ROCKY MOUNTAIN
JOURNAL OF MATHEMATICS
Volume 24, Number 1, Winter 1994

PLANTING AND HARVESTING FOR PIONEER-CLIMAX MODELS

JAMES F. SELGRADE

Dedicated to Paul Waltman on the occasion of his 60th birthday

ABSTRACT. Kolmogorov-type systems of ordinary differential equations are presented, where per capita growth rates are either monotone decreasing (pioneer) or one-humped (climax) functions of weighted population densities. Varying an intraspecific crowding parameter destabilizes an equilibrium via Hopf bifurcation. This effect may be reversed by planting the pioneer population or harvesting the climax population. Averaging methods are used to study the two-dimensional system with constant rate or periodic rate planting.

1. Introduction. Competition and cooperation among different individuals and different species in an ecosystem for its natural resources are important factors in determining the development of the ecosystem. For example, a tree in a forest competes with its neighbors for light, space, carbon dioxide, and soil nutrients. Although the intensity of this competition may or may not be affected by the species type of the neighboring trees, it is affected by neighboring population density. Analogously, an animal may not care what type of competitor is consuming its food, but the amount of food consumed will be affected by competitor population density and, possibly, by species characteristics of the competitors, for instance, physical size. We try to model the effects of population density on the survival and growth of an individual species by assuming that the species' per capita growth rate (i.e., fitness) is a function of a weighted total density variable. This total density variable is a linear combination of the densities of the interacting species with coefficients weighting the intensity of the effect of each species. An example of such a model is the Lotka-Volterra system where the per capita growth rate is just a linear combination of the

---

Received by the editors on March 9, 1993.
Research supported by NSF grant DMS-9103829 and by the USDA Forest Service, Southeastern Forest Experiment Station, Pioneering (Population Genetics of Forest Trees) Research Unit, Raleigh, NC.

densities of the interacting populations. Other studies assuming this approach include May [**11**], Comins and Hassell [**2**], Hassell and Comins [**9**], Hofbauer, Hutson and Jansen [**10**], Cushing [**3, 4**], Selgrade and Namkoong [**14, 15**], and Franke and Yakubu [**5**].

Selgrade and Namkoong [**14, 15**] study such models where a population's fitness is either a monotone decreasing function of its weighted total density (a pioneer species) or a one-humped function of its weighted total density (a climax species). They observe for two and three dimensional systems that stable equilibrium behavior may be lost by decreasing the pioneer intraspecific crowding parameter or by increasing the climax intraspecific crowding parameter. Here we show that this destabilization may be reversed by constant rate or periodic rate planting of the pioneer or harvesting of the climax. We have observed numerically that planting or harvesting may be used to maintain these systems in a "near-equilibrium" condition or in the vicinity of a large amplitude periodic solution. Using averaging methods, we prove that a two-dimensional pioneer-climax system which loses stable equilibrium behavior may be returned to stable equilibrium by constant rate planting or to near-equilibrium behavior by periodic rate planting. This is done by comparing solutions for periodic rate planting to those for constant rate planting where the constant rate is the time-average of the periodic rate. The crucial term in the bound between solutions is seen to be the product of the amplitude and the period of the periodic rate. Then the autonomous system with constant rate planting is compared to the system without planting to determine conditions for restabilizing the system. Similar analytical arguments should carry through for the case of harvesting.

Section 2 discusses the background for pioneer-climax systems. Section 3 describes the destabilizing effect of varying the intraspecific crowding parameters. Section 4 compares the asymptotic behavior for constant rate and periodic rate planting. Section 5 gives conditions for which planting of a linear or an exponential pioneer will return the system to a near-equilibrium condition. And Section 6 proves the averaging results needed in Section 4. The averaging theorems are proved for general C^1 vector fields in the plane.

2. Background and model equations.

An ecosystem of n interacting, continuously reproducing populations is modeled by an autonomous system of ordinary differential equations of Kolmogorov-type. Let x_i, $i = 1, \dots, n$, denote the density (size) of the i-th population as a function of time t and let y_i denote its *weighted total density* variable, i.e.,

$$y_i = \sum_{j=1}^{n} c_{ij} x_j$$

where c_{ij} is called the *interaction coefficient* and weights the effect of the j-th population on the i-th population. 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

$$dx_i/dt = x_i f_i(y_i), \qquad i = 1, 2, \dots, n. \tag{1}$$

In vector form (1) may be written as

$$dx/dt = F(x)$$

where the function F is called a *vector field.* This vector field is defined on the nonnegative orthant which is invariant because of the form of (1).

Introducing the weighted density variable, y_i, has the advantage of separating the i-th population's response to density, f_i, from the competitive or cooperative effect of each individual interacting population. Typically this response may be characterized by monotonicity properties of the fitness f_i as a function of the weighted density y_i. Certainly, for large enough y_i, because of the detrimental effects of crowding, f_i should be a decreasing function of y_i. In a forest ecosystem, a species which has a fitness which is monotonically decreasing for all values of density is called a *pioneer* species, and we use that terminology here. On the other hand, Allee [**1**] discusses many examples of the beneficial effects of increasing density on both reproduction and survival rates. For predator-prey interactions, Freedman and Wolkowicz [**6**] and Wolkowicz [**18**] assert that prey group defense may cause prey fitness to increase with increasing prey density. Tonkyn [**16**] suggests a one-humped fitness curve for phloem-feeding aphids because the flow of phloem sap increases due to stimulation from an increasing number of feeding aphids; and this facilitates aphid growth and reproduction up to a point where aphid crowding begins to adversely affect per capita growth. At low density, certain tree species such as oak and maple benefit from the presence of additional trees which provide protection and improved soil conditions; but ultimately individual reproduction and survival decrease at increasingly higher densities. We refer to a species as a *climax* species if its fitness monotonically increases up to a maximum value and then monotonically decreases as a function of weighted total density. For this study we assume that each fitness is either pioneer or climax.

To obtain Lotka-Volterra systems from (1), we take each f_i to be a linear pioneer fitness of the form

$$f_i(y_i) = r_i - y_i. \tag{2}$$

Since $y_i = \sum_{j=1}^{n} c_{ij} x_j$, if $c_{ij} > 0$ then the j-th population competes with the i-th population; and if $c_{ij} < 0$ then the j-th population cooperates with the i-th population. Ricker [**13**] concludes that certain fish populations have exponential pioneer fitnesses

$$f(y) = e^{r(1-y)} - a. \tag{3}$$

Hassell and Comins [**9**] study pioneer fitnesses of the form

$$f(y) = \frac{r}{(1+by)^p} - a. \tag{4}$$

Cushing [**3, 4**] in studies of age-structured populations and Selgrade and Namkoong [**14, 15**] in a model for forest succession consider climax fitnesses like

$$f(y) = ye^{r(1-y)} - a. \tag{5}$$

If f_i is a pioneer fitness, then we assume that it has exactly one positive zero, i.e., there is exactly one value $z_i > 0$ so that $f_i(z_i) = 0$. Hence the x_i-isocline is the hyperplane $z_i = \sum_{j=1}^{n} c_{ij} x_j$. Also, we assume this zero is nondegenerate, i.e., $f_i'(z_i) \neq 0$. We take each climax fitness to have exactly two positive zeroes which also are nondegenerate. Thus the isoclines of a climax population are two parallel hyperplanes. An equilibrium of (1) in the positive orthant occurs precisely where these hyperplanes intersect. If $C = (c_{ij})$ is the matrix of interaction coefficients and $z = (z_1, \dots, z_n)$ is a vector of zeroes of the fitnesses then an interior equilibrium $E = (e_1, \dots, e_n)$ is a solution to the system of linear equations

$$CE = z. \tag{6}$$

This equilibrium is isolated if $\det C \neq 0$, which we always assume. The derivative of our vector field F may be expressed in terms of two diagonal matrices and C as

$$DF(x) = \begin{bmatrix} f_1(y_1) & & 0 \\ & \ddots & \\ 0 & & f_n(y_n) \end{bmatrix} + \begin{bmatrix} x_1 f_1'(y_1) & & 0 \\ & \ddots & \\ 0 & & x_n f_n'(y_n) \end{bmatrix} C. \tag{7}$$

Note that the first diagonal matrix in (7) vanishes at an equilibrium E in the interior of the orthant. Hence, formulas for the trace and determinant of $DF(E)$ are

$$\begin{aligned} \operatorname{tr} DF(E) &= \sum_{i=1}^{n} e_i f_i'(z_i) c_{ii} \\ \det DF(E) &= \det C \prod_{i=1}^{n} e_i f_i'(z_i). \end{aligned} \tag{8}$$

3. Destabilizing E by varying intraspecific crowding. For the two-dimensional system modelling the interaction of a pioneer x_1 and a climax x_2, Selgrade and Namkoong [**14, 15**] show that a stable E may lose its stability via Hopf bifurcation. We assume that E is the interior equilibrium determined by the smaller zero z_2 of the climax fitness f_2 and so $f_2'(z_2) > 0$. Also we assume that there is intraspecific crowding determined by $c_{ii} > 0$, $i = 1, 2$. From (8) it follows that

$$\operatorname{tr} DF(E) = e_1 f_1'(z_1) c_{11} + e_2 f_2'(z_2) c_{22} \tag{9}$$

where the first term on the right is negative and the second is positive. Although e_i and z_i, $i = 1, 2$, depend on c_{11} and c_{22}, it may be possible to increase $\operatorname{tr} DF(E)$ by decreasing c_{11} or increasing c_{22}. In fact, Selgrade and Namkoong [**14**] show that if $\det C < 0$ a stable equilibrium E may become unstable via Hopf bifurcation if c_{22} is fixed and the parameter c_{11} decreases or if c_{11} is fixed and the parameter c_{22} increases. Selgrade and Namkoong [**15**] derive a formula for the stability coefficient of the resulting periodic solution which may easily be applied to many examples of biological interest. For instance, for the linear pioneer (2) and the exponential climax (5), the Hopf periodic solution is always locally, asymptotically stable.

Similar behavior may be observed in the following three-dimensional model with two linear pioneers and an exponential climax population:

$$\begin{aligned} &dx_1/dt = x_1[4-4(c_{11}x_1+(3/2)x_2+x_3)] \\ &dx_2/dt = x_2[3/4-((3/2)x_2+x_3)] \\ &dx_3/dt = x_3[-6+6(x_1+(4/3)x_2+(1/2)x_3)e^{1/2-(x_1+4x_2/3+x_3/2)/2}]. \end{aligned} \tag{10}$$

As c_{11} decreases through $c_{11} \cong .42$, a Hopf bifurcation occurs at $E \cong (.595, .051, .673)$ resulting in a stable periodic solution. If we numerically track this periodic solution as c_{11} decreases through .23, we see that it is replaced by an attracting periodic solution of roughly twice its period lying in the box $.04 < x_1 < 2.5$, $.07 < x_2 < .25$, and $.04 < x_3 < 1.41$. This occurs due to a period-doubling bifurcation of the return map. Continuing to decrease c_{11} results in a period-doubling cascade and the onset of an apparent chaotic attractor when $c_{11} < .2$. This system exhibits bistable dynamics because there is always a locally stable climax equilibrium at $(0, 0, 7.0257)$.

Thus decreasing the pioneer intraspecific crowding parameter c_{11} causes destabilization of a stable equilibrium and, in general, causes an attractor to become more complicated dynamically. From a biological perspective, reversing this reduction in pioneer crowding may be accomplished by introducing more of the pioneer population into the ecosystem. In fact, numerical studies indicate the constant rate or periodic rate planting or seeding of the pioneer returns the system to a "near-equilibrium" condition. We investigate the mathematical details of this strategy in the next three sections.

On the other hand, increasing the climax intraspecific crowding parameter c_{22} results in destabilization of the equilibrium. This increase in climax crowding may be reversed by removing some of the climax population from the ecosystem, i.e., by harvesting the climax. The numerical work of Monteiro [**12**] shows that this reversal of the dynamics does occur in two dimensions for constant rate or periodic rate harvesting.

4. Planting the pioneer. In this section we compare the asymptotic behavior of the two-dimensional pioneer-climax model with constant rate planting, equation (CRP), to the model with periodic rate planting, equation (PRP). An ecologist might try to manage a pioneer-climax ecosystem with either of these strategies. A periodic rate planting regime may be necessitated by seasonal variations in the ecosystem. We take a cosine function as the periodic rate although our arguments will work for any finite linear combination of cosines and sines of the same period. We intend to apply our results to the vector field of (1); however, Theorem 1 requires only that F be a two-dimensional, C^1 vector field. Our two systems of differential equations have the forms:

$$\dot{x} = F(x) + \left[A + B\cos\frac{2\pi t}{p}, 0\right]^* \tag{PRP}$$

$$\dot{z} = F(z) + [A, 0]^*. \tag{CRP}$$

Here $x, z \in \mathbf{R}^2$ and A, B, and p are positive constants. Also, "$\cdot$" denotes time derivative and "$*$" denotes transpose since vectors are considered as columns. The constant A in both systems is the same, because we wish to compare the dynamical behavior of the time-dependent system (PRP) near an attractor with that of the autonomous system (CRP) in which the time-periodic term is replaced by its integral average over the period p. Note that

$$A = \frac{1}{p}\int_0^p \left(A + B\cos\frac{2\pi t}{p}\right) dt. \tag{11}$$

In this study we restrict our attention to the case where the attractor for (CRP) is an equilibrium.

Assume that E is a hyperbolic equilibrium of (CRP) which is locally, asymptotically stable. Thus the eigenvalues λ_1 and λ_2 of $DF(E)$ have negative real parts, and one of the following three cases applies:

(i) If $\lambda_2 \leq \lambda_1 < 0$ and $DF(E)$ is similar to a diagonal matrix, then there is an $N > 0$ so that $|e^{tDF(E)}| \leq Ne^{\sigma t}$ for all $t \geq 0$ and all $\sigma, \lambda_1 \leq \sigma < 0$.

(ii) If $\lambda = \alpha \pm \beta i$ for $\alpha < 0$, then there is an $N > 0$ so that $|e^{tDF(E)}| \le Ne^{\sigma t}$ for all $t \ge 0$ and all $\sigma, \alpha \le \sigma < 0$.

(iii) If $\lambda_1 = \lambda_2 = \lambda < 0$ and $DF(E)$ is similar to the matrix $\left(\begin{smallmatrix} \lambda & 1 \\ 0 & \lambda \end{smallmatrix}\right)$, then there is an $N > 0$ so that $|e^{tDF(E)}| \le Ne^{\sigma t}$ for all $t \ge 0$ and all $\sigma, \lambda < \sigma < 0$.

Our first result compares solutions to (PRP) and (CRP) in a neighborhood of E. This theorem is similar to classical averaging results (see Hale [**8**] or Guckenheimer and Holmes [**7**]) but our error bound between solutions is $\mathcal{O}(pB)$ instead of $\mathcal{O}(B)$ for fixed p or $\mathcal{O}(p)$ for fixed B, as in the classical case. This allows us to compare attractors for a large set in the (p, B) parameter space. For example, if (CRP) has a stable equilibrium E then, for fixed p, (PRP) has a unique stable periodic solution near E if B is small enough (see Guckenheimer and Holmes [**7**, page 168]). This periodic attractor is clearly visible in numerical experiments. For larger values of B but for pB still relatively small, we observe more complicated attractors close to E, e.g., a period $2p$ attractor or an apparent chaotic attractor. In some numerical experiments with our pioneer-climax systems, where the coordinates of E are less than one (i.e., population densities are on a very small scale), we have observed this attractor for a product pB as large as two. The precise statement of our local result is as follows:

Theorem 1. *Let F be a C^1 vector field on $\mathbf{R}^2$ and E be a stable hyperbolic equilibrium of* (CRP)*. Then there exist positive constants ε, N, K, and γ and two convex balls $S(E)$ centered at E of radii ε and $\delta(\varepsilon) < \varepsilon$, so that if pB is sufficiently small and if $x(0)$, $z(0) \in S_{\delta(\varepsilon)}(E)$ then, for all $t \ge 0$, $x(t)$, $z(t) \in S_\varepsilon(E)$ and*

$$|x(t) - z(t)| \le KpB + Ne^{-\gamma t}|x(0) - z(0)|. \tag{12}$$

In addition, a more global result may be obtained with the same hypotheses on F and E and the same notation as Theorem 1.

Theorem 2. *Let $z(0)$ be in the domain of attraction of E, i.e., $z(t) \to E$ as $t \to \infty$. Then there is a $T > 0$ so that for B small enough there is a neighborhood G of $z(0)$ such that if $x(0) \in G$ then $z(T)$,*

$x(T) \in S_\delta(E)$. And if pB is sufficiently small then, for all $t \geq T$,

$$|x(t) - z(t)| \leq KpB + Ne^{-\gamma(t-T)}|x(T) - z(T)|. \tag{13}$$

Theorem 2 follows easily from Theorem 1 but is useful for our application because we wish to make conclusions about the asymptotic behavior of initial conditions for (PRP) by analyzing asymptotic behavior for (CRP). The proofs for these results are contained in Section 6.

5. Using planting to restabilize the system. Periodic rate planting (PRP) is more realistic biologically than constant rate planting (CRP), but (CRP) is easier to analyze mathematically since it is autonomous. The theorems in the previous section imply that if (CRP) has a stable equilibrium then (PRP) has an attractor nearby if planting amplitude and period are in appropriate ranges. In this section we obtain conditions under which a constant planting rate returns the pioneer-climax system to stable equilibrium.

Recall that the pioneer-climax system (1) undergoes Hopf bifurcation as c_{11} decreases through a critical value $\hat{c}_{11}$. We take F in (CRP) to be the pioneer-climax vector field, and we consider (CRP) to be a system with two parameters, c_{11} and A. For the cases of a linear or an exponential pioneer, we study the curve in parameter space where Hopf bifurcation occurs near the point $(c_{11}, A) = (\hat{c}_{11}, 0)$. We give conditions implying that this curve is the graph of A as a decreasing function of c_{11} as in Figure 1. Hence for $c_{11} < \hat{c}_{11}$ and no planting ($A = 0$), the system has an unstable equilibrium and a stable periodic solution. Fixing such a c_{11} and planting at a rate A above the bifurcation curve will return the system to one with a stable equilibrium. Periodic rate planting with this average A and appropriate amplitude B and period p will return the system to "near-equilibrium" behavior.

We assume that the linear pioneer has fitness f_1 given by (2) and the climax fitness is given by (5), i.e., for $0 < r_1$ and $0 < r_2 < 1$

$$f_1(y_1) = r_1 - y_1 \quad \text{and} \quad f_2(y_2) = y_2 e^{r_2(1-y_2)} - 1.$$

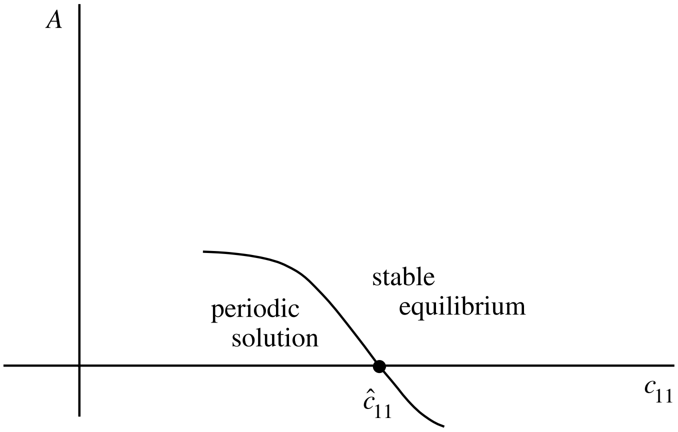

FIGURE 1. Bifurcation curve for Hopf bifurcation.

The equilibrium E of (CRP) where a Hopf bifurcation may occur solves the nonlinear system of equations:

$$\begin{aligned} r_1 - (c_{11}x_1 + c_{12}x_2) &= -A/x_1 \\ c_{21}x_1 + c_{22}x_2 &= 1. \end{aligned} \tag{14}$$

The trace of $DF(E)$ is given by

$$\operatorname{tr} DF(E) = c_{11}x_1 f_1'(y_1) + c_{22}x_2 f_2'(y_2) - (A/x_1). \tag{15}$$

To determine where the Hopf bifurcation occurs we set $\operatorname{tr} DF(E)$ equal to zero in (15) and that along with (14) provide three equations in the four unknowns x_1, x_2, A, and c_{11}. We use the second equation in (14) to eliminate x_2 and obtain two equations in the unknowns x_1, A, and c_{11}. Specifically, the first equation in (14) determines the function

$$G(x_1, A, c_{11}) = x_1(r_1 - c_{11}x_1 + (c_{12}c_{21}x_1 - c_{12})/c_{22}) + A$$

and (15) gives

$$H(x_1, A, c_{11}) = c_{11}x_1^2 + c_{21}(1 - r_2)x_1^2 - (1 - r_2)x_1 + A.$$

The set of points where Hopf bifurcation occurs is the solution set to $(G, H) = (0, 0)$. We appeal to the implicit function theorem to find conditions when the equation $(G, H) = (0, 0)$ determines x_1 and A as functions of c_{11} near the point $Q = (x_1, A, c_{11}) = ((r_1 c_{22} - c_{12})/\det C, 0, \hat{c}_{11})$. In particular, we want A to be a decreasing function of c_{11} as in Figure 1. The appropriate derivative at Q is given by:

$$\frac{\partial(G,H)}{\partial(x_1,A)}(Q) = \begin{bmatrix} \dfrac{-(r_1c_{22}-c_{12})}{c_{22}} & 1 \\ (1-r_2) & 1 \end{bmatrix}.$$

The implicit function theorem applies if

$$\det \frac{\partial(G,H)}{\partial(x_1,A)}(Q) = \frac{c_{12} - r_1c_{22} + (r_2-1)c_{22}}{c_{22}} \neq 0. \tag{16}$$

As mentioned in Section 3, $\det C < 0$ and so $c_{12} - r_1 c_{22} > 0$ since $x_1 > 0$. Hence, (16) is positive if $r_2 \approx 1$. To determine the monotonicity of A as a function of c_{11}, we compute

$$\frac{\partial(G,H)}{\partial(x_1,c_{11})}(Q) = \begin{bmatrix} \dfrac{-(r_1c_{22}-c_{12})}{c_{22}} & -x_1^2 \\ 1-r_2 & x_1^2 \end{bmatrix}. \tag{17}$$

The negative determinant of (17) divided by (16) gives

$$\frac{dA}{dc_{11}} = \frac{-x_1^2[c_{12} - r_1c_{22} + (1-r_2)c_{22}]}{[c_{12} - r_1c_{22} + (r_2-1)c_{22}]} \tag{18}$$

where $x_1 = (r_1c_{22} - c_{12})/\det C$. Thus sufficient conditions for A to be a decreasing function of c_{11} near $(A, c_{11}) = (0, \hat{c}_{11})$ are that (16) is nonzero and (18) is negative. Such a system with a linear pioneer may be returned to near-equilibrium behavior by constant rate planting or periodic rate planting.

The same procedure may be applied to the case where the pioneer population has an exponential fitness of the form

$$f_1(y_1) = e^{r_1 - y_1} - 1.$$

The functions which determine the bifurcation set are

$$\begin{aligned} G(x_1, A, c_{11}) &= x_1[-1 + e^{(r_1 - c_{11}x_1 + (c_{12}c_{21}x_1 - c_{12})/c_{22})}] + A \\ H(x_1, A, c_{11}) &= c_{11}x_1^2 + c_{21}(1-r_2)x_1^2 - c_{11}Ax_1 - (1-r_2)x_1 + A. \end{aligned}$$

We need the following Jacobian to be nonzero:

$$\det \frac{\partial(G,H)}{\partial(x_1,A)}(Q) = \frac{(1-c_{11}x_1)(c_{12}-r_1c_{22})+(r_2-1)c_{22}}{c_{22}} \tag{19}$$

where $x_1 = (r_1c_{22}-c_{12})/\det C$. And then we compute

$$\frac{dA}{dc_{11}} = \frac{-x_1^2[c_{12}-r_1c_{22}+(1-r_2)c_{22}]}{(1-c_{11}x_1)(c_{12}-r_1c_{22})+(r_2-1)c_{22}}. \tag{20}$$

So sufficient conditions for the bifurcation curve to determine A as a decreasing function of c_{11} are that (19) is nonzero and (20) is negative.

6. Proofs of theorems. In this section we prove Theorem 1 and Theorem 2 which are stated in Section 4. For our argument we need to compute an upper bound for

$$I \equiv \left| \int_T^t e^{DF(E)(t-\tau)} \left[B\cos\frac{2\pi\tau}{p}, 0\right]^* d\tau \right|.$$

This is obtained by writing $e^{DF(E)(t-\tau)}$ in terms of its real canonical form and integrating term by term. A bound is found for the norm of the resulting matrix. The integration is done first to take advantage of the oscillatory nature of $\cos(2\pi\tau/p)$. We treat the following three cases as in Section 4:

(i) If $\lambda_2 \le \lambda_1 < 0$ and $DF(E)$ is similar to a diagonal matrix, then there is an $M > 0$ so that for all $t \ge T$

$$I \le MpB(1+e^{\lambda_1(t-T)}).$$

(ii) If $\lambda = \alpha \pm \beta i$, then there is an $M > 0$ so that for all $t \ge T$,

$$I \le MpB(1+e^{\alpha(t-T)}).$$

(iii) If $\lambda_1 = \lambda_2 = \lambda < 0$ and $DF(E)$ is similar to $\left(\begin{smallmatrix}\lambda & 1\\ 0 & \lambda\end{smallmatrix}\right)$, then there is an $M > 0$ so that for all $t \ge T$

$$I \le MpB(1+e^{\lambda(t-T)}+(t-T)e^{\lambda(t-T)}).$$

The constant M depends on $DF(E)$ and on the maximum value of several bounded rational functions of p.

To estimate the difference between a solution to (PRP) and to (CRP) we begin by subtracting (CRP) from (PRP) and introducing $DF(E)$ on the right side to get:

$$\begin{aligned}\dot{x}-\dot{z} &= DF(E)(x-z)-DF(E)(x-z)\\ &\quad + F(x)-F(z)+\left[B\cos\frac{2\pi t}{p},0\right]^{*}.\end{aligned}\tag{21}$$

For each t we use the mean value theorem to write

$$F(x)-F(z)=\int_0^1 DF(w(s,t))(x-z)\,ds\tag{22}$$

where $w(s,t)$ belongs to the line segment from $z(t)$ to $x(t)$. Later we guarantee that this line segment is in an appropriate neighborhood of E. With (22), (21) becomes

$$\begin{aligned}\dot{x}-\dot{z} &= DF(E)(x-z)+\int_0^1 [DF(w(s,t))\\ &\quad - DF(E)](x-z)\,ds+\left[B\cos\frac{2\pi t}{p},0\right]^{*}.\end{aligned}\tag{23}$$

To simplify notation let $u=x-z$ and $D=DF(E)$. Then we have

$$\dot{u}-Du=\int_0^1 [DF(w(s,t))-D]u\,ds+\left[B\cos\frac{2\pi t}{p},0\right]^{*}.\tag{24}$$

Multiplying both sides by e^{-Dt} and integrating from T to any $t\geq T$, we get

$$\begin{aligned}u(t) &= e^{D(t-T)}u(T)+\int_T^t e^{D(t-\tau)}\int_0^1 [DF(w(s,\tau))-D]u(\tau)\,ds\,d\tau\\ &\quad+\int_T^t e^{D(t-\tau)}\left[B\cos\frac{2\pi\tau}{p},0\right]^{*}d\tau.\end{aligned}\tag{25}$$

Taking norms in (25) gives the inequality

$$|u(t)| \leq |e^{D(t-T)}||u(T)| + \int_T^t |e^{D(t-\tau)}| \int_0^1 |DF(w(s,\tau)) - D||u(\tau)|\,ds\,d\tau + \left| \int_T^t e^{D(t-\tau)} \left[B\cos\frac{2\pi\tau}{p}, 0\right]^* d\tau \right|. \tag{26}$$

Let $\zeta = \lambda_1, \alpha$, or λ depending on case (i), (ii) or (iii), respectively; and use the bounds for the last integral in (26) obtained for these cases. Also apply the bound $|e^{Dt}| \leq Ne^{\sigma t}$ obtained for the three cases in Section 4. Finally, assume that there is an $L > 0$ so that for all $s \in [0,1]$ and $\tau \geq T$, we have

$$|DF(w(s,\tau)) - D| \leq L. \tag{27}$$

Later we show that it is possible to find such an L. With these conditions we conclude from (26) that

$$|u(t)| \leq Ne^{\sigma(t-T)}|u(T)| + \int_T^t Ne^{\sigma(t-\tau)}L|u(\tau)|\,d\tau + MpB(1 + e^{\zeta(t-T)} + (t-T)e^{\zeta(t-T)}). \tag{28}$$

Note that the term $(t-T)e^{\zeta(t-T)}$ in (28) appears only in case (iii). Multiply both sides of (28) by $e^{-\sigma t}$ and apply the time-dependent version of Gronwall's inequality to get

$$e^{-\sigma t}|u(t)| \leq Ne^{-\sigma T}|u(T)| + e^{-\sigma t}MpB(1 + e^{\zeta(t-T)} + (t-T)e^{\zeta(t-T)}) + \int_T^t [Ne^{-\sigma T}|u(T)| + e^{-\sigma s}MpB(1 + e^{\zeta(s-T)} + (s-T)e^{\zeta(s-T)})]NLe^{NL(t-s)}\,ds. \tag{29}$$

We compute the integrals on the right of (29), multiply both sides by

$e^{\sigma t}$, and rearrange terms to get

$$
\begin{aligned}
|u(t)| \leq {} & MpB\biggl[1 - \frac{NL}{\sigma + NL}\biggr] \\
& + e^{(\sigma+NL)(t-T)}\biggl[N|u(T)| + \frac{NLMpB}{\sigma + NL} + \frac{NLMpB}{\sigma + NL - \zeta}\biggr] \\
& + MpBe^{\zeta(t-T)}\biggl[1 - \frac{NL}{\sigma + NL - \zeta}\biggr] \qquad (30) \\
& + MpBe^{\zeta(t-T)}(t-T)\biggl[1 - \frac{NL}{\sigma + NL - \zeta}\biggr] \\
& + \frac{MpBNL}{(\sigma + NL - \zeta)}\biggl[\frac{e^{(\sigma+NL)(t-T)}}{\sigma + NL - \zeta} - \frac{e^{\zeta(t-T)}}{\sigma + NL - \zeta}\biggr].
\end{aligned}
$$

Note that the last four terms in (30) are only present in case (iii). Fix $\sigma = \zeta$ in cases (i) and (ii) and $\zeta < \sigma < 0$ for case (iii). Hence $\sigma - \zeta \geq 0$. We may take L small enough so that $\sigma + 2NL < 0$. As we see later, this choice is possible because of the continuity of DF (see (27)). It follows that

$$\max_{t \geq T}\biggl[\frac{e^{(\sigma+NL)(t-T)}}{\sigma + NL - \zeta} - \frac{e^{\zeta(t-T)}}{\sigma + NL - \zeta}\biggr] \leq \frac{-1}{\zeta}$$

and

$$\max_{t \geq T}(t-T)e^{\zeta(t-T)}\biggl[1 - \frac{NL}{\sigma + NL - \zeta}\biggr] \leq \frac{-1}{\zeta e}.$$

Hence (30) leads to

$$|u(t)| \leq MpB\biggl(4 - \frac{1}{\zeta} - \frac{1}{\zeta e}\biggr) + N|u(T)|e^{(\sigma+NL)(t-T)}. \qquad (31)$$

Taking $K = M(4 - 1/\zeta - 1/(\zeta e))$ and $-\gamma = \sigma + NL$ gives (13) in Theorem 2:

$$|u(t)| \leq KpB + Ne^{-\gamma(t-T)}|u(T)|. \qquad (32)$$

This inequality is valid provided we may choose L as claimed. Note that K and N effectively depend on $DF(E)$.

Proof of Theorem 1. Fix L so that $\sigma + 2NL < 0$. Since F is C^1, there is an ε, $0 < \varepsilon < 1$, so that if $w \in S_\varepsilon(E) \equiv \{x : |x - E| < \varepsilon\}$, then

$$|DF(w) - DF(E)| < L.$$

Take δ, $0 < \delta < \varepsilon$, such that

(a) $2\delta N < \varepsilon/6$, and

(b) if $z(0) \in S_\delta(E)$ then $z(t) \in S_{\varepsilon/3}(E)$ for all $t \geq 0$.

Claim. *If $z(0), x(0) \in S_\delta(E)$ and if pB is sufficiently small, then $x(t) \in S_\varepsilon(E)$ for all $t \geq 0$ and* (32) *holds with $T = 0$.*

Proof of Claim. Assume not, i.e., there is a first time $\hat{t}$ such that $|x(\hat{t}) - E| = \varepsilon$. Then for all $t < \hat{t}$, $x(t) \in S_\varepsilon(E)$ and the line segment from $z(t)$ to $x(t)$ is in $S_\varepsilon(E)$ as needed for (22) and (23). By our choice of ε, $|DF(w(s,\tau)) - DF(E)| < L$ for all $\tau < \hat{t}$ which gives (27). Hence (28) is valid with $T = 0$ and so is (32). Thus, for all $t < \hat{t}$,

$$\begin{aligned} |x(t) - z(t)| = |u(t)| &\leq KpB + N|x(0) - z(0)|e^{-\gamma t} \\ &\leq KpB + 2\delta N < \varepsilon/3. \end{aligned} \tag{33}$$

The last inequality in (33) holds if pB is less than $\varepsilon/(6K)$. By our choice of δ it follows that for all $t < \hat{t}$

$$|x(t) - E| \leq |x(t) - z(t)| + |z(t) - E| < \varepsilon/3 + \varepsilon/3.$$

Hence $|x(\hat{t}) - E| \leq 2\varepsilon/3$ which is a contradiction. This proves the claim and Theorem 1. □

Proof of Theorem 2. Fix $z(0)$ so that $z(t) \to E$ as $t \to \infty$. Then there is a $T > 0$ so that $z(T) \in S_\delta(E)$. By continuity in initial conditions and in parameters there is a neighborhood G of $z(0)$ so that for all $x(0) \in G$, $x(T) \in S_\delta(E)$. The preceding argument now applies and results in (32). This proves Theorem 2. □

Acknowledgment. The author thanks Bob Buchanan for pointing out an error in the estimate of I for case (iii) and Gene Namkoong for helpful conversations.

REFERENCES

1. W.C. Allee, *Animal aggregations*, New York, AMS Press Reprint of ed. pub. by Univ. of Chicago Press, 1931.

2. H.N. Comins and M.P. Hassell, *Predation in multi-prey communities*, J. Theor. Biol. **62** (1976), 93–114.

3. J.M. Cushing, *Nonlinear matrix models and population dynamics*, Natur. Resource Modeling **2** (1988), 539–580.

4. ———, *The Allee effect in age-structured population dynamics*, Proceedings of the Autumn Course Research Seminars: Mathematical Ecology (T.G. Hallam, L.J. Gross and S.A. Levin, eds.), 1988, World Scientific Publishing Co., Singapore, 479–505.

5. J.E. Franke and A.-A. Yakubu, *Mutual exclusion versus coexistence for discrete competitive systems*, J. Math. Biol. **30** (1991), 161–168.

6. H.I. Freedman and G. Wolkowicz, *Predator-prey systems with group defense*: *The paradox of enrichment revisited*, Bull. Math. Biol. **48** (1986), 493–508.

7. J. Guckenheimer and P. Holmes, *Nonlinear oscillations, dynamical systems, and bifurcations of vector fields*, Springer-Verlag, New York, 1983.

8. J.K. Hale, *Ordinary differential equations*, John Wiley & Sons, Inc., New York, 1969.

9. M.P. Hassell and H.N. Comins, *Discrete time models for two-species competition*, Theoret. Population Biol. **9** (1976), 202–221.

10. J. Hofbauer, V. Hutson and W. Jansen, *Coexistence for systems governed by difference equations of Lotka-Volterra type*, J. Math. Biol. **25** (1981), 553–570.

11. R.M. May, *Ecosystem patterns in randomly fluctuating environments*, in *Progress in theoretical biology* (Rosen and Snell, eds.), Academic Press, New York, 1974.

12. R.A. Monteiro, *Dynamical behavior of pioneer-climax models with and without harvesting*, Masters project, North Carolina State University, Raleigh, 1992.

13. W.E. Ricker, *Stock and recruitment*, J. Fish. Res. Bd. Can. **11** (1954), 559–623.

14. J.F. Selgrade and G. Namkoong, *Stable periodic behavior in a pioneer-climax model*, Natur. Resource Modeling **4** (1990), 215–227.

15. ———, *Population interactions with growth rates dependent on weighted densities*, in *Differential equations models in biology, epidemiology and ecology* (S. Busenberg, M. Martelli, eds.), Lecture Notes in Biomath. **92**, Springer-Verlag, Berlin, 1991, 247–256.

16. D.W. Tonkyn, *Predator-mediated mutualism*: *Theory and tests in the homoptera*, J. Theor. Biol. **118** (1986), 15–31.

17. P. Waltman, *Competition models in population biology*, CBMS-NSF 45, SIAM, Philadelphia, 1983.

18. G. Wolkowicz, *Bifurcation analysis of a predator-prey system involving group defence*, SIAM J. Appl. Math. **48** (1988), 592–606.

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