Effects of prey refuges on a predator–prey model with a class of functional responses: The role of refuges

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ABSTRACT

In this paper, the effects of refuges used by prey on a predator–prey interaction with a class of functional responses are studied by using the analytical approach. The refuges are considered as two types: a constant proportion of prey and a fixed number of prey using refuges. We will evaluate the effects with regard to the local stability of the interior equilibrium point, the values of the equilibrium density and the long-term dynamics of the interacting populations. The results show that the effects of refuges used by prey increase the equilibrium density of prey population while decrease that of predators. It is also proved that the effects of refuges can stabilize the interior equilibrium point of the considered model, and destabilize it under a very restricted set of conditions which is disagreement with previous results in this field.

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1. Introduction

The study of the consequences of hiding behavior of prey on the dynamics of predator–prey interactions can be recognized as a major issue in applied mathematics and theoretical ecology [1–5]. Some of the empirical and theoretical work have investigated the effect of prey refuges and drawn a conclusion that the refuges used by prey have a stabilizing effect on the considered interactions and prey extinction can be prevented by the addition of refuges [6–18]. In fact, the effects of prey refuges on the population dynamics are very complex in nature, but for modelling purposes, it can be considered as constituted by two components [13]: the first effects, which affect positively the growth of prey and negatively that of predators, comprise the reduction of prey mortality due to decrease in predation success. The second one may be the trade-offs and by-products of the hiding behavior of prey which could be advantageous or detrimental for all the interacting populations [10]. A classic secondary effect is the reduction in the birth rate of prey population, because refuges are safe but rarely offer feeding or mating opportunities.

The traditional ways by which the effects of prey refuges have been incorporated in predator–prey interactions is to consider two types of refuges in the literature: those that protect a constant fraction of prey and those that protect a constant number of prey [11]. This is initially done by modifying the original Lotka–Volterra predator–prey models, and the most wildly reported conclusion is that the interior equilibrium can be stabilized by the addition of refuges for prey and the refuges which protect a constant number of prey have a stronger stabilizing impact on population dynamics than that of protecting a constant proportion of prey [1,3–9,13]. In [8], the effects of hiding behavior of prey on a continuous-time population model were studied. Prey investment in hiding behavior was modeled by a parameter. They showed that adaptive change of the parameter can speed the convergence of trajectories to equilibrium. Ruxton [9] proposed a continuous-time predator–prey model under the assumption that the rate prey move to the refuge is proportional to predator density. The results showed that the hiding behavior of prey has a stabilizing effect. In [12], the influence of refuges used by prey on predator–prey dynamics in a two-patch environment is investigated. One patch represents a refuge for prey while the other is an open habitat. It was shown that optimal antipredator behavior of prey leads to the persistence and reduction of oscillations in population densities. In this light [13–15] derived a predator–prey model with Holling type functional responses.
response incorporating prey refuges and evaluated the effects with regard to the stability of the interior equilibrium. The results showed that the refuges used by prey can increase the stability of the interior equilibrium.

However, as far as we know, no one has found that prey refuges can destabilize or decrease the stability of the predator–prey interactions. In this paper, we propose a generalized predator–prey model incorporating refuges used by prey and will investigate its both stabilizing and destabilizing effect on the dynamics of the considered model. For consistency with the previous work in this field, we consider the predator–prey interactions incorporating refuges by prey as a new ingredient. Likewise, we will consider the effects of having a constant proportion of prey and a constant number of prey using refuges. The main question of this paper is: Do refuges promote the community stability of predator–prey dynamics provided prey population incorporates refuges?

2. The mathematical model

We assume that the densities of prey and predator populations change continuously with time, uniform distribution over space and having no stage structure for neither prey or predators. The model, we will consider belong to a generalized predator–prey model incorporating logistic growth, is represented by the following differential equations:

\[
\begin{align*}
\dot{X}(t) &= rX \left(1 - \frac{X}{K}\right) - p\varphi(X)Y, \\
\dot{Y}(t) &= (q\varphi(X) - d)Y,
\end{align*}
\]

where \(X(t)\) and \(Y(t)\) denote the density of prey and predator populations at any time \(t\) respectively, and \(r, K, p, q, d\) are all positive constants and have its biological meanings accordingly. \(r\) is the intrinsic per capita growth rate of prey population, \(K\) is the environmental carrying capacity of prey population, \(p\) is the maximal per capita consumption rate of predators, \(d\) is the per capita death rate of predators, and \(q\) is the efficiency with which predators convert consumed prey into new predators. The term \(\varphi(X)\) represents the functional response of the predator population and satisfies the following assumption:

\[
\begin{align*}
\varphi(0) &= 0, \quad \varphi'(X) > 0 (X > 0).
\end{align*}
\]

According to Maynard Smith [3], there is a quantity \(X_e\) of prey population which incorporates refuges, then we modified the functional response to incorporate prey refuges in the above model [17], and it becomes as the following form:

\[
\begin{align*}
\dot{X}(t) &= rX \left(1 - \frac{X}{K}\right) - p\varphi(X - X_e)Y, \\
\dot{Y}(t) &= (q\varphi(X - X_e) - d)Y.
\end{align*}
\]

This quantity \(X_e\) is considered from two alternative points of view: (i) \(X_e = \beta X\), the quantity of hiding prey is proportional to the density of prey. (ii) \(X_e = K\), the quantity of hiding prey is a constant number.

3. Positivity and boundedness

The solutions of model (3) represent the densities of the interacting populations and have their own realistically ecological meanings, that is to say they must be positive and bounded. Therefore, we have the following theorem.

\textbf{Theorem 3.1.} All the solutions of model (3) which start in \(R^2_+\) are positive and uniformly bounded.

The proof can be seen in Appendix A.

4. A constant proportion of prey using refuges

When considering \(X_e = \beta X\), the model (3) is given as follows:

\[
\begin{align*}
\dot{X}(t) &= rX \left(1 - \frac{X}{K}\right) - p\varphi(X - \beta X)Y, \\
\dot{Y}(t) &= (q\varphi(X - \beta X) - d)Y.
\end{align*}
\]

The unique coexistent equilibrium point of model (4) is \(E_1(X, Y)\), where

\[
\begin{align*}
X &= \frac{1 - \beta}{1 - p\varphi^{-1}(d/q)} \rho^{-1}(d/q), \\
Y &= \frac{q\varphi}{pd} X \left(1 - \frac{X}{K}\right).
\end{align*}
\]

If \(0 < \beta < 1 - \frac{1}{p}\varphi^{-1}(\frac{d}{q})\), then the above equilibrium point is positive.

According to the assumption (2), we see that an increase in refuge used by prey directed to predators will increase the equilibrium density of prey population \(X\), which is natural as an increase in \(\beta\) decrease the predation risk for prey population. On the other hand, an increase in refuge using by prey can decrease the equilibrium density of predator population \(Y\) due to lack of enough foods. Because we can see from model (4) that predator population dose not have any other food resources except the prey population mentioned here as their foods. So if prey hiding in refuges increases, predators may encounter the lack of food resources, and hence its density must decrease.

Using the following change of variables:

\[
\phi: \quad \{R_+^0\}^2 \rightarrow \{R_+^0\}^2, \quad \phi(X, Y) = \left(\frac{X}{1 - p\varphi^{-1}(d/q)} \rho^{-1}(d/q)\right)
\]

and obtaining another form of model (4)

\[
\begin{align*}
\dot{x}(t) &= rX \left(1 - \frac{X}{1 - (1 - \beta)K}\right) - p\varphi(x)\rho\varphi^{-1}(d/q), \\
\dot{y}(t) &= (q\varphi(x) - d)\rho\varphi^{-1}(d/q).
\end{align*}
\]

We can easily calculate all possible equilibria of model (6) are \(E_0(0, 0), E_1((1 - \beta)K, 0)\) and \(E_2(x*, y*)\), where

\[
\begin{align*}
x* &= \varphi^{-1}(\frac{d}{q}), \\
y* &= \frac{q\varphi}{pd} \left(1 - \frac{x*}{1 - (1 - \beta)K}\right).
\end{align*}
\]

The equilibrium point \(E_2(x*, y*)\) is positive if and only if

\[
0 < \beta < 1 - \frac{1}{K}\varphi^{-1}(\frac{d}{q}).
\]

Next, we will consider the stability properties of the equilibrium points of model (6).

The Jacobian matrix of model (6) at the equilibrium point \(E_0(0, 0)\) is

\[
J_0 = \begin{pmatrix}
-r & 0 \\
0 & -d
\end{pmatrix}.
\]

Hence, \(E_0(0, 0)\) is a saddle point and is unstable.

For the predator-free equilibrium point, the Jacobian matrix is given by

\[
J_1 = \begin{pmatrix}
-r & -p\varphi((1 - \beta)K) \\
0 & q\varphi((1 - \beta)K) - d
\end{pmatrix}.
\]

Thus, \(E_1((1 - \beta)K, 0)\) is locally asymptotically stable if and only if

\[
q\varphi((1 - \beta)K) - d < 0.
\]

That is

\[
\varphi((1 - \beta)K) < \frac{d}{q} = \varphi(x').
\]

By the assumption (2), we have
Theorem 4.1. Assum ing \(d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q)) > 0\), we have

\[
0 < 1 - \frac{1}{K} \varphi^{-1} \left( \frac{d}{q} \right) < \beta < 1, \tag{7}
\]

and hence, the equilibrium point \(E_2(x^*, y^*)\) lies in the forth quadrant.

Again, the Jacobian matrix for the equilibrium point \(E_2(x^*, y^*)\) is as follows:

\[
J_2 = \begin{pmatrix}
a_{11} & a_{12} \\
a_{21} & 0
\end{pmatrix},
\]

where

\[
a_{11} = -\frac{r}{d} \left[ (d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q))) \frac{\varphi^{-1}(d/q)}{1 - \beta K} \right], \quad a_{12} = -\frac{p d}{q} < 0,
\]

\[
a_{21} = \frac{q^2 r}{pd} \varphi'(\varphi^{-1}(d/q)) \frac{\varphi^{-1}(d/q)}{1 - \beta K} > 0. \tag{8}
\]

Clearly, \(\text{Det}J_2 = a_{12}a_{21} > 0\), hence, the sign of the eigenvalues depends only on \(\text{Det}J_2 = a_{11}\).

Therefore, the equilibrium point \(E_2(x^*, y^*)\) is locally asymptotically stable if and only if \(a_{11} < 0\), that is

\[
(d - q x \varphi'(\varphi^{-1}(d/q))) (2d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q))) = \frac{\varphi^{-1}(d/q)}{1 - \beta K} < 0. \tag{9}
\]

Otherwise, the coexistent equilibrium point is asymptotically unstable.

Now, we consider three separate cases.

Case 1. If \(d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q)) > 0\), then \(2d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q)) > 0\).

The positive equilibrium point of model (6) is locally asymptotically stable if and only if

\[
0 < 1 - \frac{\varphi^{-1}(d/q)}{K} \left[ 2d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q)) \right] < \beta < 1 - \frac{\varphi^{-1}(d/q)}{K}. \nonumber
\]

Otherwise, this interior equilibrium point is asymptotically unstable.

Case 2. If \(d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q)) < 0\) and \(2d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q)) > 0\), then the positive equilibrium point is always locally asymptotically stable, because the condition (9) holds in perpetuity.

Case 3. If \(2d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q)) < 0\), then \(d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q)) < 0\).

Hence, the interior equilibrium point is locally asymptotically stable if and only if

\[
0 < \beta < 1 - \frac{\varphi^{-1}(d/q)}{K} \left[ 2d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q)) \right].
\]

Otherwise, it is asymptotically unstable.

Therefore, we obtain the following results:

Theorem 4.2. Assuming \(2d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q)) < 0\), we obtain that

\[
(1) \text{ If } 0 < \beta < 1 - \frac{\varphi^{-1}(d/q)}{K} \left[ 2d - q \varphi^{-1}(d/q) \varphi'(\varphi^{-1}(d/q)) \right], \text{ then the prey and predator populations oscillate around the unique positive equilibrium point.}
\]

\[
(2) \text{ If } 1 - \frac{\varphi^{-1}(d/q)}{K} < \beta < 1 - \frac{\varphi^{-1}(d/q)}{K}, \text{ then the two interacting populations tend to reach a locally asymptotically stable equilibrium point at the first quadrant.}
\]

\[
(3) \text{ If } 1 - \frac{\varphi^{-1}(d/q)}{K} < \beta < 1, \text{ then predators go extinct while prey population reaches its maximum environmental carrying capacity.}
\]

5. A constant number of prey using refuges

When a fixed quantity of prey \(X_e\) using refuges, the model (3) becomes as the following form:

\[
\dot{X}(t) = rX \left( 1 - \frac{X}{K} \right) - p \varphi(x - R)Y, \tag{10}
\]

\[
\dot{Y}(t) = (q \varphi(x - R) - d)Y.
\]

The unique coexistent equilibrium point of model (10) is \(Q_2(\tilde{X}, \tilde{Y})\), where

\[
\tilde{X} = \varphi^{-1} \left( \frac{d}{q} \right) + R, \quad \tilde{Y} = \frac{q r}{d} \frac{\tilde{X}}{1 - \frac{\tilde{X}}{K}}.
\]

If \(0 < R < K - \varphi^{-1} \left( \frac{d}{q} \right)\), then the above equilibrium point is positive.

Clearly, the equilibrium density of prey population increases with the constant number of prey feeding in refuges and that of predators firstly increases, then decreases as the fixed number of prey hiding in refuges increases further.

Again, using the following change of variables:

\[
\phi : (R_0)^2 \rightarrow (R_0)^2, \quad \phi(X, Y) = (x + R, y), \tag{11}
\]

and obtaining the following model:

\[
\dot{x}(t) = r(x + R) \left( 1 - \frac{X + R}{K} \right) - p \varphi(x - y), \tag{12}
\]

\[
\dot{y}(t) = (q \varphi(x) - d)y.
\]

The equilibrium points of the above model are \(P_0(0, 0), P_1(K - R, 0)\) and \(P_2(x, y)\), where

\[
\tilde{x} = \varphi^{-1} \left( \frac{d}{q} \right), \quad \tilde{y} = \frac{q r}{d} \left( 1 - \frac{x + R}{K} \right).
\]

The equilibrium point \(P_2(x, y)\) is positive if and only if

\[
0 < R < K - \varphi^{-1} \left( \frac{d}{q} \right).
\]

Now, we propose the main result about the stability of the equilibrium points of model (12).

Theorem 5.1. Assuming that \(d > 0, p > 0\), we obtain that

\[
(1) \text{ If } 0 < R < \frac{2d + q \varphi - \varphi^{-1}(d/q) - \sqrt{d^2 + 2q^2 \varphi^{-1}(d/q)^2}}{2q r \varphi^{-1}(d/q)} - \varphi^{-1}(d/q), \text{ then the prey and predator populations oscillate around the unique interior equilibrium point.}
\]

\[
(2) \text{ If } (2d + K \varphi^2 ) \left( \varphi^{-1}(d/q) - \sqrt{d^2 + 2q^2 \varphi^{-1}(d/q)^2} \right) < 0, \text{ then the two populations tend to reach a locally asymptotically stable equilibrium point in the first quadrant.}
\]

\[
(3) \text{ If } K - \varphi^{-1}(d/q) < R < \frac{K - \varphi^{-1}(d/q)}{2}, \text{ then predators go extinct while prey population reaches its maximum environmental carrying capacity.}
\]

The proof can be seen in Appendix B.
6. Applications

In this section, we will give some examples to show the robustness of our results.

The parameters of the following three models (Examples 6.1–6.3) are positive and have the same ecological meanings with those of model (3).

Example 6.1. Considering the following predator–prey model with Rosenzweig functional response incorporating refuges using by prey:

\[
\begin{align*}
    \dot{X}(t) &= rX \left(1 - \frac{X}{K}\right) - pX \frac{Y}{C_0} Y, \\
    \dot{Y}(t) &= (q - b)Y - dY,
\end{align*}
\]

in which \(0 < a < 1\).

Case 6.1.1 (A constant proportion of prey using refuges). If a constant proportion of prey apply refuges, then the model (13) becomes as the following form:

\[
\begin{align*}
    \dot{X}(t) &= rX \left(1 - \frac{X}{K}\right) - p(1 - b)X^a Y, \\
    \dot{Y}(t) &= (q - b)Y - dY.
\end{align*}
\]

Using the change (5), the above model becomes

\[
\begin{align*}
    \dot{x}(t) &= rX \left(1 - \frac{x}{(1 - \beta)K}\right) - px^a y, \\
    \dot{y}(t) &= (q) - d) y.
\end{align*}
\]

Remark 6.1.1. According to Theorem 4.1, we have the following conclusion:

(1) If \(0 < \beta < 1 - \frac{1 - \beta}{k} \left(\frac{a}{b}\right) \frac{1}{2} \), then the prey and predator populations oscillate around the unique equilibrium point in the first quadrant.

(2) If \(1 - \frac{1 - \beta}{k} \left(\frac{a}{b}\right) \frac{1}{2} < \beta < 1 - \frac{1 - \beta}{k} \left(\frac{a}{b}\right) \frac{1}{2} \), then the two interacting populations tend to reach the locally asymptotically stable equilibrium point at the first quadrant.

(3) If \(1 - \frac{1 - \beta}{k} \left(\frac{a}{b}\right) \frac{1}{2} < \beta < 1\), then the prey population tends to reach its environmental carrying capacity and predators will be depleted.

Case 6.1.2 (A constant number of prey using refuges). When considering a constant number of prey use refuges, then the model (13) becomes

\[
\begin{align*}
    \dot{X}(t) &= rX \left(1 - \frac{X}{K}\right) - p(X - R)^a Y, \\
    \dot{Y}(t) &= (qX - R)^a - dY.
\end{align*}
\]

Using the change (12), we obtain another form of the above model

\[
\begin{align*}
    \dot{x}(t) &= r(x + R) \left(1 - \frac{x + R}{K}\right) - px^a y, \\
    \dot{y}(t) &= (q) - d) y.
\end{align*}
\]

Remark 6.1.2. By Theorem 5.1, we obtain the following result:

(1) If \(0 < R < \frac{2d}{d(a+b)} \frac{q}{k}\) \(\frac{1}{2} \left(\frac{a}{b}\right) \frac{1}{2} \), then the prey and predator populations oscillate around the unique equilibrium point in the first quadrant.

(2) If \(\frac{2d}{d(a+b)} \frac{q}{k}\) \(\frac{1}{2} \left(\frac{a}{b}\right) \frac{1}{2} < R < K - \frac{1}{2} \left(\frac{a}{b}\right) \frac{1}{2} \), then the two interacting populations tend to reach the locally asymptotically stable equilibrium point at the first quadrant.

(3) If \(K - \frac{1}{2} \left(\frac{a}{b}\right) \frac{1}{2} < R < \frac{1}{2} \), the predators go extinct while prey population reaches its environmental carrying capacity.

Example 6.2. Considering the following predator–prey interaction with Ivlev functional response incorporating prey refuges:

\[
\begin{align*}
    \dot{X}(t) &= rX \left(1 - \frac{X}{K}\right) - p(1 - e^{-(X - X_0)}) Y, \\
    \dot{Y}(t) &= (q(1 - e^{-(X - X_0)}) - d) Y.
\end{align*}
\]

Case 6.2.1 (A constant proportion of prey using refuges). As considering a constant proportion of prey use refuges, the model (18) becomes

\[
\begin{align*}
    \dot{X}(t) &= rX \left(1 - \frac{X}{K}\right) - p(1 - e^{-(X - X_0)}) Y, \\
    \dot{Y}(t) &= (q(1 - e^{-(X - X_0)}) - d) Y.
\end{align*}
\]

The above model is topologically equivalent to the following model:

\[
\begin{align*}
    \dot{x}(t) &= rX \left(1 - \frac{x}{(1 - \beta)K}\right) - p(1 - e^{-x}) Y, \\
    \dot{y}(t) &= (q(1 - e^{-x}) - d) Y.
\end{align*}
\]

According to Theorem 4.1, we obtain the following conclusion:

Remark 6.2.1. Assuming that \(d + (q - d) \ln \frac{a \sqrt{d}}{b} > 0\), we have

(1) If \(0 < \beta < 1 + \frac{1}{a} \ln a \frac{d}{b} \frac{q}{k} \left(\frac{a}{b}\right) \frac{1}{2} \frac{1}{2} \), then the prey and predators oscillate around the unique positive equilibrium point.

(2) If \(1 + \frac{1}{a} \ln a \frac{d}{b} \frac{q}{k} \left(\frac{a}{b}\right) \frac{1}{2} \frac{1}{2} < \beta < 1 + \frac{1}{a} \ln a \frac{d}{b} \frac{q}{k} \left(\frac{a}{b}\right) \frac{1}{2} \frac{1}{2} \), then the two populations tend to reach a locally asymptotically stable equilibrium point at the first quadrant.

(3) If \(1 + \frac{1}{a} \ln a \frac{d}{b} \frac{q}{k} \left(\frac{a}{b}\right) \frac{1}{2} \frac{1}{2} < \beta < 1\), then the predators go extinct while prey population reaches its environmental carrying capacity.

Case 6.2.2 (A constant number of prey using refuges). If a fixed number of prey apply refuges, then the model (18) becomes as follows:

\[
\begin{align*}
    \dot{X}(t) &= rX \left(1 - \frac{X}{K}\right) - p(1 - e^{-(X - R)}) Y, \\
    \dot{Y}(t) &= (q(1 - e^{-(X - R)}) - d) Y.
\end{align*}
\]

Using the change (12), we obtain another form of the above model

\[
\begin{align*}
    \dot{x}(t) &= r(x + R) \left(1 - \frac{x + R}{K}\right) - px^a y, \\
    \dot{y}(t) &= (q(1 - e^{-x-R}) - d) Y.
\end{align*}
\]

Remark 6.2.2. By Theorem 5.1, we obtain the following result for \(q > d\):

(1) If \(0 < R < \frac{2d}{d(a+b)} \frac{q}{k} \left(\frac{a}{b}\right) \frac{1}{2} \), then the prey and predator populations oscillate around the unique equilibrium point in the first quadrant.

(2) If \(\frac{2d}{d(a+b)} \frac{q}{k} \left(\frac{a}{b}\right) \frac{1}{2} \frac{1}{2} < R < K + \frac{1}{a} \ln a \frac{d}{b} \frac{q}{k} \left(\frac{a}{b}\right) \frac{1}{2} \frac{1}{2} \), then the two interacting populations tend to reach the locally asymptotically stable equilibrium point at the first quadrant.

(3) If \(K + \frac{1}{a} \ln a \frac{d}{b} \frac{q}{k} \left(\frac{a}{b}\right) \frac{1}{2} \frac{1}{2} < R < \frac{1}{2} \), the prey population tends to reach its environmental carrying capacity and predators will be depleted.
Example 6.3. Considering the following predator–prey model with Holling type functional response incorporating refuges using by prey:

\[ \dot{X}(t) = rX \left( 1 - \frac{X}{K} \right) - \frac{p(X - X_0)}{a + (X - X_0)} Y, \]
\[ \dot{Y}(t) = \left( \frac{q(X - X_0)}{a + (X - X_0)} - d \right) Y. \]  
(23)

Case 6.3.1 (A constant proportion of prey using refuges). If a constant proportion of prey apply refuges, then the model (23) becomes

\[ \dot{X}(t) = rX \left( 1 - \frac{X}{K} \right) - \frac{(p - 1)(1 - \beta)Y}{a + (X - X_0)} Y, \]
\[ \dot{Y}(t) = \left( \frac{(p - 1)(1 - \beta)X}{a + (1 - \beta)X} - d \right) Y. \]  
(24)

Using the change (5), we obtain equivalent form of the above model

\[ \dot{x}(t) = rx \left( 1 - \frac{x}{(1 - \beta)K} \right) - \frac{pxy}{a + x}, \]
\[ \dot{y}(t) = \left( \frac{qy}{a + x} - d \right) y. \]  
(25)

According to Theorem 4.1, we have the following conclusion:

Remark 6.3.1.1. Let \( q - \gamma(q - d) > 0 \), we obtain that

(1) If \( 0 < \beta < 1 - \frac{1}{\beta} \left[ \frac{q^2}{a^2} - \frac{d^2}{q} \right] \left( \frac{a}{q} \right)^{1/\gamma} \), then the prey and predators oscillate around the unique positive equilibrium point at the first quadrant.

(2) If \( 1 - \frac{1}{\beta} \left[ \frac{q^2}{a^2} - \frac{d^2}{q} \right] \left( \frac{a}{q} \right)^{1/\gamma} < 1 - \frac{1}{\beta} \left( \frac{a}{q} \right)^{1/\gamma} \), then the two populations tend to reach a locally asymptotically stable equilibrium point in the first quadrant.

(3) If \( 1 - \frac{1}{\beta} \left( \frac{a}{q} \right)^{1/\gamma} < \beta < 1 \), then the predators go extinct while prey population reaches its environmental carrying capacity.

By Theorem 4.2, we obtain the following result:

Remark 6.3.1.2. Assuming that \( 2q - \gamma(q - d) < 0 \), we have

(1) If \( 0 < \beta < 1 - \frac{1}{\beta} \left[ \frac{q^2}{a^2} - \frac{d^2}{q} \right] \left( \frac{a}{q} \right)^{1/\gamma} \), then the two populations tend to reach a locally asymptotically stable equilibrium point in the first quadrant.

(2) If \( 1 - \frac{1}{\beta} \left[ \frac{q^2}{a^2} - \frac{d^2}{q} \right] \left( \frac{a}{q} \right)^{1/\gamma} < 1 - \frac{1}{\beta} \left( \frac{a}{q} \right)^{1/\gamma} \), then the prey and predators oscillate around the unique positive equilibrium point.

(3) If \( 1 - \frac{1}{\beta} \left( \frac{a}{q} \right)^{1/\gamma} < \beta < 1 \), then the prey population tends to reach its environmental carrying capacity and predators will be depleted.

Case 6.3.2 (A constant number of prey using refuges). When considering a constant number of prey use refuges, the model (23) becomes as follows:

\[ \dot{X}(t) = rX \left( 1 - \frac{X}{K} \right) - \frac{p(X - R)^3}{a + (X - R)} Y, \]
\[ \dot{Y}(t) = \left( \frac{q(X - R)^3}{a + (X - R)} - d \right) Y. \]  
(26)

Using the change (12), we obtain another form of the above model

\[ \dot{x}(t) = r(x + R) \left( 1 - \frac{(x + R)}{K} \right) - \frac{pxy}{a + x}, \]
\[ \dot{y}(t) = \left( \frac{qy}{a + x} - d \right) y. \]  
(27)

Remark 6.3.2. According to Theorem 5.1, we obtain the following result for \( q > d \):

(1) If \( 0 < R < \frac{(2q - \gamma(q - d))}{(2q - \gamma(q - d))} \), then the prey and predator populations oscillate around the unique equilibrium point in the first quadrant.

(2) If \( \frac{(2q - \gamma(q - d))}{(2q - \gamma(q - d))} < R < K - \left( \frac{a}{q} \right)^{1/\gamma} \), then the two interacting populations tend to reach the locally asymptotically stable equilibrium point at the first quadrant.

(3) If \( K - \left( \frac{a}{q} \right)^{1/\gamma} < R < \frac{a}{q} \), then the predators go extinct while prey population reaches its environmental carrying capacity.

Example 6.4. González-Olivos and Ramos-Jiliberto [13] have considered the following predator–prey system with Holling II functional response incorporating prey refuges:

\[ \dot{x}(t) = rX \left( 1 - \frac{x}{K} \right) - \frac{q(x - X_0)y}{a + x}, \]
\[ \dot{y}(t) = b \left( \frac{q(x - X_0)}{a + x - c} \right) y. \]  
(28)

They have investigated the two types of refuges using by prey \( (x_0 = \beta x, x_0 = \gamma) \) and obtained that the effect of prey refuges can increase the equilibrium density of prey while decrease that of predators and stabilize the interior equilibrium in the first quadrant which agrees strongly with our results.

7. Discussion

In this paper, a model describing the predator–prey interaction with a class of functional responses is proposed and the effects of refuges using by prey, as a constant proportion and a fixed number of prey, on the dynamics of the considered model and the value of the equilibrium density are investigated. Our analysis on the proposed model as a function of the values of the controlled parameter reveals that:

(I) The equilibrium density of prey population increases as refuges used by prey increases, while that of predators firstly increases and then decreases with prey refuges. In fact, it is easy to show that there is an increase in the equilibrium density of both prey and predators as the refuges increase under a very restricted set of conditions. This occurs when the equilibrium density of prey population is less than \( \frac{a}{q} \) for either a constant proportion or a fixed number of prey using refuges. Almost all work have shown that the equilibrium density of prey increases with prey refuges and its effect on that of predators is reverse when the number of prey hiding in refuges is large enough [7,13–15].

(II) Our results show that the effects of prey refuges plays an important role in determining the stability of the interior equilibrium point of the considered model. On the one hand, under a very restricted condition, the refuges used by prey have a stabilizing effect, that is, increases the local stability of the interior equilibrium which is in agreement with most previous results on simple models [1–5,7–15]. Here, stabilization or increase of stability refers to cases where a interior equilibrium point changes from repeller to an attractor due to changes in the value of a control parameter [13]. On the other hand, the refuges have a destabilizing impact on the stability of the positive equilibrium point when the certain
assumption is holden. In this paper, destabilization or decrease of stability is with regard to cases where a positive equilibrium point changes from locally stable state to an unstable state due to changes in the value of the controlled parameter. Most importantly, this destabilizing effect have not found by using the theoretical and analytical approach in previous work.


If a constant proportion of prey using refuges, the stability of the interior equilibrium is enhanced with the fraction of prey feeding in refuges when the death rate of predator population is larger than the threshold $d'$ which is defined as $q\varphi^{-1}(d/q)\varphi((\varphi^{-1}(d/q)))$. Our results referring to increase in the equilibrium density of prey population and decrease in that of predators agree with González-Olivars and Ramos-Jiliberto [13] who applied a simple model incorporating a constant proportion and number of prey using refuges. Our conclusions also agree with those of Kar [14] and Huang et al. [15], because they found a stabilizing effect on their considered system. However, if the death rate of predators is smaller than half of the threshold $d'$, the results predict an clearly destabilizing effect on dynamics of the considered interaction which strongly disagree with the previous conclusions (see in [7–15]). When the proportion of prey using refuges increases further, the results show that the considered model stabilizes at the predator-free equilibrium, that is prey reaches its environmental carrying capacity of prey and predators go extinct.

On the other hand, with a constant number of preys in refuges, we also find a clear stabilizing effect or an increase in stability of the interior equilibrium point of the considered model. A stable equilibrium point can never transform into unstable state by the increase of the fixed number of prey using refuges which is in close agreement with earlier results [see in [3,6,7,13]]. If the number of prey feeding in refuges is higher than the threshold value $K - \varphi^{-1}(d/q)$ and smaller than half of its carrying capacity, the model predicts predators will be depleted while prey population reaches its environmental carrying capacity. By comparing the conclusions obtained from analyzing stability properties of two types of refuges using by prey, we can obtain that the refuges which protect a constant number of prey have a stronger stabilizing effect on population dynamics than the refuges which protect a constant proportion of prey, which is agreement with previous work [12,13].

Appendix A. Proof of Theorem 3.1

The positively of the solutions of model (3) can be easily obtained according to their ecological meanings.

Next, we will only show the boundedness.

Defining the function $W(t) = X(t) + \frac{p}{q}Y(t)$. Hence, we have

$$W = rX \left( 1 - \frac{X}{K} \right) - p\varphi(X)Y + p\varphi(X)Y - \frac{dp}{q}Y = rX \left( 1 - \frac{X}{K} \right) - \frac{dp}{q}Y.$$

Now, for each $V > 0$, we get

$$W + VW \leq \frac{K}{4r}(V + r)^2 - \frac{p}{q}(d - V).$$

Let us choose $V > d$, then the right hand is positive.

Thus, the right-hand side is bounded for all $(X, Y) \in \mathbb{R}_+^2$. Hence, we choose a $\mu > 0$ such that $W + VW < U$.

Applying the theory of differential inequality, we obtain that

$$0 < W(X, Y) < \frac{U}{V} (1 - e^{-V}) + W(X(0), Y(0))e^{-V} - \frac{U}{V}, \quad t \to +\infty.$$

Therefore, all the solutions of model (3) starting in $\mathbb{R}_+^2$ are confined to the region $D$, where

$$D = \left\{ (X, Y) \in \mathbb{R}_+^2 \mid W = \frac{U}{V} + V, \quad t > 0 \right\}. \quad \Box$$

Appendix B. Proof of Theorem 5.1

The Jacobian matrix of model (12) at the equilibrium point $P_0(0,0)$ is

$$J_0 = \begin{pmatrix} r(1 - \frac{q}{d}) & 0 \\ 0 & -d \end{pmatrix}.$$ 

Hence, $P_0(0,0)$ is a saddle point and is unstable if $R < \frac{1}{2}$. For the predator-free equilibrium point, the Jacobian matrix is given by

$$J_1 = \begin{pmatrix} -r & -p\varphi(K - R) \\ 0 & q\varphi(K - R) - d \end{pmatrix}.$$ 

Thus, $P_1(K - R, 0)$ is locally asymptotically stable if and only if $q\varphi(K - R) - d < 0$. That is

$$\varphi(K - R) < \frac{d}{q} = \varphi(x).$$

By the assumption (2), we have

$$R > K - \varphi^{-1}(d/q).$$

and hence, the equilibrium point $P_2(x, y)$ lies in the forth quadrant. Again, the Jacobian matrix for the equilibrium point $P_2(x, y)$ is as follows:

$$J_2 = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & 0 \end{pmatrix},$$

where

$$a_{11} = \frac{r}{kd} \left[ q\varphi^{-1}(d/q) \left( \varphi^{-1}(d/q) + R \right)^2 \right.$$

$$\left. - (2d + Kq\varphi^{-1}(d/q)) \left( \varphi^{-1}(d/q) + R \right) + Kd \right],$$

$$a_{12} = -p\varphi^{-1}(d/q) < 0,$$

$$a_{21} = q\varphi^{-1}(d/q) \varphi^{-1}(d/q) + R \left[ 1 - \varphi^{-1}(d/q) + \frac{R}{K} \right] > 0.$$ 

Clearly, $\text{Det}J_2 = a_{11}a_{21} > 0$. Hence, the sign of the eigenvalues depends only on $trJ_2 = a_{11}$.

Therefore, the positive equilibrium point $P_2(x, y)$ is locally asymptotically stable if and only if $a_{11} < 0$, that is

$$\left( 2d + Kq\varphi^{-1}(d/q) \right) - \sqrt{4d^2 + K^2q^2(\varphi^{-1}(d/q))^2} < -\varphi^{-1}(d/q) < R < K - \varphi^{-1}(d/q).$$

Otherwise, the unique interior equilibrium point is locally asymptotically unstable. \(\Box\)

References
