On a Prey-Predator Model With Herd And Retaliation Behaviors In Preys*

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Abstract

The fundamental feature of any ecosystem is that no species can survive without interacting with other species. The interaction between the species is either cooperative or retaliatory and the cooperation or retaliation may be intra-species as well as inter-species. In the present article, we consider inter-species retaliation behaviour in the perspective of prey-predator model where the preys move in groups, i.e., the preys show herd behaviour and show retaliation behaviour to the attacker without running away with fear. In such models the preys are attacked by the predator along the outer corridor of the herd. So attacking rate depends not on the total number of preys but on the number of preys along the herd boundary. In the present article, we establish a model combining the retaliation phenomenon with the herd behaviour. We critically analyze the stability and bifurcation of the model. Moreover, graphical illustrations are provided to exhibit different situations.

1 Introduction

The fundamental characteristic of any ecosystem is that no species can survive alone. Numerous features on interactions between several species are seen in the realm of living plants and animals of the earth. The behaviours of the constituents of the animal kingdom are till now a fascinating topic to ecologists. During the beginning of the last century population scientists are actively engaged to uncover the behavioural mystery of the animal kingdom. In addition, mathematical formulation of the coexistence of several species of a system took a major role in population study. In this regard, it must be mentioned the masterpiece works of Lotka [9] and Volterra [12]. The characteristics of prey-predator models have been established in several perspectives by several authors. For instance, we may refer [1, 2, 3, 4, 5, 6, 7, 8, 10, 11]. Ajraldi et al. [1], developed predator-prev models that have the interaction term as the square root of the prev population. Braza [3] also has enlighten some minute aspects of such models. The importance of square root models is that they are used to study the prey-predator models equipped with herd behavior. The point behind considering such models is that when the preys show herd behaviour, the predators get chance of interacting with the preys along the outer corridor of the herd of preys. So the outer boundary is expressed as a square root function of the total population. Forest dwelling animals sometimes exhibit peculiar behaviours. In forests some predators attack from front side and sometimes they attack from behind. Again, the retaliation or revenge between two rival species are frequently seen. For example, if a herd of wild buffaloes is attacked by tiger, the herd of buffaloes take revenge by counter attacking the tiger. In the present article, we consider such retaliation behaviours of the prevs in addition to their herd behaviours. It is to be mentioned that retaliation behaviour is only exhibited by preys for self defense and not shown by predators as they are the attacker.

The article is organized as follows: After the introduction in Section 1, we present the model in Section 2. Section 3 contains the stability analysis. The aspects of bifurcation is considered in Section 4. Finally in the last section, numerical simulations are done using graphs drawn by MATLAB.

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2 Derivation of Predator-Prey Model with Herd Boundary and Retaliation Behaviour in Preys

It is known that the predator-prey model with logistic growth in the prey and Holling type II functional response is given by [3]

$$\frac{dU}{dt} = rU(1 - \frac{U}{N}) - \frac{\alpha UV}{1 + t_h \alpha U},\tag{1}$$

$$\frac{dV}{dt} = -sV + \frac{c\alpha UV}{1 + t_h \alpha U}. (2)$$

Here U(t) and V(t) denote the prey population and predator population respectively. r is the growth rate of the prey population and N is its carrying capacity. In absence of prey population the death rate of the predator is s. The search coefficient of V for U is α . c being biomass conversion or consumption rate. The average handling time of V for U is t_h . Suppose T indicate the total time that each V takes to collect food from U, T_s is the time taken by each V looking for U and the time t_h that each V takes handling U. Modifying the above model, Ajraldi et al [1], developed prey-predator models as follows that have the interaction term as the square root of the prey population.

$$\frac{dU}{dt} = rU(1 - \frac{U}{N}) - \frac{\alpha\sqrt{U}V}{1 + t_h\alpha\sqrt{U}},\tag{3}$$

$$\frac{dV}{dt} = -sV + \frac{c\alpha\sqrt{U}V}{1 + t_b\alpha\sqrt{U}}. (4)$$

Now, we consider a situation where in addition to herd behaviour, retaliation or revenge behaviour are shown by the preys. Suppose a member of the herd of preys is attacked by a predator along a boundary of the prey when the preys were not alert for possible attack of the predator, and after being attacked, they chase the predator and attack it. For this situation an additional rate of death of the predators will come into account. Let the death rate of predators due to the retaliation by preys be γ . So the model will reduce to

$$\frac{dU}{dt} = rU(1 - \frac{U}{N}) - \frac{\alpha\sqrt{U}V}{1 + t_h\alpha\sqrt{U}},\tag{5}$$

$$\frac{dV}{dt} = -sV + \frac{c\alpha\sqrt{U}V}{1 + t_h\alpha\sqrt{U}} - \gamma V. \tag{6}$$

Here U(0) > 0 and $V(0) \ge 0$.

3 Stability Analysis of Predator-Prey Model with Herd Boundary and Retaliation Behaviour in Preys

3.1 Positivity and Boundedness of the Model

Let us investigate the positivity and boundedness of the system of equations (5) and (6). The right hand sides of (5) and (3) are continuous functions of the dependent variables U and V. Integrating both sides of the equations of the system, we have

$$U(t) = U(0) exp \left[\int_0^t \left(r \left(1 - \frac{U}{N} \right) - \frac{\alpha V}{1 + t_h \alpha U} \right) dx \right],$$

$$V(t) = V(0)exp \left[\int_0^t \left(-s + \frac{c\alpha\sqrt{U}}{1 + t_h\alpha\sqrt{U}} - \gamma \right) dx \right].$$

In view of the above expressions of U(t) and V(t) it can be inferred that U(t) and V(t) remain non-negative for the infinite time, if they starts from an interior point of

$$R_{+}^{2} = \{(U(t), V(t)) \in \mathbb{R}^{2} : U(t) > 0, V(t) \ge 0\}.$$

Thus R_{+}^{2} is positively invariant for the system considered.

Regarding the uniform boundedness, let us prove the following

Theorem 3.1 The solutions of the system of equations (5) and (6) consisting the model with non-negative initial conditions (U(0), V(0)) starting from the interior of R^2_+ are uniformly bounded.

Proof. Let

$$W(t) = U(t) + \frac{1}{c}V(t). \tag{7}$$

Hence, along the solution trajectories of the model

$$\frac{dW}{dt} = rU(1 - \frac{U}{N}) - (\gamma + \frac{s}{c})V. \tag{8}$$

By virtue of (7) and (8)

$$\frac{dW}{dt} + \theta W = (r + \theta)U - \frac{r}{N}U^2 - (\gamma + \frac{s - \theta}{c})V.$$

Choosing θ such that $0 < \theta < s$, we have from above

$$\begin{split} \frac{dW}{dt} + \theta W & \leq (r+\theta)U - \frac{r}{N}U^2 \\ & = \frac{r}{N} \left(\frac{N^2(r+\theta)^2}{4r^2} - \left(\frac{N(r+\theta)}{2r} - U \right)^2 \right) \\ & \leq \frac{N(r+\theta)^2}{4r}. \end{split}$$

Thus from above

$$\frac{dW}{dt} + \theta W \le P,\tag{9}$$

where $P = \frac{N(r+\theta)^2}{4r}$. In view of differential inequality from (9), one obtains

$$0 \le W(t) \le \frac{P}{\theta}(1 - e^{-\theta t}) + W(0)e^{-\theta t}.$$

As $t \to \infty$, we infer $0 \le W(t) \le \frac{P}{\theta} + \epsilon$ for $0 < \epsilon < W(0)$. Hence, in view of positivity of U(t) and V(t), we conclude that all solutions initiating in R_+^2 are restricted in the region

$$D = \left\{ \left(U(t), V(t) \right) \in R^2 : U(t) + \frac{1}{c} V(t) \le \frac{P}{\theta} + \epsilon, \epsilon > 0 \right\}.$$

Thus the solutions of the system are uniformly bounded. Hence the model is biologically well posed.

3.2 Equilibrium Points and Their Stability:

It is seen that the equilibrium points of the above model are

(i)
$$U = N$$
, $V = \frac{cr}{(s+\gamma)} \left(N - \frac{1}{r}\right)$.

(ii)
$$U = \frac{(s+\gamma)^2}{\alpha^2(c-t_h(s+\gamma))^2}, V = \frac{c(s+\gamma)}{\alpha^2(c-t_h(s+\gamma))^2} \left(\frac{r}{\alpha^2} - \frac{r}{N} \frac{(s+\gamma)^2}{(c-t_h(s+\gamma))^2}\right).$$

(iii)
$$U = 0, V = 0.$$

The Jacobian of the system is

$$\begin{bmatrix} r - \frac{2rU}{N} - \frac{\alpha V}{2\sqrt{U}(1 + t_h \alpha \sqrt{U})^2} & -\frac{\alpha \sqrt{U}}{1 + t_h \alpha \sqrt{U}} \\ \frac{c\alpha V}{2\sqrt{U}(1 + t_h \alpha \sqrt{U})} & -s + \frac{c\alpha \sqrt{U}}{1 + t_h \alpha \sqrt{U}} - \gamma \end{bmatrix}.$$

3.3 Local Stability for Case (i)

In this subsection, we investigate the nature of stability for U = N, $V = \frac{cr}{r(s+\gamma)} \left(N - \frac{1}{r}\right)$ and prove the following:

Theorem 3.2 The equilibrium point U=N, and $V=\frac{cr}{(s+\gamma)}\left(N-\frac{1}{r}\right)$ is locally asymptotically stable if $\left(\frac{1}{r}-N\right)<2$, provided

$$s + \gamma = \frac{c\alpha\sqrt{N}}{1 + t_h\alpha\sqrt{N}}.$$

Proof. The Jacobian matrix for case (i) is of the form

$$\left[\begin{array}{cc} a_{11} & a_{12} \\ a_{21} & a_{22} \end{array}\right],$$

where

$$a_{11} = -r - \frac{\alpha}{2\sqrt{N}\left(1 + t_h\alpha\sqrt{N}\right)^2} \cdot \frac{cr}{(s+\gamma)} \cdot \left(N - \frac{1}{r}\right),$$

$$a_{12} = -\frac{\alpha\sqrt{N}}{1 + t_h\alpha\sqrt{N}},$$

$$a_{21} = \frac{\alpha c^2 r^2 \left(N - \frac{1}{r}\right)}{2r(s+\gamma)\sqrt{N}\left(1 + t_h\alpha\sqrt{N}\right)^2},$$

$$a_{22} = -s - \gamma + \frac{c\alpha\sqrt{N}}{1 + t_h\alpha\sqrt{N}}.$$

The eigenvalues λ of the above Jacobian is given by

$$\lambda^2 - B_1 \lambda + B_2 = 0.$$

where $B_1 = a_{11} + a_{12}$ and $B_2 = a_{11}a_{22} - a_{12}a_{21}$. Assume r > 0 and

$$s + \gamma = \frac{c\alpha\sqrt{N}}{1 + t_h\alpha\sqrt{N}}.$$

In that case, $a_{22} = 0$, $a_{12} < 0$, $a_{21} > 0$. So the determinant of the Jacobian is positive and thus $B_2 > 0$. Hence, by Routh Hurwitz criterion theorem [13], the solution will be asymptotically stable if $a_{11} + a_{22} < 0$. Now, by our assumed condition $a_{22} = 0$. Hence, the solution will be asymptotically stable if $a_{11} < 0$. For

$$s + \gamma = \frac{c\alpha\sqrt{N}}{1 + t_h\alpha\sqrt{N}},$$

we obtain $a_{11} = \frac{1}{2}r\left(\frac{1}{r} - N\right) - r$. Hence, the solution will be asymptotically stable if $\left(\frac{1}{r} - N\right) < 2$.

3.4 Local Stability for Case (ii)

In this subsection, we investigate the nature of stability for

$$U = \frac{(s+\gamma)^2}{\alpha^2(c - t_h(s+\gamma))^2},$$

$$V = \frac{c(s+\gamma)}{\alpha^2(c - t_h(s+\gamma))^2} \left(\frac{r}{\alpha^2} - \frac{r}{N} \frac{(s+\gamma)^2}{(c - t_h(s+\gamma))^2}\right)$$

and establish the following:

Theorem 3.3 The equilibrium point

$$U = \frac{(s+\gamma)^2}{\alpha^2 (c - t_h(s+\gamma))^2} \text{ and } V = \frac{c(s+\gamma)}{\alpha^2 (c - t_h(s+\gamma))^2} \left(\frac{r}{\alpha^2} - \frac{r}{N} \frac{(s+\gamma)^2}{(c - t_h(s+\gamma))^2} \right)$$

is locally asymptotically stable if

$$\frac{r\alpha^2}{N} \cdot \frac{(s+\gamma)^2}{(c-t_h(s+\gamma))^2} < r < \frac{r\alpha(s+\gamma)^2 \left(4rc - \alpha(c-t_h(s+\gamma))\right) + rN(c-t_h(s+\gamma))^3}{2N\alpha^3 rc(c-t_h(s+\gamma))^2}.$$

Proof. The Jacobian matrix for case (ii) is of the form

$$\left[\begin{array}{cc} a_{11} & a_{12} \\ a_{21} & a_{22} \end{array}\right],$$

where

$$a_{11} = r - \frac{r\alpha(s+\gamma)^{2} \left(4rc - \alpha(c - t_{h}(s+\gamma))\right) + rN(c - t_{h}(s+\gamma))^{3}}{2N\alpha^{3}rc(c - t_{h}(s+\gamma))^{2}},$$

$$a_{12} = -\frac{s+\gamma}{c},$$

$$a_{21} = \frac{1}{2} \left(\frac{r}{\alpha^{2}} - \frac{r}{N} \frac{(s+\gamma)^{2}}{(c - t_{h}(s+\gamma))^{2}}\right),$$

$$a_{22} = 0$$

The eigenvalues λ of the above Jacobian is given by

$$\lambda^2 - B_1 \lambda + B_2 = 0,$$

where $B_1 = a_{11} + a_{12}$ and $B_2 = a_{11}a_{22} - a_{12}a_{21}$. Assume

$$\frac{\alpha^2}{N} \cdot \frac{(s+\gamma)^2}{(c-t_h(s+\gamma))^2} < 1. \tag{10}$$

Then $a_{22} = 0$, $a_{12} < 0$ and $a_{21} > 0$. So the determinant of the Jacobian for this case is positive. Consequently, $B_2 > 0$. Hence, by Routh Hurwitz criterion theorem [13], the solution will be asymptotically stable if $a_{11} + a_{22} < 0$. Now, $a_{22} = 0$. Hence, the solution will be asymptotically stable if $a_{11} < 0$, i.e.,

$$r < \frac{r\alpha(s+\gamma)^2 \left(4rc - \alpha(c - t_h(s+\gamma))\right) + rN(c - t_h(s+\gamma))^3}{2N\alpha^3 rc(c - t_h(s+\gamma))^2}.$$
(11)

Combining (10) and (11), we get the result.

3.5 Local Stability for Case (iii)

In this subsection, we discuss the nature of stability for U=0 and V=0. Since $\frac{1}{\sqrt{U}}$ is indeterminate for U=0 and the square root function is not differentiable at U=0, the stability of this case cannot be determined by simply evaluating the Jacobian matrix at U=0 and V=0. The authors in [1] used the re-scaling $u=u'^2$ to remove such a singularity in an analogous problem. In [3], the authors tackled such a situation using some re-scaling and special assumption as follows:

$$u = \frac{U}{N}, \quad v = \frac{\alpha V}{r\sqrt{N}}, \quad t_{new} = rt_{old}, \quad s_{new} = \frac{s_{old}}{r},$$

$$a = t_h \alpha \sqrt{N}$$
 $c_{new} = c_{old} \frac{\alpha \sqrt{N}}{r}$ and $\gamma_{new} = \gamma_{old} \frac{r \sqrt{N}}{\alpha}$.

With these changes the model transforms to

$$\frac{du}{dt} = u(1-u) - \frac{\sqrt{u}v}{1+a\sqrt{u}},\tag{12}$$

$$\frac{dv}{dt} = -sv + \frac{c\sqrt{u}v}{1 + a\sqrt{u}} - \gamma v. \tag{13}$$

Further, if we assume the average handling time t_h is zero, then a=0 the model transforms to

$$\frac{du}{dt} = u(1-u) - \sqrt{u}v,\tag{14}$$

$$\frac{dv}{dt} = -(s+\gamma)v + c\sqrt{u}v. \tag{15}$$

Assuming $1-u\to 1$, i.e., u is very small compared to 1, and $c\sqrt{u}\to 0$, we have the system as

$$\frac{du}{dt} = u - \sqrt{u}v,\tag{16}$$

$$\frac{dv}{dt} = -s'v, (17)$$

where $s' = s + \gamma$. The above model is completely treated in [3].

Remark 1 Since the scale changing formulas are continuous, the change of formula will not change any topological properties of the solution, i.e., the nature of the solution will remain unaffected but due to change of scaling, numerical aspects like population number, rate of consumption etc. will be changed. So due to scaling we obtain qualitatively (topologically) same but quantitatively (numerically) different results. However, with the conversion formula, we can realize the results for the original case.

4 Bifurcation Analysis

In the following we give the bifurcation analysis of the model.

Theorem 4.1 At the equilibrium point U = N, $V = \frac{cr}{(s+\gamma)} (N - \frac{1}{r})$ for

$$s + \gamma = \frac{c\alpha\sqrt{N}}{1 + t_h\alpha\sqrt{N}},$$

the system undergoes through Hopf bifurcation with respect to the parameter r for the critical value $r_0 = \frac{1-N}{N}$.

Proof. Consider the Jacobian matrix

$$\left[\begin{array}{cc} a_{11} & a_{12} \\ a_{21} & a_{22} \end{array}\right],$$

of the system for U = N, $V = \frac{cr}{(s+\gamma)} \left(N - \frac{1}{r}\right)$ for

$$s + \gamma = \frac{c\alpha\sqrt{N}}{1 + t_h\alpha\sqrt{N}},$$

and $2r + \frac{2Nr}{Nr-1} = 0$, we have $a_{11} = 0$, $a_{22} = 0$, $a_{12} < 0$ and $a_{21} > 0$. In this case, the characteristic equation of the Jacobian matrix is $\lambda^2 = a_{12}a_{21} < 0$. Thus the eigenvalues are purely imaginary. Verifying the transversality condition, one can conclude that the model undergoes Hopf bifurcation for $r = \frac{1-N}{N}$ with r as bifurcation parameter.

Theorem 4.2 At the equilibrium point

$$U = \frac{(s+\gamma)^2}{\alpha^2(c - t_h(s+\gamma))^2}, \ V = \frac{c(s+\gamma)}{\alpha^2(c - t_h(s+\gamma))^2} \left(\frac{r}{\alpha^2} - \frac{r}{N} \frac{(s+\gamma)^2}{(c - t_h(s+\gamma))^2}\right)$$

for $\frac{\alpha^2}{N} \cdot \frac{(s+\gamma)^2}{(c-t_h(s+\gamma))^2} < 1$, the system undergoes Hopf bifurcation with respect to the parameter r for the critical values r=0 or

$$r = \frac{1}{4c} \left(\frac{1 - N(c - t_h(s + \gamma))^3}{\alpha(s + \gamma)^2} + \alpha(c - t_h(s + \gamma)) \right).$$

Proof. Consider the Jacobian matrix

$$\left[\begin{array}{cc} a_{11} & a_{12} \\ a_{21} & a_{22} \end{array}\right],$$

of the system for

$$U = \frac{(s+\gamma)^2}{\alpha^2 (c - t_h(s+\gamma))^2}, \quad V = \frac{c(s+\gamma)}{\alpha^2 (c - t_h(s+\gamma))^2} \left(\frac{r}{\alpha^2} - \frac{r}{N} \frac{(s+\gamma)^2}{(c - t_h(s+\gamma))^2} \right).$$

For $\frac{\alpha^2}{N} \cdot \frac{(s+\gamma)^2}{(c-t_h(s+\gamma))^2} < 1$ and r=0 or $r=\frac{1}{4c}\left(\frac{1-N(c-t_h(s+\gamma))^3}{\alpha(s+\gamma)^2} + \alpha(c-t_h(s+\gamma))\right)$, $a_{12}<0$ and $a_{21}>0$. Again $a_{22}=0$. Hence, as the previous case, the system undergoes Hopf bifurcation at the considered point for r=0 or $r=\frac{1}{4c}\left(\frac{1-N(c-t_h(s+\gamma))^3}{\alpha(s+\gamma)^2} + \alpha(c-t_h(s+\gamma))\right)$.

5 Numerical Simulations

In this section we exhibit graphical representation of nullclines, phase portrait and time series for different numerical values of the associated parameters.

5.1 Nullclines and Solution Curves

In the following we give nullclines and solution curves for different parameter values. Blue line denotes preys and green line denotes predators. Magenta line denotes solution curve.

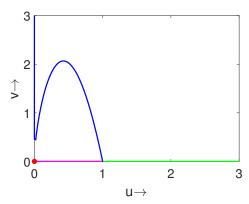


Fig. 1: Nullclines and solution curve for $c=3, s=1, \alpha=2, \gamma=2.5, r=5.$

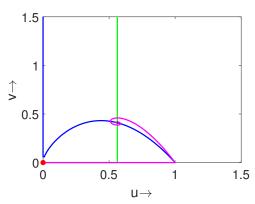


Fig. 3: Nullclines and solution curve for $c=3, s=1, \alpha=2, \gamma=.8, r=1.$

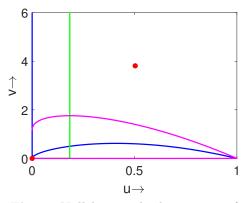


Fig. 5: Nullclines and solution curve for $c=4, s=1, \alpha=1, \gamma=.2, r=1.$

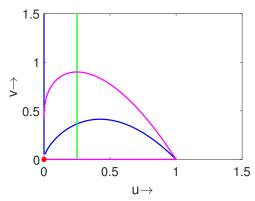


Fig. 2: Nullclines and solution curve for $c=3, s=1, \alpha=2, \gamma=.5, r=1.$

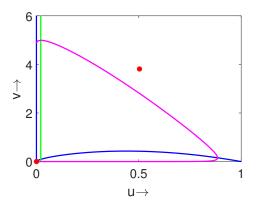


Fig. 4: Nullclines and solution curve for $c=8, s=1, \alpha=2, \gamma=.8, r=1.$

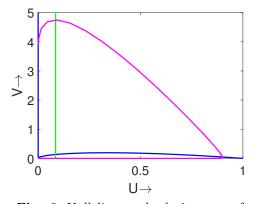


Fig. 6: Nullclines and solution curve for $c=10, s=5, \alpha=1, \gamma=.2, r=1.$

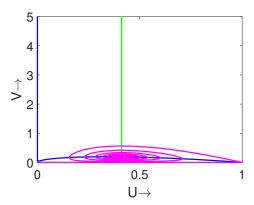


Fig. 7: Nullclines and solution curve for $c=3, s=3, \alpha=1, \gamma=.2, r=1.$

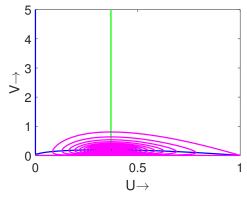


Fig. 8: Nullclines and solution curve for $c=4, s=4, \alpha=1, \gamma=.2, r=1.$

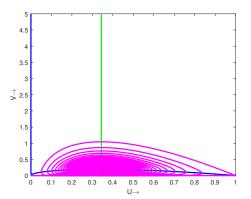


Fig. 9: Nullclines and solution curve for $c=5, s=5, \alpha=1, \gamma=.2, r=1.$

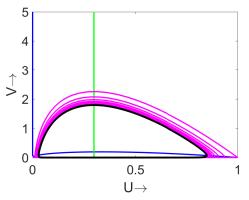


Fig. 10: Nullclines and solution curve for $c = 10, s = 10, \alpha = 1, \gamma = .2, r = 1.$

From Figure 1 to Figure 6, we exhibit how the solution i.e. the prey-predator coexistence varies for change of parameters. The values of the parameters are written bellow each figure. Figure 7 to Figure 9show existence of asymptotically stable equilibrium points. Figure 10 shows existence of unstable equilibrium point with stable limit cycle. periodic solutions for different parameters written bellow each figure.

5.2 Time Series and Phase Portrait

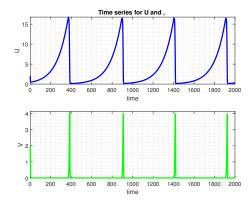


Fig. 11: Time series U-t and V-t for $s=1.5, c=3, r=.01, N=200, <math>\alpha=.8, t_h=1, \gamma=.444$

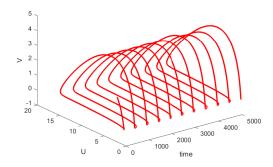


Fig. 12: Time series U - V - t for $s = 1.5, c = 3, r = .01, N = 200, \alpha = .8, t_h = 1, \gamma = .444$

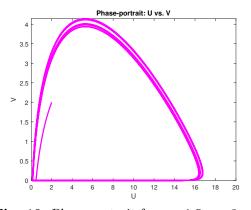


Fig. 13: Phase portrait for $s=1.5, c=3, r=0.1, N=200, \alpha=.8, t_h=1, \gamma=.444$

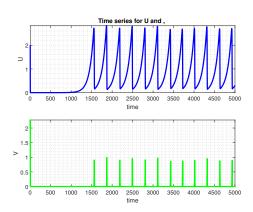


Fig. 14: Time series U-t and V-t for $s=1.5, c=4, r=.01, N=200, <math>\alpha=.9, t_h=1, \gamma=.444$

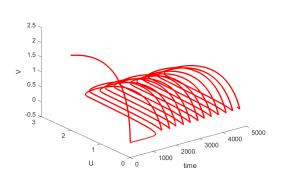


Fig. 15: U - V - t for $s = 1.5, c = 4, r = .01, N = 200, \alpha = .9, t_h = 1, \gamma = .444$

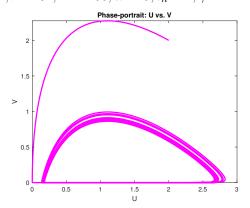


Fig. 16: Phase portrait for $s = 1.5, c = 4, r = .01, N = 200, \alpha = .9, t_h = 1, \gamma = .444$

Figure 11 and Figure 14 show the time series for different parametric values written bellow the figures. Figure 13 and Figure 16 show the existence of unstable equilibrium points with stable limit cycle. The values of the parameters are written bellow each figure. Figures 12 and 14 indicate time series in three-dimension and exhibit existence of periodic oscillatory orbits for the values of the parameters noted bellow each figure.

5.3 Bifurcation

From Figures 7, 8 and 9, we observe the existence of asymptotically stable equilibrium points, while Figures 10, 13 and 16 show existence of unstable equilibrium points with stable limit cycle. This establishes the existence of bifurcation for change of parameters mentioned bellow each figure.

6 Conclusion

Prey-predator model with preys moving in groups and exhibiting retaliation behaviour has been studied. Positivity and boundedness of the solution of the model is established. Conditions for the stability of the equilibrium points have been deduced. Existence for Hopf bifurcation has been shown by analytical proof. Different situations have been illustrated by graphical representations.

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