

## INSTABILITY IN A PREDATOR-PREY MODEL WITH DIFFUSION

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**ABSTRACT.** This paper treats the conditions for the existence and stability properties of stationary solutions of a predator-prey interaction with self and cross-diffusion. We show that at a certain critical value a diffusion driven instability occurs, i.e. the stationary solution stays stable with respect to the kinetic system (the system without diffusion) but becomes unstable with respect to the system with diffusion and that Turing instability takes place. We note that the cross-diffusion increase or decrease a Turing space ( the space which the emergence of spatial patterns is holding) compared to the Turing space with self-diffusion, i.e. the cross-diffusion response is an important factor that should not be ignored when pattern emerges

### 1. INTRODUCTION

The theory of spatial pattern formation via Turing instability (see [11])-wherein an equilibrium of a nonlinear system is asymptotically stable in the absence of diffusion but unstable in the presence of diffusion - plays an important role in ecology, embryology and elsewhere in biology and chemistry (see [4], [5], [8], [9]). Since the relation between the organisms and the space seems to be essential to stability of an ecological system, the effect of diffusion on the possibility of species coexistence in an ecological community has been an important subject in population biology (see [7], [10], [11]).

In recent years there has been considerable interest to investigate the stability behavior of a system of interacting populations by taking into account the effect of self as well as cross-diffusion. The term self-diffusion implies the per capita diffusion rate of each species is influenced only by its own density, i.e. there is no response to the density of the other one. Cross-diffusion implies the per capita diffusion rate of each species is influenced not only by its own but also by the other ones density. The value of the cross-diffusion coefficient may be positive, negative or zero. The term positive cross-diffusion coefficient denotes the movement of the species in the direction of lower concentration of another species and negative cross-diffusion coefficient denotes that one species tends to diffuse in the direction of higher concentration of another species. The dynamics of interacting population with self and cross-diffusion are investigated by several researchers (see [2], [3], [4], [6]) and others.

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In this paper we are going to study the effect of the self and cross-diffusion on the stability of the equilibria in a reaction diffusion predator-prey model of Cavani-Farkas type (see [2], [4] ) and we explore under which parameter values Turing instability can occur giving rise to non-uniform stationary solutions, this model described by the following equations:

$$\begin{aligned}\frac{\partial N}{\partial t} &= \epsilon N \left(1 - \frac{N}{K}\right) - \frac{\beta NP}{\beta + N} + d_{11} \frac{\partial^2 N}{\partial x^2} + d_{12} \frac{\partial^2 P}{\partial x^2}, & x \in [0, l], t > 0, \\ \frac{\partial P}{\partial t} &= -P \left(\frac{\gamma + \delta P}{1 + P}\right) + \frac{\beta NP}{\beta + N} + d_{21} \frac{\partial^2 N}{\partial x^2} + d_{22} \frac{\partial^2 P}{\partial x^2}, & x \in [0, l], t > 0,\end{aligned}\quad (1)$$

where  $N(t)$ ,  $P(t)$  represent the population density of prey and predator at time  $t$ , respectively. The prey grows with intrinsic growth rate  $\epsilon$  up to carrying capacity  $K$  in the absence of predation. Here  $\gamma > 0$  and  $\delta > 0$  are the minimal mortality and the limiting mortality of the predator, respectively (the natural assumption is  $0 < \gamma \leq \delta$ ),  $d_{ik} > 0$  are the diffusion coefficients,  $i, k = 1, 2$ . The meaning of the half saturation constant is that at  $N = \beta$  the specific growth rate  $\frac{\beta N}{\beta + N}$  (called also a Holling type functional response) of the predator is equal to half its maximum  $\beta$  (the conversion rate is taken to be equal to the half saturation constant for sake of simplicity). The advantage of this model over the more often used models is that here the predator mortality is neither a constant nor an unbounded function, still, it is increasing with the predator abundance.

Assuming that prey and predator are diffusing according to Fick's law in the interval  $x \in [0, l]$ . We are interested in solutions  $N : R^+ \times [0, l] \longrightarrow R^+$ ,  $P : R^+ \times [0, l] \longrightarrow R^+$  with no-flux boundary conditions

$$N_x(t, 0) = N_x(t, l) = P_x(t, 0) = P_x(t, l) = 0, \quad (2)$$

and initial conditions

$$N(x, 0) \geq 0, \quad P(x, 0) \geq 0, \quad x \in [0, l]. \quad (3)$$

Properly posed initial and boundary conditions yield well posed problem concerning this system of PDE's in forward time if

$$D = \begin{pmatrix} d_{11} & d_{12} \\ d_{21} & d_{22} \end{pmatrix}, \quad (4)$$

has eigenvalues with positive real parts, i.e.,

$$d_{11}d_{22} > d_{12}d_{21} \quad (5)$$

which means that "self-diffusion is stronger than cross diffusion", i.e. the flow of the respective densities in the spatial domain depends strongly on their own density than on the others.

Let us set  $F = (F_1, F_2)$ ,  $U = (N, P)$  where

$$F_1(N, P) = \epsilon N \left(1 - \frac{N}{K}\right) - \frac{\beta NP}{\beta + N}, \quad F_2(N, P) = -P \left(\frac{\gamma + \delta P}{1 + P}\right) + \frac{\beta NP}{\beta + N}, \quad (6)$$

the system takes the form

$$U_t = F(U) + D \frac{\partial^2 U}{\partial x^2}, \quad (7)$$

while the boundary conditions remain

$$U_x(t, 0) = U_x(t, l) = 0. \quad (8)$$

Clearly, a spatially constant solution  $U(t) = (N(t), P(t))$  of (7) satisfies the boundary conditions (8) and the kinetic system

$$U_t = F(U). \quad (9)$$

## 2. THE MODEL WITHOUT DIFFUSION

In this section, we will study system (1)-(2) without diffusion, i.e.,

$$\begin{aligned} \dot{N} &= \epsilon N \left(1 - \frac{N}{K}\right) - \frac{\beta NP}{\beta + N}, \\ \dot{P} &= -P \left(\frac{\gamma + \delta P}{1 + P}\right) + \frac{\beta NP}{\beta + N}. \end{aligned} \quad (10)$$

The following conditions are reasonable and natural:

$$\gamma < \beta \leq \delta, \quad (11)$$

$$\beta < K, \quad (12)$$

$$\gamma < \frac{\beta K}{\beta + K}. \quad (13)$$

Condition (11) ensures that the predator mortality is increasing with density, and that the predator null-cline has a reasonable concave down shape; (12) ensures that for the prey an Allée-effect zone exists where the increase of prey density is favourable to its growth rate; (13) is needed to have a positive equilibrium point of system (10). System (10) is made up by two identical uncoupled systems. Under these conditions the system has at least one equilibrium with positive coordinates. This is the point of intersection of the prey null-cline

$$P = H_1(N) = \frac{\epsilon}{\beta K} (K - N)(\beta + N) \quad (14)$$

and the predator null-cline

$$P = H_2(N) = \frac{(\beta - \gamma)N - \beta\gamma}{(\delta - \beta)N + \beta\delta}. \quad (15)$$

Thus, denoting the coordinates of a positive equilibrium by  $(\bar{N}, \bar{P})$ , these coordinates satisfy  $\bar{P} = H_1(\bar{N}) = H_2(\bar{N})$ .

Note that if  $K > \beta$ , we have an interval  $u_1 \in (0, \frac{K-\beta}{2})$ , where the Allée-effect holds, i.e., the increase of the prey quantity is beneficial to its growth rate.

In particular, we will focus our attention to the existence of equilibria and their local stability. This information will be crucial in the next section where we study the effect of the diffusion parameters on the stability of the steady states.

The Jacobian matrix of the system (10) linearized at  $(\bar{N}, \bar{P})$  is

$$A = \begin{pmatrix} \Theta_1 & -\Theta_2 \\ \Theta_3 & -\Theta_4 \end{pmatrix}, \quad (16)$$

where

$$\Theta_1 = \frac{\varepsilon \bar{N}(K - \beta - 2\bar{N})}{K(\beta + \bar{N})}, \quad \Theta_2 = \frac{\beta \bar{N}}{\beta + \bar{N}}, \quad \Theta_3 = \frac{\beta^2 \bar{P}}{(\beta + \bar{N})^2}, \quad \Theta_4 = \frac{(\delta - \gamma) \bar{P}}{(1 + \bar{P})^2}. \quad (17)$$

The characteristic equation is given by

$$\lambda^2 - \text{trace}A \lambda + \det A = 0, \quad (18)$$

where

$$\text{trace}A = \Theta_1 - \Theta_4, \quad \det A = \Theta_2 \Theta_3 - \Theta_1 \Theta_4 \quad (19)$$

If  $(\bar{N}, \bar{P})$  lies outside the Allée-effect zone then  $\Theta_1 < 0$ . Since, obviously,  $\Theta_2, \Theta_3, \Theta_4 > 0$  in this case  $\text{trace}A < 0$  and  $\det A > 0$ , i.e. all eigenvalues of the matrix  $A$ , have negative real parts.

The equilibrium point  $(\bar{N}, \bar{P})$  lies in the Allée-effect zone if

$$H_1\left(\frac{k - \beta}{2}\right) < H_2\left(\frac{k - \beta}{2}\right). \quad (20)$$

Recall that  $(\bar{N}, \bar{P})$  lies in the Allée-effect zone and is locally asymptotically stable if  $\text{Re}\lambda < 0$ , which is equivalent to have  $\text{trace}A < 0$  and  $\det A > 0$ . For this, we will assume that

$$\Theta_1 < \Theta_4 \quad \text{and} \quad \Theta_2 \Theta_3 > \Theta_1 \Theta_4. \quad (21)$$

### 3. TURING INSTABILITY

**Definition:** We say that the equilibrium  $(\bar{N}, \bar{P})$  is Turing unstable if it is an asymptotically stable equilibrium of the kinetic system (10) but is unstable with respect to solutions of (1)-(2) (see [11]).

We linearize system (1) at the point  $(\bar{N}, \bar{P})$ . Introducing the new coordinates  $V = (V_1, V_2) = (N - \bar{N}, P - \bar{P})$ , the linearized system assumes the form

$$V_t = AV + D \frac{\partial^2 V}{\partial x^2}, \quad (22)$$

while the boundary conditions remain

$$V_x(t, 0) = V_x(t, l) = 0. \quad (23)$$

We solve the linear boundary value problem by Fourier's method. Solutions are assumed in the form  $V(t, x) = y(t)\psi(x)$ . The functions  $y : [0, \infty) \rightarrow R^2$ ,  $\psi : [0, l] \rightarrow R$  are to satisfy

$$\dot{y} = (A - \lambda D)y, \quad (24)$$

where dot denotes differentiation with respect to time, and

$$\psi'' = -\lambda \psi, \quad \psi'(0) = \psi'(l) = 0, \quad (25)$$

where prime denotes differentiation with respect to the spatial variable  $x$ .

The eigenvalues of the boundary value problem (25) are

$$\lambda_j = (j\pi/l)^2, \quad j = 0, 1, 2, 3, \dots \quad (26)$$

with corresponding eigenfunctions

$$\psi_j(x) = \cos(j\pi x/l). \quad (27)$$

Clearly,  $0 = \lambda_0 < \lambda_1 < \lambda_2 < \dots$ . These eigenvalues are to be substituted into (24). Denoting two independent solutions of (27) taken with  $\lambda = \lambda_j$  by  $y_{1j}, y_{2j}$ , the solution of the boundary value problem (22)-(23) is obtained in the form

$$V(t, x) = \sum_{j=0}^{\infty} (a_{1j}y_{1j}(t) + a_{2j}y_{2j}(t)) \cos(j\pi x/l) \quad (28)$$

where  $a_{ij}$  ( $i = 1, 2; j = 0, 1, 2, \dots$ ) are to be determined according to the initial condition  $V(0, x)$ . If e.g.  $y_{1j}(0) = (1, 0), y_{2j}(0) = (0, 1)$  for  $j = 0, 1, 2, \dots$  then

$$\begin{bmatrix} a_{10} \\ a_{20} \end{bmatrix} = \frac{1}{l} \int_0^l V(0, x) dx,$$

$$\begin{bmatrix} a_{1k} \\ a_{2k} \end{bmatrix} = \frac{2}{l} \int_0^l V(0, x) \cos(j\pi x/l) dx \quad (k = 0, 1, 2, \dots).$$

The following notations will be used:

$$B(\lambda) = A - \lambda D, \quad B_j = B(\lambda_j) = A - \lambda_j D. \quad (29)$$

According to Casten, Holland (see [1]) if for all  $j$  both eigenvalues of  $B_j$  have negative real parts then the equilibrium  $(\bar{N}, \bar{P})$  of (7)-(8) is asymptotically stable; if at least one eigenvalue of at least one matrix  $B_j$  has positive real part then  $(\bar{N}, \bar{P})$  of (7)-(8) is unstable.

$$\text{trace} B_j = \Theta_1 - \Theta_4 - \lambda_j(d_{11} + d_{22}), \quad (30)$$

$$\det B_j = \det D \lambda_j^2 + [\Theta_4 d_{11} + \Theta_2 d_{12} - \Theta_1 d_{22} - \Theta_3 d_{21}] \lambda_j + \det A. \quad (31)$$

We note that  $\text{trace} B_j < 0$ , thus from Routh-Hurwitz criteria, the stability of the equilibrium  $(\bar{N}, \bar{P})$  depends on the sign of  $\det B_j$ . Since the coefficient matrix of the ODE in (24) is stable if and only if  $\det B_j > 0$  for each  $j = 0, 1, 2, \dots$ , therefore using the Theorem 1 in [1], one can easily see that in order to have Turing instability the quadratic polynomial (31) must be nonpositive for some  $j = 0, 1, 2, \dots$ . Dropping the index this condition assumes the form

$$\begin{aligned} \rho(\lambda) &:= \det D \lambda^2 - \Pi \lambda + \det A \leq 0, \\ &:= \lambda(\det D \lambda - \Pi) + \det A \leq 0 \text{ for some } \lambda > 0 \end{aligned} \quad (32)$$

where

$$\Pi = \Theta_1 d_{22} - \Theta_4 d_{11} + \Theta_3 d_{21} - \Theta_2 d_{12}.$$

The polynomial  $\rho(\lambda)$  has two positive roots  $0 < \underline{\lambda} \leq \bar{\lambda}$  and (32) holds for  $\lambda$  if and only if

$$\Pi > 0 \text{ and } \Pi^2 \geq 4 \det(AD)$$

since  $\underline{\lambda} := \frac{\Pi - \sqrt{\Pi^2 - 4 \det(AD)}}{2 \det D}$ ,  $\bar{\lambda} := \frac{\Pi + \sqrt{\Pi^2 - 4 \det(AD)}}{2 \det D}$ . This with (5) imply that the polynomial  $\rho(\lambda)$  is nonpositive for some  $\lambda > 0$  between their positive roots  $0 < \underline{\lambda} \leq \bar{\lambda}$ .

We are going to establish the conditions of a Turing instability for the following cases under the assumption that  $\text{trace} B_j < 0$  and the predator diffusion coefficient  $d_{22} > 0$  as the bifurcation parameter.

**Case 1:**  $d_{12} = d_{21} = 0$  (self-diffusion).

This shows that each species moves along its own concentration gradient.

**Theorem:** Suppose that  $\text{trace} B_j < 0$  and  $\det A > 0$ .

(i) If

$$d_{11} \geq \Theta_1 / \lambda_1 \quad (33)$$

then the zero solution of the linear problem (22)-(23) is asymptotically stable for all  $d_{22} > 0$ .

(ii) If

$$\Theta_1 / \lambda_1 > d_{11} \geq \Theta_1 / \lambda_2 \quad (34)$$

then at

$$d_{22} := d_{22crit}^* = \frac{\det A + \lambda_1 d_{11} \Theta_4}{\lambda_1 (\Theta_1 - \lambda_1 d_{11})} \quad (35)$$

the zero solution of the linear problem (22)-(23) undergoes a Turing instability.

**Proof.** (i) From (31) we have

$$\det B_j = \det A + \lambda_j d_{11} \Theta_4 - \lambda_j d_{22} (\Theta_1 - \lambda_j d_{11}).$$

Since  $\lambda_j, j = 0, 1, 2, \dots$  from a monotone increasing sequence (33) implies  $\det B_j > 0$  for all  $j = 0, 1, 2, \dots$ . From (30) we see that  $\text{trace} B_j < 0$  for all  $j = 0, 1, 2, \dots$  hence the zero solution of (22)-(23) is asymptotically stable.

(ii) If  $d_{11}$  satisfies (34) and  $d_{22}$  is chosen according to (35) then  $\det B_1 = 0$ . Clearly, for  $0 < d_{22} < d_{22crit}^*$  we have  $\det B_1 > 0$ , and for  $d_{22crit}^* < d_{22}$  we have  $\det B_1 < 0$ . In all these cases  $\det B_j > 0, j \neq 1$ . Thus, taking into account what has been quoted after formula (29), for  $0 < d_{22} < d_{22crit}^*$  the zero solution is asymptotically stable, for  $d_{22crit}^* < d_{22}$  it is unstable.

**Case 2:**  $d_{12} = 0, d_{21} \neq 0$ .

In this case under conditions (33) and (34) the matrix  $B_j$  have negative real parts and the equilibrium point  $(\bar{N}, \bar{P})$  is Turing unstable if

$$d_{22} > d_{22crit} := \frac{\det A + \lambda_1 (d_{11} \Theta_4 - d_{21} \Theta_3)}{\lambda_1 (\Theta_1 - \lambda_1 d_{11})}. \quad (36)$$

If  $d_{21} < 0$ , this implies that the predator species tends to diffuse in the direction of higher concentration of the prey species, and the prey species moves along its own concentration gradient.

We note that  $d_{22crit} > d_{22crit}^*$ . This implies that decreasing the Turing space compared to the first case, so that the emergence of spatial patterns is holding in small regions of parameter space. This situation is a usual phenomenon in nature.

If  $d_{21} > 0$ , this implies that the predator species tends to diffuse in the direction of lower concentration of the prey species, and the prey species moves along its own concentration gradient. Such a case arise in nature where the predator prefers to avoid group defense by a large number of prey and chooses to catch its prey from a smaller group unable to sufficiently resist.

We note that  $d_{22crit} < d_{22crit}^*$ . This implies that increasing the Turing space compared to the first case, so that the emergence of spatial patterns is holding in large regions of parameter space.

**Case 3:**  $d_{12} \neq 0, d_{21} = 0$ .

In this case under conditions (33) and (34) the matrix  $B_j$  have negative real parts and the equilibrium point  $(\bar{N}, \bar{P})$  is Turing unstable if

$$d_{22} > d_{22crit} := \frac{\det A + \lambda_1(d_{11}\Theta_4 + d_{12}\Theta_2)}{\lambda_1(\Theta_1 - \lambda_1 d_{11})}. \quad (37)$$

If  $d_{12} < 0$ , this implies that the prey species moves towards the higher concentration of the predator species, and the predator species moves along its own concentration gradient. This situation can be compared in nature where the predator attracts the prey towards itself as a predation technique and the suicidal tendencies among the prey exist.

Also here we note that  $d_{22crit} < d_{22crit}^*$ . This implies that increasing the Turing space compared to the first case, so that the emergence of spatial patterns is holding in large regions of parameter space.

If  $d_{12} > 0$ , this implies that the prey species moves in the direction of lower concentration of the predator species, and the predator species moves along its own concentration gradient. This situation can be compared in nature where the prey moves towards the lower concentration of the predator in search of new food.

We note that  $d_{22crit} > d_{22crit}^*$ . This implies that decreasing the Turing space compared to the first case, so that the emergence of spatial patterns is holding in small regions of parameter space. This situation is a usual phenomenon in nature.

**Case 4:**  $d_{12} \neq 0, d_{21} \neq 0$ .

In this case under conditions (33) and (34) the matrix  $B_j$  have negative real parts and the equilibrium point  $(\bar{N}, \bar{P})$  is Turing unstable if

$$d_{22} > d_{22crit} := \frac{\det A + \lambda_1 d_{11} \Theta_4 + \lambda_1 (-d_{12} d_{21} \lambda_1 + d_{12} \Theta_2 - d_{21} \Theta_3)}{\lambda_1 (\Theta_1 - \lambda_1 d_{11})}. \quad (38)$$

1) If  $d_{12} < 0, d_{21} < 0$ , this implies that the prey species tends to diffuse in the direction of higher concentration of the predator species and the predator species tends to diffuse in the direction of higher concentration of the prey species. Such situations are common in nature when prey represent the investment capital and the predator represent labour force.

We note that Turing space increase (resp. decrease) if  $\lambda_1 > \frac{d_{12}\Theta_2 - d_{21}\Theta_3}{d_{12}d_{21}}$  i.e.  $d_{22crit} < d_{22crit}^*$  (resp.  $< \frac{d_{12}\Theta_2 - d_{21}\Theta_3}{d_{12}d_{21}}$  i.e.  $d_{22crit} > d_{22crit}^*$ ), so that the emergence of spatial patterns is holding in large (resp. small) regions of parameter space.

2) If  $d_{12} > 0$ ,  $d_{21} > 0$ , this implies that the prey species moves in the direction of lower concentration of the predator species and the predator species tends to diffuse in the direction of lower concentration of the prey species. Such a case arise in nature where the prey moves towards the lower concentration of the predator in search of new food. and the predator prefers to avoid group defense by a large number of prey and chooses to catch its prey from a smaller group unable to sufficiently resist.

We note that Turing space increase (resp. decrease) if  $\lambda_1 > \frac{d_{12}\Theta_2 - d_{21}\Theta_3}{d_{12}d_{21}}$  i.e.  $d_{22crit} < d_{22crit}^*$  ( resp.  $< \frac{d_{12}\Theta_2 - d_{21}\Theta_3}{d_{12}d_{21}}$  i.e.  $d_{22crit} > d_{22crit}^*$ ), so that the emergence of spatial patterns is holding in large (resp. small) regions of parameter space.

3) If  $d_{12} > 0$ ,  $d_{21} < 0$ , this implies that the prey species tends to diffuse in the direction of lower concentration of the predator species, and the predator species tends to diffuse in the direction of higher concentration of the prey species. Such situations are common in nature for the survival of the prey predator species.

We note that  $d_{22crit} > d_{22crit}^*$ . This implies that decreasing the Turing space compared to the first case, so that the emergence of spatial patterns is holding in small regions of parameter space.

4) If  $d_{12} < 0$ ,  $d_{21} > 0$ , his implies that the prey species tends to diffuse in the direction of higher concentration of the predator species and the predator species tends to diffuse in the direction of lower concentration of the prey species.

We note that Turing space increase (resp. decrease) if  $\lambda_1 > \frac{d_{12}\Theta_2 - d_{21}\Theta_3}{d_{12}d_{21}}$  i.e.  $d_{22crit} < d_{22crit}^*$  (resp.  $< \frac{d_{12}\Theta_2 - d_{21}\Theta_3}{d_{12}d_{21}}$  i.e.  $d_{22crit} > d_{22crit}^*$ ), so that the emergence of spatial patterns is holding in large (resp. small) regions of parameter space.

#### 4. CONCLUSIONS

In this paper we have considered a Cavani-Farkas type predator-prey interacting model with self as well as cross-diffusion and investigated the stability conditions in different environmental consequences. We show that at a certain critical value a diffusion driven instability occurs, i.e. the stationary solution stays stable with respect to the kinetic system (the system without diffusion) but becomes unstable with respect to the system with diffusion and that Turing instability takes place. We note that the cross-diffusion increase or decrease a Turing space (the space which the emergence of spatial patterns is holding) compared to the Turing space with self-diffusion, i.e. the cross-diffusion response is an important factor that should not be ignored when pattern emerges.

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