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Stability analysis of predator–prey models involving cross-diffusion

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HIGHLIGHTS

- Models with two predators competing for a prey involving cross-diffusion are developed.
- Cross-diffusion accounts predators' migratory strategies and prey's defense switching.
- The models possess a continuum of equilibria unlike as in models of many real world applications.
- The analysis reveals occurrence of unsustainable zip bifurcation as Turing instability emerges.
- As switching migratory efforts are not instantaneous models involving delays have been included.

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ABSTRACT

In this paper we have considered a three dimensional system of partial differential equations to model the dynamical interactions of two predators competing for a single prey. The model is developed by introducing cross diffusion in such a way as to take into account the migratory strategy adopted by the predators, who take advantage of the defense switching behavior of the prey. Equilibria of the model are determined and a local stability analysis is discussed. The main result presented here is that for certain range of values of the cross diffusion parameters, the system has a continuum of equilibria and a *zip-type bifurcation* occurs and this is not sustainable due to the emergence of Turing type instability.

1. Introduction

Spatial ecology addresses the fundamental effects of space on the dynamics of individual species and on the structure, dynamics, diversity, and stability of multi species communities. Essentially, this subject is designed to highlight the importance of space in the areas of stability, patterns of diversity, invasions, coexistence, and pattern generation. The mathematical formulation of the ideas dealing with the spacial aspect of species leads to reaction–diffusion models. Reaction–diffusion systems have attracted much attention as prototype models for pattern formation. The above-mentioned patterns (fronts, spirals, targets, hexagons, stripes, and dissipative solitons) may be found in various types of reaction–diffusion systems in spite of large discrepancies in the local reaction terms. It has also been argued that reaction–diffusion processes are an essential basis for those connected with animal coats and skin pigmentation [1,2]. Another reason for the interest in reaction–diffusion systems is that although they represent nonlinear partial differential equations, often there exists scope for analytical treatment.

All beings, including different kinds of populations live in a spatial world and it is a natural phenomenon that a substance goes from high-density regions to low-density regions. As a result, more and more scholars use spatial artifacts to model the interactions between the prey and the predator species. In a natural setting when populations diffuse/migrate from one environment to another, they are often subject to unfavorable conditions. Naturally, predation will obligate the individuals of populations to follow defense strategies as, for example, to diffuse in the direction of lower concentrations of its predators. As a consequence, the predators also will develop some strategies to take advantage of the defense switching of the prey, looking at the migration of the prey and diffusing in that direction. In general, the escape velocity of the prey may be taken as proportional to the dispersive velocity of the predators. Also, the tendency

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of predators would be to get closer to the prey and thus the chase velocity of predators may be considered to be proportional to the dispersive velocity of the prey. This phenomenon is known as *cross-diffusion* [3]. As the predators cross diffuse, and the preys switch their defense, we might expect such an ecosystem to exhibit a rich dynamical interplay among the three species.

In this paper, we study an ecosystem consisting of two predators competing for one single prey. In such a system, we might expect the prey to develop two separate sets of defensive capabilities, one effective against each of the predators, and would switch from one set to the other depending on the relative abundance of the two predator species. Such defense switching behavior has been described, for example, for a fish species in the Lake Tanganyika against two phenotypes of the scale-eating cichlid P. microlepis [4]. On the other hand, we might also expect the predators to develop migratory strategies to take advantage of the defense switching behavior of the prey. In the present work this is indeed the case. The purpose of this paper is to investigate such a migration which involves cross-diffusion process. In particular, we will demonstrate the emergence of *Turing instability*. For a detailed discussion and examples on cross-diffusion models describing real world phenomena, we refer the readers to [1–3,5–9].

Turing instability [8] refers to "diffusion-driven instability", in the sense that the stationary solution stays stable with respect to a kinetic system (a system without diffusion) but becomes unstable with respect to the system with diffusion. This phenomenon is interesting because the general experience is that diffusion is a uniform phenomenon that helps stability by evening out differences, and now the opposite happens, and it is also of interest because Turing instability may go together with the occurrence of a spatially non constant stationary solution, which is called a *pattern*.

In a recent study on a model describing the interactions of two predator species competing for one prey [10,11], under certain natural assumptions, it has been observed that the model system admits a one dimensional continuum of equilibria leading to, what is described as a zip bifurcation phenomenon. In this model, a predator that has relatively low growth rate and survives at low carrying capacity K is identified as a k-strategist while the other predator that exhibits high growth rate is identified as an r-strategist. The model is not structurally stable however, it serves as an illustration to the intuitively evident fact that at low values of the carrying capacity K, both predators might survive but as K grows the k-strategist loses ground and only the r-strategist may survive with the prey. Subsequently a whole class of models that showed the zip phenomenon are proposed and are analyzed in the literature (see [12–18]). Interestingly enough, in all the above studies, the zip bifurcation is sustainable even in the presence of self diffusion.

This paper is organized as follows. In Section 2 we present the Models I and II and determine the equilibria. The analysis of equilibria for Model I is carried in Section 3, while Section 4 deals with Turing instability and zip bifurcation for the cross diffusion Model II. A discussion follows in Section 5.

2. Models and equilibria

Consider the following ODE system [10]

$$\begin{cases} \dot{S} &= \gamma(1-\dfrac{S}{K})S - m_1\dfrac{S}{a_1+S}u_1 - m_2\dfrac{S}{a_2+S}u_2 \\ \dot{u_1} &= m_1\dfrac{S}{a_1+S}u_1 - d_1u_1 \\ \dot{u_2} &= m_2\dfrac{S}{a_2+S}u_2 - d_2u_2, \end{cases} \tag{1}$$

in which $u=(S,u_1,u_2)$ and S is the population density of the prey, and u_i, $\quad i=1,2$, are the population densities of two predators competing for the prey. In this model, $K>0$ denotes the carrying capacity of the environment with respect to the prey, $\gamma>0$ is the intrinsic growth rate of the prey, m_i, d_i, a_i are non negative parameters and represent the maximum birth rate, the death rate and the "half saturation constant", respectively, of the ith predator.

Apart from the trivial equilibrium solutions $(S,u_1,u_2)=(0,0,0)$ and $(S,u_1,u_2)=(K,0,0)$, system (1) has biologically interesting equilibria only if $m_i>d_i$ and $\lambda=\lambda_1=\lambda_2$, where $\lambda_i=\frac{a_id_i}{m_i-d_i}$ is the prey quantity threshold for predators $i=1,2$. Thus, it follows that "non-trivial" equilibrium points of (1) belong to the straight line segment

$$\begin{aligned} L_K \;=\; \Big\{ & \big(S,u_1,u_2\big)\in R^3;\;\; S=\lambda,\;\; u_1\geq 0,\;\; u_2\geq 0 \;\text{ and} \\ & m_1\frac{S}{a_1+S}u_1+m_2\frac{S}{a_2+S}u_2=\gamma(1-\frac{\lambda}{K}) \Big\} \end{aligned} \tag{2}$$

in the positive octant of the S, u_1, u_2-space, which will be denoted by $u^*=(\lambda,\xi_1,\xi_2)$. Hence $u^*\in L_K$.

It is easy to see that the trivial equilibria $(0,0,0)$ and $(K,0,0)$ are unstable provided $0<\lambda<K$ (see [10] for details). It is clear that all equilibria on L_K are stable for all K that satisfy the inequality $\lambda<K\leq a_2+2\lambda$. This means that if food is scarce both the r and k-strategists may live together in the long run in a steady state that depends on the initial values of the species. When $a_2+2\lambda<K<a_1+2\lambda$ (i.e., when $a_1>a_2$) the family of equilibria on the line L_K undergoes a split and a part of L_K is unstable; that is, there exists a point $(\lambda,\xi_1(K),\xi_2(K))$ on L_K such that the equilibria on

$$L_U=\big\{(\lambda,\xi_1,\xi_2)\in L_K:\xi_1<\xi_1(K)\big\}$$

are unstable for the flow of (13) and the equilibria on

$$L_S=\big\{(\lambda,\xi_1,\xi_2)\in L_K:\xi_1>\xi_1(K)\big\}$$

are stable. The point $(\xi_1(K),\xi_2(K))$ is obtained by solving the system

$$\begin{cases} \dfrac{m_1\xi_1}{a_1+\lambda}+\dfrac{m_2\xi_2}{a_2+\lambda} &= \dfrac{\gamma(K-\lambda)}{K} \\ \dfrac{m_1\xi_1}{(a_1+\lambda)^2}+\dfrac{m_2\xi_2}{(a_2+\lambda)^2} &= \dfrac{\gamma}{K}. \end{cases} \tag{3}$$

As K takes on the value $a_1+2\lambda$ the equilibrium that exists in (S,u_1)-plane is stable while all other equilibria on L_K lose stability. When $K>a_1+2\lambda$ all equilibria on L_K become unstable.

Note that as K increases from $a_2+2\lambda$ to $a_1+2\lambda$ the point $(\lambda,\xi_1(K),\xi_2(K))$ moves along L_K continuously from $(\lambda,0,\xi_2(K))$ to $(\lambda,\xi_1(K),0)$ so that the points left behind become unstable. This phenomenon has been termed as *zip bifurcation* (see [10,19]). From the point of view of the competition, as the quantity of available food increases the K-strategist loses ground and those equilibria where the relative growth of K-strategist is high compared to the growth of r-strategist, are the first to be destabilized. When K reaches the value $a_1+2\lambda$ all interior equilibria become destabilized and the only stable equilibrium remaining is the endpoint of L in the (S,u_1)-plane. This means that at this value of the carrying capacity the K-strategist dies out. One may prove that if K is increased further then even the equilibrium in the (S,u_1)- plane gets destabilized but the prey and the r-strategist continue to coexist in a periodic manner due to the occurrence of Andronov–Hopf bifurcation. For a complete discussion of the zip bifurcation phenomenon we refer the readers to [10,11,19,20].

It is worth noting that in [18] the authors incorporated discrete delay and self-diffusion on model (1). They showed that the zip bifurcation is "unsustainable" for certain ranges of values of the time-delay parameter. Also, for the delay reaction–diffusion model, they showed that the zip bifurcation remains unsustainable. The results obtained in [18] are surprising, since the *zip phenomenon* is sustainable in the whole class of models studied previously. Furthermore, the dynamic interaction described by the models studied in [18] is highly desirable, as it will facilitate coexistence among the species. We also observe that time delay and cross-diffusion are not incorporated yet in model (1).

Our interest in this work is to consider a modified version of the system (1) that models the spatial segregation phenomena of the competing species. It is important to observe that the proposed system connects two particular cases depending on the values of the parameters: the coupled system of partial differential equations describes spatial segregation phenomena of the competing species connecting self-diffusion and cross-diffusion. The main result presented herein is that for certain range of values of the cross-diffusion parameter, a *zip-type bifurcation* may not sustain for the cross-diffusion model due to the emergence of Turing instability. Accordingly, we consider the system

$$-\,div\big(k(u)\nabla u\big)=G(u)\quad\text{in}\quad \Omega. \tag{4}$$

where $\Omega\subset\mathbb{R}^N$ $(N\geq 1)$ is an open connected bounded domain with smooth boundary $\partial\Omega$. Eq. (4) is equivalent to the following system of equations

$$\begin{aligned}-div\big(k(u)\nabla u\big) &= \begin{pmatrix}\nabla.\big(k_{11}\nabla S+k_{12}\nabla u_1+k_{13}\nabla u_2\big)\\ \nabla.\big(k_{21}\nabla S+k_{22}\nabla u_1+k_{23}\nabla u_2\big)\\ \nabla.\big(k_{31}\nabla S+k_{32}\nabla u_1+k_{33}\nabla u_2\big)\end{pmatrix}\\ &= \begin{pmatrix}\gamma(1-\dfrac{S}{K})S-m_1\dfrac{S}{a_1+S}u_1-m_2\dfrac{S}{a_2+S}u_2\\ m_1\dfrac{S}{a_2+S}u_1-d_1u_1\\ m_2\dfrac{S}{a_2+S}u_2-d_2u_2\end{pmatrix},\end{aligned} \tag{5}$$

where $k_{ij}=k_{ij}(u)$, $u=(S,u_1,u_2)$, $i,j=1,2,3$. We will assume that the functions S and u_i satisfy the Neumann boundary conditions

$$\frac{\partial S}{\partial\nu}(x,t)=0,\ \ \frac{\partial u_i}{\partial\nu}(x,t)=0,\quad i=1,2,\quad\text{on}\ \ \partial\Omega\times[0,\infty), \tag{6}$$

where $\nu=\vec{\nu}(x)$ denotes the outer unit normal to $\partial\Omega$. The function $G(u)$ is defined as

$$G(u)=\left(\gamma(1-\frac{S}{K})S-m_1\frac{S}{a_1+S}u_1-m_2\frac{S}{a_2+S}u_2,\,m_1\frac{S}{a_2+S}u_1-d_1u_1,\,m_2\frac{S}{a_2+S}u_2-d_2u_2\right)$$

and $k(u)=(k_{ij}(u))_{3\times 3}$ is a 3×3 matrix. In general ([3], p. 300), the diffusion coefficients may be positive, negative or zero. In the present model, we assume that these coefficients $k_{ij}(u)$ satisfy

$$k_{11},k_{22},k_{33}>0,\quad k_{12},k_{13}\geq 0\ \ \text{and}\ \ k_{21},k_{23},k_{31},k_{32}\leq 0. \tag{7}$$

The variables and parameters in (4) have the same meaning as in the model (1).

In the model (4), $J_0=-k_{11}(u)\nabla S-k_{12}(u)\nabla u_1-k_{13}(u)\nabla u_2$, $J_1=-k_{21}(u)\nabla S-k_{22}(u)\nabla u_1-k_{23}(u)\nabla u_2$ and $J_2=-k_{31}(u)\nabla S-k_{32}(u)\nabla u_1-k_{33}(u)\nabla u_2$ indicate the population fluxes of S, u_1 and u_2, respectively, where the terms $k_{11}(u)$, $k_{22}(u)$ and $k_{33}(u)$ represent the *"self-diffusion"* while the terms $k_{ij}(u)$, $i\neq j$, correspond to the *"cross-diffusion"*.

The conditions $k_{1j}(u)\geq 0$, $j=2,3$, imply that the part $-k_{12}(u)\nabla u_1-k_{13}(u)\nabla u_2$ of the flux of S is directed towards decreasing population density of u_j, that is, the prey S runs away from the predators. On the other hand, the conditions $k_{2j}(u)\leq 0$, $j=1,3$, imply that the part $-k_{21}(u)\nabla S-k_{23}(u)\nabla u_2$ of the flux of u_1 is directed towards the increasing population density of S and u_2, which means that the predator u_1 moves in anticipation of the predator u_2 and of the defense switching behavior of the prey S, that is, u_1 chases the prey. Analogously, the conditions $k_{3j}(u)\leq 0$, $j=1,2$, imply that the part $-k_{31}(u)\nabla S-k_{32}(u)\nabla u_1$ of the flux of u_2 is directed towards increasing population density of S and u_1, which means that the predator u_2 moves in anticipation of the predator u_1 and of the defense switching behavior of the prey S, that is, u_2 chases the prey. A more detailed discussion may be found in [3,21]. Thus, in order to discuss the *diffusion-driven instability* considering the strategy adopted by the predators taking advantage of the defense switching behavior of the prey, we will introduce a cross-diffusion among the species in the model (1). Noting that the relationship between the two predators in (1) is competitive, we shall introduce the cross-diffusion terms as follows:

Model I:

$$\begin{cases} -div\ (\ \delta_0 \nabla S\ ) & = \ \gamma(1-\dfrac{S}{K})S - m_1\dfrac{S}{a_1+S}u_1 - m_2\dfrac{S}{a_2+S}u_2 \\ -div\left[(\delta_1 + \dfrac{k_1}{a_1+u_2})\nabla u_1 - \dfrac{k_1u_1}{(a_1+u_2)^2}\nabla u_2\right] & = \ (m_1\dfrac{S}{a_1+S} - d_1)u_1 \\ -div\left[(\delta_2 + \dfrac{k_2}{a_2+u_1})\nabla u_2 - \dfrac{k_2u_2}{(a_2+u_1)^2}\nabla u_1\right] & = \ (m_2\dfrac{S}{a_2+S} - d_2)u_2 \quad \text{on} \quad \Omega\times[0,\infty) \end{cases} \tag{8}$$

with Neumann boundary conditions

$$\frac{\partial S}{\partial \nu}(x,t) = 0, \ \ \frac{\partial u_i}{\partial \nu}(x,t) = 0, \quad i = 1,2, \quad \text{on} \ \ \partial\Omega\times[0,\infty). \tag{9}$$

Remark 1. In the system (8), k_1 and k_2 denote the *cross-diffusion coefficients*. The predators u_1, and u_2 diffuse with flux

$$J_1 = -(\delta_1 + \frac{k_1}{a_1+u_2})\nabla u_1 + \frac{k_1u_1}{(a_1+u_2)^2}\nabla u_2.$$

We observe that, as $\frac{k_1u_1}{(a_1+u_2)^2} \geq 0$, the part $\frac{k_1u_1}{(a_1+u_2)^2}\nabla u_2$ of the flux of u_1 is directed towards the increasing population density of the predator u_2. In this way, the first predator moves in anticipation of the predator u_2 and of the defense switching behavior of the prey. Similarly, we can observe that the flux of u_2 is directed towards the increasing population density of the predator u_1 so that the second predator also moves in anticipation of predator u_1 and of the defense switching behavior of the prey, which shows the competition between the two predators.

As a starting point in this exposition, we consider the one dimensional form of the system (8)–(9) by letting $\Omega = [0,l]$, l a fixed constant. Accordingly, the corresponding system assumes the form given by

$$\begin{cases} S_t = \delta_0\Delta S + \gamma(1-\dfrac{S}{K})S - m_1\dfrac{S}{a_1+S}u_1 - m_2\dfrac{S}{a_2+S}u_2 \\ u_{1t} = \Delta\big(\delta_1u_1 + \dfrac{k_1u_1}{a_1+u_2}\big) + (m_1\dfrac{S}{a_1+S} - d_1)u_1 \\ u_{2t} = \Delta\big(\delta_2u_2 + \dfrac{k_2u_2}{a_2+u_1}\big) + (m_2\dfrac{S}{a_2+S} - d_2)u_2, \\ \\ S_x = u_{1x} = u_{2x} = 0, \quad \text{on} \ \ [0,l]\times[0,\infty). \end{cases} \tag{10}$$

or equivalently

$$\begin{cases} u_t = K(u)u_{xx} + F(u,u_x), \\ u_x = 0, \quad \text{on} \ \ [0,l]\times[0,\infty). \end{cases} \tag{11}$$

where $[0,l] \subset \mathbb{R}$ is an interval of $\mathbb{R}$ with $l \in \mathbb{R}^+$, $u_x = (S_x, u_{1x}, u_{2x})^T$, $u_{xx} = (S_{xx}, u_{1xx}, u_{2xx})^T$,

$$K(u) = \begin{pmatrix} \delta_0 & 0 & 0 \\ 0 & \delta_1 + \dfrac{k_1}{a_1+u_2} & -\dfrac{k_1u_1}{(a_1+u_2)^2} \\ 0 & -\dfrac{k_2u_2}{(a_2+u_1)^2} & \delta_2 + \dfrac{k_2}{a_2+u_1} \end{pmatrix},$$

$$\begin{aligned} F(u,u_x) \ =& \Bigg(\ \gamma(1-\frac{S}{K})S - m_1\frac{S}{a_1+S}u_1 - m_2\frac{S}{a_2+S}u_2, \ \ m_1\frac{S}{a_1+S}u_1 - d_1u_1 + 2\frac{k_1u_1}{(a_1+u_2)^3}\nabla u_2^2 \\ & -2\frac{k_1}{(a_1+u_2)^2}\nabla u_1\nabla u_2, m_2\frac{S}{a_2+S}u_2 - d_2u_2 + 2\frac{k_2u_2}{(a_2+u_1)^3}\nabla u_1^2 - 2\frac{k_2}{(a_2+u_1)^2}\nabla u_1\nabla u_2 \ \Bigg), \end{aligned}$$

and $\Delta = \sum_{j=1}^{N} \frac{\partial}{\partial x_j}$ is the Laplacian operator.

Model II:

Keeping $\Omega = [0, l]$ and l fixed, we also consider a study of the one dimensional form of the system (5)–(6). The corresponding system is given by

$$\begin{cases} S_t = \Delta\big(k_{11}S + k_{12}u_1 + k_{13}u_2\big) + \gamma(1 - \dfrac{S}{K})S - m_1\dfrac{S}{a_1+S}u_1 - m_2\dfrac{S}{a_2+S}u_2 \\ u_{1t} = \Delta\big(k_{21}S + k_{22}u_1 + k_{23}u_2\big) + (m_1\dfrac{S}{a_1+S} - d_1)u_1 \\ u_{2t} = \Delta\big(k_{31}S + k_{32}u_1 + k_{33}u_2\big) + (m_2\dfrac{S}{a_2+S} - d_2)u_2, \\ S_x = u_{1x} = u_{2x} = 0, \quad \text{on} \quad [0, l] \times [0, \infty), \end{cases} \tag{12}$$

where k_{ij}, $i, j = 1, 2, 3$ are constants.

We notice that the equilibria for Models I and II are $(S, u_1, u_2) = (0, 0, 0)$, $(S, u_1, u_2) = (K, 0, 0)$ and those described in Eq. (2).

Remark 2. The corresponding system associated with the system (5) was considered in [17] when $k_{i,j} \neq 0$ for $i = j$ and $k_{i,j} = 0$ for $i \neq j$. The results obtained in [17] suggest that, if there is no cross-diffusion included in system (1), then *diffusion-driven instability* can not happen and the zip bifurcation phenomenon is sustainable regardless of the self diffusion coefficients. The maim aim of this paper is to show that the zip bifurcation is sustainable for system (10) and that *diffusion-driven instability* emerges for system (12). We also establish that the conditions $k_{11}, k_{22}, k_{33}, k_{12}, k_{13} > 0$ and $k_{21}, k_{31}, k_{23}, k_{32} < 0$, are sufficient for the occurrence of the *diffusion-driven instability* for system (12).

3. Analysis of equilibria for Model I on the line L_K

In the following, we consider the cross-diffusion model (10) and determine the stability properties of the equilibria $u^* = (\lambda, \xi_1, \xi_2)$. Observe that

$$K(u^*) = \begin{pmatrix} \delta_0 & 0 & 0 \\ 0 & \delta_1 + \dfrac{k_1}{a_1+\xi_2} & -\dfrac{k_1\xi_1}{(a_1+\xi_2)^2} \\ 0 & -\dfrac{k_2\xi_2}{(a_2+\xi_1)^2} & \delta_2 + \dfrac{k_2}{a_2+\xi_1} \end{pmatrix}$$

and

$$F_u(u^*, 0) = G_u(u^*) = \begin{pmatrix} -\dfrac{\gamma\lambda}{K} + \lambda\displaystyle\sum_{i=1}^{2}\dfrac{m_i}{(a_i+\lambda)^2}\xi_i & -\dfrac{m_1\lambda}{a_1+\lambda} & -\dfrac{m_2\lambda}{a_2+\lambda} \\ \dfrac{\beta_1\xi_1}{a_1+\lambda} & 0 & 0 \\ \dfrac{\beta_2\xi_2}{a_2+\lambda} & 0 & 0 \end{pmatrix},$$

where $\beta_i = m_i - d_i$ since $\lambda = \frac{a_i d_i}{m_i - d_i}$, $i = 1, 2$. Hence, the linearized system of (11) at u^* is given by

$$\begin{cases} \psi_t = K(u^*)\psi_{xx} + G_u(u^*)\psi, \quad 0 < x < l, \quad t \geq 0 \\ \psi_x = 0, \quad x = 0, l, \quad t \geq 0, \end{cases} \tag{13}$$

where $\psi = (\psi_1, \psi_2, \psi_3)^T$.

Let $0 = \mu_0 < \mu_1 < \mu_2 < \cdots \to \infty$ and $\{\phi_j\}_{j=0}^{\infty}$ be the eigenvalues and eigenfunctions of the Laplacian operator in $(0, l)$ with Neumann boundary, i.e., :

$$\phi_j''(x) = \mu_j\phi_j(x) \text{ on } \quad (0, l), \quad \phi_j'(x) = 0 \quad \text{at } x = 0, l, \tag{14}$$

where $\mu_j = \frac{j^2\pi^2}{l^2}$, $j = 0, 1, 2, \ldots$. We can assume that $\{\phi_j\}_{j=0}^{\infty}$ is an orthonormal basis of $L^2(\Omega)$.

So, the solution of (13) with initial condition $u(\cdot, 0) = u_0$ is given by

$$u(x, t) = \sum_{k=0}^{\infty} e^{(G_u(u^*) - \mu_j K(u^*))t}\langle u_0, \phi_k\rangle\phi_k(x), \tag{15}$$

where $\langle u_0, \phi_j\rangle = \int_0^l u_0(x)\phi_j(x)\,dx$.

It follows from the linearization principle that a 'non-trivial' homogeneous solution of (11) is asymptotically stable if the eigenvalues of the matrix $G_u(u^*) - \mu_j K(u^*)$ have negative real parts; if there exists a $k \geq 1$ such that $G_u(u^*) - \mu_j K(u^*)$ has an eigenvalue with positive real part then the solution is unstable. Note that for $\mu_0 = 0$ the matrix $G_u(u^*)$ has zero as an eigenvalue of multiplicity 1 and two eigenvalues with positive (resp. negative) real part according as

$$\frac{m_1\xi_1}{(a_1+\lambda)^2} + \frac{m_2\xi_2}{(a_2+\lambda)^2} > \frac{\gamma}{K} \quad \text{or} \quad < \frac{\gamma}{K}. \tag{16}$$

The following result is an immediate consequence of this note.

Proposition 1. *If $K > a_1 + 2\lambda$, then all equilibria on L_K are unstable.*

Now, if u^* is an unstable equilibrium for the flow of (1) then u^* is also an unstable homogeneous equilibrium for the flow of (11), since the subspace of the functions independent of x is invariant for the flow of (11). The next theorem shows that if u^* is stable for the flow of (1) then u^* may not be stable for the flow of (11).

To simplify the computations, we introduce the notations

$$a = \lambda \sum_{i=1}^{2} \frac{m_i \xi_i}{(a_i+\lambda)^2} - \frac{\gamma\lambda}{K}, \qquad b = \frac{\beta_1 \xi_1}{a_1+\lambda}, \qquad c = \frac{\beta_2\xi_2}{a_2+\lambda}, \qquad d = -\frac{m_1\lambda}{a_1+\lambda},$$

$$e = -\frac{m_2\lambda}{a_2+\lambda}, \qquad f = \mu_j \frac{k_2\xi_2}{(a_2+\xi_1)^2}, \qquad g = \mu_j \frac{k_1\xi_1}{(a_1+\xi_2)^2}.$$

The following result presents the conditions under which the PDE system (11) and its corresponding ODE system (1) share the same stability behavior.

Theorem 1. *Suppose that u^* is an equilibrium of (11) independent of x. If u^* is stable for the flow of (1), then u^* will be stable for the flow of (11).*

Proof. Let $u^* = (\lambda, \xi_1, \xi_2)$ be an equilibrium of (11) independent of x. The hypothesis that u^* is stable for (1) is equivalent to

$$\frac{m_1\xi_1}{(a_1+\lambda)^2} + \frac{m_2\xi_2}{(a_2+\lambda)^2} < \frac{\gamma}{K} \tag{17}$$

so that the condition (17) implies that $a < 0$.

We denote by $P_k(\nu)$ the characteristic polynomial of $G_u(u^*) - \mu_j K(u^*)$. For each $k \geq 0$, the eigenvalues of $G_u - \mu_j K$ are the roots of the polynomial

$$P_j(\nu) = \nu^3 + A_j\nu^2 + B_j\nu + C_j, \tag{18}$$

The complete expressions for A_j, B_j and C_j are presented in Item 1, Appendix.

Since $a < 0$, we have $A_j > 0$, $B_j > 0$ and $C_j > 0$, for all $j \geq 1$. At $j = 0$, the polynomial

$$P_0(\nu) = \nu^3 - a\nu^2 + h\nu,$$

where $h = \frac{\beta_1\xi_1 m_1\lambda}{(a_1+\lambda)^2} + \frac{\beta_2\xi_2 m_2\lambda}{(a_2+\lambda)^2}$, has zero as a single eigenvalue and two complex conjugates with negative real parts. We claim that, for any $j \geq 1$, all eigenvalues of $G_u(u^*) - \mu_j K(u^*)$ have negative real parts. This will follow from Routh–Hurwitz's criterion if we show that $A_jB_j > C_j$, for any $j \geq 1$. To prove this, some tedious calculations were carried out using MAPLE 13, as follows. We consider the function $A_jB_j - C_j = (A_jB_j - C_j)(\mu_j)$ whose expression is presented in Item 2, Appendix, where $\mu_j > 0$ for any $j \geq 1$. Since $a < 0$, the graphs of the function $(A_jB_j - C_j)(\mu_j)$ intersect the ordinate axis at a positive point and it is strictly increasing for $\mu_j \geq 0$. In fact, the derivative of $(A_jB_j - C_j)(\mu_j)$ with respect to μ_j is a quadratic function whose graph is a parabola concave upwards since

$$\begin{aligned} E = &\left(\delta_1 + \frac{k_1}{a_1+\xi 2} + \delta_2 + \frac{k_2}{a_2+\xi_1} + \delta_0\right)\Bigg[\left(\delta_1 + \frac{k_1}{a_1+\xi_2}\right)\left(\delta_2 + \frac{k_2}{a_2+\xi_1}\right) + \left(\delta_1 + \frac{k_1}{a_1+\xi_2}\right)\delta_0 \\ &+ \left(\delta_2 + \frac{k_2}{a_2+\xi_1}\right)\delta_0 - \frac{k_2\xi_2\, k_1\xi_1}{(a_2+\xi_1)^2(a_1+\xi_2)^2}\Bigg] - \left(\delta_1 + \frac{k_1}{a_1+\xi_2}\right)\left(\delta_2 + \frac{k_2}{a_2+\xi_1}\right)\delta_0 \\ &+ \frac{k_2\xi_2\, k_1\xi_1\, \delta_0}{(a_2+\xi_1)^2(a_1+\xi_2)^2} > 0 \end{aligned} \tag{19}$$

(see Item 3, Appendix).

Furthermore, the parabola intersects the ordinate axes at a positive point (see Item 4, Appendix). Hence, u^* is stable due to the Routh–Hurwitz's criterion, the Rouché's Theorem and the results of Henry [22] p. 108, as in [17] (see Theorem 4.3, p. 51). □

Theorem 1 may be viewed as a result on the preservation of stability under self-diffusion for prey population and cross-diffusion for both predator populations for Model I. As a consequence, if $\lambda < K < a_2 + 2\lambda$, the line of equilibrium points L_K of (1) is locally asymptotically stable for the flow of (11). If $K > a_1 + 2\lambda$, then L_K is unstable. We have the following corollary.

Corollary 1. *For any K satisfying $a_2 + 2\lambda \leq K \leq a_1 + 2\lambda$, the point $(\lambda, \xi_1(K), \xi_2(K))$ splits L_K in two parts L_K^u and L_K^s; the equilibria of (11) on the set*

$$L_K^u = \{(\lambda, \xi_1, \xi_2) \in L_K : \xi_1 < \xi_1(K)\}$$

are unstable and those on the set

$$L_K^s = \{(\lambda, \xi_1, \xi_2) \in L_K : \xi_1 > \xi_1(K)\}$$

are stable, regardless the cross-diffusion coefficients given in the system (11).

Remark 3. The result in Corollary 1 shows that the zip bifurcation phenomenon is sustainable even by the introduction of cross-diffusion in the model (1). In the following, we present an example to illustrate the result obtained in Theorem 1.

Example 1. We choose the following values of parameters in system (11) which contribute to the occurrence and sustainability of the zip bifurcation: $a_1 = 0.6$; $a_2 = 0.4$; $m_1 = 0.9$; $d_1 = 0.3$; $m_2 = 0.7$; $d_2 = 0.3$; $\beta_1 = m_1 - d_1 = 0.6$; $\beta_2 = m_2 - d_2 = 0.4$; $\gamma = 0.9$; $\lambda := 0.3$; $K := 1.1$; $k_1 = 0.3$; $k_2 = 0.4$; $\delta_0 = 0.5$; $\delta_1 = 0.6$; $\delta_2 = 0.8$. In this case we have that a stable constant solution of the system (11) should satisfy

$$\frac{m_1\xi_1}{a_1+\lambda} + \frac{m_2\xi_2}{a_2+\lambda} - \gamma\left(1-\frac{\lambda}{K}\right) = 0 \quad\text{and}\quad \frac{m_1\xi_1}{(a_1+\lambda)^2} + \frac{m_2\xi_2}{(a_2+\lambda)^2} < \frac{\gamma}{K} \qquad .$$

So, a stable constant solution of system (11) is given by

$$u^* = (\lambda, \xi_1, \xi_2) = (0.3, 0.4545, 0.2).$$

Note that,

$$a = \frac{m_1\xi_1}{(a_1+\lambda)^2} + \frac{m_2\xi_2}{(a_2+\lambda)^2} - \frac{\lambda\gamma}{K} = -0.0274170274.$$

Furthermore, we have:

$$A_j = 2.743085106\mu_j + 0.008225108220;\; B_j = 2.334583521\mu_j^2 + 0.01844961774\mu_j + 0.1251948052;$$

$$C_j = 0.6065204840\mu_j^3 + 0.009977393242\mu_j^2 + 0.1659734880\mu_j \text{ and}$$

$$A_jB_j - C_j = 5.797440801\mu_j^3 + 0.05983368050\mu_j^2 + 0.1775982676\mu_j + 0.001029740821.$$

In Fig. 1 we present the graphs of A_j, B_j, C_j and $A_jB_j - C_j$ as function of μ_j, $j = 1, 2, \ldots$. Note that, for $j = 1$ and $l = 5$ we get $\mu_1 = \frac{1^2 \times 3.1416^2}{5^2} = 0.3947860224$. Thus, we have $A_j > 0$, $B_j > 0$, $C_j > 0$ and $A_jB_j - C_j > 0$ for all $j = 1, 2, \ldots$, since $0 = \mu_0 < \mu_1 < \mu_2 < \cdots \to \infty$. Hence, by Theorem 1 if u^* is stable for the flow of the system (1) then u^* is stable for the flow of the system (11).

4. Turing instability and the zip bifurcation for Model II

The Turing instability [8] refers to "diffusion-driven instability," that is the stability of the constant equilibrium $u^* = (\lambda, \xi_1, \xi_2)$ changing from stability for the ODE system (1), to instability for the PDE system (12). In the following, we perform some calculations to find a criterion for the Turing instability.

In what follows, we discuss the Turing instability for the model (12) which depends on the cross-diffusion coefficients. Following the framework of the previous section we have

$$K(u^*) = \begin{pmatrix} k_{11} & k_{12} & k_{13} \\ k_{21} & k_{22} & k_{23} \\ k_{31} & k_{32} & k_{33} \end{pmatrix}$$

and

$$F_u(u^*, 0) = G_u(u^*) = \begin{pmatrix} -\frac{\gamma\lambda}{K} + \lambda\sum_{i=1}^{2}\frac{m_i}{(a_i+\lambda)^2}\xi_i & -\dfrac{m_1\lambda}{a_1+\lambda} & -\dfrac{m_2\lambda}{a_2+\lambda} \\ \dfrac{\beta_1\xi_1}{a_1+\lambda} & 0 & 0 \\ \dfrac{\beta_2\xi_2}{a_2+\lambda} & 0 & 0 \end{pmatrix},$$

where $\beta_i = m_i - d_i$, $i = 1, 2$ and k_{ij} are constants with $k_{11}, k_{22}, k_{33}, k_{12}, k_{13} \geq 0$ and $k_{21}, k_{31}, k_{23}, k_{32} \leq 0$.

In the next theorem we show that if u^* is stable for the flow of (1) then u^* may not be stable for the flow of (12).

Theorem 2. *Suppose that u^* is an equilibrium of (12) independent of x. Then, if u^* is stable for the flow of (1), u^* will be stable for the flow of (12) provided the inequality (22) below, holds for all $j = 1, 2, \ldots$. Further, the equilibrium u^* is unstable, if any of the below mentioned inequalities (23) or (24) holds for some $j = 1, 2, \ldots$.*

Proof. To simplify the computations, we introduce the notations

$$a = \lambda\sum_{i=1}^{2}\frac{m_i\xi_i}{(a_i+\lambda)^2} - \frac{\gamma\lambda}{K}, \qquad b = \frac{\beta_1\xi_1}{a_1+\lambda} - \mu_j k_{21}, \qquad c = \frac{\beta_2\xi_2}{a_2+\lambda} - \mu_j k_{31},$$

$$d = -\frac{m_1\lambda}{a_1+\lambda} - \mu_j k_{12}, \qquad e = -\frac{m_2\lambda}{a_2+\lambda} - \mu_j k_{13}.$$

Let $u^* = (\lambda, \xi_1, \xi_2)$ be an equilibrium of (12) independent of x. The hypothesis that u^* is stable for (1) is equivalent to

$$\frac{m_1\xi_1}{(a_1+\lambda)^2} + \frac{m_2\xi_2}{(a_2+\lambda)^2} < \frac{\gamma}{K} \tag{20}$$

so that the condition (20) implies that $a < 0$.

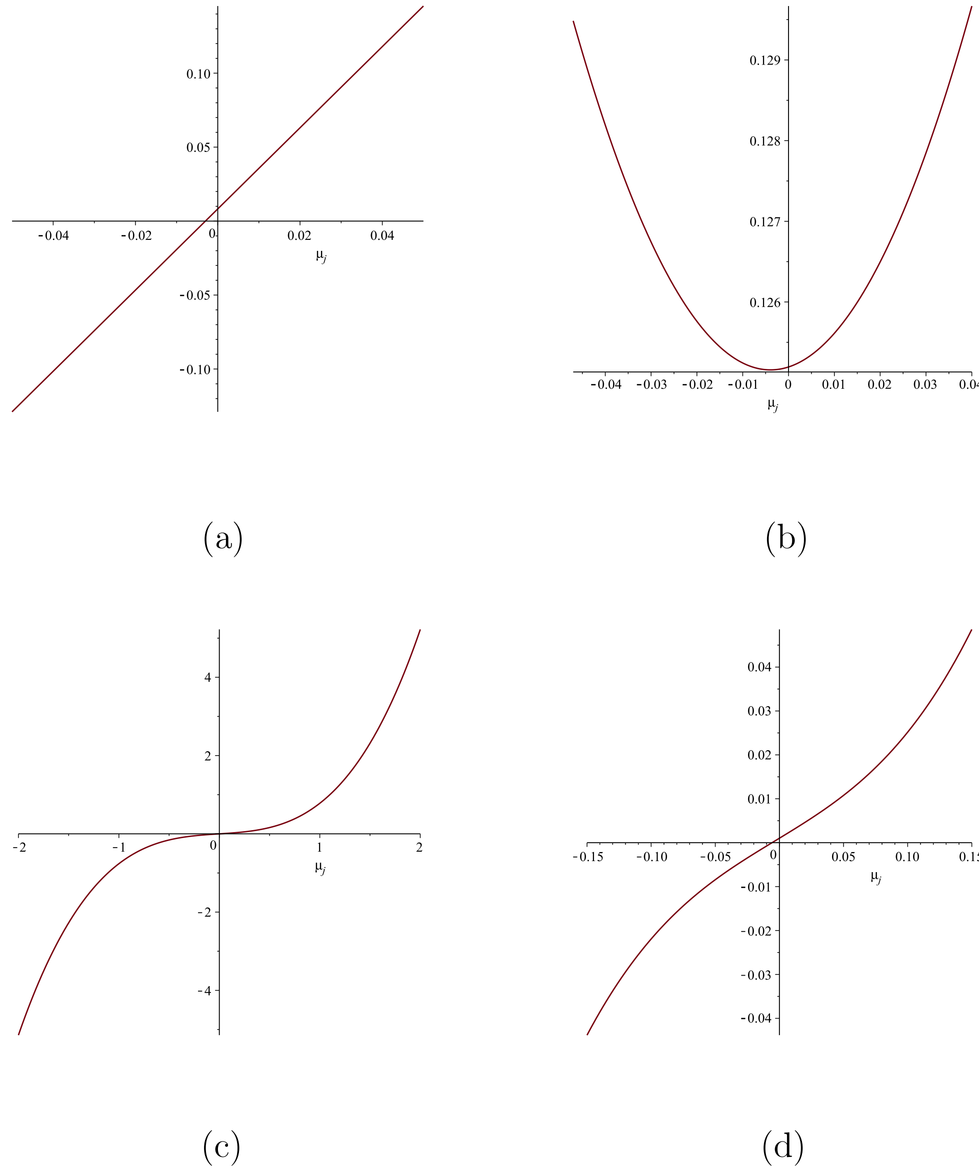

Fig. 1. Graphs of: (a) A_j, (b) B_j, (c) C_j and (d) $A_jB_j - C_j$, as functions of μ_j.

We denote by $P_k(\nu)$ the characteristic polynomial of $G_u(u^*) - \mu_j K(u^*)$. For each $k \geq 0$, the eigenvalues of $G_u - \mu_j K$ are the roots of the polynomial

$$P_j(\nu) = \nu^3 + A_j\nu^2 + B_j\nu + C_j, \tag{21}$$

The complete expressions for A_j, B_j and C_j are presented in Item 5, Appendix.

Since $a < 0$, we have $A_j > 0$, for all $j \geq 1$. On the other hand as $\frac{\beta_2\xi_2 m_2\lambda}{(a_2+\lambda)^2} + \frac{\beta_1\xi_1 m_1\lambda}{(a_1+\lambda)^2} > 0$, then if $k_{11}\big(k_{22}+k_{33}\big) - k_{12}k_{21} - k_{13}k_{31} + k_{22}k_{33} - k_{23}k_{32} < 0$ we have $B_j < 0$ for $\mu_j > 0$ big enough, otherwise if $k_{11}\big(k_{22}+k_{33}\big) - k_{12}k_{21} - k_{13}k_{31} + k_{22}k_{33} - k_{23}k_{32} > 0$ then $B_j > 0$ for all $j = 1, 2, 3\ldots$. Similarly, the coefficients of μ_j^2 and μ_j in the expression for C_j are positive since $a, k_{21}, k_{31}, k_{32}, k_{23} < 0$. So, if $\big(-k_{21}k_{33} + k_{23}k_{31}\big)k_{12} + \big(k_{22}k_{33} - k_{23}k_{32}\big)k_{11} + \big(k_{21}k_{32} - k_{22}k_{31}\big)k_{13} < 0$ then $C_j < 0$ for $\mu_j > 0$ big enough, otherwise if $\big(-k_{21}k_{33} + k_{23}k_{31}\big)k_{12} + \big(k_{22}k_{33} - k_{23}k_{32}\big)k_{11} + \big(k_{21}k_{32} - k_{22}k_{31}\big)k_{13} > 0$ then $C_j > 0$ for all $j = 1, 2, 3\ldots$. It is easy to see that the inequalities

$$A_j > 0, B_j > 0, C_j > 0 \text{ and } A_jB_j - C_j > 0 \tag{22}$$

ensure the stability of u^* while the equilibrium u^* is unstable if either of (23) or (24) holds for $j = 1, 2, \ldots$

$$A_j > 0, C_j > 0 \text{ and } B_j < 0 \tag{23}$$

$$A_j > 0, B_j < 0 \text{ and } C_j < 0. \tag{24}$$

We present the expression for $A_jB_j - C_j$ in Item 6, Appendix.

Thus, if u^* is stable for the flow of (1) u^* will be stable for the flow of (12) provided the inequality (22) holds for all $j = 1, 2, \ldots$. Further, the equilibrium u^* is unstable for the flow of (12), if any of the inequalities (23) or (24) holds for some $j = 1, 2, \ldots$. □

In Theorem 2 we observe that the stability of the equilibria for Model II is not preserved as in the case of Model I (Theorem 1), which may be due to the introduction of cross-diffusion in all interacting populations.

Corollary 2. *Suppose that u^* is an equilibrium of (12) independent of x. Moreover, suppose that one of the conditions (23)–(24) holds. Then If u^* is stable for the flow of (1), u^* may not be stable for the flow of (12).*

Remark 4. This final result shows that the Turing instability may emerge upon the introduction of cross-diffusion in the model (1) and the zip bifurcation phenomenon may not sustain.

Choosing the following values of parameters which contribute to the occurrence of zip bifurcation, we present some examples illustrating the results obtained in Theorem 2.

Example 2. Consider the following values of parameters in the system (12): $a_1 = 0.6$; $a_2 = 0.4$; $m_1 = 0.9$; $d_1 = 0.3$; $m_2 = 0.7$; $d_2 = 0.3$; $\gamma = 0.9$; $\beta_1 = m_1 - d_1 = 0.6$; $\beta_2 = m_2 - d_2 = 0.4$; $\lambda := 0.3$; $K := 1.1$; $\xi_1 = 0.4545$; $\xi_2 = 0.2$; $k_{11} = 0.3$; $k_{22} = 0.4$; $k_{33} = 0.3$; $k_{12} = 0.2$; $k_{13} = 0.3$; $k_{21} = -0.7$; $k_{23} = -0.1$; $k_{31} = -0.8$; $k_{32} = -0.1$. In this case we have that a stable constant solution of system (12) should satisfy

$$\frac{m_1\xi_1}{a_1+\lambda} + \frac{m_2\xi_2}{a_2+\lambda} - \gamma\Big(1-\frac{\lambda}{K}\Big) = 0 \ \text{ and } \ \frac{m_1\xi_1}{(a_1+\lambda)^2} + \frac{m_2\xi_2}{(a_2+\lambda)^2} < \frac{\gamma}{K}.$$

So, a stable constant solution of the system (12) is given by $u^* = (\lambda, \xi_1, \xi_2) = (0.3, 0.4545, 0.2)$ where $a = \frac{m_1\xi_1}{(a_1+\lambda)^2} + \frac{m_2\xi_2}{(a_2+\lambda)^2} - \frac{\lambda\gamma}{K} = -0.027417$.

Furthermore, we have:

$$A_j = \mu_j + 0.0274170274; \quad B_j = 0.70\mu_j^2 + 0.5640836941\mu_j + 0.1251948052;$$

$$C_j = 0.208\mu_j^3 + 0.2502886003\mu_j^2 + 0.05350649352\mu_j \text{ and}$$

$$A_jB_j - C_j = 0.492\mu_j^3 + 0.3329870130\mu_j^2 + 0.08715380978\mu_j + 0.003432469405.$$

In Fig. 2 we present the graphs of A_j, B_j, C_j and $A_jB_j - C_j$ as function of μ_j, $j = 1, 2, \ldots$. Note that, for $j = 1$ and $l = 5$ we get $\mu_1 = \frac{1^2\times 3.1416^2}{5^2} = 0.3947860224$. Thus, we have $A_j > 0$, $B_j > 0$, $C_j > 0$, and $A_jB_j - C_j > 0$ for all $j = 1, 2, \ldots$, since $0 = \mu_0 < \mu_1 < \mu_2 < \cdots \to \infty$. Hence, by Theorem 1 if u^* is stable for the flow of the system (1) then u^* is stable for the flow of the system (12).

Example 3. Consider the following values of parameters in the system (12): $a_1 = 0.6$; $a_2 = 0.4$; $m_1 = 0.9$; $d_1 = 0.3$; $m_2 = 0.7$; $d_2 = 0.3$; $\beta_1 = m_1 - d_1 = 0.6$; $\beta_2 = m_2 - d_2 = 0.4$; $\gamma = 0.9$; $\lambda := 0.3$; $K := 1.1$; $\xi_1 = 0.4545$; $\xi_2 = 0.2$; $k_{11} = 0.3$; $k_{22} = 0.1$; $k_{33} = 0.1$; $k_{12} = 0.2$; $k_{13} = 0.1$; $k_{21} = -0.9$; $k_{23} = -0.9$; $k_{31} = -0.1$; $k_{32} = -0.9$. In this case we have that a stable constant solution of system (12) should satisfy

$$\frac{m_1\xi_1}{a_1+\lambda} + \frac{m_2\xi_2}{a_2+\lambda} - \gamma\Big(1-\frac{\lambda}{K}\Big) = 0 \ \text{ and } \ \frac{m_1\xi_1}{(a_1+\lambda)^2} + \frac{m_2\xi_2}{(a_2+\lambda)^2} < \frac{\gamma}{K} \quad .$$

So, a stable constant solution of system (12) is given by $u^* = (\lambda, \xi_1, \xi_2) = (0.3, 0.4545, 0.2)$ where $a = \frac{m_1\xi_1}{(a_1+\lambda)^2} + \frac{m_2\xi_2}{(a_2+\lambda)^2} - \frac{\lambda\gamma}{K} = -0.027417$.

Furthermore, we have:

$$A_j = 0.5\mu_j + 0.0274170274; \quad B_j = -0.55\mu_j^2 + 0.3775180375\mu_j + 0.1251948052$$

and

$$C_j = -0.122\mu_j^3 + 0.3331139972\mu_j^2 + 0.1251948052\mu_j.$$

In Fig. 3 we present the graphs of A_j, B_j and C_j as function of μ_j, $j = 1, 2, \ldots$. Note that, for $j = 5$ and $l = 5$ we get $\mu_5 = \frac{5^2\times 3.1416^2}{5^2} = \pi^2$. Thus, we have $A_j > 0$, $B_j < 0$, and $C_j < 0$ for $j = 5$. Hence, by Theorem 1 if u^* is stable for the flow of the system (1) then u^* is unstable for the flow of the system (12).

Example 4. Consider the following values of parameters in the system (12): $a_1 = 0.6$; $a_2 = 0.4$; $m_1 = 0.9$; $d_1 = 0.3$; $m_2 = 0.7$; $d_2 = 0.3$; $\beta_1 = m_1 - d_1 = 0.6$; $\beta_2 = m_2 - d_2 = 0.4$; $\gamma = 0.9$; $\lambda := 0.3$; $K := 1.1$; $\xi_1 = 0.4545$; $\xi_2 = 0.2$; $k_{11} = 0.2$; $k_{22} = 0.5$; $k_{33} = 0.5$; $k_{12} = 0.2$; $k_{13} = 0.3$; $k_{21} = -0.9$; $k_{23} = -0.9$; $k_{31} = -0.4$; $k_{32} = -0.9$. In this case we have that a stable constant solution of system (12) should satisfy

$$\frac{m_1\xi_1}{a_1+\lambda} + \frac{m_2\xi_2}{a_2+\lambda} - \gamma\Big(1-\frac{\lambda}{K}\Big) = 0 \ \text{ and } \ \frac{m_1\xi_1}{(a_1+\lambda)^2} + \frac{m_2\xi_2}{(a_2+\lambda)^2} < \frac{\gamma}{K} \quad .$$

So, a stable constant solution of system (12) is given by $u^* = (\lambda, \xi_1, \xi_2) = (0.3, .4545, 0.2)$ where $a = \frac{m_1\xi_1}{(a_1+\lambda)^2} + \frac{m_2\xi_2}{(a_2+\lambda)^2} - \frac{\lambda\gamma}{K} = -0.027417$.

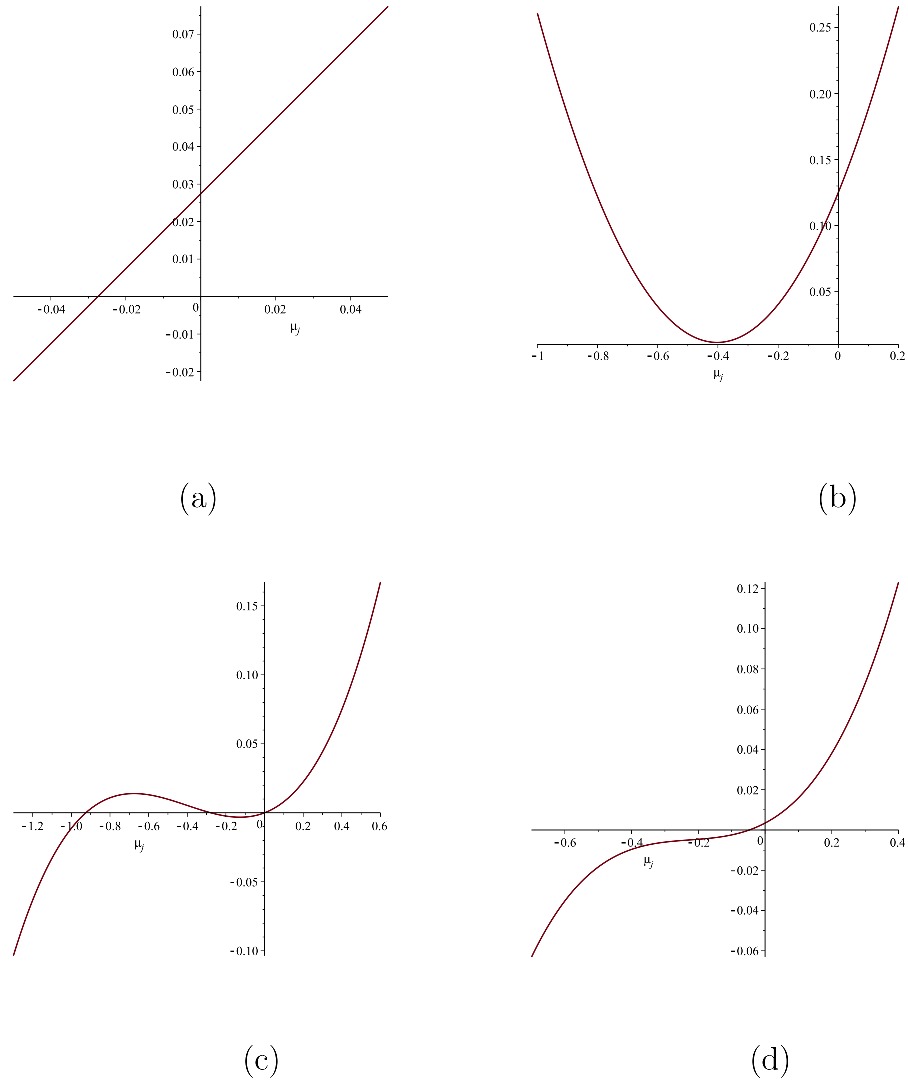

Fig. 2. Graphs of: (a) A_j, (b) B_j, (c) C_j and (d) $A_jB_j - C_j$, as functions of μ_j.

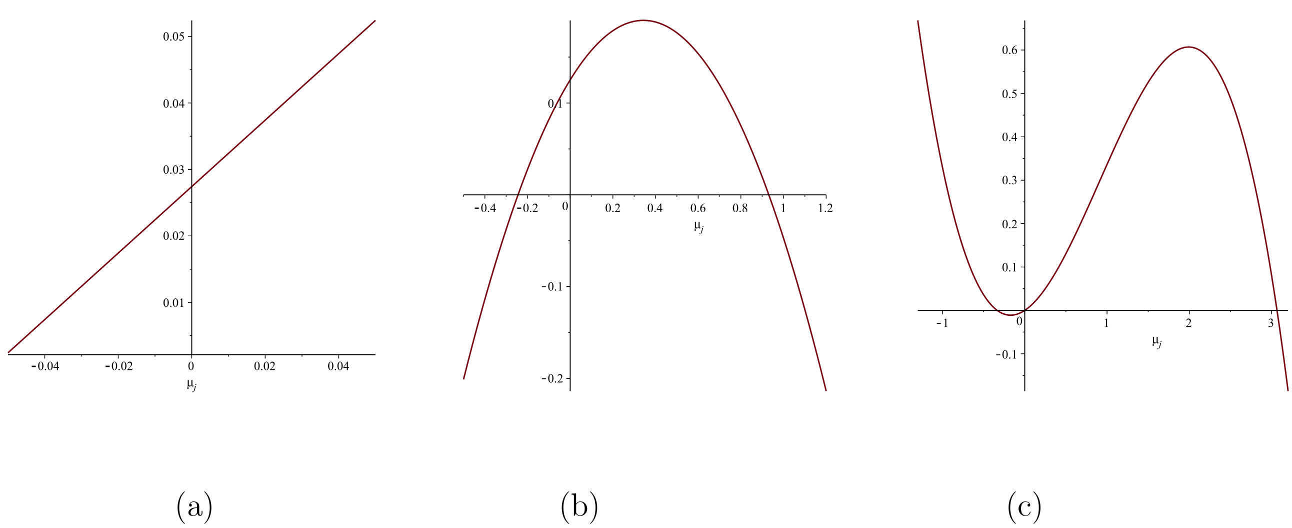

Fig. 3. Graphs of: (a) A_j, (b) B_j and (c) C_j, as functions of μ_j.

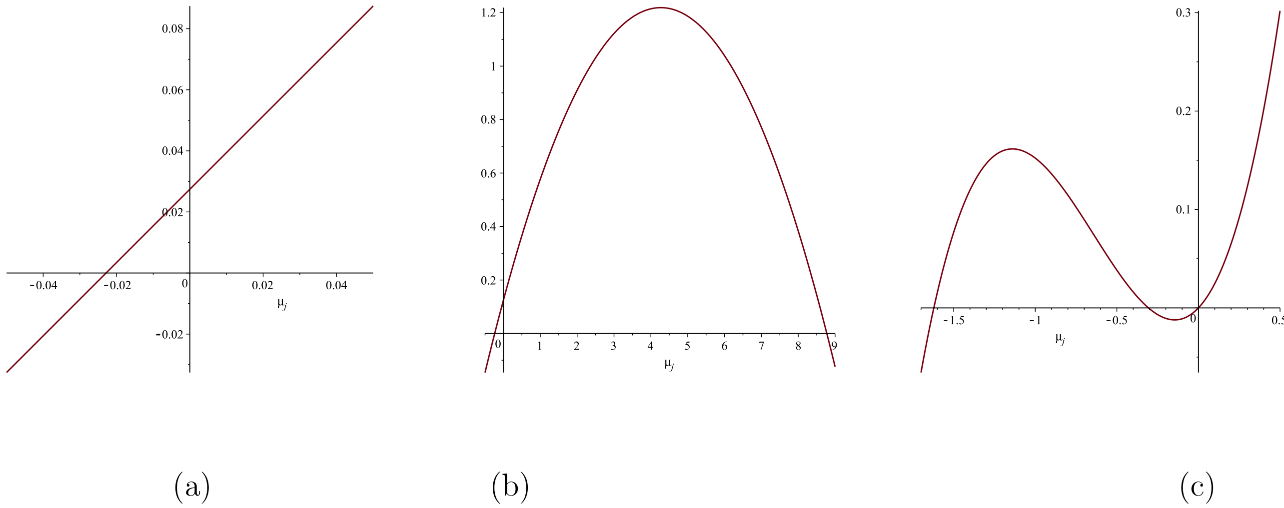

Fig. 4. Graphs of: (a) A_j, (b) B_j and (c) C_j, as functions of μ_j.

Furthermore, we have:

$$A_j = 1.2\mu_j + 0.0274170274; \quad B_j = -0.06\mu_j^2 + 0.5123088023\mu_j + 0.1251948052$$

and

$$C_j = 0.353\mu_j^3 + 0.6804819625\mu_j^2 + 0.1752727273\mu_j.$$

In Fig. 4 we present the graphs of A_j, B_j and C_j as function of μ_j, $j = 1, 2, \ldots$. Note that, for $j = 5$ and $l = 5$ we get $\mu_5 = \frac{5^2 \times 3.1416^2}{5^2} = \pi^2$. Thus, we have $A_j > 0$, $B_j < 0$, and $C_j > 0$ for $j = 5$. Hence, by Theorem 1 if u^* is stable for the flow of system (1) then u^* is unstable for the flow of system (12).

5. Discussion

In this paper we have considered a three dimensional system of partial differential equations to model the dynamical interactions among two predators competing for a single prey. It is often realistic to consider that the prey species exhibits a switching behavior which may be viewed as a strategy to defend themselves from the predators. In accordance with the strategies depicted by the prey, the predators may also develop migratory strategies, which depend on the concentration of both predators. This activity of the predators is usually known as cross diffusion effect. We have presented two models to represent the cross-diffusion phenomenon. In Model I the prey population undergoes self-diffusion while the predator populations follow cross-diffusion. On the other hand, in Model II all interacting populations follow cross-diffusion. It is evident from the present study that in the absence of the prey population developing defense strategies to move away from the predators the system that exhibits stability (Theorem 1). It is surprising to note that when both prey and predator populations develop migratory strategies due to cross-diffusion, the stability of the system is not automatically guaranteed (Theorem 1). This conclusion is a welcoming addition to the literature. Generally time delays in biological models induce instabilities in the system. It is interesting to study the effect of time delays in these models and the interplay between the cross diffusion and time delays. Indeed one of the reviewers have also agreed with the view of introducing time delays in appropriate terms of the model since the operational aspects of the switching migratory efforts in the real world environment are not instantaneous. Accordingly, our models assume the following form:

Model III:

$$\begin{cases} -div\ (\ \delta_0 \nabla S(t,x)\ ) = \gamma(1 - \dfrac{S(t-\tau,x)}{K})S(t,x) - m_1 \dfrac{S(t,x)}{a_1 + S(t,x)} u_1(t,x) - m_2 \dfrac{S(t,x)}{a_2 + S(t,x)} u_2(t,x) \\ -div \left[(\delta_1 + \dfrac{k_1}{a_1 + u_2(t,x)}) \nabla u_1(t,x) - \dfrac{k_1 u_1(t,x)}{(a_1 + u_2(t,x))^2} \nabla u_2(t,x) \right] = (m_1 \dfrac{S(t,x)}{a_1 + S(t,x)} - d_1) u_1(t,x) \\ -div \left[(\delta_2 + \dfrac{k_2}{a_2 + u_1(t,x)}) \nabla u_2(t,x) - \dfrac{k_2 u_2(t,x)}{(a_2 + u_1(t,x))^2} \nabla u_1(t,x) \right] = (m_2 \dfrac{S(t,x)}{a_2 + S(t,x)} - d_2) u_2(t,x) \\ \dfrac{\partial S}{\partial \nu}(x,t) = 0, \ \ \dfrac{\partial u_i}{\partial \nu}(x,t) = 0, \quad i = 1, 2, \quad \text{on} \ \ \partial\Omega \times [0, \infty), \end{cases} \tag{25}$$

Model IV:

$$\begin{cases} S_t(t,x) &= \Delta\Big(k_{11}S(t,x)+k_{12}u_1(t,x)+k_{13}u_2(t,x)\Big)+\gamma\Big(1-\dfrac{S(t-\tau,x)}{K}\Big)S(t,x) \\ & -m_1\dfrac{S(t,x)}{a_1+S(t,x)}u_1(t,x)-m_2\dfrac{S(t,x)}{a_2+S(t,x)}u_2(t,x) \\ u_{1t}(t,x) &= \Delta\big(k_{21}S(t,x)+k_{22}u_1(t,x)+k_{23}u_2(t,x)\big)+(m_1\dfrac{S(t,x)}{a_1+S(t,x)}-d_1)u_1(t,x) \\ u_{2t}(t,x) &= \Delta\big(k_{31}S(t,x)+k_{32}u_1(t,x)+k_{33}u_2(t,x)\big)+(m_2\dfrac{S(t,x)}{a_2+S(t,x)}-d_2)u_2(t,x), \\ & \dfrac{\partial S}{\partial\nu}(x,t)=0,\ \dfrac{\partial u_i}{\partial\nu}(x,t)=0,\quad i=1,2,\quad \text{on}\ \ \partial\Omega\times[0,\infty). \end{cases} \tag{26}$$

In models (25) and (26) the parameter $\tau\geq 0$ represents the time delay due to gestation. It would be interesting to study the inter-play among the cross-diffusion coefficients and the time delays. We defer our work in this direction to a subsequent exposition.

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Appendix

Item 1

In the following we present the expressions for the coefficients A_j, B_j and C_j of the polynomial given by (18).

$$\begin{aligned} A_j &= \mu_j\big(\delta_0+\delta_1+\delta_2+\frac{k_1}{a_1+\xi_2}+\frac{k_2}{a_2+\xi_1}\big)-a, \\ B_j &= \Bigg[\ \delta_0\big(\delta_1+\frac{k_1}{a_1+\xi_2}\big)+\delta_0\big(\delta_2+\frac{k_2}{a_2+\xi_1}\big)+\big(\delta_1+\frac{k_1}{a_1+\xi_2}\big)\big(\delta_2+\frac{k_2}{a_2+\xi_1}\big) \\ &\quad -\frac{k_2\xi_2k_1\xi_1}{(a_2+\xi_1)^2(a_1+\xi_2)^2}\ \Bigg]\mu_j^2-a\Big(\delta_1+\frac{k_1}{a_1+\xi_2}+\delta_2+\frac{k_2}{a_2+\xi_1}\Big)\mu_j-\ (ce+bd)-fg \\ &= \Big(\delta_1\delta_2+\frac{\delta_1k_2}{a_2+xi_1}+\frac{k_1\delta_2}{a_1+\xi_2}+\delta_0\delta_1+\frac{\delta_0k_1}{a_1+\xi_2}+\delta_0\delta_2+\frac{\delta_0k_2}{a_2+\xi_1}+\frac{k_1k_2(a_1a_2+a_1\xi_1+\xi_2a_2)}{(a_2+\xi_1)^2(a_1+xi_2)^2}\Big)\mu_j^2 \\ &\quad -a\Big(\delta_1+\frac{k_1}{a_1+\xi_2}+\delta_2+\frac{k_2}{a_2+\xi_1}\Big)\mu_j+\ \frac{\beta_1\xi_1m_1\lambda}{(a_1+\lambda)^2}+\frac{\beta_2\xi_2m_2\lambda}{(a_2+\lambda)^2} \\ C_j &= \Big(\big(\delta_1+\frac{k_1}{a_1+\xi_2}\big)\big(\delta_2+\frac{k_2}{a_2+\xi_1}\big)\delta_0-\frac{k_2\xi_2k_1\xi_1\delta_0}{(a_2+\xi_1)^2(a_1+\xi_2)^2}\Big)\mu_j^3 \\ &\quad +a\Big(-\big(\delta_1+\frac{k_1}{a_1+\xi_2}\big)\big(\delta_2+\frac{k_2}{a_2+\xi_1}\big)+\frac{k_2\xi_2k_1\xi_1}{(a_2+\xi_1)^2(a_1+\xi_2)^2}\Big)\mu_j^2+\ \Bigg(\ \frac{\beta_1\xi_1m_1\lambda\big(\delta_2+\frac{k_2}{a_2+\xi_1}\big)}{(a_1+\lambda)^2} \\ &\quad +\frac{\beta_2\xi_2m_2\lambda\big(\delta_1+\frac{k_1}{a_1+\xi_2}\big)}{(a_2+\lambda)^2}+\frac{\beta_1\xi_1m_2\lambda k_2\xi_2}{(a_1+\lambda)(a_2+\lambda)(a_2+\xi_1)^2}+\frac{\beta_2\xi_2m_1\lambda k_1\xi_1}{(a_1+\lambda)(a_2+\lambda)(a_1+\xi_2)^2}\ \Bigg)\ \mu_j \\ &= \Big(\delta_0\delta_1\delta_2+\frac{\delta_0\delta_1k_2}{a_2+xi_1}+\frac{\delta_0\delta_2k_1}{a_1+xi_2}+\frac{\delta_0k_1k_2(a_1a_2+a_1\xi_1+a_2\xi_2)}{(a_2+\xi_1)^2(a_1+\xi_2)^2}\Big)\mu_j^3-a\ \Bigg(\ \delta_1\delta_2+\frac{\delta_1k_2}{a_2+\xi_1} \\ &\quad +\frac{\delta_2k_1}{a_1+\xi_2}+\frac{k_1k_2(a_1\xi_1+a_2\xi_2+a_1a_2)}{(a_1+\xi_2)^2(a_2+\xi_1)^2}\ \Bigg)\ \mu_j^2+\ \Bigg(\ \frac{\beta_1\xi_1m_1\lambda\big(\delta_2+\frac{k_2}{a_2+\xi_1}\big)}{(a_1+\lambda)^2}+\frac{\beta_2\xi_2m_2\lambda\big(\delta_1+\frac{k_1}{a_1+\xi_2}\big)}{(a_2+\lambda)^2} \\ &\quad +\frac{\beta_1\xi_1m_2\lambda k_2\xi_2}{(a_1+\lambda)(a_2+\lambda)(a_2+\xi_1)^2}+\frac{\beta_2\xi_2m_1\lambda k_1\xi_1}{(a_1+\lambda)(a_2+\lambda)(a_1+\xi_2)^2}\ \Bigg)\ \mu_j. \end{aligned}$$

Item 2

In the following we present the expression for the function $(A_jB_j - C_j)(\mu_j)$.

$$
\begin{aligned}
A_jB_j - C_j = \ & \Bigg\{ \left(\delta_1 + \frac{k_1}{a_1+\xi 2} + \delta_2 + \frac{k_2}{a_2+\xi_1} + \delta_0\right) \Bigg[\left(\delta_1 + \frac{k_1}{a_1+\xi_2}\right)\left(\delta_2 + \frac{k_2}{a_2+\xi_1}\right) \\
& + \left(\delta_1 + \frac{k_1}{a_1+\xi_2}\right)\delta_0 + \left(\delta_2 + \frac{k_2}{a_2+\xi_1}\right)\delta_0 - \frac{k_2\xi_2\, k_1\xi_1}{(a_2+\xi_1)^2(a_1+\xi_2)^2} \Bigg] \\
& - \left(\delta_1 + \frac{k_1}{a_1+\xi_2}\right)\left(\delta_2 + \frac{k_2}{a_2+\xi_1}\right)\delta_0 + \frac{k_2\xi_2\, k_1\xi_1\, \delta_0}{(a_2+\xi_1)^2(a_1+\xi_2)^2} \Bigg\} {\mu_j}^3 \\
& + \Bigg\{ a\left(\delta_1 + \frac{k_1}{a_1+\xi_2}\right)\left(\delta_2 + \frac{k_2}{a_2+\xi_1}\right) - \frac{a\, k_2\xi_2\, k_1\xi_1}{(a_2+\xi_1)^2(a_1+\xi_2)^2} \\
& -a \Bigg[\left(\delta_1 + \frac{k_1}{a_1+\xi_2}\right)\left(\delta_2 + \frac{k_2}{a_2+\xi_1}\right) + \left(\delta_1 + \frac{k_1}{a_1+\xi_2}\right)\delta_0 + \left(\delta_2 + \frac{k_2}{a_2+\xi_1}\right)\delta_0 \\
& - \frac{k_2\xi_2\, k_1\xi_1}{(a_2+\xi_1)^2(a_1+\xi_2)^2} \Bigg] + \left(\delta_1 + \frac{k_1}{a_1+\xi_2} + \delta_2 + \frac{k_2}{a_2+\xi_1} + \delta_0\right) \Bigg[-a\left(\delta_2 + \frac{k_2}{a_2+\xi_1}\right) \\
& -a\left(\delta_1 + \frac{k_1}{a_1+\xi_2}\right) \Bigg]\Bigg\} {\mu_j}^2 + \Bigg\{ -a\left(-a\left(\delta_2 + \frac{k_2}{a_2+\xi_1}\right) - a\left(\delta_1 + \frac{k_1}{a_1+\xi_2}\right)\right) \\
& + \left(\delta_1 + \frac{k_1}{a_1+\xi_2} + \delta_2 + \frac{k_2}{a_2+\xi_1} + \delta_0\right)\left(\frac{\beta_1\xi_1\, m_1\lambda}{(a_1+\lambda)^2} + \frac{\beta_2\xi_2\, m_2\lambda}{(a_2+\lambda)^{e2}}\right) \\
& - \frac{\beta_1\xi_1\, m_1\lambda\left(\delta_2 + \frac{k_2}{a_2+\xi_1}\right)}{(a_1+\lambda)^2} - \frac{\beta_2\xi_2\, m_2\lambda\left(\delta_1 + \frac{k_1}{a_1+\xi_2}\right)}{(a_2+\lambda)^2} - \frac{\beta_1\xi_1\, m_2\lambda\, k_2\xi_2}{(a_1+\lambda)(a_2+\lambda)(a_2+\xi_1)^2} \\
& - \frac{\beta_2\xi_2\, m_1\lambda\, k_1\xi_1}{(a_1+\lambda)(a_2+\lambda)(a_1+\xi_2)^2} \Bigg\} \mu_j - a\left(\frac{\beta_1\xi_1\, m_1\lambda}{(a_1+\lambda)^2} + \frac{\beta_2\xi_2\, m_2\lambda}{(a_2+\lambda)^2}\right)
\end{aligned}
$$

Item 3

In the following we determine the sign of the expression (19).

$$
\begin{aligned}
E \ = \ & 2\frac{\delta_0\delta_1k_2}{a_2+\xi_1} + 2\frac{\delta_0k_1\delta_2}{a_1+\xi_2} + 2\,\delta_0\delta_1\delta_2 + \frac{{\delta_0}^2k_1}{a_1+\xi_2} + \frac{{\delta_0}^2k_2}{a_2+\xi_1} + \frac{{k_2}^2\delta_0}{(a_2+\xi_1)^2} + \frac{{k_1}^2\delta_0}{(a_1+\xi_2)^2} \\
& + \frac{{k_2}^2\delta_1}{(a_2+\xi_1)^2} + \frac{{k_1}^2\delta_2}{(a_1+\xi_2)^2} + \frac{{\delta_1}^2k_2}{a_2+\xi_1} + \frac{k_1{\delta_2}^2}{a_1+\xi_2} + 2\frac{\delta_0k_1k_2}{(a_1+\xi_2)(a_2+\xi_1)} + 2\frac{\delta_1k_1\delta_2}{a_1+\xi_2} + 2\frac{\delta_1\delta_0k_1}{a_1+\xi_2} \\
& + 2\frac{\delta_2\delta_1k_2}{a_2+\xi_1} + 2\frac{\delta_2\delta_0k_2}{a_2+\xi_1} + {\delta_1}^2\delta_2 + \delta_0{\delta_1}^2 + \delta_1{\delta_2}^2 + \delta_0{\delta_2}^2 + {\delta_0}^2\delta_1 + {\delta_0}^2\delta_2 \\
& + \frac{k_2k_1\Big[\big((\delta_1+\delta_2)\xi_2 + 2\,a_1\delta_1 + 2\,a_1\delta_2\big)\xi_1 + \big(2\,a_2\delta_1 + 2\,a_2\delta_2\big)\xi_2 + 2\,a_1a_2\delta_1 + 2\,a_1a_2\delta_2\Big]}{(a_2+\xi_1)^2(a_1+\xi_2)^2} \\
& + \frac{k_2k_1}{(a_1+\xi_2)^3(a_2+\xi_1)^3} + \Big[a_1k_1{\xi_1}^2 + \big((a_1k_2 + a_2k_1)\xi_2 + {a_1}^2k_2 + 2\,a_1k_1a_2\big)\xi_1 + a_2k_2{\xi_2}^2 \\
& + \big(2\,a_1a_2k_2 + {a_2}^2k_1\big)\xi_2 + {a_1}^2a_2k_2 + a_1{a_2}^2k_1 \Big] > 0.
\end{aligned}
$$

Item 4

The following calculations show that the parabola in Theorem 1 intersects the ordinate axes at a positive point.

$$-a\left(-a\left(\delta_2+\frac{k_2}{a_2+\xi_1}\right)-a\left(\delta_1+\frac{k_1}{a_1+\xi_2}\right)\right)+\left(\delta_1+\frac{k_1}{a_1+\xi_2}+\delta_2\right.$$

$$\left.+\frac{k_2}{a_2+\xi_1}+\delta_0\right)\left(\frac{\beta_1\xi_1 m_1\lambda}{(a_1+\lambda)^2}+\frac{\beta_2\xi_2 m_2\lambda}{(a_2+\lambda)^2}\right)-\frac{\beta_1\xi_1 m_1\lambda\left(\delta_2+\frac{k_2}{a_2+\xi_1}\right)}{(a_1+\lambda)^2}$$

$$-\frac{\beta_2\xi_2 m_2\lambda\left(\delta_1+\frac{k_1}{a_1+\xi_2}\right)}{(a_2+\lambda)^2}-\frac{\beta_1\xi_1 m_2\lambda\, k_2\xi_2}{(a_1+\lambda)(a_2+\lambda)(a_2+\xi_1)^2}-\frac{\beta_2\xi_2 m_1\lambda\, k_1\xi_1}{(a_1+\lambda)(a_2+\lambda)(a_1+\xi_2)^2}$$

$$=a^2\delta_2+\frac{a^2k_2}{a_2+\xi_1}+a^2\delta_1+\frac{a^2k_1}{a_1+\xi_2}+\frac{\delta_1\beta_1\xi_1 m_1\lambda}{(a_1+\lambda)^2}+\frac{\delta_2\beta_2\xi_2 m_2\lambda}{(a_2+\lambda)^2}+\left(\frac{\delta_0\beta_2\xi_2 m_2\lambda}{(a_2+\lambda)^2}\right.$$

$$\left.+\frac{k_2\beta_2\xi_2 m_2\lambda}{(a_2+\xi_1)(a_2+\lambda)^2}-\frac{\beta_1\xi_1 m_2\lambda\, k_2\xi_2}{(a_1+\lambda)(a_2+\lambda)(a_2+\xi_1)^2}\right)+\left(\frac{\delta_0\beta_1\xi_1 m_1\lambda}{(a_1+\lambda)^2}+\frac{k_1\beta_1\xi_1 m_1\lambda}{(a_1+\xi_2)(a_1+\lambda)^2}\right.$$

$$\left.-\frac{\beta_2\xi_2 m_1\lambda\, k_1\xi_1}{(a_2+\lambda)(a_1+\lambda)(a_1+\xi_2)^2}\right)$$

$$=a^2\delta_2+\frac{a^2k_2}{a_2+\xi_1}+a^2\delta_1+\frac{a^2k_1}{a_1+\xi_2}+\frac{\delta_1\beta_1\xi_1 m_1\lambda}{(a_1+\lambda)^2}+\frac{\delta_2\beta_2\xi_2 m_2\lambda}{(a_2+\lambda)^2}$$

$$+\frac{1}{(a_2+\lambda)^2(a_2+\xi_1)^2(a_1+\lambda)}\Big[\xi_2 m_2\lambda\,\big((\lambda\,\beta_2\delta_0+a_1\beta_2\delta_0)\xi_1{}^2+(2\,\lambda\, a_2\beta_2\delta_0+2\,a_1a_2\beta_2\delta_0$$

$$-\lambda\,\beta_1k_2\;+\lambda\,\beta_2k_2+a_1\beta_2k_2-a_2\beta_1k_2)\xi_1+\lambda\,a_2{}^2\beta_2\delta_0+a_1a_2{}^2\beta_2\delta_0+\lambda\,a_2\beta_2k_2$$

$$+a_1a_2\beta_2k_2\,\big)\Big]+\frac{1}{(a_1+\lambda)^2(a_1+\xi_2)^2(a_2+\lambda)}\times\Big[\xi_1 m_1\lambda\;\big((\lambda\,\beta_1\delta_0+a_2\beta_1\delta_0)\xi_2{}^2$$

$$+(2\,\lambda\,a_1\beta_1\delta_0+2\,a_1a_2\beta_1\delta_0+\lambda\,\beta_1k_1-\lambda\,\beta_2k_1-a_1\beta_2k_1+a_2\beta_1k_1)\xi_2$$

$$+\lambda\,a_1{}^2\beta_1\delta_0+a_1{}^2a_2\beta_1\delta_0+\lambda\,a_1\beta_1k_1+a_1a_2\beta_{1k_1)}\Big]>0.$$

The last inequality follows because the expressions

$$(\lambda\,\beta_2\delta_0+a_1\beta_2\delta_0)\xi_1{}^2+(2\,\lambda\,a_2\beta_2\delta_0+2\,a_1a_2\beta_2\delta_0-\lambda\,\beta_1k_2+\;\lambda\,\beta_2k_2+a_1\beta_2k_2-a_2\beta_1k_2)\xi_1+\lambda\,a_2{}^2\beta_2\delta_0+a_1a_2{}^2\beta_2\delta_0+\;\lambda\,a_2\beta_2k_2+a_1a_2\beta_2k_2$$

and

$$(\lambda\,\beta_1\delta_0+a_2\beta_1\delta_0)\xi_2{}^2+(2\,\lambda\,a_1\beta_1\delta_0+2\,a_1a_2\beta_1\delta_0+\lambda\,\beta_1k_1-\lambda\,\beta_2k_1-a_1\beta_2k_1+a_2\beta_1k_1)\xi_2+\lambda\,a_1{}^2\beta_1\delta_0+a_1{}^2a_2\beta_1\delta_0+\lambda\,a_1\beta_1k_1+a_1a_2\beta_1k_1$$

are positive for $\xi_1,\ \xi_2\geq 0$.

Item 5

In the following we present the expressions for the coefficients A_j, B_j and C_j of the polynomial given by (21).

$$A_j\;=(k_{11}+k_{22}+k_{33})\mu_j-a,$$

$$B_j\;=\big(k_{11}k_{22}+k_{11}k_{33}+k_{22}k_{33}-k_{23}k_{32}\big)\mu_j{}^2-a\big(k_{22}+k_{33}\big)\mu_j-bd-ce$$

$$=\Big[k_{11}\big(k_{22}+k_{33}\big)-k_{12}k_{21}-k_{13}k_{31}+k_{22}k_{33}-k_{23}k_{32}\Big]\mu_j^2$$

$$+\Big[-a\big(k_{22}+ak_{33}\big)+\frac{\beta_1\xi_1k_{12}}{a_1+\lambda}-\frac{k_{21}m_1\lambda}{a_1+\lambda}+\frac{\beta_2\xi_2k_{13}}{a_2+\lambda}-\frac{k_{31}m_2\lambda}{a_2+\lambda}\Big]\mu_j+\frac{\beta_2\xi_2\,m_2\lambda}{(a_2+\lambda)^2}$$

$$+\frac{\beta_1\xi_1\,m_1\lambda}{(a_1+\lambda)^2},$$

and

$$
\begin{aligned}
C_j &= \big(k_{11}k_{22}k_{33} - k_{11}k_{23}k_{32}\big)\mu_j{}^3 + a\big(k_{23}k_{32} - k_{22}k_{33}\big)\mu_j{}^2 + \big(-bdk_{33} \\
&\quad + bek_{32} + cdk_{23} - cek_{22} \big)\ \mu_j \\
&= \Big[\big(-k_{21}k_{33} + k_{23}k_{31}\big)k_{12} + (k_{22}k_{33} - k_{23}k_{32})k_{11} + \big(k_{21}k_{32} - k_{22}k_{31}\big)k_{13}\Big]\mu_j^3 \\
&\quad + \Big[\ k_{22}\big(\frac{\beta_2\xi_2 k_{13}}{a_2+\lambda} - \frac{k_{31}m_2\lambda}{a_2+\lambda}\big) + k_{33}\big(\frac{\beta_1\xi_1 k_{12}}{a_1+\lambda} - \frac{k_{21}m_1\lambda}{a_1+\lambda}\big) - ak_{22}k_{33} + ak_{23}k_{32} \\
&\quad + k_{32}\big(-\frac{\beta_1\xi_1 k_{13}}{a_1+\lambda} + \frac{k_{21}m_2\lambda}{a_2+\lambda}\big) + \ \big(-\frac{\beta_2\xi_2 k_{12}}{a_2+\lambda} + \frac{k_{31}m_1\lambda}{a_1+\lambda}\ \big)\ k_{23}\ \Big]\ \mu_j^2 \\
&\quad + \left(\frac{\beta_2\xi_2\, m_2\lambda\, k_{22}}{(a_2+\lambda)^2} - \frac{\beta_2\xi_2\, m_1\lambda\, k_{23}}{(a_2+\lambda)\,(a_1+\lambda)} - \frac{\beta_1\xi_1\, m_2\lambda\, k_{32}}{(a_2+\lambda)\,(a_1+\lambda)} + \frac{\beta_1\xi_1\, m_1\lambda\, k_{33}}{(a_1+\lambda)^2}\right)\mu_j.
\end{aligned}
$$

Item 6

In the following we present the expression for $A_jB_j - C_j$ given in Theorem 2.

$$
\begin{aligned}
A_jB_j - C_j &= \Big[\ \big(k_{11} + k_{22} + k_{33}\big)\big(k_{11}k_{22} + k_{11}k_{33} + k_{22}k_{33} - k_{23}k_{32}\big) \\
&\quad - k_{11}k_{22}k_{33} + k_{11}k_{23}k_{32}\ \Big]\ \mu_j^3 + a\Big[\big(\ k_{22}k_{33} - k_{23}k_{32} - k_{11}k_{22} \\
&\quad + k_{11}k_{33} + k_{22}k_{33} - k_{23}k_{32}\ \big) - \big(k_{11} + k_{22} + k_{33}\big)\big(k_{22} + k_{33}\big)\ \Big]\ \mu_j{}^2 \\
&\quad + \Big[\ a^2\big(k_{22} + k_{33}\big) + \big(k_{11} + k_{22} + k_{33}\big)\big(-bd - ce\big) + bdk_{33} - bek_{32} \\
&\quad - cdk_{23} + cek_{22}\ \Big]\ \mu_j - a\big(-bd - ce\big). \\
&= \Big[\ (k_{11} + k_{22} + k_{33})\ (-k_{12}k_{21} + k_{11}k_{22} + k_{11}k_{33} - k_{13}k_{31} + k_{22}k_{33} \\
&\quad - k_{23}k_{32}) + k_{12}k_{21}k_{33} - k_{11}k_{22}k_{33} - k_{31}k_{12}k_{23} + k_{11}k_{23}k_{32} - k_{21}k_{13}k_{32} \\
&\quad + k_{13}k_{31}k_{22}\ \Big]\ \mu_j{}^3 + \Big[\ \left(-\frac{\beta_2\xi_2\, k_{13}}{a_2+\lambda} + \frac{k_{31}m_2\lambda}{a_2+\lambda}\right)k_{22} + \left(-\frac{\beta_1\xi_1 k_{12}}{a_1+\lambda} + \frac{k_{21}m_1\lambda}{a_1+\lambda}\right)k_{33} \\
&\quad + ak_{22}k_{33} - ak_{23}k_{32} - \left(-\frac{\beta_1\xi_1 k_{13}}{a_1+\lambda} + \frac{k_{21}m_2\lambda}{a_2+\lambda}\right)k_{32} - \left(-\frac{\beta_2\xi_2 k_{12}}{a_2+\lambda} + \frac{k_{31}m_1\lambda}{a_1+\lambda}\right)k_{23} \\
&\quad - aa\ (-k_{12}k_{21} + k_{11}k_{22} + k_{11}k_{33} - k_{13}k_{31} + k_{22}k_{33} - k_{23}k_{32}) \\
&\quad + \ (k_{11} + k_{22} + k_{33})\ \left(\ -aa\, k_{22} + \frac{\beta_1\xi_1\, k_{12}}{a_1+\lambda} - \frac{k_{21}m_1\lambda}{a_1+\lambda} - aa\, k_{33} + \frac{\beta_2\xi_2\, k_{13}}{a_2+\lambda}\right. \\
&\quad \left. - \frac{k_{31}m_2\lambda}{a_2+\lambda}\ \right)\Bigg]\ \mu_j{}^2 + \Bigg[\ a\left(ak_{22} + \frac{\beta_1\xi_1\, k_{12}}{a_1+\lambda} - \frac{k_{21}m_1\lambda}{a_1+\lambda} - aa\, k_{33} + \frac{\beta_2\xi_2\, k_{13}}{a_2+\lambda} - \frac{k_{31}m_2\lambda}{a_2+\lambda}\right) \\
&\quad + \ (k_{11} + k_{22} + k_{33})\ \left(\frac{\beta_2\xi_2\, m_2\lambda}{(a_2+\lambda)^2} + \frac{\beta_1\xi_1\, m_1\lambda}{(a_1+\lambda)^2}\right) - \frac{\beta_2\xi_2\, m_2\lambda\, k_{22}}{(a_2+\lambda)^2} + \frac{\beta_2\xi_2\, m_1\lambda\, k_{23}}{(a_2+\lambda)\,(a_1+\lambda)} \\
&\quad + \frac{\beta_1\xi_1\, m_2\lambda\, k_{32}}{(a_2+\lambda)\,(a_1+\lambda)} - \frac{\beta_1\xi_1\, m_1\lambda\, k_{33}}{(a_1+\lambda)^2}\ \ \Bigg]\ \mu_j - aa\ \left(\frac{\beta_2\xi_2\, m_2\lambda}{(a_2+\lambda)^2} + \frac{\beta_1\xi_1\, m_1\lambda}{(a_1+\lambda)^2}\right).
\end{aligned}
$$

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