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Stability analysis of a prey–predator model incorporating a prey refuge

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Abstract

We consider a prey–predator model with Holling type II response function incorporating a prey refuge. The purpose of the work is to offer mathematical analysis of the model and to discuss some significant qualitative results that are expected to arise from the interplay of biological forces. Some numerical simulations are carried out.

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1. Introduction

The dynamic relationship between predators and their prey has long been and will continue to be one of the dominant themes in both ecology and mathematical ecology due to its universal existence and importance [1]. These problems may appear to be simple mathematically at first sight, they are, in fact, often very challenging and complicated. Although the predator–prey theory has seen much progress in the last 40 years, many long standing mathematical and ecological problems remain open [1–7].

Differential equation models for interactions between species are one of the classical applications of mathematics to biology. The development and use of analytic techniques and the growth of computer power have progressively improved our understanding of these types of models. In

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this paper we analyze a Lotka–Volterra type predator–prey model with Michaelis–Menten type functional response. In this particular model the population density of the prey is resource limited and each predator’s functional response to the prey approaches a constant as the prey population increases (i.e. a type II response according to Holling [8]). In addition, a spatial refuge protects a constant proportion of prey from predation.

Mite predator–prey interactions often exhibit spatial refugia which afford the prey some degree of protection from predation and reduce the chance of extinction due to predation. Maynard Smith [9] shows that the presence of a constant proportion refuge does not alter the dynamical stability of the neutrally stable Lotka–Volterra model, while a constant number refuge of any size replaces the neutrally stable behaviour with a stable equilibrium. Hassel [10] shows that adding a large refuge to a model, which in the absence of a refuge exhibits divergent oscillations, replaces the oscillatory behaviour with a stable equilibrium. These mathematical models and a number of experiments indicate that refugia have a stabilizing effect on predator–prey interactions, but, as Taylor [11] has mentioned, it would be an over simplification to assume this is always the case.

The model considered is based on the predator–prey system:

$$\begin{aligned}\frac{dx}{dt} &= \alpha x \left(1 - \frac{x}{k}\right) - \frac{\beta y x}{1 + ax}, \\ \frac{dy}{dt} &= -\gamma y + \frac{c\beta y x}{1 + ax},\end{aligned}\tag{1}$$

where x, y denote prey and predator population respectively at any time t , and $\alpha, k, \gamma, \beta, a, c$ are all positive constants. Here α represents the intrinsic growth rate and k the carrying capacity of the prey; γ is the death rate of the predator; β/a is the maximum number of prey that can be eaten by each predator in unit time; $1/a$ is the density of prey necessary to achieve one half that rate; c is the conversion factor denoting the number of newly born predators for each captured prey. The term $(\beta x/(1 + ax))$ denotes the functional response of the predator. This response function is termed as Holling type II response function [8].

This paper extends the above model by incorporating a refuge protecting mx of the prey, where $m \in [0, 1)$ is constant. This leaves $(1 - m)x$ of the prey available to the predator, and modifying system (1) accordingly yields the system:

$$\begin{aligned}\frac{dx}{dt} &= \alpha x \left(1 - \frac{x}{k}\right) - \frac{\beta(1 - m)yx}{1 + a(1 - m)x}, \\ \frac{dy}{dt} &= -\gamma y + \frac{c\beta(1 - m)xy}{1 + a(1 - m)x}.\end{aligned}\tag{2}$$

This paper is organized as follows. Basic results are given in Section 2. In this section we study the existence of equilibria and their dependence on the parameter m . We have concentrated more on the interior equilibrium of the system as we are interested in the co-existence of the species. We also study the stability and instability properties of the equilibria and existence of limit cycles for the system (2). In Section 3, we present a numerical simulation to illustrate the established results. Concluding remarks are presented in Section 4.

2. Basic results

To ensure the existence and uniqueness of system (2), we seek the solution in $R_+^2 = \{x, y : x > 0, y > 0\}$ so that all the standard results of existence, uniqueness and continuous dependence on initial conditions are evidently satisfied.

2.1. Equilibria

We now study the existence of equilibria of system (2). Particularly we are interested in the interior or positive equilibrium. Since refuge parameter m is the system parameter, positive equilibrium exists only for some restricted levels of the parameter.

To begin with we list all possible equilibria

- (i) The trivial equilibrium $P_0(0, 0)$.
- (ii) Equilibrium in the absence of predator ($y = 0$) $P_1(k, 0)$.
- (iii) The interior (positive) equilibrium $P_2(x^*, y^*)$, where

$$x^* = \frac{\gamma}{(c\beta - \gamma a)(1 - m)}, \quad y^* = \frac{\alpha c}{k} \left[\frac{k(c\beta - \gamma a)(1 - m) - \gamma}{\{(c\beta - \gamma a)(1 - m)\}^2} \right].$$

For the equilibrium $P_2(x^*, y^*)$ to be positive we first need

$$c\beta - \gamma a > 0. \tag{3}$$

For y^* to be positive, the constraint on m to be

$$0 \leq m < 1 - \frac{\gamma}{k(c\beta - \gamma a)}. \tag{4}$$

Thus, for the existence of the positive equilibrium both $c\beta > \gamma a$ and

$$0 \leq m < 1 - \frac{\gamma}{k(c\beta - \gamma a)} \text{ must be hold.}$$

We see that x^* increases with m .

2.2. Boundedness of the system

The boundedness of solutions of the system is proved in the following theorem.

Theorem 1. *All the solutions of system (2) which start in R_+^2 are uniformly bounded.*

Proof. We define the function $w = x + (1/c)y$. Therefore, time derivative

$$\frac{dw}{dt} = \frac{dx}{dt} + \frac{1}{c} \frac{dy}{dt} = \alpha x \left(1 - \frac{x}{k} \right) - \frac{\beta(1 - m)xy}{1 + a(1 - m)x} - \frac{\gamma}{c} y + \frac{\beta(1 - m)xy}{1 + a(1 - m)x}.$$

For each $v > 0$, we have

$$\frac{dw}{dt} + vw \leq \frac{k}{4\alpha}(v + \alpha)^2 - \frac{1}{c}(\gamma - v).$$

Now if we choose $v < \gamma$, then righthand side is bounded for all $(x, y) \in R_+^2$. Thus we choose a $\mu > 0$, such that

$$\frac{dw}{dt} + vw < \mu.$$

Applying the theory of differential inequality [12] we obtain

$$0 < w(x, y) < \frac{\mu}{v}(1 - e^{-vt}) + w(x(0), y(0))e^{-vt},$$

which, upon letting $t \rightarrow \infty$, yields $0 < w < (\mu/v)$. So, we have that all the solutions of system (2) that start in R_+^2 are confined to the region B , where $B = \{(x, y) \in R_+^2 : w = \frac{\mu}{v} + \varepsilon, \text{ for any } \varepsilon > 0\}$. \square

2.3. Dynamic behaviour

In this subsection we shall discuss the stability properties of the equilibria P_0 , P_1 and P_2 . The Jacobian of the system about the equilibrium point $P_0(0, 0)$ is given by

$$\begin{pmatrix} \alpha & 0 \\ 0 & -\gamma \end{pmatrix}.$$

Hence the eigenvalues of this system are the roots of the equation $(\alpha - \lambda)(-\lambda - \gamma) = 0$. Therefore, $P_0(0, 0)$ is a saddle point. Jacobian matrix for $P_1(k, 0)$ is given by

$$\begin{pmatrix} -\alpha & \frac{-\beta(1-m)k\alpha}{\alpha + \alpha k a(1-m)} \\ 0 & -\gamma + \frac{c\beta(1-m)\alpha k}{\alpha + \alpha k a(1-m)} \end{pmatrix}.$$

The eigenvalues of the matrix are $-\alpha$ and $-\gamma + \frac{c\beta(1-m)k}{1 + ak(1-m)}$. Hence $P_1(k, 0)$ is locally asymptotically stable when $m > 1 - \frac{\gamma}{k(c\beta - \alpha\gamma)}$ and unstable (saddle) when $m \leq 1 - \frac{\gamma}{k(c\beta - \alpha\gamma)}$. When both $P_0(0, 0)$ and $P_1(k, 0)$ are saddle, according to Theorem 3.1 of [13], system is *persistent*.

It is observed that, when P_2 exists, P_1 is unstable (saddle). Jacobian about P_2 is given by

$$\begin{pmatrix} X & Y \\ Z & 0 \end{pmatrix}, \text{ where}$$

$$X = \alpha - \frac{2\alpha}{k} \frac{\gamma}{(c\beta - \gamma a)(1 - m)} - \frac{\alpha}{kc\beta(1 - m)} [k(c\beta - \gamma a)(1 - m) - \gamma],$$

$$Y = -\frac{\gamma}{c},$$

$$Z = \frac{\alpha}{k\beta(1 - m)} [k(c\beta - \gamma a)(1 - m) - \gamma].$$

The characteristic equation is $\lambda^2 - \lambda X + YZ = 0$. The sum of the roots is equal to X and the product of the roots is equal to YZ , which is always positive (by virtue of condition (4)).

Now X will be negative if

$$m > 1 - \frac{\gamma}{k(c\beta - \gamma a)} - \frac{c\beta}{ka(c\beta - \gamma a)}. \tag{5}$$

From (5) it is clear that if $m > 1 - \frac{\gamma}{k(c\beta - \gamma a)} - \frac{c\beta}{ka(c\beta - \gamma a)}$, then P_2 is locally asymptotically stable. Now if m be such that $m < 1 - \frac{\gamma}{k(c\beta - \gamma a)} - \frac{c\beta}{ka(c\beta - \gamma a)}$, then P_2 is locally unstable in the xy -plane. If $m = 1 - \frac{\gamma}{k(c\beta - \gamma a)} - \frac{c\beta}{ka(c\beta - \gamma a)}$, then system (2) enters into Hopf type small amplitude periodic solutions (limit cycles) near P_2 .

2.4. Existence of limit cycles

In two dimensions it is well known that there can be no limit cycles in models of competitive or cooperative systems. Further, it is known for predator–prey systems that the existence and stability of a limit cycle is related to the existence and stability of a positive equilibrium. We assume that a positive equilibrium exists, for otherwise the predator population tends to extinction [14]. If the equilibrium is asymptotically stable, there may exist limit cycles, the innermost of which must be unstable from the inside and the outermost of which must be stable from the outside. If the limit cycles do not exist in this case, the equilibrium is globally asymptotically stable. If the positive equilibrium exists and is unstable, there must occur at least one limit cycle.

In the present subsection, we shall prove that system (2) has unique stable limit cycle, when P_2 becomes locally unstable.

Let us consider system (2) in the form

$$\begin{aligned} \frac{dx}{dt} &= xg(x) - yp(x), \quad x(0) > 0 \\ \frac{dy}{dt} &= y[-\gamma + q(x)], \quad y(0) > 0 \end{aligned} \tag{6}$$

where $g(x) = \alpha(1 - \frac{x}{k})$, $p(x) = \frac{\beta(1-m)x}{1+a(1-m)x}$, $q(x) = \frac{c\beta(1-m)x}{1+a(1-m)x}$. We have the following theorem regard uniqueness of limit cycles of system (6).

Theorem 2 [2]. *Suppose in system (6)*

$$\frac{d}{dx} \left(\frac{xg'(x) + g(x) - xg(x) \frac{p'(x)}{p(x)}}{-\gamma + q(x)} \right) \leq 0$$

in $0 \leq x < x^$ and $x^* < x \leq k$. Then system (6) has exactly one limit cycle which is globally asymptotically stable with respect to the set $\{(x, y) | x > 0, y > 0\} \setminus \{p_2(x^*, y^*)\}$.*

By employing Theorem 2, we can prove easily the following theorem.

Theorem 3. *If $m \leq 1 - \frac{\gamma}{k(c\beta - \gamma a)} - \frac{c\beta}{ka(c\beta - \gamma a)}$, then system (2) has exactly one limit cycle which is globally asymptotically stable with respect to the set $\{(x, y) | x > 0, y > 0\} \setminus \{p_2(x^*, y^*)\}$.*

Proof. This will be equivalent to proving

$$\frac{d}{dx} \left[\frac{x \left(-\frac{x}{k} \right) + \alpha \left(1 - \frac{x}{k} \right) - \alpha \left(1 - \frac{x}{k} \right) \frac{1}{1+a(1-m)x}}{-\gamma + \frac{c\beta(1-m)x}{1+a(1-m)x}} \right] \leq 0$$

or

$$\frac{d}{dx} \left[\frac{x \left(2x + \frac{1}{a(1-m)} - k \right)}{x - \lambda} \right] \geq 0,$$

where $\lambda = \frac{\gamma}{(1-m)(c\beta - a\gamma)}$. It is equivalent to proving

$$(x - \lambda)^2 + \lambda \left(\frac{k - \frac{1}{a(1-m)}}{2} \right) - \lambda^2 \geq 0$$

or

$$\frac{k - \frac{1}{a(1-m)}}{2} \geq \lambda$$

i.e.

$$m \leq 1 - \frac{\gamma}{k(c\beta - \gamma a)} - \frac{c\beta}{ka(c\beta - \gamma a)}.$$

The equality holds if and only if $m = 1 - \frac{\gamma}{k(c\beta - \gamma a)} - \frac{c\beta}{ka(c\beta - \gamma a)}$. This completes the proof. \square

Combining all these results, we have the following theorem.

Theorem 4. *If $c\beta > a\gamma$, then the constraints on m for the existence and stability of the positive equilibrium point are*

$$1 - \frac{\gamma}{k(c\beta - \gamma a)} - \frac{c\beta}{ka(c\beta - \gamma a)} < m < 1 - \frac{\gamma}{k(c\beta - \gamma a)},$$

and globally stable limit cycle exists when

$$m \leq 1 - \frac{\gamma}{k(c\beta - \gamma a)} - \frac{c\beta}{ka(c\beta - \gamma a)}.$$

Table 1

Nature of equilibria of system (2) when $c\beta > \gamma a$

Parameters	$P_0(0, 0)$	$P_1(k, 0)$	$P_2(x^*, y^*)$	Phase portrait
$m \in [0, A)$	Unstable	Unstable	Unstable, limit cycles exists	Figs. 2 and 3
$m = A$	Unstable	Unstable	Unstable, small amplitude periodic solution occurs	Fig. 4
$m(A, B)$	Unstable	Unstable	Asymptotically stable	Fig. 5
$m = B$	Unstable	Unstable	Does not exist	
$m \in (B, 1)$	Unstable	Stable	Does not exist	Fig. 8

Thus, we find that it is possible to prevent the cycles and drive the state of the considered system to a stable state by choosing the refuge parameter m appropriately (see Table 1.)

$$A = 1 - \frac{\gamma}{k(c\beta - \gamma a)} - \frac{c\beta}{ka(c\beta - \gamma a)}, \quad B = 1 - \frac{\gamma}{k(c\beta - \gamma a)}$$

3. Numerical example

Let $\alpha = 10, k = 100, a = 0.02, \gamma = 0.09, \beta = 0.6, c = 0.02$ in appropriate units. For these values of parameters, we verify the existence and stability properties of the equilibrium for the system.

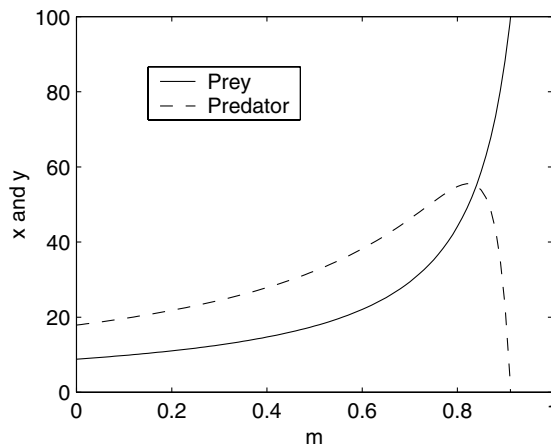


Fig. 1. A bifurcation diagram for system (2) with m as the bifurcation parameter. The vertical axis measured both x^* (solid line) and y^* (broken line).

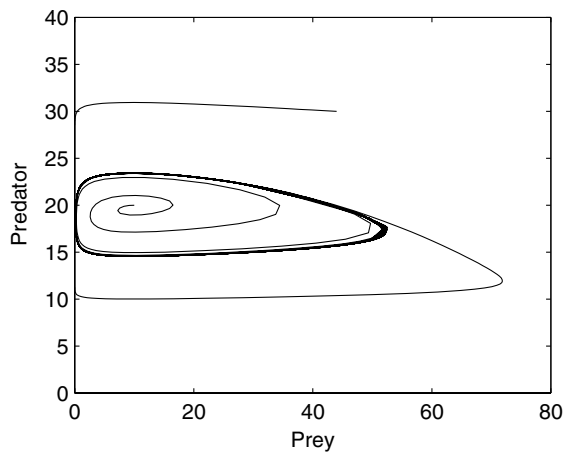


Fig. 2. The phase portrait of system (2) for $m = 0.1$.

Also we construct a limit cycle and verify its global stability. It is found that if $0.32 < m < 0.91$, then the interior equilibrium point exists and stable and if $0 \leq m \leq 0.32$ then it is unstable and hence there should exist a globally stable limit cycle.

Fig. 1 shows the bifurcation behaviour of system (2) with m as the bifurcation parameter.

Let us take $m = 0.1$, then the corresponding interior equilibrium point $(9.8, 19.65)$ is unstable. Phase diagram is shown in Fig. 2. We observe that all solutions of the system initiating in the interior of the positive quadrant of (x, y) plane, except at the equilibrium, approach a unique limit cycle eventually.

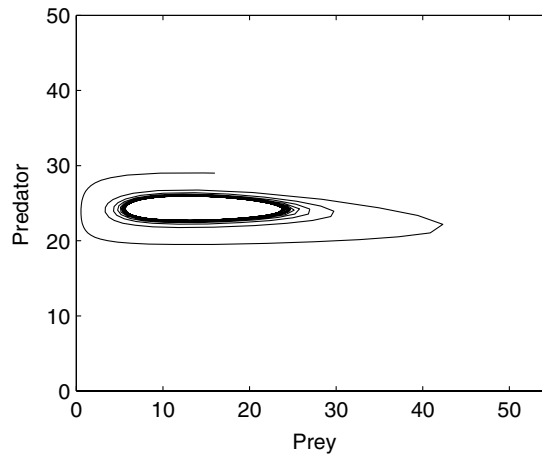


Fig. 3. The phase portrait of system (2) for $m = 0.3$.

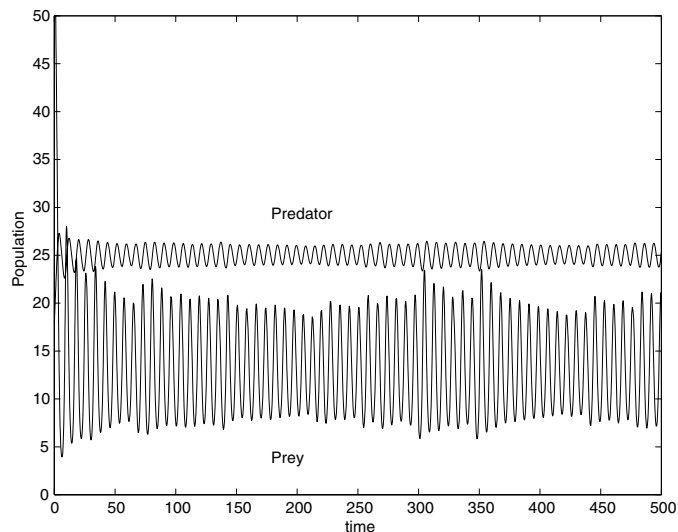


Fig. 4. Solution curves for $m = 0.32$. There is a periodic solution around the equilibrium point $P_2(13.0, 25.09)$.

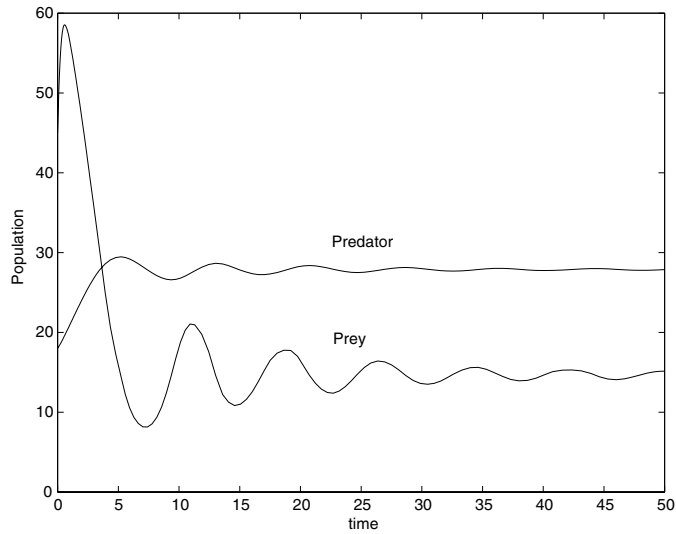


Fig. 5. Solution curves for $m = 0.4$. Both the populations converge to their equilibrium values.

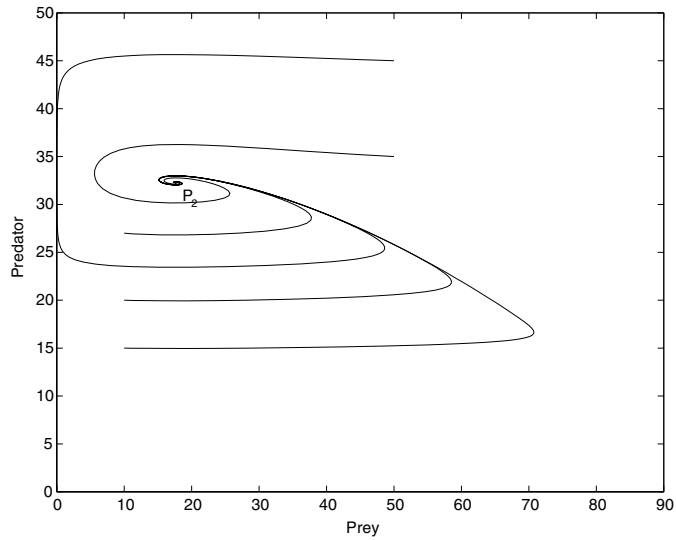


Fig. 6. The phase portrait of system (2) for $m = 0.5$. $P_2(17.65, 32.3)$ is a global attractor.

In Fig. 2 we clearly observe that two distinct solutions of the system, one with initial value in the interior of the limit cycle and the other with initial value in the exterior of the limit cycle, approaching the limit cycle.

Next let $m = 0.3$, then the corresponding interior equilibrium point $(12.6, 24.5)$ is also unstable. The phase portrait is shown in Fig. 3.

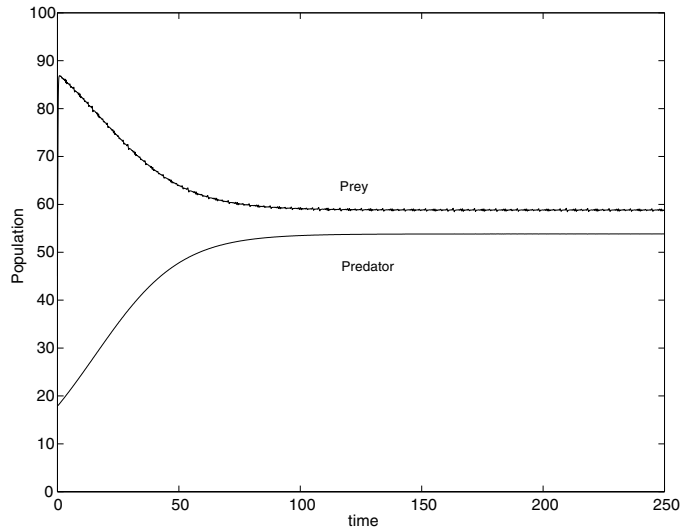


Fig. 7. Solution curves for $m = 0.85$. Both the populations converge to their equilibrium values $(58.82, 53.82)$.

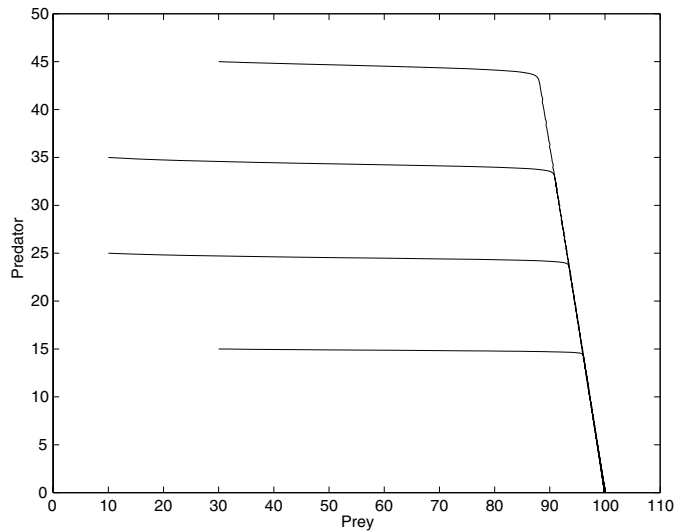


Fig. 8. The phase portrait of system (2) for $m = 0.95$. It is seen that $(100, 0)$ is a global attractor.

The behaviour of system (2) at the bifurcation point $m = 0.32$ is shown in Fig. 4. When m exceeds the bifurcation point, the behaviour of the system is shown in Figs. 5–7. We see that increasing m stabilizes the system through Hopf bifurcation at $m = 0.32$ leads to the periodic branch being replaced by a branch of stable equilibria.

The behaviour of system (2) at $m = 0.95$ is shown in Fig. 8. In this case the system has no interior equilibrium and the boundary equilibrium point $(100, 0)$ is globally asymptotically stable.

4. Concluding remarks

In this paper we have considered a prey–predator system incorporating a prey refuge. We assumed that the predator response function is of Holling type II. Incorporating a refuge into system (1) provides a more realistic model, since many prey mite populations do have some form of refuge available. A refuge can be important for the biological control of a pest, however, increasing the amount of refuge can increase prey densities and lead to population outbreaks. For example, Hoy [15] mentions that “hotspots” of high spider mite densities in almond orchards can trigger orchard-wide outbreaks. These hotspots are areas in which the predator is not successfully controlling the prey and therefore can be considered refugia. We have given conditions for existence and stability of the equilibria and persistent criteria for the system. In this study we have proved that exactly one stable limit cycle occurs in this system when the positive equilibrium is unstable. This proof also enables us to conclude that local asymptotic stability of the positive equilibrium implies its global asymptotic stability. Finally a numerical simulation is taken to verify some of the key results we obtained.

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