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Interactive effects of prey refuge and additional food for predator in a diffusive predator-prey system

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Abstract

Additional food for predators has been considered as one of the best established techniques in integrated pest management and biological conservation programs. In natural systems, there are several other factors, e.g., prey refuge, affect the success of pest control. In this paper, we analyze a predator-prey system with prey refuge and additional food for predator apart from the focal prey in the presence of diffusion. Our main aim is to study the interactive effects of prey refuge and additional food on the system dynamics and especially on the controllability of prey (pest). Different types of Turing patterns such as stripes, spots, holes, and mixtures of them are obtained. It is found that the supply of additional food to the predator is unable to control the prey (pest) population when prey refuge is high. Moreover, when both prey refuge and additional food are low, spatial distribution of prey becomes complex and once again prey control becomes **complex difficult**. However, the joint effect of reduction in prey refuge and the presence of appropriate amount of additional food can control prey (pest) population from the system.

Keywords: Prey refuge; additional food; reaction-diffusion; Turing instability; pattern formation; pest control

1. Introduction

Predator-prey systems have continuously drawn interest among mathematical biologists due to the variety of complex biological processes (May, 1974; Hassel, 1978; Anderson and May, 1979; Hastings and Powell, 1991; Turchin, 2003). The importance of studying predator-prey systems lies in gaining insight into the complex processes and solve ecological problems, e.g., the control of populations of economically damaging species, particularly of agricultural weed and insect pests. Various biological factors such as infection/disease (Chattopadhyay and Arino, 1999), predation (Roy and Chattopadhyay, 2005), migration (Chowdhury et al., 2010), group defense (Venturino and Petrovskii, 2013), mutualism (Boucher, 1988), cannibalism (Chakraborty and Chattopadhyay, 2011), omnivory (McCann and Hastings, 1997), Allee effects (Allee, 1931), alternative and additional food for the predator (Murdoch, 1969; Chakraborty and Chattopadhyay, 2008), etc., alter the dynamical behavior of the prey-predator interaction processes. Among them, prey refuge and additional food are the most common factors observed in almost every ecosystem. In real life situations, these factors can act together and the resultant dynamics become very complex.

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In predator-prey systems, the prey population shows a variety of different defense mechanisms to escape from predation (Baldwin, 1996; Chakraborty et al., 2012). Among them, behavioral changes like migration and/or refuge are most common in literature (Gonzalez-Olivares and Ramos-Jiliberto, 2003; Abrams, 2008) and this hiding behavior of prey has become a major issue in theoretical ecology (Zhuang and Wen, 2011). Generally, refuge means any strategy which decreases the rate of predation by a predator (Anderson, 2001). Some of the empirical and theoretical studies have shown a stabilizing effect of prey refuge on the system dynamics and protects prey from extinction (Taylor, 1984). For example, Connell (1970) found that spatial refuge shown by barnacle *Balanus Glandula* in the higher intertidal stabilizes its interaction with the predatory snails *Thais*. However, the effects of prey refuge on population dynamics are very complex. From a modeling point of view, prey refuge can be considered as constituted by two components. Firstly, a reduction in prey mortality due to decline in predation success affects positively the growth of prey and negatively that of predators. Secondly, the hiding behavior of prey could be beneficial or harmful for the interacting populations (Wang and Wang, 2012). Although, prey refuge is known to have stabilizing effects on system dynamics, predator-prey interactions can also be destabilized and the predator population may extinct from the system as predators suffer from lower predation success if the size of the refuge class becomes large. In spatial scale, the dynamics of a local population largely depend upon attributes of the local habitats (Johnson, 2006).

Under resource limitation, predators may deviate from their usual diet and exhibit some inclination towards the alternative prey to prolong their survivability. In contrast, the additional food always provides benefits to predator population and helps them to persist in the system. The effects of additional food to the predator and its usefulness in biological control have been studied by several researchers (Spencer and Collie, 1995). Many of the literatures addressing biological control consider prey as pest population and aim to control and eradicate the pest population (i.e. prey) through predation by providing additional food to the predator. Such type of models predict that providing additional prey increases predator population together with the predation on target prey, thus helps to decrease the abundance of the target prey population. Both theoretical and experimental works point out that the quality and quantity of additional food play a vital role in the controllability of the pest (Srinivasu and Prasad, 2011). Moreover, handling time for the additional food also plays an important role in determining the eventual state of the ecosystem (Srinivasu et al., 2007).

Predator-prey interactions generally occur over a wide range of spatial and temporal scales and the spatial components of ecological interactions play an important role in shaping ecological communities. In this respect, spatial patterns are ubiquitous in nature and often change the temporal dynamics of the system (Chakraborty, 2015; Chakraborty et al., 2015, and references therein). Pattern formation in spatial models has been investigated continuously and become a central issue to modelers since the pioneering work of Turing (1952). Till now, there are only few studies investigating the role of prey refuge (Guin et al., 2015; Wang and Wang, 2012) and additional food for predator (Kumar and Chakraborty, 2015), separately, in simple predator-prey systems affecting spatial distribution of predator and prey populations. However, since both prey refuge and additional food for predators are simultaneously present in most of the ecological systems, it would be interesting to see how their combined effect affects the spatial dynamics of predator-prey systems.

To the best of our knowledge, this is the first work considering the spatial dynamics of prey and predator with prey refuge and additional food to the predators. Here, it is assumed that a constant portion of the prey population is taking refuge and the remaining portion is exposed to predation. Moreover, the additional food is not dynamic but maintained at a specific constant level either by the nature or by an external agency. The non spatial version of our model is very close to the model by Samanta et al. (2016). The present model is made more realistic by considering predator interference

and spatial heterogeneity of populations. Here, our aim is to investigate the interactive effects of prey refuge and additional food for predator on the spatial dynamics of the system. The paper is organized as follows: in section 2, we have discussed our model. Section 3 contains the proof of boundedness and positivity of the solution. Also, the existence and stability conditions of interior equilibrium are investigated in this section. In the next section (section 4), we analyze the stability of the spatial version of the model. We validate our findings numerically and have shown the formation of different patterns w.r.t. prey refuge and additional food in section 5. The paper ends with a discussion.

2. Basic model structure

Let N be the density of prey and P be the density of predator at any time $t > 0$. In the absence of predation, the prey population follows the logistic growth with an intrinsic growth rate r and environmental carrying capacity K . The interaction between prey and predator population is assumed to be of modified Beddington type. The prey population is assumed to take refuge, which provides them a degree of protection from predator population. We consider that there exists a fraction mN of prey population that occupies a refuge. The predator population is supposed to be provided with additional food of biomass A , which is assumed to be distributed uniformly in the habitat. The additional food is non-reproducing and is supplied at a constant rate and the number of encounters per predator with additional food is proportional to the density of additional food. The consumption of additional food also reduces the consumption of the prey population. The density of predator population decreases due to natural death at a constant rate γ . If we consider the diffusion of prey and predator populations together with the above assumptions, then we have the following reaction-diffusion system:

$$\begin{aligned}\frac{\partial N}{\partial t} &= rN \left(1 - \frac{N}{K}\right) - \frac{\beta(1-m)NP}{K_1 + \delta(1-m)N + \alpha\eta A + \theta P} + D_N \nabla^2 N, \\ \frac{\partial P}{\partial t} &= \frac{c[\beta(1-m)N + \eta A]P}{K_1 + \delta(1-m)N + \alpha\eta A + \theta P} - \gamma P + D_P \nabla^2 P,\end{aligned}\tag{2.1}$$

where $\nabla^2 \equiv \partial^2/\partial x^2 + \partial^2/\partial y^2$ is the usual *Laplacian Operator* in two dimensional space; D_N , D_P are the self-diffusion coefficients for prey and predator, respectively, describing the movement of individuals from a higher to lower concentration region. We assume that the system parameters do not depend on space or time, that is, the environment is uniform. Let h_1 and e_1 be two constants representing handling time of the predator per prey item and ability of the predator to detect the prey, then $\beta = 1/h_1$ and $K_1 = 1/e_1 h_1$ represent the maximum rate of predation and half saturation value of prey uptake by the predator, respectively. Let h_2 and e_2 , respectively, be the handling time of the predator per unit quantity of additional food and ability for the predator to detect the additional food. Let us define $\eta = e_2/e_1$ and $\alpha = h_2/h_1$. The term ηA designates effectual additional food level and the constant θ scales the impact of predator interference. The description of the parameters in the model system (2.1) is given in detail in Table 1.

Let Ω be the two-dimensional bounded connected square domain. Model (2.1) is to be analyzed under the following non-zero initial condition and *zero-flux* (or Neumann) boundary conditions:

$$N(x, y, 0) > 0, P(x, y, 0) > 0, (x, y) \in \Omega = [0, R] \times [0, R],$$

$$\frac{\partial N}{\partial \hat{n}} = \frac{\partial P}{\partial \hat{n}} = 0, (x, y) \in \partial\Omega.$$

In the above, \hat{n} is the outward unit normal vector of the boundary $\partial\Omega$ which we assume is smooth. The main reason for choosing such boundary conditions is that we are interested in the self-organization of pattern; zero-flux conditions imply no external input.

3. Mathematical analysis of the non-spatial model

In this section, we restrict ourselves to the stability analysis of non-spatial model (2.1), where only the interaction part of the model system is taken into account. We find the non-negative equilibrium states of the model system and discuss their stability properties.

3.1. Boundedness of positive solution:

The solutions of model (2.1) always exist and stay positive. In fact, from the first equation of (2.1), we can get:

$$\frac{dN}{dt} \leq rN \left(1 - \frac{N}{K} \right).$$

Then by a standard comparison theorem it can be shown that

$$\limsup_{t \rightarrow \infty} N(t) \leq K.$$

As a result, for any $\epsilon > 0$, there exists a $T > 0$, such that $N(t) \leq K + \epsilon$ for $t > T$. Then from the second equation of (2.1), we obtain:

$$\frac{dP}{dt} \leq \left[\frac{c[\beta(1-m)(K+\epsilon)+\eta A]}{K_1+\delta(1-m)(K+\epsilon)+\alpha\eta A+\theta P} - \gamma \right] P.$$

Since ϵ is arbitrary, we have

$$\limsup_{t \rightarrow \infty} P(t) \leq \frac{(1-m)K(c\beta - \gamma\delta) + \eta A(1 - \alpha\gamma) - K_1\gamma}{\theta\gamma}.$$

Therefore, we get the following theorem.

Theorem 3.1. *All non-negative solutions of model (2.1) that start in \mathbb{R}_+^2 are uniformly bounded.*

Important note: It is to be noted that in the absence of refuge (i.e., $m = 0$), and/or in the absence of additional food (i.e., $A = 0$), the boundedness of the solution is similar to the results as in Theorem 3.1. That is, the solutions of the model without the above factors (single or multiple), always exist and stay positive, and all the non-negative solutions that start in \mathbb{R}_+^2 are uniformly bounded.

3.2. Equilibrium analysis

The model system (2.1) has four non-negative equilibria, which are listed as follows:

- (i) $E_0(0, 0)$, which is always feasible.
- (ii) $E_1(K, 0)$, which is always feasible.
- (iii) $E_2(0, P_2)$, where $P_2 = \frac{c\eta A - \gamma(K_1 + \alpha\eta A)}{\theta\gamma}$, which is feasible if

$$c\eta A - \gamma(K_1 + \alpha\eta A) > 0. \tag{3.1}$$

- (iv) $E^*(N^*, P^*)$, where $P^* = \frac{(1-m)(c\beta - \gamma\delta)N^* + c\eta A - \gamma(K_1 + \alpha\eta A)}{\gamma\theta}$ and N^* is the positive root of the following quadratic equation:

$$a_0N^2 + a_1N + a_2 = 0, \tag{3.2}$$

where

$$\begin{aligned} a_0 &= rc\theta\beta(1-m), \quad a_1 = rc\theta\eta A + \beta K(1-m)^2(c\beta - \gamma\delta) - rc\theta K\beta(1-m), \\ a_2 &= \beta K(1-m)[c\eta A - \gamma(K_1 + \alpha\eta A)] - rc\theta\eta AK. \end{aligned}$$

Equation (3.2) has exactly one positive root if $a_2 < 0$.

3.3. Stability analysis

The eigenvalues of the Jacobian matrix of the model system (2.1) evaluated at the equilibrium E_0 are r and $\frac{c\eta A}{K_1 + \alpha\eta A} - \gamma$. Thus, the equilibrium E_0 is always unstable.

The eigenvalues of the Jacobian matrix of the model system (2.1) evaluated at the equilibrium E_1 are $-r$ and $\frac{(1-m)(c\beta - \gamma\delta)K + c\eta A - \gamma(K_1 + \alpha\eta A)}{K_1 + \delta(1-m)K + \alpha\eta A}$. Thus, the equilibrium E_1 is stable if the following condition is satisfied:

$$(1-m)(c\beta - \gamma\delta)K + c\eta A - \gamma(K_1 + \alpha\eta A) < 0.$$

The eigenvalues of the Jacobian matrix of the model system (2.1) evaluated at the equilibrium E_2 are

$$r - \frac{\beta(1-m)[c\eta A - \gamma(K_1 + \alpha\eta A)]}{c\theta\eta A} \quad \text{and} \quad -\frac{\gamma[c\eta A - \gamma(K_1 + \alpha\eta A)]}{c\eta A}.$$

Thus, the equilibrium E_2 if exists is stable provided the following condition is satisfied:

$$rc\theta\eta A - \beta(1-m)[c\eta A - \gamma(K_1 + \alpha\eta A)] < 0.$$

The Jacobian matrix corresponding to the interior equilibrium E^* of the model system (2.1) can be written as:

$$J|_{E^*} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

where

$$\begin{aligned} a_{11} &= -\left(\frac{r}{K} - \frac{\beta\delta(1-m)^2P^*}{[K_1 + \delta(1-m)N^* + \alpha\eta A + \theta P^*]^2}\right)N^*, \quad a_{12} = -\frac{\beta(1-m)N^*[K_1 + \delta(1-m)N^* + \alpha\eta A]}{[K_1 + \delta(1-m)N^* + \alpha\eta A + \theta P^*]^2}, \\ a_{21} &= \frac{c(1-m)P^*[\beta(K_1 + \alpha\eta A + \theta P^*) - \delta\eta A]}{[K_1 + \delta(1-m)N^* + \alpha\eta A + \theta P^*]^2}, \quad a_{22} = -\frac{c\theta P^*[\beta(1-m)N^* + \eta A]}{[K_1 + \delta(1-m)N^* + \alpha\eta A + \theta P^*]^2}. \end{aligned}$$

The corresponding characteristic equation of J is

$$\lambda^2 + A\lambda + B = 0, \tag{3.3}$$

where $A = -(a_{11} + a_{22})$, $B = a_{11}a_{22} - a_{12}a_{21}$. Now, using the *Routh-Hurwitz* criterion together with the above equation, we have the following theorem:

Theorem 3.2. *The equilibrium point E^* is locally asymptotically stable iff $A > 0$ and $B > 0$.*

Since from the biological point of view the interior equilibrium E^* is the most important one, we have studied the stability behavior of the equilibrium E^* in detail.

3.4. Hopf-bifurcation analysis

In this section, we investigate the possibility of Hopf-bifurcation of interior equilibrium E^* by taking the prey refuge parameter, m , as bifurcation parameter and keeping the other parameters fixed. To determine the nature of the equilibrium E^* we require the sign of the real parts of the roots of the characteristic equation

$$\lambda^2 + A\lambda + B = 0. \quad (3.4)$$

Let $\lambda(m) = u(m) + iv(m)$ be the eigenvalues of the characteristic equation (3.4). Substituting this value in equation (3.4) and separating real and imaginary parts, we get

$$u^2 - v^2 + Au + B = 0, \quad (3.5)$$

$$2uv + Av = 0. \quad (3.6)$$

A necessary condition for the change of stability of the equilibrium E^* is that the characteristic equation (3.4) should have purely imaginary roots. We set $m = m_c$ such that $u(m_c) = 0$ and put $u = 0$ in (3.5) and (3.6). Then we have

$$-v^2 + B = 0, \quad (3.7)$$

$$Av = 0, \quad v \neq 0. \quad (3.8)$$

From equations (3.7) and (3.8), we have $A(m_c) = 0$ and $v(m_c) = \sqrt{B(m_c)}$, which implies $\lambda(m_c) = i\sqrt{B(m_c)}$.

Theorem 3.3. *The necessary and sufficient conditions for the occurrence of Hopf-bifurcation from the equilibrium E^* is that there exists $m = m_c$ such that*

$$(a) \quad A(m_c) = 0,$$

$$(b) \quad \left[\frac{dRe(\lambda(m))}{dm} \right]_{m=m_c} \neq 0.$$

Proof: The eigenvalues of the characteristic equation (3.3) are $\lambda_{1,2} = \frac{-A \pm \sqrt{A^2 - 4B}}{2}$. Here, A and B are the functions of the parameter m , when other parameter values are fixed. Moreover, we assume that there exists some $m = m_c$ such that $A(m_c) = 0$ and $B(m_c) > 0$. Therefore, the positive real parts of these eigenvalues change the sign when m passes through m_c . Subsequently, the system switches its stability provided that the transversality condition is satisfied.

Differentiating equations (3.5) and (3.6) w.r.t. m and put $u = 0$, we have

$$A \frac{du}{dm} - 2v \frac{dv}{dm} = -\frac{dB}{dm},$$

$$2v \frac{dv}{dm} + A \frac{dv}{dm} = -v \frac{dA}{dm}.$$

Solving the above system of equations, we have

$$\left[\frac{dRe(\lambda(m))}{dm} \right]_{m=m_c} = - \left[\frac{2v^2 \frac{dA}{dm} + A \frac{dB}{dm}}{A^2 + 4v^2} \right]_{m=m_c} \neq 0$$

provided $\left[2v^2 \frac{dA}{dm} + A \frac{dB}{dm} \right]_{m=m_c} \neq 0$. This completes the proof of the theorem.

4. Stability analysis of the spatial model

In this section, we will focus on the effect of diffusion on the model system (2.1) about the positive equilibrium point. Specifically, we are interested in investigating the Turing instability of the system where the uniform steady state of the system without diffusion is stable, but it is unstable in the partial differential equations with diffusion terms. Turing's revolutionary idea was that passive diffusion could interact with the chemical reaction in such a way that even if the reaction by itself has no symmetry-breaking capabilities, diffusion can destabilize the symmetry so that the system with diffusion can have them (Turing, 1952). To study this, first we consider the linearized form of system (2.1) about the equilibrium $E^*(N^*, P^*)$ as follows:

$$\begin{aligned}\frac{\partial n}{\partial t} &= a_{11}n + a_{12}p + D_N \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right), \\ \frac{\partial p}{\partial t} &= a_{21}n + a_{22}p + D_P \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right),\end{aligned}\tag{4.1}$$

where $N = N^* + n$, $P = P^* + p$. Here, (n, p) are small perturbation of (N, P) about the interior equilibrium point $E^*(N^*, P^*)$. Let us consider the solution of system (4.1) in the form

$$\begin{pmatrix} n \\ p \end{pmatrix} = \begin{pmatrix} n_k \\ p_k \end{pmatrix} e^{\xi t + i(\kappa_x x + \kappa_y y)}$$

where ξ is the growth rate of perturbation in time t , κ_x and κ_y represent the wave numbers of the solutions. The Jacobian matrix of the linearized system can be written as:

$$\tilde{J} = \begin{pmatrix} a_{11} - D_N(\kappa_x^2 + \kappa_y^2) & a_{12} \\ a_{21} & a_{22} - D_P(\kappa_x^2 + \kappa_y^2) \end{pmatrix}.$$

In the spatial model, the value of ξ depends on the sum of the square of wave numbers $\kappa_x^2 + \kappa_y^2$ (Baurmann, 2004). As a result, both wave numbers affect the eigenvalues. This makes it clear that some Fourier modes will vanish in the long-term limit whereas others will amplify. For the sake of simplicity, we can make use of ξ being rotational symmetric function on the $\kappa_x \kappa_y$ - plane and substitute $\kappa^2 = \kappa_x^2 + \kappa_y^2$ and obtain the results for the two-dimensional case from the one-dimensional formulation. The corresponding characteristic equation is given by

$$\xi^2 + \tilde{A}\xi + \tilde{B} = 0,\tag{4.2}$$

where

$$\begin{aligned}\tilde{A} &= A + \kappa^2(D_N + D_P), \\ \tilde{B} &= B - (a_{11}D_P + a_{22}D_N)\kappa^2 + D_N D_P \kappa^4.\end{aligned}$$

Using the Routh-Hurwitz criterion together with the above equation, we have the following theorem:

Theorem 4.1. *The equilibrium point E^* is locally asymptotically stable in the presence of diffusion iff $\tilde{A} > 0$ and $\tilde{B} > 0$.*

Clearly, $A > 0$ implies $\tilde{A} > 0$. Therefore, diffusive instability occurs only in the case when $B > 0$, but $\tilde{B} < 0$. Hence, the condition for diffusive instability is given by

$$H(\kappa^2) = D_N D_P \kappa^4 - (a_{11}D_P + a_{22}D_N)\kappa^2 + B < 0.\tag{4.3}$$

This shows that diffusion can induce the loss of stability with respect to perturbation of certain wave numbers. Here, H is a quadratic function of κ^2 and the graph of $H(\kappa^2) = 0$ is a parabola. Let, the minimum of $H(\kappa^2) = 0$ is reached at $\kappa^2 = \kappa_c^2$, where κ_c^2 is given by

$$\kappa_c^2 = \frac{a_{11}D_P + a_{22}D_N}{2D_N D_P} > 0. \quad (4.4)$$

As $a_{11} + a_{22} < 0$ and κ_c is real then we must have $a_{11}a_{22} < 0$. Thus, a sufficient condition for instability is that $H(\kappa_c^2) < 0$. Therefore, with the above value of κ_c^2 , the condition for diffusive instability given in equation (4.3) can be written as

$$(a_{11}D_P + a_{22}D_N)^2 > 4D_N D_P B. \quad (4.5)$$

The critical wavenumber κ_c of the growing perturbation is given by equation (4.4). After a little algebra, one can find that a change of sign in $H(\kappa^2)$ occurs when κ^2 enters or leaves the interval (κ_-^2, κ_+^2) where

$$\kappa_{\pm}^2 = \frac{a_{11}D_P + a_{22}D_N \pm \sqrt{(a_{11}D_P + a_{22}D_N)^2 - 4D_N D_P B}}{2D_N D_P}.$$

In particular, we have $H(\kappa^2) < 0$ (i.e., instability) for $\kappa_-^2 < \kappa^2 < \kappa_+^2$.

Note that the diffusive instability cannot occur unless the diffusivity ratio is sufficiently away from unity. Indeed, recall that $a_{11} + a_{22} < 0$ and therefore $a_{11} < -a_{22}$ (where $a_{22} < 0$). Then, from the condition (4.4), we obtain:

$$\frac{D_P}{D_N} > -\frac{a_{22}}{a_{11}} > 1. \quad (4.6)$$

Condition (4.6) is a general necessary condition of Turing instability applicable to any two-species system. In particular, it means that the diffusive instability cannot occur for $D_P = D_N$.

In explicit form, the condition (4.5) becomes

$$\begin{aligned} & \left[\left(\frac{r}{K} - \frac{\beta\delta(1-m)^2 P^*}{[K_1 + \delta(1-m)N^* + \alpha\eta A + \theta P^*]^2} \right) N^* D_P \right. \\ & \quad \left. + \frac{c\theta P^* [\beta(1-m)N^* + \eta A]}{[K_1 + \delta(1-m)N^* + \alpha\eta A + \theta P^*]^2} D_N \right]^2 > 4D_N D_P \\ & \left[\left(\frac{r}{K} - \frac{\beta\delta(1-m)^2 P^*}{[K_1 + \delta(1-m)N^* + \alpha\eta A + \theta P^*]^2} \right) N^* \frac{c\theta P^* [\beta(1-m)N^* + \eta A]}{[K_1 + \delta(1-m)N^* + \alpha\eta A + \theta P^*]^2} \right. \\ & \quad \left. + \frac{c(1-m)P^* [\beta(K_1 + \alpha\eta A + \theta P^*) - \delta\eta A]}{[K_1 + \delta(1-m)N^* + \alpha\eta A + \theta P^*]^2} \frac{\beta(1-m)N^* [K_1 + \delta(1-m)N^* + \alpha\eta A]}{[K_1 + \delta(1-m)N^* + \alpha\eta A + \theta P^*]^2} \right]. \quad (4.7) \end{aligned}$$

Looking at the above analytic conditions, it is not clear how the local asymptotic stability and the Turing instability depend on the prey refuge and the additional food parameters. Therefore, further investigation is carried out in the form of numerical simulation.

5. Numerical simulation

For the numerical simulation, we have chosen the parameter values as given in Table 1 and show qualitative results. Unless it is mentioned, the values of the parameters used for the numerical simulations are the same.

Table 1: The set of parameter values in the model system (2.1).

Parameter	Description	Value
r	Maximum growth rate of prey	0.5
K	Carrying capacity of prey	3
β	Maximum rate of predation	0.6
δ	Proportionality constant	1
m	Proportion of refuge protecting the prey	0.1
α	Relative handling time for additional food to prey item	0.01
η	Relative ability of the predator to detect additional food to prey	0.01
A	Amount of additional food to the predators	0.04
c	Maximum growth rate of the predator	1
γ	Death rate of predator	0.25
θ	Scaling the impact predator interference	0.4
K_1	Half saturation value of the predator	0.4
D_N	Self-diffusion coefficient of prey	0.01
D_P	Self-diffusion coefficient of predator	1

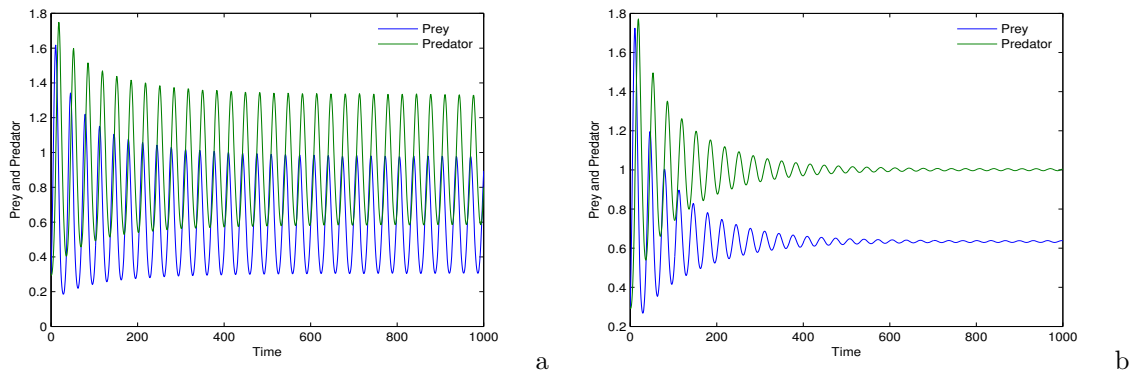


Figure 1: Temporal dynamics of prey and predator at $A = 0.04$ and different values of m : (a) $m = 0.03$ and (b) $m = 0.1$. Other parameter values are the same as in the Table 1.

5.1. Temporal dynamics

At first, we study the temporal dynamics of the system. The critical value of the prey refuge parameter (m), at which stability loss occurs, has been calculated by considering a fixed value for the additional food ($A = 0.04$) and is found to be $m_c \approx 0.0499$. At $m = 0.03$, which is less than the critical value, the dynamics of the system shows oscillatory behavior (Figure 1(a)). While at $m = 0.1$, which is greater than the critical value, the system becomes asymptotically stable (Figure 1(b)). Very large values of m results in the extinction of predator population (not shown in figure).

Next, we examine the effect of additional food (A) on the stability of the system. We keep m fixed at 0.03 and choose the value of A as $A = 1$ and find that the solution trajectories are oscillating (Figure 2(a)). Now, we increase A to $A = 11$ and find that the oscillations are damped, making equilibrium E^* stable (Figure 2(b)). The critical value of A where the stability of the system changes is found as $A = 8.5$. Very large values of A results in the extinction of prey population (not shown in figure).

In the next section, we have investigated how the stability behavior changes in the presence of diffusion in prey and predator populations and form different types of Turing patterns.

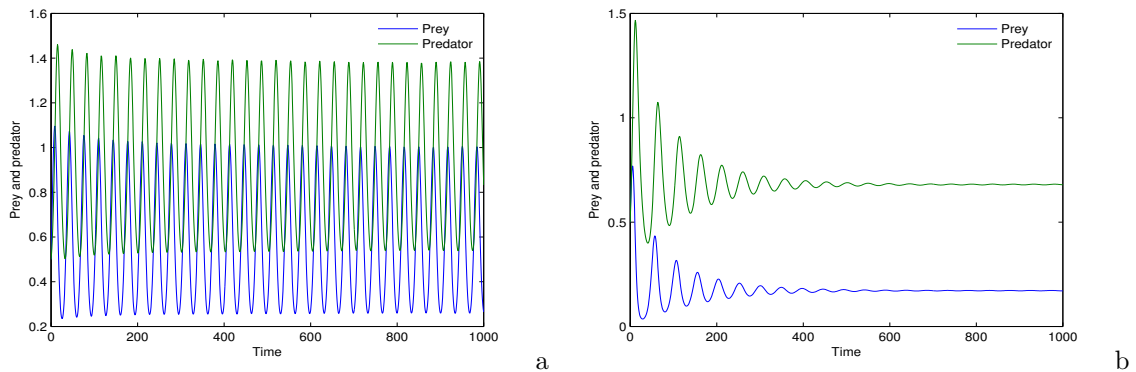


Figure 2: Temporal dynamics of prey and predator at $m = 0.03$ and different values of A : (a) $A = 1$ and (b) $A = 11$. Other parameter values are the same as in the Table 1.

5.2. Spatial dynamics

5.2.1. Proof of the existence of spatial heterogeneity

Diffusion driven instability in reaction-diffusion systems has been proposed as a mechanism for pattern formation in numerous embryological and ecological contexts. Mathematically, an equilibrium point is called diffusion-driven instability if it is asymptotically stable in the absence of diffusion but is unstable in the presence of diffusion. To check the existence of Turing instability, we look at the conditions obtained analytically. First, we plot the polynomial $H(\kappa^2)$ (equation (4.3)) w.r.t. κ^2 for different values of m and A by keeping the other parameters fixed (Figure 3). At $A = 0.04$, the range of κ^2 for which $H(\kappa^2)$ remains negative decreases as m increases and finally $H(\kappa^2)$ becomes completely positive for $m > 0.16$. That is, by increasing the value of m , the possibility of the occurrence of Turing instability decreases. On the other hand, keeping m fixed at $m = 0.1$, by increasing the value of A , the range of κ^2 for which $H(\kappa^2)$ remains negative increases. That is, by increasing the additional food, the possibility of the occurrence of Turing patterns increases. The largest real part of ξ also provides information about the existence of Turing instability and are plotted w.r.t. κ^2 for different values of m and A (eq. 4.2). With an increase in the value of m , the maximum of the real part of ξ decreases and ultimately becomes completely negative for large values of m . On the other hand, with an increase in A , the real part of ξ increases and becomes positive for a range of κ^2 at high values of A . The positivity of the largest real part of the eigenvalues for an interval of κ^2 represents the existence of diffusive instability.

5.2.2. Combined effects of prey refuge and additional food on the stability

Next, we investigate how the stability of the system changes as both prey refuge (m) and additional food (A) change simultaneously. For this reason, we vary m and A and plot stability regions in (m, A) plane (Figure 5). Here, the regions A (gray) and B (green) represent the predator and prey extinct regions, respectively. The region C (white) stands for the asymptotic stability of the coexisting equilibrium (E^*) irrespective of the presence and absence of diffusion. The regions D_1 (cyan) and D_2 (blue) represent the regions of Turing instability, i.e., where the system with diffusion becomes unstable and shows spatial pattern formation although it is stable without diffusion. The specialty of D_2 is that if we make one of the variables (either m or A) zero from here, then the system will reach to a situation with no spatial pattern formation. That is, within this region, pattern formation strictly depends on the interactive effects of prey refuge and additional food; absence of one of the factors (depending on the other one) from this situation would lead to homogeneous distribution of populations. The region E (red) represents Turing-Hopf region, where there is a possibility of the formation of inhomogeneous

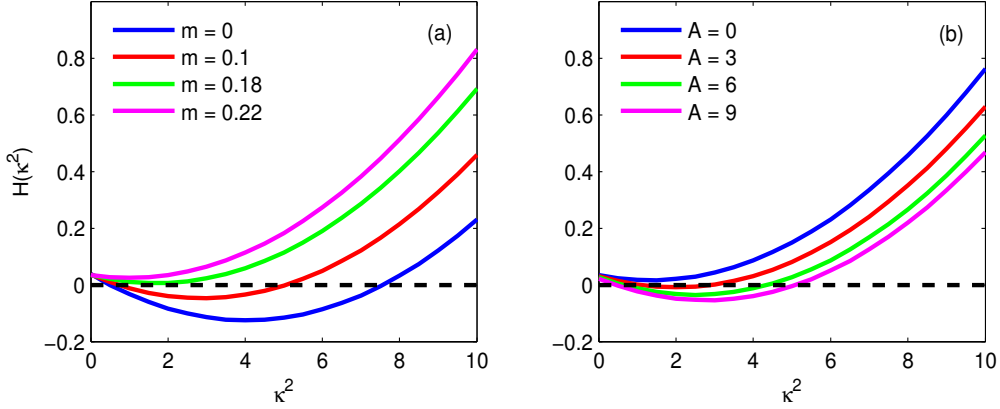


Figure 3: The graph of function $H(\kappa^2)$ w.r.t. κ^2 at (a) $A = 0.04$ and different values of m , (b) $m = 0.2$ and different values of A (using eq. (4.3)). Black dashed lines represent $H(\kappa^2) = 0$. Other parameter values are the same as in the Table 1.

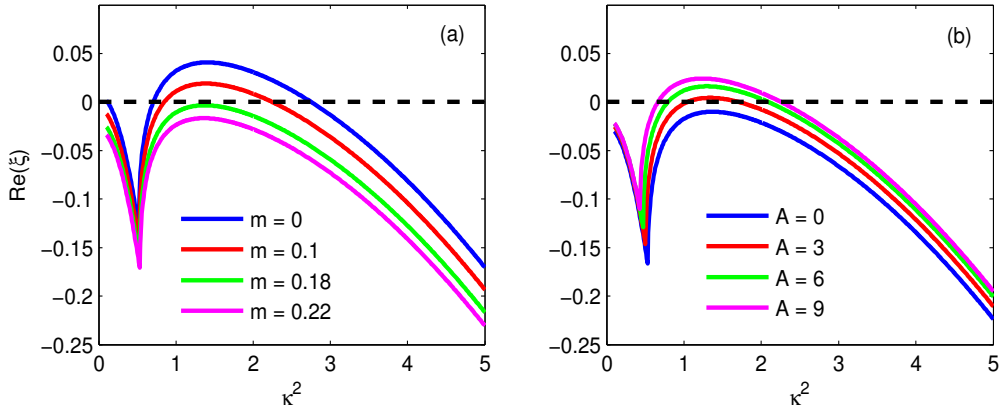


Figure 4: Dispersion relation plotting the real part of the eigenvalues at (a) $A = 0.04$ and different values of m , (b) $m = 0.2$ and different values of A (using eq. (4.2)). Black dashed lines represent $Re(\xi) = 0$. Other parameters are the same as in the Table 1.

stationary patterns due to the interaction of Turing instability and the appearance of oscillations due to Hopf-bifurcation. However, in the present study, we mainly concentrate on the Turing pattern formations. It is clear from Figure 5 that both prey refuge and additional food are important for determining different dynamics of the system. For example, if we change m when there is no additional food ($A = 0$), we see that for small values of m populations form spatial patterns whereas beyond some critical value of m , pattern formation is not possible. Very large values of m results in predator extinction. Now, in the presence of additional food ($A > 0$), the pattern formations can occur for larger values of m . However, at $A = 15$, small values of m can also result in the disappearance of the pattern formation. In this situation, Turing patterns can be observed only for intermediate values of m . Furthermore, in the presence of very large amounts of additional food for predator, prey refuge must be very high for the survival of the prey population and no pattern emerges in these scenarios. On the other hand, if we vary additional food (A) in the absence of prey refuge ($m = 0$), we see that small additional food results in spatial pattern formation. However, for a very narrow range of A , the system becomes pattern free

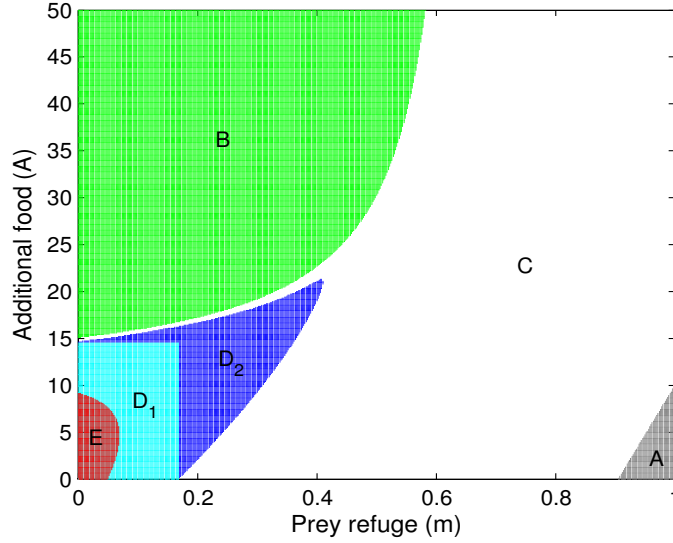


Figure 5: Different stability regions in (m, A) parametric space. Regions A (gray), B (green), C (white), D_1 (cyan), D_2 (blue) and E (red) correspond to predator extinction, prey extinction, stable regions, Turing patterns, Turing patterns and Turing-Hopf domain, respectively. The speciality of D_2 is that assigning no prey refuge or no additional food from region D_2 would lead to pattern free state. Other parameters are the same as in the Table 1.

and larger values result in prey extinction. Now, for certain intermediate values of m , e.g., $m = 0.3$, Turing patterns can be observed only for some intermediate ranges of A . Interestingly, when prey refuge becomes very high, e.g., $m = 0.7$, the presence of additional food does not affect the stability of the system; there is no possibility of Turing patterns in the system.

5.2.3. Different types of pattern formations

After establishing the existence of Turing instability and gaining information about how different stabilities change with m and A , now we investigate different Turing patterns of system (2.1). To explore the spatio-temporal dynamics of the model system (2.1) in two dimensional spatial domain, the system of partial differential equations is numerically solved using a finite difference method. The forward difference scheme is used for the reaction part and standard five point explicit finite difference scheme is used for two dimensional diffusion terms with a time step size $\Delta t = \frac{1}{40}$. The model is studied with positive initial conditions and Neumann boundary condition. The initial conditions are always a small random perturbation around the equilibrium E^* . After the initial period during which the perturbation spreads, the system goes into either a time-dependent state, or an essentially steady state solution. It is to be noted here that the time at which we stopped the simulations is sufficient to assume that the patterns attained the stationary state and they do not change further with time. During numerical simulation different types of dynamics have been observed and it is found that the distributions of predator and prey are always of the same type. Thus, we have restricted our analysis of pattern formation to one distribution and only shown the distribution of prey for instance. We look at different situations by varying one of the parameters between m and A at a time from the regions D_1 and D_2 of Figure 5 and keeping the other one fixed.

Different spatial patterns of the prey population emerge as we vary prey refuge (m) by keeping the value of additional food (A) fixed at $A = 14$ (Figure 6(a-c)). The absence of prey refuge ($m = 0$) results in spot patterns, i.e., where the prey abundance is higher in isolated zones (Figure 6(a)). In view of

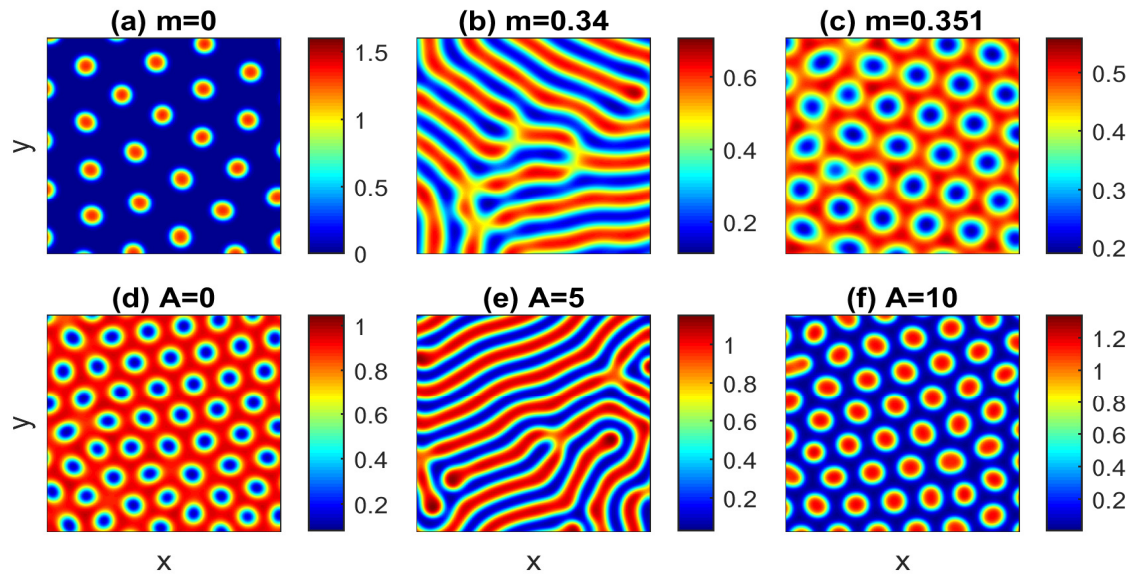


Figure 6: Stationary Turing patterns developed by prey at (a-c) $A = 14$ and different values of m , (d-f) $m = 0.15$ and different values of A at time $t = 20000$. Variations in m results in the pattern sequence spots to stripes to holes, whereas variations in A results in the opposite pattern sequence holes to stripes to spots. Other parameter values are same as in the Table 1.

population dynamics, “spots” pattern means that the prey population is driven by the predator to a very low level in majority of the spatial region and the final result is the formation of patches of high prey density surrounded by areas of low prey densities (Alonso et al., 2002). Now, as we increase the value of prey refuge, we get a mixture of stripe and spot patterns (figure is not shown). At $m = 0.34$, there is regular peaks and troughs of prey density, hence the stripe pattern emerges (Figure 6(b)). Further increase in prey refuge results in the mixture of stripes and holes (figure is not shown). However, for large prey refuge ($m = 0.351$), the model dynamics exhibits a transition from stripes-holes growth to holes replication, where the prey population is in the isolated zone with low density and the remaining region is of high density (Figure 6(c)). Therefore, by increasing the value of m , the pattern sequence “spots \rightarrow stripe-spot mixture \rightarrow stripes \rightarrow stripe-hole mixtures \rightarrow holes” is observed.

Next, we look at different pattern formations by varying additional food A by keeping prey refuge as constant ($m = 0.15$) (Figure 6(d-f)). In the absence of additional food supply ($A = 0$), we observe holes patterns (Figure 6(d)). As we increase additional food supply, the mixture of holes and stripes emerges (figure is not shown). As we reach the value $A = 5$, the whole space is dominated by stripe patterns (Figure 6(e)). Further increase in additional food supply results in the mixture of stripes and spots (figure is not shown). For larger values of additional food ($A = 10$), spot pattern dominates the space (Figure 6(f)). Therefore, in this case, an increase in additional food results in the pattern sequence “holes \rightarrow stripe-hole mixture \rightarrow stripes \rightarrow stripe-spot mixtures \rightarrow spots”. Thus, it is inferred that by increasing the level of additional food to the predator, there is a transition from the prey predominant state to predator predominant state when prey refuge is present in the system.

6. Discussion

In real world ecological systems, the mechanisms and scenarios of pattern formation in models of interacting populations have been a focus of intensive studies in theoretical ecology. A spatiotemporal predator-prey system is known to exhibit a wide variety of complex spatial pattern formations (Malchow et al., 2008). Since, predator-prey interactions affect species composition and community dynamics, the complexity in a community depends on the type of predation, which differs for different predators. In this respect, the supply of additional food to the predator strengthen predation pressure by increasing predator density and increases the chance of survival of predator populations (Chakraborty and Chattopadhyay, 2008). In response, prey species also uses different strategies, such as smell, color, injection of some poisonous agent, size, skin, body cover, refuge etc. Among them, prey refuge is considered as one of the important factors for the biological control of pests because large prey (pest) refuge can increase prey (pest) density and lead to prey (pest) population outbreaks (Hawkins et al., 1993). In the present work, we have investigated the combined effect of prey refuge and additional food for predator on the spatial distribution of predator and prey populations.

In the absence of diffusion, our result shows stabilizing effects of both prey refuge and additional food for predators which resembles the result of Samanta et al. (2016). Large prey refuge and additional food for prey predator result in predator and prey extinction, respectively. Very high prey refuge decreases food availability for predators and thus predator population get extinct. On the other hand, very high availability of additional food increases predator abundance and finally prey population get extinct due to high predation pressure, although predator population can survive solely on additional food source. However, the stable coexistence of both the populations changes in the presence of diffusion. At this point, our results differ with the results obtained by Samanta et al. (2016) since spatial heterogeneity of populations was not included in the previous study. Both the populations show spatial pattern formation in a specific region of the (m, A) parameter space. When the amount of additional food is less than a critical level, there is a possibility of spatial pattern formation depending on the prey refuge; low prey refuge can substantially form different stable patterns in space. However, both the populations show stable abundances both in time and space irrespective of additional food supply to the predator when prey refuge is high. Therefore, spatial pattern formation is possible only when both prey refuge and additional food supply to the predator remain within certain critical ranges. There are also cases when spatial patterns emerge only due to the interactive effects of prey refuge and additional food; lowering one of the values (depending on the other one) by sufficient amount would lead to homogeneous distribution of populations. As a conclusion, we can say that both prey refuge and additional food for predator interact to determine the possibility of spatial pattern formations in predator and prey populations.

Natural systems show different types of pattern formations due to the predator-prey interactions (Chakraborty, 2015). Our model also shows different types of Turing patterns: holes, stripes, spots and their mixtures. These patterns are actually representative of the distribution of predator and prey in space. Holes patterns by prey population represent prey dominance whereas spots represent predator dominance. In the absence of additional food, variations in prey refuge generate stripes, holes and their mixtures. However, in the presence of a certain amount of additional food, low prey refuge can also show spots and the mixture of spots and stripes together with the other patterns as found in the absence of additional food. In this case, the pattern sequence follows “spots \rightarrow spots-stripes mixture \rightarrow stripes \rightarrow stripes-holes mixture \rightarrow holes” as prey refuge increases. Previously, in simple diffusive predator-prey systems, prey refuge was found to be responsible for generating spots, stripes and their mixtures (Guin et al., 2015; Wang and Wang, 2012). However, our study additionally reveals that holes, which are low prey abundances at specific zones, can also be observed by increasing prey refuge for certain range of additional food for predators. On the other hand, in the absence of prey refuge, variations of additional

food show stripes, spots and their mixtures. However, for certain range of prey refuge, low additional food can also show holes and the mixture of holes and stripes together with other patterns as observed in the absence of prey refuge. In this case, the pattern sequence follows “holes \rightarrow holes-stripes mixture \rightarrow stripes \rightarrow stripes-spots mixture \rightarrow spots” as additional food supply increases. Previously, spots and holes have been documented in the presence of additional food for predators (Kumar and Chakrabarty, 2015). The present study shows that the variations of additional food can additionally show stripes and the mixture of stripes with holes and spots for certain range of prey refuge. Therefore, our study reveals that, not only the existence of pattern formation, the interactive effect of prey refuge and additional food for predator also determines the type of pattern formation by the prey and predator populations, and also establishes the importance of considering both the factors at a time.

Providing additional food to predators has been considered as one of the best established techniques in integrated pest management and biological conservation programs (Bilde and Toft, 1998; Coll and Guershon, 2002; Harmon, 2003; Harwood and Obrycki, 2005; Murdoch et al., 1985; Sabelis and van Rijn, 2005; Shannon et al., 2007; van Baalen et al., 2001; van Rijn et al., 2002; Wade et al., 2008). Additional food provided to the predator has the ability to control the ecosystem by eradicating the pest population (Srinivasu et al., 2007). However, in natural systems, there are several other factors which affect pest control. When prey (pest) refuge is relatively high, it helps pest population to escape predation and thus pest population dominates in most of the spatial region with low abundance at some specific places. In this situation, it is very difficult to control the pest population. Once we are able to regulate prey (pest) refuge, then by providing additional food to the predator it is possible to restrict the spread of pest populations in space and allow the pest population to become abundant only in isolated zones in the spatial region. At this point, it is easy to control the pest population. However, when both prey refuge and additional food are low, spatial distribution of pest population becomes complex (stripes; not shown in figures) and thus again pest control becomes difficult. In natural systems, pest population takes refuge under natural habitats within and around farms. Removal of natural habitat fundamentally alters biological communities (Philpott et al., 2008; Perfecto et al., 2009; Mendenhall et al., 2011; Melo et al., 2013; Liu et al., 2014). It is found that predators of crop pests are also very much sensitive to the natural habitat loss because the natural habitat provides predators with additional prey, refuges during the disturbances, and sites for breeding, hibernation and roosting (Landis et al., 2000; Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Jirinec et al., 2011). Thus, a complete removal of natural habitat would not only reduce prey (pest) refuge, but simultaneously it would also result in a reduction in additional food supply to the predator population, which would ultimately make the spatial distribution of pest population complex and difficult to control. However, instead of completely removing the natural habitat, we can regulate prey refuge and additional food by removing a specific portion of natural habitat to control pest population.

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