Abstract

In this paper we consider a modified spatiotemporal ecological system originating from the temporal Holling-Tanner model, by incorporating diffusion terms. The original ODE system is studied for the analysis of stability. The modified PDE system is investigated in detail with both numerical and analytical approaches. Both the Turing and non Turing patterns are examined for some fixed parametric values and some interesting results have been obtained for the prey and predator populations. Numerical simulation shows that either prey or predator population do not converge to any stationary state at any future time. Prey and predator populations exhibit spatiotemporal chaos resulting from temporal oscillation of both the population and random movement of both prey and predator species. The parametric restrictions of instabilities for both the distributions are also investigated under certain spatially inhomogeneous small perturbations. Different spatiotemporal patterns are also studied for the prey and predator populations with different time steps. The system exhibits chaotic patterns which are quantified by space time plot and also the average values of prey predator time series.

Keywords: Ratio-dependent, Holling-Tanner model, Turing instability, Pattern, Chaos.

1. Introduction

Predator-Prey dynamics continues to draw interest from both Applied Mathematicians and Ecologists due to its universal existence and importance with many concerned biological systems. While going for the mathematical modeling of predator-prey interaction, it seems to be simple initially but later it has been found that it possesses many challenging problems from the perspective of applied mathematics. The most challenging and crucial phase of modeling the population ecosystem is to examine and validate whether the concerned mathematical model can exhibit the proper behavior for the system under consideration.

From a theoretical aspect, the mechanisms that lead to these (often periodic) cycles were successfully explained by Lotka and Volterra in their now famous two-species predator-prey model which admit neutrally stable periodic solutions [35, 73]. In a more recent study, Hastings and Powell [22] examined the complex nonlinear behavior of three-species continuous-time ecological models and found them to be characterized by a far richer spectrum of dynamics than their well studied two species counterpart. In particular, they highlighted that three-species food web models are capable to exhibit chaotic oscillations and thus have relevance for the study of more complex population dynamics [67].

After the pioneering work of Alfred Lotka and Vito Volterra in the middle of 1920 for two species interactions, predator-prey models having prey-dependent functional response were
studied extensively [15, 18, 39, 49]. Recently, there is a growing explicit search for biological and physiological evidences for the choice of appropriate functional response, especially when predators have to search for food (and therefore has to share or compete for food). Based upon experimental evidences and analysis of collected field data it was revealed that a suitable predator-prey interaction should be based on the so-called ratio-dependent theory. It states that the per capita predator growth rate should be a function of the ratio of prey to predator abundance, and hence is called ratio-dependent functional response. This is supported by numerous fields and laboratory experiments and observations [34] and the references there in. Arditi and Ginzburg [4] first proposed the ratio-dependent functional response for predator-prey system. Ratio-dependent functional responses are thought to be rare compared to prey-dependent functional response but ratio-dependent functional response is considered as a reasonable alternative to model the complicated interaction between prey and predators [1, 4]. Predator-prey model with ratio-dependent functional response have revealed a wide variety of rich dynamical behavior [16, 27, 31, 11, 76, 25]. Holling-Tanner prey-predator model has received significant attention from both theoretical and mathematical biologists [30, 24, 57, 5] although little work has been done with Holling-Tanner model with ratio-dependent functional response. In a recent paper Liang and Pan [34] have studied the local and global asymptotic stability of the coexisting equilibrium point, existence and uniqueness of Poincare-Andronov-Hopf-bifurcating periodic solution for the ratio-dependent Holling-Tanner model system. This work is extended by Saha and Chakrabarti [58] to a delay differential equation model. In this they studied the local and global stability of various equilibria along with the existence criteria for small amplitude periodic solution which bifurcates from coexisting equilibrium point. They have studied the behavior of solution trajectories near the degenerate equilibrium point (0, 0) and derived the analytical criteria for the shape trajectories approaching origin.

Segel and Jackson [60] first used reaction-diffusion system to explain pattern formation in ecological context based upon the seminal work by Turing [71]. Similar ideas were used to explain spatiotemporal pattern formation in case of plankton systems [33] and semiarid vegetation [29]. Numerous papers have been published in last three decades on spatiotemporal patterns produced by reaction-diffusion models of prey-predator interactions and other types of interacting ecological systems [3, 9, 13, 17, 26, 36, 37, 40, 41, 46, 47, 52, 53, 55, 56, 61, 64, 72]. Earlier works on pattern formation were focused to study the pattern formation arising from Turing instability. Some researchers have shown their keen interest in the study of the types of Turing-patterns, namely, cold spot pattern, hot spot pattern and labyrinthine pattern depending upon the choice of parameter values within Turing domain [10, 65, 66]. Recently the focus has shifted to study the non-Turing patterns those results in spatiotemporal chaos, wave of chaos and resulting pattern near codimension two Turing-Hopf bifurcation point [10, 8, 38]. It is an established fact that formation of spontaneous spatiotemporal pattern is an intrinsic characteristic of predatorprey interaction [51, 63, 62, 55].

Most of the literature on spatiotemporal pattern formation in prey-predator models dealt with prey-dependent functional response (see [37, 55, 17, 41, 10] and references cited therein), the study of models with ratio-dependent functional response are now getting attention from the researchers [3, 7, 8, 74]. Spatiotemporal pattern formation in case of Holling-Tanner type prey-predator models with ratio-dependent functional response still remains an interesting area of research.

In this present work, we have considered ratio-dependent Holling-Tanner model for predator-prey interaction where random movement of both species are taken into account. The basic model considered in this paper is a reaction-diffusion model where the reaction part fol-
allows ratio-dependent Holling-Tanner type interaction between prey and predator population and they are capable to diffuse over a two dimensional landscape. We have arranged our paper in the following manner: In section 2, we have described Holling-Tanner predator-prey model with ratio-dependent functional response. In this section we have studied the conditions required for existence of interior equilibrium point, local asymptotic stability of interior equilibrium point, existence of small amplitude periodic solution arising from Poincare-Andronov-Hopf bifurcation and numerical investigation for existence of homoclinic orbit. In section 3, we have obtained the conditions for the occurrence of Turing instability. Linear stability analysis for spatiotemporal model [50] around homogeneous steady-state is carried out and the conditions required for the onset of Turing-instability in terms of model parameters are derived. We have obtained the domain in two dimensional parametric space where spatially uniform steady-states for both prey and predator population become unstable under spatially inhomogeneous perturbations. We have performed extensive numerical simulations for parametric values in side and outside the Turing domain and obtained results are presented in section 4. Choice of initial condition reflects small inhomogeneous perturbation from homogeneous coexisting steady state. Spatiotemporal chaotic pattern is reported for the parametric values lying outside the Turing domain. Finally we have summarized the main outcomes of present analysis in the concluding section.

2. Basic Model: Linear Stability

Robert May developed a prey-predator model Holling type functional response [23, 21] to describe the predation rate and Leslie’s formulation [39, 32] to describe predator dynamics. This model is known as Holling-Tanner model for prey-predator interaction. Holling-Tanner model is capable to capture the essential features of real ecological systems namely mite/spider mite, lynx/hare, sparrow/sparrow hawk and some other species [75, 69, 12]. Holling-Tanner predator-prey model with ratio-dependent functional response for consumption of prey by predators is governed by the following system of nonlinear coupled ordinary differential equations

\[
\frac{dN(T)}{dT} = rN(T) \left(1 - \frac{N(T)}{k}\right) - \frac{mN(T)P(T)}{N(T) + aP(T)} + aP(T)
\]

\[
\frac{dP(T)}{dT} = P(T) \left( s \left(1 - h \frac{P(T)}{N(T)}\right) \right)
\]

subjected to the biologically feasible initial conditions \(N(0) \equiv N_0 > 0\) and \(P(0) \equiv P_0 > 0\). \(N(T)\) and \(P(T)\) stand for prey and predator population (density) at any instant of time ‘\(T\)’. The parameters \(r, k, m, a, s, h\) are all positive and stand for prey intrinsic growth rate, carrying capacity for prey, capturing rate of prey by predator, handling time, predator intrinsic growth rate, conversion rate of prey into predator biomass respectively [34, 58]. In this modeling approach \(m\) and \(a\) are the characterizing parameters for the ratio-dependent functional response (detailed discussion for this type of functional response and its biological implications can be found in [6, 1, 2] and references cited there in). In a recent paper Liang and Pan [34] have studied the local and global asymptotic stability of the coexisting equilibrium point and obtained the conditions for Poincare-Andronov-Hopf-bifurcating periodic solution. For classical prey-predator models with prey-dependent functional response, \((0, 0)\) is a trivial equilibrium point as extinction of prey population imply the same for predators. But, for prey-predator models having ratio-dependent functional response like model (1), growth rates of prey and predator population is undefined at \((0, 0)\) due to presence of the
where $\alpha$ passes through the value 1. For $\alpha$ in Eq. (2a) we get $F(p)\equiv F_1(n,p)$ and $p$ is the tangent to prey nullcline at origin leading to the parametric restriction $\alpha(n,p)\leq 1$ and it is a concave curve with respect to $\alpha < n$. This idea is illustrated in Fig. 2c. Components of interior equilibrium point are given by

$$n^* = \left(1 - \frac{\beta}{\alpha \beta + 1}\right), \quad p^* = \beta n^*.$$
Figure 1: Three different plots of prey-nullcline for three different values of $\alpha$.

$n^*$ and hence $p^*$ are positive for every $\alpha \geq 1$ and for $\alpha < 1$ we need additional parametric restriction (4).

Figure 2: Three different shape of prey nullcline and position of interior equilibrium point; (a) prey nullcline (blue curve) and predator nullcline (green line) for $\alpha = 1.5$, $\beta = 1.2$; (b) prey and predator nullcline (blue curve and green line respectively) for $\alpha = 1$, $\beta = 1.2$; (c) prey nullcline for $\alpha = .5$ (blue line) and three plots of predator nullcline for $\beta = .6$ (green line), $\beta = 2$ (red line), $\beta = 5$ (sky-blue line). Interior equilibrium point coincides with $E_0$ for $\beta = 2$ and does not exist for $\beta > 2$ when $\alpha = .5$.

2.2 Stability of $E_*$

The local asymptotic stability of $E_*$ is discussed here in brief. The detailed discussion and related analysis of the stability properties of all equilibrium points for the model system (3) are available in [34, 58]. The Jacobian matrix for the model system (3) evaluated at $E_*$ is given by

$$J_* = [J(n, p)]_{E_*} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

(6a)

where

$$a_{11} = \frac{\beta(\alpha \beta + 2)}{(\alpha \beta + 1)^2} - 1, \quad a_{12} = -\frac{1}{(1 + \alpha \beta)^2} < 0, \quad a_{21} = \beta^2 \delta > 0, \quad a_{22} = -\delta \beta < 0.$$ 

(6b)
and characteristic equation for $J_*$ is

$$\lambda^2 + A_1\lambda + A_2 = 0$$

where $A_1 = -(a_{11} + a_{22}) = -\text{tr}(J_*)$ and $A_2 = a_{11}a_{22} - a_{12}a_{21} = \det(J_*)$. As $\det(J_*) = \delta\beta n^* > 0$ local asymptotic stability of $E_*$ solely depends upon the sign of $\text{Tr}(J_*)$ and hence $E_*$ is locally asymptotically stable if $\text{Tr}(J_*) < 0$ and unstable if $\text{Tr}(J_*) > 0$. The expression for $a_{11}$ can be written as

$$a_{11} = \frac{\beta^2\alpha(1 - \alpha) + 2\beta(1 - \alpha) - 1}{(\alpha\beta + 1)^2},$$

which is negative for $\alpha \geq 1$ and hence $E_*$ is locally asymptotically stable. In this case $\delta$ has no role on the local asymptotic stability of interior equilibrium point. For $\alpha < 1$, local asymptotic stability of interior equilibrium point demands parametric restriction

$$(1 + \beta\delta)(\alpha\beta + 1)^2 > (\alpha\beta + 2)\beta,$$

and magnitude of $\delta$ plays a crucial role here. The explicit restriction on $\delta$ required for local asymptotic stability of $E_*$ (when $\alpha < 1$) can be written as

$$\delta > \delta_* \equiv \left(\frac{\alpha\beta + 2}{(\alpha\beta + 1)^2} - \frac{1}{\beta}\right) = \frac{a_{11}}{\beta} > 0.$$  \hspace{1cm} (9)

The restriction $a_{11} < 0$, i.e.

$$\beta(\alpha\beta + 2) < (\alpha\beta + 1)^2,$$  \hspace{1cm} (10)

can be interpreted geometrically based upon the graphs of prey and predator nullcline. Satisfaction of inequality (10) implies that interior equilibrium point is the point of intersection of descending prey-nullcline with ascending predator nullcline passing through the origin and hence it is a stable equilibrium point (see [39]). Although $E_*$ is point of intersection of ascending predator nullcline with ascending prey nullcline when inequality (4) is satisfied and (10) is violated, its stability depends upon the satisfaction of (9). This additional condition is required as the growth rate of predators are logistic type rather than Lotka-Volterra formulation [49, 70]. The stability of $E_*$ in four different cases are illustrated in Fig. 3.

If we decrease the magnitude of $\delta^*$ through $\delta_*$ and keeping in mind the restriction $\alpha < 1$ and $\beta(\alpha\beta + 2) > (\alpha\beta + 1)^2$ then $E_*$ becomes unstable. By the Poincare criteria, there exists at least one limit cycle enclosing $E_*$. The interior equilibrium point losses its stability through Poincare-Andronov-Hopf-bifurcation; at $\delta = \delta_*$ both the conditions $\text{Tr}(J_*) = 0$ and $\frac{d\text{Tr}(J_*)}{d\delta}|_{\delta=\delta_*} \neq 0$ required for Poincare-Andronov-Hopf-bifurcation are satisfied [20]. Limit cycle arising through Poincare-Andronov-Hopf-bifurcation is a stable limit cycle which attracts all trajectories starting from a point in the interior of first quadrant [34]. Bifurcation of solution trajectories from interior equilibrium point is shown in Fig. 5 (upper panel). An important result regarding the nature of solution trajectories for $\delta < \delta_*$ we will mention here with supporting numerical simulation without going to the analytical proof. The size of limit cycle gradually increases with the decrease of $\delta$ below $\delta_*$ and ultimately it becomes a homoclinic orbit at the origin for $\delta = .21$, when other parameter values are $\alpha = .4$ and $\beta = 1.2$ (see Fig. 4). If we further decrease the magnitude of $\delta$ below .21 (keeping other two parameters fixed) then $E_0(0,0)$ becomes stable and imply extinction of both prey and predator population. For $\delta < .21$, with $\alpha = .4$ and $\beta = 1.2$, the entire first quadrant is the basin of attraction for $E_0$. Detailed discussion for stability of extinction state $E_0$, nature of phase portraits near origin depending upon the magnitudes of parameters and existence
Figure 3: Phase portrait for the model system (3) showing coexisting equilibrium point is locally asymptotically stable (green line for the prey-nullcline, blue curve for the predator-nullcline) for various choice of parametric values: (a) $\alpha = 1.5, \beta = 1.1, \delta = 1$; (b) $\alpha = 1, \beta = 1.1, \delta = 1$; (c) $\alpha = 0.4, \beta = 0.5, \delta = 1$; (d) $\alpha = 0.4, \beta = 1.1, \delta = 1$.

Figure 4: (a) - (c) limit cycle for the model system (3) with $\alpha = 0.4, \beta = 1.2$ and values of $\delta$ are mentioned in the respective figures; (d) homoclinic orbit obtained for $\alpha = 0.4, \beta = 1.2$ and $\delta = 0.21$. Of parabolic, elliptic and hyperbolic sectors in the vicinity of origin can be found in [58]. Attracting nature of $E_0$ and existence of parabolic sector as well as elliptic sector for $\alpha = 0.4, \beta = 1.2$ and $\delta = 0.18$ is presented in Fig. 5 (lower panel).
Figure 5: Upper panel: Bifurcation diagram showing maximum and minimum values of $n$ at steady-state (after neglecting initial transients) obtained for $\alpha = 0.4$ and $\beta = 1.2$. Lower panel: Solution trajectories for the model system (3) approach $E_0(0,0)$ for parametric values $\alpha = 0.4$, $\beta = 1.2$ and $\delta = 0.18$. The origin has a parabolic sector and an elliptic sector.

3. Spatiotemporal Model: Turing Instability

In this section we consider the spatiotemporal Holling-Tanner model obtained from the temporal model (3) by incorporating diffusion terms as follows

$$\frac{\partial n}{\partial t} = n(1-n) - \frac{np}{n+\alpha p} + \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2}\right) \tag{11a}$$

$$\frac{\partial p}{\partial t} = \delta p \left(\beta - \frac{p}{n}\right) + d \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2}\right) \tag{11b}$$

subjected to the no-flux boundary conditions and known positive initial distribution of populations

$$\frac{\partial n}{\partial \nu} = \frac{\partial p}{\partial \nu} = 0, \text{ on } (0, \infty) \times \partial \Omega, \tag{11c}$$

$$n(0, x, y) = n_0(x, y) > 0, \quad p(0, x, y) = p_0(x, y) > 0 \text{ for } (x, y) \in \Omega. \tag{11d}$$

$\Omega$ is the two-dimensional bounded connected domain with boundary $\partial \Omega$, $\partial / \partial \nu$ is the outward drawn normal derivative on the boundary. In the model system (11), the parameter ‘$d$’ is the ratio of diffusivity of two populations. Here $n \equiv n(t, x, y)$ and $p \equiv p(t, x, y)$ denote prey and predator population at any time ‘$t$’ at $(x, y)$.

The coexisting equilibrium point $E_*$ for the temporal model (3) is a spatially homogeneous steady-state for the reaction-diffusion model (11a) - (11b). We assume that homogeneous steady-state is locally asymptotically stable for the temporal model system (i.e. the restrictions $a_{11} + a_{22} < 0$ and $a_{11}a_{22} - a_{12}a_{21} > 0$ are satisfied). As we are interested to find out the conditions for the occurrence of Turing-instability the parametric restriction $\alpha < 1$ is only of our interest. For $\alpha \geq 1$ the homogeneous steady-state can not be destabilized by introducing spatially inhomogeneous perturbation around the steady-state for whatever may be the large magnitude of ratio of diffusivity.

Linear stability analysis for spatiotemporal model (11) around the homogeneous steady-state and the conditions required for the onset of Turing-instability are well known [50, 71, 42, 49, 60] and used by several researchers [3, 7, 8, 10, 40, 41, 43, 65, 66, 74]. Here we just
mention the basic mathematical criteria required for Turing-instability. We are interested to obtain the parametric restriction(s) for both prey and predator population. For these parametric restriction(s), both the population in spatially uniform coexisting homogeneous steady-state, become unstable under certain spatially inhomogeneous small perturbations. Three conditions required for Turing-instability of the model \((11)\) around \((n_*, p_*)\) are as follows

\[
\begin{align*}
    a_{11} + a_{22} &< 0, \tag{12a} \\
    a_{11}a_{22} - a_{12}a_{21} &> 0, \tag{12b} \\
    da_{11} + a_{22} &> 2\sqrt{d\left(a_{11}a_{22} - a_{12}a_{21}\right)}, \tag{12c}
\end{align*}
\]

and Turing-instability sets in at the critical wave number

\[
k_{cr}^2 = \frac{da_{11} + a_{22}}{2\sqrt{d}} > 0. \tag{13}
\]

\(a_{ij}, i, j = 1, 2\) have same expressions as in \((6b)\). Conditions \((12a)\) and \((12b)\) are required for local asymptotic stability of homogeneous steady-state, satisfaction of condition \((12c)\) imply homogeneous steady-state becomes unstable with smallest wavenumber \(k_{cr}\) under infinitesimally small inhomogeneous spatial perturbation and Turing pattern emerges. Type of spatial pattern depends upon the choice of parametric values and magnitude of ‘\(d\)’.

We can recall the result \(a_{11} < 0\) whenever \(\alpha \geq 1\) and hence no real \(k_{cr}\) exists to satisfy the condition \((13)\) as ‘\(d\)’ is a positive quantity and \(a_{22} < 0\). Thus small inhomogeneous spatial perturbation has no ability to induce spatial instability under any circumstances and Turing pattern do not emerge for \(\alpha \geq 1\). To see the spatial pattern arising from Turing instability we have to consider \(\alpha < 1\). Condition \((12b)\) is satisfied irrespective of the magnitude of parameters and hence \((12a)\) and \((12c)\) when written in terms of parameters of the model system \((11)\) define the domain in parameter space where homogeneous steady-state loses stability under non-uniform small spatial perturbation around steady-state. As \(a_{22} < 0\), satisfaction of inequality \((12c)\) demands \(a_{11} > 0\) and which in turn give a critical magnitude for ‘\(d\)’ as \(d_{cr} = -\frac{a_{22}}{a_{11}}\) beyond which diffusive instability sets in and this shows the magnitude of ratio of diffusivity play significant crucial role behind Turing pattern formation. In other words, for a fixed value of \(d\) the restriction \(da_{11} + a_{22} > 0\) introduce an additional boundary in Turing space. In this paper we have considered different values of \(\delta\) and \(d\), keeping other two parameters fixed to see Turing and non-Turing patterns.

3.1 Determination of Turing Space

The three conditions \((12a)\) - \((12c)\) and the supporting condition \(da_{11} + a_{22} > 0\) required for Turing instability can be written in terms of the parameters as follows

\[
\begin{align*}
    F_1(\beta, \delta) &\equiv \frac{\beta(\alpha\beta + 2)}{(\alpha\beta + 1)^2} - (1 + \delta\beta) < 0 \tag{14a} \\
    F_2(\beta, \delta) &\equiv \beta\delta \left(1 - \frac{\beta}{\alpha\beta + 1}\right) > 0 \tag{14b} \\
    F_3(\beta, \delta) &\equiv d\left(\frac{\beta(\alpha\beta + 2)}{(\alpha\beta + 1)^2} - 1\right) - \beta\delta - 2\sqrt{d}\sqrt{F_2(\beta, \delta)} > 0 \tag{14c} \\
    F_4(\beta, \delta) &\equiv d\left(\frac{\beta(\alpha\beta + 2)}{(\alpha\beta + 1)^2} - 1\right) - \beta\delta > 0, \tag{14d}
\end{align*}
\]
where four auxiliary functions $F_r(\beta, \delta), r = 1, 2, 3, 4$ are defined to describe the boundary curves in the bifurcation diagram. In $(\beta, \delta)$-parameter space the curve $F_1(\beta, \delta) = 0$ defines the Poincare-Andronov-Hopf-bifurcation curve and $F_3(\beta, \delta) = 0$ defines the Turing-bifurcation curve. Interestingly the curve $F_2(\beta, \delta) = 0$ defines one of the boundaries of Turing space as well as the boundary for feasible coexistence state $(n_*, p_*)$.

Fig. 6 shows the bifurcation diagram in $(\beta, \delta)$ parameter space for fixed $\alpha = .4$ and $d = 16$. The homogeneous steady state $(n_*, p_*)$ is feasible in the region lying on the left of the sky-blue vertical line. Turing space is bounded above by the blue curve and bounded below by the green curve and bounded by the sky-blue line on the right. Every point in the parameter space above the blue curve corresponds to the unconditionally stable homogeneous steady-state. For the parameter values within the Turing space, the coexisting homogeneous steady-state remains stable under spatially homogeneous steady state but loose their stability due to inhomogeneous spatial perturbation. We have observed the stationary inhomogeneous spatial pattern over the entire domain. The type of stationary spatial pattern solely depends upon the magnitude of parameters. For the parameter values taken from the region lying below the Poincare-Andronov-Hopf-bifurcation curve the homogeneous steady-state become unstable due to spatially homogeneous as well as inhomogeneous perturbation. The spatiotemporal chaos or extinction scenario emerges due to destabilization of homogeneous steady-state depending upon whether the chosen point lies above or below the homoclinic bifurcation curve. A part of numerically computed homoclinic bifurcation curve is shown in Fig. 6 where we have described various type of spatial pattern exhibited by the spatiotemporal model system (11a) - (11b) in $(\beta, \delta)$ parameter space. The Turing-bifurcation curve starts from $\beta = .7274861218$ (for $\alpha = .4$ and $d = 16$) as $a_{11}$ becomes negative for $\beta < .7274861218$. For parameter values taken from the region lying below the homoclinic bifurcation curve the spatially homogeneous and heterogeneous perturbation from homogeneous steady-state imply the extinction of both prey and predator species.

![Figure 6: Bifurcation diagram for the system (11a) - (11b) with $\alpha = .4$ and $d = 16$. Turing space is bounded by Turing-bifurcation curve (blue curve), Poincare-Andronov-Hopf-bifurcation curve (green curve) and the line $\beta = 1.66666667$ (sky blue line). Turing-bifurcation curve and Poincare-Andronov-Hopf-bifurcation curve intersect at the codimension two Turing-Hopf point (.83,.1). Red curve corresponds to the parametric restriction $da_{11} + a_{22} = 0.$](image)

4. Numerical Simulation: Turing and non-Turing Pattern
We take fixed values $\alpha = .4$ and $\beta = 1.2$ for numerical simulations and consider $\delta$ and $d$ as controlling parameters. The spatiotemporal model (11) becomes

$$\frac{\partial n}{\partial t} = n(1-n) - \frac{n p}{n + .4p} + \left( \frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right),$$  \hspace{1cm} (15a)

$$\frac{\partial p}{\partial t} = \delta p \left( 1.2 - \frac{p}{n} \right) + d \left( \frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right).$$  \hspace{1cm} (15b)

Numerical simulations of (15) are carried out by transforming the infinite dimensional continuous model system to finite-dimensional form using discretization of time and space. Numerical simulations were carried out over a $200 \times 200$ lattice sites and spacing between two neighboring lattice points are taken as $\Delta x = \Delta y = 1$ and time-step $\Delta t = 0.01$. It is worthy to mention that the patterns reported in this paper are independent of the choice of $\Delta t$, $\Delta x$ and $\Delta y$ as we have checked with smaller values of time and space stepping. Zero-flux boundary conditions are used at the boundary of square domain. Numerical integration of (14) are performed by using non-standard finite difference scheme [44, 45] for the reaction part and five point explicit finite difference scheme [68] for the diffusion part. In all numerical simulations the initial distribution of prey and predator population are taken as $n_0(x_i, y_j) = n_* + \epsilon \xi_{i,j}$, $p_0(x_i, y_j) = p_* + \epsilon \eta_{i,j}$ with $\epsilon = 0.001$, $\xi_{i,j}$ and $\eta_{i,j}$ are Gaussian white noise terms which are $\delta$-correlated in space [38]. The choice of initial condition reflects small inhomogeneous spatial perturbation from homogeneous steady-state.

Before looking at the Turing-pattern we demonstrate that the conditions for the Turing instability obtained analytically (see eqn. (14)) define a non-empty set in parametric space for chosen values of $\alpha$ and $\beta$. The spatially uniform steady-state of (14) is $(0, 0)$ and condition (14b) is automatically satisfied for all positive values of $\delta$. Condition (14a) offers the restriction $\delta > .2989$. Next we look at the plots of $h(k^2)$ for different values of $\delta$ keeping $d$ fixed and vice-versa, where $h(k^2)$ for our model system (15) is defined by [50, 49, 38, 7]

$$h(k^2) \equiv d(k^2)^2 - (.359d - 1.2\delta)k^2 + .227\delta.$$

Plot of $h(k^2)$ for different values of $d$ keeping $\delta$ fixed and then for a set of values of $\delta$ keeping $d$ fixed are shown in Fig. 7. Turing instability condition $\min h(k^2) < 0$ is satisfied for $d \gtrapprox 6$ when $\delta = .5$ and the interval $(k_{\min}, k_{\max})$ within which $h(k^2) < 0$ increases with increasing magnitude of $d$. For fixed $d = 10$, $\min h(k^2) < 0$ holds for $\delta \lesssim .8$ (approx) and the interval $(k_{\min}, k_{\max})$ increases with a decrease in $\delta$.

Now we are in a position to look at the Turing pattern obtained from numerical simulations of (15) subjected to necessary initial and boundary conditions. Fig. 8 depicts the stationary distribution of prey and predator population over the spatial domain at $t = 400$ for different $d$ and fixed $\delta = 1$. These patterns are obtained for the parameter values lying within Turing domain and qualitative nature of the patterns and width between the minimum and maximum prey and predator density over space are changing with increasing magnitude of $d$. The stationary spatial pattern for fixed ratio of diffusivity ($d = 16$) and three different values of $\delta$ are reported in Fig. 9, in this case similar qualitative change in pattern is observed with decreasing magnitude of $\delta$. From bifurcation diagram (see Fig. 6) it is clear that the chosen values of $\delta$ are lying within the Turing domain. The time at which we stopped the numerical simulation sufficed to assume that the patterns attained the stationary state and they no longer change with time from those we have obtained at the end of simulation. The patterns we have presented in Fig. 8 and Fig. 9 changes cold spot pattern to labyrinthine pattern as $d$ varies from 17 to 21 and $\delta$ changes from 1.1 to .7.
Figure 7: Plot of $h(k^2)$ against $k^2$ for different values of $d$ and $\delta$; (upper panel) for $\delta = .5$ and five different values of $d$ as mentioned there; (lower panel) for five different values of $\delta$ as mentioned at the right side of figure for $d = 10$.

Figure 8: Stationary prey (upper panel) and predator (lower panel) distribution over space for $\alpha = .4$, $\beta = 1.2$, $\delta = 1$ and three different values of $d$; (a),(d) $d = 17$, (b),(e) $d = 19$ and (c),(f) $d = 21$.

To see the types of spatiotemporal patterns exhibited by the model system (15a) - (15b) for fixed $d = 16$ and $\beta = 1.2$ we have performed numerical simulation for a range of values of $\delta$ within the interval $[1.15, .3]$. From bifurcation diagram it is clear that the parameter values lie inside the Turing-domain and stationary pattern ranges from spot pattern to labyrinthine
Figure 9: Steady state pattern population distribution reached by prey (upper panel) and predator (lower panel) population at $t = 400$ for fixed $\alpha = .4$, $\beta = 1.2$, $d = 16$ and three different values of $\delta$; (a),(d) $\delta = 1.1$, (b),(e) $\delta = .9$ and (c),(f) $\delta = .7$.

Figure 11 shows the dispersion relation which clearly depicts the range of wavenumbers for which the real part of largest eigenvalue of the characteristic equation is positive. We have calculated the eigenvalues of the following characteristic equation \cite{38, 50, 49} for different values of $\delta$ and $k \in [0, .9]$,

$$\lambda^2 + (17k^2 - .3586559532 + 1.2\delta)\lambda + (.2270270273\delta - 5.738495251k^2 + 1.2\delta k^2 + 16k^4) = 0.$$  

The length of the interval $(k_{\text{min}}, k_{\text{max}})$ within which the largest real part of eigenvalue is positive increases with decaying magnitude of $\delta$.

Next we examine the spatial pattern exhibited by the model \cite{15}. For $\delta = .23$ and $d = 16$, the chosen parametric values lie outside the Turing domain and lies within the Turing-Hopf domain. For this choice of parameters the homogeneous steady-state becomes unstable, breaking the the temporal and spatial symmetry of the system and spatiotemporal oscillatory pattern emerges. We have to see whether the spatiotemporal pattern reaches any stationary state or not with the advancement of time. Numerical simulation shows that either population does not converge to any stationary steady-state at any future time. Prey and predator populations exhibit spatiotemporal chaos resulting from temporal oscillation of both the population and random movement of both prey and predator species. Simulation result presented in Fig. 12 at different time steps mentioned at the caption of figure. Associated colorbar in the figure shows abrupt fluctuation in prey population density at different time steps. The observed pattern is completely different compared to the stationary pattern as depicted in Fig. 10. The stationary pattern exhibited by the prey population is presented here. The predator population develops the stationary patterns similar to those produced by prey which are not shown here for the sake of brevity. It is worthy to mention here the spot pattern emerging from Turing-bifurcation gives way to labyrinthine pattern and the labyrinthine pattern appears to be stationary at large time limit. The labyrinthine pattern reaches the stationary state for the parameter values near Turing-Hopf boundary.
Figure 10: Stationary spatial pattern exhibited by the prey population at $t = 600$ for fixed $\alpha = 4$, $\beta = 1.2$, $d = 16$ and a range of values of $\delta$ within Turing domain. (a) $\delta = 1.15$, (b) $\delta = 1$, (c) $\delta = 0.8$, (d) $\delta = 0.6$, (e) $\delta = 0.4$ and (f) $\delta = 0.3$.

Figure 11: Dispersion relations showing unstable Turing for six different values of $\delta$ as mentioned in the figure, other parameter values are $\alpha = 4$, $\beta = 1.2$ and $d = 16$.

within and just outside the Turing domain. Prey and predator population distribution never reach any stationary state at any future time and spatiotemporal chaos sustain at all future time and no drastic change in pattern is observed at a larger time step (see Fig. 13). Patterns obtained up to $t = 1800$ is presented here but we have checked the patterns for greater
values of $t$ and obtained patterns are same as we have presented here. Fig. 14 illustrate that emerging patterns do not converge to any stationary steady state as spatial average of both population oscillate in an irregular fashion and have no tendency of convergence. Fig. 14 shows the spatially average population densities $\langle n \rangle$ and $\langle p \rangle$ for prey and predator population respectively against time [8]. Spatiotemporal chaos is observed for values $.21 \leq \delta \leq .23$ keeping $d$ fixed at $d = 16$. For $\delta < .21$ we get extinction scenario for both prey and predator population.

The spot pattern we have observed within Turing domain is known as cold spot pattern [10] as spots are generated due to isolated zones with low prey and predator population densities. The cold spot patterns are observed for the parameter values near the Turing bifurcation curve. For parameter values within the Turing domain but near the Poincare-Andronov-Hopf boundary the stationary pattern is of labyrinthine type. Nearby cold spots coalesce with one another to produce labyrinthine pattern. The amplitude of population density changes at the stationary pattern as magnitude of $\delta$ decreases; cf. color bars of the panels in Fig. 10. Stationary population density fluctuates between 0.2698 and 0.0746 for $\delta = 1.15$ and it fluctuates between 0.4814 and .0216 when $\delta = .3$.

5. Conclusion

In this paper we have studied a spatio-temporal prey-predator model where the interaction between prey and predator follows Holling-Tanner formulation with ratio-dependent functional response. The local asymptotic stability condition for coexisting equilibrium point and condition for Poincare-Andronov-Hopf-bifurcating periodic solution is described briefly. We have established the existence of homoclinic orbit through numerical investigation and identified the boundary for homoclinic bifurcation. We obtained the parametric restrictions with help of linear stability analysis for reaction-diffusion model for which spatially homogeneous coexisting steady-state for both prey and predator population becomes unstable due
Figure 13: Spatiotemporal chaotic pattern exhibited by prey population with advancement of time and never reaches any stationary state. Prey population distribution at different time steps (a) $t = 2000$, (b) $t = 2100$, (c) $t = 2200$, (d) $t = 2300$, (e) $t = 2400$, (f) $t = 2500$, (g) $t = 2600$, (h) $t = 2700$. Parameter values are $\alpha = .4$, $\beta = 1.2$, $\delta = .215$ and $d = 16$.

Figure 14: Plot of spatial average values for prey and predator population against time showing chaotic oscillation.

to small spatially inhomogeneous perturbation. Both Turing and non-Turing patterns have been studied for the parametric values within Turing domain and the domain bounded by Poincare-Andronov-Hopf-bifurcation curve and homoclinic bifurcation curve.
Figure 15: Different types of patterns observed for the model system (15a) - (15b) within Turing domain and in the domain bounded by Poincare-Andronov-Hopf bifurcation curve and numerically computed homoclinic bifurcation curve. Parameter values are marked with four different symbols according to the different patterns observed: red ∗: cold spot pattern, green ♦: intermediate pattern between cold spot and labyrinthine pattern, blue △: labyrinthine pattern, magenta ◦: spatiotemporal chaotic pattern.

With the help of bifurcation diagram, we have identified the Turing instability domain and obtained cold spot pattern and labyrinthine pattern for parameters within Turing domain from extensive numerical simulations. Cold spot patterns and labyrinthine patterns are both stationary patterns. Finally we have shown that for parameter values within Turing-Hopf domain both prey and predator population show spatiotemporal chaos until the parameter values cross homoclinic bifurcation boundary. Once we cross the homoclinic bifurcation boundary the extinction scenario for both species is observed. The sufficient conditions in terms of system properties required for the formation of chaotic spatiotemporal patterns remains a controversial issue for reaction-diffusion models of prey-predator interaction [64]. Some authors demonstrated that Poincare-Andronov-Hopf-bifurcation is sufficient to ensure the onset of spatiotemporal chaos [8, 38] and others have demonstrated that spatiotemporal chaos should be observed in the vicinity of codimension two Turing-Hopf bifurcation point [10]. In this paper we have established the existence of spatiotemporal chaos for Holling-Tanner prey-predator model with ratio-dependent functional response in the Turing-Hopf domain bounded by Poincare-Andronov-Hopf-bifurcation curve and from below by homoclinic bifurcation curve. Study of spatiotemporal pattern in the vicinity of codimension two Turing-Hopf bifurcation point for the model considered here with help of nonlinear analysis used in [28, 43] would provide a better understanding. This will be our focus of research in near future. Finally we like to remark that conclusive evidence of spatiotemporal chaos in interacting ecological systems is still to be found and there are a growing number of indications of chaos in realistic ecosystems [14, 19, 54, 59]. Some recent works with continuous time models for vegetation distribution, planktonic interaction and a few work with prey-predator type interaction have argued in favor of spatiotemporal chaos [47, 56, 63].
Appendix

The non-dimensionalized version can be obtained from the following model system

\[
\frac{\partial N}{\partial T} = rN \left( 1 - \frac{N}{k} \right) - \frac{mNP}{N + AP} + D_1 \left( \frac{\partial^2 N}{\partial X^2} + \frac{\partial^2 N}{\partial Y^2} \right),
\]

\[
\frac{\partial P}{\partial T} = sP \left( 1 - \frac{P}{N} \right) + D_2 \left( \frac{\partial^2 P}{\partial X^2} + \frac{\partial^2 P}{\partial Y^2} \right),
\]

with help of the transformation of variables

\[ N = kn, \quad P = \frac{rk}{m} p, \quad T = \frac{t}{r}, \quad X = \lambda x, \quad Y = \lambda y; \quad \lambda = \sqrt{\frac{D_1}{r}}. \]

Substituting into the original model system we get the dimensionless version as follows

\[
\frac{\partial n}{\partial t} = n(1 - n) - \frac{np}{n + \alpha p} + \left( \frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \quad (4a)
\]

\[
\frac{\partial p}{\partial t} = \delta p \left( \beta - \frac{p}{n} \right) + d \left( \frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \quad (4b)
\]

where \( \alpha = \frac{ra}{m}, \delta = \frac{sh}{m}, \beta = \frac{m}{hr} \) and \( d = \frac{D_2}{D_1} \).

References


