Dedicated to the memory of Professor Andrzej Lasota

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CHAOTIC DYNAMICS IN THE VOLTERRA PREDATOR-PREY MODEL VIA LINKED TWIST MAPS

Abstract. We prove the existence of infinitely many periodic solutions and complicated dynamics, due to the presence of a topological horseshoe, for the classical Volterra predator-prey model with a periodic harvesting. The proof relies on some recent results about chaotic planar maps combined with the study of geometric features which are typical of linked twist maps.

Keywords: Volterra predator-prey system, harvesting, periodic solutions, subharmonics, chaotic–like dynamics, topological horseshoes, linked twist maps.

Mathematics Subject Classification: 34C25, 37E40, 92C20.

1. INTRODUCTION AND MAIN RESULTS

The classical Volterra predator-prey model concerns the first order planar differential system

$$\begin{cases} x' = x(a - by), \\ y' = y(-c + dx), \end{cases} \tag{E_0}$$

where $a,\ b,\ c,\ d > 0$ are constant coefficients. The study of system (E_0) is confined to the open first quadrant $(\mathbb{R}_0^+)^2$ of the plane, since $x(t) > 0$ and $y(t) > 0$ represent the size (number of individuals or density) of the prey and the predator populations, respectively. Such model was proposed by Vito Volterra in 1926 in an answer to D'Ancona's question about the percentage of selachians and food fish caught in the northern Adriatic Sea during a range of years covering the period of the World War I (see [4, 26] for a more detailed historical account).

System (E_0) is conservative and its phase-portrait is that of a global center at the point

$$P_0 := \left(\frac{c}{d}, \frac{a}{b}\right), \tag{1.1}$$

surrounded by periodic orbits (oriented counterclockwise), which are the level lines of the first integral

$$\mathcal{E}_0(x,y) := dx - c\log x + by - a\log y, \tag{1.2}$$

that we will call "energy" in analogy to mechanical systems. The choice of the sign in the definition of the first integral implies that $\mathcal{E}_0(x,y)$ achieves a strict absolute minimum at the point P_0.

According to Volterra's analysis of (E_0), the average of a periodic solution $(x(t),y(t))$, evaluated over a time-interval corresponding to its natural period, coincides with the coordinates of the point P_0.

In order to include the effects of fishing in the model, one can suppose that, during the harvesting time, both the prey and the predator populations are reduced at a rate proportional to the size of the population itself. This assumption leads to the new system

$$\begin{cases} x' = x(a_\mu - by), \\ y' = y(-c_\mu + dx), \end{cases} \tag{E_μ}$$

where

$$a_\mu := a - \mu \quad \text{and } c_\mu := c + \mu$$

are the modified growth coefficients which take into account the fishing rates $-\mu x(t)$ and $-\mu y(t)$, respectively. The parameter μ is assumed to be positive but small enough $(\mu < a)$ in order to prevent the extinction of the populations. System (E_μ) has the same form as (E_0); therefore, its phase-portrait is that of a global center at

$$P_\mu := \left(\frac{c+\mu}{d}, \frac{a-\mu}{b}\right). \tag{1.3}$$

The periodic orbits surrounding P_μ are the level lines of the first integral

$$\mathcal{E}_\mu(x,y) := dx - c_\mu \log x + by - a_\mu \log y. \tag{1.4}$$

The coordinates of P_μ coincide with the average values of the prey and the predator populations under the effect of fishing (see Figure 1). A comparison between the coordinates of P_0 and P_μ motivates the conclusion (*Volterra's principle*) that a moderate harvesting has a favorable effect on the prey population [4].

The Volterra system (also called Lotka-Volterra with reference to the work by Alfred Lotka, who in 1920 first used the same system as a description for certain chemical reactions) has been sometimes criticized by ecologists and biologists, who refused to consider such a model as accurate (see [4] for a discussion of this topic), and, in the course of years, many variants of it have been proposed. Volterra himself modified system (E_0) in [44,45], by replacing the Malthusian growth rates with logistic terms of Verhulst type (see also [26]). In order to incorporate the effects of a cyclic environment, periodic coefficients have been introduced both in the basic model and in its variants. The past forty years have witnessed a growing interest in such kind of models and several results have been obtained about the existence, multiplicity and stability of periodic solutions for Lotka-Volterra type predator-prey models with periodic coefficients [1–3, 6, 7, 9, 11–13, 15–17, 23, 24, 29, 43].

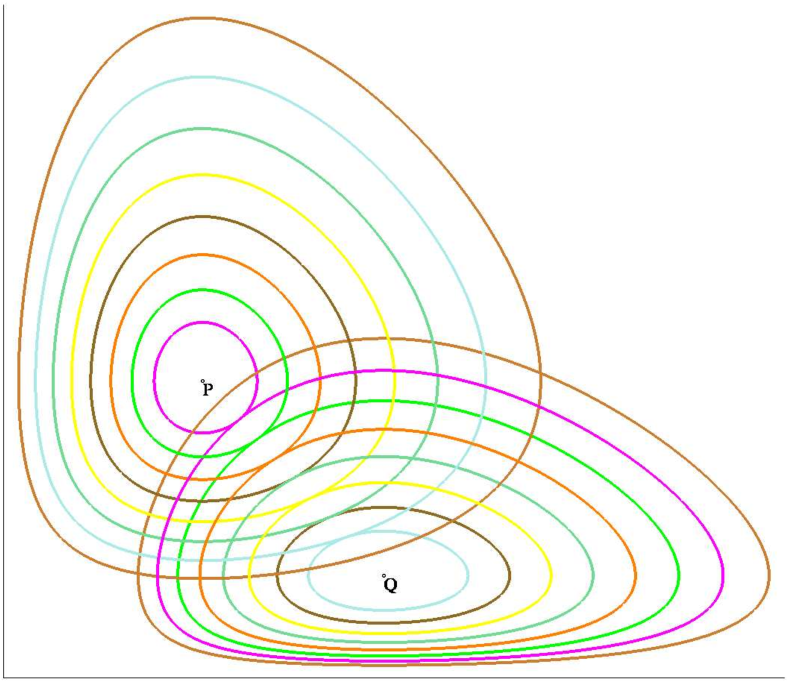

Fig. 1. In this picture we show some periodic orbits of the Volterra system (E_0) with center at $P = P_0$ as well as of the perturbed system (E_μ) with center at $Q = P_\mu$ (for a certain $\mu \in]0, a[$)

If we take the original Volterra model (E_0) and assume a seasonal effect on the coefficients, we are led to consider a new system of the form

$$\begin{cases} x' = x(a(t) - b(t)y), \\ y' = y(-c(t) + d(t)x), \end{cases} \tag{E}$$

where $a(\cdot), b(\cdot), c(\cdot), d(\cdot) : \mathbb{R} \to \mathbb{R}$ are periodic functions with a common period $T > 0$. In such a framework, it is natural to look for harmonic (i.e., T–periodic) or m-th order subharmonic solutions (i.e., mT–periodic, for some integer $m \geq 2$, with mT the minimal period in the set $\{jT : j = 1, 2, \dots\}$) having range in the open first quadrant (*positive solutions*). With this respect, we have the following theorem, which can be derived as a corollary of some results in [13] dealing with certain classes of time–periodic Kolmogorov systems. In Theorem 1.1 below, as well as in the other results of this paper, solutions are meant in the Carathéodory sense, that is, $(x(t), y(t))$ is absolutely continuous and satisfies system (E) for almost every $t \in \mathbb{R}$. Of course, such solutions are of class C^1 if the coefficients are continuous.

Theorem 1.1. *Suppose that $b(\cdot)$ and $d(\cdot)$ are continuous functions such that*

$$b(t) > 0, \ d(t) > 0, \quad \forall\, t \in [0,T]$$

and let $a(\cdot), c(\cdot) \in L^1([0,T])$ be such that

$$\bar{a} := \frac{1}{T}\int_0^T a(t)\,dt > 0, \quad \bar{c} := \frac{1}{T}\int_0^T c(t)\,dt > 0.$$

Then the following conclusions hold:

(e_1) *System (E) has at least one positive T-periodic solution;*
(e_2) *There exists an index $m^* \geq 2$ such that, for every $m \geq m^*$, there are at least two subharmonic solutions $(\tilde{x}_{1,m}, \tilde{y}_{1,m})$ and $(\tilde{x}_{2,m}, \tilde{y}_{2,m})$ of order m to (E) which do not belong to the same periodicity class and satisfy*

$$\begin{matrix} \lim_{m\to\infty} (\min \tilde{x}_{i,m}) = \lim_{m\to\infty} (\min \tilde{y}_{i,m}) = 0 \\ \lim_{m\to\infty} (\max \tilde{x}_{i,m}) = \lim_{m\to\infty} (\max \tilde{y}_{i,m}) = +\infty \end{matrix} \qquad (i = 1,2).$$

For a proof and other details, see [13]. We refer to [12] for detailed information about the subharmonic solutions of system (E) and to [1,23,29] for results about the stability and the number of solutions. See also [3, 11, 13] for more general conditions on the coefficients ensuring a priori bounds and existence of T-periodic positive solutions.

Let us for a moment come back to the original Volterra system with constant coefficients and suppose that the interaction between the two populations is governed by system (E_0) for a certain period of the season (corresponding to a time-interval of length r_0) and by system (E_μ) for the rest of the time (corresponding to a time-interval of length r_μ). Assume also that such alternation between (E_0) and (E_μ) occurs in a periodic fashion, so that

$$T := r_0 + r_\mu$$

is the period of the season. In other terms, we at first consider system (E_0) for $t \in [0, r_0[$. Next we switch to system (E_μ) at the time r_0 and assume that (E_μ) rules the dynamics for $t \in [r_0, T[$. Finally, we suppose that we switch back to system (E_0) at time $t = T$ and repeat the cycle with T-periodicity.

Such two-state alternating behavior can be equivalently described in terms of equation (E), by assuming

$$a(t) = \hat{a}_\mu(t) := \begin{cases} a & \text{for} \quad 0 \leq t < r_0, \\ a - \mu & \text{for} \quad r_0 \leq t < T, \end{cases}$$

$$c(t) = \hat{c}_\mu(t) := \begin{cases} c & \text{for} \quad 0 \leq t < r_0, \\ c + \mu & \text{for} \quad r_0 \leq t < T, \end{cases}$$

as well as

$$b(t) \equiv b, \ \ d(t) \equiv d,$$

with a, b, c, d positive constants and μ a parameter with $0 < \mu < a$. Hence we now can consider the system

$$\begin{cases} x' = x(\hat{a}_\mu(t) - by), \\ y' = y(-\hat{c}_\mu(t) + dx), \end{cases} \tag{E^*}$$

where the piecewise constant functions $\hat{a}_\mu$ and $\hat{c}_\mu$ are supposed to be extended to the whole real line by T-periodicity. Clearly, Theorem 1.1 holds for equation (E^*), ensuring the existence of at least one positive T-periodic solution and m-th order subharmonics of any sufficiently large order.

It is now our aim to prove that system (E^*) generates far richer dynamics. Indeed, we will show the presence of a *topological horseshoe* for the Poincaré map

$$\phi : (\mathbb{R}_0^+)^2 \to (\mathbb{R}_0^+)^2, \quad \phi(z) := \zeta(T, z),$$

where $\zeta(\cdot, z) = (x(\cdot, z), y(\cdot, z))$ is the solution of (E^*) starting from $z = (x_0, y_0) \in (\mathbb{R}_0^+)^2$ at the time $t = 0$. As a consequence, all the complexity which is associated with the horseshoe geometry (like, for instance, a semiconjugation to the Bernoulli shift, sensitivity to initial conditions, positive topological entropy, a compact set containing a dense subset of periodic points) will be guaranteed. To this goal, we apply recent developments [32] which connect the analysis of certain planar ODEs with the theory of *linked twist maps*. With such a term, one usually designates some geometric configurations characterized by the alternation of two planar homeomorphisms (or diffeomorphisms) which twist two overlapping annuli. More precisely, we have two annular regions $\mathcal{A}$ and $\mathcal{B}$ which cross in two disjoint topological rectangles $\mathcal{R}_1$ and $\mathcal{R}_2$. Each annulus is turned onto itself by a homeomorphism which leaves the boundaries of the annulus invariant. Both the maps act in their domains so that a twist effect is produced. This happens, for instance, when the angular speed is monotone with respect to the radius. Under certain assumptions, it is possible to prove the existence of a Smale horseshoe inside $\mathcal{R}_i$ $(i = 1, 2)$ [10]. Linked twist maps (LTMs) were originally studied in the 80s by Devaney [10], Burton and Easton [5] and Przytycki [36,37]. As observed in [10], such maps naturally appear in mathematical models for particle motions in a magnetic field and in differential geometry. Geometrical configurations related to LTMs can also be found in the restricted three-body problem [27, pp. 90–94]. In more recent years significant applications of LTMs have been found in the area of fluid mixing (see, for instance, [42, 48, 49]).

With the aid of Figure 2, we now try to explain how to show the presence of a horseshoe-type geometry for switching system (E^*). As the first step, we take two closed overlapping annuli made up by level lines of the first integrals associated to system (E_0) and (E_μ), respectively. In particular, the inner and outer boundaries of each annulus are closed trajectories surrounding the equilibrium point ($P = P_0$ for system (E_0) and $Q = P_\mu$ for system (E_μ)). Such annuli (that we call from now on $\mathcal{A}_P$ and $\mathcal{A}_Q$) intersect in two compact disjoint rectangular sets $\mathcal{R}_1$ and $\mathcal{R}_2$. The order in which we decide to name the two regions $\mathcal{R}_1$ and $\mathcal{R}_2$ is completely arbitrary. Whenever we enter a setting like that described in Figure 2, we say that the annuli $\mathcal{A}_P$ and $\mathcal{A}_Q$ are *linked together*. Technical conditions on the energy level lines defining $\mathcal{A}_P$ and $\mathcal{A}_Q$, which ensure the linking condition, are presented in Section 2.

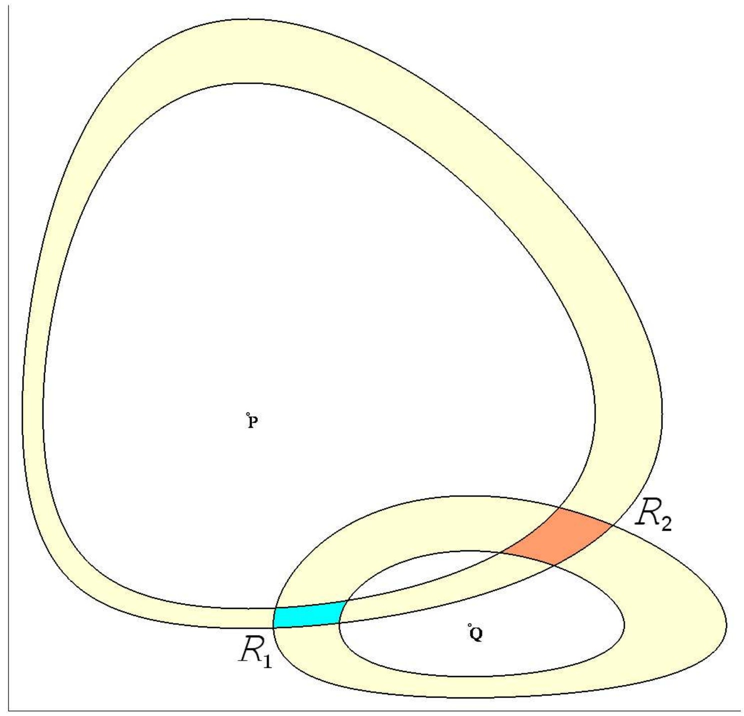

Fig. 2. The two annular regions $\mathcal{A}_P$ and $\mathcal{A}_Q$ (centered at P and Q, respectively) are linked together. We have drawn with a darker color the two rectangular sets $\mathcal{R}_1$ and $\mathcal{R}_2$ where they meet

As the second step, we give an "orientation" to $\mathcal{R}_i$ (for $i = 1, 2$) by selecting, in the boundary, two disjoint compact arcs (i.e. homeomorphic images of the compact unit interval of the real line) that we denote by $\mathcal{R}^-_{i,\,left}$ and $\mathcal{R}^-_{i,\,right}$ and call the *left* and the *right* sides of $\partial\mathcal{R}_i$. We also set

$$\mathcal{R}^-_i := \mathcal{R}^-_{i,\,left} \cup \mathcal{R}^-_{i,\,right}.$$

The closure of $\partial\mathcal{R}_i \setminus \mathcal{R}^-_i$ is denoted by $\mathcal{R}^+_i$. It consists of two disjoint components which are compact arcs that we name the *down* and *up* sides of $\partial\mathcal{R}_i$ (for a precise definition of the *oriented rectangle*, see Section 3). In the specific example of Figure 2, we orientate $\mathcal{R}_1$ and $\mathcal{R}_2$ as follows. We take as $\mathcal{R}^-_1$ the intersection of $\mathcal{R}_1$ with the inner and outer boundaries of $\mathcal{A}_P$ and as $\mathcal{R}^-_2$ the intersection of $\mathcal{R}_2$ with the inner and outer boundaries of $\mathcal{A}_Q$. The way in which we choose to name (as left/right) the two components of $\mathcal{R}^-_i$ is inessential for the rest of the discussion. Just to fix the attention, let us say that we call "left" the component of $\mathcal{R}^-_1$ which is closer to P and the component of $\mathcal{R}^-_2$ which is closer to the equilibrium point Q (of course, the "right" components will be the other ones).

As the third step, we observe that the Poincaré map associated with (E^*) can be decomposed as

$$\phi = \phi_\mu \circ \phi_0,$$

where ϕ_0 is the Poincaré map of system (E_0) on the time-interval $[0, r_0]$ and ϕ_μ is the Poincaré map for (E_μ) on the time-interval $[0, r_\mu] = [0, T - r_0]$.
Consider also a path $\gamma : [0,1] \to \mathcal{R}_1$ with $\gamma(0) \in \mathcal{R}^-_{1,\,left}$ and $\gamma(1) \in \mathcal{R}^-_{1,\,right}$. As we will see in Section 2, the points of $\mathcal{R}^-_{1,\,left}$ move faster than those belonging to $\mathcal{R}^-_{1,\,right}$ under the action of system (E_0). Hence, if we choose the first switching time r_0 large enough, it is possible to make the path

$$[0,1] \ni \theta \mapsto \phi_0(\gamma(\theta))$$

turn in a spiral-like fashion inside the annulus $\mathcal{A}_P$ and cross at least twice the rectangular region $\mathcal{R}_2$ from $\mathcal{R}^-_{2,\,left}$ to $\mathcal{R}^-_{2,\,right}$. Thus we can select two sub-intervals of $[0,1]$ such that $\phi_0 \circ \gamma$ restricted to each of these intervals is a path which lies in $\mathcal{R}_2$ and connects the two components of $\mathcal{R}^-_2$.
Now, we observe that the points of $\mathcal{R}^-_{2,\,left}$ move faster than those belonging to $\mathcal{R}^-_{2,\,right}$ under the action of system (E_μ). Therefore, we can repeat the same argument as above and conclude that for a suitable choice of $r_\mu = T - r_0$ large enough we can transform, via ϕ_μ, any path in $\mathcal{R}_2$ joining the two components of $\mathcal{R}^-_2$ onto a path which crosses at least once $\mathcal{R}_1$ from $\mathcal{R}^-_{1,\,left}$ to $\mathcal{R}^-_{1,\,right}$.

As the final step, we complete our proof of the existence of chaotic-like dynamics by applying the topological lemma that we recall in Section 3 as Lemma 3.1 for the reader's convenience.

In conclusion, our main result can be stated as follows.

Theorem 1.2. *For any choice of positive constants a, b, c, d, μ with $\mu < a$ and for every pair $(\mathcal{A}_P, \mathcal{A}_Q)$ of linked together annuli, the following conclusion holds:*
For every integer $m \geq 2$ there exist two positive constants α and β, such that for each

$$r_0 > \alpha \quad \textit{and} \quad r_\mu > \beta,$$

the Poincaré map associated with system (E^*) induces chaotic dynamics on m symbols in $\mathcal{R}_1$ and in $\mathcal{R}_2$.

In view of our result, one could conclude that complex dynamics were already hidden in Volterra's work [44], since linked twist maps (of long periods) appear as a consequence of the monotonicity of the period map and of Volterra's two principles:

— *"Se si cerca di distruggere uniformemente e proporzionalmente al loro numero gli individui delle due specie, cresce la media del numero di individui della specie mangiata e diminuisce quella degli individui della specie mangiante";*

(If one tries to destroy uniformly and proportionally to their numbers the individuals of the two species, the average of the number of individuals of the eaten species increases and the one of the eating species decreases);

— *"Se si distruggono contemporaneamente e uniformemente individui delle due specie, cresce il rapporto dell'ampiezza della fluttuazione della specie mangiata all'ampiezza della fluttuazione della specie mangiante".*
(If one destroys at the same time and uniformly the individuals of the two species, the ratio between the amplitude of the fluctuation of the eaten species and the amplitude of the fluctuation of the eating species increases).

Indeed, the first principle says that the position of the center around which the annuli can be constructed varies according to the strength of the fishing, while the second principle implies that the shapes of the annuli are suitable for a linking (see [44, fig. 6]). The twist conditions on the boundaries for the associated Poincaré maps come from an analysis of the periods of the orbits (which was carried on by Volterra in the limit case, i.e., for orbits near the equilibrium points).

In order to clarify the meaning of Theorem 1.2, we introduce the precise concept of chaotic dynamics that we consider in this work. Our definition is a modification of the corresponding one in [20] and abstracts the usual interpretation of chaos as the possibility of realizing any coin-flipping sequence, by giving also a special emphasis to the presence of periodic orbits. Definitions presenting similar features have been considered by several authors dealing with nonautonomous ODEs with periodic coefficients [8,41,50], as well as in abstract theorems about periodic points and chaotic-like dynamics in metric spaces [40]. We refer to Section 3 for a more detailed discussion of the kind of complex dynamics involved in Definition 1.1 below.

Definition 1.1. Let Z be a metric space and $\psi : Z \supseteq D_\psi \to Z$ be a map. Let also $\mathcal{D} \subseteq D_\psi$ be a nonempty set and $m \geq 2$ be an integer. We say that ψ *induces chaotic dynamics on m symbols in $\mathcal{D}$* if there exist m pairwise disjoint (nonempty) compact sets

$$\mathcal{K}_1, \mathcal{K}_2, \ldots, \mathcal{K}_m \subseteq \mathcal{D},$$

such that, for each two-sided sequence of symbols

$$(s_i)_{i\in\mathbb{Z}} \in \Sigma_m := \{1, \ldots, m\}^{\mathbb{Z}},$$

there exists a two-sided sequence of points

$$(w_i)_{i\in\mathbb{Z}} \in \mathcal{D}^{\mathbb{Z}},$$

with

$$w_i \in \mathcal{K}_{s_i} \quad \text{and } w_{i+1} = \psi(w_i), \qquad \forall\, i \in \mathbb{Z}. \tag{1.5}$$

Moreover, if $(s_i)_{i\in\mathbb{Z}}$ is a k-periodic sequence (that is, $s_{i+k} = s_i, \forall\, i \in \mathbb{Z}$) for some $k \geq 1$, then there exists a k-periodic sequence $(w_i)_{i\in\mathbb{Z}}$ satisfying (1.5). When we wish to emphasise the role of the sets $\mathcal{K}_j$'s, we also say that ψ *induces chaotic dynamics on m symbols in the set $\mathcal{D}$ relatively to* $(\mathcal{K}_1, \ldots, \mathcal{K}_m)$.

From this definition it follows that if ψ is *continuous* and *injective* [1] on the set

$$\mathcal{K} := \bigcup_{j=1}^{m} \mathcal{K}_j \subseteq \mathcal{D},$$

then there exists a nonempty compact set

$$\mathcal{I} \subseteq \mathcal{K}$$

for which the following properties are fulfilled:

— $\mathcal{I}$ is invariant for ψ (i.e., $\psi(\mathcal{I}) = \mathcal{I}$);

— $\psi|_{\mathcal{I}}$ is semiconjugate to the Bernoulli shift on m symbols, that is, there exists a continuous map g of $\mathcal{I}$ onto Σ_m such that the diagram

$$\begin{array}{ccc} \mathcal{I} & \xrightarrow{\ \psi\ } & \mathcal{I} \\ {\scriptstyle g}\downarrow & & \downarrow{\scriptstyle g} \\ \Sigma_m & \xrightarrow[\ \sigma\ ]{} & \Sigma_m \end{array} \tag{1.6}$$

commutes, where σ is the Bernoulli shift on m symbols (i.e. $\sigma : \Sigma_m \to \Sigma_m$ is the homeomorphism defined by $\sigma((s_i)_i) := (s_{i+1})_i$, $\forall i \in \mathbb{Z}$);

— The counterimage $g^{-1}(\mathbf{s}) \subseteq \mathcal{I}$ of every k-periodic sequence $\mathbf{s} = (s_i)_{i\in\mathbb{Z}} \in \Sigma_m$ contains at least one k-periodic point.

For a proof, see Lemma 3.2 in Section 3. From the above properties it also follows that

$$h_{\text{top}}(\psi|_{\mathcal{I}}) \geq h_{\text{top}}(\sigma) = \log(m),$$

where h_{top} is topological entropy [47]. Moreover, according to [18, Lemma 4], there exists a (nonempty) compact invariant set $\mathcal{I}' \subseteq \mathcal{I}$ such that $\psi|_{\mathcal{I}'}$ reveals sensitive dependence on initial conditions, i.e., $\exists\, \delta > 0 : \forall w \in \mathcal{I}'$ there is a sequence w_i of points in $\mathcal{I}'$ such that $w_i \to w$ and for each $i \in \mathbb{N}$ there exists $m = m(i)$ with $\text{dist}(\psi^m(w_i), \psi^m(w)) \geq \delta$.

As remarked in [32], if we look at Definition 1.1 and its consequences in the context of concrete examples of ODEs (for instance when ψ turns out to be the Poincaré map), condition (1.5) may be sometimes interpreted in terms of the oscillatory behavior of the solutions. Such situation occurred in [31,33] and takes place also for system (E^*). Indeed, from the proof of Theorem 1.2, one sees that it is possible to provide more precise conclusions in the statement of our main result.

[1] Such assumptions are fulfilled in our application: indeed, in Theorem 1.2, $\psi = \phi$ is a homeomorphism, being the Poincaré map associated with (E^*).

Namely, the following additional properties can be proved:
For every decomposition of the integer $m \geq 2$ *as*

$$m = m_1 m_2, \quad \text{with } m_1, m_2 \in \mathbb{N},$$

there exist nonnegative integers κ_1, κ_2, *with* $\kappa_1 = \kappa_1(r_0, m_1)$ *and* $\kappa_2 = \kappa_2(r_\mu, m_2)$, *such that, for each two-sided sequence of symbols*

$$\boldsymbol{s} = (s_i)_{i\in\mathbb{Z}} = (p_i, q_i)_{i\in\mathbb{Z}} \in \{1, \dots, m_1\}^{\mathbb{Z}} \times \{1, \dots, m_2\}^{\mathbb{Z}},$$

there exists a solution

$$\zeta_{\boldsymbol{s}}(\cdot) = \big(x_{\boldsymbol{s}}(\cdot), y_{\boldsymbol{s}}(\cdot)\big)$$

of (E^*) *with* $\zeta_{\boldsymbol{s}}(0) \in \mathcal{R}_1$ *such that* $\zeta_{\boldsymbol{s}}(t)$ *crosses* $\mathcal{R}_2$ *exactly* $\kappa_1 + p_i$ *times for* $t \in]iT, r_0 + iT[$ *and crosses* $\mathcal{R}_1$ *exactly* $\kappa_2 + q_i$ *times for* $t \in]r_0 + iT, (i+1)T[$. *Moreover, if* $(s_i)_{i\in\mathbb{Z}} = (p_i, q_i)_{i\in\mathbb{Z}}$ *is a periodic sequence, i.e.,* $s_{i+k} = s_i$ *for some* $k \geq 1$, *then* $\zeta_{\mathbf{s}}(t + kT) = \zeta_{\mathbf{s}}(t)$, $\forall\, t \in \mathbb{R}$.

Note that also the factoring $m = m_1 m_2$ with $m_1 = m$ and $m_2 = 1$ (or $m_1 = 1$ and $m_2 = m$) is allowed. For the precise connection between the role of the compact sets $\mathcal{K}_i$'s in Definition 1.1 and the oscillatory behavior of the solutions, we refer to the proof of Theorem 1.2 in the next section.
The constants α and β which represent the lower bounds for r_0 and r_μ can be estimated in terms of m_1 and m_2 and other geometric parameters, like the fundamental periods of the orbits bounding the linked annuli (see (2.1) and (2.5)).

We end this introductory section with a few observations about our main result.

First of all, we note that, according to Theorem 1.2, there is an abundance of chaotic regimes for system (E^*), provided that the time-interval lengths r_0 and r_μ (and, consequently, the period T) are sufficiently large. Indeed, we are able to prove the existence of chaotic invariant sets inside each intersection of two annular regions linked together. One could conjecture the presence of Smale horseshoes contained in such intersections, like in the classical case of the linked twist maps with circular annuli as domains [10]. On the other hand, in our approach, which is purely topological (like similar ones proposed in [14, 19, 51]), we just have to check a twist hypothesis on the boundary, without the need of verifying any hyperbolicity condition. Hence, our technique allows to detect the presence of chaotic features by means of elementary tools. This, of course, does not prevent the possibility of a further deeper analysis using more complex computations. We also observe that our result is stable with respect to small perturbations of the coefficients. Indeed, as it will be clear from the proof, whenever $r_0 > \alpha$ and $r_\mu > \beta$ are chosen in order to achieve the conclusion of Theorem 1.2, it follows that there exists a constant $\varepsilon > 0$ such that Theorem 1.2 applies to equation (E), too, provided that

$$\int_0^T |a(t) - \hat{a}_\mu(t)|\, dt < \varepsilon, \quad \int_0^T |c(t) - \hat{c}_\mu(t)|\, dt < \varepsilon,$$

$$\int_0^T |b(t) - b| \, dt < \varepsilon, \quad \int_0^T |d(t) - d| \, dt < \varepsilon.$$

Here, the T-periodic coefficients may be in $L^1([0,T])$ or even continuous or smooth functions (possibly of class C^∞).

A further remark concerns the fact that, in our model, we have assumed that the harvesting period starts and ends for both the species at the same moment. With this respect, one could face a more general situation where some phase–shift between the two harvesting intervals occurs. Such cases have been already explored in some biological models, mostly from the numerical point of view. See [28] for an example dealing with competing species and [38] for a predator-prey system. If we assume a phase-shift in the periodic coefficients, that is, if we consider

$$a(t) := \hat{a}_\mu(t - \theta_1) \quad \text{and } c(t) := \hat{c}_\mu(t - \theta_2),$$

for some $0 < \theta_1, \theta_2 < T$, and we also suppose that the length r_0 of the time-intervals without harvesting may be different for the two species (say $r_0 = r_a \in]0, T[$ in the definition of $\hat{a}_\mu$ and $r_0 = r_c \in]0, T[$ in the definition of $\hat{c}_\mu$), then the geometry of our problem turns out to be a combination of linked twist maps on two, three or four annuli (which are mutually linked together). In this manner, we increase the possibility of chaotic configurations, provided that the system is subject to the different regimes for sufficiently long time. For a pictorial comment, see Figure 3 where all the possible links among four annuli are realized.

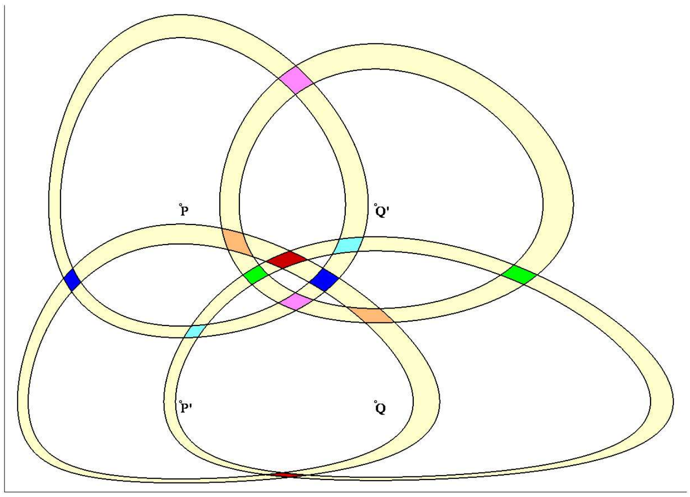

Fig. 3. We have depicted four linked annular regions bounded by energy level lines corresponding to Volterra systems with centers at $P = P_0$, $P' = (c/d, a_\mu/b)$, $Q = P_\mu$ and $Q' = (c_\mu/d, a/b)$, by highlighting the regions of mutual intersection, where it is possible to locate the chaotic invariant sets

As a final observation, we notice that our approach can also be applied (modulo more technicalities) to those time-periodic planar Kolmogorov systems [21]

$$x' = X(t,x,y), \quad y' = Y(t,x,y)$$

which possess dynamical features similar to the ones described above for the Volterra system. Investigations in this direction will be pursued elsewhere.

The paper is organized as follows. In Section 2 we provide the details for the proof of Theorem 1.2, in the sense that, following the argument described above, we justify all the steps by means of some technical estimates. In Section 3 we recall the topological tools, the corresponding notation and the abstract theorems which are employed along the paper. We conclude the article with a brief discussion on chaotic dynamics in the sense of Definition 1.1.

2. TECHNICAL ESTIMATES AND PROOF OF THE MAIN RESULT

Let us consider system (E_0) and let

$$\ell > \chi_0 := \mathcal{E}_0(P_0) = \min\{\mathcal{E}_0(x,y) : x > 0, y > 0\}.$$

The level line

$$\Gamma_0(\ell) := \{(x,y) \in (\mathbb{R}_0^+)^2 \,:\, \mathcal{E}_0(x,y) = \ell\}$$

is a closed orbit (surrounding P_0) which is run in counterclockwise sense, completing one turn over the fundamental period that we denote by $\tau_0(\ell)$. According to classical results on the period of the Lotka-Volterra system [39, 46], we know that the map

$$\tau_0 \,:]\chi_0, +\infty[\to \mathbb{R}$$

is strictly increasing with $\tau_0(+\infty) = +\infty$ and satisfies

$$\lim_{\ell \to \chi_0^+} \tau_0(\ell) = T_0 \,:= \frac{2\pi}{\sqrt{ac}}.$$

Similarly, if we consider system (E_μ) with $0 < \mu < a$, for

$$h > \chi_\mu := \mathcal{E}_\mu(P_\mu) = \min\{\mathcal{E}_\mu(x,y) : x > 0, y > 0\},$$

we denote by $\tau_\mu(h)$ the minimal period associated to the orbit

$$\Gamma_\mu(h) := \{(x,y) \in (\mathbb{R}_0^+)^2 \,:\, \mathcal{E}_\mu(x,y) = h\}.$$

Also in this case, we have that the map $h \mapsto \tau_\mu(h)$ is strictly increasing with $\tau_\mu(+\infty) = +\infty$ and

$$\lim_{h \to \chi_\mu^+} \tau_\mu(h) = T_\mu \,:= \frac{2\pi}{\sqrt{a_\mu c_\mu}}.$$

Before giving the details of the proof of our main result, we describe conditions on the energy level lines of two annuli $\mathcal{A}_P$ and $\mathcal{A}_Q$, centered at $P = P_0 = \left(\frac{c}{d}, \frac{a}{b}\right)$ and $Q = P_\mu = \left(\frac{c+\mu}{d}, \frac{a-\mu}{b}\right)$, respectively, sufficient to ensure that they are linked together. With this respect, we have to consider the intersections among the closed orbits around the two equilibria and the straight line r passing through the points P and Q, whose equation is $by + dx - a - c = 0$. We introduce an orientation on such line by defining an order "$\preceq$" between its points. More precisely, we set $A \preceq B$ (resp. $A \prec B$) if and only if $x_A \leq x_B$ (resp. $x_A < x_B$), where $A = (x_A, y_A)$, $B = (x_B, y_B)$. In this manner, the order on r is that inherited from the oriented x-axis, by projecting the points of r onto the abscissa. Assume now we have two closed orbits $\Gamma_0(\ell_1)$ and $\Gamma_0(\ell_2)$ for system (E_0), with $\chi_0 < \ell_1 < \ell_2$. Let us call the intersection points of r with such level lines $P_{1,-}, P_{1,+}$ with reference to ℓ_1, and $P_{2,-}, P_{2,+}$ with reference to ℓ_2, with

$$P_{2,-} \prec P_{1,-} \prec P \prec P_{1,+} \prec P_{2,+}.$$

Analogously, when we consider two orbits $\Gamma_\mu(h_1)$ and $\Gamma_\mu(h_2)$ for system (E_μ), with $\chi_\mu < h_1 < h_2$, we name the intersection points of r and these level lines $Q_{1,-}, Q_{1,+}$ with reference to h_1, and $Q_{2,-}, Q_{2,+}$ with reference to h_2, with

$$Q_{2,-} \prec Q_{1,-} \prec Q \prec Q_{1,+} \prec Q_{2,+}.$$

Then the two annuli $\mathcal{A}_P$ and $\mathcal{A}_Q$ turn out to be linked together if

$$P_{2,-} \prec P_{1,-} \preceq Q_{2,-} \prec Q_{1,-} \preceq P_{1,+} \prec P_{2,+} \preceq Q_{1,+} \prec Q_{2,+}.$$

For notational convenience, in the following proof, we have designated the basic set of m-symbols as $\{0, \dots, m-1\}$ instead of $\{1, \dots, m\}$.

Proof of Theorem 1.2. In line with the notation introduced above, we denote the level lines filling $\mathcal{A}_P$ by $\Gamma_0(\ell)$, where $\ell \in [\ell_1, \ell_2]$, for some $\chi_0 < \ell_1 < \ell_2$, so that

$$\mathcal{A}_P = \bigcup_{\ell_1 \leq \ell \leq \ell_2} \Gamma_0(\ell).$$

Analogously, we denote the level lines filling $\mathcal{A}_Q$ by $\Gamma_\mu(h)$, where $h \in [h_1, h_2]$, for some $\chi_\mu < h_1 < h_2$, so that we can write

$$\mathcal{A}_Q = \bigcup_{h_1 \leq h \leq h_2} \Gamma_\mu(h).$$

By construction, such annular regions turn out to be invariant under the dynamical systems generated by (E_0) and (E_μ), respectively. We now consider the two regions in which each annulus is cut by the line r (passing through P and Q) and we call such sets $\mathcal{A}_P^t$, $\mathcal{A}_P^b$, $\mathcal{A}_Q^t$ and $\mathcal{A}_Q^b$, in order to have $\mathcal{A}_P = \mathcal{A}_P^t \cup \mathcal{A}_P^b$ and $\mathcal{A}_Q = \mathcal{A}_Q^t \cup \mathcal{A}_Q^b$, where the sets with the superscript by t are the "upper" ones and the sets with the superscript by b are the "lower" ones, with respect to the line r. We will also name $\mathcal{R}^b$ the rectangular region in which $\mathcal{A}_P^b$ and $\mathcal{A}_Q^b$ meet and analogously we will denote by $\mathcal{R}^t$ the rectangular region being the intersection between $\mathcal{A}_P^t$ and $\mathcal{A}_Q^t$ (see Figure 4).

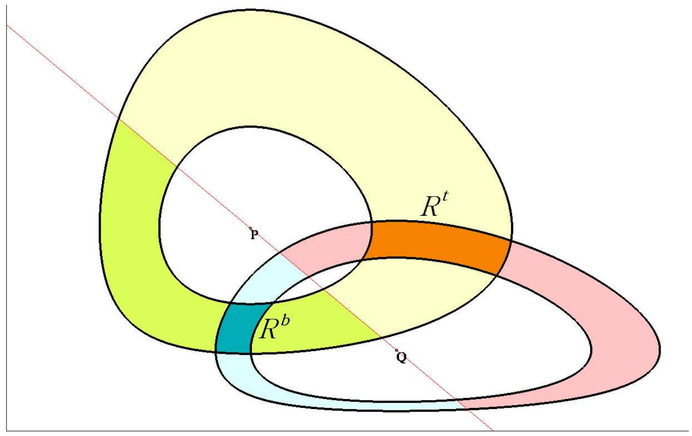

Fig. 4. For the two linked annuli in the picture (one around P and the other around Q), we have drawn in different colors the upper and lower parts (with respect to the dashed line r), as well as the intersection regions $\mathcal{R}^t$ and $\mathcal{R}^b$ between them. As a guideline for the proof, we recall that $\mathcal{A}_P$ is the annulus around P, having as its inner and outer boundaries the energy level lines $\Gamma_0(\ell_1)$ and $\Gamma_0(\ell_2)$. Similarly, $\mathcal{A}_Q$ is the annulus around Q, having as its inner and outer boundaries the energy level lines $\Gamma_\mu(h_1)$ and $\Gamma_\mu(h_2)$

Let

$$m_1 \geq 2 \quad \text{and}\; m_2 \geq 1$$

be two fixed integers (the case $m_1 = 1$ and $m_2 \geq 2$ can be treated in a similar manner and is therefore omitted).

As the first step, we are interested in the solutions of system (E_0) starting from $\mathcal{A}_P^b$ and crossing $\mathcal{A}_P^t$ at least m_1 times. After having performed the rototranslation of the plane $\mathbb{R}^2$ that brings the origin to the point P and makes the x-axis coincide with the line r, with the equations of the rototranslation being:

$$\begin{cases} \tilde{x} = (x - \frac{c}{d}) \cos \omega + (y - \frac{a}{b}) \sin \omega, \\ \tilde{y} = (\frac{c}{d} - x) \sin \omega + (y - \frac{a}{b}) \cos \omega, \end{cases}$$

where $\omega := \arctan(\frac{d}{b})$, it is possible to use the Prüfer transformation and introduce generalized polar coordinates, so that we can express the solution $\zeta(\cdot, z) = (x(\cdot, z), y(\cdot, z))$ of system (E_0) with initial point in $z = (x_0, y_0) \in \mathcal{A}_P^b$ through the radial coordinate $\rho(t, z)$ and the angular coordinate $\theta(t, z)$. Therefore, we can assume that $\theta(0, z) \in [-\pi, 0]$. For any $t \in [0, r_0]$ and $z \in \mathcal{A}_P^b$, let us also introduce the *rotation number*, that is, the quantity

$$\mathrm{rot}_0(t, z) := \frac{\theta(t, z) - \theta(0, z)}{2\pi},$$

that indicates the normalized angular displacement along the orbit of system (E_0) starting at z, during the time-interval $[0, t]$. The continuous dependence of the solutions on the initial data implies that the function $(t, z) \mapsto \theta(t, z)$ is continuous, as well as the map $(t,z) \mapsto \mathrm{rot}_0(t,z)$. From the definition of rotation number and by the star-shapedness of the level lines of $\mathcal{E}_0$ with respect to the point P, we infer that for every $z \in \Gamma_0(\ell)$ the following properties hold:

$$\begin{aligned} &\forall\, j \in \mathbb{Z}: \quad \mathrm{rot}_0(t,z) = j && \Longleftrightarrow\; t = j\,\tau_0(\ell), \\ &\forall\, j \in \mathbb{Z}: \quad j < \mathrm{rot}_0(t,z) < j+1 && \Longleftrightarrow\; j\,\tau_0(\ell) < t < (j+1)\,\tau_0(\ell) \end{aligned}$$

(if the annuli were not star-shaped, the inference "$\Longleftarrow$" would still be true). Although we have implicitly assumed that $\ell_1 \leq \ell \leq \ell_2$, such properties hold for every $\ell > \chi_0$.

Observe that, thanks to the fact that the time-map τ_0 is strictly increasing, we know that $\tau_0(\ell_1) < \tau_0(\ell_2)$. We shall use this condition to show that the twist property for the rotation number holds for sufficiently large time-intervals. Indeed, we claim that if we choose the switching time $r_0 \geq \alpha$, where

$$\alpha := \frac{(m_1 + 3 + \frac{1}{2})\,\tau_0(\ell_1)\,\tau_0(\ell_2)}{\tau_0(\ell_2) - \tau_0(\ell_1)}, \tag{2.1}$$

then, for any path $\gamma : [0,1] \to \mathcal{A}_P$, with $\gamma(0) \in \Gamma_0(\ell_1)$ and $\gamma(1) \in \Gamma_0(\ell_2)$, the following interval inclusion holds:

$$[\theta(r_0,\gamma(1)), \theta(r_0,\gamma(0))] \supseteq [2\pi n^*, 2\pi(n^* + m_1) - \pi], \text{ for some } n^* = n^*(r_0) \in \mathbb{N}. \tag{2.2}$$

To check our claim, we first note that for a path $\gamma(s)$ as above, there holds $\mathrm{rot}_0(t,\gamma(0)) \geq \lfloor t/\tau_0(\ell_1) \rfloor$ and $\mathrm{rot}_0(t,\gamma(1)) \leq \lceil t/\tau_0(\ell_2) \rceil$, for every $t > 0$ and so

$$\mathrm{rot}_0(t,\gamma(0)) - \mathrm{rot}_0(t,\gamma(1)) > t\,\frac{\tau_0(\ell_2) - \tau_0(\ell_1)}{\tau_0(\ell_1)\,\tau_0(\ell_2)} - 2 \quad \text{for} \quad t > 0.$$

Hence, for $t \geq \alpha$, with α defined as in (2.1), we obtain

$$\mathrm{rot}_0(t,\gamma(0)) > m_1 + 1 + \tfrac{1}{2} + \mathrm{rot}_0(t,\gamma(1)),$$

which, in turns, implies

$$\theta(t,\gamma(0)) - \theta(t,\gamma(1)) > 2\pi(m_1 + 1), \quad \forall\, t \geq \alpha.$$

Therefore, recalling the bound $2\pi(\lceil t/\tau_0(\ell_2) \rceil - \frac{3}{2}) < \theta(t,\gamma(1)) \leq 2\pi \lceil t/\tau_0(\ell_2) \rceil$, interval inclusion (2.2) is achieved for

$$n^* = n^*(r_0) := \left\lceil \frac{r_0}{\tau_0(\ell_2)} \right\rceil. \tag{2.3}$$

This proves our claim.

By (2.2), the continuity of $[0,1] \ni s \mapsto \theta(r_0,\gamma(s))$, and the Bolzano theorem, it now follows that

$$\{\theta(r_0,\gamma(s)),\, s \in [0,1]\} \supseteq [2\pi n^*, 2\pi(n^* + m_1 - 1) + \pi].$$

As a consequence, by the Bolzano theorem, there exist m_1 pairwise disjoint maximal intervals $[t_i', t_i''] \subseteq [0,1]$, for $i = 0, \dots, m_1 - 1$, such that

$$\theta(r_0, \gamma(s)) \in [2\pi n^* + 2\pi i, 2\pi n^* + \pi + 2\pi i],\ \forall s \in [t_i', t_i''],\ i = 0, \dots, m_1 - 1,$$

and $\theta(r_0, \gamma(t_i')) = 2\pi n^* + 2\pi i$, as well as $\theta(r_0, \gamma(t_i'')) = 2\pi n^* + \pi + 2\pi i$. Setting now

$$\mathcal{R}_1 := \mathcal{R}^b \quad \text{and} \quad \mathcal{R}_2 := \mathcal{R}^t,$$

we orientate such rectangular regions by choosing

$$\mathcal{R}^-_{1,\,left} := \mathcal{R}_1 \cap \Gamma_0(\ell_1) \quad \text{and} \quad \mathcal{R}^-_{1,\,right} := \mathcal{R}_1 \cap \Gamma_0(\ell_2),$$

as well as

$$\mathcal{R}^-_{2,\,left} := \mathcal{R}_2 \cap \Gamma_\mu(h_1) \quad \text{and} \quad \mathcal{R}^-_{2,\,right} := \mathcal{R}_2 \cap \Gamma_\mu(h_2)$$

(refer to Figure 4 for the configuration of the corresponding sets).

Finally, introducing the m_1 nonempty and pairwise disjoint compact sets

$$\mathcal{H}_i := \{z \in \mathcal{A}^b_P : \theta(r_0, z) \in [2\pi n^* + 2\pi i, 2\pi n^* + \pi + 2\pi i]\},\ i = 0, \dots, m_1 - 1,$$

we are ready to prove that

$$(\mathcal{H}_i, \phi_0) : \widetilde{\mathcal{R}_1} \Leftrightarrow\!\!\!\to \widetilde{\mathcal{R}_2}, \quad i = 0, \dots, m_1 - 1, \tag{2.4}$$

where we recall that ϕ_0 is the Poincaré map associated to system (E_0). The symbol "$\Leftrightarrow\!\!\!\to$" represents the *stretching along the paths* condition which is introduced in Definition 3.1 of Section 3.

Indeed, to prove (2.4), let us take a path $\gamma : [0,1] \to \mathcal{R}_1$, with $\gamma(0) \in \mathcal{R}^-_{1,\,left}$ and $\gamma(1) \in \mathcal{R}^-_{1,\,right}$. For $r_0 \geq \alpha$ and fixed $i \in \{0, \dots, m_1 - 1\}$, we know that there exists a sub-interval $[t_i', t_i''] \subseteq [0,1]$ such that $\gamma(t) \in \mathcal{H}_i$ and $\phi_0(\gamma(t)) \in \mathcal{A}^t_P$, for each $t \in [t_i', t_i'']$. Noting now that $\Gamma_\mu(\phi_0(\gamma(t_i'))) \leq h_1$ and $\Gamma_\mu(\phi_0(\gamma(t_i''))) \geq h_2$, it follows that there exists a sub-interval $[t_i^*, t_i^{**}] \subseteq [t_i', t_i'']$ such that $\phi_0(\gamma(t)) \in \mathcal{R}_2$, for $t \in [t_i^*, t_i^{**}]$ and $\phi_0(\gamma(t_i^*)) \in \mathcal{R}^-_{2,\,left}$, as well as $\phi_0(\gamma(t_i^{**})) \in \mathcal{R}^-_{2,\,right}$. Therefore, condition (2.4) is fulfilled.

Let us turn to system (E_μ). This time we focus our attention on the solutions of such system starting from $\mathcal{A}^t_Q$ and crossing $\mathcal{A}^b_Q$ at least m_2 times. Similarly as before, we assume to have performed a rototranslation of the plane that makes the x-axis coincide with the line r that brings the origin to the point Q, so that we can express the solution $\zeta(\cdot, w)$ of system (E_μ) with starting point in $w \in \mathcal{A}^t_Q$ through polar coordinates $(\tilde{\rho}, \tilde{\theta})$. In particular it holds that $\tilde{\theta}(0, w) \in [0, \pi]$. For any $t \in [0, r_\mu] = [0, T - r_0]$ and $w \in \mathcal{A}^t_Q$, the rotation number is now defined as

$$\text{rot}_\mu(t, w) := \frac{\tilde{\theta}(t, w) - \tilde{\theta}(0, w)}{2\pi}.$$

Since the time-map τ_μ is strictly increasing, it follows that $\tau_\mu(h_1) < \tau_\mu(h_2)$. We claim that if we choose a switching time $r_\mu \geq \beta$, with

$$\beta := \frac{(m_2 + 3 + \frac{1}{2})\, \tau_\mu(h_1)\, \tau_\mu(h_2)}{\tau_\mu(h_2) - \tau_\mu(h_1)}, \tag{2.5}$$

then, for any path $\sigma : [0,1] \to \mathcal{A}_Q$, with $\sigma(0) \in \Gamma_\mu(h_1)$ and $\sigma(1) \in \Gamma_\mu(h_2)$, the following interval inclusion is satisfied:

$$[\tilde{\theta}(r_\mu, \sigma(1)), \tilde{\theta}(r_\mu, \sigma(0))] \supseteq [\pi(2n^{**}+1), 2\pi(n^{**}+m_2)], \tag{2.6}$$

for some $n^{**} = n^{**}(r_\mu) \in \mathbb{N}$.

The claim can be proved with arguments analogous to the previous ones and therefore its verification is omitted. The nonnegative integer n^{**} has now to be chosen as

$$n^{**} := \left\lceil \frac{r_\mu}{\tau_\mu(h_2)} \right\rceil. \tag{2.7}$$

By (2.6), the continuity of $[0,1] \ni s \mapsto \tilde{\theta}(r_\mu, \sigma(s))$, and the Bolzano theorem, it follows that

$$\{\tilde{\theta}(r_\mu, \sigma(s)),\ s \in [0,1]\} \supseteq [2\pi n^{**} + \pi, 2\pi(n^{**}+m_2)].$$

As a consequence, the Bolzano theorem ensures the existence of m_2 pairwise disjoint maximal intervals $[s_i{}', s_i{}''] \subseteq [0,1]$, for $i = 0, \dots, m_2 - 1$, such that

$$\tilde{\theta}(r_\mu, \sigma(s)) \in [2\pi n^{**} + \pi + 2\pi i, 2\pi n^{**} + 2\pi + 2\pi i], \text{ for } s \in [s_i{}', s_i{}''],\ i = 0, \dots, m_2 - 1,$$

and

$$\tilde{\theta}(r_\mu, \sigma(s_i{}')) = 2\pi n^{**} + \pi + 2\pi i, \quad \text{as well as} \quad \tilde{\theta}(r_\mu, \sigma(s_i{}'')) = 2\pi n^{**} + 2\pi + 2\pi i.$$

For $\widetilde{\mathcal{R}_1}$ and $\widetilde{\mathcal{R}_2}$ as above and introducing the m_2 nonempty, compact and pairwise disjoint sets

$$\mathcal{K}_i := \{w \in \mathcal{A}_Q^t : \tilde{\theta}(r_\mu, w) \in [2\pi n^{**} + \pi + 2\pi i, 2\pi n^{**} + 2\pi + 2\pi i]\},\ i = 0, \dots, m_2 - 1,$$

we are in position to check that

$$(\mathcal{K}_i, \phi_\mu) : \widetilde{\mathcal{R}_2} \Leftrightarrow\!\!\!\!\to \widetilde{\mathcal{R}_1},\ i = 0, \dots, m_2 - 1, \tag{2.8}$$

where ϕ_μ is the Poincaré map associated to system (E_μ). Indeed, taking a path $\sigma : [0,1] \to \mathcal{R}_2$, with $\sigma(0) \in \mathcal{R}^-_{2,\,left}$ and $\sigma(1) \in \mathcal{R}^-_{2,\,right}$, for $r_\mu \geq \beta$ and for any $i \in \{0, \dots, m_2 - 1\}$ fixed, there exists a sub-interval $[s_i{}', s_i{}''] \subseteq [0,1]$ such that $\sigma(t) \in \mathcal{K}_i$ and $\phi_\mu(\sigma(t)) \in \mathcal{A}_Q^b$, for $t \in [s_i{}', s_i{}'']$. Since $\Gamma_0(\phi_\mu(\sigma(s_i{}'))) \leq \ell_1$ and $\Gamma_0(\phi_\mu(\sigma(s_i{}''))) \geq \ell_2$, there exists a sub–interval $[s_i^*, s_i^{**}] \subseteq [s_i{}', s_i{}'']$ such that $\phi_\mu(\sigma(t)) \in \mathcal{R}_1$, for $t \in [s_i^*, s_i^{**}]$ and $\phi_\mu(\sigma(s_i^*)) \in \mathcal{R}^-_{1,\,left}$, as well as $\phi_\mu(\sigma(s_i^{**})) \in \mathcal{R}^-_{1,\,right}$. Thus condition (2.8) is proved.

The stretching properties in (2.4) and (2.8) allow us to apply Lemma 3.1 of Section 3 and the thesis follows immediately. □

We observe that in our proof we have chosen the "lower" set $\mathcal{R}^b$ as $\mathcal{R}_1$ and the "upper" set $\mathcal{R}^t$ as $\mathcal{R}_2$. However, since the orbits of both systems (E_0) and (E_μ) are closed, the same argument also works (by slightly modifying some constants, if needed) if we choose $\mathcal{R}_1 = \mathcal{R}^t$ and $\mathcal{R}_2 = \mathcal{R}^b$.

3. TOPOLOGICAL TOOLS AND REMARKS ON CHAOTIC DYNAMICS

In this last section, we briefly recall the topological tools that we have employed along the paper. They are taken, with minor variations, from [32] and are based on some previous works [30, 31, 33, 35]. We start with some terminology.
Given a metric space Z, we define a *path* in Z as a continuous map $\gamma : \mathbb{R} \supseteq [0,1] \to Z$ (instead of $[0,1]$ one could take any compact interval $[s_0, s_1]$). A *sub-path* σ of γ is the restriction of γ to a compact sub-interval of its domain. An *arc* is an homeomorphic image of the compact interval $[0,1]$. By a *generalized rectangle* we mean a set $\mathcal{R} \subseteq Z$ which is homeomorphic to the unit square $\mathcal{Q} := [0,1]^2 \subseteq \mathbb{R}^2$.

If $\mathcal{R}$ is a generalized rectangle and $h : \mathcal{Q} \to h(\mathcal{Q}) = \mathcal{R}$ is a homeomorphism defining it, we call the *contour* $\vartheta\mathcal{R}$ of $\mathcal{R}$ the set

$$\vartheta\mathcal{R} := h(\partial\mathcal{Q}),$$

where $\partial\mathcal{Q}$ is the usual boundary of the unit square. Notice that $\vartheta\mathcal{R}$ is well defined, as it is independent of the choice of the homeomorphism h. We call an *oriented rectangle* the pair

$$\widetilde{\mathcal{R}} := (\mathcal{R}, \mathcal{R}^-),$$

where $\mathcal{R} \subseteq Z$ is a generalized rectangle and

$$\mathcal{R}^- := \mathcal{R}^-_{left} \cup \mathcal{R}^-_{right}$$

is the union of two disjoint compact arcs $\mathcal{R}^-_{left}, \mathcal{R}^-_{right} \subseteq \vartheta\mathcal{R}$ that we call the *left* and the *right* sides of $\mathcal{R}^-$. Once that $\mathcal{R}^-$ is fixed, we can also define $\mathcal{R}^+$ as the closure of $\vartheta\mathcal{R} \setminus \mathcal{R}^-$. In particular, we set

$$\mathcal{R}^+ := \mathcal{R}^+_{down} \cup \mathcal{R}^+_{up},$$

where $\mathcal{R}^+_{down}$ and $\mathcal{R}^+_{up}$ are two disjoint arcs. In the usual applications, the ambient space Z is just the Euclidean plane and the generalized rectangles are bounded by some orbit-segments, possibly associated with different systems.

The central concept in our approach is that of "stretching along the paths":

Definition 3.1. *Suppose that $\psi : Z \supseteq D_\psi \to Z$ is a map defined on a set D_ψ and let $\widetilde{X} := (X, X^-)$ and $\widetilde{Y} := (Y, Y^-)$ be oriented rectangles in a metric space Z. Let $\mathcal{K} \subseteq X \cap D_\psi$ be a compact set. We say that $(\mathcal{K}, \psi)$ stretches $\widetilde{X}$ to $\widetilde{Y}$ along the paths and write*

$$(\mathcal{K}, \psi) : \widetilde{X} \Leftrightarrow\!\!\!\to \widetilde{Y},$$

if the following conditions hold:

- *ψ is continuous on $\mathcal{K}$;*
- *for every path $\gamma : [0,1] \to X$ such that $\gamma(0) \in X^-_{left}$ and $\gamma(1) \in X^-_{right}$ (or $\gamma(0) \in X^-_{right}$ and $\gamma(1) \in X^-_{left}$), there exists a sub-interval $[t', t''] \subseteq [0,1]$ such that*

$$\forall\, t \in [t', t''] \quad \gamma(t) \in \mathcal{K}, \quad \psi(\gamma(t)) \in Y$$

and, moreover, $\psi(\gamma(t'))$ and $\psi(\gamma(t''))$ belong to different components of Y^-.

In the special case of $\mathcal{K} = X$, we simply write

$$\psi : \widetilde{X} \Longleftrightarrow\!\!\rightarrow \widetilde{Y}.$$

We are now in a position to introduce the result on the existence of chaotic dynamics for linked twist maps that we apply in the proof of Theorem 1.2.

Lemma 3.1. *Let Z be a metric space, let $\Phi : Z \supseteq D_\Phi \to Z$ and $\Psi : Z \supseteq D_\Psi \to Z$ be continuous maps and let $\widetilde{\mathcal{R}_1} := (\mathcal{R}_1, {\mathcal{R}_1}^-)$, $\widetilde{\mathcal{R}_2} := (\mathcal{R}_2, {\mathcal{R}_2}^-)$ be oriented rectangles in Z. Suppose that the following conditions are satisfied:*

(H_Φ) *there exist $m_1 \geq 1$ pairwise disjoint compact sets $\mathcal{H}_1, \ldots, \mathcal{H}_{m_1} \subseteq \mathcal{R}_1 \cap D_\Phi$ such that $(\mathcal{H}_i, \Phi) : \widetilde{\mathcal{R}_1} \Longleftrightarrow\!\!\rightarrow \widetilde{\mathcal{R}_2}$, for $i = 1, \ldots, m_1$;*

(H_Ψ) *there exist $m_2 \geq 1$ pairwise disjoint compact sets $\mathcal{K}_1, \ldots, \mathcal{K}_{m_2} \subseteq \mathcal{R}_2 \cap D_\Psi$ such that $(\mathcal{K}_i, \Psi) : \widetilde{\mathcal{R}_2} \Longleftrightarrow\!\!\rightarrow \widetilde{\mathcal{R}_1}$, for $i = 1, \ldots, m_2$.*

If at least one of m_1 and m_2 is greater then or equal to 2, then the composite map $\psi := \Psi \circ \Phi$ induces chaotic dynamics on $m_1 \times m_2$ symbols in the set

$$\mathcal{H}^* := \bigcup_{\substack{i=1,\ldots,m_1 \\ j=1,\ldots,m_2}} \mathcal{H}'_{i,j}, \quad \text{where } \mathcal{H}'_{i,j} := \mathcal{H}_i \cap \Phi^{-1}(\mathcal{K}_j).$$

Moreover, for each sequence of $m_1 \times m_2$ symbols

$$\boldsymbol{s} = (s_n)_n = (p_n, q_n)_n \in \{1, \ldots, m_1\}^{\mathbb{N}} \times \{1, \ldots, m_2\}^{\mathbb{N}},$$

there exists a compact connected set $\mathcal{C}_{\boldsymbol{s}} \subseteq \mathcal{H}'_{p_0,q_0}$ with

$$\mathcal{C}_{\boldsymbol{s}} \cap \mathcal{R}^+_{1,down} \neq \emptyset, \quad \mathcal{C}_{\boldsymbol{s}} \cap \mathcal{R}^+_{1,up} \neq \emptyset$$

and such that, for every $w \in \mathcal{C}_{\boldsymbol{s}}$, there exists a sequence $(y_n)_n$ with $y_0 = w$ and

$$y_n \in \mathcal{H}'_{p_n,q_n}, \quad \psi(y_n) = y_{n+1}, \; \forall\, n \geq 0.$$

Note that in Theorem 1.2 we have not used the last part of the previous lemma. Therefore, it would be possible to improve our main result on Lotka-Volterra systems by adding information about the existence of continua of points for which we have a control on the forward itineraries.

We end the paper with an attempt at clarifying the relationship between the concept of chaos expressed in Definition 1.1 and other ones available in the literature, with special reference to the semiconjugation with the Bernoulli shift and the density of the periodic points. Before giving the next lemmas, we just recall some basic definitions. We denote by $\Sigma_m = \{1, \ldots, m\}^{\mathbb{Z}}$ the set of the two-sided sequences of m symbols. Analogously, by $\Sigma_m^+ = \{1, \ldots, m\}^{\mathbb{N}}$ we mean the set of one-sided sequences of m symbols (where $\mathbb{N}$ is the set of nonnegative integers). Introducing the standard distance

$$d(\mathbf{s}', \mathbf{s}'') := \sum_{i \in \mathbb{I}} \frac{|s'_i - s''_i|}{m^{|i|+1}}, \quad \text{where } \mathbf{s}' = (s'_i)_{i\in\mathbb{I}},\ \mathbf{s}'' = (s''_i)_{i\in\mathbb{I}}, \tag{3.1}$$

for $\mathbb{I} = \mathbb{Z}$ and for $\mathbb{I} = \mathbb{N}$, we make Σ_m and Σ_m^+ compact metric spaces.

Our first result is quite classical. Indeed, the same conclusions of Lemma 3.2 have been obtained by several different authors dealing with similar situations (see, for instance, [40, Theorem 3]). Nonetheless, we give a detailed proof for the reader's convenience. We also thank Duccio Papini for useful discussions about this topic.

Lemma 3.2. *Let (Z, d_Z) be a metric space, $\psi : Z \supseteq D_\psi \to Z$ be a map which induces chaotic dynamics on $m \geq 2$ symbols in a set $\mathcal{D} \subseteq D_\psi$, relatively to $(\mathcal{K}_1, \dots, \mathcal{K}_m)$ (according to Definition 1.1). Assume also that ψ is continuous and injective on*

$$\mathcal{K} := \bigcup_{j=1}^{m} \mathcal{K}_j.$$

Define the nonempty compact set

$$\mathcal{I} := \bigcap_{j=-\infty}^{+\infty} \psi^{-j}(\mathcal{K}). \tag{3.2}$$

Then $\mathcal{I}$ is invariant for ψ and $\psi|_{\mathcal{I}}$ is semiconjugate to the two-sided m-shift, through a continuous surjection $g : \mathcal{I} \to \Sigma_m$ as in (1.6). *Moreover, the counterimage through g of any k-periodic sequence in Σ_m contains at least one k-periodic point of $\mathcal{I}$.*

Proof. First of all, we observe that $w \in \mathcal{I}$ if and only if there exists a full orbit, that is, a two-sided itinerary, $(w_i)_{i\in\mathbb{Z}}$ such that $w_0 = w$ and $\psi(w_{i-1}) = w_i \in \mathcal{K}$ for every $i \in \mathbb{Z}$. By the assumptions on ψ coming from Definition 1.1 and standard properties of compact sets, it follows immediately that $\mathcal{I}$ is a nonempty compact set such that $\psi(\mathcal{I}) = \mathcal{I}$.
As the next step, we introduce a function g_1, associating to any $w \in \mathcal{I}$ its corresponding full orbit

$$s_w := (w_i)_{i\in\mathbb{Z}},$$

that is, the sequence of points of the set $\mathcal{I}$ defined by

$$w_i := \psi^i(w), \quad \forall\, i \in \mathbb{Z},$$

with the usual convention $\psi^0 = \mathrm{Id}_{\mathcal{K}}$ and $\psi^1 = \psi$. The injectivity of ψ implies that the map

$$g_1 : w \mapsto s_w$$

is well defined. Recalling that the $\mathcal{K}_j$'s are pairwise disjoint, we know that for every term w_i of s_w there exists a unique label

$$s_i = s_i(w_i), \quad \text{with} \quad s_i \in \{1, \dots, m\},$$

such that $w_i \in \mathcal{K}_{s_i}$. Hence, also the map

$$g_2 : s_w \mapsto (s_i)_{i\in\mathbb{Z}} \in \Sigma_m \tag{3.3}$$

is well defined. Thus, if we set

$$g := g_2 \circ g_1 : \mathcal{I} \to \Sigma_m,$$

by Definition 1.1 we obtain a surjective map that makes diagram (1.6) commute. Moreover, the inverse image through g of any k-periodic sequence in Σ_m contains at least one k-periodic point of $\mathcal{I}$.
Finally, we show that g is continuous. To this end, we put

$$\epsilon := \min_{1 \leq i \neq j \leq m} d_Z(\mathcal{K}_i, \mathcal{K}_j) > 0$$

and note that the map $\psi|_{\mathcal{I}} : \mathcal{I} \to \psi(\mathcal{I}) = \mathcal{I}$ is a homeomorphism. Therefore the following property holds:

$$\forall\, n \in \mathbb{N},\ \exists\, \delta = \delta_n > 0 : \text{ for } u, v \in \mathcal{I}, \text{ with } s_u := (u_i)_{i \in \mathbb{Z}},\ s_v := (v_i)_{i \in \mathbb{Z}},$$

$$d_Z(u, v) < \delta \Longrightarrow d_Z(u_i, v_i) < \epsilon,\ \forall\, |i| \leq n \Longrightarrow s_i(u_i) = s_i(v_i),\ \forall\, |i| \leq n.$$

From this fact and the choice of the distance in Σ_m (see (3.1)), the continuity of g easily follows. □

The next result is just a more precise version of Lemma 3.2 with reference to the periodic points.

Lemma 3.3. *Under the same assumptions of Lemma 3.2, there exists a compact invariant set* $\Lambda \subseteq \mathcal{I}$ *such that* $\psi|_\Lambda$ *is semiconjugate to the two-sided* m*-shift, through the continuous surjection* $g|_\Lambda$ *(where* $g : \mathcal{I} \to \Sigma_m$ *is like in* (1.6)*). The set of the periodic points of* $\psi|_{\mathcal{I}}$ *is dense in* Λ *and, moreover, the counterimage through* g *of any* k*-periodic sequence in* Σ_m *contains at least one* k*-periodic point of* Λ.

Proof. For $\mathcal{I}$ defined as in (3.2), we consider the subset $\mathcal{P}$ of the periodic points of $\psi|_{\mathcal{I}}$, that is,

$$\mathcal{P} := \{w \in \mathcal{I} : \exists\, k \geq 1,\ \psi^k(w) = w\}$$

and define

$$\Lambda := \overline{\mathcal{P}}.$$

Since $\psi(\mathcal{P}) = \mathcal{P}$, it follows that $\psi(\Lambda) = \Lambda$. From the last statement in Lemma 3.2 we also find that $g(\mathcal{P})$ coincides with the subset of Σ_m made by the two-sided periodic sequences of m symbols, which is dense in Σ_m. This latter fact implies the surjectivity of $g|_\Lambda : \Lambda \to \Sigma_m$. The remaining properties are a straightforward consequence of the corresponding ones in Lemma 3.2. □

In both the above results, we have required the injectivity of the map ψ. This is not a heavy restriction in the applications to ODEs (like those in Section 1 and in [32, 33]), where ψ is the Poincaré map. Anyway, in the abstract setting of metric spaces and with reference to Definition 1.1, it is still possible to obtain some suitable versions of Lemma 3.2 and Lemma 3.3 for a map ψ which is continuous on $\mathcal{K}$, but without the assumption of injectivity. Such task can be accomplished in different ways. A first possibility is that of considering a semiconjugation with the Bernoulli shift on m symbols for one-sided sequences. Indeed, any initial point w uniquely determines the forward sequence $s_w^+ := (\psi^i(w))_{i\in\mathbb{N}}$, to which we can associate a well determined sequence of symbols $(s_i)_{i\in\mathbb{N}} \in \Sigma_m^+$ as in the definition of g_2 in (3.3). Another possibility is that of considering, in place of g, only the map g_2, that is, to associate to any full orbit $(w_i)_{i\in\mathbb{Z}}$, with $\psi(w_i) = w_{i+1}$, the sequence $(s_i)_{i\in\mathbb{Z}} \in \Sigma_m$ such that $w_i \in \mathcal{K}_{s_i}$. This second approach is followed by Lani-Wayda and Srzednicki in [22], where the authors obtain a variant of Lemma 3.3 for a set Λ replaced by the closure (denoted by $\mathcal{T}$) of the set of the terms of the periodic sequences in $\mathcal{K}$ which are full orbits of ψ (and project through g_2 onto a periodic sequence of Σ_m). Hence, in this case, commutative diagram (1.6) becomes

$$\begin{array}{ccc} \mathcal{T}^{\mathbb{Z}} & \xrightarrow{\psi^{\mathbb{Z}}} & \mathcal{T}^{\mathbb{Z}} \\ {\scriptstyle g_2}\downarrow & & \downarrow{\scriptstyle g_2} \\ \Sigma_m & \xrightarrow[\sigma]{} & \Sigma_m \end{array}$$

where $\psi^{\mathbb{Z}}\big((w_i)_{i\in\mathbb{Z}}\big) := (w_{i+1})_{i\in\mathbb{Z}}$.

4. CONCLUSION

It is a pleasure and an honor to have the possibility to dedicate our work to the memory of Professor Andrzej Lasota, who gave fundamental contributions in both the area of chaotic dynamics and the study of mathematical models for biological systems.

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REFERENCES

[1] Z. Amine, R. Ortega, *A periodic prey-predator system*, J. Math. Anal. Appl. **185** (1994) 2, 477–489.

[2] M. Bardi, *Predator-prey models in periodically fluctuating environments*, J. Math. Biol. **12** (1981) 1, 127–140.

[3] A. Battauz, *Coexistence states for periodic planar Kolmogorov systems*, Nonlinear Anal. **37** (1999) 6, Ser. A: Theory Methods, 735–749.

[4] M. Braun, *Differential equations and their applications*, fourth ed., Texts in Applied Mathematics, vol. 11, Springer-Verlag, New York, 1993, An introduction to Applied Mathematics.

[5] R. Burton, R.W. Easton, *Ergodicity of linked twist maps*, Global theory of dynamical systems (Proc. Internat. Conf., Northwestern Univ., Evanston, Ill., 1979) (Berlin), Lecture Notes in Math., vol. 819, Springer, Berlin, 1980, pp. 35–49.

[6] T.A. Burton, V. Hutson, *Permanence for nonautonomous predator-prey systems*, Differential Integral Equations **4** (1991) 6, 1269–1280.

[7] G.J. Butler, H.I. Freedman, *Periodic solutions of a predator-prey system with periodic coefficients*, Math. Biosci. **55** (1981) 1–2, 27–38.

[8] A. Capietto, W. Dambrosio, D. Papini, *Superlinear indefinite equations on the real line and chaotic dynamics*, J. Differential Equations **181** (2002) 2, 419–438.

[9] J.M. Cushing, *Periodic time-dependent predator-prey systems*, SIAM J. Appl. Math. **32** (1977) 1, 82–95.

[10] R.L. Devaney, *Subshifts of finite type in linked twist mappings*, Proc. Amer. Math. Soc. **71** (1978) 2, 334–338.

[11] T.-R. Ding, H. Huang, F. Zanolin, *A priori bounds and periodic solutions for a class of planar systems with applications to Lotka-Volterra equations*, Discrete Contin. Dynam. Systems **1** (1995) 1, 103–117.

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

[13] T.-R. Ding, F. Zanolin, *Periodic solutions and subharmonic solutions for a class of planar systems of Lotka-Volterra type*, World Congress of Nonlinear Analysts '92, Vol. I–IV (Tampa, FL, 1992) (Berlin), de Gruyter, Berlin, 1996, pp. 395–406.

[14] Z. Galias, P. Zgliczyński, *Computer assisted proof of chaos in the Lorenz equations*, Phys. D **115** (1998) 3–4, 165–188.

[15] A.R. Hausrath, *Periodic integral manifolds for periodically forced Volterra-Lotka equations*, J. Math. Anal. Appl. **87** (1982) 2, 474–488.

[16] A.R. Hausrath, R.F. Manásevich, *Periodic solutions of periodically harvested Lotka-Volterra systems*, Rev. Colombiana Mat. **21** (1987), no. 2–4, 337–345.

[17] A.R. Hausrath, R.F. Manásevich, *Periodic solutions of a periodically perturbed Lotka-Volterra equation using the Poincaré-Birkhoff theorem*, J. Math. Anal. Appl. **157** (1991) 1, 1–9.

[18] J. Kennedy, S. Koçak, J.A. Yorke, *A chaos lemma*, Amer. Math. Monthly **108** (2001) 5, 411–423.

[19] J. Kennedy, J.A. Yorke, *Topological horseshoes*, Trans. Amer. Math. Soc. **353** (2001) 6, 2513–2530.

[20] U. Kirchgraber, D. Stoffer, *On the definition of chaos*, Z. Angew. Math. Mech. **69** (1989) 7, 175–185.

[21] A.N. Kolmogorov, *Sulla teoria di Volterra della lotta per l'esistenza*, Giorn. Ist. Ital. Attuari **7** (1936), 74–80.

[22] B. Lani-Wayda, R. Srzednicki, *A generalized Lefschetz fixed point theorem and symbolic dynamics in delay equations*, Ergodic Theory Dynam. Systems **22** (2002) 4, 1215–1232.

[23] B. Liu, *The stability of harmonic solutions of Lotka-Volterra systems*, J. Math. Anal. Appl. **194** (1995) 3, 727–740.

[24] J. López-Gómez, R. Ortega, A. Tineo, *The periodic predator-prey Lotka-Volterra model*, Adv. Differential Equations **1** (1996) 3, 403–423.

[25] J. Mawhin, *Les héritiers de Pierre-François Verhulst: une population dynamique*, Acad. Roy. Belg. Bull. Cl. Sci. (6) **13** (2002) 7–12, 349–378 (2003).

[26] J. Mawhin, *The legacy of Pierre-François Verhulst and Vito Volterra in population dynamics*, The first 60 years of nonlinear analysis of Jean Mawhin, World Sci. Publ., River Edge, NJ, 2004, 147–160.

[27] J. Moser, *Stable and random motions in dynamical systems*, Princeton University Press, Princeton, N. J., 1973, With special emphasis on celestial mechanics, Hermann Weyl Lectures, the Institute for Advanced Study, Princeton, N. J., Annals of Mathematics Studies, No. 77.

[28] T. Namba, *Bifurcation phenomena appearing in the Lotka-Volterra competition equations: a numerical study*, Math. Biosci. **81** (1986) 2, 191–212.

[29] R. Ortega, *The number of stable periodic solutions of time-dependent Hamiltonian systems with one degree of freedom*, Ergodic Theory Dynam. Systems **18** (1998) 4, 1007–1018.

[30] D. Papini, F. Zanolin, *Fixed points, periodic points, and coin-tossing sequences for mappings defined on two-dimensional cells*, Fixed Point Theory Appl. (2004) 2, 113–134.

[31] D. Papini, F. Zanolin, *On the periodic boundary value problem and chaotic-like dynamics for nonlinear Hill's equations*, Adv. Nonlinear Stud. **4** (2004) 1, 71–91.

[32] A. Pascoletti, M. Pireddu, F. Zanolin, *Multiple periodic solutions and complex dynamics for second order ODEs via linked twist maps*, Proceedings of the 8th Colloquium on the Qualitative Theory of Differential Equations (Szeged, 2007), Electron. J. Qual. Theory Differ. Equ., Szeged, **14** (2008), 1–32.

[33] A. Pascoletti, F. Zanolin, *Example of a suspension bridge ODE model exhibiting chaotic dynamics: a topological approach*, J. Math. Anal. Appl. **339** (2008) 2, 1179–1198.

[34] M. Pireddu, F. Zanolin, *Some remarks on fixed points for maps which are expansive along one direction*, Rend. Istit. Mat. Univ. Trieste, **39** (2007), 245–274.

[35] M. Pireddu, F. Zanolin, *Cutting surfaces and applications to periodic points and chaotic−like dynamics*, Topol. Methods Nonlinear Anal. **30** (2007) 2, 279–319.

[36] F. Przytycki, *Ergodicity of toral linked twist mappings*, Ann. Sci. École Norm. Sup. (4) **16** (1983) 3, 345–354 (1984).

[37] F. Przytycki, *Periodic points of linked twist mappings*, Studia Math. **83** (1986) 1, 1–18.

[38] S. Rinaldi, S. Muratori, *Conditioned chaos in seasonally perturbed predator–prey models*, Ecological Modelling **69** (1993) 1–2, 79–97.

[39] F. Rothe, *The periods of the Volterra-Lotka system*, J. Reine Angew. Math. **355** (1985), 129–138.

[40] R. Srzednicki, *A generalization of the Lefschetz fixed point theorem and detection of chaos*, Proc. Amer. Math. Soc. **128** (2000) 4, 1231–1239.

[41] R. Srzednicki, K. Wójcik, *A geometric method for detecting chaotic dynamics*, J. Differential Equations **135** (1997) 1, 66–82.

[42] R. Sturman, J.M. Ottino, S. Wiggins, *The mathematical foundations of mixing*, Cambridge Monographs on Applied and Computational Mathematics, vol. 22, Cambridge University Press, Cambridge, 2006, The linked twist map as a paradigm in applications: micro to macro, fluids to solids.

[43] P. Táboas, *Periodic solutions of a forced Lotka-Volterra equation*, J. Math. Anal. Appl. **124** (1987) 1, 82–97.

[44] V. Volterra, *Ricerche matematiche sulle associazioni biologiche*, G. Ist. Ital. Attuari **2** (1931), 295–355.

[45] V. Volterra, *Leçons sur la théorie mathématique de la lutte pour la vie*, Éditions Jacques Gabay, Sceaux, 1990, Les Grands Classiques Gauthier-Villars [Gauthier-Villars Great Classics], Reprint of the 1931 original.

[46] J. Waldvogel, *The period in the Lotka-Volterra system is monotonic*, J. Math. Anal. Appl. **114** (1986) 1, 178–184.

[47] P. Walters, *An introduction to ergodic theory*, Graduate Texts in Mathematics, vol. 79, Springer-Verlag, New York, 1982.

[48] S. Wiggins, *Chaos in the dynamics generated by sequences of maps, with applications to chaotic advection in flows with aperiodic time dependence*, Z. Angew. Math. Phys. **50** (1999) 4, 585–616.

[49] S. Wiggins, J.M. Ottino, *Foundations of chaotic mixing*, Philos. Trans. R. Soc. Lond. Ser. A Math. Phys. Eng. Sci. **362** (2004) 1818, 937–970.

[50] K. Wójcik, P. Zgliczyński, *Isolating segments, fixed point index, and symbolic dynamics*, J. Differential Equations **161** (2000) 2, 245–288.

[51] P. Zgliczyński, *Fixed point index for iterations of maps, topological horseshoe and chaos*, Topol. Methods Nonlinear Anal. **8** (1996) 1, 169–177.

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