A PRIORI BOUNDS AND PERIODIC SOLUTIONS
FOR A CLASS OF PLANAR SYSTEMS WITH APPLICATIONS TO LOTKA–VOLTERRA EQUATIONS

Tongren Ding, Hai Huang
Department of Mathematics
Peking University, Beijing, P.R. China

Fabio Zanolin *
Dipartimento di Matematica e Informatica
Università, via Zanon 6, 33100 Udine, Italy

Abstract. The existence of periodic solutions for some planar systems is investigated. Applications are given to positive solutions for a class of Kolmogorov systems generalizing a predator–prey model for the dynamics of two species in a periodic environment.

1. Introduction. In this paper we study the first order Kolmogorov differential system in the \((p, q)\)-plane

\[
\begin{aligned}
p' &= pP(t, p, q) \\
q' &= qQ(t, p, q)
\end{aligned}
\]  

(1)

in a case which generalizes the classical Lotka–Volterra models for the interaction of a prey population \(p(t)\) with a predator population \(q(t)\). Here and in the sequel, we set \(\mathbb{R}_+ = [0, +\infty)\), \(\mathbb{R}^+ = [0, +\infty)\) and denote by \(\langle f \rangle\) the mean value of a \(T\)-periodic function \(f\), that is \(\langle f \rangle := \frac{1}{T} \int_0^T f(t) \, dt\). By \(|f|_k\), with \(1 \leq k \leq \infty\), we denote the \(L_k\)-norm of a function \(f \in L_k([0, T], \mathbb{R})\). A function \(f\) with values in \(\mathbb{R}_+\) is said to be \(T\)-periodic and \(L^k\)-periodic, while we say that \(f\) is \(T\)-periodic and \(L^k\)-periodic if its range is contained in \(\mathbb{R}_+\).

Similarly, a solution \((p, q)\) of (1) is \(T\)-periodic if it satisfies \((p(t), q(t)) \in (\mathbb{R}_+)^2\), for all \(t\) in its domain. We also use the following notation throughout, with respect to a continuous \(T\)-periodic function \(u(t)\):

\[
\begin{aligned}
\overline{u} &= \max u(t), \\
\underline{u} &= \min u(t).
\end{aligned}
\]

As is well known, the simplest example of (1) modeling a predator–prey interaction, is given by

\[
P(t, p, q) = a - c q, \quad Q(t, p, q) = -d + e p,
\]

(with \(a, c, d, e\) positive constants), as proposed by Vito Volterra [30] in his pioneering work (see also [6]). Subsequently, many variants and extensions were considered by different authors (see, e.g., [2], [17], [23]). In particular, periodic or almost periodic nonautonomous Kolmogorov systems have been proposed in more recent years in order to take into account the possibility of time-varying parameters (see the references below). Here, as in [3]–[5], [8], [10]–[14], [19]–[22], [24], [26]–[29], [32]–[34], we study the case in which the coefficients are periodic functions of the time variable.

*work performed under the auspices of GNAFA-CNR and supported by MURST (40% and 60% funds).

Keywords: Positive periodic solutions, Kolmogorov systems, Lotka-Volterra equations, continuation theorem.

AMS Subject Classifications: Primary 34C25, Secondary 92A17.
having a common period $T > 0$. This situation usually occurs for the dynamics of populations living in a periodic environment, where a typical model of Lotka-Volterra prey-predator system takes the form

$$ P(t, p, q) = a(t) - b(t)p - c(t)q, \quad Q(t, p, q) = -d(t) + e(t)p - f(t)q, \quad (2) $$

with $a, b, c, d, e, f$ continuous, $\langle a \rangle > 0$, $\langle d \rangle > 0$, $b, f$ non-negative and $c, e$ positive (see [10]). Note that with respect to the Volterra’s equation, now some logistic term $t$.

Let $P_m$ be uniformly positive periodic solution(s) is obtained under the basic assumption of a logistic growth for the prey population that is, requiring the positivity of $b$ (further conditions have to be considered too). On the other hand, if one takes $b \equiv 0$ and $f \equiv 0$ in (2), so that

$$ P(t, p, q) = a(t) - c(t)q, \quad Q(t, p, q) = -d(t) + e(t)p, \quad (3) $$

with $a, c, d, e$ positive and continuous functions of the same period, in order to have a generalization of the Volterra’s model with periodic coefficients, then there is no hope to obtain a compact attractor in $(\mathbb{R}^+)^2$, as a simple analysis for the case of constant coefficients shows. In this situation, like in [12], [22], one could try to prove at least the existence of positive $T$-periodic solutions and find a priori bounds for such solutions. In particular, let us recall that in [14, Theorem 3] the following result was obtained for the special case when $P = P(t, q)$ and $Q = Q(t, p)$ in (1):

Let $P_\infty, Q_\infty : \mathbb{R} \to \mathbb{R}$ be continuous and $T$-periodic functions such that

$$ \limsup_{y \to +\infty} P(t, y) \leq P_\infty(t), \quad \liminf_{x \to +\infty} Q(t, x) \geq Q_\infty(t), $$

uniformly in $t \in [0, T]$. Then

$$ p' = pP(t, q), \quad q' = qQ(t, p), \quad (4) $$

has at least one positive $T$-periodic solution (and all the positive $T$-periodic solutions of (4) are contained in a compact subset of $(\mathbb{R}^+)^2$) provided that

$$ \int_0^T P(t, 0) \, dt > 0 > \int_0^T P_\infty(t) \, dt, \quad \int_0^T Q(t, 0) \, dt < 0 < \int_0^T Q_\infty(t) \, dt. $$

If, in addition, $P(t, \cdot)$ is strictly decreasing or $Q(t, \cdot)$ is strictly increasing, for all $t$, then there is an index $m^* \geq 2$ such that for every $m \geq m^*$, equation (4) has at least one positive subharmonic solution $(p_m, q_m)$ of order $m$ such that $\lim_{m \to +\infty} m = \lim_{m \to +\infty} q_m = 0$, $\lim_{m \to +\infty} P_m = \lim_{m \to +\infty} q_m = +\infty$.  

---

104  
T. DING, H. HUANG, F. ZANOLIN
The plan of this article is the following. We prove a result of existence and boundedness of positive periodic solutions for (1) (Theorem 1) under some assumptions which are meaningful in view of the application to some “ecological” models. In particular, if we adapt our main result to the case of (2) we obtain a corollary which can be applied without any special assumption on the logistic coefficient b. Thus, we generalize and unify at the same time some classical [10] and recent [12], [14] existence results. We point out that the general assumptions we consider on P and Q allow us to apply our main result to conservative systems and dissipative systems as well. Thus we cannot guarantee existence of subharmonic solutions like in [12]-[14], nor the existence of a compact attractor in \((\mathbb{R}^+)^2\) like in [7], [29] and other articles dealing with “persistence”. This point will be illustrated and commented by means of some simple examples (see Remark 2). Our main existence result follows from topological degree via a priori bounds for the \(T\)-periodic solutions of a one-parameter family of equations in which system (1) will be embedded. More precisely, we deform continuously equation (1) to an Hamiltonian system of the form

\[ u' = A(t, v), \quad v' = B(t, u), \]

with \(u = \log p, v = \log q\) and \((A, B)\) satisfying suitable assumptions for the validity of [14, Theorem 1]. In this manner, we can exploit some informations about the coincidence degree previously obtained in [14] and prove our result in a more direct way.

For the reader’s convenience, we recall now some basic tools in the frame of Mawhin’s coincidence degree that we adapt to the present setting, borrowing notations and terminology from [25]. Let \(Z = Z(t, z, \lambda) : \mathbb{R} \times (\mathbb{R}^+)^2 \times [0, 1] \to \mathbb{R}^2\) be a continuous function which is \(T\)-periodic in its first variable and consider the problem

\[
\begin{aligned}
z' &= Z(t, z, \lambda) \\
z(t) &= \text{periodic and positive.}
\end{aligned}
\] (5)

For each \(\lambda \in [0, 1]\), we can write (5) as a coincidence equation of the form \(Lz = N_\lambda z\), in the Banach space \(C_T\) of the continuous and \(T\)-periodic functions \(\mathbb{R} \to \mathbb{R}^2\), endowed with the \(\| \cdot \|_\infty\)-norm. Here \(L : C_T \supset \text{dom} \ L \to C_T\) is the linear differential operator \(z \mapsto z'\), while \(N_\lambda : C_T \to C_T\) is the superposition operator \(z \mapsto Z(\cdot, z, \lambda)\) (if necessary we can extend \(Z\) by continuity and periodicity to \(\mathbb{R} \times (\mathbb{R}^+)^2 \times [0, 1]\) in order to have \(N_\lambda\) defined on all \(C_T\)). For any \(\varepsilon \in ]0, 1]\) we also define

\[
\Omega(\varepsilon) = \{ z = (x, y) \in C_T : \varepsilon < x(t) < \varepsilon^{-1} \text{ and } \varepsilon < y(t) < \varepsilon^{-1}, \forall t \in [0, T] \}. \]

If we find a compact subset \(\mathcal{R}\) of \((\mathbb{R}^+)^2\) such that

\[
\forall z(\cdot) \text{ solution of (5) : } z(t) \in \mathcal{R}, \quad \forall t \in [0, T],
\] (6)

holds for some \(\lambda \in [0, 1]\), then, by excision, the coincidence degree \(D_L(L - N_\lambda, \Omega(\varepsilon))\) is well defined and constant with respect to \(\varepsilon\) for \(\varepsilon > 0\) sufficiently small (see [25, Proposition II.1]). Hence, we can define the index

\[
i_\lambda(Z) := \lim_{\varepsilon \to 0^+} D_L(L - N_\lambda, \Omega(\varepsilon)).\]

A standard consequence of the invariance under homotopy and existence property of the degree (see [25, pages 15-16]) reads as follows.
Lemma 1. Suppose that there is a compact set $\mathcal{R} \subset (\mathbb{R}^+)^2$ such that (6) holds for each $\lambda \in [0, 1]; i_0(\mathcal{Z}) \neq 0$. Then equation $z' = Z(t, z, 1)$ has at least one $T$-periodic solution with $z(t) \in (\mathbb{R}^+)^2$, for all $t \in [0, T]$.

See [25] and the references therein and [16] for various applications of Lemma 1. See also [25, Chapter 3] and [9] for concrete examples of computation of $i_0(\mathcal{Z})$. We notice that assuming $i_0(\mathcal{Z}) \neq 0$, we implicitly suppose that $i_0(\mathcal{Z})$ is defined, that is, (6) holds for $\lambda = 0$.

2. Main results. Let $\mathcal{P}, \mathcal{Q} : \mathbb{R} \times (\mathbb{R}^+)^2 \to \mathbb{R}$ be continuous functions which are $T$-periodic in their first variable. Throughout this section we assume there is a continuous and $T$-periodic function $p_0 : \mathbb{R} \to \mathbb{R}^+$ such that any possible positive $T$-periodic solution $u$ of

$$u' = u\mathcal{P}(t, u, 0),$$

satisfies

$$u(t) \geq p_0(t), \quad \forall t \in [0, T].$$

Note that if (7) does not possess positive $T$-periodic solutions, then we can choose for $p_0$, an arbitrarily large positive constant. On the other hand, if $\int_0^T \mathcal{P}(t, 0, 0) dt > 0$ and there are $d > 0$ and a continuous and $T$-periodic function $\gamma(\cdot)$ with $\int_0^T \gamma < 0$ such that $\mathcal{P}(t, x, 0) \leq \gamma(t)$ for all $t \in [0, T]$ and $x \geq d$, then the set of positive $T$-periodic solutions of (7) is nonempty, compact and it has a minimum (cf. [32], [33]). In this case, $p_0$ is precisely such a minimal positive function.

Let us define

$$P_0(t) := \mathcal{P}(t, 0, 0)$$

and assume further there are continuous and $T$-periodic functions $A(\cdot), P_\infty(\cdot), Q_0(\cdot)$ and $Q_\infty(\cdot)$ such that

$$\limsup_{x \to +\infty} \mathcal{P}(t, x, y) \leq A(t), \quad \text{uniformly in} \quad (t, y) \in [0, T] \times \mathbb{R}_+,$$

$$\limsup_{y \to +\infty} \mathcal{P}(t, x, y) \leq P_\infty(t), \quad \text{uniformly in} \quad (t, x) \in [0, T] \times \mathbb{R}_+,$$

$$Q(t, 0, y) \leq Q_0(t), \quad \forall (t, y) \in [0, T] \times \mathbb{R}_+,$$

$$Q(t, x, 0) \geq Q_\infty(t), \quad \forall x \geq p_0(t), \quad \forall t \in [0, T].$$

If (7) has no positive $T$-periodic solutions, then we consider (11) to hold provided that $Q(t, x, 0) \geq Q_\infty(t)$ for sufficiently large $x > 0$. In this case, we can equivalently replace (11) by assuming $\liminf_{x \to +\infty} Q(t, x, 0) \geq Q_\infty(t)$, uniformly for $t \in [0, T]$.

With the above positions, we can state the following.

Theorem 1. Suppose that

$$\forall D > 0, \quad \sup \{Q(t, x, y) : (t, y) \in [0, T] \times \mathbb{R}_+, 0 \leq x \leq D\} < +\infty$$

and for each $K > 0$ there are $M_K > 0$ and a continuous and $T$-periodic function $Q_K(\cdot)$ with $(Q_K) > 0$ such that

$$Q(t, x, y) \geq Q_K(t), \quad \forall t \in [0, T], \ x \geq M_K, \ 0 \leq y \leq K.$$
Assume further that
\[ \sup \{ |Q_K| : K > 0 \} < +\infty. \] (13)
Then there is a compact set in \((\mathbb{R}^+)^2\) containing all the possible positive \(T\)-periodic solutions of system (1) and (1) has at least one positive \(T\)-periodic solution, provided that
\[ \langle P_0 \rangle > 0 > \langle P_\infty \rangle, \quad \langle Q_0 \rangle < 0 < \langle Q_\infty \rangle. \] (14)

Before starting with the proof of Theorem 1, we give a simple corollary which applies to the case when the function \(Q\) does not depend on the \(q\)-variable. A similar case was also considered in [15], [18], but we point out that here we don’t assume any monotonicity condition like in [15], [18] on the functions \(P\) and \(Q\).

Suppose that \(Q(t, x, y) = Q(t, x)\), so that equation (1) reduces to
\[
\begin{align*}
p' &= pP(t, p, q) \\
q' &= qQ(t, p)
\end{align*}
\] (15)
and also define \(Q_0(t) := Q(t, 0, 0)\), so that (10) holds. Observe that now (11) writes as
\[ Q(t, x) \geq Q_\infty(t), \quad \forall \ x \geq p_0(t), \ \forall \ t \in [0, T]. \] (16)

Then we have that assumption (12) is an obvious consequence of the continuity of \(Q\), while for any \(K > 0\) we can take \(M_K = \max_{[0,T]} p_0\) and \(Q_K = Q_\infty\) and thus have (13) satisfied. Then we can conclude with the following:

**Corollary 1.** Suppose that \(P\) is upper bounded in \([0, T] \times (\mathbb{R}^+)^2\) and (9), (16) and (14) hold. Then there is a compact set in \((\mathbb{R}^+)^2\) containing all the possible positive \(T\)-periodic solutions of (15) and system (15) has at least one positive \(T\)-periodic solution.

**Proof of Theorem 1.** First of all, we adapt some of our assumptions to a form which is more directly applicable to the computations we have to perform below. Accordingly, from (8), (9) and the second inequality in (14) take a constant \(M > 0\) and two continuous and \(T\)-periodic functions \(\alpha(\cdot) \geq 0\) and \(\tilde{P}_\infty(\cdot)\) such that
\[ P(t, x, y) \leq \alpha(t), \quad \forall \ (t, x, y) \in [0, T] \times (\mathbb{R}^+)^2 \]
and
\[ P(t, x, y) \leq \tilde{P}_\infty(t), \quad \forall \ y \geq M, \ \forall \ (t, x) \in [0, T] \times \mathbb{R}^+, \quad \text{with} \ \langle \tilde{P}_\infty \rangle < 0. \]

Then, let us set, for \(z = (x, y) \in (\mathbb{R}^+)^2\),
\[ Z(t, z, \lambda) := (xP(t, \lambda x, y), yQ(t, x, \lambda y)), \]
so that
\[ Z(t, z, 0) = (xP(t, 0, y), yQ(t, x, 0)). \]
Now we have \(P(t, x, 0) \leq \alpha(t)\), for all \(t \in [0, T]\) and \(x \geq 0\), as well as
\[ \limsup_{y \to +\infty} P(t, 0, y) \leq P_\infty(t) \quad \text{and} \quad \liminf_{x \to +\infty} Q(t, x, 0) \geq Q_\infty(t), \]
uniformly in \( t \). Recall also that (14) gives

\[
\int_0^T P(t,0,0) \, dt > 0 > \int_0^T P_\infty(t) \, dt, \quad \text{and} \quad \int_0^T Q(t,0,0) \, dt < 0 < \int_0^T Q_\infty(t) \, dt.
\]

Thus we are in the same situation as in [14, Theorem 3] for the perturbed conservative system

\[
p' = pP(t,0,q), \quad q' = qQ(t,p,0),
\]

(which corresponds to \( z' = \mathcal{Z}(t,z,0) \)) and therefore we know that all its positive \( T \)-periodic solutions are contained in a compact subset of \((\mathbb{R}^+)^2\) and also (cf. [14, proof of Theorem 1])

\[
i_0(\mathcal{Z}) = 1.
\]

Hence, thanks to Lemma 1 we have only to find “a priori bounds” in \((\mathbb{R}^+)^2\) for the \( T \)-periodic solutions of

\[
\begin{aligned}
p' &= pP(t,\lambda p,q) \\
q' &= qQ(t,p,\lambda q)
\end{aligned} \quad \lambda \in [0,1], \quad (p(t),q(t)) \in (\mathbb{R}^+)^2, \forall t \in \mathbb{R}. \quad (17)
\]

This result will be attained through some steps. From now on in the rest of the proof, \((p,q)\) is any \( T \)-periodic solution to (17) for some \( \lambda \in [0,1] \). Note that we assume \( p(t) > 0 \) and \( q(t) > 0 \) for all \( t \in \mathbb{R} \).

**Step 1.** \( \min q = q < M \). Indeed, if \( q(t) \geq M \) for all \( t \in \mathbb{R} \), then from the first equation in (17), we have

\[
0 = \int_0^T \left( p'/p \right) = \int_0^T P(t,\lambda p(t),q(t)) \, dt \leq \int_0^T \tilde{P}_\infty < 0,
\]

a contradiction.

**Step 2.** \( \exists L > 0 : \min p = p < L \). According to (13), let us take a positive constant \( C^* \) such that \( C^* > \sup \{|Q_K| : K > 0\} \) and set

\[
H := 1 + M \exp C^*, \quad L := M_H.
\]

Assume by contradiction that \( p(t) \geq L \), for all \( t \in \mathbb{R} \). If this is the case, we claim that we must have \( \max q \lambda q > H \). Otherwise, if \( \lambda q(t) \leq H \) for all \( t \), we obtain from the second equation in (17) that

\[
0 = \int_0^T \left( q'/q \right) = \int_0^T Q(t,p(t),\lambda q(t)) \, dt \geq \int_0^T Q_H > 0,
\]

which is absurd.

So we know that \( \min \lambda q \leq q < M \) (from Step 1) and \( \max \lambda q > H \) (just proved). By the periodicity of \( \lambda q \) we can find an open interval \([t_1,t_2]\) with \( t_2 - t_1 < T \), such that \( M < \lambda q(t) < H \) for all \( t \in I \) and \( \lambda q(t_1) = H, \lambda q(t_2) = M \). For all \( t \in I \), now we have

\[
\lambda q'(t)/\lambda q(t) = q'(t)/q(t) = Q(t,p(t),\lambda q(t)) \geq Q_H(t).
\]
Hence, integrating over $I$ we obtain
\[
\log(H/M) = - \int_{t_1}^{t_2} \left( \lambda q'(t)/\lambda q(t) \right) dt \leq \int_{t_1}^{t_2} -Q_H(t) dt \leq |Q_H|_1 < C^* ,
\]
that is, $H < M \exp C^*$. This contradicts the choice of $H$ and proves Step 2.

**Step 3.** $\exists D > 0 : \max p = p < D$. Indeed, we have just seen that there is $t_0 \in [0, T]$ such that $p(t_0) < L$. By the upper bound on $P$ and the first equation in (17) we have that $p'(t)/p(t) \leq \alpha(t)$ and hence, $p(t) \leq p(t_0) \exp \left| \int_{t_0}^{t} \alpha(s) ds \right|$ for all $t \geq t_0$. Then, using the periodicity of $p(\cdot)$, we find $p(t) < L \exp \left| \alpha(1) := D, \right|$ for all $t \in \mathbb{R}$.

**Step 4.** $\exists C > 0 : \max q = q < C$. Since $p(t) < D$ for all $t \in \mathbb{R}$, by the assumption (12) we know that there is a positive constant $E$ such that $Q(t, p(t), \lambda q(t)) \leq E$, for all $t \in \mathbb{R}$. Then, using Step 1 and the second equation in (17), we obtain $q < M \exp(ET) := C$.

**Step 5.** $\exists \delta > 0 : q < \delta$. Indeed, suppose by contradiction that for a sequence $(p_n, q_n)$ of positive $T$-periodic solutions of (17) for $\lambda = \lambda_n \in [0, 1]$, one has $q_n \to 0$ uniformly in $t \in \mathbb{R}$. Since from the first equation of (17) we have $\int_0^T P(t, \lambda_n p_n(t), q_n(t)) dt = 0$, and $\int_0^T \mathcal{P}(t, 0, 0) dt = T(p_0) > 0$, it is straightforward to check that there is $\varepsilon_0 > 0$ such that $\max \lambda_n p_n \geq \varepsilon_0$, for all $n$. Now, as

\[
\lambda_n p_n'(t)/\lambda_n p_n(t) = p_n'(t)/p_n(t) = \mathcal{P}(t, \lambda_n p_n, q_n(t)) \leq \alpha(t),
\]

we easily obtain that there is $\varepsilon > 0$ such that $\min \lambda_n \geq \varepsilon$ for all $n$ (use the periodicity of $\lambda_n p_n(\cdot)$ and take $\varepsilon = \varepsilon_0 \exp(-|\alpha(1)|)$). By Step 3 we know that $\varepsilon \leq \lambda_n p_n \leq D$, for all $t \in \mathbb{R}$ and each $n$. On the other hand, we have that $0 < q_n(t) \leq 1$ for all $t$ and each $n$ sufficiently large, say $n \geq n^*$ (as $q_n \to 0$). Hence, for all $t \in \mathbb{R}$ and $n \geq n^*$, $|\varepsilon_0(t)| \leq K$, where

\[
K = \sup \{ |x \mathcal{P}(t, x, y)| : t \in [0, T], 0 \leq x \leq D, 0 \leq y \leq 1 \}.
\]

Ascoli - Arzelà theorem now implies that $(\lambda_n p_n)_n$ has a subsequence converging uniformly to a positive continuous and $T$-periodic function $z(\cdot)$. For notational convention, here and below, we denote the converging subsequence with the same symbols like the original one. Moreover, from $\lambda_n p_n(t) = \lambda_n p_n(t) \mathcal{P}(t, \lambda_n p_n(t), q_n(t))$, we obtain that $z(\cdot)$ is continuously differentiable and it satisfies $z'(t) = z(t) \mathcal{P}(t, z(t), 0)$, for all $t \in \mathbb{R}$. Hence $z(\cdot)$ is a positive $T$-periodic solution of (7) and from our assumptions we conclude that $z(t) \geq p_0(t)$, for all $t \in \mathbb{R}$. Recall now Step 3 according to which we know that $0 < p_0(t) < D$, for all $t$ and $n$ and $|p_n'(t)| = |p_n(t)\mathcal{P}(t, \lambda_n p_n(t), q_n(t))| \leq K$ for all $t$ and $n \geq n^*$. Hence, repeating the above argument, it is easy to see that there are $\bar{p} \leq \bar{p}(t) \leq D$ and $\lambda \in [0, 1]$ such that, passing to the limit on a common subsequence of indexes (which will be common also to the subsequence converging to $z$), we finally have $p_n \to \bar{p}$ uniformly in $\mathbb{R} \ \text{and} \ \lambda_n \to \bar{\lambda}$. Then, $\bar{\lambda}\bar{p}(t) = z(t)$ for all $t$, so that $0 < \bar{\lambda} \leq 1$ and thus $\bar{p}(t) = z(t)/\bar{\lambda} \geq p_0(t)$, for all $t \in \mathbb{R}$. On the other hand, from the second equation in (17) we have $\int_0^T Q(t, p_n(t), \lambda_n q_n(t)) dt = 0$ and hence, passing to the limit on the above subsequence, we have $\int_0^T Q(t, \bar{p}(t), 0) dt = 0$. But now we can use condition (11) according to which $Q(t, \bar{p}(t), 0) \geq Q_{\infty}(t)$, and thus we obtain $\int_0^T Q_{\infty} \leq 0$. This contradicts the last inequality in (14) and thus our result is proved.
Step 6. \( \exists \sigma > 0 : q > \sigma \). This follows from an easy inequality, as \( \overline{q} > \delta \) and \( |q'/q| \) is bounded by
\[
\sup\{|Q(t,x,y)| : t \in [0,T], \ 0 \leq x \leq D, \ 0 \leq y \leq C\}.
\]

Step 7. \( \exists \varepsilon > 0 : \overline{p} > \varepsilon \). Indeed, if by contradiction there is a sequence \((p_n,q_n)\) of positive \(T\)-periodic solutions of (17) for \( \lambda = \lambda_n \in ]0,1[\), with \( p_n \to 0 \) uniformly in \( t \in \mathbb{R} \), then, as \( 0 < \lambda_n q_n(t) \leq C \) for all \( t \), arguing as in Step 5, by the Ascoli - Arzelá theorem and \( \lambda_n q_n(t) = \lambda_n q_n(t)Q(t,p_n(t),\lambda_n q_n(t)) \), we can find a subsequence of \((\lambda_n q_n)_n\) converging uniformly to a non-negative \(T\)-periodic function \( \tilde{y}(\cdot) \). Using \( \int_0^T Q(t,p_n(t),\lambda_n q_n(t)) dt = 0 \) and passing to the limit on this subsequence, we obtain \( \int_0^T Q(t,0,\tilde{y}(t)) dt = 0 \). Then, as \( Q(t,0,\tilde{y}(t)) \leq Q_0(t) \), for all \( t \), we conclude that \( \int_0^T Q_0 \geq 0 \), a contradiction to the third inequality in (14).

Step 8. \( \exists \eta > 0 : p > \eta \). This is like in Step 6.

At the end, we have proved that any solution \((p,q)\) of (17) satisfies \( 0 < \eta < p(t) < D \) and \( 0 < \sigma < q(t) < C \), for all \( t \in \mathbb{R} \). On the other hand, as pointed out at the beginning of the proof, for \( \lambda = 0 \), we have already the result in [14]. So all the assumptions of Lemma 1 are satisfied and therefore equation (1) has at least one \(T\)-periodic solution. Moreover, we have proved that there is a compact set \( \{x \in (\mathbb{R}^+)^2 \text{ which contains all the positive } T\text{-periodic solutions of (1)} \} . \)

Remark 1. (i) If \( \mathcal{P} = \mathcal{P}(t,q) \) and \( \mathcal{Q} = \mathcal{Q}(t,p) \), many of the assumptions in Theorem 1 are vacuously satisfied. In this case, Theorem 1 is exactly the same like the first part of the statement in Theorem 3 of [14]. From this point of view, Theorem 1 generalizes to the Kolmogorov system (1) the existence result for positive harmonic solutions obtained in [14]. (ii) In the case that the equation \( p' = \mathcal{P}(t,p,0) \) does not possess positive \(T\)-periodic solutions, then the choice of the function \( p_0(\cdot) \) is free. Hence, with respect to (11) we have only to require that \( Q(t,x,0) \geq Q_\infty(t) \) for \( x \) sufficiently large, say \( x \geq M \). (iii) The assumptions of Theorem 1 fit rather naturally when applied to prey–predator equations. To show this aspect, we present the following example.

Example 1. Consider the equation
\[
\begin{align*}
p' &= p(a(t) - b(t)p - c(t)q) \\
q' &= q(-d(t) + e(t)p - f(t)q)
\end{align*}
\]
(18)
where \( a,d : \mathbb{R} \to \mathbb{R} \) and \( b,c,e,f : \mathbb{R} \to \mathbb{R}_+ = [0, +\infty) \) are continuous functions which are all periodic of a common period \( T > 0 \). We also suppose that
\[
\langle a \rangle > 0, \quad \langle d \rangle > 0.
\]

Note that this is a typical assumption for the growth of the prey population \( p \) in absence of the predator \( q \) and the growth of \( q \) in absence of \( p \). In order to apply Theorem 1 to equation (18) we observe that \( \mathcal{P} \) and \( \mathcal{Q} \) are like in (2). Now, let us consider the assumptions of our main result. We see that (12) is always true and (8) is trivially satisfied with \( A(t) = \langle a(t) \rangle \). Moreover \( P_0 = a \) and we can take \( Q_0 = -d \), so that \( \langle P_0 \rangle > 0 \) and \( \langle Q_0 \rangle < 0 \) follow from (19). To have (9) satisfied by a suitable function \( P_\infty \) satisfying the second inequality in (14) it is sufficient to require
\[
\langle c \rangle > 0
\]
(20)
which, as $c \geq 0$, is the same like $\max c > 0$ or $c \neq 0$. On the other hand, if we assume

$$\text{either } f \equiv 0 \text{ and } \langle c \rangle > 0, \text{ or } \min c > 0$$  \hspace{1cm} (21)

then either we are in the same situation like in Corollary 1 (case $f \equiv 0$), or for each $K > 0$ we can take $M_K = (1 + d + f K)/e$ and $Q_K = 1$ in order to have (13) satisfied. Finally, it remains to consider equation (7) which now reads as

$$u' = u(a(t) - b(t)u).$$  \hspace{1cm} (22)

An elementary analysis of this equation with $\langle a \rangle > 0$ and $b \geq 0$, shows that there are no positive $T$-periodic solutions if $b \equiv 0$ and there is exactly one positive and $T$-periodic solution $w(\cdot)$ which is globally asymptotically stable with respect to $\mathbb{R}^+$ if $\langle b \rangle > 0$. The explicit form of $w$ is given by

$$w(t) = \exp \int_0^t a(s) \, ds \, w(0) - 1 + \int_0^t \exp \int_0^s a(\xi) \, d\xi \, ds,$$

where

$$w(0) = \left( \exp \int_0^T a(t) \, dt - 1 \right) / \int_0^T \exp \int_0^t a(s) \, ds \, dt.$$

In fact, $z(t) = w(t)^{-1}$ is the unique $T$-periodic solution of the linear equation $z' = b(t) - a(t)z$ which can be solved explicitly.

Therefore, we have two possibilities to discuss: $b \equiv 0$ and $b \neq 0$. In the former case we can take $p_0$ an arbitrary large constant and have (11) and the last inequality in (14) fulfilled by a suitable choice of $Q_\infty$, as a consequence of (21). In the latter case, we can take $p_0 = w$ and, using the fact that in this example $Q(t, \cdot, 0)$ is nondecreasing, we can choose $Q_\infty(t) = -d(t) + e(t)w(t)$. Thus we can conclude as follows.

**Corollary 2.** Suppose that (19), (20) (21) hold and

$$\text{either } b \equiv 0, \text{ or } \langle b \rangle > 0 \text{ and } \langle d \rangle < \langle c w \rangle,$$

where for $b \neq 0$, $w(\cdot)$ is the unique positive $T$-periodic solution of (22). Then the same conclusion of Theorem 1 holds for system (18).

Note that the case $b \equiv 0$ and $f \equiv 0$ corresponds to the Volterra prey-predator system with periodic coefficients (3) (see [12]-[14], [21], [22], [28] for some results in that direction).

**Remark 2.** Consider again equation (18) in the case that the coefficients are non-negative constants, so that we have

$$\begin{cases}
    p' = p(a - b p - c q) \\
    q' = q(-d + e p - f q)
\end{cases}$$  \hspace{1cm} (24)

For the applicability of Corollary 2 to system (24) we have to assume

$$a > 0, \ c > 0, \ d > 0, \ e > 0$$
and, either

\[ b = 0 \]

or

\[ b > 0, \quad bd < ae. \]

Note that no condition on \( f \) is required.

In the former case, if also \( f = 0 \), we have the Volterra equation and for it we know that there is a unique equilibrium point \( z^* \) in \((\mathbb{R}^+)^2\) and there is a limit positive period \( T^* \) of the orbits approaching \( z^* \) such that any other periodic solution of (24) has period larger than \( T^* \) and the period of the positive periodic solutions tends increasingly to infinity as their amplitudes increase (cf. [22], [31]). So, if \( T \leq T^* \) (with \( T^* \) computable explicitly in terms of the coefficients \( a, c, d, e \)) we have \( z^* \) as unique positive \( T \)-periodic solution of (24) and if \( T > T^* \) we have non-constant positive \( T \)-periodic solutions as well; on the other hand, we don’t have a compact attractor in \((\mathbb{R}^+)^2\) so that “permanence” does not occur. In the latter case, if also \( f = 0 \), we obtain that there is a unique equilibrium point \( z^* \) in \((\mathbb{R}^+)^2\) which is globally asymptotically stable with respect to its basin of attraction \((\mathbb{R}^+)^2\) (cf. [17]). Thus “permanence” occurs, but, on the other hand, we don’t have any other positive periodic solution (of any period). This shows that the conclusion we obtain with Theorem 1 cannot be reinforced with respect to prove the existence of a compact attractor in \((\mathbb{R}^+)^2\), like in [7] and [29] and, at the same time, we cannot prove multiplicity results of periodic solutions (harmonic or subharmonic) like in [12]-[14] and [22], as our model equation (1) contains both examples of conservative and dissipative systems.

As we already observed before, Theorem 1 is devised for the obtention of an existence result which is applicable to the case in which the dynamics of the prey population in absence of predator, given by equation (7), may be influenced or may not be influenced by some logistic growth term. Indeed, as shown in Example 1, for the corresponding single species equation (22) we can have \( b \equiv 0 \) or \( b \not\equiv 0 \) as well. Next we show how a simple change in the assumptions of Theorem 1 yields a related existence result where the presence of a self-inhibition coefficient in equation (7) can more effectively show its effects. Namely, we have the following.

**Theorem 2.** Assume conditions (8) – (12) and suppose that

\[ \langle A \rangle < 0. \quad (25) \]

Then there is a compact set in \((\mathbb{R}^+)^2\) containing all the possible positive \( T \)-periodic solutions of system (1) and (1) has at least one positive \( T \)-periodic solution, provided that (14) holds.

**Proof.** Besides the positions at the beginning of the proof of Theorem 1, we also observe that from (8) and (25) we can find a constant \( B > 0 \) and a continuous and \( T \)-periodic function \( \tilde{A}(\cdot) \) such that

\[ P(t, x, y) \leq \tilde{A}(t), \quad \forall x \geq B, \quad \forall (t, y) \in [0, T] \times \mathbb{R}_+, \quad \text{with} \quad \langle \tilde{A} \rangle < 0. \]

Then, let use set, for \( z = (x, y) \in (\mathbb{R}_+)^2 \),

\[ Z(t, z, \lambda) := \begin{cases} (xP(t, \lambda x, y), yQ(t, x, 2(\lambda - 1/2)y)), & \text{for } 1/2 \leq \lambda \leq 1 \\ (xP(t, \lambda x, y), yQ(t, x, 0)), & \text{for } 0 \leq \lambda \leq 1/2 \end{cases} \]
so that

$$Z(t, z, 0) = (xP(t, 0, y), yQ(t, x, 0)).$$

Now we repeat almost verbatim the proof of Theorem 1 taking into account that instead of equation (17) we have to consider

$$\begin{cases}
    p' = pP(t, \lambda p, q), & 1/2 < \lambda \leq 1 \\
    q' = qQ(t, p, 2(\lambda - (1/2))q), & 0 < \lambda \leq 1/2
\end{cases} \tag{26}$$

with \( (p(t), q(t)) \in (\mathbb{R}^+)^2, \forall t \in \mathbb{R} \). The only point in which some change in the proof is needed is that \( \exists \ L > 0 : \min p = \underline{p} < L \). Indeed, if \( \lambda \in [1/2, 1] \) and \( p(t) \geq 2\underline{B} \) for all \( t \in \mathbb{R} \), then \( \lambda p(t) \geq B \) and from the first equation in (26) we have

$$0 = \langle q'/p \rangle = \langle P(\cdot, \lambda p(\cdot), q(\cdot)) \rangle \leq (\bar{A}) < 0,$$

a contradiction. On the other hand, if \( \lambda \in [0, 1/2] \) and \( p(t) \geq \max \underline{p}_0 \) for all \( t \in \mathbb{R} \), then from (11) and the last equation in (26) we have

$$0 = \langle q'/q \rangle = \langle Q(\cdot, p(\cdot), 0) \rangle \geq \langle \bar{Q}_\infty \rangle > 0,$$

a contradiction. Hence the claim is proved for \( L = \max \{2\mathcal{B}, \bar{P}_0 \} \). The proof of all the other steps is just the same as above or needs only obvious changes with respect to that of Theorem 1.

□

**Example 1 (continued).** Consider again equation (18) where \( a, d : \mathbb{R} \rightarrow \mathbb{R} \) and \( b, c, e, f : \mathbb{R} \rightarrow \mathbb{R}_+ = [0, +\infty) \) are continuous functions which are all periodic of a common period \( T > 0 \). We now suppose that

$$\langle a \rangle > 0, \quad \langle b \rangle > 0, \quad \langle c \rangle > 0, \quad \langle d \rangle > 0, \quad \langle e \rangle > 0. \tag{27}$$

Since \( \langle b \rangle > 0 \), we know that equation (7) which corresponds to (22) has a unique positive and \( T \)-periodic solution \( w(\cdot) \) which is globally asymptotically stable with respect to \( \mathbb{R}_+^T \). Hence, Theorem 2 yields the following consequence.

**Corollary 3.** Suppose that (27) holds and

$$\langle d \rangle < \langle e w \rangle. \tag{28}$$

Then the same conclusion of Theorem 1 holds for system (18).

Observe that we don’t require any condition on \( f \geq 0 \). We also notice that even if there is some overlapping between Corollary 2 and Corollary 3, as well as between Theorem 1 and Theorem 2, nevertheless it is possible to give examples showing that these results are independent each other. With this respect, let us choose arbitrarily \( a : \mathbb{R} \rightarrow \mathbb{R} \) and \( b, c, e : \mathbb{R} \rightarrow \mathbb{R}_+ \) continuous, \( T \)-periodic and such that \( \langle a \rangle > 0, \langle b \rangle > 0 \) and \( \langle c \rangle > 0 \) and consider the positive and \( T \)-periodic function \( w(\cdot) \) which comes from the solvability of (22). Now define

$$e(t) = \begin{cases}
    \sin(2\pi t/T), & \text{for } kT \leq t \leq kT + (T/2) \\
    0, & \text{for } kT + (T/2) \leq t \leq (k + 1)T
\end{cases}$$

and

$$f(t) = \begin{cases}
    0, & \text{for } kT \leq t \leq kT + (T/2) \\
    -\sin(2\pi t/T), & \text{for } kT + (T/2) \leq t \leq (k + 1)T
\end{cases}$$

where \( k \in \mathbb{Z} \). Then \( e, f : \mathbb{R} \rightarrow \mathbb{R}_+ \) are continuous, \( T \)-periodic and such that \( \langle e \rangle > 0 \) and \( \langle f \rangle > 0 \). Hence, we can define

$$d(t) := e(t)w(t)/2,$$
so that \(0 < \langle d \rangle < \langle e \ w \rangle\). Now it is easy to see that, with this choice of the coefficients, Corollary 3 applies to system (18), while, neither Corollary 2, nor Theorem 1 are of use in this case. Of course, it also easy to produce examples where Corollary 2 applies while Theorem 2 does not.

**Remark 3.** Corollary 3 refines some assumptions on the coefficients of equation (18) previously obtained by Cushing [10] (see also [4], [7], [24], [29] for related conditions). Of course, we don’t claim that we do better, since in these articles more informations on the dynamics of the solutions are given, on the other hand, our result improves the above quoted ones with respect to the existence and boundedness of \(T\)-periodic solutions.

Indeed, to make a comparison with some of the preceding results, let us observe that if \(t \in \mathbb{R}\) is a point of maximum or a point of minimum of the solution \(w(t)\) of (22), then \(w'(t) = 0\) and therefore \(a(t) = b(t)w(t)\). Thus, if we further suppose that \(a(t) > 0\) and \(b(t) > 0\) for all \(t \in [0, T]\) (a condition which we don’t need in our results but we assume here for the next discussion), then we have

\[
\begin{align*}
\min_{[0, T]} \{a(t)/b(t)\} & \leq w(t) \leq \bar{w} \leq \max_{[0, T]} \{a(t)/b(t)\},
\end{align*}
\]

Hence (28) is satisfied provided that

\[
\langle d \rangle / \langle e \rangle < \min_{[0, T]} \left\{ \frac{a(t)}{b(t)} \right\}. \tag{29}
\]

Therefore, a special case of Corollary 3 yields the existence of positive \(T\)-periodic solutions for equation (18), if (29) holds, when \(a > 0\), \(b > 0\), \(c \geq 0\) and \(\langle e \rangle > 0\), \(\langle d \rangle > 0\), \(e \geq 0\) and \(\langle e \rangle > 0\), \(f \geq 0\).

On the other hand, if we suppose that \(b(t) > 0\) and \(e(t) > 0\) for all \(t \in [0, T]\), then we have

\[
\langle e \ w \rangle = \langle w \ b \ c / b \rangle \geq \langle w \ b \rangle \min_{[0, T]} \{e(t)/b(t)\}
\]

and, taking the mean value on \(w'/w = a - bw\), we also obtain \(\langle w \ b \rangle = \langle a \rangle\). Hence (28) is satisfied provided that

\[
\langle d \rangle / \langle a \rangle < \min_{[0, T]} \left\{ \frac{e(t)}{b(t)} \right\}. \tag{30}
\]

Therefore, a special case of Corollary 3 yields the existence of positive \(T\)-periodic solutions for equation (18), if (30) holds, when \(\langle a \rangle > 0\), \(\langle b \rangle > 0\), \(\langle c \rangle \geq 0\) and \(\langle e \rangle > 0\), \(\langle d \rangle > 0\), \(\langle e \rangle > 0\), \(\langle f \rangle \geq 0\). We remark that in [24, Corollary 2.1] it is required that \(\langle a(t) > \bar{a} \rangle d(t)\) for all \(t \in [0, T]\) in order to prove the existence of a positive \(T\)-periodic solution for (18), while in [4, Proposition] condition (30) is assumed. Similar hypotheses are considered in [29, Theorem 3.2] as well.

Corollary 3 may be complemented with a necessary condition for the existence of positive periodic solutions for equation (18). Namely, we have:

**Theorem 3.** Suppose that (27) holds. Then system (18) has at least one positive and \(T\)-periodic solution if and only if (28) holds, where \(w(\cdot)\) is the unique positive \(T\)-periodic solution of (22). Moreover, if \((\bar{p}, \bar{q})\) is any positive \(T\)-periodic solution of (18) then

\[
\bar{p}(t) < w(t), \quad \forall t \in \mathbb{R}.
\]
Furthermore, as (result on differential inequalities (cf. [20]) we know that \( \tilde{v} \) continuity assumptions on \( P \)

Remark 4

sufficient condition, just apply Corollary 3. and therefore (28) holds. Thus we have proved the necessary condition. For the

We have thus proved that

\[ \tilde{p}(s) = v(s) < v(s + T). \]

From here, by induction, it is easy to see that the sequence \( (v(s + nT))_n \) is strictly increasing (arguing like in the proof of the classical Massera’s theorem). On the other hand, \( v(\cdot) \) is a solution of (22) and we already know that \( w(\cdot) \) is the globally asymptotically stable \( T \)-periodic solution of (22), so that we obtain that

\[ \lim_{n \to -

We have thus proved that

\[ \tilde{p}(s) < w(s), \quad \text{for any } s \in [0, T]. \]

Now, from the second equation in (18) we have

\[ 0 = T^{-1} \int_0^T (-d(t) + e(t)\tilde{p}(t) - f(t)\tilde{q}(t)) \, dt \leq -\langle d \rangle + \langle e \tilde{p} \rangle < -\langle d \rangle + \langle e \cdot w \rangle \]

and therefore (28) holds. Thus we have proved the necessary condition. For the
sufficient condition, just apply Corollary 3. \( \square \)

Remark 4. (i) In all the article we have confined ourselves to show the applicability of Theorem 1 and Theorem 2 only to the model equation (18). Our choice has been motivated by the interest in finding some simple conditions on the coefficients for the validity of the main results as well as to the possibility of making a comparison with some preceding papers dealing with the prey - predator Lotka - Volterra equations.

It is clear that the range of applicability of our theorems is much wider and in particular there are various Kolmogorov systems of “ecological” interest where our results can be successfully employed.

(ii) In the proofs of Theorem 1 and Theorem 2 we use only integral conditions on \( P \) and \( Q \). Thus it is not difficult to extend all the above results by relaxing the continuity assumptions on \( P \) and \( Q \) to Caratheodory conditions (see [20], [25]). Of course, some of the hypotheses we used would require now a slight change, like

\[ \mathbf{PERIODIC SOLUTIONS OF LOTKA—VOLTERRA EQUATIONS 115} \]
for instance to replace systematically “for all” $t$ with “for almost every” $t$ in the inequalities concerning $P$ and $Q$, to relax the regularity of the limiting functions $A, P_0, P_\infty, Q_0, Q_\infty$ and $Q_K$, or to bound some sup{$\cdots$} by an appropriate $L^1$-function instead of a constant (in particular, it will be necessary to modify suitably condition (12)).

Acknowledgement. This paper was initiated during a visit of the third author at the Peking University and concluded in occasion of a visit of the first author at the University of Udine. The authors thanks these institutions for their kind hospitality.

REFERENCES

[1] S. Ahmad, On almost periodic solutions of the competing species problem, Proc. Amer. Math. Soc., 102 (1988), 855–861.
[2] F. Albrecht, H. Gatzke, A. Haddad and N. Wax, The dynamics of two interacting populations, J. Math. Anal. Appl., 46 (1974), 658-670.
[3] C. Alvarez and A.C. Lazer, An application of topological degree to the periodic competing species model, J. Austral. Math. Soc., Ser. B, 28 (1986), 202-219.
[4] Z. Amine and R. Ortega, A periodic prey - predator system, J. Math. Anal. Appl., 185 (1994), 477-489.
[5] M. Bardi, Predator–prey models in periodically fluctuating environments, J. Math. Biol., 12 (1981), 127-140.
[6] M. Braun, “Differential Equations and Their Applications,” Springer–Verlag, New York, 1975.
[7] T.A. Burton and V. Hutson, Permanence for non-autonomous predator–prey systems, Differential and Integral Equations, 4 (1991), 1269-1280.
[8] G.J. Butler and H.I. Freedman, Periodic solutions of a predator–prey system with periodic coefficients, Math. Biosci., 55 (1980), 27-38.
[9] A. Caplietto, J. Mawhin and F. Zanolin, Continuation theorems for periodic perturbations of autonomous systems, Trans. Amer. Math. Soc., 329 (1992), 41-72.
[10] J.M. Cushing, Periodic time - dependent predator–prey systems, SIAM J. Appl. Math., 32 (1977), 82-95.
[11] J.M. Cushing, Two species competition in a periodic enviroment, J. Math. Biol., 10 (1980), 385-400.
[12] T. Ding and F. Zanolin, Harmonic solutions and subharmonic solutions for periodic Lotka–Volterra systems, pp. 55-65 in “Dynamical Systems–Proc. Nankay Conf. Program” (ed. S. Liao, Y. Ye and T. Ding, Tianjian, 1990-91), World Scientific, Singapore, 1993.
[13] T. Ding and F. Zanolin, Subharmonic solutions of second order nonlinear equations: a time–map approach, Nonlinear Analysis, 20 (1993), 509-532.
[14] T. Ding and F. Zanolin, Periodic solutions and subharmonic solutions for a class of planar systems of Lotka–Volterra type, in “Proceedings of the First WCNA–Tampa FL.,” 1992, to appear.
[15] A.M. Fink, A two-dimensional Opial theorem and a predator–prey model, Nonlinear Analysis, 16 (1991), 55-59.
[16] A. Fonda and P. Habets, Periodic solutions of asymptotically positively homogeneous differential equations, J. Differential Equations, 81 (1989), 68-97.
[17] T.C. Gard, Uniform persistence in multispecies population models, Math. Biosci., 85 (1987), 93-104.
[18] J.A. Gatica and J. W-H. So, Predator–prey models with almost periodic coefficients, Applicable Analysis, 27 (1988), 143-152.
[19] K. Gopalsamy, Global asymptotic stability in a periodic Lotka–Volterra system, J. Austral. Math. Soc., Ser. B, 27 (1985), 66-72.
[20] J.K. Hale, “Ordinary Differential Equations,” R.E. Krieger Publishing Co., Huntington, New York, 1980.
[21] A.H. Hausrath, Periodic integral manifolds for periodically forced Volterra–Lotka equations, J. Math. Anal. Appl., 87 (1982), 474-488.
[22] A.H. Hausrath and R.F. Manásevich, *Periodic solutions of a periodically perturbed Lotka–Volterra equation using the Poincaré–Birkhoff theorem*, J. Math. Anal. Appl., 157 (1991), 1-9.

[23] A.N. Kolmogorov, *Sulla teoria di Volterra della lotta per l'esistenza*, Giornale dell'Istituto Italiano degli Attuari, 7 (1936), 74-80.

[24] Z. Ma and W. Wang, *Asymptotic behavior of predator–prey system with time dependent coefficients*, Applicable Analysis, 34 (1989), 79-90.

[25] J. Mawhin, “Topological Degree Methods for Nonlinear Boundary Value Problems,” CBMS, Reg. Conf. Ser. in Math., vol. 40, Amer. Math. Soc., Providence, R.I., 1979.

[26] P. de Mottoni and A. Schiaffino, *Competition systems with periodic coefficients: a geometric approach*, J. Math. Biol., 11 (1981), 319-345.

[27] G.H. Pimbley, Jr., *Periodic solutions of predator–prey equations simulating an immune response I*, Math. Biosci., 20 (1974), 27-51.

[28] P. Táboas, *Periodic solutions of a forced Lotka–Volterra equation*, J. Math. Anal. Appl., 124 (1987), 82-97.

[29] A. Tineo, *On the asymptotic behavior of some population models*, J. Math. Anal. Appl., 167 (1992), 516-529.

[30] V. Volterra, “Leçon sur la Théorie Mathématique de la Lutte Pour la Vie,” Gauthier–Villars, Paris, 1931.

[31] J. Waldvogel, *The period of the Lotka–Volterra system is monotonic*, J. Math. Anal. Appl., 114 (1986), 178-184.

[32] F. Zanolin, *Permanence and positive periodic solutions for Kolmogorov competing species systems*, Results in Math., 21 (1992), 224-250.

[33] F. Zanolin, “Continuation Theorems for the Periodic Problem via the Translation Operator,” preprint, Udine, 1994.

[34] X-Q. Zhao, *The qualitative analysis of N-species Lotka–Volterra periodic competition systems*, Math. Comput. Modelling, 15 (1991), 3-8.

Email addresses: dingtr@bepc2.ihep.ac.cn, zanolin@dimi.uniu.it

Received October, 1994.