PREDATOR-PREY INTERACTIONS UNDER FEAR EFFECT AND MULTIPLE FORAGING STRATEGIES

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ABSTRACT. We propose and analyze the effects of a generalist predator-driven fear effect on a prey population by considering a modified Leslie-Gower predator-prey model. We assume that the prey population suffers from reduced fecundity due to the fear of predators. We investigate the predator-prey dynamics by incorporating linear, Holling type II and Holling type III foraging strategies of the generalist predator. As a control strategy, we have considered density-dependent harvesting of the organisms in the system. We show that the systems with linear and Holling type III foraging exhibit transcritical bifurcation, whereas the system with Holling type II foraging has a much more complex dynamics with transcritical, saddle-node, and Hopf bifurcations. It is observed that the prey population in the system with Holling type III foraging of the predator gets severely affected by the predation-driven fear effect in comparison with the same with linear and Holling type II foraging rates of the predator. Our model simulation results show that an increase in the harvesting rate of the predator is a viable strategy in recovering the prey population.

1. Introduction. The predator-prey relationship is one of the predominant research areas for both ecologists and mathematicians since the last few decades. Predator-prey mathematical models predict different results based on the characteristics of prey, predator and other ecological parameters used in the model. The effects of consumption of prey by a predator is a relatively common observation in the interactions among predator and prey than the effects of predator intimidation. Researchers [3, 4] observed that besides the effects of direct consumption, the non-consumptive effect of fear due to predation risk on the prey [16] is more influential.

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to change the behaviour and physiology of the prey [20]. Triggered by the fear of predation, preys are often forced to take refuge by trading off their foraging and mating opportunities in the open habitat [27]. As a result of this trade-off, there is a reduction in the reproduction rate of the prey [28].

Mathematical models are a better way to understand the mechanism in predator-prey interactions. Wang et al. [25, 26] first proposed and analyzed a mathematical model representing the fear effect on the prey population. Researchers [25, 26] found that a high level of fear on the prey population can stabilize the predator-prey dynamics by excluding the existence of a periodic solution. Over the last few decades, Lotka-Volterra predator-prey models have been widely studied in several ecological investigations in which the functional response is linear [10, 13, 18]. However, the predator-prey interaction models that are developed based upon the Lotka-Volterra formulation are mostly structurally unstable [2, 21], thereby failing to address some ecological complexities. Towards more ecologically realistic models, Holling suggested three different kinds of functional responses [11, 12], while Leslie and Gower [14] developed the so-called Leslie-Gower functional response. In the Leslie-Gower model, the prey and predator both follow logistic growth, the carrying capacity of the predator changes proportionally with the available prey density. This model is applicable for the predator species which cannot switch over to alternative resources at a low prey density [5, 6, 7, 15, 17]. Mishra et al. [17] studied a Leslie-Gower predator-prey model with prey defence and mutual interference of predators. The researchers [17] observed that a better defence ability of the prey can destabilize the predator-prey system. Gong et al. [5] observed that the constant rate of prey harvesting in Leslie-Gower model plays a pivotal role in the dynamics of the system. In [7], Gupta et al. considered a Leslie-Gower type predator-prey model with non-linear harvesting in prey population and obtained conditions for the existence of a bi-stable regime.

In reality, many predators can switch over to an alternative resource when the prey population becomes scarce. To study such issues, researchers [1] proposed a modified version of Leslie-Gower model with Holling-type II scheme which avoids some of the singular behaviours of the original Leslie-Gower model. Zhang and Zhong [30] considered a delayed Leslie-Gower model with Holling type III scheme and identified a switching in the stability of the system by the time-delay-induced Hopf bifurcation. Zhang et al. [29] investigated the dynamics of a modified Leslie-Gower model with Holling type IV scheme and proved the existence of Hopf and saddle-node bifurcations. Zhu and Wang [31] studied the global dynamics of a modified Leslie-Gower model with periodic attractors. Gupta and Chandra [8] identified complex dynamical behaviour of a modified Leslie-Gower model with Michaelis-Menten type prey harvesting. The dynamics of predator-prey interactions with double Allee effect in the prey population governed by a modified Leslie-Gower scheme was studied by Singh et al. [22]. Wang et al. [24] studied the fear effect on the prey population on a modified Leslie-Gower model and observed that any increase in the level of fear leads to a decrease in the prey population density. Halder et al. [9] proposed and analyzed a predator-prey model by incorporating fear and Allee effect with linear and type II foraging of the predator and observed the existence of oscillatory dynamics followed by multiple switching of stability.

As an extension of our previous study [9], we implement the effect of fear on prey species induced by a generalist predator in a mathematical model. A modified logistic equation is used in the prey-growth rate to account for the cost of predation.
risk on the prey. The predator is assumed to feed primarily on the prey species and can switch over to other resources when the prey density is low. We, therefore, assume that the growth rate of the generalist predator to follow a modified Leslie-Gower functional response. Since different predator species have different feeding patterns, we have considered a linear, Holling type II and Holling type III functional responses as the foraging term in our proposed model and analyzed each of the models separately. The Holling type II functional response is described by a decelerating intake rate where the foraging rate saturates at an asymptote independent of the density of the predator as prey abundance becomes large \[23\]. Type III functional response is similar to the type II response function but is more appropriate for the predators in the generalist category that can change their predation rate based on the available prey density \[23\]. We further implemented linear harvesting for both the species in our model.

In this paper, the main emphasis is to investigate how the prey population gets affected due to the fear effect and different foraging strategies of the predator. The paper is structured as follows. The key parameters of the mathematical model and its non-dimensionalized form are described in section 2. The basic results like positivity, boundedness, and the conditions for stability of the system with type I functional response are given in section 3. We also determine the conditions of a transcritical bifurcation of the system in this section. In section 4, using the Holling type II functional response, we discuss the conditions for stability along with the criterion for the existence of a transcritical and a saddle-node bifurcation of the system. In section 5, we use the Holling type III foraging of the predator to analyze the system and then compare the model results with linear and type II foraging rates in section 6. Section 7 contains some concluding remarks.

2. Formulation of the mathematical model. We consider a bi-dimensional predator-prey system in which the densities of prey and predator at time \(T\) are \(X(T)\) and \(Y(T)\) respectively. In the absence of predator, the prey is assumed to follow logistic growth \(F(X) = R_1 X (1 - \frac{X}{K})\) with an intrinsic growth rate \(R_1\) and carrying capacity \(K\). In the presence of the predator, the intrinsic growth rate of the prey due to fear effect becomes \(R_1 H(Y; B)\), where \(H(Y; B) = \frac{1}{1+BY}\) and \(B\) represents the level of fear due to the anti-predator response of the prey. The function \(H(Y; B)\) satisfies the following conditions:

(a) \(H(Y; 0) = 1\): the prey reproduction rate remains unaltered for no fear of predation.
(b) \(H(0; B) = 1\): in the absence of the predator, the prey reproduction rate remains unaltered.
(c) \(\lim_{B \to \infty} H(Y; B) = 0\): extremely fearful prey fails to reproduce.
(d) \(\lim_{Y \to \infty} H(Y; B) = 0\): with a high predator population, the fearful prey fails to reproduce.
(e) \(\frac{\partial H(Y; B)}{\partial B} < 0\): the prey reproduction rate decreases with an increase in anti-predator behaviour.
(f) \(\frac{\partial H(Y; B)}{\partial Y} < 0\): the reproduction rate of the prey decreases with an increase in predator population density.

A modified Leslie-Gower predator-prey model under the above assumptions is given by
Theorem 2.1. Let the predation rate is half-maximal. The non-dimensional form of the system (1)
\[
\frac{dX}{dT} = R_1 H(Y; B) X \left(1 - \frac{X}{K}\right) - F_\delta(X) Y - H_1 X, \\
\frac{dY}{dT} = Y \left(R_2 - \frac{A_2 Y}{X + \eta}\right) - H_2 Y,
\]
where \(X(0) \geq 0\) and \(Y(0) \geq 0\). The parameters \(R_1, R_2, K, B, A_2, B_1\) represent
the intrinsic growth rate of prey, the intrinsic growth rate of the predator, carrying
capacity of prey, level of fear, the intra-specific competition of predator and half-
saturation constant respectively; \(H_1\) and \(H_2\) are the harvesting rates of the prey
and the predator respectively and \(\eta\) is a measure of alternative resources available
to the predator. The foraging rate of the predator on the prey is denoted by \(F_\delta(X)\),
where
\[
F_\delta(X) = \begin{cases} 
A_1 X, & \text{if } \delta = 1 \\
\frac{A_1 X}{B_1 + X}, & \text{if } \delta = 2 \\
\frac{A_1 X}{B_1 + X^2}, & \text{if } \delta = 3.
\end{cases}
\]
For \(\delta = 1\), the foraging rate of the predator is linear, whereas, for \(\delta = 2\) and \(\delta = 3\),
the predator follows Holling type II and Holling type III foraging respectively. The
parameter \(A_1\) represents the maximum per-capita consumption rate of the predator
and \(B_1\) is the half-saturation constant; that is, the density of the prey at which
the predation rate is half-maximal. The non-dimensional form of the system (1)
is represented in Table 1. The parameter values used in the system are listed in
Table 2.

| \(\delta\) | 1 (Linear) | 2 (Holling type-II) | 3 (Holling type-III) |
|---|---|---|---|
| Transformation | \(X = K x, Y = \frac{B_x y}{1 + y}, T = \frac{x}{R_1 x}, r = \frac{B_x}{B_1}, \beta = \frac{B_x}{B_1}, h_1 = \frac{B_x}{B_1}, h_2 = \frac{B_x}{B_1}, \alpha = \frac{B_x}{B_1}, \eta = \frac{B_x}{B_1}, \frac{B_1}{B_1}, \beta = \frac{B_1}{B_1}, h_1 = \frac{B_1}{B_1}, h_2 = \frac{B_1}{B_1}, \alpha = \frac{B_1}{B_1}, \eta = \frac{B_1}{B_1}, \frac{B_1}{B_1}\) | \(X = K x, Y = \frac{B_x y}{1 + y}, T = \frac{x}{R_1 x}, r = \frac{B_x}{B_1}, \beta = \frac{B_x}{B_1}, h_1 = \frac{B_x}{B_1}, h_2 = \frac{B_x}{B_1}, \alpha = \frac{B_x}{B_1}, \eta = \frac{B_x}{B_1}, \frac{B_1}{B_1}, \beta = \frac{B_1}{B_1}, h_1 = \frac{B_1}{B_1}, h_2 = \frac{B_1}{B_1}, \alpha = \frac{B_1}{B_1}, \eta = \frac{B_1}{B_1}, \frac{B_1}{B_1}\) | \(X = K x, Y = \frac{B_x y}{1 + y}, T = \frac{x}{R_1 x}, r = \frac{B_x}{B_1}, \beta = \frac{B_x}{B_1}, h_1 = \frac{B_x}{B_1}, h_2 = \frac{B_x}{B_1}, \alpha = \frac{B_x}{B_1}, \eta = \frac{B_x}{B_1}, \frac{B_1}{B_1}, \beta = \frac{B_1}{B_1}, h_1 = \frac{B_1}{B_1}, h_2 = \frac{B_1}{B_1}, \alpha = \frac{B_1}{B_1}, \eta = \frac{B_1}{B_1}, \frac{B_1}{B_1}\) |
| Non-dimensional system | \(\frac{dx}{dt} = x(1 - x) - xy(\frac{1}{x + \eta}) - h_1 x + f_1^t\) | \(\frac{dy}{dt} = y \left(\frac{r \alpha}{x + \eta} - h_2 y\right) + f_2^t\) | \(\frac{dy}{dt} = y \left(\frac{r \alpha}{x + \eta} - h_2 y\right) + f_2^t\) |
| where \(f_1(t) = \begin{cases} 1, & \text{if } \delta = 1 \\
\frac{1}{\delta - 1}, & \text{if } \delta = 2 \\
\frac{1}{\delta - 1}, & \text{if } \delta = 3, \frac{1}{\delta - 1}\end{cases}\) | | |

TABLE 1. Non-dimensionalized system

Theorem 2.1. Let \(\Gamma = \{(x, y) \in \mathbb{R}^2_+ : x(0) > 0, y(0) > 0\}\). Then all the solutions
\((x(t), y(t))\) of the system (2) are positive for all \(t \geq 0\).

Proof. From the first equation of the non-dimensionalized system (2) we get
\(\frac{dx}{dt} = \frac{1 - x}{1 + y} - y c_2(x) - h_1\). This gives \(x(t) = x(0) e^{\int_0^t \left(\frac{1 - x(s)}{1 + y(s)} - y c_2(s) - h_1\right) ds}\).

From the second equation of (2), we have \(\frac{dy}{dt} = r \frac{\alpha}{x + \eta} - h_2\) and so, we get
\(y(t) = y(0) e^{\int_0^t \left(r - h_2 - \frac{\alpha y(s)}{x(s) + \eta}\right) ds}\).

Therefore, whenever \(x(0) > 0\) and \(y(0) > 0\), we have \(x(t) > 0\) and \(y(t) > 0\) for
all \(t \geq 0\).
(a) (b)

| Parameter | Description                  | Value | Parameter | Value |
|-----------|------------------------------|-------|-----------|-------|
| $R_1$     | Intrinsic growth rate of prey | 0.03  | $r$       | 1     |
| $R_2$     | Intrinsic growth rate of predator | 0.03 | $\alpha$ | 0.03 |
| $B$       | The level of fear            | 4     | $\beta$  | 0.48  |
| $A_1$     | Consumption rate of predator | 0.5   | $\eta_1$ | 0.125 |
| $A_2$     | Intraspecific competition of predator | 0.5 | $b$      | 0.025 |
| $K$       | Carrying capacity of prey    | 2     | $h_1$    | 0.333 |
| $\eta$    | Alternative prey density     | 0.25  | $h_2$    | 0.667 |
| $B_1$     | Half saturation coefficient  | 0.1   |          |       |
| $H_1$     | Harvesting rate of prey      | 0.01  |          |       |
| $H_2$     | Harvesting rate of predator  | 0.02  |          |       |

**Table 2.** Tables of parameter values

Hence, any solution of the system (2) initiating at the positive quadrant of the $xy$-plane will stay in the first quadrant forever. Subsequently, the positive quadrant of $xy$-plane is an invariant set. Similarly, we can prove that the trajectories starting from the positive $x$-axis (or the positive $y$-axis) will remain on the positive $x$-axis (or the positive $y$-axis) for all future time. Therefore, all solutions of the system (2) are positive for all $t \geq 0$.

**Theorem 2.2.** All the non negative solutions of the system (2) are ultimately bounded.

**Proof.** From the first equation of the non-dimensionalized system (2), we have

$$\frac{dx}{dt} \leq x(1-x).$$

This gives $x(t) \to 1$ as $t \to \infty$.

Therefore, corresponding to $\epsilon_1 > 0$, there exists $t_{\epsilon_1} > 0$ such that $x(t) \leq 1 + \epsilon_1$ for all $t \geq t_{\epsilon_1}$.

For all $t \geq t_{\epsilon_1}$, from the second equation of (2), we have

$$\frac{dy}{dt} \leq y \left( r - \frac{\alpha y}{1 + \epsilon_1 + \eta_1} \right).$$

Therefore, corresponding to $\epsilon_2 > 0$ there exists $t_{\epsilon_2} > 0$ such that $0 < y(t) \leq \frac{r(1+\eta_1)}{\alpha} + \frac{\eta_1}{\alpha} + \epsilon_2$ for all $t \geq \max\left\{ t_{\epsilon_1}, t_{\epsilon_2} \right\}$.

This gives, \( \lim_{t \to \infty} \{ x(t) + y(t) \} \leq 1 + \frac{r(1+\eta_1)}{\alpha} \). This completes the proof. \( \square \)

Taking \( \psi(x, y) = \frac{1}{xy}, \) \( x > 0, y > 0 \) we obtain

$$\frac{\partial(f_1^\psi)}{\partial x} + \frac{\partial(f_2^\psi)}{\partial y} =$$

$$- \left\{ \frac{1}{y(1+\beta y)} + \frac{\alpha}{x(\delta + \eta_1)} + c'(x) \right\} < 0 \text{ (as } c'(x) \geq 0 \text{ for } \delta = 1, 3) \text{ and so, by Dulac’s criterion it follows that the system (2) has no limit cycle for } \delta = 1, 3. \text{ This gives the following Theorem} \right.$$  

**Theorem 2.3.** The system (2) with linear or Holling type-III foraging has no limit cycle.

In the following sections, we analyze the dynamics of the system (2) for different foraging types of the predator.

3. **Mathematical model with type I foraging.** In this section, the linear foraging rate of the predator (corresponding to $\delta = 1$ in Table 1) is considered to analyze the the non-dimensionalized system (2). The model equations are given by

$$\frac{dx}{dt} = \frac{x(1-x)}{1+\beta y} - xy - h_1 x$$
interior trajectories.

\[\frac{dy}{dt} = y \left( r - \frac{\alpha y}{x + \eta_1} \right) - h_2 y, \quad (3)\]

where \(x(0) \geq 0\) and \(y(0) \geq 0\).

3.1. Existence and local stability of equilibria of system (3).

**Theorem 3.1.** (i) The extinction equilibrium \(E_0 = (0, 0)\) of the system (3) is locally asymptotically stable if \(h_1 > 1\) and \(h_2 > r\).

(ii) The predator free equilibrium \(E_1 = (1-h_1, 0)\) of the system (3) is locally asymptotically stable if \(h_1 < 1\) and \(h_2 > r\).

(iii) The prey-free equilibrium \(E_2 = \left(0, \frac{(r-h_2)\eta_1}{\alpha} \right)\) of the system (3) is locally asymptotically stable if \(h_1 > h_1^*\) and \(h_2 < r\), where \(h_1^* = \frac{\alpha^2 - \beta \eta_1(r-h_2)^2 - \alpha \eta_1(r-h_2)}{\alpha^2 + \alpha \beta \eta_1(r-h_2)}\).

(iv) The system (3) is persistent at the coexistence equilibrium \(E^*\) if \(h_1 < \min\{1, h_1^*\}\) and \(h_2 < r\).

(v) The coexistence equilibrium \(E^* = (x^*, y^*)\) exists uniquely if \(h_1 < \min\{1, h_1^*\}\) and \(h_2 < r\) and is locally asymptotically stable, where \(x^* = \frac{-B \pm \sqrt{B^2 - 4AC}}{2A}, y^* = \frac{\alpha \beta \eta_1(r-h_2)^2 + \alpha (r-h_2)(1 + \beta h_1)}{\alpha \beta \eta_1(r-h_2)}\), and \(C = \alpha \{\alpha + \beta \eta_1(r-h_2)\} \{h_1 - h_1^*\}\).

**Proof.** (i) The Jacobian matrix \(J_0\) of the system (3) about the trivial equilibrium point \(E_0\) is given by

\[
J_0 = \begin{pmatrix}
1 - h_1 & 0 \\
0 & r - h_2
\end{pmatrix}
\]

The eigenvalues associated with \(J_0\) are \(1 - h_1\) and \(r - h_2\). Therefore, \(E_0\) is locally asymptotically stable whenever \(h_1 > 1\) and \(h_2 > r\).

(ii) The Jacobian matrix \(J_1\) of the system (3) about the predator-free equilibrium point \(E_1\) is given by

\[
J_1 = \begin{pmatrix}
h_1 - 1 & (h_1 - 1)(1 + \beta h_1) \\
0 & r - h_2
\end{pmatrix}
\]

The eigenvalues associated with \(J_1\) are \(h_1 - 1\) and \(r - h_2\). Therefore \(E_1\) is locally asymptotically stable if \(h_1 < 1\) and \(h_2 > r\).

(iii) The Jacobian matrix \(J_2\) of the system (3) about the prey-free equilibrium point \(E_2\) is given by

\[
J_2 = \begin{pmatrix}
h_1^* - h_1 & 0 \\
\frac{(r-h_2)^2}{\alpha} & h_2 - r
\end{pmatrix}
\]

The eigenvalues associated with \(J_2\) are \(h_1^* - h_1\) and \(h_2 - r\). Therefore \(E_2\) is locally asymptotically stable if \(h_1 > h_1^*\) and \(h_2 < r\).

(iv) The system (3) is persistent if the boundary equilibria \(E_0, E_1,\) and \(E_2\) repel interior trajectories.

It is observed that if \(h_1 < 1\) and \(h_2 < r\), then \(E_0\) and \(E_1\) are unstable.

If \(h_1 < h_1^*\) and \(h_2 < r\), the \(E_2\) is unstable.

Combining all the cases we can conclude that all the boundary equilibria of the system (3) are unstable if \(h_1 < \min\{1, h_1^*\}\) and \(h_2 < r\).

Also, by Theorem 2.2 it follows that the system (3) is bounded. Therefore, the system (3) is persistent if \(h_1 < \min\{1, h_1^*\}\) and \(h_2 < r\).
(v) For $h_1 < \min \{1, h_1^* \}$ and $h_2 < r$, we have $A > 0$, $B > 0$ and $C < 0$. Therefore, under this condition, the interior equilibrium $E^*$ of the system (3) exists uniquely. The Jacobian matrix $J^*$ of the system (3) about $E^*$ is

$$J^* = \left( \begin{array}{ccc} -\frac{\alpha y^*}{x^* + \eta_1} & -\frac{\beta x^*(u^* + h_1) + x^*(1 + \beta y^*)}{(1 + \beta y^*)} \\ \frac{-\beta x^*(u^* + h_1) + x^*(1 + \beta y^*)}{(1 + \beta y^*)} & -\frac{\alpha y^*}{x^* + \eta_1} \end{array} \right).$$

The characteristic equation associated with the Jacobian matrix $J^*$ is

$$\left( \frac{x^*}{1 + \beta y^*} + \lambda \right) \left( \frac{\alpha y^*}{x^* + \eta_1} + \lambda \right) + \frac{\alpha x^* y^2 (2 \beta y^* + \beta h_1 + 1)}{(x^* + \eta_1)^2 (1 + \beta y^*)} = 0.$$

The trace of the Jacobian matrix is $\text{Tr}(J^*) = -\left( \frac{x^*}{1 + \beta y^*} + \frac{\alpha y^*}{x^* + \eta_1} \right) < 0$ and determinant of the matrix is $\text{Det}(J^*) = \frac{\alpha x^* y^2 (2 \beta y^* + \beta h_1 + 1)}{(x^* + \eta_1)^2 (1 + \beta y^*)} > 0$. Therefore the system (3) is always asymptotically stable at $E^*$.

The stability of the system (3) at $E_0$ implies the non-existence of $E_1$, $E_2$ and $E^*$. The stability of the system (3) at $E_1$ implies that $E_0$ is unstable and the equilibria $E_2$ and $E^*$ are non existent. The stability of the system (3) at $E^*$ implies that all the boundary equilibria of the system (3) are unstable. The condition for persistence at $E^*$ precludes the possibility of extinction of any organism in the system, therefore, can be regarded as a sufficient condition for coexistence. The mutual positions of the prey-predator nullclines for different harvesting rates are given in Figs. 1(a–d). A tabular representation of the existence and stability of the system (3) is given in Table 3.

| Equilibria | Sufficient condition for existence | Local asymptotic stability |
|------------|----------------------------------|---------------------------|
| $E_0$      | Always                           | $h_1 > 1$ and $h_2 > r$   |
| $E_1$      | $h_3 < 1$                        | $h_1 < 1$ and $h_2 > r$   |
| $E_2$      | $h_2 < r$                        | $h_1 > h_1^*$ and $h_2 < r$|
| $E^*$      | $h_1 < \min \{1, h_1^*\}$ and $h_2 < r$ | $h_1 < \min \{1, h_1^*\}$ and $h_2 < r$ |

Table 3. Existence and local stability of equilibria of system (3)

**Theorem 3.2.** For $h_1 < 1$, the system (3) undergoes transcritical bifurcation at $E_1$ when $h_2$ crosses $h_2 = r$.

**Proof.** For $h_2 = r$, the Jacobian matrix $J_{1|h_2=r}$ of the system (3) around the equilibrium point $E_1$ has a simple zero eigenvalue and one negative eigenvalue $h_1 - 1$ ($h_1 < 1$). Let $V = (v_1, v_2)^T$ and $W = (w_1, w_2)$ be the eigenvectors of the matrices $J_{1|h_2=r}$ and $J^T_{1|h_2=r}$ respectively corresponding to the simple zero eigenvalue.

Then $V$ and $W$ are given by $V = \left( -1 + \beta h_1 \right)^T$ and $W = \left( 0 \ 1 \right)^T$. Let $G^3(x, y)$ represent the vector $G^3(x, y) = \left( f_1^3 \ f_2^3 \right)^T$. Then we have $G^3_{h_2}(x, y) = \left( 0 \ -y \right)^T$, $G^3_{h_2}(E_1; h_2 = r) = \left( 0 \ 0 \right)^T$ and $W^T G^3_{h_2}(E_1; h_2 = r) = 0$.

Also, $DG^3_{h_2}(x, y)V = -(1 + \beta h_1) \frac{\partial G^3_{h_2}(x, y)}{\partial x} + \frac{\partial G^3_{h_2}(x, y)}{\partial y}$ gives $DG^3_{h_2}(E_1; h_2 = r)(V) = (0, -1)^T$.

Therefore, we obtain $W^T[DG^3_{h_2}(E_1; h_2 = r)(V)] < 0$.

Further, $D^2G^3(x, y)(V, V) = (1 + \beta h_1) \left( \frac{\partial^2 G^3(x, y)}{\partial x^2} - 2(1 + \beta h_1) \frac{\partial^2 G^3(x, y)}{\partial x \partial y} + \frac{\partial^2 G^3(x, y)}{\partial y^2} \right)$ gives $W^T[D^2G^3(E_1; h_2 = r)(V, V)] = -\frac{2\alpha}{1 - h_1 + \eta_1} < 0$ (since $h_1 < 1$).
By applying Sotomayor’s theorem [19] we can conclude that the system (3) experiences a transcritical bifurcation at $E_1$ when $h_2$ crosses $h_2 = r$ (cf. Figs. 2(c–d)).

**Theorem 3.3.** For $h_2 < r$, the system (3) undergoes transcritical bifurcation at $E_2$ when $h_1$ crosses $h_1 = h_1^*$. 

**Proof.** For $h_1 = h_1^*$, the Jacobian matrix of the system (3) around the equilibrium point $E_2$ has a simple zero eigenvalue and one negative eigenvalue (since $h_2 < r$). The eigenvectors of the matrices $J_2|_{h_1 = h_1^*}$ and $J_2^T|_{h_1 = h_1^*}$ corresponding to the simple zero eigenvalue are $V_1 = \begin{pmatrix} 1 & \frac{r-h_2}{\alpha} \end{pmatrix}^T$ and $W_1 = \begin{pmatrix} 1 & 0 \end{pmatrix}^T$ respectively.
Figure 2. One-parameter bifurcation plots of the system (4) due to the changes in (a) $h_1$ where $h_2 < r$, (b) $h_1$ where $h_2 > r$, (c) $h_2$ where $h_1 < h_1^*$, and (d) $h_2$ where $h_1 > h_1^*$.

We have $G_{h_1}^1(x,y) = (-x \ 0)^T$, $G_{h_1}^1(E_2; h_1^*) = (0 \ 0)^T$ and $W_1^T G_{h_1}^1(E_2; h_1^*) = 0$.

Also, we obtain $DG_{h_1}^1(E_2; h_1 = h_1^*) V_1 = (-1, 0)^T$ and $W_1^T [DG_{h_1}^1(E_2; h_1 = h_1^*) (V_1)] < 0$.

Furthermore, $W_1^T [D^2 G^1(E_2; h_1 = h_1^*) (V_1, V_1)] = -\frac{2\alpha^2 + 2\alpha \beta (\eta_1 + 1 (r - h_2))}{(\alpha + \beta \eta_1 (r - h_2))^2} < 0$ (since $h_2 < r$). Therefore, using Sotomayor’s theorem [19] we can conclude that the system (3) experiences a transcritical bifurcation at $E_2$ when $h_1$ crosses $h_1 = h_1^*$ (cf. Figs. 2(a − b)).

Corollary 3.1. For $h_1 < 1$ and $h_2 < r$, the system (3) undergoes transcritical bifurcation at $E_2$ when $\beta$ crosses $\beta = \beta^*$, where $\beta^* = \frac{\alpha}{\eta_1 (r - h_2)} \left\{ \frac{\alpha h_1}{\alpha h_1 + \eta_1 (r - h_2)} - 1 \right\}$.

Corollary 3.2. For $h_1 < 1$, the system (3) undergoes transcritical bifurcation at $E_2$ when $h_2$ crosses $h_2 = h_2^*$, where $h_2^* = r - \frac{\alpha \sqrt{(\beta h_1 - 1)^2 + 4\beta - \alpha (\beta h_1 + 1)}}{2\beta \eta_1} < r$. 


Corollary 3.3. For $h_1 < 1$ and $h_2 < r$, the system (3) undergoes transcritical bifurcation at $E_2$ when $\eta_1$ crosses $\eta_1^* = \eta_1^* = \frac{\alpha\sqrt{\beta h_1 - 1}^2 + 4\beta - \alpha h_1 + 1}{2\beta(r - h_2)}$ (cf. Fig. 14(a))
case, the recovery of the prey population can be possible if the predator harvesting rate is increased sufficiently (cf. Fig. 3(f)).

4. **Mathematical model with type II foraging.** In this section, the Holling type II foraging of the predator (corresponding to $\delta = 2$ in Table 1) is considered. The associated non-dimensional system is given by

$$
\frac{dx}{dt} = \frac{x(1-x)}{1+\beta y} - \frac{xy}{b+x} - h_1 x \\
\frac{dy}{dt} = y \left( r - \frac{\alpha y}{x + \eta} \right) - h_2 y,
$$

(4)

where $x(0) \geq 0$ and $y(0) \geq 0$.

4.1. **Equilibrium points and their stability.** The system (4) has the following equilibrium points:

(a) The extinction equilibrium $E_0 = (0,0)$, which exists always;

(b) the predator free equilibrium $E_1 = (1-h_1,0)$, which exists if $h_1 < 1$;

(c) the prey-free equilibrium $E_2 = \left( 0, \frac{(r-h_2)\eta}{\alpha} \right)$, which exists if $h_2 < r$;

(d) the equilibria of coexistence $E_i^* = (x_i^*, y_i^*)$, where $x_i^* (i = 1, 2)$ are positive roots of the algebraic equation $F(x) = P x^2 + Q x + R = 0$, $y_i^* = \frac{(r-h_2)(x_i^*+\eta)}{\alpha}$, $P = \alpha^2 + \beta(r-h_2)^2 + \alpha\beta h_1(r-h_2)$, $Q = \alpha^2(b + h_1 - 1) + \alpha(r-h_2) + 2\beta\eta_1(r-h_2)^2 + \alpha\beta h_1(r-h_2)(b + \eta_1)$, $R = \alpha\beta\eta_1(r-h_2)(h_1-h_i^*)$, and $h_i^* = \frac{b\alpha^2 - \beta\eta_1^2(r-h_2)^2 - \alpha\eta_1(r-h_2)}{\alpha\beta\eta_1(r-h_2)}$.

The system (4) has a unique positive equilibrium if $h_1 < h_1^{**}$, $h_2 < r$ and $Q^2 > 4PR$. For $h_1^{**} < h_1 < 1$ and $h_2 < r$, a pair of positive equilibria of the system (4) exists if $Q < 0$ and $Q^2 > 4PR$.

The Jacobian matrix of the system (4) about the trivial equilibrium $E_0$ is identical to the Jacobian matrix $J_0$ of the system (3). Therefore, (3) is locally asymptotically stable at $E_0$ if $h_1 > 1$ and $h_2 > r$.

The Jacobian matrix of the system (4) about the predator-free equilibrium point $E_1$ is given by

$$
J_1 = \begin{pmatrix}
 h_1 - 1 & \frac{(h_1-1)(1+\beta h_1(1+b-h_1))}{r-h_2} \\
 0 & \frac{1}{1+b-h_1} 
\end{pmatrix}
$$

The characteristic equation associated with the Jacobian matrix $J_1$ is $(h_1 - 1 - \lambda)(r - h_2 - \lambda) = 0$ which gives the eigenvalues $h_1 - 1$ and $r - h_2$. Therefore, the predator-free equilibrium point $E_1$ of the system (4) is locally asymptotically stable if $h_1 < 1$ and $h_2 > r$.

The Jacobian matrix of the system (4) about the prey-free equilibrium point $E_2$ is given by

$$
J_2 = \begin{pmatrix}
 h_1^{**} - h_1 & 0 \\
 \frac{(r-h_2)^2}{\alpha} & h_2 - r 
\end{pmatrix}
$$

The eigenvalues associated to $J_2$ are, $h_1^{**} - h_1$ and $h_2 - r$. Therefore, the prey-free equilibrium point $E_2$ of the system (4) is locally asymptotically stable if $h_1 > h_1^{**}$ and $h_2 < r$.

We note that the boundary equilibria of the system (4) are repellers if $h_1 < \min\{1, h_1^{**}\}$ and $h_2 < r$. As the system (4) is bounded, it follows that (4) is persistent if $h_1 < \min\{1, h_1^{**}\}$ and $h_2 < r$ hold.
The Jacobian matrix $J^*_i$ of the system (4) about the coexistence equilibrium $E^*_i$ ($i = 1, 2$) is given by

$$J^*_i = \begin{pmatrix}
\frac{x_1 y_1 (1 + \beta_2 y_1^*) - x_1^* (b + x_1^*)^2}{(b + x_1^*) (1 + \beta_2 y_1^*)} & \frac{1 + b \beta_1}{(1 + \beta_2 y_1^*) (b + x_1^*)^2} \\
\frac{x_2 y_2 (1 + \beta_1 x_2^*) - x_2^* (1 + \beta_1 x_2^*)^2}{(b + x_2^*) (1 + \beta_1 x_2^*)} & \frac{1 + b \beta_1}{(1 + \beta_1 x_2^*) (b + x_2^*)^2} \\
\end{pmatrix}$$

The system (4) is locally asymptotically stable at $E^*_i$ if $\text{Tr}(J^*_i) < 0$ and $\text{Det}(J^*_i) > 0$.

A tabular representation of the existence and stability of the system (4) is given in Table 4. The mutual positions of prey-predator nullclines of the system (4) due to the changes in $h_1$ and $h_2$ are represented in Fig. 4. We have verified numerically that while $E^*_1$ is locally asymptotically stable under the given conditions, the other positive equilibrium $E^*_2$, whenever exists, is a saddle point.

| Equilibria | Sufficient condition for existence | Local asymptotic stability |
|------------|-----------------------------------|----------------------------|
| $E_0$      | Always                            | $h_1 > 1$ and $h_2 > r$   |
| $E_1$      | $h_1 < 1$                         | $h_1 < 1$ and $h_2 > r$   |
| $E_2$      | $h_2 < r$                         | $h_1 > h_1^{**}$ and $h_2 < r$ |
| $E_1^{**}$ | $h_1 < \min\{1, h_1^{**}\}$ and $h_2 < r$ | $\text{Tr}(J^*_1) < 0$ and $\text{Det}(J^*_1) > 0$ |

**Table 4.** Existence and local stability of equilibria of system (4)

**Theorem 4.1.** For $h_1 < 1$, the system (4) undergoes a transcritical bifurcation at $E_1$ when $h_2$ crosses $h_r = r$.

**Proof.** For $h_2 = r$, the Jacobian matrix $J_1$ of the system (4) around the equilibrium point $E_1$ has a simple zero eigenvalue and a negative eigenvalue $h_1 - 1$ (since $h_1 < 1$). Let $V_2$ and $W_2$ be the eigenvectors of the matrices $J_1$ and $J^*_1$ respectively corresponding to zero eigenvalue, where $V_2 = \begin{pmatrix} -1 & 1 \\ 1-b-h_1 & 1+ \frac{b \beta_1}{(1+\beta_2 y_1^*) (b+x_1^*)^2} \end{pmatrix}^T$ and $W_2 = \begin{pmatrix} 0 & 1 \end{pmatrix}^T$.

We have $G^2_{h_2}(x, y; h_2) = \begin{pmatrix} 0 & -y \end{pmatrix}^T$, $G^2_{h_2}(E_1; h_2^*) = \begin{pmatrix} 0 & 0 \end{pmatrix}^T$, and $W^T J^*_1 G^2_{h_2}(E_1; h_2^*) = 0$. This gives, $D G^2_{h_2}(E_1; h_2^*).V_2 = (0, -1)^T$, $W_2^T D G^2_{h_2}(E_1; h_2^*).V_2 < 0$, and $W_2^T [D^2 G^2(E_1; h_2^*)].(V_2, V_2) = -\frac{\alpha^2 \beta}{\alpha + \beta_1 (r-h_2)} < 0$.

Therefore, by Sotomayor’s theorem [19] we can conclude that the system (4) undergoes a transcritical bifurcation at $E_1$ when $h_2$ crosses $h_r = r$.

**Theorem 4.2.** For $h_2 < r$, the system (4) undergoes a transcritical bifurcation at $E_2$ when $h_1$ crosses $h_1^{**}$.

**Proof.** At $h_1 = h_1^{**}$, the Jacobian matrix $J_2$ of the system (4) around the equilibrium point $E_2$ has a simple zero eigenvalue and a negative eigenvalue $h_2 - r$. Let $V_3$ and $W_3$ be eigenvectors corresponding to the zero eigenvalue for $J_2|_{h_1=h_1^{**}}$ and $J^*_2|_{h_1=h_1^{**}}$ respectively, where $V_3 = \begin{pmatrix} 1 & \frac{r-h_2}{\alpha} \end{pmatrix}^T$ and $W_3 = \begin{pmatrix} 1 & 0 \end{pmatrix}^T$.

Also, we have $W_3^T G^2_{h_2}(E_2; h_1^{**}) = 0$, $W_3^T [D G^2_{h_2}(E_2; h_1^{**})].(V_3) = -1$, and $W_3^T [D^2 G^2(E_2; h_1^{**})].(V_3, V_3) = \frac{2 \alpha (r-h_2)}{\alpha + \beta_1 (r-h_2)^2} - \frac{2 \alpha^2 \beta}{\alpha + \beta_1 (r-h_2)^2} - \frac{2 \alpha (r-h_2)}{\alpha + \beta_1 (r-h_2)^2} - \frac{1}{r}$.

If $W_3^T [D^2 G^2(E_2; h_1^{**})](V_3, V_3) \neq 0$, the system (4) satisfies the Sotomayor theorem [19] for a transcritical bifurcation at $E_2$ when $h_1$ crosses $h_1^{**}$. □
Due to the complexity in the algebraic expressions involved, we will use numerical simulations to verify that $W^2_3\left[D^2G^2(E_2; h^*_1)(V_3, V_3)\right] \neq 0$.

At $h_1 = 0.6585 (h^*_1)$, we have $E_2 = (0, 0.0167)$ and the Jacobian matrix

$$J_2 =\begin{pmatrix} 0 & 0 \\ 0.111 & -0.333 \end{pmatrix}$$

has a simple zero eigenvalue and a negative eigenvalue. Corresponding to the simple zero eigenvalue, we obtain $V_3 = (1, 0.333)^T$ and $W_3 = (1, 0)^T$. This gives $W^2_3G^2_0(E_2; h^*_1) = 0, W^2_3\left[D^2G^2_0(E_2; h^*_1)\right](V_3) = -1$, and $W^2_3\left[D^2G^2(E_2; h^*_1)\right](V_3, V_3) = -2.299$, satisfying the conditions of a transcritical bifurcation at $E_2$ when $h$ crosses $h^*_1$ (cf. Fig. 5(a)).

**Corollary 4.1.** For $h_1 < 1$, the system (4) undergoes a transcritical bifurcation at $E_2$ when $h_2$ crosses $h_2^*$, where $h_2^* = r - \alpha \sqrt{(b_0 h_1 + 1)^2 + 4 b_0 (1 - h_1) - \alpha (b_0 h_1 + 1)} < r$ (cf. Fig. 5(c)).

**Corollary 4.2.** For $h_2 < r$ and $h_1 < 1$, the system (4) undergoes transcritical bifurcation at $E_2$ when $\beta$ crosses $\beta^*$, where $\beta^* = \frac{\alpha (b_0 - b_1 (r - h_2) - b_0)}{\eta_1 (r - h_2) (b_0 + b_1 (r - h_2))}$ (cf. Fig. 13(b)).

Solving $F(x) = 0 = F'(x)$ we see that the equation $F(x) = 0$ has a double root $x = x_n$ satisfying $F''(x_n) = 2P > 0$, where $x_n = -Q/2P$. The nontrivial nullclines $f''_i(x, y) = 0 (i = 1, 2)$ of the system (2) intersect at the instantaneous interior equilibrium $E_3^* = (x_n, y_n)$, where $y_n = -Q/2P_0$.

At $E_3^*$, the slopes of $f''_i(x, y) = 0 (i = 1, 2)$ are equal and so Det($J''_3^*$) = 0. Further, at $E_3^*$, the existence of a double root of $F(x) = 0$ implies $f''_3 = 0$, where $f''_3 = Q^2 - 4PR$.

Solving $f''_3 = 0$ for $h_1$, we obtain the critical value of $h_1$ given by

$$h_{1_{SN}}^\pm = \frac{2P_0 R_3 + P_1 R_0 + Q_0 Q_1 \pm \sqrt{2P_0 R_1 + 2P_1 R_0 + Q_0 Q_1)^2 - (Q_0^2 - 4P_0 R_0)(Q_1^2 - 4P_1 R_1)}{Q_0^2 - 4P_0 R_0},$$

where $P_0 = \alpha \beta (r - h_2), P_1 = \alpha^2 + \beta (r - h_2)^2, Q_0 = \alpha^2 + \alpha \beta (r - h_2) (b + \eta_1), Q_1 = \alpha^2 (1 - \beta) - \alpha (r - h_2) - 2 \beta \eta_1 (r - h_2)^2, R_0 = \alpha^2 b + \alpha \eta_1 b (r - h_2)$ and $R_1 = \beta \eta_1 (r - h_2)^2 - \alpha^2 b + \alpha \eta_1 (r - h_2)$.

The instantaneous equilibrium $E_3^*$ exists if $0 < h_2 < r$ and $0 < h_{1_{SN}}^\pm < Q_0/Q_0^*$. At $h_1 = h_{1_{SN}}^\pm$, we have $\text{Tr}(J''_3^*) = -\frac{2P_0 Q_0}{\eta_1} + \frac{Q_0}{2P_0 + \eta_1} - r + h_2 < 0 (0 < h_2 < r, P > 0$ and $Q < 0$) and so, the Jacobian of the system (4) has a simple zero eigenvalue. The eigenvectors corresponding to the zero eigenvalue for $J''_3^*$ and $J''_3^T$ are $U^* = (1, r - h_2/\alpha)^T$ and $V^* = (1, w_1)^T$ respectively, where

$$w_1 = \frac{-\alpha x_m}{(r - h_2)^2} \left\{ \frac{1}{\eta_1} + \frac{\beta}{\eta_1} \right\}. $$

Let $\bar{F}(x, y; h_1) = (\phi_1, \phi_2)^T$. Then, $\bar{F}_{h_1}(x, y; h_1 = (-x, 0)^T$ and so, $V^* T \bar{F}_{h_1}(E^*_3, h_{1_{SN}}^\pm) = -x_n < 0, V^* T (D^2 F_{h_1}(E^*_3; h_{1_{SN}}^\pm))(U^*) = -1$ and $V^* T \left[D^2 F(E_3^*; h_{1_{SN}}^\pm)(U^*, U^*)\right] = \xi \neq 0$, where $\xi = \frac{2b_2 y_m}{(b_0 + b_1)} - \frac{2}{(b_0 + b_1)} \left\{ \beta (1 - 2x_m) \right\} + \frac{2(\beta - 1)}{(b_0 + b_1)} \left\{ \alpha (1 - 2x_m) \right\}$. Due to the complexity in the algebraic expressions involved, we use numerical simulations to verify that $\xi \neq 0$ when $h_1$ approaches the critical value $h_{1_{SN}}^\pm$.

We obtain $h_{1_{SN}} = 1.0476, 0.3685$ and $Q_0/Q_0^* = 0.5869$. Since $h_{1_{SN}} < Q_0/Q_0^*$, it follows that the instantaneous positive interior equilibrium $E_3^* = (0.1008, 0.0753)$ exists.
at \( h_1 = h_{1sn} \). Further, at \( h_1 = h_{1sn} \), we obtain \( \xi = -1.4353 \). Therefore, all the conditions for the existence of a saddle-node bifurcation [19] at the interior equilibrium are satisfied when \( h_1 \) crosses \( h_1 = h_{1sn} \) (cf. Fig. 5(b)). This gives the following theorem

**Theorem 4.3.** For \( 0 < h_2 < r \), the system (4) undergoes a saddle-node bifurcation when \( h_1 \) crosses \( h_1 = h_{1sn} \).

**Corollary 4.3.** For \( h_1 < 1 \), the system (4) undergoes a saddle-node bifurcation when \( h_2 \) crosses \( h_2 = h_{2sn} \), where \( h_{2sn} \) satisfies \( f_{SN}(h_2) = 0 \) (cf. Fig. 5(d)).

From Figs. 6(a), 7(d) and 7(d) it is observed that the prey-predator coexistence is possible in the system if the predator is being harvested at a high rate. In the case of an abundance of alternative resources of the predator, the harvesting rate of the predator needs to be further increased for the prey to survive in the system (cf. Figs. 6(b) and 7(d)).

Considering \( \alpha \) as a bifurcation parameter and then solving for \( \text{Tr}(J^*_1) = 0 \), the critical value of \( \alpha \), say \( \alpha = \alpha^* \), can be obtained. Due to the complexity in the algebraic expressions involved, we will use numerical simulations to verify that

\[
\text{Det}(J^*_1) = 0 > 0 \quad \text{and} \quad \frac{d}{d\alpha} \text{Tr}(J^*_1)|_{\alpha = \alpha^*} \neq 0.
\]

For \( \alpha = 0.4993 \) and all other parameters as in Table 2 we have \( E^*_1 = (0.1893, 0.0199) \) is an interior equilibrium of the system (4) (cf. Fig. 8(a)). Evaluating the Jacobian \( J^*_1 \) of system (4) at \( E^*_1 \) we obtain

\[
J^*_1 = \begin{pmatrix}
0.1667 & -0.8578 \\
0.0556 & -1.0667
\end{pmatrix}
\]

The corresponding eigenvalues of \( J^*_1 \) are \( \pm 0.1413i \). Clearly, the trace and determinant of the Jacobian \( J^*_1 \) at \( \alpha = 0.4993 \) are 0 and 0.0199 > 0 respectively (cf. Fig. 8(b)). Furthermore, we obtain \( \frac{d}{d\alpha} \text{Tr}(J^*_1)|_{\alpha = 0.4993} < 0 \), satisfying the transversality condition (cf. Fig. 8(c)). Hence, the system (4) undergoes a Hopf bifurcation with respect to the bifurcation parameter \( \alpha \) at \( \alpha = 0.4993 \).

5. **Mathematical model with type III foraging.** In this section, the Holling type III foraging rate of the predator (corresponding to \( \delta = 3 \) in Table 1) is considered in the following non-dimensional system

\[
\begin{align*}
\frac{dx}{dt} &= \frac{x(1-x)}{1+\beta y} - \frac{x^2y}{b_1 + x^2} - h_1x, \\
\frac{dy}{dt} &= y \left( r - \frac{\alpha y}{x + \eta_1} \right) - h_2y
\end{align*}
\]

(5)

where \( x(0) \geq 0 \) and \( y(0) \geq 0 \).

5.1. **Equilibrium points and their stability.** The system (5) has the following equilibrium points:

(a) The extinction equilibrium \( E_0 = (0, 0) \), which exists always;
(b) the predator free equilibrium \( E_1 = (1-h_1, 0) \), which exists if \( h_1 < 1 \);
(c) the prey-free equilibrium \( E_2 = \left(0, \frac{r-h_2\eta_1}{\alpha} \right) \), which exists if \( h_2 < r \);
(d) the positive equilibrium \( E_* = (x_*, y_*) \), where \( x_* \) is a positive root of the equation
The characteristic equation associated with the Jacobian matrix $J$ when $\text{Tr}(J) = \text{Det}(J)$ is given by

$$\Delta = \bar{R}^2 \bar{Q}^2 - 4 \bar{S} \bar{Q}^3 - 4 \bar{R}^3 \bar{P} + 18 \bar{P} \bar{Q} \bar{R} \bar{S} - 27 \bar{Q}^2 \bar{P}^2.$$ 

The discriminant of the cubic equation is $\Delta = \bar{R}^2 \bar{Q}^2 - 4 \bar{S} \bar{Q}^3 - 4 \bar{R}^3 \bar{P} + 18 \bar{P} \bar{Q} \bar{R} \bar{S} - 27 \bar{Q}^2 \bar{P}^2$.

For $h_1^# < h_1 < 1$ and $h_2 < r$ we have $\bar{P} > 0$, $\bar{R} > 0$, and $\bar{S} < 0$. Under this condition, the positive equilibrium of the system (5) exists uniquely if either (i) $\Delta < 0$ or (ii) $\Delta > 0$ and $Q > 0$. Due to the complexities of the algebraic expressions involved, we verify the existence and uniqueness of the positive equilibrium of the system (5) numerically. Under the set of parameter values as given in Table 2, we obtain $\bar{P} = 0.0558 > 0$, $\bar{Q} = 0.0229 > 0$, $\bar{R} = 0.0021 > 0$, $\bar{S} = -10^{-5} < 0$, and $\Delta = 6.975 \times 10^{-10} > 0$, satisfying the conditions for the existence of a unique positive equilibrium of the system (5).

Since the characteristic equations of the boundary equilibria $E_0$ and $E_1$ of the systems (3), (4), and (5) are identical, the criteria for the stability at $E_0$ and $E_1$ remain the same for all these three systems.

The Jacobian matrix $\bar{J}_2$ of the system (5) about the prey-free equilibrium point $E_2$ is given by

$$\bar{J}_2 = \left( \begin{array}{c} \frac{\alpha - h_1(\alpha + \beta \eta_1(r - h_2))}{\alpha + h_1(1 + \beta \eta_1)} & 0 \\ h_2 - r \end{array} \right)$$

The characteristic equation associated with the Jacobian matrix $\bar{J}_2$ of the system (5) is given by

$$\left\{ \frac{\alpha - h_1(\alpha + \beta \eta_1(r - h_2))}{\alpha + h_1(1 + \beta \eta_1)} - \lambda \right\} (h_2 - r - \lambda) = 0.$$ 

Therefore, the prey-free equilibrium $E_2$ of the system (5) is locally asymptotically stable if $h_1^# > 0$ and $h_2 < r$.

Clearly, all boundary equilibria of the system (5) are repellers if $h_1 < \min \{1, h_1^#\}$ and $h_2 < r$. Since the system (5) is bounded, it follows that (5) is persistent at $E_*$ if $h_1 < \min \{1, h_1^#\}$ and $h_2 < r$. This implies, for the long term survival of the prey and the predator species, the prey-predator harvesting rates must satisfy $h_1 < \min \{1, h_1^#\}$ and $h_2 < r$.

The Jacobian matrix $J_*$ about the interior equilibrium point $E_*$ is given by

$$J_* = \left( \begin{array}{c} \frac{-(b_1 - x^2)x y}{(b_1 + x^2)^2} - \frac{x}{1 + \beta y} - \frac{\beta h_1 x^2 + 2 \beta x^2 y}{1 + \beta y} & \frac{x y}{1 + \beta y} - \frac{\beta h_1 x^2 + 2 \beta x^2 y}{1 + \beta y} \\ \frac{y}{1 + \beta y} & \frac{x}{1 + \beta y} - \frac{\beta h_1 x^2 + 2 \beta x^2 y}{1 + \beta y} \end{array} \right)$$

The trace of the matrix $J_*$ is $\text{Tr}(J_*) = \frac{-(b_1 - x^2)}{(b_1 + x^2)^2} - \frac{x}{1 + \beta y} - \frac{\beta h_1 x^2 + 2 \beta x^2 y}{1 + \beta y}$ and the determinant is $\text{Det}(J_*) = \frac{\beta h_1 x^2 + 2 \beta x^2 y}{1 + \beta y} \frac{x}{1 + \beta y} - \frac{\beta h_1 x^2 + 2 \beta x^2 y}{1 + \beta y} \frac{x}{1 + \beta y} = \frac{\alpha x y}{1 + \beta y}.$

Therefore, the coexistence equilibrium $E_*$ is locally asymptotically stable if $\text{Tr}(J_*) < 0$ and $\text{Det}(J_*) > 0$. The conditions for the existence and the stability of the equilibria of the system (5) is given in Table 5. The nullclines and the steady states of the system (4) for different values of $h_1$ and $h_2$ are represented in Fig. 9.

**Theorem 5.1.** For $h_2 < r$, the system (5) has a transcritical bifurcation at $E_2$ when $h_1$ crosses $h_1 = h_1^#.$
Proof. For $h_1 = h_1^\#$, the Jacobian matrix $\bar{J}_2$ of the system (5) around the equilibrium point $E_2$ has a simple zero eigenvalue and one negative eigenvalue $h_2 - r$. The eigenvectors of the matrices $\bar{J}_2$ and $\bar{J}_2^T$ corresponding to the zero eigenvalue are given by $\bar{V} = \left( \begin{array}{c} 1 \\ \frac{r-h_2}{\alpha} \end{array} \right)$ and $\bar{W} = \left( \begin{array}{c} 1 \\ 0 \end{array} \right)^T$ respectively.

We have $F_{h_1}^3(x, y) = \left( -x \quad 0 \right)^T$, $F_{h_1}^3(E_2; h_1^\#) = \left( 0 \quad 0 \right)^T$ and $\bar{W}^T F_{h_1}^3(E_2; h_1^\#) = 0$.

Furthermore, $\bar{W}^T F_{h_1}^3(E_2, h_1^\#) \bar{V} = (1, 0)^T$, $\bar{W}^T [DF_{h_1}^3(E_2; h_1^\#) \bar{V}] = -1 < 0$, and $\bar{W}^T [D^2 F_{h_1}^3(E_2; h_1^\#)](\bar{V}, \bar{V}) = -\frac{2\alpha^2 + \alpha \beta (r-h_2)(1+\eta_1)}{(\alpha + \alpha \eta_1(r-h_2))^2} < 0$ (since $h_2 < r$).

Hence, by Sotomayor’s theorem [19] we can conclude that the system (5) experiences a transcritical bifurcation at $E_2$ when $h_1$ crosses $h_1 = h_1^\#$ (cf. Fig. 10(a)).

**Corollary 5.1.** For $h_1 < 1$, the system (5) undergoes transcritical bifurcation at $E_2$ when $h_2$ crosses $h_2^\#$, where $h_2^\# = r - \frac{\alpha(1-h_1)}{\eta_1(r-h_2)} < r$.

**Corollary 5.2.** For $h_2 < r$ and $h_1 < 1$, the system (5) undergoes transcritical bifurcation at $E_2$ when $\beta$ crosses $\beta = \beta^\#$, where $\beta^\# = \frac{\alpha(1-h_1)}{\eta_1(r-h_2)}$ (cf. Fig. 13(c)).

**Corollary 5.3.** For $h_2 < r$ and $h_1 < 1$, the system (5) undergoes transcritical bifurcation at $E_2$ when $\eta_1$ crosses $\eta_1 = \eta_1^\#$, where $\eta_1^\# = \frac{\alpha(1-h_1)}{\beta \alpha (r-h_2)}$ (cf. Fig. 14(c)).

**Theorem 5.2.** The system (5) undergoes a transcritical bifurcation at $E_1$ when $h_2$ crosses $h_2 = r$.

Proof. For $h_2 = r$, the Jacobian matrix $J_1$ of the system (5) around the equilibrium point $E_1$ is

$$\bar{J}_1 = \left( \begin{array}{cc} h_1 - 1 & -\frac{\beta h_1 (1-h_1)(1-h_1^2+r)(1-h_1^2)}{b_1(1-h_1)^2} \\ 0 & 0 \end{array} \right).$$

The matrix $\bar{J}_1$ has a simple zero eigenvalue and one negative eigenvalue. The eigenvectors of the matrices $\bar{J}_1$ and $\bar{J}_1^T$ corresponding to zero eigenvalue are given by $\bar{V}_1 = \left( \begin{array}{c} \frac{\beta h_1 (1-h_1)(1-h_1^2+r)(1-h_1^2)}{b_1(1-h_1)^2} \\ 1 \end{array} \right)^T$ and $\bar{W}_1 = \left( \begin{array}{c} 0 \\ 1 \end{array} \right)^T$ respectively.

Now, we have $G_{h_2}^3(x, y) = \left( \begin{array}{c} 0 \\ -y \end{array} \right)^T$, $G_{h_2}^3(E_1; h_2 = r) = \left( \begin{array}{c} 0 \\ 0 \end{array} \right)^T$, and $\bar{W}_1^T G_{h_2}^3(E_1; h_2 = r) = 0$.

Further, we obtain $D G_{h_2}^3(E_1; h_2 = r) \bar{V}_1 = (0, -1)^T$, $D G_{h_2}^3(E_1; h_2 = r) \bar{V}_1 = -1 < 0$, and $\bar{W}_1^T [D^2 G_{h_2}^3(E_1; h_2 = r)](\bar{V}_1, \bar{V}_1) = -\frac{2\alpha^2 + \alpha \beta (r-h_2)^2}{(\alpha + \alpha \eta_1(r-h_2))^2} < 0$.

Hence, by Sotomayor’s theorem [19] we can conclude that the system (5) undergoes a transcritical bifurcation at $E_1$ when $h_2$ crosses $h_2 = r$ (cf. Fig. 10(b)).

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| Equilibria | Sufficient condition for existence | Local asymptotic stability |
|------------|-----------------------------------|---------------------------|
| $E_0$      | Always                            | $h_1 > 1$ and $h_2 > r$   |
| $E_1$      | $h_1 < 1$                         | $h_1 < 1$ and $h_2 > r$   |
| $E_2$      | $h_1 < h_2$                       | $h_1 > h_2^\#$ and $h_2 < r$ |
| $E_\ast$   | $h_1 < \min \{1, h_2^\#\}$ and $h_2 < r$ | $\text{Tr}(J_*) < 0$ and $\text{Det}(J_*) > 0$ |

**Table 5.** Existence and local stability of equilibria of system (5)
Fig. 10(c) gives a two-parameter bifurcation plot with the harvesting rates as the bifurcation parameters, showing the changes in the prey population density for different harvesting rates. It is observed that the increase in the predator harvesting rate increases the maximum permissible prey-harvesting rate for coexistence. From Fig. 11(a) it is seen that the maximum permissible prey-harvesting rate is significantly low for highly apprehensive prey. It is also seen that the initial increase in the harvesting rate of the predator leads to a little increase in the prey population density, but the prey population density starts to increase at a higher rate when the harvesting rate of the predator becomes close to its maximum admissible rate for the coexistence (cf. Figs. 10(b), 11(b) and 11(d)). While the abundance of alternative resources of the predator restricts the harvesting rate of the prey, the prey population can recover for a higher rate of harvesting of the predator (cf. Figs. 11(c) and 11(d)).

6. Comparison of model results. We compare the outcomes from the three models by considering the changes in the five common parameters (viz., $\alpha$, $\beta$, $\eta_1$, $h_1$, and $h_2$) involved in the models to account for the changes in the population densities. We first perform local sensitivity analysis of each of the non-dimensional systems to identify how the changes in the non-dimensional parameters underlying the models affect the prey and predator population densities. The local sensitivity analysis of the non-dimensional models with respect to the key parameters is determined by either increasing or decreasing each of the non-dimensional parameter values that is either 90% of its original value or 110% of its original value (cf. Figs. 12 and 15).

From Figs. 12(a−c) we observe that the prey population density is most sensitive to the changes in the harvesting rate of the predator. When the predator follows Holling type II foraging, this sensitivity is maximum due to any change in the predator-harvesting rate (cf. Fig. 12(b)). Comparing Figs. 2(c), 5(c), and 10(b) it follows that with Holling type II foraging of the predator, the prey population recovers with the least predator-harvesting effort.

From Figs. 12(a−c) it is observed that due to any changes in the prey-harvesting rate, there is a maximum change in prey population density when the predator follows Holling type II foraging. Comparing Figs. 2(a−b), 5(a−b), and 10(a) it follows that prey-harvesting is the most detrimental to its growth with Holling type II foraging of the predator.

From Figs. 12(a−c) we observe that the fear effect on the prey population density is minimum when the predator follows Holling type II foraging. The Figs. 13(a−c) confirms that the prey population gets minimally affected due to predation-driven fear effect when the predator follows Holling type II foraging. At the same time, from Fig. 13(c) it follows that the fear effect is most detrimental for the prey when the predator follows Holling III foraging. In this case, harvesting the predator at a higher rate recovers the prey population density from extinction.

From Fig. 7(c) it is observed that the increase (or decrease) in the density of alternative resources of the predator leads to a sharp decrease (or increase) in the prey population density when the predator has Holling type II foraging rate. Comparing Figs. 14(a−c) it follows that the presence of a higher quantity of alternative resources of the predator is most detrimental to the prey population even with a low harvesting rate of the prey if the predator has a Holling type II foraging rate.
From Figs. 15(a−c) we see that for Holling type III foraging rate of the predator, any increase (or decrease) in the density of alternative resource leads to a maximum increase (or decrease) in the predator population density. We also observe that the predator-intraspecific competition has the most negative effect on the predator growth for linear foraging rate of the predator (Fig. 15(a)).

Tables 6 and 7 compare the critical parameter values of one-parameter bifurcations and the size of the basins of recovery for the changes in any two parameters respectively for the three foraging types.

| Bifurcation parameter | Linear | Holling type II | Holling type III |
|-----------------------|--------|----------------|-----------------|
| $h_1$ ($h_2 < r$)     | $h_1^* = 0.8971$ TB | $h_1^{**} = 0.1475$ SNB | $h_1^* = 0.79$ TB |
| $h_1$ ($h_2 > r$)     | $h_1^* = 1$ TB | $h_1^{**} = 1$ TB | $h_1^* = 1$ TB |
| $h_2$ ($h_1 < 1$)     | $h_2^* = 1$ TB | $h_2^{**} = 0.79$ SNB | $h_2^* = 1$ TB |
| $\beta$ ($h_1 < 1 \& h_2 < r$) | $\beta^{**} = 16.8$ TB | $\beta^{**} = 16$ SNB | $\beta^{**} = 1.5$ TB |
| $\eta_1$ ($h_1 < 1 \& h_2 < r$) | $\eta_1^* = 0.825$ TB | $\eta_1^* = 0.2$ SNB | $\eta_1^* = 0.3721$ TB |

Table 6. Comparison of the critical threshold values for transcritical bifurcation (TB) and saddle-node bifurcation (SNB) of the three systems.

| Parameters | Largest basin of recovery | Smallest basin of recovery |
|------------|--------------------------|---------------------------|
| $h_1 \& h_2$ | Linear | Holling type II |
| $h_1 \& \beta$ | Linear | Holling type III |
| $h_2 \& \beta$ | Holling type III | Holling type II |
| $h_1 \& \eta_1$ | Linear | Holling type II |
| $h_2 \& \eta_1$ | Linear | Holling type II |

Table 7. Bifurcation parameters with different foraging types and corresponding basins of attraction at $E^*$.

7. Conclusion. We have studied the dynamics of three prey-predator systems by incorporating predation-mediated fear effect in the prey reproduction and three different foraging types of the generalist predator. Our models assume density-dependent harvesting of the prey and the predator as a possible control strategy. The main purpose of our study is to show how the effect of fear with different foraging types of the predator affects prey-population growth. We have analyzed the three systems and have determined the critical parameter thresholds for the changes in the dynamics of the systems. By changing the key parameters of the systems, we observed that the systems with linear and Holling type III foraging rates exhibit transcritical bifurcation only, whereas, the system with Holling type II foraging rate of the predator exhibits a qualitatively different dynamical behaviour including transcritical, saddle-node, and Hopf bifurcations.

We observed that the effect of predation-driven fear on the prey is maximum when the predator has a Holling type III foraging rate. The effect of fear on the prey population density is least for the predators having Holling type II foraging rate. We also observe that a high density of alternative resources of the predator is
detrimental for the prey population growth when the predator follows Holling type III foraging. To investigate the effect of harvesting as a possible control strategy, we plot two-parameter bifurcation diagrams with harvesting rate and another key model parameter as active parameters. It is observed that the higher rate of harvesting of the predator helps in recovering the prey population density affected by the fear effect. In case of an abundance of alternative resources of the predator, a higher rate of harvesting of the predator is necessary for protecting the prey population from possible extinction. It is also observed that harvesting of the prey at a higher rate is always detrimental to the prey population irrespective of the type of foraging of the predator.

It is observed that for the linear foraging type of the predator, the basin of recovery for varying harvesting rates is the largest compared to the same for the other two foraging types, whereas the basin of recovery is the smallest for Holling type II foraging of the predator. We also observed that the average prey density in the basin of recovery is the least for Holling type III foraging compared to the other two counterparts.

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Conflict of interest. The authors declare that they have no conflict of interest.

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Figure 4. Mutual position of prey-nullclines (red) and predator-nullclines (blue) of the system (4) due to the changes in $h_1$ and $h_2$, all other parameters are taken from Table 2. (a) The system is LAS at the unique interior equilibrium $E^*_1$ ($E_0$, $E_1$, and $E_2$ are unstable). (b) The system has bistability at $E_2$ and $E^*_1$ ($E_0$, $E_1$, and $E^*_2$ are unstable). The system is LAS at (c) $E_2$ ($E_0$ and $E_1$ are unstable; $E^*_2$ does not exist), (d) $E_2$ ($E_0$ is unstable; $E^*_2$ and $E_1$ do not exist), (e) $E_1$ ($E_0$ is unstable; $E^*_2$ and $E_2$ do not exist) and (f) $E_0$ ($E^*_1$, $E_1$, and $E_2$ do not exist) ($i = 1, 2$).
Figure 5. One-parameter bifurcation plots of the system (4) due to the changes in $h_1$ (a) for $h_2 < r$ and $\eta_1 = 0.05$, where a transcritical bifurcation occurs at $h_1^{*}=0.6585$; (b) for $h_2 < r$ and $\eta_1 = 0.125$, a transcritical and a saddle-node bifurcation occur at $h_1^{*} = 0.1475$ and $h_{1cr} = 0.3685$ respectively. One-parameter bifurcation plots of the system (4) due to the changes in $h_2$ (c) for $h_1 < h_1^{*}$ and $\eta_1 = 0.05$, where a transcritical bifurcation occurs at $h_2^{*} = 0.3495$; (d) for $h_1 < h_1^{*}$ and $\eta_1 = 0.125$, a transcritical and a saddle-node bifurcation occur at $h_2^{**} = 0.74$ and $h_{2sn} = 0.64$ respectively.
Figure 6. Two-parameter bifurcation plots with $h_1$ and $h_2$ as bifurcation parameters where (a) $\eta_1 = 0.05$ and (c) $\eta_1 = 0.25$, where $f_{SN} = 0$ is a saddle-node bifurcation curve, $h_i = h_i^{**}$ ($i = 1, 2$) and $h_2 = r$ are transcritical bifurcation curves.
Figure 7. Two-parameter bifurcation plots with the bifurcation parameters (a) $h_1$ and $\beta$, (b) $h_2$ and $\beta$, (c) $h_1$, and $\eta_1$, (d) $h_2$ and $\eta_1$; other parameter values are taken from Table 2.
Figure 8. (a) For $\alpha = 0.4993$, the phase space shows the existence of stable (in green) and unstable (in red) manifolds of the system (4). The unstable limit cycle around $E_1^*$ is represented in blue. The curves representing the changes in (b) $\text{Tr}(J_1^*)$, $\text{Det}(J_1^*)$ and (c) $\frac{d}{d\alpha}\text{Tr}(J_1^*)$ due to the changes in $\alpha$ verify the occurrence of a Hopf bifurcation of the system (4) at $\alpha = 0.4993$. 
Figure 9. Mutual position of prey-nullclines (red) and predator-nullclines (blue) of the system (5) due to the changes in $h_1$ and $h_2$, other parameters are taken from Table 1. The system is LAS at (a) $E_*$ ($E_0$, $E_1$ and $E_2$ are unstable), (b) $E_2$ ($E_0$ and $E_1$ are unstable; $E_*$ does not exist), (c) $E_1$ ($E_0$ is unstable; $E_*$ and $E_2$ do not exist) and (d) $E_0$ ($E_*$, $E_1$ and $E_2$ do not exist).
Figure 10. One-parameter bifurcation plots of the system (5) due to the changes in (a) $h_1$ where $h_2 < r$, (b) $h_2$ where $h_1 < h_1^\#$. (c) A two-parameter bifurcation plot with $h_1$ and $h_2$ as bifurcation parameters, where $h_1 = 1$, $h_1 = h_1^\#$ and $h_2 = r$ are transcritical bifurcation curves. All other parameters are taken from Table 2.
Figure 11. Two-parameter bifurcation plots of the system (5) with the bifurcation parameters (a) $h_1$ and $\beta$, (b) $h_2$ and $\beta$, (c) $h_1$ and $\eta_1$, (d) $h_2$ and $\eta_1$, where $h_1 = h_{1}^{\#}$, $h_2 = h_{2}^{\#}$, and $h_2 = r$ are transcritical bifurcation curves.
Figure 12. Local sensitivity of the prey response for (a) linear, (b) Holling type II, and (c) Holling type III foraging of the predator. For comparison, model simulations before parameter manipulations, are shown in black line. The prey density from simulations where particular parameter values were increased by 10% are shown in red lines, as are the prey density from simulations where particular parameter values were decreased by 10% in blue lines.
Figure 13. One-parameter bifurcation plots due to the changes in $\beta$, where $h_1 < 1$ and $h_2 < r$ for (a) linear, (b) Holling type II, and (c) Holling type III foraging rates.
Figure 14. One-parameter bifurcation plots due to the changes in $\eta_1$, where $h_1 < 1$ and $h_2 < r$ for (a) linear, (b) Holling type II, and (c) Holling type III foraging rates.
Figure 15. Local sensitivity of the predator response for (a) linear, (b) Holling type II, and (c) Holling type III foraging of the predator. For comparison, model simulations before parameter manipulations, are shown in black line. The predator density from simulations where particular parameter values were increased by 10% are shown in red lines, as are the predator density from simulations where particular parameter values were decreased by 10% in blue lines.