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TURING AND HOPF PATTERNS FORMATION IN A PREDATOR-PREY MODEL WITH LESLIE-GOWER-TYPE FUNCTIONAL RESPONSE

Baba Issa Camara[1] and M. A. Aziz-Alaoui[2]

Laboratoire de Mathématiques Appliquées du Havre
25 rue Philippe Lebon, 76600 Le Havre, France

[1] babaissa@yahoo.fr, [2] aziz.alaoui@univ-lehavre.fr

Abstract. In this paper we consider a predator-prey system modeled by a reaction-diffusion equation. It incorporates the Holling-type-II and a modified Lesie-Gower functional responses. We focus on spatiotemporal patterns formation. We study how diffusion affects the stability of predator-prey positive equilibrium and derive the conditions for Hopf and Turing bifurcation in the spatial domain.

Keywords. Predator-prey, Reaction diffusion, Bifurcations, Turing, Hopf.

AMS (MOS) subject classification: 34C23, 34C28, 34C37, 35B, 35G20, 35K55, 35Q88.

1 Introduction

The dynamic relationship between species 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 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 [2,5]. Similar model with delay is studied in [16,17], and a three dimensional similar system with the same functional responses is studied in [1,8,9]. Version with impulsive term is studied in [18]
This model incorporates the Holling-type-II and a modified Lesie-Gower functional responses.
Without diffusion, it reads as, see [2,5],

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

with,

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

H and P represent the 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.
The historical origin and applicability of this model is discussed in detail in [2,5,17].
Now, we suppose that both predator and prey move in space, we represent the mathematical model by reaction-diffusion equations. It is a type of spatio-temporal model most commonly used in ecology an biology. We focus on mechanisms responsible of bifurcations and the spatio-temporal organization or chaos.
We first establish the conditions of Turing and Hopf instability. Then, we present numerical simulations when this conditions are satisfied.
The mathematical model we consider consists of reaction-diffusion equations which expresses conservation of predator and prey densities. It has the following form,

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

H and P 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 2 dimensional space. X (resp. (X, Y)) is the spatial position of species when they move on a straight line (resp. 2 dimensional space). D_1 and D_2 are the diffusion coefficients of prey and predator respectively. a_1 is the growth rate of preys H. a_2 describes the growth rate of predators P. b_1 measure 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.
To investigate problem (2), we introduce the following scaling tranformations,

$$t = a_1 T,\ u(t) = \frac{b_1}{a_1} H(T),\ v(t) = \frac{c_2 b_1}{a_1 a_2} P(T),\ x = X(\frac{a_1}{D_1})^{\frac{1}{2}},\ y = Y(\frac{a_1}{D_1})^{\frac{1}{2}} \tag{3}$$

$$a = \frac{a_2 c_1}{a_1 c_2},\ b = \frac{a_2}{a_1},\ e_1 = \frac{b_1 k_1}{a_1},\ e_2 = \frac{b_1 k_2}{r_1},\ \delta = \frac{D_2}{D_1} \tag{4}$$

We obtain the following equations, for local model,

$$\begin{cases} \dfrac{du}{dt} & = & u(1-u) - \dfrac{auv}{u+e_1} = f(u,v) \\ \\ \dfrac{dv}{dt} & = & b\left(1 - \dfrac{v}{u+e_2}\right) v = g(u,v) \end{cases} \tag{5}$$

and the following system for the spatio-temporal equations:

$$\begin{cases} \dfrac{\partial u}{\partial t} & = & \triangle u + u(1-u) - \dfrac{auv}{u+e_1} = \triangle u + f(u,v) \\ \\ \dfrac{\partial v}{\partial t} & = & \delta \triangle v + b\left(1 - \dfrac{v}{u+e_2}\right) v = \delta \triangle v + g(u,v) \end{cases} \tag{6}$$

Let us make some remarks before to study the Hopf and Turing instabilities.

Remarque 1. *A steady state (u_e, v_e) of (5) is an equilibrium point of (6) because it verifies the following equations:*

$$\begin{cases} f(u_e,v_e) & = & 0 \\ \\ g(u_e,v_e) & = & 0 \end{cases} \tag{7}$$

thus, these following stationary equations are also satisfied,

$$\begin{cases} \triangle u_e + u_e(1-u_e) - \dfrac{a u_e v_e}{u_e+e_1} & = & 0 \\ \\ \delta \triangle v_e + b\left(1 - \dfrac{v_e}{u_e+e_2}\right) v_e & = & 0, \end{cases} \tag{8}$$

then (u_e, v_e) is also an equilibrium point for 6.

In [3] this model has been stadied when $\delta = 1$. In the present paper, δ is considered different from 1.

2 Turing and Hopf instabilities

The reaction-diffusion systems have led to the characterization of two basic types of symmetry-breaking bifurcations responsible for the emergence of spatiotemporal patterns. The space-independent Hopf bifurcation breaks the temporal symmetry of a system and gives rise to oscillations that are uniform in space and periodic in time. The (stationary) Turing bifurcation breaks spatial symmetry, leading to the formation of patterns that are stationary in time and oscillatory in space [13,20,21].
The Turing instability is dependent only upon the reaction rates (local interaction of species) and populations diffusion and not upon the geometry

of the system. It cannot be expected if the diffusion term is absent. It can occur only if prey population diffuses more slowly than predator one. Let us recall some results that will allow us to choice the appropriate parameters. From [2,5], the existence and the stability of the positive equilibrium (u^*, v^*) is given by the following lemma.

Lemma 1. *If $ae_2 < e_1$, system (5) admits a unique positive equilibrium (u^*, v^*).*
Let us denote by

$$\alpha_{1,2} = \frac{1-(b-e_1)\pm\sqrt{\rho}}{4}$$
$$\textit{where, } \rho = (1-(b+e_1))^2 - 8be_1$$

If $b+e_1 > 1$ or $0 < u^* < \alpha_1$ or $\alpha_2 < u^*$ then, (u^*, v^*) is asymptoticaly stable for (5).
If $\alpha_1 < u^* < \alpha_2$ then (u^*, v^*) is unstable for (5).

To perform a linear stability analysis, we linearize system (6) around the spatially homogenous fixed point (u^*, v^*) for small space and time-dependent fluctuations and expand them in Fourier space,

$$u(x,t) = u^* e^{\lambda t} e^{i\overrightarrow{k}.\overrightarrow{x}},$$
$$v(x,t) = v^* e^{\lambda t} e^{i\overrightarrow{k}.\overrightarrow{x}}$$

$\overrightarrow{k}$, is a wavenumber vector.We obtain the characteristic equation,

$$\mid A_k - \lambda I \mid = 0 \ , \tag{9}$$

with, $A_k = A - k^2 D$

$D = diag(1,\delta)$, and A is given by

$$A = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix} = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} = \begin{pmatrix} 1-2u^* - \frac{e_1(1-u^*)}{u^*+e_1} & -\frac{au^*}{u^*+e_1} \\ b & -b \end{pmatrix}$$

Now equation (9) can be solved, yielding the so-called characteristic polynomial of the original problem (6),

$$\lambda^2 - tr(A_k)\lambda + det(A_k) = 0 \tag{10}$$

where

$$tr(A_k) = f_u + g_v - k^2(1+\delta) = tr(A) - k^2(1+\delta), \tag{11}$$

$$det(A_k) = f_u g_v - f_v g_u - k^2(\delta f_u + g_v) + \delta k^4 = det(A) - k^2(\delta f_u + g_v) + \delta k^4. \tag{12}$$

The roots of equation (10) yield the dispersion relation,

$$\lambda_{1,2}(k) = \frac{1}{2}(tr(A_k) \pm \sqrt{(tr(A_k))^2 - 4det(A_k)}). \tag{13}$$

Theorem 1. *Suppose that $b + e_1 > 1$ or $0 < u^* < \alpha_1$ or $\alpha_2 < u^*$ so that (u^*, v^*) is asymptoticaly stable for local system (5), α_1, α_2 are defined in lemma 1. Then (u^*, v^*) is an unstable equilibrium solution of system (6) if we have,*

$$\delta > 2bf_u + 4det(A) + 2\sqrt{bf_u det(A) + (det(A))^2} \tag{14}$$

Proof From lemma 1 we have, $tr(A)$ is negative. Then, by the definition given in (11), $tr(A_k)$ is negative. Thus, (u^*, v^*) is an unstable equilibrium solution of system (6) if there exists k_0 so that $det(A_{k_0}) < 0$. We consider $det(A_k)$ as a polynomial of k^2, its discriminant is,

$$\Theta = (\delta_u + g_v)^2 - 4det(A) \tag{15}$$

After algebraic computations we see that Θ is positif if (14) is satisfied. Under this condition there is at least one positive k^* between k_0 and k_1 such that $det(A_{k^*}) < 0$. k_0 and k_1 satisfy $det(A_{k_{1,2}}) = 0$. This completes the proof.

Turing instability is a phenomenon that causes certain reaction-diffusion systems to lead to spontaneous stationary configuration. The key factor inducing the instability is the diffusion. It is why Turing instability is often called $diffusion - driven\ instability$. A remarkable feature as compared to other instabilities in system equilibrium is that the characteristics of the resulting patterns are not determined by external constraints but by the local interaction and the diffusion rates that are intrinsic to the system. The difference in the diffusion rates is a necessary, but not a sufficient condition for the Turing instability. Linear stability analysis is an often used method for studying the response to perturbations in the the vicinity of a fixed point.

A general linear analysis shows that the necessary conditions for yielding Turing patterns are given by,

$$tr(A) = f_u + g_v < 0, \tag{16}$$

$$det(A) = f_u g_v - f_v g_u > 0, \tag{17}$$

$$\delta f_u + g_v > 0, \tag{18}$$

$$(\delta f_u + g_v)^2 > 4\delta(f_u g_v - f_v g_u). \tag{19}$$

In fact conditions (16, 17) enssure, by definition, that the equilibrium (u^*, v^*) is stable for system (5). (u^*, v^*) becomes instable for system (6) if $Re(\lambda_{1,2}(k))$ bifurcate from negative value to positif one. From (10), a necessary condition to have $Re(\lambda_{1,2}(k)) > 0$ is $tr(A_k) > 0$. Therefore simple algebraic computations leads to (18, 19).

Remarque 2. *As we consider here a predator-prey model, then f_u must be positive, see [14]. An algebraic computation provide that $f_u > 0$ if $a > \frac{4e_1}{2-2e_1+4e_2}$. Let us also recall from (16, 17) and (18, 17) that $f_u + g_v < 0$ and $\delta f_u + g_v > 0$. Thus for a predator prey model, a necessary condition to observe a Turing instability is that the predator must diffuse faster than the prey. That is $\delta > 1$.*

Mathematically speaking, as $\delta > 1$, the Turing bifurcation occurs when $Im(\lambda(k)) = 0$ and $Re(\lambda(k)) = 0$ at $k = k_T \neq 0$, k_T is the critical wavenumber and the critical values of bifurcation parameter b equals to,

$$b_T = \frac{-B \pm \sqrt{B^2 - 4RC}}{2 * R}, \tag{20}$$

where,

$$R = \frac{-1}{(1+\delta)^2},$$
$$B = \frac{((f_u(1+\delta^2))}{(1+\delta)^2} + \frac{u^*(2u^* + a + e_1 - 1)}{u^* + e_1},$$
$$C = -\frac{(\delta f_u)^2}{(1+\delta)^2}$$

At the Turing threshold b_T, the spatial symmetry of the system is broken and patterns are stationary in time and oscillatory in space with the wavelength, see [14],

$$\lambda_T = \frac{2\pi}{k_T} = 2\pi\sqrt{\frac{\delta(u^* + e_1)}{u^*(2u^* + a + e_1 - 1)}} \tag{21}$$

The Hopf bifurcation occurs when $Im(\lambda(k)) \neq 0$ and $Re(\lambda(k)) = 0$ at $k = 0$. From roots dispersion given in equation (13), the critical value of Hopf bifurcation parameter b is,

$$b_H = 1 - 2u^* - \frac{e_1(1 - u^*)}{u^* + e_1}. \tag{22}$$

At the Hopf bifurcation threshold, the temporal symmetry of the system is broken and gives rise to uniform oscillations in space and periodic oscillations in time with the frequency,

$$w_H = Im(\lambda(k)) = \sqrt{det(A)} = \sqrt{\frac{bu^*}{u^* + e_1}(2u^* + a + e_1 - 1)}. \tag{23}$$

Here A defined by equation (12) and the corresponding wavelength is

$$\lambda_H = \frac{2\pi}{w_H} = 2\pi\sqrt{\frac{u^* + e_1}{bu^*(2u^* + a + e_1 - 1)}}. \tag{24}$$

These values are useful for our numerical experiments.

3 Numerical results

Linear stability analysis of system (6) yields the bifurcation curves with $a = 1.1$, $e_1 = 0.3$, $e_2 = 0.2$ and δ between 100 and 130. Figure 1(b) represents

the critical value of b, which allows to observe Hopf instability, when δ varies. The curves (a) and (c) in figure 1 are the minimal and maximal value of b (i.e. b_T) to observe turing instability. Curve (b) gives the critical value of b (i.e. b_H) giving rise to Hopf bifurcation.
The Hopf and the Turing bifucation curves separate the parametric space into four distinct domains.

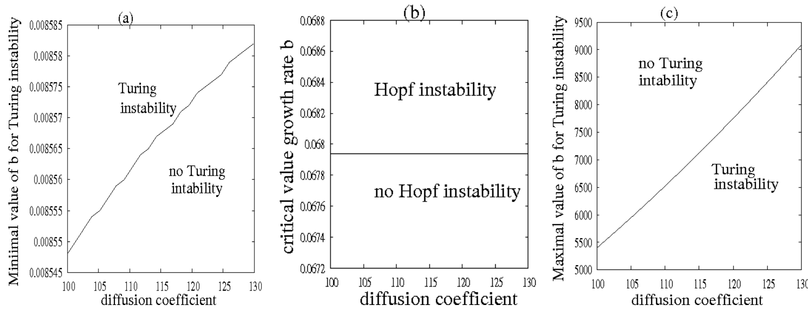

Figure 1: Critical value growth rate b leading to Hopf or Turing bifurcations, for system (6), when the diffusion coefficient varies. Other parameters are set as follow : $e1 = 0.3$, $e2 = 0.2$, $a = 1.1$.

$$a = 1.1,\ e_1 = 0.3,\ e_2 = 0.2,\ b = 0.06 \tag{25}$$

$$a = 1.1,\ e_1 = 0.3,\ e_2 = 0.2,\ b = 0.145 \tag{26}$$

Figure 2 is an example of Turing instability. The parameters are fixed as follow in (25) and, $\delta = 120.1$. Figure (3) give an example of Turing and hopf instabilities. We observe, afther the critical value given in figure 1 (b), a certain spatial symetry. With different values parameter, obtain these figures. The instabilities are also caused by Hopf bifurcations.

For other domain of parameter one can observe only Hopf instability. That can be see, in figures 4. Parameters are fixed as follows,

$$e_1 = 0.3,\ e_2 = 0.1,\ b = 0.1781,\ a = 1.1,\ \delta = 120.1$$

Let us note that we find that Hopf instability leads to the formation of symetric labirynth and Turing instability destroys a spatiotemporal chaos and leads to the formation of labirynth pattern. In fact, before the minimal critical value of Turing bifurcation the system exhibits a chaotic behaviour. Figure 5 is an illustration of this dynamics spatiotemporal chaos, parameters are fixed as follow, in (25) and $\delta = 1$

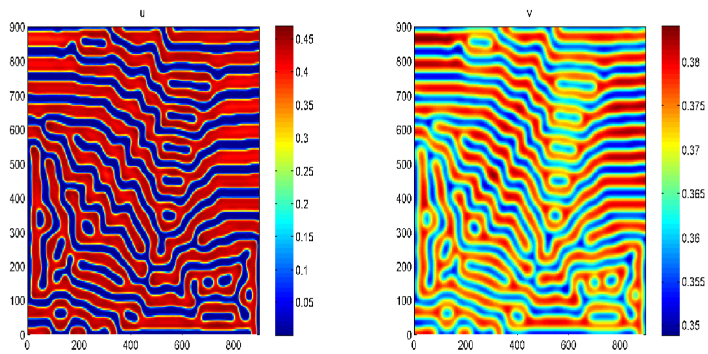

Figure 2: Stable labyrinth for system (6), in the domain where we have only Turing instability. Parameters are fixed as in (25) and $\delta = 120.1$.

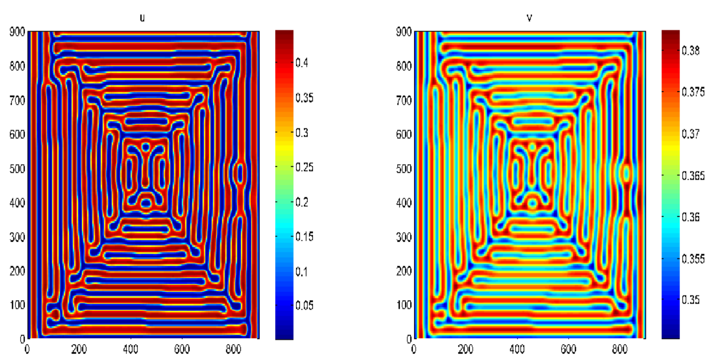

Figure 3: Stable labyrinth for system (6), in the domain where we have Turing and Hopf instability. Parameters are fixed as in (26) and $\delta = 120.1$.

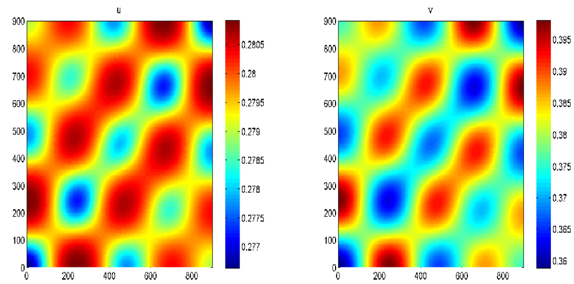

Figure 4: Hopf instability, for system (6), occurs and represents $black - eye$, with parameters $e_1 = 0.3$, $e_2 = 0.1$, $b = 0.1781$, $a = 1.1$, $\delta = 120.1$

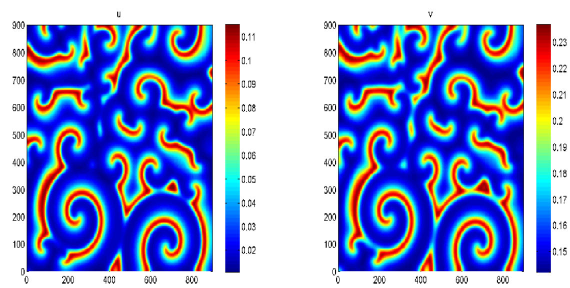

Figure 5: Spatiotemploral chaos for system (6), with $\delta = 1$ and parameters given by (25)

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