We can summarize all this graphically in the τ–Δ plane as shown in Figure 11.17. The parabola $4\Delta = \tau^2$ is the boundary line between oscillatory and nonoscillatory behavior. The line $\tau = 0$ divides the stable and the unstable regions. The line $\Delta = 0$ separates the saddle point from the node regions. The case in which the eigenvalues are identical resides on the boundary line $4\Delta = \tau^2$.

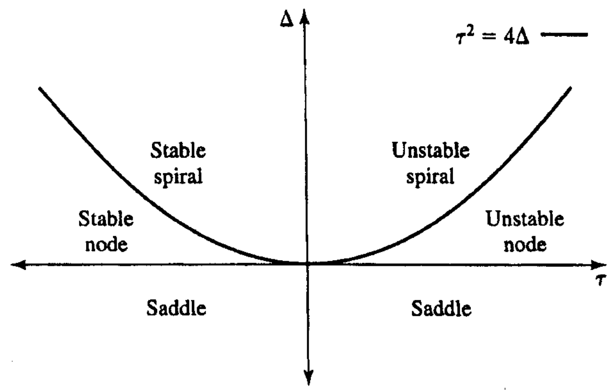

Figure 11.17 The stability behavior of a system of two linear, homogeneous differential equations with constant coefficients.

The line $\Delta = 0$ corresponds to the case in which one eigenvalue is equal to 0. As long as the other eigenvalue is not equal to 0, both eigenvalues are again distinct and the solution is of the form (11.26). However, in this case there are equilibria other than (0, 0). We will discuss two such examples in Problems 67 and 68 and one in Section 11.2.

Section 11.1 Problems

■ 11.1.1

In Problems 1–4, write each system of differential equations in matrix form.

1. $\frac{dx_1}{dt} = 2x_1 + 3x_2$

$\frac{dx_2}{dt} = -4x_1 + x_2$

2. $\frac{dx_1}{dt} = x_1 + x_2$

$\frac{dx_2}{dt} = -2x_2$

3. $\frac{dx_1}{dt} = x_3 - 2x_1$

$\frac{dx_2}{dt} = -x_1$

$\frac{dx_3}{dt} = x_1 + x_2 + x_3$

4. $\frac{dx_1}{dt} = 2x_2 - 3x_1 - x_3$

$\frac{dx_2}{dt} = -x_1 + x_2$

$\frac{dx_3}{dt} = 5x_1 + x_3$

5. Consider

$$\frac{dx_1}{dt} = -x_1 + 2x_2$$
$$\frac{dx_2}{dt} = x_1$$

Determine the direction vectors associated with the following points in the x_1–x_2 plane, and graph the direction vectors in the x_1–x_2 plane: (1, 0), (0, 1), (−1, 0), (0, −1), (1, 1), (0, 0), and (−2, 1).

6. Consider

$$\frac{dx_1}{dt} = 2x_1 - x_2$$
$$\frac{dx_2}{dt} = -x_2$$

Determine the direction vectors associated with the following points in the x_1–x_2 plane, and graph the direction vectors in the x_1–x_2 plane: (2, 0), (1.5, 1), (1, 0), (0, −1), (1, 1), (0, 0), and (−2, −2).

7. Consider

$$\frac{dx_1}{dt} = x_1 + 3x_2$$
$$\frac{dx_2}{dt} = -x_1 + 2x_2$$

Determine the direction vectors associated with the following points in the x_1–x_2 plane, and graph the direction vectors in the x_1–x_2 plane: (1, 0), (0, 1), (−1, 1), (0, −1), (−3, 1), (0, 0), and (−2, 1).

8. Consider

$$\frac{dx_1}{dt} = -x_2$$
$$\frac{dx_2}{dt} = x_1 + x_2$$

Determine the direction vectors associated with the following points in the x_1–x_2 plane, and graph the direction vectors in the x_1–x_2 plane: (1, 0), (0, 1), (−1, 0), (0, −1), (1, 1), (0, 0), and (−2, −2).

9. In Figures 11.18 through 11.21, direction fields are given. Each of the following systems of differential equations corresponds to exactly one of the direction fields. Match the systems to the appropriate figures.

(a) $\frac{dx_1}{dt} = 2x_1$

$\frac{dx_2}{dt} = x_1 + x_2$

(b) $\frac{dx_1}{dt} = x_1 + 2x_2$

$\frac{dx_2}{dt} = -2x_1$

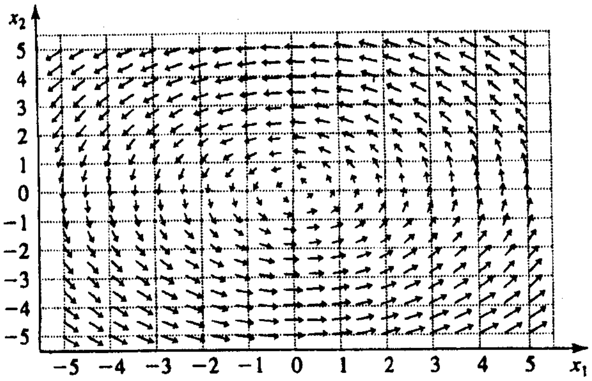

Figure 11.18

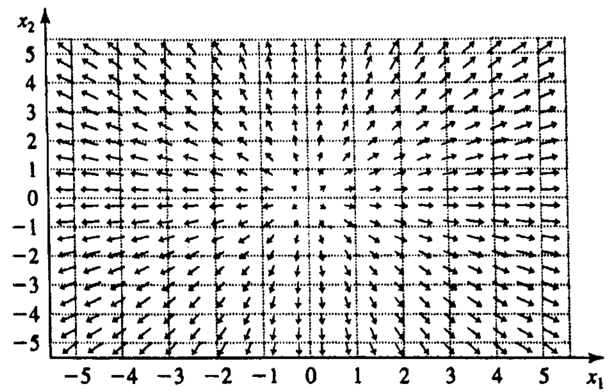

Figure 11.19

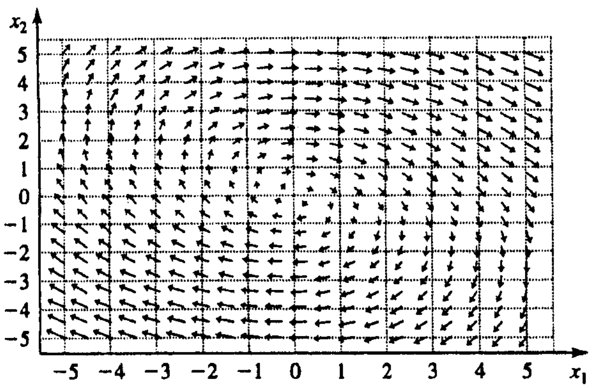

Figure 11.20

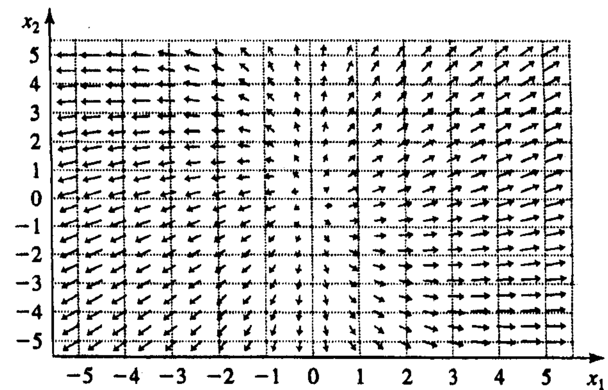

Figure 11.21

(c) $\frac{dx_1}{dt} = x_1$, $\frac{dx_2}{dt} = x_2$

(d) $\frac{dx_1}{dt} = -x_2$, $\frac{dx_2}{dt} = x_1$

10. The direction field of

$$\frac{dx_1}{dt} = x_1 + 3x_2$$

$$\frac{dx_2}{dt} = 2x_1 + 3x_2$$

is given in Figure 11.22. Sketch the solution curve that goes through the point $(1, 0)$.

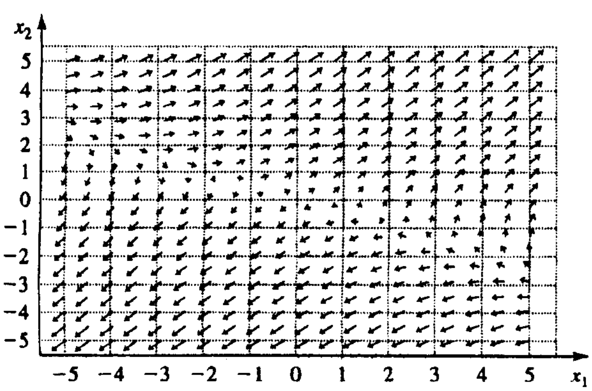

Figure 11.22

11. The direction field of

$$\frac{dx_1}{dt} = 2x_1 + 3x_2$$

$$\frac{dx_2}{dt} = -x_1 + x_2$$

is given in Figure 11.23. Sketch the solution curve that goes through the point $(2, -1)$.

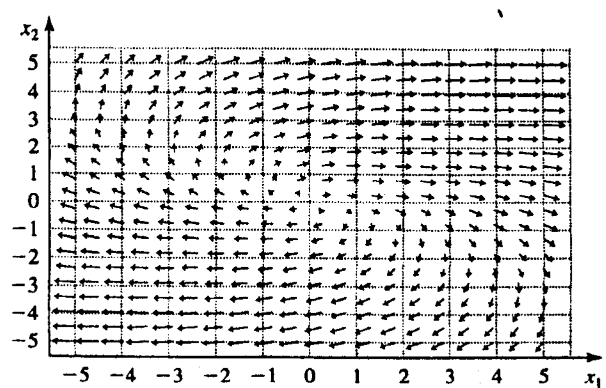

Figure 11.23

12. The direction field of

$$\frac{dx_1}{dt} = -x_1 - x_2$$
$$\frac{dx_2}{dt} = -2x_2$$

is given in Figure 11.24. Sketch the solution curve that goes through the point $(-3, -3)$.

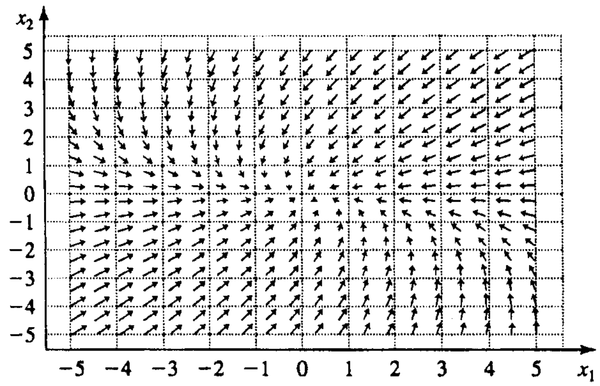

Figure 11.24

■ 11.1.2

In Problems 13–18, find the general solution of each given system of differential equations and sketch the lines in the direction of the eigenvectors. Indicate on each line the direction in which the solution would move if it starts on that line.

13. (Figure 11.25)

$$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} 1 & 3 \\ 5 & 3 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$

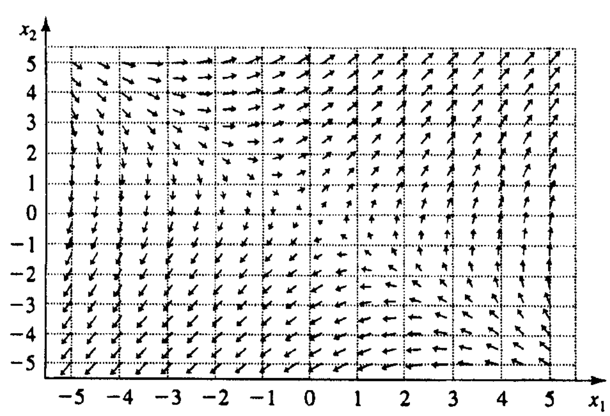

Figure 11.25

14. (Figure 11.26)

$$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} 2 & 1 \\ 4 & -1 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$

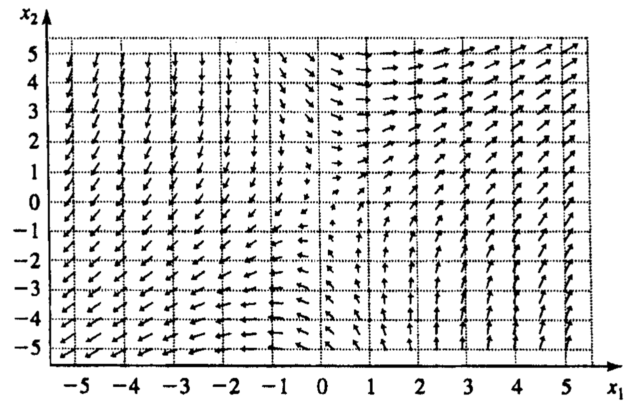

Figure 11.26

15. (Figure 11.27)

$$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} -3 & 3 \\ 6 & 4 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$

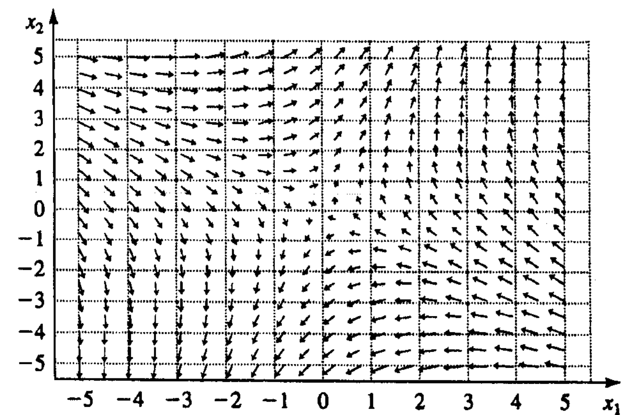

Figure 11.27

16. (Figure 11.28)

$$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} -5 & 3 \\ -2 & 0 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$

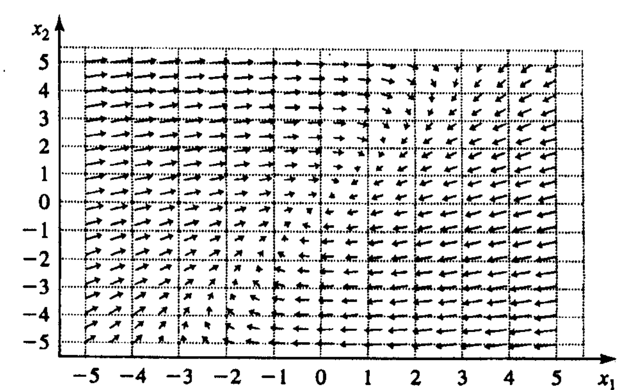

Figure 11.28

17. (Figure 11.29)

$$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} -2 & 0 \\ -3 & 1 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$

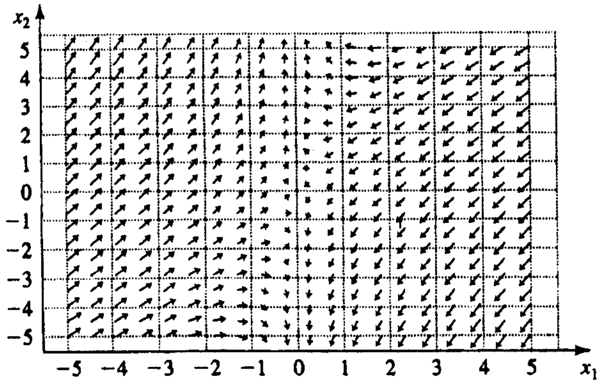

Figure 11.29

18. (Figure 11.30)

$$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} 5 & 2 \\ 1 & 6 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$

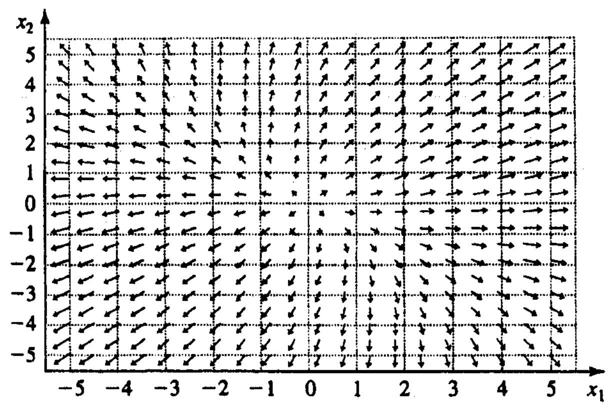

Figure 11.30

In Problems 19–26, solve the given initial-value problem.

19. $$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} -3 & 0 \\ 4 & 2 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$
with $x_1(0) = -5$ and $x_2(0) = 5$.

20. $$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} 1 & 3 \\ 0 & 2 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$
with $x_1(0) = 2$ and $x_2(0) = -1$.

21. $$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} 3 & -2 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$
with $x_1(0) = 1$ and $x_2(0) = 1$.

22. $$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} -1 & 0 \\ 1 & -2 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$
with $x_1(0) = -1$ and $x_2(0) = -2$.

23. $$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} 4 & -7 \\ 2 & -5 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$
with $x_1(0) = 13$ and $x_2(0) = 3$.

24. $$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} -3 & 4 \\ -1 & 2 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$
with $x_1(0) = 1$ and $x_2(0) = 2$.

25. $$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} 4 & 7 \\ 1 & -2 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$
with $x_1(0) = -1$ and $x_2(0) = -2$.

26. $$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} 2 & 6 \\ 1 & 3 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$$
with $x_1(0) = -3$ and $x_2(0) = 1$.

In Problems 27 and 28, we discuss the case of repeated eigenvalues.

27. Let

$$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix} \qquad (11.34)$$

(a) Show that

$$A = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$

has the repeated eigenvalues $\lambda_1 = \lambda_2 = 1$.

(b) Show that $\begin{bmatrix} 1 \\ 0 \end{bmatrix}$ and $\begin{bmatrix} 0 \\ 1 \end{bmatrix}$ are eigenvectors of A and that any vector $\begin{bmatrix} c_1 \\ c_2 \end{bmatrix}$ can be written as

$$\begin{bmatrix} c_1 \\ c_2 \end{bmatrix} = c_1 \begin{bmatrix} 1 \\ 0 \end{bmatrix} + c_2 \begin{bmatrix} 0 \\ 1 \end{bmatrix}$$

(c) Show that

$$\mathbf{x}(t) = c_1 e^t \begin{bmatrix} 1 \\ 0 \end{bmatrix} + c_2 e^t \begin{bmatrix} 0 \\ 1 \end{bmatrix}$$

is a solution of (11.34) that satisfies the initial condition $x_1(0) = c_1$ and $x_2(0) = c_2$.

28. Let

$$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{bmatrix} = \begin{bmatrix} 1 & 2 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix} \qquad (11.35)$$

(a) Show that

$$A = \begin{bmatrix} 1 & 2 \\ 0 & 1 \end{bmatrix}$$

has the repeated eigenvalues $\lambda_1 = \lambda_2 = 1$.

(b) Show that every eigenvector of A is of the form

$$c_1 \begin{bmatrix} 1 \\ 0 \end{bmatrix}$$

where c_1 is a real number different from 0.

(c) Show that

$$\mathbf{x}_1(t) = e^t \begin{bmatrix} 1 \\ 0 \end{bmatrix}$$

is a solution of (11.35).

(d) Show that

$$\mathbf{x}_2(t) = te^t\begin{bmatrix}1\\0\end{bmatrix} + e^t\begin{bmatrix}0\\0.5\end{bmatrix}$$

is a solution of (11.35).

(e) Show that

$$c_1\mathbf{x}_1(t) + c_2\mathbf{x}_2(t)$$

is a solution of (11.35). (It turns out that this is the general solution.)

■ 11.1.3

In Problems 29–42, we consider differential equations of the form

$$\frac{d\mathbf{x}}{dt} = A\mathbf{x}(t)$$

where

$$A = \begin{bmatrix}a_{11} & a_{12}\\a_{21} & a_{22}\end{bmatrix}$$

The eigenvalues of A will be real, distinct, and nonzero. Analyze the stability of the equilibrium (0, 0), and classify the equilibrium according to whether it is a sink, a source, or a saddle point.

29. $A = \begin{bmatrix}2 & -1\\0 & 3\end{bmatrix}$ **30.** $A = \begin{bmatrix}-1 & 0\\0 & -4\end{bmatrix}$

31. $A = \begin{bmatrix}-2 & 2\\2 & 1\end{bmatrix}$ **32.** $A = \begin{bmatrix}-5 & -2\\6 & 3\end{bmatrix}$

33. $A = \begin{bmatrix}-4 & 2\\-5 & 3\end{bmatrix}$ **34.** $A = \begin{bmatrix}-2 & 4\\2 & -5\end{bmatrix}$

35. $A = \begin{bmatrix}6 & -4\\-3 & 5\end{bmatrix}$ **36.** $A = \begin{bmatrix}-1 & 3\\2 & -5\end{bmatrix}$

37. $A = \begin{bmatrix}-3 & -1\\1 & -6\end{bmatrix}$ **38.** $A = \begin{bmatrix}-3 & 1\\1 & -2\end{bmatrix}$

39. $A = \begin{bmatrix}0 & -2\\-1 & 3\end{bmatrix}$ **40.** $A = \begin{bmatrix}0 & 2\\3 & 7\end{bmatrix}$

41. $A = \begin{bmatrix}-2 & -3\\1 & 3\end{bmatrix}$ **42.** $A = \begin{bmatrix}4 & -1\\5 & -1\end{bmatrix}$

In Problems 43–56, we consider differential equations of the form

$$\frac{d\mathbf{x}}{dt} = A\mathbf{x}(t)$$

where

$$A = \begin{bmatrix}a_{11} & a_{12}\\a_{21} & a_{22}\end{bmatrix}$$

The eigenvalues of A will be complex conjugates. Analyze the stability of the equilibrium (0, 0), and classify the equilibrium according to whether it is a stable spiral, an unstable spiral, or a center.

43. $A = \begin{bmatrix}2 & -1\\3 & 0\end{bmatrix}$ **44.** $A = \begin{bmatrix}-1 & -5\\4 & -3\end{bmatrix}$

45. $A = \begin{bmatrix}-2 & 4\\-3 & -2\end{bmatrix}$ **46.** $A = \begin{bmatrix}1 & 3\\-2 & 1\end{bmatrix}$

47. $A = \begin{bmatrix}1 & 3\\-2 & -2\end{bmatrix}$ **48.** $A = \begin{bmatrix}2 & -3\\2 & -1\end{bmatrix}$

49. $A = \begin{bmatrix}4 & 5\\-3 & -3\end{bmatrix}$ **50.** $A = \begin{bmatrix}2 & 2\\-6 & -4\end{bmatrix}$

51. $A = \begin{bmatrix}-1 & 1\\-3 & 1\end{bmatrix}$ **52.** $A = \begin{bmatrix}3 & -2\\1 & 3\end{bmatrix}$

53. $A = \begin{bmatrix}0 & -1\\1 & 0\end{bmatrix}$ **54.** $A = \begin{bmatrix}0 & -3\\2 & 2\end{bmatrix}$

55. $A = \begin{bmatrix}1 & 2\\-5 & -3\end{bmatrix}$ **56.** $A = \begin{bmatrix}2 & -3\\3 & -2\end{bmatrix}$

In Problems 57–66, we consider differential equations of the form

$$\frac{d\mathbf{x}}{dt} = A\mathbf{x}(t)$$

where

$$A = \begin{bmatrix}a_{11} & a_{12}\\a_{21} & a_{22}\end{bmatrix}$$

Analyze the stability of the equilibrium (0, 0), and classify the equilibrium.

57. $A = \begin{bmatrix}-1 & -2\\1 & 3\end{bmatrix}$ **58.** $A = \begin{bmatrix}-2 & 2\\-4 & 3\end{bmatrix}$

59. $A = \begin{bmatrix}-1 & -1\\5 & -3\end{bmatrix}$ **60.** $A = \begin{bmatrix}2 & 2\\2 & 3\end{bmatrix}$

61. $A = \begin{bmatrix}1 & 3\\2 & 3\end{bmatrix}$ **62.** $A = \begin{bmatrix}-1 & 5\\-3 & 0\end{bmatrix}$

63. $A = \begin{bmatrix}-2 & 3\\1 & -4\end{bmatrix}$ **64.** $A = \begin{bmatrix}-2 & -7\\1 & 2\end{bmatrix}$

65. $A = \begin{bmatrix}3 & -5\\2 & -1\end{bmatrix}$ **66.** $A = \begin{bmatrix}3 & 6\\-1 & -4\end{bmatrix}$

67. The following system has two distinct real eigenvalues, but one eigenvalue is equal to 0:

$$\frac{d\mathbf{x}}{dt} = \begin{bmatrix}4 & 8\\1 & 2\end{bmatrix}\mathbf{x}(t) \qquad (11.36)$$

(a) Find both eigenvalues and the associated eigenvectors.

(b) Use the general solution (11.26) to find $x_1(t)$ and $x_2(t)$.

(c) The direction field is shown in Figure 11.31. Sketch the lines corresponding to the eigenvectors. Compute dx_2/dx_1, and conclude that all direction vectors are parallel to the line in the direction of the eigenvector corresponding to the nonzero eigenvalue. Describe in words how solutions starting at different points behave.

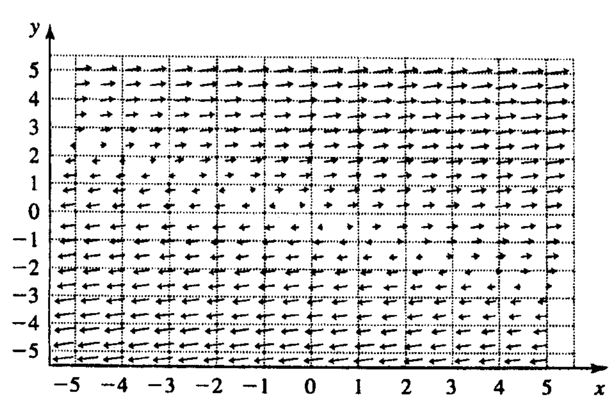

Figure 11.31

68. The following system has two distinct real eigenvalues, but one eigenvalue is equal to 0:

$$\frac{d\mathbf{x}}{dt} = \begin{bmatrix} 2 & 4 \\ 3 & 6 \end{bmatrix} \mathbf{x}(t) \tag{11.37}$$

(a) Find both eigenvalues and the associated eigenvectors.

(b) Use the general solution (11.26) to find $x_1(t)$ and $x_2(t)$.

(c) The direction field is shown in Figure 11.32. Sketch the lines corresponding to the eigenvectors. Compute dx_2/dx_1, and conclude that all direction vectors are parallel to the line in the direction of the eigenvector corresponding to the nonzero eigenvalue. Describe in words how solutions starting at different points behave.

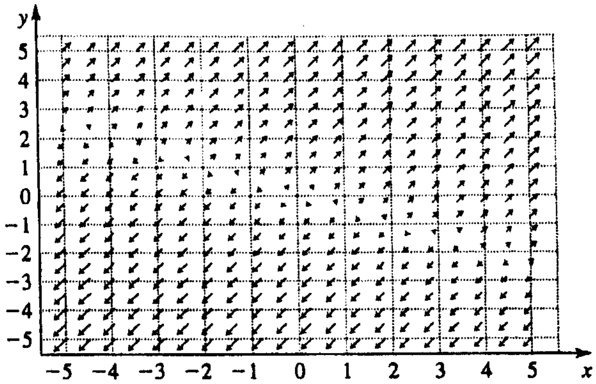

Figure 11.32

■ 11.2 Linear Systems: Applications

■ 11.2.1 Compartment Models

Compartment models (which we encountered in Chapter 8) describe flow between compartments, such as nutrient flow between lakes or the flow of a radioactive tracer between different parts of an organism. In the simplest situations, the resulting model is a system of linear differential equations.

We will consider a general two-compartment model that can be described by a system of two linear differential equations. A schematic description of the model is given in Figure 11.33.

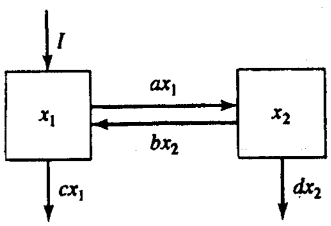

Figure 11.33 A schematic description of a general two-compartment model.

We denote by $x_1(t)$ the amount of matter in compartment 1 at time t and by $x_2(t)$ the amount of matter in compartment 2 at time t. To have a concrete example in mind, think of $x_1(t)$ and $x_2(t)$ as the amount of water in each of the two compartments, respectively. The direction of the flow of matter and the rates at which matter flows are shown in Figure 11.33. We see that matter enters compartment 1 at the constant rate I and moves from compartment 1 to compartment 2 at rate ax_1 if x_1 is the amount of matter in compartment 1. Matter in compartment 1 is lost at rate cx_1. In addition, matter flows from compartment 2 to compartment 1 at rate bx_2 if x_2 is the amount of matter in compartment 2. Matter in compartment 2 is lost at rate dx_2; there is no external input into compartment 2. The constants I, a, b, c, and d are all nonnegative.

We describe the dynamics of $x_1(t)$ and $x_2(t)$ by the following system of differential equations:

$$\begin{aligned} \frac{dx_1}{dt} &= I - (a+c)x_1 + bx_2 \\ \frac{dx_2}{dt} &= ax_1 - (b+d)x_2 \end{aligned} \tag{11.38}$$

If $I > 0$, then (11.38) is a system of inhomogeneous linear differential equations with constant coefficients. Constant input is often important in real situations, such as the flow of nutrients between soil and plants, in which nutrients might be added at a constant rate. In the discussion that follows, however, we will set $I = 0$, since this corresponds to the situation discussed in the previous section (i.e., no matter is added over time). It is not difficult to guess how the system behaves when $I = 0$: Either some matter is continually lost, so one or both compartments empty out, or no matter is lost, so at least one compartment will contain matter. We will discuss both cases.

When $I = 0$, (11.38) reduces to the linear system

$$\frac{d\mathbf{x}}{dt} = A\mathbf{x}(t) \quad \text{with} \quad A = \begin{bmatrix} -(a+c) & b \\ a & -(b+d) \end{bmatrix} \tag{11.39}$$

To avoid trivial situations, we assume that at least one of the parameters a, b, c, and d is positive. (Otherwise, no material would ever move in the system.)

We can solve (11.42) directly: Since

$$\frac{d}{dt}\sin(at) = a\cos(at)$$
$$\frac{d}{dt}\cos(at) = -a\sin(at)$$

it follows that

$$\frac{d^2}{dt^2}\sin(at) = -a^2\sin(at)$$

and

$$\frac{d^2}{dt^2}\cos(at) = -a^2\cos(at)$$

If we set $a = \sqrt{k}$, we see that $\cos(\sqrt{k}t)$ and $\sin(\sqrt{k}t)$ solve (11.42). Using the superposition principle, we therefore obtain the solution of (11.42) as

$$x(t) = c_1\sin(\sqrt{k}t) + c_2\cos(\sqrt{k}t)$$

To determine the constants c_1 and c_2, we must fix an initial condition. If we assume, for instance, that

$$x(0) = 0 \quad \text{and} \quad v(0) = v_0 \tag{11.43}$$

then

$$0 = c_2$$

Since $v(t) = dx/dt$, we have

$$v(t) = c_1\sqrt{k}\cos(\sqrt{k}t) - c_2\sqrt{k}\sin(\sqrt{k}t)$$

and, therefore,

$$v(0) = c_1\sqrt{k} = v_0$$

which implies that

$$c_1 = \frac{v_0}{\sqrt{k}}$$

Hence, the solution of (11.42) that satisfies the initial condition (11.43) is given by

$$x(t) = \frac{v_0}{\sqrt{k}}\sin(\sqrt{k}t)$$

The harmonic oscillator is quite important in physics. It describes, for instance, a frictionless pendulum when the displacement from the resting state is not too large.

Section 11.2 Problems

■ 11.2.1

In Problems 1–8, determine the system of differential equations corresponding to each compartment model and analyze the stability of the equilibrium (0, 0). *The parameters have the same meaning as in Figure 11.33.*

1. $a = 0.5, b = 0.1, c = 0.05, d = 0.02$
2. $a = 0.4, b = 1.2, c = 0.3, d = 0$
3. $a = 2.5, b = 0.7, c = 0, d = 0.1$
4. $a = 1.7, b = 0.6, c = 0.1, d = 0.3$
5. $a = 0, b = 0.1, c = 0, d = 0.3$
6. $a = 0.2, b = 0.1, c = 0, d = 0$
7. $a = 0.1, b = 1.2, c = 0.5, d = 0.05$
8. $a = 0.2, b = 0, c = 0, d = 0.3$

In Problems 9–18, find the corresponding compartment diagram for each system of differential equations.

9. $$\frac{dx_1}{dt} = -0.4x_1 + 0.3x_2$$
$$\frac{dx_2}{dt} = 0.1x_1 - 0.5x_2$$

10. $$\frac{dx_1}{dt} = -0.4x_1 + 3x_2$$
$$\frac{dx_2}{dt} = 0.2x_1 - 3x_2$$

11. $$\frac{dx_1}{dt} = -0.2x_1 + 0.1x_2$$
$$\frac{dx_2}{dt} = -0.1x_2$$

12. $$\frac{dx_1}{dt} = -0.2x_1 + 1.1x_2$$
$$\frac{dx_2}{dt} = 0.2x_1 - 1.1x_2$$

13. $\frac{dx_1}{dt} = -2.3x_1 + 1.1x_2$

$\frac{dx_2}{dt} = 0.2x_1 - 2.3x_2$

14. $\frac{dx_1}{dt} = -1.6x_1 + 0.3x_2$

$\frac{dx_2}{dt} = 0.1x_1 - 0.5x_2$

15. $\frac{dx_1}{dt} = -1.2x_1$

$\frac{dx_2}{dt} = 0.3x_1 - 0.2x_2$

16. $\frac{dx_1}{dt} = -0.2x_1 + 0.4x_2$

$\frac{dx_2}{dt} = 0.2x_1 - 0.4x_2$

17. $\frac{dx_1}{dt} = -0.2x_1$

$\frac{dx_2}{dt} = -0.3x_2$

18. $\frac{dx_1}{dt} = -x_1$

$\frac{dx_2}{dt} = x_1 - 0.5x_2$

19. Suppose that a drug is administered to a person in a single dose, and assume that the drug does not accumulate in body tissue, but is excreted through urine. Denote the amount of drug in the body at time t by $x_1(t)$ and in the urine at time t by $x_2(t)$. If $x_1(0) = 4$ mg and $x_2(0) = 0$, find $x_1(t)$ and $x_2(t)$ if

$$\frac{dx_1}{dt} = -0.3x_1(t)$$

20. Suppose that a drug is administered to a person in a single dose, and assume that the drug does not accumulate in body tissue, but is excreted through urine. Denote the amount of drug in the body at time t by $x_1(t)$ and in the urine at time t by $x_2(t)$. If $x_1(0) = 6$ mg and $x_2(0) = 0$, find a system of differential equations for $x_1(t)$ and $x_2(t)$ if it takes 20 minutes for the drug to be at one-half of its initial amount in the body.

21. A very simple two-compartment model for gap dynamics in a forest assumes that gaps are created by disturbances (wind, fire, etc.) and that gaps revert to forest as trees grow in the gaps. We denote by $x_1(t)$ the area occupied by gaps and by $x_2(t)$ the area occupied by adult trees. We assume that the dynamics are given by

$$\frac{dx_1}{dt} = -0.2x_1 + 0.1x_2 \qquad (11.44)$$

$$\frac{dx_2}{dt} = 0.2x_1 - 0.1x_2 \qquad (11.45)$$

(a) Find the corresponding compartment diagram.
(b) Show that $x_1(t) + x_2(t)$ is a constant. Denote the constant by A and give its meaning. [*Hint:* Show that $\frac{d}{dt}(x_1 + x_2) = 0$.]
(c) Let $x_1(0) + x_2(0) = 20$. Use your answer in (b) to explain why this equation implies that $x_1(t) + x_2(t) = 20$ for all $t > 0$.
(d) Use your result in (c) to replace x_2 in (11.44) by $20 - x_1$, and show that doing so reduces the system (11.44) and (11.45) to

$$\frac{dx_1}{dt} = 2 - 0.3x_1 \qquad (11.46)$$

with $x_1(t) + x_2(t) = 20$ for all $t \geq 0$.
(e) Solve the system (11.44) and (11.45), and determine what fraction of the forest is occupied by adult trees at time t when $x_1(0) = 2$ and $x_2(0) = 18$. What happens as $t \to \infty$?

22. One simple model for forest succession is a three-compartment model. We assume that gaps in a forest are created by disturbances and are colonized by early successional species, which are then replaced by late successional species. We denote by $x_1(t)$ the total area occupied by gaps at time t, by $x_2(t)$ the total area occupied by early successional species at time t, and by $x_3(t)$ the total area occupied by late successional species at time t. The dynamics are given by

$$\frac{dx_1}{dt} = 0.2x_2 + x_3 - 2x_1$$

$$\frac{dx_2}{dt} = 2x_1 - 0.7x_2$$

$$\frac{dx_3}{dt} = 0.5x_2 - x_3$$

(a) Draw the corresponding compartment diagram.
(b) Show that

$$x_1(t) + x_2(t) + x_3(t) = A$$

where A is a constant, and give the meaning of A.

■ 11.2.2

23. Solve

$$\frac{d^2x}{dt^2} = -4x$$

with $x(0) = 0$ and $\frac{dx(0)}{dt} = 6$.

24. Solve

$$\frac{d^2x}{dt^2} = -9x$$

with $x(0) = 0$ and $\frac{dx(0)}{dt} = 12$.

25. Transform the second-order differential equation

$$\frac{d^2x}{dt^2} = 3x$$

into a system of first-order differential equations.

26. Transform the second-order differential equation

$$\frac{d^2x}{dt^2} = -\frac{1}{2}x$$

into a system of first-order differential equations.

27. Transform the second-order differential equation

$$\frac{d^2x}{dt^2} + \frac{dx}{dt} = x$$

into a system of first-order differential equations.

28. Transform the second-order differential equation

$$\frac{d^2x}{dt^2} - 2\frac{dx}{dt} = 3x$$

into a system of first-order differential equations.

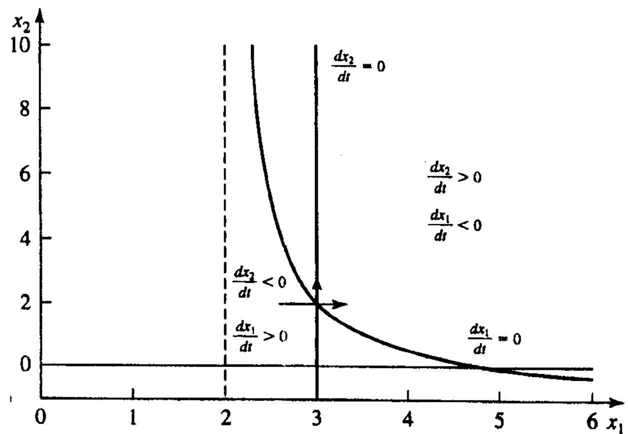

Figure 11.42 The zero isoclines in the x_1–x_2 plane.

the vertical arrow in the x_2-direction. Since the vertical arrow is on the zero isocline of x_2, the sign of dx_2/dt does not change as we cross the equilibrium in the x_2-direction. Therefore, $a_{22} = 0$. The signs of a_{12} and a_{21} follow from observing that if we cross the zero isocline of x_1 in the x_2-direction (the vertical arrow), then dx_1/dt changes from positive to negative, making $a_{12} < 0$. If we cross the zero isocline of x_2 in the direction of x_1 (the horizontal arrow), we see that dx_2/dt changes from negative to positive, making $a_{21} > 0$.

To determine the stability of $\hat{\mathbf{x}}$, we look at the trace and the determinant. Since the trace is negative and the determinant is positive, we conclude that the equilibrium is locally stable. ■

This simple graphical approach does not always give us the signs of the real parts of the eigenvalues, as illustrated in the following example: Suppose that we arrive at the Jacobi matrix in which the signs of the entries are

$$\begin{bmatrix} + & - \\ - & - \end{bmatrix}$$

The trace may now be positive or negative. Therefore, we cannot conclude anything about the eigenvalues. In this case, we would have to compute the eigenvalues or the trace and the determinant explicitly and cannot rely on the signs alone.

Section 11.3 Problems

11.3.1

n Problems 1–6, the point $(0, 0)$ *is always an equilibrium. Use the nalytical approach to investigate its stability.*

$$\frac{dx_1}{dt} = x_1 - 2x_2 + x_1x_2$$
$$\frac{dx_2}{dt} = -x_1 + x_2$$

2.
$$\frac{dx_1}{dt} = -x_1 - x_2 + x_1^2$$
$$\frac{dx_2}{dt} = x_2 - x_1^2$$

$$\frac{dx_1}{dt} = x_1 + x_1^2 - 2x_1x_2 + x_2$$
$$\frac{dx_2}{dt} = x_1$$

4.
$$\frac{dx_1}{dt} = 3x_1x_2 - x_1 + x_2$$
$$\frac{dx_2}{dt} = x_2^2 - x_1$$

$$\frac{dx_1}{dt} = x_1e^{-x_2}$$
$$\frac{dx_2}{dt} = 2x_2e^{x_1}$$

6.
$$\frac{dx_1}{dt} = -2\sin x_1$$
$$\frac{dx_2}{dt} = -x_2e^{x_1}$$

In Problems 7–12, find all equilibria of each system of differential equations and use the analytical approach to determine the stability of each equilibrium.

7.
$$\frac{dx_1}{dt} = -x_1 + 2x_1(1 - x_1)$$
$$\frac{dx_2}{dt} = -x_2 + 5x_2(1 - x_1 - x_2)$$

8.
$$\frac{dx_1}{dt} = -x_1 + 3x_1(1 - x_1 - x_2)$$
$$\frac{dx_2}{dt} = -x_2 + 5x_2(1 - x_1 - x_2)$$

9.
$$\frac{dx_1}{dt} = 4x_1(1 - x_1) - 2x_1x_2$$
$$\frac{dx_2}{dt} = x_2(2 - x_2) - x_2$$

10.
$$\frac{dx_1}{dt} = 2x_1(5 - x_1 - x_2)$$
$$\frac{dx_2}{dt} = 3x_2(7 - 3x_1 - x_2)$$

11. $$\frac{dx_1}{dt} = x_1 - x_2$$
$$\frac{dx_2}{dt} = x_1x_2 - x_2$$

12. $$\frac{dx_1}{dt} = x_1x_2 - x_2$$
$$\frac{dx_2}{dt} = x_1 + x_2$$

13. For which value of a has

$$\frac{dx_1}{dt} = x_2(x_1 + a)$$
$$\frac{dx_2}{dt} = x_2^2 + x_2 - x_1$$

a unique equilibrium? Characterize its stability.

14. Assume that $a > 0$. Find all point equilibria of

$$\frac{dx_1}{dt} = 1 - ax_1x_2$$
$$\frac{dx_2}{dt} = ax_1x_2 - x_2$$

and characterize their stability.

■ 11.3.2

15. Assume that

$$\frac{dx_1}{dt} = x_1(10 - 2x_1 - x_2)$$
$$\frac{dx_2}{dt} = x_2(10 - x_1 - 2x_2)$$

(a) Graph the zero isoclines.

(b) Show that $(\frac{10}{3}, \frac{10}{3})$ is an equilibrium, and use the analytical approach to determine its stability.

16. Assume that

$$\frac{dx_1}{dt} = x_1(10 - x_1 - 2x_2)$$
$$\frac{dx_2}{dt} = x_2(10 - 2x_1 - x_2)$$

(a) Graph the zero isoclines.

(b) Show that $(\frac{10}{3}, \frac{10}{3})$ is an equilibrium, and use the analytical approach to determine its stability.

In Problems 17–22, use the graphical approach for 2×2 systems to find the sign structure of the Jacobi matrix at the indicated equilibrium. If possible, determine the stability of the equilibrium. Assume that the system of differential equations is given by

$$\frac{dx_1}{dt} = f_1(x_1, x_2)$$
$$\frac{dx_2}{dt} = f_2(x_1, x_2)$$

Furthermore, assume that x_1 and x_2 are both nonnegative. In each problem, the zero isoclines are drawn and the equilibrium we want to investigate is indicated by a dot. Assume that both x_1 and x_2 increase close to the origin and that f_1 and f_2 change sign when crossing their zero isoclines.

17. See Figure 11.43.

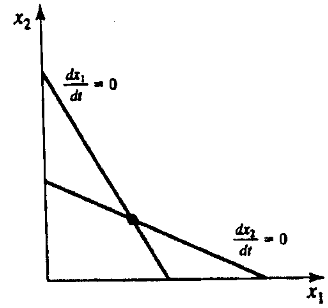

Figure 11.43

18. See Figure 11.44.

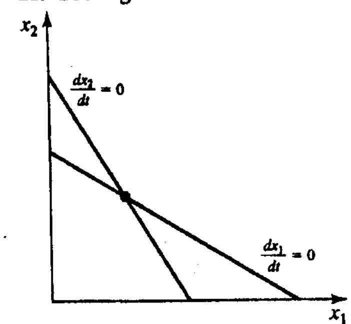

Figure 11.44

19. See Figure 11.45.

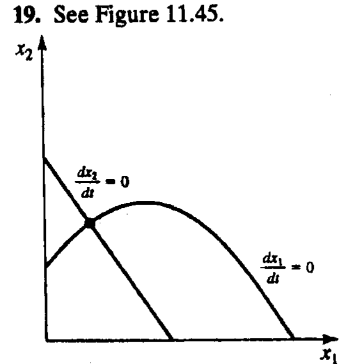

Figure 11.45

20. See Figure 11.46.

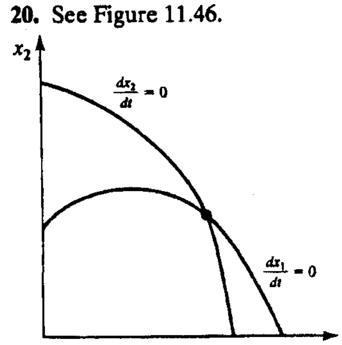

Figure 11.46

21. See Figure 11.47.

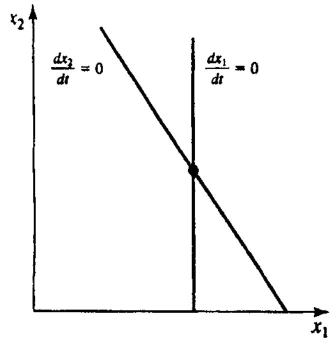

Figure 11.47

22. See Figure 11.48.

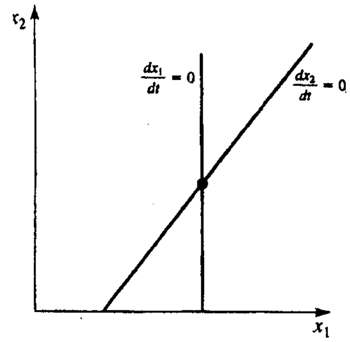

Figure 11.48

23. Let

$$\frac{dx_1}{dt} = x_1(2 - x_1) - x_1x_2$$
$$\frac{dx_2}{dt} = x_1x_2 - x_2$$

(a) Graph the zero isoclines.

(b) Show that (1, 1) is an equilibrium. Use the graphical approach to determine its stability.

24. Let

$$\frac{dx_1}{dt} = x_1(2 - x_1^2) - x_1x_2$$
$$\frac{dx_2}{dt} = x_1x_2 - x_2$$

(a) Graph the zero isoclines.

(b) Show that (1, 1) is an equilibrium. Use the graphical approach to determine its stability.

■ 11.4 Nonlinear Systems: Applications

■ 11.4.1 The Lotka–Volterra Model of Interspecific Competition

Imagine two species of plants growing together in the same plot. They both use similar resources: light, water, and nutrients. The use of these resources by one individual reduces their availability to other individuals. We call this type of interaction between individuals **competition. Intraspecific competition** occurs between individuals of the same species, **interspecific competition** between individuals of different species. Competition may result in reduced fecundity or reduced survivorship (or both). The effects of competition are often more pronounced when the number of competitors is higher.

In this subsection, we will discuss the Lotka–Volterra model of interspecific competition, which incorporates density-dependent effects of competition in the manner described previously. The model is an extension of the logistic equation to the case of two species. To describe it, we denote the population size of species 1 at time t by $N_1(t)$ and that of species 2 at time t by $N_2(t)$. Each species grows according to the logistic equation when the other species is absent. We denote their respective carrying capacities by K_1 and K_2, and their respective intrinsic rates of growth by r_1 and r_2. We assume that K_1, K_2, r_1, and r_2 are positive. In addition, the two species may have inhibitory effects on each other. We measure the effect of species 1 on species 2 by the **competition coefficient** α_{21}; the effect of species 2 on species 1 is measured by the competition coefficient α_{12}. The Lotka–Volterra model of interspecific competition is then given by the following system of differential

Section 11.4 Problems

■ 11.4.1

1. Suppose that the densities of two species evolve in accordance with the Lotka–Volterra model of interspecific competition. Assume that species 1 has intrinsic rate of growth $r_1 = 2$ and carrying capacity $K_1 = 20$ and that species 2 has intrinsic rate of growth $r_2 = 3$ and carrying capacity $K_2 = 15$. Furthermore, assume that 20 individuals of species 2 have the same effect on species 1 as 4 individuals of species 1 have on themselves and that 30 individuals of species 1 have the same effect on species 2 as 6 individuals of species 2 have on themselves. Find a system of differential equations that describes this situation.

2. Suppose the densities of two species evolve in accordance with the Lotka–Volterra model of interspecific competition. Assume that species 1 has intrinsic rate of growth $r_1 = 4$ and carrying capacity $K_1 = 17$ and that species 2 has intrinsic rate of growth $r_2 = 1.5$ and carrying capacity $K_2 = 32$. Furthermore, assume that 15 individuals of species 2 have the same effect on species 1 as 7 individuals of species 1 have on themselves and that 5 individuals of species 1 have the same effect on species 2 as 7 individuals of species 2 have on themselves. Find a system of differential equations that describes this situation.

In Problems 3–6, use the graphical approach to classify the following Lotka–Volterra models of interspecific competition according to "coexistence," "founder control," "species 1 excludes species 2," or "species 2 excludes species 1."

3. $$\frac{dN_1}{dt} = 2N_1\left(1 - \frac{N_1}{10} - 0.7\frac{N_2}{10}\right)$$
$$\frac{dN_2}{dt} = 5N_2\left(1 - \frac{N_2}{15} - 0.3\frac{N_1}{15}\right)$$

4. $$\frac{dN_1}{dt} = 3N_1\left(1 - \frac{N_1}{50} - 0.3\frac{N_2}{50}\right)$$
$$\frac{dN_2}{dt} = 4N_2\left(1 - \frac{N_2}{30} - 0.8\frac{N_1}{30}\right)$$

5. $$\frac{dN_1}{dt} = N_1\left(1 - \frac{N_1}{20} - \frac{N_2}{5}\right)$$
$$\frac{dN_2}{dt} = 2N_2\left(1 - \frac{N_2}{15} - \frac{N_1}{3}\right)$$

6. $$\frac{dN_1}{dt} = 3N_1\left(1 - \frac{N_1}{25} - 1.2\frac{N_2}{25}\right)$$
$$\frac{dN_2}{dt} = N_2\left(1 - \frac{N_2}{30} - 0.8\frac{N_1}{30}\right)$$

In Problems 7–10, use the eigenvalue approach to analyze all equilibria of the given Lotka–Volterra models of interspecific competition.

7. $$\frac{dN_1}{dt} = 3N_1\left(1 - \frac{N_1}{18} - 1.3\frac{N_2}{18}\right)$$
$$\frac{dN_2}{dt} = 2N_2\left(1 - \frac{N_2}{20} - 0.6\frac{N_1}{20}\right)$$

8. $$\frac{dN_1}{dt} = 4N_1\left(1 - \frac{N_1}{12} - 0.3\frac{N_2}{12}\right)$$
$$\frac{dN_2}{dt} = 5N_2\left(1 - \frac{N_2}{15} - 0.2\frac{N_1}{15}\right)$$

9. $$\frac{dN_1}{dt} = N_1\left(1 - \frac{N_1}{35} - 3\frac{N_2}{35}\right)$$
$$\frac{dN_2}{dt} = 3N_2\left(1 - \frac{N_2}{40} - 4\frac{N_1}{40}\right)$$

10. $$\frac{dN_1}{dt} = N_1\left(1 - \frac{N_1}{25} - 0.1\frac{N_2}{25}\right)$$
$$\frac{dN_2}{dt} = N_2\left(1 - \frac{N_2}{28} - 1.2\frac{N_1}{28}\right)$$

11. Suppose that two species of beetles are reared together in one experiment and separately in another. When species 1 is reared alone, it reaches an equilibrium of about 200. When species 2 is reared alone, it reaches an equilibrium of about 150. When both of them are reared together, they seem to be able to coexist: Species 1 reaches an equilibrium of about 180 and species 2 reaches an equilibrium of about 80. If their densities follow the Lotka–Volterra equation of interspecific competition, find α_{12} and α_{21}.

12. Suppose that two species of beetles are reared together. Species 1 wins if there are initially 100 individuals of species 1 and 20 individuals of species 2. But species 2 wins if there are initially 20 individuals of species 1 and 100 individuals of species 2. When the beetles are reared separately, both species seem to reach an equilibrium of about 120. On the basis of this information and assuming that the densities follow the Lotka–Volterra model of interspecific competition, can you give lower bounds on α_{12} and α_{21}?

■ 11.4.2

In Problems 13 and 14, use a graphing calculator to sketch solution curves of the given Lotka–Volterra predator–prey model in the N–P plane. Also graph $N(t)$ and $P(t)$ as functions of t.

13. $$\frac{dN}{dt} = 2N - PN$$
$$\frac{dP}{dt} = \tfrac{1}{2}PN - P$$
with initial conditions
(a) $(N(0), P(0)) = (2, 2)$ **(b)** $(N(0), P(0)) = (3, 3)$
(c) $(N(0), P(0)) = (4, 4)$

14. $$\frac{dN}{dt} = 3N - 2PN$$
$$\frac{dP}{dt} = PN - P$$
with initial conditions
(a) $(N(0), P(0)) = (1, 3/2)$ **(b)** $(N(0), P(0)) = (2, 2)$
(c) $(N(0), P(0)) = (3, 1)$

In Problems 15 and 16, we investigate the Lotka–Volterra predator–prey model.

15. Assume that
$$\frac{dN}{dt} = N - 4PN$$
$$\frac{dP}{dt} = 2PN - 3P$$

(a) Show that this system has two equilibria: the trivial equilibrium $(0, 0)$, and a nontrivial one in which both species have positive densities.

(b) Use the eigenvalue approach to show that the trivial equilibrium is unstable.

(c) Determine the eigenvalues corresponding to the nontrivial equilibrium. Does your analysis allow you to infer anything about the stability of this equilibrium?

(d) Use a graphing calculator to sketch curves in the N–P plane. Also, sketch solution curves of the prey and the predator densities as functions of time.

16. Assume that

$$\frac{dN}{dt} = 5N - PN$$
$$\frac{dP}{dt} = PN - P$$

(a) Show that this system has two equilibria: the trivial equilibrium (0, 0), and a nontrivial one in which both species have positive densities.

(b) Use the eigenvalue approach to show that the trivial equilibrium is unstable.

(c) Determine the eigenvalues corresponding to the nontrivial equilibrium. Does your analysis allow you to infer anything about the stability of this equilibrium?

(d) Use a graphing calculator to sketch curves in the N–P plane. Also, sketch solution curves of the prey and the predator densities as functions of time.

17. Assume that $N(t)$ denotes the density of an insect species at time t and $P(t)$ denotes the density of its predator at time t. The insect species is an agricultural pest, and its predator is used as a biological control agent. Their dynamics are given by the system of differential equations

$$\frac{dN}{dt} = 5N - 3PN$$
$$\frac{dP}{dt} = 2PN - P$$

(a) Explain why

$$\frac{dN}{dt} = 5N \tag{11.85}$$

describes the dynamics of the insect in the absence of the predator. Solve (11.85). Describe what happens to the insect population in the absence of the predator.

(b) Explain why introducing the insect predator into the system can help to control the density of the insect.

(c) Assume that at the beginning of the growing season the insect density is 0.5 and the predator density is 2. You decide to control the insects by using an insecticide in addition to the predator. You are careful and choose an insecticide that does not harm the predator. After you spray, the insect density drops to 0.01 and the predator density remains at 2. Use a graphing calculator to investigate the long-term implications of your decision to spray the field. In particular, investigate what would have happened to the insect densities if you had decided not to spray the field, and compare your results with the insect density over time that results from your application of the insecticide.

18. Assume that $N(t)$ denotes prey density at time t and $P(t)$ denotes predator density at time t. Their dynamics are given by the system of equations

$$\frac{dN}{dt} = 4N - 2PN$$
$$\frac{dP}{dt} = PN - 3P$$

Assume that initially $N(0) = 3$ and $P(0) = 2$.

(a) If you followed this predator–prey community over time, what would you observe?

(b) Suppose that bad weather kills 90% of the prey population and 67% of the predator population. If you continued to observe this predator–prey community, what would you expect to see?

19. An unrealistic feature of the Lotka–Volterra model is that the prey exhibits unlimited growth in the absence of the predator. The model described by the following system remedies this shortcoming (in the model, we assume that the prey evolves according to logistic growth in the absence of the predator; the other features of the model are retained):

$$\begin{aligned} \frac{dN}{dt} &= 3N\left(1 - \frac{N}{10}\right) - 2PN \\ \frac{dP}{dt} &= PN - 4P \end{aligned} \tag{11.86}$$

(a) Explain why the prey evolves according to

$$\frac{dN}{dt} = 3N\left(1 - \frac{N}{10}\right) \tag{11.87}$$

in the absence of the predator. Investigate the long-term behavior of solutions to (11.87).

(b) Find all equilibria of (11.86), and use the eigenvalue approach to determine their stability.

(c) Use a graphing calculator to sketch the solution curve of (11.86) in the N–P plane when $N(0) = 2$ and $P(0) = 2$. Also, sketch $N(t)$ and $P(t)$ as functions of time, starting with $N(0) = 2$ and $P(0) = 2$.

20. An unrealistic feature of the Lotka–Volterra model is that the prey exhibits unlimited growth in the absence of the predator. The model described by the following system remedies this shortcoming (in the model, we assume that the prey evolves according to logistic growth in the absence of the predator; the other features of the model are retained):

$$\begin{aligned} \frac{dN}{dt} &= N\left(1 - \frac{N}{K}\right) - 4PN \\ \frac{dP}{dt} &= PN - 5P \end{aligned} \tag{11.88}$$

Here, $K > 0$ denotes the carrying capacity of the prey in the absence of the predator. In what follows, we will investigate how the carrying capacity affects the outcome of this predator–prey interaction.

(a) Draw the zero isoclines of (11.88) for **(i)** $K = 10$ and **(ii)** $K = 3$.

(b) When $K = 10$, the zero isoclines intersect, indicating the existence of a nontrivial equilibrium. Analyze the stability of this nontrivial equilibrium.

(c) Is there a minimum carrying capacity required in order to have a nontrivial equilibrium? If yes, find it and explain what happens when the carrying capacity is below this minimum and what happens when the carrying capacity is above this minimum.

21. An unrealistic feature of the Lotka–Volterra model is that the prey exhibits unlimited growth in the absence of the predator. The model described by the following system remedies this shortcoming (in the model, we assume that the prey evolves according to logistic growth in the absence of the predator; the other features of the model are retained):

$$\frac{dN}{dt} = N\left(1 - \frac{N}{20}\right) - 5PN$$
$$\frac{dP}{dt} = 2PN - 8P \qquad (11.89)$$

(a) Draw the zero isoclines of (11.89).
(b) Use the graphical approach of Subsection 11.3.2 to determine whether the nontrivial equilibrium is locally stable.

In Problems 22–26, we will analyze how a change in parameters in the modified Lotka–Volterra predator–prey model

$$\frac{dN}{dt} = aN\left(1 - \frac{N}{K}\right) - bPN$$
$$\frac{dP}{dt} = cPN - dP \qquad (11.90)$$

affects predator–prey interactions.

22. **(a)** Find the zero isoclines of (11.90), and determine conditions under which a nontrivial equilibrium (i.e., an equilibrium in which both prey and predator have positive densities) exists.
(b) Use the graphical approach of Subsection 11.3.2 to show that if a nontrivial equilibrium exists, it is locally stable.

In Problems 23–26, we use the results of Problem 22. Assume that the parameters are chosen so that a nontrivial equilibrium exists.

23. Use the results of Problem 22 to show that an increase in a (the intrinsic rate of growth of the prey) results in an increase in the predator density, but leaves the prey density unchanged.

24. Use the results of Problem 22 to show that an increase in b (the searching efficiency) reduces the predator density, but has no effect on the equilibrium abundance of the prey.

25. Use the results of Problem 22 to show that an increase in c (the predator growth efficiency) reduces the prey equilibrium abundance and increases the predator equilibrium abundance.

26. Use the results of Problem 22 to show that an increase in K (the prey carrying capacity in the absence of the predator) increases the predator equilibrium abundance, but has no effect on the prey equilibrium abundance.

■ 11.4.3

In Problems 27–34, classify each community matrix at equilibrium according to the five cases considered in Subsection 11.4.3 and determine whether the equilibrium is stable. (Assume in each case that the equilibrium exists.)

27. $\begin{bmatrix} -1 & -1.3 \\ 0.3 & -2 \end{bmatrix}$ **28.** $\begin{bmatrix} -3 & -1.2 \\ -1 & -2 \end{bmatrix}$

29. $\begin{bmatrix} -1.5 & 1.6 \\ 2.3 & -5.1 \end{bmatrix}$ **30.** $\begin{bmatrix} -0.3 & 0 \\ 0.4 & -0.7 \end{bmatrix}$

31. $\begin{bmatrix} -1 & 1.3 \\ 2 & -1.5 \end{bmatrix}$ **32.** $\begin{bmatrix} -2.7 & 0 \\ -1.3 & -0.6 \end{bmatrix}$

33. $\begin{bmatrix} -5 & -1.7 \\ -2.3 & -0.2 \end{bmatrix}$ **34.** $\begin{bmatrix} -2.3 & -4.7 \\ 1.2 & -3.2 \end{bmatrix}$

In Problems 35–40, we consider communities composed of two species. The abundance of species 1 at time t is given by $N_1(t)$, the abundance of species 2 at time t by $N_2(t)$. Their dynamics are described by

$$\frac{dN_1}{dt} = f_1(N_1, N_2)$$
$$\frac{dN_2}{dt} = f_2(N_1, N_2)$$

Assume that when both species are at low abundances their abundances increase and that f_1 and f_2 change sign when crossing their zero isoclines. In each problem, determine the sign structure of the community matrix at the nontrivial equilibrium (indicated by a dot) on the basis of the graph of the zero isoclines. Determine the stability of the equilibria if possible.

35. See Figure 11.66.

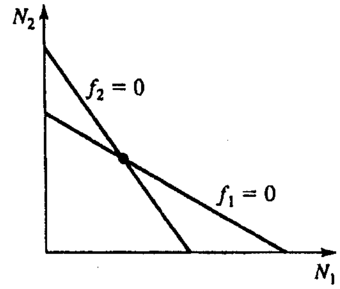

Figure 11.66

36. See Figure 11.67.

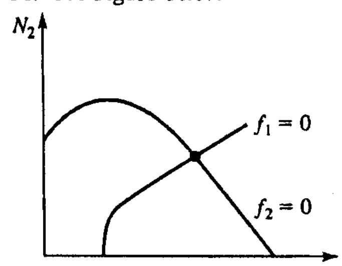

Figure 11.67

37. See Figure 11.68.

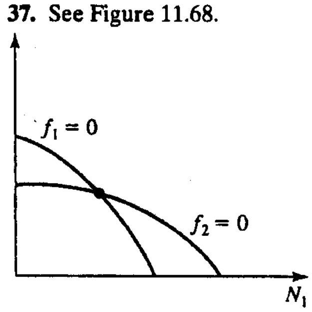

Figure 11.68

38. See Figure 11.69.

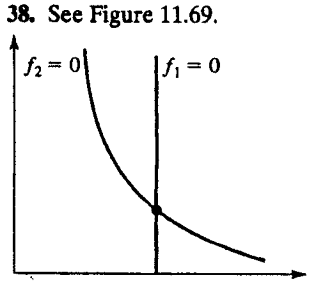

Figure 11.69

39. See Figure 11.70.

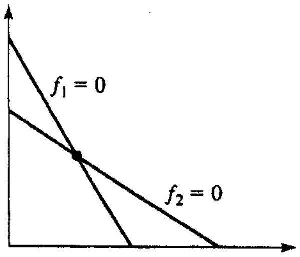

Figure 11.70

40. See Figure 11.71.

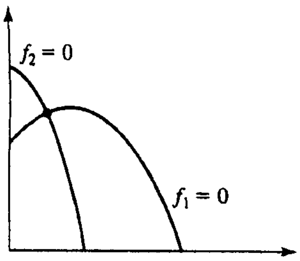

Figure 11.71

41. Assume that the diagonal elements a_{ii} of the community matrix of a species assemblage in equilibrium are negative. Explain why this assumption implies that species i exhibits self-regulation.

42. Consider a community composed of two species. Assume that both species inhibit themselves. Explain why mutualistic and competitive interactions lead to qualitatively similar predictions about the stability of the corresponding equilibria. That is, show that if $A = [a_{ij}]$ is the community matrix at equilibrium for the case of mutualism, and if $B = [b_{ij}]$ is the community matrix at equilibrium for the case of competition, then the following holds: If $|a_{ij}| = |b_{ij}|$ for $1 \leq i, j \leq 2$, then either both equilibria are locally stable or both are unstable.

43. The classical Lotka-Volterra model of predation is given by

$$\frac{dN}{dt} = aN - bNP$$
$$\frac{dP}{dt} = cNP - dP$$

where $N = N(t)$ is the prey density at time t and $P = P(t)$ is the predator density at time t. The constants a, b, c, and d are all positive.

(a) Find the nontrivial equilibrium $(\hat{N}, \hat{P})$ with $\hat{N} > 0$ and $\hat{P} > 0$.

(b) Find the community matrix corresponding to the nontrivial equilibrium.

(c) Explain each entry of the community matrix found in (b) in terms of how individuals in this community affect each other.

44. The modified Lotka-Volterra model of predation is given by

$$\frac{dN}{dt} = aN\left(1 - \frac{N}{K}\right) - bNP$$
$$\frac{dP}{dt} = cNP - dP$$

where $N = N(t)$ is the prey density at time t and $P = P(t)$ is the predator density at time t. The constants a, b, c, d, and K are positive. Assume that $d/c < K$.

(a) Find the nontrivial equilibrium $(\hat{N}, \hat{P})$ with $\hat{N} > 0$ and $\hat{P} > 0$.

(b) Find the community matrix corresponding to the nontrivial equilibrium.

(c) Explain each entry of the community matrix found in (b) in terms of how individuals in this community affect each other.

■ 11.4.4

45. Use a graphing calculator to study the following example of the Fitzhugh–Nagumo model:

$$\frac{dV}{dt} = -V(V - 0.3)(V - 1) - w$$
$$\frac{dw}{dt} = 0.01(V - 0.4w)$$

Sketch the graph of the solution curve in the V–w plane when **(i)** $(V(0), w(0)) = (0.4, 0)$ and **(ii)** $(V(0), w(0)) = (0.2, 0)$.

46. Use a graphing calculator to study the following example of the Fitzhugh–Nagumo model:

$$\frac{dV}{dt} = -V(V - 0.6)(V - 1) - w$$
$$\frac{dw}{dt} = 0.03(V - 0.6w)$$

Sketch the graph of the solution curve in the V–w plane when **(i)** $(V(0), w(0)) = (0.8, 0)$ and **(ii)** $(V(0), w(0)) = (0.4, 0)$.

47. Assume the following example of the Fitzhugh–Nagumo model:

$$\frac{dV}{dt} = -V(V - 0.3)(V - 1) - w$$
$$\frac{dw}{dt} = 0.01(V - 0.4w)$$

Assume that $w(0) = 0$. For which initial values of $V(0)$ can you observe an action potential?

48. Assume the following example of the Fitzhugh–Nagumo model:

$$\frac{dV}{dt} = -V(V - 0.6)(V - 1) - w$$
$$\frac{dw}{dt} = 0.03(V - 0.6w)$$

Assume that $w(0) = 0$. For which initial values of $V(0)$ can you observe an action potential?

■ 11.4.5

In Problems 49–52, use the mass action law to translate each chemical reaction into a system of differential equations.

49. $A + B \xrightarrow{k} C$

50. $A + B \underset{k_-}{\overset{k_+}{\rightleftharpoons}} C$

51. $E + S \xrightarrow{k_1} ES \xrightarrow{k_2} E + P$

52. $A + B \xrightarrow{k} A + C$

53. Show that the following system of differential equations has a conserved quantity, and find it:

$$\frac{dx}{dt} = 2x - 3y$$
$$\frac{dy}{dt} = 3y - 2x$$

54. Show that the following system of differential equations has a conserved quantity, and find it:

$$\frac{dx}{dt} = -4x + 2y$$
$$\frac{dy}{dt} = -y + 2x$$

55. Show that the following system of differential equations has a conserved quantity, and find it:

$$\frac{dx}{dt} = -x + 2xy + z$$
$$\frac{dy}{dt} = -2xy$$
$$\frac{dz}{dt} = x - z$$

56. Suppose that $x(t) + y(t)$ is a conserved quantity. If

$$\frac{dx}{dt} = -3x + 2xy$$

find the differential equation for $y(t)$.

57. The Michaelis–Menten law [Equation (11.76)] states that

$$\frac{dp}{dt} = \frac{v_m s}{K_m + s}$$

where $p = p(t)$ is the concentration of the product of the enzymatic reaction at time t, $s = s(t)$ is the concentration of the substrate at time t, and v_m and K_m are positive constants. Set

$$f(s) = \frac{v_m s}{K_m + s}$$

where v_m and K_m are positive constants.

(a) Show that

$$\lim_{s\to\infty} f(s) = v_m$$

(b) Show that

$$f(K_m) = \frac{v_m}{2}$$

(c) Show that, for $s \geq 0$, $f(s)$ is **(i)** nonnegative, **(ii)** increasing, and **(iii)** concave down. Sketch a graph of $f(s)$. Label v_m and K_m on your graph.

(d) Explain why we said that the reaction rate dp/dt is limited by the availability of the substrate.

58. The growth of microbes in a chemostat was described by (11.77). Using the notation of that equation, together with the relationship

$$q(s) = \frac{v_m s}{K_m + s}$$

where v_m and K_m are positive constants, we will investigate how the substrate concentration $\hat{s}$ in equilibrium depends on the uptake rate Y.

(a) Assume that the microbes have a positive equilibrium density. Find the equilibrium concentration $\hat{s}$ algebraically, and investigate how the uptake rate Y affects $\hat{s}$.

(b) Assume that the microbes have a positive equilibrium density. Sketch a graph of $q(s)$, and explain how you would determine $\hat{s}$ graphically. Use your graph to explain how the uptake rate Y affects $\hat{s}$.

59. The growth of microbes in a chemostat was described by (11.77). Using the notation of that equation, together with the relationship

$$q(s) = \frac{v_m s}{K_m + s}$$

we will investigate how the substrate concentration $\hat{s}$ in equilibrium depends on D, the rate at which the medium enters the chemostat.

(a) Assume that the microbes have a positive equilibrium density. Find the equilibrium concentration $\hat{s}$ algebraically. Investigate how the rate D affects $\hat{s}$.

(b) Assume that the microbes have a positive equilibrium density. Sketch a graph of $q(s)$, and explain how you would determine $\hat{s}$ graphically. Use your graph to explain how the rate D affects $\hat{s}$.

In Problems 60 and 61, we investigate specific examples of microbial growth described by (11.77). We use the notation of Subsection 11.4.5. In each case, determine all equilibria and their stability.

60. $$\frac{ds}{dt} = 2(4 - s) - \frac{3s}{2 + s}x$$
$$\frac{dx}{dt} = \frac{sx}{2 + s} - 2x$$

61. $$\frac{ds}{dt} = 2(4 - s) - \frac{3s}{1 + s}x$$
$$\frac{dx}{dt} = \frac{3sx}{1 + s} - 2x$$

Chapter 11 Key Terms

Discuss the following definitions and concepts:

1. Linear first-order equation
2. Homogeneous
3. Direction field, slope field, direction vector
4. Solution of a system of linear differential equations
5. Eigenvalue, eigenvector
6. Superposition principle
7. General solution
8. Stability
9. Sink, or stable node
10. Saddle point
11. Source, or unstable node
12. Spiral
13. Euler's formula
14. Compartment model
15. Conserved quantity
16. Harmonic oscillator
17. Nonlinear autonomous system of differential equations
18. Critical point
19. Zero isoclines, or null clines
20. Graphical approach to stability
21. Lotka–Volterra model of interspecific competition
22. Intraspecific competition, interspecific competition
23. Competitive exclusion, founder control, coexistence
24. Lotka–Volterra predator–prey model
25. Community matrix
26. Fitzhugh–Nagumo model
27. Action potential
28. Michaelis–Menten law

Chapter 11 Review Problems

1. Population Growth Let $N_1(t)$ and $N_2(t)$ denote the respective sizes of two populations at time t, and assume that their dynamics are respectively given by

$$\frac{dN_1}{dt} = r_1 N_1$$
$$\frac{dN_2}{dt} = r_2 N_2$$

where r_1 and r_2 are positive constants denoting the intrinsic rate of growth of the two populations. Set $Z(t) = N_1(t)/N_2(t)$, and show that $Z(t)$ satisfies

$$\frac{d}{dt} \ln Z(t) = r_1 - r_2 \tag{11.91}$$

Solve (11.91), and show that $\lim_{t\to\infty} Z(t) = \infty$ if $r_1 > r_2$. Conclude from this that population 1 becomes numerically dominant when $r_1 > r_2$.

2. Population Growth Let $N_1(t)$ and $N_2(t)$ denote the respective sizes of two populations at time t, and assume that their dynamics are respectively given by

$$\frac{dN_1}{dt} = r_1 N_1$$
$$\frac{dN_2}{dt} = r_2 N_2$$

where r_1 and r_2 are positive constants denoting the intrinsic rate of growth of the two populations. Denote the combined population size at time t by $N(t)$; that is, $N(t) = N_1(t) + N_2(t)$. Define the relative proportions

$$p_1 = \frac{N_1}{N} \quad \text{and} \quad p_2 = \frac{N_2}{N}$$

Use the fact that $p_1/p_2 = N_1/N_2$ to show that

$$\frac{dp_1}{dt} = p_1(1 - p_1)(r_1 - r_2)$$

Show that if $r_1 > r_2$ and $0 < p_1(0) < 1$, $p_1(t)$ will increase for $t > 0$ and population 1 will become numerically dominant.

3. Predator–Prey Interactions An unrealistic feature of the Lotka-Volterra model is that the prey exhibits unlimited growth in the absence of the predator. The model described by the following system remedies this shortcoming (in the model, we assume that the prey evolves according to logistic growth in the absence of the predator; the other features of the model are retained):

$$\begin{aligned} \frac{dN}{dt} &= 2N\left(1 - \frac{N}{10}\right) - 3PN \\ \frac{dP}{dt} &= PN - 3P \end{aligned} \tag{11.92}$$

(a) Draw the zero isoclines of (11.92).

(b) Use the graphical approach of Subsection 11.3.2 to determine whether the nontrivial equilibrium is locally stable.

4. Resource Competition Tilman (1982) developed a theoretical framework for studying resource competition in plants. In its simplest form, the theory posits that one species competes for a single resource—for instance, nitrogen. If $B(t)$ denotes the total biomass at time t and $R(t)$ is the amount of the resource available at time t, then the dynamics are described by the following system of differential equations:

$$\frac{dB}{dt} = B[f(R) - m]$$
$$\frac{dR}{dt} = a(S - R) - cBf(R)$$

The first equation describes the rate of change of biomass, where the function $f(R)$ describes how the species growth rate depends on the resource, and m is the specific loss rate. The second equation describes the resource dynamics; the constant S is the maximal amount of the resource in a given habitat. The rate of resource supply (dR/dt) is assumed to be proportional to the difference between the current resource level and the maximal amount of the resource; the constant a is the constant of proportionality. The term $cBf(R)$ describes the resource uptake by the plants; the constant c can be considered a conversion factor.

In what follows, we assume that $f(R)$ follows the Monod growth function

$$f(R) = \frac{dR}{k + R}$$

where d and k are positive constants.

(a) Find all equilibria. Show that if $d > m$ and $S > mk/(d - m)$, then there exists a nontrivial equilibrium.

(b) Sketch the zero isoclines for the case in which the system admits a nontrivial equilibrium. Use the graphical approach to analyze the stability of the nontrivial equilibrium.

5. Plant Competition In this problem, we describe a simple competition model in which two species of plants compete for vacant space. Assume that the entire habitat is divided into a large number of patches. Each patch can be occupied by at most one species. We denote by $p_i(t)$ the fraction of patches occupied by species i. Note that $0 \le p_1(t) + p_2(t) \le 1$. The dynamics are described by

$$\frac{dp_1}{dt} = c_1 p_1(1 - p_1 - p_2) - m_1 p_1$$
$$\frac{dp_1}{dt} = c_2 p_2(1 - p_1 - p_2) - m_2 p_2$$

where c_1, c_2, m_1, and m_2 are positive constants. The first term on the right-hand side of each equation describes the colonization of vacant patches; the second term on the right-hand side of each equation describes how occupied patches become vacant.

(a) Show that the dynamics of species 1 in the absence of species 2 are given by

$$\frac{dp_1}{dt} = c_1 p_1(1 - p_1) - m_1 p_1 \tag{11.93}$$

and find conditions on c_1 and m_1 so that (11.93) admits a nontrivial equilibrium (an equilibrium in which $0 < p_1 \le 1$).

(b) Assume now that $c_1 > m_1$ and $c_2 > m_2$. Show that if

$$\frac{c_1}{m_1} > \frac{c_2}{m_2}$$

then species 1 will exclude species 2 if species 1 initially occupies a positive fraction of the patches.

6. Paradox of Enrichment Rosenzweig (1971) analyzed a number of predator–prey models and concluded that enriching the system by increasing the nutrient supply destabilizes the nontrivial equilibrium. We will think of the predator–prey model as a plant–herbivore system in which plants represent prey and herbivores represent predators. The models analyzed were of the form

$$\frac{dN}{dt} = f(N, P) \tag{11.94}$$

$$\frac{dP}{dt} = g(N, P) \tag{11.95}$$

where $N = N(t)$ is the plant abundance at time t and $P = P(t)$ is the herbivore abundance at time t. The models all shared the property that the zero isocline for the herbivore was a vertical line and the zero isocline for the plants was a hump-shaped curve. We will look at one of the models, namely,

$$\begin{aligned} \frac{dN}{dt} &= aN\left(1 - \frac{N}{K}\right) - bP\left(1 - e^{-rN}\right) \\ \frac{dP}{dt} &= cP\left(1 - e^{-rN}\right) - dP \end{aligned} \tag{11.96}$$

(a) Find the zero isoclines for (11.96), and show that **(i)** the zero isocline of the herbivore ($dP/dt = 0$) is a vertical line in the N–P plane and **(ii)** the zero isocline for the plants ($dN/dt = 0$) intersects the N-axis at $N = K$.

(b) Plot the zero isoclines in the N–P plane for $a = b = c = r = 1$ and $d = 0.9$ and for three levels of the carrying capacity: **(i)** $K = 1$, **(ii)** $K = 4$, and **(iii)** $K = 10$.

(c) For each of the three carrying capacities, determine whether a nontrivial equilibrium exists.

(d) Use the graphical approach of Subsection 11.3.2 to determine the stability of the existing nontrivial equilibria in (c).

(e) Enriching the community could mean increasing the carrying capacity of the plants. For instance, adding nitrogen or phosphorus to plant communities frequently results in an increase in biomass, which can be interpreted as an increase in the carrying capacity of the plants (the K-value). On the basis of your answers in (d), explain why enriching the community (increasing the carrying capacity of the plants) can result in a destabilization of the nontrivial equilibrium. What are the consequences?

7. Microbial Growth The growth of microbes in a chemostat was described by Equation (11.77). We will investigate how the microbial abundance in equilibrium depends on the characteristics of the system.

(a) Assume that $q(s)$ is a nonnegative function. Show that the equilibrium abundance of the microbes is given by

$$\hat{x} = Y(s_0 - \hat{s})$$

where $\hat{s}$ is the substrate equilibrium abundance. When is $\hat{x} > 0$?

(b) Assume now that

$$q(s) = \frac{v_m s}{K_m + s}$$

Investigate how the uptake rate Y and the rate D at which new medium enters the chemostat affect the equilibrium abundance of the microbes.

8. Successional Niche Pacala and Rees (1998) discuss a simple mathematical model of competition to explain successional diversity by means of a successional niche mechanism. In this model, two species—an early successional and a late successional—occupy discrete patches. Each patch experiences disturbances (such as fire) at rate D. After a patch is disturbed, both species are present. Over time, however, the late successional species outcompetes the early successional species, causing the early successional species to become extinct. This change, from a patch that is occupied by both species to a patch that is occupied by the late successional species only, happens at rate a. We keep track of the number of patches occupied by both species at time t, denoted by $x(t)$, and the number of patches occupied by just the late successional species at time t, denoted by $y(t)$. The dynamics are given by the system of linear differential equations

$$\begin{aligned} \frac{dx}{dt} &= -ax + Dy \\ \frac{dy}{dt} &= ax - Dy \end{aligned} \tag{11.97}$$

where a and D are positive constants.

(a) Show that all equilibria are of the form $(x, ax/D)$.

(b) Find the eigenvalues and eigenvectors corresponding to each equilibrium.

(c) Show that

$$\begin{bmatrix} x(t) \\ y(t) \end{bmatrix} = C_1 \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + C_2 e^{\lambda_2 t} \begin{bmatrix} v_1 \\ v_2 \end{bmatrix}$$

where $\begin{bmatrix} u_1 \\ u_2 \end{bmatrix}$ is the eigenvector corresponding to the zero eigenvalue and $\begin{bmatrix} v_1 \\ v_2 \end{bmatrix}$ is the eigenvector corresponding to the nonzero eigenvalue λ_2, is a solution of (11.97).

(d) Show that $x(t) + y(t)$ does not depend on t. [*Hint*: Show that $\frac{d}{dt}(x(t) + y(t)) = 0$.] Show also that the line $x + y = A$ (where A is a constant) is parallel to the line in the direction of the eigenvector corresponding to the nonzero eigenvalue.

(e) Show that the zero isoclines of (11.97) are given by

$$y = \frac{a}{D}x$$

and that this line is the line in the direction of the eigenvector corresponding to the zero eigenvalue.

(f) Suppose now that $x(t) + y(t) = c$, where c is a positive constant. Show that (11.97) can be reduced to just one equation, namely,

$$\frac{dx}{dt} = -(a + D)x + Dc$$

Show that $\hat{x} = c\frac{D}{D+a}$ is the only equilibrium, and determine its stability.