# Calculus for the Life Sciences II

## Lecture Notes – More Applications of Nonlinear Dynamical Systems

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# Outline







# Introduction - Population Models

## Introduction - Population Models

- Simplest (linear) model - Malthusian or exponential growth model
- Logistic growth model is a quadratic model
  - Malthusian growth term and a term for crowding effects
  - Has a carrying capacity reflecting natural limits to populations
  - Quadratic updating function becomes negative for large populations
- Ecologists have modified the logistic growth model to make the updating function more realistic and better able to handle largely fluctuating populations
  - Ricker's model used in fishery management
  - Hassell's model used for insects
- Differentiation needed to analyze these models





# Sockeye Salmon Populations 1

## Sockeye Salmon Populations – Life Cycle

- Salmon are unique in that they breed in specific fresh water lakes and die
- Their offspring migrate to the ocean and mature for about 4-5 years
- Mature salmon migrate at the same time to return to the exact same lake or river bed where they hatched
- Adult salmon breed and die
- Their bodies provide many essential nutrients that nourish the stream of their young

## Sockeye Salmon Populations 2

### Sockeye Salmon Populations – Problems

- Salmon populations in the Pacific Northwest are becoming very endangered
- Many salmon spawning runs have become extinct
- Human activity adversely affect this complex life cycle of the salmon
  - Damming rivers interrupts the runs
  - Forestry allows the water to become too warm
  - Agriculture results in runoff pollution





## Sockeye Salmon Populations 3

### Sockeye Salmon Populations – Skeena River

- The life cycle of the salmon is an example of a complex discrete dynamical system
- The importance of salmon has produced many studies
- Sockeye salmon (*Oncorhynchus nerka*) in the Skeena river system in British Columbia
  - Largely uneffected by human development
  - Long time series of data – 1908 to 1952
  - Provide good system to model





## Sockeye Salmon Populations 4

### Sockeye Salmon Populations – Spawning Behavior

- Create table of sockeye salmon (*Oncorhynchus nerka*) in the Skeena river system
- Table lists four year averages from the starting year
- Since 4 and 5 year old salmon spawn, each grouping of 4 years is an approximation of the offspring of the previous 4 year average
- Model is complicated because the salmon have adapted to have either 4 or 5 year old mature adults spawn
- Simplify the model by ignoring this complexity





## Sockeye Salmon Populations 5

### 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

## Ricker's Model – Salmon 1

### Problems with Logistic growth model

$$P_{n+1} = P_n + rP_n\left(1 - \frac{P_n}{M}\right)$$

- Logistic growth model predicted certain yeast populations well
- This model does not fit the data for many organisms
- A major problem is that large populations in the model return a negative population in the next generation
- Several alternative models use only a **non-negative** updating function
- Fishery management has often used **Ricker's Model**





## Ricker's Model – Salmon 2

### Ricker's Model

- **Ricker's model** was originally formulated using studies of salmon populations
- **Ricker's model** is given by the equation

$$P_{n+1} = R(Pn) = aP_ne^{-bP_n}$$

- The positive constants $a$ and $b$ are fit to the data
- 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

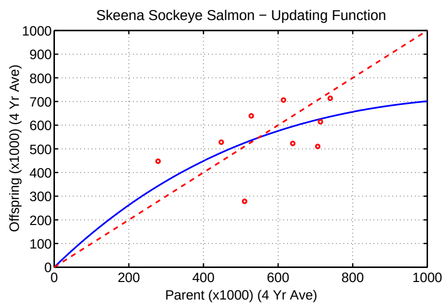




## Ricker's Model – Salmon 3

- 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

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

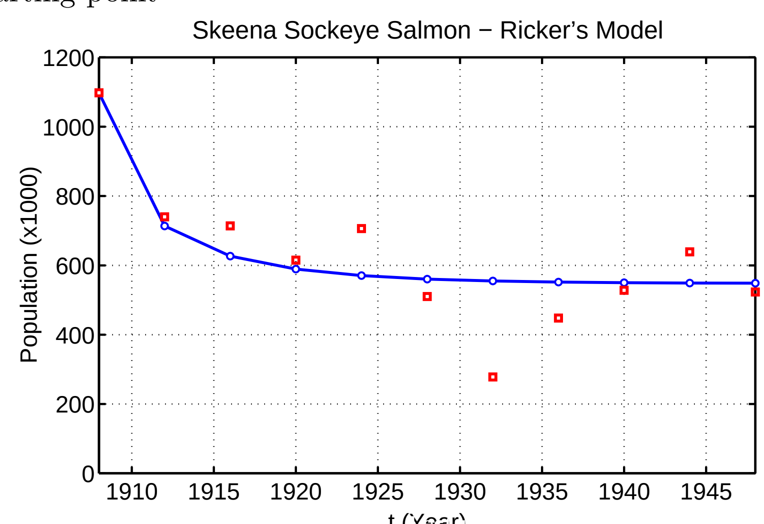







## Ricker's Model – Salmon 4

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



## Ricker's Model – Salmon 5

### Summary of Ricker's Model for Skeena river salmon

- Ricker's model levels off at a stable equilibrium around 550,000
- Model shows populations monotonically approaching the equilibrium
- 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

$$P_{n+1} = R(P_n) = aP_n e^{-bP_n}$$

### Equilibrium Analysis

The equilibria are found by setting $P_e = P_{n+1} = P_n$, thus

$$\begin{aligned} P_e &= aP_e e^{-bP_e} \\ 0 &= P_e(ae^{-bP_e} - 1) \end{aligned}$$

The equilibria are

$$P_e = 0 \qquad \text{and} \qquad P_e = \frac{\ln(a)}{b}$$

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





## Analysis of the Ricker's Model 2

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

$$R(P) = aPe^{-bP}$$

### Derivative of the Ricker Updating Function

$$R'(P) = a(P(-be^{-bP}) + e^{-bP}) = ae^{-bP}(1 - bP)$$

At the **Equilibrium** $P_e = 0$

$$R(0) = a$$

- If $0 < a < 1$, then $P_e = 0$ is stable and the population goes to extinction (also no positive equilibrium)
- If $a > 1$, then $P_e = 0$ is unstable and the population grows away from the equilibrium





## Analysis of the Ricker's Model 3

Since the **Derivative of the Ricker Updating Function** is

$$R'(P) = ae^{-bP}(1 - bP)$$

At the **Equilibrium** $P_e = \frac{\ln(a)}{b}$

$$R(\ln(a)/b) = ae^{-\ln(a)}(1 - \ln(a)) = 1 - \ln(a)$$

- The solution of Ricker's model is **stable** and **monotonically approaches** the equilibrium $P_e = \ln(a)/b$ provided $1 < a < e \approx 2.7183$
- The solution of Ricker's model is **stable** and **oscillates as it approaches** the equilibrium $P_e = \ln(a)/b$ provided $e < a < e^2 \approx 7.389$
- 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

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

From the analysis above, the equilibria are

$$P_e = 0 \qquad \text{and} \qquad P_e = \frac{\ln(1.535)}{0.000783} = 547.3$$

The derivative is

$$R'(P) = 1.535 e^{-0.000783P}(1 - 0.000783P)$$

- At $P_e = 0$, $R'(0) = 1.535 > 1$
  - This equilibrium is **unstable** (as expected)
- 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 1

**Example 1 - Ricker's Growth Model** Let $P_n$ be the population of fish in any year $n$, and assume the Ricker's growth model

$$P_{n+1} = R(P_n) = 7\, P_n e^{-0.02 P_n}$$

Skip Example

- Graph of the updating function $R(P)$ with the identity function, showing the intercepts, all extrema, and any asymptotes
- Find all equilibria of the model and describe the behavior of these equilibria
- Let $P_0 = 100$, and simulate the model for 50 years





## Example 1 - Ricker's Growth Model 2

**Solution** The Ricker's growth function is

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

- The only intercept is the origin $(0, 0)$
- Since the negative exponential dominates in the function $R(P)$, there is a horizontal asymptote of $P_{n+1} = 0$
- Extrema are found differentiating $R(P)$

$$\begin{aligned} R'(P) &= 7(P(-0.02P)e^{-0.02P} + e^{-0.02P}) \\ &= 7\, e^{-0.02P}(1 - 0.02\, P) \end{aligned}$$

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

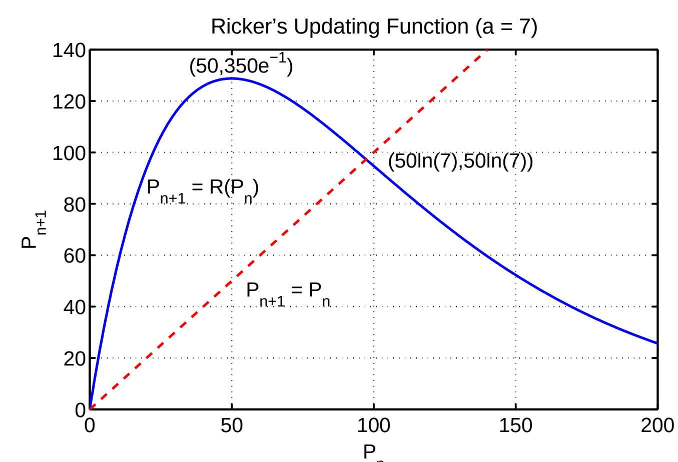




## Example 1 - Ricker's Growth Model 3

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

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



## Example 1 - Ricker's Growth Model



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

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

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

$$1 = 7\,e^{-0.02P_e} \quad \text{or} \quad e^{0.02P_e} = 7$$

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





## Example 1 - Ricker's Growth Model



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

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

- For $P_e = 0$
  - The derivative $R'(0) = 7 > 1$
  - Solutions **monotonically grow away** from $P_e = 0$
- For $P_e = 97.3$
  - 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 $P_e = 97.3$

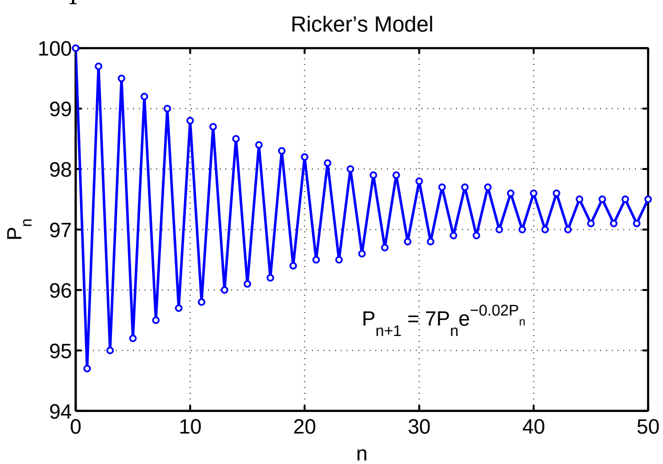




## Example 1 - Ricker's Growth Model



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








## Example 2 - Ricker's Growth Model



**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

- Graph of the updating function $R(P)$ with the identity function, showing the intercepts, all extrema, and any asymptotes
- Find all equilibria of the model and describe the behavior of these equilibria
- Let $P_0 = 100$, and simulate the model for 50 years

## Example 2 - Ricker's Growth Model



**Solution** The Ricker's growth function is

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

- The only intercept is the origin $(0, 0)$
- Since the negative exponential dominates in the function $R(P)$, there is a horizontal asymptote of $P_{n+1} = 0$
- Extrema are found differentiating $R(P)$

$$\begin{aligned} R'(P) &= 9(P(-0.02P)e^{-0.02P} + e^{-0.02P}) \\ &= 9\,e^{-0.02P}(1 - 0.02\,P) \end{aligned}$$

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



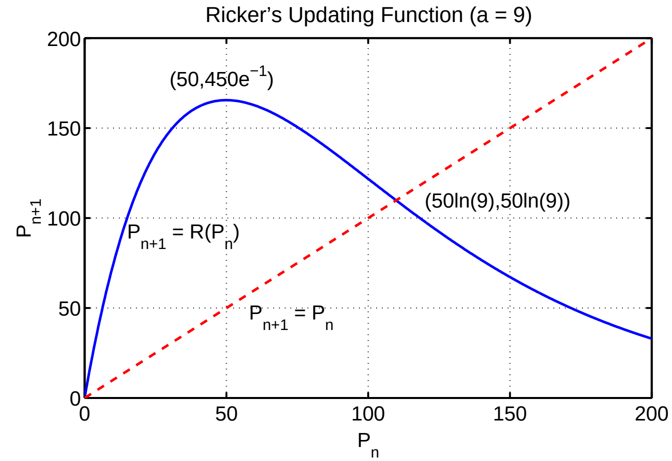


## Example 2 - Ricker's Growth Model



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

$$(P_c, R(P_c)) = (50, 450e^{-1}) \approx (50, 165.5)$$








## Example 2 - Ricker's Growth Model



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

$$P_e = R(P_e) = 9\,P_e e^{-0.02P_e}$$

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



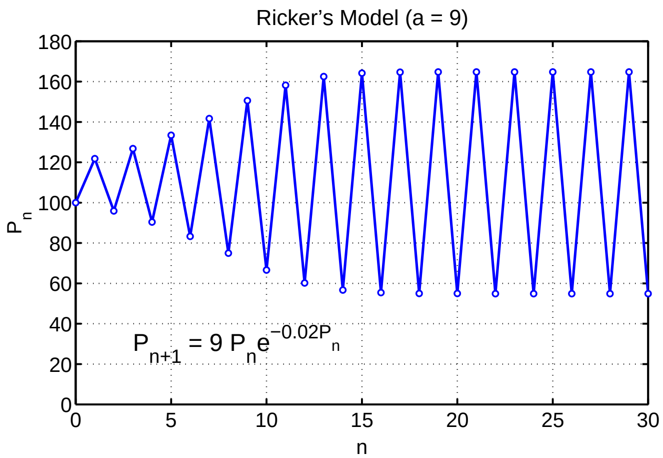
**Solution (cont)** **Stability Analysis** – Recall

$$R'(P) = 9\,e^{-0.02P}(1 - 0.02\,P)$$

- For $P_e = 0$
  - The derivative $R'(0) = 9 > 1$
  - Solutions **monotonically grow away** from $P_e = 0$
- For $P_e = 109.86$
  - 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 6

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








## Beverton-Holt Model

**Beverton-Holt Model** - Rational form

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

- Developed in 1957 for fisheries management
- Malthusian growth rate $a - 1$
- Carrying capacity
$$M = \frac{a-1}{b}$$
- Superior to **logistic** model as updating function is non-negative
- 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

$$P_{n+1} = H(P_n) = \frac{aP_n}{(1 + bP_n)^c}$$

- Often used in insect populations
- Provides alternative to **logistic** and **Ricker's** growth models, extending the **Beverton-Holt** model
- $H(P_n)$ has **3 parameters**, $a$, $b$, and $c$, while logistic, Ricker's, and Beverton-Holt models have **2 parameters**
- Malthusian growth rate $a - 1$, like Beverton-Holt model





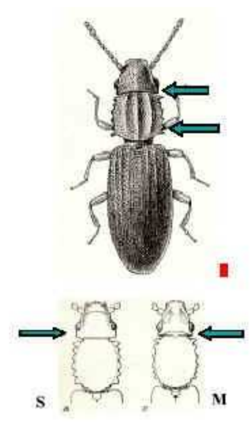
## Study of a Beetle Population 1

**Study of a Beetle Population**

- In 1946, A. C. Crombie studied several beetle populations
- 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**




Gorham, 1987





## Study of a Beetle Population 3

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 4

**Updating functions** - Least squares best fit to data

- Plot the data, $P_{n+1}$ vs. $P_n$, to fit an updating function
- **Logistic growth model** fit to data (SSE = 13,273)

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

- **Beverton-Holt model** fit to data (SSE = 10,028)

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

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

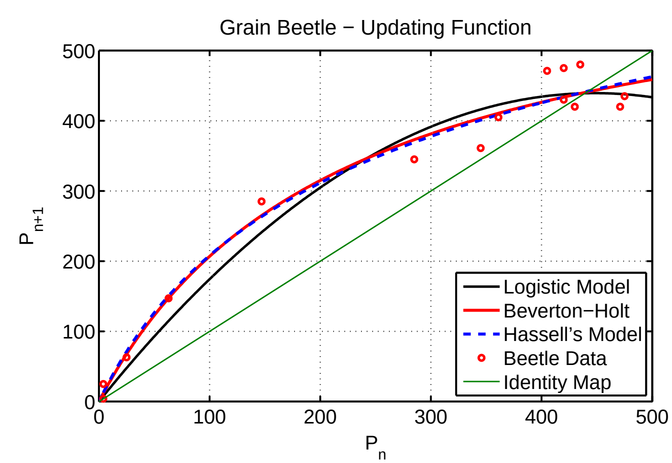
$$P_{n+1} = \frac{3.269\,P_n}{(1 + 0.00745\,P_n)^{0.8126}}$$





## Study of a Beetle Population 5

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



## Study of a Beetle Population 6

**Time Series** - Least squares best fit to data, $P_0$

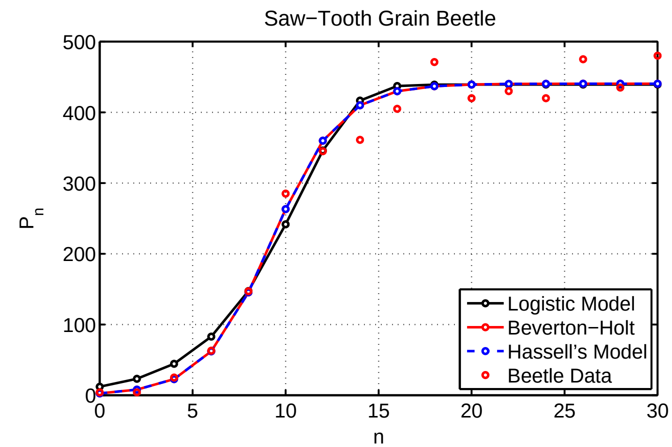
- Use the **updating functions** from fitting data before
- Adjust $P_0$ by **least sum of square errors** to time series data on beetles
- **Logistic growth model** fit to data gives $P_0 = 12.01$ with SSE = 12,027
- **Beverton-Holt model** fit to data gives $P_0 = 2.63$ with SSE = 8,578
- **Hassell's 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 7

**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

$$P_e = \frac{aP_e}{(1+bP_e)^c}$$

- Thus,

$$P_e(1+bP_e)^c = aP_e$$

- 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

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

- Differentiate using the quotient rule and chain rule
- The derivative of the denominator (chain rule) is

$$\frac{d}{dP}(1+bP)^c = c(1+bP)^{c-1}b = bc(1+bP)^{c-1}$$

- 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 3

### 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**
  - Solutions **monotonically growing away** from the **extinction equilibrium**





## Analysis of Hassell's Model 4

### Analysis of Hassell's Model – Stability Analysis

- The derivative is

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

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

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

  - 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 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

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

  - 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 $440.8$
- 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 $442.4$
- 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**
  - At $P_e = 442.4$, $H'(442.4) = 0.3766$, so this equilibrium is **monotonically stable**





## Example 1 - Beverton-Holt Model 1

**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

- 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 $p_0 = 200$

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

$$p_2 = \frac{20(800)}{(1 + 0.02(800))} = 941$$

$$p_3 = \frac{20(941)}{(1 + 0.02(941))} = 949.6$$

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

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

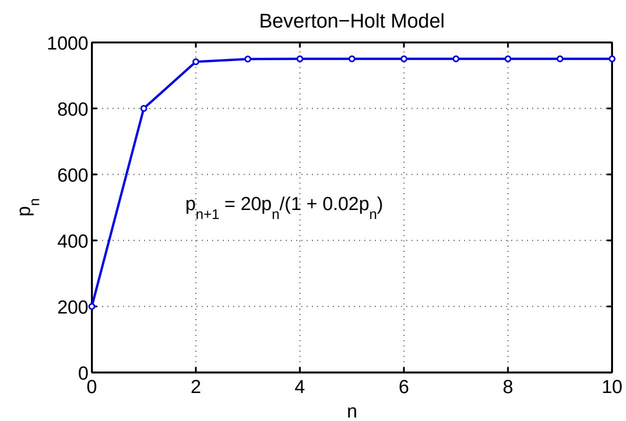




## Example 1 - Beverton-Holt Model 3

**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
- 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

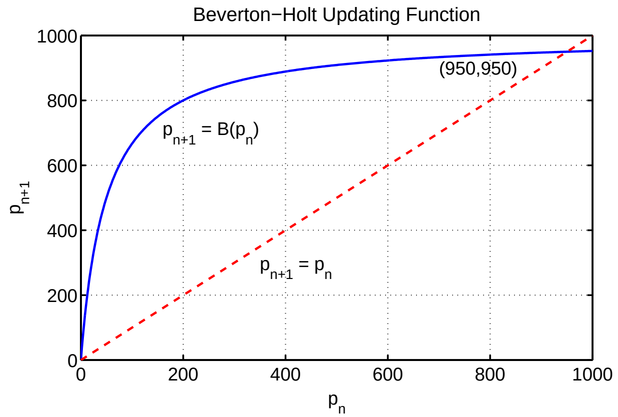




## Example 1 - Beverton-Holt Model



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








## Example 1 - Beverton-Holt Model



**Solution (cont):** **Analysis of Beverton-Holt model**

- Equilibria satisfy

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

- 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 $B'(0) = 20$
- 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 1

**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

- 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 $p_0 = 200$

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

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

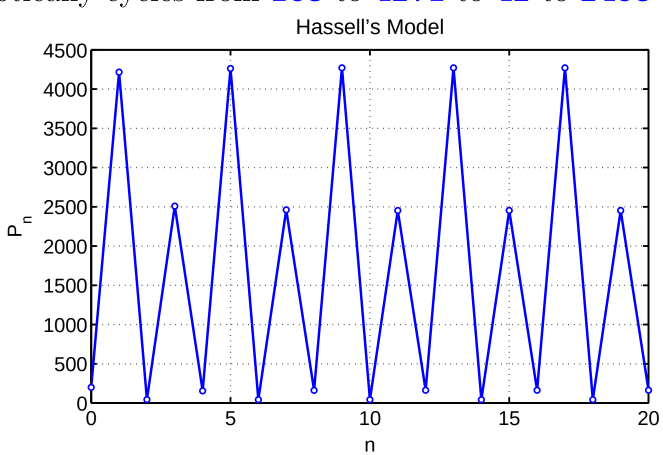
These iterations show dramatic population swings, suggesting instability in the model





## Example 2 - Hassell's Model 3

**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 4

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

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

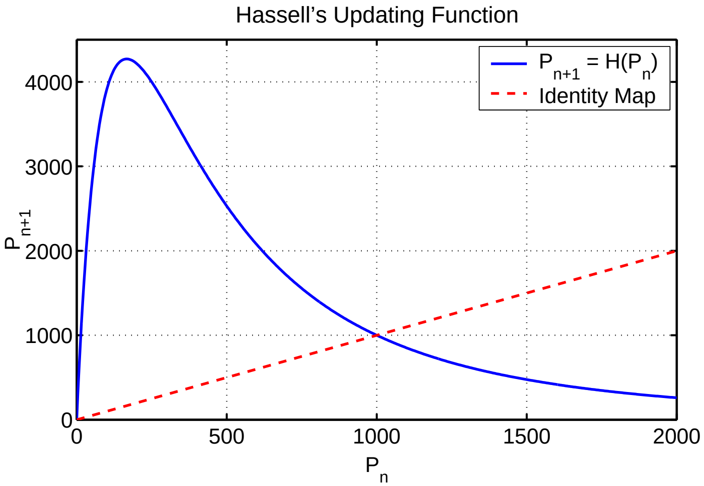
- The only intercept is the origin
- Since the power of $p$ in the denominator exceeds the power of $p$ in the numerator, there is a **horizontal asymptote** $H = 0$
- The derivative is

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

- $H'(p) = 0$ 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 5

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








## Example 2 - Hassell's Model 6

**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 7

**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 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



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

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

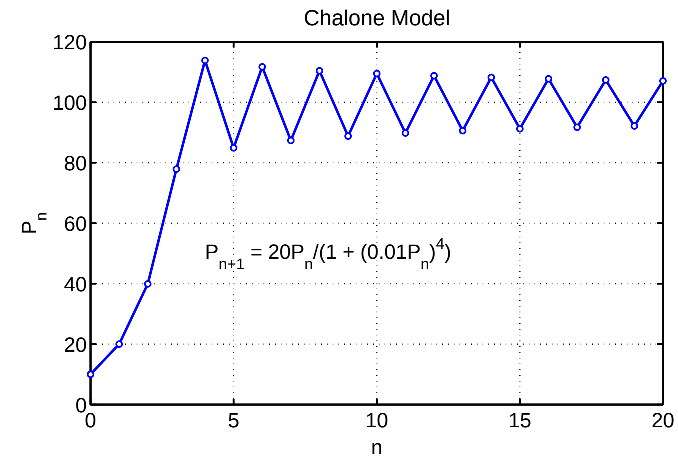




## Example 3 - Chalone Model



**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
$$p_e = f(p_e) = \frac{2\,p_e}{1+10^{-8}\,p_e^4}$$
- 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 $f'(0) = 2$
- 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** $p_e$