Calculus for the Life Sciences

Lecture Notes – Qualitative Analysis of Differential Equations

Joseph M. Mahaffy,
⟨jmahaffy@mail.sdsu.edu⟩

Department of Mathematics and Statistics
Dynamical Systems Group
Computational Sciences Research Center
San Diego State University
San Diego, CA 92182-7720

http://www-rohan.sdsu.edu/~jmahaffy

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Outline

Introduction

Modeling and Differential Equations

- **Biological Models** often use **differential equations**, which have no analytical solution
- Properties of the model and differential equation can provide some insight
- **Qualitative analysis** techniques provide simple tools for understanding models
- Analysis helps understand equilibria and behavior near the equilibria

Growth of Bacteria

Growth of Bacteria

- Bacterial growth usually follows a regular pattern
  - They are inoculated into a broth
  - Culture has a **lag period** (adjusting to the new growing conditions)
  - A period of **exponential growth** (**Malthusian growth** model)
  - Cell growth slows to **stationary growth** (nutrients become limiting or waste products build)
  - Population levels off or declines using different pathways to survive the lean times

Bacterial Growth Experiments 1

Bacterial Growth Experiments

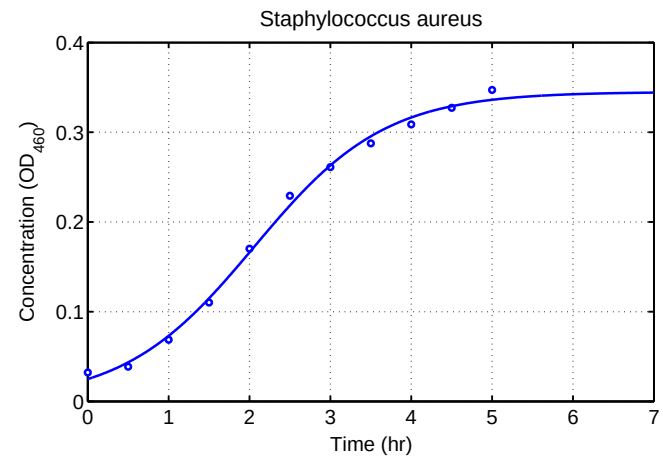
- *Staphylococcus aureus* is a common pathogen that can cause food poisoning
- Cultures of this bacterium satisfy the **logistic growth**
  - Data from one experiment by Carl Gunderson (Lab of Anca Segall)
  - Normal strain is grown to the optical density (OD_{650}), which estimates the number of bacteria

t (hr)	0	0.5	1	1.5	2	2.5
OD_{650}	0.032	0.039	0.069	0.110	0.170	0.229
t (hr)	3	3.5	4	4.5	5	
OD_{650}	0.261	0.288	0.309	0.327	0.347	

Bacterial Growth Experiments 2

Bacterial Growth Experiments

Graph of **data** and **logistic growth model**



Bacterial Growth

Bacterial Growth

- Previously studied the **discrete logistic growth**
  - Could only simulate, but not solve
  - **Qualitative analysis** of the equilibrium gave some insight to the model behavior
- Growth of bacteria is a more **continuous process**
  - Their growth is better characterized by a **differential equation**
  - Use the **continuous logistic growth** model to study growth behavior
  - Show several methods to analyze previous data, including qualitative methods, exact solution, and parameter fitting

Malthusian Growth 1

Malthusian Growth

- The experiment shows the rapid initial growth of the bacteria
  - This suggests **Malthusian growth**
- Earlier showed the **Malthusian growth model**:

$$\frac{dP}{dt} = rP, \qquad P(0) = P_0$$

- Solution satisfies:

$$P(t) = P_0 e^{rt}$$

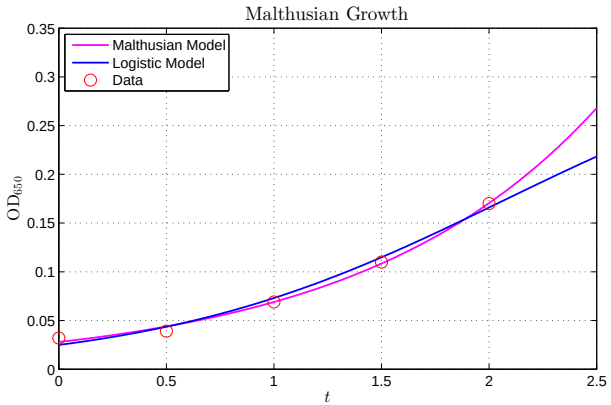
- Only later does crowding require **logistic growth model**

Malthusian Growth 2

Graph shows early data with **Malthusian** and **logistic growth models**

Best fitting Malthusian growth model is

$$P(t) = 0.0279\, e^{0.905\, t}$$



Logistic Growth 1

Logistic Growth

- After rapid growth the experiment shows bacterial growth slowing
  - This suggests **Logistic growth**
- Earlier showed the **Logistic growth model**:

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{M}\right), \qquad P(0) = P_0$$

- Solution satisfies:

$$P(t) = \frac{P_0 M}{P_0 + (M - P_0)e^{-rt}}$$

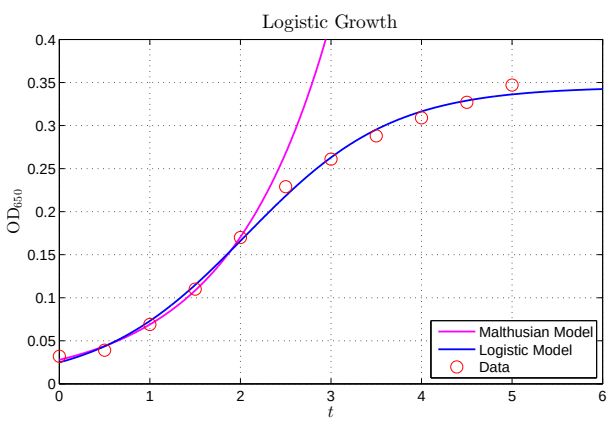
- This solution is found by:
  - Separation of Variables and special integration techniques
  - Bernoulli's method
- Want easier methods to investigate **qualitative behavior**

Malthusian Growth 2

Graph shows the **Malthusian** and **logistic growth models**

Best fitting logistic growth model is

$$P(t) = \frac{0.3450}{1 + 12.85\, e^{-1.24\, t}}$$



Qualitative Behavior of Differential Equations

Qualitative Behavior of Differential Equations

- Techniques follow analysis of discrete dynamical systems
  - Find the **equilibria**
  - Determine the behavior of the solutions near the equilibria
- Study **Autonomous Differential Equations**

$$\frac{dy}{dt} = f(y)$$

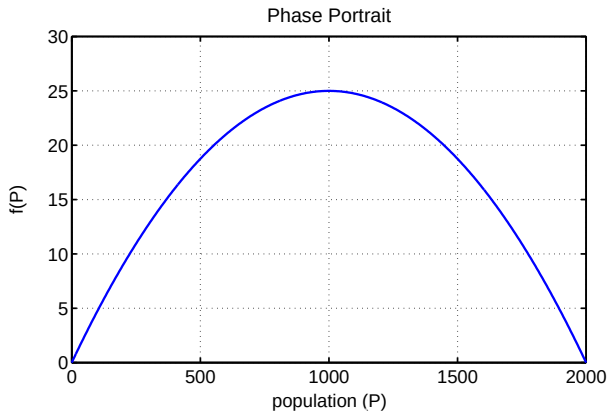
- Graph function $f(y)$
- Find **Phase Portrait** and determine local behavior near equilibria

Example: Logistic Growth Model

Example: Logistic Growth Model

Consider the logistic growth equation:

$$\frac{dP}{dt} = f(P) = 0.05P\left(1 - \frac{P}{2000}\right)$$



Example: Logistic Growth Model

For the logistic growth equation:

$$\frac{dP}{dt} = f(P) = 0.05P\left(1 - \frac{P}{2000}\right)$$

- The graph above of $f(P)$ shows
  - $f(P)$ intersects the P-axis at $P = 0$ and $P = 2000$
  - These P-intercepts are where $f(P) = 0$ or

$$\frac{dP}{dt} = 0$$

- There is **no change in the growth of the population** or the **population is at equilibrium**
- This is the first step in any **qualitative analysis**: Find all **equilibria** ($f(P) = 0$)

Example: Logistic Growth Model

Local Analysis: **Equilibria** are $P_e = 0$ and $P_e = 2000$

- The graph of $f(P)$ gives more information
- To the left of $P_e = 0$, $f(P) < 0$
  - Since $\frac{dP}{dt} = f(P) < 0$, $P(t)$ is decreasing
  - Note that this region is outside the region of biological significance
- For $0 < P < 2000$, $f(P) > 0$
  - Since $\frac{dP}{dt} = f(P) > 0$, $P(t)$ is increasing
  - Population monotonically growing in this area
- For $P > 2000$, $f(P) < 0$
  - Since $\frac{dP}{dt} = f(P) < 0$, $P(t)$ is decreasing
  - Population monotonically decreasing in this region

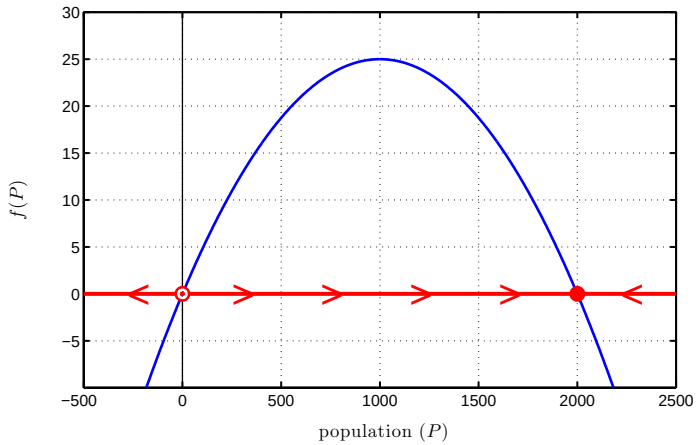
Example: Logistic Growth Model

Phase Portrait

- Use the above information to draw a **Phase Portrait** of the behavior of this differential equation along the P-axis
- The behavior of the differential equation is denoted by arrows along the P-axis
  - When $f(P) < 0$, $P(t)$ is decreasing and we draw an **arrow to the left**
  - When $f(P) > 0$, $P(t)$ is increasing and we draw an **arrow to the right**
- **Equilibria**
  - A **solid dot** represents an equilibrium that solutions approach or **stable equilibrium**
  - An **open dot** represents an equilibrium that solutions go away from or **unstable equilibrium**

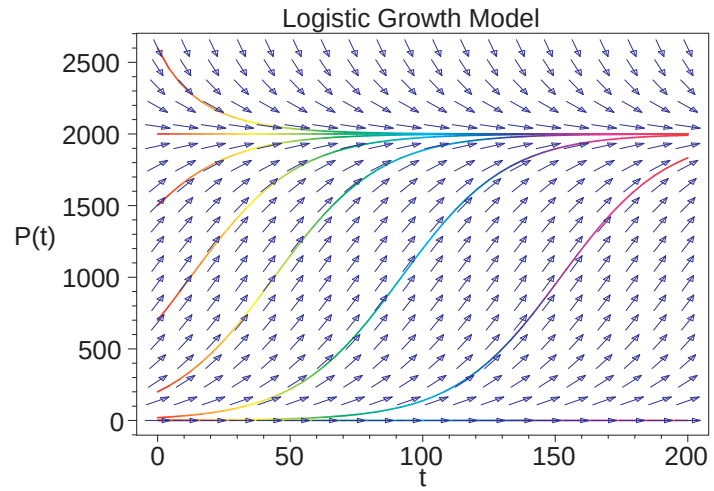
Example: Logistic Growth Model

Phase Portrait



Example: Logistic Growth Model

Diagram of Solutions for Logistic Growth Model



Example: Logistic Growth Model

Summary of Qualitative Analysis

- Graph shows solutions either moving away from the equilibrium at $P_e = 0$ or moving toward $P_e = 2000$
- Solutions are increasing most rapidly where $f(P)$ is at a maximum
- Phase portrait shows direction of flow of the solutions without solving the differential equation
- Solutions cannot cross in the tP-plane
- **Phase Portrait analysis**
  - Behavior of a scalar differential equation found by just graphing function
  - **Equilibria** are **zeros** of function
  - Direction of flow/arrows from sign of function
  - **Stability** of equilibria from whether arrows point toward or away from the equilibria

Example: Sine Function

Example: Sine Function

Consider the differential equation:

$$\frac{dx}{dt} = 2\,\sin(\pi x)$$

- Find all equilibria
- Determine the stability of the equilibria
- Sketch the phase portrait
- Show typical solutions

Example: Sine Function

For the sine function below:

$$\frac{dx}{dt} = 2\,\sin(\pi x)$$

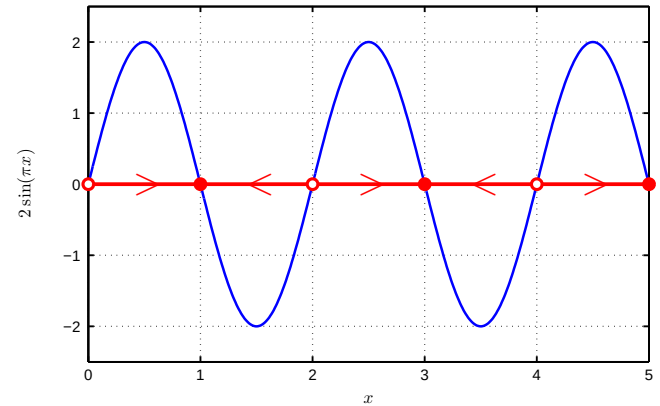
- The equilibria satisfy

$$2\,\sin(\pi x_e) = 0$$

- Thus, $x_e = n$, where n is any integer
- The sine function passes from negative to positive through $x_e = 0$, so solutions move away from this equilibrium
- The sine function passes from positive to negative through $x_e = 1$, so solutions move toward this equilibrium
- From the function behavior near equilibria
  - All equilibria of the form $x_e = 2n$ (even integer) are **unstable**
  - All equilibria of the form $x_e = 2n + 1$ (odd integer) are **stable**

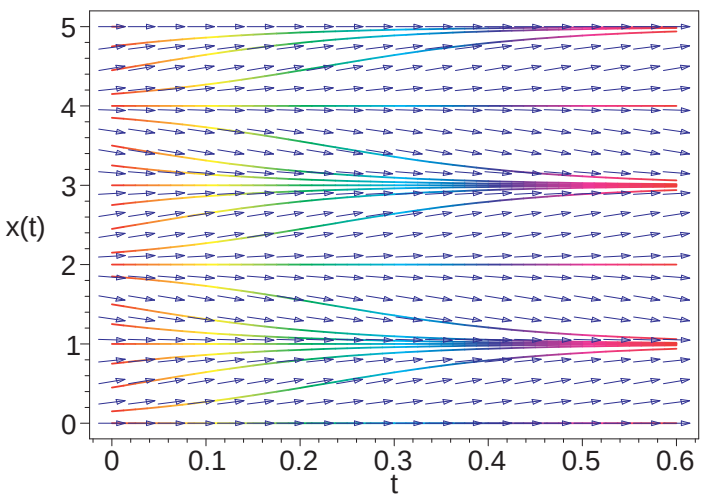
Example: Sine Function

Phase Portrait: Since $2\,\sin(\pi x)$ alternates sign between integers, the phase portrait follows below:



Example: Sine Function

Diagram of Solutions for Sine Model



Left Snail Model: Introduction

- The shell of a snail exhibits **chirality**, left-handed (sinistral) or right-handed (dextral) coil relative to the central axis
- The Indian conch shell, *Turbinella pyrum*, is primarily a right-handed gastropod [1]
- The left-handed shells are "exceedingly rare"
- The Indians view the rare shells as very holy
  - The Hindu god "Vishnu, in the form of his most celebrated avatar, Krishna, blows this sacred conch shell to call the army of Arjuna into battle"
- So why does nature favor snails with one particular handedness?
- Gould notes that the vast majority of snails grow the dextral form.

[1] S. J. Gould, "Left Snails and Right Minds," *Natural History*, April 1995, **10-18**, and in the compilation *Dinosaur in a Haystack* (1996)

Left Snail Model

- Clifford Henry Taubes [2] gives a simple mathematical model to predict the bias of either the dextral or sinistral forms for a given species
  - Assume that the probability of a dextral snail breeding with a sinistral snail is proportional to the product of the number of dextral snails times sinistral snails
  - Assume that two sinistral snails always produce a sinistral snail and two dextral snails produce a dextral snail
  - Assume that a dextral-sinistral pair produce dextral and sinistral offspring with equal probability
- By the first assumption, a dextral snail is twice as likely to choose a dextral snail than a sinistral snail
- Could use real experimental verification of the assumptions

[2] C. H. Taubes, *Modeling Differential Equations in Biology*, Prentice Hall, 2001.

Left Snail Model

Taubes Snail Model

- Let $p(t)$ be the probability that a snail is dextral
- A model that qualitatively exhibits the behavior described on previous slide:

$$\frac{dp}{dt} = \alpha p(1-p)\left(p - \frac{1}{2}\right), \qquad 0 \le p \le 1,$$

  where α is some positive constant
- What is the behavior of this differential equation?
- What does its solutions predict about the chirality of populations of snails?

Left Snail Model

Taubes Snail Model

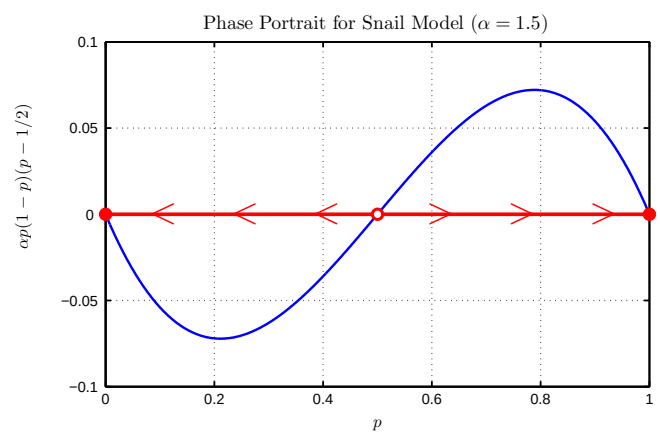
- This differential equation is not easy to solve exactly
- **Qualitative analysis** techniques for this differential equation are relatively easily to show why snails are likely to be in either the dextral or sinistral forms
- The snail model:

$$\frac{dp}{dt} = f(p) = \alpha p(1-p)\left(p - \frac{1}{2}\right), \qquad 0 \le p \le 1,$$

  - **Equilibria** are $p_e = 0, \frac{1}{2}, 1$
  - $f(p) < 0$ for $0 < p < \frac{1}{2}$, so solutions decrease
  - $f(p) > 0$ for $\frac{1}{2} < p < 1$, so solutions increase
  - The equilibrium at $p_e = \frac{1}{2}$ is **unstable**
  - The equilibria at $p_e = 0$ and 1 are **stable**

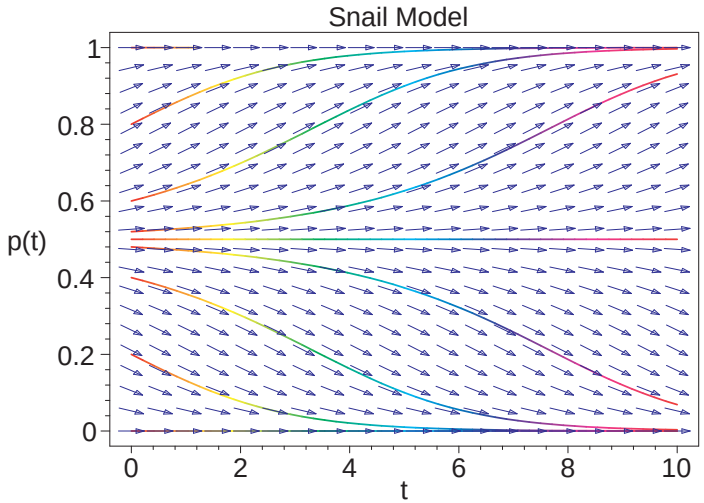
Left Snail Model

Phase Portrait: $\dfrac{dp}{dt} = \alpha p(1-p)\left(p - \dfrac{1}{2}\right)$



Left Snail Model 4

Diagram of Solutions for Snail Model



Left Snail Model 5

Snail Model - Summary

- Figures show the solutions tend toward one of the **stable equilibria**, $p_e = 0$ or 1
- When the solution tends toward $p_e = 0$, then the probability of a dextral snail being found drops to zero, so the population of snails all have the sinistral form
- When the solution tends toward $p_e = 1$, then the population of snails virtually all have the dextral form
- This is what is observed in nature suggesting that this model exhibits the behavior of the evolution of snails
- This does not mean that the model is a good model!
- It simply means that the model exhibits the basic behavior observed experimentally from the biological experiments

Pitchfork Bifurcation 1

Pitchfork Bifurcation

- **Bifurcations** are when behavior of the differential equation changes
- A **supercritical pitchfork bifurcation** has differing **numbers of equilibria** as a parameter changes
- Consider the differential equation:

$$\frac{dx}{dt} = \alpha x - x^3,$$

  where α can be positive, negative, or zero
- Find all equilibria
- Determine the stability of those equilibria as α changes
- For $\alpha = \pm 1$, sketch the phase portraits and show typical solutions in the x and t solution space

Pitchfork Bifurcation 2

For the differential equation:

$$\frac{dx}{dt} = \alpha x - x^3$$

- Find equilibria by solving

$$\alpha x_e - x_e^3 = 0 \qquad \text{or} \qquad x_e(\alpha - x_e^2) = 0$$

  - There is always an equilbrium at $x_e = 0$
  - If $\alpha < 0$, then $x_e = 0$ is the only equilibrium
  - If $\alpha > 0$, then there are **three equilibria** given by

$$x_e = 0, \pm\sqrt{\alpha}$$

Pitchfork Bifurcation 3

For the differential equation:

$$\frac{dx}{dt} = \alpha x - x^3$$

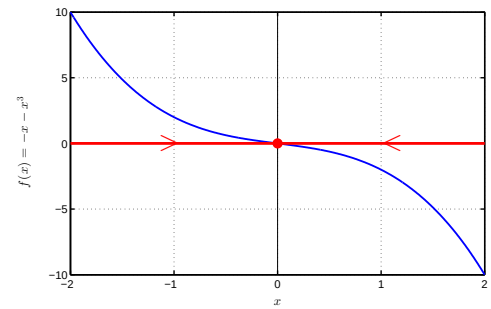
- When $x_e = 0$ is the only equilibrium, then it is **stable**
- When there are three equilibria, then $x_e = 0$ is an **unstable** equilibrium, while the equilibria, $x_e = \pm\sqrt{\alpha}$, are both **stable**
- As the parameter α changes from negative to positive, the differential equation's qualitative behavior changes
  - From having a single stable equilibrium at $x_e = 0$
  - To three equilibria with $x_e = 0$ becoming unstable and the other two being stable

Pitchfork Bifurcation 4

Phase Portrait: For $\alpha = -1$,

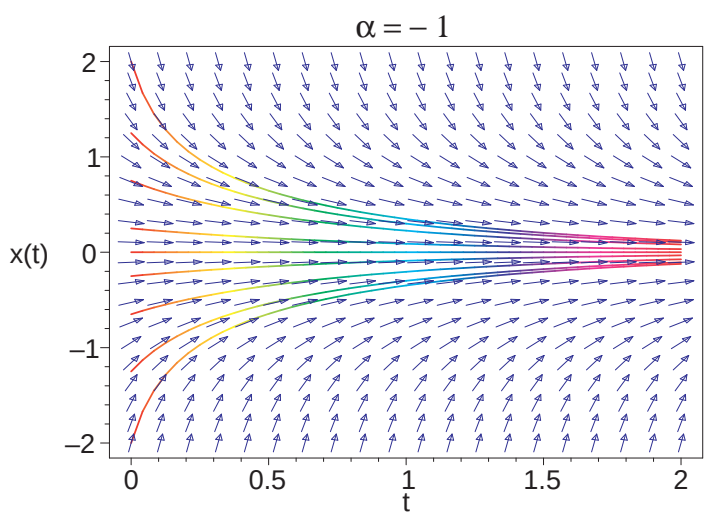
$$\frac{dx}{dt} = -x - x^3$$

The function is always decreasing, intersecting the x-axis at $x_e = 0$



Pitchfork Bifurcation 5

Diagram of Solutions: For $\alpha = -1$ with $\dfrac{dx}{dt} = -x - x^3$

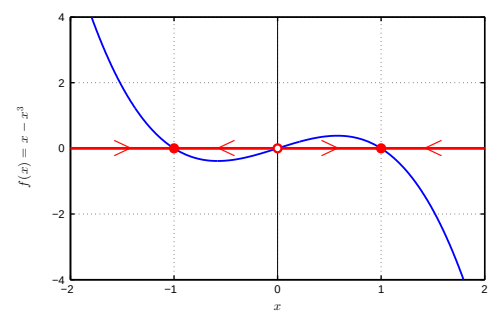


Pitchfork Bifurcation 6

Phase Portrait: For $\alpha = 1$,

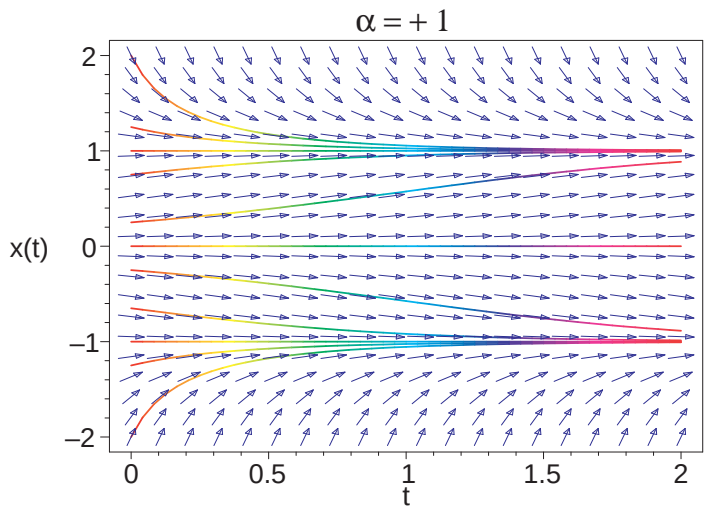
$$\frac{dx}{dt} = x - x^3$$

The function intersects the x-axis at $x_e = 0, \pm 1$



Pitchfork Bifurcation 7

Diagram of Solutions: For $\alpha = 1$ with $\dfrac{dx}{dt} = x - x^3$



Allee Effect 1

Thick-Billed Parrot: *Rhynchopsitta pachyrhycha*

Allee Effect 2

Thick-Billed Parrot: *Rhynchopsitta pachyrhycha*

- A gregarious montane bird that feeds largely on conifer seeds, using its large beak to break open pine cones for the seeds
- These birds used to fly in huge flocks in the mountainous regions of Mexico and Southwestern U. S.
- Largely because of habitat loss, these birds have lost much of their original range and have dropped to only about 1500 breeding pairs in a few large colonies in the mountains of Mexico
- The pressures to log their habitat puts this population at extreme risk for extinction

Allee Effect 3

Thick-Billed Parrot: *Rhynchopsitta pachyrhycha*

- The populations of these birds appear to exhibit a property known in ecology as the **Allee effect**
- These parrots congregate in large social groups for almost all of their activities
- The large group allows the birds many more eyes to watch out for predators
- When the population drops below a certain number, then these birds become easy targets for predators, primarily hawks, which adversely affects their ability to sustain a breeding colony

Allee Effect 4

Allee Effect:

- Suppose that a population study on thick-billed parrots in a particular region finds that the population, $N(t)$, of the parrots satisfies the differential equation:

$$\frac{dN}{dt} = N\left(r - a(N-b)^2\right),$$

where $r = 0.04$, $a = 10^{-8}$, and $b = 2200$

- Find the equilibria for this differential equation
- Determine the stability of the equilibria
- Draw a phase portrait for the behavior of this model
- Describe what happens to various starting populations of the parrots as predicted by this model

Allee Effect 5

Equilibria:

- Set the right side of the differential equation equal to zero:

$$N_e\left(r - a(N_e-b)^2\right) = 0$$

- One solution is the **trivial** or **extinction** equilibrium, $N_e = 0$
- When $\left(r - a(N_e-b)^2\right) = 0$, then

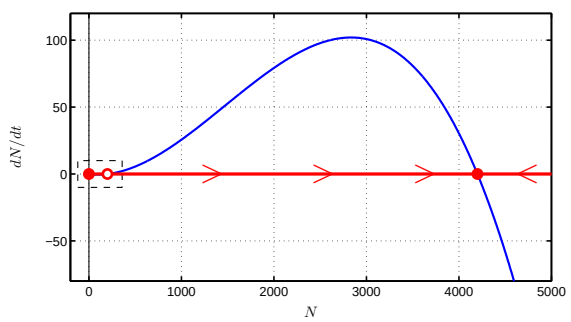
$$(N_e-b)^2 = \frac{r}{a} \qquad \text{or} \qquad N_e = b \pm \sqrt{\frac{r}{a}}$$

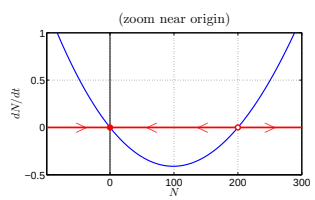
- Three distinct equilibria unless $r = 0$ or $b = \sqrt{r/a}$
- With the parameters $r = 0.04$, $a = 10^{-8}$, and $b = 2200$, the equilibria are

$$N_e = 0 \qquad N_e = 200 \qquad 4200$$

Allee Effect 6

Phase Portrait: Graph of right hand side of differential equation showing equilibria and their stability

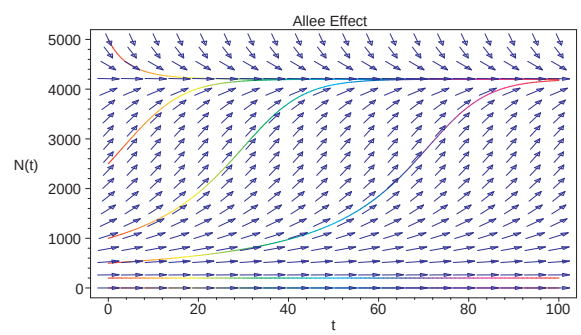


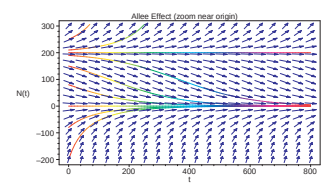


Allee Effect 7

Solutions: For

$$\frac{dN}{dt} = N\left(r - a(N-b)^2\right)$$





Allee Effect

Interpretation: Model of Allee Effect

- From the phase portrait, the equilibria at 4200 and 0 are stable
- The **threshold** equilibrium at 200 is unstable
  - If the population is above 200, then it goes to the **carrying capacity** of this region and reaches the stable population of 4200
  - If the population falls below 200, then this model predicts **extinction**, $N_e = 0$
- This agrees with the description for these social birds, which require a critical number of birds to avoid predation
- Below this critical number, the predation increases above reproduction, and the population of parrots goes to extinction
- If the parrot population is larger than 4200, then their numbers will be reduced by starvation (and predation) to the carrying capacity, $N_e = 4200$