APPENDIX

Stability Analysis

THE following information is provided as a "cookbook" example of the steps involved in a stability analysis of a simple mathematical model of a community-level interaction. Those craving a deeper understanding of the underlying mathematics—why it works, rather than how it is done—are encouraged to consult the many excellent texts that describe the process in much greater depth. Good choices include Edelstein-Keshet (1988), Bulmer (1994), and Hastings (1997).

The example considered here involves a pair of differential equations that describe the interaction between a predator and prey, where the prey population exhibits density-dependent population regulation via the inclusion of a logistic-style term. This is the same system of equations described in Chapter 5 as Equations 5.3 and 5.4. The equations, which are also two functions F_1 and F_2 of H and P, are

$b - 2bH/K - Pa$ $\quad$ $b(1 - \frac{H}{K}) - aH$

$$dH/dt = bH(1 - H/K) - PaH = F_1(H, P) \tag{A.1}$$

$bH - \frac{bH^2}{K} - PaH$

and

$$dP/dt = e(PaH) - sP = F_2(H, P) \tag{A.2}$$

where H and P are respectively the prey and predator population sizes, b is the per capita birth rate of the prey, a is a per capita attack rate, aH is the per capita consumption rate, or functional response, of predators on a given density of prey, e is the conversion efficiency of consumed prey into new predators, and $-s$ is the per capita rate at which predators die in the absence of prey.

The basic steps in the stability analysis are simply listed first to provide a general roadmap of the process and are then described in slightly greater detail. The sequence of steps involves the following operations:

1. Solving the equations for the equilibrium values of H and P, denoted H^* and P^*.

2. Creating a matrix of the partial derivatives for both equations with respect to H and P, called the Jacobian matrix.

3. Substituting the equilibrium values of H^* and P^* into the partial derivatives in the Jacobian matrix.

4. Conducting an eigenanalysis of the Jacobian matrix to determine whether the values of the model parameters will yield eigenvalues, or characteristic roots, of the matrix with negative real parts.

That said, a few words are in order to explain what these things are, and why they are useful.

Before conducting a stability analysis, it is first necessary to establish whether equilibrium values of H^* and P^* exist such that $dH/dt = 0$ and $dP/dt = 0$. These values will take the form of various combinations of the parameters included in the equations, and describe when population growth of each species is zero. Trivial cases in which H and/or P equals zero are not of interest, since one or both populations have gone extinct. We focus on the case where both populations have equilibrium population sizes that are greater than zero, which corresponds to one way in which the populations might coexist. Nonequilibrium coexistence is a possibility not considered by this analysis. When we conduct a stability analysis, we ask whether a small change in the values of either H^* or P^* will lead to an eventual return to the equilibrium values H^* and P^*. If so, the system is stable. The answer to that question depends on the properties of the Jacobian matrix.

Solving for the values of H^* and P^* simply involves a bit of algebra. Factoring H out of the prey equation and P out of the predator equation and setting both equations equal to 0 yields the following:

$$dH/dt = H(b - Hb/K - Pa) = 0 \tag{A.3}$$

and

$$dP/dt = P(eaH - s) = 0 \tag{A.4}$$

Since we are not interested in the case where $H = 0$ or $P = 0$, we want to solve for values of H and P such that

$$(b - Hb/K - Pa) = 0 \tag{A.5}$$

and

$$(eaH - s) = 0 \tag{A.6}$$

These equations describe the zero-growth isoclines for H and P, that is, the combinations of values of H and P that produce a net population growth of zero for each species. If and where the lines intersect, population growth rates of both species are simultaneously zero, and an equilibrium exists. Figure A.1 shows these isoclines for a particular set of parameter values. Solving Equa-

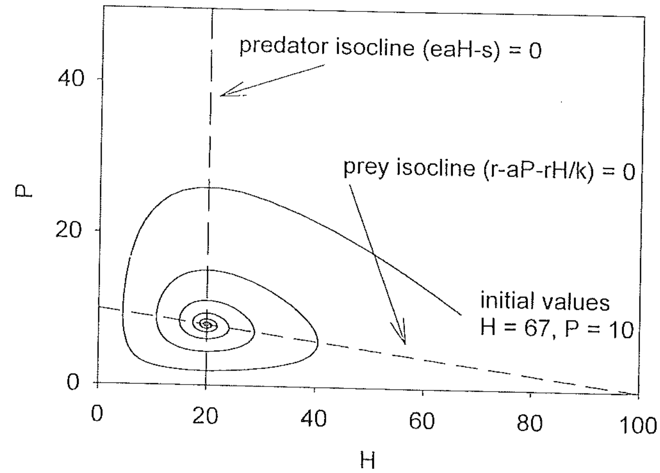

FIGURE A.1. *Zero-growth isoclines and population dynamics for Equations A.1 and A.2.*

tion A.6 for H gives $H^* = s/ea$. Solving Equation A.5 for P gives $P^* = b/[a(1 - H/k)]$. Substituting s/ea for H gives $P^* = b/[a(1 - s/eak)]$.

The Jacobian matrix consists of the partial derivatives of each equation with respect to H and P, in the two-variable, two-equation case. Referral to your freshman-year calculus book will remind you that when one takes partial derivatives with respect to a particular variable, all terms in the equation that do not contain that variable are treated like constants. Consequently, each partial derivative describes how a change in the variable of interest will change the value of the function. In this case, that description means how a change in H or P will affect the population growth rates of H or P. Since we are interested in the case where H and P are at or near H^* and P^*, we substitute the values obtained for H^* and P^* into the partial derivatives.

Whether a small change in H or P will continue to grow (unstable) or gradually decay (stable) so that values return to H^* and P^* is determined by a complex function of the elements of the Jacobian matrix. The values that function takes, called eigenvalues or characteristic roots, provide the criterion for determining whether the system is stable. The eigenvalues can be complex numbers, with real and imaginary parts. For the system to be stable, its eigenvalues must have negative real parts. If so, any perturbation away from H^* and P^* will decrease over time due to the net effects of intraspecific and interspecific interactions described by the elements of the Jacobian. The imaginary parts of the eigenvalues, if present, describe the tendency of the system to oscillate. If the eigenvalues consist solely of imaginary numbers, the system will oscillate without any tendency for the oscillations to increase or decrease in amplitude.

In the two-species, two-equation case, the eigenvalues of the Jacobian matrix , J, are given by the following relation. Where the Jacobian matrix,

$$J = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

and a, b, c, and d are the numerical values of the partial derivatives of F_1 and F_2 evaluated at equilibrium, the eigenvalues of J, denoted by λ, are given by solving the equation

$$(a-\lambda)(d-\lambda)-bc=0 \tag{A.7}$$

which can be rewritten as

$$\lambda^2-(a+d)\lambda+ad-bc=0 \tag{A.8}$$

Using the formula for the solution of a quadratic equation, we get

$$\lambda=\left\{(a+d)\left[(a+d)^2-4(ad-bc)\right]^{0.5}\right\}\Big/2 \tag{A.9}$$

However, in practice, we'll typically use the mathematical software package of our choice to painlessly do the same thing. The example below was solved using Mathcad. An example worked out for numerical values of the model parameters follows.

Consider the case of Equations A.1 and A. 2 above, where $b=0.5$, $k=100$, $a=0.05$, $e=0.5$, and $s=0.5$. These values of the parameters yield equilibrium values of $H^*=20$ and $P^*=8$, since $H^*=s/ea$ and $P^*=b/[a(1-s/eak)]$. The zero-growth isoclines are shown in Figure A.1. The Jacobian matrix of partial derivatives of Equations A.1 and A.2 is

$$\begin{array}{cc} & \begin{array}{cc} H & \quad P \end{array} \\ \begin{array}{c} H \\ P \end{array} & \begin{pmatrix} b-aP-2bH/k & -aH \\ eaP & eaH-s \end{pmatrix} \end{array} = \begin{pmatrix} \partial F_1/\partial H & \partial F_1/\partial P \\ \partial F_2/\partial H & \partial F_2/\partial P \end{pmatrix}$$

which, for these parameter values and substituting values of H^* and P^* for H and P, becomes

$$\begin{pmatrix} -0.1 & -1.0 \\ 0.2 & 0.0 \end{pmatrix}$$

The eigenvalues of this matrix are $-0.05+0.444i$ and $-0.05-0.444i$. Since the real parts of both eigenvalues are negative, the system is stable. The tendency for the system to oscillate as it returns to equilibrium is indicated by the presence of imaginary parts of the eigenvalues. The damped oscillatory return to equilibrium is shown in the phase space trace of population dynamics in Figure A.1.