SIAM J. MATH. ANAL.
Vol. 13, No. 5, September 1982

0036-1410/82/1305-0009 $01.00/0

PERIODIC KOLMOGOROV SYSTEMS*

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Abstract. The existence of nontrivial periodic solutions of periodic Kolmogorov systems of ordinary differential equations is considered. Under very general conditions, a global continuum of solutions is shown to bifurcate from a noncritical periodic solution of a reduced system using the average inherent per unit growth rate of one component of the system as a bifurcation parameter. The positivity and stability of the bifurcating branch solutions are studied. The stability is shown to depend on the stability of the solution of the reduced system as well as the direction of bifurcation. These results extend and generalize earlier work on periodic Volterra–Lotka systems. Applications to mathematical ecology are given.

Key words. Kolmogorov systems, periodic solutions, bifurcation, stability

1. Introduction. Differential equations of the form

$$x_i' = x_i h_i(x_1, \cdots, x_n), \qquad 1 \le i \le n, \quad ' = \frac{d}{dt}$$

are sometimes referred to as Kolmogorov equations. They arise in applications in which the per unit of change x_i'/x_i of dependent variables $x_i = x_i(t)$ are prescribed functions $h_i(x_1, \cdots, x_n)$ of these variables at any given time. Many models in population dynamics and mathematical ecology are of this form, of which the well-known logistic, Volterra predator-prey and Volterra–Lotka competition equations serve as perhaps the simplest and most famous examples. In such applications one is usually interested only in nonnegative solutions $x_i \ge 0$ and in positive solutions $x_i > 0$, if they exist. As indicated above the equations are autonomous and the algebraic zeros of the h_i play of course an important role as equilibria. Our concern in this paper is with Kolmogorov equations of the above type under the assumption that the h_i are no longer independent of time t, but explicitly dependent periodically on t. We will be interested in the existence of nonnegative and positive periodic solutions and in their stability or instability.

Several specific periodic Kolmogorov systems have been studied with regard to certain applications in mathematical ecology. Volterra predator-prey equations with periodic coefficients were studied by the author [2], and more general periodic predator-prey equations have recently been studied by Bardi [1]. Periodic Volterra–Lotka competition equations have been studied by de Mottoni and Schiaffino [7] and the author [3]. Volterra systems of arbitrary order with periodic coefficients were also considered by the author [4]. These papers were all motivated by the obvious fact that cyclic fluctuations in biological and environmental parameters can play an important role in the dynamics of population growth and that such periodic fluctuations might well be modelled by placing periodic coefficients in the classical equations of mathematical ecology.

The mathematical approach taken in this paper to the question of the existence of periodic solutions of periodic Kolmogorov systems is a generalization of that taken in

* Received by the editors November 4, 1980, and in revised form September 29, 1981. This material is based upon work supported by the National Science Foundation under grant MCS-7901307-01.

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previous papers by the author [2], [3], [4] and is based upon very general, abstract bifurcation theorems of Rabinowitz [8]. It will be shown (Theorem 1) for systems of size $n \geq 2$ that under rather general conditions there exists a critical value of the average inherent growth rate of one species, say x_1, at which there bifurcates a "global" branch of solutions which are positive solutions at least locally near the bifurcation point. This branch of solutions (to which, incidentally, there corresponds a branch of locally nonpositive solutions) bifurcates from a positive periodic solution of the "reduced system" of size $n-1$ obtained by eliminating x_1 from the system (i.e., by setting $x_1 \equiv 0$ in the system). Simple examples are given to show that this branch may not stay in the positive cone globally, however. Nonetheless, positive periodic solutions of periodic Kolmogorov systems of size $n \geq 2$ can be built up by repeated bifurcations of this type by applying this result repeatedly, starting from positive periodic solutions of scalar ($n=1$) periodic equations. Scalar equations are dealt with in Theorems 2 through 6. The stability of both the positive branch solutions and the periodic solutions of the reduced system are studied in §3, at least locally near the bifurcation point. As is typically the case in such bifurcation phenomena, it is found that the stability of the positive branch solutions depends on the stability properties of the solution of the reduced system and on the direction of bifurcation. In §4 the special case of planar ($n=2$) periodic Kolmogorov systems is discussed and examples of general periodic predator-prey and two-species competition models are given.

2. Periodic solutions.

(a). We begin by setting up some notation. If $v=\text{col}(v_i)$, $w=\text{col}(w_i)$ are n-vectors, then define $v \cdot w := \sum v_i w_i$ and $v_\wedge w := \text{col}(v_i w_i) = w_\wedge v$. For any $n \times n$ matrix $M=(m_{ij})$, define the $n \times n$ matrix $v \circ M := (v_i m_{ij})$. Note that $v_\wedge(Mw) = (v \circ M)w$.

Denote the Banach space of real valued, continuous p-periodic functions of a real variable t under the supremum norm $|\cdot|_0$ by B_p and denote the k-fold cross product of B_p with itself by B_p^k. Let $\text{av}(x) := p^{-1}\int_0^p x(t)\,dt$ denote the average of $x \in B_p$. Euclidean k-space will be denoted by R^k. A continuum (in a Banach space) is a closed connected set. The boundary of a set Ω will be denoted by $\partial\Omega$.

Consider the following general periodic system of n equations

$$(1) \quad \begin{aligned} &\text{(a)} \quad x' = x[a(t) + f(t,x,y)], \\ &\text{(b)} \quad y' = y_\wedge[b(t) + g(t,x,y)], \end{aligned}$$

where $x=x(t)$ is a scalar valued function of t and $y=y(t)$ is an $(n-1)$-vector valued function of t. For $n \geq 2$ let Ω^n denote an open set in $R \times R^{n-1}$ which contains the origin $(x,y)=(0,0)$. The functions f and g are assumed to satisfy the following hypotheses:

H1. $b \in B_p^{n-1}$, $n \geq 2$, and $f: R \times \Omega^n \to R$, $g: R \times \Omega^n \to R^{n-1}$ are continuous functions which are p-periodic in t and continuously differentiable in x and y with $f(t,0,0) \equiv g(t,0,0) \equiv 0$. Also, $a \in B_p$.

The system

$$(2) \qquad y' = y_\wedge[b(t) + g(t,0,y)]$$

of $n-1$ equations will be referred to as the *reduced system*. By a solution of (1) or (2) we always mean continuously differentiable functions. A positive solution $(x(t),y(t))$ of (1) [or $y(t)$ of (2)] is a solution for which $x(t)>0$, $y_i(t)>0$ for all t and i [or $y_i(t)>0$

for all t and i]. Two assumptions concerning the reduced system will be made:

H2. The reduced system (2) of $n-1$ equations, $n \geq 2$, has a positive p-periodic solution $0 < y = y_0(t) \in B_p^{n-1}$ such that $(0, y_0(t)) \in \Omega^n$ for all t.

H3. The solution $y = y_0(t)$ of (2) in H2 is noncritical, i.e., all Floquet exponents of the linearization of (2) at $y_0(t)$ have nonzero real parts.

More will be said about H2 and H3 below. Note that H2 implies the existence of a nontrivial p-periodic solution of (1) on the boundary of the positive cone in $B_p \times B_p^{n-1}$, namely $(x,y) = (0, y_0)$. We are interested, however, in solutions lying in the interior of this cone.

It is easy to show that if $0 \leq (x,y) \in B_p \times B_p^{n-1}$ is a solution of (1) ($0 \leq (x,y)$ means that $x \geq 0$ and $y_i \geq 0$ for all i) then

$$\begin{aligned} &\operatorname{av}(a(t) + f(t, x(t), y(t))) = 0 \quad \text{if } x > 0, \\ &\operatorname{av}(b_i(t) + g_i(t, x(t), y(t))) = 0 \quad \text{if } y_i > 0. \end{aligned} \tag{3}$$

To see this, given $x > 0$, divide (1a) by x and integrate over one period. A similar procedure is applied to (1b) given $y_i > 0$.

Note that (1) has the *positivity property*: if a solution of (1) satisfies $x(t_0) > 0$, $y(t_0) > 0$ for some finite t_0, then $x(t) > 0$, $y(t) > 0$ for all $t \in (-\infty, +\infty)$. Also, if $x(t_0) = 0$ or $y_i(t_0) = 0$ for some $1 \leq i \leq n$ and finite t_0, then $x(t) = 0$ or $y_i(t) = 0$ for all $t \in (-\infty, +\infty)$. These facts follow from

$$x(t) = x(t_0) \exp\left[\int_{t_0}^{t} (a(s) + f(s, x(s), y(s)))\, ds\right],$$

$$y_i(t) = y_i(t_0) \exp\left[\int_{t_0}^{t} (b_i(s) + g_i(s, x(s), y(s)))\, ds\right]$$

for $1 \leq i \leq n$ and all t.

Define $\Omega_p^n(y_0) := \{(x,y) \in B_p \times B_p^{n-1} : (x(t), y(t) + y_0(t)) \in \Omega^n \text{ for all } t\}$ for $n \geq 2$. This set is an open set in $B_p \times B_p^{n-1}$ which contains $(0, y_0)$. The following is our main theorem concerning the existence of p-periodic solutions of (1).

THEOREM 1. *Assume* H1, H2 *and* H3 *hold. Let* $a_0(t) \in B_p$ *be a given function with* $\operatorname{av}(a_0) = 0$. *There exists a continuum* $C \subset \Omega_p^n(y_0) \times R$ *with the following properties*:

(i) $(x, y, \mu) \in C$ *implies that* $(x,y) \in B_p \times B_p^{n-1}$ *solves system* (1) *with* $a(t) = \mu + a_0(t)$;

(ii) $(0, y_0, \mu_0) \in C$, *where*

$$\mu_0 := -\operatorname{av}(f(t, 0, y_0(t))); \tag{4}$$

(iii) *either* C *is unbounded or* $\partial(\Omega_p^n(y_0) \times R) \cap C \neq \varnothing$;

(iv) *in a suitably small open neighborhood of* $(0, y_0, \mu_0)$, $C = K^+ \cup K^-$, *where* K^+ *and* K^- *are continua for which* $K^+ \cap K^- = \{(0, y_0, \mu_0)\}$. *The solutions from* $K^+ - \{(0, y_0, \mu_0)\}$ *are positive while those from* $K^- - \{(0, y_0, \mu_0)\}$ *satisfy* $x(t) < 0$, $0 < y(t) < y_0(t)$ *for all* t.

In the case when $\Omega^n = R^n$ (i.e., when f and g are globally defined) and hence $\Omega_p^n(y_0) = B_p \times B_p^{n-1}$, the second alternative in (iii) is to be ruled out with the result that (iii) states simply that C is unbounded. This is the case for Volterra type systems in which the functions f and g are linear in x, y (see [2], [3], [4]). This theorem generalizes [3, Thm. 1(a)].

Proof. Define $z=y-y_0$ and let $a(t)=\mu+a_0(t)$ in (1). This results in the system

$$(5)\quad \begin{aligned} &\text{(a)} \qquad x'=[\mu+a_0(t)+f(t,0,y_0(t))]x+r_1(x,z),\\ &\text{(b)} \qquad z'=[y_0(t)_\wedge g_x(t,0,y_0(t))]x+[b(t)+g(t,0,y_0(t))]_\wedge z\\ &\qquad\qquad +y_0(t)_\wedge[g_y(t,0,y_0)z]+r_2(x,z), \end{aligned}$$

where

$$\begin{aligned} r_1(x,z) &:= x[f(t,x,z+y_0)-f(t,0,y_0)],\\ r_2(x,z) &:= z_\wedge[g_x(t,0,y_0)x+g_y(t,0,y_0)z+r_3(t,x,z)]+y_0(t)_\wedge r_3(t,x,z),\\ r_3(t,x,z) &:= g(t,x,z+y_0)-g(t,0,y_0)-g_x(t,0,y_0)x-g_y(t,0,y_0)z. \end{aligned}$$

The operators $r_1:\Omega_p^n(y_0)\to B_p$ and $r_2:\Omega_p^n(y_0)\to B_p^{n-1}$ are continuous and higher order than linear near $(0,0)\in B_p\times B_p^{n-1}$, i.e., $|r_1(x,z)|_0$ and $|r_2(x,z)|_{0,n-1}=O(|x|_0^2+|z|_{0,n-1}^2)$, where $|z|_{0,n-1}=\Sigma_1^{n-1}|z_i|_0$.

We wish to formulate (5) as an operator equation to which certain global bifurcation theorems apply. To do this we first choose a real constant c such that

$$c\neq \operatorname{av}(f(t,0,y_0(t)))$$

and rewrite (5a) as

$$(5\text{a}')\qquad x'=[-c+a_0(t)+f(t,0,y_0(t))]x+[c+\mu]x+r_1(x,z).$$

We are now interested in solving (5a')–(5b) for positive solutions in $B_p\times B_p^{n-1}$.

Let $G_1(t,s)$ and $G_2(t,s)$ be the Green's functions for the linear equations

$$\begin{aligned} x'&=[-c+a_0(t)+f(t,0,y_0(t))]x,\\ z'&=[b(t)+g(t,0,y_0(t))]_\wedge z+y_0(t)_\wedge[g_y(t,0,y_0(t))z] \end{aligned}$$

respectively. $G_1(t,s)$ exists by the choice of c which makes the p-periodic coefficient of the first (scalar) equation have nonzero average. $G_2(t,s)$ exists by H3 since the second equation is the linearization of (2) at $y=y_0$. These Green's functions define compact linear operators $L_1:B_p\to B_p$ and $L_2:B_p^{n-1}\to B_p^{n-1}$ by means of the integrals

$$\begin{aligned} L_1\xi &:= \int_0^p G_1(t,s)\xi(s)\,ds, \qquad \xi\in B_p,\\ L_2\eta &:= \int_0^p G_2(t,s)\eta(s)\,ds, \qquad \eta\in B_p^{n-1}. \end{aligned}$$

The system (5a')–(5b) is equivalent to the pair of operator equations

$$(6)\qquad x=\lambda L_1x+H_1(x,z), \qquad z=L_2[y_{0\wedge}g_x(t,0,y_0)]x+H_2(x,z)$$

for $(x,z)\in B_p\times B_p^{n-1}$, where $\lambda=c+\mu$ and $H_1:=L_1r_1:\Omega_p^n(y_0)\to B_p$ and $H_2:=L_2r_2:\Omega_p^n(y_0)\to B_p^{n-1}$ are completely continuous operators of higher order than linear near $(x,z)=(0,0)$. Equations (6) are in turn equivalent to the equations

$$(7)\qquad x=\lambda L_1x+H_1(x,z), \qquad z=\lambda L_2[y_{0\wedge}g_x(t,0,y_0)]L_1x+H_3(x,z),$$

where $H_3(x,z):=L_2[y_{0\wedge}g_x(t,0,y_0)]H_1(x,z)+H_2(x,z)$ is higher order than linear near $(x,z)=(0,0)$. Finally, (7) can be written in the concise form

$$(8)\qquad w=\lambda Lw+H(w),$$

where $w=(x,z)\in B_p\times B_p^{n-1}$, $L:B_p\times B_p^{n-1}\to B_p\times B_p^{n-1}$ is defined by

$$Lw := \left(L_1x, L_2[y_{0\wedge}g_x(t,0,y_0)]\,L_1z\right)$$

and $H:\Omega_p^n(y_0)\to B_p\times B_p^{n-1}$ is defined by $H(x,z):=(H_1(x,z),H_3(x,z))$. The operator L is linear and compact and H is completely continuous and of order higher than linear near $w=0$.

Of course, $w=0$ is a trivial solution of (8) (which corresponds to the solution $x=0$, $y=y_0$ of (1)). To find nonzero solution $w\neq 0$ of (8), we can use directly the global bifurcation theorems of Rabinowitz [8], using λ (or what amounts to the same thing μ) as a bifurcation parameter (c being held fixed). Specifically, we will use [8, Thm. 1.25, Cor. 1.12]. To do this it remains to be shown that L has a characteristic value $\lambda=\lambda_0$ of odd multiplicity. We will in fact show that L has one and only one characteristic value and it is real and simple.

The linear equation $w=\lambda Lw$ is equivalent to the linearized, homogeneous p-periodic system obtained by setting $r_1\equiv 0$, $r_2\equiv 0$ and $\mu=\lambda-c$ in (5), namely

$$(9)\quad \begin{aligned} &\text{(a)} && x'=[\mu+a_0(t)+f(t,0,y_0(t))]x,\\ &\text{(b)} && z'=[y_0(t)_\wedge g_x(t,0,y_0(t))]x+[b(t)+g(t,0,y_0(t))]_\wedge z\\ &&& \quad +y_0(t)_\wedge[g_y(t,0,y_0(t))z]. \end{aligned}$$

This system can be solved for $(x,z)\in B_p\times B_p^{n-1}$ by first solving the simpler scalar equation (9a) for p-periodic $x\in B_p$ and then solving (9b) by means of the formula $z=L_2[y_{0\wedge}g_x(t,0,y_0)]x$. Clearly, $x\equiv 0$ implies $z\equiv 0$, so (9) has a nontrivial solution if and only if $x\not\equiv 0$, which occurs if and only if $\mu=\mu_0$ as defined by (4). This shows that L has a unique characteristic value $\lambda=\lambda_0:=c+\mu_0$ which by definition of c is nonzero.

Finally we argue that $\lambda=\lambda_0$ is simple. Let $0\neq w_0=(x_0,z_0)\in B_p\times B_p^{n-1}$ be a characteristic solution: $w_0=\lambda_0 Lw_0$. Suppose $w\in B_p\times B_p^{n-1}$ satisfies $(I-\lambda_0L)^2w=0$. We wish to show that w is a multiple of w_0. Let $w^*:=(I-\lambda_0L)w$. Then $(I-\lambda_0L)w^*=0$, which implies that $w^*=mw_0$ for some real $m\in R$. Thus $w^*=m\lambda_0Lw_0$ and, hence $w=\lambda_0L(w+mw_0)$, which implies that $w=(x,z)\in B_p\times B_p^{n-1}$ solves the nonhomogeneous linear system

$$\begin{aligned} x'&=[\mu_0+a_0(t)+f(t,0,y_0)]x+\lambda_0mx_0,\\ z'&=[b(t)+g(t,0,y_0)]_\wedge z+y_0(t)_\wedge[g_y(t,0,y_0)z]+\lambda_0mz_0. \end{aligned}$$

The Fredholm alternative implies that λ_0mx_0 must be orthogonal to the adjoint solution $1/x_0$. This means, because $\lambda_0\neq 0$, that $m=0$. Hence, $w^*=0$ or, in other words, $w=\lambda_0Lw$, which implies the desired result that w is a multiple of w_0.

The results (i)–(iii) of Theorem 1 now follow from [8, Cor. 1.12] applied to the operator equation (8) on the bounded set $\Omega_p^n(y_0)\cap S(\rho)$, where $S(\rho)$ is the open sphere of arbitrary radius $\rho>0$, center $(0,0)$ in $B_p\times B_p^{n-1}$. Part (iv) follows from [8, Thm. 1.25] (also see §3 below). □

While Theorem 1 guarantees the existence of a global branch of p-periodic solutions of (1) in the sense that the branch is either unbounded or reaches the boundary of the domain of f and g, it asserts the positivity of solutions only on a subcontinuum K^+ of the branch lying in a neighborhood of the "bifurcation point" $(0,y_0,\mu_0)$. While it is shown in [8] that $C=C^+\cup C^-$, $C^+\cap C^-=\{(0,y_0,\mu_0)\}$, where $C^\pm$ are continua which are extensions of K^+ and K^- and that C^+ and C^- satisfy (iii), it does not follow that C^+ necessarily stays in the positive cone. The question which naturally arises then concerns the nature of this maximal subcontinuum C^+ containing K^+: does C^+ lie in the positive cone or does it "leave" this cone and hence contain nonpositive solutions of (1)? By "leave" the cone we mean here that the intersection of C^+ with the boundary of the positive cone contains a point other than the bifurcation point. In the latter case we can, by the positivity property of solutions of (1), distinguish three possibilities: if C^+ leaves the positive cone then there exists a $(x,y)\in C^+$ for which either

$$\text{(10)}\quad \begin{array}{lll} \text{(a)} & x\equiv 0, & y\equiv 0, \quad \text{or} \\ \text{(b)} & x\equiv 0, & 0\le y\not\equiv y_0 \text{ and } \not\equiv 0 \quad \text{or} \\ \text{(c)} & x>0, & y_i\equiv 0 \quad \text{for some } 1\le i\le n. \end{array}$$

If we define K_m^+ to be the maximal subcontinuum of C which consists of nonnegative solutions of (1) and contains K^+, then the following is immediate: *under the hypotheses of Theorem* 1, *either* K_m^+ *satisfies* (iii) *or it leaves the positive cone in the sense that* K_m^+ *contains a solution of* (1) *of one of the three types in* (10).

That K_m^+ can in fact leave the positive cone is easily established by examples. The classical Volterra predator-prey equations and Volterra–Lotka competition equations with constant coefficients and $n=2$ demonstrate this possibility as do the periodic coefficient versions of these equations studied in [2], [3]. In these examples, case (10c) always occurs, i.e., K_m^+ leaves the positive cone through a solution $(x,0,\mu^*)\in B_p\times B_p\times R$, $x>0$. We will give below a simple autonomous example to illustrate not only that K_m^+ leaves the positive cone, but that any of the three possibilities in (10) can, in fact, occur. Furthermore, this example will show that the stability of the positive solutions on K_m^+ can be lost before it leaves the cone. The stability of the positive periodic solutions on K_m^+ will be studied in §3 below.

Consider the following autonomous system of two ($n=2$) equations with constant coefficients:

$$\text{(11)}\qquad \begin{gathered} x'=x(-\gamma+y), \qquad y'=y[(y-\beta)(\alpha-y)-x], \\ \gamma>0, \quad \beta>0, \quad \alpha<\beta. \end{gathered}$$

This system serves as a model for predator-prey interaction in which the per capita growth rate of the predator x is an increasing, linear function of prey population size y and that of the prey is such that the prey zero isocline has a "hump" (see Rosenzweig [9]). The "hump" lies in the positive quadrant if and only if $(\alpha+\beta)/2>0$. Equations (11) have the form (1) with $n=2$ and

$$a(t)\equiv-\gamma, \quad f\equiv y, \quad b(t)\equiv-\alpha\beta, \quad g\equiv(\alpha+\beta)y-y^2-x.$$

In Theorem 1, $a_0(t)\equiv 0$ and $\mu=-\gamma$ with

$$y_0(t)\equiv\beta \quad \text{and} \quad \mu_0=-\beta.$$

The continuum C of periodic solutions (equilibria in this autonomous example) is explicitly given by

$$\text{(12)}\qquad x(t)\equiv(\gamma-\beta)(\alpha-\gamma), \quad y(t)\equiv\gamma, \quad \mu=-\gamma.$$

Thus, there are three cases.

1) When $\alpha=0$, the subcontinuum K_m^+ of C given by (12) for $0<\gamma<\beta$ connects the bifurcation point $(x,y,\mu)=(0,\beta,-\beta)$ with $(x,y,\mu)=(0,0,0)$ and hence case (10a) occurs.

2) When $\alpha>0$, K_m^+ is given by (12) with $\alpha<\gamma<\beta$; it leaves the positive quadrant at $(x,y,\mu)=(0,\alpha,-\alpha)$ and (10b) occurs.

3) When $\alpha<0$, K_m^+ is given by (12) with $0<\gamma<\beta$. In this case, however, it leaves the positive quadrant at $(x,y,\mu)=(-\alpha\beta,0,0)$ so that the case (10c) is seen to occur.

One can also show by standard linearization and eigenvalue techniques that when $(\alpha+\beta)/2>0$ the stability of the positive equilibrium (12) is lost as γ decreases through $(\alpha+\beta)/2$ (i.e., μ increases through $-(\alpha+\beta)/2$) and that a classical Hopf bifurcation occurs.

It is possible, of course, to set down simple conditions which rule out one or more of the possibilities in (10). For example, *if* $\operatorname{av}(b)\neq 0$, *then* (10a) *cannot occur*. This is because if $(x_n,y_n,\mu_n)\in K_m^+$ are such that $(x_n,y_n,\mu_n)\to(0,0,\mu^*)$, $\mu^*\in R$, then by (3)

$$0=\operatorname{av}\big(b(t)+g(t,x_n(t),y_n(t))\big),$$

which in the limit as $n\to+\infty$ implies the contradiction that $\operatorname{av}(b)=0$. Also, *if the reduced system* (2) *has a unique positive, p-periodic solution, then* (10b) *cannot occur*. This is because $(x_n,y_n,\mu_n)\in K_m^+$ such that $(x_n,y_n,\mu_n)\to(0,y,\mu^*)$, $y\neq y_0$, $\mu^*\in R$, implies that $y\in B_p$ solves the reduced system, a contradiction.

A simple example of the case when the subcontinuum K_m^+ of positive solutions does not leave the positive cone is given by

$$x'=x(\mu-y),\quad \mu\in R,\qquad y'=y(1+x-y)$$

for which $y_0(t)\equiv 1$, $\mu_0=1$ and $K_m^+=\{(\mu-1,\mu,\mu):\mu>\mu_0=1\}$.

Not only can C^+ leave the positive cone, but it can "leave and re-enter" the positive cone and it can even do this infinitely often. An example (again autonomous) is given by the system

$$x'=x(\mu-y),\quad \mu\in R,\qquad y'=y(x+\sin y)$$

for which $y_0(t)\equiv\pi$, $\mu_0=\pi$ and $C^+=\{(-\sin\mu,\mu,\mu):\mu>\pi\}$ which yields positive solutions for $\mu\in((2n-1)\pi,2n\pi)$ for $n=1,2,3,\cdots$. In this example $K_m^+=\{(-\sin\mu,\mu,\mu):\pi<\mu<2\pi\}$ leaves the cone at a solution of the form (10b), namely $(0,2\pi,2\pi)$. Note that in this case $C^-=\{(-\sin\mu,\mu,\mu):\mu<\pi\}$ contains no positive solutions. If, on the other hand, we take $y_0(t)\equiv 2\pi$, $\mu_0=2\pi$, then $C^+=\{(-\sin\mu,\mu,\mu):\mu<2\pi\}$ and $K^+=\{(-\sin\mu,\mu,\mu):\pi<\mu<2\pi\}$. Now $C^-=\{(-\sin\mu,\mu,\mu):\mu>2\pi\}$ contains positive solutions for $\mu\in((2n-1)\pi,2n\pi)$, $n=2,3,\cdots$.

(b) Hypothesis H2 assumes that the reduced system (2) associated with (1) has a positive p-periodic solution. This hypothesis itself can be fulfilled by use of Theorem 1 with n replaced by $n-1$ provided $n\geq 3$ and a reduced system of this reduced system has a positive p-periodic solution satisfying H3, etc. In this way positive p-periodic solutions of a general p-periodic Kolmogorov system

$$x_i'=x_ih_i(t,x_1,\cdots,x_{n-1},x_n) \tag{13}$$

can be built up from a positive p-periodic solution of a single scalar, $(n-1)$-fold reduced equation associated with one of the equations, say

$$x_n'=x_nh_n(t,0,\cdots,0,x_n), \tag{14}$$

by repeated bifurcations as given by Theorem 1. For this reason it is important to consider the scalar case $n=1$, as we do below, in order to start this algorithmic procedure. The main difficulty in carrying out this procedure is with the assumption H3 that at each step the periodic solution obtained is noncritical. While one can at least say that this hypothesis is "generic", no simple general criteria exist for testing this hypothesis when $n\geq 3$. In the case of linear functions f and g this requirement can be met by an assumption of strong diagonal dominance [4]. In §3 a criterion valid at least locally near the point of bifurcation will be obtained ($\mu_1 \neq 0$). For $n=2$ the reduced equation is a scalar equation and H3 reduces to the nonvanishing of the average of the coefficient. This case will be considered in §4. We now turn to the scalar case $n=1$.

Consider the scalar periodic equation

$$y' = y(b(t) + g(t,y)) \tag{15}$$

under the assumption

H4. $g: R \times (\alpha, \beta) \to R, -\infty \leq \alpha < 0 < \beta \leq +\infty$, is continuous in $(t,y) \in R \times (\alpha, \beta)$, is continuously differentiable in $y \in (\alpha, \beta)$, is p-periodic in t and satisfies $g(t,0) \equiv 0$.

Define $\Omega_p := \{y \in B_p : y(t) \in (\alpha, \beta) \text{ for all } t\}$, an open set in B_p which contains $y(t) \equiv 0$.

THEOREM 2. *Let* $b_0(t) \in B_p$, $\text{av}(b_0) = 0$, *be given and assume that* H4 *holds. Then there exists a continuum* $C \subset \Omega_p \times R$ *with the following properties*:

(i) $(y, \mu) \in C$ *implies* y *solves* (15) *with* $b(t) = b_0(t) + \mu$;

(ii) $(y, \mu) = (0,0) \in C$;

(iii) *either* C *is unbounded or* $C \cap \partial(R \times \Omega_p) \neq \varnothing$;

(iv) *in a suitable small open neighborhood of* $(0,0)$, $C = K^+ \cup K^-$, $K^+ \cap K^- = \{(0,0)\}$, *where* $K^{\pm}$ *are continua. The solutions from* $K^+ - \{(0,0)\}$ *are positive while those from* $K^- - \{(0,0)\}$ *are negative.*

Proof. This theorem is proved in virtually the same way as Theorem 1 (but with $n=1$, of course) except that $y_0(t)$, the p-periodic solution of the reduced system (2), is replaced by the identically zero solution of (15) and $\Omega_p^n(y_0)$ is replaced by Ω_p. Otherwise, the details are the same. □

If g is globally defined (i.e., $(\alpha, \beta) = R$ so that $\Omega_p = B_p$), then the second alternative in (iii) is to be eliminated with the result that C is unbounded.

As in the case $n \geq 2$, $C = C^+ \cup C^-$, $C^+ \cap C^- = \{(0,0)\}$, where the continua C^+ and C^- contain K^+ and K^- respectively and we again ask whether C^+ can leave the positive cone. By the positivity property of solutions of (15), C^+ can leave the positive cone only if $(0, \mu) \in C^+$ for some $\mu \in R$, $\mu \neq 0$. But this is impossible, because $(0, \mu) \in C^+$ implies that $(0, \mu)$ is a bifurcation point and, hence, $\mu = 0$ (since $w = \lambda L w$ in the proof of Theorem 1 and hence of Theorem 2 has only one characteristic value $\lambda_0 = c$, hence $\mu_0 = 0$). Thus, *under the hypotheses of Theorem* 2, $C = C^+ \cup C^-$, $C^+ \cap C^- = \{(0,0)\}$, *where* $C^{\pm}$ *are continua for which* $C^+ - \{(0,0)\}$ *and* $C^- - \{(0,0)\}$ *contain positive and negative solutions of* (15), *respectively. Both* $C^{\pm}$ *satisfy the alternative* (iii) *of Theorem* 2. *Thus, if* $\beta = +\infty$, *then* C^+ *is unbounded*. (See [8, Thm. 1.27].)

Define the *spectrum* $\Sigma^+ \subset R$ associated with C^+ to be the range of the projection mapping $C^+ \to R$ defined by $(y, \mu) \to \mu$. Thus, for $\mu \in \Sigma^+$ there exists at least one positive p-periodic solution of (15) with $a(t) = a_0(t) + \mu$. Define $S^+ \subset B_p$ to be the range of the projection $C^+ \to B_p$ defined by $(y, \mu) \to y$. Both Σ^+ and S^+ are continua which contain $\mu = 0$ and $y \equiv 0$ respectively. Σ^+ is of course an interval which is possibly open, closed or half open or closed and is possibly infinite. Let R^+ denote the positive reals.

Theorems 3–6 give results concerning S^+ and the spectrum Σ^+ of (15).

THEOREM 3. *Assume that the hypotheses of Theorem* 2 *hold. Suppose that* C^+ *is unbounded* (*which happens if* $\beta = +\infty$). *Then either* S^+ *is unbounded* (*which happens if* $\beta = +\infty$) *or else* S^+ *is bounded in which case the spectrum* Σ^+ *is unbounded*, $\beta < +\infty$ *and there exist sequences* $(y_j, \mu_j) \in C^+$ *and* $t_j \in [0,p]$ *such that* $t_j \to t_0 \in [0,p]$, $|y_j|_0 \to \beta$ *and* $|\mu_j| + |g(t_j, |y_j|_0)| \to +\infty$.

Let Γ be the set of all convergent sequences $(t_j,\xi_j)\in[0,p]\times(0,\beta)$, $0<\beta\le+\infty$, for which $\xi_j\to\beta$ and $\lim g(t_j,\xi_j)$ exists (but is not necessarily finite). Define $g_{\inf}$, $g_{\sup}\in[-\infty,+\infty]$ by

$$g_{\inf}:=\inf_\Gamma\{\lim g(t_j,\xi_j)\}\le\sup_\Gamma\{\lim g(t_j,\xi_j)\}:=g_{\sup}.$$

THEOREM 4. *Assume the hypotheses of Theorem* 2. *Then* Σ^+ *is an interval whose closure contains* $(-g_{\inf}-\min b_0(t),0]$ *if* $g_{\inf}\ge-\min b_0(t)\ge0$ *or* $[0,-g_{\sup}-\max b_0(t))$ *if* $g_{\sup}\le-\max b_0(t)\le0$.

Proofs. In everything to follow, if $(y_j,\mu_j)\in C^+$, then t_j denotes a real number which satisfies $t_j\in[0,p]$, $y_j'(t_j)=0$, $y_j(t_j)=|y_j|_0$. Since $y_j'/y_j=b_0(t)+\mu_j+g(t,y_j(t))$ for all t, it follows that

$$\mu_j=-b_0(t_j)-g(t_j,|y_j|_0). \tag{16}$$

Without loss of generality, it is assumed that $t_j\to t_0\in[0,p]$. Suppose that C^+ is unbounded, which of course implies that either S^+ or Σ^+ is unbounded.

Proof of Theorem 3. If S^+ is bounded, then Σ^+ is unbounded which means that there exists a sequence $(y_j,\mu_j)\in C^+$ for which the μ_j are unbounded. Choosing a subsequence if necessary, assume that $|\mu_j|\to+\infty$. Since $|y_j|_0$ is a bounded sequence, we can assume (by choosing another subsequence if necessary) that $|y_j|_0\to\sigma$, where $\sigma\ge0$ is finite and $\sigma\le\beta$. The conclusions of Theorem 3 follow by taking limits in (16) and noting that if $\sigma\ne\beta$ (which happens if $\beta=+\infty$), then a contradiction results because the limit on the right-hand side would be finite by the continuity of g while $|\mu_j|\to+\infty$. If $\beta<+\infty$ the only way out of the contradiction is the conclusion that S^+ is unbounded or that S^+ is bounded, but $\sigma=\beta<+\infty$.

Proof of Theorem 4. Using Theorem 2(iii) (for C^+) and Theorem 3, choose a sequence $(y_j,\mu_j)\in C^+$ for which $\xi_j:=|y_j|_0\to\beta\le+\infty$. Extracting a subsequence if necessary assume $\mu_j\to\mu^*\in[-\infty,+\infty]$. From (16)

$$\mu^*=-b_0(t_0)-\lim g(t_j,\xi_j),$$

and hence Σ^+ is an interval whose closure contains both 0 (by Theorem 2(ii)) and μ^*. Since

$$-\max b_0(t)-g_{\sup}\le\mu^*\le-\min b_0(t)-g_{\inf},$$

the result follows. □

Example 1 (A generalized logistic equation). Consider (15) when g satisfies H4 with $\beta=+\infty$. Suppose that $g(t,y)\le0$ for all $(t,y)\in[0,p]\times[0,+\infty)$ and that $\lim g(t_j,\xi_j)=-\infty$ for any convergent sequence $(t_j,\xi_j)\in[0,p]\times[0,+\infty)$ for which $\xi_j\to+\infty$. Then from the above results we conclude that (15) has at least one positive p-periodic solution whenever $\mu=\mathrm{av}(b(t))>0$ (see Theorem 4 with $g_{\sup}=-\infty$) which is unbounded in norm as $\mathrm{av}(b(t))\to+\infty$ (Theorem 3). The periodic logistic, in which $g(t,y)=-c(t)y$, $c\in B_p$, $c(t)>0$, is a simple example.

THEOREM 5. *Assume the hypotheses of Theorem* 2 *hold. If* $g(t,y)$ *is bounded for* $(t,y)\in[0,p]\times[0,\infty)$, *then* Σ^+ *is bounded.*

Proof. $(y,\mu)\in C^+$ and (16) imply that $|\mu|\le|b_0|_0+\max|g(t,y)|$. □

EXAMPLE 2. Let $g(t,y)=-c(t)y/(1+y)$, $c\in B_p$, $c(t)>0$. Then $g_{\inf}=-\max c(t)$, $g_{\sup}=-\min c(t)$ and (15) has by Theorem 4 at least one positive p-period solution for $b(t)=b_0(t)+\mu$, $\mathrm{av}(b_0)=0$, $\mu\in[0,\min c(t)-\max b_0(t)]$ provided $\min c(t)>\max b_0(t)$. By Theorem 5 the spectrum Σ^+ is bounded.

THEOREM 6. *Assume the hypotheses of Theorem 2 hold. Suppose that* $\beta<+\infty$ *and that the sequence* $g(t_j,\xi_j)$ *is unbounded for all convergent sequences* $(t_j,\xi_j)\in[0,p]\times(0,\beta)$ *for which* $\xi_j\to\beta$. *Then the spectrum* Σ^+ *is unbounded and* S^+ *is bounded.*

Proof. Since $y\in S^+$ implies $|y|_0<\beta$, S^+ is bounded. Suppose that Σ^+ is bounded. Then C^+ is bounded, and by Theorem 2(iii) applied to C^+, it follows that $C^+\cap\partial(\Omega_p\times R)\neq\varnothing$. Thus, there exists a sequence $(y_j,\mu_j)\in C^+$ for which $\xi_j=|y_j|_0\to\beta$. From (16) and the stated hypothesis on g, it follows that μ_j is unbounded, a contradiction to the boundedness of Σ^+. □

Example 3. Let $g(t,y)=-c(t)\tan y$, $0<c(t)\in B_p$. Then $\alpha=-\pi$, $\beta=\pi$ and Theorem 6 implies that Σ^+ is unbounded and S^+ is bounded. Since $g_{\sup}=-\infty$ Theorem 4 implies that there exists at least one positive p-periodic solution of (15) when $\mu=\operatorname{av}(b(t))>0$. Theorem 6 shows that for a sequence $\mu_j=\operatorname{av}(b(t))\to+\infty$ there are solutions $y_j\in B_p$, $y_j(t)>0$, of (15) for which $|y_j|_0\to\pi$.

3. Local analysis and stability. In this section the (local asymptotic) stability of the p-periodic solutions of (1) lying in a neighborhood of the bifurcation point $(x,y,\mu)=(0,y_0,\mu_0)$ will be studied as it depends on the bifurcation parameter $\mu=\operatorname{av}(a)$. Both the solutions $(0,y_0,\mu)$, $\mu\in R$, and those lying on C in a neighborhood of the bifurcation point $(0,y_0,\mu_0)$ will be considered.

THEOREM 7. *Assume* H1, H2, H3 *hold and that* $n\geq 2$, *but with the added assumption that f and g are twice continuously differentiable in x and y.*

(i) *If one of the Floquet exponents of the linearization of the reduced system* (2) *at* $y_0(t)$ *has positive real part, then* $(x,y)=(0,y_0)\in B_p\times B_p^{n-1}$ *is an unstable solution of* (1) (*for any* $a\in B_p$).

(ii) *If all Floquet exponents of the linearization of* (2) *have negative real parts, then* $(x,y)=(0,y_0)\in B_p\times B_p^{n-1}$ *is* (*locally uniformly asymptotically*) *stable as a solution of* (1) *when* $\mu=\operatorname{av}(a)<\mu_0$ *and is unstable when* $\mu>\mu_0$ (*where* μ_0 *is given by* (4)).

Proof. The linearization of (1) at $(x,y)=(0,y_0)$ yields the linear system (9), a block triangular system whose Floquet exponents are those of the reduced system (2) plus

$$\operatorname{av} s(\mu+a_0(t)+f(t,0,y_0(t)))=\mu-\mu_0.$$

The theorem follows from standard linearization theorems for periodic systems of ordinary differential equations. □

In order to study the stability of the solutions of (1) lying on the bifurcating branch C near the point of bifurcation, Lyapunov–Schmidt small parameter expansions of the solutions and their Floquet exponents will be made. Thus,

$$\begin{aligned} x(t)&=x_1(t)\varepsilon+x_2(t)\varepsilon^2+x_3(t,\varepsilon)\varepsilon^2,\\ y(t)&=y_0(t)+y_1(t)\varepsilon+y_2(t)\varepsilon^2+y_3(t,\varepsilon)\varepsilon^2,\\ \mu&=\mu_0+\mu_1\varepsilon+\mu_2(\varepsilon)\varepsilon,\end{aligned}\tag{17}$$

where $|x_3(t,\varepsilon)|_0=O(|\varepsilon|)$, $|y_3(t,\varepsilon)|_{0,n-1}=O(|\varepsilon|)$ and $|\mu_2(\varepsilon)|=O(|\varepsilon|)$. To rigorously establish that the solutions on C near the bifurcation point $(0,y_0,\mu_0)$ corresponding to $\varepsilon=0$ have the form (17) is a routine application of classical Lyapunov–Schmidt techniques and will hence not be given here. To do this requires two continuous derivative for f and g. (See [5], [6] for abstract theorems particularly suited to the operator formulation of (1) given in the proof of Theorem 1 which establish the validity of (17).) The plan here, of course, is to determine the lower order coefficients x_1, y_1 and μ_1 in the expansions (17) and then in an expansion for the Floquet exponents of the solution (17). This is done by substituting (17) into (1) and equating coefficients of like powers of ε.

The lowest order terms in ε in (1) yield the reduced equation (2) which is satisfied by $y_0(t)$ by definition. The first order terms in ε yield the linear system (1) with $\mu=\mu_0$:

$$(18)\quad \begin{aligned} &\text{(a)} && x_1'=x_1[\mu_0+a_0(t)+f(t,0,y_0(t))],\\ &\text{(b)} && y_1'=[y_0(t)_\wedge g_x(t,0,y_0(t))]x_1+y_0(t)_\wedge g_y(t,0,y_0(t))y_1\\ & && \quad +[b(t)+g(t,0,y_0(t))]_\wedge y_1 \end{aligned}$$

for $(x_1,y_1)\in B_p\times B_p^{n-1}$. Thus

$$(19)\quad \begin{aligned} x_1(t)&=\exp\left(\int_0^t[\mu_0+a_0(s)+f(s,0,y_0(s))]\,ds\right)>0,\\ y_1(t)&=\int_0^p G_2(t,s)[y_0(s)_\wedge g_x(s,0,y_0(s))]x_1(s)\,ds. \end{aligned}$$

Finally, the second order terms in ε from (1a) only yield the scalar equation

$$\begin{aligned} x_2'=x_2&[\mu_0+a_0(t)+f(t,0,y_0(t))]\\ &+x_1(t)[\mu_1+f_x(t,0,y_0(t))x_1(t)+f_y(t,0,y_0(t))\cdot y_1(t)] \end{aligned}$$

for $x_2\in B_p$. This equation is a nonhomogeneous version of (18a) and consequently the nonhomogeneous term must be orthogonal to the adjoint solution $1/x_1(t)$. This orthogonality condition yields a formula for μ_1:

$$(20)\qquad \mu_1=-\mathrm{av}[f_x(t,0,y_0(t))x_1(t)+f_y(t,0,y_0(t))\cdot y_1(t)].$$

The sign of μ_1 determines the local "direction" of bifurcation of the branches K^+ and K^- (given by $\varepsilon>0$ and $\varepsilon<0$, respectively) in Theorem 1. This is provided $\mu_1\neq 0$, of course.

Let $N_n(\rho)$ denote the open ball in $B_p\times B_p^{n-1}\times R$ of radius $\rho>0$ and center $(0,y_0,\mu_0)$.

THEOREM 8. *In addition to the hypotheses of Theorem* 7, *assume* $\mu_1\neq 0$. *There exists a* $\rho>0$ *such that the following statements hold*:

(i) $(x,y,\mu)\in C^{\pm}\cap N_n(\rho)$ *implies* $\operatorname{sign}(\mu-\mu_0)=\pm\operatorname{sign}\mu_1$.

(ii) *If at least one Floquet exponent of the linearization of the reduced system* (2) *at* $y_0(t)$ *has a positive real part* (*hence*, $y_0(t)$ *is an unstable solution of* (2)), *then for* $(x,y,\mu)\in C^{\pm}\cap N_n(\rho)-\{(0,y_0,\mu_0)\}$ *the solution* $(x,y)\in B_p\times B_p^{n-1}$ *of* (1) *with* $a(t)=a_0(t)+\mu$ *is unstable*.

(iii) *On the other hand, if all Floquet exponents of the linearization of* (2) *at* $y_0(t)$ *have negative real parts* (*hence*, $y_0(t)$ *is a stable solution of* (2)), *then for* $(x,y,\mu)\in C^+\cap N(\rho)-\{(0,y_0,\mu_0)\}$ *the positive solution* $(x,y)\in B_p\times B_p^{n-1}$ *of* (1) *with* $a(t)=a_0(t)+\mu$ *is*:

(*locally uniformly asymptotically*) *stable if* $\mu_1>0$,
unstable if $\mu_1<0$.

(*For the nonpositive solutions from* $(x,y,\mu)\in C^-\cap N(\rho)-\{(0,y_0,\mu_0)\}$, *the inequalities are reversed*.)

Proof.

(i) This follows immediately from (17) and $x_1(t)>0$.

(ii) The linearization of (1) at the branch solution (17) yields

$$\begin{aligned} z_1' &= [\mu + a_0(t) + f(t,x,y) + xf_x(t,x,y)]z_1 + [xf_y(t,x,y)]z_2, \\ z_2' &= [y_\wedge g_x(t,x,y)]z_1 + [b(t) + g(t,x,y)]_\wedge z_2 + y_\wedge [g_y(t,x,y)z_2], \end{aligned} \tag{21}$$

where $z_1(t)$ is a scalar valued function and $z_2(t)$ is an $(n-1)$-vector valued function. The stability properties of the branch solutions (17) are determined by the Floquet exponents of (21) which, because the coefficients of (21) depend on ε through (17), are functions of ε. For $\varepsilon=0$, (21) reduces to (9), which has by assumption a Floquet multiplier with positive real part. Thus, (21) has such a Floquet exponent for sufficiently small ε.

(iii) In this case (9) has $n-1$ Floquet exponents with negative real parts. The remaining exponent is $\mathrm{av}(\mu_0 + a_0(t) + f(t,0,y_0(t))) = 0$. Our problem is to determine where in the complex plane this latter Floquet exponent is located for small $|\varepsilon| > 0$.

Now e is a Floquet exponent of (21) if and only if the linear homogeneous system for $(z,w) \in B_p \times B_p^{n-1}$,

$$\begin{aligned} &\text{(a)} \quad z' = [\mu + a_0(t) + f(t,x,y) + xf_x(t,x,y) - e]z + [xf_y(t,x,y)]w, \\ &\text{(b)} \quad w' = [y_\wedge g_x(t,x,y)]z + [(b(t) + g(t,x,y)) \circ I + y \circ g_y(t,x,y) - eI]w, \end{aligned} \tag{22}$$

has a nontrivial p-periodic solution. Here I is the $(n-1)\times(n-1)$ identity matrix. (See the Appendix.)

The coefficients of (21) are at least twice continuously differentiable in ε and consequently so is $e = e(\varepsilon)$. We write

$$e = e(\varepsilon) = e_1\varepsilon + e_2(\varepsilon)\varepsilon, \qquad |e_2(\varepsilon)| = O(|\varepsilon|) \tag{23}$$

for that exponent which vanishes at $\varepsilon = 0$ and look for a nontrivial p-periodic solution of (22) of the form

$$\begin{aligned} z &= z_1(t) + z_2(t)\varepsilon + z_3(t,\varepsilon)\varepsilon \in B_p, \qquad |z_3|_0 = O(|\varepsilon|), \\ w &= w_1(t) + w_2(t)\varepsilon + w_3(t,\varepsilon)\varepsilon \in B_p^{n-1}, \qquad |w_3|_{0,n-1} = O(|\varepsilon|). \end{aligned} \tag{24}$$

It is a straightforward application of Lyapunov–Schmidt methods to show that (22) has a nontrivial solution of the form (24) for e given by (23) and, hence, these details will not be given. Instead, only enough coefficients in these expansions will be calculated in order to find a formula for the crucial coefficient e_1.

Substitute (23) and (24) into (22). The lowest order terms yield a linear system identical to (18) and hence $z_1 = x_1$ and $w_1 = y_1$ as given by (19). The coefficients of the first order ε terms in only equation (22a) yield the scalar, linear nonhomogeneous equation

$$\begin{aligned} z_2' = {} & [\mu_0 + a_0(t) + f(t,0,y_0(t))]z_2 + [x_1(t)f_y(t,0,y_0(t))]\cdot y_1 \\ & + [\mu_1 + x_1(t)f_x(t,0,y_0(t)) + y_1(t)\cdot f_y(t,0,y_0(t)) + x_1(t)f_x(t,0,y_0(t)) - e]x_1(t) \end{aligned}$$

for $z_2 \in B_p$ whose nonhomogeneous term must be orthogonal to the adjoint solution $1/x_1(t)$. Making use of the definition (20) of μ_1, one finds that this orthogonality condition reduces to

$$\mathrm{av}[y_1(t)\cdot f_y(t,0,y_0(t)) + x_1(t)f_x(t,0,y_0(t)) - e_1] = 0$$

or $e_1=-\mu_1$. Thus for small $|\varepsilon|$ we have from (i) that

$$\operatorname{sign} e(\varepsilon)=\operatorname{sign} e_1=-\operatorname{sign}\mu_1=\mp\operatorname{sign}(\mu-\mu_0).$$

Since the branch solution is stable for $e(\varepsilon)<0$ and unstable for $e(\varepsilon)>0$, the result follows. □

Note that when $\mu_1\neq 0$ and the Floquet exponents of the linearization of the reduced system (2) have negative real parts, then Theorems 7(ii) and 8(iii) show that a typical "exchange of stability" from the "trivial" solution $(0,y_0)\in B_p\times B_p^{n-1}$ to the branch solutions as the bifurcation parameter μ increases through the critical value μ_0.

It also follows from Theorem 8 and its proof that the solutions on the bifurcating branch C are noncritical, at least in a neighborhood of the bifurcation point $(0,y_0,\mu_0)$, provided $\mu_1\neq 0$. As discussed in the previous section, this fact allows the repeated application of Theorem 1 in order to build up periodic solutions of general periodic Kolmogorov systems (13).

The scalar case (15) is easier to consider. The Lyapunov–Schmidt expansions

$$\begin{aligned} y(t)&=y_1(t)\varepsilon+y_2(t,\varepsilon)\varepsilon, \qquad |y_2|_0=O(|\varepsilon|),\\ \mu&=\mu_1\varepsilon+\mu_2(\varepsilon)\varepsilon, \qquad |\mu_2|=O(|\varepsilon|)\end{aligned} \tag{25}$$

substituted into (15) with $b(t)=b_0(t)+\mu$, $b_0\in B_p$ and $\operatorname{av}(b_0)=0$, yield

$$y_1(t)=\exp\left[\int_0^t b_0(s)\,ds\right], \qquad \mu_1=-\operatorname{av}\left[g_y(t,0)y_1(t)\right]. \tag{26}$$

A linearization of (15) at (25) yields

$$z'=\left[b(t)+g(t,y)+yg_y(t,y)\right]z,$$

whose Floquet exponent is

$$\operatorname{av}\left[b(t)+g(t,y)+yg_y(t,y)\right]=-\mu_1\varepsilon+O(|\varepsilon|^2).$$

Let $N(\rho)$ denote the open ball in B_p of radius ρ centered at 0.

THEOREM 9. *Assume that* H4 *holds and that* $\operatorname{av}[g_y(t,0)\exp(\int_0^t b_0(s)\,ds)]\neq 0$.

(i) *The trivial solution* $y\equiv 0$ *of the scalar equation* (15) *is* (*locally uniformly asymptotically*) *stable if* $\mu=\operatorname{av}(b)<0$ *and unstable if* $\mu=\operatorname{av}(b)>0$.

(ii) *There is a* $\rho>0$ *such that if* $(y,\mu)\in C^+\cap N(\rho)-\{(0,0)\}$ *the positive solution* $y\in B_p$ *of* (15) *with* $b(t)=b_0(t)+\mu$ *is*:

(*locally uniformly asymptotically*) *stable if* $\operatorname{av}\left[g_y(t,0)\exp\left(\int_0^t b_0(s)\,ds\right)\right]<0$,

unstable if $\operatorname{av}\left[g_y(t,0)\exp\left(\int_0^t b_0(s)\,ds\right)\right]>0$.

(*For the negative solutions from* $(y,\mu)\in C^-\cap N(\rho)-\{(0,0)\}$, *the inequalities are reversed.*)

The hypotheses of Theorems 8 and 9 require that $\mu_1\neq 0$. If μ_1 should equal zero, then coefficients of higher order terms in the ε series expansions of the solution, the bifurcation parameter μ and the Floquet exponent e would have to be computed in order to determine the direction of bifurcation and the stability of the bifurcating solution branch. While this is in principle a straightforward repeated application of the Fredholm alternative, it quickly becomes tedious in a general setting. Although for special cases (such as the case when the lowest order terms in f and g are of order ≥ 2)

one can without too much difficulty write formulas for these coefficients, we will refrain from doing so here.

4. Systems in the plane and applications to theoretical ecology. In the subject of theoretical ecology, systems in the plane are of fundamental importance. It is, thus, of interest to consider the results of the previous sections for the special case $n=2$ and to apply them in particular to the basic types of systems which model the ecologically fundamental predator-prey and two species competition interactions.

(a) *Planar systems.* Consider the pair of scalar equations

$$x' = x[a(t)+f(t,x,y)], \qquad y' = y[b(t)+g(t,x,y)] \tag{27}$$

and the related reduced equation

$$y' = y[b(t)+g(t,0,y)]. \tag{28}$$

Assume that $y=y_0(t)\in B_p$ is a positive nontrivial solution of (28). Theorems 2–6 and 9 apply to the question of the existence of $y_0(t)$. In order to apply Theorems 1, 7 and 8 with $n=2$ to (27), the hypothesis H3 of noncriticality must be met by $y_0(t)$. Since the reduced equation (28) is scalar, $y_0(t)$ is noncritical if and only if

$$\operatorname{av}[y_0(t)g_y(t,0,y_0(t))] \neq 0. \tag{29}$$

The following theorem summarizes the application of Theorems 1, 7 and 8 to the planar system (27).

THEOREM 10. *Assume that* H1 *holds with* $n=2$. *Assume further that the scalar equation* (28) *has a positive solution* $0<y_0(t)\in B_p$ *for which* (29) *holds.*

(i) *Then the conclusions of Theorem* 1 *hold* (*with* $n=1$) *for* (27).

(ii) *Assume that f and g are twice continuously differentiable in x and y. If*

$$\operatorname{av}[y_0(t)g_y(t,0,y_0(t))] > 0, \tag{30}$$

then $(0,y_0)\in B_p\times B_p$ *is an unstable solution of* (27). *On the other hand, if*

$$\operatorname{av}[y_0(t)g_y(t,0,y_0(t))] < 0, \tag{31}$$

then $(0,y_0)\in B_p\times B_p$ *is an unstable solution of* (27) *for* $\mu=\operatorname{av}(a)>\mu_0:=-\operatorname{av}(f(t,0,y_0(t)))$ *and is a* (*locally uniformly asymptotically*) *stable solution for* $\mu<\mu_0$.

(iii) *Suppose that* $\mu_1\neq 0$ (*where* μ_1 *is given by* (20)). *Then there exists a* $\rho>0$ *such that* $(x,y,\mu)\in C^{\pm}\cap N_2(\rho)$ *implies* $\operatorname{sign}(\mu-\mu_0)=\pm\operatorname{sign}\mu_1$; (30) *implies that solutions* $(x,y)\in B_p\times B_p$ *of* (27) *corresponding to* $(x,y,\mu)\in C^{\pm}\cap N_2(\rho)-\{(0,y_0,\mu_0)\}$ *are unstable*; *and* (31) *implies that positive solutions* $(x,y)\in B_p\times B_p$ *of* (27) *corresponding to* $(x,y,\mu)\in C^{+}\cap N_2(\rho)-\{(0,y_0,\mu_0)\}$ *are unstable for* $\mu_1<0$ *and* (*locally uniformly asymptotically*) *stable for* $\mu_1>0$. (*For nonpositive solutions from* $C^-\cap N_2(\rho)-\{(0,y_0,\mu_0)\}$ *the inequalities are reversed.*)

(b) *Applications.* We consider (27) to be a model of the growth of two interacting species whose population densities are given in some units as functions of time $x=x(t)$, $y=y(t)$. The p-periodic coefficients $a(t)$ and $b(t)$ represent the inherent growth rates of each species x and y respectively in the absence of the other and in the absence of any self-inhibitory effects on its own per unit growth rate. The functions f and g, which are assumed globally defined and twice continuously differentiable in x and y, describe what effects that interspecies and intraspecies interactions have on per unit growth rates.

Assume that at least one of the species, say y, has a positive average inherent growth rate: $\operatorname{av}(b(t))>0$, so that it will, in the absence of inter- and intraspecies effects on growth rates ($g\equiv 0$), exhibit unlimited growth. Furthermore, assume that at all density levels an increase in population density y never results in an increase in per unit growth rate of y (in the absence of x):

$$g_y(t,0,y)\leq 0 \quad (\not\equiv 0). \tag{32}$$

Finally, assume that the reduced equation (28) has a positive p-periodic solution $y_0(t)\in B_p$ (see Theorems 2–6 and 9). It follows that (31) holds and, hence, $y_0(t)$ is stable, that is species y has a stable periodic "carrying capacity" in the absence of species x.

An example is the periodic version of the famous logistic equation in which $g(t,0,y)=-y/K(t)$, $0<K(t)\in B_p$, which because it is integrable in closed form is easily seen to have a unique, positive globally stable p-periodic solution. Another example is the generalized periodic logistic considered in Example 1 of §2.

Of interest are the questions of the existence and stability of positive solutions of the system (27). From Theorem 10 we find that a global branch C^+ of solutions $(x,y)\in B_p\times B_p$ for which $a(t)=a_0(t)+\mu$, $a_0\in B_p$ and $\text{av}(a_0)=0$ bifurcates from the solution $(0,y_0)\in B_p\times B_p$ at $\mu=\mu_0:=-\text{av}(f(t,0,y_0(t)))$ and that $(0,y_0)$ suffers a loss of stability as $\mu=\text{av}(a)$ increases through μ_0. The branch consists, at least locally near the bifurcation point, of positive solutions which are stable if $\mu_1>0$ (see (20)), in which case the bifurcation is "to the right" (i.e., $\mu>\mu_0$ on the branch) and unstable if $\mu_1<0$, in which case the bifurcation is "to the left". From the discussion in §2, we conclude that the global branch C^+ can leave the positive cone but only at solutions of the form $(x,y,\mu)=(0,y,\mu)$, $0<y\neq y_0$, or $(x,0,\mu)$, $x>0$, and that not all positive solutions from the branch C^+ need be stable. (Note: all of the above holds if (32) is replaced by the weaker assumption (31).)

Predator-prey systems. Let x denote a predator species which preys on species y. The restrictions

$$\begin{gathered} f_x(t,x,y)\leq 0,\quad f_y(t,x,y)\geq 0\ (\not\equiv 0),\quad g_x(t,x,y)\leq 0\ (\not\equiv 0)\\ \text{for } x>0,\quad y>0 \quad \text{and all } t\in[0,p] \end{gathered} \tag{33}$$

reflect the situation that an increase in predator density decreases the per unit growth rate of both the predator itself and the prey while an increase in prey density increases the predator's per unit growth rate at each instant of time.

Since the inequality (31) implies that the Green's function $G_2(t,s)$ is strictly positive (see the proof of Theorem 1 in §2), it follows from (19) and (33) that $y_1(t)<0$ for all t. Since $x_1(t)>0$ (see (19)) the formula (20) shows, together with (33), that $\mu_1>0$. (Note that (33) is sufficient, but not necessary for $\mu_1>0$.)

Thus for such predator-prey systems there is an exchange of stability from $(0,y_0(t))$ (*whose stability implies predator extinction*) *to the positive, p-periodic branch solutions* (*whose stability imply the stable coexistence of the prey and predator*) *as* $\mu=\text{av}(a)$ *increases through* μ_0.

If we also assume that

$$\text{av}[f(t,0,y_0(t))]>0,$$

then $\mu_0<0$. Thus, near bifurcation, that is, for $\mu<\mu_0$ close to μ_0, it follows that $\mu=\text{av}(a)<0$ or, in other words, that the predator has a negative average inherent growth rate and would go to extinction in the absence of the prey.

Note that since $y_1(t)<0$ the prey density satisfies $y(t)<y_0(t)$ for all t (see (17)). Thus, near the bifurcation point the prey and the predator coexist, but do so in such a

way that the prey's density is at all times less than what it would be in the absence of the predator.

A classical example would be the periodic version of the famous Volterra–Lotka system in which

$$f(t,x,y) = -c_1(t)x + c_2(t)y, \qquad g(t,x,y) = -c_3(t)x - c_4(t)y,$$
$$0 \le c_i(t) \in B_p, \quad c_2(t) \not\equiv 0, \quad c_3(t) \not\equiv 0$$

to which all of the above applies. For a more detailed analysis of this specific example see [2]. Also see Bardi [1].

Two-species competition. Assume $\mathrm{av}(b) > 0$. The restrictions

$$\text{(34)} \qquad \begin{aligned} &f_x(t,x,y) \le 0, \quad f_y(t,x,y) \le 0 \ (\not\equiv 0), \quad g_x(t,x,y) \le 0 \ (\not\equiv 0), \\ &g_y(t,x,y) \le 0 \quad \text{for all } x>0, y>0 \text{ and } t \in [0,p] \end{aligned}$$

describe a case in which increases in either species density results in a decrease in both species' per unit growth rates at all times. If

$$\mathrm{av}[f(t,0,y_0(t))] < 0,$$

then $\mu_0 > 0$, which implies that near bifurcation $\mu = \mathrm{av}(a) > 0$ and species x (and hence both species) have unlimited growth in the absence of both inter- and intraspecific competition.

The direction of bifurcation is in this case indeterminate since the sign of μ_1 can be either + or − under assumptions (34). Note that again $y_1(t) < 0$. In fact, the quantity μ_1 is precisely that which distinguishes between the case of stable coexistence and of competitive exclusion. It is the natural generalization to the periodic case of the determinant of the community matrix which accomplishes this same task in the autonomous case of the famous Volterra–Lotka competition model (in which f and g are linear in x and y) upon which the idea of the principle of competitive exclusion is theoretically based. This determinant, in fact, identically equals μ_1 when the above analysis and formulas are applied to this special autonomous case. For a more complete discussion of the periodic Volterra–Lotka competition equations see [3]. Also see [7].

Thus under the general assumptions (34) *two competing species can coexist if the bifurcation in Theorem* 10 *is to the "right" but do not coexist and suffer competitive exclusion if the bifurcation is to the "left".*

Appendix. Let $A(t)$ be a continuous, p-periodic $n \times n$ matrix valued function and consider the two systems

$$(*) \qquad x'(t) = A(t)x(t),$$
$$(**) \qquad y'(t) = [A(t) - \lambda I]\, y(t),$$

where I is the $n \times n$ identity matrix.

PROPOSITION. λ *is a Floquet exponent of* $(*)$ *if and only if* $(**)$ *has a nontrivial p-periodic solution.*

Proof. Let $X(t)$, $Y(t)$ be fundamental matrices of $(*)$ and $(**)$, respectively, which satisfy $X(0) = Y(0) = I$. Define $Z(t) := X(t)\exp(-\lambda t)$. A straightforward calculation shows that $Z(t)$ satisfies $(**)$ and $Z(0) = I$. Thus,

$$(\dagger) \qquad Y(t) = X(t)\exp(-\lambda t).$$

First suppose that λ is a Floquet exponent of $(*)$; that is, $\exp(\lambda p)$ is an eigenvalue of $X(p)$. Let $v \ne 0$ be a vector such that $X(p)v = \exp(\lambda p)v$ and define $y(t) := Y(t)v$.

By definition, $y(t)$ is a nontrivial soluton of $(**)$. Moreover, it is p-periodic because

$$y(p)=Y(p)v=\exp(-\lambda p)X(p)v=\exp(-\lambda p)\exp(\lambda p)v=v=y(0)$$

by (†).

Conversely, suppose that $(**)$ has a nontrivial p-periodic solution $y(t)$. Then $y(t)=Y(t)v$ for some $v\neq 0$. From (†)

$$X(p)v=\exp(\lambda p)Y(p)v=\exp(\lambda p)y(p)=\exp(\lambda p)y(0)=\exp(\lambda p)v,$$

so that λ is a Floquet exponent.

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