Equation (8.38) allows us to eliminate C. Solving (8.38) for C, we find that $C = BV^{-0.794}$ and, therefore,

$$\frac{dB}{dV} = BV^{-0.794}(0.794)V^{0.794-1} = (0.794)BV^{-1}$$

Rearranging terms yields

$$\frac{dB}{B} = (0.794)\frac{dV}{V}$$

Dividing both sides by dt, we get

$$\frac{1}{B}\frac{dB}{dt} = (0.794)\frac{1}{V}\frac{dV}{dt}$$

which is the same as (8.39). ■

EXAMPLE 9

Homeostasis The nutrient content of a consumer (e.g., the percent nitrogen of the consumer's biomass) can range from reflecting the nutrient content of its food to being constant. The former is referred to as *absence of homeostasis*, the latter as *strict homeostasis*. A model for homeostatic regulation is provided in Sterner and Elser (2002). The model relates a consumer's nutrient content (denoted by y) to its food's nutrient content (denoted by x) as

$$\frac{dy}{dx} = \frac{1}{\theta}\frac{y}{x} \tag{8.40}$$

where $\theta \geq 1$ is a constant. Solve the differential equation and relate θ to absence of homeostasis and strict homeostasis.

Solution

We can solve (8.40) by separation of variables:

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

Integrating and simplifying yields

$$\begin{aligned} \ln|y| &= \frac{1}{\theta}\ln|x| + C_1 \\ |y| &= e^{(1/\theta)\ln|x|+C_1} \\ |y| &= |x|^{1/\theta}e^{C_1} \\ y &= \pm e^{C_1}x^{1/\theta} \end{aligned}$$

Since x and y are positive (they denote nutrient contents), it follows that

$$y = Cx^{1/\theta}$$

where C is a positive constant.

Absence of homeostasis means that the consumer reflects the food's nutrient content. This occurs when $y = Cx$ and thus when $\theta = 1$. *Strict homeostasis* means that the nutrient content of the consumer is independent of the nutrient content of the food; that is, $y = C$; this occurs in the limit as $\theta \to \infty$. ■

Section 8.1 Problems

■ 8.1.1

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

1. $\frac{dy}{dx} = x + \sin x$, where $y_0 = 0$ for $x_0 = 0$

2. $\frac{dy}{dx} = e^{-3x}$, where $y_0 = 10$ for $x_0 = 0$

3. $\frac{dy}{dx} = \frac{1}{x}$, where $y_0 = 0$ when $x_0 = 1$

4. $\frac{dy}{dx} = \frac{1}{1+x^2}$, where $y_0 = 1$ when $x_0 = 0$

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

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

7. $\frac{ds}{dt} = \sqrt{3t+1}$, where $s(0) = 1$

8. $\frac{dh}{dt} = 5 - 16t^2$, where $h(3) = -11$

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 $t = 10$.

■ 8.1.2

In Problems 11–16, solve the given autonomous differential equations.

11. $\frac{dy}{dx} = 3y$, where $y_0 = 2$ for $x_0 = 0$

12. $\frac{dy}{dx} = 2(1-y)$, where $y_0 = 2$ for $x_0 = 0$

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

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

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

16. $\frac{dN}{dt} = 5 - N$, where $N(2) = 3$

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

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

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

18. 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 which 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.

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

$$\frac{1}{N}\frac{dN}{dt} = r \tag{8.41}$$

where r is a constant.

(a) Solve (8.41).

(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 evolved according to (8.41). Describe how you would determine r from your data.

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

$$\frac{dW}{dt} = -\lambda W(t) \quad \text{with } W(0) = W_0 \tag{8.42}$$

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

(a) Solve (8.42).

(b) Assume that $W(0) = 123$ gr and $W(5) = 20$ gr and that time is measured in minutes. Find the decay constant λ and determine the half-life of the radioactive substance.

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

$$\frac{dN}{dt} = \frac{1}{100}N^2, \quad \text{with } N(0) = 10 \tag{8.43}$$

(a) Solve (8.43).

(b) Graph $N(t)$ as a function of t for $0 \le t < 10$. What happens as $t \to 10$? Explain in words what this means.

22. Denote by $L(t)$ the length of a fish at time t, and assume that the fish grows according to the von Bertalanffy equation

$$\frac{dL}{dt} = k(34 - L(t)) \quad \text{with } L(0) = 2 \tag{8.44}$$

(a) Solve (8.44).

(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 $\lim_{t\to\infty} L(t)$.

23. Denote by $L(t)$ the length of a certain fish at time t, and assume that this fish grows according to the von Bertalanffy equation

$$\frac{dL}{dt} = k(L_\infty - L(t)) \quad \text{with } L(0) = 1 \tag{8.45}$$

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

(a) Use this information to determine the constants k and L_∞ in (8.45). [*Hint:* Solve (8.45).]

(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?

24. 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.

25. Use the partial-fraction method to solve

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

where $y_0 = 2$ for $x_0 = 0$.

26. Use the partial-fraction method to solve

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

where $y_0 = 2$ for $x_0 = 0$.

27. Use the partial-fraction method to solve

$$\frac{dy}{dx} = y(y-5)$$

where $y_0 = 1$ for $x_0 = 0$.

28. Use the partial-fraction method to solve

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

where $y_0 = 0$ for $x_0 = 0$.

29. Use the partial-fraction method to solve

$$\frac{dy}{dx} = 2y(3-y)$$

where $y_0 = 5$ for $x_0 = 1$.

30. Use the partial-fraction method to solve

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

where $y_0 = -3$ for $t_0 = 0$.

In Problems 31–34, solve the given differential equations.

31. $\frac{dy}{dx} = y(1+y)$ **32.** $\frac{dy}{dx} = (1+y)^2$

33. $\frac{dy}{dx} = (1+y)^3$ **34.** $\frac{dy}{dx} = (3-y)(2+y)$

35. (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

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

that passes through (i) (0, 0), (ii) (0, 2), and (iii) (0, 4).

36. Find a solution of

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

that passes through (0, 2).

37. Suppose that the size of a population at time t is denoted by $N(t)$ and that $N(t)$ satisfies the differential 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 $\lim_{t\to\infty} N(t)$.

38. Assume that the size of a population, denoted by $N(t)$, evolves according to the logistic equation. Find the intrinsic rate of growth if the carrying capacity is 100, $N(0) = 10$, and $N(1) = 20$.

39. Suppose that $N(t)$ denotes the size of a population at time t and that

$$\frac{dN}{dt} = 1.5N\left(1 - \frac{N}{50}\right)$$

(a) Solve this differential equation when $N(0) = 10$.
(b) Solve this differential equation when $N(0) = 90$.
(c) Graph your solutions in (a) and (b) in the same coordinate system.
(d) Find $\lim_{t\to\infty} N(t)$ for your solutions in (a) and (b).

40. Suppose that the size of a population, denoted by $N(t)$, satisfies

$$\frac{dN}{dt} = 0.7N\left(1 - \frac{N}{35}\right) \tag{8.46}$$

(a) Determine all equilibria by solving $dN/dt = 0$.
(b) Solve (8.46) for **(i)** $N(0) = 10$, **(ii)** $N(0) = 35$, **(iii)** $N(0) = 50$, and **(iv)** $N(0) = 0$. Find $\lim_{t\to\infty} N(t)$ for each of the four initial conditions.
(c) Compare your answer in (a) with the limiting values you found in (b).

41. Let $N(t)$ denote the size of a population at time t. Assume that the population evolves according to the logistic equation. Assume also that the intrinsic growth rate is 5 and that the carrying capacity is 30.
(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)** $N(0) = 20$, and **(iii)** $N(0) = 40$.

42. Logistic growth is described by the differential equation

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

The solution of this differential equation with initial condition $N(0) = N_0$ is given by

$$N(t) = \frac{K}{1 + (\frac{K}{N_0} - 1)e^{-rt}} \tag{8.47}$$

(a) Show that

$$r = \frac{1}{t}\ln\left(\frac{K - N_0}{N_0}\right) + \frac{1}{t}\ln\left(\frac{N(t)}{K - N(t)}\right) \tag{8.48}$$

by solving (8.47) for r.
(b) Equation (8.48) can be used to estimate r. Suppose we follow 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.

43. Selection at a Single Locus We consider one locus with two alleles, A_1 and A_2, in a randomly mating diploid population. That is, each individual in the population is either of type A_1A_1, A_1A_2, or A_2A_2. We denote by $p(t)$ the frequency of the A_1 allele and by $q(t)$ the frequency of the A_2 allele in the population at time t. Note that $p(t)+q(t) = 1$. We denote the fitness of the A_iA_j type by w_{ij} and assume that $w_{11} = 1$, $w_{12} = 1 - s/2$, and $w_{22} = 1 - s$, where s is a nonnegative constant less than or equal to 1. That is, the fitness of the heterozygote A_1A_2 is halfway between the fitness of the two homozygotes, and the type A_1A_1 is the fittest. If s is small, we can show that, approximately,

$$\frac{dp}{dt} = \frac{1}{2}sp(1-p) \quad \text{with } p(0) = p_0 \tag{8.49}$$

(a) Use separation of variables and partial fractions to find the solution of (8.49).
(b) Suppose $p_0 = 0.1$ and $s = 0.01$; how long will take until $p(t) = 0.5$?
(c) Find $\lim_{t\to\infty} p(t)$. Explain in words what this limit means.

8.1.3

In Problems 44–52, solve each differential equation with the given initial condition.

44. $\frac{dy}{dx} = 2\frac{y}{x}$, with $y_0 = 1$ if $x_0 = 1$

45. $\frac{dy}{dx} = \frac{x+1}{y}$, with $y_0 = 2$ if $x_0 = 0$

46. $\frac{dy}{dx} = \frac{y}{x+1}$, with $y_0 = 1$ if $x_0 = 0$

47. $\frac{dy}{dx} = (y+1)e^{-x}$, with $y_0 = 2$ if $x_0 = 0$

48. $\frac{dy}{dx} = x^2y^2$, with $y_0 = 1$ if $x_0 = 1$

49. $\frac{dy}{dx} = \frac{y+1}{x-1}$, with $y_0 = 5$ if $x_0 = 2$

50. $\frac{du}{dt} = \frac{\sin t}{u^2+1}$, with $u_0 = 3$ if $t_0 = 0$

51. $\frac{dr}{dt} = re^{-t}$, with $r_0 = 1$ if $t_0 = 0$

52. $\frac{dx}{dy} = \frac{1}{2}\frac{x}{y}$, with $x_0 = 2$ if $y_0 = 3$

53. *(Adapted from Reiss, 1989)* In a case study by Taylor et al. (1980) in which the maximal rate of oxygen consumption (in ml s^{-1}) for nine species of wild African mammals was plotted against body mass (in kg) on a log–log plot, it was found that the data points fall on a straight line with slope approximately equal to 0.8. Find a differential equation that relates maximal oxygen consumption to body mass.

54. Consider the following differential equation, which is important in population genetics:

$$a(x)g(x) - \frac{1}{2}\frac{d}{dx}[b(x)g(x)] = 0$$

Here, $b(x) > 0$.

(a) Define $y = b(x)g(x)$, and show that y satisfies

$$\frac{a(x)}{b(x)}y - \frac{1}{2}\frac{dy}{dx} = 0 \tag{8.50}$$

(b) Separate variables in (8.50), and show that if $y > 0$, then

$$y = C\exp\left[2\int \frac{a(x)}{b(x)}\,dx\right]$$

55. When phosphorus content in *Daphnia* was plotted against phosphorus content of its algal food on a log–log plot, a straight line with slope 1/7.7 resulted. (See Sterner and Elser, 2002; data from DeMott et al., 1998.) Find a differential equation that relates the phosphorus content of *Daphnia* to the phosphorus content of its algal food.

56. This problem addresses Malthus's concerns. 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) What assumptions do you need to make to be able to compare whether and, if so, when food supply will be insufficient? Does exponential growth eventually overtake linear growth? Explain.
(c) Do a Web search to determine whether food supply has grown linearly, as claimed by Malthus.

57. At the beginning of this section, we modified the exponential-growth equation to include oscillations in the per capita growth rate. Solve the differential equation we obtained, namely,

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

with $N(0) = 5$.

8.2 Equilibria and Their Stability

In Subsection 8.1.2, we learned how to solve autonomous differential equations and graphed their solutions as functions of the independent variable for given initial conditions. For instance, logistic growth

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{8.51}$$

with initial condition $N(0) = N_0$ has the solution given in (8.33) and graphed in Figure 8.10 for different initial values.

The solution of a differential equation can inform us about long-term behavior, as we saw in the case of logistic growth. In particular, if $N_0 > 0$, then $N(t) \to K$, the carrying capacity, as $t \to \infty$, and if $N_0 = 0$, then $N(t) = 0$ for all $t > 0$. Also, if $N_0 = K$, then $N(t) = K$ for all $t > 0$. What is so special about $N_0 = K$ or $N_0 = 0$? We see from Equation (8.51) that if $N = K$ or $N = 0$, then $dN/dt = 0$, implying that $N(t)$ is constant.

Constant solutions form a very special class of solutions of autonomous differential equations. These solutions are called **point equilibria** or, simply, equilibria. The constant solutions $N = K$ and $N = 0$ are point equilibria of the logistic equation.

A graph of $g(N)$ is shown in Figure 8.23a. Differentiating $g(N)$ yields

$$g'(N) = r\left(2N + \frac{2a}{K}N - \frac{3N^2}{K} - a\right) = \frac{r}{K}(2NK + 2aN - 3N^2 - aK)$$

We can compute the eigenvalue $g'(\hat{N})$ associated with the equilibrium $\hat{N}$:

$$\text{if} \quad \hat{N} = 0, \quad \text{then} \quad g'(0) = \frac{r}{K}(-aK) < 0$$
$$\text{if} \quad \hat{N} = a, \quad \text{then} \quad g'(a) = \frac{r}{K}a(K - a) > 0$$
$$\text{if} \quad \hat{N} = K, \quad \text{then} \quad g'(K) = \frac{r}{K}K(a - K) < 0$$

As we continue, you should compare the results from the eigenvalue method with the graph of $g(N)$.

Since $g'(0) < 0$, it follows that $\hat{N} = 0$ is locally stable. Likewise, since $g'(K) < 0$, it follows that $\hat{N} = K$ is locally stable. The equilibrium $\hat{N} = a$ is unstable, because $g'(a) > 0$. This instability is also evident from Figure 8.23a. The Allee effect is an example in which both stable equilibria are locally, but not globally, stable.

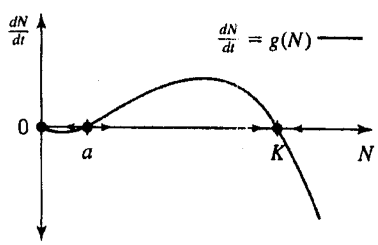

Figure 8.23a The graph of $g(N)$ illustrating the Allee effect.

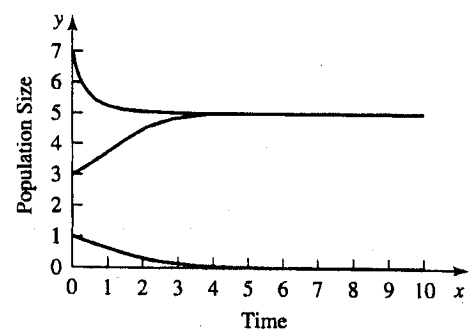

Figure 8.23b Solution curves when $r = 0.5$, $a = 2$, and $K = 5$. When the initial condition $N(0)$ is between 0 and 2, the solution curve approaches the locally stable equilibrium $\hat{N} = 0$. When the initial condition $N(0)$ is greater than 2, the solution curve approaches the locally stable equilibrium $\hat{N} = K = 5$. The approach is from below when $2 < N(0) < 5$ and from above when $N(0) > 5$.

We see from Figures 8.23a and 8.23b that if $0 \le N(0) < a$, then $N(t) \to 0$ as $t \to \infty$. If $a < N(0) \le K$ or $N(0) \ge K$, then $N(t) \to K$ as $t \to \infty$. To interpret our results, we observe that if the initial population $N(0)$ is too small [i.e., $N(0) < a$], then the population goes extinct, and if the initial population is large enough [i.e., $N(0) > a$], then the population persists. That is, the parameter a is a threshold level. The recruitment rate is large enough only when the population size exceeds this level.

Section 8.2 Problems

■ **8.2.1**

1. Suppose that

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

(a) Find the equilibria of this differential equation.

(b) Graph dy/dx as a function of y, and use your graph to discuss the stability of the equilibria.

(c) Compute the eigenvalues associated with each equilibrium, and discuss the stability of the equilibria.

2. Suppose that

$$\frac{dy}{dx} = (4 - y)(5 - y)$$

(a) Find the equilibria of this differential equation.

(b) Graph dy/dx as a function of y, and use your graph to discuss the stability of the equilibria.

(c) Compute the eigenvalues associated with each equilibrium, and discuss the stability of the equilibria.

3. Suppose that

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

(a) Find the equilibria of this differential equation.

(b) Graph dy/dx as a function of y, and use your graph to discuss the stability of the equilibria.

(c) Compute the eigenvalues associated with each equilibrium, and discuss the stability of the equilibria.

4. Suppose that

$$\frac{dy}{dx} = y(2-y)(y-3)$$

(a) Find the equilibria of this differential equation.

(b) Graph dy/dx as a function of y, and use your graph to discuss the stability of the equilibria.

(c) Compute the eigenvalues associated with each equilibrium, and discuss the stability of the equilibria.

5. **Logistic Equation** Assume that the size of a population evolves according to the logistic equation with intrinsic rate of growth $r = 1.5$. Assume that the carrying capacity $K = 100$.

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

(b) Find all equilibria, and, using the graphical approach, discuss the stability of the equilibria.

(c) Find the eigenvalues associated with the equilibria, and use the eigenvalues to determine the stability of the equilibria. Compare your answers with your results in (b).

6. **A Simple Model of Predation** 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

$$\frac{dN}{dt} = N\left(1-\frac{N}{50}\right) - \frac{9N}{5+N} \qquad (8.65)$$

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

(a) Set

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

and graph $g(N)$.

(b) Find all equilibria of (8.65).

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

(d) Use the method of eigenvalues to determine the stability of the equilibria you found in (b).

7. **Logistic Equation** Assume that the size of a population evolves according to the logistic equation with intrinsic rate of growth $r = 2$. Assume that $N(0) = 10$.

(a) Determine the carrying capacity K if the population grows fastest when the population size is 1000. (*Hint*: Show that the graph of dN/dt as a function of N has a maximum at $K/2$.)

(b) If $N(0) = 10$, how long will it take the population size to reach 1000?

(c) Find $\lim_{t\to\infty} N(t)$.

8. **Logistic Equation** The logistic curve $N(t)$ is an S-shaped curve that satisfies

$$\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right) \quad \text{with } N(0) = N_0 \qquad (8.66)$$

when $N_0 < K$.

(a) Use the differential equation (8.66) to show that the inflection point of the logistic curve is at exactly half the saturation value of the curve. [*Hint*: Do not solve (8.66); instead, differentiate the right-hand side with respect to t.]

(b) The solution $N(t)$ of (8.66) can be defined for all $t \in \mathbf{R}$. Show that $N(t)$ is symmetric about the inflection point and that $N(0) = N_0$. That is, first use the solution of (8.66) that is given in (8.33), and find the time t_0 so that $N(t_0) = K/2$ (i.e., the inflection point) is at $t = t_0$. Compute $N(t_0 + h)$ and $N(t_0 - h)$ for $h > 0$, and show that

$$N(t_0+h) - \frac{K}{2} = \frac{K}{2} - N(t_0-h)$$

Use a sketch of the graph of $N(t)$ to explain why the preceding equation shows that $N(t)$ is symmetric about the inflection point $(t_0, N(t_0))$.

9. 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?

10. 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, use the graphical approach to discuss their stability when $h = 0.1$, and find the maximal harvesting rate that maintains a positive population size.

(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 found in (b).

■ 8.2.2

11. Assume the single-compartment model defined in Subsection 8.2.2: If $C(t)$ is the concentration of the solute at time t, then dC/dt is given by (8.57); that is,

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

where q, V, and C_I are defined as in Subsection 8.2.2. Use the graphical approach to discuss the stability of the equilibrium $\hat{C} = C_I$.

12. Assume the single-compartment model defined in Subsection 8.2.2; that is, denote the concentration of the solute at time t by $C(t)$, and assume that

$$\frac{dC}{dt} = 3(20 - C(t)) \quad \text{for } t \geq 0 \qquad (8.67)$$

(a) Solve (8.67) when $C(0) = 5$.

(b) Find $\lim_{t\to\infty} C(t)$.

(c) Use your answer in (a) to determine t so that $C(t) = 10$.

13. Assume the single-compartment model defined in Subsection 8.2.2; 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) Solve the differential equation in (a) when $C(0) = 0$, and find $\lim_{t\to\infty} C(t)$.

(c) Find all equilibria of the differential equation and discuss their stability.

14. 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 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} and how much pure water is needed in each case. (Note that the rate at which water enters the tank is equal to the rate at which water leaves the tank.) Compare the amount of water needed using the pumps with the amount of water needed in part (b).

15. Assume the single-compartment model introduced in Subsection 8.2.2. Denote the concentration at time t by $C(t)$, measured in mg/L, and assume that

$$\frac{dC}{dt} = 0.37(254\text{ mg/L} - C(t)) \quad \text{for } t \geq 0$$

(a) Find the equilibrium concentration.

(b) Assume that the concentration is suddenly increased from the equilibrium concentration to 400 mg/L. Find the return time to equilibrium, denoted by T_R, which is the amount of time until the initial difference is reduced to a fraction e^{-1}.

(c) Repeat (b) for the case when the concentration is suddenly increased from the equilibrium concentration to 800 mg/L.

(d) Are the values for T_R computed in (b) and (c) different?

16. Assume the compartment model as in Subsection 8.2.2. Suppose that the equilibrium concentration is C_I and the initial concentration is C_0. Express the time it takes until the initial deviation $C_0 - C_I$ is reduced to a fraction p in terms of T_R.

17. Assume the compartment model as in Subsection 8.2.2. Suppose that the equilibrium concentration is C_I. The time T_R has an integral representation that can be generalized to systems with more than one compartment. Show that

$$T_R = \int_0^\infty \frac{C(t) - C_I}{C(0) - C_I}\, dt$$

[*Hint*: Use (8.58) to show that

$$\frac{C(t) - C_I}{C(0) - C_I} = e^{-(q/V)t}$$

and integrate both sides with respect to t from 0 to ∞.]

18. Use the compartment model defined in Subsection 8.2.2 to investigate how the size of a lake influences nutrient dynamics in the lake after a perturbation. Mary Lake and Elizabeth Lake are two fictitious lakes in the North Woods that are used as experimental lakes to study nutrient dynamics. Mary Lake has a volume of 6.8×10^3 m^3, and Elizabeth Lake has twice that volume, or 13.6×10^3 m^3. Both lakes have the same inflow/outflow rate $q = 170$ liter s^{-1}. Because both lakes share the same drainage area, the concentration C_I of the incoming solute is the same for both lakes, namely, $C_I = 0.7$ mg liter^{-1}. Assume that at the beginning of the experiment both lakes are in equilibrium; that is, the concentration of the solution in both lakes is 0.7 mg liter^{-1}. Your experiment consists of increasing the concentration of the solution by 10% in each lake at time 0 and then watching how the concentration of the solution in each lake changes with time. Assume the single-compartment model to make predictions about how the concentration of the solution will evolve. (Note that 1 m^3 of water corresponds to 1000 liters of water.)

(a) Find the initial concentration C_0 of the solution in each lake at time 0 (i.e., immediately after the 10% increase in concentration of the solution).

(b) Use Equation (8.58) to determine how the concentration of the solution changes over time in each lake. Graph your results.

(c) Which lake returns to equilibrium faster? Compute the return time to equilibrium, T_R, for each lake, and explain how it is related to the eigenvalues corresponding to the equilibrium concentration C_I for each lake.

19. Use the single-compartment model defined in Subsection 8.2.2 to investigate the effect of an increase in the input concentration C_I on the nutrient concentration in a lake. Suppose a lake in a pristine environment has an equilibrium phosphorus concentration of 0.3 mg^{-1}. The volume V of the lake is 12.3×10^6 m^3, and the inflow/outflow rate q is equal to 220 liter s^{-1}. Conversion of land in the drainage area of the lake to agricultural use has increased the input concentration from 0.3 mg liter^{-1} to 1.1 mg liter^{-1}. Assume that this increase happened instantaneously. Compute the return time to the new equilibrium, denoted by T_R, in days, and find the nutrient concentration in the lake T_R units of time after the change in input concentration. (Note that 1 m^3 of water corresponds to about 1000 liters of water.)

■ 8.2.3

20. Levins Model Denote by $p = p(t)$ the fraction of occupied patches in a metapopulation model, and assume that

$$\frac{dp}{dt} = 2p(1-p) - p \quad \text{for } t \geq 0 \tag{8.68}$$

(a) Set $g(p) = 2p(1-p) - p$. Graph $g(p)$ for $p \in [0, 1]$.

(b) Find all equilibria in (8.68) 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).

21. Levins Model Denote by $p = p(t)$ the fraction of occupied patches in a metapopulation model, and assume that

$$\frac{dp}{dt} = 0.5p(1-p) - 1.5p \quad \text{for } t \geq 0 \tag{8.69}$$

(a) Set $g(p) = 0.5p(1-p) - 1.5p$. Graph $g(p)$ for $p \in [0, 1]$.

(b) Find all equilibria of (8.69) 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).

22. A Metapopulation Model with Density-Dependent Extinction Denote by $p = p(t)$ the fraction of occupied patches in a metapopulation model, and assume that

$$\frac{dp}{dt} = cp(1-p) - p^2 \quad \text{for } t \geq 0 \tag{8.70}$$

where $c > 0$. 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 an extinction rate of p^2. The colonization of vacant patches is the same as in the Levins model.

(a) Set $g(p) = cp(1-p) - p^2$ and sketch the graph of $g(p)$.

(b) Find all equilibria of (8.70) in $[0, 1]$, and determine their stability.

(c) Is there a nontrivial equilibrium when $c > 0$? Contrast your findings with the corresponding results in the Levins model.

23. Habitat Destruction In Subsection 8.2.3, we introduced the Levins model. To study the effects of habitat destruction on a single species, we modify equation (8.63) 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. These patches have frequency $1-p(t)-D$ if $p(t)$ denotes the fraction of occupied patches at time t. Then

$$\frac{dp}{dt} = cp(1-p-D) - mp \tag{8.71}$$

(a) Explain in words the meaning of the different terms in (8.71).

(b) Show that there are two possible equilibria: the trivial equilibrium $p_1 = 0$ and the nontrivial equilibrium $p_2 = 1-D-\frac{m}{c}$. Sketch the graph of p_2 as a function of D.

(c) 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.

(d) Assume the condition that you derived in (c); that is, the nontrivial equilibrium is between 0 and 1. 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 independent of D. Show that the **effective colonization rate** in equilibrium—that is, c times the fraction of available patches—is equal to the extinction rate. This equality shows that the effective birth rate of new colonies balances their extinction rate at equilibrium.

■ **8.2.4**

24. Allee Effect Denote the size of a population at time t by $N(t)$, and assume that

$$\frac{dN}{dt} = 2N(N-10)\left(1-\frac{N}{100}\right) \quad \text{for } t \geq 0 \tag{8.72}$$

(a) Find all equilibria of (8.72).

(b) Use the eigenvalue approach to determine the stability of the equilibria you found in (a).

(c) Set

$$g(N) = 2N(N-10)\left(1-\frac{N}{100}\right)$$

for $N \geq 0$, and graph $g(N)$. Identify the equilibria of (8.72) on your graph, and use the graph to determine the stability of the equilibria. Compare your results with your findings in (b). Use your graph to give a graphical interpretation of the eigenvalues associated with the equilibria.

25. Allee Effect Denote the size of a population at time t by $N(t)$, and assume that

$$\frac{dN}{dt} = 0.3N(N-17)\left(1-\frac{N}{200}\right) \quad \text{for } t \geq 0 \tag{8.73}$$

(a) Find all equilibria of (8.73).

(b) Use the eigenvalue approach to determine the stability of the equilibria you found in (a).

(c) Set

$$g(N) = 0.3N(N-17)\left(1-\frac{N}{200}\right)$$

for $N \geq 0$, and graph $g(N)$. Identify the equilibria of (8.73) on your graph, and use the graph to determine the stability of the equilibria. Compare your results with your findings in (b). Use your graph to give a graphical interpretation of the eigenvalues associated with the equilibria.

■ 8.3 Systems of Autonomous Equations (Optional)

In the preceding two sections, we discussed models that could be described by a single differential equation. If we wish to describe models in which several quantities interact, such as a competition model in which various species interact, more than one differential equation is needed. We call this model a *system of differential equations.* We will restrict ourselves again to autonomous systems—that is, systems whose dynamics do not depend explicitly on the independent variable (which typically is time).

This section is a preview of Chapter 11, in which we will discuss systems of differential equations in detail. A thorough analysis of such systems requires a fair amount of theory, which we will develop in Chapters 9 and 10. Since we are not yet equipped with the right tools to analyze systems of differential equations, this section will be rather informal. As with movie previews, you will not know the full story after you finish reading the section, but reading it will (hopefully) convince you that systems of differential equations provide a rich tool for modeling biological systems.

We assume that $p_1 = \hat{p}_1 = 1 - 1/c_1$ and that p_2 is very small. Then $1 - \hat{p}_1 - p_2 \approx 1 - \hat{p}_1$. Hence,

$$\frac{dp_2}{dt} \approx p_2 \left[c_2 \frac{1}{c_1} - 1 - c_1 + 1 \right] = p_2 \left[\frac{c_2}{c_1} - c_1 \right] > 0$$

if

$$\frac{c_2}{c_1} - c_1 > 0, \qquad \text{or} \qquad c_2 > c_1^2$$

Since $dp_2/dt > 0$ when species 1 is in equilibrium and species 2 has a low abundance, it follows that species 2 can invade. We conclude that species 1 and 2 can coexist when $c_2 > c_1^2$.

This mechanism of coexistence is referred to as the **competition–colonization trade-off**. That is, the weaker competitor (species 2) can compensate for its inferior competitiveness by being a superior colonizer ($c_2 > c_1^2$).

Section 8.3 Problems

8.3.1

In Problems 1–4, we will investigate the classical Kermack–McKendrick model for the spread of an infectious disease in a population of fixed size N. (This model was introduced in Subsection 8.3.1, and you should refer to that subsection when working out the problems.) If $S(t)$ denotes the number of susceptibles at time t, $I(t)$ the number of infectives at time t, and $R(t)$ the number of immune individuals at time t, then

$$\frac{dS}{dt} = -bSI$$

$$\frac{dI}{dt} = bSI - aI$$

and $R(t) = N - S(t) - I(t)$.

1. Determine, in each of the following cases, whether or not the disease can spread (*Hint*: Compute R_0.):
(a) $S(0) = 1000, a = 200, b = 0.3$
(b) $S(0) = 1000, a = 200, b = 0.1$

2. Assume that $a = 100$ and $b = 0.2$. The **critical number** of susceptibles $S_c(0)$ at time 0 for the spread of a disease that is introduced into a population at time 0 is defined as the minimum number of susceptibles for which the disease can spread. Find $S_c(0)$.

3. Suppose that $a = 100, b = 0.01$, and $N = 10,000$. Can the disease spread if, at time 0, there is one infected individual?

4. Refer to the simple model of epidemics in Subsection 8.3.1.
(a) Divide (8.75) by (8.74) to show that when $I > 0$,

$$\frac{dI}{dS} = \frac{a}{b}\frac{1}{S} - 1 \tag{8.84}$$

Also, show that when $R(0) = 0, I(0) = I_0$, and $S(0) = S_0$, the solution of (8.84) satisfies

$$I(t) = N - S(t) + \frac{a}{b} \ln \frac{S(t)}{S_0}$$

where $I(t)$ denotes the number of infectives, N the total number of individuals in the population, and $S(t)$ the number of susceptibles at time t.

(b) Since $I(t)$ gives the number of infectives at time t and $dI/dt = bSI - aI$, if $S(0) > a/b$, then $dI/dt > 0$ at time $t = 0$. Also, since $\lim_{t\to\infty} I(t) = 0$, there is a time $t > 0$ at which $I(t)$ is maximal. Show that the number of susceptibles when $I(t)$ is maximal is given by $S = a/b$. [*Hint*: When $I(t)$ attains a maximum, the derivative of $I(t)$ with respect to t, dI/dt, is equal to 0.]

(c) In (a), you expressed $I(t)$ as a function of $S(t)$. Use your result in (b) to show that the maximal number of infectives is given by

$$I_{max} = N - \frac{a}{b} + \frac{a}{b} \ln \left(\frac{a/b}{S_0} \right)$$

(d) Use your result in (c) to show that I_{max} is a decreasing function of the parameter a/b for $a/b < S_0$ (i.e., in the case in which the infection can spread). Use the latter statement to explain how a and b determine the severity (as measured by I_{max}) of the disease. Does this make sense?

8.3.2

5. Assume the compartment model of Subsection 8.3.2, with $a = 5, b = 0.02, m = 1$, and $c = 1$.
(a) Find the system of differential equations that corresponds to these values.
(b) Determine which values of N_t result in a nontrivial equilibrium, and find the equilibrium values for both the autotroph and the nutrient pool.

6. Assume the compartment model of Subsection 8.2.3, with $a = 1, b = 0.01, m = 2, c = 1$, and $N_t = 500$.
(a) Find the system of differential equations that corresponds to these values.
(b) Plot the zero isoclines corresponding to this system.
(c) Use your graph in (b) to determine whether the system has a nontrivial equilibrium.

7. Assume the compartment model of Subsection 8.3.2, with $a = 1, b = 0.01, m = 2, c = 1$ and $N_t = 200$.
(a) Find the system of differential equations that corresponds to these values.
(b) Plot the zero isoclines corresponding to this system.
(c) Use your graph in (b) to determine whether the system has a nontrivial equilibrium.

■ 8.3.3

8. Assume the hierarchical competition model introduced in Subsection 8.3.3, and assume that the model describes two species. Specifically, assume that

$$\frac{dp_1}{dt} = 2p_1(1 - p_1) - p_1$$
$$\frac{dp_2}{dt} = 5p_2(1 - p_1 - p_2) - p_2 - 2p_1 p_2$$

(a) Find all equilibria.

(b) Determine whether species 2 can invade a monoculture of species 1. (Assume that species 1 is in equilibrium.)

9. Assume the hierarchical competition model introduced in Subsection 8.3.3, and assume that the model describes two species. Specifically, assume that

$$\frac{dp_1}{dt} = 2p_1(1 - p_1) - p_1$$
$$\frac{dp_2}{dt} = 3p_2(1 - p_1 - p_2) - p_2 - 2p_1 p_2$$

(a) Find all equilibria.

(b) Determine whether species 2 can invade a monoculture equilibrium of species 1. .

10. Assume the hierarchical competition model introduced in Subsection 8.3.3, and assume that the model describes two species. Specifically, assume that

$$\frac{dp_1}{dt} = 2p_1(1 - p_1) - p_1$$
$$\frac{dp_2}{dt} = 6p_2(1 - p_1 - p_2) - p_2 - 2p_1 p_2$$

(a) Use the zero-isocline approach to find all equilibria graphically.

(b) Determine the numerical values of all equilibria.

11. Assume the hierarchical competition model introduced in Subsection 8.3.3, and assume that the model describes two species. Specifically, assume

$$\frac{dp_1}{dt} = 3p_1(1 - p_1) - p_1$$
$$\frac{dp_2}{dt} = 5p_2(1 - p_1 - p_2) - p_2 - 3p_1 p_2$$

(a) Use the zero-isocline approach to find all equilibria graphically.

(b) Determine the numerical values of all equilibria.

12. *(Adapted from Crawley, 1997)* Denote plant biomass by V, and herbivore number by N. The plant–herbivore interaction is modeled as

$$\frac{dV}{dt} = aV(1 - \frac{V}{K}) - bVN$$
$$\frac{dN}{dt} = cVN - dN$$

(a) Suppose the herbivore number is equal to 0. What differential equation describes the dynamics of the plant biomass? Can you explain the resulting equation? Determine the plant biomass equilibrium in the absence of herbivores.

(b) Now assume that herbivores are present. Describe the effect of herbivores on plant biomass; that is, explain the term $-bVN$ in the first equation. Describe the dynamics of the herbivores—that is, how their population size increases and what contributes to decreases in their population size.

(c) Determine the equilibria (1) by solving

$$\frac{dV}{dt} = 0 \quad \text{and} \quad \frac{dN}{dt} = 0$$

and (2) graphically. Explain why this model implies that "plant abundance is determined solely by attributes of the herbivore," as stated in Crawley (1997).

Chapter 8 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. Levins model
15. Allee effect
16. Kermack–McKendrick model
17. Zero isocline
18. Hierarchical competition model

Chapter 8 Review Problems

1. Newton's Law of Cooling 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

$$\frac{dT}{dt} = k(T - T_a)$$

is the differential equation that expresses Newton's law of cooling.

(b) Suppose that it takes the object 20 min to cool from 30°C to 28°C in a room whose temperature is 21°C. How long will it take the object to cool to 25°C if it is at 30°C when it is brought into the room? [*Hint*: Solve the differential equation in (a) with the initial condition $T(0) = 30$°C and with $T_a = 21$°C. Use $T(20) = 28$°C to determine the constant k.]

2. *(Adapted from Cain et al., 1995)* In this problem, we discuss a model for clonal growth in the white clover *Trifolium repens*. *T. repens* is a widespread perennial clonal plant species that spreads through stolon growth. (A *stolon* is a horizontal stem.) By mapping the shape of a clone over time, Cain et al. estimated stolon elongation and dieback rates as follows. Denote by $S(t)$ the stolon length of the clone at time t. Cain et al. observed that the change in stolon length was proportional to the stolon length; that is,

$$\frac{dS}{dt} \propto S$$

Introducing the proportionality constant r, called the *net growth rate*, we find that

$$\frac{dS}{dt} = rS \tag{8.85}$$

(a) Suppose that S_f and S_0 are the final and the initial stolon lengths, respectively, and that T denotes the period of observation. Use (8.85) to show that r, the net growth rate, can be estimated from

$$r = \frac{1}{T} \ln \frac{S_f}{S_0}$$

[*Hint*: Solve the differential equation (8.85) with initial condition $S(0) = S_0$, and use the fact that $S(T) = S_f$.]

(b) The net growth rate r is the difference between the stolon elongation rate b and the stolon dieback rate m; that is,

$$r = b - m$$

Let B be the total amount of stolon elongation and D be the total amount of stolon dieback over the observation period of length T. Show that

$$B = \int_0^T bS(t)\,dt = \frac{bS_0}{r}(e^{rT} - 1)$$

$$D = \int_0^T mS(t)\,dt = \frac{mS_0}{r}(e^{rT} - 1)$$

(c) Show that $B - D = S_f - S_0$, and rearrange the equations for B and D in (b) so that you can estimate b and m from r, B, and D; that is, show that

$$b = \frac{rB}{S_f - S_0} = \frac{rB}{B - D}$$

$$m = \frac{rD}{S_f - S_0} = \frac{rD}{B - D}$$

(d) Explain how B and r can be estimated if S_f, S_0, and D are known from field measurements. Use your result in (c) to explain how you would then find estimates for b and m.

3. Diversification of Life *(Adapted from Benton, 1997, and Walker, 1985)* Several models have been proposed to explain the diversification of life during geological periods. According to Benton (1997),

> The diversification of marine families in the past 600 million years (Myr) appears to have followed two or three logistic curves, with equilibrium levels that lasted for up to 200 Myr. In contrast, continental organisms clearly show an exponential pattern of diversification, and although it is not clear whether the empirical diversification patterns are real or are artifacts of a poor fossil record, the latter explanation seems unlikely.

In this problem, we will investigate three models for diversification. They are analogous to models for population growth; however, the quantities involved have a different interpretation. We denote by $N(t)$ the diversification function, which counts the number of taxa as a function of time, and by r the intrinsic rate of diversification.

(a) *(Exponential Model)* This model is described by

$$\frac{dN}{dt} = r_e N \tag{8.86}$$

Solve (8.86) with the initial condition $N(0)$ at time 0, and show that r_e can be estimated from

$$r_e = \frac{1}{t} \ln \left[\frac{N(t)}{N(0)}\right] \tag{8.87}$$

[*Hint*: To find (8.87), solve for r in the solution of (8.86).]

(b) *(Logistic Growth)* This model is described by

$$\frac{dN}{dt} = r_l N \left(1 - \frac{N}{K}\right) \tag{8.88}$$

where K is the equilibrium value. Solve (8.88) with the initial condition $N(0)$ at time 0, and show that r_l can be estimated from

$$r_l = \frac{1}{t} \ln \left[\frac{K - N(0)}{N(0)}\right] + \frac{1}{t} \ln \left[\frac{N(t)}{K - N(t)}\right] \tag{8.89}$$

for $N(t) < K$.

(c) Assume that $N(0) = 1$ and $N(10) = 1000$. Estimate r_e and r_l for both $K = 1001$ and $K = 10,000$.

(d) Use your answer in (c) to explain the following quote from Stanley (1979):

> There must be a general tendency for calculated values of [r] to represent underestimates of exponential rates, because some radiation will have followed distinctly sigmoid paths during the interval evaluated.

(e) Explain why the exponential model is a good approximation to the logistic model when N/K is small compared with 1.

4. A Simple Model for Photosynthesis of Individual Leaves *(Adapted from Horn, 1971)* Photosynthesis is a complex mechanism; the following model is a very simplified caricature: 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 and k_2 are positive constants. Find all equilibria, and use the eigenvalue approach to study their stability.

5. Gompertz Growth Model This model is sometimes used to study the growth of a population for which the per capita growth rate is density dependent. Denote the size of a population at time t by $N(t)$; then, for $N \geq 0$,

$$\frac{dN}{dt} = kN(\ln K - \ln N) \quad \text{with } N(0) = N_0 \tag{8.90}$$

(a) Show that

$$N(t) = K \exp\left[-\left(\ln \frac{K}{N_0}\right) e^{-kt}\right]$$

is a solution of (8.90). To do this, differentiate $N(t)$ with respect to t and show that the derivaive can be written in the form (8.90). Don't forget to show that $N(0) = N_0$. Use a graphing calculator to sketch the graph of $N(t)$ for $N_0 = 100$, $k = 2$, and $K = 1000$. The function $N(t)$ is called the *Gompertz growth curve*.

(b) Use l'Hospital's rule to show that

$$\lim_{N\to 0} N \ln N = 0$$

and use this equation to show that $\lim_{N\to 0} dN/dt = 0$. Are there any other values of N where $dN/dt = 0$?

(c) Sketch the graph of dN/dt as a function of N for $k = 2$ and $K = 1000$. Find the equilibria, and use your graph to and discuss their stability. Explain the meaning of K.

6. Island Biogeography Preston (1962) and MacArthur and Wilson (1963) investigated the effect of area on species diversity in oceanic islands. It is assumed that species can immigrate to an island from a species pool of size P and that species on the island can go extinct. We denote the immigration rate by $I(S)$ and the extinction rate by $E(S)$, where S is the number of species on the island. Then the change in species diversity over time is

$$\frac{dS}{dt} = I(S) - E(S) \tag{8.91}$$

For a fixed island, the simplest functional forms for $I(S)$ and $E(S)$ are

$$I(S) = c\left(1 - \frac{S}{P}\right) \tag{8.92}$$

$$E(S) = m\frac{S}{P} \tag{8.93}$$

where c, m, and P are positive constants.

(a) Find the equilibrium species diversity $\hat{S}$ of (8.91) with $I(S)$ and $E(S)$ given in (8.92) and (8.93).

(b) It is reasonable to assume that the extinction rate is a decreasing function of island size. That is, we assume that if A denotes the area of the island, then m is a function of the island size A, with $dm/dA < 0$. Furthermore, we assume that the immigration rate I does not depend on the size of the island. Use these assumptions to investigate how the equilibrium species diversity changes with island size.

(c) Assume that $S(0) = S_0$. Solve (8.91) with $I(S)$ and $E(S)$ as given in (8.92) and (8.93), respectively.

(d) Assume that $S_0 = 0$. That is, the island is initially void of species. The time constant T for the system is defined as

$$S(T) = (1 - e^{-1})\hat{S}$$

Show that, under the assumption $S_0 = 0$,

$$T = \frac{P}{c+m}$$

(e) Use the assumptions in (b) and your answer in (d) to investigate the effect of island size on the time constant T; that is, determine whether $T(A)$ is an increasing or decreasing function of A.

7. Chemostat A chemostat is an apparatus for growing bacteria in a medium in which all nutrients but one are available in excess. One nutrient, whose concentration can be controlled, is held at a concentration that limits the growth of bacteria. The growth chamber of the chemostat is continually flushed by adding nutrients dissolved in liquid at a constant rate and allowing the liquid in the growth chamber, which contains bacteria, to leave the chamber at the same rate. If X denotes the number of bacteria in the growth chamber, then the growth dynamics of the bacteria are given by

$$\frac{dX}{dt} = r(N)X - qX \tag{8.94}$$

where $r(N)$ is the growth rate depending on the nutrient concentration N and q is the input and output flow rate. The equation for the nutrient flow is given by

$$\frac{dN}{dt} = qN_0 - qN - r(N)X \tag{8.95}$$

Note that (8.94) is (8.79) with $m = 0$, $N_I = qN_0$, and $a = e = q$ and that (8.95) is (8.78) with $m = 0$.

(a) Explain in words the meaning of the terms in (8.94) and (8.95).

(b) Assume that $r(N)$ is given by the Monod growth function

$$r(N) = b\frac{N}{k+N}$$

where k and b are positive constants. Draw the zero isoclines in the N–X plane, and explain how to find the equilibria $(\hat{N}, \hat{X})$ graphically.

(c) Show that a nontrivial equilibrium (an equilibrium for which $\hat{N}$ and $\hat{X}$ are both positive) satisfies

$$r(\hat{N}) - q = 0 \tag{8.96}$$

$$qN_0 - q\hat{N} - r(\hat{N})\hat{X} = 0 \tag{8.97}$$

Show also that (8.96) has a positive solution $\hat{N}$ if $q < b$, and find an expression for $\hat{N}$. Use this expression and (8.97) to find $\hat{X}$.

(d) Assume that $q < b$. Use your results in (c) to show that $\hat{X} > 0$ if $\hat{N} < N_0$ and $\hat{N} < N_0$ if $q < bN_0/(k + N_0)$. Furthermore, show that $\hat{N}$ is an increasing function of q for $q < b$.

(e) Use your results in (d) to explain why the following is true: As we increase the flow rate q from 0 to $bN_0/(k + N_0)$, the nutrient concentration $\hat{N}$ increases until it reaches the value N_0 and the number of bacteria decreases to 0.

8. *(Adapted from Nee and May, 1992, and Tilman, 1994)* In Subsection 8.3.3, we introduced a hierarchical competition model. We will use this model to investigate the effects of habitat destruction on coexistence. We assume that a fraction D of the sites is permanently destroyed. Furthermore, we restrict our discussion to two species and assume that species 1 is the superior and species 2 the inferior competitor. In the case in which both species have the same mortality ($m_1 = m_2$), which we set equal to 1, the dynamics are described by

$$\frac{dp_1}{dt} = c_1p_1(1 - p_1 - D) - p_1 \tag{8.98}$$

$$\frac{dp_2}{dt} = c_2p_2(1 - p_1 - p_2 - D) - p_2 - c_1p_1p_2 \tag{8.99}$$

where p_i, $i = 1, 2$, is the fraction of sites occupied by species i.

(a) Explain in words the meanings of the different terms in (8.98) and (8.99).

(b) Show that

$$\hat{p}_1 = 1 - \frac{1}{c_1} - D$$

is an equilibrium for species 1, which is in (0, 1), and is stable if $D < 1 - 1/c_1$ and $c_1 > 1$.

(c) Assume that $c_1 > 1$ and $D < 1 - 1/c_1$. Show that species 2 can invade the nontrivial equilibrium of species 1 [computed in (b)] if

$$c_2 > c_1^2(1 - D)$$

(d) Assume that $c_1 = 2$ and $c_2 = 5$. Then species 1 can survive as long as $D < 1/2$. Show that the fraction of sites that are occupied by species 1 is then

$$\hat{p}_1 = \begin{cases} \frac{1}{2} - D & \text{for } 0 \leq D \leq \frac{1}{2} \\ 0 & \text{for } \frac{1}{2} \leq D \leq 1 \end{cases}$$

Show also that

$$\hat{p}_2 = \frac{1}{10} + \frac{2}{5}D \qquad \text{for} \quad 0 \leq D \leq \frac{1}{2}$$

For $D > 1/2$, species 1 can no longer persist. Explain why the dynamics for species 2 reduce to

$$\frac{dp_2}{dt} = 5p_2(1 - p_2 - D) - p_2$$

in this case. Show, in addition, that the nontrivial equilibrium is of the form

$$\hat{p}_2 = 1 - \frac{1}{5} - D \quad \text{for } \frac{1}{2} \leq D \leq 1 - \frac{1}{5}$$

Plot $\hat{p}_1$ and $\hat{p}_2$ as functions of D in the same coordinate system. What happens for $D > 1 - 1/5$? Use the plot to explain in words how each species is affected by habitat destruction.

(e) Repeat (d) for $c_1 = 2$ and $c_2 = 3$.