

# TURING INSTABILITY IN A COUPLED PREDATOR-PREY MODEL WITH DIFFERENT HOLLING TYPE FUNCTIONAL RESPONSES

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**ABSTRACT.** In a reaction-diffusion system, diffusion can induce the instability of a positive equilibrium which is stable with respect to a constant perturbation, therefore, the diffusion may create new patterns when the corresponding system without diffusion fails, as shown by Turing in 1950s. In this paper we study a coupled predator-prey model with different Holling type functional responses, where cross-diffusions are included in such a way that the prey runs away from predator and the predator chase preys. We conduct the Turing instability analysis for each Holling functional response. We prove that if a positive equilibrium solution is linearly stable with respect to the ODE system of the predator-prey model, then it is also linearly stable with respect to the model. So diffusion and cross-diffusion in the predator-prey model with Holling type functional responses given in this paper can not drive Turing instability. However, diffusion and cross-diffusion can still create non-constant positive solutions for the model.

**1. Introduction.** In population dynamics, a spatially homogeneous predator-prey system can be modeled as a system of ordinary differential equations:

$$\mathbf{u}_t = \mathbf{G}(\mathbf{u}), \quad \mathbf{u} = \begin{bmatrix} u \\ v \end{bmatrix}, \quad \mathbf{G}(\mathbf{u}) = \begin{bmatrix} g_1(u, v) \\ g_2(u, v) \end{bmatrix}, \quad (1)$$

where  $u$  and  $v$  are the population densities of prey and predator respectively. In mathematical ecology, the classical Lotka-Volterra model, due independently to Lotka [14] and Volterra [26] in the 1920s, is the simplest model of predator-prey interactions. They chose  $g_1(u, v) = ru - auv$ , and  $g_2(u, v) = buv - mv$  and the model only reflects population changes due to predation in a situation where predator and prey densities are not spatially dependent. It does not take into consideration either the fact that predators and preys naturally develop strategies for survival or the fact that the distribution of the population is usually not homogeneous. A model taking this effect into account should capture more interesting phenomena and patterns. Such considerations involve diffusion process.

$$\mathbf{u}_t = \Delta [\mathbf{K}(\mathbf{u})] + \mathbf{G}(\mathbf{u}), \quad \mathbf{K}(\mathbf{u}) = \begin{bmatrix} u(d_1 + d_3v) \\ v\left(d_2 + \frac{d_4}{1+u}\right) \end{bmatrix}, \quad (2)$$

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where  $d_1 > 0$  and  $d_2 > 0$  are the self-diffusion coefficients,  $d_3 > 0$  and  $d_4 > 0$  are the cross-diffusion coefficients, and  $\Delta$  is the Laplacian. The positive cross-diffusion coefficients  $d_3$  and  $d_4$  represent that the prey runs away from the predator and the predator chases the prey respectively, in agreement with observed general patterns of predator-prey movements (see Okubo [21] and Murray [20] for a more detailed discussion on relevant biological models).  $\mathbf{G}(\mathbf{u})$  represents the functional response of predator and prey. Holling [9, 10] suggested a model of functional response which remains most popular among ecologists, known as Holling type function now. It illustrates the principal of time budget in behavioral ecology. It assumes that a predator spends its time on two kinds of activities: (i) Searching for prey (ii) Prey handling which includes: chasing, killing, eating and digesting. Consumption rate of a predator is limited in this model because even if prey are so abundant that no time is needed for search, a predator still needs to spend time on prey handling.

The role of diffusion  $d_1, d_2$  and cross-diffusion  $d_3, d_4$  in the modeling of many physical, chemical and biological processes has been extensively studied. A pure diffusion process usually leads to a smothering effect so that the system tends to a constant equilibrium state. However the combined effect of diffusion and chemical reaction may result in destabilizing the constant equilibrium. In 1952, Alan Turing published a paper “The chemical basis of morphogenesis” [25] which is now regarded as the foundation of basic chemical theory or reaction diffusion theory of morphogenesis. Turing suggested that, under certain conditions, chemicals can react and diffuse in such a way as to produce non-constant equilibrium solutions, which represent spatial patterns of chemical or morphogen concentration. He said that if, in the absence of the diffusion,  $\mathbf{u}$  tends to a linearly stable uniform steady state, then, with the presence of diffusion and under certain conditions, the uniform steady state can become unstable, and spatial inhomogeneous patterns can evolve through bifurcations. In another word, a constant equilibrium can be asymptotically stable without diffusion, but it is unstable with diffusion, which is called *diffusion driven instability*.

Over the years, Turing’s idea has attracted the attention of a great number of investigators and was successfully developed on the theoretical backgrounds. Not only it has been studied in biological and chemical fields, some investigations range as far as economics, semiconductor physics, and star formation. These include the predator-prey model [1]-[12], [16]-[18] and [27]-[24], the vegetation pattern formation [13, 15, 23], the chemotactic diffusion model [19, 28] and the references therein.

In [23], the authors presented a general instability analysis on cross-diffusion system with two species. They showed that cross-diffusion can destabilize a uniform equilibrium which is stable for the kinetic and self-diffusion reaction systems; on the other hand, cross-diffusion can also stabilize a uniform equilibrium which is stable for the kinetic system but unstable for the self-diffusion reaction system.

In this paper, we consider four major types of functional responses:

(i) Holling type-I function:

$$\mathbf{G}_1(\mathbf{u}) = \begin{bmatrix} g_1^{(1)}(u, v) \\ g_2^{(1)}(u, v) \end{bmatrix} = \begin{bmatrix} u(1 - u/k_1) - a_1 uv \\ v(b_1 u - 1) \end{bmatrix}. \quad (3)$$

(ii) Holling type-II function:

$$\mathbf{G}_2(\mathbf{u}) = \begin{bmatrix} g_1^{(2)}(u, v) \\ g_2^{(2)}(u, v) \end{bmatrix} = \begin{bmatrix} u(1 - u/k_2) - \frac{uv}{1+a_2 u} \\ v(\frac{b_2 u}{1+a_2 u} - 1) \end{bmatrix}. \quad (4)$$

(iii) Holling type-III function:

$$\mathbf{G}_3(\mathbf{u}) = \begin{bmatrix} g_1^{(3)}(u, v) \\ g_2^{(3)}(u, v) \end{bmatrix} = \begin{bmatrix} u(1 - u/k_3) - \frac{u^2 v}{a_3 + u^2} \\ v(\frac{b_3 u^2}{a_3 + u^2} - 1) \end{bmatrix}. \quad (5)$$

(iv) Holling type-IV function:

$$\mathbf{G}_4(\mathbf{u}) = \begin{bmatrix} g_1^{(4)}(u, v) \\ g_2^{(4)}(u, v) \end{bmatrix} = \begin{bmatrix} u(1 - u/k_4) - \frac{uv}{a_4 + u^2} \\ v(\frac{b_4 u}{a_4 + u^2} - 1) \end{bmatrix}. \quad (6)$$

The constants  $a_i, b_i, k_i$  are all positive for  $i = 1, 2, 3, 4$ .

Holling type-I function is a linear functional response which is unbounded such as the classical Lotka-Volterra model. Type I functional response is found in passive predators like spiders. Zeng [30] studied a prey-predator system with the Holling type-I functional response involving cross diffusions. The author conducted Turing instability analysis and established the existence and non-existence of its nonconstant positive solutions. Chen-Qi-Wang [1] considered a strongly coupled predator-prey system with a non-monotonic functional response—a Holling type-IV function in a bounded domain with no flux boundary condition. They proved a number of existence and non-existence results concerning non-constant steady states. A very nice review and explanation of Holling type functional responses can also be found in their introduction. There are many works on the predator-prey models such as [1]-[12], [16]-[18] and [27]-[24] and the reference therein.

The main aim of this paper is to study the effects of the diffusion pressures by conducting Turing instability analysis of (2) with four Holling type functional responses. The predator-prey model (2) is rewritten as:

$$\begin{cases} u_t = \Delta [u(d_1 + d_3 v)] + g_1^{(i)}(u, v), & \text{in } \Omega \times (0, \infty), \\ v_t = \Delta \left[ v \left( d_2 + \frac{d_4}{1+u} \right) \right] + g_2^{(i)}(u, v), & \text{in } \Omega \times (0, \infty), \\ \partial_n u = \partial_n v = 0, & \text{on } \partial\Omega \times (0, \infty), \\ u(x, 0) = u_0(x), v(x, 0) = v_0(x), & \text{in } \Omega, \end{cases} \quad (7)$$

where  $\Omega$  is a bounded domain in  $\mathbf{R}^n$  with smooth boundary  $\partial\Omega$ , and  $\partial_n$  is the outward directional derivative normal to  $\partial\Omega$ .

**Theorem 1.1.** *If  $(\bar{u}, \bar{v})$  is a positive constant solution to (7) and it is linearly stable with respect to its counterpart ODE system, then it is also linearly stable with respect to (7). So diffusion and cross-diffusion in the predator-prey model (7) with Holling types functional response given by (3), (4), (5) and (6) can not drive Turing instability.*

**Remark 1.** Although the diffusion and cross-diffusion can not produce Turing instability for (7), they still can create non-constant positive steady states. The existence of non-constant positive steady states can be found in the paper [1] and [30]. Theorem 1.1 is proved as a direct result of Theorem 2.3 – Theorem 2.6 with respect to Holling type I – Holling type IV functional responses.

**2. Turing instability.** Suppose that  $\bar{\mathbf{u}}_i = (\bar{u}_i, \bar{v}_i)$  is a positive equilibrium solution for the corresponding spatially homogeneous counterpart of problem (7):

$$\frac{d\mathbf{u}}{dt} = \mathbf{G}_i(\mathbf{u}) \quad (8)$$

The linearization of problem (8) at  $\bar{\mathbf{u}}_i$  is

$$\frac{d\mathbf{w}}{dt} = \mathbf{G}_{i\mathbf{u}}(\bar{\mathbf{u}}_i)\mathbf{w}. \quad (9)$$

Its characteristic polynomial is

$$P_{ode}(\lambda) = \lambda^2 - \text{trace}(\mathbf{G}_{i\mathbf{u}}(\bar{\mathbf{u}}_i))\lambda + \det(\mathbf{G}_{i\mathbf{u}}(\bar{\mathbf{u}}_i)). \quad (10)$$

Linearizing the reaction-diffusion system (7) about the positive equilibrium  $\bar{\mathbf{u}}_i = (\bar{u}_i, \bar{v}_i)^T$ , we have

$$\frac{\partial \Psi}{\partial t} = \mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}_i)\Delta \Psi + \mathbf{G}_{i\mathbf{u}}(\bar{\mathbf{u}}_i)\Psi, \quad (11)$$

where  $\Psi = (\Psi_1, \Psi_2)^T$  and

$$\mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}_i) = \begin{bmatrix} k_{11} & k_{12} \\ k_{21} & k_{22} \end{bmatrix}, \quad \mathbf{G}_{i\mathbf{u}}(\bar{\mathbf{u}}_i) = \begin{bmatrix} g_{11} & g_{12} \\ g_{21} & g_{22} \end{bmatrix}.$$

Let  $0 = \mu_1 < \mu_2 < \mu_3 < \dots$  be the eigenvalues of the operator  $-\Delta$  on  $\Omega$  with the homogeneous Neumann boundary condition, and  $E(\mu_m)$  be the eigenspace corresponding to  $\mu_m$  in  $C^2(\Omega)$ . Let  $\mathbf{X} = \{\mathbf{u} \in [C^1(\bar{\Omega})]^2 \mid \partial_n \mathbf{u} = 0 \text{ on } \partial\Omega\}$ ,  $\{\phi_{mj}\}_{j=1,2,\dots,\dim E(\mu_m)}$  be an orthonormal basis of  $E(\mu_m)$ , and  $\mathbf{X}_{mj} = \{\mathbf{c}\phi_{mj} \mid \mathbf{c} \in \mathbf{R}^2\}$ . Then

$$\mathbf{X} = \bigoplus_{m=1}^{\infty} \mathbf{X}_m \quad \text{and} \quad \mathbf{X}_m = \bigoplus_{j=1}^{\dim E(\mu_m)} \mathbf{X}_{mj}.$$

For each  $i \geq 1$ ,  $\mathbf{X}_m$  is invariant under the operator  $\mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}_i)\Delta + \mathbf{G}_{i\mathbf{u}}(\bar{\mathbf{u}}_i)$ . Then problem (11) has a non trivial solution of the form  $\Psi = \mathbf{c}\phi \exp(\lambda t)$  if and only if  $(\lambda, \mathbf{c})$  is an eigenpair for the matrix  $-\mu_m \mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}_i) + \mathbf{G}_{i\mathbf{u}}(\bar{\mathbf{u}}_i)$ , where  $\mathbf{c}$  is a constant vector. Then the equilibrium  $\bar{\mathbf{u}}_i$  is unstable if at least one eigenvalue  $\lambda$  has a positive real part for some  $\mu_m$ . The characteristic polynomial of  $M_i = -\mu_m \mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}_i) + \mathbf{G}_{i\mathbf{u}}(\bar{\mathbf{u}}_i)$  is given by

$$P_{pde}(\lambda) = \lambda^2 - \text{trace}(M_i)\lambda + \det(M_i), \quad (12)$$

where

$$\text{trace}(M_i) = \text{trace}(-\mu_m \mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}_i)) + \text{trace}(\mathbf{G}_{i\mathbf{u}}(\bar{\mathbf{u}}_i)) = -\mu_m(k_{11} + k_{22}) + (g_{11} + g_{22}), \quad (13)$$

$$\det(M_i) = A\mu_m^2 + B\mu_m + C, \quad (14)$$

and

$$\begin{aligned} A &= \det(\mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}_i)) = k_{11}k_{22} - k_{21}k_{12}, \\ B &= -k_{11}g_{22} + k_{21}g_{12} - k_{22}g_{11} + k_{12}g_{21}, \\ C &= \det(\mathbf{G}_{i\mathbf{u}}(\bar{\mathbf{u}}_i)) = g_{11}g_{22} - g_{12}g_{21}. \end{aligned}$$

For any positive equilibrium solution  $(\bar{u}_i, \bar{v}_i)$  of (8),  $k_{11} > 0, k_{22} > 0, k_{12} > 0, k_{21} < 0$  because

$$\mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}_i) = \begin{bmatrix} d_1 + d_3 \bar{v}_i & \bar{u}_i d_3 \\ -\frac{\bar{v}_i d_4}{(1+\bar{u}_i)^2} & d_2 + \frac{d_4}{1+\bar{u}_i} \end{bmatrix}. \quad (15)$$

So  $A = \det(\mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}_i)) > 0$ . Therefore, we have

**Lemma 2.1.** *Given any positive equilibrium solution  $(\bar{u}_i, \bar{v}_i)$  of the ODE system (8),*

- (i) *If  $g_{11} < 0, g_{22} = 0, g_{21} > 0$ , and  $g_{12} < 0$ , then  $(\bar{u}_i, \bar{v}_i)$  is linearly stable with respect to the ODE system (8).*
- (ii) *If  $g_{11} < 0, g_{22} = 0, g_{21} > 0$ , and  $g_{12} < 0$ , then  $B = -k_{11}g_{22} + k_{21}g_{12} - k_{22}g_{11} + k_{12}g_{21} > 0$ , and  $(\bar{u}_i, \bar{v}_i)$  is linearly stable with respect to the PDE system (7).*
- (iii) *If  $g_{11} > 0, g_{22} = 0, g_{21} > 0, g_{12} < 0$ , and  $\det(M_i) < 0$  for some  $\mu_m$ , then  $(\bar{u}_i, \bar{v}_i)$  is linearly unstable with respect to the PDE system (7).*
- (iv) *If  $g_{22} = 0$ , and  $g_{12} < 0$ , then  $(\bar{u}_i, \bar{v}_i)$  is linearly stable with respect to the ODE system (8) if and only if  $g_{11} < 0$  and  $g_{21} > 0$ .*

If  $\bar{\mathbf{u}}_i = (\bar{u}_i, \bar{v}_i)$  is stable with respect to (8) and at least one  $Re(\lambda)$  of (12) is positive, then  $\bar{\mathbf{u}}_i = (\bar{u}_i, \bar{v}_i)$  becomes unstable with respect to (7). This refers to *Turing instability*, i.e., the stability of the constant equilibrium  $\bar{\mathbf{u}}_i$  changing from stable, for the ODE dynamics (8), to unstable, for the PDE dynamics (7).

Note that the common characteristics of the first three types of model (Holling type-I, Holling type-II, and Holling type-III) is that the functional responses are monotonic. They satisfy the following monotonic assumptions which is studied in many predator-prey interaction models.

$$\mathbf{G}_\phi(\mathbf{u}) = \begin{bmatrix} u(1 - u/k_1) - \phi(u)v \\ v(b\phi(u) - 1) \end{bmatrix}, \quad (16)$$

where  $\phi(u)$  is a monotonic function satisfying  $\phi(0) = 0$ ,  $\phi'(u) > 0$  for  $u > 0$ , and  $\lim_{u \rightarrow \infty} \phi(u) = \phi_\infty \leq \infty$ . Function  $\phi(u)$  is the functional response of predator to prey density, which refers to the change in the density of prey attached per unit time per predator. In the Holling type-I, the functional response  $\phi(u)$  is unbounded and  $\lim_{u \rightarrow \infty} \phi(u) = \infty$ . In the Holling type-II and Holling type-III, the functional responses are bounded. But Holling type-IV is not a monotonic functional response.

**Lemma 2.2.** *If*

$$1 - \frac{\phi^{-1}(1/b)}{k} > 0, \text{ and } 1 - \frac{2\phi^{-1}(1/b)}{k} - \phi'(u)b\phi^{-1}(1/b)(1 - \frac{\phi^{-1}(1/b)}{k}) < 0,$$

*then the unique positive equilibrium solution  $(\bar{u}_\phi, \bar{v}_\phi) = (\phi^{-1}(1/b), b\phi^{-1}(1/b)(1 - \phi^{-1}(1/b)/k))$  of the predator-prey model (7) with monotonic functional response (16) is linear stable with respect to both ODE and PDE system, which is not the type of Turing instability.*

*Proof.* Because  $\phi$  is monotonic,  $\phi^{-1}(1/b)$  exists. The system (8) has a unique positive equilibrium solution  $(\bar{u}_\phi, \bar{v}_\phi) = (\phi^{-1}(1/b), b\phi^{-1}(1/b)(1 - \phi^{-1}(1/b)/k))$ . Since  $g_{11} = 1 - \frac{2\phi^{-1}(1/b)}{k} - \phi'(u)b\phi^{-1}(1/b)(1 - \frac{\phi^{-1}(1/b)}{k}) < 0$ ,  $g_{12} = -1/b < 0$ ,  $g_{21} = \bar{v}_\phi b\phi'(\bar{u}_\phi) > 0$ , and  $g_{22} = 0$ ,  $(\bar{u}_\phi, \bar{v}_\phi)$  is linear stable with respect to both ODE and PDE system by Lemma 2.1 (i) and (ii).  $\square$

From lemma 2.2,  $g_{11} > 0$  is the necessary condition that the unique equilibrium solution becomes unstable for PDE system. Therefore Turing instability can not occur in the predator-prey model with Holling type-I, II, and III functional responses because the unique equilibrium solution is linearly unstable for the ODE system if  $g_{11} > 0$ . Now we perform the Turing instability analysis for the PDE system with four types of Holling functional responses. The stability results for Holling type-I,

II, and III functional responses could be derived directly from lemma 2.2. We state the results for each functional responses and we only give the proofs for Holling type-II and Holling type-IV because we also want to explore the conditions for instability.

**Case 1 (i=1): Holling type-I functional response.**

**Theorem 2.3.** *For  $i = 1$ , we consider the predator-prey model (7) with Holling type-I functional response (3). Suppose  $b_1 k_1 - 1 > 0$ . Then the unique positive equilibrium solution  $(\bar{u}_1, \bar{v}_1)$  is linear stable with respect to both (8) and (7), which is not the type of Turning instability.*

**Case 2 (i=2): Holling type-II functional response.**

**Theorem 2.4.** *For  $i = 2$ , we consider the predator-prey model (7) with Holling type-II functional response (4). Suppose  $k_2(b_2 - a_2) - 1 > 0$ . Then (8) has a unique positive equilibrium solution  $(\bar{u}_2, \bar{v}_2) = (1/(b_2 - a_2), b_2(k_2(b_2 - a_2) - 1)/(k_2(b_2 - a_2)^2))$ . ( $\mathcal{A}_1$ ) If  $k_2 a_2(b_2 - a_2) - (b_2 + a_2) \leq 0$ , then the solution  $(\bar{u}_2, \bar{v}_2)$  is linear stable with respect to both (8) and (7), which is not the type of Turning instability. ( $\mathcal{A}_2$ ) Suppose  $k_2 a_2(b_2 - a_2) - (b_2 + a_2) > 0$ . Let  $d_1, d_3, d_4$  be fixed. There exists a positive constant  $D_2$  such that, when  $d_2 > D_2$ , the equilibrium  $(\bar{u}_2, \bar{v}_2)$  is linearly unstable with respect to both (8) and (7).*

*Proof.* When  $k_2(b_2 - a_2) - 1 > 0$ , then (8) has a unique positive equilibrium solution  $(\bar{u}_2, \bar{v}_2) = (1/(b_2 - a_2), b_2 \bar{u}_2(1 - \bar{u}_2/k_2)) = (1/(b_2 - a_2), b_2(k_2(b_2 - a_2) - 1)/(k_2(b_2 - a_2)^2))$  and

$$\mathbf{G}_{2\mathbf{u}}(\bar{\mathbf{u}}_2) = \begin{bmatrix} \frac{k_2 a_2(b_2 - a_2) - (b_2 + a_2)}{k_2 b_2(b_2 - a_2)} & -b_2^{-1} \\ \frac{k_2(b_2 - a_2) - 1}{k_2} & 0 \end{bmatrix}$$

( $\mathcal{A}_1$ ) If  $k_2 a_2(b_2 - a_2) - (b_2 + a_2) \leq 0$ , then  $g_{11} \leq 0, g_{22} = 0, g_{21} > 0, g_{12} < 0$ . Therefore the solution  $(\bar{u}_2, \bar{v}_2)$  is linear stable with respect to (8). Because  $(\bar{u}_2, \bar{v}_2)$  is positive and  $d_1, d_2, d_3, d_4$  are also positive,  $k_{11} > 0, k_{22} > 0, k_{21} < 0, k_{12} > 0$  from (15). So  $\text{trace}(M_2) < 0$  and  $\det(M_2) > 0$ . So  $(\bar{u}_2, \bar{v}_2)$  is linear stable with respect to (7).

( $\mathcal{A}_2$ ) If  $k_2 a_2(b_2 - a_2) - (b_2 + a_2) > 0$ , then  $g_{11} > 0, g_{22} = 0, g_{21} > 0, g_{12} < 0$ .  $\text{trace}(\mathbf{G}_{2\mathbf{u}}(\bar{\mathbf{u}}_2)) > 0$ . Therefore the solution  $(\bar{u}_2, \bar{v}_2)$  is linear unstable with respect to (8).  $\det(M_2) = A\mu_m^2 + B\mu_m + C$  with  $A > 0$ , and  $C = \det(\mathbf{G}_{2\mathbf{u}}(\bar{\mathbf{u}}_2)) > 0$ .  $B = -k_{11}g_{22} + k_{21}g_{12} - k_{22}g_{11} + k_{12}g_{21} = (-g_{12}\bar{v}_2/(1+\bar{u}_2)^2 - g_{11}/(1+\bar{u}_2))d_4 - g_{11}d_2 + g_{21}\bar{u}_2d_3 < 0$  for large  $d_2$ , say  $d_2 > D_2$ . By fixing  $d_1, d_3, d_4$  small,  $\det(M_2) < 0$  for some  $\mu_m$ . Then  $(\bar{u}_2, \bar{v}_2)$  is linear unstable with respect to the PDE system (7).  $\square$

**Case 3 (i=3): Holling type-III functional response.**

**Theorem 2.5.** *For  $i = 3$ , we consider the predator-prey model (7) with Holling type-III functional response (5). Suppose  $b_3 - 1 > 0$ ,  $k_3 - \sqrt{\frac{a_3}{b_3 - 1}} > 0$ , and  $2\left(k_3 - \sqrt{\frac{a_3}{b_3 - 1}}\right) - b_3 k_3 \leq 0$ . Then the ODE system (8) has a unique positive equilibrium solution*

$$(\bar{u}_3, \bar{v}_3) = \left( \sqrt{\frac{a_3}{b_3 - 1}}, b_3 \sqrt{\frac{a_3}{b_3 - 1}} \left( k_3 - \sqrt{\frac{a_3}{b_3 - 1}} \right) k_3^{-1} \right).$$

The equilibrium solution  $(\bar{u}_3, \bar{v}_3)$  is linearly stable with respect to both the ODE system (8) and the PDE system (7).

**Case 4 (i=4): Holling type-IV functional response.**

When  $b_4 > 2\sqrt{a_4}$ , there are two possible positive equilibrium solutions to  $\mathbf{G}_4(\mathbf{u}) = 0$ :

$$\begin{aligned} \bar{u}_{41} &= \frac{1}{2}(b_4 - \sqrt{b_4^2 - 4a_4}), \quad \bar{v}_{41} = b_4\bar{u}_{41}(k_4 - \bar{u}_{41})/k_4, & \text{if } k_4 > \bar{u}_{41} \\ \bar{u}_{42} &= \frac{1}{2}(b_4 + \sqrt{b_4^2 - 4a_4}), \quad \bar{v}_{42} = b_4\bar{u}_{42}(k_4 - \bar{u}_{42})/k_4, & \text{if } k_4 > \bar{u}_{42}. \end{aligned} \quad (17)$$

When  $\bar{\mathbf{u}} = (\bar{u}, \bar{v})$  is a positive solution to  $\mathbf{G}_4(\mathbf{u}) = 0$ , we have  $a_4 + \bar{u}^2 = b_4\bar{u}$  and  $\bar{v} = b_4\bar{u}(1 - \bar{u}/k_4)$ . Then

$$\begin{aligned} \mathbf{G}_{4\mathbf{u}}(\bar{\mathbf{u}}) &= \begin{bmatrix} 1 - 2\frac{\bar{u}}{k_4} - \frac{\bar{v}}{a_4 + \bar{u}^2} + 2\frac{\bar{u}^2\bar{v}}{(a_4 + \bar{u}^2)^2} & -\frac{\bar{u}}{a_4 + \bar{u}^2} \\ \bar{v}\left(\frac{b_4}{a_4 + \bar{u}^2} - 2\frac{b_4\bar{u}^2}{(a_4 + \bar{u}^2)^2}\right) & \frac{b_4\bar{u}}{a_4 + \bar{u}^2} - 1 \end{bmatrix} \\ &= \begin{bmatrix} \frac{2\bar{u}}{b_4k_4}(k_4 - \bar{u} - b_4/2) & -\frac{1}{b_4} \\ (k_4 - \bar{u})(b_4 - 2\bar{u})/k_4 & 0 \end{bmatrix}. \end{aligned} \quad (18)$$

So  $g_{11} = \frac{2\bar{u}}{b_4k_4}(k_4 - \bar{u} - b_4/2)$ ,  $g_{21} = (k_4 - \bar{u})(b_4 - 2\bar{u})/k_4$ ,  $g_{12} = -\frac{1}{b_4} < 0$ , and  $g_{22} = 0$ . By Lemma 2.1 and similar arguments as in the proofs of above theorems, we have the following results for Holling type-IV functional response.

**Theorem 2.6.** For  $i = 4$ , we consider the predator-prey model (7) with Holling type-IV functional response (6).

- (A<sub>1</sub>) Suppose  $\bar{u}_{41} < k_4 < \bar{u}_{41} + b_4/2$ . Then the equilibrium solution  $(\bar{u}_{41}, \bar{v}_{41})$  is linearly stable with respect to both the ODE system (8) and the PDE system (7).
- (A<sub>2</sub>) Suppose  $\bar{u}_{41} + b_4/2 < k_4 < \bar{u}_{42}$ . Then  $(\bar{u}_{41}, \bar{v}_{41})$  is the only equilibrium solution and it is linearly unstable with respect to the ODE system (8). For fixed  $d_1, d_3, d_4$ , there exists a large  $D_2$  such that the positive equilibrium solution is linearly unstable for the PDE system (7) when  $d_2 > D_2$ .
- (A<sub>3</sub>) Suppose  $\bar{u}_{42} < k_4$ . Then  $(\bar{u}_{42}, \bar{v}_{42})$  is linearly unstable with respect to the ODE system (8). For fixed  $d_1, d_2, d_4$ , there exists a large  $D_3$  such that the positive equilibrium solution is linearly unstable for the PDE system (7) when  $d_3 > D_3$ .

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