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Prey-predator Dynamics under Herd Behavior of Prey

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Abstract In prey-predator system prey populations take various defensive mechanism to save themselves from predator and/or to get advantage in inter-species competition. In this work, we analyzed the dynamics of prey-predator system with two prey species and single predator population in which two prey populations are fighting for the same resources. Here, it is assumed that one prey population exhibits herd behavior as their own defense mechanism and second prey population releases toxin elements which gives them advantage of inter-species competition. From the analysis of our model we observed that the strategy of herd behavior as self defense mechanism is stronger than the toxin producing strategy. Also due to herd behavior of prey the model shows ecologically meaningful dynamics near origin.

Keywords Prey-predator Model, Herd behavior of prey, Inter-species competition, Square root functional responses

AMC-2010 Classification Code: 92D25

1 Introduction

Ecosystems are characterized by the interaction between different species and natural environment. Predator-prey models have been in the focus of ecological science since the great work of Lotka (in 1925) [1] and Volterra (in 1926) [2]. Modelling predator-prey interaction has been one of the central themes in mathematical ecology. One of the important types of interaction, which has effect on population dynamics, is predation [3,4]. The several possible dynamics have been considered: we can recall here for instance Holling type II and III functional responses, Holling-Tanner systems [5-8] and ratio-dependent models [9-11]. Recent and more dated research has in fact evolved toward the modelling of more complex situations with the aim of better understanding reality. In ecological system each of the populations take various strategy viz. refuging, grouping, etc. for searching of food sources and for defensive purposes. For example, the study of the consequences of hiding behavior of prey on the dynamics of predator-prey interactions have been done [12-18]. Some of the empirical and theoretical work have been investigated the effect of prey refuges and prey extinction can be prevented by the addition of refuges [19,20]. A predator-prey model was recently considered by Ajraldi et al [21] in which the prey exhibits herd behavior, so that the predator interacts with the prey along the outer corridor of the herd of prey. As a mathematical consequence of the herd behavior, they considered competition models and predator-prey systems in which interaction terms use the square root of the prey population rather than simply the prey population. The use of the square root properly accounts for the assumption that the interactions occur along the boundary of the population. It has been shown by Peter A. Braza [22] that the origin to be either locally stable or unstable, depending on the location of the values of the predator and prey populations in the phase plane. Having different functional responses as a consequence of the prey or predator forming groups has been investigated by other authors [23-24]. Chattopadhyay et al and Coauthors [25] recognized that certain plankton (prey) aggregate in large groups so that the predator effectively only has access to them by way of surface area instead of volume. As demonstrated by these authors, using appropriate powers of the variables to properly account for the way of predators and prey aggregate is an innovation that allows for a more realistic portrayal of certain predator-prey systems. This type of advance is somewhat typical in the history of the development of predator-prey models. The models have been refined and have become more sophisticated in order to account for the many wide-ranging elements that are found in real predator-prey systems. For example, some papers have included impulsive effects that occur in harvesting [26], pest control [27], and other natural or man-made factors

[28]. All of these modifications contribute to a more accurate characterization of real predator-prey systems. In this work, we analyze the dynamics of prey-predator system with two prey species and single predator population in which two prey populations are fighting for the same resources and the first prey population exhibits herd behavior.

2 The Mathematical Model

In prey-predator system prey populations take various strategies for their defensive purpose or food resources and nature of dynamics of any prey-predator system depends on the terms of interaction. In this work, we are interested to analyze the dynamics of prey-predator system with two prey species and single predator population in which two prey populations are fighting for the same resources. Here, it is assumed that one prey population exhibits herd behavior as their own defense mechanism and second prey population releases toxin elements which gives them advantage of inter-species competition. The interaction will be happened between two prey species and also between first prey and predator population along the outer corridor of the herd of the first prey. The outer corridor of the herd is proportional to the square root of the area of the herd and area of the herd is proportional to the numbers of individuals i.e. the prey densities. Therefore, the outer corridor is proportional to the square root of the prey densities. So, in our prey-predator model we use Lotka -Volterra interaction term with square root of first prey population in both the interaction terms of two prey species and also first prey and predator population.

In formulation of mathematical model we assume the following basic assumptions:

(1) Let X denote the population density of the first prey which exhibits herd behavior, Y the population density of the second prey which releases toxin elements to get advantage of inter-species competition and Z the population density of the predator.

(2) We assume that in the absence of the predators the two prey population density grow according to a logistic curve with carrying capacity N and K ($N, K > 0$) with an intrinsic growth rate constant 'r' and 'r_1' ($r, r_1 > 0$) respectively, 'a' be the coefficient of interaction between two prey populations and the second prey (Y) get an advantage in inter-species competition though the factor 'e' which is determined by the amount of toxin produced by the prey (Y).

From the above assumptions we can write the following set of nonlinear ordinary differential equations:

$$\begin{aligned}
\frac{dX}{dt} &= rX\left(1-\frac{X}{N}\right) - a\sqrt{X}Y - c\sqrt{X}Z \\
\frac{dY}{dt} &= r_1 Y\left(1-\frac{Y}{K}\right) - e\,a\sqrt{X}Y - dYZ \\
\frac{dZ}{dt} &= \alpha_1 c\sqrt{X}Z + \alpha_2 dYZ - \mu Z.
\end{aligned} \tag{2.1}$$

Here 'c' is the predation rate of first prey and 'd' the predation rate of second prey, the constant 'α_1' the conversion rate for first prey and the constant 'α_2' the conversion rate for second prey, 'μ' the natural death rate coefficient of the predator species.

Let $P = \sqrt{X}$, then the model reduces to

$$\begin{aligned}
\frac{dP}{dt} &= \frac{r}{2}P\left(1-\frac{P^2}{N}\right) - \frac{a}{2}Y - \frac{c}{2}Z \\
\frac{dY}{dt} &= r_1 Y\left(1-\frac{Y}{K}\right) - e\,aPY - dYZ \\
\frac{dZ}{dt} &= \alpha_1 cPZ + \alpha_2 dYZ - \mu Z.
\end{aligned} \tag{2.2}$$

The variables are scaled to study how the dynamics are affected by the parameters. The model (2.2) takes the following dimensionless form:

$$\begin{aligned}
\frac{dx}{dt} &= x(1-x^2) - ay - cz \\
\frac{dy}{dt} &= my(1-y) - exy - dyz \\
\frac{dz}{dt} &= \alpha xz + \beta yz - \mu z,
\end{aligned} \tag{2.3}$$

with the rescalling variables
$x = \frac{P}{\sqrt{N}}$, $y = \frac{Y}{K}$, $z = Z$, $t_{new} = \frac{rt_{old}}{2}$, $a_{new} = \frac{a_{old}K}{r\sqrt{N}}$, $m = \frac{2r_1}{r}$, $e_{new} = \frac{2a_{old}e_{old}\sqrt{N}}{r}$, $d_{new} = \frac{2d_{old}}{r}$, $c_{new} = \frac{c_old}{r\sqrt{N}}$, $\alpha = \frac{2\sqrt{N}\alpha_1 c_{old}}{r}$, $\beta = \frac{2K\alpha_2 d_{old}}{r}$, $\mu_{new} = \frac{2\mu_old}{r}$.

3 Analysis of the Model

3.1 Equilibria and Existence

The system of equations (2.3) has five equlibria, namely $E_0(0,0,0)$, $E_1(1,0,0)$, $E_2(x_2,0,z_2) = (\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1 - \frac{\mu^2}{\alpha^2}))$, $E_3(x_3,y_3,0)$, $E_*(x_*,y_*,z_*)$.

It is easy to see that equilibria $E_0(0,0,0)$, $E_1(1,0,0)$ exist for all parametric values. The equilibrium point $E_2(x_2,0,z_2) = (\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1 - \frac{\mu^2}{\alpha^2}))$ exists if the condition $\mu < \alpha$ is satisfied.
For the existence of equilibrium point $E_3(x_3,y_3,0)$ we can find by solving following two equations as,
$x_3(1 - x_3^2) - ay_3 = 0$ and $my_3(1 - y_3) - ex_3y_3 = 0$
Positivity of y_3 gives us $x_3 < \frac{m}{e}$.
Now, from above two equations we get,
$x_3^3 - (1 + \frac{ae}{m})x_3 + a = 0$.
Let, $f(x) = x^3 - (1 + \frac{ae}{m})x + a$
Therefore, we have $f(0) = a$ which is positive and $f(\frac{m}{e}) = \frac{m^3}{e^3} - (1 + \frac{ae}{m})\frac{m}{e} + a$
$= \frac{m^3}{e^3} - \frac{m}{e}$ which is negative if $\frac{m}{e} < 1$, which implies that the equation $f(x) = 0$ has one positive root in $(0, \frac{m}{e})$ and other positive root is 1 for $\frac{m}{e} = 1$. By Descartes' rule of sign the equation $f(x) = 0$ has exactly one negative root, which implies that the equilibrium point $E_3(x_3,y_3,0)$ uniquely exists if $\frac{m}{e} < 1$.

3.2 Stability analysis

Lemma 3.2.1: $E_0(0,0,0)$ is always saddle point.
Proof: The variational matrix for $E_0(0,0,0)$ is as follows

$$V(E_0) = \begin{bmatrix} 1 & -a & -c \\ 0 & m & 0 \\ 0 & 0 & -\mu \end{bmatrix}.$$

The eigen values of $V(E_0)$ are 1, m, $-\mu$. The positive eigen values 1 and m imply $E_0(0,0,0)$ is saddle point.

Lemma 3.2.2: $E_1(1,0,0)$ is stable node if $m < e$ and $\alpha < \mu$.
Proof: The variational matrix for $E_1(1,0,0)$ is as follows

$$V(E_1) = \begin{bmatrix} -2 & -a & -c \\ 0 & m-e & 0 \\ 0 & 0 & \alpha-\mu \end{bmatrix}.$$

The eigen values are -2, $m - e$, $\alpha - \mu$. So $E_1(1,0,0)$ is stable node if $m < e$ and $\alpha < \mu$.

Lemma 3.2.3: $E_2(x_2,0,z_2) = (\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1 - \frac{\mu^2}{\alpha^2}))$ is asymptotically stable if either $\frac{1}{\sqrt{3}} < \frac{\mu}{\alpha} < 1$ and $\frac{d}{c} < \frac{e}{\sqrt{3}} - m$ or $\frac{\mu}{\alpha} = \frac{1}{\sqrt{3}}$ and $m \leq \frac{3ec-2d}{3\sqrt{3}c}$.
Proof: The variational matrix for $E_2(x_2,0,z_2) = (\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1 - \frac{\mu^2}{\alpha^2}))$ is as follows

$$V(E_2) = \begin{bmatrix} 1-3x_2^2 & -a & -c \\ 0 & m - ex_2 - dz_2 & 0 \\ \alpha z_2 & \beta z_2 & 0 \end{bmatrix}.$$

The eigen values of $V(E_2)$ are
$\lambda_1 = m - ex_2 - dz_2 = m - e\frac{\mu}{\alpha} - d\frac{\mu}{c\alpha}(1 - \frac{\mu^2}{\alpha^2})$,
$\lambda_{2,3} = \frac{1}{2}[(1 - \frac{3\mu^2}{\alpha^2}) \pm \sqrt{(1 - \frac{3\mu^2}{\alpha^2})^2 - 4\mu(1 - \frac{\mu^2}{\alpha^2})}]$.
If $\frac{1}{\sqrt{3}} < \frac{\mu}{\alpha} < 1$ the eigen values λ_2 and λ_3 will be either negative or imaginary with negative real part.
Now $\lambda_1 = m - e\frac{\mu}{\alpha} - d\frac{\mu}{c\alpha}(1 - \frac{\mu^2}{\alpha^2})$
$= m - \frac{\mu}{\alpha}(e + \frac{d}{c}) + \frac{d}{c}\frac{\mu^3}{\alpha^3}$
$< m - \frac{\mu}{\alpha}(e + \frac{d}{c}) + \frac{d}{c}$, if $(\frac{\mu}{\alpha} < 1)$
$< m - \frac{1}{\sqrt{3}}(e + \frac{d}{c}) + \frac{d}{c}$, if $(\frac{1}{\sqrt{3}} < \frac{\mu}{\alpha})$
$= m + \frac{d}{c}(1 - \frac{1}{\sqrt{3}}) - \frac{e}{\sqrt{3}}$
$< m + \frac{d}{c} - \frac{e}{\sqrt{3}}$
< 0, if $m + \frac{d}{c} < \frac{e}{\sqrt{3}}$.

Therefore, $E_2(\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1-\frac{\mu^2}{\alpha^2}))$ will be stable if the conditions $\frac{1}{\sqrt{3}} < \frac{\mu}{\alpha} < 1$ and $\frac{d}{c} < \frac{e}{\sqrt{3}} - m$ are satisfied. If $\frac{1}{\sqrt{3}} > \frac{\mu}{\alpha}$, then λ_2 and λ_3 will be positive and hence $E_2(\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1-\frac{\mu^2}{\alpha^2}))$ will be unstable. If $\frac{\mu}{\alpha} = \frac{1}{\sqrt{3}}$ then λ_2 and λ_3 will be purely imaginary.
For $\frac{\mu}{\alpha} = \frac{1}{\sqrt{3}}$,
$\lambda_1 = \left(m - \frac{e}{\sqrt{3}} - \frac{d}{c}\frac{2}{3\sqrt{3}}\right)$
$> m - \frac{e}{\sqrt{3}} - \frac{d}{c}$
$> m - e - \frac{d}{c}$
> 0, if $m > e + \frac{d}{c}$.
$\lambda_1 = 0$, if $m = \frac{3ec-2d}{3\sqrt{3}c}$ and $\lambda_1 < 0$ if $m < \frac{3ec-2d}{3\sqrt{3}c}$
Therefore, the equilibrium point $E_2(\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1-\frac{\mu^2}{\alpha^2}))$ will be stable if $\frac{\mu}{\alpha} = \frac{1}{\sqrt{3}}$ and $m \le \frac{3ec-2d}{3\sqrt{3}c}$.

For $\frac{\mu}{\alpha} = \frac{1}{\sqrt{3}}$ and $m > e + \frac{d}{c}$, $E_2(\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1-\frac{\mu^2}{\alpha^2}))$ will be unstable.

Lemma 3.2.4: $E_3(x_3, y_3, 0)$ is always unstable.
Proof: The variational matrix at $E_3(x_3, y_3, 0)$ is as follows

$$V(E_3) = \begin{bmatrix} 1-3x_3^3 & -a & -c \\ -ey_3 & -my_3 & -dy_3 \\ 0 & 0 & \alpha x_3 + \beta y_3 - \mu \end{bmatrix}.$$

One of the eigen values of $V(E_3)$ is

$$\lambda_1 = \alpha x_3 + \beta y_3 - \mu.$$

Other eigen values are obtained from

$$\begin{vmatrix} 1-3x_3^2-\lambda & -a \\ -ey_3 & -my_3-\lambda \end{vmatrix} = 0.$$

i.e. $\lambda^2 + \lambda(my_3 - 1 + 3x_3^2) - aey_3 = 0$.
The roots of the above quadratic equation in λ are

$$\lambda_{2,3} = \frac{(1-3x_3^2-my_3) \pm \sqrt{(my_3-1+3x_3^2)^2 - 4aey_3}}{2},$$

which are always real.
By Descartes' rule of sign the above quadratic equation has exactly one positive root. Hence $E_3(x_3, y_3, 0)$ will be unstable.

Lemma 3.2.5: The $E_0(0,0,0)$ will be unstable if $q = 1$ and stable if $q > 1$ where we consider the dynamic near the origin with $x = O(z_0^q)$.

For the stability of $E_0(0,0,0)$ we first consider, $y = 0$, then equation (2.3) takes the form

$$\begin{aligned} \tfrac{dx}{dt} &= x(1-x^2) - cz \\ \tfrac{dz}{dt} &= \alpha xz - \mu z \end{aligned} \tag{2.4}$$

To determine the behavior near the origin we must consider equation (2.4) for $x << 1$ and $z << 1$. With these it is clear that $1 - x^2 \approx 1$ and $\alpha xz << z$. So that near the origin,

$$\begin{aligned} \tfrac{dx}{dt} &\approx x - cz \\ \tfrac{dz}{dt} &\approx -\mu z \end{aligned} \tag{2.5}$$

Consider $x = O(z)$ and $x << 1$ so that $z(t) = z_0 e^{-\mu t}$ with $z_0 << 1$ and consider $x = O(z_0^q)$.
Now let us take two cases: namely, $q = 1$ and $q > 1$.
The first case in which $q = 1$ gives saddle behavior near the origin.
In second case i.e. for $q > 1$, the system (2.5) reduces to

$$\begin{aligned} \tfrac{dx}{dt} &\approx -cz \\ \tfrac{dz}{dt} &\approx -\mu z, \end{aligned} \tag{2.6}$$

since $x << 1$ and $x << cz$.

Now from (2.6) we have,

$$\frac{dz}{dx} = \frac{\mu}{c}$$
$$\Rightarrow \int_{z_0}^{z} dz = \int_{x_0 z_0^q}^{x} \frac{\mu}{c}\, dx$$
$$\Rightarrow z = z_0 + \frac{\mu}{c}(x - x_0\ z_0^q),$$

which is a curve that starts at $(x_0, x_0 z_0^q)$ and terminates on the z-axis at $z = z_0 - \frac{\mu}{c} x_0 z_0^q > 0$ (since $q > 1$ and $z_0 << 1$). The implication of this is that a trajectory in the phase plane with $x << cz$ terminates at $x = 0$ at some positive value of z after which the predator z declines to zero because of $\frac{dz}{dt} \approx -\mu z$. This can be explained the the following way if the x population is considerably smaller than the predator population (z), the prey (x) first goes to extinct, causing the predator (z) to follow suit. This makes perfect ecological sense, yet it is a shortcoming of other models in which, as a consequence of the origin being a saddle, the prey population recovers no matter how small it is relative to the predator population. In contrast, the net effect of the square root model (due to herd behavior of Prey) is that the interaction term effectively imposes the equivalent of a minimum sustaining level on the populations to sustain themselves, which is ecologically reasonable and meaningful. This phenomenon has been nicely explained in [22].

4 Numerical Simulation and Discussion

In this work, we are interested to analyze the dynamics of prey-predator system with two prey species and single predator population where both the prey species took different defense mechanism to protect themselves. Here, we assume the first prey (X) exhibits herd behavior, so that the predator interacts with the prey along the outer corridor of the herd of prey and second prey (Y) releases toxin elements which gives them advantage of inter-species competition. In our model analysis we observe the following facts:

i) If the demographic reproduction number $R_p = \frac{c\alpha_1}{\mu} < 1$ and toxin produced by prey (Y) is below a threshold value ($e^* = \frac{1}{e} < \frac{a\sqrt{N}}{r}$) then both the prey (Y) and predator (Z) will go to extinct and the system will reach to stable equilibrium point $E_1 = (1, 0, 0)$.

ii) If proportional logistic growth rate $\frac{r_1}{r}$ is fixed, demographic reproduction number is in moderate level ($1 < R_p < \sqrt{3}$) and toxin produced by prey (Y) is low (which is determined by the parameter $e^* = \frac{1}{e}$) then prey (Y) will go to extinct and system will be stable at boundary equilibrium point $E_2(\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1 - \frac{\mu^2}{\alpha^2}))$. Here, we preform numerical simulation in MATLAB to observe the stability of the equilibrium point $E_2(\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1 - \frac{\mu^2}{\alpha^2}))$. Figure 1 depicts the stability of $E_2(\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1 - \frac{\mu^2}{\alpha^2}))$.

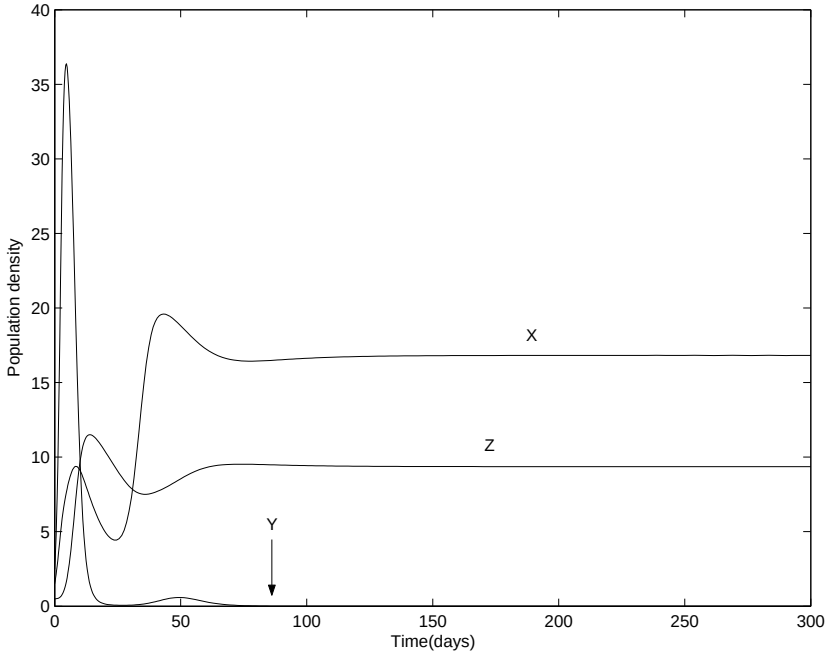

Figure 1. Show the stability of equilibrium point $E_2(\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1 - \frac{\mu^2}{\alpha^2}))$. The model system (2.1) has been solved using following set of values of parameters: r=0.8; a=0.03; c=0.154; r_1=1.3; N=30; K=245; e=0.08; α_1=0.095; α_1=0.092; μ=0.06; and d=0.15

It is to be noted that in our model analysis we did not get any equilibrium points like $E_4(0, y^*, z^*)$ or $E_4(0, y^*, 0)$, which means that the toxin producing prey (Y) can not knock down the herd behaving prey (X) just getting advantage in inter-species competition. On the other hand it is found that under certain conditions the model system can reach to stable at boundary equilibrium point $E_2(\frac{\mu}{\alpha}, 0, \frac{\mu}{c\alpha}(1 - \frac{\mu^2}{\alpha^2}))$. Thus, the strategy of herd behavior as self defense mechanism is stronger than the toxin producing strategy.

iii) Due to the mathematical complexity, we fail to perform the stability analysis at interior equilibrium point $E_*(x_*, y_*, z_*)$. Here we preform numerical simulation to study the stability of interior equilibrium point $E_*(x_*, y_*, z_*)$.

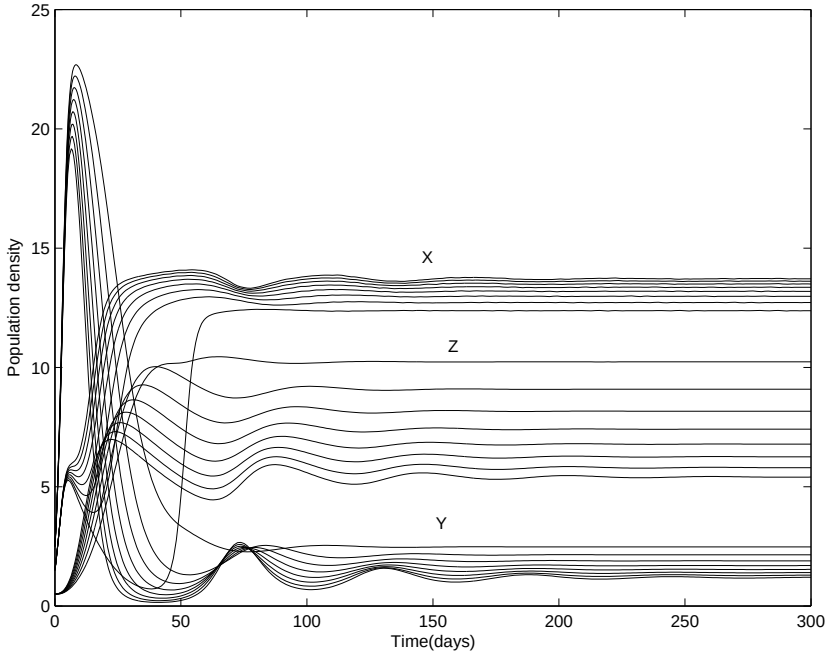

Figure 2. Depict the stability of interior equilibrium point. The model system (2.1) has been solved using following set of values of parameters: r=0.7; a=0.05; c=0.03; r_1=0.8; N=15; K=25; e=0.026; α_1=0.12; α_1=0.10; μ=0.03; and d=0.07:0.01:0.14

From Figure 2, it is observe that the interior equilibrium point $E_*(x_*, y_*, z_*)$ is stable under suitable value of parameters. It is also observed that stability of interior equilibrium point is highly sensitive with respect to the predation rate 'd' and amount of toxicities which is determined by the parameter 'e'. Here we observe that the interior equilibrium point destabilize due to high predation rate 'd' (i.e. when the predator aggressively consume the prey (Y)) and low toxicities of prey (Y) which is quite natural.

iv) Finally, we conclude that due to herd behavior of prey the equilibrium point $E_0(0, 0, 0)$ will be stable when species fail to maintain a minimum sustaining level to sustain themselves, which is ecologically reasonable and meaningful.

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