1.1 MODELING VIA DIFFERENTIAL EQUATIONS

The hardest part of using mathematics to study an application is the translation from real life into mathematical formalism. This translation is usually difficult because it involves the conversion of imprecise assumptions into very precise formulas. There is no way to avoid it. Modeling is difficult, and the best way to get good at it is the same way you get to play Carnegie Hall—practice, practice, practice.

What Is a Model?

It is important to remember that mathematical models are like other types of models. The goal is not to produce an exact copy of the "real" object but rather to give a representation of some aspect of the real thing. For example, a portrait of a person, a store mannequin, and a pig can all be models of a human being. None is a perfect copy of a human, but each has certain aspects in common with a human. The painting gives a description of what a particular person looks like; the mannequin wears clothes as a person does; and the pig is alive. Which of the three models is "best" depends on how we use the model—to remember old friends, to buy clothes, or to study biology.

We study mathematical models of systems that evolve over time, but they often depend on other variables as well. In fact, real-world systems can be notoriously complicated—the population of rabbits in Wyoming depends on the number of coyotes, the number of bobcats, the number of mountain lions, the number of mice (alternative food for the predators), farming practices, the weather, any number of rabbit diseases, etc. We can make a model of the rabbit population simple enough to understand only by making simplifying assumptions and lumping together effects that may or may not belong together.

Once we've built the model, we should compare predictions of the model with data from the system. If the model and the system agree, then we gain confidence that the assumptions we made in creating the model are reasonable, and we can use the model to make predictions. If the system and the model disagree, then we must study and improve our assumptions. In either case we learn more about the system by comparing it to the model.

The types of predictions that are reasonable depend on our assumptions. If our model is based on precise rules such as Newton's laws of motion or the rules of compound interest, then we can use the model to make very accurate quantitative predictions. If the assumptions are less precise or if the model is a simplified version of the system, then precise quantitative predictions would be silly. In this case we would use the model to make qualitative predictions such as "the population of rabbits in Wyoming will increase ...." The dividing line between qualitative and quantitative prediction is itself imprecise, but we will see that it is frequently better and easier to make qualitative use of even the most precise models.

Some hints for model building

The basic steps in creating the model are

Step 1 Clearly state the assumptions on which the model will be based. These assumptions should describe the relationships among the quantities to be studied.

Step 2 Completely describe the variables and parameters to be used in the model—"you can't tell the players without a program."

Step 3 Use the assumptions formulated in Step 1 to derive equations relating the quantities in Step 2.

Step 1 is the "science" step. In Step 1, we describe how we think the physical system works or, at least, what the most important aspects of the system are. In some cases these assumptions are fairly speculative, as, for example, "rabbits don't mind being overcrowded." In other cases the assumptions are quite precise and well accepted, such as "force is equal to the product of mass and acceleration." The quality of the assumptions determines the validity of the model and the situations to which the model is relevant. For example, some population models apply only to small populations in large environments, whereas others consider limited space and resources. Most important, we must avoid "hidden assumptions" that make the model seem mysterious or magical.

Step 2 is where we name the quantities to be studied and, if necessary, describe the units and scales involved. Leaving this step out is like deciding you will speak your own language without telling anyone what the words mean.

The quantities in our models fall into three basic categories: the **independent variable**, the **dependent variables**, and the **parameters**. In this book the independent variable is (almost) always time. Time is "independent" of any other quantity in the model. On the other hand, the dependent variables are quantities that are functions of the independent variable. For example, if we say that "position is a function of time," we mean that position is a variable that depends on time. We can vaguely state the goal of a model expressed in terms of a differential equation as "Describe the behavior of the dependent variable as the independent variable changes." For example, we may ask whether the dependent variable increases or decreases, or whether it oscillates or tends to a limit.

Parameters are quantities that don't change with time (or with the independent variable) but that can be adjusted (by natural causes or by a scientist running the experiment). For example, if we are studying the motion of a rocket, the initial mass of the rocket is a parameter. If we are studying the amount of ozone in the upper atmosphere, then the rate of release of fluorocarbons from refrigerators is a parameter. Determining how the behavior of the dependent variables changes when we adjust the parameters can be the most important aspect of the study of a model.

In Step 3 we create the equations. Most of the models we consider are expressed as differential equations. In other words, we expect to find derivatives in our equations. Look for phrases such as "rate of change of ..." or "rate of increase of ...," since rate of change is synonymous with derivative. Of course, also watch for "velocity" (derivative of position) and "acceleration" (derivative of velocity) in models from physics. The word *is* means "equals" and indicates where the equality lies. The phrase "A is proportional to B" means $A = kB$, where k is a proportionality constant (often a parameter in the model).

An important rule of thumb we use when formulating models is: *Always make the algebra as simple as possible.* For example, when modeling the velocity v of a cat falling from a tall building, we could assume:

- Air resistance increases as the cat's velocity increases.

This assumption says that air resistance provides a force that counteracts the force of gravity and that this force increases as the velocity v of the cat increases. We could choose kv or kv^2 for the air resistance term, where k is the friction coefficient, a parameter. Both expressions increase as v increases, so they satisfy the assumption. However, we most likely would try kv first because it is the simplest expression that satisfies the assumption. In fact, it turns out that kv yields a good model for falling bodies with low densities like snowflakes, but kv^2 is a more appropriate model for dense objects like raindrops.

Now we turn to a series of models of population growth based on various assumptions about the species involved. Our goal here is to study how to go from a set of assumptions to a model. These examples are not "state-of-the-art" models from population ecology, but they are good ones to consider initially. We also begin to describe the analytic, qualitative, and numerical techniques that we use to make predictions based on these models. Our approach is meant to be illustrative only; we discuss these mathematical techniques in much more detail throughout the entire book.

Unlimited Population Growth

An elementary model of population growth is based on the assumption that

- The rate of growth of the population is proportional to the size of the population.

Note that the rate of change of a population depends on only the size of the population and nothing else. In particular, limitations of space or resources have no effect. This assumption is reasonable for small populations in large environments—for example, the first few spots of mold on a piece of bread or the first European settlers in the United States.

Because the assumption is so simple, we expect the model to be simple as well. The quantities involved are

t = time (independent variable),
P = population (dependent variable), and
k = proportionality constant (parameter) between the rate of growth of the population and the size of the population.

The parameter k is often called the "growth-rate coefficient."

The units for these quantities depend on the application. If we are modeling the growth of mold on bread, then t might be measured in days and $P(t)$ might be either the area of bread covered by the mold or the weight of the mold. If we are talking about the European population of the United States, then t probably should be measured in years and $P(t)$ in millions of people. In this case we could let $t = 0$ correspond to any time we wanted. The year 1790 (the year of the first census) is a convenient choice.

Now let's express our assumption using this notation. The rate of growth of the population P is the derivative dP/dt. Being proportional to the population is expressed as the product, kP, of the population P and the proportionality constant k. Hence our assumption is expressed as the differential equation

$$\frac{dP}{dt} = kP.$$

In other words, the rate of change of P is proportional to P.

This equation is our first example of a differential equation. Associated with it are a number of adjectives that describe the type of differential equation that we are considering. In particular, it is a **first-order** equation because it contains only first derivatives of the dependent variable, and it is an **ordinary differential equation** because it does not contain partial derivatives. In this book we deal only with ordinary differential equations.

We have written this differential equation using the dP/dt Leibniz notation—the notation that we tend to use. However, there are many other ways to express the same differential equation. In particular, we could also write this equation as $P' = kP$ or as $\dot{P} = kP$. The "dot" notation is often used when the independent variable is time t.

What does the model predict?

More important than the adjectives or how the equation is written is what the equation tells us about the situation being modeled. Since $dP/dt = kP$ for some constant k, $dP/dt = 0$ if $P = 0$. Thus the constant function $P(t) = 0$ is a solution of the differential equation. This special type of solution is called an **equilibrium solution** because it is constant forever. In terms of the population model, it corresponds to a species that is nonexistent.

If $P(t_0) \neq 0$ at some time t_0, then at time $t = t_0$

$$\frac{dP}{dt} = k\,P(t_0) \neq 0.$$

As a consequence, the population is not constant. If $k > 0$ and $P(t_0) > 0$, we have

$$\frac{dP}{dt} = kP(t_0) > 0,$$

at time $t = t_0$ and the population is increasing (as one would expect). As t increases, $P(t)$ becomes larger, so dP/dt becomes larger. In turn, $P(t)$ increases even faster. That is, the rate of growth increases as the population increases. We therefore expect that the graph of the function $P(t)$ might look like Figure 1.1.

The value of $P(t)$ at $t = 0$ is called an **initial condition**. If we start with a different initial condition we get a different function $P(t)$ as is indicated in Figure 1.2. If $P(0)$ is negative (remembering $k > 0$), we then have $dP/dt < 0$ for $t = 0$, so $P(t)$ is initially decreasing. As t increases, $P(t)$ becomes more negative. The picture below the t-axis is the flip of the picture above, although this isn't "physically meaningful" because a negative population doesn't make much sense.

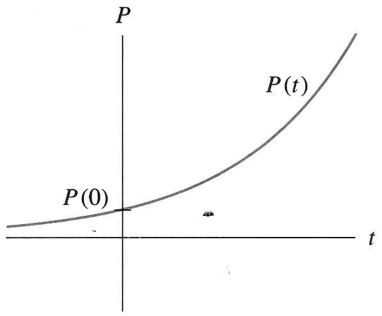

Figure 1.1
The graph of a function that satisfies the differential equation

$$\frac{dP}{dt} = kP.$$

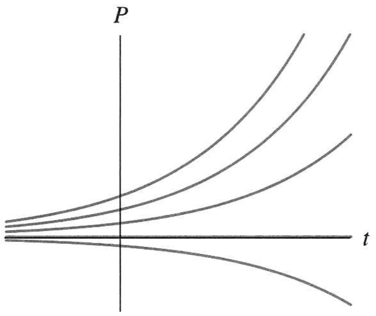

Figure 1.2
The graphs of several different functions that satisfy the differential equation $dP/dt = kP$. Each has a different value at $t = 0$.

Our analysis of the way in which $P(t)$ increases as t increases is called a **qualitative analysis** of the differential equation. If all we care about is whether the model predicts "population explosions," then we can answer "yes, as long as $P(0) > 0$."

Analytic solutions of the differential equation

If, on the other hand, we know the exact value P_0 of $P(0)$ and we want to predict the value of $P(10)$ or $P(100)$, then we need more precise information about the function $P(t)$. The pair of equations

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

is called an **initial-value problem**. A **solution** to the initial-value problem is a function $P(t)$ that satisfies both equations. That is,

$$\frac{dP}{dt} = kP \text{ for all } t \quad \text{and} \quad P(0) = P_0.$$

Consequently, to find a solution to this differential equation we must find a function $P(t)$ whose derivative is the product of k with $P(t)$. One (not very subtle) way to find such a function is to guess. In this case, it is relatively easy to guess the right form for $P(t)$ because we know that the derivative of an exponential function is essentially itself. (We can eliminate this guesswork by using the method of separation of variables, which we describe in the next section. But for now, let's just try the exponential and see where that leads us.) After a couple of tries with various forms of the exponential, we see that

$$P(t) = e^{kt}$$

is a function whose derivative, $dP/dt = ke^{kt}$, is the product of k with $P(t)$. But there are other possible solutions, since $P(t) = ce^{kt}$ (where c is a constant) yields $dP/dt = c(ke^{kt}) = k(ce^{kt}) = kP(t)$. Thus $dP/dt = kP$ for all t for any value of the constant c.

We have infinitely many solutions to the differential equation, one for each value of c. To determine which of these solutions is the correct one for the situation at hand, we use the given initial condition. We have

$$P_0 = P(0) = c \cdot e^{k \cdot 0} = c \cdot e^0 = c \cdot 1 = c.$$

Consequently, we should choose $c = P_0$, so a solution to the initial-value problem is

$$P(t) = P_0 e^{kt}.$$

We have obtained an actual formula for our solution, not just a qualitative picture of its graph.

The function $P(t)$ is called the solution to the initial-value problem as well as a **particular solution** of the differential equation. The collection of functions $P(t) = ce^{kt}$ is called the **general solution** of the differential equation because we can use it to find the particular solution corresponding to any initial-value problem. Figure 1.2 consists of the graphs of exponential functions of the form $P(t) = ce^{kt}$ with various values of the constant c, that is, with different initial values. In other words, it is a picture of the general solution to the differential equation.

The U.S. Population

As an example of how this model can be used, consider the U.S. census figures since 1790 given in Table 1.1.

Table 1.1
U.S. census figures, in millions of people (see `www.census.gov`)

Year	t	Actual	$P(t) = 3.9e^{0.03067t}$	Year	t	Actual	$P(t) = 3.9e^{0.03067t}$
1790	0	3.9	3.9	1930	140	122	286
1800	10	5.3	5.3	1940	150	131	388
1810	20	7.2	7.2	1950	160	151	528
1820	30	9.6	9.8	1960	170	179	717
1830	40	12	13	1970	180	203	975
1840	50	17	18	1980	190	226	1,320
1850	60	23	25	1990	200	249	1,800
1860	70	31	33	2000	210	281	2,450
1870	80	38	45	2010	220		3,320
1880	90	50	62	2020	230		4,520
1890	100	62	84	2030	240		6,140
1900	110	75	114	2040	250		8,340
1910	120	91	155	2050	260		11,300
1920	130	105	210				

Let's see how well the unlimited growth model fits this data. We measure time in years and the population $P(t)$ in millions of people. We also let $t = 0$ be the year 1790, so the initial condition is $P(0) = 3.9$. The corresponding initial-value problem

$$\frac{dP}{dt} = kP, \qquad P(0) = 3.9,$$

has $P(t) = 3.9e^{kt}$ as a solution. We cannot use this model to make predictions yet because we don't know the value of k. However, we do know that the population in the year 1800 was 5.3 million, and we can use this value to determine k. If we set

$$5.3 = P(10) = 3.9e^{k \cdot 10},$$

then we have

$$\begin{aligned} e^{k \cdot 10} &= \frac{5.3}{3.9} \\ 10k &= \ln\left(\frac{5.3}{3.9}\right) \\ k &\approx 0.03067. \end{aligned}$$

Thus our model predicts that the United States population is given by

$$P(t) = 3.9e^{0.03067t}.$$

As we see from Figure 1.3, this model of $P(t)$ does a decent job of predicting the population until roughly 1860, but after 1860 the prediction is much too large. (Table 1.1 includes a comparison of the predicted values to the actual data.)

Our model is fairly good provided the population is relatively small. However, as time goes on, the model predicts that the population will continue to grow without any limits, and obviously, this cannot happen in the real world. Consequently, if we want a model that is accurate over a large time scale, we should account for the fact that populations exist in a finite amount of space and with limited resources.

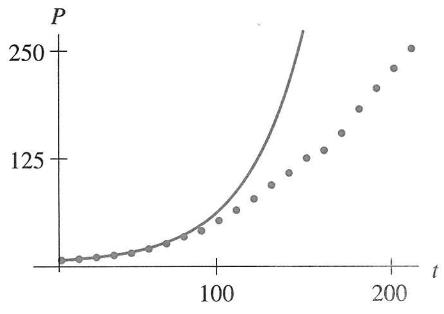

Figure 1.3
The dots represent actual census data and the solid line is the solution of the exponential growth model

$$\frac{dP}{dt} = 0.03067P.$$

Time t is measured in years since the year 1790.

Logistic Population Model

To adjust the exponential growth population model to account for a limited environment and limited resources, we add the assumptions:

- If the population is small, the rate of growth of the population is proportional to its size.
- If the population is too large to be supported by its environment and resources, the population will decrease. That is, the rate of growth is negative.

For this model, we again use

$$\begin{aligned} t &= \text{time (independent variable)}, \\ P &= \text{population (dependent variable)}, \\ k &= \text{growth-rate coefficient for small populations (parameter)}. \end{aligned}$$

However, our assumption about limited resources introduces another quantity, the size of the population that corresponds to being "too large." This quantity is a second parameter, denoted by N, that we call the "carrying capacity" of the environment. In terms of the carrying capacity, we are assuming that $P(t)$ is increasing if $P(t) < N$. However, if $P(t) > N$, we assume that $P(t)$ is decreasing.

Using this notation, we can restate our assumptions as:

- $\dfrac{dP}{dt} \approx kP$ if P is small (first assumption).
- If $P > N$, $\dfrac{dP}{dt} < 0$ (second assumption).

We also want the model to be "algebraically simple," or at least as simple as possible, so we try to modify the exponential model as little as possible. For instance, we might look for an expression of the form

$$\frac{dP}{dt} = k \cdot (\text{something}) \cdot P.$$

We want the "something" factor to be close to 1 if P is small, but if $P > N$ we want "something" to be negative. The simplest expression that has these properties is the function

$$(\text{something}) = \left(1 - \frac{P}{N}\right).$$

Note that this expression equals 1 if $P = 0$, and it is negative if $P > N$. Thus our model is

$$\frac{dP}{dt} = k\left(1 - \frac{P}{N}\right)P.$$

This is called the **logistic population model** with growth rate k and carrying capacity N. It is another first-order differential equation. This equation is said to be **nonlinear** because its right-hand side is not a linear function of P as it was in the exponential growth model.

Qualitative analysis of the logistic model

Although the logistic differential equation is just slightly more complicated than the exponential growth model, there is no way that we can just guess solutions. The method of separation of variables discussed in the next section produces a formula for the solution of this particular differential equation. But for now, we rely solely on qualitative methods to see what this model predicts over the long term.

First, let

$$f(P) = k\left(1 - \frac{P}{N}\right)P$$

denote the right-hand side of the differential equation. In other words, the differential equation can be written as

$$\frac{dP}{dt} = f(P) = k\left(1 - \frac{P}{N}\right)P.$$

We can derive qualitative information about the solutions to the differential equation from a knowledge of where dP/dt is zero, where it is positive, and where it is negative.

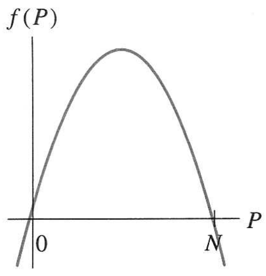

Figure 1.4
Graph of the right-hand side $f(P) = k(1 - P/N)P$ of the logistic differential equation.

If we sketch the graph of the quadratic function f (see Figure 1.4), we see that it crosses the P-axis at exactly two points, $P = 0$ and $P = N$. In either case we have $dP/dt = 0$. Since the derivative of P vanishes for all t, the population remains constant if $P = 0$ or $P = N$. That is, the constant functions $P(t) = 0$ and $P(t) = N$ are solutions of the differential equation. These two constant solutions make perfect sense: If the population is zero, the population remains zero indefinitely; if the population is exactly at the carrying capacity, it neither increases nor decreases. As before, we say that $P = 0$ and $P = N$ are *equilibria*. The constant functions $P(t) = 0$ and $P(t) = N$ are called *equilibrium solutions* (see Figure 1.5).

The long-term behavior of the population is very different for other values of the population. If the initial population lies between 0 and N, then we have $f(P) > 0$. In this case the rate of growth $dP/dt = f(P)$ is positive, and consequently the population $P(t)$ is increasing. As long as $P(t)$ lies between 0 and N, the population continues to increase. However, as the population approaches the carrying capacity N, $dP/dt = f(P)$ approaches zero, so we expect that the population might level off as it approaches N (see Figure 1.6).

If $P(0) > N$, then $dP/dt = f(P) < 0$, and the population is decreasing. As above, when the population approaches the carrying capacity N, dP/dt approaches zero, and we again expect the population to level off at N.

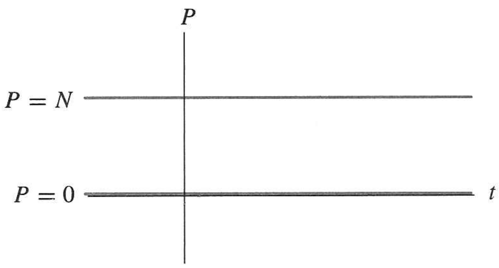

Figure 1.5
The equilibrium solutions of the logistic differential equation

$$\frac{dP}{dt} = k\left(1 - \frac{P}{N}\right)P.$$

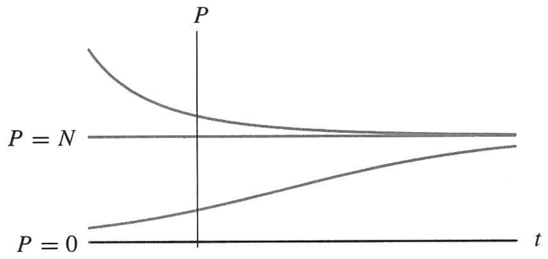

Figure 1.6
Solutions of the logistic differential equation

$$\frac{dP}{dt} = k\left(1 - \frac{P}{N}\right)P$$

approaching the equilibrium solution $P = N$.

Finally, if $P(0) < 0$ (which does not make much sense in terms of populations), we also have $dP/dt = f(P) < 0$. Again we see that $P(t)$ decreases, but this time it does not level off at any particular value since dP/dt becomes more and more negative as $P(t)$ decreases.

Thus, just from a knowledge of the graph of f, we can sketch a number of different solutions with different initial conditions, all on the same axes. The only information that we need is the fact that $P = 0$ and $P = N$ are equilibrium solutions, $P(t)$ increases if $0 < P < N$ and $P(t)$ decreases if $P > N$ or $P < 0$. Of course the exact values of $P(t)$ at any given time t depend on the values of $P(0)$, k, and N (see Figure 1.7).

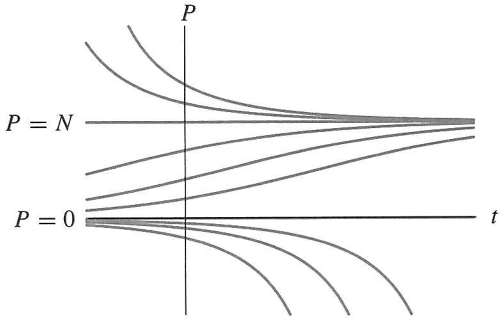

Figure 1.7
Solutions of the logistic differential equation

$$\frac{dP}{dt} = k\left(1 - \frac{P}{N}\right)P$$

approaching the equilibrium solution $P = N$ and moving away from the equilibrium solution $P = 0$.

Predator-Prey Systems

No species lives in isolation, and the interactions among species give some of the most interesting models to study. We conclude this section by introducing a simple predator-prey system of differential equations where one species "eats" another. The most obvious difference between the model here and previous models is that we have *two* quantities that depend on time. Thus our model has two dependent variables that are both functions of time. Since both predator and prey begin with "p," we call the prey "rabbits" and the predators "foxes," and we denote the prey by R and the predators by F. The assumptions for our model are:

- If no foxes are present, the rabbits reproduce at a rate proportional to their population, and they are not affected by overcrowding.

- The foxes eat the rabbits, and the rate at which the rabbits are eaten is proportional to the rate at which the foxes and rabbits interact.
- Without rabbits to eat, the fox population declines at a rate proportional to itself.
- The rate at which foxes are born is proportional to the number of rabbits eaten by foxes which, by the second assumption, is proportional to the rate at which the foxes and rabbits interact. *

To formulate this model in mathematical terms, we need four parameters in addition to our independent variable t and our two dependent variables F and R. The parameters are

α = growth-rate coefficient of rabbits,
β = constant of proportionality that measures the number of rabbit-fox interactions in which the rabbit is eaten,
γ = death-rate coefficient of foxes,
δ = constant of proportionality that measures the benefit to the fox population of an eaten rabbit.

When we formulate our model, we follow the convention that α, β, γ, and δ are all positive.

Our first and third assumptions above are similar to the assumption in the unlimited growth model discussed earlier in this section. Consequently, they give terms of the form αR in the equation for dR/dt and $-\gamma F$ (since the fox population declines) in the equation for dF/dt.

The rate at which the rabbits are eaten is proportional to the rate at which the foxes and rabbits interact, so we need a term that models the rate of interaction of the two populations. We want a term that increases if either R or F increases, but it should vanish if either $R = 0$ or $F = 0$. A simple term that incorporates these assumptions is RF. Thus we model the effects of rabbit-fox interactions on dR/dt by a term of the form $-\beta RF$. The fourth assumption gives a similar term in the equation for dF/dt. In this case, eating rabbits helps the foxes, so we add a term of the form δRF.

Given these assumptions, we obtain the model

$$\begin{aligned}\frac{dR}{dt} &= \alpha R - \beta RF\\ \frac{dF}{dt} &= -\gamma F + \delta RF.\end{aligned}$$

Considered together, this pair of equations is called a **first-order system** (only first derivatives, but more than one dependent variable) of ordinary differential equations. The system is said to be *coupled* because the rates of change of R and F depend on both R and F.

It is important to note the signs of the terms in this system. Because $\beta > 0$, the term "$-\beta RF$" is nonpositive, so an increase in the number of foxes decreases the

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*Actually, foxes rarely eat rabbits. They focus on smaller prey, mostly mice and especially grasshoppers.

growth rate of the rabbit population. Also, since $\delta > 0$, the term "δRF" is nonnegative. Consequently, an increase in the number of rabbits increases the growth rate of the fox population.

Although this model may seem relatively simpleminded, it has been the basis of some interesting ecological studies. In particular, Volterra and D'Ancona successfully used the model to explain the increase in the population of sharks in the Mediterranean during World War I when the fishing of "prey" species decreased. The model can also be used as the basis for studying the effects of pesticides on the populations of predator and prey insects.

A *solution* to this system of equations is, unlike our previous models, a pair of functions, $R(t)$ and $F(t)$, that describe the populations of rabbits and foxes as functions of time. Since the system is coupled, we cannot simply determine one of these functions first and then the other. Rather, we must solve both differential equations simultaneously. Unfortunately, for most values of the parameters, it is impossible to determine explicit formulas for $R(t)$ and $F(t)$. These functions cannot be expressed in terms of known functions such as polynomials, sines, cosines, exponentials, and the like. However, as we will see in Chapter 2, these solutions do exist, although we have no hope of ever finding them exactly. Since analytic methods for solving this system are destined to fail, we must use either qualitative or numerical methods to "find" $R(t)$ and $F(t)$.

The Analytic, Qualitative, and Numerical Approaches

Our discussion of the three population models in this section illustrates three different approaches to the study of the solutions of differential equations. The **analytic** approach searches for explicit formulas that describe the behavior of the solutions. Here we saw that exponential functions give us explicit solutions to the exponential growth model. Unfortunately, a large number of important equations cannot be handled with the analytic approach; there simply is no way to find an exact formula that describes the situation. We are therefore forced to turn to alternative methods.

One particularly powerful method of describing the behavior of solutions is the **qualitative** approach. This method involves using geometry to give an overview of the behavior of the model, just as we did with the logistic population growth model. We do not use this method to give precise values of the solution at specific times, but we are often able to use this method to determine the long-term behavior of the solutions. Frequently, this is just the kind of information we need.

The third approach to solving differential equations is **numerical**. The computer approximates the solution we seek. Although we did not illustrate any numerical techniques in this section, we will soon see that numerical approximation techniques are a powerful tool for giving us intuition regarding the solutions we desire.

All three of the methods we use have certain advantages, and all have drawbacks. Sometimes certain methods are useful while others are not. One of our main tasks as we study the solutions to differential equations will be to determine which method or combination of methods works in each specific case. In the next three sections, we elaborate on these three techniques.

EXERCISES FOR SECTION 1.1

1. Consider the population model

$$\frac{dP}{dt} = 0.4P\left(1 - \frac{P}{230}\right),$$

where $P(t)$ is the population at time t.

(a) For what values of P is the population in equilibrium?

(b) For what values of P is the population increasing?

(c) For what values of P is the population decreasing?

2. Consider the population model

$$\frac{dP}{dt} = 0.3\left(1 - \frac{P}{200}\right)\left(\frac{P}{50} - 1\right)P,$$

where $P(t)$ is the population at time t.

(a) For what values of P is the population in equilibrium?

(b) For what values of P is the population increasing?

(c) For what values of P is the population decreasing?

3. Consider the differential equation

$$\frac{dy}{dt} = y^3 - y^2 - 12y.$$

(a) For what values of y is $y(t)$ in equilibrium?

(b) For what values of y is $y(t)$ increasing?

(c) For what values of y is $y(t)$ decreasing?

4. The following table provides the land area in Australia colonized by the American marine toad (*Bufo marinis*) every five years from 1939–1974. Model the migration of this toad using an exponential growth model

$$\frac{dA}{dt} = kA,$$

where in this case $A(t)$ is the land area occupied at time t. Make predictions about the land area occupied in the years 2010, 2050, and 2100. You should do this by

(a) solving the initial-value problem,

(b) determining the constant k,

(c) computing the predicted areas, and

(d) comparing your solution to the actual data. Do you believe your prediction?

Year	Cumulative area occupied (km^2)
1939	32,800
1944	55,800
1949	73,600
1954	138,000
1959	202,000
1964	257,000
1969	301,000
1974	584,000

(Note that there are many exponential growth models that you can form using this data. Is one a more reasonable model than the others? Note also that the area of Queensland is 1,728,000 km^2 and the area of Australia is 7,619,000 km^2.)*

Remark: The American marine toad was introduced to Australia to control sugar cane beetles and, in the words of J. W. Hedgpath (see *Science*, July 1993 and *The New York Times*, July 6, 1993),

> Unfortunately the toads are nocturnal feeders and the beetles are abroad by day, while the toads sleep under rocks, boards and burrows. By night the toads flourish, reproduce phenomenally well and eat up everything they can find. The cane growers were warned by Walter W. Froggart, president of the New South Wales Naturalist Society, that the introduction was not a good idea and that the toads would eat the native ground fauna. He was immediately denounced as an ignorant meddlesome crank. He was also dead right.

Exercises 5–7 consider an elementary model of the learning process: Although human learning is an extremely complicated process, it is possible to build models of certain simple types of memorization. For example, consider a person presented with a list to be studied. The subject is given periodic quizzes to determine exactly how much of the list has been memorized. (The lists are usually things like nonsense syllables, randomly generated three-digit numbers, or entries from tables of integrals.) If we let $L(t)$ be the fraction of the list learned at time t, where $L = 0$ corresponds to knowing nothing and $L = 1$ corresponds to knowing the entire list, then we can form a simple model of this type of learning based on the assumption:

- The rate dL/dt is proportional to the fraction of the list left to be learned.

Since $L = 1$ corresponds to knowing the entire list, the model is

$$\frac{dL}{dt} = k(1 - L),$$

where k is the constant of proportionality.

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*All data taken from "Cumulative Geographical Range of *Bufo Marinis* in Queensland, Australia from 1935 to 1974," by Michael D. Sabath, Walter C. Boughton, and Simon Easteal, in *Copeia*, No. 3, 1981, pp. 676–680.

5. For what value of L, $0 \leq L \leq 1$, does learning occur most rapidly?

6. Suppose two students memorize lists according to the same model

$$\frac{dL}{dt} = 2(1 - L).$$

(a) If one of the students knows one-half of the list at time $t = 0$ and the other knows none of the list, which student is learning most rapidly at this instant?

(b) Will the student who starts out knowing none of the list ever catch up to the student who starts out knowing one-half of the list?

7. Consider the following two differential equations that model two students' rates of memorizing a poem. Jillian's rate is proportional to the amount to be learned with proportionality constant $k = 2$. Beth's rate is proportional to the square of the amount to be learned with proportionality constant 3. The corresponding differential equations are

$$\frac{dL_J}{dt} = 2(1 - L_J) \quad \text{and} \quad \frac{dL_B}{dt} = 3(1 - L_B)^2,$$

where $L_J(t)$ and $L_B(t)$ are the fractions of the poem learned at time t by Jillian and Beth, respectively.

(a) Which student has a faster rate of learning at $t = 0$ if they both start memorizing together having never seen the poem before?

(b) Which student has a faster rate of learning at $t = 0$ if they both start memorizing together having already learned one-half of the poem?

(c) Which student has a faster rate of learning at $t = 0$ if they both start memorizing together having already learned one-third of the poem?

In Exercises 8–12, we consider the phenomenon of radioactive decay which, from experimentation, we know behaves according to the law:

> The rate at which a quantity of a radioactive isotope decays is proportional to the amount of the isotope present. The proportionality constant depends only on which radioactive isotope is used.

8. Model radioactive decay using the notation

$$\begin{aligned} t &= \text{time (independent variable)}, \\ r(t) &= \text{amount of particular radioactive isotope} \\ & \text{present at time } t \text{ (dependent variable)}, \\ -\lambda &= \text{decay rate (parameter)}. \end{aligned}$$

Note that the minus sign is used so that $\lambda > 0$.

(a) Using this notation, write a model for the decay of a particular radioactive isotope.

(b) If the amount of the isotope present at $t = 0$ is r_0, state the corresponding initial-value problem for the model in part (a).

9. The **half-life** of a radioactive isotope is the amount of time it takes for a quantity of radioactive material to decay to one-half of its original amount.

(a) The half-life of Carbon 14 (C-14) is 5230 years. Determine the decay-rate parameter λ for C-14.

(b) The half-life of Iodine 131 (I-131) is 8 days. Determine the decay-rate parameter for I-131.

(c) What are the units of the decay-rate parameters in parts (a) and (b)?

(d) To determine the half-life of an isotope, we could start with 1000 atoms of the isotope and measure the amount of time it takes 500 of them to decay, or we could start with 10,000 atoms of the isotope and measure the amount of time it takes 5000 of them to decay. Will we get the same answer? Why?

10. Carbon dating is a method of determining the time elapsed since the death of organic material. The assumptions implicit in carbon dating are that

- Carbon 14 (C-14) makes up a constant proportion of the carbon that living matter ingests on a regular basis, and
- once the matter dies, the C-14 present decays, but no new carbon is added to the matter.

Hence, by measuring the amount of C-14 still in the organic matter and comparing it to the amount of C-14 typically found in living matter, a "time since death" can be approximated. Using the decay-rate parameter you computed in Exercise 9, determine the time since death if

(a) 88% of the original C-14 is still in the material.

(b) 12% of the original C-14 is still in the material.

(c) 2% of the original C-14 is still in the material.

(d) 98% of the original C-14 is still in the material.

Remark: There has been speculation that the amount of C-14 available to living creatures has not been exactly constant over long periods (thousands of years). This makes accurate dates much trickier to determine.

11. In order to apply the carbon dating technique of Exercise 10, we must measure the amount of C-14 in a sample. Chemically, radioactive Carbon 14 (C-14) and regular carbon behave identically. How can we determine the amount of C-14 in a sample? [*Hint*: See Exercise 8.]

12. The radioactive isotope I-131 is used in the treatment of hyperthyroid. When administered to a patient, I-131 accumulates in the thyroid gland, where it decays and kills part of that gland.

(a) Suppose that it takes 72 hours to ship I-131 from the producer to the hospital. What percentage of the original amount shipped actually arrives at the hospital? (See Exercise 9.)

(b) If the I-131 is stored at the hospital for an additional 48 hours before it is used, how much of the original amount shipped from the producer is left when it is used?

(c) How long will it take for the I-131 to decay *completely* so that the remnants can be thrown away without special precautions?

13. Suppose a species of fish in a particular lake has a population that is modeled by the logistic population model with growth rate k, carrying capacity N, and time t measured in years. Adjust the model to account for each of the following situations.

(a) 100 fish are harvested each year.

(b) One-third of the fish population is harvested annually.

(c) The number of fish harvested each year is proportional to the square root of the number of fish in the lake.

14. Suppose that the growth-rate parameter $k = 0.3$ and the carrying capacity $N = 2500$ in the logistic population model of Exercise 13. Suppose $P(0) = 2500$.

(a) If 100 fish are harvested each year, what does the model predict for the long-term behavior of the fish population? In other words, what does a qualitative analysis of the model yield?

(b) If one-third of the fish are harvested each year, what does the model predict for the long-term behavior of the fish population?

15. The rhinoceros is now extremely rare. Suppose enough game preserve land is set aside so that there is sufficient room for many more rhinoceros territories than there are rhinoceroses. Consequently, there will be no danger of overcrowding. However, if the population is too small, fertile adults have difficulty finding each other when it is time to mate. Write a differential equation that models the rhinoceros population based on these assumptions. (Note that there is more than one reasonable model that fits these assumptions.)

16. Consider the following assumptions concerning the fraction of a piece of bread covered by mold.

- Mold spores fall on the bread at a constant rate.
- When the proportion covered is small, the fraction of the bread covered by mold increases at a rate proportional to the amount of bread covered.
- When the fraction of bread covered by mold is large, the growth rate decreases.
- In order to survive, mold must be in contact with the bread.

Using these assumptions, write a differential equation that models the proportion of a piece of bread covered by mold. (Note that there is more than one reasonable model that fits these assumptions.)

17. The following table contains data for the population of tawny owls in Wytham Woods, Oxford, England (collected by Southern).*

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*See J. P. Dempster, *Animal Population Ecology*, Academic Press, 1975, p. 99.

(a) What population model would you use to model this population?

(b) Can you approximate (or even make reasonable guesses for) the parameter values?

(c) What does your model predict for the population today?

Year	Population	Year	Population
1947	34	1954	52
1948	40	1955	60
1949	40	1956	64
1950	40	1957	64
1951	42	1958	62
1952	48	1959	64
1953	48		

18. For the following predator-prey systems, identify which dependent variable, x or y, is the prey population and which is the predator population. Is the growth of the prey limited by any factors other than the number of predators? Do the predators have sources of food other than the prey? (Assume that the parameters α, β, γ, δ, and N are all positive.)

(a)
$$\frac{dx}{dt} = -\alpha x + \beta xy$$
$$\frac{dy}{dt} = \gamma y - \delta xy$$

(b)
$$\frac{dx}{dt} = \alpha x - \alpha\frac{x^2}{N} - \beta xy$$
$$\frac{dy}{dt} = \gamma y + \delta xy$$

19. In the following predator-prey population models, x represents the prey, and y represents the predators.

(i)
$$\frac{dx}{dt} = 5x - 3xy$$
$$\frac{dy}{dt} = -2y + \tfrac{1}{2}xy$$

(ii)
$$\frac{dx}{dt} = x - 8xy$$
$$\frac{dy}{dt} = -2y + 6xy$$

(a) In which system does the prey reproduce more quickly when there are no predators (when $y = 0$) and equal numbers of prey?

(b) In which system are the predators more successful at catching prey? In other words, if the number of predators and prey are equal for the two systems, in which system do the predators have a greater effect on the rate of change of the prey?

(c) Which system requires more prey for the predators to achieve a given growth rate (assuming identical numbers of predators in both cases)?

20. The system

$$\frac{dx}{dt} = ax - by\sqrt{x}$$
$$\frac{dy}{dt} = cy\sqrt{x}$$

has been proposed as a model for a predator-prey system of two particular species of microorganisms (where a, b, and c are positive parameters).

(a) Which variable, x or y, represents the predator population? Which variable represents the prey population?

(b) What happens to the predator population if the prey is extinct?

21. The following systems are models of the populations of pairs of species that either *compete* for resources (an increase in one species decreases the growth rate of the other) or *cooperate* (an increase in one species increases the growth rate of the other). For each system, identify the variables (independent and dependent) and the parameters (carrying capacity, measures of interaction between species, etc.) Do the species compete or cooperate? (Assume all parameters are positive.)

(a)
$$\frac{dx}{dt} = \alpha x - \alpha\frac{x^2}{N} + \beta xy$$
$$\frac{dy}{dt} = \gamma y + \delta xy$$

(b)
$$\frac{dx}{dt} = -\gamma x - \delta xy$$
$$\frac{dy}{dt} = \alpha y - \beta xy$$

1.2 ANALYTIC TECHNIQUE: SEPARATION OF VARIABLES

What Is a Differential Equation and What Is a Solution?

A first-order differential equation is an equation for an unknown function in terms of its derivative. As we saw in Section 1.1, there are three types of "variables" in differential equations—the independent variable (almost always t for time in our examples), one or more dependent variables (which are functions of the independent variable), and the parameters. This terminology is standard but a bit confusing. The dependent variable is actually a function, so technically it should be called the dependent function.

The standard form for a first-order differential equation is

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

Here the right-hand side typically depends on both the dependent and independent variables, although we often encounter cases where either t or y is missing.

A **solution** of the differential equation is a function of the independent variable that, when substituted into the equation as the dependent variable, satisfies the equation for all values of the independent variable. That is, a function $y(t)$ is a solution if it satisfies $dy/dt = y'(t) = f(t, y(t))$. This terminology doesn't tell us how to find