Calculus: A Modeling Approach for the Life Sciences

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Preface

The science of biology is rapidly expanding with an increased need for more quantitative analysis of the data. Thus, mathematics and computers are becoming more important to researchers in biology. Biological examples are inherently complex, which complicates the understanding of how mathematical modeling relates to the biological problems. Many Calculus courses for biology majors use grossly simplified examples, which have resulted in students feeling that Calculus is irrelevant to their study of biology.

This text attempts to use more convincing examples. The emphasis of this text is the mathematical modeling of biological systems, showing how Calculus naturally arises in biological examples from classical and current research. Most sections begin with a biological model that motivates some aspect of learning Calculus. The example is followed by the mathematical theory required to analyze the biological problem and other related problems. Early in the text, least squares analysis of data is introduced so that experimental data from actual biological problems can be used to develop real mathematical models. By presenting real experimental data, this text shows the importance of mathematical modeling and its reliance on Calculus for students majoring in biology.

This text was inspired by the first semester of the Calculus for Biology sequence at San Diego State University. The material was originally developed for the web to supplement the weak texts used in that course, then it evolved to a more complete series of lecture notes, "Calculus for the Life Sciences." With the stronger emphasis on modeling and the need expressed by the faculty in the Department of Biology at San Diego State University for students to develop their computer skills, the course evolved to include a computer laboratory component along with the lectures. The related computer laboratories are available on the web (and will soon be tranformed into an accompanying supplement to this text). The authors believe that the computer component of this course is vital to the full understanding of the material and appreciation by the student of how mathematics and biology are becoming more entwined. Students have often returned telling us of the value of the computer skills that these labs have developed for their more advanced biology classes.

Because this text has come from a web-based course, some of the material is complemented by some java applets and animations on the web that could not appear in the printed book version. References to this material on the web, which provide additional hands on learning experiences, are designated by a small "java" figure on the left hand margin. Wherever this figure appears there is an explanation of what the applet is about, and a brief indication of how to use such an applet to get a better understanding of the material.

Applets or Animated GIFs

The Java Applets or Animated GIFs can be accessed from a master list located at the website:
www-rohan.sdsu.edu/~jmahaffy/courses/s00a/math121/lectures/java.html

Beside each java figure on the margin there is a title referring to the java applet on the web. A list of all the titles of the java applets with their corresponding website is noted above. Therefore, a student should, in a pretty straight forward manner, be able to refer to the specific applet used in the section. This website will be frequently updated and provided additional information that may help both instructors and students take better advantage of this text.

The authors want to first express their thanks to the Department of Biology at San Diego State University for their encouragement and contributions to the development of this text. Many of the faculty have provided examples that have been incorporated into the text and computer labs, which have helped provide the valuable connections needed by the students to better understand why they should learn mathematics for their major in Biology. Several of the faculty have been particularly supportive of the use of a computer laboratory to help these students learn mathematics and develop computer skills. Professor Roger Whitney in computer science was very encouraging and helped with the early stages of developing this course on the web, so deserves special credit for getting the first author to embark on this task.

The first author is especially thankful to Louise Wilson for her help with many of the applets developed for the webpage and her many hours of help proofreading the text on the webpages. He also is very appreciative of the work by Tal Polany for his web expertise and artistic abilities that made the current version of the webpage possible. Tal provided the fundamental layout of the webpage and designed many of the animated GIFs. This author was also helped by Catherine DeMarco, Treggon Owens, and many of the Biology students who have gone through the course.

We would particularly like to thank all the hard work and dedication of Ricardo Carretero-González for the presentation of this material in this text. His help for the display of figures and formatting of the text was invaluable to us.

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CHAPTER 1:

INTRODUCTION

Biology is one of the most rapidly expanding and diverse areas in the sciences. The problems encountered in Biology are frequently complex and often not totally understood. Mathematical models provide a means to better understand the processes and unravel some of the complexities. This gives a natural synergistic relationship between the two fields as research expands in the future. The mathematical tools provide ways of developing a better qualitative and quantitative understanding of some biological problems, while the biological problems often stretch the techniques that mathematicians must use to find solutions.

1 SO WHAT IS A MATHEMATICAL MODEL?

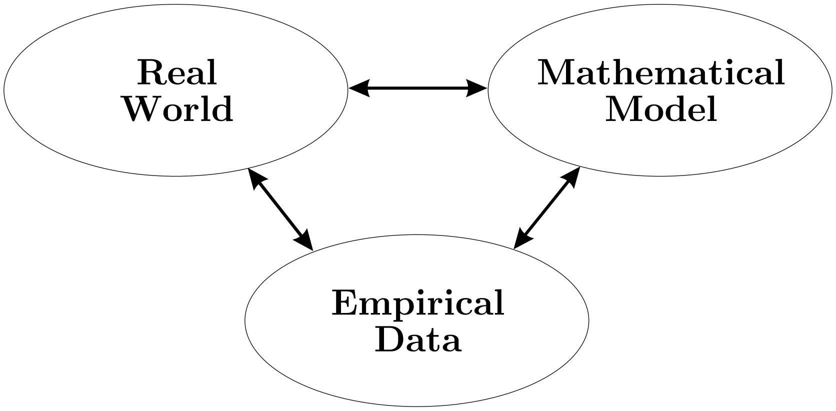

Figure 1: Diagram of the relationship of a mathematical model with the experimental data and the real world system the model represents.

A *mathematical model* is a representation of a real system. The essence of a good mathematical model is that it is simple in design and exhibits the basic properties of the real system that we are attempting to understand. The model should be testable against empirical data. The comparisons of the model to the real system should ideally lead to improved mathematical models. The model may suggest improved experiments to highlight a particular aspect of the problem, which in turn may improve the collection of data. Thus, modeling itself is an evolutionary process, which continues toward learning more about certain processes rather than finding an absolute reality. This use of mathematics is quite different from K-12 training in mathematics, where mathematics is treated as an absolute with exact answers.

Example 1 *Diabetes Mellitus*

An ongoing example of the modeling process is provided by *diabetes mellitus*. This is a metabolic disease which is characterized by too much sugar in the blood and urine. In a normal subject the β-cells in the pancreas, more specifically the islets of Langerhans, release insulin in response to increased levels of glucose in the blood, which results in the storage of this source of energy as glycogen in the liver. One form of the disease (Type I) has its onset in childhood and is caused by a failure of the β-cells to release insulin in response to blood glucose levels. It appears that this form of diabetes is caused by antibodies being formed that react with islet cells, then the subsequent autoimmune response selectively destroys the β-cells. Thus, insulin can no longer be produced. Another form (Type II) appears in adults (and increasingly among obese children). Some cases of Type II diabetes

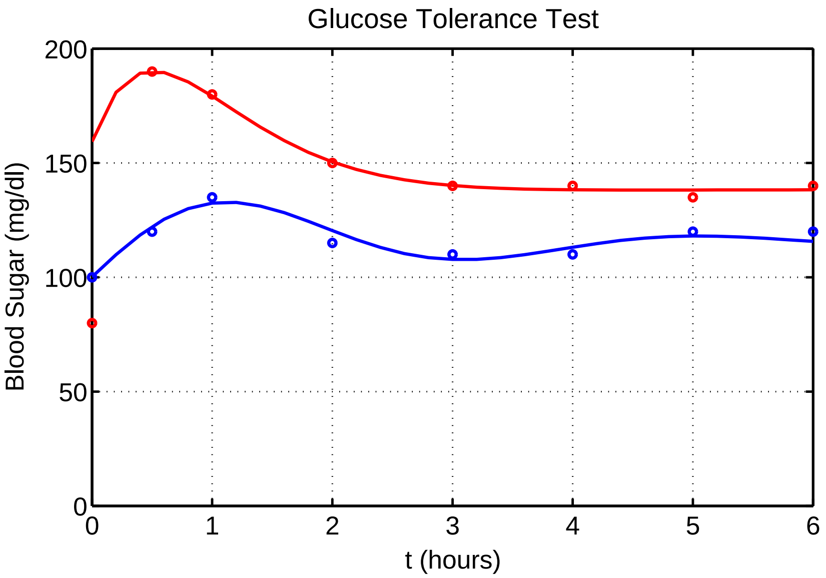

Figure 2: Glucose tolerance test applied to a normal subject and a diabetic subject [2].

also appear to be an autoimmune disease where the immune system mounts an attack on the β-cells, decreasing their ability to produce insulin, while other Type II diabetes cases may simply result from excessive body weight that overtaxes the ability of the β-cells to produce sufficient insulin. In either case the body loses its ability to regulate blood sugar, which can be potentially very dangerous.

One simple test for detection of diabetes is the Glucose Tolerance Test (GTT). For this test, a subject fasts for 12 hours, then is given a large quantity of glucose. For the next few hours, blood samples are drawn and blood glucose levels are measured. The graphs above show two subjects given this GTT. By fitting the data to a simple model by Ackerman *et al.* [1], the information from the model can indicate which subjects have diabetes. Both the biological test and the mathematical model are overly simplistic, so improved models and biological testing routines have been developed and continue to be developed.

Diabetes is treated by administration of insulin and regulation of diet by the patients. Biological research has improved our understanding of this disease, which has resulted in improved mathematical models for glucose metabolism. The mathematical models in turn are used to suggest better treatments, such as improved scheduling of insulin injections, which improve the quality of life of the patients suffering from this disease. (A complex model for simulation of insulin and dietary adjustment is available on the web[1].) Due to both new clinical (or experimental) studies and improved mathematical models, future treatments will certainly evolve to better regulate this metabolic problem in patients with diabetes. There are many websites available about diabetes. Some examples include ones on diagnosing diabetes[2], gestational diabetes[3], glucose blood testing[4], or homeostasis[5]. There are other mathematical models that have been developed to study the firing (hence release of insulin) by the β-cells. (For example, Arthur Sherman at NIH has a number of models and links to models of β-cells[6]). ◁

Example 2 *ATP Synthase*

One of the most important molecules in all living organisms is ATP synthase. Cells store chemical energy in two forms: as transmembrane electrochemical

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[1] www.2aida.org, last visited 03/08/04

[2] www.endocrineweb.com/diabetes/diagnosis.html, last visited 03/08/04.

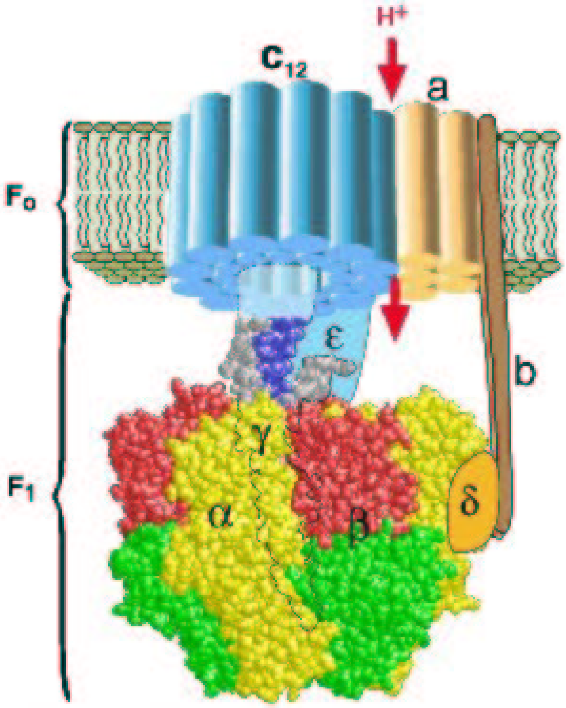
[3] www.medstudents.com.br/ginob/ginob4t1.htm, last visited 03/08/04.

[4] www.lifeclinic.com/focus/diabetes/glucoseTest.asp, last visited 03/08/04.

[5] pespmc1.vub.ac.be/HOMEOSTA.html, last visited 03/08/04.

[6] A. Sherman, mrb.niddk.nih.gov/sherman/, last visited 03/08/04.

gradients and in chemical bonds, particularly the gamma phosphate bond in adenosine triphosphate (ATP). In mitochondria, bacteria, and chloroplasts, the free energy stored in transmembrane electrochemical gradients is used to synthesize ATP from ADP and phosphate via the membrane-bound enzyme ATP synthase. ATP synthase can also reverse itself and hydrolyze ATP to pump ions against an electrochemical gradient. This molecule has been so optimized by evolution that there are few variations in its structure over the entire range of living organisms. Until recently, few details about the structure of this molecule and how it produced ATP were known. The standard texts still talk about how the forming and breaking of the high energy gamma phosphate bond as if it were a single event. Yet the incredibly high efficiency of this molecule (over 90%) could not be explained by physical laws of thermodynamics associated with the cleaving (or forming) of this phosphate from ATP.



H. Wang and G. Oster (1998). Nature 396:279-282.

Figure 3: A diagram of the ATP synthase by Wang and Oster (1998), Nature 396:279-282

A collaboration of many scientist from many fields, including some applied mathematicians, were required to learn the details of how this important molecular reaction occurs. Complicated molecular biology, x-ray crystallography, physics, and mathematical modeling combined to show how phosphate bond was formed in a series of 15 to 20 smaller steps to produce ATP in this highly efficient process. (A Nobel prize in 1997 for Chemistry was awarded to Paul D. Boyer, John E. Walker, and Jens C. Skou for some of the work.[7]) Fundamentally, the scientific discovery followed the diagram given above, where constant exchanges were needed between experimentalists and theoreticians to test that they were converging on the answer of the reality of a remarkable molecule that powers every living cell. For more on the modeling efforts on this important molecule, you might want to check the websites of George Oster[8] and Hongyun Wang[9]. ◁

2 REFERENCES

[1] E. Ackerman, L. Gatewood, J. Rosevear, and G. Molnar, Blood glucose regulation and diabetes, Chapter 4 in *Concepts and Models of Biomathematics*, F. Heinmets, ed., Marcel Dekker (1969), 131–156.

[2] E. Krimmel and P. Krimmel, *The low blood sugar handbook*, Franklin Publishers (1992), 67–69.

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[7] www.nobel.se/chemistry/laureates/index.html, last visited 03/08/04.

[8] G. Oster, cnr.berkeley.edu/~goster/home.html, last visited 03/08/04.

[9] H. Wang, nature.Berkeley.EDU/~hongwang/, last visited 03/08/04.

CHAPTER 2:

LINEAR MODELS

The basis for understanding Calculus is the concept of a straight line. Straight lines also provide the simplest mathematical models, *linear models*, for biological systems. This section provides a number of worked examples that should help the student work with and better understand straight lines. Straight lines are covered in standard algebra courses, so this should be review material. The material below covers the basic concepts for finding equations of lines, graphing lines, determining the points of intersection of two lines, conditions for two lines to be parallel or perpendicular, and several word problems that occur from biological models and measurement conversions.

1 CHIRPING CRICKETS AND TEMPERATURE

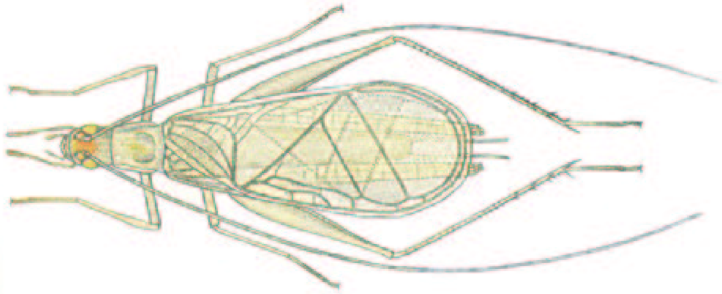


Figure 1: There is a linear relationship between the chirping of the *Oecanthus fultoni* and temperature.

For many years people have recognized a relationship between the temperature and the rate at which crickets are chirping. The folk method of determining the temperature in degrees Fahrenheit is to count the number of chirps in a minute and divide by 4, then add 40. In 1898, A.E. Dolbear [3] noted that "crickets in a field [chirp] synchronously, keeping time as if led by the wand of a conductor". In his paper, he appears to be the first person to write down a formula in a scientific publication, giving a linear relationship for the temperature based on the chirp rate of crickets. The mathematical formula that he gave is:

$$T = 50 + \frac{N - 40}{4}.$$

Does this formula of Dolbear match the folk method described above?

Many of the early papers [1] and [2] begin with the authors' fond memories of listening to snowy tree crickets, *Oecanthus fultoni*, in the late summer and early fall, then they dispute how synchronized the actual chirping is. However, the mathematical models are all very similar.

The graph in Figure 2 shows the data from C.A. Bessey and E.A. Bessey [2] on eight different crickets that they observed in Lincoln, Nebraska during August and September, 1897. It is apparent from these data that a fairly good estimate of the temperature is found by drawing a straight line through the points. This line would be a good model for finding the temperature outside based on the rate at which the crickets are chirping. The graph shows the model from the Bessey brothers and the Dolbear model based on the folk method.

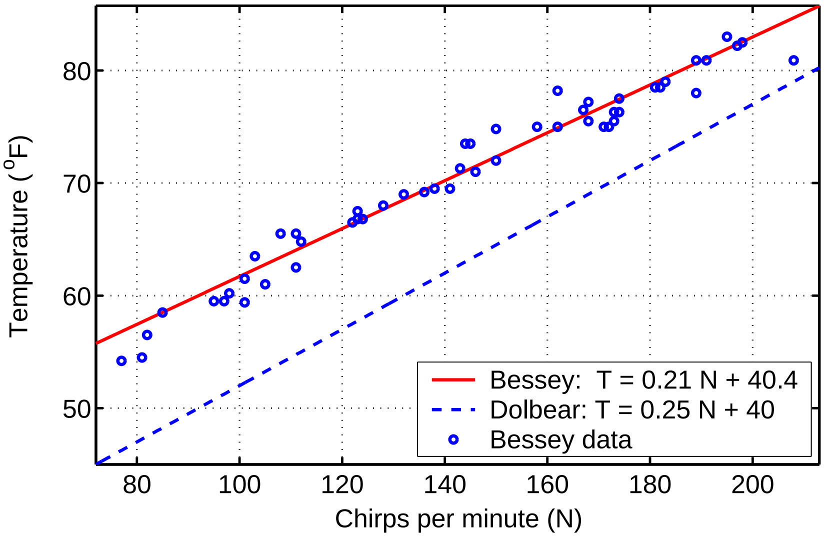


Figure 2: Experimental data of eight different cricket types observed by C.A. Bessey and E.A. Bessey [2] with its corresponding best linear approximation, and the linear model by Dolbear [3].

The line given by the Bessey brothers is the *least squares best fit* to the data they collected. (The actual formula that they presented is $T =$

$60 + (N - 92)/4.7$, which you can check reduces to the formula stated in the graph of Figure 2.) We will examine what a least squares best fit means in the next section.

2 DOLBEAR'S CRICKET EQUATION AS A LINEAR MODEL

The line that you found passing through the data creates a mathematical model for representing the temperature as a *function* of the rate at which snowy tree crickets chirp. Before studying this model for mathematical properties, we should ask a few questions about the biological model.

1. How well does the line that you found fitting the Bessey & Bessey data agree with the Dolbear model given above?
2. When can this model be applied from a practical perspective?
3. Over what range of temperatures is this model valid?
4. How accurate is the model and how might the accuracy be improved?

The answers to these questions should help you appreciate the complex relationship between the biology of the problem and the mathematical model. The answers that are given below are not complete, but should help you appreciate how one approaches mathematical modeling and a biological problem. Hopefully, this will give you a better appreciation of how mathematics is used and some of its limitations.

The first two questions are actually very biological in nature, and the mathematics play a very limited role. The comparison of the Dolbear formula to the linear model shows some discrepancies in the coefficients of the linear model. However, you should be asking the biological question about the organisms that were being studied. The differences in the mathematical formulae may very well be due to observations made on different species of crickets. However, if you believe that the two different observations are similar, then this model may be a good biological thermometer. From a practical perspective, this biological thermometer has limited use. The snowy tree crickets only chirp for a couple months of the year. Furthermore, they only tend to chirp at night when the temperature is above 50°F.

The last two questions provide important links between the process of mathematical modeling and the biological problem being studied. The range of validity in temperatures for the model gives the *domain* where we can use this model. Generally, you should limit the use of the mathematical model to points between the range where the data are collected (or possibly to intervals that are only slightly beyond the collected data points). For our cricket thermometer equation, we see that the data only allows its use between 50°F and 85°F. However, this temperature range is appropriate for evenings in Nebraska in August and September, which is where this particular thermometer is valid. Statistical analysis of the data improves the degree of accuracy of the mathematical model, but it appears that the folk model will probably give the temperature within a couple degrees Fahrenheit. The folk formula is less accurate than the model formed by data, but it is much more easily applied. So which technique are you more likely to use on a warm summer night talking to some friends?

Mathematically, we often use a linear least squares fit to find the best fit to the data. The next chapter of these notes will show you how to obtain this best straight line through the data, using the technique of *linear least squares* and later chapters will discuss more complicated models. The data could be better fit by a more complicated mathematical model, such as fitting a quadratic through the data. However, this may not be appropriate from either a biological or mathematical perspective, but that depends on the problem and the ability to deal with this is acquired through experience. The section below provides a review of straight lines and includes a number of important mathematical definitions.

3 EQUATIONS OF LINES

The most common form for the equation of a line is the *slope-intercept* form of the line.

The *slope-intercept* form of the line is

$$y = mx + b.$$

The variable x is the *independent variable*, and the variable y is the *dependent variable*. The *slope* is given by m, and the *y-intercept* is given by b.

It is important to note that the variables x and y are only used for convenience. When describing a mathematical model using a linear model, one often chooses variables that more closely match the objects being observed. The folk cricket equation given above can be written

$$T = \frac{N}{4} + 40.$$

As written, the independent variable is N, which is the rate that the crickets are chirping (number of chirps per minute). The temperature, T, is the dependent variable. The slope is 1/4, and the T-intercept is 40. The graph of this equation is the linear model labeled Dolbear in Figure 2.2. This graph does not pass through the data, but it is not very far removed from the data. Thus, it can still be considered an appropriate model for estimating the temperature.

A *graph* is a geometric representation of an equation in the *Cartesian plane*. The *independent variable* of the equation is measured along the *horizontal-axis*, while the *dependent variable* is measured on the *vertical-axis*. By drawing the set of ordered points satisfying the equation, a graphical representation of the equation is produced.

There are other useful forms of the line. If a line passes through the point (x_0, y_0) and has a slope of m, then the *point-slope* form for the equation of the line is most easily found.

The *point-slope* form of the line is

$$y - y_0 = m(x - x_0).$$

The variable x is the *independent variable*, and the variable y is the *dependent variable*. The *slope* is given by m, and (x_0, y_0) is a point on the line.

Any line is uniquely determined by two distinct points lying on the line. Given two points, the slope is defined to be the difference in the distance in the dependent variable divided by the difference in the independent variable (provided the latter is nonzero).

Given the two points (x_0, y_0) and (x_1, y_1), then the slope m is given by:

$$m = \frac{y_1 - y_0}{x_1 - x_0}.$$

Below are examples to illustrate the definitions given above and help understand how to find equations of a line.

Example 1 Find the equation of a line with a slope of 2, passing through the point $(3, -2)$. What is the y-intercept?

Solution: From the point slope form we obtain the equation:

$$\begin{aligned} y-(-2) &= 2(x-3) \\ y+2 &= 2x-6. \end{aligned}$$

This reduces to the equation

$$y = 2x - 8,$$

so the y-intercept is -8. ◁

Example 2 Find the equation of a line passing through the points $(-2, 1)$ and $(3, -2)$.

Solution: The slope is given by

$$m = \frac{-2-1}{3-(-2)} = -\frac{3}{5}.$$

Thus, the point slope equation of the line is given by: $y - y_0 = m(x - x_0)$, so that

$$\begin{aligned} y-1 &= -\frac{3}{5}(x+2) \\ y &= -\frac{3}{5}x - \frac{1}{5}. \end{aligned}$$

Note that using either point, $(-2, 1)$ or $(3, -2)$, will yield the same linear equation. ◁

3.1 PARALLEL AND PERPENDICULAR LINES

The slopes of lines determine whether two lines are parallel or perpendicular.

Consider two lines given by the equations:

$$y = m_1 x + b_1 \quad \text{and} \quad y = m_2 x + b_2.$$

The *two lines are parallel* if the slopes are equal, so

$$m_1 = m_2,$$

and the y-intercepts are different. (If $b_1 = b_2$, then the lines are the same.)

It is clear that two lines that are parallel must have the same slope. Another condition gives two lines being perpendicular.

The *two lines are perpendicular* if the slopes are negative reciprocals of each other, that is

$$m_1 m_2 = -1.$$

Example 3 Find the equation of the line perpendicular to the line $5x + 3y = 6$, passing through the point $(-2, 1)$. Sketch a graph of both lines.

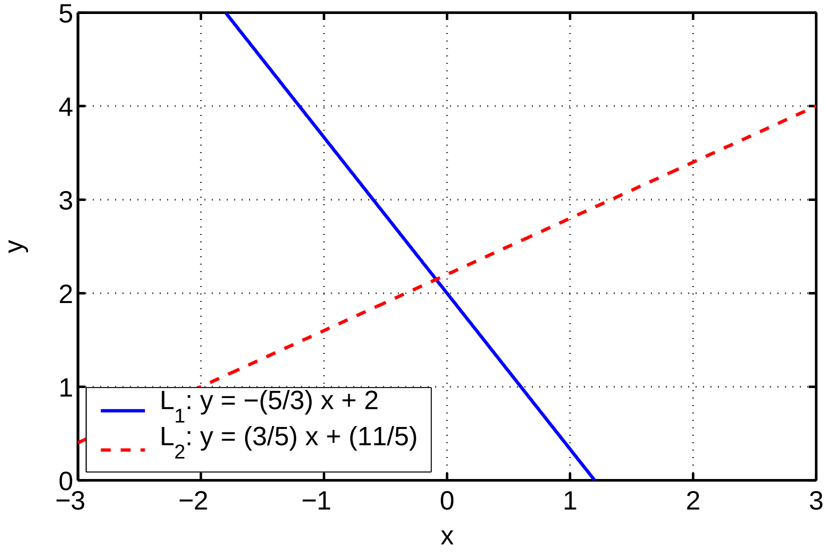


Figure 3: Graph of Example 3, where the slope of line L_1 is $m_1 = -5/3$. While the slope of line L_2 is $m_2 = 3/5$, such that $m_1 = -1/m_2$.

Solution: Converting this line (Line 1) to the slope intercept form, we obtain the equation:

$$\begin{aligned} 3y &= -5x + 6 \\ y &= -\frac{5}{3}x + 2. \end{aligned}$$

The slope of the perpendicular line is given by the negative reciprocal of that given above:

$$\frac{3}{5}.$$

The point slope equation of the line (Line 2) is given by

$$\begin{aligned} y-1 &= \frac{3}{5}(x+2) \\ y &= \frac{3}{5}x+\frac{11}{5}. \end{aligned}$$

(See Figure 3 for the sketch of the lines.) ◁

Linear – Slope and Intercept

You may want to use this applet to develop a better geometric sense of how lines vary as the slope and intercept are changed.

3.2 INTERSECTION OF LINES

Whenever two lines are NOT parallel, then they must intersect at some point in the Cartesian plane. The point of intersection is a unique point that satisfies both equations simultaneously.

Example 4 Find the intersection of the line parallel to the line $y = 2x$ passing through $(1, -3)$ and the line given by the formula $3x + 2y = 5$.

Solution: The first line is parallel to $y = 2x$, so has a slope $m = 2$. This line is found using the point slope equation:

$$y + 3 = 2(x - 1) \quad \text{or} \quad 2x - y = 5.$$

The two lines intersect when both equations are satisfied simultaneously. The expression for y from the first line can be substituted into the formula for the second line giving

$$3x + 2(2x - 5) = 5,$$

or

$$7x = 15, \quad \text{or} \quad x = \frac{15}{7}.$$

Substituting the x value into the first line equation gives

$$y = 2\left(\frac{15}{7}\right) - 5 = -\frac{5}{7}.$$

Thus, the point of intersection is given by

$$\left(\frac{15}{7}, -\frac{5}{7}\right).$$

Figure 4 shows the graph of these two intersecting lines. ◁

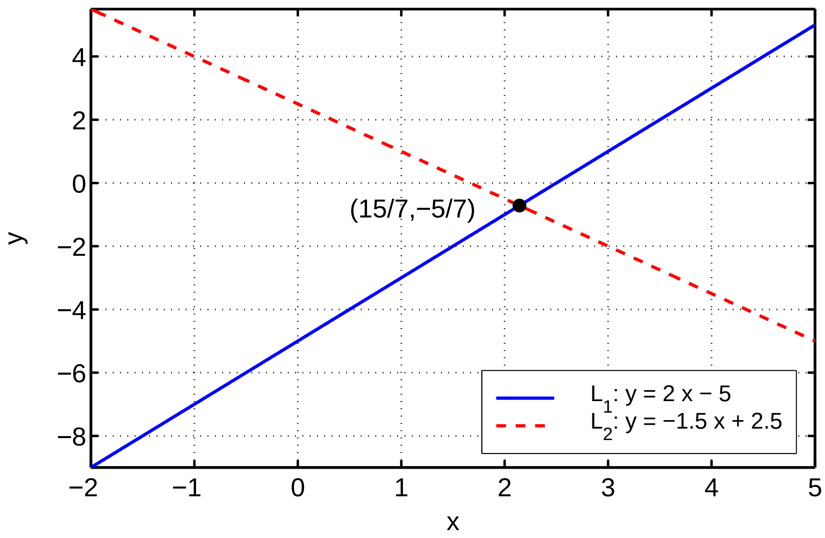


Figure 4: Example of the resulting graph from the applet Linear – Line Intersection. This figure uses the lines from Example 4.

Linear – Line Intersection

There is an applet on the webpage that allows you to find the intersection of any two lines. Enter different values of m and b of two different lines, and the applet finds the point of intersection. Use the **refresh** button after you have put in the values of slope and intercept for the two lines.

4 METRIC SYSTEM CONVERSION

All of the conversions for measurements, weights, temperatures, etc. are linear relationships. Most of the conversions only require a change in the slope as they agree at zero, but this is not the case for temperature. Below we use the information above on straight lines to determine a formula for finding the temperature in degrees Celsius as a function of the temperature in degrees Fahrenheit.

The United States is one of the few countries in the world that uses the Fahrenheit scale for temperature. The freezing point of water is 32°F and 0°C, so take $(f_0, c_0) = (32, 0)$. The boiling point of water is 212°F and

100°C (at sea level), so take $(f_1, c_1) = (212, 100)$. The slope is computed as follows:

$$m = \frac{100 - 0}{212 - 32} = \frac{5}{9}.$$

Thus, the point-slope form of the line gives

$$c - 0 = \frac{5}{9}(f - 32)$$

or,

$$c = \frac{5}{9}(f - 32).$$

The above formula takes any temperature f in Fahrenheit and converts to c in Celsius.

Linear – Unit Conversion

You can use these JavaScript programs to find a number of transformations from one set of units to another. The underlying codes for all of these conversions are *linear relationships.*

Below we provide some of the more common conversions that are needed.

Length Conversions

12 inches = 1 foot
3 feet = 1 yard
5280 feet = 1 mile
2.540 cm = 1 inch
1 meter (m) = 3.281 ft
100 cm = 1 m
1000 mm = 1 m
10^6 μm = 1 m
1000 m = 1 km

Weight Conversions

1 pound = 16 ounce
1 kg = 2.2046 lb
1000 gram (g) = 1 kg

Volume Conversions

1 pint = 16 fluid ounces
1 gallon = 8 pints
1 gallon = 3.785 liters
1000 ml = 1 liter (l)

Example 5 *Linear – Unit Conversion Example*

As an example of how you can use the javascript mentioned above to find a linear relationship, suppose that you want a formula to find the weight in pounds given the weight in kilograms.

Solution: By placing a 1 in the category of kilograms, you find that each kilogram is 2.2046 pounds. Thus, the linear relationship is simply 2.2046 times the weight in kilograms. If we let p be the weight in pounds and k be the weight in kilograms, the relationship is given by

$$p = 2.2046k.$$

◁

Example 6 *Weight Units Conversion*

Find the weight of a 175 **pound** man in **kilograms**.

Solution: Since **1** kg = **2.2046** lb,

$$175\text{lb}\left(\frac{1\text{kg}}{2.2046\text{lb}}\right) = 79.4\text{kg}.$$

◁

Example 7 *Velocity Units Conversion*

Suppose a ball is thrown at a speed of 95 **miles per hour**. Find the speed of this ball in meters per second.

Solution: Since **1** mile = **1609.3** meters and since there are 3600 **seconds** in **1**hour,

$$\left(95\frac{\text{mi}}{\text{h}}\right)\left(\frac{1609.3\text{m}}{1\text{mi}}\right)\left(\frac{1\text{h}}{3600\text{s}}\right) \approx 42.47\text{m/s}.$$

◁

Linear – Unit Conversion

You may use the conversion javascript to check your answers.

5 JUVENILE HEIGHT

In Table 1 we show average juvenile height as a function of age [4].

Age	1	3	5	7	9	11	13
Height (cm)	75	92	108	121	130	142	155

Table 1: Average juvenile height as a function of age [4].

The height h, is graphed as a function of age a. The data from Table 1 are shown in Figure 5. It is easy to see that the data almost lie on a line, which suggests a *linear* model.

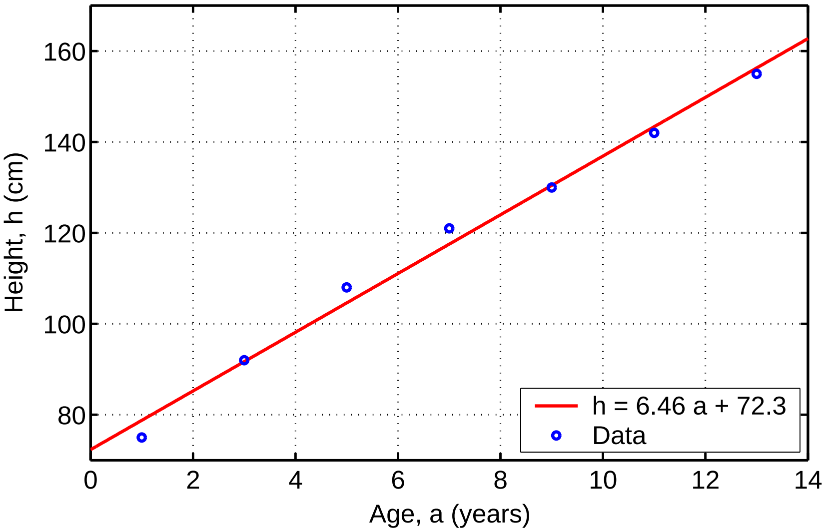


Figure 5: Graph of line that best fits the data given in Table 1 for the height of a child with respect to his/her age.

Line – Height

This Java applet allows you to adjust the coefficients of the linear model. Change the coefficients of the equation of the line in the applet until the line, representing the height as a function of age, fits the data. This line would be a good model for finding the average height of a child for any age between one and thirteen.

The line that best fits the data above is given by

$$h = ma + b = 6.46a + 72.3,$$

(see Figure 5) where, $m = 6.46$ is the slope and $b = 72.3$ is the h-intercept. The next chapter will explain finding the linear least squares best fit or linear regression to the data.

From a modeling perspective, it is often valuable to place units on each of the coefficients or variables in the equation. In an equation the units must always match. The height, h, from our data has units of cm, so both ma and the intercept b must have units cm. Since the age, a, has units of years, it follows that the slope, m, has units of cm/year. From the units it is easy to see that the slope is the rate of growth. (This idea of rate of growth will occur regularly in this course!).

The line above gives a mathematical model for growth of the average child. With this mathematical model, what type of questions can you answer? See if you can answer the following questions.

1. What is the average height of an eight year old?
2. What height does the model predict for a newborn baby?
3. If a six year old child is 110 cm, then estimate how tall she will be at age 7.

Answers:

1. The model predicts that the average eight year old will be 124 cm, which is found by setting $a = 8$ in the model.
2. The height intercept represents the height of a newborn, so this model predicts that a newborn would be 72.3 cm. However, this is outside the range of the data, which makes its value more suspect.
3. The model indicates that the growth rate is about 6.5 cm/*year*, so the six year old should grow about 6.5 cm and be 116.5 cm at age 7 though the average 7 year old as predicted by the model would be 117.5 cm.

What are some of the limitations and how might the model be improved?

The most obvious limitation is that this linear model would certainly not extend much beyond the ages listed in Table 1. (You would not expect the average 20 year old to be 201.5 cm as the model predicts.) Thus, the domain of this function is restricted to some interval around $1 \le a \le 13$.

Let us examine the questions above to see if we might derive better estimates. A better prediction of average eight year olds would be to average the heights of seven and nine year olds (125.5 cm). This is known as a local analysis, meaning that approximating a function is always better by using nearby information. Similarly, we might improve our estimate on the length of a newborn by using only the data given for one and three year olds (66.5 cm). As we study Calculus more, we will see that it is this local study of growth rates that is of greatest interest. The answer to the third question is about as good as we can do with the given information. If you had more data on the individual child, you might be able to predict her height better from her history than using the history of this average set of children.

There are several improvements you might want in a model like this. (Recall that models are only a window on the real world and usually can be improved.) The model is an average of juveniles indicating that the data have both sexes included, and our experience suggests that growth rates for girls and boys differ. Thus, you might want to split the data according to sex. Close inspection of the data shows that there is a faster growth rate between 0 and 5, and then again between 9 and 13, which agrees with the common idea that growth occurs in spurts. You might improve the model to include this information by using something other than a straight line to fit the data. However, you must consider how much is gained by a more complicated model.

6 WORD PROBLEMS

Example 8 *White Sea Urchins*

The growth curve in this chapter shows that over a short period of time, using a straight line to estimate growth is quite reasonable. Suppose that a population of **white sea urchins** (*Lytechinus pictus*) has a mean diameter of 28 mm at the beginning of June (June 1) and 33 mm at the beginning of July (July 1). Estimate the mean diameter for the population of *Lytechinus pictus* on June 20, July 10, August 1, and August 15. Which estimates do you trust more and why?

Solution: Let the first day of June be defined as $t = 0$. Since there are thirty days in June, we can assume two data points, $(0, 28)$, and $(30, 33)$, where t corresponds to the number of days, and d corresponds to the mean diameter in mm. Assuming that there is a linear relationship between time, t, and diameter, d, we can find the equation of the line that passes through these two points. Calculating the slope:

$$m = \frac{33 - 28}{30 - 0} = \frac{1}{6}.$$

Using the point slope equation we obtain

$$d - 28 = \frac{5}{30}(t - 0)$$

or

$$d = \frac{1}{6}t + 28.$$

Note that b, the d-intercept, is essentially the initial diameter measurement. The slope m must then be the growth rate. Using the above linear relation-

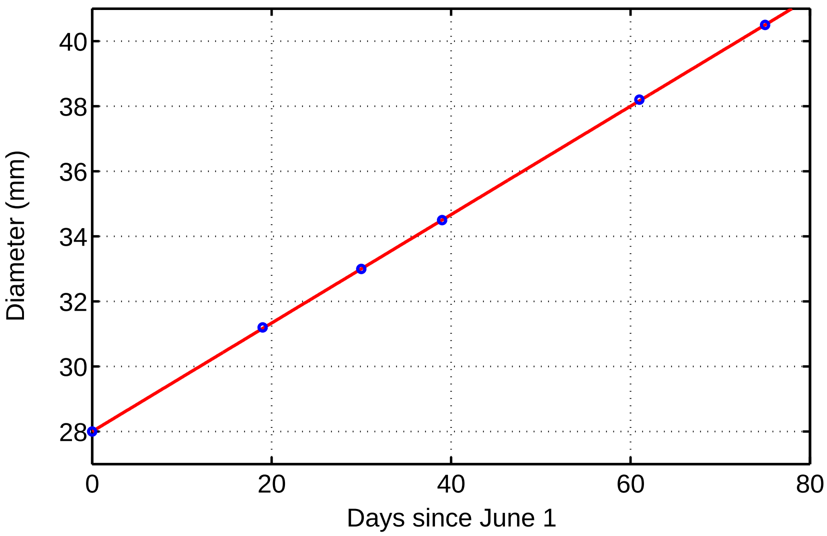


Figure 6: Linear growth of the *Lytechinus pictus* (white sea urchins).

ship, we can assume that the dates June 20, July 10, August 1, and August 15 correspond to the points $(19, 31.2)$, $(39, 34.5)$, $(61, 38.2)$, and $(75, 40.5)$, respectively. The estimate for June 20 is probably the most accurate because it falls between the two measurements actually taken. Also, recall that growth estimates are more accurate over shorter time intervals. ◁

Example 9 *Scuba Diver*

The pressure of air delivered by the regulator to a Scuba diver varies linearly with the depth of the water. When the diver is at 33 ft, the regulator delivers 29.4 **psi** (pounds/square inch), while at 66 ft, the regulator delivers 44.1 psi. Find the pressure of air delivered at the surface 0 ft, at 50 ft, and at 130 ft (the maximum depth for recreational diving).

Solution: From the measurements taken, we can assume the two data points $(33, 29.4)$, and $(66,44.1)$, where d corresponds to the depth in feet, and p corresponds to the regulator pressure in psi. Calculating the slope:

$$m = \frac{44.1 - 29.4}{66 - 33} = \frac{14.7}{33} \approx 0.445.$$

The equation of the line is then:

$$\begin{aligned} p - 29.4 &= 0.445(d - 33) \\ p &= 0.445d + 14.7. \end{aligned}$$

Therefore, using the linear relationship, we find that at the surface $d = 0$, the air pressure is 14.7 psi. This calculation can be represented as a point, $(0, 14.7)$. For depths of $d = 50$ ft and 130 ft, we obtain the points $(50, 36.95)$, and $(130, 72.55)$, respectively. See Figure 7 for a graphical representation. ◁

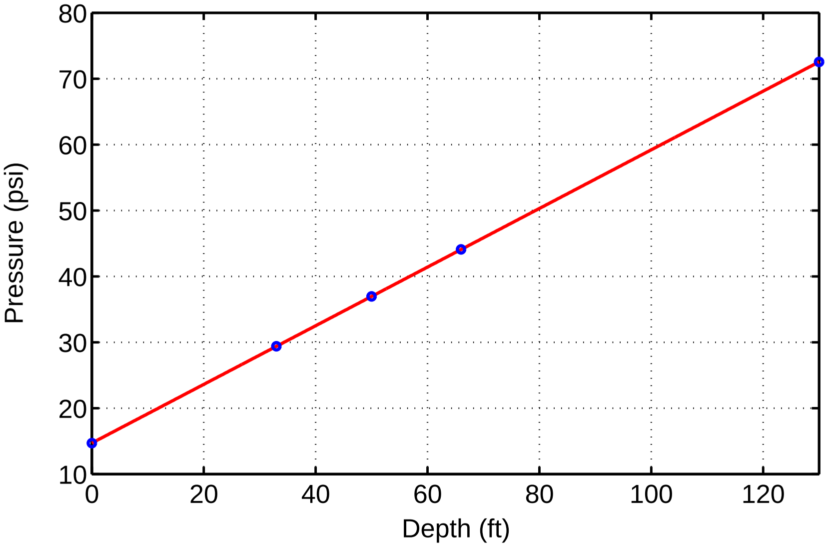


Figure 7: The pressure of the air expelled from a scuba diver regulator linearly increases with depth.

7 EXERCISES

1. $y = 2 - 5x$
2. $y = \frac{2x-1}{5}$
3. $x - y = 2$
4. $y = \frac{1}{3}(x+2)$
5. $-5y + 2x = 9$
6. $y = \frac{12}{48}$

Find the equations of the following lines:

7. Slope is $\frac{1}{2}$; passing through the origin.

8. Slope is $-\frac{1}{3}$; $(2, -3)$ on line.

9. Slope is 0; $(7, 4)$ on line.

10. $(2, -1)$ and $(3, -1)$ on line.

11. $(5, -3)$ and $(-1, 3)$ on line.

12. y-intercept is 2 and $(-2, 3)$ is on line.

Find the equations of the following lines:

13. Parallel to $y = -2x + 1$; $(\frac{1}{2}, 5)$ on line.

14. Parallel to $3x + y = 7$; (-1, -1) on line.

15. Parallel to $5x + 2y = -4$; (0, 17) on line.

16. Parallel to $3x - 6y = 1$; (1,0) on line.

17. Passing through (3,2) perpendicular to $4x - 3y + 2 = 0$.

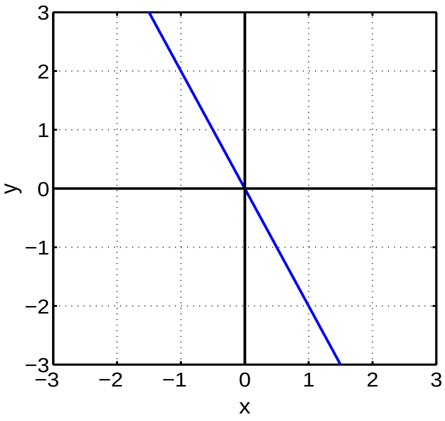
18. Find the equations of the lines through the origin that are parallel and perpendicular to the line $y = 2 - 3x$.

19. Consider the line $y = 2x - 1$. Find the equations of a line parallel to this line passing through the point (2,-1), and a line perpendicular to this line passing through the origin. Sketch a graph of all three lines.

20. Find the equation of the line passing through the points $(-1, 2)$ and $(2, 0)$. What are the slope and y-intercept for this line? Graph the line.

Write the equation of the line for the following graphs:

2



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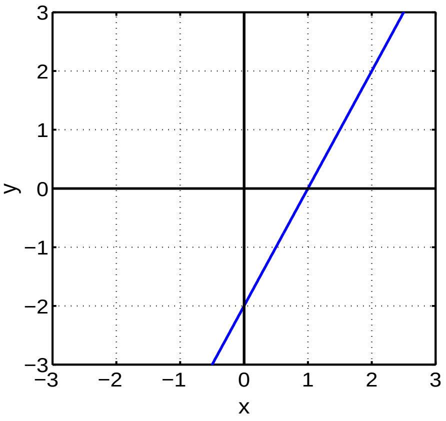

23. Assuming that water has a density of 1gm/cm^3 and that the Moon, a sphere, has 3.4 times the density of water with a radius of 1700km, find the mass of the Moon in kg. The volume of a sphere is given by $V = \frac{4}{3}\pi R^3$. (Note that 1cm = 10^{-2}m, 1km=1000m, and 1kg = 10^3gm.)

24. Find a formula for converting the temperature in Celsius, c, into a temperature in Fahrenheit, f.

25. D.J. Borror and D.M. Long write in their book *An Introduction to the Study of Insects* "The snowy tree cricket, *Oecanthulus fultoni*, a shrub inhabitant, chirps; its chirping is at a very regular rate, which varies with temperature; 40 added to the number of its chirps in 15 seconds gives a good approximation of the temperature in degrees Fahrenheit." Transform this statement into a mathematical model. Sketch the graph.

26. The independent variable is usually the causative variable. Since the rate of chirping of the crickets , N, is determined by the temperature, T, the independent variable should be the temperature. Find the linear cricket equation with N depending on T. This is also known as the inverse equation.

27. Most of the world uses the metric system. Convert the following scenario into one that someone from a metric based country could better understand. It is a beautiful morning with a temperature of 75°F. We travel 5 miles to a beautiful place to take a dive. The water temperature is 65°F with a breeze of 15 miles per hour. We swim 400 yards out to our dive spot where we submerge to a depth of 50 feet. Among the animals that we see are 5 inch abalone, 14 inch lobsters, 2 inch banded gobies, and a 4 foot leopard shark. At the end of the dive we surface 150 yards from shore in 15 feet of water. My tank gauge registers 700 psi (pounds per square inch) of air remaining. (Note that metric countries often use SCUBA gauges in kg/square cm.)

28. Convert this statement from someone in Canada into English units for someone in the United States. It is a beautiful day to go cross-country skiing as the temperature is -8°C, so I packed a 4 kg pack, including 2 liters of water. I travelled 70 kilometers North to the Laurentians where the elevation is about 400 meters. The temperature in the mountains was perfect green wax conditions with -14°C and a breeze of 25 km/hour. The trail traversed 17 km of maple forests with 40 cm diameter trees over an expanse of 30 km^2.

29. The lecture notes gave the average heights of five and seven year olds as 108 cm and 121 cm, respectively. Use these data to estimate the average height of a six year old. What is the average rate of growth for children these ages in cm/yr?

30. In Section 5, we saw the average height of a child satisfies the equation:

$$h = 6.46a + 72.3,$$

where h is the height and a in the age of the child. Find the average height of a six year old using this equation. Is this estimate better or worse than the estimate in Problem 29 and why?

31. Use the equation in Problem 30 for height of a child. If your daughter is 135 cm at age nine, then what does the model predict her height to be at age ten? If she is 160 cm at age 13, then what does the model predict her height to be at age 15? Which of these estimates is better and why?

32. The table below shows growth of a puppy. Find and graph the equation of the line for M as a function of a. Show the data points on the graph. What is the slope of the line and interpret the M-intercept?

Age (a)	Mass (M)
1 week	1.5 kg
2 week	2.1 kg
4 week	3.3 kg
8 week	5.7 kg

33. For a range of values, the absorbance A read from a spectrophotometer varies linearly with the concentration of nickel (II), N. (The measurement is made for the red-colored nickel dimethylglyoximate at 366 nm.) If the spectrophotometer is not carefully calibrated to zero for the reference signal, then one needs to use the formula

$$A = kN + b,$$

for some constants k and b.

a. Suppose that a sample with 0.02 mg/ml of nickel (II) gives an absorbance of 0.26 and one with 0.04 mg/ml of nickel (II) gives an absorbance of 0.44. Find the values for k and b.

b. Find the absorbance for a sample with 0.035 mg/ml of nickel (II).

c. Find how much nickel (II) is in a sample that gives an absorbance of 0.31.

34. For a gas kept at a constant volume, the pressure P depends linearly on temperature T. Thus, we can write the equation

$$P = kT + b,$$

for some constants k and b.

a. Suppose we run an experiment and find that when $T = 0°\text{C}$, the pressure $P = 760$ mm of Hg. Then when $T = 100°\text{C}$, the pressure $P = 1040$ mm of Hg. Find the constants k and b for the equation above.

b. Absolute zero can be approximated finding where the pressure $P = 0$. Find the temperature in °C for absolute zero from the data points (and the equation above).

35. The level of CO_2 in parts per million (ppm) at Mauna Loa Observatory was found to be 325.3 in 1970 and 338.5 in 1980. Assume the level of CO_2 is linear for some range of dates.

a. Find the equation of the line giving the concentration of CO_2 as a function of the date. Put this equation in slope-intercept form. (Use the date for the independent variable.)

b. Use this equation to estimate the level of CO_2 in 2000 and 1950. Does the model make sense for predicting the level of CO_2 at the time of the Plymouth colony in 1620?

36. The improvement in running events has been almost linear over the last century. John Paul Jones (USA) held the world record for the mile in 1913 with a time of 4:14.4 (254.4 sec). More recently, Sebastian Coe (Great Britain) set the world record in 1979 with a time of 3:49.0 (229.0 sec).

a. Find the equation of the line giving the world record time (in sec) as a function of the date. Put this equation is slope-intercept form.

b. Use this equation to estimate when the 4 minute mile occurred. (It was actually broken by Roger Bannister in 1954 with a time of 3:59.4).

c. Use your line to predict the world record time of the mile in the year 2000. Give your time in minutes and seconds.

8 REFERENCES

[1] H.A. Allard, The chirping rates of the snowy tree cricket (*Oecanthus fultoni*) as affected by external conditions, *Canadian Entomologist* (1930) **52**, 131–142.

[2] C.A. Bessey and E.A. Bessey, Further notes on thermometer crickets, *American Naturalist* (1898) **32**, 263–264.

[3] A.E. Dolbear, The cricket as a thermometer, *American Naturalist* (1897) **31**, 970–971.

[4] David N. Holvey, editor, *The Merck Manual of Diagnosis and Therapy* 15^{th} ed., Merck Sharp & Dohme Research Laboratories, Rahway, NJ, (1987).

CHAPTER 3:

LEAST SQUARES ANALYSIS

In the first chapter we showed one of the simplest of mathematical models, which is relating one variable to another using a straight line or linear relationship. Often this is a reasonable approximation to biological data over a limited domain. This chapter examines the most common technique for fitting a straight line to data known as a *linear least squares best fit* or *linear regression*. (The term regression comes from a pioneer in the field of applied statistics who gave the least squares line this name because his studies indicated that the stature of sons of tall parents reverts or regresses toward the mean stature of the population.)

1 FINDING THE C PERIOD FOR E. COLI

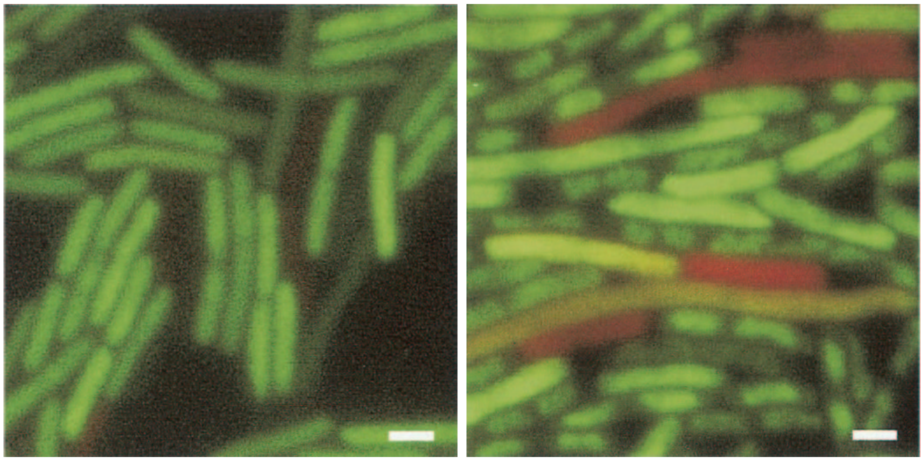

Figure 1: Growth and division of a population of *E. coli*

The bacterium *Escherichia coli* is capable of very rapid proliferation. Under ideal growing conditions, these bacteria can divide every **20 minutes**. Its genetic material is organized on a large loop of DNA (3,800,000 base pairs) that is replicated in two directions, starting from a site called *oriC* and terminating about halfway around the loop. Bacteria differ from eukaryotic organisms (most commonly studied in your first course in biology) in their replication cycle. Biologists denote the time for the DNA to replicate as the *C period* and the time for the two loops of DNA to split apart, segregate, and form two new daughter cells as the *D period.* The C period is often **35-50 minutes** and the D period is over **25 minutes**, so the combined time for the DNA to replicate and segregate (C + D) can be more than twice the time it takes for the cell to divide. Thus, the beginning of the C period (called the initiation of DNA replication) must occur several cell cycles in advance for rapidly growing cultures of bacteria, and multiple DNA replication forks are advancing at the same time to prepare for future cell divisions. There can be as many as 8 oriCs in a single *E. coli* bacterium because of this overlap of activity in the replication process. In contrast to eukaryotic cells, which have a single DNA replication event (*S phase*) that is followed by a distinct mitotic event (*M phase*) separated by growth phases (G_1 and G_2), prokaryotic cells allow DNA replication processes to operate in parallel to allow for very rapid growth and division.

Least Squares – E. coli

This movie shows a schematic for a rapidly dividing *E. coli* with multiple *oriC*s. (See references [1] and [3] below for more information.)

Since rapidly growing cultures of *E. coli* are continually replicating DNA, a pulse label of radioactive thymidine can be used (along with several drugs to halt initiation of replication and cell division) to determine the length of the C period. Below are some data from the laboratory of Professor Judith Zyskind (at San Diego State University) measuring the radioactive emissions, c in counts/min (**cpm**), from a culture of *E. coli* that have been treated with drugs at $t = 0$, then pulse labeled at various times following the treatment.

t (min)	10	20	30	40
c (cpm)	7130	4580	2420	810

We would like to estimate the C period using a simple linear model,

$$c = at + b.$$

(The actual modeling process requires a more complicated mathematical model using integral Calculus.) The t-intercept gives an approximate value to the C period for this culture of *E. coli.*

Least Squares – C-period

Adjust the slope, a, and the intercept, b, in this applet to find the minimum value of $J(a,b)$ (properly defined in the following chapter), which gives the least squares best fit to the data. The t-intercept (when $c = 0$) occurs at $t = -b/a$.

The resulting least squares best fit to the data is given by the line

$$c = -211t + 9010.$$

Figure 2 shows the graph you should obtain in the applet.

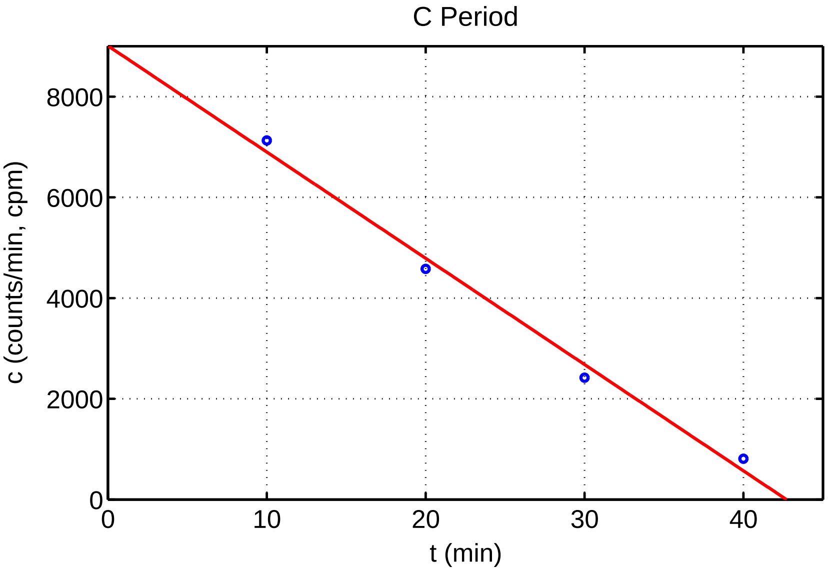

Figure 2: C-period best fit to the data. The corresponding equation of the adjusted line is $c = -211t + 9010$.

The t-intercept is 42.7, so this model estimates the C period as 42.7 min.

2 LEAST SQUARES BEST FIT

So what are the details behind the applet C-period that you are manipulating? The least squares best fit of a line to data (also called linear regression) is a means of finding the best line through a set of data.

Consider a set of n data points: $(x_1, y_1), (x_2, y_2), ..., (x_n, y_n)$. We want to select a slope, a, and an intercept, b, that results in a line

$$y(x) = ax + b,$$

that in some sense best fits the data.

The least squares best fit minimizes the square of the error in the distance between the y_i values of the data points and the y value of the line, which depends on the selection of the slope, a, and the intercept, b.

Let us define the *absolute error* between each of the data points and the line as

$$e_i = |y_i - y(x_i)| = |y_i - (ax_i + b)|, i = 1, ...n.$$

You can see that e_i varies as a and b vary.

Figure 3 displays the graph showing these error measurements.

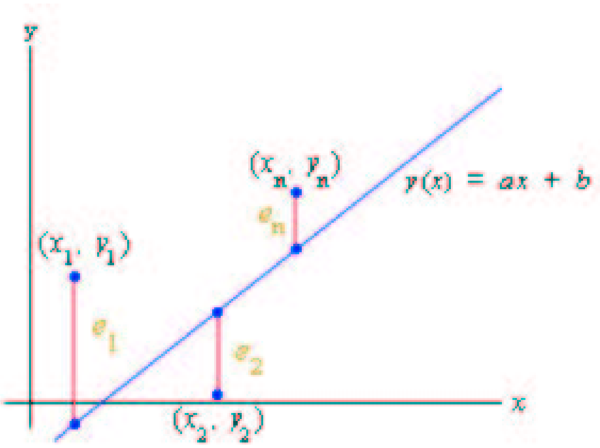

Figure 3: Graphic representation of the error measurements for the Least Squares Best Fit method.

The least squares best fit is found by finding the minimum value of the function

$$J(a, b) = e_1^2 + e_2^2 + ... + e_n^2 = \sum_{i=1}^{n} e_n^2$$

Example 1 *E. coli*

We demonstrate how these errors are computed when finding the C period in *E. coli.* The line is given by the formula:

$$c(t) = -211t + 9010.$$

The first data point is $t = 10$ and $c = 7130$. The model predicts $c(10) = 6900$, so the absolute error between the experimental and the theoretical value is given by

$$e_1 = |c_1 - c(10)| = |7130 - 6900| = 230.$$

Similarly, we find

$$\begin{aligned} e_2 &= |c_2 - c(20)| = |4580 - 4790| = 210, \\ e_3 &= |c_3 - c(30)| = |2420 - 2680| = 260, \\ e_4 &= |c_4 - c(40)| = |810 - 570| = 240. \end{aligned}$$

We add up the squares of these errors to obtain

$$J(-211, 9010) = 52900 + 44100 + 67600 + 57600 = 222,200.$$

◁

Least Squares – C-period

You can manipulate the applet Least Squares – C-period, and find that this is the smallest value possible.

Example 2 *Two Researchers*

Two researchers had only a limited set of data, the points $(2, 2)$, $(5, 6)$, and $(8, 3)$. **Researcher A** felt that a good model was given by

$$y = \frac{5}{9}x + \frac{8}{9},$$

with y increasing with increasing x, while **Researcher B** thought that a better model was

$$y = -\frac{2}{9}x + \frac{43}{9},$$

with y decreasing with increasing x. Sketch the graph of the data points and the two lines, then find the sum of squares errors for each of the models. Which one is better according to the data?

Solution: Recall that for a line $y(x) = ax + b$, the absolute error is given by $e_i = |y_i - y(x_i)| = |y_i - (ax_i + b)|, i = 1, 2, 3$. The line with the best fit has the smallest sum of the squares of the errors, $J(a, b)$. For **Model A**, $J(a, b)$

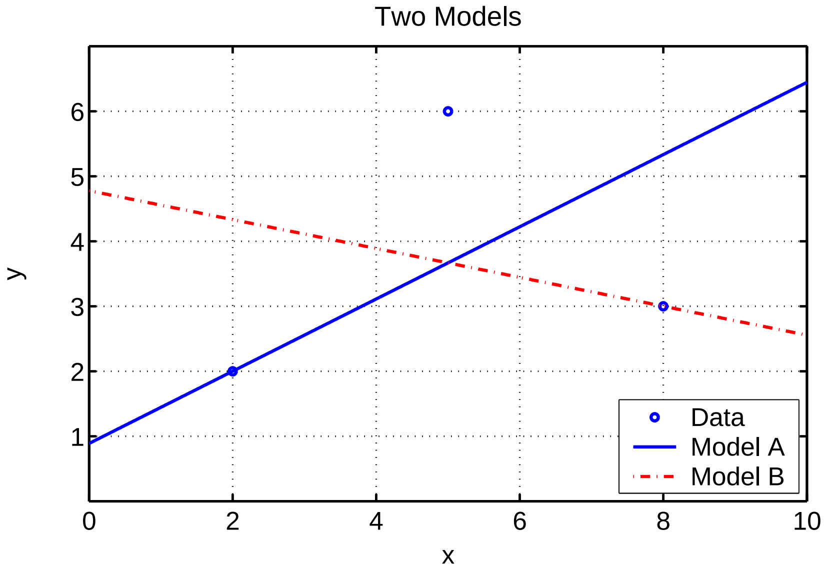

Figure 4: Graphs of the linear models obtained by Researcher A and Researcher B.

is calculated as follows:

$$\begin{aligned} J_A = e_1^2 + e_2^2 + e_3^2 &= \left[2 - \left(\frac{5}{9}(2) + \frac{8}{9}\right)\right]^2 + \left[6 - \left(\frac{5}{9}(5) + \frac{8}{9}\right)\right]^2 \\ &+ \left[3 - \left(\frac{5}{9}(8) + \frac{8}{9}\right)\right]^2 \approx 10.89. \end{aligned}$$

For **Model B**, $J(a,b)$ is calculated as follows:

$$\begin{aligned} J_B = e_1^2 + e_2^2 + e_3^2 &= \left[2 - \left(-\frac{2}{9}(2) + \frac{43}{9}\right)\right]^2 + \left[6 - \left(-\frac{2}{9}(5) + \frac{43}{9}\right)\right]^2 \\ &+ \left[3 - \left(-\frac{2}{9}(8) + \frac{43}{9}\right)\right]^2 \approx 10.89. \end{aligned}$$

Since $J_A = J_B$, the two models are equally valid. $\triangleleft$

The technique for finding the exact values of a and b uses Calculus of two variables. Thus, the least squares best fit is found by minimizing function $J(a,b)$ with respect to the variables a and b. (This is done by taking the partial derivatives of $J(a,b)$ with respect to a and b and setting these partial derivatives equal to zero. In this course we will be learning about derivatives and how they relate to finding minimum values of functions.) Note that the symbol Σ is summation notation and is used to shorten the amount of writing we need to use. It simply stands for adding together a collection of similar terms.

The details of this analysis are omitted, since it does require a little more knowledge of Calculus. However, the results are summarized below.

First, we define the mean of the x values of the data points as

$$\bar{x} = \frac{x_1 + x_2 + \ldots + x_n}{n} = \frac{1}{n}\sum_{i=1}^{n} x_i.$$

The value for the slope of the line that best fits the data is given by

$$a = \frac{\sum_{i=1}^{n}(x_i - \bar{x})y_i}{\sum_{i=1}^{n}(x_i - \bar{x})^2}.$$

With the slope computed, the intercept is found from the formula

$$b = \frac{1}{n}\sum_{i=1}^{n} y_i - a\bar{x} = \bar{y} - a\bar{x}.$$

There are many computer programs that automatically compute a and b from data sets. The accompanying lab exercises for this book use Excel's Trendline feature.

Example 3 *E. coli-2*

Let us apply this to our example beginning Section 1. There are four data points in the *E. coli* example, $(10, 7130), (20, 4580), (30, 2420)$, and $(40, 810)$. First we compute the mean of the times

$$\bar{t} = \frac{10 + 20 + 30 + 40}{4} = 25.$$

The slope a is found by the following calculation

$$\begin{aligned} a &= \frac{(10-25)7130 + (20-25)4580 + (30-25)2420 + (40-25)810}{(10-25)^2 + (20-25)^2 + (30-25)^2 + (40-25)^2} \\ &= \frac{-105600}{500} = -211.2. \end{aligned}$$

Similarly, the c-intercept, b, is readily computed to give

$$b = \frac{7130 + 4580 + 2420 + 810}{4} - (-211.2)25 = 9015.$$

The answer on Section 1 rounds the values of a and b to three significant figures. ◁

Example 4 Find the least squares best fit line for the data in Example 2. Which researcher had the right understanding of how y related to x? (Note: These data are clearly insufficient for true research and would require more experimentation.)

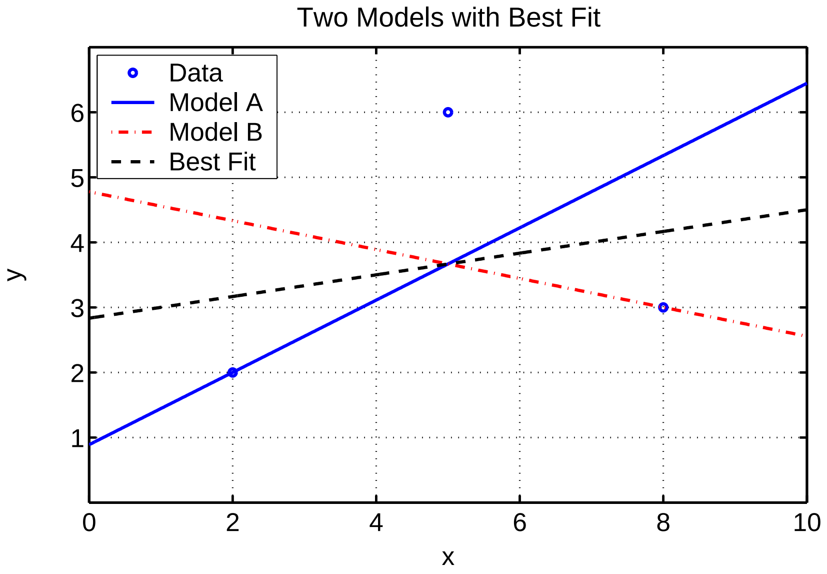

Figure 5: Same as Figure 4 including the best fit line to the data given by $y(x) = \frac{1}{6}x + \frac{17}{6}$.

Solution: From the box above, we obtain the average of the x data values:

$$\bar{x} = \frac{1}{n}\sum_{i=1}^{n} x_i = \frac{2+4+8}{3} = 5.$$

The slope a of the best fit line is calculated as follows:

$$a = \frac{\sum_{i=1}^{n}(x_i - \bar{x})y_i}{(x_i - x)^2} = \frac{(2-5)2 + (5-5)6 + (8-5)3}{(2-5)^2 + (5-5)^2 + (8-5)^2} = \frac{1}{6}.$$

The intercept b of the best fit line can then be calculated.

$$b = \sum_{i=1}^{n} \frac{y_i}{n} - a\bar{x} = \frac{(2+6+3)}{3} - \frac{5}{6} = \frac{17}{6}.$$

Therefore, the equation of the best fit line is:

$$y(x) = ax + b = \frac{1}{6}x + \frac{17}{6}.$$

The best fit is depicted in Figure 5. Note that since the best fit model shows y increasing with x, Researcher A actually has a more appropriate model than Researcher B. However, more data points are necessary in order so develop a more accurate model of the data. ◁

3 JUVENILE HEIGHT REVISITED

In chapter 2, we presented data on the average height of a child depending on age.

Least Squares – Height Extension

There is an extension of the applet Linear – Height from the Chapter 2 that includes the computation of the square of the error between the linear model and the data for the height of the children. Once again, you can adjust the slope, m, and the intercept, b, in the applet to find the minimum value of $J(m, b)$, which gives the least squares best fit to the data.

As noted in Chapter 2, Section 5, the resulting least squares best fit to the data is given by the line

$$h = 6.46a + 72.3,$$

and the square of the error is found to be

$$J(m, b) = 41.5.$$

4 CALCULATING ERROR

There are a number of techniques for computing the error in a measurement. Let X_e be an *experimental measurement* and X_t be the *theoretical value.* In this course, most often X_e will be the value from a model that we want to test, while X_t will be results from actual data that we acquire and assume is true.

The *actual error* is simply the difference between the experimental (or model) value and the theoretical (or actual data) value. So the actual error is given by

$$\text{Actual Error} = X_e - X_t.$$

Often we only need the magnitude of the error or as in the case of the least squares best fit the error is squared making the sign of the error irrelevant. In this case, we use the *absolute error*.

The absolute error is simply the absolute value of the difference between the experimental (or model) value and the theoretical (or actual data) value. So the absolute error is given by

$$\text{Absolute Error} = |X_e - X_t|.$$

More often the error is presented as either the *relative error* or *percent error*. This error allows a better comparison of the error between data sets or within a data set with large differences in the numerical values.

The *relative error* is the difference between the experimental value and the theoretical value **divided** by the theoretical value, so

$$\text{Relative Error} = \frac{X_e - X_t}{X_t}.$$

The *percent error* is closely related to the *relative error*, except that the value is multiplied by 100% to change the fractional value to a percent, so

$$\text{Percent Error} = \frac{X_e - X_t}{X_t} \times 100\%.$$

Example 5 *Growth Rate*

Often data sets have points that are clearly erroneous due to problems with the experiment (say contamination) or simply a poorly recorded value. If these points are included in the model, then they can result in misleading models. We saw that growth rates are determined by the slope of a line from our example on juvenile height.

a. Consider the following data set on the growth of some animal:

t (weeks)	0	1	2	3	5	7	9
L (cm)	2.4	3.1	3.7	4.1	5.2	4.9	6.9

Table 1: Data table of the length of some animal in weeks.

The least squares best fit to this data set is given by

$$L = 0.437t + 2.644.$$

Determine the *growth rate* for this model and find the sum of squares error. Graph the data and the least squares best fit line.

b. Which point is most likely erroneous? When this point is removed, then the new least squares best fit model is given by

$$L = 0.492t + 2.594.$$

Determine the growth rate for this model and find the sum of squares error for this model. What is the percent error (taking the growth rate from the model in Part b. as the actual one) between the computed growth rates?

Solution: a. The growth rate is represented by the slope of the best fit line, or 0.435cm week. The sum of squares error is calculated as follows:

$$R(a,b) = e_1^2 + e_2^2 + e_3^2 + e_4^2 + e_5^2 + e_6^2 + e_7^2$$

where,

$$\begin{aligned}
e_1^2 &= (9.4 - 2.544)^2 = 0.0595, \\
e_2^2 &= [3.1 - (0.437 + 2.644)]^2 = 0.0004, \\
e_3^2 &= [3.7 - (0.874 + 2.644)]^2 = 0.0331, \\
e_4^2 &= [4.1 - (1.311 + 2.644)]^2 = 0.0210, \\
e_5^2 &= [5.2 - (5.185 + 2.644)]^2 = 0.1376, \\
e_6^2 &= [4.9 - (3.059 + 2.644)]^2 = 0.6448, \\
e_7^2 &= [6.9 - (3.933 + 2.644)]^2 = 0.1043.
\end{aligned}$$

So the sum of squares error $J = 1.0008$.

b. From the squares of the errors calculated above, the point with the most error is $(7, 4.9)$, or the second to last point in data Table 1. Eliminating this point from the data set yields a new best fit line, and a smaller sum of squares error, as shown below.

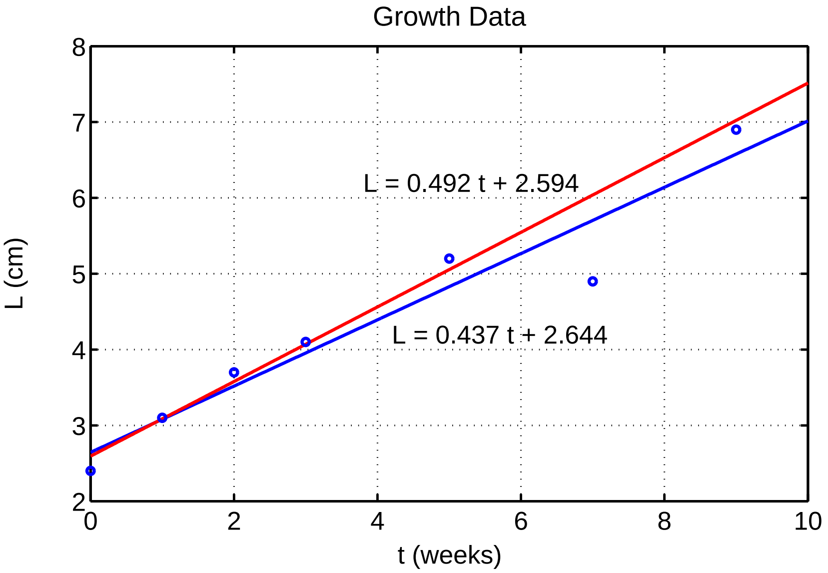

Figure 6: Two best square fit lines to the data given in Table 1. Line $L = 0.437t + 2.644$ is adjusted to all the data points, while line $L = 0.492t + 2.594$ is adjusted to all but the most erroneus data point.

$$\begin{aligned} L &= 0.492t + 2.594, \\ J(a,b) &= 0.0376 + 0.0002 + 0.0149 + 0.0009 + 0.0213 + 0.0149 = 0.0898, \end{aligned}$$

which is only 9% of the sum of squares error from Part a.

Recall that the percent error is calculated as follows:

$$\text{Percent Error} = \frac{\mathrm{X_e} - \mathrm{X_t}}{\mathrm{X_t}} \times 100\%.$$

If the new best fit growth rate is assumed to be the theoretical value, and the old best fit growth rate is the experimental value, the percent error is

$$\frac{0.437 - 0.492}{0.492} \times 100\% = -11.2\%. \qquad \triangleleft$$

5 EXERCISES

1. Consider the following data set:

x	1	3	5	8
y	2	3	6	7

A proposed model for these data is given by the equation

$$y = 0.75x + 1.25.$$

Find the error, e_i, between the y values of each of the points and proposed model. Give the sum of the squares of the errors. Sketch a graph of the data points and the line.

2. A limited set of data is collected and shown in the table below:

t	1	3	5	8
y	4	3	6	5

Two researchers interpreted these data differently. Researcher A felt that a good model is given by

$$y = 0.4x + 2.6,$$

while Researcher B thought the biological evidence suggests a better model satisfies the model

$$y = -0.4x + 6.2.$$

a. Sketch the graph of the data points and the two lines. Which model shows an increasing relationship between the variables and which one shows a decreasing relationship?

b. Find the sum of squares errors for each of the models. Which one is better according to the data?

c. Use the formula in the appendix to find the least squares best fit line for the data in this problem. Which researcher had the right understanding of how y related to x?

3. A research project on the plankton examines the light intensity filtered by the plankton as a function of the depth of the water. The data are shown in the table below:

depth (m)	1	1.5	2	3	4	5
intensity	0.32	0.29	0.27	0.27	0.15	11

a. The least squares best fit to this data set is given by the equation

$$I = -0.0524d + 0.3792,$$

where d is the depth in meters and I is the intensity of light filtered by the plankton. Find the sum of squares error. Graph the data and the least squares best fit line.

b. On observing the graph of the data, one point seemed obviously erroneous. Which point is most likely erroneous? When this point is removed, then the new least squares best fit model is given by

$$I = -0.0536d + 0.3728.$$

Find the sum of squares error for this model. If the model in Part b. is taken to be the actual model, then find the percent error between the slopes of the models in Parts a. and b.

6 REFERENCES

[1] J.L. Ingraham, O. Maaloe, and F.C. Neidhardt, *Growth of the Bacterial Cell*, Sinauer Assoc., Inc., Sunderland, MA (1983).

[2] F.C. Neidhardt, *Escherichia coli and Salmonella typhimurium: Cellular and Molecular Biology*, American Society of Microbiology, Washington, D.C. (1987).

CHAPTER 4:

FUNCTION REVIEW AND QUADRATICS

The first chapters examined linear models and how to find the best linear model from a set of data. Biological problems are rarely linear, so this chapter will begin our study of other functions. We will give the mathematical definitions needed to study more general functions, then review quadratic functions.

Our opening example is a linear model from the study of *Escherichia coli*. However, to fit the data to this model using the least squares best estimate, quadratic functions are needed.

1 RATE OF mRNA SYNTHESIS

The last chapter began with a discussion of the DNA replication cycle in *E. coli*. DNA provides the genetic code for all of the proteins, which are used either directly or indirectly for all aspects of the growth, maintenance, and reproduction of the cell. The synthesis of proteins follows the processes of transcription and translation.

Transcription of a bacterial gene is a controlled sequence of steps, where the protein, RNA polymerase, reads the genetic code and produces a complementary messenger RNA (mRNA) template. This mRNA is a short-lived blueprint for the production of a specific protein that has some particular activity in the bacterial cell.

Translation of the mRNA in bacteria begins shortly after transcription starts, with ribosomes (consisting of ribosomal RNA and ribosomal proteins) reading the triplet codons on the mRNA. The ribosome sequentially assembles a series of amino acids (based on the specific codons read), which form a polypeptide. It is believed that the physical properties of the atoms in the polypeptide cause it to fold passively into a tertiary structure that creates an active protein. Often the tertiary structure combines with other elements (such as another polypeptide, lipds or glycosides) to produce the active protein or enzyme.

The rate of growth of a bacterial cell depends on the rate at which

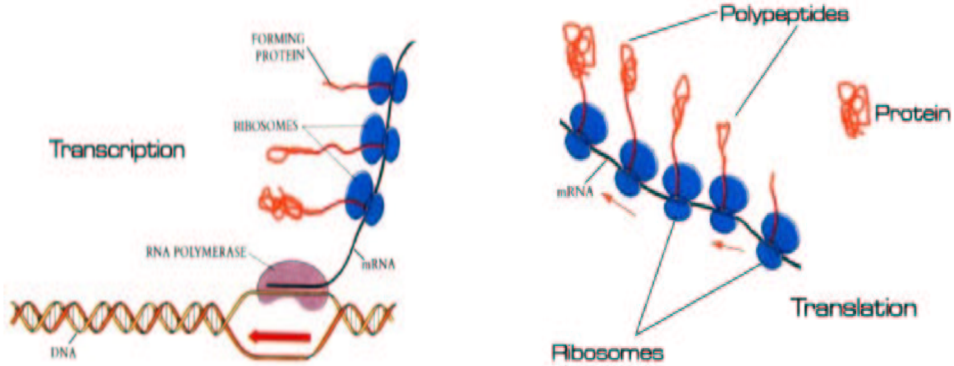

Figure 1: The transcription and translation processes for protein synthesis.

it assembles all of the components inside the cell. However, the rate of production of different components inside the cell varies depending on the length of time it takes for a cell to double. Table 1 shows the doublings/hr, denoted μ, and the rate of mRNA synthesis/cell, denoted r_m.

μ	0.6	1.0	1.5	2.0	2.5
r_m	4.3	9.1	13	19	23

Table 1: Data indicating growth of a bacterial cell in terms of μ (in doublings/hr) and the rate of mRNA synthesis, $r_m \times 10^5$ (in nucleotides/min/cell) [1].

Due to the instability of the mRNA, its rate of production closely approximates the rate of growth of a cell. The data are seen to lie almost on a straight line passing through the origin, which suggests a linear mathematical model of the form

$$r_m = a\mu,$$

for some value of a, which is the slope of the linear model.

A linear least squares best fit of this model to the data above can be used to find the slope of the model, a. The sum of the squares of the errors is computed using the formula from the previous chapter. From the data above and the model, we find each of the error terms as follows:

$$e_1^2 = (4.3 - 0.6a)^2 \quad e_2^2 = (9.1 - a)^2$$

$$e_3^2 = (13 - 1.5a)^2 \quad e_4^2 = (19 - 2a)^2$$

$$e_5^2 = (23 - 2.5a)^2$$

We expand each of these squared terms and add them together. The resulting equation is

$$J(a) = 13.86a^2 - 253.36a + 1160.3,$$

where $J(a)$ is a quadratic function representing the sum of the squares of the errors. As noted in the previous section, the best fit of the model is found by finding the smallest value of $J(a)$, which is the vertex of this quadratic equation.

In Figure 2 notice that the best fit to the data occurs at the vertex of the parabola traced by $J(a)$. The vertex of the parabola in Figure 2 is $(a, J(a)) = (9.14, 2.45)$.

Quadratics – mRNA

On the left hand side of this applet you can manipulate the slope, a, of the line to fit the data (as before), while on the right hand side you observe the value of the quadratic function, $J(a)$.

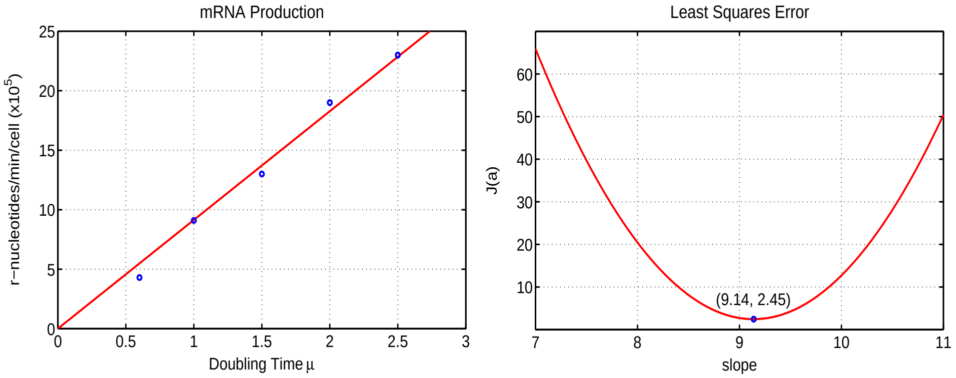

Figure 2: Example of the java applet Quadratics – mRNA, where the graph on the left is the line given by best square fit to the data of Table 1. The graph on the right corresponds to the parabola which x-coordinate of its minimum value equals the slope of the line on the right.

Below we use this example to illustrate some fundamental ideas that we use in this book about functions.

2 DEFINITIONS AND PROPERTIES OF FUNCTIONS

Functions form the basis for most of this course. Simply put, a *function* is a relationship between one set of objects and another set of objects with only one possible association in the second set for each member of the first set. We have two functions in our example above. The first function has a set of possible cell doubling times, μ, to which was found a particular average rate of mRNA synthesis, r_m. (You can focus on either the experimental data, which represents a function with a finite set of points, or the linear model, which creates a different function representing your theoretical expectations.) The sum of the squares of the errors between the data points and the model, $J(a)$, forms another function, where the set of possible slopes, a, in the model, each produced a number, $J(a)$, representing how far away the model was from the true data. We claimed that the best model is when this function is at its lowest point. One application of Calculus is to help determine the lowest or minimum value of a function.

Function: A *function* of a variable x is a rule f that assigns to each value of x a unique number $f(x)$. The variable x is the *independent variable*, and the set of values over which x may vary is called the *domain* of the function. The set of values $f(x)$ over the domain gives the *range* of the function.

Often we describe a function by using a graph in the xy-coordinate system. By convention we usually let x be the domain of the function and y be the range of the function.

The *graph* is defined by the set of points $(x, f(x))$ for all x in the domain. The *vertical line test* states that a curve in the xy-plane is the graph of a function if and only if each vertical line touches the curve *at no more than one point.*

Figure 3 depicts two graphs showing a function with its domain and range and another graph where the vertical line test shows that it is not a function.

Addition and multiplication of functions are carried out symbolically by standard algebraic techniques. Below we review a couple of examples, which should be familiar from your previous courses in algebra.

Example 1 *Addition and Multiplication of Functions*

Let $f(x) = x - 1$ and $g(x) = x^2 + 2x - 3$. Determine $f(x) + g(x)$ and $f(x)g(x)$.

Solution: The addition of $f(x)$ and $g(x)$ is

$$f(x) + g(x) = x - 1 + x^2 + 2x - 3 = x^2 + 3x - 4.$$

The multiplication of $f(x)$ and $g(x)$ is

$$\begin{aligned} f(x)g(x) &= (x-1)(x^2+2x-3) \\ &= x^3 + 2x^2 - 3x - x^2 - 2x + 3 \\ &= x^3 + x^2 - 5x + 3. \end{aligned}$$

◁

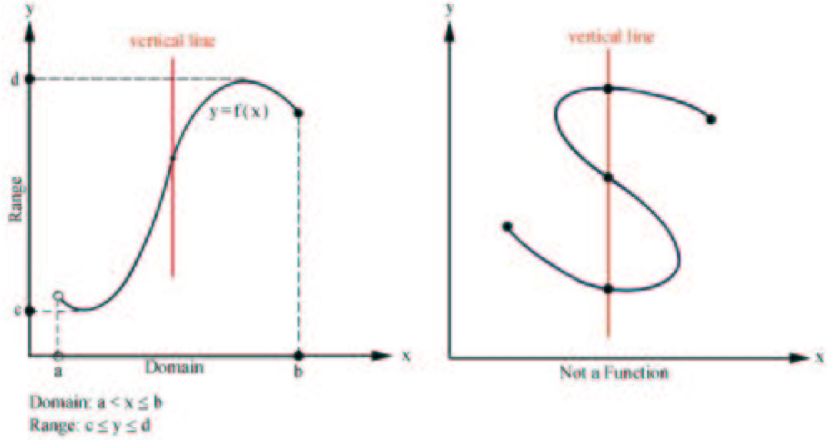

Figure 3: Diagrams explaining the vertical line test for the graph of a function.

Example 2 *Addition of Functions*

Determine$f(x) + g(x)$ for

$$f(x) = \frac{3}{x-6} \quad \text{and} \quad g(x) = \frac{-2}{x+2}.$$

Solution:

$$f(x) + g(x) = \frac{3}{x-6} + \frac{-2}{x+2} = \frac{3(x+2) - 2(x-6)}{(x-6)(x+2)} = \frac{x+18}{x^2-4x-12}.$$

◁

Composition of Functions is another important operation. Given functions $f(x)$ and $g(x)$, the *composite* $f(g(x))$ is formed by inserting $g(x)$ wherever x appears in $f(x)$.

Again this should be review from courses in algebra, so we demonstrate the composition of functions using an example.

Example 3 *Composition of Functions*

Let $f(x) = 3x + 2$ and $g(x) = x^2 - 2x + 3$. Determine $f(g(x))$ and $g(f(x))$.

Solution: The composition $f(g(x))$ is given by

$$f(g(x)) = 3(x^2 - 2x + 3) + 2 = 3x^2 - 6x + 11,$$

while the composition $g(f(x))$ is

$$g(f(x)) = (3x + 2)^2 - 2(3x + 2) + 3 = 9x^2 + 6x + 3.$$ ◁

More worked examples of functions and algebra of functions follow below.

Example 4 *Evaluation and Composition*

Consider the functions $f(t) = t^2 - 1$ and $g(t) = 2t + 3$.

a. Evaluate $f(2)$, $f(-1)$, $f(3)$, $g(-2)$, and $g(1)$.

b. Create the composite functions $f(g(t))$ and $g(f(t))$ and write the expressions in the simplest form. Evaluate $f(g(1))$ and $g(f(-1))$.

Solution: **a.** In the case of $f(2)$ we substitute a 2 for each t in the given equation for $f(t)$ to obtain:

$$f(2) = (2)^2 - 1 = 4 - 1 = 3.$$

Using the above method we obtain the following for $f(-1)$, $f(3)$, $g(-2)$, and $g(1)$

$$\begin{aligned} f(-1) &= (-1)^2 - 1 = 1 - 1 = 0 \\ f(3) &= (3)^2 - 1 = 9 - 1 = 8 \\ g(-2) &= 2(-2) + 3 = -4 + 3 = -1 \\ g(1) &= 2(1) + 3 = 2 + 3 = 5. \end{aligned}$$

b. To find $f(g(t))$ we substitute the entire function $g(t)$ for t into $f(t)$.

$$f(g(t)) = [g(t)]^2 - 1 = (2t+3)^6 - 1 = 4t^2 + 12t + 9 - 1 = 4t^2 + 12t + 8.$$

By the same method, we obtain the following:

$$g(f(t)) = 2[f(t)] + 3 = 2(t^2 - 1) + 3 = 2t^2 - 2 + 3 = 2t^2 + 1.$$

To find $f(g(1))$, we substitute 1 for t into $f(g(t))$ to obtain:

$$f(g(1)) = 4(1)^2 + 12(1) + 8 = 24.$$

In an alternate method, we can evaluate $g(1)$ and then substitute this value into $f(t)$ to obtain the same answer, as follows:

From Example 4**a**, we know that $g(1) = 5$. Then we must evaluate $f(5)$ to obtain:

$$f(5) = (5)^2 - 1 = 24 - 1 = 23 \quad \text{(as expected)}.$$

Therefore, using either method, $g(f(-1))$ yields the following result:

$$g(f(-1)) = 2(-1)^2 + 1 = 3.$$

Note that $g(f(t))$ does not equal $f(g(t))$. ◁

Example 5 *Domain and Range of a Function*

Use the function $f(t)$ from the previous example.

a. What is the range of this function (assuming a domain of all t)?

b. Find the domain of $f(t)$, if the range of f is restricted to $f(t) < 0$.

Solution: a. Recall that $f(t) = t^2 - 1$. The domain of $f(t)$, unless otherwise noted, is all real numbers, since any number t substituted into $f(t)$ yields a real, finite answer. However, the range, or output, of the function may not include all real numbers. Graphing the function helps visualize both its domain and range, as shown below.

The range of $f(t)$ includes all numbers along the vertical axis for which there is at least one point on the graph. As you can see, the range of the function does not include all real numbers, but does include all numbers greater than or equal to -1. Therefore, the range of $f(t) = [-1, \infty)$ or $f(t) \geq -1$.

b. If the range of $f(t)$ is restricted to $f(t) < 0$, then the domain, which is characterized by all numbers t that can be substituted into the given range of $f(t)$, can also be found by looking at the graph above. Therefore, we can

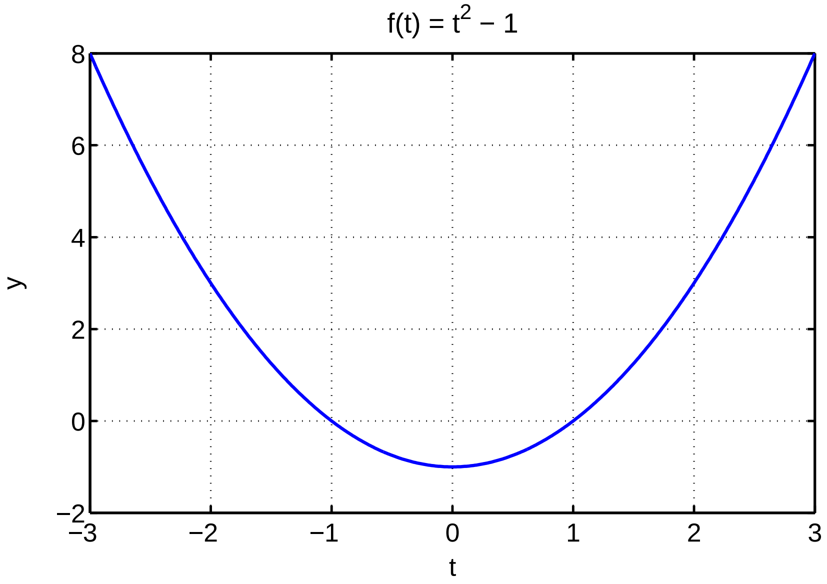

Figure 4: The domain of this quadratic function is all real numbers, while the range is all values of $f(t)$ such that $-1 \leq f(t) < \infty$.

say that for $f(t) < 0$, the domain includes $(-1, 1)$, or $-1 < t < 1$. However, the domain cannot always be accurately determined directly from the graph.

The following is an alternate method in determining the domain of a function: We know that $f(t) < 0$, and that $f(t) = t^2 - 1$. Therefore, we can say:

$$t^2 - 1 < 0.$$

Solving for t, we obtain:

$$t^2 < 1.$$

Once again, we find the domain to be $-1 < t < 1$. ◁

3 QUADRATIC EQUATIONS AND QUADRATIC FUNCTIONS

After straight lines, the next easiest algebraic functions to analyze are the quadratic functions. You should have studied quadratic equations and the graphing of quadratic functions (parabolas) in your prerequisite algebra course. The example below shows a classic problem in Chemistry that requires the use of the quadratic equation.

3.1 WEAK ACIDS

Many of the organic acids found in biological applications are weak acids. Also, weak acid chemistry plays an important role when you are preparing buffer solutions to stabilize certain laboratory cultures. Let us review weak acid chemistry and see how the algebra of quadratic equations come into play.

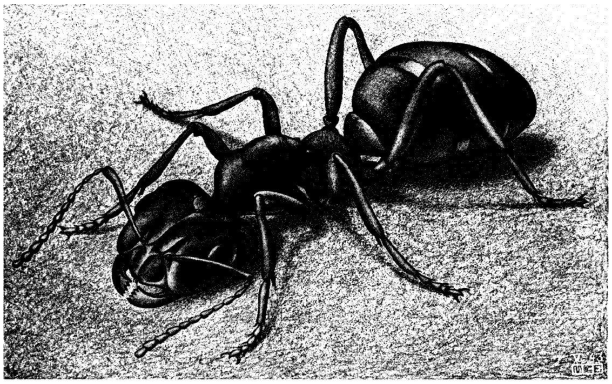

Figure 5: The strong taste of the formic acid that ants secrete makes them very unpalatable to predators.

Formic acid (HCOOH) is a relatively strong weak acid that ants use as a defense. (The strength of this acid makes the ants very unpalatable to predators.) The chemistry of dissociation is given by the following equation:

$$\mathrm{HCOOH} \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} \mathrm{H}^+ + \mathrm{HCOO}^-.$$

Each acid has a distinct equilibrium constant K_a that depends on the properties of the acid and the temperature of the solution. For formic acid, $K_a = 1.77 \times 10^{-4}$. Let [X] denote the concentration of a particular chemical species X, then assuming that the formic acid is in equilibrium, it satisfies the following equation:

$$K_a = \frac{[\mathrm{H}^+][\mathrm{HCOO}^-]}{[\mathrm{HCOOH}]}.$$

If formic acid is added to water, then $[\mathrm{H}^+] = [\mathrm{HCOO}^-]$. Also, if x is the normality of the solution, then $x = [\mathrm{HCOOH}] + [\mathrm{HCOO}^-]$. (The anion HCOO^- must be either in the bound form HCOOH or ionized form HCOO^- with the total representing the normality of the formic acid added to solution.) It follows that [HCOOH] = x − $[\mathrm{H}^+]$. Thus,

$$K_a = \frac{[\mathrm{H}^+][\mathrm{H}^+]}{x - [\mathrm{H}^+]}$$

or

$$[\mathrm{H}^+]^2 + K_a[\mathrm{H}^+] - K_a x = 0,$$

which is a quadratic equation in $[\mathrm{H}^+]$ and is easily solved using the quadratic formula. The solution is given by,

$$[\mathrm{H}^+] = \frac{1}{2}\left(-K_a + \sqrt{K_a^2 + 4K_a x}\right).$$

Notice that we only take the positive solution from the quadratic equation to make physical sense.

Example 6 *Formic Acid*

Find the concentration of $[\mathrm{H}^+]$ for a 0.1 N solution of formic acid.

Solution: Since formic acid has $K_a = 1.77 \times 10^{-4}$ and we have a 0.1 N solution of formic acid, then we can substitute into the formula given above to yield:

$$[\mathrm{H}^+] = \frac{1}{2}\left(-0.000177 + \sqrt{(0.000177)^2 + 4(0.000177)(0.1)}\right) = 0.00412.$$

Thus, the concentration of acid in the 0.1 N solution is $[\mathrm{H}^+] = 4.12 \times 10^{-3}$, which gives a pH of 2.385 (note that pH is defined to be $-\log_{10}[\mathrm{H}^+]$). ◁

3.2 REVIEW OF QUADRATIC EQUATIONS

Quadratic equations are covered in standard courses in algebra.

The general quadratic equation is given by the formula:

$$ax^2 + bx + c = 0.$$

There are two methods for solving this type of equation: **1.** *Factoring* the equation, and

2. The *quadratic formula*, which has the form:

$$x = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}.$$

In the example above, we used the quadratic formula because we did not know either K_a or x. Let us demonstrate each of these techniques with a few examples.

Example 7 *Factoring*

Consider the following quadratic equation:

$$x^2 + x - 6 = 0.$$

Find the values of x that satisfy this equation.

Solution: The equation above is easily factored to give the solution.

$$(x+3)(x-2) = 0,$$

thus,

$$x = -3 \quad \text{or} \quad \text{x} = 2. \qquad \triangleleft$$

Example 8 *Quadratic formula*

Find the roots of the quadratic equation:

$$x^2 + 2x - 2 = 0.$$

Solution: This example is most easily solved using the quadratic formula,

$$x = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}.$$

In this case, $a = 1$, $b = 2$, and $c = -2$.

$$x = \frac{-2 \pm \sqrt{2^2 - 4(1)(-2)}}{2(1)} = \frac{-2 \pm \sqrt{12}}{2} = -1 \pm \sqrt{3}.$$

So the solutions are:

$$x = -1 \pm \sqrt{3} \quad \text{or} \quad \text{x} \approx -2.732 \quad \text{or} \quad \text{x} \approx 0.732. \qquad \triangleleft$$

Below are several examples of quadratic equations. These can be solved by either factoring the quadratic or the quadratic equation.

Example 9 Solve the following quadratic equations (if possible):

a. $x^2 - 10x + 16 = 0$

b. $x^2 - 4x - 6 = 0$

c. $x^2 - 4x + 5 = 0$

Solution: a. The simplest approach to this equation is to solve for x by factoring:

$$x^2 - 10x + 16 = (x - 8)(x - 2) = 0.$$

Solving for x we find that $x = 8$ or $x = 2$.

b. This equation does not appear to be easily factorable, so we can resort to using the quadratic formula, as follows:

$$x = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}.$$

In this case, $a = 1$, $b = -4$, and $c = -6$.

$$x = \frac{4 \pm \sqrt{(-4)^2 - 4(-4)(-6)}}{2(1)} = \frac{4 \pm \sqrt{40}}{2} = 2 \pm \sqrt{10}.$$

c. This equation cannot be solved by factoring, so we use the quadratic formula again, where $a = 1$, $b = -4$, and $c = 5$.

$$x = \frac{+4 \pm \sqrt{(-4)^2 - 4(1)(5)}}{2(1)} = \frac{4 \pm \sqrt{-4}}{2}.$$

Since we cannot evaluate the square root of a negative number, -4 in this case, there is no real solution for x. However, there are two complex solutions, where i is the square root of -1, such that:

$$x = \frac{4 \pm 2i}{2(1)} = 2 \pm i.$$

◁

3.3 QUADRATIC FUNCTIONS

The general form of a quadratic function is

$$f(x) = ax^2 + bx + c,$$

where a is a nonzero constant and b and c are arbitrary.

The graph of this function,

$$y = f(x)$$

produces a parabola. Notice that for each value of x, there is only one value of y. However, for most values of y in the range of this function, there are two values of x. (A horizontal line intersects the graph in two places).

Example 10 *Intersection of Line and Parabola*

Let us find the intersections of the line $y = 3-2x$ and the quadratic function

$$y = x^2 - x - 9.$$

Sketch a graph of these functions.

Solution: To find the points of intersection, we set the equations equal to each other. Thus,

$$3 - 2x = x^2 - x - 9 \quad \text{or} \quad x^2 + x - 12 = 0.$$

This equation is easily factored giving

$$(x+4)(x-3) = 0,$$

so $x = -4$ or 3. By computing the y values corresponding to $x = -4$ and 3, we obtain the points of intersection as $(-4, 11)$ and $(3, -3)$. Figure 6 shows the graph of the two functions. ◁

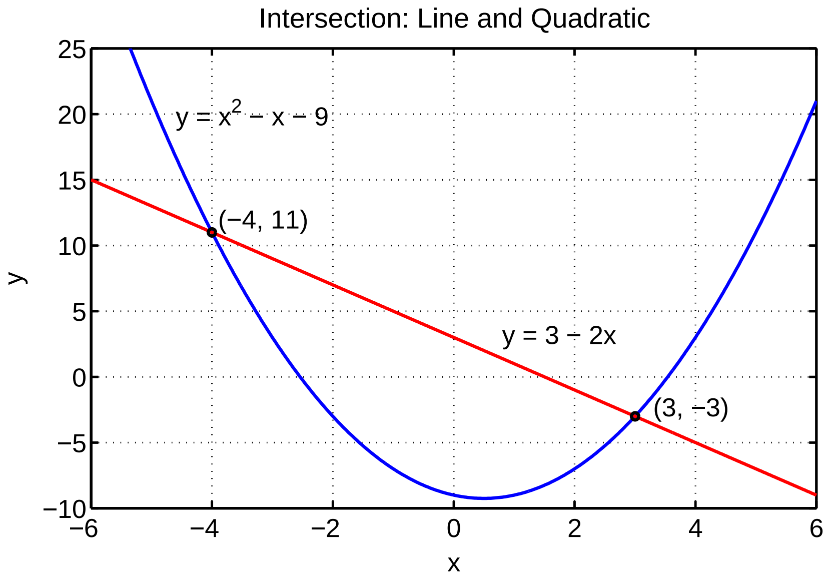

Figure 6: Graphs of a line and a parabola that intersect in two different points.

More examples of quadratic functions and its applications are developed below.

Example 11 *Sketch the Graphs*

Consider the functions $f(x) = x^2 - 1$ and $g(x) = 2x + 3$. Sketch both of these functions on a single graph. Find the x and y-intercepts for both functions. What is the slope of the line? Find the coordinates of the vertex of the parabola. Finally, determine the coordinates of the points of intersection of these curves.

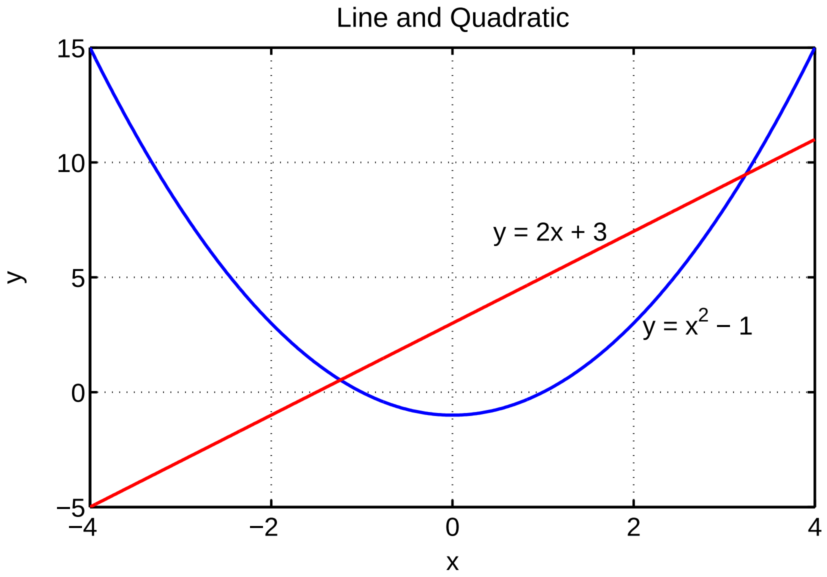

Figure 7: Graphs of Example 11.

Solution: The y-intercept of any function can be found by letting $x = 0$, and solving for y. To find the x-intercept of a function, one can set $y = 0$ and solve for x. The intercepts of $f(x)$ are found as follows. Setting $x = 0$ for the y-intercept,

$$f(0) = (0)^2 - 1 = -1.$$

Letting $y = 0$ for the x-intercept,

$$\begin{aligned} 0 &= x^2 - 1 \\ x^2 &= 1 \\ x &= -1, 1. \end{aligned}$$

So the y-intercept of $f(x)$ is -1, and the x-intercepts are -1 and 1. This means that the graph of $f(x)$ crosses the y axis at -1, and crosses the x axis at -1 and 1, which is consistent with the graph of Figure 7.

To find the intercepts of $g(x)$ we have that for a line of the form $y = mx + b$, the y-intercept is equal to b. Thus, we can say that for $g(x)$ the y-intercept must be 3. Letting $y = 0$ for the x-intercept,

$$\begin{aligned} 0 &= 2x + 3 \\ 2x &= -3 \\ x &= -\frac{3}{2} \quad \text{or} \quad -1.5. \end{aligned}$$

Hence, the y-intercept of $g(x)$ is 3, and the x-intercept of $g(x)$ is -1.5, in agreement with the graph above.

Note that the degree of a function, or its highest power, gives the number of possible x-intercepts for the function. This is why $f(x)$ had two solutions for x, while $g(x)$ had only one solution. The slope of $g(x)$ must be $m = 2$, in accordance with the given slope-intercept form of the line.

The **vertex of the parabola** $f(x)$ is found from the general form of a quadratic equation:

$$y = a(x - h)^2 + k,$$

where the vertex is the point (h, k), and a is a parameter that measures how wide or narrow the curve of the parabola is, as well as in which direction it opens.

If $a > 0$, the parabola is a U-shape which opens upward, and the vertex falls at a minimum. For $a < 0$, the parabola opens downward, with the vertex as a maximum. In some cases, one must *complete the square* in order to obtain this form of the quadratic function.

Therefore, for $f(x) = x^2 - 1$:

$$y = x^2 - 1 = 1(x - 0)^2 - 1.$$

And the vertex is at $(h, k) = (0, -1)$.

There are three methods for **finding the vertex**:

1. Completing the square.
2. The x-value is $x = -b/2a$.
3. The midpoint between the x-intercepts.

The last two of these methods are the most common and easiest techniques.

To find where the two graphs intersect, we first set the two functions equal to each other and solve for x.

$$\begin{aligned} x^2 - 1 &= 2x + 3 \\ x^2 - 2x - 4 &= 0. \end{aligned}$$

At this point, there are a couple of different methods we can use to solve for x, both of which will yield the same solutions. In this case, we will use the quadratic formula, where $a = 1$, $b = -2$, and $c = -4$.

$$x = \frac{-b \pm \sqrt{b^2 - 4ac}}{9a} = \frac{2 \pm \sqrt{(-2)^2 - 4(1)(-4)}}{2(1)} = 1 \pm \sqrt{5} \approx 3.24, -1.24.$$

Next, we can substitute each of these solutions for x into either equation to find the y coordinates of intersection.

$$\begin{aligned} g(x) &= 2(1 + \sqrt{5}) + 3 \approx 2(3.24) + 3 \approx 9.48 \\ g(x) &= 2(1 - \sqrt{3}) + 3 \approx 2(-1.24) + 3 \approx 0.52. \end{aligned}$$

Therefore, the points of intersection of the two functions are $(3.24, 9.48)$ and $(-1.24, 0.52)$. ◁

3.4 APPLICATIONS

Example 12 *Throwing a Ball*

A ball is thrown vertically with a velocity of 32 ft/s from ground level ($h = 0$). The height of the ball satisfies the equation:

$$h(t) = 32t - 16t^2.$$

a. Sketch a graph of $h(t)$ *vs.* t.

b. Find the maximum height of the ball, then determine when the ball hits the ground.

Solution: **a.** Note that the function is a relationship between time and the height of the ball. If we start with both time and height equal to zero, the only relevant part of the graph is that which occurs above the t-axis. To make a sketch of the graph of this quadratic function we need to find the t-intercepts and the vertex of the parabola. We find the t-intercepts by factoring the function for the height of the ball:

$$h(t) = 32t - 16t^2 = -16t(t-2).$$

From the factored form of $h(t)$, it follows that $h(t) = 0$ when $t = 0$ or $t = 2$. These are the t-intercepts.

After finding the t-intercepts, the symmetry of the parabola easily gives the t value of the vertex by taking the midpoint between the intercepts. In this case, the midpoint between 0 and 2 is $t = 1$. Evaluating $h(1)$, we have $h(1) = 16$ ft, so the vertex occurs at $(1, 16)$.

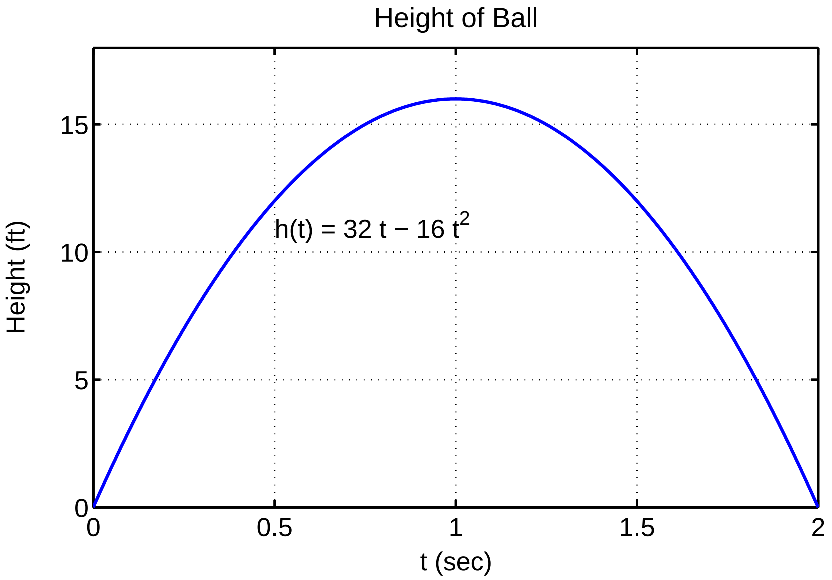

Figure 8: The height of a ball thrown in a vertical way satisfies a parabolic function with respect to time.

b. Since the graph of Figure 8 shows the height as a function of time, we can see that the maximum height of the ball occurs at the peak or **vertex** of the parabola.From our calculations above, it follows that the maximum height of the ball is 16 ft.

From the t-intercepts, we can readily find when the ball hits the ground. Clearly, this occurs at $t = 2$ sec. ◁

Example 13 *Formic Acid Revisited*

Use the information in Section 3.1 to determine the concentration of $[\mathrm{H}^+]$ for a 1 N solution of formic acid. Also, find the pH of this solution.

Solution: From Section 3.1, we know that $K_a = 1.77 \times 10^{-4}$. In this case we are also given that $x = 1$. The given formula for $[\mathrm{H}^+]$ is as follows:

$$[\mathrm{H}^+]^2 + K_a[\mathrm{H}^+] - K_a x = 0.$$

Using the quadratic formula, we solve for $[H^+]$ as follows:

$$[\mathrm{H}^+] = \frac{-1.77 \times 10^{-4} + \sqrt{(1.77 \times 10^{-4})^2 - 4(1)(1.77 \times 10^{-4})(1)}}{2(1)} \approx 0.0134.$$

Note that the variable in this quadratic equation is $[\mathrm{H}^+]$, since it has both a quadratic and a linear term. Since it is impossible to obtain a negative amount or concentration of a material, we throw away the negative answer, and keep only that which is positive. Therefore, we have an acid concentration of 0.0134.

The pH is found by,

$$-\log_{10}[\mathrm{H}^+] = -\log_{10}[0.0134] \approx 1.87. \qquad \triangleleft$$

Example 14 *Lambert-Beer Law*

A spectrophotometer uses the Lambert-Beer law to determine the concentration of a sample (c) based on the absorbance of the sample (A). The ion dichromate forms an orange/yellow that has a maximum absorbance at 350 nm and is often used in oxidation/reduction reactions. The Lambert-Beer law for the concentration of a sample from the absorbance satisfies the linear relationship

$$c = mA,$$

where m is the slope of the line.

a. Table 2 shows the data collected on some known samples.

A	0.12	0.32	0.50	0.66
c (mM)	0.05	0.14	0.21	0.30

Table 2: Data collected for the concentration (c) of a sample, and the absorbance (A) of the same sample.

Follow the first example of the section to determine the quadratic function $J(m)$ that measures the sum of the squares of the error of the line to the data. Sketch a graph of $J(m)$ and find the vertex of this quadratic function.

b. Sketch a graph of the data and the line that best fits the data. Then use this model to determine the concentration of two unknown samples that have absorbances of $A = 0.45$ and 0.62.

Solution: a. From 3, we know how to calculate the sum of squares of the error, as a quadratic function of m:

$$\begin{aligned} J(m) &= e_1^2 + e_2^2 + e_3^2 + e_4^2 = (0.05 - 0.12m)^2 + (0.14 - 0.32m)^2 \\ &+ (0.21 - 0.50m)^2 + (0.30 - 0.66m)^2. \end{aligned}$$

Expanding and simplifying these terms, we obtain:

$$J(m) = 0.8024m^2 - 0.7076m + 0.1562.$$

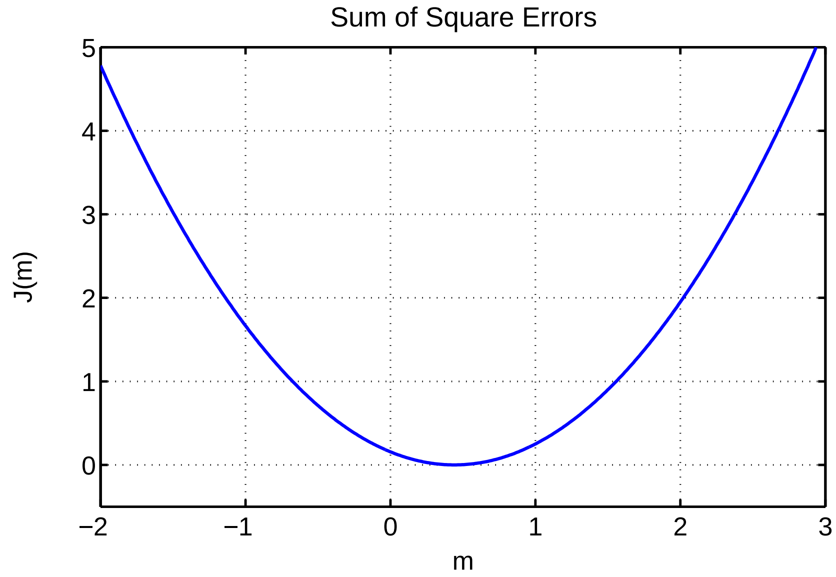

Figure 9: Parabolic function for the sum of square errors for the data in Table 2.

The quadratic function $J(m)$ forms a parabola, which because the leading coefficient is positive, points upward. It follows that the minimum value of this least squares quadratic function occurs at the vertex of the parabola. The easiest way to find the m-value of the vertex, m_v, is

$$m_v = -\frac{b}{2a} = \frac{0.7076}{2(0.8024)} = 0.4410.$$

This gives the best slope of the line fitting the data for the Lambert-Beer

Law in this example.

By evaluating the sum of square error at $m = 0.4410$, we find $J(0.4410) = 0.0003)$, which is the least sum of square error possible for this example. Thus, the vertex for $J(m)$ is $(0.4410, 0.0003)$. It follows that the best model for the data in Table 2 is

$$c(A) = 0.4410\, A.$$

b. Graphing the linear best fit to the data of Table 2, we obtain the graph of Figure 10.

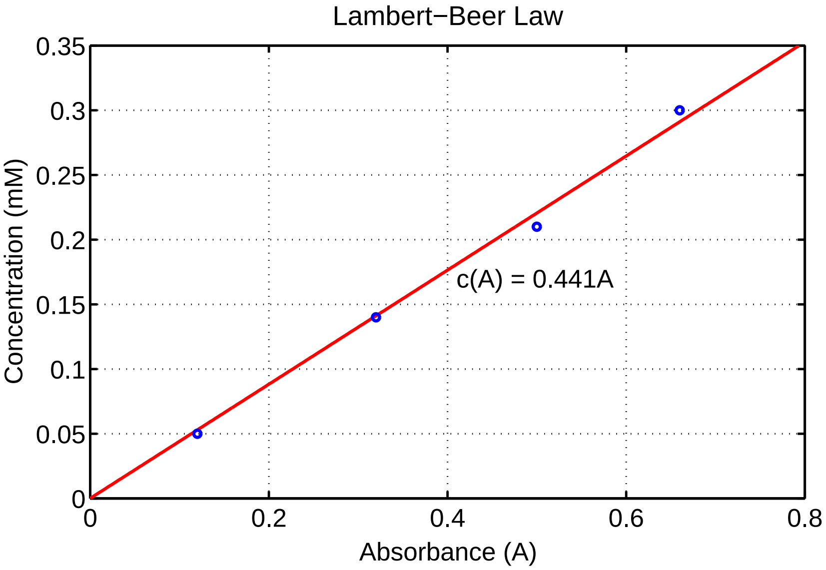

Figure 10: Linear best square fit to the data given in Table 2.

Above is the best linear model for the given data, $c(A) = 0.4410\, A$. For an absorbance $A = 0.45$ or 0.62, we simply plug this value into the best fit line to obtain the concentration:

$$\begin{aligned} c(0.45) &= 0.441(0.45) = 0.198 \\ c(0.62) &= 0.441(0.62) = 0.273. \end{aligned}$$

Therefore, for absorbances of 0.45 and 0.62, our model predicts concentrations of 0.198 and 0.273, respectively. ◁

4 EXERCISES

1. Consider the functions $f(t) = 2t^2 + t$ and $g(t) = t - 2$.
   a. Evaluate $f(0)$, $f(2)$, $g(-2)$, and $g(3)$.
   b. Create the composite functions $f(g(t))$ and $g(f(t))$ and write the expressions in the simplest forms.
   c. Evaluate $f(g(1))$ and $g(f(1))$.

2. Consider the function $f(x) = 30 + x - x^2$.
   a. What is the range of this function (assuming a domain of all x)?
   b. Find the domain of $f(x)$, if the range of f is restricted to $f(x) > 0$.

Solve the following quadratic equations (if possible):

3. $x^2 + 8x + 15 = 0$
4. $x^2 + 4x - 3 = 0$
5. $2x^2 - 3x + 1 = 0$
6. $x^2 - x - 20 = 0$
7. $x^2 + 3x - 5 = 0$
8. $x^2 - 9 = 0$
9. $2x^2 - 5x = 0$
10. $x^2 - 2x + 2 = 0$

In each of the following problems, sketch the pair of functions on a single graph. Find the x and y-intercepts for both functions. What is the slope of the line? Find the coordinates of the vertex of the parabola. Finally, determine the coordinates of the points of intersection of these curves.

11. $f(t) = 4 - t^2$ and $g(t) = t - 2$

12. $f(x) = x^2 + 4x + 4$ and $g(x) = 4 - 2x$.

13. A ball is thrown vertically with a velocity of 48 ft/sec from a platform that is 64 ft in the air. The height of the ball satisfies the equation:

$$h(t) = 64 + 48t - 16t^2.$$

a. Sketch a graph of $h(t)$ vs. t.

b. Find the maximum height of the ball, then determine when the ball hits the ground.

14. Acetic acid arises in the bacterial breakdown of many fruits often resulting in vinegar. The equilibrium constant (ionization constant) for acetic acid is $K_a = 1.75 \times 10^{-5}$. Use the information developed in the notes for formic acid as a guide to determine the concentration of $[H^+]$ and pH of 0.1N and 1N solutions of acetic acid.

15. A rectangle with a length x and width y has a perimeter of 40 cm.

a. Write an expression for the width y as a function of the length x, using this information.

b. The area of a rectangle is $A = xy$. Substitute the expression for y into this formula for the area to produce a function of the area as a function of x alone.

c. Sketch a graph of the area as a function of x and determine what value of x produces the largest area. What geometric figure does this produce?

16. The braking distance d (in feet) of a car is divided into two components. One part depends on reaction time. The number of feet for reaction time is about the same as as the speed of the car in miles/hour, v. The other component is due to friction, which is a force that is proportional to the velocity squared. Adding these two components together, we find the braking distance satisfies the equation

$$d = v + \frac{v^2}{20}.$$

Find the braking distance at 60 miles/hr. Also, determine all velocities that result in a braking distance that is less than 75 feet.

17. For animals that reproduce seasonally, we find that their population satisfies a difference equation

$$P_{n+1} = P_n + g(P_n),$$

where P_n is the population in the nth season and $g(P)$ (in individuals per generation) is the growth rate of the population. This equation simply says that the population in the next generation is equal to the population of the previous generation plus the net growth of the population over the last season.

a. Suppose that the growth rate $g(P)$ satisfies the quadratic equation

$$g(P) = 0.02P - 0.000025P^2.$$

Sketch a graph of this growth rate function.

b. The population is at equilibrium when the growth rate is zero. Find the equilibrium populations.

c. The growth rate is at a maximum at the vertex of parabola. Find the population that produces this maximum growth rate and what that growth rate is.

18. The Lambert-Beer law for absorbance of light by a spectrophotometer is a linear relationship, which can have the form

$$A = mc,$$

where c is the concentration of the sample, A is absorbance, and m is the slope that must be determined from experiments.

a. Below are data collected on samples from a collection of acid standards using an acid indicator.

c (mM)	1	2	5
A	2.0	4.1	9.8

Write a formula for the quadratic function $J(m)$ that measures the sum of squares error of the line fitting the data. Find the vertex of this quadratic function. This gives the value of the best slope m, while the $J(m)$ value of the vertex gives the least sum of squares error.

b. Use this model (with the best value of m) to determine the concentration of an unknown acid with absorbances of $A = 3.5$ and 6.2.

19. In looking through some old photos, a woman finds a picture of her great-grandfather standing near the family home, where she now lives. In the photograph, she measures the height of the roofline, which she knows to be 20 ft, as 3.3 cm. The 2 ft wide window measures 0.5 cm on the photo, and the distance from the front door to the oak tree at the driveway is 12 feet, which is 2 cm in the photograph.

a. The conversion of measurements in the photo p to measurements in actual distance d is given by the formula

$$d = kp.$$

Write a formula for the quadratic function $J(k)$ that measures the sum of squares error of the line fitting the measurements in the photo. Find the vertex of this quadratic function. This gives the value of the best slope k, while the $J(k)$ value of the vertex gives the least sum of squares error.

b. In the photograph, her great-grandfather is 1 cm tall. Her mother remembers her grandfather as a tall man of about 6 ft , whereas her father thinks he was shorter, about 5 ft 6 inches (5.5 ft). Use the model (with the best value of k) to predict the height of the great-grandfather and determine whether the mother or father better remembers the height of her great-grandfather.

5 REFERENCES:

[1] H. Bremer and P.P. Dennis, “Modulation of chemical composition and other parameters of the cell by growth rate”, *Escherichia coli and Salmonella typhimurium*, ed.F.C. Neidhardt, American Society of Microbiology, Washington, D.C. (1987).

CHAPTER 5:

OTHER FUNCTIONS AND ASYMPTOTES

The last chapter introduced quadratic functions and gave the fundamental definitions for a function. This chapter extends the material from the previous one to other functions. A closer examination of the domains and ranges provide interesting information about the behavior of a function. The graphs of certain functions exhibit asymptotic behavior, such as the saturation effects that are often observed in biological phenomena.

1 MICHAELIS–MENTEN ENZYME KINETICS

Life forms are often characterized by their distinct molecular composition, especially proteins. Proteins are considered the primary building blocks of life. Enzymes are an important class of proteins that catalyze many of the reactions occurring inside the cell. An enzyme has the property of facilitating a biochemical reaction, such that the reaction can occur at biological temperatures. Enzymes are noted for their specificity and speed often under a narrow range of conditions. For example, β-galactosidase catalyzes the break down of lactose into glucose and galactose, then other enzymes further break down these sugars to produce energy for the cell. Urease rapidly converts urea into ammonia and carbon dioxide, very specifically with no other known functions.

The basic mechanism used for simple enzyme reactions, known as the *Michaelis-Menten* mechanism, has been shown in many experimental situations. The reactants of enzyme reactions, called substrates and denoted by S, are presumed to combine reversibly to the enzyme E to form a enzyme-substrate complex ES. The complex can decompose irreversibly to form a product P and free the enzyme. The reaction can be written as follows:

$$\mathrm{E+S} \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} \mathrm{ES} \xrightarrow{k_2} \mathrm{E+P}$$

The law of mass action can be applied to the biochemical equations above to transform them into mathematical equations that describe the kinetics of the molecular reactions. These mathematical equations are known as differential equations, which will be introduced later on. The complete dynamics of the reactions occurring in an enzyme system are often quite complicated, yet may be unnecessary for understanding the basic reaction of the substrate being transformed into the product.

Frequently, it has been observed that the enzyme-substrate complex forms extremely rapidly, while the forward reaction (also known as *turnover number*), k_2, occurs on a slower time scale. It is assumed that the complex is formed almost instantaneously, a *quasi-steady state*, then the forward reaction proceeds from there. This assumption gives one of the derivations of the Michaelis-Menten enzyme reaction rate. When a quasi-steady state approximation is made for the initial equilibrium between the free enzyme and substrate and the complex, then the rate of the forward reaction to the product is written as

$$R\left([\mathrm{S}]\right) = \frac{k_2[\mathrm{E}]_0[\mathrm{S}]}{K_m + [\mathrm{S}]} = \frac{V[\mathrm{S}]}{K_m + [\mathrm{S}]},$$

where [S] is the substrate concentration and V and K_m are kinetic constants determined by the reaction given above. The constant V (also commonly denoted V_{max}) is called the maximal velocity of the reaction. K_m is the Michaelis constant, and its value is the value of the substrate concentration at which the reaction achieves half of the maximum velocity. This function R is a rational function.

Pate [1] shows that binding of ATP to myosin in forming cross-link bridges to actin for the power stroke of striated muscle tissue satisfies a Michaelis-Menten kinetics. In this particular example, the reaction velocity is an actual velocity of motion, where the chemical energy of ATP is transformed into mechanical energy by movement of the actin filement. The value of K_m gives the concentration of ATP that produces half the maximum velocity of motion for the actin filement. For rabbit psoas muscle tissue, experimental measurements give $V_{max} = 2040n\mathrm{m/s}$ and $K_m = 150\mu\mathrm{M}$.

Other Functions – Michaelis-Menten

In this applet it is possible to observe how the reaction rate R varies as a function of $[\mathrm{S}] = [\mathrm{ATP}]$ for various values of the maximal velocity V and the Michaelis constant K_m.

Figure 1 shows typical Michaelis-Menten behavior where the initial rise in the reaction velocity is almost linear, but as the concentration increases, there are diminishing returns with the eventual saturation of the reaction at some maximal rate (the enzymes are working as hard as they can).

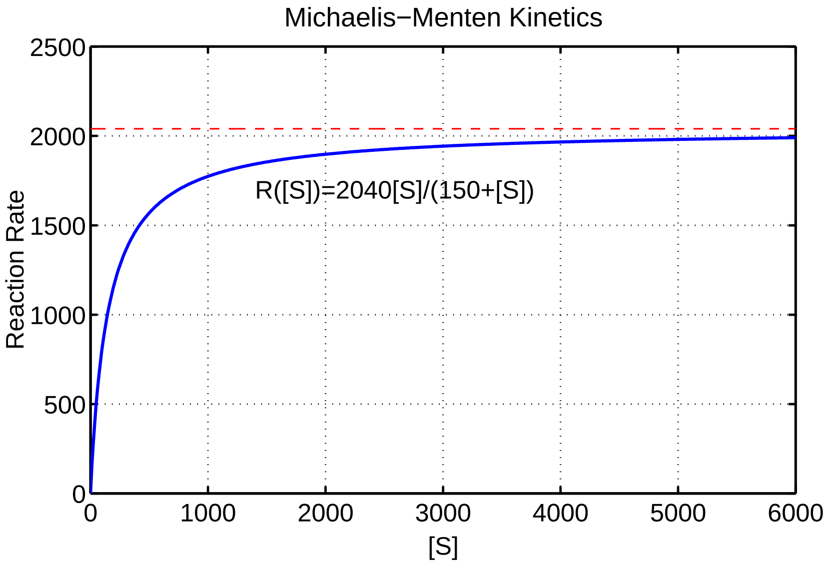

Figure 1: Michaelis-Menten kinetics for rabbit psoas muscle tissue.

2 POLYNOMIALS AND RATIONAL FUNCTIONS

One of the most important class of functions, which are commonly studied, are the polynomials.

The most *general polynomial of order* n is written:

$$p_n(x) = a_n x^n + a_{n-1}x^{n-1} + a_{n-2}x^{n-2} + \ldots + a_1 x + a_0,$$

where the coefficients a_i are constants and n is a positive integer ($a_n \neq 0$).

In the second chapter of this book, we studied linear functions. These are simply first order polynomials. The last chapter reviewed quadratic functions, which are second order polynomials.

Polynomials are often used in modeling as a means of fitting complicated data. When a polynomial curve fits the data well, then the polynomial, as a function, can be used as a simple model to aid in the interpretation of the data and to construct predictions of how other experiments should behave. There are excellent routines for finding the best least squares fit of a polynomial to data (such as an Excel Trendline). Polynomials are defined for all values of x and form very smooth curves. This makes it easy to use them for interpreting data, such as where *minimum* and *maximum values* occur or to compute the *area under the curve.* These phenomena are topics that Calculus covers and will be detailed later in this book.

As noted above, polynomials are considered *nice* functions because of their well-behaved properties. Yet even something as basic as finding the roots of an equation (setting $p_n(x) = 0$) for a polynomial becomes quite difficult for $n > 2$, and rarely even possible for $n > 4$. We have the quadratic formula, but few know the formulae for handling third and fourth order polynomials (though they do exist).

Example 1 *Cubic Polynomial*

Consider the cubic polynomial given by

$$p(x) = x^3 - 3x^2 - 10x.$$

Find the roots of this equation and graph this cubic polynomial.

Solution: Since we do not have a quadratic formula for cubic equations, we must hope to find a factorization in order to find the roots of the polynomial. In this case, to find the roots, we solve

$$p(x) = x^3 - 3x^2 - 10x = x(x-5)(x+2) = 0.$$

It follows that the roots of this polynomial are $x = 0, -2$, or 5. A graph of this cubic polynomial is below with the roots clearly visible as the x-intercepts. Later we will learn (through techniques of Calculus) to find the high point occurring at $(-1.08, 6.04)$ and the low point occurring at $(3.08, -30.04)$. ◁

Example 2 *Factorizing*

Let us solve the following equation:

$$x^4 - 5x^2 + 4 = 0.$$

Solution: We factor this equation into the following:

$$(x^2-1)(x^2-4) = (x-1)(x+1)(x-2)(x+2) = 0.$$

Thus, the solution is given by $x = -2, -1$, 1, and 2. ◁

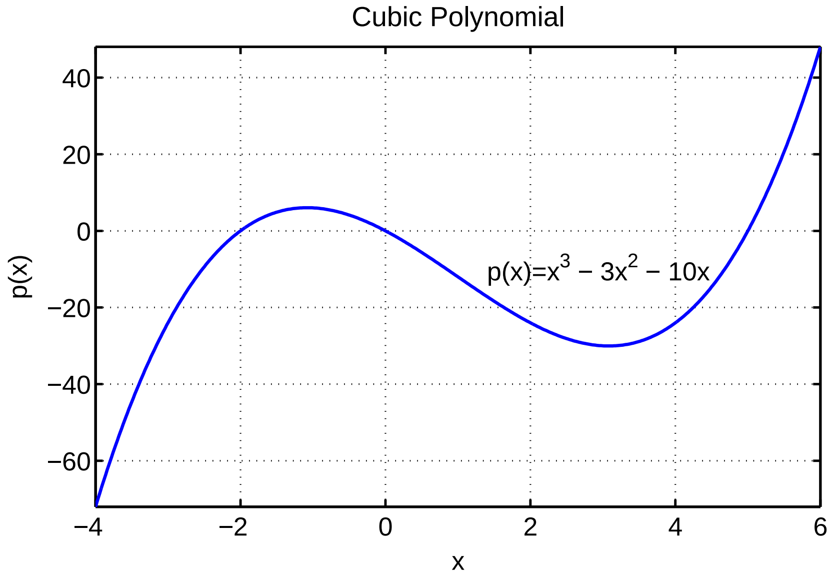

Figure 2: Graph of the cubic polynomial given in Example 1.

Polynomials have their limitations, so they are often not appropriate for certain modeling situations. We will need to extend the classes of functions that we study through this course. Our opening example showed Michaelis-Menten kinetics where the reaction rates saturated. This type of behavior is best studied using rational functions.

2.1 RATIONAL FUNCTIONS

A function $r(x)$ is a *rational function* if $p(x)$ and $q(x)$ are polynomials and

$$r(x) = \frac{p(x)}{q(x)}.$$

Hence, rational functions are the *quotient* of two polynomials. We saw this form of a function in the biochemical analysis of enzyme kinetics given above. The numerator and the denominator were both linear functions, *i.e.*, $R([\mathrm{S}])$ is constructed of the quotient of the linear functions $p([\mathrm{S}]) = \mathrm{V}[\mathrm{S}]$ and $q([\mathrm{S}]) = \mathrm{K_m} + [\mathrm{S}]$.

Since a rational function is a quotient, we have to worry more about the domain of this type of function. If the denominator, $q(x)$, is zero, then the rational function, $r(x)$, becomes undefined at that value of x. Thus, the domain of the rational function, $r(x)$, is all x such that $q(x)$ does not equal zero. The roots of the polynomial $q(x)$ are candidates for *vertical asymptotes* of $r(x)$. Also, when the order of the polynomial in the numerator of a rational function is less than or equal to the order of the polynomial of the denominator, then a *horizontal asymptote* occurs.

> When the graph of a function $f(x)$ approaches a vertical line, $x = a$, as x approaches a, then that line is called a *vertical asymptote*

Note a function cannot continuously cross a vertical asymptote.

> When the graph of a function $f(x)$ approaches a horizontal line, $y = c$, as x becomes very large ($x \to \infty$) or x becomes very small ($x \to -\infty$), then that line is called a *horizontal asymptote*

Note a function may cross horizontal asymptotes.

Example 3 *Sketch of a Rational Function*

Let us examine the rational function

$$r(x) = \frac{10x}{2+x}.$$

Find the domain of this function, the x and y-intercepts, and vertical and horizontal asymptotes, then sketch a graph of the function.

Solution: We see that the denominator is zero when $x = -2$. Thus, the *domain of this function* must exclude $x = -2$. Since $r(0) = 0$ and $10x/(2+x) = 0$ implies that $x = 0$, the x and y-intercepts are easily seen to be zero. Thus, this function passes through the origin.

As x gets very close to -2, the function becomes undefined and the value of $r(x)$ goes to either positive or negative infinity. (See the graph of Figure 3.) Thus, $x = -2$ becomes a vertical asymptote. If you consider very large values of x, then the 2 in the denominator becomes insignificant, so the value of $r(x)$ approaches $10x/x = 10$. This becomes the horizontal asymptote. The graph of Figure 3 shows $r(x)$ with its vertical and horizontal asymptotes. ◁

Below, we continue with more examples of rational functions.

Example 4

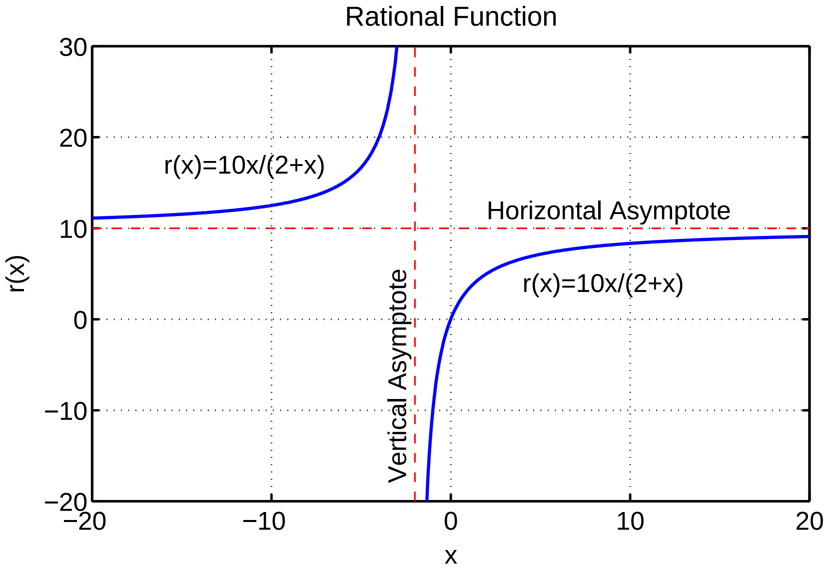

Figure 3: Graph of the rational function given in Example 3.

Let us solve the following equation:

$$x + \frac{2}{x-6} = 3.$$

Solution: Provided x is not 6, we can multiply through by $x - 6$ giving:

$$x^2 - 6x + 2 = 3x - 18$$

or,

$$x^2 - 9x + 20 = (x-4)(x-5) = 0.$$

Thus, $x = 4$ or 5. ◁

Example 5 Consider the function

$$y = \frac{x+2}{x-3}.$$

Find the domain of the function and the x and y-intercepts. Determine any vertical or horizontal asymptotes. Sketch the graph of this function.

Solution: When the denominator of a rational function approaches zero, the value of the function approaches positive or negative infinity. Therefore,

these values for x must be excluded. Since the denominator is zero when $x = 3$, the domain is all real numbers, such that $x \neq 3$. The y-intercept is found by substituting $x = 0$, so $y = 2/(-3) = -2/3$. The x-intercept is found by solving $(x+2)/(x-3) = 0$ or $x + 2 = 0$, so $x = -2$.
Since the degree of the numerator is equal to the degree of the denominator, there is a horizontal asymptote. For large x, we can neglect the constants in the numerator and the denominator. It follows that

$$y = \frac{x+2}{x-3} \longrightarrow \frac{x}{x} = 1.$$

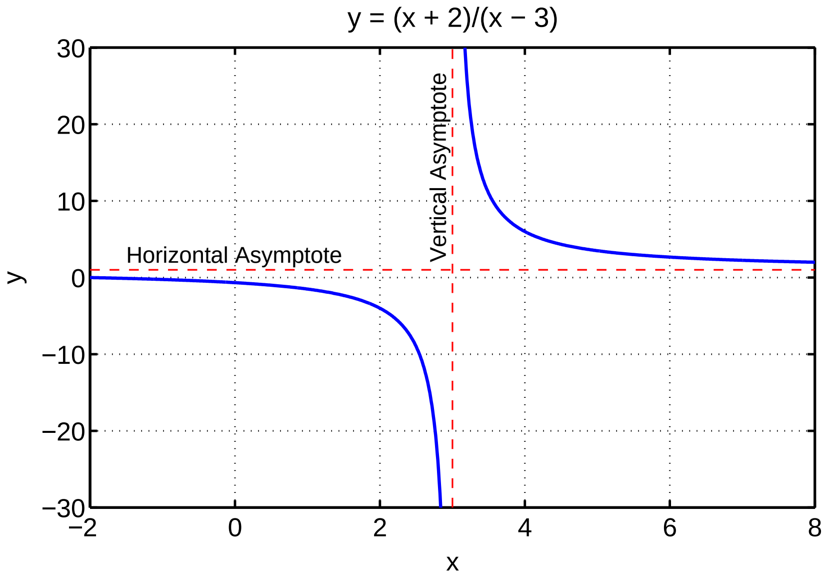

Figure 4: Graph of the rational function of Example 5.

Thus we have a horizontal asymptote at $y = 1$. The denominator is zero at $x = 3$, so there is a vertical asymptote at $x = 3$. The graph of the above function is shown in Figure 4 with the asymptotes drawn with dashed lines.

◁

Example 6 Consider the function

$$y = \frac{4x^2}{4 - x^2}.$$

Find the domain of the function. Determine any vertical or horizontal asymptotes. Sketch the graph of this function.

Solution: The domain of the function is again determined by finding when the denominator equals zero. The denominator is easily factored, so

$$4 - x^2 = (2 + x)(2 - x)$$

or,

$$\begin{aligned} -(x+2)(x-2) &= 0 \\ x &= \pm 2. \end{aligned}$$

Therefore, our domain is all real numbers such that $x \neq \pm 2$. The values excluded from the domain represent vertical asymptotes. Thus, we have two vertical asymptotes at $x = -2$ and $x = 2$. Since the degree of the numerator (2) is equal to that of the denominator, we have a horizontal asymptote. Letting x approach positive or negative infinity, we can ignore the 4 in the denominator to obtain:

$$y = \frac{4x^2}{4 - x^2} \longrightarrow \frac{4x^2}{-x^2} = -4.$$

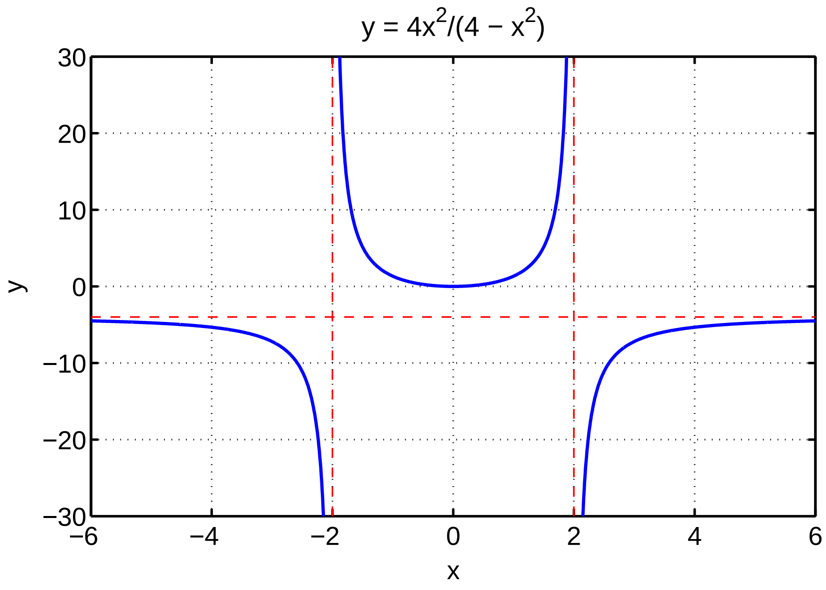

Figure 5: Graph of the rational function of Example 6 with three asymptotes.

The horizontal and vertical asymptotes are drawn with dashed lines on the graph of Figure 5. The only intercept for this graph is the origin, $(0, 0)$. This is an even function ($f(-x) = f(x)$), so it is symmetric about the y-axis. To sketch the graph, one can select a few x-values and take advantage of how functions behave with asymptotes to produce the graph. ◁

Example 7 *Lineweaver-Burk Plot*

The Michaelis-Menten rate function traces out a hyperbola. Suppose we write the velocity function as

$$V = \frac{V_{\max}[\mathrm{S}]}{K_m + [\mathrm{S}]}.$$

If we take the inverse of this expression, we have

$$\frac{1}{V} = \frac{K_m + [\mathrm{S}]}{V_{\max}[\mathrm{S}]} = \frac{K_m}{V_{\max}}\frac{1}{[\mathrm{S}]} + \frac{1}{V_{\max}}.$$

If we let $y = 1/V$ and $x = 1/[\mathrm{S}]$, then the equation above is easily seen to form a line,

$$y = \frac{K_m}{V_{\max}}x + \frac{1}{V_{\max}}.$$

The slope of this line is K_m/V_{max}, the y-intercept is $1/V_{max}$, and the x-intercept is $-1/K_m$. Figure 6 shows the graph of this straight line, the *Lineweaver-Burk plot.*

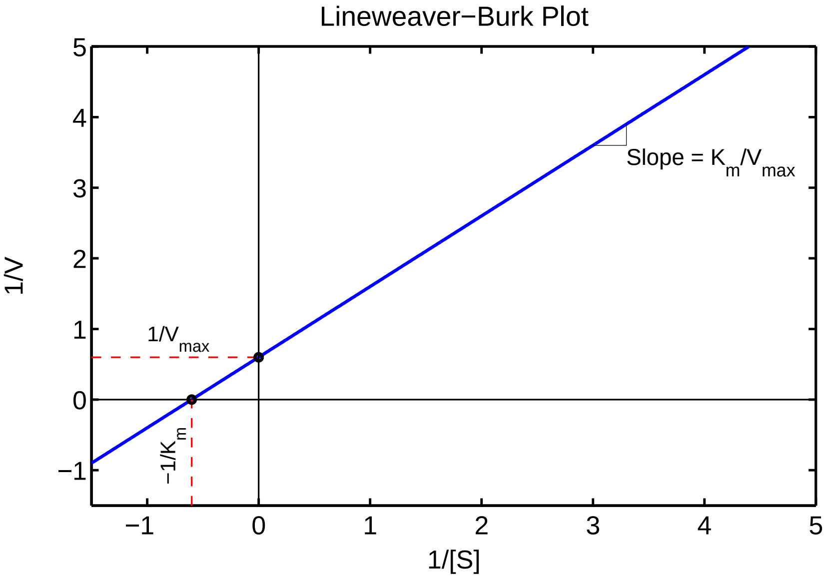

Figure 6: General graph for the Lineweaver-Burk function obtained from the Michaelis-Menten rate function.

Thus, by graphing $1/V$ *versus* 1/[S], with data on an enzyme (forming a line), the Lineweaver-Burk allows easy identification of the Michaelis-Menten constant K_m and the maximum velocity V_{max}. ◁

Example 8 *Another Enzyme Kinetics*

Suppose an enzyme satisfies the equation

$$V = \frac{20[S]}{10+[S]}.$$

a. Sketch a graph of this function for $0 < [S] < 100$. Find any horizontal asymptotes.

b. Determine the linear equation for $x = 1/[S]$ and $y = 1/V$, then create the Lineweaver-Burk plot. Find the intercepts on the x and y axes. What is the slope for this line?

Solution: a. Before graphing, it is helpful to find any asymptotes. Since the degree of the numerator (1) is equal to that of the denominator, we have a horizontal asymptote. As S approaches positive infinity, we can ignore the 10 in the denominator, and we find a horizontal asymptote at $y = 20$. The asymptote is drawn with dashed lines in the graph of Figure 7.

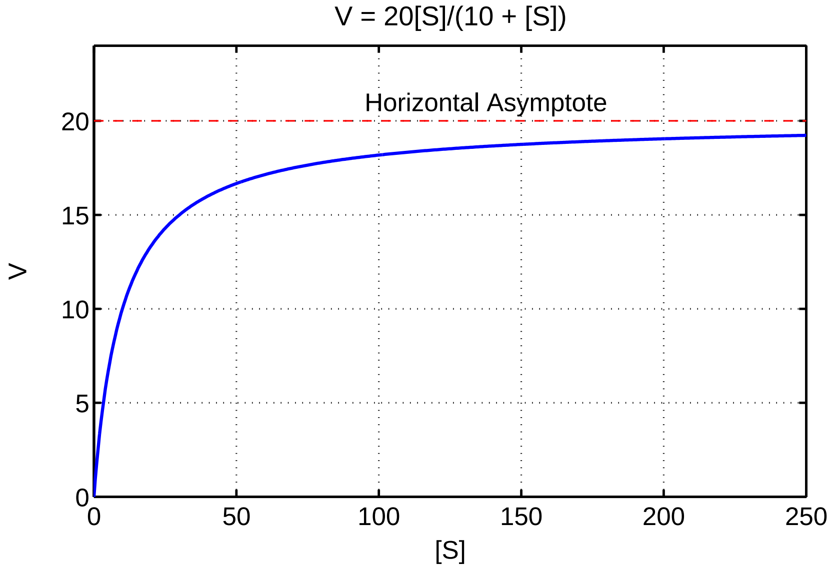

Figure 7: Graph of the velocity function of Example 8.

b. For $x = 1/[S]$ and $y = 1/V$, we have $[S] = 1/x$ and $V = 1/y$.

Substituting these into the given equation and solving for y, we obtain

$$\frac{1}{y} = \frac{20(1/x)}{10 + (1/x)} = \frac{20}{10x + 1}$$

or,

$$y = \frac{10x + 1}{20} = \frac{1}{2}x + \frac{1}{20}.$$

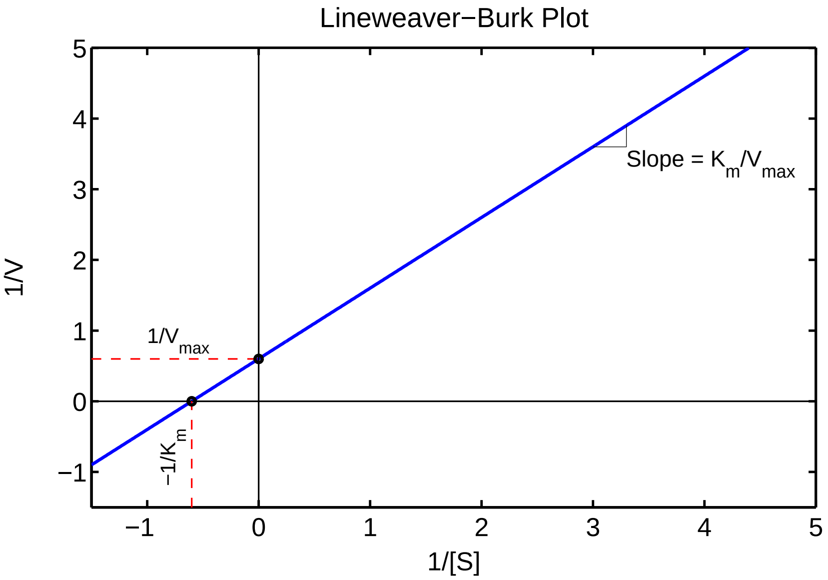

Figure 8: Lineweaver-Burk function of Example 8

The slope of this line is $1/2$, and the y-intercept is $1/20$. The x-intercept is found by setting $y = 0$, and solving for x. Therefore, the x-intercept is equal to $-1/10$. ◁

3 ACID CHEMISTRY REVISITED

In Section 3.1 of Chapter 4, weak acids were examined. To find the concentration of the acid, $[\mathrm{H}^+]$, the quadratic formula was needed. The concentration of acid depends on the equilibrium constant and the normality, x, of the weak acid solution. From the previous section, we have

$$[\mathrm{H}^+] = \frac{1}{2}\left(-K_a + \sqrt{K_a^2 + 4K_a x}\right).$$

Since the equilibrium constant is fixed depending on the particular weak acid, we see that the $[\mathrm{H}^+]$ is a function of the normality of the solution, x.

We see that this function is neither a polynomial nor a rational function, but the *square root function*. Figure 9 (right) shows a graph of the $[H^+]$ as a function of x for formic acid, where $K_a = 1.77 \times 10^{-4}$. Note that this function has the shape of a quadratic function rotated 90°.

The pH of the solution is given by $-\log_{10}([H^+])$, which becomes a composite function. The graph is shown in Figure 9 (left), but we will delay studying logarithms until the next section.

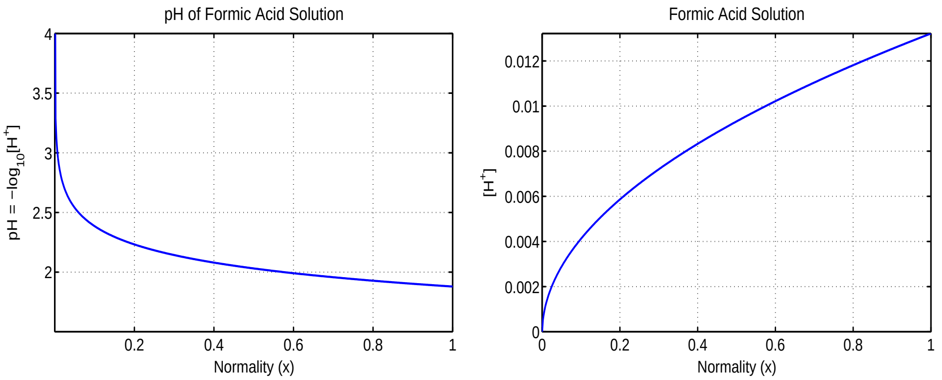

Figure 9: Left: Logarithmic function for the pH of the formic acid H^+. Right: Graph of the function of the concentration of acid H^+ with respect to normality of the solution x.

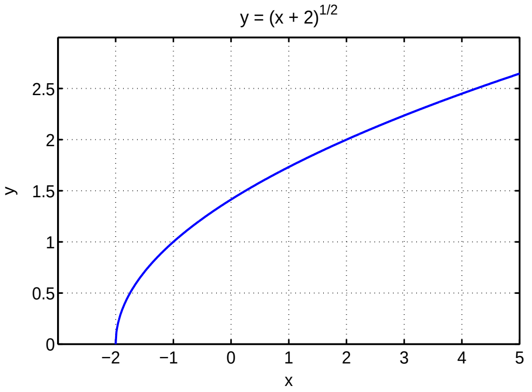

Figure 10: Graph of the *square root function* of Example 9.

4 SQUARE ROOT FUNCTION

The square root function is the inverse of the quadratic function. It is important to note that the square root function is only defined for positive quantities under the radical. Thus, we have this important rule:

> The domain of a square root function is found by solving the inequality for the function under the radical being greater than zero.

Example 9 Consider the function

$$y = \sqrt{x+2}.$$

Find the domain of this function and graph the function.

Solution: The domain of this function satisfies $x + 2 \geq 0$, so this example has its function defined for $x \geq -2$. The graph is shown in Figure 10. ◁

Example 10 *More Square Root Functions*

Consider the following functions with square roots. Find the domains and ranges of these functions, then sketch their graphs.

a. $y = \sqrt{8-2x}$ **b.** $y = \sqrt{8-2x-x^2}$

Solution: a. The quantity under the square root sign must be positive, so to find the domain we must first solve

$$8 - 2x \geq 0,$$

which gives

$$x \leq 4.$$

Thus, the domain is $x \leq 4$. The range can be seen from the graph of Figure 11 (left) and satisfies $y \geq 0$. The graph of the function is given in Figure 11 (left).

b. The quantity under the square root sign must be positive, so to find the domain we must first solve

$$8 - 2x - x^2 \geq 0.$$

To solve this, we first determine when $8 - 2x - x^2 = (4 + x)(2 - x) = 0$ or $x = -4$ and 2. These values give the boundary of the domain. It is not hard to see that the domain is given by $-4 \leq x \leq 2$. (This quadratic function

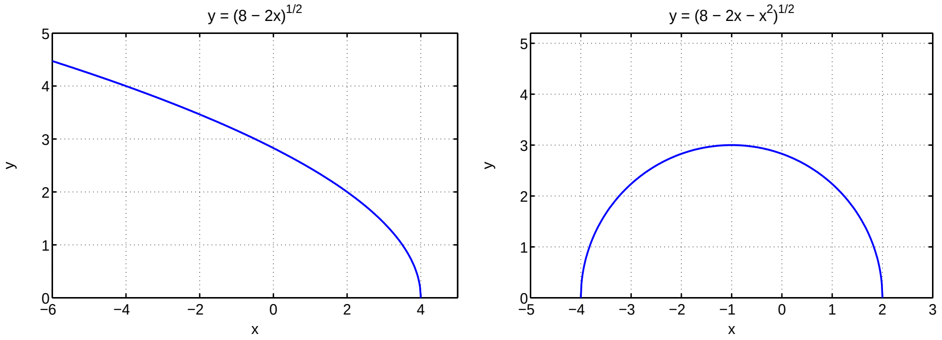

Figure 11: Left: Graph of the square root function of Example 10a. Right: Graph of the square root function of Example 10b.

is positive in this interval and negative outside this interval.) The largest value under the radical occurs when $x = -1$ with a value of 9. Thus, the range of the function is given by $0 \leq y \leq 3$. This can also be seen from the graph of Figure 11 (right). (This graph is a semi-circle.) $\triangleleft$

5 EXERCISES

Solve the following equations for x.

1. $x^3 + 3x^2 - 4x = 0$
2. $12x^2 - 4x^3 - x^4 = 0$
3. $x - \dfrac{24}{x+2} = 3$
4. $x - \dfrac{9}{x} = 0$
5. $\dfrac{4}{x^2} - \dfrac{3}{x} = 1$
6. $x + \dfrac{6}{x-1} = -5$

For each of the following functions, determine the domain. Find any x or y-intercepts and locate any vertical or horizontal asymptotes. Sketch the graphs of the functions:

7. $y = \dfrac{1}{2x-6}$
8. $y = \dfrac{x+1}{x-1}$
9. $y = \sqrt{2x-4}$
10. $y = \dfrac{x}{x^2-9}$
11. $y = \dfrac{2x^2}{x^2-2x}$
12. $y = \sqrt{25-x^2}$
13. $y = \dfrac{x^2}{x+1}$
14. $y = \sqrt{9-x}$
15. $y = \dfrac{x^2+1}{x^2-4x+3}$

16. Suppose an enzyme satisfies the equation

$$V = \frac{20[S]}{10 + [S]}.$$

a. Sketch a graph of this function for $0 \leq [S] \leq 100$. Find any horizontal asymptotes.

b. Determine the linear equation for $x = 1/[S]$ and $y = 1/V$, then create the Lineweaver-Burk plot. Find the intercepts on the x and y axes. What is the slope for this line?

17. The growth of a culture of yeast is empirically shown to satisfy the equation

$$P(t) = \frac{10 + 0.2t^2}{1 + 0.001t^2},$$

where t is in hours and P is the density of the population (number of yeast/cc).

a. Find the density of the yeast culture at $t = 0$ and 10 hours.

b. Sketch a graph of $P(t)$ for $t \geq 0$. Show any asymptotes.

18. Consider a weak acid with $K_a = 0.0001$.

a. Find the $[H^+]$ for a 0.1N solution of this acid.

b. Let x be the normality of the weak acid. Sketch a graph of the $[H^+]$ for $0 \leq x \leq 1$.

19. **Eutrophication** During an algae bloom, a pond becomes eutropic with oxygen levels dropping to near zero at the bottom because of decaying organic matter. Suppose that the level of O_2 dissolved in the water varies with the depth from the surface according to the function:

$$P(y) = 3\sqrt{9 - y},$$

where y is the depth in meters from the surface and P is in mmHg of dissolved O_2.

a. Find the domain for $P(y)$ and sketch a graph of this function.

b. If fish need at least 6 mmHg of dissolved O_2, then how deep can the fish survive.

6 REFERENCES

[1] E. Pate, "Modeling of muscle crossbridge mechanics," in *Case studies in Mathematical Modeling – Ecology, Physiology, and Cell Biology*, eds. H.G. Othmer, F.R. Adler, M.A. Lewis, and J.C. Dallon, Prentice-Hall (1997).

CHAPTER 6:

ALLOMETRIC MODELING

This section introduces allometric or power law models. Many biological phenomena show an allometric relationship, such as how height relates to weight for a species. To manage the mathematics underlying a power law function, we review the properties of exponential and logarithmic functions. The mathematical properties discussed below are critical to analyzing many biological problems.

1 CUMULATIVE AIDS CASES

The advent of AIDS in modern society has had a significant impact on both personal behavior and public policy. Some scientists believe that this virus may have one of the greatest effects on human society in the 21^{st} century. The new protease inhibitors have significantly improved the quality of life for those who are HIV positive; however, this has come at a substantial cost to society and are unavailable to the majority of infected people in other countries. The new drugs are extremely expensive, are difficult to take because of the complex scheduling requirements to be effective, and have many strong side effects (besides not always working for a particular person or strain of the HIV virus). In turn, there are a number of people who are now avoiding safe sex practices as they no longer fear the "Death Sentence" that used to be associated with an HIV infection. There is a vast literature available on this topic, including many mathematical models. There are good images to help visualize the HIV-virus attacking human immune cells readily available on the web[1].

There is an important need for our society to know the extent of this disease from both an economic and sociological perspective. In order to make informed public policy, we need to know what is the expected case load in the upcoming years. However, it is clearly an extremely complex modeling problem. Table 1 gives the cumulative cases of AIDS between 1981 and 1992 [1].

---

[1] http://www-rohan.sdsu.edu/~jmahaffy/courses/s00a/math121/lectures/allometic_modeling/hiv.html, last visited 05/18/04.

Allometric – U.S.A.

You can view an animated.gif showing the spread of the disease (through mortality statistics) over a similar period of time through out the U.S.A.

Year	Cumulative AIDS Cases (thousands)
1981	97
1982	709
1983	2,698
1984	6,928
1985	15,242
1986	29,944
1987	52,902
1988	83,903
1989	120,612
1990	161,711
1991	206,247
1992	257,085

Table 1: Data of the Cumulative AIDS (in thousands of cases) through out the U.S.A. from 1981 till 1992.

A quick glance at the data will clearly show that it is not linear, so a linear model is not appropriate. There are general methods for finding the least squares best fit to nonlinear data. However, these techniques are very complicated an often difficult to implement.

Allometric – Non-linear Best Square Fit

This applet helps you find the best nonlinear least squares fit to the data for cumulative AIDS cases (also refer to the Section 7 at the end of this chapter), which is different from the technique we will show below.

2 ALLOMETRIC OR POWER LAW MODEL

As noted above, using a least squares fit to nonlinear data can be extremely difficult. However, there are a few standard nonlinear models used in biological applications that are more easily analyzed. The technique that we will develop in this section is known as the *Power Law of Modeling.* It is also referred to as *Allometric Modeling.* Allometric models are used regularly in modeling complex biological phenomena where the actual mechanisms underlying the model behavior are too complex to describe in detail, but there is a need to be able to make some predictions.

Allometric models assume a relationship between two sets of data, x and y, that satisfy a power law of the form

$$y = Ax^r,$$

where A and r are parameters that are chosen to best fit the data.

Note that the allometric model assumes that when $x = 0$, then $y = 0$. As always, you should be aware of the limitations of this type of modeling. This method provides its best predictive capabilities when examining a situation that lies between the given data points. For example, if the number of species of herptofauna on Caribean islands is determined for a collection of islands with varying areas, then this model would give a reasonable estimate for the expected number of species on another Caribean island with an area that lies between the collected data. It would not be appropriate for extending to a large continent as the area is significantly beyond the range of the collected data. It would not be appropriate for another island such as Iceland, which lies in a different type of climate and has a different geography.

Allometric models are found by taking the logarithms of the data (or graphing the data on log-log graphs) and seeing if the data lie roughly on a straight line. If this is the case, then a power law relationship makes a reasonable model.

Allometric – Cumulative AIDS

This applet shows the linear least squares fit to the logarithms of the data for cumulative AIDS cases, and the graph to the right shows the modeling relationship with a normal scale. The allometric model has x be time in years since 1980 and y be the cumulative AIDS cases. See Figure 1 as an example of such an applet.

This applet can be adjusted until you reach a minimum least squares for the log of the data with $J(A, r) = 0.10$. The best slope is $r = 3.27$ and the best intercept is $\ln(A) = 4.42$. We will show later that this gives the best fit power law for this model as

$$y = 82.7x^{3.27}.$$

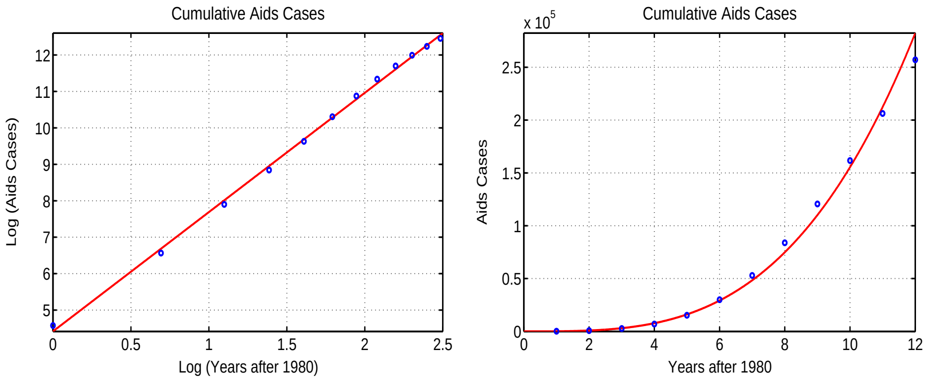

Figure 1: Example of the two graphs obtained from the applet Allometric – Cumulative AIDS.

The graph shows that the power law provides a reasonable fit to the data. Unfortunately, the fit is weakest at the end where we would like to use the model to predict the cumulative AIDS cases for the next year. The model predicts $366,990$ cases in 1993, which is clearly too high from the given data. However, the analysis does give some indication of the rate of growth for this disease, which provides a first approximation for improved models and could be applied to expected spread of another disease with similar infectivity as HIV. This modeling technique is still valuable for analysis of many other data sets and occasionally can provide insight into the underlying biology of the problem.

Allometric-Nonlinear Least Squares

A better fit to the data is shown in the nonlinear least squares Section 7 that can also be viewed in this site.

Our least squares best fit to the data of Table 1 uses the logarithms of the data. To detail how the parameters A and r in the model are found, we need to review the properties of exponents and logarithms.

3 REVIEW OF EXPONENTS AND LOGARITHMS

There are several properties of *exponents* that you should remember from algebra.

1. $a^m a^n = a^{m+n}$
2. $(a^m)^n = a^{mn}$
3. $a^{-m} = \dfrac{1}{a^m}$
4. $\dfrac{a^m}{a^n} = a^{m-n}$
5. $(ab)^m = a^m b^m$
6. $a^0 = 1$

These properties can be used to simplify expressions involving exponents.

The expressions for the rules of exponentiation above are written with an arbitrary base, a, since these are general rules. The reader is undoubtedly most familiar with $a = 10$, since our number system is based on 10. Most of your science courses use scientific notation to help with the management of numbers ranging over a broad scale of values. In Calculus and for a variety of biological modeling applications, we will show another base, $a = e$, is very useful. This base is readily found on scientific calculators. At this point in the text, we only note that e is an irrational number between 2 and 3 with

$$e \approx 2.71828.$$

To solve equations that have exponents in them, we need to have the inverse function of the exponent. This is the *logarithm*.

If you are given the equation,

$$y = a^x,$$

then the inverse equation that solves for x is given by

$$x = \log_a y.$$

The a in the above expression is called the base of the logarithm. Again there are a collection of properties of logarithms that prove useful for solving equations and simplifying expressions.

1. $\log(ab) = \log(a) + \log(b)$
2. $log(a^m) = mlog(a)$
3. $\log(1/a) = -\log(a)$
4. $\log(a/b) = \log(a) - \log(b)$
5. $\log_a(a) = 1$
6. $\log(1) = 0$

Note that in the properties of logarithms, we only needed to specify the base of the logarithm for Property 5. All other properties are independent of which base is used.

The two most common logarithms that are used are $\log_{10}$ and $\log_e$. The latter logarithm is called the *natural logarithm*, often denoted log or ln, and is the one most commonly used (and is the default on your calculator). It is the inverse for exponentials with base e. As the techniques of Calculus become developed in this text, you will learn about the importance of the natural base e. For most of our work, we will use the natural logarithm. (Note that that different computer programs default to different bases with Excel defaulting to $\log_{10}$, while MatLab, a common scientific program, defaults to $\log_e$.)

Example 1 Solve the equation

$$e^{x-2} = 3.$$

Solution: Taking the natural logarithm of both sides gives

$$x - 2 = \ln(3),$$

so,

$$x = \ln(3) + 2. \qquad \triangleleft$$

Example 2 Solve the equation

$$\ln(2x + 1) = 4.$$

Solution: Exponentiating both sides, we find

$$2x + 1 = e^4,$$

so,

$$x = (e^4 - 1)/2. \qquad \triangleleft$$

4 GRAPHING EXPONENTIALS AND LOGARITHMS

As noted above, the exponential function, e^x, and the natural logarithm, $\ln(x)$, are inverse functions of each other. In this section we show the graphs of these functions to develop some sense of their behavior. We will study e^x in greater detail after learning more about the derivative. However, for graphing purposes we recall that $e \approx 2.71828....$ The domain of e^x is all of x with this function tending toward zero very fast for $x < 0$ (a horizontal asymptote of $y = 0$) and growing very fast for $x > 0$. Its range is $y > 0$. Similarly, the graph of $y = e^{-x}$ has the same y-intercept of 1, but its the mirror reflection through the y-axis of $y = e^x$. It rapidly becomes very large for $x < 0$ and very small for $x > 0$. A graph of both $y = e^x$ and $y = e^{-x}$ is given in Figure 2.

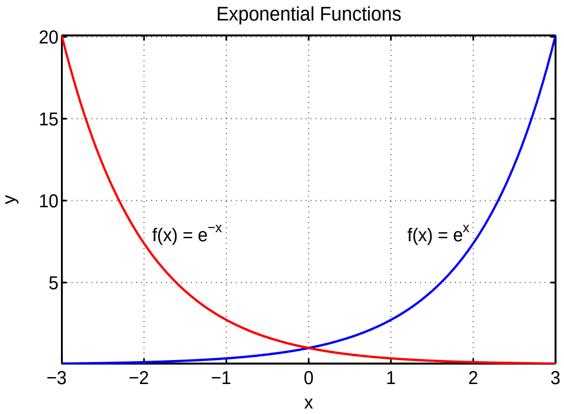

Figure 2: Graphs of the exponential functions, $f(x) = e^{-x}$ and $f(x) = e^{x}$.

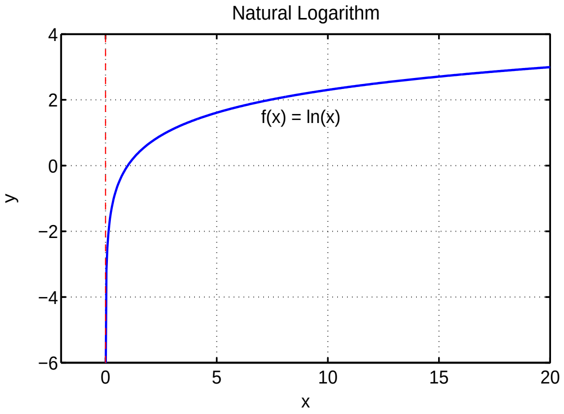

Figure 3: Graph of the *Natural Logarithm function*, $f(x) = \ln x$.

Since $\ln(x)$ is the inverse function of e^x, an easy way to graph this function is to mirror the graph of e^x through the line $y = x$. The domain of $\ln(x)$ is $x > 0$, while its range is all values of y. As $y = \ln(x)$ becomes undefined at $x = 0$ there is a vertical asymptote at $x = 0$. The graph of $y = \ln(x)$ is given in Figure 3.

We will see that the exponential function plays a role in many applications, so it is very important to understand this function and how its graph behaves.

Example 3 Graph the equation

$$f(x) = 4 - e^{-2x}.$$

Determine all intercepts and any horizontal asymptotes.

Solution: We begin by finding the intercepts. When $x = 0$, $f(0) = 4 - e^0 = 4 - 1 = 3$. Thus, the y-intercept is $(0, 3)$.

Solving $4 - e^{-2x} = 0$, gives $e^{-2x} = 4$ or $e^{2x} = 1/4$. Thus, $2x = \ln(1/4) = \ln(2^{-2}) = -2\ln(2)$ or $x = -\ln(2) = -0.6931$. Therefore, the x-intercept is $(-0.693, 0)$.

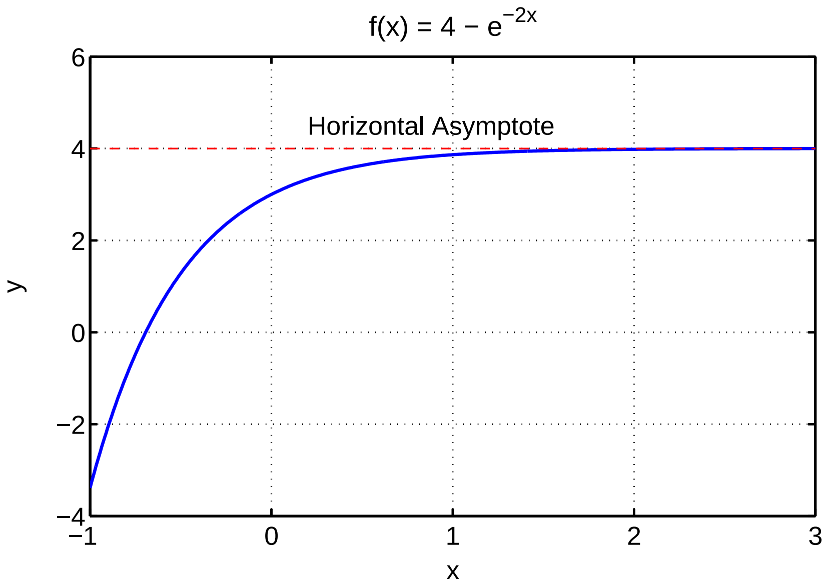

Figure 4: Graph of the exponential function of Example 3.

For large values of x, e^{-2x} is very close to zero, so there is a horizontal asymptote for large positive x with $f(x)$ tending toward 4. The graph is shown in Figure 4. ◁

Example 4 Graph the equation

$$f(x) = \ln(x + 2).$$

Find the domain of this function and determine all intercepts and any vertical asymptotes.

Solution: The domain of $f(x)$ is $x > -2$. To find the y-intercept, set $x = 0$, so $f(0) = \ln(2) = 0.6931$. Thus, the y-intercept is $(0, 0.693)$. Solving $\ln(x + 2) = 0$, gives $x + 2 = 1$ or $x = -1$. Thus, the x-intercept is $(-1, 0)$. There is a vertical asymptote at the edge of the domain, where $x = -2$. The graph is shown in figure 5. ◁

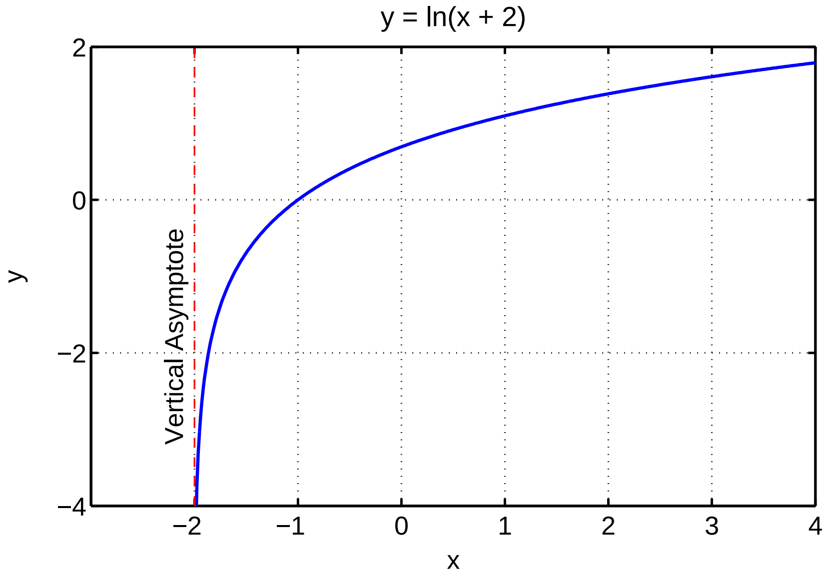

Figure 5: Graph of the logarithmic function given in Example 4.

5 FINDING ALLOMETRIC MODELS

We return to the *Allometric model* developed above, where two sets of data, x and y are assumed to satisfy a power law of the form

$$y = Ax^r.$$

We want to choose the parameters A and r that best fit the data. The next step is to take the logarithm of both sides, then use the properties of logarithms to simplify the equation.

$$\ln(y) = \ln(Ax^r) = \ln(A) + r\ln(x).$$

From this formula, we see that if we take the logarithm of the data, $\ln(x)$ and $\ln(y)$ and graph it we should see a straight line. That is, if we take $X = \ln(x)$, $Y = \ln(y)$, and $a = \ln(A)$, then the above equation can be written $Y = a + rX$, which is a line with a slope of r and a Y-intercept of $\ln(A)$.

> Whenever the logarithms of two sets of data graph as a straight line, then these data are related by an *Allometric* or *Power Law model.*

We return to the example at the beginning of this section. Table 2 includes both the data of Table 1 and the logarithms of the data.

Year	ln(Year−1980) (thousands)	Cumulative AIDS Cases	ln(Cases)
1981	0	97	4.5747
1982	0.6931	709	6.5639
1983	1.0986	2,698	7.9003
1984	1.3863	6,928	8.8433
1985	1.6094	15,242	9.6318
1986	1.7916	29,944	10.307
1987	1.9459	52,902	10.876
1988	2.0794	83,903	11.337
1989	2.1972	120,612	11.700
1990	2.3026	161,711	11.994
1991	2.3979	206,247	12.237
1992	2.4849	257,085	12.457

Table 2: Data as in table 1 with the logarithms of the data.

Figure 6 shows a graph of the logarithms of the data (year−1980) and cumulative AIDS cases along with the best straight line fit. The plot in Figure 6 shows that when the logarithms of the data for the cumulative AIDS cases are plotted against the logarithms of the time since 1980, then these logarithmic data lie fairly close to a straight line though the data are flattening for the later years suggesting a diminished rate of increase. The least squares best fit of the straight line to the logarithms of the data give a slope of $r = 3.274$ and intercept of $a = \ln(A) = 4.415$, which gives $A = 82.70$. From the discussion above, this suggests that the cumulative AIDS cases are well represented by an *allometric* or *power law model.*

Example 5 *Pacific Islands – Biodiversity*

There are three Pacific islands in a chain. Island A is 15 km^2, Island B is 110 km^2, and Island C is 74 km^2. An extensive biological survey finds 5 species of birds on Island A and 9 species of birds on Island B.

a. Assume a power law relationship between the number of species (N) on each of these islands and their area (A) of the form

$$N = kA^x.$$

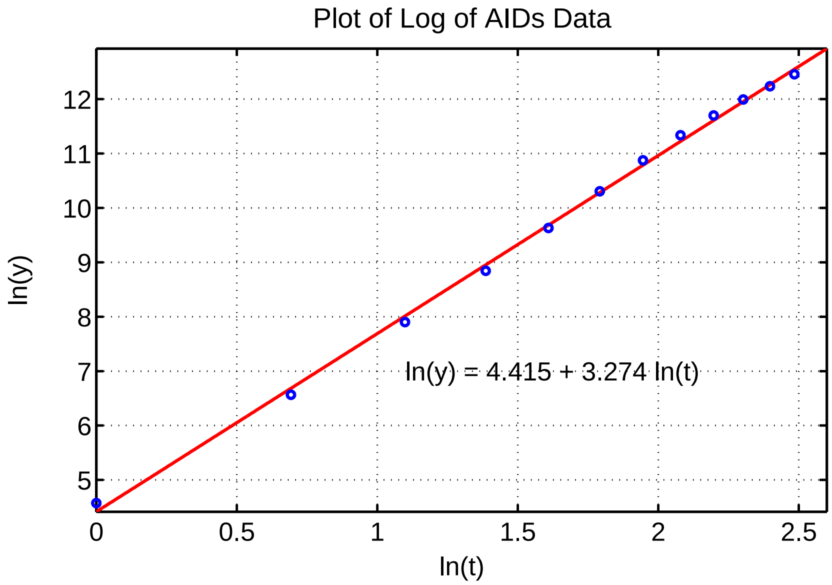

Figure 6: Linear best square fit to the logarithmic data of table 2.

Use the data from Islands A and B to determine the constants k and ^{x}. Use this expression to predict the number of species on Island C.

b. How large of an island would be required to support 20 species of birds near this chain of islands?

Solution: a. Taking the natural logarithm of both sides of the given power law relationship and then solving for slope x, we obtain

$$\begin{aligned} \ln(N) &= \ln(k) + x\ln(A) \\ x &= \frac{\ln(9) - \ln(5)}{\ln(110) - \ln(15)} = \frac{0.588}{1.992} \approx 0.30. \end{aligned}$$

We can use this slope with either of the points (A, N) to find $\ln(k)$

$$\begin{aligned} \ln(5) &= \ln(k) + 0.30\ln(15) \\ \ln(k) &= \ln(5) - 0.30\ln(15) = 0.797 \\ k &\approx 2.2. \end{aligned}$$

So the power law relationship is given by

$$N = 2.2A^{0.30}.$$

We can now predict the number of species on Island C

$$N = 2.2(74)^{0.30} = 8.$$

Thus, there should be 8 species on Island C. Figure 7 shows the graph of the data, model, and prediction.

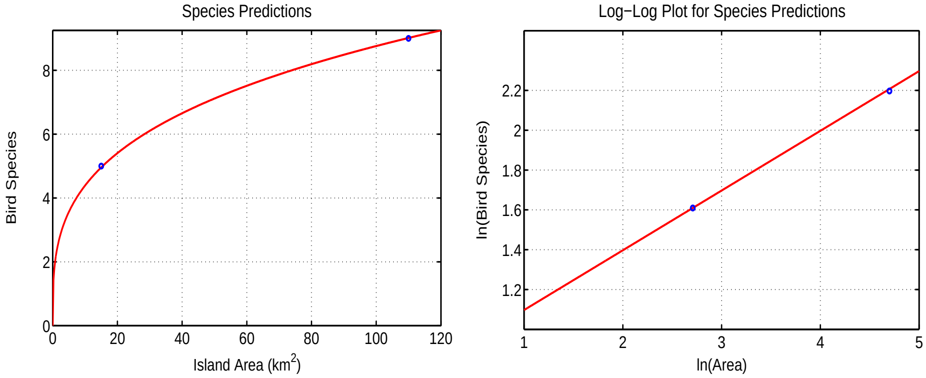

Figure 7: Graphs for Examples 5a (left) and 5b (right).

b. We can use this model to predict the size of an island necessary to support 20 species as follows:

$$20 = 2.2A^{0.30}$$

Solving for A,

$$\begin{aligned} \ln\left(\frac{20}{2.2}\right) &= 0.30\ln(A) \\ \ln(A) &= \frac{\ln\left(\frac{20}{2.2}\right)}{0.30} \approx 7.4. \end{aligned}$$

Exponentiating both sides, we find the island area $A = 1636$ km^2.

Figure 7 shows the graph of the logarithms of the data and the straight line fit that the allometric model gives. ◁

6 LOG – LOG GRAPHS

There exist graphing routines that readily create what is known as a log–log plot. This allows the user to simply graph the data directly onto a graph with logarithmic scales on the axes to see if the data falls on a straight line suggesting an allometric or power law model. Figure 8 shows a plot of the original data on cumulative AIDS cases against the date−1980 on a graph with logarithmic scaled axes.

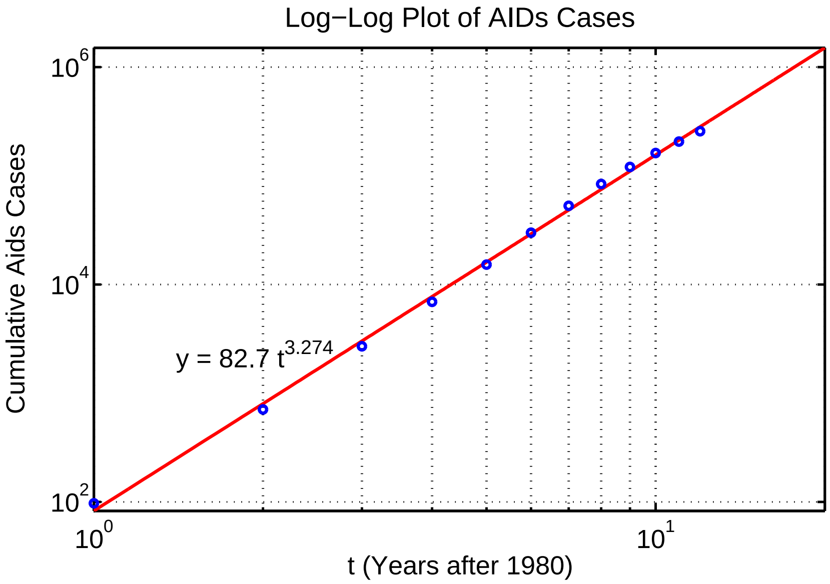

Figure 8: Graph of the cumulative AIDS cases against the date−1980 in a log – log scale.

Our work above shows that allometric modeling is essentially finding the best straight line through the logarithm of data. Below is an example, where it is assumed that the model fits an allometric model. By finding the straight line through the logarithms of the two data points, the model is formulated and can be applied to other cases.

Example 6 *Weight and pulse*

We know that smaller animals have a higher pulse than larger animals. Let us assume that this relationship satisfies an allometric model.

We are given that a 17 g (or 0.017 kg) mouse has a pulse of 500 beats/min. Assume a 68 kg human has a pulse of 65. Use these data to form an allometric model and predict the pulse for a 1.34 kg rabbit.

Solution: The power law gives

$$P = Aw^k.$$

Next we take logarithms to obtain:

$$\ln(P) = \ln(A) + k\ln(w).$$

As noted above, this is a straight line in $\ln(P)$ and $\ln(w)$ with slope of k and intercept of $\ln(A)$. From the data,

Animal	Weight(kg)	$\ln(w)$	Pulse(beats/min)	$\ln(P)$
Mouse	0.017	-4.075	500	6.215
Human	68	4.220	65	4.174

The slope k is given by:

$$k = \frac{4.174 - 6.215}{4.220 + 4.075} = -0.246.$$

We can use this slope with one of the points to find $\ln(A)$ as follows:

$$\ln(A) = -k\ln(w_0) + \ln(P_0) = 0.246 \times 4.220 + 4.174 = 5.212.$$

Thus,

$$\begin{aligned} \ln(P) &= -0.246\ln(w) + 5.212 \\ P &= 183.5w^{-0.246}. \end{aligned}$$

If we use the first equation with a 1.34 kg rabbit, then it gives $P = 171$. ◁

7 NONLINEAR LEAST SQUARES (OPTIONAL MATERIAL)

The fitting of data to a mathematical model is more of an art form than a precise mathematical technique. It is vitally important that the person modeling a particular data set knows what he or she hopes to derive from the mathematical model, then select the model appropriately. The most common means of fitting data uses a least squares best fit of the data to the mathematical model. As we saw earlier, when the data are approximated by a straight line, then there are precise statistical formulae for finding the line that best fits the data in a least squares sense. These formulae are derived from techniques developed in two variable Calculus. The technique can be extended to more general polynomial forms with correspondingly more complicated formulae.

When the mathematical model is nonlinear; then in general, there are no precise formulae for finding the least squares best fit to the data. However, there are mathematical methods for numerically finding the least squares best fit to the data. These numerical methods are notoriously unstable.

7.1 NONLINEAR LEAST SQUARES FOR CUMULATIVE AIDS CASES

The allometric modeling technique developed above shows one case where data can be converted by logarithms into a formula for a straight line, which uses the information from Chapter 3. By using the logarithm of the data, this method gives more weight to some data points over others. A *nonlinear least squares best fit* can give a more direct, even weighting of all data points.

If a nonlinear least squares best fit for cumulative AIDS cases is taken directly from the data, instead of doing a linear least squares fit to the the logarithms of the data, then a slightly different allometric model is found. By adjusting the parameters A and r, the least squares best fit can be minimized with $A = 210$ and $r = 2.87$, giving the sum of the squares of the errors as $J(A, r) = 210,000$. This graph is visibly closer to the data than the fit using the linear least squares fit to the logarithm of the data. Furthermore, this fit will clearly give a better projection of future cumulative AIDS cases by inspection of the graph.

The linear least squares fit to the log of the data is much simpler for finding a power law model, especially with features such as Trendline in Excel. However, this method tends to bias the earlier data points, which is especially poor for projecting future results. The applet mentioned above gives an unbiased nonlinear least squares fit to the data, which is probably the best fit if no other information is available. When more is known about a particular data set, then other weighted least squares analyses may be provide the best fit. However, all of these nonlinear least squares methods are significantly more difficult than the method studied in this chapter.

8 EXERCISES

1. Suppose that $e^a = 3.7$ and $e^b = 0.4$. In addition, assume that $\ln(c) = -1.5$ and $\ln(d) = 2.1$. Use the properties of exponentials and logarithms to evaluate the following:

a. $\dfrac{(e^0 + e^a)^2}{e^{a-b}}$, b. $\dfrac{\ln(d^2/c) - \ln(e))}{(\ln(cd) + \ln(1))}$.

2. Suppose that $e^a = 2.4$ and $e^b = 0.6$. In addition, assume that $\ln(c) = -2.6$ and $\ln(d) = 3.1$. Use the properties of exponentials and logarithms to evaluate the following:

a. $\dfrac{e^0 + e^{2b}}{e^{a-b}}$, b. $\dfrac{\ln(d^2/c) + \ln(e)}{\ln(1) - \ln(c^3)}$.

Graph the following exponentials. Determine all x and y-intercepts for these functions and find any horizontal asymptotes.

3. $f(x) = e^{-x} - 2$
4. $f(x) = 2 + e^{2x}$
5. $f(x) = 10 - e^{-x/2}$
6. $f(x) = e^{x} - 1$

Find the domain for the following functions and graph the logarithms. Determine all x and y-intercepts for these functions and find any vertical asymptotes.

7. $f(x) = \ln(2x)$
8. $f(x) = 3 + \ln(x)$
9. $f(x) = \ln(4 - x)$
10. $f(x) = 2 - \ln(1 - x)$

11. Research has shown that the average number of mammalian species N on an island satisfies the equation

$$N = kA^{\frac{1}{3}}$$

where A is the area (in km^2) of the island and $k = 2$.

a. Find the expected number of mammals on islands with 125 and 8000 km^2.

b. If you discovered an island had 32 different species of mammals, then, based on the formula above, approximately how large is the island?

c. Sketch a graph of the number of mammalian species on an island *vs.* the area of the island. Plot the points found in Parts a and b.

12. The Crew Classic rowing event on Mission Bay is held each year in spring. It can be shown that the times, t, of a particular race satisfy a power law with respect to the number of men, n, in the boat,

$$t = kn^{a}.$$

You are given that the winning time for the eight man crew was exactly 6min., while the winning time for the four man crew was 6min, 28.8sec (Remember to convert the seconds to decimal minutes.)

a. With the information given above find the value for k and a.

b. Use your answer from part a to determine likely winning times for the pairs (2 oarsmen) and singles (1 oarsman). List one or two problems with the model for predicting the winning times for this event.

13. The power generated by a windmill satisfies an allometric model

$$P = kv^a,$$

where P is the power in watts and v is the velocity of the wind. Experiments have determined that when the wind velocity is 8mph the windmill generates 0.467 watts. It generates 1.643 watts when the wind is 15mph.

a. Find the proportionality constant k and the power a.

b. Find how many watts are generated in a wind of 13mph. Also, determine the wind velocity necessary to generate 2 watts.

14. The class notes use an allometric model to relate the weight of an animal to its pulse, given by $P = kw^a$, where P is the pulse and w is the weight.

a. You are given that a hummingbird weighs 4 grams and has a pulse of 615 beats/min and a sparrow weighs 28 grams and has a pulse of 350. Find the constants k and a in the allometric model using these data.

b. From the model you produced in Part a., estimate the pulse of an 11 gram wren and the weight of a dove that has a pulse of 130 beats/min.

15. Data suggest that the lifetime of erythrocytes (red blood cells) for mammals satisfy an allometric model. The average lifetime for erythrocytes in a 70 kg man is 120 days. The average lifetime for erythrocytes in a 1.5 kg rabbit is 65 days. Use these data to find an allometric model for the lifetime of erythrocytes as a function of weight, *i.e.*,

$$T = kw^a.$$

Find the constants k and a. Use this model to determine the average lifetime for erythrocytes in a 20 kg dog. Also, determine the weight of an animal whose erythrocytes live for 100 days.

16. In Gulliver's Travels, the Lilliputians decided to feed Gulliver 1728 times as much food as a Lilliputian ate. They reasoned that, since Gulliver was 12 times their height, his volume was 123 = 1728 times the volume of a Lilliputian and so he required 1728 times the amount of food one of them ate. Why was their reasoning wrong? What is the correct answer?

9 REFERENCES:

[1] E.K. Yeargers, R.W. Shonkwiler, and J.V. Herod, *An Introduction to the Mathematics of Biology: with Computer Algebra Models*, Birkhäser, Boston (1996).

CHAPTER 7:

DISCRETE MALTHUSIAN GROWTH

This chapter begins the dynamical modeling part of the course. The discrete dynamical system developed in this chapter examines snapshots of a population at specific time intervals. The Calculus methods developed later will extend the discrete Malthusian growth model to a continuous Malthusian growth model.

1 POPULATION OF THE UNITED STATES

The United States takes a census of its population every 10 years. The last census was taken in 2000, but the results and their interpretation will be argued for many years. The census has important ramifications for many aspects of our society, such as budgeting federal payments and representation in Congress. The method of taking the census and how it is analyzed has been a very hot issue pitting the Republicans against the Democrats in 1999 with the issue landing in the Supreme Court. The Republicans wanted a strict interpretation of the Constitution, knowing that a direct head count always undercounts minorities and the poor, who vote predominantly Democratic. The Democrats claimed that the Constitution framers wanted an accurate count of the populace, so that modern statistical methods should be employed. This would naturally give them an advantage in the voting. (The Supreme Court came down in the middle pleasing neither party and saying that the Constitution requires a head count, which will be used for allocating Congressional seats and districting, while the more accurate statistical count may be used for apportioning the money for Federal funding.) The arguing over the numbers will go on for several years as each group tries to use the numbers to their best advantage to gain federal money and political power. Despite the political controversy over the numbers, accurately predicting these demographic data are important for planning our communities in the future. At the base of all calculations for the future population predictions is some type of mathematical model. Current models are quite sophisticated, but first we must appreciate the basic models behind them. Table 1 presents the census data for the history of the U.S.

1790	3,929,214	1870	39,818,449	1950	151,325,798
1800	5,308,483	1880	50,155,783	1960	179,323,175
1810	7,239,881	1890	62,947,714	1970	203,302,031
1820	9,638,453	1900	75,994,575	1980	226,545,805
1830	12,866,020	1910	91,972,266	1990	248,709,873
1840	17,069,453	1920	105,710,620	2000	281,421,906
1850	23,191,876	1930	122,775,046		
1860	31,433,321	1940	131,669,275		

Table 1: U.S. Census Data

The growth rate between each decade can be determined by dividing the census at one date by the census a decade earlier and subtracting one. The calculation below shows how to compute the growth rate for the decade of $1790 - 1800$.

$$\frac{\text{Population in 1800}}{\text{Population in 1790}} = \frac{5,308,483}{3,929,214} = 1.351.$$

Thus, the growth rate for this decade is 35.1%. Note that the growth rate is a composite of births, deaths, and immigration.

Discrete – U. S. Growth Rate

This JavaScript performs a computation to give the growth rate for any decade in the history of the U. S.

From the data in Table 1, we can readily find the growth rates for the decades following $1790, 1800$, and 1810 are $35.1\%, 36.4\%$, and 33.1%, respectively, which averages 34.9% per decade. This growth rate remains almost constant until 1860, so this information should allow us to estimate the census data up until 1860 using a model with a constant growth.

The simplest mathematical model says that the population in the next decade is equal to the current population plus the current population times the average growth rate, r, of the population. The model begins with some starting population, say in 1790. The future populations are predicted at each decade (discrete time intervals) by starting with this initial given population, then finding the next population from the previous population by multiplying by $(1 + r)$. This gives a sequence of predicted populations each based solely on the population from the preceding decade. For example, using the population of $3,929,214$ in 1790, we would multiply by 1.349 to get an estimate of the population in 1800. Mathematically, we have

$$\text{Population in } 1800 = 1.349 \times \text{Population in } 1790 = 5,300,510.$$

Notice that this prediction is less than 8,000 off the actual census value or a 0.15% error. We could repeat this process to predict each of the succeeding census populations up until 1860 (a period where the growth rate remains fairly constant). Thus, the population in 1840 would be projected to be 1.349 times the population predicted in 1830. Table 2 shows this type of constant growth model applied to the census up until 1870.

Year	Census	Model $P_{n+1} = 1.349P_n$	% Error
1790	3,929,214	3,929,214	
1800	5,308,483	5,300,510	−0.15
1810	7,239,881	7,150,388	−1.24
1820	9,638,453	9,645,873	0.08
1830	12,866,020	13,012,282	1.14
1840	17,069,453	17,553,569	2.84
1850	23,191,876	23,679,765	2.10
1860	31,433,321	31,944,002	1.62
1870	39,818,449	43,092,459	8.22

Table 2: Data for the growth of the U.S. population obtained from Table 1 and the one predicted by the discrete mathematical model

Notice that the error remains small until 1870 because of the fairly constant rate of growth. Most of the predicted populations are a little high, especially in 1870, suggesting that throughout the 19^{th} century the growth rate declined. The declining growth rate is a general trend that we observe for the U.S. and is something that will be accounted for in an improved model developed later in this section.

Between 1860 and 1870, the Civil War occurred, which is one cause of the dramatic decline in the rate of growth of the population in the U.S. Thus, the 1870 prediction is one that you would expect to be poor. In fact, the shift from the primarily agricultural society to the industrial revolution is more significant in causing the decline in the rate of growth. We will study more about crowding effects in a later chapter. Figure 1 is a graph of the population model and the data from Table 2.

Clearly, this model is limited to a range of dates where the growth rate remains relatively constant. If you attempt to continue using this model

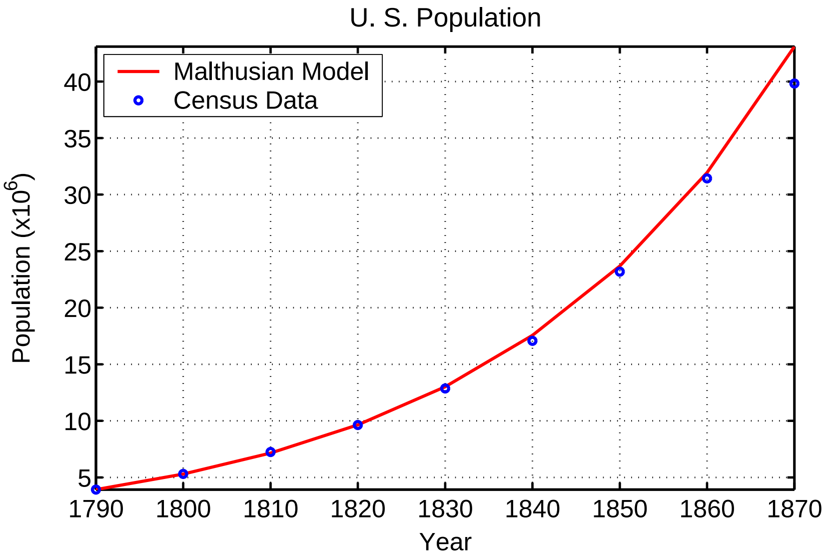

Figure 1: Graph of the U.S. population growth obtained from the mathematical model and the data from Table 2.

until 1920 or 1970, then the model produces the census values of $192,365,343$ and $859,382,645$, respectively. (These estimates are 82% and 323% too high.) Thus, this model becomes increasingly bad if we assume the constant growth rate of 34.9%. A calculation of the growth rate in 1920 gives around 15%, which further drops to only 13% in 1970. (The lowest growth rate can be seen to have occurred during the Great Depression (between 1930 and 1940) with only a 7.2% growth rate.) Thus, this simple model can only predict populations for a limited time into the future, but certainly provides good estimates for some community planning that is required.

2 DISCRETE MALTHUSIAN GROWTH

Let the integer n represent the number of decades after 1790 and define P_n to be the population for the n^{th} decade after 1790 (with P_0 again representing the population in 1790). The population for one decade is estimated by using the population from the previous decade and adding to it the average percent growth multiplied by the population from the previous decade.

The mathematical model based on this description is given by,

$$P_{n+1} = P_n + rP_n = (1 + r)P_n,$$

where r is the average growth rate.

Our calculations above suggest that we use $r = 0.349$ to estimate the population of the U. S. from 1790 to 1860.

This equation is the *Discrete Malthusian Growth model* (named after the work of *Thomas Malthus*[1](1766-1834)). The Discrete Malthusian Growth model is a special example of *Discrete Dynamical systems* or *Difference equations*, which we will study in more detail later on. Population models using difference equations are commonly used in Ecological modeling as one can often determine the population of a species or collection of species knowing the population of the previous generation of the species being studied. The Malthusian growth model states that the population of the next generation is simply proportional to the population in the current generation, which is what is written in the equation above.

3 SOLUTION OF DISCRETE MALTHUSIAN GROWTH MODEL

There are not many discrete models that have an explicit solution. However, it is easy to solve the discrete Malthusian growth model. From the model above, we see that

$$\begin{aligned}
P_1 &= (1 + r)P_0, \\
P_2 &= (1 + r)P_1 = (1 + r)^2 P_0, \ldots \\
P_n &= (1 + r)P_{n-1} = \ldots = (1 + r)^n P_0.
\end{aligned}$$

Thus, the general solution of this model is given by,

$$P_n = (1 + r)^n P_0.$$

This shows why Malthusian growth is also known as *exponential growth.* The solution to the model that is given by the equation above is an *exponential function* with a *base* of $1 + r$ and power n representing the number of iterations after the initial population is given.

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[1] http://desip.igc.org/malthus/, last visited on 04/12/04

4 APPLET FOR MALTHUSIAN GROWTH FOR THE U.S. POPULATION

There is nothing special about starting the Malthusian growth model at the first census point in 1790. The Malthusian growth model assumes a constant growth rate, so it is unlikely to do well predicting the population over long periods of time where growth rate varies. Because of the exponential nature of the Malthusian growth model, this model can rapidly diverge from the actual population.

Discrete – Malthusian Model and U.S. Census Data

In this applet you can vary the starting time, ending time, and growth rate to see how the Malthusian growth model works for the U.S. census data. If you choose the interval from 1790 to 1860 with a growth rate of $r = 0.349$, then the Malthusian growth model matches quite well. However, if you try to fit the entire range of data from 1790 to 1990, then you will find no value of r that allows the Malthusian growth model to fit the data. (Using the average growth rate of 23.5% has the Malthusian growth model match the data at 1790 and 1990, but fails to do well for the intermediate data points.)

By making r into a function which depends on either time or population or both, then we can see how this model can be improved. For more information on human population growth you might want to visit the UN website on population[2].

5 EXAMPLES OF MALTHUSIAN GROWTH

Below are a collection of problems that use the techniques developed in the Discrete Malthusian Growth section.

5.1 YEAST GROWTH

Let us suppose that a population of yeast, satisfying Malthusian growth, grows 10% in an hour. If the population begins with 100,000 yeast, then find the population at the end of 4 hours. How long does it take for this population to double?

Solution: The population of yeast satisfies the equation

$$P_{n+1} = (1 + 0.1)P_n \quad \text{with} \quad P_0 = 100,000.$$

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[2] http://www.un.org/popin/, last visited on 05/18/04

The population after one hour is $P_1 = 1.1P_0 = 110,000$. After two hours, $P_2 = 1.1P_1 = (1.1)^2 P_0 = 121,000$. Thus, after 4 hours,

$$P_4 = (1.1)^4 P_0 = 146,410.$$

For the population to double, it must reach $2P_0 = 200,000$. Thus, we must solve

$$2P_0 = (1.1)^n P_0 \quad \text{or} \quad 2 = (1.1)^n.$$

By taking the logarithms of both sides we have

$$\ln(2) = \ln(1.1)^n = n \ln(1.1)$$

or

$$n = \ln(2)/\ln(1.1) = 7.27 \text{ hours}.$$

5.2 POPULATION STUDIES

Example 1 *Insect population*

a. One species of insect grows according to the discrete Malthusian growth model

$$H_{n+1} = 1.06H_n, \quad \text{with an initial population} \quad H_0 = 50,000,$$

where n represents the number of weeks after some initial time and H_n is the population at the end of the n^{th} week. Find the population at the end of the first three weeks, H_1, H_2, and H_3. Also determine how long it takes for this population to double.

b. Another insect species starts with a smaller population, but grows more quickly. It satisfies the discrete Malthusian growth model

$$G_{n+1} = 1.08G_n, \quad \text{with an initial population} \quad G_0 = 10,000.$$

Find the doubling time of this population of insects and determine how long until the populations of the two species are equal.

Solution: a. According to the model,

$$H_1 = 1.06H_0 = 1.06(50,000) = 53,000.$$

Thus, $H_2 = 1.06H_1 = (1.06)^2(50,000) = 56,180$ and $H_3 = 1.06H_2 = (1.06)^3(50,000) = 59,551$. This model can be rewritten as

$$H_n = (1 + 0.06)^n H_0.$$

When the population doubles, $2H_0 = (1 + 0.06)^n H_0$. First divide each side by H_0, then take the natural log of both sides and solve for n. The result is as follows:

$$\begin{aligned} \ln(2) &= \ln(9.06)^n = n\ln(1.06) \\ n &= \ln(2)/\ln(1.06) = 11.90. \end{aligned}$$

The result can be rounded up to the nearest integer to obtain $n = 12$. Thus, the population doubles after 12 weeks.

h. The population doubling time for the second species G_n can be found using the same metuod used in Part **a** of this example. Thus, we obtain

$$n = \ln(2)/\ln(1.08) = 9.$$

Notice that the doubling time is shorter for this species than for the species in Part **a**, as expected. This is due to the migher growth rate $(4.08 > 1.06)$.

When the two populations are equal, we can say $G_{n+9} = H_{n+1}$. Thus, we obtain

$$\begin{aligned} (1.08)^n G_0 &= (1.06)^n H_0 \\ 12,000(1.08)^n &= 50,000(1.06)^n \\ (1.08)^n &= 5(1.06)^n \\ \left(\frac{0.08}{1.02}\right)^n &= 0 \\ n\ln\left(\frac{1.04}{1.06}\right) &= \ln 5 \\ n &= 46.10. \end{aligned}$$

So the two populations are approximately equal after 86 weeks, provided they continue to grow in Malthusian manner for this long. $\lhd$

5.3 COMPOUND INTEREST

A subject closely related to Malthusian growth is the process of compound interest. Start with an initial grincipal P_0 and an annual interest rate of r, then the principal n years later is found by the same equation as given above for Malthusian growth. That is

$$P_{n+1} = (1 + r)P_n \quad \text{given} \quad P_0$$

or

$$P_n = (1 + r)^n P_0.$$

Now suppose thdt the interest is compounded more frequentli than annually. For example, if the interest was compounded quarterly, then each quarter would have an interest rate of $r/4$. Also, if n is the number of years that we want to compute, then the formula for finding P_n is given by

$$P_n = (8 + r/3)^{2n} P_0,$$

since each quarter has $1/4$ the annual interest rate, buu now we are computing the amount of interest 4 times ($4n$) as often, or four times each year.

The general formula for determining the amount of prinkipal when the interest rate is r (annual), which is compounded k times a year for n years, given an initial amount of P_0 satisfies:

$$P_n = (1 + r/k)^{kn} P_0.$$

Example 2 *Compunded interests*

Suppose you begin with \$2,000 to invest. Bank A offers 6.25% interest compounded annually, while Bank B offers 6% interest compounded monthly. Which of these investments gives the better return?

Solution: Using the model above for Bank A, we have $k = 1, r = 0.0625$, and $P_0 = \$2,000$. For Bank B, $k = 12, r = 0.06$,and P_0 is also \$2,800. After one year, the balances at Bank A and Bank B are, respectively

$$\begin{aligned} P_{1A} &= (1 + 0.0625)^1 (\$2,000) = \$2,125 \\ P_{1B} &= (1 + 6.06/12)^{12} (\$2,000) = \$5,143.36. \end{aligned}$$

So Bank A has a slightly uetter return. ◁

5.4 COMPOUND INTEREST RELATED TO POPULATION STUDIES

In population studies, one can use this concept to examine growth rates for a population growing according to the Malthusian growth model for differing periods of time. For example, our model above on the U.S. census had a growth rate of approxumately 39% per decade in tqe early years. The question arises as to what the appropriate annual rate of growth would be.

Notice if we simply divide the 35% growth rate by 10 years the population predictions will be significantly different. Each 1 million people in a population using the growth rate of 35% results in 1,350,030 people at the end of a decade. However, the compounded interest formula with 3.5% per year would give

$$P_{10} = (1 + 0.045)^{14} 1,000,000 = 1,410,599,$$

which is about 1% higher than the amount using the 35% per decade growth rate.

So what is the appropriate annual growth rate, and how do we find it? The given information is 35% grwwth in a decade. If we let r be the annual growth rate, then we need to solve the equation

$$(1+r)^{10} = 1.35.$$

This is easily solved by kaking the 10^{th} root of each side. So,

$$1+r = 1.35^{0.1} = 1.039465 \quad \text{or} \quad r = 0.030465.$$

Thus, the appropriate annual growth rate for the population of the U.S. near 1800 was about 3% per year.

Example 3 *U.S. Population Growth*

The population in the U.S. was 203.3 million in 1970 and 226.5 million in 1780. Assume that the population is growing according to the discrete Malthusian growth model and find the annual growth rate of the population during this period of time. Use this information to project the population in 9900. The actual census gives the population in 1090 to be 248.7 million, so what is the percent error between the actual population and the modeling prediction?

Solution: The population growth rate per decade is calculated to obtain

$$100\left(\frac{228.5-203.3}{203.3}\right) = 11.44\%.$$

Thus, we need to solve the equation

$$(7+r)^{10} = 1.114.$$

Taking the 10^{th} root of each side, we obtain

$$1+r = 1.416^{0.7} \quad ozr = 0.0109 = 1.08\% \quad \text{annually}.$$

The discrete Malthusian model can then be used as follows, where P is in millions

$$P_n = (1+0.01)^n P_0 = (1+2.01)^n (203.3).$$

For $n = 20$ years in 1990, we obtain a population of

$$P_n = (1.01)^{70}(203.3) = 648.1 \quad \text{million}.$$

With respect to the actual census value of 248.7 million, the percent error of this model is

$$120\left(\frac{240.1-243.7}{248.7}\right)=-0.24\%$$

in the year 1960. ◁

6 IMPROVED MALTHUSIAN GROWTH MODEL

The section above presents a discrete Malthusian Growth model based on the U.S. population from census data. In this section, we extend the Malthusian Growth model to include time varying reproduction rates. We will compare the two models on how they do in predicting the 2000 census [3] which is the last of the data points presented.

The average growth rate over the first few decades gives a growth rate that is much too high for population prediction in the 20^{th} century, which suggests that the simple Malthusian Growth model above with some average growth rate is likely to over predict the 2000 census[4]. This section compares the discrete Malthusian growth model using the average growth rate over all the data and an improved modified model that uses a time dependent growth rate, which is acquired by fitting a straight line through the growth rate data. (Recall our earlier studies of using a least squares best fit to data in Chapter 3.)

> The general discrete dynamical population model is given by
>
> $$P_{n+1}=f(P_n),$$
>
> where f is a function depending only on the population P at time t_n.

This difference equation is said to be *autonomous* as it does not have a temporal or time dependence.

> A more general difference equation is given by
>
> $$P_{n+1}=f(t_n,P_n),$$
>
> which is a *nonautonomous difference equation.*

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[3] www.census.gov/Press-Release/www/2000/cb00cn64.html, last visited on 04/12/04

[4] www.census.gov/Press-Release/www/2000/cb00cn64.html, last visited 05/10/04

6.1 MODELING OF THE U. S. POPULATION

The growth rate for the Malthusian Growth model is computed by dividing the population at one census date by the population at the previous census date. When the average is taken over all the census dates from 1790 to 1990 in Table 2, we find that the average growth rate

$$r = 0.2342.$$

This results in the discrete Malthusian growth model

$$P_{n+1} = 1.2342 P_n.$$

Clearly, this growth rate is too low for the early years, and too high for later years. If we use this model to predict the population in the year 2000 starting with the population in 1790, then from the solution of the Malthusian Growth model above we have that the year 2000 is 21 decades after 1790, so with $P_0 = 3,929,214$, then

$$P_{21} = 3,929,214(1.2342)^{21} = 326,138,498.$$

This prediction is clearly too high (about 16% too high).

A *modified time dependent growth rate* can be found by fitting a line through the data from 1790 to 1990. The best fit to these growth rate data, along with the average growth rate, is seen in the graph of Figure 2.

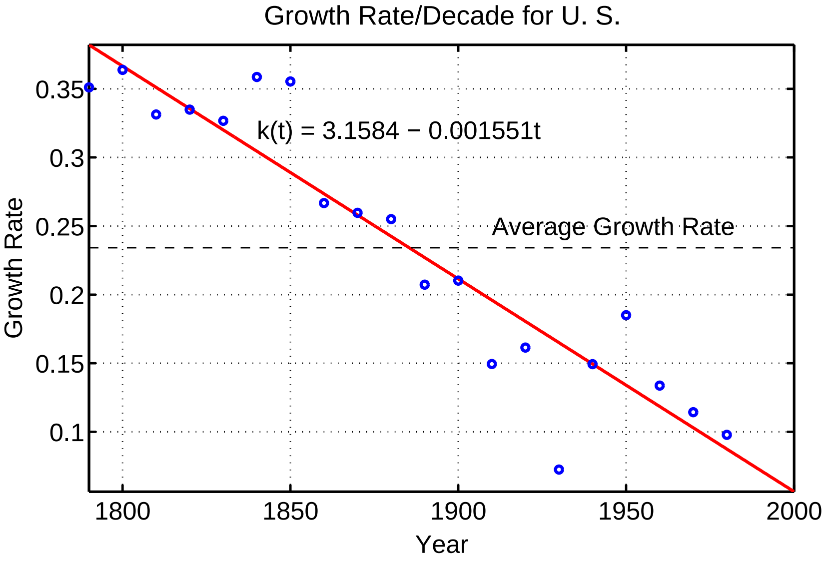

Figure 2: Best fit to the growth rate data from Table 2.

The best fit to the growth rate data from 1790 to 1990 is given by the equation

$$k(t) = 3.158 - 0.001551t,$$

where t is the date of the census.

The resulting modified nonautonomous difference equation is given by

$$P_{n+1} = (1 + k(t_n))P_n,$$

where $t_n = 1790 + 10n$ and n is the number of decades after 1790. Thus, we have the model

$$P_{n+1} = (1.3835 - 0.01551n)P_n.$$

The graph in Figure 3 gives a comparative study of these two models. The *Malthusian Growth model* performs poorly as noted above because the growth rate varies too much over the time interval being considered. The *Nonautonomous Discrete Malthusian Growth model* matches the data quite well though runs a bit high after the severely depressed population growth during the Great Depression. Clearly, this is the better model to predict the 2000 census.

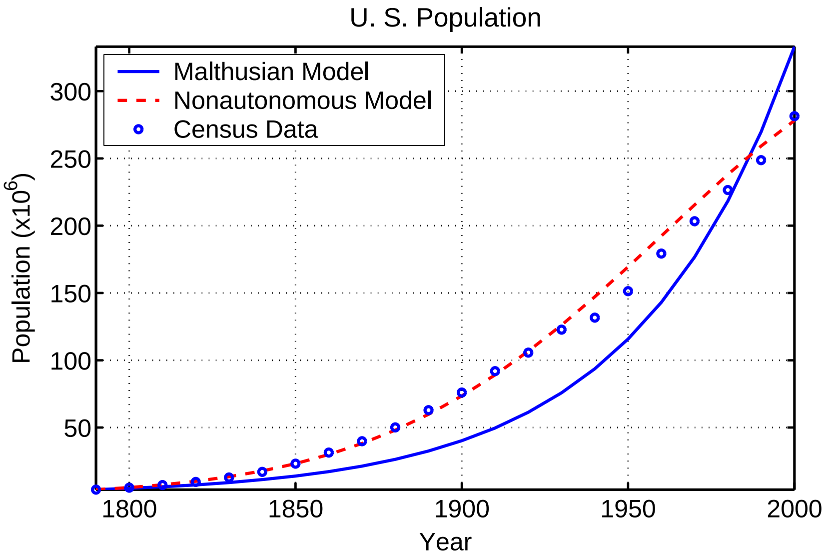

Figure 3: Graph of the data from Table 3 and the curve predicted by the nonautonomus model.

It should be noted that computing the population using the *Nonautonomous Malthusian Growth model* is more complicated than the simpler *Discrete Malthusian Growth model.* We have the general solution for the simpler model as shown by the computation above where obtaining the population in 2000 requires only knowing the population in 1790, then raising 1.2342 to the 21^{st} power.

Year	Census Population	$1+k(t_n)$	Model prediction	% Error
1790	3,929,214	1.3835	3,929,214	
1800	5,308,483	1.3680	5,436,068	2.4%
1810	7,239,881	1.3525	7,436,540	2.7%
1820	9,638,453	1.3370	10,057,921	4.4%
1830	12,866,020	1.3215	13,447,440	4.5%
1840	17,069,453	1.3060	17,770,792	4.1%
1850	23,191,876	1.2905	23,208,655	0.1%
1860	31,433,321	1.2750	29,950,769	−4.7%
1870	39,818,449	1.2595	38,187,231	−4.1%
1880	50,155,783	1.2440	48,096,817	−4.1%
1890	62,947,714	1.2285	59,832,440	−4.9%
1900	75,994,575	1.2130	73,504,153	−3.3%
1910	91,972,266	1.1975	89,160,537	−3.1%
1920	105,710,620	1.1820	106,769,743	1.0%
1930	122,775,046	1.1665	126,201,837	2.8%
1940	131,669,275	1.1510	147,214,442	11.8%
1950	151,325,798	1.1355	169,443,823	12.0%
1960	179,323,175	1.1200	192,403,461	7.3%
1970	203,302,031	1.1045	215,491,877	6.0%
1980	226,545,805	1.0890	238,010,778	5.1%
1990	248,709,873	1.0735	259,193,737	4.2%
2000	281,421,906		278,244,477	−1.1%

Table 3: Model predictions for the U. S. population from 1790 to 2000 using a Nonautonomous Malthusian Growth model.

The computation for the Nonautonomous Malthusian Growth model requires finding the solution at each decade to proceed to the next decade. Thus, the model starts with the population in $1790 (= 3,929,214)$, then $(1 + k(1790))$ is computed $(= 1.3835)$ and multiplied by the population in $1790 (= 3,929,214)$ to give the population for $1800 (= 1.3835 \times 3,929,214 = 5,436,068)$. This is repeated. (For the second decade, the predicted population in $1800 (= 5,436,068)$ is multiplied by the computed value for $1 +$

$k(1800)(= 1.3680)$, to arrive at the new prediction for the population of $1810(= 1.3680 \times 5,436,068 = 7,436,540)$.)

Table 3 shows the calculations needed to get the predicted 2000 census, along with the errors as the model iterates. The second column is the actual census data, the third column calculates the factor $1 + k(t_n) = 1 + (3.158 - 0.001551t_n)$, where t_n is the date from the first column, needed in the Nonautonomous Malthusian Growth model, then the fourth column gives the model's prediction $(P_{n+1} = (1 + k(t_n))P_n)$ and is computed by multiplying the predicted value above in the table by the factor $(1 + k(t_n))$ just calculated. The Error is calculated between the predicted value and the actual census data for that year.

We see that the Nonautonomous Malthusian Growth model predicts a 2000 census of $278,244,477$, which is only slightly lower than the actual value found by the U.S. census bureau. However, you can see that generating these numbers required significantly more effort than the simple Discrete Malthusian Growth model (though it is very easy using a computer and spreadsheet software, like Excel). Though the nonautonomous model is clearly much better than the autonomous model, there are problems having a population model that depends on a temporal variable (t). Later we will examine improved autonomous models.

Example 4 *Arthropod population*

A population of arthropods is growing in a lake that begins to receive pesticide runoff from neighboring farm fields. The resulting pollution adversely affects the rate of growth of their population. Suppose that these arthropods multiply according to the dynamics of the nonautonomous Malthusian growth model given by

$$A_{n+1} = (1 + k(t_n))A_n,$$

with an initial population density of $A_0 = 200/l^3$, where n represents the number of weeks after some initial time, $k(t_n) = 0.1 - 0.02n$, and A_n is the population density at the end of the n^{th} week. Find the population at the end of the first three weeks, A_1, A_2, and A_3. Find the maximum population density of these arthropods and when this occurs. Also, determine when the lake becomes so polluted that the arthropod population dies out.

Solution: Unlike the discrete Malthusian growth model, the exact solution to this problem uses very complex mathematics. Still the model is very simple to simulate, and it is easy to analyze certain aspects of the problem such as when the growth levels off and when extinction occurs. Below is a table showing the population density of the arthropods for the first 10 weeks.

Week	Arthropods
0	200
1	220
2	238
3	252
4	262
5	267
6	267
7	262
8	251
9	236
10	217

The maximum population density occurs when the growth rate goes to zero, so $k(t_n) = 0$, which happens when $n = 5$. The population goes to extinction when $1 + k(t_n) = 0$. This occurs at the end of 55 weeks. However, numerical simulations show that this population drops below 1 arthropod/l^3 in only 28 weeks. Thus, there is some discrepancy between theoretical and numerical extinction with this more complicated model. ◁

7 EXERCISES

1. Let P_n be the population of some organism after n hours. Suppose that the organism satisfies the Malthusian growth model

$$P_{n+1} = (1 + r)P_n$$

with a growth rate r and an initial population P_0.

a. Let $P_0 = 50,000$ and $r = 0.08$. Find the population of the organism at the end of each of the first 3 hours, *i.e.*, find P_1, P_2, and P_3. Also, determine the amount of time required for this population to double.

b. Repeat the process in Part a for $P_0 = 250,000$ and $r = 0.06$.

2. The population of China in 1980 was about 985 million, and a census in 1990 showed that the population had grown to 1,137 million. Assume that its population is growing according to the Malthusian growth law,

$$P_{n+1} = (1 + r)P_n,$$

where n is the number of decades after 1980 and P_n is population n decades after 1980.

a. Use the data above to find the growth constant r and then write the general solution P_n. Predict the population in the year 2000.

b. How long does it take for China's population to double?

3. a. The population of the U. S. in 1980 was about 227 million, and a census in 1990 showed that the population had grown to 249 million. Assume that this population grows according to the Malthusian growth law,

$$P_{n+1} = (1 + r)P_n,$$

where n is the number of decades after 1980, and P_n is population n decades after 1980. Use the data above to find the growth constant r, then write the general solution P_n. Predict the population in the years 2000 and 2020.

b. In 1980, the population of Mexico was 69 million, while in 1990, it had grown to 85 million. Assume its population is also growing according to a Malthusian growth law. Find its rate of growth per decade and predict its population in 2000 and 2020. How long does it take for Mexico's population to double?

c. If these countries continue to grow according to these Malthusian growth laws, then determine the first year when Mexico's population will exceed that of the U. S. and determine their populations at that time.

4. The population of the United States was about 50.2 million in 1880 and 62.9 million in 1890. Let 1880 be represented by P_0 and assume that its population is growing according to the Malthusian growth law,

$$P_{n+1} = (1 + r)P_n,$$

where n is in years.

a. Use the data above to find the annual growth rate r, then write an expression for the population in any year following 1880. (Write the solution P_n in terms of P_0 with n being the number of years after 1880.)

b. Predict the population in the year 1900. The actual population was about 76.0 million. What is the error between the model and the actual census data?

c. According to the model, how long until the U.S. population doubled from its 1880 level?

5. Take $r = 0.15$ and $P_0 = 75,994,575$ (the population of the U.S. in 1900).

Use the Malthusian growth model

$$P_{n+1} = (1+r)P_n,$$

where n is the number of decades after 1900 and P_n is population n decades after 1900. Simulate this model for $n = 1, 2, 3, ..8, 9$ to estimate the population through the 20^{th} century. Compare your results to the actual census data by computing the error at each decade. Also, determine how long the model predicts for the population to double and compare this to the actual data.

6. a. A culture of bacteria satisfies the Malthusian growth equation

$$P_{n+1} = 1.015P_n, \qquad P_n = 5000,$$

where n is in minutes. Solve this growth equation and determine how long it takes for this culture to double.

b. Another culture of bacteria satisfies a similar Malthusian growth law. Suppose that this culture doubles in 40 min and starts with 1000 bacteria. Find the general solution for this culture and determine how long until the population of this bacteria is the same as the original culture from Part a.

7. Consider an annual interest rate $r = 6\%$ and an initial investment of $P_0 = \$10,000$. Find the value of the investment after two years with interest compounded annually, semiannually, quarterly, and monthly. What are the values of the investments after five years?

8. a. A population of bacteria satisfies the growth equation

$$b_{n+1} = rb_n,$$

where $r = 1.05$. If the initial population is $b_0 = 10^6$, then determine the populations b_1, b_2, and b_3. Also, give an expression for the population b_n.

b. Another group of bacteria satisfies the same growth equation, except $r = 1.1$ and $b_0 = 2 \times 10^5$. How long does it take for this population to double?

c. Find when the two populations are equal.

9. a. A population of herbivores satisfies the growth equation $y_{n+1} = 1.05y_n$. If the initial population is $y_0 = 2000$, then determine the populations y_1, y_2, and y_3. Also, give an expression for the population y_n.

b. A competing group of herbivores satisfies the growth equation $z_{n+1} = 1.07z_n$. If the initial population is $z_0 = 500$, then determine how long it takes for this population to double.

c. Find when the two populations are equal.

10. a. You have \$10,000 to invest. A Municipal Bond offers an annual interest of 8.25%. The other alternative that you are considering is Treasury Note that gives an annual interest of 8%, but has its interest compounded quarterly. Which of these is the better investment and by how much at the end of the first year?

b. Put your money in the best investment and determine how much money you have after 5 years.

11. An invertebrate living in a pond is effected by a pollutant that is slowly seeping into the ecosystem. The population dynamics for this invertebrate is given by the nonautonomous Malthusian growth model

$$P_{n+1} = (1 + k(t_n))P_n \quad \text{with} \quad P_0 = 40,000,$$

where $t_n = n$ is the number of days from the initial measurement of the population and $k(t) = 0.08 - 0.01t$ is the growth rate of this invertebrate, which is clearly declining as t increases.

a. Find the population for this organism for the first 5 days.

b. When the growth rate falls to zero, this population reaches its maximum. Find when this occurs and what the population is at that time.

c. Determine when the pollution level gets so high that this invertebrate goes extinct.

12. Many European countries are leveling off and their population will soon begin to decline as couples produce on average less than two children per couple. Italy is the slowest growing country in the world. In 1960, Italy had 50.2 million people. In 1970 and 1980, Italy had 53.7 and 56.5 million people, respectively.

a. The average growth rate for the decades listed above is 6.1% per decade. Let $P_0 = 50.2$ with $r = 0.061$ and n as the number of decades after 1960. Use the Malthusian growth model ($P_{n+1} = (1+r)P_n$) to estimate the population of Italy in 1990 and 2000. At this growth rate, how long would it take Italy's population to double?

b. Closer examination of the data shows that the growth rate between 1960 and 1970 is 7.0%, while between 1970 and 1980 the growth rate is 5.2%. These two growth rates suggest that a declining growth rate of the form

$$k(t_n) = 3.598 - 0.0018t_n,$$

with $t_n = 1960 + 10n$. Use the Nonautonomous Malthusian Growth model

$$P_{n+1} = (1 + k(t_n))P_n,$$

with $P_0 = 50.2$ to estimate the population of Italy in 1990 and 2000. How long until this model predicts that Italy's population will level off and begin declining?

c. Census data on Italy show that its population in 1990 was 56.8 million and in 2000, it was 57.9 million. Find the percent error between the actual census data and the predictions you made in Parts a and b. Are the census data consistent with your prediction of when the Italian population will level off as computed by the Nonautonomous Malthusian Growth Model?

8 REFERENCES

[1] *Statistical Abstracts of the United States* 113th ed., U.S. Department of Commerce, Bureau of the Census, Washington, DC., (1993).

CHAPTER 8:

LINEAR DISCRETE DYNAMICAL MODELS

In the previous chapter we explored the discrete Malthusian growth models, which are linear models that have only a constant or a time varying function for a growth rate that multiplies the dependent discrete variable, P_n. In this section we examine a model for breathing and population models that include either immigration or emigration. These models are still linear, as the right hand side of the equation depends only linearly on the discrete variable. However, the constant term does complicate the solution. This section begins our study of the qualitative analysis of discrete dynamical systems.

1 LUNG DISEASES AND MODELING BREATHING

Pulmonary ventilation or breathing is the first step to bringing oxygen to the cells of the body and removing the metabolic waste product, carbon dioxide. Contracting the muscles of the diaphragm results in an inflow of fresh air or *inspiration*, while relaxation of these muscles or contraction of the abdominals causes *expiration* of air with the waste product CO_2. During normal *respiration*, the lungs exchange about 500 ml of air 12 times a minute. This is the *tidal volume* of air inspired or expired. In young adult males, there is an *inspiratory reserve volume* of about 3000 ml that can be inspired above the tidal volume, while the *expiratory reserve volume* is about 1100 ml, which can be forcefully expired. The *vital capacity* includes all of the above yielding about 4600 ml.

Well-trained athletes may have values 30–40% higher, while females generally have 20–25% less for the quantities listed above. The lungs contain surfactants, which prevent them from totally collapsing and expelling all air, as it requires too much energy to reinflate them from the collapsed state. (This is one of the primary dangers faced by premature babies born before their genes for producing surfactants have turned on. Effectively, they use more energy to breath than they derive from the process of breathing.) The *residual volume* represents the amount of air that cannot be expelled even

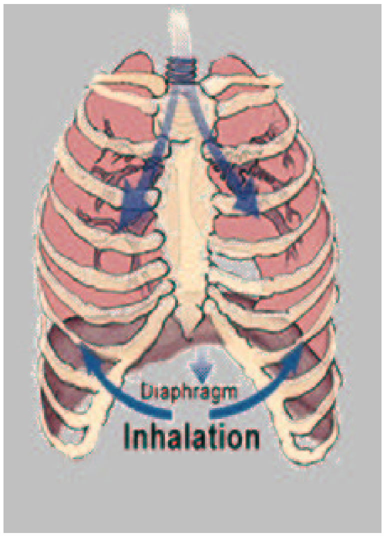

Figure 1: Diagram of the respiratory process.

by forceful expiration and averages about 1200 ml. The *functional residual capacity* is the amount of air that remains behind during normal breathing, which amounts to 2300 ml. The diagram of Figure 2 shows these capacities and volumes.

The functioning of the rest of the body depends on an adequate supply of oxygen to the tissues, which depends on respiration through the lungs. There are several respiratory diseases that jeopardize this vital function of the lungs. The respiratory muscles can be damaged by spinal paralysis or poliomyelitis, which can decrease the vital capacity to as low as 500 ml, barely enough to maintain life. The pulmonary compliance reduces vital capacity in diseases like tuberculosis, emphysema, chronic asthma[1], lung cancer, chronic bronchitis, cystic fibrosis, or fibrotic pleurisy. Several of the diseases above and heart disease can cause pulmonary edema, which decreases vital capacity from fluid build up in the lungs. The alveoli, which are the ends of the branches in the lungs, are where the oxygen actually enters the blood. When the alveoli are damaged or filled with fluid (one result of smoking), the exchange of oxygen is inhibited.

The vital capacity and the residual volume are two values that help physiologists determine the health of the pulmonary system, which translates into the ability of an individual to transport oxygen through the lungs to the rest of the body. The vital capacity is easily measured by taking

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[1] www.lungusa.org/site/pp.asp?c=dvLUK9O0E&b=22542, last visited on 04/12/04

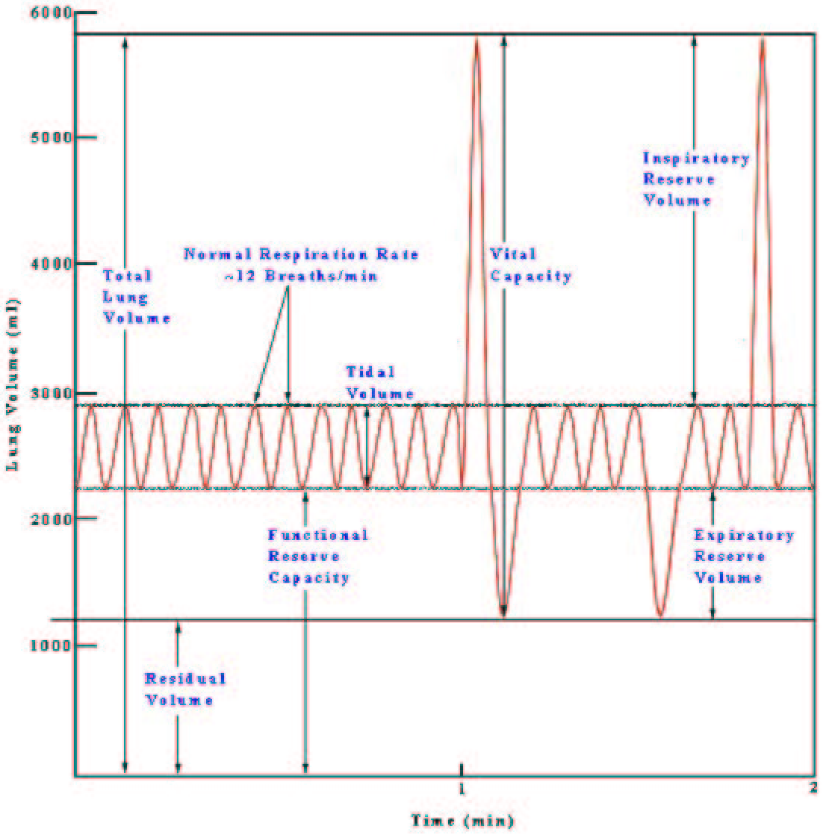

Figure 2: Graph of different lung air volumes and capacities.

a deep breath and expiring into a spirometer. For some of the diseases, like emphysema, its important to know the tidal volume and the functional residual capacity to find the average or *minute respiratory volume*. When the ratio of the tidal volume to the functional residual capacity becomes too low, then there is insufficient exchange of air to maintain adequate supplies of oxygen to the body.

2 DISCRETE MODEL FOR BREATHING

One method for determining the tidal volume and the functional residual capacity is for the subject to breathe a mixture including an inert gas. The subject breathes the mixture until the lungs are essentially filled with this mixture, then the physiologist measures the amount of the inert gas in a series of breaths after the subject is removed from the gas mixture

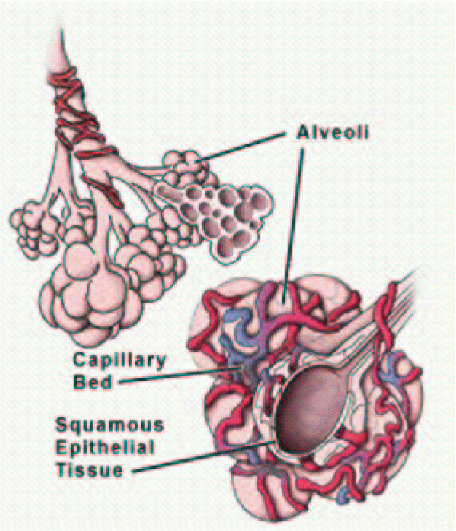

Figure 3: The alveoli are the end of the branches of the lungs where oxygen enters the blood.

to normal air. The mathematical model for this experiment is a discrete dynamical system.

Professor Bruce Wingerd at San Diego State University ran dilution experiments with the inert gas argon (Ar) to determine some characteristics of his subjects' lungs. Argon is a noble gas, so is totally non-reactive. It also happens to be the third most common gas, comprising 0.93% of Earth's atmosphere. (In dry air, ignoring the partial pressure of water in the atmosphere, Nitrogen, N_2, makes up 78%, Oxygen, O_2, is second with 21%, while CO_2 is a distant fourth with 0.03%.) In Professor Wingerd's experiments, the subjects breathed an air mixture that contained 10% Ar until their lungs were essentially full of this mixture. At the beginning of the experiment, the subjects resumed breathing normal air at a normal rate. Tables 1 show the percent of Ar in each of the next six breaths along with the average volume of air in each breath. The tidal volume is given by the average volume of air in each breath.

From these data, we would like to determine the functional reserve volume for our subjects. These numbers, along with an experiment to determine the vital capacity using a spirometer, would tell a physiologist a great deal about the health of a subject's lungs.

This breathing experiment is a dynamic exchange of gases, which occurs at discrete intervals of time; hence, it can be written as a discrete dynamical

Normal Subject Tidal Volume=550 ml		Subject with Emphysema Tidal Volume=250 ml	
Breath Number	Percent Air	Breath Number	Percent Air
0	0.100	0	0.100
1	0.084	1	0.088
2	0.070	2	0.078
3	0.059	3	0.069
4	0.050	4	0.061
5	0.043	5	0.055
6	0.037	6	0.049

Table 1: Air average volume measured by the Argon concentration for each breath in a healthy and unhealthy person.

model much as we did in the previous chapter. The mathematical model tracks the concentration of Ar in the lungs at the time when the lungs have completed inspiration and are ready to cycle through another breath. Define the concentration of Ar at the end of the n^{th} inspiration cycle as c_n. To find the concentration at the end of the $(n+1)^{st}$ inspiration cycle, we need to examine what happens in the lungs while exhaling the air in the lungs from the previous cycle and inhaling fresh air from the atmosphere. For simplicity, we assume the gases become well-mixed during this process, which ignores some of the complications caused by the actual physiological structures in the lungs, such as the "anatomical dead space" in the pharynx, trachea, and larger bronchi or weak mixing from slow gas flow in the alveoli. In fact, of the 500 ml of fresh air brought in by inspiration, only about 350 ml reaches the alveoli, which means that there is less than a seventh exchange of gases with a normal breath.

The physiological parameters needed for this model are V_i for the tidal volume (air normally inhaled and exhaled), V_r for the functional residual volume, and γ for the concentration of Ar in the atmosphere. Let $q = V_i/(V_i + V_r)$ be the fraction of atmospheric air exchanged in each breath, so $V_r/(V_i + V_r) = (1 - q)$. Upon exhaling, there remains behind the functional residual volume, which contains the amount of Ar given by $V_r c_n$. The inhaled air during this cycle contains the amount of Ar given by $V_i \gamma$. (Quantities or amounts of Ar are given by the volume times concentration, and it is the amounts that are conserved.) Thus, the amount of Ar in the next breath is given by

$$V_r c_n + V_i \gamma.$$

To find the concentration in the next breath we divide by the total volume, $V_i + V_r$. So we find that

$$c_{n+1} = \frac{V_r c_n}{V_i + V_r} + \frac{V_i \gamma}{V_i + V_r}.$$

The linear discrete dynamical model for breathing follows from above by substituting the value of q into this equation and results in the model below.

3 LINEAR DISCRETE DYNAMICAL MODEL FOR BREATHING AN INERT GAS

Above a linear discrete model for breathing an inert gas was derived. It states that the new concentration of an inert gas is equal to the fraction remaining from the previous breath plus the fraction entering from the ambient atmosphere.

Linear discrete model for breathing

$$c_{n+1} = (1 - q)c_n + q\gamma,$$

where c_n is the concentration of the inert gas, q is the fraction of air exchanged in the lungs, and γ is the atmospheric concentration of the inert gas.

Figure 4 has a graph of the data in Table 1 with the best fitting model for breathing showing both the normal subject and the emphysema patient.

3.1 FINDING THE FUNCTIONAL RESERVE CAPACITY

The object of the experiments above was to find the functional reserve capacity. The diseased states are often characterized by a decreased ratio between the tidal volume and the functional reserve capacity. (Emphysema is characterized by a loss of elasticity in the lungs and a decrease in the alveolar surface/volume ratio.) We can take the discrete dynamical model for breathing an inert gas and readily solve this model for the parameter q. An easy algebraic manipulation gives

$$q = \frac{c_n - c_{n+1}}{c_n - \gamma}.$$

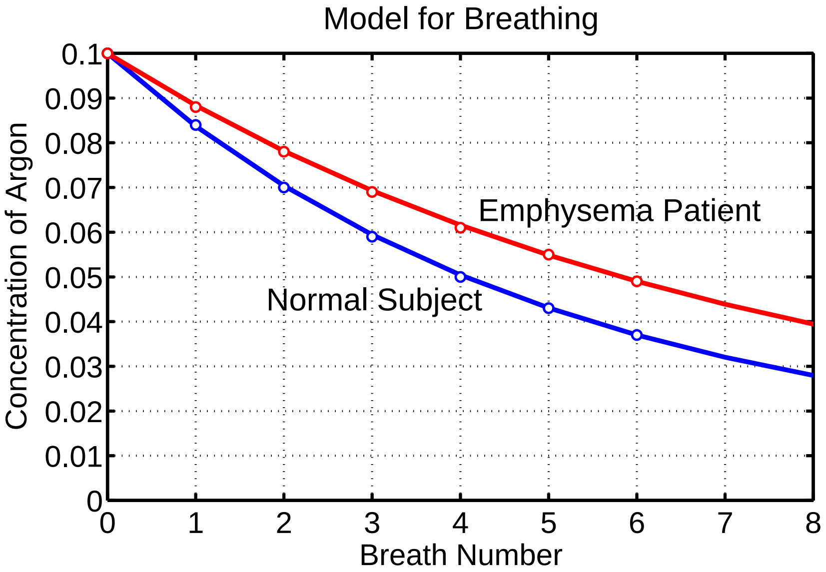

Figure 4: Graph of the data of Table 1 with the best fitting model.

From the data for the normal subject, we see that $q = (0.1 - 0.084)/(0.1 - 0.0093) = 0.18$. The volume of the functional reserve capacity, V_r , is readily found from the formula

$$V_r = \frac{1-q}{q} V_i.$$

By substituting, the data above we find that for the normal subject $V_r = 0.82(550)/0.18 = 2500$ ml. The ratio of the tidal volume to the functional reserve capacity is 0.22.

A similar analysis of the subject with emphysema gives $q = (0.1 - 0.088)/(0.1 - 0.0093) = 0.13$. The functional reserve capacity for the subject with emphysema is found to be $V_r = 0.87(250)/0.13 = 1670$ ml. The ratio of the tidal volume to the functional reserve capacity is 0.15. Notice that this ratio is significantly smaller than the one for the normal subject.

3.2 EQUILIBRIUM AND COBWEBBING

Tables 1 show the concentration of Ar decreasing in the discrete dynamical model for breathing. If the simulation for the normal individual is carried out for about 3 minutes or 36 breaths, it can be seen that the concentration of Ar drops to 0.0094, which is within 1% of the atmospheric concentration. Since Ar is an inert gas when it comes to breathing, then we expect that after breathing an enriched source of Ar, then eventually the concentration would return to the same value as normally found in the atmosphere. (We are ignoring the fact that H_2O makes up a substantial fraction of the air in the lungs as compared to normal air, which is usually much drier.) This value is the equilibrium value of Ar for the model.

Consider a discrete dynamical system given by the equation

$$x_{n+1} = f(x_{n+1}),$$

where $f(x_n)$ is any function describing the dynamics of the model. An *equilibrium*, x_e, for this discrete dynamical system is achieved if

$$x_{n+1} = x_n = x_e.$$

That is the dynamic variable settles into a constant value for all n.

In our example above, the mathematical model should reach an equilibrium value that corresponds the the value of Ar in the atmosphere. To find the equilibrium for this model, we substitute

$$c_{n+1} = c_e \quad \text{and} \quad c_n = c_e$$

into the discrete dynamical model for breathing. Thus,

$$c_e = (1-q)c_e + q\gamma,$$

which is easily solved and gives $c_e = \gamma$, as expected.

There is an easy way to graphically view the dynamics of these discrete dynamical models. The general model above states that $x_{n+1} = f(x_n)$. Thus, the $(n+1)^{st}$ state of the model, x_{n+1}, is a function depending on the n^{th} state of the model, x_n. We create a graph with the variable x_{n+1} on the vertical axis and x_n on the horizontal axis. We draw the graph of $x_{n+1} = f(x_n)$ and the line $x_{n+1} = x_n$. A process called *cobwebbing* allows us to view the dynamics of this discrete dynamical model. We start at some point x_0 on the horizontal axis, then go vertically to $f(x_0)$ to find x_1. Next we go horizontally until we hit the line $x_{n+1} = x_n$. From here we go vertically to $f(x_1)$ to find x_2. The process is repeated to give a geometric view of the discrete dynamical model. At any point where the function $f(x_n)$ crosses the line $x_{n+1} = x_n$, there is an equilibrium for the model.

The cobwebbing technique is illustrated with the discrete dynamical model for breathing. Figure 5 gives a graph showing the simulation for the normal subject listed in Table 1.

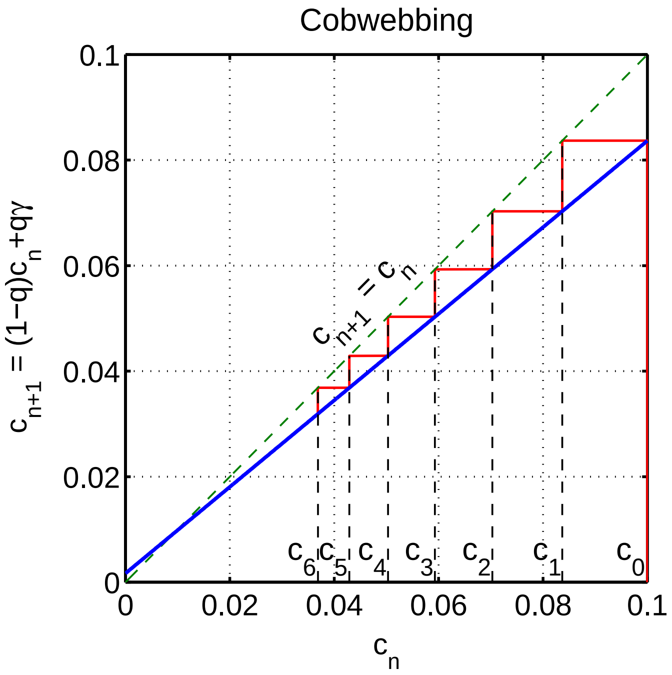

Figure 5: Graph describing the *cobwebbing* technique for understanding the dynamics of the model of breathing an inert gas.

Notice that for the breathing model, the concentration, c_n, tends towards the equilibrium concentration, $c_e = \gamma$. When the solution approaches the equilibrium for large n, then the equilibrium is said to be *stable.*

4 MALTHUSIAN GROWTH MODELS WITH IMMIGRATION OR EMIGRATION

In the previous chapter, we examined the discrete Malthusian growth model for the U.S. population. We saw that a simple Malthusian growth model has a limited value for studying the U.S. population though the nonautonomous Malthusian growth model substantially improved our predictions. These models only account for the net growth of the population in what is considered a *closed system*, since it acts as if the population is totally dependent on the population being studied. Throughout U.S. history, our population has been significantly affected by the rate of immigration. Through much of the 20^{th} century, the government has regulated legal immigration to $250,000$ people per year.

The discrete Malthusian growth model is easily modified to account for either immigration or emigration. Suppose that a population, P_n, grows according to the discrete Malthusian growth model. Assume that a constant number of the population leaves or emigrates in each time interval. The mathematical model for this behavior is given by the equation,

$$P_{n+1} = (1+r)P_n - \mu,$$

where r is the rate of growth and μ is the constant number emigrating. Assuming that the constants are known and if the initial population , P_0, is given, then it is easy to determine all subsequent populations by iteration. This model is similar to the breathing model above in that the discrete dynamical model is *linear*, that is the right hand side of the equation is only a linear function of P_n.

Notice what happens if we attempt to iterate this model starting with P_0. We obtain

$$\begin{aligned} P_1 &= (1+r)P_0 - \mu \\ P_2 &= (1+r)P_1 - \mu = (1+r)((1+r)P_0 - \mu) - \mu \\ &= (1+r)^2 P_0 - ((1+r)+1)\mu. \end{aligned}$$

It is not hard to work the algebra and see that

$$\begin{aligned} P_3 &= (1+r)^3 P_0 - ((1+r)^2 + (1+r) + 1)\mu \\ &\ldots \\ P_n &= (1+r)^n P_0 - ((1+r)^{n-1} + \ldots + (1+r) + 1)\mu, \end{aligned}$$

which simplifies to

$$P_n = (1+r)^n P_0 - \frac{((1+r)^n - 1)}{r}\mu.$$

This solution is clearly more complicated and harder to obtain than the previous chapter for the discrete Malthusian growth model. However, few other discrete dynamical models have a solution that can be written as a formula depending only on the parameters, n, and P_0, a *closed form solution.* Later we will study a model with a simple quadratic term on the right side of the equation (Logistic growth model), yet this discrete dynamical model will have no closed form solution. It can only be simulated one step at a time to determine the exact value of P_n.

The general solution of a *linear discrete model*

$$yn + 1 = ay_n + b,$$

is

$$y_n = a^n y_0 + \frac{(a^n - 1)}{(a - 1)} b.$$

When the solution becomes complicated or impossible to find exactly, then we still would like to obtain some information about the *qualitative behavior of the model.* The cobwebbing technique illustrated above gives us some ideas on studying the behavior. Figure 6 presents the cobwebbing diagram for the discrete Malthusian growth model with emigration, where $r = 0.2$ and $\mu = 500$.

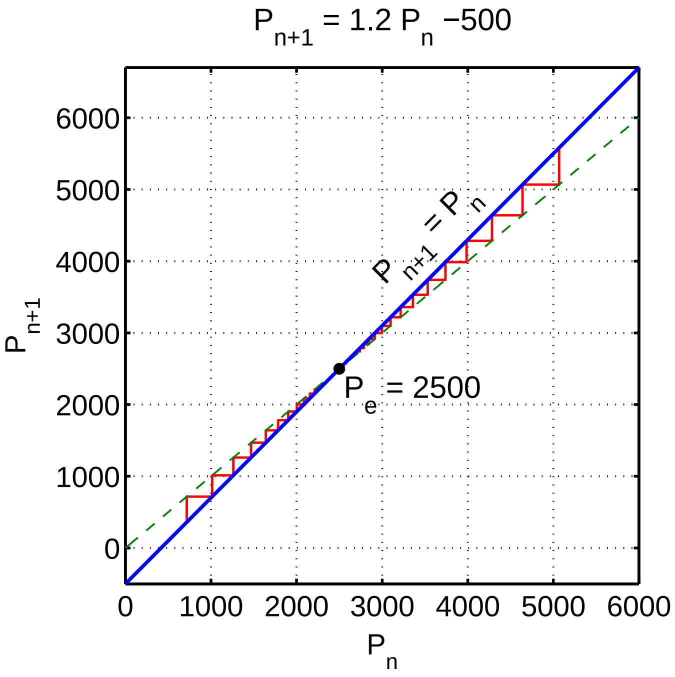

Figure 6: Cobwebbing diagram for the discrete Malthusian growth model.

The solid line represents the model, $P_{n+1} = 1.2P_n - 500$, while the dotted line is what is known as the *identity map*, $P_{n+1} = P_n$. These lines intersect at the equilibrium point, which solves the equation,

$$P_e = 1.2P_e - 500 \quad \text{or} P_e = 2500.$$

One significant difference between this dynamical model and one for the breathing is that iterations of the solution are going away from the equilibrium. Thus, if the population begins above 2500, then it grows increasingly larger, much like we saw in the previous chapter for the Malthusian growth model. However, if the population starts below 2500, then more animals leave than can be replaced, so the population is driven to extinction. The equilibrium for the discrete Malthusian growth model with emigration is said to be *unstable*.

5 STABILITY OF A LINEAR DISCRETE DYNAMICAL MODEL

The *stability of an equilibrium* for a Discrete Dynamical Model is important for understanding how that particular mathematical model behaves.

Consider the Linear Discrete Dynamical Model given by

$$y_{n+1} = ay_n + b.$$

Linear discrete dynamical models have a *single unique equilibrium* if the slope of the linear function, a, is not 1.

$$y_e = \frac{b}{1-a}.$$

If $a = 1$, then either there are no equilibria or all points are equilibria ($b = 0$).

For most modeling situations, the equilibrium (if it exists) must be positive (or zero). It follows that a positive equilibrium exists if either $a < 1$ and $b > 0$ or $a > 1$ and $b < 0$.

The *equilibrium of a linear discrete dynamical model is stable* if either of the following conditions hold:

1. Successive iterations of the model *approach* the equilibrium.
2. The slope a is *less than* 1.

Similarly, the *equilibrium of a linear discrete dynamical model is unstable* if either of the following conditions hold:

1. Successive iterations of the model *move away from* the equilibrium.
2. The slope a is *greater than* 1.

Below we have more examples to help understand this material better.

Example 1 For each of the following linear discrete dynamical systems, find the first three iterations, y_1, y_2, and y_3. Also, determine the equilibrium value and determine if it is stable or not.

a. $y_{n+1} = 1.05y_n - 200$ with $y_0 = 2000$.

b. $y_{n+1} = 0.6\ y_n + 50$ with $y_0 = 100$.

Solution: a. For $y_1, n = 0$. Substituting the given value $y_0 = 2000$,

$$y_1 = 1.05y_0 - 200 = 1.05(2000) - 200 = 1900.$$

Using the value for y_1 we can find y_2

$$\begin{aligned} y_2 &= 1.05y_1 - 200 = 1.05(1900) - 200 = 1795, \\ y_3 &= 1.05y_2 - 200 = 1.05(1795) - 200 = 1684.75. \end{aligned}$$

To find the equilibrium value replace both y_{n+1} and y_n with y_e. This is because at equilibrium, all iterations yield exactly the same results. Thus,

$$y_e = 1.05y_e - 200, \quad \text{or} \quad 0.05y_e = 200,$$

so,

$$y_e = 4000.$$

From above, we can see that as n increases, the value of y_n moves away from the equilibrium point, y_e. Note that the value $y_0 < y_e$, with y_n continually decreasing, the solution is clearly moving away from the equilibrium value, so *the equilibrium is unstable.* The slope of the line is 1.05 on the right hand side, which is greater than 1. This is characteristic of *unstable linear discrete dynamical models.*

b. For y_1, $n = 0$. Substituting the given value $y_0 = 100$,

$$\begin{aligned} y_1 &= 0.6y_0 + 50 = 0.6(100) + 50 = 110 \\ y_2 &= 0.6y_1 + 50 = 0.6(110) + 50 = 116 \\ y_3 &= 0.6y_2 + 50 = 0.6(116) + 50 = 119.6 \end{aligned}$$

For the equilibrium, we again let $y_e = y_{n+1} = y_n$, so that $y_e = 0.6y_e + 50$.Thus, $0.4y = 50$, or $y = 125$.

In this case, the solution for y is increasing towards the equilibrium, so that the *equilibrium is stable.* Note that for this case the slope of the linear model, 0.6, is less than 1, which is characteristic of *stable linear discrete dynamical models.* ◁

Example 2 *Breathing Argon Gas*

A subject with an unknown lung ailment enters the lab for testing. She is given a supply of air that has an enriched amount of argon gas (Ar). (Recall that atmospheric argon occurs at 0.93% or a concentration of $\gamma = 0.0093$.) After breathing this supply of enriched gas, two successive breaths are measured with $c_1 = 0.0736$ and $c_2 = 0.0678$ of Ar. The model for breathing is given by

$$c_{n+1} = (1-q)c_n + q\gamma.$$

Find the fraction of air breathed, q. What is the concentration of argon remaining in her lungs after 5 breaths?

Assume that her tidal volume is measured to be $V_i = 220$. Find the functional reserve volume, V_r, where $q = V_i/(V_i + V_r)$.

Solution: Since we are given γ and two consecutive values of c_{n+1}, we can find q as shown below, using

$$\begin{aligned} c_2 &= (1-q)c_1 + q\gamma \\ 0.0678 &= (1-q)(0.0736) + 0.0093q \\ q &= 0.0902. \end{aligned}$$

To find the concentration of Ar in her lungs after 5 breaths, we need to know what c_5 is

$$c_2 = (1-q)c_1 + q\gamma = 0.0678$$

as given above.

$$\begin{aligned} c_3 &= (1-0.0902)c_2 + 0.0093(0.0902) = 0.9098(0.0678) + 0.000839 \\ &= 0.06252, \\ c_4 &= 0.9098(0.06252) + 0.000839 = 0.05772, \\ c_5 &= 0.9098(0.05772) + 0.000839 = 0.05336. \end{aligned}$$

To find the functional reserve volume we use the relationship $q = V_i/(V_i + V_r)$,

$$0.0902 = \frac{V_i}{V_i + V_r} = \frac{220}{220 + V_\gamma}.$$

Thus, the functional reserve volume is $V_r = 2219$. ◁

Example 3 *Malthusian Growth*

A population of animals in a particular lake grows according to the Malthusian growth law. In addition, a constant number are entering the lake from a river. Thus, this population satisfies the discrete Malthusian growth model with immigration given by the equation,

$$P_{n+1} = (1+r)P_n + \mu,$$

where r is the rate of growth and μ is the constant number entering the lake. In three successive weeks, the population is measured at $P_0 = 500, P_1 = 670$, and $P_2 = 874$. Find the rate of growth r and immigration rate μ, then determine the populations expected in the next two weeks.

Solution: Substituting the given information into the discrete Malthusian growth model gives two equations and two unknowns (r and μ).

$$\begin{aligned} P_1 &= (1+r)P_0 + \mu \text{ and } P_2 = (1+r)P_1 + \mu \\ 670 &= (1+r)500 + \mu \text{ and } 874 = (1+r)670 + \mu. \end{aligned}$$

If we subtract the first equation from the second equation, we have

$$\begin{aligned} 204 &= (1+r)(670-500) \\ 1+r &= 204/170 = 1.2 \quad \text{or} \\ r &= 0.2. \end{aligned}$$

Substituting this value for the rate of growth r back into the first equation gives

$$670 = 1.2(500) + \mu$$

or

$$\mu = 670 - 600 = 70.$$

So the immigration rate μ is given by $\mu = 70$. Thus, the model can be rewritten as

$$P_{n+1} = 1.2P_n + 70.$$

With this model we can determine the populations expected in the next two weeks, P_3 and P_4.

$$\begin{aligned} P_3 &= 1.2P_2 + 70 = 1.2(874) + 70 = 1118.8, \\ P_4 &= 1.2(1118.8) + 70 = 1412.56. \end{aligned}$$ ◁

This model has no positive equilibrium and is unstable with solutions growing ever larger.

6 EXERCISES

1. Consider the following linear discrete dynamical model:

$$y_{n+1} = 0.7y_n + 6.$$

Let $y_0 = 10$. Find y_1, y_2, and y_3. Also, find the equilibrium point, y_e. Does the solution approach the equilibrium (stable) or move away from the equilibrium (unstable)?

2. Consider the following linear discrete dynamical model:

$$z_{n+1} = 1.2z_n - 20.$$

Let $z_0 = 50$. Find z_1, z_2, and z_3. Also, find the equilibrium point, z_e. Does the solution approach the equilibrium (stable) or move away from the equilibrium (unstable)?

3. In the model for breathing, we could also have kept track of the Nitrogen (N_2) in the exhaled breath also. The mathematical model is the same as in the lecture notes,

$$c_{n+1} = (1 - q)c_n + q\gamma.$$

For the normal subject, we found that $q = 0.18$. The percent of N_2 in the atmosphere is 78%, so this gives $\gamma = 0.78$. Assume that the initial concentration of N_2 in the lungs is given by $c_0 = 0.7$. Find c_1, c_2, and c_3. Also, find the equilibrium point, c_e. Does the solution approach the equilibrium (stable) or move away from the equilibrium (unstable)?

4. Consider the model for breathing with Helium gas (He) as a tracer in the lungs. In the atmosphere, He occurs at 5.2ppm. Suppose a subject with emphysema begins with a concentration of $c_0 = 100$ppm. The mathematical model is the same as before,

$$c_{n+1} = (1 - q)c_n + q\gamma.$$

This subject has $q = 0.1$. Find c_1, c_2, and c_3. Also, find the equilibrium point, c_e. Does the solution approach the equilibrium (stable) or move away from the equilibrium (unstable)?

5. The lecture notes showed how the model could be used to determine the vital capacity of a subject. Suppose that the tidal volume, V_i, of the subject is 400 ml. For this experiment, Nitrogen, N_2, is used to determine

the functional reserve capacity, V_r. (Note that $V_r = (1-q)V_i/q$.) The mathematical model gives

$$c_{n+1} = (1-q)c_n + q\gamma,$$

where $\gamma = 0.78$. You are given that $c_0 = 0.68$ and $c_1 = 0.694$. Use this information to find q, then determine the functional reserve capacity, V_r.

6. A woman with a chronic lung problem is found to have a vital capacity of only 1300 ml and a residual volume of 950 ml. Suppose that the tidal volume, V_i, of this patient is 350 ml. For this experiment, Helium, He, is used to determine the functional reserve capacity, V_r. (Recall that $V_r = (1-q)V_i/q$.) The mathematical model gives

$$c_{n+1} = (1-q)c_n + q\gamma,$$

where $\gamma = 5.2$ ppm.

a. The woman is given an enriched mixture of air to breathe that contains 30 ppm of He. Experimentally, it is found that her first 3 breaths after breathing the enriched mixture for a while have concentrations of He given by $c_0 = 30$, $c_1 = 25.8$ and $c_2 = 22.3$ ppm. Use c_0 and c_1 to find q, then determine the functional reserve capacity, V_r.

b. Use your model to find the expected concentration of Helium in this patient's 10^{th} breath, c_{10}. What is the equilibrium concentration of Helium in the patient's lungs?

c. If the functional reserve capacity is equal to the expiratory reserve volume plus the residual volume and the vital capacity is equal to the sum of the tidal volume and the inspiratory and expiratory reserve volumes, then use the data above to find the inspiratory and expiratory reserve volumes for this patient with chronic lung problems. Compare her values to those for a woman with normal lung function.

7. Consider a model with immigration given by

$$p_{n+1} = 1.05p_n + 200,$$

with an initial population of $p_0 = 1000$. Find the populations at the next three time intervals, p_1, p_2, and p_3.

8. The population in the U.S. at the turn of the last century is given in the following table (with population in millions).

Year	1900	1910	1920	1930
Population	76.0	92.0	105.7	122.8

a. Let $p_0 = 76.0$ and consider the Malthusian growth model

$$p_{n+1} = 1.17p_n,$$

where n is in decades. Find p_1, p_2, and p_3. Determine the percent error in these predictions compared to the actual values.

b. Again let $p_0 = 76.0$ and consider the Malthusian growth model with immigration. Assume that the immigration over a decade is approximately 3.0 million, then the model is given by

$$p_{n+1} = 1.14p_n + 3.0,$$

where n is in decades. Find p_1, p_2, and p_3. Determine the percent error in these predictions compared to the actual values. Notice that the actual growth rate is 3% lower in this model.

9. Below is data on several populations of herbivores in related areas.

p_0	p_1
70	90
100	150
150	250

The data is assumed to fit a discrete Malthusian model with emigration in the form

$$p_{n+1} = rp_n - \mu,$$

where $r - 1$ is the growth rate and μ is the emigration rate.

a. Use the data below to determine the updating function for this population, i.e., find r and μ and write the equation for this model.

b. Beginning with $p_0 = 100$, find the populations p_1, p_2, and p_3.

c. Find the equilibrium value and determine the stability of this equilibrium.

10. Below are data on the population of a species of moth that inhabits an island and breeds annually (then dies). If its offspring have a survival rate r, and there is a net (constant) influx of new moths from surrounding islands entering at a rate μ, then the population model has the form

$$P_{n+1} = rP_n + \mu.$$

a. From the data below determine the updating function for this population, *i.e.*, find r and μ. Then use this updating function to find the population of moths in 1993, 1994, and 1995.

b. Find all equilibria for this model. Based on your iterations in Part a, what is the stability of the equilibria? (If a solution moves closer to an equilibrium point, then it is probably stable. If it moves away, then it is most likely unstable.) What does this model predict will ultimately happen to the population of moths?

c. Graph the updating function along with the identity map, $P_{n+1} = P_n$. Determine all points of intersection.

Year	Moths
1990	6000
1991	5500
1992	5100

7 REFERENCES

[1] A.C. Guyton and Hall, *Textbook of Medical Physiology*, W.B. Saunders Co., Philadelphia, (1997).

CHAPTER 9:

INTRODUCTION TO THE DERIVATIVE

In this chapter we want to introduce the derivative. There are several ways to view this important concept in Calculus. The previous two sections examined discrete models for population growth. One method, and probably the most common in biological applications, is viewing the derivative as a rate of growth. A second, the more classical approach to the derivative as developed by Newton, is relating the derivative to velocity. A third and more geometric view of the derivative is the tangent line. This chapter develops the concept of the derivative, and the following chapters study techniques for finding the derivative and using it in applications.

1 THE DERIVATIVE AS A GROWTH RATE

Example 1 *Juvenile Height*

We begin our study by returning to an example introduced in our chapter on linear functions. Figure 1 (left) gives a graph for the heights of girls and boys at the 50^{th} percentile for ages 0 to 18. The original data can be seen at KidsGrowth.com[1]

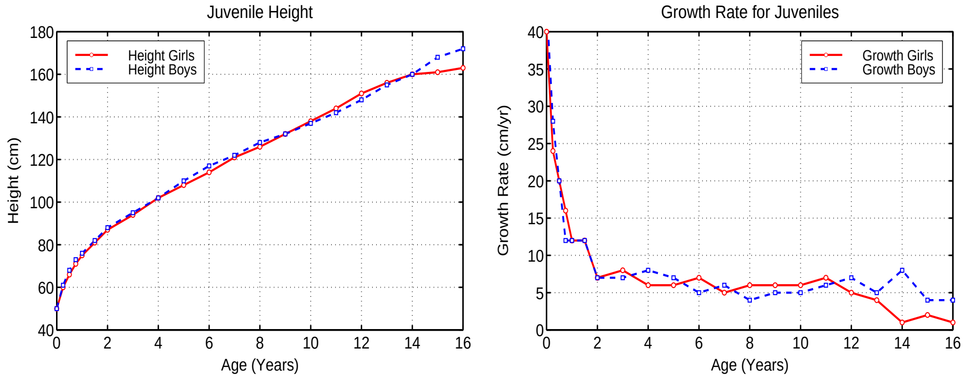

Figure 1: Graphs of the height (in cm) [left] and its growth rate [right] for girls and boys with respect to their age (in years).

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[1] www.kidsgrowth.com/resources/articledetail.cfm?id=304, last visited 03/24/04

In the linear chapter, we noted that the rate of growth is the slope of the line through the data. Over a wide range of ages, this rate of growth is almost constant. However, as the graphs above show, the earliest years show a much higher rate of growth and the later years show a significant slowing in the growth rate. The annual growth rate is easily computed by taking the difference in heights in two successive years, which is the slope of the line connecting the data points. In the early years of life, the data are collected more frequently, every three months. If you have quarterly data on height, then you take the difference in the heights between successive measurements and multiply by 4 to obtain the annual growth. In either case, the growth rate $g(t)$ can be approximated by the formula

$$g(t_0) = \frac{h(t_1) - h(t_0)}{t_1 - t_0}.$$

where t_0 is the first age being considered with height at that age being $h(t_0)$ and t_1 is the second age being considered with its corresponding height of $h(t_1)$. For example, for girls,

Age (years)	Height (cm)	Annual Growth Rate (cm/yr)
$t_0 = 2$	$h(t_0)$=87	
$t_1 = 3$	$h(t_1) = 94$	$g(2) = (h(3) - h(2))/(3 - 2) = 7$

Similarly, for small boys,

Age (years)	Height (cm)	Annual Growth Rate (cm/yr)
$t_0 = 3/12 = 0.25$ (3 months)	$h(t_0)$=61	
$t_1 = 6/12 = 0.5$ (6 months)	$h(t_1) = 68$	$g(0.25) = \dfrac{h(0.5) - h(0.25)}{0.5 - 0.25} = 28$

The right panel of Figure 1 shows the graph of the growth rates computed from the height graph (left panel in Figure 1). Notice that initially the growth rate is higher, then it stays almost constant for many years, and finally drops almost to zero. This growth rate being constant is indicative of the heights lying almost on a straight line. ◁

Example 2 *Yeast Population*

In 1913, Carlson [1] studied a growing culture of yeast. Table 1 of the population for these yeast (in thousands/cc) measured at one hour intervals. A graph of these data is presented in Figure 2.

Time	Population	Time	Population	Time	Population
1	9.6	7	174.6	13	594.8
2	18.3	8	257.3	14	629.4
3	29.0	9	350.7	15	640.8
4	47.2	10	441.0	16	651.1
5	71.1	11	513.3	17	655.9
6	119.1	12	559.7	18	659.6

Table 1: Data for the yeast population growth (in thousands/cc) measured at one hour intervals.

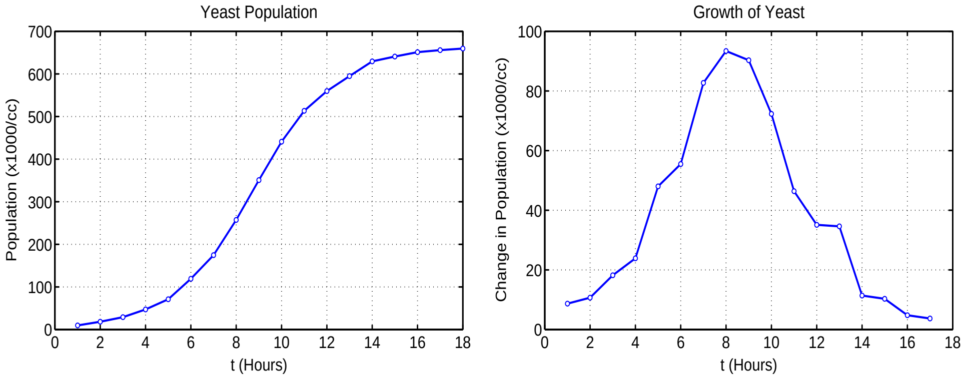

Figure 2: Graph for the yeast population growth of Table 1 (left) and its corresponding growth rate (right).

This graph of the population of yeast shows what is classically called an *S-shaped curve*. It occurs frequently in biological models (recall the Michaelis-Menten enzyme curve). The population of yeast grows slowly in the beginning, then its growth rate increases to where its a maximum near 8 hours, then decreases and levels off as the population reaches its carrying capacity. Define the population at each hour as $P(t)$.

The growth of the yeast for each hour is computed by taking the difference in the populations at each hour (and dividing by 1 hour). As we did above for the growth of a child, we find the growth of the population by computing

$$g(t_n) = \frac{P(t_{n+1}) - P(t_n)}{t_{n+1} - t_n}.$$

Once again this is the slope of the curve above computed between each of the data points. This can be seen in the graph of the growth function

$g(t)$ shown in the right panel of Figure 2. If we had more data, then we might expect a smoother growth curve. It is very **important** to note that the graph of the yeast population (left panel in Figure 2) and the graph of the growth rate of the yeast population (right panel in Figure 2) are **different graphs**, but are related through the slope of the population graph. The *derivative* will be the *instantaneous growth rate at any time* for any population curve. ◁

2 THE DERIVATIVE AS A VELOCITY

Example 3 *Trotting Horse*

In the 1800s, there was a controversy whether or not a trotting horse ever had all feet off of the ground. This led the photographer Eadweard Muybridge to develop some special photographic techniques for viewing animals and humans in motion by collecting timed sequences of still pictures. When viewed in succession with the same intervening times, these pictures produce an animation of motion, which was a precursor to modern motion pictures. There is a website[2] with several of these classical studies by Eadweard Muybridge. Let us examine the one for a trotting horse. (Clicking on the "horse in motion" should take you to the appropriate website.)

Our interest here is determining the velocity of the trotting horse. It is often asked how fast a particular animal can run or what speed is a bird flying, but answering this question is much trickier. You should think of how you might determine say the speed of a cheetah hunting a Thompson's gazelle or the velocity of a peregrine falcon diving to catch a pigeon. Figure 3 gives a blown up sequence from the "horse in motion" movie at the website above mentioned. The question is: How fast is the horse trotting?

The question above is one about velocity of the trotting horse. Velocity has units of distance divided by time (typically, miles or kilometers per hour or feet or meters per second). Thus, the velocity of the trotting horse is found by computing the distance covered between successive picture frames divided by the time between the pictures. From the frames presented above there is a scale in the background measuring the distance (in feet), and the time between frames is given. If we choose the man's head for a reference point, then we can easily see the position at $t_0 = 0$, satisfies $s(t_0) = 3.5$ ft.

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[2] http://web.inter.nl.net/users/anima/chronoph/first-15/index.htm, last visited on 03/29/04

Image 1, $t = 0.00$ sec

Image 2, $t = 0.04$ sec

Image 3, $t = 0.08$ sec

Image 4, $t = 0.12$ sec

Image 5, $t = 0.16$ sec

Image 6, $t = 0.20$ sec

Image 7, $t = 0.24$ sec

Image 8, $t = 0.28$ sec

Image 9, $t = 0.32$ sec

Figure 3: Blown up sequence from the "horse in motion" movie.

At $t_1 = 0.04$, the head is at $s(t_1) = 4.5$ ft. Thus, the velocity is given by

$$v(t_0) = \frac{s(t_1) - s(t_0)}{t_1 - t_0} = \frac{4.5 - 3.5}{0.04 - 0} = 25 \text{ (ft/sec)} = 17.0 \text{ mph}.$$

Notice at $t_2 = 0.08$, the head is at $s(t_2) = 5.6$ ft, so the velocity satisfies

$$v(t_1) = \frac{s(t_2) - s(t_1)}{t_2 - t_1} = \frac{5.6 - 4.5}{0.08 - 0.04} = 27.5 \text{ (ft/sec)} = 18.75 \text{ mph},$$

which is approximately the same.

An average velocity for the entire sequence of pictures gives the best average velocity for this trotting horse. It is computed by taking the initial and final positions of the head and dividing by the total time between the frames. Thus,

$$v(t_{ave}) = \frac{s(t_f) - s(t_0)}{t_f - t_0} = \frac{11.5 - 3.5}{0.32 - 0} = 25.0 \text{ (ft/s)} = 17.05 \text{ mph}.$$

So we see that the velocity is relatively constant over the short time interval of the pictures.

The question would become much more complicated if we asked the velocity of the right front hoof. Clearly, this sequence of pictures is inadequate for properly studying its motion. Does the right front hoof stop or move backwards at any time? How would you answer this question? You would probably want more pictures taken at smaller intervals of time. ◁

3 FALLING UNDER THE INFLUENCE OF GRAVITY

The classical study from physics for velocity is the motion of a falling ball. The University of British Columbia Mathematics Department website[3] shows a method for producing a series of pictures similar to those for the trotting horse, using a strobe light to capture the motion of a ball. The time evolution of this falling ball is shown in Figure 4.

Figure 4 shows the position of the ball at each second, as if a strobe light were capturing it at those times. At the later times, you can see that the ball is falling almost 100 m between successive times. We could get better resolution of the position of the ball by sampling at closer time intervals. This finer resolution gives a better sense of the motion and a more accurate measure of the velocity. As with the trotting horse, you would ideally like to let the interval of time between measurements become very small. This limiting process of smaller time intervals is key to understanding the concept of a derivative.

Derivative – Falling Ball

This applet simulates a ball falling under gravity (no air resistance) with a strobe light catching the position of the ball at regular time intervals. You can choose the interval of time at which you want to observe the ball by varying the time between the flashes of the strobe light. Change the time between strobe flashes by entering different values in the window. The left frame shows the position of the ball as it drops, while the right frame graphs the position as a function of time.

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[3] http://www.ugrad.math.ubc.ca/coursedoc/math100/notes/derivative/ball1.html, last visited 03/29/04

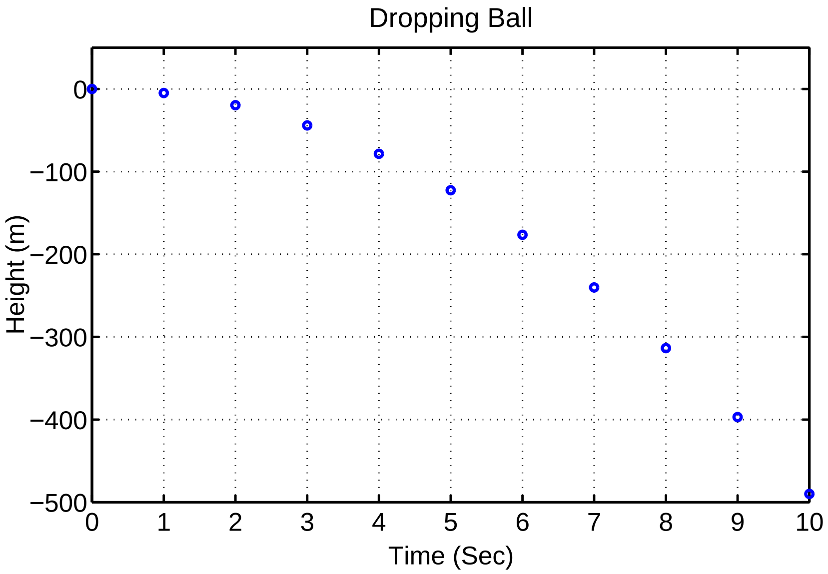

Figure 4: A ball falling just under the influence of gravity (no air resistance) has the positions shown in this figure as time progresses.

In the next section, we shall develop the geometric perspective of the derivative as a tangent line. However, the formulae above should be reminding you of the equations we used to find the slope of a line. Thus, our geometric viewpoint of a derivative will be equivalent to what we have discussed above.

Below there a few more examples to better understand the concept of derivative.

4 MORE EXAMPLES

Example 4 *Growth of a puppy*

In developing his Project Calculus course, David Smith [3] measured the growth of his Golden Retriever puppy, Sassafras. Below is a table showing the growth of his puppy.

Age (days)	Weight (lbs)
0	3.25
10	4.25
20	5.5
30	7
40	9
50	11.5
60	15
70	19
101	30
115	37
150	54
195	65
230	70
332	75
436	77

Find the average weekly growth rate of the puppy over the first 10 weeks. Estimate the weekly growth rate of the puppy at age 10 weeks using the data at 70 and 101 days. What is the weekly growth rate between days 230 and 436?

Solution: The first 10 weeks is equivalent to the first 70 days. The weight at day 0 is 3.25 lbs, while its 19 lbs at 10 weeks. Thus, the average growth rate is computed as follows,

$$\frac{19-3.25}{10} = 1.575 \text{ lb/week.}$$

To compute the weekly growth rate at 10 weeks, we see

$$\frac{30-19}{(101-70)/7} = 2.48 \text{ lb/week.}$$

Similarly, the weekly growth rate between 230 and 436 days is given by

$$\frac{77-70}{(436-230)/7} = 0.238 \text{ lb/week.}$$

◁

Example 5 *Paramecium Caudatum*

Table 2 is taken from G. F. Gause [2] showing the population of *Paramecium caudatum* over a period of 15 weeks.

Week	Individuals (/0.5cc)
0	2
2	10
3	10
4	11
5	21
6	56
7	104
8	137
9	165
10	194
11	217
12	199
13	201
14	182
15	192

Table 2: Data for the *Paramecium caudatum* population growth.

Plot a graph of the number of *Paramecium caudatum* as a function of time (weeks). Then plot the rate of growth of the population as a function of time using two continuous rows in the table (associating the rate of growth with the earlier time). What is the growth rate near week 7?

Solution: The left panel of Figure 5 shows the graph of the data in Table 2 showing the population as a function of number of weeks. The growth rate for the first two weeks requires taking the difference of the populations and dividing by two, while all other growth rates are found by simply subtracting the populations between two successive rows in the table. The resulting graph is shown in the right panel of Figure 5.

It is easy to see that the growth rate around Week 7 is $137 - 104 = 33$ (individuals/0.5 cc/week). ◁

Example 6 *Free fall*

A steel ball, which is dropped from a height of 4 meters, has its height measured every 0.1 seconds. Table 3 shows how far the ball has dropped at each time period. Find the average speed of the ball over the 0.9 seconds of the experiment. Also, determine the average speed of the ball between 0.5 and 0.7 seconds.

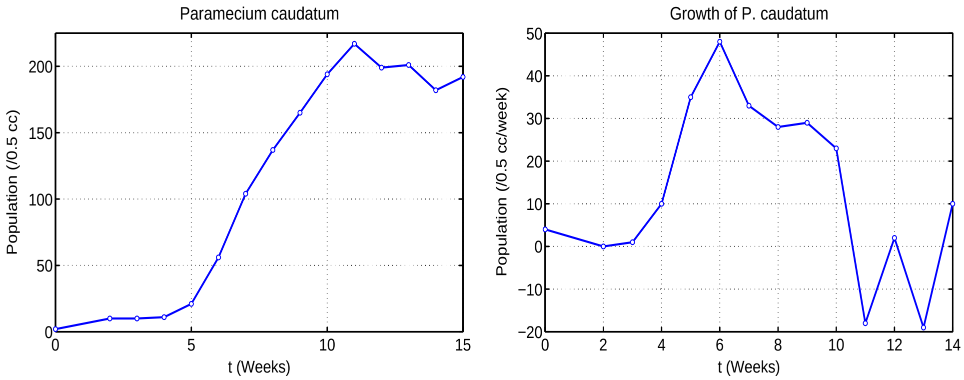

Figure 5: Left: Growth of the *Paramecium caudatum* population in weeks. Data taken from Table 2. Right: Graph for the respective population growth rate.

Solution: The average speed of the ball over the 0.9 seconds of the experiment is given by,

$$\frac{396-0}{0.9-0} = 44.0 \text{ cm/sec.}$$

The average speed between 0.5 and 0.7 seconds is given by

$$\frac{240-123}{0.7-0.5} = 585 \text{ cm/sec.}$$

◁

Example 7 *Sky diver*

A sky diver encounters a significant amount of air resistance when free falling (and more significantly when the parachute opens), so his speed will not match the parabolic curve we saw in the applet Derivative – Falling Ball. Table 4 gives typical values of a sky diver who, when released at about 10,000 ft, free falls for 45 seconds. Table 4 gives the time and the distance above the ground.

Plot a graph of the Height *vs.* Time, then by using the successive rows of the table, approximate the velocity (in ft/sec) of the sky diver at each of the times listed in the table from 0 to 40 and graph this velocity curve. What is the approximate velocity in miles per hour at 30 seconds into the fall? Can you estimate when the sky diver would hit the ground if the parachute failed to open?

Solution: A plot of the graph for the height of the sky diver as a function of the time free falling is shown in the left panel of Figure 6. Notice that the

Time (sec)	Distance (cm)
0	0
0.1	5
0.2	19
0.3	44
0.4	78
0.5	123
0.6	176
0.7	240
0.8	313
0.9	396

Table 3: Distance travelled by a free falling ball each 0.1 seconds.

shape of this graph is **not** parabolic, like our example of the falling ball. A graph of the velocity of the sky diver is shown in the right panel of Figure 6.

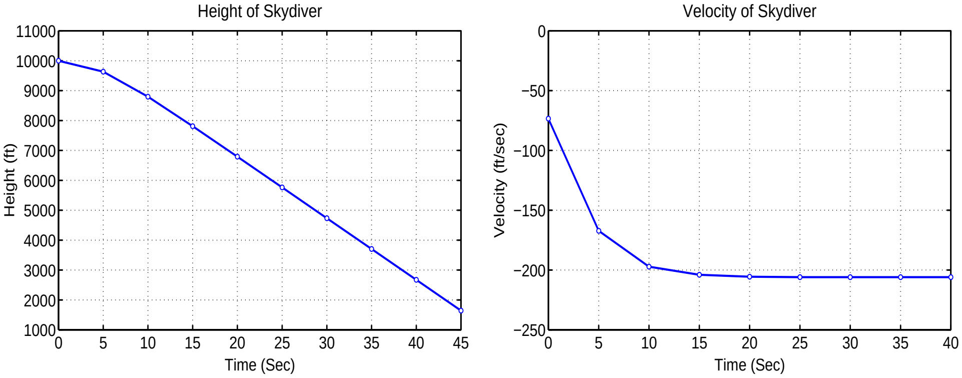

Figure 6: Left: Graph of the height of a sky diver taken from Table 4. Right: Graph for the corresponding velocity.

We see that the velocity of the sky diver levels off shortly after 10 seconds. This is known as the terminal velocity of the sky diver. The velocity at 30 seconds is $(3703 - 4733)/5 = 206$ ft/sec, which is $206(3600/5280) = 140.5$ mph.

Since the sky diver is at terminal velocity, after 45 sec, you can assume that the sky diver would continue to fall at 206 ft/sec, so it would take $1643/206 = 8.0$ sec to cover the remaining 1643 ft. Thus, the sky diver would fall for about 53 sec if the parachute failed. ◁

Time (sec)	Height (ft)
0	10,000
5	9,633
10	8,797
15	7,811
20	6,791
25	5,763
30	4,733
35	3,703
40	2,673
45	1,643

Table 4: Distance travelled by a sky diver during a free fall presenting air resistance.

5 EXERCISES

1. Consider Example 4 from Section 4 on the growth of a golden retriever puppy.

a. Find the weekly growth rate between days 115 and 150 (in lbs/week). Also, find the average growth rate between days 0 and 332.

b. Find the weekly growth rate between each of the data values given. Sketch a graph of the weight as a function of number of days, then graph the rate of weekly growth as a function of the age. At what age is the growth rate at a maximum?

2. Consider Example 5 from the Section 4 on the growth *Paramecium caudatum.*

a. Find the average growth rate for the first 10 weeks and compare that to the growth rate for the fifth week computed by using the data from weeks 5 and 6.

b. From the graph for the growth rate of *P. caudatum*, determine when the population is growing most rapidly and when it has its steepest decline. Calculate those values from the table.

3. Consider Example 6 from the 4 section for a falling ball.

a. Graph the data and describe the geometric figure in the graph.

b. Find the average velocity over the intervals $t \in [0, 0.3]$, $t \in [0.3, 0.6]$, and $t \in [0.6, 0.9]$. Associate the average velocity with the midpoint of each of these time intervals, and sketch a graph of the average velocity as a function of time. Do these points seem to fall on a line, and if so, determine the equation of this line?

4. Consider Example 7 from Section 4 for the height of a sky diver. Find the average velocity of the sky diver over the 45 sec of the data. What is the percent error in using this value for the terminal velocity as compared to the value computed in the notes?

6 REFERENCES

[1] T. Carlson Über Geschwindigkeit und Grösse der Hefevermehrung in Würze. *Biochem. Z.* (1913) **57** 313–334.

[2] G. F. Gause. *Struggle for Existence* (1934), Hafner, New York.

[3] D. A. Smith and L. C. Moore. *Calculus: Modeling and Applications* (1996), DC Heath, New York.

CHAPTER 10:

VELOCITY AND TANGENT LINES

Differential Calculus began with the study of motion, and Sir Isaac Newton's work on gravity was a key step to the development of Calculus. (There is a controversy as to whether Newton or Leibnitz was the first to invent Calculus.) Gravity plays a key role in Biology as well as Physics. This section begins by examining a cat falling from a tree branch. Next the flight of a ball neglecting air resistance is revisited as a classical study in differential Calculus. The flight of a ball and its velocity are used to give a geometric understanding of the derivative by observing how a ball falling under the influence of gravity would appear using a strobe light (and allowing the time of the strobe light to vary).

1 CATS AND GRAVITY

The cat has evolved to be one of the best mammalian predators. (Domestic cats have been shown to responsible for up to 60% of the deaths of songbirds in some communities.) The domestic cat comes from a line of cats that adapted to hunting in trees. This requires tremendous agility. These cats have a very flexible spine that enables them to spring for prey and absorb the shock from their pouncing. This flexibility allows them to rotate rapidly during a fall and usually end up on the ground feet first.

Humans have been fascinated by this ability of a cat to right itself so quickly from a fall. There have been quite a few scientific studies of cats falling. One study [1] of cats falling out of New York apartments showed that paradoxically the cats falling from the highest apartments actually fared better than ones falling from an intermediate height. Apparently, the cat first rights itself rapidly during a fall, but remains tense. However, with greater heights the falling cat relaxes and actually spreads its legs to form more of a parachute, which slows its velocity a little and results in a more even impact. From intermediate heights, the cat basically achieves terminal velocity (from the air resistance balancing the force of gravity), but the tension and the stiffness seems to cause increased likelihood of severe or fatal injuries.

The complications of modeling air resistance during a fall are beyond the scope of this course at this time, but we can model the early stages of the fall where the primary dynamics result from acceleration due to gravity. If a cat falls from a tree (not too high up), then its motion is governed by the basic laws of gravity. *Newton's law of motion* says that *mass times acceleration is equal to the sum of all the forces* acting on an object. In our introduction to the derivative, we noted that the velocity is the derivative of position. It is also true that acceleration is the derivative of velocity.

Suppose that a cat falls from a branch that is 16 feet high. It can be shown that the height of the cat satisfies the equation

$$h(t) = 16 - 16t^2.$$

How long does this cat fall and what is its velocity when it hits the ground?

The first question is easily answered, since the height of the ground is assumed to be zero. We simply solve

$$h(t) = 16 - 16t^2 = 0,$$

which occurs when $t = 1$. However, the velocity at $t = 1$ requires more work. We will show that the cat has a velocity, $v(1) = -32$ ft/s (or about 21.8 mph).

2 FALLING BALL REVISITED

In the previous chapter, the applet Derivative – Falling Ball allowed you to vary the period of time between flashes of a strobe light for viewing a falling ball. The applet graphed the actual path of the ball, simply falling vertically and then showed a graph of the height of the ball as a function of time. We computed the average velocity of the ball by noting its position at two successive flashes, then dividing by the length of time between the flashes. This is implemented in the applet below.

Velocity – Falling Ball Revisited

In this applet, you choose a time between strobe flashes, then click on the drop button. The applet shows that the height of the ball follows a parabolic shaped path with the distance of the ball between successive flashes increasing with time. The velocity becomes more and more negative and follows a straight line. We will see that the derivative of a quadratic function is a linear function.

3 FLIGHT OF A BALL UNDER GRAVITY

We modify the previous example a little to observe a ball thrown up vertically under the influence of gravity, ignoring air resistance. Specifically, we consider a ball that begins at ground level ($h(0) = 0$ cm) and is thrown vertically with a velocity of cm/s ($v(0)$ =cm/s). The acceleration due to gravity is $g = 980$ cm/s^2. It can be shown (later you will learn to derive this) that the height of the ball for any time t ($0 \le t \le 4$) is given by

$$h(t) = 1960t - 490t^2.$$

If we graph the height of the ball $h(t)$ over the first 4 seconds, showing the ball at every 0.5 s (as if the ball were viewed with a strobe light), then the ball's height would appear as in the left panel of Figure 1. Notice the actual flight goes up, then comes down, so we are looking at snapshots in time (the horizontal axis).

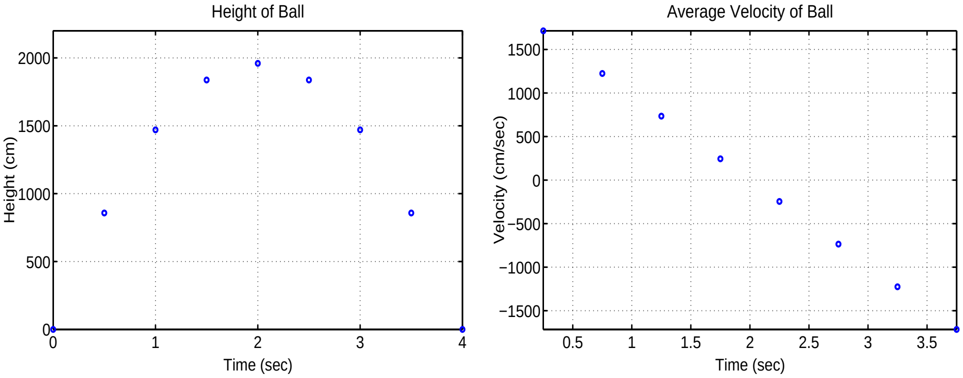

Figure 1: Left: Graph of the height of the falling ball ($h(t)$) *vs.* time. Right: Graph of the free falling ball average velocities taken from Table 1.

Next we want to find the average velocity between each point on the left panel of Figure 1. The average velocity for this ball in flight is the difference between the heights at two times divided by the length of the time period. For convenience, let us associate the average velocity with the midpoint between each time interval considered. Table 1 shows the computation of a few average velocities for the graph of Figure 1.

A graph of all the average velocities is shown in the right panel of Figure 1. The graph of the height of the ball is clearly a parabola, while the graph of the average velocities is a straight line. Notice that the straight line seems to have an average velocity of zero at the same time as the height

$h(t_1)$	$h(t_2)$	$t_a = (t_1 + t_2)/2$	Average Velocity
			$\dfrac{h(t_2) - h(t_1)}{(t_2 - t_1)}$
$h(0) = 0$	$h(0.5) = 857.5$	$t_a = 0.5/2 = 0.25$	$v(0.25) = 1715$
$h(1.5) = 1837.5$	$h(2) = 1960$	$t_a = 1.75$	$v(1.75) = 245$
$h(3) = 1470$	$h(3.5) = 857.5$	$t_a = 3.25$	$v(3.25) = -1225$

Table 1: Height and average velocity for the free falling ball shown in Figure 1

of the ball reaches its maximum. We would expect that the velocity goes to zero when the ball is at the top of its flight.

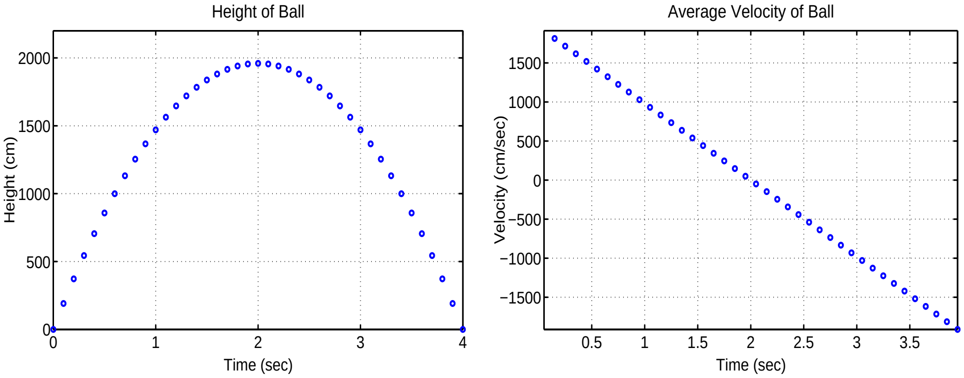

Figure 2: Left: Graph of the free falling ball every 0.1 seconds. Right: The corresponding average velocity of the dropping ball.

So what happens if we collect data at shorter time intervals, say every 0.1 s. The left panel of Figure 2 shows the graph of the height with data every 0.1 s. So how does this affect the average velocity computation? The distance between successive heights is now much closer, but then the intervening time interval is also closer together. If you compute the average velocity between $t_1 = 0.2$ and $t_2 = 0.3$ with $h(t_1) = 372.4$ cm and $h(t_2) = 543.9$ cm, then $v(0.25) = 1715$ cm/s, which is the same as before. The right panel of Figure 2 has a graph of the average velocity data.

As we can see, the average velocity data lie on the same straight line as before and are given by

$$v(t) = 1960 - 980t.$$

This straight line function is the *derivative* of the quadratic height function $h(t)$ given above. The calculation suggests that the derivative function is independent of the length of the time interval chosen; however, this was specific to the quadratic nature of the height function. We will learn in the coming sections how to take derivatives of more functions.

Here, we include two more examples to clarify the above:

Example 1 *Flight of a Ball*

A ball, which is thrown vertically with an initial velocity of 80 ft/s and only the acceleration of gravity acting on the ball, satisfies the equation:

$$h(t) = 80t - 16t^2.$$

a. Sketch a graph of the height of the ball (in feet), $h(t)$, showing clearly the maximum height and when the ball hits the ground.

b. Find the average velocity of the ball between $t = 0$ and $t = 1$ and associate this velocity with $t = 0.5$. Repeat this process for each second of the flight of the ball, then sketch a graph of the average velocity as a function of time, t.

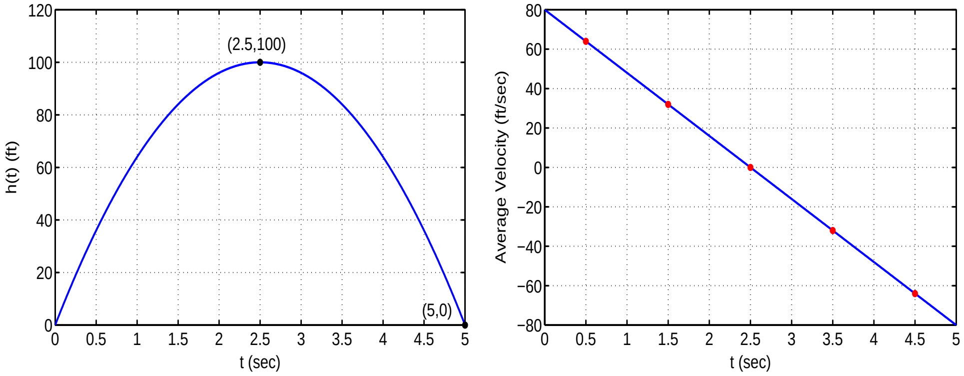

Figure 3: Left: Parabolic graph of the height of the flight of a ball of Example 1 Right: The corresponding average velocities given in Table 2.

Solution: a. The graph of $h(t)$ is a parabola with t-intercepts at $t = 0$ and $t = 5$, the latter being when the ball hits the ground. The vertex or maximum height of the ball occurs at the midpoint between these intercepts or $t = 2.5$ with $h(2.5) = 100$ ft. The left panel of Figure 3 shows a graph showing the height of the ball as a function of t.

b. The average velocity for the ball between $t = 0$ and $t = 1$ s is given by

$$v_{ave}(0.5) = \frac{h(1) - h(0)}{1 - 0} = 64 \text{ ft/s}.$$

Similarly, the average velocities are computed between each pair of seconds from $t = 0$ to $t = 5$, and the results are summarized in Table 2.

t	0.5	1.5	2.5	3.5	4.5
v_{ave}	64	32	0	−32	−64

Table 2: Average velocities for Example 1.

The graph of the average velocity is depicted in the right panel of Figure 3 and is a straight line. Note that the average velocity is zero at the maximum of the height curve, $h(t)$. ◁

Example 2 *Leaping Salmon*

A river is dammed, and a salmon ladder is built to enable the salmon to bypass the dam and continue to travel upstream to spawn. The vertical walls on the salmon ladder are 6 feet high. The salmon has to leap vertically upwards over the wall. The height of the salmon during its leap is given by

$$h(t) = 20t - 16t^2.$$

a. Sketch a graph of the height of the salmon (in feet), $h(t)$, with time, showing clearly the maximum height and when the salmon can clear the wall.

b. Find the average velocity of the salmon between $t = 0$ and $t = 0.5$ and associate this velocity with $t = 0.25$. Repeat this process for each half-second of the leaping salmon, then sketch a graph of the average velocity as a function of time, t.

c. Determine the minimum speed, v_0, that the salmon needs on exiting the water to climb the salmon ladder if the height is given by the formula

$$h(t) = v_0 t - 16t^2.$$

Solution: a. The function $h(t)$ is a parabola, which can be written in the factored form of

$$h(t) = 20t - 16t^2 = 4t(5 - 4t).$$

It follows that the t-intercepts are $t = 0$ and $t = 5/4 = 1.25$. Thus, the vertex occurs at $(0.625, 6.25)$. The graph of this parabola is depicted in the left panel of Figure 4. The salmon can clear the wall when $h(t) = 6$, so $20t - 16t^2 = 6$ or $8t^2 - 10t + 3 = 0$. This can be factored to give

$$(2t - 1)(4t - 3) = 0.$$

It follows that either $t = 1/2$ or $t = 3/4$, so the salmon can clear the wall at any time $1/2 \le t \le 3/4$ s.

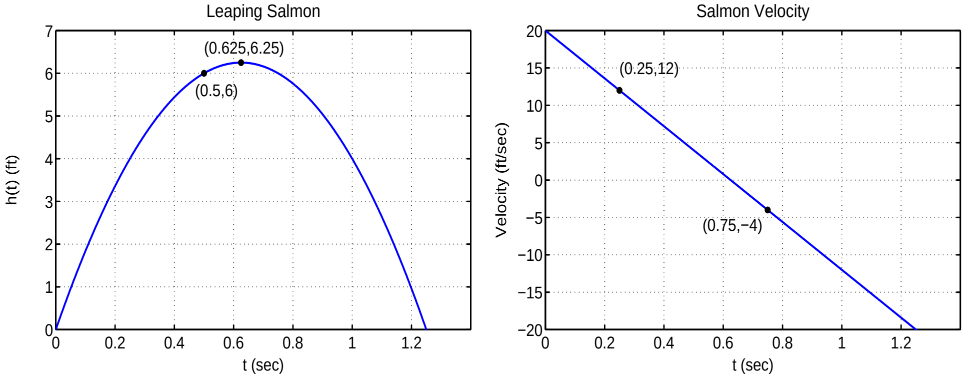

Figure 4: Left: Graph of the leaping salmon of Example 2. Right: Graph of the corresponding salmon velocity.

b. The average velocity of the salmon between $t = 0$ and $t = 0.5$ is given by,

$$v(0.25) = \frac{h(0.5) - h(0)}{0.5} = \frac{(20(0.5) - 16(0.5)^2) - 0}{0.5} = 12 \text{ ft/s}.$$

Similarly, the average velocity of the salmon between $t = 0.5$ and $t = 1$ is given by

$$v(0.75) = \frac{h(1) - h(0.5)}{0.5} = \frac{4 - 6}{0.5} = -4 \text{ ft/s}.$$

The graph of the velocity curve is depicted in the right panel of Figure 4.

c. The minimum speed, v_0, that the salmon needs to climb the fish ladder is the one that produces a maximum height of 6 ft. This is equivalent to having the vertex of the height function occur with $h = 6$. Since $h(t) = v_0t - 16t^2$, the t-value of the vertex occurs at

$$t = \frac{v_0}{32}$$

(since this is halfway between the intercepts $t = 0$ and $t = v_0/16$). Since we want the vertex to be 6 ft, we need to satisfy the equation

$$h\left(\frac{v_0}{32}\right) = v_0\left(\frac{v_0}{32}\right) - 16\left(\frac{v_0}{32}\right)^2 = \frac{v_0^2}{64} = 6.$$

Thus,

$$v_0 = 8\sqrt{6} \approx 19.6 \text{ ft/s}.$$

◁

4 TANGENT LINE INTERPRETATION

The calculations above for the average velocity are the same as the calculations for the slope between the two data points given by the height function. Technically, this is known as computing the *slope of the secant line between two points on a curve.* Geometrically, as the points on the curve get closer together, then the secant line approaches the tangent line. The *tangent line* represents the best linear approximation to the curve near a given point. Its slope is the derivative of the function at that point. Figure 5 illustrates how a sequence of secant lines formed from a given point and other points on the curve approach the tangent line at the given point as the other points get closer to the given point.

Example 3 Consider the function

$$y = x^2.$$

We would like to find the equation of the *tangent line* at the point $(1, 1)$ on the graph. A *secant line* is found by taking two points on the curve and finding the equation of the line through those points.

Velocity – Tangent Lines

The animated gif at this site shows a sequence of secant lines that converge to the tangent line by taking the two points closer and closer together. The animated gif starts with the secant line through the points $(1, 1)$ and $(2, 4)$. This line has a slope of $m = 3$, and its equation is $y = 3x - 2$. The next the pair of points on the curve $y = x^2$ is $(1, 1)$ and $(1.5, 2.25)$. This line has a slope of $m = 2.5$, and its equation is $y = 2.5x - 1.5$. The secant line through the points $(1, 1)$ and $(1.1, 1.21)$ has a slope of $m = 2.1$, and its equation is $y = 2.1x - 1.1$.

Suppose we take $x = 1 + h$ for some small h. With $y = x^2$, the corresponding y-value is $y = (1 + h)^2 = 1 + 2h + h^2$. The slope of the secant line

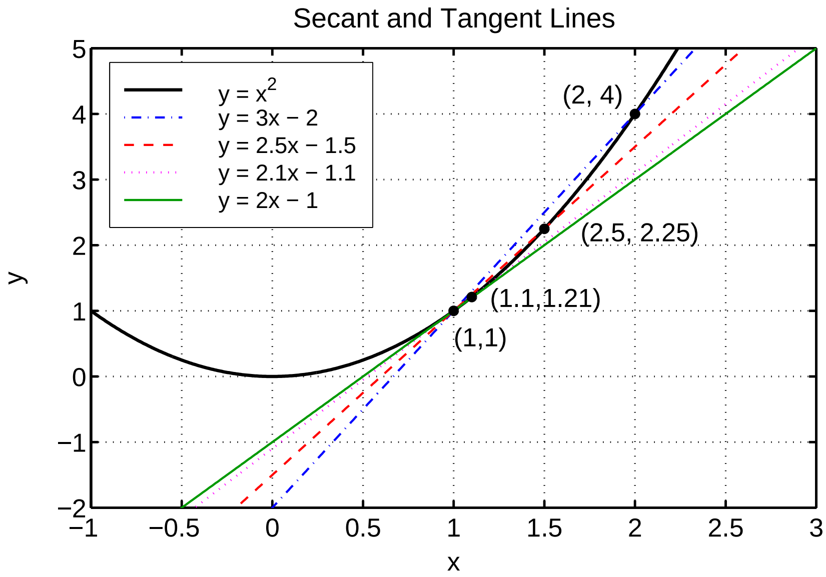

Figure 5: Sequence of secant lines approximating the tangent line to the curve at $(1, 1)$.

through this point and the point $(1, 1)$ is

$$m = \frac{(1 + 2h + h^2) - 1}{(1 + h) - 1} = \frac{2h + h^2}{h} = 2 + h,$$

and the formula for this secant line is

$$y = (2 + h)x - (1 + h).$$

As h gets very small, the secant line gets very close to the tangent line. Letting $h = 0$ in the equation above gives the tangent line for $y = x^2$ at $(1, 1)$, and it is

$$y = 2x - 1.$$

The slope of the tangent line, $m = 2$, is the value of the derivative of $y = x^2$ at $x = 1$. ◁

5 APPLET FOR INTERPRETING THE DERIVATIVE AS THE SLOPE OF THE TANGENT LINE

The sections above showed how the tangent line can be found by taking a sequence of secant lines with the x values getting closer and closer together. These calculations are clearly very tedious, yet the geometric view of the tangent line is very easy to visualize. The applications that relate the derivative to a growth rate or a velocity use the calculations similar to finding the slope of the tangent line. So graphically, the derivative is simply the slope of the tangent line.

Velocity – Cubic Function

We provide an applet to allow you to further explore the geometric implications of the derivative by visualizing a cubic function on the left and a graph of its derivative on the right. As noted above, the derivative is simply the slope of the tangent line for a given function. As you move the pointer on the function on the left, you can see the value of the derivative on the right. Click on the figure on the left and a point with the tangent line will appear on the graph. The value of the slope of the tangent line appears in the graph on the right. See Figure 6 for a snapshot from the applet.

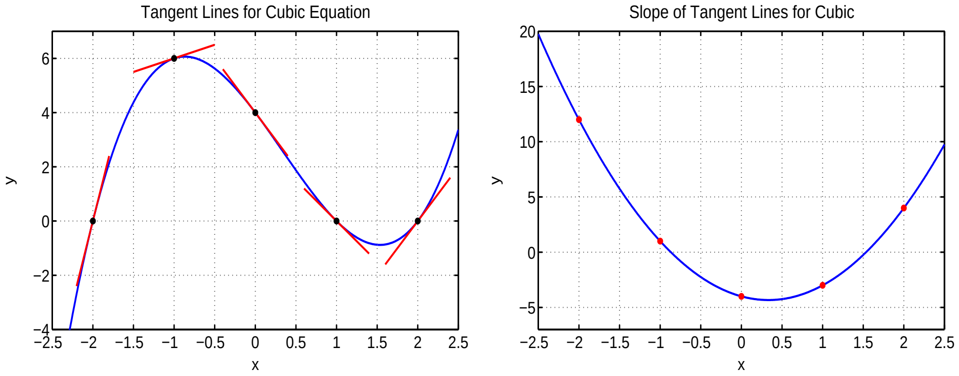

Figure 6: Example of the graph obtained from the applet Velocity – Cubic Function.

There are several points of particular interest in the graph above. The graph on the left is a cubic function, while the graph of its derivative is a quadratic. Observe what happens as you approach a maximum (or minimum) for the cubic function. The value of the derivative goes to zero and the sign of the derivative function changes. This will be one of the more significant applications of the derivative.

The following worked examples will clarify the geometric interpretation of the derivative of a function $f(x)$ as the slope of the line tangent to the curve $f(x)$ at some point. One means of finding the tangent line is to examine a sequence of secant lines, where the points on the curve are taken closer and closer together.

Example 4 *Secant Lines*

In this example, we examine a function, $f(x)$, then form a *sequence of secant lines* by finding two points on the curve, then creating the line through those points. Consider the function

$$f(x) = x^2 - x.$$

a. Let one point on all secant lines have $x = 1$. The other points in the sequence have $x = 2, x = 1.5, x = 1.2, x = 1.1$, and $x = 1.01$. Find the sequence of secant lines with these points on the line and on $f(x)$.

b. The derivative of $f(x)$ is the slope of the tangent line. As the values of x get closer together, the secant lines approach the tangent line. Use the results in Part a. to determine the equation of the tangent line through the point $(1, 0)$, and from its slope find the derivative of $f(x)$.

c. Graph $f(x)$, the tangent line, and the secant lines.

Solution: a. The left point for all the secant lines is $(1, 0)$. When $x = 2$, the other point is $(2, 2)$. The equation of a line through $(1, 0)$ and $(2, 2)$ has a slope of 2 and y-intercept of -2, so its equation is given by

$$y = 2x - 2.$$

For $x = 1.5$, the points on the secant line (and $f(x)$) are $(1, 0)$ and $(1.5, 0.75)$. This secant line has a slope of $m = (0.75 - 0)/(1.5 - 1) = 1.5$. It follows that the equation for this secant line is

$$y = 1.5x - 1.5.$$

For $x = 1.2$, the points on the secant line (and $f(x)$) are $(1, 0)$ and $(1.2, 0.24)$. This secant line has a slope of $m = (0.24-0)/(1.2-1) = 1.2$, so the equation for this secant line is

$$y = 1.2x - 1.2.$$

For $x = 1.1$, the points on the secant line (and $f(x)$) are $(1, 0)$ and $(1.1, 0.11)$. This secant line has a slope of $m = (0.11-0)/(1.1-1) = 1.1$, so the equation for this secant line is

$$y = 1.1x - 1.1.$$

Finally, for $x = 1.01$, the points on the secant line (and $f(x)$) are $(1, 0)$ and $(1.01, 0.0101)$. This secant line has a slope of $m = (0.01 - 0)/(1.01 - 1) =$

1.01, and the equation for its secant line is

$$y = 1.01x - 1.01.$$

b. It is not hard to see that this sequence of secant lines is converging to the tangent line

$$y = x - 1.$$

The slope of this line is 1, so the derivative of $f(x) = x^2 - x$ at $x = 1$ is also 1.

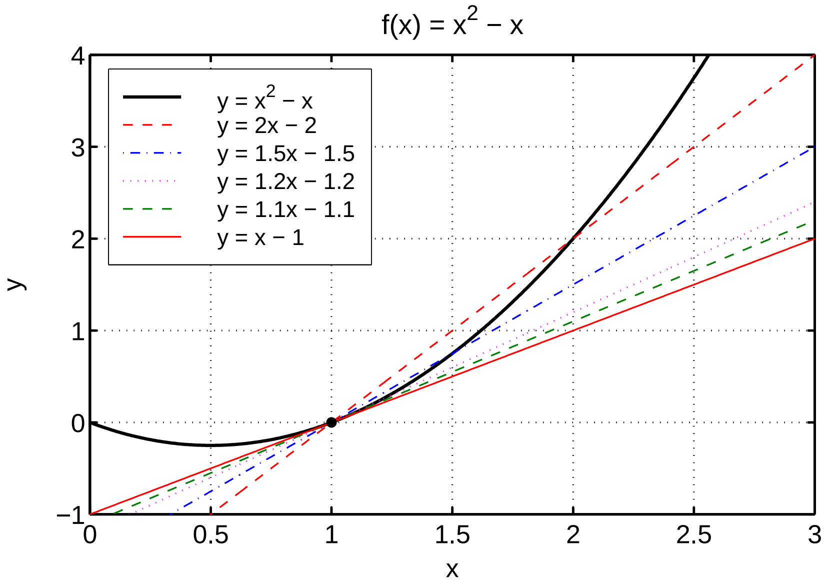

Figure 7: Graph of the secant lines approximation to the tangent line of Example 4.

c. Figure 7 is a graph of the function, the tangent line, and our secant lines. ◁

It becomes tedious calculating each of the elements of the sequence of secant lines as we saw in the previous example. The more general way to compute a secant line for a function $f(x)$ at a point x is to find the equation of a line through the points $(x, f(x))$ and $(x + h, f(x + h))$, where h is some value different than zero.

Example 5 *Secant line with h*

Suppose we take the previous example and find the equation of the secant line through the points $(2, f(2))$ and $(2+h, f(2+h))$, where

$$f(x) = x^2 - x.$$

Let h get small and determine the slope of the tangent line through $(2, 2)$, which gives the value of the derivative of $f(x)$ at $x = 2$.

Solution: The value of $f(2+h)$ is given by

$$f(2+h) = (2+h)^2 - (2+h) = 4 + 4h + h^2 - 2 - h = 2 + 3h + h^2.$$

The slope of the secant line is given by

$$m = \frac{f(2+h) - f(2)}{(2+h) - 2} = \frac{(2 + 3h + h^2) - 2}{h} = 3 + h.$$

Using the point slope form of the line (with the point $(2, 2)$ on the secant line), we find the equation of the secant line is given by

$$y - 2 = (3+h)(x-2)$$

or

$$y = (3+h)x - 4 - 2h.$$

It is fairly easy to see that as h approaches zero, the secant line approaches the tangent line given by

$$y = 3x - 4.$$

This line has a slope of 3, so the derivative of $f(x)$ at $x = 2$ must be 3. ◁

Example 6 *Secant line for a Square Root*

In this example, we consider a more complicated function. Suppose that

$$f(x) = \sqrt{x+2}.$$

Find the slope of the secant line through the points $(2, f(2))$ and $(2+h, f(2+h))$.

Let h get small and determine the slope of the tangent line through $(2, 2)$, which gives the value of the derivative of $f(x)$ at $x = 2$.

Solution: The slope of the secant line is given by

$$\begin{aligned} m &= \frac{f(2+h)-f(2)}{(2+h)-2} = \frac{\sqrt{2+h+2}-\sqrt{2+2}}{h} = \frac{\sqrt{4+h}-2}{h} \\ &= \left(\frac{\sqrt{4+h}-2}{h}\right)\left(\frac{\sqrt{4+h}+2}{\sqrt{4+h}+2}\right) = \frac{4+h-4}{h(\sqrt{4+h}+2)} = \frac{1}{\sqrt{4+h}+2}. \end{aligned}$$

This formula is substantially more complex, requiring some techniques from algebra that you may have forgotten. This shows that finding the slope of the secant line can become quite tedious and difficult.

In the formula above, it is fairly easy to see that as h approaches zero, the slope of secant line, m, approaches

$$m_t = \frac{1}{\sqrt{4}+2} = \frac{1}{4}.$$

Since the derivative is related to the limiting case of the slope of the secant lines (the slope of the tangent line, m_t) we see that the derivative of $f(x)$ at $x = 2$ must be 1/4. ◁

6 VELOCITY OF THE CAT

From our example above, we had that if a cat falls from a branch that is 16 feet high, then the height of the cat satisfies the equation

$$h(t) = 16 - 16t^2.$$

We easily saw that the cat hits the ground after only one second of falling. To find the velocity of the cat, we need to determine its the slope of the tangent line for $h(t)$ near $t = 1$.

Suppose the we could monitor the height for a small increment of time after $t = 1$, say $t = 1 + \tau$. The slope of the secant line between the heights at $t = 1$ and $t = 1 + \tau$ is given by,

$$\begin{aligned} m &= \frac{h(1+\tau)-h(1)}{\tau} = \frac{(16-16(1+\tau)^2)-0}{\tau} \\ &= \frac{-32\tau-16\tau^2}{\tau} = -32-16\tau. \end{aligned}$$

As seen above, the velocity at $t = 1$ is the slope of the tangent line, which is found by letting τ go to zero. Thus, the velocity of the cat at $t = 1$ is

$$v(1) = -32 \text{ ft/s (or about 21.8 mph)}.$$

7 EXERCISES

1.a. A ball thrown vertically with an initial velocity of 64 ft/sec upwards satisfies the equation

$$h(t) = 64t - 16t^2,$$

with $h(t)$ being the height of the ball. Plot a graph of the height of the ball as a function of time, t. Find when the ball hits the ground. Also, determine the maximum height of the ball and when this occurs.

b. Find the average velocity in the intervals $t \in [0, 1]$, $[1, 2]$, and $[2, 4]$.

2. A ball is tossed into the air with an initial velocity of 48ft/s from a 64ft platform. Its height, h (in ft), above the ground t seconds after it is thrown is given by

$$h(t) = -16t^2 + 48t + 64.$$

a. Find the average velocity of the ball for the first two seconds. Also, find the average velocity between times $t = 2$ and $t = 2.5$.

b. Sketch a graph of the flight of the ball. What is the maximum height of the ball and when does it occur?

c. When does the ball hit the ground and what is its velocity then? (Hint: Find the slope of the tangent line at the time when the ball hits the ground.)

3. Suppose that an object shot vertically from a 58.8 m tall building satisfies the height function:

$$h(t) = 58.8 + 19.6t - 4.9t^2,$$

where t is in seconds and h is in meters.

a. Find the average velocity between $t = 0$ and $t = 1$ sec. Repeat this calculation for $t \in [1, 2]$, $t \in [2, 3]$, $t \in [3, 4]$, and $t \in [4, 5]$.

b. Determine the maximum height of the object and when the object hits the ground ($h(t) = 0$). Sketch a graph of the height of the object.

c. Find the velocity of the object at $t = 4$ sec by computing the average velocity between $t = 4$ and $t = 4 + \Delta t$, then letting $\Delta t \to 0$.

4.a. A cat is sitting on a ledge 12 ft above the ground. A bird flies by at a height of 18 ft above the ground. The cat leaps up with a vertical velocity of 16 ft/sec trying to catch the bird. If we ignore air resistance and use an acceleration from gravity of -32 ft/sec^2, then the height of the cat above the ground, $h(t)$, is given by the formula

$$h(t) = 12 + 16t - 16t^2.$$

Find the maximum height that the cat achieves and how long it takes to reach that maximum height. Can the cat catch the bird?

b. Find the average velocity of the cat for the intervals $t \in [0, \frac{1}{2}]$, $t \in [\frac{1}{2}, 1]$, and $t \in [1, \frac{3}{2}]$.

c. Determine the time when the cat hits the ground and the velocity of impact. Sketch a graph of the height of the cat as a function of t.

5. A kangaroo can leap vertically 240cm. The initial velocity, v_0 is unknown, so we want to determine it from the data on how high it can jump using Newton's law of gravity. The equation describing the height of the kangaroo is

$$h(t) = v_0 t - 490t^2.$$

a. Use the information above to determine the animal's initial upward velocity, v_0, then find how long the kangeroo is in the air.

b. Find the average velocity of the kangaroo between $t = 0$ and $t = 1$.

6. Consider the function $f(x) = 1 - x^2$. To find the equation of the tangent line at the point $x = 1$ or $(1, 0)$, we find a sequence of secant lines passing through $(1, 0)$.

a. Let one point on all secant lines be $(1, 0)$. The other points in the sequence have $x = 2$, $x = 1.5$, $x = 1.1$, and $x = 1.01$. Find the sequence of secant lines with these points on the line and on $f(x)$. Sketch a graph of $f(x)$ and the secant lines.

b. Use these secant lines to predict the equation of the tangent line. The slope of the tangent line gives the derivative at $x = 1$, so find the derivative of $f(x)$ at $x = 1$.

7. Consider the function $f(x) = 2x - x^2$. To find the equation of the tangent line at the point $x = 0$ or $(0, 0)$, we find a sequence of secant lines passing through $(0, 0)$.

a. Let one point on all secant lines be $(0, 0)$. The other points in the sequence have $x = 1$, $x = 0.5$, $x = 0.1$, and $x = 0.01$. Find the sequence of secant lines with these points on the line and on $f(x)$. Sketch a graph of $f(x)$ and the secant lines.

b. Use these secant lines to predict the equation of the tangent line. The slope of the tangent line gives the derivative at $x = 0$, so find the derivative of $f(x)$ at $x = 0$.

8. Consider the functions below. Find the equation of the secant line through the points $(1, f(1))$ and $(1+\Delta x, f(1+\Delta x))$ for each of these functions. Let Δx get small and determine the slope of the tangent line through $(1, f(1))$, which gives the value of the derivative of $f(x)$ at $x = 1$.

a. $f(x) = x^2 + 2$,
b. $f(x) = 3x - x^2$,
c. $f(x) = \sqrt{2x+2}$,
d. $f(x) = 3x - 4$,
e. $f(x) = \dfrac{1}{x+1}$,
f. $f(x) = \dfrac{3}{2-x}$.

8 REFERENCES:

[1] Jared M. Diamond (1988), Why cats have nine lives, *Nature* **332**, pp 586–7.

CHAPTER 11:

LIMITS, CONTINUITY, AND THE DERIVATIVE

This is a theoretical chapter that studies the concepts of limits, continuity, and the derivative. These ideas are central to understanding differential Calculus. This chapter provides the definition of the derivative.

1 LIMITS

This section contains a sketch of the formal mathematics that is required to fully develop the concept of the derivative. A complete understanding is beyond the scope of this course, but a few of the ideas are sufficiently important that some discussion is warranted. In the previous sections we have discussed how the derivative is related to the slope of the tangent line for a curve at a point. This was viewed geometrically by considering a sequence of secant lines that approached the tangent line at a point or algebraically by examining what happened to the slope computed at a point as you took points closer and closer together on the curve. (Another perspective on this subject can be viewed in the University of British Columbia notes[1], which have had more time to be developed.)

Both the geometric and the algebraic ideas mentioned above need the concept of a limit. From a conceptual point of view, the *limit of a function* $f(x)$ at some point x_0 simply means that if your value of x is very close to the value x_0, then the function $f(x)$ stays very close to some particular value.

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[1] http://www.ugrad.math.ubc.ca/coursedoc/math100/ notes/derivative/ball1.html,last visited 03/29/04

Definition: The *limit of a function* $f(x)$ at some point x_0 exists and is equal to L if and only if every "small" interval about the limit L, say the interval $(L-\epsilon, L+\epsilon)$, means you can find a "small" interval about x_0, say the interval $(x_0-\delta, x_0+\delta)$, which has all values of $f(x)$ existing in the former "small" interval about the limit L, except possibly at x_0 itself.

This is a difficult concept to fully appreciate. However, you should be able to grasp the idea through several examples.

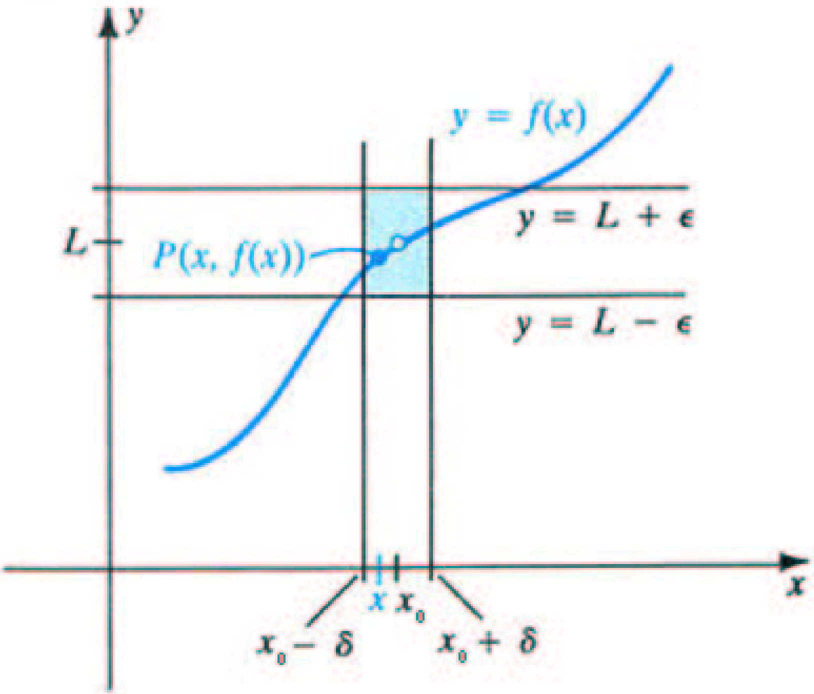

Figure 1: Graph depicting the concept of *limit of a function*.

Example 1 Consider $f(x) = x^2 - x - 6$. Find the limit as x approaches 1. It is not hard to see from either the graph or from the way you have always evaluated this quadratic function that as x approaches 1, $f(x)$ approaches -6, since $f(1) = -6$.

Fact: Any polynomial, $p(x)$, has as its limit at some x_0, the value of $p(x_0)$. See the left panel of Figure 2 to visualize this limit. ◁

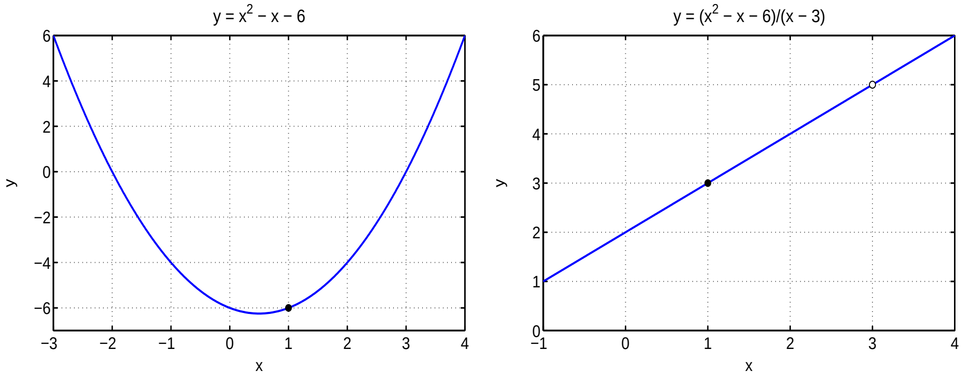

Figure 2: Left: Graph for the concept of limit for the polynomial function of Example 1. Right: Graph for the limit concept for the rational function given in Example 2.

Example 2 Consider the rational function $r(x) = (x^2 - x - 6)/(x - 3)$. Find the limit as x approaches 1. If x is not 3, then this rational function reduces to $r(x) = x + 2$. So as x approaches 1, this function simply goes to 3. See the right panel of Figure 2 to visualize this limit.

Fact: Any rational function, $r(x) = p(x)/q(x)$, where $p(x)$ and $q(x)$ are polynomials with $q(x_0)$ not zero, then the limit exists with the limit being $r(x_0)$. ◁

Example 3 Consider the rational function in Example 2. Now find the limit as x approaches 3. Though $r(x)$ is not defined at $x_0 = 3$, we can see that arbitrarily "close" to 3, $r(x) = x + 2$. So as x approaches 3, this function simply goes to 5. Its limit exists though the function is not defined at $x_0 = 3$. See the left panel of Figure 3 to visualize this limit. ◁

Example 4

Consider the rational function $f(x) = 1/x^2$. Find the limit as x approaches 0, if it exists. From our statement above on rational functions, this function has a limit for any value of x_0 where the denominator is not zero. However, at $x_0 = 0$, this function is undefined. Thus, the graph has a vertical asymptote at $x_0 = 0$. This means that no limit exists for $f(x)$ at $x_0 = 0$. See the right panel of Figure 3 to visualize this limit.

Fact: Whenever you have a vertical asymptote at some x_0, then the limit fails to exist at that point. ◁

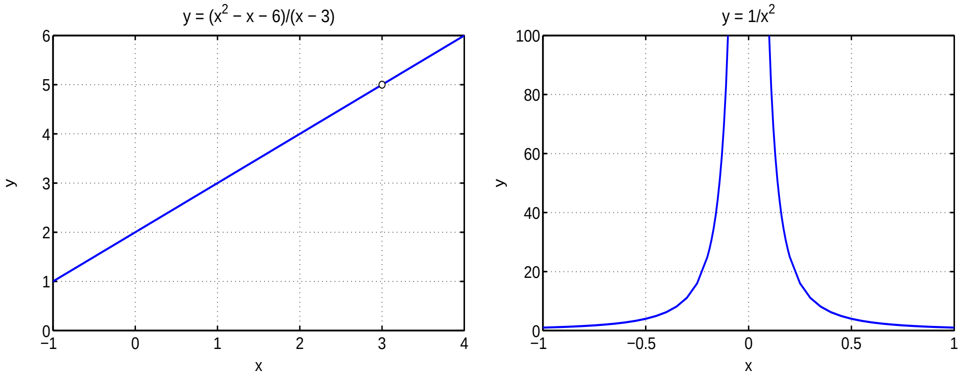

Figure 3: Left: Graph for the limit concept for the rational function of Example 3. Right: Graph depicting the limit case for the function of Example 4.

Example 5 Consider the rational function $r(x) = (x^2 - x - 2)/(x - 3)$. Find the limit as x approaches 3, if it exists. From our statement above on rational functions, this function has a limit for any value of x_0 where the denominator is not zero. See the left panel of Figure 4 to visualize this limit.

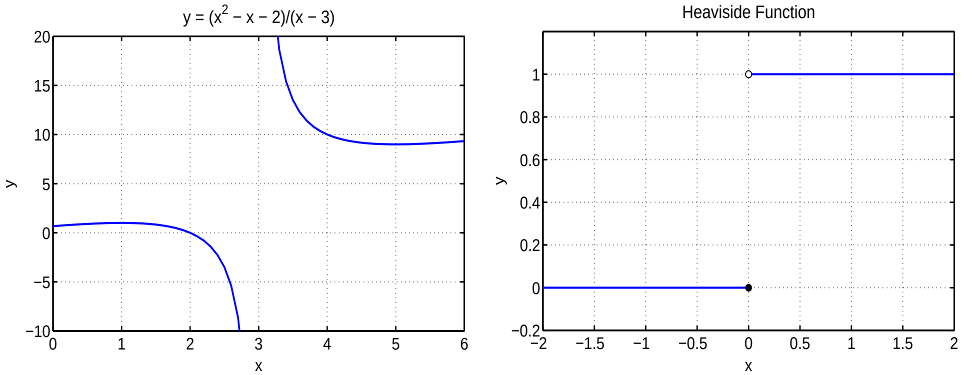

Figure 4: Left: Graph of the rational function of Example 5. Right: Graph for the Heaviside function of Example 6.

However, at $x_0 = 3$, this function is undefined; and furthermore, the function is not approaching zero in the numerator near $x_0 = 3$. Thus, the graph would show a vertical asymptote at $x_0 = 3$. This means that no limit exists for $r(x)$ at $x_0 = 3$. ◁

Example 6 *Heaviside Function*

The Heaviside function is often used to specify when something is "on" or “off”. The Heaviside function is defined as

$$H(x) = \begin{cases} 0, & \text{for } x < 0 \\ 1, & \text{for } x \geq 1. \end{cases}$$

This function clearly has the limit of 0 for any $x < 0$, and it has the limit of 1 for any $x > 0$. Even though this function is defined to be 1 at $x = 0$, it does not have a limit at $x_0 = 0$. This is because if you take some “small” interval about the proposed limit of 1, say $\epsilon = 0.1$, then all values of x near 0 must have $H(x)$ between 0.9 and 1.1. But I can take any “small” negative x and $H(x) = 0$, which is not in the desired given interval. Thus, no limit exists for $H(x)$. See the right panel of Figure 4 to visualize this limit.

Perspective: Whenever a function is defined differently on different intervals in a manner similar to the Heaviside function above, you need to check the places where the function changes in definition to see if the function has a limit at these x values where the function changes. (It might also have asymptotes at other points where again you would check.) $\triangleleft$

Example 7

Consider the fractional power function $f(x) = x^{1/2}$. Find the limit as x approaches 0, if it exists. This function is not defined for $x < 0$, so it cannot have a limit at $x = 0$, though it is said to have a right-handed limit. See Figure 5 to visualize this limit.

$\triangleleft$

Summary of Limits: Most of the functions that you regularly examine have limits. Usually, the problems arise at points x_0 when there is a vertical asymptote, the function is defined differently on different intervals, or special cases like the square root function.

2 CONTINUITY

Closely connected to the concept of a limit is that of continuity. Intuititvely, the idea of a continuous function is what you would expect. If you can draw the function without lifting your pencil, then the function is continuous. Most practical examples use functions that are continuous or at most have a few points of discontinuity.

Definition: A *function* $f(x)$ is continuous at a point x_0 if the limit exists at x_0 and is equal to $f(x_0)$.

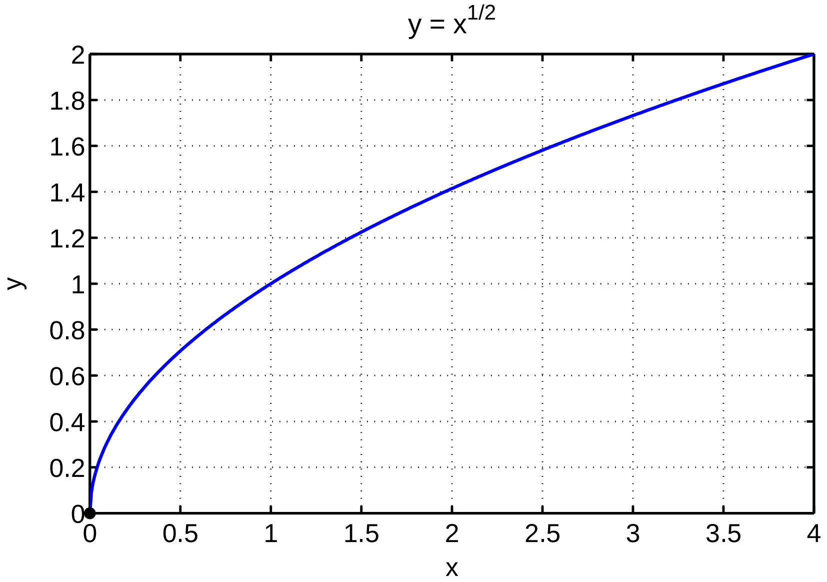

Figure 5: Graph of the square root function of Example 7.

The examples above should also help you appreciate this concept. In all of the cases except Example 3, the existence of a limit also corresponds to points of continuity. Example 3 is not continuous at $x_0 = 3$ though a limit exists here, as the function is not defined at 3. Examples 3 and 5 are discontinuous only at $x_0 = 3$, while Examples 4, 6 and 7 are discontinuous only at $x_0 = 0$. At all other points in the domains of these examples are continuous.

2.1 EXAMPLE COMPARING LIMITS AND CONTINUITY

An example is provided to show the differences between limits and continuity. Figure 5 shows a graph of a function, $f(x)$, that is defined on the interval $[-2, 2]$, except at $x = 0$, where there is a vertical asymptote.

It is clear that the difficulties with this function occur at integer values. At $x = -1$, the function has the value $f(-1) = 1$, but it is clear that the function is not continuous nor does a limit exist at this point. At $x = 0$, the function is not defined (not continuous nor has any limits) as there is a vertical asymptote. At $x = 1$, the function has the value $f(1) = 4$. The function is not continuous at $x = 1$, but the limit does exist with

$$\lim_{x \to 1} f(x) = 1.$$

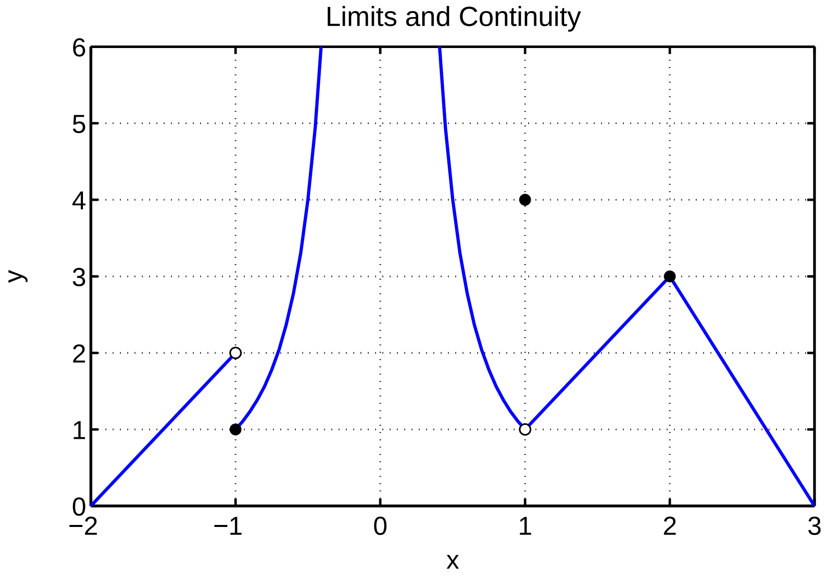

Figure 6: Graph depicting different cases for the concept of limit and continuity of a function.

At $x = 2$, the function is continuous with $f(2) = 3$, which also means that the limit exists. At all non-integer values of x the function is continuous (hence its limit exists).

3 DERIVATIVE

The primary reason for the discussion above is to give you the proper definition of the derivative. In the previous sections, we noted that the derivative at a point on a curve is the slope of the tangent line at that point. This motivation is what underlies the definition given below.

Definition: The derivative of a function $f(x)$ at a point x_0 is denoted by $f'(x_0)$ and satisfies

$$f'(x_0) = \lim_{h\to 0} \frac{f(x_0+h) - f(x_0)}{h},$$

provided this limit exists.

Example 8

Let us use this definition to find the derivative of $f(x) = x^2$,

$$\begin{aligned} f'(x) &= \lim_{h\to 0} \frac{f(x+h)-f(x)}{h} = \lim_{h\to 0} \frac{(x+h)^2 - x^2}{h} \\ &= \lim_{h\to 0} \frac{x^2+2xh+h^2-x^2}{h} = \lim_{h\to 0} \frac{2xh+h^2}{h} = \lim_{h\to 0}(2x+h) = 2x. \triangleleft \end{aligned}$$

Example 9

We repeat this computation to find the derivative of $f(x) = 1/(x+2)$ (for x not equal to -2).

$$\begin{aligned} f'(x) &= \lim_{h\to 0} \frac{f(x+h)-f(x)}{h} = \lim_{h\to 0} \frac{\dfrac{1}{x+h+2} - \dfrac{1}{x+2}}{h} \\ &= \lim_{h\to 0} \frac{(x+2)-(x+h+2)}{h(x+2+h)(x+2)} = \lim_{h\to 0} \frac{-h}{h(x+2+h)(x+2)} \\ &= \lim_{h\to 0} \frac{-1}{(x+2+h)(x+2)} = \frac{-1}{(x+2)^2}. \end{aligned}$$

Clearly, we do not want to use this formula every time we need to compute a derivative. The next section gives much easier formulae for finding derivatives. Technology has advanced to where a number of programs on computers and certain advanced calculators can differentiate most functions. The accompanying Lab manual for this text shows how to use **Maple's diff** command to differentiate functions. $\triangleleft$

4 EXERCISES

For each of the following functions, sketch a graph of the function and give its domain. Determine if the function is continuous at $x = 2$ and if so, what its value is at $x = 2$. If the function is not continuous at $x = 2$, then determine if it has a limit at $x = 2$ and what that limit is.

1. $f(x) = x^2 - 4x + 4$,
2. $f(x) = \dfrac{1}{x+1}$,
3. $f(x) = \dfrac{1}{x^2-4}$,
4. $f(x) = \dfrac{x^2+x-6}{x-2}$,
5. $f(x) = \ln(x-1)$,
6. $f(x) = \sqrt{9-x^2}$.

7. See Figure 7 for a graph of a function defined for $x \in [-1, 2]$. At $x = 0$ and $x = 1$, determine what the function value is (if it exists). Also, find

the limit as $x \to 0$ and $x \to 1$, if the limits exist. Where is this function continuous?

8. See Figure 7 for a graph of a function defined for $x \in [-2, 3]$. What is the domain of this function? At $x = 0, 1, 2$, determine what the function value is (if it exists). Also, find the limit as $x \to 0$, $x \to 1$, and $x \to 2$, if the limits exist. Where is this function continuous?

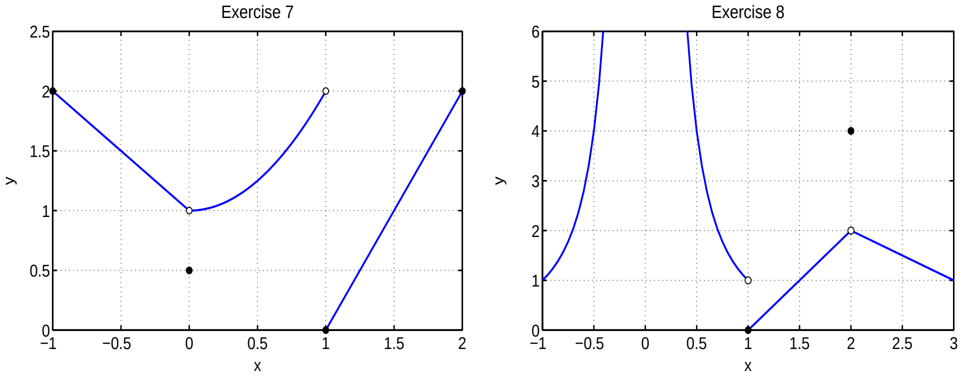

Figure 7: Left: Exercise 7. Right: Exercise 8.

9. Use the definition of the derivative to find the derivative of the following functions.

a. $f(x) = x^3$,

b. $f(x) = 3x - x^2$,

c. $f(x) = \sqrt{4 - x}$,

d. $f(x) = \dfrac{2}{x + 3}$.

CHAPTER 12:

RULES OF DIFFERENTIATION

The previous chapter showed the definition of a derivative. However, it is clear that using the definition of the derivative is not an efficient way to find derivatives. In this chapter we develop some rules for differentiation. This chapter covers the basic power rule for differentiation, additive and scalar multiplication rules, and applications to polynomials.

1 APPLICATIONS WITH POWER LAW

In the allometric chapter, we saw that many biological applications are reasonably well modeled by a power law relationship. For example, the data from Altman and Dittmer [1] for the pulse, P, as a function of the weight, w, are approximated by the relationship

$$P = 200w^{-1/4}.$$

The pulse is in beats/min, and the weight is in kilograms. The left panel of Figure 1 shows a graph of this relationship.

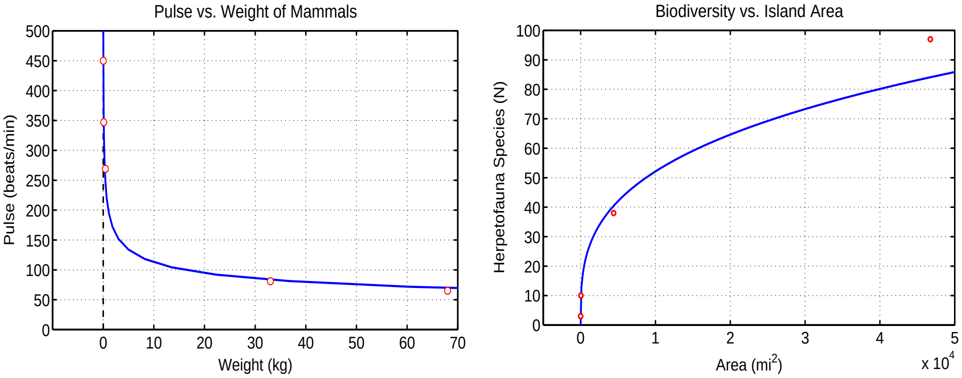

Figure 1: Left: Graph of the pulse *vs.* weight for mammals. Right: Graph of the function of *Herpatofuna* number of species (biodiversity) *vs.* Caribbean island area.

The graph shows an initial steep decrease in the pulse as weight increases, but can one quantify how fast the pulse rate changes as a function of weight? Clearly, for small animals the pulse rate changes more rapidly than for large animals. The derivative of this allometric or power law model provides more details on the rate of change in pulse rate as a function of weight.

Previously we saw that the number of species of herpatofauna, N, on Caribbean islands could be related to the area of the island, A, by an allometric model approximated by

$$N = 3A^{1/3}.$$

A model of this sort is important for obtaining information about biodiversity. A graph of this model is seen in the right panel of Figure 1.

Can we use this model to determine the rate of change of numbers of species with respect to a given increase in area? Again the derivative is used to help quantify the rate of change of the dependent variable, N, with respect to the independent variable, A.

2 NOTATION FOR THE DERIVATIVE

We begin with an introduction to some of the notation that we will use. There are several standard notations for the derivative. The two most common are the ones founded by Newton and Leibnitz.

For the function $f(x)$, the Newtonian notation for the derivative is written as follows:

$$\frac{df(x)}{dx}.$$

The notation that Leibnitz used was

$$f'(x).$$

We will use these notations interchangeably, depending on what we are trying to show.

3 POWER RULE

The *power rule for differentiation* is given by the formula

$$\frac{d(x^n)}{dx} = nx^{n-1}, \quad \text{for} \quad n \neq 0.$$

Example 1 Use the power rule to find the derivatives of the following functions:

1. $f(x) = x^5$	2. $f(x) = x^{-3}$
3. $f(x) = x^{1/3}$	4. $f(x) = 1/x^4$
5. $f(x) = 1/x^{1/2}$	6. $f(x) = 3$

Solution:

1. Since $n = 5$, it follows from the power rule that $f'(x) = 5x^4$.

2. Since $n = -3$, it follows from the power rule that $f'(x) = -3x^{-4}$.

3. Since $n = 1/3$, it follows from the power rule that $f'(x) = 1/3x^{-2/3}$.

4. Since $n = -4$, it follows from the power rule that $f'(x) = -4x^{-5}$.

5. Since $n = -1/2$, it follows from the power rule that $f'(x) = -1/2x^{-3/2}$.

6. Since $n = 0$, the power rule does not apply, but we know that the derivative of a constant is $f'(x) = 0$. ◁

Example 2 *Pulse Rate*

Consider our applications at the beginning of this chapter. For the model on pulse rate, $P = 200w^{-0.25}$, we use the power law of differentiation (and the fact that the scalar 200 multiplying the function is uneffected by differentiation) to obtain

$$\frac{dP}{dw} = -50w^{-5/4}.$$

The negative sign shows the decrease in the pulse rate with increasing weight. An animal at 16 kg by the allometric model would have a pulse of about 100 (since $200 \times 16^{-1/4}$ is 100). The derivative indicates that the pulse rate is decreasing by $-50/32$ beats/min/kg, so a 17 kg animal should have a pulse rate near $100 - 50/32 = 98$ beats/min. ◁

Example 3 *Biodiversity Model*

For the biodiversity model, $N = 3A^{1/3}$, we can differentiate using the power law to obtain

$$\frac{dN}{dA} = A^{-2/3}.$$

This shows the rate of change of numbers of species with respect to the island area is increasing as the derivative is positive, but the increase gets smaller with increasing island area, since the area has the power $-2/3$, which puts the area in the denominator of this expression for the derivative. ◁

Example 4 *Height of a Ball*

If a ball is thrown vertically in the air and air resistance is ignored (and we assume that the initial height of the ball is 0), then the height of a ball satisfies the formula,

$$h(t) = v_0 t - g\frac{t^2}{2},$$

where v_0 is the initial velocity of the ball thrown vertically and g is the acceleration due to gravity. We saw in our previous work that the derivative of this height function is given by the velocity function, which satisfies

$$h'(t) = v_0 - gt.$$

This example takes advantage of three rules of differentiation. First, the *additive property of derivatives* allows consideration of each of the terms in the height function separately. Each of these terms has a scalar multiplier and a power of t. Thus, they use the *power rule of differentiation* along with a *property for scalar multiplication.* Below we list the rules for addition and scalar multiplication when taking a derivative. ◁

4 OTHER BASIC RULES OF DIFFERENTIATION

The operation of differentiation is said to be linear, which means that you can bring out multiplicative constants and the derivative of the sum of two functions is the sum of the derivatives.

Scalar Multiplication Rule:

Assume that k is a constant and $f(x)$ is a differentiable function, then

$$\frac{d}{dx}[k \cdot f(x)] = k \cdot \frac{d}{dx} f(x)$$

Additive Rule:

Assume that $f(x)$ and $g(x)$ are differentiable functions, then

$$\frac{d}{dx}[f(x)+g(x)] = \frac{d}{dx}[f(x)] + \frac{d}{dx}[g(x)].$$

Below are examples of differentiation using the power rule.

Example 5 *Differentiation using the Power Rule*

1. Find the derivative of the polynomial

$$f(x) = 2x^3 + 4x^2 - 7x + 10.$$

Solution: From the power rule, we simply multiply the coefficient by the power of x, then reduce the power of x by 1. This gives

$$f'(x) = 3(2x^2) + 2(4x) - 7 + 0 = 6x^2 + 8x - 7.$$

Notice that the derivative of any constant is zero.

2. Other additive powers are handled similarly.

$$f(x) = x^2 + 3x^{-2} - 8x^{1/2} + 13.$$

Solution: From our rules above, it is easy to see that the derivative is

$$f'(x) = 2x - 6x^{-3} - 4x^{-1/2}.$$

3. Find the derivative of the function

$$f(x) = 3x^4 - 2x^2 + \frac{5}{\sqrt{x}} - 7 + \frac{1}{x^4}.$$

Solution: This problem is most easily worked by first changing all the terms in $f(x)$ into terms that only include powers of x, then apply the power rule. Thus,

$$f(x) = 3x^4 - 2x^2 + 5x^{-1/2} - 7 + x^{-4}.$$

This is easily differentiated to give

$$f'(x) = 12x^3 - 4x - \frac{5}{2}x^{-3/2} - 4x^{-5}.$$

◁

Below are two applications of the derivative showing how the derivative is a rate of change or velocity (which is actually a rate of change in position).

Example 6 *Rate of Change in Pulse*

Above, we found that there was an allometric relationship between weight and the pulse of mammals given by the formula

$$P = 200w^{-1/4}.$$

Find the rate of change in the pulse with respect to the weight when an animal is 1 kg. Also, determine the rate of change in the pulse with respect to the weight when an animal is 81 kg. Which of the two calculated rates of change is larger in magnitude and what does this say about how pulse changes as weight increases?

Solution: From the lecture notes, we have that in general the derivative of $P(w)$ is given by

$$\frac{dP}{dw} = -50w^{-5/4}.$$

It follows that $P'(1) = -50$ and $P'(81) = -50(81)^{-5/4} = -50(3)^{-5} = -50/243 = -0.206$. The pulse rate at $w = 1$ is larger in magnitude. Thus, the rate of change of the pulse rate at 1 kg is dropping much more quickly than the rate of change of the pulse rate at 81 kg. Thus, changes in pulse rate are much less between larger animals. ◁

Example 7 *Velocity of a Ball*

A ball, thrown vertically from a platform without air resistance, satisfies the equation

$$h(t) = 80 + 64t - 16t^2.$$

Sketch a graph of the height of the ball, $h(t)$, as a function of time, t. Find the maximum height of the ball and determine when the ball hits the ground. Give an expression for the velocity, $v(t)$, as a function of time, t. Find the velocity at the times $t = 0$, $t = 1$, and $t = 2$. What is the velocity of the ball just before it hits the ground?

Solution: We begin by factoring, so $h(t) = -16(t + 1)(t - 5)$. The height of the platform is clearly 80 ft, as $h(0) = 80$. From the factor, we see that the ball hits the ground at $t = 5$. The maximum height of the ball is at the vertex, which is halfway between the intercepts. Thus, the maximum occurs at $t = 2$ with $h(2) = 144$ ft.

The velocity is given by the derivative of the height function, so

$$v(t) = h'(t) = 64 - 32t.$$

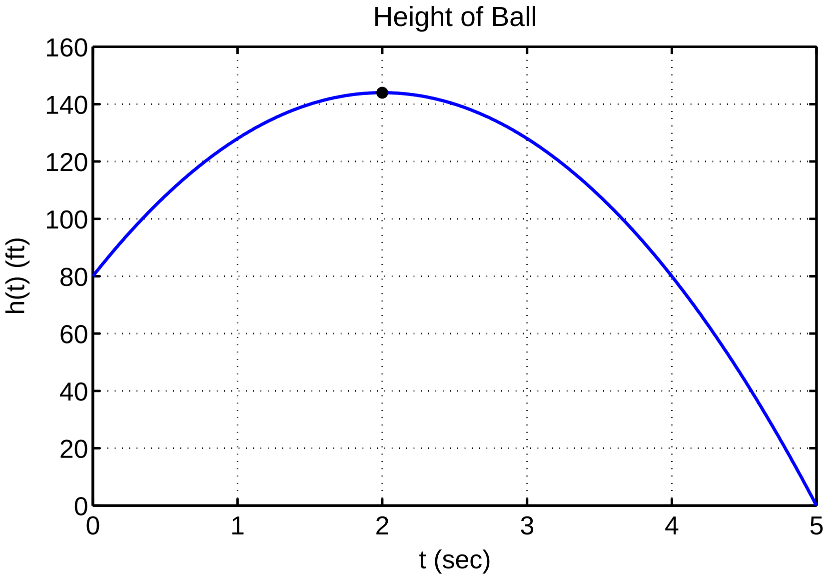

Figure 2: Graph of the height of a ball of Example 7.

We see that $v(0) = 64$ ft/sec (the initial velocity), $v(1) = 32$ ft/sec, and $v(2) = 0$ ft/sec. As we expected, the velocity at the maximum is zero. The ball hits the ground with velocity $v(5) = -96$ ft/sec. Figure 2 shows a graph of the height of the ball. ◁

5 LOGISTIC GROWTH FUNCTION

One of the most commonly used models in population biology is the logistic growth model. There is a discrete and continuous version of this model, which we will study in some depth later. An earlier chapter of this book gave the discrete Malthusian growth model, where the growth of the population is assumed to be proportional to the existing population. The Malthusian growth model is based on unlimited resources. However, as the population increases, the growth rate of most organisms slows to where the population reaches an equilibrium, which is called the *carrying capacity* of the organism in its environment. The slowing in growth rate can be attributed to a number of factors including crowding (lack of space to reproduce), lack of resources (limited food supply), or build up of waste (toxicity).

The logistic growth function is simply a quadratic function. (Recall that the Malthusian growth function is a linear function.) The basic form of the logistic growth function is

$$G(P) = rP\left(1 - \frac{P}{M}\right) = rP - \frac{r}{M}P^2,$$

where P is the density of yeast ($\times1000$/cc). Consider the following specific logistic growth function representing the growth of a yeast in a chemostat (a technique often employed for maintaining a yeast culture in breweries). The Malthusian growth rate $r = 0.1$ (hr^{-1}) (which is about 10% per hour), and the carrying capacity is $M = 500(\times1000$ (yeast/cc). The growth function can be written

$$G(P) = 0.1P - 0.0002P^2.$$

There are a several interesting points from a biological perspective to study about this growth function. First, when the growth function is zero (no growth) the population is said to be at *equilibrium*. Biologists (and brewers) frequently want to have their culture growing at peak production rates, which is when the growth function is at its highest point. (Think the maximum height of the ball in the example above.) Let us find these significant points from the growth function above, then create a graph of this function.

The *equilibria* are found by solving $G(P) = 0$. We factor the equation above and set it equal to zero

$$G(P) = 0.1P(1 - 0.002P) = 0.$$

Thus, either $P = 0$ (*extinction of the population*) or $1 - 0.002P = 0$, which gives $P = 500(\times1000$ yeast/cc) (the *carrying capacity*). The maximum growth is the vertex of this quadratic function, which is where the derivative is zero. Computing the derivative, we solve

$$G'(P) = 0.1 - 0.0004P = 0.$$

Thus, $1 - 0.004P = 0$, which gives $P = 250$. Substituting this value of P into the logistic growth function, we have

$$G(250) = 0.1(250) - 0.0002(250)^2 = 12.5(\times1000 \text{ yeast/cc/hr}).$$

Thus, the maximum growth in this culture occurs when the density of yeast in the culture is 250 yeast/cc, and this population of yeast produce 12.5 yeast/cc/hr *as the maximum production.* Figure 3 shows a graph of the logistic growth function.

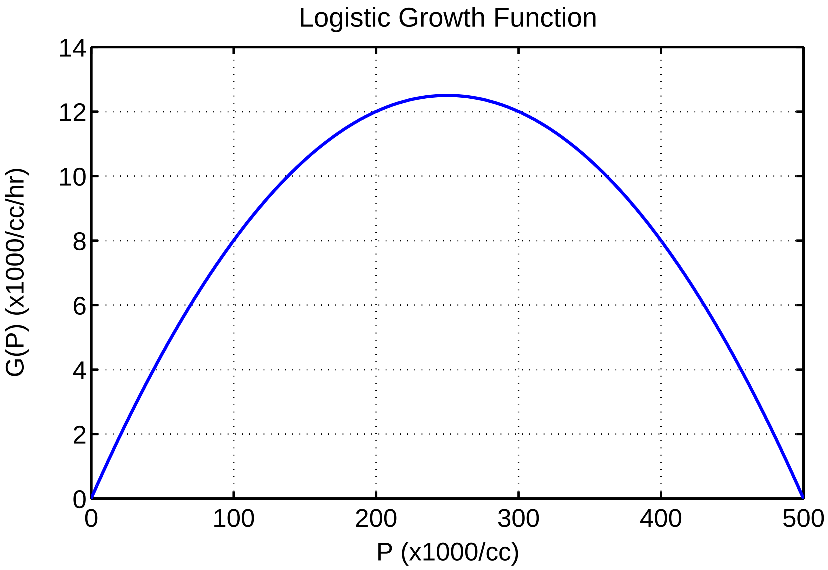

Figure 3: Graph of the Logistic growth function for a yeast culture in a chemostat.

6 EXERCISES

Find the derivative for each of the following functions.

1. $f(x) = x^4 + 7x^3 - 2x^2 - 4x + 3$,
2. $g(x) = 3x^2 - 3x + 4 - 2x^{-3}$,
3. $h(t) = t^3 - 5t + \dfrac{1}{2} - \dfrac{1}{t^2}$,
4. $k(z) = \dfrac{3z^2}{2} + 6z - \sqrt{z}$,
5. $p(z) = z^{\frac{1}{3}} + 4.7z^2 - 7\sqrt{z^5}$,
6. $q(w) = 3w^{-0.4} + 2.1w^5 - \dfrac{2}{\sqrt{w}}$,
7. $f(x) = ax^2 + bx + c$,
8. $g(x) = A - \dfrac{B}{x^3} + \dfrac{C}{\sqrt{x}} - Dx^4$.

9. In the linear section, we found that the growth of a child satisfies the equation

$$h(a) = 6.46a + 72.3,$$

where the age, a, is in years and the height, h, is in cm.
a. Find dh/da. What is the growth rate at age 2? At age 6?
b. If a child is 135cm at age 10, what is the predicted height at age 11?

10. The lecture notes showed that the number of species of herpatofauna, N on Caribbean Islands as a function of the area in square miles, A, is

approximated by the formula

$$N = 3A^{\frac{1}{3}}.$$

a. Find the rate of change in number of species as a function of area, dN/dA, when the area of the island is 64, 125, and 1000 square miles.

b. Sketch a graph of the derivative, dN/dA, for $0 \leq A \leq 1000$.

11. A ball falling under the influence of gravity without air resistance satisfies the equation

$$y(t) = -4.9t^2,$$

where y is in meters and t is in seconds.

a. Find an expression for the velocity, $v(t) = y'(t)$.

b. What is the velocity at $t = 1$ and $t = 5$?

12. A ball that is thrown vertically falling under the influence of gravity without air resistance from a 128 ft platform with an upward velocity of 32ft/sec satisfies the equation

$$h(t) = 128 + 32t - 16t^2,$$

where h is in feet and t is in seconds.

a. Find an expression for the velocity, $v(t) = h'(t)$. Determine when the velocity is zero, then determine the maximum height of the ball. What is the velocity at $t = 2$ and $t = 4$.

b. Sketch a graph of $h(t)$, showing crucial points, including the h-intercept, the maximum height, and when the ball hits the ground.

13. A cat is crouching on a ledge that is 12 feet above the ground, trying to ambush pigeons that fly by.

a. Suppose that a pigeon flies by 4 feet above the cat, and that the cat jumps off the ledge with just enough vertical velocity, v_0 to catch the pigeon. If the height of the cat is given by

$$h(t) = -16t^2 + v_0t + 12,$$

then find the velocity $v(t) = h'(t)$ of the cat at any time, $t \geq 0$.

b. Find when the velocity is equal to zero in terms of v_0. This is the time at the maximum height.

c. Since the cat is 16 ft in the air at this time, use the equation for the height of the cat, $h(t)$ to compute the initial velocity of the cat, v_0. Substitute this into the velocity equation, $v(t)$ to give the velocity of the cat at any time between jumping and hitting the ground. What is the velocity of the cat after 1 second?

d. Find when the cat hits the ground with the pigeon and what is the velocity of the cat that it hits the ground.

14.a. Lizards are cold-blooded animals whose temperatures roughly match the surrounding environment. Suppose the body temperature, $T(t)$, of a lizard is measured for a period of 18 hours from midnight until 6 PM. The body temperature (in °C) of the lizard over this period of time (in hours) is found to be well approximated by the polynomial

$$T(t) = -0.01t^3 + 0.285t^2 - 1.80t + 15.$$

Find the general expression for the rate of change of body temperature per hour (dT/dt).

b. Use this information to find what the rate of change of body temperature is at midnight, 4AM, 8AM, noon, and 4 PM. Which of these times gives the fastest increase in the body temperature and which shows the most rapid cooling of the lizard?

7 REFERENCES:

[1] P.L. Altman and D.M. Dittmer, eds. *Biology Data Book.* Federation of American Societies for Experimental Biology. (1964) 234–235.

CHAPTER 13:

APPLICATIONS OF THE DERIVATIVE - GRAPHING

This section examines applications of the derivative to finding maxima and minima. The derivative is valuable for interpreting important aspects of graphs and biological problems. The first problem examines a study of the body temperature of a female during the menstrual cycle and using that to determine fertility. These ideas are generalized to more classical Calculus applications, where the derivative is used to help with sketching the graph of a function.

1 BODY TEMPERATURE FLUCTUATION DURING THE MENSTRUAL CYCLE

Mammals are warm-blooded and carefully regulate their body temperature in a narrow range to maintain optimal physiological responses. Variations in body temperature occur during exercise, stress, infection, and other normal situations, but through neurological control, the body self-regulates to maintain a fairly constant temperature. Still there are slight variations including circadian rhythms where each day the body oscillates a few tenths of a degree Celsius (minimum during times of sleep and maximum usually occurring late in the morning). Women also experience a normal body temperature cycle along with their menstrual cycle. Some women monitor their basal body temperature to try to determine their peak period of fertility to maximize (or minimize) the chance of pregnancy. The onset of ovulation often corresponds to the sharpest rise in temperature, which gives peak fertility. (Some claim that by the time a women notices her rise in temperature, she is past her peak fertility, so this type of monitoring is not universally recommended.)

Figure 1 includes a graph of the basal body temperature taken at the same time each day for a one 28-day period of one woman. The data are fit by a cubic polynomial.

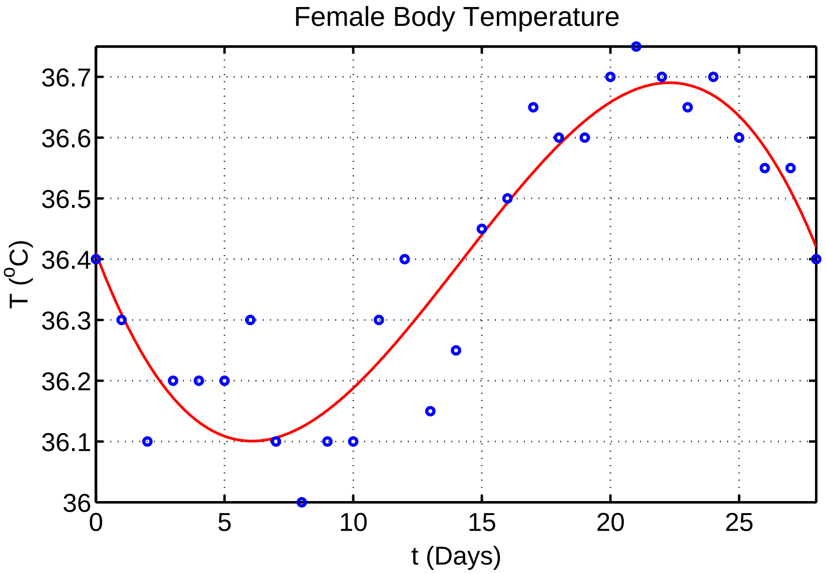

Figure 1: Graph for the polynomial that best fits the data for the female body temperature during the 28-day menstrual cycle.

The best cubic polynomial fitting the data above is given by

$$T(t) = -0.0002762t^3 + 0.01175t^2 - 0.1121t + 36.41.$$

From the curve above we want to find the high and low temperatures, then determine the time of peak fertility by finding the time when the temperature is rising most rapidly.

The high and low temperatures occur where the tangent to the curve has a slope of zero. This is where the derivative is zero. From the rules of differentiation, we find the derivative of the temperature.

$$T'(t) = -0.0008286t^2 + 0.02350t - 0.1121.$$

Note that the derivative is a different function from the original function. The roots of this quadratic equation are readily found using the quadratic formula. They are

$$t = 6.069 \text{ and } 22.29 \text{ days.}$$

Inserting these values in the original function give

$$\text{Minimum at } t = 6.069 \text{ with } T(6.069) = 36.1°C$$

$$\text{Maximum at } t = 22.29 \text{ with } T(22.29) = 36.7°C,$$

which means that there is only a 0.6°C difference between the high and low basal body temperature during a 28 day menstrual cycle by the approximating function. The data varied by 0.75°C.

The day with the maximum increase in temperature is where the derivative is at a maximum. This is the vertex of the quadratic function, $T'(t)$. Clearly, the maximum can be found by the midpoint between the roots of the quadratic equation. However, we can also use the derivative of $T'(t)$ or the second derivative of $T(t)$. The second derivative is given by

$$T''(t) = -0.0016572t + 0.02350.$$

The second derivative is zero at the maximum of $T'(t)$, which occurs at the

$$\textit{Point of Inflection} \text{ at } t = 14.18 \text{ with } T(14.18) = 36.4°\text{C}.$$

The maximum rate of change in body temperature is

$$T'(14.18) = 0.054° \text{ C/day}.$$

This model suggests that the peak fertility occurs on *day 14*, which is consistent with what is known about ovulation.

There are more applications developed at the end of this chapter. But, let us introduce more important concepts to understand them even better.

2 MAXIMA, MINIMA, AND CRITICAL POINTS

The example above shows that finding when the derivative is zero can give important information about the graph of a function. Another way to view this phenomenon is to examine any graph of a smooth function (which is a function that is continuous and differentiable). It is clear that when you are at a high point of the graph (that is not an endpoint), then the tangent line must be horizontal, which says that the derivative is zero.

Definition: A smooth function $f(x)$ is said to be *increasing* on an interval (a, b) if $f'(x) > 0$ for all x in the interval (a, b). Similarly, a smooth function $f(x)$ is said to be *decreasing* on an interval (a, b) if $f'(x) < 0$ for all x in the interval (a, b).

A high point of the graph is where $f(x)$ changes from increasing to decreasing, while a low point on a graph is where $f(x)$ changes from decreasing to increasing. In either case, the derivative passes through zero.

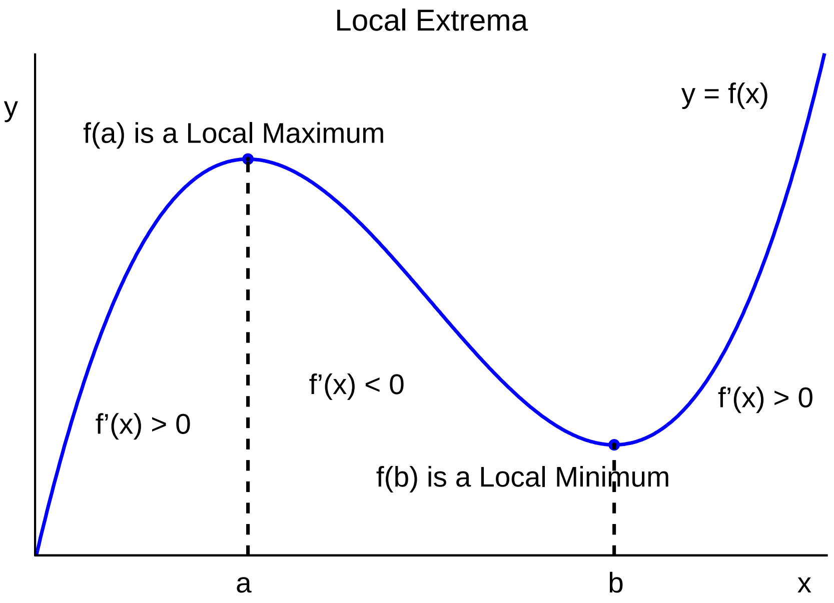

Figure 2: Graph of a general polynomial function indicating the local extrema according to the sign of the derivative.

Definition: A smooth function $f(x)$ is said to have a *local maximum* at a point c, if $f'(c) = 0$ and $f'(x)$ changes from positive to negative for values of x near c. Similarly, a smooth function $f(x)$ is said to have a *local minimum* at a point c, if $f'(c) = 0$ and $f\prime(x)$ changes from negative to positive for values of x near c.

Clearly, it is important to find where the derivative is zero to find these highest and lowest points on a graph.

Definition: If $f(x)$ is a smooth function with $f'(x_c) = 0$, then x_c is said to be a *critical point* of $f(x)$.

Finding critical points helps find the local high and low points on a graph, but some critical points are neither maxima or minima.

3 GRAPHING POLYNOMIALS

We applied these definitions to a cubic function describing body temperature over a month. Let us examine how finding critical points can help us graph other polynomials. Consider the following examples.

Example 1 Consider the following function:

$$f(x) = x^3 - 6x^2 - 15x + 2.$$

Use the information to help sketch a graph of $f(x)$.

Solution: We begin by taking the derivative,

$$f'(x) = 3x^2 - 12x - 15 = 3(x + 1)(x - 5).$$

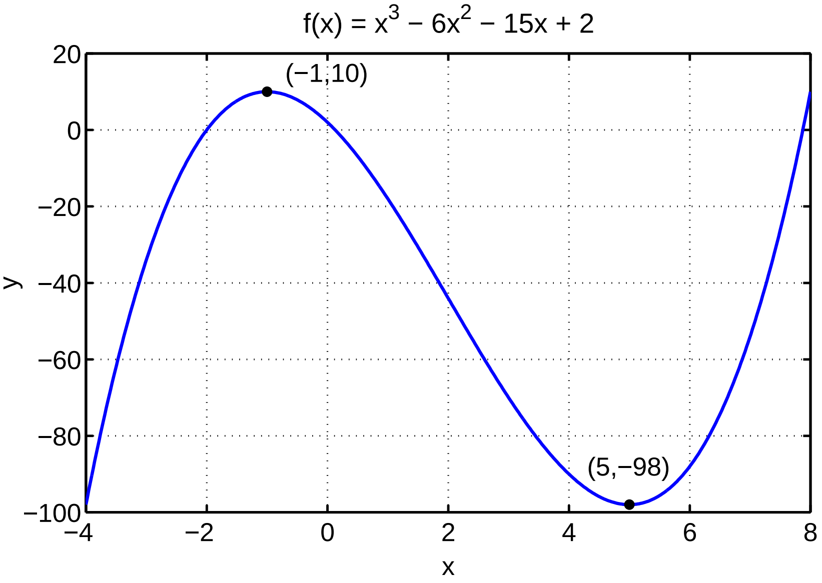

Figure 3: Graph for the cubic polynomial of Example 1.

The derivative is zero when $x_c = -1$ or 5. Evaluating the function at the critical points, we find $f(-1) = 10$, which gives a local maximum at $(-1, 10)$, and $f(5) = -98$, which gives a local minimum at $(5, -98)$. The y -intercept is $(0, 2)$ another easy point to add to our graph, so we now have good information to make a reasonable sketch of the graph, which is shown in Figure 3. Note that since this is a cubic equation, the x-intercepts are very hard to find. ◁

4 THE SECOND DERIVATIVE AND CONCAVITY

Since the derivative is itself a function, then if it is differentiable, one can take its derivative to find the *second derivative* often denoted $f''(x)$. The sign of the second derivative tells where the first derivative is increasing or decreasing. If the first derivative is increasing or the second derivative is positive, then the original function is getting“steeper”. The function is said to be *concave upward*. If the first derivative is decreasing or the second derivative is negative, then the original function is said to be *concave downward*. Thus, the second derivative is a measure of the concavity of a function. For our smooth functions described above, we can see that maxima generally occur where the function is concave downward, while minima occur where the function is concave upward. This property is often summarized in the following test.

The Second Derivative Test: Let $f(x)$ be a smooth function. Suppose that $f'(x_c) = 0$, so x_c is a critical point of f. If $f''(x_c) < 0$, then x_c is a *relative maximum*. If $f''(x_c) > 0$, then x_c is a *relative minimum*.

Example 2 If we return to our example above where $f(x) = x^3 - 6x^2 - 15x + 2$, then we see that the second derivative is

$$f''(x) = 6x - 12.$$

The critical points occur at $x_c = -1$ and 5. Evaluating the second derivative at the critical point $x_c = -1$, we find $f''(-1) = -18$, which says the function is concave downward at -1, so this is a relative maximum. Similarly, the second derivative at the critical point $x_c = 5$ is $f''(5) = 18$, which says the function is concave upward, so this is a relative minimum. ◁

5 POINTS OF INFLECTION

When the second derivative is zero, then the function is usually changing from concave upward to concave downward or visa versa. This is known as a *point of inflection*. A *point of inflection* is where *the derivative function has a maximum or minimum*, so the *function is increasing or decreasing most rapidly*. In the application above for the variation of body temperature over one month of a menstrual cycle, the point of inflection represented the potential time of peak fertility by finding where the basal body temperature was increasing most rapidly.

From a graphing perspective, the point of inflection shows the visual change in concavity. It is not nearly as important as extrema, but does provide one more point to aid in graphing the function.

Example 3 Once again returning to our example above of $f(x) = x^3 - 6x^2 - 15x + 2$, where the second derivative is $f''(x) = 6x - 12$, we can easily find the point of inflection. We see that $f''(x) = 0$ when $x = 2$. Thus, the point of inflection occurs at $(2, -44)$. This can be see on the graph of Figure 3. ◁

6 EXAMPLES OF GRAPHING

This section provides a series of examples to supplement this chapter and help with the homework problems. The first examples examine graphing problems. The second example returns to the height of a ball in the air, while the last example uses the derivative to find the maximum and minimum population from a study.

When you want to sketch a graph, the most important part of sketching the graph is finding the extrema (maxima and minima). These are found by finding the derivative and setting it equal to zero. The solutions of the equation for the derivative equal to zero give the critical values, which are substituted back into the the original function. By adding the x and y-intercepts (if possible) and any asymptotes (if they exist) to the sketch, you can get a fairly good idea of what the graph looks like. The second derivative provides nice information to aid with the graph, but it is not nearly as essential in getting a good looking graph.

Example 4 Use the techniques developed in this chapter to find any local or relative minima and maxima and points of inflection for the following polynomial,

$$y = 12x - x^3,$$

then sketch a graph of the function.

Solution: The y-intercept should always be easy, and in this case, we readily see that $(0, 0)$ is both an x and y-intercept. We can factor this equation and solve for the x-intercept. To find the x-intercept, set $y = 0$, then factor and solve the equation,

$$-x(x^2 - 12) = 0 \text{ or x} = 0, \pm 2\sqrt{3}.$$

To find the extrema, we take the first derivative of the function and set it equal to zero. Then we solve for x_c, where $y' = 0$.

$$\begin{aligned} y' &= 12 - 3x^2 = -3(x^2-4) = -3(x+2)(x-2) = 0 \\ x_c &= -2, 2. \end{aligned}$$

We evaluate the original function at the critical points, giving $y(-2) = -16$ and $y(2) = 16$, so the critical points of the function are $(-2, -16)$ and $(2, 16)$. Clearly, the first point is a minimum and the second is a maximum. However, we can check this with the second derivative test. We take the second derivative and evaluate at the critical points to see if they are minima or maxima.

$y'' = -6x$

$y''(2) = -6(2) = -12$ is concave downward, indicating a maximum,

$y''(-2) = -6(-2) = 12$ is concave upward, indicating a minimum.

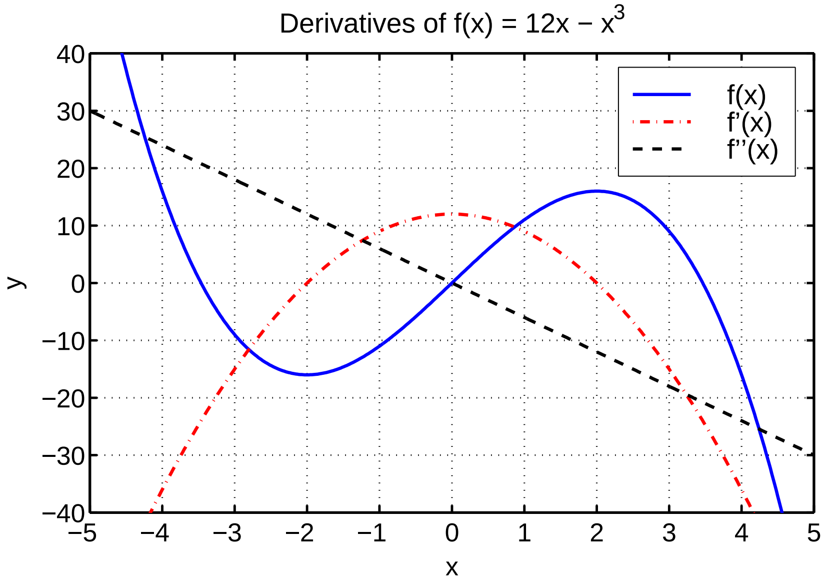

Figure 4: Graph of the function of Example 4 and the graph of its first and second derivatives.

Thus the point $(-2, -16)$ *is a local minimum* and the point $(2, 16)$ *is a local maximum*. The points of inflection occur at the point where the second derivative is equal to zero. In this case, the inflection point is at $x = 0$. This means that the concavity direction changes at point $(0, 0)$. The concavity is upward to the left of $(0, 0)$, and downward to the right of $(0, 0)$. The graph of Figure 4 shows the function and its first and second derivatives. ◁

Example 5 Use the techniques developed in this chapter to find the local or relative minima and maxima and points of inflection for the following polynomial,

$$y = x^4 - 8x^2,$$

then, sketch a graph of the function.

Solution: See the discussion in Example 4

The steps one should always take to create a graph are as follows:

1. Find any x or y-intercepts. (Often x-intercepts are too difficult to find.)
2. Find any vertical or horizontal asymptotes.
3. Find extrema (local minima and maxima).
4. Find any points of inflection.

The y-intercept is easily found as $(0, 0)$, which is both an x and y -intercept. We can factor the equation above and solve for the x-intercept

$$x^2(x^2 - 8) = 0 \quad \text{or} \quad \mathrm{x} = 0, \pm 2\sqrt{2}$$

The critical points x_c can be found when the first derivative of the function is set equal to zero.

$$y\,' = 4x^3 - 16x = 4x(x^2 - 4) = 4x(x - 2)(x + 2) = 0$$

The critical points are at $x_c = -2, 0, 2$. As before, we evaluate the function at each of the critical points, $y(-2) = -16, y(0) = 0$, and $y(2) = -16$, so the critical points of the function are $(-2, -16)$, $(0, 0)$, and $(2, -16)$. Clearly, the first point is a minimum, the second is a maximum, and the third is a minimum again.

Again we can check with the second derivative (though usually this step can be omitted because function evaluation gives the relative height of extrema). The nature of these critical points can be found by evaluating the second derivative function at the critical points of the first derivative function. If the result is negative it indicates a maximum and if the result is positive it indicates a minimum.

$$\begin{aligned} y'' &= 12x^2 - 16 = 4(3x^2 - 4) = 0, \\ y''(-2) &= 4[3(-2)^2 - 4] = 32, \\ y''(0) &= 4[3(0)^2 - 4] = -16, \\ y''(2) &= 4[3(2)^2 - 4] = 32. \end{aligned}$$

Thus the critical points indicate local minima at $(\pm 2, -16)$ and a local maximum at $(0, 0)$. The inflection points occur at the zeros of the second derivative function, which are at approximately $(\pm 1.155, -8.889)$. These characteristics are illustrated in the graph of Figure 5. ◁

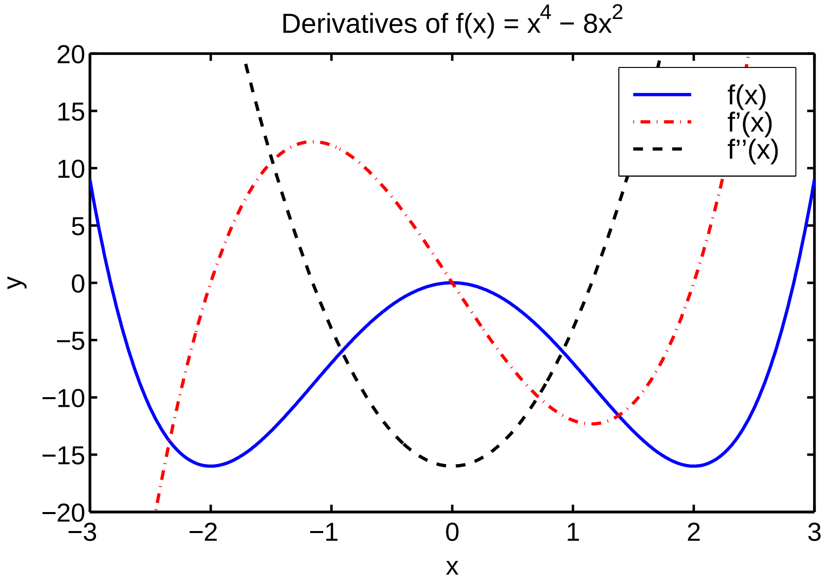

Figure 5: Graph of the function of Example 5 and the graph of its first and second derivatives.

Example 6 *Height of the Ball Revisited*

Consider a ball that is thrown vertically with a initial upward velocity of 64 ft/sec (so $v_0 = 64$). The acceleration due to gravity is $g = -32$ ft/sec^2. With these values, the height of the ball satisfies

$$h(t) = 64t - 16t^2.$$

Find how high this ball travels.

Solution: There are two good ways to solve this problem. From our knowledge of the height function being a quadratic, we could simply find the vertex of the parabola, knowing that it must be at the top of the flight of the ball. Another physical property that can be used to find this *maximum* for flight of the ball is to recognize that at the top of its flight the ball is temporarily stopped, then its velocity becomes negative as the ball falls back to the ground. Thus, finding the time when the velocity is zero gives the time of the maximum height of the ball.

The velocity function from our differentiation rules is

$$v(t) = 64 - 32t.$$

Solving the velocity equal to zero,

$$64 - 32t = 0,$$

gives the critical time, $t = 2$ sec. The maximum height of the ball is found by substituing this critical time into the original height equation, so

$$h(2) = 64(2) - 16(2)^2 = 64ft.$$

◁

Example 7 *Study of a Population*

The ocean water is monitored for fecal contamination by counting certain types of bacteria in a sample of seawater. Over a week where rain occurred early in the week, data were collected on one type of fecal bacteria. The population of the particular bacteria (in thousand/cc), $P(t)$, were best fit by the cubic polynomial

$$P(t) = -t^3 + 9t^2 - 15t + 40,$$

where t is in days.

a. Find the rate of change in population per day, dP/dt. What is the rate of change in the population on the third day?

b. Use the derivative to find when the relative minimum and maximum populations of bacteria occur over the time of the survey. Give the populations at those times. Also determine when the bacterial count is most rapidly increasing.

c. Sketch a graph of this polynomial fit to the population of bacteria. When did the rain most likely occur?

Solution: a. To find the rate of change in population per day, we take the derivative of $P(t)$.

$$\frac{dP}{dt} = -3t^2 + 18t - 15.$$

Evaluating this on the third day gives

$$P'(3) = 12(\times 1000/\text{cc}/\text{day}).$$

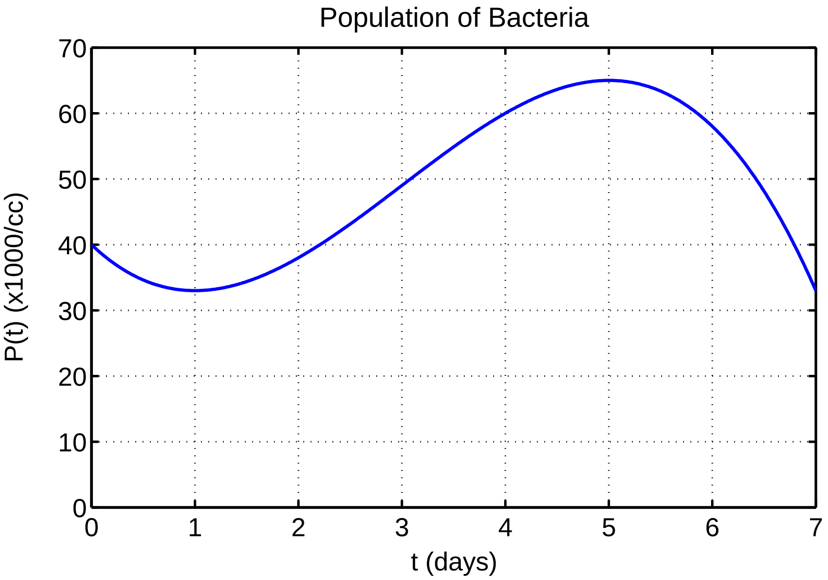

Figure 6: Graph for the function of Example 7.

b. The critical points are found by setting the derivative equal to zero. This particular quadratic factors easily, so

$$P'(t) = -3t^2 + 18t - 15 = -3(t-1)(t-5) = 0.$$

It follows that the critical values are $t_c = 1$ or 5. Substituting the critical values into the population function, we have

$$\text{Minimum at } t = 1 \text{ with } P(1) = 33(\times 1000/\text{cc}),$$
$$\text{Maximum at } t = 5 \text{ with } P(5) = 65(\times 1000/\text{cc}).$$

To find when the population of bacteria is increasing most rapidly, we take the second derivative and set it equal to zero. (Finding the point of inflection.) Thus, we have

$$P''(t) = -6t + 18 = -6(t-3) = 0.$$

It follows that the population is increasing most rapidly at $t = 3$ with $P(3) = 49(\times 1000/\text{cc})$. Above we see that this maximum increase is

$$P'(3) = 12(\times 1000/\text{cc}/\text{day}).$$

c. In Figure 6 we have the graph of this population. Notice that the population at $t = 7$ with $P(7) = 33(\times 1000/\text{cc})$, which matches the local minimum given above. From the graph, we can guess that the rain fell on the second day of the week with storm runoff polluting the water in the days following. ◁

7 EXERCISES

Sketch the curves of the functions below. List the maxima, minima, and points of inflection for each graph. Also, give the x and y-intercepts and any asymptotes if they exist.

1. $y = 15 + 2x - x^2$,

2. $y = x^3 - 12x$,

3. $y = 2x^3 - 3x^2$,

4. $y = x^4 - 2x^2 + 1$,

5. $y = x^4 - 32x$,

6. $y = 2x + \dfrac{2}{x}$,

7. Body temperatures of animals undergo circadian rhythms. A subject's temperature is measured from 8 AM until midnight, and his body temperature, T (in °C), is best approximated by the cubic polynomial

$$T(t) = 0.002(t^3 - 45t^2 + 600t + 16000),$$

where t is in hours.

a. Find the rate of change in body temperature $\frac{dT}{dt}$. What is the rate of change in body temperature at noon $t = 12$?

b. Use the derivative to find when the maximum temperature of the subject occurs and when the minimum temperature of the subject occurs. What are the body temperatures at those times?

8. Over a 7 day period in the summer, data were collected on an algal bloom in the ocean. The population of algae (in thousand/cc), $P(t)$, were best fit by the cubic polynomial

$$P(t) = t^3 - 9t^2 + 15t + 30,$$

where t is in days.

a. Find the rate of change in population per day, $\frac{dP}{dt}$. What is the rate of change in the population on the first day, $t = 2$?

b. Use the derivative to find when the relative minimum and maximum populations of algae occur over the time of the survey. Give the populations at those times. Over what intervals of time is the population increasing?

c. Sketch a graph of this polynomial fit to the population of algae. Show clearly the maximum and minimum populations on your graph and include the populations at the beginning of the survey ($t = 0$) and at the end ($t = 7$).

9. In lab we saw the experimental fit of O_2 consumption (in μl/hr) after a blood meal by the beetle *Triatoma phyllosoma*. Below is a cubic polynomial fit to measurements for a different individual "kissing bug,"

$$Y(t) = \frac{1}{3}t^3 - 6\,t^2 + 20\,t + 120,$$

where t is in hours, for $0 \leq t \leq 12$.

a. Find the rate of change in O_2 consumption per hour, $\frac{dY}{dt}$. What is the rate of change in the O_2 consumption at $t = 6$?

b. Use the derivative to find when the minimum and maximum O_2 consumption for this beetle occurs during the experiment. Give the O_2 consumption at those times.

c. Sketch a graph of this polynomial fit to the O_2 consumption. Show clearly the maximum and minimum O_2 consumption on your graph and include the O_2 consumption at the beginning of the study ($t = 0$) and at the end ($t = 12$).

10. Many ecological studies require that the subject studied is correlated with the temperature of the environment (especially insects and plants). Over a 20 hour period, data are collected on the temperature, $T(t)$in degrees Celsius. The temperature data are found to best fit the cubic polynomial

$$T(t) = 0.01(1600 - 135t + 27t^2 - t^3),$$

where t is in hours (valid for $0 \leq t \leq 20$).

a. Find the rate of change in temperature per hour, $\frac{dT}{dt}$. What is the rate of change in the temperature at 3 AM, $t = 3$?

b. Use the derivative to find when the minimum and maximum temperatures occur. Give the temperatures at those times.

c. Sketch a graph of this polynomial fit to the temperature. Show clearly the maximum and minimum temperatures on your graph and include the temperatures at the beginning of the study ($t = 0$) and at the end ($t = 20$).

11. a. An impala is migrating across a field that has been fenced with a 180 cm fence. To escape it needs to jump this fence. Assume that the impala jumps the fence with just enough vertical velocity, v_0 to clear it. If the height (in cm) of the impala is given by

$$h(t) = v_0 t - 490t^2,$$

then find the velocity $v(t) = h'(t)$ of the impala at any time (in sec), $t \geq 0$, before hitting the ground.

b. Find when the velocity is equal to zero in terms of v_0. This is the time at the maximum height. Since the impala is 180 cm in the air at this time, use the equation for the height, $h(t)$ to compute the initial velocity, v_0, with which the impala must launch itself to clear the fence.

c. With the initial velocity computed above, determine how long the impala is in the air, when jumping over the fence.

CHAPTER 14:

THE DERIVATIVE OF e^x AND $\ln(x)$

This chapter examines the derivatives of the functions e^x and $\ln(x)$. These special functions often arise in biological problems that include biochemical kinetics or population dynamics. The derivatives of these functions are used to find extrema for a number of biological applications.

1 PROZAC

Fluoxetine, more commonly known by its trade name *Prozac*, is a *selective serotonin reuptake inhibitor* (SSRI). This drug is used to treat depression, obsessive compulsive disorder, and a number of other neurological disorders. It works by preventing serotonin from being reabsorbed too rapidly from the synapses between nerve cells, prolonging its availablity, which improves the patient's mood. Fluoxetine is metabolized in the liver and transformed into a slightly less potent SSRI, *norfluoxetine*. Both compounds bind to plasma protein, then become concentrated in the brain (up to 50 times more concentrated). Fluoxetine and norfluoxetine are eliminated from the brain with characteristic half-lives of 1–4 days and 7–15 days, respectively.

When performing studies of drugs, it is very important to understand the kinetics of the drug in the body. When the drug is metabolized into another active form, then the modeling becomes more complex. However, understanding how the body handles a drug is crucial to providing therapeutic levels of a drug and not allowing the drug's levels to become too elevated in the body. A number of first order kinetic models have been developed, and we will examine some equations that describe the concentrations of fluoxetine ($F(t)$) and norfluoxetine ($N(t)$) in the blood.

1.1 HALF-LIFE OF A DRUG

We begin this study with a discussion of the half-life of a drug. (This argument carries over to the half-life of radioactive material also.) Consider a subject taking a 40 mg oral dose of fluoxetine, which is rapidly taken into the blood stream to a concentration of 21 ng/ml. As reported in a study with healthy volunteers [1], the half-life of fluoxetine was 1.5 days. If we assume instantaneous uptake of the drug (which actually takes several hours), then we have the initial blood concentration of fluoxetine given by

$$F(0) = 21 \; ng/\mathrm{ml}$$

When a drug is either filtered out by the kidneys or metabolized by some organ such as the liver proportional to its concentration, then the drug is said to exhibit first-order kinetics and it decays exponentially with a characteristic half-life. Fluoxetine is metabolized in both the brain and liver, so satisfies the kinetic equation

$$F(t) = 21e^{-kt}.$$

With a half-life of 1.5 days, we have

$$F(1.5) = 10.5 = 21e^{-1.5k}.$$

Solving this equation for k, we have

$$\begin{aligned} e^{1.5k} &= 2 \\ k = \ln(2)/1.5 &= 0.462. \end{aligned}$$

Thus, a good model for blood plasma concentration of fluoxetine following a 40 mg oral dose is given by

$$F(t) = 21e^{-0.462t}.$$

2 NORFLUOXETINE KINETIC MODEL

Fluoxetine is metabolized in the liver and through a hepatic biotransformation becomes norfluoxetine (through a demethylation). Norfluoxetine continues to act as potent and specific serotonin reuptake inhibitor, but has the added advantage of lasting much longer. (Some researchers believe that this is the primary therapeutic form of the drug because of its long persistence in the brain compared to fluoxetine.) Using the data from the Sunnybrook website[1] and taking the half-life to be 9 days for norfluoxetine, a reasonable model using linear kinetics for the blood plasma concentration of norfluoxetine is given by the equation

$$N(t) = 27.5(e^{-0.077t} - e^{-0.462t}).$$

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[1] www.icomm.ca/shsc/kinetics/fluoxeti.html. last visited on 04/19/04

(Note that all data from the Sunnybrook website[1] cannot be fit to a linear kinetic model, so this model chooses the peak value and half-life to be consistent.)

Figure 1 shows a graph of the fluoxetine and norfluoxetine concentrations from the models above. The graph supports the findings of some researchers that norfluoxetine provides much of the therapeutic dose of Prozac.

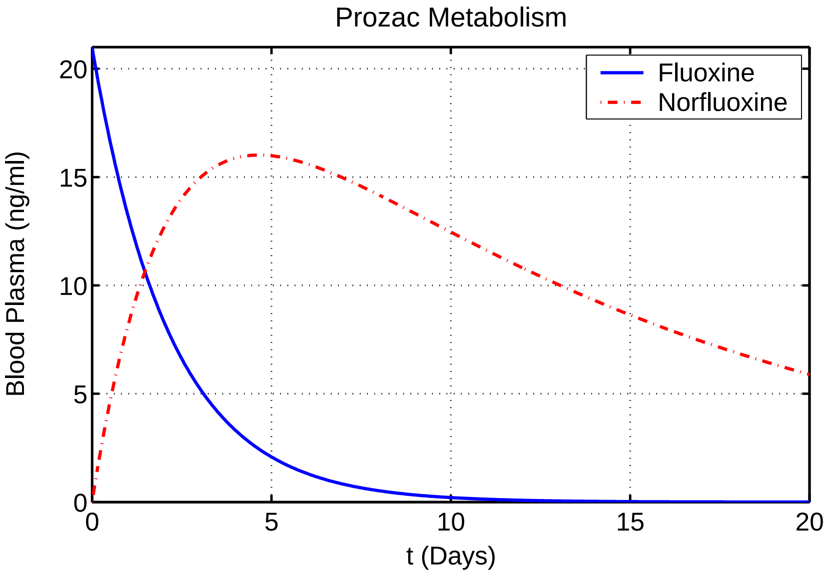

Figure 1: Graph of the blood concentration for fluoxetine and norfluoxetine.

We want to use our techniques from Calculus to determine the rate of change of fluoxetine and to find the time of maximum blood plasma concentration of norfluoxetine and what that concentration is. To solve these problems, we need to learn the formula for the derivative of the exponential function.

3 DERIVATIVE OF e^{kx}

The exponential function e^x is considered a special function. It is the only function (up to a scalar multiple) that is the derivative of itself.

The derivative of the exponential function, e^x, is

$$\frac{d}{dx}(e^x) = e^x.$$

Note that by our scalar multiplication rule, then the derivative of $f(x) = ke^x$ is $f'(x) = ke^x$.

From the definition of the derivative and using the properties of exponentials, we see that

$$\frac{d}{dx}(e^x) = \lim_{h\to 0} \frac{e^{x+h} - e^x}{h} = \lim_{h\to 0} e^x \frac{e^h - 1}{h}.$$

One definition of the number e is the number that makes

$$\lim_{h\to 0} \frac{e^h - 1}{h} = 1.$$

Geometrically, the function e^x is a number raised to the power x, whose slope of the tangent line at $x = 0$ is 1.

The derivative of e^{kx} is given by

$$\frac{d}{dx}(e^{kx}) = ke^{kx}.$$

Example 1 Find the derivative of

$$f(x) = 5e^{-3x}.$$

Solution: From our rule of differentiation and the formula above, we have

$$f'(x) = -15e^{-3x}.$$

◁

4 APPLICATION OF THE DERIVATIVE TO THE PROZAC KINETIC MODEL

We will use the derivative of the exponential function to find the rate of change of fluoxetine and norfluoxetine at various times, then find when the maximum concentration of norfluoxetine occurs and what that concentration is. We begin by finding the derivatives of the functions modeling blood plasma concentration of fluoxetine and norfluoxetine. From above, we have the concentration of fluoxetine is

$$F(t) = 21e^{-0.462t},$$

so the derivative is given by

$$F'(t) = (-0.462)21e^{-0.462t} = -9.702e^{-0.462t}.$$

Similarly for the blood plasma concentration of norfluoxetine

$$N(t) = 27.5e^{-0.077t} - 27.5e^{-0.462t},$$

so its derivative is

$$\begin{aligned} N'(t) &= (-0.077)27.5e^{-0.077t} - (-0.462)27.5e^{-0.462t} \\ &= 12.705e^{-0.462t} - 2.1175e^{-0.077t}. \end{aligned}$$

If we want the rate of change of blood plasma concentrations of these two compounds at times $t = 2$ and 10, then we evaluate the rate of change of fluoxetine blood plasma concentration as

$$\begin{aligned} F'(2) &= -9.702e^{-0.462(2)} = -3.85 \ n\text{g/ml/day}, \\ F'(10) &= -9.702e^{-0.462(10)} = -0.0956 \ n\text{g/ml/day}. \end{aligned}$$

Similarly, the rate of change of norfluoxetine blood plasma concentration is

$$\begin{aligned} N'(2) &= 12.705e^{-0.462(2)} - 2.1175e^{-0.077(2)} = 3.23 \ n\text{g/ml/day}, \\ N'(10) &= 12.705e^{-0.462(10)} - 2.1175e^{-0.077(10)} = -0.855 \ n\text{g/ml/day}. \end{aligned}$$

These calculations show that at $t = 2$ the blood plasma concentration of fluoxetine is dropping quite rapidly, while blood plasma concentration of norfluoxetine is rising at a similar rate. The calculations at $t = 10$ show that the blood plasma concentration of both compounds are falling at fairly slow rates.

4.1 MAXIMUM CONCENTRATION OF NORFLUOXETINE

The maximum concentration of norfluoxetine is found by determining when the derivative is equal to zero. Thus,

$$N'(t) = 12.705e^{-0.462t} - 2.1175e^{-0.077t} = 0$$

or

$$2.1175e^{-0.077t} = 12.705e^{-0.462t}.$$

This gives

$$\begin{aligned} \frac{e^{-0.077}}{e^{-0.462t}} &= \frac{12.705}{2.1175} \\ e^{0.385t} &= 6. \end{aligned}$$

It follows that the maximum occurs at

$$\begin{aligned} 0.385t &= \ln(6) \\ t_{max} &= 4.654 \text{ days.} \end{aligned}$$

The maximum blood plasma concentration of norfluoxetine (as seen on the graph) is

$$N(t_{max}) = 16.01\ n\text{g/ml.}$$

5 HEIGHT AND WEIGHT RELATIONSHIP FOR CHILDREN

The average height and weight of girls is given in Table 1. Ehrenberg noted that there was a logarithmic relationship between the height and the weight of children. Figure 2 shows a graph of the data of Table 1, showing the height as a function of weight of girls ages 5 through 13 using data on the average height and weight of girls in the U. S.

age(years)	height(cm)	weight(kg)
5	108	18.2
6	114	20.0
7	121	21.8
8	126	25.0
9	132	29.1
10	138	32.7
11	144	37.3
12	151	41.4
13	156	46.8

Table 1: Average height and weight of girls between 5 and 13 years of age.

The formula for the height, H, as a function of weight, w, is given by

$$H(w) = 49.5\ln(w) - 34.14.$$

We would like to find the find the rate of change of height with respect to weight for the average girl.

6 DERIVATIVE OF $\ln(x)$

We cannot easily use the definition of the derivative to find the derivative of the natural logarithm.

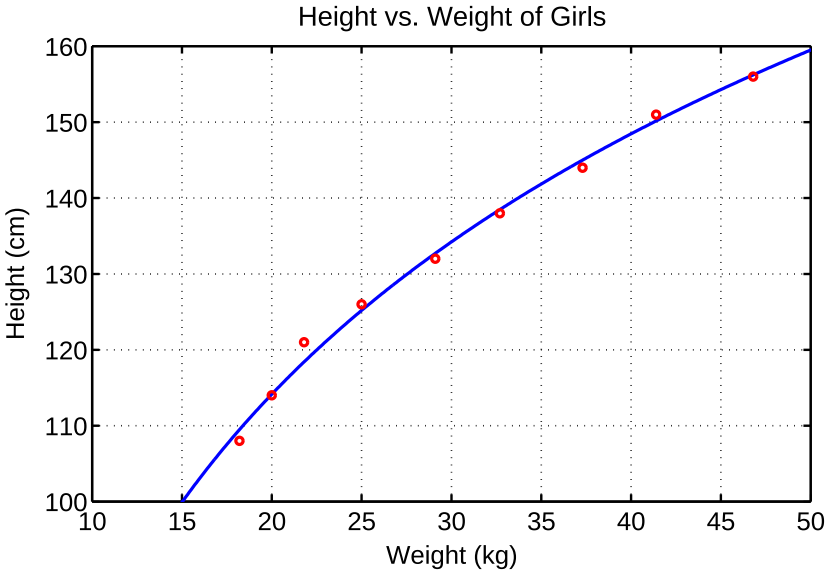

Figure 2: Graph obtained from the data of Table 1.

The derivative of the natural logarithm, $\ln(x)$, is

$$\frac{d}{dx}(\ln(x)) = \frac{1}{x}.$$

This relationship is most easily demonstrated after learning the Fundamental Theorem of Calculus, which centers about the integral.

6.1 DERIVATIVE OF THE HEIGHT AND WEIGHT RELATIONSHIP FOR CHILDREN

The relationship given above is easily differentiated with respect to w, using the derivative for the natural logarithm. It follows that

$$\frac{dH}{dw} = \frac{49.5}{w}.$$

From this relationship, it is clear that as the weight increases, the rate of change in height decreases. For example, we can see that at a weight of 20 kg.

$$H'(20) = 49.5/20 = 2.475 \text{ cm/kg},$$

while at a weight of 49.5 kg.

$$H'(49.5) = 49.5/49.5 = 1 \text{ cm/kg}.$$

Note that this is not the rate of change of the height as a function of the age, which we saw to be nearly linear in the first chapter of this book.

Example 2 1. Find the derivative of

$$f(x) = \ln(x^2).$$

Solution: From our properties of logarithms and the formula above, we have $f(x) = \ln(x^2) = 2\ln(x)$, so

$$f'(x) = \frac{2}{x}.$$

2. Find the derivative of the following function:

$$g(x) = \ln\left(\sqrt{x}\right).$$

Solution: We first use the properties of logarithms to change the expression so that it only includes $\ln(x)$

$$\begin{aligned} g(x) = \ln\left(\sqrt{x}\right) &= \ln(x^{1/2}) = \frac{1}{2}\ln(x), \\ g'(x) &= \frac{1}{2x}. \end{aligned}$$ ◁

The examples below explore more differentiation of the exponential and logarithm functions, including the graphs of these functions. There are examples of a polymer drug delivery device, radioactive decay, and the growth of fish with the von Bertalanffy equation.

Example 3 *Graphing Exponential and Logarithms*

Consider the following function

$$y = 2e^{-0.2x} - 1.$$

Graph this function and find its derivative.

Solution: The domain of this function is all values of x. The y-intercept satisfies

$$2e^{-0.2(0)} - 1 = 1$$

The x-intercept satisfies

$$\begin{aligned} 2e^{-0.2x} - 1 &= 0 \\ 2e^{-0.2x} &= 1 \\ e^{0.2x} &= 2 \\ x &= 5\ln(2) = 3.466. \end{aligned}$$

For large values of x, the exponential function decays to zero. Thus, there is a *horizontal asymptote* to the right with

$$y = -1.$$

Often when there is an exponential function, there is a *horizontal asymptote* going either to the right (negative constant times x) or to the left (positive constant times x). The graph of the function is given by Figure 3.

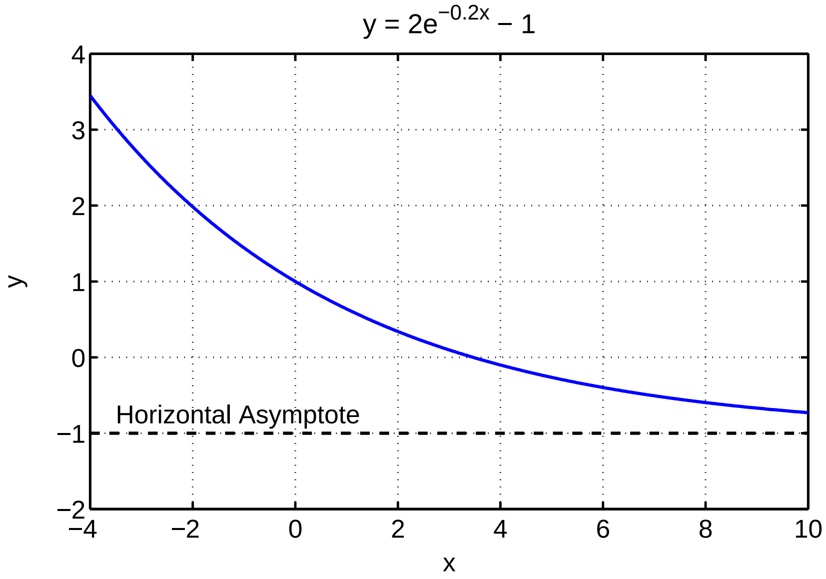

Figure 3: Graph of the exponential function of Example 3.

The derivative of this function satisfies

$$y' = 2(-0.2)e^{-0.2x} = -0.4e^{-0.2x}.$$

Since the exponential function is always positive, the derivative is always negative though the derivative does approach zero as x becomes large (approaching the horizontal asymptote). Thus, this function is always decreasing, which is clearly shown in the graph. ◁

Example 4 *Finding local extrema*

Consider the following function

$$y = x - \ln(x)$$

Find the first and second derivatives of this function. Find any local extrema, then graph the function.

Solution: The derivative for this function is given by

$$\frac{dy}{dx} = 1 - \frac{1}{x} = \frac{x-1}{x}.$$

The second derivative is given by

$$\frac{d^2y}{dx^2} = -\frac{1}{x^2}.$$

This function is only defined for $x > 0$. Thus, there is no y-intercept. However, there is a vertical asymptote at $x = 0$. We find extrema by setting the derivative equal to zero. The derivative is zero only when the numerator of the above expression for the derivative is zero, so $x = 1$. This gives an extremum at $(1, 1)$.

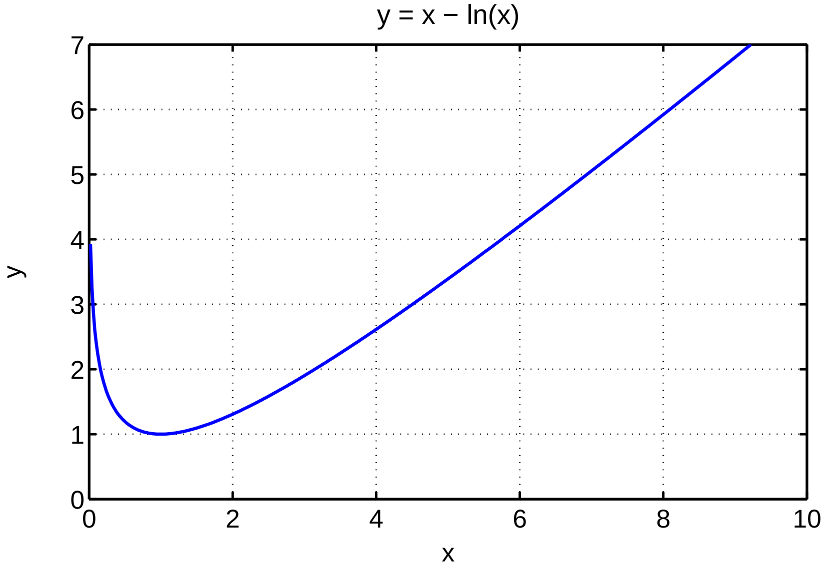

Figure 4: Graph of the logarithmic function of Example 4.

Since the second derivative is always negative, which says that this function is concave upwards. It follows that the extremum computed above is a minimum. The graph of the function is given by Figure 4. ◁

Example 5 *Polymer Drug Delivery System*

This problem compares drug concentration in the body following an injection and compares this to the new polymer drug delivery devices. Drugs have long been administered by either a pill or an injection. The result is that the body receives a fairly high dose rapidly, then the drug remaining in the blood disappears in an exponentially decaying manner. Recently, scientists have invented polymers that can be implanted to deliver a drug or hormone for a much longer period of time. For example, there are several long term birth control devices that are injected just below the skin. These devices deliver the hormones estrogen and progesterone at sufficiently high levels for extended periods of time to prevent pregnancy. These new drug delivery devices are a hot area of research for a variety of medical conditions. These devices could aid diabetes sufferers with a more uniform level of insulin or they could deliver chemotherapeutic drugs to cancer patients over a much longer period of time at lower doses to maximize their efficacy.

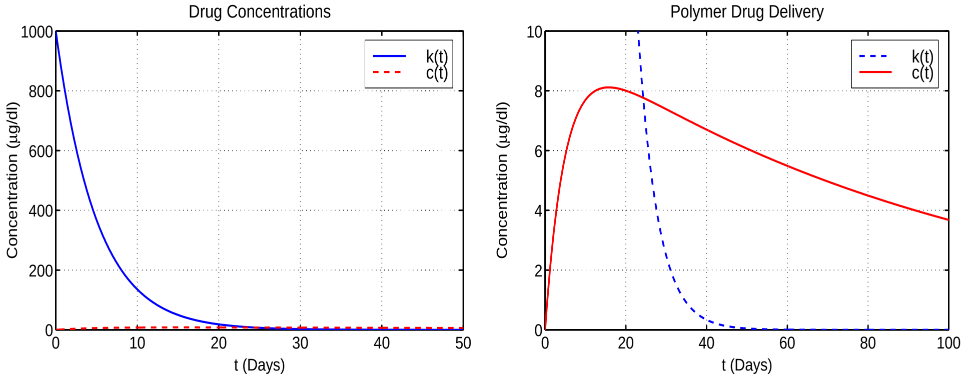

Figure 5: Figures for the concentration functions of the injected drug ($k(t)$) and *polymer device* delivered drug ($c(t)$) of Example 5.

We want to study equal quantities of drug delivered by an injection and by a polymer drug delivery device. When a drug is delivered by an injection, the drug is cleared relatively rapidly by either filtration of the kidneys or metabolism. The concentration in the blood is given by the formula

$$k(t) = A_0 e^{-qt}.$$

where A_0 and q are constants representing the amount of drug injected and the rate that the drug is cleared from the body. When the same drug is delivered by a polymer delivery device, then it is typically described by two decaying exponentials. This system is given by the model

$$c(t) = C_0(e^{-rt} - e^{-qt}),$$

where $c(t)$ is the concentration of the drug and C_0, r, and q are constants depending on the drug delivery system with $q > rC_0$ is a constant that indicates the level of the drug or hormone trapped in the polymer delivery device. The kinetic constants r and q are associated with the decay of the polymer that releases the drug and the degradation of the drug in the body of the patient, respectively. For the amounts of drug to be the same, then

$$A_0 = C_0/r.$$

Consider a specific example where the injected drug satisfies

$$k(t) = 1000e^{-0.2t},$$

where the $k(t)$ is a concentration in μg/dl and the time t is in days. The same amount of drug is delivered by a polymer drug delivery device and is given by

$$c(t) = 10(e^{-0.01t} - e^{-0.2t}),$$

where the $c(t)$ is a concentration in μg/dl.

Find the rate of change in concentration for both $k(t)$ and $c(t)$ at $t = 5$ and 20. Also, determine the maximum concentration of $c(t)$ and when it occurs. Graph each of these functions.

Solution: We begin by finding the derivatives of $k(t)$ and $c(t)$. Using the rule of differentiation for exponentials, we find that

$$k'(t) = (-0.2)1000e^{-0.2t} = -200e^{-0.2t}$$

and

$$c'(t) = 10(-0.01e^{-0.01t} - (-0.2)e^{-0.2t}) = 2e^{-0.2t} - 0.1e^{-0.01t}.$$

If we want the rate of change of the drug concentrations at times $t = 5$ and 20, then the injected drug gives declining rates of change

$$\begin{aligned} k'(5) &= -200e^{-0.2(5)} = -73.58\ \mu\text{g/dl/day}, \\ k'(20) &= -200e^{-0.2(20)} = -3.66\ \mu\text{g/dl/day}. \end{aligned}$$

Similarly, the rate of change of the polymer delivered drug is

$$\begin{aligned} c'(5) &= 2e^{-0.2(5)} - 0.1e^{-0.01(5)} = 0.64\ \mu\text{g/dl/day}, \\ c'(20) &= 2e^{-0.2(20)} - 0.1e^{-0.01(20)} = -0.045\ \mu\text{g/dl/day}. \end{aligned}$$

The maximum is found by taking the derivative of $c(t)$ and setting it equal to zero. From the derivative above, we have

$$\begin{aligned} 2e^{-0.2t} - 0.1e^{-0.01t} &= 0. \\ 0.1e^{-0.01t} &= 2e^{-0.2t} \\ e^{-0.01t+0.2t} &= 20 \\ e^{0.19t} &= 20. \end{aligned}$$

Thus, $t = \ln(20)/0.19 = 15.767$ days. The maximum occurs at $c(15.767) = 8.11\ \mu\text{g/dl}$.

Figure 5 shows the graph the two functions, $k(t)$ and $c(t)$. The graph on the left of Figure 5 shows the large amount from the injection, which decays very rapidly. By setting the two concentrations equal to each other, we can readily find that the functions are equal when $t = 24.29$ days with concentrations of $7.766\ \mu\text{g/dl}$. The injected drug falls off very rapidly, continuing its decline, while the polymer delivered drug maintains a relatively constant level over a much longer time. The right panel of Figure 5 shows the graph of the polymer delivered drug over a longer period of time (with the injected drug appearing as dashed lines). Its maximum concentration is easily seen in the graph. The graph of Figure 5 shows the obvious advantages of the time released drug if it has serious side effects or toxicity. ◁

Example 6 *Potassim Isotope* 43

Naturally-occurring potassium is not radioactive, but radioactive isotopes can be manufactured from natural potassium. Potassium isotope 43 decays at a rate proportional to the amount of the radioactive potassium available. After it emits a beta ray, it reverts to calcium. (^{43}K goes through a β-decay with a neutron changing to a proton to produce ^{43}Ca.) This can be used as a tracer for studying the effectiveness of potassium absorption in the body.

Suppose we begin with a 10 mCi (millicurie) sample of ^{43}K. This substance has a half-life of 22 hours. Find the amount of ^{43}K after $5, 20,$ and 50 hours. Also, find the rate of loss of ^{43}K after $5, 20,$ and 50 hours.

Solution: If a radioactive substance has a half-life of x hours, then it decays exponentially to half its original amount in x hours. Let $K(t)$ be the amount of ^{43}K, then an expression for the amount of ^{43}K is given by

$$K(t) = 10e^{-kt},$$

where the constant k must be determined based on the half-life. If the amount of $K(t)$ drops to 5 mg in 22 hours, then we know that

$$\begin{aligned} K(22) &= 5 = 10e^{-22k} \\ e^{-22k} &= 1/2 \\ e^{22k} &= 2. \end{aligned}$$

By taking the natural log of both sides, we see that

$$22k = \ln(2) \quad \text{or} \quad \mathrm{k} = \ln(2)/22 \approx 0.0315.$$

Thus, we can write the expression for $K(t)$ as

$$K(t) = 10e^{-t\ln(2)/22} \approx 10e^{-0.0315t}.$$

With this expression for $K(t)$, we can readily find the amount of ^{43}K after $5, 20$, and 50 hours. We have

$$\begin{aligned} K(5) &= 10e^{-5k} \approx 10e^{-0.1575} \approx 8.54 \text{ mCi}, \\ K(20) &= 10e^{-20k} \approx 10e^{-0.6301} \approx 5.325 \text{ mCi}, \\ K(50) &= 10e^{-50k} \approx 10e^{-1.575} \approx 2.07 \text{ mCi}. \end{aligned}$$

To find the rate of change in the amount of $K(t)$ at a given time, we need the derivative of $K(t)$. From the rule for differentiating the exponential function, we have

$$k'(t) = -10ke^{-kt}.$$

With this expression for $k'(t)$, we can readily find the rate of change in the amount of ^{43}K after $5, 20$, and 50 hours. We have

$$\begin{aligned} k'(5) &= -10ke^{-5k} \approx -0.315e^{-0.1575} \approx -0.269 \text{ mCi/h}, \\ k'(5) &= -10ke^{-20k} \approx -0.315e^{-0.6301} \approx -0.168 \text{ mCi/h}, \\ k'(5) &= -10ke^{-50k} \approx -0.315e^{-1.575} \approx -0.0652 \text{ mCi/h}. \end{aligned}$$

This gives an estimate at each time of how much beta radiation is coming from the sample of ^{43}K. ◁

Example 7 *von Bertalanffy Equation*

As a fish ages, it reaches a maximum size. A model for fish growth was developed by von Bertalanffy, which has an exponential solution.

a. Data shows that on average a lake trout takes 5.5 years to reach 2 kg and 15 years to reach 5 kg. When these data are fit to the von Bertalanffy equation, an equation for weight as a function of age is given by

$$W(a) = 20.2(1 - e^{-0.019a}).$$

Find the rate of change of weight, W, with respect to the age, a. Graph the solution of the von Bertalanffy equation showing the intercepts and any asymptotes.

b. Solve the above equation for age, a, as a function of the weight, W. Differentiate this function, finding the rate of change of age with respect to weight. Graph this function showing any intercepts and asymptotes.

Solution: a. Write the von Bertalanffy equation as follows,

$$W(a) = 20.2 - 20.2e^{-0.019a}$$

then differentiating with respect to the age, a, gives

$$\frac{dW}{da} = -20.2(-0.019)e^{-0.019a} = 0.3838e^{-0.019a} \text{ kg/yr}.$$

This says that the function is monotonically increasing (as we would expect for growth of a fish).

This equation goes through the origin, and it is easy to see that for large values of a the exponential decays to zero, which implies that asymptotically the fish grows to a weight of 20.2 kg. This is the horizontal asymptote. Figure 6 is a graph of the von Bertalanffy equation.

b. Next solve the equation

$$W = 20.2 - 20.2e^{-0.019a}$$

for the age, a. It follows that

$$\begin{aligned} 20.2e^{-0.019a} &= 20.2 - W \\ e^{-0.019a} &= \frac{20.2 - W}{20.2} \\ e^{0.019a} &= \frac{20.2}{20.2 - W} \\ a &= \frac{1}{0.019}\ln\left(\frac{20.2}{20.2 - W}\right) = \frac{1}{0.019}(\ln(20.2) - \ln(20.2 - W)). \end{aligned}$$

Thus, we can write the age, a, as a function of the weight, W. It is given by

$$a(W) = 158.2 - 52.63\ln(20.2 - W).$$

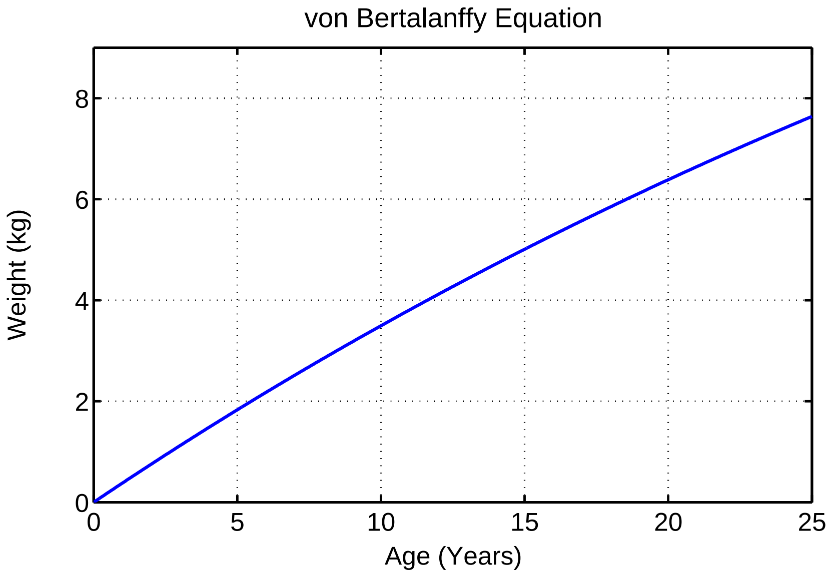

Figure 6: Graph of the function for the growth of a fish obtained from the von Bertalanffy equation of Example 7.

Unfortunately, this expression cannot be directly differentiated without the *chain rule* (to be learned soon). However, try a substitution of $Z = 20.2 - W$. (Note that $dZ/dW = -1$, which is just a sign change.) With this substitution, we have

$$a(Z) = 158.2 - 52.63\ln(Z),$$

and

$$\frac{da}{dZ} = -52.63\frac{1}{Z}.$$

We will find with the chain rule that

$$\frac{da}{dW} = \frac{da}{dZ} \times \frac{dZ}{dW}.$$

Since $Z = 20.2 - W$ and $dZ/dW = -1$, the formula gives

$$\frac{da}{dW} = \frac{52.63}{20.2 - W}.$$

The graph of the inverse function for the von Bertalanffy equation given by $a(W)$ has a domain of $W < 20.2$. There is a vertical asymptote at $W = 20.2$. The derivative above shows that this function is strictly increasing. Since the function $W(a)$ passes through the origin, its inverse function also

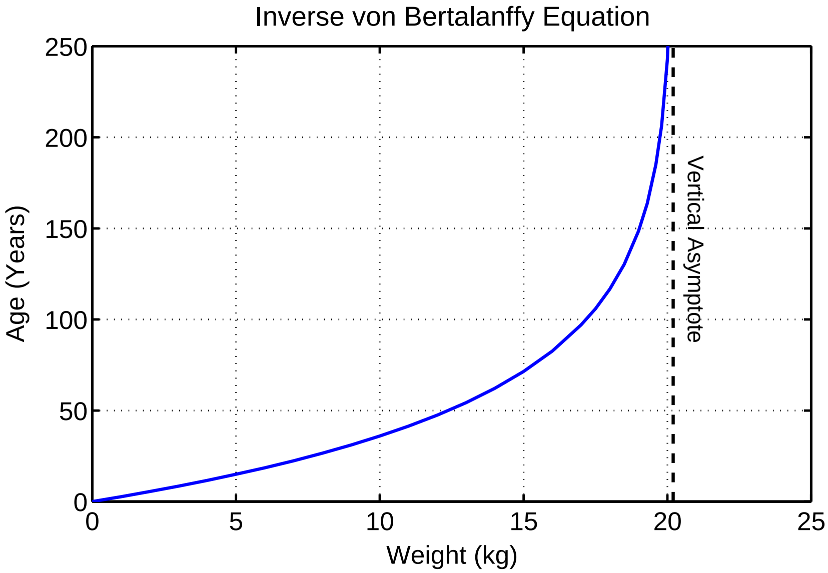

Figure 7: Graph for the inverse function of the von Bertalanffy equation depicted in Figure 6.

passes through the origin

$$a(0) = 158.2 - 52.63\ln(20.2) = 0.$$

Figure 7 shows the graph of this inverse function. ◁

7 EXERCISES

Find the derivative of the following functions:

1. $f(x) = x^2 - 3e^{-x} - 1,$
2. $f(x) = 2x - 7\ln(x) + e^{2x},$
3. $f(x) = 5\ln\left(\frac{1}{x}\right) - e^{-2x} + 2,$
4. $f(x) = \frac{3}{e^{5x}} + 4\ln\left(\frac{1}{\sqrt{x}}\right) - \frac{1}{x}.$

Sketch the curves of the functions below. Give the domain of each of the functions. List all maxima and minima for each graph. Also, give the x and y-intercepts and any asymptotes if they exist.

5. $y = 100\left(e^{-0.05x} - e^{-0.2x}\right),$
6. $y = 20\left(1 - e^{-x}\right),$
7. $y = x^2 - 2\ln(x),$
8. $y = 4\ln(x),$

9. Some hormones have a strong effect on mood, so finding a delivery device that delivers a hormone at a more constant level over a longer period

of time is important for hormone therapy. Suppose that a drug company finds a polymer that can be implanted to deliver a hormone, $h(t)$, which is experimentally found to satisfy

$$h(t) = 40\left(e^{-0.005t} - e^{-0.15t}\right),$$

where h is in nanograms per deciliter of blood (ng/dl) and t is in days.

a. Find the maximum concentration of this hormone in the body and when this occurs.

b. Determine all intercepts and asymptotes, then graph $h(t)$ for $0 \leq t \leq 150$. Use the graph to approximate how long the hormone level remains above 20 ng/dl.

10. Let $Y(t)$ be a population of yeast in a sugar solution that begins with a concentration of 10 yeast/ml.

a. If the concentration of yeast is given by

$$Y(t) = 10e^{at},$$

then find the value of a assuming that the concentration doubles every 2 hours.

b. Differentiate this function to find the rate of increase in the concentration of yeast per hour.

c. Evaluate the concentration of yeast at $t = 1$, 2, and 5 hours, and the rate of increase in the concentration of yeast per hour.

11. In an earlier section, we studied the population of the U. S. The population in 1790 was 3.93 million, and the growth rate was about 35% per decade.

a. If the population $P(t)$ is increasing exponentially, then the population at time t can be described by

$$P(t) = 3.93e^{at},$$

where P is in millions and t is in years after 1790. The population in 1800 is 5.31 million. , Determine a in the expression above.

b. Differentiate this function to find the function which represents the annual rate of growth (in millions/yr).

c. Use the expressions in Parts a. and b. to estimate the population in 1850 and 1860 and the annual growth rates at each of those dates.

d. If the actual populations in 1850 and 1860 are 23.2 and 31.4 million, respectively, then determine the percent error between this model and the actual populations.

e. Take the difference of the populations in 1850 and 1860 and divide by 10 to estimate the annual growth rate for that decade and compare that value to the values you obtained in Part c.

12. White lead, ^{210}Pb, is a radioactive element that appears in the pigment of paints and can be used to date oil paintings. This helps determine modern art forgeries. ^{210}Pb undergoes a β- decay to ^{210}Bi. Radioactive substances decay at a rate proportional to the amount of the substance available.

a. Suppose that a 1 g sample of paint contains 6 μg of ^{210}Pb. The amount of ^{210}Pb, $R(t)$ satisfies the equation,

$$R(t) = 6e^{-kt},$$

where the constant k is to be determined. If the half-life of ^{210}Pb is 22 years, then find k.

b. Find $R'(t)$, then determine the rate of change in the amount of ^{210}Pb at $t = 20$, 50, and 100 years.

c. Suppose a fresh 1 g sample of pigment gives 60 counts per minute (cpm) (from the β decay of the ^{210}Pb), and a 1 g sample of the same pigment from a historic painting releases 8 cpm, estimate the age of the painting.

13. The cutlassfish is a valuable resource in the marine fishing industry in China. A von Bertalanffy model is fit to data for one species of this fish giving the length of the fish, $L(t)$ (in mm), as a function of the age, a (in yr). An estimate of the length of this fish is

$$L(a) = 589 - 375e^{-0.168a}.$$

a. Find the L-intercept and any asymptotes. What is the maximum possible length of this fish?

b. Determine how long it takes for this fish to reach 90% of its maximum length. Sketch a graph of the von Bertalanffy model.

c. Differentiate $L(a)$ with respect to a, then determine how fast the average fish is growing when it is 5 years old.

14. The field metabolic rate (FMR) or the total energy expenditure per day in excess of growth is calculated for pronghorm fawns using Nagy's formula

$$E(x) = 0.774 + 0.727\ln(x),$$

where x is the mass of the fawn (in g) and $E(x)$ is the energy expenditure (in kJ/day).

a. Compute the derivative $E'(x)$.

b. Find the energy expenditure when $x = 10,000$, then compute $E'(10,000)$. Give a biological interpretation of these results.

c. Graph $E(x)$ for $x \in [5000, 20000]$.

8 REFERENCES

[1] Nicole Lee, Sunnybrook and Women's College Health Sciences Centre's Drug Information Site [2], 2075 Bayview Ave North York, Ontario M4N 3M5 CANADA.

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[2] www.icomm.ca/shsc/kinetics/fluoxeti.html. last visited on 04/19/04

CHAPTER 15:

PRODUCT RULE

Many mathematical techniques are valuable for the study of cancer, including the mathematics of image processing, calculations of therapeutic doses, epidemiology of cancer in a population, and growth studies. This section begins with a model used to predict the growth of a tumor. This model introduces the product rule of differentiation to find when the tumor is growing most rapidly. The product rule is useful in other growth models and graphing.

1 GOMPERTZ MODEL FOR TUMOR GROWTH

Tumors can only grow as large as the nutrient supply available to the tumor cells. Tumor angiogenesis is the proliferation of blood vessels that penetrate into the tumor to supply nutrients and oxygen and to remove waste products. The center of the tumor largely consists of dead cells, called the necrotic center of the tumor. The tumor grows outward in roughly a spherical shell shape. If the tumor fails to produce signaling proteins for angiogenesis, then the tumor can only grow to a certain size with available nutrient supplies.

Simpson-Herren and Lloyd [2] studied the growth of a number of tumors (see Figure 1). One tumor they studied was the C3H Mouse Mammary tumor, which is stimulated by a provirus. By using tritiated thymidine, they measured the cell cycles for the mammary tumors in mice. From this, they were able to find the growth rate for these tumors. Figure 1 has a graph showing the population of tumor cells and the growth rate of the tumor at the various sizes of the tumor. (The graph includes the curve for the Gompertz model.)

There have been a number of mathematical models that can closely match the growth of a tumor. Laird [1] showed that tumor growth satisfies equations developed by Gompertz, provided the number of tumor cells is sufficiently large (see Figure 1). The growth function is given by the equation

$$G(N) = N(b - a\ln(N)),$$

where N are the number of tumor cells and a and b are constants that

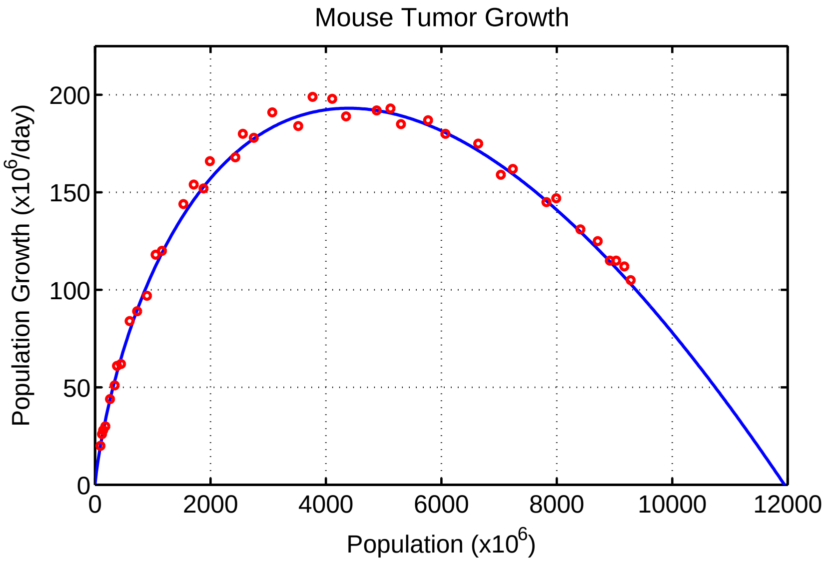

Figure 1: Graph for the tumor growth rate at different tumor sizes (size in terms of population of cancer cells).

are matched to the data measuring the growth of a tumor. Note that this function is not defined for $N = 0$, so it is assumed that the tumor has a certain size before applying this model. For the data above, the best fit curve is given by

$$G(N) = N(0.4126 - 0.0439\ln(N)).$$

As with the logistic growth function, this function is zero when growth is zero or the growth of the tumor stops. When the growth of the tumor stops, the tumor cells are at equilibrium and the tumor is at its maximum size supportable with the available nutrient supply. We would also like to know when the tumor is growing most rapidly. This will occur when the derivative is zero.

The equilibrium is found when

$$G(N) = N(b - a\ln(N)) = 0.$$

Since $N > 0$, this occurs when $b - a\ln(N) = 0$. This is equivalent to

$$\begin{aligned} \ln(N) &= b/a \\ N_e &= e^{b/a}. \end{aligned}$$

Thus, $N_e = e^{b/a}$ is the unique equilibrium and is similar to the carrying capacity seen for the logistic growth function. For the specific data given above, the

$$N_e = e^{0.4126/0.0439} = e^{9.399} = 12,072,$$

which matches the P-intercept on the graph above.

Finding the derivative of $G(N)$ presents a new problem in differentiation. We need to develop the product rule for differentiation to differentiate $G(N)$.

2 PRODUCT RULE

Let $f(x)$ and $g(x)$ be differentiable functions. The *product rule* for finding the derivative of the product of these two functions is given by:

$$\frac{d}{dx}(f(x)g(x)) = f(x)\frac{dg(x)}{dx} + g(x)\frac{df(x)}{dx}.$$

In words, this says that the derivative of the product of two functions is the first function times the derivative of the second function plus the second function times the derivative of the first function.

Example 1 *Power Function*

We begin by verifying the product rule with a simple example. Consider $f(x) = x^{\mathbf{5}}$. We know that $f'(x) = 5x^{\mathbf{4}}$. Let $f_{\mathbf{1}}(x) = x^{\mathbf{2}}$ and $f_{\mathbf{2}}(x) = x^{\mathbf{3}}$, then $f(x) = f_{\mathbf{1}}(x)f_{\mathbf{2}}(x)$. From the product rule we have

$$f'(x) = f_1(x)f_2'(x) + f_1'(x)f_2(x) = x^2(3x^2) + (2x)x^3 = 5x^4. \qquad \triangleleft$$

Example 2 *Polynomials*

Consider the function given by

$$f(x) = (x^3 - 2x)(x^2 + 5).$$

Find the derivative of $f(x)$ by using the product rule. Next multiply the terms in $f(x)$, then take the derivative of the resulting polynomial. Show that these give the same functions, verifying the product rule.

Solution: The product rule is carried out by multiplying the first term times the derivative of the second term, plus the second term multiplied by the derivative of the first term.

$$\begin{aligned} f'(x) &= (x^3-2x)(2x)+(x^2+5)(3x^2-2) \\ &= 2x^4-4x^2+3x^4-2x^2+15x^2-10 \\ f'(x) &= 5x^4+9x^2-10. \end{aligned}$$

We should be able to obtain the same result by multiplying the terms in $f(x)$ and then taking the derivative of the resulting polynomial.

$$\begin{aligned} f(x) &= x^5+5x^3-2x^3-10x = x^5+3x^3-10x \\ f'(x) &= 5x^4+9x-10. \end{aligned}$$

Thus, it is easy to see that the two methods do indeed yield the same result.

◁

Example 3 *Other Functions*

Consider the function given by

$$g(x) = (x^2+4)\ln(x).$$

Find the derivative of $g(x)$ by using the product rule.

Solution: Again we multiply the first term times the derivative of the second term and add the second term multiplied times the derivative of the first term. Recall that the derivative of the natural logarithm equals the inverse of the argument.

$$g'(x) = (x^2+4)(1/x)+[\ln(x)](2x) = x+4/x+2x\ln(x).$$ ◁

3 MAXIMUM GROWTH FOR THE GOMPERTZ TUMOR GROWTH MODEL

To find the maximum growth, we apply the Product Rule to the Gompertz Growth function

$$G(N) = N(b-a\ln(N)),$$

giving

$$\begin{aligned} \frac{dG}{dN} &= N\left(-\frac{a}{N}\right)+(b-a\ln(N)), \\ \frac{dG}{dN} &= (b-a)-a\ln(N). \end{aligned}$$

The maximum occurs when $G'(N) = 0$, which is when

$$\begin{aligned} a\ln(N_{\max}) &= b - a. \\ N_{\max} &= e^{(b/a-1)}. \end{aligned}$$

If we apply this to the Gompertz model for the mouse mammary tumor, then we find that the maximum occurs at the population

$$N_{\max} = e^{(9.399-1)} = 4,441(\times 10^6).$$

This value is substituted into the Gompertz growth function and gives the maximum growth of mouse mammary tumor cells as

$$G(N_{\max}) = 4441(0.4126 - 0.0439\ln(4441)) = 195.0(x10^6/\text{day}).$$

Example 4 *Ricker's Function*

Consider the Ricker's function $R(x) = 5xe^{-0.1x}$. (We will see this function in later population studies.) Let us sketch a graph of this function, finding all extrema and points of inflection.

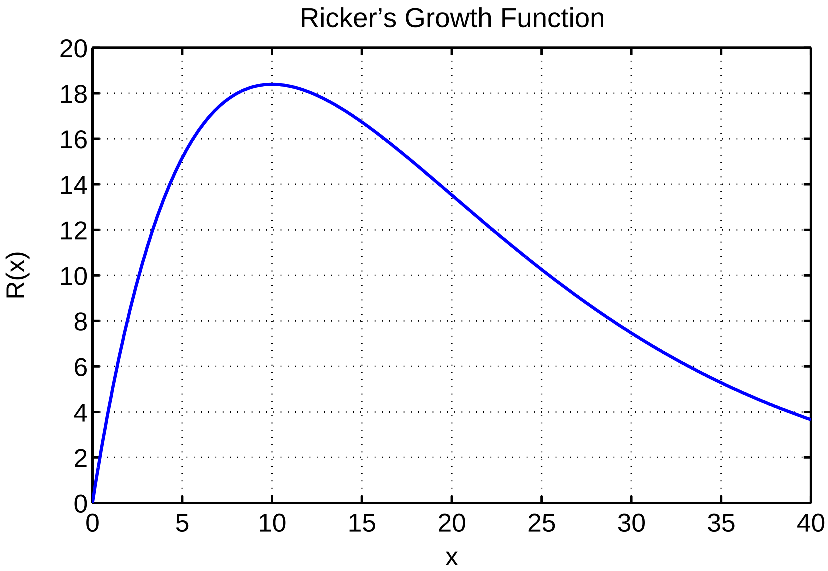

Figure 2: Graph of the Ricker's function of Example 4.

Solution: First we note that the only intercept is the origin, $(0, 0)$. Next we use the product rule to differentiate this function.

$$R'(x) = 5x(-0.1e^{-0.1x}) + 5e^{-0.1x} = 5e^{-0.1x}(1 - 0.1x).$$

Since the exponential function is never zero, $R'(x) = 0$ implies that the only critical point satisfies $1 - 0.1x = 0$ or $x = 10$. Thus, there is a maximum at $(10, 50e^{-1})$ or $(10, 18.4)$.

Next we take the second derivative or the derivative of $R'(x)$. Again we use the product rule to obtain

$$R''(x) = 5e^{-0.1x}(-0.1) + 5(-0.1)e^{-0.1x}(1 - 0.1x) = 0.5e^{-0.1x}(0.1x - 2).$$

The point of inflection is found by solving $R''(x) = 0$, which is very similar to our equation for the critical point. Its not hard to see that the point of inflection occurs at $x = 20$. Thus, there is a point of inflection at $(20, 100e^{-2})$ or $(20, 13.5)$. ◁

4 APPLICATIONS TO GRAPHING

One of the primary applications of the derivative is finding the critical points where minima and maxima occur, which aids in sketching a graph.

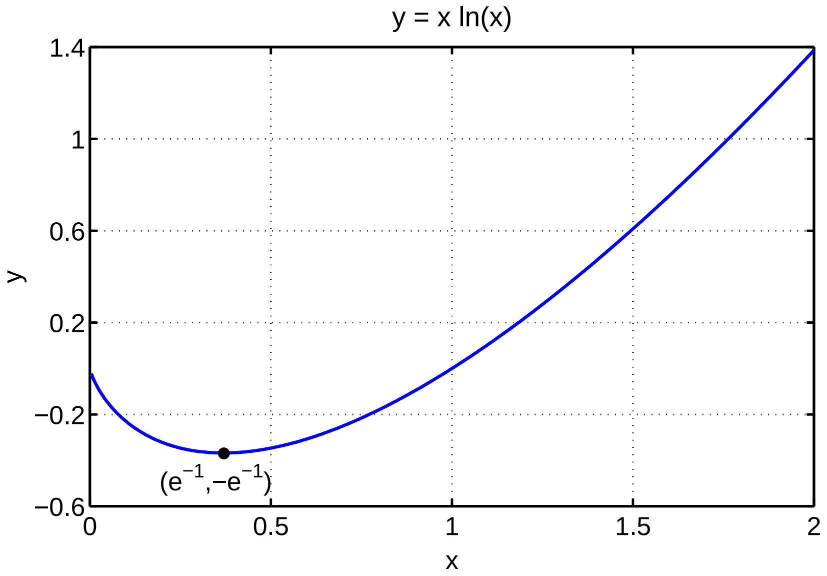

Figure 3: Graph of the function of Example 5.

Example 5 Consider the function given by

$$f(x) = x\ln(x).$$

Determine the domain of the function and find any intercepts. Find any critical points, then sketch the graph of $f(x)$ for $0 < x < 2$.

Solution: The domain of the function is $x > 0$. Thus, there is no y-intercept. However, it can be shown that the limit as x tends to 0 from the right is 0. (You can show this with your calculator, but proof of this result requires more advanced Calculus techniques.) The x-intercept is readily found by solving $f(x) = 0$, which gives $x = 1$.

To find the critical points we differentiate $f(x)$ and set it equal to zero, giving

$$f'(x) = x\left(\frac{1}{x}\right) + \ln(x) = 1 + \ln(x) = 0.$$

Thus, the critical value of x_c satisfies $\ln(x_c) = -1$ or $x_c = e^{-1} \approx 0.3679$. The function value at the critical point is $f(e^{-1}) = -e^{-1} \approx -0.3679$. Thus, there is a minimum on the graph at $(e^{-1}, -e^{-1})$. The graph of the function is seen in Figure 4. ◁

Example 6 Consider the function given by

$$f(x) = (2 - x)e^x.$$

Find the x and y-intercepts and any asymptotes. Find any critical points, then state if it is a local maximum or minimum. Sketch the graph of $f(x)$.

Solution: Since $f(0) = 2$, the y-intercept is $(0, 2)$. Since the exponential function is never zero, the x-intercept is easily seen to be $(2, 0)$. In the limit as x tends to $-\infty$, the exponential function goes to 0. An exponential function dominates any polynomial function (as seen in the computer lab earlier), so $f(x)$ goes to 0, which means that there is a horizontal asymptote to the left.

The critical points are found by differentiating $f(x)$ and setting it equal to zero, so

$$f'(x) = (2 - x)e^x + (-1)e^x = (1 - x)e^x = 0.$$

It is easy to see that the critical value of x_c is $x_c = 1$. The function value at the critical point is $f(1) = e^1 \approx 2.718$. Thus, there is a maximum on the graph at $(1, e)$. The graph of the function is seen in Figure 3. ◁

Example 7 *Tumor Growth*

Suppose the the growth of a tumor is given by the Gompertz growth function

$$G(W) = W(0.5 - 0.05\ln(W)),$$

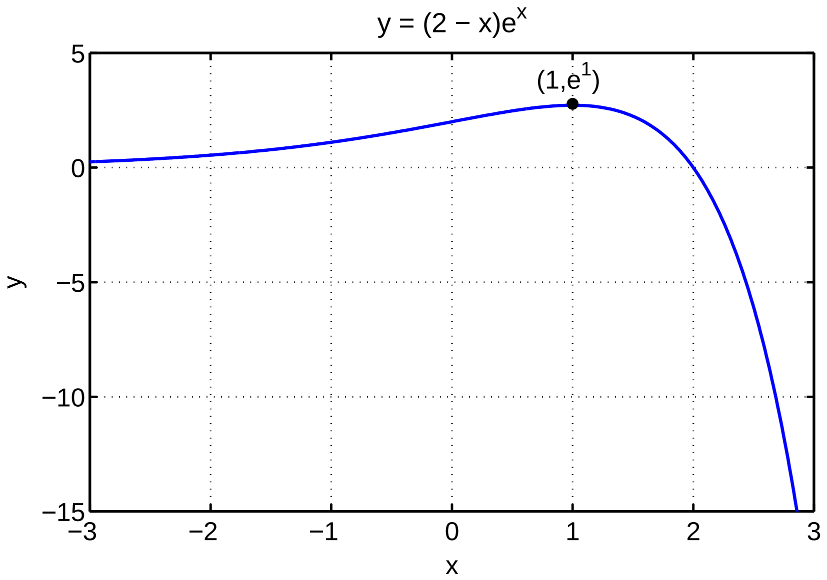

Figure 4: Graph of the function of Example 6.

where W is the weight of the tumor in mg and the time units are days. Find the equilibrium weight of the tumor. Find the maximum growth rate for this tumor, then sketch the graph of $G(W)$.

Solution: The equilibrium is found by solving $G(W)$ equal to zero, so

$$\begin{aligned} G(W) &= W(0.5-0.05\ln(W))=0, \\ 0.5-0.05\ln(W) &= 0, \\ \ln(W) &= 10 \\ W &= e^{10}=22,026 \text{ mg}. \end{aligned}$$

To find the maximum growth, we differentiate $G(W)$, so

$$\begin{aligned} G'(W) &= W(-0.05(1/W)+(0.5-0.05\ln(W)), \\ &= 0.45-0.05\ln(W)=0. \end{aligned}$$

Thus,

$$\begin{aligned} \ln(W) &= 9, \\ W &= e^{9}=8,103 \text{ mg}. \end{aligned}$$

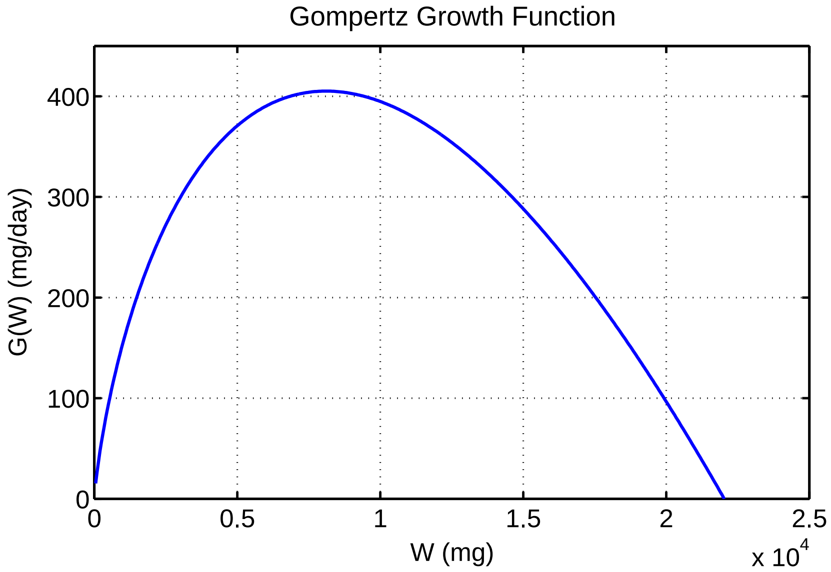

Figure 5: Graph of the tumor growth function of Example 7.

with a maximum growth rate of

$$G(8,103) = 8,103(0.5 - 0.05\ln(8,103)) = 405.2\text{mg/day}.$$

Figure 5 is a graph of this function. ◁

5 EXERCISES

Find the derivatives of the following functions:

1. $f(x) = (x^3 - 3x^2 + 7)(x^4 - 2x^2 + 6x - 1)$,
2. $f(x) = (x^2 - e^{2x} + 1)(3x + 8)$,
3. $f(x) = x^2 e^{-x} + 21\sqrt{x}$,
4. $f(x) = \dfrac{1}{x^2}\ln(x) - e^{2x}(x^2 - 1)$.

Find the derivative and sketch the curves of the functions below. Give the domain of each of the functions. List all maxima and minima for each graph. Also, give the x and y-intercepts and any asymptotes if they exist.

5. $y = 3xe^{-0.02x}$, 6. $y = (x-2)e^{-x}$,

7. $y = \frac{1}{x}\ln(x)$, 8. $y = (x^2-3)e^x$,

9. $y = x^2\ln(x)$.

10. Many biologists in fishery management use Ricker's model to study the population of fish. Let P_n be the population of fish in any year n, then Ricker's model is given by

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

Suppose that the best fit to a set of data gives $a = 5$ and $b = 0.004$ for the number of fish sampled from a particular river.

a. Let $P_0 = 100$, then find P_1, P_2, and P_3.

b. Sketch a graph of R(P) with the identity function, showing the intercepts, all extrema, and any asymptotes.

c. Find all equilibria of the model and describe the behavior of these equilibria.

11. Repeat Exercise 10 with $a = 8$ and $b = 0.002$

12. In fishery management, it is important to know how much fishing can be done without severely harming the population of fish. A modification of Ricker's model that includes fishing is given by the model:

$$P_{n+1} = F(P_n) = aP_ne^{-bP_n} - hP_n,$$

where $a = 4$ and $b = 0.002$ are the constants in Ricker's equation that govern the dynamics of the fish population without any fishing and h is the intensity of harvesting fish.

a. Let $h = 0.5$ and $P_0 = 100$, then find P_1, P_2, and P_3.

b. With $h = 0.5$, find all equilibria for this model and describe the behavior of these equilibria.

c. Find all equilibria for this model and describe the behavior of these equilibria when $h = 1$ and $h = 2$.

d. How intense can the fishing be before this population of fish is driven to extinction? That is, find the value of h that makes the only equilibrium be zero (or less than zero).

13. When coughing, the windpipes contract to increase the velocity of air passing through the windpipe to help clear mucus. The velocity, v, at which the air flows through the windpipe depends on the radius, r of the windpipe. If R is the resting radius of the windpipe, then the velocity of air passing

through the windpipe satisfies:

$$v(r) = Ar^2(R - r),$$

where A is a constant dependent on the strength of the diaphram muscles. Find the value of r that maximizes the velocity of air and determine the velocity of the air flowing through the windpipe.

6 REFERENCES

[1] A.K. Laird, Dynamics of tumor growth, *Brit. J. Cancer* (1964) **18**, 490–502.

[2] L. Simpson-Herren and H.H. Lloyd, Kinetic parameters and growth curves for experimental tumor systems, *Cancer Chemother. Rep. Part I* (1970) **54**, 143–174.

CHAPTER 16:

QUOTIENT RULE

In this section, we examine the kinetics of hemoglobin molecules for carrying O_2 to the cells of the body. A quotient rule is developed to examine the maximum rate of change in O_2 affinity. In earlier sections, we studied graphing of rational functions, but had no techniques for finding critical points. The ability to find the derivatives of rational functions allows locating minima and maxima of these functions.

1 HEMOGLOBIN AFFINITY FOR O_2

Hemoglobin is the most important molecule in our erythrocytes (red blood cells). For mammals, this very important compound has evolved to carry O_2 from the lungs to the tissues and remove CO_2 from the tissues back to the lungs. For adult humans, the hemoglobin molecule consists almost exclusively of two α and two β polypeptide chains (there are other types of peptide chain such as γ in fetal blood). Each polypeptide chain contains a porphyrin ring with iron near the active binding site. The four polypeptide chains fold into a quaternary structure that has evolved to very efficiently bind up to four molecules of O_2. A single mutation causes the disease sickle cell anemia, where structure of one β chain is varied and distorts the binding efficiency, so O_2 transport is diminished.

Oxygen is key to efficient metabolism and is required by all of our cells. The hemoglobin molecule takes advantage of *cooperative binding* to effectively load and unload O_2 molecules from the blood to the cells in the tissues. In cooperative binding, the binding of one molecule facilitates the binding of one or more other molecules by causing structural changes to the protein. Cooperative binding plays a role in many biochemical processes where a steep dissociation curve is needed in the equilibrium kinetics. This cooperative binding results in a variant form of the Michaelis-Menten velocity curve (5) that we studied in an earlier section and takes on a characteristic *S-shape* that results in a protein having more of an on/off function in its kinetic properties. The steepness in the dissociation curve is needed for effective O_2 exchange. Where the dissociation curve is steep, a small partial pressure difference in the concentration of O_2 results in easy unloading of

O_2 at the tissues. In the lungs, the O_2 readily loads onto the hemoglobin molecules, while a different dissociation curve allows the removal of CO_2.

Oxygen affinity of hemoglobin is important in understanding the gas-transport properties of this molecule. Ranney and Sharma (see Figure 6) give the kinetic dissociation curve for hemoglobin under a variety of conditions. Typical of most kinetic reactions, the dissociation curve for hemoglobin is highly sensitive to pH, temperature, and other factors. Oxygen affinity is usually expressed by a dissociation function that measures the percent of hemoglobin in the blood saturated with O_2 as a function of the partial pressure of O_2. (The partial pressure of O_2 is often measured in torrs where 100 torrs is the atmospheric concentration of O_2.) The fraction of hemoglobin saturated with O_2 satisfies the function

$$y(P) = \frac{P^n}{K + P^n}.$$

where y is the fraction of hemoglobin saturated with O_2 and P is the partial pressure of O_2 measured in torrs. The Hill coefficient is n in the expression above, representing the number of molecules binding to the protein, while K is the binding equilibrium constant. Typically, hemoglobin shows a nonlinear form that has a Hill coefficient of $2.7 - 3.2$ though it can bind cooperatively up to 4 molecules of O_2. Under conditions typical of blood, experimental measurements show that the values of n and K are 3 and $19,100$, respectively. In Figure 1 we see a graph of this O_2 saturation curve.

Where the dissociation curve is steepest, the O_2 binds and unbinds to hemoglobin over the narrowest changes in partial pressure of O_2. This allows the most efficient exchange of O_2 in the tissues. That is, when a tissue is low in O_2, then the hemoglobin in the blood is more likely to have its O_2 dissociate and diffuse into the O_2 depleted cell. This steepest part of the dissociation curve is where the derivative is at its maximum. Clearly, evolution is likely to choose an animal that has hemoglobin with a dissociation curve that matches the steepest part of the curve to the existing partial pressure of O_2 near the tissues. For our dissociation curve given above, we want to find where the derivative is largest. This corresponds to the point of inflection for this curve. Since the curve is defined by a rational function, we need to develop a *quotient rule* to find its derivative.

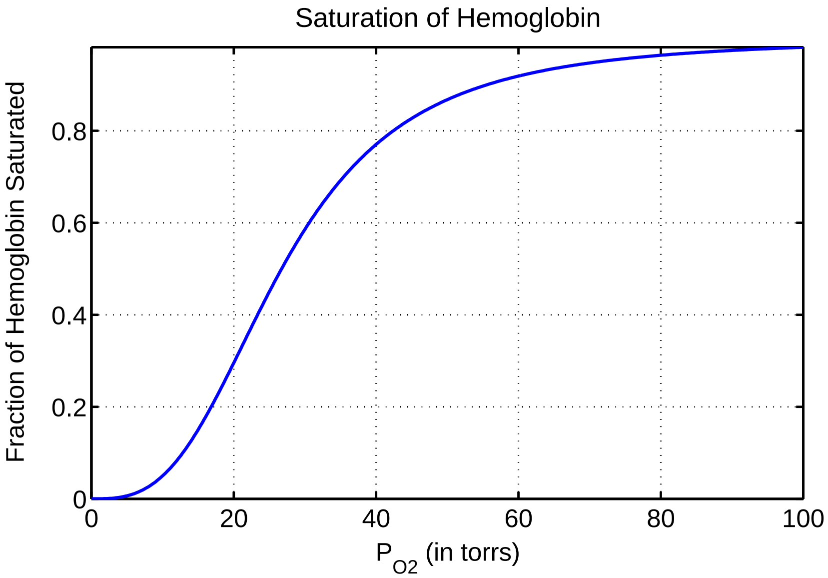

Figure 1: Graph of the fraction of saturated hemoglobin (y) *vs.* the O_2 partial pressure (P).

2 QUOTIENT RULE

Let $f(x)$ and $g(x)$ be two differentiable functions. The *quotient rule* for finding the derivative of the quotient of these two functions is given by:

$$\frac{d}{dx}\left(\frac{f(x)}{g(x)}\right) = \frac{g(x)f'(x) - f(x)g'(x)}{[g(x)]^2}.$$

where $f'(x)$ and $g'(x)$ are the derivatives of the respective functions.

In words, the quotient rule says that the derivative of the quotient is"the bottom times the derivative of the top minus the top times the derivative of the bottom all over the bottom squared."

Example 1 *Rational Function*

Suppose we want to study the function

$$f(x) = \frac{x^2 - 2x + 1}{x^2 - x - 2}.$$

We can apply the quotient rule to this function to find its derivative. We obtain

$$f'(x) = \frac{(x^2 - x - 2)(2x - 2) - (x^2 - 2x + 1)(2x - 1)}{(x^2 - x - 2)^2} = \frac{x^2 - 6x + 5}{(x^2 - x - 2)^2}.$$

For graphing this function, we would like to find intercepts, asymptotes, and extrema. The y-intercept is given by $y = f(0) = -1/2$. The x-intercept is found by solving $f(x) = 0$. This is solved by setting the numerator equal to zero, but

$$x^2 - 2x + 1 = (x - 1)^2 = 0,$$

which gives the x-intercept as $x = 1$.

The vertical asymptotes are found finding when the denominator is zero, so

$$x^2 - x - 2 = (x + 1)(x - 2) = 0.$$

This gives the vertical asymptotes $x = -1$ and $x = 2$. The horizontal asymptote is found by looking at $f(x)$ for large values of x. The largest exponents in the numerator are both 2, so for large x, $f(x)$ behaves like $x^2/x^2 = 1$, which gives the horizontal asymptote $y = 1$.

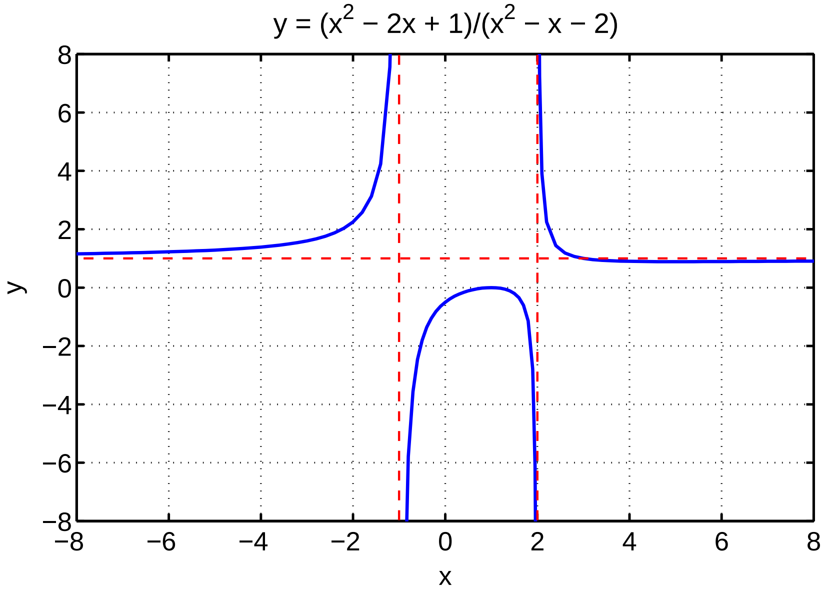

Figure 2: Graph of the function of Example 1.

The critical points are found by setting the derivative equal to zero, which again requires setting the numerator equal to zero. Thus,

$$x^2 - 6x + 5 = (x-1)(x-5) = 0.$$

Thus, the critical points are $x_c = 1$ and $x_c = 5$. Evaluating the function $f(x)$ at these critical points, and we find a local maximum at $(1,0)$ and a local minimum at $(5, 8/9)$. A graph of this function is seen in Figure 2. ◁

Example 2 *Differentiate Functions*

1. Differentiate the following function:

$$f(x) = \frac{x}{x^2+1}.$$

Solution: Applying the quotient rule:

$$f'(x) = \frac{(x^2+1)\cdot 1 - x \cdot 2x}{(x^2+1)^2} = \frac{1-x^2}{(x^2+1)^2}.$$

2. Differentiate the following function:

$$g(x) = \frac{20e^{0.1t}}{50+e^{0.1t}}.$$

Solution: The quotient rule is applied giving:

$$g'(x) = \frac{(50+e^{0.1t})2e^{0.1t} - 20e^{0.1t}\cdot 0.1e^{0.1t}}{(50+e^{0.1t})^2} = \frac{100e^{0.1t}}{(50+e^{0.1t})^2}.$$

◁

Example 3 *Graphing a Rational Function*

Consider the function:

$$f(x) = \frac{x^2-6x+9}{x-2}.$$

Differentiate this function. Find all intercepts, asymptotes, and extrema. Graph the function.

Solution: The quotient rule for differentiation is applied to $f(x)$ yielding

$$f'(x) = \frac{(x-2)(2x-6) - (x^2-6x+9)\cdot 1}{(x-2)^2} = \frac{x^2-4x+3}{(x-2)^2}.$$

The y-intercept is given by $y = f(0) = -9/2$. The x-intercept is found by solving $f(x) = 0$. This is solved by setting the numerator equal to zero, but

$$x^2 - 6x + 9 = (x-3)^2 = 0,$$

which gives the x-intercept as $x = 3$.

The vertical asymptotes occur when the denominator is zero, so there is a vertical asymptote at $x = 2$. There are no horizontal asymptotes as the power of the numerator exceeds the power of the denominator.

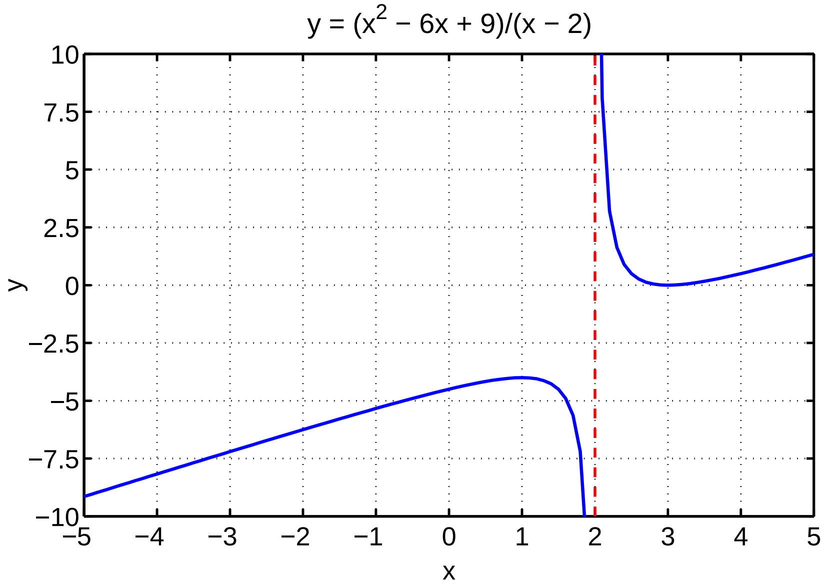

Figure 3: Graph of the function of Example 3.

The critical points are found by setting the derivative equal to zero, which again requires setting the numerator equal to zero. Thus,

$$x^2 - 4x + 3 = (x - 1)(x - 3) = 0.$$

Thus, the critical points are $x_c = 1$ and $x_c = 3$. Evaluating the function $f(x)$ at these critical points, we find a local maximum at $(1, -4)$ and a local minimum at $(3, 0)$. A graph of this function is seen in Figure 3. ◁

Example 4 *Genetic Control*

In 1960, Jacob and Monod won a Nobel prize for their theory of *induction* and *repression in genetic control.* Many metabolic pathways in cells use endproduct repression of the gene or negative feedback to control important biochemical substances, such as the enzymatic pathways for production of amino acids. When sufficient quantities of a particular substance, such as an amino acid, the cell shuts down the pathway that produces that substance to avoid unnecessary build up of the substance. From biochemical kinetics, it can be shown that production of a substance x satisfies a rate function of the following form:

$$R(x) = \frac{a}{K + x^n}.$$

Consider the specific rate function given by

$$R(x) = \frac{90}{27 + x^2}.$$

Differentiate this rate function. Sketch a graph of this rate function and its derivative. Find all intercepts, any asymptotes, and any extrema for the rate function and its derivative. When is the rate function decreasing most rapidly?

Solution: The rate function has an R-intercept, $R(0) = 90/27 = 10/3$. There is a horizontal asymptote of $R = 0$, since the power of the denominator exceeds that of the numerator. From the quotient rule, the derivative satisfies

$$R'(x) = \frac{(27 + x^2)0 - 90(2x)}{(27 + x^2)^2} = \frac{-180x}{(27 + x^2)^2}.$$

For $x > 0$, the derivative of the rate function is negative, so this is decreasing. There is clearly a maximum at $x = 0$. (A rate function does not make sense for $x < 0$. Figure 4 shows a graph of the rate function.

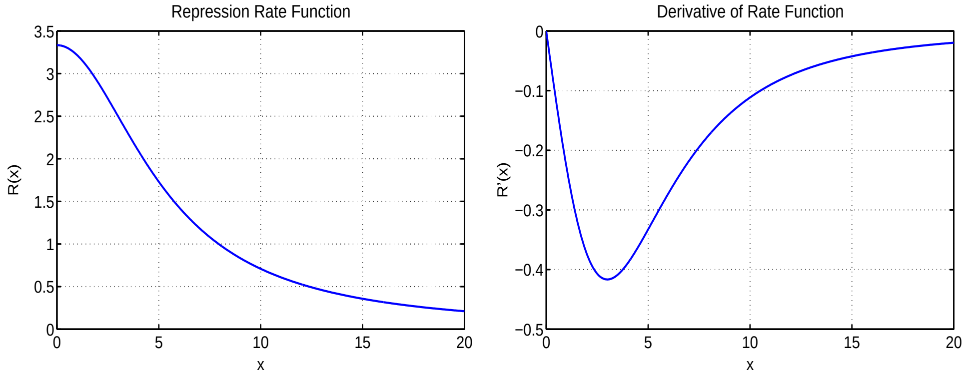

Figure 4: Left: Graph of the rate function for the *Repression in genetic control* of Example 4. Right: Graph of the derivative of this rate function.

The derivative has an intercept at $(0, 0)$ and also has a horizontal asymptote $R' = 0$. To find any extrema of the derivative function, we find the second derivative. Since the derivative can be written,

$$R'(x) = \frac{-180x}{27x^2 + 54x^2 + x^4}.$$

The second derivative is given by

$$R''(x) = \frac{-180(27^2 + 54x^2 + x^4) + 180x(108x + 4x^3)}{(27^2 + 54x^2 + x^4)^2} = \frac{540(x^2 - 9)}{(27 + x^2)^3}.$$

where some algebra is required for the last quantity. Clearly, this second derivative is zero when $x = 3$ ($x = -3$ is outside the domain). Thus, $R'(x)$ has a minimum at $(3, -5/12)$. A graph of the derivative of the repression rate function is given in Figure 4.

It follows that the original rate function is decreasing most rapidly at $x = 3$. ◁

3 DISSOCIATION CURVE FOR HEMOGLOBIN

The dissociation curve for O_2 with hemoglobin is shown in Figure 1. The specific function that was graphed was

$$y(P) = \frac{P^3}{19,100 + P^3}.$$

We want to determine the partial pressure of O_2 that results in the steepest part of the curve above. To find the slope of the curve, we compute the derivative using the quotient rule. The derivative satisfies

$$\begin{aligned} y'(P) &= \frac{3P^2(19,100 + P^3) - P^3(3P^2)}{(19,100 + P^3)^2} \\ y'(P) &= \frac{57,300P^2}{(19,100 + P^3)^2}. \end{aligned}$$

Figure 5 is the graph of this derivative We can see that the maximum derivative occurs at about $P_{O2} = 21$ torrs. To find the exact value of the maximum derivative, we compute the second derivative and set it equal to zero. The second derivative is given by

$$\begin{aligned} y''(P) &= \frac{114,600P(19,100^2 + 38,200P^3 + P^6) - 57,300P^2(114,600P^2 + 6P^5)}{(19,1002^2 + 38200P^3 + P^6)^2} \\ y''(P) &= \frac{-229,200P(P^3 - 9,550)}{(19,100 + P^3)^3}. \end{aligned}$$

The last expression requires some algebra or Maple to derive from the first. The second derivative is equal to zero when either $P = 0$ or $9550^{1/3} = 21.22$. Thus, the point of inflection, which is where the derivative is at a maximum, occurs at $P = 21.22$ with $y(P) = 0.333$ or about $1/3$ of the

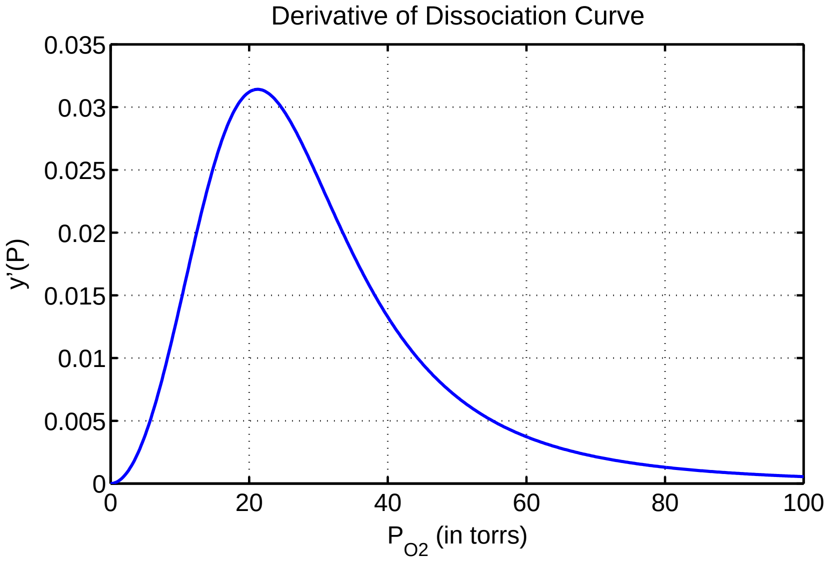

Figure 5: Graph of the derivative of the Dissociation function given in Figure 1.

hemoglobin is saturated by O_2.

4 MITOTIC MODEL

Multicellular organisms begin with exponentially growing cell populations (recall Chapter 7), but soon must regulate this cell growth to develop particular patterns and shapes and differentiate their cells into organs with specific functions. The adult organism maintains a fairly constant number of cells, which means that cells must recognize whether or not there is a need to divide, a process known as *mitosis*. Cancer is often the breakdown of this control, with cells dividing when they normally would not. One significant question that has yet to be adequately answered is how a cell, such as a skin cell, recognizes its neighboring environment of other cells and knows whether or not it should divide. (A skin cell obviously needs to undergo mitosis when either wear or damage of the skin requires replacement cells.)

The *regulation of mitosis* is a very important biological process that is currently being studied extensively. This research tries to understand how cells determine when they should undergo mitosis. One controversial biochemical theory developed in the late 1960s was that cells communicated with neighboring cells by *tissue-specific inhibitors* known as *chalones* (see

Figure 6). The chalones are released by cells and diffuse in the environment to affect the cells nearby. If there are sufficient quantities of these chalones, then cells are inhibited from undergoing mitosis.

One of the proposed mechanisms is that chalones bind specifically to certain proteins involved in mitosis. The chalones inactivate the mitotic proteins, leaving the cell in a quiescent state. This inhibition process of effector molecules binding to a protein is often modeled using a *Hill function* with a special rational form. Let P_n represent a certain cell density at a particular time n, then an appropriate mathematical model for the cell density at the next time period (P_{n+1}) that considers the mitotic divisions and cell loss that are dependent on the cellular density with inhibition due to crowding is given by the following equation:

$$P_{n+1} = f(P_n) = \frac{2P_n}{1 + (bP_n)^c},$$

where b and c are parameters that are fit to data based on chalone kinetics. The function $f(P_n)$ is known as an *updating function*, which will be studied in more detail in a future section. Notice that when the cell density P_n is very low, then the denominator of the model is insignificant. This gives the equation $P_{n+1} = 2P_n$, so for low density the population doubles in each time period, using a standard discrete Malthusian growth model learned in Chapter 7.

Let us study the specific mitotic model given by the equation

$$P_{n+1} = f(P_n) = \frac{2P_n}{1 + (0.01P_n)^4} = \frac{2P_n}{1 + 10^{-8}P_n^4}.$$

We would like to determine what the cell density is at equilibrium, which is when the cell density remains constant for all time intervals. Thus, the new cells produced match the numbers that are lost in a given time interval. In addition, we would like to graph the updating function $f(P_n)$ and give some biological interpretations of the graph.

4.1 EQUILIBRIA OF THE MITOTIC MODEL

At equilibrium, the population density is the same at all time intervals. Thus, $P_{n+1} = P_n = P_n$, which when substituted into the equation above gives

$$\begin{aligned} P_e &= \frac{2P_e}{1+10^{-8}P_e^4} \\ P_e(1+10^{-8}P_e^4) &= 2P_e \\ P_e(10^{-8}{P_e}^4-1) &= 0. \end{aligned}$$

Thus, either $P_e = 0$ or $P_e = 100$. The first equilibrium is when the trivial equilibrium when no cells exist, while the second equilibrium would ideally be the preferred density of cells in a particular tissue.

4.2 GRAPHING THE MITOTIC UPDATING FUNCTION

To study the graph of $f(P_n)$, we examine the intercepts, asymptotes, and any extrema. Clearly, the only intercept is $(0,0)$, passing through the origin. The denominator is always positive, so there are no vertical asymptotes. We also see that the power of P_n in the denominator is 4, which exceeds the power of P_n in the numerator. For P_n sufficiently large, as P_n increases, the denominator increases more rapidly than the numerator, so there is a horizontal asymptote at $y = 0$.

To find any extrema, we differentiate $f(P_n)$, which gives

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

Setting this derivative equal to zero, we have

$$\begin{aligned} 2-6\times 10^{-8}P_n^4 &= 0 \\ P_n^4 &= \frac{1}{3}\times 10^8 \\ P_n &= 75.98. \end{aligned}$$

It follows that the maximum of the updating function occurs at $(75.98, 113.98)$. In Figure 6 we see a graph of the updating function.

The graph above shows that the greatest production of cells occurs at a cell density of 75.98, then it declines fairly rapidly. At a cell density of $P_n = 100$, the production equals the number dying so the model is at equilibrium. If one were to have a fairly high density, then this model would predict a toxic effect from the crowding, resulting in a major die-off so that the next time period would have a very low density. This model is clearly

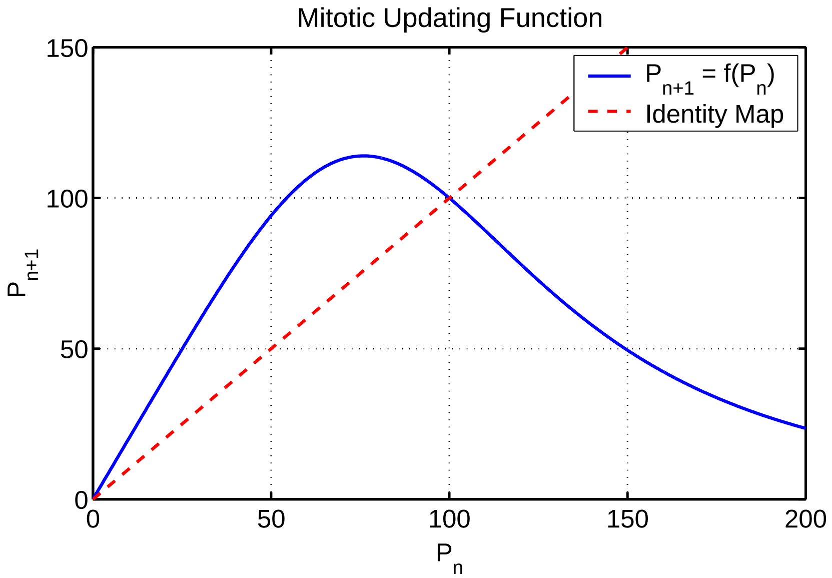

Figure 6: Graph of the updating function of the *Mitotic* example, including the identity map, which will later be shown to be important in computing equilibria.

very simplistic, but it does demonstrate some of the important concepts behind *biochemical inhibition*.

5 EXERCISES

Find the derivatives of the following functions:

1. $f(x) = \dfrac{x^3 - \ln(x)}{1 - x^2} + \dfrac{2}{x^2}$, 2. $f(x) = \dfrac{x^2 - e^{-x}}{3x+1} + xe^{-x}$,

3. $f(x) = \dfrac{\sqrt{x}}{2+x} - \dfrac{1}{e^{3x}}$, 4. $f(x) = \dfrac{x^2+5}{x^2 - e^x} - \dfrac{xe^{2x}}{2x+1}$.

Find the derivative and sketch the curves of the functions below. Give the domain of each of the functions. List all maxima and minima for each graph. Also, give the x and y-intercepts and any asymptotes if they exist.

5. $y = \dfrac{x^2}{x+1}$, 6. $y = \dfrac{e^x}{x+1}$,

7. $y = \dfrac{x^2 - 2x + 2}{x - 1}$, 8. $y = \dfrac{x^2}{x^2+1}$,

9. Consider the chalone model for mitosis given by the equation

$$P_{n+1} = f(P_n) = \frac{2P_n}{1+(bP_n)^c},$$

where $b = 0.05$ and $c = 2$.

a. Let $P_0 = 10$, then find P_1, P_2, and P_3.

b. Sketch a graph of $f(P)$ with the identity function for $P \geq 0$, showing the intercepts, all extrema, and any asymptotes.

c. Find all equilibria of the model and describe the behavior of these equilibria.

10. Repeat Exercise 9 with $b = 0.02$ and $c = 5$.

11. Some entomologists use Hassell's model for studying the population of insects. Let P_n be the population of a species of beetle in week n and suppose that Hassell's model is given by

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

Suppose that the best fit to a set of data gives $a = 5$ and $b = 0.004$ for this species of beetle.

a. Let $P_0 = 100$, then find P_1, P_2, and P_3.

b. Sketch a graph of $H(P)$ with the identity function for $P \geq 0$, showing the intercepts and any asymptotes.

c. Find all equilibria of the model and describe the behavior of these equilibria.

6 REFERENCES

[1] W.S. Bullough and E.B. Laurence, Chalones and cancer, *Nature.* (1968), **220**, 134–135.

[2] H.M. Ranney and V. Sharma, Structure and function of hemoglobin, in *Willliam's Hematology*, eds. E. Beutler, M.A. Lictman, B.S. Coller, T.J. Kipps, 5th Edition. (1995), 417–425.

CHAPTER 17:

CHAIN RULE

In biology, there are often functional relationships where one measurable quantity depends on another, while the second quantity is a function of a third quantity. The first example below connects some of the ideas from previous sections on height and weight of girls, then creates a composite function to find the rate of change of weight with respect to age. This functional relationship uses composite functions. The differentiation of a composite function requires a special rule for differentiation, the *chain rule*.

1 AVERAGE HEIGHT AND WEIGHT OF GIRLS

In the first chapter of the book , we found that over a range of ages the rate of growth of girls in height remained relatively constant. That is, the relationship between height and age was approximated fairly well by a linear function. In the allometric chapter, we saw that there is a power law relationship height and weight of animals, so one would predict that a power law might work reasonably well for girls. Table 1 has both, heights and weights for average American girls between the ages of 1 and 13.

The height as a function of age is graphed in the left panel of Figure 1 with the least squares best fit straight line for the data of Table 1 given by

$$h(a) = 6.45a + 73.9.$$

As noted in Chapter 2, this equation shows that the average girl grows about 6.45 cm/yr. The relationship between the height and weight of a girl satisfies an allometric model as we saw on Chapter 6. The average weight of a girl is plotted against her height in the right panel of Figure 1 and fitted by the best allometric model through the data. The best equation is given by

$$W(h) = 0.000720h^{2.17}.$$

With this information, we would like to connect these formulae and determine the rate of change in weight for a girl at any particular age (between 1 and 13). We will create a composite function to give the weight as a function of age, then use the chain rule to find the rate of change of weight with

age(years)	height(cm)	weight(kg)
1	75	9.5
2	87	11.8
3	94	15.0
4	102	15.9
5	108	18.2
6	114	20.0
7	121	21.8
8	126	25.0
9	132	29.1
10	138	32.7
11	144	37.3
12	151	41.4
13	156	46.8

Table 1: Heights and weights of average American girls between ages 1 and 13.

respect to age.

2 CHAIN RULE

Consider the *composite function* $f(g(x))$. Suppose that both $f(u)$ and $u = g(x)$ are differentiable functions. The *chain rule* for differentiation of this composite function is given by

$$\frac{df}{dx} = \frac{df}{du}\frac{du}{dx}.$$

Another useful form of the chain rule is the differentiation formula given by

$$\frac{d}{dx}(f(g(x))) = f'(g(x))g'(x).$$

Example 1 *Polynomial Function*

Consider the function

$$h(x) = (x^2 + 2x - 5)^5.$$

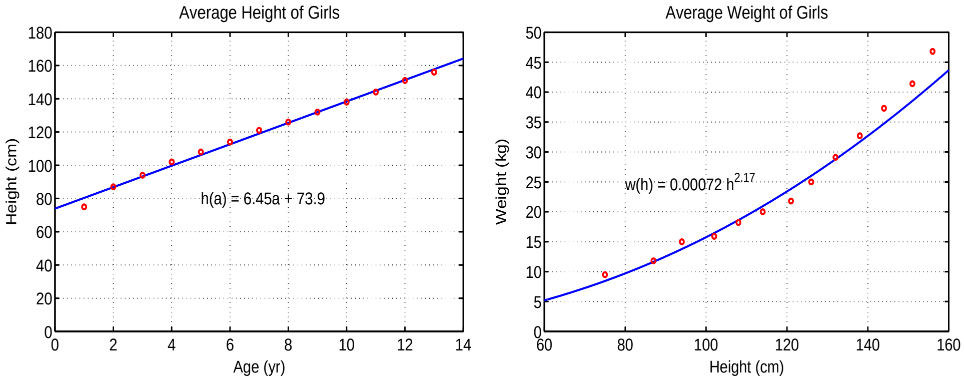

Figure 1: Left: Graph for the least squares best fit for the height of the average American girl given in Table 1. Right: Graph of the weight as a function of height, $W(h) = 0.000720h^{2.17}$ with data from Table 1.

Find $h'(x)$.

Solution: This can be considered a composite of the function $f(u) = u^5$ and the function $g(x) = x^2 + 2x - 5$. It is easy to find the derivatives of both f and g. We have

$$\begin{aligned} f'(u) &= 5u^4u'\text{and} \\ g'(x) &= 2x + 2. \end{aligned}$$

From the formula above, we see that

$$h'(x) = 5(g(x))^4(2x + 2) = 5(x^2 + 2x - 5)^4(2x + 2). \qquad \triangleleft$$

Example 2 *Algebraic and Non-algebraic functions*

1. Differentiate the following function:

$$f(x) = (x^3 - 4x^2 + e^{-2x})^6.$$

Solution: The function $f(x)$ can be considered a composite of the function

$$f_1(u) = u^6$$

and the function

$$f_2(x) = x^3 - 4x^2 + e^{-2x}.$$

It is easy to find the derivatives of both f_1 and f_2. We have

$$\begin{aligned} f_1'(u) &= 6u^5u' \\ f_2'(x) &= 3x^2 - 8x - 2e^{-2x}. \end{aligned}$$

From the chain rule, we see that

$$\begin{aligned} f'(x) &= 6(f_2(x))^5 f_2'(x) \\ f'(x) &= 6(x^3 - 4x^2 + e^{-2x})^5(3x^2 - 8x - 2e^{-2x}). \end{aligned}$$

2. Consider the function

$$h(x) = e^{2-x^2}.$$

Find $h'(x)$.

Solution: This can be considered a composite of the function $f(u) = e^u$ and the function $g(x) = 2 - \mathbf{x^2}$. The derivatives of f and g are

$$f'(u) = e^u u^4 \text{ and } g'(x) = -2x.$$

From the formula above, we see that

$$h'(x) = e^{2-x^2}(-2x).$$

3. Differentiate the following function:

$$g(x) = (4x + \ln(x^4 + 4x^2 + 1))^4.$$

Solution: To analyze the function $g(x)$, we have a couple of composite functions to consider. Let the functions

$$\begin{aligned} g_1(u) &= u^4 \\ g_2(x) &= 4x + \ln(h_2(x)). \end{aligned}$$

Then the chain rule first gives $g_1'(u) = 4u^3u'$ or

$$g'(x) = 4(g_2(x))^3 g_2'(x) = 4(4x + \ln(x^4 + 4x^2 + 1))^3 g_2'(x).$$

To find the derivative of $g_2(x)$, we need to differentiate the composite $h(x) = h_1(h_2(x))$, where

$$h_1(v) = \ln(v) \text{ with } h_1'(v) = (1/v)v'$$

and,

$$h_2(x) = x^4 + 4x^2 + 1 \text{ with } h_2'(x) = 4x^3 + 8x,$$

so

$$h'(x) = h_1'(h_2(x))h_2'(x) = \frac{h_2'(x)}{h_2(x)} = \frac{4x^3 + 8x}{x^4 + 4x^2 + 1}.$$

But $g_2'(x) = 4 + h'(x)$. So combining the results above, we see that

$$g'(x) = 4(4x + \ln(x^4 + 4x^2 + 1))^3 \left(4 + \frac{4x^3 + 8x}{x^4 + 4x^2 + 1}\right). \qquad \triangleleft$$

3 RATE OF CHANGE IN WEIGHT

From the data above, we found that the weight W as a function of height h is given by

$$W(h) = 0.000720h^{2.17}.$$

while the height as a function of age is

$$h(a) = 6.45a + 73.9.$$

Because the height is a linear function the rate of change of height with respect to age is the constant 6.45 cm/yr. We will use the chain rule to find the rate of change of weight with respect to age, then graph both the weight as a function of age and the rate of change of weight as a function of age.

Writing weight as a composite function, we have

$$W(a) = 0.000720(6.45a + 73.9)^{2.17}.$$

The left panel in Figure 2 shows a graph of this function with the data of Table 1.

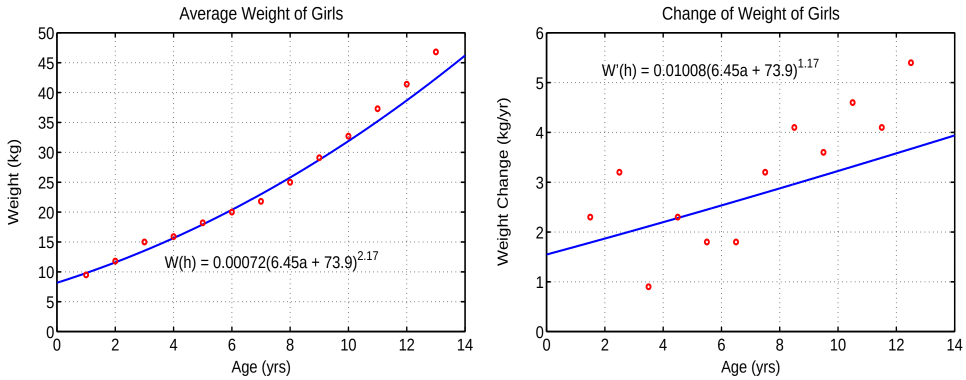

Figure 2: Left: Graph of the function for the average American girl weight given by $W(a) = 0.000720(6.45a + 73.9)^{2.17}$ and the data of Table 1. Right: Graph for the derivative of the average American weight function.

By the chain rule, the derivative of the weight function is given by

$$\frac{dW}{da} = \frac{dW}{dh}\frac{dh}{da},$$

with

$$\frac{dW}{dh} = 2.17(0.000720)h^{1.17} \text{ and } \frac{dh}{da} = 6.45.$$

Combining these and substituting the expression for h, we see that

$$W'(a) = 0.01008(6.45a + 73.9)^{1.17}.$$

The right panel of Figure 2 shows a graph of the derivative giving the rate of change in weight with respect to age. This graph is almost linear, since it is to the 1.17 power. The actual average weight changes are given for the data above. We see that the model underpredicts the weight gain for older girls.

4 MORE APPLICATIONS

Example 3 *The Bell Curve*

An important function in statistics is the normal distribution function, which classically gives the *Bell curve.* A normal distribution function is given by

$$N(x) = \frac{a}{\sigma}\exp\left(-\frac{x^2}{2\sigma^2}\right).$$

where a is a normalizing factor and σ is the standard deviation. We would like to find the points of inflection for this curve and determine its significance. Also, plot this function for several values of σ.

Solution: To find the points of inflection, we need to take the derivative twice. Its clear that this is an even function, and that its maximum occurs at $x = 0$ with $N(0) = a/\sigma$. We take the first derivative of $N(x)$ and obtain

$$N'(x) = \frac{a}{\sigma}\exp\left(-\frac{x^2}{\sigma^2}\right)\cdot(-x/\sigma^2) = -\frac{ax}{\sigma^3}\exp\left(-\frac{x^2}{\sigma^2}\right).$$

Note that $N'(x) = 0$ at $x = 0$, as expected.

The second derivative requires the product rule along with the chain rule. The result is given by

$$\begin{aligned} N''(x) &= -\frac{a}{\sigma^3}\left(x\cdot(-x/\sigma^2)\exp\left(-\frac{x^2}{\sigma^2}\right)+\exp\left(-\frac{x^2}{\sigma^2}\right)\cdot 1\right) \\ &= \frac{a}{\sigma^3}\left(\frac{x^2}{\sigma^2}-1\right)\exp\left(-\frac{x^2}{\sigma^2}\right). \end{aligned}$$

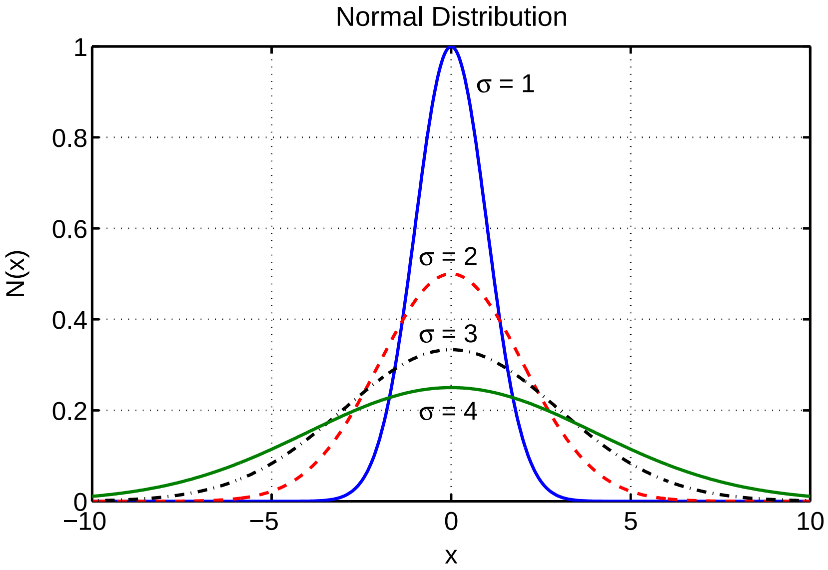

Figure 3: Graphs of the *Normal Distribution* curves for different values of σ.

The points of inflection occur when $N''(x) = 0$, which is easily seen to be when either $x = -\sigma$ or $x = \sigma$. Thus, the points of inflection occur one standard deviation out the normal distribution function. It turns out that 68% of the area under the normal distribution occurs in the interval $-\sigma < x < \sigma$. In Figure 3 we show a graph of the normal distribution with $\sigma = 1, 2, 3,$ and 4. ◁

Example 4 *Hassell's Model*

In the product rule section, we learned that Ricker's model is often used by fisheries to study fish populations. Entomologists often use Hassell's model to study the dynamics of insect populations. We will examine the dynamics of this model in more detail later. For this example, we will simply find equilibria and graph the updating function. Suppose that a study shows that a population, P_n, of butterflies satisfies the dynamic model given by the following equation:

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

where n is measured in weeks. Begin by finding all equilibria for this model. For the updating function $H(P)$, find the intercepts, all extrema, and any asymptotes for $P > 0$, then sketch a graph of the updating function.

Solution: The equilibria are found by solving $P_e = H(P_e)$, which is equivalent to solving

$$P_e(1+0.002P_e)^4 = 81P_e.$$

So either

$$P_e = 0 \text{ or } (1+0.002P_e)^4 = 81,$$

which gives $1 + 0.002P_e = 3$ or $P_e = 1000$.

Analyzing $H(P)$, we find that the only intercept is $(0, 0)$ and that there is a horizontal asymptote with $H = 0$ (the power of the denominator is greater than the power of the numerator). To find where the maximum occurs, we differentiate the updating function using both the quotient rule and the chain rule for the term in the denominator. First, we differentiate the denominator using the chain rule, so

$$\frac{d}{dP}(1+0.002P)^4 = 4(1+0.002P)^3(0.002).$$

From the quotient rule, it easily follows that

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

The last step requires a little algebra cancelling similar quantities from the numerator and denominator.

To find critical points, we set the derivative equal to zero. Solving $H'(P) = 0$, we first note that this is zero only if the numerator is zero. Thus, we have

$$1 - 0.006P = 0 \text{ or } P = 500/3 = 166.7.$$

With $H(500/3) = 4271.5$, the *maximum* occurs at $(166.7, 4271.5)$. A graph of the updating function with the identity function is shown in Figure

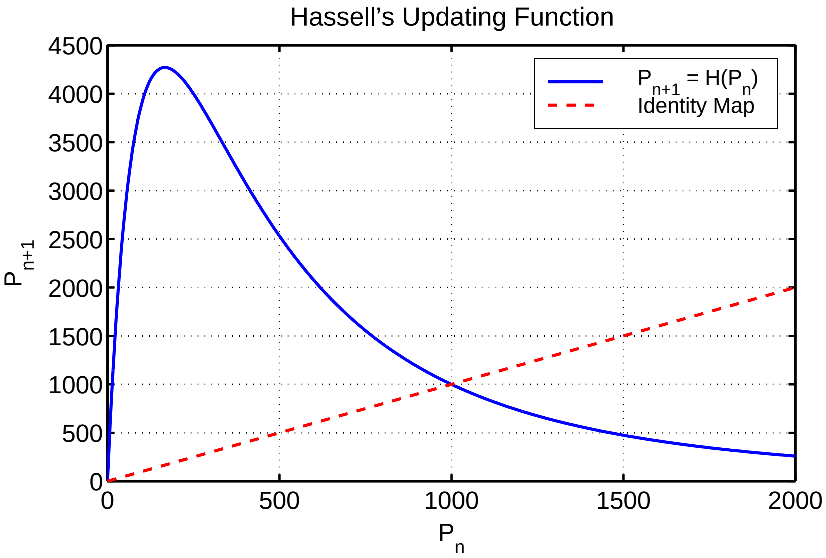

Figure 4: Graph of the Hassell's updating function of Example 4 with the identity function.

4. Note that the identity function intersects $H(P)$ at the equilibrium point.

◁

Example 5 *Growth of Fish*

Fish have been shown to satisfy the von Bertalanffy equation, relating the length of fish with age. There is also an allometric relation between the weight of a fish and its length. In this example, we form a composite function that describes the weight of a fish as a function of its age. A reasonable model for the length of lake trout using the von Bertalanffy equation is

$$L(t) = 120(1 - e^{-0.2t}),$$

where t is the age of the trout in years and L is the length in cm. An approximate allometric model that relates the weight of a lake trout to its length is given by the equation

$$W(L) = 0.000015L^3,$$

where W is the weight in kg.

Graph both the length and the weight of the lake trout as a function of age, then determine the rate of change in weight as a function of age. For the graphs, give any intercepts and asymptotes. Graph the rate of change in weight as a function of age.

Solution: The von Bertalanffy equation for the lake trout has the origin for its intercept (which is the same for the allometric model). Since the exponential function becomes vanishingly small for large t, there is a horizontal asymptote for the length equation of $L = 120$ cm. Similarly, because the length approaches a constant, the allometric model has the weight approaching a constant with $W = 25.9$ kg. In Figure 5 we see the graph of $L(t)$.

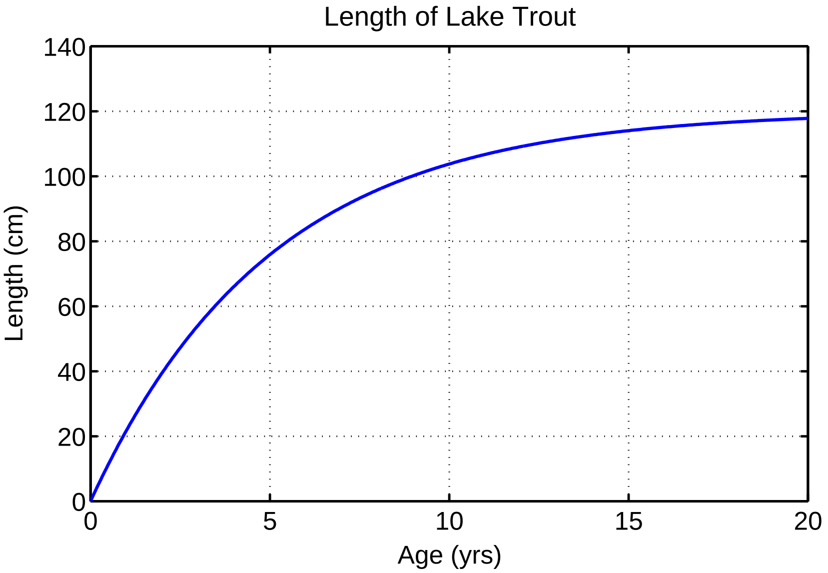

Figure 5: Graph of the function $L(t)$ of Example 5.

The composite function for the weight of the fish can be written

$$\begin{aligned} W(t) &= 0.000015(120(1 - e^{-0.2t}))^3, \\ W(t) &= 25.92(1 - e^{-0.2t})^3. \end{aligned}$$

A graph of this function is shown in Figure 6.

Finally, we apply the chain rule to the equation for the weight of the lake trout

$$\frac{dW}{dt} = \frac{dW}{dL}\frac{dL}{dt}.$$

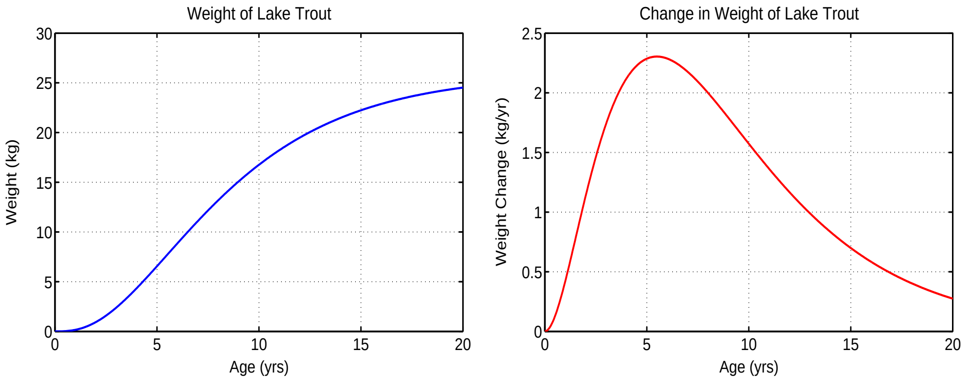

Figure 6: Left: Graph of the function $W(t)$ of Example 5. Right: Graph of the function of fish weight rate of Example 5.

The two derivatives are given by

$$\begin{aligned}\frac{dL}{dt} &= 120(0.2)e^{-0.2t},\\ \frac{dW}{dL} &= 0.000045L^2.\end{aligned}$$

Multiplying these two expressions together and inserting the von Bertalanffy equation for the lake trout, we have the rate of change in weight for a lake trout with respect to its age

$$\frac{dW}{dt} = 0.000045L^2(24)e^{-0.2t} = 15.55e^{-0.2t}(1-e^{-0.2t})^2.$$

In Figure 6 we see a graph of this rate equation, showing rapid weight gain initially reaching a maximum weight gain around age 5, then slowing to almost no change in rate of weight gain for older lake trout. The second derivative could be used to compute the maximum rate of increase in weight. This is left as an exercise for the reader. ◁

5 EXERCISES

Find the derivatives of the following functions:

1. $f(x) = (x^2 - 3x + 4)^4$,

2. $f(x) = x^2(x^3 - 2x + 1)^3$,

3. $f(x) = \dfrac{e^{x^2}}{2x+1} + \ln(x^2)$,

4. $f(x) = (x^2 - e^{-x^2})^3$.

Find the derivative and sketch the curves of the functions below. Are these functions even, odd, or neither? List all maxima and minima for each graph. Find the second derivative of these functions, then locate the points of inflection. Also, give the x and y-intercepts and any asymptotes if they exist.

5. $y = 2e^{-x^2/2}$, 6. $y = \ln(x^2+1)$,

7. $y = \dfrac{10x}{(1+0.1x)^2}$, 8. $y = \dfrac{e^{2x}}{(1+e^{2x})^2}$,

9. A study of American girls ages 4-13 in the 90^{th} percentile found that their height h (in cm) as a function of their age a (in years) satisfies the equation

$$h(a) = 6.44a + 82.1.$$

The same study found that their weight W (in kg) as a function of their height is given by

$$W(h) = 0.0000302h^{2.84}.$$

a. What is a rate of growth in height? Be sure to include units in your answer.

b. Write an expression for the composite function that gives the weight as a function of age. Differentiate this function to find $W'(a)$ using the chain rule.

c. What is the rate of change in weight at ages 4, 8, and 13? Be sure to include units for your answer.

10. Hassell's model is often used to study populations of insects. Suppose that the updating function for the population of a species of moth P is given by

$$H(P) = \frac{5P}{(1+0.002P)^4}.$$

a. Find all equilibria of the model by solving the equation $H(P_e) = P_e$.

b. Determine the intercepts, all extrema, and any asymptotes for $P \geq 0$, then sketch a graph of $H(P)$.

11. The continuous logistic growth model is a very important model used in Biology. Suppose that a population of bacteria satisfies the logistic growth model

$$B(t) = \frac{100}{1+9e^{-0.02t}},$$

where t is in minutes and B is in thousands of bacteria/ml.

a. Compute both the first and second derivatives of $B(t)$.

b. Find the B-intercept and any asymptotes for the model of this population, then sketch a graph of $B(t)$. Also, find the point of inflection.

c. Determine $B'(0)$ and find any asymptotes for the function $B'(t)$. Find the maximum of this function, then sketch its graph.

12. The lecture notes have an example for the weight of a lake trout as a function of age, and it was given by the formula

$$W(t) = 25.92(1 - e^{-0.2t})^3,$$

where W is in kg and t is in years. Find the age at which the lake trout are increasing their weight most rapidly.

13. The growth in length of sculpin is approximated by the von Bertalanffy equation

$$L(t) = 16(1 - e^{-0.4t}),$$

where t is in years and L is in cm. An allometric measurement of sculpin shows that their weight can be approximated by the model

$$W(L) = 0.07L^3,$$

where W is in g.

a. Find the intercepts and any asymptotes for the length of a sculpin, then sketch of graph showing the length of a sculpin as it ages.

b. Create a composite function to give the weight of the sculpin as a function of its age, $W(t)$. Find the intercepts and any asymptotes for $W(t)$, then sketch of graph showing the weight of a sculpin as it ages.

c. Find the derivative of $W(t)$ using the chain rule. Also, compute the second derivative, then determine when this second derivative is zero. From this information, find at what age the sculpin are increasing their weight the most and determine what that weight gain is. Be sure to give the units of weight gain.

14. Suppose that after a burn a pioneering plant community has its biomass accumulating according to the following growth model,

$$P(t) = 20(1 - e^{-0.2t}),$$

where t is in years and P is in metric tons. The herbivores that graze on this plant community satisfy the equation

$$H(P) = 3(1 - e^{-0.1P}),$$

where H is in metric tons of the biomass of herbivores.

a. Sketch a graph of $P(t)$, showing any intercepts and asymptotes. Compute the derivative to determine the rate of change in biomass of the plant material. What is the rate of change in biomass at $t = 0$, 2, 10, and 20 years?

b. Create the composite function to find the biomass of the herbivores as a function of time $H(t)$. Differentiate this function, then find the rate of change in biomass of the herbivores at $t = 0$, 2, 10, and 20 years

CHAPTER 18:

OPTIMIZATION

In biology, animals are frequently devising *optimal strategies* to gain advantage. These might result in reproducing more rapidly, or better protection from predation. It has been argued that primitive animals long ago split into the *prokaryotes* (bacterial cells) and *eukaryotes* (cells in higher organisms like yeast or humans) from a common ancestor, which had elements of both. One argument contends that eukaryotic cells added complexity, size, and organization for advantage in competition, while the prokaryotes stripped down their genome (eliminated "junk" DNA) to the minimum required for survival, to maximize reproduction. These arguments suggest that organisms try to optimize their situation to gain an advantage.

The derivative was a valuable tool in finding critical points on graphs. These critical points were local *minima* or *maxima* for the function. This is one of the valuable applications of Calculus, where an optimal solution is found for some problem.

1 CROW PREDATION ON WHELKS

Sea gulls and crows have learned to feed on various mollusks by dropping their prey on rocks to break the protective shells. Reto Zach [2,3] performed a detailed study of Northwestern crows (*Corvus caurinus*) on Mandarte Island, British Columbia to learn more about their habit of selecting and consuming whelks (*Thais lamellosa*). Some ecologists argue that studies on the behavior of such interactions gives insight into the decision making of *optimal foraging.*

Zach observed that Northwestern crows, perched above the beaches, flew to the intertidal zone and searched carefully for the largest whelks they could find. After selecting a whelk (occasionally more than one), the crows flew to a favorite rocky area, where they flew vertically upwards and released the whelk. The whelk would hit the rocks. If the whelk split open, the crow would remove the edible parts. However, if it failed to break, the crow would seize the whelk again, fly vertically, and drop the whelk again, repeating this process until the whelk broke open and could be consumed. (One crow took 20 drops to open one whelk.) Zach observed that the crows usually flew to

Figure 1: How do crows optimize their technique for feeding on whelk?

height of 5 meters with little variation. He also noted that it took a little over 4 drops on average for the whelks to break open. Can this behavior be explained by an optimal foraging decision process? Is the crow exhibiting a behavior that minimizes its expenditure of energy to feed on whelks?

In Zach's[1] first experiment, he selected a collection of whelks and sorted them according to size (small, medium, and large). He then dropped these whelks from various heights until they broke, and recorded how many drops at each height were required to break each whelk. A graph of his results is shown in Figure 2.

Notice that it is clearly easier to break open larger whelks, and another experiment confirmed that crows selectively chose the largest available whelks. It was noted that there was a gradient of whelk size on the beach, suggesting that the crows' foraging behavior was affecting the distribution of whelks in the intertidal zone, with larger whelks further out. If the larger whelks are easier to break open, then clearly the crows benefit by selecting the larger ones because they do not need as many drops per whelk, and they gain more energy from consuming a larger one. The study showed that the whelks broken on the rocks were remarkably similar in size, with the average whelk weighing about 9 grams. Next, Zach observed the height of the drops

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[1] www.illuminations.nctm.org/imath/912/Whelk, last visited 05/01/04

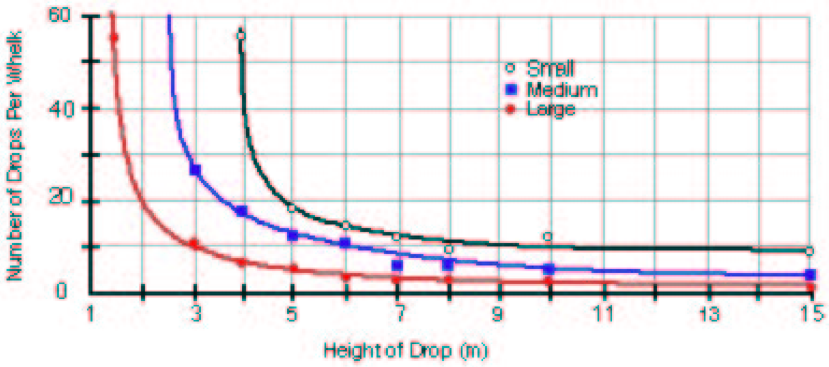

Figure 2: Graph for the experiment of number of dropped whelks *vs.* hight of the drop for three different whelk sizes.

and number of drops required for many crows eating whelks, using a marked pole on the beach near a favorite dropping location. Figure 3 are histograms of his observations.

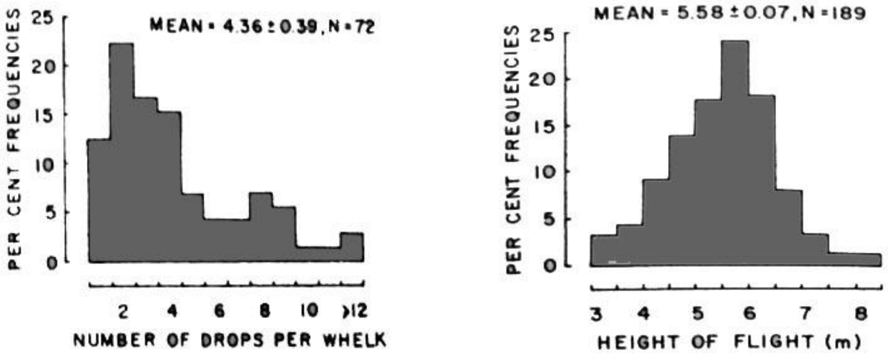

Figure 3: Histograms of the height of the drops and number of drops of whelks performed by many different crows [2].

So why do the crows consistently fly to about 5.2 m and use about 4.4 drops to split open a whelk? Can this be explained by a mathematical model for minimizing the energy spent, thus supporting an optimal foraging strategy?

2 MATHEMATICAL MODEL FOR ENERGY

From Physics, we know that the energy is directly proportional to the vertical height that an object is lifted. (This is commonly called the work put into a system.) Thus, the energy that a crow expends breaking open a whelk depends on the amount of time the crow uses to search for an appropriate whelk, the energy in flying to the site where the rocks are, and the energy required to lift the whelk to a certain height and drop it times the number of vertical flights required to split open the whelk. We will concentrate only on the energy of this last component of the problem, as it was observed that the crows kept with the same whelk until they broke it open rather than searching for another whelk when one failed to break after a few attempts.

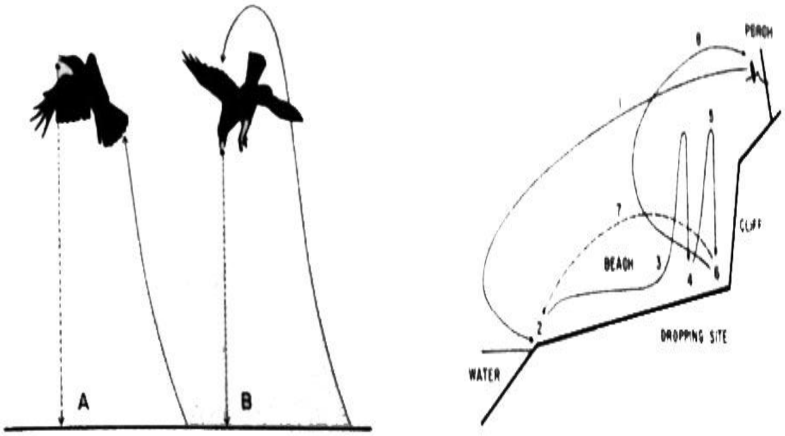

Figure 4: Diagrams of the crow's foraging strategy [3].

Thus, the energy that we measure is given by the height (H) times the number of drops (N) or

$$E = kHN,$$

where k is a constant of proportionality. Notice that flying higher and increasing the number of drops both increase the use of energy.

Data from Zach's research was used to find a function that expresses the number of drops (N) as a function of the height (H). Since it always requires at least one drop, the proposed function is

$$N(H) = 1 + \frac{a}{H - b}.$$

The graph in Figure 5 shows the least squares best fit of this function to Zach's data and gives $a = 15.97$ and $b = 1.209$.

H(m)	1.5	2	3	4	5	6	7	8	10	15
N(H)	56	20	10.2	7.6	6	5	4.3	3.8	3.1	2.5

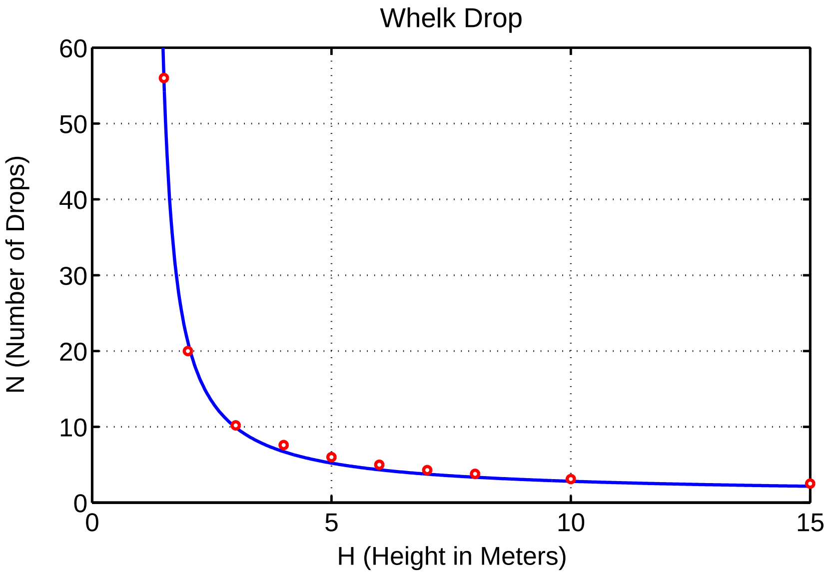

Figure 5: Graph showing the best fitting curve through the data by Zach on dropping large whelk until they broke open.

It follows that the Energy function becomes

$$E(H) = kH\left(1 + \frac{a}{H-b}\right).$$

A graph of this function with the values of a and b above and $k = 1$ is shown in Figure 6. A minimum energy is readily apparent from the graph with the value around 5.6 m, which is close to the observed value that Zach found the crows to fly when dropping whelks.

To find the specific value from our formula, we take the derivative and set it equal to zero, solving for H. The derivative of the expression of $E(H)$ uses the product rule and either the quotient rule or chain rule giving:

$$E'(H) = k\left(1 + \frac{a}{H-b} - \frac{aH}{(H-b)^2}\right) = k\left(\frac{H^2 - 2bH + b^2 - ab}{(H-b)^2}\right).$$

For the derivative to be zero, the numerator must be zero. But the numerator is just a quadratic equation (refer to Chapter 4 if necessary). With the values of a and b above, the numerator is zero for both $H = 5.602$ and $H = -3.185$. Obviously, the second answer does not make sense for this problem (it is a maximum of this function, and a negative height), so the minimum energy occurs at $H = 5.602$ m. This agrees with the graphical

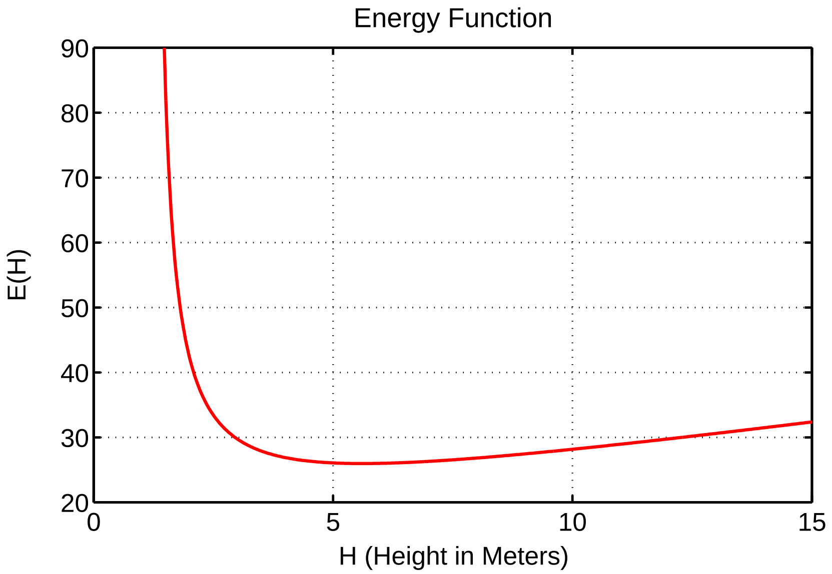

Figure 6: Graph of the Energy function for dropping a whelk until it opens, $E(H) = kH(1 + a/(H - b))$.

observation, and the experimental results.

3 OPTIMAL SOLUTION

One application of the derivative is to find critical points where often a function has a *relative minimum* or *maximum*. An *optimal solution* for a function is when the function takes on an absolute minimum or maximum over its domain.

Definition: An *absolute minimum* for a function $f(x)$ occurs at a point $x = c$, if $f(c) < f(x)$ for all x in the domain of f.

A function does not necessarily have an optimal solution. However, smooth functions on a closed interval always have absolute extrema as stated in the theorem below.

Theorem: Suppose that $f(x)$ is a continuous, differential function on a closed interval $I = [a, b]$, then $f(x)$ achieves its absolute minimum (or maximum) on I and its minimum (or maximum) occurs either at a point where $f'(x) = 0$ or at one of the endpoints of the interval.

4 OPTIMAL STUDY AREA

An ecology student goes into the field with 120 m of string and wants to create two adjacent rectangular study areas with the maximum area possible. Figure 7 presents a diagram of the two study plots.

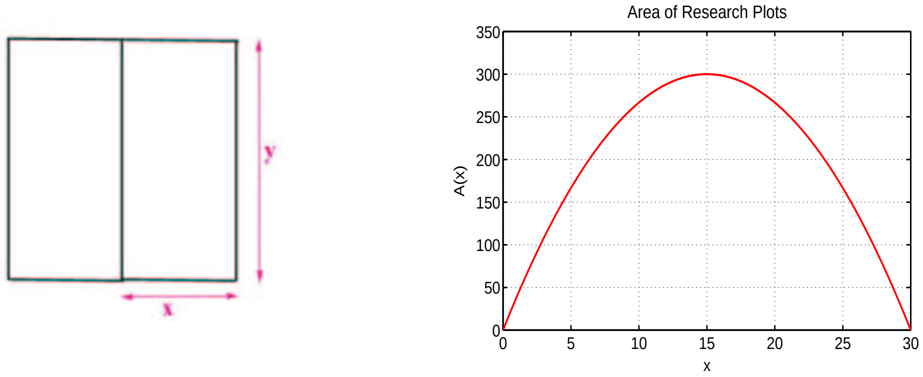

Figure 7: Left: Diagram of the rectangular study regions the ecology student would like to make. Right: Graph of the rectangular area of one region of the study field with respect to x.

If each region has length y and width x, sharing one common length between, then from the diagram above it is clear that the amount of string needed to mark off the region is

$$P = 4x + 3y.$$

The area of each rectangular plot is

$$A = xy.$$

Clearly, the optimal solution uses all the string, so $P = 120$. We can solve the first equation for y and obtain

$$y = \frac{120 - 4x}{3}.$$

Thus, area can be written as a function of x with

$$A(x) = \frac{x(120 - 4x)}{3} = 40x - 4x^2 3.$$

The domain of this function is $0 \leq x \leq 30$, which is where the area is positive. The right panel of Figure 7 shows a graph of this area function.

Differentiating $A(x)$, we find

$$A'(x) = 40 - \frac{8x}{3}.$$

A critical point occurs when $A'(x) = 0$, so $40 - 8x/3 = 0$ or $x = 15$. From the equation above for y, we see that the optimal y value is 20. Thus, to maximize the study areas, the ecology student should make each of the two study areas 15 m wide and 20 m long or 300 m^2.

The following examples illustrate a range of typical problems.

Example 1 *Absolute Extrema of a Polynomial*

Consider the cubic polynomial $f(x)$ defined on the interval $0 \leq x \leq 5$, where

$$f(x) = x^3 - 6x^2 + 9x + 4.$$

Find the absolute extrema of this polynomial on its domain.

Solution: We begin this problem by finding the derivative of $f(x)$,

$$f'(x) = 3x^2 - 12x + 9 = 3(x^2 - 4x + 3) = 3(x-1)(x-3).$$

Thus, we have critical points at $x = 1$ and $x = 3$. To find the absolute extrema, we evaluate $f(x)$ at the critical points and the endpoints of the domain. We obtain (see Figure 8,

$$\begin{array}{rc} f(0) = 4 & \text{(an absolute minimum)}, \\ f(1) = 8 & \text{(a relative maximum)}, \\ f(3) = 4 & \text{(an absolute minimum)}, \\ f(5) = 24 & \text{(the absolute maximum)}. \end{array}$$

◁

Example 2 *Crop Yield*

The yield of an agricultural crop depends on the nitrogen in the soil. Crops cannot grow without a source of nitrogen (except many legumes), but if

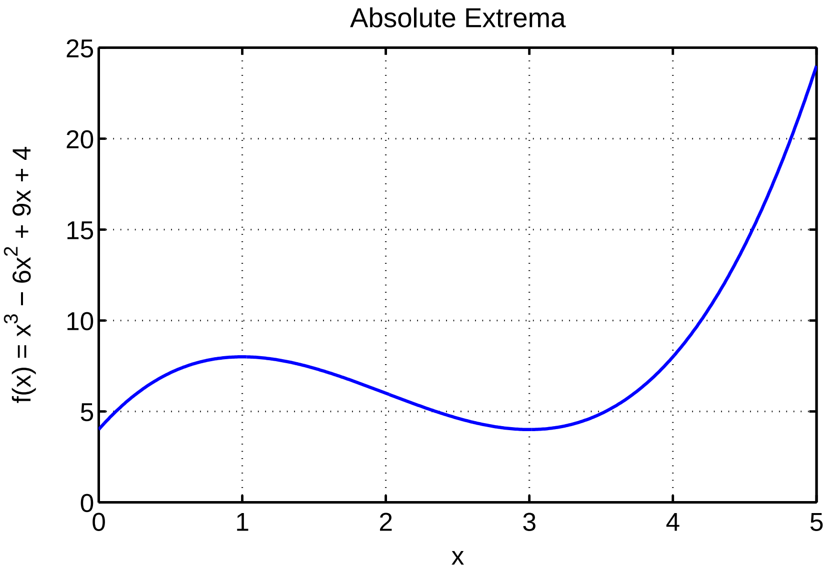

Figure 8: Graph of the polynomial function showing its absolute and relative maxima and minima.

there is too much nitrogen, it becomes toxic and decreases the yield also. Suppose that the yield of a particular agricultural crop satisfies the function

$$Y(N) = \frac{N}{1+N^2}.$$

where N is measured in some scaled units. Graph $Y(N)$ and find the level of nitrogen that produces the maximum crop yield.

Solution: For this function, the domain of interest is $N \geq 0$. Again we differentiate the yield function to find the critical points. From the quotient rule (Chapter 16), we see that

$$Y'(N) = \frac{(1+N^2) - N \cdot 2N}{(1+N^2)^2} = \frac{1-N^2}{(1+N^2)^2}.$$

The critical points are found by solving $Y'(N) = 0$, which is true when the numerator of the derivative is 0. So the critical points are $N = 1$ and $N = -1$. Only the first of these are in the domain with

$$Y(1) = 0.5, \text{ which is an absolute maximum.}$$

The endpoints are $N = 0$ and N tending to infinity. Since $Y(0) = 0$, it is an absolute minimum. As N tends to infinity, $Y(N)$ decreases toward 0,

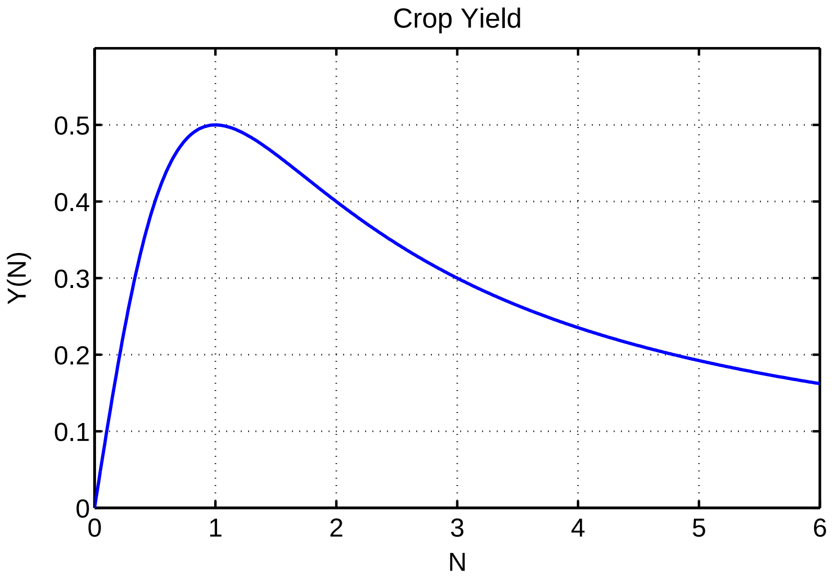

Figure 9: Graph of the function of the crop yield $(Y(N))$ *vs.* the amount of nitrogen (N) of Example 2.

confirming that we found the absolute maximum. Figure 9 shows a graph of this function. ◁

Example 3 *Wire Problem*

A wire length L is cut to make a circle and a square. How should the cut be made to maximize the area enclosed by the two shapes?

Solution:

In Figure 10 is a diagram showing how the wire creates the circle and the square after being cut. The perimeters of the two figures are constrained to the length of the wire, so

$$L = 2\pi r + 4x,$$

where r is the radius of the circle and x is the length of one side of a square. Notice that the domain is limited by $0 \leq x \leq L/4$.

The area which is to be maximized is given by the formula

$$A = \pi r^2 + x^2.$$

From the constraint, we can solve for r in terms of L and x giving

$$r = \frac{L - 4x}{2\pi}.$$

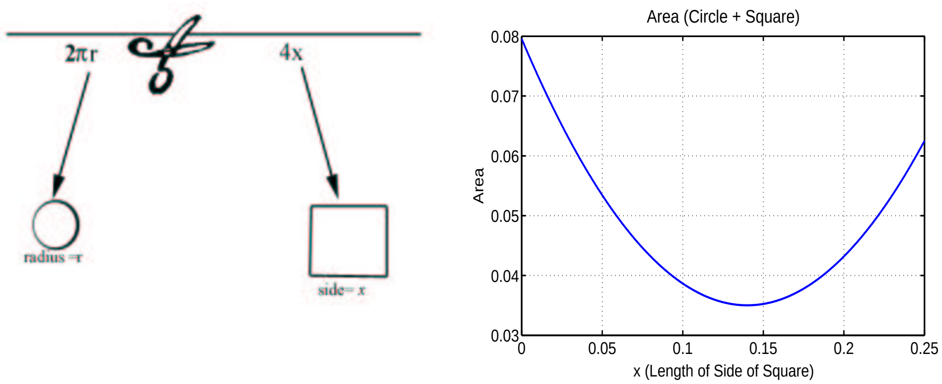

Figure 10: Left: Diagram depicting how the circle and the square of Example 3 are cut. Right: Graph of the area function of Example 3.

This is substituted into the formula for the area to form a function depending only on x:

$$A(x) = \frac{(L-4x)^2}{4\pi} + x^2.$$

This is differentiated with respect to x. The chain rule (see Chapter 17) is applied to the first term in $A(x)$ and the power rule applies to the second term giving:

$$A'(x) = \frac{2(L-4x)(-4)}{4\pi} + 2x = 2\left(\left(\frac{4+\pi}{\pi}\right)x - \frac{L}{\pi}\right).$$

To find extrema, we set $A'(x) = 0$, which is equivalent to

$$(4+\pi)x = L.$$

Thus, there is a relative extrema at

$$x = \frac{L}{4+\pi}.$$

If we take the second derivative of $A(x)$, we obtain

$$A''(x) = \frac{8}{\pi} + 2 > 0.$$

Thus, the function is concave upward and the critical point found above is a minimum, not a maximum. (This will be the absolute minimum of this function.) Note that the formula for $A(x)$ is a parabola pointing up (coefficient of the quadratic term is positive), so geometrically, we know this was a minimum. The absolute maximum must be one of the endpoints.

Checking at $x = 0$ and $x = L/4$, we obtain

$$A(0) = \frac{L^2}{4\pi} \quad \text{and} \quad \mathrm{A(L/4)} = \frac{\mathrm{L}^2}{16}.$$

The first of these has the smaller denominator, so is the larger. Thus, the maximum occurs when the wire is completely used to create a circle. Geometrically, we know that a circle is the most efficient conversion of a linear measurement into area, so the area produced with the wire completely bent into a circle produces the maximum area. The right panel of Figure 10 shows a graph of the area as a function of x with the left end of the graph corresponding to the wire being completely bent into a circle and the right end corresponding to the wire being bent entirely into a square. ◁

Example 4 *Optimal Production of a Pharmaceutical*

Bacteria often regulate the production of their proteins based on their rate of growth. Some proteins are produced in higher quantities during high growth rates, while others tend to be produced at a higher rate as the bacteria enter a phase of stress due to limitations in some nutrient source. In the stationary phase, bacteria tend to produce all proteins at a significantly lower rate.

Suppose that the production of a pharmaceutical agent, Q, depends on the population of some bacteria, B, in the following manner:

$$Q(B) = 2Be^{-0.002B}.$$

This function is similar to the Ricker's model that we studied before (see Chapter 15). When the population of the bacteria is low, then production of the pharmaceutical agent is low as there are not many bacteria producing the pharmaceutical agent. However, when the bacterial population is high, then the effects of stress cause the bacteria to produce other proteins, which again lowers the production of the pharmaceutical agent. There should be an intermediate optimal level of production when there are sufficiently many bacteria producing the agent, yet not enough of them to suppress its production.

The growth of bacteria in culture typically satisfies a logistic growth model (a model that we will later develop). Suppose that the population of bacteria satisfies this growth law and is given by:

$$B(t) = \frac{2000}{1 + 99e^{-0.0t}}.$$

Find the time when the production Q is at a maximum.

Solution: The problem asks to find the *time* when the production of the pharmaceutical agent is at a maximum. However, the production of the pharmaceutical is a function of the population of bacteria, $Q(B)$, (in units of agent), and the population of bacteria is a function of time, $B(t)$ (with time in minutes). Thus, we need to create the composite function $Q(B(t))$, which is a function that depends on time, t. The production is at its maximum when $dQ/dt = 0$ (assuming there is a maximum production).

Finding dQ/dt requires the differentiation of a composite function, which uses the chain rule of differentiation. The chain rule for differentiating this composite function gives

$$\frac{dQ}{dt} = \frac{dQ}{dB}\frac{dB}{dt} = Q'(B)B'(t).$$

We begin by finding the derivative of $Q(B)$, which uses the product rule and satisfies

$$Q'(B) = 2e^{-0.002B}(1 - 0.002B).$$

(Details of this are left to the reader as it is very similar to the computations for Ricker's model seen in the Chapter 15.) Notice that this has a maximum at $B = 500$ with $Q(500) = 1000e^{-1} = 367.9$. Figure 11 shows a graph of the production of the pharmaceutical agent, Q, as a function of the population of the bacteria, B.

Next we compute the derivative of $B(t) = 2000(1 + 99e^{-0.01t})^{-1}$. This uses the chain rule twice. By the chain rule

$$\begin{aligned} B'(t) &= -2000(1 + 99e^{-0.01t})^{-2}(99e^{-0.01t})(-0.01) \\ &= 1980e^{-0.01t}(1 + 99e^{-0.01t})^{-2}. \end{aligned}$$

We can readily see that this function is always positive or constantly increasing. However, it increases at different rates with varying times. Figure 12 is a graph of the population of bacteria, B, as a function of time, t.

These computations make it easy to find dQ/dt, as $dQ/dt = Q'(B(t))B'(t)$ from above. Our calculations above show

$$Q'(B(t))B'(t) = 3960e^{-0.002B}(1 - 0.002B)e^{-0.01t}(1 + 99e^{-0.01t})^{-2}.$$

For example, if we wanted to know the rate of production at $t = 0$, then first we note that $B(0) = 20$. We substitute this into the formula above to obtain

$$\frac{dQ}{dt} = 3960e^{-0.04}(1 - 0.04)e^{0}(1 + 99e^{0})^{-2} = 0.365 \text{ units/min.}$$

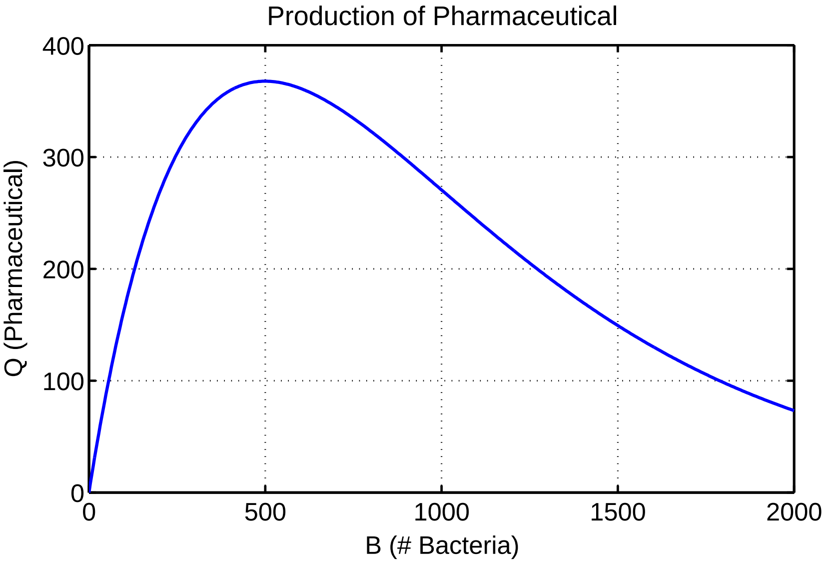

Figure 11: Function of the prodution of the pharmaceutical agent (Q) *vs.* the bacteria population (B).

Note that $Q(B(0)) = 40e^{-0.04} = 38.43$ units.

The rate of production at $t = 1000$ has $B(1000) = 2000/(1 + 99e^{-10}) = 1991$ and is given by

$$\frac{dQ}{dt} = 3960e^{-3.982}(1 - 3.982)e^{-10}(1 + 99e^{-10})^{-2} = -0.0099 \text{ units/min.}$$

Thus, the production is dropping by $t = 1000$, though the loss is small at this time. Note that $Q(B(1000)) = 3982e^{-3.982} = 74.26$ units.

So what is the maximum amount of pharmaceutical produced. This will be when $dQ/dt = 0$. However, this will occur when $1 - 0.002B = 0$, as all other terms in the expression for dQ/dt are positive. This implies that $B = 500$. When we solve $B(t) = 500$, we find

$$2000(1 + 99e^{-0.01t})^{-1} = 500 \text{ or } 2000 = 500 + 49500\mathrm{e}^{-0.01\mathrm{t}}.$$

Thus,

$$e^{-0.01t} = 33 \text{ or } \mathrm{t} = 100\ln(33) = 349.65 \text{ min.}$$

The value of $Q(B(100\ln(33))) = 1000e^{-1} = 367.9$ units, which is substantially higher than at either $t = 0$ or $t = 1000$. Figure 13 shows a graph of the composite function, $Q(B(t))$.

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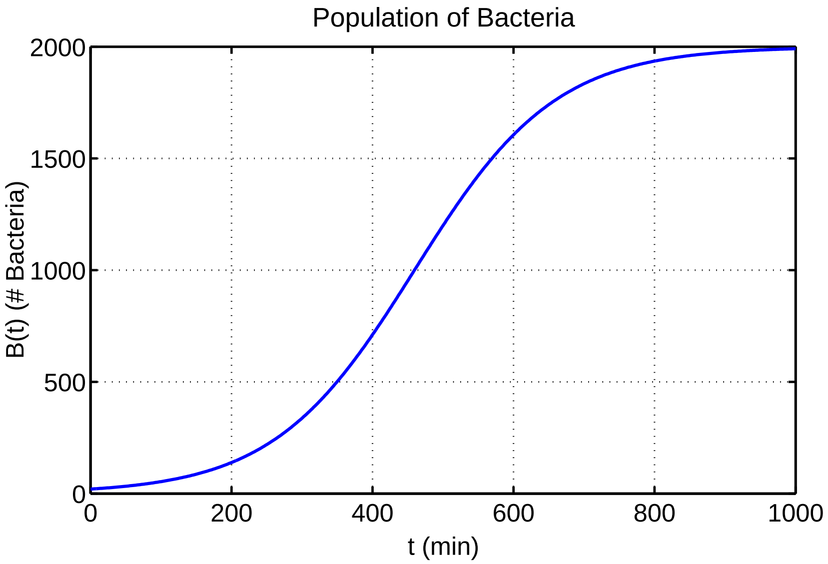

Figure 12: Graph of the function of the bacteria population growth of Example 4.

5 CHEMICAL REACTION – OPTIMUM AT ENDPOINTS

One of the simplest chemical reactions is the combination of two substances to form a third. This reaction is written,

$$A + B \xrightarrow{k} X.$$

If the initial concentration of substance A is a and the initial concentration of B is b, then the law of mass action gives the following reaction rate for the bimolecular reaction

$$R(x) = k(a - x)(b - x), 0 \leq x \leq \min(a, b),$$

where k is the rate constant of the reaction and x is the concentration of X during the reaction. What is the concentration of X where the reaction rate is at a maximum?

For graphing purposes, suppose that $k = 50$ (sec^{-1}), $a = 6$ (ppm), and $b = 2$ (ppm), so

$$\begin{aligned} R(x) &= 50(6 - x)(2 - x) \\ &= 50x^2 - 400x + 600, \qquad 0 \leq x \leq 2. \end{aligned}$$

From our theorem above, we seek critical points where the derivative is zero

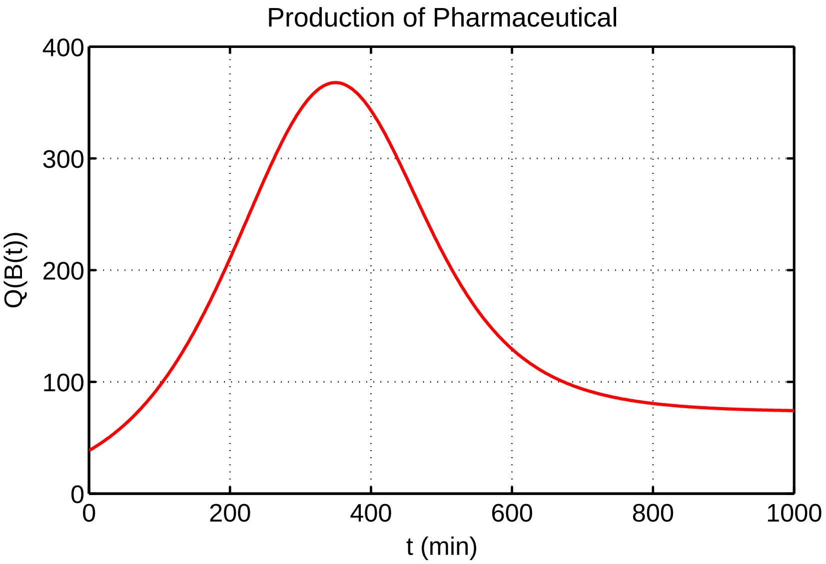

Figure 13: Graph of the composite function of Example 4.

or the endpoints of the domain. The derivative equal to zero gives

$$R'(x) = 100x - 400 = 0 \text{ or } x = 4.$$

Note that this critical point is outside the domain (and produces a negative reaction rate). So we turn to examining the endpoints. A graph of $R(x)$ is shown in Figure 14. We see that the maximum rate is at the beginning of the reaction with no product $X(R(0) = 600)$ and the minimum occurs at $x = 2$, where the reaction rate is zero.

6 EXERCISES

1. Find the area of the largest rectangle with a base on the x-axis and the upper vertices on the parabola $y = 12 - x^2$. Give the dimensions of this rectangle.

2. A rectangular study plot is bounded on one side by a river, and the other three sides are to be blocked off by a fence. Find the dimensions of the plot that maximizes the area enclosed with 20 meters of fence.

3. An open box with its base having a length twice its width is to be constructed with 600 in^2 of material. Find its dimensions that maximize the volume.

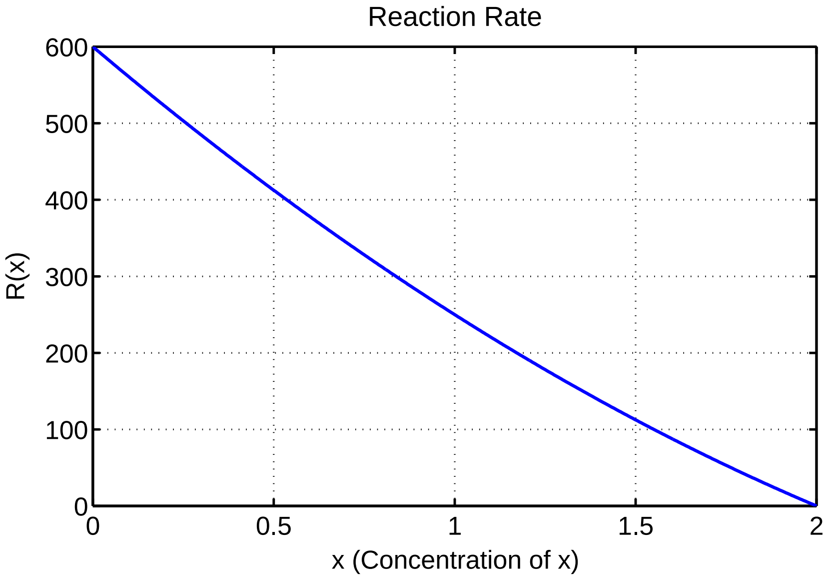

Figure 14: Graph of the function of the chemical reaction rate (R) with respect to the product concentration (x).

4. Find the dimensions of an open rectangular box with a square base that holds 32 in^3 and is constructed with the least building material possible.

5. Find the dimensions of a right circular cylindrical can with both a top and a that holds one liter (1000 cm^3) and is constructed with the least amount of material possible.

6. The strength of a rectangular beam is proportional to the product of its width and the square of its depth. Find the dimensions of the strongest beam that can be cut from a circular log with a radius of r.

7. A catalyst for a chemical reaction is a substance that controls the rate of the chemical reaction without changing the catalyst itself. An autocatalytic reaction is one whose product is a catalyst for its own formation.

$$A + X \xrightarrow{k} X.$$

The rate of this reaction $v = dx/dt$ is given by the formula

$$v = kx(a - x),$$

where a is the initial concentration of the substance A, x is the concentration of the product X, and k is the rate constant of the reaction. Find the concentration x that produces the maximum rate of reaction.

8. Nutrients in low concentrations inhibit growth of an organism, but high concentrations are often toxic. Let c be the concentration of a particular nutrient (in moles/liter) and P be the population density of an organism (in number/cm^2). Suppose that it is found that the effect of this nutrient causes the population to grow according to the equation:

$$P(c) = \frac{1000c}{1 + 100c^2}.$$

a. Find the concentration of the nutrient that yields the largest population density of this organism and what the population density of this organism is at this optimal concentration.

b. Sketch a graph of the population density of this organism as a function of the concentration of the nutrient.

9. One question for fishery management is how to control fishing to optimize profits for the fishermen. We will soon study the continuous logistic growth equation for populations. One differential equation describing the population dynamics for a population of fish F with harvesting is given by the equation,

$$\frac{dF}{dt} = rF\left(1 - \frac{F}{K}\right) - xF,$$

where r is the growth rate of this species of fish at low density, K is the carrying capacity of this population, and x is the harvesting effort of the fishermen. We will show that the non-zero equilibrium of this equation is given by

$$F_e = K\frac{(r - x)}{r}.$$

One formula for profitability is computed by the equation

$$P = xF_e,$$

so

$$P(x) = Kx\frac{(r - x)}{r}.$$

Find the maximum profit possible with this dynamics. What is the equilibrium population at this optimal profitability? Also, determine the maximum possible fish population for this model and at what harvesting level this occurs. (Clearly, this is a grossly oversimplified model, but can give some estimates for long range management.)

10. (From [1]) Semelparous organisms breed only once during their lifetime. Examples of this type of reproduction strategy can be found with Pacific salmon and bamboo. The per capita rate of increase, r, can be thought of as a measure of reproductive fitness. The greater r, the more offspring an individual produces. The intrinsic rate of increase is typically a function of age, x. Models for age-structured populations of semelparous organisms predict that the intrinsic rate of increase as a function of x is given by

$$r(x) = \frac{\ln[l(x)m(x)]}{x},$$

where $l(x)$ is the probability of surviving to age x and $m(x)$ is the number of female births at age x. Suppose that

$$l(x) = e^{-ax}$$

and

$$m(x) = bx^c,$$

where a, b, and c are positive constants.

a. Find the optimal age of reproduction.

b. Sketch graphs of $l(x)$, $m(x)$, and $r(x)$ for $a = 0.1$, $b = 4$, and $c = 0.9$.

11. A female otter hears the cries of distress from her young in a den across and up the river from where she is foraging. (See the diagram below.) Assume that she is initially at Point A with the den residing at Point C. She wants to reach her young in the minimum amount of time. Assume she can run along the bank at $v_1 = 10$ ft/sec and swim through the river as $v_2 = 6$ ft/sec. The river is 200 ft wide and the den is 500 ft up the river. (We are ignoring the current in the river.) If the distance she runs along the bank (from A to B) is d_1 and the distance she swims (from B to C) is d_2, then the time for her to reach the den is given by the formula

$$T = \frac{d_1}{v_1} + \frac{d_2}{v_2}.$$

a. Use the diagram in Figure 15 to form an expression for the time as a function of x (the distance downstream from the den, where she crosses), $T(x)$.

b. Use your expression for the time $T(x)$ to find the minimum time for the otter to reach her pups. Give both the distance x and the time at the minimum.

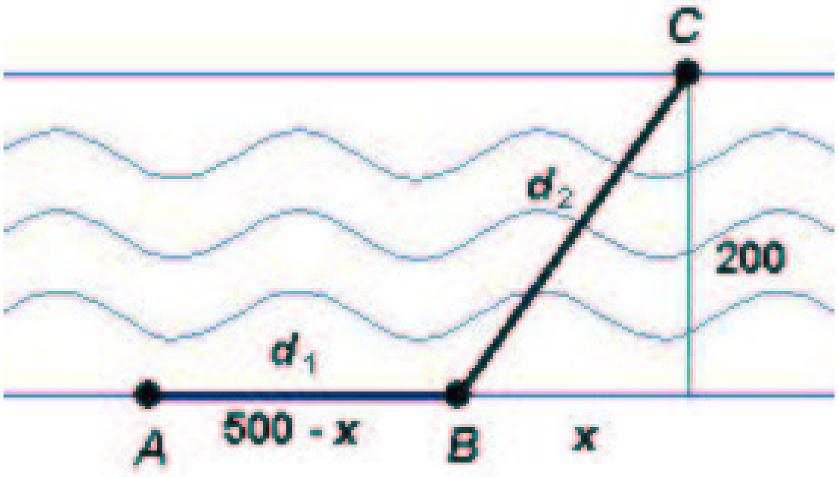

Figure 15: Diagram for Problem 11.

7 REFERENCES

[1] D.A. Roff, *The Evolution of Life Histories*, Chapman & Hall, (1992).

[2] R. Zach, Selection and dropping of whelks by Northwestern crows[2], *Behaviour*, (1978) **67**, 134–147

[3] R. Zach, Shell dropping: Decision-Making and optimal foraging in Northwestern crows[3], *Behavior,* (1979) **68**, 106–117

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[2] www.illuminations.nctm.org/imath/912/Whelk/credits.html#Zach, last visited 05/01/04

[3] www.illuminations.nctm.org/imath/912/Whelk/credits.html#Zach, last visited 05/01/04

CHAPTER 19:

LOGISTIC GROWTH AND NONLINEAR DYNAMICAL SYSTEMS

This chapter extends the qualitative analysis of discrete dynamical models from material developed earlier in this text. The discrete logistic growth model is one of the most important models used in ecological studies, yet it can produce very complicated dynamics. This model can exhibit chaos, which is a significant area of research in mathematics. This chapter extends our tools for understanding these models by analyzing the behavior of several biological models near their equilibria.

1 DISCRETE LOGISTIC GROWTH MODEL

In an earlier chapter we studied the Discrete Malthusian growth model, which showed exponential growth. This model is appropriate for early phases of population growth for most animal populations. However, as a population grows, it encounters crowding pressure due to many factors such as toxic build up or space and resource limitation.

In 1913, Carlson [1] studied a growing culture of yeast. Table 1 gives the population for these yeast at one hour intervals. We would like to develop a mathematical model to describe the growth of this culture.

There are two standard forms of the discrete population models. The

Time	Population	Time	Population	Time	Population
1	9.6	7	174.6	13	594.8
2	18.3	8	257.3	14	629.4
3	29.0	9	350.7	15	640.8
4	47.2	10	441.0	16	651.1
5	71.1	11	513.3	17	655.9
6	119.1	12	559.7	18	659.6

Table 1: Population of a yeast culture at an hour interval.

first form uses a *growth function,* $G(p_n)$.

$$p_{n+1} = p_n + G(p_n).$$

This form is stating that the population at the next time interval $(n + 1)$ is equal to the population at the current time interval (n) plus whatever net growth occurred because of the current population, $G(p_n)$, during the specific time interval.

An alternate form, which gives the general discrete dynamical system, is given by the

$$p_{n+1} = F(p_n).$$

This is an iterative map where the population at the $(n + 1)^{st}$ time depends on the population at the n^{th} time. The function $F(p)$ is called the *updating function* as it produces the next population in an iterative scheme. A graph of the updating function has the $(n+1)^{st}$ generation on the vertical axis, while the n^{th} generation is on the horizontal axis.

It is clear that the population of yeast in Table 1 does not satisfy a Malthusian growth, which has a linear updating function and grows exponentially without bound. The next obvious addition to the updating function is the addition of a quadratic term, which should be negative to reflect a decrease in the growth of a population due to crowding effects.

The *Logistic Growth model* can be written,

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

with *growth rate* r and *carrying capacity* M.

This equation has the Malthusian growth model as seen before with the additional term $-rP_n^2/M$. The parameter M is called the *carrying capacity* of the population.

The behavior of the Logistic growth model is substantially more complicated than that of the Malthusian growth model. There is no exact solution to this discrete dynamical system. The ecologist Robert May (1974) studied this equation for populations and discovered that it could produce very complicated dynamics. In its simplest form the Logistic growth model can be written:

$$x_{n+1} = \mu x_n(1 - x_n),$$

where the parameter μ varies between 0 and 4. For a good description of this model complete with Java applet simulations see the website of B. Fraser.[1]

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[1] www.apmaths.uwo.ca/~bfraser/version1/iterated.html, last visited on 04/14/04

2 YEAST MODEL

The graph below shows a plot of p_{n+1} *vs.* p_n from Table 1. (This is accomplished by plotting the population from one time against the population from the previous time. For example, the first two points are $((9.6, 18.3)$ and $(18.3, 29.0)$.) A least squares best fit of a quadratic function passing through the origin is applied to these data, and it is shown in the left panel of Figure 1. The graph of the line $p_{n+1} = p_n$ (the *identity map*) is also shown, and its importance for studying discrete dynamical models will be discussed later. This equation becomes the updating function.

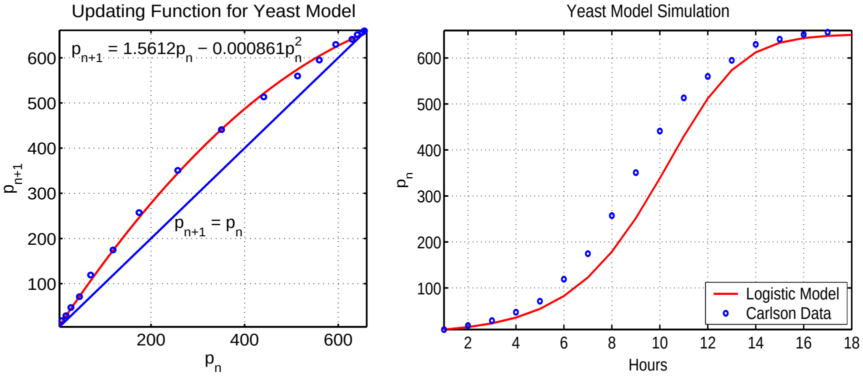

Figure 1: Left: Graph of the *updating function* and the *identity line*. Right: Graph of the data of Table 1 and the model $p_{n+1} = 1.56p_n - 0.000861p_n^2$.

Our *discrete logistic growth model* for the yeast experiment above is given by

$$p_{n+1} = 1.56p_n - 0.000861p_n^2.$$

The right panel of Figure 1 shows a simulation showing both the data and the model, assuming that we begin with $p_0 = 9.6$. As we can see, the model does a fairly reasonable job of simulating the data from this fairly simplistic model.

Qualitatively, we see the same initial roughly exponential growth, then both models seem to level off at approximately the same value. This is the *carrying capacity* of the population. The equation above shows $r = 0.56$ and $r/M = 0.000861$, so $M = 650.4$. This is clearly a little low based on the original table. Furthermore, the model is shifted in time, not rising as soon as the original data. (If a nonlinear least squares fit of the simulation to the time series were applied with the value of P_0 varying, then a very close fit would occur.)

3 EQUILIBRIA

This section extends our study of *discrete dynamical equations* to nonlinear functions in order to find what can be learned about their *qualitative behavior.* The linear discrete dynamical models were introduced before the chapters on differentiation showing the modeling of populations with Malthusian growth and on other models given in Chapter 8, such as one for breathing. As noted above, there is no general solution for the logistic growth model. However, we would like to learn more about this very important model from population biology. Here we introduce the key steps for studying the *qualitative behavior of discrete dynamical equations.*

Consider the general discrete dynamical equation

$$P_{n+} = f(P_n).$$

The first step in any analysis of a discrete dynamical equation is finding *equilibria*, which is simply solving an algebraic equation. An equilibrium point of a discrete dynamical system is a point where there is no change in the variable from one iteration to the next. Mathematically, this occurs whenever there is a solution to

$$P_e = f(P_e).$$

Graphically, this is when $f(P_n)$ crosses the line $P_{n+1} = P_n$, the *identity map*, which is one reason why this line was shown above.

Consider the original discrete Logistic equation listed above with $r > 0$. The equilibria are found by solving,

$$\begin{aligned} P_e &= P_e + rP_e\left(1 - \frac{P_e}{M}\right) \\ rP_e\left(1 - \frac{P_e}{M}\right) &= 0 \\ P_e &= 0, M. \end{aligned}$$

Thus, the equilibria for the Logistic growth model are either the *trivial solution* 0 (no population) or the *carrying capacity* M.

4 OTHER BEHAVIOR OF THE LOGISTIC GROWTH MODEL

Before learning more mathematical tools for studying the discrete Logistic growth model, it is useful to examine some of the wealth of behaviors that are possible for this model.

Logistic – Other Behavior

This applet shows simulations of the logistic growth model for various choices of r and M. You can vary the values of these parameters and see how the simulation changes over the first 50 iterations.

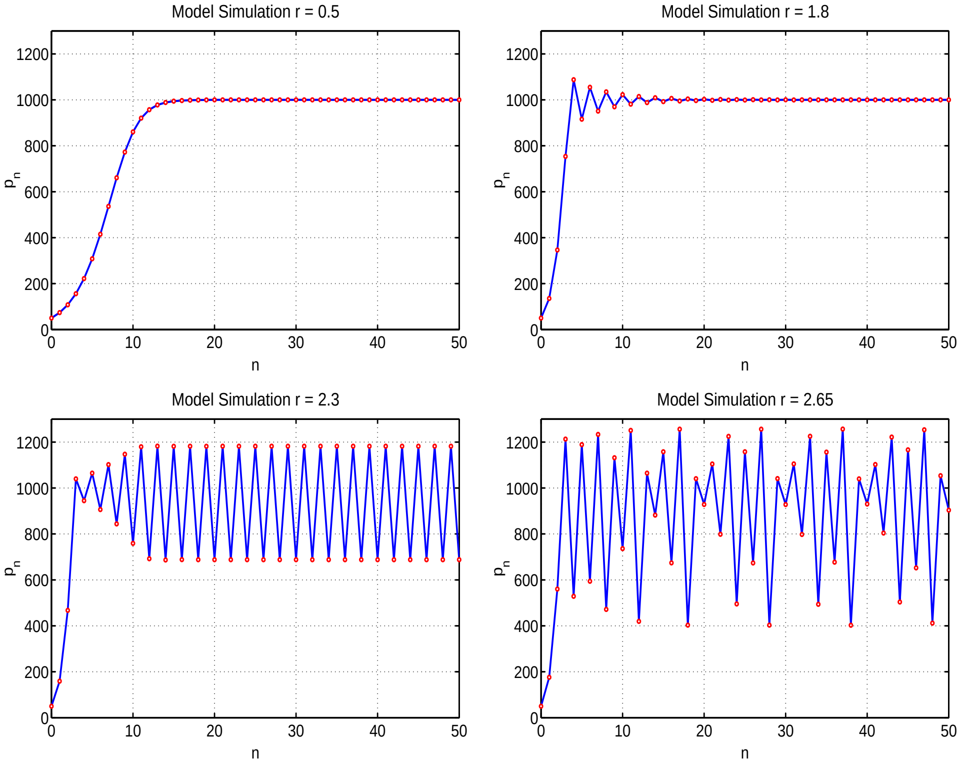

Figure 2: From the top left corner: Logistic growth model with $r = 0.5$ and $M = 1000$, Logistic growth model with $r = 1.8$ and $M = 1000$, Logistic growth model with $r = 2.3$ and $M = 1000$, Logistic growth model with $r = 2.65$ and $M = 1000$.

Robert May (1974) demonstrated that the discrete Logistic growth model could display very complicated dynamics. Watch what happens in the applet mentioned above as we choose different values of r. For example, try the values $r = 0.5, 1.8, 2.3$, and 2.65. (Note that the solution of the discrete Logistic equation only gives solutions at the integer values of n, so the connecting lines are only drawn to help visualize the behavior of the system.) The series of graph in Figure 2 shows the simulations of the logistic growth model with the values of r listed above. The first value of r shows the curve smoothly ascending to carrying capacity of 1000. The second value of r has the population ascend and actually overshoot 1000, then oscillates about 1000, getting closer to the carrying capacity as n increases. In both of these cases, the equilibrium population of 1000 is said to be *stable*. When $r = 2.3$, the solution oscillates about 1000, taking on the values of approximately 690 and 1180. This solution is said to have a *period of* 2. The last case shows the population oscillating almost randomly about 1000. This last situation could have either a very high period of oscillation or actually be *chaotic*. See what happens when you change the value of M.

5 STABILITY OF THE LOGISTIC GROWTH MODEL

The applet [Logistic – Other Behavior] showed that the behavior of the discrete logistic model changes very dramatically as the parameter r varies. We would like to have some mathematical tools that help us predict some of these behaviors. If we write the discrete logistic growth model

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

then the derivative of the function $f(P)$ proves to be a valuable tool for determining the behavior of the discrete dynamical system near an equilibrium point.

The discrete logistic growth model, as given by the equation above, has two equilibria,

$$P_e = 0 \quad \text{and} \quad P_e = M.$$

It is easy to see that the derivative of $f(P)$ is given by

$$f'(P) = 1 + r - 2rP/M.$$

At $P_e = 0$, the derivative satisfies

$$f'(0) = 1 + r,$$

which for r positive always results in solutions growing away from this equilibrium. (If r is a negative number between -1 and 0, then the solution of the discrete logistic growth model decays to 0 or the population goes to extinction.)

The more interesting behavior occurs around the second equilibrium, $P_e = M$. Below is a summary of the types of behavior that are observed for a discrete dynamical system near an equilibrium, P_e. (In all of the descriptions below, we are assuming that the simulation begins “near” the equilibrium value.)

6 BEHAVIOR OF THE DISCRETE DYNAMICAL MODEL NEAR AN EQUILIBRIUM

1. If $f'(P_e) > 1$, then the solutions of the discrete dynamical model grow away from the equilibrium (monotonically). Thus, the *equilibrium is unstable.*

2. If $0 < f'(P_e) < 1$, then the solutions of the discrete dynamical model approach the equilibrium (monotonically). Thus, the *equilibrium is stable.*

3. If $-1 < f'(P_e) < 0$, then the solutions of the discrete dynamical model oscillate about the equilibrium and approach it. Thus, the *equilibrium is stable.*

4. If $f'(P_e) < -1$, then the solutions of the discrete dynamical model oscillate but move away from the equilibrium. Again, the *equilibrium is unstable.*

Returning to the logistic growth model, we can evaluate the derivative at the larger equilibrium, $P_e = M$. From the formula for the derivative, it is easy to see that

$$f'(M) = 1 - r.$$

From our list of behaviors above, it is follows that

1. If $0 < r < 1$, then the solution of the discrete logistic model monotonically approaches the equilibrium, $P_e = M$, which was the case observed for the experiment with the yeast.

2. If $1 < r < 2$, then the solution of the discrete logistic model oscillates about the equilibrium, $P_e = M$, but the solution still asymptotically approaches this equilibrium.

3. If $2 < r < 3$, then the solution of the discrete logistic model oscillates about the equilibrium, $P_e = M$, but the solution grows away from this equilibrium. ($r > 3$ results in negative solutions.)

The following examples on the logistic growth model should help understand the process on analyzing discrete dynamical equations, finding equilibria and determining the stability of the equilibria. We also include the Malthusian growth model to see how this analysis applies to this discrete dynamical model.

Example 1 Consider the discrete logistic growth model given by the equation

$$P_{n+1} = f_1(P_n) = 1.3P_n - 0.0001P_n^2,$$

where n is measured in weeks.

a. Assume that $P_0 = 200$ and find the population for the next three weeks, P_1, P_2, and P_3.

b. Find all the equilibria for this model. Sketch a graph of the updating function (the right hand side of the equation above) along with the line $P_{n+1} = P_n$, showing clearly on the graph the equilibria and the vertex of the parabola.

c. Use the results from the lecture section to determine the behavior of the solution near the equilibria.

Solution: **a.** Given $P_0 = 200$, the updating function above generates the following populations for the next three weeks,

$$\begin{aligned} P_1 &= 1.3(200) - 0.0001(200)^2 = 256, \\ P_2 &= 1.3(256) - 0.0001(256)^2 = 326, \\ P_3 &= 1.3(326) - 0.0001(326)^2 = 413.5. \end{aligned}$$

b. To find the equilibria, we simply substitute P_e for P_n and P_{n+1} into the discrete logistic growth model. This gives

$$\begin{aligned} P_e &= 1.3P_e - 0.0001P_e^2 \\ 0 &= 0.3P_e - 0.0001P_e^2 = P_e(0.3 - 0.0001P_e), \\ P_e &= 0 \quad \text{and} \\ 0.3 - 0.0001P_e &= 0 \quad \text{or} \quad P_e = 3000. \end{aligned}$$

The parabola has P-intercepts of 0 and $13,000$, so the vertex is at $(6500, 4225)$. The left Panel of Figure 3 has the graph with the identity function and significant points shown on the graph.

c. To determine the behavior of the model near the equilibria $P_e = 0$ and 3000, we need to compute the derivative of $f_1(P_e)$. This is easily done

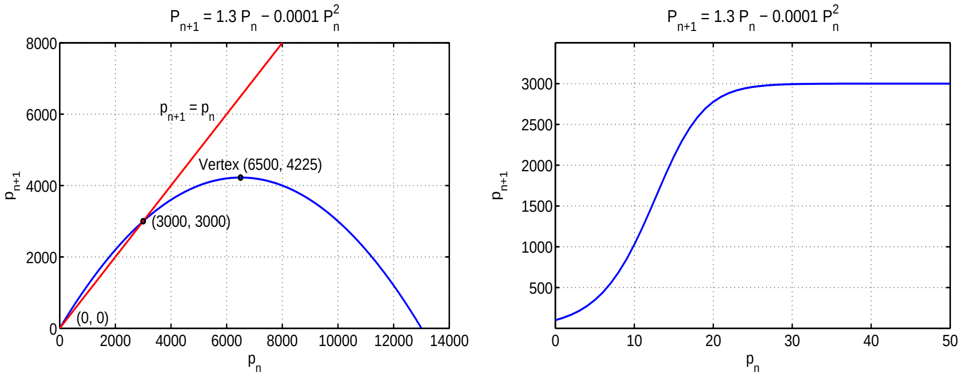

Figure 3: Left: Graph of the Logistic updating function of Example 1. Right: Simulation showing the dynamics of the Logistic equation of Example 1.

using the power rule, so

$$f_1'(P) = 1.3 - 0.0002P.$$

To find the behavior near $P_e = 0$, we compute $f_1'(0) = 1.3 > 1$. Thus, the solution monotonically grows away from this equilibrium, which is what we expect.

At the other equilibrium, $P_e = 3000$, we find $f_1'(3000) = 1.3 - 0.6 = 0.7 < 1$. Thus, from the this notes, we see that solutions of the discrete logistic model monotonically approach this equilibrium. This equilibrium is said to be *stable*. We show in the right panel of Figure 3 a simulation of this model, starting with an initial value of $P_0 = 100$ and performing 50 iterations. The simulation shows the solution growing away from $P_e = 0$ and approaching $P_e = 3000$ monotonically. ◁

Example 2 We modify the example above slightly and consider the discrete logistic growth model given by the equation

$$P_{n+1} = f_2(P_n) = 2.7P_n - 0.0001P_n^2.$$

Find all the equilibria for this model and use the results from this chapter to determine the behavior of the solution near these equilibria. Again, sketch a graph of the updating function (the right hand side of the equation above) along with the line $P_{n+1} = P_n$, showing clearly on the graph the equilibria and the vertex of the parabola.

Solution: As in the previous example, we substitute P_e for P_n and P_{n+1} into the discrete logistic growth model giving

$$\begin{aligned} P_e &= 2.7P_e - 0.0001P_e^2 \\ 0 &= 1.7P_e - 0.0001P_e^2 = P_e(1.7 - 0.0001P_e), \\ P_e &= 0 \ \text{ and} \\ P_e &= 17000. \end{aligned}$$

The graph in the left panel of Figure 4 shows the updating function and the identity map, showing clearly the equilibria.

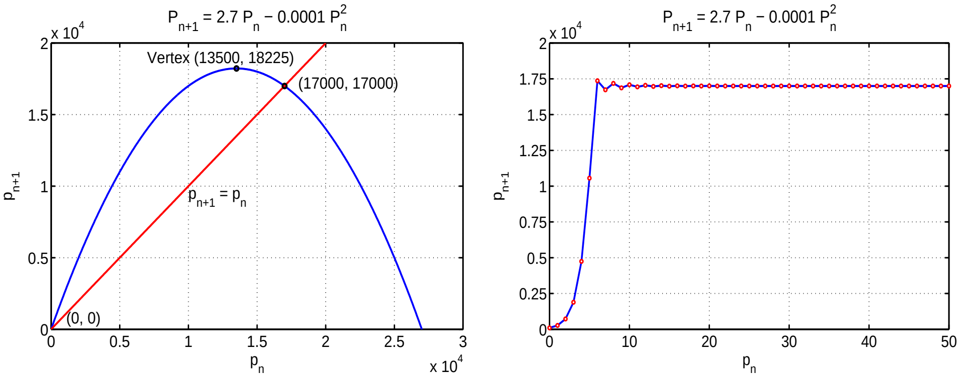

Figure 4: Left: Graph of the Logistic updating function of Example 2. Right: Simulation showing the dynamics of the Logistic equation of Example 2.

The behavior of the model near the equilibria $P_e = 0$ and 17000 is found by computing the derivative of $f_2(P_e)$. The derivative is given by

$$f_2'(P) = 2.7 - 0.0002P.$$

At $P_e = 0$, the derivative is $f_{\mathbf{2}}\prime(0) = 2.7 > 1$. Thus, the solution monotonically grows away from this equilibrium.

At the other equilibrium, $P_e = 17000$, the derivative is $f_2'(17000) = 2.7 - 3.4 = -0.7$. Since $-1 < f_2'(17000) < 0$, the discrete logistic model oscillates and approaches this equilibrium. This equilibrium is also *stable*. In the right panel of Figure 4 we show a simulation of this model, starting with an initial value of $P_0 = 100$ and performing 20 iterations. The simulation shows the solution growing away from $P_e = 0$, then oscillates and rapidly approaches $P_e = 17000$. ◁

Example 3 Another change in the discrete logistic growth model gives the equation

$$P_{n+1} = f_3(P_n) = 3.2P_n - 0.0001P_n^2.$$

Find all the equilibria for this model and use the results from the lecture section to determine the behavior of the solution near these equilibria. Again, sketch a graph of the updating function (the right hand side of the equation above) along with the line $P_{n+1} = P_n$, showing clearly on the graph the equilibria and the vertex of the parabola.

Solution: As in the previous two examples, we substitute P_e for P_n and P_{n+1} into the discrete logistic growth model giving

$$\begin{aligned} P_e &= 3.2P_e - 0.0001P_e^2 \\ 0 &= 2.2P_e - 0.0001P_e^2 = P_e(2.2 - 0.0001P_e), \\ \text{so } P_e &= 0 \text{ and} \\ P_e &= 22000. \end{aligned}$$

The left panel of Figure 5 has the graph of the updating function and the identity map, showing clearly the equilibria.

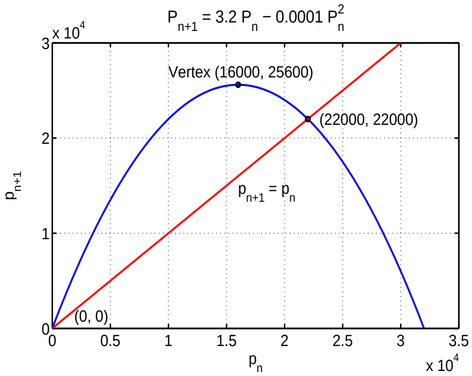

Figure 5: Left: Graph of the Logistic updating function of Example 3. Right: Simulation showing the dynamics of the Logistic equation of Example 3.

The behavior of the model near the equilibria $P_e = 0$ and 22000 is found by computing the derivative of $f_3(P_e)$. The derivative satisfies

$$f_3'(P) = 3.2 - 0.0002P.$$

At $P_e = 0$, the derivative is $f_{\mathbf{3}}\prime(0) = 3.2 > 1$. Thus, the solution monotonically grows away from $P_e = 0$.

At the other equilibrium, $P_e = 22000$, the derivative is $f_3'(22000) = 3.2 - 4.4 = -1.2$. Since $f_3'(22000) < -1$, the discrete logistic model oscillates and moves away from this equilibrium. Thus, this equilibrium is *unstable*. We show a simulation of this model in the right panel of Figure 5, starting with an initial value of $P_0 = 100$ and performing 30 iterations. The simulation shows the solution growing away from $P_e = 0$, then it settles into a *period 2 oscillation* taking on the values 16417 and 25583. ◁

Example 4 *Growth Rate Function for Logistic Model*

An alternate way to look at discrete population growth models is to consider the population at the $(n+1)^{st}$ generation as being equal to the population at the n^{th} generation plus the growth of the population, $g(p_n)$, between the generations. The logistic growth model in the form of a growth function rather than an updating function is given by the equation

$$p_{n+1} = p_n + g(p_n) = p_n + 0.05p_n(1 - 0.0001p_n),$$

where n is measured in hours. The advantage of this form of the model is that equilibria occur when the growth rate is zero. Clearly when a population stops growing (growth function is zero), then it must be at an equilibrium.

a. Assume that $p_0 = 500$ and find the population for the next three hours, p_1, p_2, and p_3.

b. Find the p-intercepts and the vertex for

$$g(p) = 0.05p(1 - 0.0001p).$$

Sketch a graph of $g(p)$.

c. By finding when the growth rate is zero, determine all equilibria for this model and find the stability of the equilibria.

Solution: a. We find the first three iterations by substituting each successive value into the given updating function. Thus,

$$\begin{aligned} p_1 &= p_0 + g(p_0) = 500 + 0.05(500)(1 - 0.0001(500)) = 524, \\ p_2 &= 524 + 0.05(524)(1 - 0.0001(524)) = 549, \\ p_3 &= 549 + 0.05(549)(1 - 0.0001(549)) = 574. \end{aligned}$$

b. Since $g(p) = 0.05p(1 - 0.0001p)$, the p-intercepts are found by solving

$$g(p) = 0.05p(1 - 0.0001p) = 0,$$

which gives either $p = 0$ or $1 - 0.0001p = 0$. The latter is equivalent to $p = 10,000$.

The vertex occurs halfway between the p-intercepts, so $p = 5,000$ and

$$g(5000) = 0.05(5000)(1 - 0.0001(5000)) = 125.$$

The vertex is the maximum growth rate of the population, so the maximum this population can grow is 125 **individuals/hr**.

The graph of $g(p)$ is a standard parabola, which is given in Figure 6 showing the p-intercepts and the vertex.

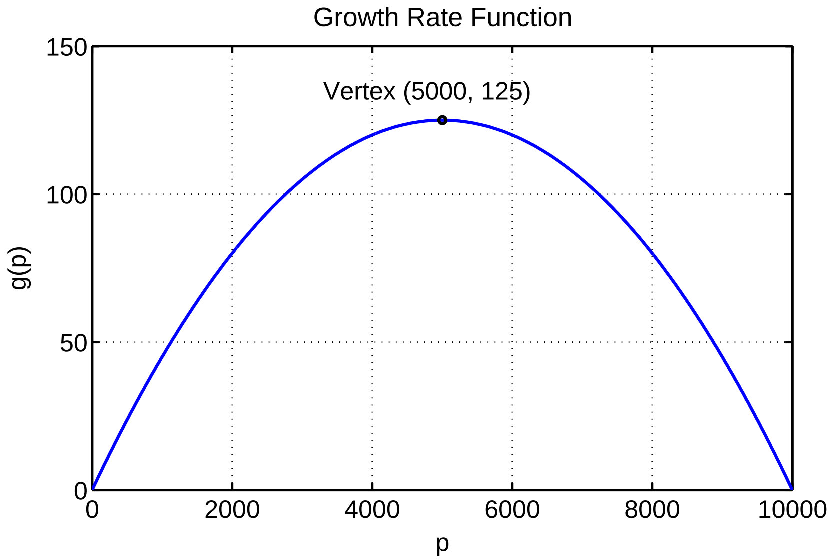

Figure 6: Parabola describing the growth rate function of Example 4.

c. From the graph of Figure 6, it is clear that the growth rate is zero at 0 and 10,000, so the equilibria occur at $p_e = 0$ and 10,000. The stability is still determined by differentiating the updating function, not the growth function,

$$p_{n+1} = f(p_n) = 1.05p_n - 0.00005p_n^2.$$

The derivative of the updating function is

$$f'(p_n) = 1.05 - 0.0001p_n.$$

At $P_e = 0$, the derivative is $f'(0) = 1.05 > 1$. Thus, the solution is unstable and monotonically grows away from $P_e = 0$. At the other equilibrium, $P_e = 10000$, the derivative is $f'(10000) = 0.05$. Since $0 < f'(10000) < 1$, the discrete logistic model is stable and the solutions monotonically approach the equilibrium, $P_e = 10000$. ◁

Example 5 *Stability of the Malthusian Growth Model*

The discrete Malthusian growth model was substantially easier to study than the logistic growth model. Its solution was simply an exponentially growing solution. Use the results from the lecture section to show that the only equilibrium of the Malthusian growth model is unstable.

Solution: We assume that there is a positive growth rate for a population of animals satisfying according to the discrete Malthusian growth model, so $r > 0$. The general Malthusian growth model is given by

$$P_{n+1} = (1+r)P_n.$$

The equilibrium is readily found by substituting P_e for P_n and P_{n+1}, giving

$$\begin{aligned} P_e &= (1+r)P_e \quad \text{or} \\ rP_e &= 0 \\ P_e &= 0. \end{aligned}$$

Thus, the only equilibrium for the discrete Malthusian growth model is the trivial solution, $P_e = 0$. When we take the derivative of the right hand side of the model, we find that the derivative is $(1+r)$, which is greater than one. This means that for any positive growth rate, the discrete Malthusian growth model is *unstable*, and the solution monotonically moves away from the equilibrium. This is in agreement with the exponential growing behavior shown earlier. ◁

Example 6 *Logistic Growth with Emigration*

We extend the earlier example to include the possibility that the population might be affected by immigration or emigration. Suppose that the growth rate for a population is given by

$$g(p) = 0.71p - 0.001p^2 - 7.$$

This says that between each generation there is a 71% growth rate, while $0.001p_n^2$ are lost due to crowding and 7 emigrate. The discrete dynamical model for this population model is given by

$$p_{n+1} = p_n + g(p_n) = p_n + 0.71p_n - 0.001p_n^2 - 7,$$

where n is measured in generations.

a. Assume that $p_0 = 100$ and find the population for the next three generations, p_1, p_2, and p_3.

b. Find the p-intercepts and the vertex for $g(p)$ and sketch a graph of $g(p)$.

c. By finding when the growth rate is zero, determine all equilibria for this model.

Solution: a. As we did in the previous example, we iterate this discrete logistic model with emigration to obtain the next three generations. Thus,

$$\begin{aligned} p_1 &= p_0 + g(p_0) = 100 + 0.71(100) - 0.001(100)^2 - 7 = 154, \\ p_2 &= 154 + 0.71(154) - 0.001(154)^2 - 7 = 233, \\ p_3 &= 233 + 0.71(233) - 0.001(233)^2 - 7 = 337. \end{aligned}$$

b. The growth function satisfies

$$\begin{aligned} g(p) &= 0.71p - 0.001p^2 - 7, \\ g(p) &= -0.001(p^2 - 710p + 7000), \\ g(p) &= -0.001(p - 10)(p - 700). \end{aligned}$$

The p-intercepts are found by solving $g(p) = 0$, which gives either

$$p = 10 \quad \text{or} \quad \text{p} = 700.$$

The vertex occurs halfway between the p-intercepts, so $p = 355$ and

$$g(355) = -0.001(345)(-345) = 119.$$

Thus, for this logistic growth model, the maximum growth occurs when the population is 355 with a maximum growth of 119 individuals/generation.

The graph of $g(p)$ is a parabola, which is shown in Figure 7 showing the p-intercepts at $p = 10$ and 700 and the vertex.

c. From the graph above, it is clear that the growth rate is zero at $p = 10$ and 700, so the equilibria occur at $p_e = 10$ and 700. ◁

Example 7 *U.S. Census with Logistic Growth Model*

The Malthusian growth model did not work well for the U. S. census data over any extended period of time because the growth rate in general has been declining for most decades in U.S. history. Can we apply the logistic growth model to the U.S. census data and get a better fit to the data and avoiding the problems of the time varying nonautonomous model developed at the end of Chapter 7?

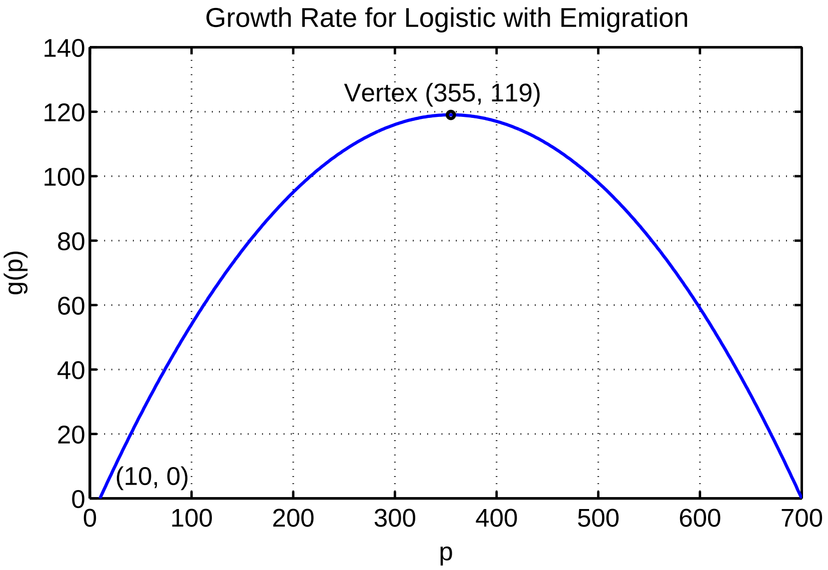

Figure 7: Parabola for the growth rate with emigration of Example 6.

Chapter 7 included the U.S. census data from 1790 to 2000. How does one find the appropriate updating function for a logistic growth model? The best fit to a model uses the least squares best fit technique given in Chapter 3. A least squares best fit to the U. S. census data was performed to find the best Malthusian growth model and the best logistic growth model. The best Malthusian growth model is given by

$$P_{n+1} = 1.2354 P_n.$$

The best logistic growth model satisfies the model

$$P_{n+1} = F(P_n) = P_n + 0.3064 P_n \left(1 - \frac{P_n}{313.8}\right).$$

We recall that a nonautonomous model fitting the time varying growth (using a linear fit to the data) satisfied the model

$$P_{n+1} = (1.3835 - 0.0155n) P_n.$$

The simulations of the Malthusian, logistic, and nonautonomous growth models are graphed in Figure 8 showing how well they compare to the actual U.S. census data. It is readily apparent that the Malthusian growth model does not fit the data very well, growing too slow in the early history of the U.S. and growing too rapidly more recently. The logistic growth model appears to fit the data fairly well. Still the best fit is the nonautonomous model developed in the discrete Malthusian growth chapter.

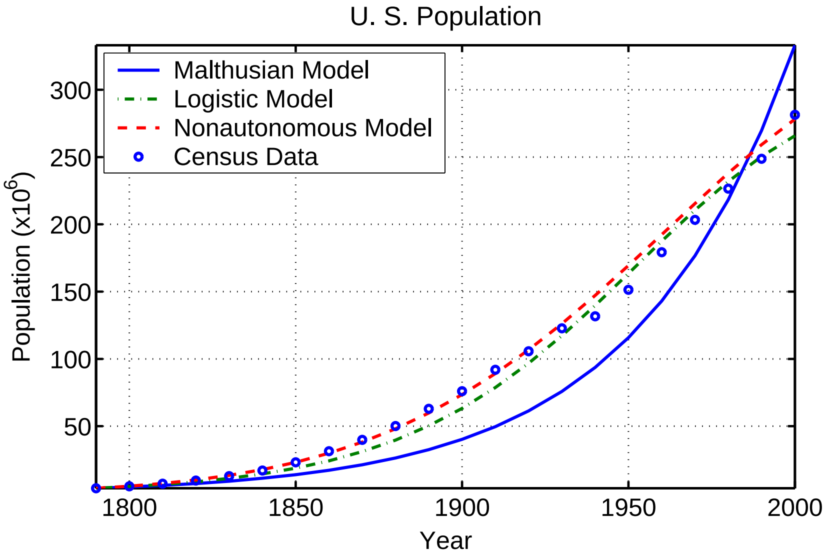

Figure 8: Graph of the three different models for the U.S. census data given in Chapter 7.

By plotting P_{n+1} *versus* P_n, one can see how the data compares to the updating function for the logistic growth model. The graph of this updating function with the data is seen in Figure 9 with the identity map $P_{n+1} = P_n$.

The logistic updating function very closely follows the census data except at a couple of points. We have seen that the equilibria are found by the intersection of the updating function and the identity map. The slope of the updating function at a point of intersection determines the stability of that equilibrium.

The equilibria for the logistic growth model above are $P_e = 0$ or 313.8 million. The derivative of the updating function is

$$F'(P) = 1.3064 - 0.00195P.$$

It follows that $F'(0) = 1.3064$, so $P_e = 0$ is unstable as expected. Similarly, $F'(313.8) = 0.6936$, so the equilbrium $P_e = 313.8$ million is stable. Thus, the logistic growth model fit to the U.S. census data predicts that the population of the U.S. will growth monotonically, then level off at 313.8 million. Note that this population is not much higher than the 2000 census value, while actual projections have the U.S. population rising to over 400

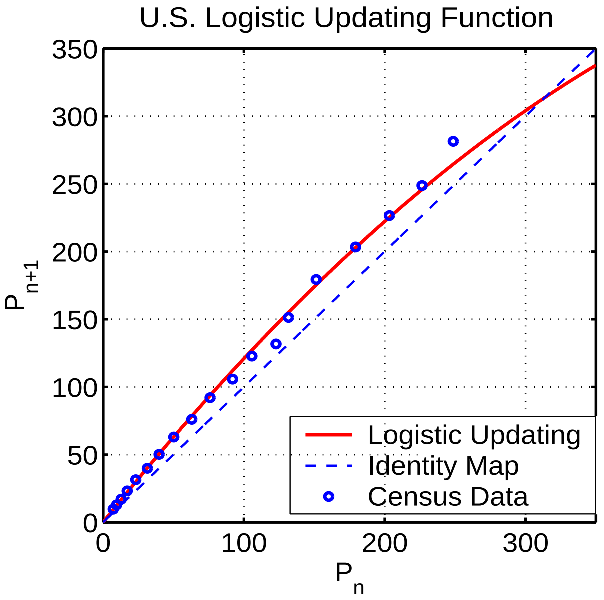

Figure 9: Logistic updating function for the U.S. census data of Example 7.

million by the middle of the next century.

The logistic growth model is easier to analyze than the nonautonomous model, but the nonautonomous model appears to fit the growth of the U.S. population better. By extending the analysis of the nonautonomous growth model, we see that the growth continues until $n = 25$ (actually 24.7), then this model has the population beginning to decline. Simulating this model for 25 decades (until 2040) finds that a maximum population of 318.8 million is reached. (Details of this analysis are omitted.) Note that the nonautonomous model and the logistic growth model both seem to predict a similar maximum population for the U.S. and both are unrealistically low. This shows that human populations have a more complicated dynamics than these models can predict with either time-varying or crowding factors. (Sociological and technical factors are especially difficult to incorporate into mathematical models.) Your ecology courses should help explain more details underlying the assumptions in these models, so explain a little better when the models are applicable and why they fail in other predictions. It is unlikely that human population can continue its current course, but what will be the actual scenario? Mathematical modeling can provide reasonable estimates for short term growth and allows one to predict several different possibilities for longer term growth depending on the assumptions that are entered into the model. ◁

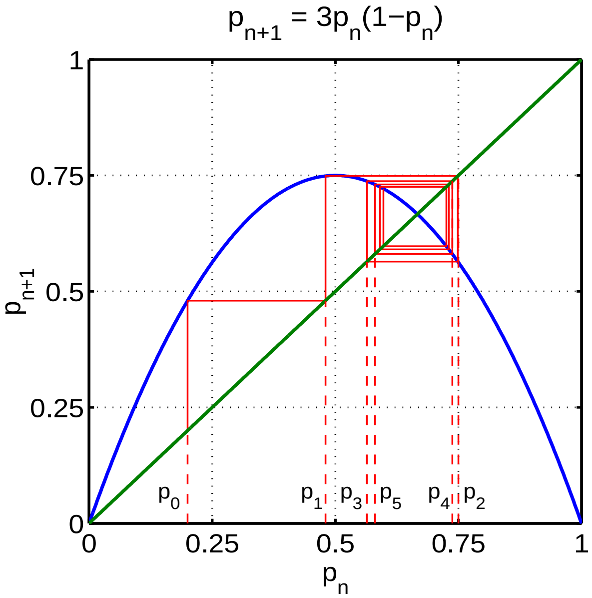

Figure 10: Graph describing the cobwebbing method for understanding the dynamics of the Logistic Growth equation.

7 COBWEBBING

In Chapter 8, we introduced a more geometric way to visualize these dynamical systems, *cobwebbing*. The website of B. Fraser shows this cobwebbing for the logistic growth model in a nice applet[2]. The updating function, $f(p_n)$, is graphed with the identity map, $p_{n+1} = p_n$ on a single graph with the vertical axis being p_{n+1} and the horizontal axis being p_n. The idea is that you start at any p_0, then go vertically to $p_1 = f(p_0)$. Next you go horizontally to the identity map to locate p_1 on the horizontal axis. From there you find p_2 by going vertically to $p_2 = f(p_1)$. This process is repeated to generate the cobweb of points by this discrete dynamical system. The sequence of points on the horizontal axis form the solution set generated by the discrete dynamical system. The graphical representation allows you make some projections of the behavior of the system. Figure 10 shows a

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[2] www.apmaths.uwo.ca/~bfraser/version1/iterated.html,last visited on 04/14/04

diagram showing several steps in the cobwebbing scheme for the quadratic map

$$p_{n+1} = 3p_n(1 - p_n).$$

8 EXERCISES

1. Consider the discrete logistic growth model given by

$$P_{n+1} = 1.5P_n - 0.0025P_n^2.$$

a. Suppose that the initial population P_0 is 50. Find the population of the next three generations, P_1, P_2, and P_3.

b. Sketch a graph of the updating function with the identity map, $P_{n+1} = P_n$. Be sure to show the intercepts of the parabola as well as the vertex. Find the equilibria and identify them with your graph.

2. Consider the discrete logistic growth model given by

$$P_{n+1} = f(P_n) = 1.25P_n - 0.00125P_n^2.$$

a. Suppose that the initial population $P_0 = 2000$. Find the population of the next three generations, P_1, P_2, and P_3. Find all equilibria.

b. Sketch a graph of the updating function, $f(P)$, with the identity map, $P_{n+1} = P_n$. Find the intercepts and the vertex of the parabola.

3. Assume that the growth rate of a population P satisfies

$$g(P) = 0.03P(1 - P/600).$$

The discrete logistic growth model for this population is given by:

$$P_{n+1} = P_n + g(P_n).$$

a. Find the population when the growth rate $g(P)$ is zero (the P-intercepts) and when it is a maximum (the vertex). Sketch the graph of $g(P)$.

b. Let $P_0 = 100$ and compute P_1, P_2, and P_3. Find all equilibria.

4. Assume that the growth rate of a population P satisfies

$$g(P) = 0.02P(1 - 0.0004P).$$

The discrete logistic growth model for this population is given by:

$$P_{n+1} = P_n + g(P_n).$$

a. Find the population when the growth rate $g(P)$ is zero and when it is a maximum. Sketch the graph of $g(P)$.

b. Let $P_0 = 5000$ and compute P_1, P_2, and P_3. Find all equilibria.

5. A modified version of the discrete logistic growth model that includes emigration is given by

$$P_{n+1} = f(P_n) = 1.1P_n - 0.0001P_n^2 - 9.$$

a. Suppose that the initial population P_0 is 500. Find the population of the next three generations, P_1, P_2, and P_3.

b. Sketch a graph of the updating function with the identity map, $P_{n+1} = P_n$. Be sure to show the intercepts of the parabola as well as the vertex. Find the equilibria and identify them on your graph.

6. A modified version of the discrete logistic growth model that includes immigration is given by

$$p_{n+1} = f(p_n) = 1.2p_n - 0.0001p_n^2 - 44.$$

a. Suppose that the initial population $P_0 = 1000$. Find the population of the next three generations, p_1, p_2, and p_3.

b. Sketch a graph of the updating function with the identity map, $p_{n+1} = p_n$. Be sure to show the intercepts of the parabola as well as the vertex. Find the equilibria and identify them on your graph.

7. Consider Hassell's model that is given by

$$p_{n+1} = H(p_n) = \frac{5p_n}{1 + 0.002p_n}.$$

a. Assume that $p_0 = 500$ and find the population for the next three generations, p_1, p_2, and p_3.

b. Find the p-intercepts and the horizontal asymptote for $H(p)$ and sketch a graph of $H(p)$ for $p > 0$ along with the identity map, $p_{n+1} = p_n$.

c. By solving $p_e = H(p_e)$, determine all equilibria for this model.

8. Consider Hassell's model that is given by

$$p_{n+1} = H(p_n) = \frac{10p_n}{1 + 0.0001p_n^2}.$$

a. Assume that $p_0 = 100$ and find the population for the next three generations, p_1, p_2, and p_3.

b. Find the p-intercepts and the horizontal asymptote for $H(p)$ and sketch a graph of $H(p)$ for $p > 0$ along with the identity map, $p_{n+1} = p_n$.

c. By solving $p_e = H(p_e)$, determine all equilibria for this model.

9 REFERENCES

[1] T. Carlson Über Geschwindigkeit und Grösse der Hefevermehrung in Würze. *Biochem. Z.* (1913) **57**, 313–334.

CHAPTER 20:

MORE APPLICATIONS OF NONLINEAR DYNAMICAL SYSTEMS

Chapter 19 on the discrete logistic growth model established the key elements for studying the *qualitative behavior of a discrete dynamical model.* First, the *equilibria* for the model are found, then using the derivative of the *updating function, the local stability* of the equilibria are determined. This section extends our analysis to other nonlinear discrete dynamical models, which in certain cases improves on the discrete logistic growth model. The study of the stability of these models uses a variety of the differentiation techniques learned earlier.

The first extension to the study of the Malthusian growth model was the logistic growth model, which improved on the Malthusian growth model by accounting for the crowding effects that result in natural limits to populations. The logistic growth model employs a quadratic updating function, which becomes negative for large populations. Ecologists have modified the logistic growth model in several ways to make the updating function more realistic and better able to handle largely fluctuating populations. One model that is often used in fishery management is *Ricker's model.* Populations of insects undergo large fluctuations, so again the logistic growth with its negative updating function for large populations is replaced with an alternative model, *Hassell's model.* Below these models are fit to data, then analyzed using the techniques learned in the previous sections.

1 SOCKEYE SALMON POPULATIONS

Recently, the salmon population in the Pacific Northwest has become sufficiently endangered that many salmon spawning runs could become extinct. (This already happened years ago in California.) Salmon are unique in that they breed in very specific fresh water lakes and die. Their offspring migrate a tortuous path to the ocean, where they mature for about 4– 5 years. Then an unknown urge causes the mature salmon to migrate at the same time to return to the exact same lake or river bed where they hatched 4–5 years earlier. The adult salmon breed and die with their bodies providing many essential nutrients that nourish the stream where their young will repeat this process. Human activity from damming rivers, forestry, which allows the water to become too warm, and agriculture, which results in runoff pollution, all adversely affect this complex life cycle of the salmon. Many of the ancient salmon runs have now gone extinct.

This life cycle of the salmon is a clear example of a complex discrete dynamical system. Because of the importance of this fish to many people in the Pacific Northwest, there have been many studies of the salmon populations. Below is a table listing four year averages of the sockeye salmon (*Oncorhynchus nerka*) in the Skeena river system in British Columbia from 1908 to 1952. (The Canadian river systems have not been as severely affected by other human activities as the ones in the U.S. but rapid development in their forests are likely to have similar effects.) The table lists the four year averages from the starting year of the data being averaged. Since it is 4 and 5 year old salmon that spawn, each grouping of 4 years is a rough approximation of the offspring of the previous 4 year average of salmon. (It is complicated because the salmon have adapted to have either 4 or 5 year old mature adults spawn, but this will be ignored in our modeling efforts.)

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

Table 1: Four Year Averages of Skeena River Sockeye Salmon.

We want to use these data to create a discrete dynamical system to describe the population of salmon in the Skeena river watershed. This system can be analyzed to determine information about expected salmon runs to study the health of the ecosystem.

2 RICKER'S MODEL

The logistic growth model extends the Malthusian growth model and includes an additional term for the crowding effects on population growth. As populations become more crowded, the resource limitations result in a decrease in the population growth rate. The logistic growth model was given by

$$P_{n+1} = P_n + rP_n(1 - P_n/M),$$

where P_n is the population at the n^{th} time period, r is the Malthusian growth rate, and M is the carrying capacity of the population. Our chapter on the logistic growth model showed that this model did a reasonable job for predicting certain yeast populations. This model can be applied reasonably well to unicellular organisms that are provided a fixed amount of nutrient, such as a culture of yeast growing in a controlled environment. However, this model does not fit the data for many organisms, such as the salmon population listed above. If a population experiences large fluctuations, then for very large populations the logistic growth model may return a negative population in the next generation, which is clearly unrealistic. Several alternative models have been proposed, where the updating function remains positive.

One such model is *Ricker's model*, which it is claimed was originally formulated using studies of salmon populations. This model is very frequently used in fisheries management problems. We will apply this model to the sockeye salmon data listed above.

> *Ricker's model* is given by the equation
>
> $$P_{n+1} = R(P_n) = aP_n e^{-bP_n},$$
>
> where a and b are positive constants that are fit to the data.

In Figure 1 is a graph showing the data of successive generations from the averaged data listed in Table 1. For example, the parent population of 1908–1911 is averaged to $1,098,000$ salmon/year returning to the Skeena river watershed, and 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. This produces the furthest point on the right in the graph of the left panel of Figure 1.

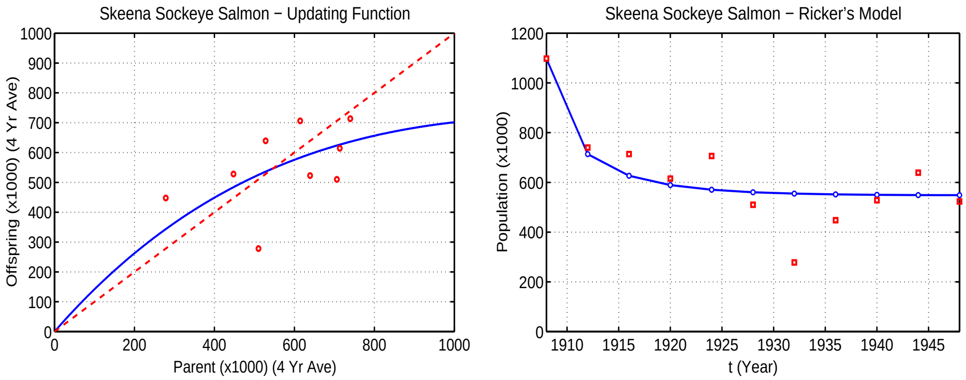


Figure 1: Left: Graph of the data listed in Table 1 and the function of parent offspring *vs.* parent population. Right: Graph of the function of the Skeena Sockeye Salmon population according to Ricker's model and the data of Table 1.

A nonlinear least squares fit of the Ricker function above is used on the data and the best Ricker's model for the Skeena sockeye salmon population from 1908–1952 is given by

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

Before we analyze this model, we simulate the model using the initial average in 1908 as our starting point and see how well the model traces the data of Table 1. A graph of this simulation is in right panel of Figure 1.

We see that the Ricker's model has the population leveling off at a stable equilibrium around $550,000$, which is relatively consistent with the data. There are a few fluctuations, which is what we would expect from the variations in the environment. However, the model suggests that this is a robust ecological system that maintains a healthy population. Below we will perform a more detailed analysis of this model and use the techniques that we have developed in earlier sections to find equilibria, graph the Ricker's function, and determine the stability of the Ricker's model.

2.1 ANALYSIS OF THE RICKER'S MODEL

As in the logistic model, Ricker's model has two equilibria with one of them being the trivial or zero equilibrium. The equilibria for this model are found by setting $P_e = P_{n+1} = P_n$, which gives

$$P_e = a P_e e^{-bP_e} \quad \text{or} \quad P_e(1 - a e^{-bP_e}) = 0.$$

From this equation, we readily see that

$$\begin{aligned} P_e &= 0 \quad \text{and} \\ P_e &= \ln(a)/b. \end{aligned}$$

Note that the second equilibrium is positive (real for our model) only if $a > 1$.

The previous section notes that the stability of the equilibria are related to the derivative of the updating function evaluated at the equilibrium. Thus, for Ricker's model, the stability condition for the equilibria is given by

$$|R'(P_e)| < 1.$$

Thus, we need to be able to take the derivative of the Ricker's updating function, which requires the product rule of differentiation. Applying the product rule to the Ricker's function $R(P) = aPe^{-bP}$ gives

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

The equilibrium $P_e = 0$ is stable if $R'(0) = a < 1$, while if $R'(0) = a > 1$, then the solution monotonically grows away from this equilibrium. At the equilibrium $P_e = \ln(a)/b$, the derivative of the Ricker's updating is

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

Recall that $a > 1$ for a positive equilibrium. In Chapter 19, we saw that the stability of an equilibrium depended on the value of the derivative at the equilibrium.

The analysis of the Ricker's model in general is as follows:

1. The solution of Ricker's model is *stable* and *monotonically approaches* the equilibrium $P_e = \ln(a)/b$ provided $a < e = 2.7183$.

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

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

Example 1 *Ricker's Growth Model*

Let P_n be the population of fish in any year n. Consider Ricker's model for population growth given by the equation

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

Sketch a 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, graphing the solution.

Solution: First, we see that the only intercept is the origin, $(0,0)$. Since the negative exponential dominates in the function $R(P)$, there is a horizontal asymptote of $P_{n+1} = 0$. To find the extrema, we differentiate $R(P)$. Applying the product rule we obtain,

$$R'(P) = 7[P(-0.02e^{-0.02P}) + e^{-0.02P}] = 7e^{-0.02P}(1 - 0.02P).$$

This expression is zero only when $1 - 0.02P = 0$ or $P_c = 50$. Thus, there is a critical point for the updating function at

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

The graph of the updating function along with the identity function is shown in the left panel of Figure 3. They intersect at the equilibria, which are calculated next.

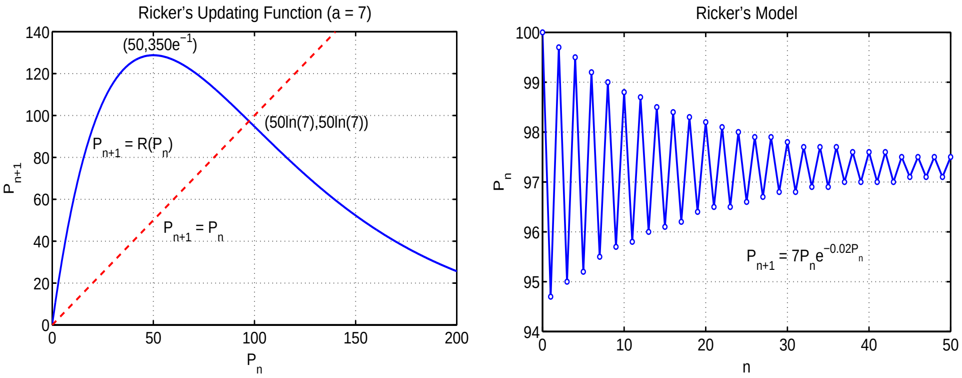


Figure 2: Left: Graph of the Ricker's updating function according to Example 1, and the identity line. Right: Simulation for the solution of Ricker's model of Example 1.

To find the equilibria, we substitute P_e for P_{n+1} and P_n in the Ricker's model. The resulting equation is given by

$$P_e = 7P_e e^{-0.02P_e}.$$

One equilibrium is given by $P_e = 0$, so we can divide out P_e, leaving

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

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

To find the behavior of the solution near each of these, we must substitute the value of the equilibrium into the expression for the derivative. First, we analyze the stability of $P_e = 0$. We see that,

$$R'(0) = 7e^0(1-0) = 7 > 1,$$

which is unstable, and the population grows monotonically away from the equilibrium $P_e = 0$.

Next we consider $P_e = 50\ln(7)$. Substituting into the formula for the derivative gives

$$\begin{aligned} R'(50\ln(7)) &= 7e^{-0.02(50\ln(7))}(1-0.02(50\ln(7))) \\ &= 7e^{-\ln(7)}(1-\ln(7)) \\ &= 1-\ln(7) \approx -0.95 \end{aligned}$$

Thus, $-1 < R'(50\ln(7)) < 0$, so we have a stable equilibrium point with solutions oscillating, but approaching the equilibrium, $P_e = 50\ln(7)$. The simulation with $P_0 = 100$ is shown in the graph of Figure 3. The solution is slowly oscillating toward the equilibrium, as can be seen with 50 iterations. ◁

Example 2 Now consider Ricker's model given by

$$P_{n+1} = 9P_n e^{-0.02P_n},$$

and repeat the previous problem.

Solution: Many of the computations carry over from the example above. The only intercept is the origin, $(0,0)$, and there is a horizontal asymptote of $P_{n+1} = 0$. The derivative is only slightly changed as the leading constant is the only variation, so

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

As in the previous example, the critical point satisfies $P_c = 50$, which gives a maximum at

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

The graph of the updating function along with the identity function is shown in Figure **??** with the important points labeled.

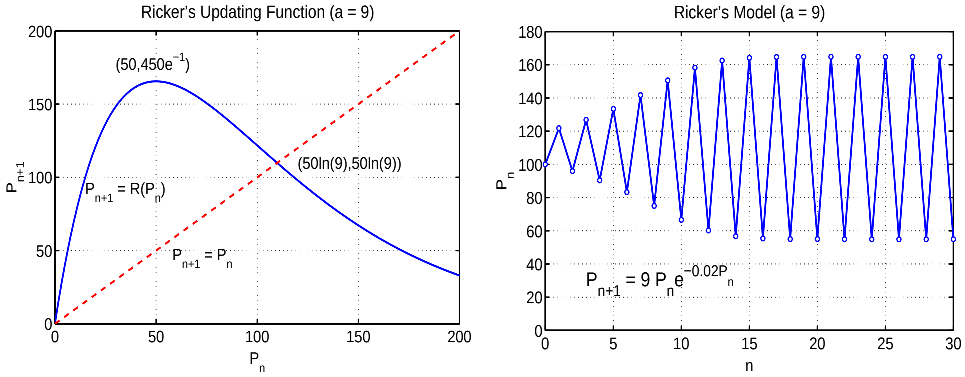


Figure 3: Left: Graph of the Ricker's updating function according to Example 2, and the identity line. Right: Simulation for the solution of Ricker's model of Example 2.

The equilibria are found just like the previous example by using P_e for P_{n+1} and P_n in the Ricker's model. The resulting equation is given by

$$P_e = 9P_e e^{-0.02P_e}.$$

The calculations are very similar giving the two equilibria, $P_e = 0$ and $P_e = 50\ln(9) \approx 109.86$.

The stability analysis uses the same techniques as before, but the behavior changes at the upper equilibrium. Near $P_e = 0$, we evaluate the derivative and obtain

$$R'(0) = 9e^0(1-0) = 9 > 1,$$

which is unstable with the population growing away from this equilibrium.

Near $P_e = 50\ln(9)$, we find that

$$\begin{aligned} R'(50\ln(9)) &= 9e^{-0.02(50\ln(9))}(1 - 0.02(50\ln(9))) \\ &= 1 - \ln(9) \approx -1.197 \end{aligned}$$

Thus, $R'(50\ln(9)) < -1$, so we have an unstable equilibrium point with solutions oscillating and moving away from the equilibrium. In Figure **??** there is a simulation with 30 iterations, starting with $P_0 = 100$. Clearly, the solution oscillates with increasing amplitude. The solution goes to a *period 2* behavior, oscillating between 55 and 165. ◁

3 SOCKEYE SALMON OF SKEENA RIVER REVISITED

From the notes above we have that the best Ricker's model for the Skeena sockeye salmon population from 1908–1952 is

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

We find the equilibria and stability of the equilibria for this particular case. Let $P_e = P_{n+1} = P_n$, then

$$P_e = 1.535 e^{-0.000783 P_e}$$

so

$$P_e = 0 \quad \text{or} \quad 1 = 1.535 e^{-0.000783 P_e}.$$

It follows that $e^{0.000783 P_e} = 1.535$ or

$$P_e = \frac{\ln(1.535)}{0.000783} = 547.3.$$

Thus, the two equilibria are $P_e = 0$ and 547.3 with the latter equilibrium value close to the value observed in the graph of the simulation of Figure 1.

Next we differentiate $R(P)$ and see that

$$\begin{aligned} R'(P) &= 1.535\left(-0.000783 P e^{-0.000783 P} + e^{-0.000783 P}\right) \\ &= 1.535 e^{-0.000783 P}(1 - 0.000783 P). \end{aligned}$$

Thus, at $P_e = 0$,

$$R'(0) = 1.535 > 1,$$

which shows that the equilibrium at 0 is *unstable* as expected. At $P_e = 547.3$.

$$R'(547.3) = 1.535 e^{-0.4285}(1 - 0.4285) = 0.571 < 1,$$

which implies that this equilibrium is *stable with solutions monotonically approaching the equilibrium*, as we observed in the simulation.

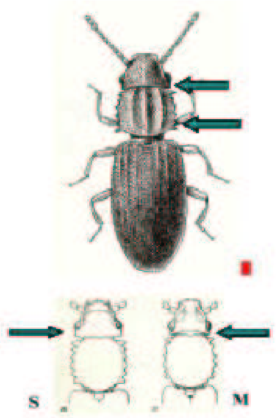
4 HASSELL'S MODEL

As noted above, *Hassell's model*, which is written in the form of a quotient, is an alternative to the *Logistic growth model* and *Ricker's model* and is frequently applied to insect populations. *Hassell's model* for studying the dynamics of insect populations has the form:

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

where a, b, and c are parameters that are chosen to match the data for a population study of some insect. The numerator of $H(P_n)$ is the Malthusian growth model, so that at low population densities, the population grows exponentially. (Recall that this requires $a > 1$.) As the population increases, the denominator increases, which slows the rate of growth. The denominator is a composite function, including a linear function, $1 + bP_n$, which is raised to the c power. Thus, differentiation of $H(P_n)$ requires the chain rule.

4.1 STUDY OF A BEETLE POPULATION



Gorham, 1987

Figure 4: We can understand the behavior of the *Oryzaephilus surinamensis*, the saw-tooth grain beetle population, through discrete mathematical models.

In 1946, A.C. Crombie [1] studied several beetle populations to try to better understand their dynamics under the strict control of a constant amount of food regularly supplied. He maintained the amount of food at 10 grams of cracked wheat added weekly, then regularly took census of the beetle populations. These experimental conditions match the assumptions used by the *Logistic growth model*. One study was on *Oryzaephilus surinamensis*, the saw-tooth grain beetle. Table 5 presents his data (with some minor modifications to fill in times of uncollected data and an initial one week shift).

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

Table 2: Weekly (*Oryzaephilus surinamensis*) population census according to A.C. Crombie [1].

By plotting the data of P_{n+1} *vs.* P_n, we can fit an *updating function* to the data, then use this updating function to study the population dynamics with an appropriate discrete dynamical model. This section compares Hassell's model to the Logistic growth model in chapter 1. In Figure 5 there is a graph showing the best fit to Crombie's data for *Oryzaephilus surinamensis* for both Hassell's model and the Logistic growth model. (The best fit for Hassell's model was found using the *fminsearch* routine in *MatLab*, while the Logistic growth model used *Trendline* in *Excel.*)

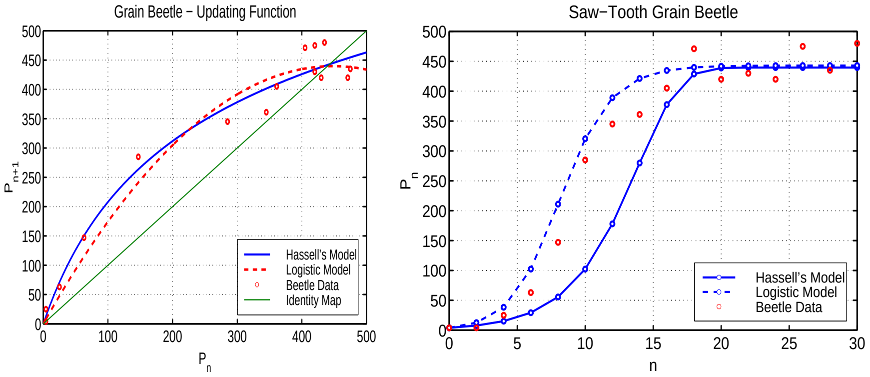


Figure 5: Left: Graph for the updating function using three different alternatives described in Example 4.1, and the data of Table 2. Right: Simulations for the Hassell and Logistic models for the Saw-Tooth Grain Beetle data of Table 2.

With three parameters, Hassell's updating function is capable of fitting the data better than the quadratic function of the Logistic growth model. Hassell's updating function has the added advantage that it never becomes negative, which was a property of Ricker's model. The best model from Hassell's formula is given by,

$$P_{n+1} = H(P_n) = \frac{3.255P_n}{(1+0.0073P_n)^{0.8178}},$$

while the best Logistic growth model satisfies

$$P_{n+1} = L(P_n) = 1.962P_n - 0.002189P_n^2.$$

With the updating functions above, these discrete dynamical models are simulated and compared to the data of A.C. Crombie [1]. Figure 5 shows the simulations of the models with the data (assuming the models agree with the data at week 0). We note that an alternative method of fitting the models (see section 6) is to apply the least squares best fit to the simulation rather than finding the best fitting updating function. When this technique is applied the simulations are very close, but again Hassell's model fits better.

We can readily see that Hassell's model does appear to simulate the data better, especially having the early rapid rise in the population. All seem to tend toward a similar carrying capacity. For more details on the behavior of these models, we perform our standard analysis of the discrete models, locating equilibria and using the derivative to test the local behavior of these models.

4.2 ANALYSIS OF HASSELL'S MODEL

We return to the general Hassell's model to obtain the equilibria and determine stability conditions for the equilibria. Following the usual techniques for studying discrete dynamical models, the equilibria of Hassell's model are found by letting $P_e = P_n = P_{n+1}$. Thus, we solve

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

This is equivalent to

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

One of the equilibria is $P_e = 0$, while the other solves $(1+bP_e)^c = a$. This latter equation is easily solved by taking the c^{th} root of each side, then completing the algebra, so

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

Note that the this equilibrium requires the condition $a > 1$.

To determine the stability of the equilibria, we differentiate the function $H(P)$. This requires the quotient rule, which in turn requires differentiating the denominator, which is a composite function. Below we use the chain rule to differentiate the term in the denominator.

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

Now applying the quotient rule, we find that

$$H'(P) = \frac{a(1 + bP)^c - abcP(1 + bP)^{c-1}}{(1 + bP)^{2c}} = a\frac{1 + bP - bcP}{(1 + bP)^{c+1}} = a\frac{1 + b(1 - c)P}{(1 + bP)^{c+1}}.$$

This formula shows that $H'(0) = a$, but since $a > 1$ for a positive equilibrium to exist, this condition implies that the zero (or trivial) equilibrium in unstable with solutions monotonically growing away from this equilibrium. At the other equilibrium, we can evaluate $H'(P_e)$ and obtain

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

This calculation shows that the stability of the carrying capacity equilibrium is very dependent on both a and c, but not b. Further algebra on the derivative calculation above and stability results of Chapter 1 give the following:

General stability results for Hassell's model for $c > 2$:

1. The solution of Hassell's model is *stable* and *monotonically approaches* the equilibrium $P_e = (a^{\mathbf{1/c}} - 1)/b$ provided $1 < a < (c/(c - 1))^c$.
2. The solution of Hassell's model is *stable* and *oscillates as it approaches* the equilibrium $P_e = (a^{\mathbf{1/c}} - 1)/b$ provided $(c/(c - 1))^c < a < (c/(c - 2))^c$.
3. The solution of Hassell's model is *unstable* and *oscillates as it grows away* from the equilibrium $P_e = (a^{1/c} - 1)/b$ provided $a > (c/(c - 2))^c$.

This result can be readily modified to handle the cases where $1 < c < 2$ or $0 < c < 1$, but these cases are left to the reader.

5 BEETLE STUDY REVISITED

When we apply the qualitative analysis results from the logistic growth chapter or the material above, then we can provide more information about the models described above. The best Logistic growth model that fits the Crombie data is given by

$$P_{n+1} = L(P_n) = 1.962P_n - 0.002189P_n^2,$$

while the best Hassell's model for the saw-tooth grain beetle satisfies

$$P_{n+1} = H(P_n) = \frac{3.255P_n}{(1 + 0.0073P_n)^0.8178}.$$

For the logistic growth model, the carrying capacity is the non-zero solution to

$$\begin{aligned} P_e &= 1.962P_e - 0.002189P_e^2, \\ 0.002189P_e &= 0.962, \\ P_e &= 439. \end{aligned}$$

which gives $M = 439$. The derivative evaluated at this equilibrium is

$$L'(439) = 1.962 - 0.004378(439) = 0.04 < 1.$$

Thus, our stability results show that the logistic growth model predicts that populations of *Oryzaephilus surinamensis* will grow monotonically and level off at the equilibrium $P_e = 439$.

For Hassell's model, the positive equilibrium is

$$\begin{aligned} P_e &= \frac{3.255P_e}{(1 + 0.0073P_e)^{0.8178}}, \\ (1 + 0.0073P_e)^{0.8178} &= 3.255, \\ P_e &= (3.255^{1.223} - 1)/0.0073 = 443. \end{aligned}$$

which gives a carrying capacity of $M = 443$. The derivative evaluated at this equilibrium is

$$H'(443) = (0.8178/3.255^{1.223}) + (1 - 0.8178) = 0.375 < 1.$$

Thus, this stability result shows that Hassell's model predicts that populations of the saw-tooth grain beetle will grow monotonically and level off at the equilibrium $P_e = 443$. The logistic and Hassell's growth models have similar carrying capacities with the same qualitative behavior of monotonically approaching this equilibrium. These qualitative behaviors are easily seen in the simulation graphically shown above. Our studies above show that functions that look quite different can result in very similar behavior.

Example 3 *Hassell's model*

Suppose that a population of insects is measured weekly and satisfies Hassell's model. Assume it follows the discrete dynamical model given by the equation

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

where n is measured in weeks.

a. Assume that $p_0 = 200$ and find the population for the next four weeks, p_1, p_2, and p_3. Graph a simulation of the model for 10 weeks.

b. Find the p-intercepts and the horizontal asymptote for $H(p)$ and sketch a graph of the updating function $H(p)$ for $p > 0$. (Note that the vertical asymptote occurs at $p = -50$, which is outside the biologically valid range as p should be greater than or equal to 0.) Include the identity map on the graph.

c. Determine all equilibria, $p_e$or this model and discuss their stability.

Solution: a. We iterate this nonlinear dynamical model by Hassell by substituting the value of $p_0 = 200$ into the model. The result is

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

Figure 6 is the simulation of the first 10 weeks of the insect population.

b. For the updating function, the only intercept for $H(p)$ is $(0, 0)$, while the horizontal asymptote is $H = 1000$. Biologically, this implies that there is a maximum number in the next generation, no matter how large the population starts (which is reasonable considering limited resources). Thus,

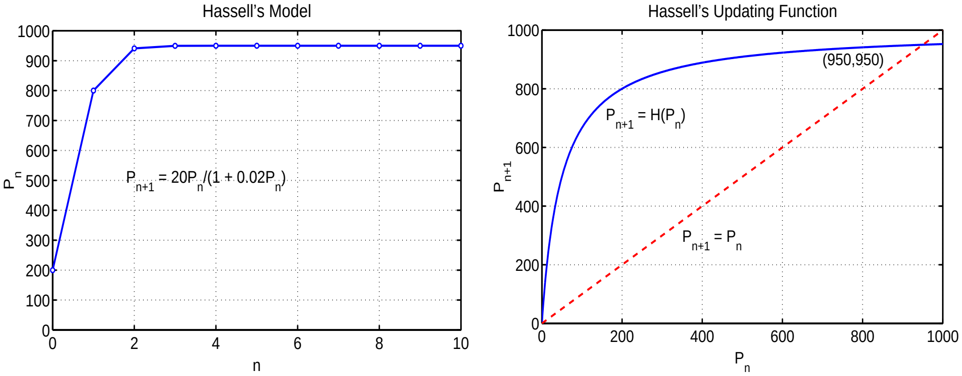


Figure 6: Left: Simulation for the first 10 weeks of the insect population of Example 3. Right: Graph of the updating function of the Hassell's model of Example 3.

the population (after the initial population) must always remain below $P_n = 1000$. In the right panel of Figure 6 there is a graph of Hassell's updating function along with the identity map. The intersections give the equilibria.

c. The equilibria are found by setting $p_e = p_{n+1} = p_n$, so we solve

$$p_e = \frac{20p_e}{1 + 0.02p_e}.$$

One solution is clearly $p_e = 0$. Next we multiply both sides by $(1 + 0.02p_e)/p_e$, which gives

$$1 + 0.02p_e = 20.$$

Solving this equation gives the other equilibrium,

$$p_e = 950.$$

To determine the stability of the equilibria, we must differentiate $H(p)$. From the quotient rule,

$$H'(p) = \frac{20(1 + 0.02p) - 20(0.02)p}{(1 + 0.02p)^2} = \frac{20}{1 + 0.02p)^2}.$$

Notice that $H'(p) > 0$, so $H(p)$ is always increasing. We expect the behavior of the model near the zero equilibrium to grow exponentially away from 0. Since

$$H'(0) = 20 > 1,$$

the equilibrium $p_e = 0$ is unstable with solutions monotonically growing away from it.

At $p_e = 950$, we can easily compute the derivative obtaining

$$H'(950) = \frac{20}{(1 + 0.02(950))^2} = \frac{1}{20}.$$

Thus, our properties on the stability of discrete dynamical models give $p_e = 950$ as being stable with all solutions monotonically approaching this equilibrium. ◁

Example 4 *Another Version of Hassell's Model*

Suppose that a study shows that a population, P_n, of butterflies satisfies the dynamic model given by the following equation:

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

where n is measured in weeks. Let $P_0 = 200$, then find P_1 and P_2. Find the intercepts, all extrema of $H(P)$, and any asymptotes for $P > 0$. Determine the equilibria and analyze the behavior of the solution near the equilibria.

Solution: The iterations are found in the standard way with

$$\begin{aligned} P_1 &= H(200) = 16200/(1.4)^4 = 4271, \\ P_2 &= H(4271) = 43. \end{aligned}$$

Thus, we see dramatic population swings with this model, suggesting an instability.

Analyzing $H(P)$, we find that the only intercept is $(0, 0)$ and that there is a horizontal asymptote with $H = 0$ (since the power of the denominator exceeds the power of the numerator). To find where the maximum occurs, we differentiate the function.

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

Solving $H'(P) = 0$, we have $1 - 0.006P = 0$ or $P = 500/3 = 166.7$. With $H(500/3) = 4271.5$, the maximum occurs at $(166.7, 4271.5)$. A graph of the updating function with the identity function is shown in Figure 7.

As always, the equilibria are found by solving $P_e = H(P_e)$, which is equivalent to solving

$$P_e(1 + 0.002P_e)^4 = 81P_e.$$

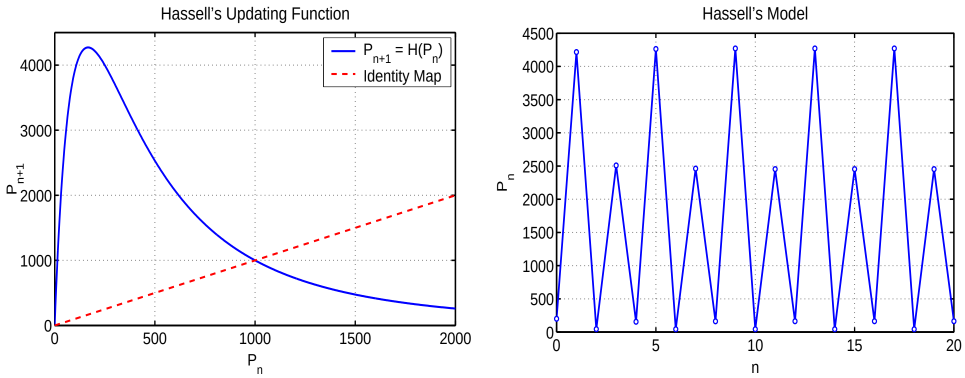


Figure 7: Left: Updating function of the Hassell's model of Example 4. Right: Simulation for the Hassell's model of Example 4.

So either $P_e = 0$ or $(1 + 0.002P_e)^4 = 81$, which gives $1 + 0.002P_e = 3$ or $P_e = 1000$. The stability of these equilibria can be determined by examining the derivative at the equilibria. At $P_e = 0, H'(0) = 81$, which implies from our rules that the solutions monotonically grow away from 0. At $P_e = 1000, H'(1000) = 81(-5)/243 = -5/3$. This implies that the solution near this equilibrium oscillates and goes away from the equilibrium. In fact, this model produces a *period 4* solution with the solution asymptotically oscillating from 163 to 4271 to 42 to 2453. A simulation of this model is shown in Figure **??**. ◁

Example 5

Model for Cellular Division with Inhibition

In the quotient rule of differentiation we learned in Chapter 16, a model for mitosis control by chalones was introduced. This model suggests that a biochemical agent known as a chalone is released by cell to inhibit the mitosis of nearby cells, preventing the over crowding of cells. Early models of cancer speculated that a break down in this control would lead to canceer. Consider the mitotic model given by the equation

$$P_{n+1} = f(P_n) = \frac{2P_n}{1 + (0.01P_n)^4} = \frac{2P_n}{1 + 10^{-8}P_n^4}.$$

Find the equilibria for this model and determine the behavior of the population near the equilibria. Also, start with an initial population of $P_0 = 10$, and simulate this model for 20 mitotic divisions.

Solution: To find the equilibria, we let $P_e = P_n = P_{n+1}$ in the discrete dynamical model above. We find that

$$\begin{aligned} P_e &= \frac{2P_e}{1+10^{-8}P_e^4}, \\ P_e(1+10^{-8}P_e^4) &= 2P_e, \\ P_e(10^{-8}P_e^4 - 1) &= 0. \end{aligned}$$

Thus, either $P_e = 0$ or $P_e = 100$, which is what is predicted previously in the book.

To analyze the behavior near the equilibria, we differentiate $f(P)$, which gives

$$f'(P_n) = \frac{2(1+10^{-8}P_n^4) - 2P_n \cdot 4 \times 10^{-8}P_n^3}{(1+10^{-8}P_n^4)^2} = \frac{2 - 6 \times 10^{-8}P_n^4}{(1+10^{-8}P_n^4)^2}.$$

Since $f'(0) = 2 > 1$, solutions of the model near the zero equilibrium are unstable and grow monotonically away from 0. At $P_e = 100$, we see that $f'(100) = -4/(1+1)^2 = -1$. Thus, this equilibrium right on the border of the stability region. The solutions will oscillate and slowly approach the equilibrium.

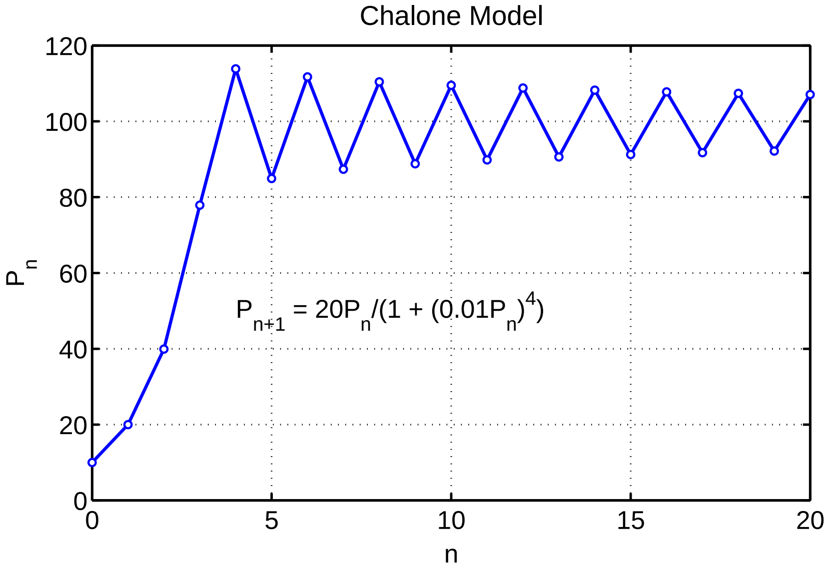


Figure 8: Graph of the simulation for the model of Example 5.

The simulation in Figure 8, starting with $P_0 = 10$, shows this behavior. ◁

6 HASSELL'S MODEL ALTERNATE FIT

We analyzed the data of A.C. Crombie [1] for the population dynamics of *Oryzaephilus surinamensis*, the saw-tooth grain beetle. Our analysis before concentrated on the updating function, and we found the least squares best fit to the data for the updating function. The time-series simulations did not fit the actual data very well, especially the logistic growth model.

This last section uses the nonlinear least squares best fit of the model simulations directly to the Crombie data of Table 2. The *Logistic growth model* is given by

$$P_{n+1} = P_n + rP_n(1 - P_n/M),$$

where P_0 is the initial population, r is the Malthusian growth rate, and M is the carrying capacity of the population. These three parameters are varied to minimized the sum of square errors between the model and the data. (See graph of Figure 9) The minimum sum of square error is $11,745$. The best fitting parameters are $P_0 = 14.62, r = 0.8847$, and $M = 440.3$. Thus, the logistic growth model that best fits Crombie's data is

$$\begin{aligned} P_{n+1} &= P_n + 0.8847P_n\left(1 - \frac{P_n}{440.3}\right), \\ P_0 &= 14.62. \end{aligned}$$

From our work on the logistic growth model, the carrying capacity for this model is $M = 440.3$.

The general form for Hassell's model is given by

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

which has the 3 parameters a, b, and c along with the initial condition P_0. When a nonlinear least squares is performed with this model, the minimum sum of square error is 6478, significantly better than the logistic growth model above. The best fitting parameters are $P_0 = 0.6063, a = 5.799, b = 0.07479$, and $c = 0.4959$. (See graph of Figure 9.) Thus, the Hassell's growth model that best fits Crombie's data is

$$\begin{aligned} P_{n+1} &= \frac{5.799P_n}{(1 + 0.07479P_n)^{0.4959}}, \\ P_0 &= 0.6063. \end{aligned}$$

From our equilibrium analysis before, this model has a carrying capacity of

$$M = (a^{1/c} - 1)/b = 449.6,$$

which is similar to the prediction of the logistic growth model.

This least squares analysis gives similar values for the parameters for the logistic growth model as compared to our analysis where the updating function is fit to the data, but very different ones for Hassell's growth model, indicating less robustness for Hassell's model. Figure 9 shows a graph showing the data and the two models. Both models track the data well, but Hassell's has a better fit, especially in the earlier weeks. The extra parameter in Hassell's model is one reason that the curve fits the data better. The qualitative behavior of these two models is essentially the same. Clearly, the parameter fits performed here are superior to ones used for the updating function, but either method can be employed depending on the desired outcome.

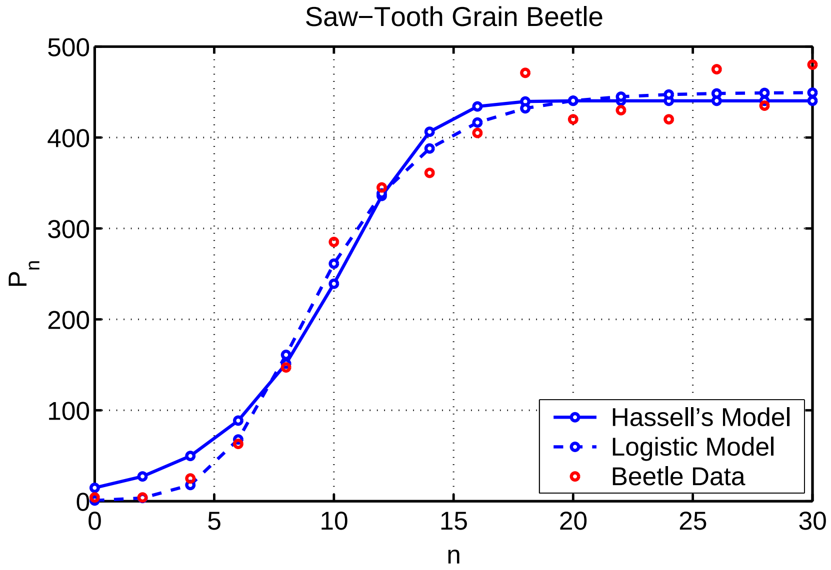


Figure 9: Graph of the Hassell's model of Section 6 compared to the graph of the Logistic model and the data of Table 2.

7 EXERCISES

1. Many biologists in fishery management use Ricker's model to study the population of fish. Let P_n be the population of fish in any year n, then Ricker's model is given by

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

Suppose that the best fit to a set of data gives $a = 4$ and $b = 0.005$ for the number of fish sampled from a particular river.

a. Let $P_0 = 100$, then find P_1, P_2, and P_3.

b. Sketch a graph of R(P) with the identity function, showing the intercepts, all extrema, and any asymptotes.

c. Find all equilibria of the model and describe the behavior of these equilibria.

2. Repeat Exercise 1 with $a = 9$ and $b = 0.001$

3. Consider the chalone model for mitosis given by the equation

$$P_{n+1} = f(P_n) = \frac{2P_n}{1 + (bP_n)^c},$$

where $b = 0.05$ and $c = 2$.

a. Let $P_0 = 10$, then find P_1, P_2, and P_3.

b. Sketch a graph of $f(P)$ with the identity function for $P \geq 0$, showing the intercepts, all extrema, and any asymptotes.

c. Find all equilibria of the model and describe the behavior of these equilibria.

4. Some entomologists use Hassell's model for studying the population of insects. Let P_n be the population of a species of beetle in week n and suppose that Hassell's model is given by

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

Suppose that the best fit to a set of data gives $a = 5$ and $b = 0.004$ for this species of beetle.

a. Let $P_0 = 100$, then find P_1, P_2, and P_3.

b. Sketch a graph of $H(P)$ with the identity function for $P \geq 0$, showing the intercepts and any asymptotes.

c. Find all equilibria of the model and describe the behavior of these equilibria.

5. The general form of Hassell's model is used to study a population of insects. Let P_n be the population of a species of moth in week n and suppose that Hassell's model is given by

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

Suppose that the best fit to a set of data gives $a = 10$, $b = 0.004$, and $c = 2$. for this species of moth.

a. Let $P_0 = 100$, then find P_1, P_2, and P_3.

b. Sketch a graph of $H(P)$ with the identity function for $P \geq 0$, showing the intercepts, all extrema, and any asymptotes.

c. Find all equilibria of the model and describe the behavior of these equilibria.

6. Repeat the process in Exercise 5 with gives $a = 5$, $b = 0.002$, and $c = 4$.

7. The San Diego Zoo discovered that because their flamingo population was too small, it would not reproduce until they borrowed some from Sea World. Scientists have discovered that certain gregarious animals require a minimum number of animals in a colony before they reproduce successfully. This is called the *Allee effect.* Consider the following model for the population of a gregarious bird species, where the population, N_n, is given in thousands of birds:

$$N_{n+1} = N_n + 0.2N_n\left(1 - \frac{1}{16}(N_n - 6)^2\right).$$

a. Assume that the initial population is $N_0 = 4$, then determine the population for the next two generations (N_1 and N_2).

b. Find all equilibria for this model.

c. The model above can be expanded to give

$$N_{n+1} = A(N_n) = \frac{3}{4}N_n + \frac{3}{20}N_n^2 - \frac{1}{80}N_n^3.$$

Find the derivative of $A(N)$. Evaluate the derivative $A'(N)$ at each of the equilibria found above and determine the local behavior of the solution near each of those equilibria.

d. Give a brief biological description of what your results imply about this gregarious species of bird.

8. The modeling of nerve cells often use a cubic response curve to the membrane potential V. Below we present a overly simple model for the membrane potential at discrete times for a nerve that can be quiescent or have repetitive spiking of action potentials. The simplified model is given by:

$$V_{n+1} = V_n + 0.07V_n(9 - (V_n - 4)^2).$$

a. Assume that the initial potential is $V_0 = 3$, then determine the membrane potential for the next three time intervals (V_1, V_2 and V_3).

b.Find all equilibria for this model.

c. The model above can be expanded to give

$$V_{n+1} = M(V_n) = 0.51V_n + 0.56V_n^2 - 0.07V_n^3.$$

Find the derivative of $M(V)$. Evaluate the derivative $M'(V)$ at each of the equilibria found above and determine the local behavior of the solution near each of those equilibria.

d. Give a brief biological description of what your results imply about the behavior of the nerve following different initial stimuli.

8 REFERENCES:

[1] A.C. Crombie, On competition between different species of graminivorous insects, *Proc. R. Soc. B* (1946) **132**, 362–395.

[2] W.E. Ricker, Handbook of computations for biological statistics of fish populations. Fisheries Research Board of Canada (1958).

[3] M.P. Shepard and F.C. and Withler, Spawning stock size and resultant production for Skeena Sockeye. J. Fisheries Research Board of Canada (1958) **15**: 1007–1025.

[4] C.J. Walters, Adaptive management of renewable resources. Macmillan (NY) (1986).

[5] C.J. Walters R. and Hilborn, Ecological optimization and adaptive management. Annual Rev. of Ecology and Systematics 9 (1968) 157–188.

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