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NECESSARY OPTIMALITY CONDITIONS FOR PREDATOR-PREY SYSTEM WITH A HUNTER POPULATION

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Abstract. An optimal control problem is studied for a predator-prey reaction-diffusion system. A hunter population is introduced in the ecosystem and it is interpreted as a control variable. One finds necessary optimality conditions in order that, in the end of a given time interval, the total density of the two populations is maximal.

Keywords: predator-prey system, optimal control, adjoint system.

Mathematics Subject Classification: 93C10, 93C20, 92D25, 35K57, 35K58.

1. INTRODUCTION

We are concerned with an optimal control problem for the predator-prey system of partial differential equations

$$\begin{cases} \frac{\partial y_1}{\partial t} = \alpha_1 \Delta y_1 + y_1 \left(a_1 - b_1 y_2 \right), \\ \frac{\partial y_2}{\partial t} = \alpha_2 \Delta y_2 + y_2 \left(-a_2 + b_2 y_1 \right), \end{cases} \quad \text{a.e. on } Q = (0, T) \times \Omega,$$

with no-flux boundary conditions

$$\frac{\partial y_1}{\partial \nu} = \frac{\partial y_2}{\partial \nu} = 0$$
 a.e. on $\Sigma = (0,T) \times \partial \Omega$

and some initial conditions

$$y_1(0,x) = y_1^0(x), \quad y_2(0,x) = y_2^0(x)$$
 a.e. on Ω .

This boundary value problem describes the dynamics of an ecosystem composed by a prey and a predator population, whose densities at time t and position x are $y_1(t, x)$

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and $y_2(t, x)$, respectively. The diffusion coefficients α_1 , α_2 , together with the parameters a_1 , a_2 , b_1 , b_2 are supposed to be positive. The habitat is modelled by an open bounded set $\Omega \subset \mathbb{R}^N$, $N \leq 3$ with the boundary $\partial\Omega$ smooth enough. The terms $\partial y_1/\partial \nu$, $\partial y_2/\partial \nu$ represent the outward normal derivatives of y_1 and y_2 on the boundary of the domain.

Now one introduces a hunter population in the ecosystem. Suppose that it acts only on the predator population and that the number of the hunted individuals is proportional to the existing individuals in the predator population. The proportionality factor at the moment $t \in [0, T]$ is denoted by u(t) and is regarded as a control function. It is assumed to be homogeneous in the space variable. The dynamics of the new ecosystem is modeled by the boundary value problem

$$\begin{cases} \frac{\partial y_1}{\partial t} = \alpha_1 \Delta y_1 + y_1 \left(a_1 - b_1 y_2 \right), \\ \frac{\partial y_2}{\partial t} = \alpha_2 \Delta y_2 + y_2 \left(-a_2 + b_2 y_1 - u \right), \end{cases}$$
 a.e. on Q , (1.1)

$$\frac{\partial y_1}{\partial \nu} = \frac{\partial y_2}{\partial \nu} = 0 \text{ a.e. on } \Sigma, \tag{1.2}$$

$$y_1(0,x) = y_1^0(x), \ y_2(0,x) = y_2^0(x)$$
 a.e. on Ω . (1.3)

Assume that u belongs to the set of controls

 $\mathcal{U} = \{ u : [0,T] \to \mathbb{R}, \ 0 \le u(t) \le 1, \ \forall t \in [0,T] \}.$

Our goal is to determine the control $u \in \mathcal{U}$ such that the mean (on Ω) density of the two populations in the habitat becomes maximal at the end of the time interval [0, T]. Therefore, the optimal control problem can be formulated as

$$\operatorname{Min}\left\{-\int_{\Omega} (y_1 + y_2)(T, x) \, dx\right\}, \ u \in \mathcal{U}, \ (y_1, y_2) \text{ solution of } (1.1) - (1.3).$$
(1.4)

Let

$$\Psi(y_1, y_2, u) = -\int_{\Omega} (y_1 + y_2) (T, x) dx$$
(1.5)

be the functional to be minimized. We work under the following hypotheses on the initial condition $y^0 = (y_1^0, y_2^0)$:

(H1)
$$y_1^0, y_2^0 \in H^2(\Omega), \ \frac{\partial y_1^0}{\partial \nu} = \frac{\partial y_2^0}{\partial \nu} = 0$$
 a.e. on $\partial\Omega, \ y_1^0 > 0, \ y_2^0 > 0$ on Ω .

To study the existence of a strong solution to problem (1.1)–(1.3), let A be the operator $A: D(A) \subset L^2(\Omega)^2 \to L^2(\Omega)^2$ given by $A(y_1, y_2) = (\alpha_1 \Delta y_1, \alpha_2 \Delta y_2)$, with the domain

$$D(A) = \left\{ y = (y_1, y_2) \in H^2(\Omega)^2, \frac{\partial y_1}{\partial \nu} = \frac{\partial y_2}{\partial \nu} = 0 \text{ a.e. on } \partial \Omega \right\}$$

and let f be the nonlinear term from system (1.1), i.e.

$$f(t,y) = (f_1(t,y), f_2(t,y)) = (y_1(a_1 - b_1y_2), y_2(-a_2 + b_2y_1 - u)).$$

Then problem (1.1)–(1.3) can be written under the form

$$\begin{cases} y'(t,x) = Ay(t,x) + f(t,y(t,x)), & \text{a.e. } t \in [0,T], \\ y(0,x) = y^{0}(x) = \left(y_{1}^{0}(x), y_{2}^{0}(x)\right), & \text{a.e. } x \in \Omega. \end{cases}$$
(1.6)

Using this equivalent form for problem (1.1)–(1.3), we can easily prove an existence result like in [7].

Theorem 1.1. If α_1 , α_2 , a_1 , a_2 , b_1 , $b_2 > 0$, $u \in \mathcal{U}$, and $y^0 = (y_1^0, y_2^0)$ satisfies hypothesis (H1), then problem (1.1)–(1.3) has a unique strong solution $y = (y_1, y_2) \in W^{1,2}\left(0,T;L^2(\Omega)^2\right)$, which is positive and bounded on Q. In addition, $y_1, y_2 \in L^2\left(0,T;H^2(\Omega)\right) \cap L^{\infty}\left(0,T;H^1(\Omega)\right)$ and

$$\left\|\frac{\partial y_i}{\partial t}\right\|_{L^2(Q)} + \|y_i(t)\|_{H^1(\Omega)} + \|y_i\|_{L^2(0,T;H^2(\Omega))} + \|y_i\|_{L^\infty(Q)} \le C, \qquad (1.7)$$

where C is a positive constant independent of u.

The case without diffusion, together with some numerical results, can be found in [3]. In [7] the author studies a similar problem, but with a different control function. A minimization problem for a predator-prey system of ODEs with logistic growth rate of the prey and general functional response was treated in [2]. In [1], a global behavior is established for an age-dependent population model with a logistic term. In [5] the authors study the global dynamics for a predator-prey model with stage structure for a predator, while in [6] an impulsively controlled predator-pest model with disease in the pest was investigated. For different models from population dynamics the reader may refer to [8]. Some basic notions and results on optimal control theory and on distributed control systems can be found in the monograph [4].

Section 2 of the present paper is devoted to the existence of an optimal solution (y^*, u^*) , where $y^* = (y_1^*, y_2^*)$. In the third section we find some necessary optimality conditions for our optimal control problem. We end with some discussions and conclusions.

2. THE EXISTENCE OF THE OPTIMAL SOLUTION

We prove now the existence of the optimal control and of the corresponding state.

Theorem 2.1. Under the above hypotheses, problem (1.1)-(1.4) admits at least one optimal control u^* .

Proof. Let $\Psi(y_1, y_2, u)$ be the cost functional defined by (1.5) and $d = \inf \{\Psi(y_1, y_2, u)\}$, subject to (1.1)–(1.3) and $u \in \mathcal{U}$. Since $u \in L^{\infty}(0, T)$, $y_1, y_2 \in L^{\infty}(Q)$ (see Theorem 1.1), it follows that d is finite. Therefore, there exists a sequence (y_{1n}, y_{2n}, u_n) of solutions to problem (1.1)–(1.3) with $u_n \in \mathcal{U}$ instead of u, such that

$$d \le \Psi(y_{1n}, y_{2n}, u_n) \le d + \frac{1}{n}, \ \forall n \ge 1.$$
 (2.1)

So (y_{1n}, y_{2n}, u_n) verifies the boundary value problem

$$\begin{cases} \frac{\partial y_{1n}}{\partial t} = \alpha_1 \Delta y_{1n} + y_{1n} \left(a_1 - b_1 y_{2n} \right), \\ \frac{\partial y_{2n}}{\partial t} = \alpha_2 \Delta y_{2n} + y_{2n} (-a_2 + b_2 y_{1n} - u_n), \end{cases}$$
 a.e. $(t, x) \in Q,$ (2.2)

$$\frac{\partial y_{1n}}{\partial \nu} = \frac{\partial y_{2n}}{\partial \nu} = 0, \text{ a.e. } (t, x) \in \Sigma,$$
(2.3)

$$y_{1n}(0,x) = y_1^0(x), \ y_{2n}(0,x) = y_2^0(x), \ \text{a.e.} \ x \in \Omega.$$
 (2.4)

Theorem 1.1 implies that

$$\left\|\frac{\partial y_{in}}{\partial t}\right\|_{L^{2}(Q)} \leq C, \ \|y_{in}(t)\|_{H^{1}(\Omega)} \leq C, \ \|y_{in}\|_{L^{2}(0,T;H^{2}(\Omega))} \leq C,$$
(2.5)

for all $n \geq 1, t \in [0, T]$ and i = 1, 2. Since (y_{in}) is bounded in $C([0, T]; L^2(\Omega))$, $(\partial y_{in}/\partial t)$ is bounded in $L^2(Q)$, and $(y_{in}(t))$ is compact in $L^2(\Omega)$, for each $t \in [0, T]$ (because $H^1(\Omega)$ is compactly imbedded in $L^2(\Omega)$), by the Ascoli-Arzela Theorem it follows that (y_{in}) is compact in $C([0, T]; L^2(\Omega))$. Thus, at least on a subsequence denoted again (y_{in}) , the following convergence holds:

$$y_{in} \to y_i^*$$
 in $L^2(\Omega)$ uniformly with respect to $t, i = 1, 2$.

In view of the boundedness of y_{in} , $\partial y_{in}/\partial t$ in $L^2(\Omega)$, by system (1.1) we find that (Δy_{in}) is also bounded in $L^2(Q)$, so it is weakly convergent on a subsequence. But for every distribution T,

$$\int_{Q} T\Delta y_{in} dt dx = \int_{Q} y_{in} \Delta T dt dx \rightarrow \int_{Q} y_i^* \Delta T dt dx = \int_{Q} T\Delta y_i^* dt dx.$$

This implies that $\Delta y_{in} \rightharpoonup \Delta y_i^*$ weakly in $L^2(Q)$. On the other hand, inequalities (2.5) infer that

$$\frac{\partial y_{in}}{\partial t} \rightharpoonup \frac{\partial y_i^*}{\partial t} \text{ weakly in } L^2(Q) ,$$

$$y_{in} \rightharpoonup y_i^* \text{ weakly star in } L^\infty\left(0, T; H^1(\Omega)\right) ,$$

$$y_{in} \rightharpoonup y_i^* \text{ weakly in } L^2\left(0, T; H^2(\Omega)\right) .$$

We also have $y_{1n}y_{2n} \to y_1^*y_2^*$ in $L^2(Q)$. On a subsequence denoted again u_n , we have $u_n \to u^*$ weakly in $L^{\infty}(0,T)$. Since \mathcal{U} is closed and convex, it is also weakly closed, hence $u^* \in \mathcal{U}$. Then we can easily see that $u_n y_{2n} \to u^* y_2^*$ in $L^2(Q)$.

Passing to the limit as $n \to \infty$ in (2.1)–(2.4), we deduce that (y_1^*, y_2^*, u^*) verifies problem (1.1)–(1.3) and minimizes the cost functional (1.4). The proof is complete.

3. NECESSARY OPTIMALITY CONDITIONS

In this section we deduce the optimality system. Let (y^*, u^*) be an optimal pair, where $y^* = (y_1^*, y_2^*)$. Consider the adjoint system defined by

$$\begin{cases} p'(t) + A^* p(t) = -f_y^*(y^*) p(t), \ t \in [0,T], \\ p(T) = -\nabla \Psi(y^*(T), u^*(T)), \end{cases}$$

where $p = (p_1, p_2)$ is the adjoint variable, A^* is the adjoint of operator A, and f_y^* is the adjoint of the Jacobian matrix f_y . In detail, this can be written under the form

$$\begin{cases} \frac{\partial p_1}{\partial t} = -\alpha_1 \Delta p_1 - a_1 p_1 + y_2^* (b_1 p_1 - b_2 p_2), \\ \frac{\partial p_2}{\partial t} = -\alpha_2 \Delta p_2 + (a_2 + u^*) p_2 + y_1^* (b_1 p_1 - b_2 p_2), \\ \frac{\partial p_1}{\partial \nu} = \frac{\partial p_2}{\partial \nu} = 0 \text{ a.e. on } \Sigma, \end{cases}$$
(3.1)

$$p_1(T, x) = p_2(T, x) = 1$$
 a.e. on Ω . (3.3)

Like in Theorem 1.1, we can easily prove the existence of the solution to this problem. More precisely, we have

Lemma 3.1. If α_i , a_i , $b_i > 0$ (i = 1, 2), then the adjoint system (3.1)–(3.3) has a unique strong solution $p = (p_1, p_2) \in W^{1,\infty}(0, T; L^2(\Omega)^2)$, such that $p_1, p_2 \in L^{\infty}(Q)$, $p_1, p_2 \in L^2(0, T; H^2(\Omega)) \cap L^{\infty}(0, T; H^1(\Omega))$.

Let $y^* = (y_1^*, y_2^*)$ and $y^{\varepsilon} = (y_1^{\varepsilon}, y_2^{\varepsilon})$ be the solutions of problem (1.1)–(1.3) corresponding to the optimal control u^* and to the control $u^{\varepsilon} = u^* + \varepsilon u_0$, respectively, where $\varepsilon > 0$ and $u_0 \in L^{\infty}(0, T)$ are chosen such that $0 \le u^* + \varepsilon u_0 \le 1$ a.e. on [0, T]. Subtracting the system corresponding to (y^*, u^*) from that corresponding to $(y^{\varepsilon}, u^{\varepsilon})$ and denoting $z_i^{\varepsilon} = (y_i^{\varepsilon} - y_i^*)/\varepsilon$, i = 1, 2, we arrive at

$$\begin{cases} \frac{\partial z_1^{\varepsilon}}{\partial t} = \alpha_1 \Delta z_1^{\varepsilon} + (a_1 - b_1 y_2^{\varepsilon}) z_1^{\varepsilon} - b_1 y_1^* z_2^{\varepsilon}, \\ \frac{\partial z_2^{\varepsilon}}{\partial t} = \alpha_2 \Delta z_2^{\varepsilon} + (-a_2 + b_2 y_1^* - u^{\varepsilon}) z_2^{\varepsilon} + b_2 y_2^{\varepsilon} z_1^{\varepsilon} - y_2^* u_0, \end{cases}$$
 a.e. on Q , (3.4)

$$\frac{\partial z_1^{\varepsilon}}{\partial \nu} = \frac{\partial z_2^{\varepsilon}}{\partial \nu} = 0 \text{ a.e. on } \Sigma, \tag{3.5}$$

$$z_1^{\varepsilon}(0,x) = z_2^{\varepsilon}(0,x) = 0$$
 a.e. on Ω . (3.6)

Lemma 3.2. There exist the limits $z_i = \lim_{\varepsilon \to 0} z_i^{\varepsilon}$ in $L^2(Q)$, i = 1, 2 and they satisfy the boundary value problem

$$\begin{cases} \frac{\partial z_1}{\partial t} = \alpha_1 \Delta z_1 + (a_1 - b_1 y_2^*) z_1 - b_1 y_1^* z_2, \\ \frac{\partial z_2}{\partial t} = \alpha_2 \Delta z_2 + (-a_2 + b_2 y_1^* - u^*) z_2 + b_2 y_2^* z_1 - y_2^* u_0, \end{cases}$$
 a.e. on Q , (3.7)

$$\frac{\partial z_1}{\partial \nu} = \frac{\partial z_2}{\partial \nu} = 0 \ a.e. \ on \Sigma, \tag{3.8}$$

$$z_1(0,x) = z_2(0,x) = 0 \ a.e. \ on \ \Omega.$$
(3.9)

Proof. Denoting by $Z^{\varepsilon} = (z_1^{\varepsilon}, z_2^{\varepsilon}),$

$$M^{\varepsilon} = \begin{pmatrix} a_1 - b_1 y_2^{\varepsilon} & -b_1 y_1^* \\ b_2 y_2^{\varepsilon} & -a_2 + b_2 y_1^* - u^{\varepsilon} \end{pmatrix}, \quad N = \begin{pmatrix} 0 \\ -y_2^* u_0 \end{pmatrix},$$

problem (3.4)–(3.6) can be written in the form

$$\begin{cases} \frac{\partial Z^{\varepsilon}}{\partial t} = A\left(Z^{\varepsilon}\right) + M^{\varepsilon}Z^{\varepsilon} + N, \text{ a.e. on } (0,T),\\ Z^{\varepsilon}\left(0\right) = 0. \end{cases}$$
(3.10)

If $\{S(t), t \ge 0\}$ is the C₀-semigroup generated by A, the solution of (3.10) can be expressed as

$$Z^{\varepsilon}(t) = S(t) 0 + \int_{0}^{t} S(t-s) \left(M^{\varepsilon} Z^{\varepsilon} + N\right)(s) ds.$$

Since S(t) = 0 and the elements of matrix M^{ε} are bounded in $L^{\infty}(Q)$ uniformly with respect to ε (see (1.7)), by Gronwall's inequality one obtains that $Z^{\varepsilon}(t)$ is bounded in $L^{2}(Q)$ uniformly with respect to ε . Thus $\|y_{i}^{\varepsilon} - y_{i}^{*}\|_{L^{2}(Q)} = \varepsilon \|z_{i}^{\varepsilon}\|_{L^{2}(Q)} \to 0$ as $\varepsilon \to 0$, i.e. $y_{i}^{\varepsilon} \to y_{i}^{*}$ (as $\varepsilon \to 0$) in $L^{2}(Q)$, i = 1, 2.

By (3.4)–(3.6) and (3.7)–(3.9) we deduce that $(z_1^{\varepsilon} - z_1, z_2^{\varepsilon} - z_2)$ verifies the boundary value problem

$$\begin{cases} \frac{\partial (z_1^{\varepsilon} - z_1)}{\partial t} = \alpha_1 \Delta (z_1^{\varepsilon} - z_1) + (z_1^{\varepsilon} - z_1)(a_1 - b_1 y_2^{\varepsilon}) - b_1 y_1^* (z_2^{\varepsilon} - z_2) - b_1 z_1 (y_2^{\varepsilon} - y_2^*), \\ \frac{\partial (z_2^{\varepsilon} - z_2)}{\partial t} = \alpha_2 \Delta (z_2^{\varepsilon} - z_2) + (z_1^{\varepsilon} - z_1)(b_2 y_2^{\varepsilon} - u^{\varepsilon}) + (-a_2 + b_2 y_1^*) (z_2^{\varepsilon} - z_2) - b_2 z_1 (y_2^{\varepsilon} - y_2^*) - \varepsilon u_0 z_1, \text{ a.e. on } Q, \\ \frac{\partial (z_1^{\varepsilon} - z_1)}{\partial \nu} = \frac{\partial (z_2^{\varepsilon} - z_2)}{\partial \nu} = 0 \text{ a.e. on } \Sigma, \end{cases}$$

$$(z_1^{\varepsilon} - z_1)(0, x) = (z_2^{\varepsilon} - z_2)(0, x) = 0$$
 a.e. on Ω

The solution of this problem can be expressed with the aid of the semigroup $\{S(t), t \ge 0\}$ generated by A:

$$\begin{pmatrix} z_1^{\varepsilon} - z_1 \\ z_2^{\varepsilon} - z_2 \end{pmatrix} = \int_0^t S\left(t - s\right) \begin{pmatrix} a_1 - b_1 y_2^{\varepsilon} & -b_1 y_1^* \\ b_2 y_2^{\varepsilon} - u^{\varepsilon} & -a_2 + b_2 y_1^* \end{pmatrix} \begin{pmatrix} z_1^{\varepsilon} - z_1 \\ z_2^{\varepsilon} - z_2 \end{pmatrix} (s) \, ds + \\ + \int_0^t S\left(t - s\right) \begin{pmatrix} -b_1 z_1 \left(y_2^{\varepsilon} - y_2^*\right) \\ -b_2 z_1 \left(y_2^{\varepsilon} - y_2^*\right) - \varepsilon u_0 z_1 \end{pmatrix} (s) \, ds.$$

Applying Gronwall's inequality and using the convergence $y_2^{\varepsilon} - y_2^* \to 0$ as $\varepsilon \to 0$ in $L^2(Q)$, together with the boundedness of all the terms under the first integral, it follows that $z_1^{\varepsilon} \to z_1, z_2^{\varepsilon} \to z_2$ in $L^2(Q)$, as $\varepsilon \to 0$. The lemma is proved.

We come back to the optimal control problem and establish the necessary optimality conditions.

Theorem 3.3. If $u^* \in \mathcal{U}$ is an optimal control and $y^* = (y_1^*, y_2^*)$ is the optimal state for problem (1.4) subject to (1.1)–(1.3), then

$$u^{*}(t) = \begin{cases} 0, & \text{if } w(t) = \int_{\Omega} y_{2}^{*} p_{2} dx > 0, \\ 1, & \text{if } w(t) = \int_{\Omega} y_{2}^{*} p_{2} dx < 0, \end{cases}$$
(3.11)

where $p = (p_1, p_2)$ satisfy the adjoint system (3.1)–(3.3).

Proof. Since (y^*, u^*) is an optimal pair, we have $\Psi(y_1^*, y_2^*, u^*) \leq \Psi(y_1^{\varepsilon}, y_2^{\varepsilon}, u^{\varepsilon}), \forall \varepsilon > 0$ such that $0 \leq u^{\varepsilon}(t) \leq 1$. Dividing by $\varepsilon > 0$ and passing to the limit as $\varepsilon \to 0$ in $L^1(\Omega)$, one arrives at

$$\int_{\Omega} (z_1 + z_2) (T, x) \, dx \le 0. \tag{3.12}$$

Now one multiplies the equations from (3.7) by p_1 and p_2 , respectively, and the equations from (3.1) by z_1 and z_2 , respectively and sum them up. One gets

$$\left(p_1 \frac{\partial z_1}{\partial t} + z_1 \frac{\partial p_1}{\partial t} \right) + \left(p_2 \frac{\partial z_2}{\partial t} + z_2 \frac{\partial p_2}{\partial t} \right) = \alpha_1 \left(p_1 \Delta z_1 - z_1 \Delta p_1 \right) + \alpha_2 \left(p_2 \Delta z_2 - z_2 \Delta p_2 \right) - u_0 y_2^* p_2.$$

Integrating over Q and using Green's formula, with the aid of (3.2), (3.3), (3.8), (3.9) and (3.12), we derive that

$$\int_{0}^{T} \int_{\Omega} u_0 y_2^* p_2 dt dx = -\int_{\Omega} (z_1 + z_2) (T, x) dx \ge 0.$$

Taking $u_0 \in \mathcal{U}$ of the form $u_0 = u - u^*$ with $u \in \mathcal{U}$, this inequality becomes

$$\int_{0}^{T} \left(u^{*}-u\right)(t) w(t) dt \leq 0, \ \forall u \in \mathcal{U}, \text{ where } w(t) = \int_{\Omega} y_{2}^{*} p_{2} dx.$$

This implies that

$$w(t) \in \begin{cases} \{0\}, & \text{if } 0 < u^*(t) < 1, \\ \mathbb{R}_+, & \text{if } u^*(t) = 1, \\ \mathbb{R}_-, & \text{if } u^*(t) = 0. \end{cases}$$

Consequently, the optimal control u^* has the form (3.11). This completes the proof.

Remark 3.4. There is a neighbourhood $(\tau, T]$ of the final time t = T such that $u^*(t) = 0$ on $(\tau, T]$.

4. CONCLUSIONS AND DISCUSSIONS

In this paper we studied an optimal control problem related to a PDE system of predator-prey type, where the control function is interpreted as the action of a hunter population. We found necessary optimality conditions in order that the total in space density of the populations becomes maximal at the end of a given time interval. When the optimal control $u^* = 0$, there is no action of the hunter population in the habitat and the system coincides with the initial (uncontrolled) one. If $u^* = 1$, then the hunter population acts at its maximum capacity.

We intend to study in a future work a similar control problem for a system of three reaction-diffusion equations which models the dynamics of an ecosystem composed by a herbivorous population, a carnivorous one and a plant.

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