A CONNECTION MATRIX APPROACH ILLUSTRATED BY MEANS OF A PREDATOR-PREY MODEL INVOLVING GROUP DEFENSE

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ABSTRACT

Our goal is firstly to show that the connection matrix is a very useful tool for analyzing biological models and secondly to show that given some fundamental results, to apply the technique requires only a knowledge of basic linear algebra and differential equations theory. Although the technique is dimension independent, we illustrate the ideas on a planar model of predator-prey dynamics. The model we use is very similar to the classical Gause type model of predator-prey interaction, but has richer dynamics. The model is of interest in itself and the results provide strong support for Rosenzweig's *paradox of enrichment*.

1. INTRODUCTION

Our aim is to show that the connection matrix is a very useful tool for analyzing biological models, perhaps the natural second step

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to follow a standard linear analysis. Because we wish to emphasize the general ideas involved, how they interrelate, and how they may be used in applications, we leave the details of the proofs to a later paper (Mischaikow and Wolkowicz in progress). Out of necessity the connection matrix is based upon rather complicated and abstract ideas from algebraic topology. However, we hope that the reader will observe that given some fundamental results, to construct and interpret these matrices requires only a knowledge of basic linear algebra and differential equations (see for example Hirsch and Smale (1974)).

Although the connection matrix technique is dimension independent, we choose to illustrate how it can be used on a two dimensional model of a predator-prey system involving group defense. Since phase portraits can be drawn this can help the reader to better relate the type of information one can derive from the matrix to the dynamics of the model. As well, for a certain parameter range, the dynamics are almost identical to a very well known model of population dynamics, the classical Gause type model of predator-prey interaction, a model with which most biologists are familiar and comfortable. However, this model has a richer dynamics, including not only a Hopf bifurcation but also a homoclinic bifurcation, making it a particularly good model for our purposes. Finally, this model is of interest in itself since its dynamics provide strong support for the so-called *paradox of enrichment* (see Freedman and Wolkowicz (1986), Gilpin (1972), May (1972), McAllister (1972), Riebesell (1974), and Rosenzweig (1971, 1972a, 1972b)). In fact, in this model there is a threshold of enrichment. If this threshold is exceeded by increasing the carrying capacity of the environment, extinction of the predator results (asymptotically) for all but a set of initial conditions of measure zero.

In Section 2 we discuss the model and explain its dynamics from a bifurcation theory point of view. For more details concerning the model and the biological implications of the results see Freedman and Wolkowicz (1986) and Wolkowicz (1988). For proofs of the results using planar techniques see Wolkowicz (1988).

In Section 3 a brief introduction to the connection matrix is given beginning with preliminary background material and culminating with the definition and some basic properties of the connection matrix. The concepts given in this section are illustrated by means of simple examples as well as examples related to the model in Section 2.

We begin Section 4 by showing how to actually construct and interpret a connection matrix for the model described in Section 2. We then indicate how the connection matrix (as an alternative to the approach discussed in Section 2) could have been used to study the predator-prey model. In particular we show how it can be used to prove the existence of a stable periodic orbit and a homoclinic orbit and how to trace bifurcations for various parameter values. We conclude this section with a brief discussion of other applications of these techniques.

We emphasize that the connection matrix is a dimension independent technique and although we illustrate its use on a two dimensional system, its primary importance is for the analysis of models of dimension three or higher.

2. PREDATOR-PREY MODEL ASSUMING GROUP DEFENSE

By group defense we mean the phenomenon whereby predation is decreased or even eliminated due to the ability of the prey to defend or disguise themselves as their numbers increase beyond some threshold. See Tener (1965) and Holmes and Bethel (1972) for examples of where this phenomenon is known to occur in nature.

As in Freedman and Wolkowicz (1986) and Wolkowicz (1988), we consider the following system of autonomous ordinary differential equations of generalized Gause-type as a model of predator-prey interaction with group defense exhibited by the prey.

$$\begin{aligned} \dot{x} &= xg(x,K) - yp(x) \triangleq p(x)(F(x,K) - y) \\ \dot{y} &= y(-s+q(x)) \\ x(0) &\geq 0,\ y(0) \geq 0, \quad \dot{} = \frac{d}{dt} \end{aligned} \qquad (1)_K$$

where $x(t)$ and $y(t)$ denote the density of prey and predator populations, respectively. It is assumed that the functions g, p and q are continuously differentiable and that s and K are positive constants. When reference is made to model $(1)_K$, if there is no ambiguity, the subscript K shall be omitted. Here, $g(x,K)$ represents the specific growth rate of the prey in the absence of predation. Logistic growth, $g(x,K) = r(1-x/K)$ is considered a prototype

This leads to the following assumptions on g:

for any $K > 0$

$$g(K,K) = 0, \quad g(0,K) > 0, \quad g_K(0,K) \geq 0 \text{ and } \lim_{K\to\infty} g(0,K) \text{ is finite} \tag{2}$$

$$g_{xK}(0,K) \geq 0, \quad g_x(0,K) \leq 0 \text{ and } \lim_{K\to\infty} g_x(0,K) = 0; \tag{3}$$

for any $K > 0$ and $x > 0$

$$g_K(x,K) > 0, \quad g_{xK}(x,K) > 0, \quad g_x(x,K) < 0 \text{ and } \lim_{K\to\infty} g_x(x,K) = 0. \tag{4}$$

The function $p(x)$ denotes the predator response function and is assumed to satisfy:

$$p(0) = 0, \quad p'(0) > 0, \quad p''(0) < 0, \quad p(x) > 0 \text{ for } x > 0. \tag{5}$$

In order to model group defense, it is assumed as well that there exists $\bar{h} > 0$ such that

$$p'(x) > 0 \quad \text{for} \quad 0 \leq x < \bar{h}, \tag{6}$$

and

$$p'(x) < 0 \quad \text{for} \quad \bar{h} < x. \tag{7}$$

For technical reasons it is assumed that

$$P(x) \triangleq p(x) - xp'(x) > 0 \quad \text{for all} \quad x > 0. \tag{8}$$

In particular, since $P'(x) = -xp''(x)$ and $P(0) = 0$ it is sufficient to assume that $p(x)$ is concave for $0 < x < \bar{h}$ (since $p'(x) \leq 0$ for $x \geq \bar{h}$, clearly $P(x) > 0$ for $x \geq \bar{h}$).

A function of the form $p(x) = mx/(ax^2 + bx + 1)$ where m, a, and b are positive constants satisfies these assumptions and approximates Holling type II dynamics for small x.

The rate of conversion of prey to predator is described by $q(x)$. In Gause's model $q(x) = cp(x)$ for some positive constant c. It is assumed that $q(x)$ has properties similar to $p(x)$. In particular

$$q(0) = 0, \quad q(x) > 0 \quad \text{for} \quad x > 0, \quad q(\bar{h}) > s, \tag{9}$$

$$q'(x) > 0 \quad \text{for} \quad 0 \leq x < \bar{h} \tag{10}$$

and

$$q'(x) < 0 \quad \text{for} \quad x > \bar{h}. \tag{11}$$

It is also assumed that $q(\bar{h}) > s$, since otherwise the predator cannot survive on the prey at any density. This implies that there exists $\lambda < \bar{h}$ such that $q(\lambda) = s$ and there may exist $\mu > \bar{h}$ such that $q(\mu) = s$.

Other examples of $g(x,K)$, $p(x)$ and $q(x)$ can be found in Boon and Laudelout (1962), Holling (1965), May (1972), Rosenzweig (1971), and Yang and Humphrey (1975).

The predator isoclines are the vertical lines $x \equiv \lambda$ and $x \equiv \mu$ (provided μ exists). If $\mu > K$ the asymptotic outcome is the same as in the classical case. It shall therefore be assumed that μ is finite throughout the remainder of this paper.

The prey isocline is given by the function $F(x,K) = xg(x,K)/p(x)$. The properties of this function play a key role in the analysis given in Wolkowicz (1988). In particular, under our assumptions it follows that

> if $H_M \triangleq H_M(K)$ is a local maximum of F satisfying $F_x(H_M,K) = 0$, then as K increases, H_M shifts to the right and is to the right of any fixed $\mu > 0$ for all sufficiently large K, (12)

and

> if $H_m \triangleq H(K)$ is a local minimum of F satisfying $F_x(H_m,K) = 0$, then as K increases, H_m shifts to the left or disappears (i.e. $H_m < 0$) and disappears for all sufficiently large K. (13)

As a consequence, if we fix $\bar{\mu} > 0$, there exists $K^* > 0$ such that for all $K > K^*$, F has no interior local minimum and any interior local maximum is to the right of $\bar{\mu}$.

For both biological realism and mathematical convenience we impose the following restriction on F.

$$\text{There are at most two values of } x \in (0,K) \text{ where } F_x(x,K) = 0. \qquad (14)$$

This holds for example, if $g(x) = r(1 - x/K)$, where r is a positive constant and $p(x) = mx/(ax^2 + bx + 1)$ where m, a and b are positive constants.

Finally we observe that there can exist at most one pair $(\bar{x},\bar{K})$ such that $F_x(x,\bar{K}) < 0$ for all $0 < x < \bar{K}$, $x \neq \bar{x}$ and $F_x(\bar{x},\bar{K}) = 0$. This forces F to have an interior local maximum, H_M for all $K > \bar{K}$. For technical reasons we shall assume that there never exists such a pair $(\bar{x},\bar{K})$ with $\bar{x} = \lambda$ or μ. This would be an extremely rare coincidence biologically. (This insures that whenever $F_x(\lambda,\hat{K}) = 0$, a Hopf bifurcation occurs as K passes through $\hat{K}$.)

Next we consider some of the properties of the different invariant sets associated with (1). (The proofs can be found in Wolkowicz (1988).) First we note that the x-axis, y-axis and hence the interior of the first quadrant are all invariant under (1). Solutions for which $x(0) > 0$ and $y(0) > 0$ are bounded in positive time and given any $\epsilon > 0$ these solutions satisfy $x(t) < K + \epsilon$ for all sufficiently large t.

There are four possible critical points of $(1)_K$. The first two, $M(0) = (0,0)$ and $M(K) = (K,0)$ always lie on the coordinate axes. The other two, $M(\lambda) = (\lambda,F(\lambda,K))$ and $M(\mu) = (\mu,F(\mu,K))$ lie inside the first quadrant if and only if $\lambda < K$ and $\mu < K$, respectively (otherwise $F(\lambda,K) \leq 0$ and $F(\mu,K) \leq 0$, respectively). If $\lambda = K$ (or $\mu = K$) then $M(\lambda)$ (or $M(\mu)$) coalesces with $M(K)$.

In order to demonstrate the connection matrix technique, it is useful to extend the dynamics of our model to the entire plane. Since the first quadrant and the coordinate axes are invariant, provided the extension agrees smoothly with (1), it will have no bearing on the dynamics in the first quadrant. (We shall also denote the extended system by (1) since this should not lead to any confusion.) It will therefore be convenient to make the following assumptions:

If $K < \lambda < \mu$ then $M(\lambda)$ is a saddle point, $M(\mu)$ is an attractor and the set of connections (see Definition 3.2) $C(M(\lambda),M(K))$ and $C(M(\lambda),M(\mu))$ consist of unique orbits. Furthermore, these are the only bounded solutions outside of the closure of the first quadrant and they lie above the line $y = -L$ for some $L > 0$.

If $\lambda < K < \mu$, then $M(\mu)$ is an attractor and $C(M(K),M(\lambda))$ consists of a unique orbit. Again this describes all the bounded solutions outside the closure of the first quadrant. We assume these bounded solutions all lie above the line $y = -L$, for some $L > 0$.

(For the reader who prefers to have a more concrete extension, define $p(x) < 0$, $q(x) < s$ and $g(x,K) > 0$ for $x < 0$, and $g(x,K) < 0$ for $x > K$. Then (1) has the dynamics described.)

The local stability analysis for all the critical points is summarized in Table 1. If $\mu > K$ or $\mu = +\infty$ then the dynamics are basically the same as the dynamics of the classical model, that is the model in which there is no group defense.

Next consider periodic orbits. By observing how solutions must cross the predator and prey isoclines (see Figure 1) it follows that any periodic orbit of our system must surround $M(\lambda)$ and cannot surround any other critical point. Denote by $M(\pi)$ the set of bounded orbits of (1) which surround $M(\lambda)$ and are also bounded away from the set of critical points $\{M(K),M(0),M(\lambda),M(\mu)\}$. (Note that $M(\pi) = \phi$ is possible.) In Wolkowicz (1988) it is shown that the slope of the portion of the prey isocline inside any periodic orbit must change sign and hence must enclose a local minimum or a local maximum of F. Thus, by (7) it follows that for all sufficiently large K, $(1)_K$ admits no nontrivial periodic orbits. As well, it is shown that if K is sufficiently close to λ, $(1)_K$ admits no periodic orbits.

As for homoclinic orbits, in Wolkowicz (1988) it was shown that the only critical point that can be involved in a homoclinic orbit is

$M(\mu)$ and any homoclinic orbit must surround $M(\lambda)$ and cannot surround any other critical point. Also, just as for periodic orbits, any homoclinic orbit must enclose either a local minimum or a local maximum of F and so $(1)_K$ admits no homoclinic orbit for all sufficiently large K.

An immediate consequence of these facts is:

<u>Theorem 2.1</u>. Assume that for some $\tilde{K} > 0$, F has a local maximum $(H_M, F(H_M, \tilde{K}))$. There exists $K^* > \mu$ such that if $K > K^*$, then all solutions of $(1)_K$ with positive initial conditions converge to $M(K)$ except those originating on the stable manifold of $M(\mu)$ or at the point $M(\lambda)$.

Thus the model predicts that too much enrichment always results in the extinction of the predator unless the prey isocline is monotone decreasing for all values of the carrying capacity K, in which case the following holds:

<u>Proposition 2.2</u>. Assume $F_x(x,K) < 0$ for all $K > \mu$ and all $0 < x < K$. Then the stable manifold of $M(\mu)$ separates the positive quadrant into two regions. Solutions originating in the inner region all converge to $M(\lambda)$. Solutions with initial conditions in the outer region all converge to $M(K)$.

Since the dynamics are more interesting and the model more realistic biologically, it is assumed that the prey isocline has a local maximum for at least one value of $\tilde{K} > 0$ (and hence for all $K > \tilde{K}$ by (2)). Otherwise $F(x,K)$ is strictly monotonically decreasing for all $K > 0$, $M(\lambda)$ is asymptotically stable, there are no periodic orbits or homoclinic orbits and if $\lambda < \mu < K$ the dynamics are similar to those shown in Figure 3.c, (though $M(\mu)$ would be lower than $M(\lambda)$).

Next we consider how the dynamics change as K varies. First note that $M(0)$ undergoes no bifurcations. It remains a saddle for all K

with stable manifold along the y-axis and unstable manifold along the x-axis. For $\lambda > K$, $M(K)$ is an asymptotically stable critical point. At $\lambda = K$, $M(\lambda)$ and $M(K)$ coalesce. As K increases, $M(K)$ loses stability becoming a saddle, whereas $M(\lambda)$ enters the first quadrant as an asymptotically stable critical point. We call this bifurcation a λ-exchange. Similarly, for $\mu = K$, $M(\mu)$ and $M(K)$ coalesce. As K increases further, $M(K)$ regains its stability and $M(\mu)$ enters the first quadrant as a saddle and remains a saddle for all K. We refer to this bifurcation as a μ-exchange.

Since any periodic orbit must surround $M(\lambda)$ and cannot surround any other critical point, $M(\lambda)$ is the only candidate for a Hopf bifurcation. Since our system is planar, and all solutions are uniformly asymptotically bounded, though semi-stable periodic orbits may appear and disappear spontaneously, the only way stable or unstable period orbits can appear or disappear is either in pairs (one stable and one unstable), or through a homoclinic bifurcation.

As K increases there is always a Hopf bifurcation about $M(\lambda)$ and a homoclinic bifurcation involving $M(\mu)$. The Hopf bifurcation occurs for the unique value $K = \hat{K}$ for which $(\lambda, \hat{K})$ is either a local maximum or a local minimum of F, the prey isocline. The direction and stability of the bifurcating periodic orbit is determined by the sign of the quantity:

$$w = \frac{-\,p(\lambda)F_{xx}(\lambda,\hat{K})q''(\lambda)}{q'(\lambda)} + p(\lambda)F_{xxx}(\lambda,\hat{K}) + 2\,p'(\lambda)F_{xx}(\lambda,\hat{K}). \qquad (15)$$

If $w < 0$ the bifurcating periodic orbit is orbitally stable and exists provided $K > \hat{K}$ and $|K - \hat{K}|$ sufficiently small. If $w > 0$ then the bifurcating periodic orbit is unstable and exists provided $K < \hat{K}$ and $|K - \hat{K}|$ sufficiently small.

If $w > 0$ and $(\lambda, \hat{K})$ is a local maximum of the prey isocline it follows that for some $K < \hat{K}$ there is either the spontaneous appearance of (a semi-stable periodic orbit which splits into) a pair of stable and unstable periodic orbits or a Hopf bifurcation and a homoclinic bifurcation occur simultaneously (because the outermost periodic orbit must be asymptotically stable). If the Hopf bifurcation occurs before the μ-exchange then only the former scenario is possible.

In Wolkowicz (1988) the homoclinic bifurcation is investigated by means of a phase plane argument, focusing attention on the stable and unstable manifolds, $E^s_{M(\mu)}$ and $E^u_{M(\mu)}$, of $M(\mu)$. Consider that part of $E^s_{M(\mu)}$ $(E^u_{M(\mu)})$ that approaches (leaves) $M(\mu)$ from (towards) the left and call it Γ^s (Γ^u). Freedman and Wolkowicz (1986) point out that there are at most three possibilities for Γ^s (see Figure 3). Case 1: In negative time Γ^s leaves the strip $0 \leq x \leq \mu$ (Figure 3a). Γ^u must therefore approach (in forward time) $M(\lambda)$ or a periodic orbit enclosing $M(\lambda)$. Case 2: Γ^s is a homoclinic orbit, that is $\Gamma^s = \Gamma^u$ (Figure 3b). Case 3: Γ^s remains in the strip $0 \leq x < \mu$ for all time and if followed as time is reversed either approaches the outermost periodic orbit surrounding $M(\lambda)$ or $M(\lambda)$ if there are no periodic orbits. In this case Γ^u approaches $M(K)$ (Figure 3c).

By Theorem 2.1 it follows that Case 3 holds for all sufficiently large K. As well it can be shown that there always exists some $K > 0$ such that Case 1 holds. Thus by continuity it follows that Case 2 must hold for some K as well, and hence there always exists a homoclinic bifurcation.

3. THE CONNECTION MATRIX

In this section we shall give various definitions and basic theorems which relate to the connection matrix. We begin with a series of basic definitions that lead us to the definition of the Conley or homology index. References for this include Conley (1976), Conley and Zehnder (1984), Moeckel (preprint), Salamon (1985), and Smoller (1983).

Let $(z,t) \longrightarrow z\cdot t$ denote a flow on $\mathbb{R}^n$ where $z \in \mathbb{R}^n$ and $t \in \mathbb{R}$. S is called an *invariant set* if $S\cdot\mathbb{R} = S$. A compact invariant set, S, is said to be an *isolated invariant set* if there exists a compact neighborhood, N, of S such that S is the maximal invariant set in N. In this case N is called an *isolating neighborhood of* S. Simple examples of isolated invariant sets include hyperbolic critical points and periodic orbits.

Definition 3.1. Given two isolated invariant sets S_1 and S_2, the *set of connections* from S_1 to S_2 is

$$C(S_1,S_2) = \{ z : \omega^*(z) \subset S_1 \text{ and } \omega(z) \subset S_2 \}, \qquad (16)$$

where

$$\omega(z) = \bigcap_{t\geq 0} \mathrm{cl}(z\cdot[t,\infty)) \text{ and } \omega^*(z) = \bigcap_{t\geq 0} \mathrm{cl}(z\cdot(-\infty,-t]) \qquad (17)$$

(i.e. $\omega(z)$ and $\omega^*(z)$ are the positive and negative omega limit sets, respectively, of the trajectory through z).

If we define the index set

$$P \triangleq \{0,K,\lambda,\mu,\pi\} \qquad (18)$$

and

$$C \triangleq \bigcup_{i,j \in P} C(M(i),M(j)) \qquad (19)$$

then the set $\mathcal{S}$ of all bounded solutions of (1),

$$\mathcal{S} \triangleq C \cup (\bigcup_{i \in P} M(i)), \qquad (20)$$

is another example of a compact, isolated invariant set.

Definition 3.2. A pair of compact sets (N_1,N_0) is an *index pair* for an isolated invariant set, S, if $N_0 \subset N_1$ and

(i) $N_1 \backslash N_0$ is a neighborhood of S and $\mathrm{cl}(N_1\backslash N_0)$ is an isolating neighborhood of S.

(ii) N_0 is *positively invariant* in N_1, i.e. if $x \in N_0$, $t \geq 0$ and $x\cdot[0,t] \subset N_1$, then $x\cdot[0,t] \subset N_0$.

(iii) N_0 is an *exit set* for N_1, i.e. if $x \in N_1$ and $[0,\infty) \not\subset N_1$, then there exists $t \geq 0$ such that $x\cdot[0,t] \subset N_1$ and $x\cdot t \in N_0$.

See Table 3 for examples of index pairs for several different isolated invariant sets. The reader who knows no algebraic topology can skip to Remark 3.5.

Given an index pair (N_1,N_0), let N_1/N_0 denote the quotient space of N_1 obtained by collapsing N_0 to a point. Let $[N_0]$ denote the special point in N_1/N_0 obtained from N_0.

Definition 3.3. Given an isolated invariant set S with index pair (N_1, N_0), the *Conley index* of S is the homotopy type of the pointed topological space $(N_1/N_0, [N_0])$. We denote the index by $h(S)$ (i.e. $h(S) \sim (N_1/N_0, [N_0])$.

Theorem 3.4. (See Conley (1976), Conley and Zehnder (1984), Salamon (1985) and Smoller (1983).) Given an isolated invariant set S, $h(S)$ exists, is well defined and any nearby flow will have a nearby isolated invariant set with the same index.

In general working with the homotopy equivalence classes of topological spaces is difficult. To simplify matters we shall restrict our attention to the singular homology vector spaces over $\mathbb{Z}_2$ (the integers mod 2) of $h(S)$, that is, $H_*(h(S), \mathbb{Z}_2)$. Then

$$H_*(h(S);\mathbb{Z}_2) \triangleq H_*(N_1/N_0,[N_0];\mathbb{Z}_2) = \{H_n(N_1/N_0,[N_0];\mathbb{Z}_2)\}_{n=0,1,2,\ldots} \quad (21)$$

where each $H_n(N_1/N_0,[N_0];\mathbb{Z}_2)$ is a vector space over $\mathbb{Z}_2$. Thus $H_*(h(S);\mathbb{Z}_2)$ is an infinite collection of vector spaces over $\mathbb{Z}_2$ indexed by the nonnegative integers. To simplify the notation let $H_*(h(S)) = H_*(h(S);\mathbb{Z}_2)$.

Remark 3.5. The Conley index associates to each isolated invariant set a pointed topological space. The homology of this topological space is an algebraic object called the Conley homology index. An important question in dynamical systems is: given different isolated invariant sets, how are they related by the flow? The connection matrix gives an algebraic answer to this by giving a relationship between the homologies that are associated with the invariant sets via the Conley index.

In order to construct connection matrices, one must be able to compute the Conley homology index

$$H_*(\mathcal{A}(S)) = (H_1(\mathcal{A}(S)), H_2(\mathcal{A}(S)), \ldots, \quad) \tag{22}$$

of certain isolated invariant sets. The index can be thought of as an ordered sequence of vector spaces over $\mathbb{Z}_2$ with most of the vector spaces isomorphic to 0. An important property of the index is that it is determined by an index pair. Thus, given (N_1, N_0), an index pair for S, the maximal invariant set contained in the interior of $N_1 \backslash N_0$, we can compute $H_*(\mathcal{A}(S))$ without explicitly knowing the structure of S. Propositions 3.7 and 3.8 are examples of this fact. The following three propositions can be used as rules for computing $H_*(\mathcal{A}(S))$. The indices of most of the isolated invariant sets we need to consider in model (1) are computed in Table 3.

<u>Proposition 3.6.</u> Let S be a hyperbolic critical point with exactly k eigenvalues having positive real part. Then

$$H_n(\mathcal{A}(S)) \approx \begin{cases} \mathbb{Z}_2 & \text{if } n = k, \\ 0 & \text{otherwise.} \end{cases}$$

<u>Proposition 3.7.</u> Let (N_1, N_0) be an index pair for S. If N_0 is a deformation retract of N_1 (i.e. there is a continuous function $H : N_1 \times [0,1] \longrightarrow N_1$ such that $H(x,0) = x$ and $H(x,1) \in N_0$ for every $x \in N_1$ and $H(a,t) = a$, for every $a \in N_0$ and $t \in [0,1]$), then $H_n(\mathcal{A}(S)) \approx 0$, $n=0,1,2,\ldots$.

$\mathcal{S}$, the set of all bounded solutions of (1) has such an index pair (see Table 3) and hence $H_n(\mathcal{A}(S)) \approx 0$, $n = 0,1,2,\ldots$.

Restricting our attention for the moment to a flow in $\mathbb{R}^2$, we have the following (see Table 3).

Proposition 3.8. Let (N_1, N_0) be an index pair for S. Assume N_1 is homeomorphic to an annulus, that is $\{z : 1 \leq \| z \| \leq 2\}$. Let $N_0 \subset \partial N_1$.

(i) If $N_0 = \Phi$, then $H_n(h(S)) \approx \begin{cases} \mathbb{Z}_2 & \text{if } n = 0,1 \\ 0 & \text{otherwise.} \end{cases}$

(ii) If N_0 is a non-empty component of ∂N_1, then $H_n(h(S)) \approx 0$

(iii) If $N_0 = \partial N_1$, then $H_n(h(S)) \approx \begin{cases} \mathbb{Z}_2 & \text{if } n = 1,2 \\ 0 & \text{otherwise.} \end{cases}$

If S is an attracting periodic orbit, we are in case (i) of the above proposition. That is, if S is an attracting periodic orbit, then any index pair for S, (N_1, N_0) could correspond to a more complicated S, for example a collection of bounded orbits where the *innermost* and *outermost* orbits are attracting orbits. If S is a semi-stable periodic orbit we are in case (ii) and if S is a repelling periodic orbit we are in case (iii).

In order to describe the structure of $\mathcal{S}$, we first define Morse decomposition. For a more detailed discussion of Morse decompositions and how they relate to connection matrices see Moeckel (preprint) and Franzosa (1986 and preprint). First we need the following definition.

Definition 3.9. A finite *partially ordered set*, $(P, >)$ is defined by choosing a set P with a finite number of elements and imposing a partial order relation, $>$, which satisfies:

(i) $i > i$ never holds for $i \in P$

and

(ii) if $i > j$ and $j > k$ then $i > k$ for all $i,j,k \in P$.

We say that two elements $i,j \in P$ are *adjacent* under $>$ if there does not exist $k \in P$ such that $i > k > j$ or $j > k > i$. Finally, given $(P, >)$, an *interval* is a subset $I \subset P$ for which $i,j \in I$ and $i > k > j$ implies that $k \in I$.

Definition 3.10. A *Morse decomposition* of S is a finite collection $\mathcal{M}(S) \triangleq \{ M(i) : i \in (P,>) \}$, of mutually disjoint, compact, invariant sets in S, indexed by P, satisfying; if $z \in S$ then either $z \in M(i)$ for some $i \in P$ or $z \in C(M(i),M(j))$, where $i > j$.

The individual sets, M(i), are called *Morse sets*. Thus a Morse decomposition of S is a collection of isolated invariant subsets with the property that each point not in one of the Morse sets tends to a single Morse set in forward time and a single Morse set in backward time. Also, Morse sets are ordered so that points move from sets which are higher in order to sets which are lower in order.

Morse sets are themselves isolated invariant sets and hence $H_*(h(M(i)))$ is defined. To simplify the notation we shall write

$$H(i) = H_*(h(M(i))) \quad \text{and} \quad H_n(i) = H_n(h(M(i))) \tag{23}$$

It is important to recognize that given S there may be different collections {M(i)} which give rise to a Morse decomposition. In fact there are two fundamental ways in which the Morse decompositions can differ. The first is that the indexing sets need not have the same number of elements. Consider the simple example where S consists of two critical points v and w. Then possible indexing sets are $P = \{p\}$ or $\bar{P} = \{p_1,p_2\}$. In the former case $M(p) = S$ and in the latter $M(p_1) = v$ and $M(p_2) = w$. The second way in which the Morse decompositions can differ is in the partial order. For example, given $\bar{P}$ there are three possible partial orders $>_1$, $>_2$ and $>_3$ where $p_1 >_1 p_2$, $p_2 >_2 p_1$, and p_1 and p_2 are not related under $>_3$. As will be seen in Examples 3.11 and 3.12, both of these differences come into play.

Any partial order which satisfies Definition 3.9 is called an *admissible* partial order. Nevertheless, having a fixed flow and a collection of Morse sets there is a minimal partial ordering which is possible. This is called the *flow defined partial ordering*, $>_F$, and is obtainable by setting $i >_F j$ if and only if there is a sequence of distinct elements of P, $j = k_0, k_1, \ldots, k_m = i$ such that $C(M(k_\ell), M(k_{\ell-1})) \neq \Phi$ for all $\ell = 1, \ldots, m$

Let I be an interval in P. Define

$$M(I) \triangleq \bigcup_{i \in I} M(i) \cup \left(\bigcup_{i,j \in I} C(M(i),M(j)) \right) \tag{24}$$

It is easily checked that M(I) is a compact isolated invariant set. This provides us with a convenient method of obtaining a different Morse decomposition, that is combining several Morse sets into one and hence changing the index set, P. Again, $\mathcal{h}(M(I))$ is defined, so let $H(I) = H_*(\mathcal{h}(M(I)))$.

<u>Example 3.11.</u> In model (1), assume that $H_m < \lambda < H_M < K < \mu$ (see Figure 2). In this case $M(\lambda)$ is unstable and there are an odd number of periodic orbits surrounding $M(\lambda)$ (not counting semi-stable periodic orbits which may also exist). For the collection of Morse sets $M(0)$, $M(\lambda)$, $M(K)$, $M(\mu)$ and $M(\pi)$ with index set $P = \{0,\lambda,K,\mu,\pi\}$ the flow defined partial order $>_F$ is:

$$0 >_F K, \quad K >_F \mu, \quad \lambda >_F \pi, \quad K >_F \pi. \tag{25}$$

Here, 0 and λ, λ and K, λ and μ, and μ and π are unrelated. We can obtain a different Morse decomposition for the same dynamics as follows. Since $I = \{\pi,\lambda\}$ is an interval of P, if we define $M(\pi\lambda) \triangleq M(I)$ then for the Morse sets $M(0)$, $M(\pi\lambda)$, $M(K)$, $M(\mu)$ and the index set $\bar{P} = \{0,\pi\lambda,K,\mu\}$ the flow-defined partial order is

$$0 >_F K, \quad K >_F \mu, \quad K >_F \pi\lambda. \tag{26}$$

<u>Example 3.12.</u> In model (1), assume that $H_m < \lambda < H_M < \mu < K$ (see Figure 2) and that there exists a unique periodic orbit surrounding $M(\lambda)$. One can obtain a Morse decomposition by selecting $P = \{0, \lambda, K, \mu, \pi\}$ and the flow defined partial order

$$0 >_F K, \quad \mu >_F K, \quad \lambda >_F \pi, \quad \mu >_F \pi. \tag{27}$$

We are now almost ready to introduce the connection matrix. By $\bigoplus_{i \in P} H(i)$, we mean the infinite sequence of vector spaces $\left(\bigoplus_{i \in P} H_0(i), \bigoplus_{i \in P} H_1(i), \bigoplus_{i \in P} H_2(i), \ldots \right)$. Let $\Delta : \bigoplus_{i \in P} H(i) \longrightarrow \bigoplus_{i \in P} H(i)$ be a linear map. We can think of Δ as a matrix of maps $\Delta = [\ \Delta(i,j)\ ]_{i,j \in P}$ where $\Delta(i,j) : H(i) \longrightarrow H(j)$. We say that Δ is a *degree -1 map* if $\Delta(i,j)\ H_n(i) \subset H_{n-1}(j)$ for all $i,j \in P$. Finally, for an interval I, in P, let $\Delta(i,j)$ denote the submatrix of maps of Δ given by $\Delta(I) \triangleq [\Delta(i,j)]_{i,j \in I}$. Thus $\Delta = \Delta(P)$.

Definition 3.13. Given an isolated invariant set, S, and a Morse decomposition $\mathcal{M}(S) = \{ M(i) : i \in (P,>) \}$,

$$\Delta : \bigoplus_{i \in P} H(i) \longrightarrow \bigoplus_{i \in P} H(i)$$

is a *connection matrix* if:

(i) $i \not> j$ implies $\Delta(i,j) = 0$,

(ii) Δ is a degree -1 map,

(iii) $\Delta \circ \Delta = 0$, the zero matrix.

(iv) For every interval $I \subset P$, if we define

$$H\Delta(I) \triangleq \text{Ker}\ \Delta(I)\ /\ \text{Im}\ \Delta(I). \tag{28}$$

then $H\Delta(I) \approx H(I)$. (In particular, if $H(I) \approx 0$ then the dimension of $\text{Ker}\ \Delta(I) = \text{rank}\ \Delta(I)$.)

Theorem 3.14. (Franzosa preprint). Given S and $\mathcal{M}(S)$ there always exists at least one connection matrix.

This result is very useful for showing that certain dynamics are impossible as we shall see in Section 4. We shall also see that connection matrices need not be unique. A trivial but important property of connection matrices is the following:

Property 3.15. Let i and j be adjacent elements of $(P,>)$. If $C(M(i),M(j)) = \phi$, then $\Delta(i,j) = 0$.

The contrapositive is:

Property 3.16. Let i and j be adjacent elements of $(P,>)$. If $\Delta(i,j) \neq 0$, then $C(M(i),M(j)) \neq \phi$.

It is important to note that $C(M(i),M(j)) \neq \phi$ does not imply that $\Delta(i,j) \neq 0$. In fact it is often the case that a double connection will result in $\Delta(i,j) = 0$. More generally,

Property 3.17. (McCord). Let S be an isolated invariant set .onsisting of the hyperbolic critical points, $M(i)$, $i=0,1$ and the connections $C(M(1),M(0))$. Assume

$$H_k(i) \approx \begin{cases} \mathbb{Z}_2 & \text{if } k = n+i, \\ 0 & \text{otherwise.} \end{cases}$$

Furthermore, let $C(M(1),M(0))$ consist of exactly p heteroclinic orbits where each orbit arises as the transverse intersection of the stable and unstable manifolds of $M(0)$ and $M(1)$, respectively. Then

$$\Delta(1,0) : H_{n+1}(1) \longrightarrow H_n(0)$$

is given by

$$\Delta(1,0) = p \mod 2.$$

(We say that two manifolds M and N in $\mathbb{R}^n$ have a *transverse intersection* at the point x if $T_x(M) \cup T_x(N)$ span $T_x(\mathbb{R}^n)$ where $T_x(V)$ is the tangent space at x to the manifold V).

In particular, it follows that

Property 3.18. Given a flow in the plane, let S consist of two hyperbolic critical points $M(i)$, $i = 1,0$ where the number of eigenvalues with positive real part for the linearized flow at $M(i)$ is $k+i$. Assume that there is a unique heteroclinic orbit from $M(1)$ to $M(0)$. Then the connection matrix $\Delta(1,0) \neq 0$.

Property 3.19. Let i and j be adjacent in $(P,>)$. Assume that

$$H_k(i) \approx \begin{cases} \mathbb{Z}_2 & \text{if } k = n - 1, \\ 0 & \text{otherwise;} \end{cases}$$

$$H_k(j) \approx \begin{cases} \mathbb{Z}_2 & \text{if } k = n, \\ 0 & \text{otherwise;} \end{cases}$$

and

$$H(ji) \sim 0.$$

Then $\Delta(i,j) \neq 0$.

Property 3.20. Let $i > j$ be adjacent in $(P,>)$. Assume that

$$H_k(i) \approx \begin{cases} \mathbb{Z}_2 & \text{if } k = n, \\ 0 & \text{otherwise;} \end{cases}$$

$$H_k(j) \approx \begin{cases} \mathbb{Z}_2 & \text{if } k = n - 1, n, \\ 0 & \text{otherwise;} \end{cases}$$

and

$$H_k(ji) \approx \begin{cases} \mathbb{Z}_2 & \text{if } k = n, \\ 0 & \text{otherwise.} \end{cases}$$

Then $\Delta(i,j) \neq 0$.

4. CONSTRUCTION AND INTERPRETATION OF CONNECTION MATRICES

We are finally in a position to actually construct a connection matrix. The steps involved in the construction are listed in Table 2. For our first example let us construct the matrix for the dynamics considered in Example 3.11, with Morse decompostition for $\mathcal{S}$ given by the index set $P = \{0,\lambda,K,\mu,\pi\}$, corresponding Morse sets $M(0)$, $M(\lambda)$,

$M(K)$, $M(\mu)$ and $M(\pi)$ and flow defined partial order given by (17). We have already done most of the steps indicated in Table 2 for this example, in particular steps 1-6. Recall that (see Table 3)

$$H_n(\mathcal{h}(\mathcal{S})) = H_n(\mathcal{S}) \approx 0, \quad n = 0,1,2, \dots .. \tag{29}$$

Also the linear analysis is summarized in Table 1.

Next we compute the homology of the index of each of the Morse sets. By Proposition 3.6,

$$H_n(\mu) \approx \begin{cases} \mathbb{Z}_2 & \text{if } n = 0, \\ 0 & \text{otherwise;} \end{cases}$$

$$H_n(0) \approx \begin{cases} \mathbb{Z}_2 & \text{if } n = 1, \\ 0 & \text{otherwise;} \end{cases}$$

$$H_n(K) \approx \begin{cases} \mathbb{Z}_2 & \text{if } n = 1, \\ 0 & \text{otherwise;} \end{cases}$$

$$H_n(\lambda) \approx \begin{cases} \mathbb{Z}_2 & \text{if } n = 2, \\ 0 & \text{otherwise.} \end{cases}$$

Since $M(\pi)$ is either an attracting periodic orbit or an annulus bounded by two periodic orbits, the innermost attracting from the inside and the outermost attracting from the outside, one can find an index pair that is homeomorphic to an annulus, with $N_0 = \Phi$ (see Table 3). Therefore by Proposition 3.8

$$H_n(\pi) \approx \begin{cases} \mathbb{Z}_2 & \text{if } n = 0,\ 1, \\ 0 & \text{otherwise.} \end{cases}$$

Finally we are in a position to determine the entries of the matrix (see Δ^3 of Proposion 4.3(iii)). Since,

$$\begin{aligned} &H(\mu) \oplus H(\pi) \oplus H(K) \oplus H(0) \oplus H(\lambda) \\ &\approx H_0(\mu) \oplus H_0(\pi) \oplus H_1(\pi) \oplus H_1(K) \oplus H_1(0) \oplus H_2(\lambda), \end{aligned} \tag{30}$$

the associated connection matrix Δ can be treated as a 6×6 matrix (we are ignoring the rows and columns that obviously consist completely of zeroes). From Definition 3.13(i), we conclude that Δ is strictly upper triangular and that the 2×2 submatrix $\Delta(\pi,\pi) = 0$. (Recall that $\Delta(i,j)$ is not the ij^{th} entry of the matrix, but rather is a map. In particular, $\Delta(i,j) : H(i) \longrightarrow H(j)$. In fact, if we let Δ_{ij} denote the ij^{th} entry of the matrix, then if $\Delta(i,j)$ corresponds to a 1×1 submatrix of Δ, it follows that $\Delta(i,j)$ corresponds to the matrix entry Δ_{ji}).

Since $\Delta(\lambda,\mu) : H_2(\lambda) \longrightarrow H_0(\mu)$ is not a degree -1 map, $\Delta(\lambda,\mu) = 0$ (i.e. the entry under $H_2(\lambda)$ and across from $H_0(\mu)$ is 0). Similarly, $\Delta(0,K) : H_1(0) \longrightarrow H_1(K)$ and so $\Delta(0,K) = 0$. Since $\Delta(\pi,\mu) : H_0(\pi) \oplus H_1(\pi) \longrightarrow H_0(\mu)$, in order for $\Delta(\pi,\mu)$ to be a degree -1 map, the entry under $H_0(\pi)$ and across from $H_0(\mu)$ must be zero. Similarly, $\Delta(\lambda,\pi) : H_2(\lambda) \longrightarrow H_0(\pi) \oplus H_1(\pi)$; $\Delta(K,\pi) : H_1(K) \longrightarrow H_0(\pi) \oplus H_1(\pi)$; and $\Delta(0,\pi) : H_1(0) \longrightarrow H_0(\pi) \oplus H_1(\pi)$; and so the entries under $H_2(\lambda)$ and across from $H_0(\pi)$; under $H_1(K)$ and across from $H_1(\pi)$; and under $H_1(0)$ and across from $H_1(\pi)$ must all be zero. Since $M(\lambda)$ is a repellor and $M(\lambda)$ is surrounded by $M(\pi)$ which is attracting from the outside, $M(\lambda)$ cannot connect (directly or indirectly) to $M(K)$ or $M(0)$ (i.e. $C(M(\lambda),M(0)) = \phi$ and $C(M(\lambda),M(K)) = \phi$). Since λ is adjacent to 0 and to K in the ordering, by Property 3.15 $\Delta(\lambda,K) = 0$ and $\Delta(\lambda,0) = 0$. Since $M(\pi)$ and $M(\mu)$ are both attracting $C(M(\pi),M(\mu)) = \phi$ and since π is adjacent to μ in the ordering $\Delta(\pi,\mu) = 0$. By Property 3.18 $\Delta(K,\mu) = 1$. By Property 3.20 the entry under $H_1(K)$ and across from $H_0(\pi)$ is 1. Since $H_n(\mathcal{S}) \approx 0$ for $n = 0, 1, 2, \ldots$, by Definition 3.13(iv), $\ker \Delta = \text{image } \Delta$. Hence the rank of Δ must equal 3. Therefore the entry under $H_2(\lambda)$ and across from $H_1(\pi)$ must be nonzero. It then follows by Definition 3.13(iii) that the entry under $H_1(\pi)$ and across from $H_0(\mu)$ must be zero. This rank condition also implies that the α and β under $H_1(0)$ must be chosen so that the vectors $\begin{bmatrix} \alpha \\ \beta \end{bmatrix}$ and $\begin{bmatrix} 1 \\ 1 \end{bmatrix}$ are linearly independent.

Remark 4.1. Both $\alpha = 0$, $\beta = 1$ and $\alpha = 1$, $\beta = 0$ give connection matrices. A reason for why this nonuniqeness is necessary it that the connection matrix *continues* under perturbation. Notice that the connection from $M(0)$ to $M(K)$ is not transverse. Thus, a generic bifurcation of (1) will destroy the invariance of the x-axis under the flow and hence one expects to either have a connection from $M(0)$ to $M(\pi)$ (i.e. $\alpha = 1$) or a connection from $M(0)$ to $M(\lambda)$ (i.e. $\beta = 1$).

Next we show how we could have used the connection matrix to prove the existence of an asymptotically stable periodic orbit in the previous example. (Of course, since this system is planar, this follows directly form the Poincaré-Bendixsonn Theorem. But that theorem only applies for planar systems, whereas the connection matrix technique is dimension independent.) Suppose we only know the flow along the axes, the local stability of the critical points, the predator and prey isoclines, and that all solutions are uniformly asymptotically bounded, and in particular that $H(\mathcal{S}) \approx 0$. For the index set $P = \{0,\lambda,\mu,K\}$ and corresponding Morse sets, the flow defined partial order would be $0 >_F K$ and $K >_F \mu$ with λ and 0 and λ and K unrelated. We note that

$$H(\mu) \oplus H(K) \oplus H(0) \oplus H(\lambda) \approx H_0(\mu) \oplus H_1(K) \oplus H_1(0) \oplus H_2(\lambda) \tag{31}$$

Therefore, the associated connection matrix can be treated as a 4×4 matrix:

$$\begin{array}{c|cccc|} & H_0(\mu) & H_1(K) & H_1(0) & H_2(\lambda) \\ H_0(\mu) & 0 & 1 & - & 0 \\ H_1(K) & 0 & 0 & 0 & 1 \\ H_1(0) & 0 & 0 & 0 & 0 \\ H_2(\lambda) & 0 & 0 & 0 & 0 \end{array}$$

From Definiton 3.13(i) it follows that Δ is strictly upper triangular. By Definition 3.13(ii), $\Delta(\lambda,\mu) = 0$, and $\Delta(0,K) = 0$. $\Delta(K,\mu) = 1$ by Property 3.19. Since $M(0)$ is a saddle with stable manifold along the y-axis, $C(M(\lambda),M(0)) = \phi$. Since λ and 0 are adjacent by Property 3.15 $\Delta(\lambda,0) = 0$. By Definition 3.13(iv), $\Delta(\lambda,K) = 1$, since the rank of Δ must equal 2 ($H(\mathcal{S}) \approx 0$). But then $\Delta \circ \Delta \neq 0$, contradicting Definition 3.13(iii). But by Theorem 3.14, to every Morse decomposition there corresponds at least one connection matrix. Thus we do not have a valid Morse decomposition. Something must be missing. In this case the only things that can be missing are periodic orbits. In fact, since $M(\lambda)$ is a repellor and any periodic orbit must surround $M(\lambda)$ there must be at least one asymptotically stable periodic orbit surrounding $M(\lambda)$ (noting that if $M(\pi)$ were to consist only of semi-stable periodic orbits, one could take $M(\lambda\pi)$ as a Morse set and the connection matrix would be identical to the one for which $M(\pi) = \phi$).

The connection matrix can also be used to keep track of *almost all* of the different bifurcations for $(1)_K$ for $K \in (0,\infty)$. The spontaneous birth of semi-stable periodic orbits is however not detected. In order to do this we need to first determine the set of all possible connection matrices for $(1)_K$ for $K \in (0,\infty)$. By Theorem 3.14, for every Morse decompositon, $\mathcal{M}(\mathcal{S})$, of $\mathcal{S}$, there exists at least one connection matrix. The first step then is to determine all the possible Morse decompositions of $\mathcal{S}$ for the index set $P = \{0, \lambda, \mu, K, \pi\}$. In order to do this we must find all the admissible, flow defined partial orders on P for various values of K.

<u>Proposition 4.2.</u> The set of admissible, flow defined, partial orderings on P for $K \in (0,\infty)$ follows:

(i) If $K < \lambda < \mu$, define

$>_1$ by $0 >_1 K$, $\lambda >_1 K$, $\lambda >_1 \mu$.

(ii) If $\lambda < K < \mu$ define

$>_2$ by $0 >_2 K$, $K >_2 \mu$, $K >_2 \pi$, $\pi >_2 \lambda$.

$>_3$ by $0 >_3 K$, $K >_3 \mu$, $K >_3 \pi$, $\lambda >_3 \pi$.

(iii) If $\lambda < \mu < K$ define

$>_4$ by $0 >_4 K, \quad \mu >_4 K, \quad \mu >_4 \pi, \quad \pi >_4 \lambda.$

$>_5$ by $0 >_5 K, \quad \mu >_5 K, \quad \pi >_5 \mu, \quad \pi >_5 \lambda.$

$>_6$ by $0 >_6 K, \quad \mu >_6 K, \quad \lambda >_6 \pi, \quad \mu >_6 \pi.$

$>_7$ by $0 >_7 K, \quad \mu >_7 K, \quad \lambda >_7 \pi, \quad \pi >_7 \mu.$

This set of partial orders was obtained by considering the analytic information described in Section 2 and then writing down all possible orderings which did not contradict that information. For example, the invariance of the x-axis allows one to conclude that $C(M(0),M(K)) \neq \phi$ for all $K \in (0,\infty)$ and hence $0 > K$ for all admissible, flow defined, partial orders. One also uses obvious facts to eliminate certain possibilities. For example, if $M(i)$ is an attractor then $i \not> j$ for any $j \in P$. Another way to eliminate certain partial orderings is by trying to construct a connection matrix. If no matrix is possible the partial order can be eliminated as inadmissible (as we did in the case where we showed a periodic orbit must exist).

Having determined the set of admissible orders, one can now determine the set of connection matrices. Let Δ^j denote the connection matrices associated with the partial order $>_j$.

<u>Proposition 4.3.</u> The set of possible connection matrices consists of:

(i) $\Delta^1 =$

	$H_0(K)$	$H_0(\mu)$	$H_1(\lambda)$	$H_1(0)$
$H_0(K)$	0	0	1	1
$H_0(\mu)$	0	0	1	0
$H_1(\lambda)$	0	0	0	0
$H_1(0)$	0	0	0	0

(ii) Δ^2 =

	$H_0(\mu)$	$H_0(\lambda)$	$H_1(K)$	$H_1(0)$
$H_0(\mu)$	0	0	1	α
$H_0(\lambda)$	0	0	1	β
$H_1(K)$	0	0	0	0
$H_1(0)$	0	0	0	0

where $\alpha \neq \beta$

(iii) Δ^3 =

	$H_0(\mu)$	$H_0(\pi)$	$H_1(\pi)$	$H_1(K)$	$H_1(0)$	$H_2(\lambda)$
$H_0(\mu)$	0	0	0	1	α	0
$H_0(\pi)$	0	0	0	1	β	0
$H_1(\pi)$	0	0	0	0	0	1
$H_1(K)$	0	0	0	0	0	0
$H_1(0)$	0	0	0	0	0	0
$H_2(\lambda)$	0	0	0	0	0	0

where $\alpha \neq \beta$

(iv) Δ^4 =

	$H_0(K)$	$H_0(\lambda)$	$H_1(\mu)$	$H_1(0)$
$H_0(K)$	0	0	1	1
$H_0(\lambda)$	0	0	1	0
$H_1(\mu)$	0	0	0	0
$H_1(0)$	0	0	0	0

(v) Δ^5 =

	$H_0(K)$	$H_0(\lambda)$	$H_1(\mu)$	$H_1(0)$	$H_1(\pi)$	$H_2(\pi)$
$H_0(K)$	0	0	0	1	*	0
$H_0(\lambda)$	0	0	0	0	1	0
$H_1(\mu)$	0	0	0	0	0	1
$H_1(0)$	0	0	0	0	0	0
$H_1(\pi)$	0	0	0	0	0	0
$H_2(\pi)$	0	0	0	0	0	0

* is undetermined

(vi) $\Delta^6 =$

$$\begin{array}{c|cccccc|} & H_0(K) & H_0(\pi) & H_1(\pi) & H_1(\mu) & H_1(0) & H_2(\lambda) \\ H_0(K) & 0 & 0 & 0 & 1 & 1 & 0 \\ H_0(\pi) & 0 & 0 & 0 & 1 & 0 & 0 \\ H_1(\pi) & 0 & 0 & 0 & 0 & 0 & 1 \\ H_1(\mu) & 0 & 0 & 0 & 0 & 0 & 0 \\ H_1(0) & 0 & 0 & 0 & 0 & 0 & 0 \\ H_2(\lambda) & 0 & 0 & 0 & 0 & 0 & 0 \end{array}$$

(vii) $\Delta^7 =$

$$\begin{array}{c|cccc|} & H_0(K) & H_1(\mu) & H_1(0) & H_2(\lambda) \\ H_0(K) & 0 & 0 & 1 & 0 \\ H_1(\mu) & 0 & 0 & 0 & 1 \\ H_1(0) & 0 & 0 & 0 & 0 \\ H_2(\lambda) & 0 & 0 & 0 & 0 \end{array}$$

Notice that we have not defined the connection matrices for all values of K. This is because if $K = \lambda$ or $K = \mu$, then we are at a bifurcation point. Furthermore, each connection matrix, Δ^j, occurs for a particular partial order, $>^j$. Thus a change in the connection matrix implies that a bifurcation has taken place. From the structure of (1), we know that only certain bifurcations can occur as K changes value. In particular, M(0) undergoes no bifurcations. M(K) and M(μ), and M(K) and M(λ) can only exchange stability. Also, M(λ) can undergo a Hopf bifurcation. On a more global level, a periodic orbit may become homoclinic to M(μ). Finally, the periodic orbit may be subject to bifurcation, (i.e. saddle node, pitchfork, etc.). We cannot pick up these bifurcations because of the way we are defining M(π), (i.e. we are intentionally ignoring these bifurcations).

Since Proposition 4.3 gives us all the possible connection matrices for values of K at which a bifurcation is not occuring, we adopt the following approach. Given Δ^j, we determine which of the four basic bifurcations, λ-exchange (M(λ) and M(K) exchange stability), μ-exchange (M(μ) and M(K) exhange stability), Hopf (M(λ) undergoes a Hopf bifurcation), or homoclinic (M(μ) is the critical point on a homoclinic orbit), is possible and given the basic bifurcation what is the new connection matrix. We can codify this information via a *bifurcation graph* (see Figure 4) where the vertices are the possible connection matrices and the edges are the possible bifurcations. See Mischaikow and Wolkowicz for a more detailed explanation of this approach and an explanation of how the homoclinic bifurcation can be detected. The edges labelled λ and μ correspond to the λ and μ-exchanges. H denotes Hopf bifurcation and h-stable and h-unstable indicates the occurence of a stable or unstable homoclinic orbit. The directed edges indicate how the connection matrices must change as K increases through the bifurcation point, (e.g. one cannot go from Δ^7 to Δ^5 via a Hopf bifurcation as K increases. Notice that the only bifurcation which is not directed is the homoclinic bifurcation. This implies that we cannot rule out the possiblility of a series of homoclinic bifurcations with the connection matrices varying between Δ^4 and Δ^5 or Δ^6 and Δ^7.

What does the bifurcation graph tell us about the set of solutions to (1) for various values of K ? By Proposition 4.2(i) it follows that for K sufficiently small (i.e. $K < \lambda$) the connection matrix is Δ^1. By Theorem 2.1 the only possible connection matrix for $K > K^*$ is Δ^7. Thus, as we vary K from below λ to above K^*, we trace a path through the bifurcation graph. From this we immediately obtain the following results:

(1) There exists a unique value of K for which a λ-exchange occurs.

(2) There exists a unique value of K for which a μ-exchange occurs.

(3) There exists a unique value of K for which a Hopf bifurcation occurs.

(4) An odd number of homoclinic bifurcations always occurs.

(5) For a particular choice of functions p, g, and q, the connection matrices which are realized are determined by the relative values of K for which the Hopf bifurcation occurs.

While these results can be obtained easily using planar techniques for our example, for problems involving more than two variables planar techniques no longer apply. However the connection matrix technique is dimension independent. In our case, (4) is obtained as a special case of a more general theorem of Mischaikow (1985b and 1986), where the primary ingredient involves checking an algebraic relation determined by Δ^6 and Δ^7 or Δ^4 and Δ^5. Finally (5) suggests how the bifurcation graph can be used to determine what structures of the flow can occur for various values of the parameter K, by knowing at what relative parameter values a particular bifurcation occurs.

The connection matrix has been used in other applications. Reineck (1985) obtained classification results for 2-dimensional symbiotic, competitive and predator-prey systems. In his situation there is no obvious parameter, but there is a long discussion of how the predator-prey systems are related depending upon the predator-prey isoclines.

Mischaikow (1985a) analyzed travelling wave solutions to n-dimensional systems of reaction diffusion equations and obtained corresponding bifurcation graphs with wave speed taken as the parameter. In this case knowledge about the connection matrices for large and small wave speeds could be used to obtain existence results for travelling wave solutions. Also, the set of realizable connection matrices (and hence dynamics) was shown to be significantly smaller than the set of algebraically permissible connection matrices.

The connection matrix might also be useful to help determine whether or not an ecological system is uniformly persistent in the sense of Butler et al. (1986) i.e. whether there is a compact attractor in the interior of the positive cone. One of their hypotheses involves verifying that solutions on the boundary of the positive cone are acyclic. Information about the set of connections could conceivably help to eliminate the possibility of cycles on the boundary.

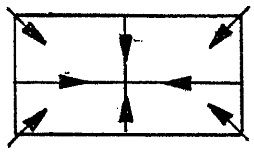
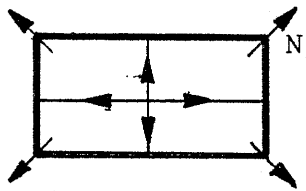
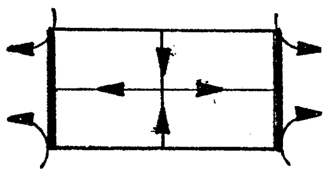
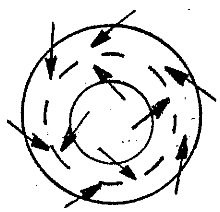
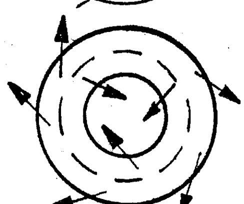
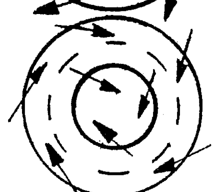
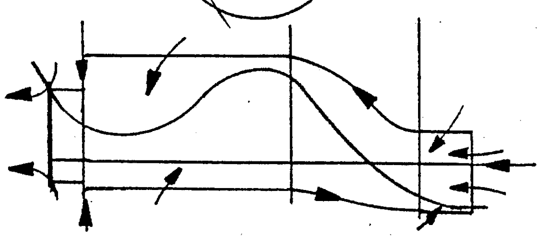
Table 1.
Linear Analysis of Critical Points

Critical Point	Parameter Range $K < \lambda < \mu$	$\lambda < K < \mu$	$\lambda < \mu < K$	
M(0)	saddle	saddle	saddle	
M(K)	attractor (node)	saddle	attractor (node)	
M(λ)	saddle	repellor	repellor	$F_x(\lambda,K) > 0$
		attractor	attractor	$F_x(\lambda,K) < 0$
M(μ)	attractor	attractor	saddle	

Table 2.
Steps Involved in Constructing a Connection Matrix

1. Determine the set of all bounded solutions for the dynamics, $\mathcal{S}$.
2. Determine an index pair for $\mathcal{S}$ (see Definition 3.2 and Table 3).
3. Compute the homology of the index of $\mathcal{S}$, H($\mathcal{S}$) (see Propositions 3.7 and 3.8 and Table 3).
4. Determine the isolated invariant subsets of $\mathcal{S}$.
5. Do a local stability analysis of the subsets of $\mathcal{S}$.
6. Determine a convenient flow-defined partial order and hence Morse decompostion of $\mathcal{S}$ (see Definitions 3.9 and 3.10).
7. Determine the homology of the index of the individual Morse sets (see Propositions 3.7 and 3.8 and Table 3).
8. Construct the connection matrix using the above information, Definition 3.13 and Properties 3.15 - 3.20.

Table 3
Index Pairs and Homology of the Index
for various
Isolated Invariant Sets in R^2.

Isolated Invariant Set S	Index Pair	Homology of the Index $H_n(S)$
Critical Point Attractor	 $N_0 = \phi$	$\begin{cases} Z_2 & \text{if } n = 0, \\ 0 & \text{otherwise.} \end{cases}$
Critical Point Repellor	 $N_0 = \partial N_1$	$\begin{cases} Z_2 & \text{if } n = 2, \\ 0 & \text{otherwise.} \end{cases}$
Critical Point Saddle		$\begin{cases} Z_2 & \text{if } n = 1 \\ 0 & \text{otherwise.} \end{cases}$
Periodic Orbit Attractor	 $N_0 = \phi$	$\begin{cases} Z_2 & \text{if } n = 0, 1 \\ 0 & \text{otherwise.} \end{cases}$
Periodic Orbit Repellor	 $N_0 = \partial N_1$	$\begin{cases} Z_2 & \text{if } n = 1, 2 \\ 0 & \text{otherwise.} \end{cases}$
Periodic Orbit Semi-stable		0 for all n
$\mathcal{S}$		0 for all n

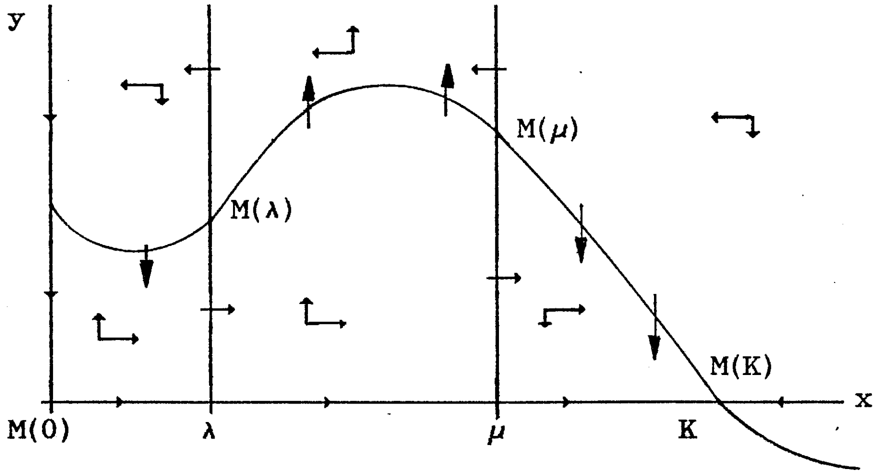


Figure 1
Typical vector field for (1).

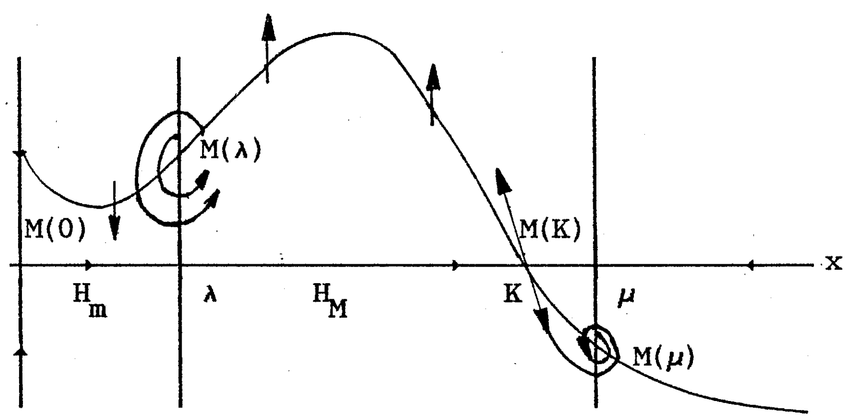


Figure 2
Dynamics for $H_m < \lambda < H_M < K < \mu$.
A stable periodic orbit must surround $M(\lambda)$.

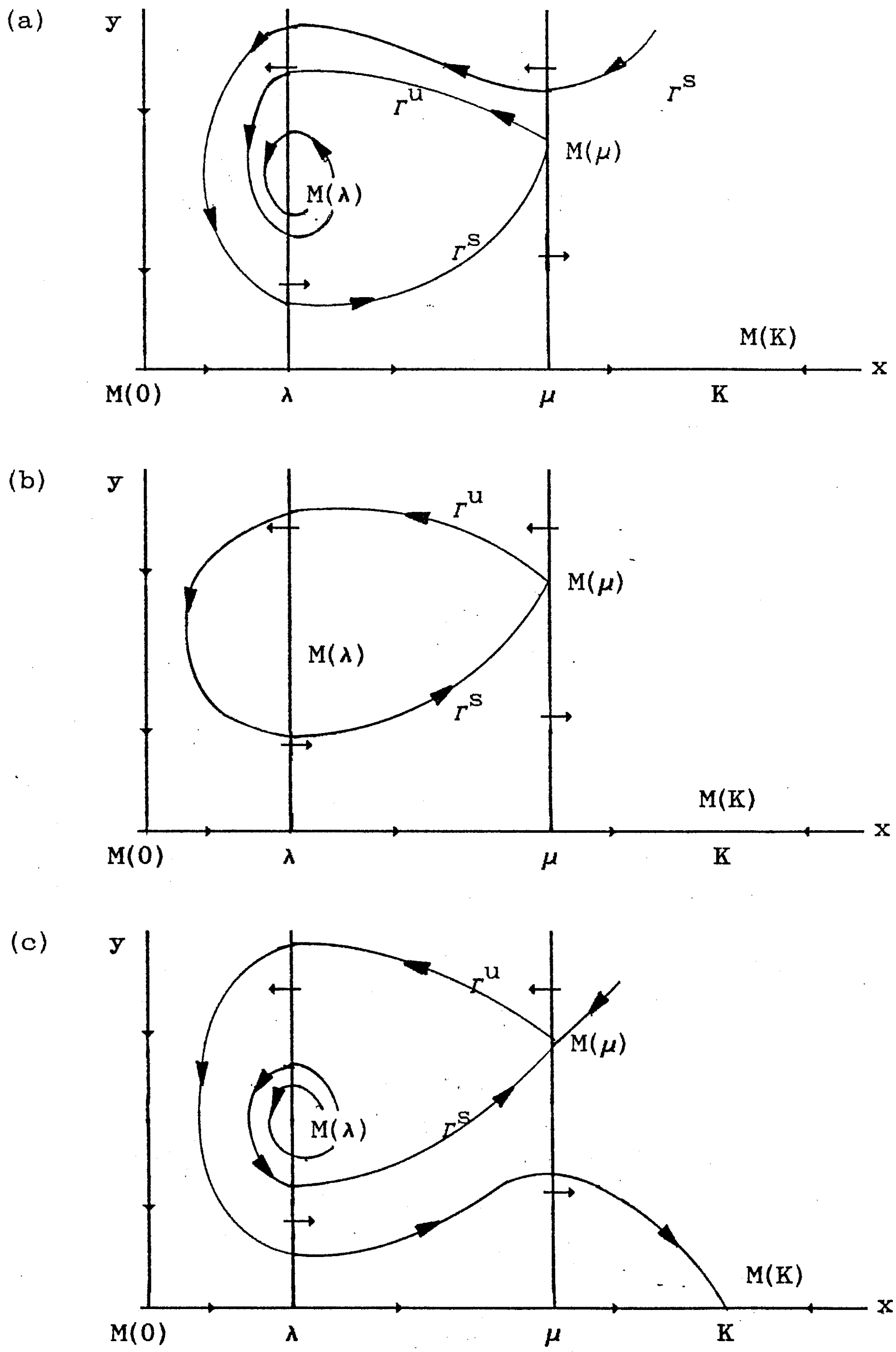


Figure 3

Three Possibilities for the Stable, Γ^s and Unstable Manifold, Γ^u of M(μ)

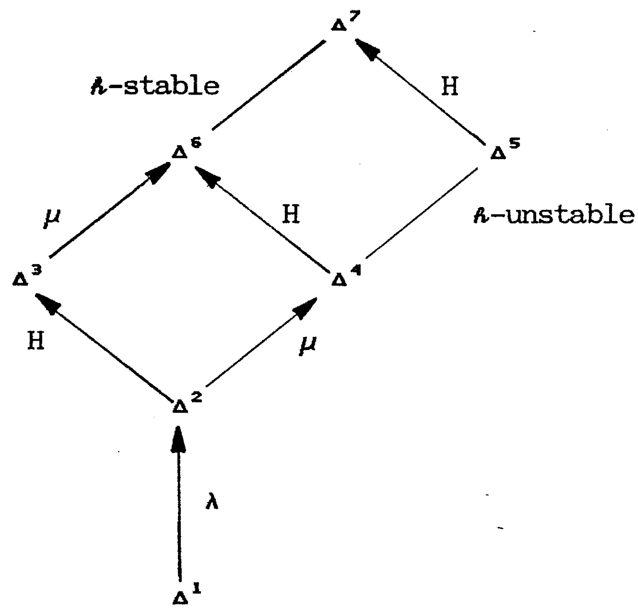


Figure 4
Bifurcation graph for (1)

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