5 Phase-Plane Methods and Qualitative Solutions

Nothing is permanent but change.

Heraclitus (500 B.C.)

Nonlinear phenomena are woven into the fabric of biological systems. Interactions between individuals, species, or populations lead to relationships that depend on the variables (such as densities) in ways more complicated than that of simple proportionality. Among other things, this means that models proporting to describe such phenomena contain nonlinear equations that are often difficult if not impossible to solve explicitly in closed analytic form.

To give a rather elementary example, consider the following two superficially similar differential equations:

$$\text{Linear:} \qquad \frac{dy}{dt} = t^2 - y, \tag{1a}$$

$$\text{Nonlinear:} \qquad \frac{dy}{dt} = y^2 - t. \tag{1b}$$

The first is linear (in the dependent variable y) and can be solved by a rather standard method (see problem 15). The second is nonlinear since it contains the term y^2; equation (1b) is not solvable in terms of elementary functions such as those encountered in calculus. While the equations both look simple, the nonlinearity in (1b) means that special methods must be applied in analyzing the nature of its solutions. Several qualitative approaches to understanding ordinary differential equations (ODEs) or systems of such equations will make up the subject of this chapter.

Our aim is to circumvent the necessity for calculating explicit solutions to ODEs; we shall be concerned with determining qualitative features of these solutions. The flavor of this approach is in large measure graphical and geometric. By blending certain geometric insights with some intuition, we will describe the behavior of solutions and thus understand the phenomena captured in a model in a pictorial form. These pictures are generally more informative than mathematical expressions and lead to a much more direct comprehension of the way that parameters and constants that appear in the equations affect the behavior of the system.

This introduction to the subject of qualitative solutions and phase-plane methods is meant to be intuitive rather than formal. While the mathematical theory underlying these methods is a rich one, the techniques we speak of can be mastered rather easily by nonmathematicians and applied to a host of problems arising from the natural sciences. Collectively these methods are an important tool that is equally accessible to the nonspecialist as to the more experienced modeler.

Reading through Sections 5.4–5.5, 5.7–5.9, and 5.11 and then working through the detailed example in Section 5.10 leads to a working familiarity with the topic. A more gradual introduction, with some background in the geometry of curves in the plane, can be acquired by working through the material in its fuller form.

Alternative treatments of this topic can be found in numerous sources. Among these, Odell's (1980) is one of the best, clearest, and most informative. Other versions are to be found in Chapter 4 of Braun (1979) and Chapter 9 of Boyce and DiPrima (1977). For the more mathematically inclined, Arnold (1973) gives an appealing and rigorous exposition in his delightful book.

5.1 FIRST-ORDER ODEs: A GEOMETRIC MEANING

To begin on relatively familiar ground we start with a single first-order ODE and introduce the concept of qualitative solutions. Here we shall assume only an acquaintance with the meaning of a derivative and with the graph of a function.

Consider the equation

$$\frac{dy}{dt} = f(y, t), \tag{2a}$$

and suppose that with this differential equation comes an initial condition that specifies some starting value of y:

$$y(0) = y_0. \tag{2b}$$

[To ensure that a unique solution to (2a) exists, we assume from here on that $f(y, t)$ is continuous and has a continuous partial derivative with respect to y.]

A solution to equation (2a) is some function that we shall call $\phi(t)$. Given a formula for this function, we might graph $y = \phi(t)$ as a function of t to display its time behavior. This graph would be a curve in the ty plane, as follows. According to equation (2b) the curve starts at the point $t = 0$, $\phi(0) = y_0$. The equation (2a) tells us that at time t, the slope of any tangent to the curve must be $f(t, \phi(t))$. (Recall that the derivative of a function is interpreted in calculus as the *slope of the tangent to its graph.*)

Let us now drop the assumption that a formula for the solution $\phi(t)$ is known and resort to some intuitive reasoning. Suppose we make a sketch of the ty plane and use only the information in equation (2a): at every point (t, y) we could draw a small line segment of slope $f(t, y)$. This can be done repeatedly for many points, resulting in a picture aptly termed a *direction field* [Figure 5.1(*a*)]. The solution curves shown in Figure 5.1(*b*), must be tangent to the directions of the line segments in Figure 5.1(*a*). Now we reconstruct an approximate graph of the solution by beginning at $(0, y_0)$ and sketching a curve that winds its way through the plane in the general direction depicted by the field. (The more line segments we have drawn, the better our approximation will be.) Starting at many different initial points one can generate a whole family of solution curves that summarize the qualitative behavior specified by the differential equation. See example 1.

Example 1

Here we explore the nature of solutions to equation (1b). We tabulate several values as follows:

Location y	t	*Slope of Tangent Line* $f(t, y) = y^2 - t$
0	0	0
1	1	0
1	2	−1
2	1	3
⋮	⋮	⋮

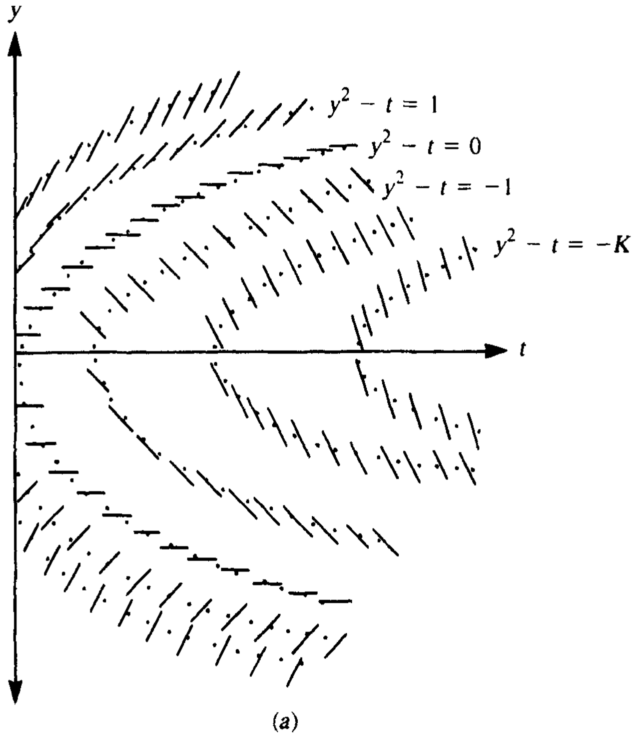
In a somewhat more systematic approach, we notice that $f(t, y) = K$ is the locus of points $K = y^2 - t$. (This is a parabola about the t axis, displaced from the origin by an amount $-K$.) Along each of these loci, tangent lines are parallel and of slope $= K$, as in Figure 5.1(*a*). Figure 5.1(*b*) is an approximate sketch of solution curves for several initial values. We have made no attempt to depict exact solutions in this picture, but rather to describe a general behavior pattern.

Example 2

The equation

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

is autonomous. Its solutions have zero slope whenever $y = 0$, 1, or 2. The slopes are positive for $0 < y < 1$ and $y > 2$ and negative for $1 < y < 2$. (The exact values of these slopes could be tabulated but are not important since the sketch is meant to be only approximate.) From the sketch in Figure 5.2b it is clear that for y initially smaller than 2, the solution approaches the value $y = 1$. For y initially larger than 2, the solution grows without bound. The values $y = 0$, 1, and 2 are steady states ($dy/dt = 0$). $y = 1$ is stable; the others are unstable.



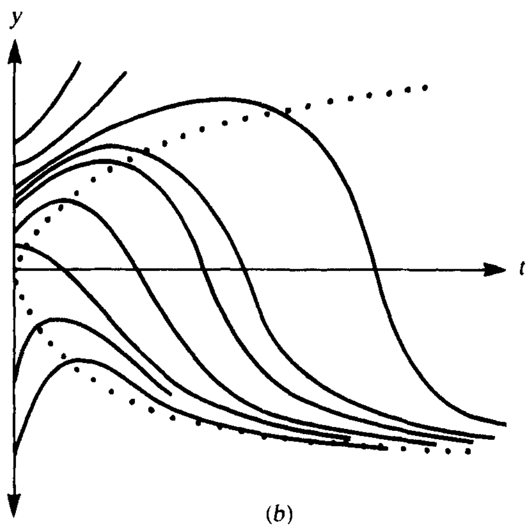


Figure 5.1 *Solutions to* $y' = y^2 - t$. *(a) For each pair of values* (t, y), *line segments whose slope is* $f(t, y) = y^2 - t$ *are shown. (Note that slopes are constant along parabolic curves for which* $K = y^2 - t$, *where* K *is any constant.) (b) Solution curves are constructed by maintaining tangency to the directions shown in (a).*

In example 2, the function appearing on the RHS of equation (3) depends explicitly only on y, not on t. A system described by such an equation would be unfolding at some inherent rate independent of the clock time or the time at which the process began. The differential equation is said to be *autonomous*, and solutions to it can be represented in an especially convenient way, as will presently be shown.

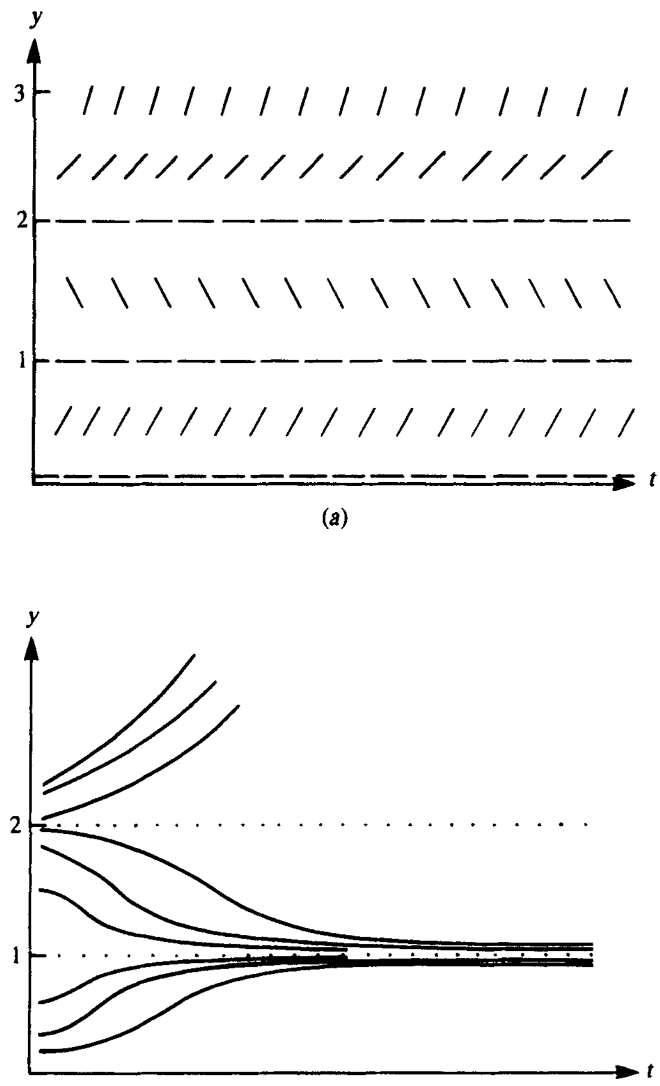


Figure 5.2 *Solutions to* $y' = y(1 - y)(2 - y)$. *(a) For each value of* y, *line segments bearing the slope* $f(y) = y(1 - y)(2 - y)$ *have been drawn. The slopes are zero when* $y = 0, 1,$ *or* 2, *and positive for* $0 < y < 1$ *or* $y > 3$. *(b) Solution curves are constructed by maintaining tangency to the line segments drawn in (a).*

The fact that a differential equation is autonomous means, pictorially, that the tangent line segments do not "wobble" along the time axis. This can be used to represent the same qualitative information in a more condensed form. Let us suppress the time dependence and instead plot dy/dt as a function of y. See Figure 5.3(*a*). Whenever $f(y)$ is positive (that is, for $0 < y < 1$ or $y > 2$), y must be increasing. Whenever $f(y)$ is negative, y must be decreasing. This can be represented by drawing arrows pointing to the left or to the right directly along the y axis, as shown in Figure 5.3(*b*). This abbreviated representation is called a *one-dimensional phase portrait*, or a *phase flow on a line*. Figure 5.3(*b*) conveys roughly the same qualitative information as does Figure 5.2, with the omission of the time course, or speed with which the solution $y(t)$ changes.

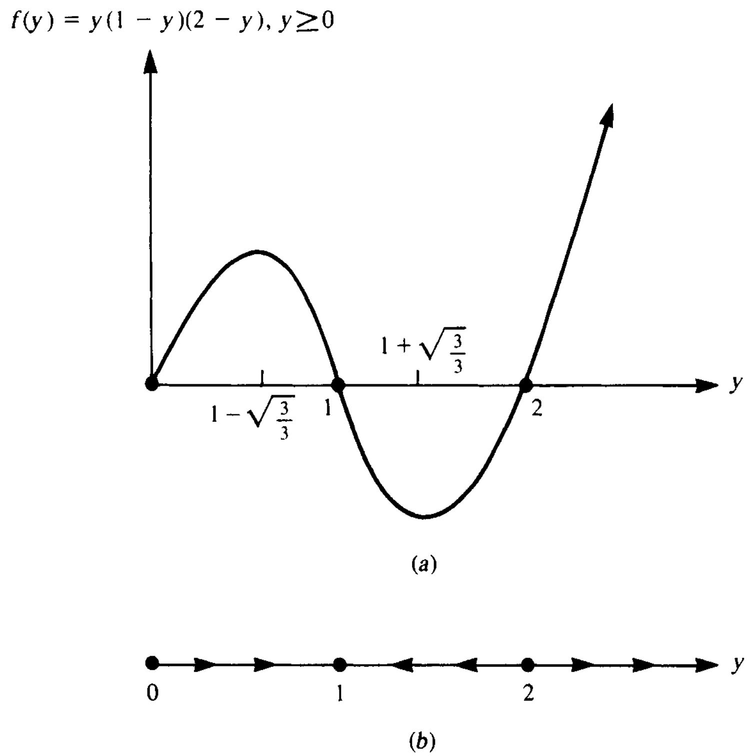


Figure 5.3 *(a) Graph of* f(y) *versus* y *for equation (3). Since* y′ = f(y), y *is increasing when* f *is positive, decreasing when* f *is negative, and stationary when* f = 0. *(b) The qualitative features described in (a) can be summarized by drawing the directions of motion along the* y *axis.*

Example 3 again illustrates the procedure of extracting information from the equation and depicting the solution as a one-dimensional flow.

As mentioned previously, when a differential equation is autonomous, the qualitative behavior of its solutions can be characterized even when time dependence is suppressed. Think of a qualitative solution as a *trajectory:* a flow that begins

Example 3

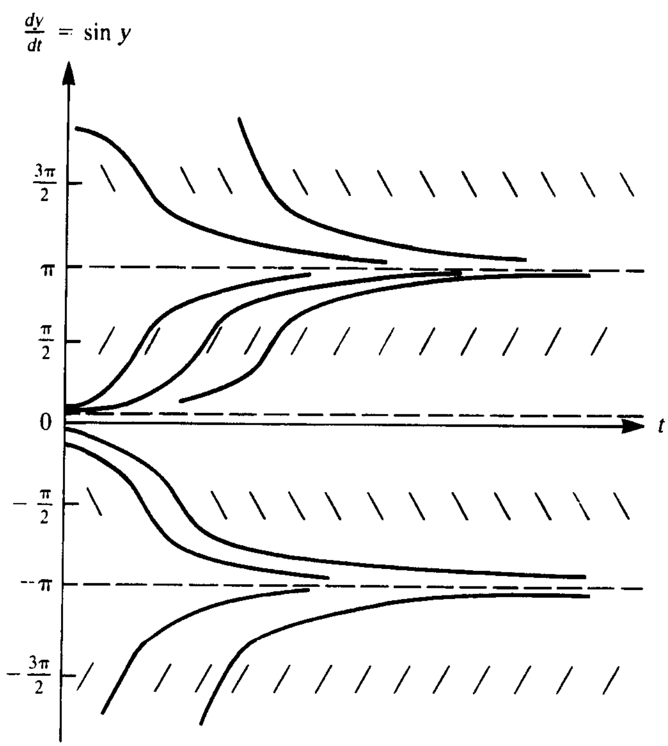
The differential equation

$$\frac{dy}{dt} = \sin y \tag{4}$$

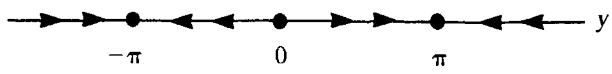
can be treated in the same way, as shown in Figure 5.4. The following are some convenient values to tabulate:

y	$dy/dt = \sin y$
0	0
$n\pi$	0
$-n\pi$	0
$\pi/2 \pm 2n\pi$	1
$-\pi/2 \pm 2n\pi$	-1

Solution curves and directions of flow are given in Figure 5.4.



(*a*)



(b)

Figure 5.4 *(a) Tangent lines and several representative solution curves to the equation* y′ = sin y. *(b) The information is again summarized by omitting time dependence and concentrating only on the direction of motion along the* y *axis.*

somewhere (at an initial point) and has an orientation consistent with increasing values of time. We shall presently see that these ideas have a natural and important generalization to systems of differential equations.

5.2 SYSTEMS OF TWO FIRST-ORDER ODEs

In modeling biological systems, which are generally composed of several *interacting variables,* we are frequently confronted with systems of nonlinear ODEs. The ideas of Section 5.1 can be extended to encompass such systems; in the present section we deal in great detail with systems of two equations that describe the interaction of two species. The reason for dealing almost exclusively with these will emerge after some preliminary familiarity is established.

Let us therefore turn attention to a system of two autonomous first-order equations, a prototype of which follows:

$$\frac{dx}{dt} = f_1(x, y), \tag{5a}$$

$$\frac{dy}{dt} = f_2(x, y). \tag{5b}$$

Technically, we assume that f_1 and f_2 are continuous functions having partial derivatives with respect to x and y; this ensures existence of a unique solution given an initial value for x and y. A solution to system (5) would be two functions, $x(t)$, and $y(t)$, that satisfy the equations together with the initial conditions, if any.

As a preliminary to understanding the equations, let us consider an approximate form of these equations, whereby derivatives are replaced by finite differences, as follows:

$$\frac{\Delta x}{\Delta t} = f_1(x, y), \tag{6a}$$

$$\frac{\Delta y}{\Delta t} = f_2(x, y). \tag{6b}$$

The changes Δx and Δy in the two independent variables are thus specified whenever x and y are known, since

$$\Delta x = f_1(x, y)\, \Delta t, \tag{7a}$$
$$\Delta y = f_2(x, y)\, \Delta t. \tag{7b}$$

These equations can be interpreted as follows: Given a value of x and y, after some small increment of time Δt, x will change by an amount Δx and y by an amount Δy. This is represented pictorially in Figure 5.5, where a point (x, y) is assigned a vector with components $(\Delta x, \Delta y)$ that describe changes in the two variables simultaneously. We see that *equations (6) and (7) are mathematical statements that assign a vector (representing a change) to every pair of values* (x, y).

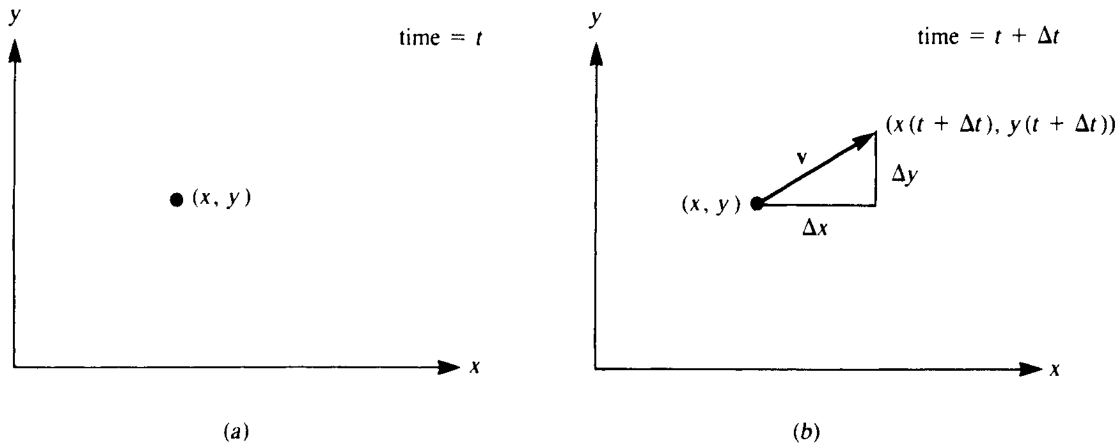


Figure 5.5 *(a) Given a point* (x, y), *(b) a change in its location can be represented by a vector* **v**.

In calculus such concepts are made more precise. Indeed, we know that derivatives are just limits of expressions such as $\Delta x/\Delta t$ when ever-smaller time increments are considered. Using calculus, we can understand equations (5a,b) directly without resorting to their approximated version. (A review of these ideas is presented in Section 5.3, which may be skipped if desired.)

5.3 CURVES IN THE PLANE

In calculus we learn that the concepts *point* and *vector* are essentially interchangeable. The pair of numbers (x, y) can be thought of as a point in the cartesian plane with coordinates x and y [as in Figure 5.6(a)] or as an arrow strung out between the origin (0, 0) and (x, y) that points to the location of this point [Figure 5.6(b)]. When the coordinates x and y vary with time or with some other parameter, the point (x, y) moves over the plane tracing a curve as it moves. Equivalently, the arrow twirls and stretches as its head tracks the position of the point $(x(t), y(t))$. For this reason, it is often called a *position vector,* symbolized by $\mathbf{x}(t)$.

As previously remarked, since the solution of a system of equations such as (5a,b) is a pair $(x(t), y(t))$, the idea that a solution corresponds geometrically to a curve carries through from the one-dimensional case. To be precise, the *graph* of a solution would be a curve $(t, x(t), y(t))$ in the three-dimensional space, depicting the time evolution of the values of x and y. We shall use the fact that equations (5a,b) are autonomous to suppress time dependence as before, that is, to depict solutions by trajectories in the plane. Such trajectories, each representing a solution, together make up a phase-plane portrait of the system of equations under consideration.

We observed in Section 5.2 that $(\Delta x, \Delta y)$ given by equations (7a,b) is a vector that depicts both the magnitude and the direction of changes in the two variables. A limiting value of this vector,

$$\left(\frac{dx}{dt}, \frac{dy}{dt}\right), \tag{8a}$$

is obtained when the time increment Δt gets vanishingly small in $(\Delta x/\Delta t, \Delta y/\Delta t)$. The latter, often symbolized

$$\frac{d\mathbf{x}}{dt} \tag{8b}$$

represents the *instantaneous change* in x and y, and can also be depicted as an arrow attached to the point $(x(t), y(t))$ and tangent to the curve. This vector is often called the *velocity vector,* since its magnitude indicates how quickly changes are occurring.

A summary of all these facts is collected here:

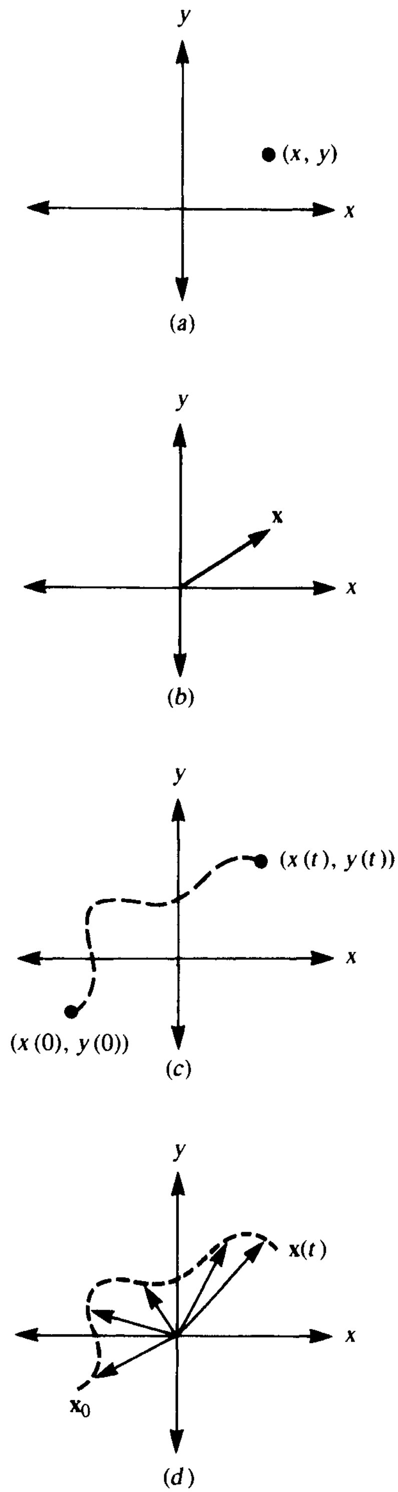
A Summary of Facts about Vector Functions (from Calculus)

1. The pair $(x(t), y(t))$ represents a curve in the xy plane with t as a parameter.
2. $\mathbf{x}(t) = (x(t), y(t))$ also represents a position vector: a vector attached to (0, 0) that points to the position along the curve, that is, the location corresponding to the value t.
3. The vector $d\mathbf{x}/dt$, which is just the pair $(dx/dt, dy/dt)$ has a well-defined geometric meaning. It is a vector that is tangent to the curve at $\mathbf{x}(t)$. Its magnitude, written $|d\mathbf{x}/dt|$ represents the speed of motion of the point $(x(t), y(t))$ along the curve.
4. The set of equations (5a,b) can be written in vector form,

$$\frac{d\mathbf{x}}{dt} = \mathbf{F}(\mathbf{x}).$$

Here the vector function $\mathbf{F} = (f_1, f_2)$ assigns a vector to every location $\mathbf{x}$ in the plane; $\mathbf{x}$ is the position vector (x, y), and $d\mathbf{x}/dt$ is the velocity vector $(dx/dt, dy/dt)$.

***Figure 5.6** (a) Point and (b) vector representations of a pair* (x, y). *(c) A curve* (x(t), y(t)) *can also be represented by moving vector* **x**(t), *as in (d).*



5.4 THE DIRECTION FIELD

From concepts that arise in calculus we surmise that solutions to ODEs, whether in one dimension or higher, correspond to curves, and differential equations are "recipes" for tangent vectors to these curves. This insight will now be applied to reconstructing a qualitative picture of solutions to a system of two equations such as (5). For such autonomous systems each point (x, y) in the plane is assigned a unique vector $(f_1(x, y), f_2(x, y))$ that does not change with time. A solution curve passing through (x, y) must have these vectors as its tangents. Thus a collection of such vectors defines a direction field, which can be used as a visual guide in sketching a family of solution curves, collectively a *phase-plane portrait*. Example 4 clarifies how this is done in practice.

Example 4
Let

$$\frac{dx}{dt} = xy - y, \tag{9a}$$

$$\frac{dy}{dt} = xy - x, \tag{9b}$$

and let $f_1(x, y) = xy - y$, $f_2(x, y) = xy - x$. In the following table the values of f_1 and f_2 are listed for several values of (x, y).

x	y	$f_1(x, y)$	$f_2(x, y)$
0	0	0	0
0	1	−1	0
1	0	0	−1
−1	0	0	1
0	−1	1	0
1	1	0	0
1	−1	2	−2
−2	−1	3	4

After tabulating arbitrarily many values of (x, y) and the corresponding values of $f_1(x, y)$ and $f_2(x, y)$, we are ready to construct the direction field. To each point (x, y) we attach a small line segment in the direction of the vector $(f_1(x, y), f_2(x, y))$.

See Figure 5.7. The slope $\Delta y/\Delta x$ of the line segment is to have the ratio $f_2(x, y)/f_1(x, y)$. Notice that a vector $(f_1(x, y), f_2(x, y))$ has the magnitude $[f_1(x, y)^2 + f_2(x, y)^2]^{1/2}$, which we shall not attempt to portray accurately. This magnitude represents a rate of motion, the speed with which a trajectory is traced. A cluttered picture emerges should we attempt to draw the vectors (f_1, f_2) in their true sizes. Since we are interested in establishing only the direction field, making all tangent vectors some uniform small size proves most convenient.

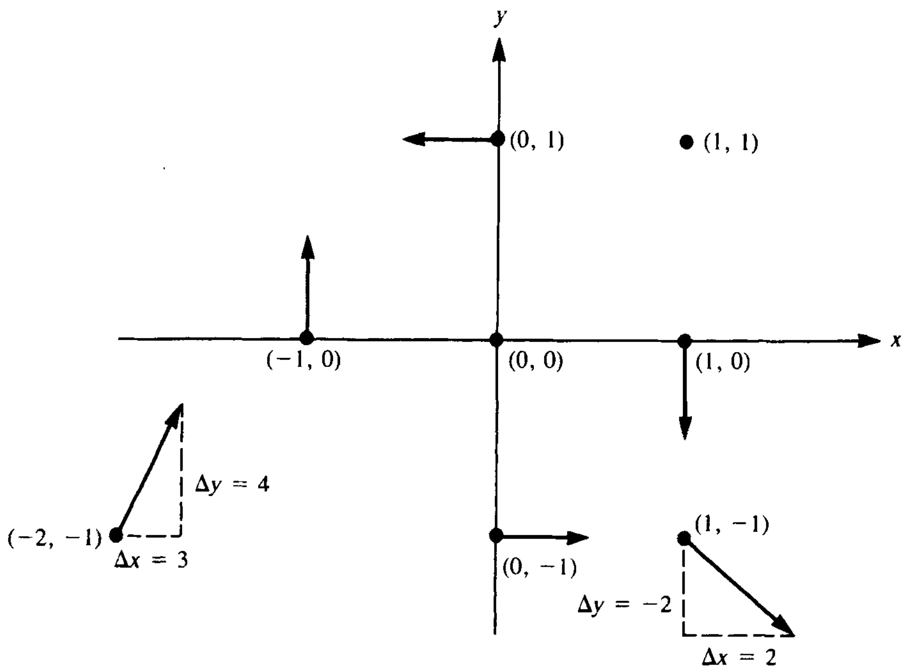
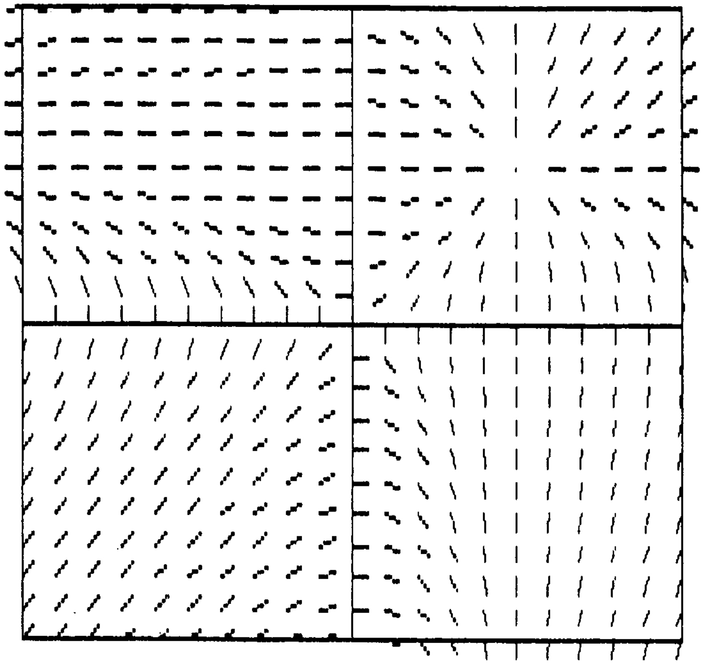


Figure 5.7 *Several points* (x, y) *and the direction vectors* (f_1, f_2) *associated with them have been sketched above for equations (9a,b).*

Two notable locations in example 4 are the points (0, 0) and (1, 1), at both of which $f_1 = 0$ and $f_2 = 0$. Neither x nor y changes given these initial values; the terms *steady state, equilibrium point,* or *singular point* are synonymously used to denote such locations. Presently we will see that such points play a central role in determining global phase-plane behavior.

The chore of tabulating and sketching direction fields is in principle straightforward but tedious. Rather than belabor the process we might consign the job to a computer, as we have done in Figures 5.8 *(a,b)*. A simple BASIC program run on an IBM personal computer produced these results.



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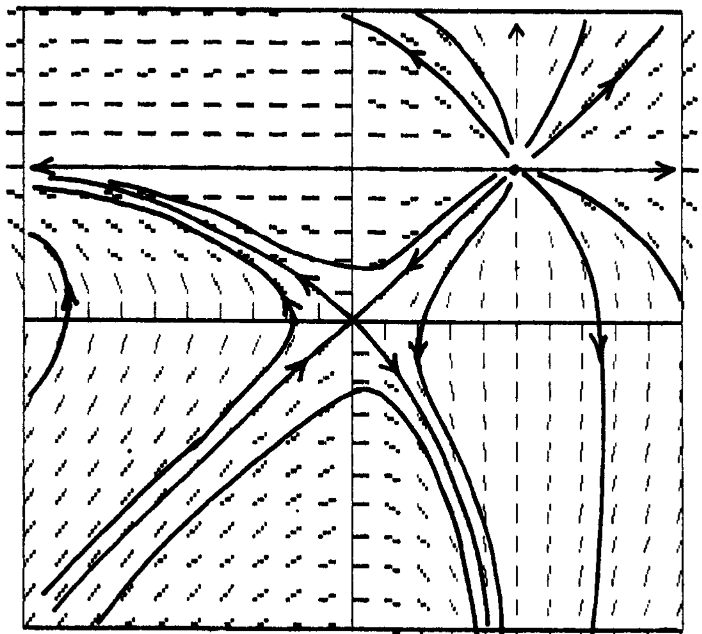


(*b*)

Figure 5.8 *(a) Computer-generated vector field for example 4. The vectors point* away *from the points to which they are attached. For example, along the positive* x *axis, they point down. (b) Hand-sketched solution curves for example 4. The directions are ascertained by noting whether vectors point into or out of the region at the boundary of the square. (Computer plot by Yehoshua Keshet.)*

From the direction field thus generated one gets a good general idea of solution curves consistent with the flow. Through every point in the plane there is a curve (by existence of a solution) and only one curve (by uniqueness). Thus curves may not intersect or touch each other, except at the steady states designated by heavy dots in Figures 5.7 and 5.8. Rules governing the possible pattern of curves will be outlined in a subsequent section.

As a word of caution, note that a phase-plane diagram is not a quantitatively accurate graph. In practice, because only a finite number of tangent vectors can be drawn in the plane, there will always be some small error in the curve that we inscribe. Such initially small mistakes could propagate if they result in an improper choice of tangent vectors along the way. For this reason, solution curves drawn in this way are approximate. There may be cases where ambiguity arises close to a steady state and where it is difficult to distinguish between several alternatives. Such situations call for a more rigorous technique. Before turning to these matters, we investigate a more systematic way of establishing the direction field in a computationally efficient way.

5.5 NULLCLINES: A MORE SYSTEMATIC APPROACH

Rather than arbitrarily plotting tabulated values, we prepare the way by noticing what happens along the locus of points for which one of the two functions, either $f_1(x, y)$ or $f_2(x, y)$ is zero. We observe that

1. If $f_1(x, y) = 0$, then $dx/dt = 0$, so x does not change. This means that the direction vector must be parallel to the y axis, since its Δx component is zero.
2. Similarly, if $f_2(x, y) = 0$, then $dy/dt = 0$, so y does not change. Thus the direction vector is parallel to the x axis, since its Δy component is zero.

The locus of points satisfying one of these two conditions is called a *nullcline*. The *x nullcline* is the set of points satisfying condition 1; similarly, the *y nullcline* is the set of points satisfying condition 2. Because the arrows are parallel to the y and x axis respectively on these loci, it proves helpful to sketch these as a first step. Example 5 illustrates the procedure.

Example 5
For equations (9a,b) the nullclines are loci for which

1. $\dot{x} = 0$ (the x nullcline); that is, $xy - y = 0$. This is satisfied when $x = 1$ or $y = 0$. See dotted lines in Figure 5.9(a). On these lines, direction vectors are vertical.
2. $\dot{y} = 0$ (the y nullcline); that is, $xy - x = 0$. This is satisfied when $x = 0$ or $y = 1$. See the dotted-dashed line in Figure 5.9(a). On these lines direction vectors are horizontal.

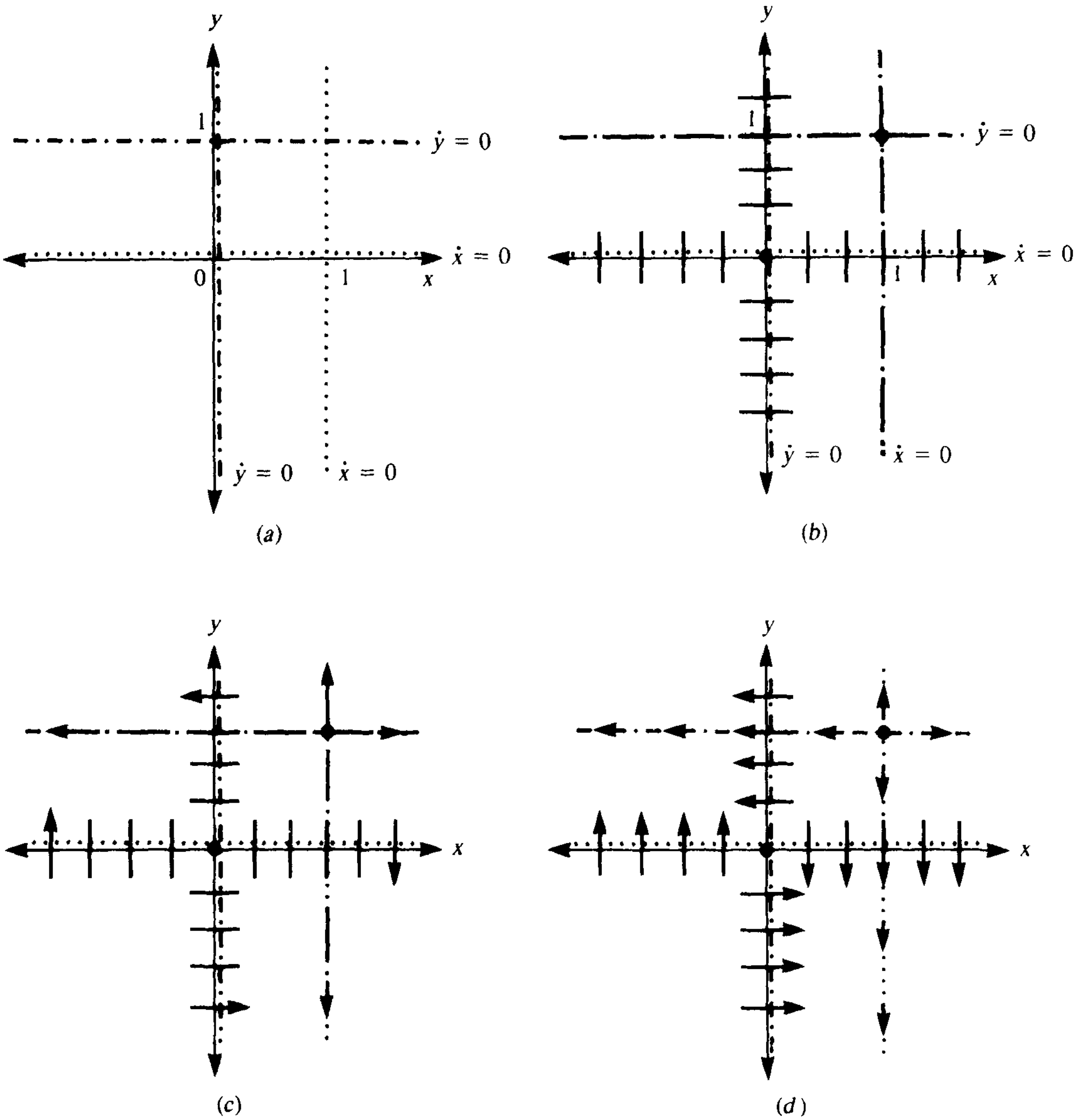


***Figure 5.9** Nullclines and flow directions for example 5. (a) Nullclines, which happen to be straight lines here, are sketched in the* xy*-plane and assigned vertical or horizontal line segments in (b). (c) Directions are determined by tabulating several values and inscribing arrowheads. (d) Neighboring arrows are deduced by preserving a continuous flow.*

Points of intersection of nullclines satisfy both $\dot{x} = 0$ and $\dot{y} = 0$ and thus represent steady states. To identify these and determine the directions of flow, several guidelines are useful.

Rules for determining steady states and direction vectors on nullclines

1. Steady states are located at intersections of an x nullcline with a y nullcline.
2. At steady states there is no change in either x or y values; that is, the vectors have zero length.
3. Direction vectors must vary continuously from one point to the next on the nullclines. Thus a change in the orientation (for example, from pointing up to pointing down) can take place only at steady states.

We note that (0, 0) and (1, 1) are the only two steady states in example 5. It is important to avoid confusing these with other intersections, for example (1, 0) and (0, 1), for which only one of the two nullcline conditions is satisfied. Generally it is a good idea to distinguish between the x and y nullclines by using different symbols or colors for each type.

It should be remarked that in affixing orientations to the arrows along nullclines we can economize on algebra by being aware of certain geometric properties. For instance, in example 5 we observe the following patterns of signs:

x	y	$f_1(x, y)$	$f_2(x, y)$
$-$	1	$-$	0
0	$-$	$+$	0
1	$-$	0	$-$
0	$+$	0	$-$
$+, > 1$	1	$+$	0
1	$+, > 1$	0	$+$
0	$+$	$-$	0
$-$	0	0	$+$

It is evident that on opposite sides of a steady-state point (along a given nullcline) the orientation of arrows is reversed. This is a property shared by most systems of equations with the exception of certain singular cases. (We shall be able to distinguish these exceptions by calculating the Jacobian **J** and evaluating it at the steady state in question. If det $\mathbf{J} \neq 0$, the property of arrow reversal holds.) In most cases where we encounter det $\mathbf{J} \neq 0$, it suffices to determine the direction vectors at one or two select places and deduce the rest by preserving continuity and switching orientation as a steady state is crossed. Thus the arrow-nullcline method can reveal a fairly complete picture with relatively little calculation (see example 6).

Example 6

Consider the equations

$$\frac{dx}{dt} = x + y^2, \qquad (10a)$$

$$\frac{dy}{dt} = x + y. \tag{10b}$$

The x nullcline is the curve $0 = x + y^2$; the y nullcline is the line $0 = x + y$. Steady states are thus (0, 0) and (−1, 1). The Jacobian of system (10) is

$$\mathbf{J}(x_0, y_0) = \begin{pmatrix} 1 & 2y \\ 1 & 1 \end{pmatrix}_{(x_0, y_0)}.$$

Thus det $\mathbf{J}(0, 0) = 1 \neq 0$, det $\mathbf{J}(-1, 1) = -1 \neq 0$, so the property of arrow reversal holds. It suffices to tabulate two values, for example, as follows:

x	y	$\dot{x} = x + y^2$	$\dot{y} = x + y$
+	$y = -x$	+	0
−	$x = -y^2$	0	−

After drawing these two arrows, all others follow by the above method. (See Figure 5.10.)

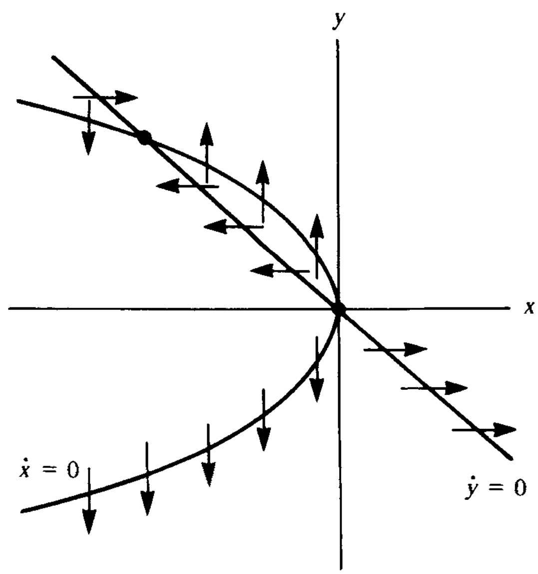


Figure 5.10 *Nullclines and arrows for example 6, equations (10a,b).*

5.6 CLOSE TO THE STEADY STATES

The examples we have seen give evidence to the notion that dramatic local changes in the flow pattern can only take place in the vicinity of steady-state points. We now invoke a metaphorical magnifying glass to scrutinize the behavior close to these locations. In the discussions of Chapter 4, we established that close to a steady state

$(\bar{x}_0, \bar{y}_0)$ [defined by $f_1(\bar{x}_0, \bar{y}_0) = f_2(\bar{x}_0, \bar{y}_0) = 0$] the nonlinear system (5) behaves very nearly like a linear one,

$$\frac{dx}{dt} = a_{11}x + a_{12}y, \tag{11a}$$

$$\frac{dy}{dt} = a_{21}x + a_{22}y, \tag{11b}$$

where a_{ij}, related to partial derivatives of f_1 and f_2, make up the coefficient of the Jacobian matrix $\mathbf{J}(\bar{x}_0, \bar{y}_0)$ as follows:

$$\mathbf{J}(\bar{x}_0, \bar{y}_0) = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} \dfrac{\partial f_1}{\partial x} & \dfrac{\partial f_1}{\partial y} \\ \dfrac{\partial f_2}{\partial x} & \dfrac{\partial f_2}{\partial y} \end{pmatrix}_{(\bar{x}_0, \bar{y}_0)} . \tag{12}$$

This result is important, as it reduces the problem to one we understand well. It remains to interpret the phase-plane equivalents of solutions to systems of linear ODEs (described in Chapter 4). This will give us the local picture of the flow pattern about the steady states.

Example 7

Equations (9a,b) can be linearized about the steady states (0, 0) and (1, 1). The Jacobian is

$$\mathbf{J}(\bar{x}_0, \bar{y}_0) = \begin{pmatrix} y & x-1 \\ y-1 & x \end{pmatrix}_{(\bar{x}_0, \bar{y}_0)}.$$

One obtains

$$\mathbf{J}(0, 0) = \begin{pmatrix} 0 & -1 \\ -1 & 0 \end{pmatrix}, \qquad \mathbf{J}(1, 1) = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}.$$

Thus close to (0, 0) the system behaves much like the linearized version,

$$\frac{dx}{dt} = -y, \qquad \frac{dy}{dt} = -x.$$

Similarly, close to (1, 1) the linearized equations are

$$\frac{dx}{dt} = x, \qquad \frac{dy}{dt} = y.$$

A summary of properties of linear systems (of two ordinary differential equations) is given in Table 5.1, in which we consider only the real, distinct eigenvalues case.

Table 5.1 ***Linear Systems of two ODEs***

	Full algebraic notation	*Equivalent Vector–Matrix Notation*
Equations	$\dfrac{dx}{dt} = a_{11}x + a_{12}y$ $\dfrac{dy}{dt} = a_{21}x + a_{22}y$ $y^1y^3 = 9$	$\dfrac{dx}{dt} = \mathbf{A}\mathbf{x}, \quad \mathbf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$
Significant quantities	$\beta = a_{11} + a_{22}$, $\gamma = a_{11}a_{22} - a_{12}a_{21}$, $\delta = \beta^2 - 4\gamma$	Tr $\mathbf{A}$, det $\mathbf{A}$, disc $\mathbf{A}$
Characteristic equation	$\lambda^2 - \beta\lambda + \gamma = 0$	$\det(\mathbf{A} - \lambda\mathbf{I}) = 0$
Eigenvalues	$\lambda_{1,2} = \dfrac{\beta \pm \sqrt{\delta}}{2}$	$\lambda_{1,2} = \dfrac{\text{Tr}\,\mathbf{A} \pm \sqrt{\text{disc}\,\mathbf{A}}}{2}$
Identities	$\lambda_1 + \lambda_2 = \beta$,	$\lambda_1 + \lambda_2 = \text{Tr}\,\mathbf{A}, \quad \lambda_1\lambda_2 = \det \mathbf{A}$
Eigenvectors	$\begin{pmatrix} a_{12} \\ \lambda_1 - a_{11} \end{pmatrix}, \begin{pmatrix} a_{12} \\ \lambda_2 - a_{11} \end{pmatrix}$	$\mathbf{v}_1, \mathbf{v}_2$ such that $(\mathbf{A} - \lambda\mathbf{I})\mathbf{v}_i = 0$
Solutions	$x = c_1a_{12}e^{\lambda_1 t} + c_2a_{12}e^{\lambda_2 t}$, $y = d_1e^{\lambda_1 t} + d_2e^{\lambda_2 t}$, where $d_1 = c_1(\lambda_1 - a_{11})$, $d_2 = c_2(\lambda_2 - a_{11})$.	$\mathbf{x} = c_1\mathbf{v}_1e^{\lambda_1 t} + c_2\mathbf{v}_2e^{\lambda_2 t}$.

5.7 PHASE-PLANE DIAGRAMS OF LINEAR SYSTEMS

We observe that a linear system can have at most one steady state, at (0, 0) provided $\gamma = \det \mathbf{A} \neq 0$. In the particular case of real eigenvalues there is a rather distinct geometric meaning for eigenvectors and eigenvalues:

1. For real λ_i the *eigenvectors* $\mathbf{v}_i$ *are directions on which solutions travel along straight lines towards or away from* (0, 0).
2. If λ_i is positive, the direction of flow along $\mathbf{v}_i$ is away from (0, 0), whereas if λ_i is negative, the flow along $\mathbf{v}_i$ is towards (0, 0).

Proof of these two statements is given below.

An Interpretation of Eigenvectors

Solutions to a linear system are of the form

$$\mathbf{x}(t) = c_1\mathbf{v}_1 e^{\lambda_1 t} + c_2\mathbf{v}_2 e^{\lambda_2 t}. \tag{13}$$

Recall that c_1 and c_2 are arbitrary constants. If initial conditions are such that $c_1 = 0$ and $c_2 = 1$, the corresponding solution is

$$\mathbf{x}(t) = \mathbf{v}_2 e^{\lambda_2 t}. \tag{14}$$

For any value of t, $\mathbf{x}(t)$ is a scalar multiple of $\mathbf{v}_2$. (This means that $\mathbf{x}(t)$ is always parallel to the direction specified by the vector $\mathbf{v}_2$.) If λ is negative, then for very large values of t $\mathbf{x}(t)$ is small. In the limit as t approaches $+\infty$, $\mathbf{x}(t)$ approaches the steady state (0, 0). Thus $\mathbf{x}(t)$ describes a straight-line trajectory moving parallel to the direction $\mathbf{v}_2$ and towards the origin.

A similar result is obtained when $c_1 = 1$ and $c_2 = 0$. Then we arrive at

$$\mathbf{x}(t) = \mathbf{v}_1 e^{\lambda_1 t}. \tag{15}$$

The solution is a straight-line trajectory parallel to $\mathbf{v}_1$.

It follows that any solution curve that starts on a straight line through (0, 0) in either direction $\pm\mathbf{v}_1$ or $\pm\mathbf{v}_2$ will stay on that line for all t, $-\infty < t < \infty$ either approaching or receding from the origin. Note also from the above that a steady state can only be attained as a limit, when t gets infinitely large, because time dependence of solutions is exponential. This tells us that the rate of motion gets progressively slower as one approaches a steady state.

Solution curves that begin along directions different from those of eigenvectors tend to be curved (because when both c_1 and c_2 are nonzero, the solution is a linear superposition of the two fundamental parts, $\mathbf{v}_1 e^{\lambda_1 t}$ and $\mathbf{v}_2 e^{\lambda_2 t}$, whose relative contributions change with time). There is a tendency for the "fast" eigenvectors (those associated with largest eigenvalues) to have the strongest influence on the solutions. Thus trajectories curve towards these directions, as shown in Figure 5.11.

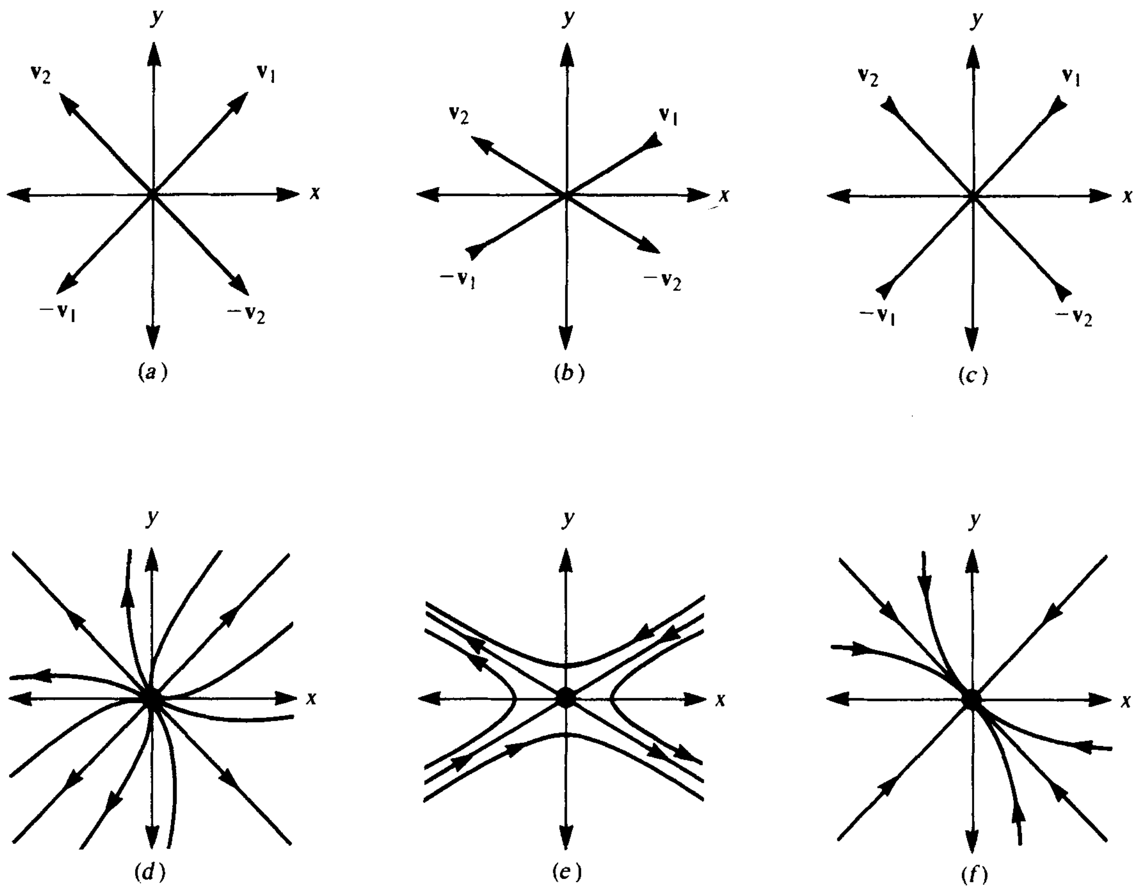


Figure 5.11 *Sketches of the eigenvectors (a–c) and solution curves (d–f) of the linear equations (11a,b) for real eigenvalues. The signs of the two eigenvalues are as follows: (a, d), both positive; (b, e), opposite; (c, f), both negative.*

Real Eigenvalues

Assuming that eigenvalues are real and distinct (with $\gamma \neq 0$, $\beta^2 - 4\gamma > 0$ where β, γ are as defined in Table 5.1 and equation (16), the behavior of solutions can be classified into one of the three possible categories:

1. Both eigenvalues are positive: $\lambda_1 > 0$, $\lambda_2 > 0$.
2. Eigenvalues are of opposite signs: e.g., $\lambda_1 > 0$, $\lambda_2 < 0$.
3. Both eigenvalues are negative: $\lambda_1 < 0$, $\lambda_2 < 0$.

In these three cases the eigenvectors also are real. Both vectors point away from the origin in case 1 and towards it in case 3. In case 2 they are of opposite orientations, with the one pointing outwards associated with the positive eigenvalue. Figure 5.11(a–c) illustrates this point.

All solutions grow with time in case 1 and decay with time in case 3; hence in each case the point (0, 0) is an *unstable* or a *stable node,* respectively. Case 2 is somewhat different in that solutions approach (0, 0) along one direction and recede from it along another. This unstable behavior is descriptively termed a *saddle point* (see Figure 5.11(*e*)).

Complex Eigenvalues

For $\lambda = a \pm bi$, we distinguish between the following cases:

4. Eigenvalues have a positive real part ($a > 0$).
5. Eigenvalues are pure imaginary ($a = 0$).
6. Eigenvalues have a negative real part ($a < 0$).

Note that when the linear equations have real coefficients, complex eigenvalues can occur only in conjugate pairs since they are roots of the quadratic characteristic equation.

The eigenvectors are then also complex and have no direct geometric significance. In building up real-valued solutions, recall that the expressions we obtained in Section 4.8 were products of exponential and sinusoidal terms. We remarked on the property that these solutions are oscillatory, with amplitudes that depend on the real part a of the eigenvalues $\lambda = a \pm bi$. In the xy plane, oscillations are depicted by trajectories that wind around the origin. When a is positive, the amplitude of oscillation grows, so the pair (x, y) spirals away from (0, 0); whereas if a is negative, it spirals towards it. The case where $a = 0$ is somewhat special. Here $e^{at} = 1$, and the amplitude of such solutions does not change. These trajectories are disjoint closed curves encircling the origin, which is then termed a *neutral center*. In this case a somewhat precarious balance exists between the forces that lead to increasing and decreasing oscillations. It is recognized that small changes in a system that oscillates in this way may disrupt the balance, and hence a neutral center is said to be *structurally unstable*. Cases 4, 5, and 6 are illustrated in Figure 5.12.

5.8 CLASSIFYING STABILITY CHARACTERISTICS

From certain combinations of the coefficients appearing in the linear equations, we can deduce criteria for each of the six classifications described in the previous section. We shall catalog the nature of the eigenvalues and thus the stability properties of a steady state using three quantities,

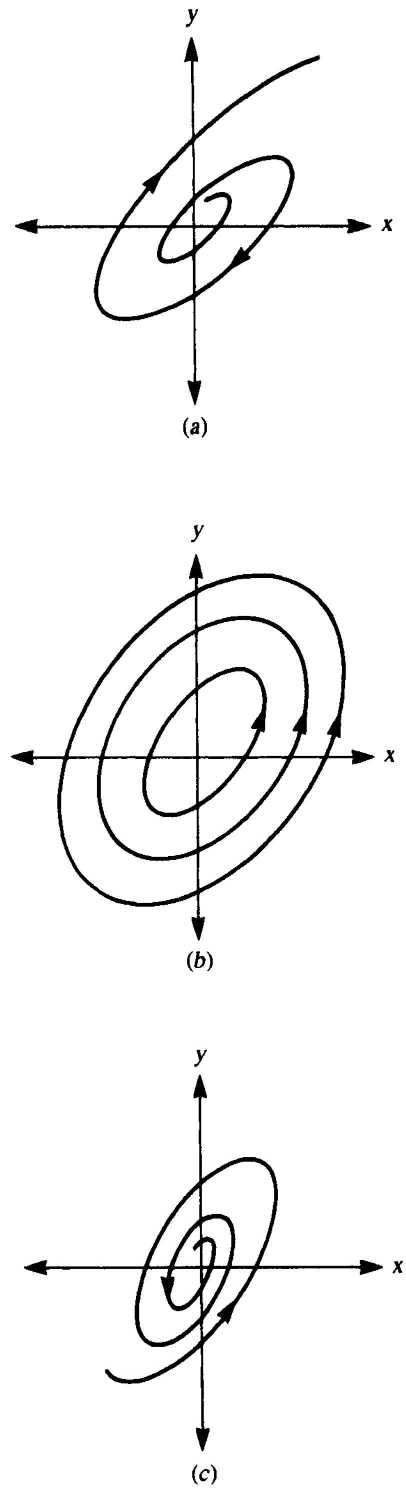
$$\beta = a_{11} + a_{22} = \text{Tr } \mathbf{A}, \tag{16a}$$

$$\gamma = a_{11}a_{22} - a_{12}a_{21} = \det \mathbf{A}, \tag{16b}$$

$$\delta = \beta^2 - 4\gamma = \text{disc } \mathbf{A}, \tag{16c}$$

where $\mathbf{A}$ is the 2×2 matrix of coefficients (a_{ij}) and $\mathbf{A} = \mathbf{J}(x_0, y_0)$. [See equation (12)] and Tr ($\mathbf{A}$) = trace, det ($\mathbf{A}$) = determinant, and disc ($\mathbf{A}$) = discriminant of $\mathbf{A}$.

Figure 5.12 *Solution curves for linear equations (11a,b) when eigenvalues are complex with (a) positive, (b) zero, and (c) negative real parts.*



Criteria stem from the fact that eigenvalues are related to these by

$$\lambda_{1,2} = \frac{\beta \pm \sqrt{\delta}}{2}. \tag{17}$$

Consult Figure 5.13 for a graphical interpretation of the arguments that follow.

For real eigenvalues, δ must be a positive number. Now if γ is positive, $\delta = \beta^2 - 4\gamma$ will be smaller than β^2 so that $\sqrt{\delta} < \beta$. In that case, $\beta + \sqrt{\delta}$ *and* $\beta - \sqrt{\delta}$ will have the same sign [see Figures 5.13(*a*) and 5.13(*c*)]. In other words, the eigenvalues will then be positive if $\beta > 0$ [case 1, Figure 5.13(*a*)] and negative if $\beta < 0$ [case 3, Figure 5.13(*c*)]. On the other hand, if γ is negative, we arrive at the conclusion that $\sqrt{\delta}$ is bigger than β. Thus $\beta + \sqrt{\delta}$ and $\beta - \sqrt{\delta}$ will have opposite signs whether β is positive or negative [case 2, Figure 5.13(*b*)].

Example 8

In Section 5.6 we saw that the Jacobian of equations (9a,b) for the two steady states (0, 0) and (1, 1) are

$$\mathbf{J}(0,0) = \begin{pmatrix} 0 & -1 \\ -1 & 0 \end{pmatrix}, \qquad \mathbf{J}(1,1) = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}.$$

Thus for (0, 0), $\beta = 0$ and $\gamma = -1$; so (0, 0) is a saddle point. For (1, 1), $\beta = 2$ and $\gamma = 1$; so (1, 1) is an unstable node.

Example 9

Consider the system of equations

$$\frac{dx}{dt} = 2x - y, \qquad \frac{dy}{dt} = 3x + 2y.$$

Then

$$\beta = (2 + 2) = 4, \qquad \gamma = (2)(2) + (1)(3) = 7,$$
$$\delta = \beta^2 - 4\gamma = 16 - 28 = -12.$$

Since $\beta^2 < 4\gamma$, the eigenvalues will be complex. Since $\beta = 4 > 0$, the behavior is that of an unstable spiral.

Example 10

Consider the system

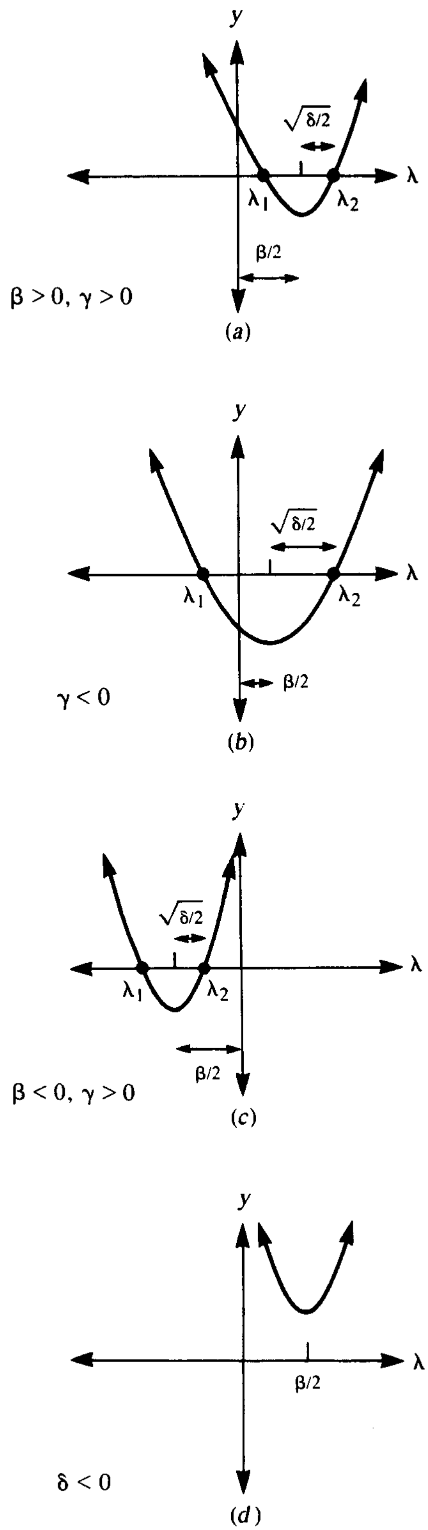
$$\frac{dx}{dt} = -4x + y, \qquad \frac{dy}{dt} = x - 2y.$$

Then

$$\beta = (-4 - 2) = -6, \qquad \gamma = (-4)(-2) - (1)(1) = 7,$$
$$\delta = \beta^2 - 4\gamma = 36 - 28 = 12.$$

Since $\beta < 0$ and $\gamma > 0$, the system is a stable node.

Figure 5.13 *Eigenvalues are those values λ at which the parabola $y = \lambda^2 - \beta\lambda + \gamma$ crosses the λ axis. Signs of these values depend on β and on the ratio of $\sqrt{\delta}$ to β where $\delta = \beta^2 - 4\gamma$. When $\gamma > 0$, both eigenvalues have the same sign as β. If $\delta < 0$, the parabola does not intersect the λ axis, so both eigenvalues are complex.*



For eigenvalues to be complex (and not real) it is necessary and sufficient that $\delta = \beta^2 - 4\gamma$ be negative. Then

$$\lambda = \frac{\beta \pm i\sqrt{-\delta}}{2}.$$

Cases 4, 5, and 6 then follow for positive, zero, or negative β respectively.

To summarize, the steady state can be classified into six cases as follows:

1. Unstable node: $\beta > 0$ and $\gamma > 0$.
2. Saddle point: $\gamma < 0$.
3. Stable node: $\beta < 0$ and $\gamma > 0$.
4. Unstable spiral: $\beta^2 < 4\gamma$ and $\beta > 0$.
5. Neutral center: $\beta^2 < 4\gamma$ and $\beta = 0$.
6. Stable spiral: $\beta^2 < 4\gamma$ and $\beta < 0$.

The *$\beta\gamma$ parameter plane,* shown in Figure 5.14, consists of six regions in which one of the above qualitative behaviors obtains. This figure captures in a com-

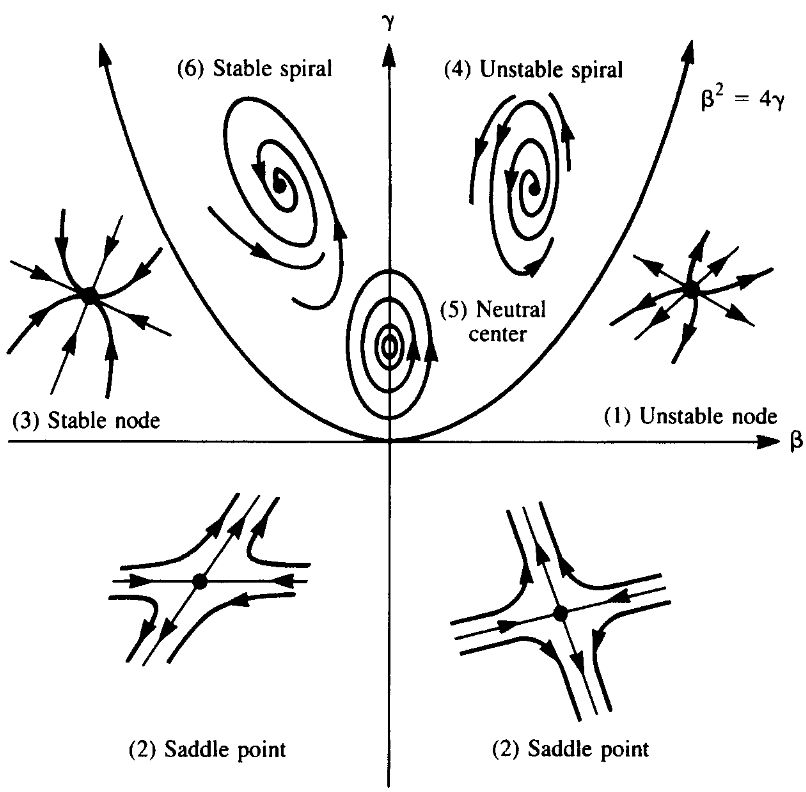


***Figure 5.14** To get a general idea of what happens in a linear system such as*

$$\dot{x} = a_{11}x + a_{12}y, \qquad \dot{y} = a_{21}x + a_{22}y,$$

we need only compute the quantities

$$\beta = a_{11} + a_{22}, \qquad \gamma = a_{11}a_{22} - a_{12}a_{21}.$$

The above parameter plane can then be consulted to determine whether the steady state (0, 0) *is a node, a spiral point, a center, or a saddle point.*

prehensive way the fundamental characteristics of a linear system. Notice that the region associated with a neutral center occupies a small part of parameter space, namely the positive γ axis.

The stability and behavior of a linear system, or the properties of a steady state of a nonlinear system can in practice be ascertained by determining β and γ and noting the region of the parameter plane in which these values occur. See examples 8, 9, and 10.

5.9 GLOBAL BEHAVIOR FROM LOCAL INFORMATION

Systems of nonlinear ODEs may have multiple steady states (see examples 5 and 6). Close to the steady states, behavior is approximated by the linearized equations, a fact that does not depend on the degree of the system; that is, it holds true in general for $n \times n$ systems.

An attribute of 2×2 systems that is *not* shared by those of higher dimensions is that local behavior at steady states can be used to reconstruct global behavior. By this we mean that stability properties of steady states and various gross features of the direction field determine a flow in the plane in an unambiguous way. The reason bigger systems of equations cannot be treated in the same way is that curves in higher dimensions are far less constrained by imposing a continuity requirement. A result that holds in the plane but not in higher dimensions is that a simple closed curve (for example, an ellipse or a circle) separates the plane into two disjoint regions, the "inside" and the "outside." It can be shown in a mathematically rigorous way that this limits the ways in which curves can form a smooth flow pattern in a planar region. Problem 16 gives some intuitive feeling for why this fact plays such a central role in establishing the qualitative behavior of 2×2 systems.

The terminology commonly used in the theory of ODEs reflects an underlying analogy between abstract mathematical equations and physical flows. We tend to associate the behavior of solutions to a 2×2 system with the motion of a two-dimensional fluid that emanates or vanishes at steady-state points. This at least imparts the idea of what a smooth phase-plane picture should look like. (We note a slight exception since saddle points have no readily apparent fluid analogy.) By smooth, or continuous flow we understand that a small displacement from a position (x_1, y_1) to one close to it (x_2, y_2) should not cause a drastic change in the direction of the flow.

There are a limited number of ways that trajectories can be combined to create a flow pattern that accommodates the local (steady-state) properties with the global property of continuity. A partial list follows:

1. Solution curves can only intersect at steady-state points.
2. If a solution curve is a closed loop, it must encircle at least one steady state that cannot be a saddle point (see Chapter 8).

Trajectories can have any one of several *asymptotic behaviors* (limiting behavior for $t \to +\infty$ or $t \to -\infty$). It is customary to refer to the *α-limit set* and *ω-limit set,* which are simply the sets of points that are approached along a trajectory for

$t \rightarrow -\infty$ and $t \rightarrow +\infty$ respectively. Limit sets may include any of the following (see Figure 5.15):

1. A steady-state point.
2. Infinity. (Trajectories emanating from or approaching infinitely large values in phase space are said to be unbounded.)
3. A *closed-loop trajectory*. (A trajectory may itself be a closed curve or else may approach or recede from one. Such solution curves represent oscillating systems; see Chapters 6 and 8.)
4. A *cycle graph* (a set containing a finite number of steady states connected by an equal number of trajectories).

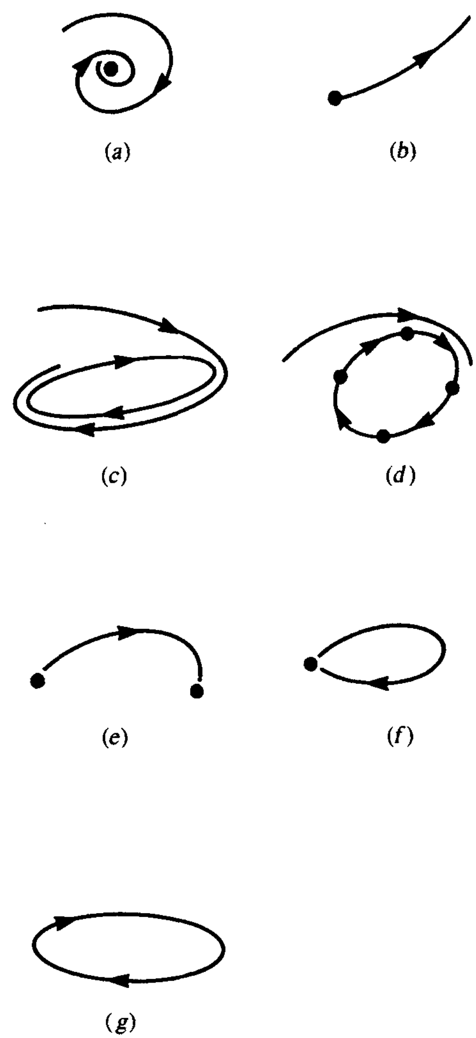


***Figure 5.15** Limit sets described in text: (a) steady-state point, (b) infinity, (c) closed-loop trajectory, (d) cycle graph, (e) heteroclinic trajectory, (f) homoclinic trajectory, and (g) limit cycle.*

Certain types of trajectories are further distinguished by name since they represent interesting or important properties. Three of these are listed here:

5. A *heteroclinic trajectory* connects two (different) steady states. (The term *connects* is often used loosely to convey that an orbit tends to each of the steady states for $t \to \pm\infty$.)
6. A *homoclinic trajectory* returns to the same steady state from whence it originates.
7. A *limit cycle* is a closed orbit that is the α or ω limit set of neighboring orbits (see Figure 5.15 and Chapter 8).

It has been shown that by linearizing a set of (nonlinear) equations about a given steady state, we can understand local behavior rather thoroughly. Indeed, this behavior falls into a small number of possible cases, six of which were described in Figure 5.14. (We did not go into details of several other singular cases, for example, if det $\mathbf{A} = 0$ or disc $\mathbf{A} = 0$. These are discussed in several sources in the references.)

Suppose we arrive at a prediction that some steady state is a spiral, a node, or a saddle point according to linear theory. The nonlinearity of the equations might distort that local behavior somewhat, but its basic features would not change. An exception to this occurs when linearization predicts a neutral center. In that case, somewhat more advanced analysis is necessary to establish whether this prediction holds true. A hint for why this prediction is not trustworthy has been given previously and involves the concept of structural stability. Briefly, even though the effect of nonlinearities is small near a steady state, it may suffice to disrupt the delicate balance of a neutral center. What happens when the delicate rings of a neutral center are broken? We postpone discussion of this to a later chapter.

5.10 CONSTRUCTING A PHASE-PLANE DIAGRAM FOR THE CHEMOSTAT

To demonstrate how to apply the theory given in Chapters 4 and 5 to a given situation, we return to the example of the chemostat. In Section 4.5 we discovered the following set of dimensionless equations depicting bacterial density N and nutrient concentration C:

$$\frac{dN}{dt} = \alpha_1\left(\frac{C}{1 + C}\right)N - N, \tag{18a}$$

$$\frac{dC}{dt} = -\left(\frac{C}{1 + C}\right)N - C + \alpha_2. \tag{18b}$$

As we saw, these nonlinear equations have two steady states, one of which represents a stable level of nutrient and cells. We now apply the method of phase-plane analysis to this example. Because only positive values of N and C are biologically meaningful, we shall restrict attention to the positive quadrant of the NC plane.

Step 1: Nullclines

The N nullcline

$\dot{N} = 0$ represents all the points such that

$$\alpha_1\left(\frac{C}{1 + C}\right)N - N = 0,$$

which are $N = 0$, or $\alpha_1 C/(1 + C) = 1$. After rearranging, the latter leads to

$$C = \frac{1}{\alpha_1 - 1}. \tag{19}$$

This horizontal line crosses the C axis at $1/(\alpha_1 - 1)$. On this line and on the line $N = 0$, the value of N cannot change, so arrows are parallel to the C axis.

The C nullcline

$\dot{C} = 0$ represents all the points satisfying

$$-\left(\frac{C}{1 + C}\right)N - C + \alpha_2 = 0.$$

For a better way of expressing this implicit equation of a nullcline, we solve for N to get

$$N = (\alpha_2 - C)\,\frac{1 + C}{C}. \tag{20}$$

This is a single curve with the following properties:

1. It passes through $(\alpha_2, 0)$.
2. It is asymptotic to $C = 0$ and tends to $+\infty$ there.
3. Arrows along this nullcline are parallel to the N axis.

The curves corresponding to the N nullclines and C nullcline are shown on Figure 5.16. Notice that we have drawn the two curves intersecting in the first quadrant; in other words, we assume that

$$\frac{1}{\alpha_1 - 1} < \alpha_2. \tag{21}$$

When this fails to be true, the picture will be quite different, as shown in problem 11. Direction of arrows will be determined by tabulating several judiciously chosen values. Having calculated the Jacobian of equations (18a,b) previously, we observe that det $\mathbf{J} \neq 0$ at either steady state. This means that arrows along nullclines have opposite orientations on opposite sides of a steady state.

In determining the signs of dC/dt and dN/dt, it is sometimes helpful to prepare the ground by rewriting the equations in a more transparent form. For example, after rearranging equation (18a) we get

$$\frac{dN}{dt} = \frac{(\alpha_1 - 1)C - 1}{(1 + C)}\,N. \tag{22}$$

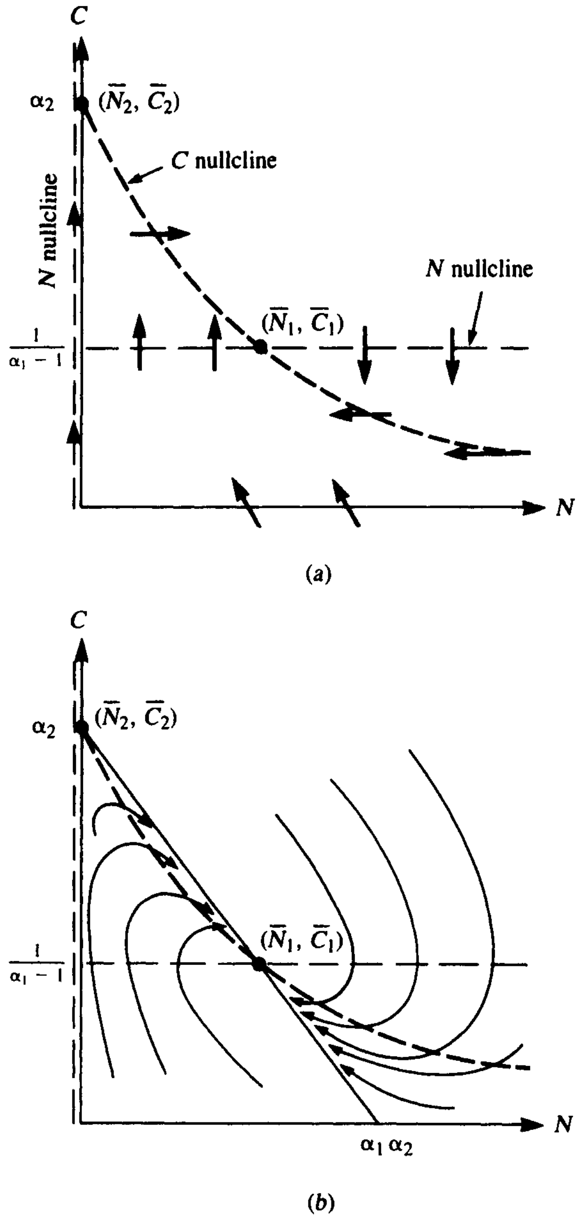


***Figure 5.16** Phase-plane portrait of the chemostat model based on equations (18a,b) showing nullclines (dashed and dotted lines) and steady-state points (heavy dots). (a) The directions of flow as given in Table 5.2. (b) The trajectories based on flow directions, steady state stability, and all other analysis.*

This allows us to conclude in a more direct way that dN/dt is negative whenever $C < 1/(\alpha_1 - 1)$ and positive when $C > 1/(\alpha_1 - 1)$. A similar procedure can be used for equation (18b). Table 5.2 summarizes these conclusions.

Table 5.2 Directions of Flow in the NC Plane (Fig. 5.16)

Case	C	N	dC/dt	dN/dt
1	small, > 0	on C nullcline	0	$\approx$ small term $\times N - N$; < 0; N must be decreasing
2	large, $> \alpha_2$	0	$\approx -C + \alpha_2 < 0$; C must be decreasing	0
3	$\dfrac{1}{\alpha_1 - 1}$	$N >$ steady-state value $\bar{N}_1$	$\approx$ −large term + small term < 0; C must be decreasing	0
4	0	0	$\alpha_2 > 0$; C must be increasing	0

Step 2: Steady States

The two steady states of the chemostat, $(\bar{N}_1, \bar{C}_1)$ and $(\bar{N}_2, \bar{C}_2)$, are given by the expressions

$$\left(\alpha_1\left(\alpha_2 - \frac{1}{\alpha_1 - 1}\right), \frac{1}{\alpha_1 - 1}\right) \qquad \text{and} \qquad (0, \alpha_2). \tag{23}$$

These are the two points of intersection of $\dot{N} = 0$ and $\dot{C} = 0$. [Note that $(0, 1/(\alpha_1 - 1))$ is not such an intersection since it satisfies only the condition $\dot{N} = 0$.] The nullclines always intersect at two places, but the first of these intersections is in the positive NC quadrant only when $\alpha_2 > 1/(\alpha_1 - 1)$ and $\alpha_1 > 1$. We have already noted that these inequalities must be satisfied in order to apply to biological systems.

Step 3: Close to Steady States

We now summarize the calculations of stability characteristics of the two steady states:

1. In the steady state $(\bar{N}_1, \bar{C}_1)$ the Jacobian is

$$\mathbf{J} = \begin{pmatrix} 0 & \alpha_1 A \\ -1/\alpha_1 & -(A + 1) \end{pmatrix}, \tag{24}$$

where $A = \bar{N}_1/(1 + \bar{C}_1)^2$. Since

$$\beta = -(A + 1) < 0, \qquad \gamma = A > 0,$$
$$\beta^2 - 4\gamma = (A - 1)^2 > 0,$$

this steady state is always a stable node.

2. In the second steady state $(\bar{N}_2, \bar{C}_2)$, the Jacobian is

$$\mathbf{J} = \begin{pmatrix} \alpha_1 B - 1 & 0 \\ -B & -1 \end{pmatrix}, \tag{25}$$

where $B = \alpha_2/(1 + \alpha_2)$. Thus

$$\beta = \alpha_1 B - 2 \qquad \text{and} \qquad \gamma = 1 - \alpha_1 B.$$

This steady state will be a saddle point whenever $1 - \alpha_1 B < 0$, that is, when

$$\alpha_1 > \frac{1}{B}. \tag{26}$$

In problem 11(a) it is shown that this is satisfied precisely when

$$\alpha_2 > \frac{1}{\alpha_1 - 1}. \tag{27}$$

This condition ensures that the nonzero steady state $(\bar{N}_1, \bar{C}_1)$ exists. Thus, when $(\bar{N}_1, \bar{C}_1)$ is a biologically meaningful steady state, $(\bar{N}_2, \bar{C}_2) = (0, \alpha_2)$ is a saddle point.

The Shape of Trajectories Close to $(\bar{N}_1, \bar{C}_1)$

Problem 12 demonstrates that eigenvalues and corresponding eigenvectors of the Jacobian in equation (24) are as follows:

$$\lambda_1 = -A, \qquad \lambda_2 = -1; \tag{28}$$

$$\mathbf{v}_1 = \begin{pmatrix} \alpha_1 \\ -1 \end{pmatrix}, \qquad \mathbf{v}_2 = \begin{pmatrix} \alpha_2 A \\ -1 \end{pmatrix}. \tag{29}$$

In problem 12(d) we show that $\mathbf{v}_1$ defines a straight line through the steady state $(\bar{N}_1, \bar{C}_1)$ and two other points $(\alpha_1\alpha_2, 0)$ and $(0, \alpha_2)$. In problem 13 it is also shown that all trajectories approach this line as t approaches infinity.

It is worth remarking that several steps carried out in the chemostat example simplify the analysis. The first was that of reducing equations to dimensionless form; this eliminated many parameters that would complicate the expressions appearing in the Jacobian. The second step was recognizing certain recurring expressions, such as $\bar{N}_1/(1 + \bar{C}_1)^2$, and representing these by suitably defined constants. Such steps are recommended as an aid to organization when analyzing the behavior of a model.

We can complete a phase-plane portrait of the chemostat by combining the nullcline-and-arrow method with knowledge of the steady-state behavior ascertained above. [See also box on the shape of trajectories near the steady state $(\bar{N}_1, \bar{C}_1)$.] Figure 5.16(b) shows a smooth flow pattern consistent with both local and global clues. Other details of the flow are worked out in problems 10 through 13. We see that no matter what the initial values of C and N, solution curves eventually approach the steady state $(\bar{N}_1, \bar{C}_1)$.

Step 4: Interpreting the Solutions

Three hypothetical ways of starting a chemostat culture are described below. Figure 5.16 is used to deduce what happens in each situation.

First, suppose that the growth chamber in the chemostat initially has no bacteria or nutrient. As the stock solution of nutrient flows into the chamber, it causes the nutrient level there to increase. From Figure 5.16 we see that after starting at $(0,0)$ we gradually approach the steady state $(0, \alpha_2)$. Thus C is building up to a level equivalent to that of the stock solution (recall the definition of α_2). N never increases, because bacteria are not present and thus cannot reproduce.

Now consider inoculating the chamber with a small bacterial population, $N = \epsilon$, and again starting with $C = 0$. Note that the solution curves through the N axis (for N small) sweep into the positive quadrant. N initially decreases, because until a nutrient level is established, bacteria cannot reproduce fast enough to replace those that are lost in the effluent. Once excess nutrient is available, bacterial densities rise dramatically, so that the solution curve has a nearly vertical "kink." At this point, rapid consumption causes decline in the nutrient and N and C approach their steady-state values. (In theory, the steady state is only attained at $t = \pm\infty$. In practice it may take only a finite time such as a few hours to be close enough to steady state as to be indistinguishable from it.)

As a third example, starting with $N > \bar{N}_1$, $C > \bar{C}_1$ we find that N initially increases, thereby causing nutrient depletion. (C drops below its steady-state value.) The bacterial population declines so that nutrient consumption is less rapid. Again, after these transients, the steady state is once more established.

In problem 14 we return once again to the original parameters of the chemostat. There it is shown that the following relevant conclusions are reached:

Summary of the Chemostat Model

1. If either

$$\frac{F}{V} \le K_{\max}, \qquad \text{or}$$

$$\frac{F}{V} > K_{\max} \qquad \text{and} \qquad C_0 \le \frac{(F/V)K_n}{K_{\max} - (F/V)},$$

$(\bar{N}_2, \bar{C}_2) = (0, C_0)$ is the only steady-state point and it is stable. This situation is called a *washout* since the microbe will be washed out of the chemostat.

2. If both

$$\frac{F}{V} > K_{\max} \qquad \text{and}$$

$$\frac{(F/V)K_n}{K_{\max} - (F/V)} < C_0,$$

then $(\bar{N}_1, \bar{C}_1)$ is a stable steady-state point. Provided $N(0)$ is initially nonzero and $C_0 > 0$, the bacterial density and nutrient concentration will converge to $\bar{N}_1$ and $\bar{C}_1$ respectively.

5.11 HIGHER-ORDER EQUATIONS

So far we have dealt only with systems of first-order equations. However, the geometric theory used here can also be applied to problems consisting of higher-order equations, such as

$$\frac{d^n y}{dt^n} = F\left(\frac{d^{n-1}y}{dt^{n-1}}, \frac{d^{n-2}y}{dt^{n-2}}, \ldots, y', y\right). \tag{30}$$

The problem will be reduced to one that is familiar by converting this nth-order equation to a set of n first-order equations. To do so, define $y_0 = y$ and $n - 1$ new variables, each of which represents the derivative of the preceding variable:

$$\begin{aligned} y_0 &= y, \\ y_1 &= \frac{dy_0}{dt} = \frac{dy}{dt}, \\ &\vdots \\ y_{n-1} &= \frac{dy_{n-2}}{dt} = \cdots = \frac{d^{n-1}y}{dt^{n-1}}. \end{aligned}$$

Now rewrite this as a "system" of equations in the variables $y_0, \ldots, y_{n-1}$, using equation (30) in the final equation:

$$\begin{aligned} \frac{dy_0}{dt} &= y_1, \\ \frac{dy_1}{dt} &= y_2, \\ &\vdots \\ \frac{dy_{n-2}}{dt} &= y_{n-1}, \\ \frac{dy_{n-1}}{dt} &= F(y_{n-1}, y_{n-2}, \ldots, y_1, y_0). \end{aligned} \tag{31}$$

The system (31) can be summarized by a vector equation,

$$\frac{d\mathbf{y}}{dt} = \mathbf{f}(\mathbf{y}) = (f_0, f_1, \ldots, f_{n-1}), \tag{32}$$

where $f_0 = y_1, f_1 = y_2, \ldots, f_{n-1} = F$, and so on.

A solution to (32), $\mathbf{y}(t)$ is a curve in n-dimensional space, parameterized by t. While $\mathbf{f}(\mathbf{y})$ again represents a direction field, it is now much more difficult to visualize. Nullclines are hyperplanes or hypersurfaces of dimension $n - 1$; in the examples given here, the subspaces are $y_1 = 0$, $y_2 = 0, \ldots,$ and $F(y_{n-1}, y_{n-2}, \ldots, y_1, y_0) = 0$. It is clear that while the geometric interpretation underlying the equations can be thus generalized, we must abandon the idea of visualizing qualitative behavior in all but the simplest cases.

In theory, steady states can be determined analytically (when equations such as $\dot{y}_0 = 0, \ldots, \dot{y}_{n-1} = 0$ can be solved). The stability of these steady states is ascertained by linearizing the equations, but technical difficulties ensue (see Section 6.4). Even given complete local information about steady states, the global qualitative behavior is generally unknown, with few exceptions. So while in theory the scope of the analysis of the 2 × 2 case can be extended, in practice we obtain valuable insights in the general case only rarely.

PROBLEMS*

1. For the following first-order ordinary differential equations, sketch solution curves $y(t)$ by first plotting the tangent vectors specified by the differential equations:
   (a) $\dfrac{dy}{dt} = y^2.$
   (b) $\dfrac{dy}{dt} = 1 - \dfrac{y}{1+y}.$
   (c) $\dfrac{dy}{dt} = y(y-2).$
   (d) $\dfrac{dy}{dt} = ye^{(y-1)}$
   (e) $\dfrac{dy}{dt} = \sin y \cos y.$

2. For problem 1(a–e) above, graph dy/dt as a function of y. Use this graph to summarize the behavior of solutions to the equations on the y axis by drawing arrows to indicate when y increases or decreases.

3. Prove that solution curves of equation (3) have inflection points at
$$y = 1 \pm \frac{\sqrt{3}}{3}.$$
(*Hint:* Consider $f'(y)$ and see Figure 5.3(*a*).)

4. *Curves in the plane*. The locus of points for which $x = y^3$ can be written in the form $(x(t), y(t))$ by choosing some parameter t. For example,
$$x(t) = t, \qquad y(t) = t^3.$$
Other choices are possible, for example,
$$x = s^{1/3}, \qquad y = s.$$
These would depict the same curve but a different rate of motion along the curve. Then, using this parameterized form we can depict any position on the curve by the vector
$$\mathbf{x}(t) = (t, t^3)$$
and any tangent vector to the curve by the vector
$$\mathbf{v}(t) = \frac{d\mathbf{x}}{dt} = \left(\frac{dx(t)}{dt}, \frac{dy(t)}{dt}\right) = (1, 3t^2).$$

* Problems preceded by an asterisk are especially challenging.

For example, at $t = 1$, $\mathbf{x} = (1, 1)$ and $\mathbf{v} = (1, 3)$.

(a) Using the parameterized form given here, sketch the curve, and compute the tangent vectors at points $(0, 0)$, $(2, 8)$, and $(-1, -1)$.

(b) Find a way of parameterizing the following curves, and determine the form of the tangent vector to the curve:

(1) $y = x(x - 1)$.
(2) $y^2 = \sin x$.
(3) $x = 1/y$.
(4) $x^2 + y^2 = 1$.
(5) $y = ax + b$.
(6) $y = 4x^2$.

5. Sketch the nullclines in the *xy* phase plane, identify steady states, and draw directions of arrows on the nullclines for the following systems of first-order equations:

(a) $\dfrac{dx}{dt} = y^2 - x^2, \quad \dfrac{dy}{dt} = x - 1.$

(b) $\dfrac{dx}{dt} = x(y^2 - y), \quad \dfrac{dy}{dt} = x - y.$

(c) $\dfrac{dx}{dt} = x^2 + y, \quad \dfrac{dy}{dt} = -y.$

(d) $\dfrac{dx}{dt} = -xy, \quad \dfrac{dy}{dt} = (1 + x)(1 - y).$

(e) $\dfrac{dx}{dt} = x^2 - y, \quad \dfrac{dy}{dt} = y^2 - x.$

(f) $\dfrac{dx}{dt} = \dfrac{-xy}{1 + x} + x, \quad \dfrac{dy}{dt} = \dfrac{xy}{1 + x} - y.$

(g) $\dfrac{dx}{dt} = xy(1 - x) + C, \quad \dfrac{dy}{dt} = y\left(1 - \dfrac{y}{x}\right).$

6. For problem 5(a–g) find the Jacobian of each system of equations and determine stability properties of each steady state.

7. Sketch the phase-plane behavior of the following systems of linear equations and classify the stability characteristic of the steady state at $(0, 0)$:

(a) $\dfrac{dx}{dt} = -2y, \quad \dfrac{dy}{dt} = x.$

(b) $\dfrac{dx}{dt} = 3x + 2y, \quad \dfrac{dy}{dt} = 4x + y.$

(d) $\dfrac{dx}{dt} = 5x + 8y, \quad \dfrac{dy}{dt} = -3x - 5y.$

(e) $\dfrac{dx}{dt} = -4 - 2y, \quad \dfrac{dy}{dt} = 3x - y.$

(c) $\dfrac{dx}{dt} = 2x + y,$

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

(f) $\dfrac{dx}{dt} = x - 4y,$

$\dfrac{dy}{dt} = x + y.$

8. Write a system of linear first-order ODEs whose solutions have the following qualitative behaviors:
(a) $(0, 0)$ is a stable node with eigenvalues $\lambda_1 = -1$ and $\lambda_2 = -2$.
(b) $(0, 0)$ is a saddle point with eigenvalues $\lambda_1 = -1$ and $\lambda_2 = 3$.
(c) $(0, 0)$ is a center with eigenvalues $\lambda = \pm 2i$.
(d) $(0, 0)$ is an unstable node with eigenvalues $\lambda_1 = 2$ and $\lambda_2 = 3$.

Hint: Use the fact that λ_1 and λ_2 are eigenvalues of a matrix **A**, then

$$\lambda_1 + \lambda_2 = \operatorname{Tr} \mathbf{A} = a_{11} + a_{22},$$
$$\lambda_1 \lambda_2 = \det \mathbf{A} = a_{11}a_{22} - a_{12}a_{21}.$$

Note that there will be many possible choices for each of the above.

9. Consider the system of equations

$$\dot{x} = y - x^2, \qquad \dot{y} = y - 2x^2.$$

(a) Show that the only steady state is $(0, 0)$.
(b) Draw nullclines and determine the directions of arrows on the nullcline. Note that $(0, 0)$ is a point of tangency of the two nullclines, which intersect but do not cross.
(c) Find the Jacobian at $(0, 0)$, show that its determinant is equal to zero, and conclude that two eigenvalues are $\lambda_1 = 0$ and $\lambda_2 = 1$.
(d) Sketch solution curves in the *xy* plane.

10. By examining Figure 5.16 describe in words what would happen if we set up the chemostat to contain the following:
(a) A small number of bacteria with excess nutrient in the growth chamber.
(b) A large number of bacteria with very little nutrient in the growth chamber.

11. In drawing the phase-plane diagram of the chemostat, we assumed that $\alpha_2 > 1/(\alpha_1 - 1)$.
(a) Show that $(\overline{N}_2, \overline{C}_2)$ is a saddle point whenever this inequality is satisfied.
(b) Now suppose this inequality is not satisfied. Sketch the resulting phase-plane diagram and interpret the biological meaning.

12. **(a)** In the chemostat model find the quantity

$$A = \frac{\overline{N}_1}{(1 + \overline{C}_1)^2}$$

in terms of α_1 and α_2 [where $(\overline{N}_1, \overline{C}_1)$ is given by (23)].
(b) Show that the two eigenvalues of the Jacobian given by (24) are

$$\lambda_1 = -A, \qquad \text{and} \qquad \lambda_2 = -1.$$

(c) Show that the corresponding eigenvectors are

$$\mathbf{v}_1 = \begin{pmatrix} \alpha_1 \\ -1 \end{pmatrix}, \qquad \mathbf{v}_2 = \begin{pmatrix} \alpha_1 A \\ -1 \end{pmatrix}.$$

***(d)** Show that the eigenvector $\mathbf{v}_1$ and the steady state $(\overline{N}_1, \overline{C}_1)$ define a straight line whose equation is

$$N - \alpha_1\alpha_2 = -\alpha_1 C.$$

[*Hint:* Use the fact that the slope is given by the ratio $\alpha_1/(-1) = -\alpha_1$ of the components of $\mathbf{v}_1$.]

(e) Show that this line passes through the points $(\alpha_1\alpha_2, 0)$ and $(0, \alpha_2)$.

13. In this problem we establish that, for the chemostat all trajectories approach the line

$$N - \alpha_1\alpha_2 = \alpha_1 C.$$

(a) Multiply equation (18b) by α_1 and add to equation (18a). Show that this leads to

$$\frac{d}{dt}(N + \alpha_1 C) = \alpha_1\alpha_2 - (N + \alpha_1 C).$$

(b) Let $x = N + \alpha_1 C$ and integrate the equation in part (a). Show that

$$x(t) = Ke^{-t} + \alpha_1\alpha_2$$

is a solution (K = a constant of integration).

(c) Show that in the limit for $t \to \infty$ one obtains $x(t) \to \alpha_1\alpha_2$; that is,

$$N + \alpha_1 C = \alpha_1\alpha_2.$$

Conclude that as t approaches infinity, all points $(N(t), C(t))$ approach this line.[1]

14. (a) Verify that conclusions outlined in the summary of the chemostat model at the end of Section 5.10 are correct.

(b) Sketch the phase-plane behavior of the original dimension-carrying variables of the problem. (Your sketch should be similar to Figure 5.16 but with relabeled axes.)

15. Equation (1a) is linear but nonhomogeneous. To solve this problem consider first the corresponding homogeneous problem

$$\frac{dy}{dt} + y = 0.$$

Find the solution $y = \Phi(t)$ of this equation and look for solutions of the equation (1a) of the form

$$y = \Phi(t)C(t)$$

where $C(t)$ is an unknown function. Solve for $C(t)$. This procedure is known as the method of *variation of parameters*.

1. This problem was kindly suggested by C. M. Biles.

16. In the accompanying figure, locations and stability properties of steady states have been indicated by arrows. Fill in the global flow pattern using the fact that continuity of the flow must be preserved (that is, no sharp transitions at neighboring points except in the vicinity of steady states). In some cases more than one qualitative flow pattern is possible. Can you determine which of the following gives ambiguous clues?

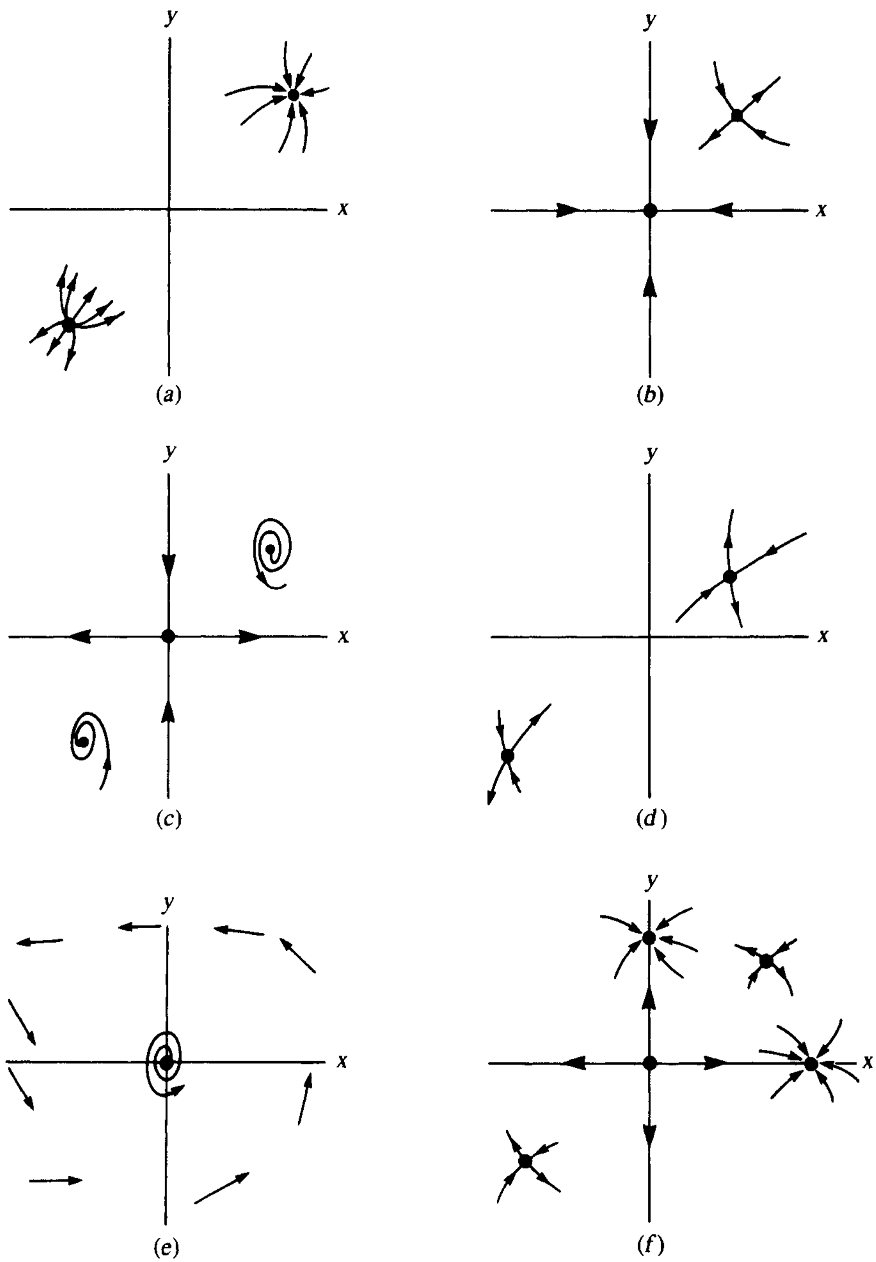


Figure for problem 16.

17. In this problem we explore one of the major distinctions between 2 × 2 systems of equations, which are represented by flows in the plane, and those of higher dimensionality.

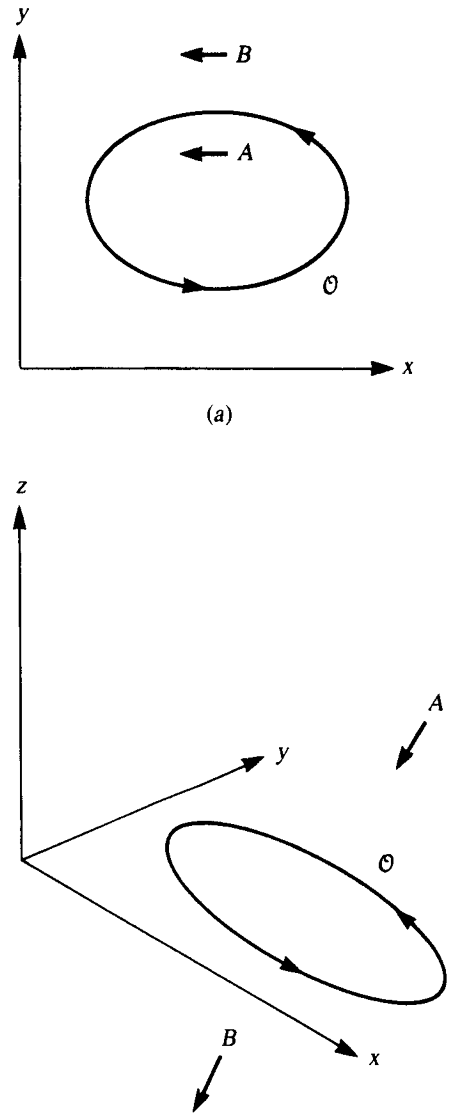


Figure for problem 17. (b)

(a) In diagram (*a*) of a 2 × 2 system, a closed orbit ($\mathcal{O}$) has been drawn in the *xy* plane. The arrows *A* and *B* represent the local directions of motion at two points on the inside and outside of the closed curve.

(1) By preserving a continuous flow, sketch several *different* qualitative flow patterns consistent with the diagram.

(2) Section 5.11 tells us there must be a steady state somewhere in the diagram. In which region must it be, and why?

(b) A similar diagram in three dimensions (for a system *xyz* of three equations) leads to some ambiguity. Is it possible to define inside and outside regions for the orbit? Give some sketches or verbal descriptions of flow patterns consistent with this orbit. Show that it is not necessary to assume that a steady state is associated with the closed orbit.

18. Use phase-plane methods to find qualitative solutions to the model for the glucose-insulin system due to Bellomo et al. (1982). (See problem 27 in Chapter 4.) Draw nullclines, identify steady states, and sketch trajectories in the *ig* plane. Interpret your graph and discuss how parameters might influence the nature of the solutions.

19. Use methods similar to those mentioned in problem 17 to explore the model for continuous chemotherapy that was suggested in problem 25 of Chapter 4.

20. *Extended problem or project.* Using plausible assumptions or sources in the literature, suggest appropriate forms for the functions $F_1(X)$, $F_2(Y)$, $F_3(X, Y)$, and $F_4(X, Y)$ in the model for insulin and glucose proposed by Bolie (1960) (see equations (84a) and (84b) in Chapter 4). Use these functions to treat the problem by phase-plane methods and interpret your solutions.

21. In this problem we examine a continuous plant-herbivore model. We shall define q as the chemical state of the plant. Low values of q mean that the plant is toxic; higher values mean that the herbivores derive some nutritious value from it. Consider a situation in which plant quality is enhanced when the vegetation is subjected to a low to moderate level of herbivory, and *declines* when herbivory is extensive. Assume that herbivores whose density is I are small insects (such as scale bugs) that attach themselves to one plant for long periods of time. Further assume that their growth rate depends on the quality of the vegetation they consume. Typical equations that have been suggested for such a system are

$$\frac{dq}{dt} = K_1 - K_2 qI(I - I_0),$$

$$\frac{dI}{dt} = K_3 I\left(1 - \frac{K_4 I}{q}\right).$$

(a) Explain the equations, and suggest possible meanings for K_1, K_2, I_0, K_3, and K_4.

(b) Show that the equations can be written in the following dimensionless form:

$$\frac{dq}{dt} = 1 - KqI(I - 1),$$

$$\frac{dI}{dt} = \alpha I\left(1 - \frac{I}{q}\right).$$

Determine K and α in terms of original parameters.

(c) Find qualitative solutions using phase-plane methods. Is there a steady state? What are its stability properties?

(d) Interpret your solutions in part (c).

22. *A continuous ventilation-volume model.* In Chapters 1 and 2 we considered a simple model for irregular patterns of breathing. It was assumed that the sensitivity of the CO_2 chemoreceptor controls the depth (volume) of breathing. Over the time scale of 10 to 100 breaths the discontinuous nature of breathing and the delay in CO_2 sensitivity play significant roles. However, suppose we now view the process over a much longer time length (t = several hours). Define

$C(t)$ = blood CO_2 concentration at time t

$V(t)$ = magnitude of ventilation volume at time t.

(a) By making the approximations

$$\frac{C_{n+1} - C_n}{\Delta t} \simeq \frac{dC}{dt}, \qquad \frac{V_{n+1} - V_n}{\Delta t} \simeq \frac{dV}{dt}$$

reason that the continuous equations for the CO_2 ventilation volume systems based on equations (49) of Chapter 1 take the form

$$\frac{dC}{dt} = -\mathcal{L}(V, C) + m,$$

$$\frac{dV}{dt} = \mathcal{S}(C) - \epsilon V,$$

where $\mathcal{L}$ = CO_2 loss rate per unit time and $\mathcal{S}$ = CO_2-induced ventilation change per unit time. What is ϵ in terms of Δt?

(b) Now investigate the problem using the following steps: First assume that $\mathcal{L}$ and $\mathcal{S}$ are linear functions (as in problem 18 in Chapter 1); that is,

$$\mathcal{L}(V, C) = \beta V, \qquad \mathcal{S}(C) = \alpha C.$$

(1) Write out the system of equations, find their steady state, and determine the eigenvalues of the equations. Show that decaying oscillations may occur if $\epsilon^2 < 4\alpha\beta$.

(2) Sketch the phase-plane diagram of the system. Interpret your results biologically.

(c) Now consider the situation where

$$\mathcal{L}(V, C) = \beta VC, \qquad \mathcal{S}(C) = \alpha C.$$

(1) Explain the biological significance of this system. When is this a more valid assumption?

(2) Repeat the analysis requested in part (b).

(d) Finally, suppose that

$$\mathcal{L}(V, C) = \beta V, \qquad \mathcal{S}(C) = \frac{V_{\max} C}{K + C}.$$

How does this model and its predictions differ from that of part (b)?

23. The following equations were given by J. S. Griffith (1971, pp. 118–122), as a model for the interactions of messenger RNA M and protein E:

$$\dot{M} = \frac{aKE^m}{1 + KE^m} - bM, \qquad \dot{E} = cM - dE.$$

(See problem 25 in Chapter 7 for an interpretation.)

(a) Show that by changing units one can rewrite these in terms of dimensionless variables, as follows

$$\dot{M} = \frac{E^m}{1 + E^m} - \alpha M, \qquad \dot{E} = M - \beta E.$$

Find α and β in terms of the original parameters.

(b) Show that one steady state is $E = M = 0$ and that others satisfy $E^{m-1} = \alpha\beta(1 + E^m)$. For $m = 1$ show that this steady state exists only if $\alpha\beta \leq 1$.

(c) *Case 1*. Show that for $m = 1$ and $\alpha\beta > 1$, the only steady state $E = M = 0$ is stable. Draw a phase-plane diagram of the system.

(d) *Case 2*. Show that for $m = 2$, at steady state

$$E = \frac{1 \pm (1 + 4\alpha^2\beta^2)^{1/2}}{2\alpha\beta}.$$

Conclude that there are two solutions if $2\alpha\beta < 1$, one if $2\alpha\beta = 1$, and none if $2\alpha\beta > 1$.

(e) *Case 2 continued*. For $m = 2$ and $2\alpha\beta < 1$, show that there are two stable steady states (one of which is at $E = M = 0$) and one saddle point. Draw a phase-plane diagram of this system.

24. In modeling the effect of spruce budworm on forest, Ludwig et al. (1978) defined the following set of variables for the condition of the forest:

$S(t)$ = total surface area of trees

$E(t)$ = energy reserve of trees.

They considered the following set of equations for these variables in the presence of a constant budworm population B:

$$\frac{dS}{dt} = r_S S\left(1 - \frac{S}{K_S}\frac{K_E}{E}\right),$$

$$\frac{dE}{dt} = r_E E\left(1 - \frac{E}{K_E}\right) - P\frac{B}{S}.$$

The factors r, K, and P are to be considered constant.

***(a)** Interpret possible meanings of these equations.

(b) Sketch nullclines and determine how many steady states exist.

(c) Draw a phase-plane portrait of the system. Show that the outcomes differ qualitatively depending on whether B is small or large.

***(d)** Interpret what this might imply biologically.

[*Note:* You may wish to consult Ludwig et al. (1978) or to return to parts (a) and (d) after reading Chapter 6.]

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