ON THE APPLICABILITY OF THE POINCARÉ–BIRKHOFF TWIST THEOREM TO A CLASS OF PLANAR PERIODIC PREDATOR-PREY MODELS

Julián López-Gómez and Eduardo Muñoz-Hernández

Universidad Complutense de Madrid
Instituto de Matemática Interdisciplinar (IMI)
Departamento de Análisis Matemático y Matemática Aplicada
Plaza de las Ciencias 3, 28040 Madrid, Spain

Fabio Zanolin*

Università degli Studi di Udine
Dipartimento di Scienze Matematiche, Informatiche e Fisiche
Via delle Scienze 2016, 33100 Udine, Italy

(Communicated by Thomas Bartsch)

Abstract. This paper studies the existence of subharmonics of arbitrary order in a generalized class of non-autonomous predator-prey systems of Volterra type with periodic coefficients. When the model is non-degenerate it is shown that the Poincaré–Birkhoff twist theorem can be applied to get the existence of subharmonics of arbitrary order. However, in the degenerate models, whether or not the twist theorem can be applied to get subharmonics of a given order might depend on the particular nodal behavior of the several weight function-coefficients involved in the setting of the model. Finally, in order to analyze how the subharmonics might be lost as the model degenerates, the exact point-wise behavior of the $T$-periodic solutions of a non-degenerate model is ascertained as a perturbation parameter makes it degenerate.

1. Introduction. This paper studies the non-autonomous Volterra predator-prey model

\[
\begin{aligned}
    u' &= \lambda \alpha(t) u(1 - v) \\
    v' &= \lambda \beta(t) v(-1 + u)
\end{aligned}
\]

(1)

where $\lambda > 0$ and $\alpha(t) \geq 0, \beta(t) \geq 0$ are $T$-periodic continuous functions. This model was introduced in [21], [19] in the special case when $\alpha \beta = 0$ in $\mathbb{R}$ and it was later analyzed in [20], where the existence of $mT$-periodic coexistence states was established for all integers $m \geq 2$. Figure 1 shows the graphs of $\alpha(t)$ and $\beta(t)$ in a case when $\alpha(t)\beta(t) = 0$ for all $t \in [0, T]$, as considered in the above quoted references.

2010 Mathematics Subject Classification. 34C25, 37B55, 37E40.

Key words and phrases. Periodic predator-prey model of Volterra type, subharmonic coexistence states, Poincaré–Birkhoff twist theorem, degenerate versus non-degenerate models, point-wise behavior of the low order subharmonics as the model degenerates.

This paper has been written under the auspices of the Ministry of Science, Technology and Universities of Spain, under Research Grant PGC2018-097104-B-100, and of the IMI of Complutense University. The second author, ORCID 0000-0003-1184-6231, has been also supported by contract CT42/18-CT43/18 of Complutense University of Madrid.

* Corresponding author: F. Zanolin.
and also in Section 3 below. An ecological justification for assuming \( \alpha(t)\beta(t) = 0 \) in a subinterval of \([0, T]\) is discussed in the Appendix.

\[
\begin{align*}
\alpha & \quad \beta \\
0 & \quad \frac{T}{2} & \quad T
\end{align*}
\]

**Figure 1.** A genuine case when \( \alpha\beta = 0 \) in \( \mathbb{R} \).

A general Volterra predator-prey system with periodic coefficients takes the form

\[
\begin{cases}
x' = x(a(t) - b(t)y) \\
y' = y(-c(t) + d(t)x)
\end{cases}
\]  

(2)

with \( a, b, c, d : \mathbb{R} \to \mathbb{R} \) \( T \)-periodic functions and \( b(t) \geq 0, \ d(t) \geq 0 \). If we are able to find a \( T \)-periodic coexistence state \( \hat{z}(t) := (\hat{x}(t), \hat{y}(t)) \) of (2), namely, a positive componentwise \( T \)-periodic solution of the system, then the change of variables

\[
x(t) = u(t)\hat{x}(t), \quad y(t) = v(t)\hat{y}(t),
\]

transforms (2) into the equivalent system

\[
\begin{cases}
u' = b(t)\hat{y}(t)u(1 - v) \\
v' = d(t)\hat{x}(t)v(-1 + u)
\end{cases}
\]  

(3)

which is of the same form as (1). In the Appendix, it will be shown that (2) admits a coexistence state if and only if

\[
\int_0^T a(t) \, dt > 0 \quad \text{and} \quad \int_0^T c(t) \, dt > 0.
\]

For system (3) as well as for (1), the constant solution \((1, 1)\) is considered as a trivial coexistence state and thus we are interested in finding nontrivial componentwise positive \( mT \)-periodic solutions, which, from a geometrical point of view, would be trajectories in the interior of the first quadrant winding around the equilibrium point. Sometimes, instead of studying (1) (or (3)), it may be convenient to perform a further change of variables, moving the equilibrium point to the origin. For instance, a typical transformation is given by

\[
x = \log u, \quad y = \log v,
\]

yielding to the equivalent Hamiltonian planar system

\[
\begin{cases}
x' = -\lambda a(t)(-1 + e^y) \\
y' = \lambda\beta(t)(-1 + e^x)
\end{cases}
\]  

(4)
On the Applicability of the Poincaré ... 2395

and now we just look for nontrivial \( mT \)-periodic solutions of (4). Due to the Hamiltonian structure of the new system, a powerful tool to prove the existence of nontrivial periodic solutions is the Poincaré–Birkhoff twist fixed point theorem. Applications of this method to Volterra–predator–prey systems can be found in [18], [10], [11], [26], [2], as well as in the recent ones [16] and [13]. A typical strategy of proof consists in showing that there is a sufficiently large gap in the rotation numbers between the small solutions and the large solutions of (4), which, in turns, guarantees a suitable twist property for the associated Poincaré map. In this context, increasing the value of the parameter \( \lambda > 0 \) in (1) may play the role of enlarging the gap in the rotation numbers. If we try to apply the above quoted results [10, 11, 13, 16, 18, 26] to (1), we find that at least one of the two coefficients \( \alpha(t), \beta(t) \) should be assumed to be always strictly positive and this prevents the applications to models where the kinetics may vanish in some time interval. On the other hand, for the special choice of \( \alpha(t) \) and \( \beta(t) \) shown in Figure 1, the results of [19] establish that (1) does not admit a nontrivial \( T \)-periodic coexistence state, independently of the value of \( \lambda \), and therefore it becomes apparent that the Poincaré–Birkhoff theorem cannot be applied to (1) for some specific coefficients like those in Figure 1. Otherwise, (1) should admit a pair of nontrivial \( T \)-periodic solutions for sufficiently large \( \lambda \).

Figure 2. Two weights such that \( \alpha \beta \geq 0 \).

Astonishingly, when the support of the product function \( \alpha(t)\beta(t) \) is non-empty, as illustrated in Figure 2, then, according to our results in Section 2, the Poincaré–Birkhoff theorem establishes that, for every \( m \geq 1 \), (1) possesses at least two \( mT \)-periodic coexistence states for sufficiently large \( \lambda \). Moreover, the number of these periodic solutions increases with \( \lambda \). And this regardless the length of the support of \( \alpha \beta \)!

Thus, a rather natural question arises. What’s going on with the (nontrivial) \( T \)-periodic coexistence states of (1) when \( \alpha(t)\beta(t) \) does approximate zero? In Section 4 we analyze what happens by considering \( \alpha(t) \) and \( \beta(t) \) like in Figure 1 and the perturbed problem

\[
\begin{align*}
\{ & u' = \lambda \alpha_{\varepsilon}(t)u(1 - v) \\
& v' = \lambda \beta(t)v(-1 + u)
\}
\end{align*}
\]

where

\[
\alpha_{\varepsilon}(t) := \begin{cases} \\
\alpha(t) & t \in [0, \frac{T}{2}] \\
\varepsilon \varphi(t) & t \in (\frac{T}{2}, T)
\end{cases}
\]

\[\varepsilon \geq 0.\]
for some function $\varphi$, as plotted in Figure 3.

![Figure 3](image-url)

**Figure 3.** The weight functions $\alpha_{\varepsilon}(t)$ and $\beta(t)$.

According to our results of Section 2, based on the Poincaré–Birkhoff theorem, for every $\varepsilon > 0$ and $m \geq 1$, there exists $\lambda_m(\varepsilon) > 0$ such that (5) admits at least two $mT$-coexistence states for each $\lambda > \lambda_m(\varepsilon)$. Our main result in Section 4 establishes that, setting

$$\lambda^*_1(\varepsilon) := \inf\{\lambda > 0 : \text{(5) has at least one } T\text{-periodic coexistence state}\},$$

either

$$\lim_{\varepsilon \downarrow 0} \lambda^*_1(\varepsilon) = \infty,$$

or the $v$-component of any $T$-periodic coexistence state of (5), $(u(t, \varepsilon), v(t, \varepsilon))$, blows-up in $[\frac{T}{2}, T]$ as $\varepsilon \downarrow 0$, which explains why the degenerate problem when $\alpha \beta = 0$ cannot admit any nontrivial $T$-periodic coexistence state.

The high multiplicity of subharmonics in these $T$-periodic predator-prey prototype models contrasts, very strongly, with the uniqueness of coexistence states established for their diffusive one-dimensional counterparts in [22], [6], [9], [23]. This confirms that the non-cooperative structure of all these models does not provoke the same dynamical effects on the dynamics of the underlying systems in the presence of temporal heterogeneities than in the presence of spatial heterogeneities.

2. **An application of the Poincaré–Birkhoff theorem.** In this section we consider the non-autonomous planar Hamiltonian system

$$\begin{align*}
x' &= -\lambda \alpha(t) f(y) \\
y' &= \lambda \beta(t) g(x)
\end{align*}$$

(6)

where $\lambda > 0$ and $\alpha \geq 0$ and $\beta \geq 0$ are $T$-periodic continuous functions such that

$$\alpha(t_0) \beta(t_0) > 0 \quad \text{for some } t_0 \in [0, T].$$

(7)

In model (6), $\lambda$ is regarded as a real parameter, and $f, g \in C(\mathbb{R})$ are locally Lipschitz functions such that $f, g \in C^1$ on a neighborhood of the origin and
Lastly, set
\[
\begin{aligned}
  f(0) = 0, & \quad f(y)y > 0 \text{ for all } y \neq 0, \\
  g(0) = 0, & \quad g(x)x > 0 \text{ for all } x \neq 0, \\
  f'(0) > 0, & \quad g'(0) > 0.
\end{aligned}
\]
Moreover, either \( f \), or \( g \), satisfies, at least, one of the following conditions:
\[
\begin{aligned}
  (f_-) & \quad f \text{ is bounded in } \mathbb{R}^-, & (f_+) & \quad f \text{ is bounded in } \mathbb{R}^+, \\
  (g_-) & \quad g \text{ is bounded in } \mathbb{R}^-, & (g_+) & \quad g \text{ is bounded in } \mathbb{R}^+.
\end{aligned}
\]
Under these conditions, \((x, y) = (0, 0)\) provides us with a steady-state solution of (6). Throughout this paper, for any given \( R > 0 \) and \( z = (x, y) \in \mathbb{R}^2 \), we will denote by \( D_R(z) \) the disc of radius \( R \) centered at \( z \). Although the next result is a direct consequence of the Lipschitz dependence of the solutions of (6) with respect to the initial conditions, we will provide with a short self-contained proof of it.

**Proposition 1.** For every integer \( m \geq 1 \) and \( \lambda, \varepsilon > 0 \), there exists \( \delta = \delta(m, \varepsilon, \lambda) > 0 \) such that if \((x_0, y_0) \in D_\delta \), then the unique solution of (6), \((x(t), y(t))\), with \((x(0), y(0)) = (x_0, y_0)\), satisfies \((x(t), y(t)) \in D_\varepsilon \) for all \( t \in [0, mT] \).

Since \( \delta(m, \varepsilon, \lambda) \downarrow 0 \) as \( m \uparrow \infty \) cannot be excluded, \((0, 0)\) is not necessarily stable in the sense of Lyapunov towards the right.

**Proof.** Let us fix \( K > \max \{f'(0), g'(0)\} \) and take \( \delta_1 > 0 \) such that
\[
\frac{g(x)}{x} < K \text{ if } 0 < |x| < \delta_1, \text{ and } \frac{f(y)}{y} < K \text{ if } 0 < |y| < \delta_1.
\]
Without loss of generality, we suppose that \((x(0), y(0)) \neq (0, 0)\) and hence \((x(t), y(t))\) is a nontrivial solution. Introducing polar coordinates, we have that
\[
\rho^2(t) = x^2(t) + y^2(t), \quad t \geq 0.
\]
Thus, differentiating with respect to \( t \), it follows from (6) that
\[
\rho(t)\rho'(t) = x(t)x'(t) + y(t)y'(t) = -\lambda \alpha(t)x(t)f(y(t)) + \lambda \beta(t)y(t)g(x(t))
\]
for all \( t \geq 0 \) for which the solution is defined, say \( t \in I := [0, T_{\max}) \).

Hence,
\[
|\rho(t)\rho'(t)| = \lambda \left| x(t)y(t) \left[ \beta(t) \frac{g(x(t))}{x(t)} - \alpha(t) \frac{f(y(t))}{y(t)} \right] \right|.
\]
Then, considering the \( T \)-periodic function
\[
\gamma(t) := K[\beta(t) + \alpha(t)], \quad t \in \mathbb{R},
\]
it is apparent that, for every \( t \in I \) such that \((x(s), y(s)) \in D_\delta \), for all \( s \in [0, t] \), the following holds:
\[
|\rho(s)\rho'(s)| \leq \lambda |x(s)y(s)||\gamma(s)| \leq \frac{\lambda}{2} (x^2(s) + y^2(s))|\gamma(s)| = \frac{\lambda}{2} \rho^2(s)|\gamma(s)|, \quad \forall s \in [0, t].
\]
This, in turn, implies
\[
|\rho'(s)| \leq \frac{\lambda}{2} \rho(s)|\gamma(s)|, \quad \forall s \in [0, t].
\]
Therefore, as long as \((x(s), y(s)) \in D_\delta \), for all \( s \in [0, t] \) with \( t \in I \), we find that
\[
\rho(s) \leq e^{|T|/2} f_s^0 |\gamma(\xi)| \, d\xi \rho(0).
\]
Lastly, set
\[
E := e^{|T|/2} f_s^0 |\gamma(\xi)| \, d\xi = e^{|k+1|T} f_s^{(k+1)T} |\gamma(\xi)| \, d\xi, \quad k \geq 1,
\]
and choose $\rho_0 := \rho(0)$ such that
$$\rho_0 < E^{-m} \min\{\varepsilon, \delta_1\} =: \delta(m, \varepsilon, \lambda).$$
Then,
$$\rho(t) < \min\{\varepsilon, \delta_1\} \leq \varepsilon$$
for all $t \in [0, mT]$, which ends the proof.

**Remark 1.** We observe that condition (8), together with $\alpha, \beta \preceq 0$, imply that if $(x(t), y(t))$ is a solution of (6) which is not globally defined in the future, then for its maximal interval of existence $[0, T_{\text{max}})$, it happens that $x^2(t) + y^2(t) \to +\infty$ as $t \to T_{\text{max}}^-$ and both $x(t)$ and $y(t)$ have infinitely many zeros accumulating at $T_{\text{max}}$. Indeed, assume, for instance that $x(t) > 0$ and $y(t) > 0$ for all $t \in [t_0, T_{\text{max}})$, for some $t_0 < T_{\text{max}}$. Then, from the first equation in (6) we have that $x(t)$ is non-increasing and therefore $0 < x(t) \leq x(t_0)$. Hence $x(t)$ is bounded and then from the second equation in (6) $y'$ is bounded and hence $y(t)$ is bounded as well. Since we have found that both $x(t)$ and $y(t)$ are bounded on $[t_0, T_{\text{max}})$, this gives a contradiction. From the above argument, we can infer that any solution entering the first quadrant must leave it and enter the second one. With a similar proof we can see that it is impossible for a blow-up solution to stay in the second quadrant and hence, it must enter the third one after some time. Repeating this process it becomes apparent that any blowing-up solution of (6) must perform infinitely many turns around the origin as $t \to T_{\text{max}}^-$. As we will see in the second part of the proof of Theorem 2.2, such a situation about solutions presenting blow-up with infinitely many rotations is not possible by condition (9). Therefore, all the solutions of (6) are globally defined in the future (and also in the past).

Our main existence result in this section, that is Theorem 2.2, is a direct consequence of the Poincaré–Birkhoff theorem as presented in [8], [15] and [26] (see also [3, Remark 1] for a short discussion about this topic). It establishes the existence of, at least, two $mT$-periodic solutions of (6) for every $m \geq 1$ provided $\lambda$ is sufficiently large.

To be more specific, to any nontrivial solution $(x(t), y(t))$ of (6) with $(x(0), y(0)) = z_0 \neq (0, 0)$ we associate an angular polar coordinate $\theta(t)$ and, for a given interval $[0, mT]$, we define a rotation number
$$\text{rot}(z_0; [0, mT]) := \frac{\theta(mT) - \theta(0)}{2\pi}. \quad (10)$$
The rotation number is an algebraic counter of the counterclockwise turns of the solution $(x(t), y(t))$ around the origin during the time-interval $[0, mT]$. The version of the Poincaré–Birkhoff fixed point theorem that we use in this paper is the following one.

**Theorem 2.1.** Assume there are $0 < r_0 < R_0$ and a positive integer $k$ such that the twist condition
$$\text{rot}(z_0; [0, mT]) > k \text{ if } ||z_0|| = r_0 \text{ and } \text{rot}(z_0; [0, mT]) < k \text{ if } ||z_0|| = R_0$$
holds. Then, system (6) has at least 2 nontrivial $mT$-periodic solutions belonging to different periodicity classes and having $k$ as a rotation number.

This is essentially an application of W.Y. Ding version of the twist theorem for planar annuli (see [12]), as presented also in [24, Theorem A] (see also [3] for an
application of the same version of the theorem). As observed in [11, §3] once that for some \( m \geq 2 \) we have a \( mT \)-periodic solution \((x, y)\), then, for each \( j = 1, 2, \ldots, m-1 \), also \((x_j, y_j)\) is a \( mT \)-periodic solution of the same system, for

\[
x_j(t) := x(t + jT), \quad y_j(t) := y(t + jT).
\]

We consider all these solutions as equivalent and we say they belong to the same periodicity class.

The information about the rotation number provided by Theorem 2.1 is crucial for different reasons. First we notice that solutions with different associated rotation numbers are essentially different since as paths in \( \mathbb{R}^2 \setminus \{(0, 0)\} \) are not homotopically equivalent. Moreover, the number \( k \) is useful in order to prove the minimality of the period of the solutions. More precisely, if \( k \) is relatively prime with \( m \), then, as consequence, the \( mT \)-periodic solutions \((x(t), y(t))\) that we find cannot be \( \ell T \)-periodic for some integer \( \ell < m \). Indeed, if, by contradiction, we suppose that \((x(t), y(t))\) is \( \ell T \)-periodic for some \( \ell = 1, \ldots, m-1 \), then the rotation number associated to the solution in the interval \([0, \ell T]\) must be an integer, say \( k_1 \). Then, by the obvious additivity property of the rotation numbers, we obtain, for \( z_0 = (x(0), y(0)) \),

\[
\text{rot}(z_0; [0, m\ell T]) = \ell k = k_1 m
\]

which contradicts the fact that \( \gcd(k, m) = 1 \). This also shows that, in particular, for \( k = 1 \) we have a periodic solution of minimal period \( mT \).

**Theorem 2.2.** For every integers \( k \geq 1 \) and \( m \geq 1 \), there exists a constant \( \lambda_m^k > 0 \) such that (6) admits, at least, two \( mT \)-periodic solutions of rotation number \( k \), for each \( \lambda > \lambda_m^k \).

**Proof.** In order to apply the version of the Poincaré–Birkhoff theorem given in Theorem 2.1 we should show that, near the origin, the solutions have a rotation number greater than \( k \), while, far from the origin, the solutions cannot complete one turn.

First, we will focus our attention on small solutions. By (8), there exists a constant \( \eta > 0 \) such that

\[
\min\{f'(0), g'(0)\} > \eta.
\]

By the limit definition, we claim that, for sufficiently small \( \zeta \sim 0 \), say for \( |\zeta| \leq \varepsilon \),

\[
f(\zeta)\zeta \geq \eta \zeta^2, \quad g(\zeta)\zeta \geq \eta \zeta^2.
\]

Let \( m \geq 1 \) be an integer that we fix from now to the end of the proof. Given \( \varepsilon \) as above, for any \( \lambda > 0 \) we can apply Proposition 1 and find a constant \( \delta(\varepsilon, \lambda) > 0 \) such that if \((x(t), y(t))\) is any solution of (6) with initial point in \( D_{\delta} \), then \((x(t), y(t)) \in D_{\varepsilon} \) for all \( t \in [0, mT] \). For these solutions with initial value in \( D_{\delta} \setminus \{(0, 0)\} \) we introduce the angular polar coordinate \( \theta(t) \). Since, locally and up to an additive constant,

\[
\theta(t) = \arctan \frac{y(t)}{x(t)}, \quad \text{or} \quad \theta(t) = -\arctan \frac{x(t)}{y(t)},
\]

differentiating with respect to time and using (6) yields

\[
\theta'(t) = \frac{y'(t)x(t) - x'(t)y(t)}{x^2(t) + y^2(t)} = \frac{\lambda \beta(t) g(x(t)) x(t) + \lambda \alpha(t) f(y(t)) y(t)}{x^2(t) + y^2(t)}
\]
for all \( t \in [0, mT] \). Hence, owing to (11), it is apparent that
\[
\theta'(t) \geq \frac{\lambda \eta \beta(t)x^2(t) + \alpha(t)y^2(t)}{x^2(t) + y^2(t)} \geq 0, \quad t \in [0, mT].
\] (12)

On the other hand, by the continuity of \( \alpha, \beta \) in \( t_0 \), it follows from (7) that there exist \( \omega > 0 \) and \( \tau > 0 \) such that
\[ \min\{\beta(t), \alpha(t)\} \geq \omega > 0 \quad \text{for all } t \in J := [t_0 - \tau, t_0 + \tau]. \]

Thus, for every \( t \in J + iT \), with \( i = 0, 1, \ldots, m - 1 \), (12) implies that \( \theta'(t) \geq \lambda \eta \omega \). Hence, we have that
\[ \theta(mT) - \theta(0) = \int_0^{mT} \theta'(s) \, ds \geq m \int_{t_0 - \tau}^{t_0 + \tau} \theta'(s) \, ds \geq m \lambda \eta \omega 2 \tau =: m \lambda \nu. \]

Therefore,
\[ \theta(mT) - \theta(0) \geq m \lambda \nu > 2 \pi k \quad \text{if } \lambda > \frac{2 \pi k}{m \nu} =: \lambda^k_m. \] (13)

At this point, we take an arbitrary (but fixed) \( \lambda > \lambda^k_m \). Then there exists \( r_0 > 0 \) with \( r_0 < \delta(m, \varepsilon, \lambda) \) such that, for every \( z_0 = (x(0), y(0)) \) with \( \|z_0\| = r_0 \), one has that
\[ (x(t), y(t)) \in D_\varepsilon \quad \text{for all } t \in [0, mT] \]
and hence,
\[ \text{rot}(z_0; [0, mT]) > k. \] (14)

Now, besides the integers \( m \) and \( k \), also the constant \( \lambda > 0 \) is fixed and we proceed by showing that the rotation number for large solutions is less than one.

In order to prove that the solutions of (6) with sufficiently large initial data, \( (x_0, y_0) \), cannot complete a rotation in the interval \([0, mT]\), we argue as follows. Suppose that (9) holds with \( g \) satisfying \((g_-)\). We shall consider only this situation as the other ones are completely symmetric.

Clearly, a solution making at least one turn around the origin must cross completely the second or the third quadrant. Indeed, if the initial point \( z_0 \) is in the first or in the fourth quadrant and \( \text{rot}(z_0; [0, mT]) \geq 1 \), then \((x(t), y(t))\) must cross completely both the second and the third quadrants; if \( z_0 \) is in the second (respectively third) quadrant, then the trajectory must cross completely the third (respectively the second) one. We shall show that these cases are prevented for large solutions, by finding some general bounds for a generic solution \((x(t), y(t))\) on the third or the second quadrant.

As a first case, we suppose that \((x(t), y(t))\) is a nontrivial solution which crosses entirely the third quadrant. Then, there exists an interval \([t_1, t_2] \subset [0, mT]\) such that \( y(t_1) = 0 = x(t_2) \) and \( x(t) < 0, y(t) < 0 \) for all \( t \in (t_1, t_2) \). Recalling also the sign condition for \( g(x) \) given in (9), there exists a constant, \( M > 0 \), such that
\[ \sup_{x \leq 0} |g(x)| \leq M. \]

Then it is clear that, for every \( t \in [t_1, t_2] \), we have that
\[ |y(t)| = |\lambda \int_{t_1}^t \beta(s)g(x(s)) \, ds| \leq \lambda M \int_{t_1}^{t_2} \beta \leq \lambda M \int_{0}^{mT} \beta = \lambda M m \int_0^T \beta. \]

Thus, setting
\[ N := \max \left\{ |f(y)| : |y| \leq \lambda M m \int_0^T \beta \right\}, \]
we also find that
\[ |x(t)| = |\lambda \int_t^T \alpha(s)f(y(s))ds| \leq \lambda N \int_0^{mT} \alpha = \lambda Nm \int_0^T \alpha. \]

Hence, denoting
\[ A := \int_0^T \alpha > 0, \quad B := \int_0^T \beta > 0, \]

and
\[ R^2 := \lambda^2 m^2 (M^2 B^2 + N^2 A^2), \]

we conclude that if \((x(t), y(t))\) is any solution of (6) such that \(x^2(\hat{t}) + y^2(\hat{t}) > R^2\) for some \(\hat{t} \in [0, mT]\), with \((x(\hat{t}), y(\hat{t}))\) in the third quadrant, then such a solution cannot cross entirely the third quadrant during a time interval containing \(\hat{t}\). Analogous estimates allow to find exactly the same constants such that the same non-crossing property holds with respect to the second quadrant where \(x \leq 0\) as well.

To complete our analysis, we now look at what happens in the other quadrants.

So, let \(s_0\) be such that \(x(s_0) = 0\) and \(0 < y(s_0) \leq R\). Let also \([s_1, s_0] \subseteq [0, s_0]\) be a maximal interval such that \(x(t) \geq 0\) and \(y(t) \geq 0\) for all \(t \in [s_1, s_0]\). From (6) we know that \(x\) is non-increasing and \(y\) is non-decreasing on \([s_1, s_0]\). Therefore, \(0 \leq y(t) \leq R\) for all \(t \in [s_1, s_0]\). Hence
\[ |f(y(t))| \leq N_1 := \max\{f(y) : 0 \leq y \leq R\} \]

for all \(t\) in the same interval. Integrating the first equation on \([t, s_0] \subseteq [s_1, s_0]\) yields to an upper bound for \(x(t)\), namely \(|x(t)| \leq \lambda N_1 mA\). Now, taking \(R_1\) as
\[ R_1^2 := \lambda^2 m^2 (M^2 B^2 + N^2 A^2 + N_1^2 A^2), \]

we conclude that if \((x(t), y(t))\) is any solution of (6) such that \(x^2(\hat{t}) + y^2(\hat{t}) > R_1^2\) for some \(\hat{t} \in [0, mT]\), with \((x(\hat{t}), y(\hat{t}))\) in the first quadrant, then such a solution cannot cross entirely the second or the third quadrant.

As a final case, let us suppose now there exists \(s_2\) such that \(y(s_2) = 0\) and \(0 < x(s_2) \leq R_1\). Let also \([s_3, s_2] \subseteq [0, s_2]\) be a maximal interval such that \(x(t) \geq 0\) and \(y(t) \leq 0\) for all \(t \in [s_3, s_2]\). Arguing as above (and using the fact that now both \(x\) and \(y\) are non-decreasing on \([s_3, s_2]\)), we define
\[ M_1 := \max\{g(x) : 0 \leq x \leq R_1\}. \]

In this manner, \(|g(x(t))| \leq M_1\) for all \(t \in [s_3, s_2]\) and thus we obtain a constant
\[ R_2^2 := \lambda^2 m^2 (M^2 B^2 + N^2 A^2 + N_1^2 A^2 + M_1^2 B^2), \]

such that if \((x(t), y(t))\) is any solution of (6) with \(x^2(\hat{t}) + y^2(\hat{t}) > R_2^2\) for some \(\hat{t} \in [0, mT]\), with \((x(\hat{t}), y(\hat{t}))\) in the fourth quadrant, then such a solution cannot cross entirely the second or the third quadrant.

Therefore, the solutions of (6) with \(x_0^2 + y_0^2 = R_0^2 > R_2^2\), satisfy
\[ \rot(z_0; [0, mT]) < 1. \]

Notice that the above proof also ensures that all the solutions are globally defined, as anticipated in Remark 1.

By (14) and (16) the twist condition holds and hence, according to Theorem 2.1, the system (6) has, at least, two \(mT\)-periodic solutions with rotation number \(k\), for each \(\lambda > \lambda_m^k\). This ends the proof.
Remark 2. Theorem 2.2 when applied for $m = 1$, guarantees the existence of $2k$ geometrically distinct $T$-periodic solutions when $\lambda > \lambda^k_1$. Indeed it provides at least two (nontrivial) $T$-periodic solutions with rotation number $j$ for each integer $j = 1, 2, \ldots, k$. In view of the analysis performed in [19], [20], the condition (7) is optimal (see the next section for a detailed discussion). System (6) can be obtained from a Volterra predator-prey equation via a change of variables. In this case $g(x) = e^x - 1$ and $f(y) = e^y - 1$ and therefore both $(f_-)$ and $(g_-)$ are satisfied. This simplifies the second part of the above proof.

We stress that Theorem 2.2 considers a situation which is not covered in the previous works dealing with periodic solutions of non-autonomous Volterra equations [18], [11], [26], [16]. For instance, we do not assume monotonicity of $\alpha(t)f(\cdot)$ or $\beta(t)g(\cdot)$ for all $t$; indeed such functions can identically vanish on some time intervals.

Remark 3. As a final observation, we should mention the fact, without any significant change in the proof, a slightly more general version of Theorem 2.2 could be proved, by assuming $f, g$ only continuous (and not locally Lipschitz) and replacing the condition on the derivatives in (8) with the following one

$$0 < \lim \inf_{|y| \to 0} \frac{f(y)}{y} \leq \lim \sup_{|y| \to 0} \frac{f(y)}{y} < \infty, \quad 0 < \lim \inf_{|x| \to 0} \frac{g(x)}{x} \leq \lim \sup_{|x| \to 0} \frac{g(x)}{x} < \infty.$$ 

To this aim, instead of Theorem 2.1, one can apply a generalized version of the Poincaré–Birkhoff theorem due to Fonda and Ureña [17] for Hamiltonian systems where the uniqueness of the solutions of the initial value problems is not required (see also [14, Theorem 10.6.1] for the precise statement). Since in our application to the Volterra system, $f$ and $g$ are smooth functions, we preferred to state our theorem in this case, instead of considering the most general situation.

3. A critical model outside the Poincaré–Birkhoff setting. In this section we will show how condition (7) is optimal for the validity of Theorem 2.2. The non-autonomous Lotka–Volterra predator-prey model

$$\begin{align*}
u' &= \lambda \alpha(t)u(1-v) \\
v' &= \lambda \beta(t)v(-1+u)
\end{align*}$$

(17)

where $\lambda > 0$ and $\alpha(t) \geq 0$, $\beta(t) \geq 0$ are $T$-periodic continuous functions such that $\alpha \beta = 0$ in $\mathbb{R}$, was introduced in [21] and later analyzed in [19] and [20], where the existence of $mT$-periodic coexistence states was analyzed for all integers $m \geq 1$. More precisely, in the rest of this paper $\alpha(t)$ and $\beta(t)$ are $T$-periodic non-negative functions such that

$$\alpha \equiv 0 \ \text{in} \ [\frac{T}{2}, T] \ \text{and} \ \beta \equiv 0 \ \text{in} \ [0, \frac{T}{2}].$$

Naturally, in searching for coexistence states of (17), i.e., componentwise positive solutions $(u, v)$, as explained in the Introduction, we can perform the change of variables

$$x = \log u, \quad y = \log v,$$

which transforms (17) into the next Hamiltonian system

$$\begin{align*}
x' &= -\lambda \alpha(t)(e^y - 1) \\
y' &= \lambda \beta(t)(e^x - 1)
\end{align*}$$

(18)

which fits within the abstract setting of Section 2 with

$$f(y) = e^y - 1, \quad g(x) = e^x - 1,$$
ON THE APPLICABILITY OF THE POINCARÉ ...

2403

except for the crucial fact that, since $\alpha \beta = 0$, the condition (7) fails to be true in the present context. As a consequence of the next result, we have that the Poincaré–Birkhoff cannot be applied to the problem (18) to infer the existence of, at least, two $T$-periodic nontrivial solutions. Therefore, the condition (7) is condition sine qua non for the validity of Theorem 2.2.

Lemma 3.1. The constant solution $(1, 1)$ provides us with the unique $T$-periodic coexistence state of (17), i.e., the equilibrium $(0, 0)$ is the unique $T$-periodic solution of (18).

Proof. Indeed, as $\alpha \beta = 0$, system (17) can be easily integrated. For every $(u_0, v_0) \in \mathbb{R}^2$, the unique solution of (17) such that $(u(0), v(0)) = (u_0, v_0)$ is given by

$$u(t) = u_0 e^{(1-v_0)\lambda \int_0^t a(s) ds}, \quad v(t) = v_0 e^{(u(T)-1)\lambda \int_0^t \beta(s) ds}, \quad t \in [0, T].$$

(19)

Hence, the associated $T$-time Poincaré map, $P_1$, is given by

$$(u_1, v_1) := P_1(u_0, v_0), \quad u_1 := u_0 e^{(1-v_0)\lambda A}, \quad v_1 := v_0 e^{(u_1-1)\lambda B},$$

(20)

where $A$ and $B$ are defined as in (15). Thus, a solution of (17) is a $T$-periodic coexistence state if, and only if,

$$u_0, v_0 > 0, \quad P_1(u_0, v_0) = (u_0, v_0).$$

Thanks to (19) and (20), this is equivalent to $(u(t), v(t)) = (1, 1)$ for all $t \in \mathbb{R}$. Therefore, $(1, 1)$ is the unique $T$-periodic coexistence state of (17). \qed

As a byproduct, since (17) cannot admit a coexistence state with minimal period $T$, the thesis of Theorem 2.2 fails to be true for the problem (18). This entails that the small solutions of (18) cannot rotate around the origin, for as, otherwise, the Poincaré–Birkhoff theorem could be applied to guarantee the existence of, at least, two $T$-periodic coexistence states. As the remaining assumptions of Theorem 2.2 hold true for model (18), it becomes apparent that condition (7) is imperative for the validity of Theorem 2.2. However, by Theorem 2.1 of [20], the problem (17) possesses some $2T$-periodic coexistence state if, and only if,

$$\lambda > \frac{2}{\sqrt{AB}},$$

and, actually, in such case it has exactly two. More generally, it has been established in [20] that, in the special case when

$$x \equiv u_0 = v_0 \quad \text{and} \quad A = B,$$

(21)

for every integer $m \geq 2$, (17) possesses, at least, $2\nu_m mT$-periodic coexistence states of (17) for each $\lambda > \frac{2}{\sqrt{AB}}$, where

$$\nu_m := \begin{cases} \frac{m}{2} & \text{if } m \in 2\mathbb{N} \\ \frac{m-1}{2} & \text{if } m \in 2\mathbb{N} + 1. \end{cases}$$

By Lemma 3.1 and a direct analysis which can be performed for $m = 2$, it seems that not all these coexistence states can be obtained as a direct application of the version of the Poincaré–Birkhoff theorem given in Section 2, as it occurs when $\alpha \beta \geq 0$.

Figure 4 provides us with a sketch of the global bifurcation diagram of subharmonics of order $m$ of (17) for all $2 \leq m \leq 13$: it has been borrowed from [20]. It should be noted that Figure 4 does not represent the true nature of the local bifurcations from $(1, 1)$ of the subharmonics of order $m \geq 2$. Indeed, by [20, Theorem 6.1], the local bifurcations of the $2T$, $3T$ and $4T$-periodic coexistence states is
Figure 4. Subharmonics of (17) under condition (21). The figure represents an ideal global bifurcation diagram for subharmonics with the parameter $A = B$ (in the abscissa) versus the value of the initial point $x = u_0 = v_0$ of the periodic solution (in the ordinate). Each bifurcation curve is labelled with the period of the corresponding subharmonic solution. For a detailed analysis of the real bifurcation diagrams, we refer to [20].

supercritical, transcritical and subcritical, respectively, while in Figure 4 all bifurcations from $(1, 1)$ have been assumed to supercritical. As the nature of the local bifurcation from $(1, 1)$ of the $mT$-periodic coexistence states, for $m \geq 5$, remains still unknown, all the local bifurcations in Figure 4 are ideal.

4. Limiting behaviour of the $T$-periodic solutions of the non-degenerate model as it degenerates. In this section we analyze the perturbed model

$$
\begin{cases}
    u' = \lambda \alpha_\varepsilon(t) u(1 - v) \\
    v' = \lambda \beta(t) v(-1 + u),
\end{cases}
$$

where $\lambda > 0$ and $\alpha(t), \beta(t)$ satisfy the same general assumptions as in Section 3, and, for sufficiently small $\varepsilon > 0$,

$$
\alpha_\varepsilon(t) := \alpha(t) + \varepsilon \varphi(t), \quad t \in \mathbb{R},
$$

where $\varphi$ is a $T$-periodic function such that

$$
\varphi(t) < 1 \text{ for each } t \in \text{supp}\varphi = [\frac{T}{2}, T].
$$

By technical reasons, $\beta$ and $\varphi$ are assumed to be differentiable functions in $[\frac{T}{2}, T]$ such that

$$
\beta(t) > 0, \quad \varphi(t) > 0, \quad \text{for all } t \in (\frac{T}{2}, T)
$$

and

$$
\beta'(\frac{T}{2}) > 0, \quad \beta'(T) < 0, \quad \varphi'(\frac{T}{2}) > 0, \quad \varphi'(T) < 0.
$$
Under these assumptions, (22) fits within the abstract setting of Section 2 by performing the change of variables

\[ x = \log u, \quad y = \log v. \]

Indeed, under this transformation, (22) becomes into

\[
\begin{align*}
    x' &= -\lambda \alpha_\varepsilon(t)(e^y - 1) \\
    y' &= \lambda \beta(t)(e^x - 1)
\end{align*}
\]

and, since

\[ \alpha_\varepsilon(t) \beta(t) > 0 \quad \text{for all} \quad t \in (\frac{T}{2}, T), \]

the problem (25) fits into the setting of Section 2 for the special choices

\[ f(y) = e^y - 1, \quad g(x) = e^x - 1. \]

Therefore, by Theorem 2.2, for every \( \varepsilon > 0 \), there exists \( \lambda_1 = \lambda_1(\varepsilon) > 0 \) (see (13) for the definition of \( \lambda_1^1 \), with \( m = 1 \) and \( k = 1 \)) such that (25) possesses, at least, two \( T \)-periodic solutions for each \( \lambda > \lambda_1 \). However, thanks to Lemma 3.1, at the particular value of the parameter \( \varepsilon = 0 \), (25) does not admit a nontrivial \( T \)-periodic solution. Thus, a natural question is to ascertain what’s going on with the particular value of the parameter \( \varepsilon \).

To state the main result of this section we need to introduce the next auxiliary constant

\[ \lambda_1^*(\varepsilon) := \inf \{ \lambda > 0 : (25) \text{ has at least one nontrivial } T\text{-periodic solution} \} \]

\[ = \inf \{ \lambda > 0 : (22) \text{ has at least one nontrivial } T\text{-periodic coexistence state} \}. \]

By definition,

\[ \lambda_1^1(\varepsilon) \leq \lambda_1(\varepsilon), \quad \text{for every} \quad \varepsilon > 0. \]

Then, the main result of this section can be stated as follows.

**Theorem 4.1.** One of the following two excluding options holds:

(a) Either \( \lambda_1^*(\varepsilon) \uparrow \infty \) as \( \varepsilon \downarrow 0 \), or

(b) there exist \( \varepsilon_0 > 0 \) and a fixed \( \lambda > 0 \), such that, for every \( 0 < \varepsilon < \varepsilon_0 \), (22) admits, at least, one (nontrivial) \( T \)-periodic coexistence state. Moreover, in such case, any nontrivial \( T \)-periodic coexistence state of (22) blows up in \( (\frac{T}{2}, T) \) as \( \varepsilon \downarrow 0 \).

The proof of this theorem will follow after a series of lemmas of technical nature. Suppose \( t \in [0, \frac{T}{2}] \). Then, as \( \beta = 0 \) in \( [0, \frac{T}{2}] \), \( v' = 0 \) and hence

\[
\begin{align*}
    v(t, \varepsilon) &= v_0(\varepsilon), \\
    u(t, \varepsilon) &= u_0(\varepsilon)e^{\lambda_1(1-v_0(\varepsilon)) \int_0^t \alpha(s) ds}.
\end{align*}
\]

Consequently, for every \( t \in [\frac{T}{2}, T] \), we have that

\[
\begin{align*}
    u(t, \varepsilon) &= u_0(\varepsilon)e^{\lambda_1 \int_{\frac{T}{2}}^t \alpha(s)(1-v(s, \varepsilon)) ds} = u_0(\varepsilon)e^{\lambda_1(1-v_0(\varepsilon)) + \lambda_1 \int_{\frac{T}{2}}^t \alpha(s)(1-v(s, \varepsilon)) ds}, \\
    v(t, \varepsilon) &= v_0(\varepsilon)e^{\lambda_1 \int_{\frac{T}{2}}^t \beta(s)(1+u(s, \varepsilon)) ds} = v_0(\varepsilon)e^{\lambda_1 \int_{\frac{T}{2}}^t \beta(s)(1+u(s, \varepsilon)) ds}.
\end{align*}
\]
As in Section 3, a solution of (22) is a $T$-periodic coexistence state if $u_0, v_0 > 0$ and 
\[ P_1(u_0, v_0) = (u_0, v_0) \]
where $P_1$ is the Poincaré map at time $T$, i.e., by (27), if
\[ \begin{cases} 
   A(1 - v_0(\varepsilon)) + \varepsilon \int_{T/2}^{T} \varphi(s)(1 - v(s, \varepsilon))ds = 0, \\
   \int_{T/2}^{T} \beta(s)(-1 + u(s, \varepsilon))ds = 0,
\end{cases} \]
which is equivalent to
\[ \int_{0}^{T} \alpha_s(s)(1 - v(s, \varepsilon))ds = 0, \quad \int_{0}^{T} \beta(s)(-1 + u(s, \varepsilon))ds = 0. \]
In particular, by the positivity of $\alpha_s$ and $\beta$, the components of any (nontrivial) $T$-periodic solution of (22) cross the constant curve 1. The next result provides us with some sharper properties of these crossings.

**Lemma 4.2.** Let $\varepsilon > 0$ be such that (22) has a (nontrivial) $T$-periodic coexistence state,
\[ (u(t), v(t)) \equiv (u(t, \varepsilon), v(t, \varepsilon)). \]
Then, the next properties hold in the interval $(\frac{T}{2}, T)$:
(a) The zeroes of $1 - v$ and $1 - u$ are simple.
(b) There exists a bijection between the critical points of $v$ (resp. $u$) and the zeroes of $1 - u$ (resp. $1 - v$).
(c) None of the functions $1 - v$ and $1 - u$ can admit a critical point which is also an inflection point.
(d) Between each two consecutive zeros of $1 - v$ (resp. $1 - u$) there is an odd number of critical points of $v$ (resp. $u$).
(e) The curvature of $v$ at $\frac{T}{2}$ is given through
\[ v''(\frac{T}{2}, \varepsilon) = \lambda \lambda'(\frac{T}{2}, \varepsilon) v_0(\varepsilon) \left[ -1 + u(\frac{T}{2}, \varepsilon) \right]. \]

**Proof.** By the assumptions, $(u, v) \neq (1, 1)$. Suppose that $v(t_0) = 1$ for some $t_0 \in (\frac{T}{2}, T)$. Then, by the uniqueness of the solutions for the Cauchy problem associated to (22), we have that $u(t_0) \neq 1$ and hence,
\[ v'(t_0) = \lambda \lambda'(t_0) v(t_0)(-1 + u(t_0)) \neq 0. \]
Similarly, if $u(t_0) = 1$, then
\[ u'(t_0) = \lambda \varepsilon \lambda'(t_0) u(t_0)(1 - v(t_0)) \neq 0. \]
This ends the proof of Part (a).
To prove Part (b), suppose that $v'(t_0) = 0$ for some $t_0 \in (\frac{T}{2}, T)$. Then,
\[ 0 = v'(t_0) = \lambda \lambda'(t_0) v(t_0)(-1 + u(t_0)) \]
and hence, $u(t_0) = 1$. Similarly, if $u'(t_0) = 0$, then
\[ 0 = u'(t_0) = \lambda \varepsilon \varphi(t_0) u(t_0)(1 - v(t_0)). \]
So, $v(t_0) = 1$, which ends the proof of Part (b).
To prove Part (c), suppose that $v'(t_0) = 0$ for some $t_0 \in (\frac{T}{2}, T)$. Then, by Part (b), $u(t_0) = 1$. Thus, by Part (a), $u'(t_0) \neq 0$. Hence, differentiating the $v$-equation of (22) yields
\[ v''(t_0) = \lambda \lambda'(t_0) v(t_0)(-1 + u(t_0)) + \lambda \lambda'(t_0) v'(t_0)(-1 + u(t_0)) + \lambda \lambda'(t_0) v(t_0) u'(t_0) \]
\[ = \lambda \lambda'(t_0) v(t_0) u'(t_0) \neq 0. \]
Similarly, \( u'(t_0) = 0 \) implies that
\[
\begin{align*}
  u''(t_0) &= \lambda \varepsilon \varphi'(t_0) u(t_0) (1 - v(t_0)) + \lambda \varepsilon \varphi(t_0) u'(t_0) (1 - v(t_0)) - \lambda \varepsilon \varphi(t_0) u(t_0) v'(t_0) \\
  &= -\lambda \varepsilon \varphi(t_0) u(t_0) v'(t_0) \neq 0.
\end{align*}
\]

Therefore, any critical point of \( v \), or \( u \), is a quadratic maximum, or minimum, which ends the proof of Part (c). Part (d) is a byproduct of this property.

Finally, since \( \beta \equiv 0 \) on the interval \([0, \frac{T}{2}]\), by (26) it becomes apparent that
\[
\begin{align*}
  v''(\frac{T}{2}) &= \lambda \beta'(\frac{T}{2}) v(\frac{T}{2}) (-1 + u(\frac{T}{2})) \\
  &= \lambda \beta'(\frac{T}{2}) v(\frac{T}{2}) (-1 + u(\frac{T}{2})) = \lambda \beta'(\frac{T}{2}) v_0(-1 + u(\frac{T}{2})),
\end{align*}
\]
which shows Part (e) and ends the proof of the lemma.

The next result provides us with the non-degeneration of the \( T \)-periodic solutions with respect to the equilibrium \((1, 1)\).

**Lemma 4.3.** There exist \( \eta > 0 \) and \( \varepsilon_0 > 0 \) such that, for every nontrivial \( T \)-periodic family of solutions, \((u(t, \varepsilon), v(t, \varepsilon))\), \(0 < \varepsilon < \varepsilon_0\), the following estimate holds
\[
\inf_{t \in [0, T]} \{|u(t, \varepsilon) - 1| + |v(t, \varepsilon) - 1|\} > \eta.
\]

**Proof.** Throughout this proof, we will use the fact that the fixed points of the Poincaré map \( P_1 \) are the zeroes of the function
\[
\Phi(u_0, v_0, \varepsilon) = (f_1, f_2) := P_1(u_0, v_0, \varepsilon) - (u_0, v_0)
\]
\[
= (u_0 e^{\lambda A(1-v_0) + \lambda \varepsilon \int_{T/2}^{T} \varphi(s)(1-v(s, \varepsilon))ds} - u_0, v_0 e^{\lambda \int_{T/2}^{T} \beta(s)(-1 + u(s, \varepsilon))ds} - v_0),
\]
where
\[
(u_0, v_0) := (u(0, \varepsilon), v(0, \varepsilon)), \quad \varepsilon \in (0, \varepsilon_0).
\]
We claim that the matrix \( D_{(u_0, v_0)} \Phi(1, 1, 0) \) is invertible. Indeed, by differentiating with respect to \( u_0 \) and \( v_0 \) yields
\[
\frac{\partial f_1}{\partial u_0} = e^{\lambda A(1-v_0) + \lambda \varepsilon \int_{T/2}^{T} \varphi(s)(1-v(s, \varepsilon))ds} + u_0 \lambda \varepsilon \frac{\partial}{\partial u_0} \left( \int_{T/2}^{T} \varphi(s)(1-v(s, \varepsilon))ds \right) e^{\lambda A(1-v_0) + \lambda \varepsilon \int_{T/2}^{T} \varphi(s)(1-v(s, \varepsilon))ds} - 1,
\]
\[
\frac{\partial f_1}{\partial v_0} = u_0 \frac{\partial}{\partial v_0} \left( \lambda A(1-v_0) \right)
\]
\[
+ \lambda \varepsilon \int_{T/2}^{T} \varphi(s)(1-v(s, \varepsilon))ds e^{\lambda A(1-v_0) + \lambda \varepsilon \int_{T/2}^{T} \varphi(s)(1-v(s, \varepsilon))ds}
\]
\[
= u_0 \left( -\lambda A + \lambda \varepsilon \frac{\partial}{\partial v_0} \int_{T/2}^{T} \varphi(s)(1-v(s, \varepsilon))ds \right) e^{\lambda A(1-v_0) + \lambda \varepsilon \int_{T/2}^{T} \varphi(s)(1-v(s, \varepsilon))ds},
\]
\[
\frac{\partial f_2}{\partial u_0} = v_0 \lambda \frac{\partial}{\partial u_0} \left( \int_{T/2}^{T} \beta(s)(-1 + u(s, \varepsilon))ds \right) e^{\lambda \int_{T/2}^{T} \beta(s)(-1 + u(s, \varepsilon))ds}
\]
\[
= v_0 \lambda \left[ \int_{T/2}^{T} \beta(s) \frac{\partial}{\partial u_0} \left( f_1(u_0, v_0, \varepsilon) + u_0 \right) ds \right] e^{\lambda \int_{T/2}^{T} \beta(s)(-1 + u(s, \varepsilon))ds}
\]
\[ v_0 \lambda \left[ \int_{T/2}^{T} \beta(s) \left( \frac{\partial f_1}{\partial u_0}(u_0, v_0, \varepsilon) + 1 \right) \, ds \right] e^{\lambda \int_{T/2}^{T} \beta(s)(-1+u_0+f_1(u_0, v_0, \varepsilon)) \, ds}. \]

Thus, since
\[ \frac{\partial f_1}{\partial u_0}(1, 1, 0) = 0, \quad \frac{\partial f_1}{\partial v_0}(1, 1, 0) = -\lambda A, \]
it is easily seen that
\[ \frac{\partial f_2}{\partial u_0}(1, 1, 0) = \lambda B. \]

Therefore,
\[ D_{(u_0, v_0)} \Phi(1, 1, 0) = \begin{pmatrix} 0 & -\lambda A \\ \lambda B & \frac{\partial f_2}{\partial v_0} \end{pmatrix} \]
and, hence,
\[ \det D_{(u_0, v_0)} \Phi(1, 1, 0) = \lambda^2 AB > 0, \]
which shows the claim above. Consequently, by the Implicit Function Theorem, since
\[ \Phi(1, 1, \varepsilon) = 0, \quad \text{for all } \varepsilon \geq 0, \]
there exist \( R > 0 \) and \( \varepsilon_0 > 0 \) such that \((1,1)\) is the unique \( T\)-periodic solution of \((22)\) in the ball \( B_R(1,1) \) of \( C_T(\mathbb{R}) \times C_T(\mathbb{R}) \) for all \( \varepsilon \in [0, \varepsilon_0] \). Therefore, by the uniqueness provided by the implicit function theorem, if \((u,v)\) is a \( T\)-periodic solution of \((22)\) for some \( \varepsilon \in [0, \varepsilon_0] \) such that
\[ ||u(\cdot, \varepsilon) - 1||_{C_T(\mathbb{R})} + ||v(\cdot, \varepsilon) - 1||_{C_T(\mathbb{R})} \leq R, \] (29)
then \( u \equiv 1 \) and \( v \equiv 1 \).

It remains to show that there exists \( \eta > 0 \) such that, whenever
\[ |u(t_0, \varepsilon) - 1| + |v(t_0, \varepsilon) - 1| \leq \eta \]
for some \( t_0 \in [0, T] \) and \( \varepsilon \in [0, \varepsilon_0] \), then the condition (29) holds. Indeed, by the Lipschitz dependence of the solutions of \((22)\) with respect to the initial data, there exists a constant \( L \) such that
\[ |u(t, \varepsilon) - 1| \leq L|u(t_0, \varepsilon) - 1|, \quad |v(t, \varepsilon) - 1| \leq L|v(t_0, \varepsilon) - 1|, \]
for all \( t \in [0, T] \) and \( \varepsilon \in [0, \varepsilon_0] \). Thus,
\[ |u(t, \varepsilon) - 1| + |v(t, \varepsilon) - 1| \leq L(|u(t_0, \varepsilon) - 1| + |v(t_0, \varepsilon) - 1|) \leq L \eta < R \]
if, and only if, \( \eta < R/L \). Therefore,
\[ \inf_{t \in [0,T]} \{|u(t, \varepsilon) - 1| + |v(t, \varepsilon) - 1|\} \leq \eta, \]
implies \( u \equiv 1 \) and \( v \equiv 1 \), which ends the proof. \( \square \)

The next result provides us with the behavior of \( v(s, \varepsilon) \) when \( v_0(\varepsilon) > 1 \).

**Lemma 4.4.** For any sequence \( \{\varepsilon_n\}_{n \geq 1} \) such that \( \lim_{n \to \infty} \varepsilon_n = 0 \) and \( v_0(\varepsilon_n) > 1 \)
for all \( n \geq 1 \), the following holds
\[ \lim_{n \to \infty} v_0(\varepsilon_n) = 1. \]

Moreover, there exists a subsequence, \( \{\varepsilon_{n_m}\}_{m \geq 1} \), such that
\[ \lim_{m \to \infty} u(t, \varepsilon_{n_m}) = u_0(0) \]
for all \( t \in [0, \frac{T}{2}] \), where \( u_0(0) \) is a suitable positive constant.
Proof. For any $A > 0$, the first equation of (28) can be expressed as

$$A = \frac{\varepsilon_n}{v_0(\varepsilon_n)} - 1 \int_{\gamma}^{T} \varphi(s)(1 - v(s, \varepsilon_n))ds.$$ 

Thus, since $(u(t, \varepsilon_n), v(t, \varepsilon_n))$ is a coexistence state, i.e. a componentwise positive solution, the next estimate holds

$$A = \frac{\varepsilon_n}{v_0(\varepsilon_n)} - 1 \int_{\gamma}^{T} \varphi(s)(1 - v(s, \varepsilon_n))ds < \frac{T\varepsilon_n}{2(v_0(\varepsilon_n) - 1)}$$

for all $n \geq 1$. Hence, since $\lim_{n \to \infty} \varepsilon_n = 0$, (30) entails that

$$\lim_{n \to \infty} v_0(\varepsilon_n) = 1.$$ 

The last assertion follows readily from the second identities of (26) and (28). This ends the proof.

We are ready to prove the main theorem of this section.

Proof of Theorem 4.1: Suppose that Alternative (a) does not occur. In this case, there exists $\lambda > 0$ such that there are coexistence states of (22), for sufficiently small $\varepsilon > 0$. Accordingly, let $(u(t, \varepsilon), v(t, \varepsilon))$ denote a family of coexistence states of (22) (for a fixed $\lambda > 0$), for $\varepsilon > 0$ small ($0 < \varepsilon < \varepsilon_0$). We must prove that $v(t, \varepsilon)$ blows-up in a finite time as $\varepsilon \downarrow 0$. To accomplish the proof we will distinguish between several different cases.

Case 1: There exists a sequence $\{\varepsilon_n\}_{n \geq 1}$ such that $\lim_{n \to \infty} \varepsilon_n = 0$ and $v_0(\varepsilon_n) > 1$ for all $n \geq 1$. Then, by Lemma 4.4,

$$\lim_{n \to \infty} v_0(\varepsilon_n) = 1.$$ 

Subcase 1.A: Suppose, in addition, that $u_0(\varepsilon_n) > 1$ for all $n \geq 1$. Then, by Lemma 4.3, there exists $n_0 \in \mathbb{N}$ and $\rho > 0$ such that $u(t, \varepsilon_n) \geq 1 + \rho > 1$ for all $n \geq n_0$ and $t \in [0, \frac{T}{2}]$. By our assumptions in this special case, we can infer from (26) that

$$v(t, \varepsilon_n) = v(0, \varepsilon_n) = v_0(\varepsilon_n) > 1$$

for all $t \in [0, \frac{T}{2}]$ and $n \geq 1$. Thus, by (22), $u'(t, \varepsilon_n) < 0$ for every $t \in [0, \frac{T}{2}]$. Let $r(\varepsilon_n)$ be the first zero, or node, of $1 - u(\cdot, \varepsilon_n)$ in $[0, T]$. As illustrated in Figure 5, for small $n$, $r(\varepsilon_n)$ might lie in $(0, \frac{T}{2})$.

Figure 5. Behavior of $u(t, \varepsilon_n)$ and $v(t, \varepsilon_n)$ in Case 1.A for small $n$. 
Nevertheless, without lost of generality, choosing an appropriate subsequence if necessary, we can assume that
\[ T > \lim_{n \to \infty} r(\varepsilon_n) = r_{\max} > \frac{T}{2}, \]
because, thanks to Lemma 4.3, \( r_{\max} \leq \frac{T}{2} \) cannot occur and, by periodicity, we cannot have \( r_{\max} \geq T \). Thus, there exists an integer \( n_0 \) such that \( r(\varepsilon_n) > \frac{T}{2} \) for every \( n \geq n_0 \). This is the situation illustrated in Figure 6. Consequently, \( u(\varepsilon_n) > 1 \) for sufficiently large \( n \), which implies, by Lemma 4.2 (e), that \( v''(\frac{T}{2}) > 0 \) as illustrated by Figure 6. So, according to the properties established by Lemma 4.2, in Case 1.A the graphs of \( u(t,\varepsilon_n) \) and \( v(t,\varepsilon_n) \) for sufficiently large \( n \) should be like sketched in Figure 6, where the number of nodes of \( 1 - u \) and \( 1 - v \) have been represented in a situation of minimal complexity.

\[ \text{Figure 6. Behavior of } u(t,\varepsilon_n) \text{ and } v(t,\varepsilon_n) \text{ in Case 1.A for large } n. \text{ Notice that } v \text{ is constant on } [0,T/2] \text{ while, on the same interval, } u \text{ is near to a constant for large } n. \]

On the other hand, due to (24), the l'Hôpital rule yields
\[ \lim_{t \to \frac{T}{2}} \frac{\beta(t)}{\varphi(t)} = \lim_{t \to \frac{T}{2}} \frac{\beta'(t)}{\varphi'(t)} = \frac{\beta'(\frac{T}{2})}{\varphi'(\frac{T}{2})} > 0, \quad \lim_{t \to T} \frac{\beta(t)}{\varphi(t)} = \lim_{t \to T} \frac{\beta'(t)}{\varphi'(t)} = \frac{\beta'(T)}{\varphi'(T)} > 0. \]

Thus, the next estimate holds
\[ \frac{1}{\varepsilon} m := \frac{1}{\varepsilon} \min_{t \in [\frac{T}{2},T]} \frac{\beta(t)}{\varphi(t)} \leq \frac{1}{\varepsilon} \frac{\beta(t)}{\varphi(t)} \leq \frac{1}{\varepsilon} \max_{t \in [\frac{T}{2},T]} \frac{\beta(t)}{\varphi(t)} =: \frac{1}{\varepsilon} M. \quad (31) \]

Moreover, according to (22), the next identity holds
\[ \frac{u'(t,\varepsilon_n)(-1 + u(t,\varepsilon_n))}{u(t,\varepsilon_n)} \frac{\beta(t)}{\varepsilon_n \varphi(t)} = \frac{v'(t,\varepsilon_n)(1 - v(t,\varepsilon_n))}{v(t,\varepsilon_n)} \quad (32) \]
for all \( t \in [\frac{T}{2},T] \). Using the estimate (31) and integrating (32) in \([\frac{T}{2},r(\varepsilon_n)]\), we find that
\[ \frac{m}{\varepsilon_n} \int_{\frac{T}{2}}^{r(\varepsilon_n)} \left( - \frac{u'(s,\varepsilon_n)}{u(s,\varepsilon_n)} + \frac{u'(s,\varepsilon_n)}{u(s,\varepsilon_n)} \right) ds \geq \int_{\frac{T}{2}}^{r(\varepsilon_n)} \left( \frac{v'(s,\varepsilon_n)}{v(s,\varepsilon_n)} - \frac{v'(s,\varepsilon_n)}{v(s,\varepsilon_n)} \right) ds. \]

We are choosing the lower estimate in (31) because
\[ \frac{u'(t,\varepsilon_n)(-1 + u(t,\varepsilon_n))}{u(t,\varepsilon_n)} < 0 \]
for all \( t \in (\frac{T}{2}, r(\varepsilon_n)) \) and \( n \geq n_0 \). Thus, developing the above integrals, shows that

\[
\frac{m}{\varepsilon_n} \left[ -\log u(r(\varepsilon_n), \varepsilon_n) + \log u(T, \varepsilon_n) + u(r(\varepsilon_n), \varepsilon_n) - u(T, \varepsilon_n) \right]
\geq \log v(r(\varepsilon_n), \varepsilon_n) - \log v(T, \varepsilon_n) - v(r(\varepsilon_n), \varepsilon_n) + v(T, \varepsilon_n)
\]

or, equivalently, since, by definition, \( u(r(\varepsilon_n), \varepsilon_n) = 1 \),

\[
\frac{m}{\varepsilon_n} \left[ \log u(T, \varepsilon_n) + 1 - u(T, \varepsilon_n) \right] \geq \log v(r(\varepsilon_n), \varepsilon_n) - \log v(0) - v(r(\varepsilon_n), \varepsilon_n) + v(0).
\]

Consequently, for sufficiently large \( n \), the next estimate holds

\[
\left( \frac{e^{u(T, \varepsilon_n) - 1}}{u(T, \varepsilon_n)} \right) \leq \frac{v(0) e^{v(r(\varepsilon_n), \varepsilon_n) - v(0)}}{v(r(\varepsilon_n), \varepsilon_n)},
\]

(33)

Now, we claim that there exists an integer \( n_1 \) such that

\[
u(T, \varepsilon_n) > 1 + \frac{\eta}{2} > 1 \quad \text{and} \quad v(r(\varepsilon_n), \varepsilon_n) > 1 + \eta > 1
\]

(34)

for all \( n \geq n_1 \). Indeed, by Lemma 4.3, we have that, for sufficiently large \( n \),

\[
|u(T, \varepsilon_n) - 1| + |v(T, \varepsilon_n) - 1| \geq \inf_{t \in [0, T]} \{ |u(t, \varepsilon_n) - 1| + |v(t, \varepsilon_n) - 1| \} > \eta.
\]

Moreover,

\[
\lim_{n \to \infty} v(T, \varepsilon_n) = 1.
\]

Thus, there exists an integer \( n_1 \) such that, for every \( n \geq n_1 \),

\[
|u(T, \varepsilon_n) - 1| > \eta - |v(T, \varepsilon_n) - 1| > \frac{\eta}{2}.
\]

On the other hand, as for every \( n \geq n_1 \)

\[
|u(r(\varepsilon_n), \varepsilon_n) - 1| + |v(r(\varepsilon_n), \varepsilon_n) - 1| \geq \inf_{t \in [0, T]} \{ |u(t, \varepsilon_n) - 1| + |v(t, \varepsilon_n) - 1| \} > \eta
\]

and

\[
u(r(\varepsilon_n), \varepsilon_n) = 1 \quad \text{for all} \quad n \in \mathbb{N},
\]

it becomes apparent that

\[
u(r(\varepsilon_n), \varepsilon_n) > 1 + \eta > 1
\]

for every \( n \geq n_1 \). Thus, (34) holds. Therefore, since function

\[
x \mapsto \frac{e^{x-1}}{x}
\]

is strictly increasing for all \( x > 1 \), the following estimate holds for every \( n \geq n_1 \):

\[
(1 + \delta) \frac{m}{\varepsilon_n} = \left( \frac{e^{1 + \frac{\eta}{2} - 1}}{1 + \frac{\eta}{2}} \right) \frac{m}{\varepsilon_n} < \left( \frac{e^{u(T, \varepsilon_n) - 1}}{u(T, \varepsilon_n)} \right) \frac{m}{\varepsilon_n} \leq \frac{v(0) e^{v(r(\varepsilon_n), \varepsilon_n) - v(0)}}{v(r(\varepsilon_n), \varepsilon_n)},
\]

(35)

where

\[
\delta := \left( 1 + \frac{\eta}{2} \right)^{-1} \sum_{k=2}^{\infty} \frac{(\eta/2)^k}{k!} > 0.
\]

Hence, by (35),

\[
\lim_{n \to \infty} \frac{v(0) e^{v(r(\varepsilon_n), \varepsilon_n) - v(\varepsilon_n)}}{v(r(\varepsilon_n), \varepsilon_n)} = \infty
\]

and, due to (34), we can conclude that

\[
\lim_{n \to \infty} v(r(\varepsilon_n), \varepsilon_n) = \infty.
\]
Therefore, the components \( v(\cdot, \varepsilon_n) \) blow up at \( r_{\text{max}} \) as \( n \to \infty \).

**Subcase 1.B:** Now, instead of \( u_0(\varepsilon_n) > 1 \), we suppose that \( u_0(\varepsilon_n) < 1 \) for all \( n \geq 1 \).

Then, by Lemma 4.3, there exists \( n_0 \in \mathbb{N} \) and \( \rho > 0 \) such that \( u(t, \varepsilon_n) \leq 1 - \rho < 1 \)
for all \( n \geq n_0 \) and \( t \in [0, \frac{T}{2}] \), like illustrated by Figure 7. As in the previous case, (26) implies that
\[
v(t, \varepsilon_n) = v(0, \varepsilon_n) = v_0(\varepsilon_n) > 1
\]
for all \( t \in [0, \frac{T}{2}] \) and \( n \geq 1 \). Thus, by (22), also in this case \( u'(t, \varepsilon_n) < 0 \) for each \( t \in [0, \frac{T}{2}] \). Moreover \( r(\varepsilon_n) > \frac{T}{2} \) for all \( n \geq n_0 \).

![Figure 7. Admissible \( u(t, \varepsilon_n) \) and \( v(t, \varepsilon_n) \) in Subcase 1.B for large \( n \). As in Figure 6, \( v \) is constant on \([0, T/2]\) while, on the same interval, \( u \) is near to a constant for large \( n \).](image)

According to Lemma 4.2 (e), since
\[
u(\frac{T}{2}, \varepsilon_n) \leq 1 - \rho < 1,
\]
it is apparent that \( v''(\frac{T}{2}, \varepsilon_n) < 0 \), as illustrated in Figure 7.

By the properties established by Lemma 4.2, the graphs of \( u(t, \varepsilon_n) \) and \( v(t, \varepsilon_n) \) for sufficiently large \( n \) look like shows Figure 7. As in the previous cases, the number of nodes of \( 1 - u \) and \( 1 - v \) have been represented in a situation of minimal complexity to be \( T \)-periodic. Let \( s(\varepsilon_n) \) be the very last node of \( u(\cdot, \varepsilon_n) - 1 \) in \([0, T]\). Since \( r(\varepsilon_n) < s(\varepsilon_n) \), it is clear that \( s(\varepsilon_n) \in (\frac{T}{2}, T) \) for sufficiently large \( n \). Finally, let \( z(\varepsilon_n) \) denote the very last node of \( v(t, \varepsilon_n) - 1 \) (see Figure 7).

Taking into account that, for every \( t \in (z(\varepsilon_n), s(\varepsilon_n)) \),
\[
\frac{u'(t, \varepsilon_n)(-1 + u(t, \varepsilon_n))}{u(t, \varepsilon_n)} < 0, \quad n \geq n_0,
\]
integrating (32) in the interval \((z(\varepsilon_n), s(\varepsilon_n))\) and using (31) yields
\[
\frac{m}{\varepsilon_n} \int_{z(\varepsilon_n)}^{s(\varepsilon_n)} \left( -\frac{u'(\sigma, \varepsilon_n)}{u(\sigma, \varepsilon_n)} + u'(\sigma, \varepsilon_n) \right) d\sigma \geq \int_{z(\varepsilon_n)}^{s(\varepsilon_n)} \left( \frac{v'(\sigma, \varepsilon_n)}{v(\sigma, \varepsilon_n)} - v'(\sigma, \varepsilon_n) \right) d\sigma.
\]

Thus, since
\[
v(z(\varepsilon_n), \varepsilon_n) = 1 \quad \text{and} \quad u(s(\varepsilon_n), \varepsilon_n) = 1,
\]
the next estimate holds for sufficiently large \( n \)
\[
\left( \frac{e^{u(z(\varepsilon_n), \varepsilon_n) - 1}}{u(z(\varepsilon_n), \varepsilon_n)} \right)^{\frac{m}{n}} \leq \frac{e^{u(s(\varepsilon_n), \varepsilon_n) - 1}}{v(s(\varepsilon_n), \varepsilon_n)}.
\]
Without loss of generality, choosing a subsequence if necessary, one can assume that
\[
\lim_{n \to \infty} z(\varepsilon_n) = z \in \left(\frac{T}{2}, T\right), \quad \lim_{n \to \infty} s(\varepsilon_n) = s_{\text{max}} \in \left(\frac{T}{2}, T\right).
\]
We claim that there exists \( \eta > 0 \) such that, for sufficiently large \( n \),
\[
u(z(\varepsilon_n), \varepsilon_n) > 1 + \eta > 1 \quad \text{and} \quad v(s(\varepsilon_n), \varepsilon_n) > 1 + \eta > 1.
\]
(37)
Indeed, by Lemma 4.3, there exists an integer \( n_0 \) such that, for every \( n \geq n_0 \),
\[
|u(z(\varepsilon_n), \varepsilon_n) - 1| + |v(z(\varepsilon_n), \varepsilon_n) - 1| \geq \inf_{t \in [0, T]} \{|u(t, \varepsilon_n) - 1| + |v(t, \varepsilon_n) - 1|\} > \eta.
\]
Thus, the first estimate of (37) holds. Similarly, since for every \( n \geq n_0 \)
\[
|u(s(\varepsilon_n), \varepsilon_n) - 1| + |v(s(\varepsilon_n), \varepsilon_n) - 1| \geq \inf_{t \in [0, T]} \{|u(t, \varepsilon_n) - 1| + |v(t, \varepsilon_n) - 1|\} > \eta,
\]
the second estimate of (37) also holds. Consequently, arguing as in the previous case, the estimate (36) provides us with the next one
\[
(1 + \delta) \frac{\varepsilon_n}{m} = \left(\frac{e^{1+\eta-1}}{1 + \eta}\right) \frac{\varepsilon_n}{m} < \left(\frac{e^{u(z(\varepsilon_n), \varepsilon_n) - 1}}{u(z(\varepsilon_n), \varepsilon_n)}\right) \frac{\varepsilon_n}{m} \leq \frac{e^{v(s(\varepsilon_n), \varepsilon_n) - 1}}{v(s(\varepsilon_n), \varepsilon_n)},
\]
where
\[
\delta := (1 + \eta)^{-1} \sum_{k=2}^{\infty} \frac{\eta^k}{k!} > 0.
\]
Therefore,
\[
\lim_{n \to \infty} v(s(\varepsilon_n), \varepsilon_n) = \infty.
\]
In other words, the components \( v(\cdot, \varepsilon_n) \) blow up at \( s_{\text{max}} \).

**Case 2:** There is a sequence \( \{\varepsilon_n\}_{n \geq 1} \), such that \( \lim_{n \to \infty} \varepsilon_n = 0, v_0(\varepsilon_n) < 1 \) for all \( n \geq 1 \), and \( \lim_{n \to \infty} v_0(\varepsilon_n) = 1 \).

When, in addition, \( u_0(\varepsilon_n) > 1 \) for all \( n \geq 1 \), arguing as in the Subcase 1.A, it is easily seen that \( v(t, \varepsilon_n) \) blows-up as \( n \to \infty \). Figure 8 shows the minimal complexity of \( T \)-periodic components in this case; \( a(\varepsilon_n) \) stands for the first node of \( v(\cdot, \varepsilon_n) - 1 \).

![Figure 8](image)

**Figure 8.** Admissible \( u(t, \varepsilon_n) \) and \( v(t, \varepsilon_n) \) in Case 2 for large \( n \).

If instead of \( u_n(\varepsilon_n) < 1 \), we assume that \( u_0(\varepsilon_n) < 1 \) for all \( n \geq 1 \), then adapting the proof of the Subcase 1.B, it is apparent that \( v(t, \varepsilon_n) \) blows-up as \( n \to \infty \). Figure 9 shows the minimal complexity of \( T \)-periodic components in this particular case.
Figure 9. Admissible $u(t, \varepsilon_n)$ and $v(t, \varepsilon_n)$ in Case 2 for large $n$.

**Case 3:** There is a sequence $\{\varepsilon_n\}_{n \geq 1}$ such that $\lim_{n \to \infty} \varepsilon_n = 0$ and, for some $\rho > 0$, $v_0(\varepsilon_n) < 1 - \rho$ for all $n \geq 1$. Then, according to (28),

$$0 < \frac{A}{\varepsilon_n} = \frac{-1}{1 - v_0(\varepsilon_n)} \int_{T/2}^{T} \varphi(s)(1 - v(s, \varepsilon_n))ds = \frac{1}{1 - v_0(\varepsilon_n)} \int_{T/2}^{T} \varphi(s)(v(s, \varepsilon_n) - 1)ds.$$

As $v_0(\varepsilon_n) < 1 - \rho$, it is clear that $\rho < 1 - v_0(\varepsilon_n)$ for every $n \geq 1$. Thus,

$$\frac{A}{\varepsilon_n} = \frac{1}{1 - v_0(\varepsilon_n)} \int_{T/2}^{T} \varphi(s)(v(s, \varepsilon_n) - 1)ds < \frac{1}{\rho} \int_{T/2}^{T} \varphi(s)(v(s, \varepsilon_n) - 1)ds \leq \frac{1}{\rho} \int_{T/2}^{T} \varphi(s) ds \left( \|v(\cdot, \varepsilon_n)\|_{C[\frac{T}{2}, T]} - 1 \right).$$

Therefore,

$$\lim_{n \to \infty} \max_{x \in [\frac{T}{2}, T]} v(x, \varepsilon_n) = \infty$$

and the proof is also completed in this case.

**Case 4:** There is a sequence $\{\varepsilon_n\}_{n \geq 1}$ such that $\lim_{n \to \infty} \varepsilon_n = 0$ and $v_0(\varepsilon_n) = 1$ for all $n \geq 1$. Then, due to (26), we have that $v(t, \varepsilon_n) = 1$ for all $t \in [0, \frac{T}{2}]$ and $n \geq 1$, like illustrated in Figure 10.

**Subcase 4.A:** Suppose, in addition, that $u_0(\varepsilon_n) > 1$ for each $n \geq 1$, like in Figure 10. According to Lemma 4.2, $1 - v(\cdot, \varepsilon_n)$ has finitely many zeroes in the interval $(\frac{T}{2}, T)$. Figure 10 shows a case with exactly one zero. Necessarily, the number of

Figure 10. Admissible components with $u_0(\varepsilon_n) > 1$ for sufficiently large $n \geq 1$. 
zeroes of $1 - v(\cdot, \varepsilon_n)$ is odd. Indeed, if it would be even, $1 - v(\cdot, \varepsilon_n)$ would have an odd number of critical points, which entails the existence of an odd number of zeroes of the function $1 - u(\cdot, \varepsilon_n)$ in the interval $(\frac{T}{2}, T)$. But this would contradict the periodicity of $u$. Therefore, $1 - v(\cdot, \varepsilon_n)$ has an odd number of zeroes. Now, adapting the argument of the Subcase 1.A, it readily follows that $v$ blows-up as $n \to \infty$.

Subcase 4.B: Now, suppose that, in addition, that $u_0(\varepsilon_n) < 1$ for all $n \geq 1$. then, the same argument of the previous case shows that $1 - v(\cdot, \varepsilon_n)$ has an odd number of zeroes in the interval $(\frac{T}{2}, T)$, like shown in Figure 11. The blow-up of $v(\cdot, \varepsilon_n)$ as $n \to \infty$ can be shown by adapting the argument of the Subcase 1.B. This ends the proof.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure11.png}
\caption{Admissible components in the Subcase 4.B for sufficiently large $n$.}
\end{figure}

Appendix: On the Volterra model with periodic coefficients. The classical predator-prey model is a planar system of the form

\begin{equation}
\begin{align*}
x' &= x(a - by), \\
y' &= y(-c + dx),
\end{align*}
\end{equation}

proposed by Vito Volterra in 1926 to explain some statistics (provided by the biologist Umberto D’Ancona) about the percentage of selachians in the north Adriatic sea (see [4], [25]). The main assumptions of the model involve the fact that all the coefficients $a, b, c, d$ are positive. In this manner, in the absence of predators, the prey population $x(t)$ is supposed to grow in a Malthusian way, exponentially, while, in absence of the prey, the predator population decays exponentially. According to [25],

“the term $xy$ can be thought of as representing the conversion of energy from one source to another: $bxy$ is taken from the prey and $dxy$ accrues to the predators”.

This model is also named after Alfred J. Lotka, who in 1920 proposed it for mimicking an hypothetical chemical reaction mechanism. A natural, more realistic, extension of (A1) considers the fact that all the dynamics occurs in the frame of a periodic (seasonally varying) environment. Incorporating seasonal effects to the prototype model (A1), one is naturally lead to

\begin{equation}
\begin{align*}
x' &= x(a(t) - b(t)y), \\
y' &= y(-c(t) + d(t)x),
\end{align*}
\end{equation}
where $a,b,c,d : \mathbb{R} \to \mathbb{R}$ are periodic coefficients of a common period $T > 0$. Although the intrinsic growth rates and the decay coefficients may change during the time interval $[0,T]$, to be consistent with the original hypotheses in the Volterra model, one has to assume the positivity of the averages of these coefficients. Similarly, to be consistent with the fact that $x(t)$ and $y(t)$ represent, respectively, the prey and the predators, requires to impose that

$$b(t) \geq 0, \quad d(t) \geq 0. \quad (A3)$$

The fact that $b(t)$ and $d(t)$ may vanish on a subinterval of $[0,T]$ mimics the (real) possibility that, seasonally, the predation/hunting is absent. The existence of periodic solutions for predator-prey systems with periodic coefficients was established by Cushing in [7] and Butler and Freedman [5] using bifurcation techniques. The next result provides a general existence principle for coexistence states of (A2) under a minimal set of assumptions. In this result, we restrict ourselves to consider the case of continuous coefficients, in the same vein as in the previous sections, though the same result holds for general $T$-periodic coefficients in $L^1(0,T)$.

**Theorem A.1.** Assume (A3). Then, the system (A2) has a $T$-periodic solution $(\tilde{x}(t), \tilde{y}(t))$ with $\tilde{x}(t) > 0$ and $\tilde{y}(t) > 0$ for all $t \in [0,T]$, if and only if

$$\int_0^T a(t) \, dt > 0 \quad \text{and} \quad \int_0^T c(t) \, dt > 0. \quad (A4)$$

**Proof.** Suppose that (A2) has a componentwise positive $T$-periodic solution, $(\tilde{x}(t), \tilde{y}(t))$. Then, by the uniqueness of the associated Cauchy problem, $\tilde{x}(t) > 0$ and $\tilde{y}(t) > 0$ for all $t \in [0,T]$ and hence, for every $t \in [0,T]$,

$$\frac{\dot{x}(t)}{x(t)} = a(t) - b(t)\tilde{y}(t), \quad -\frac{\dot{y}(t)}{y(t)} = c(t) - d(t)\tilde{x}(t).$$

Therefore, integrating on $[0,T]$ establishes the necessity of (A4) for the existence of a coexistence state.

Conversely, let us assume (A4) and re-write the system (A2) in the form

$$x' = xP(t,y), \quad y' = yQ(t,x), \quad (A5)$$

with

$$P(t,y) := a(t) - b(t)y \quad \text{and} \quad Q(t,x) := -c(t) + d(t)x.$$  

Let $M > 0$ be a sufficiently large constant such that

$$\max \left\{ \frac{\int_0^T a(t) \, dt}{\int_0^T b(t) \, dt}, \frac{\int_0^T c(t) \, dt}{\int_0^T d(t) \, dt} \right\} < M$$

and set

$$P_\infty(t) := a(t) - Mb(t), \quad Q_\infty(t) := -c(t) + Md(t).$$

Using the fact that $P(t,y)$ is non-increasing in $y$ and $Q(t,x)$ is non-decreasing in $x$, it becomes apparent that

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

uniformly in $t \in [0,T]$. Thus, we have entered in the setting of [11, Th. 3], which implies the existence of, at least, one $T$-periodic solution of (A5), and hence of (A2),
because the next conditions
\[ \int_0^T P(t,0) \, dt = \int_0^T a(t) \, dt > 0 > \int_0^T a(t) \, dt - M \int_0^T b(t) \, dt = \int_0^T P_\infty(t) \, dt \]
\[ \int_0^T Q(t,0) \, dt = - \int_0^T c(t) \, dt < 0 < - \int_0^T c(t) \, dt + M \int_0^T d(t) \, dt \]
\[ = \int_0^T Q_\infty(t) \, dt \]
are satisfied. Although the second part of [11, Th. 3], the one discussing the existence of subharmonics, requires the strict monotonicity of either \( P(t, \cdot) \) or \( Q(t, \cdot) \) for all \( t \in [0, T] \), its first part, not requiring any strict monotonicity, can be applied here.

Clearly, Theorem A.1 justifies the passage from the system (2) to the system (3), and hence our motivation in studying (1).

We conclude this paper with a brief additional discussion on our model, which is a prototype that allows \( \alpha(t) \beta(t) \) not only vanishing on a subinterval of \([0, T]\) but also the possibility that the supports of \( \alpha(t) \) and \( \beta(t) \) do not coincide. Although from the point of view of its applications in Population Dynamics, there is a strong debate concerning the validity of the classical predator-prey model of Lotka–Volterra type, which is (1) with \( \alpha(t) \) and \( \beta(t) \) positive constants, the basic features of this model still conform the basis upon which the mathematical theory of predation is built. According to ecologists, predation is essentially consumption of one organism (the prey) by another one (the predator), in which the prey is alive when the predator first attacks it. [1]. Incorporating to the simplest prototype models saturation effects for the predators does not really change the most basic features of these models, though might make them more realistic, of course.

In nature, there are many examples in which a predator, or a prey, maintains a fairly constant density in spite of the fluctuations of its prey. In general, the hunting-collecting processes adapt to these dynamics. While within a certain period of the year the predators damage the prey population by hunting their individuals and collecting them on their stocks, in another period they stop hunting the preys and simply consume the ones collected, the prey being unaffected by the action of the predators during these periods. Naturally, these periods can overlap or not, which is reflected by the length of the support of the product function \( \alpha(t) \beta(t) \) in model (1).

A very concrete example which fits very well within the setting of the model (1) takes place in the Mediterranean pine woods, where the \textit{Thaumetopoea pityocampa}, commonly refereed to as the pine processonary, defoliates the pines before being ready to pupate. Indeed, while attacking the pines and becoming pupates, the pine processonary density stays constant, whereas the pine density fluctuates. Moreover, depending on the impact of the defoliation, the new generation of caterpillars can increase or decrease before the beginning of a new cycle. Naturally, a very severe defoliation of one generation might seriously damage the individuals of the next one. The model (1) is the simplest prototype model mimicking those real situations which are far from understood yet.
REFERENCES

[1] M. Begon, C. R. Townsend and J. L. Harper, *Ecology: From Individuals to Ecosystems*, 4th Edition, Blackwell Scientific Publications, United Kingdom, 2006.

[2] A. Boscaggin, Subharmonic solutions of planar Hamiltonian systems: A rotation number approach, *Adv. Nonlinear Stud.*, 11 (2011), 77–103.

[3] A. Boscaggin and F. Zanolin, Subharmonic solutions for nonlinear second order equations in presence of lower and upper solutions, *Discrete & Continuous Dynamical Systems - A*, 33 (2013), 89–110.

[4] M. Braun, *Differential Equations and Their Applications: An Introduction to Applied Mathematics*, Third edition, Applied Mathematical Sciences, 15. Springer-Verlag, New York-Berlin, 1983.

[5] G. J. Butler and H. I. Freedman, Periodic solutions of a predator-prey system with periodic coefficients, *Math Biosci.*, 55 (1981), 27–38.

[6] A. Casal, J. C. Eilbeck and J. López-Gómez, Existence and uniqueness of coexistence states for a predator-prey model with diffusion, *Diff. Int. Eqns.*, 7 (1994), 411–439.

[7] J. M. Cushing, Periodic time-dependent predator-prey systems, *SIAM J. Appl. Math.*, 32 (1977), 82–95.

[8] F. Dalbono and C. Rebelo, Poincaré-Birkhoff fixed point theorem and periodic solutions of asymptotically linear planar hamiltonian systems, *Rend. Sem. Mat. Univ. Pol. Torino*, 60 (2003), 233–263.

[9] E. N. Dancer, J. López-Gómez and R. Ortega, On the spectrum of some linear noncooperative weakly coupled elliptic systems, *Diff. Int. Eqns.*, 8 (1995), 515–523.

[10] T. R. Ding and F. Zanolin, Harmonic solutions and subharmonic solutions for periodic Lotka-Volterra systems, *Dynamical Systems (Tianjin, 1990/1991), Nankai Ser. Pure Appl. Math. Theoret. Phys.*, World Sci. Publ., River Edge, NJ, 4 (1993), 55–65.

[11] T. R. Ding and F. Zanolin, Periodic solutions and subharmonic solutions for a class of planar systems of Lotka-Volterra type, *World Congress of Nonlinear Analyst '92*, de Gruyter, Berlin, 1-4 (1996), 395–406.

[12] W. Y. Ding, Fixed points of twist mappings and periodic solutions of ordinary differential equations, *Acta Math. Sinica*, 25 (1982), 227–235.

[13] T. Dondé and F. Zanolin, Multiple periodic solutions for one-sided sublinear systems: A refinement of the Poincaré-Birkhoff approach, preprint, (2019), arXiv:1901.09406 [math.DS].

[14] A. Fonda, *Playing Around Resonance. An Invitation to the Search of Periodic Solutions for Second Order Ordinary Differential Equations*, Birkhäuser Advanced Texts, Birkhäuser/Springer, Cham, 2016.

[15] A. Fonda, M. Sabatini and F. Zanolin, Periodic solutions of perturbed hamiltonian systems in the plane by the use of Poincaré-Birkhoff theorem, *Topol. Meth. Nonlin. Anal.*, 40 (2012), 29–52.

[16] A. Fonda and R. Toader, Subharmonic solutions of Hamiltonian systems displaying some kind of sublinear growth, *Adv. Nonlinear Anal.*, 8 (2019), 583–602.

[17] A. Fonda and A. J. Ureña, A higher dimensional Poincaré-Birkhoff theorem for Hamiltonian flows, *Ann. Inst. H. Poincaré Anal. Non Linéaire*, 34 (2017), 679–698.

[18] A. R. 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.

[19] J. López-Gómez, A bridge between operator theory and mathematical biology, *Operator Theory and its Applications, Fields Inst. Comm. Amer. Math. Soc.*, Providence, RI, 25 (2000), 383–397.

[20] J. López-Gómez and E. Muñoz-Hernández, Global structure of subharmonics in a class of periodic predator-prey models, *Nonlinearity*, 33 (2020), 34–71.

[21] J. López-Gómez, R. Ortega and A. Tineo, The periodic predator-prey Lotka-Volterra model, *Adv. Diff. Eqns.*, 1 (1996), 403–423.

[22] J. López-Gómez and R. M. Pardo, The existence and the uniqueness for the predator-prey model with diffusion, *Diff. Int. Eqns.*, 6 (1993), 1025–1031.

[23] J. López-Gómez and R. M. Pardo, Invertibility of linear noncooperative elliptic systems, *Nonlin. Anal.*, 31 (1998), 687–699.
[24] A. Margheri, C. Rebelo and F. Zanolin, Maslov index, Poincaré-Birkhoff theorem and periodic solutions of asymptotically linear planar Hamiltonian systems, *J. Differential Equations*, 183 (2002), 342–367.

[25] J. D. Murray, *Mathematical Biology. I. An Introduction*, Third edition, Interdisciplinary Applied Mathematics, 17. Springer-Verlag, New York, 2002.

[26] C. Rebelo, A note on the Poincaré-Birkhoff fixed point theorem and periodic solutions of planar systems, *Nonlin. Anal.*, 29 (1997), 291–311.

Received July 2019; revised October 2019.

E-mail address: julian@mat.ucm.es
E-mail address: eduardmu@ucm.es
E-mail address: fabio.zanolin@uniud.it