

PERIODIC TWO-PREDATOR, ONE-PREY INTERACTIONS AND THE TIME SHARING OF A RESOURCE NICHE*

J. M. CUSHING†

Abstract. A competition model involving two competing predator species and a single renewable resource prey species is studied under the assumption that the system parameters are periodic in time. It is shown by means of global bifurcation techniques that a continuum of positive periodic solutions exists as a function of a selected (averaged) parameter and that the stability of these solutions (at least locally near bifurcation) depends on the direction of bifurcation. In the special autonomous case of constant parameters the bifurcation is vertical and the spectrum of the continuum is a discrete point. This autonomous case supports the principle of competitive exclusion in that coexistence of the predators on the single resource prey is possible (in the sense that the system equilibrates) only on a parameter set of measure zero. In the more general case of periodic coefficients, however, it is shown that the spectrum can be an interval of positive length provided the predator parameter oscillations are out-of-phase in a certain sense and hence how such oscillations can promote the possibility of stable coexistence. The specific case, when all system parameters are constant except the predator resource consumption rates which are taken to be small amplitude cosine oscillations around a positive mean value, is studied in detail both analytically and numerically. Besides illustrating and corroborating the general results, this example clearly shows the effect on the spectral interval, and hence on the possibility of stable coexistence of the predators, which out-of-phase resource consumption rates can have.

1. Introduction. The great diversity of means used by different species to reduce interspecific competition and hence promote survival and coexistence can be roughly classified into three broad categories. Species can consume different resources, exploit different spatial habitats and/or be active at different times [15, p. 190]. Mathematical models have been extensively used to study the first two of these means for the avoidance of competitive exclusion. With regard to differential resource consumption, there is the well-developed theory of MacArthur and Levins upon which is founded much of the theory of competitive exclusion, ecological niche and limiting similarity [13], [14]. More recently there has appeared a growing body of mathematical research concerning the competition for space and many related phenomena such as patchiness, succession and species packing (e.g., see [20]). There has been, however, very little mathematical research into the temporal dynamics of competition, in particular into phenomena such as the time sharing of niches or the change in time of niche dimensions and habitat characteristics or vital biological parameters and into the effects that these phenomena have on coexistence and competitive exclusion.

With regard to periodic fluctuations in the system parameters, several recent papers have studied some of the basic dynamics of differential systems as models of competition [2], [3], [6], [16]. These studies focus on the questions of the existence of positive periodic solutions (in place of positive equilibria in autonomous models) and their stability, but they do not study specific periodic biological mechanisms and their effects. A more detailed study of periodicities in the theory of competition is done in [5] where periodicities are introduced into the coefficients of the classical Volterra-Lotka equations by means of the MacArthur-Levins theory which relates the coefficients in the model to the characteristics of a one-dimensional resource spectrum and its utilization rates. Ignoring periodicities in niche positions and widths [15, Chapter 13], this paper concentrates on periodicities in resource consumption rates in order to study the effects of time sharing a resource niche on competitive

* Received by the editors June 29, 1982, and in revised form March 24, 1983.

† Department of Mathematics and Program in Applied Mathematics, University of Arizona, Tucson, Arizona 85721.

coexistence. It is found that while one can roughly conclude from these model equations that out-of-phase time sharing of a resource enhances competitive coexistence and stability, the situation is quite complicated in its dependence on parameter interrelationships (such as niche separation to width ratio, length of the period and the amplitude of the oscillations) and on how one measures stable coexistence (e.g., simply by means of the existence of a positive stable solution or by means of the size of Floquet multipliers, amplitude oscillations, minimum population levels or various combinations of these things).

The purpose of the present paper is to study the effects of periodic fluctuations in parameter values on a different model of two species competition and, as an important special case, the effects of time sharing of a resource as expressed by out-of-phase periodic resource consumption rates. The model to be studied here is a periodic version of a two-predator, one-prey system studied recently by several authors [7]–[11], [18], [19]. In this model two species (the predators) are in competition for a single renewable resource (the prey) and interact only indirectly through their common consumption of this resource. The prey grows logistically in the absence of both predators and the predators decrease exponentially in the absence of the prey. The interaction terms are taken to be of Michaelis–Menten form (or Holling's type II). The model equations are given by (2.1) in § 2 below. My main reason for choosing this particular model for a study of the effects of periodicities on two species competition, quite apart from the recent mathematical interest which has been shown the model and from its usefulness in laboratory studies [11] (as opposed to the more phenomenological Volterra–Lotka equations), is that it makes, as I hope to show in this paper, dramatically clear in a straightforward and interesting way the effect that periodicities can have on the stable coexistence of competing species and how out-of-phase periodicities (in a certain sense made precise below) in key interaction parameters can promote avoidance of competitive exclusion. More specifically, in an example studied in detail in § 5, it will be seen how out-of-phase periodicities in the predator consumption rates of the prey resource can lead to significant changes in the size of the parameter region which allows stable coexistence.

The model equations will be described in § 2. In §§ 3 and 4 respectively, the existence and stability of positive solutions of the “reduced” system (2.2) of just one predator and one prey (i.e. the system in which one predator is absent) and of the full two-predator, one-prey system (2.1) will be studied. This will be done by an application of general global bifurcation results of the author for general Kolmogorov systems [3] together with some considerably detailed analysis of the specific properties of these particular systems.

Roughly, these results will show that what is true of the autonomous systems concerning positive and nonnegative equilibria is true of the periodic versions of the systems concerning positive and nonnegative periodic solutions. However, for the periodic two-predator, one-prey system there can be a crucial difference. Using d_2 in (2.1), the (averaged) inherent death rate of the second predator as a bifurcation parameter, one finds for the autonomous case that a continuum of positive equilibria exists, but only for a discrete “spectrum”, i.e. only for a single isolated value of d_2 . For the periodic case, on the other hand, this spectrum of d_2 values for which positive periodic solutions exist can be an interval with positive length.

The fact that positive equilibria exist in the autonomous system (2.1) only for a single isolated value of d_2 seemingly implies that this system of model equations supports the principle of competitive exclusion. This is true in so far as it implies that the two predator species cannot coexist in a state of stable equilibrium (except on a

parameter region of measure zero). It has, however, been shown both numerically [8], [12] and analytically [1], [18] that in certain parameter regions the two predators can coexist in a stable limit cycle sense. Roughly this can occur, provided other parameter constraints are also met, when the inherent carrying capacity K of the single prey species is sufficiently large; namely when K is large enough so that the autonomous one-predator, one-prey system (2.2) has a stable limit cycle (and an unstable equilibrium). The results below are concerned with the periodic system (2.1) only under circumstances corresponding to the former case for the autonomous system, i.e. when competitive exclusion occurs (except for an isolated value of d_2) and the one-predator, one-prey "reduced" system (2.2) has a stable equilibrium. Parameter regions which in the autonomous case give rise to limit cycle coexistence in (2.1) are excluded (by the assumption in § 4 that (S^0, x_1^0) is stably noncritical).

Theorems 2 and 3 in § 4 show that periodicities in the system's parameters can allow stable coexistence in circumstances when constant coefficients do not. This is because periodicities can yield a bifurcating branch of positive periodic solutions of (2.1) for suitable parameter values lying in a "spectral" interval of *positive* length in cases when the autonomous system (2.1) has a branch of positive equilibria only for a discrete isolated parameter value (and predicts extinction of one predator for other values). The stability of the positive periodic solutions of the periodic system (2.1) lying on this bifurcating branch is shown to depend on the direction of bifurcation.

In § 5 the specific case of small amplitude cosinusoidal oscillations in consumption rates (other parameters being held constant) is considered both analytically and numerically. Besides illustrating the results of §§ 3 and 4, this case shows that the bifurcation can be either to the right or to the left, i.e. either stable or unstable, depending on certain parameter relationships made explicit (including a case of the "paradox of enrichment") and that the length of the spectral interval which permits stable coexistence can be "substantial" (roughly, it can be commensurate with the spectral interval which permits the survival, in the positive stable equilibrium sense, of the first predator alone in the absence of the second, competing predator).

2. The model equations. Let $B(p)$ denote the Banach space of continuous, p -periodic real valued functions $x:R \rightarrow R$ under the supremum norm $\|x\|_0 := \sup_{0 \leq t \leq p} |x(t)|$. Let $av(x) := p^{-1} \int_0^p x(t) dt$ and $B_+(p) := \{x \in B(p) | x(t) > 0 \text{ for all } t\}$.

The differential systems to be considered in this paper are

$$(2.1) \quad \begin{aligned} (a) \quad S' &= rS \left(1 - \frac{S}{K}\right) - \frac{m_1}{y_1} \frac{x_1 S}{a_1 + S} - \frac{m_2}{y_2} \frac{x_2 S}{a_2 + S}, \\ (b) \quad x_1' &= \frac{m_1 x_1 S}{a_1 + S} - d_1 x_1, \\ (c) \quad x_2' &= \frac{m_2 x_2 S}{a_2 + S} - d_2 x_2, \end{aligned}$$

and the "reduced system"

$$(2.2) \quad \begin{aligned} (a) \quad S' &= rS \left(1 - \frac{S}{K}\right) - \frac{m_1}{y_1} \frac{x_1 S}{a_1 + S}, \\ (b) \quad x_1' &= \frac{m_1 x_1 S}{a_1 + S} - d_1 x_1, \end{aligned}$$

under the assumptions that

$$(2.3) \quad a_i, m_i, y_i, K, r \in B_+(p) \quad \text{and} \quad d_i \in B(p) \quad \text{for } i = 1, 2.$$

As mentioned in the introduction, (2.1) has been studied by several authors when the parameters in (2.3) are all positive constants. Further discussion of the model can be found in their work [8]–[11], [18], [19]. Our concern here, as indicated by (2.3), is with that of allowing for periodicities (of a common period) in the parameters and with the existence and stability of positive, periodic solutions.

By a solution of (2.1) is meant, of course, a differentiable triple $(S(t), x_1(t), x_2(t))$ and by a positive, periodic solution is meant a solution $(S, x_1, x_2) \in B_+^3(p) := B_+(p) \times B_+(p) \times B_+(p)$. Similar definitions are used for (2.2).

A summary of the situation concerning the existence and stability of nonnegative equilibria in the special case of constant parameters can be found in [18]. Of primary concern to us here is that (2.1) has, in this case, a positive equilibrium (S, x_1, x_2) if and only if

$$(2.4) \quad 0 < d_1 < \frac{m_1 K}{a_1 + K},$$

$$(2.5) \quad d_2 = a_1 d_1 m_2 / (a_1 d_1 + a_2 (m_1 - d_1)),$$

in which case there exists a continuum of positive equilibria given by $S = a_1 d_1 / (m_1 - d_1)$ together with any positive point $(x_1, x_2) \in \mathbb{R}^2$ on the line

$$(2.6) \quad \left(\frac{m_1}{y_1} \frac{1}{a_1 + S} \right) x_1 + \left(\frac{m_2}{y_2} \frac{1}{a_2 + S} \right) x_2 = r \left(1 - \frac{S}{K} \right).$$

Using d_2 as a bifurcation parameter and holding all other parameters fixed (but satisfying (2.4)), one can view this continuum of equilibria as a branch which bifurcates from the nonnegative equilibrium

$$S = a_1 d_1 / (m_1 - d_1), \quad x_1 = y_1 (a_1 + S) r \left(1 - \frac{S}{K} \right) / m_1, \quad x_2 = 0,$$

(the first two constants (S, x_1) of which constitute a positive equilibrium of the reduced system (2.2)) in a “vertical” manner, i.e. such that the spectrum of the branch consists of the discrete point d_2 given by (2.5). This branch leaves the positive octant at the symmetric nonnegative equilibrium

$$S = a_1 d_1 / (m_1 - d_1), \quad x_1 = 0, \quad x_2 = y_2 (a_2 + S) r \left(1 - \frac{S}{K} \right) / m_2.$$

The goal of §§ 3 and 4 is to demonstrate that, for the more general case of periodic parameters (2.3), a similar bifurcating branch of positive periodic solutions exist and to study the spectrum of this branch and the stability of the solutions on it. To do this we must begin with a study of the periodic reduced system (2.2) whose positive periodic solutions serve as the “bifurcation points” for the full system (2.1) as they do in the autonomous case just discussed above.

Solutions of Kolmogorov systems such as (2.1) and (2.2) have the property that each component of the solution either never vanishes or identically vanishes.

3. The periodic one-predator, one-prey system (2.2). It is easy to see by direct integration and the resulting general solution

$$S(t) = S(0) \exp \left(\int_0^t r(u) du \right) / \left(1 + S(0) \int_0^t (r(u)/K(u)) \exp \left(\int_0^u r(v) dv \right) du \right)$$

that the periodic logistic equation

$$(3.1) \quad S' = rS \left(1 - \frac{S}{K} \right), \quad r \in B(p) \quad \text{and} \quad K \in B_+(p),$$

provided $\text{av}(r) > 0$, has a unique positive periodic solution $S = s_0 \in B_+(p)$ and that this solution is asymptotically stable (globally attracting with respect to positive solutions). Define the real number

$$(3.2) \quad d_1^{\text{cr}} := \text{av} \left(\frac{m_1 s_0}{a_1 + s_0} \right).$$

Then $d_1^{\text{cr}} > 0$ by (2.3). Recall that a continuum is a closed, connected set.

THEOREM 1. *Assume (2.3). Then the one-predator, one-prey system (2.2) has a positive periodic solution if and only if $0 < \text{av}(d_1) < d_1^{\text{cr}}$. More specifically, if $d_1^0 \in B(p)$ is an arbitrary periodic function with $\text{av}(d_1^0) = 0$, then there exists a set $P^+ = \{(S, x_1, \mu)\} \subset B_+^2(p) \times \mathbb{R}$ where $(S, x_1) > 0$ solves (2.2) with $d_1(t) = -\mu + d_1^0(t)$ for $\mu \in (-d_1^{\text{cr}}, 0)$ whose closure is a continuum which connects the triple $(s_0, 0, \mu_0) \in B^2(p) \times \mathbb{R}$, $\mu_0 := -d_1^{\text{cr}}$, to one of the form $(0, x_1^*, 0) \in B^2(p) \times \mathbb{R}$, $x_1^*(t) > 0$. Moreover, for $\mu = -\text{av}(d_1)$ sufficiently close to the critical bifurcation value μ_0 , the corresponding positive periodic solutions are locally asymptotically stable. Furthermore, $(s_0, 0, \mu)$ as a solution of (2.2) is asymptotically stable for $\mu < \mu_0$ and unstable for $\mu > \mu_0$.*

This theorem describes a typical bifurcation and exchange of stability phenomenon as the solution $(s_0, 0, \mu)$ loses its stability to solutions on a bifurcating branch as the bifurcation parameter μ passes through the critical value μ_0 .

The following lemma concerning a priori bounds for positive solutions of (2.2) will be of use in the proof of this theorem.

LEMMA 1. *Assume (2.3). If $(S, x_1) \in B_+^2(p)$ solves (2.2) then $0 < \text{av}(d_1) < d_1^{\text{cr}}$ and for all t*

$$(3.3) \quad \begin{aligned} (a) \quad & 0 < S(t) \leq s_0(t) \leq |K|_0, \\ (b) \quad & 0 < x_1(t) \leq \frac{|r|_0}{m_1^0} |y_1|_0 (|a_1|_0 + |K|_0) \exp(p|m_1 - d_1|_0), \end{aligned}$$

where $0 < m_1^0 := \min_{0 \leq t \leq p} m_1(t)$.

Proof. If (2.2b) is divided by x_1 and the result averaged, then one gets

$$(3.4) \quad \text{av}(d_1) = \text{av} \left(\frac{m_1 S}{a_1 + S} \right) > 0.$$

From (2.2a) and (3.1) follows

$$(3.5) \quad S' \leq rS \left(1 - \frac{S}{K} \right), \quad s_0' = rs_0 \left(1 - \frac{s_0}{K} \right)$$

which, upon subtraction, leads to

$$(3.6) \quad \Delta' + b\Delta \leq -\frac{r}{K} \Delta^2 \leq 0$$

where $\Delta := S - s_0$, $b := r(2s_0K^{-1} - 1)$. Note that a division by s_0 of the equation in (3.5), followed by an average of both sides, yields $\text{av}(r) = \text{av}(rs_0/K)$ and hence

$$(3.7) \quad \text{av}(b) = \text{av} \left(\frac{s_0}{K} \right) > 0.$$

Now if (3.6) is multiplied by $\exp(\int_0^t b(u) du)$ and integrated from arbitrary t to $t^* \geq t$, then the inequality

$$\Delta(t^*) \leq \Delta(t) \exp\left(-\int_t^{t^*} b(u) du\right)$$

results. Choose $t^* = t + p$ and observe that both the difference $\Delta(t)$ and $b(t)$ are p -periodic. Thus $\Delta(t) \leq \Delta(t) \exp(-p \operatorname{av}(b))$ which, together with (3.7), implies $\Delta(t) \leq 0$ or, in other words, $S(t) \leq s_0(t)$ for all t .

If $t' \in [0, p]$ is a point where $s_0(t)$ attains its maximum, then from (3.1) one gets $|s_0|_0 = s_0(t') = K(t') \leq |K|_0$ and (3.3a) is established.

Next, (3.3a) implies the validity of the upper bound d_1^{cr} on $\operatorname{av}(d_1)$ since $S(t) \leq s_0(t)$ implies $m_1 S / (a_1 + S) \leq m_1 s_0 / (a_1 + s_0)$ for all t and the definition (3.2) of d_1^{cr} and (3.4) imply $\operatorname{av}(d_1) \leq d_1^{\text{cr}}$.

Finally, we need to establish the bound (3.3b) on $x_1(t) > 0$. From (2.2b) follows $x_1'/x_1 \leq m_1 - d_1$ and hence

$$0 < x_1(t) \leq x_1(t') \exp\left(\int_{t'}^t (m_1 - d_1) du\right)$$

for all $t \geq t'$. $x_1(t)$ is p -periodic, so it attains its maximum on every interval of length p . Let $t \in [t', t' + p]$ be chosen so that $x_1(t) = |x_1|_0$. Then

$$(3.8) \quad |x_1|_0 \leq x_1(t') \exp\left(\int_0^p |m_1 - d_1| du\right)$$

for all t' . Now choose $t' \in [0, p]$ such that $S(t') = |S|_0$. Then from (2.2a) and (3.8) we get

$$\begin{aligned} 0 &= r(t') \left(1 - \frac{|S|_0}{K(t')}\right) - \frac{m_1(t')}{y_1(t')} \frac{x_1(t')}{a_1(t') + S(t')} \\ &\leq |r|_0 - \frac{m_1^0}{|y_1|_0} \frac{|x_1|_0 \exp(-p|m_1 - d_1|_0)}{|a_1|_0 + |K|_0}, \end{aligned}$$

which implies (3.3b). \square

Proof of Theorem 1. Theorems 1, 7 and 8 (or more specifically for the 2×2 system (2.2) Theorem 10) of [3] can be applied to (2.2) with $d_1(t) = -\mu + d_1^0(t)$. To do this the open set Ω^2 in [3] can be taken to be the half plane $\Omega^2 := \{(S, x_1) \in \mathbb{R}^2 \mid S > -a_1^0, a_1^0 = \min_{0 \leq t \leq p} a_1(t)\}$ and the nondegeneracy condition H3 (or equivalently (3.1)) in [3] can be seen to hold since $-\operatorname{av}(rs_0/K) < 0$. This application results in the existence of a continuum $C^+ \subset B^2(p) \times \mathbb{R}$ of solutions (i.e. of triples (S, x_1, μ) such that $(S, x_1) \in B^2(p)$ solves (2.2) for $d_1 = -\mu + d_1^0$) which contains the ‘‘bifurcation point’’ $(s_0, 0, \mu_0)$ and which connects to the boundary of the set $\Omega_p^2 \times \mathbb{R} \subset B^2(p) \times \mathbb{R}$ (which includes ∞) where $\Omega_p^2 := \{(S, x_1) \in B^2(p) \mid S(t) + s_0(t) > -a_1^0\}$. Furthermore, in an open neighborhood of $(s_0, 0, \mu_0)$, the solutions on C^+ are positive.

The critical coefficient μ_1 in [3], which determines the direction of bifurcation and the stability of the solution branch, is easily calculated to be

$$(3.9) \quad \mu_1 = -\operatorname{av}(m_1 a_1 z_1 / (a_1 + s_0)^2),$$

where z_1 is the unique periodic solution of the linear scalar equation

$$(3.10) \quad z_1' = (b - 2rs_0/K)z_1 - x_1 m_1 s_0 / y_1 (a_1 + s_0),$$

x_1 being the periodic solution of $x_1' = (\mu_0 - d_1^0 + m_1 s_0 / (a_1 + s_0))x_1$ that satisfies $x_1(0) = 1$.

Since $av(b - 2rs_0/K) = -av(rs_0/K) < 0$, the Green's function associated with (3.10) is negative and hence, x_1 being consequently positive, it follows that $z_1 < 0$ for all t . Thus $\mu_1 > 0$ and it then follows from the results in [3] that the bifurcation of C^+ is to the right and stable; i.e. in an open neighborhood of $(s_0, 0, \mu_0)$ the set $C^+/\{(s_0, 0, \mu_0)\}$ consists of stable positive solutions $(S, x_1) > 0$ for $\mu > \mu_0$.

The continuum C^+ cannot consist entirely of positive solutions, however, because to do so C^+ would, in order to connect to the boundary of the set $\Omega_p^2 \times R$, have to be unbounded (i.e. connect to ∞) which would contradict Lemma 1 (recall $d_1 = d_1(t) = -\mu + d_1^0(t)$). Thus, as discussed in [3], C^+ must leave the "positive cone" $B_+^2(p) \times R$ at a point other than the bifurcation point.

Let C_0^+ be the maximal subcontinuum of C^+ which connects $(s_0, 0, \mu_0)$ to the boundary of $B_+^2(p) \times R$. Define P^+ to be the nonempty set of positive solutions on C_0^+ ; i.e. define $P^+ := C_0^+ \cap (B_+^2(p) \times R)$. Then the closure of P^+ is a continuum connecting $(s_0, 0, \mu_0)$ to the boundary of $B_+^2(p) \times R$; i.e. the closure of P^+ contains $(s_0, 0, \mu_0)$ and a point $(S^*, x_1^*, \mu^*) \neq (s_0, 0, \mu_0)$ where $S^* \geq 0, x_1^* \geq 0$ and either $S^* \equiv 0$ or $x_1^* \equiv 0$ or both. The proof of Theorem 1 will be complete when it is shown that $S^* \equiv 0, x_1^* > 0$ and that the spectrum associated with P^+ (i.e. the range of the projection $P^+ \rightarrow R$ defined by $(S, x_1, \mu) \rightarrow \mu$) is precisely the interval $(\mu_0, 0), \mu_0 = -d_1^{cr}$.

Let $P^+ \ni (S^n, x_1^n, \mu^n) \rightarrow (S^*, x_1^*, \mu^*)$ in $B^2(p) \times R$. First, suppose that $S^* \equiv x_1^* \equiv 0$. Then by (2.2a) for sufficiently large $n, S^{n'} > 0$ for all t , which contradicts $S^n \in B(p)$. Thus C_0^+ cannot leave the cone through the origin.

Secondly, suppose that $x_1^* \equiv 0$ and $S_1^* > 0$ for all t . Then passing $n \rightarrow +\infty$ in (2.2a) with $S = S^n, x_1 = x_1^n$ one finds that $S_1^* > 0$ satisfies the periodic logistic (3.1). Hence, because of the uniqueness of the positive periodic solution of (3.1), $S_1^* \equiv s_0$. Moreover, dividing (2.2b) with $S = S^n, x = x_1^n$ and $d_1 = -\mu^n + d_1^0$ by x_1^n and averaging both sides of the result, one further obtains $\mu^n = -av(m_1 S^n / (a_1 + S^n))$ which, in the limit as $n \rightarrow +\infty$, implies $\mu^* = \mu_0$. This results in a contradiction to $(S^*, x_1^*, \mu^*) \neq (s_0, 0, \mu_0)$.

Having ruled out the above two cases, we are left with the remaining case $S_1^* \equiv 0, x_1^* > 0$. Furthermore, by the same reasoning as above, $\mu^n = -av(m_1 S^n / (a_1 + S^n))$ which now implies $\mu^n \rightarrow \mu^* = 0$ as asserted in Theorem 1. Incidentally, (2.2b) with $S = S^n, x_1 = x_1^n$ and $d_1 = -\mu^n + d_1^0$ implies in the limit that $x_1^* > 0$ solves the equation $x_1^{*'} = -d_1^0(t)x_1^*$.

This argument also shows that if (S, x_1, μ) lies on the boundary of $B_+^2(p) \times R$ then either $\mu = \mu_0$ or $\mu = 0$.

Finally, with regard to the spectrum of P^+ we observe that since the closure C_0^+ of P^+ is a continuum in $B^2(p) \times R$ it follows that the closure of the spectrum is a continuum in R . By Lemma 1 the closure of the spectrum is bounded and hence is a compact subinterval of the interval $[\mu_0, 0]$. Since it contains, as shown above, both endpoints μ_0 and 0, the closure of the spectrum must in fact be the interval $[\mu_0, 0]$. Moreover, since only $\mu = \mu_0$ and $\mu = 0$ can correspond to solutions on the boundary of the cone, the spectrum of P^+ must be $(\mu_0, 0)$. \square

When all the parameters in (2.2)–(2.3) are positive constants, the set P^+ reduces to the set of positive equilibria given by

$$S = -a_1\mu / (m_1 + \mu), \quad x_1 = ry_1 \left(1 - \frac{S}{K} \right) (a_1 + S) / m_1,$$

with $\mu \in (-\mu_0, 0)$ where $\mu_0 = -m_1 K / (a_1 + K)$. Moreover, this equilibrium is stable if $K < a_1$ while if $K > a_1$ then it is stable for $\mu < -m_1(K - a_1) / (K + a_1)$ and unstable for $\mu > -m_1(K - a_1) / (K + a_1)$, thereby illustrating the possibility that the stability

guaranteed near bifurcation by Theorem 1 may be lost somewhere along the branch P^+ . As is typically the case in autonomous predator-prey models, the stability of the equilibrium is lost (resulting in a Hopf bifurcation to a limit cycle) when the (vertical) predator x_1 isocline moves to the left of a hump in the prey S isocline (which occurs in this example at $S = (K - a_1)/2$).

With these preliminaries for the reduced system (2.2) out of the way, it is now possible to study the full two-predator, one-prey system (2.1) using again the results and techniques in [3].

4. The periodic two-predator, one-prey system (2.1). Suppose that the coefficients (2.3) in the reduced system (2.2) are such that it has a positive periodic solution; namely, suppose that $\text{av}(d_1) \in (0, d_1^{\text{cr}})$ and let $(S, x_1) = (S^0, x_1^0) \in B_+^2(p)$ denote this solution. This solution of (2.2) yields a solution $(S, x_1, x_2) = (S^0, x_1^0, 0) \in B^3(p)$ of the two-predator, one-prey system (2.1) from which will bifurcate a continuum of positive solutions of (2.1) with $\mu = -\text{av}(d_2)$ used as a “bifurcation parameter.” The goal of this section is not only to establish the existence of this continuum but to study its stability and spectrum and to obtain conditions under which this spectrum is an interval of *positive* length.

To do this by means of the results in [3] for general periodic Kolmogorov systems it is necessary that the solution (S^0, x_1^0) of (2.2) be *noncritical*; i.e. that the system (2.2) linearized at (S^0, x_1^0) have no Floquet exponents with zero real part. *It will be assumed throughout that (S^0, x_1^0) is stably noncritical: i.e. that these Floquet exponents have negative real parts.* This will be true, in particular, if $\text{av}(d_1)$ is sufficiently close to d_1^{cr} (Theorem 1). As far as the existence of a bifurcating continuum of positive solutions of (2.1) is concerned, (S^0, x_1^0) could in fact be unstable in Theorem 2 below (so long as no Floquet exponents have zero real parts), but then as the general results in [3] show, the solutions on the continuum, at least near the bifurcation point, would be unstable. Since the concern in this paper is with the possible (stable) coexistence of x_1 and x_2 , it is necessary then (at least locally near bifurcation) to assume the stability of (S^0, x_1^0) . The stability of the positive periodic solutions on the bifurcating continuum is locally determined by the “direction of bifurcation” [3], stable solutions resulting from bifurcation to the right and unstable solutions resulting from bifurcation to the left (with respect to the parameter $\mu = -\text{av}(d_2)$). As we will see in the example of § 5, either case can arise.

Define

$$d_2^{\text{cr}} := \text{av} \left(\frac{m_2 S^0}{a_2 + S^0} \right).$$

Then $d_2^{\text{cr}} > 0$ by (2.3).

THEOREM 2. *Assume (2.3), $0 < \text{av}(d_1) < d_1^{\text{cr}}$ and that $(S^0, x_1^0) \in B_+^2(p)$ is stably noncritical as a solution of (2.2). Let $d_2^0 \in B(p)$ be an arbitrary periodic function with $\text{av}(d_2^0) = 0$. There exists a set $\Pi^+ = \{(S, x_1, x_2, \mu) \in B_+^3(p) \times \mathbb{R}\}$ where $(S, x_1, x_2) > 0$ solves (2.1) with $d_2(t) = -\mu + d_2^0(t)$ whose closure is a continuum which connects $(S^0, x_1^0, 0, \mu^0) \in B^3(p) \times \mathbb{R}$, $\mu^0 := -d_2^{\text{cr}}$, to a solution of the form $(S^*, x_1^*, x_2^*, \mu^*) \in B^3(p) \times \mathbb{R}$ where $(S^*, x_1^*, x_2^*, \mu^*) \neq (S^0, x_1^0, 0, \mu^0)$, $S^*(t) > 0$ and either $x_1^* > 0, x_2^* \equiv 0$ or $x_1^* \equiv 0, x_2^* > 0$ for all t .*

This theorem deals only with the *existence* of positive periodic solutions of (2.1). This branch of positive periodic solutions plays the role of and indeed becomes identical to the straight line branch of equilibria (2.6) when all coefficients are constants. The next theorem is concerned with the stability of those positive solutions near the

bifurcation point and with the spectrum of Π^+ ; i.e. with the range of the projection $\Pi^+ \rightarrow \mathcal{R}$ defined by $(S, x_1, x_2, \mu) \rightarrow \mu$. The autonomous case when all coefficients (2.3) are positive constants shows that this spectrum can consist solely of the point μ^0 . As the next theorem shows, however, for the more general case of periodic coefficients the spectrum can under certain circumstances be an interval of positive length.

THEOREM 3. *The closure of the spectrum of Π^+ is a finite interval $[\sigma_1, \sigma_2]$ where*

$$(4.1) \quad -\text{av}(m_2) \leq \sigma_1 \leq \mu^0 := -\text{av}(m_2 S^0 / (a_2 + S^0)) \leq \sigma_2 < 0.$$

Moreover $\sigma_1 < \sigma_2$ provided

$$(4.2) \quad \mu_1 := -\text{av}\left(\eta_2 \frac{m_2 a_2}{(a_2 + S^0)^2}\right) \neq 0,$$

where $\eta_2 \in B(p)$ is defined in (4.5) below. If $\mu_1 > 0$ (< 0) then the solutions of (2.1) lying in the intersection of Π^+ with an open neighborhood of $(S^0, x_1^0, 0, \mu^0)$ in $B^3(p) \times \mathcal{R}$ correspond to $\mu > \mu^0$ ($< \mu^0$) and are asymptotically stable (unstable). Furthermore $(S^0, x_1^0, 0, \mu)$ as a solution of (2.1) is asymptotically stable for $\mu < \mu^0$ and unstable for $\mu > \mu^0$.

With regard to the question of whether (4.2) holds, it is noteworthy that, as will be shown below,

$$(4.3) \quad \text{av}\left(\eta_2 \frac{m_1 a_1}{(a_1 + S^0)^2}\right) = 0.$$

When all coefficients (and hence S^0) are constants, this implies $\text{av}(\eta_2) = 0$ which in turn implies that $\mu_1 = 0$ and that (4.2) fails to hold. Theorem 2 is thus consistent with the fact that $\sigma_1 = \sigma_2$ in the autonomous case when Π^+ reduces to the line (2.6) and the spectrum reduces to the point (2.5).

More generally, when the coefficients are periodic, (4.2) and (4.3) constitute a notion of being "out-of-phase" which guarantees that the spectral interval of Π^+ has positive length. By this rough notion of "out-of-phase" it is meant that whereas the expression $m_1 a_1 / (a_1 + S^0)^2 \in B_+(p)$ is orthogonal by (4.3) to $\eta_2 \in B(p)$ the corresponding expression $m_2 a_2 / (a_2 + S^0)^2$ for the second predator is not (by (4.2)). The more specific example when all coefficients except the consumption rates m_1 and m_2 are constant, which is considered in § 5, will further illustrate this notion.

The possibility that the spectral interval of Π^+ can have a positive length $\sigma_2 - \sigma_1$ as guaranteed by (4.2) shows how periodicities in the system parameters can allow for competitive coexistence in circumstances when the autonomous system does not. (Roughly speaking, the constraint that (S^0, x_1^0) is stably noncritical rules out the possibility of limit cycle coexistence in the autonomous case.) To make a strong case that certain periodicities promote coexistence in a significant way would require not only that (4.2) holds, but that the length of the spectral interval be reasonably large in some sense. The example considered in § 5 demonstrates such a case where not only does (4.2) hold, but numerical results indicate that the spectral interval of (2.1) for the two-predator, one-prey interaction is "large" in the sense that it is commensurate with that of (2.2) for the one-predator, one-prey interaction.

This section closes with proofs of Theorems 2 and 3. The proof of Theorem 2 will make use of the following lemma whose proof is very similar to that of Lemma 1 and is therefore omitted.

LEMMA 2. Assume (2.3). If $(S, x_1, x_2) \in B_+^3(p)$ solves (2.1) then $0 < \text{av}(d_i) < \text{av}(m_i)$ and for all t

$$0 < S(t) \leq s_0(t) \leq |K|_0, \quad 0 < x_i(t) \leq \frac{|r|_0}{m_i^0} |y_i|_0 (|a_i|_0 + |K|_0) \exp(p|m_i - d_i|_0),$$

where $m_i^0 := \min_{0 \leq t \leq p} m_i(t) > 0$.

Proof of Theorem 2. Theorem 1 of [3] can be applied to (2.1) with $d_2(t) = -\mu + d_2^0(t)$. The open set Ω^3 in [3] can be taken to be the half space $\Omega^3 := \{(S, x_1, x_2) \in \mathbb{R}^3 | S > -a^0\}$ where $a^0 := \min(a_1^0, a_2^0) > 0$, $a_i^0 := \min_{0 \leq t \leq p} a_i(t) > 0$. This application results in the existence of a continuum $C^+ \subset B^3(p) \times \mathbb{R}$ of solutions of (2.1) which contains the ‘‘bifurcation point’’ $(S^0, x_1, 0, \mu^0)$ and which connects to the boundary of the set $\Omega_p^3 \times \mathbb{R} \subset B^3(p) \times \mathbb{R}$ where $\Omega_p^3 := \{(S, x_1, x_2) \in B^3(p) | S(t) + S^0(t) > -a^0\}$. Moreover, in an open neighborhood of $(S^0, x_1^0, 0, \mu^0)$, the set $C^+ / \{(S^0, x_1^0, 0, \mu^0)\}$ consists of positive solutions of (2.1). The continuum C^+ cannot consist entirely of positive solutions, however, because to do so C^+ would, in order to connect to the boundary of $\Omega_p^3 \times \mathbb{R}$, have to be unbounded which would contradict Lemma 2 (recall $d_2 = -\mu + d_2^0$). Thus, as discussed in [3], C^+ must leave the positive cone $B_+^3(p) \times \mathbb{R}$ at a point other than the bifurcation point.

Denote by C_0^+ the maximal subcontinuum of C^+ which connects $(S^0, x_1^0, 0, \mu^0)$ to the boundary of $B_+^3(p) \times \mathbb{R}$ and define $\Pi^+ = C_0^+ \cap (B_+^3(p) \times \mathbb{R})$. Then the closure of Π^+ is a continuum which connects $(S^0, x_1^0, 0, \mu^0)$ to the boundary of $B_+^3(p) \times \mathbb{R}$; i.e. the closure of Π^+ contains $(S^0, x_1^0, 0, \mu^0)$ and a point $(S^*, x_1^*, x_2^*, \mu^*) \neq (S^0, x_1^0, 0, \mu^0)$ where $S^* \geq 0$, $x_i^* \geq 0$ and either $S^* = 0$ or $x_1^* = 0$ or $x_2^* = 0$. The proof will be complete when it is shown that $S^* > 0$ and not both x_i^* vanish.

Let $(S^n, x_1^n, x_2^n, \mu^n) \in \Pi^+$ be a sequence which converges in $B^3(p) \times \mathbb{R}$ to $(S^*, x_1^*, x_2^*, \mu^*)$. From (2.1b) for $(S, x_1, x_2) = (S^*, x_1^*, x_2^*)$, divided by $x_1^n > 0$ and averaged, follows

$$(4.4) \quad \text{av}(d_1) = \text{av}\left(\frac{m_1 S^n}{a_1 + S^n}\right).$$

First, suppose that $S^* = 0$. Then from (4.4) in the limit $n \rightarrow +\infty$ follows a contradiction to $\text{av}(d_1) > 0$. Thus it must be the case that $S^* > 0$.

Finally, suppose that $x_1^* = x_2^* = 0$. Then from (2.1a) in the limit as $n \rightarrow +\infty$ we see that $S^* \in B_+(p)$ solves the periodic logistic and hence $S^* = s_0$. From (4.4) follows $\text{av}(d_1) = d_1^{cr}$, a contradiction to $\text{av}(d_1) < d_1^{cr}$. \square

In the event that (S^0, x_1^0) is the unique positive p -periodic solution of (2.2), then it is easy to rule out the case $x_2^* = 0$ in Theorem 2.

Proof of Theorem 3. By Lemma 2 the closure of the spectrum of Π^+ is a finite interval $[\sigma_1, \sigma_2]$ containing μ^0 with $-\text{av}(m_2) \leq \sigma_1 \leq \sigma_2 \leq 0$. Thus, to establish (4.1), it only remains to show that $\sigma_2 \neq 0$.

Suppose that $\sigma_2 = 0$ and choose a (bounded) sequence $(S^n, x_1^n, x_2^n, \mu^n) \in \Pi^+$ for which $\mu^n \rightarrow 0$. Since the set of positive solutions $(S^n, x_1^n, x_2^n, \mu^n)$ is bounded and (2.1) implies that this is also true of the set of derivatives, the Ascoli–Arzela lemma implies that we can assume (choosing a subsequence if necessary) that $(S^n, x_1^n, x_2^n, \mu^n)$ converges in $B^3(p) \times \mathbb{R}$. Let $(S^*, x_1^*, x_2^*, 0) \in B^3(p) \times \mathbb{R}$ be the limit. By the proof of Theorem 2, $S^* > 0$. Hence, by (4.4), $\mu^n \rightarrow -\text{av}(m_1 S^* / (a_1 + S^*)) < 0$, a contradiction to $\mu^n \rightarrow 0$. We conclude $\sigma_2 \neq 0$.

The remainder of Theorem 3 follows from Theorems 7 and 8 of [2] after the formula in (4.2) for the crucial quantity μ_1 in [3] is established. The real μ_1 is the

first order coefficient of μ in the Lyapunov–Schmidt expansion of the solutions lying on C^+ near bifurcation. Formulas for μ_1 and the coefficients of (S, x_1, x_2) are given in [3] and, after some calculation, these yield for small $|\varepsilon|$

$$\begin{aligned} S(t) &= S^0(t) + \eta_1(t)\varepsilon + O(\varepsilon^2), & x_1(t) &= x_1^0(t) + \eta_2(t)\varepsilon + O(\varepsilon^2), \\ x_2(t) &= \xi(t)\varepsilon + O(\varepsilon^2), & \mu &= \mu^0 + \mu_1\varepsilon + O(\varepsilon^2), \end{aligned}$$

where μ_1 is given as in (4.2) (see (20) in [3]) and where $(\eta_1, \eta_2, \xi) \in B^3(p)$, $(\eta_1, \eta_2, \xi) \neq (0, 0, 0)$, $\xi(0) = 1$, solves the periodic linear homogeneous system

$$\begin{aligned} (4.5) \quad (a) \quad \eta_1' &= \left(-d_1 + \frac{m_1 S^0}{a_1 + S^0}\right)\eta_1 + \left(\frac{m_1 a_1 x_1^0}{(a_1 + S^0)^2}\right)\eta_2, \\ (b) \quad \eta_2' &= \left(-\frac{m_1}{y_1} \frac{S^0}{a_1 + S^0}\right)\eta_1 + \left(r - 2\frac{r}{K} S^0 - \frac{m_1}{y_1} \frac{a_1 x_1^0}{(a_1 + S^0)^2}\right)\eta_2 + \left(-\frac{m_2}{y_2} \frac{S^0}{a_2 + S^0}\right)\xi, \\ (c) \quad \xi' &= \left(\mu^0 - d_2^0 + \frac{m_2 S^0}{a_2 + S^0}\right)\xi. \quad \square \end{aligned}$$

It follows from (3.4) with $(S, x_1) = (S^0, x_1^0)$ and (4.5a) that the second term on the right-hand side of (4.5a) must be orthogonal to the periodic solutions of the adjoint equation $\eta_1' = (d_1 - m_1 S^0 / (a_1 + S^0))\eta_1$ which is in fact $1/x_1^0(t)$. This orthogonality condition is just (4.3).

5. An example: similar species time sharing a resource. The results contained in Theorems 1–3 apply to the systems (2.1) and (2.2) with arbitrary periodic coefficients satisfying (2.3). In this section we study the case when all coefficients except the consumption rates $m_i(t)$ are positive constants. Thus it is assumed that the prey S grows logistically in the absence of predation and that the conversion factors y_i (measuring the per capita conversion of consumed prey into predators) and the parameters a_i (at which prey population level the predation rate of x_i reaches half its saturation level) are constants. The consumption rates $m_i(t)$ will be assumed to fluctuate cosinusoidally around a positive average value m_i^0 with a small amplitude. Time will be scaled so that the period of this fluctuation is one. Moreover, units for the predator populations can be chosen so that $y_1 = y_2 = 1$ (change dependent variables from x_i to x_i/y_i in (2.1)). Finally the predators will be assumed to be “similar” species in the sense that $a_1 = a_2$ and $m_1^0 = m_2^0$.

In summary, (2.1) and (2.2) are considered using $d_2 \in R$ as a parameter with the other coefficients given by

$$\begin{aligned} (5.1) \quad &0 < d_1, r, K \in R, \quad y_1 = y_2 = 1, \quad 0 < a_1 = a_2 = a \in R, \\ &m_1(t) = m(1 + \lambda \cos t), \quad m_2(t) = m(1 + \lambda(\rho_1 \cos t + \rho_2 \sin t)), \\ &0 < m \in R, \quad \rho_1, \rho_2 \in R, \quad \rho_1^2 + \rho_2^2 = 1, \end{aligned}$$

where $\lambda \in R$ is a small amplitude. Theorems 1–3 apply, of course, to this special case. The crucial concern here is the condition (4.2) which guarantees a spectral interval of positive length and the condition $\mu_1 > 0$ which yields a nondiscrete domain of parameter values d_2 for which x_1 and x_2 can stably coexist.

Note that if $\lambda = 0$ then this case reduces to an autonomous case for which we know that the spectrum is discrete (hence $\mu_1 = 0$). Also note that if $\lambda \neq 0$, but $\rho_2 = 0$ (hence $\rho_1 = 1$ and $m_1 = m_2$), (4.3) implies again that $\mu_1 = 0$. Thus it is necessary for the condition (4.2) of Theorem 3 that $\lambda \neq 0$ and that $\rho_2 \neq 0$, which is to say that $m_1(t)$

and $m_2(t)$ must be “out-of-phase” or in other words x_1 and x_2 must “time share” the resource S in the sense that their individual consumption rates must not be in phase.

To make this more explicit, we will treat μ_1 as a function of the small amplitude λ and calculate its lowest order terms in λ . To do this by means of the formula (4.2) for μ_1 involves calculating lowest order terms in λ of $S^0(t)$ and $\eta_2(t)$. These calculations are tedious, but in principle straightforward. As usual they involve substituting λ expansions

$$(5.2) \quad \begin{aligned} S^0(t) &= S_0^0 + S_1^0(t)\lambda + \dots, & x_1^0(t) &= x_{10}^0 + x_{11}^0(t)\lambda + \dots, \\ \eta_i(t) &= \eta_{i0} + \eta_{i1}(t)\lambda + \dots, & \xi(t) &= \xi_0 + \xi_1(t)\lambda + \dots, \end{aligned}$$

into (2.2) and (4.5) respectively and equating coefficients of like powers of λ . To do this requires the λ expansion of μ^0 :

$$\mu^0 = \mu_0^0 + \mu_1^0\lambda + \dots$$

to be obtained from

$$(5.3) \quad \mu^0 = -av \left(\frac{mS^0}{a + S^0} \right).$$

The zeroth order λ terms in (2.2) imply

$$(5.4) \quad S_0^0 = ad_1/(m - d_1), \quad x_{10}^0 = r(a + S_0^0)(K - S_0^0)/Km,$$

which are equilibria of (2.2) when $\lambda = 0$. In order that S_0^0 and x_{10}^0 be positive it is required that

$$(5.5) \quad 0 < d_1 < \frac{mK}{a_1 + K}$$

as is expected from Theorem 1.

It will be shown below that to lowest order in λ :

$$(5.6) \quad \mu_1 = (-d_1am\Delta^{-1}(a + S_0^0)[(\rho_1 - 1)^2 + \rho_2^2](d_1(B - 1) + A))\lambda^2 + O(\lambda^3)$$

where

$$A := rS_0^0K^{-1} - mS_0^0x_{10}^0(a + S_0^0)^{-2}, \quad B := d_1amx_{10}^0(a + S_0^0)^{-2}$$

and where it is assumed that

$$(5.7) \quad \Delta := A^2 + (B - 1)^2 \neq 0.$$

From this we conclude that *for the case (5.1) being considered in this section, for small amplitudes λ , the quantity μ_1 is nonzero and the spectral interval (for $d_2 = -\mu$) has positive length provided*

$$(5.8) \quad (\rho_1 - 1)^2 + \rho_2^2 \neq 0$$

and $d_1(B - 1) + A \neq 0$. The resulting positive periodic solutions are, for $d_2 < d_2^{cr}$ and $d_2 \approx d_2^{cr} = d_1 + O(\lambda^2)$, stable if

$$(5.9) \quad d_1(B - 1) + A < 0$$

and unstable if

$$(5.10) \quad d_1(B - 1) + A > 0.$$

Condition (5.8) means of course that the consumption rates $m_1(t)$ and $m_2(t)$ are out-of-phase. Note that by putting them maximally out-of-phase: $\rho_1 = -1, \rho_2 = 0$, to lowest order μ_1 is maximized (all other parameters held fixed), indicating an enhancement of the possibility of stable coexistence in the sense that the spectral interval is lengthened.

The stability condition (5.9) can be interpreted as a constraint on the inherent resource carrying capacity K (all other parameters held fixed) which must satisfy $K > S_0^0$ by (5.5). A straightforward algebraic investigation of this inequality shows that

$$r < d_1 \quad \text{implies (5.9)}$$

for all $K > S_0^0$ whereas

$$r > d_1 \quad \text{implies (5.9) for } S_0^0 < K < K_{\text{cr}} \text{ but (5.10) for } K > K^{\text{cr}},$$

where

$$K^{\text{cr}} := \frac{S_0^0}{1-w}, \quad w := \frac{m}{r} \frac{r-d_1}{d_1^3 + md_1^2 + d_1 + m} > 0.$$

We conclude that the two similar predator species in this example (5.1) can stably coexist for d_2 lying in an interval of positive length containing d_2^{cr} provided their resource consumption rates are out-of-phase and either the prey inherent growth rate r is less than the predators' inherent death rates d_i or, if this is not true, provided the prey inherent carrying capacity K is not larger than a critical value K^{cr} . This latter condition is another instance of what has come to be called the "paradox of enrichment" [4], [17].

In order to get a better understanding of the characteristics of the oscillations in this example, numerical integrations of the systems (2.1) and (2.2) with coefficients (5.1) were carried out for $r = 10.0$, $K = 1.0$, $a = 10.0$, $m = 10.0$ and $\lambda = 1.0$. Figure 1 shows the computed bifurcation diagrams for both systems (2.1) and (2.2). Confirming the results of Theorem 1, the diagram in Fig. 1a shows positive periodic solutions of (2.2) for $0 < d_1 < d_1^{\text{cr}} = 10/11$. With d_1 held fixed at $d_1 = 0.5$, the two-predator, one-prey system (2.1)–(5.1) was numerically integrated for various phase differences in the resource consumption rates. Figure 1b shows three resulting bifurcation diagrams with d_2 as the bifurcation parameter. These three bifurcation diagrams illustrate how the spectrum increases from a point when the consumption rates are in-phase to an interval of significant length (commensurate with the spectral interval in Fig. 1a) when these rates are out-of-phase.

Figure 2 shows three computed periodic solutions of (2.1)–(5.1) when the resource consumption rates are maximally out-of-phase for three different values of d_2 , one near bifurcation, one for which $d_2 = d_1$ and one "far out on the bifurcation branch" (see Fig. 1). Note that in all cases the oscillations within the three species tend to be themselves out-of-phase and that the predator oscillations are out-of-phase with their own resource consumption rates (not shown). The case when $d_2 = d_1 = 0.5$ in Fig. 2b when the species are thus similar in all regards except that their resource consumption rates are out-of-phase is especially interesting in that it shows the predators' oscillations are maximally out-of-phase and it shows that the oscillation in the prey resource population has apparently halved the period to π . The extreme case in Fig. 2c shows the resource population reaching dangerously low population level ($\leq 10^{-2}$) over a significant portion of its cycle. This suggests a danger of prey extinction and system collapse and points out that mathematical existence and stability of positive periodic solutions may not always be sufficient for measuring stable coexistence in periodic competition models [5].

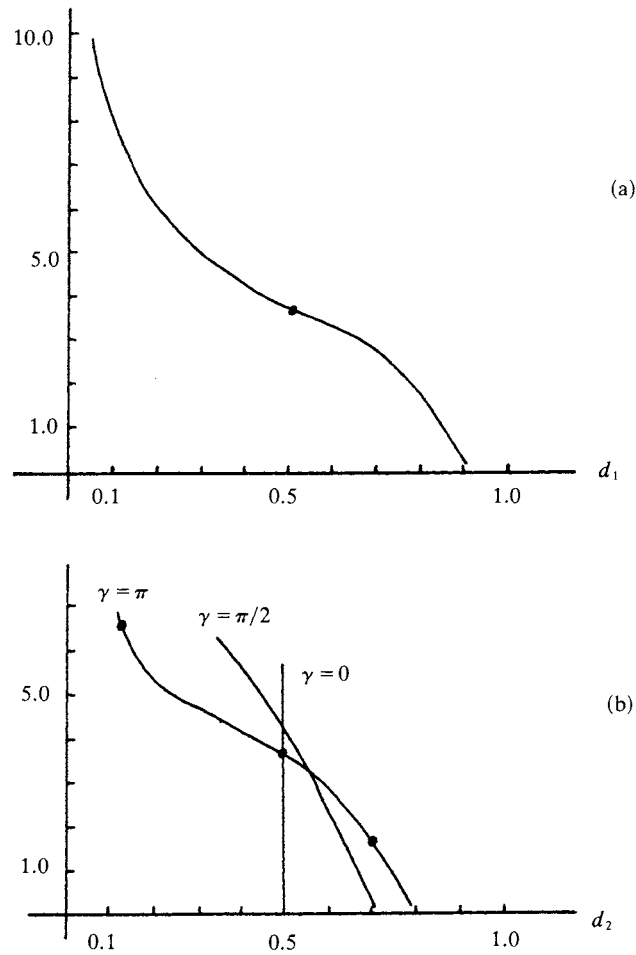


FIG. 1. In (a) the Euclidean distance $((1 - |S|_0|^2 + |x_1|_0)^{1/2}$ of the norm $(|S|_0, |x_1|_0) \in \mathbb{R}^2$ for the numerically computed positive periodic solution $(S, x_1) \in B_+^2(p)$ of (2.2)–(5.1) with $r = a = m = 10.0$ and $K = \lambda = 1.0$ from that of the “trivial solution” $(s_0, 0) = (K, 0) = (1.0, 0) \in \mathbb{R}^2$ is plotted against the death rate d_1 . Bifurcation is seen to occur at the theoretically computed $d_1^{cr} = 10/11$. The circle corresponds to that solution used in computing (b).

For the same parameter values as used in (a), but with $d_1 = 0.5$, the norm $(|S|_0^0, |x_1|_0^0) \in \mathbb{R}^2$ for the numerically computed positive periodic solution of (2.2)–(5.1) was computed to be $(|S|_0^0, |x_1|_0^0) = (0.9986, 3.9828)$. In (b) the Euclidean distance of $(|S|_0, |x_1|_0, |x_2|_0) \in \mathbb{R}^3$ from $(|S|_0^0, |x_1|_0^0, 0) = (0.9986, 3.9828, 0.0) \in \mathbb{R}^3$ for the numerically computed positive periodic solution $(S, x_1, x_2) \in B_+^3(p)$ of (2.1)–(5.1) is plotted against the parameter d_2 . The resulting graphs are shown for three selected phase angles $\gamma = 0.0, \pi/2$ and π where $\gamma = -\arctan(\rho_2/\rho_1)$. The circles on the branch for $\gamma = \pi$ correspond to the three solutions graphed in Fig. 2.

Note however that from Fig. 3 we see that low level population levels appear in this example only at the extreme end of the solution branch (i.e. smallest values of d_2 in the spectral interval) and that the spectrum which yields stable coexistence when the resource consumption rates. Figure 1b shows three resulting bifurcation diagrams large.

We conclude with some details of the calculation of μ_1 given in (5.6). As an aid to the calculation of the first order λ coefficients in (5.2) it is useful to use (4.3). The

left-hand side of (4.3) has a λ expansion all of whose coefficients must vanish. Use of (5.1) and (5.2) and a calculation of the first three coefficients in this expansion yield

$$\eta_{20} = 0, \quad \text{av}(\eta_{21}) = 0, \quad \text{av}(\eta_{22} + \eta_{21} \cos t - 2\eta_{21}S_1^0(t)/(a_1 + S_0^0)) = 0.$$

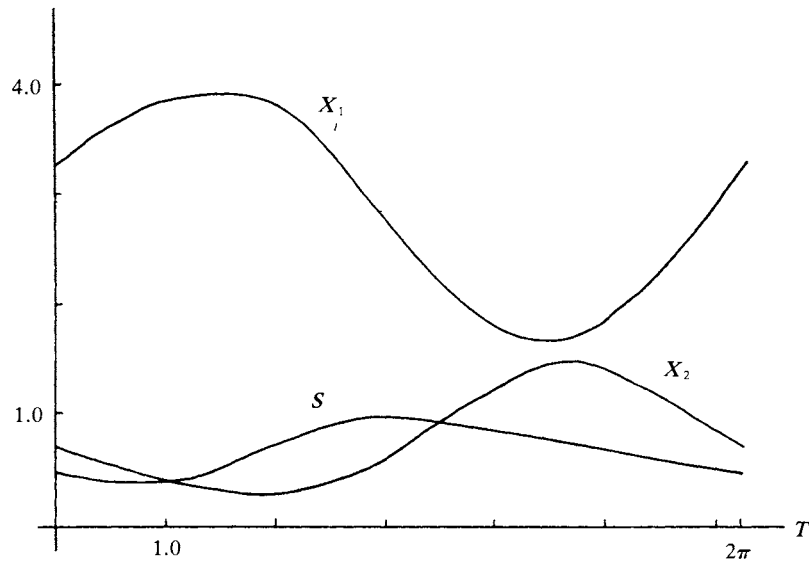
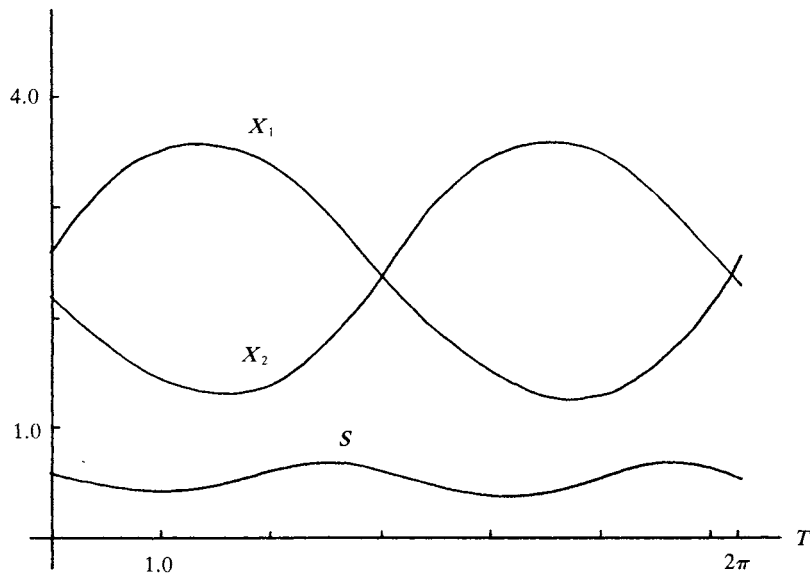
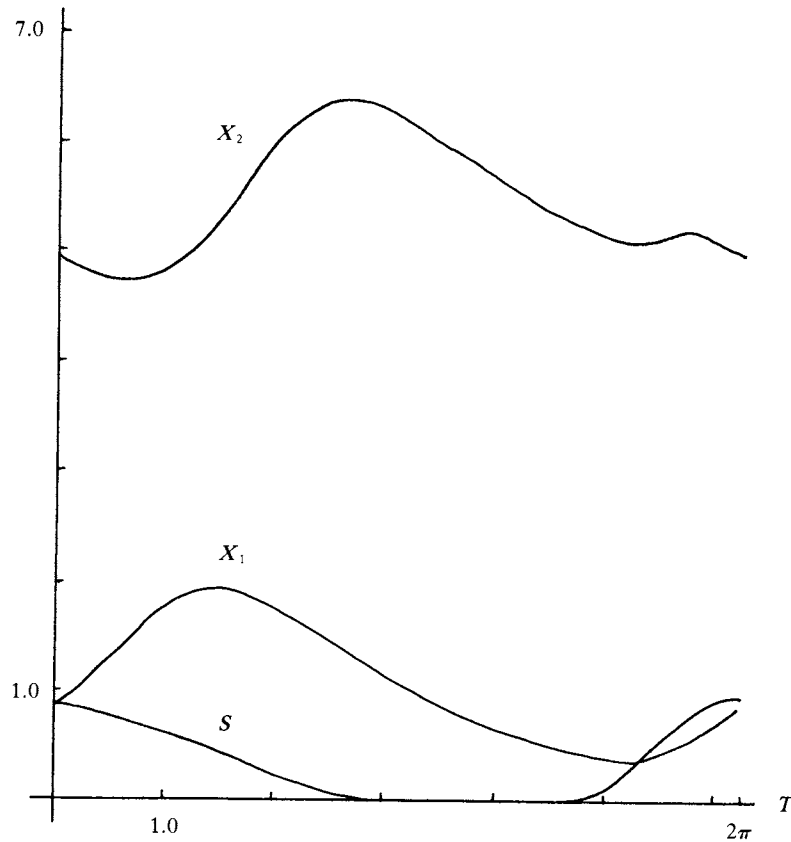
(a) $d_2 = 0.7$.(b) $d_2 = 0.5$.

FIG. 2. (Caption on p. 407.)



(c) $d_2 = 0.12$.

FIG. 2. Three computed solutions $(S, x_1, x_2) \in B^3_+(p)$ of (2.1)–(5.1) are plotted against time over one period. Here $r = a = m = 10.0$, $K = \lambda = 1.0$, $d_1 = 0.5$ and $\rho_1 = -1$, $\rho_2 = 0$. The three solutions correspond to $d_2 = 0.7, 0.5$ and 0.12 respectively and are located at the circles on the bifurcation branch graphed in Fig. 1(b) for phase angle $\gamma = \pi$.

These in turn imply from (4.3) that

$$(5.11) \quad \mu_1 = -\frac{ma}{(a + S_0^0)^2} ((\rho_1 - 1) \text{av}(\eta_{21} \cos t) + \rho_2 \text{av}(\eta_{21} \sin t)) \lambda^2 + O(\lambda^3).$$

Thus, to find the sign of μ_1 for small λ , we need only calculate the first two Fourier coefficients of $\eta_{21}(t)$, the first-order λ coefficient in the expansion (5.2) of $\eta_2(t)$. This must be done from (4.5).

The zeroth-order terms in (4.5) and (5.3) easily imply

$$\xi'_0 = \eta'_{10} = 0, \quad d_1 \eta_{10} + (mS_0^0 / (a + S_0^0)) \xi_0 = 0, \quad \mu_0^0 = -mS_0^0 / (a + S_0^0),$$

which in view of (5.4) reduces to $\eta_{10} + \xi_0 = 0$, $\mu_0^0 = -d_1$. Without loss in generality we take

$$\eta_{10} = 1, \quad \xi_0 = -1.$$

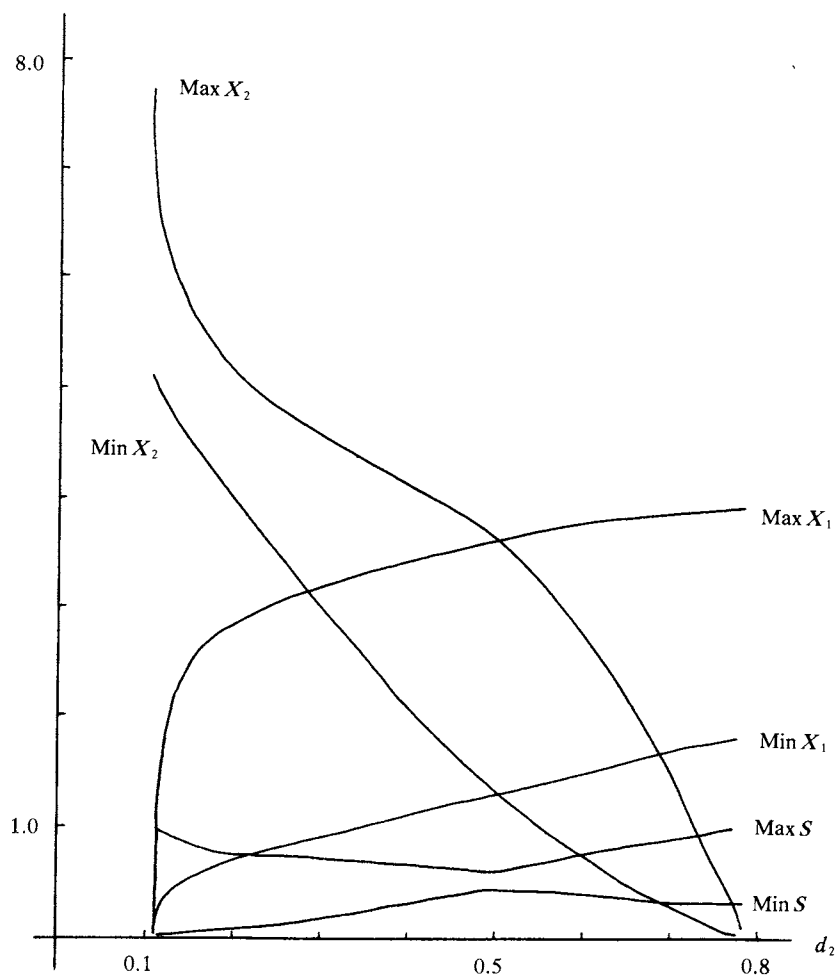


FIG. 3. The population maxima and minima for the positive periodic solutions of (2.1)–(5.1) lying on the branch $\lambda = \pi$ in Fig. 1(b) are plotted against the bifurcation parameter d_2 .

Turning now to the first order λ terms in (4.5) and (5.3), we find $\mu_1^0 = -am \operatorname{av}(S_1^0(t))/(a + S_0^0)^2$ and the equations

$$\begin{aligned}
 (a) \quad \eta'_{11} &= \left(\frac{amx_{10}^0}{(a + S_0^0)^2} \right) \eta_{21} + d_1 \cos t + \frac{amS_1^0(t)}{(a + S_0^0)^2}, \\
 (5.12) \quad (b) \quad \eta'_{21} &= -d_1 \eta_{11} + \left(-\frac{rS_0^0}{K} + \frac{mS_0^0 x_{10}^0}{(a + S_0^0)^2} \right) \eta_{21} - d_1 \xi_1 + d_1(\rho_1 - 1) \cos t + d_1 \rho_2 \sin t, \\
 (c) \quad \xi'_1 &= -d_1 \rho_1 \cos t - d_1 \rho_2 \sin t - \frac{amS_1^0(t)}{(a + S_0^0)^2},
 \end{aligned}$$

for $(\eta_{11}, \eta_{21}, \xi_1) \in B^3(p)$ and

$$(5.13) \quad \begin{aligned} (a) \quad S_1^{0'} &= \left(-\frac{rS_0^0}{K} + \frac{mS_0^0}{(a+S_0^0)^2} x_{10}^0 \right) S_1^0 - d_1 x_{11}^0, \\ (b) \quad x_{11}^{0'} &= \left(\frac{am}{(a+S_0^0)^2} x_{10}^0 \right) S_1^0 - d_1 x_{11}^0 \cos t, \end{aligned}$$

for $(S_1^0, x_{11}^0) \in B^2(p)$. While these equations appear rather formidable, recall that it is only the first two Fourier coefficients of η_{21} which are needed in (5.11).

An averaging of the equation (5.13b) for x_{11}^0 implies $\text{av}(S_1^0) = 0$. Consequently $\mu_1^0 = 0$ and

$$(5.14) \quad \mu^0 = -d_1 + O(\lambda^2).$$

A single, second order equation for η_{21} can be derived from the system (5.12) by a simple differentiation of (5.12b). This yields

$$(5.15) \quad \eta_{21}'' + A\eta_{21}' + B\eta_{21} = d_1(d_1(\rho_1 - 1) + \rho_2) \cos t + d_1(-(\rho_1 - 1) + d_1\rho_2) \sin t$$

for $\eta_{21} \in B(p)$. Thus if (5.7) holds (to avoid resonance) the periodic solution η_{21} of (5.15) is

$$\eta_{21} = d_1\Omega_1 \cos t + d_1\Omega_2 \sin t,$$

where Ω_1 and Ω_2 are given by

$$\begin{aligned} \Delta\Omega_1 &:= (B - 1)(d_1(\rho_1 - 1) + \rho_2) - A(-(\rho_1 - 1) + d_1\rho_2), \\ \Delta\Omega_2 &:= (B - 1)(-(\rho_1 - 1) + d_1\rho_2) + A(d_1(\rho_1 - 1) + \rho_2). \end{aligned}$$

The desired Fourier coefficients become

$$\text{av}(\eta_{21} \cos t) = \frac{1}{2}d_1\Omega_1, \quad \text{av}(\eta_{21} \sin t) = \frac{1}{2}d_1\Omega_2,$$

which when substituted into (5.11) yield (5.6).

REFERENCES

- [1] G. J. BUTLER AND P. WALTMAN, *Bifurcation from a limit cycle in a two predator-one prey ecosystem modeled on a chemostat*, J. Math. Biology, 12 (1981), pp. 295-310.
- [2] J. M. CUSHING, *Two species competition in a periodic environment*, J. Math. Biology, 10 (1980), pp. 385-400.
- [3] ———, *Periodic Kolmogorov systems*, SIAM J. Math. Anal., 13 (1982), pp. 811-827.
- [4] ———, *Stability and instability in predator-prey models with growth rate response delays*, Rocky Mountain J. Math., 9 (1979), pp. 43-50.
- [5] ———, *Periodicities in the Volterra-Lotka-MacArthur-Levins theory of competition*, Proceedings International Conf. on Population Biol, U. of Alberta, Lecture Notes in Biomathematics, Springer, New York, to appear.
- [6] P. DE MOTTONI AND A. SCHIAFFINO, *Competition systems with periodic coefficients: a geometric approach*, J. Math. Biology, 11 (1981), pp. 319-335.
- [7] S. B. HSU, *A mathematical analysis of competition for a single resource*, Ph.D. thesis, University of Iowa, Ames, 1976.
- [8] S. B. HSU, S. P. HUBBELL AND P. WALTMAN, *A contribution to the theory of competing predators*, Ecological Monographs, 48 (1978), pp. 337-349.
- [9] ———, *Competing predators*, SIAM J. Appl. Math., 35 (1978), pp. 617-625.
- [10] ———, *A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms*, SIAM J. Appl. Math., 32 (1977), pp. 366-383.
- [11] ———, *Theoretical and experimental investigations of microbial competition in continuous cultures*, Proc. Conference on Mathematical Modeling, Carbondale, IL, 1979.

- [12] A. L. KOCH, *Competitive coexistence of two predators utilizing the same prey under constant environmental conditions*, J. Theoret. Biol., 44 (1974), pp. 373–386.
- [13] R. MACARTHUR AND R. LEVINS, *The limiting similarity, convergence, and divergence of coexisting species*, The American Naturalist, 101 (1967), pp. 377–385.
- [14] R. M. MAY, *Stability and Complexity in Model Ecosystems* in: Monographs in Population Biology 6, Princeton University Press, Princeton, NJ, 1974.
- [15] E. R. PIANKA, *Evolutionary Ecology*, Harper and Row, New York, 1978.
- [16] S. ROSENBLATT, *Population models in a periodically fluctuating environment*, J. Math. Biology, 9 (1980), pp. 23–26.
- [17] M. L. ROSENZWEIG, *Paradox of enrichment: destabilization of exploitation ecosystems in ecological time*, Science, 171 (1971), pp. 385–387.
- [18] H. L. SMITH, *The interaction of steady state and Hopf bifurcations in a two-predator-one-prey competition model*, SIAM J. Appl. Math., 42 (1982), pp. 27–43.
- [19] ———, *Competitive coexistence in an oscillating chemostat*, SIAM J. Appl. Math., 40 (1981), pp. 498–522.
- [20] P. YODZIS, *Competition for Space and the Structure of Ecological Communities*, Lecture Notes in Biomathematics 25, Springer, Berlin, 1978.