

The impact of predator-dependent prey refuge on the dynamics of a Leslie-Gower predator-prey model

Abstract In this paper, we propose a new Leslie-Gower predator-prey model with predator-dependent prey refuge. Firstly, we obtain the positivity and boundedness of the system solution. Secondly, we prove that the origin is unstable using blow-up method, analyze the existence and local stability of the boundary equilibrium point and positive equilibrium point, and prove that the unique positive equilibrium point of the system is globally asymptotically stable by constructing a suitable Dulac function. Finally, mathematic analysis and numerical simulation show that: (1) when the strength of the predator-dependent prey refuge $k = 0$, the dynamics of the predator-prey system without predator-dependent prey refuge are consistent with the results obtained from the traditional Leslie-Gower predator-prey system; (2) when k tends to positive infinity, the predator-dependent refuge lead to prey population densities fall somewhere between without prey refuge and with proportional refuge. However, the predator densities within this new form of the predator-dependent prey refuge is greater than the densities of predators without prey refuge and with proportional refuge; (3) increasing the strength k of the predator-dependent prey refuge can increase the densities of predator and prey populations respectively.

Keywords Leslie-Gower predator-prey model; Predator-dependent prey refuge; Blow-up method; Dulac function; Global stability

1. Introduction

Predator-prey models are critical for understanding population dynamics and inter-species interactions within ecological systems. The dynamics of Leslie-Gower model and its various modifications have received great attention [1-4]. Considering the relationship between a reduction in predator numbers and the per capita availability of their preferred food, Leslie [5,6] introduced the following predator-prey model where the “carrying capacity” of the predator’s environment is proportional to the number of prey

$$\begin{aligned}\frac{dx}{dt} &= (r_1 - a_1y - b_1x)x, \\ \frac{dy}{dt} &= (r_2 - a_2\frac{y}{x})y,\end{aligned}\tag{1.1}$$

where x and y represent population densities of prey and predator at time t , respectively. Obviously, the above system admits a unique coexisting equilibrium point

$$x_1^* = \frac{r_1a_2}{a_1r_2 + a_2b_1}, \quad y_1^* = \frac{r_1r_2}{a_1r_2 + a_2b_1}.$$

By constructing a suitable Lyapunov function, they obtained that the positive equilibrium is globally asymptotically stable. For more biological background of system (1.1), one could refer to [5-8] and the references cited therein.

In the past decade, many scholars have shown great interest in predator-prey systems (1.1) based on different functional response models, which has resulted in many outstanding works. Relevant literature can be found in [9,10] and the references cited therein. However, it has been observed that some prey species survive by avoiding predators. Therefore, the predator-prey model must be adapted to incorporate the possibility of prey seeking refuge, and to account for the impact of refuge behavior on the predators functional response [11]. Typically, there are two main types of prey refuges in predator-prey models. One type considers the prey refuge as a constant number [12,13], while the other type assumes that the refuge is proportional to the size of the prey population [14-17]. Therefore, if x_r denotes the prey refuge, model (1.1) is modified as

$$\begin{aligned}\frac{dx}{dt} &= (r_1 - b_1x)x - a_1(x - x_r)y, \\ \frac{dy}{dt} &= (r_2 - a_2\frac{y}{x})y,\end{aligned}\tag{1.2}$$

where x and y represent population densities of prey and predator at time t , respectively. x_r is the number of prey population in refuge. If $x_r = m$, then the number of prey in hiding is a fixed value. When $x_r = \theta x$, the number of prey refuge varies proportionally with the size of the prey population, with $0 < \theta < 1$. In [14], the authors considered the following Leslie-Gower predator-prey model with proportional refuge

$$\begin{aligned}\frac{dx}{dt} &= (r_1 - b_1x)x - a_1(1 - \theta)xy, \\ \frac{dy}{dt} &= (r_2 - a_2\frac{y}{(1 - \theta)x})y.\end{aligned}\tag{1.3}$$

By simple calculation, they obtained that system (1.3) admits a unique positive equilibrium

$$x_2^* = \frac{r_1a_2}{a_1r_2(1 - \theta)^2 + a_2b_1}, \quad y_2^* = \frac{r_1r_2(1 - \theta)}{a_1r_2(1 - \theta)^2 + a_2b_1}.$$

They found that the prey refuge could influence the densities of both prey and predator species greatly. And they got the global stability and persistence of the system under proper conditions. As is well known, in nature, the number of prey seeking refuge may vary with the number of predators. When the number of predators is relatively high, the rate of prey refuge correspondingly increases, rather than adopting a constant rate of refuge. Therefore, it is necessary to consider the situation where the rate of prey refuge depends on the number of predators.

Motivated by the above question, we will consider a predator-prey model in which the number of prey population in refugia is nonlinear dependent on the number of predators, that is, $x_r = \theta(1 - \frac{1}{1+ky})x$, where θ is

the maximum refuge rate and k is the predator-dependent prey refuge strength. From a biological perspective, this type of refuge can be explained as follows: When the number of predators $y = 0$, $x_r = 0$, in this case, the predator does not exist, and the prey lacks refuge demand. With the number of predators $y > 0$, the proportional refuge mechanism begins to take effect. As y increases, the number of prey refuges also increases. As the number of predators increases infinitely, the refuge mechanism transforms into a proportionate refuge, and the number of refuges reaches the maximum rate, indicated by the equation $x_r = \theta x$. Compared to constant and proportional refuge, this modeling method is more precise in describing the population size of prey changes over time, especially in the presence of predators. It holds practical significance and applicability. From the above discussion, it can be seen that due to the impact of predator-dependent prey refuge, this leaves $x - x_r = x(1 - \theta(1 - \frac{1}{1+ky}))$ of the prey available to the predators, and modifying system (1.3) accordingly yields the following system

$$\begin{aligned}\frac{dx}{dt} &= (r_1 - b_1x)x - a_1(1 - \theta(1 - \frac{1}{1+ky}))xy, \\ \frac{dy}{dt} &= (r_2 - a_2\frac{y}{x})y,\end{aligned}\tag{1.4}$$

where x and y represent population densities of prey and predator at time t , respectively. r_1 is the growth rate of prey x , b_1 is the strength of competition among individuals of prey, a_1 is the maximum value of the per capita reduction of prey x due to predator y , r_2 is the growth rate of predator y , a_2 has a similar meaning to a_1 .

The rest of the paper is arranged as follows. In Section 2, we analyze the dynamical behavior of the system (1.4), including the boundedness of the system, the existence of the equilibrium point, and the local stability. In addition, we will prove the global stability of the positive equilibrium point by constructing a suitable Dulac function. In Section 3, we will analyze the effect of prey refuge on predator and prey population densities, respectively.

2. Main results

2.1 Positivity and boundedness of the solution

Lemma 2.1. *All the solutions of system (1.4), which start in R_+^2 , are always positive and bounded.*

Proof. Firstly, we want to prove that $(x(t), y(t)) \in R_+^2$ for all $t \in [0, +\infty)$. For system (1.4) with initial conditions $x(0) > 0$, $y(0) > 0$, we have

$$\begin{aligned}x(t) &= x(0) \exp \left\{ \int_0^t \left[r_1 - b_1x(s) - a_1(1 - \theta(1 - \frac{1}{1+ky(s)}))y(s) \right] ds \right\}, \\ y(t) &= y(0) \exp \left\{ \int_0^t \left[r_2 - a_2\frac{y(s)}{x(s)} \right] ds \right\}.\end{aligned}\tag{2.1}$$

Hence, the solution $(x(t), y(t))$ of model (1.4) with the initial condition $(x(0), y(0)) \in R_+^2$ remains positive.

From the first equation of (1.4), we can obtain

$$\frac{dx}{dt} \leq (r_1 - b_1x)x,\tag{2.2}$$

then from the comparison principle, we have

$$\lim_{t \rightarrow +\infty} \sup x(t) \leq \frac{r_1}{b_1}. \quad (2.3)$$

Therefore, for any $\epsilon > 0$, there exists $T > 0$ such that $x(t) \leq \frac{r_1}{b_1} + \epsilon$ for any $t > T$. Then, from the second equation of (1.4), we can get

$$\frac{dy}{dt} \leq (r_2 - a_2 \frac{y}{\frac{r_1}{b_1} + \epsilon})y, \quad t > T, \quad (2.4)$$

then again from the comparison principle, we can easily obtain that

$$\lim_{t \rightarrow +\infty} \sup y(t) \leq \frac{r_1 r_2}{b_1 a_2}. \quad (2.5)$$

Thus, all solutions of system (1.4) with initial conditions $(x(0), y(0)) \in R_+^2$ are defined in the positive bounded invariant $D := \{(x(t), y(t)) \in R_+^2 : 0 < x(t) \leq \frac{r_1}{b_1}, 0 < y(t) \leq \frac{r_1 r_2}{b_1 a_2}\}$.

2.2. The existence and stability of equilibria

It is clear that the system (1.4) allows a boundary equilibrium $E_1(\frac{r_1}{b_1}, 0)$ and a unique positive equilibrium $E^*(x^*, y^*)$, where $x^* = \frac{a_2 y^*}{r_2}$ and y^* is the root of the following equation

$$(b_1 a_2 k + a_1 r_2 (1 - \theta) k) y^{*2} + (b_1 a_2 + a_1 r_2 - r_1 r_2 k) y^* - r_1 r_2 = 0. \quad (2.6)$$

By simple computation, for all $\theta \in (0, 1)$, system (1.4) admits a unique positive equilibrium

$$x^* = \frac{a_2 y^*}{r_2}, \quad y^* = \frac{-(b_1 a_2 + a_1 r_2 - r_1 r_2 k) + \sqrt{(b_1 a_2 + a_1 r_2 - r_1 r_2 k)^2 + 4 r_1 r_2 (b_1 a_2 k + a_1 r_2 (1 - \theta) k)}}{2(b_1 a_2 k + a_1 r_2 (1 - \theta) k)}. \quad (2.7)$$

We know from system (1.4) that the origin is not defined, but it is necessary to study the dynamics behavior near the origin. Using a transformation $dt = x d\tau$ (still denoting τ by t), system (1.4) is converted into a topologically equivalent system as follows

$$\begin{aligned} \frac{dx}{dt} &= (r_1 - b_1 x)x^2 - a_1 \left(1 - \theta \left(1 - \frac{1}{1 + ky}\right)\right) x^2 y, \\ \frac{dy}{dt} &= (r_2 x - a_2 y)y. \end{aligned} \quad (2.8)$$

Lemma 2.2. *For system (1.4), the origin is unstable.*

Proof. For system (2.8), it is obvious that $\dot{y}|_{x=0} = -a_2 y^2 < 0$, thus there exists an invariant line $x = 0$ for system (2.8). Now, we will discuss the conclusion by blow-up method. Making the following transformation $x = u$, $y = uv$ and $dt = \frac{1}{u} d\tau$, (still denoting τ by t), system (2.8) is rewritten as

$$\begin{aligned} \frac{du}{dt} &= (r_1 - b_1 u)u - a_1 \left(1 - \theta \left(1 - \frac{1}{1 + kw}\right)\right) u^2 v, \\ \frac{dv}{dt} &= (r_2 - r_1)v - a_2 v^2 + b_1 uv + a_1 uv^2 \left(1 - \theta \left(1 - \frac{1}{1 + kw}\right)\right). \end{aligned} \quad (2.9)$$

When $u = 0$, system (2.9) admits two trivial boundary equilibria $E^0(0, 0)$ and $E^1(0, \frac{r_2 - r_1}{a_2})$. Then, we calculate the Jacobian matrix of system (2.9) as follows :

$$J(u, v) = \begin{pmatrix} r_1 - 2b_1u - 2a_1uv(1 - \theta \frac{ kuv }{1 + kuv}) + \frac{ a_1 \theta k u^2 v^2 }{(1 + kuv)^2} & -a_1u^2(1 - \frac{ \theta kuv }{1 + kuv}) + \frac{ a_1 k \theta u^3 v }{(1 + kuv)^2} \\ b_1v + \frac{ (1 + kuv - kuv\theta) a_1 v^2 }{1 + kuv} - \frac{ a_1 k \theta u v^3 }{(1 + kuv)^2} & r_2 - r_1 - 2a_2v + b_1u + \frac{ 2a_1uv(1 + kuv - kuv\theta) }{1 + kuv} - \frac{ a_1 k \theta u^2 v^2 }{(1 + kuv)^2} \end{pmatrix}.$$

Therefore, for the two trivial boundary equilibrium points $E^0(0, 0)$ and $E^1(0, \frac{r_2 - r_1}{a_2})$, the form of Jacobian matrix are

$$J(E^0) = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 - r_1 \end{pmatrix}$$

and

$$J(E^1) = \begin{pmatrix} r_1 & 0 \\ \frac{ b_1(r_2 - r_1) }{a_2} + \frac{ a_1(r_2 - r_1)^2 }{a_2^2} & r_1 - r_2 \end{pmatrix}.$$

When $r_2 < r_1$, $E^0(0, 0)$ is a saddle point and $E^1(0, \frac{r_2 - r_1}{a_2})$ is an unstable node. However, when $r_2 > r_1$, $E^0(0, 0)$ is an unstable node and $E^1(0, \frac{r_2 - r_1}{a_2})$ is a saddle point; when $r_2 = r_1$ according to the center manifold theorem, $E^0(0, 0)$ is a repelling saddle-node. Hence, the origin in system (1.4) is unstable after blow-down. The proof is completed.

Then, we discuss the local stability of the boundary equilibrium E_1 and the positive equilibrium E^* . We first compute the Jacobian matrix for system (1.4) to investigate the local stability of equilibria whenever they exist. $J(x, y)$ of system (1.4) at any point (x, y) is given by

$$J(x, y) = \begin{pmatrix} r_1 - 2b_1x - a_1y(1 - \theta(1 - \frac{1}{1 + ky})) & -a_1x(1 - \theta \frac{ ky }{1 + ky}) - \frac{ a_1 \theta k xy }{(1 + ky)^2} \\ \frac{ a_2 y^2 }{x^2} & r_2 - \frac{ 2a_2 y }{x} \end{pmatrix}. \quad (2.10)$$

The local stability is analyzed below by calculating eigenvalues of the Jacobian matrix corresponding to each equilibrium point. We have the following results.

Theorem 2.3. *The boundary equilibrium point $E_1(\frac{r_1}{b_1}, 0)$ is a saddle point.*

Proof. For the boundary equilibrium point $E_1(\frac{r_1}{b_1}, 0)$, the Jacobian matrix takes the form as

$$J(E_1) = \begin{pmatrix} -r_1 & -\frac{ a_1 r_1 }{b_1} \\ 0 & r_2 \end{pmatrix}.$$

The eigenvalues of $J(E_1)$ are $-r_1 < 0$ and $r_2 > 0$. Hence the boundary equilibrium point E_1 is a saddle point.

Theorem 2.4. *The positive equilibrium point E^* is always locally asymptotically stable.*

Proof. Evaluating the Jacobian matrix of the model system (1.4) at positive equilibrium point $E^*(x^*, y^*)$, we have

$$J(E^*) = \begin{pmatrix} -b_1x^* & \frac{ -a_1 k x^* y^* (1 - \theta) }{1 + ky^*} - x^* \frac{ a_1 + a_1(1 - \theta)ky^* }{(1 + ky^*)^2} \\ \frac{ r_2 y^* }{x^*} & -r_2 \end{pmatrix}.$$

The characteristic equation of the Jacobian matrix $J(E^*)$ is

$$\lambda^2 - \text{tr}(J(E^*))\lambda + \det(J(E^*)) = 0.$$

Since $\text{tr}(J(E^*)) = -b_1x^* - r_2 < 0$ and $\det(J(E^*)) = b_1r_2x^* + \frac{r_2y^*}{x^*}(\frac{a_1kx^*y^*(1-\theta)}{1+ky^*} + x^*\frac{a_1+a_1(1-\theta)ky^*}{(1+ky^*)^2}) > 0$, the characteristic equation has no positive real part root and E^* is locally asymptotically stable.

Theorem 2.5. *The unique positive equilibrium point $E^*(x^*, y^*)$ of the system (1.4) is always globally asymptotically stable.*

Proof. We denote the right-hand sides of model (1.4) as $P(x, y), Q(x, y)$, respectively. Next, taking Dulac function $B(x, y) = x^{-1}y^{-1}$ for the system (1.4) and by direct calculation, we can easily obtain that

$$\frac{\partial(B(x, y)P(x, y))}{\partial x} + \frac{\partial(B(x, y)Q(x, y))}{\partial y} = \frac{\partial(\frac{r_1}{y} - \frac{b_1x}{y} - a_1\frac{(1+(1+\theta)ky)}{1+ky})}{\partial x} + \frac{\partial(\frac{r_2}{x} - a_2\frac{y}{x^2})}{\partial y} = -\frac{b_1}{y} - \frac{a_2}{x^2} < 0.$$

Therefore, by the Dulac-Bendixson theorem [18] (Theorem 2, page 265), there is no periodic orbit in $\text{int}(R_+^2)$ for the system (1.4). Moreover, E^* is the unique positive equilibrium point in $\text{int}(R_+^2)$ and also locally asymptotically stable. Thus, E^* is globally asymptotically stable. We also show it numerically in Fig. 1. Fig. 1 reveals that the positive equilibrium point E^* of the system (1.4) is a global attractor.

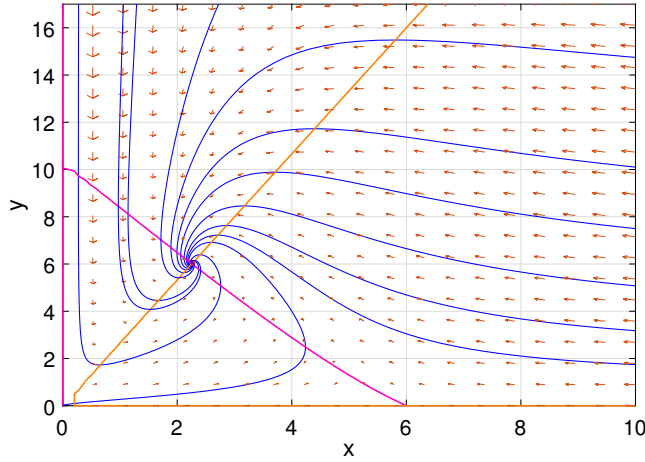


Fig. 1. The global stability of the positive equilibrium point of the system (1.4) with $r_1 = 1.2$, $r_2 = 0.8$, $a_1 = 0.18$, $a_2 = 0.3$, $b_1 = 0.2$, $k = 0.36$, $\theta = 0.45$.

3. Impact of predator-dependent prey refuge on predator and prey densities

Next, we will attempt to analyze in depth the effect of predator-dependent prey refuge on predator and prey density on the following three aspects.

Case (i) $k = 0$

In this case, from (2.7), we can easily obtain

$$x^* = \frac{r_1 a_2}{b_1 a_2 + a_1 r_2} = x_1^*, \quad y^* = \frac{r_1 r_2}{b_1 a_2 + a_1 r_2} = y_1^*, \quad (3.1)$$

where (x_1^*, y_1^*) is the unique positive equilibrium of the system (1.1) without prey refuge. Therefore, the dynamics of the system (1.4) without predator-dependent prey refuge are the same as that of the system (1.1).

Case (ii) $k \rightarrow +\infty$

For (2.7), let $k \rightarrow +\infty$, by simple calculation, we have

$$x^* = \frac{r_1 a_2}{b_1 a_2 + a_1 r_2 (1 - \theta)}, \quad y^* = \frac{r_1 r_2}{b_1 a_2 + a_1 r_2 (1 - \theta)}. \quad (3.2)$$

Obviously, for all $\theta \in (0, 1)$,

$$b_1 a_2 + a_1 r_2 (1 - \theta)^2 < b_1 a_2 + a_1 r_2 (1 - \theta) < b_1 a_2 + a_1 r_2. \quad (3.3)$$

Hence,

$$\frac{r_1 a_2}{b_1 a_2 + a_1 r_2 (1 - \theta)^2} > \frac{r_1 a_2}{b_1 a_2 + a_1 r_2 (1 - \theta)} > \frac{r_1 a_2}{b_1 a_2 + a_1 r_2}, \text{ i.e. } x_2^* > x^* > x_1^*, \quad (3.4)$$

where (x_2^*, y_2^*) is the unique positive equilibrium of the system (1.3) with proportional refuge. The inequalities above demonstrate that when the predator-dependent prey refuge strength k becomes large enough, the predator-dependent refuges lead to prey population densities fall somewhere between without prey refuge and with proportional refuge.

The impact of predator-dependent prey refuge on densities of predator populations is further discussed below. Clearly, the following inequalities hold

$$\begin{aligned} \frac{r_1 r_2}{b_1 a_2 + a_1 r_2 (1 - \theta)} &\geq \frac{r_1 r_2}{\frac{b_1 a_2}{(1 - \theta)} + a_1 r_2 (1 - \theta)}, \\ \frac{r_1 r_2}{b_1 a_2 + a_1 r_2 (1 - \theta)} &\geq \frac{r_1 r_2}{b_1 a_2 + a_1 r_2}. \end{aligned} \quad (3.5)$$

Let

$$\phi(\theta) = b_1 a_2 + a_1 r_2 - \frac{b_1 a_2}{1 - \theta} - a_1 r_2 (1 - \theta) = \frac{-\theta}{1 - \theta} b_1 a_2 + a_1 r_2 \theta = \theta (a_1 r_2 - \frac{1}{1 - \theta} b_1 a_2). \quad (3.6)$$

Next, we will discuss the sign of $\phi(\theta)$ for two cases:

(a) Assume that inequality $a_1 r_2 \geq \frac{1}{1 - \theta} b_1 a_2$ holds, then $\phi(\theta) \geq 0$, that is, $b_1 a_2 + a_1 r_2 \geq \frac{b_1 a_2}{1 - \theta} + a_1 r_2 (1 - \theta)$. Thus, we have

$$\frac{r_1 r_2}{\frac{b_1 a_2}{(1 - \theta)} + a_1 r_2 (1 - \theta)} \geq \frac{r_1 r_2}{b_1 a_2 + a_1 r_2}. \quad (3.7)$$

Further it can be obtained from (3.5) and (3.7) that

$$\frac{r_1 r_2}{b_1 a_2 + a_1 r_2 (1 - \theta)} \geq \frac{r_1 r_2}{\frac{b_1 a_2}{(1 - \theta)} + a_1 r_2 (1 - \theta)} \geq \frac{r_1 r_2}{b_1 a_2 + a_1 r_2}, \text{ i.e. } y^* \geq y_2^* \geq y_1^*. \quad (3.8)$$

(b) Assume that inequality $a_1 r_2 < \frac{1}{1-\theta} b_1 a_2$ holds, then $\phi(\theta) < 0$, that is, $b_1 a_2 + a_1 r_2 < \frac{b_1 a_2}{1-\theta} + a_1 r_2 (1-\theta)$. Thus, we have

$$\frac{r_1 r_2}{\frac{b_1 a_2}{(1-\theta)} + a_1 r_2 (1-\theta)} < \frac{r_1 r_2}{b_1 a_2 + a_1 r_2}. \quad (3.9)$$

Further it can be obtained from (3.5) and (3.9) that

$$\frac{r_1 r_2}{b_1 a_2 + a_1 r_2 (1-\theta)} \geq \frac{r_1 r_2}{b_1 a_2 + a_1 r_2} > \frac{r_1 r_2}{\frac{b_1 a_2}{(1-\theta)} + a_1 r_2 (1-\theta)}, \text{ i.e., } y^* \geq y_1^* > y_2^*. \quad (3.10)$$

The above analysis shows that when the predator-dependent prey refuge strength k becomes large enough, the predator densities within this new form of the predator-dependent prey refuge is greater than the densities of predators without prey refuge and with proportional refuge.

Case (iii) $0 < k < +\infty$

The next step is to study the effect of the predator-dependent prey refuge strength k on predator and prey densities by numerical simulation. To capture the effect of the predator-dependent prey refuge strength k on predators and prey population densities, we selected a set of parameter values: $a_1 = 0.12$, $a_2 = 0.2$, $b_1 = 0.3$, $r_1 = 1.4$, $r_2 = 0.85$, $\theta = 0.5$. It is observed that increasing the strength k of the predator-dependent prey refuge can increase the densities of predator and prey populations of the stable equilibrium point respectively in Fig. 2.

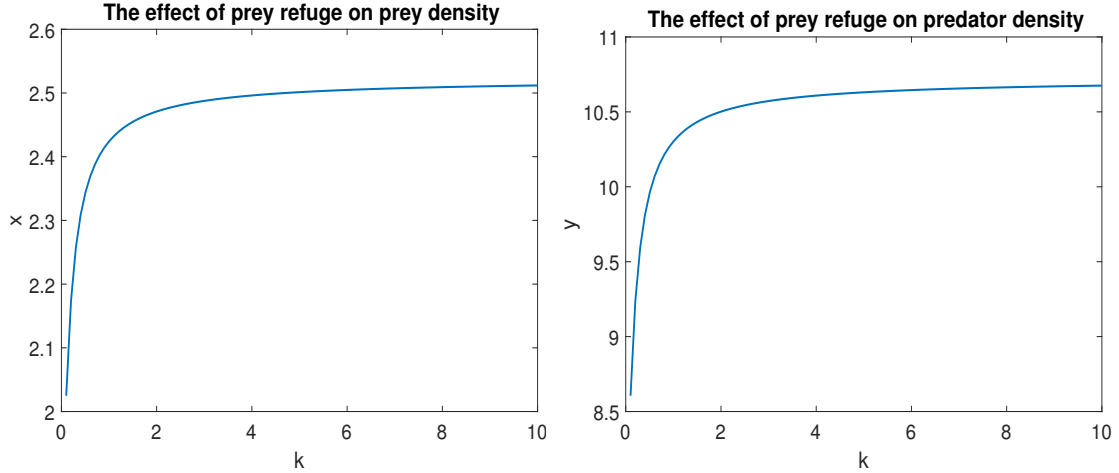


Fig. 2. The effect of the predator-dependent prey refuge on predator and prey populations of the stable equilibrium point, respectively.

Competing interests

The authors declare that there is no conflict of interests.

Acknowledgement

This work is supported by the Natural Science Foundation of Fujian Province (2022J01192).

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