Predator-prey ecosystem with group defence in prey against generalist predator

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Abstract

In this paper we proposed a population model depicting the dynamics of a prey showing group defence against a generalist predator. The group defence characteristic is represented by Hassell-Varley functional response. We studied the local and global stability and behaviour of the model around the co-existent equilibrium solution. Analysis on Hopf bifurcation and power spectra has also been done. Numerical simulations have been done to confirm the obtained analytical results as well as to validate the proposed model.

Keywords: Group Defence, Hassell-Varley Functional Response, Generalist Predator, Power Spectra, Global Stability, Indirect Control

1. Introduction

Conserving biodiversity and managing the resources of a particular ecosystem are points of major concern nowadays. Though there has been human intervention in the field of wildlife management, forestry, fishery etc.\cite{1, 2}, there are processes such as interactions among trophic levels, which also contribute to keeping the natural balance. Predator-prey was mathematically represented by Volterra in the 1920s. Later for modelling population dynamics of different ecosystems, the model has been modified to fit in various environmental and population behaviours such as growth rate, carrying capacity, food availability, mating frequency, fertility rate, predation rate etc. Among them, the predation rate plays a crucial role in the co-existence of both species, which is shown by the functional response in a model. Numerous articles on observations and applications of different types of functional responses such as Holling type (type I, II, III, IV), Beddington-deAngelis, Rosenzvig-MacArthur, Crowley-Martin etc. have been studied in past years.

The dynamics of prey may have a significant effect due to predators in trophic systems. Depending upon the type of predation, it has been pointed out by Hanski et al.\cite{3} that while the specialist predators(mustelids) contribute to the multi-annual cycles of rodent populations of northern Europe, the generalist predators, e.g. foxes, buzzards, cats may be responsible in stabilizing the rodent population in southern localities.

Taking a food chain model of generalist, specialist predators and prey, Upadhyaya et al.\cite{4} discussed the existence of chaos in an ecological model. Hassel and Varley introduced a new functional response function to consider the behaviour of grouping in 1969\cite{5}.

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After that, there had been numerous research articles showing the behaviour of the functional response in various ecosystems. This depicts the situation when in some interacting populations, predators form group to attack prey to maximize the predation rate. Several research papers are published on the study of various aspects of such ecosystem. Hsu et al. [6] studied the global dynamics of such model. Kim and Baek [7] studied the impulsive effect on such system. In such cases functional response is both prey and predator density dependant where the predators are assumed to move forming a dense colony [8]. Moreover, there are many biological shreds of evidence of group defence [9] and group vigilance (the many-eyes effect) [11] where preys form group against attacking predators to protect their species from extinction by decreasing the rate of predation. In such cases, the functional response is prey density dependant as preys are assumed to stay or move in groups and predators are assumed to have a homogeneous spatial distribution [8]. Batabyal et al. [12], in their paper, considered such functional response and studied the blow-up criterion with mutualistic preys.

Control strategies in a predator-prey system may serve several purposes such as proper utilization of resources, maintaining ecological balance etc. [10]. Generalist species can survive a wide number of different environmental conditions and may depend upon a wide variety of resources, whereas specialist species can survive a comparatively lower range of environmental conditions and prey upon limited food sources. Monophagous species are dependent upon only a particular type of food source.

1.1. The model

Here, in this paper we shall study the following prey-predator model with Hassell-Varley functional response [12] showing group defence among prey \( X \) against predation and the predator, in this model, is a generalist predator \( Y \). In this paper, we have considered that the prey species \( X \) is the favourite food source of the predators. The model is represented as follows:

\[
\begin{align*}
\frac{dX}{dT} & = RX \left(1 - \frac{X}{K}\right) - \frac{MXY}{X^p + C}, \\
\frac{dY}{dT} & = \left(D - \frac{E}{X + A}\right)Y^2,
\end{align*}
\]

where \( X(T) > 0 \) and \( Y(T) > 0 \) are respectively the densities of the prey and predator species at time \( T \). The description of model parameters along with their symbols are presented in Table 1. The value of the Hassell-Varley constant \( p \) lies between 0 to 1 [7] as \( p = 0 \) implies

| Parameters | Description |
|------------|-------------|
| \( R \)   | Intrinsic growth rate of the prey species \( X \) |
| \( K \)   | Carrying capacity for the preys |
| \( M \)   | Maximum predation rate |
| \( C \)   | The protection provided to the prey population by the environment |
| \( D \)   | Reproduction rate of the generalist predator by sexual reproduction |
| \( E \)   | Maximum rate of death of predator population |
| \( A \)   | Measures the other food sources available for the predator species |
| \( p \)   | The Hassell-Varley constant |

Table 1: Biological meaning of the parameters for model (1)

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the absence of group defence in prey and $p = 1$ implies that the whole prey population acts as one group during the defence against predation. All other parameters are considered positive.

After using the transformations $x = X/K$, $y = Y/K$ and $t = RT$, the non-dimensional form of the system (1) becomes,

$$\frac{dx}{dt} = x(1 - x) - \frac{mxy}{x^p + c},$$

$$\frac{dy}{dt} = \left(d - \frac{e}{x + a}\right)y^2,$$

(2)

where, $m = \frac{M}{RK^{p-1}}$, $c = \frac{C}{K^p}$, $d = \frac{DK}{R}$, $e = \frac{E}{R}$ and $a = \frac{A}{K}$.

The paper is organized as follows. Firstly, in section 1.1 the model is formulated. Then in section 2 some preliminary results have been obtained for the system such as positive invariance in subsection 2.1, boundedness of the system in subsection 2.2. The local stability and global stability of the interior equilibrium point of the system has been discussed along with its stability criteria in subsection 3.1 and 3.2 respectively. In section 4, Hopf bifurcation of the system is discussed. After that to check the validation of our obtained analytical results we have presented numerical simulations for stability, Lyapunov exponent, Hopf bifurcation and power spectra are presented in section 4. A method of indirect control for the system is discussed in section 6. Finally, the paper ends with the conclusion and discussion of our work in section 7.

2. Preliminary Results

2.1. Positivity

Integrating the system (2), we have,

$$x(t) = x_0 \exp \left[ \int_0^t \left( 1 - x(\tau) - \frac{my(\tau)}{x(\tau)^p + c} \right) d\tau \right],$$

$$y(t) = y_0 \exp \left[ \int_0^t \left( d - \frac{e}{x(\tau) + a} \right) y(\tau) d\tau \right],$$

(3)

where, $x_0 = x(0)$ and $y_0 = y(0)$.

From the above expression, we conclude that, $x(t), y(t) > 0$ if $x_0, y_0 > 0$. Hence, the dynamics will always stay in $\mathbb{R}_+^2$ if the initial conditions are positive. This shows that the system has positive solution.

2.2. Boundedness

In the previous subsection we can see that the system (2) has a positive solution with the positive initial condition. Now we show that the solutions of the system (2) is bounded. Before proving, we first state a lemma which will be used to prove our statement given below in Theorem 2.3.
Lemma 2.1. [13] Let $\sigma(t)$ be an absolute continuous function with $k_1, k_2 \in \mathbb{R}$ and $k_1 \neq 0$ s.t.

$$\sigma'(t) + k_1 \sigma(t) \leq k_2, \forall t \geq 0,$$

then, for all $t \geq \tilde{T} \geq 0$,

$$\sigma(t) \leq \frac{k_2}{k_1} - \left( \frac{k_2}{k_1} - \sigma(\tilde{T}) \right) \exp(-k_1(t - \tilde{T})).$$

Lemma 2.2. [19] If for $t \geq 0$ and $x(0) \geq 0$ we have $\dot{x} \geq x(c - dx)$ where $c > 0, d > 0$ then

$$\lim_{t \to \infty} \inf x(t) \geq \frac{c}{d},$$

and if for $t \geq 0$ and $x(0) \geq 0$ we have $\dot{x} \leq x(c - dx)$ where $c > 0, d > 0$ then

$$\lim_{t \to \infty} \sup x(t) \leq \frac{c}{d}.$$

Theorem 2.3. The solutions of the system (2), originating in $\mathbb{R}_+^2$, are bounded, provided the conditions $\mu < \frac{dx_+}{x_+^2 + c}$ and $d - \frac{e}{x_+ + a} < \frac{d}{m} \left( \frac{x_+}{y_+} \right)^2$ hold, where $(x_+, y_+)$ is the interior equilibrium point and $\mu = \min \{m, e\}$.

Proof. From the system (2), we can write,

$$\frac{dx}{dt} \leq x(1 - x) \implies x(t) \leq 1 = M_1. \quad (4)$$

So, $x(t)$ is bounded for all $t$.

Now, we have to show $y(t)$ is bounded in $\mathbb{R}_+^2$. To do that, let us first divide the invariant region $\mathbb{R}_+^2$ into three regions using the $x$-nullcline $1 - x - \frac{my}{x^p + c} = 0$ and the $y$-nullcline $d - \frac{e}{x + a} = 0$. Doing so, we will get three regions which can be represented by considering the signs of $x'(t)$ and $y'(t)$.

Let region I is where $y' < 0$, region II is where $x' > 0$ as well as $y' > 0$ and region III is where $x' < 0$ & $y' > 0$.

In region I, $y' < 0$. Hence, $y(t)$ is decreasing ans as $\mathbb{R}_+^2$ is invariant, so $y(t)$ will be bounded in region I.

In region II, $x' > 0$ and $y' > 0$. We have to show $y(t)$ is bounded in region II. As $x(t)$ is bounded everywhere, so $\frac{1}{m}(1 - x)(x^p + c)$ is bounded by some positive number. By contradiction, let $y(t)$ increases unboundedly. Let $\tilde{M}$ is a positive integer such that

$$\tilde{M} > \max \left\{ \frac{1}{m}(1 - x)(x^p + c) \right\},$$

then there exists a neighbourhood $N(\tilde{T})$, for an instant time $\tilde{T}$, where $y' > 0$ such that $y(t) > \tilde{M}$, $\forall t \in N(\tilde{T})$. Then

$$x' = \frac{mx}{x^p + c} \left[ \frac{1}{m}(1 - x)(x^p + c) - y \right] < 0.$$
As $y$ increases more and more, $x'$ decreases more and more. Eventually, at some point $x < x_*$ and then $y' < 0$. Hence, $y(t)$ can not increase indefinitely, which is in contrast with the assumption. Therefore, $y(t)$ is bounded in region II.

In region III, $x' < 0$ and $y' > 0$. Let $\sigma(t) = \frac{d}{m} x(t) + y(t)$, then, for $\mu = \min\{m, e\}$,

$$\sigma'(t) = \frac{d}{m} x'(t) + y'(t)$$

and

$$\sigma' + \mu \sigma = \frac{d}{m} (1 + \mu) x(t) + A_1 y + A_2 y^2,$$

where, $A_1 = \mu - \frac{dx}{x^p + c}$, and $A_2 = d - \frac{e}{x + a} - \frac{d}{m} \left( \frac{x}{y} \right)^2$.

Now, if we choose, $\mu < \frac{dx}{x^p + c} + \frac{e}{x + a}$, then $A_1 < 0$ and $A_2 < 0$, so

$$\sigma' + \mu \sigma \leq \frac{d}{m} (1 + \mu) x(t) \leq \frac{d}{m} (1 + \mu) = M_2 \mu$$

or

$$\sigma(t) \leq M_2 - M_2 \exp(-\mu (t - \tilde{T})) \leq M_2, \text{ for all } t > \tilde{T} \geq 0$$

or

$$y(t) \leq M_2, \text{ letting } \tilde{T} = 0,$$  \hspace{1cm} (5)

where $M_2 = \frac{d}{m \mu} (1 + \mu)$. Hence, $y(t)$ has upper bound in region III.

Again from the first equation (2), we can write

$$\frac{dx}{dt} \geq x \left\{ 1 - \frac{m M_2}{1 + c} - x \right\}.$$ \hspace{1cm} (6)

Using Lemma 2.2, we can write

$$\lim_{t \to \infty} x(t) \geq m_1^x,$$ \hspace{1cm} (7)

where, $m_1^x = 1 - \frac{m M_2}{1 + c}$. Similarly from the second equation of system (2), we get

$$\lim \inf_{t \to \infty} y(t) \geq m_2^y,$$ \hspace{1cm} (8)

where, $m_2^y = \frac{1 + a}{(1-a)(1+a) - a}$. Hence from (11) & (17) and (5) & (8), we have

$$m_1^x \leq \lim \inf_{t \to \infty} x(t) \leq x(t) \leq M_1,$$

$$m_2^y \leq \lim \inf_{t \to \infty} y(t) \leq y(t) \leq M_2,$$

with positive initial condition, i.e. $x(0) > 0$, $y(0) > 0$.

As $x(t)$ is bounded in $\mathbb{R}_+^2$ and $y(t)$ is bounded in all three regions of $\mathbb{R}_+^2$, hence, the system (2) is bounded in $\mathbb{R}_+^2$, when the given conditions hold.

\[3. \text{ Stability Analysis}\]

\[3.1. \text{ Local Stability}\]

In this section, we will study the local stability of the interior equilibrium point of the system (2). Computing equilibrium solutions for the system (2), we will have the only interior equilibrium point $(x_*, y_*)$, where,

$$x_* = \frac{e}{d} - a \text{ and } y_* = \frac{1}{m} \left( 1 - \frac{e}{d} + a \right) \left[ \left( \frac{e}{d} - a \right)^p + c \right].$$
Using linear analysis, the Jacobian of the system \((\mathbf{2})\) calculated at the interior equilibrium point is,

\[
J(x^*, y^*) = \begin{pmatrix}
J_{11} & J_{12} \\
J_{21} & J_{22}
\end{pmatrix},
\]

where, \(J_{11} = \frac{m x^*_p y_*}{(x^*_p + c)^2} - x_*\), \(J_{12} = -\frac{m x_*}{x^*_p + c}\), \(J_{21} = \frac{d^2 y^2_*}{e}\), \(J_{22} = 0\).

The characteristic equation is given by,

\[
\lambda^2 - P_1 \lambda + P_2 = 0,
\]

(9)

where,

\[
P_1 = \frac{m x^*_p y_*}{(x^*_p + c)^2} - x_* \quad \text{and} \quad P_2 = \frac{m x_* d^2 y^2_*}{x^*_p + c} e.
\]

From equation (9), we will have,

\[
\lambda_{1,2} = \frac{P_1 \pm \sqrt{P^2_1 - 4P^2_2}}{2}.
\]

(10)

As \(P_2 > 0\) always, so, \((x^*, y^*)\) is locally asymptotically stable when \(P_1 < 0\) and is locally asymptotically unstable when \(P_1 > 0\).

### 3.2. Global Stability

Here, we shall discuss the global stability of the system \((\mathbf{2})\) by prescribing a suitable Lyapunov function.

**Theorem 3.1.** The system \((\mathbf{2})\) is globally asymptotically stable if the following inequalities holds.

\[
y_* \left( x_* \right) - \frac{1 + a}{(1 - d)(1 + a) - d} > 0,
\]

(11)

and

\[
\frac{dx_*}{a} - \frac{1}{4} \left( \frac{cm}{(1 + c)(x^*_p + c)} - \frac{e y_*}{a(x_* + a)} \right)^2 > 0
\]

(12)

*Proof.* Let \(D = \{(x, y) \in \mathbb{R}^2: x > 0 \& y > 0\}\). Let \(V: \mathbb{D} \to \mathbb{R}\) s.t.

\[
V(x, y) = \left[ x - x_* - x_* \ln \frac{x}{x_*} \right] + \left[ y - y_* - y_* \ln \frac{y}{y_*} \right].
\]

(13)

Clearly, \(V(x^*, y^*) = 0\) and \(V(x, y) > 0\) for \((x, y) \neq (x^*, y^*)\). Now, the time derivative of the equation in (13) along the solution of the system \((\mathbf{2})\) is given by

\[
\frac{dV}{dt} = (x - x_*) \frac{x'}{x} + (y - y_*) \frac{y'}{y}
\]

\[
= (x - x_*) \left( 1 - x \frac{my}{x^*_p + c} \right) + (y - y_*) \left( dy - \frac{ey}{x + a} \right)
\]

(14)
At the equilibrium point \((x_*, y_*)\) from the system (2),

\[
1 - x_* - \frac{my_*}{x_*^p + c} = 0
\]
\[
dy_* - \frac{ey_*}{x_* + a} = 0.
\] (15)

Using the equations from (15) in (14), we have,

\[
\frac{dV}{dt} = (x - x_*) \left( x_* + \frac{my_*}{x_*^p + c} - x - \frac{my}{x^p + c} \right) + (y - y_*) \left( dy - \frac{ey}{x + a} - dy_* + \frac{ey_*}{x_* + a} \right)
\]

\[
= T_1 + T_2.
\]

Now,

\[
T_1 = -(x - x_*)^2 - m(x - x_*) \left( \frac{y}{x^p + c} - \frac{y_*/x^p}{x_* + c} \right)
\]

\[
\implies T_1 = -(x - x_*)^2 - m(x - x_*)T_3
\] (16)

Hence,

\[
T_3 = \frac{x^p y + cy - x^p y_* - cy_*}{(x^p + c)(x_*^p + c)}
\]

\[
\implies T_3 = \frac{c(y - y_*)}{(x^p + c)(x_*^p + c)} - \frac{x^p y_* - x_*^p y}{(x^p + c)(x_*^p + c)}
\] (17)

For \(x^p y_* > x_*^p y\), we can have,

\[
\frac{y_*}{x_*^p} > \frac{1 + a}{(1 - d)(1 + a) - d}.
\] (18)

So, when (11) holds, (17) becomes,

\[
T_3 \geq \frac{c(y - y_*)}{(1 + c)(x_*^p + c)}
\] (19)

From (16) & (19),

\[
T_1 \leq -(x - x_*)^2 - \frac{cm(x - x_*)(y - y_*)}{(1 + c)(x_*^p + c)}.
\] (20)

Again,

\[
T_2 = (y - y_*) \left( dy - \frac{ey}{x + a} - dy_* + \frac{ey_*}{x_* + a} \right)
\]

\[
= d(y - y_*)^2 + e(y - y_*) \frac{xy_* + ay_* - yx_* + ay}{(x_* + a)(x + a)}
\]

\[
< d(y - y_*)^2 + e(y - y_*) \frac{xy_* + ay_* - yx_* + ay}{a(x_* + a)}
\]

\[
< \left( d - \frac{e}{x_* + a} - \frac{ex_*}{a(x_* + a)} \right) (y - y_*)^2 + \frac{e}{x_* + a} (y - y_*)^2
\]

\[
+ \frac{ey_*}{a(x_* + a)} (x - x_*)(y - y_*)
\]

i.e,

\[
T_2 < - \left( \frac{e - d}{a} \right) (y - y_*)^2 + \frac{ey_*}{a(x_* + a)} (x - x_*)(y - y_*)
\] (21)

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From (20) & (21), the time derivative becomes,
\[
\frac{dV}{dt} < - (x - x_*)^2 - \frac{cm}{(1 + c)(x_p + c)}(x - x_*)(y - y_*)
- \left(\frac{e}{a - d}\right)(y - y_*)^2 + \frac{ey_*}{a(x_* + a)}(x - x_*)(y - y_*)
\]
\[
\Rightarrow \frac{dV}{dt} < -X^TAX
\]
(22)

where,
\[
X = \begin{bmatrix} x - x_* \\ y - y_* \end{bmatrix} \quad \text{and} \quad A = \begin{bmatrix} 1 & \frac{cm}{2(1+c)(x_p + c)} - \frac{ey_*}{2a(x_* + a)} \\ \frac{cm}{2(1+c)(x_p + c)} - \frac{ey_*}{2a(x_* + a)} & \frac{e}{a - d} \end{bmatrix}
\]
(23)

As \( x_* = \frac{e}{a} - d \), so, \( \frac{e}{a} - d = \frac{dy_*}{dx_*} \). When equation (12) holds then \( A \) becomes a positive definite matrix and hence \( V(x, y) \) will be a Lyapunov function for the system (2). Thus the system (2) is globally asymptotically stable if conditions (11) & (12) holds.

4. Hopf-bifurcation of the system (2)

The subject of bifurcation is a vast area to do research. In a system of differential equations Hopf-bifurcation happens when the complex conjugate set of eigenvalues of a linearised system become purely imaginary at a fixed point. So with these conditions, a system that contains at least two equations may have Hopf-bifurcation. Hopf-bifurcation occurs at a point where a system changes state from stable to unstable, i.e. it is a local bifurcation in which a fixed point of a dynamical system loses stability. Here, we shall discuss the Hopf-bifurcation of the system (2) at the interior equilibrium point \((x_*, y_*)\). From the eigenvalues, as in (10), of the Jacobian matrix of the system (2) calculated at the point \((x_*, y_*)\), will show Hopf-bifurcation when, \( P_1^2 < 4P_2 \), i.e.,
\[
\left[ \frac{mpx_*y_*}{(x_p + c)^2} - x_* \right]^2 < 4\frac{mx_*}{x_p + c} \frac{d^2y_*^2}{e}.
\]
(24)

The point of Hopf-bifurcation is obtained when \( Re(\lambda_{1,2}) = 0 \), i.e,
\[
P_1 = 0 \quad \Rightarrow \quad mpx_*^{p-1}y_* = (x_p + c)^2
\]
\[
\Rightarrow \quad p\left(1 - \frac{e}{d} + a\right) = \left(\frac{e}{d} - a\right) + c\left(\frac{e}{d} - a\right)^{1-p}.
\]
(25)

So, the system enters into Hopf-bifurcation at \( p = p_1 \) around \((x_*, y_*)\) when (24) holds and
\[
p_1\left(1 - \frac{e}{d} + a\right) = \left(\frac{e}{d} - a\right) + c\left(\frac{e}{d} - a\right)^{1-p_1}.
\]

5. Numerical simulation

The following numerical simulations have been carried out in support of the theoretical results obtained and for the clear illustration of the characteristics and behaviour of the model. All the theoretical findings are verified by numerical simulations.
At first, in Figure (1), we illustrated phase portraits and time series of the dynamics around interior equilibrium point which shows the stable nature of the interior equilibrium point of the system (2). The parameter set considered for this is $m = 1.2$, $p = 0.7$, $c = 0.3$, $d = 0.4$, $e = 0.25$, $a = 0.2$. Then, in Figure (2), the phase portrait and time series of the stable limit cycle around the unstable interior equilibrium point of the system (2) are illustrated. The parameter set considered for this is $m = 1.2$, $p = 0.7$, $c = 1$, $d = 0.7$, $e = 0.2$, $a = 0.2$.

Figure 1: (a) Phase portrait (b) Time series for the stable interior equilibrium point for parameters $m = 1.2$, $p = 0.7$, $c = 0.3$, $d = 0.4$, $e = 0.25$, $a = 0.2$.

Figure 2: (a) Phase portrait (b) Time series of the system (2) for the stable limit cycle around unstable equilibrium point for parameters $m = 1.2$, $p = 0.7$, $c = 1$, $d = 0.7$, $e = 0.2$, $a = 0.2$. 
Here, we have calculated the power spectra for the system (2) using the values of the sequence \( x_n \) \((n = 1, 2, 3, \ldots)\). The sequence \( y_n \) is not considered. The values after 1000 iterations are taken so that the long term behaviour can be taken into consideration. The sampling frequency is taken at 1 Hz. 2000 sample points are taken for analysing the attractor. The FFT length taken to calculate the power spectra is 1024. Power spectra of the system (2) are illustrated in Figure (4) for asymptotic stable interior equilibrium point and stable limit cycle around the unstable interior equilibrium point.

The global stability of the system (2) is ensured and shown in figure (5) with different initial conditions for the parameter values \( m = 1.2, \ p = 0.7, \ c = 0.3, \ d = 0.4, \ e = 0.25, \ a = 0.2 \) as these satisfy the conditions in (11) & (12).
Figure 5: Global stability of the system \( (2) \) for interior equilibrium point for parameter values \( m = 1.2, p = 0.7, c = 0.3, d = 0.4, e = 0.25, a = 0.2 \).

The Hopf bifurcation in \( p \) for the system \( (2) \) for parameter set \( m = 1.2, c = 0.25, d = 1, e = 0.45, a = 0.2 \) performed and illustrated in figure \( (6) \). The point of bifurcation is \( p_1 = 0.5 \). When \( p < 0.5 \), the interior equilibrium point is a stable node but when \( p \) crosses the bifurcation point \( p_1 = 0.5 \), the equilibrium point becomes unstable and a stable limit cycle arises surrounding the equilibrium point which is the characteristic of supercritical Hopf bifurcation.
Figure 6: (a) Phase portrait of the system (2) showing asymptotic stability of interior equilibrium point for parameters $m = 1.2$, $c = 0.25$, $d = 1$, $e = 0.45$, $a = 0.2$, $p = 0.3$. (b) Phase portrait of the system (2) showing stability of limit cycle around unstable interior equilibrium point for parameters $m = 1.2$, $c = 0.25$, $d = 1$, $e = 0.45$, $a = 0.2$, $p = 0.7$. (c) Bifurcation diagram of the system (2) showing Hopf bifurcation in $p$.

6. Indirect control

Here, in this section, we discuss an indirect control method to manipulate the behaviour of the dynamics of the system (2) to meet our objective.

In earlier cases, we saw that the stability of the system varies as the set of the parameters changes value. The parameter values for a system is dependent on the ecosystem, environment, distribution of population, nature of the species etc. So, with some environmental conditions, we may have the interior equilibrium point unstable. Hence, the main objective of introducing control to our model is to make unstable interior equilibrium point stable.
by means of introducing a control parameter. The physical interpretation of a control parameter may mean introducing juveniles to the population, taking out individuals from the population (may be by harvesting) or natural controls etc.

Considering the parameter set \( m = 1.2, p = 0.7, c = 1, d = 0.7, e = 0.2 \) and \( a = 0.2 \), we have an locally unstable interior equilibrium point. Now, our objective is to make the equilibrium point stable using a characteristic function by the method of indirect control.

Let \( \xi = \xi(t) \) be the control parameter which controls the food source of the generalist predator species \( y(t) \). Let the dynamics of \( \xi \) is determined by a characteristic function \( \varphi(\sigma) \), where \( \sigma = \sigma(t) \) is a linear combination of the population densities and the control parameter itself.

The characteristic function \( \varphi(\sigma) \) is admissible [14] if

(i) it is defined and continuous for all \( \sigma \in \mathbb{R} \);

(ii) \( \varphi(0) = 0 \) and \( \sigma \varphi(\sigma) > 0 \) when \( \sigma \neq 0 \), i.e., \( \varphi(\sigma) \) maintains the sign of \( \sigma \);

(iii) the integral \( \int_{0}^{\pm\infty} \varphi(\sigma) d\sigma \) diverges.

Incorporating \( \xi \) in the system (2), we have,

\[
\begin{align*}
\frac{dx}{dt} &= x(1 - x) - \frac{mxy}{x^p + c}, \\
\frac{dy}{dt} &= \left(d - \frac{e}{x + a - b\xi}\right) y^2, \\
\frac{d\xi}{dt} &= \varphi(\sigma),
\end{align*}
\]

(26)

where \( \sigma = b_1x + b_2y - b_3\xi \).

Considering the linear function \( \varphi(\sigma) = \sigma \), we have, all the admissibility criteria followed by \( \varphi(\sigma) \). Hence, we have, for \( \frac{d}{dt} \equiv ' \),

\[ \xi' = b_1x + b_2y - b_3\xi. \]

Along with above parameter set, let, \( b = 0.3, b_1 = 0.3, b_2 = 0.2 \) and \( b_3 = 0.7 \), the interior equilibrium point becomes locally asymptotically stable which was earlier unstable.

Numerical simulations, carried out to support the theory, is shown below.
Figure 7: Here, * & o respectively denote the interior equilibrium point and the initial point. (a) phase portrait of the system showing unstable equilibrium point with \(b = 0\) (without control) (b) phase portrait of the system showing stable interior equilibrium point with \(b = 0.3, b_1 = 0.3, b_2 = 0.2\) & \(b_3 = 0.7\) (with control).

Here, we observed that, introducing the indirect control to the system, the interior equilibrium point of the system changes but the new equilibrium point, eventually, becomes asymptotically stable.

7. Conclusion

In this paper, we have discussed the behaviour of a prey-predator system with generalist predator and prey having logistic growth with Hassell-Varley functional response which is only prey density dependent.

The stability of the interior equilibrium point is discussed and the local stability criteria are derived. Numerical simulations show the existence of a stable limit cycle around the interior equilibrium point for some parameter set. Lyapunov exponents confirm the nature of the equilibrium point and limit cycle. The global stability of the system is ensured when the system parameters satisfy the stated inequalities. Occurrence of Hopf bifurcation in \(p\), the Hassell-Varley constant, for the interior equilibrium point is observed at \(p = 0.5\) for the set of parameters \(m = 1.2, c = 0.25, d = 1, e = 0.45\) and \(a = 0.2\) for the system. Power spectra of prey population \(x(t)\) is obtained for both of the cases, i.e. when the interior equilibrium point is stable and when there a stable limit cycle around the unstable interior equilibrium point. The time series plots show the abundance of species over time, whereas the power spectra indicates at which frequencies the variations are strong or weak. We observed some cases with certain parameter sets that lead to unstable interior equilibrium and then to make the system stable, indirect control is introduced by the control parameter \(\xi\).

Presence of generalist predators has a greater contribution to the dynamics of the model as they have interesting characteristics comparing to any other predators. Habitat loss and fragmentation are thought to be essential aspects in species extinction [15]. As generalist predators have a wide number of food sources and are compatible with various changes in environmental conditions than specialist predators, so they are thought to be less susceptible
to habitat fragmentation and habitat edge than specialist predators\[16\]. Moreover, they have a stabilizing effect on a cycle driven by specialist predators\[3\]. In our model also, we observe the same that the generalist predators do not go extinct even if the prey species goes extinct as there is always a growth term $dy^2$. In this model, for most of the cases, we have either a stable limit cycle or a stable equilibrium solution.

There are many examples where generalist predators prey upon bio control agents which were introduced to control the ecosystem\[18\]. However, there are also cases of generalists wiping out the invasive species from the ecosystem\[17\]. These results may help to study these system in a better way.

Acknowledgment:

The research is funded by the Ministry of Human Resource and Development, Government of India.

References

References

[1] Perry, D. A. (1998). The scientific basis of forestry. Annual Review of Ecology and Systematics, 29(1), 435-466.

[2] Christensen, N. L., Bartuska, A. M., Brown, J. H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., Parsons, D.J. and Peterson, C.H. (1996). The report of the Ecological Society of America committee on the scientific basis for ecosystem management. Ecological applications, 6(3), 665-691.

[3] Hanski, I., Hansson, L., and Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. The Journal of Animal Ecology, 353-367.

[4] Upadhyay, R. K., Iyengar, S. R. K., and Rai, V. (1998). Chaos: an ecological reality?. International Journal of Bifurcation and Chaos, 8(06), 1325-1333.

[5] Hassell, M.P. and Varley, G.C. (1969). New inductive population model for insect parasites and its bearing on biological control. Nature, 223(5211), pp.1133-1137.

[6] Hsu, S.B., Hwang, T.W. and Kuang, Y. (2008). Global dynamics of a predator-prey model with Hassell-Varley type functional response. Discrete Contin. Dyn. Syst. Ser. B, 10(4), pp.857-871. doi: 10.3934/dcdsb.2008.10.857

[7] Kim, H.K. and Baek, H. (2013). The dynamical complexity of a predator–prey system with Hassell–Varley functional response and impulsive effect. Mathematics and Computers in Simulation, 94, pp.1-14. doi: 10.1016/j.matcom.2013.05.011

[8] Cosner, C., DeAngelis, D.L., Ault, J.S. and Olson, D.B. (1999). Effects of spatial grouping on the functional response of predators. Theoretical population biology, 56(1), pp.65-75.

[9] Hoogland, J. L., and Sherman, P. W. (1976). Advantages and disadvantages of bank swallow (Riparia riparia) coloniality. Ecological Monographs, 46(1), 33–58. doi:10.2307/1942393.

[10] Silveira, H. B., and Pagano, D. J. (2005). Piecewise-constant control signal for predator-prey systems: Application to ecological recovery. IFAC Proceedings Volumes, 38(1), 79-84.

[11] Siegfried, W. R., and Underhill, L. G. (1975). Flocking as an anti-predator strategy in doves. Animal Behaviour, 23, 504–508.

[12] Batabyal, S., Jana, D., Lu, J. and Parshad, R.D. (2020). Explosive predator and mutualistic preys: A comparative study. Physica A: Statistical Mechanics and its Applications, 541, p.123348.

[13] Aziz-Alaoui, M.A. (2002). Study of a Leslie–Gower-type tritrophic population model. Chaos, Solitons and Fractals, 14(8), pp.1275-1293.

[14] Lefschetz, S. (1965). Stability of nonlinear control systems. MARTIN MARIETTA CORP BALTIMORE MD RESEARCH INST FOR ADVANCED STUDIES.

[15] Wilson, E. O. (2002). The future of life. Vintage.

[16] Wimp, G. M., Ries, L., Lewis, D., and Murphy, S. M. (2019). Habitat edge responses of generalist predators are predicted by prey and structural resources. Ecology, 100(6), e02662.
[17] Cook, S. P., Smith, H. R., Hain, F. P., and Hastings, F. L. (1995). Predation of gypsy moth (Lepidoptera: Lymantriidae) pupae by invertebrates at low small mammal population densities. Environmental Entomology, 24(5), 1234-1238.

[18] Heinz, K. M., Brazzle, J. R., Parrella, M. P., and Pickett, C. H. (1999). Field evaluations of augmentative releases of Delphastus catalinae (Horn)(Coleoptera: Coccinellidae) for suppression of Bemisia argentifolii Bellows & Perring (Homoptera: Aleyrodidae) infesting cotton. Biological Control, 16(3), 241-251.

[19] J. Arino, L. Wang, G.S. Wolkowicz: An alternative formulation for a delayed logistic equation. J. Theor. Biol. 241(1), 109-119 (2006).