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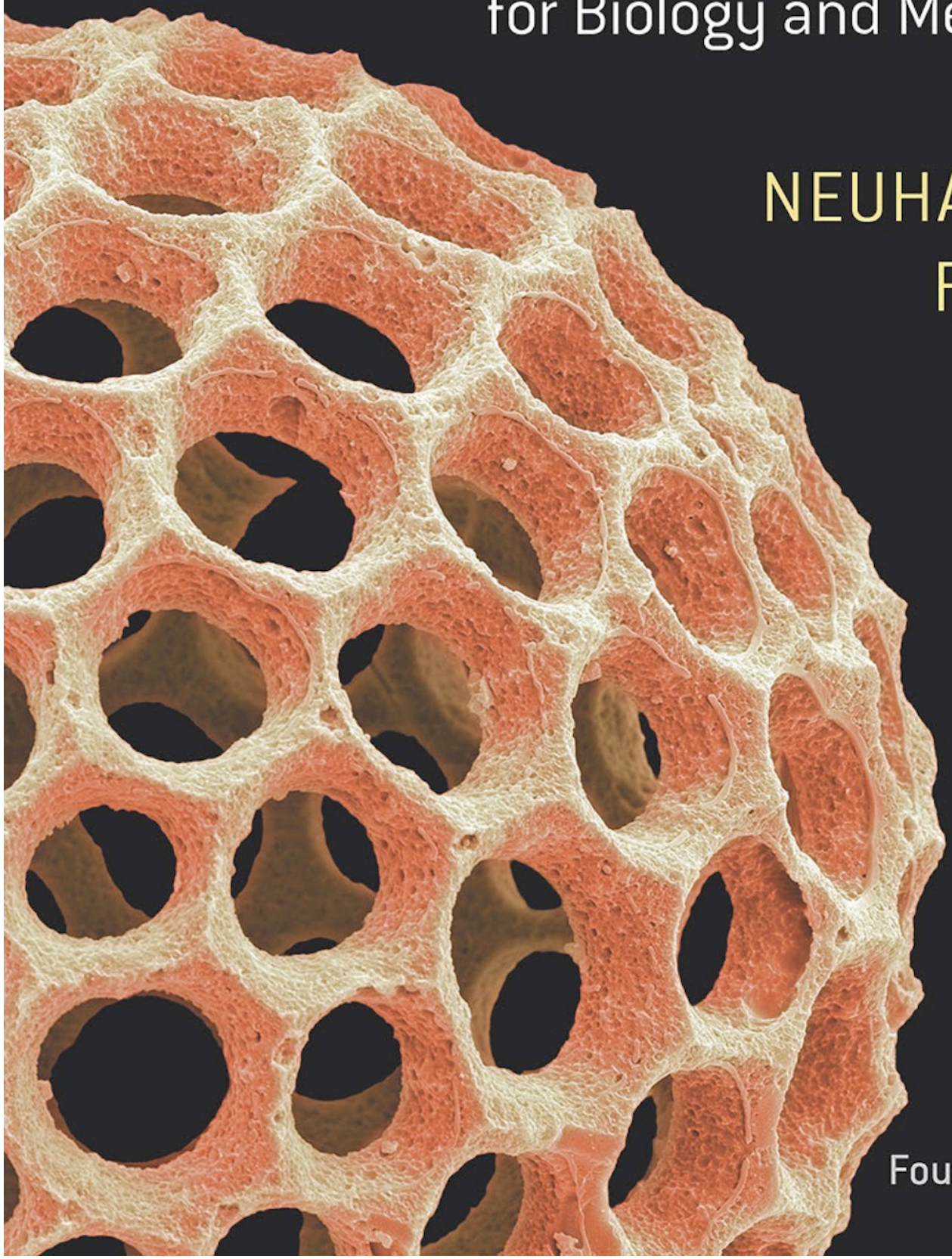

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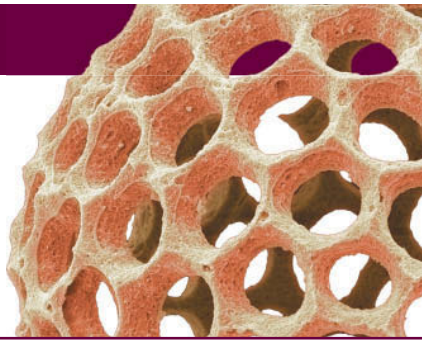
CHAPTER

8



Differential Equations

The focus of this chapter is on solving and analyzing differential equations. Specifically, we will learn how to

- use the method of separation of variables to solve separable differential equations;
- find equilibria and determine their stability graphically and analytically;
- describe the behavior of solutions of differential equations, starting from different initial conditions;
- derive differential equations to model many different biological systems;
- use the method of integrating factors to solve linear first order differential equations;
- use compartment models to analyze biological systems with multiple interacting components.

In Chapter 5 we showed how mathematical models of population growth and of the passage of medication through the human body often take the form of differential equations. For example, suppose that after t hours, the size of a population of cells is $N(t)$. If half of the cells divide every hour and if cell death can be ignored, then we may model the growth of the population by a differential equation:

$$\frac{dN}{dt} = \frac{1}{2}N \tag{8.1}$$

Previously we have shown that if the population size at time $t = 0$ is 50 (that is, $N(0) = 50$) then the function $N(t) = 50e^{t/2}$ solves (i.e., satisfies) the differential equation and matches the initial population size. But is there a way to derive the solution from the differential equation directly? In Chapter 6 we learned that integration may be thought of as being the inverse of differentiation. In Section 8.1 we will describe the most important use of this result: solving differential equations by integrating them.

We call (8.1) a **first order differential equation** because it includes the first order derivative dN/dt, but no higher order derivatives (like d^2N/dt^2, d^3N/dt^3, etc.). The techniques introduced in this chapter will enable you to solve first order differential equations. In Section 8.1 we will learn how to solve differential equations of the form:

$$\frac{dN}{dt} = f(t)g(N) \tag{8.2}$$

in which the right-hand side of the equation can be written as the product of two functions, f and g, $f(t)$ is a function of t only, and $g(N)$ is a function of N only. Equation (8.1) is an example of this kind of equation; we may set $g(N) = \frac{1}{2}N$ (a function of N) and $f(t) = 1$ (a function of t).

Using the method from Section 8.1, we will be able to solve many different mathematical models. For some types of differential equations, however, it is possible to get qualitative information about the solution (e.g., the shape of the graph of $N(t)$ against t or the limit of $N(t)$ as $t \to \infty$) without solving the equation, as we shall learn in Section 8.2. In Section 8.3 we will derive and analyze differential equation models

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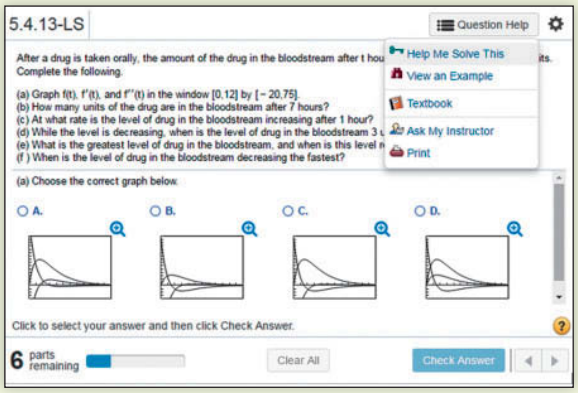

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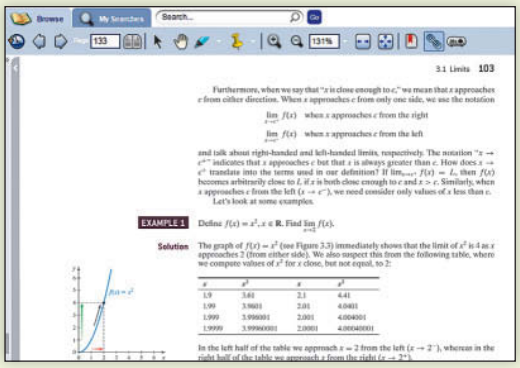

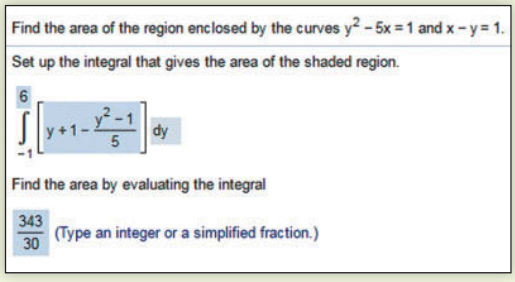

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CALCULUS

for Biology and Medicine

Fourth Edition

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for many different biological systems, either by solving the equations, or by analyzing them using the methods from Section 8.2.

In Section 8.4 we will go on to learn how to solve equations of the form:

$$\frac{dN}{dt} + a(t)N = b(t)$$

where $a(t)$ and $b(t)$ are functions of t only. An example of this type of equation is:

$$\frac{dN}{dt} + \frac{N}{t} = t^2 + 1$$

in which $a(t) = 1/t$ and $b(t) = t^2 + 1$. In addition to learning both of these techniques, an important skill for solving differential equations is to recognize which of the two types an equation belongs to, and in Section 8.4 you will practice identifying the types of different equations.

The method of Section 8.4 will enable us to solve a type of biological model called a two-compartment model. These models are useful to understand how matter moves through biological systems (e.g., how a cell exchanges salts and ions with its surroundings).

8.1 Solving Separable Differential Equations

Let's return to the growth model in (8.1):

$$\frac{dN}{dt} = \frac{1}{2}N, \ t \geq 0 \tag{8.3}$$

We are interested in finding a function $N(t)$ that satisfies (8.3). Such a function is called a **solution** of the differential equation. We already know that, with $N(0) = 50$

$$N(t) = 50e^{t/2}, \ t \geq 0$$

is a solution of (8.3). To confirm that the function $N(t)$ is a solution, we differentiate $N(t)$:

$$\frac{dN}{dt} = \frac{1}{2}\underbrace{50e^{t/2}}_{N(t)} = \frac{1}{2}N(t).$$

Let's recall how a differential equation like (8.3) might arise. (8.3) can be written in the form:

$$\frac{1}{N}\frac{dN}{dt} = \frac{1}{2}$$

So for this population, the per capita growth rate is constant. Put another way, a fixed fraction of organisms within the population will die in one unit of time, and a fixed fraction of organisms will reproduce in one unit of time. In many bacteria and fungi the rate of reproduction varies over the course of a day—reproduction is slowest at night when temperatures are lowest, and then the reproductive rate climbs during the day as temperatures increase again. Thus, the per capita growth rate may oscillate over time, as illustrated in Figure 8.1.

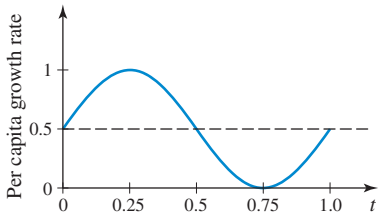


Figure 8.1 Per capita growth rate in Equation (8.4).

We can modify our original differential equation (8.3) to include these oscillations:

$$\frac{dN}{dt} = \frac{1}{2}(1 + \sin(2\pi t))N, \ t \geq 0 \tag{8.4}$$

In this section, we will learn how to solve differential equations like (8.4). To find the solution, we must integrate. We begin with a general method for solving **separable differential equations**; that is, equations of the form:

$$\frac{dy}{dt} = f(t)g(y) \tag{8.5}$$

where $f(t)$ is a function of t only and $g(y)$ is a function of y only.

We divide both sides of (8.5) by $g(y)$ [assuming that $g(y) \neq 0$]:

$$\frac{1}{g(y)}\frac{dy}{dt} = f(t)$$

Then, integrating both sides with respect to t, we find that

$$\int \frac{1}{g(y)}\frac{dy}{dt}\,dt = \int f(t)\,dt.$$

We can use the rule for integration by substitution to convert the left-hand side of this integration from an integral over t to an integral over y. We get:

$$\int \frac{1}{g(y)}\,dy = \int f(t)\,dt \qquad dy = \tfrac{dy}{dt}\,dt \tag{8.6}$$

Evaluating the two integrals in (8.6) and rearranging terms then gives y as a function of t.

In summary, to solve a separable differential equation, separate the variables t and y so that one side of the equation depends only on y and the other side only on t and then integrate both sides with respect to t. A good mnemonic for using this method is to treat dy/dt as if it were an ordinary ratio; then multiply both sides of the equation by dt when separating variables:

$$\frac{1}{g(y)}dy = f(t)\,dt.$$

Then we may integrate both sides to obtain Equation (8.6).

The method of separating the variables t and y works because the right-hand side of (8.5) can be separated into the product of two functions, $f(t)g(y)$, which gave this type of differential equation its name. Note that when we divided (8.5) by $g(y)$, we had to be careful, since $g(y)$ might be 0 for some values of y. We will address this problem in Subsection 8.1.2. Before solving general equations of form (8.5), we will first consider the special cases where either $g(y) = 1$ or $f(t) = 1$.

8.1.1 Pure-Time Differential Equations

If the rate of change of a function depends only on time, we call the resulting differential equation a **pure-time differential equation**. Such a differential equation is of the form

$$\frac{dy}{dt} = f(t),\ t \in I \tag{8.7}$$

where I is an interval and t represents time. This equation is a special case of (8.5) in which $g(y) = 1$, and Equation (8.6) can then be rewritten as

$$y = \int f(t)\,dt \qquad g(y) = 1 \Rightarrow \int \tfrac{dy}{g(y)} = \int 1\,dy = y \tag{8.8}$$

We previously solved equations like (8.7) in Section 5.10. Our derivation above shows that separation of variables produces the same answer. Namely, if $F(t)$ is an anti-derivative of $f(t)$, then (8.8) implies that:

$$y(t) = F(t) + C$$

where C is any constant. To determine C, we must, in addition to (8.7), have an initial condition on $y(t)$. If the initial condition on $y(t)$ is that $y(0) = y_0$, then we can write the solution to the initial value problem as a definite integral

$$y(t) = \int_0^t f(s)ds + y_0 \qquad \text{Since } \int_0^0 f(s)ds = 0,\ y(0) = y_0 \tag{8.9}$$

EXAMPLE 1 Suppose that the volume $V(t)$ of a cell at time t changes according to

$$\frac{dV}{dt} = \sin t \quad \text{with } V(0) = 3$$

Find $V(t)$.

Solution We can find $V(t)$ directly from (8.9), but it is not necessary to memorize the formula; we can solve the differential equation by separating variables:

$$\int dV = \int \sin t \, dt$$

$$V = -\cos t + C$$

Applying the initial condition $V(0) = 3$ we obtain:

$$3 = -1 + C$$

$$4 = C$$

So the volume of the cell at time t is:

$$V(t) = 4 - \cos t$$

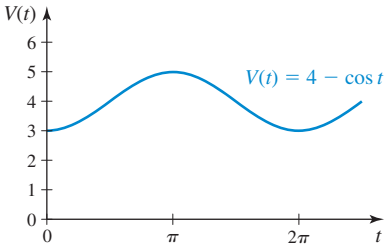


Figure 8.2 The solution $V(t) = 4 - \cos t$ in Example 1.

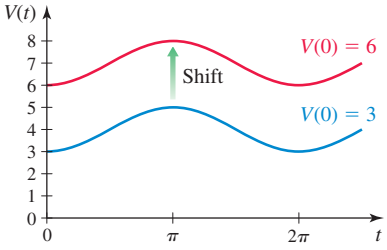


Figure 8.3 The function $V(t) = 7 - \cos t$ solves the differential equation in Example 1 with $V(0) = 6$. The solution can be obtained from the solution to Example 1 by shifting upward by 3.

See Figure 8.2 for a graph of $V(t)$. If we changed the initial condition in Example 1, the graph of the new solution could be obtained from the old solution by shifting the old solution vertically to satisfy the new initial condition. (See Figure 8.3.) •

8.1.2 Autonomous Differential Equations

A different important simplification of (8.5) comes from setting $f(t) = 1$. Then:

$$\frac{dy}{dt} = g(y) \tag{8.10}$$

These equations are called **autonomous differential equations**.

To interpret the biological meaning of *autonomous*, let's return to the growth model

$$\frac{dN}{dt} = \frac{1}{2}N \tag{8.11}$$

We will show very shortly that the general solution of (8.11) is

$$N(t) = Ce^{t/2} \tag{8.12}$$

where C is a constant that can be determined if the population size is known at one time. Suppose we conduct an experiment in which we follow a population over time, and suppose the population satisfies (8.11) with $N(0) = 20$. Using (8.12), we find that $N(0) = C = 20$. Then the size of the population at time t is given by

$$N(t) = 20e^{t/2} \tag{8.12a}$$

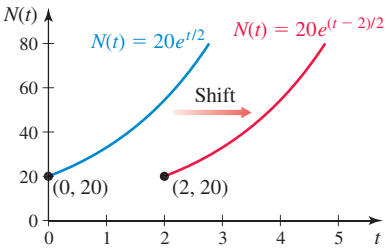


Figure 8.4 If $N(2) = 20$, then the graph of the solution $N(t) = 20e^{t/2}$ is shifted to the new starting point: $(t, N) = (2, 20)$.

If we repeat the experiment at, say, time $t = 2$ with the exact same initial population size, then, everything else being equal, the population evolves in exactly the same way as the one starting at $t = 0$. Returning to (8.12) but now setting $N(2) = 20$, we find that $N(2) = Ce = 20$, or $C = 20e^{-1}$. The size of the population is then given by

$$N(t) = 20e^{-1}e^{t/2} = 20e^{(t-2)/2}. \tag{8.12b}$$

The graph of this solution can be obtained from the graph of (8.12a), by shifting the old graph 2 units to the right to the new starting point $(t, N) = (2, 20)$ (see Figure 8.4).

This means that all populations starting with $N = 20$ grow in the same way, regardless of when we start the experiment. We can understand this biologically: If the growth conditions do not depend explicitly on time, the experiment should yield the same outcome regardless of when the experiment is performed.

We can solve (8.10) by separation of variables. We divide both sides of (8.10) by $g(y)$ and integrating both sides with respect to t.

$$\int \frac{1}{g(y)}\frac{dy}{dt}dt = \int dt$$

$$\Rightarrow \int \frac{dy}{g(y)} = \int dt \qquad \text{Special case of (8.6) with } f(t) = 1$$

Before we turn to biological applications, we give an example in which we see how to solve an autonomous differential equation and how to use the initial condition.

EXAMPLE 2 Solve $\dfrac{dy}{dx} = 2 - 3y$, where $y(1) = 1$.

Solution The independent variable is now x, but we can still separate the variables and integrate just as we did in Equation (8.6):

$$\int \frac{dy}{2-3y} = \int dx \tag{8.13}$$

We need to assume $2 - 3y \neq 0$ to divide by $2 - 3y$. We will discuss what to do if $2 - 3y = 0$ below. Since an antiderivative of $\frac{1}{2-3y}$ is $-\frac{1}{3}\ln|2-3y|$, we find that

$$-\frac{1}{3}\ln|2-3y| = x + C_1$$

We want to solve this equation for y (i.e., write y as function of x).

$$\ln|2-3y| = -3x - 3C_1$$

$$|2-3y| = e^{-3x-3C_1} \qquad \text{Exponentiate both sides}$$

$$|2-3y| = e^{-3C_1}e^{-3x} \qquad \text{Split exponential}$$

$$2-3y = \pm e^{-3C_1}e^{-3x} \qquad \text{Remove absolute value signs}$$

C_1 is an arbitrary constant, so $\pm e^{-3C_1}$ is also an arbitrary constant. We may define a new constant, $C = \pm e^{C_1}$, allowing us to write the solution in a more readable form:

$$2 - 3y = Ce^{-3x} \tag{8.14}$$

$$y = \frac{2}{3} - \frac{C}{3}e^{-3x}$$

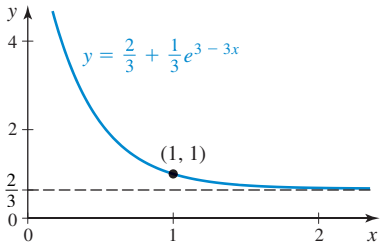


Figure 8.5 The solution to Example 2.

For any value of C the function $y = \frac{2}{3} - \frac{C}{3}e^{-3x}$ satisfies the differential equation. To determine C, we use the initial $y(1) = 1$. That is,

$$1 = \frac{2}{3} - \frac{C}{3}e^{-3}, \qquad \text{or} \qquad C = -e^3.$$

Hence,

$$y = \frac{2}{3} + \frac{1}{3}e^{3-3x}$$

(See Figure 8.5.) •

To obtain (8.13) we divided by $2-3y$, which we are only allowed to do if $2-3y \neq 0$ (i.e., if $y \neq 2/3$). Fortunately we see from the solution that $y \neq 2/3$ for all x. But if $y = 2/3$, then according to the differential equation $dy/dx = 0$, so y is a constant. In other words, if $y = 2/3$ initially, then $y(x) = 2/3$ for all x. This solution can be obtained from our general solution (8.14) by setting $C = 0$.

We now turn to two biological applications.

EXAMPLE 3 **Exponential Population Growth** We have previously modeled the growth of a population by assuming that the per capita growth rate of a population is constant

If the number of organisms is $N(t)$, then:

$$r = \frac{1}{N}\frac{dN}{dt}$$

is a constant. When $r > 0$, this model represents a growing population. When $r < 0$, the size of the population decreases. We can rearrange the terms in the formula for r into a differential equation.

$$\frac{dN}{dt} = rN. \tag{8.15}$$

To solve this differential equation we must also know the initial population size $N(0) = N_0$. (8.1) is a special case of this differential equation, in which $r = 1/2$.

We solve (8.15) by separating variables:

$$\int \frac{1}{N}dN = \int r\,dt \qquad \text{Assume } N \neq 0$$

$$\ln|N| = rt + C_1$$

$$|N| = e^{C_1}e^{rt}$$

$$N = \pm e^{C_1}e^{rt} = Ce^{rt} \qquad \text{Define a new constant } C = \pm e^{C_1}$$

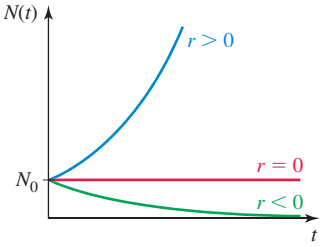


Figure 8.6 Solution curves for $dN/dt = rN$.

Our initial condition is $N(0) = N_0$. But if $N(t) = Ce^{rt}$ then $N(0) = C$, so imposing the initial condition gives $C = N_0$, or

$$N(t) = N_0e^{rt} \tag{8.16}$$

Equation (8.16) shows that the population size grows exponentially when $r > 0$. When $r < 0$, the population size decreases exponentially. When $r = 0$, the population size stays constant.

We show solution curves of $N(t) = N_0e^{rt}$ for $r > 0$, $r = 0$, and $r < 0$ in Figure 8.6. Exponential growth (or decay) is one of the most important growth phenomena in biology. You should therefore memorize both the differential equation (8.15) and its solution (8.16). •

In Example 3 when $r > 0$, the population size grows without bound ($\lim_{t\to\infty} N(t) = \infty$). Exponential growth cannot continue indefinitely in any real population. For example, if a small population of bacteria starts growing in a flask, then while the bacteria have plenty of resources, the population will grow exponentially. Eventually, however, the bacteria will run out of resources, and the population growth will slow. We will discuss one model for this **density dependent growth** in Example 6.

The type of growth in Example 3 is referred to as **Malthusian growth**, named after Thomas Malthus (1766–1834), a British clergyman and economist. Malthus warned about the consequences of unrestricted growth on the welfare of humans. He argued that while populations grow exponentially, food production can grow only linearly. He concluded that, since exponential growth ultimately overtakes linear growth, populations would eventually experience starvation (see Problem 62.)

Recall from Section 4.6 that, when $r < 0$, (8.15) has the same form as the differential equation that describes radioactive decay. $N(t)$ would then represent the amount of radioactive material left at time t. We will revisit this application in Problem 22.

EXAMPLE 4 **Restricted Growth: von Bertalanffy's Equation** Some species of fish show indefinite growth, that is, they continue to grow over their entire lifetime. However, the fish grow more slowly as they age. One model for fish growth is von Bertalanffy's equation, which models the length of a fish $L(t)$, at age t, using a differential equation:

$$\frac{dL}{dt} = k(L_\infty - L) \tag{8.17}$$

where k and L_∞ are both positive constants. Assuming that at age $t = 0$, the fish has length L_0, solve this initial value problem.

Solution Assuming that $L < L_\infty$, the right-hand side of this equation is positive, so $dL/dt > 0$ (the fish is growing). When or if L ever reaches L_∞, then $dL/dt = 0$, so growth will stop. The solution will depend on the constants k and L_∞, as well as the initial length, L_0. We solve the equation by separating variables.

$$\int \frac{dL}{L_\infty - L} = \int k\,dt$$

Hence,

$$-\ln|L_\infty - L| = kt + C_1$$

$$|L_\infty - L| = e^{-C_1}e^{-kt} \qquad \times(-1) \text{ and exponentiate both sides.}$$

$$L_\infty - L = Ce^{-kt} \qquad \text{Let: } C = \pm e^{-C_1}.$$

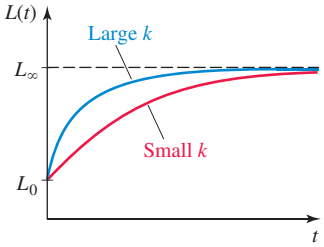


Figure 8.7 The solution of von Bertalanffy's equation.

We solve for C by setting $t = 0$ on both sides

$$L_\infty - L_0 = C \qquad L(0) = L_0$$

So, substituting for C, we obtain the solution:

$$L_\infty - L(t) = (L_\infty - L_0)e^{-kt}$$

or

$$L(t) = L_\infty - (L_\infty - L_0)e^{-kt} \tag{8.18}$$

(See Figure 8.7.)

Since $\lim_{t\to\infty} L(t) = L_\infty$ the parameter L_∞ denotes the **asymptotic length** of the fish. According to the model, if $L_0 < L_\infty$ the fish will grow over its lifetime, approaching $L = L_\infty$ asymptotically (that is, getting closer and closer to a length of L_∞ but never reaching it). k represents the rate of growth; between two fish with the same values of L_0 and L_∞, the one with the larger value of k will approach its asymptotic length quicker (see Figure 8.7). •

We now consider an important type of autonomous differential equation, in which the function $g(y)$ is a quadratic polynomial.

EXAMPLE 5 Solve

$$\frac{dy}{dt} = 2(y-1)(y+2) \quad \text{with } y(0) = 2$$

Solution Separation of variables yields

$$\int \frac{dy}{(y-1)(y+2)} = \int 2\,dt. \tag{8.19}$$

We use partial fractions to integrate the left-hand side. There are (unknown) constants A and B for which

$$\frac{1}{(y-1)(y+2)} = \frac{A}{y-1} + \frac{B}{y+2} \qquad \text{for all } y$$

$$= \frac{A(y+2) + B(y-1)}{(y-1)(y+2)}$$

Comparing numerators we have: $1 = A(y+2) + B(y-1)$. As in Section 7.3 we find A and B by substituting specific values of y into this equation:

$$y = -2 \quad \Rightarrow \quad 1 = -3B$$

$$y = 1 \quad \Rightarrow \quad 1 = 3A$$

Thus, $A = \frac{1}{3}$ and $B = -\frac{1}{3}$. So:

$$\frac{1}{3}\int\left(\frac{1}{y-1}-\frac{1}{y+2}\right)dy = \int 2\,dt$$

$$\frac{1}{3}\left[\ln|y-1| - \ln|y+2|\right] = 2t + C_1$$

So

$$\ln\left|\frac{y-1}{y+2}\right| = 6t + 3C_1 \qquad \text{Combining logarithms}$$

$$\left|\frac{y-1}{y+2}\right| = e^{3C_1}e^{6t} \qquad \text{Exponentiating}$$

$$\frac{y-1}{y+2} = \pm e^{3C_1}e^{6t} \qquad \text{Removing absolute values}$$

$$\frac{y-1}{y+2} = Ce^{6t} \qquad \text{Define } C = \pm e^{3C_1}$$

We can solve for C using the initial condition:

$$\frac{1}{4} = C \qquad \text{when } t = 0,\ y = 2, \text{ so } \frac{y-1}{y+2} = \frac{1}{4}$$

The solution is therefore

$$\frac{y-1}{y+2} = \frac{1}{4}e^{6t}$$

If we want the solution in the form $y = f(t)$, we must solve for y:

$$y - 1 = (y+2)\frac{1}{4}e^{6t}$$

$$y\left(1 - \frac{1}{4}e^{6t}\right) = \frac{1}{2}e^{6t} + 1$$

$$y = \frac{\frac{1}{2}e^{6t}+1}{1-\frac{1}{4}e^{6t}} = \frac{2e^{6t}+4}{4-e^{6t}} \qquad \text{Isolate terms in } y$$

See Figure 8.8 for a graph of this solution. •

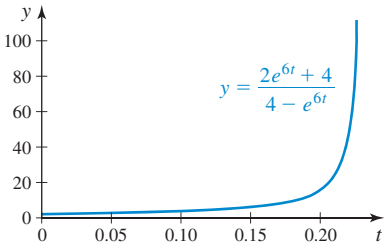


Figure 8.8 The solution for Example 5.

Why do we stress the need to study equations where $g(y)$ is a quadratic polynomial? A very important model of this type is the **logistic equation**, which can be used to analyze density dependent growth of populations. The logistic equation was introduced around 1835 by Pierre François Verhulst, and it modifies Malthus' equation from Example 3 to account for the finite **carrying capacity** of the environment that the organisms are growing in.

Malthus' equation assumes that a population has a constant per capita rate of growth (i.e., $\frac{1}{N}\frac{dN}{dt} = r$ for some constant r). In a population with density dependent growth the per capita rate will depend on the population size, N. That is,

$$\frac{1}{N}\frac{dN}{dt} = R(N)$$

for some function $R(N)$. Different growth models (we will explore others in Section 8.2) are associated with different functions $R(N)$. For the logistic equation we assume

$$R(N) = r\left(1 - \frac{N}{K}\right)$$

where r and K are both positive coefficients ($R(N)$ is graphed in Figure 8.9). Why is this form chosen? As you can see from the graph, per capita growth is positive if $N < K$ and is negative if $N > K$. Populations smaller than K will therefore grow, while populations larger than K will decrease. If $N = K$, then $\frac{dN}{dt} = 0$ (the population stays

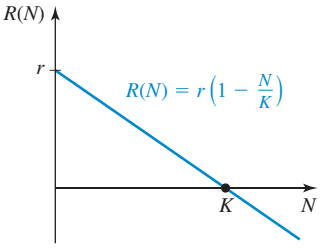


Figure 8.9 The per capita growth rate in the logistic equation is a linearly decreasing function of population size.

steady): K therefore represents the carrying capacity of the population environment. If $N > K$ then there are not enough resources for all of the organisms present, so the population will shrink. Also from Figure 8.9, we see that $R(0) = r$. This means that r is the limiting per capita growth rate when N is very small. If N is small (specifically, if N is much smaller than K), then $\frac{1}{N}\frac{dN}{dt} \approx r$, so the population will grow exponentially with per capita growth rate r until overcrowding starts to affect growth. The function $R(N)$ is the simplest function (a straight line) that incorporates both of the required features: $R(0) = r$ and $R(N)$ changes sign at $N = K$.

EXAMPLE 6 **The Logistic Equation for Population Growth** Solve the logistic equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \text{ with initial condition } N(0) = N_0 \tag{8.20}$$

where $r > 0$, $K > 0$, and $N_0 \geq 0$ are all constants.

Solution The constants r, K, and N_0 allow the logistic equation to be fit to different species and environments. It is important, therefore, to be able to solve the equation in this general form, without specifying the values of these coefficients.

To solve (8.20) we separate variables and integrate:

$$\int \frac{dN}{N(1 - N/K)} = \int r\,dt,$$

provided $N \neq 0$ and $N \neq K$.

To evaluate the integral on the left-hand side, we use the partial fraction expansion:

$$\frac{1}{N(1 - N/K)} = \frac{A}{N} + \frac{B}{1 - N/K}$$

$$1 = A(1 - N/K) + BN. \quad \times N(1 - N/K) \text{ on both sides} \tag{8.21}$$

To find A and B, substitute specific values into both sides of (8.21):

$$N = K \quad \Rightarrow \quad 1 = BK \quad \Rightarrow \quad B = 1/K$$

$$N = 0 \quad \Rightarrow \quad 1 = A \quad \Rightarrow \quad A = 1.$$

So our integrals become:

$$\int \left(\frac{1}{N} + \frac{1}{K(1 - N/K)}\right) dN = \int r\,dt$$

$$\ln|N| - \ln|1 - N/K| = rt + C_1$$

$$\ln\left|\frac{N}{1 - N/K}\right| = rt + C_1 \quad \text{Combining logarithms}$$

$$\frac{N}{1 - N/K} = \pm e^{rt}e^{C_1} = Ce^{rt} \quad \text{Defining } C = \pm e^{C_1} \tag{8.22}$$

To solve for C we can apply the initial condition:

$$\frac{N_0}{1 - N_0/K} = C. \quad N(0) = N_0$$

But the calculations will be a little easier if we leave C in the equation for the time being. Rearrange (8.22) as:

$$N\left(1 + \frac{Ce^{rt}}{K}\right) = Ce^{rt} \quad \times(1 - N/K) \text{ and then isolate terms in } N$$

$$\Rightarrow N = \frac{Ce^{rt}}{1 + Ce^{rt}/K} = \frac{C}{e^{-rt} + C/K} \quad \text{Solve for } N$$

$$\Rightarrow N = \frac{K}{\frac{Ke^{-rt}}{C} + 1} \quad \text{Multiply numerator and denominator by } \frac{K}{C}$$

Now since $C = \frac{N_0}{1-N_0/K}$, $\frac{K}{C} = \frac{K-N_0}{N_0}$, so assuming $N_0 \neq 0$ we obtain,

$$N(t) = \frac{K}{1+\left(\frac{K-N_0}{N_0}\right)e^{-rt}} = \frac{K}{1+\left(\frac{K}{N_0}-1\right)e^{-rt}} \tag{8.23}$$

Our derivation requires that $N \neq 0$ and $N \neq K$, so to complete our solution we observe that if $N_0 = 0$, then $N(t) = 0$ for all t, while if $N_0 = K$, then $N(t) = K$ for all t. •

The formula for $N(t)$ in (8.23) is a somewhat complicated function, so we spend a little time determining the shape of its graph, using the steps from Section 5.6. We may check that

$$N(0) = \frac{K}{1+\left(\frac{K}{N_0}-1\right)} = \frac{K}{\frac{K}{N_0}} = N_0,$$

so our solution does satisfy the initial conditions.

Then notice that since $r > 0$, $e^{-rt} \to 0$ as $t \to \infty$. So

$$\lim_{t\to\infty} N(t) = \frac{K}{1+\left(\frac{K}{N_0}-1\right)\cdot 0} = K.$$

That is, so long as $N_0 \neq 0$, the population size will converge to K as $t \to \infty$.

If $0 < N < K$, then

$$\frac{dN}{dt} = rN(1-N/K) > 0 \qquad r>0, N>0, 1-N/K>0$$

while if $N > K$ then $\frac{dN}{dt} = rN(1-N/K) < 0$. $\qquad r>0, N>0, 1-N/K<0$

So if $N_0 < K$ then $N(t)$ will increase monotonically until it converges to a horizontal asymptote $N = K$, while if $N_0 > K$, then $N(t)$ will decrease monotonically, approaching the horizontal asymptote $N = K$. To complete the information needed to sketch the function $N(t)$, we only need to know whether it is concave up or concave down. We may obtain the curvature from the differential equation. (Recall that $N(t)$ is concave up if $d^2N/dt^2 > 0$ and concave down if $d^2N/dt^2 < 0$.)

$$\begin{aligned}\frac{d^2N}{dt^2} &= \frac{d}{dt}\left(\frac{dN}{dt}\right) = \frac{d}{dt}\left(rN(1-N/K)\right)\\ &= r\frac{dN}{dt} - \frac{2rN}{K}\frac{dN}{dt} \qquad \tfrac{d}{dt}(N^2) = 2N\tfrac{dN}{dt} \text{ using implicit differentiation}\\ &= r\left(1-\frac{2N}{K}\right)\frac{dN}{dt}\end{aligned}$$

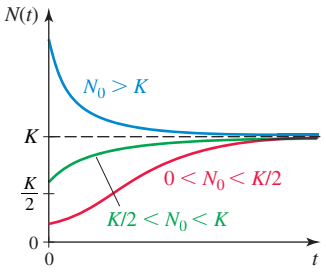


Figure 8.10 Solution curves of the logistic equation $\frac{dN}{dt} = rN(1-N/K)$ for different initial values N_0.

If $0 < N < K$ then $\frac{dN}{dt} > 0$ (the solution increases), so $\frac{d^2N}{dt^2}$ is positive if $\left(1-\frac{2N}{K}\right) > 0$ and negative if $\left(1-\frac{2N}{K}\right) < 0$; that is, $\frac{d^2N}{dt^2} > 0$ if $N < K/2$ and $\frac{d^2N}{dt^2} < 0$ if $K/2 < N < K$. So if the initial condition $0 < N_0 < K/2$, then the solution initially curves upward until the population reaches $N = K/2$; once $N(t)$ crosses $K/2$ the solution curves downward (but continues to grow) approaching a horizontal asymptote $N = K$. The point at which $N(t) = K/2$ is an inflection point. If $K/2 < N_0 < N$, then $N(t)$ grows toward $N = K$ but always curves downward. If $N > K$, then $\left(1-\frac{2N}{K}\right) < 0$, and $\frac{dN}{dt} < 0$ so $\frac{d^2N}{dt^2} > 0$. So if $N_0 > K$, then the solution curve is both monotonic decreasing and concave upward. Figure 8.10 shows some representative solution curves.

8.1.3 General Separable Equations

Although many important equations from biology are either of pure-time or autonomous forms, we can combine the techniques from 8.1.1 and 8.1.2 to solve general equations of the form: $\frac{dN}{dt} = f(t)g(N)$ (i.e., where the right-hand side includes both functions of the independent and dependent variables). As an example we first consider the problem introduced at the beginning of this chapter.

EXAMPLE 7 **Circadian Rhythm** The rate of division of some cells varies over the course of one day. One model that incorporates this effect is to have the per capita growth rate of the population be a function of the time of day. Let t represent time in fractions of one complete day, so $t = 0$ is the beginning of the first day and $t = 1$ is the end of the day. For example:

$$\frac{dN}{dt} = \frac{1}{2}(1 + \sin 2\pi t)N, \quad t \geq 0$$

Assuming $N(0) = N_0$, solve for $N(t)$.

Solution This is a separable equation with $f(t) = \frac{1}{2}(1 + \sin 2\pi t)$ and $g(N) = N$. Separate variables:

$$\frac{1}{N}\frac{dN}{dt} = \frac{1}{2}(1 + \sin 2\pi t) \qquad \text{Functions of } N \text{ on left, function of } t \text{ on right}$$

$$\int \frac{1}{N} dN = \int \frac{1}{2}(1 + \sin 2\pi t) dt \qquad \text{Integrate with respect to } t \text{ and use } \tfrac{dN}{dt}dt = dN$$

$$\ln |N| = \frac{t}{2} - \frac{1}{4\pi}\cos 2\pi t + C_1$$

$$N(t) = C \exp\left(\frac{t}{2} - \frac{1}{4\pi}\cos 2\pi t\right) \qquad \text{Define } C = \pm e^{C_1}$$

To find the value of C, apply the initial condition:

$$N_0 = C \exp\left(\frac{0}{2} - \frac{1}{4\pi}\cos 0\right) = Ce^{-1/4\pi}$$

$$\Rightarrow C = N_0 e^{1/4\pi}$$

so

$$N(t) = N_0 e^{1/4\pi} \exp\left(\frac{t}{2} - \frac{1}{4\pi}\cos 2\pi t\right) = N_0 \exp\left(\frac{t}{2} + \frac{1}{4\pi}(1 - \cos 2\pi t)\right).$$

An important application of equations of this type is **allometry**. *Allometry* is the study of how different parts of an organism (e.g., the size of two different organs, or parts) grow differently as the organism grows. We denote by $L_1(t)$ and $L_2(t)$ the respective sizes of two different parts of an individual of age t. We say that L_1 and L_2 are related through an allometric law if their *specific* (or *relative*) growth rates are proportional—that is, if

$$\frac{1}{L_1}\frac{dL_1}{dt} = k\frac{1}{L_2}\frac{dL_2}{dt} \qquad \text{Relative growth rate} = \text{growth rate}/\text{current size.} \tag{8.24}$$

for some constant k. If the constant k is equal to 1, then the growth is called **isometric**; otherwise it is called **allometric**. Integrating both sides of (8.24), we find that

$$\int \frac{dL_1}{L_1} = k\int \frac{dL_2}{L_2} \qquad \tfrac{dL_1}{dt}dt = dL_1$$

or

$$\ln |L_1| = k \ln |L_2| + C_1$$

Solving for L_1, we obtain

$$L_1 = CL_2^k \tag{8.25}$$

where $C = \pm e^{C_1}$. (Since L_1 and L_2 are typically positive, the constant C will typically be positive.) If $k = 1$ (isometric growth) then $L_1 \propto L_2$, so the two organs maintain the same relative size during growth. More generally, the relationship between L_1 and L_2 is a power law.

Section 8.1 Problems

8.1.1

In Problems 1–8, solve each pure-time differential equation.

1. $\frac{dy}{dt} = t + \sin t$, where $y(0) = 0$.

2. $\frac{dy}{dt} = e^{-3t}$, where $y(0) = 10$.

3. $\frac{dy}{dx} = \frac{1}{x}$, where $y(1) = 0$.

4. $\frac{dy}{dx} = \frac{1}{1-x^2}$, where $y(0) = 0$.

5. $\frac{dx}{dt} = \frac{1}{1-t}$, where $x(0) = 2$.

6. $\frac{dx}{dt} = \sin(2\pi(t+3))$, where $x(3) = 1$.

7. $\frac{ds}{dt} = \sqrt{t+1}$, where $s(0) = 1$.

8. $\frac{dh}{dt} = 4 - 16t^2$, where $h(1) = 0$.

9. Suppose that the volume $V(t)$ of a cell at time t changes according to

$$\frac{dV}{dt} = 1 + \cos t \quad \text{with } V(0) = 5$$

Find $V(t)$.

10. Suppose that the amount of phosphorus in a lake at time t, denoted by $P(t)$, follows the equation

$$\frac{dP}{dt} = 3t + 1 \quad \text{with } P(0) = 0$$

Find the amount of phosphorus at time $t = 10$.

11. **Drug Absorption** For a drug with zeroth order elimination kinetics, a constant amount of drug is removed from the blood per unit time. So the amount of drug in a patient's blood obeys a differential equation

$$\frac{dM}{dt} = -k_0$$

where $k_0 > 0$ is a constant. Assuming $M(0) = M_0$, find (in terms of M_0 and k_0) the time at which the level of drug will drop to 0.

12. **Drug Absorption** Drug enters a patient's blood by being absorbed from the gut. Assume that the drug enters the patient's blood at a rate that depends on time as ce^{-rt} where c and r are positive constants (the rationale for this formula will be discussed in Section 8.4) and the drug is eliminated at constant rate k. So:

$$\frac{dM}{dt} = ce^{-rt} - k.$$

(a) Assuming $c > k$ and $M(0) = 0$ (there is no drug present in the patient's blood at the start of the experiment), solve this differential equation.

(b) Suppose $k > 0$. What does your solution predict will happen to $M(t)$ as $t \to \infty$? Does your answer make sense? (In reality, drug can only be removed at a constant rate until all drug is removed from the blood. That is, the rate of elimination will be k if $M > 0$ and 0 once M drops to 0.)

(c) Assume $k = 0$ (i.e., this drug is never eliminated from blood, or is eliminated so slowly that elimination can be neglected). Show that $\lim_{t\to\infty} M(t) = \frac{c}{r}$.

(d) Suppose that $k = 0$ and you measure the following data for $M(t)$ as a function of t:

t	$M(t)$
0	0
1	1
2	1.5

Find parameters c and r that fit your model to these data.

8.1.2

In Problems 13–18, solve each autonomous differential equation.

13. $\frac{dy}{dt} = 2y$, where $y(0) = 2$

14. $\frac{dy}{dt} = 2(1-y)$, where $y(0) = 0$

15. $\frac{dx}{dt} = -2x$, where $x(1) = 3$

16. $\frac{dx}{dt} = 1 - 3x$, where $x(1) = -2$

17. $\frac{dh}{ds} = 2h + 1$, where $h(0) = 4$

18. $\frac{dN}{dt} = 5 - N$, where $N(2) = 2$

19. Suppose that a population, whose size at time t is denoted by $N(t)$, grows according to

$$\frac{dN}{dt} = 0.3N \quad \text{with } N(0) = 20$$

Solve this differential equation, and find the size of the population at time $t = 5$.

20. Suppose that you follow the size of a population over time. When you plot the size of the population versus time on a semilog plot (i.e., the horizontal axis, representing time, is on a linear scale, whereas the vertical axis, representing the size of the population, is on a logarithmic scale) you find that your data fit a straight line that intercepts the vertical axis at 1 (on the log scale) and has slope -0.43. Find a differential equation that relates the growth rate of the population at time t to the size of the population at time t.

21. Suppose that a population, whose size at time t is denoted by $N(t)$, grows according to

$$\frac{1}{N}\frac{dN}{dt} = r \tag{8.26}$$

where r is a constant.

(a) Solve (8.26).

(b) Transform your solution in (a) appropriately so that the resulting graph is a straight line. How can you determine the constant r from your graph?

(c) Suppose now that, over time, you followed a population which grew according to (8.26) with some unknown reproductive rate r. Describe how you would determine r from your data.

22. Radioactive Decay Assume that $W(t)$ denotes the amount of radioactive material in a substance at time t. Radioactive decay is described by the differential equation

$$\frac{dW}{dt} = -\lambda W(t) \quad \text{with } W(0) = W_0 \tag{8.27}$$

where λ is a positive constant called the *decay constant*.

(a) Solve (8.27).

(b) Assume that $W(0) = 123\,\text{g}$ and $W(5) = 20\,\text{g}$ and that time is measured in minutes. Find the decay constant λ and determine the half-life of the radioactive substance. (Remember that the half-life of the substance is the time taken for $W(t)$ to decrease to half of its initial value.)

23. Drug Absorption A drug has first order elimination kinetics, meaning that a fixed fraction of drug is eliminated from the body in each unit of time. So if no further drug is absorbed into the patient's blood after time $t = 0$, the amount of drug in their blood will decay with time according to:

$$\frac{dM}{dt} = -k_1 M$$

where $k_1 > 0$ is the fraction of drug eliminated in one unit of time.

(a) Assuming $M(0) = M_0$, solve the differential equation.

(b) According to your model, does $M(t)$ ever reach 0?

(c) Given that $M_0 = 10$ and $k_1 = 2$, calculate the time at which $M(t)$ drops to $M = 1$.

24. Fish Growth Denote by $L(t)$ the length of a fish at time t, and assume that the fish grows according to von Bertalanffy's equation

$$\frac{dL}{dt} = k(34 - L(t)) \quad \text{with } L(0) = 2$$

(a) Solve the differential equation.

(b) Use your solution in (a) to determine k under the assumption that $L(4) = 10$. Sketch the graph of $L(t)$ for this value of k.

(c) Find the length of the fish when $t = 10$.

(d) Find the asymptotic length of the fish; that is, find $\lim_{t\to\infty} L(t)$.

25. Fish Growth Denote by $L(t)$ the length of a certain fish at time t, and assume that this fish grows according to von Bertalanffy's equation

$$\frac{dL}{dt} = k(L_\infty - L(t)) \quad \text{with } L(0) = 1 \tag{8.28}$$

where k and L_∞ are positive constants. It is known that the asymptotic length is equal to 123 in. and that it takes the fish 27 months to reach half its asymptotic length.

(a) Use this information to determine the constants k and L_∞ in (8.28). [*Hint*: Solve (8.28).]

(b) Determine the length of the fish after 10 months.

(c) How long will it take until the fish reaches 90% of its asymptotic length?

26. Insulin Pump A diabetic patient receives insulin at constant rate from an implanted insulin pump. Insulin has first order elimination kinetics, so the amount of insulin in the blood will obey a differential equation:

$$\frac{dM}{dt} = a - k_1 M$$

where $a > 0$ is the rate at which insulin is released into their blood by the pump and k_1 is the fraction of insulin removed from the blood in one unit of time

(a) Assuming $M(0) = 0$ (i.e., there is no insulin present in the patient's blood at time $t = 0$), solve the differential equation to find $M(t)$ as a function of t.

(b) Find the limit of $M(t)$ as $t \to \infty$.

(c) Assume that a (the rate of release from the pump) is 1 IU/hr and $M(t) \to 0.2$ IU as $t \to \infty$. Calculate, k_1, the rate of insulin elimination.

27. Amnesia During Surgery During surgery a patient receives midazolam, a sedative, to produce amnesia (memory loss) and ensure they do not remember the surgery. ***Holazo et al. (1988)*** studied the rate at which midazolam is eliminated from a patient's body. They gave healthy volunteers one injection of the drug at time $t = 0$, and then measured the rate at which it disappeared from each volunteer's blood. If no further drug is added after time $t = 0$, then the concentration will obey the differential equation:

$$\frac{dC}{dt} = -k_1 C$$

where k_1 is the fraction of drug eliminated in one hour.

(a) If the concentration at $t = 0$ is C_0, solve for $C(t)$.

(b) Holazo et al. found the following data:

t	$C(t)$
1	90
4	34

where t is measured in hours, and $C(t)$ is measured in ng of midazolam per milliliter of blood. From these data estimate the rate of elimination k_1.

(c) During surgery midazolam may be infused continuously by intravenous line, at some constant rate r per milliliter of blood. Then the concentration must obey a differential equation.

$$\frac{dC}{dt} = r - k_1 C.$$

Assuming that $C(0) = 0$, find $C(t)$ as a function of t.

(d) Calculate $\lim_{t\to\infty} C(t)$ as a function of r and k_1.

(e) Using the value of k_1 from part (b), at what rate, t, must midazolam be infused into the patient's blood to maintain a constant concentration of 130 ng/milliliter?

28. Let $N(t)$ denote the size of a population at time t. Assume that the population exhibits exponential growth.

(a) If you plot $\log N(t)$ versus t, what kind of graph do you get?

(b) Find a differential equation that describes the growth of this population and sketch possible solution curves.

29. Use the partial-fraction method to solve

$$\frac{dy}{dx} = y(1 + y)$$

where $y(0) = 2$.

30. Use the partial-fraction method to solve

$$\frac{dy}{dx} = y(1 - y)$$

where $y(0) = 2$.

31. Use the partial-fraction method to solve

$$\frac{dy}{dx} = y(y-2)$$

where $y(0) = 1$.

32. Use the partial-fraction method to solve

$$\frac{dy}{dx} = (y+1)(y-2)$$

where $y(0) = 0$.

33. Use the partial-fraction method to solve

$$\frac{dy}{dt} = 2y\left(1 - \frac{y}{3}\right)$$

where $y(1) = 5$.

34. Use the partial-fraction method to solve

$$\frac{dy}{dt} = \frac{1}{2}y^2 - 2y$$

where $y(0) = -3$.

In Problems 35–38, solve each differential equation.

35. $\dfrac{dy}{dx} = y(1+y)$

36. $\dfrac{dy}{dx} = (1+y)^2$

37. $\dfrac{dy}{dx} = (1+y)^3$

38. $\dfrac{dy}{dx} = (1-y^2)$

39. (a) Use partial fractions to show that

$$\int \frac{du}{u^2 - a^2} = \frac{1}{2a}\ln\left|\frac{u-a}{u+a}\right| + C$$

(b) Use your result in (a) to find a solution of

$$\frac{dy}{dx} = y^2 - 4$$

with initial conditions **(i)** $y(0) = 0$, **(ii)** $y(0) = 2$, and **(iii)** $y(0) = 4$.

40. Find a solution of

$$\frac{dy}{dx} = y^2 + 4$$

with initial conditions $y(0) = 2$.

41. Suppose that the size of a population at time t is denoted by $N(t)$ and that $N(t)$ satisfies the logistic equation

$$\frac{dN}{dt} = 0.34N\left(1 - \frac{N}{200}\right) \quad \text{with } N(0) = 50$$

Solve this differential equation, and determine the size of the population in the long run; that is, find $\lim_{t\to\infty} N(t)$.

42. Assume that a population, whose size is denoted by $N(t)$, grows according to the logistic equation. Find the limiting growth rate for small N (i.e., find the constant r) if the carrying capacity is 100, $N(0) = 10$, and $N(1) = 30$.

43. Let $N(t)$ denote the size of a population at time t. Assume that the population grows according to the logistic equation. Assume also that the limiting growth rate for small N is 5 and that the carrying capacity is 50.

(a) Find a differential equation that describes the growth of this population.

(b) Without solving the differential equation in (a), sketch solution curves of $N(t)$ as a function of t when **(i)** $N(0) = 10$, **(ii)** $N(0) = 40$, and **(iii)** $N(0) = 50$.

44. Logistic growth is described by the differential equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

We showed in Example 6 that the solution of this differential equation with initial condition $N(0) = N_0$ is given by

$$N(t) = \frac{K}{1 + (\frac{K}{N_0} - 1)e^{-rt}}. \tag{8.29}$$

(a) Show that

$$r = \frac{1}{t}\ln\left(\frac{K - N_0}{N_0}\right) + \frac{1}{t}\ln\left(\frac{N(t)}{K - N(t)}\right) \tag{8.30}$$

by solving (8.29) for r.

(b) Equation (8.30) can be used to estimate r. Suppose we are studying a population that grows according to the logistic equation and find that $N(0) = 10$, $N(5) = 22$, $N(100) = 30$, and $N(200) = 30$. Estimate r. (*Hint*: First estimate K from the behavior of the solution for large t.)

45. **Population Genetics** Population genetics is the study of how the frequency of particular traits changes within a population over time. We are studying a gene that comes in two alleles (i.e., variants) A and a. The A allele makes individuals reproduce a little faster than the a allele. So we expect the A alleles to take over the population with time. Suppose that a proportion p of all individuals within the population carry the A allele (with the remaining proportion, $1 - p$, carrying the a allele). If the A allele boosts reproduction rate by an amount s it can be shown under some assumptions that the proportion of A-allele individuals obeys a differential equation

$$\frac{dp}{dt} = \frac{1}{2}s\,p(1-p) \tag{8.31}$$

(a) Use separation of variables and partial fractions to find the solution of (8.31), assuming $p(0) = p_0$.

(b) Show that if $p_0 \neq 0$, then $\lim_{t\to\infty} p(t) = 1$. Explain why this behavior makes sense biologically.

(c) Suppose $p_0 = 0.1$ and $s = 0.01$; how long will take until $p(t) = 0.5$?

8.1.3

In Problems 46–54, solve each differential equation with the given initial condition.

46. $\dfrac{dy}{dx} = 2\dfrac{y}{x}$, with $y(1) = 1$.

47. $\dfrac{dy}{dx} = \dfrac{x+1}{y}$, with $y(0) = 2$.

48. $\dfrac{dy}{dx} = \dfrac{xy}{x+1}$, with $y(0) = 1$.

49. $\dfrac{dy}{dx} = (y+1)e^{-x}$, with $y(0) = 2$.

50. $\dfrac{dy}{dx} = \dfrac{y^2}{x}$, with $y(1) = 1$.

51. $\dfrac{dy}{dx} = \dfrac{y+1}{x-1}$, with $y(2) = 5$.

52. $\dfrac{du}{dt} = \dfrac{\sin t}{u+1}$, with $u(0) = 3$.

53. $\dfrac{dy}{dt} = \dfrac{t}{y}$, with $y(0) = 1$.

54. $\dfrac{dx}{dy} = \dfrac{1}{2}\dfrac{x}{y}$, with $x(3) = 2$.

In Problems 55–60 you will need to solve differential equations by separation of variables. In these problems it will not always be possible to solve explicitly for y in terms of t; instead your solution may take the form of an implicit function relating the two variables.

55. $\dfrac{dy}{dt} = \dfrac{y^2 + y}{t - 1}$ where $y(0) = 1$.

56. $\dfrac{dy}{dt} = \dfrac{yt}{\ln y}$ where $y(1) = e$.

57. $\dfrac{dy}{dt} = \dfrac{t + 1}{y + y^2}$ where $y(0) = 1$.

58. $\dfrac{dy}{dt} = \dfrac{t^2 + 1}{\cos y + \sin y}$ where $y(0) = 0$.

59. $\dfrac{dy}{dt} = \sqrt{\dfrac{t + 1}{y + 1}}$ where $y(0) = 1$.

60. $\dfrac{dy}{dt} = \dfrac{t + 1}{ty + ty^3}$ where $y(1) = 1$.

61. **Circadian Rhythm** The per capita growth rate of a population of cells varies over the course of a day. Assume that time t is measured in hours and

$$\frac{dN}{dt} = 2\left(1 - \cos\frac{2\pi t}{24}\right)N$$

if $N(0) = 5$, find the number of cells after one day (that is, find $N(24)$).

62. **Malthusian Population Growth** This problem addresses Malthus's concerns, which were discussed in Example 3. Assume that a population size grows exponentially according to

$$N(t) = 1000e^t$$

and the food supply grows linearly according to

$$F(t) = 3t$$

(a) Write a differential equation for each of $N(t)$ and $F(t)$.

(b) Does exponential growth eventually overtake linear growth? Explain.

63. **Bite Strength in Carnivores** Bite strength varies as animals grow, which may mean that the animal's diet must change. ***Christiansen and Adolfsson (2005)*** studied the relationship between the strength of animal teeth with skull size in carnivores from the cat and dog families. They found that tooth strength S, and skull length L, were related in a power law:

$$S = CL^{2.85}$$

where C is some constant. Find the relationship between the relative rates of growth of S and L (i.e., between $\frac{1}{S}\frac{dS}{dt}$ and $\frac{1}{L}\frac{dL}{dt}$).

64. **Homeostasis** ***Sterner and Elser (2002)*** studied the relationship between the amount of nitrogen in an animal's body and the amount of nitrogen present in the food that it eats. Many animals maintain homeostasis (balance), that is, they control their own nitrogen content. As the amount of nitrogen present in their food increases, the amount of nitrogen in the animal's body increases more slowly. If the amount of nitrogen in the animal is N and the amount of nitrogen in its food is F, Sterner and Elser argue that:

$$\frac{1}{N}\frac{dN}{dt} = \frac{\sigma}{F}\frac{dF}{dt}$$

where σ is a constant.

(a) Show that if $\sigma = 1$, then $N \propto F$; that is, the nitrogen content of the animal increases in proportion to its food. This is called **absence of homeostasis**.

(b) If $\sigma = 0$, then N is a constant, independent of F. This is called **homeostasis** (the animal maintains a balanced amount of nitrogen, independent of its food).

(c) Show that if $0 < \sigma < 1$, then, if F doubles, N also increases but by a factor less than 2.

8.2 Equilibria and Their Stability

In Subsection 8.1.2, we learned how to solve autonomous differential equations. Once we solve a differential equation we may draw the graph of the solution. For instance, logistic growth can be modeled using the differential equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{8.32}$$

The solution of this differential equation was derived in Section 8.1 (see Equation (8.23)) and graphed in Figure 8.10. In particular we saw that so long as $N(0) \neq 0$ the population size converges to K as $t \to \infty$. We identified K as the carrying capacity of the organism's habitat. In this section we will show that this behavior could have been predicted without solving the differential equation. In particular, if $N = K$ then the right-hand side of (8.32) vanishes. This is no coincidence. If $N(t)$ converges to any constant, as $t \to \infty$, then $\frac{dN}{dt}$ must converge to 0, since the curve approaches a horizontal asymptote (i.e., a flat line) and the gradient of this flat line is 0. Since $dN/dt = 0$, the right-hand side of the equation must also vanish. In fact there are two values of N for which the right-hand side of (8.32) vanishes: $N = K$ and $N = 0$. Why don't solutions converge to 0 as $t \to \infty$? To answer this question we will need to introduce the concept of **stability**.

8.2.1 Equilibrium Points

We will consider autonomous differential equations of the form

$$\frac{dy}{dt} = g(y) \tag{8.33}$$

The point $\hat{y}$ is said to be an **equilibrium** of the differential equation if $g(\hat{y}) = 0$. Some books use the term **fixed point** instead of equilibrium. We will always refer to these points as equilibria in this book, but you should be aware of the alternate term.

Why are equilibria important? If $y(t)$ solves the differential equation $\frac{dy}{dt} = g(y)$ and $y(0) = \hat{y}$, then because $\frac{dy}{dt} = g(\hat{y}) = 0$, $y(t) = \hat{y}$ for all t (i.e., if a solution starts at one of the equilibria of the differential equation, then it will remain at that equilibrium). In other words $y(t) = \hat{y}$ is a constant solution of the differential equation.

EXAMPLE 1 Find all equilibria of the differential equations:

(a) $\frac{dy}{dt} = 2y$ **(b)** $\frac{dy}{dt} = y^3 - 3y^2 + 2y$ **(c)** $\frac{du}{dt} = \sin u$

Solution In all cases the equilibria are the zeros of the function on the right-hand side of the differential equation.

(a) $2\hat{y} = 0 \quad \Rightarrow \quad \hat{y} = 0$

(b) $\hat{y}^3 - 3\hat{y}^2 + 2\hat{y} = 0 \quad \Rightarrow \quad \hat{y}(\hat{y}^2 - 3\hat{y} + 2) = 0$

$\hat{y}(\hat{y} - 1)(\hat{y} - 2) = 0$ $\hat{y} = 0$ is a root

so $\hat{y} = 0,\ 1$ or $2.$ Factorize the quadratic

(c) $\sin \hat{u} = 0 \Rightarrow$ the equilibria are: $\hat{u} = 0, \pm\pi, \pm 2\pi, \ldots$ (alternatively: $\hat{u} = K\pi$ where $K \in \mathbf{Z}$.) •

EXAMPLE 2 **Tumor Growth** ***Laird (1969)*** showed that the growth of many different kinds of solid tumors in mice, rats, and rabbits could be described by Gompertz's equation, which predicts that the number of cells in the tumor, N, increases with time t, according to the differential equation:

$$\frac{dN}{dt} = aN \ln\left(\frac{b}{N}\right) \quad , \quad N > 0 \tag{8.34}$$

Here a and b are both positive coefficients. Find the possible equilibria of the number of cells.

Solution The function on the right-hand side of the differential equation is:

$$g(N) = aN \ln\left(\frac{b}{N}\right)$$

$g(N)$ can only be equal to zero if $N = 0$ or if $\ln\left(\frac{b}{N}\right) = 0$, since one of the two factors that make up $g(N)$ must equal 0 to make $g(N)$ equal 0. $N = 0$ is not in the domain for which $g(N)$ is defined. But $\ln\left(\frac{b}{N}\right) = 0$ if $N = b$, and this will in general be within the domain. In fact, we will show in subsection 8.2.4 that all solutions of (8.34) converge to $N = b$. •

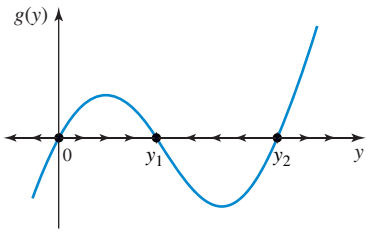


Figure 8.11 Vector field plot for the differential equation $dy/dt = g(y)$.

8.2.2 Graphical Approach to Finding Equilibria

Suppose that $g(y)$ is of the form given in Figure 8.11. To find the equilibria of $dy/dt = g(y)$, we must find all points $y = \hat{y}$ for which $g(y) = 0$. Graphically, this means that if we graph $g(y)$ as a function of y, then the equilibria are the points of intersection of $g(y)$ with the horizontal axis, which is the y-axis in this case, since y is the independent variable. We see that, for this choice of $g(y)$, the equilibria are at $y = 0$, y_1, and y_2.

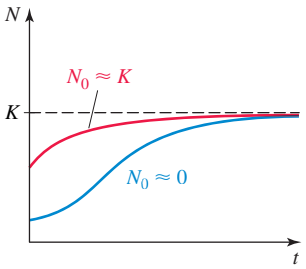


Figure 8.12 Solution curves of the logistic equation. If $N_0 \approx 0$, the population will grow away from $N = 0$ as t increases. If $N_0 \approx K$, the population will approach K as t increases.

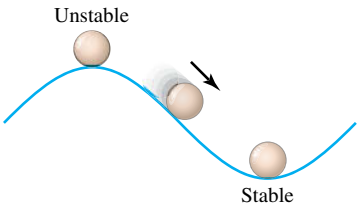


Figure 8.13 A ball rolls around on a landscape containing hills, and valleys. Equilibria occur both at the top of hills, and at the bottom of valleys.

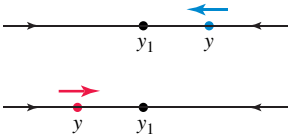


Figure 8.14 If y is perturbed from the stable equilibrium $y = y_1$ then $y(t)$ will either decrease or increase to bring $y(t)$ back toward y_1.

8.2.3 Stability of Equilibrium Points

Although the logistic equation $dN/dt = rN(1 - N/K)$ has two equilibria, at $N = 0$ and at $N = K$, the equilibria differ in the following fundamental respect. If the population starts at either equilibrium, it will remain there (i.e., $N = 0$ and $N = K$ are both valid constant solutions of the differential equation). But if the population starts with a size close to 0, but not exactly equal to 0, it will grow further from 0 as t increases, whereas if the population starts close to K, it will approach K as $t \to \infty$ (see Figure 8.12).

We say that the equilibrium point $N = 0$ is **unstable**, while the equilibrium point $N = K$ is **stable**. Whether an equilibrium is stable or unstable is determined by the behavior of the solution when the solution is **perturbed** away from the equilibrium, meaning that it doesn't start at the equilibrium but at a value close to the equilibrium. If it returns to the equilibrium, the equilibrium is stable; while if it diverges from the equilibrium, then the equilibrium is unstable.

A useful analogy is to think of a ball rolling around on a landscape that contains hills and valleys (see Figure 8.13). The ball can be balanced and at rest when it is either at the top of a hill, or at the bottom of a valley. But if it is perturbed slightly from the top of a hill, it will roll down the hill away from its rest position—these equilibria are unstable. If it starts at the bottom of a valley, and is perturbed from the bottom of a valley, it will return to its starting position—these equilibria are stable.

We will present two methods for identifying whether an equilibrium is stable or unstable. One is based on the graph of the function $g(y)$; the other requires calculating $g'(y)$. You should be comfortable using both approaches.

Suppose we are studying the differential equation

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

where the function $g(y)$ is graphed in Figure 8.11. The equilibria of this differential equation are points $\hat{y}$ at which $g(\hat{y}) = 0$. On the graph these correspond to points at which $g(y)$ crosses the horizontal axis. There are three such points: 0, y_1, and y_2.

We can also use the graph in Figure 8.11 to identify the values of y for which $y(t)$ increases with t and the values for which $y(t)$ decreases with t. (Remember, since the equation is autonomous, the value of $\frac{dy}{dt}$ depends only on y.) If $g(y) > 0$, then according to the differential equation $\frac{dy}{dt} > 0$ (i.e., $y(t)$ is an increasing function of t). Conversely, if $g(y) < 0$ (so $\frac{dy}{dt} < 0$), then $y(t)$ is a decreasing function of t. We can label the horizontal axis of Figure 8.11 with direction arrows to show the direction in which $y(t)$ travels as t increases, putting a rightward arrow to show where $y(t)$ is increasing, and a leftward arrow to show where y is decreasing. For the function $g(y)$ in the figure, this means that we add rightward arrows in the intervals $(0, y_1)$, and (y_2, ∞) and we add leftward arrows in the intervals $(-\infty, 0)$ and (y_1, y_2). This plot, which now includes the direction in which y travels with time, is called a **vector field plot** of the differential equation $\frac{dy}{dt} = g(y)$.

We may use the vector field plot to determine which of the equilibria are stable and which are unstable. Consider, for example, the equilibrium $y = y_1$. Recall that stability of an equilibrium is determined from the behavior of the solution when it is slightly perturbed away from the equilibrium. Suppose that we start with an initial condition that is slightly above y_1 (i.e., right of it on the graph); then, since the arrows are leftward, $y(t)$ will *decrease* back toward y_1. Similarly, if we solve the differential equation with an initial condition that is slightly smaller than y_1 (i.e., left of it on the graph), then the arrows show that $y(t)$ will *increase* back toward y_1. In either case the solution will tend to return to y_1 if it is started from an initial condition that is perturbed a small distance from y_1 (see Figure 8.14). Therefore y_1 is a **stable** equilibrium of the differential equation.

Let's apply the same arguments to study the stability of the point y_2. If y starts above (right of) y_2, then it will follow the rightward arrows (i.e., increase) and move further from y_2. If y starts below (left of) y_2 then it will follow the leftward arrows (i.e., decease), again moving further from y_2. Thus, however y is perturbed from y_2, it

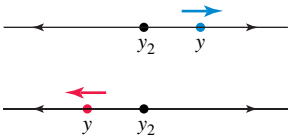


Figure 8.15 If y is perturbed from the unstable equilibrium y_2, then $y(t)$ will increase or decrease to travel further from y_2.

will tend to move further from y_2 over time, as summarized in Figure 8.15. So y_2 is an **unstable** equilibrium of the differential equation.

Our reasoning here did not require much knowledge of $g(y)$; we only needed to know the direction of arrows on either side of each equilibrium. We can examine the final equilibrium $\hat{y} = 0$ in exactly the same way. The arrows are leftward left of $y = 0$, and rightward right of $\hat{y} = 0$, so if $y(t)$ starts from an initial condition on either side of 0, it will tend to travel away from $y = 0$; the equilibrium $\hat{y} = 0$ is therefore unstable.

Graphical Criteria for Stability
If $g(y) > 0$ left of $\hat{y}$ and $g(y) < 0$ right of $\hat{y}$, then $\hat{y}$ is a stable equilibrium.
If $g(y) < 0$ left of $\hat{y}$ and $g(y) > 0$ right of $\hat{y}$, then $\hat{y}$ is an unstable equilibrium.

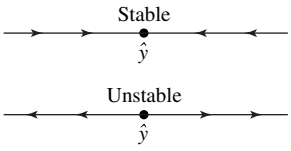


Figure 8.16 Arrows showing direction in which $y(t)$ moves near stable and unstable equilibria.

In terms of the vector field plot, stable equilibria have arrows pointing toward the equilibrium, while for unstable equilibria, the arrows point away from the equilibrium (see Figure 8.16).

An alternative way of writing the graphical criteria for stability may be easier to apply in some circumstances. Notice that if $g(\hat{y}) = 0$ and $g(y) > 0$ left of $\hat{y}$ and $g(y) < 0$ right of $\hat{y}$ (i.e., $\hat{y}$ is a stable equilibrium according to the graphical criteria), then $g(y)$ must be a decreasing function of y at $y = \hat{y}$ (since it goes from positive values to negative values as y passes from values smaller than $\hat{y}$ to values larger than $\hat{y}$). We can make similar arguments for unstable fixed points.

If $g(\hat{y}) = 0$ and $g(y)$ is decreasing at $y = \hat{y}$, then $\hat{y}$ is a stable equilibrium.
If $g(\hat{y}) = 0$ and $g(y)$ is increasing at $y = \hat{y}$, then $\hat{y}$ is an unstable equilibrium.

If g is differentiable then we may turn this criteria into one based on the derivative $g'(\hat{y})$ because $g'(\hat{y}) < 0$ implies that g is decreasing at $y = \hat{y}$, and $g'(\hat{y}) > 0$ implies that g is increasing at $y = \hat{y}$.

Derivative-Based Criterion for Stability of Equilibria
If $g(\hat{y}) = 0$ and $g'(\hat{y}) < 0$, then $\hat{y}$ is a stable equilibrium.
If $g(\hat{y}) = 0$ and $g'(\hat{y}) > 0$, then $\hat{y}$ is an unstable equilibrium.

The derivative-based criterion says nothing about the stability of an equilibrium if $g'(\hat{y}) = 0$, since the function g may be increasing, decreasing, or have a local extremum if $g'(\hat{y}) = 0$. We will discuss the last possibility after some examples.

EXAMPLE 3 Identify the equilibria of the following differential equations and determine whether they are stable or unstable.

(a) $\dfrac{dy}{dt} = y^2 - y$ **(b)** $\dfrac{dy}{dx} = y^3$

Solution Notice that the independent variables are different for the two equations. But since the right-hand side is a function of y (the dependent variable) in both cases, they are both autonomous differential equations. We plot these functions $g(y)$ for (a) and (b) in Figures 8.17 and 8.18.

(a) $g(y) = y(y-1)$ so the equilibria are at $y = 0$ and $y = 1$. In the vector field plot, the arrows point in toward $y = 0$, so $y = 0$ is stable. Arrows point out from $y = 1$, so $y = 1$ is unstable. In this case we could also have used the derivative test since

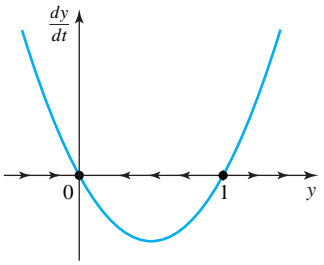


Figure 8.17 Vector field plot of $\frac{dy}{dt} = y^2 - y$ for Example 3(a).

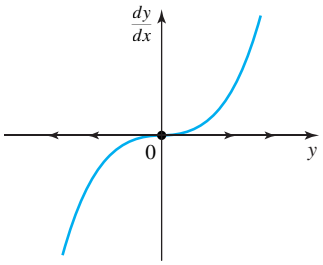


Figure 8.18 Vector field plot of $\frac{dy}{dx} = y^3$ for Example 3(b).

$g'(y) = 2y - 1$, so $g'(0) = -1$, and $g'(1) = 1$. Since $g'(0) < 0$, $y = 0$ is stable. Since $g'(1) > 0$, $y = 1$ is unstable.

(b) The only zero of $g(y) = y^3$ is $y = 0$. In the vector field plot the arrows point away from $y = 0$, so $y = 0$ is an unstable equilibrium, Although $g(y)$ is an increasing function of y at $y = 0$, $g'(0) = 0$, so the derivative criterion for stability cannot be used here. •

EXAMPLE 4 **The Logistic Equation** The logistic equation models the growth or decay of a population living in a habitat with carrying capacity K using a differential equation:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

where r, $K > 0$ are constants. Find the stable and unstable equilibria of this differential equation.

Solution The right-hand side of the differential equation is $g(N) = rN(1 - N/K)$ and is already written in factorized form, so we can read off the roots $N = 0$ and $N = K$. These roots are the equilibria of the differential equation. To determine stability we make a vector field plot (Figure 8.19). To draw the graph of $g(N)$ notice that $g(N)$ is a quadratic polynomial in N (i.e., a parabola). For large N, $g(N) \approx -rN^2/K$ (i.e., $g(N)$ can be approximated by the largest degree term; see Section 3.3), so $\lim_{N\to\infty} g(N) = -\infty$ and $\lim_{N\to-\infty} g(N) = -\infty$, meaning that the parabola bends downward for $N > K$, and $g(N) > 0$ for $0 < N < K$.

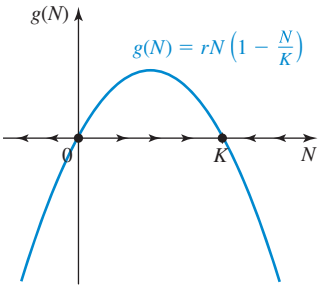


Figure 8.19 Vector field plot for Example 4.

The arrows in the vector field plot (Figure 8.19) point toward the equilibrium at $N = K$, so this equilibrium is stable; while arrows point away from the equilibrium at $N = 0$, so this equilibrium is unstable. •

Our graphical classification of stability of equilibria agrees with our direct solution of the logistic equation in Example 6 of Section 8.1. In the discussion following that example we showed that solutions tend to converge toward $N = K$ as $t \to \infty$, and tend to diverge away from $N = 0$.

EXAMPLE 5 **The Allee Effect** If a population is too small, then it may be outcompeted by other species present in the same habitat, or individuals may be forced to leave in search of mates outside the habitat. So, rather than growing exponentially, small populations may decline into extinction, an effect known as the Allee effect. We can modify the logistic equation to capture this effect by introducing another threshold, a, that represents the minimum size a population must exceed to avoid decline. (We assume that $0 < a < K$, where K is the carrying capacity.)

$$\frac{dN}{dt} = rN(N - a)\left(1 - \frac{N}{K}\right)$$

The only difference between this equation and the logistic equation is the extra factor of $(N - a)$ on the right-hand side.

Find the equilibria of the logistic equation with Allee effect and determine their stability.

Solution The right-hand side of the differential equation is already written in factorized form, so we may read off the values of the equilibria: $N = 0$, a, and K. To determine stability we refer to the vector field plot in Figure 8.20. The arrows in the vector field plot point toward the equilibria $N = 0$ and $N = K$, making these equilibria stable. The arrows point away from the equilibrium $N = a$, making $N = a$ unstable. In Example 9 we will discuss how the vector field plot represents the Allee effect. •

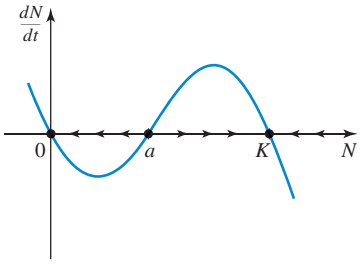


Figure 8.20 Vector field plot for Example 5.

The graphical approach can be used to find the number of equilibria, and to determine their stability, even if the function $g(y)$ is too complicated to graph directly, provided that $g(y)$ can be written as the difference between two functions that can be graphed individually.

Suppose

$$\frac{dy}{dt} = f(y) - h(y) \qquad g(y) = f(y) - h(y)$$

where $f(y)$ and $h(y)$ can both be graphed individually. Where the graphs for $f(y)$ and $h(y)$ intersect, $f(y) = h(y)$, so $g(y) = f(y) - h(y) = 0$. So the points of intersection of the two graphs are the equilibria of the differential equation. To create the vector field plot (i.e., determine whether dy/dt is positive or negative) we compare the graphs. On any interval in which $f(y) > h(y)$ (i.e., the graph of $f(y)$ is above the graph of $h(y)$), $g(y) > 0$, so we draw an arrow to the right on the horizontal axis. On any interval where $f(y) < h(y)$ (the graph of $f(y)$ is below $h(y)$), $g(y) < 0$, so we draw an arrow to the left on the horizontal axis.

EXAMPLE 6 Consider the differential equation

$$\frac{dy}{dt} = e^{-y} - y.$$

Determine how many equilibria the differential equation has and whether they are stable or unstable.

Solution To find the equilibria, we would need to solve the equation $g(y) = e^{-y} - y = 0$. This equation cannot be solved analytically, although it can be solved using a numerical method like bisection (from Section 3.5) or Newton's method (from Section 5.8). However, the graphical method allows us to find the number of equilibria and determine their stability without needing to know precisely where they are.

We cannot graph $g(y) = e^{-y} - y$ directly, but we can decompose it into two functions: $f(y) = e^{-y}$ and $h(y) = y$, whose graphs we should be familiar with (see Figure 8.21). We see from the graphs that the two functions intersect at one point, $\hat{y}$, and this point will be an equilibrium of the differential equation. In fact, since $f(y)$ is a decreasing function of y, and $h(y)$ is an increasing function of y, there can be only one intersection point. To create the vector field plot we observe that if $y < \hat{y}$ (left of the intersection point), $f(y) > h(y)$, so $g(y) = f(y) - h(y) > 0$, and we draw right pointing arrows on the horizontal axis to represent the fact that $y(t)$ is increasing. For $y > \hat{y}$ (i.e., right of the point of intersection), $f(y) < h(y)$, so $g(y) < 0$, and we draw left pointing arrows on the horizontal axis. Since the arrows point toward $\hat{y}$ on both sides, the equilibrium point is stable. •

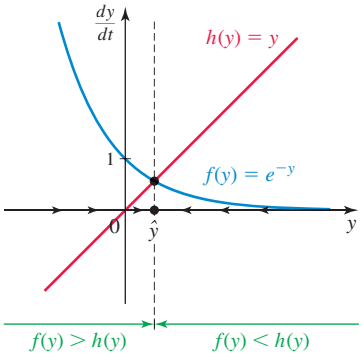


Figure 8.21 From the graphs of $f(y) = e^{-y}$ and $h(y) = y$ we can create the vector field plot for $dy/dt = f(y) - h(y)$.

The graphical approach is particularly helpful when analyzing how the locations and number of equilibria are affected by unknown coefficients that may appear in the differential equation.

EXAMPLE 7 **Sustainable Harvesting** A lake contains a managed population of fish. In the absence of any fishing, the population grows or decreases following the logistic equation with carrying capacity K, and limiting growth rate, r, as $N \to 0$. That is, absent fishing:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

Suppose time, t, is measured in months and fishing removes fish from the lake at a rate of H fish per month. So, if fishing takes place, then

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - H \tag{8.35}$$

where $H > 0$ is a constant.

Successful management of the fish stocks in the lake means finding a value of H for which the differential equation has a stable equilibrium with $N > 0$. Show that this stable equilibrium exists, provided $H < \frac{1}{4}rK$.

Solution

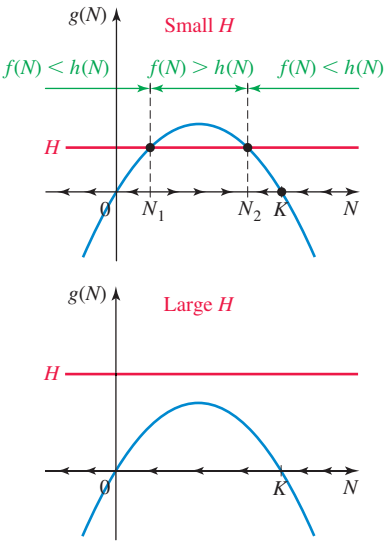


Figure 8.22 Vector field plot for $\frac{dN}{dt} = rN(1 - N/K) - H$

Since the right-hand side of (8.35) is a quadratic polynomial in N, we could find any equilibria by solving the polynomial using the quadratic formula. However, the solution is a complicated function of r, K, and H, and it is hard to see what role the different parameters play. Instead we use the graphical approach, splitting $g(N) = rN(1-N/K)-H$ into functions $f(N) = rN(1-N/K)$ and $h(N) = H$. We sketched the function $f(N)$ already for Example 4. The function $h(N)$ is just a horizontal line. Two possible scenarios can occur, depending on the value of H. If H is small, then there are two points of intersection (N_1 and N_2). If H is large, then the curves do not intersect (see Figure 8.22).

If H is small we can determine the stability of the two equilibria from the vector field plot. If $N_1 < N < N_2$ (i.e., between the equilibria), $f(N) > h(N)$, meaning that $dN/dt > 0$, so arrows are rightward. If $N < N_1$, or $N > N_2$ (i.e., left of N_1, or right of N_2 on the graph), $f(N) < h(N)$, meaning that $dN/dt < 0$, so the arrows point leftward. The arrows therefore point toward the equilibrium N_2 and away from N_1, making N_2 stable and N_1 unstable (Figure 8.22).

The equilibrium N_2 represents a sustainable state for the lake, since we expect the fish population to stay at this value, and not be strongly affected by perturbations. But this stable equilibrium does not exist if H is too large. If H is too large, then $f(N) < h(N)$ everywhere, so $dN/dt < 0$ for all values of N. What is the threshold value for H at which the two equilibria disappear? From the plot we can see that the curves stop intersecting if H exceeds the height of the parabola, $f(N)$ (i.e., if H exceeds the value f takes at its local maximum). To find the local maximum calculate

$$f'(N) = r(1 - 2N/K).$$

$f'(N) = 0$ when $N = K/2$ (from the plot we know that $f(N)$ has one local maximum and no local minima, so there is no need to check the type of extremum point). At $N = K/2$ the height of the function is:

$$f(K/2) = \frac{rK}{4}.$$

So, if $H < \frac{rK}{4}$, there is a stable equilibrium. If $H > rK/4$, then there is no stable equilibrium (in fact, $dN/dt < 0$ for all values of N, meaning that the fish population decreases over time). •

If $H > rK/4$ in the above example, then our model predicts that $N(t)$ will decrease indefinitely (i.e., $N(t) \to -\infty$ as $t \to \infty$). This is an unrealistic prediction because $N(t)$ should never drop below 0 in a real population! The problem is that in our model we assume that the same number of fish is removed from the lake each month, independent of the size of the fish population, even when the fish population

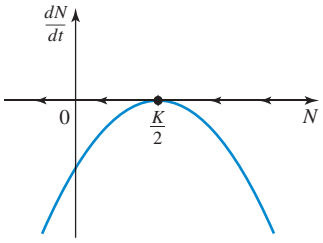


Figure 8.23 $\frac{dN}{dt} = rN(1-N/K)-K/4$ has a semi-stable equilibrium at $N = K/2$

is 0. In Problem 91 you will analyze a different fishing model, in which a fraction of fish is removed from the fish each month. In that model $N(t)$ will not drop below 0.

What happens if $H = rK/4$ in the above example? In that case $\frac{dN}{dt} < 0$ if $N \neq K/2$, and $\frac{dN}{dt} = 0$ if $N = K/2$. The vector field plot is shown in Figure 8.23. So the arrows showing whether $N(t)$ is increasing or decreasing point toward $N = K/2$ for $N > K/2$ and away from $N = K/2$ for $N < K/2$. Thus $N = K/2$ is stable to perturbations that increase N, but unstable to perturbations that decrease N. We call this kind of equation **semi-stable**: It is stable in one direction but unstable in the other.

Definition An equilibrium $\hat{y}$ is **semi-stable** if $y(t)$ returns to $\hat{y}$ if perturbed in one direction from $\hat{y}$ and diverges from $\hat{y}$ if perturbed in the other direction from $\hat{y}$.

Criterion for Semi-Stability If $g(\hat{y}) = 0$ and $\hat{y}$ is a local minimum or local maximum of $g(y)$, then $\hat{y}$ is a semi-stable equilibrium.

8.2.4 Sketching Solutions Using the Vector Field Plot

Using the information in the vector field plot, we can sketch the solutions $y(t)$ as a function of time t. To do this we make use of an important result.

Monotonicity of Solutions of Autonomous Differential Equations If $y(t)$ solves the differential equation $\frac{dy}{dt} = g(y)$, then $y(t)$ must be either constant or monotonic increasing or monotonic decreasing.

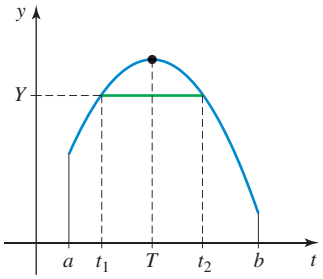


Figure 8.24 A sketch of a solution to $\frac{dy}{dt} = g(y)$ that has both increasing and decreasing intervals.

This result means that if $y(t)$ is initially increasing (i.e., if our initial condition is $y(0) = y_0$, and $g(y_0) > 0$, so that $\frac{dy}{dt}$ starts positive) then $y(t)$ will always be increasing; that is, so long as the solution exists, $\frac{dy}{dt}$ will remain positive. Similarly if $\frac{dy}{dt}$ starts off negative then it will remain negative so long as the solution exists.

We will justify, but not rigorously prove, the monotonicity result. Suppose that a solution of the differential equation $\frac{dy}{dt} = g(y)$ does not obey the monotonicity result. For example, it may start off increasing; but then switch to decreasing (the following argument can be adapted for solutions that start off decreasing but then switch to increasing; see Problem 67). For definiteness assume that this switch happens at a time $t = T$; that is, $dy/dt > 0$ over the interval $[0, T)$ and $\frac{dy}{dt} < 0$ for some interval (T, b) where $b > T$. So, $t = T$ must then be a local maximum of $y(t)$, and the solution locally will look like the sketch in Figure 8.24.

Since $y(t)$ must pass through the same values climbing up to $y(T)$ as those it passes through when it decreases again, there must be some pair of times t_1, and t_2 with $t_1 < T < t_2$, at which $y(t)$ takes the same value, say $y(t_1) = y(t_2) = Y$. However, since $t_1 < T$, $\frac{dy}{dt} > 0$ for $t = t_1$, and since $t_2 > T$, $\frac{dy}{dt} < 0$ for $t = t_2$. But $\frac{dy}{dt} = g(y)$, so $\frac{dy}{dt} \geq 0$ for $t = t_1$ requires $g(Y) \geq 0$, whereas $\frac{dy}{dt} < 0$ for $t = t_2$ requires $g(Y) \leq 0$. The only way that we may have both $g(y) \geq 0$ and $g(y) \leq 0$ is if $g(y) = 0$. In that case $y = Y$ is an equilibrium of the differential equation, meaning that $y(t) = Y$ for all $t > t_1$. This contradicts the assumption that $y(t)$ starts decreasing at $t = T$.

What else can we say about solutions? Suppose $y(t)$ is an increasing solution of the differential equation. Then as $t \to \infty$, $y(t)$ may either increase indefinitely (i.e., $y(t) \to +\infty$) or it must converge to a constant. That is $\lim_{t\to\infty} y(t) = \hat{y}$ for some

constant $\hat{y}$. If $y(t)$ converges to a constant as $t \to \infty$, then $\frac{dy}{dt} \to 0$ and $g(y) \to g(\hat{y})$. For the two sides of the equation to be equal we must have $g(\hat{y}) = 0$, which implies that $\hat{y}$ is an equilibrium of the differential equation.

Let's put all of this information together.

Rules for Sketching the Solutions of a Differential Equation.

1. If $\frac{dy}{dt} = 0$ initially then $y(t)$ is a constant.
2. If $\frac{dy}{dt} > 0$ initially, $y(t)$ will grow to $+\infty$, or converge to the first equilibrium it meets.
3. If $\frac{dy}{dt} < 0$ initially, $y(t)$ will decrease to $-\infty$, or converge to the first equilibrium it meets.

Let's use these rules to sketch the solutions for some differential equations.

EXAMPLE 8 The Gompertz law for tumor growth predicts that the number of cells in a tumor, N, changes with time t, according to $dN/dt = g(N)$ where

$$g(N) = \begin{cases} aN \ln(b/N) & \text{if } N > 0 \\ 0 & \text{if } N = 0. \end{cases}$$

Use l'Hôpital's rule to show that $g(N)$ is continuous from the right at $N = 0$

where a, b are positive coefficients that depend on the type of tumor.

By drawing the vector field plot of the differential equation, sketch possible solutions.

Solution Previously we showed that $\hat{N} = b$ is an equilibrium of this differential equation. Adding $N = 0$ to the domain of the differential equation adds the additional equilibrium $\hat{N} = 0$. To draw the vector field plot we need to know where $g(N)$ is positive and where it is negative. Since $aN > 0$ for all $N > 0$, the sign of $g(N)$ is determined by the sign of $\ln(b/N)$.

$$\ln(b/N) > 0 \text{ if } N < b \quad \text{and} \quad \ln(b/N) < 0 \text{ if } N > b$$

$\ln x > 0$ if and only if $x > 1$

The vector field plot for the differential equation is shown in Figure 8.25. Both $N = 0$ and $N = b$ are constant solutions of the differential equation if $N(0) \in (0, b)$ (that is, the initial tumor size starts somewhere between 0 and b). Then we see from the vector field plot the solution is initially growing. It must then continue to grow, but it cannot grow past $N = b$, since $dN/dt < 0$ for $N > b$. Thus $N(t)$ will converge to b as $t \to \infty$. Similarly if $N(0) > b$ (i.e., if the starting tumor size is right of b on the vector field plot, then $N(t)$ will decrease until it again converges to b). We sketch the solutions in Figure 8.26. •

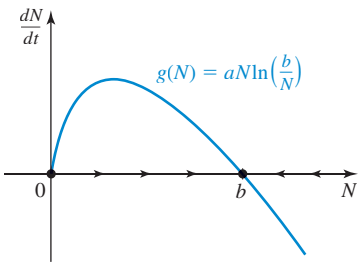


Figure 8.25 Vector field plot for the Gompertz tumor growth model.

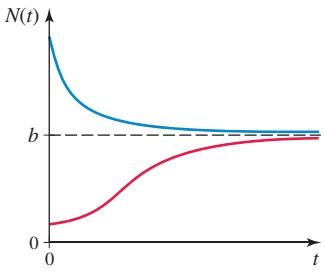


Figure 8.26 Solutions of the Gompertz tumor growth model.

EXAMPLE 9 **The Allee Effect** In Example 5 we modified the logistic equation to include the Allee effect; the tendency of small populations to shrink due to emigration and competition with other populations. The population size is modeled using a differential equation:

$$\frac{dN}{dt} = rN(N-a)\left(1-\frac{N}{K}\right).$$

Sketch the possible solutions of this differential equation.

Solution Again we start from the vector field plot that was plotted in Figure 8.20. There are three possible constant solutions: $N = 0$, a, and K. If $0 < N(0) < a$, then from the vector field plot we see that $N(t)$ starts decreasing. It will continue to decrease, converging to 0 as $t \to \infty$. If $a < N(0) < K$, then $N(t)$ will increase, converging to $N = K$. Finally, if $N(0) > K$, then $N(t)$ will decrease, again converging to $N = K$. This behavior is consistent with the Allee effect as it was described in Example 5: Populations smaller than a decline to extinction, and populations larger than a converge to the habitat's carrying capacity. A sketch of the solutions is given in Figure 8.27. •

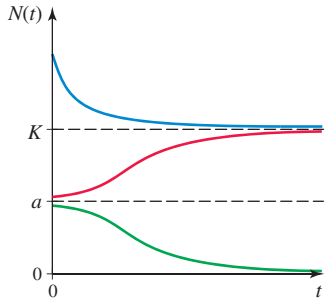


Figure 8.27 Solutions of the logistic equation with Allee effect.

8.2.5 Behavior Near an Equilibrium

The graphical method allows all equilibria of a differential equation to be identified and classified as either stable or unstable. We also showed that the stability of an equilibrium $\hat{y}$ can also be determined from the sign of $g'(\hat{y})$. What the graphical method cannot tell us is how quickly the solution converges back to $\hat{y}$, or diverges away from $\hat{y}$, if perturbed from $\hat{y}$. Put another way, are some equilibria more stable than others? To determine the rate of convergence (or divergence) we analyze the behavior of the differential equation if y is slightly perturbed from $\hat{y}$.

Consider a differential equation

$$\frac{dy}{dt} = g(y) \tag{8.36}$$

and an equilibrium $\hat{y}$. We consider a small perturbation of the solution away from the equilibrium $\hat{y}$; we express this perturbation as

$$y(t) = \hat{y} + Y(t)$$

where $Y(t)$ is small and may be either positive or negative. The function $Y(t)$ measures how far the solution has been perturbed from the equilibrium. The perturbed initial condition is $y(0) = \hat{y} + Y(0)$. Then substituting for $y(t)$:

$$\frac{dy}{dt} = \frac{d}{dt}(\hat{y}+Y) = \frac{dY}{dt} \qquad \hat{y} \text{ is a constant, so } \tfrac{d\hat{y}}{dt} = 0.$$

Substituting for y into both sides of (8.36), we find that:

$$\frac{dY}{dt} = g(\hat{y}+Y)$$

If Y is sufficiently small, we can approximate $g(\hat{y}+Y)$ by its linear approximation. The linear approximation of $g(y)$ close to $y = \hat{y}$ is given by

$$g(y) \approx g(\hat{y}) + (y-\hat{y})g'(\hat{y}) = (y-\hat{y})g'(\hat{y}) \qquad g(\hat{y}) = 0$$

Or, in terms of the perturbation variable, Y:

$$g(\hat{y}+Y) \approx Yg'(\hat{y})$$

If we set $\lambda = g'(\hat{y})$ then the linear approximation of (8.36) takes the form:

$$\frac{dY}{dt} = \lambda Y$$

This equation has the solution

$$Y(t) = Y(0)e^{\lambda t} \tag{8.37}$$

The value $Y(0)$ represents our initial perturbation; that is, how far the solution starts from the equilibrium. According to Equation (8.37), if $Y(0)$ is non-zero, then $Y(t)$ will grow exponentially (i.e., diverge from $\hat{y}$ if $\lambda > 0$), or will decay exponentially (i.e., converge back to $\hat{y}$, if $\lambda < 0$). Since we have defined $\lambda = g'(\hat{y})$, this analysis reproduces the derivative test (including the ambiguity of what must occur if $\lambda = 0$). However it also tells us the role that $g'(\hat{y})$ plays in controlling how quickly the solution converges back to $\hat{y}$. If $g'(\hat{y}) < 0$, then perturbations decay more quickly for larger values of $|g'(\hat{y})|$. If $g'(\hat{y}) > 0$, then perturbations grow faster for larger values of $g(\hat{y})$. Because the parameter λ controls the behavior of small perturbations, we need a name for it: We will call it the **eigenvalue** of the equilibrium. The main importance of the eigenvalue method for determining stability of equilibria is that it can also be used to study systems of differential equations, a problem that we will study at length in Chapter 11.

EXAMPLE 10 Find the equilibria and associated eigenvalues for each of the following differential equations. Then use the eigenvalue to determine whether each equilibrium is stable or unstable.

(a) $\dfrac{dy}{dt} = y(1-y)$ **(b)** $\dfrac{dz}{dt} = \frac{1}{z^2} - \frac{1}{z}, z > 0$ **(c)** $\dfrac{dy}{dx} = \ln y - 2, y > 0$

Solution **(a)** The function $g(y) = y(1-y)$ has roots at $\hat{y} = 0$ and $\hat{y} = 1$. $g'(y) = 1 - 2y$, so the corresponding eigenvalues are $g'(0) = 1$ and $g'(1) = -1$. Since $g'(0) > 0$, $\hat{y} = 0$ is unstable, while $g'(1) < 0$ implies that $\hat{y} = 1$ is stable.

(b) The function $g(z) = \frac{1}{z^2} - \frac{1}{z}$ has roots where:

$$\frac{1}{z^2} - \frac{1}{z} = 0 \Rightarrow 1 - z = 0 \qquad \times \text{ both sides by } z^2$$

$$z = 1.$$

$$g'(z) = -\frac{2}{z^3} + \frac{1}{z^2}$$

so the eigenvalue for this equilibrium is: $g'(1) = -2 + 1 = -1$. Since $g'(1) < 0$, the equilibrium $\hat{z} = 1$ is stable.

(c) The function $g(y) = \ln y - 2$ has roots when $\ln y - 2 = 0$ (i.e., the equilibrium is $\hat{y} = e^2$). $g'(y) = \frac{1}{y}$, so the eigenvalue is $g'(e^2) = e^{-2}$. Since $g'(e^2) > 0$, the equilibrium $\hat{y} = e^2$ is unstable. •

Section 8.2 Problems

8.2.1

Find the equilibria of the following differential equations.

1. $\dfrac{dy}{dt} = y(y^2 - 1)$

2. $\dfrac{dy}{dt} = y^3 + y$

3. $\dfrac{dx}{dt} = x^2 - 3x + 2$

4. $\dfrac{dx}{dt} = 6 + 5x + x^2$

5. $\dfrac{dy}{dt} = \dfrac{y-2}{y+1}$

6. $\dfrac{dy}{dt} = \dfrac{y-1}{y^2+1}$

7. $\dfrac{dx}{dt} = x^8 - 1$

8. $\dfrac{dy}{dt} = y^{1/3} - 1$

9. $\dfrac{dN}{dt} = Ne^{-N}$

10. $\dfrac{dN}{dt} = N \ln N, N > 0$

11. $\dfrac{dN}{dt} = \sin N$

12. $\dfrac{dN}{dt} = N \cos 2N$

8.2.2, 8.2.3

For Problems 13–28 make vector field plots of each of the differential equations. Find any equilibria of each differential equation and use your vector field plot to classify whether each equilibrium is stable or unstable.

13. $\dfrac{dy}{dt} = y - 1$

14. $\dfrac{dy}{dt} = 2 - y$

15. $\dfrac{dy}{dt} = 4 - y^2$

16. $\dfrac{dy}{dt} = y(y-2)$

17. $\dfrac{dy}{dt} = y^2 - y$

18. $\dfrac{dy}{dt} = y^2 - 2y - 8$

19. $\dfrac{dx}{dt} = x - x^3$

20. $\dfrac{dx}{dt} = x^5 - x$

21. $\dfrac{dN}{dt} = N \ln(2/N), N > 0$

22. $\dfrac{dN}{dt} = N^3 e^{-N}$

23. $\dfrac{dx}{dt} = \dfrac{x^2 - x}{x^2 + 1}$

24. $\dfrac{dx}{dt} = \dfrac{x+1}{x-1}, x \neq 1$

25. $\dfrac{dx}{dt} = \dfrac{x}{x+1}, x \neq -1$

26. $\dfrac{dx}{dt} = \dfrac{x+1}{x}, x \neq 0$

27. $\dfrac{dS}{dt} = \dfrac{1}{S^3} - \dfrac{1}{S}, S > 0$

28. $\dfrac{dS}{dt} = \dfrac{1}{S} - \dfrac{1}{S^5}, S > 0$

In Problems 29–38, by breaking down each equation into two parts that you can sketch, determine how many equilibria each differential equation has, and classify them as stable or unstable. You do not need to determine the location of the equilibria.

29. $\dfrac{dy}{dt} = e^y - (1 - y)$

30. $\dfrac{dy}{dt} = \ln y - e^{-y} \quad y > 0$

31. $\dfrac{dx}{dt} = \dfrac{1}{x} - \dfrac{x}{x+1} \quad x > 0$

32. $\dfrac{dx}{dt} = 3e^{-x^2} - x^2$

33. $\dfrac{dx}{dt} = \dfrac{1}{2} - \dfrac{x^2}{x^2+1}$

34. $\dfrac{dx}{dt} = x^2 - \dfrac{1}{x+1} \quad x \neq -1$

35. $\dfrac{dN}{dt} = N^2 - N + 1 \quad N > 0$

36. $\dfrac{dN}{dt} = 1 - N - N^3$

37. $\dfrac{dy}{dx} = y + y^5 - 1$

38. $\dfrac{dy}{dx} = y^4 + y^3 - 1$

In Problems 39–48 you should treat h as a constant. For what values of h (if any) does each equation have equilibria? Use a graphical argument to show which of the equilibria (if any) are stable.

39. $\dfrac{dy}{dt} = y(1 - y) - h$

40. $\dfrac{dy}{dt} = y - h$

41. $\dfrac{dy}{dx} = y^2 - h$

42. $\dfrac{dy}{dx} = (y - 1)(y + 3) - h$

43. $\dfrac{dy}{dx} = (y - 2)(y + 4) + h$

44. $\dfrac{dy}{dx} = y^3 - y - h$

45. $\dfrac{dx}{dt} = x^2 - hx$

46. $\dfrac{dx}{dt} = x^3 - hx$

47. $\dfrac{dx}{dt} = x(x^2 - 1) - h$

48. $\dfrac{dx}{dt} = hx - x^3$

For Problems 49–56 determine whether the equilibrium at $x = 0$ is stable, unstable, or semi-stable.

49. $\dfrac{dx}{dt} = x^3$

50. $\dfrac{dx}{dt} = -x^5$

51. $\dfrac{dx}{dt} = x^4$

52. $\dfrac{dx}{dt} = x^3 - x^5$

53. $\dfrac{dx}{dt} = x^3 + x^4$

54. $\dfrac{dx}{dt} = x^2 - x^3$

55. $\dfrac{dx}{dt} = \dfrac{x^3}{x - 1}$

56. $\dfrac{dx}{dt} = x^3 e^{-x}$

8.2.4

For Problems 57–66 draw the vector field plot of the differential equation. Then, using the given initial conditions, sketch the solutions (i.e., draw a graph showing the dependent variable as a function of the independent variable).

57. $\dfrac{dy}{dt} = 3y - 2$

(a) $y(0) = 2$, **(b)** $y(0) = 0$.

58. $\dfrac{dy}{dt} = 1 - y$

(a) $y(0) = 2$, **(b)** $y(0) = -1$.

59. $\dfrac{dy}{dt} = y(1 - y)$

(a) $y(0) = 0$, **(b)** $y(0) = 1/2$, **(c)** $y(0) = 1/4$, **(d)** $y(0) = 2$.

60. $\dfrac{dy}{dt} = y^2 - 1$

(a) $y(0) = -1$, **(b)** $y(0) = -1/2$, **(c)** $y(0) = 1/2$, **(d)** $y(0) = 2$.

61. $\dfrac{dy}{dt} = (y + 3)(1 - y)$

(a) $y(0) = -1$, **(b)** $y(0) = -1/2$, **(c)** $y(0) = -2$, **(d)** $y(0) = 2$.

62. $\dfrac{dy}{dt} = (y + 1)(y + 3)$

(a) $y(0) = -3/2$, **(b)** $y(0) = -5/2$, **(c)** $y(0) = 0$, **(d)** $y(0) = -5$.

63. $\dfrac{dN}{dt} = N(N - 1)(5 - N)$

(a) $N(0) = 1$, **(b)** $N(0) = 1/2$, **(c)** $N(0) = 3/2$, **(d)** $N(0) = 7$.

64. $\dfrac{dN}{dt} = (N - 1)(N + 1)(N - 4)$

(a) $N(0) = 0$, **(b)** $N(0) = 2$, **(c)** $N(0) = 6$, **(d)** $N(0) = -2$.

65. $\dfrac{dy}{dx} = (y - 1)(y - 2)(y - 5)$

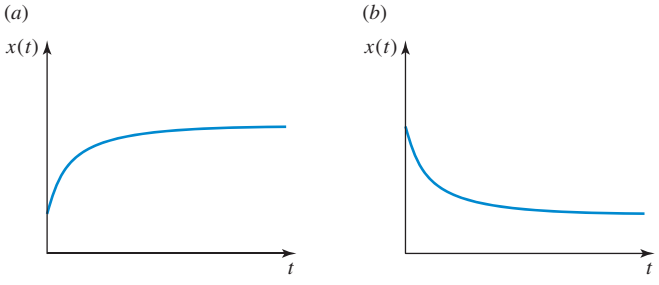
(a) $y(0) = 0$, **(b)** $y(0) = 4$, **(c)** $y(0) = 3/2$, **(d)** $y(0) = 6$.

66. $\dfrac{dy}{dx} = -y - y^3$

(a) $y(0) = 0$, **(b)** $y(0) = 1$, **(c)** $y(0) = 2$, **(d)** $y(0) = 3$.

67. **Monotonicity of Solutions** One of the key ideas for sketching solutions from vector field plots is that a solution curve must be monotonic; that is, $x(t)$ is either increasing or decreasing or constant but cannot switch from one behavior to another. We showed that a solution $x(t)$ could not start by increasing and then switch to decreasing. Suppose that $x(t)$ is a solution of the differential equation $\dfrac{dx}{dt} = g(x)$ and that $x(t)$ starts off decreasing with time. Show that $x(t)$ cannot switch to increasing.

68. **Monotonicity of Solutions** Figure 8.28 shows the graphs of some functions $x(t)$. Which of these functions could **not** arise as solutions of a differential equation $dx/dt = f(x)$ for some continuous function $f(x)$?



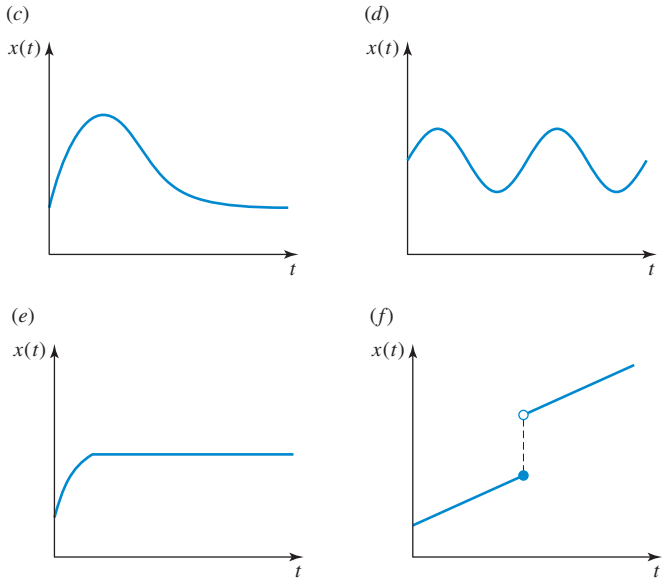


Figure 8.28 Functions $x(t)$ for Problem 68.

69. **Curvature of Solutions** In Section 5.6 we showed how knowing the curvature of a function (that is, whether it is concave up or concave down) can assist in drawing the graph of the function. Suppose that $x(t)$ solves the differential equation $dx/dt = f(x)$, where $f(x)$ is a differential function and $f'(x)$ is continuous.

(a) By applying the chain rule, show that

$$\frac{d^2x}{dt^2} = f'(x)f(x)$$

(b) If $f(x) > 0$, explain why a solution $x(t)$ is concave up if $f'(x) > 0$ and concave down if $f'(x) < 0$.

(c) What about if $f(x) < 0$? When is the solution $x(t)$ concave up and when is it concave down?

(d) Using the results of (b) and (c), show on the vector field plot in Figure 8.29 the intervals on which $x(t)$ will be concave up and the intervals on which $x(t)$ will be concave down.

(e) What happens to $x(t)$ when x passes through one of the local extrema of $f(x)$?

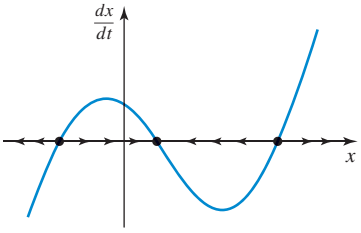


Figure 8.29 Vector field plot for $\frac{dx}{dt} = f(x)$ in Problem 69(d).

70. **Logistic Equation with Allee Effect**

You must solve Problem 69 before solving this problem.

The vector field plot for a model of density dependent growth of a population is shown in Figure 8.30.

(a) Label on the plot the intervals on which $N(t)$ is concave up.

(b) Label also the intervals on which $N(t)$ is concave down.

(c) What happens when $N = b$ or $N = c$?

(d) Suppose that $N(0) \in (a, c)$. Explain why the solution $N(t)$ will look like the sketch in Figure 8.31.

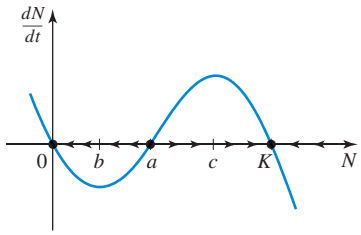


Figure 8.30 Vector field plot for a population modeling density dependent growth and the Allee effect (see Problem 70). Local extrema b and c are shown as well as equilibria $N = 0, a, K$.

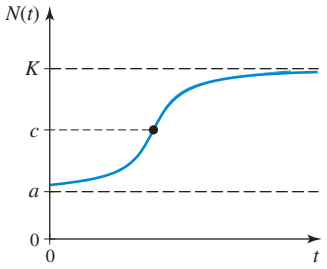


Figure 8.31 Sketch of the solution if $N(0) \in (a, c)$

(e) Draw sketches of the solution if (i) $N(0) \in (0, b)$, (ii) $N(0) \in (b, a)$, (iii) $N(0) \in (c, K)$, (iv) $N(0) \in (K, \infty)$

In Problems 71–76 you are given graphs of the function f(y) for a differential equation dy/dt = f(y). (See Figure 8.32.) You are also given initial conditions y_0 or y_1 (shown on the plot). For each graph make a sketch of the solution y(t) against t for (a) y(0) = y_0, (b) y(0) = y_1. If you have solved Problem 69, your sketch can show where y(t) is concave up and where y(t) is concave down.

71. The function shown in 8.32a.

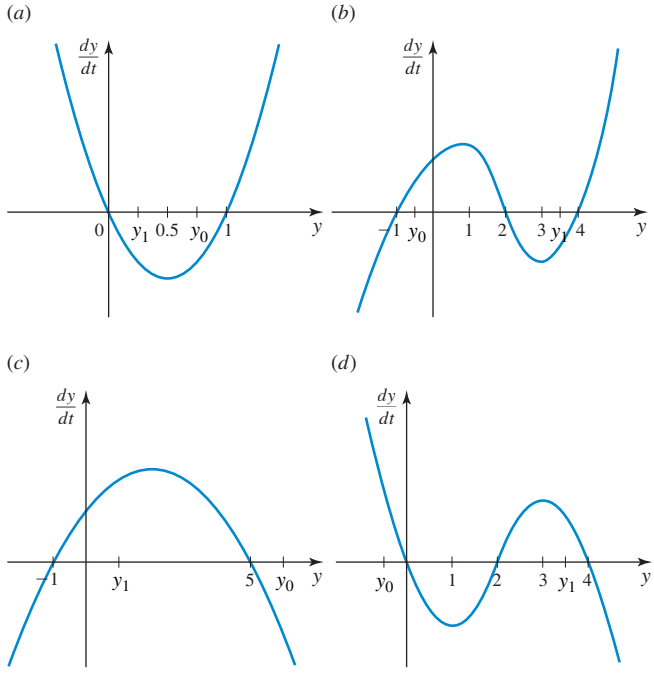
72. The function shown in 8.32b.

73. The function shown in 8.32c.

74. The function shown in 8.32d.

75. The function shown in 8.32e.

76. The function shown in 8.32f.



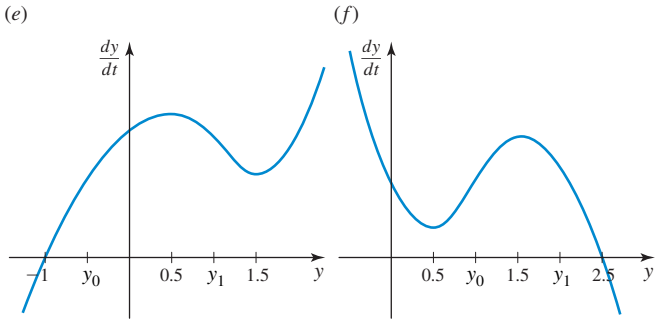


Figure 8.32 Graphs of $f(y)$ for Problems 71–76. The initial conditions $y(0) = y_0$ or $y(0) = y_1$ are marked on each graph.

8.2.5

For Problems 77–88 find all equilibria, and, by calculating the eigenvalue of the differential equation, determine which equilibria are stable and which are unstable.

77. $\dfrac{dy}{dt} = 2 - 3y$

78. $\dfrac{dy}{dt} = y - 2$

79. $\dfrac{dy}{dt} = y(2 - y)(y - 3)$

80. $\dfrac{dy}{dt} = y(y - 1)(y - 2)$

81. $\dfrac{dN}{dt} = N \ln\left(\dfrac{2}{N}\right) \qquad N > 0$

82. $\dfrac{dN}{dt} = \dfrac{N - 1}{N + 1} \qquad N \geq 0$

83. $\dfrac{dy}{dx} = \dfrac{y^2 - y}{y^2 + 1}$

84. $\dfrac{dy}{dx} = \dfrac{1}{y^3} - \dfrac{1}{y}, \quad y > 0$

85. $\dfrac{dx}{dt} = xe^{-x}$

86. $\dfrac{dx}{dt} = e^{-x} - e^{-2x}$

87. $\dfrac{dx}{dt} = hx - x^2$, where h is a constant and

(a) $h > 0$, **(b)** $h < 0$

88. $dx/dt = hx - x^3$, where h is a constant and

(a) $h > 0$, **(b)** $h < 0$

89. Effect of Predation on Population Growth Suppose that $N(t)$ denotes the size of a population at time t. The population evolves according to the logistic equation, but in addition, predation reduces the size of the population so that the rate of change is given by

$$\frac{dN}{dt} = g(N) \tag{8.38}$$

where

$$g(N) = N\left(1 - \frac{N}{50}\right) - \frac{9N}{5 + N}.$$

The first term on the right-hand side describes the logistic growth; the second term describes the effect of predation.

(a) Make the vector field plot for this differential equation.

(b) Find all equilibria of (8.38).

(c) Use your vector field plot in (a) to determine the stability of the equilibria you found in (b).

(d) Repeat your analysis from part (c) but now use the method of eigenvalues to determine the stability of the equilibria you found in (b).

90. Sustainable Harvesting Suppose that a fish population evolves according to the logistic equation and that a fixed number of fish per unit time are removed. That is,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - H$$

Assume that $r = 2$ and $K = 1000$.

(a) Find possible equilibria, and discuss their stability when $H = 100$.

(b) What is the maximal harvesting rate that maintains a positive population size?

91. Sustainable Harvesting Suppose that a fish population evolves according to a logistic equation and that fish are harvested at a rate proportional to the population size. If $N(t)$ denotes the population size at time t, then

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - hN$$

Assume that $r = 2$ and $K = 1000$.

(a) Find possible equilibria and use the graphical approach to discuss their stability, when $h = 0.1$.

(b) Show that if $h < r = 2$, then there is a nontrivial equilibrium. Find the equilibrium.

(c) Use **(i)** the eigenvalue approach and **(ii)** the graphical approach to analyze the stability of the equilibrium you found in (b).

92. Growth of a Tumor Gompertz's equation can be used to model the growth of some solid tumors. It predicts that the number of cells $N(t)$ in a tumor will grow over time according to:

$$\frac{dN}{dt} = g(N) \tag{8.39}$$

where

$$g(N) = \begin{cases} 0 \text{ if } N = 0 \\ aN \ln(b/N) \quad \text{if } N > 0 \end{cases}$$

where a and $b > 0$ are constants

(a) Find all of the equilibria of (8.39).

(b) Can you use the eigenvalues of g to calculate the stability of each equilibrium? If not, why not?

93. Logistic Equilibrium with Allee Effect A population whose growth is affected by the Allee effect is modeled using the differential equation:

$$\frac{dN}{dt} = rN(N - a)\left(1 - \frac{N}{K}\right)$$

where r, a, k are all positive constants and $a < K$.

The equilibria of this equation are $N = 0, N = a$, and $N = K$. Use the eigenvalue method to classify whether each of these equilibria is stable or unstable.

8.3 Differential Equation Models

In sections 8.1.2 and 8.2 we learned methods to solve autonomous differential equations, and to identify features of their solutions (e.g., equilibria) without solving the differential equation. We will now show how these methods can be used to study many different mathematical models.

8.3.1 Compartment Models

This example is adapted from ***DeAngelis (1992)***. A common question that many models set out to answer is how matter, nutrients, energy, or drugs move through a system like the human body. One way to model this movement is to treat the system as a series of compartments; for example, we could treat the blood as one compartment and organs as separate compartments, and model the flows of a drug between those compartments.

Let's start with a physically motivated example. A single compartment of fixed volume, V, of water contains a concentration $C(t)$ of a particular solute (e.g., salt). New water is added to the volume at a rate q. That is, in one unit of time a volume q flows into the compartment. At the same time water also flows out of the compartment. Let's assume that the rate of outflow is also q (that is, a volume, q, of water is removed in one unit of time; see Figure 8.33). We denote by $C(t)$ the concentration of the solution in the compartment at time t. Then the total mass of the solute in the compartment is $C(t)V$, where V is the volume of the compartment. For instance, if the concentration of the solution is 2 grams per liter and the volume of the compartment is 10 liters, then the total mass of the solute in the compartment is 2 g liter^{-1} $\times$ 10 liters, which is equal to 20 g. Since the inflow and outflow rates are the same, the total volume of water in the compartment will remain constant with time. However, if the concentration of solute in the water flowing into the compartment is different from the concentration flowing out of the compartment, then $C(t)$ can change over time.

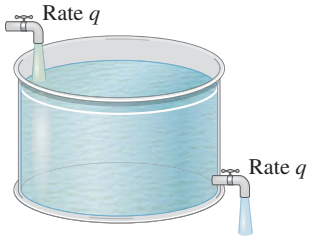


Figure 8.33 Inflows and outflows of water and solute in a single compartment.

The concentration in the outflow should be the same as the concentration in the compartment, $C(t)$, provided the solute is mixed evenly through the compartment. Suppose that the concentration in the inflow is a constant, C_I. Like q, C_I is an arbitrary constant that allows us to tailor the model to different problems. To calculate $C(t)$ we determine the rate of change of solute in the compartment.

$$\begin{pmatrix}\text{Rate of change of}\\ \text{amount of solute}\\ \text{in compartment}\end{pmatrix} = \begin{pmatrix}\text{Rate at which solute}\\ \text{flows in}\end{pmatrix} - \begin{pmatrix}\text{Rate at which solute}\\ \text{flows out}\end{pmatrix}$$

In one unit of time a volume q of water flows in, so an amount qC_I of solute flows in: The *rate* at which solute flows in is qC_I. Similarly the rate at which solute flows out is $qC(t)$. On the left-hand side, since the total amount of solute in the compartment is $C(t) \cdot V$, the rate of change is $\frac{d}{dt}(C(t) \cdot V)$. Putting these ingredients together, we obtain:

$$\frac{d}{dt}(CV) = qC_I - qC(t)$$

$$V\frac{dC}{dt} = q(C_I - C) \qquad V \text{ is a constant}$$

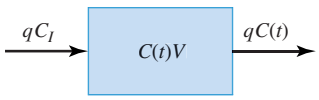


Figure 8.34 Flow diagram for the single-compartment model.

Figure 8.34 is a diagram showing the rates of flow of solute into and out of the compartment.

To analyze this equation we rearrange it into:

$$\frac{dC}{dt} = \frac{q}{V}(C_I - C) \tag{8.40}$$

and draw the vector field plot for this differential equation (Figure 8.35). Since C represents the concentration of solute we only need to consider $C \geq 0$. The graph of this equation is a straight line with slope $(-q/V)$ that meets the horizontal axis at $C = C_I$.

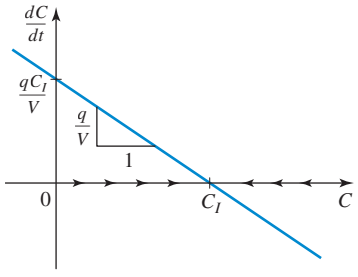


Figure 8.35 Vector field plot for the single compartment model.

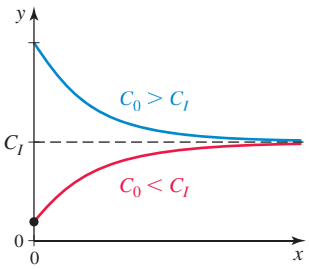


Figure 8.36 The solution curves for the single-compartment model for different values of C_0.

The equilibrium concentration is $C = C_I$, and all arrows point toward $C = C_I$, so whatever the starting concentration is, $C(t)$ will converge to C_I over time. Some possible solutions are shown in Figure 8.36 for different values of the initial concentration, C_0.

If $C(0) = C_0$, then we can solve the differential equation using separation of variables. We will just give the solution here (you will derive the solution in Problem 1).

$$C(t) = C_I - (C_I - C_0)e^{-qt/V}$$

Since $e^{-qt/V} \to 0$ as $t \to \infty$ the solution confirms that $\lim_{t\to\infty} C(t) = C_I$.

What role do the parameters q and V play? Notice from the exact solution that the exponential decay part of the solution has the form $e^{-qt/V}$. From the form of the exponential we see that C converges to C_I more rapidly if q/V is large, that is, if either q is large (fast inflow and outflow) or V is small (i.e., the compartment is small). In fact we do not need to solve the differential equation to see how q and V affect the rate at which $C(t)$ converges to C_I. Remember that, in general, near the equilibrium the solution decays with decay rate $e^{\lambda t}$ where λ is the eigenvalue. If $g(C) = \frac{q}{V}(C_I - C)$, then for Equation (8.40) $\lambda = g'(C_I) = -\frac{q}{V}$.

8.3.2 An Ecological Model

The habitats of many organisms are fragmented: Fungi, for example, may only live on certain hosts, or may only feed on logs that are spread through a forest. Ants in the same forest have a limited number of potential nest sites, depending on the availability of food and building materials and also the danger of flooding, predators, and so on. Thus the ants or fungi in a forest are broken down into small subpopulations; for example, the fungi on a single log, or the ants in a single nest. The number of organisms at each of these sites will typically vary greatly over time; each subpopulation may last only a few years before going extinct. Yet the total number of ants or fungi in the forest may remain quite stable over time: When an ant nest goes extinct, the site that it occupied is quickly recolonized by ants from nearby sites. We will study a mathematical model that was created by ***Levins (1969)*** to explain why under some conditions the total number of organisms in a particular habitat can be stable, though individual subpopulations don't last very long.

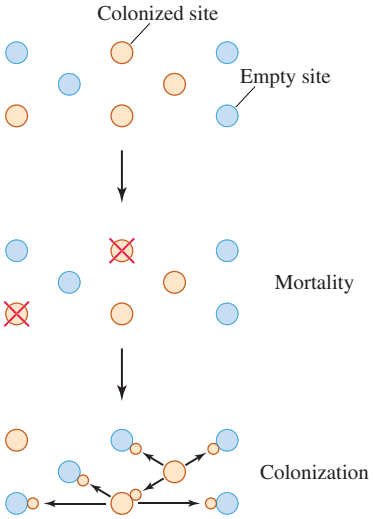


Figure 8.37 The number of occupied sites changes due to mortality and colonization.

In Levins' model, we start by imagining that the habitat is divided into a large number of sites that could contain subpopulations of the organism (e.g., potential nest sites). We will keep track of how the proportion of sites, that are occupied, p, changes with time, t. The number of occupied sites changes due to two processes.

Mortality: The subpopulation occupying a particular site may die out. Assume that in one unit of time, a fraction m of the occupied sites die out (the sites themselves remain but they cease to be occupied). The constant m is called the **mortality rate**.

Colonization: Each subpopulation sends out propagules to nearby sites. A propagule could be, for example, a fungal spore, or an insect scout that is sent out to find new potential nest sites and to colonize those sites. Suppose that in one unit of time each subpopulation sends out c propagules; these propagules are sent out indiscriminately, landing at sites that are already occupied as well as sites that are not. The constant c is called the colonization rate. The two steps, mortality and colonization, are illustrated in Figure 8.37.

Suppose that there are N sites that could be occupied by subpopulations, and that at a time t, a proportion $p(t)$ of the sites are occupied. Then the rate of change of the number of occupied sites can be written as a word equation:

$$\begin{matrix}\text{Rate of change}\\ \text{of occupied sites}\end{matrix} = -\begin{matrix}\text{Rate of loss by}\\ \text{mortality}\end{matrix} + \begin{matrix}\text{Rate of colonization}\\ \text{of new sites}\end{matrix}$$

If a proportion of p sites are occupied, the number of subpopulations is Np. In one unit of time, a fraction m of subpopulations will die out. The total number of subpopulations that die out is therefore:

$$\begin{matrix}\text{Rate of loss}\\ \text{by mortality}\end{matrix} = \begin{matrix}\text{Number of}\\ \text{subpopulations}\end{matrix} \times \begin{matrix}\text{Fraction that}\\ \text{die}\end{matrix} = Np \times m = mNp$$

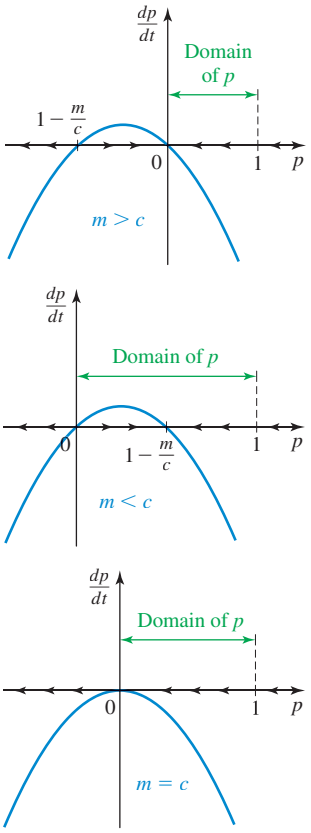


Figure 8.38 The vector field plot for the Levins' model of population growth in a patchy environment depends on whether $m \geq c$ or $m < c$.

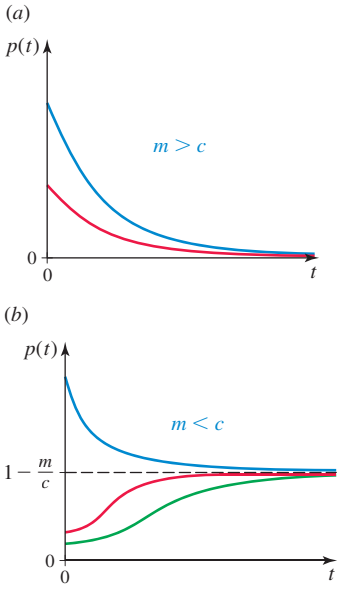


Figure 8.39 (a) If $m \geq c$, then $p(t)$ converges to 0. (b) If $m < c$, if $p(0) \neq 0$, then $p(t)$ converges to $1 - m/c$.

The rate of colonization is slightly harder to calculate. If in one unit of time each occupied site sends out c propagules, then since there are Np occupied sites, in one unit of time a total of cNp propagules (number of occupied sites $\times$ number of propagules per site) will be sent out. Only propagules that land on unoccupied sites will start new subpopulations. Since a fraction p of sites are occupied, a fraction p of propagules sent out will land on already occupied sites, and a fraction $1 - p$ will land on unoccupied sites and start new subpopulations. So the rate of colonization is:

$$\text{Rate of colonization} = \text{Number of propagules released in unit time} \times \text{Fraction of propagules that start new subpopulations} = cNp(1-p)$$

So, putting everything together, we obtain:

$$\frac{d}{dt}(Np) = -mNp + cNp(1-p)$$

$$\frac{dp}{dt} = -mp + cp(1-p) \quad \text{Divide by } N \tag{8.41}$$

Although (8.41) can be solved using a separation of variables, we will not do that here. Instead we will use the methods from Section 8.2 to analyze how the solution depends on the parameters m and c.

Let $g(p) = -mp + cp(1-p)$. Then the equilibria of (8.41) correspond to values $\hat{p}$ for which $g(\hat{p}) = 0$, that is,

$$\hat{p}((c-m) - c\hat{p}) = 0 \quad \text{Factoring } g(\hat{p})$$

This equation has two solutions, $\hat{p} = 0$ and $\hat{p} = 1 - m/c$. However, p represents the proportion of sites that are occupied, and this fraction must be between 0 and 1. Although the equilibrium $\hat{p} = 0$ always lies in this interval, $p = 1 - m/c \geq 0$ only if $m/c \leq 1$, that is, if $m \leq c$ (since $m \geq 0$ and $c \geq 0$, we certainly have $\hat{p} \leq 1$).

Thus there are three cases: If $m > c$, then there is only one equilibrium in $[0, 1]$. If $m < c$, then there are two distinct equilibria in $[0, 1]$. There is also a borderline case $m = c$ in which the two roots of $g(p) = 0$ coincide at $\hat{p} = 0$.

We draw the vector field plots corresponding to each of the cases in Figure 8.38. In the plots we have drawn $g(p)$ over a large enough interval to show both roots, but you should remember that the domain of p is always $[0, 1]$.

From the vector field plots we see that if $m \geq c$, then all solutions converge to 0, whatever the initial condition on p (remember $0 \leq p(0) \leq 1$). But if $m < c$, then the equilibrium $\hat{p} = 1 - m/c$ is stable, and $\hat{p} = 0$ is unstable. Thus $p(t) = 0$ and $p(t) = 1 - m/c$ are constant solutions. But if $p(0) > 0$, then $p(t)$ will either grow or decrease monotonically until it converges to $1 - m/c$. We show the different behaviors of $p(t)$ in these two cases in Figure 8.39.

We can interpret the two types of behaviors biologically. When $m \geq c$, mortality removes subpopulations faster than they can be replaced by colonization, so the subpopulations die out faster than sites can be recolonized; eventually all subpopulations die out. If $m < c$, then although subpopulations are continuously lost, the sites are then recolonized, maintaining a stable number of subpopulations. At the stable equilibrium the proportion of sites that are occupied is $\hat{p} = 1 - m/c$. This is always less than 1 (i.e., colonization cannot keep all sites filled), but is closer to 1 if m/c is small; that is, if either the mortality rate, m, is small, or the colonization rate, c, is large.

8.3.3 Modeling a Chemical Reaction

Now we will revisit the mass action laws that were introduced in Section 4.2. Suppose we want to build a mathematical model for a chemical reaction in which two reactants (A and B) combine to form a product (C).

$$A + B \to C$$

In Section 4.2 we argued that this reaction will proceed until either A or B is completely used up. What if the reaction is reversible; that is, C can also break down spontaneously back into A and B? We represent the reaction and the two rates (for the

forward and backward reactions) by:

$$A + B \underset{k_C}{\overset{k_{AB}}{\rightleftarrows}} C$$

where k_{AB} is the rate constant for the reaction between A and B, and k_C is the rate at which C breaks down.

Suppose that the initial amount of A present is a (this could be a total amount; e.g., measured in moles, or concentration) and the amount of B initially is b. Let x denote the amount of C present at time t. Then we derive a mathematical equation for the rate of change of x from the word equation:

$$\text{Rate of change of } x = \text{Rate at which } C \text{ is produced by } A + B \to C - \text{Rate at which } C \text{ is consumed by } C \to A + B$$

The $A + B \to C$ reaction produces C at rate $k_{AB}[A][B]$ (remember from Section 4.2 that $[A]$ denotes the amount of A present). But to produce an amount x of C, the same amount of A must be consumed, so $[A] = a - x$. Similarly $[B] = b - x$. So C is produced at a rate $k_{AB}(a - x)(b - x)$.

The reverse reaction consumes C at a rate $k_C x$. So

$$\frac{dx}{dt} = k_{AB}(a - x)(b - x) - k_C x.$$

To find the equilibria of this differential equation we can set $g(x) = k_{AB}(a-x)(b-x) - k_C x$ and use the quadratic formula to find the roots of $g(x) = 0$. However, even without knowing the precise values of the roots we can use a vector field plot to determine how many equilibria there are and to determine their stability. First, though, we need to establish the domain of x for this plot. Since $[A]$, $[B]$, $[C]$ all represent amounts of chemicals, they must all be non-negative; this constraint means that we must have $a - x \geq 0$, $b - x \geq 0$, and $x \geq 0$. To satisfy all of these constraints we must have:

$$0 \leq x \leq \min(a, b)$$

which generalizes the condition that we derived in Section 1.3, Example 5.

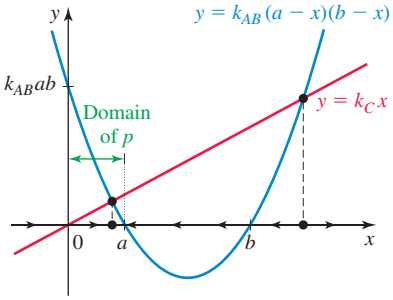


Figure 8.40 The curves $y = k_{AB}(a - x)(b - x)$ and $y = k_C x$ have two points of intersection, including one stable equilibrium with $0 < x < a$.

To identify equilibria in this interval we will use the method from Section 8.2.3 of separately plotting the two parts of $g(x)$ (i.e., make plots of $f(x) = k_{AB}(a - x)(b - x)$ and $h(x) = k_C x$ and look for points of intersection). For our plot we will assume that $a < b$ (in Problem 25, you will investigate what modifications are necessary if $a > b$ or $a = b$).

The function $f(x) = k_{AB}(a - x)(b - x)$ has roots $x = a$ and $x = b$, and $\lim_{x \to \pm\infty} f(x) = +\infty$, since the largest degree term is $k_{AB}x^2$ and $k_{AB} > 0$. So the function is a concave up parabola. $f(x)$ is a decreasing function of x over the interval $0 \leq x \leq a$, starting at $k_{AB}ab$ when $x = 0$ and decreasing to 0 when $x = a$. By contrast, $h(x) = k_C x$ is an increasing function of x on the same interval starting at $h(0) = 0$ and increasing to $h(a) = k_C a$. Thus, the two functions must intersect at exactly one point in the interval $0 < x < a$, meaning that there is a single equilibrium value $\hat{x}$. The vector field plot of the differential equation is given in Figure 8.40. From the vector field plot we see that the equilibrium is stable; and in fact, whatever the initial amount of x is, $x(t) \to \hat{x}$ as $t \to \infty$. A sketch of these solutions are shown in Figure 8.41.

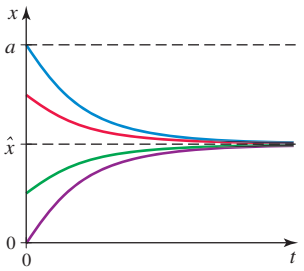


Figure 8.41 Concentration for C over time starting with different initial conditions.

The graphical method also allows us to determine how the equilibrium value, $\hat{x}$, varies as the parameters in the differential equation are changed. We will focus on the effect of varying the rate constants k_{AB} and k_C. Increasing k_{AB} dilates the curve $y = f(x)$ in the vertical direction (Figure 8.42). Since increasing k_{AB} increases $f(x)$ for all $x \in [0, a)$, the point of intersection, $\hat{x}$, between $y = f(x)$ and $y = h(x)$ moves rightward toward $x = a$ (see Figure 8.42). The change in $\hat{x}$ makes sense chemically, because as k_{AB} increases, C is produced at faster and faster rates. But the rate of decay of C back into A and B is left unaffected. So the concentration of C, at which rate of production of C equals decay, increases.

What about changing k_C? If we increase k_C, then the curve $y = k_C x$ gets steeper. It therefore intersects $y = k_{AB}(a - x)(b - x)$ at smaller and smaller values of x

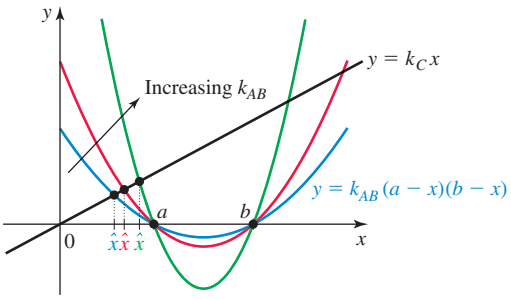


Figure 8.42 Increasing k_{AB} increases $\hat{x}$, the equilibrium amount of C.

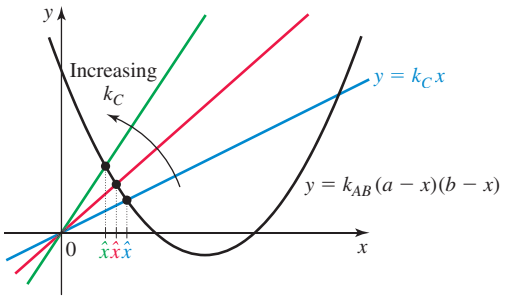


Figure 8.43 Increasing k_C decreases the equilibrium amount of C.

(see Figure 8.43), that is, the equilibrium value of x gets smaller and smaller. Again there is a chemical interpretation of this behavior: Increasing k_C increases the rate at which C decomposes back into A and B. Since the rate of production of C is unaffected, the equilibrium amount of C decreases.

8.3.4 The Evolution of Cooperation

Many organisms cooperate to perform tasks that they could not achieve working individually. For example, the cells in the human body cooperate to process food, fight off infection, and move the body around. An ant colony may contain millions of ants that work together to raise young, gather food, and defend the nest. Cooperation can also occur between different species. The health of a plant depends on **symbiotic** interactions between the plant and bacteria and fungi that the plant harbors in its root system. Despite the frequency with which it occurs, cooperation is also a paradoxical biological process. When two organisms cooperate they both contribute to a common good, but these contributions may be costly to each. For example, if a worker ant in a colony devotes her life to building the nest or defending it, she loses the opportunity to have offspring of their own. In many cooperative arrangements, the cooperating organisms are related (e.g., ants in a nest may all be sisters, born to the same queen); and so contributing to the common good may indirectly benefit each organism's genes, since these genes are shared by the organisms that they cooperate with. However, in cases where the two partners are not related we could imagine one of the organisms allowing the other to contribute to the common good but not doing so itself. That way, the organism that cheats (i.e., chooses not to cooperate) receives the benefit of cooperation but does not pay any cost. The cooperative organism pays all of the cost of cooperating.

One method for modeling these kinds of interactions is through **evolutionary game theory**. The model that we will give in this section is adapted from ***Nowak (2006)***. Imagine a population of organisms playing what evolutionary biologists call a **snowdrift game**. In this game there are two types of organisms: **cooperators** and **cheaters**. When two cooperators meet they cooperate; that is, the two organisms work together so each pays a cost $c/2$ and receives a benefit b. When a cooperator meets a cheater, then the cooperator contributes but the cheater doesn't. In that case the cooperating organism pays a cost c, and the cheating organism pays no cost. So long as one organism cooperates, the organisms still receive a benefit b.

> Bio Info • The name **snowdrift game** is used because biologists consider this form of cooperation to be analogous to two people driving on a snowy street who find themselves blocked by the same snowdrift. The benefit of shoveling through the snowdrift to each driver (i.e., getting home) is b independent of whether that driver helped to clear the snowdrift. The total cost of clearing the snowdrift so that each may drive home is c. If one person clears the snowdrift unassisted, that individual pays the entire cost, c, but if both work together they split the cost equally between them (i.e., each pays cost $c/2$). In this scenario a cooperator is one who shovels the snowdrift. A cheater, on the other hand, sits in their car, listening to

the radio, and staying warm, while the other driver shovels. You shouldn't imagine literal snowdrifts, however. Consider, for example, a plant that interacts with a fungus or bacterium in the soil. The soil fungus or bacterium can cooperate by providing the plant with nitrogen that the plant itself cannot extract from the soil. The plant cooperates by sharing with the bacterium sugars that it creates by photosynthesis. A cheating bacterium would take sugars, but not provide any nitrogen in return, while a cheating plant might take nitrogen but not provide any sugars in return.

Thus we may model the interaction by using a **pay-off matrix** that represents the net benefit each organism gets from the interaction. If we think of one organism as a player in a game, and the other organism as its opponent, then the entries in the table tell us what net return (benefit minus cost) the *player* receives from the interaction. The opponent's pay-off is not represented in the pay-off matrix.

		Opponent	
		Cooperate	Cheat
Player	Cooperate	$b - c/2$	$b - c$
	Cheat	b	0

As we can see from the table, if the opponent is a cooperator, then a player who cheats will receive a higher pay-off than a player who cooperates. But if the opponent is a cheater, then depending on whether $b > c$ or $b < c$, a cooperator may receive higher pay-off than a cheater. **Evolutionary game theory** models the effects of these different strategies on the numbers of organisms playing the game.

Imagine that we have a (large) population of N organisms, a fraction x of which are cooperators, and a fraction y of which are cheaters. In each unit of time, each organism (whether it is a cooperator or a cheater) interacts with n other organisms, which are randomly chosen (that is, a cooperator cannot choose to interact only with other cooperators; see Problem 35 for a discussion of what can occur if cooperators are able to choose whom to interact with). From each interaction it receives a payoff that can be calculated from the payoff matrix. For each organism the rate of births is proportional to the net payoff from all of its interactions with other organisms. The offspring of a cooperator organism are all cooperators, and the offspring of a cheater are all cheaters. However, we also assume that the habitat that the organisms share is at its carrying capacity. This means that for each birth that occurs, another organism must die to maintain the total size of the population at N. All organisms (cheaters and cooperators) are equally likely to die. Assume that the death rate is m for both types of organism. Figure 8.44 summarizes how the population changes from step to step.

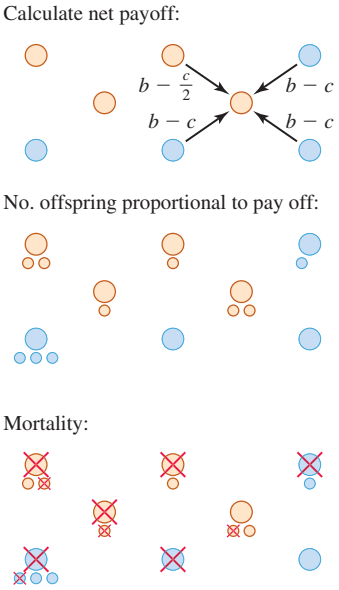


Figure 8.44 Evolutionary snowdrift game. A population contains both cheaters (blue) and cooperators (red). Each organism plays a snowdrift game with n other organisms receiving a pay-off from each game. The organism has a number of offspring proportional to its total pay-off. Organisms then die to keep population size constant.

So we can write down word equations for the rate at which the cooperator and cheater populations grow or decrease.

$$\begin{array}{c}\text{Rate of change}\\ \text{of number of}\\ \text{cooperators}\end{array} = \begin{array}{c}\text{Rate of}\\ \text{cooperator}\\ \text{births}\end{array} - \begin{array}{c}\text{Rate of}\\ \text{cooperator}\\ \text{deaths}\end{array}$$

Since x denotes the proportion of organisms that are cooperators and y represents the proportion that are cheaters, the total number of cooperators is Nx, and the total number of cheaters is Ny.

The rate of change of the number of cooperators is:

$$\frac{d}{dt}(Nx)$$

Since a fraction m of all organisms die in one unit of time, the rate of cooperator deaths is $m\times$ number of cooperators $= mNx$.

Thus:

$$\frac{d(Nx)}{dt} = \begin{array}{c}\text{Rate of cooperator}\\ \text{births}\end{array} - mNx \qquad (8.42a)$$

Similarly the word equation for the rate of change of the cheater population is:

$$\begin{array}{c}\text{Rate of change}\\ \text{of cheater}\\ \text{population}\end{array} = \begin{array}{c}\text{Rate of}\\ \text{cheater}\\ \text{births}\end{array} - \begin{array}{c}\text{Rate of}\\ \text{cheater}\\ \text{deaths}\end{array}$$

which can be rewritten as:

$$\frac{d}{dt}(Ny) = \text{Rate of cheater births} - mNy. \tag{8.42b}$$

To complete our derivation we need mathematical expressions for the birth rates that appear in Equations (8.42a) and (8.42b). To derive these expressions let's first consider the average payoff that a cooperator receives in one unit of time. In that time it interacts with n other organisms. On average, since a fraction x of those organisms are cooperators and y are cheaters, a single cooperator will interact with nx cooperators and ny cheaters. Its payoff from each cooperator is $b - c/2$, and its payoff from each cheater is $b - c$. So the total payoff from all n interactions is:

$$\begin{array}{c}\text{Payoff}\\ \text{to cooperator}\end{array} = \begin{array}{c}\text{Number of cooperators}\\ \text{interacted with}\end{array} \times \begin{array}{c}\text{Payoff from}\\ \text{interacting}\\ \text{with cooperator}\end{array} + \begin{array}{c}\text{Number of cheaters}\\ \text{interacted with}\end{array} \times \begin{array}{c}\text{Payoff from}\\ \text{interacting with}\\ \text{a cheater}\end{array}$$

$$= nx \cdot (b - c/2) + ny \cdot (b - c)$$

The number of offspring this individual will have is proportional to its total payoff. Let the constant of proportionality be k. Then

$$\text{Number of offspring per cooperator} = k \times \text{ total payoff}$$

$$= k \cdot n\,(x(b - c/2) + y(b - c))$$

So:

$$\begin{array}{c}\text{Rate of}\\ \text{cooperator births}\end{array} = \text{Number of cooperators} \times \begin{array}{c}\text{Number of offspring per}\\ \text{cooperator}\end{array}$$

$$= Nx \cdot kn\,(x(b - c/2) + y(b - c))$$

We can calculate similarly the birth rate of cheaters, by first calculating the total payoff to each cheater in one unit of time.

$$\begin{array}{c}\text{Total payoff}\\ \text{to cheater}\end{array} = \begin{array}{c}\text{Number of cooperators}\\ \text{interacted with}\end{array} \times \begin{array}{c}\text{Payoff from}\\ \text{interacting}\\ \text{with a cooperator}\end{array} + \begin{array}{c}\text{Number of cheaters}\\ \text{interacted with}\end{array} \times \begin{array}{c}\text{Payoff from}\\ \text{interaction}\\ \text{with a cheater}\end{array}$$

$$= nx \cdot b + ny \cdot 0$$

$$= nx \cdot b$$

Hence

$$\text{Rate of cheater births} = \text{Number of cheaters} \times \text{Birth rate per cheater}$$

$$= Ny \cdot knxb \qquad \text{Birth rate per cheater} = k\times \text{ Payoff to each cheater}$$

Equations (8.42a) and (8.42b) can now be written as mathematical formulas:

$$\frac{d(Nx)}{dt} = Nxkn\,(x(b - c/2) + y(b - c)) - mNx$$

and

$$\frac{d(Ny)}{dt} = Nyknxb - mNy$$

or on rearranging some of the terms:

$$\frac{dx}{dt} = knx\,(x(b - c/2) + y(b - c)) - mx \qquad \begin{array}{l}N \text{ is a constant, and can be}\\ \text{cancelled from both sides.}\end{array} \tag{8.43}$$

$$\frac{dy}{dt} = knyxb - my \tag{8.44}$$

The mortality rate, m, appears not to have been specified. But we can use Equations (8.43) and (8.44) to calculate m. The total rate of births must match the total rate of deaths, to keep the population size constant. Alternatively, since each organism can only be one of the two types (cheater or cooperator), we must have $x + y = 1$. Thus

$$\frac{dx}{dt} + \frac{dy}{dt} = \frac{d}{dt}(x + y) = \frac{d}{dt}(1) = 0.$$

And substituting in our expressions for dx/dt and dy/dt from (8.43) and (8.44) into this equation, we obtain:

$$knx\,(x(b - c/2) + y(b - c)) + knyxb - m(x + y) = 0$$

or

$$m(x + y) = knx\,(x(b - c/2) + y(2b - c)) \qquad \text{Isolating term in } m$$

so:

$$m = knx(b - c/2)(x + 2y) = knx(b - c/2)(1 + y) \qquad x + y = 1, \text{ and factorize out } (b - c/2)$$

From this equation we see that it is essential that $b - c/2 \geq 0$. Otherwise, $m < 0$ (i.e., we have negative mortality rate). The biological rationale for this inequality is that if $b - c/2 < 0$, then cooperators always receive negative payoffs, even from interacting with other cooperators. There is clearly no incentive in this case to cooperate.

Thus, substituting for m in (8.43) and (8.44), we obtain

$$\frac{dx}{dt} = knx\Big(x(b - c/2) + y(b - c) - (b - c/2)x(1 + y)\Big)$$

$$\frac{dy}{dt} = kny\Big(bx - (b - c/2)x(1 + y)\Big)$$

or

$$\frac{dx}{dt} = knxy\,(-(b - c/2)x + (b - c)) \tag{8.45}$$

and

$$\frac{dy}{dt} = knxy\left(\frac{c}{2} - (b - c/2)y\right) \tag{8.46}$$

Initially it may appear that we have to solve two differential equations; one for $x(t)$ and one for $y(t)$. But if we know x, then we can obtain y as $1 - x$, without needing to solve a second differential equation. So we only need to analyze one of the equations. Let's study the equation for $x(t)$ (i.e., (8.45)), which can be written as $\frac{dx}{dt} = g(x)$, where

$$g(x) = knx(1 - x)\Big((b - c) - (b - c/2)x\Big) \text{ and } 0 \leq x \leq 1 \qquad \text{Set } y = 1 - x \text{ in (8.45).}$$

This is a single autonomous differential equation, so we can analyze it using the methods from Section 8.2. To find the equilibria observe $g(\hat{x}) = 0$ if $\hat{x} = 0$, or $\hat{x} = 1$, or $\hat{x} = \frac{(b-c)}{(b-c/2)}$, assuming that $b \neq c/2$. You will analyze the case $b = c/2$ in Problem 31. We will assume that $b > c/2$. The first two roots certainly lie in the interval $0 \leq x \leq 1$. Whether the other root does or doesn't depends on the values of b and c. In order for the third root to lie in the interval we must have

$$0 \leq \frac{b - c}{b - c/2} \leq 1 \tag{8.47}$$

To analyze these inequalities we must multiply all sides by $b - c/2$. Since we are assuming that $b > c/2$, we do not need to reverse any of our inequalities if we multiply all three parts of the inequality by $b - c/2$. So (8.47) is satisfied if

$$0 \leq \quad b - c \quad \leq b - c/2$$

The inequality $b - c \leq b - c/2$ is automatically satisfied if $c > 0$. Thus the equilibrium $x = \frac{b-c}{b-c/2}$ lies in $[0, 1]$, provided $b \geq c$. Hence, if $b > c$, there are three equilibria in $[0, 1]$, at $x = 0, x = 1$, and $x = \frac{b-c}{b-c/2}$. If $\frac{c}{2} < b < c$, then there are two equilibria in $[0, 1]$, at $x = 0$ and $x = 1$.

Which of these equilibria are stable? We will use the derivative test to decide:

$$\begin{aligned} g'(x) &= kn(1-x)\Big((b-c)-(b-c/2)x\Big) \\ &\quad - knx\Big((b-c)-(b-c/2)x\Big) \\ &\quad - kn(b-c/2)x(1-x) \qquad \text{Using product rule} \end{aligned}$$

So:

$$\begin{aligned} g'(0) &= kn(b-c) \qquad g'(0) > 0 \text{ if } b > c \\ g'(1) &= knc/2 \qquad g'(1) > 0 \end{aligned}$$

and

$$\begin{aligned} g'\left(\frac{b-c}{b-c/2}\right) &= -kn(b-c/2)\left(\frac{b-c}{b-c/2}\right)\left(1-\frac{b-c}{b-c/2}\right) \\ &= -\frac{kn(b-c)c/2}{b-c/2} \qquad 1-\tfrac{b-c}{b-c/2} = \tfrac{c/2}{b-c/2} \\ &= -\frac{knc}{2}\left(\frac{b-c}{b-c/2}\right) \end{aligned}$$

So, if $c/2 < b < c$, then there are two equilibria in the interval at $\hat{x} = 0$ and $\hat{x} = 1$. The equilibrium $\hat{x} = 0$ is stable (since $g'(0) < 0$) and $\hat{x} = 1$ is unstable (since $g'(1) > 0$). The vector field plot is shown as Figure 8.45, and possible solutions are drawn in Figure 8.46.

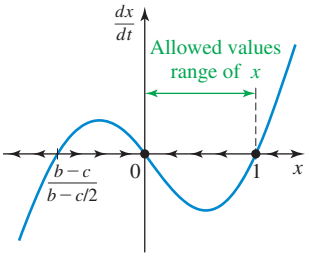


Figure 8.45 The vector field plot for the snowdrift game if $c/2 < b < c$.

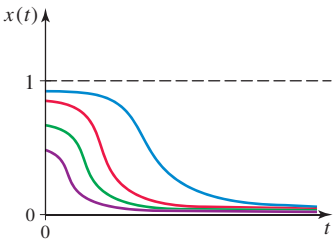


Figure 8.46 If $c/2 < b < c$, then unless $x(0) = 1$, $x(t) \to 0$ as $t \to \infty$.

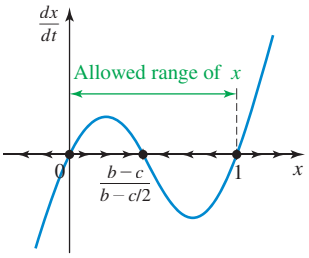


Figure 8.47 The vector field plot for the snowdrift game if $b > c$.

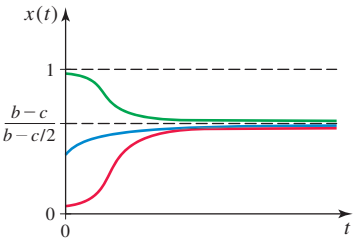


Figure 8.48 If $b > c$, unless $x(0) = 0$ or $x(0) = 1$, all solutions of the snowdrift game converge to the stable fixed point $x(t) = \frac{b-c}{b-c/2}$

Conversely, if $b > c$, there are three equilibria in the interval at $\hat{x} = 0$, $\hat{x} = \frac{b-c}{b-c/2}$, and $\hat{x} = 1$. The equilibria $\hat{x} = 0$ and $\hat{x} = 1$ are both unstable, and $\hat{x} = \frac{b-c}{b-c/2}$ is stable. The vector field plot of the differential equation is shown in Figure 8.47 and possible solutions in Figure 8.48.

Can we interpret these different behaviors biologically? First we have imposed a condition that $b > c/2$. This inequality ensures that, when two cooperators interact, their payoff $(b - c/2)$ is larger than the payoff received by two cheaters that interact (0). Unless this condition is met, there is no incentive to cooperate. If, in addition, $b < c$, when a cooperator meets a cheater, the cooperator receives a negative payoff $(b - c < 0)$, while the cheater receives a positive payoff. The ability of cheaters to take advantage of cooperators means that according to our model, cheaters will always eventually take over the entire population since $x(t) \to 0$ as $t \to \infty$, meaning that the proportion of cheaters, $y(t) \to 1$. Cooperation can be exploited by cheaters who enjoy the benefit of cooperation without paying the cost, so cooperators are eventually driven extinct. The one exception to this is if $x(0) = 1$, in which case $x(t) = 1$ for all t. If a population starts with no cheaters present $(y(0) = 0)$, then no cheaters will ever appear (since the only way a cheater can be added is when another cheater reproduces). Our analysis shows that even if the starting number of cheaters is very small, they will still eventually drive the cooperators extinct.

If, on the other hand, $b > c$, then when a cooperator and a cheater interact, the cooperator still receives a positive payoff $(b - c > 0)$, although the payoff to the cheater is larger. In an initially mixed population (that is, provided $x(0) \neq 0$ or 1), neither cheaters nor cooperators go extinct, but instead achieve some equilibrium $\hat{x} = \frac{b-c}{b-c/2}$. Notice that for larger values of b (in particular if $b \gg c$), $\hat{x}$ will be close to 1 (i.e., there will be a higher proportion of cooperators in the population's stable equilibrium).

8.3.5 Epidemic Model

Mathematical models can be used to predict disease outbreaks. Models for the spread of disease can provide critical information for efforts to control a disease. For example ***Fisman, Khoo, and Tuite (2014)*** built a mathematical model to predict the rate of growth of an Ebola epidemic in West Africa, and to show that the control measures in place at that time were not enough to stop the disease from continuing to spread.

We will study disease spread in depth in Chapter 11. In this subsection we will introduce a type of model that can be used to predict the spread of a rapidly evolving disease, like the common cold. Colds are caused by several different kinds of viruses that spread by touch, or through droplets that are produced when a person sneezes.

For our model we will consider how a cold spreads through a population of N people. We divide people into two classes: susceptible individuals (who don't currently have a cold) and infected individuals (who are currently sick with a cold). If a susceptible individual catches a cold, they are moved into the infected population. If an infected individual fights off their cold, then they re-enter the susceptible population. Let $S(t)$ represent the number of susceptible people at time t and $I(t)$ the number of infected people at that time. We write down word equations for the rate of change of $S(t)$ and $I(t)$ as follows:

$$\begin{pmatrix}\text{Rate of change of}\\ \text{no. susceptibles}\end{pmatrix} = \begin{pmatrix}\text{Rate at which}\\ \text{infected individuals}\\ \text{recover}\end{pmatrix} - \begin{pmatrix}\text{Rate at which}\\ \text{susceptible individuals}\\ \text{are infected}\end{pmatrix}$$

$$\begin{pmatrix}\text{Rate of change of}\\ \text{no. infected}\end{pmatrix} = \begin{pmatrix}\text{Rate at which}\\ \text{susceptibles}\\ \text{are infected}\end{pmatrix} - \begin{pmatrix}\text{Rate at which}\\ \text{infected individuals}\\ \text{recover}\end{pmatrix}$$

We must now derive mathematical expressions for the rates appearing in these equations. The left-hand sides are respectively dS/dt and dI/dt.

At time t there are $I(t)$ infected individuals. Let's assume that in one unit of time a fraction c of these individuals recover. Then:

$$\begin{pmatrix}\text{Rate at which}\\ \text{infected individuals}\\ \text{recover}\end{pmatrix} = \begin{pmatrix}\text{No. infected}\\ \text{individuals}\end{pmatrix} \times \begin{pmatrix}\text{Fraction that}\\ \text{recover}\end{pmatrix} = I(t)\cdot c$$

We call the coefficient c the **recovery rate**. It depends on the disease that is being studied. For example, the recovery rate for the common cold is typically around $c = 0.3$/day.

The model for infection is a little more involved. Assume that the disease can only be transmitted by direct contact between individuals (e.g., by handshakes, or when they are close enough that one inhales the droplets produced by the other's sneezes). Suppose that in one unit of time each individual comes into contact with b other individuals. We assume that the likelihood that a susceptible individual will become infected is proportional to the number of infected individuals they come into contact with. Of the b individuals, each susceptible individual contacts, a fraction $\frac{I(t)}{N}$ will be infected, and a fraction $\frac{S(t)}{N}$ will not. So;

$$\begin{pmatrix}\text{Likelihood that}\\ \text{susceptible individual}\\ \text{gets infected}\end{pmatrix} = \begin{pmatrix}k\times\text{ No.}\\ \text{infected individuals}\\ \text{contacted in unit time}\end{pmatrix} = k\times\frac{bI}{N}$$

where k is a constant of proportionality. So total rate of infection is given by

$$\begin{pmatrix}\text{Rate at which susceptibles}\\ \text{are infected}\end{pmatrix} = \text{No. susceptibles}\times\begin{pmatrix}\text{Likelihood susceptible}\\ \text{individual is infected}\\ \text{in one unit of time}\end{pmatrix}$$

$$= S(t)\times kb\frac{I(t)}{N} = \frac{kb}{N}S(t)I(t).$$

Putting these ingredients together, we obtain differential equations

$$\begin{aligned}\frac{dS}{dt} &= cI - \frac{kb}{N}SI\\ \frac{dI}{dt} &= \frac{kb}{N}SI - cI\end{aligned} \tag{8.48}$$

In these equations c, k, b, and N are all positive constants that allow the model to be used to represent different diseases and different populations.

At first look the equations in (8.48) appear very different from the equations we have previously analyzed because there are two dependent variables (S and I). We cannot solve the differential equation for $I(t)$ unless we know $S(t)$, and we cannot solve the differential equation for $S(t)$ unless we know $I(t)$. How can we proceed? A general method for analyzing systems of differential equations like (8.48) will be introduced in Chapter 11. But in this case we note that all individuals are either susceptible or infected. So:

$$S(t) + I(t) = N \tag{8.49}$$

Hence, if we know $I(t)$ at any time then we can calculate $S(t)$ from (8.49). Using (8.49) to substitute for $S(t)$ in the second equation from (8.48), we obtain:

$$\frac{dI}{dt} = \frac{kb}{N}(N - I)I - cI$$

Or:

$$\frac{dI}{dt} = (kb - c)I - \frac{kb}{N}I^2 \tag{8.50}$$

This is a single autonomous differential equation so we can analyze the solutions using the methods from Section 8.2. There are two potential equilibria: at $\hat{I} = 0$ and at $\hat{I} = \frac{(kb-c)N}{kb} = N\left(1 - \frac{c}{kb}\right)$. We call these values of $\hat{I}$ potential equilibria because in addition to satisfying (8.50), $I(t)$ must satisfy inequalities.

$$0 \le I(t) \le N$$

$\hat{I} = 0$ certainly satisfies these inequalities. The second equilibrium, $\hat{I} = N\left(1 - \frac{c}{kb}\right)$ is certainly less than N (c, k, and b are all positive numbers). But if $kb < c$, then $\hat{I} < 0$, while if $kb > c$, then $\hat{I} > 0$. There are therefore two cases to consider.

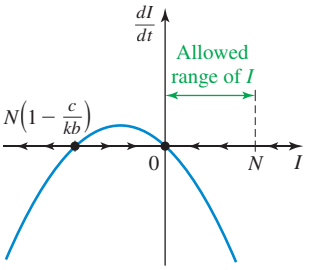


Figure 8.49 Vector field plot for (8.50) if $kb < c$.

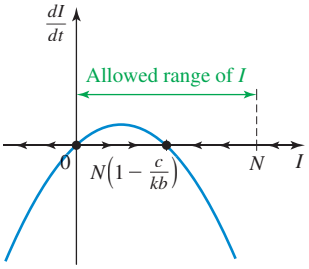


Figure 8.50 Vector field plot for (8.50) if $kb > c$.

If $kb < c$, then the only equilibrium in $[0, N]$ is $\hat{I} = 0$; the vector field plot for Equation (8.50) then shows that $\hat{I} = 0$ is a stable equilibrium (see Figure 8.49). So no matter what the initial number of infected individuals, $I(t) \to 0$ as $t \to \infty$; that is, the disease runs its course and disappears.

If, on the other hand, $kb > c$, then there are two equilibria to be considered. $\hat{I} = 0$ and $\hat{I} = \left(1 - \frac{c}{kb}\right)N$. The equilibrium $\hat{I} = 0$ is unstable, while $\hat{I} = (1 - \frac{c}{kb})N$ is stable. (see the vector field plot in Figure 8.50). $\hat{I} = 0$ is an equilibrium, because if there are initially no infected individuals (i.e., the disease is not present in the population), then no individuals will ever get sick, according to our model. However, our model now predicts that unless $I(0) = 0$, $I(t) \to \left(1 - \frac{c}{kb}\right)N$ as $t \to \infty$. That is, the disease persists in the population at some stable level. In this case we say that the disease has become **endemic**.

We can interpret the condition for determining whether a disease becomes endemic or disappears biologically. A disease will become endemic if $kb > c$, that is, if either k is large, or b is large, or c is small; in other words, if each individual has many contacts with others per unit time (large b), if these contacts have a high chance of passing the disease on (large k), or if the disease takes a long time to recover from (small c).

Section 8.3 Problems

8.3.1

1. In Section 8.3.1 we introduced single-compartment models for the motion of matter through a single tank of water. We derived an equation:

$$\frac{dC}{dt} = \frac{q}{V}(C_I - C) \tag{8.51}$$

for the concentration of solute in the tank, $C(t)$. We analyzed this equation graphically. Now let's solve the equation to confirm our analysis.

Assume that $C(0) = C_0$

(a) Solve (8.51) and use your solution to show that $C(t) \to C_I$ as $t \to \infty$, for any value of C_0.

(b) Explain how your solution from part (a) predicts that larger values of q/V lead to faster convergence of $C(t)$ to C_I, and smaller values of q/V lead to slower convergence.

2. Assume the single-compartment model defined in Section 8.3.1; that is, denote the concentration of the solute at time t by $C(t)$, and assume that

$$\frac{dC}{dt} = 3(20 - C(t)) \quad \text{for } t \ge 0 \tag{8.52}$$

(a) Solve (8.52) when $C(0) = 5$.

(b) Find $\lim_{t\to\infty} C(t)$.

(c) Use your answer in (a) to determine t so that $C(t) = 10$.

3. Use the single-compartment model defined in Section 8.3.1; that is, denote the concentration of the solution at time t by $C(t)$, and assume that the concentration of the incoming solution is 3 g liter^{-1} and the rate at which mass enters is 0.2 liter s^{-1}. Assume, further, that the volume of the compartment $V = 400$ liters.

(a) Find the differential equation for the rate of change of the concentration at time t.

(b) Find all equilibria of the differential equation and discuss their stability.

(c) Solve the differential equation in (a) when $C(0) = 0$, and find $\lim_{t\to\infty} C(t)$.

4. Suppose that a tank holds 1000 liters of water, and 2 kg of salt is poured into the tank.

(a) Compute the concentration of salt in g liter^{-1}.

(b) Assume now that you want to reduce the salt concentration. One method would be to remove a certain amount of the salt water from the tank and then replace it by pure water. How much salt water do you have to replace by pure water to obtain a salt concentration of 1 g liter^{-1}?

(c) Another method for reducing the salt concentration would be to hook up an overflow pipe and pump pure water into the tank. That way, the salt concentration would be gradually reduced. Assume that you have the choice of two pumps, one that pumps water at a rate of 1 liter s^{-1}, the other at a rate of 2 liter s^{-1}. For each pump, find out how long it would take to reduce the salt concentration from the original concentration to 1 g liter^{-1}. (Note that the rate at which water enters the tank is equal to the rate at which water leaves the tank.)

(d) Show that, whichever pump you use in part (c), you need more pure water if you use the pump method than if you follow the method in (b). Can you explain why?

5. Osmosis Through a Cell Membrane A cell constantly gains or loses small molecules to its environment because the small molecules are able to diffuse through the cell membrane. We will build a model for this process.

Suppose a molecule is present in the cell at a concentration $C(t)$, and present in its environment at a concentration C_∞ (you may assume C_∞ is a constant). One model for the diffusion of molecules across the cell membrane is that the rate at which molecules travel through the membrane is proportional to the difference in concentration between the cell and its surroundings. That is:

$$\begin{array}{c}\text{Rate at which}\\ \text{molecules flow out}\\ \text{of cell}\end{array} = k(C - C_\infty)$$

The constant k is known as the **permeability of the membrane**; $k > 0$, and k depends on the surface area of the cell and the chemistry of the membrane, as well as the type of molecule.

(a) Starting with a word equation for the amount of small molecules in the cell, show, if the cell volume is V, then:

$$\frac{dC}{dt} = -\frac{k}{V}(C - C_\infty) \tag{8.53}$$

(b) Find the equilibrium of (8.53) and use a graphical analysis to determine whether it is stable or unstable.

(c) Suppose that the molecule we are studying is produced within the cell. The cell produces the molecule at a rate r; that is, a quantity r is produced (added to the cell) in unit time. Explain why the differential equation for the concentration of molecules in the cell should be modified to:

$$\frac{dC}{dt} = -\frac{k}{V}(C - C_\infty) + \frac{r}{V} \tag{8.54}$$

(d) Analyze Equation (8.54) to find the equilibrium value of the cell concentration. Is this equilibrium stable or unstable? You may use a graphical argument or calculate the eigenvalue to determine the equilibrium's stability.

6. Chemostat A chemostat is a device that can be used to maintain a constant concentration of a chemical in a chamber.

Consider a chemostat consisting of a chamber of volume V and containing a concentration $C(t)$ of the chemical.

(a) Initially we will neglect inflows and outflows in the chamber. The chemical breaks down at a fractional rate p; that is, a proportion p of the chemical contained in the chamber is broken down in unit time. Explain why the concentration of the chemical must obey a differential equation

$$\frac{dC}{dt} = -pC \tag{8.55}$$

(b) By analyzing (8.55) determine the long-term behavior of $C(t)$; that is, find $\lim_{t\to\infty} C(t)$. (You can do this using the methods from Section 8.2. There is no need to solve the differential equation.)

(c) To maintain the concentration $C(t)$ of the chemical, at some desired concentration, fresh chemical is continuously added to the chamber. This is accomplished by adding fluid containing the chemical to the chamber continually at a rate q, and removing fluid from the chamber at the same rate. Show that if the concentration of chemical in the fluid being added to the chamber (the "inflow") is C_I, then:

$$\frac{dC}{dt} = \frac{q}{V}(C_I - C) - pC \tag{8.56}$$

(d) By analyzing (8.56) find the equilibrium concentration of chemical in the chamber as a function of q, V, C_I, and p. Determine whether the equilibrium is stable or unstable.

(e) Suppose $p = 0.2$/hr, $q = 1$ ml/hr, and $V = 10$ ml. If we want to maintain $C(t)$ at 5 g/liter, what should the concentration C_I of chemical in the inflow be?

7. The stability of the equilibrium concentration in a single compartment is often quantified using T_R, which is called the *time to return to equilibrium*. Suppose that the equilibrium concentration is C_0. Then, to measure T_R, perturb the concentration slightly, from C_0 to $C_0 + C_1$. Then T_R is defined to be the time that the tank takes for the perturbation to drop to a factor $\frac{1}{e}$ of its initial value (i.e., for $C(t)$ to drop from $C_0 + C_1$ to $C_0 + \frac{C_1}{e}$).

If the single compartment obeys the single-compartment differential Equation (8.45):

(a) Show that $T_R = V/q$.

(b) Suppose, instead of defining T_R by the time taken for the concentration to drop to $C_0 + C_1/e$, we choose a fraction p, $(p < 1)$, and define T_R to be the time taken for the concentration to drop to $C_0 + pC_1$. Calculate T_R in terms of V, q, and p.

8. Insulin Pump Insulin pumps treat patients with type I diabetes by releasing insulin continuously into the fat in the patient's stomach or thigh. We will develop a model for the transport of insulin from the site where it is released by the pump, by treating the fat as a compartment in a single-compartment model. Let's suppose that the pump releases insulin at a constant rate, r (r is the amount added in one unit of time).

(a) Explain why, if insulin is not transported from the site of release, the amount of insulin at the site of release, $a(t)$, will obey a differential equation:

$$\frac{da}{dt} = r.$$

(b) From the fat, the insulin enters the patient's bloodstream. Suppose that a fraction p of the insulin present in the patient's fat enters the blood in unit time. Explain why:

$$\frac{da}{dt} = r - pa.$$

(c) Find the equilibrium from the differential equation in part (b) and determine whether this equilibrium is stable or unstable.

9. Freeway Engineering Compartment models are used to model the flow of traffic between different roads, by treating each road as a compartment. As an example, consider how the number of cars on a freeway on-ramp, $N(t)$, changes with time. For a simplified model let's assume that cars join the on-ramp at a constant rate q (that is, q cars join the on-ramp in one unit of time). Cars then leave the on-ramp by entering the freeway itself. Assume that a fraction f of the cars on the on-ramp enter the freeway in one unit of time.

(a) Derive a differential equation for $N(t)$. Your differential equation will include the unknown constants f and q.

(b) Analyze your model from part (a) to find the equilibrium number of cars on the on-ramp, and determine whether this equilibrium is stable or unstable.

(c) Suppose that the maximum capacity of the on-ramp is 90 cars, and the rate at which cars flow onto the on-ramp is $q = 60$ cars per min. Find the value of f that is needed to keep N below the on-ramp's capacity.

10. Filling Box Model In our compartment model we assumed that inflows and outflows are matched at q to keep the volume of water in the tank constant. It's often useful when modeling, for example, the flow of pollutant into a pristine environment, to consider what can occur if the inflows and outflows do not match.

Let's assume that the tank initially contains a volume V_0 of water. Water flows into the tank at rate q_{in}, and out of the tank at rate q_{out}. (You may assume $q_{\text{in}} > q_{\text{out}}$.) Suppose that the water flowing into the tank contains a concentration C_I of solute. As usual we write $C(t)$ for the concentration in the tank.

(a) Show that the concentration in the tank can be modeled using a differential equation:

$$\frac{d}{dt}(CV) = q_{\text{in}}C_I - q_{\text{out}}C$$

(b) Previously we were able to treat V as a constant. Now V changes with time. Derive a formula for $V(t)$.

(c) By substituting your formula for $V(t)$ into (a), derive a differential equation for $C(t)$.

(d) In general we cannot analyze the behavior of the solution $C(t)$ using techniques from Section 8.2. Why not?

(e) Let's assume $C_I = 0$. Then show that your equation from (c) can be written as:

$$\frac{dC}{dt} = \frac{-q_{\text{in}}C}{V_0 + (q_{\text{in}} - q_{\text{out}})t} \tag{8.57}$$

(f) Assume some definite values for the constants in (8.57): $q_{\text{in}} = 2$, $q_{\text{out}} = 1$, and $V_0 = 20$. Assuming $C(0) = 1$, solve (8.57) to find $C(t)$. Show that $\lim_{t\to\infty} C(t) = 0$.

8.3.2

11. Levins Model Denote by $p = p(t)$ the fraction of occupied sites in the patchy habitat model, and assume that

$$\frac{dp}{dt} = 2p(1-p) - p \quad \text{for } t \geq 0 \tag{8.58}$$

(a) Set $g(p) = 2p(1-p) - p$. Graph $g(p)$ for $p \in [0, 1]$.

(b) Find all equilibria of (8.58) that are in $[0, 1]$. Use your graph from (a) to determine their stability.

(c) Now use the eigenvalue approach to analyze the stability of the equilibria that you found in (b).

12. Levins Model Denote by $p = p(t)$ the fraction of occupied sites in the patchy habitat model, and assume that

$$\frac{dp}{dt} = 0.5p(1-p) - 1.5p \quad \text{for } t \geq 0 \tag{8.59}$$

(a) Set $g(p) = 0.5p(1-p) - 1.5p$. Graph $g(p)$ for $p \in [0, 1]$.

(b) Find all equilibria of (8.59) that are in $[0, 1]$. Use your graph in (a) to determine their stability.

(c) Use the eigenvalue approach to analyze the stability of the equilibria that you found in (b).

Subpopulation Interactions in Patchy Habitats

To derive our model for patchy habitat we assumed that a fixed fraction, m, of occupied sites became extinct in each unit of time. Often, however the survival of the population at a site depends on the number of subpopulations in the surrounding sites. If different subpopulations compete for limited resources, then the per site mortality rate may not be a constant, but may increase with p because, as p increases, competition between subpopulations increases. In questions 13 and 14 we will study the effect of different models for competition between subpopulations.

13. The term p^2 describes the density-dependent extinction of patches; that is, the per-patch extinction rate is p, and a fraction p of patches are occupied, resulting in patches going extinct at a total rate of p^2. The colonization of vacant patches is the same as in the Levins model. Then the fraction of occupied patches obeys a differential equation:

$$\frac{dp}{dt} = cp(1-p) - p^2$$

where $c > 0$.

(a) Show that there are two possible equilibrium values for p in $[0, 1]$ (which you should calculate) and determine their stability.

(b) Does the patch model always predict a nontrivial equilibrium when $c > 0$? Contrast with what we found for the Levins model in Section 8.3.2.

14. Assume that the per site extinction rate is Mp, and recolonization is unaffected by competition between subpopulations. Then our model for the proportion of occupied sites becomes

$$\frac{dp}{dt} = cp(1-p) - Mp^2$$

where $M > 0$ and $c > 0$ are constants.

(a) Show that there are two possible equilibrium values for p in $[0, 1]$ for any values of c and M. You do not need to find the values of both equilibria; instead, follow the method used in Section 8.2 and graph on the same axes the functions $f(p) = cp(1-p)$ and $h(p) = Mp^2$.

(b) Which of the two equilibria from part (a) is stable?

(c) Contrast your answer (about the existence of equilibria) with the analysis from Section 8.3.2.

Competition between Subpopulations

In Problems 13 and 14 we assumed that the per colony extinction rate was proportional to p. This means that the per colony extinction rate goes to 0 for small p. This may not be realistic—subpopulations may still go extinct even if they are not competing among themselves. One way to model this is to say that the per colony extinction rate is a function m(p) of p. In Problems 15 and 16 we will assume that $m(p) = a+bp$ for some constants $a, b > 0$. That is, the extinction rate increases with p because of competition between subpopulations, but m(p) does not vanish as $p \to 0$.

Then our model for proportion of occupied sites must be modified to:

$$\frac{dp}{dt} = cp(1-p) - (a+bp)p \tag{8.60}$$

where c, a, b are all positive constants.

15. Assuming that the subpopulations obey the differential Equation (8.60) and the coefficients are $a = 1, b = 2$, but c is allowed to take any value:

(a) Find the equilibrium values of p (your answer will depend on the unknown coefficient c).

(b) What are the conditions on c for p to have a nontrivial equilibrium, that is, an equilibrium in which $p \in (0, 1]$?

(c) Show that if your condition from (b) is met, then the nontrivial equilibrium is also stable.

16. In this question we will analyze (8.60) using a graphical argument.

(a) Assuming that a, b, c are all positive, draw the graphs of $y = c(1-p)$ and $y = a+bp$ to show that the differential Equation (8.60) has an equilibrium between 0 and 1 if $a < c$. [*Hint*: If the graphs intersect, then $c(1-p) - (a+bp) = 0$.]

(b) Show additionally that if $a < c$, then the nontrivial equilibrium is stable. [*Hint*: if $c(1-p) > a + bp$ and $p > 0$, then $cp(1-p) > (a+bp)p$.]

Cooperation between Subpopulations

Interactions between different subpopulations need not be competitive. In fact, different subpopulations may share resources, and the presence of many subpopulations may provide a pool of genetic diversity that helps the population of organisms to react to changing conditions. We will model cooperation between subpopulations by again assuming that the extinction rate depends on p, but now $m(p) = a - bp$, where a and b are both positive constants. So m(p) decreases as p increases. Our model for the number of subpopulations then becomes:

$$\frac{dp}{dt} = cp(1-p) - (a-bp)p \tag{8.61}$$

We will analyze this model in Problems 17 and 18.

17. Assume that the number of subpopulations obeys (8.61) with $a = 2, b = 1$, and c some unknown (positive) constant.

(a) Find the equilibrium values of p (your answer will depend on the constant c). You may assume $c > 1$.

(b) What is the condition on c for p to have a nontrivial equilibrium (i.e., an equilibrium in which $\hat{p} \in (0, 1]$)?

(c) Show that if your condition from (b) is met, then the nontrivial equilibrium is also stable.

18. Assuming that the number of subpopulations obeys (8.61), we will analyze this model graphically.

(a) Explain why we would expect $a \geq b$. [*Hint*: What would having negative $m(p)$ imply?]

(b) Assuming that a, b, c are all positive, show by drawing the graphs of $y = c(1-p)$ and $y = a - bp$ that the differential Equation (8.60) has an equilibrium between 0 and 1 if $a < c$. [*Hint*: If the graphs intersect, then $c(1-p) - (a-bp) = 0$.]

(c) Show additionally that if $a < c$, then the nontrivial equilibrium is stable. [*Hint*: If $c(1-p) > a - bp$ and $p > 0$, then $cp(1-p) > (a-bp)p$.]

Habitat Destruction

To study the effects of habitat destruction on a single species, we modify the Levins model in the following way: We assume that a fraction D of patches is permanently destroyed. Consequently, only patches that are vacant and undestroyed can be successfully colonized. A fraction $1-p(t)-D$ of patches is both vacant and undestroyed where p(t) is the fraction of occupied patches. Then:

$$\frac{dp}{dt} = cp(1-p-D) - mp \tag{8.62}$$

19. (a) Explain in words the meaning of the different terms in (8.62).

(b) Assume that $m = 0.2$, $c = 2$, and $D = 0.2$. Show that (8.62) predicts a nontrivial equilibrium value for $p(t)$ and that this equilibrium is stable.

20. Assume that a patchy habitat that has been partly destroyed obeys Equation (8.62) with c, D, m all positive constants.

(a) Show that there are two possible equilibria: the trivial equilibrium $\hat{p}_1 = 0$ and the nontrivial equilibrium $\hat{p}_2 = 1 - D - \frac{m}{c}$. Sketch the graph of $\hat{p}_2$ as a function of D.

(b) Assume that $m < c$ such that the nontrivial equilibrium is stable when $D = 0$. Find a condition for D such that the nontrivial equilibrium is between 0 and 1, and investigate the stability of both the nontrivial equilibrium and the trivial equilibrium under that condition.

(c) Assume that the condition that you derived in is met. Show that when the system is in equilibrium, the fraction of patches that are vacant and undestroyed—that is, the sites that are *available* for colonization—is $1-D-p$ and that this available fraction is independent of D. Show that the **effective colonization rate** in equilibrium—that is, c times the fraction of available patches—is equal to the mortality rate. This equality shows that the effective birth rate of new colonies balances their mortality rate at equilibrium.

8.3.3

A reversible chemical reaction between chemicals A and B produces a product C: $A + B \rightleftharpoons C$. We modeled this reaction in Section 8.3.3 using a differential equation for the amount of C produced:

$$\frac{dx}{dt} = k_{AB}(a-x)(b-x) - k_C x \tag{8.63}$$

Here x(t) is the amount of C at time t, a is the initial amount of chemical A, b is the initial amount of B, and k_{AB} and k_C are respectively the rate constants for the reaction that creates C and for the decay of C back into A and B.

21. Explain what each term in (8.63) represents and how the equation is derived.

For Problems 22–24 find the equilibrium value of x, and use a perturbation analysis to determine the stability of the equilibrium of (8.63).

22. $k_{AB} = 2, k_C = 2, a = 2, b = 2.$

23. $k_{AB} = 2, k_C = 1, a = 2, b = 3.$

24. $k_{AB} = 1, k_C = 2, a = 3, b = 2.$

25. To show that the differential equation (8.63) always has a stable equilibrium between $x = 0$ and $x = \min(a, b)$ we assumed that a and b were different (in fact that $a < b$). Show by redrawing Figure 8.40 that the result still holds if (a) $a > b$ and (b) if $a = b$.

26. **Reactions in a Chemostat** A chemostat is a device that can be used to maintain a chemical at a particular concentration. Assume that the reaction $A + B \rightleftharpoons C$ takes place in a chemostat that maintains A and B at constant concentrations a and b respectively (that is, the concentrations do not change over time).

(a) Explain why the concentration $x(t)$ of C now obeys a differential equation:

$$\frac{dx}{dt} = k_{AB}ab - k_C x \tag{8.64}$$

(b) Find the equilibrium for x predicted by Equation (8.64).

(c) Is the equilibrium that you found in part (b) stable or unstable?

27. **Reactions in a Chemostat** A chemostat is a device that can be used to maintain a chemical at a particular concentration. Assume that the reaction $A + B \rightleftharpoons C$ takes place in a chemostat that maintains A at a constant concentration a. The chemical B has initial concentration b and is depleted by the reaction.

(a) Explain why the concentration $x(t)$ of C now obeys a differential equation:

$$dx/dt = k_{AB}a(b - x) - k_C x \tag{8.65}$$

(b) Find the equilibrium for x predicted by Equation (8.65).

(c) Is the equilibrium that you found in part (b) stable or unstable?

28. **An Irreversible Reaction** In an irreversible reaction A and B combine to produce C, but C cannot disassociate back into A and B. We can represent this reaction symbolically by $A + B \rightarrow C$. This is equivalent to setting $k_C = 0$ in our original differential equation model. So the concentration, $x(t)$, of C obeys a differential equation:

$$\frac{dx}{dt} = k_{AB}(a - x)(b - x) \tag{8.66}$$

(a) Find the equilibrium for x predicted by Equation (8.66).

(b) Is the equilibrium that you found in part (b) stable or unstable?

29. **Temperature in a Chemical Reaction** The rate constants k_{AB} and k_C in the chemical reaction we are modeling depend on temperature: Many reactions speed up at higher temperatures. Both k_{AB} and k_C will be affected by a temperature increase. Suppose that the reaction is run at a higher temperature that doubles both k_{AB} and k_C. Show that the final concentration of C will remain the same, despite the temperature increase.

30. **Autocatalytic Reactions** An autocatalytic reaction is one in which chemical C is involved in its own production, for example,

$$A + C \rightleftharpoons 2C$$

That is, one molecule of A and one molecule of C react to create two molecules of C. Suppose that the reaction occurs in a chemostat that maintains the concentration of A at a.

(a) If the concentration of C is $x(t)$, explain why we can model this process using an equation:

$$\frac{dx}{dt} = k_{AC}ax - k_C x^2 \tag{8.67}$$

where you should explain what the two terms in this equation represent.

(b) Find the equilibrium for x predicted by Equation (8.67).

(c) Is the equilibrium that you found in part (b) stable or unstable?

8.3.4

To derive the model for the growth or decline of the population of cooperators interacting in a snowdrift game, we modeled the proportion of cooperators using a model.

$$\boldsymbol{\frac{dx}{dt} = knx(1 - x)\Big(-(b - c/2)x + (b - c)\Big)} \tag{8.68}$$

where $b > 0$ represents the benefit of interaction if one player is a cooperator and $c > 0$ is the cost of cooperation.

31. In Section 8.3.4 we analyzed Equation (8.68) if $b > c/2$. Determine the equilibria and what their stability is if $b = c/2$.

Assuming that $x(t)$ is modeled by Equation (8.68) in Problems 32–34, you should locate the equilibria and find which equilibria are stable for each of the following parameter values. Draw a vector field plot for each of the three problems.

32. $k = 1, n = 1, b = 2, c = 1$

33. $k = 1, n = 1, b = 3, c = 4$

34. $k = 1, n = 1, b = 4, c = 4$

35. **Greenbeard Genes** We showed in Section 8.3.4 that if $b < c$, then cooperators will be eventually outcompeted by cheaters. One mechanism that may allow cooperators to persist under these conditions is the greenbeard gene. Richard Dawkins coined this name (see ***Dawkins, 2006***) to describe how, if the genes that are responsible for cooperation also mark cooperators in some way (e.g., by giving each cooperator a bright green beard), then cooperators can make sure that they interact only with other cooperators (and thus cheaters interact only with other cheaters).

In this case the proportion, $x(t)$, of cooperators in the population will obey a differential equation.

$$\frac{dx}{dt} = (b - c/2)knx(1 - x)$$

and again the proportion of cheaters, $y(t)$, can be obtained from $y = 1 - x$.

(a) Show that if $b > c/2$, then under the greenbeard gene model $x = 1$ is a stable equilibrium and $x = 0$ is unstable.

(b) What are the equilibria and their stability if $b < c/2$?

(c) Explain your answers from part (a) and (b) biologically in terms of the relative costs and benefits of cooperation.

(d) What happens if $b = c/2$? Again explain your answer biologically.

We discussed the snowdrift model as one example of how organisms may interact. In Problems 36–40 we will consider an alternate model for interaction.

A Hawk-Dove game

Bio Info • In the Hawk-Dove game we assume that when two organisms interact they compete for some resource (e.g., territory). Only one organism can win the competition, and the benefit to this organism is b. But the competition may also leave one organism injured. There are two possible strategies that organisms may adopt when interacting with each other. *Hawks* always fight for the resource while *Doves* always back down from a fight. When two doves meet, both back down, and the resource is shared equally between them (i.e., each receives benefit $b/2$). When a hawk meets a dove, the dove surrenders the contested resource; then the hawk automatically gets the benefit (b), while the dove gets nothing. When two hawks meet, they fight: The victor will receive the benefit. But there is a cost to losing, since the loser may be hurt. Let's call this cost c. Since a hawk does not know in advance whether they will win or lose the fight, on average costs and benefits will be evenly split (i.e., on average a hawk's benefit from fighting another hawk is $\frac{1}{2}(b-c)$). We can summarize the results of the competition in a payoff matrix:

		Opponent	
		Hawk	Dove
Player	Hawk	$\frac{1}{2}(b-c)$	b
	Dove	0	$b/2$

If we model the effect of each interaction upon the proportions of hawks $x(t)$, and doves $y(t)$, in the population we may derive a differential equation

$$\frac{dx}{dt} = knx(1-x)\left(\frac{b}{2} - \frac{cx}{2}\right) \tag{8.69}$$

Just as for the snowdrift game model, we can then calculate y, the proportion of doves, from the equation $y = 1 - x$.

In Problems 36–38 we will analyze the population dynamics that are predicted by (8.69), for different values of b and c.

36. Show that if $b > c$ (that is, the maximum benefit of fighting exceeds the maximum cost), then the only equilibria for (8.69) within $0 \le x \le 1$ are $x = 0$ and $x = 1$. Which equilibrium is stable and which is unstable?

37. Show that if $b < c$, then there are three equilibria for (8.69) with $0 \le x \le 1$. What are these equilibria and which one(s) are stable?

38. Suppose $b = c$; then $\frac{dx}{dt} = \frac{knb}{2}x(1-x)^2$. Assuming $k = 1$, $n = 1$, and $b = 1$, sketch the vector field plot for x.

Assuming that x(t) is modeled by Equation (8.69), in Problems 39–40, you should find the equilibria and determine which equilibria are stable for each of the following parameter values. Draw a vector field plot for each problem.

39. $k = 1, n = 1, b = 2, c = 1$

40. $k = 1, n = 1, b = 2, c = 3$

8.3.5

To model the spread of a disease in a population of size N we derived a differential equation model:

$$\frac{dI}{dt} = (kb - c)I - \frac{kb}{N}I^2 \tag{8.70}$$

where I(t) is the number of infected individuals at time t, and k, b, and c are all positive coefficients.

Assuming that I(t) is modeled by Equation (8.70), in Problems 41–44, you should locate the equilibria of the model, and find which of these equilibria are stable. Draw a vector field plot for each problem.

41. $k = 1, b = 1, c = 0.5, N = 50$.

42. $k = 1, b = 1, c = 0.5, N = 200$.

43. $k = 2, b = 2, c = 1, N = 100$.

44. $k = 2, b = 2, c = 4, N = 100$.

45. In this question we will interpret the *recovery rate*, c, that appears in the model. Assume that a population of infected individuals is quarantined (that is, they are unable to transmit the disease to others, or to catch it again once they recover).

(a) Explain why under these assumptions we expect:

$$\frac{dI}{dt} = -cI \tag{8.71}$$

(b) Assuming $I(0) = I_0$, find $I(t)$ by solving (8.71).

(c) How long will it take for the number of infected individuals to decrease from I_0 to $I_0/2$?

(d) Assume that it takes 7 days for the number of infected individuals to decrease from 50 to 25. Calculate the recovery rate c for this disease.

46. **Quarantining** Quarantining is an effective way to prevent diseases from spreading. Infectious individuals are told to stay at home to avoid spreading the disease. However, when a person is in the early stages of a disease, they may not realize they are ill and they then spread the disease to others.

Suppose that a fraction p of infectious individuals continue to spread the disease.

(a) Explain why, if a person contacts b individuals in a unit of time, then a fraction $\left(\frac{pI}{S+pI}\right)$ will be infectious.

(b) Show that the differential equation for the number of infectious individuals needs to be modified to

$$\frac{dI}{dt} = kb\frac{pIS}{(S+pI)} - cI.$$

(c) Use the relationship $S = N - I$ to rewrite your equation from part (b) in terms of I only (i.e., to eliminate $S(t)$ from the equation).

(d) Assume that $p = 1/2$. Analyze the differential equation from (c) to find its equilibria, and determine which are stable.

(e) Under what conditions on k, b, and c will the disease be endemic? (You may continue to assume $p = 1/2$). Compare this condition with the one that we derived in Section 8.3.5.

47. **Handwashing** One way to control the spread of a disease is to run public health programs that educate people on how to limit their exposure to the disease. For example, frequent handwashing can prevent people from picking up a virus after touching surfaces that it may live on.

(a) Explain why in our model such efforts to control the disease would affect the value of the parameter k, but would not affect b or c.

(b) Suppose that for a particular disease $c = 0.3$/day, and $b = 10$/day. What value must k remain below to prevent the disease from becoming endemic?

48. **Public Health** In our analysis of the spread of a disease we showed that a disease will become endemic if $kb > c$. Thinking about the meanings of the coefficients k, b, and c, discuss how the following public health measures can help to prevent a disease from becoming endemic. In particular, explain which coefficients in the model are affected by each measure, and whether the measure increases or decreases the coefficients it affects:

(a) Quarantining sick people (i.e., requiring that sick people stay at home).

(b) Encouraging frequent hand-washing.

(c) Educating people to cover their mouths and noses when they sneeze.

(d) Providing medications to people with the disease.

8.4 Integrating Factors and Two-Compartment Models

In Section 8.1 we learned the method of separation of variables for solving differential equations of the form:

$$\frac{dN}{dt} = f(t)g(N) \tag{8.72}$$

In Section 8.2 we learned how to analyze the solutions of these kinds of differential equations graphically as in the case where $f(t) = 1$ (i.e., the right-hand side of (8.72) is a function of N only). As we saw in Section 8.3 many differential equations that arise as models of biological phenomena are of this form. However, not all equations are of this form, and it is important to recognize when separation of variables can be used and when it cannot be used. For example, the equation:

$$\frac{dN}{dt} = N + t \tag{8.73}$$

cannot be solved by separation of variables—the right-hand side is not the product of a function of N with a function of t. To see why, try pulling out the t (i.e., writing $N + t = t(1 + N/t)$). Then we have one factor, $f(t) = t$, that is truly a function of t only, but the other factor is a function of both N and t, $g(N, t) = 1 + N/t$.

In this section we will learn a technique that can be used to solve any equation of the form:

$$\frac{dN}{dt} + a(t)N = b(t) \tag{8.74}$$

where $a(t)$ and $b(t)$ are both functions of t only. Equation (8.73) is of this form because it can be written as

$$\frac{dN}{dt} - N = t$$

which is of the correct form if we set $a(t) = -1$ and $b(t) = t$ in (8.74). The method that we will use is called integrating factors, because it involves multiplying (8.74) by a new function (a factor) in order to turn both sides of the equation into functions that we can integrate with respect to t. Equations of the form (8.74) are needed for the study of two-compartment models—these are differential equations that are used throughout life sciences, but particularly to study how medications or drugs move through the body, and we will present this important application at the end of this section.

8.4.1 Integrating Factors

Let's start with a specific example, namely the differential equation from (8.73), with an initial condition added

$$\frac{dN}{dt} - N = t \qquad N(0) = 0$$

To solve this differential equation we will start with an unintuitive step: We will multiply both sides of the differential equation by e^{-t}

$$\frac{dN}{dt}e^{-t} - Ne^{-t} = te^{-t}$$

Although it looks like we have, needlessly, made our differential equation even more complicated, we notice that the left-hand side can now be rewritten to put the equation in the form

$$\frac{d}{dt}(Ne^{-t}) = te^{-t} \qquad \begin{aligned} \tfrac{d}{dt}(Ne^{-t}) &= \tfrac{dN}{dt}\cdot e^{-t} + N\cdot \tfrac{d}{dt}(e^{-t}) \\ &= \tfrac{dN}{dt}\cdot e^{-t} - N\cdot e^{-t} \end{aligned}$$

This simplification seems like magic, but it is part of the integrating factor method. We can then integrate both sides of the equation with respect to t:

$$\begin{aligned} Ne^{-t} &= \int te^{-t}dt \qquad \text{Fundamental theorem of calculus on left-hand side.} \\ &= -te^{-t} + \int e^{-t}dt \qquad \text{Integrating by parts with } u = t,\ v' = e^{-t}. \\ &= -te^{-t} - e^{-t} + C \end{aligned}$$

Thus:

$$N(t) = -(t+1) + Ce^{t}$$

To calculate C we apply the initial condition:

$$0 = -1 + C \Rightarrow C = 1 \qquad e^0 = 1$$

so

$$N(t) = -(t+1) + e^{t}.$$

Now let's develop a more general version of the integrating factor method. Suppose that we are trying to solve the general form of Equation (8.74). In general we will assume that $a(t)$ is continuous and $b(t)$ is differentiable for all of the values of t for which a solution of the equation is sought. Because $a(t)$ is continuous, it has an antiderivative; that is, there is a function $A(t)$ for which $A'(t) = a(t)$. Multiply both sides of (8.74) by $e^{A(t)}$. For the example studied previously, $a(t) = -1$, so $A(t) = -t$ and $e^{A(t)} = e^{-t}$, which is the factor that we multiplied (8.73) by. The factor $e^{A(t)}$ is known as the **integrating factor** of the equation. (In this section we will use IF as an abbreviation for integrating factor in the help text.) Then (8.74) becomes

$$e^{A(t)}\frac{dN}{dt} + a(t)e^{A(t)}N = e^{A(t)}b(t) \tag{8.75}$$

But we recognize that the left-hand side of (8.75) can be rewritten as $\frac{d}{dt}(N(t)e^{A(t)})$, so

$$\frac{d}{dt}(Ne^{A(t)}) = e^{A(t)}b(t) \qquad \tfrac{d}{dt}(Ne^{A(t)}) = \tfrac{dN}{dt}e^{A(t)} + N\tfrac{d}{dt}(e^{A(t)})$$

Or on integrating both sides with t:

$$Ne^{A(t)} = \int e^{A(t)}b(t)dt$$

$$N(t) = e^{-A(t)}\int e^{A(t)}b(t)dt \tag{8.76}$$

Note that the differential equation is solved only in the sense that we have converted the problem of calculating $N(t)$ to the problem of finding the integral $\int e^{A(t)}b(t)dt$. Since $b(t)$ is differentiable, $b(t)$ is certainly continuous and so is $A(t)$, so the integral exists, but you may not be able to write it in terms of functions that you know. It is not necessary to memorize Equation (8.76); in general, you can memorize the sequence of steps that led to the result and perform them for any equation of the form (8.74).

EXAMPLE 1 Solve the differential equation:

$$\frac{dy}{dt} = k(y-a), \quad y(0) = 0 \tag{8.77}$$

using the method of integrating factors.

Solution The function on the right-hand side of this differential equation is a function of the dependent variable, y, only; that is, the differential equation is autonomous. It can therefore be solved by separation of variables. However, (8.77) can also be rearranged into the form of (8.74):

$$\frac{dy}{dt} - ky = -ka, \quad y(0) = 0. \qquad a(t) = -k,\ b(t) = -ka$$

We may then solve the equation using integrating factors. For this equation, $\int a(t)dt = -kt$, so:

$$e^{-kt}\frac{dy}{dt} - ke^{-kt}y = -kae^{-kt} \qquad \text{IF is } e^{-kt}$$

$$\frac{d}{dt}(e^{-kt}y) = -kae^{-kt}$$

$$e^{-kt}y = \int (-kae^{-kt})\,dt \qquad \text{Integrate both sides with respect to } t$$

$$= ae^{-kt} + C \qquad \text{We only need one constant of integration}$$

so $y(t) = a + Ce^{kt}$. We calculate the constant of integration, C, by applying the initial conditions

$$0 = a + C \qquad \text{Set } t = 0$$

$$\Rightarrow y(t) = a - ae^{kt}$$

•

EXAMPLE 2 Solve the differential equation

$$\frac{dy}{dx} + \frac{y}{x} = \frac{1}{x^2}, \quad \text{for } x > 0$$

with initial condition $y(1) = 1$.

Solution This equation is of the form (8.74), with x as the independent variable and y as the dependent variable. $a(x) = \frac{1}{x}$ and $b(x) = \frac{1}{x^2}$. Since $\int a(x)dx = \ln x$, the integrating factor is $e^{\ln x} = x$. So

$$x\frac{dy}{dx} + y = \frac{1}{x} \qquad \text{Multiply both sides by } x.$$

$$\frac{d}{dx}(xy) = \frac{1}{x}$$

$$xy = \int \frac{1}{x}dx$$

$$= \ln x + C$$

So

$$y = \frac{\ln x}{x} + \frac{C}{x}$$

We calculate the constant of integration by applying our initial conditions

$$1 = 0 + C \qquad \text{Substitute } x = 1,\ y = 1$$

so

$$y(x) = \frac{\ln x}{x} + \frac{1}{x}$$

•

Solving differential equations using integrating factors often requires us to use integration methods from Chapter 7.

EXAMPLE 3 Solve the differential equation:

$$\frac{dy}{dt} + \left(\frac{2t}{1+t^2}\right)y = t \tag{8.78}$$

with initial condition $y(0) = 0$.

Solution Here $a(t) = \frac{2t}{1+t^2}$. To calculate the integrating factor we need to find the antiderivative of $a(t)$:

$$A(t) = \int \frac{2t}{1+t^2}dt$$

We can evaluate this integral by the method of substitution. Let $u = 1 + t^2$. Then $du = 2tdt$ and $A(t) = \int \frac{du}{u} = \ln u = \ln(t^2 + 1)$.

So, the integrating factor is $e^{A(t)} = e^{\ln(t^2+1)} = t^2 + 1$, and

$$(t^2+1)\frac{dy}{dt} + 2ty = t(t^2+1)$$

$$\frac{d}{dt}\left((t^2+1)y\right) = t(t^2+1) \qquad \text{Multiply both sides by the IF.}$$

$$(t^2+1)y = \int t(t^2+1)dt = \frac{1}{4}t^4 + \frac{1}{2}t^2 + C \qquad \text{Integrate both sides with } t.$$

Or:

$$y(t) = \frac{\frac{1}{4}t^4 + \frac{1}{2}t^2}{t^2+1} + \frac{C}{t^2+1}$$

Calculate the constant C from the initial condition:

$$0 = 0 + C \qquad t = 0,\ y = 0$$

So

$$y(t) = \frac{t^2}{4}\frac{(t^2+2)}{(t^2+1)} \qquad \text{Factorize the numerator.}$$

•

One of the most important skills for solving differential equations is to recognize which equations are separable and which are in a form where integrating factors can be used (remember that in some cases, such as Example 1 in this section, both methods of solution can be used).

EXAMPLE 4 Find the general solution of the following equations:

(a) $\frac{dN}{dt} = 3Nt + t^3$ **(b)** $\frac{dy}{dx} = y^2x + x$ **(c)** $\frac{dx}{dt} = x + t - xt - 1$

Solution **(a)** The right-hand side is not separable. If we try to separate out the function of N, we get $3Nt + t^3 = N(3t + t^3/N)$, but the second factor contains both N and t, rather than being a function of t alone. But we can rewrite the equation in the form of (8.74):

$$\frac{dN}{dt} - 3tN = t^3 \qquad a(t) = -3t,\ b(t) = t^3$$

So the integrating factor is $\exp\left(\int(-3t)dt\right) = e^{-3t^2/2}$:

$$e^{-3t^2/2}\frac{dN}{dt} - 3te^{-3t^2/2}N = t^3e^{-3t^2/2}$$

$$\frac{d}{dt}(e^{-3t^2/2}N) = t^3e^{-3t^2/2}$$

$$e^{-3t^2/2}N = \int t^3e^{-3t^2/2}dt \qquad \text{Integrate both sides with } t.$$

To evaluate the integral we make a change of variables: $s = 3t^2/2$, $ds = 3tdt$:

$$e^{-3t^2/2}N = \frac{2}{9}\int se^{-s}ds \qquad t^3dt = \tfrac{t^2}{3}3tdt = \tfrac{2}{9}s\,ds$$

$$= \frac{2}{9}\left(-se^{-s} + \int e^{-s}ds\right) \qquad \text{Integrate by parts } \tfrac{dv}{ds} = e^{-s},\ u = s$$

$$= \frac{2}{9}(-se^{-s} - e^{-s} + C)$$

$$= -\frac{2}{9}\left(\frac{3t^2}{2} + 1\right)e^{-3t^2/2} + C_1 \qquad \text{Define a new constant } C_1 = 2C/9 \text{ and substitute } s = 3t^2/2$$

So:

$$N(t) = -\frac{2}{9}\left(\frac{3t^2}{2} + 1\right) + C_1 e^{3t^2/2}$$

(b) This differential equation is separable; the right-hand side can be written as:

$$y^2 x + x = \overbrace{(y^2+1)}^{g(y)}\overbrace{x}^{f(x)}$$

So we can separate variables:

$$\frac{1}{y^2+1}\frac{dy}{dx} = x$$

$$\int \frac{1}{y^2+1}dy = \int x dx \qquad \text{Integrate both sides with } x.$$

$$\tan^{-1}(y) = \frac{1}{2}x^2 + C \qquad \text{Use Table 6.1 in Section 6.2.3.}$$

$$y = \tan\left(\frac{1}{2}x^2 + C\right)$$

(c) The right-hand side is factorizable.

$$x + t - xt - 1 = (x-1)(1-t)$$

So, we can separate variables

$$\frac{1}{x-1}\frac{dx}{dt} = (1-t)$$

$$\int \frac{1}{x-1}dx = \int (1-t)dt \qquad \text{Integrate both sides with } t.$$

$$\ln|x-1| = t - \frac{t^2}{2} + C$$

$$x - 1 = \pm e^C \exp\left(t - \frac{t^2}{2}\right)$$

So, $x(t) = 1 + C_1 \exp(t - t^2/2)$ if we define a new constant $C_1 = \pm e^C$.

This equation can also be written in the form of (8.74) by pulling the terms in x to the left-hand side:

$$\frac{dx}{dt} + x(t-1) = t - 1.$$

It can then be solved using integrating factors (see Problem 9). •

8.4.2 Two-Compartment Models

Solution of equations by integrating factors is particularly useful to solve two-compartment problems. The flow of a drug through a body is often modeled by treating the body as two linked compartments. One compartment might represent the gut (e.g., the intestines), and the other compartment, the blood. Pills containing the drug enter the gut, and from there the drug passes into the blood, where it is used by the body.

Let's start the analysis of two-compartment models by adapting the single-compartment model from Section 8.3.1. Imagine we have two tanks, of volume V_1 and V_2, that contain both water and solute. Suppose that the concentration in the first tank is C_1, and in the second the concentration is C_2 (both $C_1(t)$ and $C_2(t)$ will vary with time). Water flows into the first tank at a rate q. There is also an outflow, also q, of water from the first tank. (Remember, q represents the volume of water being added to or removed from the tank in one unit of time.) However, unlike the scenario described in Section 8.3.1, the water flowing out of the first tank is not lost, but flows directly into the second tank. Water must then flow out of the second tank, also at rate

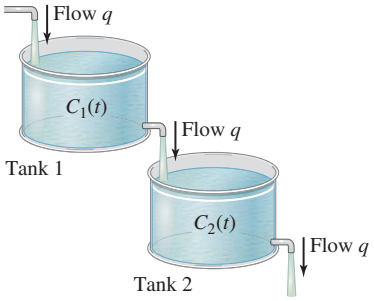


Figure 8.51 Flows of water between two tanks.

q, to keep the volume of water in this tank constant. Figure 8.51 represents the flows of water into and out of each tank.

Suppose that the concentration of solute in the water flowing into tank 1 is C_∞. We also assume, as we did in Section 8.3.1, that the solute in each tank is stirred up well enough to mix through all of the water in the tank. Then the concentration of solute in the flow coming out of tank 1 will be $C_1(t)$, while the concentration in the water coming out of tank 2 will be $C_2(t)$.

We will derive differential equations for the concentration of solute in the two tanks by starting with the word equations:

$$\begin{array}{c}\text{Rate of change of}\\ \text{amount of solute}\\ \text{in tank 1}\end{array} = \begin{array}{c}\text{Rate at which}\\ \text{solute flows into}\\ \text{tank 1}\end{array} - \begin{array}{c}\text{Rate at which}\\ \text{solute flows out}\\ \text{of tank 1}\end{array}$$

Since a volume q of water enters tank 1 in one unit of time, and the concentration of solute in this inflow is C_∞, the total amount of solute flowing into tank 1 in one unit of time is (volume $\times$ concentration) $= qC_\infty$. Similarly, the rate at which solute flows out of the tank is (volume outflow in one unit of time) $\times$ (concentration) $= qC_1$.

So

$$\frac{d}{dt}(C_1V_1) = qC_\infty - qC_1 \qquad \text{Total amount of solute in tank 1 is } C_1 \times V_1.$$

We can write down a similar equation for the solute in tank 2.

$$\frac{d}{dt}(C_2V_2) = qC_1 - qC_2 \qquad \text{Rate of solute inflow into tank 2 is } qC_1.$$

Because V_1 and V_2 are both constants, we can rewrite these equations in the form:

$$\frac{dC_1}{dt} = \frac{q}{V_1}(C_\infty - C_1) \tag{8.79}$$

and

$$\frac{dC_2}{dt} = \frac{q}{V_2}(C_1 - C_2) \tag{8.80}$$

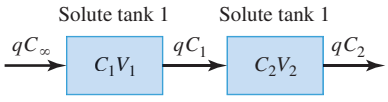


Figure 8.52 Diagram showing flows of solute in the two-compartment model.

We therefore have two differential equations to solve: one for C_1 and one for C_2. But to solve the differential equation for $C_2(t)$ we need to know the value of $C_1(t)$. This is an example of a general problem in math modeling—differential equations with **coupled** variables (i.e., where the terms in one differential equation change with time due to a differential equation of their own). We will develop a general theory for solving this kind of problem in Chapter 11. But in Equation (8.79) the concentration of solute in tank 1 (i.e., C_1) does not depend on the concentration in tank 2. This is made clear if we draw a diagram of the flows of solute in this system (Figure 8.52). If we consider only flows into and out of tank 1, these flows depend only on the concentration C_1 (and on C_∞, which represents the constant concentration of solute in the inflow to tank 1). So we can calculate the concentration $C_1(t)$ without knowing $C_2(t)$ (i.e., solve Equation (8.79) separately from (8.80)).

Equation (8.79) is of a form where we can use either integrating factors or separation of variables to solve the equation. The full solution that accounts for arbitrary initial conditions on C_1 and C_2 is messy and difficult to interpret. So we will solve the system of differential equations in the special case where $C_1(0) = C_2(0) = 0$ (that is, neither tank initially contains any solute). So (8.79) becomes

$$\frac{dC_1}{dt} = \frac{q}{V_1}(C_\infty - C_1) \quad , \quad C_1(0) = 0$$

We solved this equation originally in Section 8.3.1. But the equation is the same as Example 1 in this section, if we rename the variables $y \to C_1$, $a \to C_\infty$, and $k \to -\frac{q}{V_1}$. From Example 1 we may read off the solution:

$$C_1(t) = C_\infty - C_\infty e^{-qt/V_1} = C_\infty(1 - e^{-qt/V_1})$$

To calculate $C_2(t)$ we must substitute our solution for $C_1(t)$ into (8.80):

$$\frac{dC_2}{dt} = \frac{q}{V_2}C_\infty\left(1 - e^{-qt/V_1}\right) - \frac{qC_2}{V_2}. \tag{8.81}$$

Equation (8.81) is not separable, but it can be solved by integrating factors if it is first rewritten as

$$\frac{dC_2}{dt} + \frac{qC_2}{V_2} = \frac{qC_\infty}{V_2}\left(1 - e^{-qt/V_1}\right) \qquad a(t) = q/V_2,\ b(t) = \tfrac{qC_\infty}{V_2}(1 - e^{-qt/V_1}).$$

Then:

$$e^{qt/V_2}\frac{dC_2}{dt} + \frac{q}{V_2}e^{qt/V_2}C_2 = \frac{qC_\infty}{V_2}\left(e^{qt/V_2} - e^{qt(1/V_2 - 1/V_1)}\right) \qquad \text{IF} = e^{qt/V_2}$$

$$\frac{d}{dt}\left(C_2 e^{qt/V_2}\right) =$$

$$C_2 e^{qt/V_2} = \frac{qC_\infty}{V_2}\int \left(e^{qt/V_2} - e^{qt(1/V_2 - 1/V_1)}\right) dt$$

$$= \frac{qC_\infty}{V_2}\left(\frac{V_2}{q}e^{qt/V_2} - \frac{V_1V_2}{q(V_1 - V_2)}e^{qt(1/V_2 - 1/V_1)}\right) + C \qquad \text{Assume } V_1 \neq V_2;\ (1/V_2 - 1/V_1)^{-1} = \tfrac{V_1V_2}{V_1 - V_2}.$$

In our derivation we have assumed that $V_1 \neq V_2$ (i.e., the tanks have different sizes).

Hence:

$$C_2(t) = C_\infty - C_\infty\frac{V_1}{V_1 - V_2}e^{-qt/V_2} + Ce^{-qt/V_2}$$

To calculate the constant of integration, C, apply the initial conditions:

$$0 = C_\infty - C_\infty\left(\frac{V_1}{V_1 - V_2}\right) + C. \qquad C_2(0) = 0$$

We find $C = -C_\infty + \frac{V_1}{V_1 - V_2}C_\infty$ and so:

$$C_2(t) = C_\infty\left(1 - e^{-qt/V_2}\right) + C_\infty\left(\frac{V_1}{V_1 - V_2}\right)\left(e^{-qt/V_2} - e^{-qt/V_1}\right) \tag{8.82}$$

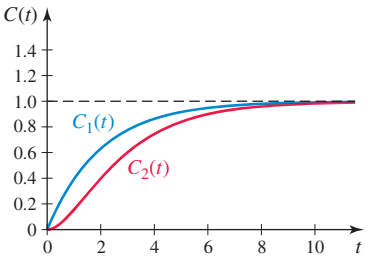


Figure 8.53 Solutions of (8.79) and (8.80) with $C_\infty = 1$, $q = 1$, $V_1 = 2$, $V_2 = 1$, $C_1(0) = C_2(0) = 0$.

Figure 8.53 shows one solution of the model.

Our solution for $C_2(t)$ in Equation (8.82) is quite complicated, and it is hard, even using the techniques from Section 5.6, to determine how the shape of the graph will depend on all of the constants in our model. From our solution for $C_1(t)$ we can see that $C_1(t) \to C_\infty$ as $t \to \infty$ because $C_1(t)$ can be decomposed as C_∞ plus an exponential term that decays to 0 as $t \to \infty$.

Since all of the exponential terms in (8.82) decay to 0 as $t \to \infty$, $C_2(t)$ must also converge to C_∞ as $t \to \infty$. That is, the concentration of solute in both tanks converges to C_∞, (i.e., to match the concentration in the water flowing into the first tank).

To understand how the solutions behave, it is often helpful to consider what happens if one of the constants in the equation is very small or very large. We will show how this kind of analysis can be used, focusing on the effect of the size of the second tank, V_2, on $C_2(t)$.

If $V_2 \ll V_1$ (the second tank is much smaller than the first), then $\frac{V_1}{V_1 - V_2} \approx \frac{V_1}{V_1} = 1$, because we can neglect the V_2 term in the denominator. We can approximate $\frac{V_2}{V_1 - V_2} \approx 0$, so:

$$C_2(t) \approx C_\infty\left(1 - e^{-qt/V_1}\right)$$

But this is the same expression as we found for $C_1(t)$. So the concentrations in the two tanks are almost identical. If V_2 is very small, then the concentration in the second tank quickly reaches equilibrium with the concentration in the inflow to the second tank (i.e., to $C_1(t)$). But $C_1(t)$ changes with time t. So the second tank matches the concentration of the first tank and eventually reaches the same equilibrium concentration C_∞. Because $C_2(t)$ is being fed with an inflow whose concentration is $C_1(t)$ rather than C_∞, it is not possible for the second tank to converge to the equilibrium concentration C_∞ faster than the first tank.

On the other hand, if $V_2 \gg V_1$ (the second tank is much larger than the first), then $\frac{V_1}{V_1 - V_2} \approx -\frac{V_1}{V_2} \approx 0$. In this case we may approximate (8.82) by

$$C_2(t) \approx C_\infty \left(1 - e^{-qt/V_2}\right)$$

Our expression for $C_2(t)$ is then the same as the expression for $C_1(t)$, only with the volume V_1 replaced by the (much larger) volume V_2. In fact $C_2(t)$ doesn't depend on V_1 at all in this limit. Our solution for $C_2(t)$ is the same as for a tank of volume V_2 that receives an inflow with constant concentration C_∞. We can understand this as follows: If $V_1 \ll V_2$, then the concentration in the first tank converges to C_∞ much quicker than the second tank. So quickly, in fact, that when considering the second tank we can assume that the first tank reaches C_∞ effectively instantly. So the second tank receives an almost constant inflow concentration C_∞, and can be analyzed as a single tank reaching equilibrium at this concentration.

As we noted in the introduction, one of the most important applications of two-compartment models is the study of how drugs move through the human body. Here we don't have physical tanks with flow between them, but matter moves from one compartment to another, and equations very similar to the above can be used to represent this movement.

EXAMPLE 5 **A Two-Compartment Model for Drug Metabolization** A patient takes a pill containing a drug. The pill enters her gut. From there it then passes into her bloodstream. A fraction f of the drug from the gut enters the patient's bloodstream in each unit of time. Once the drug enters the blood it is used by the patient's body or eliminated. A fraction k of the drug present in the patient's blood is removed in each unit of time. Calculate the amount of drug in the patient's blood as a function of time. Assume that f and k are constants.

Solution Here we model the flow of drug using two compartments: the gut and the blood. Let the amount of medication in the patient's gut be $g(t)$ and the amount in her blood be $b(t)$. We start with word equations for $g(t)$ and $b(t)$.

$$\text{Rate of change of drug in gut} = -\left(\text{Rate at which drug passes from gut to blood}\right)$$

$$\frac{dg}{dt} = -fg \qquad \text{No extra drug enters gut unless the patient takes more pills.} \tag{8.83}$$

At time $t = 0$, when the pill first enters the patient's gut, if no drug was previously present, then $g(t)$ will be equal to the total amount of drug contained in a pill. Let's call the amount of drug in one pill g_0. Then $g(0) = g_0$.

Since the drug leaving the gut enters the patient's blood,

$$\text{Rate of change of drug in blood} = \begin{matrix}\text{Rate at which}\\ \text{drug passes from}\\ \text{gut to blood}\end{matrix} - \begin{matrix}\text{Rate at which}\\ \text{drug is removed}\\ \text{from the blood}\end{matrix}$$

$$\frac{db}{dt} = fg - kb \tag{8.84}$$

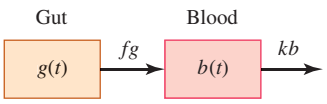


Figure 8.54 Flow of drug between gut and blood for Example 5.

If we assume that this is the first time the patient has taken this particular medication, then at time $t = 0$ there should be no medication present in the patient's blood (i.e., $b(0) = 0$).

We can represent the flow of drug between the two compartments by a diagram (Figure 8.54).

Just as in the two tank problem, the flow to the gut (there is no inflow) does not depend on the level of drug in the blood. That is, Equation (8.83) can be solved

independently of Equation (8.84). In fact we can solve (8.83) by either of the methods (separation of variables or integrating factors) that we have studied in this chapter. We will use separation of variables:

$$\int \frac{dg}{g} = -\int f\,dt \quad \Rightarrow \quad g(t) = g_0 e^{-ft}$$

To solve (8.84) we substitute our expression for $g(t)$ into the equation:

$$\frac{db}{dt} = fg - kb = fg_0 e^{-ft} - kb \tag{8.85}$$

Equation (8.85) is not separable but can be solved using integrating factors:

$$\frac{db}{dt} + kb = fg_0 e^{-ft} \qquad \text{First, write in the form of (8.74).}$$

$$e^{kt}\frac{db}{dt} + ke^{kt}b = fg_0 e^{(k-f)t} \qquad \text{IF} = e^{kt}$$

$$\frac{d}{dt}(e^{kt}b) = \int fg_0 e^{(k-f)t}dt.$$

Let's assume that $k \neq f$ (the case where $k = f$ is left to you; see Problem 30). Then we can evaluate the integral on the right hand side, giving

$$e^{kt}b(t) = \frac{fg_0}{k-f}e^{(k-f)t} + C \qquad C \text{ is a constant of integration.}$$

so

$$b(t) = \frac{fg_0}{k-f}e^{-ft} + Ce^{-kt}.$$

To find the constant C, apply initial conditions:

$$0 = \frac{fg_0}{k-f} + C \quad \Rightarrow \quad C = -\frac{fg_0}{k-f}$$

Thus

$$b(t) = \frac{fg_0}{k-f}\left(e^{-ft} - e^{-kt}\right). \tag{8.86}$$

To understand our solution better it is useful to sketch a graph of how $b(t)$ varies over time. We can use the techniques from Section 5.6 to draw this graph. We will assume for definiteness that $k > f$. Modifications for $k < f$ will be discussed as we proceed.

Step 1 Find zeros. $b(t) = 0$ only when:

$$e^{-ft} - e^{-kt} = 0 \text{ (i.e., } e^{(k-f)t} = 1).$$

Since $k \neq f$, this occurs only when $t = 0$.

Step 2 Find where function is positive or negative. Since $b(t) = 0$ only when $t = 0$, $b(t)$ must be positive over the entire interval $(0, \infty)$ or negative over the entire interval). Since $b(t)$ represents an amount of drug, we expect only the first case to be possible. But to reason from Equation (8.86) rather than from the science of the model, consider the two factors in (8.86): $(e^{-ft} - e^{-kt})$ and $\frac{fg_0}{k-f}$. Since we are assuming $k > f$, $k - f > 0$, so $\frac{fg_0}{k-f} > 0$. Meanwhile $e^{(k-f)t} > 1$ since e raised to any power is positive, so $e^{-ft} > e^{-kt}$. Thus, both factors are positive, and so $b(t)$ is positive.

Step 3 and 4 Find $b'(t)$ and points where $b(t)$ or $b'(t)$ are undefined. Both $b(t)$ and db/dt are defined for all $t \geq 0$, and:

$$\frac{db}{dt} = \frac{fg_0}{k-f}\left(-fe^{-ft} + ke^{-kt}\right)$$

Steps 5 and 6 Locate local extrema and increasing and decreasing intervals of $b(t)$. From Step 3 we see $\frac{db}{dt} = 0$ only when $ke^{-kt} = fe^{-ft}$, that is, when $e^{(k-f)t} = k/f$ so the only candidate for a local extrema with $t > 0$ is at time $t_1 = \frac{\ln(k/f)}{k-f}$.

Notice that t_1 is a positive number whether $k > f$ or $k < f$. If $k > f$, then $k - f > 0$ and $\ln(k/f) > 0$ (since $\ln x > 0$ if $x > 1$). But if $k < f$, then $k - f < 0$ and $\ln(k/f) < 0$. Since our expression has both a negative numerator and a negative denominator, t_1 will be positive. The derivative $b'(t)$ can only change sign at points where $b'(t) = 0$ (i.e., at the local extremum t_1). We also observe that:

$$b'(0) = \frac{fg_0}{k-f}(k-f) = fg_0 > 0$$

so $b(t)$ starts off increasing for $0 \le t < t_1$. Moreover, since $b(t) \to 0$ as $t \to \infty$, and $b(t) > 0$, $b(t)$ must be decreasing as $t \to \infty$, so $b(t)$ is decreasing for $t > t_1$.

Step 7 Classify extrema. $b(t)$ switches from increasing to decreasing at $t = t_1$, and so $t = t_1$ is a local maximum.

Step 8 Behavior at end points of the interval. Since $b(t) > 0$ for $t > 0$ and $b(t) = 0$, $t = 0$ is a local (in fact a global) minimum point. The other end point of interest is the behavior of $b(t)$ as $t \to \infty$:

$$\lim_{t\to\infty} b(t) = \lim_{t\to\infty}\left(\frac{fg_0}{k-f}e^{-ft}\right) - \lim_{t\to\infty}\left(\frac{fg_0}{k-f}e^{-kt}\right)$$
$$= 0 - 0 = 0$$

Figure 8.55 is a sketch of the solution, containing all of this information.

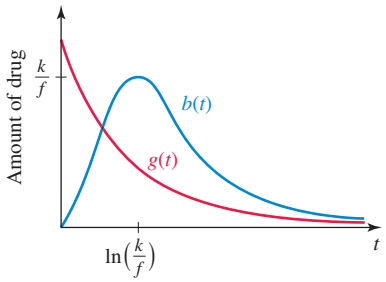


Figure 8.55 Sketch of the solution to the differential equations (8.83 and 8.84). Finding the maximum level of the drug in the patient's blood is left as an exercise (see Problem 30).

Two-compartment models are commonly used to predict how the body uses medications. For example, ***Albert and Gernaat (1984)*** collected data on the levels of ibuprofen (sold under the name Motrin®) in the blood of patients being treated for arthritis. We can fit the model to these data, that is, estimate the parameters k and f that make the mathematical model match experimental measurements: to determine how quickly the ibuprofen enters and leaves a patient's blood. The data and fit are shown in Figure 8.56.

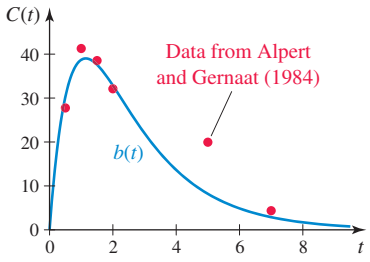


Figure 8.56 We fit our two-compartment model to the data of ***Albert and Gernaat (1984)*** (red crosses). From the fit we can estimate the parameters in our model: $k = 0.53\ \text{hr}^{-1}$ and $f = 1.35\ \text{hr}^{-1}$.

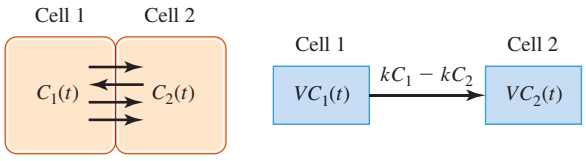


Figure 8.57 Two cells exchange a small molecule through the small region of membrane between them. In the second panel we represent the flow between the two cells.

EXAMPLE 6 **Equilibration Across a Membrane** Although the membrane of a cell may appear to be solid when the cell is viewed through a microscope, at the molecular scale the membrane is riddled with holes that allow small molecules to diffuse into and out of the cell, either into the cell's environment or into nearby cells. Controlling what enters and what leaves is one of the cell's most important tasks. Here we will consider a simplified model for the process by which two cells exchange small molecules.

Imagine the cells are in contact via a region of membrane. The two cells have the same volume V, and their respective concentrations of the molecule are $C_1(t)$ and $C_2(t)$ (see Figure 8.57).

The flow of molecules between the two cells will depend on the difference in concentration between the two cells. A commonly used model for the process of diffusion states that:

$$\begin{matrix}\text{Rate of flow from} \\ \text{cell 1 to cell 2}\end{matrix} = k(C_1 - C_2). \tag{8.87}$$

The constant k is called the **permeability** of the membrane—it depends both on the properties of the membrane (the area of contact between the two cells, the size of the holes in the membrane) and upon the molecule (e.g., small molecules typically diffuse across the membrane more readily—that is, they have higher values of k than large molecules).

Now if $C_1 < C_2$, then the rate of flow predicted by (8.87) is negative. In that case molecules flow from cell 2 to cell 1. That is, molecules always tend to diffuse from the cell where the concentration is higher to the cell where the concentration is lower.

Hence, we can write down a word equation for the concentration in the two cells starting with the first cell:

$$\begin{matrix}\text{Rate of change of} \\ \text{number of molecules} \\ \text{in cell 1}\end{matrix} = - \begin{matrix}\text{Rate at which} \\ \text{molecules diffuse} \\ \text{from cell 1 to cell 2}\end{matrix}$$

which may then be written in mathematical form, i.e.:

$$\frac{d}{dt}(C_1 V) = -k(C_1 - C_2).$$

Similarly for cell 2:

$$\begin{matrix}\text{Rate of change of} \\ \text{number of molecules} \\ \text{in cell 2}\end{matrix} = \begin{matrix}\text{Rate at which} \\ \text{molecules diffuse} \\ \text{from cell 1 to cell 2}\end{matrix}$$

Molecules diffusing from cell 1 to cell 2 are subtracted from cell 1 and added to cell 2.

$$\frac{d}{dt}(C_2 V) = k(C_1 - C_2)$$

Or, on dividing all equations by the constant V:

$$\frac{dC_1}{dt} = -\frac{k}{V}(C_1 - C_2) \tag{8.88}$$

$$\frac{dC_2}{dt} = \frac{k}{V}(C_1 - C_2) \tag{8.89}$$

Previously we were able to solve one of our equations independently of the other. In this model, however, to calculate the concentration C_1, we need to solve an equation that involves C_2. But to solve the equation for C_2, we need to solve an equation that involves C_1. The two equations are *coupled*. In general, solving this kind of differential equation system requires techniques that will be introduced in Chapter 11. However, in this case a trick allows us to decouple the equations. Suppose that instead of solving (8.88) and (8.89) directly for C_1 and C_2 we try to solve for the quantity

$$C(t) = \frac{1}{2}(C_1(t) + C_2(t)),$$

which represents the average concentration of molecules in the two cells.

Why do we introduce this new dependent variable? If we look at how $C(t)$ changes with time we see:

$$\begin{aligned}\frac{dC}{dt} &= \frac{d}{dt}\left[\frac{1}{2}(C_1 + C_2)\right] = \frac{1}{2}\frac{dC_1}{dt} + \frac{1}{2}\frac{dC_2}{dt} \\ &= -\frac{k}{2V}(C_1 - C_2) + \frac{k}{2V}(C_1 - C_2) = 0\end{aligned} \tag{8.90}$$

So C is a constant. This makes sense, physically. When a molecule leaves cell 1, it enters cell 2, and conversely, so the total number of molecules in both cells must remain constant, so the average must also be constant.

Now if we know C, we can substitute for $C_2(t)$ in Equation (8.88) because $C_2(t) = 2C(t) - C_1(t)$. So:

$$\begin{aligned}\frac{dC_1}{dt} &= -\frac{k}{V}\Big(C_1 - (2C(t) - C_1(t)\Big) \\ &= -\frac{2k}{V}C_1 + \frac{2k}{V}C \qquad C(t) \text{ is a constant.}\end{aligned}$$

We can then solve this differential equation by the method of integrating factors.

$$\begin{aligned}\frac{dC_1}{dt} + \frac{2kC_1}{V} &= \frac{2kC}{V} \qquad \text{Write in the form of (8.74)} \\ \frac{dC_1}{dt}e^{2kt/V} + \frac{2kC_1}{V}e^{2kt/V} &= \frac{2kC}{V}e^{2kt/V} \qquad \int a(t)\,dt = \tfrac{2kt}{V} \\ \frac{d}{dt}\left(C_1(t)e^{2kt/V}\right) &= \frac{2kC}{V}e^{2kt/V} \\ C_1(t)e^{2kt/V} &= \frac{2kC}{V}\int e^{2kt/V}\,dt \\ &= Ce^{2kt/V} + A\end{aligned}$$

that is,

$$C_1(t) = C + Ae^{-2kt/V} \tag{8.91}$$

where A is a constant that is determined by the initial conditions on $C_1(t)$. We then solve for $C_2(t)$ from:

$$\begin{aligned}C_2(t) &= 2C - C_1(t) \\ &= C - Ae^{-2kt/V}.\end{aligned} \tag{8.92}$$

Now let's consider a specific problem. Assume that at time $t = 0$, the concentration in cell 1 is A_1 and the concentration in cell 2 is A_2. Find $C_1(t)$ and $C_2(t)$.

Solution To solve the problem we need to use the initial conditions to solve for the coefficients C and A that appear in our expressions for $C_1(t)$ and $C_2(t)$.

First, note that:

$$C = \frac{1}{2}\left(C_1(t) + C_2(t)\right)$$

and since C is a constant:

$$C = \frac{1}{2}\Big(C_1(0) + C_2(0)\Big) = \frac{1}{2}(A_1 + A_2)$$

Now since $C_1(0) = A_1$, substituting into (8.91) we obtain:

$$C + A = A_1$$

$$\text{or} \quad A = A_1 - C = \frac{1}{2}(A_1 - A_2)$$

So by substituting for C and A in (8.91) and (8.92) we obtain:

$$C_1(t) = \frac{1}{2}(A_1 + A_2) + \frac{1}{2}(A_1 - A_2)e^{-2kt/V}$$

$$C_2(t) = \frac{1}{2}(A_1 + A_2) - \frac{1}{2}(A_1 - A_2)e^{-2kt/V}$$

That is, both C_1 and C_2 converge monotonically to $\frac{1}{2}(A_1 + A_2)$. The level of small molecule in cells equilibrates at the same value $(\frac{1}{2}(A_1 + A_2))$. A plot of the solution is given in Figure 8.58. •

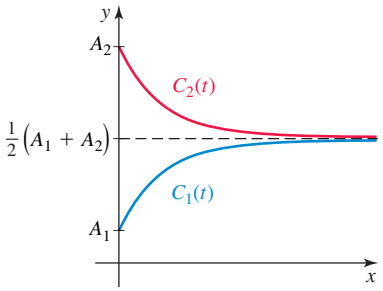


Figure 8.58 Plot of the solution of the two-compartment model for equilibration of the concentration of a small molecule between two cells.

Section 8.4 Problems

8.4.1

Find the general solution of the differential equations in Problems 1–12 using the method of integrating factors:

1. $\frac{dy}{dt} + \frac{y}{t} = \frac{1}{t^2}$

2. $\frac{dy}{dt} + \frac{3y}{t} = t$

3. $\frac{dy}{dt} - y = t + 1$

4. $\frac{dy}{dt} + y = t^2$

5. $\frac{dy}{dx} + \frac{y}{x+2} = x - 1$

6. $\frac{dy}{dx} + \frac{y}{x+2} = x$

7. $\frac{dy}{dx} - \frac{y}{x(x+1)} = 1$

8. $\frac{dy}{dx} + \frac{2(x+1)y}{x(x+2)} = x$

9. $\frac{dx}{dt} + (t-1)x = t - 1$

10. $\frac{dx}{dt} + \frac{tx}{t^2+1} = t$

11. $\frac{dy}{dx} + \frac{y}{x} = y$

12. $\frac{dy}{dx} + x = y$

For each of the Problems 13–24 you should determine whether the problem needs to be solved using separation of variables or integrating factors (some of the problems may be solved using either method). Then solve the differential equation.

13. $\frac{dy}{dt} = \frac{y}{t} - t^2$

14. $\frac{dy}{dt} = \frac{y}{t+1}$

15. $\frac{dy}{dt} = y^2 t + y^2$

16. $\frac{dy}{dt} = y - yt$

17. $\frac{dy}{dt} = \cos t$

18. $\frac{dy}{dt} = 1 - y$

19. $\frac{dy}{dt} = t^3 + yt$

20. $\frac{dy}{dt} = t + yt$

21. $\frac{dy}{dx} = (x+1)y + (x+1)$

22. $\frac{dy}{dx} = (x+1)y + (x+1)y^2$

23. $\frac{dy}{dx} = \frac{xy}{x+1}$

24. $\frac{dy}{dx} = \frac{x}{y+1}$

8.4.2

In Problems 25–28 consider the two-compartment model for two tanks with respective volumes V_1 and V_2.

$$\frac{dC_1}{dt} = \frac{q}{V_1}(C_\infty - C_1) \tag{8.93}$$

$$\frac{dC_2}{dt} = \frac{q}{V_2}(C_1 - C_2) \tag{8.94}$$

where $C_1(t)$ is the concentration in the first tank and $C_2(t)$ is the concentration in the second tank, and q is the volume of water flowing between the two tanks in one unit of time.

25. When we analyzed (8.93) and (8.94) in the main text we assumed that $V_1 \neq V_2$. Now consider how the analysis must be modified if $V_1 = V_2$, and $C_1(0) = C_2(0) = 0$.

(a) Show that $C_1(t) = C_\infty(1 - e^{-qt/V_1})$ and $C_2(t) = C_\infty\left(1 - \left(1 + \frac{qt}{V_1}\right)e^{-qt/V_1}\right)$

(b) Show that $\lim_{t\to\infty} C_1(t) = C_\infty$ and $\lim_{t\to\infty} C_2(t) = C_\infty$.

26. Let $C_\infty = 0$, so that the fresh water is pumped into tank 1 and flushes solute from tank 1 into tank 2. Now assume that $C_1(0) = 1$ and $C_2(0) = 0$. If $q = 1$, $V_1 = 1$, and $V_2 = 2$, solve the pair of differential equations to find $C_1(t)$ and $C_2(t)$. Sketch both functions of time.

27. Let $C_\infty = 0$, so that the fresh water is pumped into tank 1 and flushes solute from tank 1 into tank 2. Now assume that $C_1(0) = 1$ and $C_2(0) = 0$. If $q = 1$, $V_1 = 3$, and $V_2 = 1$, solve the pair of differential equations to find $C_1(t)$ and $C_2(t)$, and sketch both functions of time.

28. Let $C_\infty = 0$, so that the fresh water is pumped into tank 1 and flushes solute from tank 1 into tank 2. Now assume that $C_1(0) = 1$ and $C_2(0) = 0$. If $q = 1$ and $V_1 = V_2 = 1$, solve the pair of differential equations to find $C_1(t)$ and $C_2(t)$, and sketch both functions of time.

29. Consider a two-compartment model where, instead of having a separate reservoir feeding into tank 1, the two tanks are separated by two pipes, one of which carries water from tank 1 to tank 2, at rate q, and the other carries water from tank 2 to tank 1, at the same rate q. A schematic and diagram of the flows is given in Figure 8.59.

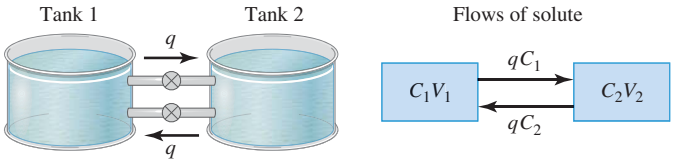


Figure 8.59 Schematic of two-compartment model for Problem 29.

(a) Explain why, although there is no net flow between the tanks, we would expect the concentrations in the tanks to change over time.

(b) Explain why the change in concentrations over time can be modeled using differential equations:

$$\frac{dC_1}{dt} = \frac{q}{V_1}(C_2 - C_1)$$

$$\frac{dC_2}{dt} = \frac{q}{V_2}(C_1 - C_2) \tag{8.95}$$

(c) To solve the differential equations in (8.95) start by assuming that $V_1 = V_2$. Then define $C(t) = \frac{1}{2}(C_1 + C_2)$ and by deriving a differential equations for dC/dt and explain why $C(t)$ is constant.

(d) Using the fact that $C(t)$ is a constant, eliminate $C_2(t)$ from the equation for $\frac{dC_1}{dt}$. Solve the equation you then obtain, and write down expressions for $C_1(t)$ and $C_2(t)$.

(e) Use the expression from part (d) to explain why, no matter what the starting values for $C_1(0)$ and $C_2(0)$ are, we expect $C_1(t)$ and $C_2(t)$ to converge to the same limit as $t \to \infty$.

(f) To solve the differential equations in (8.95) in the most general case ($V_1 \neq V_2$), let $C(t) = \frac{V_1C_1 + V_2C_2}{V_1 + V_2}$ (the weighted average of the concentrations in the two tanks). Explain why $C(t)$ is a constant.

(g) Using the fact that $C(t)$ is a constant, eliminate $C_2(t)$ from the equation for $\frac{dC_1}{dt}$. Solve the equation you then obtain, and write down expressions for $C_1(t)$ and $C_2(t)$.

(h) Use the expression from part (g) to explain why, no matter what the starting values for $C(t)$ and $C_2(t)$ are, we expect $C_1(t)$ and $C_2(t)$ to converge to the same limit as $t \to \infty$.

30. **Drug Modeling** In Example 5 we analyzed the flow of a medication from a patient's gut to their blood. Reanalyze this model assuming the rate of elimination of medication from the patient's

blood is the same as the rate at which medication passes from the gut into blood. Then, if the amount of medication in the patient's blood is $b(t)$ and the amount in the patient's gut is $g(t)$:

$$\frac{dg}{dt} = -fg$$

and

$$\frac{db}{dt} = fg - fb$$

where f is a positive constant.

(a) Show that just as in Example 5, $g(t) = g_0 e^{-ft}$ where g_0 is the amount of drug in the pill the patient takes at time $t = 0$.

(b) Solve for $b(t)$, assuming $b(0) = 0$, and sketch the graph of $b(t)$ against t.

31. Find the maximum level of medication in a patient's blood, if the passage of medication through the patient's body is modeled using Equation (8.86).

32. Filling Box Models In Problem 10 of Section 8.3 we analyzed the concentration in a tank whose volume changes over time because the inflows and outflows are not matched. For such a tank it can be shown that if the concentration in the inflow is C_I, and the inflow and outflow rates are respectively q_{in} and q_{out}, then both concentration, $C(t)$, and volume of water in the tank, $V(t)$, vary with time and can be modeled by a pair of differential equations:

$$\frac{d}{dt}(CV) = q_{\text{in}}C_I - q_{\text{out}}C$$

and (8.96)

$$\frac{dV}{dt} = q_{\text{in}} - q_{\text{out}}.$$

(a) Show that the differential equations (8.96) imply that

$$((q_{\text{in}} - q_{\text{out}})t + V_0)\frac{dC}{dt} + q_{\text{in}}C = q_{\text{in}}C_I \qquad (8.97)$$

where V_0 is the initial volume of water in the tank.

(b) Assuming that $q_{\text{in}} = 2$, $q_{\text{out}} = 1$, $V_0 = 1$, $C(0) = 0$, and $C_I = 1$, solve (8.97) using integrating factors to find $C(t)$.

(c) Assuming that $q_{\text{in}} = 1$, $q_{\text{out}} = 2$, $V_0 = 1$, $C(0) = 0$, and $C_I = 1$, solve (8.97) using integrating factors to find $C(t)$. What does your model predict will occur when $t = 1$? Explain whether this answer makes sense given that $V(1) = 0$.

Chapter 8 Review

Key Terms

Discuss the following definitions and concepts:

1. Differential equation
2. Separable differential equation
3. Solution of a differential equation
4. Pure-time differential equation
5. Autonomous differential equation
6. Exponential growth
7. Von Bertalanffy equation
8. Logistic equation
9. Allometric growth
10. Equilibrium
11. Stability
12. Eigenvalue
13. Single-compartment model
14. Patchy habitat model
15. Colonization rate
16. Mortality rate
17. Allee effect
18. Chemical reaction model
19. Reaction rate
20. Evolutionary game theory
21. Snow-drift game
22. Cooperator
23. Cheater
24. Pay-off matrix
25. Epidemic model
26. Susceptible
27. Infected
28. SI-model
29. Infection rate
30. Recovery rate
31. Endemic disease
32. Integrating factor
33. Two-compartment model
34. Coupled equations

Review Problems

1. ***For each of the following differential equations, find the general solution:***

(a) $dx/dt = 2 - x$,

(b) $dy/dx = \frac{1}{y} - \frac{1}{y^2}$,

(c) $dy/dx = yx - x$,

(d) $dy/dx = \frac{y}{x} + x^2$.

2. ***For each of the following differential equations, sketch the vector field plot, and identify any equilibria as well as determining their stability.***

(a) $\frac{dN}{dt} = N(N-1)(3-N)$,

(b) $dN/dt = N(1-N)$,

(c) $dx/dt = x^3 - 1$.

3. Newton's Law of Cooling and Time of Death Suppose that an object has temperature T and is brought into a room that is kept at a constant temperature T_a. Newton's law of cooling states that the rate of temperature change of the object is proportional to the difference between the temperature of the object and the surrounding medium.

(a) Denote the temperature at time t by $T(t)$, and explain why

$$\frac{dT}{dt} = k(T_a - T) \qquad (8.98)$$

is the differential equation that expresses Newton's law of cooling.

(b) Derive the solution to the differential equation, assuming that at time $t = 0$, the temperature of the object is $T = T_0$.

Newton's law of cooling can be used to estimate the time of death of a person during criminal investigations. When we

are alive, our bodies tend to maintain a constant temperature of around 37°C. On death, bodies start to cool. Assume that a cooling dead body obeys Equation (8.98). ***Molnar et al. (1969)*** found that cooling bodies have a cooling coefficient between $k = 0.04\ \text{hr}^{-1}$ and $k = 0.09\ \text{hr}^{-1}$.

(c) A body is found at 10 p.m. The body's temperature when it was found was 27.0°C, and the temperature of the room is 20.0°C. Estimate the range of possible times of death if k is between 0.04 hr and 0.09 hr.

(d) To make a more accurate estimate of time of death it can be helpful to measure k directly. To do this, the body's temperature is measured at 11 p.m. At this time, the body temperature is found to be 26.4°C (you may assume the room temperature remains constant at 20.0°C). Using the temperatures measured at 10 p.m. and 11 p.m., estimate k.

(e) Use your new measurement of k from part (d) to make a new estimate of the time of death.

4. Photosynthesis *(Adapted from **Horn, 1971**)* The following model is a simplified model of photosynthesis: Suppose that a leaf contains a number of traps that can capture light. If a trap captures light, the trap becomes energized. The energy in the trap can then be used to produce sugar, which causes the energized trap to become unenergized. The number of traps that can become energized is proportional to the number of unenergized traps and the intensity of the light. Denote by T the total number of traps (unenergized and energized) in a leaf, by I the light intensity, and by x the number of energized traps. Then the following differential equation describes how the number of energized traps changes over time:

$$\frac{dx}{dt} = k_1(T - x)I - k_2 x$$

Here, k_1, k_2, and I are positive constants. Find all equilibria and their stability.

5. Chemical Reactions A chemical reaction between chemical A and chemical B produces chemical C. Two molecules from chemical C can then combine to produce chemical D. The chain of reactions can be written as

$$A + B \to C \quad \text{with rate constant } k_{AB}$$
$$2C \to D \quad \text{with rate constant } k_C.$$

Chemicals A and B are continuously added to the system to keep A and B at constant concentrations a and b respectively. Then, the concentration $x(t)$ of C can be modeled using a differential equation:

$$\frac{dx}{dt} = k_{AB}ab - 2k_C x^2 \tag{8.99}$$

(a) Analyze (8.99); that is, find the equilibria of the equation and their stability.

(b) Assume that $k_{AB} = 1, k_C = 1, a = 1, b = 1$. Draw the vector field plot for (8.99).

(c) Now sketch the graph of the solution $x(t)$ against t if $x(0) = 0$ (it is not necessary to solve the differential equation to sketch the solution).

6. Island Biogeography ***Preston (1962)*** and ***MacArthur and Wilson (1963)*** investigated the effect of area on species diversity in oceanic islands. In their model, animals and plants of different species continuously travel to the island from the mainland. The fraction of mainland species that can be found on the island is p, which we call the **diversity of the island**. We want to derive a model for how $p(t)$ will change with time, t.

The number of different species present on the island will be affected by extinction and immigrations; species may die out, while other species from the mainland start new populations on the island. In general we expect:

$$\frac{dp}{dt} = \text{Rate of immigrations} - \text{Rate of extinctions}$$

Assume that a fraction m of species go extinct in one unit of time. Assume that, if a species is present on the mainland, then there is a probability c that it will emigrate to the island in one unit of time. But only species not present already on the island will add to the number of species there.

(a) Explain why we may model the diversity of the island using a model:

$$\frac{dp}{dt} = c(1 - p) - mp. \tag{8.100}$$

(b) Find the equilibria for p and determine their stability.

(c) Assume that, for a particular island, $c = 2$ and $m = 1$. If $p(0) = 1$ (that is, initially the island contains all species found on the mainland) solve Equation (8.100) to calculate $p(t)$.

(d) One question of interest in the field of biogeography—how diversity is affected by the physical environment—is how the area of the island affects its diversity. Assume that the extinction rate m decreases as island area, A, increases. But the rate of colonization, c, is unaffected. Will the equilibrium value of p increase or decrease if A is increased?

7. The Prisoner's Dilemma In this problem we will discuss a classic model for organism interactions based on ***Nowak (2006)***. This model is based on a game called **prisoner's dilemma**. Two individuals are charged with a crime. If neither confesses (i.e., they cooperate with each other) then it cannot be proven that they committed the crime, and they will be sentenced for a more minor crime. However, each prisoner has the option of confessing, and blaming their partner for the crime. In this case the person who confesses walks free, while the other person is sent to jail. We may regard this as a form of cheating—the cheater (person who confesses) receives a reward (no prison time), but at the expense of the cooperator (the partner who doesn't confess). But if both partners confess, then both will be sent to prison (though sharing the blame means that their sentences are reduced). We will imagine a community of organisms interacting via this game. We can summarize net benefit to each player using a payoff matrix.

We will put specific numbers in the payoff matrix to make the analysis clearer.

		Opponent	
		Cooperate	Cheat
Player	Cooperate	3	0
	Cheat	6	1

Assuming that each organism interacts with n others in unit time, and that reproductive rate is proportional to the total benefit from all of these interactions, then it can be shown that the proportion $x(t)$ of cooperators will obey a differential equation:

$$\frac{dx}{dt} = knx(x - 1)(2x + 1) \tag{8.101}$$

where $k > 0$ is a constant (as in Section 8.3.4). The proportion $y(t)$ of cheaters can be determined from $y = 1 - x$.

(a) Find the stable and unstable equilibria of Equation (8.101).

(b) What is the long time behavior of $x(t)$?

(c) Consider a population made up only of cooperators ($x = 1$). What is the total benefit that each individual in this population receives in one unit of time?

(d) Now consider a population made up only of cheaters ($x = 0$). What is the total benefit that each individual in this population receives in one unit of time?

Your answers from (c) and (d) illustrate an effect known as **tragedy of the commons**. Although in populations of cooperators all individuals get more benefits than in populations of cheaters, cheaters always prosper and eventually take over in a mixed population.

8. Insulin Infusion An insulin pump is used to treat diabetes by continuously infusing insulin into the fat in a patient's abdomen or thigh. From there the insulin enters the patient's bloodstream. We will model this process using a two-compartment model.

Assume that insulin is pumped into a small region of fat at a constant rate r. This region will be the first compartment in our model. A fraction f of the insulin in the fat then diffuses into the patient's blood in each unit of time. Within the patient's blood, a fraction k of the insulin present is eliminated in one unit of time r, and f and k are constants. So if we denote the amount of insulin in the patient's fat by x, and the amount in their blood by y then:

$$\frac{dx}{dt} = r - fx. \tag{8.102}$$

$$\frac{dy}{dt} = fx - ky. \tag{8.103}$$

(a) By analyzing Equation (8.102) find the equilibrium level of insulin in the patient's fat (that is, the equilibrium value of x) and determine whether this equilibrium is stable or unstable.

(b) Assuming that $x(t)$ converges to its equilibrium value (found in part (a)), what is the equilibrium value for $y(t)$; that is, find the value of y that ensures that $dy/dt = 0$?

(c) Assuming the following parameter values: $r = 2$, $f = 1$, $k = 1$, and that at time $r = 0$, there is no insulin present either in the patient's fat or in their blood (that is, $x(0) = y(0) = 0$), solve the system of equations (8.102) and (8.103), and confirm that $x(t)$ and $y(t)$ converge to the equilibrium values that you calculated in parts (a) and (b).