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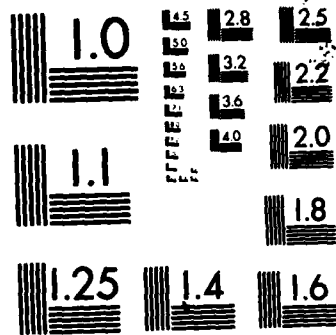
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(A)

# Monotone Semiflows Generated by Functional Differential Equations

by

Hal Smith

## ABSTRACT

In this paper we obtain sufficient condition for an autonomous functional differential equation to generate a strongly monotone semiflow on a suitable state space. This allows the application to functional differential equations of very powerful recent results on strongly monotone semiflows due to M.W. Hirsch and H. Matano. In addition, a very striking relationship is established between such functional differential equations and corresponding ordinary differential equations. An example, involving a biochemical feedback loop is considered.

Keywords:

stability; steady states



## Monotone Semiflows Generated by Functional Differential Equations

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Recently, there has been a considerable advance in our understanding of the qualitative as well as the asymptotic behavior of semiflows on partially ordered spaces which preserve the partial ordering. In large part, this advance is due to recent work of M.W. Hirsch [9-12] and H. Matano [14-16]. The most striking result, due to Hirsch [10,11,12], implies that "almost every" precompact orbit converges to the set of equilibria (under suitable hypotheses, see section 4). These results have been applied to ordinary differential equations in  $R^n$  (see e.g. [10,23]) where the well-known Kamke theorem applies and to nonlinear reaction diffusion systems with quasimonotone reaction term (see e.g. [11,12,14,15,23]) where maximum principles apply. The aim of this paper is to develop the machinery necessary to apply the above mentioned results to the class of functional differential equations, FDE's, and to investigate the qualitative behavior of the subclass of these equations which generate an order preserving semiflow.

More precisely, we consider the FDE

$$(0.1) \quad x'(t) = f(x_t), \quad ' = \frac{d}{dt}$$

where  $f: C([-r,0], R^n) \rightarrow R^n$  and  $x_t$  denotes the element of  $C = C([-r,0], R^n)$ , the space of continuous maps of  $[-r,0]$  into  $R^n$ , given by  $x_t(\theta) = x(t+\theta)$ ,  $-r \leq \theta \leq 0$ . For more details concerning FDE's we refer the reader to the text [6]. Assume that (0.1), together with the initial data  $x_0 = \phi \in C$ , gives rise to a unique solution on  $[0, \sigma)$ ,  $\sigma > 0$ , which we denote by  $x(t, \phi)$  or  $x_t(\phi)$  depending on whether we view the solution in  $R^n$  or  $C$ . Then, under suitable conditions, the collection of maps,

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$\phi \rightarrow x_t(\phi)$ , is a local semiflow on  $C$ . If  $\phi, \psi \in C$ , we write  $\phi \leq \psi$  ( $\phi < \psi$ ) if the indicated inequality holds pointwise, with the usual (componentwise) partial ordering on  $\mathbb{R}^n$ . The semiflow is order preserving (we will say that  $f$  is cooperative) if whenever  $\phi \leq \psi$  we have  $x_t(\phi) \leq x_t(\psi)$  for all  $t$ ,  $0 \leq t < \min\{\sigma_\phi, \sigma_\psi\}$ . Sufficient conditions for  $f$  to be cooperative appear not to be well-known. After, obtaining such conditions, this author found references to work of K. Kunisch and W. Schappacher [25], R.H. Martin [13] and Y. Ohta [18] who had earlier obtained the same sufficient conditions. Most likely, others before them have obtained the following sufficient condition

(H) Whenever  $\phi \leq \psi$  and  $\phi_i(0) = \psi_i(0)$  it follows that  $f_i(\phi) \leq f_i(\psi)$ .

For those familiar with the Kamke (quasimonotone) condition for ordinary differential equations, (H) will seem quite natural, it reduces to the Kamke condition.

The order preserving property of a semiflow is not sufficient for the strong result of Hirsch mentioned above; one requires strongly order preserving semiflows, that is, if  $\phi \leq \psi$ ,  $\phi \neq \psi$  then  $x_t(\phi) < x_t(\psi)$ , at least for all large  $t$  (it is only reasonable to expect such an inequality for  $t \geq r$ ).

In section 2 of this paper we develop sufficient conditions for (0.1) to generate a strongly order preserving semiflow (we say, in this case, that  $f$  is cooperative and irreducible).

In section 3, we consider the stability of steady states of cooperative FDE's and the existence of connecting orbits between steady states.

In section 4, we state the relevant results of Hirsch which apply in our setting.

The main result of our work can be roughly summarized as follows. Let  $f$  be cooperative and irreducible (see section 2) and assume all orbits of (0.1) are

precompact (e.g. all orbits are bounded and  $f$  maps bounded sets to bounded sets). Then, for a dense set of initial conditions for (0.1), the qualitative behavior of the solutions of (0.1) is the same as for the ordinary differential equation

$$(0.2) \quad \begin{aligned} x'(t) &= F(x(t)) \\ F(x) &= f(\hat{x}) \end{aligned}$$

where  $x \rightarrow \hat{x}$  is the inclusion of  $R^n$  into  $C$  given by  $\hat{x}(\theta) \equiv x$ . Equations (0.1) and (0.2) have the same steady states and the stability properties of a steady state  $\hat{x}$  of (0.1) are the same as for the steady state  $x$  of (0.2). Moreover, Equation (0.2) is cooperative in the sense of Hirsch [9] and hence there are simple tests for stability and instability of steady states of (0.2) (see [23] and Corollary 3.2). These rather striking results represent a considerable improvement in the connection made between (0.1) and (0.2) by R.H. Martin [13].

The results of the first four sections of this paper are applied in section 5 of this paper to a model of biochemical feedback in protein synthesis which goes back to Goodwin [4] and has been the object of much study [13,20,21,24] particularly in the nondelay case. Under very reasonable hypotheses, we obtain an essentially complete picture of the qualitative behavior of the solutions of the model equations.

It is convenient to establish some notation here. Let  $R_+^n$  be the cone of non-negative vectors in  $R^n$ . If  $x, y \in R^n$  we write  $x \leq y$  ( $x < y$ ) if  $x_i \leq y_i$  ( $x_i < y_i$ ) for  $1 \leq i \leq n$ . Let  $\{e_1, \dots, e_n\}$  denote the standard basis in  $R^n$  and let  $1 = e_1 + e_2 + \dots + e_n$ . If  $x \leq y$ , we write  $[x, y] = \{z \in R^n: x \leq z \leq y\}$ . Set  $N = \{1, 2, \dots, n\}$ . Let  $r \geq 0$  and  $C = C([-r, 0], R^n)$  be the Banach space of continuous functions mappings  $\phi: [-r, 0] \rightarrow R^n$  with supremum norm. If  $\phi, \psi \in C$ , we write  $\phi \leq \psi$  ( $\phi < \psi$ ) in case the indicated inequality holds at each point of  $[-r, 0]$ . If  $\phi \leq \psi$ , we write  $[\phi, \psi] = \{\beta \in C: \phi \leq \beta \leq \psi\}$ .

Let  $C^+ = \{\phi \in C: \phi \geq 0\}$ . Let  $\hat{\cdot}$  denote the inclusion  $R^n \rightarrow C([-r,0], R^n)$  by  $x \rightarrow \hat{x}$ ,  $\hat{x}(\theta) \equiv x$ ,  $\theta \in [-r,0]$ . Denote the space of functions of bounded variation on  $[-r,0]$  by  $BV[-r,0]$ . If  $A$  and  $B$  are subsets of a linear space, then  $A+B = \{a+b: a \in A, b \in B\}$  and similarly for  $A-B$ . If  $X$  and  $Y$  are Banach spaces, let  $L(X,Y)$  denote the space of bounded linear maps from  $X$  to  $Y$ . Let  $A$  and  $B$  be  $n \times n$  matrices. We write  $A \leq B$  if the equality holds componentwise. The matrix  $A$  is irreducible if it does not leave invariant any proper subspace of  $R^n$  spanned by a subset of the standard basis elements. We write  $s(A) = \max \operatorname{Re} \lambda$  where  $\lambda$  runs over the eigenvalues of  $A$ , the stability modulus of  $A$ . If  $a \in R^n$  we write  $\operatorname{diag}(a)$  for the  $n \times n$  diagonal matrix with  $a_i$  in the  $(i,i)$  entry.

# 1. Comparison results.

Let  $\Omega$  be an open subset of  $\mathbb{R} \times \mathbb{C}$  and  $f: \Omega \rightarrow \mathbb{R}^n$  be continuous. Consider the FDE

$$(1.1) \quad x'(t) = f(t, x_t).$$

We assume throughout this paper that solutions of the initial value problem (1.1) together with  $x_{t_0} = \phi$ , for  $(t_0, \phi) \in \Omega$ , are unique. If  $f$  is Lipschitz continuous in  $\phi$  on compact subsets of  $\Omega$  then uniqueness holds [6]. We write  $x(t, t_0, \phi, f)$  ( $x_t(t_0, \phi, f)$ ) for the solution of the initial value problem and we drop the  $f$  when no confusion results.

The results of this section have probably been proved by many authors. However we are only aware of the work of contained in [13],[18], and [25]. These authors proved both results of this section.

Consider the hypothesis:

(H): If  $(t, \phi), (t, \psi) \in \Omega$ ,  $\phi \leq \psi$  and  $\phi_i(0) = \psi_i(0)$  for some  $i$ , then

$$f_i(t, \phi) \leq f_i(t, \psi).$$

The main result of this section is the following.

Proposition 1.1: Let  $f, g: \Omega \rightarrow \mathbb{R}^n$  be as above and assume either  $f$  or  $g$  satisfies

(H). Assume  $f(t, \phi) \leq g(t, \phi)$  for all  $(t, \phi) \in \Omega$ . If  $(t_0, \phi), (t_0, \psi) \in \Omega$  with  $\phi \leq \psi$  then

$$x(t, t_0, \phi, f) \leq x(t, t_0, \psi, g)$$

for all  $t \geq t_0$  for which both are defined.

Proof: Assume that  $f$  satisfies (H). Let  $g_\epsilon(t, \phi) = g(t, \phi) + \epsilon 1$  and  $\psi_\epsilon = \psi + \epsilon \hat{1}$  for  $\epsilon \geq 0$ . If  $x(t, t_0, \psi, g)$  is defined on  $[t_0 - r, t_1]$  for some  $t_1 > t_0$  then  $x(t, t_0, \psi_\epsilon, g_\epsilon)$  is defined on  $[t_0 - r, t_1]$  for all sufficiently small positive  $\epsilon$  by Theorem 2.2 of [6]. We will show that  $x(t, t_0, \phi, f) < x(t, t_0, \psi_\epsilon, g_\epsilon)$  on  $[t_0 - r, t_1]$  for small positive  $\epsilon$ . The proposition will then follow by letting  $\epsilon \rightarrow 0$  and applying Theorem 2.2 of [6]. Suppose the above assertion is false. Then there exists a small positive  $\epsilon$  for

which  $x(t, t_0, \psi_\epsilon, g_\epsilon)$  is defined on  $[t_0 - r, t_1]$  and a  $t' \in (t_0, t_1]$  such that  $x(t, t_0, \phi, f) < x(t, t_0, \psi_\epsilon, g_\epsilon)$  on  $[t_0 - r, t')$  and  $x_i(t', t_0, \phi, f) = x_i(t', t_0, \psi_\epsilon, g_\epsilon)$  for some value of  $i$ . Clearly  $x_i'(t', t_0, \phi, f) \geq x_i'(t', t_0, \psi_\epsilon, g_\epsilon)$ . But

$$\begin{aligned} x_i'(t', t_0, \psi_\epsilon, g_\epsilon) &= g_i(t', x_{t'}(t_0, \psi_\epsilon, g_\epsilon)) + \epsilon \\ &\geq f_i(t', x_{t'}(t_0, \psi_\epsilon, g_\epsilon)) + \epsilon \\ &> f_i(t', x_{t'}(t_0, \psi_\epsilon, g_\epsilon)) \\ &\geq f_i(t', x_{t'}(t_0, \phi, f)) \\ &= x_i'(t', t_0, \phi, f) \end{aligned}$$

where the latter inequality follows from (H). This contradiction implies that such a  $t'$  cannot exist and establishes the above assertion (and the proposition).

Suppose that  $\Omega = \mathbb{R} \times U$  where  $U$  is an open subset of  $C$  containing  $C^+$ . The following invariance result will be useful. The proof involves ideas similar to those used in the proof of Proposition 1.1 and is therefore omitted.

**Proposition 1.2:** Assume that whenever  $\phi \in C^+$  with  $\phi_i(0) = 0$  and  $t \in \mathbb{R}$ ,  $f_i(t, \phi) \geq 0$ . If  $\phi \in C^+$  and  $t_0 \in \mathbb{R}$  then  $x(t, t_0, \phi) \geq 0$  for all  $t \geq t_0$  in the maximal interval of existence.

Proposition 1.2 is a very special case of much more general invariance result due to G. Seifert [19].

## 2. Cooperative Irreducible FDE's

The ultimate goal of this section is to find sufficient conditions for the autonomous FDE

$$(2.1) \quad x'(t) = f(x_t), \quad f : C \rightarrow \mathbb{R}^n$$

to have the property that whenever  $\phi, \psi \in C$  are distinct with  $\phi \leq \psi$ ,

$$\text{then } x_t(0, \phi) \leq x_t(0, \psi) \quad \text{for } t \geq 0$$

$$\text{and } x_t(0, \phi) < x_t(0, \psi) \quad \text{for } t \geq t_0 > 0,$$

$t_0$  sufficiently large (independent of  $\phi$  and  $\psi$ ). The following example will show us that we need to modify slightly our notion of the state space of (2.1).

Consider the initial value problem

$$x_1'(t) = ax_1(t) + bx_2(t-1/2) \quad t \geq 0$$

$$x_2'(t) = cx_1(t-1) + dx_2(t)$$

$$x_1(\theta) \equiv 0 \quad , -1 \leq \theta \leq 0$$

$$x_2(\theta) = \phi_2(\theta)$$

$$\text{supp } \phi_2 \subseteq [-1, -2/3], \quad \phi_2 \geq 0, \quad \phi_2 \neq 0.$$

The initial value problem can easily be integrated by steps and one finds  $x(t) \equiv 0$  for  $t \geq -2/3$ . The problem is that  $x_2(t-1/2)$ ,  $t \geq 0$ , "never sees" the support of  $\phi_2$  so  $x_1'(t) \equiv 0$ . Hence, although the initial condition  $\phi = (0, \phi_2) \geq 0$  satisfies  $\phi \neq 0$ , we nevertheless have  $x(t, 0, \phi)$  agreeing with the identically zero solution.

The source of the failure of the solution operator to distinguish between the two initial conditions  $\phi$  and  $0$  is our (implicit) choice of the state space as  $C = C([-1, 0], \mathbb{R}^2)$ . We will show that this pathology can be removed by taking our state space to be  $C_{(1, 1/2)} \equiv C([-1, 0], \mathbb{R}) \times C([-1/2, 0], \mathbb{R})$ . To this end, consider the above linear equation where  $b > 0$ ,  $c > 0$ . Let  $(\phi_1, \phi_2) \in C_{(1, 1/2)}^+$  and assume

$(\phi_1, \phi_2) \neq 0$ . We can associate to  $(\phi_1, \phi_2) = \phi$  a solution  $x(t, 0, \phi)$  and it is not difficult to see that  $x(t, 0, \phi) > 0$  for  $t > 3/2$  (the worst case is where the support of  $\phi_1$  belongs to, say,  $[-\epsilon, -\epsilon/2]$  for small  $\epsilon$  and  $\phi_2 \equiv 0$ ). In addition, for each small  $\epsilon > 0$ , one can select a nontrivial  $\phi$  as above such that  $x_1(t, 0, \phi) \equiv 0$  on  $[0, 3/2 - \epsilon]$  but  $x(t, 0, \phi) > 0$  for  $t \geq 3/2$ .

It is worth emphasizing this last point. Namely that, with our new choice of state space, if  $\phi \geq 0$  and  $\phi \neq 0$ , the solution  $x(t, 0, \phi)$  has the property that  $x(t, 0, \phi) > 0$  for  $t \geq 3/2$ . In other words, it takes time for nontrivial nonnegative initial conditions to become a positive state. Fortunately, we can bound from above this time lapse independently of the initial conditions.

Motivated by this example, we develop some notation. Let  $r \in \mathbb{R}_+^n$ ,  $r = (r_1, r_2, \dots, r_n)$ ,  $|r| = \max r_i$  and let

$$C_r = C([-r_1, 0], \mathbb{R}) \times C([-r_2, 0], \mathbb{R}) \times \dots \times C([-r_n, 0], \mathbb{R})$$

$$C = C([-|r|, 0], \mathbb{R}^n).$$

Given an element  $\phi = (\phi_1, \dots, \phi_n) \in C_r$  we will identify  $\phi$  with an element of  $C$ , which again we label  $\phi$ , by the correspondence

$$\phi(\theta) = (\phi_1(\theta), \dots, \phi_n(\theta)) \text{ where } \phi_i : [-|r|, 0] \rightarrow \mathbb{R}$$

$$\text{is defined by } \phi_i(\theta) = \begin{cases} \phi_i(\theta) & -r_i \leq \theta \leq 0 \\ \phi_i(-r_i) & -|r| \leq \theta \leq -r_i \end{cases}$$

This inclusion,  $I$ , of  $C_r$  into  $C$  is injective but not surjective. Similarly, given an element  $\phi$  of  $C$  we will identify  $\phi$  with an element of  $C_r$ , which we label  $\phi$  again, by  $\phi = (\phi_1, \dots, \phi_n) \in C_r$ ,  $\phi_i = \phi(\cdot) \big|_{[-r_i, 0]}$ .

This latter map,  $R$ , of  $C$  into  $C_r$  is surjective but of course, not injective. We write  $C_r^+$  for the cone of  $n$ -tuples of nonnegative functions and if  $\phi, \psi \in C_r^+$  we



write  $\phi \leq \psi$  ( $\phi < \psi$ ) if  $\psi - \phi \in C_r^+$  ( $\psi - \phi \in \text{interior } C_r^+$ ). Note that we use the same symbol for inequality in both  $C$  and  $C_r$ . This should not cause a problem since  $\phi \leq \psi$  in  $C_r$  if and only if  $\phi \leq \psi$  in  $C$  (upon making identifications as above). Finally, let  $\text{Ker}(R) = \{\phi \in C : \phi_i(\theta) = 0, -r_i \leq \theta \leq 0, 1 \leq i \leq n\}$ .

It will be convenient to define the semigroup on  $C$  generated by the trivial FDE :  $x' = 0$ . For  $\tau \geq 0$ , define  $S(\tau) : C \rightarrow C$  by

$$[S(\tau)\phi](\theta) = \begin{cases} \phi(\theta) & -|r| \leq \theta \leq -\tau \\ \phi(0) & -\tau \leq \theta \leq 0 \end{cases} \quad \text{if } \tau < |r|$$

and

$$[S(\tau)\phi] = \hat{\phi}(0) \quad \text{if } \tau \geq |r|.$$

With this notation, we begin by considering a nonautonomous linear equation. Our aim is to establish sufficient conditions for certain nonnegative nonzero initial conditions to give rise to eventually positive solutions.

Consider the linear FDE

$$(2.2) \quad x'(t) = L(t, x_t)$$

where  $L(t, \cdot) : C \rightarrow \mathbb{R}^n$  is a bounded linear map and  $t \mapsto L(t, \cdot)$  is continuous from  $\mathbb{R}$  to  $L(C, \mathbb{R}^n)$ , the space of bounded linear maps of  $C$  into  $\mathbb{R}^n$ . The following hypotheses will be required

(K): For all  $\phi \in C^+$  with  $\phi_i(0) = 0$ ,  $L_i(t, \phi) \geq 0$  for  $t \in \mathbb{R}$ .

(I): The matrix  $A(L)(t)$  defined by

$$A(L)(t) = \text{col}(L(t, \hat{e}_1), L(t, \hat{e}_2), \dots, L(t, \hat{e}_n))$$

is irreducible for every  $t \in \mathbb{R}$

(R): If  $\phi \in C^+$ ,  $\phi \notin \text{Ker}(R)$  and  $\phi(0) = 0$ ,  $t_0 \in \mathbb{R}$  then there exists  $i \in N$  and  $\tau \in [0, |r|)$  such that

$$L_i(t_0 + \tau, S(\tau)\phi) > 0.$$

In order to get another perspective on the hypotheses (K) and (I), consider the standard representation of  $L$  as  $L = (L_1, \dots, L_n)$  where

$$L_i(t, \phi) = \sum_{j=1}^n \int_{-|r|}^0 \phi_j(\theta) d_{\theta} \eta_{ij}(\theta, t), \quad 1 \leq i \leq n$$

in which  $\eta_{ij} : \mathbb{R} \times \mathbb{R} \rightarrow \mathbb{R}$  satisfies

$$\begin{aligned} \eta_{ij}(\theta, t) &= \eta_{ij}(0, t) & \theta \geq 0 \\ \eta_{ij}(\theta, t) &= \eta_{ij}(-|r|, t) \equiv 0 & \theta \leq -|r| \\ \eta_{ij}(\cdot, t) &\in BV[-|r|, 0] \\ \eta_{ij}(\cdot, t) &\text{ is continuous from the left on } (-|r|, 0). \end{aligned}$$

If we set

$$a_i(t) \equiv \eta_{ii}(0, t) - \eta_{ii}(0-, t), \quad 1 \leq i \leq n$$

$$\bar{\eta}_{ii}(\theta, t) = \begin{cases} \eta_{ii}(\theta, t), & \theta < 0 \\ \eta_{ii}(0-, t), & \theta \geq 0 \end{cases}$$

then

$$\begin{aligned} L_i(t, \phi) &= a_i(t) \phi_i(0) + \int_{-|r|}^0 \phi_i(\theta) d_{\theta} \bar{\eta}_{ii}(\theta, t) + \sum_{j \neq i} \int_{-|r|}^0 \phi_j(\theta) d_{\theta} \eta_{ij}(\theta, t) \\ &\equiv a_i(t) \phi_i(0) + \bar{L}_i(t, \phi). \end{aligned}$$

It is easy to see that (K) holds if and only if  $\bar{\eta}_{ii}$  and  $\eta_{ij}$ ,  $i \neq j$ , are nondecreasing in

$\theta$  for fixed  $t$ . Hence (K) holds if and only if  $\bar{L}(t, \cdot) : C^+ \rightarrow \mathbb{R}_+^n$ .

It is not difficult to see that due to the continuity of the map  $t \rightarrow L(t, \cdot)$ ,  $a_i(t)$  is continuous in  $t$ .

Finally, we note that the matrix  $A(L)(t)$  has entries

$$(2.3) \quad A(L)(t)_{ij} = \int_{-|r|}^0 d_{\theta} \eta_{ij}(\theta, t) = \eta_{ij}(0, t).$$

The next several results concern solutions  $x(t, t_0, \phi)$  of (2.2). We begin by showing that (K) implies that if a solution  $x(t, t_0, \phi)$  ( $\phi \in C^+$ ) ever has a positive component then ever after that component is positive.

Lemma 2.1: Let (K) hold,  $\phi \in C^+$  and  $x(t) = x(t, t_0, \phi)$ ,  $t \geq t_0$ , satisfy (2.2). If  $x_j(t_1) > 0$  for some  $t_1 \geq t_0$  then  $x_j(t) > 0$  for  $t \geq t_1$ .

Proof: Note that (K) implies the hypotheses of Proposition 1.2 so  $x(t, t_0, \phi) \geq 0$  for  $t \geq t_0$ . Now

$$x_j'(t) = -a_j(t)x_j(t) + \bar{L}_j(t, x_t) \geq -a_j(t)x_j(t).$$

Hence, if  $x_j(t_1) > 0$  then  $x_j(t) > 0$  for  $t \geq t_1$  by a standard differential inequality argument.

The next lemma is the rationale for assuming (R). It guarantees "ignition" of some component of  $x(t, t_0, \phi)$ .

Lemma 2.2: Let (R) hold. If  $\phi \in C^+$ ,  $\phi \notin \text{Ker}(R)$ ,  $t_0 \in \mathbb{R}$  then there exists  $i \in N$  and  $t \in [t_0, t_0 + |r|)$  such that  $x_i(t, t_0, \phi) > 0$ .

Proof: If  $\phi(0) \neq 0$  then the conclusion follows by taking  $i \in N$  such that  $\phi_i(0) > 0$  and  $t = t_0$ .

Assume  $\phi(0) = 0$ . By (R), there exists  $i \in N$  and  $\tau \in [0, |r|)$  such that  $L_i(t_0 + \tau, S(\tau)\phi) > 0$ . Since  $[S(\tau)\phi](0) = 0$ ,  $\bar{L}_i(t_0 + \tau, S(\tau)\phi) = L_i(t_0 + \tau, S(\tau)\phi)$ . Clearly  $x_t(t_0, \phi) \geq S(t - t_0)\phi$  for  $t \geq t_0$  so  $\bar{L}_i(t_0 + \tau, x_{t_0 + \tau}(t_0, \phi)) \geq \bar{L}_i(t_0 + \tau, S(\tau)\phi) > 0$ . Hence  $x_{t_0 + \tau}(t_0, \phi) \neq 0$  and this implies our result.

Putting together (K) and (R), we see that if  $\phi \in C^+$ ,  $\phi \notin \text{Ker}(R)$  then some component of  $x(t, t_0, \phi)$  becomes and remains positive. To "turn on" the other components is the job of (I).

Proposition 2.3: Let (K), (I) and (R) hold. If  $\phi \in C^+$ ,  $\phi \notin \text{Ker}(R)$ ,  $t_0 \in R$  then  $x(t, t_0, \phi) > 0$  for  $t \geq t_0 + n|r|$ .

Proof: By Lemmas 2.1 and 2.2, there exists an  $i \in N$  such that  $x_i(t) > 0$  for  $t \geq t_0 + |r|$ . It follows that there exists  $\alpha(t) > 0$  for  $t \geq t_0 + 2|r|$  such that  $x_t \geq \alpha(t)\hat{e}_i$  for  $t \geq t_0 + 2|r|$ . Hence  $\bar{L}(t, x_t) \geq \alpha(t)\bar{L}(t, \hat{e}_i)$  for  $t \geq t_0 + 2|r|$ . Now since  $A(L)(t) = -[\text{diag } a(t)] + A(\bar{L})(t)$ ,  $A(\bar{L})(t)$  is irreducible. It follows that there exists  $j \neq i$  such that  $\bar{L}_j(t_0 + 2|r|, \hat{e}_i) > 0$ . Either  $x_j(t_0 + 2|r|) > 0$  or  $x_j(t_0 + 2|r|) = 0$  and  $x'_j(t_0 + 2|r|) = L_j(t_0 + 2|r|, x_{t_0 + 2|r|})$

$$= \bar{L}_j(t_0 + 2|r|, x_{t_0 + 2r}) \geq \alpha(t_0 + 2|r|) \bar{L}_j(t_0 + 2|r|, \hat{e}_i) > 0.$$

But  $x_j(t_0 + 2|r|) = 0$  and  $x'_j(t_0 + 2|r|) > 0$  contradicts  $x_j(t) \geq 0$  for  $t \geq t_0$ . Hence we must have  $x_j(t_0 + 2|r|) > 0$  and by Lemma 2.2,  $x_j(t) > 0$  for  $t \geq t_0 + 2|r|$ .

It follows that there exists  $\beta(t) > 0$  for  $t \geq t_0 + 3|r|$  such that  $x_t \geq \alpha(t)\hat{e}_i + \beta(t)\hat{e}_j$  for  $t \geq t_0 + 3|r|$ . Hence  $\bar{L}(t, x_t) \geq \alpha(t)\bar{L}(t, \hat{e}_i) + \beta(t)\bar{L}(t, \hat{e}_j) = A(\bar{L})(t)(\alpha(t)e_i + \beta(t)e_j)$ . Now  $A(\bar{L})(t_0 + 3|r|)$  is irreducible so  $A(\bar{L})(t_0 + 3|r|)(\alpha(t_0 + 3|r|)e_i + \beta(t_0 + 3|r|)e_j) \cdot e_k > 0$  for some  $k \notin \{i, j\}$ . The reasoning is as follows. Since  $A(\bar{L})(t_3)$  ( $t_3 = t_0 + 3|r|$ ) is

irreducible  $A(\bar{L})(t_3)$  does not leave invariant the span of  $e_i$  and  $e_j$ . It follows that  $A(\bar{L})(t_3)(\mu\alpha(t_3)e_i + \lambda\beta(t_3)e_j) \cdot e_k > 0$  for some choice of  $\mu \in (0,1)$ ,  $\lambda \in (0,1)$  and  $k \in N - \{i,j\}$ . Since  $A(\bar{L})(t_3)$  is nonnegative the assertion above follows. Now, if  $x_k(t_3) = 0$  then

$$x'_k(t_3) = \bar{L}(t_3, x_{t_3}) \geq A(\bar{L})(t_3)(\alpha(t_3)e_i + \beta(t_3)e_j) \cdot e_k > 0.$$

But this is incompatible with  $x_k(t) \geq 0$  for  $t \geq t_0$ , hence  $x_k(t_3) > 0$ . By Lemma 2.2,  $x_k(t) > 0$  for  $t \geq t_0 + 3|r|$ .

Continuing in this manner, we obtain  $x(t) > 0$  for  $t \geq t_0 + n|r|$ .

Recall our earlier example where

$$L(t, \phi) = \text{col}(a\phi_1(0) + b\phi_2(-1/2), c\phi_1(-1) + d\phi_2(0))$$

where  $b > 0$  and  $c > 0$ . Then (K) holds with  $\bar{L}(t, \phi) = \text{col}(b\phi_2(-1/2), c\phi_1(-1))$ . The matrix  $A(L)(t)$  is given by

$$A(L)(t) = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

and is clearly irreducible since both  $b$  and  $c$  are positive. It is easy to check that (R) holds for this example if  $r = (1, 1/2)$  determines the restriction map  $R$ . Notice that (R) fails if " $\phi \notin \text{Ker}(R)$ " is omitted from (R).

We now turn to the main goal of this section. Let  $r \in R_+^n$  and  $C = C([-|r|, 0], R^n)$ . Consider (2.1) where  $f : U \rightarrow R^n$  is a continuously differentiable map on the open subset  $U$  of  $C$ . Assume  $U$  is order convex, that is, if  $\phi, \psi \in U$  with  $\phi \leq \psi$  then  $t\phi + (1-t)\psi \in U$  for  $0 \leq t \leq 1$ .

**Definition:**  $f$  is cooperative in  $U$  if for every  $\psi \in U$ ,  $L = df(\psi)$  satisfies (K).  
 $f$  is cooperative and irreducible in  $U$  if  $f$  is cooperative in  $U$  and the following hold:

- (1) If  $\phi \in U$  and  $\psi \in C$  with  $\phi - \psi \in \text{Ker}(R)$  then  $\psi \in U$  and  $f(\phi) = f(\psi)$ .
- (2) For all  $\psi \in U$ ,  $L = df(\psi)$  satisfies (I) and (R) with the provision that  $i$  and  $\tau$  are independent of  $\psi$ .

We will write  $x(t, \phi)$  ( $x_t(\phi)$ ) for  $x(t, 0, \phi) \in \mathbb{R}^n$  ( $x_t(0, \phi) \in C$ ). Thus  $x(t, \phi)$  is the solution of (2.1) satisfying  $x_0(\phi) = \phi$ . The next lemma, together with Proposition 1.1 implies that if  $f$  is cooperative in  $U$  and  $\phi \leq \psi$  then  $x_t(\phi) \leq x_t(\psi)$  for  $t \geq 0$  on their common interval of existence.

**Lemma 2.4:** If  $f$  is cooperative in  $U$  then  $f$  satisfies (H) of section 1.

**Proof:** Suppose  $\phi, \psi \in U$ ,  $\phi \leq \psi$  and  $\phi_i(0) = \psi_i(0)$ . Since  $U$  is order convex and  $f$  is continuously differentiable

$$f_i(\psi) - f_i(\phi) = \int_0^1 df_i(s\psi + (1-s)\phi)(\psi - \phi) ds \geq 0$$

where the inequality holds since the integrand is pointwise nonnegative by (K).

The next result is the main theorem of this section. It will allow us to define a local semi-flow on  $C_T$  which is eventually strongly monotone.

**Theorem 2.5:** Let  $f$  be cooperative and irreducible in  $U$ . If  $\phi$  and  $\psi$  are elements of  $U$  with  $\phi \leq \psi$ ,  $\psi - \phi \notin \text{Ker}(R)$  and  $[0, \sigma)$ ,  $0 < \sigma < \infty$ , is the intersection of the maximal intervals of existence of  $x(t, \phi)$  and  $x(t, \psi)$ , then

$$x(t, \phi) < x(t, \psi) \text{ for } n|r| \leq t < \sigma.$$

Proof: By Lemma 2.4 and Proposition 1.1 we have  $x(t, \phi) \leq x(t, \psi)$  on  $0 \leq t < \sigma$ .

Now

$$x(t, \psi) - x(t, \phi) = \int_0^1 d_\phi x(t, s\psi + (1-s)\phi)(\psi - \phi) ds.$$

If  $\xi \in U$  and  $\beta \in C$ ,  $d_\phi x(t, \xi)\beta = y(t, \beta)$  satisfies the linear variational equation

$$y'(t) = df(x_t(\xi))_{y_t}, \quad y_0 = \beta$$

(See Theorem 4.1 of [6].) Let  $L(t, \cdot) = df(x_t(\xi))$ . It is apparent that  $L$  satisfies (K) and (I). In order to see that (R) holds for  $L$ , suppose  $\mu \in C$ ,  $\mu \notin \text{Ker}(R)$  and  $\mu(0) = 0$ . By our assumption that  $f$  is cooperative and irreducible, there exists  $i$  and  $\tau \geq 0$  such that  $df(\xi)_i(S(\tau)\mu) > 0$  for all  $\xi \in U$ . In particular, if  $\xi = x_\tau(\xi)$ ,  $\xi \in U$ , we have  $L_i(\tau, S(\tau)\mu) > 0$  which is just (R).

We can now apply Proposition 2.3: if  $\beta \in C^+$ ,  $\beta \notin \text{Ker}(R)$  then  $y(t, \beta) = d_\phi x(t, \xi)\beta > 0$  for  $t \geq n|r|$ . Now  $\psi - \phi \in C^+$  and  $\psi - \phi \notin \text{Ker}(R)$  so for each fixed  $s$ , the integrand above is positive for  $t \geq n|r|$ . Hence the integral above is positive and we have proved the theorem.

If  $f$  is cooperative and irreducible in  $U$ , we would like to think of the state space for (2.1) as  $C_r$  rather than  $C$ . The reason for this is simple. In order to apply a very powerful result of Hirsch for strongly monotone flows [11,12] (see section 4) we need the semi-flow generated by the maps  $\phi \rightarrow x_t(\phi)$  to have the strong monotonicity property that if  $\phi \leq \psi$  and  $\phi \neq \psi$  then  $x_t(\phi) < x_t(\psi)$ , at least for large  $t$ . Theorem 2.5 does not give us this in  $C$ . However, in  $C_r$ , we have this

property as we shall show. First note that if  $\phi, \psi \in C$  and  $\psi - \phi \in \text{Ker}(R)$  then  $x(t, \phi) \equiv x(t, \psi)$  for  $t \geq 0$ . Here is where (1) of the definition of cooperative and irreducible plays a role (a proof can be given following the proof of Theorem 2.5).

Consider the collection of maps

$$\phi \in C_r \xrightarrow{\Phi_t} R \ x_t(I\phi), \quad t \geq 0$$

defined on open subsets of  $U$ , depending on  $t$ . It is apparent that  $\{\Phi_t\}$  defines a local semi-flow in the sense of Hirsch [11,12]. Moreover, if  $\phi, \psi \in C_r$ ,  $\phi \leq \psi$ ,  $\phi \neq \psi$ , then clearly  $I\phi \leq I\psi$  and  $I\psi - I\phi \notin \text{Ker}(R)$ . Hence, by Theorem 2.5,  $x_t(I\psi) > x_t(I\phi)$  for all  $t \geq (n+1)|r|$  for which both exist and thus  $\Phi_t(\phi) < \Phi_t(\psi)$  for  $t \geq (n+1)|r|$ .



### 3. Stability of steady states and connecting orbits.

In this section we are concerned with the stability of a steady state of the FDE

$$(3.1) \quad x'(t) = f(x_t)$$

where  $f$  is a continuously differentiable cooperative map  $f : U \rightarrow \mathbb{R}^n$ ,  $U$  an open order convex subset of  $C$ ,  $r \in \mathbb{R}_+^n$ . Suppose there exists  $v \in \mathbb{R}^n$  with  $\hat{v} \in U$  and

$$f(\hat{v}) = 0$$

and consider the linear variational equation about the steady state  $\hat{v}$ :

$$(3.2) \quad y'(t) = L(y_t), \quad L = df(\hat{v}).$$

Let  $L$  be represented as

$$L\phi = (L_1\phi, \dots, L_n\phi)$$

$$L_i\phi = \sum_{j=1}^n \int_{-|r|}^0 \phi_j(\theta) d\eta_{ij}(\theta), \quad 1 \leq i \leq n$$

$$\eta_{ij} \in BV[-|r|, 0], \quad \eta_{ij}(-|r|) = 0, \quad \eta_{ij}(\theta) \text{ continuous from the left on } (-|r|, 0).$$

The characteristic values associated with the linearized equation (3.2) are roots of

$$\det \Delta(\lambda) = 0$$

$$(3.3) \quad \Delta(\lambda) = \lambda I - A(\lambda)$$

$$A(\lambda)_{ij} = \int_{-|r|}^0 e^{\lambda\theta} d\eta_{ij}(\theta).$$

Define the stability modulus of  $L$  as

$$s(L) = \max\{\operatorname{Re} \lambda : \det \Delta(\lambda) = 0\}.$$

The stability modulus is a well-defined quantity since for any  $\beta \in \mathbb{R}$  there are at most a finite number of zeros of  $\det \Delta(\lambda)$  with  $\operatorname{Re} \lambda \geq \beta$ . It is well known that

the steady state  $\hat{v}$  is asymptotically stable if  $s(L) < 0$  and is unstable if  $s(L) > 0$ .

Since  $f$  is cooperative  $L$  satisfies

(K) Whenever  $\phi \in C^+$  and  $\phi_i(0) = 0$ ,  $L_i \phi \geq 0$ .

Hence the  $\eta_{ij}$  satisfy

$\eta_{ij}(\theta)$ ,  $i \neq j$ , is nondecreasing in  $\theta \in [-|r|, 0]$

$$(3.4) \quad \bar{\eta}_{ii}(\theta) = \begin{cases} \eta_{ii}(\theta), & \theta \in [-|r|, 0) \\ \eta_{ii}(0-), & \theta = 0 \end{cases}$$

$\bar{\eta}_{ii}(\theta)$  is nondecreasing in  $\theta \in [-|r|, 0]$ .

Our first result says that the stability of a steady state of a cooperative system is determined by a real "most unstable" characteristic root

**Theorem 3.1:** Let  $f$  be cooperative. Then  $s(L)$  is a root of  $\det \Delta(\lambda) = 0$ . If  $\lambda$  is a characteristic root different from  $s(L)$  then  $\operatorname{Re} \lambda < s(L)$ . If  $L$  satisfies the hypotheses of Proposition 2.3 then  $s(L)$  is a simple root of  $\det \Delta(\lambda) = 0$ .

**Proof:** Consider  $A(\lambda)$  for real values of  $\lambda$ . For  $i \neq j$ , it follows from (3.3), (3.4) that  $A(\lambda)_{ij} \geq 0$ . Hence  $A(\lambda)$  is a matrix with nonnegative off diagonal elements. Similarly, if  $\lambda_1 \leq \lambda_2$ , then  $A(\lambda_2)_{ij} \leq A(\lambda_1)_{ij}$ . This is immediate from (3.3) and

(3.4) for  $i \neq j$ . For  $i=j$ , note  $A(\lambda)_{ii} = \eta_{ii}(0) - \eta_{ii}(0-) + \int_{-|r|}^0 e^{\lambda\theta} d\bar{\eta}_{ii}(\theta)$  and  $\bar{\eta}_{ii}$  is non-

decreasing so  $A(\lambda_2)_{ii} \leq A(\lambda_1)_{ii}$ . Thus we have that  $\lambda_1 \leq \lambda_2$  implies  $A(\lambda_2) \geq A(\lambda_1)$ .

Consider what happens as  $\lambda \rightarrow \infty$ . From (3.3) we have that

$\lim_{\lambda \rightarrow \infty} A_{ij}(\lambda) = \eta_{ij}(0) - \eta_{ij}(0-)$ , hence  $\lim_{\lambda \rightarrow \infty} A(\lambda) = A(\infty) = (\eta_{ij}(0) - \eta_{ij}(0-))$  and observe

$A(\infty)_{ij} \geq 0$   $i \neq j$ .

Let us write  $s(A(\lambda))$  for the stability modulus of the matrix  $A(\lambda)$ . Since for real  $\lambda$ ,  $A(\lambda)$  has nonnegative off diagonal elements, it is known that  $s(A(\lambda))$  is an eigenvalue of  $A(\lambda)$ . Furthermore, if  $\lambda_1 \leq \lambda_2$ ,  $A(\lambda_2) \leq A(\lambda_1)$  and so  $s(A(\lambda_2)) \leq s(A(\lambda_1))$ . It is also known that  $s(\cdot)$  is continuous, thus the map  $\lambda \rightarrow s(A(\lambda))$  is a nonincreasing continuous map from  $\mathbb{R}$  into itself which has a finite limit at  $+\infty$ . It follows that there exists a unique value of  $\lambda$ ,  $\lambda_0$ , for which  $s(A(\lambda_0)) = \lambda_0$ . We will show that  $s(L) = \lambda_0$ .

Since  $s(A(\lambda_0)) = \lambda_0$  and  $s(A(\lambda_0))$  is an eigenvalue of  $A(\lambda_0)$ , it follows that

$$\det(s(A(\lambda_0))I - A(\lambda_0)) = \det(\lambda_0 I - A(\lambda_0)) = 0$$

and hence  $\lambda_0$  is a characteristic root of (3.2). Assume  $\lambda$  is a real characteristic root of (3.2) so that  $\det(\lambda I - A(\lambda)) = 0$ . Then  $\lambda$  is an eigenvalue of  $A(\lambda)$  so  $\lambda \leq s(A(\lambda))$ . It follows that  $\lambda \leq \lambda_0$ . Indeed, if  $\lambda > \lambda_0$  then  $\lambda \leq s(A(\lambda)) \leq s(A(\lambda_0)) = \lambda_0 < \lambda$ . Thus  $\lambda_0$  is greater than or equal to any real characteristic root of (3.2).

Let  $T(t)\phi \equiv y_t(\phi)$  denote the solution of (3.2) with  $\phi \in C$ . Then  $T(t)(C^+) \subset C^+$  and  $T(t)$  is a compact linear operator for  $t \geq |r|$ . That is,  $\{T(t)\}_{t \geq 0}$  is a strongly continuous positive semigroup consisting of compact operators for  $t \geq |r|$ . Now if  $\rho(T(t))$  denotes the spectral radius then it is known that [6]

$$\rho(T(t)) = e^{t\mu}, \quad \mu = \max\{\operatorname{Re} \lambda : \det \Delta(\lambda) = 0\}.$$

On the other hand the set of characteristic roots is precisely the spectrum of the infinitesimal generator of  $\{T(t)\}$  (see [6]). It has been shown that  $\mu$  belongs to the spectrum of the generator of a strongly continuous positive semigroup, [5]. In particular,  $\mu$  is a characteristic root so  $\mu = \lambda_0$ .

Moreover, by Theorem 7.2 in [8, see also 17],  $\lambda_0$  is the only characteristic root  $\lambda$  satisfying  $\operatorname{Re} \lambda = \lambda_0$ .

Finally, if  $L$  satisfies the hypotheses of Proposition 2.3 then  $T(t)C_1^+$  belongs to the interior of  $C_1^+$  for  $t \geq (n+1)|r|$ . In this case  $\rho(T(t))$  is a simple

eigenvalue of  $T(t)$  and thus  $\lambda_0$  is a simple characteristic root [1]. This completes our proof of Theorem 3.1.

The proof of Theorem 3.1 yields much more than has been stated. In the next few remarks, we bring out other consequences of the proof.

Remark 1: There exists  $u \geq 0$  in  $R^n$  such that  $y(t) = ue^{s(L)t}$  satisfies the variational equation (3.2). This is an immediate consequence of the well known fact [2] that corresponding to  $s(A(\lambda_0)) (= s(L) = \lambda_0)$  there is a nonnegative eigenvector in  $R^n$ . If, in addition,  $L$  satisfies the hypotheses of Proposition 2.3, then one can take  $u > 0$ . Again, this follows from the fact that  $A(\lambda_0)$  is irreducible which in turn follows from (I) of the previous section.

Remark 2: The importance of the fact that  $s(L)$  is itself a characteristic root of (3.2) will be clear to anyone who has had experience in computing characteristic roots of FDE's -- even one dimensional equations. They are notoriously difficult to find. It is very important to be able to determine stability by only considering the real characteristic roots of (3.2).

Remark 3: The second assertion of Theorem 3.1 is especially important in the context of bifurcation theory. One naturally asks the question "how can a one parameter family of steady state of a parametrized family of FDE's lose stability at a critical value of the parameter?" According to Theorem 3.1, if the family consists of cooperative maps, the answer is that a real eigenvalue must change sign giving rise to a steady state bifurcation (generically) and an exchange of stability. In particular, although a Hopf bifurcation is not precluded for cooperative FDE's (see [21]), a steady state can never lose stability to a Hopf bifurcation. Put another way, a local Hopf bifurcating periodic solution cannot be asymptotically

stable (see also Theorem 4.2 of section 4).

The following result, a corollary to the proof of Theorem 3.1, provides a relatively simple test for stability and instability.

Corollary 3.2:  $s(L) < 0$  ( $s(L) > 0$ ) if and only if  $s(A(0)) < 0$  ( $s(A(0)) > 0$ ).  
Moreover  $s(A(0)) < 0$  if and only if

$$(-1)^j \begin{bmatrix} A(0)_{11} & \dots & A(0)_{1j} \\ \vdots & & \vdots \\ A(0)_{j1} & \dots & A(0)_{jj} \end{bmatrix} > 0, \quad j = 1, 2, \dots, n.$$

where  $A(0)_{ij} = \eta_{ij}(0)$ .

Proof: The second equivalence is well known [2]. Recall  $s(L) = \lambda_0$ , the unique root of  $\lambda - s(A(\lambda)) = 0$ . But  $\lambda \rightarrow \lambda - s(A(\lambda))$  is an increasing continuous function. Hence  $\lambda_0 < 0$  if and only if  $0 - s(A(0)) > 0$ , that is, if and only if  $s(A(0)) < 0$ . Similarly  $\lambda_0 > 0$  if and only if  $0 - s(A(0)) < 0$ .

Corollary 3.2 has an interest interpretation. It is saying that the zero solution of the linear FDE is asymptotically stable or unstable according as the zero solution of the linear ODE

$$Z' = A(0)Z$$

is asymptotically stable or unstable. Notice how  $A(0)$  is obtained:  $A(0)_{ij} = \eta_{ij}(0)$ ; the magnitude of the delays are completely ignored! There is an appealing way to look at  $A(0)$ , that is

$$A(0)v = L(\hat{v})$$

in other words,  $A(0)$  is the restriction of  $L$  to the constant functions. This observation leads to another interesting observation. Consider the nonlinear ordinary differential equation

$$(3.5) \quad x'(t) = F(x(t)), \quad F(x) = f(\hat{x}).$$

It is easy to see that (3.5) is cooperative in the sense of Hirsch [9] (see also [23]). The steady states of (3.5) and (3.1) are identical. Even more, the stability type of a steady state is the same for (3.5) as for (3.1)! One only need check that

$$DF(x) = df(\hat{x}) \frac{\partial \hat{x}}{\partial x} = df(\hat{x})(\hat{e}_1, \dots, \hat{e}_n) = A(0).$$

Hence as far as steady states and their stability goes, one can trade in a cooperative FDE for a cooperative ODE. The first person to see a connection between (3.5) and (3.1) appears to have been R.H. Martin [13]. He did not make the observation that steady states have the same stability type, however.

If  $L$  satisfies the hypotheses of Proposition 2.3 and  $s(L) > 0$  then by our earlier remark, there exists a solution of (3.2) of the form  $y(t) = ue^{s(L)t}$ ,  $u > 0$ . In terms of our state space  $C_r$ , this solution gives rise to a monotone orbit  $t \rightarrow y_t(\bar{u})$ ,  $t \in \mathbb{R}$ , of (3.2) where  $\bar{u} \in C_r^+$  is given by

$$(3.6) \quad \begin{aligned} \bar{u} &= (\bar{u}_1, \dots, \bar{u}_n) \\ \bar{u}_i(0) &= u_i e^{s(L)\theta}, \quad -r_i \leq \theta \leq 0. \end{aligned}$$

The orbit connects the trivial solution of (3.2) to  $\infty$ . This "most unstable" manifold for the variational equation should have a counterpart for the nonlinear equation (3.1). This is precisely the content of the next theorem.

**Theorem 3.3:** Let  $f$  be cooperative and irreducible. Suppose  $f(\hat{v}) = 0$ ,  $s = s(df(\hat{v})) > 0$  and suppose  $df$  is Lipschitz continuous in a neighborhood of  $\hat{v}$ . Suppose  $\hat{v} + C^+$  belongs to the domain of  $f$  and  $f$  is bounded on bounded subsets of  $U$ . Then there exists a unique  $C^1$  function  $y: [0, \infty) \rightarrow \hat{v} + C^+$  satisfying

- (1)  $y(\tau) = \hat{v} + \tau \bar{u} + o(\tau)$  as  $\tau \rightarrow 0$   
where  $\bar{u} > 0$  is as in (3.6).
- (2)  $x_t(y(\tau)) = y(e^{st}\tau)$ ,  $t \geq 0, \tau \geq 0$ .
- (3)  $0 \leq \tau_1 \leq \tau_2$  implies  $y(\tau_1) \leq y(\tau_2)$ .
- (4) Either (a)  $\lim_{\tau \rightarrow \infty} \|y(\tau)\| = \infty$  or (b)  $\lim_{\tau \rightarrow \infty} y(\tau) = \hat{w}$  where  $w \in \mathbb{R}^n$ ,  $w > v$  and,  $f(\hat{w}) = 0$  and  $s(df(\hat{w})) \leq 0$ .
- (5) If (4)(a) holds, then for all  $\phi \geq \hat{v}$ ,  $\phi \neq \hat{v}$ ,  $\|x_t(\phi)\| \rightarrow \infty$  as  $t$  tends to the right hand limit of the maximal interval of existence of  $x_t(\phi)$ . If (4)(b) holds, then for all  $\phi$ ,  $\hat{v} \leq \phi \leq \hat{w}$ ,  $\phi \neq \hat{v}$ ,  $x_t(\phi) \rightarrow \hat{w}$  as  $t \rightarrow \infty$ .

Theorem 3.3 says that the monotone curve  $\Gamma = \{y(\tau): \tau \geq 0\}$  is a heteroclinic orbit of (3.1) connecting the unstable steady state  $\hat{v}$  to the steady state  $\hat{w}$  (or  $\infty$ ). In addition, the steady state  $\hat{w}$ , if not asymptotically stable ( $s(df(\hat{w})) \leq 0$ ), at least attracts all initial conditions  $\phi$  different from  $\hat{v}$  with  $\hat{v} \leq \phi \leq \hat{w}$ . When  $\hat{w}$  in Theorem 3.3 exists, we will paraphrase Theorem 3.3 by simply saying that there exists a monotone increasing trajectory connecting  $\hat{v}$  to  $\hat{w}$ .

Actually, we have only stated half of the story. If  $\hat{v} - C^+$  belongs to the domain of  $f$  then one can find a monotone decreasing trajectory connecting  $\hat{v}$  to  $\hat{p}$  (or  $\infty$ ) with the obvious changes in (1)-(5) above.

The assumption that  $\hat{v} + C^+$  belongs to the domain of  $f$  can be significantly weakened. For example, if it is known that there exists a steady

state  $\hat{w}$  with  $w > v$  and  $[\hat{v}, \hat{w}]$  belongs to the domain of  $f$  then one can show that  $\Gamma \subset [\hat{v}, \hat{w}]$ .

The proof of Theorem 3.3 is very similar to the proof of Theorem 2.7 in [23] and uses Theorems 1.1 and 2.1 in [22]. Hence we will not give the proof here. It should be remarked that Matano [15,16] has stated a similar result, although requiring a second steady state  $\hat{w} \geq \hat{v}$  but less smoothness than we require.



#### 4. Strongly monotone local semiflows and FDEs.

In this section we state some very powerful results due to M.W. Hirsch [9-12] for monotone semi-flows which have direct application in our setting. We will not state these results in their greatest generality. Let  $X$  be a separable Banach space and  $K$  a cone in  $X$ , that is,  $K$  is a nonempty closed subset of  $X$  with the closure properties  $R^+ \cdot K \subset K$ ,  $K+K \subset K$  and  $K \cap (-K) = \{0\}$ . We assume that  $K$  has nonempty interior,  $K^0$ . We write  $x \leq y$  ( $x < y$ ) if and only if  $y-x$  belongs to  $K$  ( $K^0$ ). Let  $U$  be an open order convex subset of  $X$ . Let  $\Phi = \{\Phi_t\}_{t \geq 0}$  be a local semi-flow on  $U$  (see e.g. [11,16]), in particular, each  $\Phi_t$  is a continuous map on a subset  $U_t$  of  $U$  and the semigroup property  $\Phi_t \Phi_s = \Phi_{s+t}$  holds under appropriate conditions. We say that  $\Phi$  is a monotone flow if each  $\Phi_t$  is monotone:  $x, y \in U_t$  and  $x \leq y$  implies  $\Phi_t(x) \leq \Phi_t(y)$ ;  $\Phi$  is strongly monotone if each  $\Phi_t$  is strongly monotone:  $x \leq y$ ,  $x \neq y$ ,  $t > 0$  implies  $\Phi_t(x) < \Phi_t(y)$ .

As an example, consider a cooperative FDE defined on an order convex subset of  $C_r$ ,  $r \in R_+^n$ . Then  $X = C_r$  and the local semi-flow is given by  $\Phi_t \rightarrow x_t(\phi)$ . This semi-flow is monotone in the above sense. If  $f$  is cooperative and irreducible then  $\Phi_t$  is eventually strongly monotone but not strongly monotone. That is, there exists  $\tau > 0$  such that if  $x \leq y$ ,  $x \neq y$  then  $\Phi_t(x) < \Phi_t(y)$  for  $t \geq \tau$  (provided  $\Phi_t(x), \Phi_t(y)$  exist). For FDE's we may take  $\tau = (n+1)|r|$  by Theorem 2.5. Note that  $\tau$  is independent of  $x$  or  $y$ . The results of Hirsch which we state below for strongly monotone flows are true for what we term eventually strongly monotone flows (see also Matano [16]).

The first two results require only a monotone flow (See [11], Theorem 2.3 and Corollary 2.4.)

Theorem 4.1: Let  $x \in U$  be such that  $\phi^+(x) = \{\phi_t(x) : t \geq 0\}$  is compact in  $U$ . Assume for some real  $T > 0$ ,  $\phi_T(x) > x$  ( $\phi_T(x) < x$ ). Then  $\phi_t(x)$  converges to an equilibrium as  $t \rightarrow \infty$ .

Theorem 4.2: A monotone flow does not have an attracting periodic orbit.

By an equilibrium, we mean a point  $y \in U$  such that  $\phi_t(y) = y$  for all  $t \geq 0$ . By periodic orbit we mean a non-constant closed orbit. Such an orbit is attracting if it attracts an open set. It is not difficult to see that Theorem 4.1 implies Theorem 4.2.

The following results require the flow to be strongly monotone. For simplicity, we assume that the domain of  $\phi_t$  is  $U$  for every  $t \geq 0$  and that all orbits have compact closure in  $U$ . The following result is a special case of Theorems 5.2 and 5.5 in [11].

Theorem 4.3: Let  $S$  be a totally ordered subset of  $U$  and let  $E$  be the set of equilibria. Assume  $E$  consists of isolated points. Then the subset of points of  $S$ , the orbits of which do not converge to a point of  $E$ , is at most countably infinite.

In particular, Theorem 4.3 implies that a dense set of points of  $U$  have convergent orbits.

The following result of Hirsch [12] sharpens the conclusion of Theorem 4.3 at the expense, of course, of additional hypotheses. It does not require that  $X$  be separable though (see Theorem 10.1 in [12]).

Theorem 4.4: Let  $X_0$  be an open positively invariant set for  $(\phi_t)_{t \geq 0}$  and suppose  $X_0$  contains a compact attractor which attracts points of  $X_0$ . Assume  $E$  is a finite set. Then there is a dense open subset  $D_0$  of  $X_0$  consisting of "asymptotically stable" points  $x$  for which  $\omega(x) \subset E$ .

By  $\omega(x)$ , we mean that Omega limit set,  $\bigcap_{\tau \geq 0} \text{cl}(\bigcup_{t \geq \tau} \phi_t(x))$ , of the orbit

through  $x$ . A compact attractor  $K$  is a compact invariant set which attracts a neighborhood of itself. In Theorem 4.4, we assume  $\omega(x) \subset K$  for all  $x \in X_0$ . We remark that  $E \cap K$  is nonempty (see [11]).

We now make use of our remarks concluding section 2, together with Theorem 4.4 and Lemma 2.2 in [6].

Theorem 4.5: Assume (2.1) is cooperative and irreducible in  $U$  and that  $f$  maps bounded subsets of  $U$  to bounded subsets of  $\mathbb{R}^n$ . Assume that  $U$  is positively invariant for (2.1), there is a closed bounded subset  $B$  of  $U$  such that for all  $\phi \in U$ ,  $\omega(\phi) \subset B$  and the map  $\phi \rightarrow x_t(\phi)$  maps bounded sets to bounded sets for each  $t \geq 0$ . Then  $B$  contains a compact attractor which attracts points of  $U$ . If  $E$  is a finite set consisting of nondegenerate equilibria, then the union of the basins of attraction of the equilibria  $e$  with  $s(df(e)) < 0$  is an open dense subset of  $U$ .

Proof: By Lemma 2.2 in [6],  $B$  contains a compact attractor which attracts points of  $U$ . By Theorem 4.4, there is a dense open subset  $U_0$  of  $U$  consisting of asymptotically stable points  $\phi$  for which  $\omega(\phi) \subset E$ . But if  $\phi$  is an asymptotically stable point with  $\omega(\phi) = \{e\}$ ,  $e \in E$ , then necessarily  $s(df(e)) < 0$ . Hence  $U_0$  is a subset of the union of basins of attraction of equilibria  $e$  with  $s(df(e)) < 0$ .

## 5. An example

As an application of the ideas in the previous section we consider a mathematical model of biochemical feedback in protein synthesis developed by Goodwin [4] and which has been the object of much study [13,20,21,24]. We refer the interested reader to [4] for details concerning the model. The quantities  $x_1, x_2, \dots, x_n$  denote concentrations of mRNA ( $x_1$ ), various enzyme-intermediates ( $x_2, \dots, x_{n-1}$ ) and a final product protein ( $x_n$ ) in a sequence of first order reactions  $x_1 \rightarrow x_2 \rightarrow \dots \rightarrow x_n$ . The product protein is assumed to induce (positive feedback) the transcription of mRNA.

The equations derived from the model are given below as (5.1). In (5.1), we have used the notation  $x_{j,t}$  to denote the function  $x_{j,t}(\theta) = x_j(t+\theta)$ ,  $-r_j \leq \theta \leq 0$ .

$$(5.1) \quad \begin{aligned} x_1'(t) &= h(L_n x_{n,t}) - \alpha_1 x_1(t) \\ x_j'(t) &= L_{j-1} x_{j-1,t} - \alpha_j x_j(t), \quad 2 \leq j \leq n \end{aligned}$$

$$L_i \phi = \int_{-r_i}^0 \phi(\theta) d\eta_i(\theta)$$

$\eta_i : [-r_i, 0] \rightarrow \mathbb{R}$  is nondecreasing

$\eta_i(-r_i) = 0$ ,  $\eta_i(0) = 1$ ,  $\eta_i(\theta) > 0$  for  $\theta > -r_i$

$h : \mathbb{R}^+ \rightarrow \mathbb{R}^+$  is a smooth function with  $h'(u) > 0$  for  $u \geq 0$

$\alpha_i > 0$ ,  $1 \leq i \leq n$ .

R.H. Martin has considered equation (5.1) in the special case that  $h(u) = u/(1+u)$  and  $L_j \phi_j = \phi_j(-r_j)$  in [13]. We have borrowed techniques from Martin as well as from previous authors (e.g. Selgrade [20], Hirsch [10]) who have treated simpler versions of (5.1). Allwright [24] also treats a version of (5.1).

A brief word on the assumptions listed below (5.1) is appropriate. Concerning the integrators  $\eta_i$ , we set  $\eta_i(-r_i) = 0$  merely as a normalization (recall

$\eta_i$  and  $\eta_i + c$ ,  $c \in \mathbb{R}$ , give equivalent integrals). Our requirement that  $\eta_i(0) = 1$  can always be achieved by a scaling of the  $x_i$  and an appropriate redefinition of  $h$ . If our requirement that  $\eta_i(\theta) > 0$  for  $\theta > -r_i$  does not hold then  $\eta_i(\theta) = 0$  on some subinterval  $[-r_i, -s_i]$  and hence one could replace  $-r_i$  by  $-s_i$ . This assumption, given  $\eta_i(0) = 1$ , is thus without loss of generality. On the other hand, it is essential for the proper choice of state space, namely  $C_r$ ,  $r = (r_1, r_2, \dots, r_n) \geq 0$ , for (5.1) to be cooperative and irreducible. We require  $h'$  to be locally Lipschitz in order to apply Theorem 3.3.

We write the right hand side (5.1) as  $f(x_t)$  where

$$f(\phi) = \text{col}(h(L_n \phi_n) - \alpha_1 \phi_1(0), L_1 \phi_1 - \alpha_2 \phi_2(0), \dots, L_{n-1} \phi_{n-1} - \alpha_n \phi_n(0))$$

and  $f : C \rightarrow \mathbb{R}^n$ .

Since  $h$  and  $L_j$  are nondecreasing in their arguments,  $f$  satisfies (H), in fact,  $f$  is cooperative. Note that this would not be the case if  $-\alpha_i x(t - \tau_i)$  replaced  $-\alpha_i x(t)$ . In addition  $f$  satisfies the hypotheses of Proposition 1.2 so that the flow  $\phi \rightarrow x_t(\phi)$ ,  $t \geq 0$  leaves  $C^+$  positively invariant (so long as solutions are defined).

Our first task is to insure that solutions with nonnegative initial conditions are globally defined and to seek conditions for boundedness of these solutions. The following inequality will be useful.

$$(5.2) \quad \limsup_{u \rightarrow +\infty} \frac{h(u)}{u} = a < \infty.$$

**Lemma 5.1:** Suppose (5.2) holds. If  $\phi \in C^+$  then  $x(t, \phi)$  is defined for  $t \geq 0$  and  $x(t, \phi) \geq 0$ . If

$$(5.3) \quad a < \pi \alpha_i$$

then  $\Theta^+(\phi) = \{x_t(\phi) : t \geq 0\}$  has compact closure.

Proof: By (5.2) there exists  $b \geq 0$  such that  $h(u) \leq au+b$  for  $u \geq 0$ . Let  $g(u) = au+b$  and write  $x(t,\phi,h)$ ,  $x(t,\phi,g)$  for the solution of (5.1) and (5.1) with  $g$  replacing  $h$ , respectively. The solution  $x(t,\phi,g)$ ,  $\phi \in C^+$  is globally defined since it satisfies a linear FDE. By Proposition 1.1 and Proposition 1.2 we have  $0 \leq x(t,\phi,h) \leq x(t,\phi,g)$  on the maximal interval of existence of  $x(t,\phi,h)$ . Now  $f$  maps bounded subsets of  $C^+$  to bounded subsets of  $R^n$  so by Theorem 3.2 in [6],  $x(t,\phi,h)$  can fail to be globally defined only by becoming unbounded, a possibility that our inequality precludes. It follows that  $x(t,\phi,h)$  is defined for  $t \geq 0$ .

Now suppose (5.3) holds. The function  $x(t,\phi,g)$  satisfies a linear non-homogeneous equation which we write

$$(5.4) \quad Z'(t) = LZ_t + be_1$$

where  $L\phi = \text{col}(aL_n\phi_n - \alpha_1\phi_1(0), L_1\phi_1 - \alpha_2\phi_2(0), \dots, L_{n-1}\phi_{n-1} - \alpha_n\phi_n(0))$ . We will show that  $s(L) < 0$  by making use of Corollary 3.2. First we calculate  $A(0)$  (see (3.3))

$$(5.5) \quad A(0) = \begin{bmatrix} -\alpha_1 & 0 & \dots & 0 & a \\ 1 & -\alpha_2 & 0 & \dots & 0 \\ 0 & 1 & -\alpha_3 & 0 & \dots & 0 \\ \vdots & & & & & \\ 0 & \dots & & 0 & 1 & -\alpha_n \end{bmatrix}$$

Note that the subdiagonal of ones arises due to our normalization  $\eta_j(0) = 1$ . Now it is easy to check that the  $n$  principal minors of Corollary 3.2 have the correct sign if (5.3) holds. Hence the zero solution of the linear homogeneous equation  $Z'(t) = LZ_t$  is asymptotically stable. But this implies that the positive steady state  $x_n = b/(\alpha_1\alpha_2\dots\alpha_n - a)$ ,  $x_j = \alpha_{j+1}x_{j+1}$ ,  $j=1, \dots, n-1$ , of the nonhomogeneous equation (5.4) is globally attracting. The boundedness of  $x(t,\phi) = x(t,\phi,h)$  follows from the

comparison  $0 \leq x(t, \phi, h) \leq x(t, \phi, g)$ . The compactness of the orbit  $\vartheta^+(\phi)$  follows from the fact that it is bounded, that  $f$  maps bounded sets to bounded sets, and the Ascoli-Arzelà theorem.

We have observed that  $f$  is cooperative. In fact, it is cooperative and irreducible as we now show. For  $\psi \in C^+$ ,

$$df(\psi)\phi = \text{col}(\beta L_n \phi_n - \alpha_1 \phi_1(0), L_1 \phi_1 - \alpha_2 \phi_2(0), \dots, L_{n-1} \phi_{n-1} - \alpha_n \phi_n(0))$$

$$\beta = \beta(\psi) = h'(L_n \psi_n) > 0.$$

In order to check (I), we need to show that the matrix  $A(df(\psi))$  is irreducible for each  $\psi \in C^+$ . But  $A(df(\psi))$  is identical to the matrix  $A(0)$  in (5.5) except that  $a = \beta(\psi)$ . Hence  $A(df(\psi))$  is irreducible if and only if  $\beta(\psi) = h'(L_n \psi_n) > 0$ .

Consider the requirement (R) ( $t_0=0$ ). Let  $\phi \in C^+$ ,  $\phi \notin \text{Ker } R$  and  $\phi(0)=0$ . Then for some  $j$  and some  $\theta_0 \in (-r_j, 0]$ ,  $\phi_j(\theta_0) > 0$ . Set  $i=j+1$  where we agree that  $n+1=1$  and set  $\tau = r_j + \theta_0 \geq 0$ . Note that both  $i$  and  $\tau$  depend only on  $\phi$  and not on

$\psi$ . If  $j < n$  then  $df(\psi)_i(S(\tau)\phi) = L_j(S(\tau)\phi) = \int_{-r_j}^0 (S(\tau)\phi)_j(\theta) d\eta_j(\theta)$ , where

$(S(\tau)\phi)_j(-r_j) = \phi_j(\theta_0) > 0$ . Since we assumed  $\eta_j(\theta) > \eta_j(-r_j) = 0$  for  $\theta > -r_j$ , it follows that the integral is positive since the support of  $(S(\tau)\phi)_j$  and the support of  $d\eta_j$  overlap. If  $j=n$  and  $\beta(\psi) > 0$ , a similar calculation shows  $df(\psi)_1(S(\tau)\phi) > 0$ .

We have proved the following

**Lemma 5.2:**  $f$  is cooperative and irreducible in  $C^+$ .

We now turn to the question of existence and stability of steady states of (5.1). We assume that (5.3) holds. The steady states of (5.1),  $\hat{x}$ ,  $x \in R_+^n$  are solutions of

$$h(x_n) = \alpha_1 x_1$$

$$x_{j-1} = \alpha_j x_j, \quad 2 \leq j \leq n.$$

and are in one-to-one correspondence with solutions of

$$h(x_n) - \alpha_1 \alpha_2 \dots \alpha_n x_n = 0, \quad x_n \geq 0.$$

We assume that

$$(5.6) \quad 0 \text{ is a regular value of } q(u) \equiv h(u) - \alpha_1 \dots \alpha_n u.$$

It follows from (5.3) and (5.6) that there exists at least one steady state and there are finitely many steady states. Moreover, the steady states are totally ordered

$$\hat{x}^1 < \hat{x}^2 < \dots < \hat{x}^m.$$

The stability of  $\hat{x}^i$  depends, according to Corollary 3.2, on the stability of the matrix

$$A_i = \begin{bmatrix} -\alpha_1 & 0 & \dots & 0 & h'(x_n^i) \\ 1 & -\alpha_2 & 0 & \dots & 0 \\ 0 & 1 & -\alpha_3 & 0 & \dots & 0 \\ \vdots & & & & \\ 0 & \dots & 0 & 1 & -\alpha_n \end{bmatrix}$$

The principal minors alternate in sign as in Corollary 3.2 if and only if  $h'(x_n^i) < \alpha_1 \dots \alpha_n$ . The reverse inequality implies  $s(A_i) > 0$  as is easy to check. We have proved part of the following

**Theorem 5.3:** Assume (5.3) and (5.6) hold. Then  $\hat{x}^m, \hat{x}^{m-2}, \hat{x}^{m-4}, \dots$  are asymptotically stable and  $\hat{x}^{m-1}, \hat{x}^{m-3}, \dots$  are unstable. There exists a monotone increasing orbit connecting  $\hat{x}^{m-1}$  to  $\hat{x}^m$  and a monotone decreasing orbit connecting  $\hat{x}^{m-1}$  to  $\hat{x}^{m-2}$ . An identical assertion holds for the other unstable steady states  $\hat{x}^{m-3}, \dots$ .



Proof: (5.3) and (5.6) imply that  $h'(x_n^m) - \alpha_1 \dots \alpha_n < 0$ , thus  $\hat{x}^m$  is asymptotically stable. By (5.6) the sign of  $h'(x_n^i) - \alpha_1 \dots \alpha_n$  must alternate with  $i$ . The existence of connecting orbits follows from Theorem 3.3.

The main result of this section follows. We write  $B(\hat{x}^i)$  for the domain of attraction of  $\hat{x}^i$ ,  $i=m, m-2, m-4, \dots$ . That is,  $B(\hat{x}^i) = \{\phi \in C^+ : \omega(\phi) = \{\hat{x}^i\}\}$ .

Theorem 5.4: Assume (5.3) and (5.6) hold. Then  $[0, \hat{x}^m]$  attracts all orbits of (5.1) with  $\phi \in C^+$ . If  $m=1$  then  $B(\hat{x}^1) = C^+$ . If  $m > 1$ , then  $\bigcup_{j \geq 0} B(\hat{x}^{m-2j})$  is open and

dense in  $C^+$ .

Proof: In Lemma 5.1 we showed that every orbit has compact closure in  $C^+$  and in fact is attracted to a bounded subset of  $C^+$ , namely, to  $[0, \hat{y}]$  where  $y \in R^n$  is the equilibrium of the linear inhomogeneous comparison equation. Hence the hypotheses of Theorem 4.5 are satisfied. We only need to verify the conclusion  $B(\hat{x}^1) = C^+$  when  $m=1$ . We first observe that  $\hat{x}^1 + C^+$  belongs to  $B(\hat{x}^1)$ . In fact, if  $\phi \geq \hat{x}^1$  then there exists  $\psi$  with  $\hat{x}^1 \leq \phi < \psi$  such that  $\psi \in B(\hat{x}^1)$  (use Theorem 4.4 or Theorem 4.5). But then  $\phi \in B(\hat{x}^1)$  since  $\hat{x}^1 \leq x_t(\phi) \leq x_t(\psi)$  for  $t \geq 0$ . Similarly, if  $\phi \in C^+$  and  $\phi \leq \hat{x}^1$  then  $\phi \in B(\hat{x}^1)$ . Hence, if  $\phi \in C^+$  there exist  $\phi_1, \phi_2 \in B(\hat{x}^1)$  with  $\phi_1 \leq \phi \leq \phi_2$  and hence  $\phi \in B(\hat{x}^1)$ . This completes our proof.

One might conjecture that every orbit of (5.1) with nonnegative initial condition converges to an  $\hat{x}^i$  even when  $m > 1$ . However, this is, in general, false. There can be periodic orbits of (5.1), necessarily unstable (Theorem 4.2). Indeed, Selgrade [21] has shown for the ODE version ( $L_j x_{j,t} = x_j(t)$ ) of (5.1)

that a Hopf bifurcation can occur at an unstable steady state.

It is worth mentioning that by Theorem 4.5, (5.1) possesses a compact attractor in  $[0, \hat{x}^m] \subset C^+$ . This compact attractor,  $J$ , is invariant and connected. Of course, when  $m=1$ ,  $J = \{\hat{x}^1\}$ , but if  $m > 1$  then  $J$  consists of the equilibria, their connecting orbits described in Theorem 5.3, and the unstable manifolds of the equilibria  $\hat{x}^{m-1}, \hat{x}^{m-3}, \dots$ . Any exotic, but necessarily unstable, dynamics together with its attracting set must be connected in  $J$  by the unstable manifolds of the unstable equilibria.

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