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COMPLEXITY IN THREE SPECIES RATIO DEPENDENT PREDATOR-PREY MODEL

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Abstract. In this work we study the three species ratio dependent predator-prey model. We investigated the global dynamical behavior of the model through (local) stability results for its equilibriums and large time computer simulations. The chaotic attractors are obtained for the suitable choice of parametric values.

Keywords: Three species food chain models, Ratio dependent predator prey models, Kolmogrov system, Equilibrium points, Chaotic attracter, Limit cycles.

2000 AMS Subject Classifications: 92B05

1. Introduction

The classical Lotka-Volterra model [4,5] for prey-predator species was developed on the basis of chemical principle of mass action, where their responses were assumed to be proportional to the product of their densities. These models, though used extensively, suffer from two problems: the paradox of enrichment and that of biological control. The ratio dependent predator prey models are free of these problems [1].

Ariditi and Ginzburg [2] were the first to introduce the “ratio-dependent predation” in which the feeding rate of predators (the functional response) depends on the ratio of prey to predator rather than on prey density alone (prey-dependent), as is the case in most conventional models.

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Interestingly, consideration of ratio-dependent models helps understand the paradox of enrichment and biological control related problems [1]. In these models the functional response depends on the ratio of prey and predator densities emphasizing the fact that the predators must share the available prey. It has been observed that while earlier models are more suitable in homogeneous situations, the ratio dependent models are more suitable in heterogeneous situations.

Recently, Gakkhar and Naji [3] have given the following three species food chain model:

$$\frac{1}{X_1}\frac{dX_1}{dT} = a_1 - b_1X_1 - \frac{d_1X_2}{\gamma_1+X_1},$$
$$\frac{1}{X_2}\frac{dX_2}{dT} = a_2 - b_2X_2 - \frac{X_2}{c_2X_1} - \frac{d_2X_3}{\gamma_2+X_2},$$
$$\frac{1}{X_3}\frac{dX_3}{dT} = a_3 - b_3X_3 - \frac{X_3}{c_3X_2} \quad (1)$$

where X_i is the biomass density of the species in the trophic chain at ith level, the parameter b_i defines the effect of intra-species competition for food. The ratio $a_i/b_i = K_i$ represents the carrying capacity in the logistic growth model. The parameter c_i represents the effect of individual in the lower trophic level while d_i is the impact of individual in upper trophic level on the per capita growth of the ith species. In the model (1.1) the feeding relationship among X_1, X_2 and X_3 is such that the prey X_1 is eaten by middle predator X_2 and middle predator X_2 is eaten by top predator X_3 and there is no explicit relationship between the prey X_1 and top predator X_3.

2. Our model

We form our model by modifying the model of [3]. It is assumed in this model that the middle predator X_2 feeds on X_1 whereas the top predator feeds on both X_1andX_2. Under these assumptions, our model becomes

$$\frac{1}{X_1}\frac{dX_1}{dT} = a_1 - b_1X_1 - \frac{d_1X_2}{\gamma_1+X_2} - \frac{d_3X_3}{\gamma_3+X_1},$$
$$\frac{1}{X_2}\frac{dX_2}{dT} = a_2 - b_2X_2 - \frac{X_2}{c_2X_1} - \frac{d_2X_3}{\gamma_2+X_2},$$
$$\frac{1}{X_3}\frac{dX_3}{dT} = a_3 - b_3X_3 - \frac{X_3}{c_3X_2} - \frac{X_3}{c_4X_1} \quad (2)$$

The system of equations (1.2) has 15 parameters in all. Too many parameters in a model make mathematical analysis complex. The model is simplified by considering the interspecies competitions for the topmost prey only i.e. $b_i = 0\; for\; i = 2,3$. To reduce the number of parameters in system (1.2) the following non-dimensional variables are introduced:

$$t = a_1 T,\;\; u_1 = \frac{X_1}{K_1},\;\; u_2 = \frac{d_1 X_2}{a_1 K_1},\;\; and\;\; u_3 = \frac{d_1 d_2 X_3}{a_1^2 K_1} \tag{3}$$

The non-dimensionalized equations are:

$$\frac{du_1}{dt} = \left[1 - u_1 - \frac{u_2}{w_1+u_1} - \frac{u_3}{w_2+u_1}\right] u_1,$$
$$\frac{du_2}{dt} = \left[w_3 - w_4 \frac{u_2}{u_1} - \frac{u_3}{w_5+u_2}\right] u_2,$$
$$\frac{du_3}{dt} = \left[w_6 - w_7 \frac{u_3}{u_2} - w_8 \frac{u_3}{u_1}\right] u_3. \tag{4}$$

Here the non-dimensional parameters are defined as:

$$w_1 = \frac{\gamma_1}{K_1},\; w_2 = \frac{\gamma_2}{K_1}\;\; w_3 = \frac{a_2}{a_1},\;\; w_4 = \frac{1}{c_2 d_1},\;\; w_5 = \frac{d_1 \gamma_2}{a_1 K_1},\;\; w_6 = \frac{a_3}{a_1},\;\; w_7 = \frac{1}{c_3 d_2}$$
$$w_8 = \frac{a_1}{d_1 d_2 c_4}. \tag{5}$$

Hence in the non-dimensional form the numbers of parameters are reduced from 15 to 8.

3. Analysis

For the analysis and to study the long-term dynamic behavior of the interacting system (1.4), we follow the approach adopted in [3] and divide the system (1.4) into three subsystems. The first subsystem is obtained by assuming the absence of third species i.e. $u_3 = 0$.

$$\frac{du_1}{dt} = \left[1 - u_1 - \frac{u_2}{w_1+u_1}\right] u_1$$
$$\frac{du_2}{dt} = \left[w_3 - w_4 \frac{u_2}{u_1}\right] u_2 \tag{6}$$

The second subsystem is obtained when the first species is at non-trivial equilibrium ($u_1 = u_1^*$):

$$\frac{du_2}{dt} = \left[w_3 - w_4 \frac{u_2}{u_1^*} - \frac{u_3}{w_5+u_2}\right] u_2,$$
$$\frac{du_3}{dt} = \left[\left(w_6 - w_7 \frac{u_3}{u_2} - w_8 \frac{u_3}{u_1^*}\right)\right] u_3, \tag{7}$$

The third subsystem is obtained when the second species is at non-trivial equilibrium ($u_2 = u_2^*$):

$$\frac{du_1}{dt} = \left[1 - u_1 - \frac{u_2^*}{w_1+u_1} - \frac{u_3}{w_2+u_1}\right] u_1$$
$$\frac{du_3}{dt} = \left[w_6 - w_7 \frac{u_3}{u_2^*} - w_8 \frac{u_3}{u_1}\right] u_3, \tag{8}$$

It may be noted that while the subsystem (1.6) qualifies as Kolmogorov system the subsystems (1.7) and (1.8) are not Kolmogrov systems.

For studying the behavior of the subsystem (1.6), a substitution $v_1 = u_2/u_1$ is made into it and this gives

$$\frac{du_1}{dt} = u_1\left[1 - u_1 - v_1\frac{u_1}{w_1+u_1}\right],$$
$$\frac{dv_1}{dt} = v_1\left[w_3 - w_4 v_1 - 1 + u_1 + v_1\frac{u_1}{w_1+u_1}\right]. \tag{9}$$

The equilibrium points for subsystem (1.9) are given as:

1. First equilibrium point for subsystem (1.9) is $E_{01} = (0,0)$.
2. Second equilibrium point for subsystem (1.9) is $E_{11} = (1,0)$.
3. Third equilibrium point for subsystem (1.9) is $E_{21} = (0,(w_3-1)/w_4)$ such that $w_3 > 1$.
4. Fourth nontrivial equilibrium point for subsystem (1.9) is $E_{31} = (u_1^*, v_1^*)$, where

$$u_1^* = \frac{1}{2}\left[1 - w_1 - \frac{w_3}{w_4} + R_1\right], \qquad v_1^* = \frac{w_3}{w_4} \tag{10}$$

with

$$R_1 = \left[\left(\frac{w_3}{w_4} + w_1 - 1\right)^2 + 4w_1\right]^{1/2}$$

It may be noted that E_{31}always exists and is unique. The necessary and sufficient condition for the equilibrium point E_{31} of subsystem (1.9) to be locally stable is

$$w_3 > \frac{2\big((w_3/w_4) - R_1\big)}{1 + (w_3/w_4) + w_1 + R_1}\,. \tag{11}$$

Further the subsystem (1.9) will have a limit cycle if

$$w_3 < \frac{2\big((w_3/w_4) - R_1\big)}{1 + (w_3/w_4) + w_1 + R_1} \tag{12}$$

System (1.7) can be analyzed on similar lines. The substitution $v_2 = u_3/u_2$ transforms the subsystem (1.7) to

$$\frac{du_2}{dt} = u_2\left[w_3\left(1 - \frac{u_2}{H}\right) - v_2\frac{u_2}{w_5+u_2}\right],$$
$$\frac{dv_2}{dt} = v_2\left[w_6 - w_7 v_2 - \frac{u_2 v_2}{H_1} - w_3\left(1 - \frac{u_2}{H}\right) + v_2\frac{u_2}{w_5+u_2}\right], \tag{13}$$

where $H = (w_3/w_4)u_1^*$ and $H_1 = (u_1^*/w_8)$.

The equilibrium points for subsystem (1.13) are given as:

1. First equilibrium point for subsystem (1.13) is $E_{02} = (0,0)$.
2. Second equilibrium point for subsystem (1.13) is $E_{12} = (H, 0)$.

3. Third equilibrium point for subsystem (1.13) is $E_{22} = (0, (w_3 - w_6)/w_7)$ such that $w_3 > w_6$.
4. Nontrivial equilibrium points $E_{32} = (u_2{}^*, v_2{}^*)$ for subsystem (1.13) are such that $u_2{}^*$ is a root of

$$u_2^3 + (w_5 + w_7H_1 - H)u_2^2 + \left(HH_1\frac{w_6}{w_3} + w_7HH_1 + w_5w_7H_1 - w_5H\right)u_2 - w_7w_5HH_1 = 0$$

satisfying $0 < u_2{}^* < H$ (14)

and $v_2{}^*$ is given by

$$v_2{}^* = (w_5 + u_2{}^*)\frac{w_3}{u_2{}^*}\left(1 - \frac{u_2{}^*}{H}\right) \tag{15}$$

The discriminant for the cubic equation (1.14) is given as

$$D = \frac{1}{4}\left[\frac{2}{27}(w_5 + w_7H_1 - H)^3 - (w_5 + w_7H_1 - H)\left(HH_1\frac{w_6}{w_3} + w_7HH_1 + w_5w_7H_1 - w_5H\right) - w_7w_5HH_1\right]^2 + \frac{1}{27}\left[\left(HH_1\frac{w_6}{w_3} + w_7HH_1 + w_5w_7H_1 - w_5H\right) - \frac{(w_5+w_7H_1-H)^2}{3}\right]^3 \tag{16}$$

- All roots of equation (1.14) are real and distinct if $D < 0$.
- Exactly one root of equation (1.14) is real if $D > 0$.

Biologically, we will be only interested in positive real roots of (1.14). We focus more on this aspect in the following section.

Lastly we turn to finding the equilibrium solutions of the system (1.8). For this purpose, we substitute $v_3 = u_1/u_3$ and transform subsystem (1.8) into

$$\frac{du_3}{dt} = u_3\left[w_6 - \frac{u_3}{H_2} - \frac{w_8}{v_3}\right]$$
$$\frac{dv_3}{dt} = v_3\left[1 - u_3v_3 - \frac{H_3}{(w_1+u_3v_3)} - \frac{u_3}{(w_2+u_3v_3)} - w_6 + \frac{u_3}{H_2} + \frac{w_8}{v_3}\right] \tag{17}$$

where $H_2 = u_2^*/w_7$ and $H_3 = u_2^*$.

The equilibrium points for subsystem (1.17) are given as:

1. First equilibrium point for subsystem (1.17) is $E_{03} = (0,0)$.
2. Second equilibrium point for subsystem (1.17) is $E_{13} = (0, w_1w_8/(H_3 + w_1w_6 - w_1))$ such that $H_3 + w_1w_6 - w_1 > 0$.
3. Nontrivial equilibrium points $E_{33} = (u_3{}^*, v_3{}^*)$ for subsystem (1.17) are such that $v_3{}^*$ is a root of

$$v_3^4 + \frac{1}{(H_2w_6)}[w_2 + w_1 - 3H_2w_8 - 1]v_3^2 + \frac{1}{(H_2w_6)^2}[H_2w_6 + w_1w_2 - 2H_2w_8w_1$$

$$-2H_2w_8w_2 + 3(H_2w_8)^2 - w_1 - w_2 + 2H_2w_8 + H_3]v_3^2 + \frac{1}{(H_2w_6)^3}[H_2w_6w_1 -$$
$$2w_6w_8H_2^2 - w_1w_2w_8H_2 + w_2(w_8H_2)^2 + w_1(w_8H_2)^2 - (w_8H_2)^3 - w_1w_2 - w_1w_8H_2$$
$$+ w_2w_8H_2 - (w_8H_2)^2 + w_2H_3 - H_3H_2w_8]v_3 + \frac{1}{(H_2w_6)^3}((w_8H_2)^2 - w_1w_8H_2) = 0 \quad (18)$$

such that $\frac{w_8}{w_6} < v_3{}^*$.

and $u_3{}^*$ is given by

$$u_3{}^* = H_2\left(w_6 - \frac{w_8}{v_3{}^*}\right) \quad (19)$$

It is obvious that the quartic equation (1.18) can only be analyzed numerically for its roots. For specific choices of parameters, existence of equilibrium solutions of (1.17) and their stability results are given in the following section.

4. Discussion

The stability of the subsystem (1.9) is shown in Table1.1 when parameters $w_1 = 0.2, w_3 = 0.1$ are kept constant and w_4 is varied.

Table 1.1

Behavior of nonlinear subsystem (1.9) for different choices of parameters

Parameters kept constant	Parameter varied	Analytical behavior of linearized system
$w_1 = 0.2$	$0 < w_4 \le 0.014$	Stable
$w_3 = 0.1$	$0.015 \le w_4 \le 0.09$	Unstable
	$w_4 \ge 0.091$	Stable

Similarly, the stability of the subsystem (1.13) is shown in Table 1.2 when parameters $w_1 = 0.2$, $w_3 = 0.1$, $w_4 = 0.05$, $w_5 = 0.0344531$, $w_6 = 0.01$ *and* $w_7 = 0.04$ are kept constant and w_8 is varied.

Table 1.2

Behavior of nonlinear subsystem (1.13) for different choices of parameters

Parameters	Parameter varied	Analytical behavior of linearized system
$w_1 = 0.2, w_3 = 0.1,\ w_4 = 0.05$	$0 < w_8 \leq 0.027$	Stable
$w_5 = 0.0344531, w_6 = 0.01$	$0.027 \leq w_8 \leq 0.27$	Unstable
$w_7 = 0.04\ H = 0.296662$	$w_8 \geq 0.28$	Stable

Table 1.3

Behavior of nonlinear subsystem (1.17) for different choices of parameters

Parameters kept constant	Parameter varied	Analytical behavior of linearized system
$w_1 = 0.2, w_3 = 0.1,\ w_4 = 0.05$	$0 \leq w_2 \leq 0.2$	Unstable
$w_5 = 0.0344531, w_6 = 0.01$	$0.3 \leq w_2 \leq \infty$	Stable
$w_7 = 0.04,\ w_8 = 0.03,\ H_2 = 6.33$		
$H_3 = 0.190$		

Numerical integration is used to investigate the global dynamic behavior of the model system (1.4). The objective is to explore the possibility of chaotic behavior. Extensive numerical simulations were carried out for various values of parameters and for different sets of initial conditions.

The parameters w_8 *and* w_2 have been taken as controlling parameters in the following cases with other parameters kept fixed at:

$w_1 = 0.2,\ \ w_3 = 0.1,\ \ w_4 = 0.05,\ \ w_5 = 0.0344531,\ \ and\ \ w_6 = 0.01\ and\ w_7 = 0.04$

Case 1: $w_2 = 0.02\ and\ \ w_8 = 0.1$

In this case Fig 1.1(a) shows the presence of chaotic attracter.

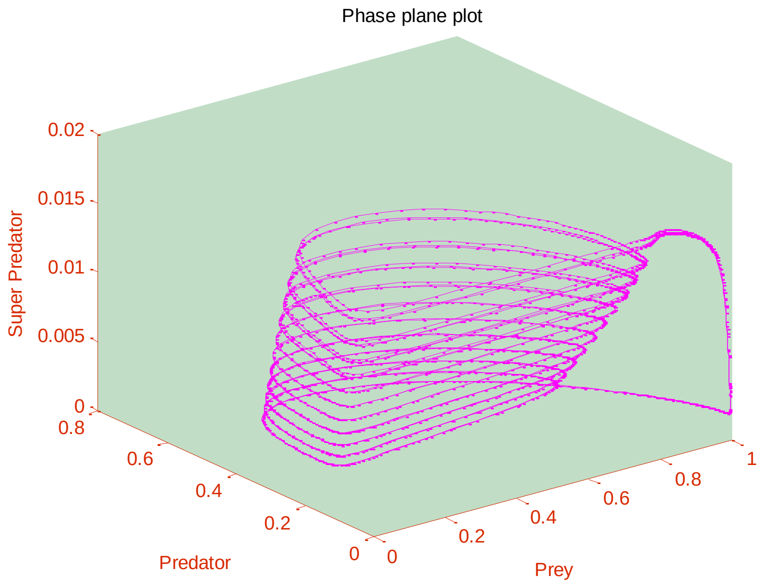

Fig 1.1(a)

Case 2: $w_2 = 0.02 \; and \;\; w_8 = 0.12$

In this case Fig 1.1(b) shows the presence of chaotic attracter.

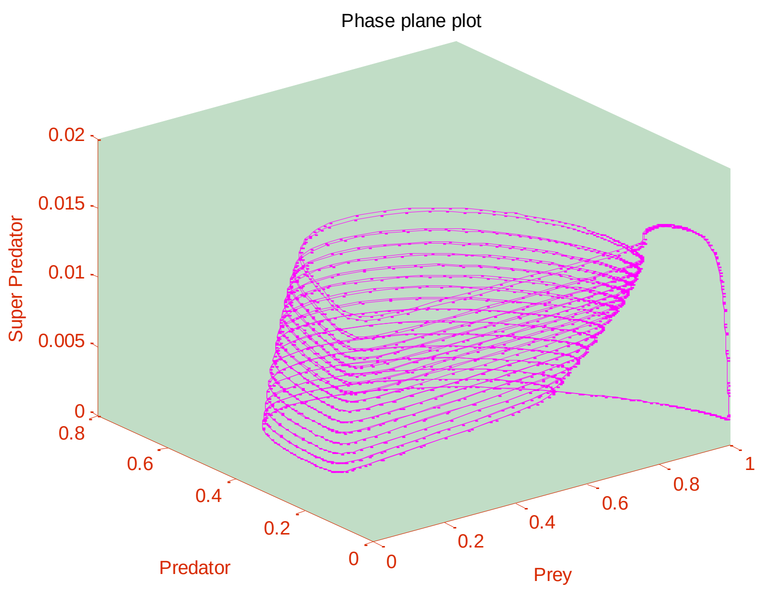

Fig 1.1(b)

Case 3: $w_2 = 0.02$ *and* $w_8 = 0.2$

In this case Fig 1.1(c) shows the presence of limit cycle.

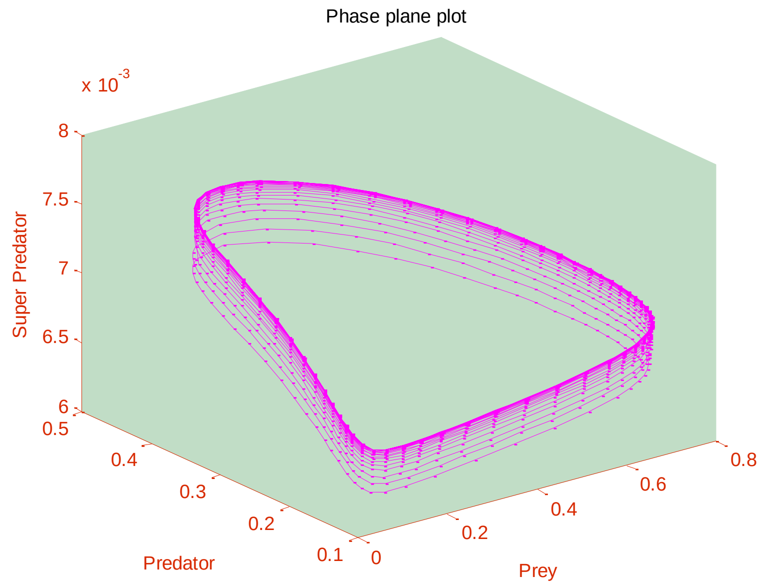

Fig 1.1(c)

Case 4: $w_2 = 0.02$ *and* $w_8 = 0.25$

In this case Fig 1.1(d) shows the presence of limit cycle.

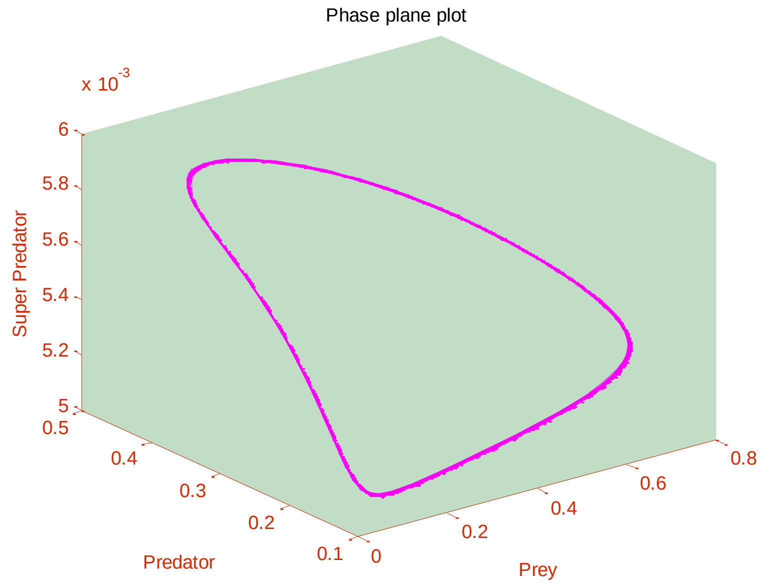

Fig 1.1(d)

Now we will take $w_2 = 0.2$ and vary the value of w_8.

Case 5: $w_2 = 0.2 \; and \; w_8 = 0.05$

In this case Fig 1.1(e) shows the presence of chaotic attracter.

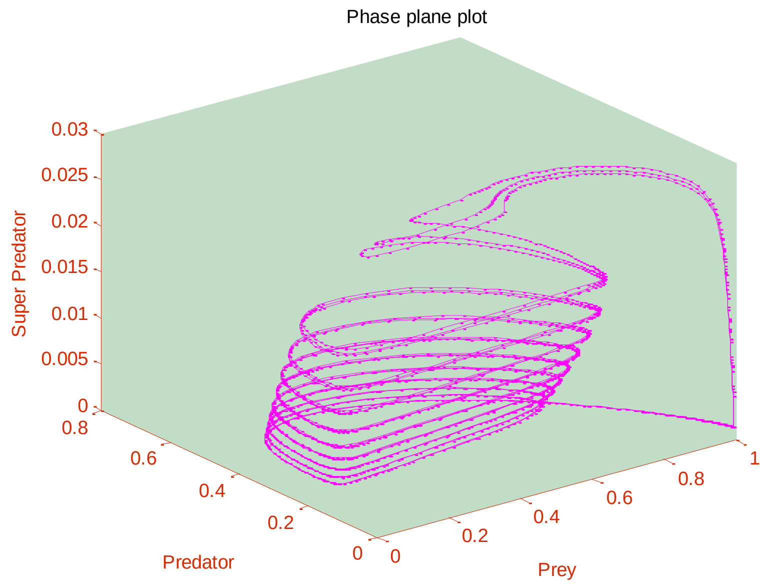

Fig 1.1(e)

Case 6: $w_2 = 0.2 \; and \; w_8 = 0.08$

In this case Fig 1.1(f) shows the presence of chaotic attracter.

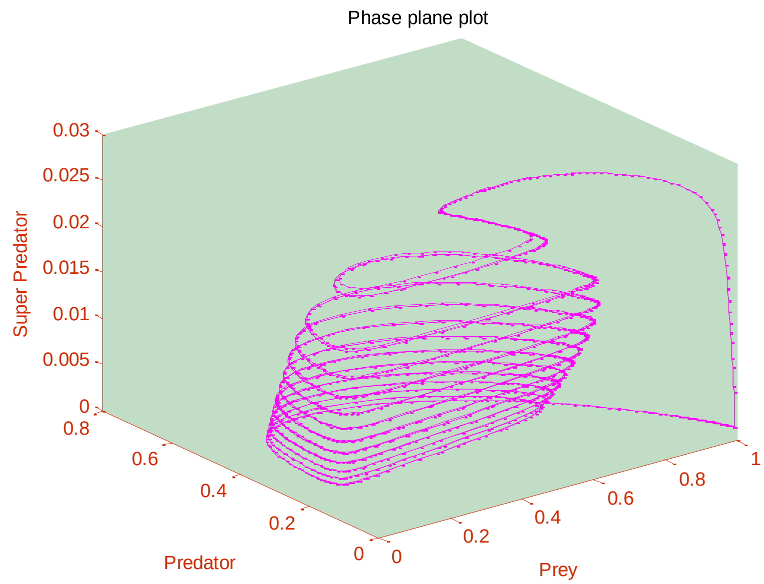

Fig 1.1(f)

Case 7: $w_2 = 0.2 \; and \; w_8 = 0.12$

In this case Fig 1.1(g) shows the presence of chaotic attracter.

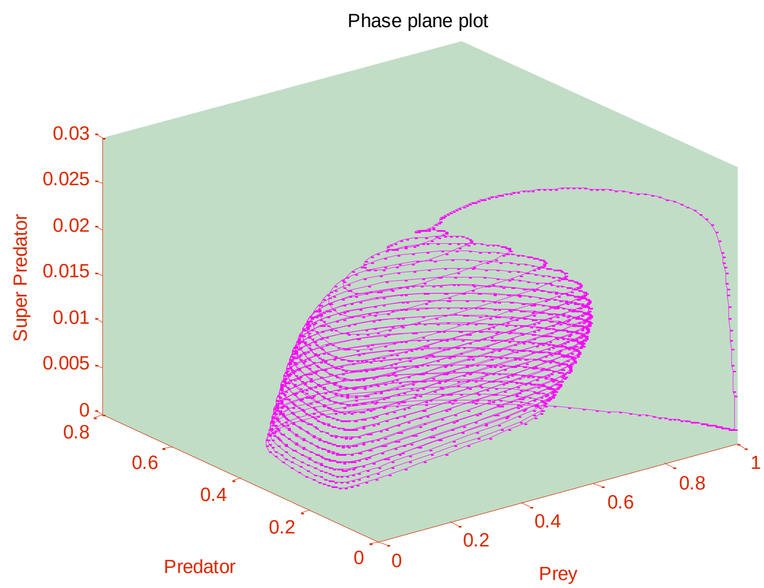

Fig 1.1(g)

Case 8: $w_2 = 0.2 \; and \; w_8 = 0.8$

In this case Fig 1.1(h) shows the presence of limit cycle.

Fig 1.1(h)

5. Conclusions

Gakkhar and Naji [3] have shown the existence of chaotic dynamics in three species ratio dependent food chain model. They have taken the food chain in such a way that their prey exists at the topmost level, a predator at the next level and then a super predator at the lowest level. There is no explicit relationship between the prey and the topmost predator and by choosing one parameter as the control parameter they have shown chaotic dynamics in their food chain. In a modified version of their model we have taken a feeding relationship between the prey and topmost predator and by choosing two parameters as the control parameter we have shown that complex dynamics in terms of chaotic behavior is also possible in our model.

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