
Explosive tritrophic food chain model with herd behaviour of prey and finite time blow-up of the top predator

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Abstract: In this work, we have discussed the dynamical behaviours of a three species food chain model where the prey species exhibits herd behaviour and sexually reproductive top predator are of generalist type. Positivity and uniform boundedness of the system are studied to verify its well-posedness. Some conditions for extinction of prey and predators are derived. Feasibility criteria and stability analysis of all the equilibrium points are discussed here. Hopf-bifurcation condition for interior equilibrium point is carried out analytically. Mathematical conditions for finite time blow-up of top predator are established. Numerical simulations are carried out to validate our analytical findings.

Keywords: square root functional response; generalist predator; sexual reproduction; Hopf-bifurcation; finite time blow-up.

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1 Introduction

In order to survive in a better way, every population must eat in different strategic ways. For certain predator species this necessarily implies to pursue and bring down a sufficient amount of prey. Prey population must be on the alert when predator population always on the lookout for food. Scattering and zigzagging of prey to confuse the predator is a popular strategy of herd prey to escape from predator (Chen and Kolokolnikov, 2014; Olson et al.,

2013). Several anti-predator protocols of animal aggregations have been proposed and one potential method among them is by which fish schools or bird flocks may thwart predators is the 'predator confusion effect' (Milinski and Heller, 1978; Jeschke and Tollrian, 2007; Ioannou et al., 2008; Krakauer, 1995; Olson et al., 2013; Demsar et al., 2015). This theory is based on the idea that it becomes difficult for predators to pick out individual prey from groups because the many moving targets create a sensory overload of the predator's visual channel. Other potential anti-predator effects of animal aggregations are the 'many eyes' hypothesis where the size of the group increases, the task of scanning the environment for predators can be spread out over many individuals and 'encounter dilution'. Predation by large fields accounted for more than 50% of mortality of adult white-coatis (Hass and Valenzuela, 2002). Predation rates were higher on solitary coatis than on group coatis where the predation rate was inversely related to group size. Herd formation can decrease individual predation risk for several reasons (Cressman and Garay, 2011). In summary, we can claim that the individual prey's survival probability is dependent on whether the individual in question is solitary or in the herd. It is a 'group defense' strategy of prey population, such that when the predators make contact with the prey population, they cannot reach the inside of the prey group which means that the predators hunt only on the boundary of prey herd. It is the reason of defining this dynamics of prey by the square root of the prey population in the functional response term (Tang and Song, 2015; Cagliero and Venturino, 2016; Venturino, 2011, 2013; Lv et al., 2016; Tanner, 1975; Ajraldi et al., 2011; Venturino and Petrovskii, 2013; Yuan et al., 2013; Maiti et al., 2016).

In ecology, predation provides a biological relationship where a predator feeds the prey. In multi species food chain model, energy flow from lower trophic level to higher trophic level is very interesting and these individual steps from one energy level to the next constitute the ecological community structure. Specialist predators are supposed to feed only on its preferable prey species where generalist predator can survive without its preferred prey. Specialist predator are considered to be limited to the regular habitat as their prey; subsequently loss of the habitat is, therefore, also loss of predator habitat. Whereas generalist predator are assumed to be live mainly in the focal prey species (Cronin, 2003; Prakash and Ross, 2002; Swihart et al., 2001). In general the generalist predators are sexually reproducing (Priyadarshi and Gakkhar, 2013; Jana et al., 2015; Parshad et al., 2016b). It is predictable that the growth of sexually reproducing population will be proportional to densities of the two species, because sexual selection is based on the success of definite individuals over others of the same sex and contains behavioural habits such as choosiness and species recognition (Jana and Tripathi, 2016).

In the ecological perspective, it is very difficult to derive the particular conditions of population explosion/blow-up for any ecological model system. Parshad et al. (2002) establishes the solution to a three species model studied by Aziz-Alaoui (Aziz-Alaoui, 2002), can blow-up in finite time even under the restriction derived in Aziz-Alaoui (2002). It is also useful then to study ecological mechanisms that can prevent such explosive phenomenon (Parshad et al., 2016c). Recently, many researchers culture the blow-up behaviour of different dynamical systems. Zhang and Yang (2010) obtained the conditions under which the solutions may exist globally or blow up in a finite time for a nonlinear parabolic equation subject to mixed boundary conditions. Ling and Wang (2013) studied blow-up criteria and global boundedness of non-negative solutions using super/sub solution method techniques. The exact conditions of blow-up and global existence of a nonlinear wave equation are studied by Jiang and Zhang (2014). Also, the sufficient conditions for the blow-up and global solutions are presented for nonlinear parabolic equation with different

kinds of boundary conditions studied by Zhang and He (2010). Zhou et al. (2016) illustrated that the blow-up behaviours of differential equations with piecewise constant arguments are quite different from those of the corresponding ordinary differential equations.

In this paper, we have proposed a tri-trophic food chain model with one prey that shows herd behaviour, one intermediate specialist predator and a sexually reproductive generalist top predator which shows finite time blow-up. The paper is organised as follows. In Section 2, we have presented the mathematical model with basic consideration. Positivity and uniform boundedness are studied in Section 3. In Section 4, the extinction criteria of all the populations are discussed. Stability behaviours of the equilibrium points and Hopf-bifurcation analysis of the interior equilibrium point are discussed in the Section 5. In Section 6, finite time blow-up analysis is there. To illustrate our analytical findings, numerical simulations results are presented in Section 7. Section 8 contains the general discussion on the results of our mathematical findings.

2 The mathematical model

In this work, we have introduced and discussed a three-species food chain model: one prey (X) with logistic growth rate (with growth rate constant r and environmental carrying capacity K), intermediate specialist predator (Y) and sexually reproductive generalist (governed by the modified Holling-Tanner/Leslie-Grower model) top predator (Z) (Jana and Tripathi, 2016). We have assumed that the prey population (X) lives in herds. As the population exhibits herd behaviour, here we have used the modified square root functional response mentioned earlier (Braza, 2012). The top predator (Z) has preferred food source (Y) and their interaction is assumed to be governed by the usual Holling type-II functional response. The model under investigation is as follows:

$$\begin{aligned}\frac{dX}{dT} &= rX \left(1 - \frac{X}{K}\right) - \frac{\alpha_1 \sqrt{XY}}{1 + T_1 \alpha_1 \sqrt{X}}, \\ \frac{dY}{dT} &= \frac{C_1 \alpha_1 \sqrt{XY}}{1 + T_1 \alpha_1 \sqrt{X}} - d_1 Y - \frac{\alpha_2 Y Z}{1 + T_2 \alpha_2 Y}, \\ \frac{dZ}{dT} &= C_2 Z^2 - \frac{\alpha_3 Z^2}{m + T_2 Y},\end{aligned}\tag{1}$$

with initial conditions $X(0) > 0$, $Y(0) > 0$, $Z(0) > 0$. Here the parameters α_1, α_2 are the search efficiencies and T_1, T_2 are the handling times of the intermediate predator and top predator respectively. The parameter C_1 denotes the biomass conversion factor for prey population to intermediate predator and it dies with mortality rate d_1 . The residual loss in Z population due to severe scarcity of its preferred food Y is denoted by α_3 . The top predator Z is a sexually reproducing species. For most sexual species over most population densities, reproduction is determined primarily by female densities; however, the growth of a sexually reproducing population is proportional to the square of the biomass of individual's present in situation when the population is at very low densities. The square term Z^2 signifies the fact that mating frequency is directly proportional to the biomass of males as well as that of females present at any instant of time T and because of severe scarcity of its preferred food Y , C_2 is the top predator's sexual reproduction rate and m normalises the residual reduction in the top predator Z .

To reduce the number of parameters and to simplify system (1) a little bit, we non-dimensionalise the system with the following scaling:

$$x = \frac{X}{K}, y = \frac{Y}{K}, z = \frac{Z\alpha_2}{\gamma} \text{ and } t = rT.$$

Then the system (1) takes the form (after some simplifications):

$$\frac{dx}{dt} = x(1-x) - \frac{a_1\sqrt{xy}}{1+b_1\sqrt{x}}, \quad (2)$$

$$\frac{dy}{dt} = \frac{c\sqrt{xy}}{1+b_1\sqrt{x}} - dy - \frac{yz}{1+b_2y}, \quad (3)$$

$$\frac{dz}{dt} = ez^2 - \frac{a_2z^2}{b_3+y}, \quad (4)$$

where

$$a_1 = \frac{\alpha_1\sqrt{K}}{r}, b_1 = T_1\alpha_1\sqrt{K}, c = \frac{C_1\alpha_1\sqrt{K}}{r}, d = \frac{d_1}{r}, b_2 = T_2\alpha_2K, e = \frac{C_2}{\alpha_2},$$

$$a_2 = \frac{\alpha_3}{\alpha_2T_2K}, b_3 = \frac{m}{T_2K},$$

with initial conditions $x(0) > 0, y(0) > 0, z(0) > 0$.

3 Positivity and uniform boundedness

Positivity and uniform boundedness of a model guarantee that the model is biologically well behaved or well posed. For positivity of the system (2)–(4), we have the following lemma.

Lemma 3.1: $(x(t), y(t), z(t))^T \in \mathbb{R}^3 : x(t_0) > 0, y(t_0) > 0, z(t_0) > 0$ for some $t_0 \in \mathbb{R}$ is positively invariant for the model system (2)–(4).

Proof: For $x(t_0) > 0, y(t_0) > 0, z(t_0) > 0$, we have

$$x(t) = x(t_0) \exp\left(\int_0^t \left\{1 - x(s) - \frac{a_1y(s)}{\sqrt{x(s)} + b_1x(s)}\right\} ds\right) > 0,$$

$$y(t) = y(t_0) \exp\left(\int_0^t \left\{\frac{c\sqrt{x(s)}}{1+b_1\sqrt{x(s)}} - d - \frac{z(s)}{1+b_2y(s)}\right\} ds\right) > 0,$$

$$z(t) = z(t_0) \exp\left(\int_0^t \left\{ez(s) - \frac{a_2z(s)}{b_3+y(s)}\right\} ds\right) > 0,$$

which complete the proof. □

Theorem 3.1: All the solutions of the three species food chain model system (2)–(4) are uniformly bounded, provided

$$\frac{c}{4da_1} + \frac{c}{a_1} + b_3 < \frac{a_2}{e},$$

and finally entering the region

$$\Omega = \left\{ (x, y, z) \in \mathbb{R}_+^3 : 0 < x \leq 1, 0 < x + \frac{a_1}{c}y \leq \frac{1}{4d} + 1, \right. \\ \left. 0 < x + \frac{a_1}{c}y + z < \frac{1}{4d} + 1 + \frac{d}{\frac{c}{4da_1} + \frac{c}{a_1} + b_3} - 4e \right\}.$$

Proof: First, we prove that $x(t)$ is bounded for all $t \geq 0$. From equation (2) we can write

$$\frac{dx}{dt} \leq x(1-x) \Rightarrow \lim_{t \rightarrow +\infty} \sup x(t) \leq 1$$

Now, we show that both $x(t)$ and $y(t)$ are bounded for all $t \geq 0$. Let $W_1(t) = x + \frac{a_1}{c}y$, then

$$\begin{aligned} \frac{dW_1}{dt} &= x(1-x) - \frac{a_1}{c}dy - \frac{a_1}{c} \frac{yz}{1+b_2y} \\ &\Rightarrow \frac{dW_1}{dt} \leq \frac{1}{4} - \frac{a_1}{c}dy - dx + dx \\ &\Rightarrow \frac{dW_1}{dt} + dW_1 \leq \frac{1}{4} + d \text{ (for large } t) \\ &\Rightarrow 0 < W_1(t) \leq \frac{1}{4d} + 1 \text{ as } t \rightarrow \infty. \end{aligned}$$

Finally, let us prove that $x(t)$, $y(t)$ and $z(t)$ are all bounded for all $t \geq 0$.

Suppose $W_2 = x + \frac{a_1}{c}y + z$.

$$\begin{aligned} \therefore \frac{dW_2}{dt} &= x(1-x) - \frac{a_1}{c}dy + z^2 \left(e - \frac{a_2}{b_3 + y} \right) \\ &\Rightarrow \frac{dW_2}{dt} \leq \frac{1}{4} - \frac{a_1}{c}dy - dx + dx - dz + dz + z^2 \left(e - \frac{a_2}{b_3 + y} \right) \\ &\Rightarrow \frac{dW_2}{dt} + dW_2 \leq \frac{1}{4} + d + dz + z^2 \left(e - \frac{a_2}{b_3 + y} \right) \\ &< \frac{1}{4} + d + z \left\{ d - z \left(\frac{a_2}{\frac{c}{4da_1} + \frac{c}{a_1} + b_3} - e \right) \right\} \end{aligned}$$

Now, let us find the maximum value of the function $z \left\{ d - z \left(\frac{a_2}{\frac{c}{4da_1} + \frac{c}{a_1} + b_3} - e \right) \right\}$.

Let, $f(z) = zd - \beta z^2$, where $\beta = \left(\frac{a_2}{\frac{c}{4da_1} + \frac{c}{a_1} + b_3} - e \right)$

Then, the maximum value of $f(z)$ is $\frac{d^2}{4\beta}$, provided $\beta > 0$, i.e. $\frac{a_2}{e} > \frac{c}{4da_1} + \frac{c}{a_1} + b_3$.

$$\therefore \frac{dW_2}{dt} + dW_2 < \frac{1}{4} + d + \frac{d^2}{4\beta} \Rightarrow 0 < W_2(t) < \frac{1}{4d} + 1 + \frac{d}{4\beta} \text{ as } t \rightarrow \infty$$

$$\Rightarrow 0 < x + \frac{a_1}{c}y + z < \frac{1}{4d} + 1 + \frac{d}{\frac{c}{4da_1} + \frac{c}{a_1} + b_3 - 4e} \text{ as } t \rightarrow \infty.$$

Hence, the theorem is proved. \square

4 Extinction scenarios

In this section, some conditions for extinction of the prey or predators are noticed. The symbols \bar{x} , \bar{y} and \underline{y} represent $\limsup_{t \rightarrow \infty} x(t)$, $\limsup_{t \rightarrow \infty} y(t)$ and $\liminf_{t \rightarrow \infty} y(t)$, respectively. Here, we use the fact that $0 < \bar{x} \leq 1$, which is proved in Theorem 3.1.

Theorem 4.1: *If $\underline{y} > \frac{\sqrt{2}(1 + b_1\sqrt{2})}{a_1}$, then $\lim_{t \rightarrow \infty} x(t) = 0$.*

Proof: If possible, let $\lim_{t \rightarrow \infty} x(t) = \mu > 0$. Since $\bar{x} \leq 1$ then for any $0 < \epsilon < 1$, there exists $t_\epsilon > 0$ such that $x(t) < 1 + \epsilon$ for $t > t_\epsilon$.

From the definition of y , it follows that, for any $0 < \epsilon' < \underline{y} - \frac{\sqrt{2}(1 + b_1\sqrt{2})}{\alpha}$, there exists $t_{\epsilon'} > 0$ such that $y(t) > \underline{y} - \epsilon'$ for $t > t_{\epsilon'}$.

Then, for $t > \max\{t_\epsilon, t_{\epsilon'}\}$, the equation (2) can be written as

$$\begin{aligned} \frac{dx}{dt} &< x - \frac{a_1\sqrt{x}y}{1 + b_1\sqrt{x}}, \\ &< x - \frac{a_1xy}{\sqrt{1 + \epsilon}(1 + b_1\sqrt{1 + \epsilon})}, \\ &< x \left\{ 1 - \frac{a_1(\underline{y} - \epsilon')}{\sqrt{2}(1 + b_1\sqrt{2})} \right\}, \\ &< -\frac{a_1x}{\sqrt{2}(1 + b_1\sqrt{2})} \left(\underline{y} - \epsilon' - \frac{\sqrt{2}(1 + b_1\sqrt{2})}{a_1} \right) < 0 \end{aligned}$$

which implies that $\lim_{t \rightarrow \infty} x(t) = 0$, a contradiction. Hence the theorem is established. \square

Theorem 4.2: If $d > c$, then $\lim_{t \rightarrow \infty} y(t) = 0$.

Proof: Since $\bar{x} \leq 1$, for any $0 < \epsilon < \frac{d^2}{c^2} - 1$, there exists $t_\epsilon > 0$ such that $x(t) < 1 + \epsilon$ for $t > t_\epsilon$. For $t > t_\epsilon$, we have from equation (3):

$$\begin{aligned} \frac{dy}{dt} &< \left(-d + \frac{c\sqrt{x}}{1 + b_1\sqrt{x}} \right) y, \\ &< y(-d + c\sqrt{x}), \\ &< -cy \left(\frac{d}{c} - \sqrt{1 + \epsilon} \right) < 0. \end{aligned}$$

Therefore, $\lim_{t \rightarrow \infty} y(t) = 0$. □

Theorem 4.3: If $\bar{y} < \frac{a_2}{e} - b_3$, then $\lim_{t \rightarrow \infty} z(t) = 0$.

Proof: Let $0 < \epsilon < \frac{a_2}{e} - b_3 - \bar{y}$, which is possible due to Theorem 3.1. Then there exists $t_\epsilon > 0$ such that $y(t) < \bar{y} + \epsilon$ for $t > t_\epsilon$. For $t > t_\epsilon$, from equation (4):

$$\begin{aligned} \frac{dz}{dt} &< z^2 \left\{ e - \frac{a_2}{\bar{y} + b_3} \right\}, \\ &< z^2 \left\{ e - \frac{a_2}{\bar{y} + \epsilon + b_3} \right\} < 0. \end{aligned}$$

Therefore, $\lim_{t \rightarrow \infty} z(t) = 0$. □

5 Stability analysis

The system (2)–(4) has five different boundary equilibrium points: (i) $E_0(0, 0, 0)$, (ii) $E_1(1, 0, 0)$, (iii) $E_2(0, 0, \tilde{z})$ (where \tilde{z} represents nonzero positive value, provided $e = \frac{a_2}{b_3}$), (iv) $E_3(\hat{x}, \hat{y}, 0)$ and (v) $E_4(1, 0, \bar{z})$. It is noted that the system (2)–(4) can not be linearised about the equilibrium points $E_0(0, 0, 0)$ and $E_2(0, 0, \tilde{z})$. But if the conditions of the Theorems (4.1), (4.2) and (4.3) hold simultaneously, then $E_0(0, 0, 0)$ is globally asymptotically stable. Let us establish a theorem to study the nature of the equilibrium point E_0 .

Theorem 5.1: If $\frac{a_2}{e} - b_3 < 0$, then $E_0(0, 0, 0)$ is an unstable equilibrium point.

Proof: From equation (4) we have

$$\frac{dz}{dt} = ez^2 - \frac{a_2z^2}{y + b_3}$$

$\therefore \frac{dz}{dt} > 0$, when $\frac{a_2}{e} - b_3 < 0$. So, E_0 is unstable equilibrium point. □

Table 1 Stability analysis of boundary equilibria of model system (2)–(4)

	Equilibrium and coordinate	Feasibility condition	Jacobian matrix and eigenvalues	Stability status
(i)	$E_1 = (1, 0, 0)$	Always	$\begin{pmatrix} -1 & -\frac{a_1}{1+b_1} & 0 \\ 0 & \frac{c}{1+b_1} - d & 0 \\ 0 & 0 & 0 \end{pmatrix}$ $\lambda_1 = -1, \lambda_2 = \frac{c}{1+b_1} - d,$ $\lambda_3 = 0$	Neutral
(ii)	$E_3 = (\hat{x}, \hat{y}, 0)$	$(c - b_1 d)^2 > d^2$	$\begin{pmatrix} p_1 - \frac{a_1 d}{c} & 0 \\ p_2 & 0 - \frac{\hat{y}}{1+b_2 \hat{y}} \\ 0 & 0 & 0 \end{pmatrix}$ $\lambda_1 = 0, \lambda_{2,3} = \frac{p_1 \pm \sqrt{p_1^2 - \frac{4a_1 d p_2}{c}}}{2}$ $\left[\begin{array}{l} p_1 = 1 - 2\hat{x} - \frac{a_1 \hat{y}}{2\sqrt{\hat{x}}(1+b_1\sqrt{\hat{x}})^2}, \\ p_2 = \frac{c\hat{y}}{2\sqrt{\hat{x}}(1+b_1\sqrt{\hat{x}})^2} \end{array} \right]$	Neutral
(iii)	$E_4(1, 0, \bar{z})$	$e = \frac{a_2}{b_3}$	$\begin{pmatrix} -1 & -\frac{a_1}{1+b_1} & 0 \\ 0 & \frac{c}{1+b_1} - d - \bar{z} & 0 \\ 0 & \frac{a_2 \bar{z}^2}{b_3^2} & 2\bar{z}(e - \frac{a_2}{b_3}) \end{pmatrix}$ $\lambda_1 = -1, \lambda_2 = \frac{c}{1+b_1} - d - \bar{z},$ $\lambda_3 = 2\bar{z}(e - \frac{a_2}{b_3}) = 0$	Neutral

Feasibility and stability of the other boundary equilibrium points are given in Table 1.

Feasibility conditions and dynamical behaviour of the interior equilibrium point: Interior equilibrium point is $E^*(x^*, y^*, z^*)$, where $y^* = \frac{a_2 - eb_3}{e}$ (provided $a_2 > eb_3$), $z^* = \left(\frac{c\sqrt{x^*}}{1+b_1\sqrt{x^*}} - d \right) (1 + b_2 y^*)$ (provided $\left(\frac{c\sqrt{x^*}}{1+b_1\sqrt{x^*}} - d \right) > 0$) and x^* is the real positive root of the equation: $b_1 x^2 + x^{\frac{3}{2}} - b_1 x - x^{\frac{1}{2}} + \frac{a_1(a_2 - eb_3)}{e} = 0$. The variational matrix $V(E^*)$ of system (2)–(4) at E^* is given by

$$V(E^*) = \begin{bmatrix} a_{11} & a_{12} & 0 \\ a_{21} & a_{22} & a_{23} \\ 0 & a_{32} & 0 \end{bmatrix},$$

where

$$a_{11} = 1 - 2x^* - \frac{a_1 y^*}{2\sqrt{x^*}(1+b_1\sqrt{x^*})^2}, a_{12} = -\frac{a_1 \sqrt{x^*}}{1+b_1\sqrt{x^*}},$$

$$a_{13} = 0, a_{21} = \frac{c y^*}{2\sqrt{x^*}(1+b_1\sqrt{x^*})^2},$$

$$a_{22} = \frac{b_2 y^* z^*}{(1+b_2 y^*)^2}, a_{23} = -\frac{y^*}{1+b_2 y^*}, a_{31} = 0, a_{32} = \frac{a_2 z^{*2}}{(b_3 + y^*)^2} \text{ and } a_{33} = 0.$$

The characteristic equation of $V(E^*)$ is

$$\lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 = 0,$$

where $A_1 = -(a_{11} + a_{22})$, $A_2 = (a_{11}a_{22} - a_{12}a_{21} - a_{23}a_{32})$ and $A_3 = a_{11}a_{23}a_{32}$. By Routh-Hurwitz criterion, the coexistence equilibrium point $E^*(x^*, y^*, z^*)$ is locally asymptotically stable if $A_1 > 0$, $A_3 > 0$ and $A_1A_2 - A_3 > 0$.

5.1 Hopf bifurcation at $E^*(x^*, y^*, z^*)$

The characteristic equation of system (2)–(4) at $E^*(x^*, y^*, z^*)$ is given by

$$\lambda^3 + A_1(b_2)\lambda^2 + A_2(b_2)\lambda + A_3(b_2) = 0, \quad (5)$$

where

$$\begin{aligned} A_1(b_2) &= - \left[1 - 2x^* - \frac{a_1y^*}{2\sqrt{x^*}(1+b_1\sqrt{x^*})^2} + \frac{b_2y^*z^*}{(1+b_2y^*)^2} \right], \\ A_2(b_2) &= \left\{ 1 - 2x^* - \frac{a_1y^*}{2\sqrt{x^*}(1+b_1\sqrt{x^*})^2} \right\} \frac{b_2y^*z^*}{(1+b_2y^*)^2} \\ &\quad + \frac{a_1cy^*\sqrt{x^*}}{2\sqrt{x^*}(1+b_1\sqrt{x^*})^3} + \frac{a_2y^*z^{*2}}{(1+b_2y^*)(b_3+y^*)^2}, \\ A_3(b_2) &= - \left\{ 1 - 2x^* - \frac{a_1y^*}{2\sqrt{x^*}(1+b_1\sqrt{x^*})^2} \right\} \frac{a_2y^*z^{*2}}{(1+b_2y^*)(b_3+y^*)^2}. \end{aligned}$$

In order to see the instability of system (2)–(4), let us consider b_2 as bifurcation parameter. For this purpose let us state and prove the following theorem:

Theorem 5.2 (Hopf Bifurcation Theorem (Murray, 1993)): *If $A_i(b_2)$, $i = 1, 2, 3$ are smooth functions of b_2 in an open interval about $b_2^* \in \mathbb{R}$ such that the characteristic equation (5) has*

- *a pair of complex eigen values $\lambda = p_1(b_2) \pm ip_2(b_2)$ (with $p_1(b_2), p_2(b_2) \in \mathbb{R}$) so that they become purely imaginary at $b_2 = b_2^*$ and*

$$\left. \frac{dp_1}{db_2} \right|_{b_2=b_2^*} \neq 0,$$

- *the other eigen value is negative at $b_2 = b_2^*$, then a Hopf bifurcation occurs around E^* at $b_2 = b_2^*$ (i.e., a stability change of E^* accompanied by the creation of a limit cycle at $b_2 = b_2^*$).*

Theorem 5.3: *The system (2)–(4) possesses a Hopf-bifurcation around E^* when b_2 passes through b_2^* provided $A_1(b_2^*), A_3(b_2^*) > 0$ and $A_1(b_2^*)A_2(b_2^*) = A_3(b_2^*)$.*

Proof: For $b_2 = b_2^*$, the characteristic equation of the system (2)–(4) at E^* becomes

$$(\lambda^2 + A_2)(\lambda + A_1) = 0,$$

providing roots $\lambda_1 = i\sqrt{A_2}$, $\lambda_2 = -i\sqrt{A_2}$, and $\lambda_3 = -A_1$. Thus there exists a pair of purely imaginary eigenvalues and a strictly negative real eigenvalue. Also $A_i (i = 1, 2, 3)$

are smooth functions of b_2 . So, for b_2 in a neighbourhood of b_2^* , the roots have the form $\lambda_1(b_2) = p_1(b_2) + ip_2(b_2)$, $\lambda_2(b_2) = p_1(b_2) - ip_2(b_2)$, $\lambda_3 = -p_3(b_2)$, where $p_i(b_2)$, $i = 1, 2, 3$ are real.

Next, we shall verify the transversality condition:

$$\left. \frac{d}{db_2} (Re(\lambda_i(b_2))) \right|_{b_2=b_2^*} \neq 0, i = 1, 2.$$

Substituting $\lambda(b_2) = p_1(b_2) + ip_2(b_2)$ into the characteristic equation (5), we get

$$(p_1 + ip_2)^3 + A_1(p_1 + ip_2)^2 + A_2(p_1 + ip_2) + A_3 = 0. \quad (6)$$

Now, taking derivative of both sides of equation (6) with respect to b_2 , we get

$$3(p_1 + ip_2)^2(\dot{p}_1 + i\dot{p}_2) + 2A_1(p_1 + ip_2)(\dot{p}_1 + i\dot{p}_2) + \dot{A}_1(p_1 + ip_2)^2 + A_2(\dot{p}_1 + i\dot{p}_2) + \dot{A}_2(p_1 + ip_2) + \dot{A}_3 = 0. \quad (7)$$

Comparing real and imaginary parts from both sides of equation (7)), we get

$$D_1\dot{p}_1 - D_2\dot{p}_2 + D_3 = 0 \quad (8)$$

and

$$D_2\dot{p}_1 + D_1\dot{p}_2 + D_4 = 0, \quad (9)$$

where

$$\begin{aligned} D_1 &= 3(p_1^2 - p_2^2) + 2A_1p_1 + A_2, \\ D_2 &= 6p_1p_2 + 2A_1p_2, \\ D_3 &= \dot{A}_1(p_1^2 - p_2^2) + \dot{A}_2p_1 + \dot{A}_3, \\ D_4 &= 2\dot{A}_1p_1p_2 + \dot{A}_2p_2. \end{aligned}$$

From equations (8) and (9), we get

$$\dot{p}_1 = -\frac{D_2D_4 + D_1D_3}{D_1^2 + D_2^2}. \quad (10)$$

Now,

$$D_3 = \dot{A}_1(p_1^2 - p_2^2) + \dot{A}_2p_1 + \dot{A}_3 \neq \dot{A}_1(p_1^2 - p_2^2) + \dot{A}_2p_1 + \dot{A}_1A_2 + \dot{A}_2A_1.$$

At $b_2 = b_2^*$

Case-I : $p_1 = 0, p_2 = \sqrt{A_2}$

$$D_1 = -2A_2, D_2 = 2A_1\sqrt{A_2}, D_3 \neq A_1\dot{A}_2, D_4 = \dot{A}_2\sqrt{A_2}.$$

$$\therefore D_2D_4 + D_1D_3 \neq 2A_1A_2\dot{A}_2 - 2A_1A_2\dot{A}_2 = 0.$$

So, $D_2D_4 + D_1D_3 \neq 0$ at $b_2 = b_2^*$, when $p_1 = 0, p_2 = \sqrt{A_2}$.

Case-II : $p_1 = 0, p_2 = -\sqrt{A_2}$

$D_1 = -2A_2, D_2 = -2A_1\sqrt{A_2}, D_3 \neq A_1\dot{A}_2, D_4 = -\dot{A}_2\sqrt{A_2}$.

$\therefore D_2D_4 + D_1D_3 \neq 2A_1A_2\dot{A}_2 - 2A_1A_2\dot{A}_2 = 0$.

So, $D_2D_4 + D_1D_3 \neq 0$ at $b_2 = b_2^*$, when $p_1 = 0, p_2 = -\sqrt{A_2}$.

Therefore,

$$\left. \frac{d}{db_2} (Re(\lambda_i(b_2))) \right|_{b_2=b_2^*} = - \left. \frac{D_2D_4 + D_1D_3}{D_1^2 + D_2^2} \right|_{b_2=b_2^*} \neq 0$$

and

$$-p_3(b_2^*) = -A_1(b_2^*) < 0.$$

Hence by Theorem 5.2, the result follows. \square

6 Finite time blow-up

In this section, we present results on finite time blow-up of the system (2)–(4). We first provide some background to this approach. We are motivated primarily to control non-native species, which is a central problem in spatial ecology. Data on species such as the invasive Burmese python (*Python bivittatus*) in the Florida everglades, show an exponential increase in python population, which have resulted in local prey populations reducing severely (Dorcas et al., 2012). An *invasive* species is formally defined as any species capable of propagating itself in a nonnative environment and thus establish a self-sustained population. The environment may turn favourable for a certain species while becoming unfavourable for its competitors or natural enemies. This can result in the favoured species to *outbreak* (Berryman, 1987). For example, in the European Alps certain seasonal environmental conditions enable the population of the larch budmoth to become large enough to defoliate entire forests (Ludwig et al., 1978). In United States alone damages caused by invasive species to agriculture, forests, fisheries and businesses, have been estimated to be \$120 billion a year (Pimentel et al., 2005).

Biological control is an adopted strategy to limit harmful populations (Van Driesche and Bellows, 1996). The objective of a biological control is to establish a management strategy that best controls and decreases the harmful population to healthy levels as opposed to high and risky levels. Naturally, how does one define *high* level, and further, how well does the biological control actually work, at various high levels We have recently started investigating this question via the mathematical property of finite time blow-up (Parshad et al., 2016c, 2013, 2016a).

Definition 6.1: A given ODE model of a nonlinear system say,

$$\frac{d\mathbf{u}}{dt} = f(\mathbf{u}), \tag{11}$$

we say finite time blow-up occurs if,

$$\lim_{t \rightarrow T^* < \infty} \|\mathbf{u}\| \rightarrow \infty, \quad (12)$$

where $\|\cdot\|$ is the standard sup norm on \mathbb{R}^n , \mathbf{u} is the state variable in question that depends on time (t) and T^* is the blow-up time.

In the context of population biology, finite time blow-up has also been well investigated (Kim and Lin, 2004; Lou et al., 2001; Lou and Munther, 2012; Hillen and Painter, 2009). Note, we have now introduced an alternate viewpoint: finite time blow-up, can be viewed as *mimicing* the explosive growth of an invasive species. This is formalised by equating:

$$\text{finite time blow-up} = \text{uncontrollable and unmanageable population level.} \quad (13)$$

Here, the blow-up time T^* is viewed as the *disaster* time, for the ecosystem.

Remark 6.2: Although populations cannot reach infinite values in finite time, they can grow rapidly (Berryman, 1987). For example, experimental evidence suggest that the human population may be growing hyperbolically, rather than logistically (Grinn et al., 2010). Data on the Burmese python suggests, that its population is growing at least exponentially (Dorcas et al., 2012).

Our approach investigates biological control mechanisms, that attempt to lower and control the targeted population *before time* T^* . This approach has distinct advantages:

- there is no ambiguity as to what is a disastrous high level of population
- there is a clear demarcation between when or if the disaster occurs
- our controls focus on *avoiding* classical chemical and biological controls
- this method provides a predictive modelling tool for various ecological settings.

6.1 Finite time blow-up for large initial data

Here, we show that the model system (2)–(4) blow-up in finite time with suitable positive initial condition (x_0, y_0, z_0) .

Theorem 6.3: Consider the three species food chain model (2) – (4). Even if

$$e < \frac{a_2}{b_3},$$

$z(t)$ the solution to (4) blows up in finite time, that is

$$\lim_{t \rightarrow T^{**} < \infty} \|z\| \rightarrow \infty$$

as long as the initial data (y_0, z_0) are large enough.

Proof: Consider (2)–(4) with positive initial conditions.

Integrating (4), we obtain

$$-\frac{1}{z} + \frac{1}{z_0} = et - a_2 \int_0^t \frac{ds}{y + b_3}$$

which gives

$$z = \frac{1}{\frac{1}{z_0} - et + a_2 \int_0^t \frac{ds}{y + b_3}}$$

Let

$$\phi(t) = \frac{1}{z_0} - et + a_2 \int_0^t \frac{ds}{y + b_3}$$

Our mission is to show that the function $\phi(t) \rightarrow 0, t \rightarrow T^{**} > 0$. Essentially, for y_0 chosen sufficiently large, there exists a $\delta > 0$ such that

$$\frac{1}{z_0} - et + a_2 \int_0^t \frac{ds}{y + b_3} < \frac{1}{z_0} - \frac{et}{2}, \forall t \in (0, \delta)$$

Now if we take a sufficient large value of z_0 , then we can find a finite value $T^* \in (0, \delta)$ such that

$$\frac{1}{z_0} - \frac{e}{2}T^* = 0$$

thus, $\phi(T^*) \leq 0$ while $\phi(0) = \frac{1}{z_0} > 0$. So, by using Intermediate value theorem there exists a $T^{**} < T^*$, where $\phi(T^{**}) = 0$. So, z blows up at finite time T^{**} .

Hence, the theorem is proved. \square

6.2 Finite time blow-up for small initial data

Theorem 6.4: Consider the three species food chain model (2)–(4). Even if

$$e > \frac{a_2}{b_3},$$

$z(t)$ the solution to (4) blows up in finite time, that is

$$\lim_{t \rightarrow T^{**} < \infty} \|z\| \rightarrow \infty$$

for possibly small initial data (x_0, y_0, z_0) , that is, $x_0 \ll x^*$, $z_0 \ll z^*$ and $y_0 \approx y^*$, as long as the following relation holds:

$$\frac{d}{e} < z_0 \log \left(\frac{y_0}{\int_0^t \frac{\exp(d(s-t))}{\phi(y,s)} ds + y^*} \right), \text{ provided } b_2 \geq 1.$$

Here (x^*, y^*, z^*) represents the interior equilibrium point for the given parameter set.

Proof: By simple comparison of the equation (3), we get

$$\frac{dy}{dt} > -dy - z. \quad (14)$$

It is obtained by integrating (4), $z = \frac{1}{\frac{1}{z_0} - et + a_2 \int_0^t \frac{ds}{y+b_3}}$

$$\text{Now we set, } \phi(y, t) = \frac{1}{z_0} - et + a_2 \int_0^t \frac{ds}{y+b_3}$$

Thus, integrating equation (14), we have

$$y > - \int_0^t \frac{\exp(d(s-t))}{\phi(y, s)} ds + y_0 \exp(-dt) \quad (15)$$

In order for blow up: $y > \frac{a_2}{e} - b_3$, for as long as it takes

$$\frac{dz}{dt} = ez^2 \quad (16)$$

to blow up. This follows by a simple comparison. Here blow-up occurs at $T^* = \frac{1}{ez_0}$.

From equation (16), we get

$$t < \frac{1}{d} \log \left(\frac{y_0}{\int_0^t \frac{\exp(d(s-t))}{\phi(y, s)} ds + y^*} \right). \quad (17)$$

Let $t = T^{**}$, then blow up is certain if $T^* < T^{**} \Rightarrow \frac{d}{e} < z_0 \log \left(\frac{y_0}{\int_0^t \frac{\exp(d(s-t))}{\phi(y, s)} ds + y^*} \right)$.

Hence, the theorem is proved. \square

7 Numerical simulations

For the purpose of visualisation of the dynamical aspects of the system of equations (2)–(4), we choose the parameter set as: $a_1 = 0.7, b_1 = 0.3, c = 0.55, d = 0.3, e = 1.4, a_2 = 0.5$ and $b_3 = 0.13$. But keep the parameter b_2 aside because we'll see stability switching w.r.t this parameter. If we consider $b_2 \in (0, 2.5)$, then we see that the system experiences stable focus to unstable focus dynamics at the coexistence equilibrium point E^* with increasing b_2 via Hopf-bifurcation at $b_2 = b_2^* = 1.27$ (Fig.1(iv)). So, if we choose $b_2 = 1.02$ from its stable range $(0, 1.27)$, then we see E^* equilibrium point is stable focus, we represent it by time series in Figure 1(i) and phase-space diagram in Figure 1(iii), black trajectory in xyz -space which starts at initial point marked by blue bullet and with increasing time converges to E^* which is marked by green bullet. Also, if we choose $b_2 = 2.02$ from its stable range $b_2 > 1.27$, then we see E^* equilibrium point is unstable focus, we represent it by time series in Figure 1(ii) and phase-space diagram in Figure 1(iii), red trajectory in xyz -space which starts at initial point marked by blue bullet and with increasing time converges to stable limit cycle around E^* which is marked by blue closed loop. Now if we choose parameter set as: $a_1 = 0.7, b_1 = 0.3, c = 0.55, d = 0.3, b_2 = 1.02, a_2 = 0.05$ and

$b_3 = 0.13$, by this parameter set $\frac{a_2}{b_3} = 0.3846$. Now if we consider $e = 3.4 > \frac{a_2}{b_3}$, then we see z population blows-up obviously (Figure 2(i) and its enlarged form in Figure 2(ii) for comparison of z value with x and y). Also, if we consider $e = 0.2 < \frac{a_2}{b_3}$, then w.r.t very high initial data (0.9, 0.08, 50) we see z population blows-up (Figure 2(iii) and its enlarged form in Figure 2(iv) for comparison of z value with x and y). For the rest of the figures we've considered initial data as (0.9, 0.08, 0.01).

Figure 1 Time series (i)–(ii), phase-space (iii) and Hopf-bifurcation diagram w.r.t parameter b_2 (iv) of system (2)–(4). Parameter values and description are in the text (see online version for colours)

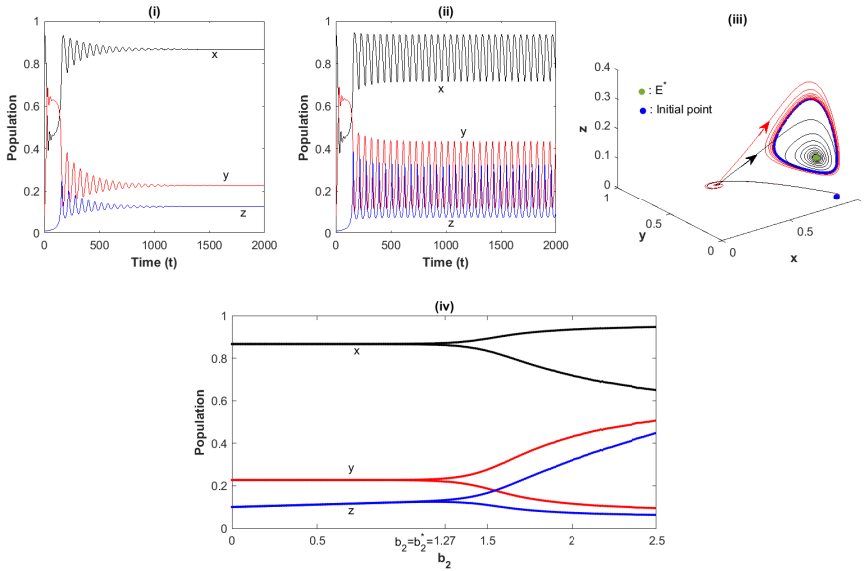
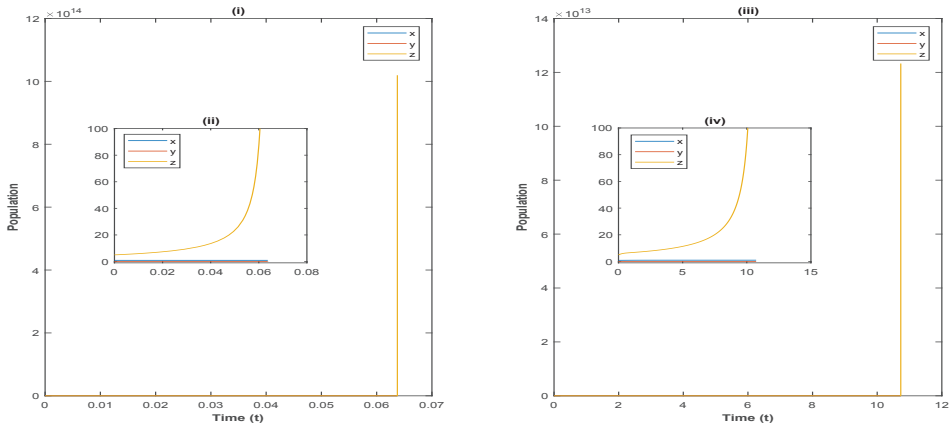


Figure 2 System (2)–(4) blow-up in finite time, (i) for $e > \frac{a_2}{b_3}$ and (ii) for $e < \frac{a_2}{b_3}$. Parameter values and description are in the text (see online version for colours)



8 General discussion

Recently, the research of the significance of herd behaviour when two or more populations are in same ecological relationship has drawn the attention of the scientists for its own virtue. In this work, we have considered a tri-trophic food chain model in which prey population exhibits herd behaviour and also the influence of generalist type top predator which grows by sexual reproduction. The main feature of group-living of prey population has been accented using square root of prey density (biomass) in the functional response. The predation process of specialist middle predator and generalist top predator is assumed to be governed by Holling type -II functional response where the generalist predator's equation is governed by the modified Holling-Tanner/Leslie-Grower model. The number of parameters of the model has been reduced by proper scaling. The dynamical behaviours of the model system (2)–(4) is studied. It is observed that the solution of the system is positively invariant and uniformly bounded which indicates its wellposedness. This actually shows that the system is well-behaved. We have also studied the extinction criteria of both prey and predator. We have discussed the feasibility criteria and stability behaviour of all the boundary equilibrium points. Interestingly due to the model formulation, x^* , the prey abundance solutions at coexistence equilibrium E^* is the unique positive solution of the algebraic equation. Local stability by using Routh-Hurwitz criteria of coexistence equilibrium E^* and switching of the stability of the system at E^* via Hopf bifurcation are also investigated analytically. Blow-up phenomena of top predator z in finite time has been observed for the system. Numerical simulations are presented to verify the analytical predictions.

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