



On the dynamics of two classes of periodic ecological models

Philip Korman^{a,b}

^a *Institute for Dynamics, University of Cincinnati, Cincinnati, OH 45221, United States*

^b *Department of Mathematical Sciences, University of Cincinnati, Old Chemistry Building (ML 0025), Cincinnati, OH 45221-0025, United States*

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Abstract

We give a detailed description of dynamics for periodic Lotka–Volterra systems with constant interaction rates. We also give an exact multiplicity result for a periodic species with a threshold. We present some numerical computations, which both illustrate our results and indicate possibilities for further developments.

Keywords: Periodic Lotka–Volterra systems; Global dynamics; Computations

1. Introduction

We begin by considering Lotka–Volterra systems of the type

$$\dot{x}(t) = x(t)(a(t) - b(t)x(t) - c(t)y(t)), \quad \dot{y}(t) = y(t)(d(t) - e(t)x(t) - f(t)y(t)), \quad (1.1)$$

with continuous p -periodic coefficients $a(t), \dots, f(t)$, and we are interested in positive solutions $x(t) > 0$, $y(t) > 0$. We assume that the carrying capacities $a(t)$ and $d(t)$ have positive averages and that self-limitation coefficients $b(t)$ and $f(t)$ are positive. The signs of the interaction coefficients $c(t)$ and $e(t)$ determine the type of interaction: competing species if $c(t)$ and $e(t)$ are positive, predator–prey if one of the signs is reversed, and cooperating species if both signs are reversed. We show that dynamics of (1.1) can be described in detail if the coefficients b , c , e and f are constant. It appears reasonable to assume that self-limitation and crowding coefficients change less with time (or seasons) than the carrying capacities. Section 2 is devoted mostly to the cooperating-species case, for which we obtain a complete description of the dynamics. We then recall our results in [4], which give a complete understanding of the dynamics for the competing-species case (for constant b , c , e and f). For the predator–prey case we obtain a necessary and sufficient condition for existence of a positive p -periodic solution (for constant b , c , e and f). This solution is globally stable under an additional

condition: $ce < bf$. Our numerical experiments indicate that this restriction may be relaxed.

In Section 3 we consider a periodic model for a species with a threshold:

$$\dot{x}(t) = x(t)(x(t) - a(t))(b(t) - x(t)). \quad (1.2)$$

Assuming $\max_t a(t) < \min_t b(t)$ and a technical condition, we prove existence of exactly two positive p -periodic solutions. We then study numerically competition of a Lotka–Volterra species with a species of a threshold type.

2. Remarks on periodic Lotka–Volterra systems

We begin with a general Lotka–Volterra system describing interaction of two cooperating species in a periodic environment ($x = x(t)$, $y = y(t)$):

$$\dot{x} = x(a(t) - b(t)x + c(t)y), \quad \dot{y} = y(d(t) + e(t)x - f(t)y). \quad (2.1)$$

Here $a(t), \dots, f(t)$ are continuous p -periodic functions such that

$$b(t), c(t), e(t) \text{ and } f(t) \text{ are positive functions,} \quad (2.2)$$

$$A = \int_0^p a(t) dt > 0, \quad D = \int_0^p d(t) dt > 0. \quad (2.3)$$

Lemma 1. *Let $(x(t), y(t))$ and $(u(t), v(t))$ be two positive (componentwise) solutions of (2.1) such that $u(0) \geq x(0)$ and $v(0) \geq y(0)$ with at least one inequality being strict. Then $u(t) > x(t)$ and $v(t) > y(t)$ for all $t > 0$.*

Proof. Denote $z = u - x$, $w = v - y$. Then,

$$\begin{aligned} \dot{z} &= (a + cy - bx - bu)z + cuw, & z(0) &\geq 0, \\ \dot{w} &= evz + (d + ex - fy - fv)w, & w(0) &\geq 0, \end{aligned} \quad (2.4)$$

and $z^2(0) + w^2(0) > 0$. Let now $z = e^{-\lambda t}\xi$, $w = e^{-\lambda t}\eta$, with a constant λ to be determined. Then (2.4) becomes

$$\begin{aligned} \dot{\xi} &= (\lambda + a + cy - bx - bu)\xi + cu\eta, & \xi(0) &= z(0) \geq 0, \\ \dot{\eta} &= ev\xi + (\lambda + d + ex - fy - fv)\eta, & \eta(0) &= w(0) \geq 0. \end{aligned} \quad (2.5)$$

For any $T > 0$ we can choose $\lambda > 0$ so large that all the coefficients in (2.5) are positive for $0 \leq t \leq T$. This implies that $\xi(t)$ and $\eta(t)$ are positive on $(0, T]$, and so are $x(t)$ and $y(t)$. Since T was arbitrary, the proof follows. \square

The following result is an adaptation of a theorem of [3].

Theorem 2 (Essentially of de Mottoni and Schiaffino [3]). *Every positive solution of (2.1) either tends to a positive p -periodic solution as $t \rightarrow +\infty$ or to infinity (in both components).*

Proof. We begin by introducing the natural directions in the (x, y) -plane. We say that a point $P = (p_1, p_2)$ lies northeast of $Q = (q_1, q_2)$ if $p_1 \geq q_1$ and $p_2 \geq q_2$. The other three directions (northwest, southeast and southwest) are defined similarly. We say that the point P lies strictly northeast of Q if the above inequalities are strict, and similarly for other directions. Let $P = (x(0), y(0))$. By P' we denote $(x(t'), y(t'))$ the solution of (2.1) for some $t' > 0$, and Q' is defined similarly. By P'' we denote $(x(t''), y(t''))$, etc.

It follows from Lemma 1 that if Q lies northeast (southwest) of P , then Q' lies strictly northeast (southwest) of P' for any $t' > 0$. If the point Q lies northwest (southeast) of P , then we claim that only one of two possibilities occurs.

(i) Q' is either northeast or southwest of P' for some $t' > 0$. Then, by the above, Q'' will lie correspondingly strictly northeast or strictly southwest of P'' for all $t'' > t'$.

(ii) Q' is strictly northwest (southeast) of P' for all $t' > 0$.

We show that the other possibilities cannot occur. Assume for definiteness that Q lies strictly northwest of P , Q' is strictly southeast of P' for some $t' > 0$. By continuous dependence on data for (2.1), this would imply the existence of $0 < t'' < t'$, such that Q'' is either northeast or southwest of P'' . By (i) it is then impossible for Q' to be southeast of P' .

Starting with an arbitrary point $(x(0), y(0))$, we now consider its images under the Poincaré map, denoting $P_n = (x(np), y(np))$, $n = 0, 1, \dots$. It follows from the above that for $n > n_0 \geq 0$, P_n moves in either of four strict directions, i.e., its components are monotone. If P_n lies in a bounded region, then $P_n \rightarrow P$, with P a fixed point of the Poincaré map. Finally, we remark that P cannot lie on either of the coordinate axes, since, e.g., the x -component of the periodic solution of (2.1) is bounded below by the p -periodic solution of $\dot{z} = z(a(t) - b(t)z)$, which is strictly positive (as can be seen by a direct integration). \square

Theorem 3. Assume that the interaction coefficients b, c, e and f are constant while $a(t)$ and $d(t)$ satisfy (2.3). Then for existence of a positive p -periodic solution of (2.1) it is necessary and sufficient that $ec < bf$. In such a case the positive p -periodic solution is unique, and it attracts all other positive solutions when $t \rightarrow +\infty$. If $ec = bf$, then both components of any positive solution of (2.1) go to $+\infty$ in infinite time (i.e., solution of (2.1) exists for all $t > 0$). If $ec > bf$, then any positive solution of (2.1) blows up in finite time.

Proof. If $(x(t), y(t))$ is a positive p -periodic solution of (2.1), then dividing the first equation in (2.1) by $x(t)$, the second one by $y(t)$ and integrating from 0 to p , we express

$$\int_0^p x(\tau) d\tau = \frac{Af + cD}{bf - ec}, \quad \int_0^p y(\tau) d\tau = \frac{Ae + bD}{bf - ec}, \quad (2.6)$$

which proves necessity of $ec < bf$.

(i) Assume $ec < bf$. Denote $a_m = \max a(t)$, $d_m = \max d(t)$. Choose $M > 0$, $N > 0$ such that $a_m - bM + cN < 0$ and $d_m + eM - fN < 0$.

Then (2.1) has an invariant rectangle $(0, M) \times (0, N)$ and hence a positive p -periodic solution exists by Theorem 2. To show that it is unique, we first show that there is a maximal p -periodic solution by constructing standard monotone iterates, and then use formulas (2.6). (Alternatively, we could show that the local index of any p -periodic solution is 1, and use the degree

theory. The last approach was introduced in [1].) By Theorem 2, the unique p -periodic solution is a global attractor.

(ii) $ec = bf$. No positive p -periodic solution exists. Referring to the proof of the Theorem 2, the points P_n must eventually move strictly northeast and tend to ∞ , i.e., both $x(t)$ and $y(t)$ tend to ∞ .

We show next that solution exists for all $t > 0$. The proof is almost identical to the one we used in [5]. Denote $\mu_1(t) = \exp(-\int_0^t a(\tau) d\tau)$, $\mu_2 = \exp(-\int_0^t d(\tau) d\tau)$. Rewrite (2.1) as

$$\frac{d}{dt}(\mu_1 x) = \mu_1 x(-bx + cy), \quad \frac{d}{dt}(\mu_2 y) = \mu_2 y\left(ex - \frac{c}{b}ey\right). \quad (2.7)$$

Denote $X = \mu_1 x$, $Y = \mu_2 y$ and divide the second equation in (2.7) by the first:

$$\frac{dY}{dX} = -\frac{e}{b} \frac{Y}{X}.$$

Integrating and returning to the original x and y gives

$$\mu_2 y = \frac{c_2}{\mu_1^{c_1} x^{c_1}}, \quad c_1 = \frac{e}{b}, \quad c_2 \text{ a constant of integration.}$$

This implies that $x(t)$ cannot go to ∞ in finite time, since otherwise $y(t)$ would have to go to zero.

(iii) $ec > bf$. Choose $\alpha, \beta > 0$ so that

$$\frac{e}{f+\beta} > \frac{b+\alpha}{c}, \quad (2.8)$$

and divide the positive quadrant \mathbb{R}_+^2 into the regions $A_1 = \{0 < x < \infty, y > ex/(f+\beta)\}$, $A_2 = \{0 < x < \infty, (b+\alpha)x/c \leq y \leq ex/(f+\beta)\}$ and $A_3 = \{0 < x < \infty, y < (b+\alpha)x/c\}$. If a trajectory eventually stays outside A_3 , then $x(t)$ blows up in finite time, since then $\dot{x}(t) \geq x(t)(a(t) + \alpha x)$. Similarly, if a trajectory stays eventually outside A_1 , then $y(t)$ blows up. As in (ii), we know that $x(t)$ and $y(t)$ go to ∞ as t increases. In order for a solution to exist for all t , the trajectory would have to visit both A_1 and A_3 infinitely often on its way to infinity. We show next that this is impossible.

Let $y = \gamma x$, with $(b+\alpha)/c < \gamma < e/(f+\beta)$. Then,

$$\lim_{x \rightarrow \infty} \frac{dy}{dx} = \lim_{x \rightarrow \infty} \frac{y(d+ex-fy)}{x(a-bx+cy)} = \gamma \frac{e-f\gamma}{-b+c\gamma} > \gamma,$$

if we choose γ sufficiently close to b/c (decreasing $\alpha > 0$ if necessary). This implies that the vector field crosses the line $y = \gamma x$ only in one direction for large x , completing the proof. \square

Remark 4. In case $ce < bf$ our numerical experiments have shown the convergence to a p -periodic solution to be very fast. In fact even with $(x(0), y(0))$ taken rather far from the periodic solution, by time $t = 2p$ the solution usually is very close to the periodic one. This remains true also in the case when b, c, e and f depend on t .

Example 5. In Fig. 1 we present a computation for the system

$$\dot{x} = x(9 + 2 \sin(2\pi t) - 4x + 1.5 y), \quad \dot{y} = y(11 - 8 \sin(2\pi t) + 0.1 x - y).$$

The system was integrated using a program written by D. Schmidt, which is using a fifth- and sixth-order Runge–Kutta method with automatically adjusted time steps (Fehlberg's method). We started with $x(0) = y(0) = 1$. One sees quick convergence to a periodic pattern in the (x, y) -plane. The fact that $x(t)$ and $y(t)$ converge to one-periodic functions was verified by a separate computation of $x(t)$ and $y(t)$ (keep in mind that the system is nonautonomous).

Similar detailed description of dynamics is also possible for the case of competing species with constant and positive b, c, e and f :

$$\dot{x} = x(a(t) - bx - cy), \quad \dot{y} = y(d(t) - ex - fy). \quad (2.9)$$

The following result we proved in [4] (it can also be deduced from [3]).

Theorem 6. Assume $a(t)$ and $d(t)$ satisfy (2.3). Then for the existence of a positive p -periodic solution of (2.9) it is necessary and sufficient that

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

In order for this solution to attract all other positive solutions as $t \rightarrow \infty$, it is necessary and sufficient that $Af - cD > 0$ and $bD - eA > 0$.

Next we consider the periodic predator–prey model

$$\dot{x} = x(a(t) - bx - cy), \quad \dot{y} = y(d(t) + ex - fy), \quad (2.10)$$

with constant interaction rates $b, c, e, f > 0$.

Theorem 7. Assume $a(t)$ and $d(t)$ satisfy (2.3). Then condition

$$Af - cD > 0 \quad (2.11)$$

is necessary and sufficient for existence of a positive p -periodic solution of (2.10). If in addition $ec < bf$, then this solution is unique and attracts all other positive solutions as $t \rightarrow \infty$.

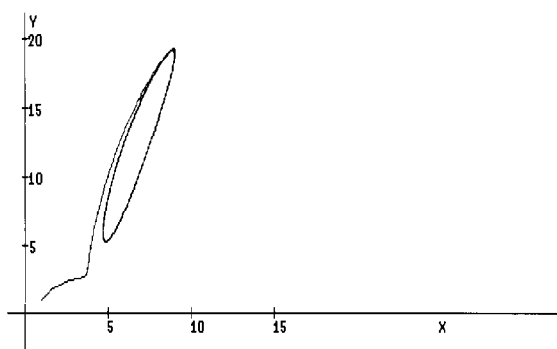


Fig. 1.

Proof. Expressing as before

$$\int_0^p x(t) dt = \frac{Af - cD}{bf + ce}, \quad \int_0^p y(t) dt = \frac{Ac + bD}{bf + ce},$$

we see the necessity of (2.11). Sufficiency easily follows by using the degree theory, in a similar way as we used in [4]. The stability assertion follows from [7] (or by setting up monotone iterations as in [6] and then using the iterates to prove global stability similarly to [2]. This approach would carry over to a class of n -species systems with constant interaction rates). \square

3. On a periodic model with a threshold

We begin with the equation ($u = u(t)$)

$$\dot{u} = u(u - a(t))(b(t) - u) \quad (3.1)$$

with positive continuous and p -periodic functions $a(t)$ and $b(t)$. We assume that

$$\max_t a(t) < \min_t b(t). \quad (3.2)$$

Here we have a species whose growth rate is negative when $u < a(t)$ (the threshold) and positive for $a(t) < u < b(t)$.

Theorem 8. Assume, in addition to (3.2), that the following two conditions hold:

$$\max_t a(t) < \frac{1}{2}[a(t) + b(t)], \quad (3.3)$$

$$\sqrt{a(t)b(t)} < \min_t b(t). \quad (3.4)$$

Then the problem (3.1) has exactly two positive p -periodic solutions, with $0 < u_1(t) < u_2(t)$ for all t . Moreover, $u_2(t)$ is asymptotically stable as $t \rightarrow +\infty$, while $u_1(t)$ is unstable. Also, we have

$$\min_t a(t) \leq u_1(t) \leq \max_t a(t), \quad (3.5)$$

$$\min_t b(t) \leq u_2(t) \leq \max_t b(t). \quad (3.6)$$

Proof. Define the Poincaré map $u_0 \in \mathbb{R}_+ \rightarrow T(u_0) \in \mathbb{R}_+$ by $T(u_0) = u(p, u_0)$, where $u(t, u_0)$ is the solution of (3.1) with $u(0, u_0) = u_0$. It is clear that T maps the interval $[\min_t b(t), \max_t b(t)]$ into itself, while T^{-1} maps $[T(\min_t a(t)), T(\max_t a(t))]$ into itself. Since the fixed points of T correspond to periodic solutions, it follows that (3.1) has at least two p -periodic solutions, with at least one satisfying (3.5) and (3.6), respectively. Also notice that all p -periodic solutions must satisfy either (3.5) or (3.6), since outside these regions \dot{u} is either positive or negative.

Next we establish the stability claim, from which the exact multiplicity of solutions will easily follow. The variational equation of (3.1) is

$$\dot{v} = [-3u^2 + 2(a + b)u - ab]v. \quad (3.7)$$

Its Floquet multiplier is

$$f = v(p, 1) = \exp\left(\int_0^p (-3u^2 + 2(a+b)u - ab) dt\right). \quad (3.8)$$

We show next that for any p -periodic solution satisfying (3.6), $f < 1$, which implies asymptotic exponential stability of the solution.

Dividing (3.1) by u and integrating, we get in view of periodicity

$$\int_0^p (-u^2 + (a+b)u - ab) dt = 0. \quad (3.9)$$

Motivated by [1], we now rewrite (3.7):

$$\dot{v} = [-u^2 + (a+b)u - ab]v + [-2u^2 + (a+b)u]v = \frac{\dot{u}}{u}v + [-2u^2 + (a+b)u]v. \quad (3.10)$$

Letting $\xi = v/u$, we express

$$\dot{\xi} = [-2u^2 + (a+b)u]\xi. \quad (3.11)$$

Using (3.9),

$$\int_0^p [-2u^2 + (a+b)u] dt = \int_0^p (-u^2 + ab) dt. \quad (3.12)$$

It follows from (3.11) that if (3.4) holds, $\xi(t) \rightarrow 0$ as $t \rightarrow +\infty$. But then $v(t) \rightarrow 0$ as $t \rightarrow +\infty$, which implies that $f < 1$ (since the integral in (3.8) has to be negative). Instability of any solution satisfying (3.5) follows similarly, using (3.12) (here $f > 1$).

Next, we show uniqueness of the p -periodic solution satisfying (3.6). We use the Brouwer degree theory similarly to [1]. Define the function $F(r): \mathbb{R}_+ \rightarrow \mathbb{R}_+$ by $F(r) = r - T(r)$. Choose any number $s \in (\min_t b(t), \max_t b(t))$. Then for any $\epsilon > 0$ sufficiently small and any $0 \leq \theta \leq 1$,

$$\theta F(r) + (1 - \theta)(r - s) < 0, \quad \text{for } r = \min_t b(t) - \epsilon, \quad (3.13)$$

and the opposite inequality holds for $r = \max_t b(t) + \epsilon$. It follows that with $I = (\min_t b(t) - \epsilon, \max_t b(t) + \epsilon)$,

$$\deg(F(r), I, 0) = \deg(r - s, I, 0) = 1. \quad (3.14)$$

The C^1 function $F(r)$ will have a finite number of roots on I , provided we can show that $F'(\bar{r}) > 0$ at any root \bar{r} , and then its degree (3.10) is the sum of indices of each root. But the index at \bar{r} is

$$\text{sign } F'(\bar{r}) = \text{sign}(1 - T'(\bar{r})) = \text{sign}(1 - f_{\bar{r}}) = 1,$$

where $f_{\bar{r}} < 1$ is the Floquet multiplier of $u(t, \bar{r})$. Hence $F(r)$ has only one root in I , satisfying (3.6).

Uniqueness of the p -periodic solution satisfying (3.5) can be reduced to the above argument by reversing time, i.e., defining $T(u_0) = u(-p, u_0)$. \square

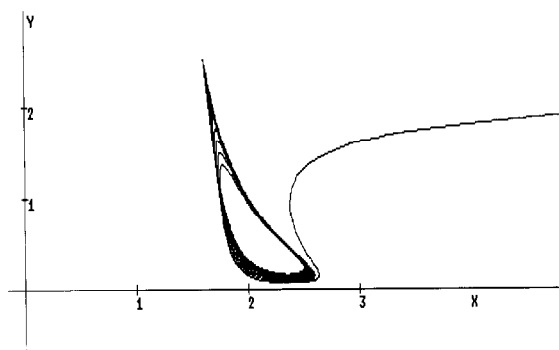


Fig. 2.

Remark 9. We had no difficulty numerically computing both periodic solutions, the stable (higher) one by considering the long-time behavior of $u(t, u_0)$ for $t > 0$ and $u_0 > 0$ large, and the unstable (lower) one when $t < 0$ and $u_0 > 0$ small (stability of $u_1(t)$ and $u_2(t)$ is reversed for $t < 0$).

Based on Theorem 8, one can consider various interaction models. We present a numerical example.

Example 10. We consider competition of a Lotka–Volterra species with one of threshold type:

$$\dot{x} = x(x-1)(9+p \sin(2\pi t) - 4x - y), \quad \dot{y} = y(7+q \sin(2\pi t) - 3x - y), \quad (3.15)$$

with constant p and q . If $p = q = 0$, then (3.15) has a fixed point $(2, 1)$, which attracts as $t \rightarrow +\infty$ all solutions of (3.15) with $x(0) > 1$ and $y(0) > 0$. For all constants p and q that we tried, we found that (3.15) had a one-periodic solution, attracting all other solutions with $x(0) > 1$ and $y(0) > 0$. In Fig. 2 we present the (x, y) -picture of the solution for $p = 2$ and $q = -8$, with $x(0) = 7$, $y(0) = 2$. We used the program of D. Schmidt, which was described previously.

4. Note added in proof

Recently we found another proof of Theorem 8, which does not require conditions (3.3) and (3.4). It will appear elsewhere.

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