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Computing the heteroclinic bifurcation curves in predator–prey systems with ratio-dependent functional response

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Abstract Predator–prey models with Michaelis–Menten–Holling type ratio-dependent functional response exhibit very rich and complex dynamical behavior, such as the existence of degenerate equilibria, appearance of limit cycles and heteroclinic loops, and the coexistence of two attractive equilibria. In this paper, we study heteroclinic bifurcations of such a predator–prey model. We first calculate the higher order Melnikov functions by transforming the model into a Hamiltonian system and then provide an algorithm for computing higher order approximations of the heteroclinic bifurcation curves.

Keywords Approximation · Melnikov functions · Heteroclinic loop · Hamiltonian system · Beta functions · Predator–prey system

Mathematics Subject Classification (2000) 34C05 · 34C60 · 92D25

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1 Introduction

In population dynamics of predator–prey models, the functional response describes the behavior of searching predators on a fast behavioral time scale, in minutes or hours, whereas the differential equations operate on a slow dynamical time scale, in days or years. To overcome this problem, Arditi and Ginzburg [1] suggested that the functional response should be expressed in terms of the ratio of prey to predators and proposed the following predator–prey model with Michaelis–Menten–Holling type ratio-dependent functional response:

$$\begin{cases} \frac{dx}{dt} = x\left(a - bx - \frac{cy}{x + my}\right), \\ \frac{dy}{dt} = y\left(-d + \frac{fx}{x + my}\right), \end{cases}$$

where a, b, c, d, f, m are positive coefficients and $x(t)$, $y(t)$ are the density of prey and predators, respectively, at time t. This system can be simplified as

$$\begin{cases} \frac{dx}{dt} = \alpha x(1 - x) - \frac{xy}{x + y}, \\ \frac{dy}{dt} = -\beta y + \frac{\kappa xy}{x + y} \end{cases} \tag{1.1}$$

with the changes of variables $x \mapsto (a/b)x,\ \ y \mapsto (a/mb)y,\ \ t \mapsto (m/c)t$, where $\alpha = ma/c,\ \beta = md/c,\ \kappa = mf/c.$

In the last decade, both biologists and mathematicians have paid great attention to this type of predator–prey models since many complicated dynamical phenomena, such as the existence of degenerate equilibria, appearance of limit cycles and heteroclinic loops, and the coexistence of two attractive equilibria, have been observed. In 1998, Kuang and Beretta [9] showed, by using the divergency criterion, that it has no nontrivial positive periodic solutions if the positive equilibrium is asymptotically stable. They also gave sufficient conditions on global asymptotic stability for each of the three possible equilibria $O = (0, 0)$, $A = (1, 0)$ and $B = (x_1, y_1)$, where $x_1 = (\alpha\kappa - \kappa + \beta)/\alpha\kappa$ and $y_1 = (\kappa - \beta)x_1/\beta$. In 2001, Hsu et al. [8] gave more results on the degenerate equilibrium O and proved that a periodic solution exists only in the case when

$$(\mathbf{HHK}): \qquad \beta < \kappa < \alpha + \beta < 1, \quad \alpha\kappa - \kappa + \beta > 0,$$

where the equilibrium B is unstable, and that such a periodic solution must be unique and stable. It was pointed out in [8] that a heteroclinic loop, formed by the equilibria O and A together with their joint separatrices, may exist when the unstable manifold of the saddle A happens to coincide with the orbit γ_0 which goes towards the degenerate equilibrium O in the direction of the polar angle $\theta = \arctan((\kappa - \alpha - \beta)/(\alpha + \beta - 1))$.

Efforts were made in studying the existence of the heteroclinic loop in system (1.1), among other dynamical properties, by Berezovskaya et al. [2] and Xiao and Ruan [16] at the same time (these two papers appeared in the same issue of the J Math Biol).

Under the condition (HHK), Berezovskaya et al. [2] used the continuity of the vector field to establish the existence of a constant κ_L between κ_H (the parameter value for the Hopf bifurcation at equilibrium B) and κ_{OB} (the parameter value for B to coincide with O), so that a heteroclinic loop exists at $\kappa = \kappa_L$. By investigating the topological structures in the neighborhood of the degenerate equilibrium O and the global dynamics involving all three equilibria, Xiao and Ruan [16] showed that, under certain parameter values, there is a heteroclinic loop, and when it is broken there exists a stable limit cycle surrounding the unstable positive equilibrium. Using the package XPP (see [6]), they demonstrated numerically the existence of a heteroclinic loop (Fig. 1) and the existence of a stable limit cycle (Fig. 2).

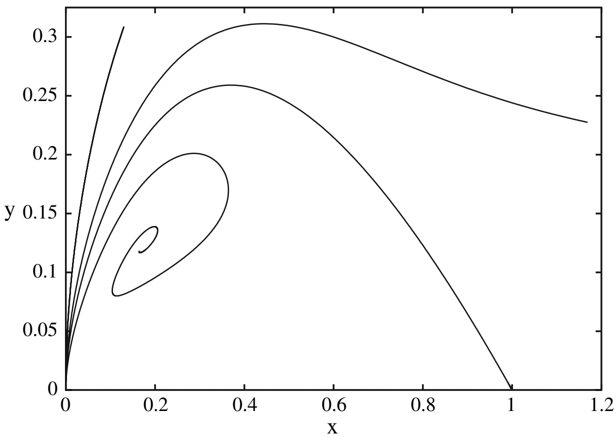

Fig. 1 The phase portrait of system (1.1) when $\alpha = 0.5$, $\beta = 1$, and $\kappa = 1.6$. $O = (0, 0)$ is an attractor, $A = (1, 0)$ is a saddle, and $B = (0.25, 0.15)$ is an unstable focus. There is a heteroclinic loop consisting of the origin O, the saddle A, the heteroclinic orbit connecting A and O, and the seperatrices between O and A. This is Fig. 4.8 in Xiao and Ruan [16]

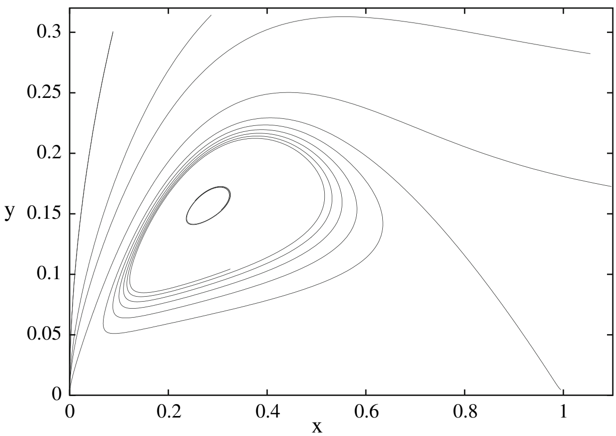

Fig. 2 The phase portrait of system (1.1) when $\alpha = 0.5$, $\beta = 1$, and $\kappa = 1.564$. The heteroclinic loop is broken and there is a stable limit cycle surrounding the unstable positive equilibrium $B = (0.2788, 0.1568)$. This is Fig. 4.7 in Xiao and Ruan [16]

Consider a prey species growing to its carrying capacity with logistic growth in a habitat [represented by the boundary equilibrium $A = (1, 0)$ in Fig. 1]. Now a predator species invades the habitat. Figure 1 indicates that, no matter what the initial densities of the prey and predators are, the predation will always drive both species to extinction. The heteroclinc orbit connecting the equilibria A and O describes the transition from positive density to extinction of both prey and predator populations. All solutions with initial values from either side of the heteroclinc orbit will eventually approach the origin. This is the catastrophe or overexploitation (van Voorn et al. [15]) scenario in predator–prey systems.

The interesting scenario is in Fig. 2. Though solutions with initial values outside the just-disappeared heteroclinc orbit still tend to the origin, solutions starting inside the previous heteroclinc orbit will approach the stable limit cycle surrounding the unstable positive equilibrium. Thus, both prey and predator populations coexist in oscillatory modes. Therefore, it is biologically significant and important to determine the heteroclinic bifurcation curves, *analytically and precisely,* in terms of the model parameters. In fact, mathematically heteroclinic bifurcation is also a very challenging and very active problem in dynamical systems (see, for example, Guckenheimer and Holmes [7], Zhang and Li [17]).

Motivated by these facts, in 2005, two of us gave an analytical condition on parameters for the existence of the heteroclinic loop in [14]. Blowing up the degenerate equilibrium O with a Briot–Bouquet transformation and reducing the transformed system of (1.1) to a perturbation of a Hamiltonian system possessing a triangular-like heteroclinic loop, we obtained an explicit expression of κ in terms of α and β, that is,

$$\kappa = \beta + \left(\frac{\beta}{2 - 2\alpha - \beta}\right)\alpha + O(\alpha^2), \tag{1.2}$$

by finding zeros of the Melnikov function ([7, 13]). The dependence defines a bifurcation curve in the (α, κ)-plane for the heteroclinic loop. Most recently, Li and Kuang [10] found a flaw in the dependence on β in our computation in [14]. Applying the same ideas and techniques to a different Hamiltonian system, they obtained a new explicit relation

$$\kappa = \beta + \left(\frac{\beta}{2 - \beta}\right)\alpha + \left(\frac{6\beta}{(4 - \beta)(2 - \beta)^2}\right)\alpha^2 + O(\alpha^3) \tag{1.3}$$

in a higher order expansion for the bifurcation curve of the heteroclinic loop.

In this paper we calculate the Melnikov functions of higher orders as in [5, 17] and present an algorithm for computing the higher order approximations to the bifurcation curves. The computational procedure of the first order Melnikov function, which was applied in [14] and [10], is simplified with properties of the Beta function. One can observe by comparing (1.2) and (1.3) that a further expansion with respect to α was neglected in [14]. We then employ the improved computational procedure to the same type of Hamiltonian system as considered in [14], where the further expansion is applied, and obtain the same expression (1.3) of the bifurcation curve as in [10]. In order to illustrate our algorithm, the second order Melnikov function is computed so that a third order approximation of the bifurcation curve of the heteroclinic loop is obtained.

The paper is organized as follows. Section 2 deals with the second order approximation. Higher order approximations are discussed in Sect. 3. Section 4 provides the algorithm for calculating the Melnikov functions.

2 Second order approximation

We still follow the steps in [14]. Under the condition (HHK) we only need to consider the equivalent system of (1.1), where (1.1) is multiplied by a factor $x + y$. Using the Briot–Bouquet transformation $\tilde{x} = x,\ u = y/x,\ d\tilde{t} = x\,dt$ and the substitutions of variables $\tilde{x} = x_1^2/\alpha,\ u = u_1^2/(1-\alpha-\beta),\ \tilde{t} = -2t_1$, respectively, the system can be transformed into the form

$$\begin{cases} x_1' = x_1\left(-\alpha + x_1^2 + \frac{1-\alpha}{1-\alpha-\beta}u_1^2 + \frac{1}{1-\alpha-\beta}x_1^2u_1^2\right), \\ u_1' = u_1\left(\alpha+\beta-\kappa - x_1^2 - u_1^2 - \frac{1}{1-\alpha-\beta}x_1^2u_1^2\right), \end{cases} \tag{2.1}$$

where x_1', u_1' represent the derivatives of x_1, u_1 with respect to t_1, respectively. System (2.1) has a unique equilibrium

$$B'' = \left(\sqrt{\frac{\alpha\kappa-\kappa+\beta}{\kappa}}, \sqrt{\frac{(\kappa-\beta)(1-\alpha-\beta)}{\beta}}\right)$$

in the interior of the first quadrant and three boundary equilibria:

$$O'' = (0,0), \quad O_1'' = (0, \sqrt{\alpha+\beta-\kappa}), \quad A'' = (\sqrt{\alpha}, 0).$$

Choose

$$\lambda_1 := -\alpha, \quad \lambda_2 := \alpha+\beta-\kappa \tag{2.2}$$

as the unfolding parameters. In order to reduce the highest order terms in (2.1) to small perturbations, we introduce a small parameter $\delta > 0$ and construct the invertible transformations $(x_1, u_1, t_1) \mapsto (v_1, v_2, \tau)$, $(\lambda_1, \lambda_2) \mapsto (\delta, \mu)$ such that

$$\begin{cases} x_1 = \sqrt{\delta}v_1, \quad u_1 = \sqrt{\delta}v_2, \quad t_1 = \delta^{-1}\tau, \\ \lambda_1 = -\delta, \quad \lambda_2 = \frac{2(1-\beta)}{2-\beta}\delta + \delta^2\mu, \end{cases} \tag{2.3}$$

which transfer system (2.1) into the form

$$\begin{cases} \frac{dv_1}{d\tau} = v_1(-1 + v_1^2 + \frac{1}{1-\beta}v_2^2) + \delta v_1\left[\frac{\beta}{(1-\beta)^2}v_2^2 + \frac{1}{1-\beta}v_1^2v_2^2 + O(|\delta|)\right], \\ \frac{dv_2}{d\tau} = v_2(\frac{2(1-\beta)}{2-\beta} - v_1^2 - v_2^2) + \delta v_2\left[\mu - \frac{1}{1-\beta}v_1^2v_2^2 + O(|\delta|)\right]. \end{cases} \tag{2.4}$$

In contrast to (3.5) in [14], an expansion of a coefficient $(1-\alpha)/(1-\alpha-\beta)$ with respect to δ is applied in (2.4), i.e.,

$$\frac{1-\alpha}{1-\alpha-\beta} = \frac{1}{1-\beta} + \left(\frac{\beta}{(1-\beta)^2}\right)\delta + O(\delta^2).$$

Multiplying system (2.4) by the integrating factor $v_1^{\xi-1}v_2^{\eta-1}$, where

$$\xi = \frac{4(1-\beta)}{\beta} > 0, \qquad \eta = \frac{2(2-\beta)}{\beta} > 0, \tag{2.5}$$

we obtain a perturbed Hamiltonian system H_δ:

$$\begin{cases} \frac{dv_1}{d\tau} = v_1^{\xi}v_2^{\eta-1}\left(-1+v_1^2+\frac{1}{1-\beta}v_2^2\right) + \delta v_1^{\xi}v_2^{\eta-1}\left[\frac{\beta}{(1-\beta)^2}v_2^2 + \frac{1}{1-\beta}v_1^2v_2^2 + O(|\delta|)\right], \\ \frac{dv_2}{d\tau} = v_1^{\xi-1}v_2^{\eta}\left(\frac{2(1-\beta)}{2-\beta} - v_1^2 - v_2^2\right) + \delta v_1^{\xi-1}v_2^{\eta}\left[\mu - \frac{1}{1-\beta}v_1^2v_2^2 + O(|\delta|)\right], \end{cases} \tag{2.6}$$

which is equivalent to system (2.4) in the sense that they have the same phase portrait. Here we only consider small α so that $|\delta|$ is small. Note that (2.2) and the second line in (2.3) make a one-to-one correspondence between (α, κ) and (δ, μ) for each fixed β. Thus, one can treat β in (2.4) as a parameter independent of the small δ. In this sense no coefficients in the Hamiltonian system H_0 (i.e., system (2.6) with $\delta = 0$) depend on the perturbation parameter δ.

Let

$$\sigma := \sqrt{\frac{1-\beta}{2-\beta}}, \qquad h_B := \frac{1}{\eta}\sigma^{\xi+\eta}\left(-1+\sigma^2+\frac{\eta}{\xi}\sigma^2\right) = -\frac{1}{\eta}\sigma^{\xi+\eta}\frac{\beta}{2(2-\beta)}.$$

Obviously, $\sigma > 0$ and $h_B < 0$ under the condition (HHK).

Lemma 2.1 *Under the condition (HHK) system H_0, that is system (2.6) for $\delta = 0$, is Hamiltonian with the Hamiltonian function $H(v_1, v_2) = \frac{1}{\eta}v_1^{\xi}v_2^{\eta}(-1+v_1^2+\frac{\eta}{\xi}v_2^2)$. The system has three saddles at $\mathcal{O}_0 = (0,0)$, $\mathcal{O}_1 = (0, \sqrt{2}\sigma)$, $\mathcal{A}_1 = (1,0)$, and a center at $\mathcal{B}_1 = (\sigma, \sigma)$ in the first quadrant. Moreover, for $h = h_B$ the curve $H(v_1, v_2) = h$ is just the center $\mathcal{B}_1$; for $h_B < h < 0$ the curve $H(v_1, v_2) = h$ is a periodic orbit around the center; and for $h = 0$ the curve is a heteroclinic orbit Γ_0 formed by the equilibria $\mathcal{O}_0$, $\mathcal{A}_1$ and $\mathcal{O}_1$ of system H_0 together with their joint separatries, as shown in Fig. 3.*

The proof of this lemma is almost the same as the proof of Lemma 3 in [14] except that we note that the linearized system at $\mathcal{O}_0$ has eigenvalues -1 and $2\sigma^2$ and the linearized system at $\mathcal{B}_1$ has a pair of purely imaginary eigenvalues $\pm 2i\sqrt{\beta(1-\beta)}/(2-\beta)$. The branch of the curve $H(v_1, v_2) = 0$, which is a heteroclinic orbit connecting

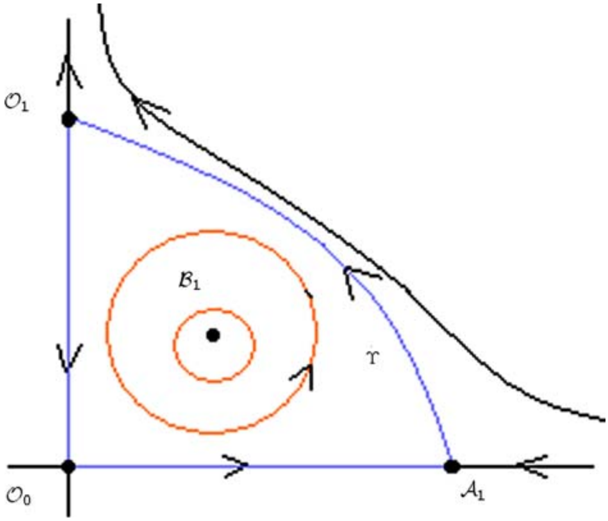

Fig. 3 The Hamiltonian system H_0

saddles $\mathcal{O}_1$ and $\mathcal{A}_1$, is Υ:

$$v_1^2 + \frac{\eta}{\xi} v_2^2 = 1. \tag{2.7}$$

Lemma 2.1 enables us to reduce the problem of the heteroclinic loop to the bifurcation of the heteroclinic orbit Υ in the system H_δ (for $\delta \neq 0$).

Theorem 2.2 *Under the condition (HHK), for small $|\delta|$ system (2.6) (i.e., H_δ) has a heteroclinic orbit when*

$$\mu = -\frac{6\beta}{(4-\beta)(2-\beta)^2} + O(\delta). \tag{2.8}$$

Proof We need to investigate how the perturbation term of the lowest degree

$$\begin{aligned}&(\varphi_1(v_1, v_2), \varphi_2(v_1, v_2))^T\\ &:= \left(v_1^{\xi} v_2^{\eta-1} \left[\frac{\beta}{(1-\beta)^2} v_2^2 + \frac{1}{1-\beta} v_1^2 v_2^2 \right],\ v_1^{\xi-1} v_2^{\eta} \left[\mu - \frac{1}{1-\beta} v_1^2 v_2^2 \right] \right)^T\end{aligned}$$

affects the Hamiltonian system H_0. As known in [7], system (2.6) for $\delta \neq 0$ has a heteroclinic loop near Γ_0 if the Melnikov function

$$M_1(\mu) := \int\limits_{\Upsilon} \{\varphi_2(v_1, v_2)dv_1 - \varphi_1(v_1, v_2)dv_2\}$$

$$= \left(\frac{\xi}{\eta}\right)^{\frac{\eta}{2}} \int\limits_0^1 \left\{\mu v_1^{\xi-1}\left(1-v_1^2\right)^{\frac{\eta}{2}} - \frac{\xi}{(1-\beta)\eta} v_1^{\xi+1}\left(1-v_1^2\right)^{\frac{\eta+2}{2}}\right.$$

$$\left. + \frac{\xi}{(1-\beta)\eta} v_1^{\xi+3}\left(1-v_1^2\right)^{\frac{\eta}{2}} + \frac{\beta\xi}{(1-\beta)^2\eta} v_1^{\xi+1}\left(1-v_1^2\right)^{\frac{\eta}{2}}\right\} dv_1, \quad (2.9)$$

has a zero, where Υ denotes a heteroclinic orbit in Γ_0 connecting saddles $\mathcal{O}_1$ and $\mathcal{A}_1$, as shown in (2.7). Solving $M_1(\mu) = 0$, we obtain a unique solution

$$\mu = \frac{\frac{\xi}{(1-\beta)\eta} J(\xi+1, \eta+2) - \frac{\xi}{(1-\beta)\eta} J(\xi+3, \eta) - \frac{\beta\xi}{(1-\beta)^2\eta} J(\xi+1, \eta)}{J(\xi-1, \eta)}, \quad (2.10)$$

where

$$J(s_1, s_2) = \int\limits_0^1 v_1^{s_1}(1-v_1^2)^{\frac{s_2}{2}} dv_1 = \frac{1}{2} B\left(\frac{s_1+1}{2}, \frac{s_2+2}{2}\right) \quad (2.11)$$

and $B(p, q)$ is the Beta function for $p > 0$ and $q > 0$. In the computation of (2.11) the expression (2.7) of curve Υ is used. Note that $B(p, q) = \Gamma(p)\Gamma(q)/\Gamma(p+q)$ and $\Gamma(s+1) = s\Gamma(s)$ for $s > 0$, where $\Gamma(s)$ is the Gamma function. It follows from (2.10) that

$$\mu = \frac{\xi^2}{(1-\beta)\eta(\xi+\eta+2)}\left(\frac{\eta+2}{\xi+\eta+4} - \frac{\xi+2}{\xi+\eta+4} - \frac{\beta}{1-\beta}\right)$$

$$= -\frac{6\beta}{(4-\beta)(2-\beta)^2}, \quad (2.12)$$

that is, the bifurcation curve for the heteroclinic orbit is given by (2.8), as shown in the Melnikov's theory (see, e.g., [7]). □

With the changes of parameters (2.2) and the second line in (2.3), the expression (2.8) can be equivalently rewritten as

$$\kappa = \beta + \left(\frac{\beta}{2-\beta}\right)\alpha + \left(\frac{6\beta}{(4-\beta)(2-\beta)^2}\right)\alpha^2 + O(\alpha^3), \quad (2.13)$$

the same expression as (1.3). By the equivalence among those reduced systems, Theorem 2.2 indicates that system (1.1) has the heteroclinic loop when parameters α, β, κ lie on the bifurcation curve (2.13), denoted by $\kappa_L(\alpha, \beta)$. One can observe that the expression (1.2) (i.e., (3.20) in [14]) has the same first two terms as the expression

(2.13) if we expand the coefficient $\beta/(2-2\alpha-\beta)$ in (1.2) with respect to α. The more precise expression (2.13) is actually the second order approximation to the bifurcation curve $\kappa_L(\alpha, \beta)$.

We remark that the first order Melnikov function for a heteroclinic loop near Γ_0 was computed inappropriately by

$$M_1(\mu) := \int\int_{\mathrm{int}\Gamma_0} \text{trace } D(\varphi_1(v_1, v_2), \varphi_2(v_1, v_2))^T \, dv_1 dv_2 \tag{2.14}$$

in both [10] and [14], where $\mathrm{int}\Gamma_0$ denotes the region with boundary Γ_0, but it is corrected in the proof of our Theorem 2.2. From [7] we see that the correct expression of $M_1(\mu)$ is given as in (2.9) by an integral on the curve Υ. Note that Υ is not a closed curve and therefore we cannot apply the Green formula to reduce the integral on curve in (2.9) to the form of (2.14).

3 Higher order approximation

From (2.12) in the proof of Theorem 2.2 we easily see that the first order Melnikov function $M_1(\mu) \equiv 0$ when $\mu \equiv -6\beta/\{(4-\beta)(2-\beta)^2\}$. By the Melnikov theory in dynamical systems (see Zhang and Li [17]), we have to calculate higher order Melnikov functions as done in [5,11,17]. We will calculate coefficients of α^k ($k \geq 3$) in (2.13) and give a higher order approximation to the bifurcation curve.

We present the detailed procedure of calculating the coefficient of α^3 in (2.13). Firstly, applying the substitution of variables

$$\tilde{x} = x_1^2/\alpha, \quad u = u_1^2/(1-\beta), \quad \tilde{t} = -2t_1$$

together with a Briot-Bouquet transformation, we transform system (1.1) into the form

$$\begin{cases} x_1' = x_1 \left(-\alpha + x_1^2 + \frac{1-\alpha}{1-\beta} u_1^2 + \frac{1}{1-\beta} x_1^2 u_1^2\right), \\ u_1' = u_1 \left(\alpha + \beta - \kappa - x_1^2 - \frac{1-\beta-\alpha}{1-\beta} u_1^2 - \frac{1}{1-\beta} x_1^2 u_1^2\right), \end{cases} \tag{3.1}$$

a form similar to (2.1). Then, introducing some new parameters μ_i ($i \geq 2$) for higher order terms, we improve the second transformation (2.3) as

$$\lambda_1 = -\delta, \qquad \lambda_2 = \frac{2(1-\beta)}{2-\beta}\delta + \sum_{i=1}^{k} \mu_i \delta^{i+1}, \tag{3.2}$$

where $k \geq 1$. When $\mu_i = 0$ $(i \geq 2)$ this transformation is exactly the same as (2.3). With (3.2) system (3.1) is transformed into

$$\begin{cases} \frac{dv_1}{d\tau} = v_1\left(-1+v_1^2+\frac{1}{1-\beta}v_2^2\right)+\delta v_1\left(\frac{-1}{1-\beta}v_2^2+\frac{1}{1-\beta}v_1^2v_2^2\right), \\ \frac{dv_2}{d\tau} = v_2\left(\frac{2(1-\beta)}{2-\beta}-v_1^2-v_2^2\right)+\delta v_2\left(\frac{1}{1-\beta}v_2^2-\frac{1}{1-\beta}v_1^2v_2^2+\mu_1\right)+v_2\sum_{i=2}^k \mu_i\delta^i. \end{cases} \tag{3.3}$$

Using the same integrating factor as for (2.6), we obtain

$$\begin{cases} \frac{dv_1}{d\tau} = f_1(v_1, v_2) + g_1(v_1, v_2)\delta, \\ \frac{dv_2}{d\tau} = f_2(v_1, v_2) + \sum_{i=1}^k g_{2i}(v_1, v_2)\delta^i, \end{cases} \tag{3.4}$$

a form similar to the perturbed Hamiltonian system H_δ in (2.6), where

$$\begin{aligned} f_1(v_1, v_2) &= v_1^{\xi}v_2^{\eta-1}\left\{-1+v_1^2+\frac{1}{1-\beta}v_2^2\right\}, \\ f_2(v_1, v_2) &= v_1^{\xi-1}v_2^{\eta}\left\{\frac{2(1-\beta)}{2-\beta}-v_1^2-v_2^2\right\}, \\ g_1(v_1, v_2) &= v_1^{\xi}v_2^{\eta-1}\left\{\frac{-1}{1-\beta}v_2^2+\frac{1}{1-\beta}v_1^2v_2^2\right\}, \\ g_{21}(v_1, v_2) &= v_1^{\xi-1}v_2^{\eta}\left\{\mu_1+\frac{1}{1-\beta}v_2^2-\frac{1}{1-\beta}v_1^2v_2^2\right\}, \\ g_{2i}(v_1, v_2) &= \mu_i v_1^{\xi-1}v_2^{\eta}, \quad i \geq 2. \end{aligned}$$

Let

$$\begin{cases} f(v_1, v_2) := (f_1(v_1, v_2), \quad f_2(v_1, v_2))^T, \\ g^1(v_1, v_2) := (g_1(v_1, v_2), \quad g_{21}(v_1, v_2))^T, \\ g^i(v_1, v_2) = (0, g_{2i}(v_1, v_2))^T, \quad i \geq 2. \end{cases} \tag{3.5}$$

Consider the equivalent 1-form of system (3.4), i.e.,

$$\omega_\delta := -\left(f_2 + \sum_{i=1}^k g_{2i}\delta^i\right)dv_1 + (f_1 + g_1\delta)dv_2 = 0. \tag{3.6}$$

Clearly, $\omega_\delta = \Sigma_{i=0}^k \omega_i\delta^i$, where $\omega_1 = -g_{21}\, dv_1 + g_1\, dv_2$, $\omega_i = -g_{2i}\, dv_1$ for $i \geq 2$ and $\omega_0 = dH(v_1, v_2)$, the differential of the Hamiltonian function $H(v_1, v_2)$ defined in Lemma 2.1. As shown in [11,12,17], the Melnikov function along Υ

can be written as

$$M(\mu) = \sum_{i=1}^{k} M_i(\mu)\delta^i + O\left(|\delta|^{k+1}\right),$$

where $\mu := (\mu_1, \ldots, \mu_k)$, $M_1(\mu) = -\int_\Upsilon \omega_1$, which can be presented in exactly the same form as given in (2.9), and

$$M_i(\mu) = \int\limits_\Upsilon \left(\sum_{j=1}^{i-1} a_j\omega_{i-j} - \omega_i\right) \tag{3.7}$$

if $M_j(\mu) \equiv 0$ for all $1 \le j \le i-1$. In (3.7) all a_j's are analytic functions in (v_1, v_2) except at equilibria and satisfy

$$\omega_j - a_j dH = \sum_{\ell=1}^{j-1} a_\ell\omega_{j-\ell} + dR_j, \tag{3.8}$$

where R_j is an analytic function.

From [11,12,17] we see that $\omega_1 = a_1 dH + dR_1$. So we can obtain the differential equation

$$d\omega_1 = da_1 \wedge dH.$$

Moreover, we get

$$d\omega_1 = (\mathrm{div}\ g^1)\ dv_1 \wedge dv_2$$

by the expression of ω_1 in equation (3.6). Thus we can solve

$$a_1(t) = \int\limits_0^t (\mathrm{div}\ g^1)dt + C,$$

where C is a constant. Therefore, we have

$$\left.\frac{da_1(v_1(\tau), v_2(\tau))}{d\tau}\right|_\Upsilon = \mathrm{div}\ g^1(v_1(\tau), v_2(\tau)). \tag{3.9}$$

On the other hand, restricted to Υ system (3.4) can be simplified as

$$\begin{cases} v_1' = \frac{2}{\xi} v_1^\xi v_2^{\eta+1}, \\ v_2' = -\frac{2}{\eta} v_1^{\xi+1} v_2^\eta. \end{cases} \tag{3.10}$$

Therefore, by (3.9) and (3.10), we obtain

$$\left.\frac{da_1(v_1,v_2)}{d\tau}\right|_{\Upsilon} = \frac{\xi-\eta}{1-\beta}v_1^{\xi+1}v_2^{\eta+1} + \frac{\xi-\eta-2}{\beta-1}v_1^{\xi-1}v_2^{\eta+1} + \eta\mu_1 v_1^{\xi-1}v_2^{\eta-1}$$
$$= \frac{(\xi-\eta)}{(1-\beta)}\frac{\xi}{2}v_1v_1' + \frac{(\xi-\eta-2)}{(\beta-1)}\frac{\xi}{2}\frac{v_1'}{v_1} + \eta\mu_1\frac{\xi}{2}\frac{v_1'}{v_1v_2^2},$$

from which we have

$$a_1(v_1,v_2) = \frac{(\xi-\eta)}{(1-\beta)}\frac{\xi}{2}\int v_1dv_1 - \frac{(\xi-\eta-2)}{(1-\beta)}\frac{\xi}{2}\int\frac{dv_1}{v_1} + \eta\mu_1\frac{\xi}{2}\int\frac{dv_1}{v_1(1-v_1^2)\xi/\eta} + C$$
$$= -\frac{2}{\beta}v_1^2 + \frac{8}{\beta}\ln v_1 - \frac{6}{\beta(4-\beta)}\ln\frac{v_1^2}{1-v_1^2} + C,$$

where C is a constant. Substituting $a_1(v_1,v_2)$ into formula (3.7), the second Melnikov function of the heteroclinic loop Γ_0 can be expressed as

$$\begin{aligned}
M_2(\mu) &= \int_{\Upsilon}\{a_1(v_1,v_2)(-g_{21}\,dv_1 + g_1\,dv_2) + g_{22}\,dv_1\} \\
&= \int_{\Upsilon}\Big\{a_1(v_1,v_2)[-v_1^{\xi-1}v_2^{\eta}\left(\mu_1 + \frac{1}{1-\beta}v_2^2 - \frac{1}{1-\beta}v_1^2v_2^2\right)dv_1 \\
&\qquad + v_1^{\xi}v_2^{\eta-1}\left(\frac{-1}{1-\beta}v_2^2 + \frac{1}{1-\beta}v_1^2v_2^2\right)dv_2] + \mu_2v_1^{\xi-1}v_2^{\eta}\,dv_1\Big\} \\
&= \int_{\Upsilon}\Big\{-a_1(v_1,v_2)\,v_1^{\xi-1}v_2^{\eta}\left[\frac{2(1-\beta)(8-\beta)}{(4-\beta)(2-\beta)^2} - \frac{6}{2-\beta}v_1^2 + \frac{4}{2-\beta}v_1^4\right]dv_1 \\
&\qquad + \mu_2v_1^{\xi-1}v_2^{\eta}\,dv_1\Big\} \\
&= -I_0 - I_1 + \mu_2I_2 \\
&= I_2\{\mu_2 - \frac{I_0}{I_2} - \frac{I_1}{I_2}\},
\end{aligned} \tag{3.11}$$

where

$$\begin{aligned}
I_0 &:= -\frac{4}{\beta}\int_{\Upsilon}v_1^{\xi+1}v_2^{\eta}\left[\frac{(1-\beta)(8-\beta)}{(4-\beta)(2-\beta)^2} - \frac{3}{2-\beta}v_1^2 + \frac{2}{2-\beta}v_1^4\right]dv_1 \\
&= -\frac{4}{\beta}\left(\frac{\xi}{\eta}\right)^{\frac{\eta}{2}}\int_0^1 v_1^{\xi+1}(1-v_1^2)^{\frac{\eta}{2}}\left[\frac{(1-\beta)(8-\beta)}{(4-\beta)(2-\beta)^2} - \frac{3}{2-\beta}v_1^2 + \frac{2}{2-\beta}v_1^4\right]dv_1,
\end{aligned}$$

$$\begin{aligned}
I_1 :=\ & 4 \int\limits_{\Upsilon} \left(\frac{4}{\beta} \ln v_1 - \frac{3}{\beta(4-\beta)} \ln \frac{v_1^2}{1-v_1^2} \right) v_1^{\xi-1} v_2^{\eta} \left[\frac{(1-\beta)(8-\beta)}{(4-\beta)(2-\beta)^2} \right. \\
& \left. - \frac{3}{2-\beta} v_1^2 + \frac{2}{2-\beta} v_1^4 \right] dv_1 \\
=\ & 4 \left(\frac{\xi}{\eta} \right)^{\frac{\eta}{2}} \int\limits_0^1 \left(\frac{4}{\beta} \ln v_1 - \frac{3}{\beta(4-\beta)} \ln \frac{v_1^2}{1-v_1^2} \right) v_1^{\xi-1} \left(1 - v_1^2\right)^{\frac{\eta}{2}} \left[\frac{(1-\beta)(8-\beta)}{(4-\beta)(2-\beta)^2} \right. \\
& \left. - \frac{3}{2-\beta} v_1^2 + \frac{2}{2-\beta} v_1^4 \right] dv_1, \\
I_2 :=\ & \left(\frac{\xi}{\eta} \right)^{\frac{\eta}{2}} \int\limits_0^1 v_1^{\xi-1} \left(1 - v_1^2\right)^{\frac{\eta}{2}} dv_1 > 0
\end{aligned}$$

because $v_1^{\xi-1}(1-v_1^2)^{\frac{\eta}{2}} > 0$ for $v_1 \in (0, 1)$. From the relation (2.11) we can calculate

$$\begin{aligned}
\frac{I_0}{I_2} &= \frac{-\frac{4}{\beta}\left[\frac{(1-\beta)(8-\beta)}{(4-\beta)(2-\beta)^2} J(\xi+1, \eta) - \frac{3}{2-\beta} J(\xi+3, \eta) + \frac{2}{2-\beta} J(\xi+5, \eta) \right]}{J(\xi-1, \eta)} \\
&= \frac{4(1-\beta)(1+\beta)}{(4-\beta)(2-\beta)^3},
\end{aligned} \tag{3.12}$$

the first quotient in (3.11). Although it is difficult to calculate the second quotient I_1/I_2 in (3.11) by using the same method as for (3.12) because the transcendental function of logarithm ln is involved, integrals I_1, I_2 exist surely and the second quotient I_1/I_2 in (3.11) defines a function of β by (2.5), denoted by $I_{12}(\beta)$.

Solving the equation $M_2(\mu) = 0$ with (3.11) and (3.12), we obtain

$$\mu_2 = \frac{I_0 + I_1}{I_2} = \frac{4(1-\beta)(1+\beta)}{(4-\beta)(2-\beta)^3} + I_{12}(\beta). \tag{3.13}$$

Let $\tilde{\mu_2}$ denote the right hand side of (3.13). Thus, with the change (2.2) of parameters and the relations in the second line of (2.3), the condition (3.13) of parameters can be presented equivalently as

$$\begin{aligned}
\kappa = \beta + \left(\frac{\beta}{2-\beta} \right) \alpha + \left(\frac{6\beta}{(4-\beta)(2-\beta)^2} \right) \alpha^2 \\
- \left\{ \frac{4(1-\beta)(1+\beta)}{(4-\beta)(2-\beta)^3} + I_{12}(\beta) \right\} \alpha^3 + O(\alpha^4).
\end{aligned} \tag{3.14}$$

Therefore, we conclude the following:

Theorem 3.1 *Under the condition (HHK) the bifurcation curve $\kappa_L(\alpha,\beta)$ of the heteroclinic loop of system* (1.1) *has the third order approximation* (3.14) *for small α.*

The above procedure of calculating the third order approximation actually exhibits the algorithm for higher orders. Suppose that we have obtained the kth order approximation

$$\kappa=\beta+\left(\frac{\beta}{2-\beta}\right)\alpha+\left(\frac{6\beta}{(4-\beta)(2-\beta)^2}\right)\alpha^2-\tilde{\mu}_2\alpha^3-\cdots-\tilde{\mu}_{k-1}\alpha^k+O(\alpha^{k+1}). \tag{3.15}$$

It implies that

$$M_2(\tilde{\mu}_2)\equiv M_3(\tilde{\mu}_3)\equiv\ldots\equiv M_{k-1}(\tilde{\mu}_{k-1})\equiv 0.$$

Solving $\mu_k=\tilde{\mu}_k$ from the equation $M_k(\mu)=0$ by formula (3.7) in a similar procedure, the $(k+1)$th order approximation to the bifurcation curve $\kappa_L(\alpha,\beta)$ can be obtained.

4 Algorithm for $I_{12}(\beta)$

Although the third order approximation of the bifurcation curve is given in (3.14), it is still difficult to compute the analytic expression of the quotient $I_{12}(\beta):=I_1/I_2$. Our strategy is to apply an appropriate numerical integration rule to approximate the integral

$$I_\psi:=\int_0^1\psi(v_1)v_1^{s_1}\left(1-v_1^2\right)^{\frac{s_2}{2}}dv_1,$$

where $s_1=\xi-1$, $s_2=\eta$ and $\psi(v_1)$ is a smooth function in $v_1\in(0,1)$, because I_ψ is equal to I_1 (resp. I_2) when

$$\begin{aligned}\psi(v_1)=4\left(\frac{\xi}{\eta}\right)^{\frac{\eta}{2}}&\left(\frac{4}{\beta}\ln v_1-\frac{3}{\beta(4-\beta)}\ln\frac{v_1^2}{1-v_1^2}\right)\\&\times\left[\frac{(1-\beta)(8-\beta)}{(4-\beta)(2-\beta)^2}-\frac{3}{2-\beta}v_1^2+\frac{2}{2-\beta}v_1^4\right]\end{aligned}$$

(resp. $\psi(v_1)=(\xi/\eta)^{\frac{\eta}{2}}$). Although many numerical integration rules (for example, the Newton–Cotes integration rule of $n+1$ partition points, [3,4]) can be applied to I_ψ, the main difficulties come from estimating and controlling the approximation precision to a desired level. For instance, the error in the Newton–Cotes rule requires derivatives of the integrand in I_ψ of at least $(n+1)$th order but the integrand in I_1 is so complicated that it is hard to compute its higher order derivatives for a higher precision. The *Composite Trapezoidal Rule*, stated in Sect. 4.1 of [3], is an appropriate integration rule for a high-order approximation with a lower order continuity of integrand. Applying this integration rule we get

$$I_\psi = I(n) + E(n), \tag{4.16}$$

where n is an integer,

$$I(n) := \frac{1}{n}\left[\sum_{j=1}^{n-1} \psi(t_j) t_j^{s_1}(1-t_j^2)^{\frac{s_2}{2}}\right] \quad \text{and}$$
$$E(n) := -\frac{1}{12\,n^2}\left(\frac{d^2}{dv_1^2}\right)(\psi(\tilde{v})\tilde{v}^{s_1}(1-\tilde{v}^2)^{\frac{s_2}{2}})$$

are the approximation of the integral I_ψ and its error, respectively, $t_j = j/n$ and $\tilde{v} \in (0,1)$ is a certain constant. Here we choose $s_1 > 2$ and $s_2 > 4$ so that $\psi(v_1)v_1^{s_1}(1-v_1^2)^{\frac{s_2}{2}} \in C^2[0,1]$. Thus, for an arbitrary small positive constant ε, the approximation error $E(n)$ in (4.16) can be estimated as

$$|E(n)| < \frac{1}{12\,n^2} \sup_{0\le\tilde{v}\le 1}\left|\left(\frac{\partial^2}{\partial v_1^2}\right)\left(\psi(\tilde{v})\tilde{v}^{s_1}(1-\tilde{v}^2)^{\frac{s_2}{2}}\right)\right| < \varepsilon$$

by choosing a sufficiently large integer n (and appropriate choices of s_1 and s_2).

Let us demonstrate the algorithm for $n = 100$ and $n = 1{,}000$. Let

$$F_1(v_1) := 4\left(\frac{4}{\beta}\ln v_1 - \frac{3}{\beta(4-\beta)}\ln\frac{v_1^2}{1-v_1^2}\right)v_1^{\xi-1}(1-v_1^2)^{\frac{\eta}{2}}$$
$$\times\left[\frac{(1-\beta)(8-\beta)}{(4-\beta)(2-\beta)^2} - \frac{3}{2-\beta}v_1^2 + \frac{2}{2-\beta}v_1^4\right],$$
$$F_2(v_1) := v_1^{\xi-1}\left(1-v_1^2\right)^{\frac{\eta}{2}}.$$

Then, for $n = 100$,

$$\frac{I_1}{(\xi/\eta)^{\frac{\eta}{2}}} = I_1(100) + E_1(100), \quad \frac{I_2}{(\xi/\eta)^{\frac{\eta}{2}}} = I_2(100) + E_2(100), \tag{4.17}$$

where

$$I_1(100) = \frac{1}{100}\sum_{j=1}^{99} F_1(j/100), \quad I_2(100) = \frac{1}{100}\sum_{j=1}^{99} F_2(j/100),$$
$$|E_1(100)| < \frac{1}{12\cdot 10^4}\sup_{0\le v_1\le 1}|F_1''(v_1)|, \quad |E_2(100)| < \frac{1}{12\cdot 10^4}\sup_{0\le v_1\le 1}|F_2''(v_1)|.$$

For $n = 1000$,

$$\frac{I_1}{(\xi/\eta)^{\frac{\eta}{2}}} = I_1(1000) + E_1(1000), \quad \frac{I_2}{(\xi/\eta)^{\frac{\eta}{2}}} = I_2(1000) + E_2(1000), \quad (4.18)$$

where

$$I_1(1000) = \frac{1}{1000}\sum_{j=1}^{999} F_1(j/1000), \quad I_2(1000) = \frac{1}{1000}\sum_{j=1}^{999} F_2(j/1000),$$

$$|E_1(1000)| < \frac{1}{12\cdot 10^6}\sup_{0\le v_1\le 1}|F_1''(v_1)|, \quad |E_2(1000)| < \frac{1}{12\cdot 10^6}\sup_{0\le v_1\le 1}|F_2''(v_1)|.$$

More concretely, choosing $\beta = 0.2$ for example, we can calculate with (4.17) or (4.18) that

$$\begin{aligned}
-12n^2E_1(n) = {} & -(200/9747)(251160\ln(\tilde{v}) + 316236\tilde{v}^8 \\
& -803472\tilde{v}^6 + 6777042\ln(\tilde{v})\tilde{v}^4 \\
& +81900\ln(-(\tilde{v}-1)(\tilde{v}+1)) - 2239464\ln(\tilde{v})\tilde{v}^2 - 8314362\ln(\tilde{v})\tilde{v}^6 \\
& +2209905\ln(-(\tilde{v}-1)(\tilde{v}+1))\tilde{v}^4 + 716395\tilde{v}^4 - 266393\tilde{v}^2 + 34684 \\
& -730260\ln(-(\tilde{v}-1)(\tilde{v}+1))\tilde{v}^2 - 2711205\ln(-(\tilde{v}-1)(\tilde{v}+1))\tilde{v}^6 \\
& +3492504\ln(\tilde{v})\tilde{v}^8 + 1138860\ln(-(\tilde{v}-1)(\tilde{v}+1))\tilde{v}^8) \\
& \times(\tilde{v}-1)^7(\tilde{v}+1)^7\tilde{v}^{13}, \\
-12n^2E_2(n) = {} & -6\tilde{v}^{13}(176\tilde{v}^4 - 163\tilde{v}^2 + 35)(\tilde{v}-1)^7(\tilde{v}+1)^7.
\end{aligned}$$

The diagrams of $-12n^2E_1(n)$ and $-12n^2E_2(n)$ are plotted by Maple V.7 in Figs. 4 and 5. Therefore, we have

$$|12n^2E_1(n)| < 0.006, \quad |12n^2E_2(n)| < 0.0015, \quad \forall n \in \mathbf{N}. \quad (4.19)$$

For $n = 100$, by (4.17) and (4.19) we calculate

$$\frac{I_1(100)}{I_2(100)} = \frac{-0.08352691394}{0.3085150144} = -0.270738574803$$

and

$$\frac{I_1}{I_2} = \frac{-0.08352691394 - 12\cdot 10^4E_1(100)}{0.3085150144 - 12\cdot 10^4E_2(100)} \in (-0.29160435, -0.25007471),$$

showing that the error for I_1/I_2 can be controlled within 0.02086577.

For $n = 1000$, by (4.17) and (4.19) we calculate

$$\frac{I_1(1000)}{I_2(1000)} = \frac{-8.352691526}{30.85150143} = -0.270738574748$$

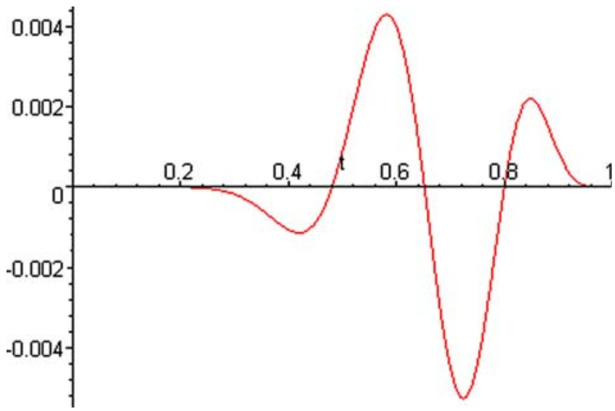

Fig. 4 Function $12n^2E_1(n)$

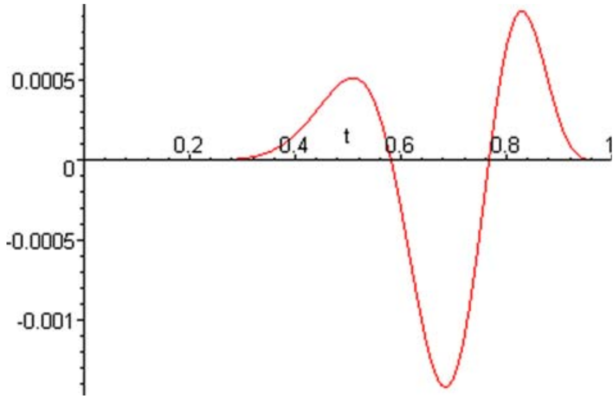

Fig. 5 Function $12n^2E_2(n)$

and

$$\frac{I_1}{I_2} = \frac{-8.352691526 - 12 \cdot 10^6 E_1(1000)}{30.85150143 - 12 \cdot 10^6 E_2(1000)} \in (-0.2709462282, -0.2705309415),$$

showing that the error for I_1/I_2 can be controlled within 0.000207653, much less than the error for $n = 100$. Thus for $n = 1000$ we can calculate by (3.13) that

$$\tilde{\mu}_2 = \frac{4(1-\beta)(1+\beta)}{(4-\beta)(2-\beta)^3} + \frac{I_1}{I_2} \approx -0.0974658869$$

and the third order approximation of the bifurcation curve $\kappa_L(\alpha, \beta)$ is given by

$$\kappa = \kappa_L := 0.2 + 0.1111111111\,\alpha + 0.09746588694\,\alpha^2 + 0.0974658869\,\alpha^3 + O(\alpha^4).$$

5 Discussion

In the classical predator–prey models with Michaelis–Menten–Holling type functional response, predator species can always invade the habit of the prey population successfully in the following sense: both predator and prey populations can co-exist in terms of either a stable steady state or a stable limit cycle. Recently, the traditional predator–prey models with prey-dependent functional response have been challenged by some biologists (see Arditi and Ginzburg [1]) based on the fact that functional responses over typical ecological timescales ought to depend on the densities of both predators and prey, especially when predators have to search for food. Such a functional response is called a ratio-dependent functional response.

Predator–prey models with Michaelis–Menten–Holling type ratio-dependent functional response have been studied by several researchers (Kuang and Beretta [9], Hsu et al. [8]), very rich and complex dynamical behavior, such as the existence of degenerate equilibria, appearance of limit cycles and heteroclinic loops, and the coexistence of two attractive equilibria, have been observed. The existence of heterclinic bifurcation in the model has attracted particular attention (Berezovskaya et al. [2], Xiao and Ruan [16], Tang and Zhang [14], and Li and Kuang [10]) since it leads to the collapse of both predator and prey populations, that is, such models can exhibit catastrophe or overexploitation scenario due to the ratio-dependent predation.

In this paper, we studied heteroclinic bifurcations of the predator–prey model with Michaelis–Menten–Holling type ratio-dependent functional response. By transforming the model into a Hamiltonian system, we first calculated the higher order Melnikov functions. The computational procedure of the first order Melnikov function was simplified with properties of the Beta function. We also provided an algorithm for computing higher order approximations of the heteroclinic bifurcation curves. The second Melnikov function was computed so that a third order approximation of the bifurcation curve of the heteroclinic loop is obtained.

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