Population Dynamics in a Patchy Space and Turing Bifurcation

Shaban Anwar Hassan Aly

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Abstract

This thesis is a systematic presentation of our results in the field of population dynamics in patchy space with self and cross-diffusion. The results presented in the thesis and those connecting to them were published during the past two years (see [3, 4, 5, 6, 7, 8, 9]). The research reported in this thesis was carried out in the Budapest University of Technology and Economics, Institute of Mathematics, Department of Differential Equations.

In Chapter 1, I briefly review models of two-species, pattern formation in ecological systems and the two types of spatio-temporal models of populations.

In Chapter 2, I have treated a two-species models in a habitat of two identical patches linked by migration in which the migration rate of each species is influenced only by its own density, i.e. there is no response to the density of the other one described by the equations:

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)f_1(u_1(t,1),u_2(t,1)) + d_1(u_1(t,2)-u_1(t,1)),\\
\dot{u}_2(t,1) &= u_2(t,1)f_2(u_1(t,1),u_2(t,1)) + d_2(u_2(t,2)-u_2(t,1)),\\
\dot{u}_1(t,2) &= u_1(t,2)f_1(u_1(t,2),u_2(t,2)) + d_1(u_1(t,1)-u_1(t,2)),\\
\dot{u}_2(t,2) &= u_2(t,2)f_2(u_1(t,2),u_2(t,2)) + d_2(u_2(t,1)-u_2(t,2)),
\end{aligned} \tag{1}$$

where $u_i(t,j) :=$ density of species i in patch j at time t, f_i is continuously differentiable, $d_i > 0$ is a constant characterizing the rate of migration when individuals of species i migrate from a certain patch according to Fick's law, $i = 1,2$; $j = 1,2$; $t \in R$.

In section 2.1, I have considered a Lotka-Volterra system and I have shown that instability of a uniform state can not arise via the well known Turing mechanism of diffusion driven instability. In section 2.2, I have considered a two species predator-prey system in which the predator consumes the prey with Holling type functional response and the per capita mortality is an increasing linear function of its quantity. In section 2.3, I have considered a two species predator-prey model of Cavani-Farkas type in which the predator consumes the prey with Holling type functional response and the per capita mortality is neither a constant nor an unbounded function, still, it is increasing with quantity. I have shown that the equilibrium of a standard (self-diffusion) system may be either stable or unstable and at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation. Numerical studies show that if the bifurcation parameter is increased through a critical value the spatially homogeneous equilibrium loses its stability and two new equilibria emerge (see [3, 4]).

Chapter 3 is devoted to studied two-species models in a habitat of two identical patches linked by migration in which the migration rate of each species is influenced not only by its own but also by the other one's density, i.e. there is cross diffusion present described by the equations:

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)f_1(u_1(t,1),u_2(t,1)) + d_1(\rho_1(u_2(t,2))u_1(t,2)-\rho_1(u_2(t,1))u_1(t,1)),\\
\dot{u}_2(t,1) &= u_2(t,1)f_2(u_1(t,1),u_2(t,1)) + d_2(\rho_2(u_1(t,2))u_2(t,2)-\rho_2(u_1(t,1))u_2(t,1)),\\
\dot{u}_1(t,2) &= u_1(t,2)f_1(u_1(t,2),u_2(t,2)) + d_1(\rho_1(u_2(t,1))u_1(t,1)-\rho_1(u_2(t,2))u_1(t,2)),\\
\dot{u}_2(t,2) &= u_2(t,2)f_2(u_1(t,2),u_2(t,2)) + d_2(\rho_2(u_1(t,1))u_2(t,1)-\rho_2(u_1(t,2))u_2(t,2)),
\end{aligned} \tag{2}$$

where f_i is continuously differentiable, $d_i > 0$ is a constant characterizing the rate of migration when individuals of species i migrate from a certain patch according to Fick's law, $\rho_i(u)$ is a positive function of u characterizing the decrease or the increase of the rate of migration if it depends on the densities of the species $(i = 1, 2)$.

In section 3.1, I have considered a Lotka-Volterra system and I show that for competitive (or cooperative) type interaction, a cross-diffusion may lead to Turing instability but for a predator-prey type of interaction, instability of a uniform state can not arise via the well known Turing mechanism of diffusion driven instability(see [5, 6]). In section 3.2, I have considered a two species predator-prey system in which the predator consumes the prey with Holling type functional response and the per capita mortality is an increasing linear function of its quantity. In section 3.3, I have considered a predator-prey model of Cavani-Farkas type in which the predator consumes the prey with Holling type functional response and the per capita mortality is neither a constant nor an unbounded function, still, it is increasing with quantity. I have shown that a cross-diffusion response can stabilize an unstable equilibrium of standard system and destabilize a stable equilibrium of standard system. I have shown that at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation, and numerical studies shown that if the bifurcation parameter is increased through a critical value the spatially homogeneous equilibrium loses its stability and two new stable equilibria emerge. I conclude that the cross migration response is an important factor that should not be ignored when pattern emerges .(see [7, 8]).

Two Appendices in Chapter 4 contain all Tables and Figures of the numerical investigations.

The thesis ends with Bibliography, my curriculum vitae and list of publications.

Contents

Chapter 1

Introduction

Because 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. The effects of self and cross-diffusion, Turing bifurcation and pattern formation are the subjects of this thesis.

1.1 Models of Two-Species

The classical approach to modelling ecological systems (see [24], [37]) simplifies by ignoring space completely and in essence assumes that the per capita growth rates of the participating species are linear functions of the quantities (densities) of the species. The classical Lotka-Volterra model takes the form:

$$\text{predator-prey} \left\{ \begin{array}{l} \dot{u}_1 = u_1(r_1 - a_{11}u_1 - a_{12}u_2) \\ \dot{u}_2 = u_2(-r_2 + a_{21}u_1 - a_{22}u_2) \end{array} \right. , \tag{1.1}$$

$$\text{competition} \quad \left\{ \begin{array}{l} \dot{u}_1 = u_1(r_1 - a_{11}u_1 - a_{12}u_2) \\ \dot{u}_2 = u_2(r_2 - a_{21}u_1 - a_{22}u_2) \end{array} \right. , \tag{1.2}$$

$$\text{mutualism} \quad \left\{ \begin{array}{l} \dot{u}_1 = u_1(r_1 - a_{11}u_1 + a_{12}u_2) \\ \dot{u}_2 = u_2(r_2 + a_{21}u_1 - a_{22}u_2) \end{array} \right. , \tag{1.3}$$

where r_i is the growth or death rate, $a_{ii} > 0$ is the coefficient of intra-specific competition, $a_{ij} > 0 (i \neq j)$ is the coefficient of inter-specific competition.

The general Kolmogorov-type model of a two species community is

$$\begin{aligned} \dot{u}_1 &= u_1 f_1(u_1, u_2), \\ \dot{u}_2 &= u_2 f_2(u_1, u_2), \end{aligned} \tag{1.4}$$

where the partial derivatives of $f_i (i = 1, 2)$ determine the classification of the community:

- If $f'_{1u_2} < 0$ and $f'_{2u_1} > 0$ we say that (1.4) represents a predator-prey system such that $u_1$is prey for u_2.

- If $f'_{1u_2} < 0$ and $f'_{2u_1} < 0$ we say that (1.4) represents a competitive system. etc.

- If $f'_{1u_2} > 0$ and $f'_{2u_1} > 0$ we say that (1.4) represents a cooperative system.

A predator-prey model has received great attention in the last forty years in mathematical ecology due to its universal existence and importance. Standard Lotka-Volterra models for predator prey species assume that the per capita rate of predation depends on the prey numbers only, but in many situations, especially when predators have to search, share or compete for food, a more suitable predator-prey model should be based on the "ratio-dependent " theory.

A predator-prey model in which the predator consumes the prey with Holling type functional response (see [19, 20]) (or ratio-dependent) take the form

$$\begin{aligned} \dot{u}_1 &= u_1(r_1 - a_{11}u_1 - \frac{u_2}{a+u_1}), \\ \dot{u}_2 &= u_2(-r_2 + \frac{bu_1}{a+u_1} - a_{22}u_2). \end{aligned} \tag{1.5}$$

where $r_1 > 0$ and $-r_2 < 0$ are the intrinsic growth rate and intrinsic mortality of the respective species, $a_{11} > 0$ and $a_{22} > 0$ represent the strength of the intraspecific competition (the competition within the species, $\frac{r_1}{a_{11}}$ is the carrying capacity for the prey), $b > 0$, $a > 0$ are the maximum birth rate and the half saturation constant of the predator, respectively. The meaning of the half saturation constant is that at $u_1 = a$ the specific growth rate $\frac{bu_1}{a+u_1}$ (called also a Holling type functional response) of the predator is equal to half its maximum b. The Holling type terms are more realistic than those in a Lotka-Volterra system because they increase with u_1 but do not tend to infinity and are concave down.

A predator-prey system of Cavani-Farkas type (see [11]) takes the form:

$$\begin{aligned} \dot{u}_1 &= \varepsilon u_1(1 - \tfrac{u_1}{K}) - \tfrac{\beta u_1 u_2}{\beta + u_1}, \\ \dot{u}_2 &= -\tfrac{u_2(\gamma+\delta u_2)}{1+u_2} + \tfrac{\beta u_1 u_2}{\beta+u_1}, \end{aligned} \tag{1.6}$$

where $\varepsilon > 0$ is the specific growth rate of the prey in the absence of predation and without environmental limitation, $\beta > 0$, $K > 0$ are the conversion rate and carrying capacity with respect to the prey, respectively, $\gamma > 0$ and $\delta > 0$ are the minimal mortality and the limiting mortality of the predator, respectively (the natural assumption is $\gamma < \delta$). 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.

1.2 Pattern Formation in Ecological Systems

The fifty three years since Turing (1952) have witnessed the unfolding of a vast literature of theoretical investigations of the pattern formation mechanisms as well as numerous applications to real patterns in a large number of ecological systems (see [10], [17], [25, 26, 27, 28, 29], [32]).

It was Turing who first exposed that unforced systems of reaction-diffusion equations can exhibit inhomogeneous spatial structures via a symmetry-breaking bifurcation. More precisely, in a reaction-diffusion system a homogeneous equilibrium which would be stable without diffusion becomes unstable. It is, hence, diffusion that destabilizes the homogeneous equilibrium. This idea is known as Turing Instability, or Diffusion-Driven Instability (DDI) nowadays.

Segel and Jackson (see [34]) introduced this idea to the ecological field. By a predator-prey system of reaction-diffusion equations they demonstrated the same diffusion-driven instability and gave a biological explanation which is well-known now. In the absence of dispersal, the prey and the predator arrive at a stable equilibrium so that any increase in prey is consumed by the predator, and any increase in predator is reduced by self-limitation. When diffusion is added and the diffusion rate of the predator is sufficiently larger than that of the prey, the stabilizing influence of the predator may be dissipated by diffusion, yielding regular peaks and troughs of prey and predator densities. The striking aspect of the theory is that spatially periodic patterns are formed due to the Brownian motion of individuals in a homogeneous environment. Under such an assumption of random movement a criterion has been established for DDI in two-species systems, by which it is concluded that a standard reaction-diffusion system of two- species competition can not exhibit DDI (see [25], [30]). There are also some new theories which extend the old reaction-diffusion models (see [26, 27]). The analytical methods developed for reaction-diffusion models continue to be of use in the investigation of these alternative models.

1.3 Simple Spatio -Temporal Models of Population Dynamics

To formulate a spatio-temporal model, one has to make some basic choices about space, time, and state variables. Each of them may be continuous or discrete (see [13]). Here we briefly introduce two kinds of classical spatial models of population dynamics which are relevant to the approaches in this thesis.

One of the classical methods is the standard reaction diffusion equation (see [18]) that takes into account space as well as the movement of organisms:

$$u_t = f(u) + D\Delta u, \tag{1.7}$$

where $u = u(t;x) \in R^n$ is the vector of population densities at time t at place $x \in \Omega \subset R^2$ (Ω is a bounded domain with no-flux on the boundary), f is a smooth map, D is a diagonal matrix with constant positive diagonal elements known as diffusion coefficients. Δ is the Laplace operator. It is seen that the equation is obtained by simply adding a diffusion term (i.e., $D\Delta u$) to the reaction term describing local interaction and growth of populations (i.e. $f(u)$). The basic assumption concerning the diffusion term is that organisms follow Brownian motion in space with a rate which is invariant in time and space.

In a patchy world (either the habitat is patchy or the species assumes a patchy distribution) spatially discrete models ($''$patch models$''$ or $''$cell models $''$), in which patches are coupled by dispersal while the within patch dynamics is described explicitly, turns out to be one of the relevant approaches (see [12], [33]). When organisms migrate among patches by way of unbiased random walk and the rate of migration is constant, this type of models for two-species living in two identical patches takes the form:

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)f_1(u_1(t,1),u_2(t,1)) + d_1(u_1(t,2)-u_1(t,1)),\\
\dot{u}_2(t,1) &= u_2(t,1)f_2(u_1(t,1),u_2(t,1)) + d_2(u_2(t,2)-u_2(t,1)),\\
\dot{u}_1(t,2) &= u_1(t,2)f_1(u_1(t,2),u_2(t,2)) + d_1(u_1(t,1)-u_1(t,2)),\\
\dot{u}_2(t,2) &= u_2(t,2)f_2(u_1(t,2),u_2(t,2)) + d_2(u_2(t,1)-u_2(t,2)),
\end{aligned} \tag{1.8}$$

where $u_i(t,j) :=$ density of species i in patch j at time t, f_i is continuously differentiable, $d_i > 0$ is a constant characterizing the rate of migration when individuals of species i migrate from a certain patch according to Fick's law, $i = 1,2$; $j = 1,2$; $t \in R$.

It has been the basic assumption behind most early mathematical models of spatial population dynamics that organisms move or disperse in space randomly, which allows for a simple mathematical approach to population dynamics and yet is sufficient to study the fundamental influence of space and dispersal on population dynamics. In the classical applications of partial differential equations to population biology, for instance, organisms are assumed to do Brownian motion the rate of which is invariant in time and space. The assumption leads to the standard reaction-diffusion type model (1.7).

There is an extensive mathematical literature on reaction-diffusion systems applied to ecological problems (see [1, 2], [21], [30, 31]). However, in spite of all work that has been devoted to diffusion theory in ecology, the suitability of the most naive diffusion model for the description of animal movements requires scrutiny. For most insect and mammal species the reality of individuals' movement may be far different from standard diffusion. For instance, individuals may move in response to the local abundance of populations. In some predator-prey systems prey at a certain position usually have increasing inclination to leave when the number of predators near-by increases because of the increasing danger, whereas predators, in contrast, usually have decreasing inclination to leave when the number of prey increases because of the increasing food resource. Obviously, the standard reaction-diffusion model (1.7) or the standard diffusively coupled patchy model (1.8) are too naive to describe such interactions. When a cross-diffusion response is incorporated, the corresponding reaction diffusion model for a two-species living in two identical patches has the form:

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)f_1(u_1(t,1),u_2(t,1)) + d_1(\rho_1(u_2(t,2))u_1(t,2)-\rho_1(u_2(t,1))u_1(t,1)),\\
\dot{u}_2(t,1) &= u_2(t,1)f_2(u_1(t,1),u_2(t,1)) + d_2(\rho_2(u_1(t,2))u_2(t,2)-\rho_2(u_1(t,1))u_2(t,1)),\\
\dot{u}_1(t,2) &= u_1(t,2)f_1(u_1(t,2),u_2(t,2)) + d_1(\rho_1(u_2(t,1))u_1(t,1)-\rho_1(u_2(t,2))u_1(t,2)),\\
\dot{u}_2(t,2) &= u_2(t,2)f_2(u_1(t,2),u_2(t,2)) + d_2(\rho_2(u_1(t,1))u_2(t,1)-\rho_2(u_1(t,2))u_2(t,2)),
\end{aligned} \tag{1.9}$$

where f_i is continuously differentiable, $d_i > 0$ is a constant characterizing the rate of migration when individuals of species i migrate from a certain patch according to Fick's law, $\rho_i(u)$ is a positive function of u characterizing the decrease or the increase of the rate of migration if it depends on the densities of the species ($i = 1,2$).

- If $\rho_i(u) \equiv 1$, $i = 1,2$ we refer to the system (1.9) as the self-diffusion system.

- If the system of equations (1.9) involves a cross-diffusion response (i.e., $\frac{\partial \rho_i(u)}{\partial u_j} \neq 0$, $i \neq j$), we call it a cross-diffusion system.

The system

$$\begin{aligned}\dot{u}_1(t,1) &= u_1(t,1)f_1(u_1(t,1),u_2(t,1)),\\ \dot{u}_2(t,1) &= u_2(t,1)f_2(u_1(t,1),u_2(t,1)),\\ \dot{u}_1(t,2) &= u_1(t,2)f_1(u_1(t,2),u_2(t,2)),\\ \dot{u}_2(t,2) &= u_2(t,2)f_2(u_1(t,2),u_2(t,2)),\end{aligned} \tag{1.10}$$

is called the kinetic system of (1.9).

I assume that the kinetic system (1.10) has a positive equilibrium

$$(u_1(t,1),u_1(t,2),u_2(t,1),u_2(t,2)) \equiv (\overline{u}_1,\overline{u}_2,\overline{u}_1,\overline{u}_2). \tag{1.11}$$

Because the patches are identical, the first two coordinates are equal to the second two coordinates, i.e. this equilibrium is $''$ spatially homogeneous$''$.

There are three important special cases:

- If $\rho_1'(u_2) > 0$ and $\rho_2'(u_1) < 0$ we say that (1.9) represents a predator-prey system such that $u_1$is prey for u_2.
- If $\rho_1'(u_2) > 0$ and $\rho_2'(u_1) > 0$ we say that (1.9) represents a competitive system. etc.
- If $\rho_1'(u_2) < 0$ and $\rho_2'(u_1) < 0$ we say that (1.9) represents a cooperative system.

1.4 The Aims and The Strategy

One of the fundamental issues in spatial ecology is how explicit considerations of space alter the prediction of population models. Classical theories, such as diffusion-driven instability and meta-population dynamics which are developed via simple spatial population models, have profoundly increased our understanding of the issue. In this thesis I scrutinize these theories by considering more complicated processes of spatial interaction of populations. For this purpose I consider spatio-temporal models as systems of ODE which describe two-identical patch-two-species systems linked by migration, where the phenomenon of the Turing bifurcation occurs. In the models it is assumed that either the migration rate of each species is influenced only by its own density (self-diffusion) or that not only by its own but also by the other one's density (cross diffusion). I show that the equilibrium of a standard (self-diffusion) system may be either stable or unstable, a cross-diffusion response can stabilize an unstable equilibrium of standard system and destabilize a stable equilibrium of standard system. For the models I show that at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation and numerical studies show that if the bifurcation parameter is increased through a critical value the spatially homogeneous equilibrium loses its stability and two new equilibria emerge. I conclude that the cross migration response is an important factor that should not be ignored when pattern emerges.

Chapter 2

The Effects of a Self-Diffusion Response

The Turing bifurcation (see [36]) is the basic bifurcation generating spatial pattern, wherein an equilibrium of a nonlinear system is asymptotically stable in the absence of diffusion but unstable in the presence of diffusion. This lies at the heart of almost all mathematical models for patterning in ecology, embryology and elsewhere in biology and chemistry (see [11], [14, 15, 16], [30]). 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 [22], [25], [35, 36]). In this chapter I treat a two-species model in a habitat of two identical patches linked by migration in which the migration rate of each species is influenced only by its own density, i.e. there is no response to the density of the other one. In section 2.1, I consider a Lotka-Volterra system and I show that instability of a uniform state can not arise via the well known Turing mechanism of diffusion driven instability. In section 2.2, I consider a two species predator-prey system in which the predator consumes the prey with Holling type functional response and the per capita mortality is an increasing linear function of its quantity. In section 2.3, I consider a two species predator-prey model of Cavani-Farkas type in which the predator consumes the prey with Holling type functional response and the per capita mortality is neither a constant nor an unbounded function, still, it is increasing with quantity. I show that the equilibrium of a standard (self-diffusion) system may be either stable or unstable and at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation. Numerical studies show that if the bifurcation parameter is increased through a critical value the spatially homogeneous equilibrium loses its stability and two new equilibria emerge.

2.1 Lotka-Volterra Systems

I consider a two-species Lotka–Volterra system living in a habitat of two identical patches linked by migration and we show that instability of a uniform state can not arise via the well known Turing mechanism of diffusion driven instability.

Let $u_i(t, j) :=$ density of species i in patch j at time t, $i = 1, 2$; $j = 1, 2$; $t \in R$. The interaction is described as a system of differential equations as follows:

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)(r_1 - a_{11}u_1(t,1) - a_{12}u_2(t,1)) + d_1(u_1(t,2) - u_1(t,1)),\\
\dot{u}_2(t,1) &= u_2(t,1)(r_2 - a_{21}u_1(t,1) - a_{22}u_2(t,1)) + d_2(u_2(t,2) - u_2(t,1)),\\
\\
\dot{u}_1(t,2) &= u_1(t,2)(r_1 - a_{11}u_1(t,2) - a_{12}u_2(t,2)) + d_1(u_1(t,1) - u_1(t,2)),\\
\dot{u}_2(t,2) &= u_2(t,2)(r_2 - a_{21}u_1(t,2) - a_{22}u_2(t,2)) + d_2(u_2(t,1) - u_2(t,2)),
\end{aligned} \tag{2.1}$$

where r_1 and r_2 are the intrinsic growth rates of the respective species, the matrix $A = [a_{ik}]$ is the interaction matrix, $a_{ii} > 0$, $(i = 1, 2)$ represent the strength of the intraspecific competition, the signs of a_{12} and a_{21} determine the type of interaction, $d_i > 0$, $(i = 1, 2)$ are the diffusion coefficients.

First I consider the kinetic system without migration, i.e. $d_1 = d_2 = 0:$

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)(r_1 - a_{11}u_1(t,1) - a_{12}u_2(t,1)),\\
\dot{u}_2(t,1) &= u_2(t,1)(r_2 - a_{21}u_1(t,1) - a_{22}u_2(t,1)),\\
\\
\dot{u}_1(t,2) &= u_1(t,2)(r_1 - a_{11}u_1(t,2) - a_{12}u_2(t,2)),\\
\dot{u}_2(t,2) &= u_2(t,2)(r_2 - a_{21}u_1(t,2) - a_{22}u_2(t,2)).
\end{aligned} \tag{2.2}$$

We assume that

$$r_1a_{22} - r_2a_{12} > 0, r_2a_{11} - r_1a_{21} > 0 \text{ and } \det A = a_{11}a_{22} - a_{21}a_{12} > 0. \tag{2.3}$$

Then system (2.2) has a positive equilibrium

$$(u_1(t,1), u_2(t,1), u_1(t,2), u_2(t,2)) \equiv (\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2), \tag{2.4}$$

where

$$\overline{u}_1 = \frac{r_1a_{22} - r_2a_{12}}{\det A}, \overline{u}_2 = \frac{r_2a_{11} - r_1a_{21}}{\det A}. \tag{2.5}$$

The Jacobian matrix of the system without diffusion linearized at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is

$$J_k = \begin{pmatrix} -a_{11}\overline{u}_1 & -a_{12}\overline{u}_1 & 0 & 0 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 & 0 & 0 \\ 0 & 0 & -a_{11}\overline{u}_1 & -a_{12}\overline{u}_1 \\ 0 & 0 & -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 \end{pmatrix}. \tag{2.6}$$

The characteristic polynomial is

$$D_4(\lambda) = (D_2(\lambda))^2, D_2(\lambda) = \lambda^2 + \lambda(a_{11}\overline{u}_1 + a_{22}\overline{u}_2) + \overline{u}_1\overline{u}_2 \det A, \tag{2.7}$$

since $(a_{11}\overline{u}_1 + a_{22}\overline{u}_2) > 0$, $\det A > 0$, the coexistence equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is linearly asymptotically stable. Now we are ready to check how self-diffusion affects the stability of $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$. To proceed I distinguish different types of interaction.

2.1.1 Competitive Interaction

For competitive interaction, $r_1 > 0$ and $r_2 > 0$, the entries of the matrix $A = [a_{ik}]$ are positive.

We see that $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is also a spatially homogeneous equilibrium of system (2.1) with self-diffusion. The Jacobian matrix of the system with self-diffusion at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can be written as:

$$J_D = \begin{pmatrix} -a_{11}\overline{u}_1 - d_1 & -a_{12}\overline{u}_1 & d_1 & 0 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - d_2 & 0 & d_2 \\ d_1 & 0 & -a_{11}\overline{u}_1 - d_1 & -a_{12}\overline{u}_1 \\ 0 & d_2 & -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - d_2 \end{pmatrix}, \tag{2.8}$$

$\det(J_D - \lambda I) =$

$$\begin{vmatrix} -a_{11}\overline{u}_1 - d_1 - \lambda & -a_{12}\overline{u}_1 & d_1 & 0 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - d_2 - \lambda & 0 & d_2 \\ d_1 & 0 & -a_{11}\overline{u}_1 - d_1 - \lambda & -a_{12}\overline{u}_1 \\ 0 & d_2 & -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - d_2 - \lambda \end{vmatrix}. \tag{2.9}$$

Using the properties of determinant we get

$$\begin{vmatrix} -a_{11}\overline{u}_1 - \lambda & -a_{12}\overline{u}_1 & d_1 & 0 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - \lambda & 0 & d_2 \\ 0 & 0 & -a_{11}\overline{u}_1 - 2d_1 - \lambda & -a_{12}\overline{u}_1 \\ 0 & 0 & -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - 2d_2 - \lambda \end{vmatrix} \tag{2.10}$$

$$\begin{aligned} &= D_2(\lambda)(\lambda^2 + \lambda(a_{11}\overline{u}_1 + a_{22}\overline{u}_2 + 2(d_1 + d_2)) + \overline{u}_1\overline{u}_2 \det A \\ &\quad +2(\overline{u}_1 d_2 a_{11} + \overline{u}_2 d_1 a_{22}) + 4d_1 d_2. \end{aligned} \tag{2.11}$$

We know that $D_2(\lambda)$ has two roots with negative real parts and

$$\begin{aligned} (a_{11}\overline{u}_1 + a_{22}\overline{u}_2 + 2(d_1 + d_2)) &> 0, \\ \overline{u}_1\overline{u}_2 \det A + 2(\overline{u}_1 d_2 a_{11} + \overline{u}_2 d_1 a_{22}) + 4d_1 d_2 &> 0. \end{aligned} \tag{2.12}$$

Thus, the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can not be destabilized by self-diffusion.

2.1.2 Cooperative Interaction

For cooperative interaction, the case to be considered is when each species survives if left alone and follows the logistic dynamics, that is, the intrinsic growth rates of the respective species are positive, r_1, $r_2 > 0$, this is called facultative cooperation,

$$a_{12} < 0 \text{ and } a_{21} < 0, \tag{2.13}$$

where $|a_{12}|$ and $|a_{21}|$ represent the strength of the cooperation.

Returning to system (2.1), we see that $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is also a spatially homogeneous equilibrium of the system with self-diffusion. The Jacobian matrix of the system with self-diffusion at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can be written as:

$$J_D = \begin{pmatrix} -a_{11}\overline{u}_1 - d_1 & -a_{12}\overline{u}_1 & d_1 & 0 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - d_2 & 0 & d_2 \\ d_1 & 0 & -a_{11}\overline{u}_1 - d_1 & -a_{12}\overline{u}_1 \\ 0 & d_2 & -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - d_2 \end{pmatrix}, \tag{2.14}$$

$\det(J_D - \lambda I) =$

$$\begin{vmatrix} -a_{11}\overline{u}_1 - d_1 - \lambda & -a_{12}\overline{u}_1 & d_1 & 0 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - d_2 - \lambda & 0 & d_2 \\ d_1 & 0 & -a_{11}\overline{u}_1 - d_1 - \lambda & -a_{12}\overline{u}_1 \\ 0 & d_2 & -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - d_2 - \lambda \end{vmatrix}. \tag{2.15}$$

Using the properties of determinant we get

$$\begin{vmatrix} -a_{11}\overline{u}_1 - \lambda & -a_{12}\overline{u}_1 & d_1 & 0 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - \lambda & 0 & d_2 \\ 0 & 0 & -a_{11}\overline{u}_1 - 2d_1 - \lambda & -a_{12}\overline{u}_1 \\ 0 & 0 & -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - 2d_2 - \lambda \end{vmatrix} \tag{2.16}$$

$$\begin{aligned} &= D_2(\lambda)(\lambda^2 + \lambda(a_{11}\overline{u}_1 + a_{22}\overline{u}_2 + 2(d_1 + d_2)) + \overline{u}_1\overline{u}_2 \det A \\ &\quad +2(d_1 a_{22}\overline{u}_2 + d_2 a_{11}\overline{u}_1) + 4d_1 d_2. \end{aligned} \tag{2.17}$$

We know that $D_2(\lambda)$ has two roots with negative real parts and

$$\begin{aligned} (a_{11}\overline{u}_1 + a_{22}\overline{u}_2 + 2(d_1 + d_2)) &> 0 \\ \overline{u}_1\overline{u}_2 \det A + +2(d_1 a_{22}\overline{u}_2 + d_2 a_{11}\overline{u}_1) + 4d_1 d_2. &> 0. \end{aligned} \tag{2.18}$$

Thus, the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can not be destabilized by self-diffusion.

Remark 1 *The situation is different if the cooperation is obligatory, $r_1, r_2 < 0$,the condition of having a point of intersection in the positive quadrant is*

$$\det A = a_{11}a_{22} - a_{21}a_{12} < 0. \tag{2.19}$$

The characteristic polynomial of the linearized system without diffusion at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is

$$D_4(\lambda) = (D_2(\lambda))^2, D_2(\lambda) = \lambda^2 + \lambda(a_{11}\overline{u}_1 + a_{22}\overline{u}_2) + \overline{u}_1\overline{u}_2 \det A, \tag{2.20}$$

since $(a_{11}\overline{u}_1 + a_{22}\overline{u}_2) > 0$, $\det A < 0$, hence, the coexistence equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is a saddle point and self-diffusion never stabilizes an equilibrium which is unstable for the kinetic system.

2.1.3 Predator-Prey Interaction

For predator-prey interaction,

$$r_1 > 0, r_2 < 0, a_{12} > 0 \text{ and } a_{21} < 0. \tag{2.21}$$

Returning to system (2.1), we see that $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is also a spatially homogeneous equilibrium of the system with self-diffusion.

The Jacobian matrix of the system with self-diffusion at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can be written as:

$$J_D = \begin{pmatrix} -a_{11}\overline{u}_1 - d_1 & -a_{12}\overline{u}_1 & d_1 & 0 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - d_2 & 0 & d_2 \\ d_1 & 0 & -a_{11}\overline{u}_1 - d_1 & -a_{12}\overline{u}_1 \\ 0 & d_2 & -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - d_2 \end{pmatrix}, \tag{2.22}$$

$\det(J_D - \lambda I) =$

$$\begin{vmatrix} -a_{11}\overline{u}_1 - d_1 - \lambda & -a_{12}\overline{u}_1 & d_1 & 0 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - d_2 - \lambda & 0 & d_2 \\ d_1 & 0 & -a_{11}\overline{u}_1 - d_1 - \lambda & -a_{12}\overline{u}_1 \\ 0 & d_2 & -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - d_2 - \lambda \end{vmatrix}. \tag{2.23}$$

Using the properties of determinant we get

$$\begin{vmatrix} -a_{11}\overline{u}_1 - \lambda & -a_{12}\overline{u}_1 & d_1 & 0 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - \lambda & 0 & d_2 \\ 0 & 0 & -a_{11}\overline{u}_1 - 2d_1 - \lambda & -a_{12}\overline{u}_1 \\ 0 & 0 & -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - 2d_2 - \lambda \end{vmatrix} \tag{2.24}$$

$$\begin{aligned} = \quad & D_2(\lambda)(\lambda^2 + \lambda(a_{11}\overline{u}_1 + a_{22}\overline{u}_2 + 2(d_1 + d_2)) \\ & + \overline{u}_1\overline{u}_2 \det A + 2(d_2 a_{11}\overline{u}_1 + d_1 a_{22}\overline{u}_2) + 4d_1 d_2. \end{aligned} \tag{2.25}$$

We know that $D_2(\lambda)$ has two roots with negative real parts and

$$\begin{aligned} (a_{11}\overline{u}_1 + a_{22}\overline{u}_2 + 2(d_1 + d_2)) & > 0, \\ \overline{u}_1\overline{u}_2 \det A + 2(d_2 a_{11}\overline{u}_1 + d_1 a_{22}\overline{u}_2) + 4d_1 d_2 & > 0. \end{aligned} \tag{2.26}$$

Thus, we can not destabilize the equilibrium point by self-diffusion.

2.2 A Predator-Prey System with Holling Type II Functional Response

I consider a two species predator-prey system living in a habitat of two identical patches linked by migration in which the predator consumes the prey with Holling type functional response and the per capita mortality is an increasing linear function of its quantity. The Holling type terms are more realistic than those in a Lotka-Volterra system because they increase with the quantity of prey but do not tend to infinity and are concave down. I show that a standard (self-diffusion) system may have an either stable or unstable equilibrium point. I show that at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation (see [3]).

Let $u_1(t,j)$:= density of prey in patch j at time t and $u_2(t,j)$:= density of predator in patch j at time t, $j = 1,2$; $t \in R$.

The interaction between the two species is described as a system of differential equations as follows:

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)(r_1 - a_{11}u_1(t,1) - \tfrac{u_2(t,1)}{a+u_1(t,1)}) + d_1(u_1(t,2) - u_1(t,1)),\\
\dot{u}_2(t,1) &= u_2(t,1)(-r_2 + \tfrac{b\,u_1(t,1)}{a+u_1(t,1)} - a_{22}u_2(t,1)) + d_2(u_2(t,2) - u_2(t,1)),\\
\\
\dot{u}_1(t,2) &= u_1(t,2)(r_1 - a_{11}u_1(t,2) - \tfrac{u_2(t,2)}{a+u_1(t,2)}) + d_1(u_1(t,1) - u_1(t,2)),\\
\dot{u}_2(t,2) &= u_2(t,2)(-r_2 + \tfrac{b\,u_1(t,2)}{a+u_1(t,2)} - a_{22}u_2(t,2)) + d_2(u_2(t,1) - u_2(t,2)),
\end{aligned} \tag{2.27}$$

where $r_1 > 0$ and $-r_2 < 0$ are the intrinsic growth rate and intrinsic mortality of the respective species, $a_{11} > 0$ and $a_{22} > 0$ represent the strength of the intraspecific competition (the competition within the species, $\frac{r_1}{a_{11}}$ is the carrying capacity for the prey), $b > 0$, $a > 0$ are the maximum birth rate and the half saturation constant of predator, respectively. The meaning of the half saturation constant is that at $u_1 = a$ the specific growth rate $\frac{bu_1}{a+u_1}$ (called also a Holling type functional response) of the predator is equal to half its maximum b, the constants $d_i > 0$, $(i = 1,2)$ are the diffusion coefficients.

First I consider the kinetic system without diffusion i.e. $d_1 = d_2 = 0$:

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)(r_1 - a_{11}u_1(t,1) - \tfrac{u_2(t,1)}{a+u_1(t,1)}),\\
\dot{u}_2(t,1) &= u_2(t,1)(-r_2 + \tfrac{bu_1(t,1)}{a+u_1(t,1)} - a_{22}u_2(t,1)),\\
\\
\dot{u}_1(t,2) &= u_1(t,2)(r_1 - a_{11}u_1(t,2) - \tfrac{u_2(t,2)}{a+u_1(t,2)}),\\
\dot{u}_2(t,2) &= u_2(t,2)(-r_2 + \tfrac{bu_1(t,2)}{a+u_1(t,2)} - a_{22}u_2(t,2)).
\end{aligned} \tag{2.28}$$

The following conditions are reasonable and natural:

$$b > r_2, \tag{2.29}$$

$$r_1/a_{11} > a, \tag{2.30}$$

$$\begin{aligned}
b(r_1 - aa_{11}) &> r_2(r_1 + aa_{11}),\\
b(r_1 - aa_{11}) &> \frac{a_{22}}{4a}(r_1 + aa_{11})^3 + r_2(r_1 + aa_{11}).
\end{aligned} \tag{2.31}$$

Condition (2.29) ensures that the predator may have eventually, a positive net growth rate; (2.30) ensures that for the prey an Allée-effect zone exists where the increase of prey density is favourable to its growth rate; (2.31) is needed to have a positive equilibrium point of system (2.28). System (2.28) is made up by two identical uncoupled systems. Under these conditions each has (the same) positive equilibrium which is the intersection of the null-clines:

$$u_2 = H_1(u_1) := (a + u_1)(r_1 - a_{11}u_1), \tag{2.32}$$

$$u_2 = H_2(u_1) := \frac{1}{a_{22}}(-r_2 + \frac{bu_1}{a+u_1}). \tag{2.33}$$

Thus, denoting the coordinates of a positive equilibrium by $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$, these coordinates satisfy $\overline{u}_2 = H_1(\overline{u}_1) = H_2(\overline{u}_1)$.

Note that if $r_1/a_{11} > a$, we have an interval $u_1 \in (0, \frac{r_1/a_{11}-a}{2})$, where the Allée-effect holds, i.e., the increase of the prey quantity is beneficial to its growth rate.

The Jacobian matrix of system (2.28) linearized at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is

$$J_k = \begin{pmatrix} -a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} & -\frac{\overline{u}_1}{a+\overline{u}_1} & 0 & 0 \\ \frac{ab\overline{u}_2}{(a+\overline{u}_1)^2} & -a_{22}\overline{u}_2 & 0 & 0 \\ 0 & 0 & -a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} & -\frac{\overline{u}_1}{a+\overline{u}_1} \\ 0 & 0 & \frac{ab\overline{u}_2}{(a+\overline{u}_1)^2} & -a_{22}\overline{u}_2 \end{pmatrix}. \tag{2.34}$$

The characteristic polynomial is

$$\begin{aligned} D_4(\lambda) &= (D_2(\lambda))^2, D_2(\lambda) = \lambda^2 + \lambda(a_{11}\overline{u}_1 + a_{22}\overline{u}_2 - \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2}) \\ &\quad +(a_{11}a_{22} + \frac{ab}{(a+\overline{u}_1)^3} - \frac{a_{22}\overline{u}_2}{(a+\overline{u}_1)^2})\overline{u}_1\overline{u}_2. \end{aligned} \tag{2.35}$$

The equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ lies in the Allée-effect zone if

$$H_1((-a + \frac{r_1}{a_{11}})/2) < H_2((-a + \frac{r_1}{a_{11}})/2), \tag{2.36}$$

i.e.

$$\frac{a^2 a_{11}}{4}(1 + \frac{r_1}{aa_{11}}) < \frac{1}{a_{22}}(-r_2 + b\frac{r_{1-}aa_{11}}{r_{1+}aa_{11}}). \tag{2.37}$$

Assume that

$$a_{11}\overline{u}_1 + a_{22}\overline{u}_2 - \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} > 0 \;\text{ and }\; a_{11}a_{22} + \frac{ab}{(a+\overline{u}_1)^3} - \frac{a_{22}\overline{u}_2}{(a+\overline{u}_1)^2} > 0, \tag{2.38}$$

then the coexistence equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is linearly asymptotically stable.

2.2.1 The Linearized Problem

Returning to system (2.27), we see that $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is also a spatially homogeneous equilibrium of the system with self-diffusion.

The Jacobian matrix of system (2.27) at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can be written as:

$$J_D = \begin{pmatrix} -a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} - d_1 & -\frac{\overline{u}_1}{a+\overline{u}_1} & d_1 & 0 \\ \frac{ab\overline{u}_2}{(a+\overline{u}_1)^2} & -a_{22}\overline{u}_2 - d_2 & 0 & d_2\rho_2 \\ d_1 & 0 & -a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} - d_1 & -\frac{\overline{u}_1}{a+\overline{u}_1} \\ 0 & d_2 & \frac{ab\overline{u}_2}{(a+\overline{u}_1)^2} & -a_{22}\overline{u}_2 - d_2 \end{pmatrix}, \tag{2.39}$$

$\det(J_D - \lambda I) =$

$$\begin{vmatrix} -a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} - d_1 - \lambda & -\frac{\overline{u}_1}{a+\overline{u}_1} & d_1 & 0 \\ \frac{ab\overline{u}_2}{(a+\overline{u}_1)^2} & -a_{22}\overline{u}_2 - d_2 - \lambda & 0 & d_2 \\ d_1 & 0 & -a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} - d_1 - \lambda & -\frac{\overline{u}_1}{a+\overline{u}_1} \\ 0 & d_2 & \frac{ab\overline{u}_2}{(a+\overline{u}_1)^2} & -a_{22}\overline{u}_2 - d_2 - \lambda \end{vmatrix}. \tag{2.40}$$

Using the properties of determinant we get

$$\begin{vmatrix} -a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} - \lambda & -\frac{\overline{u}_1}{a+\overline{u}_1} & d_1 & 0 \\ \frac{ab\overline{u}_2}{(a+\overline{u}_1)^2} & -a_{22}\overline{u}_2 - \lambda & 0 & d_2 \\ 0 & 0 & -a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} - 2d_1 - \lambda & -\frac{\overline{u}_1}{a+\overline{u}_1} \\ 0 & 0 & \frac{ab\overline{u}_2}{(a+\overline{u}_1)^2} & -a_{22}\overline{u}_2 - 2d_2 - \lambda \end{vmatrix} \tag{2.41}$$

$$\begin{aligned} = \;& D_2(\lambda)(\lambda^2 + \lambda(a_{11}\overline{u}_1 + a_{22}\overline{u}_2 - \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} + 2(d_1+d_2)) \\ & +(a_{11}a_{22} + \frac{ab}{(a+\overline{u}_1)^3} - \frac{a_{22}\overline{u}_2}{(a+\overline{u}_1)^2})\overline{u}_1\overline{u}_2 \\ & +2a_{22}d_1\overline{u}_2 - 2d_2(-a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} - 2d_1). \end{aligned} \tag{2.42}$$

We know that $D_2(\lambda)$ has two roots with negative real parts. By (2.38), clearly, $a_{11}\overline{u}_1 + a_{22}\overline{u}_2 - \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} + 2(d_1+d_2) > 0$. The other polynomial will have a negative and a positive root if the constant term is negative. By the properties of the model and conditions (2.38) the first two terms are positive. If (2.37) holds and the parameters have been chosen so that

$$-a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} - 2d_1 > 0, \tag{2.43}$$

we may increase d_2 and the constant term becomes negative. The calculations lead to the following Theorem.

Theorem 1 *Under conditions (2.37), (2.38), (2.43) If*

$$d_2 > d_{2crit} = \frac{[(a_{11}a_{22} + \frac{ab}{(a+\overline{u}_1)^3} - \frac{a_{22}\overline{u}_2}{(a+\overline{u}_1)^2})\overline{u}_1\overline{u}_2 + 2a_{22}d_1\overline{u}_2]}{2(-a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} - 2d_1)}, \tag{2.44}$$

then Turing instability occurs.

Remark 2 *If (2.37) and (2.38) hold and the parameters have been chosen so that*

$$-a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2} - 2d_1 < 0, \tag{2.45}$$

then self-diffusion never destabilizes the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ which is asymptotically stable for the kinetic system, i.e. the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is diffusively stable for all values of d_2.

2.2.2 Numerical Investigations

In this section I illustrate the results by the following example and we are looking for conditions which imply Turing instability (diffusion driven instability).

Example 1: *We choose* $r_1 = 10.5$, $r_2 = 1$, $a_{11} = 0.5$, $a_{22} = 5, d_1 = 1$, $a = 2.3$, $b = 547.8$ *then*

$\overline{u}_1 = 1$, $\overline{u}_2 = 33$.

We consider d_2 as a bifurcation parameter. For the above values of the parameters the positive critical value of the bifurcation is $d_{2crit} \cong 1008.357143$. In this case at $d_2 = d_{2crit}$, we have four eigenvalues $\lambda_i (i = 1, 2, 3, 4)$ such that $\operatorname{Re}\lambda_i < 0, (i = 1, 2, 3)$ and $\lambda_4 = 0$.

If $d_2 < d_{2crit} \Rightarrow \operatorname{Re}\lambda_i < 0$, $(i = 1, 2, 3, 4)$ then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable

If $d_2 > d_{2crit} \Rightarrow \operatorname{Re}\lambda_i < 0, (i = 1, 2, 3)$ and $\lambda_4 > 0$, then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is unstable.

Thus as d_2 is increased through $d_2 = d_{2crit}$ the spatially homogeneous equilibrium loses its stability by Turing bifurcation. Numerical calculations show that two new spatially non-constant equilibria emerge (see Table 1 and Figure 1), and these equilibria are asymptotically stable.

2.3 A Predator-Prey System of Cavani-Farkas Type

I consider a two-species predator-prey system of Cavani-Farkas type (see [11]) living in a habitat of two identical patches linked by migration. The advantage of the present 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 quantity. I show that a standard (self-diffusion) system may have an either stable or unstable equilibrium point. I show that at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation (see [4]).

Let $u_1(t, j)$ = density of prey in patch j at time t and $u_2(t, j)$ = density of predator in patch j at time t, $j = 1, 2$; $t \in R$. The interaction is described as a system of differential equations as follows:

$$
\begin{aligned}
\dot{u}_1(t,1) &= \varepsilon u_1(t,1)\left(1 - \tfrac{u_1(t,1)}{K}\right) - \tfrac{\beta u_1(t,1) u_2(t,1)}{\beta + u_1(t,1)} + d_1(u_1(t,2) - u_1(t,1)),\\
\dot{u}_2(t,1) &= -\tfrac{u_2(t,1)(\gamma + \delta u_2(t,1))}{1 + u_2(t,1)} + \tfrac{\beta u_1(t,1) u_2(t,1)}{\beta + u_1(t,1)} + d_2(u_2(t,2) - u_2(t,1)),\\
\\
\dot{u}_1(t,2) &= \varepsilon u_1(t,2)\left(1 - \tfrac{u_1(t,2)}{K}\right) - \tfrac{\beta u_1(t,2) u_2(t,2)}{\beta + u_1(t,2)} + d_1(u_1(t,1) - u_1(t,2)),\\
\dot{u}_2(t,2) &= -\tfrac{u_2(t,2)(\gamma + \delta u_2(t,2))}{1 + u_2(t,2)} + \tfrac{\beta u_1(t,2) u_2(t,2)}{\beta + u_1(t,2)} + d_2(u_2(t,1) - u_2(t,2)),
\end{aligned}
\tag{2.46}
$$

where $\varepsilon > 0$ is the specific growth rate of the prey in the absence of predation and without environmental limitation, $\beta > 0$, $K > 0$ are the half saturation constant and carrying capacity with respect to the prey, respectively, $\gamma > 0$ and $\delta > 0$ are the minimal mortality and the limiting mortality of the predator, respectively (the natural assumption is $\gamma < \delta$). The meaning of the half saturation constant is that at $u_1 = \beta$ the specific growth rate $\frac{\beta u_1}{\beta + u_1}$ (called also a Holling type functional response) of the predator is equal to half its maximum β (the conversion rate is taken to be equal to the half saturation constant for sake of simplicity). $d_i > 0$, $(i = 1, 2)$ are the diffusion coefficients.

First we consider the kinetic system without diffusion, i.e. $d_1 = d_2 = 0$:

$$\begin{array}{rl} \dot{u}_1(t,1) = & \varepsilon u_1(t,1)(1-\frac{u_1(t,1)}{K}) - \frac{\beta u_1(t,1)u_2(t,1)}{\beta+u_1(t,1)}, \\ \dot{u}_2(t,1) = & -\frac{u_2(t,1)(\gamma+\delta u_2(t,1))}{1+u_2(t,1)} + \frac{\beta u_1(t,1)u_2(t,1)}{\beta+u_1(t,1)}, \\ & \\ \dot{u}_1(t,2) = & \varepsilon u_1(t,2)(1-\frac{u_1(t,2)}{K}) - \frac{\beta u_1(t,2)u_2(t,2)}{\beta+u_1(t,2)}, \\ \dot{u}_2(t,2) = & -\frac{u_2(t,2)(\gamma+\delta u_2(t,2))}{1+u_2(t,2)} + \frac{\beta u_1(t,2)u_2(t,2)}{\beta+u_1(t,2)}. \end{array} \tag{2.47}$$

The following conditions are reasonable and natural:

$$\gamma < \beta \leq \delta, \tag{2.48}$$

$$\beta < K, \tag{2.49}$$

$$\gamma < \frac{\beta K}{\beta + K}. \tag{2.50}$$

Condition (2.48) ensures that the predator mortality is increasing with density, and that the predator null-cline has a reasonable concave down shape; (2.49) ensures that for the prey an Allée-effect zone exists where the increase of prey density is favourable to its growth rate; (2.50) is needed to have a positive equilibrium point of system (2.47). System (2.47) is made up by two identical uncoupled systems. Under these conditions each has (the same) positive equilibrium which is the intersection of the null-clines:

$$u_2 = H_1(u_1) := \frac{\varepsilon}{\beta K}(K - u_1)(\beta + u_1), \tag{2.51}$$

$$u_2 = H_2(u_1) := \frac{(\beta-\gamma)u_1 - \beta\gamma}{(\delta-\beta)u_1 + \beta\delta}. \tag{2.52}$$

Thus, denoting the coordinates of a positive equilibrium by $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$, these coordinates satisfy $\overline{u}_2 = H_1(\overline{u}_1) = H_2(\overline{u}_1)$.

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.

The Jacobian matrix of the system (2.47) linearized at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is

$$J_k = \begin{pmatrix} \frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)} & -\frac{\beta\overline{u}_1}{\beta+\overline{u}_1} & 0 & 0 \\ \frac{\beta^2\overline{u}_2}{(\beta+\overline{u}_1)^2} & -\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2} & 0 & 0 \\ 0 & 0 & \frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)} & -\frac{\beta\overline{u}_1}{\beta+\overline{u}_1} \\ 0 & 0 & \frac{\beta^2\overline{u}_2}{(\beta+\overline{u}_1)^2} & -\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2} \end{pmatrix}. \tag{2.53}$$

The characteristic polynomial is

$$\begin{aligned} D_4(\lambda) &= (D_2(\lambda))^2, \qquad (2.54) \\ D_2(\lambda) &= \lambda^2 + \lambda(\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2} - \frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)}) \\ &\quad + \frac{\beta\overline{u}_1\overline{u}_2}{(\beta+\overline{u}_1)}(-\frac{\varepsilon(\delta-\gamma)(K-\beta-2\overline{u}_1)}{K\beta(1+\overline{u}_2)^2} + \frac{\beta^2}{(\beta+\overline{u}_1)^2}), \end{aligned}$$

The equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ lies in the Allée-effect zone if

$$H_1(\frac{k-\beta}{2}) < H_2(\frac{k-\beta}{2}), \tag{2.55}$$

i.e.

$$\frac{\varepsilon}{4\beta K}(K+\beta)^2 < -1 + \frac{(\delta-\gamma)K}{\beta^2 - \beta K + \delta K}. \tag{2.56}$$

If

$$\frac{K-\beta}{2} < \overline{u}_1, \tag{2.57}$$

then, in view of (2.48), clearly

$$\begin{aligned} \frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2} - \frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)} \quad &> \quad 0, \\ -\frac{\varepsilon(\delta-\gamma)(K-\beta-2\overline{u}_1)}{K\beta(1+\overline{u}_2)^2} + \frac{\beta^2}{(\beta+\overline{u}_1)^2} \quad &> \quad 0, \end{aligned} \tag{2.58}$$

i.e. the coexistence equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is linearly asymptotically stable.

In the sequel we assume that

$$0 < \overline{u}_1 < \frac{K-\beta}{2}, \tag{2.59}$$

and that still (2.58) holds. In this case the equilibrium point lies in the Allée-effect zone, still the coexistence equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is linearly asymptotically stable.

2.3.1 The Linearized Problem

Returning to system (2.46), we see that $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is also a spatially homogeneous equilibrium of the system with self-diffusion. The Jacobian matrix of the system at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can be written as:

$$J_D = \begin{pmatrix} \frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)} - d_1 & -\frac{\beta\overline{u}_1}{\beta+\overline{u}_1} & d_1 & 0 \\ \frac{\beta^2\overline{u}_2}{(\beta+\overline{u}_1)^2} & -\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2} - d_2 & 0 & d_2 \\ d_1 & 0 & \frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)} - d_1 & -\frac{\beta\overline{u}_1}{\beta+\overline{u}_1} \\ 0 & d_2 & \frac{\beta^2\overline{u}_2}{(\beta+\overline{u}_1)^2} & -\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2} - d_2 \end{pmatrix}, \tag{2.60}$$

$\det(J_D - \lambda I) =$

$$\begin{vmatrix} \frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)} - d_1 - \lambda & -\frac{\beta\overline{u}_1}{\beta+\overline{u}_1} & d_1 & 0 \\ \frac{\beta^2\overline{u}_2}{(\beta+\overline{u}_1)^2} & -\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2} - d_2-\lambda & 0 & d_2 \\ d_1 & 0 & \frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)} - d_1-\lambda & -\frac{\beta\overline{u}_1}{\beta+\overline{u}_1} \\ 0 & d_2 & \frac{\beta^2\overline{u}_2}{(\beta+\overline{u}_1)^2} & -\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2} - d_2-\lambda \end{vmatrix}. \tag{2.61}$$

Using the properties of determinant we get

$$\begin{vmatrix} \frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)}-\lambda & -\frac{\beta\overline{u}_1}{\beta+\overline{u}_1} & d_1 & 0 \\ \frac{\beta^2\overline{u}_2}{(\beta+\overline{u}_1)^2} & -\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2}-\lambda & 0 & d_2 \\ 0 & 0 & \frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)}-2d_1-\lambda & -\frac{\beta\overline{u}_1}{\beta+\overline{u}_1} \\ 0 & 0 & \frac{\beta^2\overline{u}_2}{(\beta+\overline{u}_1)^2} & -\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2}-2d_2-\lambda \end{vmatrix}, \tag{2.62}$$

$$\begin{aligned} &= D_2(\lambda)(\lambda^2+\lambda(-\frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)}+\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2}+2(d_1+d_2)) \\ &+\frac{\beta\overline{u}_1\overline{u}_2}{(\beta+\overline{u}_1)}(-\frac{\varepsilon(\delta-\gamma)(K-\beta-2\overline{u}_1)}{K\beta(1+\overline{u}_2)^2}+\frac{\beta^2}{(\beta+\overline{u}_1)^2}) \\ &++2d_1\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2}-2d_2(\frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)}-2d_1). \end{aligned} \tag{2.63}$$

If $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ lies outside the Allée-effect zone i.e. $\frac{(K-\beta)}{2} < \overline{u}_1$ then, obviously all the eigenvalues of matrices J_k and J_D have negative real parts, so no Turing instability may occur.

We know that $D_2(\lambda)$ has two roots with negative real parts. By (2.58), clearly, $-\frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)} + \frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2} + 2(d_1 + d_2) > 0$. The other polynomial will have a negative and a positive root if the constant term is negative. By the properties of the model and condition (2.56) the first two terms of the constant are positive. If (2.56) hold and the parameters have been chosen so that

$$\frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)} - 2d_1 > 0. \tag{2.64}$$

we may increase d_2 and the constant term becomes negative, i.e. .the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ becomes diffusively unstable. The calculations lead to the following Theorem.

Theorem 2 *Under conditions (2.56), (2.58), (2.64) if*

$$d_2 > d_{2crit} = \frac{\frac{\beta\overline{u}_1\overline{u}_2}{(\beta+\overline{u}_1)}(-\frac{\varepsilon(\delta-\gamma)(K-\beta-2\overline{u}_1)}{K\beta(1+\overline{u}_2)^2}+\frac{\beta^2}{(\beta+\overline{u}_1)^2})+2d_1\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2}}{2(\frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)}-2d_1)}, \tag{2.65}$$

or

$$0 < d_1 < \frac{2\frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)}d_2-\frac{\beta\overline{u}_1\overline{u}_2}{(\beta+\overline{u}_1)}(-\frac{\varepsilon(\delta-\gamma)(K-\beta-2\overline{u}_1)}{K\beta(1+\overline{u}_2)^2}+\frac{\beta^2}{(\beta+\overline{u}_1)^2})}{2\frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2}+4d_2}, \tag{2.66}$$

then Turing instability occurs.

Remark 3 *Note that as d_2 tends to infinity the right hand side of (2.66) is increasing and tends to $\frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{2K(\beta+\overline{u}_1)}$. An easy estimate shows that this is less than $\frac{\varepsilon}{2}$. This means that irrespective of how large the predator diffusion rate d_2 is,the prey diffusion rate d_1 must satisfy*

$$d_1 < \frac{\varepsilon}{2}, \tag{2.67}$$

in order to have Turing instability.

Remark 4 *If (2.56) and (2.58) hold and the parameters have been chosen so that*

$$\frac{\varepsilon \overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)} - 2d_1 < 0, \tag{2.68}$$

then self-diffusion never destabilizes the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ *which is asymptotically stable for the kinetic system, i.e. the equilibrium* $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ *is diffusively stable for all values of* d_2.

2.3.2 Numerical Investigations

We apply our analytical approach to the following example and we are looking for conditions which imply Turing instability (diffusion driven instability).

Example 2: Trying to prepare an example comparable to that of [11], we choose $\beta = 0.1$, $\gamma = 0.01$, $\delta = 0.1055$, $\varepsilon = 1$, $K = 1$, $d_1 = 0.0001$. The unique positive equilibrium is $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2) = (0.4486, 3.0250, 0.4486, 3.0250)$. We see that this point is in the Allée-effect zone $(0.4486 < 0.45)$ and it is asymptotically stable for the kinetic system (2.47).

We consider d_2 as a bifurcation parameter. In this case at $d_{2crit} \cong 2.02447842$, we have four eigenvalues $\lambda_i (i = 1, 2, 3, 4)$ such that $\operatorname{Re} \lambda_i < 0, (i = 1, 2, 3)$ and $\lambda_4 = 0$.

If $d_2 < d_{2crit} \Rightarrow \operatorname{Re} \lambda_i < 0$, $(i = 1, 2, 3, 4)$ then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable

If $d_2 > d_{2crit} \Rightarrow \operatorname{Re} \lambda_i < 0, (i = 1, 2, 3)$ and $\lambda_4 > 0$, then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is unstable.

Thus as d_2 is increased through $d_2 = d_{2crit}$ the spatially homogeneous equilibrium loses its stability. Numerical calculations show that two new spatially non-constant equilibria emerge (see Table 2). The dynamics after the bifurcation is strange: none of the equilibria are stable and computer simulations indicate that there exists an attractive closed path of a peculiar form (see Figure 2).

Chapter 3

The Effects of a Cross-Diffusion Response

In population dynamics there are a lot of problems which are described by a cross-diffusion system (see [14], [25], [30]). In this chapter I consider a two-species model in a habitat of two identical patches linked by migration in which the per capita migration rate of each species is influenced not only by its own but also by the other one's density, i.e. there is cross-diffusion present. In section 3.1, I consider a Lotka-Volterra system and I show that for competitive (or cooperative) type interaction, a cross-diffusion may lead to Turing instability but for a predator-prey type of interaction, instability of a uniform state can not arise via the well known Turing mechanism of diffusion driven instability. In section 3.2, I consider a two species predator-prey system in which the predator consumes the prey with Holling type functional response and the per capita mortality is an increasing linear function of its quantity. In section 3.3, I consider a predator-prey model of Cavani-Farkas type in which the predator consumes the prey with Holling type functional response and the per capita mortality is neither a constant nor an unbounded function, still, it is increasing with quantity. I show that a cross-diffusion response can stabilize an unstable equilibrium of standard system and destabilize a stable equilibrium of standard system. I show that at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation, and numerical studies show that if the bifurcation parameter is increased through a critical value the spatially homogeneous equilibrium loses its stability and two new stable equilibria emerge. I conclude that the cross migration response is an important factor that should not be ignored when pattern emerges (see [5, 6, 7, 8]).

3.1 Lotka-Volterra Systems

I consider a two-species Lotka–Volterra system living in a habitat of two identical patches linked by migration and we show that for competitive (or cooperative) type interaction, cross-diffusion may lead to Turing instability but for a predator-prey type of interaction, instability of a uniform state can not arise via the well known Turing mechanism of diffusion driven instability

Let $u_i(t, j) :=$ density of species i in patch j at time t, $i = 1, 2$; $j = 1, 2$; $t \in R$. The interaction is described as a system of differential equations as follows:

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)(r_1 - a_{11}u_1(t,1) - a_{12}u_2(t,1)) \\
&\qquad + d_1(\rho_1(u_2(t,2))u_1(t,2) - \rho_1(u_2(t,1))u_1(t,1)), \\
\dot{u}_2(t,1) &= u_2(t,1)(r_2 - a_{21}u_1(t,1) - a_{22}u_2(t,1)) \\
&\qquad + d_2(\rho_2(u_1(t,2))u_2(t,2) - \rho_2(u_1(t,1))u_2(t,1)), \\
\dot{u}_1(t,2) &= u_1(t,2)(r_1 - a_{11}u_1(t,2) - a_{12}u_2(t,2)) \\
&\qquad + d_1(\rho_1(u_2(t,1))u_1(t,1) - \rho_1(u_2(t,2))u_1(t,2)), \\
\dot{u}_2(t,2) &= u_2(t,2)(r_2 - a_{21}u_1(t,2) - a_{22}u_2(t,2)) \\
&\qquad + d_2(\rho_2(u_1(t,1))u_2(t,1) - \rho_2(u_1(t,2))u_2(t,2)),
\end{aligned} \tag{3.1}$$

where r_1 and r_2 are the intrinsic growth rates of the respective species, the matrix $A = [a_{ik}]$ is the interaction matrix, $a_{ii} > 0$ $(i = 1, 2)$ represent the strength of the intraspecific competition, the signs of a_{12} and a_{21} determine the type of interaction, $d_i > 0$, $(i = 1, 2)$ are the diffusion coefficients and $\rho_i \in C^1$ $(i = 1, 2)$ are positive functions modeling the cross-diffusion effect. We say that the cross diffusion is strong if $\left|\rho'_{iu_k}\right|$ $(i \neq k)$ is large. If $\rho_i = 1$ $(i = 1, 2)$ then we have mere $''$ self-diffusion$''$.

First we consider the kinetic system without migration, i.e. $d_1 = d_2 = 0$:

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)(r_1 - a_{11}u_1(t,1) - a_{12}u_2(t,1)), \\
\dot{u}_2(t,1) &= u_2(t,1)(r_2 - a_{21}u_1(t,1) - a_{22}u_2(t,1)), \\
\dot{u}_1(t,2) &= u_1(t,2)(r_1 - a_{11}u_1(t,2) - a_{12}u_2(t,2)), \\
\dot{u}_2(t,2) &= u_2(t,2)(r_2 - a_{21}u_1(t,2) - a_{22}u_2(t,2)).
\end{aligned} \tag{3.2}$$

We assume that

$$r_1a_{22} - r_2a_{12} > 0, r_2a_{11} - r_1a_{21} > 0 \text{ and } \det A = a_{11}a_{22} - a_{21}a_{12} > 0. \tag{3.3}$$

Then system (3.2) has a positive equilibrium

$$(u_1(t,1), u_2(t,1), u_1(t,2), u_2(t,2)) \equiv (\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2), \tag{3.4}$$

where

$$\overline{u}_1 = \frac{r_1a_{22} - r_2a_{12}}{\det A}, \overline{u}_2 = \frac{r_2a_{11} - r_1a_{21}}{\det A}. \tag{3.5}$$

The Jacobian matrix of the system without diffusion linearized at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is

$$J_k = \begin{pmatrix} -a_{11}\overline{u}_1 & -a_{12}\overline{u}_1 & 0 & 0 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 & 0 & 0 \\ 0 & 0 & -a_{11}\overline{u}_1 & -a_{12}\overline{u}_1 \\ 0 & 0 & -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 \end{pmatrix}. \tag{3.6}$$

The characteristic polynomial is

$$D_4(\lambda) = (D_2(\lambda))^2, D_2(\lambda) = \lambda^2 + \lambda(a_{11}\overline{u}_1 + a_{22}\overline{u}_2) + \overline{u}_1\overline{u}_2 \det A, \tag{3.7}$$

since $(a_{11}\overline{u}_1 + a_{22}\overline{u}_2) > 0$, $\det A > 0$, hence, the coexistence equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is linearly asymptotically stable. Now we are ready to check how cross-diffusion affect the stability of $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$. To proceeds, we distinguish different types of interaction.

3.1.1 Competitive Interaction

For competitive interaction (see [5]), $r_1 > 0$ and $r_2 > 0$, the entries of the matrix $A = [a_{ik}]$ are positive and $\rho_1 \in C^1$ is a positive increasing function of u_2, the density of the competitor, with analogous conditions on ρ_2. The idea is that high density of the competitor increases the diffusion rate of the species (see [22, 23]).

We see that $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is also a spatially homogeneous equilibrium of the system with cross-diffusion. The Jacobian matrix of system (3.1) with cross-diffusion at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can be written as:

$J_D =$

$$\begin{pmatrix} -a_{11}\overline{u}_1 - d_1\rho_1 & -a_{12}\overline{u}_1 - d_1\rho_1'\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ -a_{21}\overline{u}_2 - d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - d_2\rho_2 & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ d_1\rho_1 & d_1\rho_1'\overline{u}_1 & -a_{11}\overline{u}_1 - d_1\rho_1 & -a_{12}\overline{u}_1 - d_1\rho_1'\overline{u}_1 \\ d_2\rho_2'\overline{u}_2 & d_2\rho_2 & -a_{21}\overline{u}_2 - d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - d_2\rho_2 \end{pmatrix}, \tag{3.8}$$

where $\rho_1$and $\rho_1^{'}$ are to be taken at $\overline{u}_2$ and ρ_2, $\rho_2^{'}$ at $\overline{u}_1$.

$\det(J_D - \lambda I) =$

$$\begin{vmatrix} -a_{11}\overline{u}_1 - d_1\rho_1 - \lambda & -a_{12}\overline{u}_1 - d_1\rho_1'\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ -a_{21}\overline{u}_2 - d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - d_2\rho_2 - \lambda & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ d_1\rho_1 & d_1\rho_1'\overline{u}_1 & -a_{11}\overline{u}_1 - d_1\rho_1 - \lambda & -a_{12}\overline{u}_1 - d_1\rho_1'\overline{u}_1 \\ d_2\rho_2'\overline{u}_2 & d_2\rho_2 & -a_{21}\overline{u}_2 - d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - d_2\rho_2 - \lambda \end{vmatrix}. \tag{3.9}$$

Using the properties of determinant we get

$$\begin{vmatrix} -a_{11}\overline{u}_1 - \lambda & -a_{12}\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - \lambda & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ 0 & 0 & -a_{11}\overline{u}_1 - 2d_1\rho_1 - \lambda & -a_{12}\overline{u}_1 - 2d_1\rho_1'\overline{u}_1 \\ 0 & 0 & -a_{21}\overline{u}_2 - 2d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - 2d_2\rho_2 - \lambda \end{vmatrix} \tag{3.10}$$

$$\begin{aligned} = \quad & D_2(\lambda)(\lambda^2 + \lambda(a_{11}\overline{u}_1 + a_{22}\overline{u}_2 + 2(d_1\rho_1 + d_2\rho_2)) + \overline{u}_1\overline{u}_2 \det A \\ & +2\overline{u}_1 d_2(a_{11}\rho_2 - a_{12}\rho_2'\overline{u}_2) + 2\overline{u}_2 d_1(a_{22}\rho_1 - a_{21}\rho_1'\overline{u}_1) \\ & +4d_1d_2(\rho_1\rho_2 - \overline{u}_1\overline{u}_2\rho_1'\rho_2')). \end{aligned} \tag{3.11}$$

We know that $D_2(\lambda)$ has two roots with negative real parts. The other polynomial will have a negative and a positive root if the constant term is negative. Clearly, $(a_{11}\rho_2 - a_{12}\rho_2'\overline{u}_2) = \rho_2(a_{11} - a_{12}\frac{\rho_2'}{\rho_2}\overline{u}_2) < 0$ if $\frac{\rho_2'}{\rho_2}$ is big enough, $(a_{22}\rho_1 - a_{21}\rho_1'\overline{u}_1) = \rho_1(a_{22} - a_{21}\frac{\rho_1'}{\rho_1}\overline{u}_1) < 0$ if $\frac{\rho_1'}{\rho_1}$ is big enough and $(\rho_1\rho_2 - \overline{u}_1\overline{u}_2\rho_1'\rho_2') = \rho_1\rho_2(1 - \overline{u}_1\overline{u}_2\frac{\rho_1'\rho_2'}{\rho_1\rho_2}) < 0$ if $\frac{\rho_1'\rho_2'}{\rho_1\rho_2}$ is big enough. If we have achieved this we may increase d_1 and/or d_2 and the constant term becomes negative. The calculations lead to the following Theorem.

Theorem 3 *The equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ of system (3.1) is asymptotically stable if $\frac{\rho_1'}{\rho_1}, \frac{\rho_2'}{\rho_2}, \frac{\rho_1'\rho_2'}{\rho_1\rho_2}, d_1$ and d_2 are sufficiently small; if $\frac{\rho_1'}{\rho_1}, \frac{\rho_2'}{\rho_2}, \frac{\rho_1'\rho_2'}{\rho_1\rho_2}$ and either d_1 or d_2 are sufficiently large the $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ loses its stability by a Turing bifurcation.*

Numerical Investigations

I consider two examples of migration function and we are looking for conditions which imply Turing instability (diffusion driven instability).

Example 3: *We choose*

$$\rho_1(u_2) = \exp(m_1 u_2), \rho_2(u_1) = \exp(m_2 u_1), \; m_1, \; m_2 > 0. \tag{3.12}$$

If $r_1 = 11$, $r_2 = 10$, $a_{11} = 5$, $a_{22} = 4$, $a_{12} = 4$, $a_{21} = 3$, $m_1 = 2$, $m_2 = 1$, $d_1 = 1$, then

$\det A = a_{11}a_{22} - a_{21}a_{12} = 8$, $\overline{u}_1 = \frac{r_1 a_{22} - r_2 a_{12}}{\det A} = 0.5, \overline{u}_2 = \frac{r_2 a_{11} - r_1 a_{21}}{\det A} = \frac{17}{8}$.

At $d_{2crit} = \frac{\frac{17}{2} + \frac{17}{4}\exp(\frac{17}{4})}{\frac{7}{2}\exp(\frac{1}{2}) + \frac{9}{2}\exp(\frac{19}{4})} \cong 0.582712$, we have four eigenvalues $\lambda_i (i = 1, 2, 3, 4)$ such that $\lambda_i < 0$ $(i = 1, 2, 3)$ and $\lambda_4 = 0$.

If $d_2 < d_{2crit} \Rightarrow \lambda_i < 0$ $(i = 1, 2, 3, 4)$, then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable .

If $d_2 > d_{2crit} \Rightarrow \lambda_i < 0$ $(i = 1, 2, 3)$ and $\lambda_4 > 0$, then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is unstable.

Thus if d_2 is increased through $d_2 = d_{2crit}$ then the spatially homogeneous equilibrium loses its stability. Numerical calculations show that two new spatially non-constant equilibria emerge (see Table 3 and Figure 3), and these equilibria are asymptotically stable; so that this is a pitchfork bifurcation.

Example 4: *We choose*

$$\rho_1(u_2) = \frac{u_2}{1+u_2}, \rho_2(u_1) = \frac{u_1}{1+u_1}. \tag{3.13}$$

If $r_1 = 11$, $r_2 = 10$, $a_{11} = 5$, $a_{22} = 4$, $a_{12} = 4$, $a_{21} = 3, d_1 = 1$ then we have:

$\det A = a_{11}a_{22} - a_{21}a_{12} = 8$, $\overline{u}_1 = \frac{r_1 a_{22} - r_2 a_{12}}{\det A} = 0.5$, $\overline{u}_2 = \frac{r_2 a_{11} - r_1 a_{21}}{\det A} = \frac{17}{8}$.

At $d_{2crit} = \frac{72777}{5242} \cong 13.88344143$, we have four eigenvalues $\lambda_i (i = 1, 2, 3, 4)$ such that $\lambda_i < 0$ $(i = 1, 2, 3)$ and $\lambda_4 = 0$.

If $d_2 < d_{2crit} \Rightarrow \lambda_i < 0$ $(i = 1, 2, 3, 4)$, then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable.

If $d_2 > d_{2crit} \Rightarrow \lambda_i < 0$ $(i = 1, 2, 3)$ and $\lambda_4 > 0$, then $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is unstable.

Thus as d_2 is increased through $d_2 = d_{2crit}$ the spatially homogeneous equilibrium loses its stability. Numerical calculations show that two new spatially non-constant equilibria emerge (see Table 4 and Figure 4) and these equilibria are asymptotically stable; so that this is a pitchfork bifurcation.

It is to be noted that after the bifurcation the sum of the stable equilibrium values of species 1 (and, similarly, that of species 2) is equal to the double of its spatially homogeneous equilibrium value $\overline{u}_1$ (resp. $\overline{u}_2$).

3.1.2 Cooperative Interaction

For cooperative interaction (see [6]), the case to be considered is when each species survives if left alone and follows the logistic dynamics, that is, the intrinsic growth rates of the respective species are positive, r_1, $r_2 > 0$, this is called facultative cooperation,

$$a_{12} < 0 \text{ and } a_{21} < 0, \tag{3.14}$$

where $|a_{12}|$ and $|a_{21}|$ represent the strength of the cooperation, $\rho_1 \in C^1$ is a positive decreasing function of u_2, with analogous conditions on ρ_2. The idea is that these migration functions describe the inclination of individuals of one species to stay at a certain patch due to the attraction by the other species in the patch (see [22, 23]).

Returning to system (3.1), we see that $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is also a spatially homogeneous equilibrium of the system with cross-diffusion. The Jacobian matrix of the system with cross-diffusion at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can be written as:

$$J_D =$$

$$\begin{pmatrix} -a_{11}\overline{u}_1 - d_1\rho_1 & -a_{12}\overline{u}_1 - d_1\rho_1'\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ -a_{21}\overline{u}_2 - d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - d_2\rho_2 & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ d_1\rho_1 & d_1\rho_1'\overline{u}_1 & -a_{11}\overline{u}_1 - d_1\rho_1 & -a_{12}\overline{u}_1 - d_1\rho_1'\overline{u}_1 \\ d_2\rho_2'\overline{u}_2 & d_2\rho_2 & -a_{21}\overline{u}_2 - d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - d_2\rho_2 \end{pmatrix}, \quad (3.15)$$

where $\rho_1$and $\rho_1^{'}$ are to be taken at $\overline{u}_2$ and ρ_2, $\rho_2^{'}$ at $\overline{u}_1$.

$$\det(J_D - \lambda I) =$$

$$\begin{vmatrix} -a_{11}\overline{u}_1 - d_1\rho_1 - \lambda & -a_{12}\overline{u}_1 - d_1\rho_1'\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ -a_{21}\overline{u}_2 - d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - d_2\rho_2 - \lambda & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ d_1\rho_1 & d_1\rho_1'\overline{u}_1 & -a_{11}\overline{u}_1 - d_1\rho_1 - \lambda & -a_{12}\overline{u}_1 - d_1\rho_1'\overline{u}_1 \\ d_2\rho_2'\overline{u}_2 & d_2\rho_2 & -a_{21}\overline{u}_2 - d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - d_2\rho_2 - \lambda \end{vmatrix} \quad (3.16)$$

Using the properties of determinant we get

$$\begin{vmatrix} -a_{11}\overline{u}_1 - \lambda & -a_{12}\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - \lambda & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ 0 & 0 & -a_{11}\overline{u}_1 - 2d_1\rho_1 - \lambda & -a_{12}\overline{u}_1 - 2d_1\rho_1'\overline{u}_1 \\ 0 & 0 & -a_{21}\overline{u}_2 - 2d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - 2d_2\rho_2 - \lambda \end{vmatrix} \quad (3.17)$$

$$\begin{aligned} = \; & D_2(\lambda)(\lambda^2 + \lambda(a_{11}\overline{u}_1 + a_{22}\overline{u}_2 + 2(d_1\rho_1 + d_2\rho_2)) + \overline{u}_1\overline{u}_2 \det A \quad (3.18) \\ & +2\overline{u}_1 d_2(a_{11}\rho_2 - a_{12}\rho_2'\overline{u}_2) + 2\overline{u}_2 d_1(a_{22}\rho_1 - a_{21}\rho_1'\overline{u}_1) \\ & +4d_1d_2(\rho_1\rho_2 - \overline{u}_1\overline{u}_2\rho_1'\rho_2')). \end{aligned}$$

We know that $D_2(\lambda)$ has two roots with negative real parts. The other polynomial will have a negative and a positive root if the constant term is negative. Clearly, $(\rho_1\rho_2 - \overline{u}_1\overline{u}_2\rho_1'\rho_2') = \rho_1\rho_2(1 - \overline{u}_1\overline{u}_2\frac{\rho_1'\rho_2'}{\rho_1\rho_2}) < 0$ if $\frac{\rho_1'\rho_2'}{\rho_1\rho_2}$ is big enough. If we have achieved this we may increase d_1 and/or d_2 and the constant term becomes negative. These calculations lead to the following Theorem.

Theorem 4 *The equilibrium* $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ *of system (*3.1*) is asymptotically stable if* $\frac{\rho_1'\rho_2'}{\rho_1\rho_2}$, d_1 *and* d_2 *are sufficiently small; if* $\frac{\rho_1'\rho_2'}{\rho_1\rho_2}$ *and either* d_1 *or* d_2 *are sufficiently big then* $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ *loses its stability by a Turing bifurcation.*

Remark 5 *The situation is different if the cooperation is obligatory,* $r_1, r_2 < 0$,*the condition of having a point of intersection in the positive quadrant is*

$$\det A = a_{11}a_{22} - a_{21}a_{12} < 0. \quad (3.19)$$

The characteristic polynomial of the linearized system (3.2) without diffusion at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ *is*

$$D_4(\lambda) = (D_2(\lambda))^2, D_2(\lambda) = \lambda^2 + \lambda(a_{11}\overline{u}_1 + a_{22}\overline{u}_2) + \overline{u}_1\overline{u}_2 \det A, \tag{3.20}$$

since $(a_{11}\overline{u}_1 + a_{22}\overline{u}_2) > 0$, $\det A < 0$, *hence, the coexistence equilibrium point* $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ *is a saddle point and diffusion never stabilizes an equilibrium which is unstable for the kinetic system.*

Numerical Investigations

We apply our analytical approach to the following example of migration function and we are looking for conditions which imply Turing instability (diffusion driven instability).

Example 5: *We choose*

$$\rho_1(u_2) = m_1 \exp(-u_2/m_1), \rho_2(u_1) = m_2 \exp(-u_1/m_2), \ m_1, \ m_2 > 0. \tag{3.21}$$

If $r_1 = 2$, $r_2 = 1$, $a_{11} = 5$, $a_{22} = 4$, $a_{12} = -4$, $a_{21} = -3$, $m_1 = 1$, $m_2 = 1$, $d_1 = 1$, then

$\det A = a_{11}a_{22} - a_{21}a_{12} = 8$, $\overline{u}_1 = \frac{r_1 a_{22} - r_2 a_{12}}{\det A} = \frac{3}{2}, \overline{u}_2 = \frac{r_2 a_{11} - r_1 a_{21}}{\det A} = \frac{11}{8}$.

At $d_{2crit} = \dfrac{-\frac{33}{2} + \frac{11}{8\exp(\frac{11}{8})}}{-\frac{17}{4\exp(\frac{23}{8})} - \frac{3}{2\exp(\frac{3}{2})}} \cong 28.11725408$, we have four eigenvalues $\lambda_i (i = 1, 2, 3, 4)$ such that $\lambda_i < 0$ $(i = 1, 2, 3)$ and $\lambda_4 = 0$.

If $d_2 < d_{2crit} \Rightarrow \lambda_i < 0$ $(i = 1, 2, 3, 4)$, then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable .

If $d_2 > d_{2crit} \Rightarrow \lambda_i < 0$ $(i = 1, 2, 3)$ and $\lambda_4 > 0$, then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is unstable.

Thus as d_2 is increased through $d_2 = d_{2crit}$ then the spatially homogeneous equilibrium loses its stability. Numerical calculations show that two new spatially non-constant equilibria emerge (see Table 5 and Figure 5), and these equilibria are asymptotically stable; so that this is a pitchfork bifurcation.

Remark 6 *It is to be noted that after the bifurcation the sum of the stable equilibrium values of species 1 (and, similarly, that of species 2) is equal to the double of its spatially homogeneous equilibrium value* $\overline{u}_1$ *(resp.* $\overline{u}_2$*).*

3.1.3 Predator-Prey Interaction

For predator-prey interaction,

$$r_1 > 0, r_2 < 0, a_{12} > 0 \text{ and } a_{21} < 0,$$

and $\rho_1 \in C^1$ is a positive increasing function of u_2, the density of the predator, $\rho_1' > 0$ and $\rho_2 \in C^1$ is a positive decreasing function of u_1 the density of the prey, $\rho_2' < 0$. The idea is that the dependence of the diffusion coefficient on the density of the other species reflects the inclination of a prey (or an activator) to leave a certain patch because of the danger (or the inhibition) and the tendency of a predator (or the inhibition) to stay at a certain patch because of the abundance of prey (or an activator).

Returning to system (3.1), we see that $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is also a spatially homogeneous equilibrium of the system with cross-diffusion. The Jacobian matrix of the system with cross-diffusion at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can be written as:

$J_D =$

$$\begin{pmatrix} -a_{11}\overline{u}_1 - d_1\rho_1 & -a_{12}\overline{u}_1 - d_1\rho_1'\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ -a_{21}\overline{u}_2 - d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - d_2\rho_2 & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ d_1\rho_1 & d_1\rho_1'\overline{u}_1 & -a_{11}\overline{u}_1 - d_1\rho_1 & -a_{12}\overline{u}_1 - d_1\rho_1'\overline{u}_1 \\ d_2\rho_2'\overline{u}_2 & d_2\rho_2 & -a_{21}\overline{u}_2 - d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - d_2\rho_2 \end{pmatrix}, \tag{3.22}$$

where $\rho_1$and $\rho_1^{'}$ are to be taken at $\overline{u}_2$ and ρ_2, $\rho_2^{'}$ at $\overline{u}_1$.

$\det(J_D - \lambda I) =$

$$\begin{vmatrix} -a_{11}\overline{u}_1 - d_1\rho_1 - \lambda & -a_{12}\overline{u}_1 - d_1\rho_1'\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ -a_{21}\overline{u}_2 - d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - d_2\rho_2 - \lambda & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ d_1\rho_1 & d_1\rho_1'\overline{u}_1 & -a_{11}\overline{u}_1 - d_1\rho_1 - \lambda & -a_{12}\overline{u}_1 - d_1\rho_1'\overline{u}_1 \\ d_2\rho_2'\overline{u}_2 & d_2\rho_2 & -a_{21}\overline{u}_2 - d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - d_2\rho_2 - \lambda \end{vmatrix} \tag{3.23}$$

Using the properties of determinant we get

$$\begin{vmatrix} -a_{11}\overline{u}_1 - \lambda & -a_{12}\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ -a_{21}\overline{u}_2 & -a_{22}\overline{u}_2 - \lambda & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ 0 & 0 & -a_{11}\overline{u}_1 - 2d_1\rho_1 - \lambda & -a_{12}\overline{u}_1 - 2d_1\rho_1'\overline{u}_1 \\ 0 & 0 & -a_{21}\overline{u}_2 - 2d_2\rho_2'\overline{u}_2 & -a_{22}\overline{u}_2 - 2d_2\rho_2 - \lambda \end{vmatrix} \tag{3.24}$$

$$\begin{aligned} = \; & D_2(\lambda)(\lambda^2 + \lambda(a_{11}\overline{u}_1 + a_{22}\overline{u}_2 + 2(d_1\rho_1 + d_2\rho_2)) \\ & +(a_{11}\overline{u}_1 + 2d_1\rho_1)(a_{22}\overline{u}_2 + 2d_2\rho_2) \\ & -(a_{21}\overline{u}_2 + 2d_2\rho_2'\overline{u}_2)(a_{12}\overline{u}_1 + 2d_1\rho_1'\overline{u}_1). \end{aligned} \tag{3.25}$$

We know that $D_2(\lambda)$ has two roots with negative real parts, $\rho_2(u_1) > 0$, $\rho_2'(u_1) < 0$, $\rho_1(u_2) > 0$ and $\rho_1'(u_2) > 0$, then we can not destabilize the equilibrium point by cross diffusion.

3.2 A Predator-Prey System with Holling Type II Functional Response

I consider a two-species predator-prey system living in a habitat of two identical patches linked by migration and I show that at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation, i. e. the stable constant steady state loses its stability and spatially non-constant stationary solutions, pattern emerge (see [7]).

Let $u_1(t, j) :=$ density of prey in patch j at time t and $u_2(t, j) :=$ density of predator in patch j at time t, $j = 1, 2$; $t \in R$. The interaction is described as a system of differential equations as follows:

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)(r_1 - a_{11}u_1(t,1) - \tfrac{u_2(t,1)}{a+u_1(t,1)}) \\
&\qquad +d_1(\rho_1(u_2(t,2))u_1(t,2) - \rho_1(u_2(t,1))u_1(t,1)), \\
\dot{u}_2(t,1) &= u_2(t,1)(-r_2 + \tfrac{bu_1(t,1)}{a+u_1(t,1)} - a_{22}u_2(t,1)) \\
&\qquad +d_2(\rho_2(u_1(t,2))u_2(t,2) - \rho_2(u_1(t,1))u_2(t,1)), \\
\dot{u}_1(t,2) &= u_1(t,2)(r_1 - a_{11}u_1(t,2) - \tfrac{u_2(t,2)}{a+u_1(t,2)}) \\
&\qquad +d_1(\rho_1(u_2(t,1))u_1(t,1) - \rho_1(u_2(t,2))u_1(t,2)), \\
\dot{u}_2(t,2) &= u_2(t,2)(-r_2 + \tfrac{bu_1(t,2)}{a+u_1(t,2)} - a_{22}u_2(t,2)) \\
&\qquad +d_2(\rho_2(u_1(t,1))u_2(t,1) - \rho_2(u_1(t,2))u_2(t,2)),
\end{aligned} \tag{3.26}$$

where $r_1 > 0$ and $-r_2 < 0$ are the intrinsic growth rate and intrinsic mortality of the respective species, $a_{11} > 0$ and $a_{22} > 0$ represent the strength of the intraspecific competition (the competition within the species, $\frac{r_1}{a_{11}}$ is the carrying capacity for the prey), $b > 0$, $a > 0$ are the maximum birth rate and the half saturation constant of predator respectively. The meaning of the half saturation constant is that at $u_1 = a$ the specific growth rate $\frac{bu_1}{a+u_1}$ (called also a Holling type functional response) of the predator is equal to half its maximum b. $d_i > 0$, $(i = 1, 2)$ are the diffusion coefficients and $\rho_1 \in C^1$ is a positive increasing function of u_2 the density of the predator, $\rho_1' > 0$ and $\rho_2 \in C^1$ is a positive decreasing function of u_1 the density of the prey, $\rho_2' < 0$. The idea is that the dependence of the diffusion coefficient on the density of the other species reflects the inclination of a prey (or an activator) to leave a certain patch because of the danger (or the inhibition) and the tendency of a predator (or the inhibition) to stay at a certain patch because of the abundance of prey (or an activator), (see [14], [22]). The functions ρ_i model the cross-diffusion effect. We say that the cross-diffusion is strong if $\left|\rho'_{iu_k}\right|$ $(i \neq k)$ is large. If by varying a parameter $\left|\rho'_{iu_k}\right|$ $(i \neq k)$ is increasing then we say that the cross diffusion effect is increasing. If $\rho_i = 1$, $i = 1$, 2 then we have mere "self-diffusion".

First we consider the kinetic system without migration, i.e. $d_1 = d_2 = 0$:

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)(r_1 - a_{11}u_1(t,1) - \tfrac{u_2(t,1)}{a+u_1(t,1)}), \\
\dot{u}_2(t,1) &= u_2(t,1)(-r_2 + \tfrac{bu_1(t,1)}{a+u_1(t,1)} - a_{22}u_2(t,1)), \\
\dot{u}_1(t,2) &= u_1(t,2)(r_1 - a_{11}u_1(t,2) - \tfrac{u_2(t,2)}{a+u_1(t,2)}), \\
\dot{u}_2(t,2) &= u_2(t,2)(-r_2 + \tfrac{bu_1(t,2)}{a+u_1(t,2)} - a_{22}u_2(t,2)).
\end{aligned} \tag{3.27}$$

The following conditions are reasonable and natural:

$$b > r_2, \tag{3.28}$$

$$r_1/a_{11} > a, \tag{3.29}$$

$$\begin{aligned}
b(r_1 - aa_{11}) &> r_2(r_1 + aa_{11}), \\
b(r_1 - aa_{11}) &> \frac{a_{22}}{4a}(r_1 + aa_{11})^3 + r_2(r_1 + aa_{11}).
\end{aligned} \tag{3.30}$$

Condition (3.28) ensures that the predator may have eventually, a positive net growth rate; (3.29) ensures that for the prey an Allée-effect zone exists where the increase of prey density is favourable to its growth rate; (3.30) is needed to have a positive equilibrium point of system (3.27). System (3.27) is made up by two identical uncoupled systems. Under these conditions each has (the same) positive equilibrium which is the intersection of the null-clines:

$$u_2 = H_1(u_1) := (a+u_1)(r_1 - a_{11}u_1), \tag{3.31}$$

$$u_2 = H_2(u_1) := \frac{1}{a_{22}}(-r_2 + \frac{bu_1}{a+u_1}). \tag{3.32}$$

Thus, denoting the coordinates of a positive equilibrium by $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$, these coordinates satisfy $\overline{u}_2 = H_1(\overline{u}_1) = H_2(\overline{u}_1)$.

Note that if $r_1/a_{11} > a$, we have an interval $u_1 \in (0, \frac{r_1/a_{11}-a}{2})$, where the Allée-effect holds, i.e., the increase of the prey quantity is beneficial to its growth rate.

The Jacobian matrix of the system without diffusion linearized at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is

$$J_k = \begin{pmatrix} \Theta_1 & -\Theta_2 & 0 & 0 \\ \Theta_3 & -\Theta_4 & 0 & 0 \\ 0 & 0 & \Theta_1 & -\Theta_2 \\ 0 & 0 & \Theta_3 & -\Theta_4 \end{pmatrix}. \tag{3.33}$$

The characteristic polynomial is

$$D_4(\lambda) = (D_2(\lambda))^2, D_2(\lambda) = \lambda^2 + \lambda(\Theta_4 - \Theta_1) + \Theta_2\Theta_3 - \Theta_1\Theta_4, \tag{3.34}$$

where

$$\begin{aligned} \Theta_1 &= -a_{11}\overline{u}_1 + \frac{\overline{u}_1\overline{u}_2}{(a+\overline{u}_1)^2}, \quad \Theta_2 = \frac{\overline{u}_1}{a+\overline{u}_1}, \\ \Theta_3 &= \frac{ab\overline{u}_2}{(a+\overline{u}_1)^2}, \qquad \Theta_4 = a_{22}\overline{u}_2. \end{aligned}$$

The equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ lies in the Allée-effect zone if

$$H_1((-a + \frac{r_1}{a_{11}})/2) < H_2((-a + \frac{r_1}{a_{11}})/2). \tag{3.35}$$

Assume that

$$\Theta_4 - \Theta_1 > 0 \text{ and } \Theta_2\Theta_3 - \Theta_1\Theta_4 > 0; \tag{3.36}$$

then the coexistence equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is linearly asymptotically stable.

3.2.1 The Linearized Problem

Returning to system (3.26), we see that $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is also a spatially homogeneous equilibrium of the system with cross-diffusion. The Jacobian matrix of the system with cross-diffusion at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can be written as:

$$J_D = \begin{pmatrix} \Theta_1 - d_1\rho_1 & -\Theta_2 - d_1\rho_1'\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ \Theta_3 - d_2\rho_2'\overline{u}_2 & -\Theta_4 - d_2\rho_2 & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ d_1\rho_1 & d_1\rho_1'\overline{u}_1 & \Theta_1 - d_1\rho_1 & -\Theta_2 - d_1\rho_1'\overline{u}_1 \\ d_2\rho_2'\overline{u}_2 & d_2\rho_2 & \Theta_3 - d_2\rho_2'\overline{u}_2 & -\Theta_4 - d_2\rho_2 \end{pmatrix}, \tag{3.37}$$

where $\rho_1$and $\rho_1^{'}$ are to be taken at $\overline{u}_2$ and ρ_2, $\rho_2^{'}$ at $\overline{u}_1$.

Theorem 5 *Under conditions (3.35), (3.36) if*

$$\Theta_1 - 2d_1\rho_1 > 0, \tag{3.38}$$

and $\rho_2(\overline{u}_1)$ *is sufficiently large then Turing instability occurs.*

Proof: $\det(J_D - \lambda I) =$

$$\begin{vmatrix} \Theta_1 - d_1\rho_1 - \lambda & -\Theta_2 - d_1\rho_1'\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ \Theta_3 - d_2\rho_2'\overline{u}_2 & -\Theta_4 - d_2\rho_2 - \lambda & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ d_1\rho_1 & d_1\rho_1'\overline{u}_1 & \Theta_1 - d_1\rho_1 - \lambda & -\Theta_2 - d_1\rho_1'\overline{u}_1 \\ d_2\rho_2'\overline{u}_2 & d_2\rho_2 & \Theta_3 - d_2\rho_2'\overline{u}_2 & -\Theta_4 - d_2\rho_2 - \lambda \end{vmatrix}. \tag{3.39}$$

Using the properties of determinant we get

$$\begin{vmatrix} \Theta_1 - \lambda & -\Theta_2 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ \Theta_3 & -\Theta_4 - \lambda & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ 0 & 0 & \Theta_1 - 2d_1\rho_1 - \lambda & -\Theta_2 - 2d_1\rho_1'\overline{u}_1 \\ 0 & 0 & \Theta_3 - 2d_2\rho_2'\overline{u}_2 & -\Theta_4 - 2d_2\rho_2 - \lambda \end{vmatrix} \tag{3.40}$$

$$\begin{aligned} = \quad & D_2(\lambda)\{\lambda^2 + \lambda[\Theta_4 - \Theta_1 + 2(d_1\rho_1 + d_2\rho_2)] + \Theta_2\Theta_3 - \Theta_1\Theta_4 \\ & +2d_1\Theta_4\rho_1 - 2d_2\rho_2(\Theta_1 - 2d_1\rho_1) + 2d_1\overline{u}_1\Theta_3\rho_1' \\ & -2d_2\rho_2'\overline{u}_2(\Theta_2 + 2d_1\rho_1'\overline{u}_1)\}. \end{aligned} \tag{3.41}$$

We know that $D_2(\lambda)$ has two roots with negative real parts. By (3.36), clearly, $\Theta_4 - \Theta_1 + 2(d_1\rho_1 + d_2\rho_2) > 0$. The other polynomial will have a negative and a positive root if the constant term is negative. This can be achieved if $\rho_2(\overline{u}_1)$ is increased.

Remark 7 *As I have mentioned in Chapter 2, if (2.45) holds and there is no cross-diffusion then the equilibrium remains stable for any* $d_2 > 0$. *Still, (3.38) may hold, i.e. in this case only the cross-diffusion effect may destabilize the equilibrium.*

Remark 8 *If the parameters have been chosen so that*

$$\Theta_1 - 2d_1 > 0 \text{ and } \Theta_1 - 2d_1\rho_1 < 0, \tag{3.42}$$

then the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ *remains asymptotically stable for any* $d_2 > 0$ *and* $\rho_2 > 0$ *in the cross-diffusion case while, as we have seen, it will undergo a Turing bifurcation in the absence of cross-diffusion.*

3.2.2 Numerical Investigations

We apply our analytical approach to the following example of migration function and we are looking for conditions which imply Turing instability (diffusion driven instability).

Example 6: *We choose*

$$\rho_1(u_2) = \frac{m_1 u_2}{1 + u_2}, \rho_2(u_1) = m_2 \exp(\frac{-u_1}{m_2}), \; m_1, \; m_2 > 0. \tag{3.43}$$

If $r_1 = 10.5$, $r_2 = 1$, $a_{11} = 0.5$, $a_{22} = 5$, $m_1 = 1$, $d_2 = 1$, $d_1 = 1$, $a = 2.3$, $b = 547.8$ then $\overline{u}_1 = 1$, $\overline{u}_2 = 33$.

We consider m_2 as a bifurcation parameter. In this case at $m_{2crit} \cong 923.0945$, we have four eigenvalues $\lambda_i (i = 1, 2, 3, 4)$ such that $\operatorname{Re} \lambda_i < 0 \ (i = 1, 2, 3)$ and $\lambda_4 = 0$.

If $m_2 < m_{2crit} \Rightarrow \operatorname{Re} \lambda_i < 0 \ (i = 1, 2, 3, 4)$, then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable .

In this example $\left|\rho'_{2u_1}(u_1, u_2)\right| = \exp(-\frac{u_1}{m_2})$. As we see if m_2 is increased for fixed $u_1$this derivative is increasing, i.e. the cross-diffusion effect is increasing.

If $m_2 > m_{2crit} \Rightarrow \operatorname{Re} \lambda_i < 0 \ (i = 1, 2, 3)$ and $\lambda_4 > 0$, then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is unstable.

Thus as m_2 is increased through $m_2 = m_{2crit}$ then the cross-diffusion response is strong and the spatially homogeneous equilibrium loses its stability. Numerical calculations show that two new spatially non-constant equilibria emerge (see Table 6 and Figure 6), and these equilibria are asymptotically stable.

Remark 9 *This result does not contradict that of [22] where a situation is treated in which the spatially homogeneous equilibrium is stable for all values of the "self-diffusion" coefficients (without cross-diffusion). Here this is not the case.*

3.3 A Predator-Prey System of Cavani-Farkas Type

In Chapter 2, I considered a predator-prey system of Cavani-Farkas type (see [11]) living in a habitat of two identical patches in which the migration rate of each species is influenced only by its own density and I show that at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation, pattern emerge. In this Section, I consider the case when the migration rate of each species is influenced not only by its own but also by the other one's density, i.e. there is cross-diffusion present.

Let $u_1(t, j) :=$ density of prey in patch j at time t and $u_2(t, j) :=$ density of predator in patch j at time t, $j = 1, 2$; $t \in R$. The interaction between two species is described as a system of differential equations as follows:

$$\begin{aligned}
\dot{u}_1(t,1) &= \varepsilon u_1(t,1)(1 - \tfrac{u_1(t,1)}{K}) - \tfrac{\beta u_1(t,1) u_2(t,1)}{\beta + u_1(t,1)} \\
&\qquad + d_1(\rho_1(u_2(t,2)) u_1(t,2) - \rho_1(u_2(t,1)) u_1(t,1)), \\
\dot{u}_2(t,1) &= -\tfrac{u_2(t,1)(\gamma + \delta u_2(t,1))}{1 + u_2(t,1)} + \tfrac{\beta u_1(t,1) u_2(t,1)}{\beta + u_1(t,1)} \\
&\qquad + d_2(\rho_2(u_1(t,2)) u_2(t,2) - \rho_2(u_1(t,1)) u_2(t,1)), \\
\dot{u}_1(t,2) &= \varepsilon u_1(t,2)(1 - \tfrac{u_1(t,2)}{K}) - \tfrac{\beta u_1(t,2) u_2(t,2)}{\beta + u_1(t,2)} \\
&\qquad + d_1(\rho_1(u_2(t,1)) u_1(t,1) - \rho_1(u_2(t,2)) u_1(t,2)), \\
\dot{u}_2(t,2) &= -\tfrac{u_2(t,2)(\gamma + \delta u_2(t,2))}{1 + u_2(t,2)} + \tfrac{\beta u_1(t,2) u_2(t,2)}{\beta + u_1(t,2)} \\
&\qquad + d_2(\rho_2(u_1(t,1)) u_2(t,1) - \rho_2(u_1(t,2)) u_2(t,2)),
\end{aligned} \tag{3.44}$$

where $\varepsilon > 0$ is the specific growth rate of the prey in the absence of predation and without environmental limitation, $\beta > 0$, $K > 0$ are the half saturation constant and carrying capacity with respect to the prey respectively, $\gamma > 0$ and $\delta > 0$ are the minimal mortality and the limiting mortality of the predator, respectively (the natural assumption is $\gamma < \delta$). The meaning of the half saturation constant is that at $u_1 = \beta$ the specific growth rate $\frac{\beta u_1}{\beta + u_1}$ (called also a Holling type functional response) of the predator is equal to half its maximum β (the conversion rate is taken to be equal to the half saturation constant for sake of simplicity). The advantage of the present 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 quantity. $d_i > 0$, $(i = 1, 2)$ are the diffusion coefficients and $\rho_1 \in C^1$ is a positive increasing function of u_2, the density of the predator, $\rho_1' > 0$ and $\rho_2 \in C^1$ is a positive decreasing function of u_1 the density of the prey, $\rho_2' < 0$. The idea is that the dependence of the diffusion coefficient on the density of the other species reflects the inclination of a prey (or an activator) to leave a certain patch because of the danger (or the inhibition) and the tendency of a predator (or the inhibition) to stay at a certain patch because of the abundance of prey (or an activator). The functions ρ_i model the cross-diffusion effect. We say that the cross-diffusion is strong if $\left|\rho'_{iu_k}\right|$ $(i \neq k)$ is large. If by varying a parameter $\left|\rho'_{iu_k}\right|$ $(i \neq k)$ is increasing then we say that the cross diffusion effect is increasing. If $\rho_i = 1$, $i = 1$, 2 then we have mere "self-diffusion".

First we consider the kinetic system without migration, i.e. $d_1 = d_2 = 0$:

$$\begin{aligned} \dot{u}_1(t,1) &= \varepsilon u_1(t,1)(1 - \tfrac{u_1(t,1)}{K}) - \tfrac{\beta u_1(t,1) u_2(t,1)}{\beta + u_1(t,1)}, \\ \dot{u}_2(t,1) &= -\tfrac{u_2(t,1)(\gamma + \delta u_2(t,1))}{1 + u_2(t,1)} + \tfrac{\beta u_1(t,1) u_2(t,1)}{\beta + u_1(t,1)}, \\ \\ \dot{u}_1(t,2) &= \varepsilon u_1(t,2)(1 - \tfrac{u_1(t,2)}{K}) - \tfrac{\beta u_1(t,2) u_2(t,2)}{\beta + u_1(t,2)}, \\ \dot{u}_2(t,2) &= -\tfrac{u_2(t,2)(\gamma + \delta u_2(t,2))}{1 + u_2(t,2)} + \tfrac{\beta u_1(t,2) u_2(t,2)}{\beta + u_1(t,2)}. \end{aligned} \tag{3.45}$$

The following conditions are reasonable and natural:

$$\gamma < \beta \leq \delta, \tag{3.46}$$

$$\beta < K, \tag{3.47}$$

$$\gamma < \frac{\beta K}{\beta + K}. \tag{3.48}$$

Condition (3.46) ensures that the predator mortality is increasing with density, and that the predator null-cline has a reasonable concave down shape; (3.47) ensures that for the prey an Allée-effect zone exists where the increase of prey density is favourable to its growth rate; (3.48) is needed to have a positive equilibrium point of system (3.45). System (3.45) is made up by two identical uncoupled systems. Under these conditions each has (the same) positive equilibrium which is the intersection of the null-clines:

$$u_2 = H_1(u_1) := \frac{\varepsilon}{\beta K}(K - u_1)(\beta + u_1), \tag{3.49}$$

$$u_2 = H_2(u_1) := \frac{(\beta - \gamma) u_1 - \beta\gamma}{(\delta - \beta) u_1 + \beta\delta}. \tag{3.50}$$

Thus, denoting the coordinates of a positive equilibrium by $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$, these coordinates satisfy $\overline{u}_2 = H_1(\overline{u}_1) = H_2(\overline{u}_1)$.

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.

The Jacobian matrix of the system (3.45) linearized at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is

$$J_k = \begin{pmatrix} \Phi_1 & -\Phi_2 & 0 & 0 \\ \Phi_3 & -\Phi_4 & 0 & 0 \\ 0 & 0 & \Phi_1 & -\Phi_2 \\ 0 & 0 & \Phi_3 & -\Phi_4 \end{pmatrix}. \tag{3.51}$$

The characteristic polynomial is

$$D_4(\lambda) = (D_2(\lambda))^2, D_2(\lambda) = \lambda^2 + \lambda(\Phi_4 - \Phi_1) + \Phi_2\Phi_3 - \Phi_1\Phi_4, \tag{3.52}$$

where

$$\begin{aligned} \Phi_1 &= \frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)}, \ \Phi_2 = \frac{\beta\overline{u}_1}{\beta+\overline{u}_1}, \\ \Phi_3 &= \frac{\beta^2\overline{u}_2}{(\beta+\overline{u}_1)^2}, \quad \Phi_4 = \frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2}. \end{aligned} \tag{3.53}$$

The equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ lies in the Allée-effect zone if

$$H_1(\frac{k-\beta}{2}) < H_2(\frac{k-\beta}{2}), \tag{3.54}$$

i.e.

$$\frac{\varepsilon}{4\beta K}(K+\beta)^2 < -1 + \frac{(\delta-\gamma)K}{\beta^2 - \beta K + \delta K}. \tag{3.55}$$

Assume that

$$\Phi_4 - \Phi_1 > 0 \ \text{ and } \ \Phi_2\Phi_3 - \Phi_1\Phi_4 > 0, \tag{3.56}$$

then the coexistence equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is linearly asymptotically stable.

3.3.1 The Linearized Problem

For model (3.44) with cross-diffusion response (i.e., $\frac{\partial\rho_i(u)}{\partial u_j} \neq 0$, $i \neq j$) we see that $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is also a spatially homogeneous equilibrium of the system with cross-diffusion.

The Jacobian matrix of the system with cross-diffusion at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can be written as:

$J_D =$

$$\begin{pmatrix} \Phi_1 - d_1\rho_1 & -\Phi_2 - d_1\rho_1'\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ \Phi_3 - d_2\rho_2'\overline{u}_2 & -\Phi_4 - d_2\rho_2 & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ d_1\rho_1 & d_1\rho_1'\overline{u}_1 & \Phi_1 - d_1\rho_1 & -\Phi_2 - d_1\rho_1'\overline{u}_1 \\ d_2\rho_2'\overline{u}_2 & d_2\rho_2 & \Phi_3 - d_2\rho_2'\overline{u}_2 & -\Phi_4 - d_2\rho_2 \end{pmatrix}, \tag{3.57}$$

where $\rho_1$and ρ_1' are to be taken at $\overline{u}_2$ and ρ_2, ρ_2' at $\overline{u}_1$.

Theorem 6 *Under conditions (3.55), (3.56) if*

$$\Phi_1 - 2d_1\rho_1 > 0, \tag{3.58}$$

and $\rho_2(\overline{u}_1)$ is sufficiently large then Turing instability occurs.

Proof. $\det(J_D - \lambda I) =$

$$\begin{vmatrix} \Phi_1 - d_1\rho_1 - \lambda & -\Phi_2 - d_1\rho_1'\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ \Phi_3 - d_2\rho_2'\overline{u}_2 & -\Phi_4 - d_2\rho_2 - \lambda & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ d_1\rho_1 & d_1\rho_1'\overline{u}_1 & \Phi_1 - d_1\rho_1 - \lambda & -\Phi_2 - d_1\rho_1'\overline{u}_1 \\ d_2\rho_2'\overline{u}_2 & d_2\rho_2 & \Phi_3 - d_2\rho_2'\overline{u}_2 & -\Phi_4 - d_2\rho_2 - \lambda \end{vmatrix}. \tag{3.59}$$

Using the properties of determinant we get

$$\begin{vmatrix} \Phi_1 - \lambda & -\Phi_2 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ \Phi_3 & -\Phi_4 - \lambda & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ 0 & 0 & \Phi_1 - 2d_1\rho_1 - \lambda & -\Phi_2 - 2d_1\rho_1'\overline{u}_1 \\ 0 & 0 & \Phi_3 - 2d_2\rho_2'\overline{u}_2 & -\Phi_4 - 2d_2\rho_2 - \lambda \end{vmatrix}, \tag{3.60}$$

$$\begin{aligned} = \; & D_2(\lambda)\{\lambda^2 + \lambda[\Phi_4 - \Phi_1 + 2(d_1\rho_1 + d_2\rho_2)] + \Phi_2\Phi_3 - \Phi_1\Phi_4 \\ & +2d_1\Phi_4\rho_1 - 2d_2\rho_2(\Phi_1 - 2d_1\rho_1) + 2d_1\overline{u}_1\Phi_3\rho_1' \\ & -2d_2\rho_2'\overline{u}_2(\Phi_2 + 2d_1\rho_1'\overline{u}_1)\}. \end{aligned} \tag{3.61}$$

We know that $D_2(\lambda)$ has two roots with negative real parts. By (3.56), clearly, $\Phi_4 - \Phi_1 + 2(d_1\rho_1 + d_2\rho_2) > 0$. The other polynomial will have a negative and a positive root if its constant term is negative. This can be achieved if $\rho_2(\overline{u}_1)$ is increased.

Remark 10 *As I have mentioned in Chapter 2, if (2.68) holds and there is no cross-diffusion then the equilibrium remains stable for any $d_2 > 0$. Still, (3.58) may hold, i.e. in this case only the cross-diffusion effect may destabilize the equilibrium.*

Remark 11 *If the parameters have been chosen so that*

$$\Phi_1 - 2d_1 > 0 \text{ and } \Phi_1 - 2d_1\rho_1 < 0, \tag{3.62}$$

then the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ remains asymptotically stable for any $d_2 > 0$ and $\rho_2 > 0$ in the cross-diffusion case while, as we have seen, it will undergo a Turing bifurcation in the absence of cross-diffusion.

3.3.2 Numerical Investigations

I illustrate the results by the following example and we are looking for conditions which imply Turing instability (diffusion driven instability).

Example 7: We choose

$$\rho_1(u_2) = \frac{m_1 u_2}{1 + u_2}, \rho_2(u_1) = m_2 \exp(\frac{-u_1}{m_2}), \; m_1, \; m_2 > 0. \tag{3.63}$$

If $\beta = 0.1$, $\gamma = 0.01$, $\delta = 0.1055$, $\varepsilon = 1$, $K = 1$. The unique positive equilibrium is $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2) = (0.4486,\ 3.0250,\ 0.4486,\ 3.0250)$. We see that this point is in the Allée-effect zone $(0.4486 < 0.45)$ and it is asymptotically stable with respect to the kinetic system (3.45).

If $d_2 = 1$ (resp.2.5) then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable (resp. unstable).

For the cross-diffusion system we consider m_2 as a bifurcation parameter. In this case at $d_1 = 1, .d_2 = 1, m_1 = 0.001$ and $m_{2crit} \cong 350.7$, we have four eigenvalues $\lambda_i (i = 1, 2, 3, 4)$ such that $\operatorname{Re} \lambda_i < 0, (i = 1, 2, 3)$ and $\lambda_4 = 0$.

If $m_2 < m_{2crit} \Rightarrow \operatorname{Re} \lambda_i < 0,\ (i = 1, 2, 3, 4)$, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable .

If $m_2 > m_{2crit} \Rightarrow \operatorname{Re} \lambda_i < 0, (i = 1, 2, 3)$ and $\lambda_4 > 0$, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is unstable.

If $d_1 = 0.0001$, $d_{2crit} = 2.5$ and $m_1 = 100$, then, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable for all m_2.

In this example $\left|\rho'_{2u_1}(u_1, u_2)\right| = \exp(-\frac{u_1}{m_2})$. As we see if m_2 is increased for fixed $u_1$this derivative is increasing, i.e. the cross-diffusion effect is increasing and the spatially homogeneous equilibrium loses its stability. Numerical calculations show that two new spatially non-constant equilibria emerge (see Table 7 and Figure 7), and these equilibria are asymptotically stable.

Chapter 4

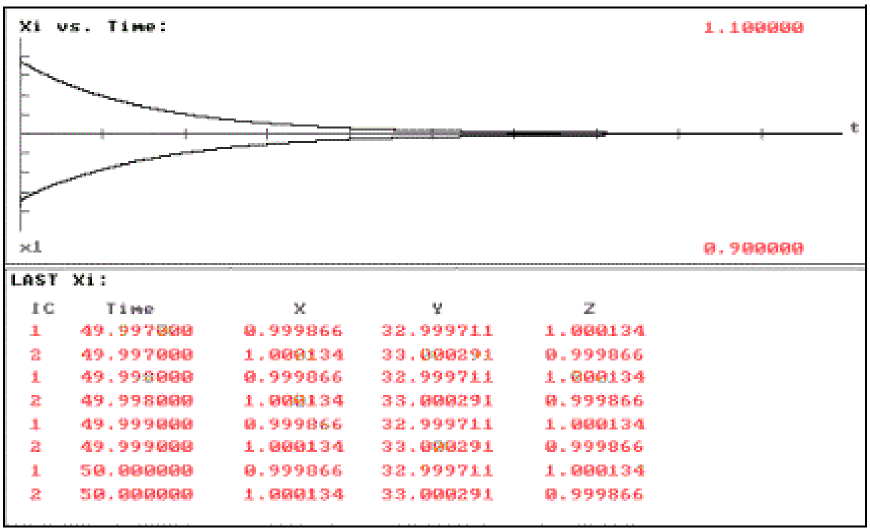
Appendices

4.1 Appendix to Chapter 2

Table 1: Equilibria of Example 1 before and after bifurcation.

d_2	$u_1(t,1)$	$u_2(t,1)$	$u_1(t,2)$	$u_2(t,2)$
1000	1.000000000	33.00000000	1.000000000	33.00000000
	1.036370925	33.07433937	.9653313619	32.95021445
1010	1.000000000	33.00000000	1.000000000	33.00000000
	.9653313619	32.95021445	1.036370925	33.07433937
	1.074868882	33.17381736	.9320140124	32.92539437
1015	1.000000000	33.00000000	1.000000000	33.00000000
	.9320140124	32.92539437	1.074868882	33.17381736
	1.100598745	33.25055797	.9114645403	32.92320726
1020	1.000000000	33.00000000	1.000000000	33.00000000
	.9114645403	32.92320726	1.100598745	33.25055797
	1.140164553	33.38238717	.8822598022	32.94018541
1030	1.000000000	33.00000000	1.000000000	33.00000000
	.8822598022	32.94018541	1.140164553	33.38238717
	1.200526588	33.61072042	.8426276092	33.00836211
1050	1.000000000	33.00000000	1.000000000	33.00000000
	.8426276092	33.00836211	1.200526588	33.61072042
	1.313535754	34.10544965	.7815757376	33.24970043
1100	1.000000000	33.00000000	1.000000000	33.00000000
	.7815757376	33.24970043	1.313535754	34.10544965

Figure 1a: Graphs of the coordinate $u_1(t,1)$ of two solutions of Example 1 corresponding to the respective initial conditions (0.932, 33.925, 1.074, 33.173), (1.0748, 33.1738, 0.932, 33.925); before bifurcation at $d_2 = 900$ and after bifurcation at $d_2 = 1015$ (see Table 1); (Figure produced by applying PHASER).



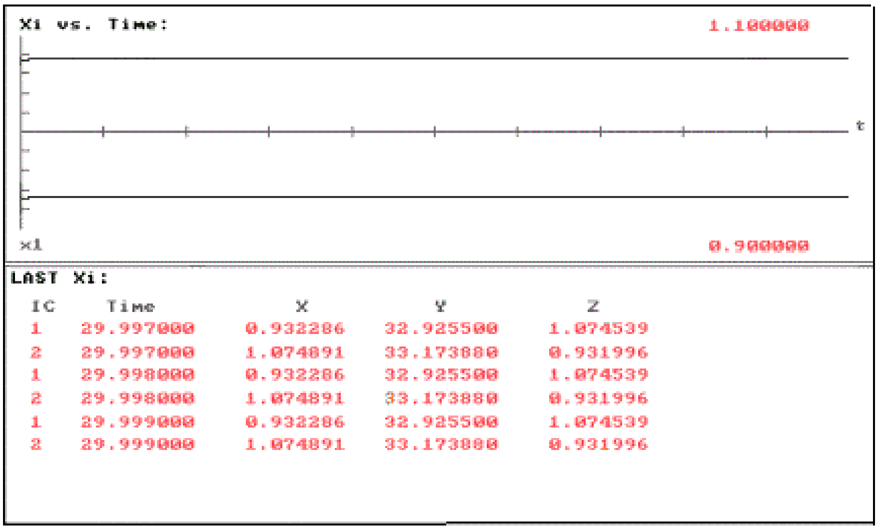
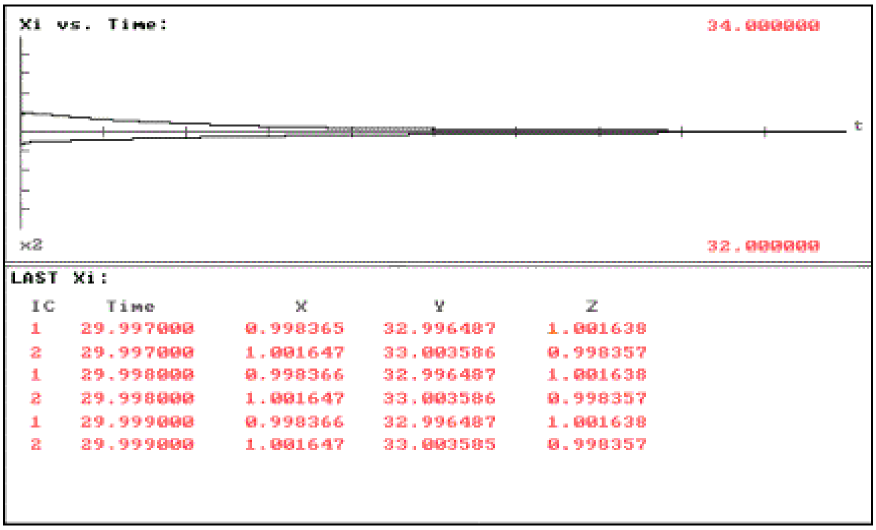


Figure 1b: Graphs of the coordinate $u_1(t, 1)$ of two solutions of Example 1 corresponding to the respective initial conditions (0.932, 33.925, 1.074, 33.173), (1.0748, 33.1738, 0.932, 33.925); before bifurcation at $d_2 = 900$ and after bifurcation at $d_2 = 1015$ (see Table 1); (Figure produced by applying PHASER).



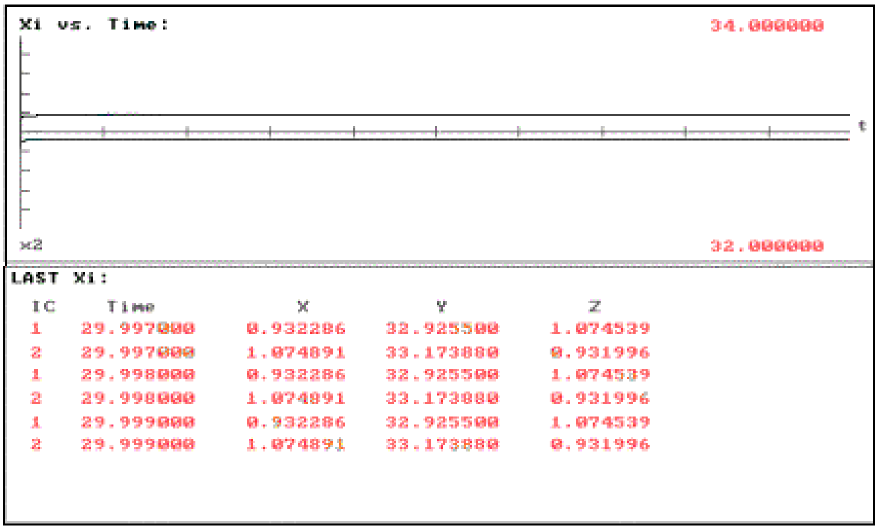
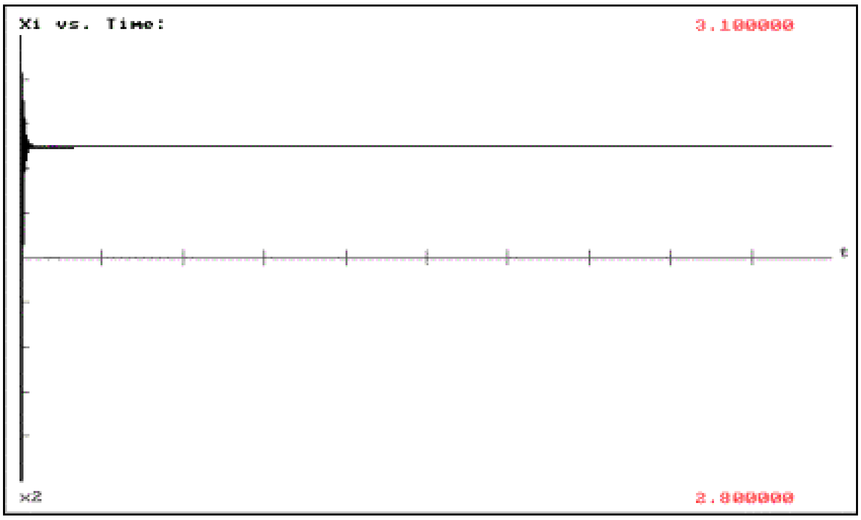


Table 2 : Equilibria of the Example 2 before and after bifurcation.

d_2	$u_1(t,1)$	$u_2(t,1)$	$u_1(t,2)$	$u_2(t,2)$
2.024	.4486421535	3.024981563	.4486421535	3.024981563
2.025	.4458431186	3.024834058	.4514418231	3.024972373
	.4486421535	3.024981563	.4486421535	3.024981563
	.4514418231	3.024972373	.4458431186	3.024834058
2.05	.4293231321	3.020772347	.4679918523	3.021716001
	.4486421535	3.024981563	.4486421535	3.024981563
	.4679918523	3.021716001	.4293231321	3.020772347
2.5	.3788250727	2.974518384	.5189281294	2.977322028
	.4486421535	3.024981563	.4486421535	3.024981563
	.5189281294	2.977322028	.3788250727	2.974518384
3	.3612552241	2.946467825	.5368308539	2.949395746
	.4486421535	3.024981563	.4486421535	3.024981563
	.5368308539	2.949395746	.3612552241	2.946467825
5	.3380800939	2.900027778	.5606719399	2.902254925
	.4486421535	3.024981563	.4486421535	3.024981563
	.5606719399	2.902254925	.3380800939	2.900027778
10	.3256132296	2.870603510	.5736383640	2.871844287
	.4486421535	3.024981563	.4486421535	3.024981563
	.5736383640	2.871844287	.3256132296	2.870603510

Figure 2a Graphs of the coordinate $u_2(t,1)$ of five solutions of Example 2 corresponding to the initial conditions (0.33, 2.85, 0.5, 2.91), (3.332, 2.88, 0.542, 2.85), (3.1, 2.851, 3.2, 2.9), (0.542, 2.85, 0.332, 2.88), (0.5, 3.0, 0.3, 3.1); before bifurcation at $d_2 = 2$; and the projection to the $u_2(.,1)$, $u_1(.,2)$ plane of the phase portrait of the same solutions (Figure produced by applying PHASER).



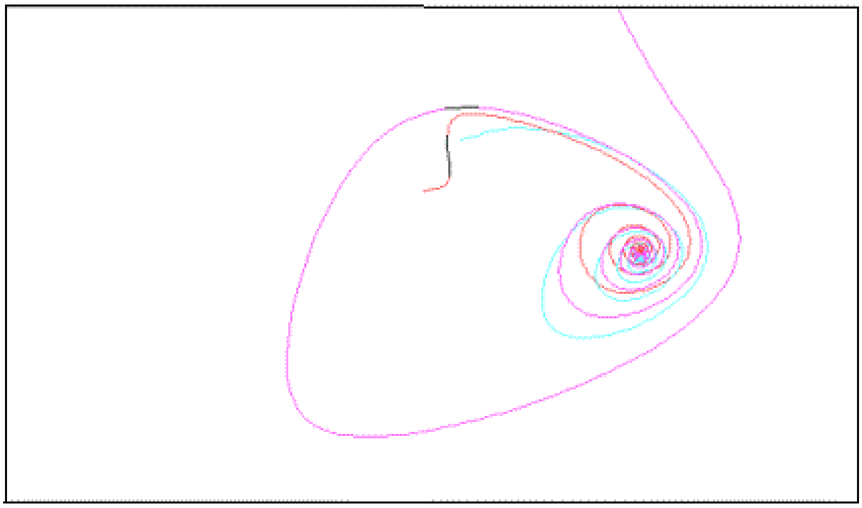
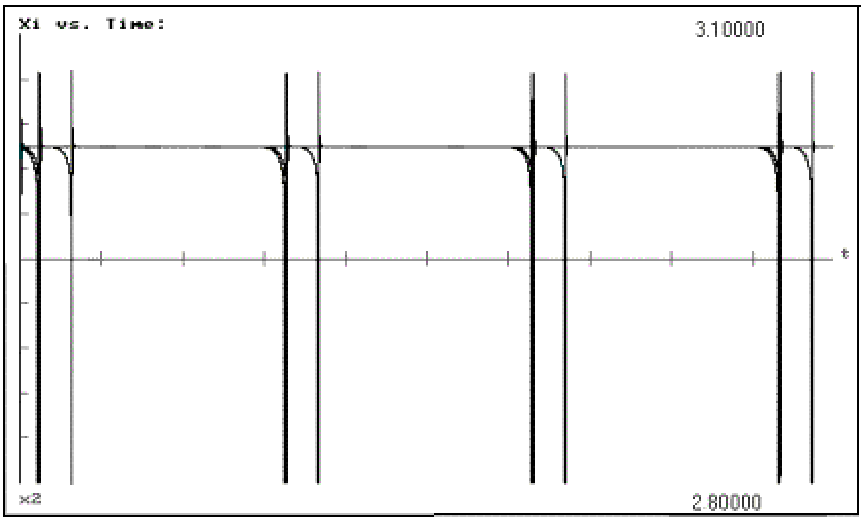
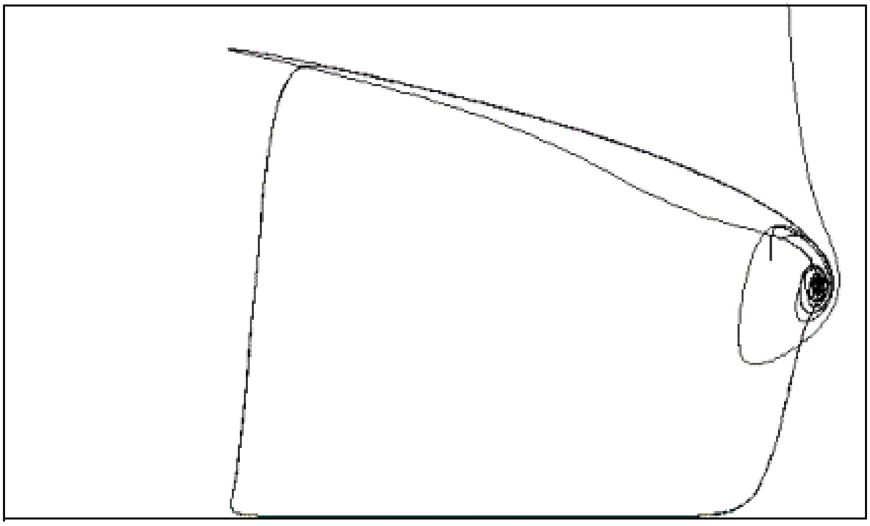


Figure 2b Graphs of the coordinate $u_2(t,1)$ of five solutions of Example 2 corresponding to the initial conditions (0.33, 2.85, 0.5, 2.91), (3.332, 2.88, 0.542, 2.85), (3.1, 2.851, 3.2, 2.9), (0.542, 2.85, 0.332, 2.88), (0.5, 3.0, 0.3, 3.1); after bifurcation at $d_2 = 2.5$; and the projection to the $u_2(.,1)$, $u_1(.,2)$ plane of the phase portrait of the same solutions (Figure produced by applying PHASER).



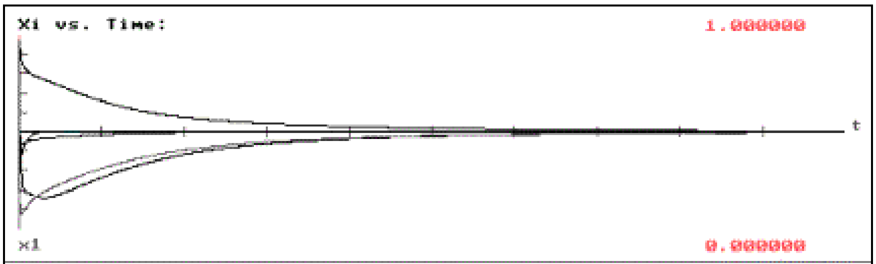


4.2 Appendix to Chapter 3

Table 3. Equilibria of Example 3 before and after bifurcation.

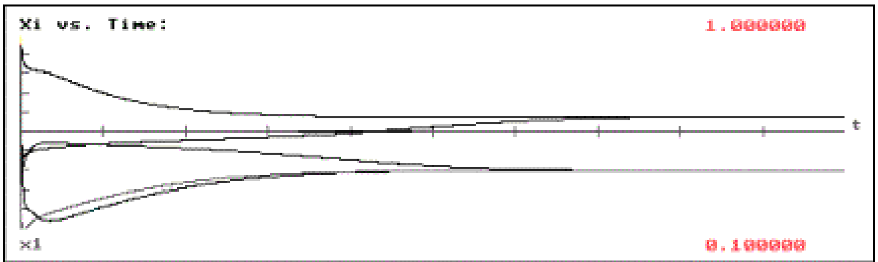
d_2	$u_1(t,1)$	$u_2(t,1)$	$u_1(t,2)$	$u_2(t,2)$
0.5827	.5000000000	2.125000000	.5000000000	2.125000000
	.5010077539	2.123988386	.4989907276	.4693014611
0.58272	.5000000000	2.125000000	.5000000000	.5000000000
	.4989907276	2.126012509	.5010077539	.5293725729
	.5021693912	2.122821494	.4978235602	2.127182662
0.58275	.5000000000	2.125000000	.5000000000	2.125000000
	.4978235602	2.127182662	.5021693912	2.122821494
	.5059395913	2.119027941	.4940072986	2.131003365
0.583	.5000000000	2.125000000	.5000000000	2.125000000
	.4940072986	2.131003365	.5059395913	2.119027941
	.5166055295	2.108235670	.4829743642	2.142011446
0.585	.5000000000	2.125000000	.5000000000	2.125000000
	.4829743642	2.142011446	.5166055295	2.108235670
	.5293725729	2.095171870	.4693014611	2.155603969
0.59	.5000000000	2.125000000	.5000000000	2.125000000
	.4693014611	2.155603969	.5293725729	2.095171870
	.5651072032	2.057393659	.4284802446	2.196228829
0.62	.5000000000	2.125000000	.5000000000	2.125000000
	.4284802446	2.196228829	.5651072032	2.057393659
	.6149762005	2.000472689	.3679939971	2.257933065
0.7	.5000000000	2.125000000	.5000000000	2.125000000
	.3679939971	2.257933065	.6149762005	2.000472689
	.7090000193	1.881442605	.2686398427	2.367505431
0.9	.5000000000	2.125000000	.5000000000	2.125000000
	.2686398427	2.367505431	.7090000193	1.881442605
	.7647806699	1.808440651	.2260228448	2.418691192
1	.5000000000	2.125000000	.5000000000	2.125000000
	.2260228448	2.418691192	.7647806699	1.808440651

Figure 3a. Graphs of the coordinate $u_1(t, 1)$ of five solutions of Example 3 corresponding to the respective initial conditions (0.55, 1.50, 0.20, 0.60), (0.30, 1.50, 0.40, 1.50), (0.40, 2.40, 0.50, 1.00), (1.00, 2.20, 0.40, 2.50), (0.70, 2.00, 0.10, 2.00); before bifurcation at $d_2 = 0.5$ and after bifurcation at $d_2 = 0.7$ (see Table 3); (Figure produced by applying PHASER).



LAST Xi:

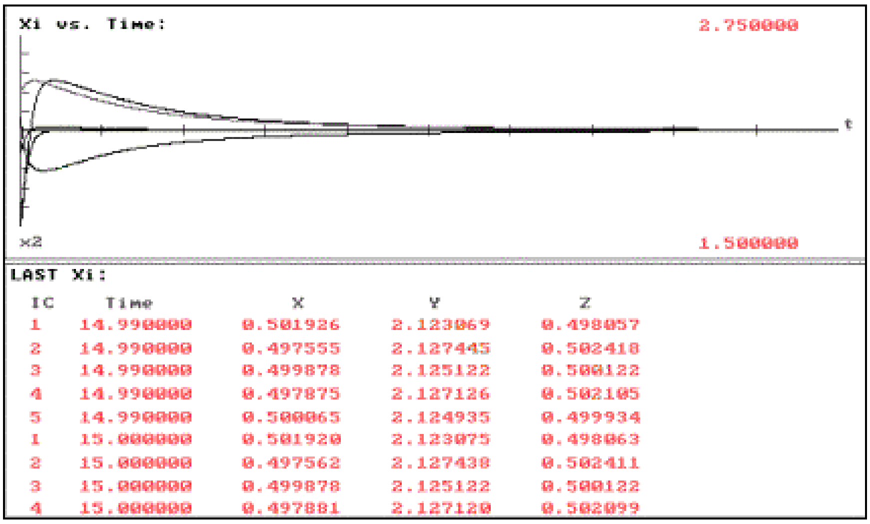
IC	Time	X	Y	Z
1	14.990000	0.501926	2.123069	0.498057
2	14.990000	0.497555	2.127445	0.502418
3	14.990000	0.499878	2.125122	0.500122
4	14.990000	0.497875	2.127126	0.502105
5	14.990000	0.500065	2.124935	0.499934
1	15.000000	0.501920	2.123075	0.498063
2	15.000000	0.497562	2.127438	0.502411
3	15.000000	0.499878	2.125122	0.500122
4	15.000000	0.497881	2.127120	0.502099



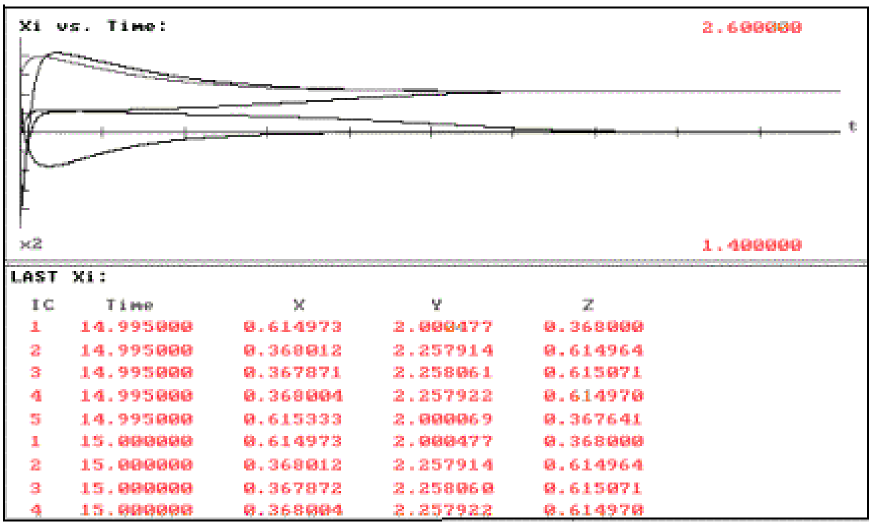
LAST Xi:

IC	Time	X	Y	Z
1	14.990000	0.614973	2.000477	0.368000
2	14.990000	0.368012	2.257914	0.614964
3	14.990000	0.367871	2.258061	0.615071
4	14.990000	0.368004	2.257922	0.614970
5	14.990000	0.615336	2.000066	0.367639
1	15.000000	0.614973	2.000477	0.368000
2	15.000000	0.368012	2.257914	0.614964
3	15.000000	0.367872	2.258060	0.615071
4	15.000000	0.368004	2.257922	0.614970

Figure 3b. Graphs of the coordinate $u_2(t, 1)$ of five solutions of Example 3 corresponding to the respective initial conditions (0.55, 1.50, 0.20, 0.60), (0.30, 1.50, 0.40, 1.50), (0.40, 2.40, 0.50, 1.00), (1.00, 2.20, 0.40, 2.50), (0.70, 2.00, 0.10, 2.00); before bifurcation at $d_2 = 0.5$ and after bifurcation at $d_2 = 0.7$ (see Table 3); (Figure produced by applying PHASER).



IC	Time	X	Y	Z
1	14.990000	0.501926	2.123069	0.498057
2	14.990000	0.497555	2.127445	0.502418
3	14.990000	0.499878	2.125122	0.500122
4	14.990000	0.497875	2.127126	0.502105
5	14.990000	0.500065	2.124935	0.499934
1	15.000000	0.501920	2.123075	0.498063
2	15.000000	0.497562	2.127438	0.502411
3	15.000000	0.499878	2.125122	0.500122
4	15.000000	0.497881	2.127120	0.502099

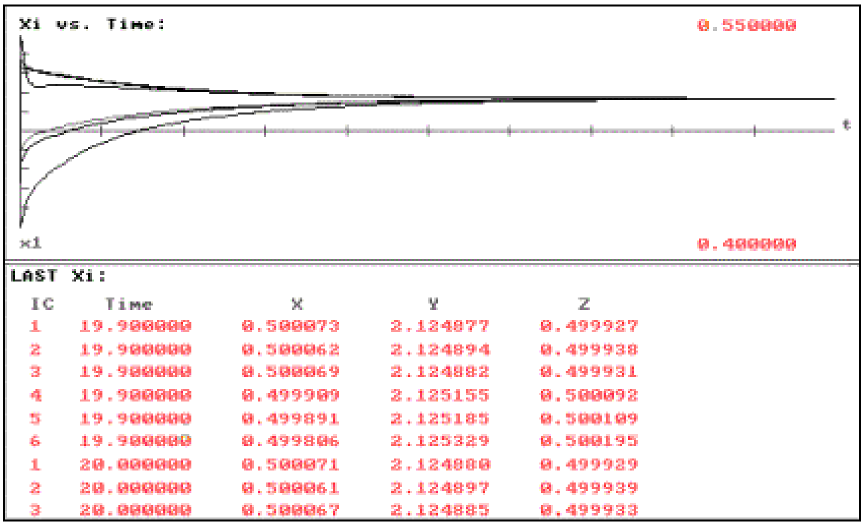


IC	Time	X	Y	Z
1	14.995000	0.614973	2.000477	0.368000
2	14.995000	0.368012	2.257914	0.614964
3	14.995000	0.367871	2.258061	0.615071
4	14.995000	0.368004	2.257922	0.614970
5	14.995000	0.615333	2.000069	0.367641
1	15.000000	0.614973	2.000477	0.368000
2	15.000000	0.368012	2.257914	0.614964
3	15.000000	0.367872	2.258060	0.615071
4	15.000000	0.368004	2.257922	0.614970

Table 4. Equilibria of Example 4 before and after bifurcation.

d_2	$u_1(t,1)$	$u_2(t,1)$	$u_1(t,2)$	$u_2(t,2)$
13.883	.5000000000	2.125000000	.5000000000	2.125000000
	.5014814431	2.122287989	.4985368540	2.127694220
13.884	.5000000000	2.125000000	.5000000000	2.125000000
	.4985368540	2.127694220	.5014814431	2.122287989
	.5024848312	2.120459963	.4975662194	2.129490400
13.885	.5000000000	2.125000000	.5000000000	2.125000000
	.4975662194	2.129490400	.5024848312	2.120459963
	.5231171757	2.084228374	.4806680566	2.162088813
14	.5000000000	2.125000000	.5000000000	2.125000000
	.4806680566	2.162088813	.5231171757	2.084228374
	.5813860699	1.991069850	.4523622714	2.225928186
15	.5000000000	2.125000000	.5000000000	2.125000000
	.4523622714	2.225928186	.5813860699	1.991069850
	.6686054058	1.864463939	.4343277017	2.283720787
18	.5000000000	2.125000000	.5000000000	2.125000000
	.4343277017	2.283720787	.6686054058	1.864463939
	.7062101228	1.812453409	.4308733557	2.301200284
20	.5000000000	2.125000000	.5000000000	2.125000000
	.4308733557	2.301200284	.7062101228	1.812453409
	.7693452176	1.727299697	.4283289249	2.324188044
25	.5000000000	2.125000000	.5000000000	2.125000000
	.4283289249	2.324188044	.7693452176	1.727299697

Figure 4a. Graphs of the coordinate $u_1(t,1)$ of five solutions of Example 4 corresponding to the respective initial conditions (0.53, 2.10, 0.485, 2.20), (0.55, 2.30, 0.485, 2.19), (0.525, 2.088, 0.482, 2.18), (0.46, 2.14, 0.52, 2.06), (0.45, 2.15, 0.515, 2.02); before bifurcation at $d_2 = 10$ and after bifurcation at $d_2 = 14$ (see Table 4); (Figure produced by applying PHASER).



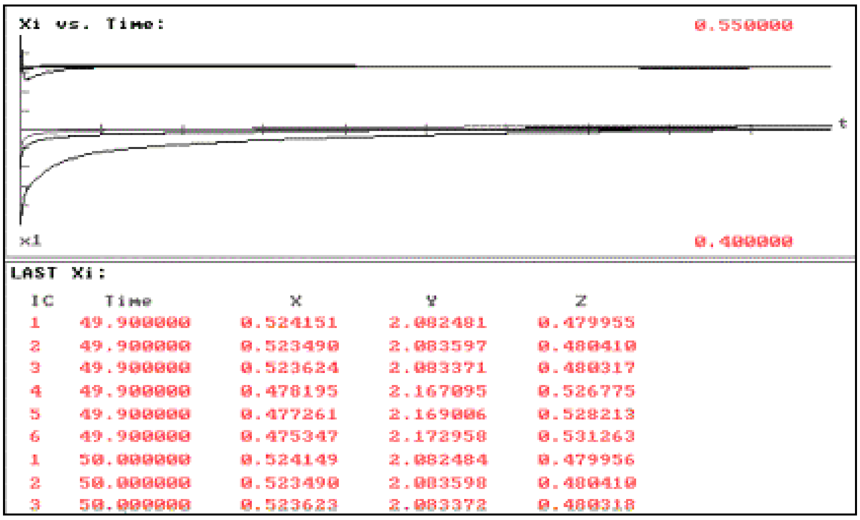
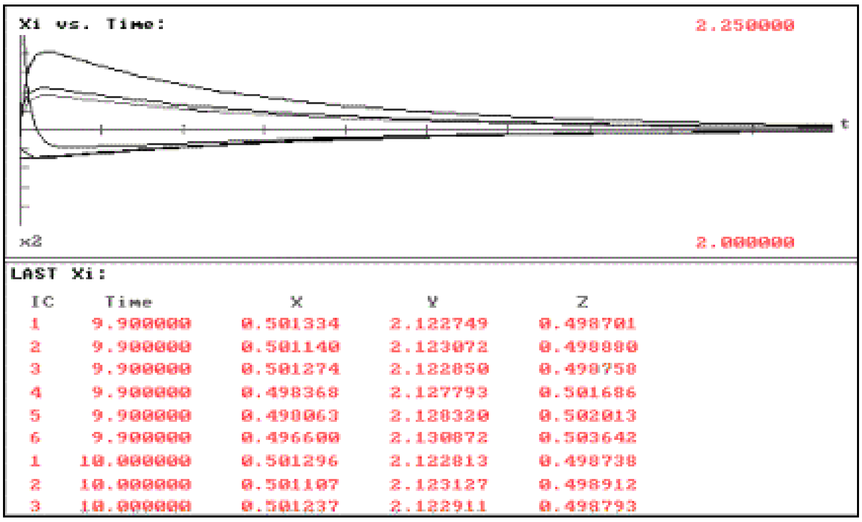


Figure 4b. Graphs of the coordinate $u_2(t,1)$ of five solutions of Example 4 corresponding to the respective initial conditions (0.53, 2.10, 0.485, 2.20), (0.55, 2.30, 0.485, 2.19), (0.525, 2.088, 0.482, 2.18), (.46, 2.14, 0.52, 2.06), (0.45, 2.15, 0.515, 2.02); before bifurcation at $d_2 = 10$ and after bifurcation at $d_2 = 14$ (see Table 4); (Figure produced by applying PHASER).



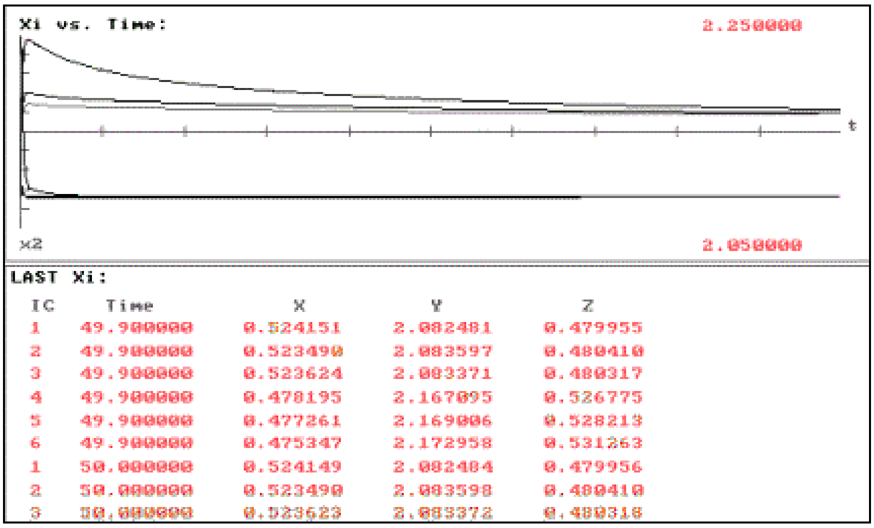
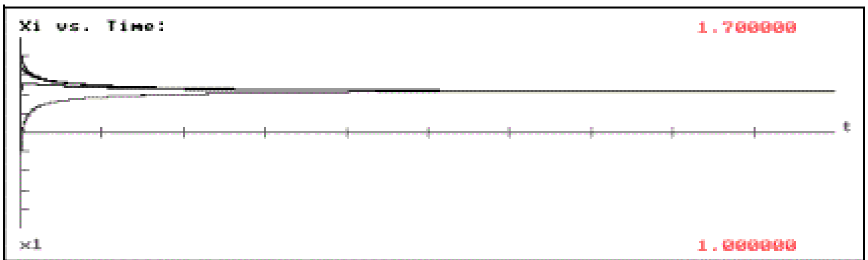


Table 5: Equilibria of Example 5 before and after bifurcation.

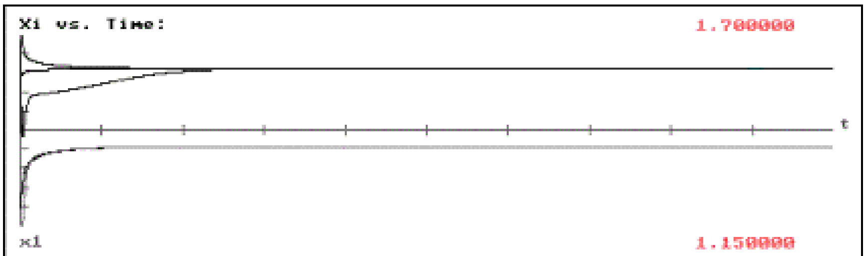
d_2	$u_1(t,1)$	$u_2(t,1)$	$u_1(t,2)$	$u_2(t,2)$
28	1.500000000	1.375000000	1.500000000	1.375000000
	1.524440807	1.403943678	1.474516967	1.344807960
28.2	1.500000000	1.375000000	1.500000000	1.375000000
	1.474516967	1.344807960	1.524440807	1.403943678
	1.574289053	1.462917090	1.415068046	1.274335600
29	1.500000000	1.375000000	1.500000000	1.375000000
	1.415068046	1.274335600	1.574289053	1.462917090
	1.602257674	1.495956494	1.376189993	1.228230906
30	1.500000000	1.375000000	1.500000000	1.375000000
	1.376189993	1.228230906	1.602257674	1.495956494
	1.683294096	1.591314489	1.225824281	1.049861530
40	1.500000000	1.375000000	1.500000000	1.375000000
	1.225824281	1.049861530	1.683294096	1.591314489
	1.704327936	1.615899482	1.169559919	.9830950704
50	1.500000000	1.375000000	1.500000000	1.375000000
	1.169559919	.9830950704	1.704327936	1.615899482
	1.714081033	1.627253651	1.138343964	.9460399293
60	1.500000000	1.375000000	1.500000000	1.375000000
	1.138343964	.9460399293	1.714081033	1.627253651
	1.723234442	1.637870036	1.104276166	.9055833674
80	1.500000000	1.500000000	1.500000000	1.500000000
	1.104276166	.9055833674	1.723234442	1.637870036
	1.727536907	1.642841684	1.085923814	.8837801086
100	1.500000000	1.500000000	1.500000000	1.500000000
	1.085923814	.8837801086	1.727536907	1.642841684

Figure 5a. Graphs of the coordinate $u_1(t,1)$ of five solutions of Example 5 corresponding to the respective initial conditions (1.80, 1.60, 1.50, 1.25), (1.20, 1.10, 1.59, 1.47), (1.58, 1.45, 1.36, 1.22), (1.00, 1.10, 1.585, 1.47), (1.65, 1.100, 1.320, 1.500); before bifurcation at $d_2 = 28$ and after bifurcation at $d_2 = 30$, (see Table 5) (Figure produced by applying PHASER).



LAST Xi:

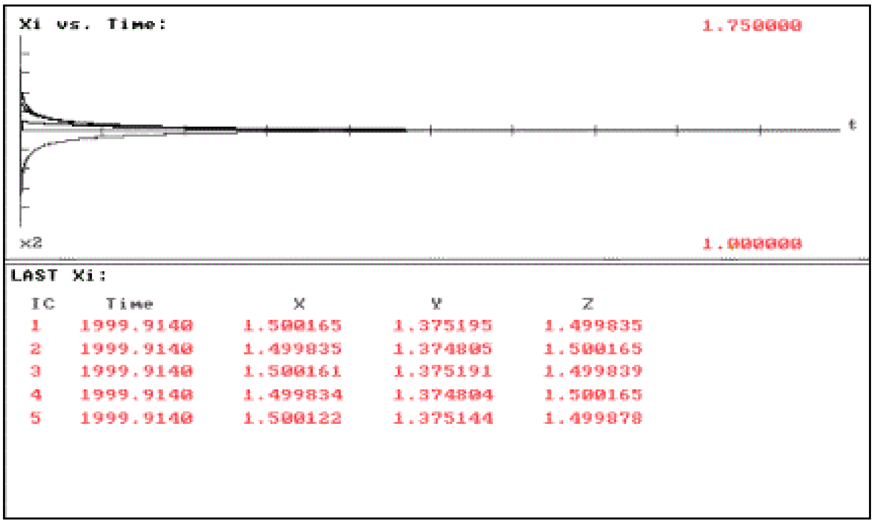
IC	Time	X	Y	Z
1	1999.9140	1.500165	1.375195	1.499835
2	1999.9140	1.499835	1.374805	1.500165
3	1999.9140	1.500161	1.375191	1.499839
4	1999.9140	1.499834	1.374804	1.500165
5	1999.9140	1.500122	1.375144	1.499878



LAST Xi:

IC	Time	X	Y	Z
1	299.90000	1.602258	1.495956	1.376190
2	299.90000	1.376190	1.228231	1.602258
3	299.90000	1.602258	1.495956	1.376190
4	299.90000	1.376190	1.228231	1.602258
5	299.90000	1.602258	1.495956	1.376190
1	300.00000	1.602258	1.495956	1.376190
2	300.00000	1.376190	1.228231	1.602258
3	300.00000	1.602258	1.495956	1.376190
4	300.00000	1.376190	1.228231	1.602258

Figure 5b. Graphs of the coordinate $u_2(t, 1)$ of five solutions of Example 5 corresponding to the respective initial conditions (1.80, 1.60, 1.50, 1.25), (1.20, 1.10, 1.59, 1.47), (1.58, 1.45, 1.36, 1.22), (1.00, 1.10, 1.585, 1.47), (1.65, 1.100, 1.320, 1.500); before bifurcation at $d_2 = 28$ and after bifurcation at $d_2 = 30$, (see Table 5) (Figure produced by applying PHASER).



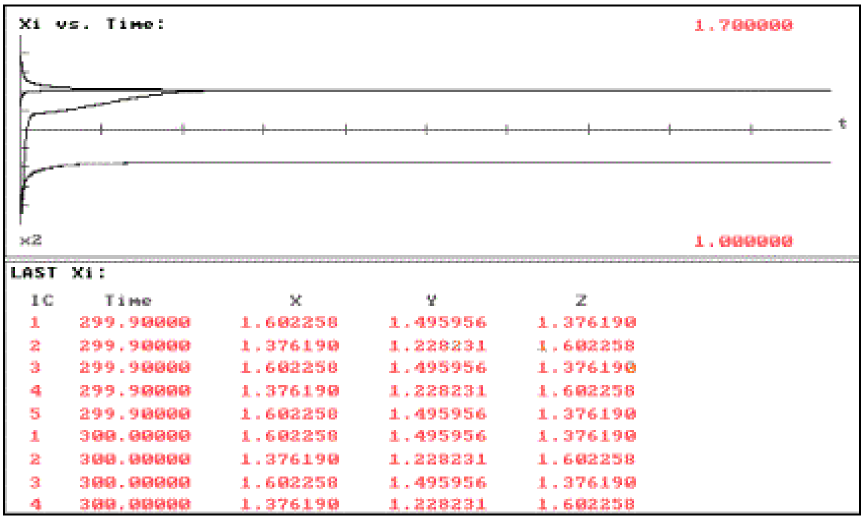
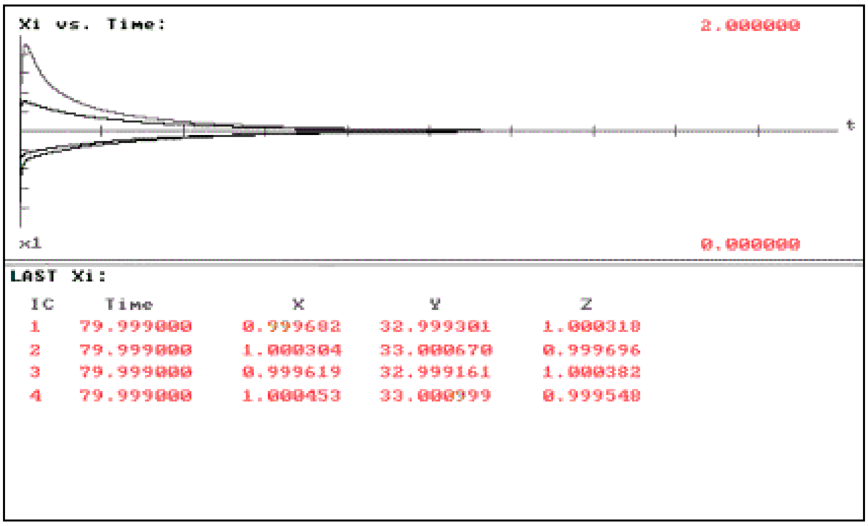


Table 6: Equilibria of Example 6 before and after bifurcation.

m_2	$u_1(t,1)$	$u_2(t,1)$	$u_1(t,2)$	$u_2(t,2)$
923	1.000000000	33.00000000	1.000000000	33.00000000
	0.972054740	32.95268025	1.029013814	33.06268396
924	1.000000000	33.00000000	1.000000000	33.00000000
	1.029013814	33.06268396	0.972054740	32.95268025
	0.925412134	32.90756707	1.082739872	33.20954082
930	1.000000000	33.00000000	1.000000000	33.00000000
	1.082739872	33.20954082	0.925412134	32.90756707
	0.886882196	32.90928234	1.133078158	33.37702687
940	1.000000000	33.00000000	1.000000000	33.00000000
	1.133078158	33.37702687	0.886882196	32.90928234
	0.860562652	32.93541297	1.171211561	33.51966483
950	1.000000000	33.00000000	1.000000000	33.00000000
	1.171211561	33.51966483	0.860562652	32.93541297
	0.839838937	32.97292415	1.203757263	33.65052577
960	1.000000000	33.00000000	1.000000000	33.00000000
	1.203757263	33.65052577	0.839838937	32.97292415
	0.782414455	33.17586301	1.308603529	34.11782822
1000	1.000000000	33.00000000	1.000000000	33.00000000
	1.308603529	34.11782822	0.782414455	33.17586301

Figure 6a. Graphs of the coordinate $u_1(t, 1)$ of four solutions of Example 6 corresponding to the respective initial conditions (0.77, 33.10, 1.30, 34.00), (1.30, 37.00, 0.77, 33.10), (0.784, 33.20, $1.32, 34.20$), (1.31, 34.20, 0.80, 33.30); before bifurcation at $m_2 = 900$ and after bifurcation at $m_2 = 1000$ (see Table 6); (Figure produced by applying PHASER).



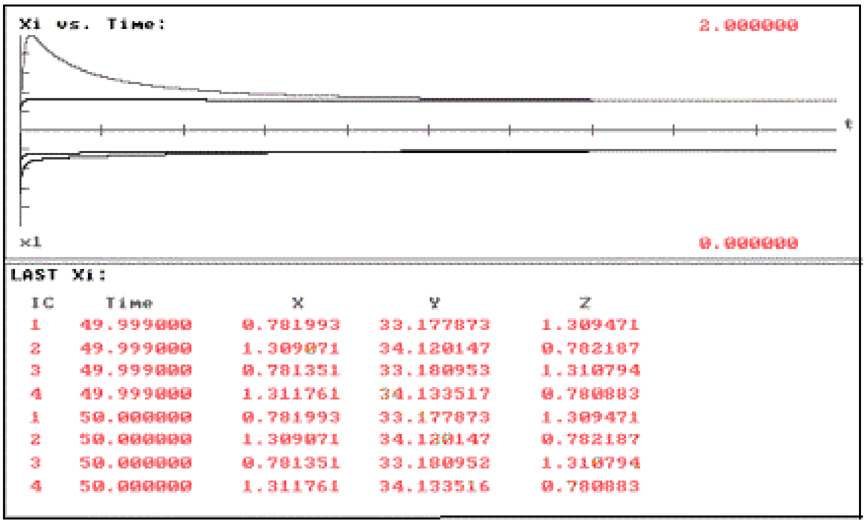
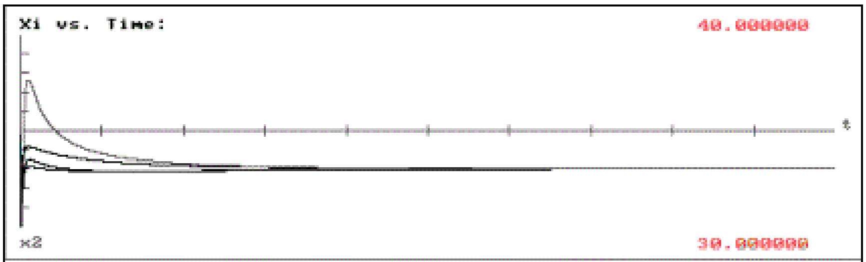
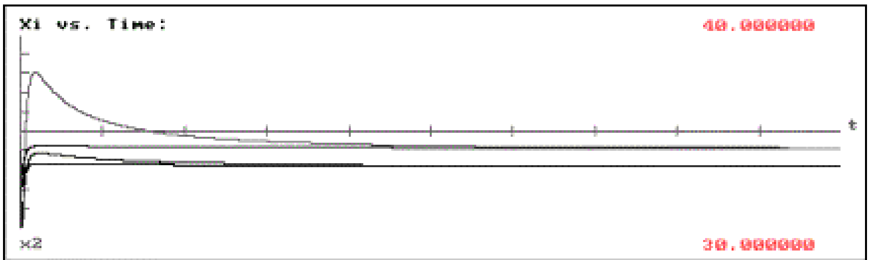


Figure 6b. Graphs of the coordinate $u_2(t, 1)$ of five solutions of Example 6 corresponding to the respective initial conditions (0.77, 33.10, 1.30, 34.00), (1.30, 37.00, 0.77, 33.10), (0.784, 33.20, 1.32, 34.20), (1.31, 34.20, 0.80, 33.30); before bifurcation at $m_2 = 900$ and after bifurcation at $m_2 = 1000$ (see Table 6); (Figure produced by applying PHASER).



LAST Xi:

IC	Time	X	Y	Z
1	79.999000	0.999682	32.999301	1.000318
2	79.999000	1.000304	33.000670	0.999696
3	79.999000	0.999619	32.999161	1.000382
4	79.999000	1.000453	33.000999	0.999548



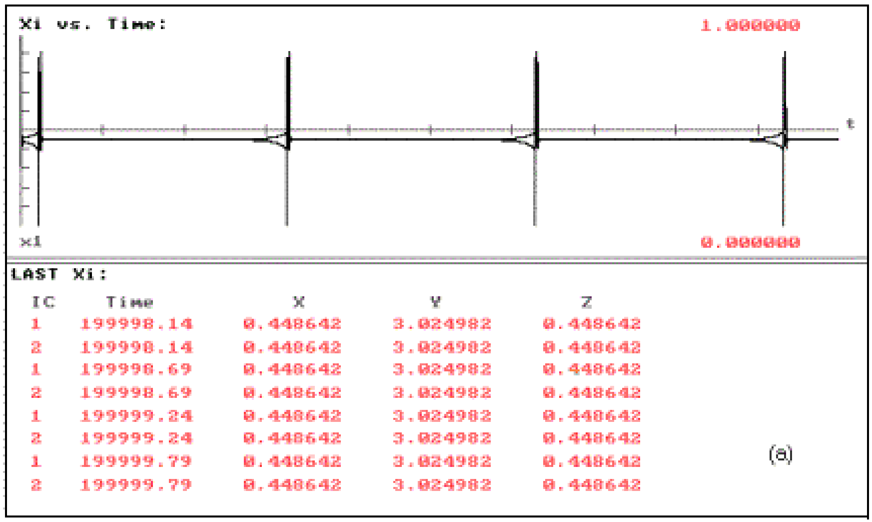
LAST Xi:

IC	Time	X	Y	Z
1	49.999000	0.781993	33.177873	1.309471
2	49.999000	1.309071	34.120147	0.782187
3	49.999000	0.781351	33.180953	1.310794
4	49.999000	1.311761	34.133517	0.780883
1	50.000000	0.781993	33.177873	1.309471
2	50.000000	1.309071	34.120147	0.782187
3	50.000000	0.781351	33.180952	1.310794
4	50.000000	1.311761	34.133516	0.780883

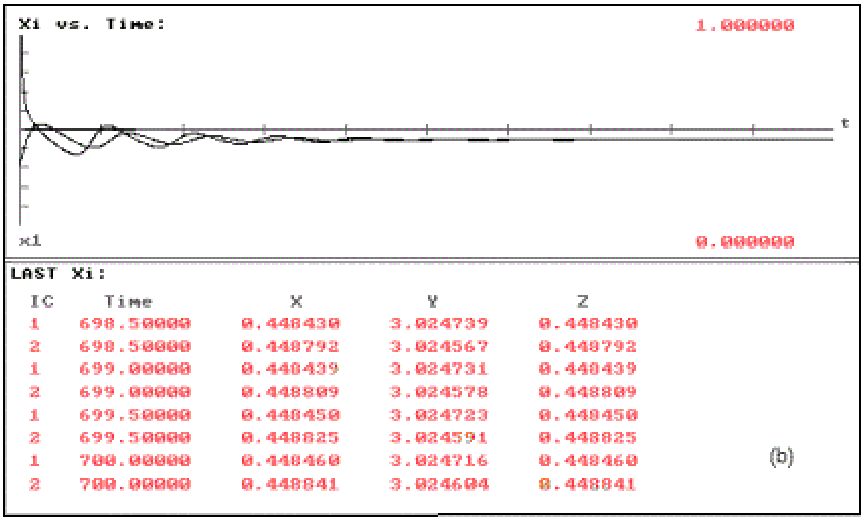
Table 7: Equilibria of Example 7 before and after Turing bifurcation.

m_2	$u_1(t,1)$	$u_2(t,1)$	$u_1(t,2)$	$u_2(t,2)$
350	.4486421535	3.024981563	.4486421535	3.024981563
	.4378285520	3.023718369	.4594667816	3.023905740
355	.4486421535	3.024981563	.4486421535	3.024981563
	.4594667816	3.023905740	.4378285520	3.023718369
	.4293426859	3.021090741	.4679770577	3.021415850
365	.4486421535	3.024981563	.4486421535	3.024981563
	.4679770577	3.021415850	.4293426859	3.021090741
	..4239447856	3.018670501	.4733980189	3.019075240
375	.4486421535	3.024981563	.4486421535	3.024981563
	.4733980189	3.019075240	.4239447856	3.018670501
	.4198086580	3.016422000	.4775559683	3.016882011
385	.4486421535	3.024981563	.4486421535	3.024981563
	.4775559683	3.016882011	.4198086580	3.016422000
	.4149242890	3.013326528	.4824709584	3.013843903
400	.4486421535	3.024981563	.4486421535	3.024981563
	.4824709584	3.013843903	.4149242890	3.013326528

Figure 7a: Graphs of the coordinate $u_1(t,1)$ of two solutions of Example 7 corresponding to the respective initial conditions (0.33, 2.85, 0.5, 2.91), (3.332, 2.88, 0.542, 2.85); (a) for self-diffusion at $d_1 = 0.0001$, $d_2 = 2.5$,(b) for cross-diffusion at $d_1 = 0.0001$, $d_2 = 2.5$, $m_1 = 100$ and $m_2 = 1$, (Figure produced by applying PHASER).

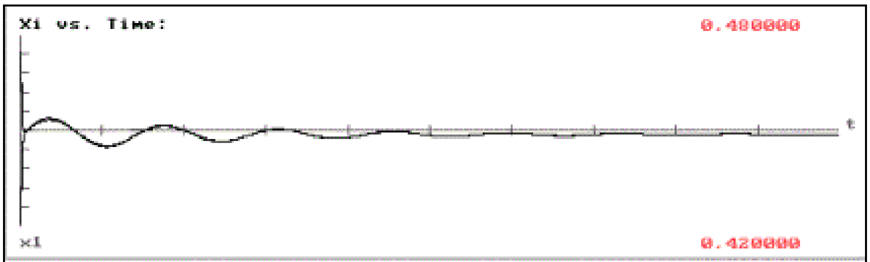


IC	Time	X	Y	Z
1	199998.14	0.448642	3.024982	0.448642
2	199998.14	0.448642	3.024982	0.448642
1	199998.69	0.448642	3.024982	0.448642
2	199998.69	0.448642	3.024982	0.448642
1	199999.24	0.448642	3.024982	0.448642
2	199999.24	0.448642	3.024982	0.448642
1	199999.79	0.448642	3.024982	0.448642
2	199999.79	0.448642	3.024982	0.448642



IC	Time	X	Y	Z
1	698.50000	0.448430	3.024739	0.448430
2	698.50000	0.448792	3.024567	0.448792
1	699.00000	0.448439	3.024731	0.448439
2	699.00000	0.448809	3.024578	0.448809
1	699.50000	0.448450	3.024723	0.448450
2	699.50000	0.448825	3.024591	0.448825
1	700.00000	0.448460	3.024716	0.448460
2	700.00000	0.448841	3.024604	0.448841

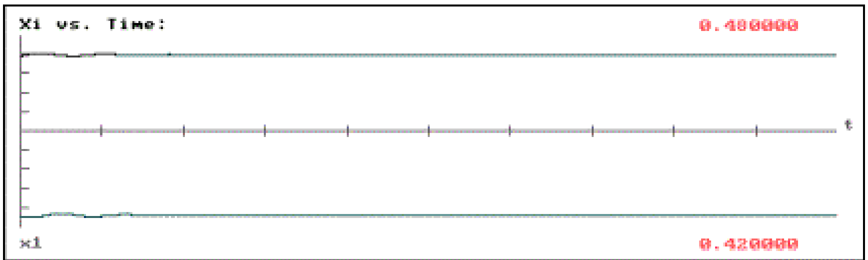
Figure 7b: Graphs of the coordinate $u_1(t,1)$ of two solutions of Example 7 corresponding to the respective initial conditions (0.423, 3.018, 0.473, 3.02), (0.4733, 3.018, 0.423, 3.0186);(a) for self-diffusion at $d_1 = 1$, $d_2 = 1$, (b) for cross-diffusion at $d_1 = 1$, $d_2 = 1$, $m_1 = 0.001$ and $m_2 = 375$, (Figure produced by applying PHASER).



LAST Xi:

IC	Time	X	Y	Z
1	498.30000	0.448717	3.024905	0.448717
2	498.30000	0.448728	3.024900	0.448728
1	498.85000	0.448720	3.024910	0.448720
2	498.85000	0.448732	3.024906	0.448732
1	499.40000	0.448723	3.024915	0.448723
2	499.40000	0.448735	3.024912	0.448735
1	499.95000	0.448726	3.024920	0.448726
2	499.95000	0.448738	3.024918	0.448738

(a)



LAST Xi:

IC	Time	X	Y	Z
1	999.99400	0.423511	3.018450	0.473834
2	999.99400	0.473667	3.018944	0.423677
1	999.99600	0.423511	3.018450	0.473834
2	999.99600	0.473667	3.018944	0.423677
1	999.99800	0.423511	3.018450	0.473834
2	999.99800	0.473667	3.018944	0.423677
1	1000.0000	0.423511	3.018450	0.473834
2	1000.0000	0.473667	3.018944	0.423677

(b)

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Curriculum Vitae

Shaban A. H. Aly was born in Assiut, Egypt in 1970. He received his BSc degree in Mathematics from Assiut University, Egypt 1992. From January 1994 he has been working in the Department of Mathematics , Faculty of Science, Al-Azhar University (Assiut). In June of 1999 he received the MSc degree in Mathematics (Dynamical Systems). He was supervised by **Prof. Dr. Gamal M. Mahmoud** from Assiut University. From October 2001 to the present time he has been working on his Ph.D. thesis supervised by **Prof. Dr. Miklós Farkas** at the Department of Differential Equations, Institute of Mathematics, Budapest University of Technology and Economics.

Lectures:

1- Two lectures in the graduate seminar series of the Institute of Mathematics, Budapest University of Technology, 2002, 2003.

2- Lecture in The Second International Workshop Constructive Methods for Non-linear Boundary Value Problems, June 4-6, 2003 Miskolc, Hungary.

3- Lecture in The Seventh Colloquium on the Qualitative Theory of Differential Equations, July 14-18, 2003 Szeged, Hungary (an important international conference).

4- Lecture in The International Conference 2004-Dynamical Systems and Applications, July 5-10, 2004, Antalya, Turkey.

5- Lecture in The International Conference on Nonlinear Operators, Differential Equations and Applications, August 24-27, 2004, Cluj-Napoca, Romania.

Conferences Participation:

1- The Second International Workshop Constructive Methods for Non-linear Boundary Value Problems, June 4-6, 2003 Miskolc, Hungary.

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4- The International Conference on Nonlinear Operators, Differential Equations and Applications, August 24-27, 2004, Cluj-Napoca, Romania.

List of Publications

PhD. Results

1- **Aly S., Farkas M.**, Bifurcation in a predator-prey model in patchy Environment with diffusion, Nonlinear Analysis:Real World Applications, 5 (2004) 519-526.

2- **Aly S., Farkas M.**, Competition in patchy environment with cross diffusion, Nonlinear Analysis: Real World Applications, 5 (2004) 589-595.

3- **Aly S.,** Cooperation in patchy environment with cross-diffusion, Miskolc Math. Notes, 5 (2004) 83-90.

4- **Aly S., Farkas M.**, Prey-predator in patchy environment with cross-diffusion, accepted for publication in Journal of Differential Equations and Dynamical System (DEDS).

5- **Aly S., Farkas M.**, Bifurcation in a predator-prey model in patchy environment with cross-diffusion, accepted for publication in Annales Univ. Sci. Budapest. Sect. Math.

6- **Aly S.,** Stable oscillations in a predator-prey model with delay, submitted for publication to The Australian Journal of Mathematical Analysis and Applications (AJMAA).

7- **Aly S.,** Bifurcations in a predator-prey model with diffusion and memory, submitted for publication to International Journal of Bifurcation and Chaos (IJBC).

8- **Aly S., Farkas M.**, Interaction of species in patchy space with diffusion, International Conference: 2004-Dynamical Systems and Applications, July 05-10, 2004, Antalya-Pamukkale (Hierapolis), Turkey (Proceeding).

9- **Aly S.,** Predator-prey model in patchy space with diffusion, Aplimat 4$^{\text{th}}$ International Conference, February 1-4, 2005, Bratislava, Slovak Republic (Proceeding).

10- **Aly S.,** Cooperation in patchy environment with cross-diffusion, The Second International Workshop Constructive Methods for Non-linear Boundary Value Problems, June 4-6, 2003 Miskolc, Hungary (Abstract).

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MSc. Results

1- **Mahmoud G. M., Aly S.**, On periodic solutions of parametrically excited complex nonlinear dynamical systems, Physica A 278 (2000) 390-404.

2- **Mahmoud G. M., Aly S.**, Periodic attractors of complex damped nonlinear systems, Int. J. Non-Linear Mech., Vol. 35 6 (2000) 309-323.

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