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CONSTANT AND PERIODIC RATE STOCKING AND HARVESTING FOR KOLMOGOROV-TYPE POPULATION INTERACTION MODELS

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To the memory of Geoffrey James Butler

ABSTRACT. Averaging methods are used to compare solutions to n-dimensional systems of ordinary differential equations with constant or periodic forcing. These results are applied to population models of Kolmogorov-type where per capita growth rates are either monotone decreasing (pioneer) or one-humped (climax) functions of weighted population densities. The asymptotic behavior of such systems may be controlled, to some extent, by stocking or harvesting a population.

1. Introduction. The effects of population density on the reproduction and survival of individuals of a species are widely studied and accepted, e.g., see [**1, 16, 11**]. Here we model the interaction of populations of animals or plants by a system of ordinary differential equations where the per capita replacement rate is a function (called the *fitness*) of a linear combination of the densities of the interacting populations. Other studies assuming this approach include Comins and Hassell [**3**], Hassell and Comins [**12**], Hofbauer, Hutson and Jansen [**13**], Cushing [**4, 5**], Selgrade and Namkoong [**19, 20**], Franke and Yakubu [**6**], and Selgrade [**18**]. These systems are generalizations of Lotka-Volterra equations where the fitnesses are linear functions of the densities.

For our study we take the population fitnesses to be either monotone decreasing functions or one-humped functions. Borrowing from the forestry terminology, we refer to the former as *pioneer* fitnesses and to the latter as *climax* fitnesses. Such a pioneer fitness is a decreasing function of density, it simply captures the detrimental effects of crowding on per capita replacement rates. Ricker [**17**] concludes that

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certain fish populations have exponential pioneer fitnesses, and Hassell and Comins [**12**] study pioneer fitnesses which are rational functions. On the other hand, Allee [**1**], Freedman and Wolkowicz [**7**], Tonkyn [**22**], Cushing [**5**], and Wolkowicz [**23**] discuss examples of the beneficial effects of increasing density on both reproduction and survival rates. Thus, we take a climax fitness to be monotonically increasing up to a maximum value and then monotonically decreasing as a function of density. Populations with such climax fitnesses are studied in Cushing [**4, 5**], Selgrade and Namkoong [**19, 20**], and Selgrade [**18**].

For population interaction models with pioneer and climax fitnesses, Selgrade and Namkoong [**19, 20**] observe that varying an intraspecific crowding parameter may destabilize an equilibrium via Hopf bifurcation. In fact, continuing to vary this intrinsic parameter may produce a period-doubling cascade resulting in an apparent strange attractor. Selgrade [**18**] analyzes the dynamical behavior of the interaction between a linear pioneer and an exponential climax and shows that such a two-dimensional system may be returned to "near-equilibrium" by stocking or planting the pioneer population. Constant rate stocking and periodic rate (a sine or cosine function) stocking are studied. Selgrade [**18**] shows that if the system with constant rate stocking has an asymptotically stable equilibrium then solutions of the periodic rate system near this equilibrium stay close to solutions of the constant rate system if the constant rate is the time-average of the periodic rate function. Here we use averaging methods to extend this result to n-dimensional C^1 vector fields where each component of the vector field is forced (which represents stocking or harvesting) with a sine or a cosine function of different amplitude and frequency. We show (Theorem 1) that if the autonomous system with constant forcing vector whose components are the time-averages of the periodic forcing functions has an asymptotically stable equilibrium, then solutions to both systems near this equilibrium stay close for all positive time. The error bound between solutions depends on the sum over the components of the products of amplitude and period. We suspect that similar results are true for a neighborhood of any hyperbolic attractor of the system with constant forcing. For example, Kot, Sayler and Schultz [**14**] study nutrient forcing in a three-dimensional model of the chemostat. They are interested in dynamical behavior for periodic forcing near a stable periodic orbit of the system with constant forcing which is the time-average of the periodic forcing. From their work, it appears that solution components normal to the periodic orbit stay close with a bound depending on the product of amplitude and period of the forcing function.

Our general result is applied to two- and three-dimensional interaction models of pioneer and climax populations. For the interaction of one pioneer and one climax, we investigate the Hopf bifurcation curve with respect to the intrinsic crowding parameter and the constant rate stocking or harvesting parameter. We show that either stocking or harvesting may return the system to a stable equilibrium; and the strategy which will accomplish this depends on the first two derivatives of the fitnesses and on intraspecific and interspecific competition parameters. Hence, the corresponding periodic rate stocking or harvesting will return the system to "near-equilibrium" behavior because of Theorem 1. For the three-dimensional system which models the interaction of two linear pioneers and an exponential climax, we consider a two-parameter example, determine the Hopf bifurcation curve, and show that harvesting the first pioneer is the strategy which restabilizes the system at equilibrium. Without harvesting, this system exhibits a period-doubling cascade to a strange attractor. Numerically, we illustrate how appropriate levels of harvesting may reverse this cascade and maintain the system at any periodic attractor along the cascade. Thus the asymptotic behavior of this population interaction model may be controlled by harvesting.

Section 2 states and proves our averaging result for n-dimensional C^1 vector fields. Section 3 presents the model equations and background for the Kolmogorov-type population interaction models which we study. Sections 4 and 5 discuss stocking and harvesting strategies for two- and three-dimensional systems, respectively.

2. Averaging result.

Let F be an n-dimensional C^1 vector field. In this section we compare the asymptotic behavior of two systems obtained by adding external forcing to F. These two systems have the forms:

$$\text{(C)} \qquad \frac{dz}{dt} = F(z) + (A_1, \dots , A_n)^*$$

$$\text{(P)} \qquad \frac{dx}{dt} = F(x) + \left(A_1 + B_1 \cos\frac{2\pi t}{p_1}, \dots , A_n + B_n \cos\frac{2\pi t}{p_n}\right)^*,$$

where * represents the transpose operation and $x = (x_1, \dots, x_n)^*$, $z = (z_1, \dots, z_n)^*$. System (C) has constant forcing. The ith component of the forcing in (P) is a cosine function of period p_i which may be different from the periods of the other components; and A_i is the time-average over the period of the ith component of the forcing. This component may be taken to be any finite linear combination of sines and cosines of period p_i, but here we use a single cosine to simplify the mathematical analysis. A system with periodic forcing may be more realistic for biological applications, e.g., because of seasonal variations in ecosystems.

Assume that E is a hyperbolic equilibrium of (C) which is locally, asymptotically stable. Thus, the eigenvalues of $DF(E)$, the derivative of F at E, have negative real parts. Let $B = (B_1, \dots, B_n)^*$ and $p = (p_1, \dots, p_n)^*$ denote the amplitude and period vectors, respectively. Using dot product notation, we have $p \cdot B = \sum_{i=1}^n p_i B_i$. Our result compares solutions to (C) and (P) in a neighborhood of E. This theorem is similar to the classical averaging results (see Hale [**10**] or Guckenheimer and Holmes [**9**]), but our error bound between solutions is $O(p \cdot B)$ instead of $O(|B|)$ for fixed p or $O(|p|)$ for fixed B, as in the classical case.

Theorem 1. *Let F be a C^1 vector field on $\Re^n$ and E a stable hyperbolic equilibrium of* (C). *Assume that $B_i \geq 0$ and $p_i > 0$ for $i = 1, 2, \dots, n$. Then there exist positive constants ε, N, M and γ and two balls $S_\varepsilon(E)$ and $S_\delta(E)$ centered at E of radius ε and $\delta(\varepsilon) < \varepsilon$, so that if $p \cdot B$ is sufficiently small and if $x(0)$, $z(0) \in S_\delta(E)$, then $x(t)$, $z(t) \in S_\varepsilon(E)$ for all $t \geq 0$, and*

$$|x(t) - z(t)| \leq Mp \cdot B + Ne^{-\gamma t}|x(0) - z(0)|. \tag{1}$$

Proof. First we subtract (C) from (P) which eliminates A_i and gives

$$\dot{x} - \dot{z} = F(x) - F(z) + \left(B_1 \cos \frac{2\pi t}{p_1}, \dots, B_n \cos \frac{2\pi t}{p_n} \right)^*. \tag{2}$$

For each fixed $t > 0$, use the mean value theorem to write

$$F(x) - F(z) = \int_0^1 DF(w(s,t))(x - z)\, ds \tag{3}$$

where $w(s,t) = sx(t)+(1-s)z(t)$ for some s, $0 \leq s \leq 1$, which depends on $x(t)$ and $z(t)$. Let $D = DF(E)$ and $u = x-z$; then (2) and (3) give

$$\begin{aligned}\dot{u} - Du = &\int_0^1 [DF(w(s,t)) - D]u\,ds \\ &+ \left(B_1 \cos\frac{2\pi t}{p_1}, \dots, B_n \cos\frac{2\pi t}{p_n}\right)^*.\end{aligned} \tag{4}$$

Multiplying both sides of (4) by e^{-Dt} and integrating from T to t yields

$$\begin{aligned}u(t) = &e^{D(t-T)}u(T) \\ &+ \int_T^t e^{D(t-\tau)} \int_0^1 [DF(w(s,\tau)) - D]u(\tau)\,ds\,d\tau \\ &+ \int_T^t e^{D(t-\tau)} \left(B_1 \cos\frac{2\pi\tau}{p_1}, \dots, B_n \cos\frac{2\pi\tau}{p_n}\right)^* d\tau.\end{aligned} \tag{5}$$

Take norms in (5) and assume $|DF(w(s,t)) - D| \leq L$, where L will be determined later, to get

$$\begin{aligned}|u(t)| = &|e^{D(t-T)}||u(T)| \\ &+ \int_T^t L|e^{D(t-\tau)}||u(\tau)|\,d\tau \\ &+ \left|\int_T^t e^{D(t-\tau)} \left(B_1 \cos\frac{2\pi\tau}{p_1}, \dots, B_n \cos\frac{2\pi\tau}{p_n}\right)^* d\tau\right|.\end{aligned} \tag{6}$$

The last term in (6) is bounded by using the Jordan canonical form of D to evaluate integrals before taking norms. The required bounds are obtained by the following lemma which is proved by induction on k and some tedious computation, see Buchanan [**2**].

Lemma 1. *Fix $i = 1, 2, \dots, n$, and let k be a nonnegative integer. Assume $\operatorname{Re}\lambda < 0$. Then there exists a positive number M_k such that the following inequalities hold.*

$$\begin{aligned}&\left|\int_T^t \left(a_0 + a_1(t-\tau) + \cdots + a_k\frac{(t-\tau)^k}{k!}\right) e^{\lambda(t-\tau)} B_i \cos\frac{2\pi\tau}{p_i}\,d\tau\right| \\ &\qquad\qquad\qquad\qquad \leq M_k p_i B_i\end{aligned}$$

$$\left|\int_T^t \left(b_0+b_1(t-\tau)+\cdots+b_k\frac{(t-\tau)^k}{k!}\right)e^{\lambda(t-\tau)}B_i\sin\frac{2\pi\tau}{p_i}\,d\tau\right| \\ \le M_k p_i B_i.$$

From Lemma 1 there is an $M > 0$ so that (6) becomes

$$|u(t)| = |e^{D(t-T)}||u(T)| + \int_T^t L|e^{D(t-\tau)}||u(\tau)|\,d\tau + \frac{M}{2}p\cdot B. \tag{7}$$

Since $\operatorname{Re}\lambda < 0$ for all the eigenvalues of D, then there exists $N > 0$ and σ with

$$\max_{\lambda_i\in\operatorname{spec}(D)} \operatorname{Re}\lambda_i < \sigma < 0$$

such that $|e^{D(t-\tau)}| \le Ne^{\sigma(t-\tau)}$ for all $t \ge \tau \ge T$. Hence, $u(t)$ is bounded by

$$\begin{aligned}|u(t)| \le N|u(T)|e^{\sigma(t-T)} + \frac{M}{2}p\cdot B \\ + \int_T^t NLe^{\sigma(t-\tau)}|u(\tau)|\,d\tau.\end{aligned} \tag{8}$$

Multiplying both sides by $e^{-\sigma t}$ gives

$$\begin{aligned}|u(t)|e^{-\sigma t} \le N|u(T)|e^{-\sigma T} + \frac{M}{2}p\cdot Be^{-\sigma t} \\ + \int_T^t NLe^{-\sigma\tau}|u(\tau)|\,d\tau.\end{aligned} \tag{9}$$

Apply a time dependent version of Gronwall's inequality to get

$$\begin{aligned}|u(t)|e^{-\sigma t} \le N|u(T)|e^{-\sigma T} + \frac{M}{2}p\cdot Be^{-\sigma t} \\ + \int_T^t NLe^{NL(t-\tau)}[N|u(T)|e^{-\sigma T} + \frac{M}{2}p\cdot Be^{-\sigma\tau}]\,d\tau.\end{aligned} \tag{10}$$

Multiply both sides in (10) by $e^{\sigma t}$ and integrate

$$\begin{aligned}|u(t)| \le N|u(T)|e^{(NL+\sigma)(t-T)} + \frac{M}{2}p\cdot B \\ + \frac{NLMp\cdot B}{2(NL+\sigma)}(e^{(NL+\sigma)(t-T)} - 1).\end{aligned} \tag{11}$$

Since F is C^1 and $DF(E)$ is fixed, then there exists $\varepsilon > 0$ so that if $w \in S_\varepsilon(E)$ then $|DF(w) - DF(E)| < L$ where L is chosen small enough that $\sigma + 2NL < 0$. The last inequality implies $NL + \sigma < -NL < 0$ and hence $0 < -NL/(NL+\sigma) < 1$. Then (11) becomes

$$|u(t)| \leq N|u(T)|e^{(NL+\sigma)(t-T)} + Mp \cdot B. \tag{12}$$

Since E is locally asymptotically stable there exists $0 < \delta < \varepsilon$ such that $\delta < \varepsilon/(6N)$, and for all $z(0) \in S_\delta(E)$ then $z(t) \in S_{\varepsilon/3}(E)$ for all $t \geq 0$. Now if $z(0), x(0) \in S_\delta(E)$ and if $p \cdot B < \varepsilon/(6M)$, then $x(t) \in S_\varepsilon(E)$ for all $t \geq 0$. To see this, assume the last statement is false; then there is a first time $\hat{t}$ such that $|x(\hat{t}) - E| = \varepsilon$. Consequently, for all $t < \hat{t}$ we have $|x(\hat{t}) - E| < \varepsilon$. The constant δ has been chosen so that $z(t) \in S_{\varepsilon/3}(E) \subset S_\varepsilon(E)$ for all $t \geq 0$. Thus, if $x(t)$, $z(t) \in S_\varepsilon(E)$ for all $t < \hat{t}$, then the line segment connecting them is also contained in $S_\varepsilon(E)$. By our choice of ε we have $|DF(w(s,t)) - DF(E)| < L$ for all $t < \hat{t}$. Hence, if we let $\gamma = -(NL+\sigma)$ and $T = 0$ and use (12), we have

$$|x(t) - z(t)| \leq Mp \cdot B + Ne^{-\gamma t}|x(0) - z(0)| < \varepsilon/2$$

for all $t < \hat{t}$ since $NL + \sigma < 0$, $x(0)$, $z(0) \in S_\delta(E)$, and by our choice of $p \cdot B$. Since $z(t) \in S_{\varepsilon/3}(E)$ for all $t \geq 0$, then using the triangle inequality we have

$$|x(t) - E| \leq |x(t) - z(t)| + |z(t) - E| < \varepsilon/2 + \varepsilon/3 < \varepsilon$$

for all $t < \hat{t}$. This contradicts the assumption that $|x(\hat{t}) - E| = \varepsilon$. Consequently, $x(t)$, $z(t) \in S_\varepsilon(E)$ for all $t \geq 0$ and (12) holds for all $t \geq 0$. Thus, Theorem 1 is proved. $\square$

3. Model equations and background.

An ecosystem of n interacting, continuously reproducing populations is modeled by an autonomous system of ordinary differential equations of Kolmogorov-type. Let x_i, $i = 1, \ldots, n$, denote the density of the ith 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 jth population on the ith population. The per capita replacement rate, the fitness f_i, of the ith population is a smooth function of y_i. Our model equations are

$$\frac{dx_i}{dt} = x_i f_i(y_i), \qquad i = 1, 2, \dots, n. \tag{13}$$

This vector field is defined on the nonnegative orthant which is invariant because of the form of (13). Introducing the weighted density variable, y_i, has the advantage of separating the ith 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. Here we restrict our attention to pioneer and climax fitnesses.

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 zeros which also are nondegenerate. Thus, the isoclines of a climax population are two parallel hyperplanes. An equilibrium of (13) 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 zeros of the fitnesses, then an interior equilibrium $E = (e_1, \dots, e_n)^*$ is a solution to the system of linear equations

$$CE = z. \tag{14}$$

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

$$\begin{aligned} DF(x) = &\begin{pmatrix} f_1(y_1) & & 0 \\ & \ddots & \\ 0 & & f_n(y_n) \end{pmatrix} \\ &+ \begin{pmatrix} x_1 f_1'(y) & & 0 \\ & \ddots & \\ 0 & & x_n f_n'(y_n) \end{pmatrix} C. \end{aligned} \tag{15}$$

Note that the first diagonal matrix in (15) vanishes at an equilibrium E in the interior of the orthant. Hence, formulas for the trace and determinant of $DF(E)$ are

$$\begin{aligned} \operatorname{tr} DF(E) &= \sum_{i=1}^{n} e_i f_i'(z_i) c_{ii} \\ \det DF(E) &= \det C \prod_{i=1}^{n} e_i f_i'(z_i). \end{aligned} \tag{16}$$

4. Interactions of one pioneer and one climax.

For the two-dimensional system modeling the interaction of a pioneer, x_1, and a climax, x_2, Selgrade and Namkoong [**19, 20**] show that an asymptotically stable, interior equilibrium E may lose its stability via Hopf bifurcation where the parameter is either intraspecific crowding coefficient $c_{ii} > 0$, $i = 1, 2$. This bifurcation occurs only if $\det C < 0$ and only if E is determined by the smaller zero z_2 of the climax fitness, f_2, i.e., where $f_2'(z_2) > 0$. Selgrade and Namkoong [**20**] derive a formula for the stability coefficient of the resulting periodic solution and show that this solution is asymptotically stable for many examples of biological interest. Since increasing or decreasing appropriate intraspecific crowding parameters destabilizes an equilibrium, we try to reverse this behavior by harvesting or stocking the appropriate population.

First we consider system (C) for the vector field of (13) with $A_1 = A$ and $A_2 = 0$, i.e., we stock or harvest the pioneer. If $A = 0$, a Hopf bifurcation occurs as c_{11} decreases through the critical value $\hat{c}_{11}$. We use the implicit function theorem to determine the curve in the (c_{11}, A) parameter space along which the Hopf bifurcation occurs near the point $(c_{11}, A) = (\hat{c}_{11}, 0)$. For specific cases of a linear or exponential pioneer and an exponential climax, Selgrade [**18**] obtains conditions implying that this curve is the graph of A as a decreasing function of c_{11}. Hence, for $c_{11} < \hat{c}_{11}$ and $A = 0$ where the equilibrium E is unstable, the system (C) will be returned to stable equilibrium by stocking at a rate A above the bifurcation curve. Here we do a similar analysis for arbitrary pioneer and climax fitnesses and present an example where stocking or harvesting may be required to return (C) to stable equilibrium.

Recall that z_2 is the smaller zero of f_2. For $A_1 = A$ and $A_2 = 0$, the interior equilibrium E of (C) where the Hopf bifurcation must occur solves the nonlinear system of equations:

$$\begin{aligned} 0 &= x_1 f_1(c_{11}x_1 + c_{12}x_2) + A \\ z_2 &= c_{21}x_1 + c_{22}x_2. \end{aligned} \tag{17}$$

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

$$\operatorname{tr} DF(E) = c_{11}x_1 f_1'(y_1) + c_{22}x_2 f_2'(y_2) - \frac{A}{x_1}. \tag{18}$$

To determine where the Hopf bifurcation occurs, we set $\operatorname{tr} DF(E)$ equal to zero in (18) and that equation along with (17) provide three equations in the four unknowns x_1, x_2, A, and c_{11}. We use the second equation in (17) to eliminate x_2 and to obtain two equations in the unknowns x_1, A and c_{11}. Specifically, the first equation in (17) determines the function

$$G(x_1, A, c_{11}) = x_1 f_1\left(c_{11}x_1 + \frac{c_{12}z_2 - c_{12}c_{21}x_1}{c_{22}}\right) + A$$

and (18) gives

$$\begin{aligned} H(x_1, A, c_{11}) = -c_{11}x_1^2 f_1'&\left(c_{11}x_1 + \frac{c_{12}z_2 - c_{12}c_{21}x_1}{c_{22}}\right) \\ &+ c_{21} f_2'(z_2) x_1^2 - z_2 f_2'(z_2) x_1 + A. \end{aligned}$$

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 $Q = (x_1, A, c_{11}) = (\hat{x}_1, 0, \hat{c}_{11})$. The appropriate derivative at Q is given by:

$$\frac{\partial(G, H)}{\partial(x_1, A)}(Q) = \begin{pmatrix} \hat{x}_1 f_1'(z_1)(\det C)/c_{22} & 1 \\ z_2 f_2'(z_2) - c_{11} f_1''(z_1)\hat{x}_1^2(\det C)/c_{22} & 1 \end{pmatrix}. \tag{19}$$

The implicit function theorem applies if the determinant of the matrix in (19) is nonzero. If so, the monotonicity of A as a function of c_{11} at $\hat{c}_{11}$ is determined by

$$\frac{dA}{dc_{11}} = \frac{\hat{x}_1^2 f_1'(z_1)[\hat{x}_1 f_1'(z_1) \det C + z_2 c_{22} f_2'(z_2)]}{\hat{x}_1 \det C[f_1'(z_1) + \hat{c}_{11} f_1''(z_1)\hat{x}_1] - z_2 c_{22} f_2'(z_2)}. \tag{20}$$

The numerator of (20) is always negative because $f_1'(z_1) < 0$, $f_2'(z_2) > 0$ and $\det C < 0$. Thus the sign of (20) is determined by the sign of the denominator, i.e., the sign of the determinant of (19). This sign crucially depends on the first two derivatives of the pioneer fitness, on the first derivative of the climax fitness, and on the competition coefficients. Even for a linear pioneer where $f_1''(z_1) = 0$, this denominator may be positive or negative as we see in the following example. Let

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

where $r < 1$. Then the denominator of (20) is

$$c_{12} - (2-r)c_{22}. \tag{21}$$

Essentially, (21) measures the difference between the competitive effect of the climax on the pioneer and the climax intraspecific competition. Thus, if $c_{12} > (2-r)c_{22}$, then $dA/dc_{11} < 0$ at $\hat{c}_{11}$, so for $c_{11} < \hat{c}_{11}$ stocking the pioneer returns system (C) to stable equilibrium. But if $c_{12} < (2-r)c_{22}$, then harvesting the pioneer returns the system to stable equilibrium.

For the system (P) with $A_1 = A$, $A_2 = 0$, and $c_{11} < \hat{c}_{11}$, if the parameters are such that (C) has an attracting periodic orbit then the corresponding system (P) has a toral attractor surrounding this orbit for small B_1, see Levinson [**15**]. If A is chosen so that stocking or harvesting at rate A yields a stable equilibrium for (C) then, in light of Theorem 1, the corresponding periodic rate stocking or harvesting with sufficiently small product $p_1 B_1$ will return system (P) to "near-equilibrium" behavior.

For (C) with $A_1 = 0$ and $A_2 = A$, i.e., for stocking or harvesting the climax, an argument analogous to the preceding may be used to find the Hopf bifurcation curve in the (c_{22}, A) parameter space near $(\hat{c}_{22}, 0)$. A stable equilibrium bifurcates to a periodic orbit as c_{22} increases through $\hat{c}_{22}$, see Selgrade and Namkoong [**20**]. So if the bifurcation curve is increasing as a function of c_{22}, then stocking the climax is needed to restore (C) to stable equilibrium; and if the bifurcation curve is decreasing, then harvesting the climax restores (C) to stable equilibrium. The system (P) may be returned to "near-equilibrium" with the corresponding periodic stocking or harvesting. The bifurcation curve determines A as a function of c_{22} with derivative at $\hat{c}_{22}$ given by

$$\frac{dA}{dc_{22}} = \frac{-\hat{x}_2^2 f_2'(z_2)[\hat{x}_2 f_2'(z_2) \det C + z_1 c_{11} f_1'(z_1)]}{\hat{x}_2 \det C[f_2'(z_2) + \hat{c}_{22} f_2''(z_2)\hat{x}_2] - z_1 c_{11} f_1'(z_1)}. \tag{22}$$

Notice the similarities between (22) and (20).

5. Interactions of two pioneers and one climax.

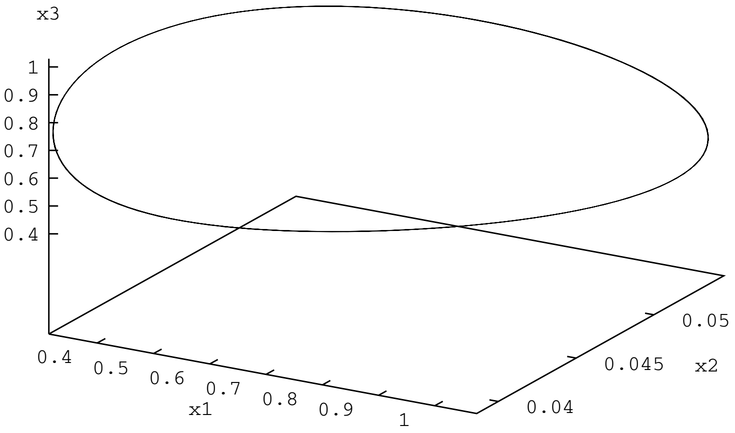
Gardini, Lupini and Messia [**8**] report the occurrence of strange attractors for three-dimensional Lotka/Volterra systems, which are included in (13). For (13) with two linear pioneers and one exponential climax, we observe these attractors arising from repeated period-doubling of the return map of a stable Hopf periodic orbit as the self-crowding parameter c_{11} decreases. With forcing on the first pioneer, our system is:

$$\begin{aligned} \frac{dx_1}{dt} &= x_1[4 - 4(c_{11}x_1 + c_{22}x_2 + x_3)] + A \\ \frac{dx_2}{dt} &= x_2[.75 - (c_{22}x_2 + x_3)] \\ \frac{dx_3}{dt} &= x_3[-6 + 6(x_1 + x_2 + c_{33}x_3)e^{.5-.5(x_1+x_2+c_{33}x_3)}]. \end{aligned} \tag{23}$$

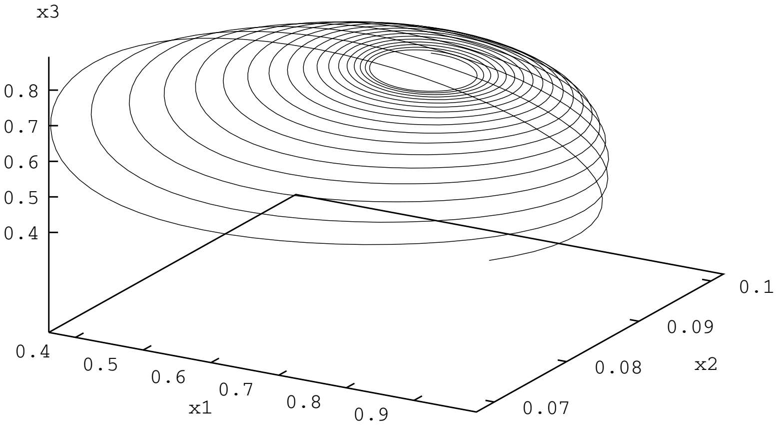
Equation (23) represents a class of interactions where the climax has the same effect on both pioneers, i.e., $c_{13} = c_{23} = 1$; each pioneer has the same effect on the climax, i.e., $c_{31} = c_{32} = 1$; and the second pioneer affects itself and the first pioneer equally so $c_{12} = c_{22}$. The formulas for Hopf bifurcation in (23) are complicated so we restrict our attention to a two parameter problem by choosing $c_{22} = 1.5$ and $c_{33} = .5$. When $A = 0$, a Hopf bifurcation occurs at $E \cong (.616371, .034517, .698225)$ as c_{11} decreases through $\hat{c}_{11} \cong .4056$. We examine the Hopf bifurcation curve in the (c_{11}, A) parameter space near $(c_{11}, A) = (\hat{c}_{11}, 0)$.

An interior equilibrium E of (23) where our Hopf bifurcation occurs must satisfy the following three equations:

$$\begin{aligned} 0 &= x_1(4 - 4(c_{11}x_1 + 1.5x_2 + x_3)) + A \\ .75 &= 1.5x_2 + x_3 \\ 1 &= x_1 + x_2 + .5x_3. \end{aligned} \tag{24}$$



(a) $A = 0$, stable periodic solution.



(b) $A = -.05$, stable equilibrium.

FIGURE 1. $c_{11} = .38$.

For a pair of eigenvalues of E to cross the imaginary axis, the following equation must be satisfied:

$$(J_{11} + J_{22} + J_{33})\operatorname{tr} DF(E) - \det DF(E) = 0 \tag{25}$$

where J_{ii} denotes the cofactor of $DF(E)$ corresponding to the ii entry, see Sumner [**21**] for a detailed discussion. With the aid of the symbolic manipulator MAPLE, we find that

$$\begin{aligned} \operatorname{tr} DF(E) &= 1 - 8c_{11}x_1 + 1.5(x_3 - x_2) \\ \det DF(E) &= -.75x_2x_3(1 - 8c_{11}x_1) \\ J_{11} + J_{22} + J_{33} &= 1.5(x_3 - x_2)(1 - 8c_{11}x_1) \\ &\qquad + 12x_1x_3 + .75x_2x_3. \end{aligned} \tag{26}$$

Using (24) to eliminate x_2 and x_3 and inserting (26) into (25), we obtain two equations in the unknowns x_1, c_{11} and A:

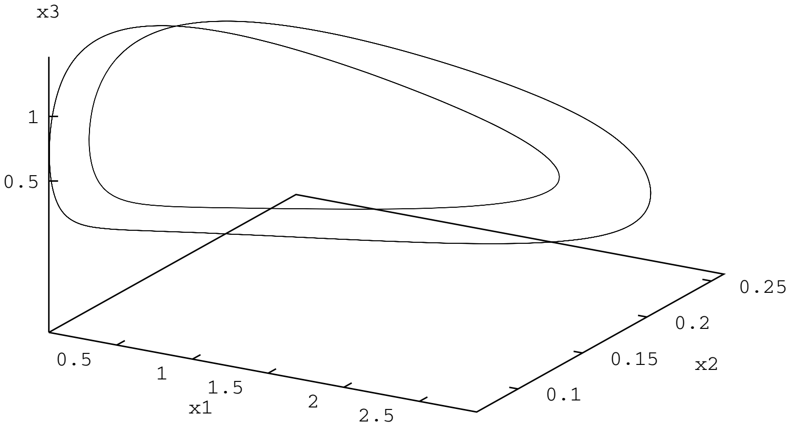
$$\begin{aligned} G(x_1, c_{11}, A) &\equiv x_1(1 - 4c_{11}x_1) + A = 0 \\ H(x_1, c_{11}, A) &\equiv (810 - 2376c_{11} + 960c_{11}^2)x_1^3 \\ &\qquad + (2028c_{11}528c_{11}^2 - 1539/4)x_1^2 \\ &\qquad - 825c_{11}/2 + 3567/16)x_1 + 3399/32 = 0. \end{aligned} \tag{27}$$

The equation $(G, H) = (0, 0)$ determines x_1 and A as functions of c_{11} near the point $Q \equiv (x_1, c_{11}, A) \cong (.616371, .4056, 0)$ since the following determinant is nonzero at Q:

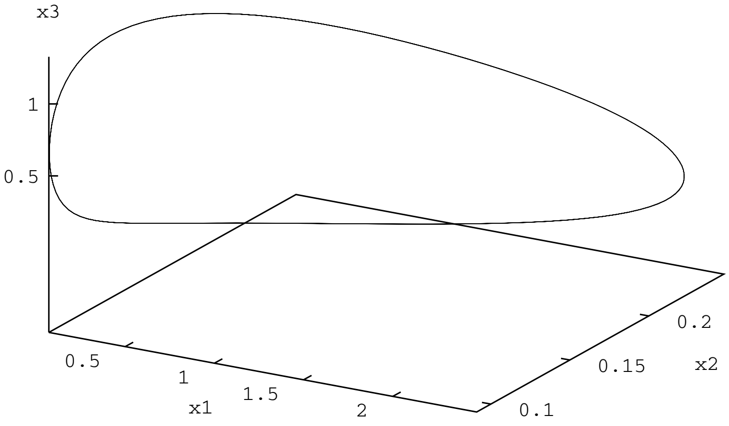
$$\det \frac{\partial(G, H)}{\partial(x_1, A)}(Q) \cong -47.1926.$$

The bifurcation curve in the (c_{11}, A)-space is the graph of A as an increasing function of c_{11} near .4056 because dA/dc_{11} is positive at .4056, i.e., $dA/dc_{11} \cong 1.95478$. Hence, for c_{11} less than .4056, system (23) has a stable equilibrium for negative A below the bifurcation curve, i.e., harvesting is needed to restore (23) to stable equilibrium (see Figure 1).

Numerical experiments indicate that appropriate levels of harvesting will reverse the period-doubling cascade in (23) and will maintain the system at any periodic attractor along the cascade. For example, when $c_{11} = .21$ and $A = 0$, (23) has a period-2 attractor with initial

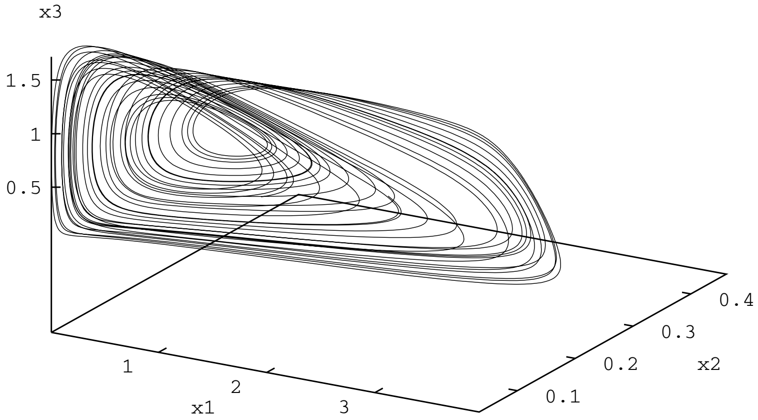


(a) $A = 0$.

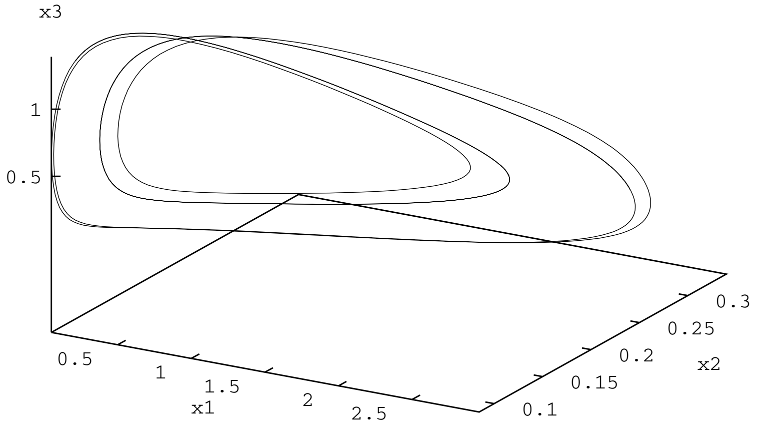


(b) $A = -.02$.

FIGURE 2. $c_{11} = .21$.



(a) $A = 0$.



(b) $A = -.03$.

FIGURE 3. $c_{11} = .19$.

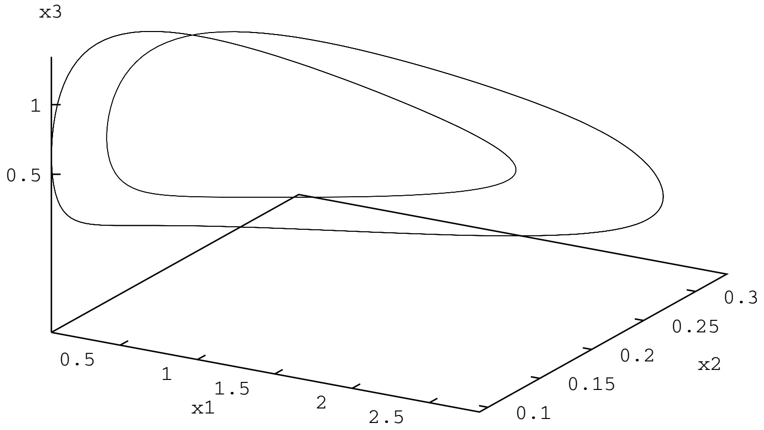


FIGURE 3. $c_{11} = .19$. (c) $A = -.04$.

condition $(x_1, x_2, x_3) = (2.22669, .20737, .27923)$, see Figure 2a. If (23) is harvested at a level of .02, i.e., $A = -.02$, then the attractor is an orbit of period roughly one half that of the period-2 attractor, see Figure 2b.

For $c_{11} = .19$ and $A = 0$, (23) appears to have a strange attractor containing the orbit of the point $(x_1, x_2, x_3) = (1.30014, .155198, .286801)$, see Figure 3a. If $A = -.03$, then this strange attractor is replaced with a period-4 attractor with initial condition $(x_1, x_2, x_3) = (2.65342, .286699, .118539)$, see Figure 3b. If $A = -.04$, then (23) has a period-2 attractor with initial condition $(x_1, x_2, x_3) = (1.93927, .25526, .30584)$, see Figure 3c. Hence, the local asymptotic behavior of (23) may be controlled by harvesting the first pioneer.

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