

REVERSING PERIOD-DOUBLING BIFURCATIONS IN MODELS OF POPULATION INTERACTIONS USING CONSTANT STOCKING OR HARVESTING

JAMES F. SELGRADE AND JAMES H. ROBERDS

Dedicated to the memory of Geoffrey James Butler

ABSTRACT. This study considers a general class of two-dimensional, discrete population models where each per capita transition function (fitness) depends on a linear combination of the densities of the interacting populations. The fitness functions are either monotone decreasing functions (pioneer fitnesses) or one-humped functions (climax fitnesses). Conditions are derived which guarantee that an equilibrium loses stability through a period-doubling bifurcation with respect to the pioneer self-crowding parameter. A constant term which represents stocking or harvesting of the pioneer population is introduced into the system. Conditions are determined under which this stocking or harvesting will reverse the bifurcation and restabilize the equilibrium, and comparisons are made with the effects of density dependent stocking or harvesting. Examples illustrate the importance of the concavity of the pioneer fitness in determining whether stocking or harvesting has a stabilizing effect.

1. Introduction. Systems of nonlinear difference equations are used to model the effects of population density on the interactions of discretely reproducing populations of animals and plants. The types of interactions include competition, cooperation, and predation. It is now well known that such systems can possess complex dynamical behavior, even a single population with a quadratic growth function might exhibit a cascade of period-doubling (or flip) bifurcations culminating in chaotic oscillations as illustrated by R.M. May [17]. Typically a period-doubling bifurcation occurs when varying a parameter of the system causes an eigenvalue of an equilibrium to pass through -1 .

Received by the editors on October 4, 1996, and in revised form on May 12, 1997.

Research supported by a grant from the British Columbia Forest Renewal Plan Research Project No: OPS. EN-109, British Columbia, Canada, and by the USDA-Forest Service, Southern Research Station, Southern Institute of Forest Genetics, Saucier, MS.

Copyright ©1998 Rocky Mountain Mathematics Consortium

The equilibrium often loses stability and a stable cycle of period 2 appears. Continued parameter changes may result in a cascade of period-doubling bifurcations and the onset of chaos. Costantino et al. [6] report period-doubling bifurcations in data from experiments with flour beetle populations which they model with a three stage age-structured, discrete system. Franke and Yakubu [12, 13] observe cascades of period-doubling bifurcations in models for competitive interactions of pioneer and climax populations. Such cascades occur for systems of ordinary differential equations which model the interactions of continuously reproducing populations. For example, Gardini et al. [14] illustrate a period-doubling transition to a chaotic attractor for three-dimensional Lotka-Volterra systems, and Buchanan and Selgrade [2] discuss similar behavior for a three-dimensional model of the interaction among pioneer and climax populations.

Usually chaotic behavior is undesirable in an ecological system. Selgrade [21] shows how systems which undergo period-doubling bifurcations due to variations in intrinsic parameters may be restabilized by extrinsic stocking or harvesting which is proportional to population density. Here we compare and contrast the results for density dependent stocking or harvesting with results for constant rate stocking or harvesting. We consider a general class of Kolmogorov models where each per capita transition map (called the *fitness*) is a function of a linear combination of the densities of the interacting populations. This lumped density assumption allows a population's response (fitness) to density pressure to be separated from intraspecific and interspecific competitive effects. Previous studies of such systems include Comins and Hassell [4], Hassell and Comins [15], Hofbauer, Hutson, and Jansen [16], Cushing [7, 8], Selgrade and Namkoong [22, 23], Franke and Yakubu [9–13], Selgrade [20], Sumner [27, 28], Yakubu [29], Buchanan and Selgrade [2, 3], Selgrade and Roberds [24, 25], and Selgrade [21].

The fitness functions in our models will be either monotone decreasing functions (pioneer fitnesses) or one-humped functions (climax fitnesses). The interaction of a pioneer population and a climax population permits competition and predation in different regions of the same phase space. Yakubu [29] shows that stocking or harvesting may be used to obtain stable coexistence in a system of two competing pioneer populations where there is exclusionary dynamics without stocking or

harvesting. Stone [26] discusses reversing period-doubling bifurcations in a model for a single pioneer population with a constant immigration (stocking) term. Stone's bifurcation parameter is the intrinsic growth rate and the period-doubling reversals appear as "bubbles" in the bifurcation diagram where the population density is plotted against the growth rate. Our intention is to determine when period-doubling bifurcations can be reversed by varying the stocking or harvesting parameter which is extrinsic to the population interaction,

Section 2 discusses the model equations and conditions for a period-doubling bifurcation with respect to the pioneer self-crowding parameter which destabilize an equilibrium. We show that if any of four sets of necessary conditions are satisfied then either a subcritical or a supercritical period-doubling bifurcation must occur. In Section 3 we introduce a constant stocking or harvesting term into the pioneer transition equation. We determine conditions under which this stocking or harvesting will reverse the bifurcation and restabilize the equilibrium. This is accomplished by studying the geometry of the bifurcation curve in the space of parameters given by the intrinsic crowding parameter and the extrinsic stocking/harvesting parameter. Section 4 discusses restabilizing the equilibrium of prey-predator type. For density dependent stocking or harvesting, Selgrade [21] shows that if the pioneer fitness function has nonnegative concavity, which is the case for all familiar examples in the modeling literature, then an equilibrium of prey-predator type may be restabilized if and only if stocking is done. Here we present an example where constant rate harvesting is needed to restabilize an equilibrium of prey-predator type. In Section 5 we illustrate the importance of the size of the concavity of the pioneer fitness in determining whether stocking or harvesting will restabilize the equilibrium of competitive type. Also we discuss an example where stocking reverses a cascade of period-doubling bifurcations.

2. Model equations and conditions for period-doubling.

In order to study period-doubling bifurcations we consider systems of two-dimensional, nonlinear difference equations which model the interactions of discretely reproducing populations. Let x_1 and x_2 denote the densities of two populations. Let y_i , for $i = 1, 2$, denote the *weighted total density* variable for x_i , i.e.,

$$y_i = c_{i1} x_1 + c_{i2} x_2$$

where $c_{ij} \geq 0$ is called the *interaction coefficient* and reflects the effect of the j th population on the i th population. The 2×2 matrix $C = (c_{ij})$ is called the *interaction matrix*. The per capita transition function, the fitness f_i , of the i th population is a smooth function of y_i . Our model equations are

$$(2.1) \quad x'_i = x_i f_i(y_i), \quad i = 1, 2$$

where x'_i denotes the density of the i th population at the next generation. Because (2.1) is of Kolmogorov-type, if the values of f_i are always nonnegative then the nonnegative quadrant is invariant for solutions to (2.1). However, we will not assume that this is always the case.

An equilibrium in the interior of the positive quadrant occurs where each fitness has the value 1. Since f_1 is a pioneer fitness then we assume that there is exactly one value $y_1^* > 0$ so that $f_1(y_1^*) = 1$. Hence the x_1 -isocline is the line $y_1^* = c_{11} x_1 + c_{12} x_2$. Also we assume this value y_1^* is nondegenerate, i.e., $f'_1(y_1^*) \neq 0$. We take the climax fitness f_2 to have exactly two positive values where it assumes the value 1, which also are nondegenerate. Thus the isoclines of the climax population are two parallel lines. An equilibrium in the positive quadrant occurs precisely where the pioneer isocline intersects one of the climax isoclines, see Figure 1. If $y^* = (y_1^*, y_2^*)$ is a vector such that $f_i(y_i^*) = 1$, for each i , then an interior equilibrium $E = (e_1, e_2)$ is a solution to the system of linear equations

$$(2.2) \quad CE = y^*.$$

Hence we find

$$(2.3) \quad e_1 = \frac{y_1^* c_{22} - y_2^* c_{12}}{\det C}, \quad e_2 = \frac{y_2^* c_{11} - y_1^* c_{21}}{\det C},$$

For E to be in the positive quadrant, both numerators in (2.3) must have the same sign as $\det C$. This equilibrium is isolated if $\det C \neq 0$, which we always assume.

The stability of an interior equilibrium E may be determined by the Jacobian matrix of the right side of (2.1). At $x = (x_1, x_2)$ this matrix is given by:

$$(2.4) \quad J(x) = \begin{bmatrix} f_1(y_1) & 0 \\ 0 & f_2(y_2) \end{bmatrix} I + \begin{bmatrix} x_1 f'_1(y_1) & 0 \\ 0 & x_2 f'_2(y_2) \end{bmatrix} C.$$

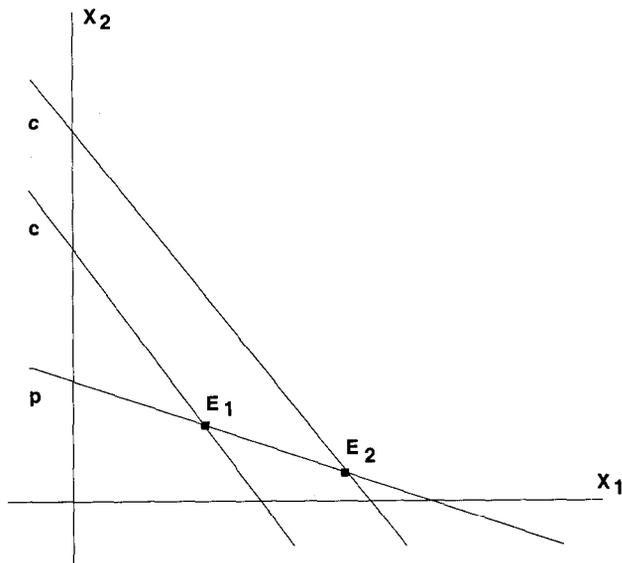


FIGURE 1. Pioneer (p) and climax (c) isoclines; equilibria E_1 and E_2 .

When (2.4) is evaluated at \bar{E} , the first matrix in (2.4) becomes the identity. Let $D(E)$ denote the 2×2 diagonal matrix in (2.4) with entries $e_1 f'_1(y_1^*)$ and $e_2 f'_2(y_2^*)$. Notice that the eigenvalues of the product $D(E) C$ are left-translations by the amount 1 of the eigenvalues of $J(E)$. If the eigenvalues of $J(E)$ are inside the unit circle in the complex plane, which implies that E is asymptotically stable, then the eigenvalues of $D(E) C$ are inside the circle of radius 1 centered at -1 in the complex plane. Hence, the trace of $D(E) C$ is between -4 and 0 and the determinant of $D(E) C$ is between 0 and 4, i.e.,

$$(2.5) \quad 0 < \det [D(E) C] = e_1 e_2 f'_1(y_1^*) f'_2(y_2^*) \det C < 4.$$

Since $f'_1(y_1^*)$ is negative, for (2.5) to hold we must have

$$(2.6) \quad f'_2(y_2^*) \det C < 0.$$

Notice that (2.5) and (2.6) still hold if one eigenvalue of $J(E)$ is -1 and the other is inside the unit circle. If one eigenvalue of $J(E)$ is -1 then $\det [D(E) C] \neq 0$ is equivalent to the other eigenvalue of $J(E)$

not equal to 1 ; if one eigenvalue of $J(E)$ is -1 then $\det [D(E) C] \neq 4$ is equivalent to the other eigenvalue of $J(E)$ not equal to -1 . Thus, for an equilibrium to lose stability by its smaller eigenvalue passing through -1 , it is necessary that (2.5) holds and that the slope of the climax fitness $f'_2(y_2^*)$ and $\det C$ have opposite signs. The term $\det C$ measures the difference between the intraspecific and the interspecific competition. If the intraspecific competition is less than the interspecific competition ($\det C < 0$) then $f'_2(y_2^*)$ must be positive and, hence, the equilibrium E_1 must occur where the pioneer isocline intersects the climax isocline which is closer to the origin (Figure 1). The off-diagonal terms of $J(E_1)$ have opposite signs and, hence, at E_1 the pioneer and climax populations interact like prey and predator, respectively. We refer to E_1 as an equilibrium of *prey-predator type*. On the other hand, if the intraspecific competition is greater than the interspecific competition then $f'_2(y_2^*)$ must be negative; so the bifurcation equilibrium E_2 is the intersection of the pioneer isocline and the climax isocline farther from the origin. The off-diagonal terms of $J(E_2)$ are negative and the populations truly compete with each other at this equilibrium. We refer to E_2 as an equilibrium of *competitive type*.

Computing the eigenvalues λ_{\pm} of $J(E)$, we obtain

$$(2.7) \quad \lambda_{\pm} = \frac{1}{2}(2 + e_1 f'_1(y_1^*)c_{11} + e_2 f'_2(y_2^*)c_{22}) \pm \frac{1}{2} \sqrt{(e_1 f'_1(y_1^*)c_{11} - e_2 f'_2(y_2^*)c_{22})^2 + 4e_1 e_2 c_{12} c_{21} f'_1(y_1^*) f'_2(y_2^*)}.$$

From (2.7) observe that the eigenvalues of an equilibrium of competitive type are real and distinct. However, an equilibrium of prey-predator type may have complex eigenvalues and, in fact, undergo Hopf bifurcation, see Selgrade and Roberds [24]. But our bifurcation equation, (2.8) below, will not be valid if the eigenvalues have nonzero imaginary parts. For a stable equilibrium to undergo period-doubling, we need λ_- to pass through -1 . Solving (2.7) for $\lambda_- = -1$, we obtain

$$(2.8) \quad 0 = 4 + 2e_1 f'_1(y_1^*)c_{11} + 2e_2 f'_2(y_2^*)c_{22} + e_1 e_2 f'_1(y_1^*) f'_2(y_2^*) \det C.$$

The right side of (2.8) may be rewritten as

$$1 + \text{tr } J(E) + \det J(E).$$

This sum is positive if the eigenvalues of \mathbf{E} have nonzero imaginary parts; hence, an equilibrium whose coordinates satisfy (2.8) must have real eigenvalues-one eigenvalue is -1 and the other is inside the unit circle if (2.5) holds.

Selgrade and Roberds [24, 25] indicate that the intraspecific competition coefficients c_{11} and c_{22} are convenient, intrinsic bifurcation parameters. For simplicity we choose c_{11} as our bifurcation parameter and solve (2.8) for c_{11} in terms of parameters which are independent of c_{11} , i.e., the other interaction coefficients, the total density variables y_i^* at equilibrium, and the slope of each fitness at the appropriate y_i^* :

$$(2.9) \quad \hat{c}_{11} = \frac{4c_{12}c_{21} + 2y_1^*c_{21}c_{22}f_2'(y_2^*) + c_{21}y_1^*(y_1^*c_{22} - y_2^*c_{12})f_1'(y_1^*)f_2'(y_2^*)}{[2 + y_2^*f_2'(y_2^*)]\{2c_{22} + f_1'(y_1^*)(y_1^*c_{22} - y_2^*c_{12})\}}$$

For the bifurcation to occur, it is necessary that the right side of (2.9) be positive.

To determine the direction of bifurcation we need to find $d\lambda_-/dc_{11}$ at $c_{11} = \hat{c}_{11}$. From (2.3) we compute

$$(2.10) \quad \frac{\partial e_1}{\partial c_{11}} = \frac{-c_{22}e_1}{\det C} \quad \text{and} \quad \frac{\partial e_2}{\partial c_{11}} = \frac{c_{21}e_1}{\det C}.$$

We differentiate λ_- with respect to c_{11} and use (2.8) and (2.10) to evaluate at $c_{11} = \hat{c}_{11}$. Some tedious algebraic manipulation yields

$$(2.11) \quad \frac{d\lambda_-}{dc_{11}} = \frac{-2e_1c_{21}[2 + y_1^*f_1'(y_1^*)]}{e_2 \det C [4 + e_1f_1'(y_1^*)\hat{c}_{11} + e_2f_2'(y_2^*)c_{22}]}$$

Using (2.5) and (2.8) we conclude that the term in brackets in the denominator of (2.11) is positive. Hence the signs of $\det C$ and $[2 + y_1^*f_1'(y_1^*)]$ determine the sign of (2.11). If (2.11) is negative then \mathbf{E} loses stability as c_{11} increases; and if (2.11) is positive, then \mathbf{E} loses stability as c_{11} decreases.

Sufficient conditions for a bifurcation depend on the type of equilibrium. For instance, if E_1 is of prey-predator type where the slope of the climax population $f_2'(y_2^*)$ is positive, then from (2.6) $\det C$ must be negative and so is the term $y_1^*c_{22} - y_2^*c_{12}$ which is the numerator of the first coordinate of E_1 . However, this term must be positive if the

equilibrium is of competitive type because the slope of the climax population $f'_2(y_2^*)$ is negative and $\det C$ is positive. The numerator of the second coordinate of the equilibrium at \hat{c}_{11} is obtained by substituting (2.9) into (2.3) to get

$$(2.12) \quad y_2^* \hat{c}_{11} - y_1^* c_{21} = \frac{-2c_{21}[2 + y_1^* f'_1(y_1^*)](y_1^* c_{22} - y_2^* c_{12})}{[2 + y_2^* f'_2(y_2^*)]\{2c_{22} + f'_1(y_1^*)(y_1^* c_{22} - y_2^* c_{12})\}}.$$

Inequality conditions on the terms on the right side of (2.12) are needed to guarantee the appropriate sign for (2.12). Selgrade [21] derives four sets of inequalities which guarantee bifurcation and are listed below. We assume that (2.5) holds and obtain the value in (2.9), \hat{c}_{11} , for the bifurcation parameter by solving the bifurcation equation (2.8). In this situation, necessary and sufficient conditions for a bifurcation to occur at E_1 are:

Case (i).

$$(2.13) \quad y_1^* c_{22} - y_2^* c_{12} < 0 \quad \text{and} \quad 2 + y_1^* f'_1(y_1^*) < 0.$$

The inequalities in (2.13) guarantee that $\hat{c}_{11} > 0$, $\det C < 0$, and the numerators of the coordinates of E_1 are negative; hence, E_1 is in the positive quadrant when $c_{11} = \hat{c}_{11}$. The corresponding conditions for bifurcation at E_2 are more complicated, see Selgrade [21], and are arranged according to the signs of $[2 + y_2^* f'_2(y_2^*)]$ and $[2 + y_1^* f'_1(y_1^*)]$.

Case (ii).

$$y_1^* c_{22} - y_2^* c_{12} > 0, \quad 2 + y_2^* f'_2(y_2^*) < 0, \quad 2 + y_1^* f'_1(y_1^*) < 0,$$

and

$$(2.14) \quad 2c_{22} + f'_1(y_1^*)(y_1^* c_{22} - y_2^* c_{12}) < 0.$$

Case (iii).

$$y_1^* c_{22} - y_2^* c_{12} > 0, \quad 2 + y_2^* f'_2(y_2^*) < 0, \quad 2 + y_1^* f'_1(y_1^*) > 0,$$

and

$$(2.15) \quad 4c_{12} + y_1^* f_2'(y_2^*) \{2c_{22} + f_1'(y_1^*) (y_1^* c_{22} - y_2^* c_{12})\} < 0.$$

Case (iv).

$$\begin{aligned} y_1^* c_{22} - y_2^* c_{12} > 0, \quad 2 + y_2^* f_2'(y_2^*) > 0, \quad 2 + y_1^* f_1'(y_1^*) < 0, \\ 4c_{12} + y_1^* f_2'(y_2^*) \{2c_{22} + f_1'(y_1^*) (y_1^* c_{22} - y_2^* c_{12})\} > 0, \end{aligned}$$

and

$$(2.16) \quad 2c_{22} + f_1'(y_1^*) (y_1^* c_{22} - y_2^* c_{12}) > 0.$$

The inequality conditions in Cases (i) through (iv) guarantee that E loses stability as c_{11} passes through \hat{c}_{11} because the smaller eigenvalue passes through -1, which generically is a period-doubling bifurcation. However, it is much more difficult to prove that the curve of period-2 points is “parabolic” in shape. Sufficient conditions for this are derived in Selgrade and Roberds [25] and involve applications of the implicit function theorem. Specifically, when considering the phase variables graphed against the parameter c_{11} in three dimensions, we are interested in describing the set of points of prime period-2 as c_{11} varies through its bifurcation value \hat{c}_{11} . This set is a subset of the two-dimensional center manifold parameterized by c_{11} and a phase variable. Selgrade and Roberds [25] provide sufficient conditions for showing that this set may be viewed locally as the graph of c_{11} as a function of the phase variable and for determining the direction of bifurcation, i.e., the concavity of the graph. The condition for existence of this function is that the following combination of the first and second derivatives of the fitness functions is nonzero at (\hat{c}_{11}, E) where $F_i(c_{11}, x_1, x_2) \equiv x_i f_i(y_i)$:

$$(2.17) \quad \sum_{j=1}^2 a_{j1} \sum_{i=1}^2 b_{1i} \left[\frac{\partial^2 F_i}{\partial c_{11} \partial x_j} + \frac{\partial e_1}{\partial c_{11}} \frac{\partial^2 F_i}{\partial x_1 \partial x_i} + \frac{\partial e_2}{\partial c_{11}} \frac{\partial^2 F_i}{\partial x_2 \partial x_j} \right].$$

The matrices $A = (a_{ij})$ and $A' = (b_{ij})$ are obtained from changes of coordinates needed to put (2.1) in standard form, see Selgrade and

Roberds [25] for details. We compute the partial derivatives needed to evaluate (2.17) for $i, j = 1, 2$ and $i \neq j$ as

$$\begin{aligned}
 \frac{\partial^2 F_i}{\partial x_i^2} &= 2f'_i(y_i)c_{ii} + x_i f''_i(y_i)c_{ii}^2, \\
 \frac{\partial^2 F_i}{\partial x_j^2} &= x_i f''_i(y_i)c_{ij}^2, \\
 (2.18) \quad \frac{\partial^2 F_i}{\partial x_j \partial x_i} &= f'_i(y_i)c_{ij} + x_i f''_i(y_i)c_{ii}c_{ij}, \\
 \frac{\partial^2 F_1}{\partial c_{11} \partial x_1} &= 2x_1 f'_1(y_1) + x_1^2 f''_1(y_1)c_{11}, & \frac{\partial^2 F_2}{\partial c_{11} \partial x_1} &= 0, \\
 \frac{\partial^2 F_1}{\partial c_{11} \partial x_2} &= x_1^2 f''_1(y_1)c_{12} \text{ and } \frac{\partial^2 F_2}{\partial c_{11} \partial x_2} = 0.
 \end{aligned}$$

If β is the eigenvalue of E inside the unit circle, then the matrix A is given by

$$(2.19) \quad A = \begin{bmatrix} -c_{12}e_1 f'_1(y_1^*) & -c_{12}e_1 f'_1(y_1^*) \\ 2 + c_{11}e_1 f'_1(y_1^*) & 1 - \beta + c_{11}e_1 f'_1(y_1^*) \end{bmatrix}.$$

After a lengthy computation using (2.10), (2.18) and (2.19), the expression in (2.17) is found to be

$$(2.20) \quad \frac{[2 + y_2^* f'_2(y_2^*)] \{2c_{22} + f'_1(y_1^*)(y_1^* c_{22} - y_2^* c_{12})\}}{(1 + \beta) \det C}$$

The facts that $\beta \neq -1$ and that one of the cases (i) through (iv) holds assure that each factor in (2.20) is nonzero. Thus, we have the following result :

Proposition 2.1. *Suppose that $E = (e_1, e_2)$ is an equilibrium of (2.1) in the positive quadrant. Assume that*

$$0 < e_1 e_2 f'_1(y_1^*) f'_2(y_2^*) \det C < 4$$

and that one of the sets of inequalities (i), (ii), (iii), or (iv) holds. Then the expression (2.20) is nonzero at E and a period-doubling bifurcation occurs at (\hat{c}_{11}, E) where \hat{c}_{11} is given by (2.9).

To determine the concavity of the set of period-2 points and, hence, to establish whether the bifurcation is subcritical or supercritical, additional combinations of first, second, and third derivatives of the fitness functions like (2.17) are needed, see Selgrade and Roberds [25]. However, these formulas do not simplify for the general system (2.1) as (2.17) does. They will be determined for specific examples in Sections 4 and 5.

3. Constant rate stocking and harvesting. Since varying the pioneer self-crowding parameter c_{11} destabilizes the equilibrium, one might suspect that stocking or harvesting the pioneer population may restabilize the equilibrium. One approach to stocking or harvesting is to add a term to the pioneer difference equation which is directly proportional to the current pioneer density. Density-dependent stocking or harvesting retains the Kolmogorov form of the difference equations and the isoclines are still lines. Hence, mathematical analysis proceeds without much additional algebraic complication, see Selgrade [21]. However, from a practical point of view, a manager of an ecosystem would have to know the pioneer density to stock or harvest at a proportional rate. Therefore, here we add a constant term to the pioneer difference equation to represent constant rate stocking or harvesting and we obtain:

$$(SH) \quad \begin{aligned} x'_1 &= x_1 f_1(c_{11} x_1 + c_{12} x_2) + a \\ x'_2 &= \mathbf{52} f_2(c_{21} x_1 + c_{22} x_2). \end{aligned}$$

Notice that the second equation in (SH) is of Kolmogorov form so the climax isoclines are still lines. However, this is not true for the pioneer population. Although (SH) is more complicated mathematically than density-dependent stocking or harvesting, we feel that (SH) is more realistic biologically. We consider (SH) as a system in the two parameters a and c_{11} and study destabilizing period-doubling bifurcations with respect to c_{11} for $a = 0$ and restabilizing period-doubling bifurcations with respect to a for a near 0. In general, harvesting ($a < 0$) may cause the pioneer population density to become negative. In their study of the harvesting of one population, Cooke, Elderkin, and Witten [5] use a step function to curtail harvesting if the population density of the next generation will be negative. However, since a is always small in our studies, we do not encounter negative population density and do not need to consider a discontinuous harvesting function.

An equilibrium $E = (e_1, e_2)$ of (SH) is a solution (x_1, x_2) to the system

$$(3.1) \quad \begin{aligned} x_1 &= x_1 f_1(c_{11} x_1 + c_{12} x_2) + a \\ 1 &= f_2(c_{21} x_1 + c_{22} x_2). \end{aligned}$$

The x_2 -isoclines are determined by $f_2(y_2) = 1$ and, hence, are the pair of parallel lines given by $y_2^* = c_{21} x_1 + c_{22} x_2$. Notice that they are the same as the case without stocking or harvesting, i.e., they do not depend on a or c_{11} . To study the x_1 -isocline consider $H(x_1, x_2) \equiv x_1 - x_1 f_1(c_{11} x_1 + c_{12} x_2)$. For different a 's, the isoclines are the level curves

$$\mathcal{L}_a \equiv \{(x_1, x_2) : H(x_1, x_2) = a\}.$$

When $a = 0$, the pioneer isocline \mathcal{L}_0 is a line. Along \mathcal{L}_0 we compute the gradient vector of H ,

$$\vec{\nabla} H = -x_1 f_1'(y_1) [c_{11} \vec{i} + c_{12} \vec{j}],$$

which points in the positive direction. Hence for $a > 0$, the pioneer isoclines \mathcal{L}_a are curves above and to the right of the line \mathcal{L}_0 in the positive quadrant, see Figure 2. Similarly, for $a < 0$ the pioneer isoclines lie below and to the left of the line \mathcal{L}_0 .

As before, let y_1^* and y_2^* denote the values of the total density variables at equilibrium. y_2^* is independent of the two parameters a and c_{11} . However, y_1^* depends on both parameters. To understand how the coordinates of E depend on a and c_{11} , we apply the implicit function theorem to (3.1) to solve for (x_1, x_2) as a function of (a, c_{11}) near $(a, c_{11}) = (0, \hat{c}_{11})$. Without relating the details, the appropriate nonzero Jacobian at $(e_1, e_2, 0, \hat{c}_{11})$ which guarantees the application of the implicit function theorem is

$$(3.2) \quad e_1 f_1'(y_1^*) f_2'(y_2^*) \det C.$$

Notice that (3.2) is always positive because (2.6) holds. Then the partial derivatives of the coordinates of E at $(a, c_{11}) = (0, \hat{c}_{11})$ may be computed as

$$(3.3) \quad \begin{aligned} \frac{\partial e_1}{\partial a} &= \frac{-c_{22}}{e_1 f_1'(y_1^*) \det C} & \text{and} & \quad \frac{\partial e_2}{\partial a} = \frac{c_{21}}{e_1 f_1'(y_1^*) \det C} \\ \frac{\partial e_1}{\partial c_{11}} &= \frac{-c_{22} e_1}{\det C} & \text{and} & \quad \frac{\partial e_2}{\partial c_{11}} = \frac{c_{21} e_1}{\det C}. \end{aligned}$$

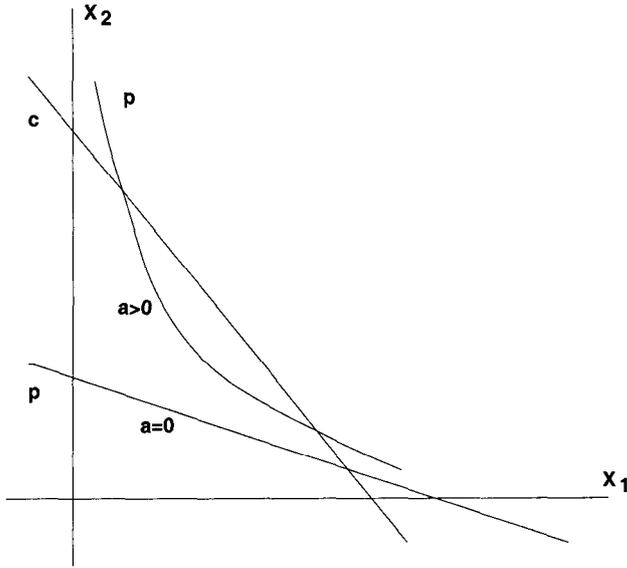


FIGURE 2. Pioneer (p) and climax (c) isoclines for $a \geq 0$.

The dependence of y_1^* on a and c_{11} may be obtained by rewriting the first equation in (3.1) at equilibrium as

$$(3.4) \quad 1 = f_1(y_1^*(a, c_{11})) + \frac{a}{e_1}.$$

Since $f_1(y_1)$ is decreasing, (3.4) implies that if $a > 0$ then $f_1(y_1^*) < 1$ and if $a < 0$ then $f_1(y_1^*) > 1$. Differentiating (3.4) and evaluating at $a = 0$ gives

$$(3.5) \quad \frac{\partial y_1^*}{\partial a} = \frac{-1}{e_1 f_1'(y_1^*)} \quad \text{and} \quad \frac{\partial y_1^*}{\partial c_{11}} = 0.$$

Hence, at $a = 0$, $y_1^*(a, c_{11})$ is an increasing function of a .

We discuss the geometric changes which accompany the destabilizing bifurcation at the equilibrium of prey-predator type, E_1 . Consider the bifurcation with respect to c_{11} when $a = 0$. Since the numerators of the coordinates of E_1 are negative then the x_1 -intercept, y_1^*/c_{11} , of the pioneer isocline is to the right of the climax isocline and the x_2 -intercept of the pioneer isocline is below the climax isocline. Hence,

the positions of the linear isoclines determining E_1 when $a = 0$ are as depicted in Figure 2. From (2.11) and (2.13), E_1 loses stability as c_{11} increases through \hat{c}_{11} . When c_{11} increases, the pioneer isocline pivots to the left about its fixed x_2 -intercept. This causes E_1 to slide down the climax isocline as it destabilizes, which is consistent with the facts that $\partial e_1/\partial c_{11} > 0$ and $\partial e_2/\partial c_{11} < 0$ from (3.3). To move E_1 back up the climax isocline by varying a from 0 requires that a be positive as shown in Figure 2. This is consistent with the facts that $\partial e_1/\partial a < 0$ and $\partial e_2/\partial a > 0$ from (3.3). Hence, one might suspect that increasing pioneer stocking ($a > 0$) would restabilize E_1 . In fact, in the case of density-dependent stocking or harvesting, Selgrade [21] proves that if the pioneer fitness function has nonnegative concavity, which is the case for all familiar examples in the modeling literature, then E_1 is restabilized if and only if stocking is done. However, the geometric heuristics are somewhat deceptive because the stability of E_1 does not actually depend on the position of E_1 but on the eigenvalues of E_1 which vary with both a and c_{11} and are subtly related to a balance between the predatory effect of the climax on the pioneer and the pioneer self-crowding. In Section 4, for constant rate stocking or harvesting, we illustrate an example where harvesting a pioneer with fitness having nonnegative concavity restabilizes E_1 .

Similar geometric changes occur when the equilibrium of competitive type, E_2 , loses stability via a bifurcation when $a = 0$ and c_{11} varies through \hat{c}_{11} . Since $\det C > 0$ and so the numerators of the coordinates of E_2 are positive, the positions of the linear isoclines are interchanged from that depicted in Figure 2. Conditions (ii), (iii), and (iv) guarantee destabilizing bifurcations at E_2 which may occur as c_{11} increases or decreases. Stocking or harvesting will restabilize E_2 depending on the situation.

To study the bifurcations rigorously we need a formula for the eigenvalues of E . The derivative matrix of the right side of (SH) is given by (2.4). Evaluating at E and using (3.4) to write $f_1(y_1^*(a, c_{11}))$ as $1 - a/e_1$, we get

$$(3.6) \quad J(E) = \begin{bmatrix} 1 - a/e_1 & 0 & \mathbf{1} \\ 0 & 1 & \mathbf{1} \end{bmatrix} \begin{bmatrix} e_1 f_1'(y_1^*) & 0 \\ 0 & e_2 f_2'(y_2^*) \end{bmatrix} C.$$

The eigenvalues λ_{\pm} of $J(E)$ are given by

$$\begin{aligned}
 \lambda_{\pm} = & \frac{1}{2} \left(2 + e_1 f_1'(y_1^*) c_{11} + e_2 f_2'(y_2^*) c_{22} - \frac{a}{e_1} \right) \\
 (3.7) \quad & \pm \frac{1}{2} \left[(e_1 f_1'(y_1^*) c_{11} - e_2 f_2'(y_2^*) c_{22})^2 \right. \\
 & + 4e_1 e_2 c_{12} c_{21} f_1'(y_1^*) f_2'(y_2^*) \\
 & \left. + \frac{a^2}{e_1^2} - \frac{2a}{e_1} (e_1 f_1'(y_1^*) c_{11} - e_2 f_2'(y_2^*) c_{22}) \right]^{1/2}
 \end{aligned}$$

E loses stability when the smaller eigenvalue λ_- passes through -1 . Solving (3.7) for $\lambda_- = -1$ we get the bifurcation equation

$$\begin{aligned}
 (3.8) \quad 0 = & 4 + 2e_1 f_1'(y_1^*) c_{11} + 2e_2 f_2'(y_2^*) c_{22} \\
 & + e_1 e_2 f_1'(y_1^*) f_2'(y_2^*) \det C \\
 & - \frac{2a}{e_1} - \frac{ac_{22} e_2 f_2'(y_2^*)}{e_1} \\
 \equiv & G(a, c_{11}).
 \end{aligned}$$

Notice that this bifurcation equation differs from (2.8) because of the last two terms which depend on a . Define the bifurcation curve \mathcal{BC} as the set of points

$$\mathcal{BC} \equiv \{(a, c_{11}) : G(a, c_{11}) = 0\}.$$

Each of the four inequality conditions (i), (ii), (iii), or (iv) guarantees that the equation $G(a, c_{11}) = 0$ has a solution $(a, c_{11}) = (0, \hat{c}_{11})$ where \hat{c}_{11} is given by (2.9). Thus, near $(0, \hat{c}_{11})$, the set of points \mathcal{BC} is nonempty. To determine if stocking or harvesting will restabilize E , we need to understand the nature of the curve \mathcal{BC} near $(0, \hat{c}_{11})$.

We appeal to the implicit function theorem to show that \mathcal{BC} may be considered the graph of c_{11} as a function of a near $(0, \hat{c}_{11})$. The appropriate sufficient condition is

$$\frac{\partial G}{\partial c_{11}}(0, \hat{c}_{11}) \neq 0.$$

Differentiating (3.8) at $(a, c_{11}) = (0, \hat{c}_{11})$, using (3.3) and (3.5), and simplifying, we obtain

$$(3.9) \quad \frac{\partial G}{\partial c_{11}} = \frac{-2c_{21} e_1}{e_2 \det C} [2 + y_1^* f_1'(y_1^*)].$$

The term $[2 + y_1^* f_1'(y_1^*)]$ is nonzero because of conditions (i) through (iv). Hence, we have the following result:

Proposition 3.1. *With the same assumptions as Proposition 2.1, consider the period-doubling bifurcation in the two-parameter bifurcation space determined by (a, c_{11}) . Then the expression (3.9) is nonzero and the bifurcation curve \mathcal{BC} is the graph of c_{11} as a function of a in a neighborhood of $(a, c_{11}) = (0, \hat{c}_{11})$.*

The slope of \mathcal{BC} at $(0, \hat{c}_{11})$ is the negative of $\partial G/\partial a$ divided by $\partial G/\partial c_{11}$. Computing $\partial G/\partial a$ from (3.8) and evaluating at $(0, \hat{c}_{11})$, we get

$$(3.10) \quad \frac{\partial G}{\partial a} = \frac{c_{21} f_2'(y_2^*) \{2c_{22} + f_1'(y_1^*) (y_1^* c_{22} - y_2^* c_{12})\}^2 - 4c_{12} c_{21} c_{22} f_1'(y_1^*)}{e_1 f_1'(y_1^*) \det C \{2c_{22} + f_1'(y_1^*) (y_1^* c_{22} - y_2^* c_{12})\}} - \frac{4c_{12} c_{21} f_1''(y_1^*) (y_1^* c_{22} - y_2^* c_{12}) - 2c_{12} c_{21} [f_1'(y_1^*)]^2 (y_1^* c_{22} - y_2^* c_{12})}{e_1 f_1'(y_1^*) \det C \{2c_{22} + f_1'(y_1^*) (y_1^* c_{22} - y_2^* c_{12})\}}.$$

If we compare (3.10) to the analogous formula for density-dependent stocking or harvesting (see Selgrade [21]), we see that the terms in the numerator are identical except that the last term is absent in the density-dependent case. As we discuss in Section 4, this term which depends on the square of the pioneer derivative may change the sign of $\partial G/\partial a$ and provide for greater variety in the bifurcation curves for the case of constant rate stocking or harvesting.

Before discussing the strategies for restabilizing the two types of equilibria, we mention the significance of the term $[2 + y_1^* f_1'(y_1^*)]$ which is essential to the nondegeneracy of the bifurcation curve via (3.9) and the original period-doubling bifurcation via (2.11). The product $y_1^* f_1'(y_1^*)$ is the linear drop in pioneer fitness from its maximal value when total population is zero to its value of 1 at equilibrium. Because the pioneer fitness is usually concave up, the actual fitness drop is greater than the linear fitness drop. Since 2 is the sum of pioneer and climax fitnesses at equilibrium, the term $[2 + y_1^* f_1'(y_1^*)]$ measures the difference between the pioneer fitness drop and the total ecosystem fitness at equilibrium. We refer to $[2 + y_1^* f_1'(y_1^*)]$ as the *pioneer fitness variation*. If the pioneer fitness variation is negative, then there is a significant decrease in pioneer fitness from its maximum to its equilibrium level. If the pioneer

fitness variation is positive then this decrease is not so great. For two of the most common pioneer fitnesses, this pioneer fitness variation may be written in terms of the maximum pioneer fitness. If the pioneer fitness has either the exponential or the linear form, i.e.,

$$(3.11) \quad f_1(y_1) = b e^{-my_1} \quad \text{or} \quad f_1(y_1) = b - my_1,$$

then the term $[2 + y_1^* f_1'(y_1^*)]$ becomes $2 - \log(b)$ or $3 - b$, respectively. Obviously, $b = f_1(0)$ which is the maximum for the pioneer fitness.

4. Restabilizing the equilibrium of prey-predator type. The equilibrium, E_1 , of prey-predator type loses stability as c_{11} increases through \hat{c}_{11} when the inequalities in (i) are satisfied. If the graph of the bifurcation curve \mathcal{BC} has positive slope at $(0, \hat{c}_{11})$, then stocking ($a > 0$) will restabilize E_1 . The familiar pioneer fitnesses in the modeling literature have nonnegative concavity, i.e., $f_1'' \geq 0$. For instance, the exponential and rational fitnesses are concave up and the linear fitness has zero concavity. Selgrade [21] proves that for density-dependent stocking or harvesting if the pioneer fitness has nonnegative concavity then the bifurcation curve \mathcal{BC} always has positive slope. Hence, E_1 is restabilized if and only if stocking is done. However, for constant rate stocking or harvesting the derivative $\partial G/\partial a$ has a term that is lacking in the case of density-dependent stocking or harvesting. When this new term is large enough, the sign of $\partial G/\partial a$ changes which causes the bifurcation curve to have negative slope.

At E_1 we have $\det C < 0$ and $[2 + y_1^* f_1'(y_1^*)] < 0$, so $\partial G/\partial c_{11}$ is negative from (3.9). The denominator in (3.10) is positive. Since $f_2'(y_2^*) > 0$, it is clear that the first two terms in the numerator in (3.10) are positive. For the third term in the numerator to be positive we assume that $f_1''(y_1^*) \geq 0$. In the case of density-dependent stocking or harvesting, these three terms force $\partial G/\partial a$ to be positive and, hence, the curve \mathcal{BC} has positive slope at $(0, \hat{c}_{11})$. By combining the third and fourth terms in the numerator of (3.10), we see that if $[f_1'(y_1^*)]^2 - 2f_1''(y_1^*) < 0$ then $\partial G/\partial a$ is positive and, hence, the curve \mathcal{BC} also has positive slope in the case of constant rate stocking or harvesting. However, below we discuss an example in the constant rate case where $[f_1'(y_1^*)]^2$ is large enough so that the fourth term in the numerator of (3.10) forces $\partial G/\partial a$ to be negative and, thus, the bifurcation curve \mathcal{BC} has negative slope at $(0, \hat{c}_{11})$, see Figure 3.

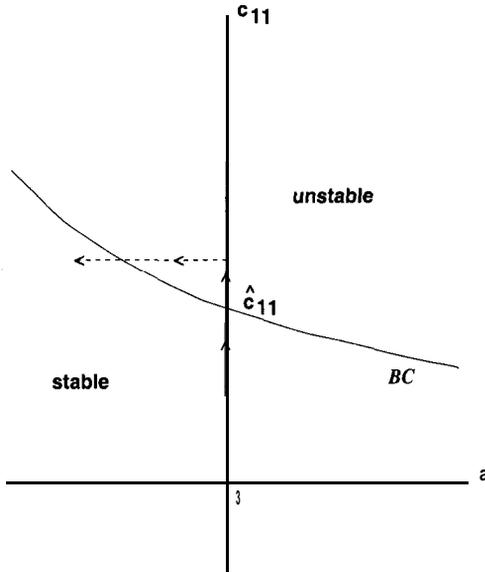


FIGURE 3. Bifurcation curve for (4.1) and arrows indicating parameter variations.

Consider a pioneer population with the linear fitness and a climax population with the quadratic fitness given by the following forms:

$$(4.1) \quad f_1(y_1) = 3.5 - 2y_1 \quad \text{and} \quad f_2(y_2) = \frac{3}{2}y_2 - \frac{1}{4}y_2^2 - \frac{1}{4}.$$

With these fitnesses $y_1^* = 1.25$, $y_2^* = 1$, $f_1'(y_1^*) = -2$, and $f_2'(y_2^*) = 1$. We assume that $c_{12} = c_{21} = 1$ and $c_{22} = 0.2$. The inequality conditions in (i) hold and the period-doubling bifurcation occurs at $\hat{c}_{11} = 85/76 \approx 1.1184$ where $E_1 = (57/59, 10/59) \approx (0.9661, 0.1695)$. Computing (3.9) and (3.10) we have

$$(4.2) \quad \frac{\partial G}{\partial c_{11}} = \frac{-2166}{295} \approx -7.3424 \quad \text{and} \quad \frac{\partial G}{\partial a} = \frac{\quad}{285} \approx -0.27719.$$

Thus the slope of the bifurcation curve BC is approximately -0.03775 . When $a = 0$, E_1 loses stability as c_{11} increases through \hat{c}_{11} into the region above the bifurcation curve as indicated by the arrows on the c_{11} -axis in Figure 3. To restabilize E_1 by varying a we must proceed back below BC which is accomplished by moving left along the dashed line in Figure 3, i.e., we must harvest the pioneer population.

Numerical experiments suggest that the period-doubling bifurcations which occur as c_{11} increases through \hat{c}_{11} are subcritical, i.e., there is an unstable 2-cycle for $c_{11} < \hat{c}_{11}$ which coalesces with the stable equilibrium E_1 when $c_{11} = \hat{c}_{11}$ and which results in E_1 being unstable for $c_{11} > \hat{c}_{11}$. From Selgrade and Roberds [25], signs of two formulas must be calculated to establish rigorously that this bifurcation is subcritical. One sign is for equation (2.20) which is always negative in case (i) because $\det C < 0$ and the remaining terms in (2.20) are positive. The other formula needed to determine the direction of bifurcation is equation (3) in Selgrade and Roberds [25]. For a pair of general fitnesses satisfying (i), the sign of this formula is too difficult to determine. However, for the linear pioneer and the quadratic climax in (4.1) this formula yields ≈ -44.1676 . Thus the curve of period-2 points has negative concavity and, hence, the bifurcation is subcritical.

5. Restabilizing the equilibrium of competitive type. For the equilibrium E_2 of competitive type to lose stability at \hat{c}_{11} , one of the conditions (ii), (iii), or (iv) must be satisfied. Since $\partial G/\partial c_{11} \neq 0$, the bifurcation curve \mathcal{BC} is still the graph of c_{11} as a function of a near $(0, \hat{c}_{11})$; but its slope is more difficult to determine. Recall that $f'_2(y_2^*) < 0$ and $\det C > 0$. Assuming $f''_1(y_1^*) > 0$, from (3.10) we see that the first and third terms of the numerator of $\partial G/\partial a$ are negative and the second and fourth terms are positive. Here we illustrate that in some situations $\partial G/\partial a$ is positive and in other situations it is negative.

First we illustrate how varying the size of $f''_1(y_1^*)$ can change the sign of $\partial G/\partial a$. Consider the inequality conditions in Case (iv) and assume that the pioneer fitness is linear so $f''_1(y_1) = 0$. By expanding and rearranging terms in (3.10), we see that the numerator of $\partial G/\partial a$ becomes

$$(5.1) \quad \begin{aligned} & c_{12}c_{21}[2 - y_2^*f'_2(y_2^*)][f'_1(y_1^*)]^2(y_1^*c_{22} - y_2^*c_{12}) \\ & - 2c_{12}c_{21}c_{22}f'_1(y_1^*)[2 + y_2^*f'_2(y_2^*)] \\ & + c_{21}c_{22}f'_2(y_2^*)[2 + y_1^*f'_1(y_1^*)]\{2c_{22} + f'_1(y_1^*)(y_1^*c_{22} - y_2^*c_{12})\}. \end{aligned}$$

Each term in (5.1) is positive so the numerator of $\partial G/\partial a$ is positive, and the denominator is negative. Hence, $\partial G/\partial a < 0$. From (3.9) we see that $\partial G/\partial c_{11} > 0$. Thus the slope of the bifurcation curve is positive. Since (2.11) is positive, E_2 loses stability as c_{11} decreases through \hat{c}_{11} . In this case harvesting is needed to restabilize E_2 .

However, if we take a pioneer fitness with large positive concavity, we can produce an example where $\partial G/\partial a > 0$ and stocking is required to restabilize E_2 . When $f_1''(y_1^*) > 0$, we see from (3.10) that we add the following negative term to (5.1) to obtain the numerator of $\partial G/\partial a$:

$$(5.2) \quad -4c_{12}c_{21}f_1''(y_1^*)(y_1^*c_{22} - y_2^*c_{12}).$$

In Selgrade [21], an exponential pioneer is used to produce a negative numerator for $\partial G/\partial a$. However, the same function will not work here because of the presence of an additional term in (5.1) with $[f_1'(y_1^*)]^2$. Instead we use a rational function for the pioneer fitness similar to those studied by Hassel and Comins [15]. Consider the following fitnesses where $p > 0$:

$$(5.3) \quad f_1(y_1) = \frac{1}{(0.5 + y_1)^p} \quad \text{and} \quad f_2(y_2) = y_2 \exp(2 - 2y_2).$$

For these fitnesses $y_1^* = 0.5$, $y_2^* = 1$, $f_1'(y_1^*) = -p$, $f_1''(y_1^*) = p(p + 1)$, and $f_2'(y_2^*) = -2$. Assume that $c_{12} = c_{21} = 1$ and $c_{22} = 3$. So the bifurcation occurs at $E_2 = (1/19, 6/19)$ when $\hat{c}_{11} = 3.5$. The exponent $p = 10$ is the smallest integral value of p so that the numerator of $\partial G/\partial a$ is negative. With $p = 10$, we compute

$$\frac{\partial G}{\partial a} = \frac{1}{5} \quad \text{and} \quad \frac{\partial G}{\partial c_{11}} = \frac{2}{19}.$$

Thus for this pioneer fitness the slope of the bifurcation curve \mathcal{BC} is equal to -1.9 at $(a, \hat{c}_{11}) = (0, 3.5)$, and stocking is needed to restabilize E_2 .

Finally, we discuss an example where a cascade of period-doubling bifurcations resulting in a strange attractor may be reversed by constant rate stocking. Consider a linear fitness for the pioneer and a quadratic fitness for the climax having the forms:

$$(5.2) \quad f_1(y_1) = 2 - y_1 \quad \text{and} \quad f_2(y_2) = 4y_2 - y_2^2 - 2.$$

With these fitnesses $y_1^* = 1$, $y_2^* = 3$, $f_1'(y_1^*) = -1$, and $f_2'(y_2^*) = -2$. We assume that $c_{12} = c_{21} = 1$ and $c_{22} = 3.6$. The inequality conditions in (iii) hold and the period-doubling bifurcation occurs at $\hat{c}_{11} = 23/66 \approx 0.34848$ where $E_2 = (33/14, 5/28)$. Selgrade and

Roberds [25] prove that a period-doubling bifurcation occurs as c_{11} increases through \hat{c}_{11} giving rise to a stable 2-cycle, and numerical experiments indicate that as c_{11} increases up to 0.391 a period-doubling cascade results in a strange attractor. From (3.9) and (3.10), we conclude that the slope of the bifurcation curve \mathcal{BC} is approximately 0.17414 at $(a, \hat{c}_{11}) = (0, 23/66)$. Hence stocking is needed to reverse the first period-doubling bifurcation and to restabilize the equilibrium, as indicated by the dashed arrows in Figure 4. Using the tangent line to the bifurcation curve as a guide, we surmise that if $c_{11} = 0.36$ then stocking at a rate of $a = .07$ will result in a stable equilibrium. Numerical experiments confirm our predictions. In addition, if $c_{11} = 0.391$ and a varies from 0 to 0.26, then the cascade of bifurcations is reversed and a stable equilibrium is restored. Such a reversal is similar to that observed by Selgrade [21] for density dependent stocking with the parameter ranging from 0 to 0.11. Thus the interval over which the parameter must vary to reverse the cascade is more than twice as long for the constant rate stocking as compared to the density dependent stocking.

6. Summary and biological interpretations. Here we study period-doubling bifurcations for two-dimensional, discrete population models of Kolmogorov type, where each per capita fitness function depends on a linear combination of the densities of the interacting populations. We assume that one population has a pioneer (decreasing) fitness and the other, a climax (one-humped) fitness. For an equilibrium of such a system to lose stability via period-doubling, it is necessary that the slope of the climax fitness at equilibrium has sign opposite that of the difference between the intraspecific and the interspecific competition, i.e., $\det C$. If the interspecific competition is greater than the intraspecific competition and the climax fitness is increasing at equilibrium so that the climax population is behaving like a predator, then this provides two sources of stress on the pioneer and permits destabilizing bifurcation. We say that such an equilibrium is of prey-predator type. On the other hand, if the intraspecific competition is greater than the interspecific competition and the climax fitness is decreasing at equilibrium so that both populations are truly competing with each other, then the climax population is under stress and destabilizing bifurcation may occur. We say that such an equilibrium is of competitive type. In each case, we obtain necessary and sufficient conditions

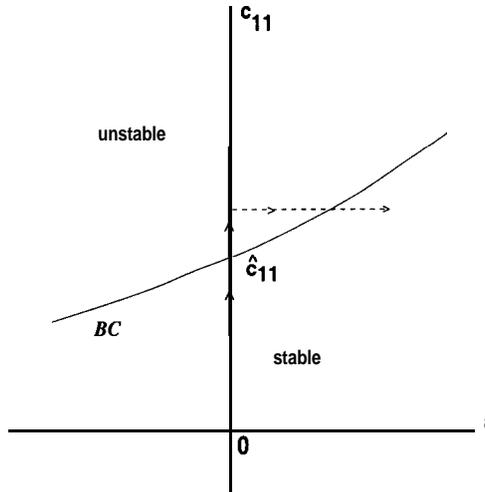


FIGURE 4. Bifurcation curve for (5.2) and arrows indicating parameter variations.

for destabilizing period-doubling bifurcation, see Proposition 2.1, with respect to the pioneer self-crowding parameter. Similar results may be obtained for other intrinsic interaction parameters, i.e., the entries in the interaction matrix C .

To reverse the period-doubling bifurcation and restabilize the equilibrium we consider stocking or harvesting the pioneer population, which is an extrinsic strategy that could be used by an ecosystem manager to re-establish stability. We show that, generically, it is always possible to restabilize the equilibrium, see Proposition 3.1. We compare the effects of constant rate stocking or harvesting to a stocking or harvesting rate proportional to the pioneer density.

A crucial factor in determining whether stocking or harvesting will restabilize the equilibrium is the pioneer fitness variation

$$(6.1) \quad 2 + y_1^* f_1'(y_1^*)$$

where y_1^* is the weighted total density of the pioneer at equilibrium and f_1 is the pioneer fitness. If (6.1) is negative then there is a significant

decrease in pioneer fitness from its maximum value to its value at equilibrium. This is precisely the case when an equilibrium of prey-predator type loses stability, i.e., the pioneer's (the prey) diminished ability to reproduce and the climax's (the predator) reliance on the pioneer result in equilibrium instability. In this case, biological intuition suggests that stocking the pioneer may restabilize the system. In fact, we show that stocking the pioneer is the only way to restabilize the equilibrium if the stocking is proportional to density and the pioneer density has nonnegative concavity (which is the case for all familiar examples in the modeling literature). However, if the stocking is at a constant rate then the situation is more complex and, in Section 4, we present examples where either stocking or harvesting the pioneer will restabilize the equilibrium.

When an equilibrium of competitive type loses stability, (6.1) may be positive or negative, see inequalities (2.14), (2.15), and (2.16). Section 5 discusses reversing this bifurcation using stocking or harvesting. However, there appears to be little biological motivation for determining which strategy will restabilize an equilibrium of competitive type.

REFERENCES

1. W.C. Allee, *Animal aggregations*, reprint of edition published by Univ. of Chicago Press, 1931, Amer. Math. Soc. Press, New York, 1978.
2. J.R. Buchanan and J.F. Selgrade, *Constant* and periodic *rate* stocking and harvesting for Kolmogorov-type population interaction models, Rocky Mountain J. Math. 25 (1995), 67-85.
3. ——— Discontinuous forcing of C^1 vector fields and applications to population interaction models, Canad. Appl. Math. Quart. 3 (1995), 113-136.
4. H.N. Comins and M.P. Hassell, Predation in multi-prey communities, J. Theor. Biol. 62 (1976), 93-114.
5. K.L. Cooke, R. Elderkin and M. Witten, *Harvesting procedures with* management policy *in iterative density-dependent* population models, Natur. Resource Modeling 2 (1988), 383-420.
6. R.F. Costantino, J.M. Cushing, B. Dennis and R.A. Desharnais, Experimentally induced transitions *in the dynamic behavior* of insect populations, Nature 375 (1995), 227-230.
7. J.M. Cushing, *Nonlinear* matrix models and population dynamics, Natur. Resource Modeling 2 (1988), 539-580.
8. J.M. Cushing, *The Allee effect* in age-structured *population* dynamics, Proceed. of the Autumn Course Research Seminars, Mathematical *ecology* (T.G. Hallam, L.J. Gross, and S.A. Levin, eds.), World Scientific Publ. Co., Singapore, 1988, 479-505.

9. J.E. Franke and A.-A. Yakubu, **Mutual exclusion vertices** coexistence for **discrete** competitive systems, *J. Math. Biol.* 30 (1991), 161-168.
10. ———, **Geometry of** exclusion principles in discrete systems, *J. Math. Anal. Appl.* 168 (1992), 385-400.
11. ———, **Species extinction using geometry of** level surfaces, *Nonlinear Anal.: Theory, Methods, Appl.* 21 (1993), 369-378.
12. ———, **Exclusion principles for** density dependent **discrete** pioneer-climax **models**, *J. Math. Anal. Appl.* 187 (1994), 1019-1046.
13. ———, Pioneer exclusion in a one-hump discrete pioneer-climax competitive **system**, *J. Math. Biol.* 32 (1994), 771-787.
14. L. Gardini, R. Lupini and M.G. Messia, **Hopf** bifurcation and transition **to chaos in Lotka-Volterra** equation, *J. Math. Biol.* 27 (1989), 259-272.
15. M.P. Hassell and H.N. Comins, **Discrete time models for two-species competition**, *Theor. Pop. Biol.* 9 (1976), 202-221.
16. J. Hofbauer, V. Hutson and W. Jansen, **Coexistence for** systems governed by **difference equations of Lotka-Volterra type**, *J. Math. Biol.* 25 (1987), 533-570.
17. R.M. May, Biological populations **with** nonoverlapping **generations: stable points, stable cycles, and chaos**, *Science* 186 (1974), 645-647.
18. P.A.B. Moran, Some remarks on animal population dynamics, *Biometrics* 6 (1950), 250-258.
19. W.E. Ricker, **Stock and recruitment**, *J. Fish. Res. Bd. Can.* 11 (1954), 559-623.
20. J.F. Selgrade, Planting and harvesting for pioneer-climax models, *Rocky Mountain J. Math.* 24 (1994), 293-310.
21. ———, Using stocking or harvesting **to reverse period-doubling** bifurcations in discrete **population models**, *J. Difference Eq. and Appl.*, to appear.
22. J.F. Selgrade and G. Namkoong, Stable periodic behavior in a pioneer-climax model, *Natur. Resource Modeling* 4 (1990), 215-227.
23. J.F. Selgrade and G. Namkoong, **Population interactions with growth rates** dependent on **weighted** densities, in *Differential equations models in biology, epidemiology and ecology*, *Lect. Notes in Biomath.* 92, 1991, 247-256.
24. J.F. Selgrade and J.H. Roberds, Lumped-density population models of pioneer-climax **type and stability analysis of Hopf** bifurcations, *Math. Biosci.* 135 (1996), 1-21.
25. J.F. Selgrade and J.H. Roberds, Period-doubling bifurcations **for systems of** difference equations and applications **to** models in population **biology**, *Nonlinear Anal.: Theory, Methods, Appl.* 29 (1997), 185-199.
26. L. Stone, Period-doubling reversals and chaos in simple ecological **models**, *Nature* 365 (1993), 617-620.
27. S. Sumner, Competing species models for pioneer-climax forest dynamical systems, *Proc. Dynamic Systems Appl.* 1 (1994), 351-358.
28. S. Sumner, **Hopf bifurcation in** pioneer-climax **competing species models**, *Math. Biosci.* 137 (1996), 1-24.

29. A.-A. Yakubu, *The effects of planting and harvesting on endangered species in discrete competitive systems*, Math. Biosci. 126 (1995), 1-20.

DEPARTMENT OF MATHEMATICS, NORTH CAROLINA STATE UNIVERSITY, RALEIGH,
NC 276954205
E-mail address: selgrade@math.ncsu.edu

USDA FOREST SERVICE, SOUTHERN INSTITUTE OF FOREST GENETICS, SAUCIER,
MS 39574