Dynamics and Bifurcations in Variable Population Interactions

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Typical Predator-Prey Model:

\[
\frac{dx}{dt} = \ldots - \frac{a}{c + mx} xy \\
\frac{dy}{dt} = \ldots + \frac{b}{c + mx} xy
\]  

(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.
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.
Instead, generalize (1) to

\[
\begin{align*}
\frac{dx}{dt} &= \ldots + \frac{\alpha_1(x, y)}{c + mx} xy \\
\frac{dy}{dt} &= \ldots + \frac{\alpha_2(x, y)}{c + mx} xy
\end{align*}
\]  

(2)

where the functions \(\alpha_1\) and \(\alpha_2\) 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 $\alpha$ function used affects the magnitude of benefit or detriment the species undergo when they interact:

\[ \alpha(x) = ax(b-x) \quad (a>0, b>0) \]

\[ \alpha(x) = (ax-x^2)/(1+bx^2) \quad (a>0, b>0) \]
First Model

\[
\begin{align*}
\frac{dx}{dt} &= x(r_1 - k_1 x) + ay(b - y)xy - \frac{hx}{e+x} \\
\frac{dy}{dt} &= y(r_2 - k_2 y) + cx(d - x)xy
\end{align*}
\]

This model includes the harvesting function \( H(x) = \frac{hx}{e+x} \) and has quadratic \( \alpha \) 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.
**Definition**

**Equilibrium Point:**
A point $x_0 \in \mathbb{R}^n$ is an equilibrium of

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

if $f(x_0) = 0 \quad \forall t$.

- Boundary Equilibria
- Coexistence Equilibria
A Boundary Equilibrium occurs along the x or y axis, when either one or both species is extinct. For $x_0$ a boundary equilibrium, $x_0$ 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 $x_0 = (x^*, y^*)$, $x^* > 0$, $y^* > 0$. Remember the system is:

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

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

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

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

$$r_2 - k_2 y + cx(d - x)x = 0 \quad (4)$$

These are the nullclines for the system.
Coexistence Equilibria

To find $x^*$, have:

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

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

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$$\frac{ac^3}{k_2^3}x^{10} + \left(\frac{ac^3e}{k_2^3} - \frac{3ac^3d}{k_2^3}\right)x^9 + \ldots + \left(r_1e - h + \frac{aber_2^2}{k_2^2} - \frac{aer_3^3}{k_2^3}\right) = 0$$

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- Slope Method
Coexistence Equilibria

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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:

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

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

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:

\[ \dot{x} = f(x). \]  

(5)

For a linear system:

\[ \dot{x} = Ax \quad \text{with} \quad x(0) = x_0, \]

solutions are of the form

\[ x(t) = e^{At}x_0, \quad t \in \mathbb{R}, \quad \text{for} \quad e^{At} = \sum_{k=0}^{\infty} \frac{A^k t^k}{k!}. \]
To linearize system, have this definition:

**Definition**

The linearization of (5) is defined as

\[ \dot{x} = Ax \]

where \( A = Df(x) \), 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:

\[
J(x, y) = \begin{bmatrix}
    r_1 + ay^2(b - y) - 2k_1 x - \frac{he}{(e+x)^2} & axy(2b - 3y) \\
    cxy(2d - 3x) & r_2 + cx^2(d - x) - 2k_2 y
\end{bmatrix}
\]

For coexistence equilibria, the Jacobian simplifies to:

\[
J(x^*, y^*) = \begin{bmatrix}
    -Bx^* & \frac{Bx^*}{m_1} \\
    m_2 k_2 y^* & -k_2 y^*
\end{bmatrix}
\]

For \( B = \frac{k_1(e+x^*)^2 - h}{(e+x^*)^2} \) and \( m_1, m_2 \) the slopes of the nullclines evaluated at \((x^*, y^*)\).
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
- $\lambda = a \pm bi$ for $a, b \in \mathbb{R}$: Focus
- $\lambda = \pm bi$ for $b \in \mathbb{R}$: Center

Note: If $\lambda$ 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 $(0, \frac{r_2}{k_2})$:

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

For \((x_+, 0)\):
\[\lambda_1 \leq 0 \text{ for } h \leq \frac{(r_1+k_1e)^2}{4k_1}, \text{ but } h \leq \frac{(r_1+k_1e)^2}{4k_1} \text{ is necessary for } x_+ \in \mathbb{R}.\]
Make inequality strict so as to keep \(\lambda_1\) 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 \((x_-, 0)\):
\[\lambda_1 > 0 \text{ for } h < \frac{(r_1+k_1e)^2}{4k_1}, \text{ but } h < \frac{(r_1+k_1e)^2}{4k_1} \text{ is necessary for } x_- \in \mathbb{R}\]
and for \(x_-\) to exist.
\((\text{At } h = \frac{(r_1+k_1e)^2}{4k_1}, x_+ = x_-).\)
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 $F = 2cd^3 + 27r_2 + 3\sqrt{12cd^3r_2 + 81r_2^2}$.

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

- 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 \((x^*, y^*)\):

- 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 \(e < \sqrt{\frac{h}{k_1}}\), \(x < x_B\), \(Bx + k_2y \neq 0\), and \(\frac{m_2}{m_1} < 1\): Saddle Point.
- If \((Bx + k_2y)^2 < 4Bk_2(1 - \frac{m_2}{m_1})xy\)
  - and \(Bx + k_2y > 0\): Stable Focus.
  - and \(Bx + k_2y < 0\): Unstable Focus.
- and \(h > k_1(e + x)^2\), \(\frac{m_2}{m_1} > 1\), and \(Bx + k_2y = 0\): Center.
Examples

Parameter Values:
\[ a=0.9; \quad b=0.8; \quad c=0.9; \quad d=0.8; \quad e=0.6; \quad h=0.2; \]
\[ k_1=0.6; \quad k_2=0.6; \quad r_1=0.8; \quad r_2=0.8; \]
Parameter Values:
\[ a=0.6; \quad b=0.9; \quad c=0.8; \quad d=1.2; \quad e=0.7; \quad h=0.2; \]
\[ k_1=0.3; \quad k_2=0.5; \quad r_1=0.9; \quad r_2=0.7; \]
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;
The system depends on 10 parameters, so it is of the form:

\[ \dot{x} = f(x, \mu) \]  \hspace{2cm} (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 \( \mu_0 \) for which (6) is not structurally stable, then \( \mu_0 \) 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:

\[ \mu = -0.25 \]

\[ \mu = 0 \]

\[ \mu = 0.25 \]
Sotomayor’s Theorem

Assume have an n-dimensional system $\dot{x} = f(x, \mu)$ and have $f(x_0, \mu_0) = 0$, $J(x_0, \mu_0) = A$ has a simple eigenvalue $\lambda = 0$, $\nu$ is an eigenvector of $A$ corresponding to $\lambda = 0$, $\omega$ 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 $\omega^T f_\mu(x_0, \mu_0) \neq 0$ and $\omega^T [D^2 f(x_0, \mu_0)(\nu, \nu)] \neq 0$, then there is a saddle-node bifurcation at $x_0$ 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:
\( a = 0.3; \quad b = 1.3; \quad c = 0.4; \quad d = 1.5; \quad e = 0.6; \quad h = \text{varied}; \)
\( k_1 = 0.1; \quad k_2 = 0.4; \quad r_1 = 0.5; \quad r_2 = 0.4; \)

Results from XPPAUT with \( h \) as free parameter:
Bifurcations in Model

XPPAUT output:

- 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:
\( a = \text{varied}; \quad h = \text{varied}; \)
\( b = 1.3; \quad c = 0.4; \quad d = 1.5; \quad e = 0.6; \)
\( k_1 = 0.1; \quad k_2 = 0.4; \quad r_1 = 0.5; \quad r_2 = 0.4; \)

Parameter Values:
\( k_1 = \text{varied}; \quad h = \text{varied}; \)
\( a = 0.3; \quad b = 1.3; \quad c = 0.4; \quad d = 1.5; \)
\( e = 0.6; \quad k_2 = 0.4; \quad r_1 = 0.5; \quad r_2 = 0.4; \)
First some necessary tools:

**Differential Inequality**

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

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

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 $\Omega \subseteq \mathbb{R}^2$ and be such that the initial value problem for the scalar equation

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

(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

\[
x \geq \frac{d + \sqrt{d^2 + b^2}}{2} \quad \text{or} \quad y \geq \frac{b + \sqrt{b^2 + d^2}}{2}
\]  

is bounded.

**Proof**

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

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

and for each \(k > 0\) we have

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

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

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

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

\[ u(t) = \frac{B}{k} \left( 1 - e^{-kt} \right) + u_0 e^{-kt} \]  

(10)

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

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

\[ \square \]
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

$$\begin{align*}
\dot{x} &= F_1(x, y) \\
\dot{y} &= F_2(x, y)
\end{align*}$$

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

$$\frac{\partial}{\partial x} [\phi(x, y)F_1(x, y)] + \frac{\partial}{\partial y} [\phi(x, y)F_2(x, y)] = \frac{hx - (k_1x + k_2y)(e + x)^2}{xy(e + x)^2}.$$

Which can be written as

$$-k_1x^3 - 2ek_1x^2 + (h - e^2k_1)x - k_2(e + x)^2y \quad \frac{xy(e + x)^2}{xy(e + x)^2}.$$
Conditions for no Periodic Solutions

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

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

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:

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

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 \textit{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 \textit{mutualistic} 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
Instead of using parabolic $\alpha$ function, use a rational $\alpha$ function:

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

Compare to Dr. Hernandez’s model:

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

\[
a = 0.2, \quad b = 1.3, \quad c = 0.2, \quad d = 1.5, \quad e = 0.6, \quad h = 0.7816406, \\
\quad r_1 = 0.5, \quad r_2 = 0.4, \quad k_1 = 0.1, \quad k_2 = 0.4.
\]
Mathematical analysis of second model (rational $\alpha$ 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.


