Breeding Suppression in Prey due to Fear of Predator

Qamar J.A. Khan, Fatma A. Al-Kharousi and Hamed Al Shamsi

***Abstract*—This paper presents a theoretical model of the impact on a prey's breeding due to short term heavy predation. The prey suppresses breeding due to short term heavy predation only to restart breeding when predation pressure lowers. The predator consumes both suppressor and breeder of the prey and this prey population is more prone to predation at higher densities. Equilibrium and stability analyses are carried out. Taking a fraction of newborn breeder prey q, a bifurcation parameter, it is shown that Hopf bifurcation could occur.**

***Index Terms*—Prey, Predator, Stability, Bifurcation, Optimal harvesting.**

I. INTRODUCTION

ECOLOGISTS for several decades have observed with great interest the population growth of small mammals [1]. In prey-predator interactions it is observed that prey population is reduced through direct killing by predators. It has also been verified by field studies that the mere presence of predators alters the behaviour and physiology of prey to such an extent that it is more effective than direct killing. When prey perceive the presence of predators they fear a reduction in birth rate and the associated negative impact on their population. Due to this, they relocate to low-risk habitats. Thus, the interaction of prey and predator should consider the cost of fear in addition to direct predation [2]-[5]. Studies into environmental stressors have pointed to stress as the probable cause of delayed small mammal reproduction. Stress of social life, competition for food etc. are all conditions which were thought to lead to delayed mammal reproduction [6], [7]. The other reason for the delayed reproduction is density-dependent predation. Krebs and Myers [8], Taitt and Krebs [9] and Ostfeld et al. [10] have confirmed through many field studies and experiments that there is little evidence to show that stress is a cause of mammal delayed reproduction. On the other hand, in the case of small mammals such as bank voles (clethrionomys glareolus) and snowshoe hare, the works of Lima [11], Ylönen [12], Ylönen [13], Hanski et al. [14], Hik [15], Korpimäki [16] and Norrdahl and Korpimäki [17], among others, established that the presence of predators induced breeding suppression (PIBS) influenced the population cycles. Furthermore, Ruxton and Lima [18] studied a mathematical model and showed that the presence of PIBS occurs as a part of the predator-prey dynamics. Based on the above works and other recent studies on breeding suppression, researchers believe that certain small mammals suppress breeding in response to strong predation pressure. This is because for non-breeding individuals, the suppressors have a better chance of avoiding predation than those in a reproductive stage. They assumed that the suppressor populations experienced no predation. Kokko and Ruxton [19] studied a general model in which breeding suppression is observed in both predator and prey populations. Later, Ruxton et al. [20] improved this model by taking into consideration the fact that a predator catches small sized prey species proportional to their abundances. The predator feeds preferentially on the most numerous species which is thus over-represented in the predator diet. In this model, breeder and suppressor populations are both exposed (to varying degrees) to the predator. This implies a kind of switching from breeder to suppressor as changes occur in numerical superiority.

Switching may simply come about due to changing individual behaviour with changes in the abundance of that class of prey. Moreover, breeding small mammals suffer higher predation risk than nonbreeders. This may be because the breeding process impairs a mammal's defenses. Several examples can be cited where cruising predators prefer to hunt small prey species with limited defense capabilities such as small antelope or whichever species is most abundant at any given time [21]- [24]. The mathematical models that have generally been proposed to describe switching involve the interaction of one predator with two prey species (see, e.g. [20], [25]-[33]). If prey species are large or have the ability to defend themselves in groups, then the predator will be attracted towards a habitat where prey are fewer in number, that is, switching will be in the opposite direction [34], [35] and [36].

Models including time delays are much more realistic, as in reality, time-delays occur in almost every biological situation [37] - [39]. The process in which breeder populations convert to suppressor populations or vice versa is not instantaneous and there is always a time lag. Therefore, to make the model biologically realistic, one has to consider delays in breeders becoming suppressors or vice versa. For simplicity, in this model, we are assuming a time delay in suppressor populations becoming breeder populations. We thus assume that the transition of the suppressor population into a breeder population is subject to a time lag z. In this time z, one may predict that there will be less predation pressure in future. In our present work, we consider a three species prey-predator system, namely, breeder prey, suppressor prey and predator. The breeder class always breeds while the suppressor prey class suppresses breeding in the short-term in response to increased predation pressure. The predation risk for prey is reduced by suppressing breeding. We assume that predators eat breeder prey preferentially because during pregnancy breeder individuals are less active and can be caught more easily. In much the same way, for example wolves attack moose more successfully when they are heavily infected by

Manuscript received January 21, 2020; revised July 27, 2020.

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"Echinococcus granulosus" Petrson and Page [40]. Ruxton et al. [20] formulated a functional differential equation model where past events affect current behaviour. A population cycle is a phenomenon where the population rises and falls over a predictable period of time. Prey population rapidly increases and this is followed by an increase in the predator population. As predators eat the prey, the prey population declines. In turn, the predator population also decreases because there is less to eat. Hence, both predator and prey play a crucial role in the smooth running of an ecosystem. When the predator population is high, prey suppress breeding and when predator population decline, suppressor prey take a decision in advance to breed because they feel safe in mating due to less predation. Our model is represented in terms of a differential difference equation. The concept of advance is related to potential future events which can be known at the present time and could be useful for decision making Kalecki [41]. Suppressor individuals make transition to breeding class by sensing the breeder and predator population after time z.

II. The Model

Our model is represented in terms of a system of differential difference equations that describe the behaviour of the breeder, suppressor and predator populations relationship and is given by

$$\begin{aligned}\frac{dB}{dZ} &= \gamma Bq - \frac{\ell_b B^2 P}{B+S} - \frac{\psi_{mb} PB}{P+P_0+aB} \\ &\quad + \frac{\psi_{ms} B(Z+z)S}{B(Z+z)+B_0+bP(Z+z)}, \\ \frac{dS}{dZ} &= \gamma B(1-q) - \frac{\ell_s S^2 P}{B+S} \\ &\quad + \frac{\psi_{mb} PB}{P+P_0+aB} - \frac{\psi_{ms} B(Z+z)S}{B(Z+z)+B_0+bP(Z+z)}, \\ \frac{dP}{dZ} &= \frac{\alpha_1 \ell_b B^2 P}{B+S} + \frac{\alpha_2 \ell_s S^2 P}{B+S} - \mu P,\end{aligned} \tag{1}$$

where population densities of breeder and suppressor prey are denoted by B and S respectively. The predator population density is denoted by P. Both breeder and suppressor prey population are exposed to predator but predator feeds preferentially on the most numerous species.

γ is the intrinsic birth rate constant of the breeding subpopulation.

and, $\frac{\psi_{mb} PB}{P+P_0+aB}$ is the rate at which breeding population move to suppressor population. The per capita rate of movement into the suppressor population increases with predator density but is reduced with an increasing breeding population. The positive parameters a and P_0 control the shape of response. Furthermore, $\frac{\psi_{ms} B(Z+z)S}{B(Z+z)+B_0+bP(Z+z)}$ is the rate at which the suppressor population returns to breeding population and it depends on the future population of breeder and predator. The positive parameters B_0 and b control the shape of response.

The quantities ℓ_b and ℓ_s are the predator response rate towards the breeder and suppressor populations, and the quantities α_1 and α_2 are the efficiencies with which captured breeders and suppressors, respectively, are converted to predators.

Also, μ is the predator death rate constant, and q is a fraction of newborn breeder prey.

We assume all the parameters are positives.

For the sake of simplicity, we reduce one parameter from the model equations (1) by rescaling the parameters on the predator death rate constant μ. We define

$$\epsilon = \frac{\gamma}{\mu},\ \ell_b = \frac{I_b}{\mu},\ I_s = \frac{\ell_s}{\mu},\ \phi_{mb} = \frac{\psi_{mb}}{\mu},\ \phi_{ms} = \frac{\psi_{ms}}{\mu} \\ t = \mu Z. \tag{2}$$

This leads to the equations

$$\begin{aligned}\frac{dB}{dt} &= \epsilon Bq - \frac{I_b B^2 P}{B+S} - \frac{\phi_{mb} PB}{P+P_0+aB} \\ &\quad + \frac{\phi_{ms} B(t+z)S}{B(t+z)+B_0+bP(t+z)}, \\ \frac{dS}{dt} &= \epsilon B(1-q) - \frac{I_s S^2 P}{B+S} + \frac{\phi_{mb} PB}{P+P_0+aB} \\ &\quad - \frac{\phi_{ms} B(t+z)S}{B(t+z)+B_0+bP(t+z)}, \\ \frac{dP}{dt} &= \frac{\alpha_1 I_b B^2 P}{B+S} + \frac{\alpha_2 I_s S^2 P}{B+S} - P.\end{aligned} \tag{3}$$

III. The Equilibrium

The co-existing equilibrium point is

$$\bar{B} = \frac{\bar{X}(\bar{X}+1)}{\alpha_1 I_b \bar{X}^2 + \alpha_2 I_s},\quad \bar{S} = \frac{(1+\bar{X})}{\alpha_1 I_b \bar{X}^2 + \alpha_2 I_s}, and \\ \bar{P} = \frac{\epsilon \bar{X}(1+\bar{X})}{I_s + I_b \bar{X}^2}, \tag{4}$$

where $\bar{X} = \frac{\bar{B}}{\bar{S}}$ is the positive root of the ten degree polynomial.

$$a_{10}\bar{X}^{10} + a_9\bar{X}^9 + a_8\bar{X}^8 + a_7\bar{X}^7 + a_6\bar{X}^6 + a_5\bar{X}^5 \\ + a_4\bar{X}^4 + a_3\bar{X}^3 + a_2\bar{X}^2 + a_1\bar{X} + a_0 = 0, \tag{5}$$

where (5) is obtained from the first equation of (3) by substituting the values of $\bar{B}$, $\bar{S}$, and $\bar{P}$ at equilibrium point. See appendix A.

IV. Stability and Hopf bifurcation analysis

Let $\bar{E} = (\bar{B},\ \bar{S},\ \bar{P})$ denotes the unique interior equilibrium point where $\bar{B},\ \bar{S},\ \bar{P} > 0$. Consider a small perturbation around the equilibrium point $B = \bar{B} + u, S = \bar{S} + v$ and $P = \bar{P} + w$. We substitute these into the system of equations (3) and neglect products of small quantities. Then the characteristic equation about $\bar{E}$ is given by

The characteristic equation about $\bar{E}$ gives

$$\lambda^3 + K_1\lambda^2 + K_2\lambda + K_3 + e^{z\lambda}(U_1\lambda^2 + U_2\lambda + U_3) \\ + e^{2z\lambda}(a_{32}c_{23}a_{13} - a_{32}a_{22}c_{13}) = 0. \tag{6}$$

where

$$
\begin{aligned}
&K_1 = -b_{21} - a_{11},\\
&K_2 = -a_{31}c_{11} - a_{32}c_{21} - b_{11}a_{21} + b_{21}a_{11},\\
&K_3 = -a_{31}b_{11}c_{21} - a_{32}a_{21}c_{11} + a_{31}c_{11}b_{21} + a_{32}c_{21}a_{11},\\
&\cup_1 = -a_{13},\\
&\cup_2 = -a_{31}c_{13} - a_{32}c_{23} - b_{11}a_{22} + b_{21}a_{13},\\
&\cup_3 = -a_{31}b_{11}c_{23} - a_{32}a_{21}c_{13} - a_{32}a_{22}c_{11} + a_{31}c_{13}b_{21}\\
&\quad + a_{32}c_{21}a_{13} + a_{32}c_{23}a_{11},\\
&M = \bar{P} + P_0 + a\bar{B},\\
&N = \bar{B} + B_0 + b\bar{P},\\
&L = \bar{B} + \bar{S},\\
&a_{11} = -\frac{I_b\bar{B}\bar{P}}{L} + \frac{I_b\bar{B}^2\bar{P}}{L^2} - \frac{\phi_{ms}\bar{S}}{N} + \frac{\phi_{mb}\bar{P}\bar{B}a}{M^2},\\
&a_{13} = -\frac{\phi_{ms}\bar{B}\bar{S}}{N^2} + \frac{\phi_{ms}\bar{S}}{N},\\
&b_{11} = \frac{I_b\bar{B}^2\bar{P}}{L^2} + \frac{\phi_{ms}\bar{B}}{N},\\
&c_{11} = -\frac{I_b\bar{B}^2}{L} - \frac{\phi_{mb}\bar{B}}{M} + \frac{\phi_{mb}\bar{P}\bar{B}}{M^2},\\
&c_{13} = -\frac{\phi_{ms}\bar{B}\bar{S}b}{N^2},\\
&a_{21} = \epsilon(1-q) + \frac{I_sS^2\bar{P}}{L^2} + \frac{\phi_{mb}\bar{P}}{M} - \frac{\phi_{mb}\bar{P}\bar{B}a}{M^2},\\
&a_{22} = -\frac{\phi_{ms}\bar{S}}{N} + \frac{\phi_{ms}\bar{B}\bar{S}}{N^2},\\
&b_{21} = -\frac{2I_s\bar{S}\bar{P}}{L} + \frac{I_s\bar{S}^2\bar{P}}{L^2} - \frac{\phi_{ms}\bar{B}}{N},\\
&c_{21} = \frac{-I_s\bar{S}^2}{L} - \frac{\phi_{mb}\bar{P}\bar{B}}{M^2} + \frac{\phi_{mb}\bar{B}}{M},\\
&c_{23} = \frac{\phi_{ms}\bar{B}\bar{S}b}{N^2},\\
&a_{31} = \frac{\alpha_1 I_b\bar{B}\bar{P}(\bar{S}+L)}{L^2} - \frac{\alpha_2 I_s\bar{S}^2\bar{P}}{L^2},\\
&a_{32} = \frac{\alpha_2 I_s\bar{S}\bar{P}(\bar{B}+L)}{L^2} - \frac{\alpha_1 I_b\bar{B}^2\bar{P}}{L^2}.
\end{aligned}
$$

Since $a_{13}c_{23} = a_{22}c_{13}$, so coefficient of $e^{2z\lambda}$ will be zero and the characteristic equation (6) reduces to

$$\lambda^3 + K_1\lambda^2 + K_2\lambda + K_3 = e^{z\lambda}(B_1\lambda^2 + B_2\lambda + B_3), \quad (7)$$

where $B_1 = -\cup_1$, $B_2 = -\cup_2$ and $B_3 = -\cup_3$, when $z = 0$, the characteristic equation(6) reduces to

$$\lambda^3 + P_1\lambda^2 + P_2\lambda + P_3 = 0.$$

where

$$
\begin{aligned}
P_1 &= K_1 - B_1,\\
P_2 &= K_2 - B_2,\\
P_3 &= K_3 - B_3. \qquad (8)
\end{aligned}
$$

Hence, according to the Routh-Hurwitz criterion for stability, we have the following:

Proposition 1: For $z = 0$, the equilibrium $\bar{E} = (\bar{B}, \bar{S}, \bar{P})$ locally asymptotically stable if and only if

(i) $P_1 > 0$, $P_3 > 0$,
(ii) $P_1P_2 > P_3$.

If $z \neq 0$, we consider a characteristic equation (7). We let $\lambda = u + i\ \upsilon$, u, $\upsilon \in \Re$ and rewrite (7) in terms of its real and imaginary parts as

$$
\begin{aligned}
&u^3 - 3u\upsilon^2 + K_1(u^2 - \upsilon^2) + K_2u + K_3\\
&= e^{zu}((B_1(u^2-\upsilon^2) + B_2u + B_3)cos(z\upsilon)\\
&- (2u\upsilon B_1 + B_2\upsilon)\sin(z\upsilon)),\\
&3u^2\upsilon - \upsilon^3 + 2K_1u\upsilon + K_2\upsilon\\
&= e^{zu}((B_1(u^2-\upsilon^2) + B_2u + B_3)\ sin(z\upsilon) \qquad (9)\\
&+ (2u\upsilon B_1 + B_2\upsilon)\cos(z\upsilon)).
\end{aligned}
$$

Let $z = z^*$ be such that $u(z^*) = 0$ and $\upsilon(z^*) = \upsilon^*$. Then equations (9) reduce to

$$
\begin{aligned}
&-K_1\upsilon^{*2} + K_3 = (-B_1\upsilon^{*2} + B_3)\cos(z^*\upsilon^*)\\
&- B_2\upsilon^*\sin(z^*\upsilon^*),\\
&-\upsilon^{*3} + K_2\upsilon^* = (-B_1\upsilon^{*2} + B_3)\sin(z^*\upsilon^*) \qquad (10)\\
&+ B_2\upsilon^*\cos(z^*\upsilon^*),
\end{aligned}
$$

equations (10) can be rewritten as

$$
\begin{aligned}
-K_1\upsilon^{*2} + K_3 &= X_1\cos(z^*\upsilon^*) - X_2\sin(z^*\upsilon^*),\\
-\upsilon^{*3} + K_2\upsilon^* &= X_1\sin(z^*\upsilon^*) + X_2\cos(z^*\upsilon^*), \qquad (11)
\end{aligned}
$$

where

$$
\begin{aligned}
X_1 &= -B_1\upsilon^{*2} + B_3,\\
X_2 &= B_2\upsilon^*,
\end{aligned}
$$

It follows by taking sum of squares of equations (11) that

$$
\begin{aligned}
&\upsilon^{*6} + \upsilon^{*4}(K_1^2 - 2K_2 - B_1^2) + \upsilon^{*2}(K_2^2 - 2K_1K_3\\
&+ 2B_1B_3 - B_2^2) + (K_3^2 - B_3^2) = 0. \qquad (12)
\end{aligned}
$$

Let $\upsilon^{*2} = s$ equation (12) reduces to

$$
\begin{aligned}
&\phi(s) = s^3 + s^2(K_1^2 - 2K_2 - B_1^2)\\
&+ s(K_2^2 - 2K_1K_3 + 2B_1B_3 - B_2^2) + (K_3^2 - B_3^2) = 0. \qquad (13)
\end{aligned}
$$

$$
\begin{aligned}
&\frac{d\phi}{ds} = 3s^2 + 2s(K_1^2 - 2K_2 - B_1^2) + (K_2^2 - 2K_1K_3 +\\
&2B_1B_3 - B_2^2) > 0, \qquad (14)
\end{aligned}
$$

if υ^* is the largest positive root of (12).

Proposition 2: Necessary and sufficient conditions for the cubic equation

$$s^3 + \ell_1 s^2 + \ell_2 s + \ell_3 = 0,$$

where

$$
\begin{aligned}
\ell_1 &= K_1^2 - 2K_2 - B_1^2,\\
\ell_2 &= K_2^2 - 2K_1K_3 + 2B_1B_3 - B_2^2,\\
\ell_3 &= K_3^2 - B_3^2,
\end{aligned}
$$

to have at least one simple positive root is $\ell_3 < 0$ and $\ell_1 > 0$. Now equation (11) can be written as

$$X_1\cos(z^*\upsilon^*) - X_2\sin(z^*\upsilon^*) = Q,$$

$$X_1\sin(z^*\upsilon^*) + X_2\cos(z^*\upsilon^*) = R,$$

where $-K_1 \upsilon^{*2} + K_3 = Q$ and $-\upsilon^{*3} + K_2\upsilon^* = R$ so, $Q^2 + R^2 = X_1^2 + X_2^2 = d^2$(say), where $d > 0$.
The equations

$$X_1 = d\cos\alpha, \quad \text{and} \quad X_2 = d\sin\alpha,$$

determine a unique $\alpha \in [0, 2\pi]$. With this α,

$$d\cos(z^*\upsilon^* - \alpha) = Q,$$

$$d\sin(z^*\upsilon^* - \alpha) = -R.$$

These equation show $z^*\upsilon^* - \alpha$ uniquely in $(0, 2\pi)$, and hence υ^* uniquely in $(\frac{\alpha}{z^*}, \frac{2\pi+\alpha}{z^*})$.
To establish the Hopf bifurcation theorem, we state and prove the following theorem.

Theorem 3: $\upsilon(z^*) = \upsilon^*$ is a simple root of (7) and $u(z^*) + i\upsilon(z^*)$ is analytic in a neighbourhood of $z = z^*$.

Proof: To show that $\upsilon(z^*) = \upsilon^*$ is a simple root, equation (7) can be written as $g(\lambda) = 0$, where

$$g(\lambda) = \lambda^3 + K_1\lambda^2 + K_2\lambda + K_3 - e^{z\lambda}(B_1\lambda^2 + B_2\lambda + B_3) = 0.$$

Any double root λ satisfies

$$g(\lambda) = 0 \ and \ g'(\lambda) = 0,$$

where

$$g'(\lambda) = 3\lambda^2 + 2K_1\lambda + K_2 - ze^{z\lambda}(B_1\lambda^2 + B_2\lambda + B_3) - e^{z\lambda}(2B_1\lambda + B_2) = 0.$$

Substituting $\lambda = i\ \upsilon^*$ and $z = z^*$ in $g(\lambda) = 0$, $g'(\lambda) = 0$ and equating the real and imaginary parts, we get that if iz^* is a double root,

$$-K_1\upsilon^{*2} + K_3 = X_1\cos(z^*\upsilon^*) - X_2\sin(z^*\upsilon^*),$$
$$-\upsilon^{*3} + K_2\upsilon^* = X_1\sin(z^*\upsilon^*) + X_2\cos(z^*\upsilon^*),$$

and

$$\begin{aligned}-3\upsilon^{*2} + K_2 &= \cos(z^*\upsilon^*)(z^*X_1 + B_2) - \sin(z^*\upsilon^*)(2B_1\upsilon^* + z^*X_2),\\ &= z^*X_1\cos(z^*\upsilon^*) - z^*X_2\sin(z^*\upsilon^*) + Y_1\cos(z^*\upsilon^*) - Y_2\sin(z^*\upsilon^*).\end{aligned}$$

$$2K_1\upsilon^* = z^*X_2\cos(z^*\upsilon^*) + z^*X_1\sin(z^*\upsilon^*) + Y_2\cos(z^*\upsilon^*) + Y_1\sin(z^*\upsilon^*).$$

where

$$Y1 = B_2, \quad \text{and} \quad Y_2 = 2B_1\upsilon$$

Equation (12) can be written as

$$H(\upsilon^*) = (-K_1\upsilon^{*2} + K_3)^2 + (-\upsilon^{*3} + K_2\upsilon^*)^2 - (-B_1\upsilon^{*2} + B_3)^2 - B_2^2\upsilon^{*2},$$

or

$$H(\upsilon^*) = [X_1\cos(z^*\upsilon^*) - X_2\sin(z^*\upsilon^*)]^2 + [X_1\sin(z^*\upsilon^*) + X_2\cos(z^*\upsilon^*)]^2 - X_1^2 - X_2^2 = 0.$$

where

TABLE I
REPRESENTATIVE SET OF PARAMETER VALUES USED FOR MODEL EQUATION (3).

ϵ	I_s	P_0	B_0	α_1	α_2	I_b	ϕ_{ms}	ϕ_{mb}	a	b
0.7791	0.2	0.21	1	0.2925	0.2412	1	0.1	0.1	1	0.3

$$\begin{aligned}H'(\upsilon^*) &= 2(-K_1\upsilon^{*2} + K_3)(-2K_1\upsilon^*) + 2(-\upsilon^{*3} + K_2\upsilon^*)(-3\upsilon^{*2} + K_2) - 2(-B_1\upsilon^{*2} + B_3)(-2B_1\upsilon^*) - 2B_2^2\upsilon^*,\\ &= [X_1\cos(z^*\upsilon^*) - X_2\sin(z^*\upsilon^*)][-z^*X_2\cos(z^*\upsilon^*) - z^*X_1\sin(z^*\upsilon^*) - Y_2\cos(z^*\upsilon^*) - Y_1\sin(z^*\upsilon^*)] + [X_1\sin(z^*\upsilon^*) + X_2\cos(z^*\upsilon^*)]\\ &\quad [z^*X_1\cos(z^*\upsilon^*) - z^*X_2\sin(z^*\upsilon^*) + Y_1\cos(z^*\upsilon^*) - Y_2\sin(z^*\upsilon^*)] = 0.\end{aligned}$$

As $H(\upsilon^*) = H'(\upsilon^*) = 0$, υ^* is a double root of $H(\upsilon^*) = 0$, this is a contradiction. Hence $i\upsilon^*$ is a simple root of the equation $g(\lambda) = 0$. ■

Using the analytic version of the Implicit Function Theorem (Chow and Hale [42]), $u(z) + i\upsilon(z)$ is defined and analytic in a neighbourhood of $z = z^*$.
To establish Hopf bifurcation of $z = z^*$, as given in Marsden and McCracken [43], we need to show

$$\frac{du}{dz}|_{z=z^*} \neq 0.$$

We differentiate equations (9) with respect to z and substitute $u = 0$ and $z = z^*$, then solve for $\frac{du}{dz}$ and $\frac{dv}{dz}$ and use equations (10), we get

$$\frac{du}{dz} = \frac{-\upsilon^{*2}(3\upsilon^{*4} + \upsilon^{*2}(2K_1^2 - 4K_2 - 2B_1^2)}{J_1^2 + J_2^2} + \frac{(2B_1B_3 + K_2^2 - B_2^2 - 2K_1K_3)}{J_1^2 + J_2^2}.$$

where

$$J_1 = 2K_1\upsilon^* - z^*X_1\sin(z^*\upsilon^*) - z^*X_2\cos(z^*\upsilon^*) - B_2\sin(z^*\upsilon^*) - 2B_1\upsilon^*\cos(z^*\upsilon^*),$$
$$J_2 = -3\upsilon^{*2} + K_2 + 2B_1\upsilon^*\sin(z^*\upsilon^*) - z^*X_1\cos(z^*\upsilon^*) - B_2\cos(z^*\upsilon^*) + z^*X_2\sin(z^*\upsilon^*),$$

Using (14) it is obvious that $\frac{du}{dz} > 0$.

V. NUMERICAL RESULTS

Hence System (3) (when $z = 0$) undergoes Hopf bifurcation when q passes through $\bar{q}$. The Hopf bifurcation analysis of $\bar{E} = (\bar{B}, \bar{S}, \bar{P})$ has been performed to investigate the dynamics when all three species co-exist.
ϵ, I_s, P_0, B_0, α_1, α_2, I_b, ϕ_{ms}, ϕ_{mb}, a and b have a units of 'per day', while B, S and P have units of 'number per area'.

The system (3) has been integrated numerically using a Runge-Kutta-Fehlberg fourth-fifth order method. Table (I)

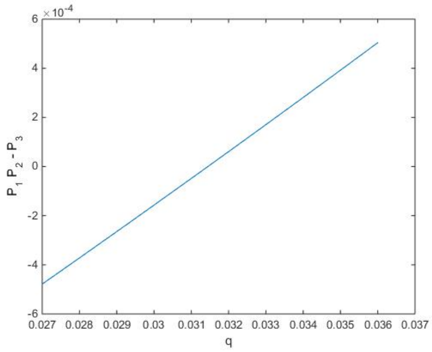

Fig. 1. Plot of $P_1P_2 - P_3$ as a function of the parameter q.

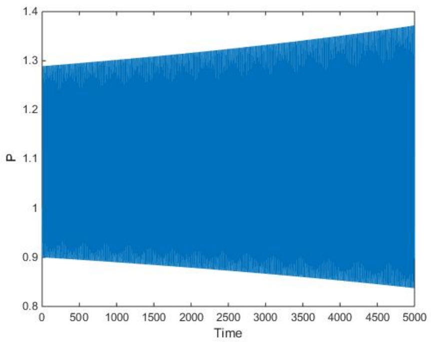

Fig. 2. Hopf bifurcation of P with respect to q when $q = 0.031$.

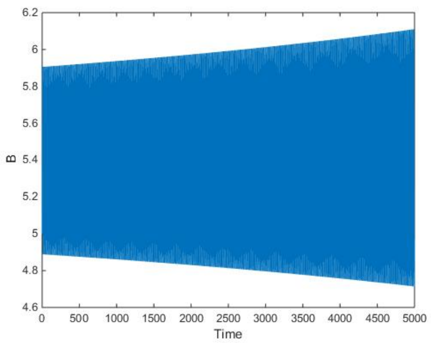

Fig. 3. Hopf bifurcation of B with respect to q when $q = 0.031$.

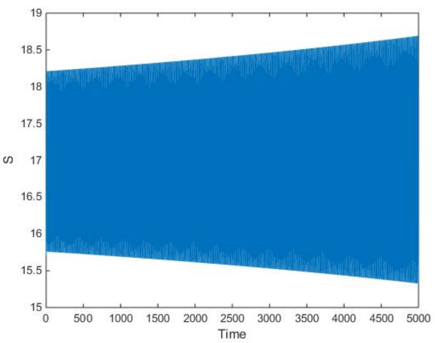

Fig. 4. Hopf bifurcation of S with respect to q when $q = 0.031$.

contains a representative set of values used for the hypothetical parameters in the simulation. For initial data, a slight perturbation of the equilibrium values were used. The numerical results show that there is a Hopf bifurcation for

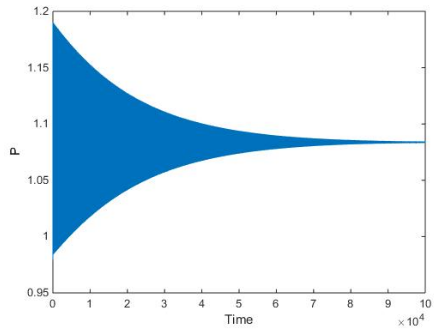

Fig. 5. Hopf bifurcation of P with respect to q when $q = 0.032$.

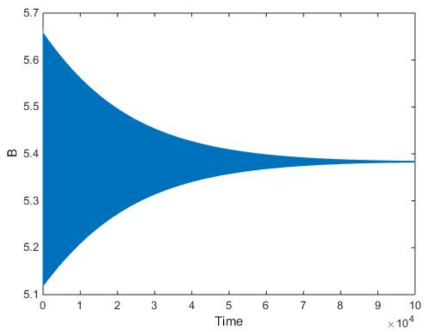

Fig. 6. Hopf bifurcation of B with respect to q when $q = 0.032$.

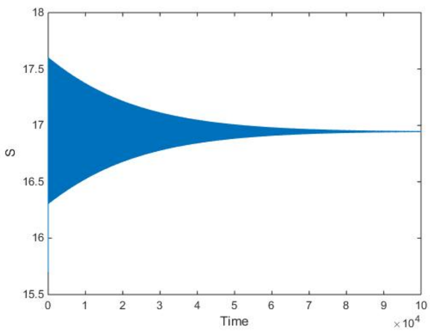

Fig. 7. Hopf bifurcation of S with respect to q when $q = 0.032$.

this system where unstable behaviour changes to stable as the parameter q is varied. This bifurcation point is between $q = 0.031$ and 0.032 , and it is approximately when $q = 0.0315$ as illustrated in Figure (1) which contains a plot of $P_1P_2 - P_3$ as a function of the parameter q. Figures (2, 3 and 4) show an unstable solution for the system when $q = 0.031$ while figures (5, 6 and 7) show a stable solution when the value $q = 0.032$ is used.

VI. Conclusion

Recent studies have explored the change in a prey's behaviour including reproduction, due to fear of predators. A field study Zanette et al. [44] verified that the growth of the prey species in an ecological system is influenced by the fear induced from predators. Experiments verified that intimidation by predators can reduce reproduction in song sparrows by 40%. Direct killing in these experiments was stopped by some means. In this paper we studied the effects of fear in the prey-predator system and discussed the dynamics of the predator-prey system in the light of the Fennoscandian vole cycle. We considered a mathematical model based on Ruxton and Lima [18] as the basic model. Also, our model considers prey small in size, and predators large in size. Prey populations suppress breeding in response to heavy predation as a non-breeding individual has a better chance of avoiding predation than those in a reproductive stage. Both breeding and suppressor populations are exposed to predator populations depending on their numerical superiority as predators feed preferentially on the most numerous class prey species. Furthermore, the prey species would be more willing to exhibit anti-predator defenses when the rate of predation becomes high.The cost of fear due to predators by which breeders turn into suppressor or vice versa has influenced the predator-prey relationship.

To keep the model simple, we considered a time delay only when the suppressor population restarted breeding. This is in anticipation that after time z, predator pressure will be reduced to a level that it will be safe again for mating. If $\ell_3 < 0$ and $\ell_1 > 0$ then there exists only one non-zero equilibrium and it will be locally stable if the Routh-Hurwitz criteria are satisfied. By taking q as a bifurcation parameter we found that Hopf bifurcation could occur. Figure 1 shows that $P_1P_2 - P_3 = 0$ at $q \simeq 0.0315$. If $q < 0.0315$, then population starts oscillating and as $q > 0$, the population will be stable. Where $q \simeq 0.0315$ is called the point of Hopf bifurcation. Finding the exact point of bifurcation is difficult. Analytical conditions for local stability analysis and bifurcations for co-existing equilibrium have highlighted the role played by parameter values in obtaining the results of predator-prey system. In the context of ecology, Hopf bifurcation helped us in determining the existence of a region of instability in the neighbourhood of co-existing equilibrium where prey and predator populations will both survive undergoing regular fluctuations.

In future to make the model more realistic ecologically we can introduce a fear factor in the growth of prey population i.e γ can be replaced by $\dfrac{\gamma}{1+\theta P}$. Using this term growth of prey decreases as the population of predators becomes large, and increases as the population of prey becomes less. We can also study the same model by introducing another time delay when the breeder population turns to a suppressor population. It will give a dual time delays effect.

Due to non-availability of suitable software we left the sketching of the figures obtained from the model equations for future time.

Appendix A

$a_{10} = a \epsilon I_b^3 q - a \epsilon I_b^3 - \alpha_1^2 b \epsilon^3 I_b^3 - P_0 \alpha_1 \epsilon I_b^4 - \alpha_1 \epsilon I_b^3 \phi_{mb} - \alpha_1 \epsilon^2 I_b^3 + \alpha_1 \epsilon^2 I_b^3 q - B_0 \alpha_1^2 \epsilon^2 I_b^4 - B_0 \alpha_1^2 \epsilon I_b^4 \phi_{mb} - a \alpha_1 b \epsilon^2 I_b^3 - P_0 \alpha_1^2 b \epsilon^2 I_b^4 + B_0 \alpha_1^2 \epsilon^2 I_b^4 q - \alpha_1^2 b \epsilon^2 I_b^3 \phi_{mb} + \alpha_1^2 b \epsilon^3 I_b^3 q - B_0 a \alpha_1 \epsilon I_b^4 + P_0 \alpha_1 \epsilon I_b^4 q - B_0 P_0 \alpha_1^2 \epsilon I_b^5 + B_0 a \alpha_1 \epsilon I_b^4 q + B_0 P_0 \alpha_1^2 \epsilon I_b^5 q + a \alpha_1 b \epsilon^2 I_b^3 q + P_0 \alpha_1^2 b \epsilon^2 I_b^4 q.$

$a_9 = a I_b^3 \phi_{ms} - 2 a \epsilon I_b^3 - 2 \alpha_1 \epsilon^2 I_b^3 - 2 \alpha_1^2 b \epsilon^3 I_b^3 - P_0 \alpha_1 \epsilon I_b^4 + P_0 \alpha_1 I_b^4 \phi_{ms} - 2 \alpha_1 \epsilon I_b^3 \phi_{mb} + \alpha_1 \epsilon I_b^3 \phi_{ms} + 2 a \epsilon I_b^3 q + 2 \alpha_1 \epsilon^2 I_b^3 q - B_0 \alpha_1^2 \epsilon^2 I_b^4 - B_0 \alpha_1^2 \epsilon I_b^4 \phi_{mb} - 2 a \alpha_1 b \epsilon^2 I_b^3 - P_0 \alpha_1^2 b \epsilon^2 I_b^4 + B_0 \alpha_1^2 \epsilon^2 I_b^4 q - 2 \alpha_1^2 b \epsilon^2 I_b^3 \phi_{mb} + 2 \alpha_1^2 b \epsilon^3 I_b^3 q - B_0 a \alpha_1 \epsilon I_b^4 + P_0 \alpha_1 \epsilon I_b^4 q + B_0 a \alpha_1 \epsilon I_b^4 q + 2 a \alpha_1 b \epsilon^2 I_b^3 q + P_0 \alpha_1^2 b \epsilon^2 I_b^4 q.$

$a_8 = 2 a I_b^3 \phi_{ms} - a \epsilon I_b^3 - \alpha_1 \epsilon^2 I_b^3 - \alpha_1^2 b \epsilon^3 I_b^3 + P_0 \alpha_1 I_b^4 \phi_{ms} - 2 a \epsilon I_b^2 I_s - \alpha_1 \epsilon I_b^3 \phi_{mb} + 2 \alpha_1 \epsilon I_b^3 \phi_{ms} + a \epsilon I_b^3 q - \alpha_1 \epsilon^2 I_b^2 I_s - \alpha_2 \epsilon^2 I_b^2 I_s + \alpha_1 \epsilon^2 I_b^3 q - a \alpha_1 b \epsilon^2 I_b^3 + 2 \alpha_1 \epsilon^2 I_b^2 I_s q + \alpha_2 \epsilon^2 I_b^2 I_s q - B_0 \alpha_1^2 \epsilon^2 I_b^3 I_s - \alpha_1^2 b \epsilon^2 I_b^3 \phi_{mb} + \alpha_1^2 b \epsilon^3 I_b^3 q - 2 P_0 \alpha_1 \epsilon I_b^3 I_s - P_0 \alpha_2 \epsilon I_b^3 I_s - 2 \alpha_1 \epsilon I_b^2 I_s \phi_{mb} - \alpha_2 \epsilon I_b^2 I_s \phi_{mb} + 3 a \epsilon I_b^2 I_s q - 2 B_0 a \alpha_1 \epsilon I_b^3 I_s - B_0 a \alpha_2 \epsilon I_b^3 I_s + 3 P_0 \alpha_1 \epsilon I_b^3 I_s q + P_0 \alpha_2 \epsilon I_b^3 I_s q - 2 B_0 P_0 \alpha_1^2 \epsilon I_b^4 I_s - 2 B_0 \alpha_1 \alpha_2 \epsilon^2 I_b^3 I_s - 2 B_0 \alpha_1^2 \epsilon I_b^3 I_s \phi_{mb} - a \alpha_1 b \epsilon^2 I_b^2 I_s - a \alpha_2 b \epsilon^2 I_b^2 I_s - 2 \alpha_1 \alpha_2 b \epsilon^3 I_b^2 I_s + a \alpha_1 b \epsilon^2 I_b^3 q - P_0 \alpha_1^2 b \epsilon^2 I_b^3 I_s + 2 B_0 \alpha_1^2 \epsilon^2 I_b^3 I_s q - \alpha_1^2 b \epsilon^2 I_b^2 I_s \phi_{mb} + \alpha_1^2 b \epsilon^3 I_b^2 I_s q + 2 P_0 \alpha_1^2 b \epsilon^2 I_b^3 I_s q - 2 B_0 P_0 \alpha_1 \alpha_2 \epsilon I_b^4 I_s - 2 B_0 \alpha_1 \alpha_2 \epsilon I_b^3 I_s \phi_{mb} + 3 B_0 a \alpha_1 \epsilon I_b^3 I_s q + B_0 a \alpha_2 \epsilon I_b^3 I_s q + 3 B_0 P_0 \alpha_1^2 \epsilon I_b^4 I_s q - 2 P_0 \alpha_1 \alpha_2 b \epsilon^2 I_b^3 I_s + 2 B_0 \alpha_1 \alpha_2 \epsilon^2 I_b^3 I_s q - 2 \alpha_1 \alpha_2 b \epsilon^2 I_b^2 I_s \phi_{mb} + 2 a \alpha_1 b \epsilon^2 I_b^2 I_s q + a \alpha_2 b \epsilon^2 I_b^2 I_s q + 2 \alpha_1 \alpha_2 b \epsilon^3 I_b^2 I_s q + 2 P_0 \alpha_1 \alpha_2 b \epsilon^2 I_b^3 I_s q + 2 B_0 P_0 \alpha_1 \alpha_2 \epsilon I_b^4 I_s q.$

$a_7 = a I_b^3 \phi_{ms} - 4 a \epsilon I_b^2 I_s + \alpha_1 \epsilon I_b^3 \phi_{ms} + 3 a I_b^2 I_s \phi_{ms} - 2 \alpha_1 \epsilon^2 I_b^2 I_s - 2 \alpha_2 \epsilon^2 I_b^2 I_s + 4 \alpha_1 \epsilon^2 I_b^2 I_s q + 2 \alpha_2 \epsilon^2 I_b^2 I_s q - B_0 \alpha_1^2 \epsilon^2 I_b^3 I_s - 2 P_0 \alpha_1 \epsilon I_b^3 I_s - P_0 \alpha_2 \epsilon I_b^3 I_s + 3 P_0 \alpha_1 I_b^3 I_s \phi_{ms} + P_0 \alpha_2 I_b^3 I_s \phi_{ms} - 4 \alpha_1 \epsilon I_b^2 I_s \phi_{mb} - 2 \alpha_2 \epsilon I_b^2 I_s \phi_{mb} + 2 \alpha_1 \epsilon I_b^2 I_s \phi_{ms} + \alpha_2 \epsilon I_b^2 I_s \phi_{ms} + 6 a \epsilon I_b^2 I_s q - 2 B_0 a \alpha_1 \epsilon I_b^3 I_s - B_0 a \alpha_2 \epsilon I_b^3 I_s + 3 P_0 \alpha_1 \epsilon I_b^3 I_s q + P_0 \alpha_2 \epsilon I_b^3 I_s q - 2 B_0 \alpha_1 \alpha_2 \epsilon^2 I_b^3 I_s - 2 B_0 \alpha_1^2 \epsilon I_b^3 I_s \phi_{mb} - 2 a \alpha_1 b \epsilon^2 I_b^2 I_s - 2 a \alpha_2 b \epsilon^2 I_b^2 I_s - 4 \alpha_1 \alpha_2 b \epsilon^3 I_b^2 I_s - P_0 \alpha_1^2 b \epsilon^2 I_b^3 I_s + 2 B_0 \alpha_1^2 \epsilon^2 I_b^3 I_s q - 2 \alpha_1^2 b \epsilon^2 I_b^2 I_s \phi_{mb} + 2 \alpha_1^2 b \epsilon^3 I_b^2 I_s q + 2 P_0 \alpha_1^2 b \epsilon^2 I_b^3 I_s q - 2 B_0 \alpha_1 \alpha_2 \epsilon I_b^3 I_s \phi_{mb} + 3 B_0 a \alpha_1 \epsilon I_b^3 I_s q + B_0 a \alpha_2 \epsilon I_b^3 I_s q - 2 P_0 \alpha_1 \alpha_2 b \epsilon^2 I_b^3 I_s + 2 B_0 \alpha_1 \alpha_2 \epsilon^2 I_b^3 I_s q - 4 \alpha_1 \alpha_2 b \epsilon^2 I_b^2 I_s \phi_{mb} + 4 a \alpha_1 b \epsilon^2 I_b^2 I_s q + 2 a \alpha_2 b \epsilon^2 I_b^2 I_s q + 4 \alpha_1 \alpha_2 b \epsilon^3 I_b^2 I_s q + 2 P_0 \alpha_1 \alpha_2 b \epsilon^2 I_b^3 I_s q.$

$a_6 = 6 a I_b^2 I_s \phi_{ms} - 2 a \epsilon I_b^2 I_s - a \epsilon I_b I_s^2 - \alpha_1 \epsilon^2 I_b^2 I_s - \alpha_2 \epsilon^2 I_b I_s^2 - \alpha_2 \epsilon^2 I_b^2 I_s - P_0 \alpha_1 \epsilon I_b^2 I_s^2 - 2 P_0 \alpha_2 \epsilon I_b^2 I_s^2 + \alpha_1 \epsilon^2 I_b I_s^2 q + 2 \alpha_1 \epsilon^2 I_b^2 I_s q + 2 \alpha_2 \epsilon^2 I_b I_s^2 q + \alpha_2 \epsilon^2 I_b^2 I_s q - \alpha_2^2 b \epsilon^3 I_b I_s^2 + 3 P_0 \alpha_1 I_b^3 I_s \phi_{ms} + P_0 \alpha_2 I_b^3 I_s \phi_{ms} - B_0 \alpha_2^2 \epsilon^2 I_b^2 I_s^2 - \alpha_1 \epsilon I_b I_s^2 \phi_{mb} - 2 \alpha_1 \epsilon I_b^2 I_s \phi_{mb} - 2 \alpha_2 \epsilon I_b I_s^2 \phi_{mb} - \alpha_2 \epsilon I_b^2 I_s \phi_{mb} + 4 \alpha_1 \epsilon I_b^2 I_s \phi_{ms} + 2 \alpha_2 \epsilon I_b^2 I_s \phi_{ms} + 3 a \epsilon I_b I_s^2 q + 3 a \epsilon I_b^2 I_s q - P_0 \alpha_2^2 b \epsilon^2 I_b^2 I_s^2 + B_0 \alpha_1^2 \epsilon^2 I_b^2 I_s^2 q + B_0 \alpha_2^2 \epsilon^2 I_b^2 I_s^2 q - B_0 a \alpha_1 \epsilon I_b^2 I_s^2 - 2 B_0 a \alpha_2 \epsilon I_b^2 I_s^2 + 3 P_0 \alpha_1 \epsilon I_b^2 I_s^2 q + 3 P_0 \alpha_2 \epsilon I_b^2 I_s^2 q - a \alpha_1 b \epsilon^2 I_b^2 I_s - a \alpha_2 b \epsilon^2 I_b I_s^2 - a \alpha_2 b \epsilon^2 I_b^2 I_s - 2 \alpha_1 \alpha_2 b \epsilon^3 I_b^2 I_s - B_0 P_0 \alpha_1^2 \epsilon I_b^3 I_s^2 - B_0 P_0 \alpha_2^2 \epsilon I_b^3 I_s^2 - 2 B_0 \alpha_1 \alpha_2 \epsilon^2 I_b^2 I_s^2 - B_0 \alpha_1^2 \epsilon I_b^2 I_s^2 \phi_{mb} - B_0 \alpha_2^2 \epsilon I_b^2 I_s^2 \phi_{mb} - \alpha_1^2 b \epsilon^2 I_b^2 I_s \phi_{mb} - \alpha_2^2 b \epsilon^2 I_b I_s^2 \phi_{mb} + \alpha_1^2 b \epsilon^3 I_b^2 I_s q + \alpha_2^2 b \epsilon^3 I_b I_s^2 q + 3 B_0 P_0 \alpha_1^2 \epsilon I_b^3 I_s^2 q + B_0 P_0 \alpha_2^2 \epsilon I_b^3 I_s^2 q - 2 P_0 \alpha_1 \alpha_2 b \epsilon^2 I_b^2 I_s^2 + 4 B_0 \alpha_1 \alpha_2 \epsilon^2 I_b^2 I_s^2 q + P_0 \alpha_1^2 b \epsilon^2 I_b^2 I_s^2 q + P_0 \alpha_2^2 b \epsilon^2 I_b^2 I_s^2 q - 4 B_0 P_0 \alpha_1 \alpha_2 \epsilon I_b^3 I_s^2 - 4 B_0 \alpha_1 \alpha_2 \epsilon I_b^2 I_s^2 \phi_{mb} + 3 B_0 a \alpha_1 \epsilon I_b^2 I_s^2 q + 3 B_0 a \alpha_2 \epsilon I_b^2 I_s^2 q - 2 \alpha_1 \alpha_2 b \epsilon^2 I_b I_s^2 \phi_{mb} -$

$2\ \alpha_1\ \alpha_2\ b\ \epsilon^2\ I_b^2\ I_s\ \phi_{mb} + a\ \alpha_1\ b\ \epsilon^2\ I_b\ I_s^2\ q + 2\ a\ \alpha_1\ b\ \epsilon^2\ I_b^2\ I_s\ q + 2\ a\ \alpha_2\ b\ \epsilon^2\ I_b\ I_s^2\ q + a\ \alpha_2\ b\ \epsilon^2\ I_b^2\ I_s\ q + 2\ \alpha_1\ \alpha_2\ b\ \epsilon^3\ I_b\ I_s^2\ q + 2\ \alpha_1\ \alpha_2\ b\ \epsilon^3\ I_b^2\ I_s\ q + 6\ B_0\ P_0\ \alpha_1\ \alpha_2\ \epsilon\ I_b^3\ I_s^2\ q + 4\ P_0\ \alpha_1\ \alpha_2\ b\ \epsilon^2\ I_b^2\ I_s^2\ q.$

$a_5 = 3\ a\ I_b\ I_s^2\ \phi_{ms} - 2\ a\ \epsilon\ I_b\ I_s^2 + 3\ a\ I_b^2\ I_s\ \phi_{ms} - 2\ \alpha_2\ \epsilon^2\ I_b\ I_s^2 - P_0\ \alpha_1\ \epsilon\ I_b^2\ I_s^2 - 2\ P_0\ \alpha_2\ \epsilon\ I_b^2\ I_s^2 + 3\ P_0\ \alpha_1\ I_b^2\ I_s^2\ \phi_{ms} + 3\ P_0\ \alpha_2\ I_b^2\ I_s^2\ \phi_{ms} + 2\ \alpha_1\ \epsilon^2\ I_b\ I_s^2\ q + 4\ \alpha_2\ \epsilon^2\ I_b\ I_s^2\ q - 2\ \alpha_2^2\ b\ \epsilon^3\ I_b\ I_s^2 - B_0\ \alpha_2^2\ \epsilon^2\ I_b^2\ I_s^2 - 2\ \alpha_1\ \epsilon\ I_b\ I_s^2\ \phi_{mb} - 4\ \alpha_2\ \epsilon\ I_b\ I_s^2\ \phi_{mb} + \alpha_1\ \epsilon\ I_b\ I_s^2\ \phi_{ms} + 2\ \alpha_1\ \epsilon\ I_b^2\ I_s\ \phi_{ms} + 2\ \alpha_2\ \epsilon\ I_b\ I_s^2\ \phi_{ms} + \alpha_2\ \epsilon\ I_b^2\ I_s\ \phi_{ms} + 6\ a\ \epsilon\ I_b\ I_s^2\ q - P_0\ \alpha_2^2\ b\ \epsilon^2\ I_b^2\ I_s^2 + B_0\ \alpha_1^2\ \epsilon^2\ I_b^2\ I_s^2\ q + B_0\ \alpha_2^2\ \epsilon^2\ I_b^2\ I_s^2\ q - B_0\ a\ \alpha_1\ \epsilon\ I_b^2\ I_s^2 - 2\ B_0\ a\ \alpha_2\ \epsilon\ I_b^2\ I_s^2 + 3\ P_0\ \alpha_1\ \epsilon\ I_b^2\ I_s^2\ q + 3\ P_0\ \alpha_2\ \epsilon\ I_b^2\ I_s^2\ q - 2\ a\ \alpha_2\ b\ \epsilon^2\ I_b\ I_s^2 - 2\ B_0\ \alpha_1\ \alpha_2\ \epsilon^2\ I_b^2\ I_s^2 - B_0\ \alpha_1^2\ \epsilon\ I_b^2\ I_s^2\ \phi_{mb} - B_0\ \alpha_2^2\ \epsilon\ I_b^2\ I_s^2\ \phi_{mb} - 2\ \alpha_2^2\ b\ \epsilon^2\ I_b\ I_s^2\ \phi_{mb} + 2\ \alpha_2^2\ b\ \epsilon^3\ I_b\ I_s^2\ q - 2\ P_0\ \alpha_1\ \alpha_2\ b\ \epsilon^2\ I_b^2\ I_s^2 + 4\ B_0\ \alpha_1\ \alpha_2\ \epsilon^2\ I_b^2\ I_s^2\ q + P_0\ \alpha_1^2\ b\ \epsilon^2\ I_b^2\ I_s^2\ q + P_0\ \alpha_2^2\ b\ \epsilon^2\ I_b^2\ I_s^2\ q - 4\ B_0\ \alpha_1\ \alpha_2\ \epsilon\ I_b^2\ I_s^2\ \phi_{mb} + 3\ B_0\ a\ \alpha_1\ \epsilon\ I_b^2\ I_s^2\ q + 3\ B_0\ a\ \alpha_2\ \epsilon\ I_b^2\ I_s^2\ q - 4\ \alpha_1\ \alpha_2\ b\ \epsilon^2\ I_b\ I_s^2\ \phi_{mb} + 2\ a\ \alpha_1\ b\ \epsilon^2\ I_b\ I_s^2\ q + 4\ a\ \alpha_2\ b\ \epsilon^2\ I_b\ I_s^2\ q + 4\ \alpha_1\ \alpha_2\ b\ \epsilon^3\ I_b\ I_s^2\ q + 4\ P_0\ \alpha_1\ \alpha_2\ b\ \epsilon^2\ I_b^2\ I_s^2\ q.$

$a_4 = a\ \epsilon\ I_s^3\ q - \alpha_2\ \epsilon\ I_s^3\ \phi_{mb} - a\ \epsilon\ I_b\ I_s^2 + 6\ a\ I_b\ I_s^2\ \phi_{ms} - \alpha_2\ \epsilon^2\ I_b\ I_s^2 + \alpha_2\ \epsilon^2\ I_s^3\ q + 3\ P_0\ \alpha_1\ I_b^2\ I_s^2\ \phi_{ms} + 3\ P_0\ \alpha_2\ I_b^2\ I_s^2\ \phi_{ms} + \alpha_1\ \epsilon^2\ I_b\ I_s^2\ q + 2\ \alpha_2\ \epsilon^2\ I_b\ I_s^2\ q - B_0\ \alpha_2^2\ \epsilon^2\ I_b\ I_s^3 - \alpha_2^2\ b\ \epsilon^3\ I_b\ I_s^2 - \alpha_2^2\ b\ \epsilon^2\ I_s^3\ \phi_{mb} + \alpha_2^2\ b\ \epsilon^3\ I_s^3\ q - P_0\ \alpha_2\ \epsilon\ I_b\ I_s^3 - \alpha_1\ \epsilon\ I_b\ I_s^2\ \phi_{mb} - 2\ \alpha_2\ \epsilon\ I_b\ I_s^2\ \phi_{mb} + 2\ \alpha_1\ \epsilon\ I_b\ I_s^2\ \phi_{ms} + 4\ \alpha_2\ \epsilon\ I_b\ I_s^2\ \phi_{ms} + 3\ a\ \epsilon\ I_b\ I_s^2\ q - B_0\ a\ \alpha_2\ \epsilon\ I_b\ I_s^3 + P_0\ \alpha_1\ \epsilon\ I_b\ I_s^3\ q + 3\ P_0\ \alpha_2\ \epsilon\ I_b\ I_s^3\ q - 2\ B_0\ \alpha_2^2\ \epsilon\ I_b\ I_s^3\ \phi_{mb} - a\ \alpha_2\ b\ \epsilon^2\ I_b\ I_s^2 + a\ \alpha_2\ b\ \epsilon^2\ I_s^3\ q - 2\ B_0\ P_0\ \alpha_2^2\ \epsilon\ I_b^2\ I_s^3 - P_0\ \alpha_2^2\ b\ \epsilon^2\ I_b\ I_s^3 + 2\ B_0\ \alpha_2^2\ \epsilon^2\ I_b\ I_s^3\ q - \alpha_2^2\ b\ \epsilon^2\ I_b\ I_s^2\ \phi_{mb} + \alpha_2^2\ b\ \epsilon^3\ I_b\ I_s^2\ q + B_0\ P_0\ \alpha_1^2\ \epsilon\ I_b^2\ I_s^3\ q + 3\ B_0\ P_0\ \alpha_2^2\ \epsilon\ I_b^2\ I_s^3\ q + 2\ P_0\ \alpha_2^2\ b\ \epsilon^2\ I_b\ I_s^3\ q - 2\ B_0\ \alpha_1\ \alpha_2\ \epsilon\ I_b\ I_s^3\ \phi_{mb} + B_0\ a\ \alpha_1\ \epsilon\ I_b\ I_s^3\ q + 3\ B_0\ a\ \alpha_2\ \epsilon\ I_b\ I_s^3\ q - 2\ B_0\ P_0\ \alpha_1\ \alpha_2\ \epsilon\ I_b^2\ I_s^3 + 2\ B_0\ \alpha_1\ \alpha_2\ \epsilon^2\ I_b\ I_s^3\ q - 2\ \alpha_1\ \alpha_2\ b\ \epsilon^2\ I_b\ I_s^2\ \phi_{mb} + a\ \alpha_1\ b\ \epsilon^2\ I_b\ I_s^2\ q + 2\ a\ \alpha_2\ b\ \epsilon^2\ I_b\ I_s^2\ q + 2\ \alpha_1\ \alpha_2\ b\ \epsilon^3\ I_b\ I_s^2\ q + 6\ B_0\ P_0\ \alpha_1\ \alpha_2\ \epsilon\ I_b^2\ I_s^3\ q + 2\ P_0\ \alpha_1\ \alpha_2\ b\ \epsilon^2\ I_b\ I_s^3\ q.$

$a_3 = a\ I_s^3\ \phi_{ms} - 2\ \alpha_2\ \epsilon\ I_s^3\ \phi_{mb} + \alpha_2\ \epsilon\ I_s^3\ \phi_{ms} + 2\ a\ \epsilon\ I_s^3\ q + 3\ a\ I_b\ I_s^2\ \phi_{ms} + 2\ \alpha_2\ \epsilon^2\ I_s^3\ q - B_0\ \alpha_2^2\ \epsilon^2\ I_b\ I_s^3 - 2\ \alpha_2^2\ b\ \epsilon^2\ I_s^3\ \phi_{mb} + 2\ \alpha_2^2\ b\ \epsilon^3\ I_s^3\ q - P_0\ \alpha_2\ \epsilon\ I_b\ I_s^3 + P_0\ \alpha_1\ I_b\ I_s^3\ \phi_{ms} + 3\ P_0\ \alpha_2\ I_b\ I_s^3\ \phi_{ms} + \alpha_1\ \epsilon\ I_b\ I_s^2\ \phi_{ms} + 2\ \alpha_2\ \epsilon\ I_b\ I_s^2\ \phi_{ms} - B_0\ a\ \alpha_2\ \epsilon\ I_b\ I_s^3 + P_0\ \alpha_1\ \epsilon\ I_b\ I_s^3\ q + 3\ P_0\ \alpha_2\ \epsilon\ I_b\ I_s^3\ q - 2\ B_0\ \alpha_2^2\ \epsilon\ I_b\ I_s^3\ \phi_{mb} + 2\ a\ \alpha_2\ b\ \epsilon^2\ I_s^3\ q - P_0\ \alpha_2^2\ b\ \epsilon^2\ I_b\ I_s^3 + 2\ B_0\ \alpha_2^2\ \epsilon^2\ I_b\ I_s^3\ q + 2\ P_0\ \alpha_2^2\ b\ \epsilon^2\ I_b\ I_s^3\ q - 2\ B_0\ \alpha_1\ \alpha_2\ \epsilon\ I_b\ I_s^3\ \phi_{mb} + B_0\ a\ \alpha_1\ \epsilon\ I_b\ I_s^3\ q + 3\ B_0\ a\ \alpha_2\ \epsilon\ I_b\ I_s^3\ q + 2\ B_0\ \alpha_1\ \alpha_2\ \epsilon^2\ I_b\ I_s^3\ q + 2\ P_0\ \alpha_1\ \alpha_2\ b\ \epsilon^2\ I_b\ I_s^3\ q.$

$a_2 = 2\ a\ I_s^3\ \phi_{ms} - \alpha_2\ \epsilon\ I_s^3\ \phi_{mb} + 2\ \alpha_2\ \epsilon\ I_s^3\ \phi_{ms} + a\ \epsilon\ I_s^3\ q + \alpha_2\ \epsilon^2\ I_s^3\ q - B_0\ \alpha_2^2\ \epsilon\ I_s^4\ \phi_{mb} + B_0\ \alpha_2^2\ \epsilon^2\ I_s^4\ q - \alpha_2^2\ b\ \epsilon^2\ I_s^3\ \phi_{mb} + \alpha_2^2\ b\ \epsilon^3\ I_s^3\ q + P_0\ \alpha_2\ \epsilon\ I_s^4\ q + P_0\ \alpha_1\ I_b\ I_s^3\ \phi_{ms} + 3\ P_0\ \alpha_2\ I_b\ I_s^3\ \phi_{ms} + B_0\ a\ \alpha_2\ \epsilon\ I_s^4\ q - B_0\ P_0\ \alpha_2^2\ \epsilon\ I_b\ I_s^4 + a\ \alpha_2\ b\ \epsilon^2\ I_s^3\ q + P_0\ \alpha_2^2\ b\ \epsilon^2\ I_s^4\ q + 3\ B_0\ P_0\ \alpha_2^2\ \epsilon\ I_b\ I_s^4\ q + 2\ B_0\ P_0\ \alpha_1\ \alpha_2\ \epsilon\ I_b\ I_s^4\ q.$

$a_1 = a\ I_s^3\ \phi_{ms} + P_0\ \alpha_2\ I_s^4\ \phi_{ms} + \alpha_2\ \epsilon\ I_s^3\ \phi_{ms} - B_0\ \alpha_2^2\ \epsilon\ I_s^4\ \phi_{mb} + B_0\ \alpha_2^2\ \epsilon^2\ I_s^4\ q + P_0\ \alpha_2\ \epsilon\ I_s^4\ q + B_0\ a\ \alpha_2\ \epsilon\ I_s^4\ q + P_0\ \alpha_2^2\ b\ \epsilon^2\ I_s^4\ q.$

$a_0 = B_0\ P_0\ \epsilon\ q\ \alpha_2^2\ I_s^5 + P_0\ \phi_{ms}\ \alpha_2\ I_s^4.$

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