PREY-PREDATOR MODEL WITH NONLOCAL AND GLOBAL CONSUMPTION IN THE PREY DYNAMICS

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ABSTRACT. A prey-predator model with a nonlocal or global consumption of resources by prey is studied. Linear stability analysis about the homogeneous in space stationary solution is carried out to determine the conditions of the bifurcation of stationary and moving pulses in the case of global consumption. Their existence is confirmed in numerical simulations. Periodic travelling waves and multiple pulses are observed for the nonlocal consumption.

1. Introduction. In conventional models of population dynamics, consumption of resources by the individuals occurs at the same spatial location as reproduction and death. We assume in this work that the individual located at a point in the spatial domain can consume resources not only at that point but also at some neighboring region surrounding that point. Movement of the individuals to the nearby location occurs in a faster time scale compared to the movement from one location to the other one. This modifies the modeling approach and gives rise to an integro-differential equation describing the nonlocal consumption of resources [8, 10, 27]. This type of models manifest stationary patchy distribution, and periodic traveling waves in addition to the steady traveling wave solutions. Interesting results on complex dynamics of single species population models with reaction kinetics comprising of logistic growth law, Allee effect, sexual reproduction etc. along with nonlocal consumption can be found in [4, 3, 18, 19, 26]. Reaction-diffusion equation with the nonlocal term is also used to explain the emergence and evolution of biological species and speciation [14, 17, 18, 19, 20, 25]. The models with nonlocal consumption of resources present complex dynamics for the single species models [4, 3, 18, 19, 26]. A limiting case of nonlocal consumption of resources, where the individual can consume resource not only from the neighboring region, but from any point of the entire considered domain, is termed to be global consumption [10, 27]. Models with global consumption of resources, under proper parametric
conditions and appropriate choice of initial conditions, give rise to pulse solutions. A stationary pulse (spike) solution with zero limits at infinity and a moving pulse solution are observed. Multiple pulse solutions are also observed depending on wider initial conditions as described in [27].

Let us recall that Turing patterns are stationary in time and inhomogeneous in space solutions of a reaction-diffusion system of equations resulting from the so-called Turing instability [5, 7, 11, 12, 15, 21]. Prey-predator model with specialist predator, prey dependent functional response and linear intrinsic death rate of predator cannot produce Turing patterns in the presence of self-diffusion terms. Instead, such type of models show spatio-temporal chaos and traveling wave solutions when the spatial aspect is taken into account [24]. A similar model is used in [23], where the authors are interested to find a minimal spatio-temporal model showing spatio-temporal chaos. Due to the inclusion of nonlocal consumption of resources by the prey in the spatio-temporal Rosenzweig-MacArthur model, the conditions for Turing instability are satisfied, and Turing patterns are produced [9]. Hence, such modeling approaches, when adopted for prey-predator interactions, help to understand the prey-predator dynamics in a better way. Moreover, system of reaction-diffusion equations for two or three species, with nonlocal consumption of resources for inter-specific regulation is also helpful to explain several ecological phenomena [1, 2, 3, 13]. In a modified version of the Lotka-Volterra prey-predator model, where intra-predator interaction is incorporated, complex and diverse spatio-temporal patterns are observed due to the inclusion of nonlocal interactions of prey and predator populations [8]. They include vivid description of stationary patterns, traveling waves and their bifurcations to spatio-temporal chaos, periodic and modulated traveling waves. Interesting results are found when nonlocal consumption of resources by prey is included into a generalist predator-prey model with Holling type II functional response [22].

In a similar manner, when a prey-predator model with bistable reaction kinetics for prey (in the absence of predators) is considered, and nonlocal consumption of resources by prey is included into the system, various spatio-temporal patterns are reported in [6]. The model has the form:

\[
\frac{\partial u}{\partial t} = d_1 \frac{\partial^2 u}{\partial x^2} + au^2(b - J(u)) - \sigma_1 u - \frac{\alpha uv}{\kappa + u}, \tag{1}
\]
\[
\frac{\partial v}{\partial t} = d_2 \frac{\partial^2 v}{\partial x^2} + \frac{\beta uv}{\kappa + u} - \sigma_2 v, \tag{2}
\]

subjected to a non-negative initial condition and periodic boundary condition. Here

\[
J(u) = \int_{-\infty}^{\infty} \phi(x-y)u(y,t)dy, \quad \phi(y) = \begin{cases} \frac{1}{2N} & , \quad |y| \leq N \\ 0 & , \quad |y| > N \end{cases}.
\]

The consumption of prey by the predator follows the Holling type-II functional response, \(\alpha\) is the rate of consumption of prey by an individual predator, \(\kappa\) is the half-saturation constant and \(\beta\) is the rate of conversion of prey to predator biomass. The conversion efficiency \(\beta/\alpha\) has value between 0 and 1, which implies \(\beta < \alpha\). The reproduction of prey is proportional to the second power of the population density specific for sexual reproduction. In the absence of predator (\(\alpha = 0\)) dynamics of prey is described by a reaction-diffusion equation with bistable reaction kinetics. The conditions for Turing instability and spatial Hopf bifurcation are explicitly derived and validated with numerical examples in [6]. The nonlocal model is capable of producing stationary Turing pattern, periodic traveling wave, modulated traveling
wave in addition to oscillatory solutions and spatio-temporal chaos produced by the model without the nonlocal term.

In this work, we will consider the prey-predator model with the same reaction kinetics and with the global consumption of resources by prey together with the nonlocal consumption. Inclusion of the global consumption leads to the following system of equations:

\[
\begin{align*}
\frac{\partial u}{\partial t} &= d_1 \frac{\partial^2 u}{\partial x^2} + au^2 (b - I(u)) - \sigma_1 u - \frac{\alpha uv}{k_1 + u}, \\
\frac{\partial v}{\partial t} &= d_2 \frac{\partial^2 v}{\partial x^2} + \frac{\beta uv}{k_2 + u} - \sigma_2 v,
\end{align*}
\]

(3)

(4)

considered on the interval \(0 \leq x \leq L\) with the periodic boundary conditions. The integral

\[I(u) = \int_0^L u(y,t)dy.\]

corresponds to the global consumption of resources by prey. The main motivation of considering this modification is to explore the conditions for stationary pulse solutions and their bifurcation into moving pulse solutions. Section 2 deals with linear stability analysis and Section 3 with numerical simulations. We conclude this work with the discussion of obtained results.

2. Bifurcation of pulses. In this section we briefly mention the condition for bifurcation of pulses from stationary homogeneous solution for single species prey growth. Next we derive the condition for bifurcation of pulses from stationary homogeneous solution of the prey-predator model (3) - (4).

2.1. For the single species model. In the absence of predator, we obtain a decoupled equation for the prey density

\[
\frac{\partial u}{\partial t} = d_1 \frac{\partial^2 u}{\partial x^2} + au^2 (b - I(u)) - \sigma_1 u, \quad I(u) = \int_0^L u(y,t)dy,
\]

(5)

on a bounded interval \(0 < x < L\) with the periodic boundary conditions. We look for homogeneous in space stationary solutions of equation (5). If \(\sigma_1 < ab^2/(4L)\), then this problem has three homogeneous in space solutions, \(w = 0\), and two positive solutions of the equation

\[aw(b - I(w)) = \sigma_1.\]

(6)

We denote them by \(w_1\) and \(w_2\) assuming that \(w_1 < w_2\). Let us next consider the eigenvalue problem for the equation (5) linearized about a constant solution \(u_*\):

\[
d_1 u'' + 2au_* (b - I(u_*))u - \sigma_1 u - au_*^2 I(u) = \lambda u, \quad u'(0) = u'(L) = 0.
\]

(7)

Taking into account (6), we can write it as follows:

\[
d_1 u'' + \sigma_1 u - au_*^2 I(u) = \lambda u, \quad u'(0) = u'(L) = 0.
\]

(8)

We will search for its solutions in the form of

\[u(x) = \cos(n\pi x/L), \quad n = 0, 1, 2, \cdots .\]

Then we get

\[\lambda_0 = \sigma_1 - au_*^2 L, \quad \lambda_n = -d_1(n\pi/L)^2 + \sigma_1, \quad n = 1, 2, \cdots .\]
Hence the presence of the integral term influences only the eigenvalue \( \lambda_0 \). From (6) we get
\[
\lambda_0 = au_*(b - 2Lu_*).
\]
If equation (6) has two solutions, then \( \lambda_0 > 0 \) for \( u_* = w_1 \) and \( \lambda_0 < 0 \) for \( u_* = w_2 \).

Thus, the problem linearized about solution \( w_2 \) has negative eigenvalue \( \lambda_0 \). The eigenvalue \( \lambda_1 \) can be negative or positive. If it is negative, this solution is stable, otherwise it is unstable and another solution bifurcates from it. We can consider \( d_1 \) as bifurcation parameter with the critical value \( d_1^* = \sigma_1 L^2 / \pi^2 \). If \( d_1 < d_1^* \), then a non-homogeneous stable solution emerges. Since the eigenfunction \( \cos(\pi x/L) \) corresponding to the eigenvalue \( \lambda_1 \) has its extrema at the boundary, then the emerging solution also has its maximum at the boundary of the interval. If we consider a double interval, then this solution corresponds to the pulse solution.

2.2. For the prey-predator model. Let \((u_0, v_0)\) be a positive stationary solution of system (3) - (4). It is determined as a solution of the algebraic system of equations:
\[
a u_0(b - u_0 L) - \sigma_1 - \frac{\alpha u_0}{k_1 + u_0} = 0, \quad \frac{\beta u_0}{k_2 + u_0} - \sigma_2 = 0.
\]
(9)

Then for \( \alpha \neq 0 \),
\[
u_0 = \frac{k_2 \sigma_2}{\beta - \sigma_2}, \quad v_0 = \frac{1}{\alpha} \left( k_1 + u_0 \right) (au_0(b - u_0 L) - \sigma_1).
\]

(10)
The stationary solution \((u_0, v_0)\) is positive if
\[
\sigma_2 < \beta, \quad \frac{\sigma_1 (\beta - \sigma_2)}{\alpha k \sigma_2} + \frac{k_2 \sigma_2 L}{\beta - \sigma_2} < b.
\]

(11)

In order to study the stability of this solution, we linearize system (3) - (4) about it and obtain the following eigenvalue problem:
\[
d_1 u'' + pu - au_0^2 \int_0^L u(x) dx - \frac{\alpha u_0}{k_1+u_0} v = \lambda u
\]
\[
d_2 v'' + q u = \lambda v,
\]

(12)

(13)

where
\[
p = au_0(b - u_0 L) + \frac{\alpha u_0 v_0}{(k_1 + u_0)^2}, \quad q = \frac{\beta v_0}{k_2 + u_0} - \frac{\beta u_0 v_0}{(k_2 + u_0)^2}.
\]

We look for a solution of problem (12)-(14) in the form
\[
u_n(x) = r_n \cos(\mu_n x), \quad v_n(x) = r_2 \cos(\mu_n x),
\]
where \( \mu_n = n \pi / L, \ n = 0, 1, 2, ... \) Let \( \lambda_n \) be the corresponding eigenvalues. Then \( \lambda_0 \) can be found from the system of equations:
\[
(p - au_0^2 L) r_1 - \frac{\alpha u_0}{k_1 + u_0} r_2 = \lambda_0 r_1, \quad qr_1 = \lambda_0 r_2
\]

(15)

and \( \lambda_n, \ n = 1, 2, ... \) from the equations:
\[
d_1 \mu_n^2 r_1 + pr_1 - \frac{\alpha u_0}{k_1 + u_0} r_2 = \lambda_n r_1, \quad -d_2 \mu_n^2 r_2 + qr_1 = \lambda_n r_2.
\]

(16)

Thus, the introduction of the integral term changes the eigenvalue \( \lambda_0 \) and it does not change other eigenvalues. In the problem without the integral term, the
eigenvalue \( \lambda_0 \) is positive. Assuming the presence of the integral, we obtain the following equation for \( \lambda_0 \):

\[
\lambda_0^2 - (p - au_0^2 L)\lambda_0 + \frac{\alpha qu_0}{k_1 + u_0} = 0.
\]

Hence

\[
\lambda_0 = \frac{1}{2} (p - au_0^2 L) \pm \sqrt{\frac{1}{4} (p - au_0^2 L)^2 - \frac{\alpha qu_0}{k_1 + u_0}}.
\]

The eigenvalue \( \lambda_0 \) has a negative real part if \( p < au_0^2 L \). This condition can be written as \( b < 2u_0L \) or

\[
b < \frac{2k\sigma_2 L}{\beta - \sigma_2} \tag{18}
\]

(cf. (11)). Suppose that this condition is satisfied. Then stability of the stationary solution \((u_0, v_0)\) is determined by the other eigenvalues \( \lambda_n (= \lambda_n^*) \). Solving (16) we get:

\[
\lambda_n = S \pm \sqrt{R}, \tag{19}
\]

where

\[
S = \frac{1}{2} \left( p - \mu_n^2 (d_1 + d_2) \right), \quad R = \frac{1}{4} \left( p - \mu_n^2 (d_1 + d_2) \right)^2 + M, \]

\[
M = d_2 \mu_n^2 (p - d_1 \mu_n) - \frac{\alpha qu_0}{k_1 + u_0}.
\]

If \( M \) is positive, then some of the eigenvalues in (19) are real and positive leading to the emergence of stationary non-homogeneous solutions. If \( M \) is negative, then condition \( p = \mu_n^2 (d_1 + d_2) \) implies the existence of pure imaginary eigenvalues leading to the bifurcation of time periodic non-homogeneous solutions.

Thus, similar to the single equation, introduction of global consumption in the prey-predator model can lead to the emergence of pulses. In addition to stationary pulses which appear due to the real eigenvalue crossing the origin, we can also expect moving pulses due to the complex conjugate eigenvalues crossing the imaginary axis.

3. Numerical simulation. The instability of the homogeneous in space stationary solution leads to the bifurcation of various spatial or spatio-temporal patterns. In the case of the scalar equations, pulses and waves for the nonlocal and global consumptions were studied in [18, 19, 20, 27].

3.1. Stationary and moving pulses. We now consider the prey-predator system (3)-(4) with the periodic boundary conditions. We fix the values of parameter: \( a = 1, \sigma_1 = 0.1, k_1 = k_2 = 0.35, \alpha = \beta = 0.35 \) and \( \sigma_2 = 0.2 \). Parameters \( b, d_1, d_2 \) and \( L \) will be varied in order to study spatio-temporal pattern formation. In the case where the stationary solution \((u_0, v_0)\) is positive, the initial condition is taken in the following form:

\[
u(x, 0) = \begin{cases} u_0 + 0.001, & \text{if } |x - \frac{L}{2}| < 1 \\ u_0, & \text{elsewhere} \end{cases} \quad v(x, 0) = \begin{cases} 0.1 v_0, & \text{if } |x - \frac{L}{2}| < 0.5, \\ 0, & \text{elsewhere} \end{cases}
\]

It follows from (10) that \( u_0 \) is independent of \( L \) whereas \( v_0 \) depends on it. For \( b = 10 \), we get \( u_0 = 0.4667 \) and \( v_0 = 10.655 - 0.5081L \). The latter equals 0 for \( L^* = 20.969 \). Hence we set \( L = 20 < L^* \), for which \( v_0 = 0.49259 \) is positive.

For \( b = 10, d_1 = 0.1 \) and \( d_2 = 0.1 \), a stationary pulse solution is formed (Fig. 1). The corresponding eigenvalue \( \lambda_1 = 0.3822 \) is positive satisfying the condition of the bifurcation of pulses (Section 2). For \( d_1 = 0.3 \) and for the same values of other parameters, we observe moving pulses (or travelling waves) instead of stationary
pulses (Fig. 2). Due to the periodic boundary conditions, they cross the domain with a constant speed. Let us note that the eigenvalue \( \lambda_1 \) remains positive. However, the next eigenvalues are complex with a positive real part. Therefore, we can expect that moving pulses are unstable near the bifurcation point, and they become stable far from it.

3.2. Bifurcation diagrams. We construct a bifurcation diagram in the \((L,d_1)\)-plane where the length of the interval satisfies the inequality \( L < L^* \). Then there exists a unique stationary solution \((u_0,v_0)\) with \( v_0 > 0 \). Numerical simulations of system (3)-(4) with the periodic boundary conditions and initial conditions (20) show four types of solutions (Figure 3a). For sufficiently small values of \( d_1 \) and any value of \( L \), we get stationary pulse solutions for both prey and predator. For \( d_1 > 0.3 \) fixed, we observe extinction of both species if \( L \) is small enough and moving pulse solutions for \( L \) sufficiently large. For \( L > 9.5 \) and \( d_1 \geq 0.4 \), the positive stationary state exists, and it is stable.

If \( L \) exceed the critical value \( L^* \), then the component \( v_0 \) of the stationary solution becomes negative, and initial condition (20) cannot be used. In this case we use the continuation technique, where the value of \( L \) is gradually increased, and the result of the previous simulation is taken as initial condition for the next simulation. Using this approach we extend the bifurcation diagram beyond \( L^* \). In this case, stationary and moving pulses are observed for the same values of \( d_1 \). Instead of the stable homogeneous positive solution for sufficiently large \( d_1 \), we observe extinction of predator. Finally predator goes to extinction and prey persists at homogeneous stationary state for \( L > 11 \) and \( d_1 > 0.4 \).

We finish this subsection with the representation of solutions at the \((d_1,b)\)-plane (Figure 3b). As before, there are stationary or moving pulses, and extinction of predator or of both species.

3.3. Nonlocal consumption. If we consider nonlocal consumption of resources instead of the global consumption, the integral \( I(u) \) should be replaced by \( J(u) \):

\[
\frac{\partial u}{\partial t} = d_1 \frac{\partial^2 u}{\partial x^2} + au^2 (b - J(u)) - \sigma_1 u - \frac{\alpha uv}{k_1 + u},
\]  

(21)
Figure 2. Moving pulse for $b = 10, d_1 = 0.3, d_2 = 0.1$ (a) after time $t = 500$; (b) after time $t = 600$; (c) $x$-$t$ profile for $L = 20$.

Figure 3. For two bifurcation diagrams, $a = 1, \sigma_1 = 0.1, k_1 = k_2 = 0.35, \sigma_2 = 0.2$ are fixed. (a) Bifurcation diagram in $(L, d_1)$-plane for the values of parameters $b = 5, \alpha = \beta = 0.35, d_2 = 0.1$. (b) Bifurcation diagram in $(d_1, b)$-plane for the values of other parameters $\alpha = \beta = 0.363, d_2 = 1$. 
\[ \frac{\partial v}{\partial t} = d_2 \frac{\partial^2 v}{\partial x^2} + \frac{\beta uv}{k_2 + u} - \sigma_2 v, \]  

(22)

where

\[ J(u) = \int_{-\infty}^{\infty} \phi(x-y)u(y,t)dy, \quad \phi(y) = \begin{cases} \frac{1}{2N}, & |y| \leq N \\ 0, & |y| > N \end{cases}. \]

This system is considered in the interval \(-L \leq x \leq L\) with the periodic boundary conditions.

If the support of the kernel function \(\phi(y)\) is sufficiently wide, then the solutions in the case of nonlocal consumption converges to the solutions with global consumption. Behavior of solutions become quite different for lesser values of \(N\). The main difference of the nonlocal model is that it can manifest travelling waves, including periodic travelling waves where the density distributions and the wave speed oscillate periodically in time. Figure 4 shows propagation of a periodic wave followed by a spatio-temporal structure emerging due to the instability of the homogeneous in space stationary solution [8, 9]. The support of the initial condition is located at the center of the interval. Therefore, the wave propagates symmetrically from the center towards the border of the interval.

Another regime observed in the case of nonlocal consumption, but not for the global consumption, consists of multiple moving pulses (Figure 5). They are similar to moving pulses for the global consumption but there are several spikes and not only a single spike, as before.

Different regimes observed in the case of nonlocal consumption are summarized in the diagrams in Figure 6. Considering \((d_1, N)\) parameter plane for single species prey growth model, we conclude that increase of \(N\) leads to the succession of travelling waves, periodic travelling waves, and stationary pulses, qualitatively similar to the single equation [27]. The partition of the parameter plane is more complex for the \((N, \alpha)\)-plane for the resulting patterns exhibited by the prey-predator model. Extinction of one or of both species can be observed, as well as travelling waves, moving and stationary pulses.
4. Discussion. We consider in this work a prey-predator model with nonlocal and global consumption of resources in the prey reproduction term. This means that consumption of resources by prey individuals occurs in some area around their average location. From the mathematical point of view this assumption leads to the appearance of an integral term in the growth equation for prey. We will discuss here mathematical and ecological implications of this hypothesis.

4.1. Pulses and waves in nonlocal equations. A single reaction-diffusion equation with a bistable nonlinearity possesses two types of non-homogeneous in space solutions, waves and pulses. As it is well known, a monotone wave exists for a unique value of speed, and it is globally asymptotically stable. A pulse is a positive stationary solution with zero limits at infinity. It exists if and only if the wave speed...
is positive, and it is unstable, as it is the case of any non-monotone solution of the scalar equation.

An important observation is that introduction of global consumption makes the pulse solution stable [26, 27]. If we consider this equation on a bounded interval, then the emergence of pulses can be studied by the conventional stability and bifurcation analysis of the homogeneous in space solution. The integral term in the equation moves the principal (positive) eigenvalue to the left-half plane, and stability of this homogeneous solution is determined by the second eigenvalue. If it crosses the origin, then the homogeneous solution loses its stability leading to the appearance of a stable pulse solution.

In the case of systems of equations, the proof of the existence of pulses becomes much more involved. Existence of waves for monotone reaction-diffusion equations is well known [26]. Existence of pulses is recently proved for some classes of monotone systems arising in various applications [16]. It is interesting to note that the condition of the existence of pulses can be formulated similarly to the scalar equation: the pulse exists if and only if the wave speed is positive. The pulses for the monotone systems are unstable, and they can become stable under the introduction of the integral terms.

The same approach to study the existence and stability of pulses is not applicable for the prey-predator model. Here, we use the stability analysis to determine the condition of the bifurcation of pulses from the homogeneous in space solution. In addition to stationary pulses observed for the single equation and for monotone systems, there exist also moving pulses. As before, the bifurcation of pulses is determined by the second eigenvalue since the principal eigenvalue is removed by the integral.

In the case of nonlocal consumption of resources, dynamics of solutions are characterized by the existence of simple and periodic waves and by spatio-temporal patterns bifurcating from the homogeneous in space solution. Their interaction leads to various regimes of wave propagation. Some of them are indicated above. More detailed analysis of wave propagation will be presented in the subsequent works.

4.2. Speciation and evolution. The models with nonlocal and global consumption are particularly interesting due to their possible applications to the investigation of the emergence and evolution of biological species. Let us consider the space variable $x$ as some morphological characteristics, and the function $u(x,t)$ as a population density distribution with respect to this characteristics at time $t$. Then a stable population can be characterized by a stationary pulse solution of the corresponding equation for the population density. In the case of a single reaction-diffusion equations such solutions exist in the bistable case but they are unstable. As we have indicated above, they become stable if we introduce global consumption of resources. In the case of nonlocal consumption of resources, we can observe the process of speciation where the population distribution splits into sub-populations separated in the morphological space.

Note that these results are also applicable to cell populations where the existence of stable distributions with respect to the genotype is a necessary condition of normal functioning of tissues and organs. Emergence of new cells lines (clones) due to mutations is often considered as a characteristics of tumor instability and heterogeneity.
Prey-predator models with nonlocal consumption provide a new dimension to these evolutionary dynamics. The interaction with predator imposes an evolutionary pressure on the prey leading to its possible motion in the morphological space (moving pulse solution). Let us emphasize that such behavior occurs under the constant fitness conditions, that is, the prey population does not evolve in the absence of predator. In the case of nonlocal consumption of resources, the evolutionary dynamics can become more complex.

REFERENCES

[1] A. Apreutesei, A. Ducrot and V. Volpert, Competition of species with intra-specific competition, *Math. Model. Nat. Phenom.*, 3 (2008), 1–27.
[2] N. Apreutesei, A. Ducrot and V. Volpert, Travelling waves for integro-differential equations in population dynamics, *Discrete Contin. Dyn. Syst. Ser. B*, 11 (2009), 541–561.
[3] N. Apreutesei, N. Bessonov, V. Volpert and V. Vougalter, Spatial structures and generalized travelling waves for an integro-differential equation, *Discrete Contin. Dyn. Syst. Ser. B*, 13 (2010), 537–557.
[4] O. Aydogmus, Patterns and transitions to instability in an intraspecific competition model with nonlocal diffusion and interaction, *Math. Model. Nat. Phenom.*, 10 (2015), 17–19.
[5] M. Banerjee and S. Banerjee, Turing instabilities and spatio-temporal chaos in ratio-dependent Holling-Tanner model, *Math. Biosci.*, 236 (2012), 64–76.
[6] M. Banerjee, N. Mukherjee and V. Volpert, Prey-predator model with a nonlocal bistable dynamics of prey, *Mathematics*, 6 (2018), 1–13.
[7] M. Banerjee and S. Petrovskii, Self-organized spatial patterns and chaos in a ratio-dependent predator-prey system, *Theor. Ecol.*, 4 (2011), 37–53.
[8] M. Banerjee and V. Volpert, Prey-predator model with a nonlocal consumption of prey, *Chaos*, 26 (2016), 12pp.
[9] M. Banerjee and V. Volpert, Spatio-temporal pattern formation in Rosenzweig-MacArthur model: Effect of nonlocal interactions, *Ecol. Complex.*, 30 (2017), 2–10.
[10] M. Banerjee, V. Vougalter and V. Volpert, Doubly nonlocal reaction–diffusion equations and the emergence of species, *Appl. Math. Model.*, 42 (2017), 591–599.
[11] M. Baumann, W. Ebenhoh and U. Feudel, Turing instabilities and pattern formation in a benthic nutrient-microorganism system, *Math. Biosci. Eng.*, 1 (2004), 111–130.
[12] M. Baumann, T. Gross and U. Feudel, Instabilities in spatially extended predator-prey systems: Spatio-temporal patterns in the neighborhood of Turing-Hopf bifurcations, *J. Theoret. Biol.*, 245 (2007), 220–229.
[13] A. Bayliss and V. A. Volpert, Patterns for competing populations with species specific nonlocal coupling, *Math. Model. Nat. Phenom.*, 10 (2015), 30–47.
[14] N. Bessonov, N. Reinberg and V. Volpert, Mathematics of Darwin’s diagram, *Math. Model. Nat. Phenom.*, 9 (2014), 5–25.
[15] S. Fasani and S. Rinaldi, Factors promoting or inhibiting Turing instability in spatially extended prey-predator systems, *Ecol. Model.*, 222 (2011), 3449–3452.
[16] T. Galochkina, M. Marion and V. Volpert, Initiation of reaction-diffusion waves of blood coagulation, *Phys. D*, 376–377 (2018), 160–170.
[17] G. F. Gause, *The Struggle for Existence*, Williams and Wilkins, Baltimore, 1934.
[18] S. Genieys, N. Bessonov and V. Volpert, Mathematical model of evolutionary branching, *Math. Comput. Modelling*, 49 (2009), 2109–2115.
[19] S. Genieys, V. Volpert and P. Auger, Pattern and waves for a model in population dynamics with nonlocal consumption of resources, *Math. Model. Nat. Phenom.*, 1 (2006), 65–82.
[20] S. Genieys, V. Volpert and P. Auger, Adaptive dynamics: Modelling Darwin’s divergence principle, *Comp. Ren. Biol.*, 329 (2006), 876–879.
[21] J. D. Murray, *Mathematical Biology. II: Spatial Models And Biomedical Applications*, Interdisciplinary Applied Mathematics, 19, Springer-Verlag, New York, 2003.
[22] S. Pal, S. Ghorai and M. Banerjee, Analysis of a prey-predator model with non-local interaction in the prey population, *Bull. Math. Biol.*, 80 (2018), 906–925.
[23] S. V. Petrovskii and H. Malchow, A minimal model of pattern formation in a prey-predator system, *Math. Comput. Modelling*, 29 (1999), 49–63.
[24] J. A. Sherratt, B. T. Eagan and M. A. Lewis, Oscillations and chaos behind predator-prey invasion: Mathematical artifact or ecological reality?, Phil. Trans. R. Soc. Lond. B, 352 (1997), 21–38.

[25] V. Volpert, Branching and aggregation in self-reproducing systems, in MMCS, Mathematical Modelling of Complex Systems, ESAIM Proc. Surveys, 47, EDP Sci., Les Ulis, 2014, 116–129.

[26] V. Volpert, Elliptic Partial Differential Equations, Monographs in Mathematics, 104, Birkhäuser/Springer Basel AG, Basel, 2014.

[27] V. Volpert, Pulses and waves for a bistable nonlocal reaction-diffusion equation, Appl. Math. Lett., 44 (2015), 21–25.

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