interval which is disjoint from the down-interval $[t_3, t_4)$, contradicting Proposition 2.5.

Suppose $F(p)>0$ and $p\in\omega(Z)$. Then $p(\varepsilon)>p$ for sufficiently small $\varepsilon>0$. Since $p(\varepsilon)\in\omega(z)$ this contradicts what has already been proved. The other cases are similar. Q.E.D.

Proof of Theorem 2.3. By time-reversal we may assume (2.1) is cooperative. We also assume $y(t)$ is not constant. The interval $I=\{t\geqq 0: y(t) \text{ is defined}\}$ is the union of the following sets:

$$A_1=\{t\in I: F_i(y(t))\geqq 0, i=1, 2\},$$

$$A_2=\{t\in I: F_2(y(t))>0>F_1(y(t))\},$$

$$A_3=\{t\in I: F_i(y(t))\leqq 0, i=1, 2\},$$

$$A_4=\{t\in I: F_2(y(t))<0<F_1(y(t))\}.$$

Notice that these sets are pairwise disjoint. And if $t\in A_1$ and $s>t$ and $s\in I$ then $s\in A_1$. For

$$D\phi_{s-t}(y(t))F(y(t))=F(y(s))$$

and, from Proposition 2.6 below, $D\phi_r(x)$ is a nonnegative matrix for all $x\in\Gamma$, $r\in I(x)$, $r>0$. Similarly if, $t\in A_3$ and $s>t$, $s\in I$ then $s\in A_3$. This proves that *either A_1 or A_3 is empty.*

Let $k\in\{1, 2, 3, 4\}$ be such that $0\in A_k$. If $k=1$ or 3 then $I\subset A_k$, so $y_i(t)$ is monotone, $i=1, 2$. If $k=2$ or 4 and $I\not\subset A_k$ there must be a smallest $t_0\in I$ with $t_0\in A_j$, $j=1$ or 3. Then $I\subset A_k\cup A_j$. This proves the last sentence of Theorem 2.3. Q.E.D.

Theorem 2.3 is true even without p-convexity of Γ: the proof uses only the following result.

PROPOSITION 2.6. *Let $\{\phi_t\}$ denote the flow of a cooperative system defined in a set $\Gamma\subset\mathbb{R}^n$ which satisfies the assumptions above except that Γ is not assumed to be p-convex. Then $D\phi_t(x)$ is a nonnegative matrix for all $t\geqq 0$, $x\in\Gamma$.*

Proof. We apply Kamke's theorem (which holds for nonautonomous systems) to the variational equation along a fixed solution $x(t)=\phi_t(x)$:

$$\frac{dA}{dt}=DF(\phi_t(x))A. \tag{2.4}$$

Here $A(t)$ is an $n\times n$ matrix. It is easily seen that the right-hand side of (2.4), that is, the matrix function

$$G(t,A)=(DF(\phi_t(x))A,$$

satisfies

$$\frac{\partial G_{ij}}{\partial A_{rs}}\geqq 0 \quad \text{for } (i,j)\neq(r,s),$$

so that Kamke's comparison theorem applies to solutions to (2.4). Now the solution $B(t)$ to (2.4) with initial condition $B(0)=0$ is the constant solution $B(t)=0$, while the solution with initial condition $A(0)=I$ is $D\phi_t(x)$. Since $0\leqq I$ we have $B(t)\leqq A(t)$, for all $t\geqq 0$, i.e., $D\phi_t(s)$ is a nonnegative matrix. Q.E.D.

Proposition 2.6 has an interesting consequence for competitive systems, due to S. Grossberg [5]. We say a solution $x(t)$ is *switched on* at time t_0 if $F_i(x(t_0))>0$ for some $i\in\{1,\dots,n\}$. Grossberg calls the following result the *ignition principle.*

PROPOSITION 2.7. *Let Γ be as in Proposition* 2.6 *and let $x(t)$ be a solution to a competitive system in Γ. If $x(t)$ is switched on at t_0 then $x(t)$ is switched on all $t_1>t_0$.*

Proof. Let the competitive system be

$$\frac{dx}{dt}=G(x).$$

Consider the corresponding cooperative system obtained by time-reversal,

$$\frac{dy}{dt}=F(y)\equiv -G(y).$$

Fix $t_1>t_0$, and observe that the curve $y(t)=x(t_1-t)$ is a solution to the cooperative system.

If $x(t)$ is not switched on at time t_1 then $G(x(t_1))\leqq 0$, so $F(y(0))\geqq 0$. Therefore $F(y(s))\geqq 0$ for all $s>0$ by Proposition 2.6, since

$$F(y(s))=D\phi_s(y(0))F(y(0)),$$

and $D\phi_s(y(0))\geqq 0$. Putting $s=t_1-t_0$ shows that $F(y(t_1-t_0))\geqq 0$, so $G(x(t_0))\leqq 0$, contradicting $x(t)$ being switched on at t_0. Q.E.D.

3. Extension and proof of Theorem A. In this section we consider a cooperative or competitive system

$$\frac{dx}{dt}=F(x). \tag{3.1}$$

THEOREM 3.1. *Let L be a limit set. Then L is compressible along any positive vector v.*

Proof. It suffices to consider only unit vectors v. Let $\pi_v:\mathbb{R}^n\to E^{n-1}=v^\perp$ be an orthogonal projection onto the hyperplane orthogonal to v. We first show that $\pi_v|L$ is injective.

Suppose $p, q \in L$ and $\pi_v(p) = \pi_v(q)$. Then $p - q = \lambda v$, $\lambda \in \mathbb{R}$. If $p \neq q$ then p, q are related since $\lambda \neq 0$ and $v > 0$. But this contradicts Theorem 2.2; therefore $\pi_v|L$ is injective.

For distinct nonzero vectors $a, b \in \mathbb{R}^n$ let $A(a, b)$ denote the positive acute angle between the lines $\{\lambda a : \lambda \in \mathbb{R}\}$ and $\{\lambda b : \lambda \in \mathbb{R}\}$. It is easy to see that if $\pi_v|L$ is *not* Lipschitz then there exist sequences p_j, q_j in L such that $p_j \neq q_j$ and

$$A(v, p_j - q_j) \to 0.$$

Suppose this holds, and let w_j denote the unit vector $(p_j - q_j)/|p_j - q_j|$. Then $A(v, w_j) \to 0$. Passing to a subsequence we may assume that $w_j \to \pm v$. Interchanging p_j and q_j where necessary we may assume $w_j \to v$. Choose k so large that $w_k > 0$ and set $w = w_k$. Then $\pi_w(p_k) = \pi_w(q_k)$, contradicting the injectivity of π_w proved above. This shows that $\pi_v|L$ is Lipschitz.

Set $\pi_v = \pi$ and define

$$H : \pi(L) \to E^{n-1}, \qquad H = \pi \circ F \circ (\pi|L)^{-1}.$$

Now F is C^1 so $F : L \to \mathbb{R}^n$ is locally Lipschitz. Therefore H is locally Lipschitz. By a result of McShane [14] H can be extended to a locally Lipschitz vector field on E^{n-1}. Notice that $H(\pi x) = 0$ if and only if $F(x) = 0$, by the last statement of Theorem 2.2.

To say that $\pi : L \to E^{n-1}$ is equivariant means that if $x(t)$ is an integral curve of F in L then $\pi(x(t))$ is an integral curve of H. This follows from the definition of H. Q.E.D.

We conclude this section with another compressibility theorem for cooperative systems.

THEOREM 3.2. *Suppose* (3.1) *is cooperative and* $K \subset \Gamma$ *is a compact set which is the closure of the image of a solution* $x : [0, \infty) \to K$. *If* $x(t)$ *does not converge to an equilibrium then* K *is compressible along any positive vector.*

Proof. Observe that $K = O_+(x) \cup \omega(x)$. Let $\pi_v : \mathbb{R}^n \to v^\perp$ be an orthogonal projection where $v > 0$. Using arguments similar to those above, one can show that if $\pi_v|K$ is not injective, or $(\pi_v|K)^{-1}$ is not Lipschitz, then $x(t_0)$ and $x(t_1)$ are related for some $t_0, t_1 \geqq 0$. But then by Theorem 2.1 $x(t)$ converges to an equilibrium. The rest of the proof is like that of Theorem 3.1. Q.E.D.

4. Proof of Theorem C. In this section we assume given a competitive or cooperative system

$$\frac{dx_i}{dt} = F_i(x_1, x_2, x_3), \qquad i = 1, 2, 3 \tag{4.1}$$

defined in a set $\Gamma \subset \mathbb{R}^3$ satisfying the conditions in § 2.

THEOREM 4.1. *Let* L *be a compact limit set which contains no equilibrium. Then*:

(a) *L is either a closed orbit or a cylinder of closed orbits.*

(b) *L is a closed orbit if the system is cooperative and L is an ω-limit set.*

(c) *L is a closed orbit if L contains a hyperbolic closed orbit.*

Proof. Let $\pi : \mathbb{R}^3 \to E^2$ be an orthogonal projection onto a plane perpendicular to a positive vector. By Theorem 3.1, π maps L homeomorphically and equivariantly onto an invariant set of some locally Lipschitz vector field Y in E^2. Clearly $\pi(L)$ is compact and connected, and it contains no equilibrium.

Let ψ_t denote the flow of Y.

The Poincaré–Bendixson theorem (see, e.g., Hartman [4]) implies that $\pi(L)$ is a union of closed orbits and trajectories that spiral down to closed orbits in both positive and negative time. We shall prove that such spiralling cannot in fact occur, so that $\pi(L)$ is a union of closed orbits. From this part (a) of the theorem follows easily.

Let $z \in \pi(L)$. Suppose z is not on a closed orbit. Then, as $t \to \infty$, $\psi_t(z)$ spirals down to a closed orbit $\gamma \subset \pi(L)$.

Let A denote the component of $E^2 - \gamma$ which contains z; let B denote the other component. Let $T > 0$ be the period of γ.

It is well known that γ is an attractor for the flow restricted to $\bar{A}$. Thus there is a compact neighborhood N or γ in $\bar{A}$ such that

$$\psi_T(N - \gamma) \subset \operatorname{Int} N.$$

Define $W = \pi(L) \cap (B \cup N)$. Then W is a compact subset of $\pi(L)$ and

$$\psi_T(W) \subset \operatorname{Int} W.$$

Put $V = (\pi|L)^{-1}(W)$. Then V is a compact subset of L and

$$\phi_T(V) \subset \operatorname{Int}_L V.$$

This, however, is impossible for a compact limit set L by a result of Franke and Selgrade [3]. This contradiction shows that z, which is an arbitrary point of $\pi(L)$, must lie on a closed orbit. This completes the proof of (a).

Now assume the system is cooperative.

Suppose that L is not a single closed orbit, but is a cylinder of closed orbits. Then $\pi(L)$ contains a 2-disk D. Let $p \in L$ be such that $\pi(p)$ is the center of D.

Let $x(t)$, $t > 0$ be a solution of (1) whose ω-limit set is L. There exists $t_0 > 0$ such that $x(t_0) \in \operatorname{Int} D$. Let $q \in L$ be such that $\pi(x(t_0)) = \pi(q)$. It follows that $x(t_0)$ is related to q.

There exists $t_1 > t_0$ such that $x(t_1)$ is so near q that $x(t_0)$ is related to $x(t_1)$. It now follows from Proposition 2.1 that $x(t)$ converges to an equilibrium as $t \to \infty$. Thus L is an equilibrium; this contradiction completes the proof of (b).

Part (c) follows from (a) since a cylinder of closed orbits cannot contain a hyperbolic closed orbit. Q.E.D.

By exploiting Theorem 3.2 we can establish other criteria for L to be a closed orbit in the cooperative case. Suppose L is a compact ω-limit set of a cooperative system (4.1), say $L = \omega(x)$. Suppose L contains a nonequilibrium closed orbit γ. Then $x(t)$ does not converge, and so Theorem 3.2 implies that the closure of $\{x(t): t \geqq 0\}$ is compressible. Set $z = \pi x(0)$. Thus (in the notation above) $\psi_t(z)$ has the ω-limit set $\pi(L)$. Since $\pi(L)$ contains the closed orbit $\pi(\gamma)$, the Poincaré–Bendixson theorem implies $\pi(L) = \pi(\gamma)$. Since π is injective it follows that $L = \gamma$.

Now suppose L does not contain a closed orbit, L contains only a finite number of equilibria, and $x(t)$ does not converge. Then by using Theorem 3.2 and Poincaré–Bendixson one can show that L must contain a *cycle of equilibria* $p_1, \cdots, p_k$ $(k \geqq 1)$: this means that for each $i = 1, \cdots, k$ there is a solution $y_i(t)$ in L whose α-limit in p_i and whose ω-limit is p_{i+1}, with $p_{k+1} = p_1$. Thus we obtain:

THEOREM 4.2. *Assume that* (4.1) *is cooperative and contains no cycle of equilibria. Then every compact ω-limit set is a closed orbit* (*possibly an equilibrium*).

It is well known that existence of a cycle of equilibria is a highly unstable phenomenon. It cannot occur if all the equilibria are hyperbolic and their stable and unstable manifolds meet only transversely—a generic property of C^1 vector fields (see Smale [16], Abraham and Robbin [17]).

In applying approximation theorems to cooperative systems there arises the difficulty that the cooperative condition is not stable. However, the property of being *strongly cooperative*—$\partial F_i/\partial x_j > 0$ for $i \neq j$—*is* stable. Given a cooperative field F every neighborhood of F in the compact-open C^1 topology contains a strongly cooperative field G of the form

$$G_i(x) = F_i(x) + \delta \sum_{j=1}^{n} x_j, \qquad \delta > 0.$$

The field G can then be approximated by fields having generic properties. In this way, using standard approximation methods of differentiable dynamical systems, one can prove the following result:

THEOREM 4.3. *Let F be a cooperative vector field in $\Gamma \subset \mathbb{R}^n$. Let $K \subset \Gamma$ be a compact set and ε a positive number. There exists a strongly cooperative vector field G on Γ with the following properties*:

(a) *For all $x \in K$,*

$$|F(x) - G(x)| + \|DF(x) - DG(x)\| < \varepsilon.$$

(b) *All equilibria and closed orbits of G are hyperbolic, and their stable and unstable manifolds meet only transversely.*

(c) *If $n = 3$ then every compact ω-limit set is a closed orbit (perhaps degenerate).*

5. A criterion for unlinking. In this section we prove a topological result, Proposition 5.2, needed for the proof of Theorem B.

An *isotopy* of $\mathbb{R}^n$ is a family of C^1 diffeomorphisms $h_t: \mathbb{R}^n \to \mathbb{R}$, $0 \leqq t \leqq 1$, such that h_0 is the identity and $h_t(x)$ is C^∞ in (t, x).

Let $\mathscr{A} = \{A_i\}$, $\mathscr{B} = \{B_i\}$ be two collections of subsets of $\mathbb{R}^n$ indexed by the same set S. We say $\mathscr{A}$ and $\mathscr{B}$ are *isotopic* if there is an isotopy h_t of $\mathbb{R}^n$ such that $h_1(A_i) = B_i$ for all $i \in S$. This is an equivalence relation.

The family $\mathscr{A}$ is *unlinked* if it is isotopic to a family $\mathscr{B}$ such that there exist disjoint convex sets $C_i \subset \mathbb{R}^n$ with $B_i \subset C_i$ for all $i \in S$.

Let $f_1, \cdots, f_r$ be continuous real-valued functions on $\mathbb{R}^{n-1}$. Let L_i be the graph of f_i; we consider L as a subset of $\mathbb{R}^{n-1} \times \mathbb{R} = \mathbb{R}^n$.

LEMMA 5.1. *If $f_1 < \cdots < f_r$ then $\{L_1, \cdots, L_r\}$ is unlinked.*

Proof. Given real numbers $u_1 < \cdots < u_r$ there is a single isotopy of $\mathbb{R}$ carrying each u_i into the open interval $(i, i+1)$. Moreover, the isotopy can be chosen to be C^∞ in the parameters $(u_1, \cdots, u_r)$. We assume such a family of isotopies has been chosen once and for all; for fixed $u_1 < \cdots < u_r$ we denote the isotopy by

$$y \to g(t, u_1, \cdots, u_r, y), \qquad y \in \mathbb{R},$$

where g is C^∞.

An isotopy of $\mathbb{R}^{n-1} \times \mathbb{R}$ is defined by

$$h_t: \mathbb{R}^{n-1} \times \mathbb{R} \to \mathbb{R}^{n-1} \times \mathbb{R},$$

$$h_t(x, y) = (x, g(t, f_1(x), \cdots, f_r(x), y)).$$

Evidently h_1 takes the graph of f_i into the convex set $C_i = \{(x, z) \in \mathbb{R}^{n-1} \times \mathbb{R}: i < z < i + 1\}$. Since these sets are disjoint the L_i are unlinked. Q.E.D.

PROPOSITION 5.2. *For $i = 1, \cdots, r$ let $K_i \subset \mathbb{R}^{n-1}$ be a compact set and $g_i: K_i \to \mathbb{R}$ a continuous map. Let $L_i \subset \mathbb{R}^{n-1} \times \mathbb{R}$ denote the graph of g_i. Suppose that $g_i(x) < g_j(x)$ whenever $i < j$ and $x \in K_i \cap K_j$. Then $\{L_1, \cdots, L_r\}$ is unlinked.*

Proof. This follows from Lemma 5.1 provided the g_i extend to continuous maps $f_i: \mathbb{R}^{n-1} \to \mathbb{R}$ such that $f_i < f_j$ for $i < j$. Such extensions can be found as follows.

By Tietze's theorem the g_i extend to continuous maps $\hat{g}_i : \mathbb{R}^{n-1} \to \mathbb{R}$. Let

$$m_i < \min \{f_j(x) : 2 \leqq j \leqq r, x \in K_j\}.$$

Let U be a neighborhood of K so small that $\hat{g}_i < m_i$ on U. Let $\rho : \mathbb{R}^{n-1} \to [0, 1]$ be a continuous function which is 1 on K_1 and 0 on $\mathbb{R}^{n-1} = U$.

Define

$$f_1 : \mathbb{R}^{n-1} \to \mathbb{R},$$

$$f_1(x) = \rho(x)\hat{g}_1(x) + (1 - \rho(x))m_1.$$

Then $f_1(x) < g_j(x)$ for $j > 1$, $x \in K_j$. A similar procedure extends g_2 to $f_2 : \mathbb{R}^{n-1} \to \mathbb{R}$ with $f_2 > f_1$ and $f_2(x) < g_j(x)$ for $j > 2$, $x \in K_j$, etc. In this way the required f_j are successively defined. Q.E.D.

6. Extension and proof of Theorem B. Theorem B is a special case of a more general result, Theorem 6.1, proved below.

We suppose given a cooperative or competitive system

$$\frac{dx}{dt} = F(x) \tag{6.1}$$

defined in a set $\Gamma \subset \mathbb{R}^n_+$ as in § 2.

Let L be an invariant set. We call L a *pseudo-limit* set if it satisfies the following condition. Given two points of L and $\varepsilon > 0$, there is a trajectory (not necessarily in L) that comes within ε of each of the points. Evidently limit sets and orbit closures are examples of pseudo-limit sets.

A set L is *balanced* if p, q are unrelated for all p, q in L.

THEOREM 6.1. *Let $L_1, \cdots, L_s$ be disjoint compact pseudo-limit sets. Suppose that each L_i is balanced. Then $\{L_1, \cdots, L_s\}$ is unlinked.*

The proof depends on the following lemma. Define a relation $<$ on $\{L_1, \cdots, L_s\}$: $L_i < L_j$ if $p < q$ for some $p \in L_i$, $q \in L_j$.

LEMMA 6.2. *The relation $<$ is a partial ordering.*

Proof. Since each L_i is balanced it is impossible that $L_i < L_i$.

Suppose $L_i < L_j < L_m$. We want to prove $L_i < L_m$. There exist points

$$p \in L_i, \quad q, q' \in L_j, \quad r \in L_m$$

such that $p < q$, $q' < r$. Let U, U' be neighborhoods in Γ of q, q' respectively such that $p < U$, $U' < r$. Let $y(t)$ be a solution entering both U and U'. Suppose $y(t_0) \in U$, $y(t_1) \in U'$.

By time-reversal we assume $t_1 \geqq t_0$.

Suppose the system is cooperative. Let $x(t)$ be the solution such that $x(t_0) = p$. We have $x(t_0) < y(t_0)$. Since $t_0 \leqq t_1$, the order-preserving property (Theorem D of § 1) implies $x(t_1) < y(t_1)$. Now $y(t_1) \in U'$ so $y(t_1) < r$. Since $x(t_1) \in L_i$ it follows that $L_i < L_m$.

Suppose the system is competitive. Let $z(t)$ be the solution such that $z(t_1) = r$. By a similar argument one sees that

$$p = x(t_0) < y(t_0) < z(t_0)$$

and $z(t_0) \in L_m$. Thus in all cases $L_i < L_m$. This completes the proof of Lemma 6.2. Q.E.D.

Proof of Theorem 6.1. It follows from Lemma 6.1 that the L_k are partially ordered by $<$. We relabel the L_k so that if $L_i < L_j$ then $i < j$.

Let $E^{n-1} \subset \mathbb{R}^n$ be a hyperplane orthogonal to a positive unit vector v. Let $\pi: \mathbb{R}^n \to E^{n-1}$ be the orthogonal projection. Define continuous maps

$$g_k: \pi(L_k) \to \mathbb{R}, \qquad x \to \langle x, v \rangle,$$

where $\langle \cdot, \cdot \rangle$ is the standard inner product.

Identify $\mathbb{R}^n$ isometrically with $E^{n-1} \times \mathbb{R}$ in such a way that E^{n-1} is identified with $E^{n-1} \times 0$ in the natural way, and λv is identified with $(0, \lambda v)$ for all $\lambda \in \mathbb{R}$. Then L_k is identified with the graph of g_k.

The partial ordering of the L_k by $<$ implies that whenever $i<j$ then $g_i < g_j$ on $\pi(L_i) \cap \pi(L_j)$. It follows from Proposition 6.2 (with $K_i = \pi(L_i)$) that $\{L_1, \cdots, L_s\}$ is unlinked. Q.E.D.

REFERENCES

[1] J. G. Conlon, *A theorem in ordinary differential equations with an application to hyperbolic conservation laws*, Adv. Math., 35 (1980), pp. 1–18.

[2] W. A. Coppel, *Stability and Asymptotic Behavior of Differential Equations*, D. C. Heath, Boston, 1965.

[3] J. E. Franke and J. F. Selgrade, *Abstract ω-limit sets, chain recurrent sets, and basic sets for flows*, Proc. Amer. Math. Soc., 60 (1976), pp. 309–316.

[4] P. Hartman, *Ordinary Differential Equations*, John Wiley, New York, 1964.

[5] S. Grossberg, *Competition, decision and consensus*, J. Math. Anal. Appl., 66 (1978), pp. 470–493.

[6] M. Hirsch and S. Smale, *Differential Equations, Dynamical Systems, and Linear Algebra*, Academic Press, New York, 1974.

[7] E. Kamke, *Zur Theorie der Systeme gewöhnlicher differential-gleichungen*, II, Acta Math., 58 (1932), pp. 57–85.

[8] A. Lajmanovich and J. Yorke, *A deterministic model for gonorrhea in a nonhomogeneous population*, Math. Biosci., 28 (1976), pp. 221–236.

[9] W. J. Leonard and R. May, *Nonlinear aspects of competition between species*, SIAM J. Appl. Math., 29 (1975), pp. 243–275.

[10] E. J. McShane, *Extension of range of functions*, Bull. Amer. Math. Soc., 40 (1934), pp. 837–842.

[11] A. Rescigno and I. Richardson, *The struggle for life*; I, *Two species*, Bull. Math. Biophys., 29 (1967), pp. 377–388.

[12] J. Selgrade, *Mathematical analysis of a cellular control process with positive feedback*, SIAM J. Appl. Math., 36 (1979), pp. 219–229.

[13] ———, *Asymptotic behavior of solutions to single loop positive feedback systems*, J. Differential Equations, 38 (1980), pp. 80–103.

[14] S. Smale, *On the differential equations of species in competition*, J. Math. Biol., 3 (1976), pp. 5–7.

[15] ———, *The Mathematics of Time*, Springer-Verlag, New York, 1980.

[16] ———, *Stable manifolds for differential equations and diffeomorphisms*, Annali della Scuola Normale Superiore di Pisa (Serie III), 17 (1963), pp. 97–116.

[17] R. Abraham and J. Robbin, *Transversal Mappings and Flows*, W. A. Benjamin, New York, 1967.