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DYNAMICS OF A PREDATOR-PREY MODEL WITH DIFFUSION

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Abstract. In this paper we consider a predator-prey model given by a reaction-diffusion system. It incorporates the Holling-type-II and a modified Leslie-Gower functional responses. We focus on the positive equilibrium global stability, bifurcations and mecanisms responsible for transitions between different kind of dynamics.

Keywords. Predator-prey, Lyapunov function, Bifurcation, Chaos, Self-organization.

AMS (MOS) subject classification: 34, 37, 65

1 Introduction

The dynamics relationships between species and their complex properties are at heart of many important ecological and biological processes. Predator-prey dynamics are a classic and relatively well-studied example of interactions. This paper adresses the analysis of the global stability of the endemic equilibrium, the bifurcations and spatio-temporal dynamics of a system of this type. We assume that only basic qualitative features of the system are known, namely the invasion of a prey population by predators. The local dynamics has been studied in [3, 6]. Similar three dimensional systems with the same functional responses are studied in [2, 8, 9] and in [13, 14] with the delay case. Versions with impulsive term are studied for instance in [19].
This model incorporates the Holling-type-II and a modified Leslie-Gower functional responses. Without diffusion it reads as,

$$\left\{\begin{array}{rcl} \dfrac{dH}{dT} &=& \left(a_1 - b_1 H - \dfrac{c_1 P}{H + k_1}\right) H \\[2ex] \dfrac{dP}{dT} &=& \left(a_2 - \dfrac{c_2 P}{H + k_2}\right) P \end{array}\right. \tag{1}$$

with,

$$H(0) \geq 0\ ,\ P(0) \geq 0.$$

H and P represent population densities at time T. r_1, a_1, b_1, k_1, r_2, a_2, and k_2 are model parameters assuming only positive values. a_1 is the growth rate

of preys H. a_2 describes the growth rate of predators P. b_1 measures the strength of competition among individuals of species H. c_1 is the maximum value of the *per capita* reduction of H due to P. c_2 has a similar meaning to c_1. k_1 measures the extent to which environment provides protection to prey H. k_2 has a similar meaning to k_1 relatively to the predator P.
The historical origin and applicability of this model is discussed in detail in [3, 6, 13, 14]. The corresponding PDE version has been first done and partially studied in [5].
In This paper, we suppose that both predator and prey move in space, we represent the mathematical model by reaction-diffusion equations, see [5]. It is a type of spatio-temporal model most commonly used in ecology and biology. We focus on mechanisms responsible of bifurcations and spatio-temporal chaos. We first study the positive boundednes and global stability conditions of the interior equilibrium. Then, we give a bifurcation analysis leading to chaotic behavior when the species move on a straight line, or on a bounded square.

2 Mathematical model

The mathematical model we consider here consists of reaction-diffusion equations which express conservation of predator and prey densities. It has the following form,

$$\begin{cases} \dfrac{\partial H}{\partial T} = D_1 \Delta H + \left(a_1 - b_1 H - \dfrac{c_1 P}{H + k_1}\right) H \\ \\ \dfrac{\partial P}{\partial T} = D_2 \Delta P + \left(a_2 - \dfrac{c_2 P}{H + k_2}\right) P \end{cases} \tag{2}$$

$H = H(T, X)$ and $P = P(T, X)$ are the densities of prey and predators, respectively. ΔH (resp. ΔP) denotes $\dfrac{\partial^2 H}{\partial X^2}$ (resp $\dfrac{\partial^2 P}{\partial X^2}$) when preys (resp predators) move on a straight line X or ΔH (resp. ΔP) denotes $\dfrac{\partial^2 H}{\partial X^2} + \dfrac{\partial^2 H}{\partial Y^2}$ (resp $\dfrac{\partial^2 P}{\partial X^2} + \dfrac{\partial^2 P}{\partial Y^2}$) when the populations move on a two dimensional space. X (resp. (X, Y)) is the spatial position of species when they move on a straight line (resp. two dimensional space). D_1 and D_2 are the diffusion coefficients of prey and predator respectively.
To investigate problem (2), we introduce the following scaling tranformations,

$$t = a_1 T,\ x = X(\frac{a_1}{D_1})^{\frac{1}{2}},\ y = Y(\frac{a_1}{D_1})^{\frac{1}{2}},\ u(t) = \frac{b_1}{a_1} H(T),\ v(t) = \frac{c_2 b_1}{a_1 a_2} P(T)$$

$$a = \frac{a_2 c_1}{a_1 c_2},\ b = \frac{a_2}{a_1},\ e_1 = \frac{b_1 k_1}{a_1},\ e_2 = \frac{b_1 k_2}{r_1},\ \delta = \frac{D_2}{D_1}$$

We obtain the following equations, for the local model,

$$\begin{cases} \dfrac{du}{dt} &= u\left(1-u-\dfrac{av}{u+e_1}\right)=f(u,v) \\ \dfrac{dv}{dt} &= bv\left(1-\dfrac{v}{u+e_2}\right)=g(u,v) \end{cases} \tag{3}$$

and the following system for the spatio-temporal equations :

$$\begin{cases} \dfrac{\partial u(t,x)}{\partial t} &= \triangle u + u\left(1-u-\dfrac{av}{u+e_1}\right) \\ &= \triangle u + f(u,v), \quad x\in\Omega,\ t>0 \\ \\ \dfrac{\partial v(t,x)}{\partial t} &= \delta\triangle v + bv\left(1-\dfrac{v}{u+e_2}\right) \\ &= \delta\triangle v + g(u,v), \quad x\in\Omega,\ t>0 \end{cases} \tag{4}$$

With general boundary conditions, the permanence and the predator extinction for this model have been studied in [5]. We consider here the Neumann boundary conditions given by,

$$\frac{\partial u}{\partial n}=\frac{\partial v}{\partial n}=0$$

$$u(0,x)=u_0(x) \quad x\in\Omega, \quad v(0,x)=v_0(x) \quad x\in\Omega\subset\mathbb{R}^n, \quad n=1,2.$$

Here, Ω is a bounded domain and the initial data u_0, v_0, are non-negative functions.

This kind of problem is well studied, related results can be seen for example in [4, 10]. In this section we investigate the existence of positive solutions and the stability of the positive uniform steady state. As in standard existence theory (see [1, 18, 15]), in the first step, we give an invariant bounded domain for system (4).

Theorem 2.1 *Let us denote by,*

$$\Sigma=\left\{(u,v)\in\mathbb{R}^2,\ 0\le u\le 1,\ 0\le u+v\le \frac{5b+(1+b)^2(1+e_2)}{4b}\right\}$$

i) Σ is positively invariant region for equation (3).
ii) Σ is positively invariant region for equation (4).

proof For the proof of i) see [3, 6]. Let us denote by $\partial\Sigma$ the boundary of Σ, $\partial\Sigma=\{u=0\}\cup\{v=0\}\cup\{u=1\}\cup\left\{v=\frac{5b+(1+b)^2(1+e_2)}{4b}-1\right\}$. The vector field $(f(u,v),g(u,v))$ does not point out of Σ see [3, 6]. So ii) follows from theorems 14.11 and 14.2 of [18]. Thus, the following theorem is obvious.

Theorem 2.2 *For any smooth non-negative functions $u_0(x)$, $v_0(x)$ in Σ, system (4) has a unique smooth bounded global solution.*

System (3) admits a unique steady state $(u*, v*)$ in the region $u > 0$,$v > 0$ if $ae_2 < e_1$, see [3, 6].

Remark 2.3
A steady state for system (3) is also a steady state for system (4).

Here, we address the question of stability of $(u*, v*)$ for equation (4). So, we assume the following conditions,

$$1 \leq e_1 \leq e_2 \tag{5}$$

$$\left(\frac{\delta}{u*+e_1}\left(2u*^2+(e_1-1)\,u*\right)+b\right)^2 \leq \frac{4\delta bu*}{u*+e_1}\left(2u*+a+e_1-1\right) \tag{6}$$

Theorem 2.4 *If (5) and (6) are satisfied, then the steady state $(u*, v*)$ is globaly asymptoticaly stable for equation (4).*

proof Let us denote by,

$$l(u,v) = \int_{u*}^{u} \frac{(\eta-u*)\,(\eta+e_1)}{a\eta\,(\eta+e_2)}d\eta + \frac{u*+e_2}{bv*}\int_{v*}^{v}\frac{\eta-v*}{\eta}d\eta$$

and

$$\begin{aligned} L(u,v) &= \int_\Omega l(u,v)\ dx \\ &= \int_\Omega \left(\int_{u*}^{u} \frac{(\eta-u*)\,(\eta+e_1)}{a\eta\,(\eta+e_2)}d\eta + \frac{u*+e_2}{bv*}\int_{v*}^{v}\frac{\eta-v*}{\eta}d\eta\right)\ dx \end{aligned}$$

Ω is the domain where the species move.
The aim is to prove that L is a Lyapunov function, with a negative orbital derivative. $l(u, v)$ is a Lyapunov function of system (3), see [6] for more details. $L(u, v)$ is positive for all (u, v) in the positive quadrant, except for $(u*, v*)$, for which $L(u*, v*) = 0$. Therefore, we only have to show the inequality $\dfrac{dL}{dt} < 0$. The orbital derivative of L, along the flow of system (4) is,

$$\begin{aligned} \frac{dL}{dt} &= \int_\Omega \left(\frac{(u-u*)\,(u+e_1)}{au\,(u+e_2)}\right)\left(\triangle u + u\,(1-u) - \frac{auv}{u+e_1}\right)\ dx \\ &\quad + \int_\Omega \frac{u*+e_2}{bv*}\frac{v-v*}{v}\left(\delta\triangle v + b\left(1-\frac{v}{u+e_2}\right)v\right)\ dx \\ \frac{dL}{dt} &= \int_\Omega \left(\frac{(u-u*)(u+e_1)}{au(u+e_2)}\left(u(1-u)-\frac{auv}{u+e_1}\right)\right)\ dx \\ &\quad + \int_\Omega \frac{u*+e_2}{bv*}\frac{v-v*}{v}bv\left(1-\frac{v}{u+e_2}\right)\ dx \\ &\quad + \int_\Omega \left(\triangle u\frac{(u-u*)(u+e_1)}{au(u+e_2)} + \delta\triangle v\frac{u*+e_2}{bv*}\frac{v-v*}{v}\right)\ dx \end{aligned} \tag{7}$$

Let us denote by S_1 the first two integrals of equation (7) and S_2 the last integral.
After simple algebraic computations, S_1 becomes,

$$S_1 = -\int_\Omega \left((u + u* + e_1 - 1)\frac{(u-u*)^2}{a(u+e_2)} + \frac{(v-v*)^2}{u+e_2} \right) dx \tag{8}$$

For S_2 we use the Green formula, assuming that the flux on the boundary is zero. Thus, we obtain,

$$\begin{aligned} S_2 &= -\int_\Omega \left(|\nabla u|^2 \frac{d}{du}\left(\frac{(u-u*)(u+e_1)}{au(u+e_2)} \right) + \delta \frac{u*+e_2}{bv*}|\nabla v|^2 \frac{d}{dv}\left(\frac{v-v*}{v} \right) \right) dx \\ &= -\int_\Omega |\nabla u|^2 \left(\frac{e_2 - e_1 + 1 + u*}{a(u+e_2)^2} + \frac{u* e_1(2u+e_2)}{a(u^2+e_2u)^2} \right) dx \\ &\qquad - \int_\Omega \left(\delta \frac{u*+e_2}{bv*}|\nabla v|^2 \frac{v*}{v^2} \right) dx \end{aligned} \tag{9}$$

Equations (8) and (9) show that the derivative of $L(u, v)$ along the flow of system (4) is negative. Therefore, by La Salle's theorem given in [7], $(u*, v*)$ is globally asymptotically stable for equation (4).

3 Local bifurcation in one-dimensional space

In this section, we present our numerical results in one dimensional space. We suppose that the two species diffuse on a line, $\Omega \subset \mathbb{R}$. At boundaries we use the zero-flux condition. Let us consider the two following intial conditions :

$$\begin{aligned} u(0,x) &= u_0 \text{ for } L_{1u} < x < L_{2u}, \text{ otherwise } u(0,x) = 0 \\ v(0,x) &= v_0 \text{ for } L_{1v} < x < L_{2v}, \text{ otherwise } v(0,x) = 0 \end{aligned} \tag{10}$$

The initial domain, where the prey move, is larger than that of the predator for making, during the simulation, the impact of the boundaries as small as possible. Thus, we assume,

$$0 < L_{1u} \leq L_{1v} < L_{2v} \leq L_{2u} < L$$

We choose the parameters so that the species do not disappear when the increase or the decrease degree vary, (that is (birth quantity of species)/(death quantity of species)). In the following of this section, the parameters are fixed as follows,

$$L = 100, L_{1u} = 40,\ L_{1v} = 48,\ L_{2v} = 56,\ L_{2u} = 60,\ u_0 = 1.0,\ v_0 = 0.1 \tag{11}$$

$$e_1 = 0.08,\ e_2 = 0.01,\ a = 3.0,\ \delta = 1. \tag{12}$$

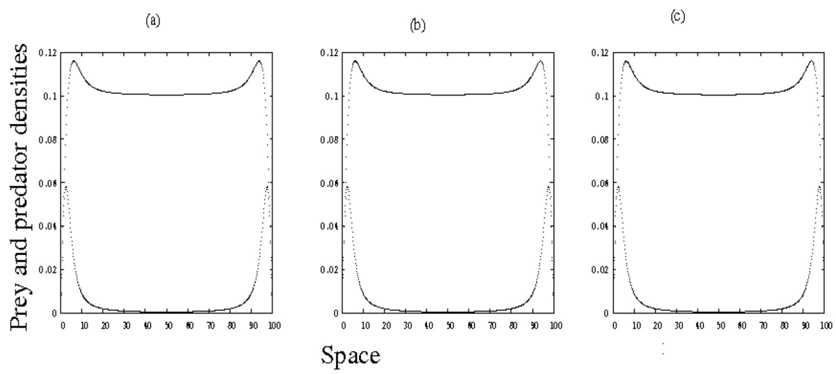


Figure 1: System (4) density of spatial distribution, the parameters and initial data are fixed as given in (11) and (12) and $b = 0.256$.

Figure 1 is an example of species spatial distribution, observed for $b = 0.256$, at (a) $t = 250$, (b) $t = 750$ and (c) $t = 1200$. With these fixed parameters and these initial distributions, there are two patches at the beginning and the end of the field which are formed as of the first moments of simulation. Between these patches, the densities remain constant with respect to the time parameter. Therefor the figure does not give enough informations.
For better examining the properties of the population dynamics as a whole,

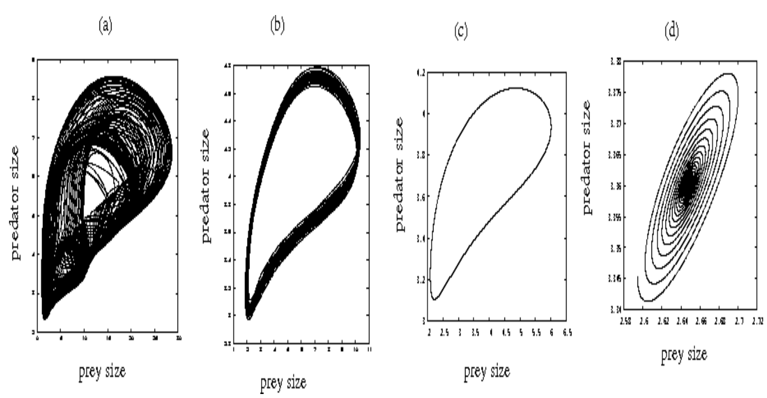


Figure 2: A cascade of bifurcations leading to the onset of chaotic oscillations in the phase plane (U,V) for different values of b : (a) $b = 0.197$, (b) $b = 0.203$, (c) $b = 0.23$, (d) $b = 0.26$. The other parameters are given in (11) and (12).

we estimate the species size of prey and predator by,

$$U(t) = \int_0^L u(t,x)dx \text{ and } V(t) = \int_0^L v(t,x)dx \tag{13}$$

The aim is to study the properties of the oscillations of the dynamics of the populations when one varies the control parameter, the choice of this parameter is then important. We will choose b as control parameter since it determines the ratio of two factors which are the birth rates of the prey and the predator. Therefore, while b varies between 0.195 and 0.26, other parameters will be fixed as in equation (12) and initial conditions are given as in (11). We leave a rather large transitory time, so that the total quantities of the species U and V are in the attractor domain. We start with $b = 0.26$ and make b decreasing. For $b = 0.26$, the system presents an attractor focus in (U, V), see figure 2(d). The same phase plane is obtained as long as the ratio of the birth rate of the predator by the prey one is higher than 0.255. We have a first bifurcation when this ratio is equals to 0.255. When b belongs to $[0.208\ ,\ 0.255]$ the system exhibits periodic attractors, see figure 2(c). A second bifurcation leads to the dynamics of the species in quasi-periodic attractors, for b between 0.208 and 0.199, see figure 2(b). Finally for b between 0.199 and 0.195, it becomes chaotic, see figure 2(a). These results are summarized by the bifurcation diagram given in figure 3.

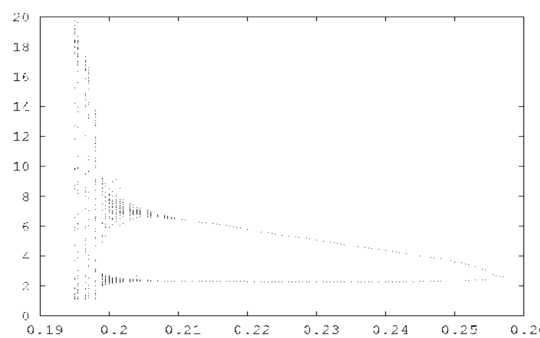


Figure 3: Bifurcation diagram when the parameter b varies.

4 Dynamics in two-dimensional space

In this last section we study the problem in the limited field $D = [0\ ,\ 900] \times [0\ ,\ 900]$ of $\mathbb{R}^2$. We are interesting in the emerging structures if the homogenous equilibrium $(u*, v*)$ of system (4) is unstable an the species diffuse in the same way.

Let us remark that, if $(u*, v*)$ is unstable for equation (3) it becomes also unstable for (4) as soon as the coefficient of diffusion is equals to one. In this part, we suppose that the prey and the predator diffuse in the same way ($\delta = 1$). The global emerging structures are given only by the local interactions of the functional response $(f(u,v), g(u,v))$. We start from an initial condition rather close to (u^*, v^*), having a low disparity of the space distribution. These initial conditions have been chosen as,

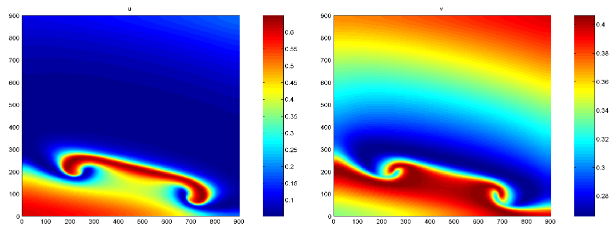
$$u(0,x,y) = u^* - 2\ 10^{-7}(x - 0.1y - 231)(x - 0.1y - 632) \tag{14}$$

$$v(0,x,y) = v^* - 3\ 10^{-5}(x - 450) - 1.2\ 10^{-4}(y - 150) \tag{15}$$

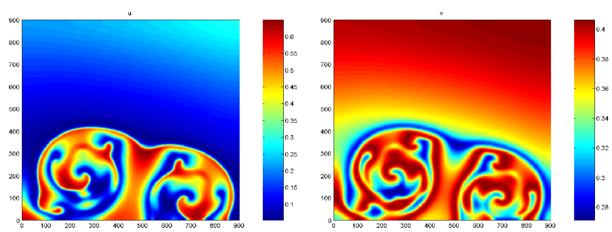
Now, we fix the following parameters values, so that the equilibrium is unstable,

$$e_1 = 0.3,\ e_2 = 0.1,\ b = 0.02,\ a = 1.1,\ \delta = 1 \tag{16}$$

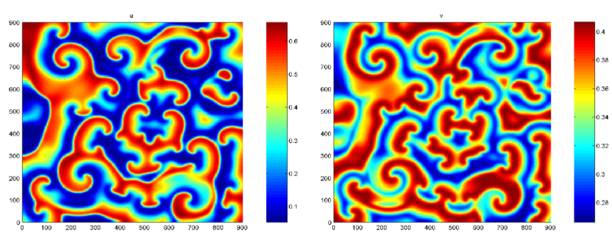
We observe the following time evolution of spatial distributions. The left figures are the evolution of the prey spatial distribution and the right are the predator's. After a while, the behavior becomes complex and remains very semilar.



$t = 500$



$t = 2000$



$t = 8000$

5 Conclusions

In this paper, we have considered a spatio-temporal prey-predator system given by a reaction-diffusion equations which is based on a holling-type II modified fontional responses. The global stability of the interior steady state is studied as well as bifurcations which lead to the instability of this equilibrium. We investigate spatio-temporal dynamics in one an two dimensions. Let us remark that these properties ensure also the permananence and the persistence of the model.

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