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A DELAY NONAUTONOMOUS PREDATOR–PREY MODEL FOR THE EFFECTS OF FEAR, REFUGE AND HUNTING COOPERATION

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Fear of predation may assert privilege to prey species by restricting their exposure to potential predators, meanwhile it can also impose costs by constraining the exploration of optimal resources. A predator–prey model with the effect of fear, refuge, and hunting cooperation has been investigated in this paper. The system's equilibria are obtained and their local stability behavior is discussed. The existence of Hopf-bifurcation is analytically shown by taking refuge as a bifurcation parameter. There are many ecological factors which are not instantaneous processes, and so, to make the system more realistic, we incorporate three discrete time delays: in the effect of fear, refuge and hunting cooperation, and analyze the delayed system for stability and bifurcation. Moreover,

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for environmental fluctuations, we further modify the delayed system by incorporating seasonality in the fear, refuge and cooperation. We have analyzed the seasonally forced delayed system for the existence of a positive periodic solution. In the support of analytical results, some numerical simulations are carried out. Sensitivity analysis is used to identify parameters having crucial impacts on the ecological balance of predator–prey interactions. We find that the rate of predation, fear, and hunting cooperation destabilizes the system, whereas prey refuge stabilizes the system. Time delay in the cooperation behavior generates irregular oscillations whereas delay in refuge stabilizes an otherwise unstable system. Seasonal variations in the level of fear and refuge generate higher periodic solutions and bursting patterns, respectively, which can be replaced by simple 1-periodic solution if the cooperation and fear are also allowed to vary with time in the former and latter situations. Higher periodicity and bursting patterns are also observed due to synergistic effects of delay and seasonality. Our results indicate that the combined effects of fear, refuge and hunting cooperation play a major role in maintaining a healthy ecological environment.

Keywords: Predator–Prey Model; Fear; Refuge; Hunting Cooperation; Time Delay; Seasonality.

1. Introduction

The species interactions are the major driving forces behind evolution. The predator–prey interactions are the interactions between an organism and its natural enemies. These interactions include plant-herbivore, host-parasitoid, herbivore–carnivore and host–pathogen interactions. The predator–prey interactions are one of the most important evolutionary driving forces as they determine the mortality of prey and birth of new predators, and play a key role in energy movement through food chains. Due to the role of predator–prey interactions in shaping the ecosystem structure, these interactions are one of the central themes in mathematical ecology.[1,2] Following the pioneering work of Lotka[3] and Volterra,[4] numerous predator–prey models have been proposed with the inclusion of different kinds of functional responses to depict various realistic scenarios.[5–12] The various kinds of functional responses depict only the effect of direct killing by predator on the predator–prey dynamics. However, predator not only influences the ecology of prey directly by consuming them but also indirectly by inflecting the behavior and physiology of the prey population. The physiological and behavioral characteristics of the prey population are greatly influenced due to the presence of the predator population.[13–17] In order to escape the predation risk, the prey population adopts many behavioral traits such as spatial or temporal refuge, reduction in the foraging activity, prey aggregation, etc.

The use of physical refuge is one of the most important traits used by prey populations to protect themselves from possible predator attacks. Refuge is an important factor in the population ecology as it is found to increase the stability of predator–prey interactions.[18] Lots of theoretical models are analyzed to investigate the effect of prey refuge on the coexistence of the predator and prey populations.[18–30] These studies show that the refuge used by prey causes an increase in the equilibrium prey density and yields a stabilizing effect on the predator–prey dynamics. It is also found that the existence of refuge protecting a constant proportion of prey has little effect on the predator–prey system's stability compared to the refuge, which protects a constant number of prey.[18] The reason behind this is that in the case of a constant proportion refuge, the prey death rate does not increase with population density, and hence the existence of refuge does not cause a negative feedback effect needed for stabilization.[31] However, constant proportion refuge increases the persistence of the predator–prey interaction by making the prey extinction difficult. On the other hand, the refuge which protects a constant number of prey creates a negative feedback effect, as in this case, the prey death rate increases with the population density once the population exceeds the number of prey taking refuge.[32]

The anti-predator behaviors, such as vigilance, aggregation, changes in habitat use, movement patterns, etc., adopted by the prey in response to the fear of predation undoubtedly lower the predation risk and hence may increase the chances of survival of prey species.[33–35] However, the defense against predators has an associated fear cost in terms of the reduction in the growth rate of the prey population. Some field studies have shown that the fear of predation may influence the behavior and psychology of prey species to such an extent that it may decrease the prey reproduction and survival.[36–42] For instance, the fear of predators causes a reduction in forage activities of prey, which may reduce the reproduction and survival of prey.[36] The predation risk can push the bird species to temporally escape from their eyries, reducing the reproduction rate as a long-run cost.[37] In a field study by Zanette *et al.*,[39] it is found that under the predation risk, the number of offspring of song sparrows successfully reared decreased by 40%. This happened because to escape the perceived predation risk, the song sparrow selects more secluded nest sites and reduced foraging trips, putting their offspring to a disadvantage. An experiment examining the effect of the predation risk of a caged predator *Trachemys scripta elegans* on the invasive freshwater snail *P. canaliculata* has reported that the predation risk can inhibit the growth of juvenile and adult *P. canaliculata*, most likely due to a drop in the food intake.[41] The drop in food intake has resulted from the reduction in feeding time since the predator avoidance activities are performed at the cost of feeding time. This study also reports the lethal effect of predation risk on the juvenile snails.

Wang *et al.*[43] proposed the first mathematical model of predator–prey dynamics which incorporates the cost of fear in prey reproduction. This study has shown a richer spectrum of predator–prey dynamics, including bi-stability phenomenon, in which depending upon the initial start, the solutions either attain an equilibrium state or oscillate periodically. The increase in the fear level among prey is found to make a change in the direction of Hopf-bifurcation and very high level of fear among prey is found to stabilize the predator–prey system by excluding the existence of periodic solutions. After the work of Wang *et al.*,[43] a number of predator–prey models incorporating the cost of fear in prey reproduction are studied by several researchers.[44–52] Some of these studies have considered the effects of fear factor and prey refuge on the predator–prey system.[47,48,51,53] In particular, Wang *et al.*[48]

studied the effect of fear on predator–prey system with a constant proportion of prey refuge and found that prey and predator population densities decrease with the increase in fear effect. This study has shown the rich and complex effect of fear on the stability of the interior equilibrium in the presence of refuge and identified the different range of values for the portion of prey taking refuge, whereas an increase in fear factor destabilizes the interior equilibrium and benefit the emergency of the periodic behavior, stabilizes the interior equilibrium and prevent the occurrence of periodic solution or yields no effect on stability. Kumar and Dubey[53] studied the effect of fear factor and refuge on the dynamics of predator–prey system by incorporating gestation delay of the predator population and found that the delayed system shows chaotic behavior for higher values of gestation delay.

The anti-predator behavior of the prey population to escape from the perceived predation risk yields negative effect on the density of predator population. In order to increase the predation rate, several predator populations adopt hunting cooperation strategy. Some studies have investigated the effect of predator hunting cooperation on the predator–prey systems.[54,55] These studies have shown that the hunting cooperation may be beneficial for predator population through an increase in the predation rate but it can also be detrimental for predators if prey density drastically reduces due to increased predation pressure. Pal *et al.*[56] explored the rich dynamics of predator–prey system subjected to the combined effects of fear and hunting cooperation, and showed that the system exhibits two different types of bi-stabilities due to subcritical Hopf-bifurcation and backward bifurcation. The combined effects of prey refuge, fear factor and hunting cooperation have not been studied yet. The goal of this study is to examine the impact of prey refuge, fear factor, and hunting cooperation on the predator–prey system. The fear of predation does not have an instantaneous effect on the reproduction rate of the prey species, rather there must be some time lag required.[57] Further, there exists some time lag in the process of taking refuge after realizing the attack cue of predator. Also, the cooperative predators do not aggregate in a group instantly, but there is a delay involved in forming a group and prepare to attack prey.[58] We study the effects of these delays involved in the processes of fear, refuge, and hunting cooperation on the system dynamics by extending the model to incorporate these time delays in the modeling process.

The ecological communities are significantly affected by the seasonal fluctuations of their environments. There are several environmental factors which vary periodically with change in seasons and affect various parameters of the predator–prey models.[42,59,60] Thus, it is important to study the dynamics of predator–prey systems under the seasonal fluctuations of the key biological parameters of the system. The experimental studies have shown that the fear of predation has cross-seasonal effect on reproduction rate and the level of fear is affected by the seasonal variations.[61,62] The cooperative hunting generally occurs in areas of prey scarcity and the pattern of this behavior is influences by the seasonal fluctuations of resource availability.[63] The seasonal changes in habitat structure and resource availability may also affect the refuge used by prey population, thus it is also important to incorporate seasonal fluctuation in refuge to depict more realistic scenario.[60] In view of this, the proposed delayed model system is further extended by considering the seasonal variations in the level of fear, prey refuge, and hunting cooperation.

The rest of the paper is organized in the following way. In the next section, we introduce our model for the combined effects of fear, refuge, and hunting cooperation. The model is analyzed for its basic properties such as boundedness and permanence; biologically feasible equilibria are obtained and their local stability behaviors are discussed. Existence of Hopf bifurcation is discussed by taking the coefficient of prey refuge as a bifurcation parameter; direction and stability of bifurcating periodic solutions are also discussed. In Sec. 3, the proposed model is extended by including the effects of time lags concealed in the processes of fear factor, prey refuge, and hunting cooperation. The delayed model is analyzed for the existence of Hopf bifurcation by taking delay factors as bifurcation parameters. In Sec. 4, we further modify the delayed model by considering the seasonal patterns of fear, refuge, and hunting cooperation. The delay nonautonomous model is analyzed for the existence of periodic solutions. The analytical findings are well supported through numerical simulations in Sec. 5. Finally, we close the paper with conclusion and discussion in Sec. 6.

2. The Mathematical Model

We consider an ecological community consisting of single prey and single predator populations. Let us assume that the density of prey and predator populations, at any time $t > 0$, are $N(t)$ and $P(t)$, respectively. The populations are measured in terms of number per unit area. We construct the model to describe the predator–prey interactions based on the following aspects:

(1) Prey population grows logistically with r_0 as its growth rate and r_2 as mortality rate due to intraspecific competition when there is no predation and fear effect. The reason behind considering the intraspecific competition among the species of prey population is that for high density of populations and less availability of resources, the individuals of prey population compete with each other for the available resources. Also, the prey population undergoes natural death at the rate r_1.

(2) The anti-predator behavior adopted by the prey population due to fear has an associated cost in terms of reduction in the reproduction rate of prey population. Thus, the reproduction rate should be multiplied by a factor that decreases with the increase in level of fear and the density of predator population. In view of this, the reproduction rate is multiplied by a factor $\frac{1}{1+kP}$, which accounts for the cost of anti-predator behavior of prey due to fear of predation.[43] Here, the constant k measures the level of fear.

(3) The derivation of predation term is based on the classical Lotka–Volterra predator–prey model in which a linear functional response αN is considered,

where α is the attack rate of predator. This linear functional response modifies due to the incorporation of prey refugia and hunting cooperation of predators.

(4) The prey refugia to avoid the perceived predation risk depends upon the frequency of encounter of prey with predator, which in turn depends on both prey and predator densities.[22,64] Therefore, it is reasonable to take the number of prey taking refuge to be proportional to the direct interaction between predator and prey[57] i.e., NP, so the prey population available for predation is given by $(N - mNP) = (1 - mP)N$, where $0 \leq m \leq 1$. Throughout this paper, we consider the acceptable range $0 \leq (1 - mP) \leq 1$, i.e., $P \leq \frac{1}{m}$. Hence, due to the incorporation of prey refuge, the functional response gets modified to $\alpha(1 - mP)N$.

(5) The hunting cooperation of predators helps them to capture more prey, and thus, the attack rate should increase with an increase in the predator density. Following Refs. 55, 56, we consider the attack rate as the linear increasing function of predator density, i.e., $\alpha(1 + cP)$, where c denotes the degree of hunting cooperation among predators. Thus, after incorporating the hunting cooperation of predators and prey refuge, the functional response takes the form $\alpha(1 + cP)(1 - mP)N$.

(6) The growth rate of predator depends wholly on the consumption of prey population. We denote by α_1 the conversion efficiency of prey biomass into predator biomass. The predator population also has natural death at rate d_1 and faces intraspecific competition for prey at the rate d_2.

Keeping the above facts in mind, we get the following system of nonlinear ordinary differential equations:

$$\begin{aligned} \frac{dN}{dt} &= \frac{r_0 N}{1 + kP} - r_1 N - r_2 N^2 - \alpha(1 - mP)[1 + cP]NP, \\ \frac{dP}{dt} &= \alpha_1 \alpha(1 - mP)[1 + cP]NP - d_1 P - d_2 P^2. \end{aligned} \tag{2.1}$$

Our model (2.1) is different from the models considered in previous studies[42,44–48,51,53,56,58,60,65] in the following sense:

(1) It captures the combined effects of fear factor, prey refuge and hunting cooperation of predators, which are the important behavioral traits observed in predator and prey populations.

(2) The functional response of predator to prey density incorporates the hunting cooperation of predators alongside the prey refuge, which depends on the direct interaction between prey and predator.

All parameters involved in the system (2.1) are positive constants, and the system (2.1) is to be analyzed with the non-negative initial conditions. All the parameters appearing in the system (2.1) are described in Table 1.

Table 1. Descriptions of parameters in system (2.1) and their values used for numerical simulations.

Parameters	Descriptions	Units	Values	References
r_0	Growth rate of prey	1/time	2	[60]
r_1	Natural death rate of prey	1/time	0.03	Assumed
r_2	Death rate of prey due to intraspecific competition	unit area/number/time	0.02	Assumed
k	Level of fear	unit area/number	0.6	[60]
α	Rate of predation	unit area/number/time	0.64	Assumed
m	Refuge coefficient	unit area/number	0.33	Assumed
c	Coefficient of hunting cooperation	unit area/number	0.85	Assumed
α_1	Conversion efficiency	—	0.6	Assumed
d_1	Natural death rate of predator	1/time	0.09	Assumed
d_2	Death rate of predator due to intraspecific competition	unit area/number/time	0.001	Assumed

2.1. *Mathematical analysis of system* (2.1)

2.1.1. *Boundedness and persistence of solutions*

In an ecological subsystem, boundedness of a system implies that the system is well behaved. Boundedness of the solutions means that the interacting populations cannot grow exponentially or abruptly for a long-time interval due to limited resources. Moreover, the permanence of a system means the long-term survival of all populations of the system, irrespective of the initial populations. From the mathematical point of view, permanence of a system means that strictly positive solutions do not have omega limit points on the boundary of the non-negative cone.

Theorem 2.1. *Solutions of the system* (2.1) *which initiate in* $\mathbb{R}^2_+ - \{(0,0)\}$ *are uniformly bounded, and the set* $\Omega^* = \{(N,P) : 0 \le N \le \frac{r_0 - r_1}{r_2}, 0 \le P \le \frac{1}{m}\}$ *contains a region of attraction for all solutions initiating in the positive quadrant.*

Proof. From the first equation of system (2.1), we have

$$\frac{dN}{dt} \le (r_0 - r_1)N - r_2 N^2.$$

This yields,

$$\limsup_{t\to\infty} N(t) \le \frac{r_0 - r_1}{r_2}.$$

From the second equation of system (2.1), we have

$$\frac{dP}{dt} \le \alpha_1 \alpha \frac{r_0 - r_1}{r_2}(1 - mP)(1 + cP)P.$$

Let $\lambda = \alpha_1 \alpha \frac{r_0 - r_1}{r_2}$, then

$$P(t) \le \frac{1}{m} - \frac{1}{m} \frac{P^{\frac{m+c}{m}}}{(e^{\lambda t})^{\frac{m+c}{m}} (1 + cP)^{\frac{c}{m}}}.$$

Thus, we have

$$\limsup_{t\to\infty} P(t) \le \frac{1}{m}. \qquad \square$$

Lemma 2.1. *If $\alpha, \beta > 0$ and $x(0) > 0$, then for the differential equation $\frac{dx}{dt} \ge x(t)(\alpha - \beta x(t))$, $\liminf_{t\to\infty} x(t) \ge \frac{\alpha}{\beta}$.*

Theorem 2.2. *System (2.1) is permanent if the following condition holds*:

$$\alpha_1\alpha\left[\frac{r_0 m}{m+k} - r_1 - \frac{\alpha(c+m)}{m^2}\right] > r_2 d_1. \tag{2.2}$$

Proof. From Theorem 2.1, we have

$$\limsup_{t\to\infty} N(t) \le \frac{r_0 - r_1}{r_2}, \tag{2.3}$$

$$\limsup_{t\to\infty} P(t) \le \frac{1}{m}. \tag{2.4}$$

Using (2.4), from the first equation of system (2.1), we have

$$\frac{dN}{dt} \ge N\left\{\frac{r_0}{1+k/m} - r_1 - r_2 N - \alpha\left(1 + \frac{c}{m}\right)\frac{1}{m}\right\} = N(\widetilde{M} - r_2 N),$$

where $\widetilde{M} = \frac{r_0 m}{m+k} - r_1 - \frac{\alpha(c+m)}{m^2}$.

If $\widetilde{M} > 0$, by Lemma 2.1, we have

$$\liminf_{t\to\infty} N(t) \ge \frac{\widetilde{M}}{r_2}. \tag{2.5}$$

Using (2.5), from the second equation of system (2.1), we obtain

$$\begin{aligned}\frac{dP}{dt} &\ge \alpha_1\alpha\frac{\widetilde{M}}{r_2}(1 - mP)P - d_1 P - d_2 P^2 \\ &= P\left\{\left(\frac{\alpha_1\alpha\widetilde{M}}{r_2} - d_1\right) - \left(\frac{\alpha_1\alpha m\widetilde{M}}{r_2} + d_2\right)P\right\}.\end{aligned}$$

For $\alpha_1\alpha\widetilde{M} > r_2 d_1$, by Lemma 2.1, we get

$$\liminf_{t\to\infty} P(t) \ge \frac{\alpha_1\alpha\widetilde{M} - r_2 d_1}{\alpha_1\alpha m\widetilde{M} + r_2 d_2}.$$

Note that if $\alpha_1\alpha\widetilde{M} > r_2 d_1$, then obviously $\widetilde{M} > 0$.

Now, we choose

$$M_1 = \min\left\{\frac{\widetilde{M}}{r_2}, \frac{\alpha_1\alpha\widetilde{M} - r_2 d_1}{\alpha_1\alpha m\widetilde{M} + r_2 d_2}\right\}, \quad M_2 = \max\left\{\frac{r_0 - r_1}{r_2}, \frac{1}{m}\right\}.$$

Hence,

$$\min\left\{\liminf_{t\to\infty} N(t, N_0, P_0), \liminf_{t\to\infty} P(t, N_0, P_0)\right\} \geq M_1,$$

$$\max\left\{\limsup_{t\to\infty} N(t, N_0, P_0), \limsup_{t\to\infty} P(t, N_0, P_0)\right\} \leq M_2.$$

Therefore, system (2.1) is permanent if the condition (2.2) holds. □

Remark 2.1. It is apparent from condition (2.2) that the increment in growth rate of prey population enhances the permanence of the system (2.1). On the other hand, for larger values of fear of predator and hunting cooperation, the system (2.1) may not be permanent. Similarly, on increasing the natural death rate of prey, intraspecific competition among prey species and natural death rate of predator, the condition (2.2) may not be satisfied, i.e., for higher values of these parameters the system (2.1) may not be permanent. The effect of refuge on the permanence of the system (2.1) is not clear from the condition (2.2).

2.1.2. *System's equilibria*

Due to nonlinearity of model system (2.1), it is not possible to find exact solutions to the system. Instead, we determine the long-term behavior of the system. In general, a nonlinear system either gravitates towards an equilibrium point or it blows up. An equilibrium point represents the rest state of a dynamical system. Once the dynamical system attains an equilibrium state, it remains at that state for all future times. These points can be obtained by putting the growth rate of different variables of model system (2.1) equal to zero.

System (2.1) has the following three equilibria:

(1) Population-free equilibrium point $E_0 = (0, 0)$, which always exists. This equilibrium represents an ecological situation where neither prey nor predator population is present.
(2) Predator-free equilibrium point $E_1 = (\frac{r_0 - r_1}{r_2}, 0)$, which is feasible if $r_0 > r_1$. This equilibrium represents an ecological situation where only prey exist in the system with a condition that its growth rate should be greater than its natural death rate.
(3) Coexistence equilibrium point $E^* = (N^*, P^*)$, where

$$N^* = \frac{d_1 + d_2 P^*}{\alpha_1 \alpha (1 - mP^*)(1 + cP^*)} > 0$$

and P^* is (are) positive root(s) of the following equation:

$$a_6 P^6 + a_5 P^5 + a_4 P^4 + a_3 P^3 + a_2 P^2 + a_1 P + a_0 = 0, \tag{2.6}$$

where

$$a_6 = \alpha^2 \alpha_1 k c^2 m^2,$$

$$a_5 = \alpha^2 \alpha_1 c m \{2k(m - c) + mc\},$$

$$a_4 = \alpha^2\alpha_1\{2cm(m-c-2k)+k(c^2+m^2)\},$$

$$a_3 = \alpha^2\alpha_1\{c^2+m^2-4cm+2k(c-m)\} - kr_1\alpha\alpha_1 cm,$$

$$a_2 = \alpha^2\alpha_1\{2(c-m)+k\} + r_1\alpha\alpha_1\{k(c-m)-cm\} + kr_2d_2 + cmr_0\alpha\alpha_1,$$

$$a_1 = \alpha^2\alpha_1 + r_1\alpha\alpha_1(c-m+k) + r_2(d_2+d_1k) - r_0\alpha\alpha_1(c-m),$$

$$a_0 = r_2d_1 + \alpha\alpha_1(r_1-r_0).$$

Since $a_6 > 0$, Eq. (2.6) has at least one positive root if $a_0 < 0$, i.e.,

$$r_2d_1 + \alpha\alpha_1(r_1-r_0) < 0. \tag{2.7}$$

The coexistence equilibrium is very common in natural ecosystem and can be visualized in almost every ecological system. As all the dynamical variables are present here, this equilibrium is of utmost importance.

Now, we study the local stability of the equilibrium points by using standard stability analysis with an application of the Routh–Hurwitz criterion. An equilibrium point of the system (2.1) is locally asymptotically stable if all the eigenvalues of the Jacobian matrix evaluated at the equilibrium point are negative or have negative real parts. Regarding local stability of the equilibria of system (2.1), we have the following theorem.

Theorem 2.3. (1) *The equilibrium E_0 is stable if $r_0 < r_1$ and unstable if $r_0 > r_1$.* (2) *The equilibrium E_1 is stable if $d_1 > \frac{\alpha_1\alpha(r_0-r_1)}{r_2}$ and unstable if $d_1 < \frac{\alpha_1\alpha(r_0-r_1)}{r_2}$.* (3) *The equilibrium E^*, if exists, is locally asymptotically stable if and only if*

$$A_1 > 0, \quad A_2 > 0, \tag{2.8}$$

where A_1 and A_2 are defined in the proof.

Proof. (1) Eigenvalues of the Jacobian matrix of system (2.1) evaluated at the equilibrium point E_0 are $r_0 - r_1$ and $-d_1$. Clearly, one eigenvalue is always negative and the other is negative (positive) if $r_0 - r_1 < 0(>0)$. Thus, the equilibrium E_0 is stable (unstable) whenever the equilibrium E_1 does not exist (exists).

(2) Eigenvalues of the Jacobian matrix of system (2.1) corresponding to the equilibrium point E_1 are $-(r_0-r_1)$ and $-(\frac{\alpha_1\alpha(r_1-r_0)}{r_2} + d_1)$. In view of feasibility condition for the equilibrium point E_1, one eigenvalue is always negative while the other is negative (positive) provided $\alpha_1\alpha(r_0-r_1) - r_2d_1 < 0(>0)$. That is, for the stability of the equilibrium E_1, we must have $d_1 > \frac{\alpha_1\alpha(r_0-r_1)}{r_2}$ while for the instability, the inequality is reversed. Thus, the equilibrium E_1, if exists, is stable (unstable) whenever the equilibrium E^* does not exist (exists).

(3) The Jacobian matrix of system (2.1) corresponding to the coexistence equilibrium point E^* is given by

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

where

$$a_{11} = -r_2 N^*, \quad a_{12} = N^* \left\{ -\frac{r_0 k}{(1 + kP^*)^2} - \alpha[1 + 2(c - m)P^* - 3cmP^{*2}] \right\},$$

$$a_{21} = \alpha\alpha_1(1 - mP^*)(1 + cP^*)P^*, \quad a_{22} = [\alpha_1 \alpha N^* \{(c - m) - 2cmP^*\} - d_2]P^*.$$

The corresponding characteristic equation is given by

$$\lambda^2 + A_1\lambda + A_2 = 0, \tag{2.9}$$

where $A_1 = -(a_{11} + a_{22})$ and $A_2 = a_{11}a_{22} - a_{12}a_{21}$. Employing Routh–Hurwitz criterion, the equilibrium E^* is locally asymptotically stable if and only if $A_1, A_2 > 0$. □

Remark 2.2. Eigenvalues of the Jacobian matrix of system (2.1) at the equilibrium E_0 indicate that it is possible to observe the population-free equilibrium in natural ecosystem if the growth rate of prey is lesser than its natural death rate. In contrast, if the growth rate of prey is more than its natural death rate, the population-free equilibrium is no longer stable and the predator-free equilibrium comes into the picture. The predator-free equilibrium is visible in realistic scenario, if the natural death rate of the predator population is sufficiently large. Our stability result also indicates that stability of predator-free equilibrium is directly linked with feasibility of the coexistence equilibrium. One cannot see the predator-free system whenever the coexistence equilibrium exists. Moreover, if the initial state of system (2.1) is near the equilibrium point E^*, then the solution trajectories not only stay near the equilibrium E^* for all $t > 0$, but, also approaches the equilibrium E^* as $t \to \infty$ under the conditions in (2.8). Thus, if the initial values of state variables N and P are close to N^* and P^*, respectively, then the system (2.1) will eventually get stabilized provided conditions in (2.8) hold. That is, small perturbations in the system's variables do not affect stability of the system at the coexistence equilibrium.

2.1.3. *Hopf-bifurcation analysis*

Nonlinear mathematical models of interacting populations show rich and complex dynamical behaviors even when system complexity is low (two or three species). Oscillating behavior is the most frequent dynamical property in population dynamics. Oscillating behavior or the existence of a limit cycle leads to the Hopf bifurcation of the system. Hopf bifurcation is defined as the appearance or disappearance of a periodic orbit through a local change in the stability properties of an equilibrium point. Analytically, we study the Hopf bifurcation about the coexistence equilibrium E^* with respect to the parameter representing the refuge coefficient (m), while other parameters are fixed. We have the following results for the existence of Hopf bifurcation.

Theorem 2.4. *The necessary and sufficient conditions for the occurrence of Hopf-bifurcation about the equilibrium E^* are that there exists $m = m^c$ such that $A_1(m^c) = 0$, $A_2(m^c) > 0$ and $[\frac{dA_1}{dm}]_{m=m^c} \neq 0$.*

For proof of this theorem, see Appendix A.

3. Effects of Time Delays

In this section, we modify the nondelayed model (2.1) by incorporating three discrete time delays. After sensing the chemical cue or vocal cue, prey takes some time for assessing the predation risk. Therefore, the fear of predation risk does not respond instantaneously to the growth of prey species, rather there must be some time lag required.[65] In order to incorporate this time lag in the model, we consider that at time t, the fear of predator is in accordance with the predator density at time $t - \tau_1$ (for some $\tau_1 > 0$). Moreover, prey cannot take refuge instantly; they need some time to take refuge. Let $\tau_2 > 0$ be the time delay to hide from predation risk. Furthermore, the cooperative predators do not aggregate in a group instantly, but individuals use different stages and strategies such as tactile, visual, vocal cues, or a suitable combination of these to communicate with each other.[58] Let $\tau_3 > 0$ be the time delay during cooperative hunting. Incorporating these time lags in system (2.1), we get the following system of delay differential equations:

$$\begin{aligned}\frac{dN}{dt} &= \frac{r_0 N}{1 + kP(t-\tau_1)} - r_1 N - r_2 N^2 \\ &\quad - \alpha[1 - mP(t-\tau_2)][1 + cP(t-\tau_3)]NP, \\ \frac{dP}{dt} &= \alpha_1 \alpha[1 - mP(t-\tau_2)][1 + cP(t-\tau_3)]NP - d_1 P - d_2 P^2. \end{aligned} \tag{3.1}$$

Initial conditions for the system (3.1) take the form

$$N(\phi) = \psi_1(\phi), \quad P(\phi) = \psi_2(\phi), \quad -\tau \leq \phi \leq 0, \tag{3.2}$$

where $\psi = (\psi_1, \psi_2)^T \in \mathcal{C}_+$ such that $\psi_i(\phi) \geq 0, i = 1, 2\ \forall\, \phi \in [-\tau, 0]$ and $\mathcal{C}_+$ denotes the Banach space $\mathcal{C}_+([-\tau, 0], \mathbf{R}^2_{+0})$ of continuous functions mapping the interval $[-\tau, 0]$ into $\mathbf{R}^2_{+0}$. Denote the norm of an element ψ in $\mathcal{C}_+$ by $\|\psi\| = \sup_{-\tau \leq \phi \leq 0} \{|\psi_1(\phi)|, |\psi_2(\phi)|\}$, where $\tau = \max\{\tau_1, \tau_2, \tau_3\}$. For biological feasibility, we further assume that $\psi_i(0) \geq 0$ for $i = 1, 2$. By the fundamental theory of functional differential equations,[66] we know that there is a unique solution $(N(t), P(t))$ to system (3.1) with initial conditions (3.2).

3.1. *Stability and bifurcation analysis in the presence of time delays*

Here, we study the stability dynamics of the delay model (3.1) around the coexistence equilibrium $E^*(N^*, P^*)$. The linearized form of system (3.1) around the coexistence equilibrium E^* is

$$\frac{dX}{dt} = M_0X(t) + M_1X(t-\tau_1) + M_2X(t-\tau_2) + M_3X(t-\tau_3), \tag{3.3}$$

where $X = (N, P)^T$, and

$$M_0 = \begin{pmatrix} M_{01} & M_{02} \\ M_{03} & M_{04} \end{pmatrix}, \quad M_1 = \begin{pmatrix} 0 & M_{12} \\ 0 & 0 \end{pmatrix}, \quad M_2 = \begin{pmatrix} 0 & M_{22} \\ 0 & M_{24} \end{pmatrix}, \quad M_3 = \begin{pmatrix} 0 & M_{32} \\ 0 & M_{34} \end{pmatrix}$$

with

$$\begin{aligned}
&M_{01} = -r_2N^*, \quad M_{02} = -\alpha N^*(1+cP^*)(1-mP^*),\\
&M_{03} = \alpha_1\alpha(1-mP^*)(1+cP^*)P^*,\\
&M_{04} = -d_2P^*, \quad M_{12} = -\frac{r_0kN^*}{(1+kP^*)^2},\\
&M_{22} = \alpha m(1+cP^*)N^*P^*, \quad M_{24} = -\alpha_1\alpha m(1+cP^*)N^*P^*,\\
&M_{32} = -\alpha cN^*P^*(1-mP^*), \quad M_{34} = \alpha_1\alpha cN^*P^*(1-mP^*).
\end{aligned}$$

The variational matrix of system (3.3) around the coexistence equilibrium is given by

$$J_\tau(E^*) = \begin{pmatrix} M_{01}-\lambda & M_{02} + M_{12}e^{-\lambda\tau_1} + M_{22}e^{-\lambda\tau_2} + M_{32}e^{-\lambda\tau_3} \\ M_{03} & M_{04} + M_{24}e^{-\lambda\tau_2} + M_{34}e^{-\lambda\tau_3} - \lambda \end{pmatrix}.$$

Therefore, the characteristic equation is given by

$$\lambda^2 + B_1\lambda + B_0 + C_0e^{-\lambda\tau_1} + (D_1\lambda + D_0)e^{-\lambda\tau_2} + (E_1\lambda + E_0)e^{-\lambda\tau_3} = 0, \tag{3.4}$$

where

$$\begin{aligned}
&B_1 = -(M_{01}+M_{04}), \quad B_0 = M_{01}M_{04} - M_{02}M_{03},\\
&C_0 = -M_{03}M_{12}, \quad D_1 = -M_{24}, \quad D_0 = M_{01}M_{24} - M_{03}M_{22},\\
&E_1 = -M_{34}, \quad E_0 = M_{01}M_{34} - M_{03}M_{32}.
\end{aligned}$$

Case I. $\tau_1 = \tau_2 = \tau_3 = 0$.
In the absence of time delays (i.e., $\tau_1 = \tau_2 = \tau_3 = 0$), the local stability behavior of the equilibrium E^* is already discussed in Theorem 2.3.

Case II. $\tau_1 > 0$ and $\tau_2 = \tau_3 = 0$.
In this case, the characteristic equation (3.4) takes the following form:

$$\lambda^2 + f_1\lambda + f_0 + c_0 e^{-\lambda\tau_1} = 0, \tag{3.5}$$

where $f_1 = B_1 + D_1 + E_1$, $f_0 = B_0 + D_0 + E_0$, $c_0 = C_0$. A necessary condition for stability changes of the equilibrium E^* is that the characteristic equation (3.5) should have purely imaginary solutions. Thus, putting $\lambda = i\omega$ $(\omega > 0)$ in Eq. (3.5), and separating real and imaginary parts, we get

$$c_0\cos(\omega\tau_1) = \omega^2 - f_0, \tag{3.6}$$

$$c_0\sin(\omega\tau_1) = \omega f_1. \tag{3.7}$$

Squaring and adding Eqs. (3.6) and (3.7), we get

$$c_0^2 = (\omega^2 - f_0)^2 + (\omega f_1)^2. \tag{3.8}$$

Substituting $\omega^2 = \zeta$ in Eq. (3.8) and simplifying, we obtain the following equation in ζ:

$$\Psi(\zeta) \equiv \zeta^2 + g_1\zeta + g_0 = 0, \tag{3.9}$$

where $g_1 = f_1^2 - 2f_0$ and $g_0 = f_0^2 - c_0^2$. Note that Eq. (3.9) has exactly one positive root if g_0 is negative, and two positive roots if g_0 is positive and g_1 is negative.

Theorem 3.1. *Suppose that the equilibrium E^* exists and is locally asymptotically stable for $\tau_1 = \tau_2 = \tau_3 = 0$, i.e., conditions in (2.7) and (2.8) hold. Also, let $\zeta_0 = \omega_{10}^2$ be a positive root of Eq. (3.9). Then, there exists $\tau_1 = \tau_1^0$ such that the equilibrium E^* is asymptotically stable for $0 \le \tau_1 < \tau_1^0$ and unstable for $\tau_1 > \tau_1^0$, where*

$$\tau_1^n = \frac{1}{\omega_{10}}\tan^{-1}\left[\frac{f_1\omega_{10}}{\omega_{10}^2 - f_0}\right] + \frac{n\pi}{\omega_{10}},$$

for $n = 0, 1, 2, 3, \ldots$. Moreover, the system (3.1) undergoes a Hopf-bifurcation at the equilibrium E^* when $\tau_1 = \tau_1^0$ provided

$$\operatorname{sgn}\left[\frac{d(\mathrm{Re}(\lambda))}{d\tau_1}\right]_{\tau_1=\tau_1^0} = \operatorname{sgn}\left[\frac{2\omega_{10}^2 + g_1}{c_0^2}\right] > 0.$$

Proof. Since $\zeta_0 = \omega_{10}^2$ is a solution of Eq. (3.9), the characteristic equation (3.5) possesses a pair of purely imaginary roots $\pm i\omega_{10}^2$. It follows from Eqs. (3.6) and (3.7) that τ_1^n is a function of ω_{10}^2 for $n = 0, 1, 2, 3, \ldots$. Thus, if the system (3.1) is locally asymptotically stable around the coexistence equilibrium E^* for $\tau_1 = \tau_2 = \tau_3 = 0$, then by *Butler's lemma*, the equilibrium E^* will remain stable for $\tau_1 < \tau_1^0$, such that $\tau_1^0 = \min_{n\ge 0}\tau_1^n$ and unstable for $\tau_1 > \tau_1^0$ provided the following transversality condition holds:

$$\operatorname{sgn}\left[\frac{d(\mathrm{Re}(\lambda))}{d\tau_1}\right]_{\tau_1=\tau_1^0} \neq 0.$$

Differentiating Eq. (3.5) with respect to τ_1, we obtain

$$\frac{d\lambda}{d\tau_1} = \frac{c_0 \lambda e^{-\lambda\tau_1}}{2\lambda + f_1 - c_0\tau_1 e^{-\lambda\tau_1}}.$$

This implies,

$$\left(\frac{d\lambda}{d\tau_1}\right)^{-1} = \frac{2\lambda + f_1}{c_0\lambda e^{-\lambda\tau_1}} - \frac{\tau_1}{\lambda}.$$

Now,

$$\begin{aligned}\operatorname{sgn}\left[\frac{d(\mathrm{Re}(\lambda))}{d\tau_1}\right]_{\tau_1=\tau_1^0} &= \operatorname{sgn}\left[\frac{d(\mathrm{Re}(\lambda))}{d\tau_1}\right]^{-1}_{\tau_1=\tau_1^0} = \operatorname{sgn}\left[\mathrm{Re}\left(\frac{d\lambda}{d\tau_1}\right)^{-1}\right]_{\lambda=i\omega_{10}}\\ &= \operatorname{sgn}\left[\frac{2\omega_{10}^2 + g_1}{c_0^2}\right] = \operatorname{sgn}\left[\frac{\Psi'(\omega_{10}^2)}{c_0^2}\right].\end{aligned}$$

Clearly, $\Psi'(\omega_{10}^2) \neq 0$, since ω_{10}^2 is a simple positive root of Eq. (3.9). Therefore, the transversality condition is verified and hence Hopf-bifurcation occurs at $\tau_1 = \tau_1^0$ i.e., a family of periodic solutions bifurcate from the equilibrium E^* as τ_1 passes through τ_1^0.[67] □

Case III. $\tau_1 = \tau_3 = 0$ and $\tau_2 > 0$.
In this case, the characteristic equation (3.4) becomes

$$\lambda^2 + b_1\lambda + b_0 + (d_1\lambda + d_0)e^{-\lambda\tau_2} = 0, \tag{3.10}$$

where

$$b_1 = B_1 + E_1, \quad b_0 = B_0 + C_0 + E_0, \quad d_1 = D_1, \quad d_0 = D_0.$$

Following the similar analysis as in Case II, we can state the following theorem.

Theorem 3.2. *Suppose that the equilibrium E^* exists and is locally asymptotically stable for $\tau_1 = \tau_2 = \tau_3 = 0$, i.e., conditions in (2.7) and (2.8) hold. Also, let $b_0^2 - d_0^2 < 0$, then there exists $\tau_2 = \tau_2^0$ such that the equilibrium E^* is asymptotically stable for $0 \leq \tau_2 < \tau_2^0$ and unstable for $\tau_2 > \tau_2^0$, where*

$$\tau_2^n = \frac{1}{\omega_{20}}\tan^{-1}\left[\frac{b_1 d_0\omega_{20} + \omega_{20} d_1(\omega_{20}^2 - b_0)}{d_0(\omega_{20}^2 - b_0) - b_1 d_1 \omega_{20}^2}\right] + \frac{n\pi}{\omega_{20}},$$

for $n = 0, 1, 2, 3, \ldots$ and $i\omega_{20}$ is root of the characteristic equation (3.10). Moreover, the system (3.1) undergoes a Hopf-bifurcation at the equilibrium E^* when $\tau_2 = \tau_2^0$ provided

$$\operatorname{sgn}\left[\frac{d(\mathrm{Re}(\lambda))}{d\tau_2}\right]_{\tau_2=\tau_2^0} = \operatorname{sgn}\left[\frac{2\omega_{20}^2 + b_1^2 - d_1^2 - 2b_0}{d_1^2\omega_{20}^2 + d_0^2}\right] > 0.$$

Proof. Proof is similar as in Case II. □

Case IV. $\tau_1 = \tau_2 = 0$ and $\tau_3 > 0$.
In this case, the characteristic equation (3.4) becomes

$$\lambda^2 + c_1\lambda + c_0 + (e_1\lambda + e_0)e^{-\lambda\tau_3} = 0, \tag{3.11}$$

where

$$c_1 = B_1 + D_1, \quad c_0 = B_0 + C_0 + D_0, \quad e_1 = E_1, \quad e_0 = E_0.$$

Following the similar analysis as in Case II, we can state the following theorem.

Theorem 3.3. *Suppose that the equilibrium E^* exists and is locally asymptotically stable for $\tau_1 = \tau_2 = \tau_3 = 0$, i.e., conditions in (2.7) and (2.8) hold. Also, let $c_0^2 - e_0^2 < 0$, then there exists $\tau_3 = \tau_3^0$ such that the equilibrium E^* is asymptotically stable for $0 \le \tau_3 < \tau_3^0$ and unstable for $\tau_3 > \tau_3^0$, where*

$$\tau_3^n = \frac{1}{\omega_{30}} \tan^{-1}\left[\frac{c_1 e_0 \omega_{30} + \omega_{30} e_1(\omega_{30}^2 - c_0)}{e_0(\omega_{30}^2 - e_0) - c_1 e_1 \omega_{30}^2}\right] + \frac{n\pi}{\omega_{20}},$$

for $n = 0, 1, 2, 3, \ldots$ and $i\omega_{30}$ is root of the characteristic equation (3.11). Moreover, the system (3.1) undergoes a Hopf-bifurcation at the equilibrium E^* when $\tau_3 = \tau_3^0$ provided

$$\mathrm{sgn}\left[\frac{d(\mathrm{Re}(\lambda))}{d\tau_3}\right]_{\tau_3=\tau_3^0} = \mathrm{sgn}\left[\frac{2\omega_{30}^2 + c_1^2 - e_1^2 - 2c_0}{e_1^2\omega_{30}^2 + e_0^2}\right] > 0.$$

Proof. Proof is similar as in Case II. □

4. Combined Effects of Seasonality and Time Delays

Again, we extend our delayed model system (3.1) by allowing some of the rate parameters to vary with time. In system (3.1), we assumed that the parameters representing the effect of fear, prey refuge and hunting cooperation are constants, and do not change with time. But, in realistic scenarios, these parameters are not constant. Indeed, the fear of predator, prey refuge and hunting cooperation depend upon several ecological and environmental factors, and hence vary with time.[52,60,63] Thus, by considering seasonal variations in the parameters k, m and c, we get the following modified delay nonautonomous system:

$$\begin{aligned}\frac{dN}{dt} &= \frac{r_0 N}{1 + k(t)P(t-\tau_1)} - r_1 N - r_2 N^2 \\ &\quad - \alpha[1 - m(t)P(t-\tau_2)][1 + c(t)P(t-\tau_3)]NP, \\ \frac{dP}{dt} &= \alpha_1\alpha[1 - m(t)P(t-\tau_2)][1 + c(t)P(t-\tau_3)]NP - d_1 P - d_2 P^2.\end{aligned} \tag{4.1}$$

We assume that the seasonally forced parameters $k(t)$, $m(t)$ and $c(t)$ are positive, continuous and bounded functions with positive lower bounds, and are ω-periodic. For simplicity, we assume the period of 365 days.

4.1. *Existence of periodic solution*

In this section, we show that the delay nonautonomous system (4.1) possesses at least one positive periodic solution. To this, we use the following lemma[68]:

Lemma 4.1. *Let X and Y be two Banach spaces, $L : \mathrm{Dom}(L) \subset X \to Y$ be a Fredholm operator with index zero, $\Omega \subset Y$ be any open bounded set, and let $M : \overline{\Omega} \to X$ be L-compact on $\overline{\Omega}$. Assume that*

(1) *For each $\psi \in (0, 1)$, $x \in \partial\Omega \cap \mathrm{Dom}(L)$, $Lx \neq \psi Mx$.*
(2) *For each $x \in \partial\Omega \cap \mathrm{Ker}(L)$, $QMx \neq 0$.*
(3) *The Brouwer degree $\deg\{JQM, \Omega \cap \mathrm{Ker}(L), 0\} \neq 0$, where $J : \mathrm{Im}(Q) \to \mathrm{Ker}(L)$ is an isomorphism.*

Then, the equation $Lx = Mx$ has at least one solution in $\mathrm{Dom}(L) \cap \overline{\Omega}$.

Theorem 4.1. *System (4.1) has at least one positive ω-periodic solution if the following conditions hold*:

$$r_0 > r_1, \quad d_1 > \alpha_1 \alpha e^{H_1}, \tag{4.2}$$

$$\frac{r_0}{1 + \overline{k} e^{H_2}} > \alpha[1 + \overline{c} e^{H_2}] e^{H_2} + r_1, \tag{4.3}$$

where H_1 and H_2 are defined in the proof.

For proof of this theorem, see Appendix B.

Remark 4.1. The existence of positive periodic solution indicates that the prey and predator population densities fluctuate in periodic manner in an ecological subsystem, that means, prey and predator populations survive for long time. From the conditions (4.2) and (4.3), we note that if predation rate, level of fear and natural death rate of prey are very low and growth rate of prey is sufficiently high, then both prey and predator populations survive for long time. Hence, we can conclude that the prey and predator populations survive if their interaction becomes weak; on the other hand, for strong interaction, they may extinct.

5. Numerical Simulations

In this section, we simulate systems (2.1), (3.1) and (4.1) by choosing a set of hypothetical parameter values. Unless otherwise mentioned, the parameters are at the same values as in Table 1.

5.1. *Simulation results of system* (2.1)

5.1.1. *Sensitivity results*

At first, we identify key parameters having crucial impacts on the equilibrium abundances of prey and predator populations. By using the method described in Refs. 69

and [70], we perform global sensitivity analysis. Basically, we utilize two statistical techniques: Latin Hypercube Sampling (LHS) and Partial Rank Correlation Coefficients (PRCCs). The former allows us to vary several parameters simultaneously in an efficient way while the latter correlate the output of model with the input parameters. We checked monotone relationships of our input parameters with the response function, which is necessary for computing PRCCs. Type of relationships between input parameters and model output is determined by the signs of PRCCs whereas the strength of correlation can be measured by values of PRCCs which lie between -1 and 1. We pick r_0, k, α, m, c and α_1 as the input parameters and set the density of prey population (N) as the response function. The reason behind choosing these parameters for sensitivity analysis is that the dynamic interactions of prey and predator depend on the growth rate of prey, fear of predators, predation rate, prey refuge and hunting cooperation of predators. We run 200 simulations for the chosen parameters by assuming uniform distribution for each of them. We take baseline values of parameters from Table 1 and allow them to deviate $\pm 25\%$ from their nominal values. In Fig. 1, we represent PRCCs for the parameters of interest using prey population as the response function. Notably, the parameters r_0 and m posses positive correlation with the prey population while the parameters having negative correlations with the prey population are k, α, c and α_1. We find that all the considered parameters have significant correlations with density of prey population. That is, for these parameters the p-values are less than 0.05. Having ideas about the positive/negative correlation of parameters with prey density can help to formulate the effectual control strategy necessary for maintenance of ecological balance of the predator–prey system.

Next, we plot equilibrium abundances of prey and predator populations by varying two parameters at a time viz. (k, m), (k, c) and (m, c), Fig. 2. It can be noted

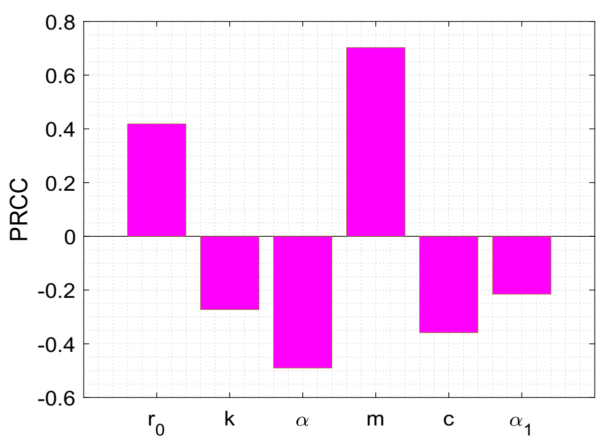
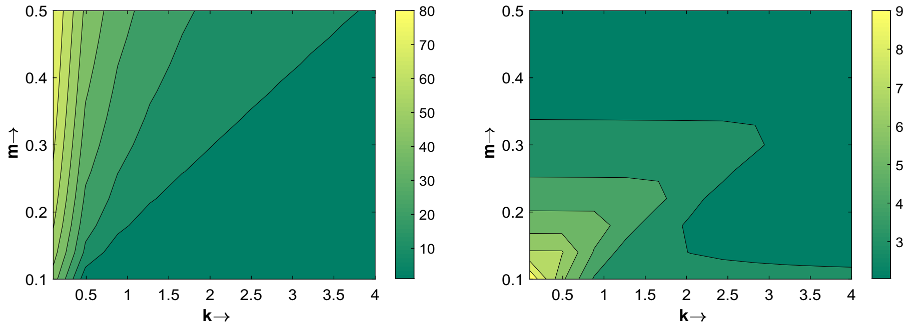
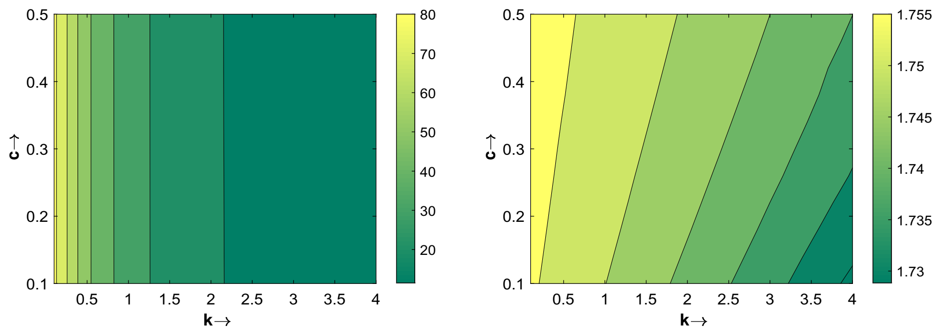


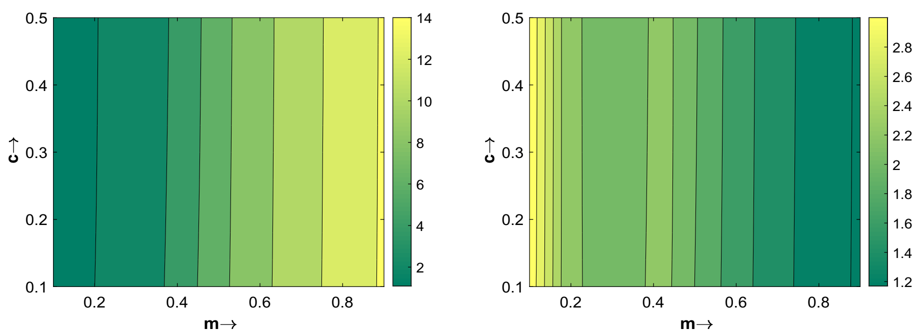
Fig. 1. (Color online) Effect of uncertainty of the model (2.1) on prey population (N). Baseline values of parameters are same as in Table 1.



(a)



(b)



(c)

Fig. 2. Contour lines representing the equilibrium values of prey population (first column) and predator population (second column) as functions of (a) k and m, (b) k and c, and (c) m and c. Rest of the parameters are at the same values as in Table 1.

from the contour plots that for lower levels of fear (k), that the prey and predator populations are at higher equilibrium densities. But, the prey and predator populations decrease as the level of fear increased. Increments in the refuge coefficient (m) lead to incline in the prey density but decline in the predator density.

If refuge is very high, the prey population reach a healthier equilibrium level while the density of predator population becomes very low. Hunting cooperation helps predator population to grow but can cause decline in the prey density. At the time of cooperation, refuge behavior of prey helps them to persist in the system.

5.1.2. *Bifurcation results*

Next, we see how the predation rate, fear of predator, refuge property of prey and hunting cooperation by predator regulate the dynamics of system (2.1). First, we set the system (2.1) in oscillatory state (see Fig. 3(a)) and change the values of parameters α, k, m and c one-by-one. We observe that on reducing the value of α from 0.64 to 0.2, the unstable dynamics of the system is replaced by stability (see Fig. 3(b)). Decreasing the value of k from 5 to 0.6, the oscillatory behavior of system (2.1) is replaced by stable dynamics (see Fig. 3(c)). Increase in the value of m from 0.33 to 0.59 evacuate the persistent oscillations in the system and push back the system to stable state (see Fig. 3(d)). The limit cycle oscillations also disappear as the value of c changes from 0.85 to 0.1 (see Fig. 3(e)). To have a clear picture, we draw bifurcation diagrams of system (2.1) with respect to k, m and c (see Fig. 4). The destabilizing roles of k and c, and stabilizing effect of m are clearly apparent from the bifurcation diagrams. We also plot two parameter stability regions of system (2.1), Fig. 5. It can be seen from Fig. 5(a) that for lower ranges of k and c, the system shows stable dynamics while stability is lost and the system becomes unstable on increasing the values of parameters k and c on the diagonal. Figure 5(b) shows that for lower values of m, the system is unstable for all values of k but as the parameter m crosses certain threshold values, the system remains stable irrespective of the level of fear.

5.2. *Simulation results of system* (3.1)

Now, we see the dynamics of the delayed system (3.1) for different values of time delays τ_1, τ_2 and τ_3. First, we see the dynamical behavior of system (3.1) in time series solutions, which are solved by MATLAB software, using dde23 solver. Keeping the original nondelayed system (2.1) in stable state (see Fig. 6(a)), we introduce time delays τ_1 or τ_3 or both, setting $\tau_2 = 0$. When we introduce single delay (τ_1 or τ_3) in the system (3.1), it gives limit cycle oscillations (see Figs. 6(b) and 6(d)). But, higher values of τ_1 or τ_3 push back the system in stable state (see Figs. 6(c) and 6(e)). Moreover, we observe that if the system is in oscillatory state due to single delay (τ_1 or τ_3), then introduction of other delay makes the system stable again (see Fig. 6(f)). Thus, we find that single delay induces multiple stability switches in the system. However, limit cycle oscillations produced by one delay can be terminated and the system regains its stability for suitable value of another delay parameter. This indicates that considering simultaneous delays in fear and cooperation evacuate the persistent oscillations induced by anyone of them, returning the system to stable

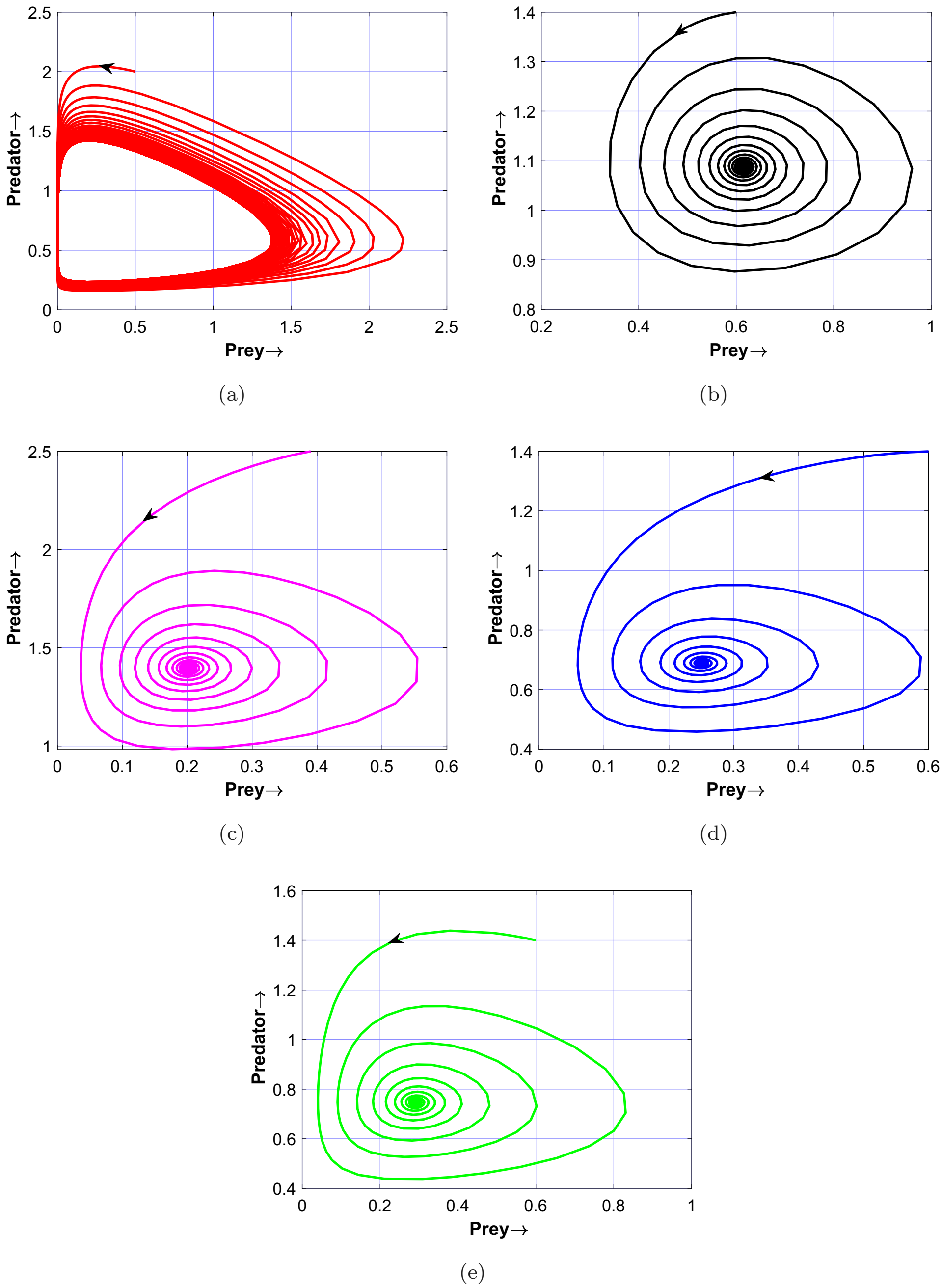
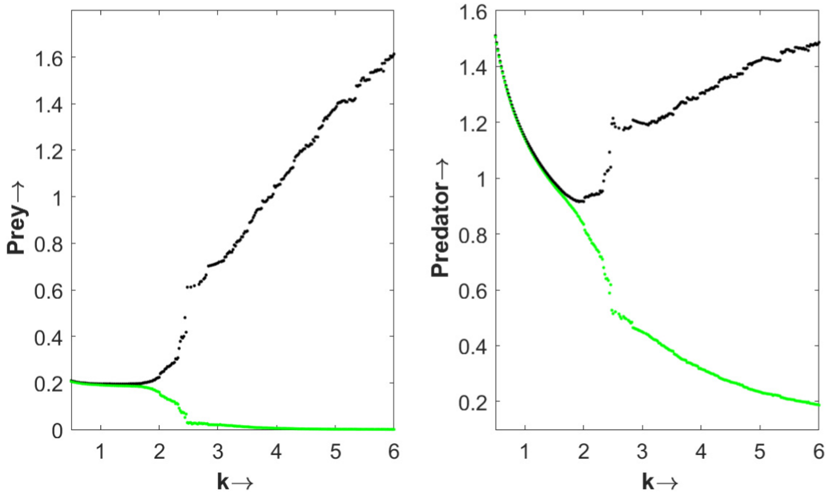


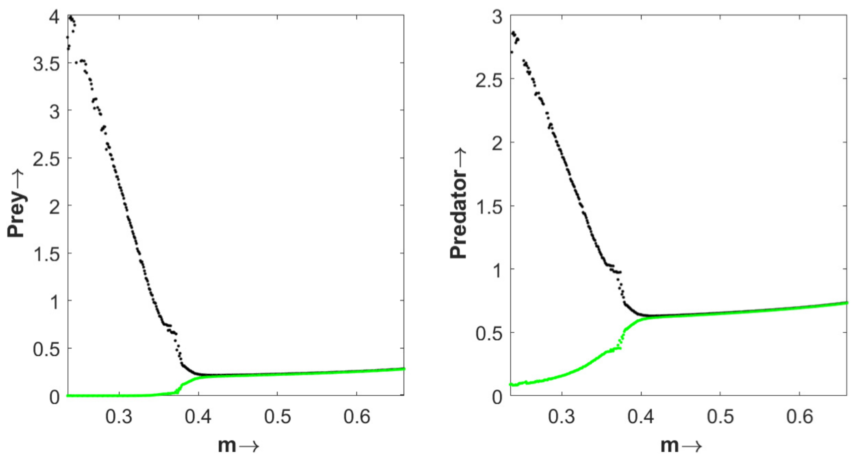
Fig. 3. Phase portrait of system (2.1). System (2.1) shows (a) limit cycle oscillations at $k = 5$, (b) stable focus at $\alpha = 0.2$, (c) stable focus at $k = 0.6$, (d) stable focus at $k = 5$, $m = 0.59$, and (e) stable focus at $k = 5$, $c = 0.1$. Rest of the parameters are at the same values as in Table 1.

state. We note that the time delay in refuge (τ_2) has no effect on the dynamics of a stable system.

Next, we set the system (2.1) in oscillatory state (see Fig. 7(a)), and see the impacts of delays in refuge (τ_2) and cooperation (τ_3) by fixing $\tau_1 = 0$. For $\tau_3 = 13$, we observe that the persistent oscillations are killed out by simple stable state, Fig. 7(b). Further, we note that at $\tau_3 = 30$, system (3.1) exhibits 2-periodic solutions (see Fig. 7(c)). On increasing the value of τ_3 from 30 to 55, system (3.1) shows chaotic behavior, a complicated natural phenomenon in predator–prey system (see

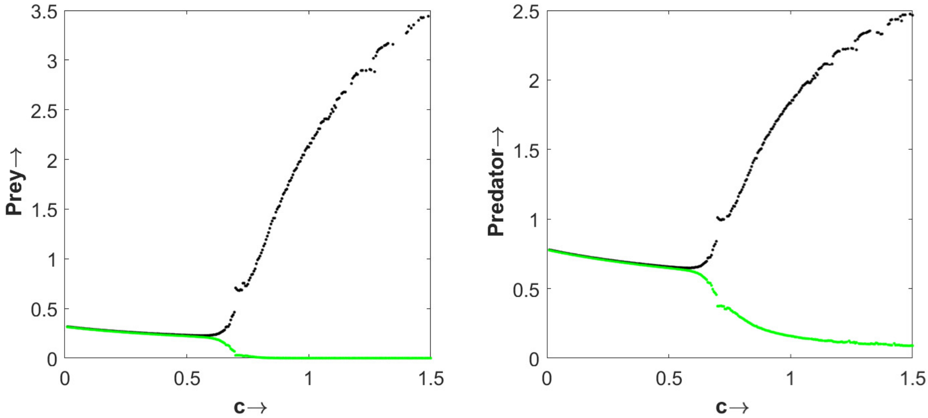


(a)



(b)

Fig. 4. Bifurcation diagrams of system (2.1) with respect to (a) k, (b) m and (c) c. Rest of the parameters are at the same values as in Table 1 except $k = 5$ in (b) and (c).

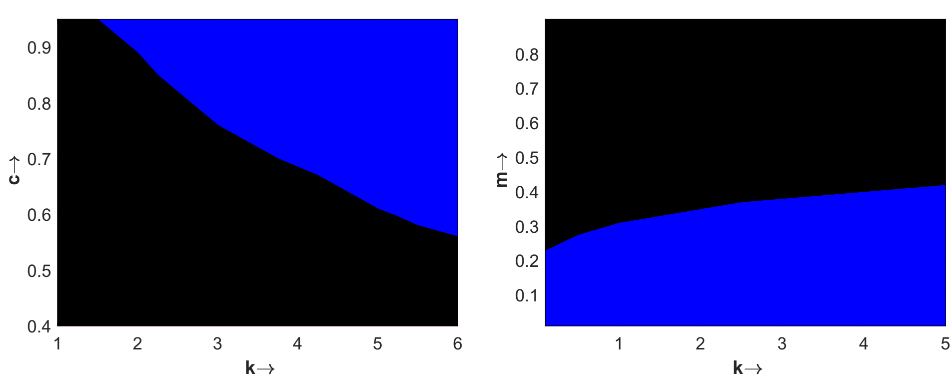


(c)

Fig. 4. (*Continued*)

Fig. 7(d)). The occurrence of chaotic oscillation may be explained through incommensurate limit cycles.[71] Hence, we find that delay in cooperation (τ_3) can induce complex dynamics in the system. Chaotic behavior of predator–prey system due to delay in cooperation is also observed by Pal *et al.*[58] In Fig. 7(e), we see the effect of delay in refuge (τ_2) on an otherwise unstable system. We find that an oscillating system becomes stable due to delay in refuge.

Now, to get a clear picture of impact of cooperation delay, we plot bifurcation diagrams of prey and predator populations with respect to the delay parameter τ_3 by fixing $\tau_1 = \tau_2 = 0$. It is clear from Fig. 8 that there exists a critical value of τ_3 below which the delayed system (3.1) exhibits limit cycle oscillations. But,



(a) (b)

Fig. 5. Two-parameter bifurcation diagrams of system (2.1) in (a) (k, c) and (b) (k, m) planes. Here, black and blue regions correspond to stable and unstable coexistence, respectively. Rest of the parameters are at the same values as in Table 1.

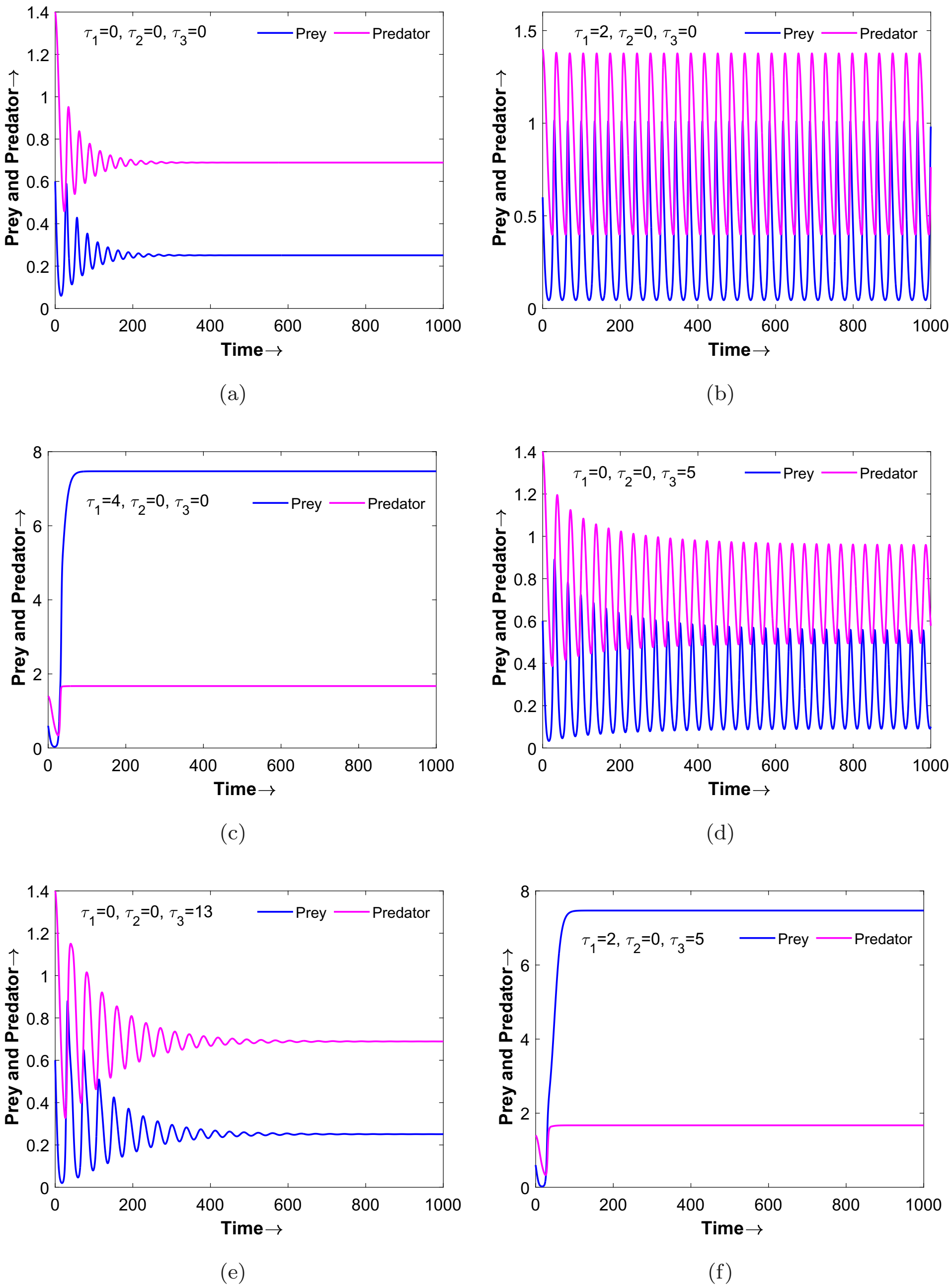


Fig. 6. Time series solutions of system (3.1) for different values of τ_1 and τ_3, setting $\tau_2 = 0$. Parameters are at the same values as in Fig. 3(d).

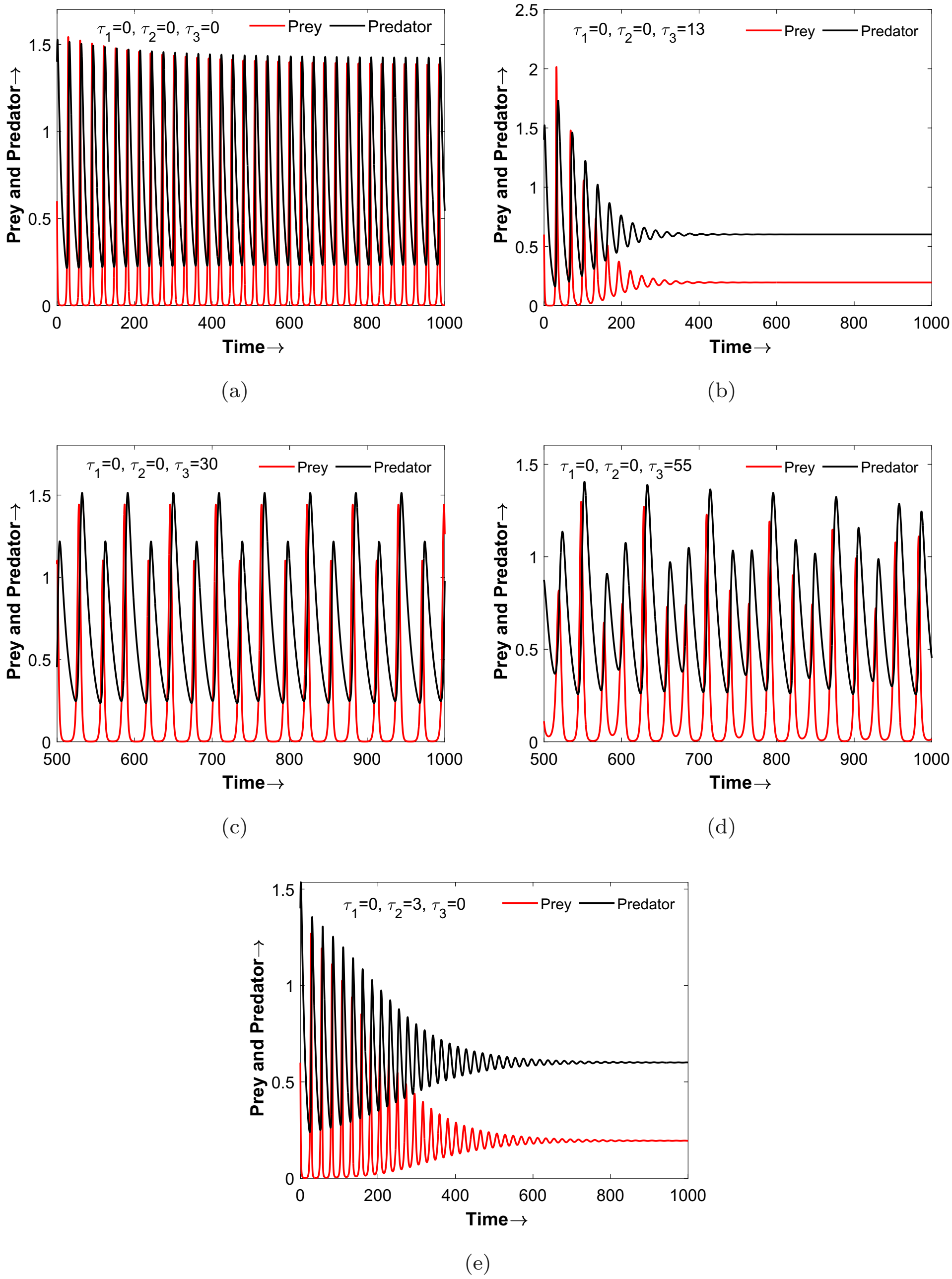


Fig. 7. Time series solutions of system (3.1) for different values of τ_2 and τ_3, setting $\tau_1 = 0$. Parameters are at the same values as in Fig. 3(a).

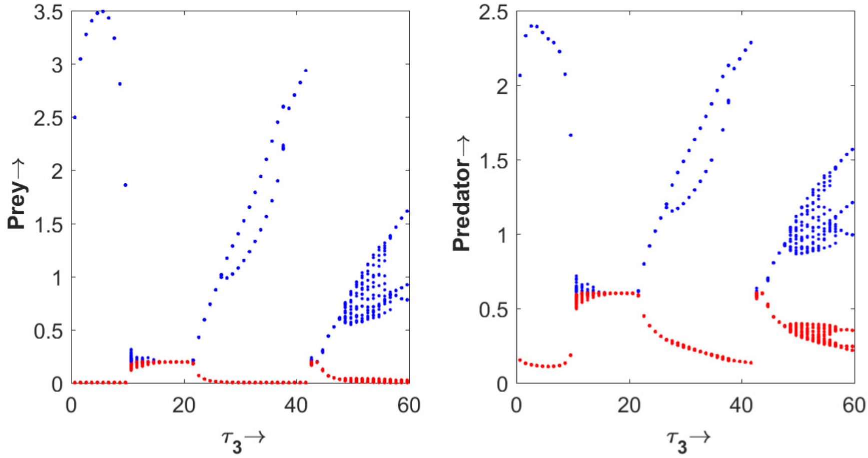


Fig. 8. Bifurcation diagram of system (3.1) with respect to τ_3, setting $\tau_1 = \tau_2 = 0$. Parameters are at the same values as in Fig. 3(a).

as the value of τ_3 increases, the amplitude of oscillations reduce and after a critical value, it becomes stable. However, system (3.1) remains in stable state up to a certain range of τ_3, and again system oscillates and experiences 2-periodic oscillations as the value of τ_3 increased. We observe that there is again a narrow range of τ_3 in which the system possesses stable dynamics. Ultimately, the system enters into chaotic state for higher values of τ_3. Now, we specify the maximum Lyapunov exponent as the noticeable measure for estimation of dynamical stability of a nonlinear system. The basic objective of calculating the maximum Lyapunov

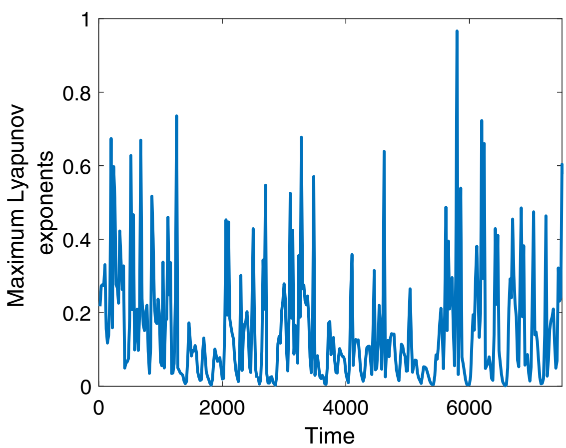


Fig. 9. Maximum Lyapunov exponent of the system (3.1) for $\tau_3 = 55$, setting $\tau_1 = \tau_2 = 0$. Parameters are at the same values as in Fig. 3(a). In the figure, positive values of the maximum Lyapunov exponent confirm the occurrence of chaotic oscillation.

exponent is to calculate the average logarithmic rate of separation of two nearby orbits by following them. Whenever they get too far apart, one of the orbits has to be moved back to the vicinity of the other along the line of separation. The maximum Lyapunov exponent is positive corresponding to a chaotic attractor, the maximum Lyapunov exponent is zero corresponding to a bifurcation point, and the maximum Lyapunov exponent is negative corresponding to a fixed point or a periodic attractor. For the confirmation of chaotic behavior of the delayed system (3.1), the maximum Lyapunov exponents have been plotted in Fig. 9. We compute the Lyapunov exponents by using the approach of Refs. 72 and 73. The positivity of maximum Lyapunov exponents ensures that the system is in chaotic state.

5.3. *Simulation results of system* (4.1)

Now, we numerically investigate the dynamical behaviors of delay nonautonomous system (4.1). We choose the time dependent parameters $k(t)$, $m(t)$ and $c(t)$ as sinusoidal functions:

$$k(t) = k + k_{11}\sin(\omega t), \quad m(t) = m + m_{11}\sin(\omega t), \quad c(t) = c + c_{11}\sin(\omega t)$$

with period of 365 days. We assume that these parameters vary depending on the several ecological and environmental factors which alter the fear effect, prey refuge and cooperative behavior of predators. For simplicity, we neglect the phase shift in these biological processes, and simply incorporate the effect of seasonal changes by considering the periodic parameters with a period of one year. It is to be noted that consideration of different periodic functions for these parameters may give different results.

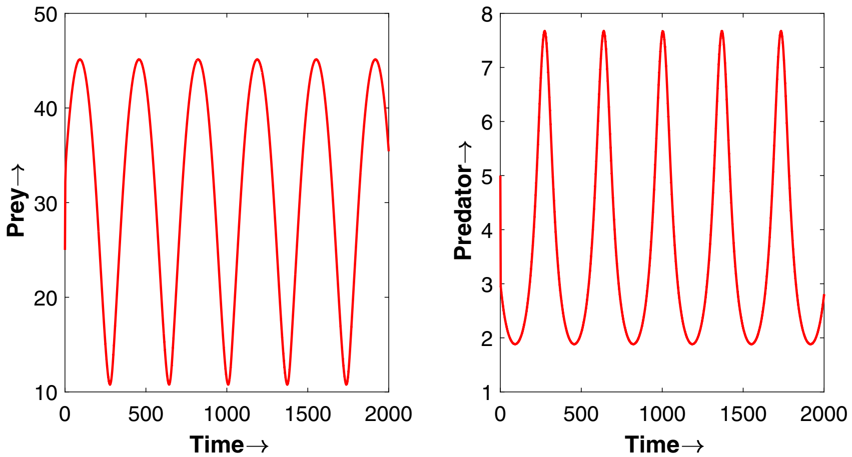


Fig. 10. Time series solutions of system (4.1) in the absence of time delays. Parameters are at the same values as in Fig. 3(c), and $m_{11} = 0.2$, $k_{11} = c_{11} = 0$.

First, we see the dynamical behavior of the solution trajectories of system (4.1) for different parametric setups of the seasonally varied parameters, $m(t)$, $k(t)$ and $c(t)$, in the absence of time delays (i.e., $\tau_1 = \tau_2 = \tau_3 = 0$). We get that for $m_{11} = 0.2$ and $k_{11} = c_{11} = 0$, system (4.1) gives periodic solution (see Fig. 10) whereas the corresponding autonomous system (2.1) shows stable behavior. Interestingly, on increasing the strength of seasonality in prey refuge to $m_{11} = 0.3$, system (4.1) exhibits bursting patterns (see Fig. 11(a)). Bursting is a result of mutual influence between different scales, and can be classified by bifurcation analysis of a fast

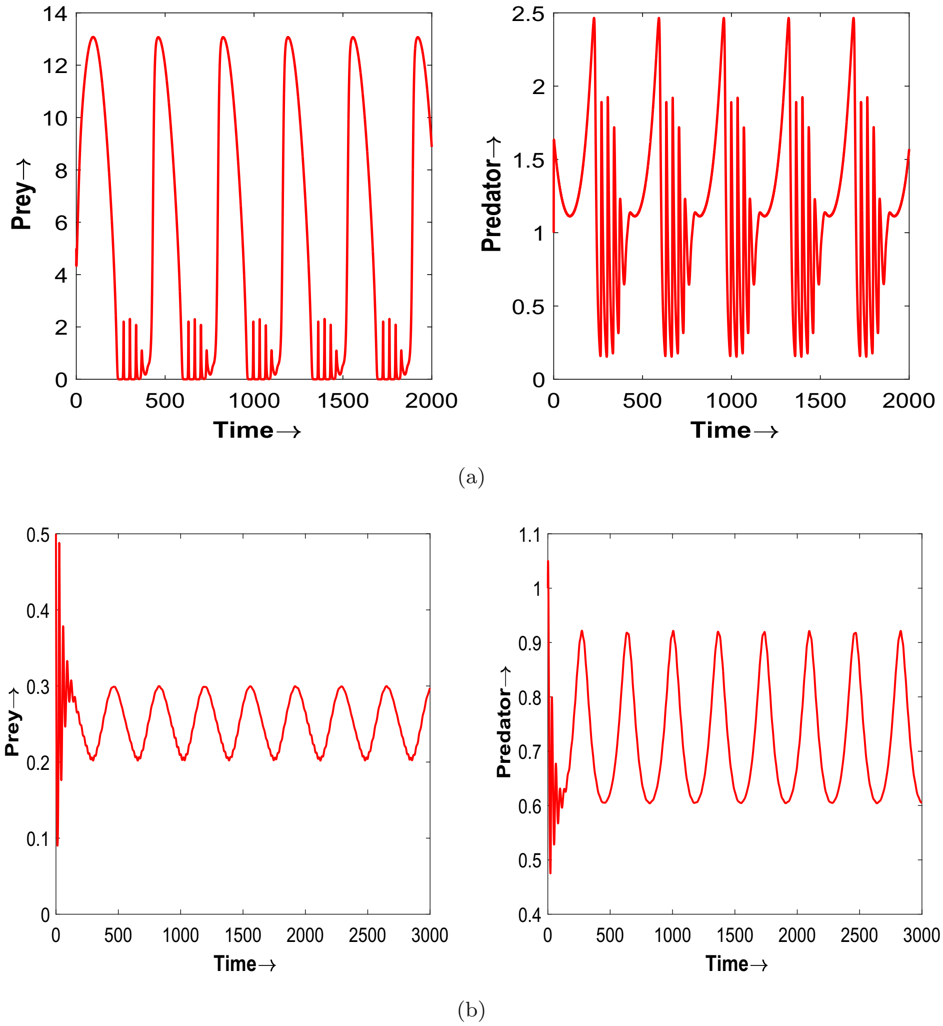
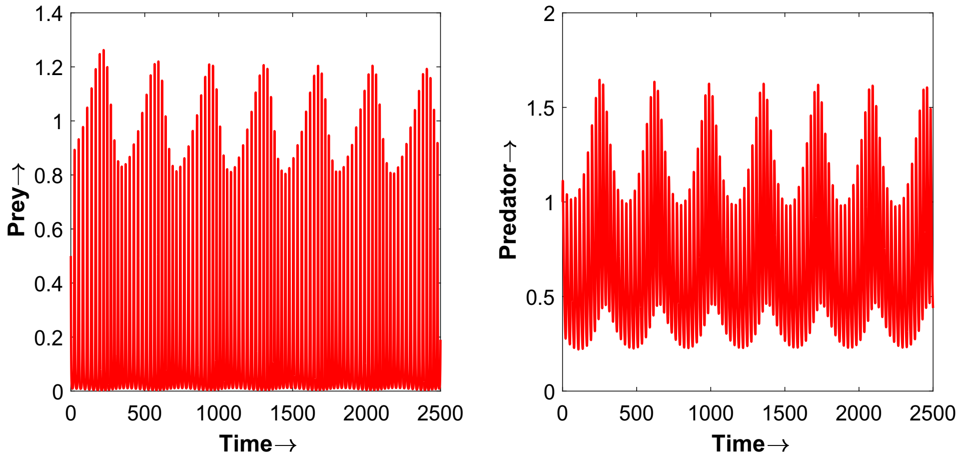
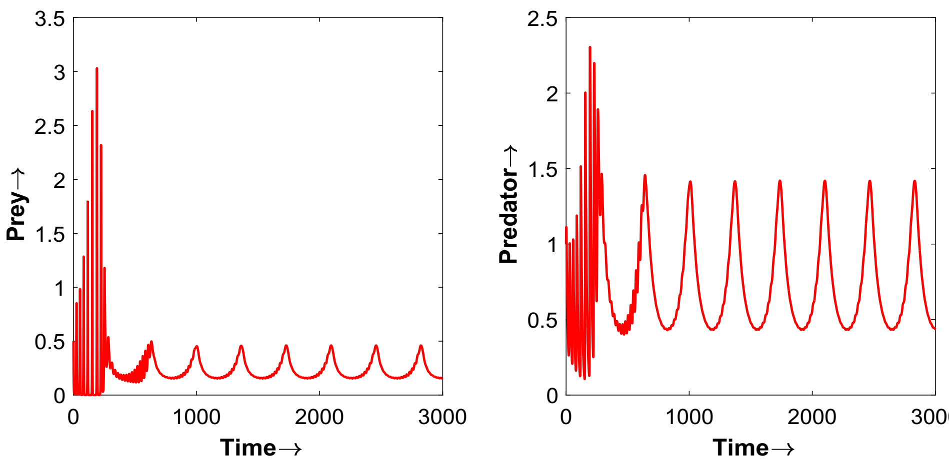


Fig. 11. Time series solutions of system (4.1) in the absence of time delays. Parameters are at the same values as in Fig. 3(d), and in (a) $m_{11} = 0.3$, $k_{11} = c_{11} = 0$, (b) $k_{11} = 3$, $m_{11} = 0.3$, $c_{11} = 0$.

subsystem in respect of slow variables.[74] The fast subsystem can be different states, rest and active, modulated by the slow variables. Whenever the slow variables visit the fast subsystem's different parameter areas containing different states,[75] bursting patterns appear. In the process of modulating the behaviors of the fast subsystem, the slow variables may not get feedback from the fast variables. Indeed, the slow variables do not depend on the fast ones, and change by their own. The appearance of bursting patterns can be eliminated by introducing seasonal variation in the level of fear also (see Fig. 11(b)).



(a)



(b)

Fig. 12. Time series solutions of system (4.1) in the absence of time delays. Parameters are at the same values as in Fig. 3(a), and in (a) $k_{11} = 3$, $m_{11} = c_{11} = 0$, (b) $k_{11} = 3$, $m_{11} = 0$, $c_{11} = 0.84$.

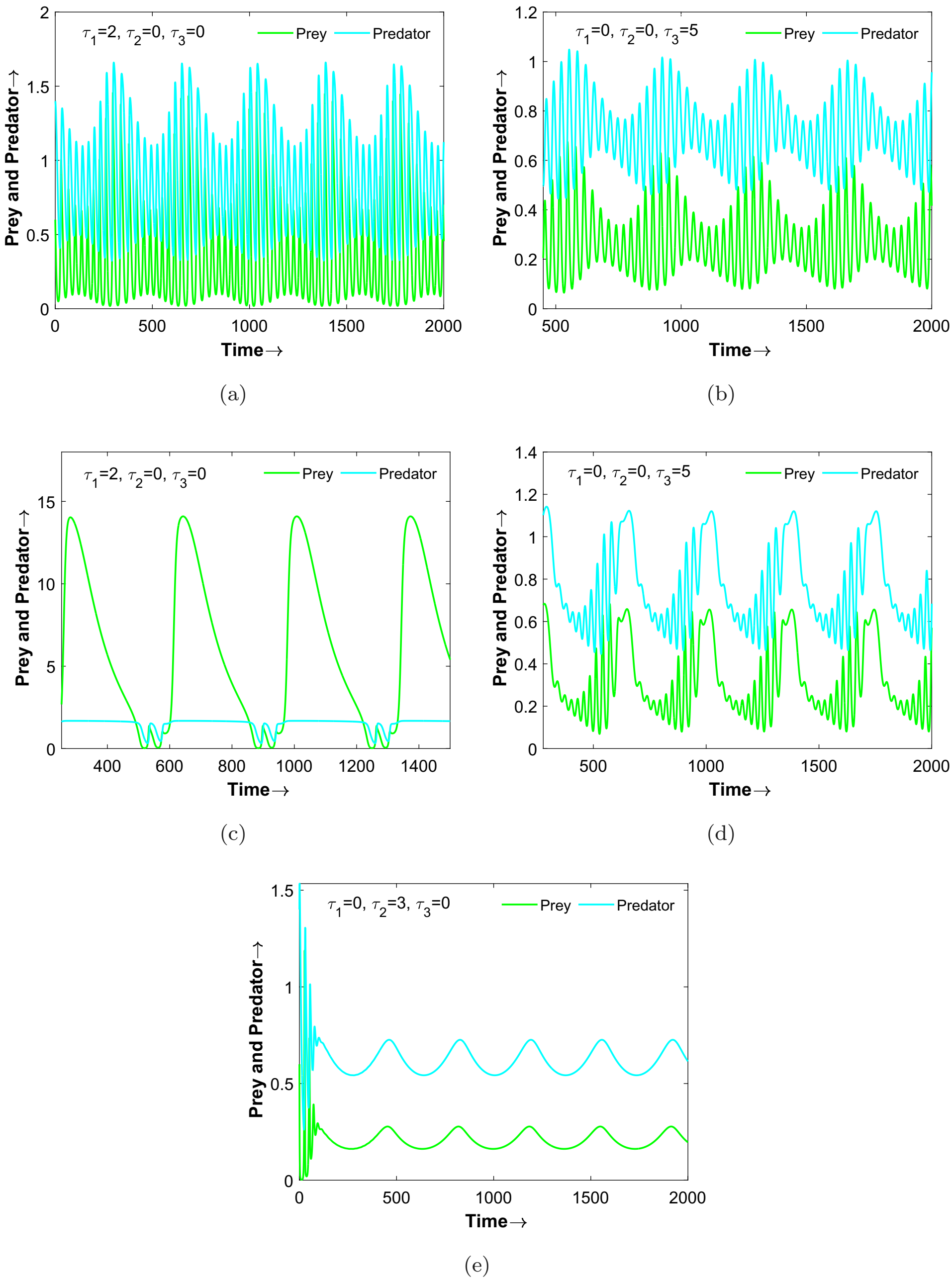


Fig. 13. Time series solutions of system (4.1) for different values of τ_1, τ_2 and τ_3. Parameters are at the same values as in Fig. 3(d) except in (a) $m_{11} = 0.05$, $k_{11} = c_{11} = 0$, (b) $k_{11} = 0 = m_{11}$, $c_{11} = 0.3$, (c) $k_{11} = 2$, $m_{11} = c_{11} = 0$, (d) $k_{11} = m_{11} = 0$, $c_{11} = 0.8$, (e) $m = 0.33$, $k_{11} = c_{11} = 0$, $m_{11} = 0.32$.

We also see the effect of seasonal forcing when the autonomous system (2.1) is in oscillatory state, Fig. 12. We find that if the system without seasonality is in unstable mode, then the seasonal variations in the level of fear generates higher periodic solutions, Fig. 12(a). However, seasonal forcing in the hunting cooperation plays a great role by bringing the system back to exhibit simple periodic solution in place of higher periodic solutions, Fig. 12(b).

Now, we observe the behavioral change of time series solutions for delay nonautonomous system (4.1). We see that if the delayed system (3.1) exhibits limit cycle oscillations due to delay involved in fear (or cooperation), then seasonal variation in refuge (or cooperation) induces higher periodic solutions (see Figs. 13(a) and 13(b)). On the other hand, keeping delayed system (3.1) in oscillatory state due to τ_1 (or τ_3), we find that the seasonal forcing in the fear (or cooperation) parameter can give rise to complex bursting patterns (see Figs. 13(c) and 13(d), respectively). Further, we note that if the original system (2.1) is in unstable state (see Fig. 3(a)), then delay in refuge (τ_2) destroys the persistent oscillations and stabilize the system (see Fig. 7(e)) whereas seasonality in refuge again induces periodic oscillations (see Fig. 13(e)).

6. Conclusion and Discussion

In this paper, we have investigated a predator–prey model with the effects of fear of predator, prey refuge, and hunting cooperation by predator. We have seen the effects of these three ecologically important parameters on the dynamical behaviors of predator–prey system. The sensitivity results confirm that refuge taken by prey help them to survive while fear of predator and hunting cooperation can cause decline in the prey population. These show that if the levels of fear and hunting cooperation are too high, it is only the refuge behavior of prey which can prevent extinction of prey population in the ecological community. We found that the fear of predator and hunting cooperation have destabilizing effects on the dynamics of system, whereas prey refuge stabilize an otherwise unstable system. Looking at the combined actions of these features of ecological community, we observed that if fear of predator and hunting cooperation are low, the system attains stable coexistence of prey and predator. But, the system loses its stability and exhibits persistent oscillations whenever fear and cooperation are much higher. Further, we noted that if only a small portion of prey population is taking refuge, then fear of predator always keep the system in unstable mode. However, if the refuge level is above certain value, fear of predator cannot break stability of the system.

Next, we see the effects of time delays involved in the processes of fear, refuge and hunting cooperation. First, we set the system in stable state in the absence of time delays and see the impacts of single as well as different combinations of time delays. The simulation results show that the delay in fear makes the system unstable. But, higher values of this delay terminate limit cycle oscillations and push back the system to stable state. Similar behavior is noted for the delay in cooperation. Importantly, if the system shows limit cycle oscillations due to the presence of any of the delay factors, then the other delay factor has capability to destroy the oscillations and drive the system to a stable state. However, if the system in the absence of time delays produces limit cycle oscillations, then the delay in cooperation can induce multiple stability switches and system showcases complex behaviors including higher periodic oscillations and chaos. On the other hand, delay involved in the process of taking refuge has tendency to stabilize an otherwise unstable system.

Considering seasonal changes in the level of fear, prey refuge, and hunting cooperation, we found that the nonautonomous system generates periodic solution due to lower strength of seasonality in refuge, while the corresponding autonomous system exhibits stable coexistence. However, on increasing the strength of seasonality in refuge, the nonautonomous system shows complex bursting patterns. The bursting patterns induced by higher strength of seasonality in prey refuge are replaced by a simple periodic state on introducing seasonality in the level of fear. The emergence of higher periodic solutions is observed due to seasonality in the level of fear if the autonomous system is at unstable state. But, on introducing seasonality in the hunting cooperation, higher periodicity is replaced by periodicity. Finally, we see the combined effects of time delays and seasonality on the dynamics of predator-prey interactions. Our simulation results showed that seasonality in prey refuge and hunting cooperation can generate higher periodic solutions whenever delayed unforced system produces limit cycle oscillations due to presence of time delays in fear and hunting cooperation, respectively. However, higher strength of seasonality in fear and cooperation induce complex bursting patterns whenever the delayed system is in unstable state due to time lags in the respective processes. We also observe that delay in refuge stabilize an unstable system while the action of seasonality in the refuge behavior causes existence of periodic solution.

Biologically, above results imply that the avoiding/anti-predator behavior prevents prey species from extinction due to the level of fear and group forming ability of predator. Consequently, the combined effects of these three important biological phenomena maintain the biodiversity. Moreover, the time required for assessing the predation risk by prey and to form groups by the predators makes a situation so that populations density fluctuates from a stable state, whereas more time lags again push the fluctuating biomass of species to a balanced state. Furthermore, the time to form a hunting group by the predators pushes the simple population density fluctuation into an irregular fluctuation, which is more accurate to natural environment. We also note that the time lag in the process of taking refuge after realizing the attack cue of predator makes a system stable from the oscillating situation. Due to the environmental factors, the effects of fear, refuge and cooperation vary in time. Changes in the level of fear by time exhibit higher order fluctuations of population density whereas seasonal changes of cooperation push the population density into simple fluctuation. On the other hand, seasonal changes of refuge shows another kind of populations density fluctuation known as bursting patterns, which is controlled by the time varying level of fear. Overall, our results show that the three ecologically important factors — fear, refuge, and cooperation, the delay effects on these phenomena, and the seasonality in the respective parameters, play crucial roles in the persistence/extinction of species, and hence affect the biodiversity of the ecosystem.

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Appendix A

To determine the nature of equilibrium E^*, we require the signs of the real parts of the roots of the characteristic equation (2.9). Let $\lambda(m) = u(m) + iv(m)$ be the eigenvalues of the characteristic equation (2.9). Substituting this value in Eq. (2.9), and separating real and imaginary parts, we get

$$u^2 - v^2 + A_1 u + A_2 = 0, \tag{A.1}$$

$$2uv + A_1 v = 0. \tag{A.2}$$

A necessary condition for the change of stability through the equilibrium E^* is that the characteristic equation (2.9) should have purely imaginary roots. We set $m = m^c$ such that $u(m^c) = 0$, and put $u = 0$ in Eqs. (A.1) and (A.2). Then, we have

$$-v^2 + A_2 = 0, \tag{A.3}$$

$$A_1 v = 0, \quad v \neq 0. \tag{A.4}$$

From Eqs. (A.3) and (A.4), we have $A_1(m^c) = 0$ and $v(m^c) = \sqrt{A_2(m^c)}$, which implies $\lambda(m^c) = i\sqrt{A_2(m^c)}$.

The eigenvalues of the characteristic equation (2.9) are $\lambda_{1,2} = \frac{-A_1 \pm \sqrt{A_1^2 - 4A_2}}{2}$. Here, A_1 and A_2 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 $A_1(m^c) = 0$ and $A_2(m^c) > 0$. Therefore, the positive real parts of these eigenvalues change the sign when m passes through m^c. Consequently, the system switches its stability provided that the transversality condition is satisfied.

Differentiating Eqs. (A.1) and (A.2) with respect to m, and put $u = 0$, we have

$$A_1 \frac{du}{dm} - 2v \frac{dv}{dm} = -\frac{dA_2}{dm},$$

$$2v \frac{du}{dm} + A_1 \frac{dv}{dm} = -v \frac{dA_1}{dm}.$$

Solving the above system of equations, we have

$$\left[\frac{d\mathrm{Re}(\lambda(m))}{dm}\right]_{m=m^c} = -\left[\frac{2v^2 \frac{dA_1}{dm} + A_1 \frac{dA_2}{dm}}{A_1^2 + 4v^2}\right]_{m=m^c}.$$

Since at $m = m^c$, $A_1 = 0$, we have

$$\left[\frac{d\mathrm{Re}(\lambda(m))}{dm}\right]_{m=m^c} = -\frac{1}{2}\left[\frac{dA_1}{dm}\right]_{m=m^c} \neq 0$$

provided $[\frac{dA_1}{dm}]_{m=m^c} \neq 0$.

Now, we discuss the direction and stability properties of the bifurcating periodic solutions originating from the equilibrium point E^* via Hopf-bifurcation. For this, we calculate the first Lyapunov coefficient.[76]

First, we transform the equilibrium point $E^* = (N^*, P^*)$ of the system (2.1) into the origin by letting $x_1 = N - N^*$ and $x_2 = P - P^*$. Then, the system (2.1) takes the form

$$\begin{aligned}
\frac{dx_1}{dt} &= \frac{r_0(x_1 + N^*)}{1 + k(x_2 + P^*)} - r_1(x_1 + N^*) - r_2(x_1 + N^*)^2 \\
&\quad - \alpha\{1 - m(x_2 + P^*)\}\{1 + c(x_2 + P^*)\}(x_1 + N^*)(x_2 + P^*), \\
\frac{dx_2}{dt} &= \alpha_1 \alpha\{1 - m(x_2 + P^*)\}\{1 + c(x_2 + P^*)\}(x_1 + N^*)(x_2 + P^*) - d_1(x_2 + P^*) \\
&\quad - d_2(x_2 + P^*)^2.
\end{aligned} \tag{A.5}$$

Expanding Taylor's series of system (A.5) at $(x_1, x_2) = (0, 0)$ up to terms of order three, and neglecting higher order terms, we get

$$\begin{aligned}\dot{x}_1 &= S_{10}x_1 + S_{01}x_2 + S_{20}x_1^2 + S_{02}x_2^2 + S_{11}x_1x_2\\&\quad + S_{30}x_1^3 + S_{21}x_1^2x_2 + S_{12}x_1x_2^2 + S_{03}x_2^3 + \mathcal{O}(|x|^4)\\\dot{x}_2 &= W_{10}x_1 + W_{01}x_2 + W_{20}x_1^2 + W_{02}x_2^2 + W_{11}x_1x_2 + W_{30}x_1^3\\&\quad + W_{21}x_1^2x_2 + W_{12}x_1x_2^2 + W_{03}x_2^3 + \mathcal{O}(|x|^4),\end{aligned} \tag{A.6}$$

where

$$\begin{aligned}&S_{10} = a_{11}, \quad S_{01} = a_{12}, \quad W_{10} = a_{21}, \quad W_{01} = a_{22},\\&S_{30} = 0, \quad S_{21} = 0, \quad W_{20} = W_{21} = W_{30} = 0,\\&S_{20} = -r_2, \quad S_{02} = \frac{r_0k^2N^*}{(1+kP^*)^3} - \alpha(c - m - 3mcP^*)N^*,\\&S_{11} = -\frac{r_0k}{(1+kP^*)^2} - \alpha\{1 + (2c - 2m - 3mcP^*)P^*\},\\&S_{12} = \frac{r_0k^2}{(1+kP^*)^3} - \alpha(c - m - 3mcP^*), \quad S_{03} = -\frac{r_0k^3N^*}{(1+kP^*)^4} + \alpha cmN^*,\\&W_{02} = \alpha_1\alpha N^*(c - m - 3mcP^*) - d_2, \quad W_{11} = \alpha_1\alpha\{1 + (2c - 2m - 3mcP^*)P^*\},\\&W_{12} = \alpha_1\alpha(c - m - 3mcP^*), \quad W_{03} = -\alpha_1\alpha cmN^*.\end{aligned}$$

Thus, system (A.6) can be written as

$$\dot{Q} = J_{E^*}Q + F'(Q), \tag{A.7}$$

where

$$Q = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}, \quad F' = \begin{pmatrix} F_1 \\ F_2 \end{pmatrix} = \begin{pmatrix} S_{20}x_1^2 + S_{02}x_2^2 + S_{11}x_1x_2 + S_{12}x_1x_2^2 + S_{03}x_2^3 \\ W_{02}x_2^2 + W_{11}x_1x_2 + W_{12}x_1x_2^2 + W_{03}x_2^3 \end{pmatrix}.$$

The eigenvector V^* of the Jacobian J_{E^*} corresponding to the eigenvalue $i\omega_0$ at $m = m^c$ is $V^* = (S_{01}, i\omega_0 - S_{10})^T$, where $\omega_0 = \sqrt{A_2(m^c)}$.

Now, we define

$$P = (\mathrm{Re}(V^*), -\mathrm{Im}(V^*)) = \begin{pmatrix} S_{01} & 0 \\ -S_{10} & -\omega_0 \end{pmatrix}.$$

Let $Q = PZ$ and $Z = P^{-1}Q$, where $Z = (z_1, z_2)^T$. Under this transformation, system (A.7) becomes

$$\dot{Z} = (P^{-1}J_{E^*}P)Z + P^{-1}F'(PZ).$$

This can be written as

$$\begin{pmatrix} \dot{z}_1 \\ \dot{z}_2 \end{pmatrix} = \begin{pmatrix} 0 & -\omega_0 \\ \omega_0 & 0 \end{pmatrix}\begin{pmatrix} z_1 \\ z_2 \end{pmatrix} + \begin{pmatrix} G^1(z_1, z_2; m = m^c) \\ G^2(z_1, z_2; m = m^c) \end{pmatrix}, \tag{A.8}$$

where G^1 and G^2 are nonlinear in z_1 and z_2, and are given by

$$G^1(z_1, z_2; m = m^c) = \frac{1}{S_{01}}F_1, \quad G^2(z_1, z_2; m = m^c) = -\frac{1}{\omega_0 S_{01}}(S_{10}F_1 + S_{01}F_2),$$

with

$$\begin{aligned} F_1 &= (S_{20}S_{01}^2 - S_{11}S_{01}S_{10} + S_{02}S_{10}^2)z_1^2 + \omega_0(2S_{02}S_{10} - S_{11}S_{01})z_1z_2 + \omega_0^2 S_{02}z_2^2 \\ &\quad + (S_{12}S_{01}S_{10}^2 - S_{03}S_{10}^3)z_1^3 + \omega_0(2S_{12}S_{10}S_{01} - 3S_{03}S_{10}^2)z_1^2z_2 \\ &\quad + \omega_0^2(S_{12}S_{01} - 3S_{03}S_{10})z_1z_2^2 - \omega_0^3 S_{03}z_2^3, \\ F_2 &= (W_{02}S_{10}^2 - W_{11}S_{01}S_{10})z_1^2 + \omega_0(2W_{02}S_{10} - W_{11}S_{01})z_1z_2 + \omega_0^2 W_{02}z_2^2 \\ &\quad + (W_{12}S_{01}S_{10}^2 - W_{03}S_{10}^3)z_1^3 + \omega_0(2W_{12}S_{10}S_{01} - 3W_{03}S_{10}^2)z_1^2z_2 \\ &\quad + \omega_0^2(W_{12}S_{01} - 3W_{03}S_{10})z_1z_2^2 - \omega_0^3 W_{03}z_2^3. \end{aligned}$$

Now, we calculate the first Lyapunov coefficient, based on the normal form (A.8), which determines the stability and direction of periodic solution. The first Lyapunov coefficient is obtained as

$$\begin{aligned} l_1 &= \frac{1}{16}[G^1_{z_1z_1z_1} + G^1_{z_1z_2z_2} + G^2_{z_1z_1z_2} + G^2_{z_2z_2z_2}] \\ &\quad + \frac{1}{16\omega_0}[G^1_{z_1z_2}(G^1_{z_1z_1} + G^1_{z_2z_2}) - G^2_{z_1z_2}(G^2_{z_1z_1} + G^2_{z_2z_2}) \\ &\quad - G^1_{z_1z_1}G^2_{z_1z_1} + G^1_{z_2z_2}G^2_{z_2z_2}], \end{aligned}$$

where all the partial derivatives are calculated at the bifurcation point, i.e., $(z_1, z_2; m) = (0, 0; m^c)$. The Hopf-bifurcation is supercritical if $l_1 < 0$ and subcritical if $l_1 > 0$.[76] It is to be noted that when $l_1 = 0$, system (2.1) exhibits generalized Hopf-bifurcation (or Bautin bifurcation) at which the equilibrium E^* has a pair of purely imaginary eigenvalues. The generalized Hopf-bifurcation point separates branches of subcritical and supercritical Hopf-bifurcation in the parameter plane.

Appendix B

At first, we change the variables N and P in such a way that they remain positive for all $t > 0$ as the solutions of system (4.1) are always positive. For this, we consider the following transformations:

$$N(t) = e^{x(t)}, \quad P(t) = e^{y(t)}. \tag{B.1}$$

Then, system (4.1) becomes

$$\begin{aligned} \frac{dx(t)}{dt} &= \frac{r_0}{1 + k(t)e^{y(t-\tau_1)}} - r_1 - r_2 e^{x(t)} \\ &\quad - \alpha(1 - m(t)e^{y(t-\tau_2)})[1 + c(t)e^{y(t-\tau_3)}]e^{y(t)}, \\ \frac{dy(t)}{dt} &= \alpha_1\alpha(1 - m(t)e^{y(t-\tau_2)})[1 + c(t)e^{y(t-\tau_3)}]e^{x(t)} - d_1 - d_2 e^{y(t)}. \end{aligned} \tag{B.2}$$

Consider the set

$$X = Z = \{(x,y)^T \in C(\mathbb{R},\mathbb{R}^2) \,|\, x(t+\omega) = x(t), y(t+\omega) = y(t)\}$$

and the norm defined by

$$\|(x,y)\| = \max_{t\in[0,\omega]} |x(t)| + \max_{t\in[0,\omega]} |y(t)|.$$

Note that X and Z are both Banach spaces with respect to the above norm $\|\cdot\|$.

Let,

$$M\begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} \overline{M}_1(t) \\ \overline{M}_2(t) \end{bmatrix} = \begin{bmatrix} \dfrac{r_0}{1+k(t)e^{y(t-\tau_1)}} - r_1 - r_2 e^{x(t)} \\ \quad - \alpha(1-m(t)e^{y(t-\tau_2)})[1+c(t)e^{y(t-\tau_3)}]e^{y(t)} \\ \alpha_1\alpha(1-m(t)e^{y(t-\tau_2)})[1+c(t)e^{y(t-\tau_3)}]e^{x(t)} - d_1 - d_2 e^{y(t)} \end{bmatrix}$$

and

$$L\begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} \dfrac{dx}{dt} \\ \dfrac{dy}{dt} \end{bmatrix}, \quad P\begin{bmatrix} x \\ y \end{bmatrix} = Q\begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} \dfrac{1}{\omega}\displaystyle\int_0^\omega x(t)dt \\ \dfrac{1}{\omega}\displaystyle\int_0^\omega y(t)dt \end{bmatrix}, \quad \begin{bmatrix} x \\ y \end{bmatrix} \in X.$$

Then,

$$\mathrm{Ker}(L) = \{(x,y) \in X : (x,y) = (h_1,h_2) \in \mathbb{R}^2\},$$
$$\mathrm{Im}(L) = \left\{(x,y) \in Z : \int_0^\omega x(t)dt = 0, \int_0^\omega y(t)dt = 0\right\}$$

and $\dim\mathrm{Ker}(L) = 2 = \mathrm{codim}\,\mathrm{Im}(L)$.

Since $\mathrm{Im}(L)$ is closed in Z, L is a Fredholm mapping of index zero. It is easy to show that P and Q are continuous projections such that,

$$\mathrm{Im}(P) = \mathrm{Ker}(L), \quad \mathrm{Im}(L) = \mathrm{Ker}(Q) = \mathrm{Im}(I-Q).$$

However, the generalized inverse to L, $K_P : \mathrm{Im}(L) \to \mathrm{Dom}(L) \cap \mathrm{Ker}(P)$ exists and is given by

$$K_P\begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} \displaystyle\int_0^t x(s)ds - \frac{1}{\omega}\int_0^\omega \int_0^t x(s)dsdt \\ \displaystyle\int_0^t y(s)ds - \frac{1}{\omega}\int_0^\omega \int_0^t y(s)dsdt \end{bmatrix}.$$

Thus,

$$QM\begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} \frac{1}{\omega}\int_0^\omega \overline{M}_1(t)dt \\ \frac{1}{\omega}\int_0^\omega \overline{M}_2(t)dt \end{bmatrix}$$

and

$$K_P(I-Q)M\begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} \int_0^t \overline{M}_1(s)ds - \frac{1}{\omega}\int_0^\omega\int_0^t \overline{M}_1(s)dsdt - \left(\frac{t}{\omega}-\frac{1}{2}\right)\int_0^\omega \overline{M}_1(t)dt \\ \int_0^t \overline{M}_2(s)ds - \frac{1}{\omega}\int_0^\omega\int_0^t \overline{M}_2(s)dsdt - \left(\frac{t}{\omega}-\frac{1}{2}\right)\int_0^\omega \overline{M}_2(t)dt \end{bmatrix}.$$

Clearly, QM and $K_P(I-Q)M$ are continuous. By Arzela–Ascoli theorem, it is easy to show that $\overline{K_P(I-Q)M(\overline{\Omega})}$ is compact and $QM(\overline{\Omega})$ is bounded for any open bounded set $\Omega \subset X$. Therefore, M is L-compact on $\overline{\Omega}$ for any open bounded set $\Omega \subset X$.

Now, we find an appropriate open bounded set Ω for the application of Continuation theorem. From the operator equation $Lx = \psi Mx$, $\psi \in (0,1)$, we have

$$\begin{aligned} \frac{dx}{dt} &= \psi\Bigg[\frac{r_0}{1+k(t)e^{y(t-\tau_1)}} - r_1 - r_2 e^{x(t)} \\ &\quad - \alpha(1-m(t)e^{y(t-\tau_2)})[1+c(t)e^{y(t-\tau_3)}]e^{y(t)}\Bigg], \\ \frac{dy}{dt} &= \psi[\alpha_1\alpha(1-m(t)e^{y(t-\tau_2)})[1+c(t)e^{y(t-\tau_3)}]e^{x(t)} - d_1 - d_2e^{y(t)}]. \end{aligned} \tag{B.3}$$

Assume that $(x(t), y(t)) \in X$ is an arbitrary solution of system (B.2) for a certain $\psi \in (0,1)$. Integrating on both sides of (B.3) over the interval $[0,\omega]$, we have

$$\begin{aligned} r_1\omega &= \int_0^\omega \Bigg[\frac{r_0}{1+k(t)e^{y(t-\tau_1)}} - r_2e^{x(t)} \\ &\quad - \alpha(1-m(t)e^{y(t-\tau_2)})[1+c(t)e^{y(t-\tau_3)}]e^{y(t)}\Bigg]dt, \end{aligned} \tag{B.4}$$

$$d_1\omega = \int_0^\omega [\alpha_1\alpha(1-m(t)e^{y(t-\tau_2)})[1+c(t)e^{y(t-\tau_3)}]e^{x(t)} - d_2e^{y(t)}]dt. \tag{B.5}$$

Using Eqs. (B.3)–(B.5), we obtain

$$\int_0^\omega \left|\frac{dx}{dt}\right|dt \le 2r_1\omega, \tag{B.6}$$

$$\int_0^\omega \left|\frac{dy}{dt}\right|dt \le 2d_1\omega. \tag{B.7}$$

Since $(x, y) \in X$, there exist $\xi_i, \eta_i \in [0, \omega]$ $(i = 1, 2)$ such that

$$x(\xi_1) = \min_{t\in[0,\omega]} x(t), \quad x(\eta_1) = \max_{t\in[0,\omega]} x(t),$$
$$y(\xi_2) = \min_{t\in[0,\omega]} y(t), \quad y(\eta_2) = \min_{t\in[0,\omega]} y(t). \tag{B.8}$$

From Eqs. (B.4) and (B.8), we get

$$r_1\omega \le \int_0^\omega (r_0 - r_2 e^{x(\xi_1)})dt \Rightarrow x(\xi_1) \le \ln\left[\frac{r_0 - r_1}{r_2}\right]. \tag{B.9}$$

Hence, from (B.6) and (B.9), we have for some H_1

$$x(t) \le x(\xi_1) + \int_0^\omega \left|\frac{dx}{dt}\right| dt \le \ln\left[\frac{r_0 - r_1}{r_2}\right] + 2r_1\omega = H_1.$$

From Eqs. (B.5) and (B.8), we get

$$d_1\omega \le \int_0^\omega \alpha_1\alpha(1 + ce^{y(\eta_2)})e^{H_1} dt \Rightarrow y(\eta_2) \ge \ln\left[\frac{1}{\overline{c}}\left(\frac{d_1}{\alpha_1\alpha e^{H_1}} - 1\right)\right]. \tag{B.10}$$

Hence, from (B.6) and (B.10), we have for some L_2

$$y(t) \ge y(\eta_2) - \int_0^\omega \left|\frac{dy}{dt}\right| dt \ge \ln\left[\frac{1}{\overline{c}}\left(\frac{d_1}{\alpha_1\alpha e^{H_1}} - 1\right)\right] - 2d_1\omega = L_2.$$

From Eqs. (B.4) and (B.8), we get

$$r_1\omega \le \int_0^\omega \frac{r_0}{1 + ke^{y(\xi_2)}} dt \Rightarrow y(\xi_2) \le \ln\left[\frac{1}{\overline{k}}\left(\frac{r_0}{r_1} - 1\right)\right]. \tag{B.11}$$

Hence, from (B.6) and (B.11), we have for some H_2

$$y(t) \le y(\xi_2) + \int_0^\omega \left|\frac{dy}{dt}\right| dt \le \ln\left[\frac{1}{\overline{k}}\left(\frac{r_0}{r_1} - 1\right)\right] + 2d_1\omega = H_2.$$

From Eqs. (B.4) and (B.8), we get

$$r_1\omega \le \int_0^\omega \left(\frac{r_0}{1 + ke^{H_2}} - r_2 e^{x(\eta_1)} - \alpha[1 + ce^{H_2}]e^{H_2}\right) dt$$
$$\Rightarrow x(\eta_1) \ge \ln\left[\frac{1}{r_2}\left(\frac{r_0}{1 + \overline{k}e^{H_2}} - \alpha[1 + \overline{c}e^{H_2}]e^{H_2} - r_1\right)\right]. \tag{B.12}$$

Hence, from (B.6) and (B.12), we have for some L_1

$$x(t) \ge x(\eta_1) - \int_0^\omega \left|\frac{dx}{dt}\right| dt \ge \ln\left[\frac{1}{r_2}\left(\frac{r_0}{1 + \overline{k}e^{H_2}} - \alpha[1 + \overline{c}e^{H_2}]e^{H_2} - r_1\right)\right]$$
$$- 2r_1\omega = L_1.$$

Now, for some $\overline{B}_1$ and $\overline{B}_2$, we choose

$$\max_{t\in[0,\omega]} |x(t)| \le \max\{|H_1|, |L_1|\} = \overline{B}_1,$$
$$\max_{t\in[0,\omega]} |y(t)| \le \max\{|H_2|, |L_2|\} = \overline{B}_2. \tag{B.13}$$

Clearly, $\overline{B}_1$ and $\overline{B}_2$ are independent of ψ. Now, we consider the following algebraic equations:

$$\frac{r_0}{1+\overline{k}e^y} - r_1 - r_2e^x - \alpha(1-\overline{m}e^y)[1+\overline{c}e^y]e^y = 0,$$
$$\alpha_1\alpha(1-\overline{m}e^y)[1+\overline{c}e^y]e^x - d_1 - d_2e^y = 0. \tag{B.14}$$

Let $\overline{B} = \overline{B}_1 + \overline{B}_2 + \epsilon$, where ϵ is sufficiently large such that for each solution (x^*, y^*) of the above system of algebraic equations (B.14) satisfies $\|(x^*, y^*)\| < \overline{B}$ provided that the system (B.14) has one or a number of solutions.

Let us define $\Omega = \{(x,y)^T \in X : \|(x,y)^T\| < \overline{B}\}$. Then, for each $\psi \in (0,1)$, $x \in \partial\Omega \cap \mathrm{Dom}(L)$ and $Lx \neq \psi Mx$. Therefore, the first condition of Lemma 4.1 is satisfied.

Whenever $(x,y) \in \partial\Omega \cap \mathrm{Ker}(L) = \partial\Omega \cap \mathbb{R}^2$, (x,y) is a constant vector with $\|(x,y)\| = |x| + |y| = \overline{B}$.

If the system (B.14) has at least one solution, we have

$$QM\begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} \dfrac{r_0}{1+\overline{k}e^y} - r_1 - r_2e^x - \alpha(1-\overline{m}e^y)[1+\overline{c}e^y]e^y \\ \alpha_1\alpha(1-\overline{m}e^y)[1+\overline{c}e^y]e^x - d_1 - d_2e^y \end{bmatrix} \neq \begin{bmatrix} 0 \\ 0 \end{bmatrix}.$$

Hence, the second condition of Lemma 4.1 is also satisfied.

Now, we define the homomorphism $J\colon \mathrm{Im}(Q) \to \mathrm{Ker}(L)$. Since $\mathrm{Im}(Q) = \mathrm{Ker}(L)$, J is the identity mapping and hence J is an isomorphism. By direct calculation, we have

$$\deg\{JQM, \Omega \cap \mathrm{Ker}(L), 0\} = \sum_{z_i^* \in QM^{-1}(0)} \mathrm{sgn} JQM(z_i^*) \neq 0.$$

Thus, the third condition of Lemma 4.1 is verified. Therefore, we can conclude that the system (B.2) has at least one positive ω-periodic solution in $\Omega \cap \mathrm{Dom}(L)$. Hence, the system (4.1) has at least one periodic solution.