DIMACS
Center for Discrete Mathematics &
Theoretical Computer Science

DIMACS EDUCATIONAL MODULE SERIES

MODULE 08-4
Modeling Biological Populations
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Module Description Information

- **Title:**

  Modeling Biological Populations

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- **Abstract:**

  This module introduces three discrete-time population models: the logistic model, the Ricker model, and the Beverton-Holt model. These models are studied using real data sets from biological populations. Students use techniques from dynamical systems (iterations, cobwebs, fixed points, stability, and sensitivity analysis) to analyze population models.

- **Informal Description:**

  In this module we use mathematical models to study biological populations such as the pine-looper moth, coho salmon, the common wasp, and the paramecium aurelia. Exercises throughout the module allow students to work with a model and a data set to determine how well the model fits the data, and what it predicts about the population's long-term survival. The exercises range from simple computations requiring a graphing calculator or Microsoft Excel (assumes Office 2003), to more challenging problems requiring calculus.

- **Target Audience:**

  This module is aimed at high school students in their junior or senior years, and at freshman college students. It would be an appropriate module for an applied mathematics course.

- **Prerequisites:**

  This module assumes some familiarity with composing functions, and with using exponential functions and logarithms. Some exercises require first semester calculus.

- **Mathematical Field:**

  Mathematical Biology, Dynamical Systems, Difference Equations

- **Applications Areas:**

  This module uses difference equations and technology to model population dynamics.

- **Mathematics Subject Classification:**

  37N25, 39A11, 92D25

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- **Other DIMACS modules related to this module:**

  Module 07–3: Using Population Models in the Teaching of Eigenvalues

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1 Introduction and Definitions

The population of a biological species depends on many factors, such as birth and death rates, immigration and emigration rates, competition, harvesting, and environmental influences. The simplest types of populations to study are those with non-overlapping generations. In a population with non-overlapping generations, one generation dies out before the next generation is born. This is the case for some species of fish and for seasonally breeding insects.

A *basic population model* for a population with non-overlapping generations is an equation that attempts to describe how the population in one generation depends on the population in the previous generation. Say $x(n+1)$ is the population in generation $n+1$, and $x(n)$ is the population in generation n. A basic population model is an equation of the form $x(n+1) = f(x(n))$ for some function f. We call f a *generating function.* Different choices of generating functions produce different population models. The choice of generating function depends on the assumptions that are made about how a population grows. In this module we will consider four different population models, i.e., four different generating functions.

In order to simplify the notation, we will write x_n for $x(n)$. If we have a basic population model $x_{n+1} = f(x_n)$, with initial population x_0, then $x_1 = f(x_0)$ is the population in generation 1, $x_2 = f(x_1) = f(f(x_0)) = f^2(x_0)$ is the population in generation 2, and, in general, $x_n = f^n(x_0)$ is the population in generation n. Here f^n represents the composition or *iteration* of f with itself n times. The sequence of iterations $\{x_0, x_1, x_2, x_3, \ldots\}$ is called the *orbit* of x_0 under f.

Example: Suppose $f(x) = x^2$ and $x_0 = 1/2$. Then

$$\begin{aligned} x_1 = (x_0)^2 &= (1/2)^2 = 1/4 \\ x_2 = (x_1)^2 &= (1/4)^2 = 1/16 \\ x_3 = (x_2)^2 &= (1/16)^2 = 1/256 \\ &\vdots \end{aligned}$$

and so forth, and the orbit of $x_0 = 1/2$ is $\{1/2, 1/4, 1/16, 1/256, \ldots\}$. We can see that as n increases, the values of x_n are getting closer and closer to 0. Similar limiting behavior occurs for any initial value x_0 with $|x_0| < 1$. The values of x_n would increase without bound (as n increases) if $x_0 > 1$.

Exercise 1.1: What happens if $x_0 < -1$?

Since $f(0) = 0$, the orbit of $x_0 = 0$ is $\{0, 0, 0, \ldots\}$. That is, the orbit of $x_0 = 0$ remains fixed at 0. We say that x_0 is a *fixed point* of a generating function f if $f(x_0) = x_0$. In order to find the fixed points of $f(x) = x^2$ we solve $f(x) = x$. Solving $x^2 = x$, we find f has two fixed points: $x = 0$ and $x = 1$.

In some of the exercises in this module you will be asked to determine if population values over time move toward a fixed point or away from a fixed point. In our example, we've seen that for any initial value x_0 near the fixed point 0, the values of x_n approach the fixed point 0 as n increases. In this case, we say that 0 is an *attracting* fixed point of f. Similarly, for any initial population value near (but not equal to) the fixed point 1, the values of x_n either approach 0 (for $x_0 = 0.9$, for instance) or grow without bound (for $x_0 = 1.1$, for instance) as n increases. In either case, the values of x_n move away from 1. Therefore we say that 1 is a *repelling* fixed point of f. (It's worth noting that we cannot classify every fixed point of every generating function as either attracting or repelling.)

One of the first population models was introduced by Thomas Malthus in 1798 to describe the population of Great Britain. The Malthus model is based on the simplifying assumption that the population at time $n+1$ is proportional to the population at time n. For example, suppose that a population at time n is given by x_n and that in any given time period, the number of births is equal to 20% of the population, and the number of deaths is equal to 13% of the population. The net change in population between times n and $n+1$ would be the difference between the number of births and the number of deaths during that time period. Mathematically, we have $x_{n+1} - x_n = 0.20x_n - 0.13x_n$, or simply $x_{n+1} = 1.07x_n$. In general, we can write the Malthus model as

$$x_{n+1} = kx_n \tag{1}$$

for some constant k. We can also write the Malthus model as $x_{n+1} = f(x_n)$, where $f(x) = kx$ is the generating function. The constant k will always be 1 + birth rate − death rate.

Exercise 1.2: What can you say about the birth rate and death rate for the population if $k > 1$? What implication would that have for the population?

Exercise 1.3: What can you say about the birth rate and death rate for the population if $k = 1$? And if $0 < k < 1$? What implications would that have for the population?

You can verify your answers above with the following observation. If x_0 is the initial population, then

$$\begin{aligned} x_1 &= kx_0, \\ x_2 &= kx_1 = k^2x_0, \\ \text{and, in general, } x_n &= k^n x_0. \end{aligned}$$

We can see from this equation, for example, that if $k > 1$, then k^n increases without bound as n increases. Over time the population would increase without bound.

The Malthus model assumes that a population is always growing at a rate of k. This is a reasonable assumption for short-term growth of small populations with vast resources, such as the first bacteria in a bacteria colony. However, the Malthus model is not reasonable for describing long-term population growth. For instance, if $k = 1.07$ and $x_0 = 1$, then x_{325} is over one billion!

No generating function can possibly capture all the factors affecting a population's growth. A mathematical population model attempts to capture some of the main factors that govern a population. In the following sections we will consider three population models (logistic, Ricker, and Beverton-Holt) which, unlike the Malthus model, assume that the rate at which a population grows decreases as the population increases.

2 The Logistic Model

2.1 Introduction

The maximum population that an environment can sustain is called the *carrying capacity* of the environment. The simplest population model which takes into account the carrying capacity is the logistic model. We will denote the carrying capacity for a population by L, and the population in generation n by y_n.

The logistic model is given by the difference equation

$$y_{n+1} = ry_n \left(1 - \frac{y_n}{L}\right), \tag{2}$$

where L is the carrying capacity and r is a constant combining the birth and death rates. We will assume $r > 0$.

Note the following two features of the logistic model. First, if the current population y_n is relatively small compared to the carrying capacity L, so that $(1 - \frac{y_n}{L})$ is close to 1, the environment contains an abundance of resources for the current population. As a result, the population behaves in the short-term as though its growth were unrestricted. That is, when y_n is much smaller than L, the logistic model is approximately the Malthus model because y_{n+1} is approximately ry_n. The second feature to note is that $(1 - \frac{y_n}{L})$ approaches 0 as y_n approaches L. So the growth rate of the population slows down as the population nears the carrying capacity L.

Though the logistic model makes unrealistic predictions (such as negative populations if $y_n > L$), it is useful for describing how a population would grow in the absence of outside intervention. The model can be modified to incorporate intervening factors such as harvesting or migration (see Exercise 2.4). From a mathematical perspective, the logistic model is interesting to study. Though it seems very simple, it displays rather complicated behaviors. (For a classic paper with examples of simple models that have very complex behaviors see [8].)

If we let $x_n = \frac{y_n}{L}$, it can be shown that the equation

$$x_{n+1} = rx_n (1 - x_n) \tag{3}$$

is equivalent to Equation (2). Note that in Equation (3), the population values are scaled as a fraction of the carrying capacity, so that x_n will take values between zero and one. In making this adjustment, the "1" now represents carrying capacity as 100%, and the factor $(1 - x)$ tells us how close the population is to the carrying capacity as x is a fraction of the carrying capacity. For the remainder of this module, we will refer to Equation (3) as the logistic model. We can also write the logistic model as $x_{n+1} = f(x_n)$, where $f(x) = rx(1 - x)$ is the generating function for the logistic model.

Exercise 2.1: Show that if $x_n = \frac{y_n}{L}$ then Equation (2) can be rewritten as Equation (3).

Exercise 2.2: Find the fixed points of the logistic model by solving the equation $rx(1 - x) = x$ for x.

Exercise 2.3: Consider $x_{n+1} = f(x_n)$ where $f(x) = rx(1 - x)$.

(a) Suppose $x_n > 0$. Show that the logistic model predicts $x_{n+1} < 0$ if and only if $x_n > 1$.

(b) What is the maximum value of f, and where does it occur?

(c) Show that $x_{n+1} > 1$ is possible only if $r > 4$.

(d) What are conditions on r and x_0 that guarantee $x_n > 0$ for $n = 1, 2, 3, \ldots$?

2.2 Iterations Using Excel

In this section we give steps to easily compute iterations of a function using Excel. Consider the logistic model $x_{n+1} = rx_n(1 - x_n)$.

- We will use the A column to keep track of the time (or generation). Enter **0** for the initial time in cell A1. In A2 enter **=A1+1**. Next, drag the fill handle in A2 (the small box in the lower right corner of the cell) downward until, say, A20. This will copy and update the formula in A2 into the cells below. (Each time 1 will be added to the entry in the preceding cell.)
- We will keep track of the parameter r in C1. For now let's enter **2** in C1.
- Enter the initial population x_0 in B1. For now let's enter **0.1** in B1.
- In the B column we will calculate the iterations of the generating function $f(x) = rx(1 - x)$ by entering **=$C$1*B1*(1-B1)** in B2. (The $ symbol in the reference to C1 signifies that the reference is absolute and will not be updated as we iterate. The references to B1 are relative and will change in subsequent formulas.) Now drag the fill handle in B2 downward until B20.
- Every time you enter a new value for x_0, the initial population, in B1 or change the parameter r in C1, your iterations will be updated. (See Figure 1.)

A	B	C
0	0.1	2
1	0.18	
2	0.2952	
3	0.416114	
4	0.485926	
5	0.499604	
6	0.5	
7	0.5	
8	0.5	
9	0.5	
10	0.5	

Figure 1: Excel iterations of the logistic model with $r = 2$ and $x_0 = 0.1$.

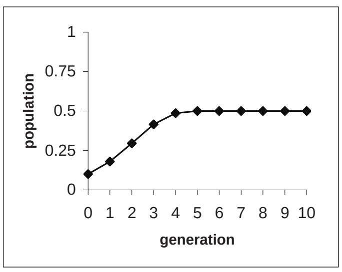

Figure 2: Excel plot of iterations with $r = 2$ and $x_0 = 0.1$.

In order to graph the data points as in Figure 2, select **Chart** under the **Insert** menu. Then select **XY (Scatter)** and choose the sub-chart "Scatter with data points connected by lines". After clicking **Next**, a **Data Range** box will appear. Click on the small square to the right of this box, and then highlight the data points in columns A and B that are to be graphed. Finally, follow the steps in the **Chart Wizard** to label your chart and the axes, and choose the scale of your graph. When you select **Finish**, the data will be displayed on a chart as shown in Figure 2. Your graph will be automatically updated every time you enter a new value of r in C1 or a new value of x_0, the initial population, in B1.

2.3 Iteration Exercises

In the exercises in this section you'll work with logistic population models for biological populations. Keep in mind that the predictions the model makes about the size of the population are what we might expect to observe if outside conditions remain approximately the same.

Exercise 2.4: The wheat bulb fly is a common pest to wheat crops. Wheat bulb flies have one brood per year and have non-overlapping generations. Each fall the flies lay their eggs. The eggs hatch in mid-winter, and the adult flies are present from mid-June through September. In [9] W. Morris fit logistic models to previously published life-table data of eight generations of the wheat bulb fly from a wheat growing area of England. It was estimated that the carrying capacity for wheat bulb flies is 0.72×10^6 flies per ha (hectare) and that $r = 1.5$.

Suppose that there are 0.06×10^6 flies per ha. Because we have scaled the population values to be a fraction of the carrying capacity, to find x_0 for our model we must divide the initial population 0.06×10^6 by 0.72×10^6 to get the fraction $x_0 = 0.06/0.72 = 0.0833$.

(a) Find the first 20 iterations of this model and show that the model predicts that the population stabilizes at 0.333 of the carrying capacity. What is the actual number of wheat bulb flies that this fraction represents?

(b) Suppose 0.5×10^5 flies per ha migrated to this region each year. How would you modify the model to take into account this migration?

Exercise 2.5: Understanding how tumors grow is an important part of understanding how to treat cancer. In [5], Cross and Cotton use a logistic model $x_{n+1} = rx_n(1 - x_n)$ to predict tumor growth. Assume that the tumor cells are in a container in a laboratory and that the container can support a maximum number of cells, which is the carrying capacity of the container. Instead of specifying a container carrying capacity of, say, 2 million cells, and also the actual number of cells, we instead represent populations as fractions of the carrying capacity. Therefore the population x_n is always between 0 and 1. For each of the following values of r find the first 30 iterations of three different initial populations between 0 and 1, and plot your results. Based on your results, what (if anything) does the model predict will happen to the tumor cell population over time?

(a) $r = 2.5$

(b) $r = 3$

(c) $r = 3.5$

Exercise 2.6: Consider a population modeled by the logistic equation $x_{n+1} = 2x_n(1 - x_n)$.

(a) Find the fixed points.

(b) For each value of x_0 given below, determine the corresponding values of x_n for times $n = 1, 2, 3, 4, 5$. Describe the patterns you observe and interpret them in terms of the population.

i. $x_0 = 0.1$

ii. $x_0 = 1.1$

iii. $x_0 = 0.6$

iv. $x_0 = 0.5$

(c) Based on your calculations in part (b), determine whether each fixed point is attracting or repelling.

2.4 Cobweb Diagrams

A cobweb diagram is a graphical representation of the orbit of a point x_0 under a generating function $f(x)$ that does not require any computations. To start, we graph both $y = f(x)$ and the line $y = x$. Note that the $x-$coordinates of the intersection points are precisely the fixed points of f since they are the solutions to the equation $f(x) = x$.

The coordinates of any point on the graph of the generating function $f(x)$ represent successive population values. That is, a point on the graph of $f(x)$ has coordinates (x_n, x_{n+1}). Also note that a point on the graph of $y = x$ has coordinates (x_n, x_n). The cobweb diagram is constructed by alternately drawing a sequence of vertical and horizontal line segments.

Let's consider the logistic model $x_{n+1} = 2x_n(1 - x_n)$ with initial population $x_0 = 0.2$. We first graph the generating function $y = 2x(1 - x)$ and the line $y = x$. (The intersection points occur at $x = 0$ and $x = 0.5$, the fixed points of f.) Locate the initial population $x_0 = 0.2$ on the horizontal axis. Sketch a vertical line segment up to the graph of $y = 2x(1 - x)$. The y-coordinate of this point on the parabola is the value of the population at time 1, or x_1. (See Figure 3.)

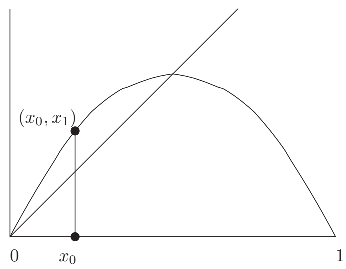

Figure 3: Starting a cobweb diagram.

From the point (x_0, x_1) on the parabola, sketch a horizontal line segment over to the line $y = x$. The horizontal line segment intersects the line $y = x$ at the point (x_1, x_1). We repeat this process of drawing a vertical line segment from (x_1, x_1) up to the parabola and a horizontal line segment over to the line $y = x$. We should now be at the point (x_2, x_2). (See Figure 4.) In repeating this process we are graphically iterating x_0 under the function f. The result is a diagram that looks like a cobweb or staircase. We can visualize the orbit $\{x_0, x_1, x_2, \ldots\}$ and its behavior, in this case increasing toward the fixed point at 0.5, without doing any calculations! (See Figure 5.)

A cobweb diagram provides a way to visualize the long-term behavior of orbits. From the cobweb diagram of $x_{n+1} = 2x_n(1 - x_n)$ we see that the orbit of any point x_0 near 0.5 always approaches the fixed point at 0.5. This verifies your observation in Exercise 2.6 that 0.5 is an attracting fixed point. However, the orbit of any point x_0 near 0 (but not equal to 0) always goes away from 0, which verifies that 0 is a repelling fixed point.

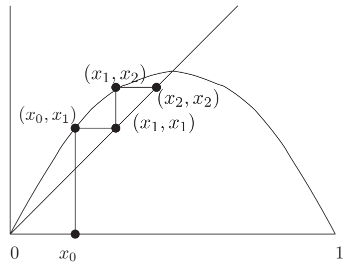

Figure 4: Two iterations

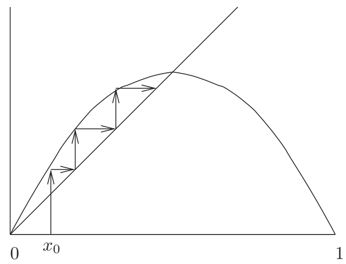

Figure 5: The orbit of x_0 approaches the fixed point 0.5.

Exercise 2.7: Draw cobweb diagrams for the Malthus model $x_{n+1} = kx_n$, for $0 < k < 1$, $k > 1$ and for $k = 1$. (Here the generating function is the line with slope k that passes through the origin.) Based on your cobweb diagrams, is the fixed point $x = 0$ attracting, repelling or neither attracting nor repelling?

The following theorem is useful for classifying fixed points. It says that the slope of the generating function at a fixed point determines whether a fixed point is attracting or repelling, confirming what you observed in the previous exercise with the Malthus model. (The theorem is proved using the Mean Value Theorem and can be found in [6])

Theorem 2.1 *Let f be a continuous function whose derivative is also continuous, and let p be a fixed point of f. If $|f'(p)| < 1$, then p is an attracting fixed point. If $|f'(p)| > 1$, then p is a repelling fixed point.*

Exercise 2.8: Consider the logistic model $x_{n+1} = rx_n(1 - x_n)$. Use Theorem 2.1 to determine the values of r for which each fixed point is attracting.

2.5 Cobweb Diagrams using Excel

We next describe how to use Excel to draw a cobweb diagram (as in Figure 6) for the logistic function $x_{n+1} = rx_n(1 - x_n)$.

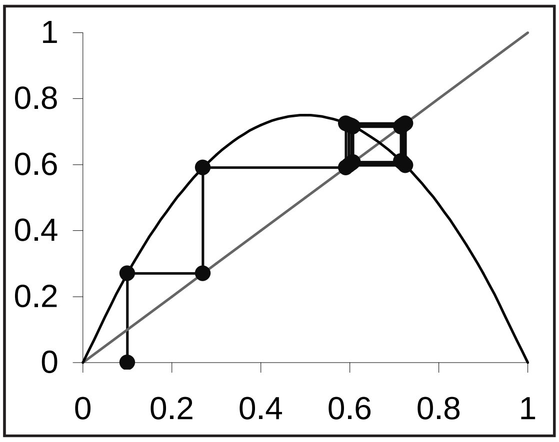

Figure 6: Cobweb of the logistic model using Excel with $r = 3$

- Enter the parameter(s) of the model and the initial population in column A. For the logistic model, the only parameter is r, so enter a value of r in A1, and enter a value of x_0 in A2.
- The first point on the cobweb diagram lies on the $x-$axis at $(x_0, 0)$. Enter **= $A$2** in B1, and enter **0** in C1.
- The second point lies on the graph of the generating function at (x_0, x_1). Enter **=B1** in B2 and the formula for the generating function in C2. For the logistic example we would enter **=$A$1*B2*(1-B2)** in C2.
- The third point lies on the line $y = x$ at (x_1, x_1). Enter **=C2** in both B3 and C3.
- Highlight the four cells B2, C2, B3 and C3. Drag the fill handle down until you've filled up to B50, C50. The formula pattern from the four cells will be repeated. (Note that the $x-$coordinates for the cobweb diagram are in column B, and the $y-$ coordinates are in column C.)
- Next we generate data points that will be used to sketch the generating function $f(x) = rx(1 - x)$. The $x-$coordinates will be in column D. Enter **0** in D1 and **=D1+0.1** in D2. Drag D2 down to D11. To generate the $y-$coordinates, we need to enter the generating function in E1. For the logistic example, we enter **= $A$1*D1*(1-D1)** in E1. Then drag this down to E11.
- Select **Chart** under the **Insert** menu. Next, select **XY (Scatter)** and choose the sub-chart "Scatter with data points connected by lines". After clicking **Next**, a **Data Range** box will appear. Click on the small square to the right of this box, and then highlight the data points in columns B and C that are to be graphed. Finally, follow the steps in the Chart Wizard to label your chart and the axes, and choose the scale of your graph. You now should have a chart with the cobweb, but it still needs the graph of $y = x$ and the generating function. Right click on the chart and select **Source data** and then select **Add** under **Series**. Click on the small square to the right of the x-values box and then highlight the data in column D. Next, click on the small square to the right of the y-values box and highlight the data in column E. This produces a graph of the generating function. (If you right click on its graph you can change the sub-type to "scatter with data points connected by smooth lines without

markers".) Finally, to sketch the line $y = x$, repeat these instructions but use the data in column D for both the x and y values on your graph.

- Now you can change both r and x_0 to construct new cobweb graphs.

Exercise 2.9: Find the fixed points of the logistic model $x_{n+1} = 2.5x_n(1 - x_n)$ and use a cobweb diagram to classify each fixed point as attracting or repelling.

Exercise 2.10: Let $r > 0$ and let x_0 be in $(0, 1)$. Use cobweb diagrams on $x_{n+1} = rx_n(1 - x_n)$ to find

(a) an interval of values of r for which the fixed point $x = 0$ is attracting.

(b) an interval of values of r for which the second (nonzero)fixed point is attracting.

(c) a value of r for which the long-term behaviors of orbits cannot be determined.

A *period* k point p is a point such that $f^k(p) = p$ but $f^j(p) \neq p$ for $0 < j < k$. The orbit of a period k point is called a k-*cycle*. In Exercise 2.5 you saw that for some choice of r there was an attracting 2-cycle or 4-cycle. In fact, it can be shown that there are values of r that give cycles of every period.

Exercise 2.11: Find the values of r for which there will there be a 2-cycle. (Hint: To find the period 2 points, you need to solve the equation $f^2(x) = x$. Note that $f^2(x) - x$ is degree 4 polynomial, and two of its roots will be the fixed points of f. Why? Factoring out the fixed points of f will simplify your calculations.)

Exercise 2.12: For what values of r will the 2-cycle found in the previous exercise be attracting? Use Theorem 2.1 and the chain rule.

3 The Ricker Model

3.1 Introduction

When determining the optimal stocking rates for fisheries, mathematical biologists often use a mathematical model developed in 1954 by W.E. Ricker to study the salmon population in the Pacific northwest. In this section, we'll examine the Ricker model and some of its applications to mathematical biology.

The Ricker model is given by the difference equation

$$x_{n+1} = \alpha e^{-\beta x_n} x_n. \tag{4}$$

The constants α and β are positive and are estimated from population data. We can regard α as the maximum value of the growth rate, and β as a constant that scales the carrying capacity. We will see how to estimate these constants in Section 3.2.

Recall that the logistic model can give unrealistic predictions, such as negative populations. This situation does not occur in the Ricker model because its generating function $f(x) = \alpha e^{-\beta x}$ is positive for $x > 0$. In the exercises you'll show that, like the logistic function, the the graph of the Ricker generating function has one-hump. That is, f is increasing for $0 < x < L$ for some L, and f is decreasing for $x > L$.

A population model of the form $x_{n+1} = g(x_n)x_n$ is called *density dependent* because $g(x)$, the per-capita growth rate, depends on the size of the population. Generally, the greater the population, the more competition there is for resources, so g will be a decreasing function. Both the logistic and Ricker models are density dependent. In the logistic model $g(x) = r(1-x)$. In the Ricker model $g(x) = \alpha e^{-\beta x}$. The growth rate in the Malthus model does not depend on the size of the population; it is always k.

Note, in the logistic model the population values were scaled to take values between 0 and 1. The population values are not scaled in the Ricker model.

Exercise 3.1: The Ricker model has been used to study the population of the Mexican bean beetle in the soybean fields of North Carolina. (See [11].) These beetles can have three generations in one year. Occasionally the beetle causes serious damage to a soybean crop. By fitting the beetle population data with a Ricker model it was found that, for one variety of soybean, $\alpha = 8.86$ and $\beta = 0.148$.

(a) Suppose that initially there are 20 beetles per square meter. Determine the first 10 iterations of the Ricker model. What patterns for the beetle population does this model predict? If you are using the Excel directions in Section 2.2, you'll need to keep track of two parameters, say, α in C1 and β in D1. The A column would be the same as described in Section 2.2, and B1 would contain the initial population. The generating function in B2 would be written as $= \$\mathbf{C}\$\mathbf{1} * \mathbf{Exp}(-\$\mathbf{D}\$\mathbf{1} * \mathbf{B1}) * \mathbf{B1}$.

(b) Suppose that other varieties of soybeans yield different values of α. For each of the following values of α find the first 30 iterations and plot your results. Based on your results, what (if anything) does the model predict will happen to the beetle population over time?

 i. $\alpha = 0.5$
 ii. $\alpha = 1.5$
 iii. $\alpha = 10$

(c) For one of the values of α in part (b) you should have observed the population bouncing back and forth between two values, i.e., a two-cycle. Experiment with different values of α until you find a value that gives a 4-cycle.

3.2 Finding a Ricker Model

If we have a data set for a population with non-overlapping generations that we want to fit it with a Ricker model, we need a method of finding α and β. In this section we give directions for using Excel to find these constants. We'll illustrate the method with population data of the pine looper moth found in [4] that is taken from annual pupal surveys conducted in Great Britain by the British Forestry service since the 1950s.

The pine looper moth is a threat to many species of conifers. It is found in the western United States, in western Canada, and in northern Europe. Adult moths emerge in early summer and live without feeding for 10–14 days. The females lay their eggs on the pine needles. After three weeks the larvae hatch and feed on new and old pine needles for four to five months. The needles are often eaten down to the sheath, which can lead to needle loss and the death of trees. Sometime between mid October and December, the larvae drop to the ground and burrow under the leaves, needles, and twigs on the forest floor. It overwinters in the pupa stage. In the chart below are the mean totals of pupal densities in the Cannock Chase forest from 1960 to 1969. The densities are given per square meter.

Year	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
pupae per sq. m.	15.09	9.15	9.32	1.02	0.35	0.26	1.75	9.09	5.93	1.53

Exercise 3.2: Show that if we divide both sides of the Ricker equation $x_{n+1} = \alpha e^{-\beta x_n} x_n$ by x_n and take the natural log of both sides, we obtain

$$\ln\left[\frac{x_{n+1}}{x_n}\right] = \ln(\alpha) - \beta x_n \tag{5}$$

We can treat Equation (5) as a linear regression $y = b + mx$ where $y = \ln\left[\frac{x_{n+1}}{x_n}\right]$, $b = \ln(\alpha)$, and $m = -\beta$. Here y is the dependent variable and x_n the independent variable. Say $n = 0$ corresponds to 1960. We next compute the y values, which are displayed in the following table.

n	x_n	x_{n+1}	$y = \ln\left[\frac{x_{n+1}}{x_n}\right]$
0	15.09	9.15	-0.500
1	9.15	9.32	0.018
2	9.32	1.02	-2.212
3	1.02	0.35	-1.070
4	0.35	0.26	-0.297
5	0.26	1.75	1.907
6	1.75	9.09	1.648
7	9.09	5.93	-0.427
8	5.93	1.53	-1.355

To find b and m, enter the data from the x_n column in cells A1-A9, and enter the data from the y column in cells B1-B9. To find m enter $=$ **Slope(B1 : B9, A1 : A9)** in an empty cell. To find b enter $=$ **Intercept(B1 : B9, A1 : A9)** in another empty cell. Then set $\beta = -m$ and $\alpha = e^b$. For this data set, we find that $\beta = 0.111$ and $\alpha = e^{0.388} = 1.474$. So the Ricker model would be

$$x_{n+1} = 1.474e^{0.111x_n}x_n \tag{6}$$

Exercise 3.3: Find the first 15 iterations of Equation (6). What does this model predict for the pine looper pupae population per square meter in the Cannock Chase forest for 1975?

Exercise 3.4: Below are data of the pine looper moth from the the Moray forest district. Find a Ricker model for this data. Then find the first 8 iterations. What does the model predict for the population of pine looper pupae in 2000?

Year	1992	1993	1994	1995	1996	1997
pupae per sq. m.	6.0	3.2	4.4	10.0	24.0	30.0

Exercise 3.5: The Ricker model was recently used to study the density of wasp nests in New Zealand beech forests. (See [1].) Each year wasps build nests in the trees of New Zealand's South Island. The wasps compete with rare birds for honeydew sap, and an overabundance of wasps threatens both the birds and the trees. In the model, x_n is the number of wasp nests per hectare at each site.

Site	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
Mt Misery	16.0	11.8	10.0	15.7	25.3	28.3	30.5	4.4	16.5	11.4	17.1	11.4	11.9
Watson	20.5	19.8	12.9	15.7	10.6	18.3	12.9	6.8	1.1	12.2	9.0	6.9	8.0

(a) Use the Watson data to find a Ricker model for the number of wasp nests, and sketch the graph of the generating function. What does your model predict about the number of wasp nests in 2002?

(b) If we use a model $x_{n+1} = f(x_n)$ to make predictions about a population, then ordered pairs of actual population values (p_n, p_{n+1}) should lie approximately on the graph of the generating function. Recall that if (x, y) is a point on the graph of the generating function $f(x)$, the $x-$coordinate represents the current population value x_n, and the $y-$coordinate represents x_{n+1} the predicted population value at the next time period. Plot the ordered pairs (p_n, p_{n+1}) of actual Watson population values given in the chart below together with the generating function you found in part (a).

p_n	20.5	19.8	12.9	15.7	10.6	18.3	12.9	6.8	1.1	12.2	9.0	6.9
p_{n+1}	19.8	12.9	15.7	10.6	18.3	12.9	6.8	1.1	12.2	9.0	6.9	8.0

(c) Based on part (b), does it seem reasonable to fit this data with a Ricker model?

Exercise 3.6: Coho salmon are one of the main fish varieties caught off the coast of southeastern Alaska, and they have a life span of about three years. When the adult salmon are ready to spawn, they swim from the ocean to the river bed where they were born. After this arduous journey, the females lay their eggs, which the males then fertilize. Several months later, the eggs hatch. In about a year, the young salmon start their migration to the ocean, where they live between one and two years before they begin their own journey to the river bed spawning grounds.

The following data set can be found in [10]. The fish counted here are called *recruits.* Recruits are the salmon that are ready to begin migration from the river to the ocean, and which will be available for fishing the following year.

Year	1980	1983	1986	1989	1992	1995	1998	2001
Coho Population in Auke Creek fishery	10714	6901	5617	7011	6596	4884	7420	5980

(a) Fit this data with a Ricker model, and find the first 8 iterations. What does this model predict the population of Coho salmon will be in the Auke Creek fishery in 2004 (when $n = 8$)?

(b) As in Exercise 3.5, plot the generating function and the actual population points (p_n, p_{n+1}). Compare your plot with the Watson-wasp plot in Exercise 3.5. In which case does the Ricker model appear to better fit the data?

(c) If $f(x_n) > x_n$ (that is, the graph of f lies above the diagonal line $y = x$) then the fishery could catch the surplus $f(x) - x$ and be left with a fish population of the same size as the last generation. The largest harvest of this type is called the *maximum sustainable yield.* Use technology to find the maximum sustainable yield if $\alpha = 10$ and $\beta = 0.05$, and determine the population size that gives this harvest size.

3.3 Additional Exercises

Exercise 3.7: Find the fixed points of the Ricker model $x_{n+1} = \alpha e^{-\beta x_n} x_n$.

Exercise 3.8: In this exercise you will show that the graph of the Ricker model's generating function has a "one hump" shape.

(a) Find $f'(x)$ and determine where f is increasing or decreasing.

(b) Show that $\lim_{x\to\infty} f(x) = 0$.

(c) At what value of x is $f(x)$ the greatest?

(d) What is the maximum value of $f(x)$?

(e) Based on the information in parts (a) through (c), sketch the graph of f.

Exercise 3.9: In the beetle exercise (Exercise 3.1) we saw that when $\alpha = 0.5$, the model predicted that the population would become extinct. When $\alpha = 1.5$, the model showed that the population would approach 2.73, which was (approximately) the fixed point $\frac{\ln\alpha}{\beta}$. So for some values of α the fixed points are attracting, and for other values they are repelling. In this exercise you will find the values of α for which the fixed points are attracting or repelling. To simplify the calculations, let $\beta = 1$ so that $f(x) = \alpha x e^{-x}$.

(a) Show that the fixed points of f are $x = 0$ and $x = \ln\alpha$.

(b) Use cobweb diagrams to find an interval of values of α for which $x = 0$ is attracting.

(c) Use cobweb diagrams to find an interval of values of α for which $x = \ln\alpha$ is attracting.

(d) Use Theorem 2.1 to confirm your answers to parts (b) and (c).

Exercise 3.10: As with the logistic model, the Ricker model can exhibit very complicated behaviors. Let $\beta = 1$. Use cobwebbing to find a value of α for which an attracting 2-cycle appears. Also, find a value of α for which an attracting 4-cycle appears.

4 The Beverton-Holt Model

4.1 Introduction

The Beverton-Holt model, introduced by Beverton and Holt in 1957 (see [3]) is one of the most commonly used stock and recruitment models in fishery management. It is used to describe the population of insect or fish species, such as the pacific salmon, which reproduce just once during their lifetime after which death is inevitable. The Beverton-Holt model depicts density dependent recruitment of a population in which resources are limited and unequally shared.

Let x_n represent the total population at time n of a species with initial population x_0. (Time can be given in minutes, days, years, etc.) Then x_{n+1} is the population at time $n+1$. The Beverton-Holt model is given by

$$x_{n+1} = \frac{\alpha x_n}{1+\beta x_n}. \tag{7}$$

The constants α and β are estimated from population data, and α is positive. (We regard α as the maximum growth rate and β as a measure of growth inhibition.) Equation (7) can be written as $x_{n+1} = f(x_n)$ where $f(x) = \frac{\alpha x}{1+\beta x}$ is the generating function for the Beverton-Holt model.

Exercise 4.1: Equation (7) can also be written as $x_{n+1} = g(x_n)x_n$ where $g(x) = \dfrac{\alpha}{1+\beta x}$ is the per-capita growth rate. What are some reasons why we need g to be positive and decreasing?

Exercise 4.2: Suppose that for a species of Atlantic salmon in the Western Arm Brook River it was estimated that $\alpha = 84.2$ and $\beta = 0.0036$. Graph the generating function. If $x_0 = 500,000$, find the first 4 iterations of this model.

Exercise 4.3: Find the fixed points of the Beverton-Holt model.

Exercise 4.4: In this exercise you will examine the graph of the generating function $f(x) = \frac{\alpha x}{1+\beta x}$. Assume $x \geq 0$.

(a) Find $f'(x)$.

(b) Determine the intervals of increase and decrease of f.

(c) Find $\lim\limits_{x\to\infty} f(x)$.

(d) Find $f''(x)$.

(e) Determine the values of β and intervals of x where f is concave up or concave down.

Exercise 4.5: Consider a Beverton-Holt model with $\alpha = 2.5$ and $\beta = 1.5$.

(a) Show that the fixed points are $x = 0$ and $x = 1$.

(b) Suppose $x_0 = 0.55$. Find the first 20 iterations of f and describe the limiting behavior of the iterations.

(c) Repeat part (b) for $x_0 = 1.4$.

(d) Draw cobweb diagrams for three different values of x_0. Based on your diagrams and calculations, is $x = 0$ attracting or repelling? Is $x = 1$ attracting or repelling?

If K is the nonzero fixed point, it can be shown that $\beta = \dfrac{\alpha - 1}{K}$ and that the generating function for the Beverton-Holt model has the form

$$f(x) = \frac{\alpha x}{1 + \left(\frac{\alpha-1}{K}\right) x} \tag{8}$$

Exercise 4.6: Verify that if K is the nonzero fixed point, then the generating function has the form in Equation (8).

Exercise 4.7: Consider the Beverton-Holt model given by Equation (8), and suppose $K = 1$.

(a) Construct a cobweb diagram for the following α values and initial conditions.

i. $\alpha = 2$, $x_0 = 0.4$

ii. $\alpha = 2$, $x_0 = 1.4$

iii. $\alpha = 0.7$, $x_0 = 0.4$

iv. $\alpha = 0.7$, $x_0 = 1.1$

(b) From your cobweb diagrams, make a conjecture about when the fixed point $x = 0$ will be attracting or repelling. Make a conjecture about when the fixed point $x = 1$ will be attracting or repelling.

Exercise 4.8: Consider the generating function f, given by Equation (8). Use Theorem 2.1 to find values of α for which $x = 0$ is attracting. Repeat for the nonzero fixed point K.

4.2 Finding a Beverton-Holt Model

In this section we describe how to find a model of the form $x_{n+1} = f(x_n)$ where f is given by Equation (8). That is, given a set of data, how does one find the parameters α and K that best fit it? The data set in Table 1 is from experiments conducted by G. F. Gauss (1934a) on a single cell organism, *paramecium aurelia*, a protozoa found in a number of fresh water ponds. In the data set in Table 1, time n is measured in days and x_n is the mean population density of paramecium, measured in numbers of individuals per 0.5 cm^3.

Exercise 4.9: Construct a scatter plot of the data in Table 1. Does it look like the graph of a possible generating function $f(x)$ for the Beverton-Holt model?

We can use Excel as we did in Section 3.2 to estimate the parameters α and K.

Exercise 4.10: Show that if we invert both sides of the Beverton-Holt equation $x_{n+1} = \frac{\alpha x_n}{1+\left(\frac{\alpha-1}{K}\right)x_n}$ and then multiply by x_n and simplify, we obtain $\dfrac{x_n}{x_{n+1}} = \dfrac{1}{\alpha} + \left(\dfrac{\alpha - 1}{\alpha K}\right) x_n$.

We can treat the equation in Exercise 4.10 as a linear regression $y = b + mx$ where $y = \dfrac{x_n}{x_{n+1}}$, $b = \dfrac{1}{\alpha}$ and $m = \dfrac{\alpha - 1}{\alpha K}$. Here y is the dependent variable and x_n is the independent variable.

Table 1: growth of paramecium aurelia in isolation

Day (n)	Mean Density of P. Aurelia x_n
0	2
1	–
2	14
3	34
4	56
5	94
6	189
7	266
8	330
9	416
10	507
11	580
12	610
13	513
14	593
15	557
16	560
17	522
18	565
19	517
20	500
21	585
22	500
23	495
24	525
25	510

Exercise 4.11: Use linear regression to find a Beverton-Holt model for the paramecium in Table 1. What does the Beverton-Holt model predict about the number of paramecium on day 50?

Exercise 4.12: Recall that in Exercise 3.6 we found a Ricker model for the salmon population in the Auke Creek fishery from the following data set found in [10]:

Year	1980	1983	1986	1989	1992	1995	1998	2001
Population	10714	6901	5617	7011	6596	4884	7420	5980

Fit this data with a Beverton-Holt model and find the first 8 iterations of this model. What does this model predict the population of Coho salmon will be in the Auke Creek fishery in 2004? Sketch the graph of the generating function and the ordered pairs of actual population values (p_n, p_{n+1}). Is it realistic to make predictions about the salmon population with this model? Why or why not? How do your results compare with those you found using the Ricker model?

4.3 Finding a Closed Form

Unlike the Ricker model, the Beverton-Holt model may be rewritten in closed form. That is, we can find an expression for x_n in terms of x_0, namely,

$$x_n = \frac{\alpha^n (\alpha - 1) x_0}{(\alpha - 1) + \beta (\alpha^n - 1) x_0}. \tag{9}$$

Exercise 4.13: This exercise will guide you through the derivation of Equation (9).

(a) Use mathematical induction to show that if Equation (7) is iterated starting at x_0, we obtain the closed form solution

$$x_n = \frac{\alpha^n x_0}{1 + \beta \left(\sum_{i=0}^{n-1} \alpha^i \right) x_0} \tag{10}$$

(b) Show that $\displaystyle\sum_{i=0}^{n-1} \alpha^i = \frac{\alpha^n - 1}{\alpha - 1}$. (Hint: Let $s_n = 1 + \alpha + \cdots + \alpha^{n-1}$. Then consider $\alpha s_n - s_n$.)

(c) Use part (b) to show that Equation (10) can be rewritten as Equation (9).

Exercise 4.14: The closed-form solution allows us to readily determine the long-term behavior of populations predicted by the model. Suppose $x_0 > 0$.

(a) Let $\alpha = 0.5$. Use Equation (9) to determine the behavior of the population over time predicted by the model.

(b) Repeat if $\alpha = 2$.

(c) In general, what can you say if $\alpha > 1$ or if $\alpha < 1$ about the population over long periods of time?

(d) Will the Beverton-Holt model ever have unpredictable results like the Ricker model? Why or why not?

5 Selected Solutions

Exercise 1.1: If $x_0 < -1$, then $|x_n|$ grows without bound with x_n alternating between positive and negative values.

Exercise 1.2: If $k > 1$, then the birth rate is greater than the death rate. The population would grow without bound.

Exercise 1.3: If $k = 1$ the birth rate equals the death rate. The population would remain at x_0 forever. If $0 < k < 1$, then the population would die out over time.

Exercise 2.1: Substitute $y_n = Lx_n$ into Equation (2) and simplify.

Exercise 2.2: The fixed points are $x = 0$ and $x = \frac{r-1}{r}$.

Exercise 2.3: Consider $x_{n+1} = f(x_n)$ where $f(x) = rx(1-x)$ and $r > 0$.

(a) Note that $x_n > 1$ if and only if $(1 - x_n) < 0$. Moreover, $(1 - x_n) < 0$ if and only if $rx_n(1 - x_n) < 0$.

(b) The graph of f is a parabola that opens downward with vertex at $(\frac{1}{2}, \frac{r}{4})$. Thus the maximum value of f is $\frac{r}{4}$ and it occurs at $x = \frac{1}{2}$, half the carrying capacity.

(c) If $r > 4$ then we can show that there is some $x_0 \in (0, 1)$ such that the logistic model predicts a negative population. If $x_0 = \frac{1}{2}$, then by part (b) $x_1 = f(\frac{1}{2}) = \frac{r}{4} > 1$. By part (a), $x_2 < 0$.

(d) If $r < 4$ then $0 < f(x) < 1$ for all $x \in (0, 1)$. (Note: if $r = 4$ and $x_0 = \frac{1}{2}$, then $x_2 = 0$.) The two conditions $0 < x_0 < L$ and $r < 4$ guarantee that $x_n > 0$ for $n = 1, 2, 3, \ldots$.

Exercise 2.4:

(a) About 240,000 flies.

(b) $x_{n+1} = 1.5x_n(1 - x_n) + \frac{0.5\times10^6}{0.72\times10^6}$

Exercise 2.5:

(a) It approaches 60% of the carrying capacity.

(b) In this case the population alternates between 62% and 70% of the carrying capacity.

(c) Over time, the population alternates between 38%, 83%, 50%, and 87% of the carrying capacity.

Exercise 2.6: Logistic model $x_{n+1} = 2x_n(1 - x_n)$.

(a) The fixed points are $x = 0$ and $x = 0.5$.

(b) Iterations:

i. For the initial value $x_0 = 0.1$, we have the following population sequence: $x_1 = 0.18, x_2 = 0.2952, x_3 = 0.4161, x_4 = 0.4859, x_5 = 0.4996$. The population appears to approach 50% of the carrying capacity.

ii. For the initial value $x_0 = 1.1$, we have the following population sequence: $x_1 = -0.22, x_2 = -0.5368, x_3 = -1.6499, x_4 = -8.7442, x_5 = -170.411$. The model is giving negative values.

iii. For the initial value $x_0 = 0.6$, we have the following population sequence: $x_1 = 0.48, x_2 = 0.4992, x_3 = 0.4999, x_4 = 0.5, x_5 = 0.5$. As in part (i), the population approaches 50% of the carrying capacity.

iv. For the initial value $x_0 = 0.5$, we have the following population sequence: $x_1 = 0.5, x_2 = 0.5, x_3 = 0.5, x_4 = 0.5, x_5 = 0.5$. Again, the population is approaching 50% of the carrying capacity.

(c) It appears that $x = 0$ is a repelling fixed point and $x = 0.5$ is an attracting fixed point.

Exercise 2.7: The fixed point $x = 0$ is attracting when $0 < k < 1$ and repelling when $k > 1$. If $k = 1$, then every point is fixed, and $x = 0$ is neither attracting nor repelling.

Exercise 2.8: Note that $f'(x) = r - 2rx$. So $|f'(0)| = |r|$. Thus $x = 0$ is attracting when $0 < r < 1$. For the nonzero fixed point we have $|f'(\frac{r-1}{r})| = |2 - r|$. We set $|2 - r| < 1$ to find that $x = \frac{r-1}{r}$ is attracting when $1 < r < 3$.

Exercise 2.9: The fixed points are $x = 0$ and $x = 0.6$. From cobweb diagrams, $x = 0$ is repelling and $x = 0.6$ is attracting.

Exercise 2.10: From cobweb diagrams we find

(a) if $0 < r < 1$, the fixed point $x = 0$ is attracting,

(b) if $1 < r < 3$, the second fixed point $x = \frac{r-1}{r}$ is attracting,

(c) When $r = 3.7$ we cannot determine the long-term behavior using cobwebbing.

Exercise 2.11: We find that $f^2(x) = r^2x(1 - x)(1 - rx(1 - x))$. The next step is to factor $f^2(x) - x$. Using the hint, we find that $f^2(x) - x = -x(rx + 1 - r)(r^2x^2 - r^2x - rx + r + 1)$. The period 2 points are found by solving $r^2x^2 - r^2x - rx + r + 1 = 0$. Using the quadratic formula and simplifying, we find the roots are $x = \dfrac{r + 1 \pm \sqrt{r^2 - 2r - 3}}{2r}$. Therefore, there are period two points when $\sqrt{r^2 - 2r - 3} > 0$, which is the case when $r > 3$.

Exercise 2.12: Let $p = \frac{r+1+\sqrt{r^2-2r-3}}{2r}$ and $q = \frac{r+1-\sqrt{r^2-2r-3}}{2r}$ be the period-2 points. By the Chain Rule, $(f^2)'(p) = f'(f(p))f'(p) = f'(q)f'(p)$. After some algebra we find $f'(p)f'(q) = -[(r-1)^2 - 5]$. We then find $|f'(p)f'(q)| < 1$ if $3 < r < \sqrt{6} + 1$.

Exercise 3.1:

(a) From ten iterations of the Ricker model with $\alpha = 8.86$, $\beta = 0.148$ and an initial population of 20 beetles, the model predicts that the beetle population will oscillate between approximately 21.8 and 7.6 beetles.

(b) i. For $\alpha = 0.5$, the model predicts the beetle would become extinct.

ii. For $\alpha = 1.5$ the model predicts the beetle population would reach 2.7 at generation 9 and will remain there.

iii. For $\alpha = 10$, the model predicts the population will oscillate between 24.8 and 6.3 beetles.

(c) One answer is $\alpha = 14$.

Exercise 3.2: After dividing both sides by x_n and taking the natural log of both sides we have $\ln\left[\dfrac{x_{n+1}}{x_n}\right] = \ln(\alpha e^{-\beta x_n} x_n)$. Simplifying the right hand side using properties of the natural log gives the desired result.

Exercise 3.3: It predicts the population will approach 3.5 per square meter.

Exercise 3.4: Using the linear regression process, we find that $\alpha = 1.396$ and $\beta = 0.001$. The first 8 iterations using this model are

Year	1992	1993	1994	1995	1996	1997	1998	1999	2000
population	6.0	8.3	11.5	15.9	21.9	29.9	40.4	54.2	71.7

Exercise 3.5: (a) Using linear regression we find $\alpha = 2.112$ and $\beta = 0.067$. The model predicts 11.156 nests per hectare in 2002.

Exercise 3.6:
(a) We find that $\alpha = 2.367$ and $\beta = 0.00013$. The model predicts the population will be 6627 salmon in 2004.
(c) Let $H(x) = f(x) - x$. Then $H(x)$ is maximum when $H'(x) = 0$ or when $f'(x) = 1$. If solve this equation with the given α and β (using a numerical solver) we find x is approximately 15.63.

Exercise 3.7: We set $\alpha e^{-\beta x} x = x$ and solve for x to find the fixed points are $x = 0$ and $x = \frac{\ln \alpha}{\beta}$ provided $\alpha > 1$.

Exercise 3.8:

(a) $f'(x) = \alpha e^{-\beta x}(1 - \beta x)$. f is increasing on $(0, \frac{1}{\beta})$ and decreasing for $x > \frac{1}{\beta}$.

(b) Use L'Hopital's rule.

(c) The maximum value occurs at $\frac{1}{\beta}$.

(d) The maximum value is $\frac{\alpha}{e\beta}$.

Exercise 3.9: (d) The fixed point $x = 0$ is attracting for $\alpha < 1$ and repelling for $\alpha > 1$. The nonzero fixed point is attracting for $1 < \alpha < e^2$. This is confirmed using Theorem 2.1, since $|f'(0)| = \alpha$ and $|f'(\ln \alpha)| = |1 - \ln \alpha|$.

Exercise 3.10: From cobwebbing, it appears there's a 2-cycle when $\alpha = 11$ and a 4-cycle when $\alpha = 14$.

Exercise 4.1: If g is positive, then the model will never predict negative populations. As the population increases, the availability of resources decreases and so does the per capita growth rate.

Exercise 4.2: $x_0 = 500,000$, $x_1 = 23,376$, $x_2 = 23,114$, $x_3 = 23,111$, $x_4 = 23,111$.

Exercise 4.3: There are two fixed points: $x = 0$ and $x = \dfrac{\alpha - 1}{\beta}$. In order for the non-zero fixed point to be positive we need $\alpha > 1$.

Exercise 4.4:

(a) $f'(x) = \frac{\alpha}{(1+\beta x)^2}$.

(b) f is always increasing.

(c) $\lim_{x\to\infty} f(x) = \frac{\alpha}{\beta}$.

(d) $f''(x) = \frac{-2\alpha\beta}{(1+\beta x)^3}$.

(e) If $\beta > 0$, then f is concave down. If $\beta < 0$ then f is concave up for $x < \frac{-1}{\beta}$ and concave down for $x > \frac{-1}{\beta}$.

Exercise 4.5:

(a) To find the fixed points, solve $\frac{2.5x}{1+1.5x} = x$.

(b) The iterations increase and approach 1.

(c) The iterations decrease and approach 1.

(d) $x = 0$ is repelling, and $x = 1$ is attracting.

Exercise 4.6: Set K equal to the nonzero fixed point $\frac{\alpha-1}{\beta}$ and solve for β. Then substitution gives the desired result.

Exercise 4.8: We find $|f'(0)| = \alpha$ and $|f'(K)| = \frac{1}{\alpha}$. Thus $x = 0$ is attracting if $\alpha < 1$ and K is attracting if $\alpha > 1$.

Exercise 4.11: We find $x_{n+1} = \frac{2.074x_n}{1+0.002x_n}$. The model predicts there will be 537 paramecium on day 50.

Exercise 4.12: We find $x_{n+1} = \frac{8.899x_n}{1+0.0013x_n}$. The model predicts there will be 6076 salmon in 2004.

Exercise 4.14:

(a) Substituting $\alpha = 0.5$ and taking the limit as $n \to \infty$ we have that $x_n \to 0$.

(b) Substituting $\alpha = 2$ and taking the limit as $n \to \infty$ we have that $x_n \to \frac{1}{\beta}$.

(c) If $\alpha < 1$, then $x_n \to 0$. If $\alpha > 1$, then $x_n \to \frac{\alpha-1}{\beta}$.

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