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THE PERIODIC PREDATOR-PREY LOTKA-VOLTERRA MODEL

Julián López-Gómez
Department of Mathematics, Heriot-Watt University
Riccarton Campus, Edinburgh EH14 4AS, Scotland

Rafael Ortega
Departamento de Matemática Aplicada, Facultad de Ciencias
Universidad de Granada, 18071-Granada, Spain

Antonio Tineo
Departamento de Matemáticas, Facultad de Ciencias
Universidad de Los Andes, 5101-Mérida, Venezuela

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Abstract. In this paper we characterize the existence of coexistence states for the classical Lotka-Volterra predator-prey model with periodic coefficients and analyze the dynamics of positive solutions of such models. Among other results we show that if some trivial or semi-trivial positive state is linearly stable, then it is globally asymptotically stable with respect to the positive solutions. In fact, the model possesses a coexistence state if, and only if, any of the semi-trivial states is unstable. Some permanence and uniqueness results are also found. An example exhibiting a unique coexistence state that is unstable is given.

1. Introduction. In this work we study the dynamical behavior of positive solutions of the classical nonautonomous predator-prey Lotka-Volterra model under the assumption that the coefficients are periodic functions of a common period

$$\begin{cases} u'(t) = \lambda\, \ell(t)\, u(t) - a(t)\, u^2(t) - b(t)\, u(t)v(t)\,, \\ v'(t) = \mu\, m(t)\, v(t) + c(t)\, u(t)v(t) - d(t)\, v^2(t)\,. \end{cases} \tag{1.1}$$

To be precise, we assume that $\ell(t)$, $m(t)$, $a(t)$, $b(t)$, $c(t)$ and $d(t)$ are continuous T-periodic functions such that $a \geq 0$, $b \geq 0$, $c \geq 0$, $d \geq 0$, $a(t_1) > 0$, $d(t_2) > 0$ for some $t_1, t_2 \in \mathbb{R}$, and

$$\frac{1}{T}\int_0^T \ell(t)\,dt = 1\,, \qquad \frac{1}{T}\int_0^T m(t)\,dt = 1\,. \tag{1.2}$$

The coefficients $\lambda, \mu \in \mathbb{R}$ will be eventually regarded as bifurcation parameters. This work is a natural prolongation of some previous research carried out by the authors, [1], [6], [9], [10], [13]. Here, we mainly focus our attention into the problem of analyzing the attractivity properties of the positive solutions of (1.1) to complete the analysis done in

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the previous references. In the sequel we shortly describe the main results obtained in this paper.

The problem (1.1) exhibits three types of T-periodic component-wise nonnegative solutions: the solution $(0,0)$, usually known as the *trivial* one; those with one component vanishing, often known as the *semi-trivial* positive solutions; and the *coexistence states,* which are the solutions with both components positive. To describe our results we need some notation. The model (1.1) admits a semi-trivial positive state of the form $(u,0)$ (respectively $(0,v)$) if, and only if, $\lambda > 0$ (respectively $\mu > 0$). Moreover, if $\lambda > 0$ (respectively $\mu > 0$), then the semi-trivial state is given by $(\theta_\lambda, 0)$ (respectively $(0,\theta_\mu)$), where θ_λ (respectively θ_μ) is the unique positive T-periodic solution of $u' = \lambda \ell u - au^2$ (respectively $v' = \mu m v - dv^2$). Given $(u_0, v_0) \in [0,\infty)^2$ we shall denote by $(u(t;u_0,v_0), v(t;u_0,v_0))$ the unique solution of the Cauchy problem associated with (1.1) having initial data (u_0,v_0). As far as the attractivity properties of $(0,0)$ and the T-periodic semi-trivial states are concerned, our main result can be summarized as follows:

- If $(0,0)$ is linearly stable, then
$$\lim_{t\to\infty} (|u(t;u_0,v_0)| + |v(t;u_0,v_0)|) = 0\,,$$
for any $(u_0,v_0) \in (0,\infty)^2$. Moreover, we are in this situation if, and only if, $\lambda \le 0$ and $\mu \le 0$.
- If $(\theta_\lambda, 0)$ is linearly stable, then
$$\lim_{t\to\infty} (|u(t;u_0,v_0) - \theta_\lambda(t)| + |v(t;u_0,v_0)|) = 0\,,$$
for any $(u_0,v_0) \in (0,\infty) \times [0,\infty)$. Moreover, this happens if, and only if, $\lambda > 0$ and $\mu \le \frac{-1}{T}\int_0^T c\theta_\lambda$.
- If $(0,\theta_\mu)$ is linearly stable, then
$$\lim_{t\to\infty} (|u(t;u_0,v_0)| + |v(t;u_0,v_0) - \theta_\mu(t)|) = 0\,,$$
for any $(u_0,v_0) \in [0,\infty) \times (0,\infty)$. Moreover, this happens if, and only if, $\mu > 0$ and $\lambda \le \frac{1}{T}\int_0^T b\theta_\mu$.

In particular, a necessary condition for the existence of a coexistence state is the instability of any semi-trivial positive solution. In other words,

$$\mu > \frac{-1}{T}\int_0^T c\theta_\lambda\,, \qquad \lambda > \frac{1}{T}\int_0^T b\theta_\mu\,. \tag{1.3}$$

The previous results are given in Section 4 as an easy consequence of some abstract monotone schemes introduced in Section 4, which will be used also in Section 6 to get some sufficient conditions for permanence. In Section 5 we use global bifurcation theory and Brouwer degree to show that condition (1.3) is also sufficient for the existence of a coexistence state. Therefore, the model (1.1) admits a coexistence state if, and only if, any semi-trivial positive solution is unstable. This result is related to the main theorem of [9], obtained for a periodic parabolic problem under homogeneous Dirichlet boundary conditions. It is precisely this fact which makes it impossible to deduce the results for (1.1) as a particular case of the main theorem of [9] by simply switching off the diffusivities to zero. In fact, the positive solutions will develop boundary layers as the diffusivities tend to zero. A posteriori, it is clear that (1.3) may be obtained from the characterization of the existence of coexistence states for the periodic parabolic model under homogeneous Dirichlet boundary conditions by switching off to zero both diffusivities. This is precisely one of the consequences of our analysis. When $\mu \leq 0$, there is a recent proof in [7].

As far as the problem of the uniqueness and the stability of the coexistence states is concerned, things are much more difficult to deal with. The linearization of (1.1) at any coexistence state has a noncooperative structure in the sense that the off-diagonal entries of the coupling matrix of the system have contrary signs, and for such problems any general comparison principle is not available. Therefore it is not clear how to ascertain the signs of the Floquet exponents of a given coexistence state. It is known that the one-dimensional predator-prey model with diffusion under homogeneous Dirichlet boundary conditions admits at most a coexistence state, [10]. Moreover, there are choices of several coefficient functions in the setting of (1.1) for which this model admits at least three T-periodic component-wise positive solutions, [1], [5]. Therefore, the uniqueness result for the one-dimensional elliptic model does not extend in general to the periodic prototype models.

Proposition 3.3 of [1] shows that if the product of the interactions b and c is sufficiently small, then the model admits at most a coexistence state. In fact, the techniques of [13] adapt to show that if this is the case then the coexistence state is globally asymptotically stable. In this paper we shall give examples which do not fit into the setting of these results, because b and c are as large as we wish, possessing a unique coexistence state which is asymptotically stable. Therefore, some further work is needed to show whether uniqueness of a coexistence state occurs or not. In Section 5 we obtain an uniqueness result of a different nature than those just commented upon. We show that if (u_0, v_0) is a coexistence state of (1.1) with either u_0 or v_0 sufficiently small, then it is unique and asymptotically stable. In Section 6 we use the monotone scheme introduced in Section 3 to give some sufficient conditions for permanence in the sense that there is a compact attractor within the interior of the positive cone in $\mathbb{R}^2$. By a theorem of Massera ([11]) this guarantees the existence of a coexistence state. In Section 7 we construct an example exhibiting a unique coexistence state which is unstable. In that case second-order subharmonic solutions must appear. In Section 2 we introduce some notation and basic results used throughout this work.

2. The single logistic equation. Basic properties. Throughout this work we deal with the Banach spaces of T-periodic functions $X := C^1_T(\mathbb{R})$ and $Y := C_T(\mathbb{R})$ ordered by their cones of nonnegative functions, P_X and P_Y, respectively. We will always focus our attention on nonnegative solutions in X or X^2, depending on each specific situation, even if not explicitly stated. The interior of P_X (respectively P_Y), denoted by $\operatorname{int} P_X$ (respectively $\operatorname{int} P_Y$), is the set of functions $u \in X$ (respectively $u \in Y$) such that $u(t) > 0$ for all $t \in \mathbb{R}$. Given an ordered Banach space (E, P) and $u, v \in E$ we write $u \geq v$ if $u - v \in P$, $u > v$ if $u - v \in P \setminus \{0\}$, and $u \gg v$ if $u - v \in \operatorname{int} P$. Moreover, for any $y \in Y$ we shall denote

$$\overline{y} := \frac{1}{T} \int_0^T y \,, \qquad y_L := \min_{t \in [0,T]} y(t) \,, \qquad y_M := \max_{t \in [0,T]} y(t) \,.$$

Given $\alpha, \beta \in Y$, $\beta > 0$, we consider the logistic equation

$$w'(t) = \alpha(t)\, w(t) - \beta(t)\, w^2(t) \,. \tag{2.1}$$

It is very easy to see that (2.1) admits a positive periodic solution if and only if $\overline{\alpha} > 0$. Moreover, it is unique if it exists. We shall denote it by $\theta_{[\alpha;\beta]}$. Note that $\theta_{[\alpha;\beta]}(t) > 0$ for all $t \in \mathbb{R}$. In fact, since (2.1) is a Riccati equation we can integrate it to obtain

$$\theta_{[\alpha;\beta]}(t) = \frac{1 - e^{-\int_0^T \alpha(s) ds}}{\int_0^T e^{-\int_0^s \alpha(t-\sigma)\, d\sigma} \beta(t-s)\, ds} \,. \tag{2.2}$$

Dividing $\theta'_{[\alpha;\beta]} = \alpha \theta_{[\alpha;\beta]} - \beta \theta^2_{[\alpha;\beta]}$ by $\theta_{[\alpha;\beta]}$ and integrating over a period, we find that

$$\overline{\alpha} = \frac{1}{T} \int_0^T \beta\, \theta_{[\alpha;\beta]} \,. \tag{2.3}$$

Throughout this work we extend the definition of $\theta_{[\alpha;\beta]}$ to any α by setting

$$\theta_{[\alpha;\beta]} \equiv 0 \qquad \text{if} \qquad \overline{\alpha} \leq 0 \,.$$

The next result can be easily derived from (2.2).

Corollary 2.1. *Let $\alpha_j\,, \beta_j \in Y$, $j = 1\,, 2$, be such that $\alpha_1 \leq \alpha_2$ and $\beta_1 \geq \beta_2 > 0$. Then, $\theta_{[\alpha_1;\beta_1]} \leq \theta_{[\alpha_2;\beta_2]}$. Moreover, if $\overline{\alpha}_2 > 0$ and either $\alpha_1 < \alpha_2$, or $\beta_1 > \beta_2$, then $\theta_{[\alpha_1;\beta_1]} \ll \theta_{[\alpha_2;\beta_2]}$.*

Given $t_0\,, w_0 \in \mathbb{R}$ and two continuous functions $a\,, b \in C([t_0, \infty); \mathbb{R})$ with $b > 0$ we denote by $\Phi_{[a;b]}(\cdot; t_0, w_0)$ the unique solution of the Cauchy problem

$$w' = a\, w - b\, w^2 \,, \quad w(t_0) = w_0 > 0 \,, \tag{2.4}$$

which is positive and globally defined for $t \geq t_0$. The following result gives the global attractive character of $\theta_{[\alpha;\beta]}$. It follows by direct integration.

Proposition 2.2. *Given $\alpha\,, \beta \in Y$, for any $t_0 \in \mathbb{R}$ and $w_0 > 0$ we have*

$$\lim_{t \to \infty} |\Phi_{[\alpha;\beta]}(t; t_0, w_0) - \theta_{[\alpha;\beta]}(t)| = 0 \,.$$

The following comparison result is very useful and rather standard.

Proposition 2.3. *Let $t_0\,, w_0 \in \mathbb{R}$ be given with $w_0 > 0$ and consider two continuous functions $a\,,\, b \in C([t_0,\infty);\mathbb{R})$ with $b > 0$. Suppose that w is a differentiable function such that $w' \le a\,w - b\,w^2$ for $t \ge t_0$, and $w(t_0) \le w_0$. Then, $w(t) \le \Phi_{[a;b]}(t;t_0,w_0)$ for all $t \ge t_0$. Similarly, if $w' \ge a\,w - b\,w^2$ for $t \ge t_0$ and $w(t_0) \ge w_0$, then $w(t) \ge \Phi_{[a;b]}(t;t_0,w_0)$ for all $t \ge t_0$.*

We now introduce the class of asymptotically T-periodic functions. Given a continuous function $a : [t_0,\infty) \to \mathbb{R}$, ($t_0 \in \mathbb{R}$) we say that a is asymptotic to $\alpha \in Y$ if $\lim_{t\to\infty} |a(t) - \alpha(t)| = 0$. The following generalization of Proposition 2.2 will be very useful.

Theorem 2.4. *Consider $\beta \in Y$, $\beta > 0$, and a a function having the previous conditions that is asymptotic to $\alpha \in Y$. Then, for any $w_0 > 0$,*

$$\lim_{t\to\infty} |\Phi_{[a;\beta]}(t;t_0,w_0) - \theta_{[\alpha;\beta]}(t)| = 0\,.$$

Proof. Given $\varepsilon > 0$ there exists $t_\varepsilon > t_0$ such that

$$\alpha(t) - \varepsilon \le a(t) \le \alpha(t) + \varepsilon\,, \qquad t \ge t_\varepsilon\,.$$

Hence, it follows from Proposition 2.3 that

$$\begin{aligned}\Phi_{[\alpha-\varepsilon;\beta]}(t;t_\varepsilon,\Phi_{[a;\beta]}(t_\varepsilon;t_0,w_0)) &\le \Phi_{[a;\beta]}(t;t_0,w_0)\\ &\le \Phi_{[\alpha+\varepsilon;\beta]}(t;t_\varepsilon,\Phi_{[a;\beta]}(t_\varepsilon;t_0,w_0))\,,\end{aligned}$$

for all $t \ge t_\varepsilon$. Moreover, thanks to Proposition 2.2 we get

$$\lim_{t\to\infty} |\Phi_{[\alpha\pm\varepsilon;\beta]}(t;t_\varepsilon,\Phi_{[a;\beta]}(t_\varepsilon;t_0,w_0)) - \theta_{[\alpha\pm\varepsilon;\beta]}(t)| = 0\,.$$

On the other hand, we have from the definition of $\theta_{[\alpha\pm\varepsilon;\beta]}$ that $\lim_{\varepsilon\downarrow 0}\theta_{[\alpha\pm\varepsilon;\beta]} = \theta_{[\alpha;\beta]}$ in X. This completes the proof. $\square$

To conclude this section we apply the previous remarks to (1.1). The system (1.1) has a semi-trivial positive solution of the form $(u,0)$ if and only if $\lambda > 0$, namely, $(\theta_{[\lambda\,\ell;a]},0)$. Similarly, (1.1) admits a semi-trivial positive solution of the form $(0,v)$ if and only if $\mu > 0$, given by $(0,\theta_{[\mu\,m;d]})$. To shorten notation we write $\theta_\lambda := \theta_{[\lambda\,\ell;a]}$ and $\theta_\mu := \theta_{[\mu\,m;d]}$. We find from (1.2) and (2.3) that

$$\lambda = \frac{1}{T}\int_0^T a\,\theta_\lambda\,, \qquad \mu = \frac{1}{T}\int_0^T d\,\theta_\mu\,. \tag{2.5}$$

Note that if (u,v) is a T-periodic component-wise positive solution of (1.1) with $u > 0$, then $u \gg 0$. Similarly, $v \gg 0$ if $v > 0$. In particular, if (u_0,v_0) is a coexistence state of (1.1), then $u_0 \gg 0$ and $v_0 \gg 0$. Hence,

$$\frac{u_0'}{u_0} = \lambda\,\ell - a\,u_0 - b\,v_0\,, \qquad \frac{v_0'}{v_0} = \mu\,m + c\,u_0 - d\,v_0\,,$$

and integrating in $[0,T]$ yields

$$\lambda = \frac{1}{T}\,(\int_0^T a\,u_0 + \int_0^T b\,v_0)\,, \qquad \mu = \frac{1}{T}\,(-\int_0^T c\,u_0 + \int_0^T d\,v_0)\,. \tag{2.6}$$

In particular, if (1.1) admits a coexistence state, then $\lambda > 0$.

3. The monotone scheme. In this section we analyze the properties of the following scheme:

$$U_0 := 0\,, \qquad V_n := \theta_{[\mu\,m + c\,U_{n-1};d]}\,, \qquad U_n := \theta_{[\lambda\,\ell - b\,V_n;a]}\,, \qquad n \geq 1\,. \tag{3.1}$$

Notice that it makes sense for all values of the coefficients of (1.1).

Lemma 3.1. *For each $n \geq 1$ the following inequalities hold:*

$$V_1 \leq \cdots \leq V_{2n-1} \leq V_{2n} \leq \cdots \leq V_2\,, \qquad U_2 \leq \cdots \leq U_{2n} \leq U_{2n-1} \leq \cdots \leq U_1\,. \tag{3.2}$$

Moreover, the limits

$$\underline{V} := \lim_{n\to\infty} V_{2n-1} \leq \overline{V} := \lim_{n\to\infty} V_{2n}\,, \qquad \underline{U} := \lim_{n\to\infty} U_{2n} \leq \overline{U} := \lim_{n\to\infty} U_{2n-1}\,, \tag{3.3}$$

are well defined (in X) and $(\overline{V}, \overline{U}, \underline{V}, \underline{U})$ is a component-wise nonnegative T-periodic solution of

$$\begin{aligned} \overline{U}' &= (\lambda\,\ell - a\,\overline{U} - b\,\underline{V})\,\overline{U}\,, \quad & \underline{U}' &= (\lambda\,\ell - a\,\underline{U} - b\,\overline{V})\,\underline{U}\,, \\ \overline{V}' &= (\mu\,m + c\,\overline{U} - d\,\overline{V})\,\overline{V}\,, \quad & \underline{V}' &= (\mu\,m + c\,\underline{U} - d\,\underline{V})\,\underline{V}\,. \end{aligned} \tag{3.4}$$

Furthermore, if either
(i) $b \gg 0$, $\underline{U} > 0$, $\overline{V} > 0$, and $\underline{U}(t) = \overline{U}(t)$ for some $t \in \mathbb{R}$, or
(ii) $c \gg 0$, $\underline{V} > 0$, $\overline{U} > 0$, and $\underline{V}(t) = \overline{V}(t)$ for some $t \in \mathbb{R}$,
then $\underline{U} = \overline{U}$, $\underline{V} = \overline{V}$.

Proof. We shall argue by induction using Corollary 2.1. By definition of the θ's we have $U_n \geq 0$ and $V_n \geq 0$ for all $n \geq 1$. Thus, it follows from Corollary 2.1 that $\theta_{[\mu\,m;d]} \leq \theta_{[\mu\,m + cU_1;d]}$; that is, $V_1 \leq V_2$. This inequality implies $\lambda\,\ell - bV_1 \geq \lambda\,\ell - bV_2$ and once again it follows from Corollary 2.1 that $U_1 \geq U_2$. Now, suppose that (3.2) is satisfied for $n \in \{1\,, \ldots\,, k\}$. We have to see that

$$V_{2k-1} \leq V_{2k+1} \leq V_{2k+2} \leq V_{2k}\,, \qquad U_{2k} \leq U_{2k+2} \leq U_{2k+1} \leq U_{2k-1}\,.$$

Since we are assuming that $U_{2k-2} \leq U_{2k}$, it follows from (3.1) that $V_{2k-1} \leq V_{2k+1}$. This implies that $U_{2k-1} \geq U_{2k+1}$. Thus, $V_{2k} \geq V_{2k+2}$ and so $U_{2k} \leq U_{2k+2}$. On the other hand, we find from $U_{2k} \leq U_{2k-1}$ that $V_{2k+1} \leq V_{2k}$. So, $U_{2k+1} \geq U_{2k}$ and hence $V_{2k+2} \geq V_{2k+1}$. Therefore, $U_{2k+2} \leq U_{2k+1}$. This completes the proof of (3.2).

The fact that the limits in (3.3) are pointwise well defined follows from the monotonicity of the scheme. On the other hand, it follows from the definition of the θ's that

$$\begin{aligned} U'_{2n-1} &= (\lambda\,\ell - a\,U_{2n-1} - b\,V_{2n-1})\,U_{2n-1}\,, \\ U'_{2n} &= (\lambda\,\ell - a\,U_{2n} - b\,V_{2n})\,U_{2n}\,, \\ V'_{2n} &= (\mu\,m + c\,U_{2n-1} - d\,V_{2n})\,V_{2n}\,, \\ V'_{2n-1} &= (\mu\,m + c\,U_{2n-2} - d\,V_{2n-1})\,V_{2n-1}\,. \end{aligned} \tag{3.5}$$

Thus, since the U_k's and the V_k's are uniformly bounded, we find from (3.5) that each of the sequences U_{2n-1}, U_{2n}, V_{2n} and V_{2n-1} is equicontinuous. So, it follows from (3.2) and the Ascoli-Arzela Theorem that the limits in (3.3) are uniform; that is, the convergence occurs in Y. Now, passing to the limit as $n \to \infty$ in (3.5), we find that the convergence actually occurs in X and so (3.4) holds.

We now show the last claim of the lemma. Suppose that $b \gg 0$ and that $\underline{U} > 0$, $\overline{V} > 0$. Under these assumptions, if $\underline{V} < \overline{V}$, then $-b\underline{V} > -b\overline{V}$ and hence it follows from Corollary 2.1 applied to the U-equations of (3.4) that $\underline{U} \ll \overline{U}$. Therefore, condition (i) implies $\underline{V} = \overline{V}$ and by the uniqueness of the positive solution for the logistic-type equations we find that $\underline{U} = \overline{V}$ as well. Similarly, (ii) implies $\underline{U} = \overline{U}$, $\underline{V} = \overline{V}$. $\square$

Now, given $(u_0, v_0) \in \mathbb{R}^2$ we denote by $(u(t;t_0,u_0,v_0), v(t;t_0,u_0,v_0))$ the unique positive solution of the Cauchy problem

$$\begin{cases} u' = \lambda\,\ell\,u - au^2 - buv \\ v' = \mu\,m\,v + cuv - dv^2 \end{cases} \qquad (u(t_0), v(t_0)) = (u_0, v_0)\,. \tag{3.6}$$

Our interest in the scheme (3.1) comes from the next result.

Theorem 3.2. *For any $t_0 \in \mathbb{R}$ and $(u_0, v_0) \in (0,\infty)^2$ the following estimates hold:*

$$\begin{aligned} &\limsup_{t\to\infty}[u(t;t_0,u_0,v_0) - \overline{U}(t)] \le 0 \le \liminf_{t\to\infty}[u(t;t_0,u_0,v_0) - \underline{U}(t)]\,, \\ &\limsup_{t\to\infty}[v(t;t_0,u_0,v_0) - \overline{V}(t)] \le 0 \le \liminf_{t\to\infty}[v(t;t_0,u_0,v_0) - \underline{V}(t)]\,. \end{aligned} \tag{3.7}$$

Proof. To simplify the notation we set $(u(t), v(t)) := (u(t;t_0,u_0,v_0), v(t;t_0,u_0,v_0))$. Consider the iterative scheme

$$\mathcal{U}_0 := 0\,, \quad \mathcal{V}_n := \Phi_{[\mu\,m + c\,\mathcal{U}_{n-1};d]}(\cdot;t_0,v_0)\,, \quad \mathcal{U}_n := \Phi_{[\lambda\,\ell - b\,\mathcal{V}_n;a]}(\cdot;t_0,u_0)\,, \quad n \ge 1\,. \tag{3.8}$$

Arguing as in the proof of Lemma 3.1, but this time applying Proposition 2.3, instead of Corollary 2.1, it can be easily seen that for any $n \ge 1$ we have

$$\begin{aligned} &\mathcal{V}_1 \le \cdots \le \mathcal{V}_{2n-1} \le v \le \mathcal{V}_{2n} \le \cdots \le \mathcal{V}_2\,, \\ &\mathcal{U}_2 \le \cdots \le \mathcal{U}_{2n} \le u \le \mathcal{U}_{2n-1} \le \cdots \le \mathcal{U}_1\,. \end{aligned} \tag{3.9}$$

In particular, $(u(t), v(t))$ is well defined for any $t \geq t_0$. Finally, an induction argument together with Proposition 2.2 and Theorem 2.4 show that

$$\lim_{t\to\infty}[\mathcal{U}_n(t) - U_n(t)] = \lim_{t\to\infty}[\mathcal{V}_n(t) - V_n(t)] = 0\,, \qquad n \geq 1\,.$$

This identity together with the uniformity in the convergence of (3.3) complete the proof. $\square$

Similarly, if we consider the monotone scheme

$$\hat{V}_0 := 0\,, \qquad \hat{U}_n := \theta_{[\lambda\,\ell - b\,\hat{V}_{n-1};a]}\,, \qquad \hat{V}_n := \theta_{[\mu\,m + c\,\hat{U}_n;d]}\,, \qquad n \geq 1\,, \tag{3.10}$$

then the following result holds.

Theorem 3.3. *For each $n \geq 1$ the following inequalities hold:*

$$\hat{U}_2 \leq \cdots \leq \hat{U}_{2n} \leq \hat{U}_{2n-1} \leq \cdots \leq \hat{U}_1\,, \qquad \hat{V}_2 \leq \cdots \leq \hat{V}_{2n} \leq \hat{V}_{2n-1} \leq \cdots \leq \hat{V}_1\,.$$

Moreover, the limits

$$V_* := \lim_{n\to\infty} \hat{V}_{2n} \leq V^* := \lim_{n\to\infty} \hat{V}_{2n-1}\,, \quad U_* := \lim_{n\to\infty} \hat{U}_{2n} \leq U^* := \lim_{n\to\infty} \hat{U}_{2n-1}\,, \tag{3.11}$$

are well defined (in X) and (V^*, U^*, V_*, U_*) is a component-wise nonnegative T-periodic solution of (3.4). Furthermore, for any $t_0 \in \mathbb{R}$ and $(u_0, v_0) \in (0,\infty)^2$ the following estimates hold:

$$\begin{aligned} &\limsup_{t\to\infty}[u(t;t_0,u_0,v_0) - U^*(t)] \leq 0 \leq \liminf_{t\to\infty}[u(t;t_0,u_0,v_0) - U_*(t)]\,, \\ &\limsup_{t\to\infty}[v(t;t_0,u_0,v_0) - V^*(t)] \leq 0 \leq \liminf_{t\to\infty}[v(t;t_0,u_0,v_0) - V_*(t)]\,. \end{aligned} \tag{3.12}$$

Remark 3.4. As in Lemma 3.1, if either
(i) $b \gg 0$, $U_* > 0$, $V^* > 0$, and $U_*(t) = U^*(t)$ for some $t \in \mathbb{R}$, or
(ii) $c \gg 0$, $V_* > 0$, $U^* > 0$, and $V_*(t) = V^*(t)$ for some $t \in \mathbb{R}$,
then $U_* = U^*$, $V_* = V^*$.

To conclude this section we look at an example for which the monotone scheme can be computed explicitly. Consider the system

$$u' = \lambda\,\ell(t)\,u - u^2 - buv\,, \qquad v' = \lambda\,\ell(t)\,v + cuv - v^2\,, \tag{3.13}$$

where $\ell \in Y$ with $\frac{1}{T}\int_0^T \ell = 1$, and $b\,, c \in \mathbb{R}$ with $b > 0$, $c > 0$. Assume that λ is positive and let θ_λ denote the unique T-periodic positive solution of $w' = \lambda\ell(t)w - w^2$. It is easy to verify that

$$\theta_{[\lambda\,\ell + \alpha\theta_\lambda;1]} = (1+\alpha)^+\,\theta_\lambda\,, \qquad \alpha \in (-\infty, \infty)\,.$$

Using this identity one can compute the sequences U_n,V_n, given by (3.1), in each of the following cases:
(i) $b \geq 1$

$$U_n = 0\,, \quad V_n = \theta_\lambda\,, \quad n = 1, 2, \ldots$$

(ii) $b < 1$, $bc \geq 1$

$$U_{2n} = 0\,, \quad U_{2n-1} = (1-b)\theta_\lambda\,; \quad V_{2n} = (1+c-bc)\theta_\lambda\,, \quad V_{2n-1} = \theta_\lambda\,, \quad n = 1, 2, \ldots$$

(iii) $b < 1$, $bc < 1$

$$U_n = (1-b)\sum_{j=0}^{n-1}(-bc)^j\,\theta_\lambda\,, \quad V_n = [(1+c)\sum_{j=0}^{n-2}(-bc)^j + (bc)^{n-1}]\,\theta_\lambda\,, \quad n = 1, 2, \ldots,$$

On the other hand it is possible to perform two successive changes of variables and transform (3.13) into the autonomous system

$$x' = x(1-x-by), \qquad y' = y(1+cx-y)\,. \tag{3.14}$$

The changes are

$$(t,u,v) \to (t,x,y), \quad x = \frac{u}{\theta_\lambda}\,, \quad y = \frac{v}{\theta_\lambda}\,; \quad (t,x,y) \to (s,x,y), \quad s = \int_0^t \theta_\lambda(\tau)\,d\tau.$$

A phase portrait analysis shows that when $b \geq 1$ every positive solution tends to $(0, \theta_\lambda)$ while if $b < 1$ every positive solution goes to the coexistence state $(\frac{1-b}{1+bc}\theta_\lambda\,, \frac{1+c}{1+bc}\theta_\lambda)$. Thus, our previous computations show that Theorem 3.2 gives a sharp conclusion in cases (i) and (iii) while it only provides a rough estimate in case (ii).

4. Extinction.

In this section we characterize whether some of the states $(\theta_\lambda, 0)$, $(0, \theta_\mu)$, or $(0, 0)$, are globally asymptotically stable with respect to the positive solutions of (1.1). The next theorem is optimal.

Theorem 4.1. (a) *If $(0,0)$ is not linearly unstable, then*

$$\lim_{t\to\infty}(u(t;t_0,u_0,v_0), v(t;t_0,u_0,v_0)) = (0,0)\,,$$

for any $(u_0, v_0) \geq 0$.

(b) *If $\lambda > 0$ and $(\theta_\lambda, 0)$ is not linearly unstable, then*

$$\lim_{t\to\infty}[(u(t;0,u_0,v_0), v(t;0,u_0,v_0)) - (\theta_\lambda(t), 0)] = (0,0)\,,$$

for any (u_0, v_0) such that $u_0 > 0$ and $v_0 \geq 0$.

(c) *If $\mu > 0$ and $(0, \theta_\mu)$ is not linearly unstable, then*

$$\lim_{t\to\infty}[(u(t;0,u_0,v_0), v(t;0,u_0,v_0)) - (0, \theta_\mu(t))] = (0,0)\,,$$

for all (u_0, v_0) with $u_0 \geq 0$ and $v_0 > 0$.

To prove this result we shall use the following characterization of the linear stabilities of the trivial and semi-trivial states.

Proposition 4.2. (i) *The trivial solution* $(0,0)$ *is linearly unstable if, and only if,* (1.1) *admits a semitrivial positive solution, that is, if and only if either* $\lambda > 0$ *or* $\mu > 0$.

(ii) *Assume that* $\lambda > 0$. *Then,* $(\theta_\lambda, 0)$ *is linearly unstable if, and only if,* $\mu > \frac{-1}{T}\int_0^T c\theta_\lambda$, *and linearly stable if, and only if,* $\mu < \frac{-1}{T}\int_0^T c\theta_\lambda$.

(iii) *Assume that* $\mu > 0$. *Then,* $(0, \theta_\mu)$ *is linearly unstable if, and only if,* $\lambda > \frac{1}{T}\int_0^T b\theta_\mu$, *and linearly stable if, and only if,* $\lambda < \frac{1}{T}\int_0^T b\theta_\mu$.

Proof. (i) A direct calculation shows that the Floquet multipliers of $(0,0)$ are $e^{\lambda T}$ and $e^{\mu T}$. This completes the proof of Part (i).

(ii) Assume that $\lambda > 0$. Then, (1.1) admits the semitrivial state $(\theta_\lambda, 0)$. The linearization of (1.1) at $(\theta_\lambda, 0)$ is given by

$$u' = (\lambda\,\ell - 2\,a\,\theta_\lambda)\,u - b\,\theta_\lambda\,v\,, \qquad v' = (\mu\,m + c\,\theta_\lambda)\,v\,. \tag{4.1}$$

A direct calculation from (4.1) shows that $\nu_1 := e^{\int_0^T(\lambda\,\ell - 2a\theta_\lambda)} = e^{-\int_0^T a\theta_\lambda} < 1$ is a Floquet multiplier with associated eigenvector $(1,0)$. Let ν_2 denote the other multiplier. We know from Liouville's formula that $\nu_1\,\nu_2 = e^{\int_0^T(\lambda\,\ell - 2\,a\,\theta_\lambda) + \int_0^T(\mu\,m + c\,\theta_\lambda)}$. Thus, the other multiplier is given by $\nu_2 := e^{\int_0^T(\mu\,m + c\,\theta_\lambda)}$ and therefore the linearized stability of $(\theta_\lambda, 0)$ is given by the sign of $\mu + \frac{1}{T}\int_0^T c\theta_\lambda$. If $\mu > \frac{-1}{T}\int_0^T c\theta_\lambda$, then $\nu_2 > 1$ and hence the unstable manifold of $(\theta_\lambda, 0)$ is one-dimensional. If $\mu = \frac{-1}{T}\int_0^T c\theta_\lambda$, then $\nu_2 = 1$ and $(\theta_\lambda, 0)$ is neutrally stable. If $\mu < \frac{-1}{T}\int_0^T c\theta_\lambda$, then $\nu_2 < 1$ and so $(\theta_\lambda, 0)$ is linearly asymptotically stable.

Similarly, the linear stability of $(0, \theta_\mu)$ is given by the sign of $\lambda\,T - \int_0^T b\,\theta_\mu$. The proof is completed. □

Proof of Theorem 4.1. (a) Suppose that $(0,0)$ is not linearly unstable. Then, thanks to Proposition 4.2 we have $\lambda \le 0$ and $\mu \le 0$. Thus, if U_n, V_n, $n \ge 1$, are the sequences constructed by (3.1), we have that $U_n = V_n = 0$ for all $n \ge 1$. Hence, $\underline{U} = \overline{U} = \underline{V} = \overline{V} = 0$ and Theorem 3.2 completes the proof.

(b) Suppose that $\lambda > 0$ and that $(\theta_\lambda, 0)$ is not linearly unstable. Then, thanks to Proposition 4.2 we have that $\mu \le \frac{-1}{T}\int_0^T c\theta_\lambda$. In this case, the sequences constructed from (3.1) are given by $U_n = \theta_\lambda$ and $V_n = 0$ for all $n \ge 0$. Therefore, $\underline{U} = \overline{U} = \theta_\lambda$, $\underline{V} = \overline{V} = 0$, and using Theorem 3.2 the proof is completed.

(c) Suppose that $\mu > 0$ and that $(0, \theta_\mu)$ is not linearly unstable. Then, thanks to Proposition 4.2 we have that $\lambda \le \frac{1}{T}\int_0^T b\theta_\mu$. Let $\hat{U}_n$, $\hat{V}_n$, $n \ge 1$, be the sequences given by (3.10). We have that $\hat{V}_1 = \theta_{[\mu\,m + c\,\theta_\lambda; d]} \ge \theta_\mu$. Thus, $\lambda\,T - \int_0^T bV_1^* \le \lambda\,T - \int_0^T b\theta_\mu \le 0$. Hence, $\hat{U}_2 = 0$. Therefore, $\hat{U}_n = 0$ and $\hat{V}_n = \theta_\mu$ for all $n \ge 2$. Due to Theorem 3.3 the proof of this part is completed. □

As an immediate consequence of Theorem 4.1 and Proposition 4.2 we get the following result.

Corollary 4.3. *Suppose that* (1.1) *admits a coexistence state. Then,*

$$\lambda > \frac{1}{T}\int_0^T b\theta_\mu\,, \qquad \mu > \frac{-1}{T}\int_0^T c\theta_\lambda\,. \tag{4.2}$$

In other words, all the trivial and semitrivial coexistence states are linearly unstable.

In Section 5 we shall show that (4.2) is also sufficient for the existence of a coexistence state.

Remark 4.4. Due to (2.3), we find from Corollary 4.3 that if $a \gg 0$ and $d \gg 0$, then the following relations are necessary for the existence of a coexistence state:

$$\lambda > \big(\frac{b}{d}\big)_L \mu\,, \qquad \mu > -\big(\frac{c}{a}\big)_M \lambda\,. \tag{4.3}$$

5. Existence and number of coexistence states. The following result characterizes the existence of coexistence states and provides us with some uniqueness and stability results of a local nature.

Theorem 5.1. (i) *The model* (1.1) *admits a coexistence state if, and only if, its trivial and semi-trivial states are linearly unstable, that is, if* (4.2) *holds. Moreover, the number of coexistence states is always finite.*

(ii) *If $\lambda > 0$ and $\mu + \frac{1}{T}\int_0^T c\theta_\lambda > 0$ is sufficiently small, then* (1.1) *admits a unique coexistence state which is linearly asymptotically stable.*

(iii) *If $\mu > 0$ and $\lambda - \frac{1}{T}\int_0^T b\theta_\mu > 0$ is sufficiently small, then the same conclusion as in part* (ii) *holds.*

Remark 5.2. Due to (2.3), we find from Theorem 5.1 that if $a \gg 0$ and $d \gg 0$, then the following relations are sufficient for the existence of a coexistence state:

$$\lambda > \big(\frac{b}{d}\big)_M \mu\,, \qquad \mu > -\big(\frac{c}{a}\big)_L \lambda\,. \tag{5.1}$$

In fact, if there exist constants B and C such that $\frac{b}{d} \equiv B$ and $\frac{c}{a} \equiv C$, then the following condition is necessary and sufficient for the existence of a coexistence state:

$$\lambda > B\,\mu\,, \qquad \mu > -C\,\lambda\,. \tag{5.2}$$

The necessary and sufficient condition for the existence of coexistence states was obtained in [9] for the periodic-parabolic model with Dirichlet boundary conditions. The proof was based on the fixed-point index in cones. Another proof based on Leray-Schauder degree has been recently obtained in [7] for the case $\mu < 0$. Here we will use global bifurcation theory because this technical tool provides us with parts (i), (ii) and gives the topological structure of the set of coexistence states as λ, or μ, varies. We shall also present a second proof based on Brouwer degree that is quite simple.

In general it is not possible to guarantee the uniqueness for the coexistence state ([5], [1]). The finiteness of the set of coexistence states was obtained in [1] under some additional conditions.

In the sequel the solutions of (1.1) will be regarded as zeros of the operator $\mathcal{F}$: $\mathbb{R}^2 \times X^2 \mapsto Y^2$ defined by

$$\mathcal{F}(\lambda, \mu, u, v) := (\,u' - (\lambda\,\ell - au - bv)\,u\,,\, v' - (\mu\,m + cu - dv)\,v\,)\,. \tag{5.3}$$

Notice that this operator is analytic in all its arguments. The following result is needed for the proof of Theorem 5.1.

Lemma 5.3. (i) *If $\lambda > 0$ and there exists a sequence $(\lambda_n, \mu_n, u_n, v_n)$, $n \geq 1$, of zeros of $\mathcal{F}$, with $v_n \neq 0$ for $n \geq 1$, such that* $\lim_{n\to\infty}(\lambda_n, \mu_n, u_n, v_n) = (\lambda, \mu, \theta_\lambda, 0)$ *for some $\mu \in \mathbb{R}$, then*

$$\mu = \mu_\lambda := \frac{-1}{T}\int_0^T c\,\theta_\lambda\,. \tag{5.4}$$

(ii) *If $\mu > 0$ and there exists a sequence $(\lambda_n, \mu_n, u_n, v_n)$, $n \geq 1$, of zeros of $\mathcal{F}$, with $u_n \neq 0$ for $n \geq 1$, such that* $\lim_{n\to\infty}(\lambda_n, \mu_n, u_n, v_n) = (\lambda, \mu, 0, \theta_\mu)$ *for some $\lambda \in \mathbb{R}$, then*

$$\lambda = \lambda_\mu := \frac{1}{T}\int_0^T b\,\theta_\mu\,. \tag{5.4}$$

(iii) *If $\mathcal{F}$ admits a sequence of zeros $(\lambda_n, \mu_n, u_n, v_n)$, $n \geq 1$, such that $u_n \neq 0$ and $v_n \neq 0$ for $n \geq 1$ and* $\lim_{n\to\infty}(\lambda_n, \mu_n, u_n, v_n) = (\lambda, \mu, 0, 0)$ *for some $(\lambda, \mu) \in \mathbb{R}^2$, then $\lambda = \mu = 0$.*

Proof. (i) If there exists such a sequence, then it follows from the implicit function theorem that $\mathcal{L}(\lambda,\mu) := D_{(u,v)}\mathcal{F}(\lambda,\mu,\theta_\lambda,0)$ is not invertible. We have that

$$\mathcal{L}(\lambda,\mu) := \begin{pmatrix} \frac{d}{dt} - \lambda\,\ell + 2\,a\,\theta_\lambda & b\,\theta_\lambda \\ 0 & \frac{d}{dt} - \mu\,m - c\,\theta_\lambda \end{pmatrix}.$$

Moreover, since $\int_0^T (2\,a\,\theta_\lambda - \lambda\,\ell) = \int_0^T a\,\theta_\lambda > 0$, we find that $(\frac{d}{dt} - \lambda\,\ell + 2\,a\,\theta_\lambda)^{-1}$ is well defined and $\mathcal{L}(\lambda,\mu)$ is not invertible if and only if $\frac{d}{dt} - \mu\,m - \,c\,\theta_\lambda$ has not an inverse. Therefore, $\mu = \mu_\lambda$. Similarly, part (ii) follows.

(iii) Assume that there exists such a sequence. Then, it follows from the implicit function theorem that either $\lambda = 0$, or $\mu = 0$. Suppose that $\lambda = 0$. We have to see that $\mu = 0$. Set $V_n := \frac{v_n}{\|v_n\|_Y}$, $n \geq 1$. Then,

$$V_n' = \mu_n\,m\,V_n + cu_nV_n - dv_nV_n\,, \qquad n \geq 1\,. \tag{5.6}$$

From (5.6) we deduce that V_n' is uniformly bounded and by the Ascoli-Arzela Theorem one can extract a subsequence (relabeled V_n) such that $V_n \to V$ in Y. It is clear that $||V||_Y = 1$. Letting $n \to \infty$ in (5.6) it is easy to prove that V satisfies the linear equation $V' = \mu m V$. Therefore V is a nontrivial periodic solution and this is possible whenever $\mu = 0$. $\square$

Proof of Theorem 5.1. We first prove (ii) and (iii). Fixing $\lambda > 0$ and regarding μ as the bifurcation parameter, we shall apply the main result of [2] to show that $\mu = \mu_\lambda$ is a bifurcation value from the semi-trivial branch $(\theta_\lambda, 0)$ to an analytic curve of coexistence states. We have that $\mathcal{F}(\lambda,\mu,\theta_\lambda,0) = 0$ for all $\mu \in \mathbb{R}$. So, $(\mu, u, v) = (\mu, \theta_\lambda, 0)$ can be regarded as the known curve of zeros of $\mathcal{F}(\lambda,\cdot)$ from which a new solution curve will emanate. It can be easily seen that

$$N\left[\mathcal{L}(\lambda,\mu_\lambda)\right] = \text{span}\ \left[(u_1,\varphi)\right], \quad \varphi := e^{\int_0^\cdot (\mu_\lambda\,m + c\,\theta_\lambda)}\,,$$

$$u_1 := -\left(\frac{d}{dt} - \lambda\,\ell + 2\,a\,\theta_\lambda\right)^{-1}(b\,\theta_\lambda\,\varphi)\,.$$

Observe that $\varphi \gg 0$ and that $u_1 \ll 0$ by the periodic maximum principle. Moreover,

$$R\,[\mathcal{L}(\lambda,\mu_\lambda)] = \{\,(u,v)\in Y^2 \;:\; \int_0^T v\,\varphi^* = 0\,\}\,, \qquad \varphi^*(t) := e^{-\int_0^t(\mu_\lambda\,m + c\,\theta_\lambda)}\,.$$

If we decompose $\mathcal{L}(\lambda,\mu)$ into the form

$$\mathcal{L}(\lambda,\mu) = \mathcal{L}(\lambda,\mu_\lambda) + (\mu-\mu_\lambda)\mathcal{L}_1\,, \qquad \mathcal{L}_1 := \begin{pmatrix} 0 & 0 \\ 0 & -m \end{pmatrix},$$

then we have that $\mathcal{L}_1(N\,[\mathcal{L}(\lambda,\mu_\lambda)]) = \text{span}\,[(0,-m\,\varphi)]$. Moreover, $\int_0^T m\,\varphi\,\varphi^* = \int_0^T m > 0$ and hence $(0,-m\,\varphi) \notin R\,[\mathcal{L}(\lambda,\mu_\lambda)]$. Therefore, it follows from the main theorem of [2] that there exists $\varepsilon_0 > 0$ and an analytic mapping $(\mu,u,v) : (-\varepsilon_0,\varepsilon_0) \mapsto \mathbb{R}\times X^2$, $|s| < \varepsilon_0$, of the form

$$(\mu(s),u(s),v(s)) = (\mu_\lambda + O(s), \theta_\lambda + s\,u_1 + O(s^2), s\,\varphi + O(s^2))\,, \quad s\to 0\,, \tag{5.7}$$

such that $\mathcal{F}(\lambda,\mu(s),u(s),v(s)) = 0$ for all $s \in (-\varepsilon_0,\varepsilon_0)$. Moreover, there exists a neighborhood Q of $(\mu_\lambda,\theta_\lambda,0)$ in $\mathbb{R}\times X^2$ such that if $\mathcal{F}(\lambda,\mu,u,v) = 0$ for some $(\mu,u,v)\in Q$, then either $(\mu,u,v) = (\mu(s),u(s),v(s))$ for some $s\in(-\varepsilon_0,\varepsilon_0)$, or $(\mu,u,v) = (\mu,\theta_\lambda,0)$. Since $\varphi \gg 0$, we have that $u(s) \gg 0$ and $v(s) \gg 0$ if s is positive and small, and that $u(s) \gg 0$ and $v(s) \ll 0$ if s is negative and small. In particular, μ_λ is a bifurcation value to coexistence states. Moreover, it follows from Corollary 4.3 that $\mu(s) > \mu_\lambda$ if $s > 0$ and therefore, since the dimension of the unstable manifold of $(\theta_\lambda,0)$ increases the unity when μ passes by μ_λ, it follows from the exchange stability principle that $(\mu(s),u(s),v(s))$ is linearly asymptotically stable for $s > 0$ small enough, [3]. The following lemma completes the proof of part (ii).

Lemma 5.4. *There exists $\varepsilon_1 > 0$ such that if $\mu \in (\mu_\lambda,\mu_\lambda+\varepsilon_1)$ and $\mathcal{F}(\lambda,\mu,u,v) = 0$ for some $(u,v)\in X^2$ with $u > 0$ and $v > 0$, then there exists $s\in(0,\varepsilon_0)$ such that $(\mu,u,v) = (\mu(s),u(s),v(s))$.*

Proof. To prove the lemma we argue by contradiction assuming that there exists a sequence $(\mu_n,u_n,v_n)\notin Q$, $n\geq 1$, such that $u_n > 0$, $v_n > 0$, $\mathcal{F}(\lambda,\mu_n,u_n,v_n) = 0$, for all $n \geq 1$, and $\lim_{n\to\infty}\mu_n = \mu_\lambda$. From the results of Section 3 we deduce that

$$0 \leq u_n \leq \theta_\lambda\,; \quad 0 \leq v_n \leq \theta_{[\mu m + c\theta_\ell;d]}\,. \tag{5.8}$$

Now, from the differential equations we obtain a uniform bound on (u_n,v_n) in X. Let (u_n,v_n) be a subsequence that converges to (u_ω,v_ω) in Y^2. It is easy to check that (u_ω,v_ω) is a solution of (1.1) with $\mu = \mu_\lambda$. Due to Corollary 4.3, (u_ω,v_ω) can not be a coexistence state. Moreover, since (u_n,v_n) is bounded away from $(\theta_\lambda,0)$, $(u_\omega,v_\omega)\neq(\theta_\lambda,0)$. As $\mu_\lambda < 0$, necessarily $(u_\omega,v_\omega) = (0,0)$. Thanks to Lemma 5.3 this is also impossible, because $\lambda > 0$. This contradiction completes the proof. $\square$

Similarly, if we fix $\mu > 0$ and consider λ as the main bifurcation parameter, then from the branch $(\lambda, u, v) = (\lambda, 0, \theta_\mu)$ emanates a curve of coexistence states of (1.1) at the value of the parameter $\lambda = \lambda_\mu$. Moreover, these coexistence states are linearly asymptotically stable and are unique provided that $\lambda - \lambda_\mu < 0$ is sufficiently small.

To prove the existence result stated in (i) we shall use the global bifurcation theorem of Rabinowitz, [12]. Observe that the solutions of (1.1) in X^2 are the fixed points (u, v) of the compact operator $\mathcal{K} : \mathbb{R}^2 \times Y^2 \mapsto Y^2$ defined by

$$\mathcal{K}(\lambda, \mu, u, v) := (\frac{d}{dt} + M)^{-1} \left((\lambda \ell + M)u - au^2 - buv \, , \, (\mu m + M)v + cuv - dv^2 \right), \quad (5.9)$$

where $M \neq 0$. We distinguish two cases:

(I) $\lambda > 0$, $\mu \leq 0$. Let λ be fixed and regard μ as a bifurcation parameter. Since $\mu = \mu_\lambda$ is an algebraically simple eigenvalue of $D_{(u,v)}\mathcal{K}(\lambda, \mu, \theta_\lambda, 0)$, we can apply Theorem 1.40 of [12]. Consider the solution set

$$\mathcal{S}_\lambda := \{ (\mu, u, v) \in \mathbb{R} \times X^2 \ : \ \mathcal{F}(\lambda, \mu, u, v) = 0 \, , \ (u, v) \neq (\theta_\lambda, 0) \}$$

and let $\mathcal{C}_\lambda$ denote the maximal connected component of $\mathcal{S}_\lambda$ such that $(\mu_\lambda, \theta_\lambda, 0) \in \bar{\mathcal{S}}_\lambda$. Let $\mathcal{C}_\lambda^+$ denote the maximal connected component of $\mathcal{C}_\lambda \setminus \{ (\mu(s), u(s), v(s)) \ : \ 0 \simeq s \leq 0 \}$ that contains the positive branch that bifurcates at $(\mu_\lambda, \theta_\lambda, 0)$. Since for $\mu \neq \mu_\lambda$ the solution $(\mu, \theta_\lambda, 0)$ is isolated, the component $\mathcal{C}_\lambda^+$ can not contain a point of the form $(\hat{\mu}, \theta_\lambda, 0)$ with $\hat{\mu} \neq \mu_\lambda$. Therefore, it follows from Theorem 1.40 of [12] that $\mathcal{C}_\lambda^+$ is unbounded in $\mathbb{R} \times X^2$. For $(\mu, u, v) \simeq (\mu_\lambda, \theta_\lambda, 0)$, $\mathcal{C}_\lambda^+$ is constituted by the curve $(\mu(s), u(s), v(s))$, $s > 0$, and so there exists a neighborhood B of $(\mu_\lambda, \theta_\lambda, 0)$ such that $\mathcal{C}_\lambda^+ \cap B \subset \mathbb{R} \times (\text{int } P_X)^2$. Let $\mathcal{C}_{\lambda,int}^+$ denote the corresponding maximal component of $\mathcal{C}_\lambda^+ \cap \mathbb{R} \times (\text{int } P_X)^2$. If $\mathcal{C}_{\lambda,int}^+ = \mathcal{C}_\lambda^+$ we obtain bounds as in (5.8) for compact subsets of the parameter space and this allows us to deduce that the μ-projection of $\mathcal{C}_\lambda^+$ is $(\mu_\lambda, +\infty)$. Thus, in such a case (1.1) admits a coexistence state for all $\mu > \mu_\lambda$ and the proof is complete. Now, assume that $\mathcal{C}_{\lambda,int}^+$ is a proper subset of $\mathcal{C}_\lambda^+$. Then, there exists $(\mu_\omega, u_\omega, v_\omega) \in \mathcal{C}_\lambda^+ \cap (\mathbb{R} \times \partial P_X^2)$, $(\mu_\omega, u_\omega, v_\omega) \notin B$, such that $\lim_{n\to\infty}(\mu_n, u_n, v_n) = (\mu_\omega, u_\omega, v_\omega)$ for some sequence $(\mu_n, u_n, v_n) \in \mathcal{C}_\lambda^+$, $n \geq 1$. Since $\mathcal{F}(\lambda, \mu_\omega, u_\omega, v_\omega) = 0$ and $(u_\omega, v_\omega) \in \partial P_X^2$, either $u_\omega = 0$, or $v_\omega = 0$. Lemma 5.3 completes the proof. Indeed, since $\lambda > 0$ we have that $(u_\omega, v_\omega) \neq (0, 0)$. Moreover, $(\mu_\omega, u_\omega, v_\omega) \notin B$ implies that $(\mu_\omega, u_\omega, v_\omega) \neq (\mu_\lambda, \theta_\lambda, 0)$ and hence $(u_\omega, v_\omega) \neq (\theta_\lambda, 0)$. Therefore, $(u_\omega, v_\omega) = (0, \theta_\mu)$ for some μ. It follows from Lemma 5.3 that $\lambda = \lambda_\mu$ and this implies that $\mu > 0$. Summing up, we have proved that the μ-projection of $\mathcal{S}_\lambda$ contains $(\mu_\lambda, 0]$ and each corresponding solution (μ, u, v) with $\mu \leq 0$ is a coexistence state. This completes the proof of case (I).

(II) $\lambda > 0$, $\mu > 0$. We now fix μ and look at λ as a bifurcation parameter and repeat the previous reasoning for the component emanating from $(\lambda_\mu, 0, \theta_\mu)$. $\square$

We now give a proof of the existence result in (i) using a degree argument. Given $\mu \in \mathbb{R}$ and $\varepsilon \in [0, 1]$, we define

$$\sigma_\mu(\varepsilon) = \begin{cases} 1, & \text{if } \mu \leq 0 \\ \varepsilon, & \text{if } \mu > 0 \end{cases}$$

and consider the homotopy for $\varepsilon \in [0,1]$

$$\left\{\begin{array}{l} u'(t) = \lambda\,\ell(t)\,u(t) - a(t)\,u^2(t) - \sigma_{-\mu}(\varepsilon)b(t)\,u(t)v(t)\,, \\ v'(t) = \mu\,m(t)\,v(t) + \sigma_{\mu}(\varepsilon)c(t)\,u(t)v(t) - d(t)\,v^2(t)\,. \end{array}\right. \tag{5.10}$$

Lemma 5.5. *Suppose* (4.2)*. Then, there exist positive constants c and C, independent of ε, such that*

$$c \le u(t) \le C, \quad c \le v(t) \le C, \quad \forall t \in \mathbb{R}$$

for every $(u, v; \varepsilon)$ positive solution of (5.10)*.*

Proof. We shall assume $\mu \le 0$ (the remaining case is similar). The bounds given by (5.8) are also valid in our case. Thus, it is enough to show the existence of a positive lower bound. Before doing that we point out some useful estimates. From (5.8) and (5.10) we deduce that for every positive solution $|\frac{u_n'}{u_n}|_Y + |\frac{v_n'}{v_n}|_Y \le K$, where K is a fixed constant. In consequence

$$u_M \le Ke^T u_L, \quad v_M \le Ke^T v_L. \tag{5.11}$$

To prove the existence of a lower bound we use a contradiction argument and assume the existence of a sequence of positive solutions $(u_n, v_n; \varepsilon_n)$ such that $(u_n)_L \to 0$ or $(v_n)_L \to 0$. Assume first that $(u_n)_L \to 0$. Then (5.11) implies that $u_n \to 0$ in Y. The second equation in (5.10) and the continuity of $\theta_{[\alpha,\beta]}$ with respect to α implies that $v_n = \theta_{[\mu m + c u_n; d]} \to \theta_\mu = 0$ in Y. As in (2.6) we obtain $\frac{1}{T}(\int_0^T \varepsilon b v_n + a u_n) = \lambda$ and, letting $n \to \infty$ we reach a contradiction with the positivity of λ. Assuming now that $(v_n)_L \to 0$ we deduce in the same way that $v_n \to 0$ in Y and $u_n \to \theta_\lambda$. From (5.10), $\mu = -\frac{1}{T}\int_0^T (c u_n - d v_n) \to -\frac{1}{T}\int_0^T c\theta_\lambda$, a contradiction with (4.2).

We now assume that (4.2) holds and prove the existence of a coexistence state of (5.10) for each $\varepsilon \in [0,1]$. We shall use the same notation as [1]. The change of variables $u = e^p$, $v = e^q$ reduces our problem to the search of T-periodic solutions of the system

$$\left\{\begin{array}{l} p' = \lambda\,\ell(t)\; - a(t)\,e^p - \sigma_{-\mu}(\varepsilon)b(t)\,e^q\,, \\ q' = \mu\,m(t)\; + \sigma_{\mu}(\varepsilon)c(t)\,e^p - d(t)\,e^q\,. \end{array}\right. \tag{5.12}$$

Let P_ε denote the associated Poincaré operator. It is well defined in $\mathbb{R}^2$ and we shall prove the existence of fixed points for each $\varepsilon \in [0,1]$. For $\varepsilon = 0$ there exists a unique T-periodic solution (p_0, q_0) given by $(\log\theta_\lambda, \log\theta_{[\mu m + c\theta_\lambda; d]})$ if $\mu \le 0$ and $(\log\theta_{[\lambda\ell - b\theta_\mu; a]}, \log\theta_\mu)$ if $\mu > 0$. (Notice that (4.2) guarantees that such a solution is well defined.) If follows from Proposition 2.2 that this solution is globally asymptotically stable and, in consequence the index is one; that is, $\gamma_T(p_0, q_0) = 1$. Moreover, Lemma 5.5 guarantees that the possible fixed points of P_ε have an a priori bound independent of $\varepsilon \in [0,1]$. Therefore, P_ε is a homotopy in large balls B of $\mathbb{R}^2$ and

$$\deg[I - P_\varepsilon, B] = \deg[I - P_0, B] = \gamma_T(p_0, q_0) = 1.$$

This proves that (5.12) has at least one T-periodic solution for each $\varepsilon \in [0,1]$.

Due to Lemma 5.5, the model possesses at most a finite number of coexistence states. The proof given in [1] can be adapted to cover our general situation.

6. Persistence and global attractivity. In this section we obtain some further consequences of the results of Section 3 and analyze some examples to see how the theory applies.

Definition 6.1. It is said that (1.1) is persistent if there exist positive numbers $0 < \rho < R$ such that any component-wise positive solution of (1.1) satisfies

$$\rho \le \liminf_{t\to+\infty} u(t) \le \limsup_{t\to+\infty} u(t) \le R, \quad \rho \le \liminf_{t\to+\infty} v(t) \le \limsup_{t\to+\infty} v(t) \le R.$$

Since (1.1) is a two-dimensional system we can apply the second theorem of Massera ([11]) to show that if the model is persistent, then it admits a coexistence state.

Proposition 6.2. *Assume that* (1.1) *has a component-wise positive solution such that*

$$\liminf_{t\to+\infty} u(t) > 0\,, \qquad \liminf_{t\to+\infty} v(t) > 0\,. \tag{6.1}$$

Then (1.1) *possesses a coexistence state.*

Proof. It follows from Theorem 3.2 that the solution (u,v) has also an upper bound at infinity. Using again the change of variables $u = e^p$, $v = e^q$ the system (1.1) is reduced to

$$\begin{cases} p' = \lambda\,\ell(t)\ - a(t)\,e^p - b(t)\,e^q\,, \\ q' = \mu\,m(t)\ + c(t)\,e^p - d(t)\,e^q\,, \end{cases} \tag{6.2}$$

and the solution (u,v) is transformed into a solution of (3.14) that is bounded in $[0,+\infty)$. Since all the solutions of (3.14) can be extended up to infinity, the results in [11] imply the existence of a T-periodic solution. Undoing the change we obtain a coexistence state for the original system. $\square$

We do not know of an example that is not persistent but has a coexistence state. In the next result we obtain some sufficient conditions for persistence.

Theorem 6.3. (i) *If* $\mu > 0$, $\lambda > \frac{1}{T}\int_0^T b\theta_\mu$, *and*

$$\lambda > \frac{1}{T}\int_0^T b\theta_{[\mu\,m + c\,\theta_{[\lambda\,\ell - b\,\theta_\mu;a]};d]}\,, \tag{6.3}$$

then (1.1) *is persistent.*

(ii) *If* $\lambda > 0$, $\frac{-1}{T}\int_0^T c\theta_\lambda < \mu \le 0$, *and*

$$\lambda > \frac{1}{T}\int_0^T b\theta_{[\mu\,m + c\theta_\lambda;d]}\,, \qquad \mu > \frac{-1}{T}\int_0^T c\theta_{[\lambda\,\ell - b\theta_{[\mu\,m+c\theta_\lambda;d]};a]}\,, \tag{6.4}$$

then (1.1) *is persistent.*

Proof. (i) Let U_n, V_n, $n \ge 1$, denote the sequences given by the scheme (3.1). Since $\mu > 0$ and $\lambda > \frac{1}{T}\int_0^T b\theta_\mu$, we have $V_1 > 0$ and $U_1 > 0$. Moreover, condition (6.1) implies that $U_2 > 0$. Now, Theorem 3.2 completes the proof. Similarly, Part (ii) follows from (3.10) and Theorem 3.3. $\square$

Corollary 6.4. (i) *If* $a \gg 0$, $d \gg 0$, $\mu > 0$ *and*

$$\lambda > \Big(\frac{b}{d}\Big)_M \mu\,, \qquad \Big[\lambda - \Big(\frac{b}{d}\Big)_M \mu\Big] > \Big(\frac{b}{d}\Big)_M \Big(\frac{c}{a}\Big)_M \Big[\lambda - \Big(\frac{b}{d}\Big)_L \mu\Big]\,, \tag{6.5}$$

then (1.1) *is persistent.*

(ii) *If* $\lambda > 0$, $0 \geq \mu > -\left(\frac{c}{a}\right)_L \lambda$, $[1 - \left(\frac{b}{d}\right)_M \left(\frac{c}{a}\right)_M] \lambda > \left(\frac{b}{d}\right)_M \mu$, *and*

$$\Big[-1 + \Big(\frac{c}{a}\Big)_L \Big(\frac{b}{d}\Big)_M\Big]\mu > \Big(\frac{c}{a}\Big)_L \Big[\lambda - \Big(\frac{c}{a}\Big)_M \Big(\frac{b}{d}\Big)_M\Big]\lambda\,, \tag{6.6}$$

then (1.1) *is persistent.*

Theorem 6.5. *If* $\overline{U} = \underline{U} \gg 0$ *and* $\overline{V} = \underline{V} \gg 0$ (*respectively* $U_* = U^*$ *and* $V_* = V^*$), *then* $(\overline{U}, \overline{V})$ *is globally asymptotically stable. In particular,* (1.1) *is persistent.*

To conclude this section we apply the previous corollary to the following family of models:

$$u' = A(t)\, u\, (1 - u - bv)\,, \qquad v' = B(t)\, v\, (n + cu - v)\,, \tag{6.7}$$

where $A\,, B \in Y$, $A \gg 0$, $B \gg 0$, and $n, b, c \in \mathbb{R}$ satisfy $b > 0$, $c > 0$. It is easy to see that there exists a positive constant solution if and only if $bn < 1$ and $c + n > 0$. In view of Corollary 4.3 this condition is also necessary and sufficient for the existence of a coexistence state. In this case it is easy to compute explicitly the monotone scheme given by (3.1) and verify that if $bc < 1$ then $\overline{U} = \underline{U} = \frac{1-bn}{1+bc}$, $\overline{V} = \underline{V} = \frac{c+n}{1+bc}$. It follows from Theorem 6.5 that under these conditions the constant solution is the unique coexistence state and it is globally asymptotically stable with respect to the first quadrant.

7. An example.

In this section we construct a prey-predator system having a unique T-periodic coexistence state that is unstable. This example answers a question posed at the end of [1]. Throughout the section α and β will denote two fixed functions in Y such that $\alpha > 0$, $\beta > 0$ and

$$\alpha(t) = 0 \;\; \forall\, t \in [\frac{T}{2}, T]\,, \qquad \beta(t) = 0 \;\; \forall\, t \in [0, \frac{T}{2}]\,.$$

We denote $A := \int_0^T \alpha$, $B := \int_0^T \beta$. Notice that $A > 0$, $B > 0$ and $\alpha\beta \equiv 0$.

First, we consider

$$u' = u(\alpha - \alpha v)\,, \qquad v' = v(-\beta + \beta u)\,. \tag{7.1}$$

However this system does not fit into the general framework of this paper, because some of the coefficients are identically zero; it can be regarded as a limit of a one-parameter family of admissible systems. Namely,

$$u' = u(\alpha_\varepsilon + \varepsilon\beta_\varepsilon - \varepsilon\beta_\varepsilon u - \alpha_\varepsilon v), \qquad v' = v(-\beta_\varepsilon + \varepsilon\alpha_\varepsilon + \beta_\varepsilon u - \varepsilon\alpha_\varepsilon v)\,, \tag{7.2}$$

where $\varepsilon > 0$ is a parameter and $\alpha_\varepsilon := \alpha + \varepsilon$, $\beta_\varepsilon = \beta + \varepsilon$. It is clear that $(u, v) = (1, 1)$ is a T-periodic coexistence state of both models (7.1) and (7.2).

An interesting feature of system (7.1) is that it can be integrated. This is due to the property $\alpha\beta = 0$. The solution of the initial value problem associated with (7.1) is

$$u(t) := u(t; u_0, v_0) = u_0 e^{(1-v_0)\int_0^t \alpha(s)ds}, \qquad t \in [0, T],$$

$$v(t) := v(t; u_0, v_0) = \begin{cases} v_0\,, & \text{if } t \in [0, \frac{T}{2}]\,, \\ v_0 e^{(u(T)-1)\int_{\frac{T}{2}}^t \beta(s)ds}, & \text{if } t \in [\frac{T}{2}, T]\,. \end{cases}$$

Proposition 7.1. *The couple $(u, v) = (1, 1)$ is the unique positive T-periodic solution of (7.1). Moreover, it is linearly unstable if $AB > 4$.*

Proof. The corresponding Poincaré map is defined by the equations

$$(u_1, v_1) = P(u_0, v_0)\,, \qquad u_1 = u_0 e^{A(1-v_0)}\,, \qquad v_1 = v_0 e^{B(u_1-1)}\,.$$

An easy computation shows that $(1, 1)$ is the unique positive fixed point of P. The Jacobian matrix at the fixed point is

$$\partial_{(u_0,v_0)} P(1, 1) = \begin{pmatrix} 1 & -A \\ B & 1 - AB \end{pmatrix}. \tag{7.3}$$

If $AB > 4$, then the matrix $\partial_{(u_0,v_0)} P(1, 1)$ has eigenvalues $\nu_1 < -1 < \nu_2 < 0$. The proof is completed. $\square$

We now state a result for system (7.2) that provides us with the example promised at the beginning of the section.

Theorem 7.2. *There exists $\varepsilon_0 > 0$ such that if $0 < \varepsilon < \varepsilon_0$, then the only positive T-periodic solution of (7.2) is $(u, v) = (1, 1)$. Moreover, if $AB > 4$, then there exists $\varepsilon_1 \in (0, \varepsilon_0)$ such that the solution $(1, 1)$ is linearly unstable for $0 < \varepsilon < \varepsilon_1$.*

The proof will be obtained after two lemmas.

Lemma 7.3. *There exist $\varepsilon_2 > 0$ and $\delta > 0$ (depending on α and β) such that if $\varepsilon \in (0, \varepsilon_2)$, then $(u, v) = (1, 1)$ is the unique T-periodic solution of (7.2) satisfying*

$$|u(0) - 1| + |v(0) - 1| < \delta\,. \tag{7.4}$$

Proof. Let $P = P(u_0, v_0; \varepsilon)$ denote the Poincaré map associated to (7.2). It is easy to see that P is well defined and smooth on the first quadrant $u_0 > 0$, $v_0 > 0$. Thanks to (7.3), the function $\Phi(u_0, v_0; \varepsilon) = (u_0, v_0) - P(u_0, v_0; \varepsilon)$ satisfies

$$\Phi(1, 1; \varepsilon) = 0, \qquad \partial_{(u_0,v_0)} \Phi(1, 1; 0) = \begin{pmatrix} 0 & A \\ -B & AB \end{pmatrix}.$$

The implicit function theorem can now be applied to deduce that the only solutions of $\Phi = 0$ in a neighborhood of $(u_0, v_0; \varepsilon) = (1, 1; 0)$ are $(1, 1; \varepsilon)$. The proof is completed. $\square$

Lemma 7.4. *There exist positive constants* ϵ_3*,* c *and* C *such that*

$$c \le u(t) + v(t) \le C\,, \qquad \forall\, t \in \mathbb{R}\,,$$

for every positive T*-periodic solution of* (7.2) *with* $\varepsilon \in [0, \varepsilon_3]$*.*

Proof. In what follows the K_i's stand for positive constants that are independent of the solution (u, v). Dividing the first equation of (7.2) by u and the second by v and integrating over a period we obtain

$$\varepsilon \int_0^T \beta_\varepsilon u + \int_0^T \alpha_\varepsilon v = \int_0^T (\alpha_\varepsilon + \varepsilon\beta_\varepsilon)\,, \tag{7.5}$$

$$\int_0^T \beta_\varepsilon u - \varepsilon \int_0^T \alpha_\varepsilon v = \int_0^T (\beta_\varepsilon - \varepsilon\alpha_\varepsilon)\,. \tag{7.6}$$

From (7.5) we find that

$$\int_0^T \alpha_\varepsilon v \le \int_0^T \alpha_\varepsilon + \varepsilon\beta_\varepsilon \le K_1\,. \tag{7.7}$$

Now, substituting this estimate into (7.6) gives

$$\int_0^T \beta_\varepsilon u \le \varepsilon K_1 + |\int_0^T (\beta_\varepsilon - \varepsilon\alpha_\varepsilon)| \le K_2\,. \tag{7.8}$$

From these estimates one can easily obtain uniform upper bounds for u_L and v_L, say

$$u_L \le K_3\,, \qquad v_L \le K_3\,. \tag{7.9}$$

Going back to the system (7.2) we find that

$$\int_0^T |\frac{u'}{u}| \le \varepsilon \int_0^T \beta_\varepsilon u + \int_0^T \alpha_\varepsilon v + |\int_0^T (\alpha_\varepsilon + \varepsilon\beta_\varepsilon)|\,, \tag{7.10}$$

$$\int_0^T |\frac{v'}{v}| \le \int_0^T \beta_\varepsilon u + \varepsilon \int_0^T \alpha_\varepsilon v + |\int_0^T (\beta_\varepsilon - \varepsilon\alpha_\varepsilon)|\,. \tag{7.11}$$

Thus, substituting (7.7) and (7.8) into (7.10) and (7.11) we find that

$$\int_0^T |\frac{u'}{u}| + \int_0^T |\frac{v'}{v}| \le K_4\,. \tag{7.12}$$

Moreover, it follows from (7.12) that

$$\log u_M \le \log u_L + \int_0^T |\frac{u'}{u}| \le \log K_3 + K_4\,, \tag{7.13}$$

and therefore $u_M \leq K_3 e^{K_4} := K_5$. Similarly, $v_M \leq K_6$.

It remains to show that u_L and v_L are uniformly bounded away from zero. Using (7.6) we find that

$$(B+\varepsilon T)u_M \geq \int_0^T \beta_\varepsilon u \geq \int_0^T (\beta_\varepsilon - \varepsilon\alpha_\varepsilon) = B + \varepsilon T - \varepsilon(A+\varepsilon T)$$

and, since ε is small, we get $u_M \geq K_7$. Thus, it follows from the first inequality of (7.13) that

$$u_L \geq u_M e^{-K_4} \geq K_7 e^{-K_4} := K_8\,.$$

Similarly, from (7.5) we find that

$$(A+\varepsilon T)v_M \geq \int_0^T \alpha_\varepsilon v = \int_0^T (\alpha_\varepsilon + \varepsilon\beta_\varepsilon) - \varepsilon \int_0^T \beta_\varepsilon u \geq A + \varepsilon T + \varepsilon(B+\varepsilon T) - \varepsilon K_2$$

and therefore v_L is uniformly bounded away from zero as well. The proof of this lemma is completed. □

Proof of Theorem 7.2. First we prove the uniqueness. On the contrary, assume that there exists a sequence $\varepsilon_n > 0$, $n \geq 1$, such that $\varepsilon_n \to 0$ as $n \to \infty$ and (7.2) admits at least two coexistence states, $(1,1)$ and $(u_{\varepsilon_n}, v_{\varepsilon_n}) \neq (1,1)$, for each $n \geq 1$. Due to Lemma 7.3, condition (7.4) cannot be satisfied by $(u_{\varepsilon_n}, v_{\varepsilon_n})$ if n is sufficiently large. Moreover, from Lemma 7.4 we deduce the estimate $u_{\varepsilon_n} + v_{\varepsilon_n} \leq C$ which combined with (7.2) provides us with a uniform upper estimate of $\|u_{\varepsilon_n}\|_X + \|v_{\varepsilon_n}\|_X$. A compactness argument based on Ascoli-Arzela Theorem allows us to extract a subsequence converging to a solution of (7.1). Since for n large we have that $u_{\varepsilon_n} + v_{\varepsilon_n} \geq c$ the limit state is a coexistence state which can not satisfy (7.4). This contradiction with Proposition 7.1 completes the proof of the uniqueness.

To prove the instability of $(1,1)$ with respect to (7.2) we consider the Floquet multipliers of the linearization of (7.2) at $(1,1)$, say $\nu_1(\varepsilon)$, $\nu_2(\varepsilon)$. They depend continuously on ε, so that $\nu_i(\varepsilon) \to \nu_i(0)$ as $\varepsilon \to 0$. The conclusion now follows from Proposition 7.1. The proof of the theorem is completed. □

Remark 7.5. When $AB > 4$ the index of the solution $(1,1)$ changes from period T to period $2T$. In fact, following the notation of [1], $\gamma_T(1,1) = 1$ and $\gamma_{2T}(1,1) = -1$. As in large balls the degree of $I - P_1$ is one and the model possesses a finite number of $2T$-periodic coexistence states; there exist at least two periodic solutions with minimal period $2T$ and fixed point index 1. Thus, our example is also useful to construct systems with more than one coexistence state, [1], [5].

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