Dynamics and Bifurcations in Variable Population Interactions

Jordan Whitener

REU 2013

Model Formulation

Typical Predator-Prey Model:

$$\begin{aligned}\frac{dx}{dt} &= \ldots - \frac{a}{c+mx}xy \\ \frac{dy}{dt} &= \ldots + \frac{b}{c+mx}xy\end{aligned} \tag{1}$$

Where x and y represent the number of prey and predators respectively, $\frac{dx}{dt}$ and $\frac{dy}{dt}$ represent the growth rates of the populations, t represents time, and a, b, c, and m are positive parameters representing ecological factors.

For this model, the relationship between x and y is fixed.

Model Formulation

However in nature, some interactions between two species are not necessarily static, but rather depend on the state of the system:

- Rock Lobsters vs. Whelks
- Ants vs Aphids

In such cases, a fixed classification and modeling of the interaction between x and y is inadequate.

Generalize Model

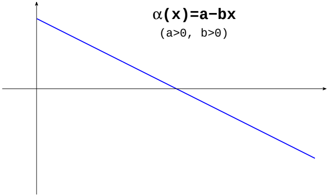
Instead, generalize (1) to

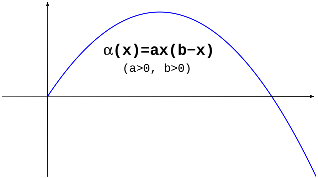
$$\frac{dx}{dt} = \ldots + \frac{\alpha_1(x,y)}{c+mx}xy$$
$$\frac{dy}{dt} = \ldots + \frac{\alpha_2(x,y)}{c+mx}xy \qquad (2)$$

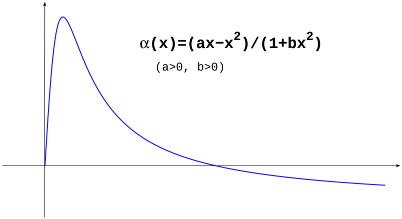
where the functions α_1 and α_2 can take positive and negative values. Since these functions are not constant, the interaction between x and y can shift from mutualistic to host-parasitic to competitive, depending on the signs.

Some Examples

The type of α function used affects the magnitude of benefit or detriment the species undergo when they interact:







First Model

$$\frac{dx}{dt} = x(r_1 - k_1x) + ay(b-y)xy - \frac{hx}{e+x}$$
$$\frac{dy}{dt} = y(r_2 - k_2y) + cx(d-x)xy$$

This model includes the harvesting function $H(x) = \frac{hx}{e+x}$ and has quadratic α functions.

All parameters $\in \mathbb{R}^+$, r_1, r_2 represent the intrinsic growth rates, k_1, k_2 represent the intra-specific competition coefficients, h represents the rate of harvesting limit, e represents the number of species x it takes to reach half of the rate of harvesting limit, and a, b, c, d represent changes in environmental conditions.

Equilibrium Points

Definition

Equilibrium Point:

A point $\mathbf{x}_0 \in R^n$ is an equilibrium of

$$\dot{\mathbf{x}} = f(\mathbf{x})$$

if $f(\mathbf{x}_0) = 0 \quad \forall t$.

- Boundary Equilibria
- Coexistence Equilibria

Boundary Equilibria

A Boundary Equilibrium occurs along the x or y axis, when either one or both species is extinct.
For $\mathbf{x_0}$ a boundary equilibrium, $\mathbf{x_0}$ may have the form:

- $(0, 0)$
- $(x_{\pm}, 0)$
- $(0, \frac{r_2}{k_2})$

where $x_{\pm}$ and $\frac{r_2}{k_2}$ are the carrying capacities for the respective species.

Restrictions for $x_\pm$

$$x_\pm = \frac{(r_1 - k_1 e) \pm \sqrt{(r_1 + k_1 e)^2 - 4k_1 h}}{2k_1}.$$

Have restrictions on parameter values to get at least one positive, real x_k. Must have:

- $h \leq \frac{(r_1+k_1 e)^2}{4k_1}$.
    - If $h < r_1 e$, then only $x_+ > 0$.
    - If $h = r_1 e$ and $r_1 > k_1 e$, then $x_+ = \frac{r_1 - k_1 e}{k_1}$ and $x_- = 0$.
    - If $r_1 e < h < \frac{(r_1+k_1 e)^2}{4k_1}$
        - and $r_1 > k_1 e$, then $x_\pm > 0$.
        - and $r_1 < k_1 e$, then $x_\pm < 0$.

Coexistence Equilibria

A coexistence equilibrium is of the form $\mathbf{x_0} = (x^*, y^*)$, $x^* > 0$, $y^* > 0$. Remember the system is:

$$\frac{dx}{dt} = x\left[r_1 - k_1 x + ay(b-y)y - \frac{h}{e+x}\right]$$

$$\frac{dy}{dt} = y[r_2 - k_2 y + cx(d-x)x]$$

Thus a coexistence equilibrium (x^*, y^*) is a solution of:

$$r_1 - k_1 x + ay(b-y)y - \frac{h}{e+x} = 0 \tag{3}$$

$$r_2 - k_2 y + cx(d-x)x = 0 \tag{4}$$

These are the nullclines for the system.

Coexistence Equilibria

To find x^*, have:

$$\frac{ac^3}{k_2^3}x^{10}+(\frac{ac^3e}{k_2^3}-\frac{3ac^3d}{k_2^3})x^9+\ldots+(r_1e-h+\frac{aber_2^2}{k_2^2}-\frac{aer_2^3}{k_2^3})=0$$

Then put x^* values in to:

$$y=\frac{1}{k_2}[r_2+cx^2(d-x)]$$

Coexistence Equilibria are classified as mutualistic, host-parasitic, or competitive, and I use two methods of classification:

Coexistence Equilibria

To find x^*, have:

$$\frac{ac^3}{k_2^3}x^{10}+(\frac{ac^3e}{k_2^3}-\frac{3ac^3d}{k_2^3})x^9+\ldots+(r_1e-h+\frac{aber_2^2}{k_2^2}-\frac{aer_2^3}{k_2^3})=0$$

Then put x^* values in to:

$$y=\frac{1}{k_2}[r_2+cx^2(d-x)]$$

Coexistence Equilibria are classified as mutualistic, host-parasitic, or competitive, and I use two methods of classification:

- Slope Method

Coexistence Equilibria

To find x^*, have:

$$\frac{ac^3}{k_2^3}x^{10}+(\frac{ac^3e}{k_2^3}-\frac{3ac^3d}{k_2^3})x^9+\ldots+(r_1e-h+\frac{aber_2^2}{k_2^2}-\frac{aer_2^3}{k_2^3})=0$$

Then put x^* values in to:

$$y=\frac{1}{k_2}[r_2+cx^2(d-x)]$$

Coexistence Equilibria are classified as mutualistic, host-parasitic, or competitive, and I use two methods of classification:

- Slope Method
- Carrying Capacity Method

Slope Method

Through implicit differentiation, find equations for the slopes of the nullclines:

$$m_1 = \frac{k_1(e+x)^2 - h}{ay(2b-3y)(e+x)^2}$$

$$m_2 = \frac{1}{k_2}[cx(2d-3x)]$$

To determine the type of coexistence equilibrium, evaluate the slopes at (x^*, y^*):

- mutualistic if $m_1 > 0$ and $m_2 > 0$
- host-parasitic if $m_1 > 0$ and $m_2 < 0$ or $m_1 < 0$ and $m_2 > 0$
- competitive if $m_1 < 0$ and $m_2 < 0$

Conditions for Classifications

Mutualistic:

- Must have $x < \frac{2d}{3}$.
  - For $h \leq k_1 e^2$, must have:
    - $y < \frac{2b}{3}$.
  - For $h > k_1 e^2$, must have:
    - either $x > \sqrt{\frac{h}{k_1}} - e$ and $y < \frac{2b}{3}$
    - or $0 < x < \sqrt{\frac{h}{k_1}} - e$ and $y > \frac{2b}{3}$.

Conditions for Classifications

Competitive:

- Must have $x > \frac{2d}{3}$.
  - For $h \leq k_1 e^2$, must have:
    - $y > \frac{2b}{3}$.
  - For $h > k_1 e^2$, must have:
    - either $x > \sqrt{\frac{h}{k_1}} - e$ and $y > \frac{2b}{3}$
    - or $0 < x < \sqrt{\frac{h}{k_1}} - e$ and $y < \frac{2b}{3}$.

Conditions for Classifications

Host-Parasitic:

- For $x > \frac{2d}{3}$:
  - For $h \leq k_1 e^2$, must have:
    - $y < \frac{2b}{3}$.
  - For $h > k_1 e^2$, must have:
    - either $x > \sqrt{\frac{h}{k_1}} - e$ and $y < \frac{2b}{3}$
    - or $0 < x < \sqrt{\frac{h}{k_1}} - e$ and $y > \frac{2b}{3}$.

Conditions for Classifications

Host-Parasitic:

- For $x > \frac{2d}{3}$:
  - For $h \leq k_1 e^2$, must have:
    - $y < \frac{2b}{3}$.
  - For $h > k_1 e^2$, must have:
    - either $x > \sqrt{\frac{h}{k_1}} - e$ and $y < \frac{2b}{3}$
    - or $0 < x < \sqrt{\frac{h}{k_1}} - e$ and $y > \frac{2b}{3}$.
- For $x < \frac{2d}{3}$:
  - For $h \leq k_1 e^2$, must have:
    - $y > \frac{2b}{3}$.
  - For $h > k_1 e^2$, must have:
    - either $x > \sqrt{\frac{h}{k_1}} - e$ and $y > \frac{2b}{3}$
    - or $0 < x < \sqrt{\frac{h}{k_1}} - e$ and $y < \frac{2b}{3}$.

Carrying Capacity Method

Again the system is:

$$\frac{dx}{dt} = x\left[r_1 - k_1 x + ay(b-y)y - \frac{h}{e+x}\right]$$

$$\frac{dy}{dt} = y[r_2 - k_2 y + cx(d-x)x]$$

Find the carrying capacities:

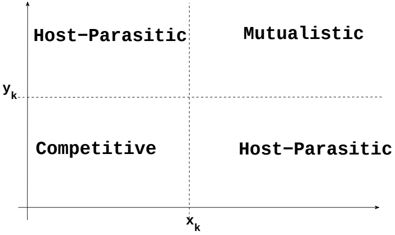
$$y_k = \frac{r_2}{k_2}$$

$$x_k = \frac{(r_1 - k_1 e) \pm \sqrt{(r_1 + k_1 e)^2 - 4k_1 h}}{2k_1}$$

Carrying Capacity Method

Compare coexistence equilibrium (x^*, y^*) to carrying capacities:

- mutualistic if $x^* > x_k$ and $y^* > y_k$
- host-parasitic if $x^* > x_k$ and $y^* < y_k$ or $x^* < x_k$ and $y^* > y_k$
- competitive if $x^* < x_k$ and $y^* < y_k$



Local Stability Analysis

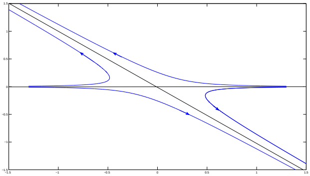
For either type of equilibrium, I analyze the behavior of the system around the points.
There are two methods for analyzing the points:

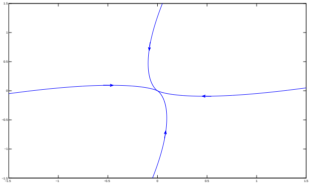
- Eigenvalue Analysis
- Trace-Determinant Analysis

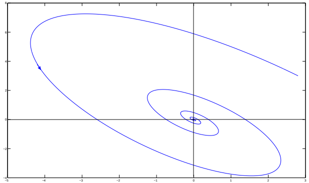
There are four types of behavior for a 2-D system:

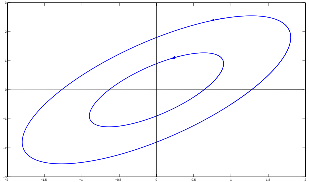
- Saddle
- Node
- Focus
- Center

Simple Examples









Linearization of System

Have non-linear system:

$$\dot{\mathbf{x}} = f(\mathbf{x}). \tag{5}$$

For a linear system:

$$\dot{\mathbf{x}} = A\mathbf{x} \qquad \text{with} \qquad \mathbf{x}(0) = \mathbf{x_0},$$

solutions are of the form

$$\mathbf{x}(t) = e^{At}\mathbf{x_0}, \qquad t \in \mathbb{R}, \qquad \text{for} \qquad e^{At} = \sum_{k=0}^{\infty} \frac{A^k t^k}{k!}.$$

Linearization of System

To linearize system, have this definition:

Definition

The linearization of (5) is defined as

$$\dot{\mathbf{x}} = A\mathbf{x}$$

where $A = Df(\mathbf{x})$, the Jacobian of f.

Evaluate the Jacobian at the equilibrium to linearize around that point; use eigenvalue or trace-determinant methods for behavior of linear systems (good local approximation to non-linear system: **Hartman-Grobman Thm**. and **Stable Manifold Thm**.).

Jacobian of System

The general Jacobian for the system is:

$$\mathbf{J}(x,y) = \begin{bmatrix} r_1 + ay^2(b-y) - 2k_1x - \frac{he}{(e+x)^2} & axy(2b-3y) \\ cxy(2d-3x) & r_2 + cx^2(d-x) - 2k_2y \end{bmatrix}$$

For coexistence equilibria, the Jacobian simplifies to:

$$\mathbf{J}(x^*,y^*) = \begin{bmatrix} -Bx^* & \frac{Bx^*}{m_1} \\ m_2k_2y^* & -k_2y^* \end{bmatrix}$$

For $B = \frac{k_1(e+x^*)^2 - h}{(e+x^*)^2}$ and m_1, m_2 the slopes of the nullclines

evaluated at (x^*, y^*).

Eigenvalue Analysis

Once I have the eigenvalues of the Jacobian, can determine the type of equilibrium:

- $\lambda_1, \lambda_2 \in \mathbb{R}$, $\lambda_1 < 0 < \lambda_2$ or $\lambda_1 > 0 > \lambda_2$: Saddle point
- $\lambda_1, \lambda_2 \in \mathbb{R}$, $\lambda_1 \leq \lambda_2 < 0$ or $\lambda_1 \geq \lambda_2 > 0$: Node
- $\lambda = \mathrm{a} \pm \mathrm{bi}$ for a, b $\in \mathbb{R}$: Focus
- $\lambda = \pm \mathrm{bi}$ for b $\in \mathbb{R}$: Center

Note: If λ is purely imaginary, then the equilibrium is said to be non-hyperbolic.

Trace-Determinant Analysis

Use this method when finding an explicit expression for the eigenvalues is difficult.
The formula for the eigenvalues can be written as:

$$\lambda = \frac{T \pm \sqrt{T^2 - 4D}}{2}$$

for A=the Jacobian of the system evaluated at the equilibrium, $T = trA$, and $D = detA$. Thus

- if $D<0$: Saddle Point
- if $D>0$ and $T^2-4D \geq 0$: Node
  (Stable if $T<0$, unstable if $T>0$)
- if $D>0$ and $T^2-4D<0$: Focus
  (Stable if $T<0$, unstable if $T>0$)
- if $D>0$ and $T=0$: Center

Conditions for Solution Behavior

For $(0, 0)$:

- $h < r_1 e$: Unstable Node.
- $h > r_1 e$: Saddle Point.
- Cannot be a stable node, focus, or of center-type.

For $(0, \frac{r_2}{k_2})$:

- $h < r_1 e + \frac{a e r_2^2}{k_2^2}(b - \frac{r_2}{k_2})$: Saddle Point.
- $h > r_1 e + \frac{a e r_2^2}{k_2^2}(b - \frac{r_2}{k_2})$: Stable Node.
- Cannot be an unstable node, focus, or of center-type.

Conditions for Solution Behavior

For $(\mathbf{x}_+, \mathbf{0})$:

$\lambda_1 \leq 0$ for $h \leq \frac{(r_1+k_1 e)^2}{4k_1}$, but $h \leq \frac{(r_1+k_1 e)^2}{4k_1}$ is necessary for $x_+ \in \mathbb{R}$.

Make inequality strict so as to keep λ_1 hyperbolic.

Also have $\lambda_1 \in \mathbb{R}$ for $x_+ \in \mathbb{R}$.

Thus $\lambda_1 < 0$ and $\lambda_1 \in \mathbb{R}$, so x_+ *may only be a saddle point or stable node*.

For $(\mathbf{x}_-, \mathbf{0})$:

$\lambda_1 > 0$ for $h < \frac{(r_1+k_1 e)^2}{4k_1}$, but $h < \frac{(r_1+k_1 e)^2}{4k_1}$ is necessary for $x_- \in \mathbb{R}$ and for x_- to exist.

(At $h = \frac{(r_1+k_1 e)^2}{4k_1}$, $x_+ = x_-$).

Also $\lambda_1 \in \mathbb{R}$ for $x_- \in \mathbb{R}$.

Thus x_- *may only be a saddle point or unstable node*.

Conditions for Solution Behavior

Special case for $h = r_1 e$.

$x_- = 0$ and $x_+ = \frac{r_1 - k_1 e}{k_1}$.

Let $F = 2cd^3 + 27r_2 + 3\sqrt{12cd^3 r_2 + 81r_2^2}$.

- If $r_1 > \frac{k_1}{3}\left[d + \sqrt[3]{\frac{F}{2c}} + \sqrt[3]{\frac{2cd^6}{F}}\right] + k_1 e$, then $(x_+, 0)$ is a stable node.
- If $r_1 < \frac{k_1}{3}\left[d + \sqrt[3]{\frac{F}{2c}} + \sqrt[3]{\frac{2cd^6}{F}}\right] + k_1 e$, then $(x_+, 0)$ is a saddle point.

Conditions for Solution Behavior

Let $x_B = \frac{-k_1 e + \sqrt{k_1 h}}{k_1}$, with B, m_1, and m_2 the same as before.

Then for $(\mathbf{x}^*, \mathbf{y}^*)$:

- If $(Bx + k_2 y)^2 - 4Bk_2(1 - \frac{m_2}{m_1})xy \geq 0$
  - and $e > \sqrt{\frac{h}{k_1}}$ and $\frac{m_2}{m_1} < 1$: Stable Node.
  - and $e < \sqrt{\frac{h}{k_1}}$, $x > x_B$, and $\frac{m_2}{m_1} < 1$: Stable Node.
  - and $e < \sqrt{\frac{h}{k_1}}$, $x < x_B$, $\frac{m_2}{m_1} > 1$, and $Bx + k_2 y > 0$: Stable Node.
  - $e < \sqrt{\frac{h}{k_1}}$, $x < x_B$, $Bx + k_2 y < 0$, and $\frac{m_2}{m_1} > 1$: Unstable Node.

Conditions for Solution Behavior

For $(\mathbf{x}^*, \mathbf{y}^*)$:

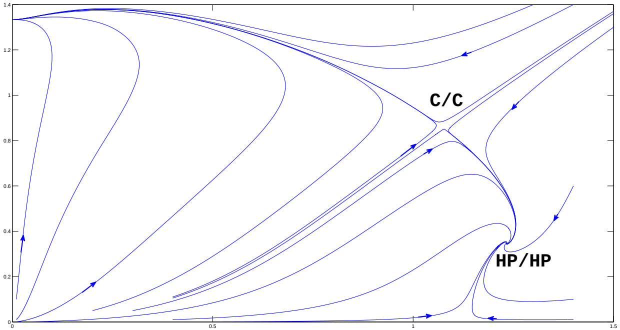
- If $e > \sqrt{\frac{h}{k_1}}$ and $\frac{m_2}{m_1} > 1$: Saddle Point.
- If $e < \sqrt{\frac{h}{k_1}}$, $x > x_B$, and $\frac{m_2}{m_1} > 1$: Saddle Point.
- If $e < \sqrt{\frac{h}{k_1}}$, $x < x_B$, $Bx + k_2 y \neq 0$, and $\frac{m_2}{m_1} < 1$: Saddle Point.
- If $(Bx + k_2 y)^2 < 4Bk_2(1 - \frac{m_2}{m_1})xy$
    - and $Bx + k_2 y > 0$: Stable Focus.
    - and $Bx + k_2 y < 0$: Unstable Focus.
    - and $h > k_1(e + x)^2$, $\frac{m_2}{m_1} > 1$, and $Bx + k_2 y = 0$: Center.

Examples

Parameter Values:

a=0.9; b=0.8; c=0.9; d=0.8; e=0.6; h=0.2;

k_1=0.6; k_2=0.6; r_1=0.8; r_2=0.8;

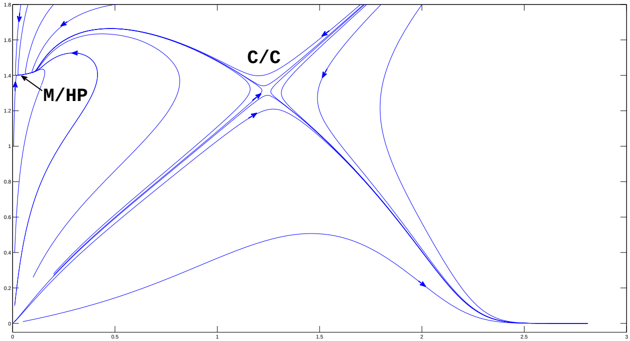


Examples

Parameter Values:

a=0.6; b= 0.9; c=0.8; d=1.2; e=0.7; h=0.2;

k_1=0.3; k_2=0.5; r_1=0.9; r_2=0.7;

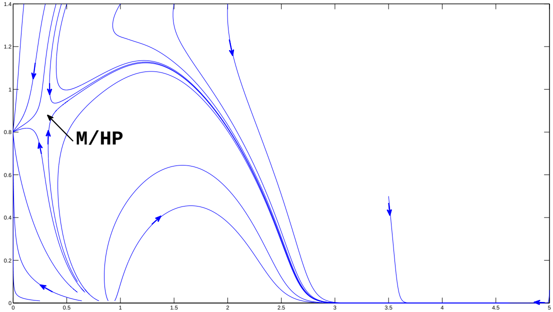


Examples

Parameter Values:

a=1; b=1.3; c=0.4; d=1.5; e=0.5; h=0.72;

k_1=0.1; k_2=0.5; r_1=0.6; r_2=0.4;



Bifurcations

The system depends on 10 parameters, so it is of the form:

$$\dot{\mathbf{x}} = f(\mathbf{x}, \mu) \quad (6)$$

with $\mu \in \mathbb{R}^{10}$.

The solutions and behavior of the system change with variations in the parameters, but occasionally drastic changes (**bifurcations**) take place for an arbitrarily small change in one or more parameters.

If there exists a μ_0 for which (6) is not structurally stable, then μ_0 is called a **bifurcation value**.

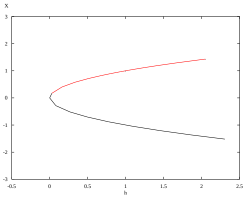
Bifurcations

Types of bifurcations I looked for:

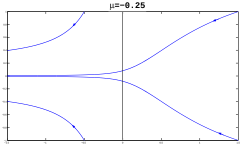
- Transcritical: Exchange of stability.
- Saddle-Node(Fold): Number of equilibria goes from two to one to none or vice versa, stability properties change at bifurcation value.
- Pitchfork: One equilibrium bifurcates into three equilibria, initial equilibrium changes stability and two new equilibria keep stability quality.
- Hopf: An equilibrium bifurcates into a periodic orbit.
- Cusp: A two-parameter bifurcation, occurs where saddle-node bifurcations form.

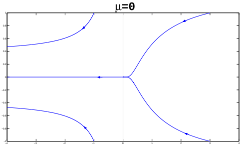
Saddle-Node Bifurcation

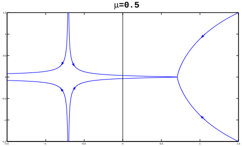
Bifurcation Diagram:



Phase Portrait:

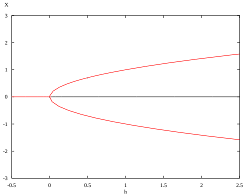




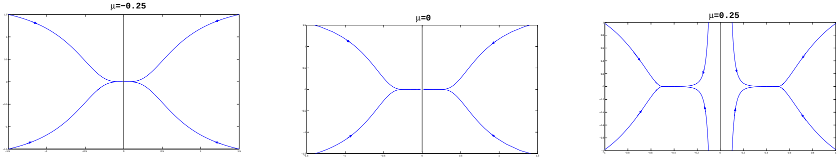


Pitchfork Bifurcation

Bifurcation Diagram:



Phase Portrait:



Finding Bifurcations

Sotomayor's Theorem

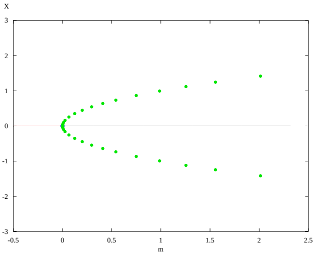
Assume have an n-dimensional system $\dot{\mathbf{x}} = f(\mathbf{x}, \mu)$ *and have* $f(\mathbf{x_0}, \mu_0) = 0$, $J(\mathbf{x}_0, \mu_0) = A$ *has a simple eigenvalue* $\lambda = 0$, ν *is an eigenvector of* A *corresponding to* $\lambda = 0$, ω *is a left eigenvector of* A *corresponding to* $\lambda = 0$, *and* A *has* k *eigenvalues with negative real part and n-k-1 eigenvalues with positive real part.*
If $\omega^T f_\mu(\mathbf{x}_0, \mu_0) \neq 0$ *and* $\omega^T[D^2 f(\mathbf{x}_0, \mu_0)(\nu, \nu)] \neq 0$, *then there is a* **saddle-node bifurcation** *at* $\mathbf{x}_0$ *when* $\mu = \mu_0$.
Have similar sufficient conditions to prove existence of **transcritical** *and* **pitchfork bifurcations**.

Finding Bifurcations

To have a Hopf bifurcation, must meet conditions for center behavior (purely imaginary eigenvalues, i.e. $detA > 0$ and $trA = 0$) and have Liapunov number $\sigma \neq 0$.

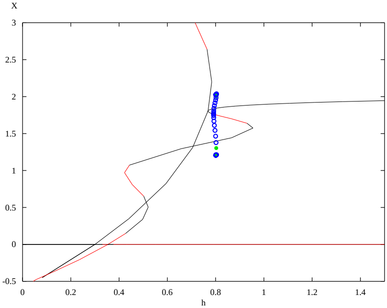
Initially use XPPAUT to see if any bifurcations exist.

Example Hopf Bifurcation Diagram:



Bifurcations in Model

Parameter Values:
a=0.3; b=1.3; c=0.4; d=1.5; e=0.6; h=varied;
k_1=0.1; k_2=0.4; r_1=0.5; r_2=0.4;
Results from XPPAUT with h as free parameter:



Bifurcations in Model

XPPAUT output:

```
BR    PT TY LAB    PAR(1)        L2-NORM         U(1)          U(2)
 1     1 EP   1  3.000000E-01  4.400000E+00  4.400000E+00  9.881313-324
 1    11 LP   2  7.840000E-01  2.200000E+00  2.200000E+00  0.000000E+00
 1    12 BP   3  7.685116E-01  1.806442E+00  1.806442E+00  0.000000E+00
 1    16 BP   4  2.999869E-01  2.222243E-05 -2.222243E-05  0.000000E+00
 1    19 EP   5 -2.000001E-01  2.208811E-27 -2.208811E-27  0.000000E+00

BR    PT TY LAB    PAR(1)        L2-NORM         U(1)          U(2)
 2     7 HB   6  7.917271E-01  1.772165E+00  1.762547E+00  1.843790E-01
 2    11 LP   7  9.550545E-01  1.773096E+00  1.574433E+00  8.154938E-01
 2    15 LP   8  4.225300E-01  1.786045E+00  9.713761E-01  1.498794E+00
 2    18 LP   9  5.207979E-01  1.350943E+00  5.043540E-01  1.253265E+00
 2    21 BP  10  3.539988E-01  1.000000E+00 -1.844286E-06  1.000000E+00
 2    26 EP  11 -1.138562E-03  1.905265E+00 -6.160023E-01  1.802936E+00

BR    PT TY LAB    PAR(1)        L2-NORM         U(1)          U(2)
 2    17 EP  12  2.284388E+00  2.196034E+00  1.988538E+00 -9.318173E-01

BR    PT TY LAB    PAR(1)        L2-NORM         U(1)          U(2)
 3    10 EP  13  2.271861E+00  1.064440E-53 -1.064440E-53  0.000000E+00

BR    PT TY LAB    PAR(1)        L2-NORM         U(1)          U(2)
 3     7 EP  14 -1.918603E-01  4.129194E-31 -4.129194E-31  0.000000E+00

BR    PT TY LAB    PAR(1)        L2-NORM         U(1)          U(2)
 4    10 EP  15  2.078648E+00  1.000000E+00  1.747150E-52  1.000000E+00

BR    PT TY LAB    PAR(1)        L2-NORM         U(1)          U(2)
 4     7 EP  16 -1.864762E-02  1.000000E+00 -2.571394E-38  1.000000E+00

BR    PT TY LAB    PAR(1)        L2-NORM       MAX U(1)      MAX U(2)        PERIOD
 6     9 LP  17  8.024750E-01  1.758325E+00  2.007497E+00  9.170014E-01  3.425564E+01
 6    11 LP  18  8.010738E-01  1.773379E+00  2.026095E+00  1.200470E+00  4.869325E+01
 6    19 LP  19  8.015567E-01  1.813863E+00  2.026656E+00  1.205150E+00  1.142182E+02
 6    31 LP  20  8.012050E-01  1.833071E+00  2.025949E+00  1.206438E+00  3.307053E+02
 6    35 LP  21  8.019144E-01  1.836337E+00  2.024345E+00  1.204727E+00  4.941244E+02
 6    37 LP  22  8.010759E-01  1.837749E+00  2.024512E+00  1.206049E+00  6.119847E+02
 6    40 LP  23  8.011757E-01  1.839380E+00  2.023052E+00  1.206188E+00  8.753723E+02
 6    42 LP  24  8.011173E-01  1.839625E+00  2.025670E+00  1.205815E+00  9.332094E+02
 6    43 MX  25  8.011173E-01  1.838080E+00  2.025461E+00  1.205860E+00  9.332094E+02
```

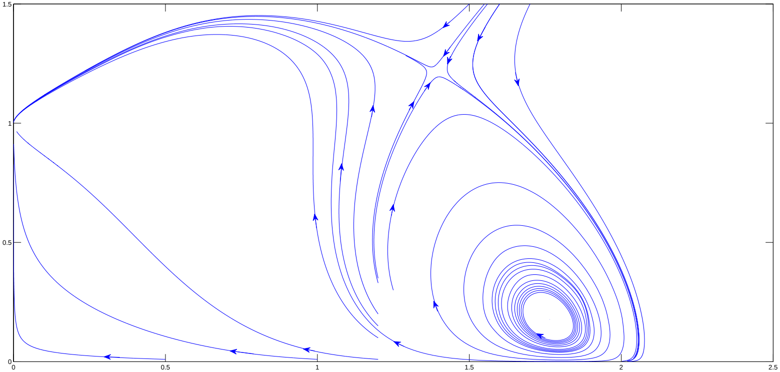
- Used theorems to prove existence of transcritical, saddle-node, and Hopf bifurcations.

Bifurcations in Model

Parameter Values:

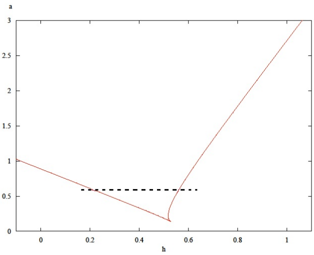
a=0.3; b=1.3; c=0.4; d=1.5; e=0.6; h=0.8024750;

k_1=0.1; k_2=0.4; r_1=0.5; r_2=0.4;

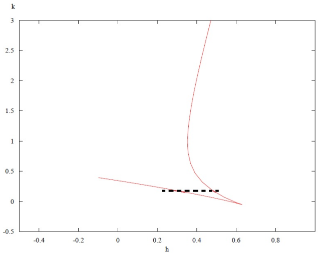


Two-Parameter Bifurcations in Model

Parameter Values:
a=varied; h=varied;
b=1.3; c=0.4; d=1.5; e=0.6;
k_1=0.1; k_2=0.4; r_1=0.5; r_2=0.4;



Parameter Values:
k_1=varied; h=varied;
a=0.3; b=1.3; c=0.4; d=1.5;
e=0.6; k_2=0.4; r_1=0.5; r_2=0.4;



Boundedness of Coexistence Solutions

First some necessary tools:

Differential Inequality

If $\omega(t, u)$ is a scalar function of the scalars t, u in some open connected set Ω, we say a function $v(t)$, $a \leq t \leq b$, is a solution of the **differential inequality**

$$\dot{v}(t) \leq \omega(t, v(t)) \tag{7}$$

on $[a, b)$ if $v(t)$ is continuous on $[a, b)$ and has a derivative on $[a, b)$ that satisfies (7).

Boundedness of Coexistence Solutions

Theorem (1)

Let $\omega(t,u)$ be continuous on an open connected set $\Omega \sqsubset \mathbb{R}^2$ and be such that the initial value problem for the scalar equation

$$\dot{u} = \omega(t,u) \tag{8}$$

has a unique solution.
If $u(t)$ is a solution of (8) on $a \leq t \leq b$ and $v(t)$ is a solution of (7) on $a \leq t < b$ with $v(a) \leq u(a)$, then $v(t) \leq u(t)$ for $a \leq t \leq b$.

Boundedness of Coexistence Solutions

Every solution (x, y) starting in $\mathbb{R}^2_+$ which satisfies either

$$x \geq \frac{d + \sqrt{d^2 + b^2}}{2} \text{ or } y \geq \frac{b + \sqrt{b^2 + d^2}}{2} \tag{9}$$

is bounded.

Proof

Let $w = x + \frac{a}{c}y$. Then

$$\dot{w} = x(r_1 - k_1 x) + ay(b - y)xy - H(x) + \frac{a}{c}[y(r_2 - k_2 y) + cx(d - x)xy],$$

and for each $k > 0$ we have

$$\dot{w} + kw = x(r_1 + k - k_1) + axy[y(b - y) + x(d - x)] + \frac{a}{c}y[r_2 + k - k_2 y] - H(x).$$

Note: both $x(r_1 + k - k_1)$ and $\frac{a}{c}y[r_2 + k - k_2 y]$ form downward opening parabolas.

Boundedness of Coexistence Solutions

Replacing the parabolas with their corresponding maximum values, get

$$\dot{w} + kw \leq \frac{(r_1 + k)^2}{4k_1} + axy[y(b-y) + x(d-x)] + \frac{a}{c}[\frac{(r_2+k)^2}{4k_2}] - H(x).$$

Note that $H(x) = \frac{hx}{e+x}$, so $\lim_{x \to \infty^+} H(x) = h$.

Thus $0 \leq H(x) \leq h$ and $h > 0$.

Set restriction that $y(b-y) + x(d-x) < 0$, which gives rise to (9).

Thus $\exists B > 0$ such that $\dot{w} + kw \leq B$, or $\dot{w} \leq B - kw$.

Let $\dot{u} = B - ku$ with $u(0) = w(0)$. Then $\dot{u} + ku = B$, which can be solved explicitly by using an integrating factor. Get

$$u(t) = \frac{B}{k}(1 - e^{-kt}) + u_0 e^{-kt} \tag{10}$$

where $u_0 = w_0 = x_0 + \frac{a}{c} y_0$.

Boundedness of Coexistence Solutions

Let $w(t)$ be a solution of $\dot{w} \leq B - kw$.

Then by Theorem 1, $w(t) \leq u(t)$ for $0 \leq t < \infty$.

Thus $0 < w(t) \leq \frac{B}{k}(1 - e^{-kt}) + w_0 e^{-kt}$, and

$\lim_{t\to\infty} \frac{B}{k}(1 - e^{-kt}) + w_0 e^{-kt} = \frac{B}{k}$. □

Conditions for no Periodic Solutions

Can establish conditions under which periodic solutions are not possible, using what is called Dulac's Criterion:

Dulac's Criterion

Let D be a simply connected open set of $\mathbb{R}^2$. If there exists a real-valued function $\phi(x, y) \in C^1$ in D such that

$$\frac{\partial}{\partial x}[\phi(x,y)F_1(x,y)] + \frac{\partial}{\partial y}[\phi(x,y)F_2(x,y)]$$

is not identically zero and does not change sign in D, then the dynamical system

$$\dot{x} = F_1(x,y)$$

$$\dot{y} = F_2(x,y)$$

has no closed periodic orbits contained in D.

Conditions for no Periodic Solutions

Let D be $\mathbb{R}_+^2$ and use $\phi(x,y) = \frac{1}{xy}$.

Then get

$$\frac{\partial}{\partial x}[\phi(x,y)F_1(x,y)] + \frac{\partial}{\partial y}[\phi(x,y)F_2(x,y)] = \frac{hx - (k_1 x + k_2 y)(e+x)^2}{xy(e+x)^2}.$$

Which can be written as

$$\frac{-k_1 x^3 - 2ek_1 x^2 + (h - e^2 k_1)x - k_2(e+x)^2 y}{xy(e+x)^2}.$$

Conditions for no Periodic Solutions

For $e \geq \sqrt{\frac{h}{k_1}}$, all coefficients of

$$\frac{-k_1x^3 - 2ek_1x^2 + (h - e^2k_1)x - k_2(e+x)^2y}{xy(e+x)^2}$$

are negative $\forall x, y \in \mathbb{R}^2_+$.

Then by Dulac's Criterion, when $e \geq \sqrt{\frac{h}{k_1}}$ the system has no closed periodic orbits contained in $\mathbb{R}^2_+$.

Corollary: For $h = 0$ (no harvesting), simply have $e \geq 0$, which is always true. Thus without harvesting, no closed periodic solutions are contained in $\mathbb{R}^2_+$.

So the harvesting function allows for periodic solutions, given that $e < \sqrt{\frac{h}{k_1}}$.

Impact of Harvesting

System without harvesting:

$$\begin{aligned}\frac{dx}{dt} &= x(r_1 - k_1 x) + ay(b - y)xy \\ \frac{dy}{dt} &= y(r_2 - k_2 y) + cx(d - x)xy\end{aligned}$$

Boundary equilibria are: $(0,0)$, $(0, \frac{r_2}{k_2})$, and $(\frac{r_1}{k_1}, 0)$.

versus $(0,0)$, $(0, \frac{r_2}{k_2})$, and $(x_{\pm}, 0)$ with harvesting.

Impact of Harvesting

Without harvesting:

- $(0, 0)$ is always an unstable node.
- $(0, \frac{r_2}{k_2})$ is always a saddle or stable node.
- $(\frac{r_1}{k_1}, 0)$ is always a saddle or stable node.
- (x^*, y^*) is always either a saddle, stable node, or stable focus.

With harvesting:

- $(0, 0)$ is always a saddle or unstable node.
- $(0, \frac{r_2}{k_2})$ is always a saddle or stable node, though different conditions are necessary for a saddle.
- $(x_\pm, 0)$ is always either a saddle, stable node, or unstable node.
- (x^*, y^*) can be a saddle, stable node, unstable node, stable focus, unstable focus, or of center-type.

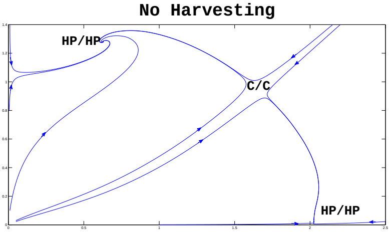
Impact of Harvesting

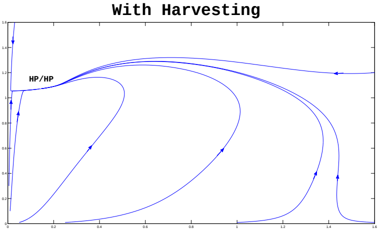
For these parameter values,
$a = 1.09$, $b = 1.28$, $c = 0.4$, $d = 0.21$, $r_1 = 0.53$, $r_2 = 0.57$,
$k_1 = 0.76$, $k_2 = 0.91$, $h = 0$, $e = 0$,
have one coexistence equilibrium, $(0.89072, 0.38898)$,
which is a stable focus.
By the slope and carrying-capacity classifications, $(0.89072, 0.38898)$ is a *host-parasitic* equilibrium.

With $h = 1.29$ and $e = 1.63$, have one coexistence equilibrium, $(0.062363, 0.62663)$, which is a stable node.
By the slope classification, $(0.062363, 0.62663)$ is a *mutualisitc* equilibrium (x_k is complex).

Impact of Harvesting

For these parameter values,
$a = 1.09,\ b = 0.63,\ c = 0.76,\ d = 1.6,\ r_1 = 1.68,\ r_2 = 1.36,$
$k_1 = 0.83,\ k_2 = 1.29,\ h = 1.35,\ e = 1.2,$ have





Second Model

Instead of using parabolic α function, use a rational α function:

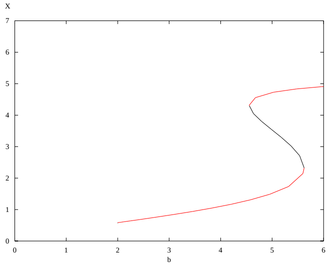
$$\begin{aligned}\frac{dx}{dt} &= x(r_1 - k_1 x) + k_1\left(\frac{by-y^2}{1+ay^2}\right)xy - \frac{hx}{e+x}\\ \frac{dy}{dt} &= y(r_2 - k_2 y) + k_2\left(\frac{dx-x^2}{1+cx^2}\right)xy\end{aligned}$$

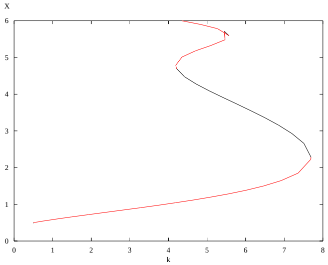
Compare to Dr. Hernandez's model:

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(r_1 - (\frac{r_1}{k_1})N_1) + \frac{r_1}{k_1}\left(\frac{b_1 N_2 - N_2^2}{1+c_1 N_2^2}\right)N_1 N_2\\ \frac{dN_2}{dt} &= N_2(r_2 - (\frac{r_2}{k_2})N_2) + \frac{r_2}{k_2}\left(\frac{b_2 N_1 - N_1^2}{1+c_2 N_1^2}\right)N_1 N_2\end{aligned}$$

Graphical Analysis of Bifurcations

For Dr. Hernandez's model:

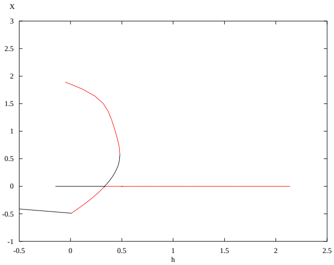


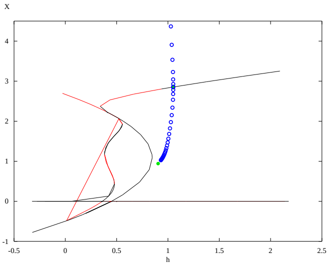


Note: Dr. Hernandez only had saddle-node bifurcations in her model.

Graphical Analysis of Bifurcations

For Second Model:





For parameters:

$a = 1,\ b = 1.3,\ c = 0.4,\ d = 1.5,\ e = 0.5,\ h = \text{varied},\ r_1 = 0.6,\ r_2 = 0.4,$

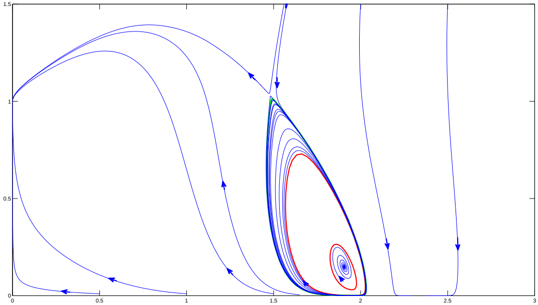
$k_1 = 0.337,\ k_2 = 0.5.$ For $h = 1.0515$, had a hopf bifurcation.

Periodic Orbits in Second Model

For parameters:

$$a = 0.2,\ b = 1.3,\ c = 0.2,\ d = 1.5,\ e = 0.6,\ h = 0.7816406,$$

$$r_1 = 0.5,\ r_2 = 0.4,\ k_1 = 0.1,\ k_2 = 0.4.$$



Next Step

- Mathematical analysis of second model(rational α function).
- Add a refuge component to one or both species.
- Make stage-structured populations.
- Use more than two species, with either static or variable interactions.

References

[1] Hale, J. (1980). *Ordinary Differential Equations*. Wiley.

[2] Hernandez, M., & Barradas, I. (2003). Variation in the outcome of population interactions: bifurcations and catastrophes. *Journal of Mathematical Biology, 46,* 571-594.

[3] Hernandez, M. (2009). Disentangling nature, strength and stability issues in the characterization of population interactions. *Journal of Theoretical Biology, 261,* 107-119.

[4] Rebaza, J. (2012). *A First Course in Applied Mathematics*. Wiley.

References

[5] Rebaza, J. (2012). Dynamics of prey threshold harvesting and refuge. *Journal of Computational and Applied Mathematics, 236,* 1743-1752.

[6] Rebaza, J. (2013). Bifurcations and periodic orbits in variable population interactions. *Communications on Pure and Applied Analysis, 12* (6), 2997-3012.

[7] Zhang, B., Zhang, Z., Zhenqing, L., & Tao, L. (2007). Stability analysis of a two-species model with transitions between population interactions. *Journal of Theoretical Biology, 248,* 145-153.