Diffusive Holling-Tanner predator-prey models in periodic environments

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Abstract

In this paper, by using the Lyapunov method, we establish sufficient conditions for the global asymptotic stability of the positive periodic solution to diffusive Holling-Tanner predator-prey models with periodic coefficients and no-flux conditions.

Keywords. Predator-prey. Diffusive system. Periodicity. Global stability.

2010 Mathematics Subject Classification. 35K52, 35K57, 92D25.

1 Introduction

The main object of this paper is studying the stability of the periodic solution to a reaction-diffusion Holling-Tanner predator-prey model of the form

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1(t)\Delta u + u\left(a(t) - u - \dfrac{v}{u+m(t)}\right) \\ \dfrac{\partial v}{\partial t} = d_2(t)\Delta v + v\left(b(t) - \dfrac{v}{\gamma(t)\, u}\right) \\ u(x,0) = u_0(x) > 0, v(x,0) = v_0(x) > 0 \quad x \in \overline{\Omega} \\ \dfrac{\partial u}{\partial \mathbf{n}} = \dfrac{\partial v}{\partial \mathbf{n}} = 0 \quad \text{on } \partial\Omega \times \mathbf{R}_+, \end{cases} \tag{1.1}$$

where Ω is a bounded domain of $\mathbf{R}^n$, with sufficiently smooth boundary $\partial\Omega$, $d_1(t), d_2(t)$, $a(t), b(t), m(t), \gamma(t)$ are continuous T-periodic functions, and $u_0(x), v_0(x)$ are continuous functions. The unknowns $u(x,t)$, $v(x,t)$ represent, respectively, the density of preys and predators, and $\mathbf{n}$ is the outward unit vector on $\partial\Omega$.

The ODE Holling-Tanner model, proposed by Tanner ([9]) and May ([6]), has received considerable attention by many researchers because it well describes the real ecological interactions between certain species (see [9]). It exhibits rich dynamical behaviours, such as global stability of the unique positive equilibrium, periodic solutions, limit cycles, bifurcation and so on. A recent contribution to the Holling-Tanner system with periodic coefficients is due to Lisena ([5]).

To take into consideration the movement of the species in different spatial locations within a fixed domain, the corresponding PDE system has to be analyzed. Indeed, the role of spatial effect to maintain the biodiversity can be better investigated through reaction-diffusion system (1.1). The Neumann boundary conditions biologically can be interpreted as the ecosystem being impermeable to the external environment, so that there is no population flux across its boundary. The periodic coefficients account for the fact that, as a result of seasonal alternation, life-cycles and other factors, there might be cyclic fluctuations in the biological parameters of the model.

From a mathematical point of view, the presence of periodic coefficients can be linked to the study of the so-called free-boundary reaction-diffusion problems, i.e., those reaction-diffusion problems on domains evolving in time. In [4, 10], in fact, it was proven that, under suitable assumptions, one can turn an autonomous reaction-diffusion problem, on a periodically and isotropically evolving domain, into a reaction-diffusion problem with periodic coefficients on a fixed domain.

In this paper we focus on system (1.1) with the aim of generalizing the results in ([3, 7]) in the case the environment is assumed to be temporally periodic and spatially homogeneous.

2 Preliminary results

We begin the section with presenting some results (see [1]) about the periodic solutions to a logistic reaction-diffusion equation, whose coefficient are supposed to be T-periodic in time.

First of all, if f is a continuous T-periodic function, we denote by

$$[f(t)] = \frac{1}{T}\int_0^T f(t)\,dt$$

its integral average (or mean value).

Moreover, given a smooth bounded domain $\Omega \subset \mathbf{R}^n$, consider the diffusive logistic equation

$$\frac{\partial w}{\partial t} = k(t)\Delta w + w(a(t) - b(t)w). \tag{2.1}$$

Lemma 2.1. *If $a(t), b(t), k(t)$ are continuous, T-periodic functions with $[a(t)] > 0$, $b(t), k(t) > 0$, then the unique positive solution to*

$$\begin{cases} \dfrac{\partial w}{\partial t} = k(t)\Delta w + w(a(t) - b(t)w) \\ \dfrac{\partial w}{\partial \mathbf{n}}|_{\partial\Omega\times\mathbf{R}_+} = 0 \\ w(x, t+T) = w(x,t) \quad (x,t) \in \overline{\Omega}\times\mathbf{R}_+ \end{cases}$$

is the positive T-periodic solution $w^*(t)$ to the logistic equation ([2])

$$u' = u(a(t) - b(t)u).$$

Moreover, for any positive solution $w(x,t)$ to (2.1) with homogeneous Neumann conditions and $w(x,0) = w_0(x) \in C^2(\Omega) \cap C^(\overline{\Omega})$, one has

$$\lim_{t\to+\infty} |w(x,t) - w^*(t)| = 0 \text{ uniformly w.r.t. } x \in \overline{\Omega}. \tag{2.2}$$

Proof. The first part follows from the investigations carried on in [1]. Statement (2.2) may be easily obtained by using the comparison theorem for parabolic equations ([8]). □

Let us recall some recent results concerning ODE Holling-Tanner predator-prey models with periodic coefficients (see [5]).

Theorem 2.1. *Consider the system*

$$\begin{cases} u' = u\left(a(t) - u - \dfrac{v}{u+m(t)}\right) \\ v' = v\left(b(t) - \dfrac{v}{\gamma(t)\,u}\right), \end{cases} \tag{2.3}$$

where $a(t), b(t), m(t), \gamma(t)$ are continuous T-periodic functions, $m(t), \gamma(t) > 0$, and $[a(t)], [b(t)] > 0$. Denote, respectively, by $\widetilde{u}(t)$ and $\widetilde{v}(t)$ the positive T-periodic solution to the logistic equations

$$x' = x(a(t) - x) \quad \text{and} \quad y' = y\left(b(t) - \frac{y}{\gamma(t)\,\widetilde{u}(t)}\right).$$

If the inequality

$$[a(t)] > \left[\frac{\widetilde{v}(t)}{m(t)}\right] \tag{2.4}$$

holds, then, for any positive solution $(u(t), v(t))$ to (2.3)*, there exists $\bar{t} > 0$ such that*

$$\overline{u}(t) \le u(t) \le \widetilde{u}(t), \quad \overline{v}(t) \le v(t) \le \widetilde{v}(t), \quad \text{for } t > \bar{t},$$

where $\overline{u}(t)$, $\overline{v}(t)$ are, respectively, the positive periodic solution to

$$x' = x\left(\left(a(t) - \frac{\widetilde{v}(t)}{m(t)}\right) - x\right) \quad \text{and} \quad y' = y\left(b(t) - \frac{y}{\gamma(t)\,\overline{u}(t)}\right).$$

As a consequence of Theorem 2.1, we get the existence of a positive T-periodic solution to system (2.3). In fact, the following result (see [5]) holds true.

Theorem 2.2. *Suppose that inequality* (2.4) *is satisfied; then system* (2.3) *has at least a positive, T-periodic solution $(u^*(t), v^*(t))$ such that*

$$\overline{u}(t) \le u^*(t) \le \widetilde{u}(t), \quad \overline{v}(t) \le v^*(t) \le \widetilde{v}(t), \quad t \in [0, T]\,.$$

To prove our main result, an additional property of system (2.3) will be needed.

Lemma 2.2. *Under the notation and assumptions of Theorem 2.1 and Theorem 2.2, if additionally*

$$v^*(t) \le m(t)u^*(t), \quad t \in [0, T], \tag{2.5}$$

then $u^*(t) > \frac{\widetilde{u}(t)}{2}$ for every $t > 0$.

Proof. From (2.5) it follows that, for each $t > 0$,

$$\frac{v^*(t)}{u^*(t) + m(t)} \le \frac{u^*(t)m(t)}{u^*(t) + m(t)} < u^*(t). \tag{2.6}$$

Accordingly,

$$(u^*)' = u^*\left(a(t) - u^*(t) - \frac{v^*(t)}{u^*(t) + m(t)}\right) > u^*(a(t) - 2u^*).$$

We notice that $\frac{\widetilde{u}(t)}{2}$ is a periodic solution to the logistic equation

$$u' = u(a(t) - 2u).$$

Moreover $[u^*(t)] > \frac{[\widetilde{u}(t)]}{2}$; in fact, from (2.6) it follows that

$$[\widetilde{u}(t)] = [a(t)] = [u^*(t)] + \left[\frac{v^*(t)}{u^*(t)+m(t)}\right] < 2[u^*(t)].$$

As a consequence, there exists $t_0 > 0$ such that $u^*(t_0) > \frac{\widetilde{u}(t_0)}{2}$. For the comparison theorem, for every $t > t_0$, $u^*(t) > \frac{\widetilde{u}(t)}{2}$; since $u^*(t), \widetilde{u}(t)$ are T-periodic functions, there exists $K \in \mathbf{N}$ such that $KT > t_0$, so that $u^*(0) = u^*(KT) > \frac{\widetilde{u}(KT)}{2} = \frac{\widetilde{u}(0)}{2}$; hence, $u^*(t) > \frac{\widetilde{u}(t)}{2}$ for every $t > 0$. □

3 Global stability

Consider the reaction-diffusion Holling-Tanner predator-prey model (1.1) and assume that $d_1(t), d_2(t)$, $m(t), \gamma(t) > 0$, $[a(t)], [b(t)] > 0$ and $u_0(x), v_0(x) \in C^2(\Omega) \cap C^0(\overline{\Omega})$.

The presence of an invariant region is shown below.

Theorem 3.1. *Under the assumptions and notation of Theorem 2.1, the region* $\Sigma(t) := [\overline{u}(t), \widetilde{u}(t)] \times [\overline{u}(t), \widetilde{u}(t)]$ $(t > 0)$ *is invariant and attractive for* (1.1)*, i.e.,*

(a) If $(u(x,t), v(x,t))$ *is a positive solution to* (1.1) *with* $(u_0(x), v_0(x)) \in \Sigma(0)$ *for every* $x \in \overline{\Omega}$*, then* $(u(x,t), v(x,t)) \in \Sigma(t)$ *for every* $t > 0$ *and* $x \in \overline{\Omega}$*.*

(b) If $(u(x,t), v(x,t))$ *is a positive solution to* (1.1)*, there exists* $\overline{t} > 0$ *such that* $(u(x,t), v(x,t)) \in \Sigma(t)$ *for every* $t > \overline{t}$ *and* $x \in \overline{\Omega}$*.*

Proof. Assume that $u_0(x) = u(x,0) \le \widetilde{u}(0)$ for every $x \in \overline{\Omega}$; since $\widetilde{u}(t)$ is a positive periodic solution to

$$u'(t) = u(t)(a(t) - u(t)),$$

it satisfies the equation

$$\frac{\partial u}{\partial t} = d_1(t)\Delta u + u\,(a(t) - u)\,,$$

subject to $\dfrac{\partial u}{\partial \mathbf{n}} = 0$ on $\partial\Omega \times \mathbf{R}_+$. Accordingly, by using the comparison theorem for parabolic equations, we get $u(x,t) \le \widetilde{u}(t)$ for every $t > 0$ and $x \in \overline{\Omega}$.

Assume now that $\max_{x\in\overline{\Omega}} u(x,0) > \widetilde{u}(0)$. Let us denote by $u(t)$ the solution to the logistic equation

$$\begin{cases} u' = u(a(t) - u) \\ u(0) = \max_{x\in\overline{\Omega}} u(x,0). \end{cases}$$

By applying the comparison theorem for parabolic equations, we have that $u(x,t) \le u(t)$ for every $t > 0$ and $x \in \overline{\Omega}$. On the other hand, taking Theorem 2.1 into account, there exists $t_0 > 0$ such that, for every $t > t_0$, $u(t) \le \widetilde{u}(t)$. Consequently, for $t \ge t_0$ and $x \in \overline{\Omega}$,

$$u(x,t) \le u(t) \le \widetilde{u}(t).$$

Similarly, one can prove all the remaining parts of the statement. □

Lemma 3.1. *Let* $(u^*(t), v^*(t))$ *be a positive periodic solution to* (2.3)*. If* $(u(x,t), v(x,t))$ *is a solution to* (1.1)*, by applying the substitution*

$$z(x,t) = \frac{u(x,t)}{u^*(t)} - 1, \quad w(x,t) = \frac{v(x,t)}{v^*(t)} - 1, \tag{3.1}$$

system (1.1) *turns into*

$$\begin{cases} \dfrac{\partial z}{\partial t} = d_1(t)\Delta z + (1+z)\left(\left(-u^*(t) + \dfrac{v^*(t)}{(u^*(t)\theta(t))(z+\theta(t))}\right)z - \dfrac{v^*(t)}{u^*(t)}\dfrac{w}{(z+\theta(t))}\right) \\ \dfrac{\partial w}{\partial t} = d_2(t)\Delta w + (1+w)\dfrac{v^*(t)}{\gamma(t)\, u^*(t)}\left(\dfrac{z}{z+1} - \dfrac{w}{z+1}\right) \\ z(x,0) = z_0(x) > -1, w(x,0) = w_0(x) > -1 \\ \dfrac{\partial z}{\partial \mathbf{n}} = \dfrac{\partial w}{\partial \mathbf{n}} = 0 \quad \text{on } \partial\Omega \times \mathbf{R}_+, \end{cases} \tag{3.2}$$

where

$$\theta(t) = \frac{m(t)}{u^*(t)} + 1, \quad z_0(x) = \frac{u_0(x)}{u^*(0)} - 1, \quad w_0(x) = \frac{v_0(x)}{v^*(0)} - 1. \tag{3.3}$$

Proof. The initial and boundary conditions (3.3) derive directly from (3.1) and the initial and boundary conditions in (1.1). Moreover, we notice that

$$\frac{\partial z}{\partial t} = \frac{1}{u^*(t)}\left(d_1(t)\Delta u + u\left(a(t) - u - \frac{v}{u+m(t)}\right)\right) - \frac{u}{u^*(t)}\left(a(t) - u^*(t) - \frac{v^*(t)}{u^*(t)+m(t)}\right)$$
$$= d_1(t)\Delta z + \frac{u}{u^*(t)}\left(-u + u^*(t) - \frac{v}{u+m(t)} + \frac{v^*(t)}{u^*(t)+m(t)}\right).$$

In the same way,

$$\frac{\partial w}{\partial t} = d_2(t)\Delta w + \frac{v}{v^*(t)}\left(-\frac{v}{\gamma(t)u} + \frac{v^*(t)}{\gamma(t)u^*(t)}\right).$$

At this point, arguing as in [5, Lemma 4.1], we obtain (3.2). □

The following result is a straightforward consequence of Theorem 3.1 and Lemma 3.1.

Lemma 3.2. *Let us assume that* (2.4) *holds true and let* $(u(x,t), v(x,t))$ *be a solution to* (1.1) *and* $(u^*(t), v^*(t))$ *a positive periodic solution to* (2.3). *Then, for any* $t > \bar{t}$ *and* $x \in \overline{\Omega}$, $(z(x,t), w(x,t)) \in \mathcal{Q}(t) = [\overline{z}(t), \widetilde{z}(t)] \times [\overline{w}(t), \widetilde{w}(t)]$ *(see* (3.1)*), where*

$$\overline{z}(t) = \frac{\overline{u}(t)}{u^*(t)} - 1, \quad \widetilde{z}(t) = \frac{\widetilde{u}(t)}{u^*(t)} - 1, \quad \overline{w}(t) = \frac{\overline{v}(t)}{v^*(t)} - 1, \quad \widetilde{w}(t) = \frac{\widetilde{v}(t)}{v^*(t)} - 1.$$

We pass now to study the global stability of (1.1). To this end, we set

$$\alpha := \left[\frac{m(t)}{u^*(t)}\right], \quad \theta_\alpha := \alpha + 1, \quad \sigma := [\gamma(t)].$$

Moreover, let $H(z,w)$ be defined as

$$H(z,w) = \int_1^{z+1}\left(1 - \frac{1}{s}\right)\left(1 + \frac{\alpha}{s}\right) ds + \sigma \int_1^{w+1}\left(1 - \frac{1}{s}\right) ds\,. \tag{3.4}$$

Theorem 3.2. *Assume that condition* (2.4) *holds and let* $(u^*(t), v^*(t))$ *be a positive periodic solution to* (2.3). *Such solution is globally attractive for* (1.1) *under assumption* (2.5) *and the following inequality*

$$\Gamma(t,z) < 0 \quad \text{for every } t > 0 \text{ and } z \in [\overline{z}(t), \widetilde{z}(t)], \tag{3.5}$$

where, for $t > 0$ *and* $z > -1$,

$$\Gamma(t,z) = \left(\frac{v^*(t)}{u^*(t)}\right)^2\left(\frac{\sigma}{\gamma(t)} - \frac{z+\theta_\alpha}{z+\theta(t)}\right)^2 - 4\,\frac{\sigma v^*(t)(z+\theta_\alpha)}{\gamma(t)u^*(t)}\left(u^*(t) - \frac{v^*(t)}{u^*(t)\theta(t)(z+\theta(t))}\right).$$

Proof. The proof is based on a positive definite Lyapunov function. Given a solution $(u(x,t), v(x,t))$ to (1.1), let $(z(x,t), w(x,t))$ be the corresponding solution to system (3.2) under substitution (3.1). Consider the Lyapunov function

$$V(t) = \int_\Omega H(z(x,t), w(x,t))\, dx,$$

where $H(z,w)$ is defined by (3.4). Since, taking Lemma 3.2 into account, for $t > \bar{t}$, the solutions to (3.2) ultimately enter $\mathcal{Q}(t)$, we restrict the study to this set. In particular, for $t > \bar{t}$,

$$V'(t) = \int_\Omega \left(\frac{z(z+\theta_\alpha)}{(z+1)^2} \frac{\partial z}{\partial t} + \frac{\sigma w}{w+1} \frac{\partial w}{\partial t} \right) dx + d_1(t) \int_\Omega \frac{z(z+1+\alpha)}{(z+1)^2} \Delta z dx + \sigma d_2(t) \int_\Omega \frac{w \Delta w}{w+1}\, dx.$$

Using Lemma 3.1 and integrating by parts in the second and third integral, we get

$$V'(t) = \int_\Omega \frac{G(t,z,w)}{z+1} dx - d_1(t) \int_\Omega \left(\frac{\alpha(1-z)}{(1+z)^3} + \frac{1}{(z+1)^2} \right) |\nabla z|^2 dx - \sigma d_2(t) \int_\Omega \frac{|\nabla w|^2}{(w+1)^2} dx, \tag{3.6}$$

where

$$\begin{aligned} G(t,z,w) = &-(z+\theta_\alpha) \left(u^*(t) - \frac{v^*(t)}{u^*(t)\theta(t)(z+\theta(t))} \right) z^2 \\ &+ \frac{v^*(t)}{u^*(t)} \left(\frac{\sigma}{\gamma(t)} - \frac{z+\theta_\alpha}{z+\theta(t)} \right) z\, w - \frac{\sigma v^*(t)}{\gamma(t) u^*(t)} w^2. \end{aligned}$$

The function $G(t,\cdot,\cdot)$ can be treated as a quadratic form in z, w, so that, under assumption (3.5), it is negative. In addition, taking into account that (z,w) belongs to the compact region $\mathcal{Q}(t)$, there exists $\lambda > 0$ such that

$$\frac{G(t,z,w)}{z+1} \le -\lambda(z^2 + w^2). \tag{3.7}$$

Concerning the sign of the second addendum in (3.6), we use hypothesis (2.5), ensuring, by Lemma 2.2, that $u(x,t) < 2u^*(t)$. As an immediate consequence, one yields $z(x,t) < 1$. Therefore $V'(t) < 0$ and, from (3.7), it follows

$$V'(t) \le -\lambda \int_\Omega (z^2 + w^2)\, dx. \tag{3.8}$$

Integrating (3.8) from $\bar{t}$ to t, we obtain

$$\lambda \int_{\bar{t}}^t ds \left(\int_\Omega (z^2 + w^2)\, dx \right) \le V(\bar{t}) - V(t) < V(\bar{t}) < +\infty;$$

thus

$$\int_{\bar{t}}^{+\infty} ds \left(\int_\Omega (z^2 + w^2)\, dx \right) < +\infty$$

and, consequently (see [11, Lemma 2.1]),

$$\lim_{t \to +\infty} \|z(\cdot,t)\|_{L^2(\Omega)} = 0 = \lim_{t \to +\infty} \|w(\cdot,t)\|_{L^2(\Omega)}. \tag{3.9}$$

Using standard arguments ([8]) we get our statement. Indeed, let $p > \max\{n, 2\}$; then the Sobolev inequality yields that, for $(x,t) \in \overline{\Omega} \times \mathbf{R}^+$,

$$|z(x,t)|^p \le \int_\Omega |z(\cdot,t)|^p\, dx + \int_\Omega |\nabla z(\cdot,t)|^p\, dx \le c_1 \int_\Omega |z(\cdot,t)|^2\, dx + c_2 \int_\Omega |\nabla z(\cdot,t)|^2\, dx. \tag{3.10}$$

Moreover,

$$\lim_{t\to\infty} \int_\Omega |\nabla z(\cdot,t)|^2\, dx = 0;$$

in fact, multiplying by z the first equation in (3.2) and integrating over Ω, there exists $c > 0$ such that

$$d_1(t) \int_\Omega |\nabla z|^2\, dx \le -\frac{1}{2}\frac{d}{dt}\int_\Omega z^2\, dx + c\int_\Omega (z^2 + w^2)\, dx.$$

From this, (3.9) and (3.10), it follows that $\lim_{t\to+\infty} |z(x,t)| = 0$ uniformly w.r.t. $x \in \overline{\Omega}$. Arguing in the same way, $\lim_{t\to+\infty} |w(x,t)| = 0$ uniformly w.r.t. $x \in \overline{\Omega}$.

Going back to $u(x,t)$, $v(x,t)$ through (3.1), we conclude

$$\lim_{t\to+\infty} |u(x,t) - u^*(t)| = 0 = \lim_{t\to+\infty} |v(x,t) - v^*(t)| \text{ uniformly w.r.t. } x \in \overline{\Omega}.$$

□

Corollary 3.1. *Suppose that all coefficients in system* (1.1) *are constant and*

$$(b\gamma) < m. \tag{3.11}$$

Then the unique positive solution (u^*, v^*) *to* (1.1) *attracts all other positive solutions, as* t *goes to infinity.*

Proof. As shown in [5, Corollary 4.2], it turns out that, in this particular case, (3.11) implies both conditions (2.5) and (3.5). Consequently, Theorem 3.2 can be applied. □

Remark 3.1. *The above result was proven in [3], by using the upper and lower solutions method. From an ecological point of view, assumptions* (2.5) *and* (3.5) *generalize the known condition* (3.11) *when the biological parameters of system* (1.1) *present periodic fluctuations in time.*

In the next example we apply our theoretical findings to a special case of model (1.1) with 2π-periodic coefficients.

Example 3.1. *Consider the reaction-diffusion predator-prey system*

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1(t)\Delta u + u\left(a(t) - u - \dfrac{v}{u + m(t)}\right), x \in \Omega, t \ge 0 \\ \dfrac{\partial v}{\partial t} = d_2(t)\Delta v + v\left(2 - \dfrac{8v}{7\,u}\right) \end{cases} \tag{3.12}$$

with the same initial and boundary conditions as (1.1)*, where*

$$a(t) = 5 - 0.2\cos t, \qquad m(t) = \frac{3 + 0.8\cos t}{1 - 0.2\cos t},$$

and $d_1(t), d_2(t)$ *are continuous, positive and* 2π*-periodic. It turns out that*

$$(u^*, v^*) = (4, 7)$$

is a positive (2π*-periodic) solution to* (3.12)*. The validity of the inequalities*

$$v^* \le m(t)u^* \quad \Gamma(t,z) > 0,\, z \in [\overline{z}(t), \widetilde{z}(t)]$$

required in Theorem 3.2 can be checked as in [5, Section 5].

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