digraph
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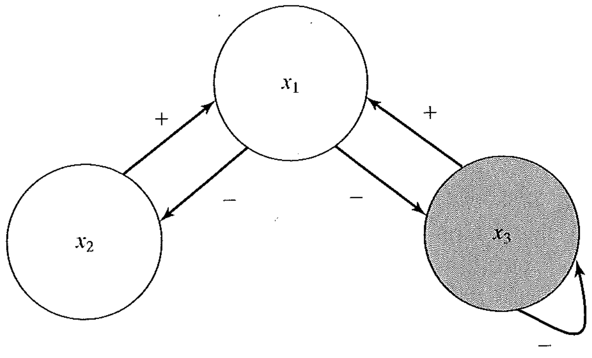


As an example, consider Figure 5.19. Node x_3 is gray and the other two nodes are white. There is at least one white node and each white node is connected by a predation link to one other white node. However, condition (iii) is not satisfied because the gray node is only connected to one white node. Now we state the criteria for qualitative stability.

eorem 5.13 *Let $Q = sign\,(J) = (q_{ij})$. If matrix J satisfies the five necessary conditions for qualitative stability and if, in addition, each predation community in the digraph associated with matrix Q fails at least one of the three conditions (i)–(iii) in the color test, then matrix J is qualitatively stable.* □

The conditions for qualitative stability can be applied to Example 5.23.

ample 5.25 **(Example 5.23 Revisited).** The predation community in this example is given in Figure 5.21. We have already shown that the five criteria are satisfied for the matrix Q and that conditions (i) and (ii) are satisfied in the color test. Since condition (iii) is not satisfied, the signed digraph fails the color test. Hence, the underlying Jacobian matrix J corresponding to the predator-prey system, where $Q = sign\,(J)$, is qualitatively stable. Thus, if the predator-prey system has a positive equilibrium with Jacobian matrix J, then the equilibrium is locally asymptotically stable. ■

5.11 Global Stability and Liapunov Functions

An important technique in stability theory for differential equations is known as the *direct method of Liapunov*. A function with particular properties known as a *Liapunov function* is constructed to prove stability or asymptotic stability of an equilibrium in a given region. The construction of Liapunov functions is often difficult for particular systems, but for Lotka-Volterra systems, there has been some success.

A procedure referred to as the direct method of Liapunov for studying the stability of a equilibrium is discussed in this section (Hale and Koçak, 1991; LaSalle and Lefschetz, 1961). This method has practical importance because estimates for the *basin of attraction* of the equilibrium can be obtained. (A basin of attraction is a subset U in $\mathbf{R}^n$ containing the equilibrium with the property

that solutions beginning in U approach the equilibrium.) The method can be applied to autonomous and nonautonomous systems consisting of n differential equations. The method is demonstrated for the following two-dimensional autonomous system:

$$\frac{dx}{dt} = f(x, y) \quad \text{and} \quad \frac{dy}{dt} = g(x, y). \tag{5.22}$$

The objective is to find a particular function, a Liapunov function, having certain properties in relation to system (5.22). In the following discussion, it is assumed that the equilibrium of interest is at the origin. If the equilibrium is not at the origin, a change of variable translates the equilibrium to the origin, $u = x - \bar{x}$ and $v = y - \bar{y}$.

Definition 5.10. Let U be an open subset of $\mathbf{R}^2$ containing the origin. A real-valued $C^1(U)$ function V, $V: U \to \mathbf{R}$, $[(x, y) \in U, V(x, y) \in \mathbf{R})]$ is said to be *positive definite* on the set U if the following two conditions hold:

(i) $V(0, 0) = 0$.

(ii) $V(x, y) > 0$ for all $(x, y) \in U$ with $(x, y) \neq (0, 0)$.

The function V is said to be *negative definite* if $-V$ is positive definite.

Example 5.26 The function $V(x, y) = x^2 + y^2$ is positive definite on all of $\mathbf{R}^2$, while the function $V(x, y) = x^2 + y^2 - y^3$ is positive definite only near the x-axis. On the other hand, the functions $V(x, y) = x + y^2$, $V(x, y) = (x + y)^2$, and $V(x, y) = x^2$ are not positive definite in any open neighborhood of the origin. Figure 5.22 shows the set of points in the x-y plane at which $V(x, y) = 0$ for these latter three examples. ■

If V is a positive definite function on the set U, then V has a minimum at the origin. This extreme point of V is isolated so that the surface $z = V(x, y)$, near the origin, has the general shape of a paraboloid with vertex at the origin. The intersections of this graph with the horizontal plane $z = k$, that is, the *level sets* of V,

$$V^{-1}(k) \equiv \{(x, y) \in \mathbf{R}^2 : V(x, y) = k\},$$

are closed curves for small $k > 0$. The projection of these level sets onto the x-y plane results in concentric ovals encircling the origin. See Figure 5.23.

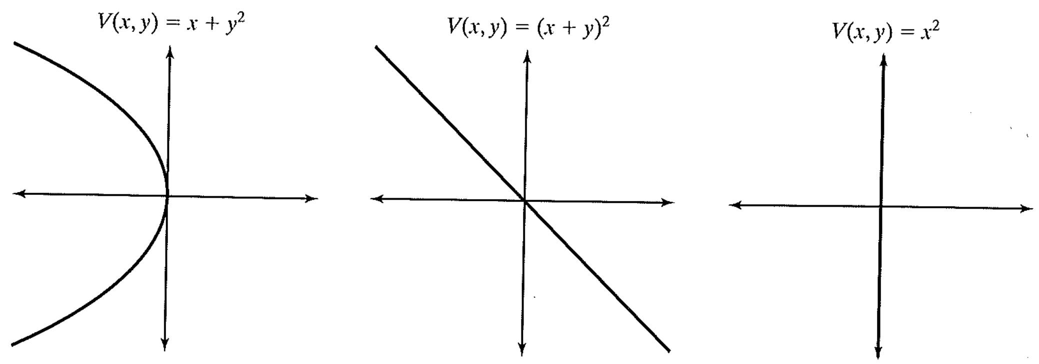
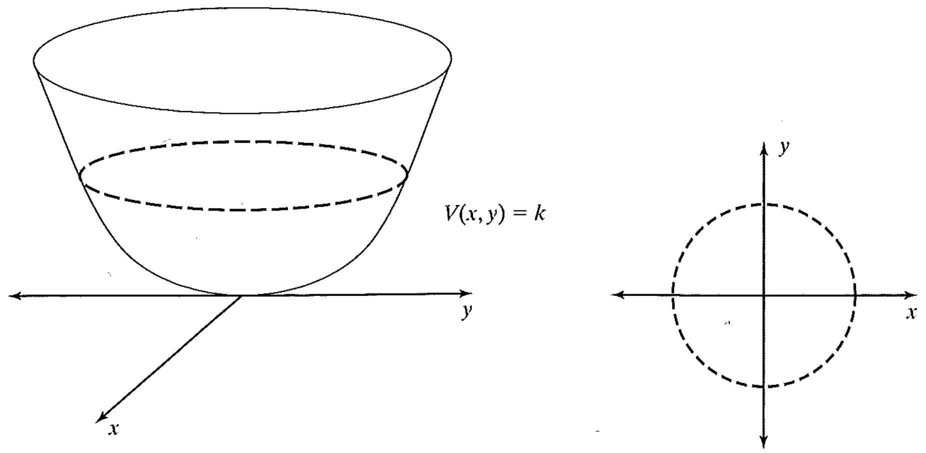


Figure 5.22 The set in the x-y plane (bold curves) such that $V(x, y) = 0$.

level sets of
$(x, y) =$



It is important to know how solutions of the two-dimensional autonomous system cross the level sets of a positive definite function V. Let $(x(t), y(t))$ be a solution of the differential system. Then

$$\frac{dV(x(t), y(t))}{dt} = \frac{\partial V}{\partial x}\frac{dx}{dt} + \frac{\partial V}{\partial y}\frac{dy}{dt}.$$

The preceding expression is the inner product of the vector (f, g) with the gradient vector,

$$\frac{dV(x, y)}{dt} = (f(x, y), g(x, y)) \cdot \nabla V(x, y) = \|(f(x, y), g(x,y))\| \, \|\nabla V(x, y)\| \cos\theta,$$

where θ is the angle between (f, g) and the gradient of V, and $\|(a, b)\|$ means the Euclidean norm, $\|(a, b)\| = \sqrt{a^2 + b^2}$. The gradient vector is the outward normal vector to the level curve of V at (x, y). Thus, if $dV(x, y)/dt < 0$, then the angle between (f, g) and ∇V at (x, y) is obtuse, which implies that the orbit through (x, y) is crossing the level curve from the outside to the inside. Similarly, if $dV(x, y)/dt = 0$, then the orbit is tangent to the level curve; if $dV(x, y)/dt > 0$, the orbit is crossing the level curve from the inside to the outside. See Figure 5.24.

The definition of a Liapunov function is given next. Then Liapunov's stability theorem is stated and verified. Although the definitions and theorem are stated for the equilibrium at the origin, remember that the results can be applied to any equilibrium.

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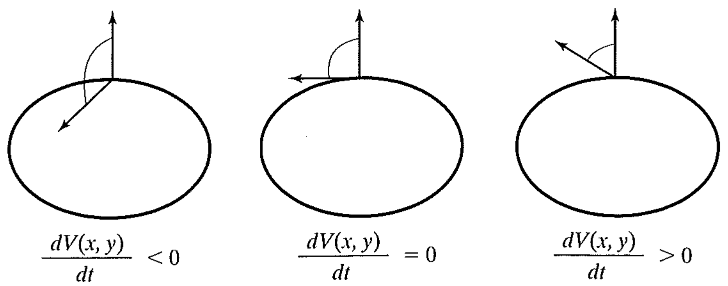

Definition 5.11. A positive definite function V in an open neighborhood of the origin is said to be a *Liapunov function* for the autonomous differential system, $dx/dt = f(x, y), dy/dt = g(x, y)$, if $dV(x, y)/dt \le 0$ for all $(x, y) \in U - \{(0, 0)\}$. If $dV(x, y)/dt < 0$ for all $(x, y) \in U - \{(0, 0)\}$, the function V is called a *strict Liapunov function*.

Theorem 5.14 **(Liapunov's Stability Theorem).** *Let $(0, 0)$ be an equilibrium of the autonomous system (5.22) and let V be a positive definite C^1 function in a neighborhood U of the origin.*

(i) If $dV(x, y)/dt \le 0$ for $(x, y) \in U - \{(0, 0)\}$, then $(0, 0)$ is stable.
(ii) If $dV(x, y)/dt < 0$ for $(x, y) \in U - \{(0, 0)\}$, then $(0, 0)$ is asymptotically stable.
(iii) If $dV(x, y)/dt > 0$ for $(x, y) \in U - \{(0, 0)\}$, then $(0, 0)$ is unstable.

In Case (i) the function V is a *Liapunov function* and in Case (ii) V is a *strict Liapunov function.*

Proof Cases (i) and (ii) are verified.

Case (i) Let $\epsilon > 0$ be sufficiently small so that the neighborhood of the origin consisting of the points $\|(x, y)\| \le \epsilon$ is contained in U ($\|\cdot\|$ denotes the Euclidean norm). Let m be the minimum value of V on the boundary of the neighborhood, $\|(x, y)\| = \epsilon$. Since V is positive definite and the set $\|(x, y)\| = \epsilon$ is closed and bounded, it follows that $m > 0$. Now, choose a $\delta > 0$ with $0 < \delta \le \epsilon$ such that $V(x, y) < m$ for $\|(x, y)\| \le \delta$. Such a δ always exists because V is continuous with $V(0, 0) = 0$. If $\|(x_0, y_0)\| \le \delta$, then the solution with initial conditions (x_0, y_0) satisfies $\|(x, y)\| \le \epsilon$ for $t \ge 0$ since $dV/dt \le 0$ implies that $V(x(t), y(t)) \le V(x_0, y_0) < m$ for $t \ge 0$. The origin is stable.

Case (ii) The function $V(x(t), y(t))$ decreases along solutions that lie in U. Thus, as $t \to \infty$, $V(x(t), y(t))$ approaches a limit. Suppose $V \to l > 0$. Then it follows from the uniform continuity of $dV(x(t), y(t))/dt$ (solutions are bounded and f and g are C^1) that $dV(x(t), y(t))/dt \to 0$ in an annular region excluding the origin. This is impossible, since $-dV/dt$ is positive definite, $dV/dt = 0$ only at the origin, and $(x(t), y(t))$ does not tend to the origin when $V \to l$. It follows that $V(x(t), y(t))$ approaches 0, which implies $(x(t), y(t))$ approaches $(0, 0)$. The origin is asymptotically stable. □

The difficulty in verifying stability using Liapunov's direct method is finding a suitable Liapunov function V.

Example 5.27 Consider the logistic differential equation,

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right),$$

where $r, K > 0$. There are two equilibria $\bar{x} = 0, K$. We know from previous analyses that K is globally asymptotically stable for positive initial conditions. Let $U = (0, \infty) = \mathbf{R}_+$, the positive x axis. A strict Liapunov function is given by

$$V(x) = (x - K)^2.$$

Since

$$\frac{dV(x)}{dt} = 2(x - K)\frac{dx}{dt} = 2(x - K)rx\left(1 - \frac{x}{K}\right) = -2rx\frac{(x - K)^2}{K}.$$

The function V is a $C^1(U)$ function that is positive except at $x = K$, $V(K) = 0$. Also, $-dV/dt$ is positive in U except at $x = K$, $dV(K)/dt = 0$. Thus, according to part (ii) of Liapunov's Stability Theorem, the equilibrium $x = K$ is asymptotically stable for all initial values in U. ■

xample 5.28 Consider the Lotka-Volterra predator-prey system,

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

$$\frac{dy}{dt} = y(-b + x), \quad a, b > 0$$

The positive equilibrium is $(\bar{x}, \bar{y}) = (b, a)$. The equilibrium is stable but not asymptotically stable. A Liapunov function for this system has the form

$$V(x, y) = \left(x - b - b\ln\left(\frac{x}{b}\right)\right) + \left(y - a - a\ln\left(\frac{y}{a}\right)\right).$$

First note that $V(x, y)$ is continuous and differentiable for $x, y > 0$ and $V(b, a) = 0$. Next, we show that $V(x, y) > 0$ for $x, y > 0$ and $x \neq b, y \neq a$. Note that the partial derivatives are $V_x = 1 - b/x$, $V_y = 1 - a/y$, $V_{xx} = b/x^2$, $V_{yy} = a/y^2$, and $V_{xy} = 0$. Thus, a critical point of V occurs when $V_x = 0 = V_y$ at $x = b$ and $y = a$. This critical point is a local minimum because we can apply the following test: $V_{xx}V_{yy} - V_{xy}^2 > 0$ and $V_{xx} > 0$. At the local minimum $V(b, a) = 0$ and (b, a) is the only local minimum for $x, y > 0$ so it is a global minimum for $x, y > 0$. Thus, $V(x, y) > 0$ for $x, y > 0$ and $x \neq b, y \neq a$ (positive definite in $\mathbf{R}^2_+$). Next, we calculate the derivative of V along solutions:

$$\begin{aligned}\frac{dV}{dt} &= V_x\frac{dx}{dt} + V_y\frac{dy}{dt}\\ &= \left(1 - \frac{b}{x}\right)x(a - y) + \left(1 - \frac{a}{y}\right)y(-b + x)\\ &= (x - b)(a - y) + (y - a)(x - b) = 0.\end{aligned}$$

Thus, according to part (i) of Liapunov's stability theorem, the equilibrium (b, a) is stable in the region $\mathbf{R}^2_+ = \{(x, y) | x > 0, y > 0\}$; that is, globally stable in $\mathbf{R}^2_+$. ■

Example 5.29 Goh (1977) has shown that in many Lotka-Volterra systems with a unique positive equilibrium given by $(\bar{x}_1, \ldots, \bar{x}_n)$, there exists a Liapunov function in $\mathbf{R}^n_+$ which has a form similar to the one given in the previous example. The Liapunov function has the form

$$V(x_1, \ldots, x_n) = \sum_{i=1}^{n} c_i\left[x_i - \bar{x}_i - \bar{x}_i\ln\left(\frac{x_i}{\bar{x}_i}\right)\right],$$

where the constants c_i are positive and are chosen dependent on the parameters of the particular system. ■

5.12 Persistence and Extinction Theory

We end this chapter by discussing the concept of persistence and extinction, an important concept for biological systems. Basically, persistence of a system means no state of the system approaches zero, that is, there can be no extinction of any of the populations that make up the biological system.

Definition 5.12. Given a system of differential equations, $dX/dt = F(X, t)$, $X(0) = X_0$, where $X(t) = (x_1(t), x_2(t), \ldots, x_n(t))^T$, the system is said to be *persistent* if for any positive initial conditions, $X_0 > 0$, the solution $X(t)$, satisfies

$$\liminf_{t\to\infty} x_i(t) > 0$$

for $i = 1, 2, \ldots, n$.

There are other definitions of persistence that either weaken or strengthen the previous definition. For example, the system is said to be *weakly persistent* if

$$\limsup_{t\to\infty} x_i(t) > 0$$

for $i = 1, 2, \ldots, n$; *uniformly persistent* if there exists $\delta > 0$ such that

$$\liminf_{t\to\infty} x_i(t) > \delta$$

for $i = 1, 2, \ldots, n$; *permanent* if there exists a time $T > 0$ and a compact set K in the interior of the positive cone, $\mathbf{R}^n_+ = \{(x_1, x_2, \ldots, x_n) \in \mathbf{R}^n | x_i > 0, i = 1, 2, \ldots, n\}$ such that $X(t) \in K$ for $t > T$. (Solutions enter the compact set K and remain in K.) Persistence or extinction of a subset of the set $\{x_i\}_{i=1}^n$ can also be defined (e.g., some populations survive and some do not).

Weak persistence and persistence are generally not very good indications of population survival because solutions may be initial condition dependent. For example, in the case of persistence, there could be a set of initial conditions $\{X_0^k\}_{k=1}^\infty$ such that the corresponding solution $X^k(t) = (x_i^k(t))$ satisfies

$$\epsilon_k > \liminf_{t\to\infty} x_i^k(t) > 0,$$

where $\epsilon_k \to 0$ as $k \to \infty$ for some i. Even uniform persistence and permanence may not be very good measures of survival since solutions may approach very close to the extinction boundaries if δ is small or the compact set K is close to the extinction boundaries. Another more reasonable type of persistence criterion is referred to as *practical persistence*. Practical persistence requires that the bounds on the solutions be specified a priori (dependent on population data). Given $L_i > 0$ and $M_i > 0$, solutions $x_i(t)$ exhibit *practical persistence* if $0 < L_i < \liminf_{t\to\infty} x_i(t) \leq \limsup_{t\to\infty} x_i(t) \leq M_i$, $i = 1, 2, \ldots, n$ (Cantrell and Cosner, 1996; Cao and Gard, 1997).

In general, practical persistence implies permanence. Persistence implies weak persistence. If solutions are uniformly bounded, $\limsup_{t\to\infty} x_i(t) < M$, $i = 1, \ldots, n$, then uniform persistence and permanence are equivalent. If a system has a globally stable equilibrium in $\mathbf{R}^n_+$, then it is permanent. The converse of this statement is not true. If a system is permanent, it may not have a globally stable equilibrium. Further discussion and examples of systems that are permanent or persistent may be found in Hofbauer and Sigmund (1988, 1998) or Freedman and Moson (1990).