Heteroclinic Bifurcation and Multistability in a Ratio-dependent Predator-Prey System with Michaelis-Menten Type Harvesting Rate

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Abstract—**In this article, we study a ratio-dependent predator-prey system where predator population is subjected to harvesting with Michaelis-Menten type harvesting rate. We study the existence of heteroclinic bifurcations in an exploited predator-prey system by using Melnikov's method. Our simulation results also show that the system may exhibit monostability, bistability and tristability depending on the initial values of the system populations and the harvesting effort.**

***Keywords**—predator-prey model, ratio-dependence, harvesting, Melnikov functions, heteroclinic bifurcation.*

1 Introduction

The standard Lotka-voltera type models assume that the per-capita rate of predation depends on the prey numbers only. This means that the predator's functional response is a function of prey density only. In general, predator's functional response should certainly be a function of both prey and predator densities [1, 2] as there is often competition among the predators for their food. A simple alternative assumption is that the per capita rate of predation depends on the ratio of prey to predator densities.

It is well known that classical prey-dependent predator prey model exhibits the "paradox of enrichment" [3, 4] which states that enriching a predator prey system (by increasing the carrying capacity) will cause an increase in the equilibrium density of the predator but not in that of prey and will destabilize the positive equilibrium, and thus increases the possibilities of the stochastic extinction of the predator. However, numerus field observations provide contrary to this paradox of enrichment. It is often observed in nature that fertilization increases the prey density, but does not destabilize a stable steady state and fails to increase the amplitude of the oscillations in system that already cycle [5]. Another paradox that the predator-prey model with prey-dependent Michaelis-Menten functional response exhibits is the so-called "biological control paradox" [6], which states that we cannot have both a low and stable prey equilibrium density. However, there are many examples of successful biological control where the prey is maintained at very low densities compared with its carrying capacity [7]. A ratio dependent predator-prey model with Michaelis-Menten functional response does not show these paradoxes ([10]-[15]) and assumed, therefore, to be superior than their prey-dependent counter part. Kuang and Beretta [10] observed that ratio-dependent predator-prey models are richer in boundary dynamics and showed that if the positive steady state of the system is locally asymptotically stable then the system has no nontrivial positive periodic solutions. Jost et. al [11] demonstrated that the equilibrium for a ratio dependent predator prey model can either be a saddle point or an attractor. Xiao and Ruan [12] and Berezovskaya et. al. [14] observed that there exist different kinds of topological structures in the vicinity of the origin of a ratio dependent predator prey model. Hsu et. al. [16] considered a ratio dependent food chain model and studied the extinction dynamics as well as the sensitivity of the system to initial population densities. Berezovskoya et. al. [15] presented an algorithmic approach to analyze the behavior of ratio dependent predator prey system. Tang and Zhang [17] gave an analytical condition on parameters for the existence of the hetroclinic loop. Most recently Li and Kuang [18], applying the same ideas and techniques to a different Hamiltonian system, obtained a new explicit relation in higher order expansion for the bifurcation curve of a heteroclinic loop. The heteroclinic bifurcation plays an important role in understanding the dynamics of the system [13, 14] because heteroclinic bifurcation may trigger a catastrophic shift from the state of large oscillations of predator and prey populations to the state of extinction of both populations [18].

Harvesting in a predator prey system may be two fold. The primary objective is optimal exploitation of the harvested stock to maximize the profit ([20]-[22]). In contrast, some researchers ([23]-[26]) considered harvesting from ecological point of view. Xiao and Jennings [27] observed numerous kinds of bifurcation in a ratio-dependent predator-prey model where prey is being harvested at a constant rate. Xiao et al. [28] considered a constant harvesting term in predator equation and observed subcritical, supercritical and the cusp bifurcation of codimension 2. We also studied a ratio-dependent predator-prey model in presence of parasite where the prey population was subjected to harvesting [29]. The dynamics of

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zero equilibria was thoroughly investigated to find out conditions on the system parameters such that trajectories starting from the domain of interest can reach the zero equilibrium following any fixed direction. Meza et al. [30] studied a ratio-dependent predator-prey model where predator is subject to an on-off control, known as threshold policy. They showed that an equilibrium on the boundary may slide to an stable interior equilibrium point due to on-off control and thus avoid the extinction of species. One important question in the bioeconomic modeling of productive resources is the rate of harvesting. It is shown that Michaelis-Menten type functional form of catch rate, $h(t)$, given by

$$h(t) = \frac{qEx}{bE + lx},$$

where b and l are positive constants, q is the catchability coefficient and E is the external effort devoted to harvesting, is better than the constant rate of harvesting and catch-per-unit-effort harvesting [31, 32]. None of these studies ([27]-[30]), however, considered the Michaelis-Menten type functional form of catch rate in their model systems. The objective of this paper is to rigorously study the existence of heteroclinic bifurcation in a ratio-dependent predator-prey model where the predator population is subjected to harvesting with Michaelis-Menten type harvesting rate.

The organization of the paper is as follows: Section 2 deals with the model development. Section 3 is devoted to the study of heteroclinic bifurcations. Numerical studies and discussion are presented in Section 4.

2 The model

The following assumptions are made in formulating the mathematical model:

- Let $x(t)$ and $y(t)$ be, respectively, the prey and predator densities at time t.

- Assume that the prey population grows logistically to its carrying capacity K with intrinsic growth rate r.

- Let d_0 be the food independent death rate and b_0 be the conversion efficiency of the predator.

- Assume that predator follows ratio-dependent Type II functional response $\frac{\alpha xy}{ay+x}$, where α is the maximum prey consumption rate and a is the half-saturation constant.

- Let predator is harvested following the Michaelis-Menten type catch rate.

Based on these assumptions, we formulate the following ratio-dependent predator-prey model with predator harvesting:

$$\begin{aligned} \frac{dx}{dt} &= rx(1-\frac{x}{K}) - \frac{\alpha xy}{ay+x}, \\ \frac{dy}{dt} &= \frac{\alpha b_0 xy}{ay+x} - d_0 y - \frac{qEy}{bE+ly}. \end{aligned} \tag{2.1}$$

All parameters are assumed to be positive. Taking $x = Kx^{'}$, $y = \frac{Ky^{'}}{a}$ and $t = \frac{at^{'}}{\alpha}$, we can write down the system (2.1) as

$$\begin{aligned} \frac{dx^{'}}{dt^{'}} &= \alpha_0 x^{'}(1-x^{'}) - \frac{x^{'}y^{'}}{x^{'}+y^{'}}, \\ \frac{dy^{'}}{dt^{'}} &= \frac{\beta_0 x^{'}y^{'}}{x^{'}+y^{'}} - \gamma_0 y^{'} - \frac{E_0 y^{'}}{E^{'}+y^{'}}, \end{aligned} \tag{2.2}$$

where $\alpha_0 = \frac{ar}{\alpha}, \beta_0 = ab_0, E_0 = \frac{a^2qE}{\alpha Kl}, \gamma_0 = \frac{ad_0}{\alpha}, E^{'} = \frac{abE}{Kl}$ and $E_0^{'} = \frac{aq}{b\alpha}$.

For convenience, we replace $x^{'}$, $y^{'}$, $t^{'}$ by x, y t, respectively, and rewrite the above system as

$$\begin{aligned} \frac{dx}{dt} &= \alpha_0 x(1-x) - \frac{xy}{x+y}, \\ \frac{dy}{dt} &= \frac{\beta_0 xy}{x+y} - \gamma_0 y - \frac{E_0 y}{E^{'}+y}. \end{aligned} \tag{2.3}$$

Changing the independent variable t to $(x+y)t^{''}$ and replacing $t^{''}$ by t for convenience, the system (2.3) becomes

$$\begin{aligned} \frac{dx}{dt} &= \alpha_0 x(1-x)(x+y) - xy, \\ \frac{dy}{dt} &= \beta_0 xy - \gamma_0 y(x+y) - \frac{E_0 y(x+y)}{E^{'}+y}. \end{aligned} \tag{2.4}$$

It is easy to show that the system (2.3) in the first quadrant is equivalent to the polynomial system (2.4) [14, 17, 12]. Using Briot Boughet's transformations

$$x \to x^{'''},\ y \to x^{'''}y^{'''},\ t \to \frac{t^{'''}}{x^{'''}}, \tag{2.5}$$

the system (2.4) can be written as

$$\begin{aligned} \frac{dx}{dt} &= x[\alpha_0 - \alpha_0 x - (1-\alpha_0)y - \alpha_0 xy], \\ \frac{dy}{dt} &= y[(\beta_0 - \alpha_0 - \gamma_0) + \alpha_0 x + (1-\alpha_0-\gamma_0)y + \alpha_0 xy \\ &\quad - \frac{E_0(1+y)}{E^{'}+xy}]. \end{aligned} \tag{2.6}$$

For convenience, we have written x, y, t in place of $x^{'''}$, $y^{'''}$, $t^{'''}$, respectively, in (2.6). Transformation (2.5) is a homomorphism in the first quadrant and its inverse maps the y-axis to the point $(0,0)$. Now changing the variables

$$x \to \frac{x}{\alpha_0},\ y \to y,\ t \to t, \tag{2.7}$$

the equation (2.6) can be transformed into the following simpler system:

$$\begin{aligned} \frac{dx}{dt} &= x[\alpha_0 - x - (1-\alpha_0)y - xy], \\ \frac{dy}{dt} &= y[(\beta_0 - \alpha_0 - \gamma_0) + x + (1-\alpha_0-\gamma_0)y + xy \\ &\quad - \frac{\alpha_0 E_0(1+y)}{\alpha_0 E^{'}+xy}]. \end{aligned} \tag{2.8}$$

System (2.8) has to be analyzed with the following initial conditions:

$$x(0) > 0,\ y(0) > 0.$$

3 Heteroclinic Bifurcation

In the system (2.8), we simply use α_0 and $\gamma^{'} = \beta_0 - \alpha_0 - \gamma_0$ (or equivalently α_0 and β_0) as our unfolding parameters while fixing γ_0 and get the following transformed equations as

$$\begin{aligned} \frac{dx}{dt} &= x(\alpha_0 - x - y) + x(\alpha_0 y - xy), \\ \frac{dy}{dt} &= y\left[\gamma^{'} + x + (1-\gamma_0)y\right] + y(xy - \alpha_0 y) - \frac{\alpha_0 E_0(1+y)}{\alpha_0 E^{'}+xy}. \end{aligned} \tag{3.1}$$

This system can then be viewed as a perturbation of the system

$$\begin{aligned} \frac{dx}{dt} &= x(\alpha_0 - x - y), \\ \frac{dy}{dt} &= y\left[\gamma + x + (1-\gamma_0)y\right], \end{aligned} \tag{3.2}$$

as α_0, γ, x and y all are very small. Here $\gamma = \gamma^{'} - \frac{E_0}{E^{'}} = \beta_0 - \alpha_0 - \gamma_0 - E_0^{'}$. Note that the coefficients of second order terms in (3.2) do not depend on α_0 and γ, and we shall assume that $\gamma_0 < 1$.

The system (3.2) is integrable if

$$\gamma = -\frac{2(1-\gamma_0)}{2-\gamma_0}\alpha_0 < 0 \tag{3.3}$$

and in this case the function

$$F_{\alpha_0}(x,y) = \frac{1}{b}x^a y^b \left(\alpha_0 - x - \frac{2-\gamma_0}{2}y\right), \tag{3.4}$$

where

$$a = \frac{2(1-\gamma_0)}{\gamma_0} \text{ and } b = \frac{2-\gamma_0}{\gamma_0} \tag{3.5}$$

are constant along the solution curves. In fact, when (3.3) holds along any solution curve $(x(t), y(t))$ of (3.2), we have

$$\frac{d}{dt}F_{\alpha_0}(x,y) = \frac{1}{b}y^b x(\alpha_0 - x - y)\times$$
$$\left[ax^{a-1}\left(\alpha_0 - x - \frac{2-\gamma_0}{2}y\right) - x^a\right]$$
$$+\frac{1}{b}x^a y\left[\gamma + x + (1-\gamma_0)y\right]\times$$
$$\left[by^{b-1}\left(\alpha_0 - x - \frac{2-\gamma_0}{2}y\right) - \frac{y^b(2-\gamma_0)}{2}\right] = 0.$$

This gives,

$$x(\alpha_0 - x - y)\left[a\alpha_0 x^{a-1}y^b - (a+1)x^a y^b - \frac{a(2-\gamma_0)}{2}x^{a-1}y^{b+1}\right]$$
$$+y\{\gamma + x + (1-\gamma_0)y\}\times$$
$$\left[b\alpha_0 x^a y^{b-1} - (b+1)\frac{2-\gamma_0}{2}x^a y^b - bx^{a+1}y^{b-1}\right] = 0.$$

Using the transformations $x \to \epsilon x, y \to \epsilon y, \alpha_0 = \epsilon\gamma_1$ and $\gamma = -\frac{2(1-\gamma_0)}{2-\gamma_0}\epsilon\gamma_1 + \gamma_2\epsilon^2$ and rescaling time $t \to \frac{1}{\epsilon}dt$, equation (3.1) transforms into

$$\begin{aligned}\tfrac{dx}{dt} &= x(\gamma_1 - x - y) + \epsilon x(\gamma_1 y - xy),\\ \tfrac{dy}{dt} &= y\left[-\tfrac{2(1-\gamma_0)}{2-\gamma_0}\gamma_1 + x + (1-\gamma_0)y\right] + \epsilon(\gamma_2 y - \gamma_1 y^2 + xy^2)\\ &\quad - \tfrac{E_0}{E'}\epsilon y(1+\epsilon y)(1 + \tfrac{\epsilon xy}{\gamma_1 E'})^{-1}.\end{aligned} \tag{3.6}$$

Multiplying (3.6) by the integrating factor $x^{a-1}y^{b-1}$, we obtain the equivalent perturbed Hamiltonian system

$$\begin{aligned}\tfrac{dx}{dt} &= x^a y^{b-1}\left[(\gamma_1 - x - y) + \epsilon x(\gamma_1 y - xy)\right],\\ \tfrac{dy}{dt} &= x^{a-1}b^b\left[-\tfrac{2(1-\gamma_0)}{2-\gamma_0}\gamma_1 + x + (1-\gamma_0)y + \epsilon(\gamma_2 - \gamma_1 y + xy)\right]\end{aligned} \tag{3.7}$$
$$-x^{a-1}b^b\left[\frac{E_0}{E'}\epsilon(1+\epsilon y)(1 + \frac{\epsilon xy}{\gamma_1 E'})^{-1}\right].$$

One can check that $F_{\gamma_1}(x,y) = \frac{1}{b}x^a y^b\left(\gamma_1 - x - \frac{2-\gamma_0}{2}y\right)$ is the Hamiltonian for (3.7) when $\epsilon = 0$, where a and b are given in (3.5).

We use the Melnikov theory [33, 34, 35] to locate the parameter values that produce a heteroclinic cycle for (3.7) in case $\epsilon \neq 0$. In the following, we have employed the technique used in [33, 34]. We can set $\gamma_1 = 1$, without any loss of generality. The heteroclinic cycle for $\epsilon = 0$ lies on the level curve $F_{\gamma_1}(x,y) = 0$, denoted by Γ_0, which corresponds to a triangle formed by the three line segments determined by $x = 0, y = 0$ and $x + \frac{2-\gamma_0}{2}y = 1$. Let

$$G(x,y) = \left(x^a y^{b-1}(y - xy), x^{a-1}y^b(\gamma_2 - y + xy)\right).$$

The Melnikov function is

$$M(\gamma_2) = \int\int_{int\ \Gamma_0} traceDG(x,y)dxdy,$$

where

$$traceDG(x,y) = (a-b-1)x^{a-1}y^b + (b-a)x^a y^b$$
$$+\gamma_2 bx^{a-1}y^{b-1}$$

and $int\ \Gamma_0$ denotes the region bounded by Γ_0. $M(\gamma_2) = 0$ has a unique solution

$$\gamma_2 = -\left[\frac{(a-b-1)I(a-1,b) + (b-a)I(a,b)}{bI(a-1,b-1)}\right],$$

where

$$I(u,v) = \int\int_{\Gamma_0} x^u y^v dxdy, u > -1, v > -1.$$

It is easy to see that

$$\begin{aligned}I(u,v) &= \textstyle\int_0^1 x^u \int_0^{\frac{1-x}{s}} y^v dydx\\ &= \tfrac{1}{(v+1)s^{v+1}}\textstyle\int_0^1 x^u(1-x)^{v+1}dx,\end{aligned}$$

where $s = \frac{2-\gamma_0}{2}$. We also have,

$$I(u+1,v) = -\frac{v+2}{v+1}sI(u,v+1) + I(u,v).$$

Using integration by parts, we obtain

$$I(u,v+1) = \frac{(v+1)}{(u+1)s}I(u+1,v).$$

Thus, we get

$$I(u+1,v) = \frac{(u+1)}{(u+v+3)}I(u,v)$$

and

$$I(u,v+1) = \frac{(v+1)}{s(u+v+3)}I(u,v).$$

Therefore,

$$\gamma_2 = -\frac{1}{s(a+b+1)}\left[a - b - 1 + \frac{a(b-a)}{a+b+2}\right].$$

Now, we have

$$a + b = \frac{4-3\gamma_0}{\gamma_0}, a - b = -1, s = \frac{2-\gamma_0}{2}.$$

Putting these values we get,

$$\gamma_2 = \frac{6\gamma_0}{(2-\gamma_0)^2(4-\gamma_0)}.$$

The Melnikov theory [34] shows that if

$$\gamma = -\frac{2(1-\gamma_0)}{2-\gamma_0}\alpha_0 + \frac{6\gamma_0}{(2-\gamma_0)^2(4-\gamma_0)}\alpha_0^2 + O(\alpha_0^3) \tag{3.8}$$

then the system (3.1) has a heteroclinic cycle and it is stable [14].

Condition (3.8) is equivalent to

$$\beta_0 = \gamma + \alpha_0 + \gamma_0 + \frac{E_0}{E'} = \gamma_0 + \frac{E_0}{E'} + \frac{\gamma_0}{2-\gamma_0}\alpha_0$$
$$+\frac{6\gamma_0}{(2-\gamma_0)^2(4-\gamma_0)}\alpha_0^2 + O(\alpha_0^3). \tag{3.9}$$

We thus state the following lemma.

Lemma 5.3.1. *We assume that* γ_0, $\frac{E_0}{E'}$ *are fixed and* $\gamma_0 < 1$, $\frac{E_0}{E'} < 1$, $\gamma_0 + \frac{E_0}{E'} < 1$. *For small* α_0, *if condition* (3.9) *holds, the system* (3.1) *has a stable heteroclinic cycle connecting saddles at* $(0,0), (\alpha_0, 0)$ *and* $\left(0, \frac{-(\beta_0-\alpha_0-\gamma_0-\frac{E_0}{E'})}{1-\gamma_0}\right)$.

In this case, foloowing Tang and Zhang [17], there exists a stable heteroclinic cycle. The positive coexistence equilibrium $\left(\frac{\alpha_0\gamma_0++\gamma_0-\beta_0+\frac{E_0}{E'}}{\gamma_0}, \frac{\beta_0-\gamma_0-\frac{E_0}{E'}}{\gamma_0}\right)$ lies inside the heteroclinic cycle and it is a spiral source.

Conditions of Lemma 5.3.1 shows that for small α_0,

$$\gamma_0 + \frac{E_0}{E'} < \beta_0 < \alpha_0\gamma_0 + \gamma_0 + \frac{E_0}{E'},\ \gamma_0 < 1. \tag{3.10}$$

The system (2.8) in [13] shows that in this case a limit cycle in the system is always stable and unique once it exists. We therefore conclude that there is no limit cycle inside the heteroclinic cycle, since it is attracting.

Lemma 5.3.1 and the transformation used to convert (2.2) to (2.9) give the following theorem.

Theorem 5.3.1. Assume that γ_0 is fixed and $\gamma_0 < 1$. If for small α_0 condition (3.10) holds, system (2.3) has a stable heteroclinic cycle connecting saddles at $(0,0)$ and $(1,0)$.

4 Simulations and discussion

To illustrate the analytical results, we consider the following fixed parameter values: $\alpha_0 = 0.5, \beta_0 = 0.16, \gamma_0 = 0.1, E' = 0.05$ and $E_0 = 0.001$. This parameter set satisfies conditions of the Theorem 5.3.1 and the system (2.3) exhibit heteroclinic bifurcations (Fig. 1). Here $(0,0)$ is an attractor, $(1,0)$ is a saddle and the interior equilibrium is an unstable focus. There is a heteroclinic loop consisting of the origin $(0,0)$, the saddle equilibrium $(1,0)$, the heteroclinic orbit connecting $(0,0)$ & $(1,0)$ and the seperatrices between $(0,0)$ & $(1,0)$. The solid line denotes the seperatrices. Any trajectory started below the seperatrices (denoted by dash-dot line) converges to $(0,0)$ spirally and any trajectory above the seperatrices (denoted by dotted line) converges to $(0,0)$ monotonically (Fig. 1). If we slightly increase the parameter value of E_0 from 0.001 to 0.0022, keeping other parameter values unaltered, some trajectories (denoted by dotted lines) go to $(0,0)$ and some produces limit cycle (denoted by dash-dot lines), which is unique, depending on the initial values of the system populations (Fig. 2). If we again increase the parameter value of E_0 from 0.0022 to 0.004, keeping other parameter values unaltered, the system exhibits bistability (Fig. 3). In this case, some trajectories (denoted by dotted lines) go to $(0,0)$ and some converge to the interior equilibrium (denoted by dash-dot lines).

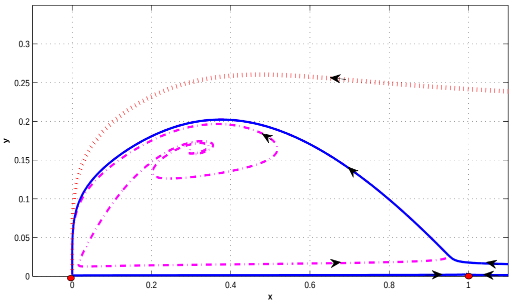

Figure 1: The phase portrait of the system (2.3) for $\alpha_0 = 0.5, \beta_0 = 0.16, \gamma_0 = 0.1, E' = 0.05$ and $E_0 = 0.001$. Here $(0,0)$ is an attractor, $(1,0)$ is a saddle and the interior equilibrium is an unstable focus. The figure shows existence of heteroclinic loop in the system (2.3).

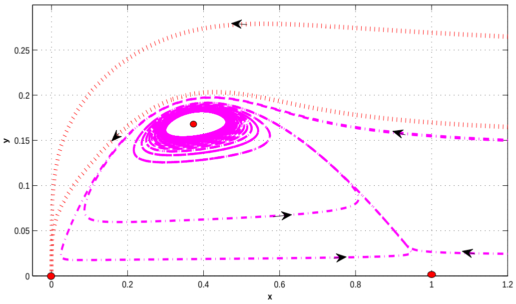

Figure 2: The phase portrait of the system (2.3) for $E_0 = 0.0022$. Other parameters are as in the Fig. 1. Here some trajectories go to $(0,0)$ and some converge to the unique limit cycle surrounding the interior equilibrium.

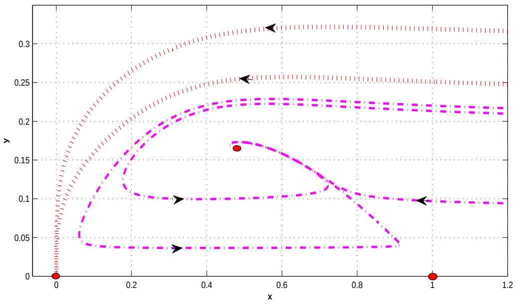

Figure 3: The phase portrait of the system (2.3) for $E_0 = 0.004$. Other parameters are as in the Fig. 1. The system, in this case, exhibits bistability. Here some trajectories go to $(0,0)$ and some converge to the interior equilibrium depending on the initial value.

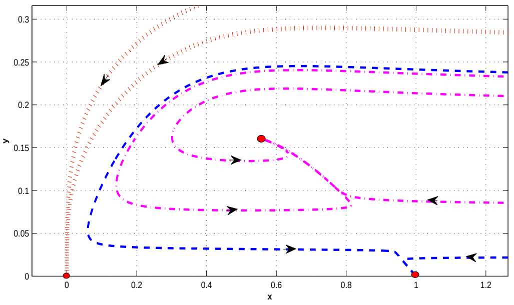

Figure 4: The phase portrait of the system (2.3) for $E_0 = 0.005$. Other parameters are as in the Fig. 1. The system, in this case, exhibits tristability.

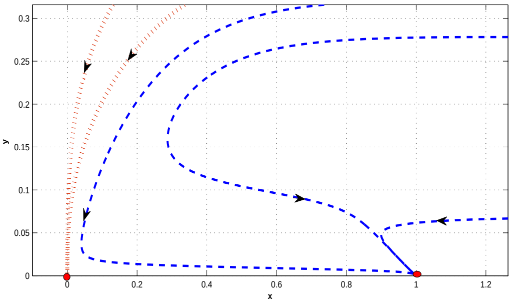

Figure 5: The phase portrait of the system (2.3) for $E_0 = 0.01$. Other parameters are as in the Fig. 1. The system, in this case, exhibits bistability.

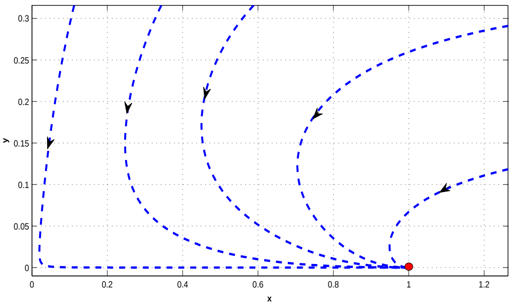

Figure 6: The phase portrait of the system (2.3) for $E_0 = 0.05$. Other parameters are as in the Fig. 1. The system, in this case, exhibits monostability.

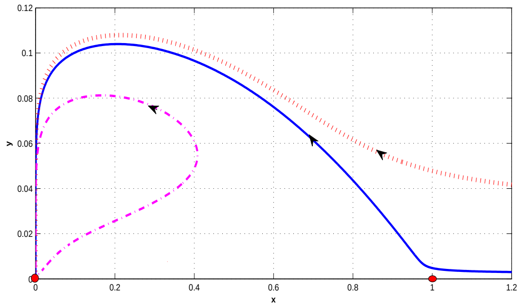

Figure 7: The phase portrait of the system (2.3) for $\alpha = 0.2$. Other parameters are as in the Fig. 1. Here all trajectories, independent of the initial values, go to $(0, 0)$.

If we further increase the parameter value of E_0 from 0.004 to 0.005, the system exhibits tristability (Fig. 4). Here, some trajectories (denoted by dotted lines) converge to $(0, 0)$, some converge to $(1, 0)$ (denoted by dashed lines) and some converge to the interior equilibrium (denoted by dash-dot lines), depending on the initial values of the system populations. If the parameter value of E_0 is increased again from 0.005 to 0.01, keeping other parameter values intact, the system exhibits bistability (Fig. 5).

It is observed that some trajectories (denoted by dotted lines) go to $(0, 0)$ and some converge to $(1, 0)$ (denoted by dashed lines). A further increment in E_0 from 0.01 to 0.05 leads the system to monostability (Fig. 6). All trajectories, in this case, converges to $(1, 0)$ (denoted by dashed lines). If we reduce the value of the parameter α from 0.5 to 0.2, keeping other parameter values as in the Fig. 1, then all trajectories converge to $(0, 0)$ (Fig. 7). It is to be observed that we have obtained different dynamics (see, Fig. 1 to Fig 6) of the system (2.3) only by changing the parameter value of E_0, which is directly related to the harvesting effort (E) of the predator population. Thus, an exploited ratio-dependent predator-prey system, where the predator population is subjected to harvesting with Michaelis-Menten type harvesting rate, may exhibit very rich dynamics including heteroclinic bifurcation and multistabilities.

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