

ORDINARY DIFFERENTIAL EQUATIONS WITH STAR STRUCTURE

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ABSTRACT. We consider sets of differential equations with quadratic force terms that have a structure that can be diagrammed on star polygons. These can be seen as complementary equations to the "well-known replicator equations used, for example, to study " *hypercycles*. Where as the hypercycle equations describe systems in which interactions between components contribute to the "replication of components, the equations studied in this paper" correspond to systems in which such interactions catalyze the transformation of one component into another. Both similarities and differences to hypercycles are noted. Equilibrium manifolds are determined and their stability is studied. It turns out that equilibrium manifolds for these equations are sometimes unstable or neutrally stable when the corresponding hypercycle equilibrium manifolds are stable. In cases where equilibrium manifolds are stable there are interesting structures that are exhibited in the specific cases analyzed.

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1. INTRODUCTION

The importance of molecular interaction cycles in biological systems is well known. The ATP cycle, for example, has been extensively mapped as it provides the basis for energy exchange in metabolism [1]. In the early 1970's the idea of a hypercycle was introduced [2,3,4,5] as a means of explaining pre-Darwinian molecular evolution. A hypercycle consists of a set of n self-replicating units with the property that the replication of unit i is

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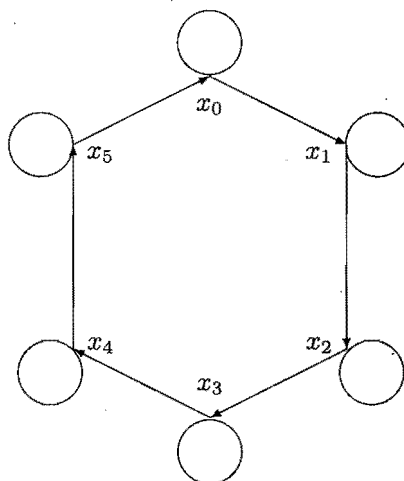


FIGURE 1. Simple Hypercycle on Six Variables

catalyzed by the presence of unit $i - 1$, and perhaps other units as well. The system is closed into a cycle by taking unit indices $\text{mod } (n)$.

In the abstract, a hypercycle on n replicators can be schematically represented by a directed graph with n vertices. Each vertex is labeled by one of the replicators, and if there is an edge directed from vertex i to vertex j it is labeled with a rate constant indicating the degree to which replicator i acts to catalyze the reproductive rate of replicator j . Since each unit is self-replicating, there is a loop at each vertex as well. Figure 1 shows the graph representing a simple hypercycle on 6 replicators.

Hypercycle behavior is then modelled by sets of differential equations of

$$\begin{aligned}
 \dot{x}_i &= x_i [f_i(\underline{x}) - \bar{f}(\underline{x})] \\
 \bar{f}(\underline{x}) &= \frac{1}{\sqrt{n}\nu} \sum_{j=0}^{n-1} x_j f_j(\underline{x}) \\
 \sqrt{n}\nu &= \sum_{i=0}^{n-1} x_i, \quad 0 \leq i < n,
 \end{aligned}
 \tag{1.1}$$

where $x_i \geq 0$ is the concentration of replicator species i . These equations have been called replicator equations [6]. The $\bar{f}(\underline{x})$ term is included as a "dilution flux" in order to maintain a constant overall concentration.

In addition to providing models of hypercycles in molecular evolution, replicator equations of the form (1.1) have many other applications. As indicated in [6], they have been used in sociobiology to model the evolution of behavioral phenotypes. They are also a continuous version of the selection equations of population genetics, and under a simple transformation they become the well known Lotka-Volterra equations of mathematical ecology. More recently, they have also been considered as models of oscillatory behavior in neural networks [7].

In the case of simple hypercycles, equations (1.1) are written as [2]:

$$(1.2) \quad \dot{x}_i = k_i x_i + k'_i x_i x_{i-1} - \frac{x_i}{\sqrt{nv}} \sum_{j=0}^{n-1} (k_j x_j + k'_j x_j x_{j-1})$$

with all indices taken mod (n) . Total concentration is a constant of motion:

$$(1.3) \quad \sum_{i=0}^{n-1} x_i = \sqrt{nv} = \text{constant}.$$

A comprehensive analysis of the fixed point behavior of equations (1.2) is provided by Eigen & Schuster [2] for the case in which all rate constants are equal. Restricting consideration to the concentration simplex

$$(1.4) \quad x_i \geq 0, \quad \sum_{i=0}^{n-1} x_i = \sqrt{nv}$$

they find that there is a stable fixed point at the center

$$(1.5) \quad x_i = \frac{v}{\sqrt{n}},$$

and there are n fixed points at its vertices. In addition, there may be higher dimensional equilibrium manifolds on the edges and faces of this simplex.

More generally, the functions f_i in equation (1.1) are taken as multinomials in the components of the concentration vector $\underline{x}$:

$$(1.6) \quad f_i(\underline{x}) = k_i + \sum_{j=0}^{n-1} A_{ij} x_j + \sum_{j,k=0}^{n-1} A_{ijk} x_j x_k + \dots$$

In most cases, only the linear terms in this expansion are retained. With this assumption, equation (1.1) becomes

$$(1.7) \quad \dot{x}_i = k_i x_i + x_i \sum_{j=0}^{n-1} A_{ij} x_j - \frac{x_i}{\sqrt{nv}} \sum_{j=0}^{n-1} \left[k_j x_j + \sum_{k=0}^{n-1} A_{jk} x_j x_k \right]$$

The constants k_i are growth rates, describing the increase of species i due to self-replication. The entries A_{ij} of the interaction matrix A describe the influence of species j on the replication of species i . In the case of a hypercycle $A_{ij} \geq 0$ and the interpretation of equation (1.7) is that it describes n self-replicating units joined in a closed cycle with species j helping to catalyze the replication of species i whenever $A_{ij} \neq 0$. Thus, in addition to the self-replication and catalytic terms, the negative dilution flux is required to maintain a constant total concentration. Thus, systems described by hypercycle models have the following general properties:

- A. All catalytic interactions influence replication rather than transformation. No term in equation (1.7) represents a case in which species j catalyzes the transformation of another species to species i , or vice versa.
- B. All catalytic interaction coefficients are positive, hence excitatory. In application to neural nets, this means that the dilution flux is to be interpreted as an inhibitory background, determined by the total activity of the neural assembly being modeled.

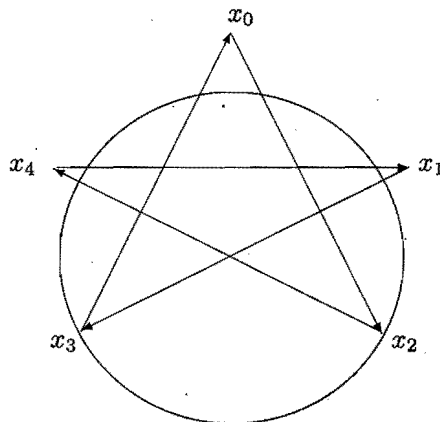


FIGURE 2. (5,2)-Star Representing Interaction Terms in Equation 1,10.

In the present paper, some simple systems of equations lacking these two properties are considered. In the equations to be studied, there are no self-replication terms. All direct catalytic interactions are inhibitory, catalyzing transformations rather than replication. As a result, no dilution flux is required. Such systems could model, for example, inhibitory interactions in a system residing in an ambient excitatory background.

The basic equations considered have the form

$$(1.8) \quad \dot{x}_i = -x_i x_{i-s} + x_{i-1} x_{i-s-1}$$

with all indices taken mod (n) . These equations can also be written in the form

$$(1.9) \quad \dot{\underline{x}} = \underline{x}^T \cdot (\sigma \otimes \sigma^{n-s-1} - \sigma^s \otimes I) \cdot \underline{x},$$

where $\sigma(x_0, \dots, x_{n-1}) = (x_{n-1}, x_0, \dots, x_{n-2})$ is the shift on indices of $\underline{x}$.

Equations of the form (1.8) or (1.9) will be said to have star structure. That is, their quadratic terms can be read off from the (n, s) -star polygon inscribed in a circle. For example, if $(n, s) = (5, 2)$ then equations (1.8) become

$$(1.10) \quad \begin{aligned} \dot{x}_0 &= -x_0 x_3 + x_2 x_4 \\ \dot{x}_1 &= -x_1 x_4 + x_0 x_3 \\ \dot{x}_2 &= -x_0 x_2 + x_1 x_4 \\ \dot{x}_3 &= -x_1 x_3 + x_0 x_2 \\ \dot{x}_4 &= -x_2 x_4 + x_1 x_3, \end{aligned}$$

and the pattern of interactions is schematically represented by the $(5, 2)$ -star polygon shown in Figure 2.

For a (n, s) -star inscribed in a circle σ^{-1} is the left shift so that $\sigma \underline{x}$ corresponds to a clockwise shift around the circle, corresponding to the transformation $x_i \rightarrow x_{i+1}$. The shift around the inscribed star is given by $\sigma^{-s} \underline{x}$. The connectivity of the complete graph is then described by numbers a and b such that $\sigma^{-a-sb} = I$, or equivalently, $\sigma^{sb} = \sigma^{-a}$.

Taking $\gcd(n, s) = d$, these numbers are the integer solutions of

$$(1.11) \quad \begin{aligned} a + sb &= rn, & 0 \leq a, b \leq n \\ 1 \leq s &< \left\lfloor \frac{n}{2} \right\rfloor \\ 1 \leq r &\leq \frac{s}{d}. \end{aligned}$$

If $d > 1$, equations (1.8) and (1.9) can be considered as representing d identical coupled subsystems, each represented by a $(n/d, s/d)$ -star. The $(5, 2)$ -star of Figure 2, on the other hand, represents a situation in which a single system supports two coupled cycles with state transitions in either cycle directly catalyzed by a state transition in the other cycle. (In Figure 2, for example, x_3 catalyzes the transition $x_0 \rightarrow x_1$ and x_1 then catalyzes the transition $x_3 \rightarrow x_4$.) For arbitrary n this kind of coupling requires that if x_{i-s} catalyzes the transition $x_i \rightarrow x_{i+1}$ then x_{i+1} must catalyze the transition $x_{i-s} \rightarrow x_{i-s+1}$ and this requires that $i+1 = i-2s \pmod{n}$, or equivalently $2s = n-1$. Thus, this pattern of interactions is only found in $(n, \frac{n-1}{2})$ -stars with n odd.

2. DETERMINATION OF EQUILIBRIUM MANIFOLDS

For determination of equilibrium manifolds, equations (1.8) will be embedded in a more general system of equations exhibiting what will be called weighted star structure.

$$(2.1) \quad \dot{x}_i = -k_i x_i x_{i-s} + k_{i-1} x_{i-1} x_{i-s-1} \quad k_j > 0$$

This corresponds to labelling the edge from vertex x_{j-s} to vertex x_j with a rate constant k_j . It is easy to verify that the total concentration remains constant so that equation (1.3) remains valid.

There are two distinct types of equilibria for equations (2.1). The first will be called the *central equilibrium* since it corresponds to the stable fixed point of equation (1.5). It turns out, however, that this equilibrium may no longer be point-like, and may not be stable. The second type of equilibrium is obtained by finding minimal subsets E of $\{0, \dots, n-1\}$ such that $\dot{x}_i = 0$ for all i if $x_j = 0$ when $j \in E$. Determination of the subsets E is equivalent to finding maximally independent sets of vertices in the (n, s) -star [8]. If $V(n, s)$ is the (n, s) -star vertex set and D is a maximally independent subset of $V(n, s)$ then setting $x_j = 0$ for $x_j \in V \setminus D$ yields an equilibrium manifold of dimension $|D| - 1$. Equilibrium manifolds determined by this procedure are independent of the values of the rate constants k_i . Because they are determined by setting subsets of the x_i to zero, they lie on edges or faces of the concentration simplex. The number of such equilibrium manifolds depends on the number of distinct maximally independent subsets of $V(n, s)$. Table 1 gives an enumeration of the equilibrium manifolds for $3 \leq n \leq 16$.

The central equilibrium is obtained from equations (2.1). Setting $\dot{x}_i = 0$ for all i , the star structure of these equations allows substitutions of the form $k_j x_j x_{j-s} = k_{j-1} x_{j-1} x_{j-s-1}$ and this can be iterated until one of the x variables can be divided out. This procedure yields:

Lemma 1. *The central equilibrium for quadratic ODE's with star structure (n, s) is given by*

$$(2.2) \quad x_i = \frac{k_{i+2s}}{k_{i+s}} x_{i+2s}$$

TABLE 1. Numbers of Equilibrium Manifolds Other Than Central Equilibrium ($n(p, q)$ indicates n distinct cases in which there are p equilibrium manifolds of dimension q)

(n,s)	1	2	3	4	5	6	7
3	(3,0)						
4	(2,1) (1,1)						
5	(5,1)	(5,1)					
6	(2,2) (3,1)	(3,1) (6,1)					
7	(7,2)	(7,2)	(7,2)				
8	(2,3) (8,2)	(4,3)	(2,3) (8,2)				
9	(9,3) (3,2)	(9,3) (3,2)	(3(9,2)	(9,3) (3,2)			
10	(2,4) (10,3) (5,3)	2(10,3) (5,3)	(10,4) (10,3) (5,3)	2(10,3) (5,3)			
11	(11,4) (11,3)	(11,4) (11,3)	(11,4) (11,3)	(11,4) (11,3)	(11,4) (11,3)		
12	(2,5) 2(12,4) (3,3)	(4,5) (12,4) (6,3) (3,3)	(6,5) (2,5)	6(12,3) (6,3) (3,3)	(2,5) 2(12,4) (3,3)		
13	(13,5) 2(13,4)	(13,5) 2(13,4)	(13,5) 2(13,4)	(13,5) 2(13,4)	(13,5) 2(13,4)	(13,5) 2(13,4)	
14	(2,6) 2(14,5) (7,5) (14,4)	3(14,5) (7,5)	(2,6) (14,5) (7,5) 2(14,4)	3(14,5) (7,5)	(2,6) (14,5) (7,5) (14,4)	4(14,5) (7,5)	
15	(15,6) 3(15,5) (5,5) (3,4)	(15,6) 3(15,5) (5,5) (3,4)	7(15,5) (5,5)	(15,6) 3(15,5) (3,4)	15(15,4)	7(15,5)	(15,6) 3(15,5) (5,5) (3,4)
16	(2,7) 3(16,6) 2(16,5) (8,5)	(4,7) 2(16,6) 4(16,5)	(2,7) 3(16,6) 2(16,5) (8,5)	2(8,7)	(2,7) 2(16,6) 3(16,5) (8,5)	(4,7) 2(16,6) 4(16,5)	(2,7) 3(16,6) 2(16,5) (8,5)

Equation (2.2) can be written in matrix form as $x = Ax$ where A is given by

$$(2.3) \quad A_{ij} = \begin{cases} \frac{k_{i+2s}}{k_{i+s}}, & j = i + 2s \\ 0, & \text{otherwise.} \end{cases}$$

By construction, it must be true that $A^n = I$ for every (n, s) -star. If n is even and $\gcd(n, s) = 1$ this leads to a constraint on the possible values of the rate constants.

Theorem 1. *Let n be even with $\gcd(n, s) = 1$. There exists a central equilibrium for equations (2.1) if and only if*

$$(2.4) \quad \prod_{r=1}^{\frac{n}{2}-1} k_{2r} = \prod_{r=1}^{\frac{n}{2}} k_{2r-1}$$

Further, if this is the case, the equilibrium manifold has dimension one and is structurally unstable.

Proof: The result follows by demonstration that under the stated conditions

$$(2.5) \quad [A^{\frac{n}{2}}]_{ij} = \begin{cases} 0, & i \neq j, \\ \frac{\prod_{r=1}^{\frac{n}{2}-1} k_{2r}}{\prod_{r=1}^{\frac{n}{2}} k_{2r-1}}, & i = j, j \text{ even}, \\ \frac{\prod_{r=1}^{\frac{n}{2}} k_{2r-1}}{\prod_{r=1}^{\frac{n}{2}-1} k_{2r}}, & i = j, j \text{ odd}. \end{cases}$$

This result is obtained from equations (2.2) and (2.3) by observing that since $2s$ is even, the non-zero entry $A_{0,2s}$ of A will be in an even column. Hence in computing powers A^m of A , this entry will always end up multiplying the unique non-zero entry from an even row of A^{m-1} . Further, the result will occur in some other even column, in the position $A_{0,2r}$ of A . Since $\gcd(n, s) = 1$, the smallest r such that $2rs = 0 \pmod{n}$ is $r = n/2$. Thus it will require $m = n/2$ multiplication's for this non-zero entry to appear in the A_{00} position, and the product obtained will have the form

$$\frac{\prod_{r=1}^{\frac{n}{2}-1} k_{2r}}{\prod_{r=1}^{\frac{n}{2}} k_{2r-1}}.$$

This same form will appear in $[A^{n/2}]_i$, whenever i is even, while if i is odd a similar line of reasoning leads to the reciprocal of this form.

Thus, if equation (2.4) is not satisfied then there is no consistent set of x_i that can satisfy equation (2.2) so that no central equilibrium exists. On the other hand, if equation (2.4) is satisfied then there is a central equilibrium, but it is clearly structurally unstable since a change in the value of any of the k_i which leads to the failure of equation (2.4) will destroy this equilibrium.

Equation (1.3) leads to the further conclusion that the equilibrium manifold must have dimension one. For $1 \leq m < n/2$ let $[A^m]_{j0}$ be the non-zero entry of the 0-th column of A^m . But this quantity is 0 for all odd j , while for every even j there will be a unique value $m(j)$ of m such that $[A^{m(j)}]_{j0} \neq 0$. Thus if j is even there is an $m(j)$ such that $x_j = [A^{m(j)}]_{j0} x_0$. Likewise, $[A^{m(j)}]_{j1} = 0$ for all even j , and for odd j , there is a unique $m(j)$ such that $x_j = [A^{m(j)}]_{j1} x_1$. Making these substitutions into equation (1.3) yields

$$(2.6) \quad x_0 \sum_{j \text{ even}} [A^{m(j)}]_{j0} + x_1 \sum_{j \text{ odd}} [A^{m(j)}]_{j1} = \sqrt{nv}$$

where the sums in each case are taken over the appropriate $m(j)$ values. This indicates, however, that the equilibrium manifold will have dimension one. $\square$

The central equilibrium will be a point equilibrium if equation (2.2) can be used to express all x_j in terms of x_i for some fixed value of i . Without loss of generality, this can be taken as x_0 .

For $\gcd(n, s) = d$, let $S(i) = \{j = i + 2rs \pmod{n} \mid 1 \leq r \leq \lceil \frac{n-1}{2d} \rceil\}$.

That is, $S(i)$ contains those indices labelling vertices of the (n, s) -star, together with their corresponding rate constants, obtained by starting at vertex x_i and proceeding along the directed edges in moves of length two until either vertex x_{i-s} ($\frac{n}{d}$ odd) or vertex x_{i-2s} ($\frac{n}{d}$ even) are reached.

Lemma 2. . Let $p_i = \prod_{r \in S(i)} k_r$ and take $1 \leq m < n/d$. Then for $j = i \pmod{d}$, if $[A^m]_{ij} \neq 0$,

$$(2.7) \quad [A^m]_{ij} = \begin{cases} \frac{p_i}{p_{i-s}} & \frac{n}{d} \text{ even} \\ \frac{p_i}{p_j} & \text{otherwise} \end{cases}$$

Proof: By equation (2.2), for any m

$$(2.8) \quad x_i = \frac{\prod_{r=1}^m k_{i+2rs}}{\prod_{r=1}^m k_{i+(2r-1)s}} x_{i+2rs}.$$

Hence the matrix element $[A^m]_{i0}$ will be non-zero if m is such that $i + 2ms \equiv 0 \pmod{n}$, and if this is so then $x_i = [A^m]_{i0} x_0$. If there is such an m then for $i \neq 0$, $m \leq (n-1)/d$. In addition, the k_j appearing in the numerator and denominator of equation (2.8) can be read off from the labelled (n, s) -star by starting at vertex i and proceeding along edges in moves of length two. For the numerator, the label of the second edge of each move is included (corresponding to k_{i+2rs} , $1 \leq r \leq m$), and for the denominator the label of the first edge of each move is included (corresponding to $k_{i+(2r-1)s}$).

If n/d is odd then, after $\lceil \frac{n-1}{2d} \rceil$ moves this process will have reached the vertex labelled x_{i-s} while if n/d is even the process will have reached the vertex labelled x_{i-2s} .

In the first case, the process returns to x_i after half a move, so in this and the following moves the edge labels selected for numerator and denominator are interchanged. If the process continues for the full $\lceil \frac{n-1}{d} \rceil$ moves then the second $\lceil \frac{n-1}{2d} \rceil$ edge labels in the numerator are identical to the first $\lceil \frac{n-1}{2d} \rceil$ in the denominator while the final $\lceil \frac{n-3}{2d} \rceil$ edge labels in the denominator are equal to the first $\lceil \frac{n-3}{2d} \rceil$ edge labels of the numerator.

There are three cases to consider. We first assume that $d = 1$. The more general case will be considered later.

Case 1: $m = \lceil \frac{n-1}{2d} \rceil$. In this case there are no common edge labels between numerator and denominator. Further, the numerator is by definition p_i , and since $i + 2ms \equiv 0 \pmod{n}$, $i = s$. Hence vertex x_i is half a move from vertex x_0 so that the denominator equals p_0 .

Case 2: $\lceil \frac{n-1}{2d} \rceil < m \leq \lceil \frac{n-1}{d} \rceil$. Now the first $\lceil \frac{n-1}{2d} \rceil$ edge labels from the numerator yield p_i while the final $\lceil \frac{n-1}{2d} \rceil$ edge labels in the denominator will equal p_0 . The remaining edge labels in numerator and denominator will cancel. Note, however, that there may in this case be common edge labels in numerator and denominator.

Case 3: $1 \leq m < \lceil \frac{n-1}{2d} \rceil$. In this case the product appearing in the numerator of $[A^m]_{i0}$ will be an incomplete portion of p_i . This can be changed to p_i by continuing another $\lceil \frac{n-1}{2d} \rceil - m$ moves, while multiplying the denominator by the same k_j terms that this continuation

adds to the numerator. What remains to be shown is that the new denominator is just p_0 . Since this process of extension begins at x_0 , these additional terms are clearly a portion of p_0 . That the initial m terms of the denominator provide the remaining elements of the product p_0 follows from the equation $i + 2ms \equiv 0 \pmod{n}$, and the form of the denominator in equation (2.8). In the present case, this denominator will have the form $k_{i+s}k_{i+3s} \dots k_{i+(2m-1)s}$. But in general, $i + 2ms$ can be written as $i + (2r-1)s + (2m-2r+1)s$ and thus $i + (2r-1)s = n - (2m-2r+1)s$ with $1 \leq r \leq m$. For $r = m$ this yields $i = n - s$, with the corresponding final element k_{n-s} of p_0 . Likewise, for $r = m-1$ this yields the penultimate element k_{n-3s} of p_0 , and so on until $r = 1$. That is, the initial m elements in the denominator are the final m elements of p_0 .

If $d > 1$ then $(n, s) = d(a, b)$ with a odd and $\gcd(a, b) = 1$. Thus the situation reduces to a set of $d(a, b)$ -stars with the only difference from previous considerations being that for $j \equiv i \pmod{d}$ the matrix element $[A^m]_{i0}$ is replaced by $[A^m]_{ij}$. Again this leads to the second part of equation (2.7).

What remains is to consider the case in which n/d is even. Now the process returns from x_{i-2s} to x_i after $\lceil \frac{n-1}{2d} \rceil + 1$ moves. Thus,

$$A^{\lceil \frac{n-1}{2d} \rceil + 1} = 1$$

and the situation has reduced to a set of $d(a, b)$ -stars with a even. To each of these stars, the conclusions of Theorem 1 apply: there are constraints imposed on the k_i for each of these stars, and the x_i on any one such star are not expressible in terms of a single x_i on that star. Therefore, all that can be said is that the denominator of equation (2.8) has the form p_{i-s} . $\square$

For cases in which n/d is even, Theorem 1 and Lemma 2 imply that the central equilibrium manifold has dimension $2d-1$ and is structurally unstable. If n/d is odd the central equilibrium is a point and is structurally stable with respect to equations (2.1). The location of this equilibrium is obtained by use of equations (2.7) and (1.3) to obtain

$$\sum_{j=0}^{d-1} x_j \sum_{r=0}^{\frac{n}{2}-1} [A^{m(r)}]_{j+rd,j} = \sqrt{nv},$$

$$(2.9) \quad m(r) = \left(\frac{an-1}{2s} \right) r,$$

where a is the smallest number such that the coefficient of r is an integer.

If $d = 1$ this simplifies to

$$(2.10) \quad x_0 \sum_{r=0}^{n-1} [A^{m(r)}]_{r0} = \sqrt{nv},$$

which by equation (2.7) yields

$$(2.11) \quad x_0 = \frac{\sqrt{np_0v}}{\sum_{r=0}^{n-1} p_r},$$

(2.11) from which the remaining x_i can be seen to be

$$(2.12) \quad x_i = \frac{\sqrt{np_i v}}{\sum_{r=0}^{n-1} p_r}.$$

If $d > 1$ then use of equations (2.7) and (2.9) yields

$$(2.13) \quad \sum_{j=0}^{d-1} x_j \sum_{r=0}^{\frac{n}{d}-1} \frac{p_{j+rd}}{p_j} = \sqrt{n}v.$$

In this case a further reduction is possible through use of the equilibrium versions of equations (2.1). These can be written as

$$k_i x_i x_{i-s} = k_{i-1} x_{i-1} x_{i-s-1}.$$

With $(n, s) = d(a, b)$ and for all j , x_j and x_{j-s} lie on the same (a, b) -star. Thus, equation (2.7) can be used in these equilibrium equations to express x_{i-s} and x_{i-s-1} in terms of x_i and x_{i-1} . This gives the equations

$$(2.14) \quad \frac{k_i p_{i-s}}{p_i} x_i^2 = \frac{k_{i-1} p_{i-s-1}}{p_{i-1}} x_{i-1}^2$$

and since $x_j > 0$ for all j this gives

$$(2.15) \quad x_i = \left[\frac{k_{i-1} p_i p_{i-s-1}}{k_i p_{i-1} p_{i-s}} \right]^{\frac{1}{2}} x_{i-1}.$$

This same process can be used to obtain x_{i-1} in terms of x_{i-2} , eventually leading to an expression in terms of x_0 :

$$(2.16) \quad x_i = \left[\frac{k_0 p_i p_{n-s}}{k_i p_0 p_{i-s}} \right]^{\frac{1}{2}} x_0.$$

Substitution into equation (2.13) and use of equation (2.7) now determines the coordinates of the central equilibrium as

$$(2.17) \quad x_{i+md} = \frac{\sqrt{n} p_{i+md} v}{p_i k(n, s)} \left[\frac{k_0 p_i p_{n-s}}{k_i p_0 p_{i-s}} \right]^{\frac{1}{2}}, \quad 0 \leq m < d, \quad 0 \leq i < d,$$

$$k(r, s) = \sum_{j=0}^{d-1} \sum_{r=0}^{\frac{n}{d}-1} \left[\frac{k_{j-1} p_j p_{j-s-1}}{k_j p_{j-1} p_{j-s}} \right]^{\frac{1}{2}} \frac{p_{j+rd}}{p_j}.$$

It is of interest to note that although the position of the central equilibrium depends on the rate constants, the other equilibria do not. That is, they are embodiments of the basic star structure while the central equilibrium involves the rate constant structure.

3. STABILITY OF THE CENTRAL EQUILIBRIUM

In this section consideration is restricted to the case in which all rate constants are equal to one. Thus the central equilibrium is given by equation (1.5). The perturbation $x_i \rightarrow \frac{v}{\sqrt{n}} + \varepsilon_i$ in equations (1.8) leads to the set of linearized equations

$$(3.1) \quad \dot{\varepsilon}_i = -\frac{v}{\sqrt{n}} (\varepsilon_i + \varepsilon_{i+s}) + \frac{v}{\sqrt{n}} (\varepsilon_{i-1} + \varepsilon_{i-s-1}).$$

The coefficient matrix for this system is the circulant matrix $C = \frac{v}{\sqrt{n}} \text{circ}(c_0, c_1, \dots, c_{n-1})$ with the c_i defined by

$$(3.2) \quad c_i = \begin{cases} -1 & i = \overline{0, n-s}, s > 1, \\ 1 & i = \overline{n-s-1, n-1}, s > 1, \\ 0 & \text{otherwise,} \end{cases}$$

$$c_i = \begin{cases} -1 & i = \overline{0}, s = 1, \\ 1 & i = \overline{n-2}, s = 1. \end{cases}$$

Properties of circulant matrices are well known. A matrix is circulant if and only if it commutes with the shift operator σ , and in fact can be expressed as a polynomial in σ . If this polynomial is denoted P for the matrix C , then the eigenvalues of C are given by $P(\omega^r)$ for $0 \leq r \leq n-1$ where $\omega = e^{2\pi i/n}$ is the first of the n -th roots of unity. P is the complex polynomial defined by

$$(3.3) \quad P(z) = z^{n-1} - z^{n-s} + z^{n-s-1} - 1$$

For $r = 0$, $P(1) = 0$ indicating neutral stability. The corresponding eigenvector lies along the line $x_i = t(0 \leq i < n)$, hence is orthogonal to the surfaces defined by equation (1.3). Within these surfaces, stability of the central equilibrium is determined by the sign of $\text{Re}(P(\omega^r))$ for $1 \leq r \leq n-1$.

Theorem 2. *If n is odd, the central equilibrium of the $(n, 1)$ -star is a structurally stable attractor in the hypersurfaces of constant v . If n is even this central equilibrium is neutrally stable in the direction corresponding to the eigenvalue $P(-1)$ of C .*

Proof. For $s = 1$, equation (3.3) becomes $P(z) = z^{n-2} - 1$. Thus $P(\omega^r) = \omega^{(n-2)r} - 1$ and since $\text{Re}(\omega^m) < 1$ for all $m \neq 0$ this can never have a positive real part. Further, the real part of $P(\omega^r)$ will be zero if and only if $\omega^{(n-2)r} = 1$ for some value of r . This requires that $(n-2)r \equiv 0 \pmod{n}$ for some r between 1 and $n-1$. This can occur only if $r = n/m$ for some m , in which case $\left(\frac{n-2}{m}\right)n \equiv 0 \pmod{n}$. But both of these conditions are satisfied only if both n and $n-2$ are divisible by m and this occurs if and only if n is even and $m = 2$. Thus for every even n , $P(\omega^{n/2}) = 0$. Also, since n is even, so is $n-2$ and use of equation (3.2) indicates that the vector with components $e_i(z) = \frac{(-1)^i}{\sqrt{n}}$ is an eigenvector of C with eigenvalue 0, lying along the line equilibrium for the $(n, 1)$ -star with n even, which exists by Theorem 1. $\square$

Theorem 3. *If n is odd then the $(n, \frac{n-1}{2})$ -star has a stable central equilibrium.*

Proof. For this case, equation (3.3) becomes $P(\omega^r) = \omega^{(n-1)r} - \omega^{(n+1)r/2} + \omega^{(n-1)r/2} - 1$, but $\omega^{(n+1)r/2} - \omega^{(n-1)r/2}$ has zero real part, hence $\text{Re}(P(\omega^r)) = \text{Re}(\omega^{(n-1)r} - 1) < 0$. $\square$

Theorem 4. *Let n be even. Then for $s = (n-2)/r$ the real part of $P(\omega^r)$ is zero if r is even and negative if r is odd.*

Proof. $P(\omega^r) = \omega^{(n-1)r} - \omega^{(n+2)r/2} + \omega^{(n-2)r/2} - 1$ and $\omega^n = 1$, $\omega^{n/2} = -1$. Hence this becomes $P(\omega^r) = \omega^{-r} - (-1)^r \omega^r + (-1)^r - 1$. If r is even this becomes $\omega^{-r} - \omega^r$ which has zero real part. If r is odd, it becomes $\omega^{-r} + \omega^r - 2$ which has negative real part. $\square$

Lemma 3. *Let $P_n(\omega^r)$ be the r -th eigenvalue for perturbations about the central equilibrium of the (n, s) -star. Then $P_{mn}(\omega^{mr}) = P_n(\omega^r)$.*

Theorem 5. *Sufficient conditions for neutral stability of the central equilibrium of the (n, s) -star are:*

- A. *For some $r < n$, $(s+1)r \equiv 0 \pmod{n}$.*
- B. *If n is even there exists an r such that $sr \equiv -1 \pmod{n}$.*

Evaluation of $P(\omega^r)$ for various (n, s) -stars indicates that unlike the case of hypercycles, the central equilibrium for equations (1.8) may sometimes be unstable.

Table 2 lists the values of r for which this equilibrium is unstable for $n \leq 16$.

TABLE 2. Stability of Central Equilibrium for Different r Values. (All r -values not listed are stable)

n/s	2	3	4	5	6	7
5	stable					
6	neutral 2,4					
7	unstable 2,5	stable				
8	neutral 2,6	neutral 2,4,6				
9	neutral 3,6	unstable 2,7	stable			
10	unstable 3,7	unstable 2,8	neutral 2,4,6,8			
11	unstable 3,8	unstable 2,9	unstable 2,9			
12	neutral 3,4,8,9	neutral 2,3,9,10	unstable 2,10	neutral 2,4,6,8 10		
13	unstable 4,9	unstable 3,10	unstable 2,5,8,11	unstable 2,4,9,11	stable	
14	unstable 4,10	unstable 3,11 neutral 7	unstable 2,12	unstable 2,12 neutral 7	neutral 2,4,6,8 10,12	
15	unstable 4,11 neutral 5,10	unstable 3,12	unstable 2,13 neutral 3,6,9,12	unstable 2,13 neutral 5,10,	unstable 2,4,11,13	stable
16	unstable 5,11 neutral 4,12	unstable 3,13 neutral 4,8,12	unstable 3,13 neutral 2,6,10,14	unstable 2,5,11,14 neutral 8	unstable 2,14 neutral 4,12	neutral 2,4,6,8 10,12,14

4. EXAMPLES

- A. $(n, s) = (3, 1)$.

The simplest case is the (3, 1)-star, for which equations (1.8) become

$$(4.1) \quad \begin{aligned} \dot{x}_0 &= -x_2(x_0 - x_1) \\ \dot{x}_1 &= -x_0(x_1 - x_2) \\ \dot{x}_2 &= -x_1(x_2 - x_0) \end{aligned}$$

Since $x_0 + x_1 + x_2 = \sqrt{3}v$ is a constant of motion, the system orbits are most easily represented in coordinates (x, y, v) defined by:

$$(4.2) \quad \begin{pmatrix} x \\ y \\ v \end{pmatrix} = \frac{1}{\sqrt{2}} \begin{pmatrix} \frac{2}{\sqrt{3}} & -\frac{1}{\sqrt{3}} & -\frac{1}{\sqrt{3}} \\ 0 & 1 & -1 \\ \frac{\sqrt{2}}{\sqrt{3}} & \frac{\sqrt{2}}{\sqrt{3}} & \frac{\sqrt{2}}{\sqrt{3}} \end{pmatrix} \begin{pmatrix} x_0 \\ x_1 \\ x_2 \end{pmatrix}$$

In these coordinates equations (4.1) become

$$(4.3) \quad \begin{aligned} \dot{x} &= \frac{\sqrt{3}}{2\sqrt{2}}(x^2 - y^2) + \frac{xy}{\sqrt{2}} - \frac{\sqrt{3}}{2}vx + \frac{v}{2}y, \\ \dot{y} &= \frac{1}{2\sqrt{2}}(x^2 - y^2) - \frac{\sqrt{3}}{\sqrt{2}}xy - \frac{v}{2}x - \frac{\sqrt{3}}{2}vy. \end{aligned}$$

The central equilibrium is now located at the origin $(x, y) = (0, 0)$ in the two dimensional surfaces orthogonal to the v axis. By Theorem 2 it is a stable attractor. Eigenvalues for linear perturbations about this equilibrium are $-\frac{\sqrt{3}}{2}v \pm \frac{i}{2}v$. There is only one maximal set of independent vertices, $\{x_0, x_1, x_2\}$ which gives rise to three point equilibria: $(\sqrt{3}v, 0, 0)$, $(0, \sqrt{3}v, 0)$, and $(0, 0, \sqrt{3}v)$. In the (x, y) coordinates these become respectively the points

$$\left(\sqrt{2}v, 0\right), \left(-\frac{v}{\sqrt{2}}, \frac{\sqrt{3}}{\sqrt{2}}v\right), \text{ and } \left(-\frac{v}{\sqrt{2}}, -\frac{\sqrt{3}}{\sqrt{2}}v\right).$$

Eigenvalues for linearized perturbations about each of these points are $-\frac{\sqrt{3}v}{2}(1 \pm \sqrt{5})$, indicating that each of these points is a hyperbolic saddle.

Figure 3 shows equilibrium manifolds, some plots of system orbits, and the basin of attraction for this example.

Similar results hold for the more general case of equations (2.1). The three saddle equilibria remain the same, but the eigenvalues for linearized perturbations about them are now, respectively,

$$\begin{aligned} \frac{\sqrt{3}vk^2}{2} \left[1 \pm \sqrt{1 + \frac{4k_0}{k^2}} \right], \frac{\sqrt{3}vk_0}{2} \left[1 \pm \sqrt{1 + \frac{4k_1}{k_0}} \right], \\ \text{and } \frac{\sqrt{3}vk_1}{2} \left[1 \pm \sqrt{1 + \frac{4k_2}{k_1}} \right] \end{aligned}$$

while the central equilibrium is located at

$$(4.5) \quad \begin{aligned} x_0 &= \frac{\sqrt{3}vk_2}{K(3, 1)}, \quad x_1 = \frac{\sqrt{3}vk_0}{K(3, 1)}, \quad x_2 = \frac{\sqrt{3}vk_1}{K(3, 1)}, \\ K(3, 1) &= k_0 + k_1 + k_2, \\ x &= \frac{\sqrt{2}v(2k_2 - k_0 - k_1)}{K(3, 1)}, \quad y = \frac{\sqrt{3}v(k_0 - k_1)}{\sqrt{2}K(3, 1)} \end{aligned}$$

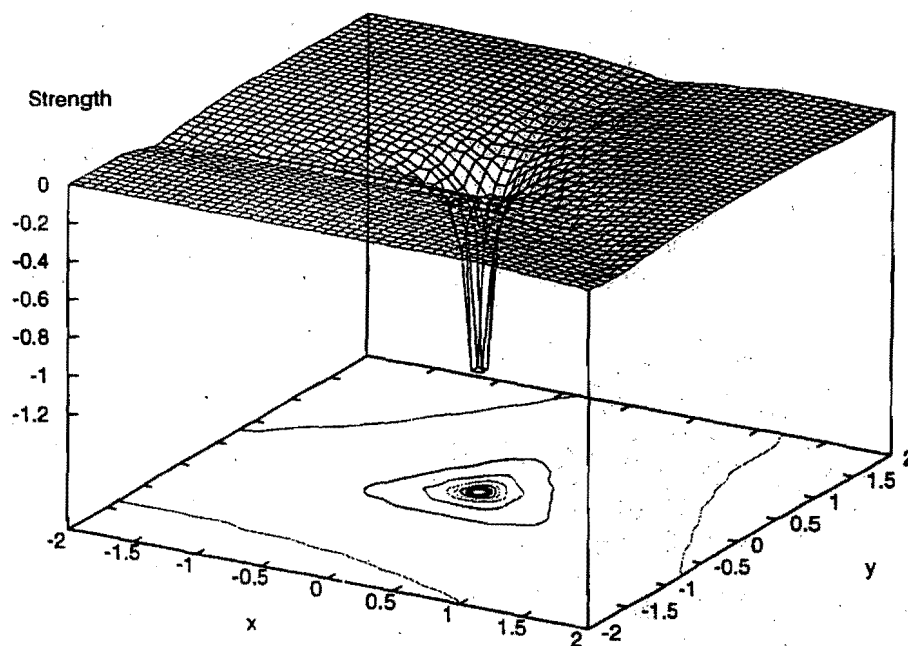
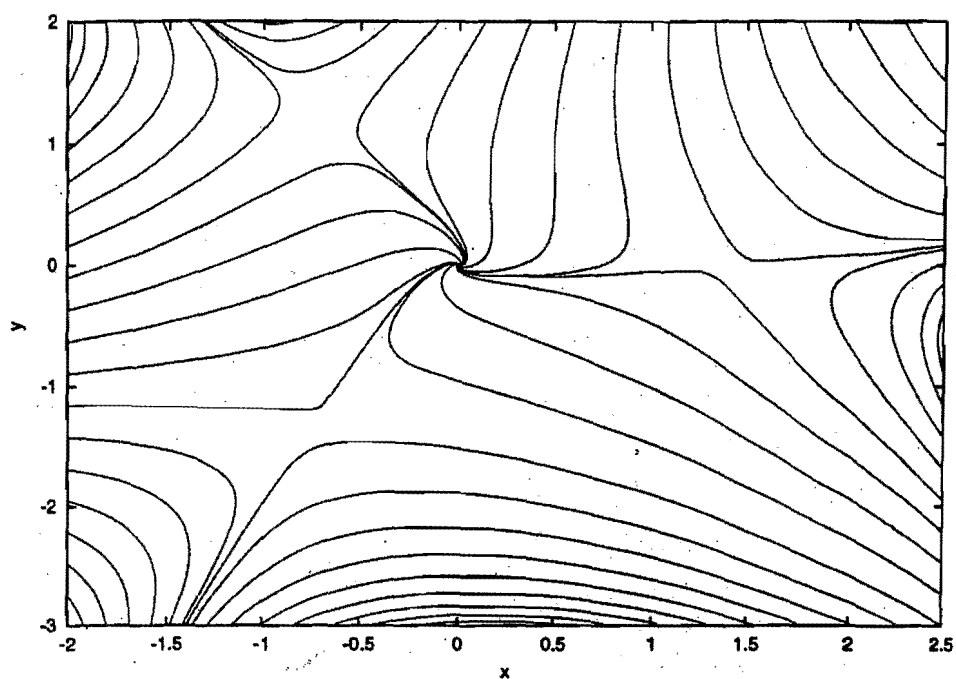


FIGURE 3. Orbits and Basin of Attraction for Equation (1.8) for $(n, s) = (3, 1)$.

with eigenvalues for linearized perturbations given by

$$(4.6) \quad \frac{\sqrt{3}v}{K(3,1)} \left[-(k_0k_1 + k_0k_2 + k_1k_2) \pm \sqrt{k_0^2k_1^2 + k_0^2k_2^2 + k_1^2k_2^2 - 4k_0k_1k_2K(3,1)} \right]$$

$$\text{B. } (n, s) = (4, 1).$$

By Theorem 2, the central equilibrium manifold is one dimensional. There are two maximal sets of independent vertices, $\{x_0, x_2\}$ and $\{x_1, x_3\}$, so there will also be two line equilibria defined by $x_1 = x_3 = 0$ and $x_0 = x_2 = 0$.

Again, it is useful to introduce new coordinates:

$$(4.7) \quad \begin{pmatrix} x \\ y \\ z \\ v \end{pmatrix} = \frac{1}{\sqrt{2}} \begin{pmatrix} 0 & 1 & 0 & -1 \\ 1 & 0 & -1 & 0 \\ \frac{1}{\sqrt{2}} & -\frac{1}{\sqrt{2}} & \frac{1}{\sqrt{2}} & -\frac{1}{\sqrt{2}} \\ \frac{1}{\sqrt{2}} & \frac{1}{\sqrt{2}} & \frac{1}{\sqrt{2}} & \frac{1}{\sqrt{2}} \end{pmatrix} \begin{pmatrix} x_0 \\ x_1 \\ x_2 \\ x_3 \end{pmatrix}$$

In these coordinates, equations (1.8) take the form

$$(4.8) \quad \begin{aligned} \dot{x} &= -\sqrt{2}x(z+v), \\ \dot{y} &= \sqrt{2}y(z-v), \\ \dot{z} &= 2xy. \end{aligned}$$

The central equilibrium line is the z -axis while the two other equilibrium manifolds are the lines $z = v, x = 0$ and $z = -v, y = 0$. Orbits for initial conditions chosen as small circles about the z -axis for z values of $\pm 1.1, \pm 1.5$, and 0 are shown in Figure 4, with $v = 1$.

Eigenvalues for perturbations about the z -axis are $0, \sqrt{2}(z+v)$, and $\sqrt{2}(z-v)$. These have corresponding eigendirections along the z, x , and y axes respectively. Thus, stability of the z -axis against perturbations in the (x, y) plane depends on the value of z :

$$(4.9) \quad \begin{aligned} z &< -v \text{ unstable in } x \text{ direction,} \\ -v &< z < v \text{ stable,} \\ z &> v \text{ unstable in } y \text{ direction.} \end{aligned}$$

The lines $z = v, x = 0$ and $z = -v, y = 0$ are neutrally stable in the y and x directions respectively, and stable in the respective directions

$$\left(-\frac{x^2}{2\sqrt{2}v^2}, 1, \frac{x}{\sqrt{2}v} \right) \text{ and } \left(1, \frac{y^2}{2\sqrt{2}v^2}, -\frac{y}{\sqrt{2}v} \right).$$

$$\text{C. } (n, s) = (5, 2)$$

By Theorems 2 and 3 the central equilibrium for these cases is a stable point attractor. For both cases, there are five maximal sets of independent vertices. For the $(5, 1)$ -star these are $\{x_1, x_3\}, \{x_2, x_4\}, \{x_0, x_3\}, \{x_1, x_4\}, \{x_0, x_2\}$, while for the $(5, 2)$ -star they are $\{x_0, x_1\}, \{x_1, x_2\}, \{x_2, x_3\}, \{x_3, x_4\}, \{x_0, x_4\}$. Thus, each case admits five line equilibria. Linearization of equations (1.8) about these equilibrium lines yields two zero

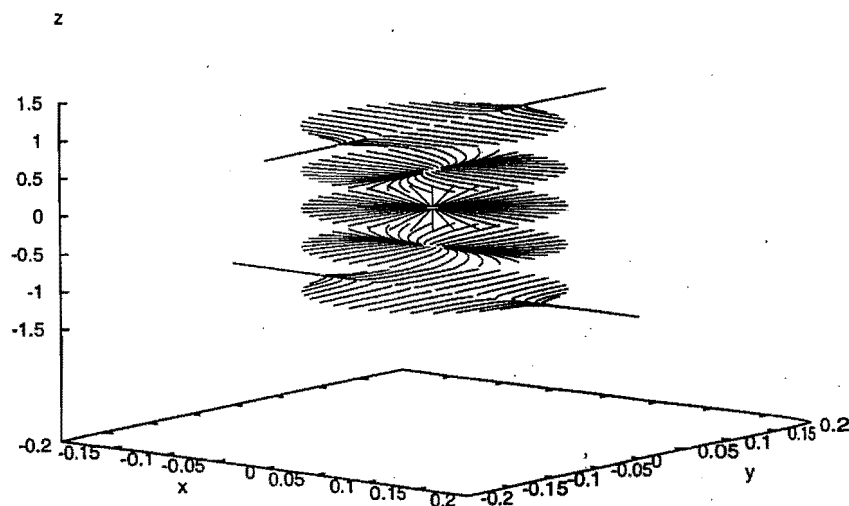


FIGURE 4. Initial conditions taken as small circles about z -axis for $z = -1, -0.5, 0, 0.5, 1$.

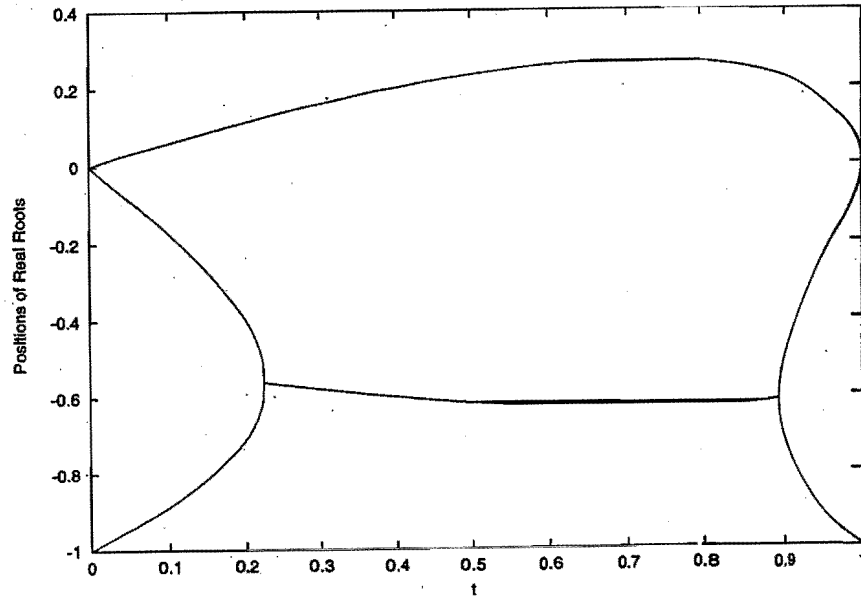
eigenvalues, with corresponding eigenvectors along the equilibrium line, and orthogonal to the hypersurfaces of constant v . The remaining eigenvalues are obtained from solutions of

$$(4.10) \quad \lambda^3 + \lambda^2 + t(1-t)\lambda - t^2(1-t) = 0$$

with the actual eigenvalues being equal to $\sqrt{5}v\lambda$. The parameter t varies from 0 to 1 along the equilibrium line $x_i = \sqrt{5}vt$, $x_j = \sqrt{5}v(1-t)$, $x_k = 0$, $k \neq i, j$. Figure 5 shows a plot of the real part of the roots of equation (4.10) for values $0 \leq t \leq 1$. Near 0 and 1 there are three real roots, two negative and one positive. The positive root is real for all values of t while the two negative roots become complex, with identical real parts.

Thus, at least within the concentration simplex, these equilibrium manifolds are unstable. Figures 6 - 9 show some typical orbits, both near the central equilibrium and near the equilibrium lines.

These figures show orbits in both the x_i coordinates, and in a coordinate system adapted to the hypersurfaces of constant v , determined in terms of the x_i by the orthonormal transformation shown in equation (4.11). Orbits shown in Figures 6 and 7 are near the central equilibrium. In the (x, y, p, q) coordinates these show convergence to the central equilibrium in the (p, q) plane, and a more complicated form of convergence in the (x, y) plane. In Figures 8 and 9, initial conditions are taken as small circles about the equilibrium line defined by $\underline{v} = (0, 0, 1, 0, -1)t + (0, 0, 0, 0, \sqrt{5})$. The orbits show divergence away from

FIGURE 5. Real part of roots of $\lambda^3 + \lambda^2 + t(1-t)\lambda - t^2(1-t)$.

this line both toward the central equilibrium, and away from it.

$$\begin{pmatrix} x \\ y \\ p \\ q \\ v \end{pmatrix} = \begin{pmatrix} \frac{\sqrt{2}}{\sqrt{5}} & \sqrt{2}\alpha_+^2 & -\sqrt{2}\alpha_-^2 & -\sqrt{2}\alpha_-^2 & \sqrt{2}\alpha_+^2 \\ \frac{\sqrt{2}}{\sqrt{5}} & -\sqrt{2}\alpha_-^2 & \sqrt{2}\alpha_+^2 & \sqrt{2}\alpha_+^2 & -\sqrt{2}\alpha_-^2 \\ 0 & \alpha_+ & -\alpha_- & \alpha_- & -\alpha_+ \\ 0 & \alpha_- & \alpha_+ & -\alpha_+ & -\alpha_- \\ \frac{1}{\sqrt{5}} & \frac{1}{\sqrt{5}} & \frac{1}{\sqrt{5}} & \frac{1}{\sqrt{5}} & \frac{1}{\sqrt{5}} \end{pmatrix} \begin{pmatrix} x_0 \\ x_1 \\ x_2 \\ x_3 \\ x_4 \end{pmatrix}, \quad (4.11)$$

$$\alpha_+ = \frac{1}{2} \left[\frac{\sqrt{5}+1}{\sqrt{5}} \right]^{1/2}, \quad \alpha_- = \frac{1}{2} \left[\frac{\sqrt{5}-1}{\sqrt{5}} \right]^{1/2}$$

D. $(n, s) = (6, 2)$

This example shows some particularly interesting structures, most apparent in coordinates adapted to the three equilibrium lines defined by $x_0 = x_1 = x_3 = x_4 = 0$, $x_1 = x_2 = x_4 = x_5 = 0$, $x_0 = x_2 = x_3 = x_5 = 0$.

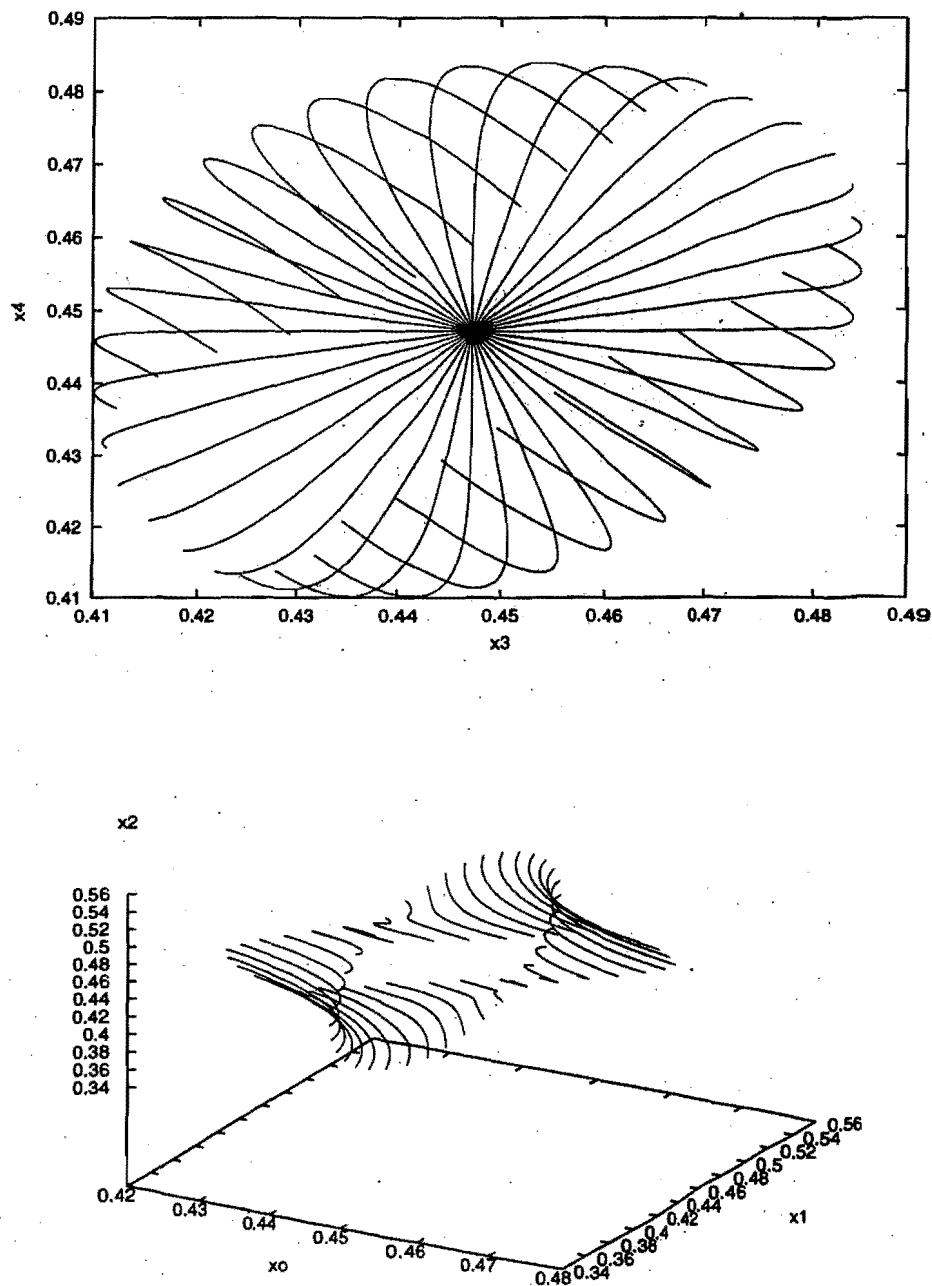


FIGURE 6. Projection of orbits of equations of (1.8) in original coordinates. Initial conditions taken as a small circle about the origin in the (x_0, x_1) plane.

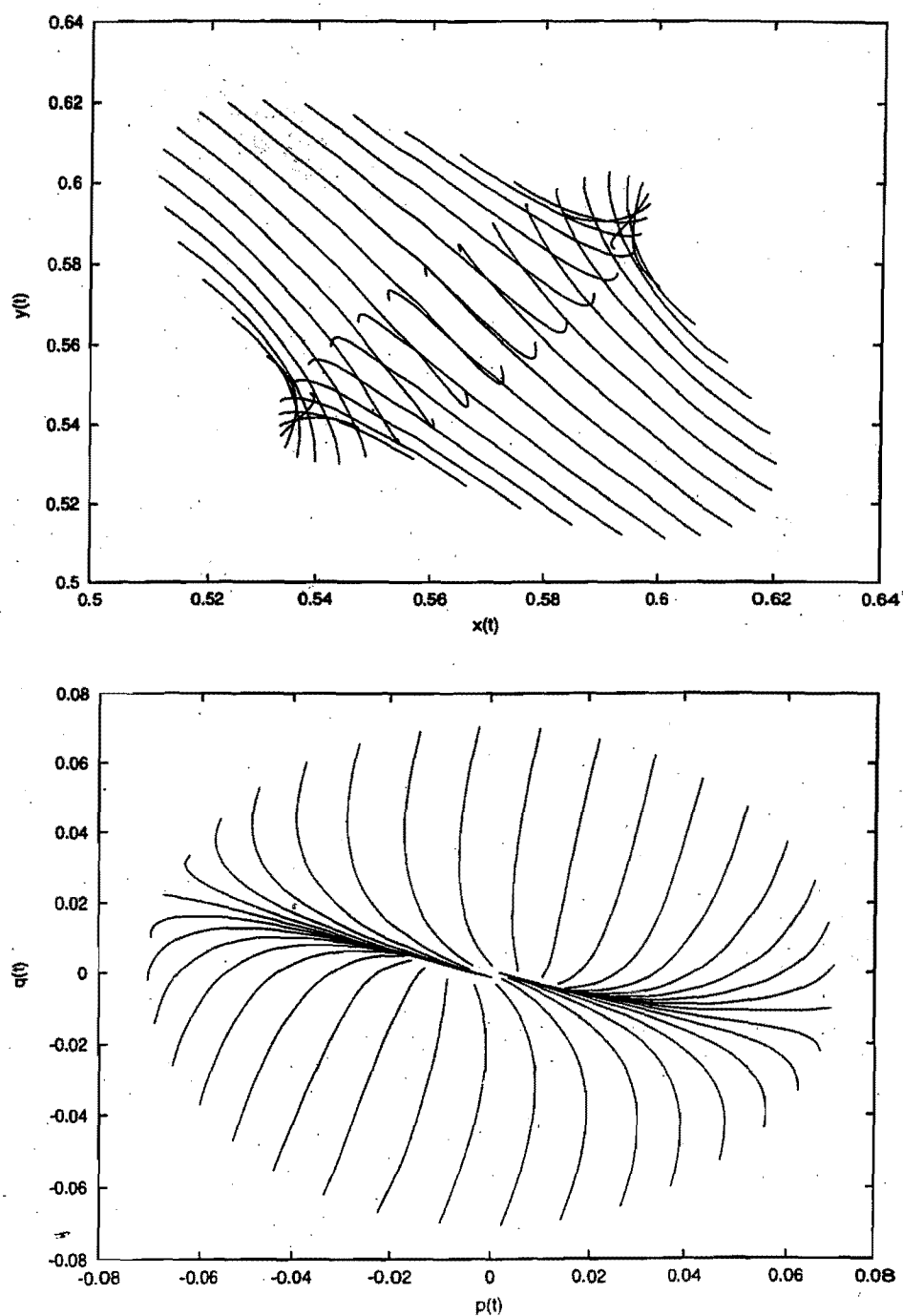


FIGURE 7. Projection of orbits of equations of (1.8) for $(n, s) = (5, 2)$ in simplex coordinates. Initial conditions taken as a small circle about the origin in the (x_0, x_1) plane.

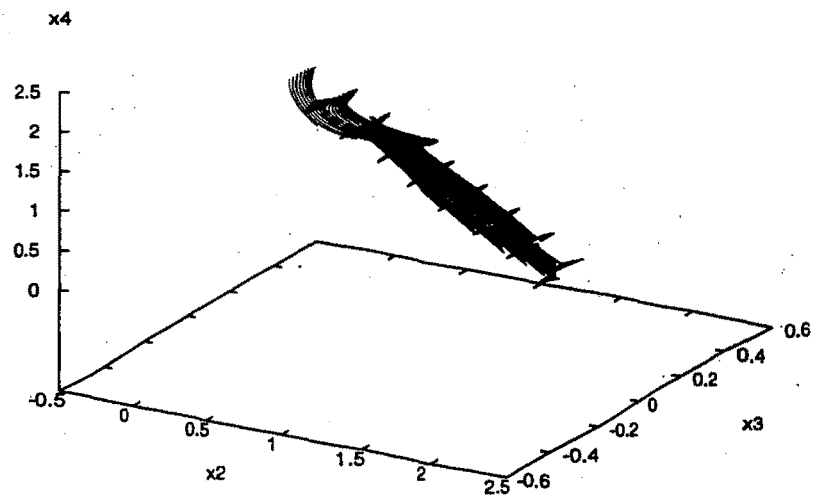
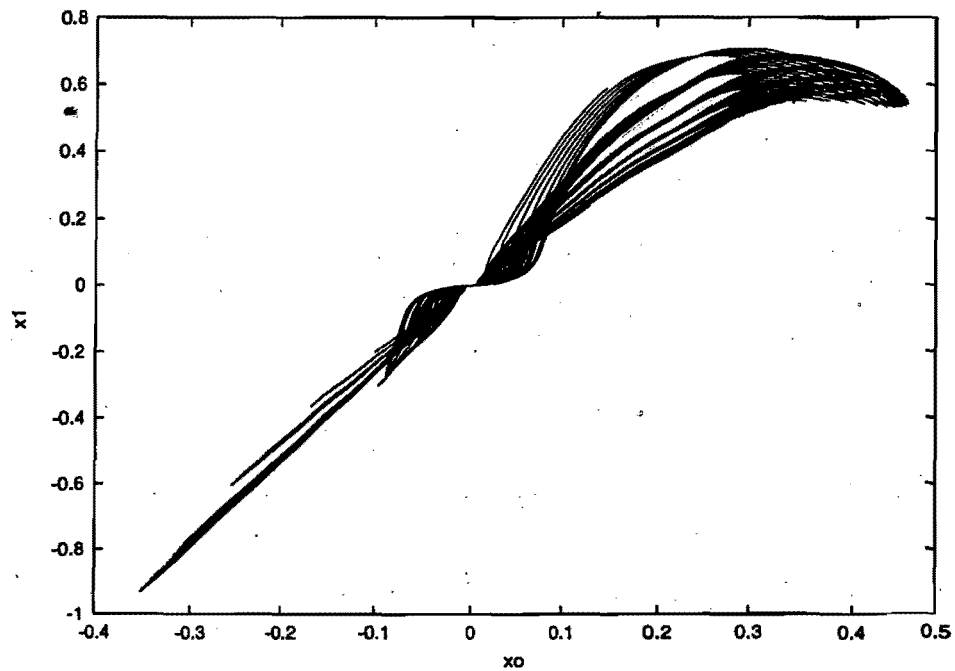


FIGURE 8. Projection of orbits of equations of (1.8) for $(n, s) = (5, 2)$ in original coordinates. Initial conditions taken as a small circle about an equilibrium line.

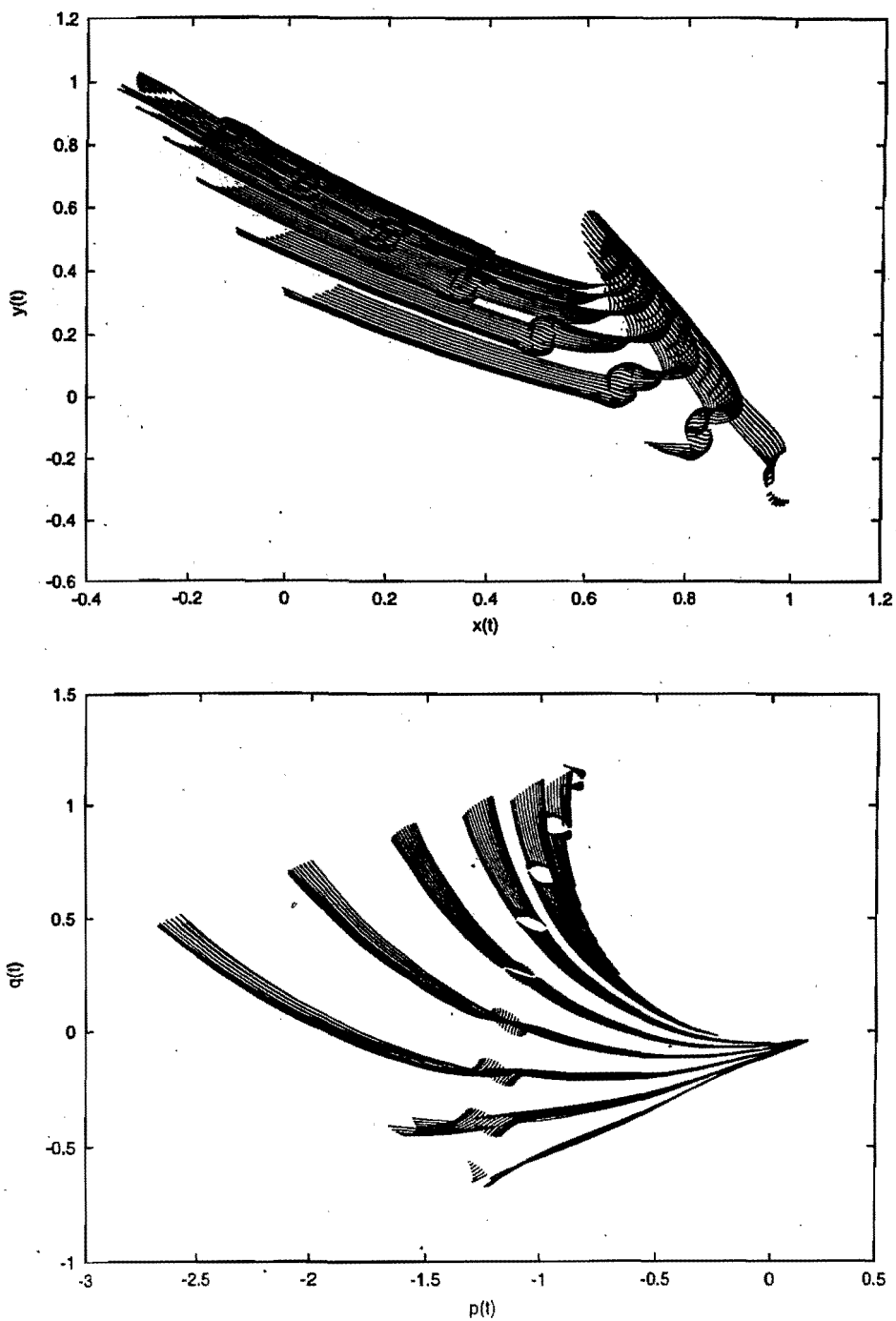


FIGURE 9. Projection of orbits of equations of (1.8) for $(n, s) = (5, 2)$ in simplex coordinates. Initial conditions taken as a small circle about an equilibrium line. Note the instability as orbits either go to infinity or to the central equilibrium.

These are defined by the transformation

$$(4.12) \quad \begin{pmatrix} \eta \\ \xi \\ \gamma \\ \mu \\ \nu \\ v \end{pmatrix} = \frac{1}{\sqrt{2}} \begin{pmatrix} 0 & 0 & -1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 & -1 & 0 \\ 1 & 0 & 0 & -1 & 0 & 0 \\ \frac{\sqrt{2}}{\sqrt{3}} & -\frac{1}{\sqrt{6}} & -\frac{1}{\sqrt{6}} & \frac{\sqrt{2}}{\sqrt{3}} & -\frac{1}{\sqrt{6}} & -\frac{1}{\sqrt{6}} \\ 0 & \frac{1}{\sqrt{2}} & -\frac{1}{\sqrt{2}} & 0 & \frac{1}{\sqrt{2}} & -\frac{1}{\sqrt{2}} \\ \frac{1}{\sqrt{3}} & \frac{1}{\sqrt{3}} & \frac{1}{\sqrt{3}} & \frac{1}{\sqrt{3}} & \frac{1}{\sqrt{3}} & \frac{1}{\sqrt{3}} \end{pmatrix} \begin{pmatrix} x_0 \\ x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \end{pmatrix}$$

In these coordinates, equations (1.8) become

$$(4.13) \quad \begin{aligned} \dot{\eta} &= \frac{1}{2\sqrt{3}} (\mu + \sqrt{3}\nu - \sqrt{2}v) (\eta - \xi + \gamma) - \frac{\sqrt{3}}{\sqrt{2}} v\eta, \\ \dot{\xi} &= \frac{1}{2\sqrt{3}} (\mu - \sqrt{3}\nu - \sqrt{2}v) (\eta - \xi - \gamma) - \frac{\sqrt{3}}{\sqrt{2}} v\xi, \\ \dot{\gamma} &= \frac{1}{\sqrt{6}} (\sqrt{2}\mu + v) (\eta + \xi + \gamma) - \frac{\sqrt{3}}{\sqrt{2}} v\gamma, \\ \dot{\mu} &= -\frac{\sqrt{3}}{2} (\eta - \xi)\gamma - \left(\mu + \frac{v}{\sqrt{2}}\right) \nu, \\ \dot{\nu} &= -\eta\xi - \frac{(\eta - \xi)\gamma}{2} - \frac{\mu^2 - \nu^2}{2} + \frac{v}{\sqrt{2}} \mu \end{aligned}$$

The five dimensional hypersurfaces of constant v partition naturally into three dimensions coordinatized by (η, ξ, γ) and two dimensions coordinatized by (μ, ν) with the central equilibrium located at the origin $(0, 0, 0, 0, 0)$. There are nine equilibrium lines. Three of these are the η, ξ , and γ axes, which project to points in the (μ, ν) -plane. The remaining six of these equilibrium lines are obtained by taking $x_i = x_{i+1} = x_{i+2} = x_{i+3} = 0$ for $0 \leq i \leq 5$. Equations for all of these lines are given in Table 3.

TABLE 3. Equilibrium Lines for (6, 2)-Star

$\xi = \gamma = 0,$	$\mu = -\frac{v}{\sqrt{2}},$	$\nu = -\frac{\sqrt{3}}{\sqrt{2}}v$	η - axis
$\eta = \gamma = 0,$	$\mu = -\frac{v}{\sqrt{2}},$	$\nu = \frac{\sqrt{3}}{\sqrt{2}}v$	ξ - axis
$\xi = \eta = 0,$	$\mu = \sqrt{2}v,$	$\nu = 0$	γ - axis
1. $\xi = \eta - \sqrt{3}v,$	$\gamma = 0,$	$\mu = -\frac{v}{\sqrt{2}},$	$\nu = \frac{\sqrt{3}}{\sqrt{2}}v - \sqrt{2}\eta$
2. $\gamma = \sqrt{3}v - \eta,$	$\xi = 0,$	$\mu = \sqrt{2}v - \frac{\sqrt{3}}{\sqrt{2}}\eta,$	$\nu = \frac{\mu}{\sqrt{3}} - \frac{\sqrt{2}}{\sqrt{3}}v$
3. $\gamma = \sqrt{3}v - \xi,$	$\eta = 0,$	$\mu = \sqrt{2}v - \frac{\sqrt{3}}{\sqrt{2}}\xi,$	$\nu = \frac{\sqrt{2}}{\sqrt{3}} - \frac{\mu}{\sqrt{3}}$
4. $\xi = \sqrt{3}v - \eta,$	$\gamma = 0,$	$\mu = -\frac{v}{\sqrt{2}},$	$\nu = \frac{\sqrt{3}}{\sqrt{2}}v + \sqrt{2}\eta$
5. $\gamma = -\sqrt{3}v - \eta,$	$\xi = 0,$	$\mu = \sqrt{2}v + \frac{\sqrt{3}}{\sqrt{2}}\eta,$	$\nu = \frac{\mu}{\sqrt{3}} - \frac{\sqrt{2}}{\sqrt{3}}v$
6. $\gamma = -\sqrt{3}v - \xi,$	$\eta = 0,$	$\mu = \sqrt{2}v + \frac{\sqrt{3}}{\sqrt{2}}\xi,$	$\nu = \frac{\sqrt{2}}{\sqrt{3}}v - \frac{\mu}{\sqrt{3}}$

Figure 10 shows the projections of these six equilibrium lines in the (η, ξ, γ) and (μ, ν) spaces.

Only segments of the lines, labelled 1 – 6 are shown in the (η, ξ, γ) space—it is only along these segments that these line equilibria are stable. The six lines project into the (μ, ν) space in pairs, as indicated, and the three points of intersection are the point projections of the η, ξ , and γ axes.

Linearization of equations (4.13) about the central equilibrium yields a coefficient matrix having eigenvalues

$$(4.14) \quad -\frac{v}{\sqrt{6}}(\text{twice}), -\frac{2\sqrt{2}}{\sqrt{3}}v, \pm i\frac{v}{\sqrt{2}}.$$

In a neighborhood of the origin, $(\eta, \xi, \gamma, \mu, \nu)$ are normal coordinates. The (μ, ν) plane is a center manifold in this neighborhood, and the corresponding stable manifold is the (η, ξ, γ) 3-space.

Eigenvectors for the negative eigenvalues are:

$$(4.15) \quad -\frac{2\sqrt{2}}{\sqrt{3}}v : \frac{1}{\sqrt{3}}(1, 1, -1, 0, 0),$$

$$-\frac{v}{\sqrt{6}} : \frac{1}{\sqrt{2}}(1, 0, 1, 0, 0), \quad \frac{1}{\sqrt{2}}(0, 1, 1, 0, 0),$$

while the imaginary eigenvalues indicate closed orbits about $(\mu, \nu) = (0, 0)$. The center manifold lies in the interior of the triangle in the (μ, ν) plane formed by the projections of the equilibrium lines 1 - 6. Perturbation of equations (4.13) about $(\eta, \xi, \gamma) = (0, 0, 0)$, with (μ, ν) located at one of the vertices of this triangle yields eigenvalues $0, \pm \frac{\sqrt{3}}{\sqrt{2}}v$.

Table 4 shows the corresponding eigenspaces for each case.

TABLE 4. Eigenvectors for Perturbations About $(\eta, \xi, \gamma) = (0, 0, 0)$

	$\left(-\frac{v}{\sqrt{2}}, -\frac{\sqrt{3}}{\sqrt{2}}v\right)$	$\left(-\frac{v}{\sqrt{2}}, \frac{\sqrt{3}}{\sqrt{2}}v\right)$	$(\sqrt{2}v, 0)$
0	$(1, 0, 0, 0, 0)$ η - axis	$(0, 1, 0, 0, 0)$ ξ - axis	$(0, 0, 1, 0, 0)$ γ - axis
$-\frac{\sqrt{3}}{\sqrt{2}}v$	$(r + s, r, -s, 0, t)$ $\eta - \xi + \gamma = 0$ $\mu = -\frac{v}{\sqrt{2}}$	$(r + s, r, s, -t, t)$ $\eta - \xi - \gamma = 0$ $\nu = -\frac{\mu}{\sqrt{3}} + \frac{\sqrt{2}}{\sqrt{3}}v$	$(r + s, -r, -s, \sqrt{3}t, t)$ $\eta + \xi + \gamma = 0$ $\nu = \frac{\mu}{\sqrt{3}} - \frac{\sqrt{2}}{\sqrt{3}}v$
$\frac{\sqrt{3}}{\sqrt{2}}v$	$(0, 0, 0, \sqrt{3}, 1)$ $\nu = \frac{\mu}{\sqrt{3}} - \frac{\sqrt{2}}{\sqrt{3}}v$	$(0, 0, 0, 0, 1)$ $\mu = -\frac{v}{\sqrt{2}}$	$(0, 0, 0, -\sqrt{3}, 1)$ $\nu = -\frac{\mu}{\sqrt{3}} + \frac{\sqrt{2}}{\sqrt{3}}v$

Inspection of this table indicates that the η, ξ , or γ axis whose projection is a particular vertex of the triangle in the μ, ν plane will be the neutrally stable direction out of $\eta, \xi, \gamma = (0, 0, 0)$ at that vertex. The eigenspaces corresponding to the negative eigenvalue are three dimensional, breaking down into a two dimensional plane in the η, ξ, γ space and one of the pairs of projected equilibrium lines in the μ, ν plane. Eigenspaces corresponding to the positive eigenvalue lie in the μ, ν plane along the projections of the equilibrium lines. Each vertex of the triangle formed by these projections is a saddle for η, ξ, γ near $(0, 0, 0)$, as indicated by the direction of the arrows in Figure 10.

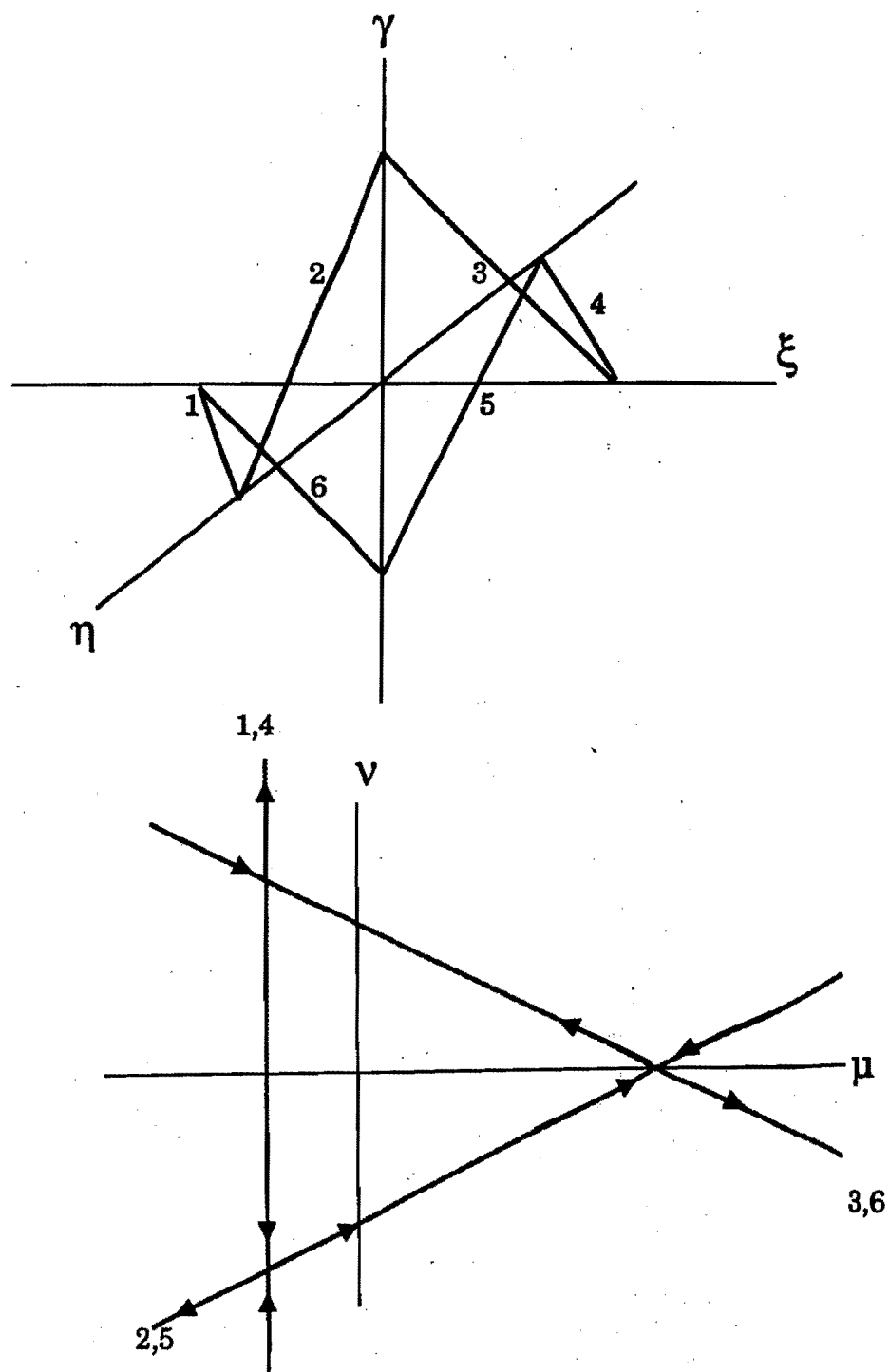


FIGURE 10. Equilibrium lines projected into (η, ξ, γ) space and (μ, ν) plane. Arrows indicate directions in and out of saddle points in (μ, ν) plane.

	η - axis ($\eta = kv$)	ξ - axis ($\xi = kv$)	γ = axis ($\gamma = kv$)
0	$(1, 0, 0, 0) k \neq \pm\sqrt{3}$ $\left(t, r, s, \frac{\sqrt{3}s}{\sqrt{2}}, \frac{s-2r}{\sqrt{2}}\right) k = \sqrt{3}$ $\left(t, r, s, -\frac{\sqrt{3}s}{\sqrt{2}}, -\frac{s-2r}{\sqrt{2}}\right) k = -\sqrt{3}$	$(0, 1, 0, 0) k \neq \pm\sqrt{3}$ $\left(t, r, s, \frac{\sqrt{3}s}{\sqrt{2}}, -\frac{s-2t}{\sqrt{2}}\right) k = \sqrt{3}$ $\left(t, r, s, -\frac{\sqrt{3}s}{\sqrt{2}}, \frac{s-2t}{\sqrt{2}}\right) k = -\sqrt{3}$	$(0, 0, 1, 0) k \neq \pm\sqrt{3}$ $\left(t, r, s, -\frac{\sqrt{3}(t+r)}{\sqrt{2}}, -\frac{t-r}{\sqrt{2}}\right) k = \sqrt{3}$ $\left(t, r, s, \frac{\sqrt{3}(t+r)}{\sqrt{2}}, \frac{t-r}{\sqrt{2}}\right) k = -\sqrt{3}$
$-\frac{(\sqrt{3}-k)}{\sqrt{2}}v$	$(1, 1, 0, 0, -\sqrt{2}) k \neq 0, \sqrt{3}$ $(r-s, r, s, 0, t) k = 0$	$\left(0, 1, -1, -\frac{\sqrt{3}}{\sqrt{2}}, \frac{1}{\sqrt{2}}\right) k \neq 0, \sqrt{3}$ $(r+s, -r, -s, -\sqrt{3}t, t) k = 0$	$\left(1, 0, -1, -\frac{\sqrt{3}}{\sqrt{2}}, -\frac{1}{\sqrt{2}}\right) k \neq 0, \sqrt{3}$ $(r+s, -r, s, \sqrt{3}t, t) k = 0$
$-\frac{(\sqrt{3}+k)}{\sqrt{2}}v$	$(1, 1, 0, 0, \sqrt{2}) k \neq 0, -\sqrt{3}$ $(r-s, r, s, 0, t) k = 0$	$\left(0, 1, -1, \frac{\sqrt{3}}{\sqrt{2}}, \frac{-1}{\sqrt{2}}\right) k \neq 0, -\sqrt{3}$ $(r+s, -r, -s, -\sqrt{3}t, t) k = 0$	$\left(1, 0, -1, \frac{\sqrt{3}}{\sqrt{2}}, \frac{1}{\sqrt{2}}\right) k \neq 0, -\sqrt{3}$ $(r+s, -r, s, \sqrt{3}t, t) k = 0$
$\sqrt{\frac{3-k^2}{2}}v$	$\left(1, 0, -1, \frac{-3\alpha+}{\sqrt{2}k}, \frac{-\sqrt{3}\alpha+}{\sqrt{2}k}\right) k \neq 0$ $(0, 0, 0, \sqrt{3}, 1) k = 0$	$\left(1, 1, 0, 0, \frac{\sqrt{6}\alpha+}{k}\right) k \neq 0$ $(0, 0, 0, 0, 1) k = 0$	$\left(0, 1, -1, \frac{-3\alpha+}{\sqrt{2}k}, \frac{\sqrt{3}\alpha+}{\sqrt{2}k}\right) k \neq 0$ $(0, 0, 0, \sqrt{3}, -1) k = 0$
$-\sqrt{\frac{3-k^2}{2}}v$	$\left(1, 0, -1, \frac{-3\alpha-}{\sqrt{2}k}, \frac{-\sqrt{3}\alpha-}{\sqrt{2}k}\right) k \neq 0$ $(r-s, r, s, 0, t) k = 0$	$\left(1, 1, 0, 0, \frac{\sqrt{6}\alpha-}{k}\right) k \neq 0$ $(r+s, -r, -s, -\sqrt{3}t, t) k = 0$	$\left(0, 1, -1, \frac{-3\alpha-}{\sqrt{2}k}, \frac{\sqrt{3}\alpha-}{\sqrt{2}k}\right) k \neq 0$ $(r+s, -r, s, \sqrt{3}t, t) k = 0$

TABLE 5. Eigenvectors corresponding to eigenvalues in (4.16).

Introducing a scale factor k such that distance along the η, ξ and γ axes is measured by kv , linear perturbations about each of these axes, with μ and ν perturbed about the corresponding point in the μ, ν plane, yields eigenvalues

$$(4.16) \quad 0, -\frac{(\sqrt{3} \pm k)v}{2}, \pm \sqrt{\frac{3-k^2}{2}}v.$$

Corresponding eigenvectors are listed in Table 5.

With this parametrization, the points determined by $k = \pm\sqrt{3}$ are the points where each axis intersects two of the equilibrium lines 1 - 6. Inspection of Table 5 indicates that for $-\sqrt{3} < k < \sqrt{3}$ the η, ξ , and γ axes are stable and the dimension of the eigenspace for the eigenvalues $-\left(\frac{\sqrt{3} \pm k}{2}\right)v$ changes from one to three at $k = 0$, corresponding to $(\eta, \xi, \gamma) = (0, 0, 0)$.

A similar analysis for perturbations about the equilibrium lines 1 - 6 yields three 0 eigenvalues, and eigenvalues $-\sqrt{2}kv$ and $-\sqrt{2}(\sqrt{3} - k)v$.

Table 6: Eigenvectors for perturbations about equilibrium lines 1-6.

$\lambda = 0$		
	$k \neq 0, \sqrt{3}$	$k = 0, \sqrt{3}$
1	$(1, 1, 0, 0, -\sqrt{2})$	$\begin{pmatrix} t, r, s, \frac{-\sqrt{3}s}{\sqrt{2}}, \frac{s-2t}{\sqrt{2}} \end{pmatrix} k = 0$ $\begin{pmatrix} t, r, s, \frac{\sqrt{3}s}{\sqrt{2}}, \frac{s-2r}{\sqrt{2}} \end{pmatrix} k = \sqrt{3}$
2	$\left(1, 0, -1, \frac{-\sqrt{3}}{\sqrt{2}}, \frac{-1}{\sqrt{2}}\right)$	$\begin{pmatrix} t, r, s, \frac{\sqrt{3}s}{\sqrt{2}}, \frac{s-2r}{\sqrt{2}} \end{pmatrix} k = 0$ $\begin{pmatrix} t, r, s, \frac{-\sqrt{3}(t+r)}{\sqrt{2}}, \frac{r-t}{\sqrt{2}} \end{pmatrix} k = \sqrt{3}$
3	$\left(0, 1, -1, \frac{-\sqrt{3}}{\sqrt{2}}, \frac{-1}{\sqrt{2}}\right)$	$\begin{pmatrix} t, r, s, \frac{-\sqrt{3}(t+r)}{\sqrt{2}}, \frac{r-t}{\sqrt{2}} \end{pmatrix} k = 0$ $\begin{pmatrix} t, r, s, \frac{\sqrt{3}s}{\sqrt{2}}, \frac{-s-2t}{\sqrt{2}} \end{pmatrix} k = \sqrt{3}$
4	$(1, 1, 0, 0, \sqrt{2})$	$\begin{pmatrix} t, r, s, \frac{\sqrt{3}s}{\sqrt{2}}, \frac{-s-2t}{\sqrt{2}} \end{pmatrix} k = 0$ $\begin{pmatrix} t, r, s, \frac{-\sqrt{3}s}{\sqrt{2}}, \frac{-s-2r}{\sqrt{2}} \end{pmatrix} k = \sqrt{3}$
5	$\left(1, 0, -1, \frac{\sqrt{3}}{\sqrt{2}}, \frac{1}{\sqrt{2}}\right)$	$\begin{pmatrix} t, r, s, \frac{-\sqrt{3}s}{\sqrt{2}}, \frac{-s-2r}{\sqrt{2}} \end{pmatrix} k = 0$ $\begin{pmatrix} t, r, s, \frac{\sqrt{3}(t+r)}{\sqrt{2}}, \frac{-r-t}{\sqrt{2}} \end{pmatrix} k = \sqrt{3}$
6	$\left(0, 1, -1, \frac{\sqrt{3}}{\sqrt{2}}, \frac{1}{\sqrt{2}}\right)$	$\begin{pmatrix} t, r, s, \frac{\sqrt{3}(t+r)}{\sqrt{2}}, \frac{-r-t}{\sqrt{2}} \end{pmatrix} k = 0$ $\begin{pmatrix} t, r, s, \frac{-\sqrt{3}s}{\sqrt{2}}, \frac{s-2t}{\sqrt{2}} \end{pmatrix} k = \sqrt{3}$
$\lambda = -\sqrt{2}kv$		
		$k = \sqrt{3}$
1	$\left(1, 1, 0, 0, -\frac{\sqrt{2}(\sqrt{3}-2k)}{\sqrt{3}}\right)$	$(1, 1, 0, 0, \sqrt{2})$
2	$\left(1, 0, -1, -\frac{(\sqrt{3}-2k)}{\sqrt{2}}, -\frac{(\sqrt{3}-2k)}{\sqrt{6}}\right)$	$\left(1, 0, -1, \frac{\sqrt{3}}{\sqrt{2}}, \frac{1}{\sqrt{2}}\right)$
3	$\left(0, 1, -1, -\frac{\sqrt{3}-2k}{\sqrt{2}}, \frac{\sqrt{3}-2k}{\sqrt{6}}\right)$	$\left(0, 1, -1, \frac{\sqrt{3}}{\sqrt{2}}, -\frac{1}{\sqrt{2}}\right)$
continued on the next page		

4	$\left(1, 1, 0, 0, \frac{\sqrt{2}(\sqrt{3}-2k)}{\sqrt{3}}\right)$	$(1, 1, 0, 0, -\sqrt{2})$
5	$\left(1, 0, -1, \frac{\sqrt{3}-2k}{\sqrt{2}}, \frac{\sqrt{3}-2k}{\sqrt{6}}\right)$	$\left(1, 0, -1, -\frac{\sqrt{3}}{\sqrt{2}}, -\frac{1}{\sqrt{2}}\right)$
6	$\left(0, 1, -1, \frac{\sqrt{3}-2k}{\sqrt{2}}, -\frac{\sqrt{3}-2k}{\sqrt{6}}\right)$	$\left(0, 1, -1, -\frac{\sqrt{3}}{\sqrt{2}}, \frac{1}{\sqrt{2}}\right)$
$\lambda = -\sqrt{2}(\sqrt{3}-k)v$		
$k = 0$		
1	$\left(\frac{2k}{\sqrt{3}}, 1, -\frac{\sqrt{3}-2k}{\sqrt{3}}, -\frac{\sqrt{3}-2k}{\sqrt{2}}, \frac{\sqrt{3}-2k}{\sqrt{6}}\right)$	$\left(0, 1, -1, -\frac{\sqrt{3}}{\sqrt{2}}, \frac{1}{\sqrt{2}}\right)$
2	$\left(1, \frac{\sqrt{3}-2k}{\sqrt{2}}, -\frac{2k}{\sqrt{3}}, 0, \frac{\sqrt{2}(\sqrt{3}-2k)}{\sqrt{3}}\right)$	$(1, 1, 0, 0, \sqrt{2})$
3	$\left(\frac{\sqrt{3}-2k}{\sqrt{3}}, \frac{2k}{\sqrt{3}}, -1, \frac{\sqrt{3}-2k}{\sqrt{2}}, \frac{\sqrt{3}-2k}{\sqrt{6}}\right)$	$\left(1, 0, -1, \frac{\sqrt{3}}{\sqrt{2}}, \frac{1}{\sqrt{2}}\right)$
4	$\left(\frac{2k}{\sqrt{3}}, 1, -\frac{\sqrt{3}-2k}{\sqrt{3}}, \frac{\sqrt{3}-2k}{\sqrt{2}}, -\frac{\sqrt{3}-2k}{\sqrt{6}}\right)$	$\left(0, 1, -1, \frac{\sqrt{3}}{\sqrt{2}}, -\frac{1}{\sqrt{2}}\right)$
5	$\left(1, \frac{\sqrt{3}-2k}{\sqrt{2}}, -\frac{2k}{\sqrt{3}}, 0, -\frac{\sqrt{2}(\sqrt{3}-2k)}{\sqrt{3}}\right)$	$(1, 1, 0, 0, -\sqrt{2})$
6	$\left(\frac{\sqrt{3}-2k}{\sqrt{3}}, \frac{2k}{\sqrt{3}}, -1, -\frac{\sqrt{3}-2k}{\sqrt{2}}, -\frac{\sqrt{3}-2k}{\sqrt{6}}\right)$	$\left(1, 0, -1, -\frac{\sqrt{3}}{\sqrt{2}}, -\frac{1}{\sqrt{2}}\right)$

Parameterization has been chosen so that $0 \leq k \leq \sqrt{3}$ corresponding for each of the equilibrium lines to the segments shown in Figures 8 and 9. The lines themselves are the eigenspaces corresponding to the 0 eigenvalues. Thus, the indicated segments are stable for $0 < k < \sqrt{3}$ and unstable for values of k outside of this range.

Eigenvectors for perturbations about these equilibrium lines are shown in Table 6.

Some system orbits are shown in Figures 11-14.

In Figures 11-13 initial conditions are taken as small circles about the origin with (μ, ν) equal to $(0, 0)$ in 11, $(0, .25)$ in 12, and $(0, -.25)$ in 13. Orbits converge towards the origin in the (η, ξ, γ) -space and show an orbital flow about $(0, 0)$ in the (μ, ν) -space.

Figure 14 shows orbits computed for initial conditions taken as small circles about the η -axis for $-2 < \eta < 2$ and $(\mu, \nu) = \left(-\frac{\nu}{\sqrt{2}}, -\frac{\sqrt{3}\nu}{\sqrt{2}}\right)$. Note the complex behavior that appears for $|\eta| \geq \sqrt{3}$ which is where the η -axis intersects the other equilibrium lines, and also the point where these lines become unstable.

5. DISCUSSION

We have considered a family of ordinary differential equations with quadratic force terms exhibiting a structure diagrammed by (n, s) -star polygons. These equations are taken as representing n component systems in which interactions catalyze transformations between components rather than replication of components. Results on equilibrium manifolds are given for these systems, showing both similarities to, and differences from the usual replicator equations used to describe hypercycles.

If n is even there will be a central equilibrium if and only if equation (2.4) is satisfied and if this equilibrium exists it will be structurally unstable in the more general parameter space. If n is odd, the central equilibrium is stable. There are also equilibrium manifolds that reside on the edges and faces of the concentration simplex and while the location of the central equilibrium depends on the rate constants, the locations of these other equilibria do not.

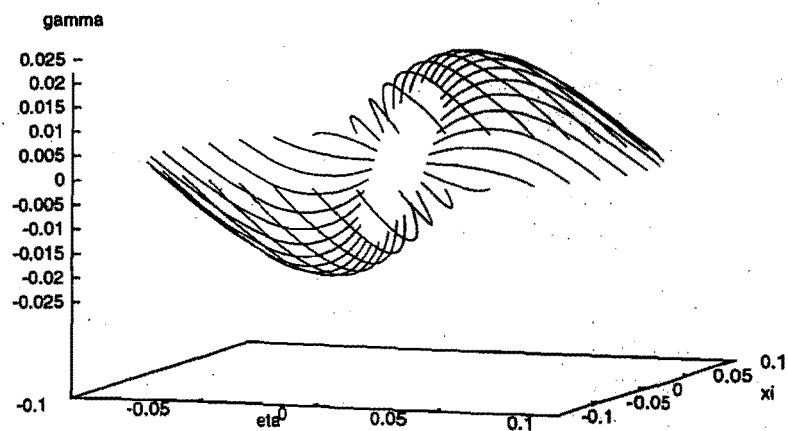
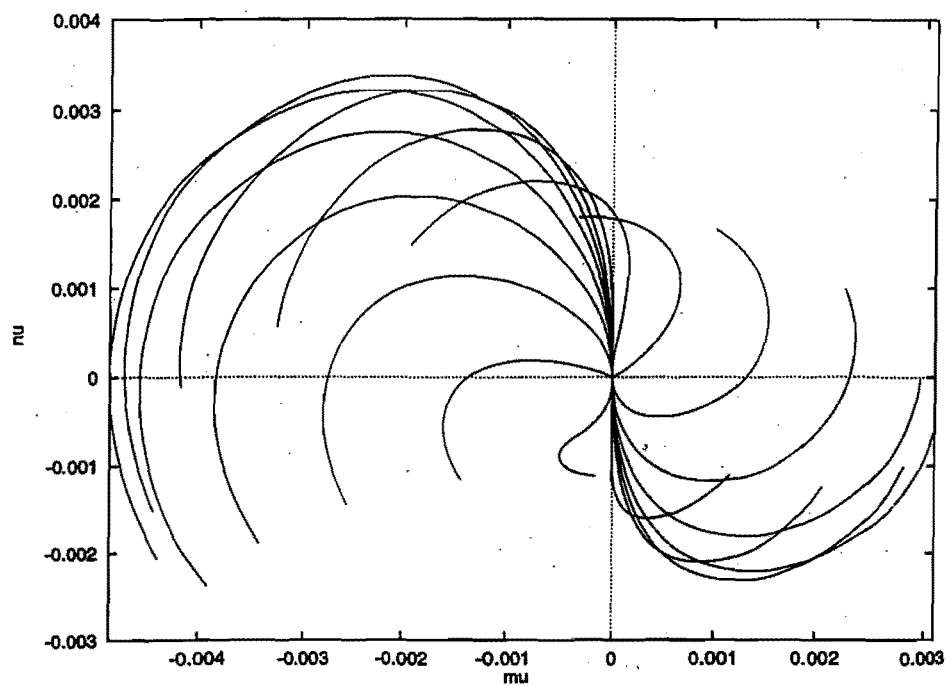


FIGURE 11. Orbits of equations (4.13) for $(n, s) = (6, 2)$ with initial conditions taken as a small circle about the origin in (η, ξ, γ) -space and at $(0, 0)$ in (μ, ν) plane.

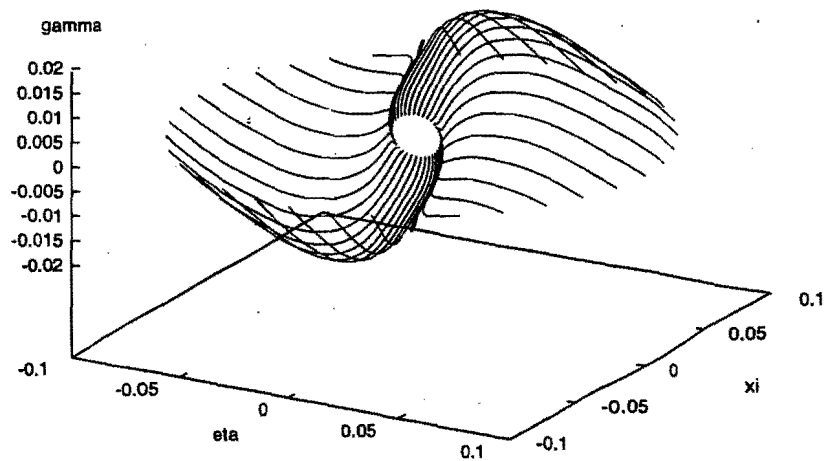
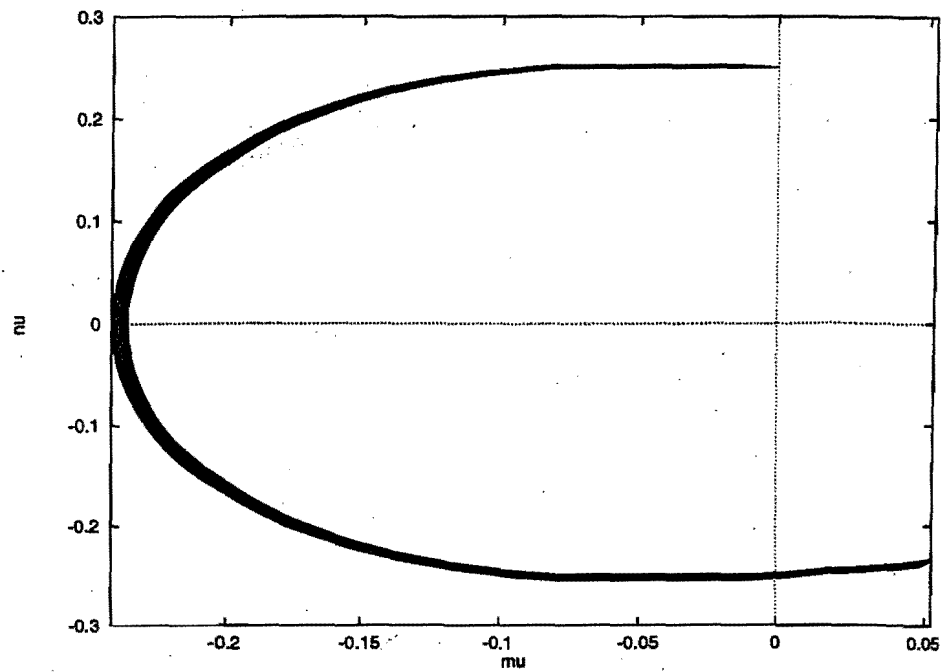


FIGURE 12. Orbits of equations (4.13) for $(n, s) = (6, 2)$ with initial conditions taken as a small circle about the origin in (η, ξ, γ) -space and at $(0, .25)$ in (μ, ν) plane.

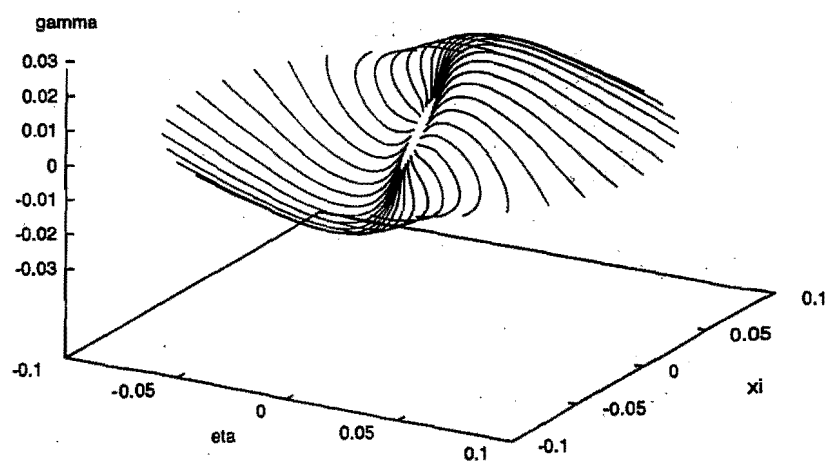
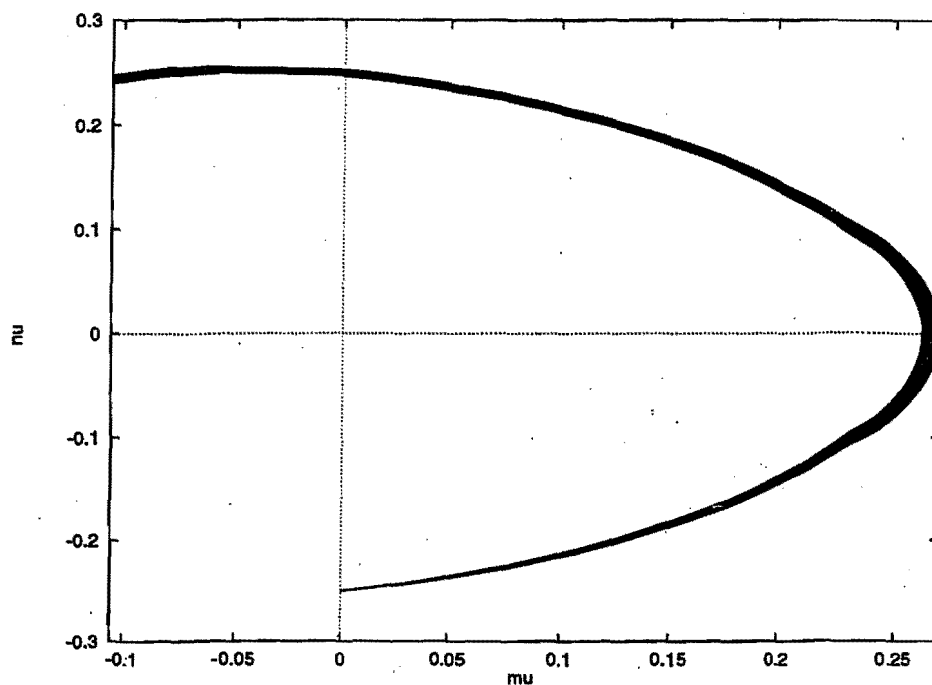


FIGURE 13. Orbits of equations (4.13) for $(n, s) = (6, 2)$ with initial conditions taken as a small circle about the origin in (η, ξ, γ) -space and at $(0, -0.25)$ in (μ, ν) plane.

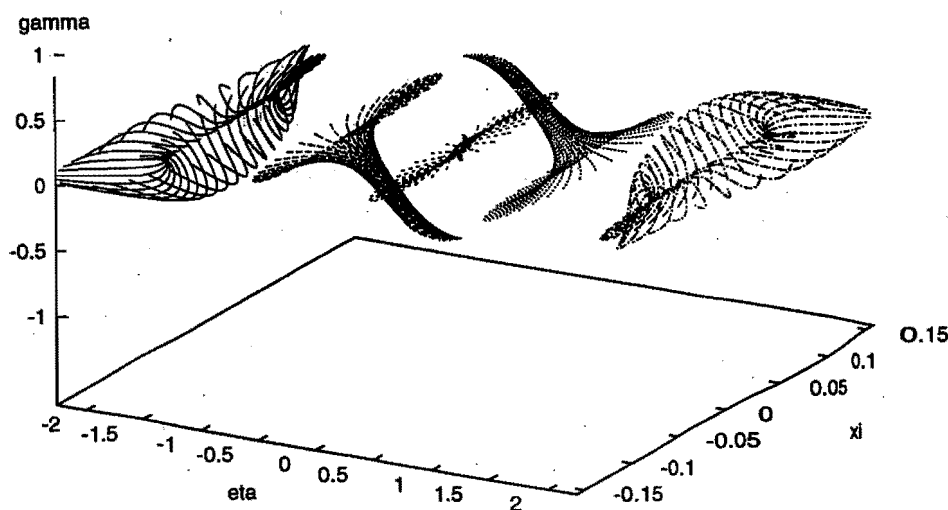


FIGURE 14. Orbits of equations (4.13) for $(n, s) = (6, 2)$ with initial conditions taken as a small circle about the η -axis and at point of projection of η -axis in (μ, ν) plane.

Examples have been discussed for dimensions 3, 4, 5, and 6 with the most interesting geometric configurations of the equilibrium manifolds showing up in dimensions 3 and 6. In dimension 5 the five equilibrium lines lying along boundaries of the concentration simplex are unstable, with orbits either running off to infinity, or into the central equilibrium.

In computing the stability criteria the rate constants k_i were all set equal to one. This allowed use of well-known results on circulant matrices for computation of eigenvalues of the perturbation coefficient matrix. An interesting question remains as to whether or not there are results on the eigenvalues for the matrices that would result from allowing arbitrary rate constants.

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