

Dynamics of a predator-prey system with fear and group defense

Sourav Kumar Sasmal*, Yasuhiro Takeuchi

Department of Physics and Mathematics, Aoyama Gakuin University, Kanagawa 252-5258, Japan



ARTICLE INFO

Article history:

Received 3 April 2019
Available online 5 September 2019
Submitted by Y. Yamada

Keywords:

Fear effect
Group defense
Predator-prey system
Predator-taxis sensitivity

ABSTRACT

We study the dynamics of a prey-predator interaction model that incorporates: (1) reduction of prey growth rate, in the form of fear effect, in presence of predator; and (2) group defense of prey, against predation, by using the Monod-Haldane type functional response. Moreover, we interrelate these two factors, through the predator-taxis sensitivity, as the total time or energy for foraging and defense is constant for prey. If the prey invests more time or energy for group defense, then reproduction may decrease due to that investment. We provide detailed mathematical results, including, basic dynamical properties, existence of positive equilibria, asymptotic stability of all equilibria, Hopf-bifurcation, direction and stability of bifurcated periodic solutions. We also provide some global features and possible occurrence of multi-stability in our model. Furthermore, we perform detailed numerical simulations to validate our mathematical results numerically. Our mathematical and numerical results suggest that the predator-taxis sensitivity should be less than some threshold density, for possible survivability of predator. We provide some sensitivity analysis of our model solutions with respect to the three important model parameters, namely, the predator-taxis sensitivity, level of fear, and the tolerance limit of predator. We can observe that the perturbation of the tolerance limit of predator has the greatest influence over model dynamics. Initially, the predator-taxis sensitivity has a positive effect on prey as its decreases the killing rate, however, for long run, its effect is negative on both the solutions, as it decreases the growth rate of prey, which affects overall fitness of both the populations. Our results may provide some useful biological insights on predator-prey interactions.

© 2019 Elsevier Inc. All rights reserved.

1. Introduction

One of the central topics in ecology and evolutionary biology, is to study the different mechanisms related to the predator-prey interaction. Among these mechanisms, predation is relatively easy to observe in nature, as it involves direct killing, thus removing individuals from the population [12,16]. Consequently, predation is the most powerful force in a prey-predator interaction, particularly in altering behavior, which

* Corresponding author.

E-mail addresses: sourav.sasmal@gmail.com, sourav.sasmal@gem.aoyama.ac.jp (S.K. Sasmal), takeuchi@gem.aoyama.ac.jp (Y. Takeuchi).

can shape traits, associated with both prey and predator, but especially traits related to prey's behavior [23]. Every prey species adjust their activity budgets, and show a variety of anti-predator responses, like change of habitat (move from high-risk habitat and relocate to low-risk habitat), foraging activity (reduction of foraging activity to reduce the probability of detection by predators), vigilance (increase vigilance to detect a predator more in advance), some physiological changes, defense and grouping tendencies, etc. [32,16,27].

It is well established that prey grouping is a form of anti-predator behavior in many prey species [25, 13], and some studies also examined that how group size responds to the predation risk [5,9,14]. The advance predator detection is the main benefit when the preys are in a group. However, sometimes larger groups are more detectable by predators. It is widely accepted that increasing the defense against the predator is costly and leads to a decline preys foraging intake, and the selection will favor individuals who optimally balance the benefits of risk reduction against its costs [20]. Therefore, many prey (like ungulates, *Ungulata*) gather into large groups to reduce the individual defense cost by using “many eyes” effects and enhance their survival through the “safety in number” [4]. Ungulates show many anti-predator responses, however these can be categorized into two, reduction of probability of detection by the predators and enhancement the probability of surviving after detection by a predator by increasing their group defense or group size [22]. Group defense and the risk of predation have been studied in many natural populations, including birds, fish, and invertebrates (sparrowhawks, *Accipiter niscus*, preying on redshanks, *Tringa tetanus* [17]; cichlids, *Aequidens pulcher*, preying on guppies, *Poecilia reticulate* [21]; wasps preying on orb-weaving spiders, *Metapeira incrassate* [31]) as well as mammalian predators and prey (cheetahs, *Acinonyx jubatus*, preying on gazelles, *Gazella thompsoni* [18]; lions, *Panthera leo*, preying on mixed ungulate herds, [30]). Japanese honeybees form a “hot defensive ball” around the hornet to defend the attack [24].

In the present paper, we consider the group defense among preys as an anti-predator behavior of prey population. Mathematical model on group defense was first introduced by Freedman and Wolkowicz Freedman and Wolkowicz [19], after that several attempts have been made. The most common and simplest way to incorporate group defense is by considering Holling type IV functional response or Monod-Haldane functional Response [3,19]. In Holling type IV functional response predator cannot survive above some upper threshold of prey density. Another approach is to consider that the predation mostly occurs on the perimeter of the herd (prey gathers together to graze and that the outermost individuals suffering most by the predator attacks from outside), which is modeled by the square root term [1,33]. Here, we consider the Holling type IV functional response to incorporate the group defense of prey.

However, there are two important factors, namely energy and time limitations, which restraining wild animal activities. To survive under the risk of predation, prey may shorten its activity periods and sacrifice some of its foraging time to vigilance, however prey need to balance between defense time and foraging intake. Because, high level of anti-predator behavior over long time results shorten foraging and leads to starvation, which impacts on growth. Therefore, there are both costs and benefits for prey in prey defense. Here, we incorporate the cost as a form of growth reduction of prey due to predation fear. Predation extremely affects prey population, not only because it associates with direct killing but also predation fear is a predominant factor in the feeding ecology. Almost all aspects of prey biology may be affected due to predation fear [15], such as decreased feeding rate [8], altered diets [10], as well as the force to change the habitat, which may carry a high cost, especially if the new habitat is of suboptimal quality [7,2,17]. In order to survive under risk of predation, scared prey forage less, which forced them to adopt survival mechanisms like starvation, and could reduce their birth rate [12,16]. Sometimes higher level of anti-predator response causes prey to leave their habitat temporarily, which greatly affects juvenile prey's physical condition and harmful impact on their survival as adults [12,11]. As an anti-predator behavior bird flees away from their nests at the first sign of danger, which may increase their probability of survival in short-term but reduce their reproduction as a long-term cost, which may affect overall population [16].

Many biologists realized that in prey-predator interaction, the cost of fear should be incorporated along with direct predation [28]. However, due to the lack of field experimental evidence, this fear effect has

not been incorporated into mathematical models, except some recent studies [34,29]. Recent experiment by Zenette et al. [35], on song sparrows *Melospiza Melodia*, showed that the offspring production can be reduced up to 40% due to predation fear only, without direct killing. Prey-predator models with varieties of functional response have been studied in literature; however such functional responses only considered direct killing, no matter how complicated they are. Very few mathematical models are there, where this reduction of prey growth rate has been considered [34].

In the literature, authors only consider the group defense, which is beneficial for prey, as it decreases the rate of predation. However, defense is not always beneficial, as due to this investment, there may be a reduction in prey growth. Therefore, in the present study, we consider the reduction of prey growth rate, in the form of fear factor, in presence of group defense through Monod-Haldane type functional response. Our study objective includes, (i) What are the dynamical effects of growth rate reduction in the form of fear, when prey shows group defense as an anti-predator response? (ii) Moreover, we are interested in how these two factors are interrelated with each other through predator-taxis sensitivity? The remainder of the paper is organized as follows: Section 2 is designated for the development of our model, which considers both fear and group defense, and how they are interrelated through predator-taxis sensitivity. Detailed equilibrium analysis and their stability are given in the Section 3. In this section, we also discuss about some global features of the proposed model, multi-stability, direction and stability of Hopf-bifurcation, etc. Also, we validate our analytical results numerically in this section. Sensitivity of model solutions to some important model parameters is discussed in Section 4. The paper ends with the results and conclusions, which are presented in Section 5.

2. Formulation of mathematical model

First, we assume that the preys growth follows the logistic dynamics, which can be split into three different parts, namely, the birth, the natural death, and the density dependent death due to intra-specific competition among preys. Therefore, in the absence of predator, the prey dynamics is governed by the following ordinary differential equation

$$\frac{dx}{dt} = rx - d_1x - d_2x^2 \quad (2.1)$$

where x is the population density of prey, r is the birth rate of prey, d_1 is the natural death rate of prey, and d_2 is the death rate due to intra-prey competition. It is easy to show that the solution $x(t)$ for any positive initial value for (2.1) tends to 0 when $r \leq d_1$, that is, the prey always goes to extinction. Hereafter, we assume that $r > d_1$.

Next, in the presence of predator, we incorporate the predation term $p(x)$ in prey dynamics and also include the predator dynamics explicitly into (2.1). In this study, we consider prey group defense as an anti-predator response. Mainly two well known approaches are there to incorporate the group defense in predator-prey competition. One is by considering Holling type IV or Monod-Haldane type functional response [19] and another is to consider that the predation mostly occurs on the perimeter of herd which is modeled by the square root term [1,33]. Therefore, our general predator-prey model with group defense is given by

$$\begin{aligned} \frac{dx}{dt} &= rx - d_1x - d_2x^2 - p(x)y \\ \frac{dy}{dt} &= cp(x)y - m(y)y. \end{aligned} \quad (2.2)$$

Here, y is the density of predator population, c is the conversion efficiency from prey biomass to predator biomass and $m(y)$ is the death of predator, which could be density dependent or density independent. Here we consider density independent death rate of predator, i.e., $m(y) = m$. In this study, we consider the

group defense following Holling type *IV* functional response, i.e., $p(x) = \frac{\beta x}{a + bx + x^2}$, where β is the rate of predation, $a > 0$ is the half-saturation constant, and the parameter b is the tolerance limit of predator. The successful predation rate of predator decreases if the defense level or equivalently the tolerance limit of predator increases.

As we discussed in the introduction section, due to energy and time limitations, high level of anti-predator behavior over long time may have a cost also, which can reduce the prey growth rate. In fact, some field experiments suggest that the predation fear can significantly reduce the reproduction of prey [34]. Therefore, in the present study we incorporate the cost through predation fear, in the presence of predator population, which depends on predator population density. Thus, in the presence of predator population, we modify the above equation (2.2) by multiplying the reproduction term of prey rx by a factor $f(k, y) = \frac{1}{1 + ky}$ which accounts for the cost of anti-predator defense due to predation fear [34,29]. Thus our model (2.2) becomes

$$\begin{aligned}\frac{dx}{dt} &= rx f(k, y) - d_1 x - d_2 x^2 - p(x)y \\ \frac{dy}{dt} &= cp(x)y - m(y)y.\end{aligned}\quad (2.3)$$

Here, the parameter k refers to the level of fear which reflects the reduction of prey growth rate due to the anti-predator behavior. As k increases the growth rate of prey decreases. Moreover, in the current study, we consider d_1 and d_2 as constant. Although, without any direct experimental evidence, some research suggests that predator fear may lead to lower survival rates of adult preys, due to some physiological impacts when they are young [11]. Therefore, one may consider d_1 and d_2 as a function of predator density (e.g., d_1 and d_2 may be an increasing function of y).

In the above formulation, both the cost (in the form of fear factor) and benefit due to group defense are independent to each other. However, they may not be independent to each other, as total time and energy is limited. That is, if prey invest more time and energy for group defense then reproduction may decrease more due to that investment. Therefore, we interrelate these two factors through a parameter called predator-taxis sensitivity ' α '. As the predator-taxis sensitivity increases, in other words, when preys are more sensitive to predation, they will increase their group defense and successful predation rate will decrease. However, at the same time their reproduction rate also decreases as foraging time and energy decrease, in other words level of fear increases. Here we consider both the tolerance limit of predator b and the level of fear k increases linearly with respect to the predator-taxis sensitivity α (i.e., $b \mapsto b\alpha$ and $k \mapsto k\alpha$). Therefore, we modify the functions $f(k, y)$ and $p(x)$ in model (2.3), as $f(k, y) \equiv f(k, \alpha, y) = \frac{1}{1 + k\alpha y}$, and $p(x) \equiv p(\alpha, x) = \frac{\beta x}{a + b\alpha x + x^2}$, i.e., both the successful reproduction rate of prey and the successful predation rate of predator decrease if the defense level or equivalently predator-taxis sensitivity α increases. Therefore, our final model becomes,

$$\begin{aligned}\frac{dx}{dt} &= \frac{rx}{1 + k\alpha y} - d_1 x - d_2 x^2 - \frac{\beta xy}{a + b\alpha x + x^2} \\ \frac{dy}{dt} &= \frac{c\beta xy}{a + b\alpha x + x^2} - my\end{aligned}\quad (2.4)$$

Description of parameters and their values are given in the Table 1. In the above model (2.4), if we consider $\alpha = 1$, then the group defense and the cost of fear are independent to each other. By the definition of k , α , y , $f(k, \alpha, y)$ and $p(\alpha, x)$, we have the following properties:

$$\begin{aligned}f(0, \alpha, y) &= 1, & f(k, \alpha, 0) &= 1, & f(k, 0, y) &= 1, & \lim_{k \rightarrow \infty} f(k, \alpha, y) &= 0, \\ \lim_{y \rightarrow \infty} f(k, \alpha, y) &= 0, & \lim_{\alpha \rightarrow \infty} f(k, \alpha, y) &= 0, & \frac{\partial f(k, \alpha, y)}{\partial k} &< 0, & \frac{\partial f(k, \alpha, y)}{\partial \alpha} &< 0, \\ \frac{\partial f(k, \alpha, y)}{\partial y} &< 0, & \lim_{\alpha \rightarrow \infty} p(\alpha, x) &= 0, & \frac{\partial p(\alpha, x)}{\partial \alpha} &< 0.\end{aligned}$$

The basic dynamical property of the model (2.4) is summarized in the following theorem:

Table 1

Description of parameters and their fixed values for Model (2.4).

Parameter	Description	Value
r	birth rate of prey	0.2
k	level of fear	0.5
α	predator-taxis sensitivity	0.25
d_1	natural death rate of prey	0.1
d_2	death due to intra-prey competition	0.2
β	rate of predation	0.5
a	half-saturation constant	0.1
b	tolerance limit of predator	0.5
c	conversion efficiency of biomass	1
m	natural death rate of predator	0.25

Theorem 2.1. For the system (2.4), \mathbb{R}_+^2 is positively invariant. Moreover, the system (2.4) is dissipative, i.e., every solution of (2.4) is ultimately bounded in \mathbb{R}_+^2 , with the following properties

$$\lim_{t \rightarrow \infty} \sup x(t) \leq \frac{r-d_1}{d_2}$$

$$\lim_{t \rightarrow \infty} \sup \left[x(t) + \frac{1}{c}y(t) \right] \leq \begin{cases} \frac{r-d_1}{d_2} & \text{if } m > r-d_1 \\ \frac{(r-d_1+m)^2}{4d_2m} & \text{if } m \leq r-d_1. \end{cases}$$

Proof. For any $x \geq 0$ and $y \geq 0$, we have

$$\left. \frac{dx}{dt} \right|_{x=0} = 0 \text{ and } \left. \frac{dy}{dt} \right|_{y=0} = 0,$$

which implies that $x = 0$ and $y = 0$ are invariant manifolds, respectively. Due to the uniqueness of a solution, we can conclude that the set \mathbb{R}_+^2 is positively invariant for the system (2.4).

Now,

$$\begin{aligned} \frac{dx}{dt} &\leq \frac{rx}{1+k\alpha y} - d_1x - d_2x^2 \\ &\leq (r-d_1)x - d_2x^2. \end{aligned}$$

Consider the system

$$\frac{dz}{dt} = (r-d_1)z - d_2z^2,$$

whose solution satisfies that

$$\lim_{t \rightarrow \infty} \sup z(t) \leq \frac{r-d_1}{d_2}.$$

By the comparison theory, we have

$$\lim_{t \rightarrow \infty} \sup x(t) \leq \frac{r-d_1}{d_2}.$$

Now we define $w(t) = x(t) + \frac{1}{c}y(t)$, then

$$\begin{aligned} \frac{dw}{dt} &= \frac{rx}{1+k\alpha y} - d_1x - d_2x^2 - \frac{m}{c}y \\ &< rx - d_1x - d_2x^2 - m(w-x) \\ &= (r-d_1+m)x - d_2x^2 - mw. \end{aligned}$$

Define $f(x) = (r-d_1+m)x - d_2x^2$,

$$\max_{x \geq 0} f(x) = f\left(\frac{r-d_1+m}{2d_2}\right) = \frac{(r-d_1+m)^2}{4d_2}.$$

Since $\lim_{t \rightarrow \infty} \sup x(t) \leq \frac{r-d_1}{d_2}$, $\forall \epsilon > 0$, $\exists T > 0$, s.t. $x(t) \leq \frac{r-d_1}{d_2} + \epsilon$ for $t > T$.

Case I: $\frac{r-d_1}{d_2} < \frac{r-d_1+m}{2d_2}$ (i.e., $m > r - d_1$)

First, choose some $\epsilon > 0$ such that $\frac{r-d_1}{d_2} + \epsilon < \frac{r-d_1+m}{2d_2}$. Now,

$$\begin{aligned} \max_{x \leq \frac{r-d_1}{d_2} + \epsilon} f(x) &= f\left(\frac{r-d_1}{d_2} + \epsilon\right) \\ &= \left[r - d_1 + m - d_2\left(\frac{r-d_1}{d_2} + \epsilon\right)\right]\left(\frac{r-d_1}{d_2} + \epsilon\right) \\ &= (m - d_2\epsilon)\left(\frac{r-d_1}{d_2} + \epsilon\right). \end{aligned}$$

Hence,

$$\begin{aligned} \frac{dw}{dt} &\leq (m - d_2\epsilon)\left(\frac{r-d_1}{d_2} + \epsilon\right) - mw \\ \text{and } \lim_{t \rightarrow \infty} \sup w(t) &\leq \frac{(m-d_2\epsilon)\left(\frac{r-d_1}{d_2} + \epsilon\right)}{m} \end{aligned}$$

letting $\epsilon \rightarrow 0$, we have

$$\lim_{t \rightarrow \infty} \sup \left[x(t) + \frac{1}{c}y(t)\right] \leq \frac{r-d_1}{d_2} \quad (\text{if } m > r - d_1).$$

Note that $\frac{r-d_1}{d_2} + \epsilon < \frac{r-d_1+m}{2d_2} \Leftrightarrow 0 < \epsilon < \frac{m-r+d_1}{2d_2}$. Therefore,

$$\min_{0 \leq \epsilon \leq \frac{m-r+d_1}{2d_2}} (m - d_2\epsilon)\left(\frac{r-d_1}{d_2} + \epsilon\right) = (m - d_2\epsilon)\left(\frac{r-d_1}{d_2} + \epsilon\right)\Big|_{\epsilon=0} = \frac{m(r-d_1)}{d_2}.$$

Case II: $m \leq r - d_1$

$$\begin{aligned} \max_{x \leq \frac{r-d_1}{d_2} + \epsilon} f(x) &= f\left(\frac{r-d_1+m}{2d_2}\right) = \frac{(r-d_1+m)^2}{4d_2} \\ \Rightarrow \frac{dw}{dt} &\leq \frac{(r-d_1+m)^2}{4d_2} - mw \\ \Rightarrow \lim_{t \rightarrow \infty} \sup w(t) &\leq \frac{(r-d_1+m)^2}{4d_2m}. \quad \square \end{aligned}$$

The theorem shows that, when the death rate of the predator is large ($m > r - d_1$), we have

$$\lim_{t \rightarrow \infty} \sup \left(x(t) + \frac{1}{c}y(t)\right) \leq \frac{r-d_1}{d_2},$$

when it is small ($m \leq r - d_1$), we have

$$\lim_{t \rightarrow \infty} \sup \left(x(t) + \frac{1}{c}y(t)\right) \leq \frac{(r-d_1+m)^2}{4d_2m}.$$

Note that

$$\frac{(r-d_1+m)^2}{4d_2m} - \frac{r-d_1}{d_2} = \frac{1}{4d_2m}(r-d_1-m)^2 \geq 0.$$

Hence, when the predator's death rate is small ($m \leq r - d_1$), then the upper bound of limit supremum of the 'total population' is higher, compared to the higher predator's death rate ($m > r - d_1$), which is reasonable from the biological point of view.

3. Equilibrium analysis

The Model (2.4) has three non-negative equilibria:

1. The trivial extinction equilibrium $E_0 = (0, 0)$, which always exists.
2. The axial equilibrium, where only prey population survive is given by $E_1 = \left(\frac{r-d_1}{d_2}, 0\right)$, which exists if $r > d_1$.
3. Other non-negative interior steady states of (2.4) can be solved from the following equations

$$\begin{aligned} \frac{r}{1+k\alpha y} - d_1 - d_2 x - \frac{\beta y}{a+b\alpha x+x^2} &=: g(x, y) \\ \frac{c\beta x}{a+b\alpha x+x^2} - m &=: f(x) \end{aligned} \quad (3.1)$$

From $f(x) = 0$, we can get the expression of x as follows:

$$x_i = \frac{(c\beta - mb\alpha) \mp \sqrt{(c\beta - mb\alpha)^2 - 4m^2a}}{2m}, \quad i = 1, 2, \quad (3.2)$$

where $x_1 \leq x_2$. From $g(x, y) = 0$, we can get a quadratic polynomial of y in terms of x as follows:

$$\begin{aligned} (m^2k\alpha)y^2 + \left[\left((c^2\beta d_2 + cmd_1 - mb\alpha cd_2)x - macd_2 \right) k\alpha + m^2 \right] y \\ + \left[\left((c^2\beta d_2 + cmd_1 - mb\alpha cd_2)x - macd_2 \right) - cmrx \right] = 0. \end{aligned} \quad (3.3)$$

Depending on the parameter values and corresponding x_i for $i = 1, 2$, our proposed system (2.4) would have none, one or two interior steady states.

We provide the following theorem regarding the number of interior equilibrium corresponding to the system (2.4).

Theorem 3.1.

- (a) The system (2.4) has no interior steady states if any of the following conditions hold:

$$\frac{ma}{x_1} + \frac{m(r-d_1)}{d_2} \leq c\beta - mb\alpha \text{ or } c\beta - mb\alpha < 2m\sqrt{a}.$$

- (b) The system (2.4) has a unique interior steady state $E_1^* = (x_1, y_1)$ if the following conditions hold:

$$\max \left\{ 2m\sqrt{a}, \frac{ma}{x_2} + \frac{m(r-d_1)}{d_2} \right\} < c\beta - mb\alpha < \frac{ma}{x_1} + \frac{m(r-d_1)}{d_2}.$$

- (c) The system (2.4) has two interior steady states $E_1^* = (x_1, y_1)$ and $E_2^* = (x_2, y_2)$ if the following conditions hold:

$$2m\sqrt{a} < c\beta - mb\alpha < \frac{ma}{x_2} + \frac{m(r-d_1)}{d_2}.$$

Proof. From the expression of x_i in the equation (3.2),

$$\begin{aligned} x_i > 0 \text{ iff } c\beta - mb\alpha > 0 \text{ and } (c\beta - mb\alpha)^2 \geq 4m^2a, \\ \text{i.e.,} \quad x_i > 0 \text{ iff } c\beta - mb\alpha > 2m\sqrt{a}. \end{aligned}$$

A straightforward application of the Descartes sign rule, we can easily verify that the equation (3.3) has at most one real positive root for suitable values of different parameters and variable x as follows. We rename the coefficients of the equation (3.3) as

$$\begin{aligned} C_1 &= m^2 k \alpha \quad (> 0) \\ C_2 &= \left[\left\{ (c^2 \beta d_2 + c m d_1 - m b \alpha c d_2) x - m a c d_2 \right\} k \alpha + m^2 \right] \\ C_3 &= \left[\left\{ (c^2 \beta d_2 + c m d_1 - m b \alpha c d_2) x - m a c d_2 \right\} - c m r x \right] \\ \text{Now, } C_3 > 0 &\implies (c^2 \beta d_2 + c m d_1 - m b \alpha c d_2) x - m a c d_2 > c m r x \\ &\implies [(c^2 \beta d_2 + c m d_1 - m b \alpha c d_2) x - m a c d_2] k \alpha + m^2 > c m r x k \alpha + m^2 \\ &\implies C_2 > (c r k \alpha x + m) m > 0. \end{aligned}$$

Therefore, by Descartes sign rule, equation (3.3) cannot have any positive real solution, if $C_3 > 0$.

Thus, the equation (3.3) has unique real positive root if and only if

$$C_3 < 0, \text{ which gives } c\beta - mb\alpha < \frac{ma}{x} + \frac{m(r-d_1)}{d_2}.$$

Therefore, under the conditions $c\beta - mb\alpha > 2m\sqrt{a}$, the system (2.4) has

- (a) no interior equilibrium if $\max\{\frac{ma}{x_i} + \frac{m(r-d_1)}{d_2}, i = 1, 2\} < c\beta - mb\alpha$, i.e., if $\frac{ma}{x_1} + \frac{m(r-d_1)}{d_2} < c\beta - mb\alpha$,
- (b) unique positive interior equilibrium if $\frac{ma}{x_2} + \frac{m(r-d_1)}{d_2} < c\beta - mb\alpha < \frac{ma}{x_1} + \frac{m(r-d_1)}{d_2}$, and
- (c) two positive interior equilibrium if $c\beta - mb\alpha < \min\{\frac{ma}{x_i} + \frac{m(r-d_1)}{d_2}, i = 1, 2\}$, i.e., if $c\beta - mb\alpha < \frac{ma}{x_2} + \frac{m(r-d_1)}{d_2}$. \square

Note: From the existence conditions, we have $c\beta - mb\alpha > 2m\sqrt{a}$, which gives $\alpha < \frac{c\beta - 2m\sqrt{a}}{mb}$. Thus the predator taxis sensitivity α must be less than the threshold density $\left(\frac{c\beta - 2m\sqrt{a}}{mb}\right)$ for possible survivability of predator at a positive equilibrium point.

In the Fig. 1, we fix the parameters as $r = 0.2$, $k = 0.5$, $d_1 = 0.1$, $d_2 = 0.2$, $\beta = 0.5$, $a = 0.1$, $b = 0.5$, $c = 1$, $m = 0.25$ and varied the parameter α . For $\alpha = 3$, there is no interior steady state for the system (2.4) (Fig. 1(a)), for $\alpha = 2.5$ there is unique interior steady state $E_1^* = (0.1734, 0.0388)$ (Fig. 1(b)) and for $\alpha = 2.7$ there are two interior steady states $E_1^* = (0.25, 0.0398)$ and $E_2^* = (0.4, 0.0225)$ (Fig. 1(c)).

Next, we provide the following theorems regarding the stability of equilibria corresponding to the system (2.4).

Theorem 3.2. *The extinction equilibrium E_0 is locally asymptotically stable if $r - d_1 < 0$. In fact, E_0 is globally asymptotically stable under this condition.*

Proof. The eigenvalues at the extinction equilibrium E_0 are given by $\lambda_1 = r - d_1$ and $\lambda_2 = -m$ (< 0). Thus E_0 is locally asymptotically stable if $r - d_1 < 0$.

The global asymptotic stability of E_0 under the condition $r - d_1 < 0$ follows from the Theorem 2.1 and the local stability of E_0 . \square

Theorem 3.3. *The unique prey-only equilibrium E_1 exists and is locally asymptotically stable if $r - d_1 > 0$ and $c\beta - mb\alpha < \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2}$. Moreover, E_1 is globally asymptotically stable when $r - d_1 > 0$ and $c\beta - mb\alpha < 2m\sqrt{a}$. In particular, E_1 is globally asymptotically stable when $r - d_1 > 0$, $c\beta - mb\alpha < \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2}$, and $\frac{r-d_1}{d_2} < \sqrt{a}$.*

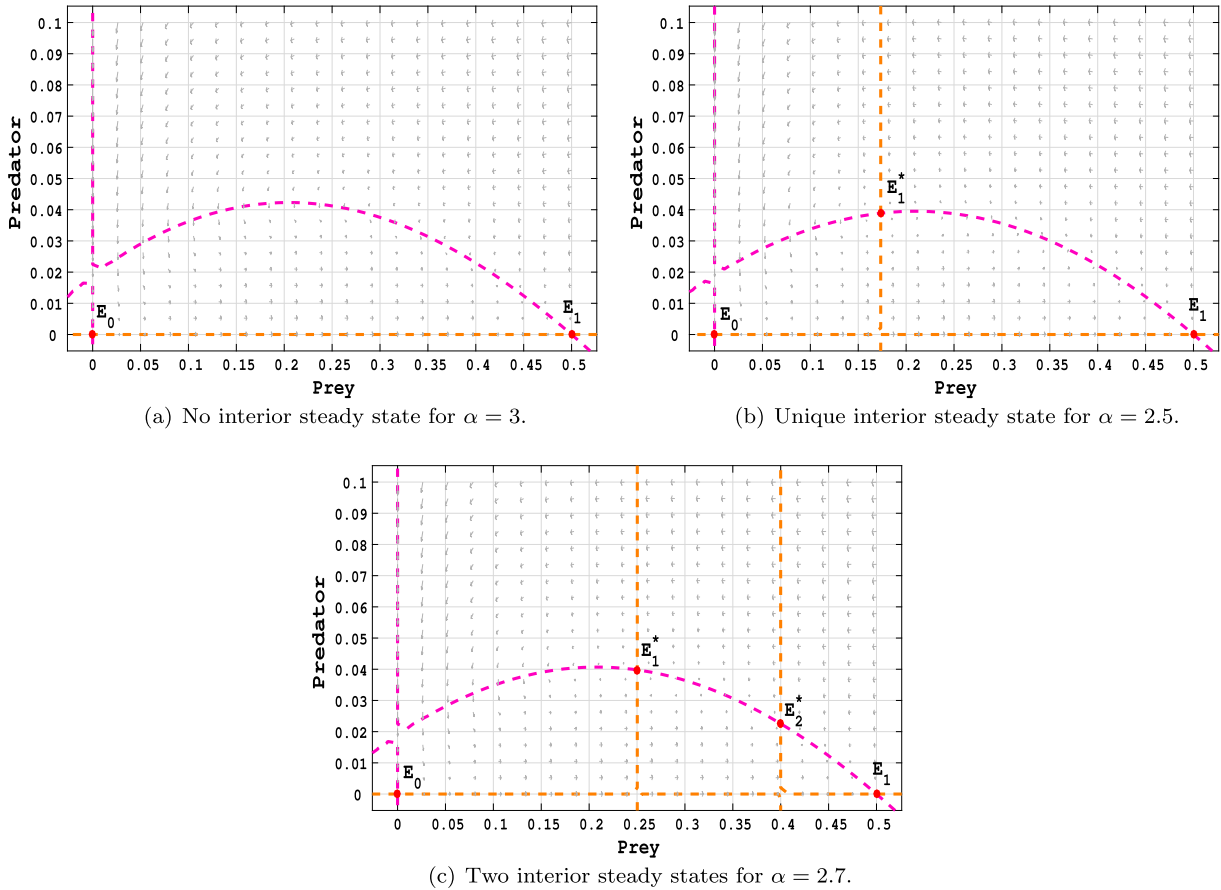


Fig. 1. Number of interior steady states for model (2.4) with varying α . The other parameter values are fixed as mentioned in the Table 1.

Proof. The eigenvalues at the axial equilibrium E_1 are given by $\lambda_1 = -(r - d_1)$ (< 0) and $\lambda_2 = \frac{(r-d_1)[d_2(c\beta - mb\alpha) - m(r-d_1)] - mad_2^2}{\alpha bd_2(r-d_1) + (r-d_1)^2 + ad_2^2}$, where $\lambda_2 < 0$ if $(r - d_1)[d_2(c\beta - mb\alpha) - m(r - d_1)] < mad_2^2$, i.e., if $c\beta - mb\alpha < \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2}$. Thus, E_1 is locally asymptotically stable if $r - d_1 > 0$ and $c\beta - mb\alpha < \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2}$.

From (2.4), we define $g(x)$ as follows:

$$\frac{1}{y} \frac{dy}{dt} = \frac{c\beta x}{a + b\alpha x + x^2} - m \equiv g(x).$$

It is easy to show that $g(x)$ attains its maximum at $x = \sqrt{a}$.

First, consider the case $\frac{r-d_1}{d_2} \geq \sqrt{a}$.

Now

$$\begin{aligned} g(\sqrt{a}) &= \frac{c\beta\sqrt{a}}{2a + b\alpha\sqrt{a}} - m, \\ &= \frac{\sqrt{a}(c\beta - mb\alpha - 2m\sqrt{a})}{2a + b\alpha\sqrt{a}}. \end{aligned}$$

By the assumption $c\beta - mb\alpha < 2m\sqrt{a}$, define $\epsilon = 2m\sqrt{a} - (c\beta - mb\alpha) > 0$, we have

$$g(\sqrt{a}) = -\frac{\epsilon\sqrt{a}}{2a + b\alpha\sqrt{a}} < 0.$$

Hence,

$$\begin{aligned}\frac{1}{y} \frac{dy}{dt} &= g(x) \leq -\frac{\epsilon\sqrt{a}}{2a+b\alpha\sqrt{a}} = -\bar{\epsilon}, \text{ with } \bar{\epsilon} > 0, \\ \Rightarrow y(t) &\leq Ce^{-\bar{\epsilon}t} \text{ for some constant } C > 0, \\ \Rightarrow y(t) &\rightarrow 0 \text{ as } t \rightarrow \infty.\end{aligned}$$

Now we need to exclude the possibility that some subsequence of $(x(t), y(t))$ converges to E_0 . Choose $\epsilon_y > 0$, sufficiently small, then

$$\begin{aligned}& \left. \operatorname{sgn} \left(\frac{1}{x} \frac{dx}{dt} \right) \right|_{y=\epsilon_y} \\ &= \operatorname{sgn} \left(\frac{r}{1+k\alpha\epsilon_y} - d_1 - d_2x - \frac{\beta\epsilon_y}{a+b\alpha x+x^2} \right) \\ &= \operatorname{sgn} [r(a+b\alpha x+x^2) - (d_1+d_2x)(1+k\alpha\epsilon_y)(a+b\alpha x+x^2) - \beta\epsilon_y(1+k\alpha\epsilon_y)] \\ &= \operatorname{sgn} [-\beta k\alpha\epsilon_y^2 - (k\alpha(d_1+d_2x)(a+b\alpha x+x^2) + \beta)\epsilon_y + (a+b\alpha x+x^2)(r-d_1-d_2x)] \\ &> 0 \quad \forall x < \frac{r-d_1}{d_2} \text{ and for sufficiently small } \epsilon_y > 0 \\ \Rightarrow \frac{dx}{dt} &> 0 \quad \forall x < \frac{r-d_1}{d_2} \text{ and for sufficiently small } y > 0.\end{aligned}$$

This proves that there exist no solution converging to E_0 , when $x < \frac{r-d_1}{d_2}$ and sufficiently small $y > 0$. Now, since $y(t) \rightarrow 0$ as $t \rightarrow \infty$, we have

$$\begin{aligned}\frac{dx}{dt} &\rightarrow (r-d_1)x - d_2x^2, \\ \Rightarrow x(t) &\rightarrow \frac{r-d_1}{d_2}.\end{aligned}$$

Note that

$$\frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2} - 2m\sqrt{a} = \frac{m(r-d_1-\sqrt{a}d_2)^2}{d_2(r-d_1)} > 0,$$

which implies that $2m\sqrt{a} < \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2}$. Now, $c\beta - mb\alpha < 2m\sqrt{a}$ ensures that

$$c\beta - mb\alpha < \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2}.$$

This shows that E_1 is globally asymptotically stable if $c\beta - mb\alpha < 2m\sqrt{a}$.

Next, consider the case $\frac{r-d_1}{d_2} < \sqrt{a}$.

It is easy to check that $g\left(\frac{r-d_1}{d_2}\right) < 0$, if $c\beta - mb\alpha < \frac{amd_2}{r-d_1} + \frac{m(r-d_1)}{d_2}$.

Note that $\limsup_{t \rightarrow \infty} x(t) \leq \frac{r-d_1}{d_2}$. These show that $y(t) \rightarrow 0$ as $t \rightarrow \infty$. Similarly, we can prove E_1 is globally asymptotically stable if $c\beta - mb\alpha < \frac{amd_2}{r-d_1} + \frac{m(r-d_1)}{d_2}$ when $\frac{r-d_1}{d_2} < \sqrt{a}$. \square

Theorem 3.4. *The interior equilibrium E_1^* exists and is locally asymptotically stable if $2m\sqrt{a} < c\beta - mb\alpha < \frac{ma}{x_1} + \frac{m(r-d_1)}{d_2}$ and $y_1 < \frac{d_2c^2\beta x_1^2}{m^2(b\alpha+2x_1)}$, however, the other interior equilibrium E_2^* is always a saddle, when it exists.*

Proof. Now, the Jacobian matrix at the interior equilibrium is given by

$$J_{E_i^*} = \begin{bmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{bmatrix} = \begin{bmatrix} x_i \left(\frac{\beta y_i(b\alpha+2x_i)}{(a+b\alpha x_i+x_i^2)^2} - d_2 \right) & -x_i \left(\frac{rk\alpha}{(1+k\alpha y_i)^2} + \frac{\beta}{a+b\alpha x_i+x_i^2} \right) \\ \frac{c\beta y_i(a-x_i^2)}{(a+b\alpha x_i+x_i^2)^2} & 0 \end{bmatrix}.$$

Thus, the characteristic equation at the interior equilibrium is

Table 2

Existence and stability conditions of equilibria for model (2.4).

Equilibrium	Existence conditions	Stability conditions
$E_0 = (0, 0)$	always exists	$r < d_1$
$E_1 = \left(\frac{r-d_1}{d_2}, 0\right)$	$r > d_1$	$c\beta - mb\alpha < \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2}$
$E_1^* = (x_1, y_1)$	$2m\sqrt{a} < c\beta - mb\alpha < \frac{ma}{x_1} + \frac{m(r-d_1)}{d_2}$	$y_1 < \frac{d_2 c^2 \beta x_1^2}{m^2(b\alpha + 2x_1)}$
$E_2^* = (x_2, y_2)$	$2m\sqrt{a} < c\beta - mb\alpha < \frac{ma}{x_2} + \frac{m(r-d_1)}{d_2}$	always saddle

$$\begin{aligned} \lambda^2 - J_{11}\lambda - J_{12}J_{21} &= 0, \\ \lambda^2 + \frac{x_i [d_2(a+b\alpha x_i+x_i^2)^2 - \beta y_i(b\alpha+2x_i)]}{(a+b\alpha x_i+x_i^2)^2} \lambda + \frac{c\beta x_i y_i (a-x_i^2) [rk\alpha(a+b\alpha x_i+x_i^2) + \beta(1+k\alpha y_i)^2]}{(a+b\alpha x_i+x_i^2)^3(1+k\alpha y_i)^2} &= 0. \end{aligned} \quad (3.4)$$

The roots will be real negative or complex conjugate with negative real parts if

$$x_i^2 < a \text{ and } y_i < \frac{d_2(a+b\alpha x_i+x_i^2)^2}{\beta(b\alpha+2x_i)} = \frac{d_2 c^2 \beta x_i^2}{m^2(b\alpha+2x_i)}.$$

However, x_2^2 can not be less than a . In fact $x_2^2 < a$ implies $[(c\beta - mb\alpha)^2 - 4m^2a] + (c\beta - mb\alpha) \times \sqrt{(c\beta - mb\alpha)^2 - 4m^2a} < 0$ which is not possible. Thus the interior equilibrium E_2^* is always unstable (saddle, since the constant term of the characteristic equation is negative, thus by the Descartes sign rule, one eigenvalue is positive and one is negative).

On the other hand, $x_1^2 < a$ implies $(c\beta - mb\alpha)^2 > 4m^2a$ which is true whenever E_1^* exists. Thus, the interior equilibrium E_1^* is locally asymptotically stable when it exists and the condition $y_1 < \frac{d_2 c^2 \beta x_1^2}{m^2(b\alpha+2x_1)}$ holds. \square

We summarize the existence and stability conditions of all the equilibria in the Table 2.

Next, we investigate the possibility of Hopf-bifurcation at the interior equilibrium E_1^* by considering the parameter α , the predator-taxis sensitivity, as the bifurcation parameter.

The interior equilibrium E_1^* loses its stability through Hopf-bifurcation when the eigenvalues are complex conjugate with zero real parts. We consider α as the bifurcation parameter. Let $\lambda(\alpha) = \lambda_r(\alpha) + i\lambda_i(\alpha)$ be an eigenvalue of the characteristic equation (3.4). After substituting the value of $\lambda(\alpha)$ in equation (3.4), and separating the real and imaginary parts, we get

$$\begin{aligned} \lambda_r^2 - \lambda_i^2 - J_{11}\lambda_r - J_{12}J_{21} &= 0, \\ 2\lambda_r\lambda_i - J_{11}\lambda_i &= 0. \end{aligned} \quad (3.5)$$

At the Hopf-bifurcation point, we have $\lambda_r(\alpha) = 0$. We set $\alpha = \alpha_H$, $\lambda_r(\alpha_H) = 0$, and put $\lambda_r = 0$ in (3.5). Therefore,

$$\begin{aligned} \lambda_i^2 + J_{12}J_{21} &= 0, \\ J_{11}\lambda_i &= 0, \text{ where } \lambda_i \neq 0. \end{aligned}$$

Therefore, from the above equations, we have $J_{11}(\alpha_H) = 0$, and $\lambda_i(\alpha_H) = \sqrt{-J_{12}(\alpha_H)J_{21}(\alpha_H)} > 0$, i.e., $\det(J_{E_1^*})|_{\alpha=\alpha_H} = -J_{12}(\alpha_H)J_{21}(\alpha_H) > 0$.

Thus, at the Hopf-bifurcation point, we have

$$J_{11}(\alpha_H) = 0 \Rightarrow \alpha_H = \frac{[\beta y_1 - 2d_2x_1(a+x_1^2)] \pm \sqrt{\beta y_1 [\beta y_1 - 4d_2x_1(a-x_1^2)]}}{2d_2bx_1^2}.$$

Differentiating equations (3.5), w.r.t. α and putting $\lambda_r(\alpha) = 0$, we have

$$\begin{aligned} -J_{11} \frac{d(\lambda_r)}{d\alpha} - 2\lambda_i \frac{d(\lambda_i)}{d\alpha} &= \frac{d(J_{12}J_{21})}{d\alpha}, \\ 2\lambda_i \frac{d(\lambda_r)}{d\alpha} - J_{11} \frac{d(\lambda_i)}{d\alpha} &= \lambda_i \frac{d(J_{11})}{d\alpha}. \end{aligned}$$

By solving the above system of equations, we have

$$\left. \frac{d(\lambda_r)}{d\alpha} \right|_{\alpha=\alpha_H} = \frac{2\lambda_i^2 \frac{d(J_{11})}{d\alpha} - J_{11} \frac{d(J_{12}J_{21})}{d\alpha}}{J_{11}^2 + 4\lambda_i^2} \Big|_{\alpha=\alpha_H} \neq 0,$$

provided $\left[2\lambda_i^2 \frac{d(J_{11})}{d\alpha} - J_{11} \frac{d(J_{12}J_{21})}{d\alpha} \right] \Big|_{\alpha=\alpha_H} \neq 0$.

Theorem 3.5. If $\det(J_{E_1^*}) \Big|_{\alpha=\alpha_H} = -J_{12}(\alpha_H)J_{21}(\alpha_H) > 0$, and $\frac{d(\lambda_r(\alpha))}{d\alpha} \Big|_{\alpha=\alpha_H} \neq 0$, hold, then the interior equilibrium E_1^* of model (2.4) is locally asymptotically stable when $\alpha < \alpha_H$, and undergoes Hopf-bifurcation at E_1^* when $\alpha = \alpha_H$.

The following theorem will give the direction and stability of Hopf-bifurcation around the interior steady state E_1^* .

Theorem 3.6. Let define L as

$$\begin{aligned} L := & 3f_{xxx}f_y^2 - f_y g_x f_{xyy} + (2\sqrt{-f_y g_x} f_{xyy} y_1 - f_{xy} - 2f_{xxy} f_y x_1) \\ & [f_{xx} f_y + 3f_{xxx} f_y^2 x_1 - g_x f_{yy} - f_y g_x f_{xyy} x_1 - \sqrt{-f_y g_x} (f_y f_{xxy} - 3g_x f_{yyy}) y_1]. \end{aligned}$$

Then the Hopf bifurcation is supercritical if $L < 0$ and it is subcritical if $L > 0$, where

$$\begin{aligned} f_y &= J_{12} = -\frac{rx_1 k\alpha}{(1+k\alpha y_1)^2} - \frac{\beta x_1}{a+b\alpha x_1+x_1^2} \\ f_{xx} &= -2d_2 + \frac{2\beta y_1(b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} - \frac{2\beta x_1 y_1(b\alpha+2x_1)^2}{(a+b\alpha x_1+x_1^2)^3} + \frac{2\beta x_1 y_1}{(a+b\alpha x_1+x_1^2)^2} \\ f_{xy} &= -\frac{rk\alpha}{(1+k\alpha y_1)^2} - \frac{\beta}{(a+b\alpha x_1+x_1^2)} + \frac{x_1 \beta(b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} \\ f_{yy} &= \frac{2x_1 r k^2 \alpha^2}{(1+k\alpha x_1)^3} \\ f_{xxx} &= -\frac{6\beta y_1(b\alpha+2x_1)^2}{(a+b\alpha x_1+x_1^2)^3} + \frac{6\beta y_1}{(a+b\alpha x_1+x_1^2)^2} + \frac{6\beta x_1 y_1(b\alpha+2x_1)^3}{(a+b\alpha x_1+x_1^2)^4} - \frac{12\beta x_1 y_1(b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^3} \\ f_{xxy} &= \frac{2\beta(b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} - \frac{2\beta x_1(b\alpha+2x_1)^2}{(a+b\alpha x_1+x_1^2)^3} + \frac{2\beta x_1}{(a+b\alpha x_1+x_1^2)^2} \\ f_{xyy} &= \frac{2rk^2 \alpha^2}{(1+k\alpha y_1)^3} \\ f_{yyy} &= -\frac{6x_1 r k^3 \alpha^3}{(1+k\alpha y_1)^4} \\ g_x &= J_{21} = \frac{c\beta y_1}{(a+b\alpha x_1+x_1^2)} - \frac{c\beta x_1 y_1(b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} \end{aligned}$$

The proof is given in the appendix.

Multi-stability: From the existence and stability conditions for different equilibria, there is a possibility of bi-stability. Our system (2.4) is bi-stable between the equilibria E_1 and E_1^* , if the following conditions hold

$$r - d_1 > 0, 2m\sqrt{a} < c\beta - mb\alpha < \min \left\{ \frac{ma}{x_1} + \frac{m(r-d_1)}{d_2}, \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2} \right\} \text{ and } y_1 < \frac{d_2 c^2 \beta x_1^2}{m^2 (b\alpha + 2x_1)}.$$

For the following set of parameters values $\alpha = 2.7$, $r = 0.2$, $k = 0.5$, $d_1 = 0.1$, $d_2 = 0.2$, $\beta = 0.5$, $a = 0.1$, $b = 0.5$, $c = 1$ and $m = 0.25$, we have

$$r - d_1 = 0.1 > 0, y_1 = 0.0398 < \frac{d_2 c^2 \beta x_1^2}{m^2 (b\alpha + 2x_1)} = 0.2250,$$

and

$$2m\sqrt{a} = 0.1581 < c\beta - mb\alpha = 0.1625 < \min \left\{ \frac{ma}{x_1} + \frac{m(r-d_1)}{d_2} = 0.2250, \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2} = 0.175 \right\}.$$

In the Fig. 4, the red region is the bi-stable region of both the equilibria E_1 and E_1^* .

In addition to the local and global stability of different equilibria for Model (2.4), the following theorem shows the stability and instability of prey-only equilibrium when there exists one or two interior attractors.

Theorem 3.7.

- (a) When there exist two interior equilibria E_1^* and E_2^* , the prey-only equilibrium E_1 is always locally asymptotically stable.
- (b) When there exists unique interior equilibrium E_1^* , the prey-only equilibrium E_1 is always unstable.

Proof. (a) Two interior equilibria exist if

$$2m\sqrt{a} < c\beta - mb\alpha < \frac{ma}{x_i} + \frac{m(r-d_1)}{d_2}; \quad i = 1, 2. \quad (3.6)$$

Under this condition the equation (3.3) has positive real solution, which satisfies the first equation of (3.1),

$$\begin{aligned} \text{i.e., } & \frac{r}{1+k\alpha y} - d_1 - d_2 x_i - \frac{\beta y}{a+b\alpha x_i + x_i^2} = 0 \\ \implies & \frac{r}{1+k\alpha y} - d_1 - d_2 x_i \geq 0 \\ \implies & r - d_1 - d_2 x_i > 0 \\ \implies & \frac{1}{x_i} > \frac{d_2}{r-d_1}. \end{aligned}$$

Now, the prey-only equilibrium E_1 is locally asymptotically stable if

$$\begin{aligned} & c\beta - mb\alpha < \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2} \\ \implies & c\beta - mb\alpha < \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2} < \frac{ma}{x_i} + \frac{m(r-d_1)}{d_2}; \quad i = 1, 2. \end{aligned} \quad (3.7)$$

Now, we exclude the possibility of

$$\frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2} < c\beta - mb\alpha < \frac{ma}{x_i} + \frac{m(r-d_1)}{d_2}; \quad i = 1, 2. \quad (3.8)$$

From the left inequality of (3.8):

$$\begin{aligned} & \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2} < c\beta - mb\alpha, \\ \iff & m(r-d_1)^2 - (c\beta - mb\alpha)d_2(r-d_1) + mad_2^2 < 0, \\ \iff & \frac{(c\beta - mb\alpha)d_2 - \sqrt{(c\beta - mb\alpha)^2 d_2^2 - 4m^2 ad_2^2}}{2m} < r - d_1 < \frac{(c\beta - mb\alpha)d_2 + \sqrt{(c\beta - mb\alpha)^2 d_2^2 - 4m^2 ad_2^2}}{2m}, \\ \iff & d_2 x_1 < r - d_1 < d_2 x_2 \end{aligned}$$

From the second equation of (3.1), we have

$$(c\beta - mb\alpha)x_i = mx_i^2 + am; \quad i = 1, 2.$$

By using the above equation, the right inequality of (3.8) is written as

$$\begin{aligned} c\beta - mb\alpha &< \frac{ma}{x_i} + \frac{m(r-d_1)}{d_2}; \quad i = 1, 2 \\ \iff (mx_i^2 + am)d_2 &< mad_2 + m(r-d_1)x_i; \quad i = 1, 2 \\ \iff d_2x_i &< r - d_1; \quad i = 1, 2 \\ \Rightarrow d_2x_2 &< r - d_1. \end{aligned}$$

Therefore, in (3.8), left and right inequalities contradict each other. Hence (3.6) and (3.7) imply that E_1 is locally asymptotically stable when there exist two interior equilibria.

(b) System (2.4) has unique interior equilibrium if the following conditions hold

$$\max\{2m\sqrt{a}, \frac{ma}{x_2} + \frac{m(r-d_1)}{d_2}\} < c\beta - mb\alpha < \frac{ma}{x_1} + \frac{m(r-d_1)}{d_2}.$$

These x_i ($i = 1, 2$) satisfy the first equation of (3.1) which gives $\frac{1}{x_i} > \frac{d_2}{r-d_1}$, i.e., $\frac{1}{x_2} > \frac{d_2}{r-d_1}$. Thus

$$\frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2} < \frac{ma}{x_2} + \frac{m(r-d_1)}{d_2} < c\beta - mb\alpha,$$

therefore E_1 is unstable when there exists unique interior equilibrium E_1^* . \square

Theorem 3.8. *The unique interior equilibrium E_1^* is globally asymptotically stable if $y_1 < \frac{d_2c^2\beta x_1^2}{m^2(b\alpha+2x_1)}$ and $0 < r - d_1 < \min\{d_2b\alpha, \frac{ad_2}{b\alpha}\}$, i.e., E_1^* is globally asymptotically stable if $\max\{2m\sqrt{a}, \frac{ma}{x_2} + \frac{m(r-d_1)}{d_2}\} < c\beta - mb\alpha < \frac{ma}{x_1} + \frac{m(r-d_1)}{d_2}$, $y_1 < \frac{d_2c^2\beta x_1^2}{m^2(b\alpha+2x_1)}$ and $0 < r - d_1 < \min\{d_2b\alpha, \frac{ad_2}{b\alpha}\}$.*

Proof. From the Theorems 3.2, 3.4 and 3.7, for the global stability of E_1^* , it is sufficient to prove that under the above conditions there are no periodic orbits in $\{(x, y) | x \geq 0, y \geq 0\}$. First, we make the substitution $dt = (a + b\alpha x + x^2)d\tau$, then the model (2.4) becomes

$$\begin{aligned} \frac{dx}{d\tau} &= \left(\frac{rx}{1+k\alpha y} - d_1x - d_2x^2 \right) (a + b\alpha x + x^2) - \beta xy \\ \frac{dy}{d\tau} &= c\beta xy - my (a + b\alpha x + x^2). \end{aligned} \quad (3.9)$$

Taking Dulac function $D(x, y) = \frac{1}{xy}$ for the system (3.9), we have

$$\begin{aligned} \operatorname{div} \Big|_{(PD, QD)} &= \frac{\partial}{\partial x} (P(x, y)D(x, y)) + \frac{\partial}{\partial y} (Q(x, y)D(x, y)) \\ &= \frac{1}{y} \left[-3d_2x^2 - 2 \left(d_1 + d_2b\alpha - \frac{r}{1+k\alpha y} \right) x - \left(ad_2 + d_1b\alpha - \frac{rb\alpha}{1+k\alpha y} \right) \right], \end{aligned}$$

where

$$P(x, y) = \left(\frac{rx}{1+k\alpha y} - d_1x - d_2x^2 \right) (a + b\alpha x + x^2) - \beta xy \text{ and } Q(x, y) = c\beta xy - my (a + b\alpha x + x^2).$$

Now if $d_1 + d_2b\alpha - r > 0$ (i.e., $r - d_1 < d_2b\alpha$) and $ad_2 + d_1b\alpha - rb\alpha > 0$ (i.e., $r - d_1 < \frac{ad_2}{b\alpha}$) then $d_1 + d_2b\alpha - \frac{r}{1+k\alpha y} > 0$ and $ad_2 + d_1b\alpha - \frac{rb\alpha}{1+k\alpha y} > 0$ for any $y \geq 0$. Moreover, above two conditions are sufficient for

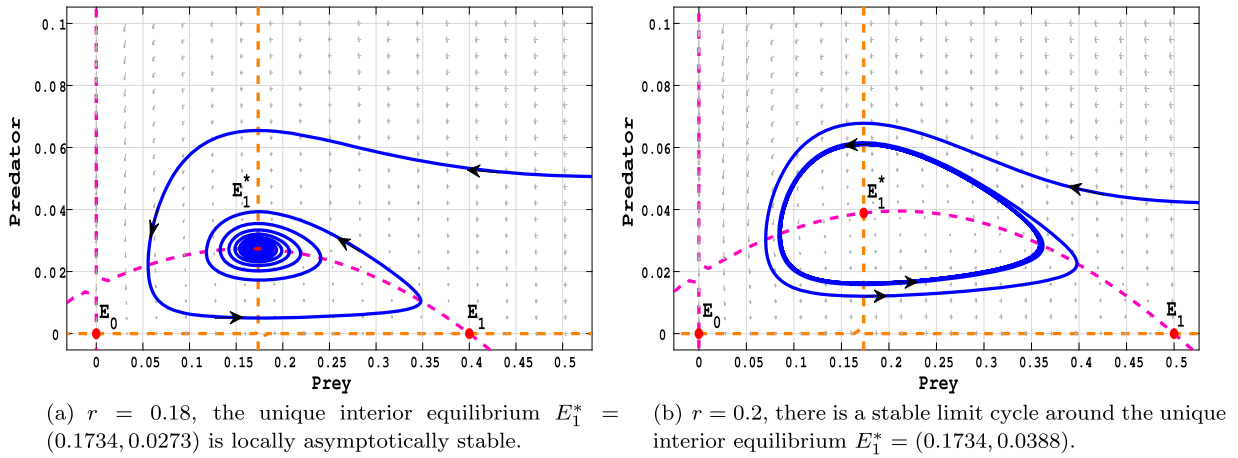


Fig. 2. Here $\alpha = 2.5$, and the other parameters are fixed as mentioned in the Table 1. In this case the other two equilibria E_0 and E_1 are always saddle.

$\text{div}|_{(PD, QD)} < 0$ in $\{(x, y) | x \geq 0, y \geq 0\}$. Therefore, by Dulac criteria and together with the Theorems 3.2, 3.4 and 3.7, the interior equilibrium E_1^* is globally asymptotically stable if $0 < r - d_1 < \min\{d_2 b \alpha, \frac{a d_2}{b \alpha}\}$. \square

Here, we provide some numerical simulations to show the dynamics when system (2.4) has unique or two interior equilibria, with prey-only equilibrium, being unstable or locally asymptotically stable, respectively.

When the unique interior steady state $E_1^* = (x_1, y_1)$ exists, it is locally asymptotically stable if $y_1 < \frac{d_2 c^2 \beta x_1^2}{m^2(b\alpha + 2x_1)}$ and spiral source otherwise. In this case, both prey-only equilibrium E_1 and extinction equilibrium E_0 are saddle.

In Fig. 2, we fix $\alpha = 2.5$, $k = 0.5$, $d_1 = 0.1$, $d_2 = 0.2$, $\beta = 0.5$, $a = 0.1$, $b = 0.5$, $c = 1$, $m = 0.25$. Then for $r = 0.18$ the system (2.4) has a stable unique interior steady state $E_1^* = (0.1734, 0.0273)$ (Fig. 2(a)) and for $r = 0.2$ there exists a stable limit cycle around the unique interior steady state $E_1^* = (0.1734, 0.0388)$ (Fig. 2(b)). In this case, the system (2.4) has only one attractor: if $y_1 < \frac{d_2 c^2 \beta x_1^2}{m^2(b\alpha + 2x_1)}$ the system goes to the stable unique interior steady state E_1^* or there can be a stable limit cycle around E_1^* if $y_1 > \frac{d_2 c^2 \beta x_1^2}{m^2(b\alpha + 2x_1)}$.

Now when the system (2.4) has two interior steady states E_1^* and E_2^* , E_1^* is stable for $y_1 < \frac{d_2 c^2 \beta x_1^2}{m^2(b\alpha + 2x_1)}$. However E_2^* is always saddle. In this case the prey-only equilibrium E_1 is always locally asymptotically stable, whereas the extinction equilibrium E_0 is always saddle.

In Fig. 3, we fix the parameters $\alpha = 2.7$, $k = 0.5$, $d_1 = 0.1$, $d_2 = 0.2$, $\beta = 0.5$, $a = 0.1$, $b = 0.5$, $c = 1$, $m = 0.25$. Then for $r = 0.2$ (Fig. 3(a)) the system (2.4) has two interior equilibria: $E_1^* = (0.25, 0.0398)$, which is a spiral sink and $E_2^* = (0.4, 0.0225)$, which is a saddle. In this case the system (2.4) has two attractors: the stable interior equilibrium E_1^* and stable prey only equilibrium E_1 . For $r = 0.23$ (Fig. 3(b)), the system (2.4) has two interior equilibria: $E_1^* = (0.25, 0.0622)$, which is a spiral source and $E_2^* = (0.4, 0.0546)$ which is a saddle. There is a stable limit cycle around E_1^* . Also in this case, there are two attractors for system (2.4): the stable limit cycle around E_1^* and the stable prey-only equilibrium E_1 . Finally, for $r = 0.24$ (Fig. 3(c)), the system has two interior equilibria $E_1^* = (0.025, 0.0694)$ which is a spiral source and E_2^* which is a saddle. However, in this case the equilibrium prey-only state E_1 attracts the solution starting at almost all the initial conditions. The oscillation of E_1^* becomes so large, such that it touches the stable manifold of E_1 and leads to the extinction of predator population.

Moreover, we plot the existence and stability of all equilibria in the Fig. 4. In this figure, we fix the parameters $k = 0.5$, $d_1 = 0.1$, $d_2 = 0.2$, $\beta = 0.5$, $a = 0.1$, $b = 0.5$, $c = 1$, $m = 0.25$ and vary the other two important parameters r and α from 0 to 0.5 and 0 to 3, respectively. Here, in the black region ($r < d_1$), the extinction equilibrium E_0 is globally asymptotically stable, and no other equilibria exist

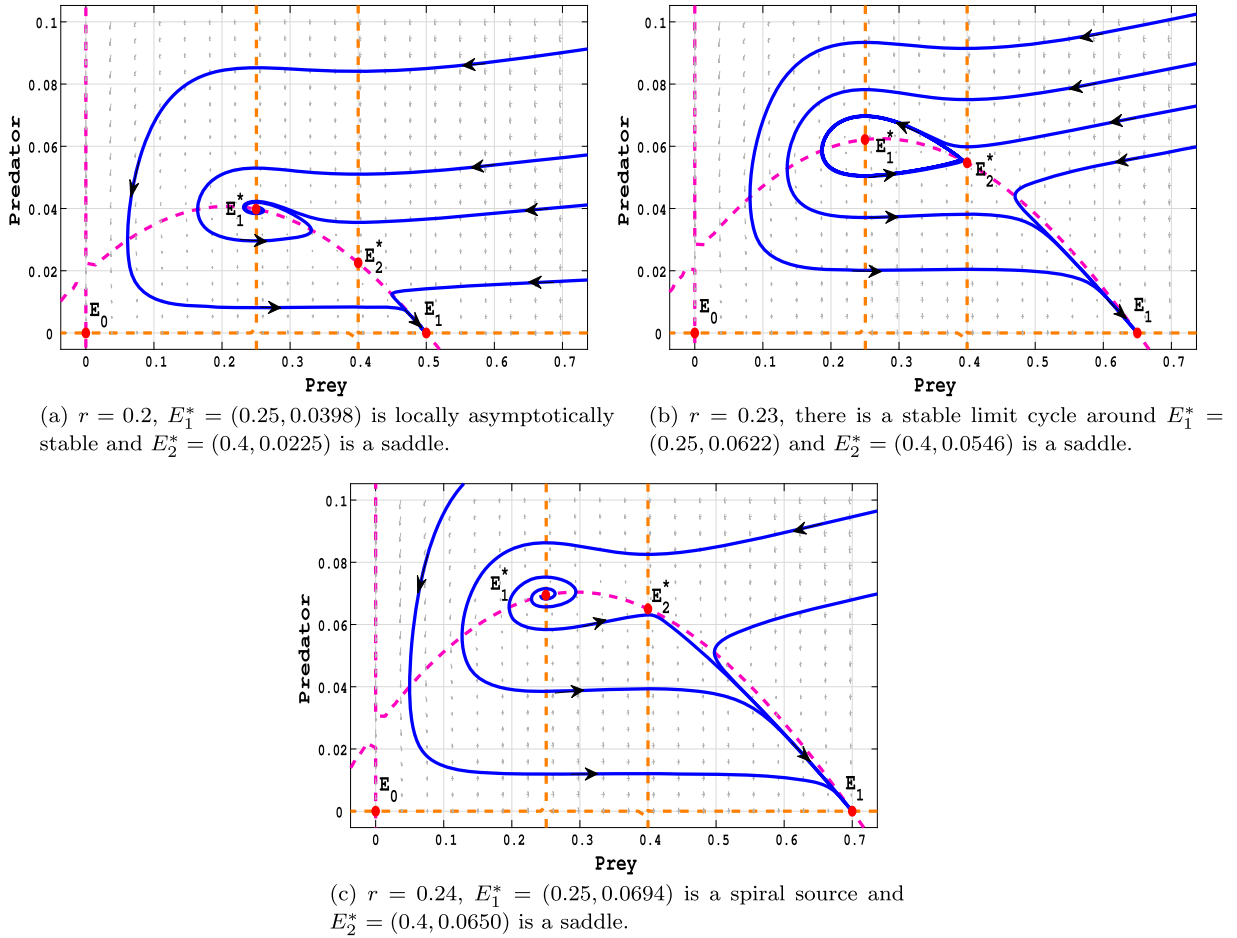


Fig. 3. Here $\alpha = 2.7$, and the other parameters are fixed as mentioned in the Table 1. In this case the prey-only equilibrium E_1 is always locally asymptotically stable, whereas the extinction equilibrium E_0 is always saddle.

in this region (E_0 is the only attractor, i.e., every solution curve will go to the extinction state). The prey only equilibrium E_1 exists and is locally asymptotically stable in the regions yellow, red and green ($c\beta - mb\alpha < \frac{mad_2}{r-d_1} + \frac{m(r-d_1)}{d_2}$), whereas in yellow region there does not exist any interior equilibria (E_1 is the only attractor), however, in red and green region there always exist two interior equilibria E_1^* and E_2^* . In red region the interior equilibrium E_1^* is locally asymptotically stable (here E_1 and E_1^* are two attractors for the system (2.4)), however in green region both the interior equilibria are unstable (here also there may be two attractors, one is a stable E_1 , and another may be a stable limit cycle around E_1^*). Finally, the unique interior attractor E_1^* exists in the blue and cyan regions, however it is locally asymptotically stable only in the blue region. Only a unique attractor exists in this case. In the blue region the unique attractor is the stable unique interior steady state E_1^* and in the cyan region the unique attractor is stable limit cycle around E_1^* .

Fig. 5, shows the existence of the number of interior equilibria and their stability, as well as the stability of all boundary equilibria with respect to varying α . When there exists two interior equilibria, one is always saddle (E_2^*), and the other one is always locally asymptotically stable (E_1^*). When there exists unique interior equilibrium (E_1^*), it either could be stable or a source, where the other two boundary equilibria E_0 and E_1 are saddle.

Next, we draw the bifurcation diagram of both prey and predator, with respect to the parameter α (the predator-taxis sensitivity) in the Fig. 6. From this figure, we can see that the predator population can survive only for the small values of α . If the value of the predator-taxis sensitivity is high ($\alpha > 2.736$),

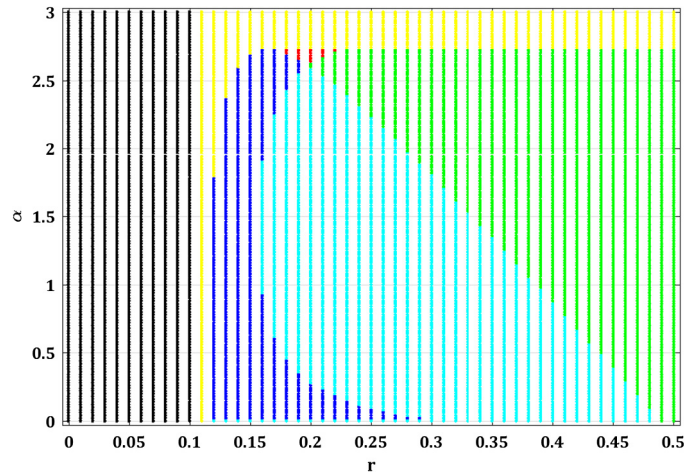
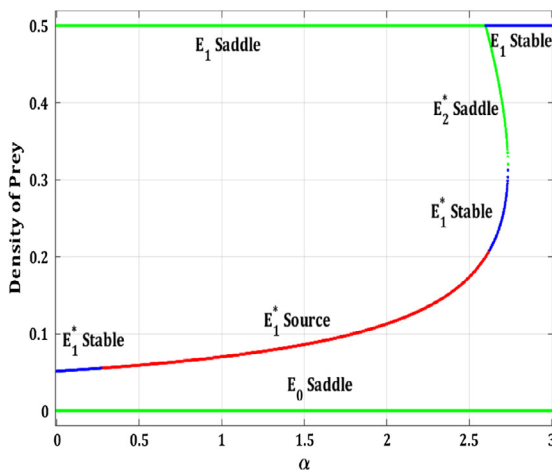
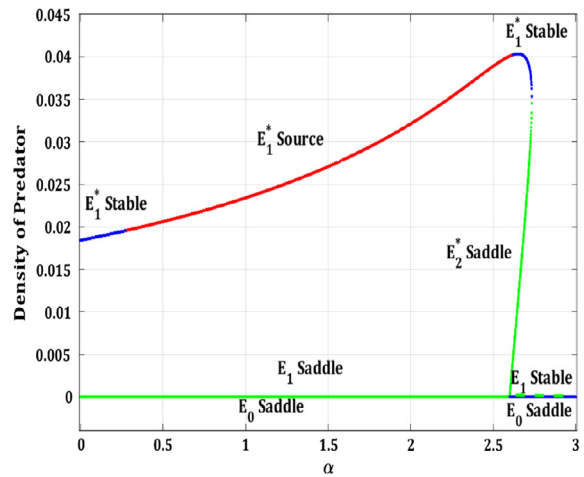


Fig. 4. Existence and stability of all equilibria in $\alpha - r$ parameter plane. The other parameters are fixed as mentioned in the Table 1. Black: E_0 is globally asymptotically stable, no other equilibria exist, yellow: E_1 exists and stable, interior equilibria do not exist, green: both the interior equilibria E_1^* and E_2^* exist but both are unstable, however E_1 exists and stable, red: both interior equilibria exist, with E_1^* stable and E_2^* exists and stable, blue: unique interior attractor exists and stable, no other equilibria exist, cyan: unique interior equilibrium exists with spiral source E_1^* . (For interpretation of the colors in the figure(s), the reader is referred to the web version of this article.)



(a) α V.S. prey population x at different equilibria



(b) α V.S. predator population y at different equilibria.

Fig. 5. The figure shows the stability of boundary equilibria (E_0 and E_1) and describes the number of interior equilibria and their stability when α changes from 0 to 3, where y -axis is the population size at corresponding equilibria. Blue represents the sink (stable); green represents the saddle; and red represents the source. All the parameter (except α) values are taken from the Table 1.

then the predator population can not survive (panel D in the figure). As we increase the value of α the coexistence of prey-predator changes at stable equilibrium (panel A) to stable oscillatory coexistence (panel B) to stable equilibrium (panel C) and finally to extinction of predator (panel D).

4. Sensitivity of model solutions

In this section, we analyze the sensitivity of model (2.4) solutions for both the variables prey and predator, with respect to some important model parameters, namely, the predator-taxis sensitivity (α), the level of fear (k), and the tolerance limit of predator (b), respectively. Here, the sensitivity system given by the partial derivatives of variables $X = \{x, y\}$ of the model (2.4) is derived with respect to the parameters $q = \{\alpha, k, b\}$ (the details method is given in [6]). The semi-relative sensitivity curves for prey $[q \frac{\partial x}{\partial q}]$ and predator $[q \frac{\partial y}{\partial q}]$

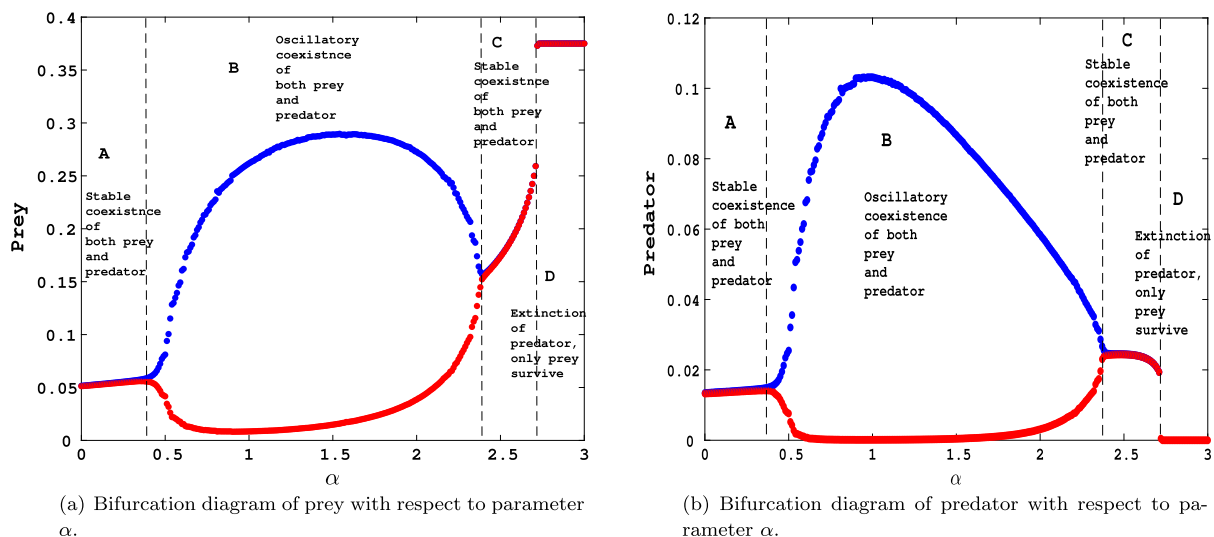


Fig. 6. Here $r = 0.175$, and all the other parameters are fixed as mentioned in the Table 1. A: stable coexistence of prey and predator at the equilibrium, B: oscillatory coexistence of both prey and predator, C: stable coexistence of prey and predator at the equilibrium, and D: extinction of predator and only prey population survives.

are presented in Figs. 7(a) and 7(b), whereas the logarithmic sensitivity curves for prey $\left[\frac{q}{x} \frac{\delta x}{\delta q}\right]$ and predator $\left[\frac{q}{y} \frac{\delta y}{\delta q}\right]$ are presented in Figs. 7(c) and 7(d), respectively.

From the semi-relative sensitivity solutions, we can observe that the perturbation of b (the tolerance limit of predator) exhibit its greatest influence over both prey and predator. At the initial stage ($t \approx 3$ time unit), the effect of α is just opposite to the effect of other two parameters, k and b , for both prey and predator, whereas at later stage, all the parameters have similar effect on solutions. Initially, the effect of α is positive for the prey and negative for the predator. However, for long run its effect is negative for both prey and predator populations. It may be due to the fact that initially it is beneficial for prey as it decreases the death of prey due to predation (which increases the adult survivability), however for long run, it is not beneficial for prey as it decreases the growth rate of prey, which greatly affects overall fitness of the population. All the parameters have largest negative effects on both prey and predator at around 40 time unit, but a decreased effect over time.

From the logarithmic sensitivity solution curves we can interpret the percentage changes in the solutions induced by positive perturbations of the parameters. The graphs in Fig. 7(c), suggests that perturbations of α , k and b have a negative impact upon solution of prey population, however, the impact decreases over time and after $t = 50$ time unit the effect is negligible. The graphs also suggest that at time $t \approx 25$ unit the parameter b causes more than 400% change in solution of prey population. Similarly, perturbations of all the studied parameters have a negative impact upon predator solution and this negative effect increases over time Fig. 7(d). At time $t = 200$ unit the parameter b causes a roughly 700% change in the solution of predator population.

5. Conclusions

In the present paper, we formulate an ODE model on predator-prey interactions by considering both fear and group defense of prey in the presence of predator. We consider the Monod-Haldane-type response function (also known as Holling type IV functional response) for predation, which can capture the group defense of prey. We consider the fear factor as a reduction of prey birth rate due to the time and energy investment for defense. Moreover, we interrelate the reduced growth rate (the fear effect) and group defense by the parameter predator-taxis sensitivity. Since, the total time and/or energy are limited for the prey, then

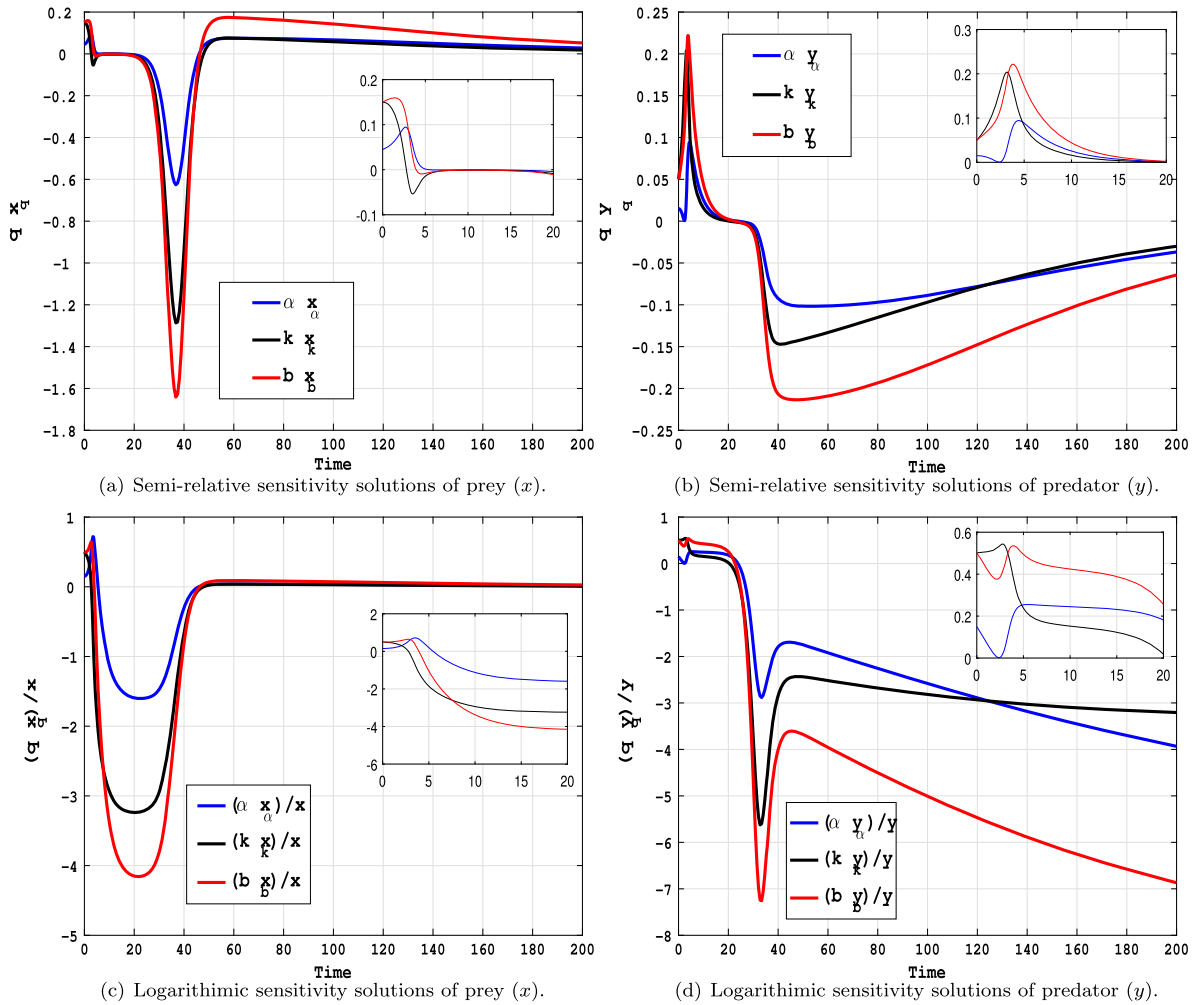


Fig. 7. Here, $r = 0.5$, $\alpha = 0.15$, and all the other parameters are fixed as given in the Table 1. The figure describes the semi-relative and logarithmic sensitivity solutions of both prey and predator, with respect to the important model parameters, namely, the predator-taxis sensitivity (α), level of fear (k), and tolerance limit of predator (b), respectively.

if the prey invests more time and/or energy (i.e., when predator-taxis sensitivity increases) towards group defense, then their birth rate should be decreased (though it increases their survival against predation).

We provide complete dynamics of our proposed ODE model. We provide the positivity and boundedness of solutions, for both cases, when the predator death rate is below and above some threshold density. Also, the upper bound of the limit supremum of the total population is high when the predator death rate is below the threshold density, compared to the other case. We provide the conditions for existence of the number of positive equilibria and their stability. Some global features of boundary equilibria and coexistence equilibria are also provided. We discuss about the possible attractors of our system solutions in the entire parameter's space, and validate our results numerically. In addition, we provide the additional results on the cases, (1) when the system has two interior equilibria then the prey-only equilibrium is always stable, and (2) when the system has unique interior equilibrium then the prey-only equilibrium is always a saddle.

Our mathematical analysis and numerical simulations suggest that the large predator-taxis sensitivity could destabilize the system, and the predator population could be extinct. Sensitivity of model solutions with respect to three studied parameters, namely, the predator-taxis sensitivity, level of fear, and the tolerance limit of predator, shows that the perturbation of tolerance limit of predator has the greatest influence over both prey and predator. Interestingly, at the initial time, the predator-taxis sensitivity has a positive effect on prey; however, at the later time, it could have negative effect on both prey and predator.

Studies on prey-predator interactions with different important mechanisms, have been a motivation in theoretical ecology, which generally could enhance our understanding on real-world ecological systems. It would be interesting to study the dynamics of our proposed model with various realistic time delays, with or without the reaction-diffusion effect. Moreover, group defense can be incorporated in the model by choosing some other response functions. It would be interesting to consider how these response functions change dynamical properties obtained by the present study. These are some of our future research goals.

Acknowledgments

The authors thank the editor and anonymous reviewer for their constructive comments that improved the manuscript. SKS's research is supported by the Japan Society for the Promotion of Science (JSPS) post-doctoral fellowship. YT's research is supported by the JSPS through the "Grant-in-Aid 26400211," and by Aoyama Gakuin University research grant "Ongoing Research Support." SKS would like to thank Prof. Frank Hilker of Osnabruck University for the fruitful discussions.

Appendix A

Proof of the Theorem 3.6. To find the stability and direction of Hopf bifurcation, we calculate the 1st Lyapunov coefficient. Let $u = x - x_1$ and $v = y - y_1$, then the system (2.4) becomes

$$\begin{aligned}\frac{du}{dt} &= \frac{r(u+x_1)}{1+k\alpha(v+y_1)} - d_1(u+x_1) - d_2(u+x_1)^2 - \frac{\beta(u+x_1)(v+y_1)}{a+b\alpha(u+x_1)+(u+x_1)^2} := f(u, v), \\ \frac{dv}{dt} &= \frac{c\beta(u+x_1)(v+y_1)}{a+b\alpha(u+x_1)+(u+x_1)^2} - m(v+y_1) := g(u, v)\end{aligned}$$

Now, considering the Taylor's series expansion at $(u, v) = (0, 0)$ up to 3rd order, we have

$$\begin{aligned}\frac{du}{dt} &= J_{11}u + J_{12}v + f_1(u, v), \\ \frac{dv}{dt} &= J_{21}u + J_{22}v + g_1(u, v),\end{aligned}\tag{A.1}$$

$f_1(u, v)$ and $g_1(u, v)$ are the higher order terms of u and v , given by

$$\begin{aligned}f_1(u, v) &= f_{uu}u^2 + f_{uv}uv + f_{vv}v^2 + f_{uuu}u^3 + f_{uuv}u^2v + f_{uvv}uv^2 + f_{vvv}v^3, \\ g_1(u, v) &= g_{uu}u^2 + g_{uv}uv + g_{vv}v^2 + g_{uuu}u^3 + g_{uuv}u^2v + g_{uvv}uv^2 + g_{vvv}v^3\end{aligned}$$

where

$$\begin{aligned}f_u &= J_{11} = \frac{r}{1+k\alpha y_1} - d_1 - 2d_2x_1 - \frac{\beta y_1}{(a+b\alpha x_1+x_1^2)} + \frac{\beta x_1 y_1 (b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} \\ &= -d_2x_1 + \frac{\beta x_1 y_1 (b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} \\ f_v &= J_{12} = -\frac{r x_1 k \alpha}{(1+k\alpha y_1)^2} - \frac{\beta x_1}{a+b\alpha x_1+x_1^2} \\ f_{uu} &= -2d_2 + \frac{2\beta y_1 (b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} - \frac{2\beta x_1 y_1 (b\alpha+2x_1)^2}{(a+b\alpha x_1+x_1^2)^3} + \frac{2\beta x_1 y_1}{(a+b\alpha x_1+x_1^2)^2} \\ f_{uv} &= -\frac{r k \alpha}{(1+k\alpha y_1)^2} - \frac{\beta}{(a+b\alpha x_1+x_1^2)} + \frac{x_1 \beta (b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} \\ f_{vv} &= \frac{2x_1 r k^2 \alpha^2}{(1+k\alpha y_1)^3} \\ f_{uuu} &= -\frac{6\beta y_1 (b\alpha+2x_1)^2}{(a+b\alpha x_1+x_1^2)^3} + \frac{6\beta y_1}{(a+b\alpha x_1+x_1^2)^2} + \frac{6\beta x_1 y_1 (b\alpha+2x_1)^3}{(a+b\alpha x_1+x_1^2)^4} - \frac{12\beta x_1 y_1 (b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^3} \\ f_{uuv} &= \frac{2\beta (b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} - \frac{2\beta x_1 (b\alpha+2x_1)^2}{(a+b\alpha x_1+x_1^2)^3} + \frac{2\beta x_1}{(a+b\alpha x_1+x_1^2)^2} \\ f_{uvv} &= \frac{2r k^2 \alpha^2}{(1+k\alpha y_1)^3} \\ f_{vvv} &= -\frac{6x_1 r k^3 \alpha^3}{(1+k\alpha y_1)^4}\end{aligned}$$

and

$$\begin{aligned}
g_u &= J_{21} = \frac{c\beta y_1}{(a+b\alpha x_1+x_1^2)} - \frac{c\beta x_1 y_1 (b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} \\
g_v &= J_{22} = \frac{c\beta x_1}{(a+b\alpha x_1+x_1^2)} - m = 0 \\
g_{uu} &= -\frac{2c\beta y_1 (b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} + \frac{2c\beta x_1 y_1 (b\alpha+2x_1)^2}{(a+b\alpha x_1+x_1^2)^3} - \frac{2c\beta x_1 y_1}{(a+b\alpha x_1+x_1^2)^2} \\
g_{uv} &= \frac{c\beta}{(a+b\alpha x_1+x_1^2)} - \frac{c\beta x_1 (b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} \\
g_{vv} &= 0 \\
g_{uuu} &= \frac{6c\beta y_1 (b\alpha+2x_1)^2}{(a+b\alpha x_1+x_1^2)^3} - \frac{6c\beta y_1}{(a+b\alpha x_1+x_1^2)^2} - \frac{6c\beta x_1 y_1 (b\alpha+2x_1)^3}{(a+b\alpha x_1+x_1^2)^4} + \frac{12c\beta x_1 y_1 (b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^3} \\
g_{uuv} &= -\frac{2c\beta (b\alpha+2x_1)}{(a+b\alpha x_1+x_1^2)^2} + \frac{2c\beta x_1 (b\alpha+2x_1)^2}{(a+b\alpha x_1+x_1^2)^3} - \frac{2c\beta x_1}{(a+b\alpha x_1+x_1^2)^2} \\
g_{uvv} &= 0 \\
g_{vvv} &= 0
\end{aligned}$$

Here all the partial derivatives are calculated at the bifurcation point, i.e., $(u, v) = (0, 0)$. Thus system (A.1) can be written as

$$\dot{U} = J_{E_1^*} U + F(U),$$

where $U = (u, v)^T$ and $F = (f_1(u, v), g_1(u, v))^T = (f_{uu}u^2 + f_{uv}uv + f_{vv}v^2 + f_{uuu}u^3 + f_{uuv}u^2v + f_{uvv}uv^2 + f_{vvv}v^3, g_{uu}u^2 + g_{uv}uv + g_{uuu}u^3 + g_{uuv}u^2v)^T$.

Now, Hopf bifurcation occurs when $f_u = J_{11} = 0$, i.e., at the Hopf bifurcation point, the eigenvalue will be purely imaginary, which is given by $i\sqrt{-f_v g_u}$. Eigenvector corresponding to this eigenvalue $i\sqrt{-f_v g_u}$ is given by $\bar{v} = (f_v, i\sqrt{-f_v g_u})^T$. Now, we define $Q = (Re(\bar{v}), -Im(\bar{v})) = \begin{bmatrix} f_v & 0 \\ 0 & -\sqrt{-f_v g_u} \end{bmatrix}$. Now, let $U = QZ$ or $Z = Q^{-1}U$, where $Z = (z_1, z_2)^T$. Therefore, under this transformation, the system is reduced to

$$\dot{Z} = (Q^{-1}J_{E_1^*}Q)Z + Q^{-1}F(QZ).$$

This can be written as

$$\begin{bmatrix} \dot{z}_1 \\ \dot{z}_2 \end{bmatrix} = \begin{bmatrix} 0 & -\sqrt{-f_v g_u} \\ \sqrt{-f_v g_u} & 0 \end{bmatrix} \begin{bmatrix} z_1 \\ z_2 \end{bmatrix} + \begin{bmatrix} F_1(z_1, z_2) \\ F_2(z_1, z_2) \end{bmatrix},$$

where $F_1(z_1, z_2)$ and $F_2(z_1, z_2)$ are given by

$$\begin{aligned}
F_1(z_1, z_2) &= \frac{1}{f_v} \left[f_{uu}f_v^2 z_1^2 - \sqrt{-f_v g_u} f_{uv} f_v z_1 z_2 - f_v g_u f_{vv} z_2^2 + f_{uuu}f_v^3 z_1^3 - \sqrt{-f_v g_u} f_{uuv} f_v^2 z_1^2 z_2 \right. \\
&\quad \left. - f_v g_u f_{uvv} f_v z_1 z_2^2 - f_v g_u \sqrt{-f_v g_u} f_{vvv} z_2^3 \right] \\
F_2(z_1, z_2) &= -\frac{1}{\sqrt{-f_v g_u}} \left[g_{uu}f_v^2 z_1^2 - \sqrt{-f_v g_u} f_v g_{uv} z_1 z_2 + g_{uuu}f_v^3 z_1^3 - \sqrt{-f_v g_u} g_{uuv} f_v^2 z_1^2 z_2 \right]
\end{aligned}$$

The direction of Hopf bifurcation is determined by the sign of the 1st Lyapunov coefficient, which is given by

$$\begin{aligned}
L := & \frac{1}{16} \left[\frac{\partial^3 F_1}{\partial z_1^3} + \frac{\partial^3 F_1}{\partial z_1 \partial z_2^2} + \frac{\partial^3 F_2}{\partial z_1^2 \partial z_2} + \frac{\partial^3 F_2}{\partial z_2^3} \right] \\
& + \frac{1}{16\sqrt{-f_v g_u}} \left[\frac{\partial^2 F_1}{\partial z_1 \partial z_2} \left(\frac{\partial^2 F_1}{\partial z_1^2} + \frac{\partial^2 F_1}{\partial z_2^2} \right) - \frac{\partial^2 F_2}{\partial z_1 \partial z_2} \left(\frac{\partial^2 F_2}{\partial z_1^2} + \frac{\partial^2 F_2}{\partial z_2^2} \right) - \frac{\partial^2 F_1}{\partial z_1^2} \frac{\partial^2 F_2}{\partial z_1^2} + \frac{\partial^2 F_1}{\partial z_2^2} \frac{\partial^2 F_2}{\partial z_2^2} \right].
\end{aligned}$$

We use maple software to simplify the expression of L , which is given as follows:

$$L := 3f_{uuu}f_v^2 - f_v g_u f_{uvv} + (2\sqrt{-f_v g_u} f_{uvv} y_1 - f_{uv} - 2f_{uvv} f_v x_1) \\ [f_{uu} f_v + 3f_{uuu} f_v^2 x_1 - g_u f_{vv} - f_v g_u f_{uvv} x_1 - \sqrt{-f_v g_u} (f_v f_{uvv} - 3g_u f_{vvv}) y_1].$$

Now by Perko [26], Hopf-bifurcation is supercritical if $L < 0$ and it is subcritical if $L > 0$. \square

References

- [1] V. Ajraldi, M. Pittavino, E. Venturino, Modeling herd behavior in population systems, *Nonlinear Anal. Real World Appl.* 12 (4) (2011) 2319–2338.
- [2] K.B. Altendorf, J.W. Laundré, C.A. López González, J.S. Brown, Assessing effects of predation risk on foraging behavior of mule deer, *J. Mammal.* 82 (2) (2001) 430–439.
- [3] J.F. Andrews, A mathematical model for the continuous culture of microorganisms utilizing inhibitory substrates, *Biotechnol. Bioeng.* 10 (6) (1968) 707–723.
- [4] D. Blank, Vigilance, staring and escape running in antipredator behavior of goitered gazelle, *Behav. Process.* 157 (2018) 408–416.
- [5] C.R. Boland, An experimental test of predator detection rates using groups of free-living emus, *Ethology* 109 (3) (2003) 209–222.
- [6] D. Bortz, P. Nelson, Sensitivity analysis of a nonlinear lumped parameter model of HIV infection dynamics, *Bull. Math. Biol.* 66 (5) (2004) 1009–1026.
- [7] J.S. Brown, Vigilance, patch use and habitat selection: foraging under predation risk, *Evol. Ecol. Res.* 1 (1) (1999) 49–71.
- [8] J.S. Brown, B.P. Kotler, Hazardous duty pay and the foraging cost of predation, *Ecol. Lett.* 7 (10) (2004) 999–1014.
- [9] T. Caro, C. Graham, C. Stoner, J. Vargas, Adaptive significance of antipredator behaviour in artiodactyls, *Anim. Behav.* 67 (2) (2004) 205–228.
- [10] D. Christianson, S. Creel, Risk effects in elk: sex-specific responses in grazing and browsing due to predation risk from wolves, *Behav. Ecol.* 19 (6) (2008) 1258–1266.
- [11] M. Clinchy, M.J. Sheriff, L.Y. Zanette, Predator-induced stress and the ecology of fear, *Funct. Ecol.* 27 (1) (2013) 56–65.
- [12] S. Creel, D. Christianson, Relationships between direct predation and risk effects, *Trends Ecol. Evol.* 23 (4) (2008) 194–201.
- [13] S. Creel, P. Schuette, D. Christianson, Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community, *Behav. Ecol.* 25 (4) (2014) 773–784.
- [14] S. Creel, J.A. Winnie Jr., Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves, *Anim. Behav.* 69 (5) (2005) 1181–1189.
- [15] C.E. Cressler, A.A. King, E.E. Werner, Interactions between behavioral and life-history trade-offs in the evolution of integrated predator-defense plasticity, *Amer. Nat.* 176 (3) (2010) 276–288.
- [16] W. Cresswell, Predation in bird populations, *J. Ornithol.* 152 (1) (2011) 251–263.
- [17] W. Cresswell, J. Quinn, Faced with a choice, sparrowhawks more often attack the more vulnerable prey group, *Oikos* 104 (1) (2004) 71–76.
- [18] C.D. Fitzgibbon, Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits, *Anim. Behav.* 39 (6) (1990) 1116–1126.
- [19] H. Freedman, G. Wolkowicz, Predator-prey systems with group defence: the paradox of enrichment revisited, *Bull. Math. Biol.* 48 (5–6) (1986) 493–508.
- [20] A. Illius, C. Fitzgibbon, Costs of vigilance in foraging ungulates, *Anim. Behav.* (1994).
- [21] J. Krause, J.-G.J. Godin, Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk, *Anim. Behav.* 50 (2) (1995) 465–473.
- [22] R.B. Langerhans, Evolutionary consequences of predation: avoidance, escape, reproduction, and diversification, in: *Predation in Organisms*, Springer, 2007, pp. 177–220.
- [23] S. Lingle, Anti-predator strategies and grouping patterns in white-tailed deer and mule deer, *Ethology* 107 (4) (2001) 295–314.
- [24] M. Ono, T. Igarashi, E. Ohno, M. Sasaki, Unusual thermal defence by a honeybee against mass attack by hornets, *Nature* 377 (6547) (1995) 334–336.
- [25] O. Pays, E. Sirot, H. Fritz, Collective vigilance in the greater kudu: towards a better understanding of synchronization patterns, *Ethology* 118 (1) (2012) 1–9.
- [26] L. Perko, *Differential Equations and Dynamical Systems*, vol. 7, Springer Science & Business Media, 2013.
- [27] N. Pettorelli, T. Coulson, S.M. Durant, J.-M. Gaillard, Predation, individual variability and vertebrate population dynamics, *Oecologia* 167 (2) (2011) 305.
- [28] E.L. Preisser, D.I. Bolnick, The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations, *PLoS ONE* 3 (6) (2008) e2465.
- [29] S.K. Sasmal, Population dynamics with multiple Allee effects induced by fear factors—a mathematical study on prey-predator interactions, *Appl. Math. Model.* 64 (2018) 1–14.
- [30] D. Scheel, Profitability, encounter rates, and prey choice of African lions, *Behav. Ecol.* 4 (1) (1993) 90–97.
- [31] G.W. Uetz, C.S. Hieber, Group size and predation risk in colonial web-building spiders: analysis of attack abatement mechanisms, *Behav. Ecol.* 5 (3) (1994) 326–333.

- [32] A. Vainikka, T. Jokelainen, R. Kortet, H. Ylönen, Predation risk allocation or direct vigilance response in the predator interaction between perch (*perca fluviatilis* L.) and pike (*esox lucius* L.)?, *Ecol. Freshw. Fish* 14 (3) (2005) 225–232.
- [33] E. Venturino, A minimal model for ecoepidemics with group defense, *J. Biol. Systems* 19 (04) (2011) 763–785.
- [34] X. Wang, L. Zanette, X. Zou, Modelling the fear effect in predator–prey interactions, *J. Math. Biol.* 73 (5) (2016) 1179–1204.
- [35] L.Y. Zanette, A.F. White, M.C. Allen, M. Clinchy, Perceived predation risk reduces the number of offspring songbirds produce per year, *Science* 334 (6061) (2011) 1398–1401.