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On the Dynamics of a General Predator-Prey System

[1]M.M.A. El-Sheikh, [1,2]S.A.A. El-Marouf and [2]Z.M. Alaofy
[1]Department of Mathematics, Faculty of Science,
Menoufia University, Sheben El-Koom, Egypt
[2]Department of Mathematics, Faculty of Science,
Taibah University, Saudi Arabia

Abstract: Problem statement: In this study a general two dimensional predator-prey model is considered. The dynamic and existence of equilibrium points are studied. **Conclusion/Recommendations:** Hopf bifurcation is discussed. The existence and uniqueness of limit cycles is proved. Special cases are considered to justify our results.

Key words: Predator-prey system, functional response, limit cycles, hopf bifurcation, mathematics subject classification, analyzing models, interacting species, predator population, efficiency rate

INTRODUCTION

There has been a demanding need for developing and analyzing models of interacting species in ecosystems. Predator-prey models are one of the most important models of two-species interaction. In this study we are concerned with a general 2-dimensional predator-prey system of the form

$$\begin{aligned} \frac{dx}{dt} &= xg(x) - yp(x) - q_1E_1x, \\ \frac{dy}{dt} &= -Dy + syp(x) - q_2E_2y \end{aligned} \tag{1}$$

where, x and y are the prey and the predator population sizes, respectively. The parameters s, D and k are positive and represent the conversion efficiency rate of prey to predator, predator death rate and the carrying capacity of the prey population, respectively. The parameters $E_1 \geq 0$, $E_2 \geq 0$ denote the harvesting efforts for the predator and prey respectively. The expressions q_1E_1x and q_2E_2x represent the catch of the respective species, where $q_1$and q_2 denote the catch ability coefficients of the prey and predator, respectively. The functions g(x) and p(x) denote the functional response of the prey and predator, respectively and satisfy the assumptions p(0) = 0 and g(0)>0, for all x>0. There have been considerable interests in the dynamics of the predator-prey models of some special cases of (1) by several authors (Attili, 2001; Attili and Mallak, 2006; Xiao and Ruan, 2001; Hesaaraki and Moghadas, 2001; Kar and Matsuda, 2007; Moghadas and Corbett, 2008; Moghadas and Alexander, 2005; Sugie *et al*., 1997; Ruan and Xiao, 2001). Hasik (2000); Sesay *et al*. (2010); Moghadas and Alexander (2006); Saha and Bandyopadhyay (2005) and Tao *et al*. (2011) the authors considered Eq. 1 in the special case $g(x) = r(1-\frac{x}{k})$.

The aim of this study is to discuss the qualitative properties of the general predator-prey system (1). We discuss the existence and stability of equilibria and nonexistence criteria for limit cycles. We explore the uniqueness of limit cycles using Kuang and Freedmann approach (Moghadas and Corbett, 2008) and some applications. It is natural due to biological considerations to expect that the solutions of (1) must to be positive and bounded. So we give the following result which is a partial extension of those of (Freedman and So, 1985) and (Saha and Bandyopadhyay, 2005).The paper end with a brief discussion.

Theorem 1.1: All the solutions of Eq. 1 which start in $\mathbb{R}_+^2$ are positive and uniformly bounded.

Proof: According to the ecological consideration the positivity of the solutions of (1) is obtained. To show the roundedness', we set:

Corresponding Author: M.M.A. El-Sheikh, Department of Mathematics, Faculty of Science, Menoufia University, Sheben El-Koom, Egypt

$$w(x,y) = x + \frac{1}{s}y$$

Then we easily obtain:

$$\frac{dw}{dt} = \frac{dx}{dt} + \frac{1}{s}\frac{dy}{dt} = xg(x) - q_1E_1x - \frac{D}{s}y - \frac{q_2}{s}E_2y$$

i.e. for any r, we have:

$$\frac{dw}{dt} + rw \le x(\alpha + r - q_1E_1) \le M^2 = M_1, \text{say}$$

where, α = max g(x) and $x \le M = (\alpha + r - q_1E_1)$.

Thus applying the theory of differential inequality (Freedman and So, 1985), we obtain:

$$0 < w(x,y) < \frac{M_1}{r}(1 - e^{-rt}) + w(x(0), y(0))e^{-rt}.$$

So the limits as tends to ∞ yields $0 < w(x,y) < \frac{M_1}{r}$. Thus we have that all solutions of (1) start in $\mathbb{R}^2_+$ are confirmed to the region D where $D = \left\{(x,y) \in R^2_+ : w = \frac{M_1}{r} + \in \text{ for } > 0\right\}$. The equilibria of (1) are the intersection points of the prey and predator isoclines $\frac{dx}{ds} = 0$ and $\frac{dy}{ds} = 0$, respectively. It is clear that all possiple equilibria are:

- The trivial equilibrium $P_0(0,0)$,
- The equilibrium corresponding to predator absence $P_1(x_1, 0)$, where

$$x_1 = g^{-1}(q_1E_1), \ y_1 = 0$$

- The positive Equilibrium $P_2(x^*, y^*)$, where

$$x^* = p^{-1}\left(\frac{D + q_2E_2}{s}\right), \ y^* = \left(\frac{x^*[g(x^*) - q_1E_1]}{p(x^*)}\right)$$

It is clear that y* increases with s and decrease with D. This is a natural conclusion because an increase in the predator death rate will cause decrease in the predator population and hence enhances the survival rate of prey. It is also clear that the positive equilibrium $P_2(x^*, y^*)$ exists for (1) only if the harvesting satisfies $0 < g^{-1}(q_1E_1) < x^*$.

The nature of Equilibria: We discuss the stability properties of the equilibria $p_0(0,0)$, $p_1(x_1, 0)$ and $p_2(x^*, y^*)$. The Jacobian matrix of (1) around $P_0(0,0)$ is:

$$J_{P_0(0,0)} = \begin{bmatrix} g(0) = q_1E_1 & 0 \\ 0 & -D - q_2E_2 \end{bmatrix}$$

i.e., we have two eigenvalues $\lambda_1 = -D - q_2E_2$ and $\lambda_2 = g(0) - q_1E_1$.

Therefore if $g(0) > q_1E_1$ then $P_0(0,0)$ is a saddle point, while if $g(0) < q_1E_1$, then $P_0(0,0)$ is asymptotically stable. Further at the boundary equilibrium $P_1(x_1, 0)$, the Jacobian matrix has the eigenvalues:

$$\lambda_1 = x_1g'(x_1) + g(x_1) - q_1E_1 \text{ and } \lambda_2 = -(D + q_2E_2 - sp(x_1))$$

i.e. if we assume that $D + q_2E_2 > sp(x_1)$, then for $x_1g'(x_1) + g(x_1) > q_1E_1$, $P_1(x_1,0)$ is a saddle point while if $x_1g'(x_1) + g(x_1) > q_1E_1$ then $p_1(x_1, 0)$ is asymptotically stable.

Now to discuss the stability of the interior equilibrium $P_2(x^*, y^*)$, the Jacobean matrix around P_2 is:

$$J_{P_2(x^*,y^*)} = \begin{bmatrix} x^*g'(x^*) + g(x^*) - y^*p'(x^*) - q_1E_1 & -p(x^*) \\ sy^*p'(x^*) & 0 \end{bmatrix}$$

The eigenvalues of J_{P_2} obey the equation:

$$\lambda^2 - (\text{trace}J_{P_2})\lambda + \det J_{P_2} = 0$$

Since it is clear that $\det J_{P_2} = sy^*p'(x^*)p(x^*) > 0$, so the sign of the characteristic roots depend only on trace $J_{P_2}(x^*, y^*)$. Following (Pimply, 1974), we introduce an auxiliary parameter β such that J_{P_2} takes the form:

$$J_{\beta P_2} = \begin{bmatrix} \beta[x^*g'(x^*) + g(x^*)] - y^*p'(x^*) - q_1E_1 & -p(x^*) \\ sy^*p'(x^*) & 0 \end{bmatrix}$$

Since by the Routh-Hurwitz criterion $P_2(x^*, y^*)$ is stable or unstable if (trace J_{P_2}) <0 or > 0, respectively. This leads to if $\beta < \frac{y^*p'(x^*) + q_1E_1}{x^*g'(x^*) + g(x^*)}$, then critical point $P_2(x^*, y^*)$ is locally asymptotically stable. On the other hand if β is chosen such that $\beta > \frac{y^* p'(x^*) + q_1 E_1}{x^* g'(x^*) + g(x^*)}$, then $P_2(x^*, y^*)$ is unstable in the positive quadrant.

However in the case $\beta = \beta^*$, trace $J_{\beta p_2} = 0$. In this case the characteristic roots are pure imaginary. Further since $\frac{d}{d\beta}(\text{trace } J_{\beta p_2})_{\beta=\beta^*} \neq 0$, then by Hopf bifurcation Theorem (Hassard *et al*., 1981), we have small amplitude periodic solution at $\beta = \beta^{**}$. Therefore the two interacting populations oscillate around the unique nontrivial positive equilibrium $P_2(x^*, y^*)$.

Existence of limit cycles: Now we discuss the existence and nonexistence of limit cycles of the general system (1). (Attili, 2001; Attili and Mallak, 2006; Hesaaraki and Moghadas, 2001; Kar and Matsuda, 2007; Moghadas and Corbett, 2008; Sesay *et al*., 2010). We start with a criterion for nonexistence of limit cycles.

Proposition 3.1: If $x^* g'(x^*) + g(x^*) - y^* p'(x^*) - q_1 E_1 < 0$, then there is no periodic solutions of (1).

Proof: Since for any real function $\alpha(x, y)$ we have:

$$\operatorname{div}F(x,y) = \operatorname{div}\begin{bmatrix}\alpha(x,y)[xg(x) - yp(x)] \\ \alpha(x,y)[-Dy + syp(x)]\end{bmatrix} =$$
$$x^* g'(x^*) + g(x^*) - y^* p'(x^*)\_q_1 E_1 + [-Dy + sp(x)],$$

choosing Dulac function $\alpha=1$, then:

$$\operatorname{div}\{F(x,y)\} = x^* g'(x^*) + g(x^*) - y^* p'(x^*)\_q_1 E_1 < 0$$

By Bendixon-Dulac Theorem (Kelley and Peterson, 2003), this is sufficient for nonexistence of periodic solutions of (1). The following result discusses the existence of limit cycles.

Theorem 3.1: The system (1) has at least one limit cycle in $\Omega = \{(x,y): x > 0, y > 0\}$ if and only if Eq. 2:

$$x^* g'(x^*) + g(x^*) - y^* p'(x^*)\_q_1 E_1 < 0 \quad (2)$$

In order to prove sufficient condition of Theorem 3.1, we first note that one can show ((Freedman and So, 1985; Moghadas and Corbett, 2008) that, if:

$$\vartheta = \left\{(x,y) \in \mathbb{R}_+^2 : 0 \le x \le \frac{M}{2}, 0 \le x + \frac{y}{s} \le \frac{M_1}{r}\right\}$$

where, $\frac{M}{2}$ =max x then:

- The set ϑ is positively invariant
- For $(x_0, y_0) \in \mathbb{R}_+^2$, $(x(t), y(t)) \to \vartheta$ as $t \to \infty$

Now since by above, the characteristic polynomial at the nontrivial positive equilibrium $P_2(x^*, y^*)$ is:

$$p(\lambda) = \lambda^2 + \begin{bmatrix} y^* p'(x^*) - x^* g'(x^*) - \\ g(x^*) + q_1 E_1 \end{bmatrix}\lambda + sy^* p'(x^*)p(x^*)$$

Since $sy^* p'(x^*)$ p $(x^*)>0$, the roots of $p(\lambda)$ have positive real parts if and only if (2) holds. Cosequently $P_2(x^*, y^*)$ is unstable if (2) holds. It is easy to check that the stable and unstable manifolds at (0, 0) are on the x-axis and y-axis, respectively. If $P_2(x^*, y^*)$ is unstable, then by above discussion and Poincaré Bendixson Theorem, it follows that the ω-limit set of every solution initiating at a point in the first quadrant is a limit cycle. Therefore, we have established that if (2) holds, then the system (1) has at least one limit cycle. This proves the sufficient condition.

Remark 3.1: We note that it can be shown that this condition is not only sufficient but also necessary (Attili, 2001; Attili and Mallak, 2006; Hesaaraki and Moghadas, 2001; Moghadas and Corbett, 2008).

Uniqueness of limit cycles: We discuss the uniqueness of limit cycles of the general system (1). Our criterion improves and partially generalizes those of (Hasik, 2000; Kuang and Freedman, 1988; Sugie *et al*., 1997). We first start with the most famous uniqueness result which was the motivation for several authors and criteria. As in (Kuang and Freedman, 1988) we consider the system Eq. 3:

$$\begin{aligned}\frac{dx}{dt} &= xp(x) - y\phi(x), \\ \frac{dy}{dt} &= y(-\gamma + \psi(x))\end{aligned} \quad (3)$$

where, $\gamma>0$, all the functions are sufficiently smooth on $[0,\infty)$ and satisfy Eq. 4:

$$\varphi(0) = \psi(0) = 0 \text{ and } \varphi'(x) > 0, \psi'(x) > 0 \text{ for } x > 0 \quad (4)$$

The authors in (Kuang and Freedman, 1988) gave the following result on the uniqueness of limit cycles.

Theorem 4.1: Kuang and Freedman (1988) if there exist constants x^* and m with $0< x^* < m$ such that:

$$\psi(x^*) = \gamma \text{ and } (x-m)\rho(x) < 0 \text{ for } x \neq m,$$

$$\frac{d}{dx}\left(\frac{x(\rho(x))}{\varphi(x)}\right)\Big|_{x=x^*} > 0,$$

$$\frac{d}{dx}\left(\frac{xp'(x)+\rho(x)-x\rho(x)\frac{\varphi'(x)}{\varphi(x)}}{\psi(x)-\gamma}\right) \leq 0 \text{ for } x \neq x^*,$$

Then the system (3) has exactly one limit cycle which is globally asymptotically stable. In view of Theorem 4.1 and those of (Sugie *et al*., 1997; Hasik, 2000), we give the following uniqueness theorem for the limit cycles of our general system (1).

Theorem 4.2: Assume that $H(x) = x^*g'(x^*)+g(x^*)-y^*P'(x^*)-q_1E_1 \geq 0$. Then the system (1) has a unique limit cycle.

Proof: Rewriting the system (1) as the system (3) of Kuang and Freedman (1988) with:

$$\gamma = D+q_2E_2, \rho(x) = g(x)-q_1E_1, \varphi(x) = p(x) \text{ and } \psi(x) = sp(x)$$

Then it is clear that our functions satisfy the conditions (4) of (Kuang and Freedman 1988). Moreover:

$$\frac{d}{dx}\left(\frac{x(\rho(x)),}{\psi(x)}\right)\Big|_{x=x^*} = \frac{d}{dx}\left(\frac{x^*[g(x^*)-q_1E_1]}{P(x^*)}\right)\Big|_{x=x^*} =$$
$$\frac{xg'(x^*)+g(x^*)-q_1E_1}{p(x^*)} - \frac{x^*[g(x^*)-q_1E_1]p'(x^*)}{p^2(x^*)} =$$
$$\frac{xg'(x^*)+g(x^*)-q_1E_1}{p(x^*)} - \frac{y^*p'(x^*)}{p(x^*)} = \frac{H(x)}{p(x^*)} > 0$$

Setting $W(x) = \frac{H(x)}{sp(x)-D=q_2E_2}$' then:

$$\frac{d}{dx}\left(\frac{xp'(x)+\rho(x)-x\rho(x)\frac{\varphi'(x)}{\varphi(x)}}{\psi(x)-\gamma}\right) = W'(x^*) =$$
$$\left\{\frac{(H'(x))}{sp(x)-D-q_2E_2} - \frac{H'(x).sp'(x)}{(sp(x)-D-q_2E_2)^2}\right\}$$

Hence since $H(x)>0$, $sp'(x)>0$, $D+q_2E_2>sp(x^*)$, then $W'(x^*)<0$.

Therefore the condition of Theorem 4.1 (Freedman and So, 1985) is satisfied and this completes the uniqueness of limit cycles.

Applications: Now we give some examples from the ecological literature. The numerical simulations may justify the results.

Example 5.1: Consider the special case:

$$g(x) = r\left(1-\frac{x}{k}\right), p(x) = \frac{mx}{\alpha+bx}$$

Then we have the system:

$$\frac{dx}{dt} = rx\left(1-\frac{x}{k}\right) - y\frac{mx}{\alpha+bx} - q_1E_1x,$$
$$\frac{dy}{dt} = -Dy + sy\frac{mx}{\alpha+bx} - q_2E_2y$$

Clearly all the assumptions hold. Thus the critical point

$$(x^*, y^*) = \left(\frac{\alpha D+\alpha q_2E_2}{sm-bD-bq_2E_2}, \left[r\left(1-\frac{x^*}{k}\right)-q_1E_1\right]\left(\frac{\alpha+bx^*}{x}\right)\right)$$

and the Jacobian is:

$$A = \begin{bmatrix} r-\frac{2rx^*}{k}-\frac{amy^*}{(\alpha+bx^*)^2}-q_1E_1 & \frac{-mx^*}{\alpha+bx^*} \\ \frac{asmy^*}{(\alpha+bx^*)^2} & 0 \end{bmatrix}$$

choosing r = 1, k = 0.5, m = 2, α = 0.51, b = 1, q_1 = 0.001, E_1 = 1,D = 1,s = 10, q_2 = 0.02, E_2 = 0.5, x(0) = 0.01, y(0) = 0.2, T1 = 200.

It is clear that $r-\frac{2rx^*}{k}-\frac{amy^*}{(\alpha+bx^*)^2}-q_1E_1<0$. Thus the condition of Theorem 3.1. holds. Then there exists at least one limit cycle (Fig. 1).

Example 5.2: Consider the special case:

$$g(x,k) = r(1-\frac{x}{k}), \quad p(x) = \frac{x^p}{\alpha+x^p}$$

Then we have the Holling system:

$$\frac{dx}{dt} = rx\left(1-\frac{x}{k}\right) - y\frac{x^p}{\alpha+x^p} - q_1E_1x,$$
$$\frac{dy}{dt} = -Dy + sy\frac{x^p}{\alpha+x^p} - q_2E_2y$$

Clearly the conditions (H_1)-(H_3) and (H_4)-(H_6) hold. Thus the critical point

$$(x^*, y^*) = \left(\left(\frac{\alpha D + \alpha q_2 E_2}{s - D - q_2 E_2}\right)^{\frac{1}{p}}, \left[rx^*\left(1 - \frac{x^*}{k}\right) - q_1 E_1 x^*\right]\left(\frac{\alpha + x^{*p}}{x^{*p}}\right)\right)$$

and the Jacobian is:

$$A = \begin{bmatrix} r - \frac{2rx^*}{k} - \frac{\alpha P y^* x^{*p-1}}{(\alpha + x^{*p})^2} - q_1 E_1 & -\frac{x^{*p}}{\alpha + x^{*p}} \\ \frac{\alpha s p y^* x^{*p-1}}{(+bx^{*p})^2} & 0 \end{bmatrix}$$

choosing r = 0.1, k = 20, α = 0.51, q_1 = 0.001, E_1 = 1, D = 1, s =10, q_2 = 0.02, E_2 = 0.5, T= 150, x(0) = 0.5, y(0) = 0.001, p = 3.

It is clear that $r - \frac{2rx^*}{k} - \frac{\alpha P y^* x^{*p-1}}{(\alpha + x^{*p})^2} - q_1 E_1 < 0$. Thus the condition of Theorem 3.1. Holds.

Then there exists at least one limit cycles (Fig. 2).

Example 5.3: Consider the special case:

$$g(x,k) = r(1 - \frac{x}{k}), \qquad p(x) = \frac{x^2}{\alpha + x^2}$$

Then we have the system:

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{k}\right) - y\frac{x^2}{\alpha + x^2} - q_1 E_1 x,$$
$$\frac{dy}{dt} = -Dy + sy\frac{x^2}{\alpha + x^2} - q_2 E_2 y.$$

Clearly the assumptions (H_1)-(H_3) and (H_4)-(H_6) hold. Thus the critical point $(x^*, y^*) = \left(\sqrt{\frac{\alpha D + \alpha q_2 E_2}{s - D - q_2 E_2}}, \left[r\left(1 - \frac{x^*}{k}\right) - q_1 E_1\right]\left(\frac{\alpha + bx^{*2}}{x^*}\right)\right)$ and the Jacobian is:

$$A = \begin{bmatrix} r - \frac{2rx^*}{k} - \frac{2\alpha x^* y^*}{(\alpha + x^{*2})^2} - q_1 E_1 & -\frac{x^{*2}}{\alpha + x^{*2}} \\ \frac{2\alpha s x^* y^*}{(\alpha + bx^{*2})^2} & 0 \end{bmatrix}$$

choosing r = 0.1, k = 20, α = 0.51, q_1 = 0.001, E_1 = 1, D = 1, s =10, q_2 = 0.02, E_2 = 0.5, T= 150, x(0) = 0.5, y(0) = 0.001, p = 2.

It is clear that $r - \frac{2rx^*}{k} - \frac{\alpha P y^* x^{*p-1}}{(\alpha + x^{*p})^2} - q_1 E_1 < 0$. Thus the condition of Theorem 3.1. holds.

Then there exists at least one limit cycles (Fig. 3).

Example 5.4: Consider the special case:

$$g(x,k) = r(1 - \frac{x}{k}), \qquad p(x) = 1 - e^{-\alpha x}$$

Then we have the system:

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{k}\right) - y(1 - e^{-\alpha x}) - q_1 E_1 x,$$
$$\frac{dy}{dt} = -Dy + sy(1 - e^{-\alpha x}) - q_2 E_2 y$$

Clearly the conditions (H_1)-(H_3) and (H_4)-(H_6) hold. Thus the critical point:

$$(x^*, y^*) = \left(-\frac{1}{\alpha}\mathrm{In}\left|1 - \frac{D + q_2 E_2}{s}\right|, \frac{rx^*\left(1 - \frac{x^*}{k}\right) - q_1 E_1 x^*}{1 - e^{-\alpha x^*}}\right)$$

And the Jacobian is:

$$J = \begin{bmatrix} r - \frac{2rx^*}{k} - \alpha y^* e^{-\alpha x^*} - q_1 E_1 x^* & e^{-\alpha x^*} - 1 \\ \alpha s y^* e^{-\alpha x^*} & 0 \end{bmatrix}$$

choosing r = 1,k = 0.5, α = 0.51,q_1 = 0.001,E_1 = 1, D = 1,s = 10,q_2 = 0.02, E_2 = 0.5, x(0) = 0.01, y(0) = 0.5, T1 = 100.

It is clear that $r - \frac{2rx^*}{k} - \alpha y^* e^{-\alpha x^*} - q_1 E_1 < 0$. Thus the condition of Theorem 3.1. holds.

Then there exists at least one limit cycle (Fig. 4).

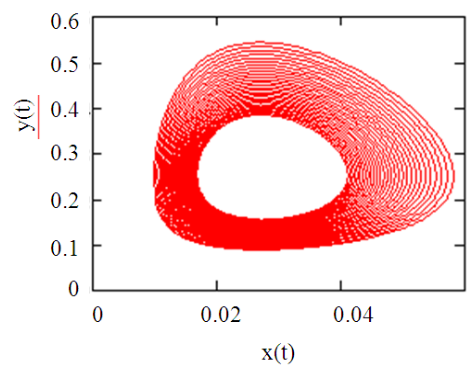

Fig. 1: Existence of limit cycles for choosing r = 1,k = 0.5, α = 0.51,q_1 = 0.001,E_1 = 1, D = 1,s = 10,q_2 = 0.02, E_2 = 0.5

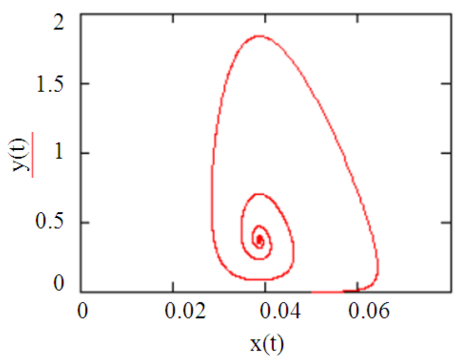

Fig. 2: Existence of limit cycles for choosing r = 0.1, k = 20, α = 0.51, q_1 = 0.001, E_1 = 1, D = 1, s =10, q_2 = 0.02, E_2 = 0.5, T= 150, x(0) = 0.5, y(0) = 0.001, p = 3

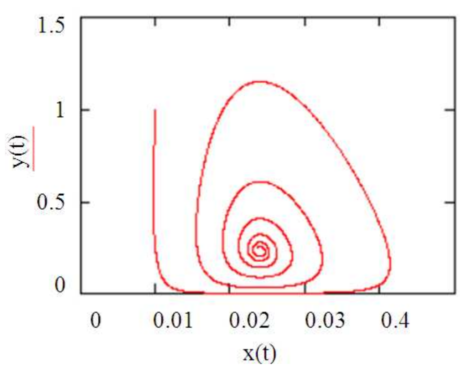

Fig. 3: Existence of limit cycles for r = 1, k = 0.5,m = 2, α = 0.51, b = 1,q_1 = 0.001,E_1 = 1,D = 1,s = 10,q_2 = 0.02, E_2 = 0.5, x(0) = 0.01, y(0) = 1, T1 = 100, p = 2

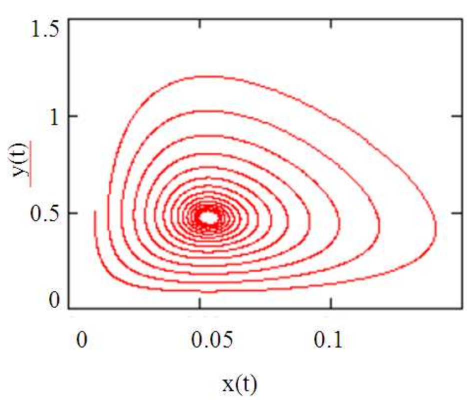

Fig. 4: Existence of limit cycles for choosing r = 1, k = 0.5, m = 2, α = 0.51, b = 1, q_1 = 0.001,E_1 = 1,D = 1,s = 10,q_2 = 0.02, E_2 = 0.5, x(0) = 0.01, y(0) = 0.5, T1 = 100, p = 2

Remark 5.2: we may note that our examples and graphs are different from those exist in (Kar and Matsuda, 2007; Moghadas and Corbett, 2008).

COUCLUSION

In this article we discuss the existence and stability of equilibrium points using Routh-Hurwitz approach. Theorem1 shows that all solutions of the model are positive and bounded. We give sufficient condition guarantees that the model has at least one limit cycle in the first quadrant of the xy plane. We give sufficient condition guarantees that the model has at least one limit cycle in the first quadrant of the xy plane. We give sufficient condition guarantees that the model has at least one limit cycle in the first quadrant of the xy plane if:

$$x^*g'(x^*)+g(x^*)-y^*p'(x^*)-q_1E_1<0$$

Using Bendixon Dulac Theorem we discuss the case for which the predator-prey model (1) has no periodic solution. Using Kuang and Freedman technique we give sufficient condition for the uniqueness of limit cycles of (1). Numerical examples for some special cases of g(x) are given to justify the results with graphs showing the existence of limit cycles.

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