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SYSTEMS OF DIFFERENTIAL EQUATIONS THAT ARE COMPETITIVE OR COOPERATIVE II: CONVERGENCE ALMOST EVERYWHERE*

MORRIS W. HIRSCH[†]

Abstract. A vector field in n -space determines a competitive (or cooperative) system of differential equations provided all of the off-diagonal terms of its Jacobian matrix are nonpositive (or nonnegative). The main results in this article are the following. A cooperative system cannot have nonconstant attracting periodic solutions. In a cooperative system whose Jacobian matrices are irreducible the forward orbit converges for almost every point having compact forward orbit closure. In a cooperative system in 2 dimensions, every solution is eventually monotone. Applications are made to generalizations of positive feedback loops.

Introduction. This paper studies the limiting behavior of solutions of systems

$$(1) \quad \frac{dx^i}{dt} = F^i(x^1, \dots, x^n) \quad (i = 1, \dots, n)$$

which are either cooperative:

$$\frac{\partial F^i}{\partial x^j} \geq 0 \quad \text{for } i \neq j,$$

or competitive:

$$\frac{\partial F^i}{\partial x^j} \leq 0 \quad \text{for } i \neq j.$$

The main results are as follows:

If (1) is cooperative, there are no attracting nonconstant periodic solutions (Theorem 2.4).

If (1) is cooperative and irreducible and its flow is $\{\phi_t\}$, then $\phi_t(x)$ approaches the equilibrium set for almost every point x whose forward orbit has compact closure (Theorem 4.1).

If $n = 2$ every solution to (1) is eventually monotone (Theorem 2.7).

The author's earlier paper [6] investigated compact limit sets of (1) from a geometrical and topological point of view. The present paper is concerned more directly with dynamical behavior. While it is formally independent of [6], it uses some of the same techniques.

Most of the results concern cooperative systems which are irreducible in the sense that the matrices $[(\partial F^i / \partial x^j)(p)]$ are irreducible. This has the important consequence that the flow $\{\phi_t\}$ corresponding to (1) has positive derivatives for $t > 0$, i.e. the matrices $D\phi_t(p)$ have only positive entries. By Kamke's theorem such a flow is strongly

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monotone, that is,

$$\phi_t(x) < \phi_t(y) \quad \text{if } x \leq y, \quad x \neq y, \quad t > 0.$$

The class of irreducible cooperative vector fields is contained in the wider class of vector fields whose flows have eventually positive derivatives: $D\phi_t > 0$ for all $t > t_0$, for some $t_0 \geq 0$. A flow of this type is eventually strongly monotone, which is as useful as being strongly monotone for most purposes. Moreover suitably small perturbations (in the weak C^1 topology) of such a vector field have positive derivatives in a given compact set, and thus are eventually strongly monotone in such a set. This has the great advantage of allowing the use of perturbation methods. In particular we make crucial use of the Closing Lemma of C. Pugh in the proof of Theorem 4.1.

Section 1 contains results on the monotonicity of various kinds of flows. Section 2 studies equilibria and closed orbits of eventually monotone flows. The key result is Theorem 2.2 which gives a useful sufficient condition for a solution to converge.

In §3 the Closing Lemma is exploited to prove basic results (3.7), (3.8), (3.9) about the relative position of ω -limit sets. These are applied in §4 to derive conditions under which almost all bounded forward trajectories converge (Theorems 4.1 and 4.4). Theorem 4.6 implies that compact attractors contain equilibria. Theorem 4.7 shows that invariant functions are usually constant.

Section 5 shows how the theorems proved in earlier sections can be applied to systems in the nonnegative orthant $\mathbb{R}_+^n$. The positive feedback loop (Selgrade [13], [14]) is used as an example. The Closing Lemma is discussed in the Appendix.

Many of the results in this paper can be extended to strongly monotone semiflows in ordered Banach spaces, including those defined by solutions to certain parabolic evolution equations. For these results see the author's paper [19].

The following terminology will be used throughout the paper: $\mathbb{R}$ is the field of real numbers; real n -space is $\mathbb{R}^n$, the vector space of n -tuples $x = (x^1, \dots, x^n)$ of real numbers. $F: W \rightarrow \mathbb{R}^n$ is a C^1 (continuously differentiable) vector field on a nonempty open set $W \subset \mathbb{R}^n$. For any $x \in W$ we denote the maximally defined solution of the vector differential equation

$$\frac{d\xi}{dt} = F(\xi), \quad \xi(0) = x$$

by $t \rightarrow \phi_t(x)$, $t \in I(x) \subset \mathbb{R}$. For each $t \in \mathbb{R}$ the set of $x \in W$ for which $\phi_t(x)$ is defined is a (possibly empty) open set $W(t) \subset W$ and $\phi_t: W(t) \rightarrow W(-t)$ is a C^1 diffeomorphism. The collection of maps $\{\phi_t\}_{t \in \mathbb{R}}$ is called the *flow* of F , or of the differential equation $dx/dt = F(x)$. For $x \in W$ we also write $x(t)$ for $\phi_t(x)$.

The forward trajectory of $x \in W$ is the parametrized curve $t \rightarrow \phi_t(x)$ ($t \geq 0$, $t \in I(x)$). Its image is the *forward orbit* of x , $O_+(x)$. The backward trajectory of x and the backward orbit $O_-(x)$ are analogously defined.

A subset $X \subset W$ is *positively* (respectively, *negatively*) *invariant* if $O_+(x) \subset X$ (resp. $O_-(x) \subset X$) for all $x \in X$. It is *invariant* if it is both positively and negatively invariant.

The ω -*limit set* $\omega(x)$ of a point $x \in W$, or of a solution $x(t)$, is the set of $p \in W$ such that $x(t_k) \rightarrow p$ for some sequence $t_k \rightarrow \infty$. The α -*limit set* $\alpha(x)$ is similarly defined with $t_k \rightarrow -\infty$.

If $O_+(x)$ has compact closure in W then $\omega(x)$ is a nonempty compact connected invariant set. An analogous statement is true of $\alpha(x)$.

We say a forward trajectory $x(t)$ *approaches* a subset $S \subset W$ if $O_+(x)$ has compact closure in W and $\omega(x) \subset S$. This implies

$$\lim_{t \rightarrow \infty} \inf_{y \in S} |x(t) - y| = 0.$$

If $V \subset \mathbb{R}^n$ is open, $h: V \rightarrow \mathbb{R}^n$ is C^1 and $p \in V$, then $Dh(p)$ denotes the $n \times n$ matrix $[(\partial h^i / \partial x^j)(p)]$. In particular there are the matrices $DF(p)$ and $D\phi_i(p)$.

Let $x, y \in \mathbb{R}^n$. We write:

$$\begin{aligned} x < y & \quad \text{if } x^i < y^i \quad \text{for all } i, \\ x \leq y & \quad \text{if } x^i \leq y^i \quad \text{for all } i. \end{aligned}$$

The notations $y > x$, $y \geq x$ have the obvious meaning. We call x positive if $x > 0$ (the zero vector). Similar notation applies to matrices.

The *closed positive orthant* is the set

$$\mathbb{R}_+^n = \{x \in \mathbb{R}^n: x \geq 0\}.$$

If $X, Y \subset \mathbb{R}^n$ are any subsets we write $X < Y$ if $x < y$ for all $x \in X, y \in Y$. We analogously define $X > Y, X \leq Y$, etc.

An $n \times n$ matrix $A = [A_{ij}]$ is *irreducible* if whenever the set $\{1, \dots, n\}$ is expressed as the union of two disjoint proper subsets S, S' , then for every $i \in S$ there exists $j, k \in S'$ such that $A_{ij} \neq 0, A_{ki} \neq 0$. This means the linear map $A: \mathbb{R}^n \rightarrow \mathbb{R}^n$ does not map into itself any nonzero proper linear subspace spanned by a subset of the standard basis. Equivalently: the directed graph with vertices $1, \dots, n$ and directed edges (i, j) for $A_{ij} \neq 0$, is connected by directed paths.

If $x \in \mathbb{R}^n$ then $|x|$ is the Euclidean norm $(\sum x_i^2)^{1/2}$. If A is a real $n \times n$ matrix then $\|A\|$ is the operator norm

$$\max\{|Ax|: x \in \mathbb{R}^n \text{ and } |x| = 1\}.$$

If K, L are sets then

$$K \setminus L = \{x \in K: x \notin L\}.$$

1. Monotone flows. For reference we quote a corollary of a result of Kamke [8].

KAMKE'S THEOREM. Let $V \subset \mathbb{R}^n$ be an open set and $G: \mathbb{R} \times V \rightarrow \mathbb{R}^n$ a continuous map such that $G^i(t, x^1, \dots, x^m)$ is a nondecreasing in x^k , for all $k \neq i$. Let

$$\xi, \eta: [a, b] \rightarrow V$$

be solutions of

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

such that $\xi(a) < \eta(a)$ (resp. $\xi(a) \leq \eta(a)$). Then $\xi(t) < \eta(t)$ (resp. $\xi(t) \leq \eta(t)$) for all $t \in [a, b]$.

For a proof see Coppel [2] or W. Walter [16].

Notice that the assumption on G is satisfied if $\partial G^i / \partial x^k \geq 0$ whenever $k \neq i$ and V is convex. In fact V need only be p -convex: whenever $x, y \in V$ and $x \leq y$ then V contains the entire line segment joining x and y .

Now consider the system

$$(1) \quad \frac{dx^i}{dt} = F^i(x), \quad i = 1, \dots, n$$

defined by the C^1 vector field $F: W \rightarrow \mathbb{R}^n$. The flow $\{\phi_t\}$ of the system is called:

cooperative if the off-diagonal entries of $DF(z)$ are ≥ 0 for all $z \in W$;

competitive if the off-diagonal entries of $DF(t)$ are ≤ 0 for all $z \in W$;

irreducible if $DF(t)$ is irreducible for all $z \in W$.

These adjectives will also be applied to the system (1) or the vector field F , with the same meaning.

It is a well-known consequence of Kamke's theorem that when W is convex, the flow of a cooperative system (1) preserves the ordering $\leq$ in $\mathbb{R}^n$. In 1.4 and 1.5 below we extend this result.

We say $\{\phi_t\}$ has *nonnegative* (resp. *positive*) derivatives if $D\phi_t \geq 0$ (resp. > 0) for all $t > 0, z \in W$.

THEOREM 1.1. *Let F be a cooperative vector field. Then:*

(a) $\{\phi_t\}$ has nonnegative derivatives.

(b) If F is also irreducible then $\{\phi_t\}$ has positive derivatives.

Proof. Fix $t \in W$. For all $t \in J(z)$ define matrices

$$A(t) = DF(\phi_t(z)), \quad M(t) = D\phi_t(z).$$

Then $M(t)$ satisfies the variational equation

$$(2) \quad \frac{dM}{dt} = A(t)M$$

with initial condition

$$(3) \quad M(0) = I,$$

where I is the $n \times n$ identity matrix. The right-hand side of (2) is a matrix function $G(t, M)$ whose entries are

$$G_{ik}(t, M_{11}, \dots, M_{nn}) = \sum_{j=1}^n A_{ij}(t) M_{jk}.$$

It is easily verified that (because F is cooperative)

$$\frac{\partial G_{ij}}{\partial M_{rs}} \geq 0 \quad \text{if } (i, k) \neq (r, s).$$

It follows from Kamke's theorem that the solution $M(t)$ to (2), (3) satisfies $M_{ik}(t) \geq 0$ for all i, k and all $t \geq 0$ because the constant map $N(t) = 0$ (the $n \times n$ zero matrix) is also a solution to (2), and $M(0) \geq N(0)$. Thus $M(t) \geq 0$ for all $t \geq 0$.

Now assume F irreducible. If $t_0 > 0$ and $M(t_0) > 0$ then Kamke's theorem implies $M(t) > 0$ for all $t > t_0$. Suppose it is not the case that $M(t) > 0$ for all $t > 0$. Then there exists $t_1 > 0$ such that $M_{ij}(t_1) = 0$ for some i, j . It follows that for every $t \in [0, t_1]$, $M_{ij}(t) = 0$ for some i, j (depending on t). One of the sets

$$[0, t_1] \cap M_{ij}^{-1}(0)$$

must have an interior point. Therefore there exist i, j and an interval $[a, b] \subset \mathbb{R}_+$ such that $M_{ij}(t) = 0$ for all $t \in [a, b]$. But the following lemma contradicts this.

LEMMA. Suppose $i, k \in \{1, \dots, n\}$ and $t_0 > 0$ are such that $M_{ik}(t_0) = 0$. Then $(d/dt)M_{ik}(t_0) > 0$.

To prove the lemma define

$$S = \{r: M_{rk}(t_0) = 0\}.$$

Then S is nonempty (since $i \in S$) and $S \neq \{1, \dots, m\}$ (since the matrix $M(t_0)$ is nonsingular for all t). Now the matrix $A(t_0)$ is irreducible. Therefore there exists $j \in \{1, \dots, \} \setminus S$ with $A_{ij}(t_0) \neq 0$. Clearly $j \neq i$, so $A_{ij}(t_0) > 0$ since F is cooperative. We now have

$$\frac{d}{dt}M_{ik}(t_0) = \sum_{r=1}^n A_{ir}(t_0)M_{rk}(t_0).$$

Since $M_{ik}(t_0) = 0$ we can write the sum as

$$\sum_{\substack{r=1 \\ r \neq i}}^n A_{ir}(t_0)M_{rk}(t_0).$$

In this expression each summand is the product of nonnegative numbers, and the terms with $r = j$ are positive. Thus all $M_{ik}(t_i) > 0$. This proves the lemma; the proof of the theorem is now complete. QED.

Perturbations of a cooperative irreducible vector field need not preserve the property that its flow have positive derivatives. But a slightly weaker, equally useful property is preserved: that of having *eventually positive derivatives*. A flow $\{\phi_t\}$ has this property in a set V provided there exists $t_0 > 0$ such that $D\phi_t(z) > 0$ for all $t \geq t_0, z \in V$.

THEOREM 1.2. Assume $K \subset W$ is a compact set in which the flow $\{\phi_t\}$ has eventually positive derivatives. Then there exists $\delta > 0$ with the following property. Let $\{\psi_t\}$ denote the flow of a C^1 vector field G such that

$$(4) \quad |F(x) - G(x)| + \|DF(x) - DG(x)\| < \delta \quad \text{for all } x \in K.$$

Then there exists $t_* > 0$ such that if $t \geq t_*$ and $\psi_s(z) \in K$ for all $s \in [0, t]$ then $D\psi_t(z) > 0$. In particular: if K is positively invariant under $\{\psi_t\}$ then $\{\psi_t\}$ has eventually positive derivatives in K .

Proof. Fix $t_0 > 0$ so that $D\phi_t(z) > 0$ for all $t \geq t_0, z \in K$. Fix $\delta > 0$ so small that (4) implies

$$D\psi_t(z) > 0 \quad \text{if } t_0 \leq t \leq 2t_0 \quad \text{if } z \in K.$$

Now fix $t \geq 2t_0$. Write

$$t = r + kt_0$$

where

$$t_0 \leq r < 2t_0 \quad \text{and} \quad k \text{ is an integer } \geq 1.$$

Put $jt_0 = s_j$ for $j = 0, \dots, k$. Let z be such that $\psi_s(z) \in K$ for all $s \in [0, t]$. Put $\psi_{s_j}(z) = z_j$. By the chain rule

$$(5) \quad D\psi_t(z) = D\psi_r(z_k) D\psi_{t_0}(z_{k-1}) \cdots D\psi_{t_0}(z_0).$$

Now $D\psi_{t_0}(z_i) > 0$ for $i = 0, \dots, k-1$ because $z_i \in K$. Also $D\psi_r(t_k) > 0$ because $z_k \in K$ and $t_0 \leq r < 2t_0$. QED.

Let $W' \subset \mathbb{R}^n$ be a subset. A map $f: W' \rightarrow \mathbb{R}^n$ is *monotone* in W' (resp. *strongly monotone*) provided $x \leq y$ implies $f(x) \leq f(y)$ (resp. $f(x) < f(y)$ when $x \neq y$).

LEMMA 1.3. Suppose $f: W' \rightarrow \mathbb{R}^n$ is C^1 . If $Df(z) \geq 0$ (resp. $Df(z) > 0$) for all $z \in W'$ and W' is p -convex then f is monotone (resp. strongly monotone) in W' .

Proof. Let $a, b \in W$ with $a \leq b$. For $s \in [0, 1]$ put $a_s = a + s(b - a)$. The lemma follows from the formula

$$f(b) - f(a) = \int_0^1 Df(a_s)(b - a) ds. \quad \text{QED.}$$

The flow $\{\phi_t\}$ is *eventually (strongly) monotone* if there exists $t_0 \geq 0$ such that ϕ_t is (strongly) monotone for all $t > t_0$. If this holds with $t_0 = 0$ then the flow is called *(strongly) monotone*.

THEOREM 1.4. Let $V \subset W$ be p -convex. If the flow $\{\phi_t\}$ has (eventually) positive derivatives in V then it is (eventually) strongly monotone in V . If the flow has (eventually) nonnegative derivatives in V then it is (eventually) monotone in V .

Proof. This follows from Lemma 1.3. QED.

THEOREM 1.5. Let $V \subset W$ be p -convex. If the vector field F is cooperative (resp., cooperative and irreducible) then its flow $\{\phi_t\}$ is monotone (resp. strongly monotone) in V .

Proof. Apply Theorems 1.1 and 1.4. QED.

Notice also that every open set W is locally convex, hence the flow of a cooperative vector field in W monotone in some neighborhood of any point.

The following theorem is a converse to Theorem 1.4.

THEOREM 1.6. Suppose $\{\phi_t\}$ is (eventually) monotone in an open set $V \subset W$. Then $\{\phi_t\}$ has (eventually) nonnegative derivatives in V .

Proof. Fix $t > 0$ such that ϕ_t is monotone in V . Fix $x \in V$ and $v \in \mathbb{R}_+^n$. Then

$$D\phi_t(x)v = \lim_{h \rightarrow 0} h^{-1}(\phi_t(x + hv) - \phi_t(x)).$$

If $h > 0$ is sufficiently small we have $x + hv \in V$ and $\phi_t(x + hv) \geq \phi_t(x)$. Thus $D\phi_t(x)v$ is a limit of vectors in $\mathbb{R}_+^n$, so $D\phi_t(x)v \geq 0$. This shows $D\phi_t(x)$ maps $\mathbb{R}_+^n$ into itself. QED.

For convenience we present a summary of some of the implications between various kinds of systems. The following abbreviations are used:

- C: cooperative,
- CI: cooperative and irreducible,
- ND: nonnegative derivatives,
- PD: positive derivatives,
- EPD: eventually positive derivatives,
- M: monotone,
- SM: strongly monotone,
- ESM: eventually strongly monotone,
- $\Rightarrow$: implications,
- $\overset{x}{\Rightarrow}$: implication is valid in p -convex sets.

THEOREM 1.7.

$$\begin{array}{ccccc}
 & & M & & \\
 C & \Rightarrow & ND & \xRightarrow{x} & M \\
 \uparrow & & \uparrow & & \uparrow \\
 CI & \Rightarrow & PD & \xRightarrow{x} & SM \\
 & & \downarrow & & \downarrow \\
 & & EPD & \xRightarrow{x} & ESM
 \end{array}$$

2. Equilibria and close orbits. Let $\{\phi_t\}$ denote the flow of a C^1 vector field F defined on the open set $W \subset \mathbb{R}^n$.

A point $p \in W$ is an *equilibrium* if $F(p) = 0$, or equivalently, if $\phi_t(p) = p$ for all $t \in \mathbb{R}$.

Let p be an equilibrium. Then $D\phi_t(p) = \exp(tDF(p))$. The spectrum (set of complex eigenvalues) of $D\phi_t(p)$ is related to that of $DF(p)$ by

$$\text{Spec } D\phi_t(p) = \{e^{t\lambda} : \lambda \in \text{Spec } DF(p)\}.$$

The equilibrium p is called:

simple if $0 \notin \text{Spec } DF(p)$; or equivalently, if $1 \notin \text{Spec } D\phi_t(p)$ for some $t \in \mathbb{R}$;

hyperbolic if $\text{Re } \lambda \neq 0$ for all $\lambda \in \text{Spec } DF(p)$; or equivalently, if $|\mu| \neq 1$ for all $\mu \in \text{Spec } D\phi_t(p)$ and some (hence all) $t \neq 0$;

a *sink* if $\text{Re } \lambda < 0$ for all $\lambda \in \text{Spec } DF(p)$; or equivalently, if $|\mu| < 1$ for all $\mu \in \text{Spec } D\phi_t(p)$ and some (hence all) $t > 0$.

It is well known that a sink p is asymptotically stable; that is, every neighborhood of p contains a positively invariant neighborhood N of p such that

$$(1) \quad \phi_t(x) \text{ converges to } p \text{ uniformly in } x \in N \text{ as } t \rightarrow \infty.$$

A weaker notion is that of a *trap*: an equilibrium p such that there is some open set N , not necessarily containing p , such that (1) holds.

It is not known how to characterize traps in terms of the vector field without integrating it. It is easy to see, however, if p is a trap then $\text{Re } \lambda \leq 0$ for all λ in $\text{Spec } DF(p)$. It follows that a simple trap is a sink, and $\text{Div } F \leq 0$ at a trap.

An ω -*colimit point* of points u, v in W is a point $p \in W$ such that

$$p = \lim_{k \rightarrow \infty} u(t_k) = \lim_{k \rightarrow \infty} v(t_k)$$

for some sequence $t_k \rightarrow \infty$.

LEMMA 2.1. *Let $\{\phi_t\}$ be eventually monotone in an open set $W_0 \subset W$. Let $p \in W$ be an ω -colimit point of points x, y in W_0 where $x < y$. Then p is an equilibrium.*

Proof. Let $T > 0$ be so large that $x(t) < y(t)$ for all $t \geq T$. Let $t_k \rightarrow \infty$, $p, y(t_k) \rightarrow p$. Choose $k_0 \in \mathbb{Z}_+$ so large that $t_k \geq T$ for all $k \geq k_0$. Put $t_{k_0} = s$. The set

$$U = \phi_s^{-1}\{z \in W_0 : x(s) < z < y(s)\}$$

is a nonempty open set. If $u \in U$ then

$$x(s) < u(s) < y(s).$$

Therefore for $r \geq T$

$$\phi_r(x(s)) < \phi_r(u(s)) < \phi_r(y(s)),$$

i.e.

$$x(r+s) < u(r+s) < y(r+s).$$

It follows that for all k such that $t_k \geq T+s$,

$$x(t_k) < u(t_k) < y(t_k).$$

This implies $u(t_k) \rightarrow p$ as $k \rightarrow \infty$, uniformly in $u \in U$.

As a consequence,

$$\lim_{k \rightarrow \infty} \text{diam } \phi_{t_k}(U) = 0$$

where for any $X \subset \mathbb{R}^n$,

$$\text{diam } X = \sup \{ |a - b| : a, b \in X \}.$$

Now each ϕ_{t_k} maps solution curves to solution curves, preserving parameterization up to an additive constant. It follows that there exists $\tau > 0$ with the following property. For every $t \in [0, \tau]$ and every $\varepsilon > 0$ there exists z in the ε -neighborhood of p such that

$$|z(t) - z| < \varepsilon \quad \text{for all } t \in [0, \tau].$$

Letting $\varepsilon \rightarrow 0$ we get

$$|p(t) - p| = 0 \quad \text{for all } t \in [0, \tau]$$

which implies p is an equilibrium. QED.

The following result is basic to the rest of the paper.

THEOREM 2.2. *Assume the flow $\{\phi_t\}$ is eventually monotone in an open set W_0 : let $t_1 \geq 0$ be such that $\phi_t|_{W_0}$ is monotone for all $t > t_1$. Let $x(t)$ be a solution defined for all $t \geq 0$. Suppose $T > 0$ is such that $x(0) \in W_0$ and $x(t) \in W_0$, and either $x(0) < x(T)$ or $x(0) > x(T)$. If $p \in W$ is a limit point of $\{x(kT) : k \in \mathbb{Z}_+\}$ then the following are true:*

(a) p is a trap.

(b) $p = \lim_{t \rightarrow \infty} x(t)$.

(c) Assume $p \in W_0$. If $x(T) > x(0)$ (resp. $x(T) < x(0)$) then $p > x(t)$ (resp. $p < x(t)$) for all $t > t_1$.

Proof. We assume $x(0) < x(T)$, the other case being similar.

For all $t > t_1$ we have

$$x(t) < x(t+T).$$

Letting $t = T, 2T, 3T, \dots$, we find that for all sufficiently large integers $k > 0$:

$$(2) \quad x(kT) < x((k+1)T).$$

It follows that

$$(3) \quad p = \lim_{k \rightarrow \infty} x(kT), \quad (k \in \mathbb{Z}_+).$$

Now apply Lemma 2.1 with $x = x(0)$, $y = x(T)$: clearly p is an ω -colimit point of x, y so p is an equilibrium. For all $s \in [0, T]$, $k \in \mathbb{Z}_+$, we have:

$$\phi_{kT+s}(x) = \phi_s(\phi_{kT}x) \rightarrow \phi_s(p) = p$$

as $k \rightarrow \infty$. This shows

$$\phi_t(x) \rightarrow p \quad \text{as } t \rightarrow \infty.$$

Similarly $\phi_t(y) \rightarrow p$ as $t \rightarrow \infty$. Finally, p is a trap because if $x < z < y$, $z \in W_0$ then

$$\phi_t(x) < \phi_t(z) < \phi_t(y)$$

which shows $\phi_t(z) \rightarrow p$ uniformly for z is the nonempty open set

$$\{z \in W_0: x < z < y\}.$$

To prove (c) assume $p \in W_0$ and set

$$C = \{y \in W_0: y < p\}.$$

Since $\phi_t(p) = p$ it follows that $\phi_t(C) \subset C$ for all $t > t_1$. By (2) and (3), $x \in c$. Therefore $x(t) \in C$ for all $t > t_1$, proving (c). QED.

THEOREM 2.3. *Let $\{\phi_t\}$ be eventually monotone.*

(a) *If $y \in \omega(x)$ and $y < x$ or $y > x$ then y is a trap and $\lim_{t \rightarrow \infty} x(t) = y$.*

(b) *There cannot exist u, v in $\omega(x)$ with $u < v$.*

(c) *If the flow is eventually strongly monotone there cannot exist u, v in $\omega(x)$ with $u \leq v$, $u \neq v$.*

Proof. (a) Suppose $y > x$, the other case being similar. There exist arbitrarily large $T > 0$ such that $\phi_T(x) > x$. The conclusion now follows from Theorem 2.2(a) and 2.2(b).

(b) There exists x' in the forward orbit of x so close to u that $x' < v$. Part (a) implies $\lim_{t \rightarrow \infty} x'(t) = v$. Therefore $\omega(x) = \{v\}$, contradicting $u \neq v$.

(c) Apply part (b) to $u(t_0)$, $v(t_0)$ where $t_0 > 0$ is so large that $u(t_0) < v(t_0)$.

QED.

COROLLARY. *Let $\{\phi_t\}$ be eventually strongly monotone and suppose E is totally ordered. If $x \in W$ is such that $\omega(x)$ is a nonempty compact subset of E then $x(t)$ converges to an equilibrium as $t \rightarrow \infty$.*

Proof. Suppose $\phi(x)$ contains two equilibria u and v . Then $u < v$ by strong monotonicity, contradicting Theorem 2.3(b). QED.

By a *closed orbit* we mean the image of a nonconstant periodic solution.

THEOREM 2.4. *An eventually monotone flow cannot have an attracting closed orbit.*

Proof. Let γ be a closed orbit of an eventually monotone flow. Let $y \in \gamma$. In every neighborhood of y there exists a point $x > y$. Since y is not an equilibrium it follows from 2.3(a) that $y \notin \omega(x)$. Since γ is invariant, $\gamma \cap \omega(x) = \emptyset$. This shows that γ is not an attractor. QED.

More generally, a similar argument shows that if a minimal set M is an attractor then M is a single point. We consider attractors again in Theorem 4.6.

The following convergence criterion can be considered an infinitesimal analogue of Theorem 2.2. For cooperative systems it is well known.

THEOREM 2.5. *Let $\{\phi_t\}$ have eventually nonnegative derivatives. Suppose $x \in W$ is such that $F(x) \geq 0$ (or $F(x) \leq 0$). Then all coordinates $x^i(t)$ are eventually nondecreasing (or eventually nonincreasing). If $\omega(X) \neq \emptyset$ then $x(t)$ converges to an equilibrium p . If $F(x) > 0$ (or $F(x) < 0$) then p is a trap. If $\{\phi_t\}$ has eventually positive derivatives then p is a trap.*

Proof. Suppose $F(x) \leq 0$, the other case being similar. Let $t_0 \geq 0$ be large enough so that $D\phi_t(x) \geq 0$ for all $t \geq t_0$. Now

$$F(x(t)) = D\phi_t(x)F(x).$$

Therefore for all $t \geq t_0$ it follows that $F(x(t)) \leq 0$. In other words $(d/dt)x^i(t) \leq 0$ for all $i = 1, \dots, n, t \geq t_0$. Thus $x(t)$ is eventually nonincreasing.

If $p \in \omega(x)$ then $x(t)$ must converge to p . Each of the last three hypotheses implies the existence of $t_1 > 0$ such that $F(x(t)) < 0$ for all $t \geq t_1$. Put $y = x(t_1)$. Then $y(T) < y$ for sufficiently small $T > 0$. By Theorem 2.3(a) $v(t)$ converges to a trap as $t \rightarrow \infty$. QED.

The following lemma says that solutions lying in certain two-dimensional affine subspaces are eventually monotone.

LEMMA 2.6. *Let $y(t)$ be a trajectory of a flow having eventually nonnegative derivatives. Suppose $y(t)$ defined for all $t \geq 0$. Suppose there exist $t_0 \geq 0$, and distinct $j, k \in \{1, \dots, n\}$, such that $y_i(t)$ is constant for all $t \geq t_0, i \neq j, k$. Then $y_j(t)$ and $y_k(t)$ are monotone for sufficiently large t . If $\omega(y) \neq \emptyset$ then $y(t)$ converges.*

Proof. We may assume $F(y(t)) \neq 0$ for all $t \geq t_0$. If $F(y(t_1)) \geq 0$ or $F(y(t_1)) \leq 0$ for some $t \geq t_0$ the conclusion follows from Theorem 2.5. In the contrary case, the vector $(F_j(y(t)), F_k(y(t))) \in \mathbb{R}^2$ is confined, for all $t \geq t_0$, to the second or fourth open quadrant. This implies eventual monotonicity of $y_j(t)$ and $y_k(t)$. QED.

THEOREM 2.7. *Let F be a vector field in an open subset of the plane. Assume that F is cooperative, or competitive, or that the flow has eventually nonnegative derivatives. Let $x(t)$ be a solution defined for $-\infty < t \leq 0$, or for $0 \leq t < \infty$. Then each $x^i(t)$ is monotone for $|t|$ sufficiently large.*

Proof. It suffices to consider the case where the flow has eventually nonnegative derivatives: this holds if F is cooperative; and if F is competitive it suffices to prove the lemma for $-F$ (which is cooperative).

If $x(t)$ is constant there is nothing more to prove. Assume $x(t)$ is not constant. Suppose $x(t)$ is defined for $-\infty < t \leq 0$. Let $t_0 > 0$ be such that ϕ_t has nonnegative derivatives for $t \geq t_0$.

Case 1. Assume there exists $t_1 \leq 0$ such that $F(x(t_1))$ is in open quadrant II or IV (i.e. it is neither ≤ 0 nor ≥ 0). Then Theorem 2.6 implies that for all $t \leq t_1 - t_0$, $F(x(t))$ is in quadrant II or IV. Since $F(x(t)) \neq 0$, $F(x(t))$ cannot pass directly from II to IV. Therefore $F(x(t))$ is in the same quadrant for all $t \leq t_1 - t_0$. Therefore $x^1(t), x^2(t)$ are monotone for $t \leq t_1 - t_0$.

Case 2. $F(t)$ is never in II or IV. Then $F(t)$ must stay in I or III for all $t < 0$ and again $x^i(t)$ is monotone, $i = 1, 2$.

When $x(t)$ is defined for all $t > 0$ a similar argument applies. QED.

COROLLARY 2.8. *Let $\{\phi_t\}$ be a cooperative or competitive flow in $\mathbb{R}^2$ for which the nonnegative quadrant $\mathbb{R}_+^2$ is positively invariant. Then every bounded trajectory $[0, \infty) \rightarrow \mathbb{R}_+^2$ converges.*

Versions of the last result have been proved many times: see for example Albrecht et al. [1], Grossberg [4], Hirsch–Smale [7], Kolmogorov [9], Rescigno–Richardson [12].

3. ω -Limits. Throughout this section we assume given a C^1 vector field F on a p -convex open set $W \subset \mathbb{R}^n$, whose flow $\{\phi_t\}$ has eventually positive derivatives. It follows from Theorem 1.5 that $\{\phi_t\}$ is eventually strongly monotone.

The following notation is used:

$E \subset W$ is the set of equilibria;

x, y are distinct points of W and $x \leq y$.

The main results of this section are Theorems 3.7, 3.8 and 3.9.

LEMMA 3.1. *Let p be an ω -colimit point of x, y (see §2). Then $p \in E$. If $x(t), y(t)$ converge to p as $t \rightarrow \infty$, then p is a trap.*

Proof. Follows from Lemma 2.1. QED.

Throughout the rest of this section we assume that $\omega(x)$ and $\omega(y)$ are compact and nonempty.

LEMMA 3.2. If $p \in \omega(x) \setminus E$ then $p < q$ for some $q \in \omega(y)$.

Proof. It is easy to see that there exists $q \in \omega(y)$ such that for some sequence $t_k \rightarrow \infty$,

$$p = \lim_{k \rightarrow \infty} x(t_k), \quad q = \lim_{k \rightarrow \infty} y(t_k).$$

Monotonicity implies $p \leq q$. If $p = q$ then p is an ω -colimit point of x, y . Then $p \in E$ by Lemma 3.1, a contradiction. Therefore $p \neq q$.

Let $T > 0$ be so large that ϕ_t is strongly monotone for all $g \geq T$. Since $\omega(x)$ and $\omega(y)$ are compact and negatively invariant, we can define

$$\begin{aligned} p_0 &= \phi_{-T}(p) \in \omega(x), \\ q_0 &= \phi_{-T}(q) \in \omega(y). \end{aligned}$$

Clearly $p_0 \neq q_0$, and

$$\begin{aligned} p_0 &= \lim_{k \rightarrow \infty} \phi_{t_k - T}(x), \\ q_0 &= \lim_{k \rightarrow \infty} \phi_{t_k - T}(y). \end{aligned}$$

By the argument above it follows that $p_0 \leq q_0$. Therefore

$$p = \phi_T(p_0) < \phi_T(q_0) = q. \quad \text{QED.}$$

COROLLARY 3.3. $\omega(X) \cap \omega(y) \subset E$.

Proof. Suppose $p \in \omega(x) \cap \omega(y) \setminus E$. Then by Lemma 3.2 there exists $q \in \omega(y)$ with $q > p$; and also $p \in \omega(y)$. But this is impossible by Theorem 2.3(b). QED.

LEMMA 3.4. Let K, L be compact invariant sets such that $K \geq L$. Then either $K > L$ or else there is an equilibrium b such that $K \cap L = \{b\}$ and $a < b < c$ for all $a \in K \setminus \{b\}$, $c \in L \setminus \{b\}$.

Proof. Clearly $K \cap L$ is compact and invariant and $K \geq K \cap L \geq L$. Suppose $b, d \in K \cap L$. Then $b \leq d$ and $d \leq b$, so $b = d$. Therefore $K \cap L = \{b\}$. Since $\{b\}$ is invariant $b \in E$.

Choose $T > 0$ so large that ϕ_T is strongly monotone. Let $x \in K, y \in L$ be distinct. Then $\phi_{-T}(x) \geq \phi_{-T}(y)$ because $K \geq L$, so $x > y$. This implies $K > L$ if $K \cap L = \emptyset$; and also if $K \cap L = \{b\}$ then $K \setminus b > b > L \setminus b$. QED.

LEMMA 3.5. Let $K \subset \omega(x)$, $M \subset \omega(y)$ be nonempty subsets with $K < M$. If one of the sets K, M is compact and positively invariant then $\omega(x) \leq \omega(y)$.

Proof. First assume K is compact and positively invariant. Set

$$V = \{z \in W : z > K\}.$$

Then $V \cap \omega(y) \neq \emptyset$ and monotonicity implies $y(t) \in V$ for all sufficiently large $t > 0$. This implies $\omega(y) \geq K$. I claim $\omega(y) > K$. If not, by Lemma 3.4 there exists an equilibrium b such that $K \leq b \leq \omega(y)$ and $K \cap \omega(y) = \{b\}$. Now $\{b\} = \omega(y)$, otherwise $c > b$ for some $c \in \omega(y)$, contradicting Theorem 2.3(a). But then $b \in K \cap M$, contradicting $K < M$. Therefore $\omega(y) > K$.

Put $M_0 = \omega(y)$. Then M_0 is compact and positively invariant and nonempty. By what has already been proved it follows that $\omega(x) < M_0$, i.e. $\omega(x) < \omega(y)$. In a similar way one shows that if M is compact and positively invariant then $\omega(x) < \omega(y)$. QED.

LEMMA 3.6. Let $p \in \omega(x)$, $q \in \omega(y)$, $p < q$. If p or q is a periodic point then $\omega(x) < \omega(y)$.

Proof. If p is an equilibrium, apply Lemma 3.5 with $K = \{p\}$, $M = \{q\}$.

A similar argument is used if q is an equilibrium.

Suppose p belongs to a closed orbit γ and q is not an equilibrium. By Lemma 3.4 γ is disjoint from $\omega(y)$. By the Closing Lemma (Pugh [10], or see Appendix) there is a C^1 vector field G whose flow $\{\psi_t\}$ has a closed orbit β through q . Moreover G can be chosen to coincide with F outside any given neighborhood of the orbit closure of Q , and to C^1 -approximate F as closely as desired. Now the orbit closure of q is in the compact set $\omega(y) \subset W \setminus \gamma$. Therefore we can choose G so close to F that $\{\psi_t\}$ is eventually strongly monotone, by Theorems 1.3 and 1.5; and we can choose G to coincide with F in a neighborhood of γ . Therefore γ is a closed orbit of $\{\psi_t\}$.

We have closed orbits γ, β of $\{\psi_t\}$ and points $p \in \gamma$, $q \in \beta$ with $p < q$. It follows from Corollary 2.9 that $\gamma < \beta$. In particular, $\gamma < q$.

We now consider the original flow $\{\phi_t\}$. From Lemma 3.5 (with $K = \gamma$ and $M = \{q\}$) we conclude that $\omega(x) < \omega(y)$. QED.

THEOREM 3.7. Suppose there exist $p \in \omega(x)$, $q \in \omega(y)$ with $p < q$. Then $\omega(x) < \omega(y)$.

Proof. If p is an equilibrium then the theorem follows from Theorem 3.5. From now on assume p is not an equilibrium.

By Corollary 3.3 the orbit of p is disjoint from $\omega(y)$. We apply the Closing Lemma of Pugh [10] (see Appendix) to obtain a vector field G whose flow $\{\psi_t\}$ has a closed orbit γ through p . As in the proof of Lemma 3.6, we can choose $\{\psi_t\}$ so close to $\{\phi_t\}$ as to be eventually strongly monotone. Moreover there exists $T > 0$ with the following property. For any $\varepsilon > 0$ we can choose G so that $G = F$ outside the ε -neighborhood N_ε of the solution arc

$$\{\phi_t(p) : |t| \leq T\}.$$

For small ε , N_ε is disjoint from $\omega(y; \{\phi_t\})$. Therefore for sufficiently small ε , $\omega(y; \{\phi_t\})$ is also an ω -limit set for the flow $\{\psi_t\}$, of some point y_0 . It is easy to see that we can choose $y_0 > p$. It now follows from Lemma 3.6 that

$$\gamma = \omega(p; \{\psi_t\}) < \omega(y_0; \{\psi_t\}).$$

Thus

$$p < \omega(y_0; \{\psi_t\}) = \omega(y, \{\phi_t\}).$$

Now apply Lemma 3.5 to $\{\phi_t\}$, with $K = p$, $M = \omega(y; \{\phi_t\})$. QED.

THEOREM 3.8. Exactly one of the following conditions holds:

- (a) $\omega(x) < \omega(y)$.
- (b) $\omega(x) = \omega(y) \subset E$.

Proof. For any $p \in \omega(x)$ there exists $q \in \omega(y)$ such that $x(t_k) \rightarrow p$, $y(t_k) \rightarrow q$ for some sequence $t_k \rightarrow \infty$. Then $p \leq q$. If $p \neq q$ then $p < q$ by eventual strong monotonicity; and then $\omega(x) < \omega(y)$ by Theorem 3.7. If $p = q$ then p is an ω -colimit point of x, y and so $p \in E$ by Lemma 2.1.

Suppose (a) is false. Then the results just proved show that for all $p \in \omega(x)$, whenever q is chosen as above then $p = q \in E$. Thus $\omega(x) \subset \omega(y) \cap E$. A similar argument shows $\omega(y) \subset \omega(x) \cap E$, and thus (b) holds. QED.

4. Convergence almost everywhere. We continue the assumption of §3: $W \subset \mathbb{R}^n$ is a p -convex open set and $\{\phi_t\}$ is a flow in W having eventually positive derivatives.

Let $W^c \subset W$ be the set of points whose forward orbit has compact closure in W .

THEOREM 4.1. *There is a set $Q \subset W^c$ having Lebesgue measure zero, such that $x(t)$ approaches the equilibrium set E as $t \rightarrow \infty$, for all $x \in W^c \setminus Q$.*

The proof of Theorem 4.1 uses Lemma 4.2 and 4.3 below. Put

$$Q = \{x \in W^c : \omega(x) \not\subset E\}.$$

It is easy to prove that W^c and Q are Borel sets. We must prove that Q has measure zero.

Fix a vector $v > 0$ in $\mathbb{R}^n$. Let $E^{n-1} \subset \mathbb{R}^n$ be the hyperplane orthogonal to v and let $\pi: \mathbb{R}^n \rightarrow E^{n-1}$ be orthogonal projection. To prove that Q has measure zero it suffices by Fubini's theorem to prove:

- (1) For all $w \in E^{n-1}$, $Q \cap \pi^{-1}(w)$ is countable.

We need two lemmas. Let $\pi_i: \mathbb{R}^n \rightarrow \mathbb{R}$ be the i th coordinate projection. Let a and $b > a$ be two points of W . Since W is a p -convex, W contains the line segment L from a to b . For each $i \in \{1, \dots, n\}$ define

$$S_i(L) = \{x \in Q \cap L : \pi_i(\omega(x)) \text{ has more than one element}\}.$$

LEMMA 4.2. $S_i(L)$ is countable for $i = 1, \dots, n$.

Proof. For any $z \in S_i(L)$ let $K_z \subset \mathbb{R}$ be the interval spanned by $\pi_i(\omega(z))$. Let $x, y \in S_i(L)$ be distinct. Since $a < b$ we may assume $x < y$. Since $x, y \in Q$, Theorem 3.8 implies $\omega(x) < \omega(y)$. Therefore $K_x \cap K_y = \emptyset$. Thus the intervals K_x , $x \in S_i(L)$, are pairwise disjoint. Each interval contains a rational number, so this family of intervals is countable. Hence $S_i(L)$ is countable. QED.

LEMMA 4.3. $Q \cap L$ is countable.

Proof. If $x \in Q \cap L$ then $\omega(x)$ is not a single point. Therefore $x \in S_i(L)$ for some $i \in \{1, \dots, n\}$, so $Q \cap L = \bigcup_{i=1}^n S_i(L)$. It follows from Lemma 4.2 that $Q \cap L$ is countable. QED.

Proof of 4.1. Lemma 4.3 implies (1) since $W \cap \pi^{-1}(w)$ is the union of a countable family of line segments of the type L . This completes the proof of Theorem 4.1.

By imposing some slightly generic behavior on the equilibria we obtain stronger conclusions.

THEOREM 4.4. (a) *Assume E is countable. Then $x(t)$ converges to a trap as $t \rightarrow \infty$, for almost all $x \in W^c$.*

(b) *Assume all equilibria are simple. Then $x(t)$ converges to a sink as $t \rightarrow \infty$, for almost all $x \in W^c$.*

Proof. Since a simple trap is a sink, (b) follows from (a). Recall the definition

$$Q = \{x \in W^c : \omega(x) \not\subset E\},$$

and define

$$N = \{x \in W^c \setminus Q : \omega(x) \text{ is not a trap}\}.$$

If $x \in W^c \setminus Q$ then $\omega(x)$ is a compact connected nonempty subset of E . Therefore, since E is countable, $\omega(x)$ is a single equilibrium, which we denote by $e(x)$. We obtain a map $e: W^c \setminus Q \rightarrow E$.

Let L be a line segment in W parallel to a positive vector. The map

$$e: L \cap N \rightarrow E$$

is injective: If x, y are distinct points of $L \cap N$ we may assume $x < y$; then $e(x)$ is not a trap so $e(x) \neq e(y)$ by Lemma 3.1.

This proves that $L \cap N$ is countable. In Lemma 4.3 we proved that $L \cap Q$ is countable. Therefore an argument using Fubini's theorem, similar to the proof of Theorem 4.1, shows that $Q \cup N$ has measure zero, which proves Theorem 4.4. QED.

The *stable set* of an equilibrium p is

$$S(p) = \{x \in W: \omega(x) = \{p\}\}.$$

COROLLARY 4.5. *Assume E is countable. If $p \in E$ is not a trap, then $S(p)$ has measure zero.*

Proof. Use Lemma 4.3(a). QED.

Even without assuming countability of E one can sometimes prove the existence of traps.

THEOREM 4.6. *Let $K \subset W$ be a compact attractor. Then K contains a trap. If all equilibria in K are simple then K contains a sink.*

Proof. By definition K is a compact nonempty positively invariant set having a neighborhood U such that

$$\emptyset \neq \omega(x) \subset K \quad \text{for all } x \in U.$$

It follows easily from Theorem 4.1 that K contains an equilibrium. Let $p \in K \cap E$ be maximal for the vector ordering $\leq$. By Theorem 4.1 there exists $y \in U$ such that $y > p$ and $\omega(y) \cap K \cap E \neq \emptyset$. Let $q \in \omega(y) \cap K \cap E$. Then $q \geq p$ since $y > p$ and the flow is eventually monotone. Therefore $q = p$ by maximality. In this way we can find $y_2 > y_1 > p$ such that $y_i(t) \rightarrow p$ as $t \rightarrow \infty$, $i = 1, 2$. This implies p is a trap (hence a sink if it is simple), since $y(t) \rightarrow p$ uniformly in $y \in \{x \in W: y_2 > x > y_1\}$. QED.

We turn to invariant functions. As an example, consider the cooperative irreducible system

$$\begin{aligned}\frac{dx}{dt} &= -2x^3 + y + z, \\ \frac{dy}{dt} &= x^3 - 2y + 2z, \\ \frac{dz}{dt} &= x^3 + y - 3z.\end{aligned}$$

The function $x + y + z$ is invariant, as is seen by adding up the right-hand sides of the equations. The equilibrium set is the curve $z = (3/4)x^4$, $y = (5/4)x^3$. Thus the equilibria are quite degenerate. This is not an accident: Theorem 4.3 shows that when E is nondegenerate there are very likely to be traps, whereas a continuous invariant function must be constant on the domain of attraction of a trap. The following result strengthens this conclusion.

THEOREM 4.7. *Suppose the equilibrium set is countable. Let $A \subset W$ be a connected open set such that almost every point of A has compact forward orbit closure. Then every continuous invariant function f is constant on A .*

Proof. Let the traps be $p_1, p_2, \dots$; let the domain of attraction of p_i be D_i . By Theorem 4.4(a) the set $\bigcup_i A \cap D_i$ is dense in A .

Clearly f is constant on each $\bar{D}_i$. Therefore $f(A)$ is countable. Since A is connected, $f(A)$ is connected and countable, hence $f(A)$ is a single point, and the theorem is proved. QED.

5. Systems in $\mathbb{R}_+^n$. In this section we consider a C^1 vector field $F: \mathbb{R}^n \rightarrow \mathbb{R}^n$ and the corresponding system

$$(1) \quad \frac{dx^i}{dt} = F^i(x^1, \dots, x^n), \quad i = 1, \dots, n$$

such that

- (2) the system is cooperative and irreducible;
 - (3) $F(0) \geq 0$;
 - (4) for any $x \in \mathbb{R}_+^n$ there exists $y > x$ with $F^i(y) < 0$, $i = 1, \dots, n$.
- An example is a “positive feedback loop” of n species, of the form

$$(5) \quad \begin{aligned} \frac{dx^1}{dt} &= f(x^n) - A_1 x^1, \\ \frac{dx^j}{dt} &= x^{j-1} - A_j x^j \quad \text{for } j = 2, \dots, n \end{aligned}$$

where $f: \mathbb{R} \rightarrow \mathbb{R}$ is C^1 and the following conditions obtain:

- (5a) $A_j > 0$, $j = 1, \dots, n$;
- (5b) $f(s) > 0$ for all $s > 0$ and $f'(s) > 0$ for all $s \geq 0$;
- (5c) $f(s_k)/s_k < A_1 \cdots A_n$ for some sequences $s_k \rightarrow \infty$.

Systems of this kind have been studied by Selgrade [13], [14] and Griffiths [3]. See also Walter [15].

THEOREM 5.1. *Let system (1) satisfy (2), (3), (4). Then:*

- (a) $\mathbb{R}_+^n$ is positively invariant;
- (b) every forward orbit closure in $\mathbb{R}_+^n$ is compact;
- (c) the forward trajectory of almost every point of $\mathbb{R}_+^n$ approaches the set of equilibria.

The next result shows that small perturbations of (1) enjoy similar properties. Let $\mathcal{V}(\mathbb{R}^n)$ denote the space of C^1 vector fields on $\mathbb{R}^n$ with the weak topology (see Appendix).

THEOREM 5.2. *Let $K \subset \mathbb{R}_+^n$ be a compact set. Then there exists a weak C^1 neighborhood $\mathcal{N} \subset \mathcal{V}(\mathbb{R}^n)$ of F such that if $G \in \mathcal{N}$ and $\mathbb{R}_+^n$ is positively invariant for the flow of G , then:*

- (a) the forward orbit closure of any point of K is compact;
- (b) the forward trajectory of almost every point of K approaches the set of equilibria.

Proof of Theorem 5.1. By (1), (2) and Theorem 1.5 the flow $\{\phi_t\}$ is strongly monotone. Evidently (3) implies (a), and (3) and (4) imply (b); given $y > x$ as in (4), for all $g \geq 0$ we have

$$0 \leq \phi_t(0) \leq \phi_t(x) < \phi_t(y) \leq y$$

showing that the forward orbit of x is bounded. Finally, (c) follows from Theorem 4.1.

Proof of Theorem 5.2. Fix $q \in \text{int } \mathbb{R}_+^n$ such that

$$q > K \quad \text{and} \quad F(q) < 0,$$

using property (4). Set

$$\Gamma = \{x \in \mathbb{R}_+^n : 0 \leq x \leq q\}.$$

Because F is cooperative and irreducible and $F(x) < 0 < F(q)$, it follows that $F(x)$ points into $\text{int } \Gamma$ for any $x \in \partial F \setminus \{0\}$. If G is sufficiently near F then $G(x)$ points into Γ for all $x \in \partial \Gamma$ such that $x^i = q^i$ for some $i \in \{1, \dots, n\}$. If we assume that $\mathbb{R}_+^n$ is

positively invariant for the flow $\{\psi_t\}$ of such a G , then $\psi_t(\Gamma) \subset \Gamma$ under $\{\psi_t\}$ for all $t > 0$. Conclusion (a) is now obvious.

If, in addition to the properties above, G is sufficiently near F , then $\{\psi_t\}$ has eventually positive derivatives in Γ by Theorem 1.2. Conclusion (b) follows from Theorem 4.1. QED.

THEOREM 5.3. *In the feedback loop (5) assume that 0 is a regular value of the function*

$$s \rightarrow f(s) - A_1 \cdots A_n s.$$

Then the forward trajectory of almost every point of $\mathbb{R}_+^n$ converges to a sink.

Proof. The hypothesis is exactly the condition that the vector field in (5) have simple equilibria. The theorem now follows from Theorems 5.1 and 4.4(b).

THEOREM 5.4. *In the system (5) we have:*

- (a) *The forward trajectory of almost every point in $\mathbb{R}_+^n$ converges to an equilibrium.*
- (b) *If $f(s)$ is analytic for $s > 0$ then every invariant function on $\mathbb{R}_+^n$ is constant.*

Proof. Part (a) follows from the Corollary to Theorem 2.3 because the set E of equilibria of (5) is totally ordered. Part (b) follows from Theorem 5.1 and (5a, b) once we show that E is countable. But in the contrary case one proves easily that $f(s) \equiv A_1 \cdots A_n s$, violating (5c). QED.

Appendix. The Closing Lemma.

Let M be a smooth manifold without boundary. Denote by $\mathcal{V}(M)$ the set of C^1 vector fields on M in the weak C^1 topology.

THEOREM (Closing Lemma). *Let $F \in \mathcal{V}(M)$ have flow $\{\phi_t\}$. Let $p \in M$ be a nonwandering point of $\{\phi_t\}$ which is not an equilibrium, and which belongs to some compact invariant set. Let $\mathcal{N} \subset \mathcal{V}(M)$ be a neighborhood of F . Then there exists $T > 0$ with the following property. For every neighborhood $U \subset M$ of the solution curve $\{\phi_t(p) : -T \leq t \leq T\}$ there exists $G \in \mathcal{N}$ such that $G = F$ in $M \setminus U$ and the flow of G has a closed orbit through p .*

COROLLARY. *For every $F, p, \mathcal{N}$ as above and every neighborhood $N \in M$ of the closure of the orbit of p there exists $G \in \mathcal{N}$ having a closed orbit through p , such that $G = F$ in $M \setminus N$.*

In this paper we need only the case where M is an open set in $\mathbb{R}^n$. From now on we assume M is of this kind.

A basic neighborhood of $F \in \mathcal{V}(M)$ is then a set of the form

$$\mathcal{N} = \mathcal{N}(F; K, \epsilon)$$

where $K \subset M$ is compact, $\epsilon > 0$, and $g \in \mathcal{N}$ if and only if

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

for all $x \in K$.

A point $p \in M$ is *nonwandering* for a flow $\{\phi_t\}$ provided that for every neighborhood $V \subset M$ of p and every real number $T > 0$ there exists $t > T$ such that $\phi_t(U) \cap U$ is not empty. In particular, α - and ω -limit points are nonwandering.

The Closing Lemma was proved in Pugh [10]. The proof has a gap, but a complete proof has been given by Robinson [11]; see also Robinson [17] and a forthcoming paper by Pugh and Robinson [18]. The gap has also been filled by D. Hart [5].

The gap concerns the topology of $\mathcal{V}(M)$. What is actually proved in [10] is that the vector field G can be chosen so that for a given $\epsilon > 0$, compact $K \subset M$, and $s > 0$ the

flow $\{\psi_t\}$ of G satisfies

$$|F(x) - G(x)| + |\psi_t(x) - \phi_t(z)| + \|D\psi_t(x) - D\phi_t(x)\| < \varepsilon$$

for all $x \in K$, $t \in [-s, s]$. This result in fact suffices for the applications of the Closing Lemma in this paper.

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