Heteroclinic Cycles in Competitive Populations

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Abstract. We investigate heteroclinic cycles of the famous Lotka-Volterra system modeling a system of 3 competitive populations.

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1 Introduction

Robust heteroclinic cycles in competitive population models have been the subject of many papers in fields ranging through chemistry, ecology, network flows, just to name a few. We are mainly concerned with systems of ordinary differential equations of the form:

\[ x'_1 = f_1(x_1, x_2, \ldots, x_n) \]
\[ x'_2 = f_2(x_1, x_2, \ldots, x_n) \]
\[ \vdots \]
\[ x'_n = f_n(x_1, x_2, \ldots, x_n). \]

Let us begin the discussion by reviewing some terminology first.

2 Preliminaries

Consider the following system of ordinary differential equations \( \mathbf{f} \):

\[ x'_1 = f_1(x_1, x_2, \ldots, x_n) \]
\[ x'_2 = f_2(x_1, x_2, \ldots, x_n) \]

\[ \vdots \]

\[ x'_n = f_n(x_1, x_2, \ldots, x_n) \]

The \textit{ith nullcline} is the set of points \((x_1, x_2, \ldots, x_n)\) for which

\[ f_i((x_1, x_2, \ldots, x_n) = 0. \]

The intersection(s) of all the nullclines i.e the point(s) where \(x'_i = 0\) for \(i \in \{1 \ldots n\}\) are called the \textbf{fixed points} of the system. We are concerned with the behavior of the system at the fixed points. In particular, we desire to find the stable, unstable, and center manifolds of the system at the fixed points. It is the interplay between the stable and unstable manifolds of different fixed points that suggest the existence of heteroclinic cycles.

Our main tools for analysis of these systems lie within the realm of stability theory. Before we begin, we review these tools. These methods can be found in \cite{2.1}.

\section*{2.1 The Flow}

Consider the system

\[ \mathbf{x}' = \mathbf{f}(\mathbf{x}). \quad (*) \]

\[ \mathbf{x}(0) = \mathbf{x}_0. \]

The definition of the flow of the system \((*)\) is given below:

Let \(E\) be an open subset of \(\mathbb{R}^n\) and let \(\mathbf{f} \in C^1(E)\). For \(\mathbf{x}_0 \in E\), let \(\phi(t, \mathbf{x}_0)\) be solution of the initial value problem \((*)\) defined on its maximal interval of existence \(I(\mathbf{x}_0)\). Then for \(t \in I(\mathbf{x}_0)\), the set of mappings \(\phi_t\) defined by

\[ \phi_t(\mathbf{x}_0) = \phi(t, \mathbf{x}_0) \]

is called the \textbf{flow} of the differential equation \((*)\).

The standard approach for analysis of the behavior of the system \((*)\) at a fixed point \(\mathbf{x}_0\) is to near the fixed points is to compute the stable, unstable, and center manifolds tangent to \(\mathbf{x}_0\). For the sake of simplicity, we assume that \(x_0 = 0\) for the remainder of the discussion. The open set \(E\), of the preceding definition decomposes as:

\[ E = E^s \oplus E^u \oplus E^c \]
where

\[ E^s = \{ x \in E : \lim_{t \to \infty} \phi_t(x) = x_0 \}, \]

\[ E^u = \{ x \in E : \lim_{t \to -\infty} \phi_t(x) = x_0 \}. \]

3 Stable and Unstable Manifolds

**Theorem** Let \( E \) be an open subset of \( \mathbb{R}^n \) containing the origin, let \( f \in C^1(E) \), and let \( \phi_t \) be the flow of the system \((*)\). Suppose that \( f(0) = 0 \) and that \( Df(0) \) has \( k \) eigenvalues with negative real part and \( n - k \) eigenvalues with positive real part. Then there exists a \( k \)-dimensional differentiable manifold \( S \) tangent to the stable subspace \( E^s \) of the linear system \((*)\) at \( 0 \) such that for all \( t \geq 0 \), \( \phi_t(S) \subset S \) and for all \( x_0 \in S \),

\[ \lim_{t \to \infty} \phi_t(x_0) = 0; \]

and there exists an \( n - k \) dimensional differentiable manifold \( U \) tangent to the unstable subspace \( E^u \) of \((*)\) at \( 0 \) such that for all \( t \geq 0 \), \( \phi_t(U) \subset U \) and for all \( x_0 \in U \),

\[ \lim_{t \to -\infty} \phi_t(x_0) = 0. \]

4 Limit Sets

[1] gives the definition of a limit set as: Let \( E \) be an open subset of \( \mathbb{R}^n \). A point \( p \in E \) is an \( \omega \) limit point of the trajectory \( \phi(\cdot, x) \) of the system \((*)\) if there is a sequence

\[ \lim_{n \to \infty} \phi(t_n, x) = p. \]

The set of all \( \omega \)-limit points of a trajectory is called a \( \omega \) limit set.

5 Heteroclinic Cycles

Let \( x_1, \ldots x_m \) represent relative equilibria of a vector field. If there exists trajectories \( \{y_1(t), \ldots, y_m(t)\} \) such that \( y_j(t) \) is forward asymptotic to \( x_{j+1} \) and backward asymptotic to \( x_j \) then the collection of trajectories \( \{x_j, y_j(t)\} \) is called a **heteroclinic cycle**.
6 Competitive Population Model (2 species model)

We consider competitive population models in the case of two populations. We focus our attention to a special case called the Lotka-Volterra equations given for two populations $x$ and $y$ by:

\[
\begin{align*}
x' &= x(x_0 + ax + by) \\
y' &= y(y_0 + cx + dy).
\end{align*}
\]

- $x_0$ and $y_0$ correspond to the initial populations of $x$ and $y$, respectively.
- The parameter $a$ corresponds to the effect of population $x$ on itself.
- The parameter $b$ corresponds to the effect of population $y$ on population $x$.
- The parameter $c$ corresponds to the effect of population $x$ on population $y$.
- The parameter $d$ corresponds to the effect of population $y$ on itself.

Since we are considering competitive populations, we assume that each of the parameters $a$, $b$, $c$, $d$ are all negative. We consider the special case when $a$ and $d = -1$. Equivalently, we may write the system as:

\[
\begin{align*}
x' &= x(x_0 - x - by) \\
y' &= y(y_0 - cx - y).
\end{align*}
\]

6.1 Find the Nullclines

We find the nullclines by finding the values of $x$ and $y$ such that $x' = 0$ and $y' = 0$. First, if $x' = 0$, then

\[
x' = x(x_0 - x - by) \Rightarrow
\]

- $x = 0$, or
- \((x_0 - x - by) = 0\).
Then \( x' = 0 \) on the line

\[
y = \frac{-1}{b} x + \frac{x_0}{b}.
\]

Similarly, if \( y' = 0 \), then

\[
y' = y(y_0 - cx - y) \Rightarrow
\]

- \( y = 0 \), or

- \( (y_0 - cx - y) = 0 \).

Then \( y' = 0 \) on the line

\[
y = -cx + y_0.
\]

The nullclines are the lines \( N_y \) (through the points \((0, y_0)\) and \((\frac{y_0}{c}, 0)\)), and \( N_x \) (through the points \((x_0, 0)\) and \((0, \frac{y_0}{b})\)). To find the fixed point of the system, we simply compute where the two nullclines intersect.

\[
-cx + y_0 = \frac{-1}{b} x + \frac{x_0}{b},
\]

then

\[
x^* = \frac{x_0 - y_0 b}{1 - cb}.
\]

7 Competitive Population Model (3 species)

We now consider competitive population models in the case of three populations. We focus our attention to a special case of the Lotka-Volterra equations given for three populations \( x, y, \) and \( z \) by:

\[
x' = x(1 - x - ay - bz)
\]

\[
y' = y(1 - bx - y - az)
\]
we also require that:

1. \[0 < b < 1 < a,\]

2. \[2 < a + b.\]

7.1 Compute the Fixed Points and Nullclines

We begin by finding the \( x \) of \( \mathbb{R}^3 \) such that

\[ f_i(x) = 0 \quad \text{for } i = 1, 2, 3. \]

The fixed points are given by:

\[ x_1 = (1, 0, 0), \]
\[ x_2 = (0, 1, 0), \]
\[ x_3 = (0, 0, 1), \]
\[ x_4 = \left( \frac{1}{1 + a + b}, \frac{1}{1 + a + b}, \frac{1}{1 + a + b} \right). \]

Here are some of the nullclines:

\[ x = 0, \]
\[ y = 0, \]
\[ z = 0, \]
\[ x + y + z = 1. \]
7.2 Analysis of $f$ at $x_1$

We compute $Df(x_1)$ to arrive at the following eigenvalues and eigenvectors:

$$\lambda_1(x_1) = -1, \quad v_1(x_1) = (1, 0, 0)^T,$$

$$\lambda_2(x_1) = 1 - b, \quad v_2(x_1) = \left(\frac{a}{b-2}, 1, 0\right)^T,$$

$$\lambda_3(x_1) = 1 - a, \quad v_3(x_1) = \left(\frac{b}{a-2}, 0, 1\right)^T.$$

By the restrictions given to $a$ and $b$, we know that $\lambda_2(x_1) > 0$ and $\lambda_3(x_1) < 0$. This allows us to compute:

$$E^s(x_1) = \{(x, 0, z) \cdot \left(\frac{a}{b-2}, 1, 0\right)^T : x, z \in \mathbb{R}\} \cup \{(x, 0, 0) \cdot (1, 0, 0)^T,$$

$$E^u(x_1) = \{(0, y, 0) \cdot \left(\frac{a}{b-2}, 1, 0\right) : y \in \mathbb{R}\},$$

7.3 Analysis of $f$ at $x_2$

We compute $Df(x_2)$ to arrive at the following eigenvalues and eigenvectors:

$$\lambda_1(x_2) = -1, \quad v_1(x_2) = (0, 1, 0)^T,$$

$$\lambda_2(x_2) = 1 - a, \quad v_2(x_2) = \left(\frac{a-2}{b}, 1, 0\right)^T,$$

$$\lambda_3(x_2) = 1 - b, \quad v_3(x_2) = \left(0, \frac{b}{a-2}, 1\right)^T.$$

By the restrictions given to $a$ and $b$, we know that $\lambda_3(x_2) > 0$ and $\lambda_2(x_2) < 0$. This allows us to compute:

$$E^s(x_2) = \{(x, y, 0) \cdot \left(\frac{a}{b-2}, 1, 0\right)^T : x, y \in \mathbb{R}\} \cup \{(0, y, 0) \cdot (0, 1, 0)^T,$$

$$E^u(x_2) = \{(0, 0, z) \cdot \left(0, \frac{a}{b-2}, 1\right)^T : z \in \mathbb{R}\}.$$
7.4 Analysis of $f$ at $x_3$

We compute $Df(x_3)$ to arrive at the following eigenvalues and eigenvectors:

- $\lambda_1(x_3) = -1$, $v_1(x_3) = (0, 0, 1)^T$,
- $\lambda_2(x_3) = 1 - a$, $v_2(x_3) = (\frac{a - 2}{b}, 1)^T$,
- $\lambda_3(x_3) = 1 - b$, $v_3(x_3) = (\frac{b}{a - 2}, 0, 1)^T$.

By the restrictions given to $a$ and $b$, we know that $\lambda_3(x_3) > 0$ and $\lambda_2(x_3) < 0$. This allows us to compute:

$$E^s(x_3) = \{(0, y, z) \cdot (0, \frac{a - 2}{b}, 1)^T : y, z \in \mathbb{R}\} \cup \{(0, 0, z) \cdot (0, 0, 1)^T,\}
$$

$$E^u(x_2) = \{(0, 0, z) \cdot (\frac{b - 2}{a}, 0, 1)^T : z \in \mathbb{R}\}.$$  

7.5 Analysis of $f$ at $x_4$

We compute $Df(x_4)$ to arrive at the following eigenvalues and eigenvectors:

- $\lambda_1(x_4) = \frac{-1}{1 + a + b}$, $v_1(x_3) = (1, 1, 1)^T$,
- $(\lambda_2(x_4)) = \omega_1$, $v_2(x_4)$,
- $\lambda_3(x_4) = \omega_2$, $v_3(x_4)$.

By the restrictions given to $a$ and $b$, we know that the real part of $\lambda_2(x_4) > 0$ and $\lambda_3(x_4) > 0$. This allows us to compute:

$$E^s(x_3) = \{(x, y, z) \cdot (1, 1, 1)^T : x, y, z \in \mathbb{R}\}
$$

$$E^u(x_2) = \{(x, y, z) \notin E^s(x_4).\}
$$

Now observe that:

$$E^u(x_1) \subset E^s(x_2) \subset \{(x, y, 0) : x, y \in \mathbb{R}\}.$$
\[ E^u(x_2) \subset E^s(x_3) \subset \{(0, y, z) : y, z \in \mathbb{R}\} \]
\[ E^u(x_3) \subset E^s(x_1) \subset \{(x, 0, z) : x, z \in \mathbb{R}\}. \]

Thus, all three fixed points are connected by stable and unstable manifolds. The dynamics of the system can be described as follows: The orbit cycles around the fixed points \(x_1, x_2, x_3\) in succession. It follows that the Lotka-Volterra system with three competitive populations contains heteroclinic cycles for the parameters given above. We now check the stability of this cycle.

### 7.6 Stability of Heteroclinic Cycles

Let \(c_j, e_j, t_j\) denote the real parts of the, strongest contracting eigenvalue, the strongest expanding eigenvalue, the weakest contracting eigenvalue, respectively. Then [2] has stated the following result:

**Theorem** Let \(c_j, e_j, t_j\) denote the real parts of the, strongest contracting eigenvalue, the strongest expanding eigenvalue, the weakest contracting eigenvalue, respectively of a system having a heteroclinic cycle. Then the heteroclinic cycle is stable provided that:

\[
\prod_{j=1}^{m} \min(c_j, e_j - t_j) > \prod_{j=1}^{m} e_j.
\]

### 7.7 Finding Heteroclinic Cycles

Finding heteroclinic cycles in general is a very difficult problem. We investigate the behavior of the Lotka-Volterra system with the parameters:
\[ a = 1 + \frac{1}{100000}, b = 1 - \frac{1}{100000}, \]
with the initial condition
\[ x_0 = \left(\frac{1}{3}, \frac{1}{6}, \frac{1}{6}\right). \]

The solution is given by:
\[ x(t) = \frac{1}{9}e^{-3t} + \frac{1}{3} + e^{3t}\cos\left(\frac{\sqrt{3}t}{100000}\right), \]
\[ y(t) = \frac{1}{9}e^{-3t} - \frac{1}{3} + e^{3t}\cos\left(\frac{\sqrt{3}t}{100000}\right) - \sqrt{3}\sin\left(\frac{\sqrt{3}t}{100000}\right), \]
\[ z(t) = \frac{1}{9}e^{-3t} - \frac{1}{3} + e^{3t}\cos\left(\frac{\sqrt{3}t}{100000}\right) + \sqrt{3}\sin\left(\frac{\sqrt{3}t}{100000}\right). \]

The trajectories for the solution are given by:
Heteroclinic Cycles

Figure 1: \((t, x(t))\)

Figure 2: \((t, y(t))\)

Figure 3: \((t, z(t))\)
Figure 4: 1,000,000 iterations

Figure 5: $10^8$ iterations
Figure 6: $10^9$ iterations

Figure 7: $5 \times 10^{10}$ iterations
Of the system above, we see that the strongest contracting eigenvalue is -1, and the strongest expanding eigenvalue is \(1 - \left(1 - \frac{1}{10^{100000}}\right) = \frac{1}{10^{100000}}\), and the weakest contracting eigenvalue \(1 - (1 + \frac{1}{10^{100000}}) = -\frac{1}{10^{100000}}\) for each of the equilibria. Using the above theorem we see that this cycle is stable.

References
