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Dynamical complexity of a predator-prey model with a prey refuge and Allee effect

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Abstract: We consider a predator-prey model with a non-monotonic functional response encompassing a prey refuge and a strong Allee effect on the prey. The multiple existence and stability of interior equilibria are investigated. The bifurcation analysis shows this model can exhibit numerous kinds of bifurcations (e.g., saddle-node, Hopf-Andronov and Bogdanov-Takens bifurcations). It is found that there exist diverse parameter values for which the model exhibits a limit cycle, a homoclinic orbit, and even many heteroclinic curves. The results obtained reveal the prey refuge in the model brings rich dynamics and makes the system more sensitive to parameter values. The main purpose of the present work is to offer a complete mathematical analysis of the effect that the refuge brings about.

Key words: Allee effect, Hopf bifurcation, B-T bifurcation, predator-prey system, refuge, non-monotonic functional response

1. Introduction

The qualitative theory of differential systems has been one of the main method for biological mathematicians to reveal numerous processes encountered in the biosciences, particularly in ecological systems. And this trend is bound to continue in the foreseeable future. Predator-prey interaction, one of the dominant themes in ecology, has been modelled for many years and plenty of excellent works have been done for this kind of model [9, 15, 16, 19]. The common predator-prey system can be generalized as follows:

$$\begin{cases} \frac{dx}{d\tau} = xg(x) - y\varphi(x), \\ \frac{dy}{d\tau} = (\varepsilon\varphi(x) - c)y, \end{cases} \tag{1.1}$$

where $x(\tau)$, $y(\tau)$ are the prey and the predator density, respectively; ε characterizes the conversion e iciency of predator; c represents the predator natural mortality rate; $g(x)$ and $\varphi(x)$ are smooth functions with respect to x and represent the natural per capita growth function and the functional response, respectively.

In (1.1), the classical choices of $g(x)$ are exponential growth ($g(x) = r$), or logistic growth ($g(x) = r(1 - x/K)$), which has been modelled to explain various ecological phenomena, see, e.g., [25]. Allee effect, observed by Allee in the 1930s [1], shows a phenomenon to the effect that the per-individual growth rate will be positively correlated to the density of population in the case of low population densities. An Allee effect occurs

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2010 *AMS Mathematics Subject Classification:* 34C23,34D20,92B05 when there is a positive relationship between a component of fitness and population size or density [5–7, 39]. Plenty of causes can bring about the Allee effect in a population such as mating limitation [11], inbreeding depression [36], food exploitation and predator avoidance of defence. Recently, an epidemic model to describe the joint interplay of a strong Allee effect and infectious diseases in a single population was introduced by Hilker et al. [14], which complete bifurcations were studied by Cai et al. [3]. It is widely acknowledged that the Allee effect greatly increases the likelihood of extinction of the population [39], and can lead to a variety of dynamical effects. Allee effect has been roughly divided into two categories, namely strong and weak ones [6]. A threshold will be introduced when the population is subject to a strong Allee effect and the growth rate can be negative if the population density drops below the threshold [6, 7]. The population with weak Allee effect, though the per capita population growth rate is lower when at low density than at higher density, does not undergo threshold phenomena [6, 24]. Practically the continuous growth function considering the strong Allee effect usually takes the mathematical form:

$$g(x) = r(1 - \frac{x}{K})(x - m),$$

where r and K are the intrinsic growth rate and the environment carrying capacity of prey, respectively; m denotes the Allee threshold [6] which belongs to $(0, K)$. We can model the Allee effect in other mathematical forms which are available in [6], even though [27] has shown the topological equivalence among these forms.

The other function $\varphi(x)$ in (1.1) is called a functional response or trophic function, which is to character the capacity of the predator to consume the prey. The conventional forms of functional response are Holling types I, II, and III, and clearly, these types of functional response $\varphi(x)$ have inherent monotonicity which can be explained in many predator- prey interactions [9, 16, 19, 20]. However, a cluster of experimental and observational findings illustrate that when it comes to the "inhibition" in microbial and "group defence" in population dynamics, it is unrealistic to put forward the assumption that the functional response $\varphi(x)$ is monotonic [2]. Group defence, which has been investigated for many years, is used to describe the situation whereby predation is decreased or even prevented altogether due to the increased ability of the prey to better defend or disguise themselves when their number is large enough. To study the predator-prey interaction when the prey exhibits group defence, many modellers change the inherent monotonicity of the functional response $\varphi(x)$ and assume the following condition that $\varphi(x)$ should satisfy:

$$\varphi'(x) \begin{cases} > 0, & \text{if } 0 \le x < \tilde{M}, \\ < 0, & \text{if } x > \tilde{M}, \end{cases} \tag{1.2}$$

where $\tilde{M} > 0$ is a constant. In [2], Andrews proposed a function

$$\varphi(x) = \frac{qx}{a + bx + x^2}, \tag{1.3}$$

which satisfies (1.2). The function (1.3) is also called the Monod-Haldane function or Holling type-IV function. Afterwards, Sokol and Howell [35] proposed a simplified Monod-Haldane function of the form

$$\varphi(x) = \frac{qx}{a + x^2}, \tag{1.4}$$

and found that it fitted their experimental data. Ruan and Xiao [31] have discussed the following predator-prey system with non-monotonic functional response

$$\begin{cases} \frac{dx}{d\tau} = rx(1-\frac{x}{K}) - \frac{qxy}{a+x^2}, \\ \frac{dy}{d\tau} = \frac{\varepsilon qxy}{a+x^2} - cy. \end{cases} \tag{1.5}$$

Olivares et al. [28] incorporate the Allee effect into (1.5), that is,

$$\begin{cases} \frac{dx}{d\tau} = rx(1-\frac{x}{K})(x-m) - \frac{qxy}{a+x^2}, \\ \frac{dy}{d\tau} = \frac{\varepsilon qxy}{a+x^2} - cy. \end{cases} \tag{1.6}$$

The authors of [28] provided the dynamics analysis of system (1.6) and proved the uniqueness of limit cycle in this system.

Due to over-exploitation, over-predation, environmental pollution, etc, many kinds of species have been driven to extinction and others are on the brink of extinction. To take this situation on hold, some preventive measures, both human intervention and prey themselves prevention, should be taken such as restriction on harvesting, creating refuges (burrows, trees, thick vegetation or rock talus), and so on. The method of creating a refuge for the endangered species enlightens many researchers to insert a refuge in the conventional prey-predator dynamics from various angles [4, 8, 12, 13, 17, 18, 22, 23, 26, 32, 34, 37]. Two traditional ways [37] help workers to incorporate a refuge in predator-prey model for the studying of refuge: one is to assume that the reserve areas protect a constant proportion of prey; the other is to consider that a constant number of prey are protected by the refuge. The conclusions of the traditional literature about the role of refuge is that the addition of refuge for prey can enhance the stability of the positive equilibrium and affect positively the survival of prey and threaten the survival of predator. In [12], the oscillatory behaviour which is the case in the absence of a refuge will be replaced by a stable equilibrium when considering a huge refuge. McNair [23] found that prey predator oscillations will be amplified rather than damped be a prey refuge. Ruxton [32] considered a continuous-time predator-prey model where the rate that prey taken to the refuge is assumed to be proportional to the density of the predator, and the author showed that prey refuge has a stabilizing effect. With the propose of Holling types functional response [15], many works such as [17, 26] have considered a refuge in the model with Holling types functional response and got the conclusion that refuges used by prey can increase the stability of interior equilibrium. Ma [22] investigated a generalised predator-prey model with monotonous functional response which included the cases of Holling types I-III and found that the refuge used by prey also can destabilize the stability of the predator-prey interactions. Zhou et al. [40] gave a Hopf bifurcation of a predator-prey model with Holling type II functional response and prey refuge. Xiang et al. [38] obtained several high codimension bifurcation analysis for a Holling-Tanner model with generalist predator and prey refuge. For more investigations on biological models with refuge, we can refer the reader to [10, 33] and references therein.

Motivated by the above works, we extend model (1.5) and (1.6) by incorporating a refuge which is proportional to the density of prey. Our purpose is to identify the role of the refuge in a predator-prey model with a non-monotonic functional response. We assume that the reserve areas protect βx of the prey, where $\beta \in [0, 1)$. This leaves $(1-\beta)x$ of prey available to the predator, then system (1.6) yields that

$$\begin{cases} \frac{dx}{d\tau} = [r(1-\frac{x}{K})(x-m) - \frac{q(1-\beta)y}{(1-\beta)^2x^2+a}]x, \\ \frac{dy}{d\tau} = [\frac{p(1-\beta)x}{(1-\beta)^2x^2+a} - c]y, \end{cases} \tag{1.7}$$

where $p = \varepsilon q$ and β is refuge parameter. If $\beta = 0$, system (1.7) becomes system (1.6). It is not difficult to realise that system (1.7) is qualitatively equivalent to the system (1.6) and thus some dynamics of the system (1.7) are similar to those in the system (1.6). Yet the main purpose of this article is to illustrate the influence of the refuge on the existence of the positive equilibria in the system (1.7) and the effects of the refuge on the system (1.7) by giving a bifurcation analysis of system (1.7) in terms of the refuge parameter. The results obtained illustrate the additional refuge on prey brings about ample dynamics and makes the system more sensitive to parameter value.

Using the rescaling $u = \frac{x}{K}$, $v = \frac{y}{K}$, $t = rK\tau$, we have

$$\begin{cases} \frac{du}{dt} = [(1-u)(u-\alpha_1) - \frac{A\gamma v}{\gamma^2u^2+B}]u := F_1(u,v), \\ \frac{dv}{dt} = (\frac{C\gamma u}{\gamma^2u^2+B} - D)v := F_2(u,v), \end{cases} \tag{1.8}$$

where

$$C = \frac{p}{rK^2}, \quad B = \frac{a}{K^2} \in (0,1), \quad A = \frac{q}{rK^2}, \quad 0 < \alpha_1 = \frac{m}{k} \ll 1, \quad D = \frac{c}{rk},$$

and $\gamma = (1-\beta) \in (0,1]$ is anti-refuge parameter. We assume all the other parameters are positive. For convenience, in the next, we will consider the effect of γ, instead of β, on the dynamics of (1.8).

This paper is organized as follows. In section 2, the cases of no-existence, the existence of one or two interior equilibria, and their stability analysis are investigated. Bifurcation analysis is given in section 3. In the last section, we discuss our findings in terms of β and summarize our conclusions.

2. Existence and stability analysis

2.1. Dissipative

The following lemma shows the system (1.8) is dissipative.

Lemma 2.1 *Any solutions of (1.8) with a positive initial value are positive and bounded.*

Proof Since $\{(u,v) : u = 0\}$ and $\{(u,v) : v = 0\}$ are manifolds of (1.8), then the positive quadrant $\{(u,v) : u > 0, v > 0\}$ is an invariant region of (1.8). Therefore, any solutions of (1.8) with the initial value $u(0) > 0$ and $v(0) > 0$ are positive. For any $u(0) > 1$, then

$$\frac{du}{dt} = [(1-u)(u-\alpha_1) - \frac{A\gamma v}{\gamma^2u^2+B}]u < 0,$$

as long as $u > 1$. Along $u = 1$, we have:

$$\frac{du}{dt} = -\frac{A\gamma v}{\gamma^2u^2+B} < 0.$$

Then no equilibria of (1.8) can be found in the region $\{(u,v) : u > 1, v \geq 0\}$. Hence any positive solution satisfies $u(t) \leq \max\{u(0), 1\}$ for $t \geq 0$. Let

$$V(t) = u(t) + \frac{Av(t)}{C},$$

then differentiating V with respect to t, we yield

$$\begin{aligned} V'(t) &= u'(t) + \frac{Av'(t)}{C} \\ &= u(1-u)(u-\alpha_1) - \frac{ADv}{C} \\ &= u(1-u)(u-\alpha_1) + Du - D(u + \frac{Av}{C}). \end{aligned}$$

Let

$$\eta = \max_{t\geq 0} |u(1-u)(u-\alpha_1) + Du|,$$

then

$$V' \leq \eta - DV(t).$$

From Gronwall's inequality, we obtain that

$$V(t) \leqslant V(0)e^{-Dt} + \frac{\eta(1-e^{-Dt})}{D}.$$

Hence $v(t)$ is also bounded. Therefore, system (1.8) is dissipative. This completes the proof. □

2.2. Equilibria analysis

Now we discuss all the possible equilibria of the system (1.8). Clearly, system (1.8) has three equilibria $E_0(0,0)$, $E_1(1,0)$ and $E_2(\alpha_1, 0)$ which exist for all possible parameters. We now focus on the existence of equilibria interior to the positive quadrant. It is easy to see that the necessary condition for system (1.8) admitting a positive equilibrium is that the following equation has a positive root:

$$\frac{C\gamma u}{\gamma^2 u^2 + B} - D = 0.$$

Therefore, for $\gamma \in (0,1]$, we let

$$f(x) = \gamma^2 D x^2 - C\gamma x + BD, \qquad \Delta_1 = C^2 - 4BD^2,$$

then the existence of solution for $f(x) = 0$ is determined by the sign of Δ_1. We also should determine the v value of the equilibrium. Note that

$$(1-u')(u'-\alpha_1) = \frac{A\gamma v}{\gamma^2 u^2 + B}$$

where u' satisfies $f(u') = 0$, then we get

$$v' = \frac{(1-u')(u'-\alpha_1)(\gamma^2 u^2 + B)}{A\gamma}.$$

To guarantee $v' > 0$, the value of u' should satisfy $\alpha_1 < u' < 1$, which implies that the u value of a possible positive equilibrium of (1.8) belongs to the interval $(\alpha_1,\ 1)$. Let $E^*(u^*, v^*)$ be the unique interior equilibrium of system (1.8) and $E^1(u_1, v_1)$, $E^2(u_2, v_2)$ be the two different interior equilibria of system (1.8). We have the following several different cases:

(H1) $\Delta_1 < 0$. In this case, system (1.8) has no interior equilibria.

(H2) $\Delta_1 = 0$ and $D \le \frac{C}{2\gamma}$ or $D \ge \frac{C}{2\gamma\alpha_1}$. In this case, we know that $u^* = \frac{C}{2D\gamma}$. But u^* does not belong to $(\alpha_1, 1)$. Hence there is no positive equilibria for the system (1.8).

(H3) $\Delta_1 = 0$ and $\frac{C}{2\gamma} < D < \frac{C}{2\gamma\alpha_1}$. In this case, system (1.8) has unique positive equilibrium $E^*(u^*, v^*)$ where $u^* = \frac{C}{2D\gamma}$ and $v^* = g(u^*)$ with

$$g(x) = \frac{(1-x)(x-\alpha_1)}{\gamma^2 x^2 + B}.$$

(H4) $\Delta_1 > 0$, $\frac{C}{2\gamma} < D < \frac{C}{2\gamma\alpha_1}$, $f(1) > 0$, $f(\alpha_1) > 0$. We can easily see that two different inferior equilibria can be found for system (1.8) in this case, which are $E^1(u_1, v_1)$ and $E^2(u_2, v_2)$ where

$$u_1 = \frac{C - \sqrt{\Delta_1}}{2\gamma D}, \qquad v_1 = g(u_1),$$

$$u_2 = \frac{C + \sqrt{\Delta_1}}{2\gamma D}, \qquad v_2 = g(u_2).$$

(H5) $f(1) < 0$, $f(\alpha_1) > 0$. In this case, system (1.8) has two equilibria but one of them does not lie in the positive quadrant. So only $E^1(u_1, v_1)$ will be obtained for system (1.8).

(H6) $f(1) > 0$, $f(\alpha_1) < 0$. Then the system (1.8) only has $E^2(u_2, v_2)$ just because $u_1 < \alpha_1$.

(H7) $f(1) < 0$, $f(\alpha_1) < 0$. No interior equilibria can be detected for system (1.8) since $u_1 < \alpha_1$ and $u_2 > 1$.

(H8) $\Delta_1 > 0$, $D < \frac{C}{2\gamma}$, $f(1) > 0$. System (1.8) has no interior equilibria for $u_1 > 1$.

(H9) $\Delta_1 > 0$, $D > \frac{C}{2\gamma\alpha_1}$, $f(\alpha_1) > 0$. System (1.8) has no interior equilibria for $u_2 < \alpha_1$.

The following theorem summarizes what we have discussed above:

Theorem 2.2 *There are two different interior equilibria in the system (1.8) if (H4) holds, and only one interior equilibrium if (H3), (H5) or (H6) holds, while no interior equilibrium for cases of (H1), (H2), (H7), (H8) or (H9).*

Remark 2.3 *Assume that* $\Delta_1 = 0$*, then* $E^*(u^*, v^*)$ *coincides with* $E_1(1, 0)$ *and* $E_2(\alpha_1, 0)$ *if* $D = \frac{C}{2\gamma}$ *and* $D = \frac{C}{2\gamma\alpha_1}$*, respectively. When* $\Delta_1 > 0$*, the condition* $f(1) = 0$ *implies that either* $E^1(u_1, v_1)$ *or* $E^2(u_2, v_2)$ *coincides with* $E_1(1, 0)$*, while* $f(\alpha_1) = 0$ *implies either* $E^1(u_1, v_1)$ *or* $E^2(u_2, v_2)$ *coincides with* $E_2(\alpha_1, 0)$*. Moreover, if* $\Delta_1 > 0$*,* $f(1) = 0$ *and* $f(\alpha_1) = 0$*, then* $E^1(u_1, v_1)$ *and* $E^2(u_2, v_2)$ *coincide with* $E_2(\alpha_1, 0)$ *and* $E_1(1, 0)$ *respectively at the same time.*

2.3. Stability analysis

Let

$$G = \begin{pmatrix} F_1(u,v) \\ F_2(u,v) \end{pmatrix},$$

and the Jacobian matrix associated to system (1.8) is given by

$$J = \begin{pmatrix} F_{1u} & F_{1v} \\ F_{2u} & F_{2v} \end{pmatrix},$$

where

$$F_{1u} = (1-u)(u-\alpha_1) - \frac{A\gamma v}{\gamma^2u^2+B} - u(u-\alpha_1) + u(1-u) + \frac{2A\gamma^3u^2v}{(\gamma^2u^2+B)^2},$$

$$F_{1v} = -\frac{A\gamma u}{\gamma^2u^2+B},\ F_{2u} = \frac{(CB\gamma - C\gamma^3u^2)v}{(\gamma^2u^2+B)^2},\ F_{2v} = \frac{C\gamma v}{\gamma^2u^2+B} - D.$$

As far as $E_1(1,0)$ and $E_2(\alpha_1,0)$ are concerned, the Jacobian matrix evaluated at these points are:

$$J(E_1) = \begin{pmatrix} -(1-\alpha_1) & -\frac{A\gamma}{\gamma^2+B} \\ 0 & -\frac{1}{\gamma^2+B}f(1) \end{pmatrix},$$

$$J(E_2) = \begin{pmatrix} -\alpha_1(1-\alpha_1) & -\frac{A\gamma\alpha_1}{\gamma^2\alpha_1^2+B} \\ 0 & -\frac{1}{\gamma^2\alpha_1^2+B}f(\alpha_1) \end{pmatrix},$$

respectively. By standard stable analysis, we have following theorem.

Theorem 2.4 (1) $E_0(0,0)$ *is always a stable node for all possible parameters;*

(2) $E_1(1,0)$ *is a stable node for the cases of (H1), (H2), (H3), (H4), (H6) (H8) or (H9), while is a saddle for (H5) or (H7);*

(3) $E_2(\alpha_1,0)$ *is a saddle for the cases of (H1), (H2), (H3), (H4), (H5) (H8) or (H9), while is an unstable node for (H6) or (H7).*

By Theorem 2.2, system (1.8) has a unique equilibrium $E^*(u^*,v^*)$ in the case of (H3). Let

$$J(E^*) = \begin{pmatrix} -\frac{C^2}{8D^4\gamma^2}\Theta(D) & -\frac{2ACD}{C^2+4BD^2} \\ 0 & 0 \end{pmatrix},$$

where

$$\Theta(x) = 4\gamma^2\alpha_1x^2 - 4\gamma C(1+\alpha_1)x + 3C^2.$$

To obtain the stability of E^*, we need to decide the sign of $\Theta(D)$. Note the function $\Theta(x)$ is a parabola that opens up with a symmetry given by

$$x = \frac{C(1+\alpha_1)}{2\gamma\alpha_1} > 0.$$

Furthermore,

$$\Theta(\frac{C}{2\gamma}) = C^2(1-\alpha_1) > 0, \quad \Theta(\frac{C}{2\gamma\alpha_1}) = C^2(1-\frac{1}{\alpha_1}) < 0,$$

and

$$\frac{C}{2\gamma} < \frac{C}{2\gamma\alpha_1} < \frac{C(1+\alpha_1)}{2\gamma\alpha_1},$$

then we know there exists a $D^* \in (\frac{C}{2\gamma}, \frac{C}{2\gamma\alpha_1})$ with $\Theta(D^*) = 0$. A simply calculating yields

$$D^* = \frac{C(1+\alpha_1) - C\sqrt{1-\alpha_1+\alpha_1^2}}{2\gamma\alpha_1}.$$

Meanwhile, $\Theta(x)$ is monotone decreasing in the interval of $(\frac{C}{2\gamma}, \frac{C}{2\gamma\alpha_1})$. Thus we have the following theorem:

Theorem 2.5 *Assume the condition (H3) holds, then we have*

(1) E^* *is a saddle-node attractor (see Figure 1(a)) when* $D < D^*$*;*

(2) E^* *is a saddle-node repellor (see Figure 1(b)) when* $D > D^*$*;*

(3) E^* *can be a cusp (see Figure 1(c)) when* $D = D^*$*.*

In the case of (H4), system (1.8) has two different equilibria $E^1(u_1, v_1)$ and $E^2(u_2, v_2)$. It is apparent to see that E^2 is a saddle. For $E^1(u_1, v_1)$, one has

$$J(E^1) = \begin{pmatrix} F_{1u}(E^1) & F_{1v}(E^1) \\ F_{2u}(E^1) & 0 \end{pmatrix}.$$

Clearly, $\det(J(E^1)) > 0$. Then the stability of E^1 is dependent of the sign of $\mathrm{tr}(J(E^1))$, where

$$\begin{aligned} tr(J(E^1)) &= F_{1u}(E^1) \\ &= \frac{C-\sqrt{\Delta_1}}{2\gamma^2D^2[(C-\sqrt{\Delta_1})^2+4BD^2]}[-2(C-\sqrt{\Delta_1})^3 \\ &\quad + 2\gamma D(1+\alpha_1)(C-\sqrt{\Delta_1})^2 + 4B\gamma D^3(1+\alpha_1) \\ &\quad - 4D^2(B+\alpha_1\gamma^2)(C-\sqrt{\Delta_1})] \\ &\triangleq \frac{C-\sqrt{\Delta_1}}{2\gamma^2D^2[(C-\sqrt{\Delta_1})^2+4BD^2]} \cdot P^*(B,C,D,\gamma,\alpha_1). \end{aligned}$$

Therefore we have the following theorem,

Theorem 2.6 *Assume the condition (H4) holds, then we have*

(1) E^2 *is a saddle;*

(2) *when* $P^* > 0$, E^1 *is an unstable node (focus);*

(3) *when* $P^* < 0$, E^1 *is a stable node (focus);*

(4) *when* $P^* = 0$, E^1 *is a weak focus or center.*

Similarly, we can have the following theorems,

Theorem 2.7 *Assume the condition (H5) holds, then we have*

(1) E^1 *is an unstable node (focus) if* $P^* > 0$;

(2) E^1 *is a stable node (focus) if* $P^* < 0$;

(3) E^1 *is a weak focus or center if* $P^* = 0$.

Theorem 2.8 E^2 *is a saddle if (H6) holds.*

Remark 2.9 (1) *According to Theorem 2.4, the topological structure around* E_1 *and* E_2 *may change when parameter vector* $(A, B, C, D, \gamma, \alpha_1)$ *varies from certain case to another.*

(2) *According to Remark 2.3, the existence of interior equilibria of system (1.8) with parameter vector* $(A, B, C, D, \gamma, \alpha_1)$ *satisfying* $f(1) = 0$ *and* $f(\alpha_1) = 0$ *is very sensitive, since at any arbitrarily small neighbourhood of this kind of parameter, there exist some parameters such that it has none, one or two interior equilibria.*

(3) *System (1.8) may exhibit many heteroclinic curves joining* E_0 *and* E_2 *(see Figure 2).*

3. bifurcation analysis

3.1. Hopf bifurcation

In this subsection, we investigate the Hopf bifurcation in the system (1.8) which may occur only at E^1 for the cases of (H4) and (H5). We consider γ as the bifurcation parameter and set

$$P_1 = \{(A, B, C, D, \gamma, \alpha_1) : \Delta_1 > 0,\ \frac{C}{2\gamma} < D < \frac{C}{2\alpha_1\gamma},\ f(1) > 0,\ f(\alpha_1) > 0,\ \gamma = \gamma_h\},$$
$$P_2 = \{(A, B, C, D, \gamma, \alpha_1) : f(1) < 0,\ f(\alpha_1) > 0,\ \gamma = \gamma_h\},$$

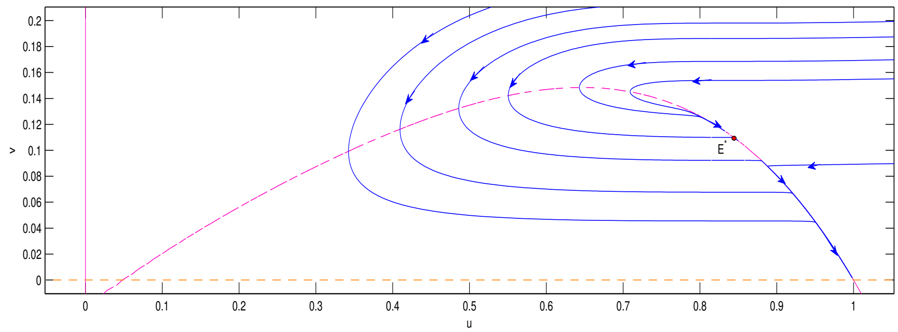
where γ_h satisfies

$$P^*(A, B, C, D, \gamma_h, \alpha_1) = 0. \tag{3.1}$$

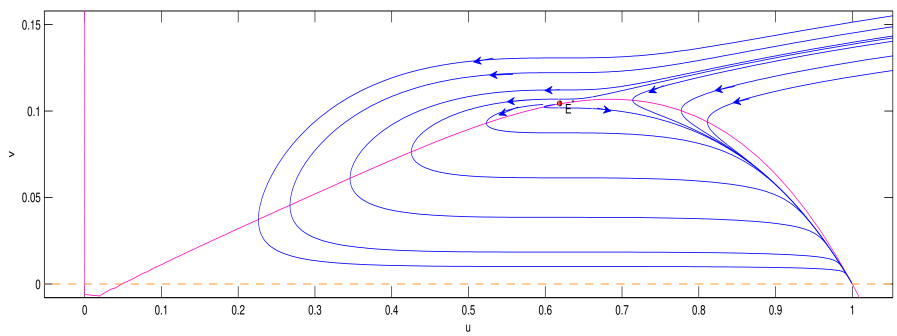
Clearly, $det(J(E^1)) > 0$ in the cases of (H4) and (H5). Since there are many parameters and it is hard to get the analytic expression. Then next we will use the numerical method to show that some parameters can be got in P_1 or P_2 which satisfies the following condition:

$$\frac{d}{d\gamma}\mathrm{tr}(J(E^1))\Big|_{\gamma=\gamma_h} > 0, \tag{3.2}$$

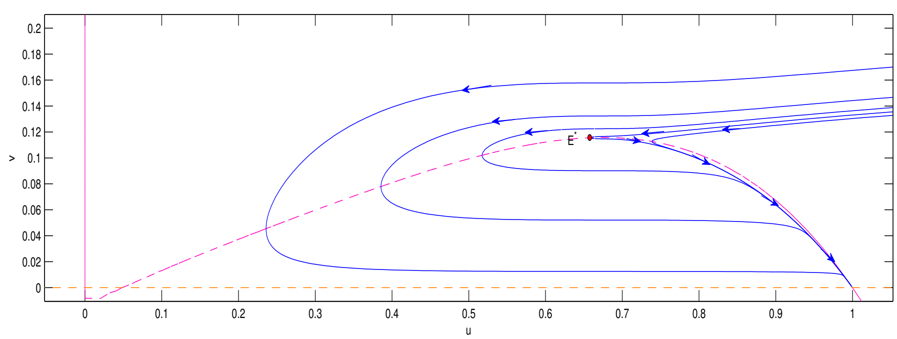
For $A = 0.8$, $B = 0.112$, $C = 0.5$, $D = 0.7404$, $\alpha_1 = 0.05$, we have Figure 3(a) and we know $\gamma_h = 0.4434$, which $(0.8, 0.112, 0.5, 0.7404, 0.4434, 0.05)$ belongs to P_1; for $A = 0.8$, $B = 0.6$, $C = 0.5$, $D = 0.2$, $\alpha_1 = 0.05$, we have Figure 3(b) and we know $\gamma_h = 0.474$, which $(0.8, 0.6, 0.5, 0.2, 0.474, 0.05)$ belongs to P_2. From what has been discussed above, we know that a parameter $(A, B, C, D, \gamma, \alpha_1)$ will be detected in P_1 or P_2 which satisfies (3.1) and (3.2). Now we know system (1.8) can undergo a Hopf bifurcation at E^1 for $\gamma = \gamma_h$ in the



(a) Saddle-node attractor.



(b) Saddle-node respellor.



(c) Cusp point.

Figure 1. Saddle-node attractor for $A = 0.8,\ B = 0.17715,\ C = 0.5,\ D = 0.594,\ \gamma = 0.5,\ \alpha_1 = 0.05$; saddle-node respellor for $A = 0.8,\ B = 0.0964,\ C = 0.5,\ D = 0.8052,\ \gamma = 0.5,\ \alpha_1 = 0.05$; cusp point for $A = 0.8,\ B = 0.111405,\ C = 0.5,\ D = 0.7404,\ \gamma = 0.5,\ \alpha_1 = 0.05$.

cases of (H4) and (H5). We further discuss the stability of E^1 and the limit cycle of the system (1.8) as a Hopf bifurcation occurs by calculating the first Lyapunov coefficient l [29] at E^1. Making the transformation

$$x_1 = u - u_1, \quad y_1 = v - v_1$$

to translate (u_1, v_1) to the origin, we have

$$\begin{cases} \dot{x_1} = a_{10}x_1 + a_{01}y_1 + a_{20}x_1^2 + a_{11}x_1y_1 + a_{02}y_1^2 + a_{30}x_1^3 + a_{21}x_1^2y_1 + a_{12}x_1y_1^2 \\ \qquad +a_{03}y_1^3 + O_1(x_1, y_1), \\ \dot{y_1} = b_{10}x_1 + b_{01}y_1 + b_{20}x_1^2 + b_{11}x_1y_1 + b_{02}y_1^2 + b_{30}x_1^3 + b_{21}x_1^2y_1 + b_{12}x_1y_1^2 \\ \qquad +b_{03}y_1^3 + O_2(x_1, y_1), \end{cases} \tag{3.3}$$

where

$$a_{10} = -(u_1 - \alpha_1)u_1 + (1 - u_1)u_1 + \frac{2A\gamma^3u_1^2v_1}{(\gamma^2u_1^2 + B)^2} = 0, \; a_{01} = -\frac{A\gamma u_1}{\gamma^2u_1^2 + B} < 0,$$

$$a_{20} = \frac{1}{2}\big[-2(u_1 - \alpha_1) - 2u_1 + 2(1 - u_1) + \frac{2A\gamma^3u_1v_1}{(\gamma^2u_1^2 + B)^2} + \frac{4AB\gamma^3u_1v_1 - 4A\gamma^5u_1^3v_1}{(\gamma^2u_1^2 + B)^3}\big],$$

$$a_{11} = \frac{A\gamma^3u_1^2 - AB\gamma}{2(\gamma^2u_1^2 + B)^2}, \; a_{02} = 0,$$

$$a_{30} = \frac{1}{6}\big[-6 + \frac{2AB\gamma^3v_1 - 6A\gamma^5u_1^2v_1}{(\gamma^2u_1^2 + B)^3} + \frac{-40AB\gamma^5u_1^2v_1 + 20A\gamma^7u_1^4v_1 + 4AB^2\gamma^3v_1}{(\gamma^2u_1^2 + B)^5}\big],$$

$$a_{21} = \frac{1}{6}\big[\frac{2A\gamma^3u_1}{(\gamma^2u_1^2 + B)^2} + \frac{4AB\gamma^3u_1 - 4A\gamma^5u_1^3}{(\gamma^2u_1^2 + B)^4}\big], \; a_{12} = 0, \; a_{03} = 0,$$

$$b_{10} = v_1\frac{C\gamma B - C\gamma^3u_1^2}{(\gamma^2u_1^2 + B)^2} > 0, \; b_{01} = 0, \; b_{20} = v_1\frac{C\gamma^5u_1^3 - 3BC\gamma^3u_1}{(\gamma^2u_1^2 + B)^3},$$

$$b_{11} = \frac{C\gamma B - C\gamma^3u_1^2}{(\gamma^2u_1^2 + B)^2}, \; b_{02} = 0, \; b_{30} = v_1\frac{6BC\gamma^5u_1^2 - B^2C\gamma^3 - C\gamma^7u_1^4}{(\gamma^2u_1^2 + B)^4},$$

$$b_{21} = \frac{C\gamma^5u_1^3 - 3BC\gamma^3u_1}{3(\gamma^2u_1^2 + B)^3}, \; b_{12} = 0, \; b_{03} = 0,$$

and $O_1(x_1, y_1)$, $O_2(x_1, y_1)$ are the smooth functions with at least the fourth order with respect to (x_1, y_1). Hence using the formula of the first Lyapunov coefficient l at the origin of system (3.3), we have

$$\begin{aligned} l = -\tfrac{3\pi}{2a_{01}\Delta^{3/2}}&([a_{10}b_{10}(a_{11}^2 + a_{11}b_{02} + a_{02}b_{11}) + a_{10}a_{01}(b_{11}^2 + a_{20}b_{11} + a_{11}b_{02}) \\ &+b_{10}^2(a_{11}a_{02} + 2a_{02}b_{02}) - 2a_{10}b_{10}(b_{02}^2 - a_{20}a_{02}) - 2a_{10}a_{01}(a_{20}^2 - b_{20}b_{02}) \\ &-a_{01}^2(2a_{20}b_{20} + b_{11}b_{20}) + (a_{01}b_{10} - 2a_{10}^2)(b_{11}b_{02} - a_{11}a_{20})] \\ &-(a_{10}^2 + a_{01}b_{10})[3(b_{10}b_{03} - a_{01}a_{30}) + 2a_{10}(a_{21} + b_{12}) + (b_{10}a_{12} - a_{01}b_{21})]), \end{aligned}$$

where $\Delta = a_{10}b_{01} - a_{01}b_{10}$. According to [28] and the equivalence between system (1.7) and system (1.6), we have $l \neq 0$, which guarantees the uniqueness of limit cycle, then the origin of system (3.3) is a weak focus of multiplicity one that is stable if $l < 0$ and unstable if $l > 0$ [29]. With the aid of numerical calculations, we can see that the sign of l can be negative at certain parameter $(A, B, C, D, \gamma, \alpha_1)$. For example, when the parameter $(A, B, C, D, \gamma, \alpha_1) = (0.8, 0.6, 0.5, 0.2, 0.474, 0.05)$ belongs to P_2, then $l = -1.068760e + 00 < 0$. Since the complexity of the expression of l, we have the following theorem theoretically:

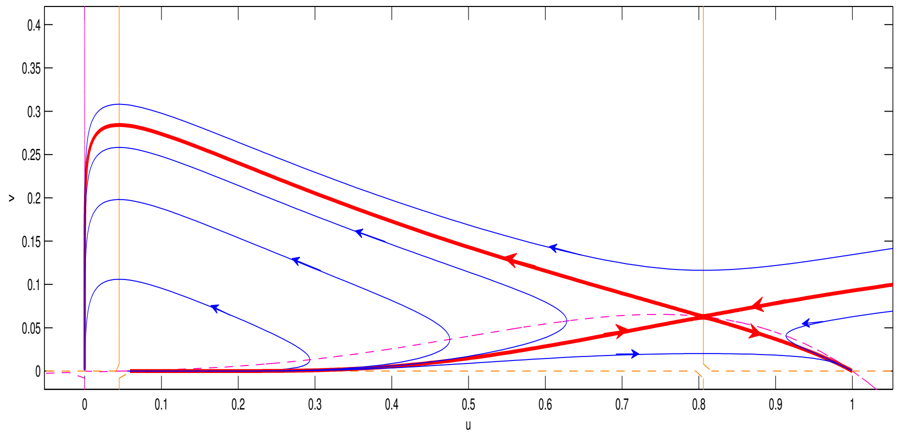


Figure 2. For $A = 0.8$, $B = 0.009$, $C = 0.5$, $D = 1.176$, $\gamma = 0.5$, α_1=0.05, there exists E^2 which is saddle and the red line is saddle point separatrix. Many heteroclinic curves connecting E_0 and E_2 can be found.

Theorem 3.1 *Let*

$$P_3 = \{(A, B, C, D, \gamma, \alpha_1) : (A, B, C, D, \gamma, \alpha_1) \in P_1 \ \textit{or} \ P_2, \ l < 0\},$$

$$P_4 = \{(A, B, C, D, \gamma, \alpha_1) : (A, B, C, D, \gamma, \alpha_1) \in P_1 \ \textit{or} \ P_2, \ l > 0\},$$

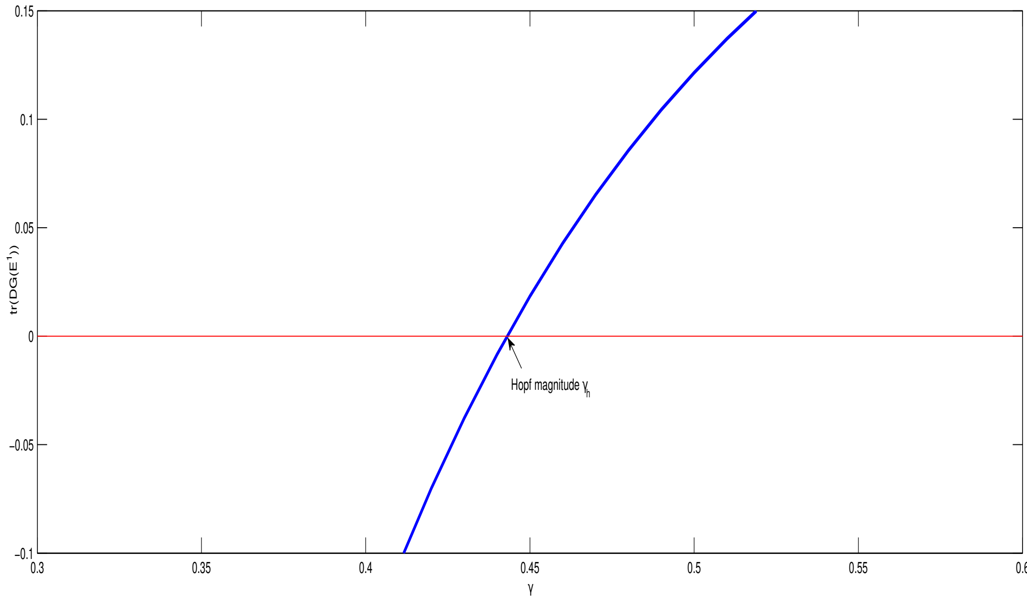
then

(1) if the parameter $(A, B, C, D, \gamma, \alpha_1)$ is in P_3, then the equilibrium E^1 of the system (1.8) is a weak focus of multiplicity one and is stable;

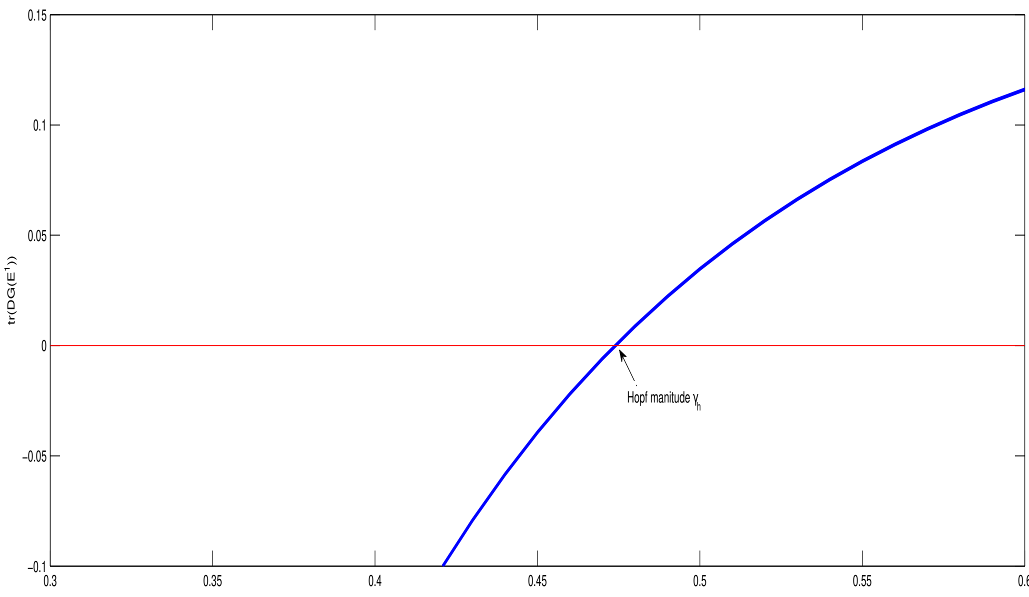
(2) if the parameter $(A, B, C, D, \gamma, \alpha_1)$ is in P_4, then the equilibrium E^1 of the system (1.8) is a weak focus of multiplicity one and is unstable.

We regard the sets $P_i, i = 3, 4$ as three surfaces. From Theorem 2.6, Theorem 2.7, and the first case in Theorem 3.1 coupled with the condition (3.2), we know that a stable limit cycle can be generated by the weak focus E^1 as γ passes through the bifurcation value $\gamma = \gamma_h$. When the parameter $(A, B, C, D, \gamma_h, \alpha_1)$ varies from one side of the surface P_3 to the other side, system (1.8) can experience a supercritical Hopf bifurcation [29] and a stable limit cycle occurs in the small neighbourhood of E^1 when $\gamma > \gamma_h$ and $(A, B, C, D, \gamma_h, \alpha_1) \in P_3$. Those phenomena can be numerically presented in (Figure 4).

On the other hand, from Theorem 2.6, Theorem 2.7 and the third case in Theorem 3.1 couple with the condition (3.2), we know that an unstable limit cycle can be generated by the weak focus E^1 as γ passes through the bifurcation value $\gamma = \gamma_h$. When the parameter $(A, B, C, D, \gamma_h, \alpha_1)$ varies from one side of the surface P_4 to the other side, system (1.8) may undergo a subcritical Hopf bifurcation [29] and an unstable limit cycle occurs in the small neighbourhood of E^1 when $\gamma < \gamma_h$ and $(A, B, C, D, \gamma_h, \alpha_1) \in P_4$.



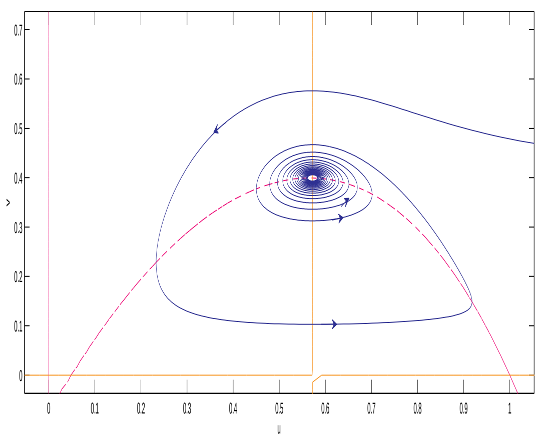
(a) $(A, B, C, D, \gamma_h, \alpha_1) \in P_1$.



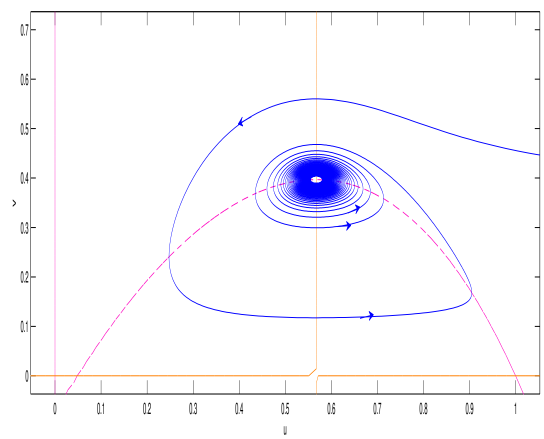
(b) $(A, B, C, D, \gamma_h, \alpha_1) \in P_2$.

Figure 3. Existence of Hopf bifurcation parameter γ.

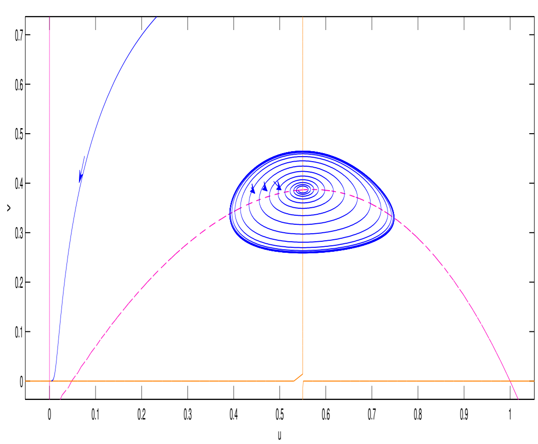
Now we show that Hopf bifurcation can be observed by changing the bifurcation parameter γ in the small neighbourhood of bifurcation value γ_h. We again use numerical way (Figure 4). If $0 < \gamma < \gamma_h$, system (1.8) has a stable equilibrium E^1 (Figure 4(a)). A stable limit cycle appears when γ passes through γ_h (Figures 4(b), 4(c), 4(d)) and the limit cycle expands with the increasing γ. As γ becomes larger, the stable limit cycle disappears and a homoclinic orbit is created by joining the stable and unstable manifolds of the saddle. By the



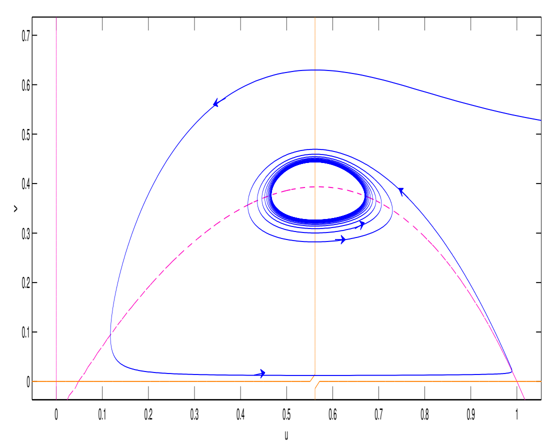
(a) $\gamma = 0.473$ $(\gamma < \gamma_h)$, E^1 is a stable focus.



(b) $\gamma = 0.474(\gamma = \gamma_h)$, a weak focus of multiplicity one occurs.



(c) $\gamma = 0.489(\gamma > \gamma_h)$, inside the stable limit cycle.



(d) $\gamma = 0.489(\gamma > \gamma_h)$, outside the stable limit cycle.

Figure 4. Bifurcation structure of E^1 for Hopf bifurcation for $A = 0.8$, $B = 0.6$, $C = 0.5$, $D = 0.2$, $\alpha_1 = 0.05$.

above statements, we have:

Theorem 3.2 (1) *System (1.8) has at least one stable limit cycle under the condition that the parameter* $(A, B, C, D, \alpha_1) \in P_3$, $\gamma > \gamma_h$ *and* $| \gamma - \gamma_h | \ll 1$.

(2) *System (1.8) has at least one unstable limit cycle under the condition that the parameter* $(A, B, C, D, \alpha_1) \in P_4$, $0 < \gamma < \gamma_h$ *and* $| \gamma - \gamma_h | \ll 1$.

3.2. Saddle-node bifurcation

Let

$$P_6 = \{(A, B, C, D, \gamma, \alpha_1) : \Delta_1 = 0,\ \frac{C}{2\gamma} < D < \frac{C}{2\gamma\alpha_1}\},$$

then from the theorem (2.2), we can see that when $(A_0, B_0, C_0, D_0, \gamma_0, \alpha_{10}) \in P_6$, system (1.8) has only one interior equilibrium $E^*(u^*, v^*)$. Let γ^* has following property:

$$D^* = \frac{C_0(1+\alpha_{10}) - C_0\sqrt{1-\alpha_{10}+\alpha_{10}^2}}{2\gamma^*\alpha_{10}}.$$

Now we choose B as the bifurcation parameter, then we have the following theorem.

Theorem 3.3 *For* $B = B_0$ *and* $\gamma_0 \neq \gamma^*$, *a saddle-node bifurcation occurs at the unique positive equilibrium* $E^*(u^*, v^*)$ *of system (1.8).*

Proof First, we have $\det(J(E^*)) = 0$. Then, $J(E^*)$ has an eigenvalue $\lambda_1 = 0$. According to Theorem 2.5, we know thast if $\gamma_0 \neq \gamma^*$, then $\lambda_1 = 0$ is simple. Let W_1 and W_2 be the eigenvectors corresponding to the $\lambda_1 = 0$ for $J(E^*)$ and $J(E^*)^T$ respectively. Then we have

$$W_1 = \begin{pmatrix} 1 \\ \frac{C_0^2+4B_0D_0^2}{2A_0C_0D_0} H_1 \end{pmatrix} := \begin{pmatrix} w_{11} \\ w_{12} \end{pmatrix},$$

and

$$W_2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}.$$

From the expressions for W_1 and W_2, we get

$$W_2^T G_B(E^*; B_0) = -\frac{C_0\gamma_0 u^* v^*}{(\gamma_0^2 u^{*2} + B_0)^2} \neq 0,$$

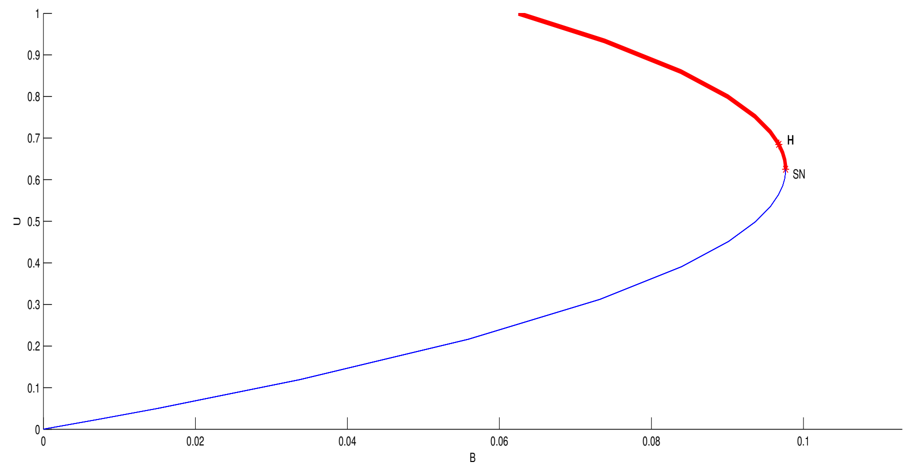
$$W_2^T D^2G(W_1, W_1) = -\frac{2C_0\gamma_0^3 u^* v^*}{(\gamma_0^2 u^{*2} + B_0)^2} \neq 0,$$

where $G_B = \frac{\partial G}{\partial B}$ and

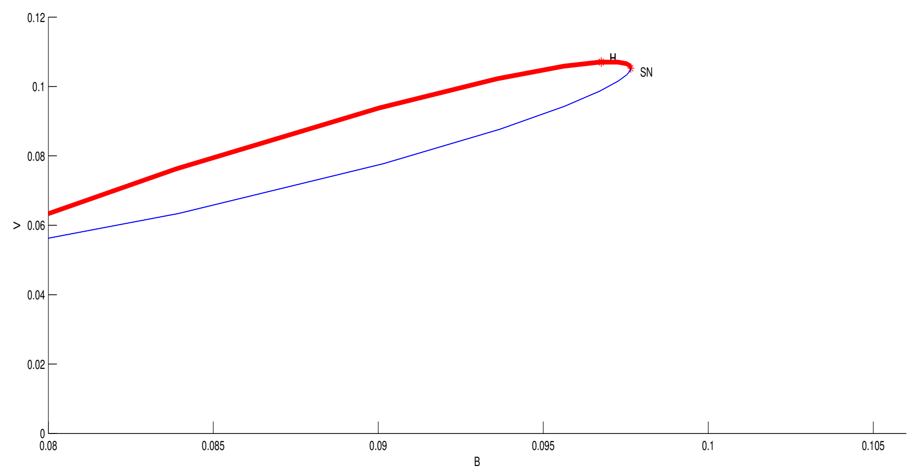
$$D^2G(W_1, W_1) = \frac{\partial^2 G}{\partial u^2} w_{11}w_{11} + \frac{\partial^2 G}{\partial u \partial v} w_{11}w_{12} + \frac{\partial^2 G}{\partial v \partial u} w_{12}w_{11} + \frac{\partial^2 G}{\partial v^2} w_{12}w_{12}.$$

By Sotomayor's theorem [29], system (1.8) undergoes a saddle-node bifurcation at E^* as B passes B_0 if $\gamma_0 \neq \gamma^*$. $\square$

We have a numerical example to illustrate a saddle-node bifurcation of system (1.8) (Figure 5). This example illustrates that when $B > B_0$ where B_0 represents saddle-node bifurcation parameter value, system (1.8) does not have any interior equilibria; when B passes through B_0 (in this example, $B_0 = 0.097656$), then system (1.8) has two different interior equilibria: the smaller equilibrium (blue) is unstable node and the larger one (red) is saddle.



(a) Prey population scenario.



(b) Predator population scenario.

Figure 5. A saddle-node bifurcation of system (1.8) at B_0=0.097656 (mark as SN), for $A = 0.8$, $C = 0.5$, $D = 0.8$, $\gamma = 0.5$, $\alpha_1 = 0.05$. A neutral saddle also occurs.

3.3. Bogdanov-Takens bifurcation

From the analysis in section 2, we know that when $(A, B, C, D, \gamma, \alpha_1) \in P_6$ and $D = D^*$, system (1.8) has an interior equilibrium E^* which can be a cusp. We use parameter $(A_0, B_0, C_0, D_0, \gamma_0, \alpha_{10})$ again and now

$\gamma_0 = \gamma_*$ (namely $D_0 = D^*$), then

$$det(J(E^*)) = 0, \quad tr(J(E^*)) = 0.$$

The following theorem indicates that system (1.8) could exhibit the BT bifurcation under a small parameter perturbation if we choose apt bifurcation parameters,

Theorem 3.4 *The interior equilibrium E^* of the system (1.8) is a cusp of codimension 2.*

Proof First of all, we translate the interior equilibrium E^* to the origin and expand the system (1.8) in a power series around the origin. Let

$$X = u - u^*, \quad Y = v - v^*,$$

then system (1.8) can be rewritten as

$$\begin{cases} \dot{X} &= -\frac{A_0\gamma_0 u^*}{\gamma_0^2 u^{*2}+B_0}Y + h(u^*)X^2 + R_{10}(X,Y), \\ \dot{Y} &= -\frac{2C_0\gamma_0^3 u^*}{(\gamma_0^2 u^{*2}+B_0)^2}X^2 + R_{20}(X,Y), \end{cases} \tag{3.4}$$

where

$$h(u^*) = \frac{-7u^{*2} + 3\alpha_{10}u^* + 3u^* - \alpha_{10}}{2u^*},$$

$R_{10}(X,Y)$ and $R_{20}(X,Y)$ are C^∞ functions in (X,Y) at least of the third order. Next, we study the normal form of system (1.8) in the two-dimensional center manifold. Making the affine transformation

$$X = X, \qquad Z = -\frac{A_0\gamma_0 u^*}{\gamma_0^2 u^{*2} + B_0}Y.$$

We can rewrite system (3.4) as follows:

$$\begin{cases} \dot{X} &= Z + h(u^*)X^2 + R_{11}(X,Z), \\ \dot{Z} &= \delta_1 X^2 + R_{21}(X,Z), \end{cases} \tag{3.5}$$

where

$$\delta_1 = \frac{2A_0C_0\gamma_0^4 u^{*2}}{(\gamma_0^2 u^{*2} + B_0)^3},$$

$R_{11}(X,Z)$ and $R_{21}(X,Z)$ are C^∞ functions in (X,Z) at least of the third order. In order to find the canonical form of the cusp, we take

$$f = X, \qquad e = Z + h(u^*)X^2 + R_{21}(X,Z),$$

and the system (3.5) becomes

$$\begin{cases} \dot{f} &= e, \\ \dot{e} &= \delta_1 f^2 + \delta_2 fe + R_{30}(f,e), \end{cases} \tag{3.6}$$

where $R_{30}(f,e)$ is a C^∞ function in (f,e) at least of the third order, and

$$\delta_2 = \frac{-7u^{*2} + 3\alpha_{10}u^* + 3u^* - \alpha_{10}}{4u^*}.$$

It is easy to see that $\delta_1 > 0$ and $\delta_2 < 0$, then $E^*(u^*, v^*)$ is a cusp of codimension 2. □

Next we are interested in the bifurcation of the cusp E^* as the parameters vary in a small neighbourhood of $(A_0, B_0, C_0, D_0, \alpha_{10})$. According to the Theorem (3.3), we choose B and γ as bifurcation parameters, then we obtain

Theorem 3.5 *The system (1.8) undergoes a Bogdanov-Takens bifurcation around the equilibrium point E^* when $B = B_0$ and $\gamma_0 = \gamma^*$.*

Proof Using the method in [21], we consider the neighbourhood of (B_0, γ^*), i.e. $\gamma = \gamma^* + \varepsilon_1$, $B = B_0 + \varepsilon_2$, where ε_i, $i = 1, 2$ are sufficient small, and system (1.8) becomes

$$\begin{cases} \frac{du}{dt} = [(1-u)(u-\alpha_{10}) - \frac{A_0(\gamma^*+\varepsilon_1)v}{(\gamma^*+\varepsilon_1)^2u^2+B_0+\varepsilon_2}]u, \\ \frac{dv}{dt} = [\frac{C_0(\gamma^*+\varepsilon_1)u}{(\gamma^*+\varepsilon_1)^2u^2+B_0+\varepsilon_2} - D_0]v. \end{cases} \tag{3.7}$$

We translate E^* to the origin and expand system (3.7) in a power series around the origin. Let

$$x_2 = u - u^*, \qquad y_2 = v - v^*.$$

Then we have

$$\begin{cases} \dot{x_2} = L_{10} + L_{11}x_2 + L_{12}y_2 + \frac{1}{2}L_{13}x_2^2 + L_{14}x_2y_2 + \frac{1}{2}L_{15}y_2^2 + T_1(x_2, y_2, \varepsilon_1, \varepsilon_2) \\ \quad := Q_1(x_2, y_2, \varepsilon_1, \varepsilon_2), \\ \dot{y_2} = L_{20} + L_{21}x_2 + L_{22}y_2 + \frac{1}{2}L_{23}x_2^2 + L_{24}x_2y_2 + \frac{1}{2}L_{25}y_2^2 + T_2(x_2, y_2, \varepsilon_1, \varepsilon_2) \\ \quad := Q_2(x_2, y_2, \varepsilon_1, \varepsilon_2), \end{cases} \tag{3.8}$$

and

$$L_{10} = \frac{A_0\gamma^*u^*v^*}{(\gamma^{*2}u^{*2}+B_0)^2}\varepsilon_2 + \xi_1(\varepsilon_1,\varepsilon_2),\ L_{11} = \frac{4A_0\gamma^{*4}u^{*4}v^*}{(\gamma^{*2}u^{*2}+B_0)^3}\varepsilon_1 - \frac{2A_0\gamma^{*3}u^{*2}v^*}{(\gamma^{*2}u^{*2}+B_0)^3}\varepsilon_2 + \xi_2(\varepsilon_1,\varepsilon_2),$$

$$L_{12} = -\frac{A_0\gamma^*u^*}{\gamma^{*2}u^{*2}+B_0} + \frac{A_0\gamma^*u^*}{(\gamma^{*2}u^{*2}+B_0)^2}\varepsilon_2 + \xi_3(\varepsilon_1,\varepsilon_2),\ L_{13} = h(u^*) - \frac{4A_0\gamma^{*4}u^{*3}v^*}{(\gamma^{*2}u^{*2}+B_0)^3}\varepsilon_1 + \xi_4(\varepsilon_1,\varepsilon_2),$$

$$L_{14} = \frac{2A_0\gamma^{*2}u^{*2}}{(\gamma^{*2}u^{*2}+B_0)^2}\varepsilon_1 - \frac{A_0\gamma^*}{(\gamma^{*2}u^{*2}+B_0)^2}\varepsilon_2 + \xi_5(\varepsilon_1,\varepsilon_2),\ L_{15} = 0,$$

$$L_{20} = -\frac{C_0\gamma^*u^*v^*}{(\gamma^{*2}u^{*2}+B_0)^2}\varepsilon_2 + \xi_6(\varepsilon_1,\varepsilon_2),\ L_{21} = -\frac{2C_0\gamma^{*2}u^{*2}}{(\gamma^{*2}u^{*2}+B_0)^2}\varepsilon_1 + \frac{C_0\gamma^*}{(\gamma^{*2}u^{*2}+B_0)^2}\varepsilon_2 + \xi_7(\varepsilon_1,\varepsilon_2),$$

$$L_{22} = -\frac{C_0\gamma^*u^*}{(\gamma^{*2}u^{*2}+B_0)^2}\varepsilon_2 + \xi_8(\varepsilon_1,\varepsilon_2),\ L_{23} = -\frac{4C_0\gamma^{*5}u^{*3}v^*}{(\gamma^{*2}u^{*2}+B_0)^3} + \frac{8C_0\gamma^{*6}u^{*5}v^*}{(\gamma^{*2}u^{*2}+B_0)^4}\varepsilon_1 + \xi_9(\varepsilon_1,\varepsilon_2),$$

$$L_{24} = -\frac{2C_0\gamma^{*2}u^{*2}}{(\gamma^{*2}u^{*2}+B_0)^2}\varepsilon_1 + \frac{C_0\gamma^*}{(\gamma^{*2}u^{*2}+B_0)^2}\varepsilon_2 + \xi_{10}(\varepsilon_1,\varepsilon_2),\ L_{25} = 0,$$

where $\xi_i(\varepsilon_1, \varepsilon_2)$, $i = 1, \cdots, 10$, are smooth functions at least of the second order, $T_1(x_2, y_2, \varepsilon_1, \varepsilon_2)$ and $T_2(x_2, y_2, \varepsilon_1, \varepsilon_2)$ are C^∞ functions at least of the third order with respect to (x_2, y_2), and the coefficients depend smoothly on ε_1 and ε_2, respectively. Making the parameter-dependent affine transformation

$$m = x_2, \quad n = L_{11}x_2 + L_{12}y_2,$$

system (3.7) becomes

$$\begin{cases} \dot{m} = L_{10} + n + (\frac{1}{2}L_{13} - \frac{L_{14}}{L_{12}}L_{11})m^2 + \frac{L_{14}}{L_{12}}mn + \tilde{T}_1(m,n,\varepsilon_1,\varepsilon_2), \\ \dot{n} = L_{11}L_{10} + L_{12}L_{20} + (L_{11} + L_{22}))n + (L_{12}L_{21} - L_{11}L_{22})m \\ \qquad +(\frac{1}{2}L_{11}L_{13} - \frac{L_{11}^2 L_{14}}{L_{12}} + \frac{L_{12}L_{13}}{2} - L_{11}L_{24})m^2 + (\frac{L_{11}L_{14}}{L_{12}} + L_{24})mn \\ \qquad +\bar{T}_2(m,n,\varepsilon_1,\varepsilon_2), \end{cases} \tag{3.9}$$

where $\bar{T}_1(m,n,\varepsilon_1,\varepsilon_2)$ and $\bar{T}_2(m,n,\varepsilon_1,\varepsilon_2)$ are C^∞ functions in variables (m,n) at least of the third order, the coefficients depend smoothly on ε_1 and ε_2.

Furthermore, if $\varepsilon_1 = \varepsilon_2 = 0$, we can see that

(BT0)

$$J(E^*,0,0) = \begin{pmatrix} 0 & -\frac{2A_0C_0D_0}{C_0^2+4B_0D_0^2} \\ 0 & 0 \end{pmatrix} \neq \theta_{2\times 2},$$

(BT1)

$$\Big[\frac{L_{13}}{2} - \frac{L_{11}L_{14}}{L_{12}} + \frac{L_{11}L_{14}}{L_{12}} + L_{24}\Big]\Big|_{\varepsilon_1=0,\varepsilon_2=0} = \frac{h(u^*)}{2} < 0,$$

(BT2)

$$\Big[-\frac{L_{11}L_{13}}{2} - \frac{L_{11}^2L_{14}}{L_{12}} + \frac{L_{12}L_{13}}{2} - L_{11}L_{24}\Big]\Big|_{\varepsilon_1=0,\varepsilon_2=0} = \frac{2C_0\gamma^{*6}u^{*4}v^*}{(\gamma^{*2}u^{*2}+B_0)^4} > 0,$$

(BT3) the map

$$\left(\begin{pmatrix} x_2 \\ y_2 \end{pmatrix}, \begin{pmatrix} \varepsilon_1 \\ \varepsilon_2 \end{pmatrix}\right) \longrightarrow \left(\begin{pmatrix} Q_1 \\ Q_2 \end{pmatrix}, \mathrm{tr}(M), \det(M)\right), i = 1,2$$

is regular at

$$\begin{pmatrix} x_2 \\ y_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix} \; and \; \begin{pmatrix} \varepsilon_1 \\ \varepsilon_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix},$$

where

$$M = \frac{\partial(Q_1,Q_2)}{\partial(x_2,y_2)}.$$

By the theorem in [21], the system (1.8) can undergo a Bogdanov-Takens bifurcation around the interior equilibrium point E^* when $B = B_0$ and $\gamma_0 = \gamma^*$. This completes the proof. □

Remark 3.6 *The quantity ω [21] which determines the structure of the bifurcation is given by*

$$\omega = sign[\frac{h(u^*)c_0\gamma^{*6}u^{*4}v^*}{(\gamma^{*2}u^{*2}+B_0)^4}] = -1.$$

The bifurcation diagram of system (1.8) in (γ, B) is presented in (Figure 6). Now we make a roundtrip near the Bogdanov-Takens point $(\gamma, B) = (0.498, 0.114)$ and sketch all the possible dynamical structures of the system (1.8) near the BT point. We start from domain 1 where there are no positive equilibria (and thus no limit cycles are possible). When through the horizontal line at the left part of BT point into domain 2, there are two possible structures that the system (1.8) can exhibit. The first case is that when entering from domain 1 into domain 2 through the left part of mark CP (which means the unique positive equilibrium E^* coincides with E_1), system (1.8) has no positive equilibria even though the change of number of equilibria can be from one to two. Yet one positive equilibrium (a stable node) can be detected after a certain point in domain 2; the second case is two interior equilibria (a stable node and a saddle) can be found when entering from domain 1 into domain 2 through the limit point curve (magenta) part between the mark CP and BT. Then the nodes in both cases turn into a focus and lose stability as we cross the Hopf curve (green). A stable limit cycle is presented for close parameter values to the right of the Hopf cure (green). If we continue the journey anticlockwise and finally return to domain 1 where no limit cycle can remain, there must be global bifurcations "destroying" the cycle somewhere between the hopf curve and limit point curve. According to [21], we know of only two such bifurcations of codim 1 in planar systems: a saddle homoclinic bifurcation and a saddle-node homoclinic bifurcation. Since the saddle-node equilibrium at the fold bifurcation cannot have a homoclinic orbit [21], the only possible candidate for global bifurcation is the appearance of an orbit homoclinic to the saddle. On the homoclinic curve (blue), an orbit homoclinic to the saddle $E_1(1,0)$ (Figure 7(a)) or an orbit homoclinic to the saddle E^2 (Figure 7(b)) can be found. As we trace the homoclinic orbit along the homoclinic curve toward the Bogdanov-Takens point, the looplike orbit shrinks and disappears. There exists a non-bifurcation line corresponding to a neutral saddle (black) between domain 4 and domain 5.

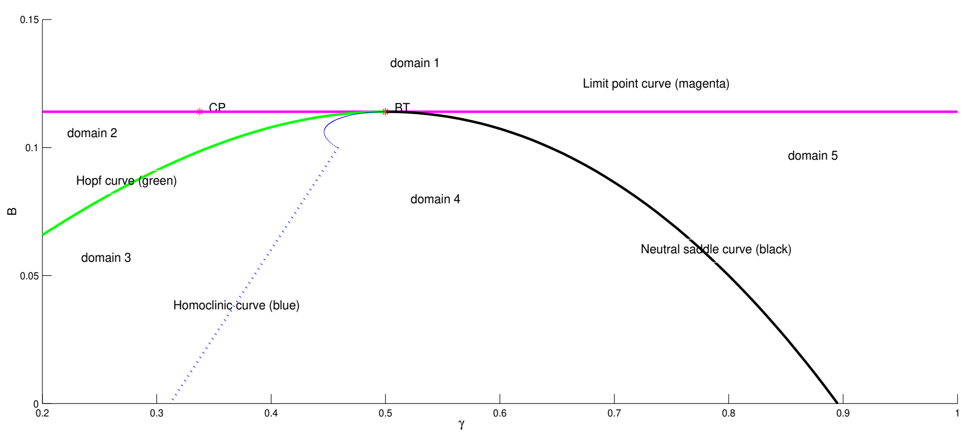
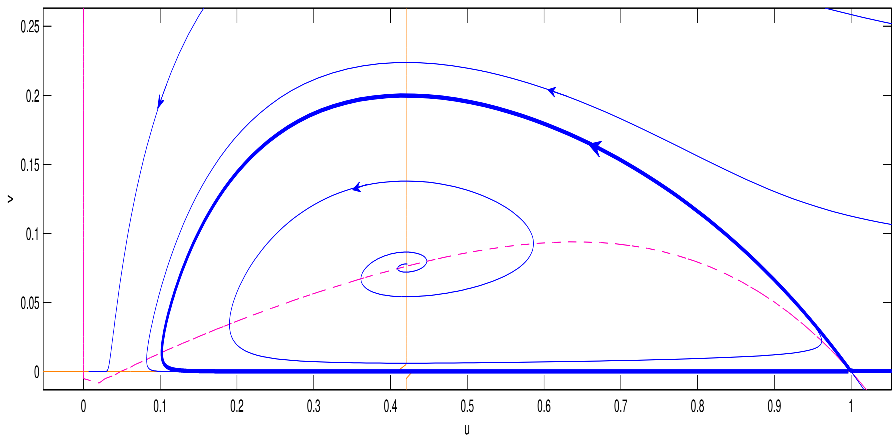


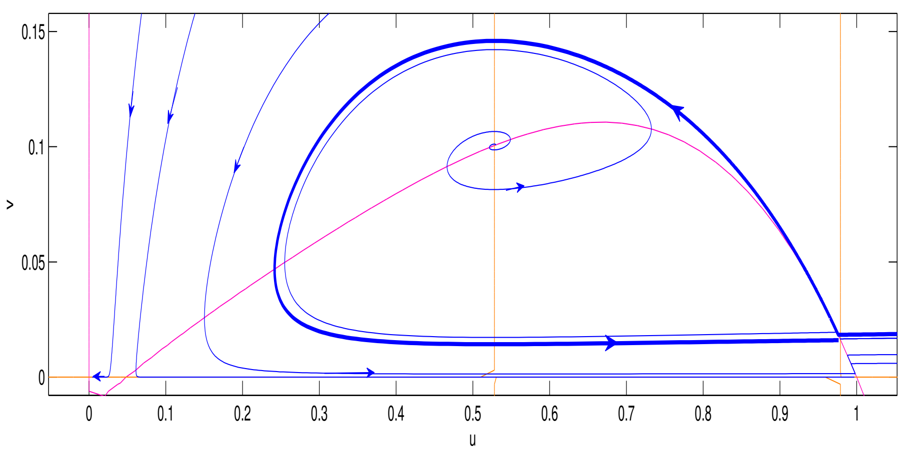
Figure 6. Bifurcation structure of system (1.8) in (γ, B) with a Bogdanov-Takens bifurcation for $A = 0.8$, $C = 0.5$, $D = 0.7404$, $\alpha_1 = 0.05$.

4. Discussion

In this paper, a model, equivalently extended by the model in [28], has been erected by considering a refuge which can protect prey proportionally to the density of prey. As mentioned in the introduction, the equivalence



(a) Homoclinic to E_1, $(\gamma, B) = (0.3, 0.06924)$.



(b) Homoclinic to E^2, $(\gamma, B) = (0.4482, 0.1038)$.

Figure 7. Homoclinic orbits for $A = 0.8$, $C = 0.5$, $D = 0.7404$, $\alpha_1 = 0.05$.

between system (1.7) and system (1.6) makes the stability analysis for both models have some similarities and also guarantees the uniqueness of limit cycle of the model in this paper, if it has. However, in this paper, we intend to analyse the influence that the refuge produced on the existence of positive equilibrium of the system (1.7) and make a well-round analysis. In addition, we conduct the bifurcation analysis of the system (1.7) mainly in terms of the refuge parameter to study the effect that variant values of refuge exert on the dynamics of the system (1.7), which was not considered in [28]. Noting the relationship between the anti-refuge parameter γ and the refuge parameter β, we can discuss the effect of refuge on the system (1.8) merely in terms of β.

According to the discussion in Section 2, we know that there are nine cases for the existence of the solution of system (1.8) and each case has a relationship with the value of β except the case (H1). In the case of (H1), because of the sign of Δ_1 fixed once we choose a certain value for (C, B, D), it has nothing to do with the value of β which explains why we take other parameter B rather than β as the parameter for saddle-node bifurcation that also can be explained by (Figure 6). Hence, when $\Delta_1 < 0$, the value of β does not have any effect on the system (1.8) and the system exhibits a bistability phenomenon for the existence of strong Allee effect. However, β plays a very important role in determining the existence of positive equilibria for the system (1.8) when the rest of the parameters are deterministic and $\Delta_1 \geq 0$. In the cases of (H2) and (H3), system (1.8) may have none or one interior equilibrium in which β can play a significant role. In cases of (H4) to (H9), just as the predator-prey system which considers a non-monotonic functional response in [28, 31], system (1.8) may have up to two positive equilibria (see the case (H4)). When we regard the parameter (A, B, C, D, α_1) as constant and $\Delta_1 > 0$, system (1.8) may have none, one or two positive equilibria when we increase refuge parameter β from 0. From what has been discussed above, we can conclude that considering refuge can alter the number of interior equilibria of the system (1.8) and make the system more complex. Meanwhile, contrasting to the case without refuge, adding refuge on the prey (increase the value of β) may increase the equilibrium density of the prey population which is natural as an increase in refuge parameter β decreases the predation risk for the prey population.

Due to the existence of a strong Allee effect, it is interesting to note that the origin E_0 is a locally asymptotically stable equilibrium point of system (1.8) for any set of parameter values and there exists a separatrix curve determined by the stable (unstable) manifold of E_2 which divides the behaviour of trajectories of the system into two domain in the phase plane, suggesting that the model is sensitive enough to the initial conditions which is also true in [28]. Consequently, the refuge used by prey does not decrease or diminish the effect that the Allee effect brings about.

In section 3, we consider β as the bifurcation parameter and find that system (1.8) can exhibit a subcritical Hopf bifurcation (because $\gamma = 1 - \beta$) and co-2 Bogdanov-Takens bifurcations with the other bifurcation parameter B. When in the cases of (H4) and (H5), then system (1.8) has either one interior equilibrium E^1 or two interior equilibria E^1 and E^2. In these cases, E^2 is saddle and the stability of E^1 is determined by the value of β. E^1 will be a unstable node when $\beta < \beta_h$ where $\beta_h + \gamma_h = 1$; the prey and predator populations oscillate around E^1 when $\beta = \beta_h$; when $\beta > \beta_h$, E^1 turns into a local stable node which means the two interacting populations tend to a stable equilibrium at some initial conditions; when the proportion of prey using refuge β increases further, the result shows that the considered model stabilizes at the predator-free equilibrium under some initial conditions, that is prey reaches its environment carrying capacity of prey and predators go extinct. When in the case of (H3), we detect a codimension-2 Bogdanov-Takens bifurcation with parameters B and γ. For the relationship between γ and β and according to the analysis of (Figure 6), we find that increasing β under proper initial conditions will also increase the local stability of the interior equilibrium. To sum up, under proper conditions, protecting a fraction of prey in the system (1.6) may alter the stability of interior equilibria and have a stabilizing effect.

Therefore, by the mathematical results established in this paper, we should take proper actions to protect the endangered species as soon as possible in case the quantity of the species is inferior to a certain threshold under which the strong Allee effect can urge the species goes extinction even without predation. Because once the number of species is below the threshold, the refuge on prey will play no role. Hence considering refuge is a good choice for the department concerned to preserve the endangered species at the beginning.

This paper admits improvement and leaves some questions for further discussion. For starters, what if we consider the quantity of hiding prey to be a constant number; the other one is what will happen if system (1.8) takes the form of the original Monod-Haldane, i.e.

$$\varphi(x) = \frac{qx}{a + bx + x^2}$$

and incorporates a proportion of refuge on prey. We surmise the system can have bifurcations of codimension-3 as a similar outcome has been observed in [30] without the Allee effect and refuge on prey.

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