

# Prey and polyphagous predator species with diffusion

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## Abstract

*This paper deals with a ratio-dependent polyphagous predator–prey system taking into account the spatial movement of the species. We will investigate under what conditions Turing stability or instability occurs in higher dimensions.*

*Key words and phrases:* Predator–prey system, functional response, sign stability, ratio-dependence, diffusion, Turing instability

## 1. Model setup

We consider a ratio-dependent ecological system in which a single predator species is consuming  $n$  different prey species (the quantity or density of predator and prey  $i$  at time  $t$  and at place  $\xi$  is denoted by  $y(t, \xi)$ , and  $x_i(t, \xi)$ ,  $i = 1, 2, \dots, n$ , respectively) assuming that preys and predators are diffusing according to Fick's law in the interval  $\xi \in [0, l]$  (modeling a long island or a river), i.e:

$$\left. \begin{aligned} x'_{i\xi} &= d_i x''_{i\xi\xi} + r_i x_i g_i(x_i, K_i) - y p_i\left(\frac{y}{x_i}, a_i\right) \\ y'_t &= d_{n+1} y''_{\xi\xi} + \sum_{i=1}^n y p_i\left(\frac{y}{x_i}, a_i\right) - d y, \end{aligned} \right\} \quad (1)$$

$i = 1, 2, \dots, n$ , where  $(t, \xi) \in (0, \infty) \times (0, l)$ ,  $l > 0$ . The diffusion coefficients are  $d_i > 0$ ,  $i = 1, 2, \dots, n + 1$ . We are interested in solutions  $x_i, y : [0, \infty) \times [0, l] \rightarrow [0, \infty)$ ,  $i = 1, 2, \dots, n$ , that satisfy the no-flux boundary conditions

$$x'_{i\xi}(t, 0) = x'_{i\xi}(t, l) = y'_\xi(t, 0) = y'_\xi(t, l) = 0, \quad (2)$$

$(t \in (0, \infty), i = 1, 2, \dots, n)$  and the initial conditions:

$$x_i(0, \xi) = x_{i0}(\xi), \quad y(0, \xi) = y_{j0}(\xi), \quad (\xi \in [0, l]).$$

The constants are supposed to be positive. We assume that the per capita growth rate of prey species  $i$  in absence of predators is  $r_i g_i(x_i, K_i)$  where  $r_i > 0$  is in fact

the maximal growth rate of prey  $i$  while  $K_i > 0$  is the carrying capacity of the environment with respect to the prey species  $i$ . Only the case where there is no competition between prey species will be considered. The increase of each prey species is advantageous for the predator, and there may be intraspecific competition within the predator species. We suppose that the presence of the different prey species increases the growth rate of predator by the amount equal to the consumed prey quantity. The functional response is  $p_i\left(\frac{y}{x_i}, a_i\right)$ . Functions  $g$  and  $p_i$  both satisfy some natural conditions, (see the details in [5]):

$$g_i \in C^2((0, \infty) \times (0, \infty), \mathbb{R}), g_i \in C^0([0, \infty) \times (0, \infty), \mathbb{R}),$$

$$g_i(0, K_i) = 1, \quad g'_{i x_i}(x_i, K_i) < 0 < g''_{i x_i K_i}(x_i, K_i), \quad (3)$$

(for  $x_i > 0, K_i > 0$ ),

$$\lim_{K_i \rightarrow \infty} g'_{i x_i}(x_i, K_i) = 0, \quad (4)$$

$$(K_i - x_i)g_i(x_i, K_i) > 0 \quad (x_i \geq 0, x_i \neq K_i > 0). \quad (5)$$

Generally the functional response  $p_i$  is the following three-variable function  $p_i(x_i, y, a_i)$ , where  $p_i \in C^1((0, \infty) \times (0, \infty) \times (0, \infty), \mathbb{R})$ ,  $p_i \in C^0([0, \infty) \times (0, \infty) \times (0, \infty), \mathbb{R})$ . An important natural condition is that  $p_i(0, y, a_i) = 0$  ( $y > 0, a_i > 0$ ). We will keep this condition, see later at (10) meaning that the predator cannot survive without prey. Now we consider the so-called ratio-dependent functional responses and we give the remaining natural conditions in this respect:

$$p'_{i \frac{y}{x_i}}\left(\frac{y}{x_i}, a_i\right) < 0 \quad (x_i, y, a_i > 0), \quad (6)$$

$$-p'_{i \frac{y}{x_i}}\left(\frac{y}{x_i}, a_i\right) < \frac{p_i\left(\frac{y}{x_i}, a_i\right)}{y/x_i} \quad (x_i, y, a_i > 0), \quad (7)$$

$$p'_{i a_i}\left(\frac{y}{x_i}, a_i\right) \leq 0 \quad (x_i, y, a_i > 0), \quad (8)$$

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where

$$p_i' \frac{y}{x_i} = \frac{dp_i}{d\left(\frac{y}{x_i}\right)}.$$

A possible choice of function  $g_i(x_i, K_i)$  may be the so-called logistic growth rate of prey:

$$g_i(x_i, K_i) = 1 - \frac{x_i}{K_i}, \tag{9}$$

The functional response is of ratio-dependent type, which can be for example a Holling type one

$$p_i\left(\frac{y}{x_i}, a_i\right) = m_i \frac{1}{a_i \frac{y}{x_i} + 1} = m_i \frac{x_i}{a_i y + x_i}. \tag{10}$$

In this case condition  $p_i(0, y, a_i) = 0$  is satisfied for the three-variable function of the general functional response. Parameter  $a_i$  is the so-called "half saturation constant", namely in the case where  $p_i$  is a bounded function for fixed  $a_i > 0$ ,  $m_i = \sup_{x_i, y > 0} p_i\left(\frac{y}{x_i}, a_i\right)$  is the "maximal birth rate"  $i$  of the predator coming from prey  $i$ . The constants  $a_i, m_i$  are supposed to be positive. The birth rate of the predator species is equal to the sum of the functional responses, namely  $\sum_{i=1}^n p_i\left(\frac{y}{x_i}, a_i\right)$ . Thus, its maximal birth rate is equal to  $\sum_{i=1}^n m_i$ . For the survival of the predator species it is, clearly, necessary that the maximal birth rate be larger than its death rate  $d > 0$ , namely:

$$\sum_{i=1}^n m_i > d. \tag{11}$$

It is easy to see that the positive orthant is positively invariant. The proof of dissipativeness is more complicated. The second author with Lizana and Duque have already proven dissipativeness in the case of  $n$  different predators and a single prey species with functional response (10) in [6]. In this dual model a similar proof can be done which is complicated and it will be published in a forthcoming paper. Thus, the model is biologically well-posed.

Introducing the  $(n + 1)$ -dimensional vector  $U = (x_1, \dots, x_n, y)^T$ , the diagonal matrix  $D = \text{diag}(d_1, d_2, \dots, d_n, d_{n+1})$  and the vector

$$F(U) = \begin{bmatrix} r_1 x_1 g_1(x_1, K_1) - y p_1\left(\frac{y}{x_1}, a_1\right) \\ \vdots \\ r_n x_n g_n(x_n, K_n) - y p_n\left(\frac{y}{x_n}, a_n\right) \\ \sum_{i=1}^n y p_i\left(\frac{y}{x_i}, a_i\right) - d y \end{bmatrix} \tag{12}$$

system (1) and boundary conditions (2) assume the form

$$U_t' = DU_{\xi\xi}'' + F(U) \tag{13}$$

$$U_{\xi}'(t, 0) = U_{\xi}'(t, l) = 0. \tag{14}$$

Initial conditions assume the following form:

$$U(t = 0) = U_0. \tag{15}$$

Clearly, a spatially constant solution  $U(t) = (x_1(t), \dots, x_n(t), y(t))^T$  of (13) satisfies the boundary conditions (14) and the kinetic system

$$\dot{U} = F(U). \tag{16}$$

## 2. Kinetic system

The equilibrium of (16) is a constant solution of (13) at the same time. We shall be concerned with the positive equilibrium, namely it is supposed that there exists an equilibrium point  $E^*(x_1^*, \dots, x_n^*, y^*)$  in the positive orthant, where  $x_i^*$ , and  $y^*$  are the solutions of the following equations:

$$r_i x_i^* g_i(x_i^*, K_i) = y^* p_i\left(\frac{y^*}{x_i^*}, a_i\right), \quad \sum_{i=1}^n p_i\left(\frac{y^*}{x_i^*}, a_i\right) = d, \tag{17}$$

(i=1, ..., n). This implies

$$\sum_{i=1}^n r_i x_i^* g_i(x_i^*, K_i) = d y^*. \tag{18}$$

There is a necessary condition of the existence of a positive equilibrium point in a special case as follows.

**Theorem 2.1.** Consider system (1) in the case of logistic birth rate of prey species (9) and in the case of Holling type functional response (10). If

$$x_i^* < K_i \quad i = 1, 2, \dots, n$$

and if there exists a positive equilibrium point of (16) then

$$\sum_{i=1}^n a_i r_i > \left(\sum_{i=1}^n m_i\right) - d \tag{19}$$

is satisfied.

The Jacobian of the kinetic system (16) at the equilibrium point is denoted by  $J|_{E^*} = A$  which is the so-called interaction matrix.

$$A = \begin{bmatrix} a_{11} & 0 & \dots & 0 & a_{1\ n+1} \\ 0 & a_{22} & \ddots & \vdots & a_{2\ n+1} \\ \vdots & \ddots & \ddots & 0 & \vdots \\ 0 & \dots & 0 & a_{nn} & a_{n\ n+1} \\ a_{n+1\ 1} & a_{n+1\ 2} & \dots & a_{n+1\ n} & a_{n+1\ n+1} \end{bmatrix}, \tag{20}$$

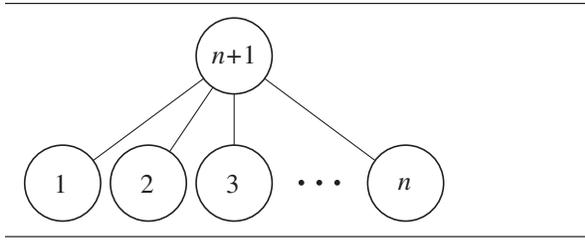


Figure 1. The graph of matrix A

$$a_{ii} = r_i g_i(x_i^*, K_i) + r_i x_i^* g'_{ix_i}(x_i^*, K_i) + \left(\frac{y^*}{x_i^*}\right)^2 p_i^*, \quad (21)$$

$$a_{in+1} = -p_i^* - \frac{y^*}{x_i^*} p_i^*, \quad (22)$$

$$a_{n+1i} = -\left(\frac{y^*}{x_i^*}\right)^2 p_i^*, \quad (23)$$

$$a_{n+1n+1} = \sum_{i=1}^n p_i^* + \sum_{i=1}^n \frac{y^*}{x_i^*} p_i^* - d \stackrel{(17)}{=} \sum_{i=1}^n \frac{y^*}{x_i^*} p_i^*, \quad (24)$$

where  $p_i' \left(\frac{y}{x_i}, a_i\right) = \frac{dp_i \left(\frac{y}{x_i}, a_i\right)}{d \left(\frac{y}{x_i}\right)}$  and  $p_i^* =$

$$p_i' \left(\frac{y^*}{x_i^*}, a_i\right) \quad i = 1, 2, \dots, n.$$

Natural conditions imply that A has the following sign pattern:

$$A = \begin{bmatrix} * & 0 & \dots & 0 & - \\ 0 & * & \ddots & \vdots & - \\ \vdots & \ddots & \ddots & 0 & \vdots \\ 0 & \dots & 0 & * & - \\ + & + & \dots & + & - \end{bmatrix}, \quad (25)$$

where the sign of the entries denoted by \* can be arbitrary.

**Theorem 2.2.** *If functions g and p satisfy the natural conditions (3)–(8) and  $a_{ii} \leq 0$  ( $i = 1, 2, \dots, n$ ) in (20) (given by (21)) and at most one  $a_{ii} = 0$  ( $i \in \{1, 2, \dots, n\}$ ) then  $E^*$  is an asymptotically stable equilibrium point of system (16).*

*Proof.* Let us consider the graph of matrix A (see in Figure 1) and check the conditions of Theorem 2.6 of [3]. We obtain that matrix A is sign-stable.  $\square$

Condition  $a_{ii} \leq 0$  ( $i = 1, 2, \dots, n$ ) of Theorem 2.2 is in connection with the Allee-effect zone of the different prey species. In the Allee-effect zone prey is scarce and an increase in prey quantity is beneficial for the

growth rate of prey, see [2] the two-dimensional case. Since there is no interspecific competition between the different prey species hence the  $(n + 1)$ -dimensional case is close to this one, more precisely every prey species has a well-defined own Allee-effect zone. Condition  $a_{ii} \leq 0$  ( $i = 1, 2, \dots, n$ ) of Theorem 2.2 means that the equilibrium point is situated outside of the Allee-effect zone of all prey species. Inside of these zones all prey species are scarce, thus, there is not enough food for predator species while outside of these zones there is enough food. In the three-dimensional case typical nullcline surfaces are presented in Figure 2.

**Example 2.1.** *The first picture in Figure 2 shows that  $E^*(1.48879, 2.76681, 1.90506)$  is unique and situated in the Allee-effect zone of both prey species. Parameters are chosen as follows:  $r_1 = 2, r_2 = 3, K_1 = 20, K_2 = 15, m_1 = 7, m_2 = 6, a_1 = 3, a_2 = 1, d = 5$ .*

*It can be proven that in this case  $E^*$  cannot be asymptotically stable. This is natural because there is not enough food for predator species.*

**Example 2.2.** *The second picture in Figure 2 shows that there are two positive equilibrium points:  $(23.025, 115.463, 24.1008)$  which is asymptotically stable and  $(92.1265, 11.8102, 26.4042)$  which is unstable and they are situated in the Allee-effect zone of exactly one prey species. Parameters are chosen as follows:  $r_1 = 2, r_2 = 3, K_1 = 100, K_2 = 150, m_1 = 7, m_2 = 4, a_1 = 3, a_2 = 1, d = 5$ .*

**Example 2.3.** *In the third case in Figure 2  $E^*$  is the unique positive equilibrium point and it is situated in the Allee-effect zone of one prey, but it not asymptotically stable. Parameters are chosen as follows:  $r_1 = 2, r_2 = 4, K_1 = 200, K_2 = 150, m_1 = 7, m_2 = 5.1, a_1 = 3, a_2 = 1, d = 5$ .*

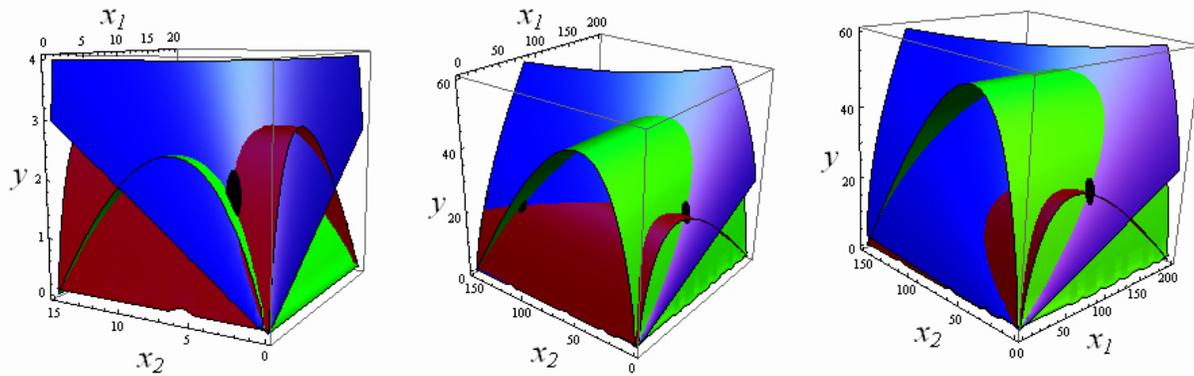
**Remark 2.1.** *The meaning of Theorem 2.2 is the following: If the equilibrium point  $E^*$  is situated outside of the Allee-effect zone of all prey species then it is asymptotically stable with respect to system (16).*

### 3. Stability in case of diffusion

We linearize system (13) around point  $E^*$ . Introducing the new coordinates  $V = (x_1 - x_1^*, \dots, x_n - x_n^*, y - y^*)^T$  the linearized system takes the form

$$V_t' = DV_{\xi\xi}'' + AV \quad (26)$$

$$V_{\xi}'(t, 0) = V_{\xi}'(t, l) = 0, \quad (27)$$



**Figure 2.** Nullclines and equilibrium points are presented in Examples 2.1, 2.2, 2.3.

where  $A$  is given by (20). We solve the linear boundary value problem (26)–(27) by Fourier’s method. The eigenvalues of the boundary value problem are

$$\alpha_k^2 = \left(\frac{k\pi}{l}\right)^2, \quad k \in \mathbb{N}. \quad (28)$$

Clearly,  $0 = \alpha_0 < \alpha_1 < \alpha_2 < \dots$ . It is known that the stability of  $E^*$  with respect to system (1) is in connection with the stability behaviour of the following matrices:

$$B_k = B(\alpha_k^2) = A - \alpha_k^2 D, \quad k \in \mathbb{N}. \quad (29)$$

The following definition is similar as it is used by [7]:

**Definition 3.1.** An  $n \times n$  matrix  $A = [a_{ij}]$  is said to be strongly stable if  $A$  is stable and if for all  $k$  all the eigenvalues of  $B_k$  (given by (29)) have negative real parts for all nonnegative diagonal matrices  $D$ . Matrix  $A = [a_{ij}]$  is excitable or stable without being strongly stable if it is stable and there exists a nonnegative diagonal matrix  $D$  and a  $k \in \mathbb{N}$  such that  $B_k$  has at least one eigenvalue with positive real part.

**Remark 3.1.** Usually strong stability of an  $n \times n$  matrix  $A$  is defined more generally:  $A$  is strongly stable if  $A - \hat{D}$  is stable for all nonnegative  $n \times n$  diagonal matrices  $\hat{D}$ . (E.g. [7].)

But Definition 3.1 is equivalent to this, and it is much more applicable in case of system (26)–(27).

**Definition 3.2.** We say that the equilibrium  $E^*$  of (13) is Turing (diffusionally) unstable if it is an asymptotically stable equilibrium of the kinetic system (16) but it is unstable with respect to solutions of (13)–(14).

**Theorem 3.1.** If functions  $g$  and  $p$  satisfy the natural conditions (3)–(8) and  $a_{ii} \leq 0$  ( $i = 1, 2, \dots, n$ ) in (20) (given by (21)) and at most one  $a_{ii} = 0$  ( $i \in \{1, 2, \dots, n\}$ )

then matrix  $A$  defined by (20) is strongly stable and the equilibrium  $E^*$  of (13) is asymptotically stable.

*Proof.* It is enough to prove that (20) is sign-stable. We have already proven this in Theorem 2.2.  $\square$

Theorem 3.1 means that in case of a sign-stable interaction matrix Turing instability cannot occur.

#### 4. Turing instability in three dimensions

**Theorem 4.1.** Let the interaction matrix  $A$  of system (1) be given by (20) and let  $n = 2$ . Functions  $g$  and  $p$  satisfy the natural conditions (3)–(8). A necessary condition of Turing instability is  $a_{11}a_{22} < 0$ .

*Proof.* If functions  $g$  and  $p$  satisfy the natural conditions (3)–(8) then the sign pattern of  $A$  is given by (25). If  $a_{11}, a_{22} > 0$  then matrix  $A$  cannot be stable. This can be proven indirectly. It is a long calculation. Now we omit it, but we note that Example 2.1 demonstrates the phenomenon. In the case  $a_{11}, a_{22} < 0$  the equilibrium  $E^*$  of (13) is asymptotically stable as it was proven in Theorem 3.1. This means that Turing instability may occur only in the case when  $a_{11}a_{22} < 0$ .  $\square$

The meaning of this theorem is that Turing instability may occur in the case when the quantity of one prey species is low while the quantity of another prey species is sufficient compared with their carrying capacity.

Without loss of generality we suppose that  $a_{11} > 0$  and  $a_{22} < 0$ , thus, the sign pattern of  $A$  is the following (in case of  $n = 2$ ):

$$A = \begin{bmatrix} + & 0 & - \\ 0 & - & - \\ + & + & - \end{bmatrix}. \quad (30)$$

From this point the method is similar to the one that is applied in [4].

**Lemma 4.1.** *Suppose that the sign pattern of  $A$  is given by (30) and its characteristic polynomial is given by*

$$D(\lambda) = \lambda^3 + a_2\lambda^2 + a_1\lambda + a_0. \quad (31)$$

If

$$a_{11} + \frac{a_{22}}{2} < 0, \quad (32)$$

$$a_{11} + \frac{a_{33}}{2} < 0, \quad (33)$$

are satisfied then  $a_2, a_1 > 0$ ,  $a_2a_1 - a_0 > 0$  and  $a_0$  can be either positive or negative.

*Proof.* It can be checked directly by a long calculation which we omit now.  $\square$

Thus, conditions of the Routh–Hurwitz criterion are fulfilled except that  $a_0 > 0$ . This gives us later a possibility to find Turing bifurcation. Conditions (32), (33) mean that the intraspecific competition in the prey species 2 and in the predator species is strong enough.

**Theorem 4.2.** *Suppose that the interaction matrix  $A$  of system (1) is given by (20) and  $n = 2$ . Functions  $g$  and  $p$  satisfy the natural conditions (3)–(8). Let  $a_{11} > 0$  and  $a_{22} < 0$ .*

*If  $\det A < 0$ , (32)–(33) are satisfied, and*

$$\exists k : 0 < \alpha_k^2 < \frac{a_{11}}{d_1} \quad (34)$$

*then for fixed  $d_1 > 0$  and  $d_2 > 0$  there exists a  $d_{3_{\text{krit}}} > 0$  (by increasing  $d_3$  from a low value) at which Turing bifurcation occurs. The exact value of  $d_{3_{\text{krit}}}$  can be calculated as follows:*

$$d_{3_{\text{krit}}} = \min_{k \in \mathbb{N}: 0 < \alpha_k^2 < \frac{a_{11}}{d_1}} -\frac{v_0(\alpha_k^2)}{v_1(\alpha_k^2)}, \quad (35)$$

where  $\alpha_k^2 < \frac{a_{11}}{d_1}$ ,  $k = 1, 2, \dots, N$ ,  $\alpha_{N+1}^2 \geq \frac{a_{11}}{d_1}$ ,  $N \in \mathbb{N}$ ,

$$\begin{aligned} v_0(\alpha_k^2) &= -d_1d_2a_{33}\alpha_k^4 + (a_{11}a_{33}d_2 + a_{22}a_{33}d_1 - \\ &a_{13}a_{31}d_2 - a_{23}a_{32}d_1)\alpha_k^2 + a_0, \end{aligned} \quad (36)$$

$$v_1(\alpha_k^2) = d_1d_2 \left( \alpha_k^2 - \frac{a_{11}}{d_1} \right) \left( \alpha_k^2 - \frac{a_{22}}{d_2} \right) \alpha_k^2. \quad (37)$$

*Proof.* Using lemma 4.1 it is easy to see that  $A$  is stable. Let us consider the following characteristic polynomial:

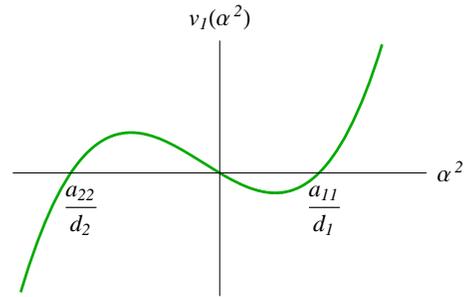
$$-\det(A - \alpha^2 D - \mu I) = \mu^3 + \tilde{a}_2\mu^2 + \tilde{a}_1\mu + \tilde{a}_0.$$

Using again lemma 4.1 it is easy to see that  $\tilde{a}_2, \tilde{a}_1, \tilde{a}_2\tilde{a}_1 - \tilde{a}_0 > 0$  for all  $\alpha^2, d_1, d_2, d_3 > 0$ . Thus, the

stability of this characteristic polynomial depends only on the sign of  $\tilde{a}_0(\alpha^2)$ . We have to see that for fixed  $d_1, d_2 > 0$  there exists a  $k \geq 1$  at which  $\tilde{a}_0(\alpha_k^2) = 0$  if  $d_3 = d_{3_{\text{krit}}} > 0$  and  $\tilde{a}_0(\alpha_k^2)$  changes its sign at  $d_{3_{\text{krit}}}$ , more precisely it becomes negative from a positive value as  $d_3$  increases. After long calculation we obtain:

$$\tilde{a}_0(\alpha_k^2) = v_1(\alpha_k^2)d_3 + v_0(\alpha_k^2),$$

where  $v_0(\alpha_k^2)$  is given by (36) and it is positive for all  $\alpha_k^2$ , and  $v_1(\alpha_k^2)$  is given by (37) which can be positive or negative depending on  $\alpha_k^2$ . The graph of  $v_1(\alpha^2)$  can be seen in Figure 3.



**Figure 3.** Function  $v_1(\alpha^2)$

The method is the following. Let us consider the set of the following indices  $\{k \in \mathbb{N} : 0 < \alpha_k^2 < \frac{a_{11}}{d_1}\}$ . The cardinality of this set is finite, let us denote it by  $N$ . Determine the value  $d_{3_{\text{krit}}}(\alpha_k^2)$  at which  $\tilde{a}_0(\alpha_k^2) = 0$ . Then calculate  $\min_{k \in \mathbb{N}: 0 < \alpha_k^2 < \frac{a_{11}}{d_1}} d_{3_{\text{krit}}}(\alpha_k^2)$ .

It can be seen that this is exactly:  $d_{3_{\text{krit}}}$ .  $\square$

**Remark 4.1.** *With Theorem 4.2 we gave a method to determine  $d_{3_{\text{krit}}}$  at which pattern may occur.*

**Corollary 4.1.** *It is obvious that if  $\exists k : 0 < \alpha_k^2 < \frac{a_{11}}{d_1}$ , then by monotonicity  $\alpha_1^2 < \frac{a_{11}}{d_1}$ . If  $\alpha_1^2 > \frac{a_{11}}{d_1}$ , conditions (32)–(33) are satisfied and let  $\det A < 0$  then by increasing  $d_3$  Turing instability cannot occur.*

**Remark 4.2.** *Condition (34) of Theorem 4.2 holds in the case of one-dimensional spatial region if  $d_1 < \frac{a_{11}l^2}{\pi^2k^2}$  for some  $k \geq 1$ . If this is the case then by monotonicity of  $\alpha_k^2$ ,  $d_1 < \frac{a_{11}l^2}{\pi^2}$ . This means that if  $d_1$  is large compared to  $l$  then local asymptotic stability of  $E^*$  remains for any diffusion rate of the species, while if  $d_1$  is small then  $E^*$  can be unstable. This corresponds to our expectation: if for example the island is short then agility has no importance.*

**Theorem 4.3.** *If  $E^*$  is locally asymptotically stable with respect to the kinetic system (16) and if it is in the Allee-effect zone of prey  $i_1, i_2, \dots, i_k$  ( $k \leq n$ ) and*

$$0 < \frac{a_{i_j i_j} \pi^2}{l^2} < d_{i_j} \quad j = 1, \dots, k$$

(where  $a_{i_j i_j}$  is given by (21)) then  $B_k$  is stable for all  $k \in \mathbb{Z}$ , thus Turing instability does not occur.

*Proof.* It is obvious from the definition.  $\square$

## 5. CONCLUSIONS

This work is partly the generalization of a paper of Cavani and Farkas [1]. System (1) describes the dynamics of an  $n$  prey–predator interaction. It can be considered as a problem dual to the model published in [4]. In absence of predation prey quantity grows by a function  $g$  which can be for example given by (9). Predator mortality is constant. The functional response is of ratio-dependent type, which can be for example a Holling type one (given by (10)). All species are subject to Fickian diffusion in a one–dimensional spatial habitat from which and into which there is no migration. It is assumed that the system has a positive equilibrium in the positive orthant. If this equilibrium is outside of the Allee–effect zone of all prey species — i.e. in a neighbourhood of the equilibrium the increase of prey density is not beneficial to prey’s growth rate and this is true for all prey species — then the interaction matrix of the kinetic system is sign–stable and the equilibrium point remains locally asymptotically stable for any diffusion rate of species.

If this equilibrium is not outside the Allee–effect zone of all prey species, i.e. there are prey species for which an increase of prey density is beneficial to prey’s growth rate (in a neighbourhood of the equilibrium) then the equilibrium point remains locally asymptotically stable if the prey diffusion rate is relatively high compared e.g. to the square of the length of the spatial domain for any diffusion rate of predator species. If the prey diffusion rate is lower then one may increase the predator diffusion rate to a value at which equilibrium loses its stability, i.e. a so–called diffusional instability occurs. We detailed the three–dimensional case when the equilibrium point is inside the Allee–effect zone of the prey species number 1 while the equilibrium point is outside the Allee–effect zone of the prey species number 2. If the diffusion coefficient of the prey species 1 (describing its mobility) is not too large compared to the size of its habitat where it lives, and the diffusion coefficients of both prey species are fixed then the diffusion coefficient of the predator species can be determined in order

to achieve Turing bifurcation. We gave a method to determine its critical value. This means that if predators are fast enough then they can catch the preys belonging to species 1 and this leads to instability. If the mobility of the prey species 1 is large enough, that is, their diffusion coefficients are large then Turing instability cannot occur in this case.

These results correspond to the result of [1] proven in two dimensions. Importance of the Allee–effect zone is also proven.

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