

13

Stability of Predator–Prey Systems: Analytical Methods (Advanced)

In this chapter we develop general tools for the mathematical evaluation of the stability of equilibria in coupled population growth equations. While we develop these methods for two-species models, these techniques can be generalized to several interacting species including additional trophic levels (Chapters 14 and 15) or even additional age or stage groups. You might think that the graphical analysis of Chapter 12 is adequate for this task and that more sophisticated tools aren't needed. However, the graphical analysis works only when you can visualize the system in two or at most three dimensions, so models with more interacting species still need additional attention. Also, even in two dimensions, it is sometimes difficult to predict when an equilibrium point will be stable or unstable, based on graphical analysis alone. For example, take another look at Box 12.2. In Figure 12.34, with predator interference, the feasible equilibrium point can sometimes be stable and sometimes unstable even when it lies to the left of the peak of the prey zero-isocline. Without simulation we would not be able to predict which points are stable and which are not. The analytical techniques that we present in this Chapter can provide this ability.

THE CLASSICAL LOTKA–VOLTERRA PREDATOR–PREY EQUATIONS

We start with the simplest possible predator–prey system, known as the **classical Lotka–Volterra predator-prey equations**:

$$\frac{dV}{dt} = V[b - aP] = f_1(V, P) \quad (13.1)$$

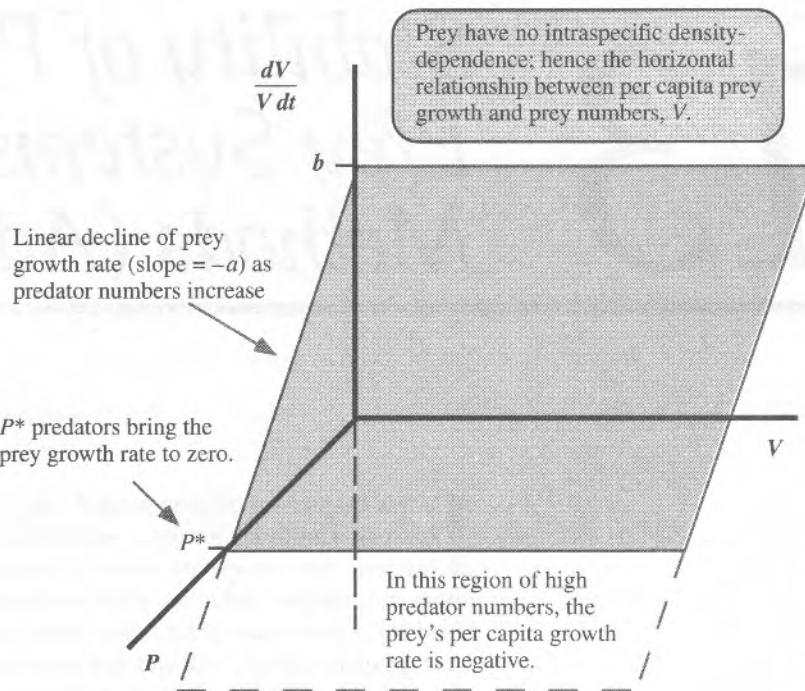
and

$$\frac{dP}{dt} = P[-d + kaV] = f_2(V, P). \quad (13.2)$$

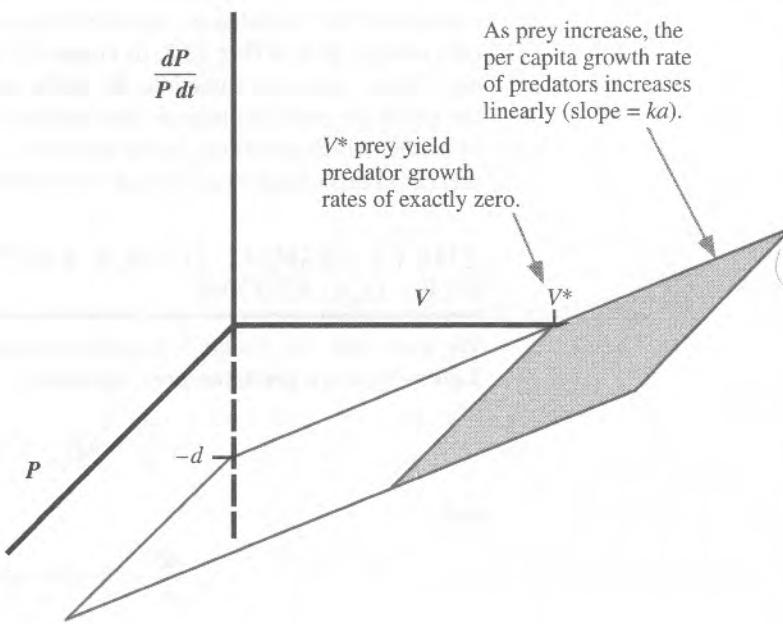
In the absence of a predator, the prey population, V , grows exponentially with an intrinsic growth rate, b . The prey death rate increases linearly with the number of predators. Predators have a type 1 functional response, aV , with a capture rate parameter per prey per predator of a . Prey captured are converted into new predator offspring at a rate determined by the proportionality constant, k . For example, if a predator must consume 10 prey before it has enough energy to produce one predator offspring, then $k = 1/10$ or 0.1. In addition, predators have a constant per capita death rate, d . Thus predator numbers decline exponentially (with exponent $-d$) in the absence of prey for them to eat. The per capita growth rate of prey and predators is plotted as a function of both prey and predator numbers in Figures 13.1 and 13.2.

Figure 13.1

The relationship between per capita growth of prey, $dV/V dt$, prey numbers, V , and predator numbers, P , for the classical Lotka–Volterra predator–prey model.

**Figure 13.2**

Predator per capita growth, $dP/P dt$ as a function of prey numbers, V , and predator numbers, P .



Superimposing these two planes for the per capita growth of each species gives the situation in Figure 13.3.

The zero-isoclines for prey and predators can be found algebraically by setting the growth rates of the two populations, as given by eq. (13.1) and (13.2), to zero:

$$V[b - aP] = 0 \quad (13.3)$$

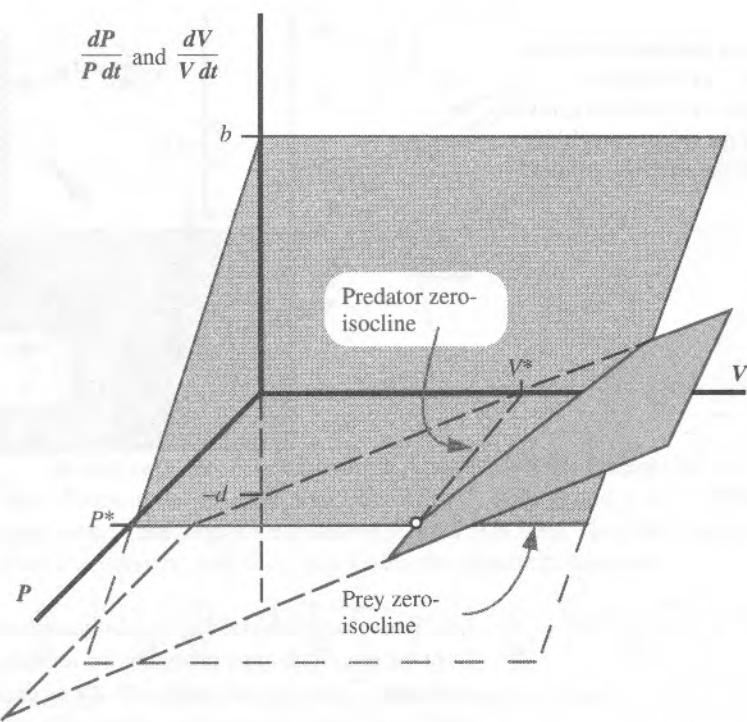
and

$$P[-d + kaV] = 0. \quad (13.4)$$

There are only two ways that each of these equations may become zero. Either the term outside the brackets equals zero (i.e., $V = 0$ or $P = 0$) or the terms inside the brackets,

Figure 13.3

The combination of Figures 13.1 and 13.2. The interior equilibrium point where the two growth planes cross on the plane of zero-zero growth is shown as a white dot.



which are the per capita growth rates, equal zero. The latter condition for both species defines the interior equilibrium point. By setting the prey per capita growth equation, Eq. (13.3), to zero, we get

$$b - aP^* = 0,$$

which yields a solution for the predator's equilibrium density as

$$P^* = \frac{b}{a}.$$

This is also, by definition, the equation for the zero-isocline of the prey from Eq. (13.3). It is a horizontal line placed on the P axis (y axis) at $P = b/a$. If predators exceed this level, the prey population declines; if predators are below this level, the prey population increases.

By setting the predator growth equation to zero Eq. 13.4, we find that the prey's equilibrium density is

$$V^* = \frac{d}{ka}.$$

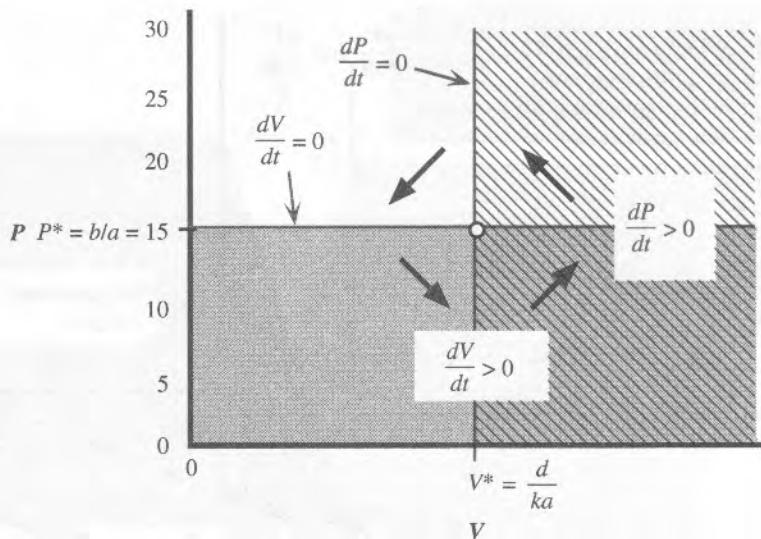
This also defines the equation for the predator zero-isocline from Eq. (13.4). It is a vertical line placed on the V axis (x axis) at $V = d/ka$. If the prey population exceeds this level, then the predator population increases; if prey are below this level, then the predator population must decline.

Phase space is the bottom P - V plane in Figure 13.3 flipped on its side. Figure 13.4 shows the zero-isoclines for the equations derived.

Exercise: Look at the point on the y axis in Figure 13.4, where $P^* = 15$ and $V = 0$. Why isn't this a boundary equilibrium point?

Figure 13.4

The predator and prey zero-isoclines for the classical Lotka–Volterra equations. Regions of positive growth rate, based on Eqs. (13.1) and (13.2), are shaded. The equilibrium point is (V^*, P^*) .



To evaluate the stability of an equilibrium point we need to nudge the system away from the equilibrium by changing the abundances of predator and/or prey by some small deviation. Then we determine how these deviations change over time (see Figures 5.42 and 5.43). For a two-species system with coupled growth equations, as for Eqs. (13.1) and (13.2), we may write the deviations of the two state variables, V and P , from their equilibrium values, V^* and P^* , as

$$v = V - V^* \quad (13.5a)$$

and

$$p = P - P^*. \quad (13.5b)$$

Substituting Eqs. (13.5a) and (13.5b) into Eqs. (13.1) and (13.2) and noting that $dv/dt = dV/dt$ and $dp/dt = dP/dt$ (because V^* and P^* are constants), we obtain

$$\frac{dv}{dt} = f_1(v + V^*, p + P^*) \quad \text{and} \quad \frac{dp}{dt} = f_2(v + V^*, p + P^*).$$

Here the f notation is shorthand for the actual equations, Eqs. (13.1) and (13.2); it also reminds us that while we are specifically analyzing Eqs. (13.1) and (13.2), the method being applied is general for any functions f_1 and f_2 . To reach the linearized dynamics of the system around this equilibrium point, we perform a Taylor's expansion on f_1 and f_2 in the neighborhood of an equilibrium point. Recall from Chapter 5 that a continuous function $F(x)$ evaluated at an equilibrium point may be decomposed into a polynomial using a Taylor's expansion:

$$F(x) \approx F(x^*) + \frac{F'(x^*)(x - x^*)}{1!} + \frac{F''(x^*)(x - x^*)^2}{2!} + \frac{F'''(x^*)(x - x^*)^3}{3!} + \dots$$

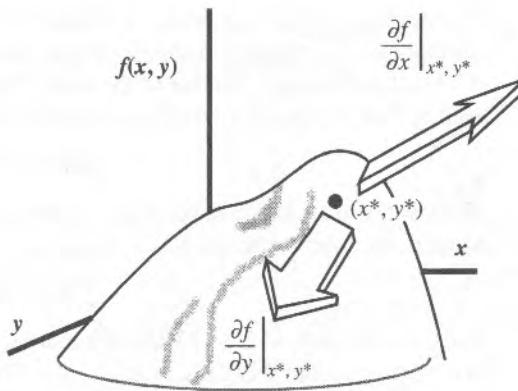
For a function F of two variables, x and y , a similar expansion may be performed. Now, however, we need to evaluate the partial derivatives of $F(x, y)$ with respect to x and then again with respect to y . A graphical depiction of these partial derivatives is the slope of $F(x, y)$ in the two directions x and y as depicted in Figure 13.5.

The Taylor's expansion of $F(x, y)$ at point (x^*, y^*) is

$$F(x, y) \approx F(x^*, y^*) + \frac{1}{1!} \left[(x - x^*) \frac{\partial F(x^*, y^*)}{\partial x} + (y - y^*) \frac{\partial F(x^*, y^*)}{\partial y} \right] + \frac{1}{2!} \left[\left((x - x^*) \frac{\partial}{\partial x} + (y - y^*) \frac{\partial}{\partial y} \right)^2 F(x^*, y^*) \right] + \dots \quad (13.6)$$

Figure 13.5

A graphical representation of the partial derivatives of a function, f , of two variables, x and y . The partial derivative of f with respect to x is positive, but the partial derivative of f with respect to y is negative.



In this case the F functions are f_1 and f_2 , which themselves are derivatives over time. Since at the equilibrium point (V^*, P^*) both f_1 and $f_2 = 0$, by definition the constant term in the Taylor's expansion, $F(x^*, y^*)$ is zero. Thus the change in the deviations from equilibrium over time as a first-order approximation are

$$\frac{dv}{dt} = \frac{\partial f_1(V^*, P^*)}{\partial V} v + \frac{\partial f_1(V^*, P^*)}{\partial P} p \quad \text{and} \quad \frac{dp}{dt} = \frac{\partial f_2(V^*, P^*)}{\partial V} v + \frac{\partial f_2(V^*, P^*)}{\partial P} p,$$

which can be expressed more compactly in matrix form as

$$\begin{bmatrix} \frac{dv}{dt} \\ \frac{dp}{dt} \end{bmatrix} = \begin{bmatrix} \frac{\partial f_1}{\partial V} & \frac{\partial f_1}{\partial P} \\ \frac{\partial f_2}{\partial V} & \frac{\partial f_2}{\partial P} \end{bmatrix}_{V^*, P^*} \begin{bmatrix} v \\ p \end{bmatrix}. \quad (13.7)$$

As usual, the partial derivative $\partial f_1/\partial V$ means to take the derivative of f_1 with respect to the variable V , holding fixed the value of the other variable, P . These partial derivatives are then evaluated at the equilibrium point V^*, P^* . To simplify notation still more, we write Eq. (13.7), using boldface type to signify matrices and vectors:

$$\mathbf{n} = \begin{bmatrix} v \\ p \end{bmatrix} \quad (13.8)$$

and

$$\frac{d\mathbf{n}}{dt} = \mathbf{J}\mathbf{n}. \quad (13.9)$$

We now have two coupled first-order (i.e., linear) differential equations. The matrix of partial derivatives, \mathbf{J} , in Eq. (13.9) is called the **Jacobian matrix**. It describes the dynamic forces acting around the equilibrium point. The local stability of the equilibrium point can be determined very simply from the Jacobian matrix. Recall that, for single species exponential growth, we also had a first-order differential equation,

$$\frac{dN}{dt} = rN, \quad (13.10)$$

whose solution is

$$N(t) = N_0 e^{rt}.$$

The resemblance between the scalar differential equation, Eq. (13.10), and the matrix differential equation, Eq. (13.9), is so striking that without the boldface type we could not distinguish them. This example suggests that the solution to the matrix differential equation, Eq. (13.9), might have a form similar to the solution for exponential growth, or

$$\mathbf{n}(t) = \mathbf{n}_0 e^{\mathbf{J}t}. \quad (13.11)$$

But what does it mean to raise e to the power of a matrix? Perhaps there is some number that can be extracted from the matrix that makes a sensible expression out of Eq. (13.11). Let's explore this line of thought. If there is such a number, let's call it λ , it will need to have the property that for some vector $\tilde{\mathbf{n}}$,

$$\mathbf{n}(t) = e^{\lambda t} \tilde{\mathbf{n}}. \quad (13.12)$$

Moreover, if Eq. (13.12) is indeed a solution to Eq. (13.9) for some particular values of λ and $\tilde{\mathbf{n}}$, then we could write

$$\mathbf{J} \tilde{\mathbf{n}} = \lambda \tilde{\mathbf{n}}. \quad (13.13)$$

The left-hand side of Eq. (13.13) is a matrix, \mathbf{J} , times a (2×1) vector; for the dimension of the product this yields $(2 \times 2)(2 \times 1) = (2 \times 1)$. The right-hand side is a scalar times a (2×1) vector and, of course, this also yields a (2×1) vector, so this equation is dimensionally consistent. If you return to Chapter 3, you will see that Eq. (13.13) is identical, except for notation, to Eq. (3.21), which we used to define the eigenvalues, λ , and the eigenvectors, $\tilde{\mathbf{n}}$, of a matrix. Equation (13.13) makes the proposition that the matrix multiplication, $\mathbf{J} \tilde{\mathbf{n}}$, can be simplified to a multiplication of a scalar times a vector, $\lambda \tilde{\mathbf{n}}$. So if a number λ and vector $\tilde{\mathbf{n}}$ exist that have the property specified by Eq. (13.13), we could use λ (a scalar), in place of \mathbf{J} (a matrix) to follow the dynamics of the system via Eq. (13.12). As we demonstrated in Chapter 3, an $n \times n$ matrix will have n eigenvalues and n eigenvectors (although some may be duplicates of others).

In Chapter 3 we used eigenvalues to examine geometric population growth, whereas here we are looking at growth only in a small region around the equilibrium point. With the Jacobian matrix, we have rescaled the equilibrium point to be zero.

The simplest case is that the eigenvalues are real numbers. If the sign of each eigenvalue is negative, then $\mathbf{n}(t) = e^{\lambda t} \tilde{\mathbf{n}}$ will grow smaller and smaller, approaching zero (the equilibrium point) as time goes on. In other words, the deviations \mathbf{p} and \mathbf{v} grow smaller over time. Since perturbations are reduced over time, we can infer that the equilibrium point is locally stable. **Thus there is a connection between the sign of the eigenvalues of the Jacobian matrix and the local stability of the equilibrium point.** Since eigenvalues can be complex numbers, things can become a bit more complicated, but not much. A complex number $a + bi$ has real (a) and imaginary (bi), parts where i equals the square root of -1 . Consider a general solution in the vicinity of the equilibrium point, like Eq. (13.12):

$$\mathbf{n}(t) = g_1 \tilde{\mathbf{n}}_1 e^{\lambda_1 t} + g_2 \tilde{\mathbf{n}}_2 e^{\lambda_2 t} + g_3 \tilde{\mathbf{n}}_3 e^{\lambda_3 t} \dots + g_n \tilde{\mathbf{n}}_n e^{\lambda_n t},$$

when the g 's are scalars determined by the initial conditions and the eigenvectors are $\tilde{\mathbf{n}}_i$. If the eigenvalues are complex, $\lambda = a + bi$, then each e term can also be expressed as

$$e^{(a+bi)t} = e^{at} e^{bit}.$$

This last expression is the product of two parts—one real and the other imaginary. The number e raised to an imaginary number can also be expressed as

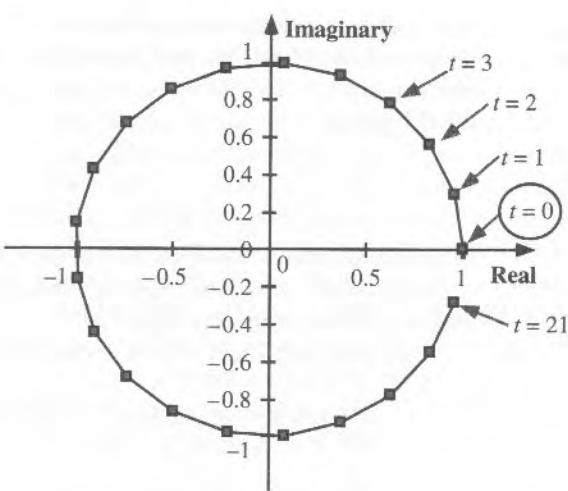
$$e^{bit} = \cos(bt) + i \sin(bt).$$

The graph of this last function for $t = 0$ to 21 is shown in Figure 13.6.

Note in Figure 13.6 that the imaginary exponential term e^{bit} neither winds in nor out, but simply oscillates on a circle; thus this term represents an **undamped oscillation** of unit amplitude ($r = 1$), regardless of the particular value of b , which only determines the frequency of the oscillation. In contrast the real exponential part, e^{at} , which multiplies the imaginary part, can exhibit a variety of behaviors, depending on whether a is positive, negative, or zero. **Local stability requires that the real part of each eigenvalue of \mathbf{J} be strictly negative** so that perturbations decline exponentially to zero with time. In Box 13.1 we explore the consequences of the sign of the real part and the presence of an imaginary part in solutions.

Figure 13.6

The graph of $e^{bit} = \cos(bt) + i \sin(bt)$ in the imaginary–real plane with a choice of $b = 0.3$ and time t varying from 0 to 21. Line segments connect successive points in the time series. Note that all the points fall on a circle of radius 1. The value of b represents the frequency of oscillation around the circle.



Box 13.1

Figure 13.7 presents examples of eigenvalues (red dots on the right) for a coupled pair of differential equations in the real–imaginary plane. Both eigenvalues of the Jacobian matrix must fall in the shaded region (real part < 0) for local stability. Samples trajectories for each case are shown on the left.

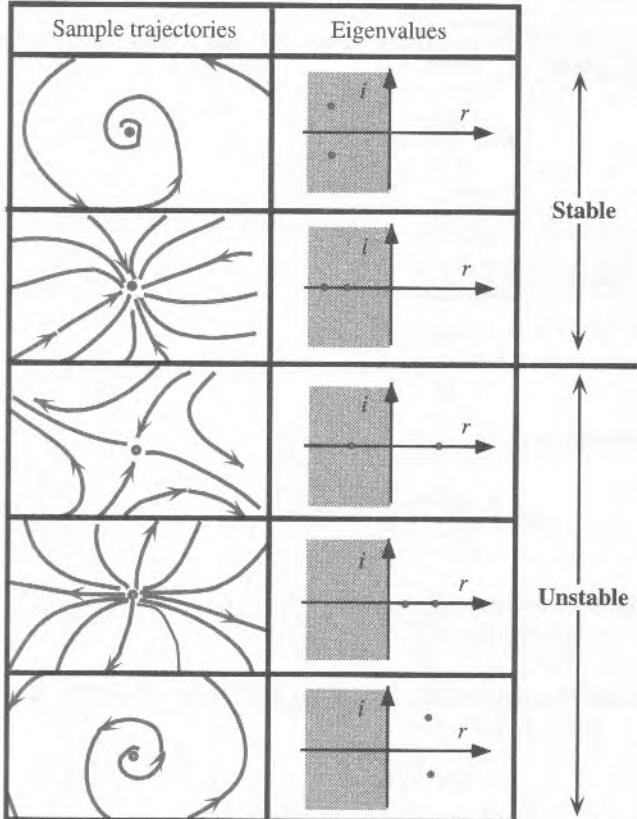


Figure 13.7
Eigenvalues and stability.

Figure 13.8 a topographical depiction, using a gravity metaphor for stability in two dimensions. The direction and steepness of the slope of the landscape are determined by the sign and magnitude of the real part of the two eigenvalues. In the case of neutral stability, the landscape is completely flat and the real part of both eigenvalues is zero.

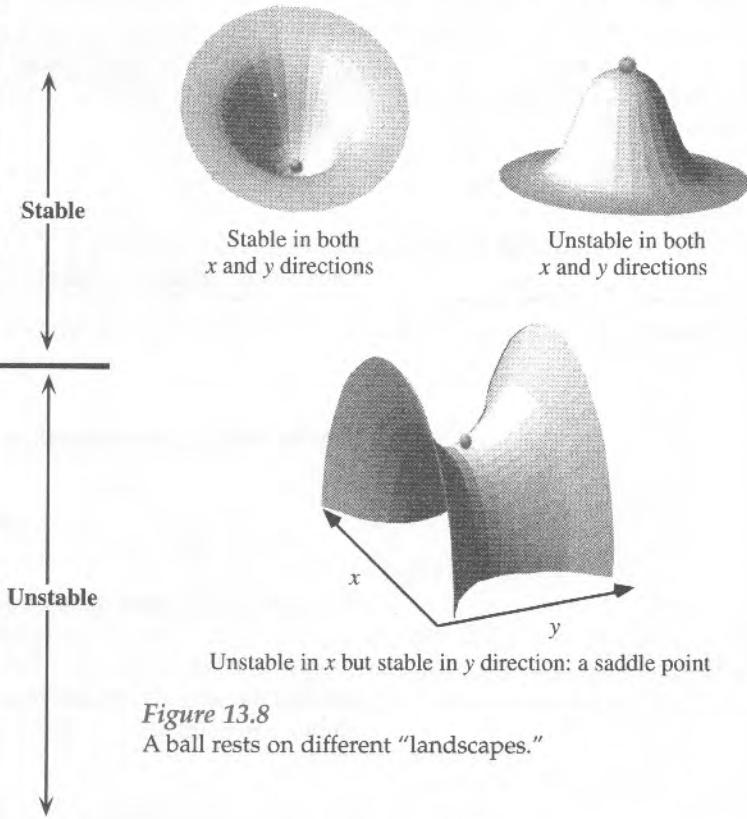


Figure 13.8
A ball rests on different “landscapes.”

Let's now return to the Jacobian matrix, \mathbf{J} , which contains the partial derivatives of the growth equations. We want to evaluate the forces of population growth at a particular equilibrium. The partial of the prey population growth, f_1 , with respect to V , holding P fixed, is

$$\frac{\partial f_1}{\partial V} = b - aP.$$

In words: the rate at which the rate of increase of the prey population, f_1 , changes with changes in their own numbers, V , equals the prey per capita birth rate, b , minus their per capita death rate from predation, $-aP$.

The other partial derivatives in the Jacobian matrix are

$$\frac{\partial f_1}{\partial P} = -aV \quad (\text{the effect of predators on prey growth rate});$$

$$\frac{\partial f_2}{\partial V} = kaP \quad (\text{the effect of prey on predator's growth rate});$$

$$\frac{\partial f_2}{\partial P} = -d + kaV \quad (\text{the effect of predators on their own growth rate}).$$

In general, these partial derivatives are functions of V and P , so the changes in their magnitudes depend on the particular values of V and P at which the partial derivatives are evaluated. To test the local stability of an equilibrium point, we evaluate these partial derivatives (i.e., determine their magnitudes) at that equilibrium point. We begin by evaluating the stability of the interior equilibrium point.

The Jacobian matrix containing the terms that we just determined is

$$\mathbf{J} = \begin{bmatrix} b - aP & -aV \\ kaP & -d + akV \end{bmatrix}. \quad (13.14)$$

Now we substitute into Eq. (13.14) the particular values of P and V at the interior equilibrium point, $V^* = d/ka$ and $P^* = b/a$,

$$\mathbf{J} = \begin{bmatrix} b - \frac{ab}{a} & -\frac{ad}{ka} \\ \frac{kab}{a} & -d + \frac{akd}{ka} \end{bmatrix}.$$

After canceling terms, we have

$$\mathbf{J} = \begin{bmatrix} 0 & -\frac{d}{k} \\ kb & 0 \end{bmatrix}.$$

Now we solve for the eigenvalues of \mathbf{J} :

$$\det \begin{bmatrix} 0 - \lambda & -\frac{d}{k} \\ kb & 0 - \lambda \end{bmatrix} = 0.$$

This leads to the characteristic equation

$$\lambda^2 + db = 0 \quad \text{or} \quad \lambda^2 = -bd,$$

and thus the solutions for the two eigenvalues describing the forces around the interior equilibrium point are

$$\lambda = 0 \pm i\sqrt{bd}.$$

The eigenvalues of \mathbf{J} when evaluated at the interior equilibrium point are purely imaginary numbers—the real parts are zero. This explains why the forces on (V^*, P^*) are

neutral and why undamped (or unmagnified) oscillations occur. (Recall the connection between imaginary numbers as exponents of e and sin and cos functions developed in Chapter 3.)

This neutral stability is somewhat artifactual for two reasons. First, it rests on differential equations. Converting this predator-prey model to a discrete time analog inevitably adds a time lag as we showed in Chapter 5. Even for the smallest conceivable finite birth and death rate terms, b and d , the equilibrium point now becomes unstable, not simply neutrally stable. Second, as we indicated in Chapter 12, the incorporation of more realistic assumptions about the growth and interaction of predator and prey creates models wherein the equilibrium point becomes either stable or unstable. We pursue some more complicated predator-prey systems a bit later.

Next, let's evaluate the stability of one of the boundary equilibrium points, namely, $(0, 0)$. We return to the general form of the Jacobian matrix of Eq. (13.14), but this time we substitute the values $V^* = 0$ and $P^* = 0$ to get

$$\mathbf{J} = \begin{bmatrix} b & 0 \\ 0 & -d \end{bmatrix}.$$

The eigenvalues of this diagonal matrix are simply the diagonal elements themselves. Since

$$\det \begin{bmatrix} b - \lambda & 0 \\ 0 & -d - \lambda \end{bmatrix} = 0.$$

yields the characteristic equation

$$(b - \lambda)(-d - \lambda) = 0,$$

therefore $\lambda_1 = b$ and $\lambda_2 = -d$. These eigenvalues are pure real numbers with no imaginary parts. Since the eigenvalue associated with prey growth is positive, the $(0, 0)$ equilibrium is unstable (thus verifying our graphical analysis). The other eigenvalue is negative, so the stability picture here is that of a saddle point. The absence of imaginary parts means that in the vicinity of $(0, 0)$ the growth of the prey is exponential (not oscillatory), trending upward, while that of the predator is exponential, trending downward.

STABILITY EVALUATION APPLIED TO MORE REALISTIC MODELS

We can now apply the technique that we just developed to a slightly more elaborate predator-prey system:

$$\frac{dV}{dt} = f_1(V, P) = \frac{rV}{K}[K - V] - aVP \quad (13.15)$$

and

$$\frac{dP}{dt} = f_2(V, P) = P[-d + kaV]. \quad (13.16)$$

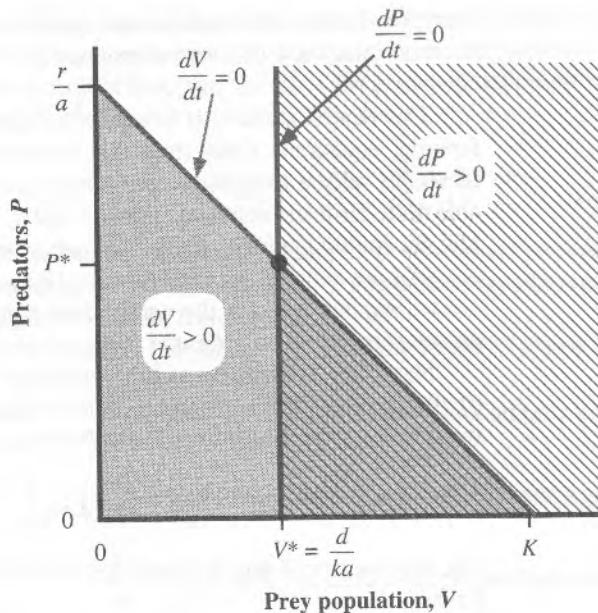
This predator-prey system is modified from the one that we just explored in that the prey now grow logistically, rather than exponentially, in the absence of any predators. The predator zero-isocline is found by setting the term in brackets in Eq. (13.16) to zero, which yields

$$V^* = \frac{d}{ka}, \quad (13.17)$$

and thus the interior equilibrium point for the prey is $V^* = d/ka$.

Figure 13.9

Predator and prey zero-isoclines based on Eqs. (13.17) and (13.18).



To determine the equilibrium number of predators, P^* , we first need to solve for the prey zero-isocline. Setting Eq. (13.15) to zero and solving gives

$$\frac{r(K - V^*)}{K} = aP^*.$$

Rearranging gives

$$P^* = \frac{r}{a} \left(1 - \frac{V^*}{K} \right). \quad (13.18)$$

Thus the prey zero-isocline is a line with a negative slope of $-r/(aK)$ and a y intercept of r/a , intersecting the horizontal prey axis at the prey K . The prey will reach K in the absence of any predators. Figure 13.9 displays the two zero-isoclines based on Eqs. (13.17) and (13.18).

The next step is to find an expression for the equilibrium abundance of predators, P^* . We substitute $V^* = d/ka$ from Eq. (13.17) into Eq. (13.18) and solve for P^* :

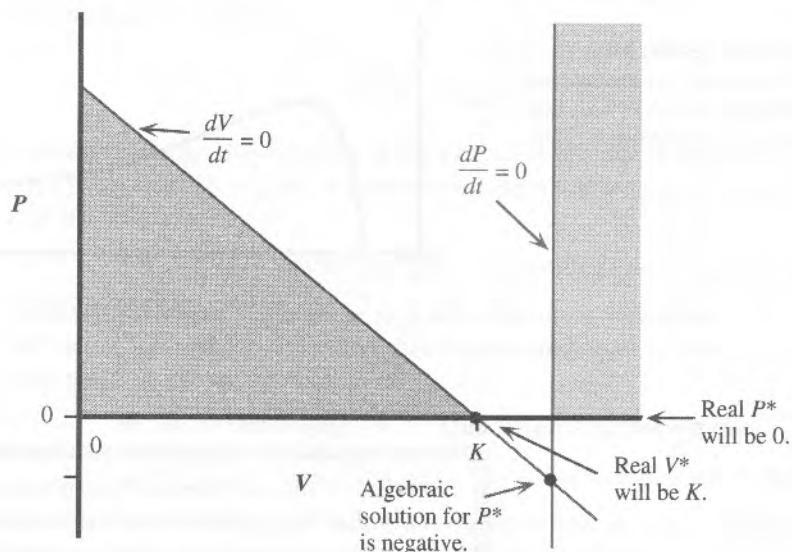
$$P^* = \frac{r}{a} \left(1 - \frac{d}{kaK} \right). \quad (13.19)$$

Before moving on to the rest of the stability analysis, it is useful to examine the graphical relationship between P^* , V^* , and some of the parameters of this model. Note, for example, that both zero-isoclines (Eqs. 13.17 and 13.18) contain the term for the capture rate, a . The equilibrium prey density, V^* , declines continuously as the capture rate, a , increases (Eq. 13.17), but the relationship between a and P^* is more complex in Eq. (13.19). Very high values of a will allow P^* to be negative, but clearly this is impossible, so we must discard any algebraic analysis based on these unfeasible values of P^* , as illustrated in Figure 13.10.

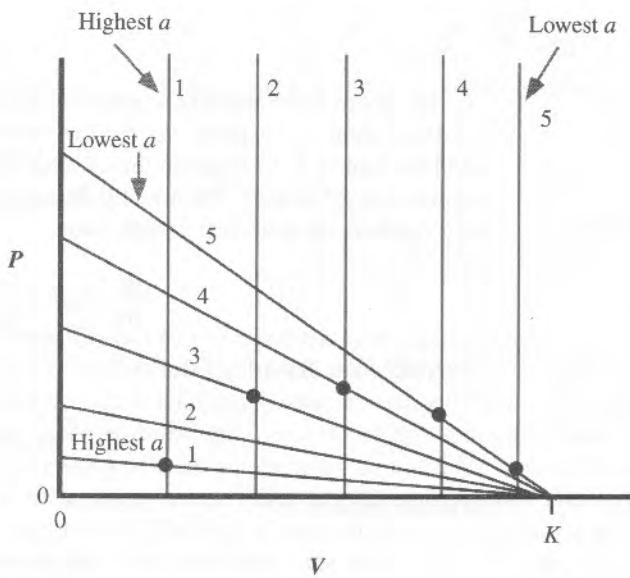
Equation (13.19) contains a term in a^{-2} , so this equation describes a humped relationship for P^* as a function of a . As the capture rate, a , increases from zero, P^* first increases from zero and later decreases as the capture rate increases still more. This effect is illustrated in Figure 13.11, which shows five different values of the capture rate, a , as it affects the position of the zero-isocline for both prey, V and predator, P .

Figure 13.10

An unfeasible equilibrium point in this case means that the predator will not be able to exist and that the prey goes to its carrying capacity, K .

**Figure 13.11**

The effect of increasing the capture rate, a , on the predator and prey zero-isoclines and thus the position of the predator–prey interior equilibrium point.

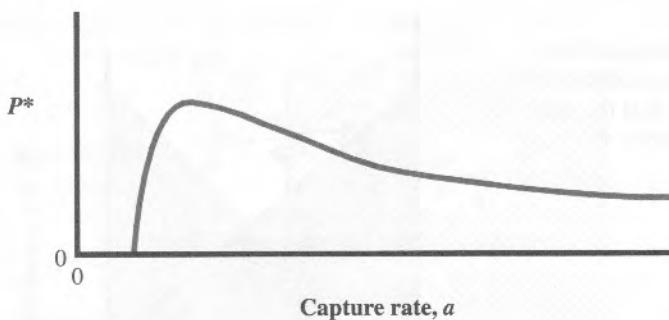


Note the equilibrium points (black dots) for this family of different prey and predator zero-isoclines. Here V^* continuously decreases as the capture rate, a , increases, but P^* rises and then falls. As predators become increasingly successful at capturing prey, their own densities (at equilibrium) ultimately decrease as they overexploit their prey population. This trend is shown in Figure 13.12, which is based on Figure 13.11 but shows the effect of continuously varying a .

This up-then-down feature of P^* is common in predator–prey interactions, but it is not ubiquitous (see the Problems at the end of this chapter).

Figure 13.12

A summary of the results from Figure 13.11, showing an example of the relationship between P^* and the capture rate, a , for equations (13.15) and (13.16).



Exercise: If the prey population contained genetic variation for the capture rate, a , such that the different zero-isoclines drawn in Figure 13.12 were associated with different genotypes, which genotype would be most favored by natural selection? How might this affect the ultimate population sizes of the prey and predator populations and their long term persistence?

We return to the stability analysis for the predator–prey system of Eqs. (13.15) and (13.16). Using our expressions for the interior equilibrium point, we may form the Jacobian matrix \mathbf{J} , to evaluate the stability of this equilibrium point. The partials are evaluated at V^* and P^* . We now fill in the elements of \mathbf{J} , beginning with the effect of prey numbers on their own growth rate:

$$\frac{\partial f_1}{\partial V} = rK - \frac{2rV}{K} - aP.$$

At equilibrium, from Eq. (13.15)

$$rK - \frac{rV^*}{K} - aP^* = 0,$$

so $\partial f_1 / \partial V$ reduces to

$$\frac{\partial f_1}{\partial V} = -\frac{rV^*}{K}.$$

Similarly, after solving for the other partial derivatives and evaluating each at (V^*, P^*) , we reach

$$\mathbf{J} = \begin{bmatrix} -\frac{rV^*}{K} & -aV^* \\ kaP^* & 0 \end{bmatrix}.$$

At this point we could substitute the algebraic expressions for V^* and P^* from Eqs. (13.17) and (13.19), but we save this step for later. Instead, we go ahead and evaluate the eigenvalues of \mathbf{J} , using

$$\det \begin{bmatrix} -\frac{rV^*}{K} - \lambda & -aV^* \\ kaP^* & 0 - \lambda \end{bmatrix} = 0.$$

The characteristic equation is

$$\lambda^2 + \left(\frac{rV^*}{K} \right) \lambda + a^2 k P^* V^* = 0. \quad (13.20)$$

Note that the sign of every term in Eq. (13.20) is positive as long as the equilibrium point is feasible. Thus, if we factor this quadratic into the product of two terms, it will look like this:

$$(\lambda_1 + \text{"something"}) (\lambda_2 + \text{"something else"}) = 0,$$

where we must have plus signs in each of the factors in parentheses. This immediately tells us that the *real parts* of both λ 's are negative and equal to "something" and "something else." Moreover,

$$\text{If } (\lambda_1 + \text{"something"}) = 0, \text{ then } \lambda_2 = -\text{"something else,"}$$

$$\text{and if } (\lambda_2 + \text{"something else"}) = 0, \text{ then } \lambda_1 = -\text{"something."}$$

Therefore without doing any more math we know that, as long as the interior equilibrium is feasible (i.e., $V^* > 0$ and $P^* > 0$), this equilibrium point is locally stable, since both eigenvalues for the Jacobian matrix will have negative real parts. To solve for "something" and "something else" we apply the quadratic root formula:

$$\lambda_1 = \frac{-rV^*}{K} + \sqrt{\left(\frac{rV^*}{K} \right)^2 - 4a^2 k P^* V^*}$$

and

$$\lambda_2 = \frac{-rV^*}{K} - \sqrt{\left(\frac{rV^*}{K} \right)^2 - 4a^2 k P^* V^*}.$$

From this last pair of equations, you can also see that, even for positive V^* and P^* , it's quite possible that the radical contains a negative number, implying that the eigenvalues may have imaginary parts. Referring to Box 13.1, you can see that this means that trajectories would spiral into the equilibrium point (since the real parts are both negative). Also, if there are complex numbers for roots to the characteristic equation, they come in pairs that are called **complex conjugates**. That is, they both have the same real part, and only the sign of their imaginary part is different. We may plot these complex numbers in the plane where the x axis represents the real part and the y axis the imaginary part. We then have, for example, one of the situations depicted in Box 13.1.

A complementary way to see that the interior equilibrium point of the system described by Eqs. (13.15) and (13.16) is necessarily stable, if it is feasible, is to apply a graphical analysis that parallels the development in Chapter 10, Figure 10.22.

Box 13.2 shows how the condition for stability of an equilibrium point needs to be modified for coupled difference equations instead of differential equations.

FISHING INTENSITY AND FISH POPULATION SIZES

A young Umberto D'Ancona worked in the fishery industry in Italy after World War I. He noticed that predatory fish seemed to have increased in the Adriatic Sea following the war, while smaller prey fish had decreased. Naturally the war had interrupted most commercial fishing. He interested his mathematician father-in-law, Vito Volterra, into trying to understand and explain this phenomenon. Thus began Volterra's interest in the

Box 13.2. Discrete Time Predator-Prey Models

A general form for a single predator, P and prey, V , species interacting according to a difference equation is

$$P_{t+1} = f_1(P_t, V_t) \quad \text{and} \quad V_{t+1} = f_2(P_t, V_t).$$

An equilibrium point occurs when

$$P_{t+1} = P_t \quad \text{and} \quad V_{t+1} = V_t.$$

An alternative notation that matches more the form of a differential equation is based on just the change in population size on the left-hand side of the equation, or

$$P_{t+1} - P_t = F_1(P_t, V_t) \quad \text{and} \quad V_{t+1} - V_t = F_2(P_t, V_t).$$

By this formulation, an equilibrium point occurs when

$$F_1(V_t, P_t) = 0 \quad \text{and} \quad F_2(V_t, P_t) = 0.$$

Contrasting these two formulations, we see that

$$\begin{array}{c} f_1(P_t, V_t) - P_t = F_1(P_t, V_t). \\ \text{The function} \quad \text{minus } P_t = \text{the function for } \frac{\Delta P}{\Delta t} = 1. \\ \text{for } P_{t+1} \end{array}$$

And, similarly,

$$f_2(P_t, V_t) - V_t = F_2(P_t, V_t).$$

Now let's go ahead and apply the Jacobian approach to the equations for $\Delta P/\Delta t$ and $\Delta V/\Delta t$, just as we did with differential equations:

$$\frac{\partial F_1}{\partial P} = \frac{\partial f_1}{\partial P} - 1$$

$$\frac{\partial F_2}{\partial V} = \frac{\partial f_2}{\partial V} - 1$$

$$\frac{\partial F_1}{\partial V} = \frac{\partial f_1}{\partial V}$$

$$\frac{\partial F_2}{\partial P} = \frac{\partial f_2}{\partial P}.$$

The Jacobian matrix therefore has the structure

$$\mathbf{J} = \begin{bmatrix} \frac{\partial f_1}{\partial P} - 1 & \frac{\partial f_1}{\partial V} \\ \frac{\partial f_2}{\partial P} & \frac{\partial f_2}{\partial V} - 1 \end{bmatrix}$$

Note that the diagonal terms have a value of 1 subtracted from them in contrast to the structure of the Jacobian matrix for differential equations. To find the eigenvalues of \mathbf{J} , we get

$$\det \begin{bmatrix} \frac{\partial f_1}{\partial P} - 1 - \lambda & \frac{\partial f_1}{\partial V} \\ \frac{\partial f_2}{\partial P} & \frac{\partial f_2}{\partial V} - 1 - \lambda \end{bmatrix} = 0. \quad (13.21)$$

Naturally, we want to evaluate these partials at the equilibrium point of interest. But regardless of what point that is, we can also write this last equation as

$$\det \begin{bmatrix} \frac{\partial f_1}{\partial P} - \lambda' & \frac{\partial f_1}{\partial V} \\ \frac{\partial f_2}{\partial P} & \frac{\partial f_2}{\partial V} - \lambda' \end{bmatrix} = 0, \quad (13.22)$$

where $\lambda' = 1 + \lambda$. In Chapter 3, we found that, for age-structured growth modeled as a difference equation, general solutions of difference equations have the form

$$\mathbf{n}(t) = g_1 \mathbf{x}_1 \lambda_1^t + g_2 \mathbf{x}_2 \lambda_2^t + g_3 \mathbf{x}_3 \lambda_3^t + \cdots + g_n \mathbf{x}_n \lambda_n^t.$$

For local stability the absolute value of each $\lambda_i < 1$, which implies that, based solely on the difference equation formulation (i.e., the f_1 and f_2 functions in the Jacobian of matrix Eq. 13.22) we have the requirement that

$$|\lambda'| < 1$$

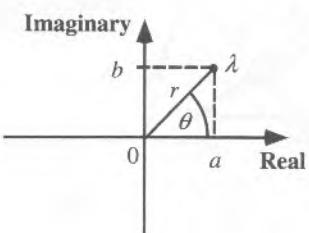
dynamical modeling of ecological systems, beginning with the development of the predation equations that we have already discussed. Volterra reasoned that, without much commercial fishing during the war, predatory fish, P , experienced lower death rates while prey fish, V , probably had higher recruitment rates, r . The per capita capture rates, he reasoned, probably stayed about the same. While Volterra modeled these changes, using the artificial model of the classical Lotka–Volterra predator equations, the same conclusions emerge from more realistic models as well, as illustrated in Figure 13.14.¹

1. Apparently, unbeknownst to Volterra, these equations had been analyzed earlier by Alfred Lotka (1920). However, his work contained some serious errors. For example, Lotka initially did not realize that the cycle's amplitude and frequency depended on the initial conditions. These errors were later corrected in Lotka's 1924 book *Elements of Physical Biology*, which came out 2 years before Volterra's apparently parallel discovery of the same predator-prey dynamics (Volterra 1926).

for each eigenvalue. The absolute value condition arises from the fact that a complex number, $\lambda = a + bi$, can be raised to the power t to reach

$$\lambda^t = r^t(\cos t\theta + i \sin t\theta), \quad (13.23)$$

where r and θ are defined in the following diagram.

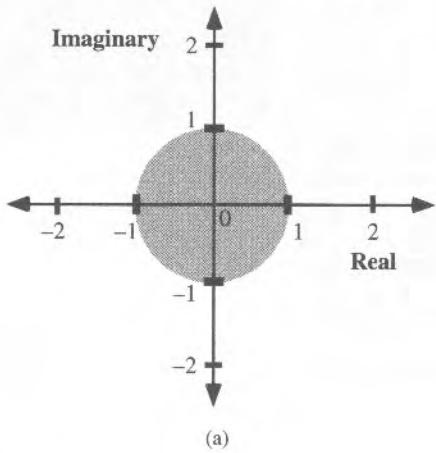


The **absolute value r** (also called the magnitude or modulus) of a complex number is

$$r = |\lambda'| = \sqrt{a^2 + b^2}.$$

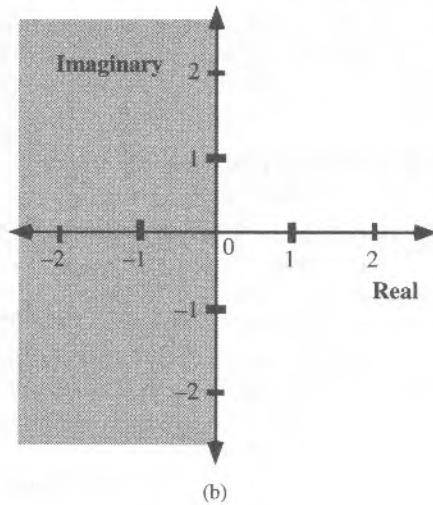
Now the second part of Eq. (13.23), $\cos t\theta + i \sin t\theta$, is just an undamped oscillation with an amplitude of 1 and a frequency of b (see Figure 13.6). This term alone causes deviations from equilibrium to get neither closer to nor farther from equilibrium with time. However, this part is multiplied by r^t , where $r = |\lambda'|$ is the absolute value. Thus, if and only if $|\lambda'| < 1$, for each eigenvalue, deviations from equilibrium become smaller over time. The condition that $|\lambda'| < 1$ is plotted in Figure 13.13 and compared to the analogous condition for differential equations.

Difference equations with $\Delta t = 1$



(a)

Differential equations with dt



(b)

Figure 13.13

For local stability, all the eigenvalues of the Jacobian matrix must fall in the shaded regions. This figure should be compared to the analogous development in Box 5.3 for a single-species dynamical model described by either difference equations or differential equations and to Box 13.1.

A SHORTCUT FOR STABILITY EVALUATION OF 2-SPECIES SYSTEMS

We have seen that an equilibrium point will be stable if and only if the real parts of the eigenvalues of the Jacobian matrix are both negative. Consider the following general representation for a two-by-two Jacobian matrix:

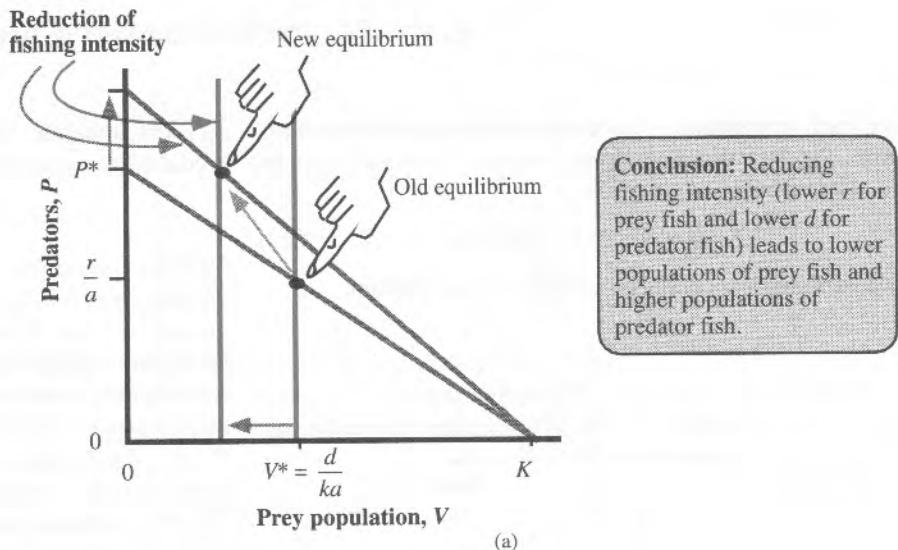
$$\mathbf{J} = \begin{bmatrix} a & b \\ c & d \end{bmatrix}.$$

Its eigenvalues are found by solving the equation

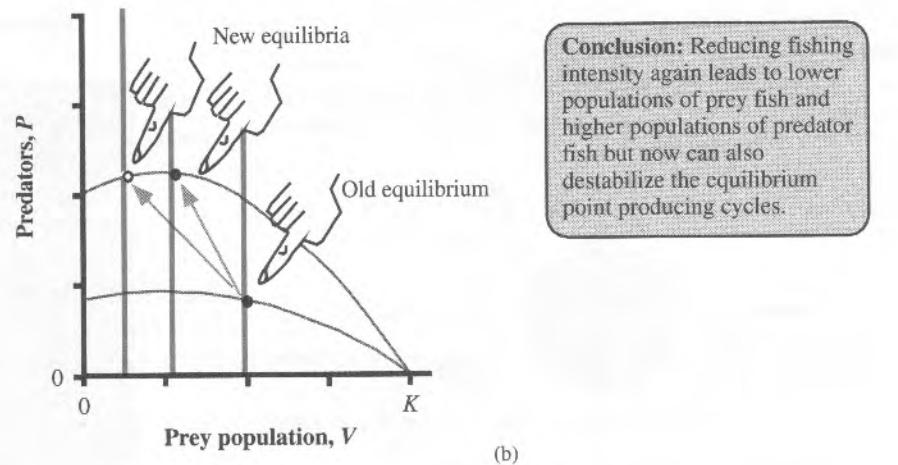
$$\det \begin{bmatrix} a - \lambda & b \\ c & d - \lambda \end{bmatrix} = 0,$$

Figure 13.14

A way to explain the increase in large predatory fish and the decrease in smaller fish after World War I, as originally suggested by Volterra (1926) but illustrated here with different predator-prey equations.



(a)



(b)

which yields

$$\lambda^2 - a\lambda - d\lambda + ad - bc = 0.$$

Note that this last equation can also be written as

$$\lambda^2 - (\text{trace of } \mathbf{J})\lambda + (\det \text{of } \mathbf{J}) = 0$$

where the **trace of \mathbf{J}** is simply the sum of the diagonal elements ($a + d$). For both roots of this last equation to be negative, the middle term, the trace of \mathbf{J} , must be negative and the determinant of \mathbf{J} must be positive. Then we will have an equation of the form,

$$(\lambda + \text{something})(\lambda + \text{something else}) = 0.$$

Hence a two-species system will be stable if and only if the trace of \mathbf{J} is negative *and* the determinant of \mathbf{J} is positive.

While it is difficult to translate the condition on the determinant of \mathbf{J} into graphical terms, the condition on the trace of \mathbf{J} is readily evaluated from the depiction of the two zero-isoclines. Let's return to the more complicated predator-prey equations with a type 2 functional response explored in Chapter 12. In the absence of predator interference the Jacobian matrix has the sign structure

$$\begin{bmatrix} - \text{ or } + & + \\ - & 0 \end{bmatrix}.$$

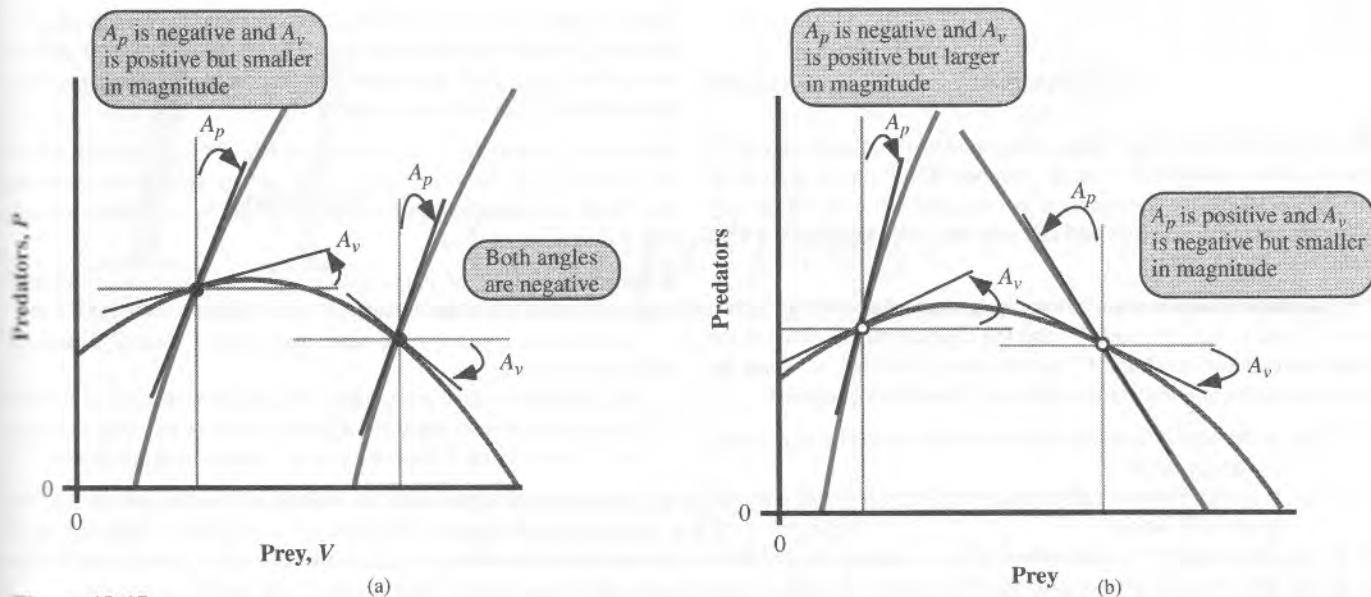


Figure 13.15

A graphical means of evaluating a necessary condition for stability. The trace of the Jacobian matrix will be negative when the sum of angles A_p and A_v is negative. The light gray lines are simply vertical and horizontal construction lines through the equilibrium point to facilitate the measurement of the critical angles A_p and A_v . The black lines are the tangent lines for the predator and prey zero-isoclines at the feasible equilibrium point. Angles are measured from the construction line to the tangent line. By this convention a clockwise angle is negative and represents a negative partial derivative on the diagonal of the Jacobian matrix. The two examples in (a) pass this necessary stability test while the two examples in (b) fail it.

The $J(1,1)$ element, corresponding to the prey-prey interaction is ambiguous in sign, an expression of the rising and then falling shape of the prey zero-isocline. However, the determinant of this matrix is necessarily positive regardless of the ambiguous sign of $J(1,1)$. On the other hand, the trace will only be negative if $J(1,1)$ is negative. Graphically $J(1,1)$ represents the slope of the prey zero-isocline at the equilibrium point. When this equilibrium point lies to the right of the peak of the prey zero-isocline this slope is negative, but it is positive when it falls on the left side of the hump.

Now let's tackle the case of systems with non-zero predator self-interactions. These matrices will have a sign structure for the Jacobian:

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

The $J(2,2)$ term will be negative for predator-predator interference and positive for predator-predator mutualism. Figure 13.15 shows four examples where we graphically evaluate the “trace is negative” test since it boils down to a condition on the angles of the zero-isoclines at the equilibrium point. The two examples in (a) pass this test while the two examples in (b) fail it. We are not assured of stability even for the two examples in (a), however, because we still have the “determinant is positive” test to evaluate, but we can at least see how it is possible that equilibrium points that lie to the left of the prey peak can be stable if predator interference is strong enough. The other side of the coin is that equilibrium points to the right of the peak can be unstable if predator mutualism is strong enough.

PROBLEMS

1. What are the eigenvalues associated with the equilibrium point $(0, 0)$ for the predator-prey system of eqs. (13.15) and (13.16)?
2. Robert MacArthur (1972) introduced the following predator-prey equations to describe a situation where the rate that resources, R , enter an area is independent of the number already there:

$$\frac{dR}{dt} = F - aRP \quad (13.24a)$$

and

$$\frac{dP}{dt} = P(kaR - d). \quad (13.24b)$$

He called this system the “falling fruit” model since the resources, R , are like fruit falling from trees; the number of fruit on the ground, R , and thus available for consumption by consumers, P , does not directly affect the rate that new fruit will fall onto the ground, which is a constant, F , in Eq. (13.24a).

For this model, what is the relationship between the equilibrium levels of R and P (i.e., R^* , and P^*) and the capture rate, a ? What is the relationship between R^* and P^* and the rate of fruit fall, F ? Form the Jacobian matrix and answer the following True/False questions.

- T F a. If the equilibrium point is positive for both R and P , it will be locally stable.
- T F b. If the equilibrium point is positive for both R and P , it will be globally stable.
- T F c. Resource growth is self-inhibited (i.e., density dependent).
- T F d. Per capita consumer growth has a positive feedback term (intraspecific mutualism).
- T F e. Consumers have negative growth in the absence of resources.
- T F f. Increasing k will decrease the equilibrium (or standing crop) of resources.
- T F g. In the absence of consumers, resources will grow exponentially.
- T F h. As the capture rate, a , increases, the equilibrium density of consumers will necessarily increase.

3 The Nicholson–Bailey model of host–parasite interactions differs from all other models in this chapter in that it is expressed as discrete time difference equations (Nicholson and Bailey 1935), as shown in Figure 13.16.

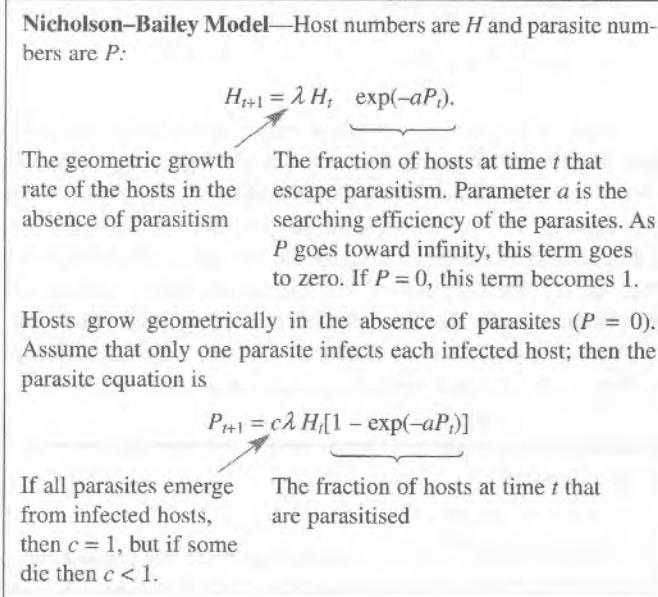


Figure 13.16
The Nicholson–Bailey host–parasite model.

Similar to the Lotka–Volterra predation equation, the prey grow geometrically in the absence of predators. The predators, however, decline immediately to zero in the absence of prey, unlike in the exponential decay of the Lotka–Volterra equation.

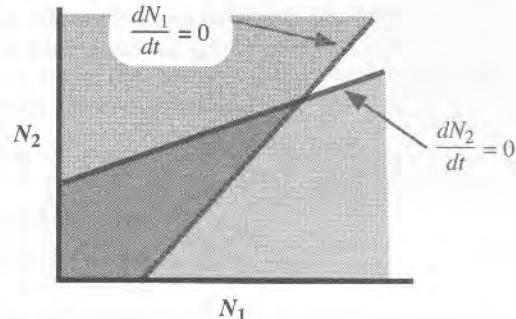
Show that the interior equilibrium point is $P^* = \ln(\lambda)/a$ and $H^* = \ln(\lambda)/[ca(\lambda - 1)]$. (Hint: $e^{zlna} = a^z$). This interior equilibrium is unstable. Small perturbations from equilibrium lead to oscillations of rapidly increasing amplitude.

4. Construct one set of linear two-species zero-isoclines consistent with all the following assumptions.

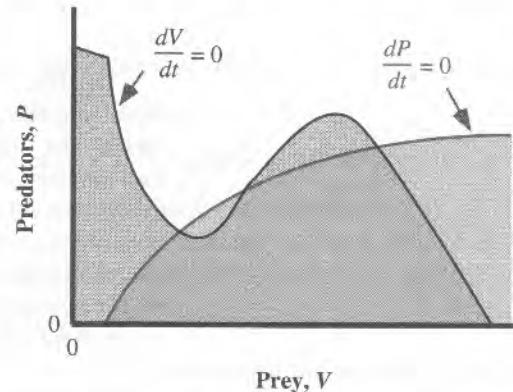
- a. Species 1 and 2 each have intraspecific density dependent population growth.
- b. Species 1 and 2 are interspecifically mutualistic (i.e., higher numbers of one species enhances the growth rate of the other species).
- c. Species 1 and 2 can coexist at a stable equilibrium point.

On your diagram, cross-hatch the regions of positive growth rate for both species; label the axes, zero-isoclines, and points of intersection of the zero-isoclines with each axis. Draw circles around each equilibrium point. Indicate which of these equilibria are stable and unstable.

Partial Answer:



5. For the zero-isocline situation depicted in the following diagram, identify and label each equilibrium point. For each equilibrium point state whether it is or is not locally stable. (The shaded and hatched regions yield positive growth.)



Answer the following True/False questions about the system.

- T F a. Predators exhibit self-interference at high densities.
- T F b. Predators have a type 1 functional response.
- T F c. Prey experience intraspecific density dependence.
- T F d. Prey have a carrying capacity.
- T F e. This model has just one domain of attraction.
- T F f. Point (0, 0) is locally stable.