MATH 4010/6010: Mathematical Biology

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Lecture 3 – May 21, 2014

Non-linear Difference Methods
2.5 Graphical Methods 4 first-order Eqs

- Numerical check for stability of $x_{\text{bar}} = 0$

- [http://math.bu.edu/DYSYS/applets/nonlinear-web.html](http://math.bu.edu/DYSYS/applets/nonlinear-web.html)

- Point and click java applet for some of the simple functions used in class (logistic, cubic, ...)

- Numerical exploration
2.5 Graphical Methods 4 first-order Eqs

- Check for bifurcations

De Vries et al textbook
2.5 Graphical Methods 4 first-order Eqs

- Correspondent of cobweb

De Vries et al. textbook
2.5 Graphical Methods 4 first-order Eqs

- Another coweb example
- $x_{n+1} = -x_n$
- $f(x) = -x$

- Fixed points? Stability?
2.5 Graphical Methods 4 first-order Eqs

- % Syntax: \( x = \text{cobweb}(\text{fcnName}, \text{domain}, \text{initVal}, \text{nStart}, \text{nStop}) \)

- % fcnName - The function to be iterated,
- % domain - The domain of the x variable,
- % initVal - The initial x value(s); can be a vector,
- % nStart - The first iterate to be plotted,
- % nStop - The last iterate to be plotted.
- % x - The forward orbit of 'initVal'.
2.5 Graphical Methods 4 first-order Eqs

- cobweb('-x', [-10 10], 4, 1, 40)
- cobweb('2.9*x*(1-x)', [0 1], 0.3, 1, 40)
- cobweb('x + sin(x)', [0 10], 4, 1, 40)
- cobweb('30*tanh(x)^2/(1 + x)', [0 10], 4, 1, 40)
- cobweb('x/(1 + 0.1*sin(x))', [0 100], 4, 1, 40)
- cobweb('3*x - x^2', [0 5], 0.2, 1, 40)

\[
J = \begin{bmatrix}
\frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\
\frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*)
\end{bmatrix}
\]
Outline for today’s lecture

• 2.6 A WORD ABOUT THE COMPUTER

• 2.7 SYSTEMS OF NONLINEAR DIFFERENCE EQUATIONS

• 2.8 STABILITY CRITERIA FOR SECOND-ORDER EQUATIONS
2.6 A WORD ABOUT THE COMPUTER

• Evil
2.7 Systems of nonlinear difference equations

- Extend some of the math discussed here to systems of equations of dimension $n$

- Keep things simple, use $n = 2$

- In general form:
  - $x_{n+1} = f(x_n, y_n)$,
  - $y_{n+1} = g(x_n, y_n)$,
2.7 Systems of nonlinear difference equations

- \( x_{n+1} = f(x_n, y_n), \)
- \( y_{n+1} = g(x_n, y_n), \)

- In general, \( f \) and \( g \) are nonlinear functions
- We look at the steady state solutions
- \( x_{\text{bar}} = f(x_{\text{bar}}, y_{\text{bar}}), \)
- \( y_{\text{bar}} = g(x_{\text{bar}}, y_{\text{bar}}), \)

\[
\begin{bmatrix}
\frac{\partial f}{\partial x}(x^*, y^*) \\
\frac{\partial f}{\partial y}(x^*, y^*)
\end{bmatrix}
\begin{bmatrix}
\frac{\partial g}{\partial x}(x^*, y^*) \\
\frac{\partial g}{\partial y}(x^*, y^*)
\end{bmatrix}
\]
2.7 Systems of nonlinear difference equations

- We analyze what happens near the fixed points by looking at the small perturbations (let’s call them $x'$ and $y'$)

- Use Taylor series expansions of the functions of two variables for $f$ and $g$ to approximate

$$f(x + x', y + y') \quad g(x + x', y + y')$$

$$J = \begin{bmatrix} \frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\ \frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*) \end{bmatrix}$$
2.7 Systems of nonlinear difference equations

- Expand the terms:

\[ f(\bar{x} + x', \bar{y} + y') = f(\bar{x}, \bar{y}) + \frac{\partial f}{\partial x}\bigg|_{x=\bar{x}, y=\bar{y}} x' + \frac{\partial f}{\partial y}\bigg|_{x=\bar{x}, y=\bar{y}} y' + \ldots \]

- Easy to see that when substituting in the original equations: \( x_{\text{bar}} = f(x_{\text{bar}}, y_{\text{bar}}) \):

- \( x_{n+1}' = a_{11} x_n' + a_{12} y_n' \)
- \( y_{n+1}' = a_{21} x_n' + a_{22} y_n' \)
2.7 Systems of nonlinear difference equations

- Where:

\[
a_{11} = \left. \frac{\partial f}{\partial x} \right|_{x=\bar{x}, y=\bar{y}} \quad a_{11} = \left. \frac{\partial f}{\partial x} \right|_{x=\bar{x}, y=\bar{y}}
\]

\[
a_{21} = \left. \frac{\partial g}{\partial x} \right|_{x=\bar{x}, y=\bar{y}} \quad a_{22} = \left. \frac{\partial g}{\partial y} \right|_{x=\bar{x}, y=\bar{y}}
\]

- We can now construct a matrix of coefficients

\[
J = \begin{bmatrix}
\left. \frac{\partial f}{\partial x} \right|_{(x^*, y^*)} & \left. \frac{\partial f}{\partial y} \right|_{(x^*, y^*)} \\
\left. \frac{\partial g}{\partial x} \right|_{(x^*, y^*)} & \left. \frac{\partial g}{\partial y} \right|_{(x^*, y^*)}
\end{bmatrix}
\]
2.7 Systems of nonlinear difference equations

- The Jacobian of the system is then defined as:

\[
A = \begin{pmatrix}
a_{11} & a_{12} \\
a_{21} & a_{22}
\end{pmatrix}
\]

- We can write in a compact way: \( v_{n+1}' = A \, v_n' \)
- Where \( v_n = (x_n, y_n)^T \)
2.7 Systems of nonlinear difference equations

- linear system of equations for states that are in proximity to the steady state \((x_{\text{bar}}, y_{\text{bar}})\).

1. Finding the characteristic equation of

- \(x_{n+1} = a_{11} x_n + a_{12} y_n\)
- \(y_{n+1} = a_{21} x_n + a_{22} y_n\)

- \(\det (A - \lambda I) = 0\)
2.7 Systems of nonlinear difference equations

• Expanding: \( \det (A - \lambda I) = 0 \), one gets:

\[ \lambda^2 - \beta \lambda + \gamma = 0 \]

• \( \beta = a_{11} + a_{22} \)
• \( \gamma = a_{11} a_{22} - a_{12} a_{21} \)

• Remember the love affairs problem?
2.7 Systems of nonlinear difference equations

• Q: Are magnitudes of the roots of equation ($\lambda^2 - \beta \lambda + \gamma = 0$) smaller than 1?

• A: Depends on the parameter. If yes, then solutions are stable

• We can phrase the question in a mathematical way and see under what conditions the solutions are stable.
2.7 Systems of nonlinear difference equations

- We do not need to compute explicitly the solutions every time to determine stability

- \( \lambda^2 - \beta \lambda + \gamma = 0 \)

- Compute the solutions (general formula)
- Determine the parameter range for which both eigenvalues have magnitude less than 1
2.7 Systems of nonlinear difference equations

- \( \lambda^2 - \beta \lambda + \gamma = 0 \)

\[
\lambda_{1,2} = \frac{\beta \pm \sqrt{\beta^2 - 4\gamma}}{2}
\]

- \( |\lambda_1| < 1, \ |\lambda_2| < 1 \)
- It is necessary to have \( |\beta|/2 < 1 \)
- Why?
2.7 Systems of nonlinear difference equations

• Assume, without loss of generality that $\beta > 0$

$$\lambda_{1,2} = \frac{\beta \pm \sqrt{\beta^2 - 4\gamma}}{2}$$

• Then the bigger danger of having an eigenvalue exceed 1 comes from

$$\lambda_2 = \left(\beta + \sqrt{\beta^2 - 4\gamma}\right)/2$$
2.7 Systems of nonlinear difference equations

Therefore let’s look at the following inequality

$$\lambda_2 = \left( \beta + \sqrt{\beta^2 - 4\gamma} \right)/2 < 1$$

$$\beta + \sqrt{\beta^2 - 4\gamma} < 2$$
$$\sqrt{\beta^2 - 4\gamma} < 2 - \beta$$

$$\beta^2 - 4\gamma < (2 - \beta)^2 = 4 - 4\beta + \beta^2$$

$$-4\gamma < 4 - 4\beta$$
$$\beta < 1 + \gamma$$
2.7 Systems of nonlinear difference equations

- We determined that
  - $|\beta| < 2$ and $\beta < 1 + \gamma$ (this one for $\beta > 0$)

- $|\beta| < 2$ and $|\beta| < 1 + \gamma$

- Finally, we want the roots to be real
  - If $1 + \gamma > 2$, then $\gamma > 1$, then $\beta^2 - 4\gamma < 0$, unreal!
2.7 Systems of nonlinear difference equations

- Things are similar for $\beta < 0$
- Therefore, in a compact form:

$$|\beta| < 1 + \gamma < 2$$

- Fig 2.10/pg 58
2.7 Systems of nonlinear difference equations

- We showed that $\lambda^2 - \text{trace}(J) \lambda + \text{det}(J) = 0$ and
- $|\text{trace}(J)| < 1 + \text{det}(J) < 2$
- $|\beta| < 1 + \gamma < 2$

- Stable inside triangle
2.7 Systems of nonlinear difference equations

• The vector $v_n = (x_n, y_n)^T$ is a 2-dimensional vector.
• The Jacobian matrix is a 2 x 2 matrix.
• In general, if we start with an $m$-dimensional system, $v$ is an $m$-vector, and the Jacobian matrix has dimension $m \times m$.
• Look for solutions of form $v_n = \lambda^n w$.
• Show that $\lambda$ is an eigenvalue and $w$ is an eigenvector.
2.7 Systems of nonlinear difference equations

- Start from \( v_{n+1} = A v_n \)

- \( \lambda^{n+1} w = A \lambda^n w = \lambda^n A w \)

- Hence \( A w = \lambda w \)

- Or: \( (A - \lambda I)w = 0 \)

- \( \text{det} (A - \lambda I)w = 0 \)
2.7 Systems of nonlinear difference equations

- \( \det(A - \lambda I)w = 0 \)
- In general a m-degree poly with m solutions

\[
v_{n+1} = \sum_{i=1}^{m} c_i \lambda_i^{n+1} w_i
\]

- If all eigenvalues \( |\lambda_i| < 1 \), then \( |v_{n+1}| \to 0 \) as \( n \to \infty \)
- If at least one eigenvalue \( |\lambda_i| > 1 \), then \( |v_{n+1}| \to \infty \) as \( n \to \infty \)
Love Affairs: Model Analysis

- Love affair of Romeo and Juliet
- Attempt to understand the outcome of their affair

\[ R_{n+1} = a_R R_n + p_R J_n \]
\[ J_{n+1} = p_J R_n + a_J J_n \]

- Determine the fixed points
Love Affairs: Model Analysis

- \( R^* = a_R R^* + p_R J^* \)
- \( J^* = p_J R^* + a_J J^* \)

- Rearrange:
  - \((a_R - 1)R^* + p_R J^* = 0\)
  - \(p_J R^* + (a_J - 1)J^* = 0\)
Love affairs example

• In matrix form

\[
A \begin{pmatrix} R^* \\ J^* \end{pmatrix} = \begin{pmatrix} a_R - 1 & p_R \\ p_J & a_J - 1 \end{pmatrix} \begin{pmatrix} R^* \\ J^* \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}
\]

• homogeneous linear system.
• This system has a unique solution
• \((R^*, J^*) = (0,0), \text{ provided that } \det(A) \neq 0,\)
Love affairs example

• \((R^*, J^*) = (0,0), \text{ provided that } \det(A) \neq 0,\)

• **Stable**

• **Unstable**

• **Stable**
Love affairs example

- Jacobian is simply

\[ \tilde{M} = \begin{pmatrix} a_R & p_R \\ p_J & a_J \end{pmatrix} \]

- \( \text{tr} \ J = a_R + a_J \)

- \( \det \ J = a_R a_J - P_R P_J \)

- \( | a_R + a_J | < 1 + a_R a_J - P_R P_J < 2 \)
Love affairs example

- Numerical variations
  - $a_R = 0.5; a_J = 0.7$
  - $p_R = 0.2; p_J = 0.5$
  - Stable

- $| a_R + a_J | < 1 + a_R a_J - P_R P_J < 2$
- $| 0.5 + 0.2 | < 1 + 0.5*0.2 - 0.7*0.5 < 2$
Love affairs example

- Numerical variations
  - $a_R = 0.5$; $a_J = 0.7$;
  - $p_R = 0.7$; $p_J = 0.9$;

  - $| a_R + a_J | < 1 + a_R a_J - P_R P_J < 2$
  - $| 0.5 + 0.7 | < 1 + 0.5*0.7 - 0.7*0.9 < 2$
  - $1.2 < 0.72 < 2$  Unstable
Love affairs example

- Numerical variations
- $a_R = 1; a_J = 1$
- $p_R = 0.2; p_J = -0.2$

\[
| a_R + a_J | < 1 + a_R a_J - P_R P_J < 2 \\
| 1 + 1 | < 1 + 1 \times 1 + 0.2 \times 0.2 < 2 \\
1 < 2.04 < 2 \quad \text{Unstable, oscillations}
\]
Love affairs example

- Numerical variations
- \( a_R = 1; \) \( a_J = 1; \)
- \( p_R = 0.2; \) \( p_J = -0.2; \)

- \(| a_R + a_J | < 1 + a_R a_J - p_R p_J < 2\)
- \(| 1 + 1 | < 1 + 1*1 + 0.2*0.2 < 2\)
- \(1 < 2.04 < 2\)  \textit{Unstable, oscillations}
Love affairs example

- Numerical variations
  - \( a_R = 0.5; \)
  - \( a_J = 0.8; \)
  - \( p_R = 0.2; \)
  - \( p_J = 0.5; \)
- Equilibrium
- Perpetual love
- Unequal love

\[
J = \begin{bmatrix}
\frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\
\frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*)
\end{bmatrix}
\]
Love affairs example

- Numerical variations
- $a_R = 0.5; \ a_J = 0.8;$
- $p_R = 0.2; \ p_J = 0.5;$
- Equilibrium, Perpetual love

$$\det\begin{pmatrix} a_R - 1 & p_R \\ p_J & a_J - 1 \end{pmatrix} = \det\begin{pmatrix} 0.5 - 1 & 0.2 \\ 0.5 & 0.8 - 1 \end{pmatrix} = \det\begin{pmatrix} -0.5 & 0.2 \\ 0.5 & -0.2 \end{pmatrix} = 0$$

- Solution is not unique anymore
Love affairs example

• All fixed points of form

\[
A \left( \begin{array}{c}
R^* \\
J^*
\end{array} \right) = \left( \begin{array}{cc}
\alpha_R - 1 & p_R \\
p_J & \alpha_J - 1
\end{array} \right) \left( \begin{array}{c}
R^* \\
J^*
\end{array} \right) = \left( \begin{array}{c} 0 \\
0
\end{array} \right)
\]

• \((R^*, J^*) = (R^*, 1 - \alpha_R/p_R \ R^*)\) are fixed points

• \((\alpha_R = 0.5, \alpha_J = 0.8, P_R = 0.2, P_J = 0.5),\)

• \((R^*, J^*) = (R^*, 2.5 \ R^*)\)
Love affairs example

• $a_R + p_J = 0.5 + 0.5 = 1$ and $p_R + a_J = 0.2 + 0.8 = 1.$

• Total amount of love/hate that Romeo and Juliet feel for each other initially is preserved on all subsequent days.

• Each day, Romeo’s love/hate for Juliet is split 50/50 between Romeo and Juliet.

• Similarly, Juliet's love/hate for Romeo is split unequally, with 20% transferred to Romeo and the remaining 80% retained by Juliet herself.
Love affairs example

- Show that $\det(A) = 0$

- whenever Romeo and Juliet preserve their love/hate from day to day

- $a_R + P_J = 1$
- $P_R + a_J = 1$
Love affairs example

• Then $R^* + J^* = R_0 + J_0$

• $J^* = 1 - \frac{a_R}{p_R} R^*$

• Therefore we can compute
  
  • $R^* = \frac{p_R}{p_R + p_R} (R_0 + J_0) = 0.571429$
  
  • $J^* = 1.428571$
Love affairs example

- $\lambda_1 = 1$
- $\lambda_2 = a_R + a_J - 1 > -1$

- *Stability is determined by second eigenvalue*
- $|\lambda_2| = a_R + a_J - 1 < 1$
- $|\lambda_2| = 0.5 + 0.8 - 1 = 0.3$
- *Stable!*
Waves of disease

- H1N1

- Wiki: Influenza A (H1N1) virus is a subtype of influenza A virus

- swine flu pandemic
Waves of disease

• Consider a simple discrete model for the spread of disease due to infection in a population.
• Consider a population with some contagious and some susceptible people
• Does the disease cycle through population?
• How long does it take?
• Let 1 unit of time to be the average period of infection
Waves of disease

- Write a model
- Infected people and susceptible people
- Define VARIABLES

- $C_t = \text{the number of infected people at time } t$
- $S_t = \text{the number of susceptible people at time } t$

- Both populations change at each moment in time
Waves of disease

- $C_{t+1} = \text{newly infected}$
- $S_{t+1} = S_t + B - \text{newly susceptible}$

- Variables:
  - $C_t$
  - $S_t$
  - Other options?
Waves of disease

- $C_{t+1} = f \, C_t \, S_t$
- $S_{t+1} = S_t + B - f \, C_t \, S_t$

- The number of new cases at time $t + 1$ is the fraction of the product of the current cases and the current susceptible.

- Why? Assume that the product $C_t \, S_t$ approximates the likelihood that an encounter will take place between infected and susceptible.
Waves of disease

• The underlying assumption is that both population move about randomly and are uniformly distributed over the habitat.
Waves of disease

- The encounter rate is derived from the law of mass action

- The rate of molecular collisions of two chemical species in a dilute gas is proportional to the product of their two concentrations

- Q: Do humans behave like dilute gases? Move randomly?
Waves of disease

- Q: Do humans behave like dilute gases? Move randomly?
- A: No, but use encounter rate anyways.

Assumptions

- Therefore the number of new cases at time $t + 1$ is some fraction $f$ of the product of current cases $C_t$ and current susceptible $S_t$
- A case lasts only for a single time period (i.e. sick at time $t$, then well at $t + 1$ (or ...))
Waves of disease

• Assumptions

• The current number of susceptible is increased at each time by a fixed number B, and decreases by the number of new cases

• Individual recovered from the disease are immune or dead (hence not susceptible of contagious anymore)
Waves of disease

• Let’s look at the equations in detail:
• \( C_{t+1} = f \ C_t \ S_t \)
• Current # of new cases = some fraction \( X \) (past number of current number) \( X \) susceptible
Waves of disease

• $S_{t+1} = S_t + B - f C_t S_t$

• Current number of susceptibles = number of susceptibles in the past generation + new susceptibles - new cases of susceptible who got sick
Waves of disease

• Solve the equations
• Q: Where are the fixed points?
• A: Remember we solve equations of the form:

\[
\begin{align*}
  x_{n+1} &= f(x_n, y_n) \\
  y_{n+1} &= g(x_n, y_n)
\end{align*}
\]

\[
\begin{align*}
  \bar{x} &= f(\bar{x}, \bar{y}) \\
  \bar{y} &= g(\bar{x}, \bar{y})
\end{align*}
\]

• Substitute in our equations
Waves of disease

• $C^* = f C^* S^*$
• $S^* = S^* + B - f C^* S^*$

• Where $C^*, S^*$ are the fixed points ($C_{bar}, S_{bar}$)

• Rewrite first equation as:
  • $C^* (1 - f S^*) = 0$
  • Obtain: $C^* = 0, S^* = 1/f$
Waves of disease

- Look first at the case: $C^* = 0$, substitute in the second equation

- $S^* = S^* + B - f C^* S^*

- We obtain: $S^* = S^* + B$

- Hence $B = 0$? This case is non-physical, as new individuals are always added to the population
Waves of disease

• Consider $S^* = 1/f$ instead

• $1/f = 1/ + B - f C^* 1/f$

• Therefore: $C^* = B$

• Fixed points: $C^* = B, S^* = 1/f$
Waves of disease

• Q: Is this steady state stable?
• A: We need to linearize around the fixed point, compute the Jacobian, and so on.

• Define: \( A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \)

\[
\begin{align*}
a_{11} &= \frac{\partial f}{\partial x} \bigg|_{x = \bar{x}, y = \bar{y}} \\
a_{11} &= \frac{\partial f}{\partial x} \\
a_{21} &= \frac{\partial g}{\partial x} \\
a_{22} &= \frac{\partial g}{\partial y} \bigg|_{x = \bar{x}, y = \bar{y}}
\end{align*}
\]

• Use \( x = C, y = S \)
Waves of disease

- \( f(C, S) = f \begin{pmatrix} C \\ S \end{pmatrix} \)
- \( g(C, S) = S + B - f \begin{pmatrix} C \\ S \end{pmatrix} \)

\[
A = \begin{pmatrix}
\frac{\partial f}{\partial C} \bigg|_{\bar{C}, \bar{S}} & \frac{\partial f}{\partial S} \bigg|_{\bar{C}, \bar{S}} \\
\frac{\partial g}{\partial C} \bigg|_{\bar{C}, \bar{S}} & \frac{\partial g}{\partial S} \bigg|_{\bar{C}, \bar{S}}
\end{pmatrix}
= \begin{pmatrix}
f \begin{pmatrix} S \\ 1 \end{pmatrix} & f \begin{pmatrix} C \\ 0 \end{pmatrix}
\end{pmatrix}
\bigg|_{\bar{C}, \bar{S}}
\]
Waves of disease

• Fixed points: $C^* = B, S^* = 1/f$

\[
A = \begin{pmatrix}
  fS & fC \\
  -fS & 1-fC \\
\end{pmatrix}_{C,S} = \begin{pmatrix}
  1 & fB \\
  -1 & 1-fB \\
\end{pmatrix}
\]

• Now find the eigenvalues

from equation

\[
\det(A - \lambda I) = 0 \\
\det\begin{pmatrix}
  1 - \lambda & fB \\
  -1 & 1-fB - \lambda \\
\end{pmatrix} = 0
\]
Waves of disease

- Compute eigenvalues

- \((1 - \lambda) (1 - fB - \lambda) + fB = 0\)
- \(\lambda^2 - \lambda + \lambda fB - \lambda + 1 - fB + fB = 0\)
- \(\lambda^2 + \lambda (fB - 2) + 1 = 0\)

\[
\lambda_{1,2} = \frac{2 - fB \pm \sqrt{(2 - fB)^2 - 4}}{2}
\]
Waves of disease

• We have obtained

\[ \lambda_{1,2} = 1 - \frac{fB}{2} \pm \sqrt{(1 - \frac{fB}{2})^2 - 1} \]

• Consider the case: \( f = \frac{2}{B} \)

\[ \lambda_{1,2} = 1 - \frac{2}{B} * \frac{B}{2} \pm \sqrt{(1 - \frac{2}{B} * \frac{B}{2})^2 - 1} \]

\[ \lambda_{1,2} = \pm \sqrt{-1} = \pm i \]
Waves of disease

- Compute eigenvectors

- Set $\lambda = i$, use $f = 2/B$

\[
A = \begin{pmatrix} 1 & fB \\ -1 & 1-fB \end{pmatrix} = \begin{pmatrix} 1 & 2 \\ -1 & -1 \end{pmatrix}
\]

\[
Av = \lambda v = \begin{pmatrix} 1 & 2 \\ -1 & -1 \end{pmatrix} \begin{pmatrix} a \\ b \end{pmatrix} = i \begin{pmatrix} a \\ b \end{pmatrix}
\]
Waves of disease

• For $A \nu = \lambda \nu = \begin{pmatrix} 1 & 2 \\ -1 & -1 \end{pmatrix} \begin{pmatrix} a \\ b \end{pmatrix} = -i \begin{pmatrix} a \\ b \end{pmatrix}$

• We obtain:
  • $a + 2b = -i a$
  • $-a - b = -i b$
  • Set $b = 1$, then from 2$^{nd}$ equation: $a = -1 + i$
Waves of disease

For \( A v = \lambda v = \begin{pmatrix} 1 & 2 \\ -1 & -1 \end{pmatrix} \begin{pmatrix} a \\ b \end{pmatrix} = i \begin{pmatrix} a \\ b \end{pmatrix} \)

We obtain:

- \( a + 2b = i a \)
- \(-a - b = i b \)
- Set \( b = 1 \), then from 2\(^{nd} \) equation: \( a = -1 - i \)
Waves of disease

• In conclusion, we find:

\[
\lambda_1 = -i \rightarrow \begin{pmatrix} a \\ b \end{pmatrix} = \begin{pmatrix} -1 + i \\ 1 \end{pmatrix}, \quad \lambda_2 = i \rightarrow \begin{pmatrix} a \\ b \end{pmatrix} = \begin{pmatrix} -1 - i \\ 1 \end{pmatrix}
\]

• Thus, the linear system has solution

\[
\begin{pmatrix} x_n \\ y_n \end{pmatrix} = C_1 (-i)^n \tilde{v}_1 + C_2 (i)^n \tilde{v}_2
\]
Waves of disease

- Q: What are the dynamics of the solutions as $n$ increases?
- A: Useful to move to complex plane Rotation or oscillation (counterclockwise)

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</tbody>
</table>

$$J = \begin{bmatrix} \frac{\partial^2 f(x, y^*)}{\partial x^2} & \frac{\partial^2 f(x, y^*)}{\partial x \partial y} \\ \frac{\partial^2 f(x, y^*)}{\partial y \partial x} & \frac{\partial^2 f(x, y^*)}{\partial y^2} \end{bmatrix}$$
Waves of disease

• It is actually useful to transform into polar coordinates

• \( a = x = r \cos(\theta) \)
• \( b = y = r \sin(\theta) \)

• \( r = \sqrt{a^2 + b^2} \)
• \( \theta = \arctan(b/a) \)
Waves of disease

• Now it’s easy to raise at the $n^{th}$ power

• $(a + b\,i)^n = (r\,e^{i\theta})^n = r^n\,e^{i\,n\theta}$

• Q: what happens as $n \to \infty$
• A: depends on $r$
• $r < 1$, $r^n \to 0$, $r > 1$, $r^n \to \infty$
Waves of disease

- Mathematica example

- $y[n_] = (1.1 \exp[\sqrt{-1} \pi/4])^n$
- $(0.777817 + 0.777817 i)^n$
- `ListLinePlot[Table[{Re[y[k]], Im[y[k]]}, {k, 1, 10}]]`
Waves of disease

• Back to our problem
• Q: are the fixed points stable?
• A: Compute the magnitude of the eigenvalues
  
  • $|\lambda_1| = |-i| = 1$
  • $|\lambda_2| = |i| = 1$
  • Stability test is inconclusive
Waves of disease

• Express our solution in polar coordinates

\[
\begin{pmatrix}
  x_n \\
  y_n
\end{pmatrix} = C_1 (e^{-i\pi/4})^n \begin{pmatrix}
  -1 - i \\
  1
\end{pmatrix} + C_2 (e^{i\pi/4})^n \begin{pmatrix}
  -1 + i \\
  1
\end{pmatrix}
\]

\[
\begin{pmatrix}
  x_n \\
  y_n
\end{pmatrix} = C_1 \left( \cos\left(-n\pi/4\right) + i \sin\left(-n\pi/4\right) \right) \begin{pmatrix}
  -1 - i \\
  1
\end{pmatrix} +
\]

\[
C_2 \left( \cos\left(n\pi/4\right) + i \sin\left(n\pi/4\right) \right) \begin{pmatrix}
  -1 + i \\
  1
\end{pmatrix}
\]
Waves of disease

• Express our solution in polar coordinates

\[
\begin{pmatrix}
x_n \\
y_n
\end{pmatrix} = C_1 \left( \cos(-n \varphi) + i \sin(-n \varphi) \right) \begin{pmatrix}
-1 \\
1
\end{pmatrix} + \\
C_2 \left( \cos(n \varphi) + i \sin(n \varphi) \right) \begin{pmatrix}
-1 \\
1
\end{pmatrix}
\]

\[x_n = C_1 \left( \cos(-n \varphi) + i \sin(-n \varphi) \right)(-1 - i) + \\
C_2 \left( \cos(n \varphi) + i \sin(n \varphi) \right)(-1 + i)\]
Waves of disease

- Simplify

\[ x_n = -C_1 \cos(-n\phi) - C_2 \cos(n\phi) + C_1 \sin(-n\phi) - C_2 \sin(n\phi) + \]
\[ i\left(-C_1 \cos(-n\phi) + C_2 \cos(n\phi) - C_1 \sin(-n\phi) - C_2 \sin(n\phi)\right) \]

- Use \( \cos(-\phi) = \cos(\phi), \sin(\phi) = -\sin(\phi) \)

\[ x_n = -C_1 \cos(n\phi) - C_2 \cos(n\phi) - C_1 \sin(n\phi) - C_2 \sin(n\phi) + \]
\[ i\left(-C_1 \cos(n\phi) + C_2 \cos(n\phi) + C_1 \sin(n\phi) - C_2 \sin(n\phi)\right) \]
Waves of disease

• Simplify

\[ x_n = -C_1 \cos(n\varphi) - C_2 \cos(n\varphi) - C_1 \sin(n\varphi) - C_2 \sin(n\varphi) + \]
\[ i\left(-C_1 \cos(n\varphi) + C_2 \cos(n\varphi) + C_1 \sin(n\varphi) - C_2 \sin(n\varphi)\right) \]

\[ x_n = -(C_1 + C_2)(\cos(n\varphi) + \sin(n\varphi)) + \]
\[ i(C_1 - C_2)(-\cos(n\varphi) + \sin(n\varphi)) \]
Waves of disease

• Express our solution in polar coordinates

\[
\begin{bmatrix}
\begin{pmatrix}
\frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\
\frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*) 
\end{pmatrix}
\end{bmatrix}
\]

\[
\begin{pmatrix}
x_n \\
y_n
\end{pmatrix}
= C_1 \left( \cos(-n\varphi) + i \sin(-n\varphi) \right) \begin{pmatrix}
-1 & -i \\
1 & \phantom{-}1
\end{pmatrix} + \\
C_2 \left( \cos(n\varphi) + i \sin(n\varphi) \right) \begin{pmatrix}
-1 & -i \\
1 & \phantom{-}1
\end{pmatrix}
\]

\[
y_n = C_1 \left( \cos(-n\varphi) + i \sin(-n\varphi) \right)(1) + \\
C_2 \left( \cos(n\varphi) + i \sin(n\varphi) \right)(1)
\]
Waves of disease

• Simplify

\[ y_n = C_1 \left( \cos(-n\phi) + i\sin(-n\phi) \right) + C_2 \left( \cos(n\phi) + i\sin(n\phi) \right) \]

• Use \( \cos(-\phi) = \cos(\phi) \), \( \sin(\phi) = -\sin(\phi) \)

\[ y_n = (C_1 + C_2) \cos(n\phi) + i(-C_1 + C_2) \sin(n\phi) \]
Waves of disease

- Simplify

\[ x_n = -(C_1 + C_2)(\cos(n\varphi) + \sin(n\varphi)) + i(C_1 - C_2)(-\cos(n\varphi) + \sin(n\varphi)) \]

\[ y_n = (C_1 + C_2)\cos(n\varphi) + i(-C_1 + C_2)\sin(n\varphi) \]

\[
\begin{pmatrix}
   x_n \\
   y_n
\end{pmatrix} = (C_1 + C_2)
\begin{pmatrix}
   -\cos(n\varphi) + \sin(n\varphi) \\
   \cos(n\varphi)
\end{pmatrix} + i(C_1 - C_2)
\begin{pmatrix}
   -\cos(n\varphi) + \sin(n\varphi) \\
   -\sin(n\varphi)
\end{pmatrix}
\]
Waves of disease

- Wait!

$$\begin{pmatrix} x_n \\ y_n \end{pmatrix} = (C_1 + C_2) \begin{pmatrix} -(\cos(n\varphi) + \sin(n\varphi)) \\ \cos(n\varphi) \end{pmatrix} + i(C_1 - C_2) \begin{pmatrix} -\cos(n\varphi) + \sin(n\varphi) \\ -\sin(n\varphi) \end{pmatrix}$$

- Why imaginary?

- Imaginary people, cells, plants

- Actually, we can set $C_1$ and $C_2$ in such a way that they match the initial real conditions

- As a matter of fact, the imaginary and real parts are also solutions themselves

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Waves of disease

• Check

\[
\begin{pmatrix} x_n \\ y_n \end{pmatrix} = (C_1 + C_2) \begin{pmatrix} -(\cos(n\varphi) + \sin(n\varphi)) \\ \cos(n\varphi) \end{pmatrix} + \\
i(C_1 - C_2) \begin{pmatrix} -\cos(n\varphi) + \sin(n\varphi) \\ -\sin(n\varphi) \end{pmatrix}
\]

• Substitute the real part and verify that it is a solution of the system

• Think $C_1 + C_2$ REAL, and $C_1 + C_2$ imaginary
Waves of disease

• Then
\[
\begin{pmatrix}
  x_n \\
y_n
\end{pmatrix} = C_1' \begin{pmatrix}
  -(\cos(n\varphi) + \sin(n\varphi)) \\
  \cos(n\varphi)
\end{pmatrix} + iC_2' \begin{pmatrix}
  -\cos(n\varphi) + \sin(n\varphi) \\
  -\sin(n\varphi)
\end{pmatrix}
\]

• This is a real-valued solution to the linear approximation of the system. Valid close to the fixed points. Oscillations. Good, good stuff.
Waves of disease

• We have obtained

\[ \lambda_{1,2} = 1 - \frac{fB}{2} \pm \sqrt{(1 - \frac{fB}{2})^2 - 1} \]

• Consider the case: 1-f B/2 < 1
Waves of disease

• Set $B = 200$, Vary $f$ from 0 to $6/B$
Waves of disease

• C components of the eigenvectors

\[ J = \begin{bmatrix} \frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\ \frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*) \end{bmatrix} \]
Waves of disease

- S components of the eigenvectors

\[ J = \begin{bmatrix} \frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\ \frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*) \end{bmatrix} \]
Waves of disease

- Numerical evolution of C and S
Waves of disease

• What’s wrong with this model?

• Assumptions about infected-susceptible interaction (uniform): think urban settings

• Time to become immune (1 time unit?)

• Natural immunity (native south americans vs spanish conquistadors) or more susceptible (vitamin D status – red blinking lights)
Waves of disease

- What’s wrong with this model?

- Time units: what happens if we want to describe things at a smaller (or larger) time scale?
Nonlinear difference equation

• Another example with similarly oscillatory behavior

\[ x_{n+1} = - x_n - y_n - x_n y_n^2 \]
\[ y_{n+1} = - \frac{1}{2} x_n - x_n^2 \]

• Leave as an exercise to find the fixed points and check stability
Ventilation Volume and Blood CO$_2$ Levels

• Simplify the problem by assuming that breathing takes place at constant in time, at $t$, $t + \tau$, $t + 2\tau$, ...

• The volume $V_n = V(t + n\tau)$ is controlled by the concentration in the blood in the previous time interval, $C_{n-1}$
Ventilation Volume and Blood CO\textsubscript{2} Levels

- CO\textsubscript{2} in the bloodstream = previous CO\textsubscript{2} in the bloodstream MINUS amount lost to breathing PLUS amount gained by metabolism

- $C_{n+1} = C_n - L(V_n, C_n) + m$
- $V_{n+1} = L_2(C_n)$
Ventilation Volume and Blood CO$_2$ Levels

- Q: Specific forms for the amount of CO$_2$ lost
- Q: What are the steady states of the system?

- Hw problem – linear terms
- Section 2.10 nonlinear extensions
- Problem 17/Chapter 2/Page 66
Ventilation Volume and Blood CO₂ Levels

• In problem 1.16 we assumed that the amount of CO₂ lost, \( L(V_n, C_n) \), was simply proportional to \( V_n \) and independent of \( C_n \).

• Now consider the case in which

\[ L(V_n, C_n) = \beta V_n C_n \]

• Explain the biological difference between these distinct hypotheses.
Ventilation Volume and Blood CO₂ Levels

- \( C_{n+1} = C_n - \beta V_n C_n + m, \)
- \( V_{n+1} = \alpha C_n \)

- For steady state solutions
- \( C^* = C^* - \beta V^* C^* + m \)
- \( V^* = \alpha C^* \)

- \( 0 = -\beta \alpha (C^*)^2 + m \)

\[
C^* = \sqrt{\frac{m}{\alpha \beta}} \quad V^* = \sqrt{\frac{\alpha m}{\beta}}
\]
Ventilation Volume and Blood CO₂ Levels

• Stability?

\[ C^* = \sqrt{\frac{m}{\alpha\beta}} \quad V^* = \sqrt{\frac{\alpha m}{\beta}} \]

• \( f(x, y) = x - \beta x y + m \)

• \( g(x, y) = \alpha x \)

\[ A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \]

\[ a_{11} = \frac{\partial f}{\partial x} \bigg|_{x=\bar{x},y=\bar{y}} \quad a_{11} = \frac{\partial f}{\partial x} \bigg|_{x=\bar{x},y=\bar{y}} \]

\[ a_{21} = \frac{\partial g}{\partial x} \bigg|_{x=\bar{x},y=\bar{y}} \quad a_{22} = \frac{\partial g}{\partial y} \bigg|_{x=\bar{x},y=\bar{y}} \]
Ventilation Volume and Blood CO₂ Levels

• Stability?
• $f(x, y) = x - \beta x y + m$
• $g(x, y) = \alpha x$

$$A = \begin{pmatrix} 1 - \beta y & -\beta x \\ \alpha & 0 \end{pmatrix}$$

$$C^* = \sqrt{\frac{m}{\alpha \beta}} \quad V^* = \sqrt{\frac{\alpha m}{\beta}}$$

• Compute eigenvalues

$$A = \begin{pmatrix} 1 - \sqrt{\alpha \beta m} & -\sqrt{\frac{\beta m}{\alpha}} \\ \alpha & 0 \end{pmatrix}$$
Ventilation Volume and Blood CO₂ Levels

• Compute eigenvalues

\[
\det(A - \lambda I) = \det\begin{pmatrix}
1 - \sqrt{\alpha \beta m} - \lambda & -\sqrt{\frac{\beta m}{\alpha}} \\
\alpha & -\lambda
\end{pmatrix}
\]

\[
\lambda^2 - (1 - \sqrt{\alpha \beta m})\lambda + \sqrt{\alpha \beta m} = 0
\]

• Define: \( \eta = \sqrt{\alpha \beta m} \)
Ventilation Volume and Blood CO₂ Levels

- Compute eigenvalues

\[ \eta = \sqrt{\alpha \beta m} \]
\[ \lambda^2 - (1 - \eta) \lambda + \eta = 0 \]
\[ \lambda_{1,2} = \frac{(1 - \eta) \pm \sqrt{(1 - \eta)^2 - 4\eta}}{2} \]

- Eigenvectors

\[ \nu_1 = \left( \frac{[(1 - \eta) - \sqrt{(1 - \eta)^2 - 4\eta}]}{2\alpha, 1} \right)^T \]
\[ \nu_2 = \left( \frac{[(1 - \eta) + \sqrt{(1 - \eta)^2 - 4\eta}]}{2\alpha, 1} \right)^T \]
Ventilation Volume and Blood CO$_2$ Levels

• Compute eigenvalues

$$\eta = \sqrt{\alpha \beta m}$$

$$\lambda^2 - (1 - \eta)\lambda + \eta = 0$$

$$\lambda_{1,2} = \frac{(1 - \eta) \pm \sqrt{(1 - \eta)^2 - 4\eta}}{2}$$

• For $\eta$ small, both eigenvalues are between 0 and 1 - Stable
Ventilation Volume and Blood CO$_2$ Levels

- Very similar to wave of diseases

$$\lambda_{1,2} = \frac{(1 - \eta) \pm \sqrt{(1 - \eta)^2 - 4\eta}}{2}$$

- For $\eta$ small, both eigenvalues are between 0 and 1 – Stable

- Are oscillations in $V_n$ and $C_n$ possible for certain ranges of the parameters?

- For $\eta = 1$, $\lambda_1 = -i$, $\lambda_2 = i$
Ventilation Volume and Blood CO₂ Levels

- Are oscillations in $V_n$ and $C_n$ possible for certain ranges of the parameters?
Ventilation Volume and Blood CO$_2$ Levels

- Magnitude of $\lambda_1$ and $\lambda_2$

\[
\text{abs}(\lambda_1(\eta)) \text{ (red), abs}(\lambda_2(\eta)) \text{ (blue)}
\]
Ventilation Volume and Blood CO$_2$ Levels

- Real and imaginary parts of $\lambda_1$ and $\lambda_2$
Ventilation Volume and Blood CO$_2$ Levels

- $C_{n+1} = C_n - \beta V_n C_n + m,$
- $V_{n+1} = V_{\text{max}} C_n^p / (K^p + C_n^p)$
- Where $L_2(C) = C_n^p / (K^p + C_n^p)$
Ventilation Volume and Blood CO₂ Levels

• \( L_2(C) = \frac{C_n^p}{(K^p + C_n^p)}, \ p = 0 \)

\[
f(x) = \frac{1\cdot x^0}{(1^0 + x^0)}
\]
Ventilation Volume and Blood CO₂ Levels

- \( L2(C) = \frac{C_n^p}{(K^p + C_n^p)} \), \( p = 1 \)
Ventilation Volume and Blood CO$_2$ Levels

- L2(C) = $C_n^p / (K_p + C_n^p)$, $p = 2$

$$f(x) = \frac{1 \cdot x^2}{(1^2 + x^2)}$$
Ventilation Volume and Blood CO$_2$ Levels

- $C_{n+1} = C_n - \beta V_n C_n + m,$
- $V_{n+1} = V_{\text{max}} C_n p / (K^p + C_n^p)$
- $f(x, y) = x - \beta x y + m$
- $g(x, y) = \alpha x^n / (k^n + x^n)$
- Keep $n = p$, $\alpha = V_{\text{max}}$
Ventilation Volume and Blood CO$_2$ Levels

- $C_{n+1} = C_n - \beta \ V_n \ C_n + m$
- $V_{n+1} = V_{\text{max}} \ C_n^p / (K^p + C_n^p)$

$\begin{align*}
C_{n+1} &= C_n - \beta \ V_n \ C_n + m = \\
&= C_n - \beta \ V_{\text{max}} \ C_{n-1}^p / (K^p + C_{n-1}^p) \ C_n + m
\end{align*}$
Ventilation Volume and Blood CO₂ Levels

\[ C_{n+1} = C_n - \beta V_n C_n + m \]

\[ V_{n+1} = V_{\text{max}} C_n^p /(K^p + C_n^p) \]

\[ y \rightarrow a - \frac{ak}{k + \frac{m - \sqrt{m\sqrt{4abk + m}}}{2ab}} \quad x \rightarrow \frac{m - \sqrt{m\sqrt{4abk + m}}}{2ab} \]

\[ y \rightarrow a - \frac{ak}{k + \frac{m + \sqrt{m\sqrt{4abk + m}}}{2ab}} \quad x \rightarrow \frac{m + \sqrt{m\sqrt{4abk + m}}}{2ab} \]

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VenNlaNon
Volume
and Blood CO₂ Levels

Compute the Jacobian

\[ a = V_{\text{max}}, \ b = \beta \]

At the fixed points

\[ J = \begin{bmatrix}
\frac{2\beta}{\alpha} (x^*, y^*) & \frac{2\alpha}{\beta} (x^*, y^*) \\
\frac{\alpha}{\beta} (x^*, y^*) & \frac{\beta}{\alpha} (x^*, y^*)
\end{bmatrix} \]
Ventilation Volume and Blood CO$_2$ Levels

• This is an example where it is simpler to compute the trace and the determinant in order to figure out stability

$$\begin{align*}
1 - \sqrt{a}\sqrt{b}\sqrt{m} \\
\frac{a}{k + \frac{\sqrt{m}}{\sqrt{a}\sqrt{b}}} - \frac{\sqrt{a}\sqrt{m}}{\sqrt{b}(k + \frac{\sqrt{m}}{\sqrt{a}\sqrt{b}})^2} \\
- \frac{\sqrt{b}\sqrt{m}}{\sqrt{a}} \\
0
\end{align*}$$

$$J = \begin{bmatrix}
\frac{\partial f(x, y)}{\partial x} & \frac{\partial f(x, y)}{\partial y} \\
\frac{\partial g(x, y)}{\partial x} & \frac{\partial g(x, y)}{\partial y}
\end{bmatrix}$$
VenNlaNon	
  Volume	
  and	
  Blood	
  CO_2	
  Levels

• In normal resting humans, ventilation volume is approximately constant from one breath to another.

• Cheyne-Stokes breathing consists of a repeated waxing and waning of the depth of breathing, with an amplitude of ventilation volume that oscillates over intervals of 0.5 to 1 min.
Reading

• 2.7 SYSTEMS OF NONLINEAR DIFFERENCE EQUATIONS

• 2.8 Stability CRITERIA FOR SECOND-ORDER EQUATIONS

• Problems 1 and 2/Chapter 2/page 61
Topics covered so far

- Chapter 1: The Theory of Linear Difference Equations Applied to Population Growth
- Chapter 2: Nonlinear Difference Equations
- Homework 1: Due May 27, 2014
New topics to be covered

- Chapter 3 Applications of Nonlinear Difference Equations to Population Biology

- 3.1 DENSITY DEPENDENCE IN SINGLE-SPECIES POPULATIONS

- 3.6 FOR FURTHER STUDY: POPULATION GENETICS
Nonlinear growth models

- Discrete logistical equation
- \( x_{n+1} = r x_n (1 - x_n) \)

- If \( x_n > 1 \), then the population reverses sign
- Huh?

- Let’s consider some alternative models
Nonlinear growth models

- In general the growth models can be written in the general form:
  \[ x_{n+1} = f(x_n) = x_n g(x_n) \]

- Geometric growth: \( g(x) = r \); growth in the geometric model is \textit{density independent}

- Logistic growth: \( g(x) = r (1 - x) \)

- Regulatory mechanism – density-dependent
Nonlinear growth models

- Populations are influenced by
- changes in the weather (global warming)
Nonlinear growth models

• Populations are influenced by
  a limited food supply

• seabirds carefully
  corralling unwieldy
  shoals of herring into
  tightly packed "bait balls"
• Sharks, Whales, dolphins
• BBC wildlife series Nature's
  Great Events: The Great Feast.
Nonlinear growth models

• Populations are influenced by competition for resources such as nutrients and space

• Cut your own Christmas tree
Nonlinear growth models

- Populations are influenced by territoriality, predation, Diseases, and Prostate cancer.
Nonlinear growth models

- 3.1 Density dependence in single-species population
- Human population (wiki)
Nonlinear growth models

• 3.1 Density dependence in single-species population
  
• Hassell model
  
• The Beverton-Holt model
  
• Ricker model
Nonlinear growth models


• Population dynamics of fisheries
• Accounts for model competition (resources, mating)
Nonlinear growth models

• New model: (compare with model 1/page 74)
  \[ N_{t+1} = \lambda N_t / (1 + a N_t)^b \]

• Numerator is same as in geometric growth
• \(a, b\) are parameters related to density feedback
• As \(N_t\) increases, so does the denominator, effectively slowing down the growth rate
• Three parameters \(\{\lambda, a, b\}\), assume all positive
Nonlinear growth models

- Solve the model
- 1. Find the fixed points of the system
  \[ N^* = \frac{\lambda N^*}{(1 + a N^*)^b} \]
  \[ N^* (1 + a N^*)^b = \lambda N^* \]
  \[ N^* [(1 + a N^*)^b - \lambda] = 0 \]
  \[ N^* = 0 – trivial solution \]
  \[ OR \text{ use: } (1 + a N^*)^b - \lambda = 0 \text{ to compute } N^* \]
Nonlinear growth models

- $N^* = 0$ – trivial solution

- $N^* = (\lambda^{1/b} - 1)/a$

- Determine if solutions are stable

- Compute the derivative of $f(x)$, where $f(x) = \lambda x / (1 + a x)^b$
Nonlinear growth models

- $f(x) = \frac{\lambda x}{(1 + ax)^b}$

- $f'(x) = \frac{\lambda}{(1 + ax)^b} + \lambda x \left[ -b (1 + ax)^{-b-1} a \right] = \frac{\lambda}{(1 + ax)^b} \left( 1 - ab x/(1 + ax) \right)$

- $f'(0) = \frac{\lambda}{(1 + a 0)^b} \left( 1 - ab 0/(1 + ax) \right) = \lambda$

- $N^* = 0$ is STABLE if $-1 < \lambda < 1$

- $N^* = 0$ is UNSTABLE if $1 < \lambda$
Nonlinear growth models

• Actually, we choose $\lambda > 0$ to keep $N_t$ positive (no negative population)

• To prevent extinction (stable $N^* = 0$), we choose $\lambda > 1$

• We can now look at the stability of the other fixed point
Nonlinear growth models

• Stability of the other fixed point

\[ N^* = \frac{\lambda^{1/b} - 1}{a} \]

• Use:

\[ a N^* = \lambda^{1/b} - 1 \]

• \( f'(N^*) = \lambda / (1 + a x)^b + \lambda x [-b (1 + a x)^{-b-1} a] = \lambda / (\lambda^{1/b})^b - \lambda (\lambda^{1/b} - 1)/a [-b (\lambda^{1/b})^{-b-1} a] \]
Nonlinear growth models

- Stability of the other fixed point

\[ N^* = \frac{\lambda^{1/b} - 1}{a} \]

- \( f'(N^*) = \lambda / (1 + a x)^b + \lambda x [-b (1 + a x)^{-b-1} a] = \lambda / (\lambda^{1/b})^b - \lambda (\lambda^{1/b} - 1)/a [-b (\lambda^{1/b})^{-b-1} a] = 1 - b (\lambda^{1/b} - 1)/\lambda^{1/b} = 1 - b (1 - \lambda^{-1/b}) \)

Stable if: \(-1 < 1 - b (1 - \lambda^{-1/b}) < 1\)
Nonlinear growth models

• Stability of the other fixed point

\[ N^* = \frac{\lambda^{1/b} - 1}{a} \]

• Stable if: \(-1 < 1 - b \left(1 - \lambda^{-1/b}\right) < 1\)

• Stable if: \(0 < 2 - b \left(1 - \lambda^{-1/b}\right) < 2\)

• Note: stability of both fixed points is independent of \(a\)? Why?
Nonlinear growth models

• Note: stability of both fixed points is independent of a? Why?

• There are really less than 3 parameters in the system

• Scaling idea, change of variable to remove constant, let $N_t = k n_t$, where $k$ is constant
Nonlinear growth models

• Substitute into equations and select k conveniently to obtain simpler equations

\[ k \, n_{t+1} = \lambda \, k \, n_t / (1 + a \, k \, n_t)^b \]

\[ n_{t+1} = k \, n_t / (1 + a \, k \, n_t)^b \]

• Choose \( k = 1/a \) and get rid of parameter \( a \)
• The choice of a new unit gives a simpler equation
Nonlinear growth models

- E. g. $k = 1/12$

- $n_t = 12 N_t$

- $n_t = 1$, then $N_t = \text{one dozen}$
- $n_t = 2$, then $N_t = \text{two dozen}$

- $n_t$ is the number of dozens of $N_t$
Nonlinear growth models

- New system: equivalent to old equation, but with different units

\[ n_{t+1} = k \frac{n_t}{(1 + n_t)^b} \]

- Easy to prove that \( n^* = 0 \) and \( n^* = \lambda^{1/b} - 1 \)
- Stability as before: \( f'(0) = \lambda \), \( f'(n^*) = 1 - b \left( 1 - \lambda^{-1/b} \right) \)
- (leave as an exercise)
Nonlinear growth models - Beverton-Holt

- Other alternatives to the discrete logistic growth

\[ x_{n+1} = f(x_n) = x_n \cdot g(x_n) = r \cdot x_n / (1 + (r - 1)/K \cdot x^n) \]

- Fixed points of the system:
- Trivial fixed point \( x^* = 0 \)
- Non-trivial fixed point \( x^* = k \) (carrying capacity)
Nonlinear growth models - Beverton-Holt

- \( x_{n+1} = f(x_n) = x_n \cdot g(x_n) \)
Nonlinear growth models - Beverton-Holt

- Check stability: \[ f'(x) = \frac{k^2r}{(k + (-1 + r)x)^2} \]

- Check: \[ f'(0) = r, \quad f'(K) = 1/r \]

- When \( r < 1 \)
  - the trivial fixed point, \( x^* = 0 \), is STABLE
  - the nontrivial fixed point \( x^* = K \), is UNSTABLE
Nonlinear growth models - Beverton-Holt

- Check stability:  \( f'(x) = \frac{k^2 r}{(k + (-1 + r)x)^2} \)

- Check: \( f'(0) = r, \quad f'(K) = 1/r \)

- When \( r > 1 \)
  - the trivial fixed point, \( x^* = 0 \), is UNSTABLE
  - the nontrivial fixed point \( x^* = K \), is STABLE
Nonlinear growth models - Beverton-Holt

- Cobwebbing: use $r = \frac{1}{2}$, $k = 2$, $x^* = 0$ STABLE

- $x_0 = 1.9$
Nonlinear growth models - Beverton-Holt

- Cobwebbing: use $r = 2$, $k = 2$, $x^* = 2$ STABLE

- $x_0 = 0.1$
Nonlinear growth models - Beverton-Holt

- Easy to verify with cobwebbing that convergence to \( x^* = K \) is monotonic.
- Start with small initial condition \( 0 < x_0 << K \)
- Population initially increases quickly.
- Growth slows down when the population approaches the carrying capacity \( K \).
Nonlinear growth models - Beverton-Holt

- Convergence to $x^* = K$ is monotonic.
- Fast initial steps
- Slower convergence

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$$J = \begin{bmatrix} \frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\ \frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*) \end{bmatrix}$$
Nonlinear growth models - Beverton-Holt

- if $x_0 > K$, population decreases smoothly to $K$.
- No cycles and chaos
Nonlinear growth models - Beverton-Holt

• The Beverton-Holt model, is one of the few nonlinear models which has a solution in closed form

• \( x_n \) can be expressed in terms of the model parameters and the initial condition \( x_0 \).

\[
x_n = \frac{r x_0}{1 + \frac{r^n - 1}{K} x_0}
\]
Nonlinear growth models – Ricker model

• Another non-linear model

\[ x_{n+1} = f(x_n) = x_n \cdot g(x_n) = x_n \exp(r(1 - x_n/k)) \]

• Factor \( \exp(r) \) as a constant reproduction factor
• \( \exp(-r \, x_n / k) \): density-dependent mortality factor.
• The larger the population \( x_n \), the more severe the mortality factor.
Nonlinear growth models – Ricker model

- \( x_{n+1} = f(x_n) = x_n \cdot g(x_n) = x_n \exp(r(1 - x_n/k)) \)
Nonlinear growth models – Ricker model

- $x_{n+1} = f(x_n) = x_n g(x_n) = x_n \exp(r(1 - x_n/k))$

- Shape of the graph of $g(x)$ is similar to that for the Beverton-Holt model.
- Exponential function decreases more quickly than the inverse function
- Ricker map has a single local maximum
Nonlinear growth models – Ricker model

- \( x_{n+1} = f(x_n) = x_n \cdot g(x_n) = x_n \exp(r(1 - x_n/k)) \)

- Fixed points: as always \( n^* = 0 \) is a fixed point

- The non-trivial fixed point is \( x_n = k \)

- Determine stability of the fixed points
Nonlinear growth models – Ricker model

- $x_{n+1} = f(x_n) = x_n \ g(x_n) = x_n \ \exp(r(1 - x_n/k))$

- $f'(x) = \frac{e^r \cdot \frac{rx}{K} \ (K - rx)}{K}$

- Evaluate derivative in the fixed points
- $f'(0) = e^r > 1; \quad$ Always UNSTABLE
- $f'(k) = 1 - r$
Nonlinear growth models – Ricker model

- $x_{n+1} = f(x_n) = x_n g(x_n) = x_n \exp(r(1 - x_n/k))$

- $f'(k) = 1 - r$
- Since $|1-r| < 1$ when $0 < r < 2$
- The nontrivial fixed point is stable for $0 < r < 2$
- Unstable for $r > 2$ (cycles and chaos are observed)
- Detailed analysis of the Ricker model mirrors the investigation of the discrete logistic equation
Nonlinear growth models – Ricker model

- The nontrivial fixed point is stable for $0 < r < 2$
- $K = 2$, $r = 0.5$, $x_0 = 0.2$
- Fast initial steps
- Slower convergence

$f(x) = x \cdot \exp(0.5(1 - x/2))$. Showing iterates 1 to 40.
Nonlinear growth models – Ricker model

• The nontrivial fixed point is stable for $0 < r < 2$
• $K = 2$, $r = 0.5$, $x_0 = 0.2$
• Fast initial steps
• Slower convergence

• Same situation
• ZOOM out
Nonlinear growth models – Ricker model

• The nontrivial fixed point is stable for $0 < r < 2$
• $K = 2$, $r = 1.5$, $x_0 = 2.4$

• Damped oscillations
Nonlinear growth models – Ricker model

- The nontrivial fixed point is UNSTABLE for $r > 2$
- $K = 2$, $r = 2.1$, $x_0 = 1.5$
- Period DOUBLING
Nonlinear growth models – Ricker model

- The nontrivial fixed point is UNSTABLE for $r > 2$
- $K = 2$, $r = 2.55$, $x_0 = 1.5$
- Period Quadrupling
Nonlinear growth models – Ricker model

- The nontrivial fixed point is UNSTABLE for $r > 2$
- $K = 2$, $r = 3$, $x_0 = 1.5$
- Chaotic behavior
Nonlinear growth models – Ricker model

• Advantage of Ricker model over the logistic growth

• Initial conditions and parameter values may lead to negative population sizes for the logistic map (non-biological)

• This is avoided in the Ricker model (both have bifurcation maps)
3.2 TWO-SPECIES INTERACTIONS: HOST-PARASITOID SYSTEMS

- World of insects: host-parasitoid systems
- Both species have a number of life-cycle stages that include eggs, larvae, pupae and adults
3.2 TWO-SPECIES INTERACTIONS: HOST-PARASITOID SYSTEMS

• Eggs of the parasite may lay inside or outside

• The larval parasitoids develop and grow at the expense of their host, consuming it and eventually killing it before they pupate.
3.2 TWO-SPECIES INTERACTIONS: HOST-PARASITOID SYSTEMS

• Host-parasite diagram

\[ J = \begin{bmatrix} \frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\ \frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*) \end{bmatrix} \]
3.2 TWO-SPECIES INTERACTIONS: HOST-PARASITOID SYSTEMS

• 1. Hosts that have been parasitized will give rise to the next generation of parasitoids.

• 2. Hosts that have not been parasitized will give rise to their own progeny.

• 3. The fraction of hosts that are parasitized depends on the rate of encounter of the two species; in general, this fraction may depend on the densities of one or both species.
3.2 TWO-SPECIES INTERACTIONS: HOST-PARASITOID SYSTEMS

- Define terms:
- \( N_t \) = density of host species in generation \( t \),
- \( P_t \) = density of parasitoid in generation \( t \),
- \( f = f(N_t, P_t) \) = fraction of hosts not parasitized,
- \( \lambda \) = host reproductive rate,
- \( c \) = average number of viable eggs laid by a parasitoid on a single host
3.2 TWO-SPECIES INTERACTIONS: HOST-PARASITOID SYSTEMS

• Then we obtain

• \( N_{t+1} = \text{density of host species in generation } t+1\)

• \( N_{t+1} = \text{number of hosts in previous generation } \times \frac{\text{fraction not parasitized}}{\text{reproductive rate } \lambda} \)
3.2 TWO-SPECIES INTERACTIONS: HOST-PARASITOID SYSTEMS

• Then we obtain

• \( P_{t+1} \) = density of parasite species at \( t+1 \)

• \( P_{t+1} \) = *number of hosts parasitized in previous generation* \( \times \) *fecundity of parasitoids* (c).

• \( 1 - f \) is the fraction of hosts that are parasitized
3.2 TWO-SPECIES INTERACTIONS: HOST-PARASITOID SYSTEMS

- \( N_{t+1} = \lambda N_t f(N_t, P_t) \)
- \( P_{t+1} = c N_t [1 - f(N_t, P_t)] \)

- Need to specify the term \( f(N_t, P_t) \) and how it depends on the two populations.

- Particular form suggested by Nicholson and Bailey (1935)
3.3 THE NICHOLSON-BAILEY MODEL

• After the parasite eggs have been laid, supplementary eggs would not create additional parasites

• Why?

• Presumably many eggs are laid, and the number of parasites is related to the host capacity
3.3 THE NICHOLSON-BAILEY MODEL

• Law of mass action:
• Encounters occur randomly.
• Number of encounters $N_t$ of hosts by parasitoids: proportional to the product of their densities ($a$ is related to searching efficiency)

$$N_{\text{encounters}} = a \ N_t \ P_t$$
3.3 THE NICHOLSON-BAILEY MODEL

• Random encounters with Constant probability

• Lead to the Poisson Distribution and Escape from Parasitism

• In the case of host-parasitoid encounters, the *average number* of encounters per host per unit time is \( N_e/N_t = a N_t P_t / N_t = a P_t \)
The Poisson Distribution

- Evaluates the probability of a (usually small) number of occurrences out of many opportunities in a ...
  - Period of time
  - Area
  - Volume
  - Weight
  - Distance
  - Other units of measurement
The Poisson Distribution

\[ P(x) = \frac{\lambda^x e^{-\lambda}}{x!} \]

- \( \lambda \) = mean number of occurrences in the given unit of time, area, volume, etc.
- \( e = 2.71828 \ldots \)
- \( \mu = \lambda \)
- \( \lambda^2 = \lambda \)
The Poisson Distribution

- Say in a given stream there are an average of 3 striped trout per 100 yards. What is the probability of seeing 5 striped trout in the next 100 yards, assuming a Poisson distribution?

\[ P(x = 5) = \frac{\lambda^x e^{-\lambda}}{x!} = \frac{3^5 e^{-3}}{5!} = .1008 \]
The Poisson Distribution

- How about in the next 50 yards, assuming a Poisson distribution?
- Since the distance is only half as long, $\lambda$ is only half as large.

$$P(x = 5) = \frac{\lambda^x e^{-\lambda}}{x!} = \frac{1.5^5 e^{-1.5}}{5!} = .0141$$
The Poisson Distribution

\[ P(x) = \frac{\lambda^x e^{-\lambda}}{x!} \]

Poisson Distribution for \( \lambda = 1 \)
The Poisson Distribution

\[ P(x) = \frac{\lambda^x e^{-\lambda}}{x!} \]
The Poisson Distribution

\[ P(x) = \frac{\lambda^x e^{-\lambda}}{x!} \]
The Poisson Distribution

Poisson data should be skewed right, though the skewness becomes less pronounced as the mean increases

\[ P(x) = \frac{\lambda^x e^{-\lambda}}{x!} \]
The Poisson Distribution

Poisson data should be skewed right, though the skewness becomes less pronounced as the mean increases (skew to the right means that there are more outliers to the right)

\[ P(x) = \frac{\lambda^x e^{-\lambda}}{x!} \]
3.3 THE NICHOLSON-BAILEY MODEL

• Probability of exactly two encounters would be given by

\[ P(2) = \frac{(aP_t)^2 e^{-aP_t}}{2!} \]

• Likelihood of escaping parasitism is

\[ P(0) = \frac{(aP_t)^0 e^{-aP_t}}{0!} = e^{-aP_t} \]
3.3 THE NICHOLSON-BAILEY MODEL

- Fraction that *escapes parasitism*

\[ f(N_t, P_t) = e^{-aP_t} \]

- We can (finally) write the equations:

\[ N_{t+1} = \lambda N_t \ e^{-aP_t} \]
\[ P_{t+1} = c \ N_t \ [1 - e^{-aP_t}] \]
3.3 THE NICHOLSON-BAILEY MODEL

• Following the textbook’s suggestion

• 1. Solving for steady states.
• 2. Finding the coefficients of the Jacobian matrix (for the system linearized about the steady state).
• 3. Checking the stability condition derived in Section 2.8.
3.3 THE NICHOLSON-BAILEY MODEL

• 1. Solving for steady states
• Write down the system of equations as:

- \( N_{t+1} = F(N_t, P_t) \)
- \( P_{t+1} = G(N_t, P_t) \)

- \( F(N, P) = \lambda N \exp(-\alpha P) \)
- \( G(N, P) = c N (1 - \exp(-\alpha P)) \)
3.3 THE NICHOLSON-BAILEY MODEL

1. Solving for steady states

\[ N^* = F(N^*, P^*) \]
\[ P^* = G(N^*, P^*) \]

\[ N^* = \lambda N^* \exp(-\alpha P^*) \]
\[ P^* = c N^* (1 - \exp(-\alpha P^*)) \]
3.3 THE NICHOLSON-BAILEY MODEL

- Trivial solution:
- \( N^* = 0 \)
- \( P^* = c \ N^* \ (1 - \exp(-a \ P^*)) = c \ 0(1 - \exp(-a \ P^*)) = 0 \)

- The trivial solution is obvious, no hosts and no parasites
- Let’s look at non-zero solutions
3.3 THE NICHOLSON-BAILEY MODEL

1. Solving for steady states

\[ N^* = \lambda N^* \exp(-a P^*), \quad 1 = \lambda \exp(-a P^*) \]

Then \( P^* = \ln(\lambda)/a \)

Substitute in the second equation

\[ P^* = c N^* (1 - \exp(-a P^*)) \]

\[ \ln(\lambda)/a = c N^* (1 - 1/\lambda), \]

\[ N^* = \lambda \ln(\lambda)/(a c (\lambda - 1)) \]
3.3 THE NICHOLSON-BAILEY MODEL

- We found
- \( P^* = \ln(\lambda)/a \)
- \( N^* = \lambda \ln(\lambda)/(a c (\lambda - 1)) \)

2. Finding the coefficients of the Jacobian matrix (for the system linearized about the steady state).

- Compute the partial derivatives
3.3 THE NICHOLSON-BAILEY MODEL

• 2. Compute the partial derivatives

\begin{align*}
\alpha_{11} &= F_N(N^*, P^*) = \left[ \frac{\partial (\lambda \ N \ \text{exp}(-\alpha \ P))}{\partial N} \right]_{N^*, P^*} \\
\alpha_{11} &= \lambda \ \text{exp}(-\alpha \ P^*) = 1 \\
\alpha_{12} &= F_P(N^*, P^*) = \lambda \ \text{N} \ \text{exp}(-\alpha \ P) \ * \ (-\alpha) = -\alpha N^*
\end{align*}
3.3 THE NICHOLSON-BAILEY MODEL

- 2. Compute the partial derivatives

  - $a_{21} = G_N(N^*, P^*) = \left[\frac{\partial (c N(1-\exp(-a P)))}{\partial N}\right]_{N^*, P^*}$
  - $a_{21} = c \left(1 - \exp(-a \cdot P^*)\right) = c \left(1 - \frac{1}{\lambda}\right)$

  - $a_{22} = G_P(N^*, P^*) = a \cdot c \cdot N^* \cdot \exp(-a \cdot P^*) = c \cdot a \cdot N^*/\lambda$
3.3 THE NICHOLSON-BAILEY MODEL

• 2. *Compute the partial derivatives*

  • $a_{11} = 1$
  • $a_{12} = -aN^*$
  • $a_{21} = c \left(1 - 1/\lambda\right)$
  • $a_{22} = c \alpha N^*/\lambda$

• *Obtain the Jacobian:* 
  \[
  J = \begin{pmatrix}
  1 & -aN^* \\
  c(1-1/\lambda) & caN^*/\lambda
  \end{pmatrix}
  \]
3.3 THE NICHOLSON-BAILEY MODEL

• 3. Checking the stability condition derived in Section 2.8
• Compute the trace and determinant of J

\[ J = \begin{pmatrix} 1 & -aN^* \\ c(1-1/\lambda) & caN^*/\lambda \end{pmatrix} \]

- \( a_{11} = 1 \)
- \( a_{12} = -aN^* \)
- \( a_{21} = c(1 - 1/\lambda) \)
- \( a_{22} = ca N^*/\lambda \)
3.3 THE NICHOLSON-BAILEY MODEL

- Trace:

- $\beta = a_{11} + a_{22} = 1 + c a N^*/\lambda = 1 + \lambda \frac{\ln(\lambda)}{(a c (\lambda - 1))} c a/\lambda = 1 + \lambda / (\lambda - 1)$

$$J = \begin{pmatrix} 1 & -aN^* \\ c(1 - 1/\lambda) & caN^*/\lambda \end{pmatrix}$$
3.3 THE NICHOLSON-BAILEY MODEL

• Determinant

\[ \gamma = a_{11} a_{22} - a_{12} a_{21} = c a N^*/\lambda - (-aN^*) c \left(1 - 1/\lambda \right) \]
\[ = c a N^*/\lambda + c a N^*(1 - 1/\lambda) = caN^* = \lambda \ln(\lambda)/(\lambda-1) \]

• \( \beta = 1 + \lambda / (\lambda - 1) \)

• \( \gamma = \lambda \ln(\lambda)/(\lambda-1) \)

\[
J = \begin{pmatrix}
1 & -aN^* \\
(1 - 1/\lambda) c & caN^*/\lambda \\
\end{pmatrix}
\]
3.3 THE NICHOLSON-BAILEY MODEL

- Show that $\gamma > 1$

- $\gamma = \lambda \ln(\lambda)/(\lambda-1)$

- Show that $\lambda \ln(\lambda)/(\lambda-1) > 1$ OR $\lambda-1 - \lambda \ln(\lambda) < 0$

- Define $h(x) = (x - 1) - x \ln(x)$
3.3 THE NICHOLSON-BAILEY MODEL

- Define \( h(x) = (x - 1) - x \ln(x) \)
- \( h(1) = 0 \)
- \( h'(x) = 1 - \ln(x) - x \frac{1}{x} = -\ln(x) \)

Therefore \( h'(\lambda) < 1 \) for \( \lambda > 1 \)
- Decreasing function of \( \lambda \), \( h(\lambda) < 0 \)
- Therefore \( \gamma > 1 \), therefore equilibrium is unstable
3.3 THE NICHOLSON-BAILEY MODEL

• Numerics: figure 3.3 from page 83
• Implement model with $\lambda = 2$, $c = 1$, $a = 0.068$

• Green - host
• Red – parasite

• Note log(10) scale
Chapter 3 reading

- 3.1 DENSITY DEPENDENCE IN SINGLE-SPECIES POPULATIONS
- 3.2 TWO-SPECIES INTERACTIONS: HOST·PARASITOID SYSTEMS
- 3.3 THE NICHOLSON-BAILEY MODEL

Problems 2, 3 and 4 from pages 102/103
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

• It is unreasonable to use the original form of the NICHOLSON-BAILEY model
• There are no stable solutions and the populations undergo growing oscillations
• Modify the model and include stabilizing factors
• One potential problem is that the host population grows to infinity: carrying capacity
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

• 6. In the absence of parasitoids, the host population grows to some limited density (determined by the carrying capacity K of its environment)

• \( N_{t+1} = F(N_t, P_t) \)

• \( P_{t+1} = G(N_t, P_t) \)

• \( F(N, P) = \lambda(N) N \exp(-\alpha P) \)

• \( G(N, P) = c \, N \, (1 - \exp(-\alpha P)) \) (set \( c = 1 \))
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- Formula for the growth rate
  \[ \lambda(N_t) = \exp [r \left( 1 - \frac{N_t}{K} \right)] \]

- In the absence of predators
  \[ N_{t+1} = \exp \left[ r \left( 1 - \frac{N_t}{K} \right) \right] N \]

- the host population grows up to density \( N \), and declines if \( N_t > K \).
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- \( N_{t+1} = \exp \left[ r \left( 1 - \frac{N_t}{K} \right) - a P_t \right] N_t \)
- \( P_{t+1} = N_t (1 - \exp(-a P_t)) \)

- Beddington, Free, and Lawton modified the NICHOLSON-BAILEY model
- Study it as a function of the ratio of steady-state host density and carrying capacity: \( \frac{N^*}{K} \)
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

• Look at the fixed states

• $N^* = \exp [r \ (1 - N^*/K) - \alpha \ P^*] \ N^*$

• $P^* = N^* \ (1 - \exp(-\alpha \ P^*))$

• Trivial state $(N^* = 0, P^* = 0)$

• First equation: $r \ (1 - N^*/K) - \alpha \ P^* = 0$
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- \( N^* = \exp [r (1 - N^*/K) - \alpha P^*] N^* \)
- \( P^* = N^* (1 - \exp(-\alpha P^*)) \)

- \( r (1 - N^*/K) - \alpha P^* = 0 \)
- \( N^* = K(1 - \alpha P^*/r) \)

- \( P^* = K(1 - \alpha P^*/r) (1 - \exp(-\alpha P^*)) \)
- Transcendental equation – numerical solutions
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- Can’t solve it? Simulate it!

- Use matlab to replicate the TURBO - PASCAL program, written by David F. Dabbs and run on a personal computer.
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- Need to figure out the parameters
- Figure from page 85 is a good starting point
- \( R = 0.5, \ K = 14.47 \)
- \( N_0 = 11, \ P_0 = 1 \)

- Need to obtain \( N^* = 5.79, \ P^* = 1.5 \)
- The only problem is that parameter \( a \) is not given, instead we have \( q = N^*/k = 0.4 \) (depends on \( a \))
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- Parameter $a$ is not given,
- Instead we have $q = \frac{N^*}{k} = 0.4$ (depends on $a$)
- Figure it out numerically, using matlab
  
  use $a = 0.2$
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- Oscillations!
- Not spirals!

\[
J = \begin{bmatrix}
\frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\
\frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*)
\end{bmatrix}
\]
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- Oscillations!
- Not spirals!

\[ J = \begin{bmatrix} \frac{\partial f(x^*, y^*)}{\partial x} & \frac{\partial f(x^*, y^*)}{\partial y} \\ \frac{\partial g(x^*, y^*)}{\partial x} & \frac{\partial g(x^*, y^*)}{\partial y} \end{bmatrix} \]
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- Oscillations!
- Not spirals!

$J = \begin{bmatrix}
\frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\
\frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*)
\end{bmatrix}$
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

• Stable limit cycle
• Jagged edges
• Choose \( a = 0.1981 \)
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- Stable limit cycle
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- Stable limit cycle, stable oscillations
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- Cycle with period 5

- Further increasing \( r \) slowly would produce cycles of periods 10, 20, 40, and so on
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- Cycle with period 5
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- This sharply bounded figure shows definable areas without any points.
- Lower $r$ values these areas are better defined;
- For higher $r$ values they tend to fill in.
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- Chaotic oscillations
3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL

- **Other Stabilizing Factors**
- **1. Efficiency of the parasitoids**
  - efficiency generally decreases somewhat when the parasitoid population is too large
  - \( f(N_t, P_t) = \exp (-a P_t)^{1-m} \)
- **2. (Spatial and temporal) Heterogeneity of the environment (refuges)**
  - Part of the host population may be less exposed (see problem 11/Chapter 3)
Chapter 3 reading

- 3.1 DENSITY DEPENDENCE IN SINGLE-SPECIES POPULATIONS
- 3.2 – 3.4 NICHOLSON-BAILEY MODEL
- 3.6 POPULATION GENETICS

- 3.5 A MODEL FOR PLANT-HERBIVORE INTERACTIONS (not covered in class)

- Problems 2, 3 and 4 from pages 102/103
Non-linear growth model fitting

• How do we decide which model works best for some experimental data sets?
• Need to try a few models, and see which one produces a better fit
• Do not use a model with too many parameters, can lead to overfit, etc
• Example: generate some data for the logistic growth model, add noise, repeat ...

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Non-linear growth model fitting

- Example: generate some data for the logistic growth model, add noise, repeat …
- Advantage: we know what we put in the model, this is a working example to see how to use additional tools
- Allows us to get some experience with different methods before testing them on real data
- \( x_{n+1} = rx(1-x) \), use say \( r = 2.3 \) and \( x_0 = 0.05 \)
Non-linear growth model fitting

- $x_{n+1} = r \times (1 - x)$, use say $r = 2.3$ and $x_0 = 0.05$

- Add some noise

- $x_{n+1} = r \times (1 - x) + \eta \times \text{noise}$

Where $\eta = 0.05$
Non-linear growth model fitting

- $x_{n+1} = r x (1 - x) + \eta^* \text{noise}$
Non-linear growth model fitting

• Now fit the logistic model to the noise-free data

• Not surprisingly

• Perfect fit
Non-linear growth model fitting

- Now look at the data with noise
- Fit the logistic
  - (magenta)
- In addition
- Beverton-Holt
- Green line
  - \( x_{n+1} = f(x_n) = x_n g(x_n) = \frac{r x_n}{1 + x_n (r - 1)/K} \)
Non-linear growth model fitting

- Logistic: $x_{n+1} = 2.603 \times x_n \times (0.9482 - x_n)$

- Logistic is better than Beverton-Holt fit

- That’s because we generated the data

- Beverton-Holt
  - $x_{n+1} = 4.32 \times x_n / (1 + x_n(4.32 - 1)/0.5637)$
Non-linear growth model fitting

• Gauge the effectiveness of the fit by looking at the graphed data
• Look at the particular values for parameters
• If the carrying capacity is 0.56, it seems natural that the data seems to be around 0.55 to 0.6
• Look at the confidence intervals for fitted parameters
  • \( a = 2.603 \ (2.124, 3.082) \) - logistic
  • \( a = 4.32 \ (2.782, 5.859) \) – Beverton-Holt