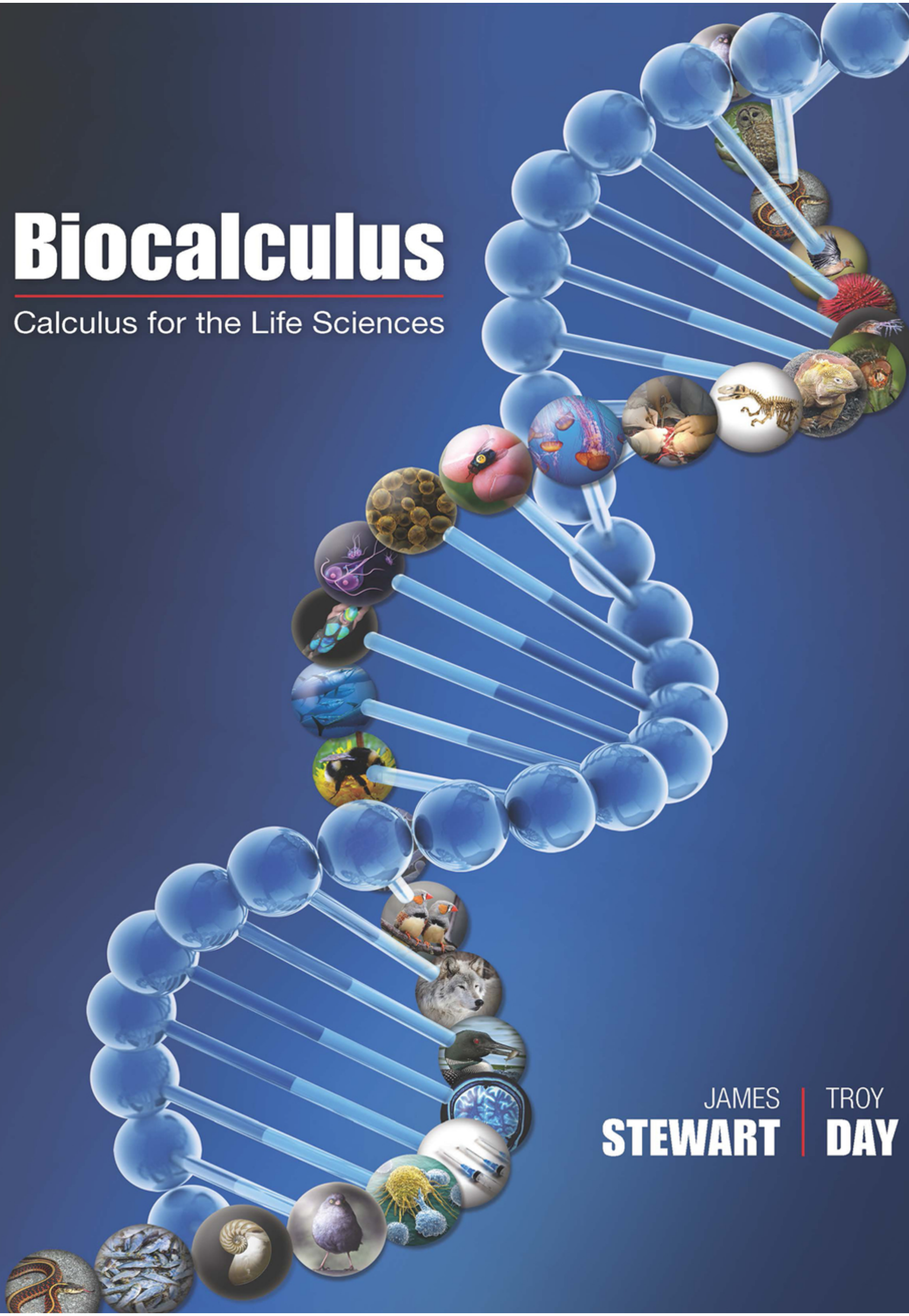
Biocalculus

Calculus for the Life Sciences

JAMES STEWART | TROY DAY



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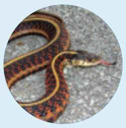
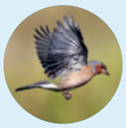
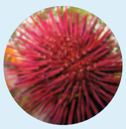
About the Cover Images

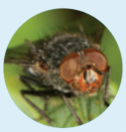

Spotted owl populations are analyzed using matrix models (Exercise 8.5.22).

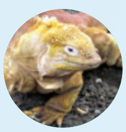

The fitness of a garter snake is a function of the degree of stripedness and the number of reversals of direction while fleeing a predator (Exercise 9.1.7).

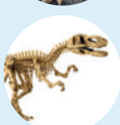

The project on page 297 asks how birds can minimize power and energy by flapping their wings versus gliding.


The population size of some species, like this sea urchin, can be measured by evaluating a certain integral, as explored in Exercise 5.3.49.

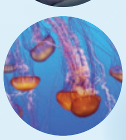

The interaction between *Daphnia* and their parasites is analyzed in Case Study 2 (page xlvi).


Populations of blowflies are modeled by chaotic recursions (page 430).

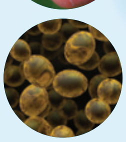

The energy needed by an iguana to run is a function of two variables, weight and speed (Exercise 9.2.47).

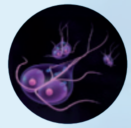

Dinosaur fossils can be dated using potassium-40 (Exercise 3.6.12).


The project on page 222 illustrates how mathematics can be used to minimize red blood cell loss during surgery.


Jellyfish locomotion is modeled by a differential equation in Exercise 10.1.34.


The screw-worm fly was effectively eliminated using the sterile insect technique (Exercise 5.6.24).


The growth of a yeast population leads naturally to the study of differential equations (Section 7.1).


The doubling time of a population of the bacterium *G. lamblia* is determined in Exercise 1.4.29.

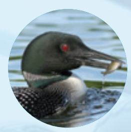

The Speedo LZR Racer reduces drag in the water, resulting in dramatically improved performance. The project on page 603 explains why.

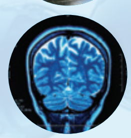

In Example 9.4.2 we use the Chain Rule to discuss whether tuna biomass is increasing or decreasing.


The optimal foraging time for bumblebees is determined in Example 4.4.2.

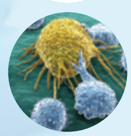

The vertical trajectory of zebra finches is modeled by a quadratic function (Figure 1.2.8).

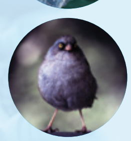

The size of the gray-wolf population depends on the size of the food supply and the number of competitors (Exercise 9.4.21).


Example 4.4.4 investigates the time that loons spend foraging.


The area of a cross-section of a human brain is estimated in Exercise 6.Review.5.


The project on page 479 determines the critical vaccination coverage required to eradicate a disease.


Natural killer cells attack pathogens and are found in two states described by a pair of differential equations developed in Section 10.3.


In Example 4.2.6 a junco has a choice of habitats with different seed densities and we determine the choice with the greatest energy reward.


The project on page 467 investigates logarithmic spirals, such as those found in the shell of a nautilus.

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To Dolph Schluter and Don Ludwig, for early inspiration

About the Authors

JAMES STEWART received the M.S. degree from Stanford University and the Ph.D. from the University of Toronto. After two years as a postdoctoral fellow at the University of London, he became Professor of Mathematics at McMaster University. His research has been in harmonic analysis and functional analysis. Stewart's books include a series of high-school textbooks as well as a best-selling series of calculus textbooks published by Cengage Learning. He is also coauthor, with Lothar Redlin and Saleem Watson, of a series of college algebra and precalculus textbooks. Translations of his books include those into Spanish, Portuguese, French, Italian, Korean, Chinese, Greek, Indonesian, and Japanese.

A talented violinist, Stewart was concertmaster of the McMaster Symphony Orchestra for many years and played professionally in the Hamilton Philharmonic Orchestra. Having explored the connections between music and mathematics, Stewart has given more than 20 talks worldwide on Mathematics and Music and is planning to write a book that attempts to explain why mathematicians tend to be musical.

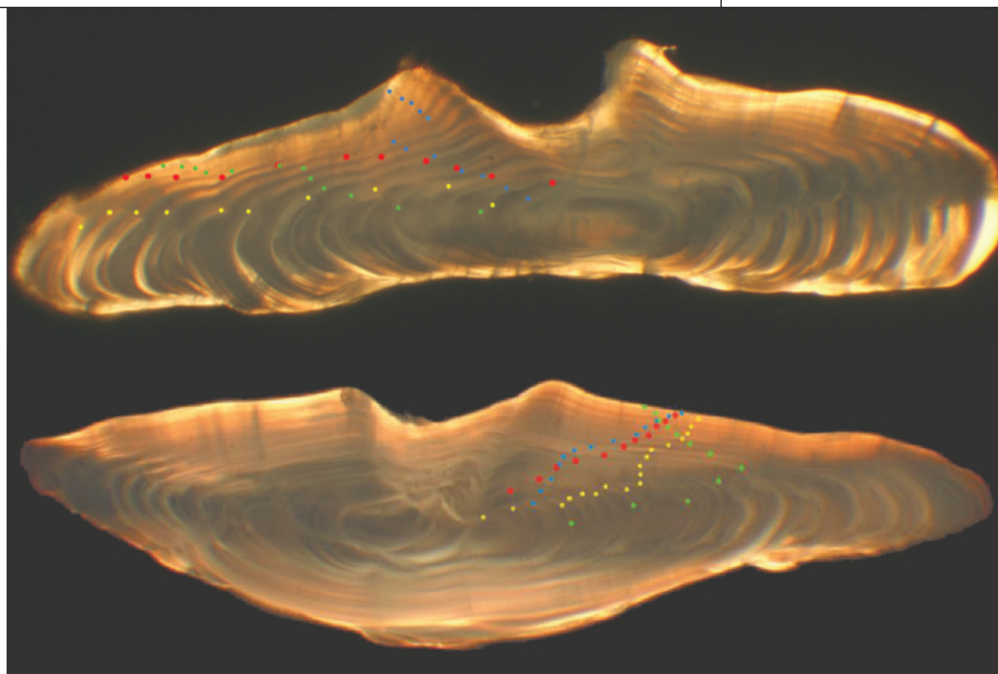
Stewart was named a Fellow of the Fields Institute in 2002 and was awarded an honorary D.Sc. in 2003 by McMaster University. The library of the Fields Institute is named after him. The James Stewart Mathematics Centre was opened in October, 2003, at McMaster University.

James Drewry Stewart (1941-2014) - Obit

TROY DAY received the M.S. degree in biology from the University of British Columbia and the Ph.D. in mathematics from Queen's University. His first academic position was at the University of Toronto, before being recruited back to Queen's University as a Canada Research Chair in Mathematical Biology. He is currently Professor of Mathematics and Statistics and Professor of Biology. His research group works in areas ranging from applied mathematics to experimental biology. Day is also coauthor of the widely used book *A Biologist's Guide to Mathematical Modeling,* published by Princeton University Press in 2007.

Differential Equations

7



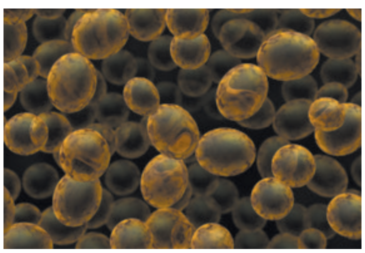
Shown are otoliths from Atlantic redfish—they were used to estimate fish age when fitting the von Bertalanffy differential equation in Example 7.4.2.

Dr. Cristoph Stransky / Thuenen Institute of Sea Fisheries

ONE OF THE MOST IMPORTANT applications of calculus is to differential equations. A wide variety of biological processes can be modeled using differential equations, and such equations have provided enormous insight into our understanding of the dynamics of living organisms—how individuals and populations change over time.

7.1 Modeling with Differential Equations

Many biological processes occur continuously through time. Examples include the change in concentration of a drug in the bloodstream of a patient, or the growth in mass of individual organisms. Even the population dynamics of many species, from size of bacteria colonies to the size of the human population, are sometimes best modeled by assuming the quantity of interest (population size, in this case) changes continuously through time. (For example, see page 146.) As we will see in this chapter, differential equations provide a convenient and natural way to construct such models.



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Models of Population Growth

A **differential equation** is an equation that contains an unknown function and one or more of its derivatives. Such equations arise in a variety of situations but one of the most common is in models of population growth.

Consider the growth of a population of yeast. Yeast are single-celled organisms used for a variety of purposes, including alcohol production and baking. Researchers collected the data in Table 1 from a yeast population grown in liquid culture, measuring the population size (in number of individuals per mL of culture) at different points in time (in hours).[1] Figure 1 is a scatter plot of these data.

Table 1

Time (h)	Pop. size ($\times 10^6$/mL)	Time (h)	Pop. size ($\times 10^6$/mL)
0	0.200	19	209
1	0.330	20	190
2	0.500	21	210
3	1.10	22	200
4	1.40	23	215
5	3.10	24	220
6	3.50	25	200
7	9.00	26	180
8	10.0	27	213
9	25.4	28	210
10	27.0	29	210
11	55.0	30	220
12	76.0	31	213
13	115	32	200
14	160	33	211
15	162	34	200
16	190	35	208
17	193	36	230
18	190		

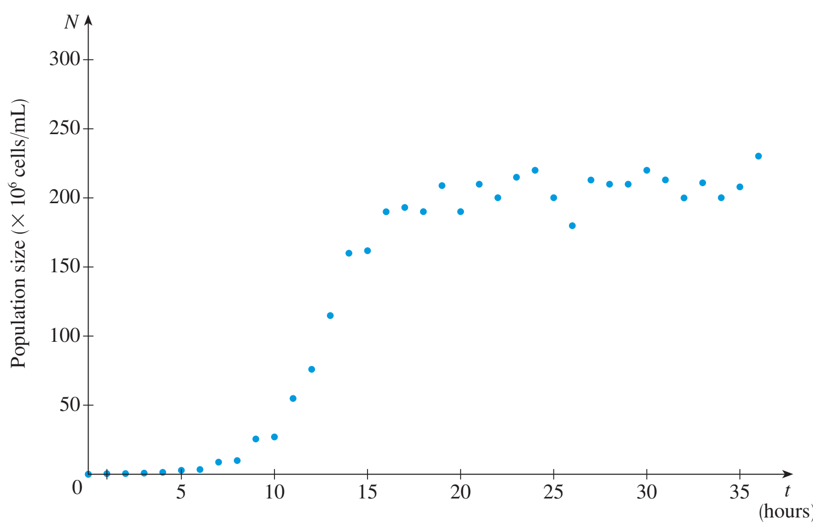


FIGURE 1 A scatter plot of the data in Table 1

1. B. K. Mable et al., "Masking and Purging Mutations following EMS Treatment in Haploid, Diploid, and Tetraploid Yeast (*Saccharomyces cerevisiae*)," *Genetical Research* 77 (2001): 9–26.

Although the population size in Table 1 was measured at one-hour intervals, the yeast themselves are replicating in a way that is nearly continuous in time. In other words, no matter how small we make the interval of time between successive measurements, some reproduction and death will likely have occurred.

BB

How can we model such processes? Let's start simply and assume that each individual yeast cell produces offspring at a constant rate β. Thus the total rate of offspring production (that is, the total birth rate) at time t is $\beta N(t)$, where $N(t)$ is the number of yeast cells present at time t. Likewise, suppose the total loss rate of yeast cells through death at time t is $\mu N(t)$, where μ is a constant death rate per individual cell.

With the preceding assumptions, we see that the rate of change of the number of yeast cells at time t is the total birth rate minus the total death rate, $\beta N(t) - \mu N(t)$. And since the rate of change of $N(t)$, the number of yeast cells, can also be written as $dN(t)/dt$, we can write

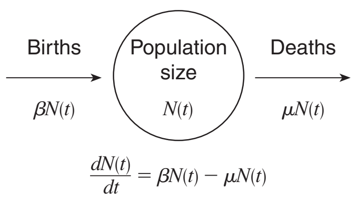


FIGURE 2

$$\textbf{(1)} \qquad \frac{dN(t)}{dt} = \beta N(t) - \mu N(t)$$

(See Figure 2.) Now if we define the constant r as

$$\textbf{(2)} \qquad r = \beta - \mu$$

then Equation 1 can be written more simply as

$$\textbf{(3)} \qquad \frac{dN(t)}{dt} = rN(t)$$

Equation 3 can be derived directly by simply *assuming* that the yeast population grows at a rate proportional to its size. The rate of growth of the population is the derivative dN/dt, and therefore we obtain Equation 3, where r is a constant of proportionality. See Equation 3.6.1, where it was called the *law of natural growth*.

The quantity r in Equation 2 is called the **per capita growth rate**. It is the rate of growth of the population *per individual* in the population. Since dN/dt is the rate of growth of the population, the rate of growth *per individual* is dN/dt divided by $N(t)$. From Equation 3, we get

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

showing that r is indeed the per capita growth rate.

Equation 3 involves the unknown function $N(t)$ along with its first derivative and is therefore a differential equation. The population size N is the *dependent variable* and time t is the *independent variable*. This differential equation tells us that the rate of change of the population size of yeast at any time is proportional to the size of the population at that time. Put another way, the rate of reproduction of each individual in the population (that is, the *per capita* rate of reproduction) is constant and equal to r.

The model given by Equation 3 is one of the simplest models for population growth. Let's see how well it predicts the data in Table 1. First notice that if $r > 0$, then from Equation 3

$$\frac{dN(t)}{dt} = rN(t) > 0$$

Biologically, if the per capita growth rate is positive (meaning that the birth rate β is larger than the death rate μ), then the yeast population will increase. On the other hand, if $r < 0$ (the birth rate β is smaller than the death rate μ), then from Equation 3

$$\frac{dN(t)}{dt} = rN(t) < 0$$

and the yeast population will decrease.

To make more progress, we would like to obtain an explicit function $N(t)$ that tells us exactly what the population size will be at any time. Such a function $N(t)$ is called a *solution* of the differential equation. It is a function that, when substituted into both sides of the differential equation, produces an equality.

Equation 3 tells us that $N(t)$ is a function whose derivative is equal to the function itself, multiplied by a constant, r. As we have seen in Chapter 3, exponential functions have exactly this property. In fact we can see that the function $N(t) = Ce^{rt}$ satisfies the differential equation. In particular, substituting this choice of $N(t)$ into Equation 3, we obtain

$$N'(t) = C(re^{rt}) = r(Ce^{rt}) = rN(t)$$

demonstrating that $N(t) = Ce^{rt}$ does, in fact, satisfy the differential equation. (We will see in Section 7.4 that there is no other solution.) Here C is an arbitrary constant. We can obtain a biological interpretation of this constant by setting $t = 0$: This gives $N(0) = Ce^{r(0)} = C$, revealing that C is the population size at $t = 0$. Figure 3 shows examples of the solution curves for different values of C when $r > 0$.

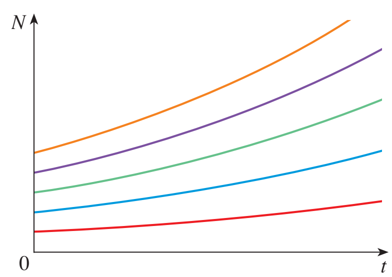


FIGURE 3
The family of solutions $N(t) = Ce^{rt}$ with $r > 0$, $t \geqslant 0$, and different values of C

We can already see from Figure 3 that Equation 3 does not capture all of the features of the data in Figure 1. For example, it appears to predict continued population growth. To obtain a more satisfying comparison, however, we should choose appropriate values for the constants C and r.

From the data in Table 1 we see that $N(0) = 0.200$ and therefore $C = 0.200$. One way to obtain a suitable value for r is to consider the factor by which the population of yeast grew over some fixed period of time. For example, in the first hour the yeast population grew by a factor of

$$\frac{0.330}{0.200} = 1.65$$

On the other hand, according to the model, the factor by which this population is predicted to have grown is

$$\frac{N(1)}{N(0)} = \frac{Ce^{r \cdot 1}}{Ce^{r \cdot 0}} = e^r$$

Therefore a reasonable choice for r would be the value for which $e^r = 1.65$. Solving this equation for r gives $r = \ln 1.65 \approx 0.5$. Thus, our final model is

$$N(t) = 0.2e^{0.5t}$$

Figures 4(a) and 4(b) both plot this equation along with the data from Table 1, but on two different intervals of time. The model provides remarkably accurate predictions over the first 13 or so hours, as shown in Figure 4(a), but its predictions are extremely inaccurate for later time points in the data [see Figure 4(b)].

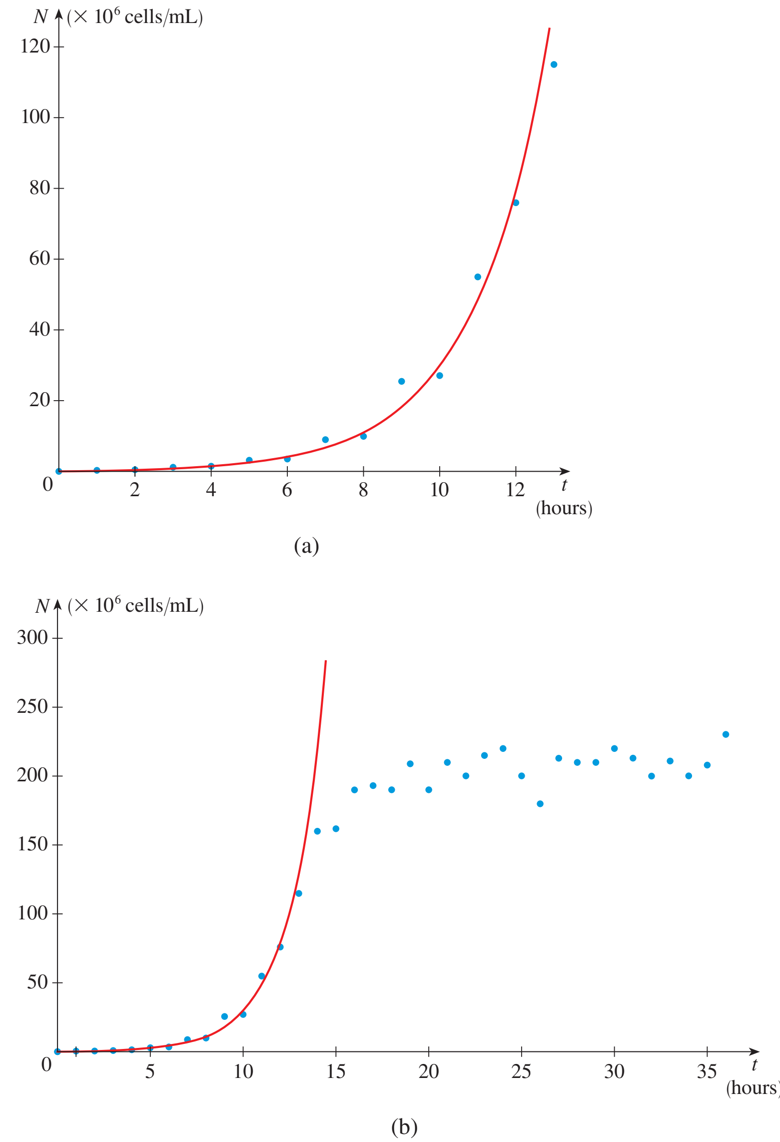


FIGURE 4

In retrospect, one obvious biological reason for this discrepancy is that the model assumes the per capita growth rate remains constant at r, regardless of the population size. In reality, as the population gets large, we might expect that crowding and resource depletion will cause the per capita growth rate to decline.

BB In fact, using the data in Table 1, it is possible to show that the per capita growth rate for the yeast population varies as a function of population size according to the equation

See Exercise 11.3.25.

$$\text{per capita growth rate} \approx 0.55 - 0.0026N$$

In other words,

$$\frac{dN(t)}{dt}\frac{1}{N(t)} \approx 0.55 - 0.0026N(t)$$

Thus a better differential equation for modeling the yeast population is

$$\frac{dN}{dt} = (0.55 - 0.0026N)N$$

We will learn how to analyze differential equations of this form in later sections. For now we simply note that these techniques can be used to show that the solution is

$$N(t) = \frac{42e^{0.55t}}{209.8 + 0.2e^{0.55t}}$$

(See Exercise 18.) This function is plotted in Figure 5 along with the data from Table 1. We see that this model provides quite accurate predictions over the entire time period of the experiment.

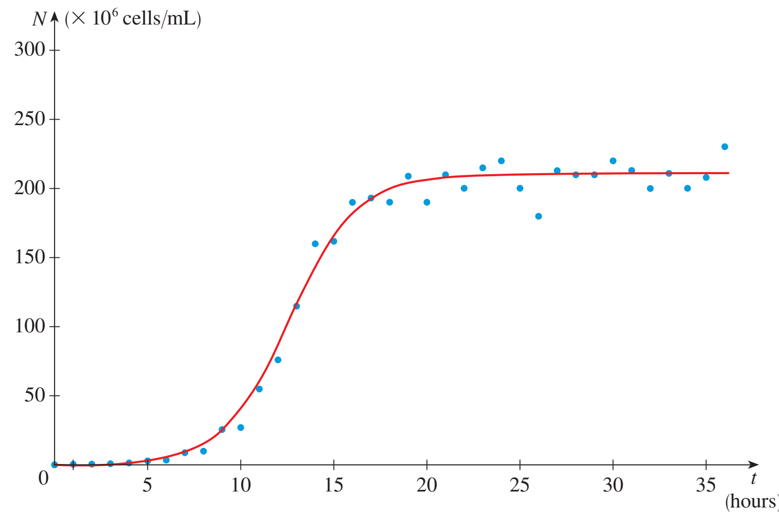


FIGURE 5

Our revised yeast model is a specific example of a more general model for population growth called the *logistic differential equation*. Suppose that the per capita growth rate of a population decreases linearly as the population size increases, from a value of r when $N = 0$ to a value of 0 when $N = K$. The positive constant K is referred to as the *carrying capacity*; it is the population size at which crowding and resource depletion cause the per capita growth rate to be zero. In Exercise 16 you are asked to show that this results in the differential equation

The logistic growth equation was first proposed by Dutch mathematical biologist Pierre-François Verhulst in the 1840s as a model for world population growth.

$$\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right)N \tag{4}$$

Equation 4 is called the **logistic differential equation**, or more simply the **logistic equation**. In Exercise 17 you are asked to show that, for the yeast model, $r = 0.55$ and $K \approx 210$.

We can obtain some qualitative features of the solutions of Equation 4 by inspection. We first observe that the constant functions $N(t) = 0$ and $N(t) = K$ are solutions because, in either case, the left side of Equation 4 is then zero (the derivative of a constant is zero), and the right side is zero as well. Such constant solutions are called *equilibrium solutions*. (A formal definition of an equilibrium solution will be given in Section 7.2.)

If the initial population $N(0)$ lies between 0 and K, then the right side of Equation 4 is positive, so $N'(t) > 0$ and the population increases (assuming $r > 0$). But if the population exceeds the carrying capacity ($N > K$), then $1 - N/K$ is negative, so $N'(t) < 0$ and the population decreases. In either case, if the population approaches the carrying capacity ($N \to K$), then $N'(t) \to 0$, which means the population levels off.

■ Classifying Differential Equations

Differential equations involve an unknown function and its derivatives. The **order** of the differential equation is the order of the highest derivative appearing in the equation. For example, $y'(t) + 2y(t) = 3$ is a first-order differential equation, whereas $5y''(t) - y'(t) = y(t)$ is a second-order differential equation. The **solution** of a differential equation is a function that, when substituted into the equation, produces an equality. For example, we can verify that the function $y(t) = e^t - 2$ is a solution of the differential equation $dy/dt = 2 + y(t)$ as follows: Substituting the function into the left side of this differential equation gives

$$\frac{dy}{dt} = \frac{d}{dt}(e^t - 2) = e^t$$

and substituting it into the right side gives

$$2 + (e^t - 2) = e^t$$

The right and left sides evaluate to the same expression, demonstrating that the function $y(t) = e^t - 2$ is indeed a solution.

Typically, there are several solutions to a differential equation. In many problems we need to find the particular solution that satisfies an additional condition of the form $y(t_0) = y_0$. This is called an **initial condition**. The problem of finding a solution of the differential equation that also satisfies an initial condition is called an **initial-value problem**. Graphically, when we impose an initial condition, we look at the family of solution curves and pick the one that passes through the point (t_0, y_0). For an example involving the logistic equation, see Figure 6. This corresponds to measuring the state of a system at time t_0 and using the solution of the initial-value problem to predict the future behavior of the system.

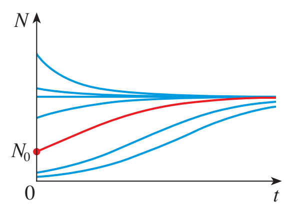


FIGURE 6
The family of solutions of the logistic equation. The solution curve satisfying the initial condition $N(0) = N_0$ is shown in red.

Verifying a solution is relatively easy, but obtaining a solution in the first place may not be. The difficulty of this task—and indeed whether or not it is even possible—is determined by the type of the differential equation. We consider three types of first-order differential equations: pure time, autonomous, and nonautonomous differential equations.

Pure-Time Differential Equations

Pure-time differential equations involve the derivative of the function but not the function itself. For example, if the rate of change of population size y depends on time only, this results in a differential equation of the form

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

We have already studied this type of equation in the context of antidifferentiation (in Section 4.6) and integration (in Chapter 5). We can obtain the solution $y(t)$ by calculating the antiderivative of $f(t)$. Although we refer to such equations as *pure-time differential equations*, the independent variable need not be time.

EXAMPLE 1 | **Spatial species distributions** As we move up a stream from its mouth toward its source, suppose that the population size n of a species of insect at a fixed point in time changes over space according to

$$\frac{dn}{dx} = 1 - 2e^{-x}$$

where $0 \leqslant x \leqslant 10$ is the spatial location (in km) between the mouth ($x = 0$ km) and a dam ($x = 10$ km). (This situation is described in Figure 7.) Suppose the population size at the dam is $n(10) = 20$. Obtain an expression for the population size as a function of distance from the mouth.

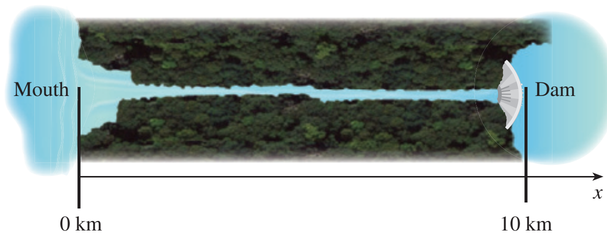


FIGURE 7
Population density along a stream

SOLUTION We first seek a function $n(x)$ that satisfies the given differential equation. This function can be obtained by integrating both sides of the differential equation with respect to x:

$$\frac{dn}{dx} = 1 - 2e^{-x}$$

$$\int \frac{dn}{dx}\,dx = \int (1 - 2e^{-x})\,dx$$

$$n(x) = x + 2e^{-x} + C$$

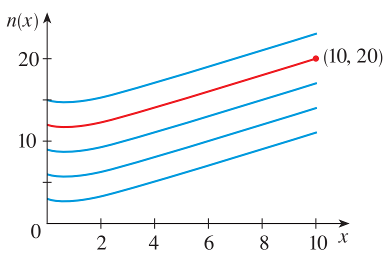


FIGURE 8
The family of solutions giving population size along the stream. The solution curve satisfying the initial condition $n(10) = 20$ is shown in red.

The function $n(x) = x + 2e^{-x} + C$ is a family of solutions. We now need to choose the specific function from this family that satisfies the condition $n(10) = 20$. Substituting $x = 10$ into $n(x)$ gives

$$n(10) = 10 + 2e^{-10} + C = 20$$

This tells us that we must choose $C = 10 - 2e^{-10}$. Therefore the population size as a function of x is $n(x) = x + 2e^{-x} + 10 - 2e^{-10}$. See Figure 8. ■

Autonomous Differential Equations

Autonomous differential equations arise when the equation involves both the derivative of the function and the function itself, but when there is no explicit dependence on the independent variable. Such equations have the general form

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

where y is the unknown function of the independent variable t. Equations 3 and 4 are examples of autonomous differential equations.

EXAMPLE 2 | **BB** **Modeling intravenous drug delivery** Often the rate at which the body metabolizes a drug is proportional to the current concentration of the drug. In other words, if $y(t)$ is the concentration of a drug in the bloodstream at time t

(measured in mg/mL), then

$$\text{outflow of drug through metabolism} = ky$$

where k is a positive constant of proportionality (with units 1/hour).

For drugs administered through a constant intravenous supply, the concentration in the bloodstream will also be replenished at a rate that is determined by the drug concentration in the supply:

$$\text{inflow of drug through IV supply} = A$$

where A is a positive constant with units mg/(mL hour). The total rate of change of concentration resulting from both processes (that is, dy/dt) is therefore

$$\frac{dy}{dt} = \text{inflow} - \text{outflow}$$

or

$$\frac{dy}{dt} = A - ky \tag{5}$$

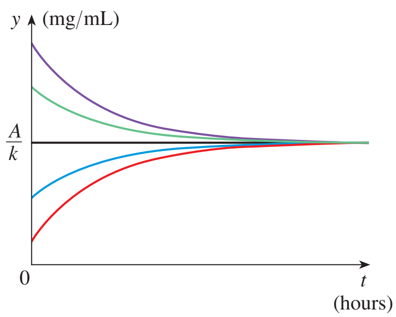


FIGURE 9
The family of solutions of Equation 5

Equation 5 is an autonomous differential equation because it involves the dependent variable y but not the independent variable t. Figure 9 shows a family of solutions to differential equation (5), and suggests that the drug concentration is predicted to approach a limiting value of A/k at time passes, regardless of the initial concentration. ■

Nonautonomous Differential Equations

Nonautonomous differential equations are a combination of pure-time and autonomous differential equations. They arise when the equation involves the function and its derivative, and the independent variable appears explicitly as well.

EXAMPLE 3 | Administering drugs A drug is administered to a patient intravenously at a time-varying rate of $A(t) = 1 + \sin t$ mg/(mL hour), and is metabolized at a rate of $y(t)$ mg/(mL hour), where $y(t)$ is the concentration at time t (in units of mg/mL). Thus y obeys the differential equation

$$\frac{dy}{dt} = 1 + \sin t - y \tag{6}$$

Verify that the family of functions $y(t) = Ce^{-t} + \frac{1}{2}(2 - \cos t + \sin t)$ satisfies the differential equation.

SOLUTION Substituting $y(t)$ into the left side of the differential equation (6) gives $-Ce^{-t} + \frac{1}{2}(\sin t + \cos t)$. Substituting it into the right side gives

$$\begin{aligned} 1 + \sin t - y &= 1 + \sin t - Ce^{-t} - \tfrac{1}{2}(2 - \cos t + \sin t) \\ &= -Ce^{-t} + \tfrac{1}{2}(\sin t + \cos t) \end{aligned}$$

Since both quantities are the same, this family of functions y satisfies the differential equation. ■

EXAMPLE 4 | Administering drugs (continued) What is the drug concentration as a function of time for the model in Example 3 if the initial drug concentration at $t = 0$ is zero?

SOLUTION We seek the specific member from the family of functions, $y(t) = Ce^{-t} + \frac{1}{2}(2 - \cos t + \sin t)$, that also satisfies $y(0) = 0$. Evaluating, we obtain

$$y(0) = Ce^{-0} + \tfrac{1}{2}(2 - \cos 0 + \sin 0) = C + \tfrac{1}{2} = 0$$

and therefore $C = -\frac{1}{2}$. Thus the solution to the *initial-value problem* is $y(t) = \frac{1}{2}(2 - e^{-t} - \cos t + \sin t)$, as shown in Figure 10. ■

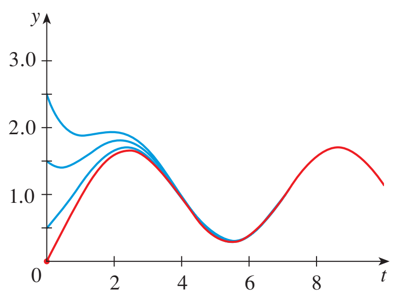


FIGURE 10
The family of solutions giving drug concentration $y(t)$. The solution curve satisfying the initial condition $y(0) = 0$ is shown in red.

EXERCISES 7.1

1. Show that $y = \frac{2}{3}e^x + e^{-2x}$ is a solution of the differential equation $y' + 2y = 2e^x$. Is this differential equation pure-time, autonomous, or nonautonomous?

2. Verify that $y = -t\cos t - t$ is a solution of the initial-value problem

$$t\frac{dy}{dt} = y + t^2 \sin t \qquad y(\pi) = 0$$

Is this differential equation pure-time, autonomous, or nonautonomous?

3. Show that $y = e^{-at}\cos t$ is a solution of the differential equation $y' = -e^{-at}(a\cos t + \sin t)$. Is this differential equation pure-time, autonomous, or nonautonomous?

4. (a) Show that every member of the family of functions $y = (\ln x + C)/x$ is a solution of the differential equation $x^2y' + xy = 1$.
(b) Illustrate part (a) by graphing several members of the family of solutions on a common screen.
(c) Find a solution of the differential equation that satisfies the initial condition $y(1) = 2$.
(d) Find a solution of the differential equation that satisfies the initial condition $y(2) = 1$.

5. (a) What can you say about a solution of the equation $y' = -y^2$ just by looking at the differential equation?
(b) Verify that all members of the family $y = 1/(x + C)$ are solutions of the equation in part (a).
(c) Can you think of a solution of the differential equation $y' = -y^2$ that is not a member of the family in part (b)?
(d) Find a solution of the initial-value problem

$$y' = -y^2 \qquad y(0) = 0.5$$

6. (a) What can you say about the graph of a solution of the equation $y' = xy^3$ when x is close to 0? What if x is large?
(b) Verify that all members of the family $y = (c - x^2)^{-1/2}$ are solutions of the differential equation $y' = xy^3$.
(c) Graph several members of the family of solutions on a common screen. Do the graphs confirm what you predicted in part (a)?
(d) Find a solution of the initial-value problem

$$y' = xy^3 \qquad y(0) = 2$$

7. Logistic growth A population is modeled by the differential equation

$$\frac{dN}{dt} = 1.2N\left(1 - \frac{N}{4200}\right)$$

where $N(t)$ is the number of individuals at time t (measured in days).
(a) For what values of N is the population increasing?
(b) For what values of N is the population decreasing?
(c) What are the equilibrium solutions?

8. The Fitzhugh-Nagumo model for the electrical impulse in a neuron states that, in the absence of relaxation effects, the electrical potential in a neuron $v(t)$ obeys the differential equation

$$\frac{dv}{dt} = -v[v^2 - (1 + a)v + a]$$

where a is a constant and $0 < a < 1$.

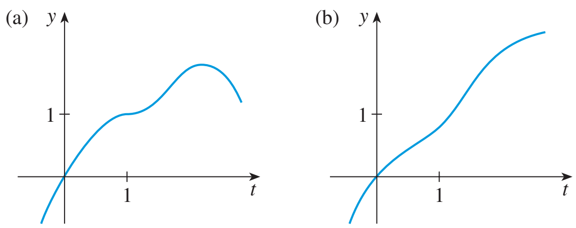
(a) For what values of v is v unchanging (that is, $dv/dt = 0$)?

(b) For what values of v is v increasing?

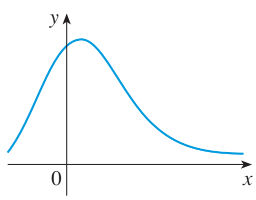
(c) For what values of v is v decreasing?

9. Explain why the functions with the given graphs *can't* be solutions of the differential equation

$$\frac{dy}{dt} = e^t(y - 1)^2$$



10. The function with the given graph is a solution of one of the following differential equations. Decide which is the correct equation and justify your answer.

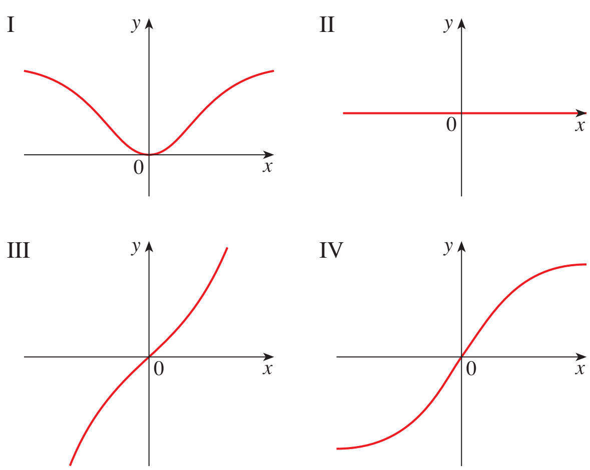


A. $y' = 1 + xy$ **B.** $y' = -2xy$ **C.** $y' = 1 - 2xy$

11. Match the differential equations with the solution graphs labeled I–IV. Give reasons for your choices.

(a) $y' = 1 + x^2 + y^2$ (b) $y' = xe^{-x^2-y^2}$

(c) $y' = \dfrac{1}{1 + e^{x^2+y^2}}$ (d) $y' = \sin(xy)\cos(xy)$



12. Von Bertalanffy's equation states that the rate of growth in length of an individual fish is proportional to the difference between the current length L and the asymptotic length L_∞ (in cm).

(a) Write a differential equation that expresses this idea.

(b) Make a rough sketch of the graph of a solution to a typical initial-value problem for this differential equation.

13–15 Drug dissolution Differential equations have been used extensively in the study of drug dissolution for patients given oral medications. The three simplest equations used are the zero-order kinetic equation, the Noyes-Whitney equation, and the Weibull equation. All assume that the initial concentration is zero but make different assumptions about how the concentration increases over time during the dissolution of the medication.

13. The **zero-order kinetic equation** states that the rate of change in the concentration of drug c (in mg/mL) during dissolution is governed by the differential equation

$$\frac{dc}{dt} = k$$

where k is a positive constant. Is this differential equation pure-time, autonomous, or nonautonomous? State in words what this differential equation says about how drug dissolution occurs. What is the solution of this differential equation with the initial condition $c(0) = 0$?

14. The **Noyes-Whitney equation** for the dynamics of the drug concentration is

$$\frac{dc}{dt} = k(c_s - c)$$

where k and c_s are positive constants. Is this differential equation pure-time, autonomous, or nonautonomous? State in words what this differential equation says about how drug dissolution occurs. Verify that $c = c_s(1 - e^{-kt})$ is the solution to this equation for the initial condition $c(0) = 0$.

15. The **Weibull equation** for the dynamics of the drug concentration is

$$\frac{dc}{dt} = \frac{k}{t^b}(c_s - c)$$

where k, c_s, and b are positive constants and $b < 1$. Notice that this differential equation is undefined when $t = 0$. Is this differential equation pure-time, autonomous, or nonautonomous? State in words what this differential equation says about how drug dissolution occurs. Verify that

$$c = c_s\left(1 - e^{-\alpha t^{1-b}}\right)$$

is a solution for $t \neq 0$, where $\alpha = k/(1 - b)$.

16. The logistic differential equation Suppose that the per capita growth rate of a population of size N declines linearly from a value of r when $N = 0$ to a value of 0 when $N = K$.

Show that the differential equation for N is

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

17. Modeling yeast populations Use the fact that the per capita growth rate of the yeast population in Table 1 is $0.55 - 0.0026N$ to show that, in terms of the logistic equation (4), $r = 0.55$ and $K \approx 210$.

18. Modeling yeast populations (cont.) Verify that

$$N(t) = \frac{42e^{0.55t}}{209.8 + 0.2e^{0.55t}}$$

is an approximate solution of the differential equation

$$\frac{dN}{dt} = (0.55 - 0.0026N)N$$

■ PROJECT Chaotic Blowflies and the Dynamics of Populations

BB

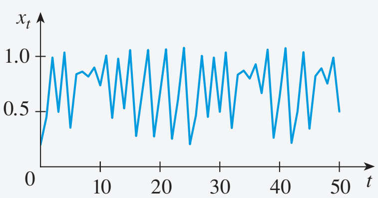


FIGURE 1
x is plotted against time with $x_0 = 0.1$ and $R_{max} = 3.89$.

In Section 1.6 we explored the dynamics of the logistic difference equation. After some simplification, the population size in successive times steps was given by the recursion

(1) $$x_{t+1} = R_{max}x_t(1 - x_t)$$

where R_{max} is a positive constant. See Equation 1.6.7. For large enough values of R_{max} the recursion exhibits very complicated behavior, as shown in Figure 1. In fact, Equation 1 is famous for being one of the simplest recursions that exhibits chaotic dynamics.[1]

The plots for the logistic differential equation that we have seen in Section 7.1 do not exhibit this type of complicated behavior. Here we explore why. To do so, we will derive the logistic differential equation from the logistic difference equation.

1. In Section 1.6 we obtained Equation 1 by starting with the equation

$$N_{t+1} = [1 + r(1 - N_t/K)]N_t$$

(See Equation 1.6.5.) If the time interval is of length h instead, where $h < 1$, then this equation becomes

$$N_{t+h} = [1 + rh(1 - N_t/K)]N_t$$

Use this result to derive a differential equation for N by writing an expression for $\dfrac{N_{t+h} - N_t}{h}$ and then letting $h \to 0$.

2. Show that with the change of variables $y = N/K$ the differential equation from Problem 1 can be written as $dy/dt = ry(1 - y)$.

3. In Section 7.4 we will learn how to solve differential equations like the one in Problem 2. If $y(0) = y_0$, the solution is $y(t) = y_0/[e^{-rt} + y_0(1 - e^{-rt})]$. Sketch this solution for different choices of y_0 and r. This solution can never exhibit the sort of behavior of Equation 1 that is displayed in Figure 1. Explain why from a biological standpoint.

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A blowfly

The reason for the complicated dynamics in Figure 1 is the existence of a time-lag between the current population size x_t and its effects on population regulation. This allows the population to overshoot its carrying capacity. Once an overshoot occurs, a dramatic population decline will ensue. The resulting low population size then sets the stage for a large population rebound and another overshoot of the carrying capacity. Some

1. R. May, "Simple Mathematical Models with Very Complicated Dynamics," *Nature* 261 (1976): 459–67.

7.4 Separable Equations

We have looked at first-order differential equations from a geometric point of view (phase plots and direction fields) and from a numerical point of view (Euler's method). What about the symbolic point of view? It would be helpful to have an explicit formula for a solution of a differential equation. Although this is not always possible, in this section we examine a commonly encountered type of differential equation that *can* be solved explicitly.

A **separable equation** is a first-order differential equation in which the expression for dy/dt can be factored as a function of t times a function of y. In other words, it can be written in the form

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

The name separable comes from the fact that the expression on the right side can be separated into a function of t and a function of y. Equivalently, if $g(y) \neq 0$, we could write

$$\textbf{(1)} \qquad \frac{dy}{dt} = \frac{f(t)}{h(y)}$$

where $h(y) = 1/g(y)$. To solve this equation we rewrite it in the differential form

$$h(y)\, dy = f(t)\, dt$$

The technique for solving separable differential equations was first used by James Bernoulli (in 1690) in solving a problem about pendulums and by Leibniz (in a letter to Huygens in 1691). John Bernoulli explained the general method in a paper published in 1694.

so that all y's are on one side of the equation and all t's are on the other side. Then we integrate both sides of the equation:

$$\textbf{(2)} \qquad \int h(y)\, dy = \int f(t)\, dt$$

Equation 2 defines y implicitly as a function of t. In some cases we may be able to solve for y in terms of t.

We can verify that Equation 2 is indeed a solution using the Chain Rule: If h and f satisfy (2), then

$$\frac{d}{dt}\left(\int h(y)\, dy\right) = \frac{d}{dt}\left(\int f(t)\, dt\right)$$

so $$\frac{d}{dy}\left(\int h(y)\, dy\right)\frac{dy}{dt} = f(t)$$

and $$h(y)\frac{dy}{dt} = f(t)$$

Thus Equation 1 is satisfied.

One of the simplest applications of the technique of separation of variables is to the differential equation for exponential growth introduced in Sections 3.6 and 7.1. In particular, if $y(t)$ is the value of some quantity at time t and if the rate of change of y with respect to t is proportional to its size $y(t)$, then

$$\frac{dy}{dt} = ky$$

where k is a constant. If $y \neq 0$ we can write this equation in terms of differentials and integrate both sides as follows:

$$\int \frac{dy}{y} = \int k\,dt$$

$$\ln |y| = kt + C$$

$$|y| = e^{kt+C} = e^C e^{kt}$$

$$y = Ae^{kt}$$

The absolute value can be cleared by noting that we can write

$$y = e^C e^{kt} \quad \text{if } y > 0$$

$$y = -e^C e^{kt} \quad \text{if } y < 0$$

Therefore $y = Ae^{kt}$, where $A = \pm e^C$.

where A ($= \pm e^C$) is an arbitrary constant. This is the solution presented in Sections 3.6 and 7.1. If $y = 0$ we cannot divide the differential equation by y. However, we can readily verify that, in this case, $y = 0$ is also a solution. Therefore the constant A in the solution $y = Ae^{kt}$ can also be 0. This corresponds to an equilibrium solution.

EXAMPLE 1

(a) Solve the differential equation $\dfrac{dy}{dx} = \dfrac{x^2}{y^2}$.

(b) Find the solution of this equation that satisfies the initial condition $y(0) = 2$.

SOLUTION

(a) We write the equation in terms of differentials and integrate both sides:

$$y^2 dy = x^2 dx$$

$$\int y^2 dy = \int x^2 dx$$

$$\tfrac{1}{3}y^3 = \tfrac{1}{3}x^3 + C$$

where C is an arbitrary constant. (We could have used a constant C_1 on the left side and another constant C_2 on the right side. But then we could combine these constants by writing $C = C_2 - C_1$.)

Solving for y, we get

$$y = \sqrt[3]{x^3 + 3C}$$

We could leave the solution like this or we could write it in the form

$$y = \sqrt[3]{x^3 + K}$$

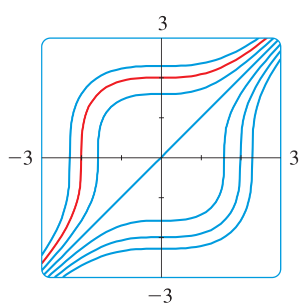


FIGURE 1
Graphs of several members of the family of solutions of the differential equation in Example 1. The solution of the initial-value problem in part (b) is shown in red.

where $K = 3C$. (Since C is an arbitrary constant, so is K.) Figure 1 plots this family of solutions.

(b) If we put $x = 0$ in the general solution in part (a), we get $y(0) = \sqrt[3]{K}$. To satisfy the initial condition $y(0) = 2$, we must have $\sqrt[3]{K} = 2$ and so $K = 8$. Thus the solution of the initial-value problem is

$$y = \sqrt[3]{x^3 + 8}$$

■

EXAMPLE 2 | **The von Bertalanffy growth equation** A commonly used differential equation for the growth, in length, of an individual fish is

$$\frac{dL}{da} = k(L_\infty - L)$$

Von Bertalanffy

Ludwig von Bertalanffy (1901–1972) was an Austrian-born biologist who first published this differential equation for individual growth in 1934. It captures the idea that the rate of growth in length is proportional to the difference between current length and asymptotic length.

where $L(a)$ is length (in cm) at age a (in years), L_∞ is the asymptotic length, and k is a positive constant whose units are $1/\text{year}$.

(a) Find a family of solutions for length as a function of age.

(b) Find the solution that has an initial length of $L(0) = 2$.

SOLUTION

(a) Assuming $L \neq L_\infty$, we can write the equation in differential form as

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

Now integrate to obtain

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

or

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

Now we can solve for L:

$$|L_\infty - L| = e^{-ka}e^{-C_1}$$

or

$$L = L_\infty - Ce^{-ka}$$

where $C = \pm e^{-C_1}$ is an arbitrary constant. An example of this solution with particular constant values is shown in Figure 2.

If $L = L_\infty$, we cannot divide the differential equation by $L - L_\infty$, but we can verify that $L = L_\infty$ is itself another solution. Thus the constant C in the preceding solution can be 0 as well, and this again corresponds to an equilibrium solution.

(b) Setting $a = 0$ in the family of solutions from part (a) gives $L(0) = L_\infty - C$. To satisfy the initial condition $L(0) = 2$, we therefore require that $L_\infty - C = 2$, or $C = L_\infty - 2$. The desired solution is thus $L = L_\infty - (L_\infty - 2)e^{-ka}$ or

$$L = L_\infty(1 - e^{-ka}) + 2e^{-ka}$$

From this we can see why L_∞ is called the asymptotic length. As $a \to \infty$, $L \to L_\infty$. ■

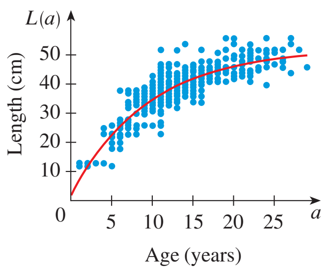


FIGURE 2
Age-length relationship for Atlantic redfish along with the solution to the von Bertalanffy equation with constants specific to redfish.

Source: Adapted from C. Stransky et al., "Age Determination and Growth of Atlantic Redfish (*Sebastes marinus* and *S. mentella*): Bias and Precision of Age Readers and Otolith Preparation Methods," *ICES Journal of Marine Science* 62 (2005): 655–70.

EXAMPLE 3 | Allometric growth During growth, the claw of fiddler crabs increases in length at a *per unit rate* that is 1.57 times larger than that of its overall body width. In other words, if L and B denote claw length and body width, respectively (in mm), then

$$\frac{dL}{dt}\frac{1}{L} = 1.57\,\frac{dB}{dt}\frac{1}{B}$$

(See Figure 3.) Find an equation that specifies claw length as a function of body width at any point during growth.

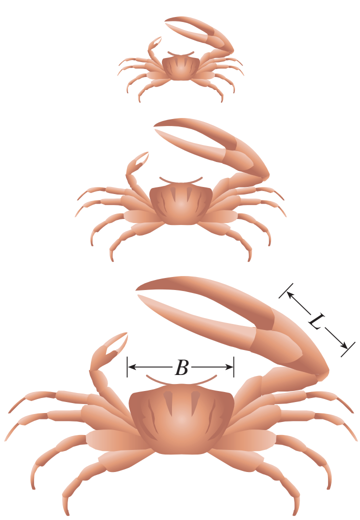


FIGURE 3
Three crabs of different sizes, along with their claw lengths

SOLUTION Multiplying both sides by dt gives

$$\frac{dL}{L} = 1.57\,\frac{dB}{B}$$

Now integrate both sides to get

$$\ln L = 1.57 \ln B + C$$

On a log-log plot this is a straight line. Figure 4 plots data displaying this relationship. We can also rearrange our solution to the differential equation to obtain a power function for allometric scaling like those in Sections 1.2 and 1.5. Defining $k = e^C$, we obtain

$$L = kB^{1.57}$$

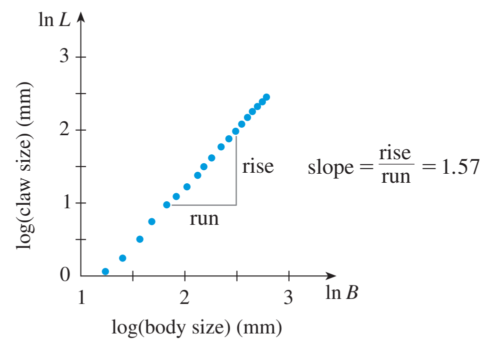


FIGURE 4
Data for the relationship between claw length and body width on a log-log plot

EXAMPLE 4 | Population dynamics Suppose the *per capita growth rate* of a population decreases as the population size n increases, in a way that is described by the expression $1/(1 + n)$. The differential equation for n is therefore

$$\frac{1}{n}\frac{dn}{dt} = \frac{1}{1+n}$$

Solve this differential equation.

SOLUTION Writing the equation in differential form gives

$$\int \frac{1+n}{n}\,dn = \int dt$$

(3) $$\ln n + n = t + C$$

where C is an arbitrary constant. Equation 3 gives the family of solutions implicitly. In this case it's impossible to solve the equation to express n explicitly as a function of t.

The Gompertz differential equation assumes that the *per volume growth rate* of the tumor declines as the tumor volume gets larger according to the expression $a(\ln b - \ln V)$. Notice that the tumor growth rate is zero when $V = b$, where b represents the asymptotic tumor volume.

EXAMPLE 5 | Gompertz model of tumor growth The Gompertz differential equation models the growth of a tumor in volume V (in mm^3) and is given by

$$\frac{dV}{dt} = a(\ln b - \ln V)V$$

where a and b are positive constants.

(a) Find a family of solutions for tumor volume as a function of time.

(b) Find the solution that has an initial tumor volume of $V(0) = 1\ \text{mm}^3$.

SOLUTION First note that $\ln b - \ln V = \ln(b/V)$. Therefore, assuming $V \neq 0$ and $V \neq b$, we can write the equation in differential form and integrate as

$$\int \frac{dV}{V[\ln(b/V)]} = \int a\,dt$$

We can then integrate the left side using the substitution $u = \ln(b/V)$. We get

$$-\ln|\ln(b/V)| = at + C_1$$

Now we can solve for V by exponentiating both sides twice:

$$\ln(b/V) = Ce^{-at}$$

and then

$$b/V = e^{Ce^{-at}}$$

or

$$V = be^{-Ce^{-at}}$$

where $C = \pm e^{-C_1}$ is an arbitrary constant.

On the other hand, we can verify that $V = b$ is also an (equilibrium) solution.

(b) Setting $t = 0$ in the family of solutions from part (a) gives $V(0) = be^{-C}$. To satisfy the initial condition $V(0) = 1$, we therefore require that $1 = be^{-C}$ or $0 = \ln b - C$. Therefore the desired solution is $V = be^{-(\ln b)e^{-at}}$ or

$$V = b(e^{-\ln b})^{e^{-at}} \quad \Rightarrow \quad V = b\left(\frac{1}{b}\right)^{e^{-at}}$$

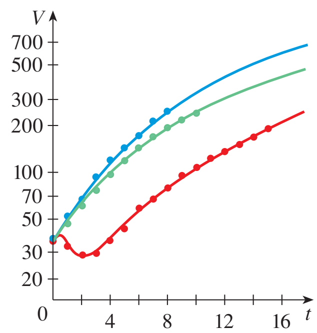


FIGURE 5
The solution of the Gompertz model fitted to tumor data.

Source: Adapted from D. Miklavčič et al., "Mathematical Modelling of Tumor Growth in Mice Following Electrotherapy and Bleomycin Treatment," *Mathematics and Computers in Simulation* 39 (1995): 597–602.

Figure 5 shows model predictions and data for three different sets of constant values with initial condition $V(0) = 35$. ■

EXAMPLE 6 | **The logistic equation** Find the solution to the following initial-value problem involving the logistic equation:

$$\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right)N \qquad N(0) = N_0$$

SOLUTION Assuming $N \neq 0$ and $N \neq K$, we can write the equation in differential form and integrate as

(4)
$$\int \frac{dN}{(1 - N/K)N} = \int r\,dt$$

To evaluate the integral on the left side, we write

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

Using partial fractions (see Section 5.6), we get

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

This enables us to rewrite Equation 4:

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

$$\ln|N| - \ln|K - N| = rt + C$$

$$\ln \left| \frac{K - N}{N} \right| = -rt - C$$

$$\left| \frac{K - N}{N} \right| = e^{-rt-C} = e^{-C}e^{-rt}$$

(5) $$\frac{K - N}{N} = Ae^{-rt}$$

where $A = \pm e^{-C}$. Solving Equation 5 for N, we get

$$\frac{K}{N} - 1 = Ae^{-rt} \qquad \Rightarrow \qquad \frac{N}{K} = \frac{1}{1 + Ae^{-rt}}$$

so $$N = \frac{K}{1 + Ae^{-rt}}$$

We find the value of A by putting $t = 0$ in Equation 5. If $t = 0$, then $N = N_0$ (the initial population), so

$$\frac{K - N_0}{N_0} = Ae^0 = A$$

Thus the solution to the logistic equation is

$$N(t) = \frac{K}{1 + Ae^{-rt}} \qquad \text{where } A = \frac{K - N_0}{N_0}$$

On the other hand, if $N = 0$, then we can verify that this is also an (equilibrium) solution. Likewise, $N = K$ is an equilibrium solution.

We can now return to the model of yeast growth from page 424. As mentioned in Section 7.1, the model output in Figure 7.1.5 comes from the logistic growth equation with constant values $N_0 = 0.2$, $K = 210$, and $r = 0.55$. Substituting these values into the solution that we just obtained gives (after some rearrangement)

$$N(t) = \frac{42e^{0.55t}}{209.8 + 0.2e^{0.55t}}$$

This is exactly the solution presented on page 424. ■

EXERCISES 7.4

1–10 Solve the differential equation.

1. $\dfrac{dy}{dx} = xy^2$

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

3. $(x^2 + 1)y' = xy$

4. $(y^2 + xy^2)y' = 1$

5. $(y + \sin y)y' = x + x^3$

6. $\dfrac{du}{dr} = \dfrac{1 + \sqrt{r}}{1 + \sqrt{u}}$

7. $\dfrac{dy}{dt} = \dfrac{te^t}{y\sqrt{1 + y^2}}$

8. $\dfrac{dy}{d\theta} = \dfrac{e^y \sin^2\theta}{y \sec\theta}$

9. $\dfrac{du}{dt} = 2 + 2u + t + tu$

10. $\dfrac{dz}{dt} + e^{t+z} = 0$

11–18 Find the solution of the differential equation that satisfies the given initial condition.

11. $\dfrac{dy}{dx} = \dfrac{x}{y}, \quad y(0) = -3$

12. $\dfrac{dy}{dx} = \dfrac{\ln x}{xy}, \quad y(1) = 2$

13. $\dfrac{du}{dt} = \dfrac{2t + \sec^2 t}{2u}, \quad u(0) = -5$

14. $y' = \dfrac{xy \sin x}{y + 1}, \quad y(0) = 1$

15. $x \ln x = y\left(1 + \sqrt{3 + y^2}\right)y', \quad y(1) = 1$

16. $\dfrac{dP}{dt} = \sqrt{Pt}, \quad P(1) = 2$

17. $y' \tan x = a + y, \; y(\pi/3) = a, \quad 0 < x < \pi/2$

18. $\dfrac{dL}{dt} = kL^2 \ln t, \; L(1) = -1$

19. Find an equation of the curve that passes through the point $(0, 1)$ and whose slope at (x, y) is xy.

20. Find the function f such that $f'(x) = f(x)[1 - f(x)]$ and $f(0) = \frac{1}{2}$.

21. Solve the differential equation $y' = x + y$ by making the change of variable $u = x + y$.

22. Solve the differential equation $xy' = y + xe^{y/x}$ by making the change of variable $v = y/x$.

23. (a) Solve the differential equation $y' = 2x\sqrt{1 - y^2}$.
(b) Solve the initial-value problem $y' = 2x\sqrt{1 - y^2}$, $y(0) = 0$, and graph the solution.
(c) Does the initial-value problem $y' = 2x\sqrt{1 - y^2}$, $y(0) = 2$, have a solution? Explain.

24. Solve the equation $e^{-y}y' + \cos x = 0$ and graph several members of the family of solutions. How does the solution curve change as the constant C varies?

CAS 25. Solve the initial-value problem $y' = (\sin x)/\sin y$, $y(0) = \pi/2$, and graph the solution (if your CAS does implicit plots).

CAS 26. Solve the equation $y' = x\sqrt{x^2 + 1}/(ye^y)$ and graph several members of the family of solutions (if your CAS does implicit plots). How does the solution curve change as the constant C varies?

CAS **27–28**
(a) Use a computer algebra system to draw a direction field for the differential equation. Get a printout and use it to sketch some solution curves without solving the differential equation.
(b) Solve the differential equation.
(c) Use the CAS to draw several members of the family of solutions obtained in part (b). Compare with the curves from part (a).

27. $y' = y^2$

28. $y' = xy$

29–31 An **integral equation** is an equation that contains an unknown function $y(x)$ and an integral that involves $y(x)$. Solve the given integral equation. [*Hint:* Use an initial condition obtained from the integral equation.]

29. $y(x) = 2 + \int_2^x [t - ty(t)]\, dt$

30. $y(x) = 2 + \int_1^x \dfrac{dt}{ty(t)}, \quad x > 0$

31. $y(x) = 4 + \int_0^x 2t\sqrt{y(t)}\, dt$

32–34 Seasonality and habitat destruction The per capita growth rate of many species varies temporally for a variety of reasons, including seasonality and habitat destruction. Suppose $n(t)$ represents the population size at time t, where n is measured in individuals and t is measured in years. Solve the differential equation for habitat destruction and describe the predicted population dynamics.

32. $$n' = e^{-t}n \qquad n(0) = n_0$$

Here the per capita growth rate declines over time, but always remains positive. It is modeled by the function e^{-t}.

33. $$n' = (e^{-t} - 1)n \qquad n(0) = n_0$$

Here the per capita growth rate declines over time, starting at zero and becoming negative. It is modeled by the function $e^{-t} - 1$.

34. $$n' = (r - at)n \qquad n(0) = n_0$$

Here the per capita growth rate declines over time, going from positive to negative. It is modeled by the function $r - at$, where r and a are positive constants.

35. Noyes-Whitney drug dissolution Solve the initial-value problem in Exercise 7.1.14 for the Noyes-Whitney drug dissolution equation.

36. Weibull drug dissolution Solve the Weibull drug dissolution equation given in Exercise 7.1.15.

37–38 Bacteria colony growth In Exercises 1.6.35–36, we obtained difference equations for the growth of circular and spherical colonies of bacteria. These equations are based on the idea that nutrients for growth are available only at the colony–environment interface. Continous-time versions of these equations are presented here, where k is a positive constant and n is the number of bacteria (in thousands). Solve each differential equation to find the size of the colony as a function of time. Assume $n(0) = 1$.

37. $\dfrac{dn}{dt} = kn^{1/2}$ (circular colony)

38. $\dfrac{dn}{dt} = kn^{2/3}$ (spherical colony)

39. Tumor growth The Gompertz equation in Example 5 is not the only possibility for modeling tumor growth. Suppose that a tumor can be modeled as a spherical collection of cells and it acquires resources for growth only through its surface area (like the spherical bacterial colony in Exercise 38). All cells in a tumor are also subject to a constant per capita death rate. The dynamics of tumor mass M (in grams) might therefore be modeled as

$$\frac{dM}{dt} = kM^{2/3} - \mu M$$

where μ and k are positive constants. The first term represents tumor growth via nutrients entering through the surface. The second term represents a constant per capita death rate.

(a) Assuming that $k = 1$ and $M(0) = 1$, find M as a function of t.

(b) What happens to the tumor mass as $t \to \infty$?

(c) Assuming tumor mass is proportional to its volume, the diameter of the tumor is related to its mass as $D = aM^{1/3}$, where $a > 0$. Derive a differential equation for D and show that it has the form of the von Bertalanffy equation in Example 2.

40. In an elementary chemical reaction, single molecules of two reactants A and B form a molecule of the product C: $A + B \to C$. The law of mass action states that the rate of reaction is proportional to the product of the concentrations of A and B:

$$\frac{d[C]}{dt} = k[A][B]$$

Thus, if the initial concentrations are $[A] = a$ moles/L and $[B] = b$ moles/L and we write $x = [C]$, then we have

$$\frac{dx}{dt} = k(a - x)(b - x)$$

CAS (a) Assuming that $a \neq b$, find x as a function of t. Use the fact that the initial concentration of C is 0.

(b) Find $x(t)$ assuming that $a = b$. How does this expression for $x(t)$ simplify if it is known that $[C] = \frac{1}{2}a$ after 20 seconds?

41. Population genetics Exercise 7.2.16 derives the following equation from population genetics that specifies the evolutionary dynamics of the frequency of a bacterial strain of interest:

$$\frac{dp}{dt} = sp(1 - p) \qquad p(0) = p_0$$

where s is a constant. Find the solution, $p(t)$.

42. Mutation-selection balance The equation of Exercise 41 can be extended to account for a deleterious mutation that destroys the bacterial strain of interest. The differential equation becomes

$$\frac{dp}{dt} = sp(1 - p) - \mu p \qquad p(0) = p_0$$

where μ is the mutation rate and $\mu > 0$ (see Exercise 7.2.19). Solve this initial-value problem for $s \neq \mu$.

43. Glucose administration A glucose solution is administered intravenously to the bloodstream at a constant rate r. As the glucose is added, it is converted into other substances and removed from the bloodstream at a rate that is proportional to the concentration at that time. Thus a model for the concentration $C(t)$ (in mg/mL) of the glucose solution in the bloodstream is

$$\frac{dC}{dt} = r - kC$$

where k is a positive constant.

(a) Suppose that the concentration at time $t = 0$ is C_0. Determine the concentration at any time t by solving the initial-value problem.

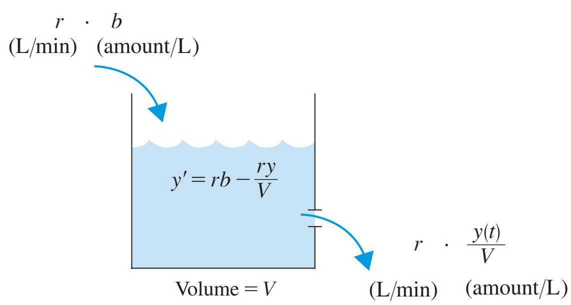
(b) Assuming that $C_0 < r/k$, find $\lim_{t\to\infty} C(t)$ and interpret your answer.

44. mRNA transcription The intermediate molecule mRNA arises in the decoding of DNA: it is produced by a process called transcription and it eventually decays. Suppose that the rate of transcription is changing exponentially according to the expression e^{bt}, where b is a positive constant and mRNA has a constant per capita decay rate of k. The number of mRNA transcript molecules T thus changes as

$$\frac{dT}{dt} = e^{bt} - kT$$

Although the form of this equation is similar to that from Exercise 43, the first term on the right side is now time-varying. As a result, the differential equation is no longer separable; however, the equation can be solved using the change of variables $y(t) = e^{kt}T(t)$. Solve the differential equation using this technique.

45–48 Mixing problems Mixing problems arise in many areas of science. They typically involve a tank of fixed capacity filled with a well-mixed solution of some substance (such as salt). Solution of a given concentration enters the tank at a fixed rate and the mixture, thoroughly stirred, leaves at a fixed rate. We will focus on examples where the inflow and outflow rates are the same, so that the volume of solution in the tank remains constant. If $y(t)$ denotes the amount of substance in the tank at time t, then $y' = (\text{rate in}) - (\text{rate out})$.



45. A tank contains 1000 L of brine with 15 kg of dissolved salt. Pure water enters the tank at a rate of 10 L/min. The solution is kept thoroughly mixed and drains from the tank at the same rate. How much salt is in the tank (a) after t minutes? (b) After 20 minutes?

46. Dialysis treatment removes urea and other waste products from a patient's blood by diverting some of the blood flow externally through a machine called a dialyzer. Suppose that a patient's blood volume is V mL and blood is diverted through the dialyzer at a rate of K mL/min. At the start of treatment the patient's blood contains $c(0) = c_0$ mg/mL of urea.

(a) Formulate the process of dialysis as an initial-value problem.

(b) What is the concentration of urea in the patient's blood after t minutes of dialysis? Compare your answer to Exercise 1.5.53.

47. A vat with 500 gallons of beer contains 4% alcohol (by volume). Beer with 6% alcohol is pumped into the vat at a rate of 5 gal/min and the mixture is pumped out at the same rate. What is the percentage of alcohol after an hour?

48. Lung ventilation A patient is placed on a ventilator to remove CO_2 from the lungs. Suppose that the rate of ventilation is 100 mL/s, with the percentage of CO_2 (by volume) in the inflow being zero. Suppose also that air is absorbed by the lungs at a rate of 10 mL/s and gas consisting of 100% CO_2 is excreted back into the lungs at the same rate. The volume of a typical pair of lungs is around 4000 mL. If the patient starts ventilation with 20% of lung volume being CO_2, what volume of CO_2 will remain in the lungs after 30 minutes?

49. When a raindrop falls, it increases in size and so its mass at time t is a function of t, namely, $m(t)$. The rate of growth of the mass is $km(t)$ for some positive constant k. When we apply Newton's Law of Motion to the raindrop, we get $(mv)' = gm$, where v is the velocity of the raindrop (directed downward) and g is the acceleration due to gravity. The terminal velocity of the raindrop is $\lim_{t\to\infty} v(t)$. Find an expression for the terminal velocity in terms of g and k.

50. Homeostasis refers to a state in which the nutrient content of a consumer is independent of the nutrient content of its food. In the absence of homeostasis, a model proposed by Sterner and Elser is given by

$$\frac{dy}{dx} = \frac{1}{\theta}\frac{y}{x}$$

where x and y represent the nutrient content of the food and the consumer, respectively, and θ is a constant with $\theta \geqslant 1$.

(a) Solve the differential equation.

(b) What happens when $\theta = 1$? What happens when $\theta \to \infty$?

Source: Adapted from R. Sterner et al., *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere* (Princeton, NJ: Princeton University Press, 2002).

51. Tissue culture Let $A(t)$ be the area of a tissue culture at time t and let M be the final area of the tissue when growth is complete. Most cell divisions occur on the periphery of the tissue and the number of cells on the periphery is proportional to $\sqrt{A(t)}$. So a reasonable model for the growth of tissue is obtained by assuming that the rate of growth of the area is jointly proportional to $\sqrt{A(t)}$ and $M - A(t)$.

(a) Formulate a differential equation and use it to show that the tissue grows fastest when $A(t) = \frac{1}{3}M$.

CAS (b) Solve the differential equation to find an expression for $A(t)$. Use a computer algebra system to perform the integration.

52. According to Newton's Law of Universal Gravitation, the gravitational force on an object of mass m that has been projected vertically upward from the earth's surface is

$$F = \frac{mgR^2}{(x + R)^2}$$

where $x = x(t)$ is the object's distance above the surface at time t, R is the earth's radius, and g is the acceleration due to gravity. Also, by Newton's Second Law, $F = ma = m(dv/dt)$ and so

$$m\frac{dv}{dt} = -\frac{mgR^2}{(x + R)^2}$$

(a) Suppose a rocket is fired vertically upward with an initial velocity v_0. Let h be the maximum height above the surface reached by the object. Show that

$$v_0 = \sqrt{\frac{2gRh}{R + h}}$$

[*Hint:* By the Chain Rule, $m(dv/dt) = mv(dv/dx)$.]

(b) Calculate $v_e = \lim_{h\to\infty} v_0$. This limit is called the *escape velocity* for the earth.
(c) Use $R = 3960$ mi and $g = 32\ \text{ft/s}^2$ to calculate v_e in feet per second and in miles per second.

53. Species–area relationship The number of species found on an island typically increases with the area of the island. Suppose that this relationship is such that the rate of increase with island area is always proportional to the density of species (that is, number of species per unit area) with a proportionality constant between 0 and 1. Find the function that describes the species-area relationship. Compare your answer to Example 1.5.14.

■ PROJECT Why Does Urea Concentration Rebound after Dialysis?

A patient undergoes dialysis treatment to remove urea from the bloodstream when the kidneys are not functioning properly. Blood is diverted from the patient through a machine that filters out the urea. In many patients, once a dialysis session ends there is a relatively rapid rebound in the concentration of urea in the blood—too rapid to be accounted for by the production of new urea (see Figure 1).

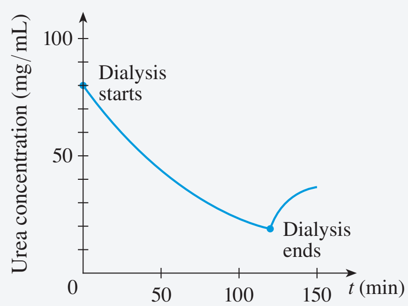


FIGURE 1
Urea rebound after dialysis

One explanation for this rebound is that urea also exists in other parts of the body, and there is continual movement of urea from these other areas into the bloodstream. Modeling this movement results in a so-called "two-compartment" model, as shown in Figure 2.

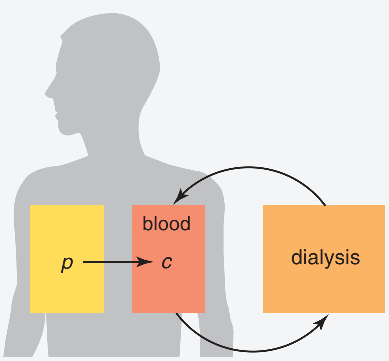


FIGURE 2
A schematic diagram of the two-compartment model

In Exercise 7.4.46 we saw that a common, one-compartment model for dialysis is

$$\frac{dc}{dt} = -\frac{K}{V}c$$

where K and V are positive constants and c is the concentration of urea in the blood (in mg/mL). To construct a two-compartment model we need to describe the dynamics using two variables, c for the concentration in the blood and p for the concentration in the inaccessible pool (both measured in mg/mL). A model for this process is

$$\textbf{(1)} \qquad \frac{dc}{dt} = -\frac{K}{V}c + ap \qquad \frac{dp}{dt} = -ap$$

where K, V, and a are positive constants.

1. Explain the terms in Equations 1 and the assumptions that underlie them.

2. The dynamics of c depend on both the concentration in the blood c and in the inaccessible pool p. However, the dynamics of p depend only on p and so we can solve the differential equation for p independently of the differential equation for c. What is this solution, assuming that the initial concentration of urea in the pool is c_0?