3.5 Modeling populations

In Section 3.1, we saw how population growth, under appropriate conditions, can be modeled by an exponential function. In this section, we examine this model a bit more closely, and consider some other models that arise through altering the assumptions behind the exponential model.

Single-species models: rabbits

The problem. If we turn 2,000 rabbits loose on a large, unpopulated island, how might the number of rabbits vary over time? If we let $R = R(t)$ be the number of rabbits at time t – measured in months, let us say – we would like to be able to make some predictions about the function $R(t)$. It would be ideal to have a formula for $R(t)$ – but this is not always possible. Nevertheless, there may still be a great deal we can say about the behavior of R. To begin our explorations we will construct a model of the rabbit population that is obviously too simple. After we analyze the predictions it makes, we'll look at various ways to modify the model so that it approximates reality more closely.

The first model. Let's assume that, at any time t, the rate at which the rabbit population changes is simply proportional to the number of rabbits present at that time. We then have the familiar differential equation

$$R' = kR. \tag{3.5.1}$$

If t is in months and R in number of rabbits, then the multiplier k, called the **per capita growth rate** (or the **reproductive rate**), should have units of month^{-1}, so that the units on the two sides of our differential equation agree with the other.

There is another, perhaps more suggestive, way of understanding k, and its units. We divide both sides of the differential equation (3.5.1) by R, to get

$$k = \frac{R'}{R}. \tag{3.5.2}$$

Since R' has units of rabbits/month, and R has units of rabbits, equation (3.5.2) tells us that k has units of rabbits per month per rabbit. Mathematically, these are the same units as month^{-1}. However, the "rabbits per month per rabbit" interpretation is more indicative of what k measures: it measures how many rabbits per month result from *each* rabbit (on average, of course). Or to put it another way: $1/k$ months is the average length of time required for a rabbit to produce one new rabbit.

For the sake of discussion, let's suppose that $k = 0.1$ rabbits per month per rabbit. We also assume, as above, that there are 2,000 rabbits at the start. We can now state a clearly defined initial value problem for the function $R(t)$:

$$R' = 0.1R, \qquad R(0) = 2,000. \tag{3.5.3}$$

As we saw in Section 3.1, this initial value problem has solution

$$R(t) = 2{,}000e^{0.1t}$$

rabbits after t months.

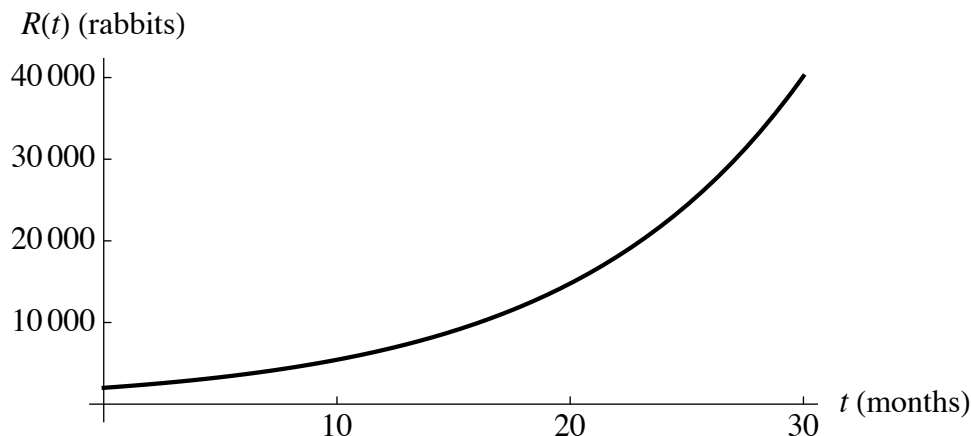The graph of $R(t)$ looks like this:

Figure 3.3. Growth of rabbits according to the initial value problem (3.5.3)

This model is too simple to be able to describe what happens to a rabbit population very well. One of the obvious difficulties is that it predicts the rabbit population just keeps growing – forever. For example, if we used the formula for $R(t)$ given above, our model would predict that after 20 years – $t = 240$ – there will be $2{,}000e^{0.1 \cdot 240}$, or more than 50 *trillion,* rabbits! While rabbit populations can, under good conditions, grow at a nearly constant per capita rate for a surprisingly long time (this happened in Australia during the 19th century), our model is ultimately unrealistic.

> It is a good idea to think qualitatively about the functions determined by a differential equation and make some rough estimates before doing extensive calculations. Your sketches may help you see ways in which the model doesn't correspond to reality. Or, you may be able to catch errors in your computations if they differ noticeably from what your estimates led you to expect.

The second model. One way out of the problem of unlimited growth is to modify equation (3.5.1) to take into account the fact that any given ecological system can support only some finite number of creatures over the long term. This number is called the **carrying capacity** of the system. We expect that, as a population approaches the carrying capacity of the system, the growth of the population should slow way down. That is: near carrying capacity, a population should hold nearly steady – its rate of change should be close to zero.

Let's denote this carrying capacity by b. What we would like to do, then, is to find an expression for R' which is in some ways similar to equation (3.5.1), but which approaches 0 as R approaches b. One model which captures these features is the **logistic equation**, first proposed by the Belgian mathematician Otto Verhulst in 1845:

$$R' = kR\left(1 - \frac{R}{b}\right). \tag{3.5.4}$$

In this equation, the coefficient k is called the **natural growth rate**. It plays much the same role as the per capita growth rate in equation (3.5.1), and it has the same units (if R and t have the

same units as in (3.5.1)). The carrying capacity b is measured in rabbits (or whatever the units of R are).

Logistic growth – that is, growth according to equation (3.5.4) – has several key features:

1. Suppose that, at some point or interval in time, R is small compared to b. Then the quantity R/b in (3.5.4) will be small, so that the quantity $1 - R/b$ in parentheses will be close to 1. So (3.5.4) will "look like" the simpler, exponential growth differential equation $R' = kR$. In other words: as long as the population is much smaller than the carrying capacity, logistic growth looks a lot like exponential growth.

2. Suppose, on the other hand, that R is close to b, but less than b. Then $1 - R/b$ will be close to zero, but positive, so by (3.5.4), R' will be too. In other words: as the population grows close to the carrying capacity, its growth slows down.

3. If, on the other hand, R is initially *larger* than b, then by (3.5.4), R' will be negative. So a population that exceeds the carrying capacity will decrease – which makes sense because, again, the carrying capacity is the maximum value of R that our system can support. (If R is larger than b, but becomes close to b, then R' will become negative and small, signifying that the attrition in population has slowed.)

Returning to our island of rabbits: for the sake of specificity, let's suppose that the carrying capacity of the island is 25,000 rabbits. If we keep the natural growth rate at 0.1 rabbits per month per rabbit, then our logistic initial value problem for the rabbit population is

$$R' = 0.1R\left(1 - \frac{R}{25{,}000}\right), \qquad R(0) = 2{,}000. \qquad (3.5.5)$$

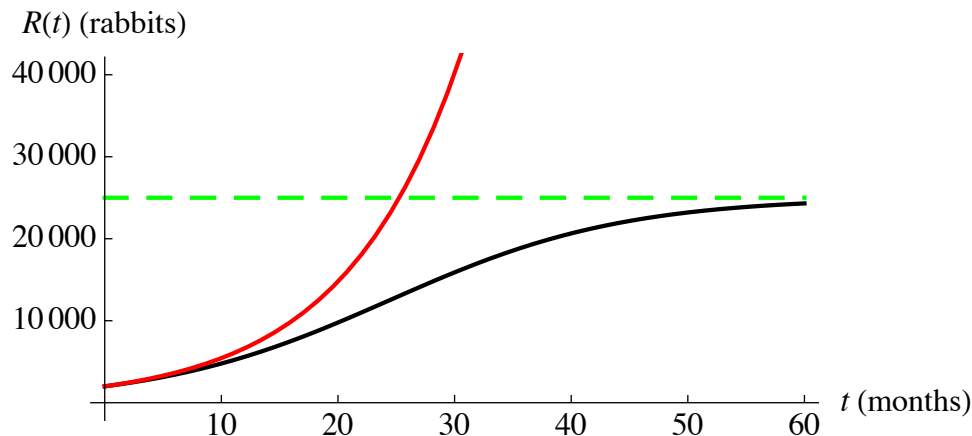The solution to this initial value problem has the following graph.

Figure 3.4. Growth of rabbits according to the logistic initial value problem (3.5.5) (black curve)

For comparison we have also graphed, in red, the solution to the exponential growth initial value problem (3.5.3). Notice that the two graphs look similar when R is near 2,000, but look quite different later on. (The dashed green line is an "asymptote" for the logistic model – a line that the logistic curve approaches as time elapses.)

To graph logistic curves like the one above, one can, of course, apply Euler's method to the logistic equation (3.5.4). Actually though, this equation, like the exponential growth differential equation, admits a closed-form solution. Specifically one may show that (3.5.4), together with the initial condition $R(0) = R_0$, have solution

$$R(t) = \frac{R_0 b}{R_0 + (b - R_0)e^{-kt}}. \tag{3.5.6}$$

We will see how to derive equation (3.5.6) in Section 5.3.

Two-species Models: Rabbits and Foxes

No species lives alone in an environment, and the same is true of the rabbits on our island. The rabbit population will probably have to deal with predators of various sorts. Some are microscopic – disease organisms, for example – while others loom as obvious threats. We will enrich our population model by adding a second species – foxes – that will prey on the rabbits. Can we say what will happen? Will the number of foxes and rabbits level off and reach a "steady state" where their numbers don't vary? Or will one species perhaps become extinct?

Let F denote the number of foxes, and R the number of rabbits. As before, measure the time t in months. Then F and R are functions of t: $F(t)$ and $R(t)$. We seek differential equations that describe how the growth rates F' and R' are related to the population sizes F and R. We make the following assumptions.

- In the absence of foxes, the rabbit population grows logistically.

- The population of rabbits declines at a rate proportional to the product RF. This is reasonable if we assume rabbits never die of old age – they just get a little too slow. Their death rate, which depends on the number of fatal encounters between rabbits and foxes, will then be approximately proportional to both R and F – and thus to their product. (This is the same kind of interaction effect we used in our SIR epidemic model to predict the rate at which susceptibles become infected.)

- In the absence of rabbits, the foxes die off at a rate proportional to the number of foxes present.

- The fox population increases at a rate proportional to the number of encounters between rabbits and foxes. To a first approximation, this says that the birth rate in the fox population depends on maternal fox nutrition, and this depends on the number of rabbit-fox encounters, which is proportional to RF.

Our assumptions are about birth and death rates, so we can convert them quite naturally into differential equations. Pause here and check that the assumptions translate into these differential equations:

$$R' = aR\left(1 - \frac{R}{b}\right) - cRF = aR - \frac{a}{b}R^2 - cRF$$
$$F' = dRF - eF$$

These are called the **Lotka–Volterra equations** for bounded (that is, logistic) growth of rabbits. The coefficients a, b, c, d, and e are **parameters** – constants that have to be determined through field observations in particular circumstances.

An example. To see what kind of predictions the Lotka–Volterra equations make, we'll work through an example with specific values for the parameters. Let

$$
\begin{aligned}
a &= & 0.1 & \quad \text{rabbits per month per rabbit} \\
b &= & 10{,}000 & \quad \text{rabbits} \\
c &= & 0.005 & \quad \text{rabbits per month per rabbit-fox} \\
d &= & 0.00004 & \quad \text{foxes per month per rabbit-fox} \\
e &= & 0.04 & \quad \text{foxes per month per fox}
\end{aligned}
$$

(Check that these five parameters have the right units.) Let's also suppose that there are 2,000 rabbits and 10 foxes at time $t = 0$. These choices give us the specific initial value problem

$$
\begin{aligned}
R' &= 0.1\,R - 0.00001\,R^2 - 0.005\,RF, & R(0) &= 2{,}000; \\
F' &= 0.00004\,RF - 0.04\,F, & F(0) &= 10.
\end{aligned}
\tag{3.5.7}
$$

Then the two populations will vary in the following way over the next 300 months.
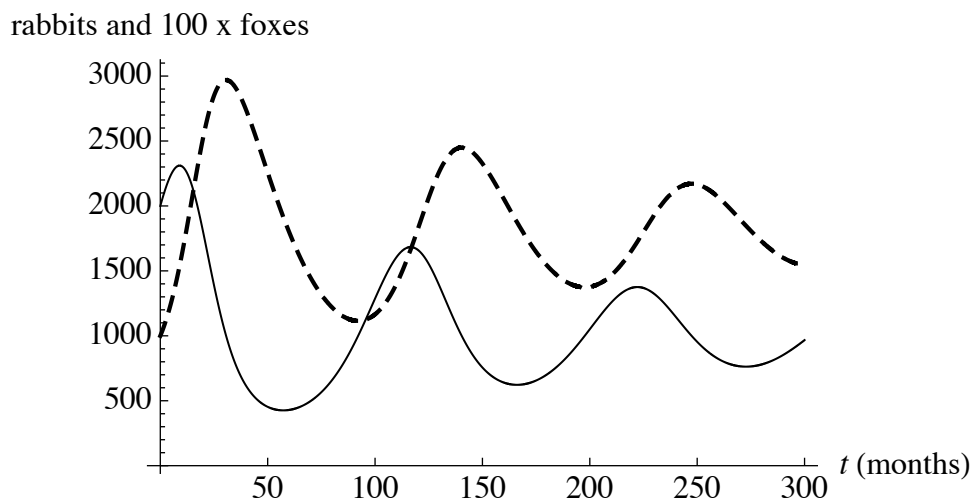

Figure 3.5. Rabbits (solid) and $100 \times$ foxes (dashed), in the two-species model (3.5.7)

A variant of the program SIR.sws (see Section 1.7) was used to produce these graphs. Notice that we have plotted $100F$ rather than F itself. This is because the number of foxes is about 100 times smaller than the number of rabbits. Consequently, $100F$ and R are about the same size, so their graphs fit nicely together on the same screen.

The graphs have several interesting features. The peak fox population is about 30, while the peak rabbit population is about 2,300. The rabbit and fox populations rise and fall in a regular manner. They rise and fall less with each repeat, though, and if the graphs were continued far enough into the future, we would see R and F level off to nearly constant values.

The illustration below shows what happens to an initial rabbit population of 2,000 in the presence of three different initial fox populations $F(0)$. Note that the peak rabbit populations are different, and they occur at different times. The size of the intervals between peaks also depends on $F(0)$.
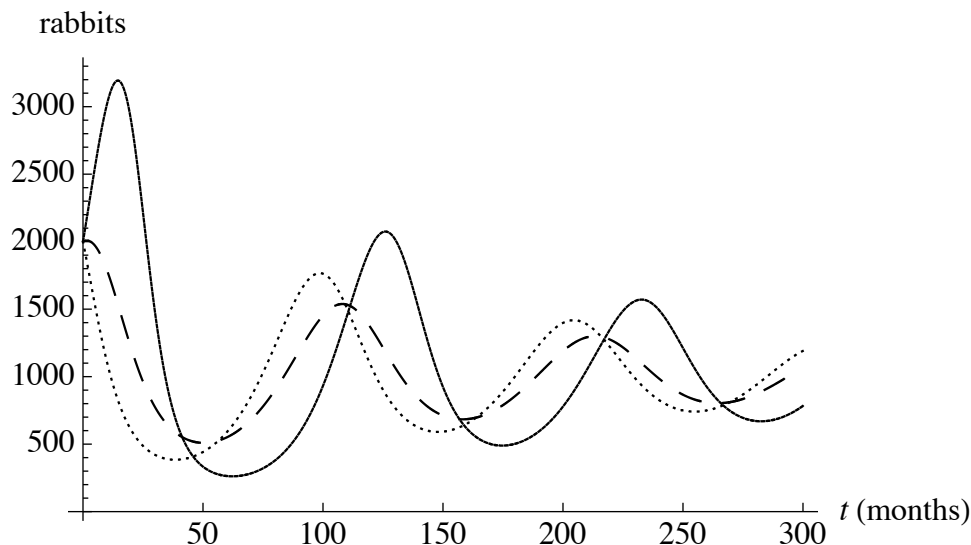

Figure 3.6. Rabbit populations in the two-species model (3.5.7), but with initial fox populations $F(0) = 5$ (solid), $F(0) = 15$ (dashed), and $F(0) = 25$ (dotted)

We have looked at three models, each a refinement of the preceding one. The first was the simplest. It accounted only for the rabbits, and it assumed the rabbit population grew at a constant per capita rate. The second was also restricted to rabbits, but it assumed logistic growth to take into account the carrying capacity of the environment. The third introduced the complexity of a second species preying on the rabbits. In the exercises, you will have an opportunity to explore these and other models. Remember that when you use Euler's method to find the functions determined by an initial value problem, you must construct a sequence of successive approximations, until you obtain the level of accuracy desired.

Exercises

Part 1: Single-species models

1. **Constant per capita Growth**. This question considers the initial value problem given in the text:

$$R' = 0.1\,R \text{ rabbits per month}; \qquad R(0) = 2{,}000 \text{ rabbits}.$$

(a) Use Euler's method to determine how many rabbits there are after 6 months. Present a table of successive approximations from which you can read the exact value to whole-number accuracy.

(b) Determine, to whole-number accuracy, how many rabbits there are after 24 months.

(c) How many months does it take for the rabbit population to reach 25,000?

2. **Logistic Growth**. The following questions concern a rabbit population described by the logistic model

$$R' = 0.1\,R \left(1 - \frac{R}{25000}\right) \text{ rabbits per month}.$$

(a) What happens to a population of 2,000 rabbits after 6 months, after 24 months, and after 5 years? To answer each question, present a table of successive approximations that allows you to give the exact value to the nearest whole number.

(b) Sketch the functions determined by the logistic equation if you start with either 2,000 or 40,000 rabbits. (Suggestion: you can modify the program SIR.sws of Section 1.7 to answer this question.) Compare the two functions. How do they differ? In what ways are they similar?

3. **Seasonal Factors.** Living conditions for most wild populations are not constant throughout the year – due to factors like drought or cold, the environment is less supportive during some parts of the year than at others. Partially in response to this, most animals don't reproduce uniformly throughout the year. This problem explores ways of modifying the logistic model to reflect these facts.

(a) For the eastern cottontail rabbit, most young are born during the months of March–May, with reduced reproduction during June–August, and virtually no reproduction during the other six months of the year. Write a program to generate the solution to the differential equation $R' = k(1 - R/25000)$, where $k = 0.2$ during March, April, and May; $k = 0.05$ during June, July, and August; and $k = 0$ the rest of the year. Start with an initial population of 2,000 rabbits on January 1.

(b) How would you modify the model to take into account the fact that rabbits don't reproduce during their first season?

4. **World population**. The world's population in 1990 was about 5 billion, and data show that birth rates range from 35 to 40 per thousand per year and death rates from 15 to 20. Take this

to imply a net annual growth rate of 20 per thousand. One model for world population assumes constant per capita growth, with a per capita growth rate of $20/1000 = 0.02$.

(a) Write a differential equation for P that expresses this assumption. Use P to denote the world population, measured in billions.

(b) According to the differential equation in (a), at what rate (in billions of persons per year) was the world population growing in 1990?

(c) By applying Euler's method to this model, using the initial value of 5 billion in 1990, estimate the world population in the years 1980, 2,000, 2040, and 2230. Present a table of successive approximations that stabilizes with one decimal place of accuracy (in billions). What step size did you have to use to obtain this accuracy?

5. **Supergrowth**. Another model for the world population, one that actually seems to fit recent population data fairly well, assumes "supergrowth" – the rate P' is proportional to a *higher power* of P, rather than to P itself. The model is

$$P' = 0.015\, P^{1.2}.$$

As in the previous exercise, assume that P is measured in billions, and that the population in 1990 was about 5 billion.

(a) According to this model, at what rate (in billions of persons per year) was the population growing in 1990?

(b) Using Euler's method, estimate the world population in the years 1980, 2,000 and 2040. Use successive approximations until you have one decimal place of accuracy (in billions). What step size did you have to use to obtain this accuracy?

(c) Use an Euler approximation with a step size of 0.1 to estimate the world population in the year 2230. What happens if you repeat your calculation with a step size of 0.01? [Comment: Something strange is going on here. We will look again at this model in Section 5.3.]

Part 2: Two-species models

Here are some other differential equations that model a predator-prey interaction between two species.

6. **The May Model**. This model has been proposed by the contemporary ecologist, R.M. May, to incorporate more realistic assumptions about the encounters between predators (foxes) and their prey (rabbits). So that you can work with quantities that are about the same size (and therefore plot them on the same graph), let y be the number of foxes and let x be the number of rabbits *divided by* 100 – we are thus measuring rabbits in units of "hectorabbits".

> While a term like "hectorabbits" is deliberately whimsical, it echoes the common and sensible practice of choosing units that allow us to measure things with numbers that are neither too small nor too large. For example, we wouldn't describe the distance from the earth to the moon in millimeters, and we wouldn't describe the mass of a raindrop in kilograms.

In his model, May makes the following assumptions.

- In the absence of foxes, the rabbits grow logistically.

- The number of rabbits a single fox eats in a given time period is a function $D(x)$ of the number of rabbits available. $D(x)$ varies from 0 if there are no rabbits available to some value c (the **saturation value**) if there is an unlimited supply of rabbits. The total number of rabbits consumed in the given time period will thus be $D(x) \cdot y$.

- The fox population is governed by the logistic equation, and the carrying capacity is proportional to the number of rabbits.

(a) Explain why $D(x) = \dfrac{c\,x}{x + d}$ (d some constant) might be a reasonable model for the function $D(x)$. Include a sketch of the graph of D in your discussion. What is the role of the parameter d? That is, what feature of rabbit – fox interactions is reflected by making d smaller or larger?

(b) Explain how the following system of equations incorporates May's assumptions.

$$x' = a\,x \left(1 - \frac{x}{b}\right) - \frac{c\,x\,y}{x + d}$$

$$y' = e\,y \left(1 - \frac{y}{f x}\right)$$

The parameters a, b, c, d, e and f are all positive.

(c) Assume you begin with 2,000 rabbits and 10 foxes. (Be careful: $x(0) \neq 2{,}000$.) What does May's model predict will happen to the rabbits and foxes over time if the values of the parameters are $a = .6$, $b = 10$, $c = .5$, $d = 1$, $e = 0.1$ and $f = 2$? Use a suitable modification of the program SIR.sws.

(d) Using the same parameters, describe what happens if you begin with 2,000 rabbits and 20 foxes; with 1,000 rabbits and 10 foxes; with 1,000 rabbits and 20 foxes. Does the eventual long-term behavior depend on the initial condition? How does the long-term behavior here compare with the long-term behavior of the two populations in the Lotka–Volterra model of the text?

(e) Using 2,000 rabbits and 20 foxes as the initial values, let's see how the behavior of the solutions is affected by changing the values of the parameter c, the saturation value for the number of rabbits (measured in centirabbits, remember) a single fox can eat in a month. Keeping all the other parameters $(a, b, d, \ldots)$ fixed at the values given above, get solution curves for $c = 0.5$, $c = 0.45$, $c = 0.4$, $\ldots$, $c = 0.15$, and $c = 0.1$. The solutions undergo a qualitative change somewhere between $c = 0.3$ and $c = 0.25$. Describe this change. Can you pinpoint the crucial value of c more closely? This phenomenon is an example of **Hopf bifurcation**, which we will look at more

closely in chapter 8. The May model undergoes a Hopf bifurcation as you vary each of the other parameters as well. Choose a couple of them and locate approximately the associated bifurcation values.

7. **The Lotka–Volterra Equations**. This model for predator and prey interactions is slightly simpler than the "bounded growth" version we consider in the text. It is important historically, though, because it was one of the first mathematical population models, proposed as a way of understanding why the harvests of certain species of fish in the Adriatic Sea exhibited cyclical behavior over the years. For the sake of variety, let's take the prey to be hares and the predators to be lynx.

Let $H(t)$ denote the number of hares at time t and $L(t)$ the number of lynx. This model, the basic Lotka–Volterra model, differs from the bounded growth model in only one respect: it assumes the hares would experience constant per capita growth if there were no lynx.

(a) Explain why the following system of equations incorporates the assumptions of the basic model. (The parameters a, b, c, and d are all positive.)

$$H' = a\,H - b\,HL$$
$$L' = c\,HL - d\,L$$

(These are called the **Lotka–Volterra equations**. They were developed independently by the Italian mathematical physicist Vito Volterra in 1925–26, and by the mathematical ecologist and demographer Alfred James Lotka a few years earlier. Though simplistic, they form one of the principal starting points in ecological modeling.)

(b) Explain why a and b have the units hares per month per hare and hares per month per hare-lynx, respectively. What are the units of c and d? Explain why.

Suppose time t is measured in months, and suppose the parameters have values

$$
\begin{aligned}
a &= 0.1 && \text{hares per month per hare} \\
b &= 0.005 && \text{hares per month per hare-lynx} \\
c &= 0.00004 && \text{lynx per month per hare-lynx} \\
d &= 0.04 && \text{lynx per month per lynx}
\end{aligned}
$$

This leads to the system of differential equations

$$H' = 0.1\,H - 0.005\,HL$$
$$L' = 0.00004\,HL - 0.04\,L.$$

(c) Suppose that you start with 2,000 hares and 10 lynx – that is, $H(0) = 2{,}000$ and $L(0) = 10$. Describe what happens to the two populations. A good way to do this is to draw graphs of the functions $H(t)$ and $L(t)$. It will be convenient to have the H scale run from 0 to 3000, and the L scale from 0 to 50. If you modify the program SIR.sws, have it plot H and $60L$.
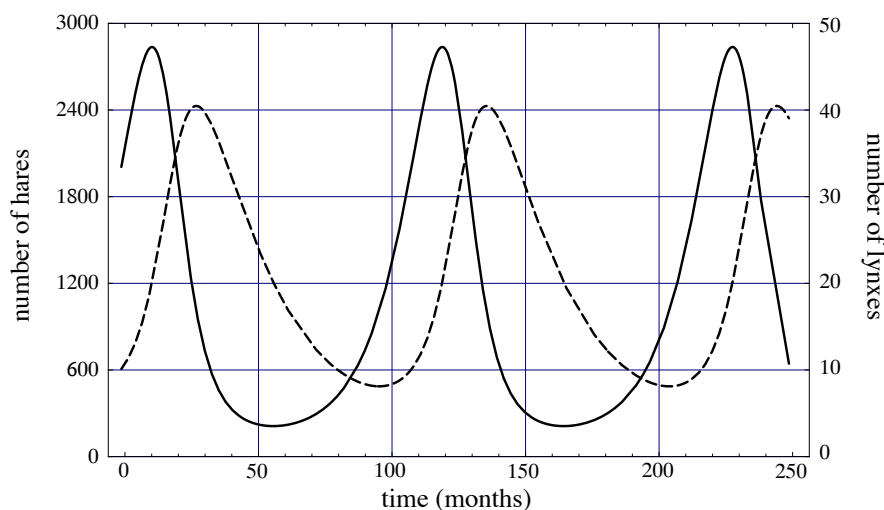
Figure 3.7. Hare and lynx populations as a function of time

You should get graphs like those above. Notice that the hare and lynx populations rise and fall in a fashion similar to the rabbits and foxes, but here they oscillate – returning *periodically* to their original values.

(d) What happens if you keep the same initial hare population of 2,000, but use different initial lynx populations? Try $L(0) = 20$ and $L(0) = 50$. (In each case, use a stepsize of 0.1 month.)

(e) Start with 2,000 hares and 10 lynx. From part (c), you know the solutions are periodic. The goal of this part is to analyze this periodic behavior. First find the maximum number of hares. What is the length of one **period** for the hare population? That is, how long does it take the hare population to complete one cycle (e.g., to go from one maximum to the next)? Find the length of one period for the lynx. Do the hare and lynx populations have the same periods?

(f) Plot the hare populations over time when you start with 2,000 hares and, successively, 10, 20, and 50 lynx. Is the hare population periodic in each case? What is the period? Does it vary with the size of the initial lynx population?