Calculus for the Life Sciences I

Lecture Notes – More Applications of Nonlinear Dynamical Systems

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Outline

Introduction - Population Models

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- Simplest (linear) model - Malthusian or exponential growth model

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- Differentiation needed to analyze these models

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- Their bodies provide many essential nutrients that nourish the stream of their young

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- Simplify the model by ignoring this complexity

Sockeye Salmon Populations

Sockeye Salmon Populations – Skeena River Table

Population in thousands

Year	Population	Year	Population
1908	1,098	1932	278
1912	740	1936	448
1916	714	1940	528
1920	615	1944	639
1924	706	1948	523
1928	510		

Four Year Averages of Skeena River Sockeye Salmon

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- Fishery management has often used **Ricker's Model**

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- Consider the Skeena river salmon data
  - The parent population of 1908-1911 is averaged to 1,098,000 salmon/year returning to the Skeena river watershed
  - It is assumed that the resultant offspring that return to spawn from this group occurs between 1912 and 1915, which averages 740,000 salmon/year

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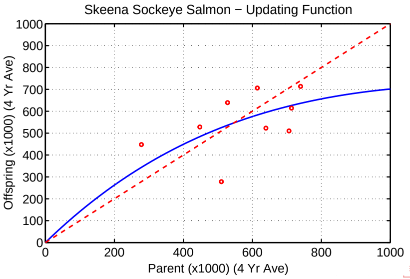
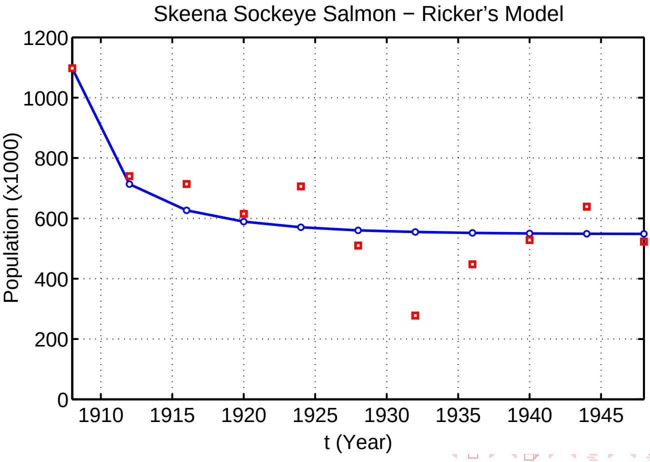
- Successive populations give data for updating functions
  - P_n is parent population, and P_{n+1} is surviving offspring
  - Nonlinear least squares fit of Ricker's function

$$P_{n+1} = 1.535\, P_n e^{-0.000783\, P_n}$$



Ricker's Model – Salmon

Simulate the Ricker's model using the initial average in 1908 as a starting point



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- There are a few fluctuations from the variations in the environment
- Low point during depression, suggesting bias from economic factors

Analysis of the Ricker's Model 1

Analysis of the Ricker's Model: General Ricker's Model

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Note that $a > 1$ required for a positive equilibrium

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Stability Analysis of the Ricker's Model: Find the derivative of the updating function

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- The solution of Ricker's model is **unstable** and **oscillates as it grows away** the equilibrium $P_e = \ln(a)/b$ provided $a > e^2 \approx 7.389$

Skeena River Salmon Example

The best Ricker's model for the Skeena sockeye salmon population from 1908-1952 is

$$P_{n+1} = R(P_n) = 1.535\, P_n e^{-0.000783\, P_n}$$

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- At $P_e = 0$, $R'(0) = 1.535 > 1$
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- At $P_e = 547.3$, $R'(547.3) = 0.571 < 1$
  - This equilibrium is **stable** with solutions monotonically approaching the equilibrium, as observed in the simulation

Example 1 - Ricker's Growth Model

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- Find all equilibria of the model and describe the behavior of these equilibria
- Let $P_0 = 100$, and simulate the model for 50 years

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Solution The Ricker's growth function is

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- This gives a critical point at $P_c = 50$

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Solution (cont) The Ricker's function has a **maximum** at

$$(P_c, R(P_c)) = (50, 350e^{-1}) \approx (50, 128.76)$$

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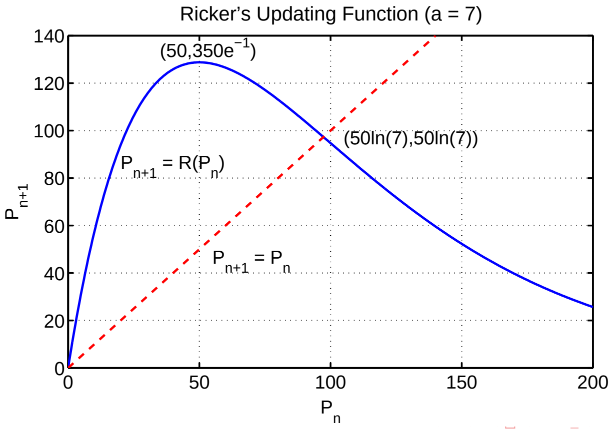

Example 1 - Ricker's Growth Model

Solution (cont) For **equilibria**, let $P_e = P_{n+1} = P_n$, then

$$P_e = R(P_e) = 7\,P_e e^{-0.02P_e}$$

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This gives the other equilibrium $P_e = 50\ln(7) \approx 97.3$

Example 1 - Ricker's Growth Model 5

Solution (cont) **Stability Analysis** – Recall

$$R'(P) = 7\,e^{-0.02P}(1 - 0.02\,P)$$

Example 1 - Ricker's Growth Model

Solution (cont) **Stability Analysis** – Recall

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Example 1 - Ricker's Growth Model

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$$R'(P) = 7\,e^{-0.02P}(1 - 0.02\,P)$$

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  - The derivative $R'(0) = 7 > 1$

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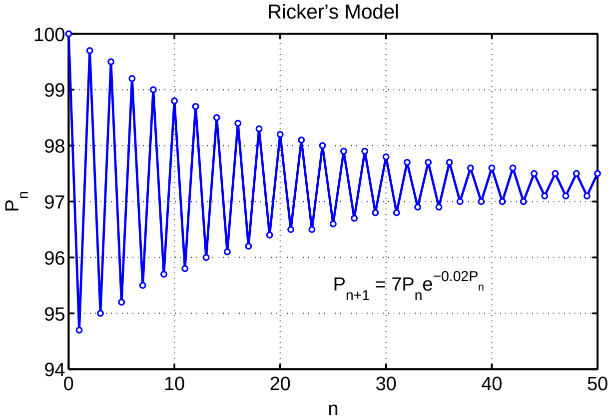
  - The derivative $R'(97.3) = 1 - \ln(7) \approx -0.95$
  - Solutions **oscillate**, but **approach** $P_e = 97.3$
  - This is a **stable equilibrium**, so populations eventually settle to $P_e = 97.3$

Example 1 - Ricker's Growth Model

Solution (cont) Starting with $P_0 = 100$, the simulation shows the behavior predicted above



Example 2 - Ricker's Growth Model 1

Example 2 - Ricker's Growth Model Let P_n be the population of fish in any year n, and assume the Ricker's growth model

$$P_{n+1} = R(P_n) = 9\,P_n e^{-0.02P_n}$$

Skip Example

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Example 2 - Ricker's Growth Model 2

Solution The Ricker's growth function is

$$R(P) = 9\,Pe^{-0.02P}$$

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- This gives a critical point at $P_c = 50$

Example 2 - Ricker's Growth Model 3

Solution (cont) The Ricker's function has a **maximum** at

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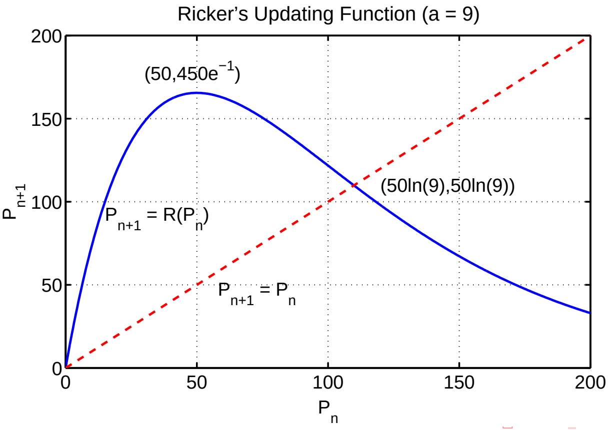

Example 2 - Ricker's Growth Model 4

Solution (cont) For **equilibria**, let $P_e = P_{n+1} = P_n$, then

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Example 2 - Ricker's Growth Model 4

Solution (cont) For **equilibria**, let $P_e = P_{n+1} = P_n$, then

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One equilibrium is $P_e = 0$, so dividing by P_e

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Example 2 - Ricker's Growth Model 4

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One equilibrium is $P_e = 0$, so dividing by P_e

$$1 = 9\,e^{-0.02P_e} \quad \text{or} \quad e^{0.02P_e} = 9$$

This gives the other equilibrium $P_e = 50\ln(9) \approx 109.86$

Example 2 - Ricker's Growth Model 5

Solution (cont) **Stability Analysis** – Recall

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Example 2 - Ricker's Growth Model 5

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Example 2 - Ricker's Growth Model

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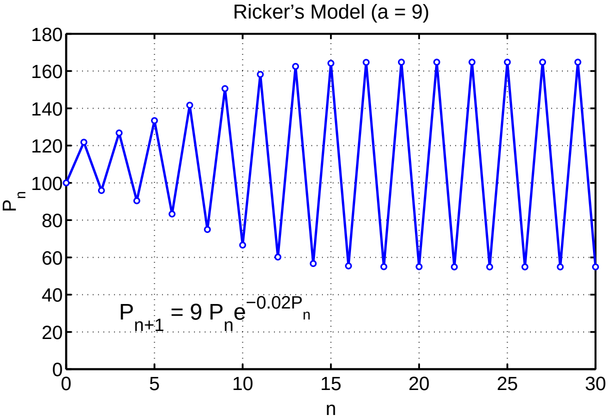
  - The derivative $R'(109.86) = 1 - \ln(9) \approx -1.197$
  - Solutions **oscillate** and **grow away** from $P_e = 109.86$
  - This is a **unstable equilibrium**, and populations oscillate with **Period 2** between 55 and 165

Example 2 - Ricker's Growth Model

Solution (cont) Starting with $P_0 = 100$, the simulation shows the behavior predicted above



Beverton-Holt Model

Beverton-Holt Model - Rational form

$$P_{n+1} = \frac{aP_n}{1 + bP_n}$$

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- Rare amongst nonlinear models - Has an explicit solution
- Given an initial population, P_0

$$P_{n+1} = \frac{MP_0}{P_0 + (M - P_0)a^{-n}}$$

Hassell's Model

Hassell's Model - Alternate Rational form

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- Malthusian growth rate $a - 1$, like Beverton-Holt model

Study of a Beetle Population 1

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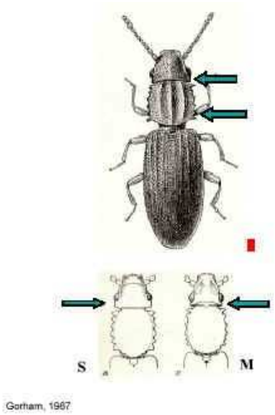
- The food was strictly controlled to maintain a constant supply
- 10 grams of cracked wheat were added weekly
- Regular census of the beetle populations recorded
- These are experimental conditions for the **Logistic growth model**

Study of a Beetle Population 2

Study of *Oryzaephilus surinamensis*, **the saw-tooth grain beetle**



Study of a Beetle Population

Data on ***Oryzaephilus surinamensis*, the saw-tooth grain beetle**

Week	Adults	Week	Adults
0	4	16	405
2	4	18	471
4	25	20	420
6	63	22	430
8	147	24	420
10	285	26	475
12	345	28	435
14	361	30	480

Study of a Beetle Population

Updating functions - Least squares best fit to data

- Plot the data, P_{n+1} vs. P_n, to fit an updating function

Study of a Beetle Population

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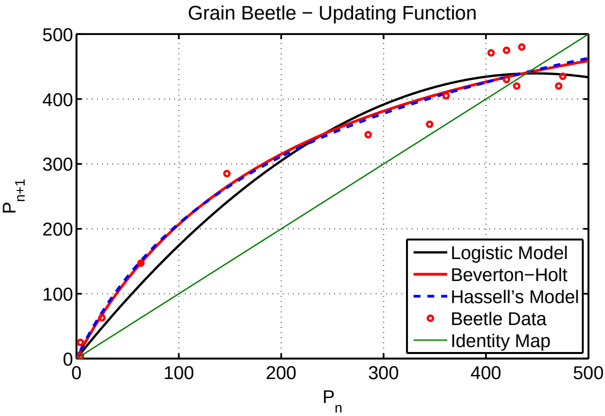
$$P_{n+1} = \frac{3.010\, P_n}{1 + 0.00456\, P_n}$$

- **Hassell's growth model** fit to data (SSE = 9,955)

$$P_{n+1} = \frac{3.269\, P_n}{(1 + 0.00745\, P_n)^{0.8126}}$$

Study of a Beetle Population

Graph of **Updating functions** and **Beetle data**



Study of a Beetle Population

Time Series - Least squares best fit to data, P_0

- Use the **updating functions** from fitting data before
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Study of a Beetle Population 6

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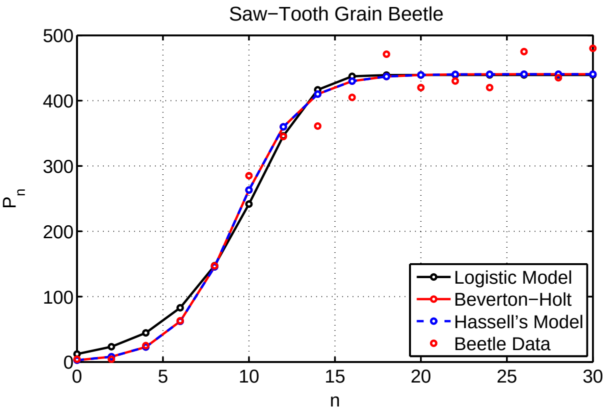
- **Hassell's growth model** fit to data gives $P_0 = 2.08$ with SSE = 7,948
- Beverton-Holt and Hassell's models are very close with both significantly better than the logistic growth model

Study of a Beetle Population

Time Series graph of Models with Beetle Data



Analysis of Hassell's Model 1

Analysis of Hassell's Model – Equilibria

- Let $P_e = P_{n+1} = P_n$, so

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Analysis of Hassell's Model 1

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Analysis of Hassell's Model 1

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- One equilibrium is $P_e = 0$ (as expected the extinction equilibrium)
- The other satisfies

$$\begin{aligned}(1 + bP_e)^c &= a \\ 1 + bP_e &= a^{1/c} \\ P_e &= \frac{a^{1/c} - 1}{b}\end{aligned}$$

Analysis of Hassell's Model 2

Analysis of Hassell's Model – Stability Analysis

- Hassell's updating function is

$$H(P) = \frac{aP}{(1+bP)^c}$$

Analysis of Hassell's Model 2

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Analysis of Hassell's Model

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- By the quotient rule

$$\begin{aligned} H'(P) &= \frac{a(1+bP)^c - abcP(1+bP)^{c-1}}{(1+bP)^{2c}} \\ &= a\frac{1+b(1-c)P}{(1+bP)^{c+1}} \end{aligned}$$

Analysis of Hassell's Model

Analysis of Hassell's Model – Stability Analysis

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Analysis of Hassell's Model

Analysis of Hassell's Model – Stability Analysis

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- At $P_e = 0$, $H'(0) = a$

Analysis of Hassell's Model

Analysis of Hassell's Model – Stability Analysis

- The derivative is

$$H'(P) = a\frac{1 + b(1-c)P}{(1+bP)^{c+1}}$$

- At $P_e = 0$, $H'(0) = a$
  - Since $a > 1$, the zero equilibrium is **unstable**

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  - Since $a > 1$, the zero equilibrium is **unstable**
  - Solutions **monotonically growing away** from the **extinction equilibrium**

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- At $P_e = (a^{1/c}-1)/b$, we find

$$\begin{aligned} H'(P_e) &= a\frac{1+(1-c)(a^{1/c}-1)}{(1+(a^{1/c}-1))^{c+1}} \\ &= \frac{c}{a^{1/c}} + 1 - c \end{aligned}$$

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  - The stability of the **carrying capacity equilibrium** depends on both a and c, but not b
  - When $c=1$ (**Beverton-Holt** model) $H'(P_e)=\frac{1}{a}$, so this equilibrium is **monotonically stable**

Beetle Study Analysis

Beetle Study Analysis – Logistic Growth Model

$$P_{n+1} = F(P_n) = P_n + 0.962\,P_n\left(1 - \frac{P_n}{439.2}\right)$$

- The **equilibria** are $P_e = 0$ and 439.2

Beetle Study Analysis 1

Beetle Study Analysis – Logistic Growth Model

$$P_{n+1} = F(P_n) = P_n + 0.962\, P_n \left(1 - \frac{P_n}{439.2}\right)$$

- The **equilibria** are $P_e = 0$ and 439.2
- The derivative of the updating function is

$$F'(P) = 1.962 - 0.00438\, P$$

Beetle Study Analysis

Beetle Study Analysis – Logistic Growth Model

$$P_{n+1} = F(P_n) = P_n + 0.962\, P_n \left(1 - \frac{P_n}{439.2}\right)$$

- The **equilibria** are $P_e = 0$ and 439.2
- The derivative of the updating function is

$$F'(P) = 1.962 - 0.00438\, P$$

  - At $P_e = 0$, $F'(0) = 1.962$, so this equilibrium is **monotonically unstable**

Beetle Study Analysis

Beetle Study Analysis – Logistic Growth Model

$$P_{n+1} = F(P_n) = P_n + 0.962\, P_n \left(1 - \frac{P_n}{439.2}\right)$$

- The **equilibria** are $P_e = 0$ and 439.2
- The derivative of the updating function is

$$F'(P) = 1.962 - 0.00438\, P$$

- At $P_e = 0$, $F'(0) = 1.962$, so this equilibrium is **monotonically unstable**
- At $P_e = 439.2$, $F'(439.2) = 0.038$, so this equilibrium is **monotonically stable**

Beetle Study Analysis 2

Beetle Study Analysis – Beverton-Holt Growth Model

$$P_{n+1} = B(P_n) = \frac{3.010\,P_n}{1 + 0.00456\,P_n}$$

- The **equilibria** are $P_e = 0$ and 440.8

Beetle Study Analysis 2

Beetle Study Analysis – Beverton-Holt Growth Model

$$P_{n+1} = B(P_n) = \frac{3.010\,P_n}{1 + 0.00456\,P_n}$$

- The **equilibria** are $P_e = 0$ and 440.8
- The derivative of the updating function is

$$B'(P) = \frac{3.010}{(1 + 0.00456\,P)^2}$$

Beetle Study Analysis 2

Beetle Study Analysis – Beverton-Holt Growth Model

$$P_{n+1} = B(P_n) = \frac{3.010\, P_n}{1 + 0.00456\, P_n}$$

- The **equilibria** are $P_e = 0$ and 440.8
- The derivative of the updating function is

$$B'(P) = \frac{3.010}{(1 + 0.00456\, P)^2}$$

  - At $P_e = 0$, $B'(0) = 3.010$, so this equilibrium is **monotonically unstable**

Beetle Study Analysis

Beetle Study Analysis – Beverton-Holt Growth Model

$$P_{n+1} = B(P_n) = \frac{3.010\,P_n}{1 + 0.00456\,P_n}$$

- The **equilibria** are $P_e = 0$ and 440.8
- The derivative of the updating function is

$$B'(P) = \frac{3.010}{(1 + 0.00456\,P)^2}$$

  - At $P_e = 0$, $B'(0) = 3.010$, so this equilibrium is **monotonically unstable**
  - At $P_e = 440.8$, $B'(440.8) = 0.332$, so this equilibrium is **monotonically stable**

Beetle Study Analysis 2

Beetle Study Analysis – Hassell's Growth Model

$$P_{n+1} = H(P_n) = \frac{3.269\,P_n}{(1+0.00745\,P_n)^{0.8126}}$$

- The **equilibria** are $P_e = 0$ and 442.4

Beetle Study Analysis

Beetle Study Analysis – Hassell's Growth Model

$$P_{n+1} = H(P_n) = \frac{3.269\,P_n}{(1 + 0.00745\,P_n)^{0.8126}}$$

- The **equilibria** are $P_e = 0$ and 442.4
- The derivative of the updating function is

$$H'(P) = 3.269\frac{1 + 0.001396\,P}{(1 + 0.00745P)^{1.8126}}$$

Beetle Study Analysis

Beetle Study Analysis – Hassell's Growth Model

$$P_{n+1} = H(P_n) = \frac{3.269\,P_n}{(1 + 0.00745\,P_n)^{0.8126}}$$

- The **equilibria** are $P_e = 0$ and 442.4
- The derivative of the updating function is

$$H'(P) = 3.269\frac{1 + 0.001396\,P}{(1 + 0.00745P)^{1.8126}}$$

  - At $P_e = 0$, $H'(0) = 3.269$, so this equilibrium is **monotonically unstable**

Beetle Study Analysis

Beetle Study Analysis – Hassell's Growth Model

$$P_{n+1} = H(P_n) = \frac{3.269\, P_n}{(1 + 0.00745\, P_n)^{0.8126}}$$

- The **equilibria** are $P_e = 0$ and 442.4
- The derivative of the updating function is

$$H'(P) = 3.269 \frac{1 + 0.001396\, P}{(1 + 0.00745 P)^{1.8126}}$$

  - At $P_e = 0$, $H'(0) = 3.269$, so this equilibrium is **monotonically unstable**
  - At $P_e = 442.4$, $H'(442.4) = 0.3766$, so this equilibrium is **monotonically stable**

Example 1 - Beverton-Holt Model

Example 1 - Beverton-Holt Model: Suppose that a population of insects (measured in weeks) grows according to the discrete dynamical model

$$p_{n+1} = B(p_n) = \frac{20\,p_n}{1 + 0.02\,p_n}$$

Skip Example

Example 1 - Beverton-Holt Model 1

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$$p_{n+1} = B(p_n) = \frac{20\,p_n}{1 + 0.02\,p_n}$$

Skip Example

- Assume that $p_0 = 200$ and find the population for the next 3 weeks
- Simulate the model for 10 weeks
- Graph the **updating function** with the identity map
- Determine the **equilibria** and analyze their **stability**

Example 1 - Beverton-Holt Model 2

Solution - Beverton-Holt Model: Iterate the model with $p_0 = 200$

$$p_1 = \frac{20(200)}{(1 + 0.02(200))} = 800$$

Example 1 - Beverton-Holt Model 2

Solution - Beverton-Holt Model: Iterate the model with $p_0 = 200$

$$
\begin{aligned}
p_1 &= \frac{20(200)}{(1+0.02(200))} = 800 \\
p_2 &= \frac{20(800)}{(1+0.02(800))} = 941
\end{aligned}
$$

Example 1 - Beverton-Holt Model

Solution - Beverton-Holt Model: Iterate the model with $p_0 = 200$

$$
\begin{aligned}
p_1 &= \frac{20(200)}{(1+0.02(200))} = 800 \\
p_2 &= \frac{20(800)}{(1+0.02(800))} = 941 \\
p_3 &= \frac{20(941)}{(1+0.02(941))} = 949.6
\end{aligned}
$$

Example 1 - Beverton-Holt Model 2

Solution - Beverton-Holt Model: Iterate the model with $p_0 = 200$

$$\begin{aligned} p_1 &= \frac{20(200)}{(1+0.02(200))} = 800 \\ p_2 &= \frac{20(800)}{(1+0.02(800))} = 941 \\ p_3 &= \frac{20(941)}{(1+0.02(941))} = 949.6 \end{aligned}$$

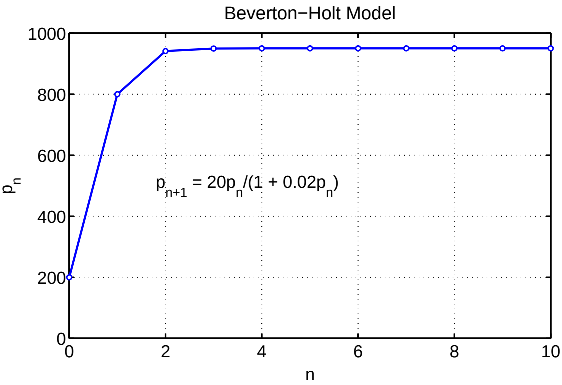
From before, the **carrying capacity** for the Beverton-Holt model is

$$M = \frac{a-1}{b} = \frac{19}{0.02} = 950$$

Example 1 - Beverton-Holt Model 3

Solution (cont): The explicit solution for this model is

$$p_n = \frac{950\, p_0}{p_0 + (950 - p_0)20^{-n}} = \frac{950}{1 + 3.75(20)^{-n}}$$



Example 1 - Beverton-Holt Model

Solution (cont): Graphing the **Updating function**

$$B(p) = \frac{20\,p}{1 + 0.02\,p}$$

- The only intercept is the origin

Example 1 - Beverton-Holt Model

Solution (cont): Graphing the **Updating function**

$$B(p) = \frac{20\,p}{1 + 0.02\,p}$$

- The only intercept is the origin
- There is a **horizontal asymptote** satisfying

$$\lim_{p\to\infty} B(p) = \frac{20}{0.02} = 1000$$

Example 1 - Beverton-Holt Model

Solution (cont): Graphing the **Updating function**

$$B(p) = \frac{20\,p}{1 + 0.02\,p}$$

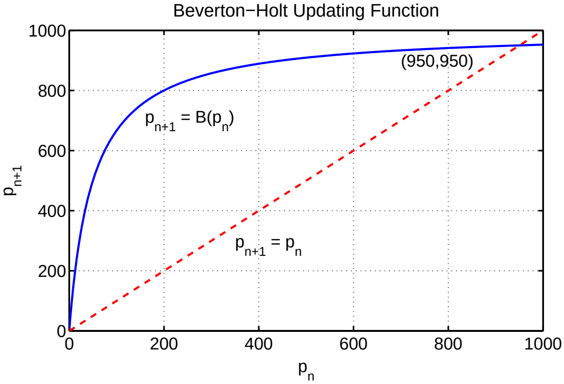
- The only intercept is the origin
- There is a **horizontal asymptote** satisfying

$$\lim_{p\to\infty} B(p) = \frac{20}{0.02} = 1000$$

- Biologically, this asymptote means that there is a maximum number in the next generation no matter how large the population starts

Example 1 - Beverton-Holt Model

Solution (cont): The **updating function** and **identity map**



Example 1 - Beverton-Holt Model

Solution (cont): Analysis of Beverton-Holt model

- Equilibria satisfy

$$p_e = B(p_e) = \frac{20\,p_e}{1 + 0.02\,p_e}$$

Example 1 - Beverton-Holt Model

Solution (cont): Analysis of Beverton-Holt model

- Equilibria satisfy

$$p_e = B(p_e) = \frac{20\,p_e}{1 + 0.02\,p_e}$$

- One equilibrium is $p_e = 0$

Example 1 - Beverton-Holt Model

Solution (cont): Analysis of Beverton-Holt model

- Equilibria satisfy

$$p_e = B(p_e) = \frac{20\,p_e}{1 + 0.02\,p_e}$$

- One equilibrium is $p_e = 0$
- The other satisfies

$$1 + 0.02\,p_e = 20 \quad \text{or} \quad p_e = 950$$

Example 1 - Beverton-Holt Model

Solution (cont): Analysis of Beverton-Holt model

- Equilibria satisfy

$$p_e = B(p_e) = \frac{20\,p_e}{1 + 0.02\,p_e}$$

- One equilibrium is $p_e = 0$
- The other satisfies

$$1 + 0.02\,p_e = 20 \quad \text{or} \quad p_e = 950$$

- The derivative of the updating function is

$$B'(p) = \frac{20}{(1 + 0.02\,p)^2}$$

Example 1 - Beverton-Holt Model

Solution (cont): Analysis of Beverton-Holt model –
Since the derivative of the updating function is

$$B'(p) = \frac{20}{(1 + 0.02\,p)^2}$$

- Equilibrium $p_e = 0$ has $B'(0) = 20$

Example 1 - Beverton-Holt Model

Solution (cont): **Analysis of Beverton-Holt model** –
Since the derivative of the updating function is

$$B'(p) = \frac{20}{(1 + 0.02\,p)^2}$$

- Equilibrium $p_e = 0$ has $B'(0) = 20$
- The **extinction equilibrium** is **unstable** with solutions **monotonically growing away**

Example 1 - Beverton-Holt Model

Solution (cont): Analysis of Beverton-Holt model –
Since the derivative of the updating function is

$$B'(p) = \frac{20}{(1 + 0.02\,p)^2}$$

- Equilibrium $p_e = 0$ has $B'(0) = 20$
- The **extinction equilibrium** is **unstable** with solutions **monotonically growing away**
- The equilibrium $p_e = 950$ has $B'(950) = \frac{1}{20}$

Example 1 - Beverton-Holt Model

Solution (cont): **Analysis of Beverton-Holt model** –
Since the derivative of the updating function is

$$B'(p) = \frac{20}{(1 + 0.02\,p)^2}$$

- Equilibrium $p_e = 0$ has $B'(0) = 20$
- The **extinction equilibrium** is **unstable** with solutions **monotonically growing away**
- The equilibrium $p_e = 950$ has $B'(950) = \frac{1}{20}$
- The **carrying capacity equilibrium** is **stable** with solutions **monotonically approaching**

Example 2 - Hassell's Model

Example 2 - Hassell's Model: Suppose that a population of butterflies (measured in weeks) grows according to the discrete dynamical model

$$p_{n+1} = H(p_n) = \frac{81\, p_n}{(1 + 0.002\, p_n)^4}$$

Skip Example

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Skip Example

- Assume that $p_0 = 200$ and find the population for the next 2 weeks
- Simulate the model for 20 weeks
- Graph the **updating function** with the identity map
- Determine the **equilibria** and analyze their **stability**

Example 2 - Hassell's Model 2

Solution - Hassell's Model: Iterate the model with $p_0 = 200$

$$p_1 = \frac{81(200)}{(1 + 0.002(200))^4} = 4217$$

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$$p_1 = \frac{81(200)}{(1+0.002(200))^4} = 4217$$

$$p_2 = \frac{81(4217)}{(1+0.002(4217))^4} = 43$$

Example 2 - Hassell's Model 2

Solution - Hassell's Model: Iterate the model with $p_0 = 200$

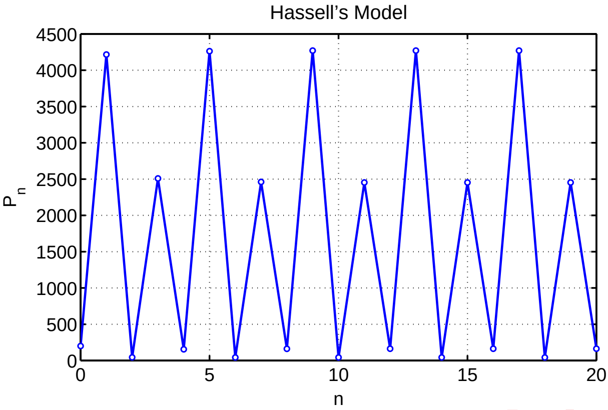
$$p_1 = \frac{81(200)}{(1+0.002(200))^4} = 4217$$
$$p_2 = \frac{81(4217)}{(1+0.002(4217))^4} = 43$$

These iterations show dramatic population swings, suggesting instability in the model

Example 2 - Hassell's Model

Solution (cont): This model is iterated 20 times, and the observed behavior is a **Period 4** solution

Asymptotically cycles from **163** to **4271** to **42** to **2453**



Example 2 - Hassell's Model

Solution (cont): Graphing the **Updating function**

$$H(p) = \frac{81\,p}{(1 + 0.002\,p)^4}$$

- The only intercept is the origin

Example 2 - Hassell's Model

Solution (cont): Graphing the **Updating function**

$$H(p) = \frac{81\,p}{(1 + 0.002\,p)^4}$$

- The only intercept is the origin
- Since the power of p in the denominator exceeds the power of p in the numerator, there is a **horizontal asymptote** $H = 0$

Example 2 - Hassell's Model

Solution (cont): Graphing the **Updating function**

$$H(p) = \frac{81\,p}{(1+0.002\,p)^4}$$

- The only intercept is the origin
- Since the power of p in the denominator exceeds the power of p in the numerator, there is a **horizontal asymptote** $H = 0$
- The derivative is

$$\begin{aligned} H'(p) &= 81\frac{(1+0.002\,p)^4 - p\cdot 4(1+0.002\,p)^3 0.002}{(1+0.002\,p)^8} \\ &= 81\frac{(1-0.006\,p)}{(1+0.002\,p)^5} \end{aligned}$$

Example 2 - Hassell's Model

Solution (cont): Graphing the **Updating function**

$$H(p) = \frac{81\,p}{(1+0.002\,p)^4}$$

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- $H'(p) = 0$ when $1 - 0.006\,p = 0$ or $p_{max} = \frac{500}{3}$

Example 2 - Hassell's Model

Solution (cont): Graphing the **Updating function**

$$H(p) = \frac{81\,p}{(1+0.002\,p)^4}$$

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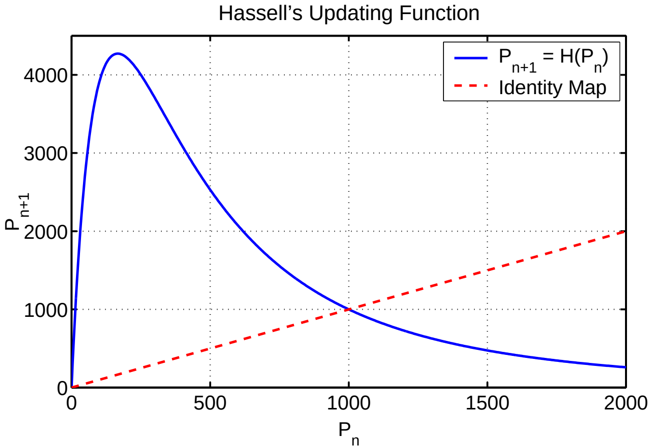
- $H'(p) = 0$ when $1 - 0.006\,p = 0$ or $p_{max} = \frac{500}{3}$
- There is a **maximum** at $(166.7, 4271.5)$

Example 2 - Hassell's Model

Solution (cont): The **updating function** and **identity map**



Example 2 - Hassell's Model

Solution (cont): Analysis of Hassell's model

- Equilibria satisfy

$$p_e = H(p_e) = \frac{81\, p_e}{(1 + 0.002\, p_e)^4}$$

Example 2 - Hassell's Model

Solution (cont): Analysis of Hassell's model

- Equilibria satisfy

$$p_e = H(p_e) = \frac{81\, p_e}{(1 + 0.002\, p_e)^4}$$

- One equilibrium is $p_e = 0$

Example 2 - Hassell's Model

Solution (cont): Analysis of Hassell's model

- Equilibria satisfy

$$p_e = H(p_e) = \frac{81\,p_e}{(1 + 0.002\,p_e)^4}$$

- One equilibrium is $p_e = 0$
- The other satisfies

$$(1 + 0.002\,p_e)^4 = 81$$

Example 2 - Hassell's Model

Solution (cont): Analysis of Hassell's model

- Equilibria satisfy

$$p_e = H(p_e) = \frac{81\, p_e}{(1 + 0.002\, p_e)^4}$$

- One equilibrium is $p_e = 0$
- The other satisfies

$$(1 + 0.002\, p_e)^4 = 81$$

- Thus,

$$1 + 0.002\, p_e = 3 \quad \text{or} \quad p_e = 1000$$

Example 2 - Hassell's Model

Solution (cont): Analysis of Hassell's model – Since the derivative of the updating function is

$$H'(p) = 81\frac{(1-0.006\,p)}{(1+0.002\,p)^5}$$

- Equilibrium $p_e = 0$ has $H'(0) = 81$

Example 2 - Hassell's Model

Solution (cont): Analysis of Hassell's model – Since the derivative of the updating function is

$$H'(p) = 81\frac{(1-0.006\,p)}{(1+0.002\,p)^5}$$

- Equilibrium $p_e = 0$ has $H'(0) = 81$
- The **extinction equilibrium** is **unstable** with solutions **monotonically growing away**

Example 2 - Hassell's Model

Solution (cont): **Analysis of Hassell's model** – Since the derivative of the updating function is

$$H'(p) = 81\frac{(1 - 0.006\,p)}{(1 + 0.002\,p)^5}$$

- Equilibrium $p_e = 0$ has $H'(0) = 81$
- The **extinction equilibrium** is **unstable** with solutions **monotonically growing away**
- The equilibrium $p_e = 1000$ has $H'(1000) = -\frac{5}{3}$

Example 2 - Hassell's Model

Solution (cont): **Analysis of Hassell's model** – Since the derivative of the updating function is

$$H'(p) = 81\frac{(1-0.006\,p)}{(1+0.002\,p)^5}$$

- Equilibrium $p_e = 0$ has $H'(0) = 81$
- The **extinction equilibrium** is **unstable** with solutions **monotonically growing away**
- The equilibrium $p_e = 1000$ has $H'(1000) = -\frac{5}{3}$
- The $p_e = 1000$ **equilibrium** is **unstable** with solutions **oscillating** and **moving away** from p_e

Example 3 - Chalone Model

Example 3 - Chalone Model or Model for Cellular Division with Inhibition: A biochemical agent, **chalone**, is released by a cell to inhibit mitosis of nearby cells, preventing the over crowding of cells.

Example 3 - Chalone Model 1

Example 3 - Chalone Model or Model for Cellular Division with Inhibition: A biochemical agent, **chalone**, is released by a cell to inhibit mitosis of nearby cells, preventing the over crowding of cells.

This was an early model for **cancer**, speculating that this control breaks down

$$p_{n+1} = f(p_n) = \frac{2\,p_n}{1 + 10^{-8} p_n^4}$$

Skip Example

Example 3 - Chalone Model 1

Example 3 - Chalone Model or Model for Cellular Division with Inhibition: A biochemical agent, **chalone**, is released by a cell to inhibit mitosis of nearby cells, preventing the over crowding of cells.

This was an early model for **cancer**, speculating that this control breaks down

$$p_{n+1} = f(p_n) = \frac{2\,p_n}{1 + 10^{-8} p_n^4}$$

Skip Example

- Let $p_0 = 10$ and find the population for the next 2 generations
- Simulate the model for 20 weeks
- Determine the **equilibria** and analyze their **stability**

Example 3 - Chalone Model 2

Solution - Chalone Model: Iterate the model with $p_0 = 10$

$$p_1 = \frac{2(10)}{1 + 10^{-8}(10)^4} = 20.0$$

Example 3 - Chalone Model 2

Solution - Chalone Model: Iterate the model with $p_0 = 10$

$$\begin{aligned} p_1 &= \frac{2(10)}{1+10^{-8}(10)^4} = 20.0 \\ p_2 &= \frac{2(20)}{1+10^{-8}(20)^4} = 39.94 \end{aligned}$$

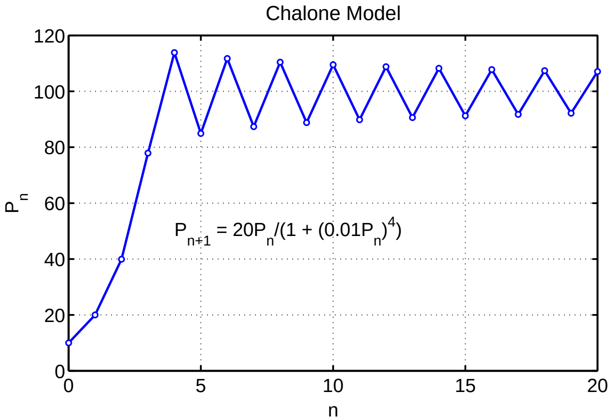
Example 3 - Chalone Model

Solution - Chalone Model: Iterate the model with $p_0 = 10$

$$\begin{aligned} p_1 &= \frac{2(10)}{1 + 10^{-8}(10)^4} = 20.0 \\ p_2 &= \frac{2(20)}{1 + 10^{-8}(20)^4} = 39.94 \\ p_3 &= \frac{2(39.94)}{1 + 10^{-8}(39.94)^4} = 77.90 \end{aligned}$$

Example 3 - Chalone Model

Solution (cont): This model is iterated 20 times, and the model shows oscillations



Example 3 - Chalone Model

Solution (cont): Analysis of Chalone model

- Equilibria satisfy

$$p_e = f(p_e) = \frac{2\,p_e}{1 + 10^{-8}\,p_e^4}$$

Example 3 - Chalone Model

Solution (cont): Analysis of Chalone model

- Equilibria satisfy

$$p_e = f(p_e) = \frac{2\,p_e}{1 + 10^{-8}\,p_e^4}$$

- One equilibrium is $p_e = 0$

Example 3 - Chalone Model

Solution (cont): Analysis of Chalone model

- Equilibria satisfy

$$p_e = f(p_e) = \frac{2\,p_e}{1 + 10^{-8}\,p_e^4}$$

- One equilibrium is $p_e = 0$
- The other satisfies

$$1 + 10^{-8}\,p_e^4 = 2$$

Example 3 - Chalone Model

Solution (cont): Analysis of Chalone model

- Equilibria satisfy

$$p_e = f(p_e) = \frac{2\,p_e}{1 + 10^{-8}\,p_e^4}$$

- One equilibrium is $p_e = 0$
- The other satisfies

$$1 + 10^{-8}\,p_e^4 = 2$$

- Thus,

$$p_e^4 = 10^8 \quad \text{or} \quad p_e = 100$$

Example 3 - Chalone Model

Solution (cont): **Analysis of Chalone model** – The derivative of the updating function is

$$f'(p) = 2\frac{(1 + 10^{-8}p^4) - p(4 \times 10^{-8}p^3)}{(1 + 10^{-8}p^4)^2}$$

$$= \frac{2 - 6 \times 10^{-8}p^4}{(1 + 10^{-8}p^4)^2}$$

- Equilibrium $p_e = 0$ has $f'(0) = 2$

Example 3 - Chalone Model

Solution (cont): Analysis of Chalone model – The derivative of the updating function is

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- The **extinction equilibrium** is **unstable** with solutions **monotonically growing away**

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- Equilibrium $p_e = 0$ has $f'(0) = 2$
- The **extinction equilibrium** is **unstable** with solutions **monotonically growing away**
- The equilibrium $p_e = 100$ has $f'(100) = -1$

Example 3 - Chalone Model

Solution (cont): **Analysis of Chalone model** – The derivative of the updating function is

$$\begin{aligned} f'(p) &= 2\frac{(1+10^{-8}p^4) - p(4\times 10^{-8}p^3)}{(1+10^{-8}p^4)^2} \\ &= \frac{2-6\times 10^{-8}p^4}{(1+10^{-8}p^4)^2} \end{aligned}$$

- Equilibrium $p_e = 0$ has $f'(0) = 2$
- The **extinction equilibrium** is **unstable** with solutions **monotonically growing away**
- The equilibrium $p_e = 100$ has $f'(100) = -1$
- The $p_e = 100$ **equilibrium** is on the **border of stability** with solutions **oscillating** and **slowly approaching** p_e