

Codimension two and three bifurcations of a predator–prey system with group defense and prey refuge*

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Abstract. A predator–prey system with nonmonotonic functional response and prey refuge is considered. We mainly obtain that the system has the bifurcations of cusp-type codimension two and three, these illustrate that the dynamic behaviors of the model with prey refuge will become more complicated than the system with no refuge.

Keywords: prey refuge, saddle-node bifurcation, Bogdanov–Takens bifurcation.

1 Introduction

The predator–prey systems with group defense due to the increased ability of the prey to better defend or disguise themselves when their numbers are large enough have been researched by several papers, see [4, 7, 15] and the references therein.

Particularly, when the prey exhibits group defense, Freedman and Ruan [4] proposed a nonmonotonic functional response $p(x) = \alpha x e^{-\beta x}$, where α and β are positive constants. Xiao and Ruan [15] have studied a predator–prey system with the functional response $p(x)$ of the form

$$\begin{aligned}\dot{x} &= rx \left(1 - \frac{x}{K}\right) - \alpha xy e^{-\beta x}, \\ \dot{y} &= y(\mu \alpha x e^{-\beta x} - D).\end{aligned}\tag{1}$$

They have shown that system (1) undergoes a series of bifurcations including a supercritical Hopf bifurcation, a saddle-node bifurcation and a homoclinic bifurcation. In general, the system has codimension two bifurcation but no codimension three bifurcation.

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In the real environment, there always exists refuge for prey to protect them from the capture of the predator, which also can avoid the extinction of the prey and maintain the permanence of the species to some extent. The dynamics of some predator–prey systems with constant prey refuge have attracted some authors' attention, one can refer to [2, 5, 8, 10, 12, 13, 14] and the references therein, the effect of prey refuge on the stability and the existence of limit cycle of the corresponding systems has been discussed.

Hence, when considering the prey refuge in system (1), we can obtain the following model:

$$\begin{aligned}\dot{x} &= rx \left(1 - \frac{x}{K}\right) - \alpha(x - m)ye^{-\beta(x-m)}, \\ \dot{y} &= y(-D + \mu\alpha(x - m)e^{-\beta(x-m)}),\end{aligned}\quad (2)$$

where x and y denote the prey and predator populations, respectively, r , K , α , β , m , D and μ are positive constants. Here r denotes the intrinsic growth rate and K the carrying capacity of the prey; m is a constant number of prey using refuges, which protects m of prey from predation; D is the death rate of the predator; μ is the conversion factor of newly born predators for each captured prey. The term $\alpha xe^{-\beta x}$ represents the functional response of the predator.

For simplicity, let $\tau = rt$, $X = x$, $Y = \alpha y/r$ (still denote τ , X and Y as t , x and y), then system (2) is transformed to

$$\begin{aligned}\dot{x} &= x \left(1 - \frac{x}{K}\right) - y(x - m)e^{-\beta(x-m)} = P(x, y), \\ \dot{y} &= y(-d + c(x - m)e^{-\beta(x-m)}) = Q(x, y),\end{aligned}\quad (3)$$

where $c = \mu\alpha/r$, $d = D/r$.

For ecological meaning, we only study (3) in the first quadrant.

The organization of this paper is as follows. In Section 2, we mainly discuss the existence and the properties of the equilibria of system (3). In Section 3, we analyze all possible bifurcations according to the parameters of system (3). Especially, by choosing two parameters as bifurcation parameters, the versal unfolding of the Bogdanov–Takens singularity is given.

2 The existence and properties of positive equilibria

System (3) has a boundary equilibrium $E_0 = (K, 0)$, and about the properties of E_0 we have the following lemma.

Lemma 1. *Let $0 < m < K$. Then system (3) has equilibrium $E_0 = (K, 0)$ and:*

- E_0 is a hyperbolic saddle if $d < c(K - m)e^{-\beta(K-m)}$;
- E_0 is a hyperbolic stable node if $d > c(K - m)e^{-\beta(K-m)}$ and $d \neq -1 + c(K - m) \times e^{-\beta(K-m)}$;
- E_0 is a degenerate node if $d = -1 + c(K - m)e^{-\beta(K-m)}$;
- E_0 is a saddle-node if $d = c(K - m)e^{-\beta(K-m)}$.

Proof. The Jacobian matrix of system (3) at E_0 takes the form

$$J_{E_0} = \begin{pmatrix} -1 & -(K-m)e^{-\beta(K-m)} \\ 0 & -d + c(K-m)e^{-\beta(K-m)} \end{pmatrix}, \quad (4)$$

then the characteristic equation is

$$\lambda^2 + (1 + d - c(K-m)e^{-\beta(K-m)})\lambda + d - c(K-m)e^{-\beta(K-m)} = 0,$$

by above equation we can obtain the results of the lemma. \square

It is a more interesting topic to discuss the dynamical behaviors of system (3) at the interior positive equilibria. About the existence conditions and properties of interior positive equilibria, see the following lemma.

Lemma 2. Assume $0 < m < K - 1/\beta$, then system (3) has at least one positive equilibrium if $c/d \geq e\beta$. More precisely:

- (i) when $c/d = e\beta$, system (3) has a unique positive equilibrium $E_* = (m + 1/\beta, (m + 1/\beta)(\beta - (m\beta + 1)/K)e)$, which is a degenerate singularity;
- (ii) when $e\beta < c/d < e^{\beta(K-m)}/(K-m)$, system (3) has two distinct positive equilibria $E_1^* = (x_{1*}, y_{1*})$ and $E_2^* = (x_{2*}, y_{2*})$, where E_2^* is a hyperbolic saddle; when $c/d \geq e^{\beta(K-m)}/(K-m)$, only has E_1^* ; E_1^* is always stable if $K[m(1 + x_{1*}\beta) - x_{1*}^2\beta] > x_{1*}[m - (x_{1*} - m)(1 + x_{1*}\beta)]$ and $e\beta < c/d$.

Proof. To obtain the interior equilibria of system (3) we need solve the equation

$$d - c(x - m)e^{-\beta(x-m)} = 0, \quad \text{i.e.,} \quad f_1(x) = f_2(x) \quad (5)$$

in the interval (m, K) , where $f_1(x) = e^{\beta(x-m)}$, $f_2(x) = c/d(x - m)$.

By $f_1(x) = f_2(x)$ and $f_1'(x) = f_2'(x)$, Eq. (5) has a unique solution $x_* = m + 1/\beta$ if $c/d = e\beta$. $x_* \in (m, K)$ if and only if

$$0 < m < K - \frac{1}{\beta}. \quad (6)$$

Comparing the slopes and values of the curves f_1 and f_2 at x_* and K , respectively, one can obtain that Eq. (5) in the interval (m, K) has two positive solutions $x_{1*} \in (m, m + 1/\beta)$ and $x_{2*} \in (m + 1/\beta, K)$ if $e\beta < c/d < e^{\beta(K-m)}/(K-m)$ and $0 < m < K - 1/\beta$; one positive solution x_{1*} if $c/d \geq e^{\beta(K-m)}/(K-m)$ and $0 < m < K - 1/\beta$. The relation of the functions $f_1(x)$ and $f_2(x)$ also can be seen in Fig. 1.

Let $E = (x, y)$ be any positive equilibrium, then the Jacobian matrix of system (3) at E is

$$J_E = \begin{pmatrix} 1 - 2x/K - ye^{-\beta(x-m)}(1 - \beta(x-m)) & -(x-m)e^{-\beta(x-m)} \\ yce^{-\beta(x-m)}(1 - \beta(x-m)) & 0 \end{pmatrix}, \quad (7)$$

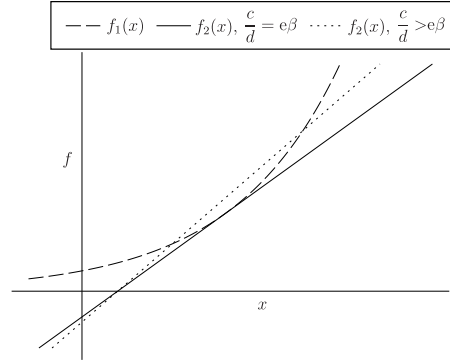


Fig. 1. The possible cases about the solutions of Eq. (5).

where $y = x(1 - x/K)e^{\beta(x-m)}/(x - m)$. Then we have

$$\det(J_E) = \frac{d\beta x}{x - m} \left(\frac{x}{K} - 1 \right) \left(x - m - \frac{1}{\beta} \right),$$

$$\text{tr}(J_E) = - \frac{[m(1 + x\beta) - x^2\beta]K + x[(x - m)(1 + x\beta) - m]}{K(x - m)}.$$

One can see that $\det(J_{E_*}) = 0$, thus, E_* is a degenerate singularity. Together with $\det(J_{E_1^*}) > 0$ and $\det(J_{E_2^*}) < 0$, we obtain the results of the lemma. \square

2.1 Properties of E_*

To discuss the properties of E_* of system (3) in detail, we need the following proposition.

Proposition 1. (See [11].) *By changes of coordinates and a rescaling of time, system*

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= x^2 + c_{30}x^3 + c_{40}x^4 + y(c_{21}x^2 + c_{31}x^3) + y^2(c_{22}x^2 + c_{12}x) + O(|(x, y)|^5) \end{aligned}$$

is equivalently transformed to the system

$$\begin{aligned} \dot{X} &= Y, \\ \dot{Y} &= X^2 + (c_{31} - c_{30}c_{21})X^3Y + O(|(X, Y)|^5). \end{aligned}$$

About the properties of the degenerate equilibrium E_* , we have the following theorem.

Theorem 1. *Let $0 < m < K - 1/\beta$ and $c/d = e\beta$. Then E_* is a unique degenerate equilibrium. More precisely:*

- when $m \neq K/2 - 1/\beta$, E_* is a saddle-node;

- when $m = K/2 - 1/\beta$ and $\beta \neq 2\sqrt{2}/K$, E_* is a cusp singularity of codimension 2;
- when $m = K/2 - 1/\beta$ and $\beta = 2\sqrt{2}/K$, E_* is a cusp singularity of codimension 3.

Proof. By the transformation $X = x - m - 1/\beta$ and $Y = y - (m + 1/\beta)(\beta - (m\beta + 1/K)e)$, we translate E_* to the origin, then system (3) can be rewritten as (still denote X, Y as x, y)

$$\begin{aligned}\dot{x} &= \left(1 - \frac{2}{K} \left(m + \frac{1}{\beta}\right)\right)x - \frac{y}{e\beta} + \frac{m(K-m)\beta^2 + (K-2m)\beta - 3}{2K}x^2 \\ &\quad + O(|(x, y)|^3), \\ \dot{y} &= \frac{(m\beta + 1)(m\beta + 1 - \beta K)e\beta d}{2K}x^2 + O(|(x, y)|^3).\end{aligned}\tag{8}$$

Since E_* is multiplicity 2, then E_* is a saddle node when $m \neq K/2 - 1/\beta$.

When $m = K/2 - 1/\beta$, system (8) can be written as

$$\begin{aligned}\dot{x} &= -\frac{y}{e\beta} + \frac{(K\beta)^2 - 8}{8K}x^2 - \frac{K\beta^3}{12}x^3 + \frac{\beta}{2e}x^2y + \frac{K\beta^4}{32}x^4 - \frac{\beta^2}{3e}x^3y \\ &\quad + O(|(x, y)|^5), \\ \dot{y} &= -\frac{eK\beta^3d}{8}x^2 + \frac{\beta^4eKd}{12}x^3 - \frac{d\beta^2}{2}x^2y - \frac{K\beta^5ed}{32}x^4 + \frac{d\beta^3}{3}x^3y \\ &\quad + O(|(x, y)|^5).\end{aligned}\tag{9}$$

In a small neighborhood of $(0, 0)$, we perform the first change of coordinates $X = x$, $Y = -y/(e\beta) + ((K\beta)^2 - 8)/(8K)x^2$, then (9) becomes (rewrite X, Y as x, y)

$$\begin{aligned}\dot{x} &= y - \frac{K\beta^3}{12}x^3 - \frac{\beta^2}{2}x^2y + \frac{\beta^2(3K^2\beta^2 - 16)}{32K}x^4 + \frac{\beta^3}{3}x^3y + O(|(x, y)|^5), \\ \dot{y} &= \frac{K\beta^2d}{8}x^2 + \frac{K^2\beta^2 - 8}{4K}xy - \frac{K\beta^3d}{12}x^3 - \frac{d\beta^2}{2}x^2y + w_{40}x^4 + w_{31}x^3y \\ &\quad + O(|(x, y)|^5),\end{aligned}\tag{10}$$

where

$$w_{40} = \frac{\beta^2}{2} \left(\frac{\beta}{3} - \frac{K^2\beta^3}{24} + \frac{3K\beta^2d}{16} - \frac{d}{K} \right), \quad w_{31} = \frac{\beta^3d}{3} + \frac{\beta^2}{K} - \frac{K\beta^4}{8}.$$

Notice that the coefficients of the terms x^2 and xy in system (10) are not zero if $\beta \neq 2\sqrt{2}/K$, hence, the equilibrium $(0, 0)$ of system (10) is a cusp of codimension 2, as used in [1, 15].

On the other hand, if $\beta = 2\sqrt{2}/K$, then (10) becomes

$$\begin{aligned}\dot{x} &= y - \frac{4\sqrt{2}}{3K^2}x^3 - \frac{4}{K^2}x^2y + \frac{2}{K^3}x^4 + \frac{16\sqrt{2}}{3K^3}x^3y + O(|(x, y)|^5), \\ \dot{y} &= \frac{d}{K}x^2 - \frac{4\sqrt{2}d}{3K^2}x^3 - \frac{4d}{K^2}x^2y + \frac{2d}{K^3}x^4 + \frac{16\sqrt{2}d}{3K^3}x^3y + O(|(x, y)|^5).\end{aligned}$$

Performing the second change of coordinates $X = x + 4/(3K^2)x^3$, $Y = y - 4\sqrt{2}/(3K^2)x^3$ (rewrite X, Y as x, y), we have

$$\begin{aligned}\dot{x} &= y + \frac{2}{K^3}x^4 + \frac{16\sqrt{2}}{3K^3}x^3y + O(|(x, y)|^5), \\ \dot{y} &= \frac{d}{K}x^2 - \frac{4\sqrt{2}d}{3K^2}x^3 - \frac{4(d + \sqrt{2})}{K^2}x^2y - \frac{2d}{3K^3}x^4 + \frac{16\sqrt{2}d}{3K^3}x^3y \\ &\quad + O(|(x, y)|^5).\end{aligned}\tag{11}$$

Taking the third change of coordinates $X = x - 4\sqrt{2}/(3K^3)x^4$, $Y = y + 2/K^3x^4 + O(|(x, y)|^5)$ (rewrite X, Y as x, y), we obtain that

$$\begin{aligned}\dot{x} &= y, \\ \dot{y} &= \frac{d}{K}x^2 - \frac{4\sqrt{2}d}{3K^2}x^3 - \frac{4(d + \sqrt{2})}{K^2}x^2y - \frac{2d}{3K^3}x^4 + \frac{8(2\sqrt{2}d + 3)}{3K^3}x^3y \\ &\quad + O(|(x, y)|^5).\end{aligned}$$

Let $X = (d/K)x$, $Y = (d/K)y$, then above system can be transformed to (still denote X, Y as x, y)

$$\begin{aligned}\dot{x} &= y, \\ \dot{y} &= x^2 - \frac{4\sqrt{2}}{3d}x^3 - \frac{4(d + \sqrt{2})}{d^2}x^2y - \frac{2}{3d^2}x^4 + \frac{8(2\sqrt{2}d + 3)}{3d^3}x^3y \\ &\quad + O(|(x, y)|^5).\end{aligned}\tag{12}$$

It follows from the Proposition 1 that system (12) is equivalent to the system

$$\begin{aligned}\dot{X} &= Y, \\ \dot{Y} &= X^2 - \frac{8}{3d^3}X^3Y + O(|(x, y)|^5).\end{aligned}\tag{13}$$

By [3], we know that the equilibrium $(0, 0)$ of system (13) is a cusp singularity of codimension 3 due to $-8/3d^3 < 0$. This completes the proof. \square

Remark. When system (3) has a cusp singularity $(\sqrt{2}/\beta, \sqrt{2}e/2)$ of codimension 3, if there exists an unfolding, then the unfolding of system (3) is equivalent to

$$\begin{aligned}\dot{x} &= y, \\ \dot{y} &= \mu_1 + \mu_2y + \mu_3xy + x^2 - x^3y + O(|(x, y)|^5).\end{aligned}$$

The bifurcation diagram of this form has been studied in [3].

3 Bifurcation analysis

In this section, we study all possible bifurcations of system (3) at its equilibria, which are not hyperbolic.

3.1 Saddle-node bifurcation

From Lemma 2 and Theorem 1 we see that the unique positive equilibrium E_* of system (3) is a saddle-node when $c/d = e\beta$, $0 < m < K - 1/\beta$ and $m \neq K/2 - 1/\beta$. Notice that

$$\begin{aligned} & \lim_{\hat{x} \rightarrow m+1/\beta} D(\hat{x}) \\ &= \lim_{\hat{x} \rightarrow m+1/\beta} (\operatorname{tr}(J_{\hat{E}})^2 - 4 \det(J_{\hat{E}})) = \operatorname{tr}(J_{E_*})^2 - 4 \det(J_{E_*}) > 0, \end{aligned}$$

when $m \neq K/2 - 1/\beta$, together with the continuity and the differentiability of function $D(\hat{x})$, which lead to $D(x_{1*}) > 0$ when x_{1*} is sufficiently near $m + 1/\beta$. Also notice that $\det(J_{E_1^*}) > 0$ and $\det(J_{E_2^*}) < 0$. Thus, when c/d passes $e\beta$ to the right-hand side, E_* splits into a hyperbolic node E_1^* and a hyperbolic saddle E_2^* . Therefore, there is a saddle-node bifurcation surface

$$SN = \left\{ (c, b, d, m): \frac{c}{d} = e\beta, 0 < m < K - \frac{1}{\beta}, m \neq \frac{K}{2} - \frac{1}{\beta} \right\}.$$

3.2 Bogdanov–Takens bifurcation

By Theorem 1, we know that system (3) has a cusp $(K/2, Ke\beta/4)$ of codimension 2 when $c/d = e\beta$, $m = K/2 - 1/\beta$ and $\beta \neq 2\sqrt{2}/K$, in this section, we will choose K and d as bifurcation parameters and show that system (3) exists the Bogdanov–Takens bifurcation. Consider the system

$$\begin{aligned} \dot{x} &= x \left[1 - x \left(\frac{1}{K} + \lambda_1 \right) \right] - y(x - m)e^{-\beta(x-m)}, \\ \dot{y} &= y(-d - \lambda_2 + c(x - m)e^{-\beta(x-m)}), \end{aligned} \quad (14)$$

where λ_1 and λ_2 are very small parameters.

Let $X = x - K/2$ and $Y = y - Ke\beta/4$. Then system (14) becomes (rewrite X, Y as x, y)

$$\begin{aligned} \dot{x} &= -\frac{K^2\lambda_1}{4} - \lambda_1 Kx - \frac{y}{e\beta} - \frac{8 + 8\lambda_1 - K^2\beta^2}{8K}x^2 + O(|(x, y)|^3), \\ \dot{y} &= -\frac{Ke\beta\lambda_2}{4} - \lambda_2 y - \frac{K\beta^3 de}{8}x^2 + O(|(x, y)|^3). \end{aligned} \quad (15)$$

Performing the transformations $X = x$ and $Y = -K^2\lambda_1/4 - \lambda_1 Kx - y/(e\beta) - (8 + 8\lambda_1 - K^2\beta^2)/(8K)x^2 + O(|(x, y)|^3)$ and rewriting X, Y as x, y , system (15) becomes

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= n_0 + n_1x + n_2y + n_3x^2 + n_4xy + O(|(x, y, \lambda)|^3), \end{aligned} \quad (16)$$

where $O(|(x, y, \lambda)|^3)$ is a smooth function of x, y and $\lambda = (\lambda_1, \lambda_2)$ at least of order three, and

$$\begin{aligned} n_0 &= -\frac{\lambda_2 K}{4}(\lambda_1 K - 1), & n_1 &= -\lambda_2 \lambda_1 K, & n_2 &= \lambda_2 - \lambda_1 K, \\ n_3 &= \frac{\beta^2}{8}(\lambda_2 + d)K - \lambda_2 \left(\lambda_1 + \frac{1}{K} \right), & n_4 &= -2\lambda_1 + \frac{K^2 \beta^2 - 8}{4K}, \end{aligned}$$

clearly, $n_3 > 0$ and $n_4 > 0$ ($n_4 < 0$) for $K\beta > 2\sqrt{2}$ ($K\beta < 2\sqrt{2}$),

Take $X = x + n_2/n_4$, $Y = y$ and substitute X, Y into system (16) and writing (X, Y) as (x, y) , we get that

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= m_0 + m_1 x + n_3 x^2 + n_4 xy + O(|(x, y, \lambda)|^3), \end{aligned} \quad (17)$$

where $m_0 = n_0 - n_1 n_2/n_4 + n_3 n_2^2/n_4^2$, $m_1 = n_1 - 2n_2 n_3/n_4$ and $O(|(x, y, \lambda)|^3)$ is a smooth function of x, y and $\lambda = (\lambda_1, \lambda_2)$ at least of order three.

Let $X = (n_4^2/n_3)x$, $Y = (n_4^3/n_3^2)y$, $t = (n_3/n_4)\tau$ and write (X, Y, τ) as (x, y, t) . Then system (17) becomes

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= \tau_1 + \tau_2 x + xy + x^2 + O(|(x, y, \lambda)|^3), \end{aligned} \quad (18)$$

where $O(|(x, y, \lambda)|^3)$ is a smooth function of x, y and $\lambda = (\lambda_1, \lambda_2)$ at least of order three, and

$$\tau_1 = \frac{m_0 n_4^4}{n_3^3}, \quad \tau_2 = \frac{m_1 n_4^2}{n_3^2}.$$

Hence, for system (18), the following bifurcation curves exists in a small neighborhood of the origin, see [6, 9].

Theorem 2. Assume $c/d = e\beta$, $m = K/2 - 1/\beta$ and $\beta K \neq 2\sqrt{2}$, then system (18) admits the following bifurcations:

- the saddle-node bifurcation curve $SN = \{(\lambda_1, \lambda_2): \tau_1 = \tau_2^2/4\}$, i.e., $SN = \{(\lambda_1, \lambda_2): 4n_3 m_0 = m_1^2\}$;
- the Hopf bifurcation curve $H = \{(\lambda_1, \lambda_2): \tau_1 = 0, \tau_2 < 0\}$, i.e., $H = \{(\lambda_1, \lambda_2): m_0 = 0, m_1 < 0\}$;
- the homoclinic bifurcation curve $HL = \{(\lambda_1, \lambda_2): \tau_1 = -6/25\tau_2^2, \tau_2 < 0\}$, i.e., $HL = \{(\lambda_1, \lambda_2): 25m_0 n_3 + 6m_1^2 = 0, m_1 < 0\}$.

Moreover, if $\beta K > 2\sqrt{2}$, then there exists a repelling B-T bifurcation; if $0 < \beta K < 2\sqrt{2}$, then there exists an attracting B-T bifurcation.

Take $\beta = 1$, $K = 3$ and $d = 2$, then $\beta K > 2\sqrt{2}$. The repelling bifurcation diagram is shown in Fig. 2.

Take $\beta = 0.5$, $K = 3$ and $d = 2$, then $\beta K < 2\sqrt{2}$. The attracting bifurcation diagram is shown in Fig. 3.

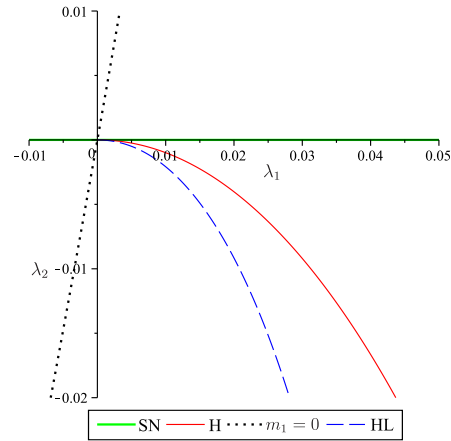
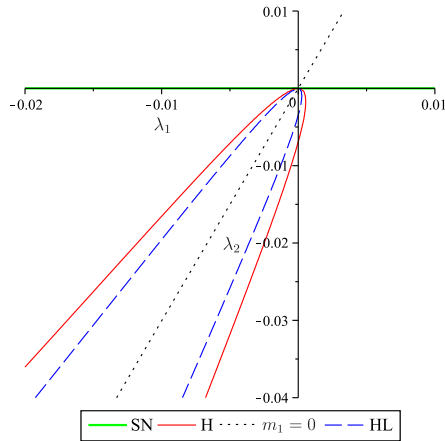


Fig. 2. The repelling bifurcation curve of Theorem 2. Fig. 3. The attracting bifurcation curve of Theorem 2. $m_1 < 0$ lies in the left-hand side of $m_1 = 0$.

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