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Using Stocking or Harvesting to Reverse Period-Doubling Bifurcations in Discrete Population Models*

JAMES **F. SELGRADE**[†]

Department of Mathematics, North Carolina State University, Raleigh, NC 27695-8205

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This study considers a general class of 2-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). Four sets of necessary inequality conditions are derived which guarantee generically that an equilibrium loses stability through a period-doubling bifurcation with respect to the pioneer self-crowding parameter. A stocking or harvesting term which is proportional to the pioneer density is introduced into the system. Conditions are determined under which this stocking or harvesting will reverse the bifurcation and restabilize the equilibrium. A numerical example illustrates how pioneer stocking can be used to reverse a period-doubling cascade and to maintain the system at any attracting cycle along the cascade.

Keywords: Discrete models; period-doubling bifurcations and reversals; pioneer and climax populations.

Classification Categories: 39A10, 39A12, 92D25

1. INTRODUCTION

Nonlinear difference equations and ordinary differential equations are used to model the effects of the population densities of animals or plants on ecosystems. These models of population interactions possess complex dynamical behavior; even a single, discretely reproducing population with a quadratic transition func-

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[†] Email: selgrade@math.ncsu.edu. Tel: (919) 515 8589.

tion exhibits a cascade of period-doubling bifurcations culminating in chaotic oscillations as illustrated by R. M. May [1]. Typically a period-doubling bifurcation occurs when varying a parameter of the system causes an eigenvalue of an equilibrium of the transition map (in the case of difference equations) or of the return map for a periodic solution (in the case of differential equations) to pass through -1. For the difference equations, the equilibrium often loses stability and a stable cycle of period 2 appears; for the differential equations, the stable periodic solution becomes unstable and a stable solution of roughly twice its period appears. Continued parameter changes may result in a cascade of period-doubling bifurcations and the onset of chaos. Franke and Yakubu [2,3] observe cascades of period-doubling bifurcations in discrete models for competitive interactions of pioneer and climax populations. For differential equation models of population interactions, Gardini *et al.* [4] illustrate a period-doubling transition to a chaotic attractor for 3-dimensional Lotka-Volterra systems, and Buchanan and Selgrade [5] discuss similar behavior for a 3-dimensional model of the interaction among pioneer and climax populations.

Usually chaotic behavior is undesirable in an ecological system. Here we study how systems which undergo destabilizing period-doubling bifurcations due to variations in intrinsic parameters may be restabilized by extrinsic stocking or harvesting strategies. Buchanan and Selgrade [5] observe numerically that varying a crowding parameter in a 3-dimensional interaction model with a periodic solution produces a period-doubling cascade to a strange attractor. They show that harvesting reverses this cascade and illustrate numerically that an appropriate level of harvesting may be chosen to maintain the system at any periodic attractor along the cascade. Thus the asymptotic behavior of this population interaction model may be controlled by harvesting. Unfortunately, obtaining an analytical representation for the return map is not possible so a rigorous examination of the bifurcations cannot be carried out in this example. This is a common difficulty in the case of differential equations because it is not possible to obtain a simple surface transverse to the periodic solution where the return map may be analyzed. However, in the case of difference equations a rigorous mathematical analysis may be carried out. Here we restrict our attention to 2-dimensional difference equations which are analogues of the 3-dimensional ordinary differential equations studied by Buchanan and Selgrade [5]. Period-doubling for higher dimensional discrete systems may be reduced to two dimensions, where one dimension is the bifurcation direction and the other dimension includes all the remaining hyperbolic directions.

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. Previous studies of such systems include

Comins and Hassell [6], Hassell and Comins [7], Hofbauer, Hutson, and Jansen [8], Cushing [9,10], Selgrade and Namkoong [11,12], Franke and Yakubu [2,3,13,14,15], Yakubu [16], Buchanan and Selgrade [5,17], and Selgrade and Roberds [18,19]. One fitness function in our model will be a monotone decreasing function (pioneer fitness) and the other, a one-humped function (*climax* fitness). The interaction of a pioneer population and a climax population permits competition and predation in different regions of the same phase space. Yakubu [16] 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 [20] 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. Bubbling in our setting will occur when the 2-parameter bifurcation curve has a critical point, and we will consider this possibility in future studies.

Section 2 discusses some specific properties of the model equations and biological rationale for these properties. In section 3 we derive four sets of necessary inequality conditions which also guarantee generically that an equilibrium loses stability through a period-doubling bifurcation with respect to an intrinsic pioneer self-crowding parameter. Section 4 introduces into the system a stocking or harvesting term which is proportional to the pioneer density. We determine conditions under which this stocking or harvesting will reverse the bifurcation and restabilize the equilibrium. In section 5 we show 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. Section 6 studies the case of the equilibrium of competitive type. We discuss an example where the size of the concavity of the pioneer fitness function determines whether stocking or harvesting will restabilize the equilibrium. Small positive concavity requires harvesting and large positive concavity requires stocking. Finally, we illustrate numerically how pioneer stocking can be used to reverse a period-doubling cascade and to maintain the system at any attracting cycle along the cascade. Since these results are local, they may be applied to any Kolmogorov system of difference equations where each per capita growth rate is a function of a linear combination of the population densities and where the bifurcating equilibrium is either of prey-predator type or of competitive type.

2. BACKGROUND AND MODEL EQUATIONS

In order to study period-doubling bifurcations we consider systems of 2-dimensional, nonlinear difference equation 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 x 2 matrix C = (c_{ij}) is called the ***interaction matrix.*** The per capita growth rate, the fitness f_i, of the i-th population is a smooth function of y_i. Our model equations are

$$x_i' = x_i f_i(y_i) \qquad i = 1,2 \tag{2.1}$$

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.

Introducing the weighted density variable, y, has the advantage of separating the i-th population's response to density, f_i, from the competitive or cooperative effect of each population. Typically this response may be characterized by monotonicity properties of the fitness f_i as a function of the weighted density y_i. Because of the detrimental effects of crowding, f_i may be a decreasing function of y_i. If f_i is monotonically decreasing for all values Of y_i, (see Figure 1), then x_i is referred to as a *pioneer* population. A variety of pioneer fitness functions appears in the modeling literature. For instance, exponential (see Moran [21] and Ricker [22]), rational (see Hassell and Comins [7]), and linear (see Selgrade and Roberds [18,19]) functions are used. On the other hand, Allee [23] discusses many examples of the beneficial effects of increasing density on both reproduction and survival rates, especially at low density levels. In forest ecosystems, certain tree populations such as oak and maple benefit from the presence of additional trees which provide protection and improved soil conditions. However, as total density increases, ultimately the adverse effects of crowding reduce individual fitness. If f_i monotonically increases up to a unique maximum value and then monotonically decreases as a function of weighted total density, (see Figure 1), then x_i is called a *climax* population. Examples of climax fitnesses are exponential and quadratic functions, see Cushing [9,10] and Selgrade and Namkoong [12]. Henceforth, we assume the x_1 is a pioneer population and x_2 is a climax population.

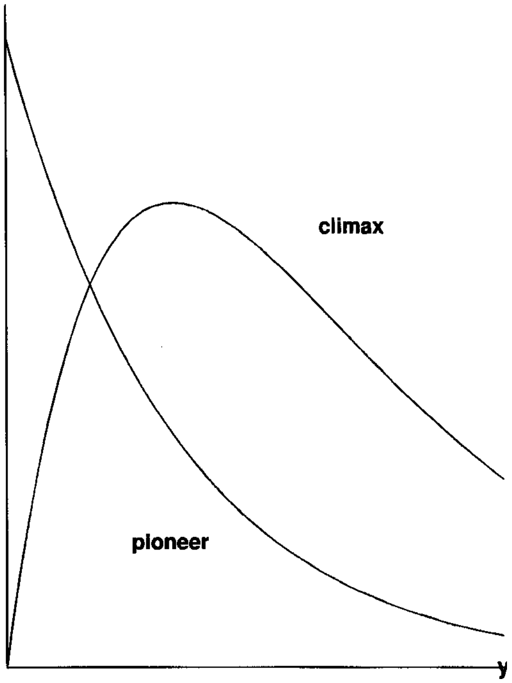

FIGURE 1 Pioneer and climax fitnesses

An equilibrium in the interior of the nonnegative quadrant occurs where all fitnesses assume 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. 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

$$CE = y^* . \tag{2.2}$$

Hence we find

$$e_1 = \frac{y_1^* c_{22} - y_2^* c_{12}}{detC}, \qquad e_2 = \frac{y_2^* c_{11} - y_1^* c_{21}}{detC}. \tag{2.3}$$

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

3. PERIOD-DOUBLING WITHOUT STOCKING OR HARVESTING

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:

$$J(x) = \begin{bmatrix} f_1(y_1) & 0 \\ 0 & f_2(y_2) \end{bmatrix} + \begin{bmatrix} x_1 f_1'(y_1) & 0 \\ 0 & x_2 f_2'(y_2) \end{bmatrix} C. \tag{3.1}$$

When (3.1) is evaluated at E, the first matrix in (3.1) becomes the identity. Let $D(E)$ denote the 2 x 2 diagonal matrix in (3.1) 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.,

$$0 < det[D(E)C] = e_1 e_2 f_1'(y_1^*) f_2'(y_2^*)\ detC < 4. \tag{3.2}$$

Since $f'_1(y_1^*)$ is negative, for (3.2) to hold we must have

$$f_2'(y_2^*)\ detC < 0. \tag{3.3}$$

Notice that (3.2) and (3.3) 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 the other eigenvalue of $J(E)$ not equal to 1 is equivalent to $det[D(E)C] \neq 0$; if one eigenvalue of $J(E)$ is -1 then the other eigenvalue of $J(E)$ not equal to -1 is equivalent to $det[D(E)C] \neq 4$. Thus, for an equilibrium to lose stability by its smaller eigenvalue passing through -1, it is necessary that (3.2) holds and that the slope of the climax fitness $f_2'(y_2^*)$ and $detC$ have opposite signs. The term $detC$ measures the difference between the intraspecific and the interspecific competition. If the intraspecific competition is less than the interspecific competition ($detC < 0$) 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. At such an equilibrium, the pioneer and climax populations interact like prey and predator, respectively. We refer to E_1 as the 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, and the populations truly compete with each other at this equilibrium. We refer to E_2 as the equilibrium of *competitive type.*

Computing the eigenvalues $\lambda_\pm$ of $J(E)$, we obtain

$$\lambda_\pm = \frac{1}{2}\left(2+e_1f'_1(y_1^*)\,c_{11} + e_2f'_2(y_2^*)\,c_{22}\right)$$

$$\pm\frac{1}{2}\left[(e_1f'_1(y_1^*)\,c_{11} - e_2f'_2(y_2^*)\,c_{22})^2 + 4e_1e_2c_{12}c_{21}f'_1(y_1^*)f'_2(y_2^*)\right]^{1/2}. \qquad (3.4)$$

From (3.4) observe that the eigenvalues of the equilibrium of competitive type are real and distinct. However, the equilibrium of prey-predator type may have complex eigenvalues and, in fact, undergo Hopf bifurcation, see [18]. But our bifurcation equation, (3.5) 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 (3.4) for $\lambda_- = -1$, we obtain

$$0 = 4 + 2e_1f'_1(y_1^*)\,c_{11} + 2e_2f'_2(y_2^*)\,c_{22} + e_1e_2f'_1(y_1^*)f'_2(y_2^*)\,detC. \qquad (3.5)$$

The right side of (3.5) may be rewritten as

$$1 + tr\,J(E) + det\,J(E).$$

Clearly this sum is positive if the eigenvalues of E have nonzero imaginary parts. Selgrade and Roberds [18,19] 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 (3.5) 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^* :

$$\hat{c}_{11}=\frac{4c_{12}c_{21} + 2y_1^*c_{21}c_{22}f_2'(y_2^*) + c_{21}y_1^*(y_1^*c_{22} - y_2^*c_{12})f_1'(y_1^*)f_2'(y_2^*)}{[2 + y_2^*f_2'(y_2^*)]\{2c_{22} + f_1'(y_1^*)(y_1^*c_{22} - y_2^*c_{12})\}} \qquad (3.6)$$

For the bifurcation to occur, it is necessary that the right side of (3.6) 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

$$\frac{\partial e_1}{\partial c_{11}} = \frac{-c_{22}e_1}{detC} \quad \text{and} \quad \frac{\partial e_2}{\partial c_{11}} = \frac{c_{21}e_1}{detC} \qquad (3.7)$$

We differentiate λ_- with respect to c_{11} and use (3.5) and (3.7) to evaluate at $c_{11} = \hat{c}_{11}$. This is a tedious algebraic computation which begins by differentiating λ_- in (3.4) yielding two terms, one of which has a square root in the denominator. But when $c_{11} = \hat{c}_{11}$ and $\lambda_- = -1$ then (3.4) may be used to replace this square root term by $[4 + e_1f_1'(y_1^*)\hat{c}_{11} + e_2f_2'(y_2^*)\,c_{22}]$. Then a common denominator is obtained and (3.5) and (3.7) are used to simplify the expression giving

$$\frac{d\lambda_-}{dc_{11}} = \frac{-2e_1c_{21}[2+y_1^*f_1'(y_1^*)]}{e_2detC[4 + e_1f_1'(y_1^*)\hat{c}_{11} + e_2f_2'(y_2^*)c_{22}]} \qquad (3.8)$$

Using (3.2) and (3.4) we conclude that the term in brackets in the denominator of (3.8) is positive. Hence the signs of $detC$ and $[2 + y_1^*f'_1(y_1^*)]$ determine the sign of (3.8). If (3.8) is negative then E loses stability as c_{11} increases; and if (3.8) is positive then E loses stability as c_{11} decreases.

If the bifurcation occurs at the equilibrium E_1 of prey-predator type, where the slope of the climax population $f_2'(y_2^*)$ is positive, then from (3.3) $detC$ must be negative and so is the term $y_1^* c_{22} - y_2^* c_{12}$ because of (2.3). Thus each term in both the numerator and the denominator of (3.6) is positive, and there is always a positive solution $\hat{c}_{11}$ to (3.5) given by (3.6). In fact, at the value $\hat{c}_{11}$, a computation shows that $detC < 0$; so assuming $detC < 0$ is extraneous. Also the numerator of the second coordinate of E_1 must be negative at $\hat{c}_{11}$. Substituting (3.6) into (2.3) and simplifying gives this numerator as

$$y_2^*\hat{c}_{11} - y_1^*c_{21} = \frac{-2c_{21}[\,2 + y_1^*f'_1(y_1^*)](y_1^*c_{22} - y_2^*c_{12})}{[2 + y_2^*f_2'(y_2^*)\,]\{2c_{22} + f_1'(y_1^*)(y_1^*c_{22} - y_2^*c_{12})\}}. \tag{3.9}$$

Since the denominator in (3.9) is positive, we require that 2 t $y_1^*f'_1(y_1^*) < 0$ so that the fraction is negative. Hence, for a period-doubling bifurcation with respect to the parameter c_{11} at the equilibrium E_1, we must assume that

$$\text{case (i):} \qquad y_1^*c_{22} - y_2^*c_{12} < 0 \quad \text{and} \quad 2 + y_1^*f'_1(y_1^*) < 0. \tag{3.10}$$

The inequalities in (3.10) guarantee that the numerators of the coordinates of E_1 are negative and, hence, E_1 is in the positive quadrant when $c_{11} = \hat{c}_{11}$. In addition, the second inequality in (3.10) and the fact that $detC < 0$ imply that (3.8) is negative. Thus E_1 loses stability as c_{11} increases through $\hat{c}_{11}$. Figure 2 indicates the positions of the pioneer and climax isoclines in this case. The fact that the numerators of the coordinates of E_1 are negative results in the x,-intercept, y_1^*/c_{11}, of the pioneer isocline being to the right of the climax isocline and the x,-intercept of the pioneer isocline being below the climax isocline. As c_{11} increases, the x,-intercept of the pioneer isocline moves to the left which causes E_1 to slide down the climax isocline as E_1 loses stability. This agrees with the signs of the derivatives in (3.7). Hence as the pioneer self-crowding parameter, c_{11}, increases, the equilibrium of prey-predator type moves down and to the right in phase space and loses stability.

If the bifurcation occurs at the equilibrium E_2 of competitive type, where the slope of the climax population $f_2'(y_2^*)$ is negative, then from (3.3) $detC$ must be positive and so are the numerators in (2.3). Thus the pioneer and the climax isoclines interchange positions in Figure 2, i.e., see Figure 7. This implies that period-doubling bifurcations with respect to the parameter c_{11} may not occur in the same system at both E_1 and E_2. Since $f_2'(y_2^*) < 0$, the numerator and the denominator of (3.6) for $\hat{c}_{11}$ may not agree in sign and, in fact, the denominator may be zero; and so the feasibility of a period-doubling bifurcation with respect to the parameter

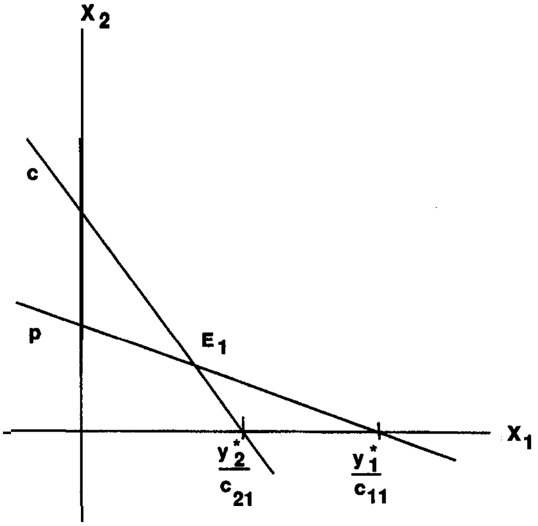

FIGURE 2 Pioneer (p) and climax (c) isoclines and E_1

c_{11} at E_2 requires additional assumptions. We consider cases depending on the signs of $[2 + y_2^* f_2'(y_2^*)]$ and $[2 + y_1^* f_1'(y_1^*)]$. If both $[2 + y_2^* f_2'(y_2^*)]$ and $[2 + y_1^* f_1'(y_1^*)]$ are positive then (3.9) is negative which precludes E_2 from being in the positive quadrant.

If both $[2 + y_2^* f_2'(y_2^*)]$ and $[2 + y_1^* f_1'(y_1^*)]$ are negative then the numerator in (3.9) is positive and we need

$$2c_{22} + f_1'(y_1^*)(y_1^* c_{22} - y_1^* c_{12}) < 0 \tag{3.11}$$

for the denominator in (3.9) to be positive. Also $\hat{c}_{11} > 0$ follows from (3.11). Hence the following assumptions permit a bifurcation at E_2,

$$\text{case (ii):}\quad y_1^* c_{22} - y_2^* c_{12} > 0,\quad 2 + y_2^* f_2'(y_2^*) < 0,\quad 2 + y_1^* f_1'(y_1^*) < 0,$$
$$\text{and}\quad 2c_{22} + f_1'(y_1^*)(y_1^* c_{22} - y_2^* c_{12}) < 0. \tag{3.12}$$

Given (3.12), $d\lambda_- /dc_{11} > 0$ so E_2 loses stability as c_{11} decreases.

If $[2 + y_2^* f_2'(y_2^*)] < 0$ and $[2 + y_1^* f_1'(y_1^*)] > 0$ then the inequality in (3.11) is reversed, and so (3.9) is positive. But to get $\hat{c}_{11} > 0$ we need to assume

$$4c_{12} + y_1^* f_2'(y_2^*)\{2c_{22} + f_1'(y_1^*)(y_1^* c_{22} - y_2^* c_{12})\} < 0. \tag{3.13}$$

Thus the following conditions permit a bifurcation at E_2,

$$\text{case (iii):}\quad y_1^* c_{22} - y_2^* c_{12} > 0,\quad 2 + y_2^* f_2'(y_2^*) < 0,\quad 2 + y_1^* f_1'(y_1^*) > 0,$$
$$\text{and}\quad 4c_{12} + y_1^* f_2'(y_2^*)\{2c_{22} + f_1'(y_1^*)(y_1^* c_{22} - y_2^* c_{12})\} < 0. \tag{3.14}$$

In this case $d\lambda_- /dc_{11} < 0$, so E_2 loses stability as c_{11} increases.

If $[2 + y_2^* f_2'(y_2^*)] > 0$ and [2 t $y_1^* f_1'(y_1^*)$] < 0 then we need to assume that the inequality in (3.11) is reversed so that (3.9) is positive and to assume that the inequality in (3.13) is reversed so that $\hat{c}_{11} > 0$. Hence bifurcation occurs at E_2 if,

$$\text{case (iv):}\quad y_1^* c_{22} - y_2^* c_{12} > 0, \quad 2 + y_2^* f_2'(y_2^*) > 0, \quad 2 + y_1^* f_1'(y_1^*) < 0,$$

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

$$\text{and } 2c_{22} + f_1'(y_1^*)\;(y_1^* c_{22} - y_2^* c_{12}) > 0. \tag{3.15}$$

Here $d\lambda_-/dc_{11} > 0$, so E_2 loses stability as c_{11} decreases. For cases (ii), (iii), and (iv) computations show that $detC > 0$ at $\hat{c}_{11}$, which is required for E_2 to be in the positive quadrant.

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 determine the shape of the curve of period-2 points. Conditions sufficient to prove that this curve is "parabolic" in shape are derived in [19] and involve combinations of the first three derivatives of the fitness functions.

The preceding discussion in section 3 establishes the following result:

PROPOSITION 3.1. *Suppose that E is an equilibrium of (2.1) in the positive quadrant. Assume that*

$$0 < e_1 e_2 f_1'(y_1^*) f_2'(y_2^*)\, detC < 4$$

and that one of the sets of inequalities (i), (ii), (iii), or (iv) holds. Then E loses stability as c_{11} *either increases or decreases through* $\hat{c}_{11}$ *given by (3.6), because its smaller eigenvalue passes through* -1. *Its larger eigenvalue remains inside the unit circle.*

4. DENSITY-DEPENDENT STOCKING AND HARVESTING

Since varying the pioneer self-crowding parameter c_{11} destabilizes the equilibrium, one would suspect that stocking or harvesting the pioneer population may restabilize the equilibrium. We investigate this possibility by adding a density-dependent stocking $(a > 0)$ or harvesting $(a < 0)$ term to the pioneer difference equation in (2.1) to get:

$$\begin{aligned} x_1' &= x_1 f_1(c_{11}x_1 + c_{12}x_2) + ax_1 \\ x_2' &= x_2 f_2(c_{21}x_1 + c_{22}x_2) \end{aligned} \tag{SH}$$

The amount of stocking or harvesting is directly proportional to the current pioneer density with proportionality constant "a". Mathematically, this is the simplest way to include stocking or harvesting because (SH) retains the Kolmogorov form and the isoclines are still lines. 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. We consider (SH) as a system in the two parameters a and c_{11}.

An equilibrium $E = (e_1, e_2)$ in the positive quadrant is a solution of the simultaneous equations:

$$1 = f_1(c_{11}e_1 + c_{12}e_2) + a \tag{4.1}$$
$$1 = f_2(c_{21}e_1 + c_{22}e_2).$$

The climax isoclines are the two parallel lines determined by the values of the weighted density variable y_2 where $f_2(y_2) = 1$ as in the case when $\boldsymbol{a = 0}$. The two values for y_2^* such that $f_2(y_2^*) = 1$ are independent of c_{11} and a. The pioneer **isocline** is determined by the value of y_1 where $f_1(y_1) = 1 - a$ which we denote y_1^* (a), see Figure 3.

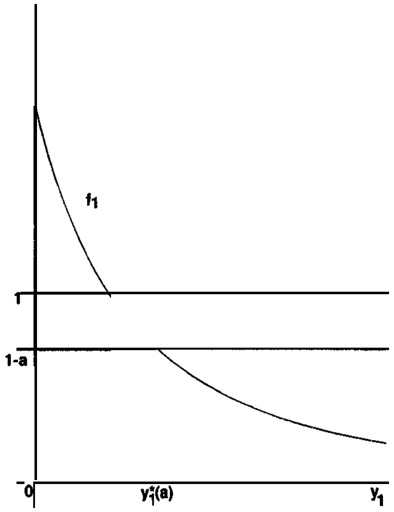

FIGURE 3 Pioneer fitness f_1 with stocking (a > 0)

Since $f_1(y_1)$ is decreasing, it is clear that y_1^* (a) is an increasing function of a. In fact, $dy_1^*/da = -1/f_1'(y_1^*) > 0$. Notice that y_1^* (a) is independent of c_{11}. The coordinates of $\boldsymbol{E}$ are still given by (2.3) except that y_1^* is a function of a. From (2.3) we compute

$$\frac{\partial e_1}{\partial a} = \frac{-c_{22}}{f_1'(y_1^*(a))\, detC} \text{ and } \frac{\partial e_2}{\partial a} = \frac{c_{21}}{f_1'(y_1^*(a))\, detC}. \tag{4.2}$$

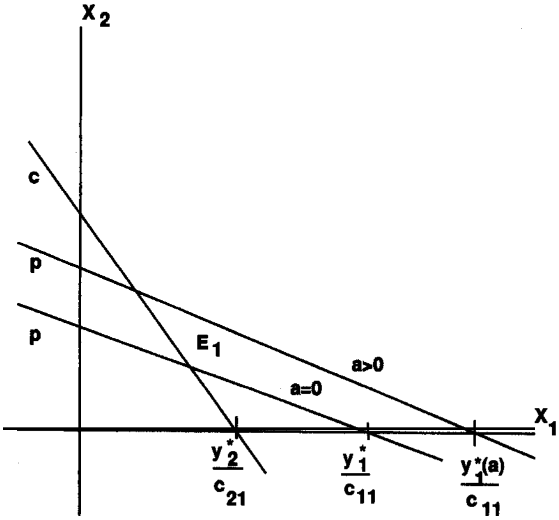

FIGURE 4 Pioneer (p) and climax (c) isoclines near E_1 for a $\geq$ 0

The pioneer isocline is given by the linear equation

$$c_{11}x_1 + c_{12}x_2 = y_1^*(a). \tag{4.3}$$

Since y_1^* (a) is increasing as a increases, the x,-intercept and x,-intercept of this isocline move away from the origin as a increases but its slope is always $-c_{11}/c_{12}$. In the case of the equilibrium E_1 of prey-predator type, increasing a moves E_1 up and left along the climax isocline but increasing c_{11} moves E_1 down and right, see Figure 4. The opposite behavior occurs at E_2 because the positions of the isoclines interchange, see Figure 7.

The derivative of the right side of (SH) evaluated at an equilibrium E is:

$$J(E) = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} + \begin{bmatrix} e_1 f_1'(y_1^*(a)) & 0 \\ 0 & e_2 f_2'(y_2^*) \end{bmatrix} C. \tag{4.4}$$

This matrix is analogous to (3.1) except that e_1, e_2, and y_1^* depend on the parameters c_{11} and a. A period-doubling occurs when the smaller eigenvalue λ_- in (3.4) passes through -1. Hence we need a solution (a,c_{11}) to equation (3.5). We define the bifurcation function $G(a,c_{11})$ to be the right side of (3.5) and repeat that equation here:

$$0=4+2e_1 f_1'(y_1^*(a))\ c_{11}+2e_2 f_2'(y_2^*)\ c_{22}+e_1 e_2 f_1'(y_1^*(a))\ f_2'(y_2^*)\ detC \equiv G(a,c_{11}). \tag{4.5}$$

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 (3.6). Thus, near $(0, \hat{c}_{11})$, the bifurcation curve BC is a nonempty set of points:

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

If a = 0 and if the equilibrium E loses stability because of a variation in c_{11} then we would like to determine if stocking or harvesting (a $\neq$ 0) will restabilize E. Understanding the nature of the curve BC near (0, $\hat{c}_{11}$) will answer this question.

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

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

From (4.5) we compute $\partial G/\partial c_{11}$ where $y_1^* = y_1^*(0)$:

$$\frac{\partial G}{\partial c_{11}} = 2\hat{c}_{11} f_1'(y_1^*) \frac{\partial e_1}{\partial c_{11}} + 2e_1 f_1'(y_1^*) + 2c_{22} f_2'(y_2^*) \frac{\partial e_2}{\partial c_{11}} +$$

$$\frac{\partial e_1}{\partial c_{11}} e_2 f_1'(y_1^*) f_2'(y_2^*) \, detC$$

$$+ e_1 \frac{\partial e_2}{\partial c_{11}} f_1'(y_1^*) f_2'(y_2^*) \, detC + c_{22} e_1 e_2 f_1'(y_1^*) f_2'(y_2^*) . \tag{4.6}$$

Inserting (3.7) into (4.6) and rearranging terms gives

$$\frac{\partial G}{\partial c_{11}} = \frac{c_{21} e_1}{e_2 detC} [-2c_{12} f_1'(y_1^*) e_2 + 2 c_{22} f_2'(y_2^*) \quad e_2 +$$

$$e_1 e_2 f_1'(y_1^*) f_2'(y_2^*) \, detC]. \tag{4.7}$$

From (4.5) we obtain

$$2c_{22} f_2'(y_2^*) e_2 + e_1 e_2 f_1'(y_1^*) f_2'(y_2^*) \, detC = -4 - 2\hat{c}_{11} f_1'(y_1^*) e_1$$

and substitute into (4.7) to get

$$\frac{\partial G}{\partial c_{11}} = \frac{-2c_{21} e_1}{e_2 detC} [2 + y_1^* f_1'(y_1^*)]. \tag{4.8}$$

Using (2.3) for e_1 and e_2 in (4.8) leads to the alternate form

$$\frac{\partial G}{\partial c_{11}} = \frac{[2 + y_2^* f_2'(y_2^*)]\{2c_{22} + f_1'(y_1^*) (y_1^* c_{22} - y_2^* c_{12})\}}{detC} \tag{4.9}$$

The advantage of (4.9) is that the right side is easily computed from the interaction coefficients and the weighted density variables. The sign of $\partial G/\partial c_{11}$, is determined by the signs of $detC$ and $[2 + y_1^* f_1'(y_1^*)]$, the latter is given in conditions (i) through (iv). For cases (i) and (iii), $\partial G/\partial c_{11}$ is negative; for cases (ii) and (iv), $\partial G/\partial c_{11}$ is positive. Hence we have established the following result:

PROPOSITION 4.1. *Suppose that one of the sets of inequalities (i), (ii), (iii), or (iv) holds. Then the bifurcation curve BC in the (a, c_{11})-space of parameters is the graph of c_{11} as a function of a near the point $(0, \hat{c}_{11})$.*

The slope of this graph 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 (4.5) and evaluating at $(0, \hat{c}_{11})$, we obtain

$$\begin{aligned}\frac{\partial G}{\partial a} &= 2\hat{c}_{11} f_1'(y_1^*)\frac{\partial e_1}{\partial a} + 2\hat{c}_{11} e_1 f_1''(y_1^*)\frac{\partial y_1^*}{\partial a} + 2c_{22} f_2'(y_2^*)\frac{\partial e_2}{\partial a} + \\ &\quad \frac{\partial e_1}{\partial a} e_2 f_1'(y_1^*) f_2'(y_2^*)\, detC \\ &\quad + e_1\frac{\partial e_2}{\partial a} f_1'(y_1^*) f_2'(y_2^*)\, detC + e_1 e_2 f_1''(y_1^*)\frac{\partial y_1^*}{\partial a} f_2'(y_2^*)\, detC. \end{aligned} \tag{4.10}$$

Inserting (4.2) into (4.10) and rearranging terms gives

$$\begin{aligned}\frac{\partial G}{\partial a} &= \frac{1}{f_1'(y_1^*)\, detC}\big[(c_{22} f_1'(y_1^*) + e_1 f_1''(y_1^*)\, detC)\{-2\hat{c}_{11} - \\ &\quad f_2'(y_2^*)\,(y_2^*\hat{c}_{11} - y_1^* c_{21})\} \\ &\quad + c_{21} f_2'(y_2^*)\,\{2c_{22} + f_1'(y_1^*)\,(y_1^* c_{22} - y_2^* c_{12})\}\big]. \end{aligned} \tag{4.11}$$

Using (3.6) to substitute for $\hat{c}_{11}$ and (3.9) to substitute for $y_2^*\hat{c}_{11} - y_1^* c_{21}$, we get

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

and inserting this into (4.11) we obtain

$$\begin{aligned}\frac{\partial G}{\partial a} &= \frac{c_{21} f_2'(y_2^*)\{2c_{22} + f_1'(y_1^*)(y_1^* c_{22} - y_2^* c_{12})\}}{f_1'(y_1^*)\, detC} \\ &\quad - \frac{4c_{12}c_{21}[c_{22} f_1'(y_1^*) + e_1 f_1''(y_1^*)\, detC]}{f_1'(y_1^*)\, detC\{2c_{22} + f_1'(y_1^*)(y_1^* c_{22} - y_2^* c_{12})\}}. \end{aligned} \tag{4.12}$$

For each of our four cases, the sign of $\partial G/\partial a$ may not be determined in general. However, reasonable biological assumptions will permit us to establish the sign of (4.12) and to conclude appropriate stocking or harvesting strategies to restabilizing the equilibrium.

5. 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. Since $f_2'(y_2^*) > 0$ and $detC$ *c 0* at

E_1, it is clear that the first term in (4.12) is positive. For the second term in (4.12) to be positive we need that the term in brackets in the numerator is negative. This term depends on the concavity of the pioneer fitness. For the pioneer fitnesses in the modeling literature, $f_1'' \geq 0$. For instance, the exponential and rational fitnesses are concave up and the linear fitness has zero concavity. Hence, it is reasonable to assume that

$$f_1''(y_1^*) \geq 0 \tag{5.1}$$

From (5.1) it follows that (4.12) is positive. Since $\partial G/\partial c_{11} < 0$ in case (i), the graph of the bifurcation curve *BC* has positive slope at $(0, \hat{c}_{11})$, see Figure 5.

At a point in parameter space $(0, c_{11})$ where $c_{11} > \hat{c}_{11}$, E_1 is unstable. To restabilize E_1 by varying a only, we must reach a point in parameter space below and to the right of the bifurcation curve, i.e., stocking the pioneer restabilizes the equilibrium. Biologically this is somewhat counterintuitive. Since increasing pioneer self-crowding destabilizes E_1, one might suspect that reducing the self-crowding by harvesting would restabilize E_1. However, from Figure 5, it is clear that above $(0, \hat{c}_{11})$ but near $(0, \hat{c}_{11})$ harvesting will keep E_1 unstable. In fact, harvesting the pioneer in this system-increases pioneer density and decreases climax density at equilibrium. Thus the predatory effect of the climax population on the pioneer population is reduced by harvesting; apparently, this predation is crucial to maintaining equilibrium stability. The geometry of Figure 4 may help in understanding this phenomenon. With a = 0 as c_{11} increases through $\hat{c}_{11}$, the pioneer isocline

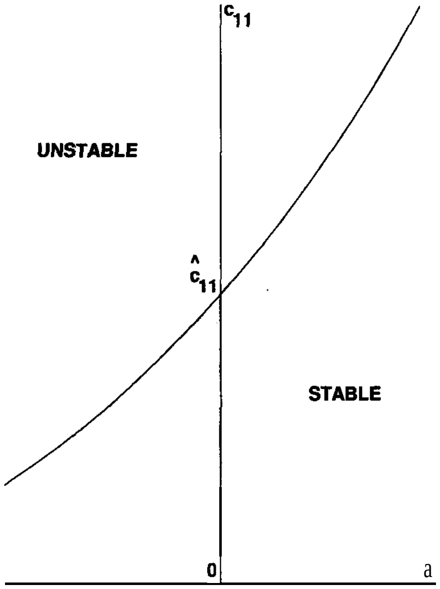

FIGURE 5 Bifurcation curve near $(0, \hat{c}_{11})$

swings to the left and the equilibrium E_1 loses stability as it moves down the climax isocline. As E_1 moves down the climax isocline, the pioneer density is increasing and the climax density is decreasing. Stocking or harvesting displaces the pioneer isocline parallel to itself (see Figure 4) - upward for stocking and downward for harvesting. Hence, harvesting would move E_1 farther down the climax isocline. Stocking moves E_1 up the climax isocline to a larger climax density and a smaller pioneer density and restabilizes E_1. The restabilization depends on factors more subtle than the position of E_1. It depends on a balance between the predatory effect of the climax on the pioneer and the pioneer self-crowding. This is reflected in the eigenvalues of the matrix $J(E_1)$ which vary with both a and c_{11}, see (4.4). Thus, for all biologically reasonable fitness functions, the loss of stability of the equilibrium of prey-predator type via a period-doubling bifurcation with respect to c_{11} may be reversed only by stocking. Specifically, we have obtained:

PROPOSITION 5.1. *Assume that (i) holds and that $f''_1(y_1^*) \geq 0$. Then the equilibrium E_1 of prey-predator type is restabilized if and only if stocking is done (i.e., $a > 0$).*

6. 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 BC is still the graph of c_{11} as a function a near $(0, \hat{c}_{11})$; but its slope is more difficult to determine. Here we illustrate that in some situations this slope is positive and in other situations it is negative. Recall that at E_2 we have $f'_2(y_2^*) < 0$ and $detC > 0$. The fact that $detC > 0$ is pivotal to determining the sign of $\partial G/\partial a$. The sign of the second term in (4.12) depends on the sign of the term in brackets in the numerator. The first addend is negative but the second addend is nonnegative because typically $f''_1(y_1^*) \geq 0$. We present two examples of how the concavity of the pioneer fitness affects the slope of the bifurcation curve.

Consider the inequality conditions in (iv). First assume that the pioneer fitness is linear so $f''_1 = 0$. By finding a common denominator, we combine the two terms in (4.12) to get the numerator:

$$\begin{aligned}&c_{21}c_{22}f'_2(y_2^*)\ [2+y_1^* f'_1(y_1^*)]\{2c_{22}+f'_1(y_1^*)(y_1^*c_{22}-y_2^*c_{12})\}\\&-2c_{12}c_{21}c_{22}f'_1(y_1^*)\,[2+y_2^*f'_2(y_2^*)]-c_{12}c_{21}\,y_2^*f'_2(y_2^*)\\&[f'_1(y_1^*)]^2(y_1^*c_{22}-y_2^*c_{12})\,. \qquad (6.1)\end{aligned}$$

Each term in (6.1) is positive so the numerator of $\partial G/\partial a$ is positive, and the denominator

$$(f_1'(y_1^*)\,detC\{2c_{22} + f_1'(y_1^*)(y_1^*c_{22} - y_1^*c_{12})\}) \tag{6.2}$$

is negative. Hence, $\partial G/\partial a < 0$. From (4.8) or (4.9), we see that $\partial G/\partial c_{11} > 0$. Thus the slope of the bifurcation curve is positive. Since (3.8) is positive, E_2 loses stability as c_{11} decreases through $\hat{c}_{11}$. In this case harvesting is needed to restabilize E_2, see Figure 5 except that the region of stability is above the curve and the region of instability is below.

However, if we take a pioneer fitness with positive concavity, we can produce an example where stocking is required to restabilize E_2. When $f_1''(y_1^*) > 0$, we see from (4.12) that we add the following negative term to (6.1) to obtain the numerator of $\partial G/\partial a$:

$$-4c_{12}c_{21}f_1''(y_1^*)(y_1^*c_{22} - y_2^*c_{12}). \tag{6.3}$$

Consider exponential fitnesses for both the pioneer and the climax populations of the forms:

$$f_1(y_1) = exp(r - ry_1) \qquad \text{and} \qquad f_2(y_2) = y_2exp(2 - 2y_2). \tag{6.4}$$

Here $r > 0$ is the pioneer decay rate and measures the decrease in pioneer per capita growth with respect to an increase in weighted total density at equilibrium. For these fitness functions, $y_1^* = y_2^* = 1$ and we find that $f_1'(y_1^*) = -r$, $f_1''(y_1^*) = r^2$, and $f_2'(y_2^*) = -1$. We assume that $c_{12} = c_{21} = 1$ and $c_{22} = \frac{5}{4}$. As r increases, the term in (6.3) becomes more dominant in the numerator of $\partial G/\partial a$. For instance, if r = 3 then the period-doubling bifurcation occurs at $\hat{c}_{11} = \frac{9}{7}$ where $E_2 = \left(\frac{7}{17}, \frac{8}{17}\right)$. Adding (6.1) and (6.3) and dividing by (6.2) we obtain

$$\frac{\partial G}{\partial a} = \frac{-47}{51}.$$

Thus for this pioneer fitness the slope of the bifurcation curve is positive, and harvesting is needed to restabilize E_2 as with the linear pioneer above. However, if $r = 6$ the period doubling-bifurcation occurs at $\hat{c}_{11} = 3$ where $E_2 = \left(\frac{1}{11}, \frac{8}{11}\right)$. We compute

$$\frac{\partial G}{\partial a} = \frac{14}{33} \quad \text{and} \quad \frac{\partial G}{\partial c_{11}} = \frac{4}{11},$$

Thus the slope of this bifurcation curve is -7/6. Hence E_2 loses stability as c_{11} decreases through $\hat{c}_{11} = 3$ and stability is restored by increasing a enough so that the system corresponds to a point in parameter space above and to the right of the bifurcation curve (see Figure 6). Numerical experiments show that the destabilizing effect of decreasing c_{11} below 3 by increments of 0.01 may be compensated for by increasing a by increments of 0.01, which is consistent with our calculation of $-7/6$ as the slope of the bifurcation curve.

If we study the position of the isoclines near the equilibrium E_2 (see Figure 7), we see that increasing c_{11} swings the pioneer isocline to the left and moves E_2 up the climax isocline and decreasing c_{11} swings the pioneer isocline to the right and moves E_2 down the climax isocline. In case (iv) decreasing c_{11} moves E_2 down and destabilizes it. Our arguments show that stocking or harvesting may be required to restabilize E_2 depending on the concavity of the pioneer fitness. If the concavity is large then stocking is needed, which causes E_2 to move farther down the climax isocline and to attain a higher pioneer density. If the concavity is small then harvesting is needed, which causes E_2 to move back up the climax isocline and to reduce pioneer density. However, E_2 may require stocking to restabilize even with zero concavity as shown by our next example which satisfies (iii).

For our last example, we take the interaction between a pioneer and a climax population which occurs when the pioneer fitness is linear and the climax fitness is quadratic:

$$f_1(y_1) = 2 - y_1 \quad \text{and} \quad f_2(y_2) = 4y_2 - y_2^2 - 2. \tag{6.5}$$

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 $\hat{c}_{11} = \frac{23}{66} \approx 0.34848$ where $E_2 = \left(\frac{33}{14}, \frac{5}{28}\right)$. Selgrade and Roberds [19] prove that a period-doubling bifurcation occurs as c_{11} increases through $\hat{c}_{11}$ giving rise to a stable 2-cycle. In fact, as c_{11} continues to increase, a cascade of period-doubling bifurcation occurs and culminates in a strange attractor with two connected components when $c_{11} \approx 0.391$. Here we consider system (SH) as a two parameter bifurcation problem in a and c_{11}. Using (4.9) and (4.12), we find that the slope of the bifurcation curve is approximately 0.41736 at $(a, \hat{c}_{11}) = (0, \frac{23}{66})$. Hence stocking is needed to reverse the first period-doubling and to restabilize the equilibrium. In fact, numerical studies indicate that each bifurcation in the cascade may be reversed by an appropriate level of stocking. If c_{11} is fixed at 0.391 and a increases from 0 to 0.11 then the strange attractor is transformed back to a stable equilibrium. Figure 8 depicts period-halving which occurs as a increases from a = 0.0026 to a ≈ 0.006 – an attracting 16-cycle bifurcates to an 8-cycle and then to a 4-cycle.

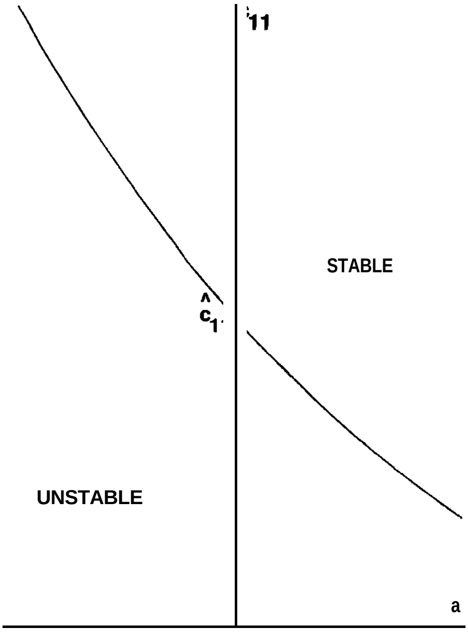

FIGURE 6 Bifurcation curve near (0, $\hat{c}_{11}$) for exponential pioneer (6.4) with r = 6, which shows that stocking restabilizes E_2

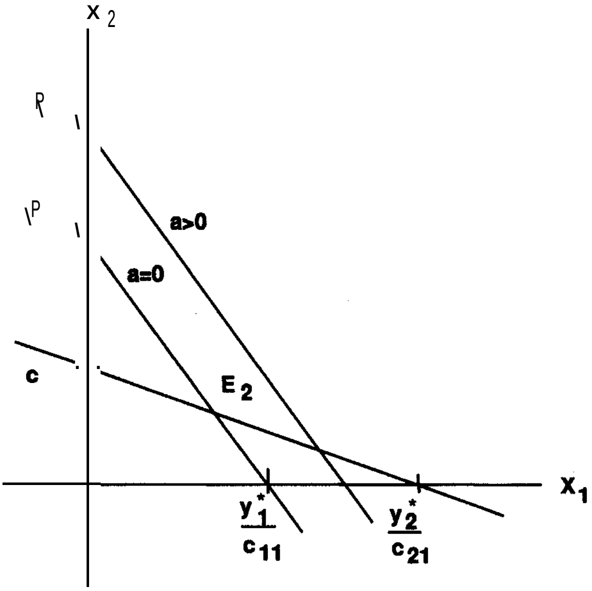

FIGURE 7 Pioneer (p) and climax (c) isoclines near E_2 for a ≥ 0

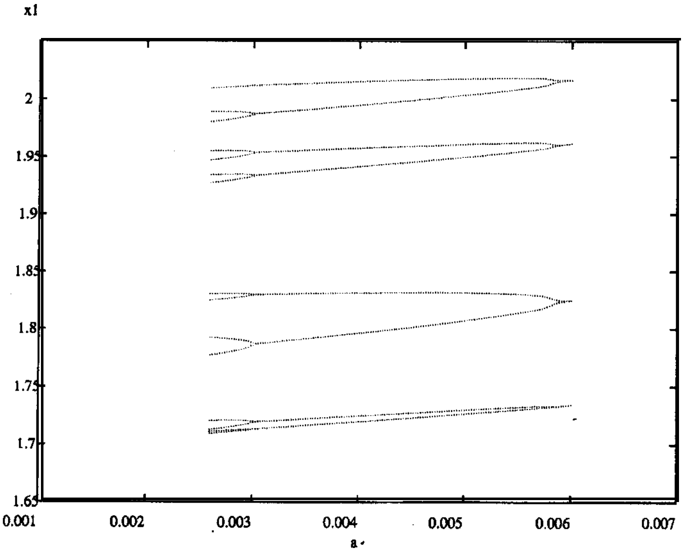

FIGURE 8 Period-halving for c_{11} = 0.391 and 0.0026 ≤ a ≤ 0.006 and fitnesses (6.5)

7. SUMMARY

Here we derive four sets of inequality conditions (see (3.10), (3.12), (3.14), and (3.15)) which guarantee that an equilibrium loses stability through a period-doubling bifurcation with respect to the intrinsic pioneer crowding parameter cu. We introduce into the system a stocking or harvesting term which is proportional to the pioneer density. The constant of proportionality is the parameter a. The character of the bifurcation curve in the (a&-parameter space near the point $(0, \hat{c}_{11})$, where the equilibrium loses stability, determines whether stocking or harvesting restabilizes the equilibrium. In the case of the equilibrium E_1 of prey-predator type, if the pioneer fitness has nonnegative concavity then E_1 is restabilized if and only if stocking is done. For the equilibrium E_2 of competitive type, we exhibit examples which show that the size of the concavity of the pioneer fitness function determines whether stocking or harvesting is needed to restabilize E_2. Finally we discuss an example where a period-doubling cascade may be reversed and maintained at any attracting cycle along the cascade by appropriate levels of pioneer stocking.

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