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Some New Results on the Periodic Competition Model*

PHILIP KORMAN

Institute for Dynamics and Department of Mathematical Sciences, University of Cincinnati, Cincinnati, Ohio 45221-0025

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1. INTRODUCTION

We study existence and stability of periodic solutions for the Lotka–Volterra systems with periodic coefficients,

$$\begin{aligned} \dot{x}(t) &= x(t)(a(t) - b(t)\,x - c(t)\,y) \\ \dot{y}(t) &= y(t)(d(t) - e(t)\,x - f(t)\,y). \end{aligned} \tag{1.1}$$

Throughout the paper we assume the functions $a(t), ..., f(t)$ to be continuous and periodic with period $p > 0$, and that

$$A \equiv \int_0^p a(\tau)\,d\tau > 0, \qquad D \equiv \int_0^p d(\tau)\,d\tau > 0, \tag{1.2}$$

$$b(t), c(t), e(t), f(t) \quad \text{are positive for all } t. \tag{1.3}$$

Existence and local stability of positive p-periodic solutions of (1.1) were studied by J. Cushing [2]. P. de Mottoni and A. Schiaffino [7] have studied extensively the geometric properties of the period map $T\colon (x(0), y(0)) \to (x(p), y(p))$. In particular they noticed the monotonicity property: if the point $(\bar{x}(0), \bar{y}(0))$ lies northwest of $(x(0), y(0))$, then $(\bar{x}(t), \bar{y}(t))$ lies northwest of $(x(t), y(t))$ for all t, in particular $t = np$. This implies that any positive solution of (1.1) tends to a p-periodic solution as $t \to \infty$ (with possibly one component equal to zero). They go on to study multiplicity, location, and domains of attraction of the fixed points of T. However, their uniqueness results are rather restrictive.

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Our work was motivated by the paper of C. Alvarez and A. C. Lazer [1], who study (1.1) under the additional assumption that $a(t)$ and $d(t)$ are positive.

They define $a_L = \min_t a(t)$, $a_M = \max_t a(t)$, and b_L, b_M,... similarly. By an ingenious use of the degree theory, they showed that the conditions (introduced earlier by K. Gopalsamy [4])

$$a_L f_L > c_M d_M, \qquad d_L b_M > e_M d_M \tag{1.4}$$

imply existence and uniqueness of a p-periodic solution of (1.1), which attracts all other positive solutions as $t \to \infty$.

It turns out that the dynamics of (1.1) depend strongly on the stability properties of semitrivial solutions of (1.1), $(x_0(t), 0)$, and $(0, y_0(t))$, where $x_0(t)$ and $y_0(t)$ are positive p-periodic solutions of the equations $\dot{x} = x(a(t) - b(t)\,x)$ and $\dot{y} = y(d(t) - f(t)\,y)$, whose existence (and uniqueness) is obtained by direct integration. If both semitrivial solutions are unstable then the system (1.1) has a positive p-periodic solution. It is an open question if such a solution is unique in general. We conjecture that multiple solutions are possible. If this is so, the dynamics of (1.1) are then analyzed in H. Smith [9]. Under an additional assumption we show uniqueness (see Theorem 2.2), extending the results of [1, 7]. If both semitrivial solutions are unstable, again we conjecture non-uniqueness in general. Under an additional assumption we prove in the Theorem 2.3 both existence and uniqueness of the solution, using the degree theory similarly to [1]. We discuss the dynamics of (1.1) in that case, and present a numerical example. If one of the semitrivial solutions is stable and the other one unstable, then multiple solutions are known to occur, see [7]. Finally, we discuss our numerical experiments related to the above conjectures.

2. Periodic Coexistence States and the Dynamics

We begin by showing that if both semitrivial solutions of (1.1) are unstable then there is a positive coexistence state.

THEOREM 2.1. *In addition to the conditions* (1.2) *and* (1.3), *assume that*

$$\int_0^p (a(\tau) - c(\tau)\,y_0(\tau))\,d\tau > 0, \qquad \int_0^p (d(\tau) - e(\tau)\,x_0(\tau))\,d\tau > 0. \tag{2.1}$$

Then the system (1.1) *has a positive p-periodic solution.* (*Notice that the conditions* (2.1) *can be written explicitly in terms of the coefficients of* (1.1).)

Proof. It is a straightforward computation to verify that conditions

(2.1) are included in Theorem 5.3 of P. de Mottoni and A. Schiaffino [7]. Alternatively, we could apply Schauder's fixed point theorem to a map $T: (u, v) \to (\bar{u}, \bar{v})$, which takes positive p-periodic functions $u(t)$ and $v(t)$ into positive p-periodic solutions of

$$\dot{\bar{u}} = \bar{u}(a - b\bar{u} - cv), \qquad \dot{\bar{v}} = \bar{v}(d - eu - f\bar{v}).$$

The second proof generalizes also to $n \geqslant 2$ competing species.

It is known that the stability question for the n species Lotka–Volterra problems can be reduced to that for a linear system

$$\dot{x} = A(t)\,x, \qquad x(t) \in R^n, \qquad A(t+p) = A(t), \tag{2.2}$$

with a real $n \times n$ matrix. Stability of (2.2) is not a trivial question, as for example negativity of real parts of all eigenvalues of $A(t)$ does not imply in general even boundness of $x(t)$, see, e.g., [5, p. 121]. The following lemma is extracted with some generalizations from the proof of Lemma 1 in [1]. It could also be derived from more general results on exponential dichotomies, see, e.g., [8]; however, checking the conditions of [8] would occupy about as much space as the self-contained proof below. All vector inequalities below are understood componentwise.

LEMMA 2.1. *Assume that* $a_{ij}(t) > 0$ *for all* $i \neq j$ *and all* $t \geqslant 0$. *Assume there exists a constant row vector* $\alpha = (\alpha_1, ..., \alpha_n) > 0$, *such that*

$$\alpha A \leqslant 0\ (\geqslant 0) \qquad \textit{and} \qquad \|\alpha A\| > 0 \qquad \textit{for all} \quad t \geqslant 0. \tag{2.3}$$

Then the system (2.2) *is asymptotically stable* (*unstable*).

Proof. According to the Floquet theory, stability is governed by the eigenvalues of the monodromy matrix $X(p)$, where $X(t)$ is the solution of

$$\dot{X}(t) = A(t)\,X(t), \qquad X(0) = E - \text{the identity matrix.} \tag{2.4}$$

Observe next that all entries of $X(t)$ are strictly positive for all $t > 0$. Indeed, setting $X(t) = e^{-\mu t}Y(t)$, we obtain for $\mu > 0$ sufficiently large a system

$$\dot{Y}(t) = (A(t) + \mu E)\,Y(t), \qquad Y(0) = E,$$

whose matrix has all entries strictly positive, and hence $Y(t) > 0$ for all $t > 0$.

By the Perron–Frobenius theorem $X(p)$ has a simple positive eigenvalue, call it λ, which is strictly greater than the modulus of any other eigenvalue; moreover, the corresponding eigenvector z, $X(p)\,z = \lambda z$, can be chosen positive. If $\lambda < 1$, the system (2.2) is asymptotically stable, and if $\lambda > 1$ then unstable. If we now set $x(t) = X(t)\, z$, then $x(t)$ is strictly positive for $t \geqslant 0$ solution of (2.2), with $x(0) = z$ and $x(p) = \lambda z$. Using (2.3),

$$\alpha_1 \dot{x}_1 + \cdots + \alpha_n \dot{x}_n = \sum_{j=1}^{n} \left(\sum_{i=1}^{n} a_{ij} \alpha_i \right) x_j < 0 \qquad \text{for all} \quad t \geqslant 0.$$

Integrating from 0 to p,

$$\lambda(\alpha_1 z_1 + \cdots + \alpha_n z_n) < \alpha_1 z_1 + \cdots + \alpha_n z_n,$$

and hence $\lambda < 1$. The instability is proved similarly.

Assuming instability of both semitrivial solutions, we now give a condition for uniqueness, generalizing the results of of [1, 7]. A similar result was proved by A. Tineo and C. Alvarez [10]. They consider $n \geqslant 2$ competing species; however, for the $n = 2$ case their result is more restrictive.

THEOREM 2.2. *Assume that the conditions of Theorem 2.1 are satisfied. Assume also existence of a constant vector $\alpha = (\alpha_1, \alpha_2) > 0$ so that for $A(t) = \begin{pmatrix} -b(t) & c(t) \\ e(t) & -f(t) \end{pmatrix}$ one has $\alpha A \leqslant 0$, $\|\alpha A\| > 0$ for all $t \geqslant 0$. Then the problem (1.1) has a unique positive p-periodic solution, which attracts all other positive solutions of (1.1) as $t \to \infty$.*

Proof. Let $(x(t), y(t))$ be a positive p-periodic solution of (1.1), whose existence follows by Theorem 2.1. Its variational system is

$$\begin{aligned} \dot{\xi} &= (a - 2bx - cy)\, \xi - cx\eta = -bx\xi - cx\eta + \frac{\dot{x}}{x}\, \xi \\ \dot{\eta} &= -ey\xi + (d - ex - 2fy)\, \eta = -ey\xi - fy\eta + \frac{\dot{y}}{y}\, \eta. \end{aligned} \tag{2.5}$$

Letting $u = \xi/x$, $v = -\eta/y$, we obtain from (2.5)

$$\begin{aligned} \dot{u} &= -bxu + cyv \\ \dot{v} &= exu - fyv. \end{aligned} \tag{2.6}$$

Using Lemma 2.1, we conclude that any positive p-periodic solution of (1.1) is stable (by [1] the Floquet multipliers of (2.5) and (2.6) are identical). It follows by the results of [7] that such a solution is then unique (alternatively, we could use the degree theory, as in Theorem 2.3 below, to prove uniqueness). Finally, by [7] any positive solution of (1.1) tends to a p-periodic solution. Since both semitrivial solutions are unstable, the proof follows.

Next we prove existence and uniqueness results in case both case semi-trivial solutions are stable.

THEOREM 2.3. *In addition to the conditions* (1.2) *and* (1.3), *assume that*

$$\int_0^p (a(\tau)-c(\tau)\,y_0(\tau))\,d\tau<0, \qquad \int_0^p (d(\tau)-e(\tau)\,x_0(\tau))\,d\tau<0. \quad (2.7)$$

Assume also existence of a constant positive vector $\alpha=(\alpha_1,\alpha_2)$, *so that for* $A(t)=\left(\begin{smallmatrix}-b(t) & c(t)\\ e(t) & -f(t)\end{smallmatrix}\right)$ *one has* $\alpha A\geqslant 0$ *and* $\|\alpha A\|>0$ *for all* $t\geqslant 0$. *Then the problem* (1.1) *has a unique positive p-periodic solution* (*which is unstable*).

Proof. If the system (1.1) has a p-periodic solution $(x(t),y(t))$, then we can consider the variational systems (2.5) and (2.6) again. Applying Lemma 2.1 to the system (2.6), we conclude that it is unstable, i.e., it has a Floquet multiplier greater than one. Since the systems (2.5) and (2.6) have identical Floquet multipliers (see [1]), we get the same conclusion for (2.5). We show next that the index of $(x(t),y(t))$ is -1, and then use the degree theory to obtain both existence and uniqueness.

We make a general remark. Let $x(t,x_0)$ denote the solution of $\dot{x}=f(t,x)$, $x(0)=x_0$, where $x\in R^n$ and $f(t+p,x)=f(t,x)$. Denote by T the period map: $T(x_0)=x(p,x_0)$. Let the matrix $X(t)$ be the solution of the variational system $\dot{X}(t)=f_x(t,x(t,x_0))\,X(t)$, $X(0)=E$. Then differentiating the original ODE in x_0, we conclude that $T'(x_0)=X(p)$.

For the problem (1.1) the variational equation at the positive p-periodic solution $(x(t),y(t))$ is given by (2.5). If $X(p)$ denotes the fundamental matrix of (2.5) with the eigenvalues λ_1 and λ_2, then by the above remark the index of T at $(x(0),y(0))$ is equal to $(1-\lambda_1)(1-\lambda_2)$. From the above remarks we know that say $\lambda_2>1$. By Liouville's formula

$$\begin{aligned}\lambda_1\lambda_2&=\det X(p)=\exp\left(\int_0^p (a-2bx-cy+d-ex-2fy)\,dt\right)\\&=\exp\left(\int_0^p (-bx-fy)\,dt\right)<1.\end{aligned}$$

Hence $0<\lambda_1<1$, and so the index of T at the fixed point $(x(0),y(0))$ is -1.

The map T also has the trivial fixed points: $(0,0)$, $(x_0(0),0)$, and $(0,y_0(0))$, where $x_0(t)$ denotes the positive p-periodic solution of $\dot{x}=x(a(t)-b(t)\,x)$, and $y_0(t)$ is defined similarly. It is easy to check that $(0,0)$ is a repeller and the other two are attractors, so that they all have index 1 (the variational equations at these points are easily analyzed).

Recall that $a_M=\max_t a(t)$, etc. To avoid having to use the degree theory in cones, we extend T from the positive quadrant to

$D=[-a_M/b_L, a_M/b_L]\times[-d_M/f_L, d_M/f_L]$ by reflecting the picture with respect to the x and y axes. Each positive fixed point of T gives rise to four fixed points of index -1 on D. The five trivial fixed points $(0,0)$, $(\pm x_0(0), 0)$, $(0, \pm y_0(0))$ still have index 1 each (as they still are a repeller and attractors, respectively). Let $n \geqslant 0$ be the number of positive fixed points of T. Then, since $\deg(I-T, D, 0)=1$ $(TD \subset D)$, we conclude that (see Fig. 1)

$$1=5+4n(-1),$$

i.e., $n=1$, and the theorem follows.

By [7] any positive solution of (1.1) approaches a p-periodic one. Hence, in the conditions of Theorem 2.3, generically one of the species becomes extinct. Which one of them actually dies out depends on the coefficients and initial conditions, sometimes in a surprising way as the following example shows.

NUMERICAL EXAMPLE. We computed the solution of $(2\pi \simeq 6.283)$

$$\dot{x}=x(a+b\sin 2\pi t-x-cy)$$
$$\dot{y}=y(d-ex-y),$$

for various values of parameters and initial conditions.

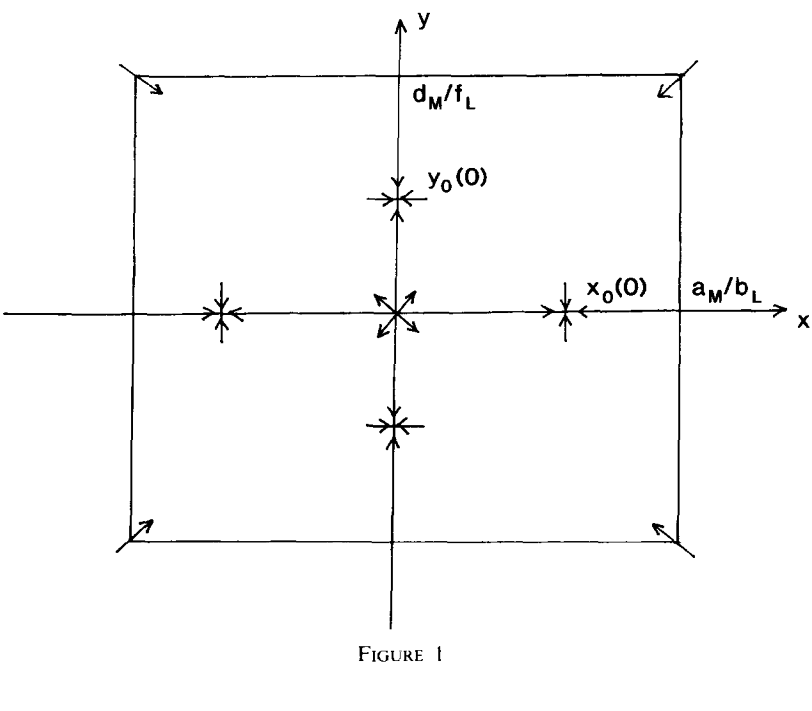

FIGURE 1

(i) $a=d=4$, $b=1$, $e=c=2$, $x(0)=y(0)=5$, i.e., we have identical on the average species. Result: $y(t) \to 0$ as $t \to \infty$.

(ii) The same as above but $b=-1$. This time $x(t)$ died out.

(iii) $a=4.1$, $d=4$, $b=-1$, $c=e=2$, $x(0)=y(0)=5$. Here $x(t)$ went extinct (although it is on the average a superior species).

(iv) The same as in (iii), but $x(0)=5.3$. This time $y(t)$ became extinct.

As an application of our results we obtain a complete understanding of the dynamics of the system (1.1) in the case of constant interaction rates b, c, e, and f. Since the above coefficients quantify the "crowding" and "interaction" effects, it appears reasonable to suppose that they change less with time than the carrying capacities $a(t)$ and $d(t)$, explaining our interest in this case.

PROPOSITION 2.1. *Assume that b, c, e, and f are positive constants. For the existence of a positive p-periodic solution of* (1.1) *it is necessary and sufficient that $A>0$, $D>0$, and*

$$\frac{Af-cD}{bf-ce}>0 \quad \text{and} \quad \frac{Db-eA}{bf-ce}>0. \tag{2.8}$$

The solution is then unique.

Proof. Dividing the equations in (1.1) by $x(t)$ and $y(t)$, respectively, and integrating from 0 to p, we see that the expressions in (2.8) are proportional to the averages of $x(t)$ and $y(t)$, respectively, proving necessity. For the sufficiency part, it is easy to see that the case $bf-ce>0$ is covered by Theorem 2.2, while the case $bf-ce<0$ is covered by Theorem 2.3.

The following result now follows easily.

PROPOSITION 2.2 *Assume that b, c, e, and f are positive constants. In order for* (1.1) *to have a unique positive p-periodic solution which attracts all other positive solutions, it is necessary and sufficient that $A>0$, $D>0$ and $Af-cD>0$, $Db-eA>0$.*

Finally we describe our attempts to find an example when both semitrivial solutions are unstable and multiple coexistence states occur. It follows from the results of [7, 9] that if uniqueness fails, one can expect at least two locally stable p-periodic solutions, and solutions starting with (M, ε) and (ε, M), with $\varepsilon>0$ small and $M>0$ large, will tend to two different coexistence states. We integrated (1.1), using the standard fourth-order Runge–Kutta method, and tried various examples, which violated the conditions of Theorem 2.2. However, in all cases we saw convergence to a unique p-periodic coexistence state.

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