# Effect of prey refuge on the dynamics and equilibrium density of

a predator-prey system

Zhi-hui Ma<sup>1</sup> Zi-zhen Li<sup>1,2\*</sup> Shu-fan Wang<sup>2</sup>

1. Key Laboratory of Arid and Grassland Agroecology of Ministry of Education , Lanzhou, 730000, China

2. School of Mathematics and Statistics, Lanzhou University, Lanzhou, 730000, China

Abstract: In this paper, we use an analytical approach to study the dynamics of the simplest forms of refuge using by prey. Here we incorporate prey refuge in a widely known continuous model—the Lotka-Volterra model. We will evaluate the effect of prey refuge with regard to the local stability of equilibrium points in the first quadrant and equilibrium density values. The results show that the effect of prey refuge can enhance the stability of equilibrium points and equilibrium density of prey and predator populations.

Keywords: Predator-prey models; Stability; Limit cycles; Prey refuge

## 5 1 Introduction

Interspecies interactions are the primary subject of ecology, in which predation is one of the most inportant factors influencing the consequences of natural selection[1]. Research on predation system is always the popular issue in contemporary theoretical ecology[2]. Results based on simple, non-spatial systems show that increasing the productivity or carrying capacity of

<sup>\*</sup>Corresponding author. Tel: +86-931-8913370; Fax: +86-931-8912823.

E\_mail address: ZizhenLee@lzu.edu.cn(Z. Li); wishufedom@163.com(Z. Ma)

conditions in their refuges[17].

prey result in the so called "paradox of enrichment", forcing the equilibrium density of prey and 10 predator to move from a stable state to limit cycles which characterize as periodic oscillations in population densities [2,3,4]. However, dynamics of the natural predation systems are always not consistent with the predictions of such theoretical models [5,6]. There are several reasons for this discrepancy, such as the rescue effect of the prey[7], the presence of predator interferences[8,9], and the effect of predator pursuit(PE) and prey evasion(PE)[2]. Besides the above factors, prey 15 refuge is recognized as playing an important role in determining the dynamics of predator-prey models. This was initially done by modifying the originally simple predator-prey models and the most widely reported conclusions were the community equilibrium being stabilized and the equilibrium density of prey and/or predator was enhanced by the addition of prey refuges [10-16]. The effect of prey refuge on population growth is complex in nature, but for modeling and 20 mathematical analysising, it can be considered as constituted by two components: the first one is a primary effect. Secondary effects could conclude trade-offs and by-products of the prey refuging that could be either advantageous or disadvantageous, even detrimental for the involved populations [15]. The primary effect comprises the reduction of death rate of prey population due to decreasing in predation success. Thus, the first effect impacts positively on the population 25 growth of prey and negatively on that of predators. One of the classic secondary effects is the reduction in the birth rate of prey population due to the sub-optimal states of resources and

As a comparatively larger extent, the effect of prey refuge has been incorporated as a new <sup>30</sup> ingredient of simple predator-prey models and it's major influencing on the community stability and the equilibrium density have been studied many ecologists[12,14-16,17-19]. In [15], which incorporated the effect of prey refuge in the well-known Rosenzweig-MacArthur model and obtained that there is a trend from limit cycles through non-zero stable point up to predator extinction and prey stabilizing at it's carrying capacity as hidden prey increasing in proportion or

<sup>35</sup> number. In [16], which obtained that the non-zero equilibrium point could change from unstable state surrounded by a stable limit cycle to globally asymptotically stable state as increasing in the refuge using by prey, they also found a clear stabilizing effect on the community equilibrium. In [18], which used a model with a constant proportion of prey using refuge(founded on complex assumptions) and found a clear stabilizing effect and an increase of the equilibrium density of

40 prey.

The model we will use here to incorporate the primary effect of prey refuge is a natural extension of the Lotka-Volterra model with prey self-limitation and Holling ||| functional response. There is a huge variety of predator-prey models presenting in the ecological literature, one of those best known and understood in the mathematical and biological terms is likely to be the Lotka-Volterra model. For consistence with the previous works on this researching filed, we will consider refuge as an environmental place where predation rate is lower than any other places. Here the ways in which the effect of refuge using by prey has been incorporated in the predator-prey model is to consider either a constant proportion or a constant number of prey population being protected from predation.

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This paper is organized as follows. In the next section, we formulate the basic model. the main results are given in the third section. In the fourth section, we discuss the main results presented in the third section. the proof of the theorem can be seen in the appendix.

## 2 The basic model

In this paper, we assume that populations change continuously with time, uniformly distribute over space and have neither sex structure or stage structure. Therefore, we will consider the following Lotka-Volterra type predator-prey model with prey self-limitation and Holling type ||| functional response, where the population growth of prey is logistic in the absence of predation

and the functional response is hyperbolic:

$$\dot{x}(t) = rx(1 - \frac{x}{K}) - \frac{\alpha x^2 y}{\beta^2 + x^2}$$

$$\dot{y}(t) = b(\frac{p\alpha x^2}{\beta^2 + x^2} - c)y$$
(1)

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Here, x(t) and y(t) are the density of prev and predator populations at time t, respectively. The other parameters have the following biological meanings: r is the intrinsic per capita growth rate of prev population: K is the prev environmental carrying capacity; c is the per capita death rate of predators; p is the conversion rate denoting the number of newly born predators for each captured prey. the function  $\frac{\alpha x^2}{\beta^2 + x^2}$  is a saturating functional response of the kind of Holling type ||| and represents the amount of prey killed per unit time by an individual predator, where  $\alpha, \beta$  are all positive. Noting that predators do not exhibit self-interference since  $\frac{\partial f}{\partial u} = 0$ , but 60 when predators apply the ratio-dependent functional response, they will exhibit the negative self-interference. As a bioeconomic model, b is the stiffness parameter that measures the speed with which the effort reacts in the perceived cent flow [14,20,21]. Here the predator reproductivity rate responds only to the rate of prey killed by predators, thus obeying the principle of biomass conversion. 65

This paper extends the above model by incorporating the effect of prey refuge. According to Maynard Simth[12], there exists a quantity  $x_r$  of prey population that occupies a refuge. This quantity is considered from two alternative points of views [22]: (1) the quantity of hidden prey is proportional to the size of prey population, i.e.  $x_r = \gamma x$ . (2) the quantity of refuged prey is a constant, i.e.  $x_r = R$ . The quantity of hidden prey depends on the capacity of places found in the habitat. According to Collings [18], we have the following model incorporating the effect of prey refuge:

$$\dot{x}(t) = rx(1 - \frac{x}{K}) - \frac{\alpha(x - x_r)^2 y}{\beta^2 + (x - x_r)^2}$$
  
$$\dot{y}(t) = b(\frac{p\alpha(x - x_r)^2}{\beta^2 + (x - x_r)^2} - c)y$$
(2)

Considering the existence of the equilibria and feasibility of the system (2), throughout this paper, we assume that:  $c < p\alpha < 2c$ .

## 75 **3** Statement of the main results

#### Case 1: A constant proportion of prey using refuge:

when considering  $x_r = \gamma x (0 \le \gamma < 1)$ , the model (2) becomes the following form:

$$\dot{x}(t) = rx(1 - \frac{x}{K}) - \frac{\alpha(1 - \gamma)^2 x^2 y}{\beta^2 + (1 - \gamma)^2 x^2}$$
  
$$\dot{y}(t) = b(\frac{p\alpha(1 - \gamma)^2 x^2}{\beta^2 + (1 - \gamma)^2 x^2} - c)y$$
(3)

Which can be rewrited as :

$$\dot{x}(t) = rx(1 - \frac{x}{K}) - \frac{\alpha x^2 y}{\bar{\beta}^2 + x^2}$$

$$\dot{y}(t) = b(\frac{p\alpha x^2}{\bar{\beta}^2 + x^2} - c)y$$
(4)

Where  $\bar{\beta} = \frac{\beta}{1-\gamma}$ , that is, the only change relative to the model (1) is the new value of parameter  $\beta$ . It is easy to show that the system (4) is topologically equivalent to the system (3). When  $\gamma \to 0$ , the new parameter  $\bar{\beta}$  is close to the original one, while  $\gamma \to 1$ , the value of the parameter  $\bar{\beta}$  increases indefinitely.

The equilibrium points of model (4) are:  $E_0(0,0)$ ,  $E_K(K,0)$ ,  $\tilde{E}(\tilde{x},\tilde{y})$ , where  $\tilde{x} = \frac{\bar{\beta}\sqrt{c}}{\sqrt{p\alpha-c}}$ ;  $\tilde{y} = \frac{pr\bar{\beta}\sqrt{c}(K\sqrt{p\alpha-c}-\bar{\beta}\sqrt{c})}{Kc(p\alpha-c)}$ , If  $K\sqrt{p\alpha-c}-\bar{\beta}\sqrt{c} = 0$ , the equilibrium point  $\tilde{E}(\tilde{x},\tilde{y})$  collapses

with the point  $E_K(K, 0)$ . Using the following change of variables

$$\varphi: (R_0^+)^2 \times R \to (R_0^+)^2 \times R, \varphi(x, y, t) = (K\bar{x}, \frac{Kr}{\alpha}\bar{y}, \frac{x^2 + A^2}{r}\bar{t})$$

and rewriting  $\bar{x}, \bar{y}, \bar{t}$  as x, y, t, we obtain another form of model (4):

$$\dot{x}(t) = x(1-x)(x^2 + A^2) - x^2 y$$
  

$$\dot{y}(t) = B(x^2 - C(x^2 + A^2))y$$
(5)

Which has only three parameters, where  $A = \frac{\bar{\beta}}{K}$ ,  $B = \frac{bp\alpha}{r}$ ,  $C = \frac{c}{p\alpha}$ . The system (5) is topologically equivalent to the system (4) since  $det D\varphi(x, y, t) = \frac{K^2(x^2 + A^2)}{\alpha} > 0$ . The equilibrium points of this model are:  $E_0(0,0)$ ,  $E_1(1,0)$ ,  $\bar{E}(\bar{x},\bar{y})$ , where  $\bar{x} = \frac{A\sqrt{C}}{\sqrt{1-C}}$ ,  $\bar{y} = \frac{A(\sqrt{1-C} - A\sqrt{C})}{(1-C)\sqrt{C}}$ . The equilibrium point  $\bar{E}(\bar{x},\bar{y})$  is positive if and only if  $M = \sqrt{1-C} - A\sqrt{C}$  $A\sqrt{C} > 0$ . If M = 0, the positive equilibrium point collapses with the equilibrium point  $E_1(1,0)$ , and if M < 0, the equilibrium point  $\bar{E}(\bar{x},\bar{y})$  lies in the fourth quadrant.

**Theorem1:** Let A, B, C are all positive, then we have:

(1) If  $0 < A < \frac{(2C-1)\sqrt{1-C}}{2C\sqrt{C}}$ , the system (5) has a unique limit cycle surrounding the

positive equilibrium point  $\bar{E}(\bar{x}, \bar{y})$ .

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(2) If  $\frac{(2C-1)\sqrt{1-C}}{2C\sqrt{C}} < A < \frac{\sqrt{1-C}}{\sqrt{C}}$ , the system (5) has a locally asymptotically stable

equilibrium point  $\bar{E}(\bar{x}, \bar{y})$  at the first quadrant.

95 (3) If  $\frac{\sqrt{1-C}}{\sqrt{C}} < A < 1$ , the system (5) has a stable equilibrium point  $E_1(1,0)$  and the equilibrium point  $\bar{E}(\bar{x},\bar{y})$  lies in the fourth quadrant.

Proof: The Jacobia matrix of system (5) at the equilibrium point  $E_1(1,0)$  is:

$$\left(\begin{array}{cc} -(1+A^2) & -1 \\ 0 & B(A\sqrt{C}+\sqrt{1-C})M \end{array}\right)$$

When  $M = \sqrt{1 - C} - A\sqrt{C} > 0$ , the equilibrium point  $E_1(1,0)$  is a saddle point. Otherwise, the equilibrium point  $E_1(1,0)$  is locally stable. For the positive equilibrium point, the Jacobia matrix is:

$$\left(\begin{array}{cc} \frac{A^2N}{(1-C)\sqrt{1-C}} & -\frac{A^2C}{1-C}\\ \frac{2A^2BM}{\sqrt{1-C}} & 0 \end{array}\right)$$

where  $N = 2C(\sqrt{1-C} - A\sqrt{C}) - \sqrt{1-C}$ ,  $Det(J) = \frac{2A^4BCM}{\sqrt{1-C}} > 0$ , therefore, the sign of the eigenvalues depends only on  $Tr(J) = \frac{A^2N}{(1-C)\sqrt{1-C}}$ , then we have:

(1) If N > 0, the positive equilibrium point is unstable and a limit cycle exists according to

the Poincare-Bendison theorem.

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(2) If N < 0, the positive equilibrium point is locally asymptotically stable.

(3) If N = 0, the positive is a central point, i.e. neutrally stable cycles.

Figuring out the parameter A explicitly, we obtain the above theorem.

Clearly, the parameter B does not have any influences on the stability properties and equi-

librium densities of this system.

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In reference to the original parameters, the above results can be expressed as follows:

**Theorem2:** Let  $p, \alpha, \beta, \gamma, c$  are all positive constant, then we have:

(1) If  $0 < \gamma < 1 - \frac{2\beta c\sqrt{c}}{K(2c - p\alpha)\sqrt{p\alpha - c}}$ , the prey and predator populations stably oscillate

around the unique positive equilibrium point.

(2) If 
$$1 - \frac{2\beta c\sqrt{c}}{K(2c - p\alpha)\sqrt{p\alpha - c}} < \gamma < 1 - \frac{\beta\sqrt{c}}{K\sqrt{p\alpha - c}}$$
, the two populations tend to reach a

<sup>115</sup> locally stable equilibrium point in the first equdrant.

(3) If  $1 - \frac{\beta\sqrt{c}}{\sqrt{K\sqrt{p\alpha - c}}} < \gamma < 1$ , the prey population reaches it's carrying capacity and the redators are extinct eventually.

predators are extinct eventually.

#### Case 2: A constant number of prey using refuge:

When considering  $x_r = R(0 \le R < K)$ , a different model is obtained. Under this assumption, <sup>120</sup> we have :

$$\dot{x}(t) = rx(1 - \frac{x}{K}) - \frac{\alpha(x - R)^2 y}{\beta^2 + (x - R)^2}$$
  
$$\dot{y}(t) = b(\frac{p\alpha(x - R)^2}{\beta^2 + (x - R)^2} - c)y$$
(6)

The equilibrium points of system (6) are:  $E_0(0,0)$ ,  $E_K(K,0)$ ,  $\tilde{E}(\tilde{x},\tilde{y})$ , where  $\tilde{x} = \frac{\beta\sqrt{c}}{\sqrt{p\alpha-c}}$ ,  $\tilde{y} = \frac{pr(R\sqrt{p\alpha-c}+\beta\sqrt{c})[(K-R)\sqrt{p\alpha-c}-\beta\sqrt{c}]}{Kc(p\alpha-c)}$ . If  $(K-R)\sqrt{p\alpha-c}-\beta\sqrt{c}=0$ , the equilibrium points of system (6) are:  $E_0(0,0)$ ,  $E_K(K,0)$ ,  $\tilde{E}(\tilde{x},\tilde{y})$ , where  $\tilde{x} = \frac{\beta\sqrt{c}}{\sqrt{p\alpha-c}}$ ,

rium point  $\tilde{E}(\tilde{x}, \tilde{y})$  collapse with  $E_K(K, 0)$ . Using the following changes of variables:

$$\varphi: (R_0^+)^2 \times R \to (R_0^+)^2 \times R, \varphi(x, y, t) = (K\bar{x}, \frac{Kr}{\alpha}\bar{y}, \frac{D^2 + (x - A)^2}{r}\bar{t})$$

and rewriting  $\bar{x}$ ,  $\bar{y}$ ,  $\bar{t}$  as x, y, t, we obtain the following model:

$$\dot{x}(t) = x(1-x)(D^2 + (x-A)^2) - (x-A)^2y$$
  
$$\dot{y}(t) = B((x-A)^2 - C(D^2 + (x-A)^2))y$$
(7)

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Which has only four parameters, where  $A = \frac{R}{K}$ ,  $B = \frac{b}{r}$ ,  $C = \frac{c}{p\alpha}$ ,  $D = \frac{\beta}{K}$ . The system (7) is topologically equivalent to the the system (6) since  $det D\varphi(x, y, t) = \frac{K^2(D^2 + (x - A)^2)}{\alpha} > 0$ . the equilibrium point of system (7) are:  $E_0(0,0)$ ,  $E_1(1,0)$ ,  $\bar{E}(\bar{x},\bar{y})$ , where  $\bar{x} = A + \frac{D\sqrt{C}}{\sqrt{1-C}}$ ,  $\bar{y} = \frac{(A\sqrt{1-C} + D\sqrt{C})[(1-A)\sqrt{1-C} - D\sqrt{C}]}{C(1-C)}$ . If  $S = (1-A)\sqrt{1-C} - D\sqrt{C} > 0$ , the equilibrium point  $\bar{E}(\bar{x},\bar{y})$  is a positive equilibrium point. We interest only in the point  $E_1(1,0)$ 

130 and  $\overline{E}(\overline{x}, \overline{y})$  since x > A.

**Theorem3:** Let  $S = (1 - A)\sqrt{1 - C} - D\sqrt{C}$ .

(1) If S > 0, the equilibrium point  $E_1(1,0)$  is a saddle point and the equilibrium point  $\overline{E}(\bar{x},\bar{y})$  is the unique positive equilibrium point of system (7).

(2) If S < 0, the equilibrium point  $E_1(1,0)$  is locally asymptotically stable and the equilibrium point  $\bar{E}(\bar{x},\bar{y})$  lies in the fourth quadrant.

(3) If S = 0, the equilibrium point  $\overline{E}(\overline{x}, \overline{y})$  collapses with the point  $E_1(1, 0)$ , which is locally stable.

Proof: The Jacobia matrix of system (7) at the equilibrium point  $E_1(1,0)$  is:

$$\begin{pmatrix} -[(1-A)^2 + D^2] & -(1-A)^2 \\ 0 & B[(1-A)\sqrt{1-C} + D\sqrt{C})]S \end{pmatrix}$$
 then  $Tr(J) = -((1-A)^2 + D^2) < 0$ ,  $Det(J) = -B[(1-A)^2 + D^2][(1-A)\sqrt{1-C} + D\sqrt{C})]S$ .

(1) If S > 0, then Det(J) < 0, the point  $E_1(1,0)$  is a saddle point.

(2) If S < 0, then Det(J) > 0, the point  $E_1(1,0)$  is locally asymptotically stable and the equilibrium point  $\bar{E}(\bar{x},\bar{y})$  lies in the fourth quadrant.

(3) If S = 0, the equilibrium point  $\overline{E}(\overline{x}, \overline{y})$  collapses with the point  $E_1(1, 0)$  which is locally stable.

Theorem4: Let 
$$S = (1 - A)\sqrt{1 - C} - D\sqrt{C} > 0$$
 and  $\overline{T} = [2A(C - \sqrt{1 - C}) + (2C - 1)D\sqrt{C}][(1 - A)\sqrt{1 - C} - D\sqrt{C}] - D\sqrt{C}(D\sqrt{C} + A\sqrt{1 - C})$ , then we have:

(1) If  $\overline{T} > 0$ , the positive equilibrium point  $\overline{E}(\overline{x}, \overline{y})$  is unstable and surrounded by a limit cycle.

(2) If  $\overline{T} < 0$ , the positive equilibrium point  $\overline{E}(\overline{x}, \overline{y})$  is locally asymptotically stable.

Proof: The Jacobia matrix of system (7) at the equilibrium point  $\overline{E}(\overline{x}, \overline{y})$  is:

$$\left(\begin{array}{cc} \frac{D\bar{T}}{(1-C)\sqrt{C(1-C)}} & -\frac{D^2C}{1-C}\\ \frac{2BD(A\sqrt{1-C}+D\sqrt{C})S}{\sqrt{C(1-C)}} & 0 \end{array}\right)$$

Where  $\bar{T} = [2A(C - \sqrt{1 - C}) + (2C - 1)D\sqrt{C}][(1 - A)\sqrt{1 - C} - D\sqrt{C}] - D\sqrt{C}(D\sqrt{C} + A\sqrt{1 - C})$ . Clearly, Det(J) > 0, then the sign of the eigenvalues depends only on  $Tr(J) = \frac{D\bar{T}}{(1 - C)\sqrt{C(1 - C)}}$ , and we obtain that

(1) If  $\overline{T} > 0$ , the positive equilibrium point  $\overline{E}(\overline{x}, \overline{y})$  is unstable and surrounded by a limit cycle.

(2) If  $\overline{T} < 0$ , the positive equilibrium point  $\overline{E}(\overline{x}, \overline{y})$  is locally asymptotically stable.

Clearly, the parameter B does not have any influences on the stability properties and equi-

librium densities of system (7).

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In terms of the original parameters, the above results reveal the following conclusions:

**Theorem5:** Let  $p, \alpha, \beta, c, K, R$  are all positive, then we have:

(1) If  $0 < R < \frac{K\sqrt{p\alpha - c} - \beta\sqrt{c}}{\sqrt{p\alpha - c}}$ , the predators are depleted and the prey population tends

to reach it's carrying capacity.

(2) If  $\frac{K\sqrt{p\alpha-c}-\beta\sqrt{c}}{\sqrt{p\alpha-c}} < R < K$ , the equilibrium point  $E_1(1,0)$  is a saddle point. (3) If  $R = \frac{K\sqrt{p\alpha-c}-\beta\sqrt{c}}{\sqrt{p\alpha-c}}$ , the equilibrium point  $\tilde{E}(\tilde{x},\tilde{y})$  collapse with  $E_K(K,0)$  which is

165 locally stable.

**Theorem6:** Let  $\frac{K\sqrt{p\alpha-c}-\beta\sqrt{c}}{\sqrt{p\alpha-c}} < R < K$  and  $T = [(2c-p\alpha)\sqrt{c}-2R\sqrt{p\alpha}(c-\sqrt{p\alpha(p\alpha-c)}))][(K - R)\sqrt{p\alpha-c}] - p\alpha\beta\sqrt{c}(p\alpha\sqrt{p\alpha-c}+\beta\sqrt{c})$ , then we have:

(1) If T > 0, the prey and predator populations stably oscillate around the unique positive equilibrium point.

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(2) If T < 0, the two populations tend to reach a stably coexisting state.

## 4 Discussion

The generally reported results were the effect of prey refuge had the stabilizing effect on simple predator-prey models, particularly when a constant number of hidden prey is considered[8,10,12-16]. Nevertheless, other results obtained from different models show no such dynamics[17,18].

On the other hand, the effect of prey refuge could increase the equilibrium density of prey population or that of prey and predator populations[15,18]. The refuge can be important for biological control of a pest, however, increasing the amount of refuge can lead to population outbreak, for example, Hoy[23] mentioned that "hotspots" of high spider mite density in almond orchards can trigger orchards-wide outbreaks. These hotspots are areas in which the predator is not successfully controlling the prey and therefore can be considered as refuga. In this paper, we considered the impact of prey refuge on the dynamic consequences of the predator-prey model with prey self-limitation and Holling type ||| functional repones. We note that the parameter B has no influences on the equilibrium densities of prey and predators and stability properties of the system, since the parameter B does not take part on the determination of equilibrium points

The equilibrium density of prey increases as refuge using by prey increases, and/or predation

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inefficiency increases. we refer to the predation inefficiency as the parameter C, which represents the ratio of predator death rate to the product of the predator conversion rate and parameter  $\alpha$ . If a constant proportion of prey using refuge, the predator's equilibrium density increases as refuge using by prey increases, and then decreases. The equilibrium density reaches it's maximum value if  $A = \frac{\sqrt{1-C}}{2\sqrt{C}}$ , i.e. the equilibrium density of prey is equal to  $\frac{K}{2}$ . If a constant number of prey using refuge, it is easy to show that under a restricted set of conditions we also predict an increase in the predator's equilibrium density. This occurs when the equilibrium density of prey is less than  $\frac{K}{2}$ . Therefore, the equilibrium density of predator population increase with the constant proportion or number of prey using refuge, only when that of prey is less than  $\frac{K}{2}$ .

Secondly, as can be seen from our results, if refuge using by prey is high, the model predicts that prey population reaches it's carrying capacity and predator goes extinct, a behavior also observed by Collings[18] and González-Olivares and Ramos-Jiliberto[15] for a certain parameter space. Thirdly, the refuge using by prey can increase the stability of the community equilibrium in the first quadrant, which agrees with most previous results on simple models[8,15,16,18]. In this paper, stabilization or increase of stability refers to cases where a community equilibrium point changes from a repeller to an attractor due to changes in the value of controlled parameter(see [15]). Three kind of states can be reached: unstable state surrounded by a limit cycle, stable coexistent state and prey population reaches it's carrying capacity and while predators extinct.

If a constant number of prey using refuge, it is difficult to figure out the value of the parameter R explicitly, the consequences are more complex than that of a constant proportion prey using refuge. Populations oscillate can occur only under a very restricted set of conditions(T > 0). We can see from the theorem 6, if very few prey hiding in the refuge, the prey and predator populations can oscillate stably around the equilibrium point in the first quadrant. Our results

also predict that predator must capture and digest their prey efficiently to survive form the habitat in which prey build the refuge where resources and/or conditions are sub-optimal.

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Although our results are reasonable under a restricted set of assumptions derived from the basic model. they are robust and comparable to previous conclusions. We expect the dynamic consequences to be studied if more realistic information is added to the model. For instance, prey population and/or predators have the stage structure—the immature stage and the mature stage, or predators apply the ratio-dependent functional response.

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### References

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 J.M. McGlade, Adevanced Ecology Theory: Pinciples and Applications. Blackwell Scientific Poblications, Oxford, 1999.

- [2] Z. Li, M. Gao, C. Xu, X. Han, Impact of predator pursuit and prey evasion on synchrony and spatial patterns in metapopulation, Ecol.Model. 185(2005)245-254.
  [3] M.L. Rosenzweig, Paradox of enrichment: destabilization of exploitation ecosystem in ecological time, Science. 171(1971)385-387.
  - [4] C. Xu, Z. Li, Effects of diffusion and spatially varing predation risk on the dynamics and equilibrium density of a predator-prey model, J.Theor.Biol. 219(2002a)73-82.
  - [5] E. McCauley, W.W. Murdonch, Cyclic and stable populations: plankton as paradigm, Am. Nat. 129(1987)98-121.
  - [6] E. McCauley, W.W. Murdonch, Predator-prey dynamics in environments rich and poor

in nutrients, Nature. 343(1990)455-457.

[7] A.C. Kent, P. Doncaster, T. Sluckin, Consequences for predators of rescue and Allee effects on prey, Ecol.Model. 162(2003)233-2453.

[8] G.D. Ruxton, W.S.C. Gurney, A.M. De Ross, Interference and generation cycles, Thoer.Popul.Biol. 42(1992)235-253.

[9] P.A. Abrams, Effect of increased preductivity on the abundances of tropic levels, Am.Nat. 144(1993)351-371.

[10] G.W. Harrison, Global stability of predator-prey interactions, J.Math.Biol. 8(1979)39-174.

[11] C.S. Holling, Some characteristics of simple types of predation and parasitism, The Can.Entomol. 91(1959)385-398.

[12] J. Maynard Smith, Models in Ecology. Cambridge University Press, Cambridge, 1974.
 [13] W.W. Murdoch, A. Oaten, Predation and population stability, Adv.Ecol.Res.
 9(1975)2-132.

[14] A. Sih, Prey refuges and predatorCprey stability, Theor.Popul.Biol. 31(1987)1-12.

[15] E. González-Olivares, R. Ramos-Jiliberto, Dynamic consequences of prey refuges in a simple model system: more prey, fewer predators and enhanced stability, Ecol.Model. 166(2003)135-146.

[16] Y. Huang, F. Chen, Z. Li, Stability analysis of prey-predator model with Holling type response function incorporating a prey refuge, Appl.Math.Copul. 182(2006)672-683.

[17] J.M. McNair, The effects of refuges on predator-prey interactions: a reconsideration, Theor.Popul.Biol. 29(1986)38-63.

[18] J.B. Collings, Birfurcation and stability analysis of a temperature-dependent mite predator-prey interaction model incorporating a prey refuge, Bull.Math.Biol. 57(1)(1995)63-76.

245

240



255

250

13

[19] M. Scheffer, R.J. De Boer, Implications of spatial heterogeneity for the paradox of enrichment, Ecology, 76(7)(1995)2270-2277.

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[20] C.W. Clark, Mathematical Bioeconomic: The Optimal Management of Renewable Resources, 2nd ed. Wiley, New York, 1990.

[21] A.A. Berryman, A.P. Gutierrez, R. Arditi, Credible, parsimonious and useful predatorprey models—a reply to Abrams, Gleeson, and Sarnelle, Ecology. 76(6)(1995)1980-1985.

[22] R.J. Taylor, Predation. Chapman and Hall, New York, 1984.

<sup>[23]</sup> M.A. Hoy, Almonds (California). In: Helle W, Sabelis M.W, editors. Spider mites: their Biology, natural enemies and control. World crop pests, vol.1B. Amsterdam: Elsevier, 1985.

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