

PREDATOR-PREY IN PATCHY SPACE WITH DIFFUSION

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ABSTRACT. In this paper we formulate a predator-prey system in two patches in which the per capita 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. Numerical studies 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, a pattern emerge

1. INTRODUCTION

The development of a spatial pattern from a homogeneous steady-state via diffusion-driven instability is well known and so-called " Turing bifurcation " (see [5]) have been postulated to explain the occurrence of pattern formation. This lies at the heart of almost all mathematical models for patterning in ecology, embryology and elsewhere in biology and chemistry (see [1]). 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 [2], [3], [4]). We consider a two-species predator-prey system living in a habitat of two identical patches linked by migration and we 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. The aim of the present paper is to show how the phenomenon looks like in this ODE setting.

This paper is organized as follows: In Section 2 the model is built, in Section 3 its linearization is treated and the conditions for the Turing bifurcation are established (these are the main results of this paper), in Section 4 we consider an example to illustrate what can be expected, in Section 5 we summarize the main conclusions of the study.

2. THE MODEL

We consider a two-species prey-predator system living in a habitat of two identical patches linked by migration.

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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:

$$\begin{aligned} \dot{u}_1(t, 1) &= u_1(t, 1)(r_1 - a_{11}u_1(t, 1) - \frac{u_2(t, 1)}{a+u_1(t, 1)}) + d_1(u_1(t, 2) - u_1(t, 1)), \\ \dot{u}_2(t, 1) &= u_2(t, 1)(-r_2 + \frac{bu_1(t, 1)}{a+u_1(t, 1)} - a_{22}u_2(t, 1)) + d_2(u_2(t, 2) - u_2(t, 1)), \\ \dot{u}_1(t, 2) &= u_1(t, 2)(r_1 - a_{11}u_1(t, 2) - \frac{u_2(t, 2)}{a+u_1(t, 2)}) + d_1(u_1(t, 1) - u_1(t, 2)), \\ \dot{u}_2(t, 2) &= u_2(t, 2)(-r_2 + \frac{bu_1(t, 2)}{a+u_1(t, 2)} - a_{22}u_2(t, 2)) + d_2(u_2(t, 1) - u_2(t, 2)), \end{aligned} \quad (2.1)$$

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.

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

$$\begin{aligned} \dot{u}_1(t, 1) &= u_1(t, 1)(r_1 - a_{11}u_1(t, 1) - \frac{u_2(t, 1)}{a+u_1(t, 1)}), \\ \dot{u}_2(t, 1) &= u_2(t, 1)(-r_2 + \frac{bu_1(t, 1)}{a+u_1(t, 1)} - a_{22}u_2(t, 1)), \\ \dot{u}_1(t, 2) &= u_1(t, 2)(r_1 - a_{11}u_1(t, 2) - \frac{u_2(t, 2)}{a+u_1(t, 2)}), \\ \dot{u}_2(t, 2) &= u_2(t, 2)(-r_2 + \frac{bu_1(t, 2)}{a+u_1(t, 2)} - a_{22}u_2(t, 2)). \end{aligned} \quad (2.2)$$

The following conditions are reasonable and natural:

$$b > r_2, \quad (2.3)$$

$$r_1/a_{11} > a, \quad (2.4)$$

$$b(r_1 - aa_{11}) > r_2(r_1 + aa_{11}), \quad (2.5)$$

$$b(r_1 - aa_{11}) > \frac{a_{22}}{4a}(r_1 + aa_{11})^3 + r_2(r_1 + aa_{11}).$$

Condition (2.3) ensures that the predator may have eventually, a positive net growth rate; (2.4) ensures that for the prey an Allée-effect zone exists where the increase of prey density is favorable to its growth rate; (2.5) is needed to have a positive equilibrium point of system (2.2). System (2.2) 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:

$$u_2 = H_1(u_1) := (a + u_1)(r_1 - a_{11}u_1), \quad (2.6)$$

$$u_2 = H_2(u_1) := \frac{1}{a_{22}}(-r_2 + \frac{bu_1}{a + u_1}). \quad (2.7)$$

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

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 zone 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 $(\bar{u}_1, \bar{u}_2, \bar{u}_1, \bar{u}_2)$ is

$$J_k = \begin{pmatrix} \Theta_1 & -\Theta_2 & 0 & 0 \\ \Theta_3 & -\Theta_4 & 0 & 0 \\ 0 & 0 & \Theta_1 & -\Theta_2 \\ 0 & 0 & \Theta_3 & -\Theta_4 \end{pmatrix}. \quad (2.8)$$

The characteristic polynomial is

$$D_4(\lambda) = (D_2(\lambda))^2, D_2(\lambda) = \lambda^2 + \lambda(\Theta_4 - \Theta_1) + \Theta_2\Theta_3 - \Theta_1\Theta_4. \quad (2.9)$$

where

$$\Theta_1 = -a_{11}\bar{u}_1 + \frac{\bar{u}_1\bar{u}_2}{(a + \bar{u}_1)^2}, \Theta_2 = \frac{\bar{u}_1}{a + \bar{u}_1}, \Theta_3 = \frac{ab\bar{u}_2}{(a + \bar{u}_1)^2}, \Theta_4 = a_{22}\bar{u}_2.$$

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

$$H_1((-a + \frac{r_1}{a_{11}})/2) < H_2((-a + \frac{r_1}{a_{11}})/2), \quad (2.10)$$

i.e.

$$\frac{a^2 a_{11}}{4} (1 + \frac{r_1}{a a_{11}}) < \frac{1}{a_{22}} (-r_2 + b \frac{r_1 - a a_{11}}{r_1 + a a_{11}}). \quad (2.11)$$

Assume that

$$\Theta_4 - \Theta_1 > 0 \text{ and } \Theta_2\Theta_3 - \Theta_1\Theta_4 > 0; \quad (2.12)$$

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

3. THE LINEARIZED PROBLEM

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

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

$$J_D = \begin{pmatrix} \Theta_1 - d_1 & -\Theta_2 & d_1 & 0 \\ \Theta_3 & -\Theta_4 - d_2 & 0 & d_2 \\ d_1 & 0 & \Theta_1 - d_1 & -\Theta_2 \\ 0 & d_2 & \Theta_3 & -\Theta_4 - d_2 \end{pmatrix}, \quad (3.1)$$

$$\det(J_D - \lambda I) = \begin{vmatrix} \Theta_1 - d_1 - \lambda & -\Theta_2 & d_1 & 0 \\ \Theta_3 & -\Theta_4 - d_2 - \lambda & 0 & d_2 \\ d_1 & 0 & \Theta_1 - d_1 - \lambda & -\Theta_2 \\ 0 & d_2 & \Theta_3 & -\Theta_4 - d_2 - \lambda \end{vmatrix} \quad (3.2)$$

Using the properties of determinant we get

$$\begin{vmatrix} \Theta_1 - \lambda & -\Theta_2 & d_1 & 0 \\ \Theta_3 & -\Theta_4 - \lambda & 0 & d_2 \\ 0 & 0 & \Theta_1 - 2d_1 - \lambda & -\Theta_2 \\ 0 & 0 & \Theta_3 & -\Theta_4 - 2d_2 - \lambda \end{vmatrix} \quad (3.3)$$

$$\begin{aligned} &= D_2(\lambda)(\lambda^2 + \lambda(\Theta_4 - \Theta_1 + 2(d_1 + d_2)) + \Theta_2\Theta_3 - \Theta_1\Theta_4 \\ &+ 2d_1\Theta_4 - 2d_2(\Theta_1 - 2d_1)). \end{aligned} \quad (3.4)$$

We know that $D_2(\lambda)$ has two roots with negative real parts. By (2.12), clearly, $\Theta_4 - \Theta_1 + 2(d_1 + d_2) > 0$. 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 (2.12) the first three terms are positive. Suppose that the parameters have been chosen so that

$$\Theta_1 - 2d_1 > 0. \quad (3.5)$$

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

Theorem. *If (2.11), (2.12), (3.5) hold and if*

$$d_2 > d_{2crit} = \frac{(\Theta_2\Theta_3 - \Theta_1\Theta_4 + 2d_1\Theta_4)}{2(\Theta_1 - 2d_1)}, \quad (3.6)$$

then Turing instability occurs.

4. NUMERICAL INVESTIGATIONS

In this section we show what happens by numerical simulation on the following example and we are looking for conditions which imply Turing instability (diffusion driven instability).

Example: *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*

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

We consider d_2 as a bifurcation parameter. In this case at $d_{2crit} \cong 1008.357143$, we have four eigenvalues $\lambda_i (i = 1, 2, 3, 4)$ such that $\text{Re } \lambda_i < 0, (i = 1, 2, 3)$ and $\lambda_4 = 0$.

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

If $d_2 > d_{2crit} \Rightarrow \text{Re } \lambda_i < 0, (i = 1, 2, 3)$ and $\lambda_4 > 0$, then, $(\bar{u}_1, \bar{u}_2, \bar{u}_1, \bar{u}_2)$ 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 1), and these equilibria are asymptotically stable.

5. CONCLUSIONS

In the present article our interest is to study a predator-prey system in two patches in which the per capita 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. We show that at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation, pattern emerges, also as d_2 is increased

TABLE 1. Equilibria of the Example 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	33.000000000	1.000000000	33.000000000
1010	1.036370925	33.07433937	.9653313619	32.95021445
	1.000000000	33.000000000	1.000000000	33.000000000
	.9653313619	32.95021445	1.036370925	33.07433937
1015	1.074868882	33.17381736	.9320140124	32.92539437
	1.000000000	33.000000000	1.000000000	33.000000000
	.9320140124	32.92539437	1.074868882	33.17381736
1020	1.100598745	33.25055797	.9114645403	32.92320726
	1.000000000	33.000000000	1.000000000	33.000000000
	.9114645403	32.92320726	1.100598745	33.25055797
1030	1.140164553	33.38238717	.8822598022	32.94018541
	1.000000000	33.000000000	1.000000000	33.000000000
	.8822598022	32.94018541	1.140164553	33.38238717
1050	1.200526588	33.61072042	.8426276092	33.00836211
	1.000000000	33.000000000	1.000000000	33.000000000
	.8426276092	33.00836211	1.200526588	33.61072042
1100	1.313535754	34.10544965	.7815757376	33.24970043
	1.000000000	33.000000000	1.000000000	33.000000000
	.7815757376	33.24970043	1.313535754	34.10544965

through $d_2 = d_{2crit}$ the spatially homogeneous equilibrium loses its stability and two new equilibria emerge.

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