

HETEROCLINIC BIFURCATION IN THE MICHAELIS–MENTEN-TYPE RATIO-DEPENDENT PREDATOR-PREY SYSTEM*

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Abstract. The existence of a heteroclinic bifurcation for the Michaelis–Menten-type ratio-dependent predator-prey system is rigorously established. Limit cycles related to the heteroclinic bifurcation are also discussed. It is shown that the heteroclinic bifurcation is characterized by the collision of a stable limit cycle with the origin, and the bifurcation triggers a catastrophic shift from the state of large oscillations of predator and prey populations to the state of extinction of both populations. It is also shown that the limit cycles related to the heteroclinic bifurcation originally bifurcate from the Hopf bifurcation.

Key words. ratio-dependent predator-prey model, heteroclinic cycle, bifurcation

AMS subject classifications. 34C05, 34D20, 92D25

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1. Introduction. In studying the interaction between predators and their prey, it is crucial to determine what specific form of the functional response that describes the amount of prey consumed per predator per unit of time is biologically plausible and provides a sound basis for theoretical development. Traditionally, dependence on prey density has been the starting point, giving a functional response function of the form $p(x)$. In the simplest case, such a function is a linear function of x , which is incorporated into the classical Lotka–Volterra predator-prey model. The linear functional response is a limiting case of the more general and useful Michaelis–Menten or Holling type II response function of the form $p(x) = \frac{cx}{m+x}$. Because $p(x)$ varies solely with prey density, it is usually labeled as “prey-dependence.”

Sole dependence of the functional response on prey density has been questioned by several biologists (e.g., DeAngelis, Goldstein, and O’Neill [10], Arditi and Ginzburg [4], Arditi, Ginzburg, and Akcakaya [5], Akcakaya [1], Gutierrez [12]). It has been recognized that predators might interfere with each other’s foraging, requiring the functional response to depend on densities of both predators and prey (DeAngelis, Goldstein, and O’Neill [10], Arditi and Akcakaya [2], Beddington [6]). Arditi and Ginzburg [4] have argued that a functional response depending on the ratio of prey to predator abundance is a suitable representation of some of these phenomena. With the Michaelis–Menten or Holling type II-type ratio-dependence functional response $p(x/y)$ and logistic prey growth, the predator-prey system takes the form of

$$(1.1) \quad \begin{aligned} x'(t) &= rx \left(1 - \frac{x}{K}\right) - \frac{cxy}{x + my}, \\ y'(t) &= y \left(\frac{fx}{x + my} - d\right), \end{aligned}$$

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where $x(t)$, $y(t)$ represent population densities of prey and predator, respectively, and r , K , c , m , f , d are positive constants that stand for prey intrinsic growth rate, carrying capacity, capturing rate, half saturation constant, maximal predator growth rate, and predator mortality rate, respectively.

The ratio-dependent predator-prey system (1.1) exhibits original dynamic properties that have never been observed in the early prey-dependent predator-prey systems. Specifically, the ratio-dependent predator-prey system (1.1) does not produce the so-called paradox of enrichment (Hairston, Smith, and Slobodkin [13], Rosenzweig [19]) or the paradox of biological control (Arditi and Berryman [3]). It also allows the predator population or both populations to either become extinct or coexist, depending on the initial population values. These are realistic features of predator-prey models that have been observed experimentally (Huffaker [14], Luckinbill [17]).

The dynamics of the ratio-dependent predator-prey system (1.1) has been systematically studied by Kuang and Beretta [16], Hsu, Hwang, and Kuang [15], Berezovskaya, Karev, and Arditi [7], and Xiao and Ruan [22]. These authors have shown that system (1.1) has very rich dynamics. In particular, the origin is a complicated equilibrium point whose characteristics determine some important properties of the system (see [7, 22]), the limit cycle exists and is unique and stable (see [15]), and the heteroclinic bifurcation plays an important role in understanding the dynamics of the system (see [7, 15]). Berezovskaya, Karev, and Arditi [7] have found numerically the heteroclinic cycle in (1.1) that corresponds to the disappearance of the limit cycle. It is thus interesting to rigorously establish the existence of heteroclinic bifurcation and to study the properties associated with the bifurcation. In a recent paper [20], Tang and Zhang reduced the system to a perturbed Hamiltonian system with a Delta-shape heteroclinic loop and computed Melnikov's function by eliminating some complicated terms in establishing the heteroclinic bifurcation. This is a valid and novel approach, yet its implementation is subtle since it involves intensive steps of variable manipulations and computations. The analysis presented in [20] contains a flaw that failed to ensure a proper application of Melnikov's method.

The objective of this paper is to rigorously establish the existence of heteroclinic bifurcation and determine the associated dynamics in system (1.1). This paper is organized as follows. The main results of the paper are provided in section 2. In this section, we use Melnikov's method to determine the existence of heteroclinic bifurcation. It is shown that the heteroclinic bifurcation is characterized by the collision of a stable limit cycle with the origin, and the bifurcation triggers a catastrophic shift from the state of large oscillations of predator and prey populations to the state of extinction of both populations. We also employ Melnikov's method to study limit cycles related to the heteroclinic bifurcation. It is shown that the limit cycles related to the heteroclinic bifurcation originally bifurcate from the Hopf bifurcation. The biological interpretations of the theoretical results are also provided. Some concluding remarks are given in section 3.

2. Bifurcations.

2.1. Heteroclinic bifurcation. For simplicity, we nondimensionalize system (1.1) as in Tang and Zhang [20] with the following scaling:

$$x \rightarrow Kx, \quad y \rightarrow Ky/m, \quad t \rightarrow mt/c.$$

(Throughout this paper the variable on the left-hand side of \rightarrow always represents the old variable.) With this scaling, system (1.1) takes the form

$$(2.1) \quad \begin{aligned} x'(t) &= \alpha x(1-x) - \frac{xy}{x+y}, \\ y'(t) &= -\beta y + \frac{\kappa xy}{x+y}, \end{aligned}$$

where

$$(2.2) \quad \alpha = \frac{rm}{c}, \beta = \frac{dm}{c}, \kappa = \frac{fm}{c}.$$

As shown in [7, 20, 22], system (2.1) in the first quadrant is equivalent to the polynomial system

$$(2.3) \quad \begin{aligned} x'(t) &= \alpha x(1-x)(x+y) - xy \\ y'(t) &= -\beta y(x+y) + \kappa xy \end{aligned}$$

obtained from (2.1) by a change of the independent variable

$$t \rightarrow (x+y)t.$$

As in [7, 20, 22], one can then use Briot–Bouquet’s transformation

$$(2.4) \quad x \rightarrow x, \quad y \rightarrow yx, \quad t \rightarrow t/x$$

to convert (2.3) to

$$(2.5) \quad \begin{aligned} x'(t) &= x[\alpha - \alpha x - (1-\alpha)y - \alpha xy], \\ y'(t) &= y[(\kappa - \alpha - \beta) + \alpha x + (1-\alpha-\beta)y + \alpha xy]. \end{aligned}$$

Transformation (2.4) is a homomorphism in the first quadrant, and its inverse maps the y axis to the point $(0, 0)$.

Tang and Zhang [20] used variable changes to transform (2.5) to

$$(2.6) \quad \begin{aligned} v_1'(t) &= v_1 \left[\mu_1 + v_1^2 + \frac{1-\alpha}{1-\alpha-\beta} v_2^2 \right] + \delta v_1 \left(\mu_2 + \frac{1}{1-\alpha-\beta} v_1^2 v_2^2 \right), \\ v_2'(t) &= v_2 \left[\frac{-2(1-\alpha-\beta)}{2-2\alpha-\beta} \mu_1 - v_1^2 - v_2^2 \right] + \delta v_2 \left(\mu_2 - \frac{1}{1-\alpha-\beta} v_1^2 v_2^2 \right), \end{aligned}$$

where δ , μ_1 , and μ_2 are related to α and $\alpha + \beta - \kappa$, and in particular $\alpha = -(\delta\mu_1 + \delta^2\mu_2)$. In [20] the coefficient term $(1-\alpha)/(1-\alpha-\beta)$ is treated as a constant when Melnikov’s method is used to carry out bifurcation analysis with respect to parameters δ, μ_1, μ_2 . This is not appropriate. One needs to split this coefficient term into a term independent of bifurcation parameters and a perturbation term in applying Melnikov’s method.

Instead of working on (2.6), we study the following simpler system

$$(2.7) \quad \begin{aligned} x'(t) &= x[\alpha - x - (1-\alpha)y - xy], \\ y'(t) &= y[(\kappa - \alpha - \beta) + x + (1-\alpha-\beta)y + xy], \end{aligned}$$

obtained from (2.5) by the change of variable

$$x \rightarrow x/\alpha.$$

We simply use α and $\nu = \kappa - \alpha - \beta$ (or equivalently α and κ) as our unfolding parameters while fixing β . In (2.7) there are two second order terms whose coefficients depend on α . We decompose these terms and rewrite (2.7) as

$$(2.8) \quad \begin{aligned} x'(t) &= x(\alpha - x - y) + x(\alpha y - xy), \\ y'(t) &= y(\nu + x + (1 - \beta)y) + y(-\alpha y + xy). \end{aligned}$$

This system can then be viewed as a perturbation of the system

$$(2.9) \quad \begin{aligned} x'(t) &= x(\alpha - x - y), \\ y'(t) &= y(\nu + x + (1 - \beta)y), \end{aligned}$$

as α, ν, x , and y are all small. Note that the coefficients of second order terms in (2.9) do not depend on α and ν .

We shall assume that

$$\beta < 1.$$

System (2.9) is integrable if

$$(2.10) \quad \nu = -\frac{2(1 - \beta)}{2 - \beta}\alpha < 0,$$

and in this case the function

$$(2.11) \quad F_\alpha(x, y) = \frac{1}{b}x^a y^b \left(\alpha - x - \frac{2 - \beta}{2}y \right),$$

where

$$(2.12) \quad a = 2\frac{1 - \beta}{\beta}, \quad b = \frac{2 - \beta}{\beta},$$

is constant along solution curves. In fact, when (2.10) holds, along any solution curve $(x(t), y(t))$ of (2.9), $\frac{dF_\alpha(x,y)}{dt} = \frac{\partial F_\alpha}{\partial x}x'(t) + \frac{\partial F_\alpha}{\partial y}y'(t) = \frac{1}{b}[\alpha ax^{a-1}y^b - (a + 1)x^a y^b - \frac{2-\beta}{2}ax^{a-1}y^{b+1}]x(\alpha - x - y) + \frac{1}{b}[\alpha bx^a y^{b-1} - bx^{a+1}y^{b-1} - \frac{2-\beta}{2}(b + 1)x^a y^b]y(\nu + x + (1 - \beta)y) = 0$. The level curves of F_α take the form shown in Figure 1. Here we have a family of periodic orbits encircling the center at $(\bar{x}, \bar{y}) = (\frac{(1-\beta)\alpha}{2-\beta}, \frac{\alpha}{2-\beta})$ and limiting on the heteroclinic cycle $F_\alpha(x, y) = 0$, which is a triangle connecting the saddles at $(0, 0)$, $(\alpha, 0)$, and $(0, \frac{2\alpha}{2-\beta})$.

Using the transformations

$$x \rightarrow \epsilon x, \quad y \rightarrow \epsilon y, \quad \alpha = \epsilon \nu_1, \quad \nu = -\frac{2(1 - \beta)}{2 - \beta}\epsilon \nu_1 + \nu_2 \epsilon^2$$

and rescaling time $t \rightarrow t/\epsilon$, we convert system (2.8) into

$$(2.13) \quad \begin{aligned} x'(t) &= x[\nu_1 - x - y] + \epsilon(\nu_1 xy - x^2 y), \\ y'(t) &= y \left[-\frac{2(1 - \beta)}{2 - \beta}\nu_1 + x + (1 - \beta)y \right] + \epsilon(\nu_2 y - \nu_1 y^2 + xy^2). \end{aligned}$$

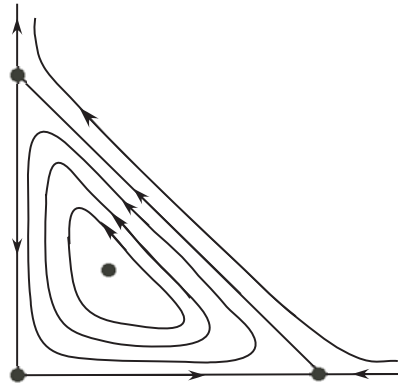


FIG. 1. The level curves of $F_\alpha(x, y)$.

Multiplying (2.13) by the integrating factor $x^{a-1}y^{b-1}$, we obtain the “equivalent” perturbed Hamiltonian system:

$$(2.14) \quad \begin{aligned} x'(t) &= x^a y^{b-1} \{ [\nu_1 - x - y] + \epsilon(\nu_1 y - xy) \} \\ y'(t) &= x^{a-1} y^b \left\{ \left[-\frac{2(1-\beta)}{2-\beta} \nu_1 + x + (1-\beta)y \right] + \epsilon(\nu_2 - \nu_1 y + xy) \right\}. \end{aligned}$$

One can check that

$$(2.15) \quad F_{\nu_1}(x, y) = \frac{1}{b} x^a y^b \left(\nu_1 - x - \frac{2-\beta}{2} y \right)$$

is the Hamiltonian function for (2.14) when $\epsilon = 0$, where a and b are given in (2.12).

We use the Melnikov theory [9, 11, 21] to locate parameter values that produce a heteroclinic cycle for (2.14) in the case $\epsilon \neq 0$. The analysis that we perform here is similar to what is carried out in section 7.5 of [11] and section 4.7 of [9]. We can set $\nu_1 = 1$ without loss of generality. The heteroclinic cycle for $\epsilon = 0$ lies on the level curve $F_1(x, y) = 0$, denoted by Γ_0 , which corresponds to a triangle formed by the three line segments determined by $x = 0$, $y = 0$, and $x + \frac{2-\beta}{2}y = 1$. Let

$$\mathbf{G}(x, y) = (x^a y^{b-1}(y - xy), x^{a-1} y^b (\nu_2 - y + xy)).$$

The Melnikov function is

$$(2.16) \quad \begin{aligned} M(\nu_2) &= \int \int_{\text{int}\Gamma_0} \text{trace} D\mathbf{G}(x, y) dx dy \\ &= \int \int_{\text{int}\Gamma_0} [(a-b-1)x^{a-1}y^b + (b-a)x^a y^b + bx^{a-1}y^{b-1}\nu_2] dx dy, \end{aligned}$$

where $\text{int}\Gamma_0$ denotes the region bounded by Γ_0 . $M(\nu_2) = 0$ has a unique solution

$$(2.17) \quad \nu_2 = -\frac{(a-b-1)I(a-1, b) + (b-a)I(a, b)}{bI(a-1, b-1)},$$

where

$$I(u, v) = \int \int_{\text{int}\Gamma_0} x^u y^v dx dy, \quad u > -1, v > -1.$$

It is easy to see that

$$I(u, v) = \int_0^1 x^u \int_0^{\frac{1-x}{s}} y^v dy dx = \frac{1}{(v+1)s^{v+1}} \int_0^1 x^u (1-x)^{v+1} dx,$$

where $s = \frac{2-\beta}{2}$.

We have

$$\begin{aligned} I(u+1, v) &= \frac{1}{(v+1)s^{v+1}} \int_0^1 x^{u+1} (1-x)^{v+1} dx \\ &= \frac{1}{(v+1)s^{v+1}} \int_0^1 x^u (1-x)^{v+1} (x-1+1) dx \\ (2.18) \quad &= -\frac{1}{(v+1)s^{v+1}} \int_0^1 x^u (1-x)^{v+2} dx + I(u, v) \\ &= -\frac{v+2}{v+1} s I(u, v+1) + I(u, v). \end{aligned}$$

Using integration by parts, we obtain

$$\begin{aligned} I(u, v+1) &= \frac{1}{(v+2)s^{v+2}} \int_0^1 x^u (1-x)^{v+2} dx \\ (2.19) \quad &= \frac{1}{(v+2)s^{v+2}} \left[\frac{x^{u+1} (1-x)^{v+2}}{u+1} \Big|_0^1 - \int_0^1 \frac{x^{u+1}}{u+1} (-1)(v+2)(1-x)^{v+1} dx \right] \\ &= \frac{v+1}{(u+1)s} I(u+1, v). \end{aligned}$$

Using (2.18) and (2.19), we find

$$(2.20) \quad I(u+1, v) = \frac{u+1}{u+v+3} I(u, v), \quad I(u, v+1) = \frac{v+1}{(u+v+3)s} I(u, v).$$

It follows from (2.12), (2.17), and (2.20) that

$$\begin{aligned} \nu_2 &= - \left[\frac{a-b-1}{b} \frac{I(a-1, b)}{I(a-1, b-1)} + \frac{b-a}{b} \frac{I(a, b)}{I(a, b-1)} \frac{I(a, b-1)}{I(a-1, b-1)} \right] \\ &= - \left[\frac{a-b-1}{(a+b+1)s} + \frac{a(b-a)}{(a+b+1)(a+b+2)s} \right] \\ &= \frac{6\beta}{(4-\beta)(2-\beta)^2}. \end{aligned}$$

The Melnikov theory [11] shows that if

$$(2.21) \quad \nu = -\frac{2(1-\beta)}{2-\beta} \alpha + \frac{6\beta}{(4-\beta)(2-\beta)^2} \alpha^2 + O(\alpha^3),$$

then system (2.8) has a heteroclinic cycle. It is shown in [7] that the heteroclinic cycle is stable.

Condition (2.21) is equivalent to

$$(2.22) \quad \kappa = \beta + \frac{\beta}{2-\beta} \alpha + \frac{6\beta}{(4-\beta)(2-\beta)^2} \alpha^2 + O(\alpha^3).$$

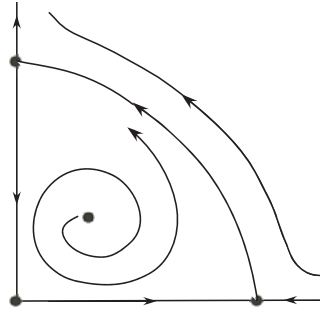


FIG. 2. Dynamics of system (2.7) if the conditions of Lemma 1 hold.

We have obtained the following result.

LEMMA 1. Assume that β is fixed and $\beta < 1$. For small α , if condition (2.22) holds, then system (2.7) has a stable heteroclinic cycle connecting saddles at $(0, 0)$, $(\alpha, 0)$, and $(0, \frac{\kappa - \alpha - \beta}{1 - \alpha - \beta})$.

The dynamics of the system in the case that there exists a stable heteroclinic cycle was discussed by Tang and Zhang [20]. For the sake of completeness, we describe the dynamics in this case based on our analytical results. The positive coexistence equilibrium $(\frac{\beta + \alpha\kappa - \kappa}{\kappa}, \frac{\kappa - \beta}{\beta})$ lies inside the heteroclinic cycle. One can check that it is a spiral source. Conditions of Lemma 1 show that for small α

$$(2.23) \quad \beta < \kappa < \alpha + \beta < 1, \quad \beta + \alpha\kappa - \kappa > 0,$$

which implies that the condition (2.9) in Hsu, Hwang, and Kuang [15] holds. Theorem 2.7 in [15] shows that in this case a limit cycle in the system is always stable and unique once it exists. We therefore conclude that there is no limit cycle inside the heteroclinic cycle since it is attracting. The dynamics of the system in this case is depicted in Figure 2.

Lemma 1 and the transformations used to convert (2.1) to (2.7) imply the following result.

THEOREM 1. Assume that β is fixed and $\beta < 1$. If for small α condition (2.22) holds, then system (2.1) has a stable heteroclinic cycle connecting saddles at $(0, 0)$ and $(1, 0)$.

The conditions of Theorem 1 imply that

$$(2.24) \quad c - rm - dm > 0, \quad f - r - d < 0, \quad d < f < \frac{cd}{c - rm}$$

in the original system (1.1). In view of the properties of the heteroclinic cycle described in Lemma 1, and after Theorem 2.3 and Theorem 2.5 of Xiao and Ruan [22], we see that the heteroclinic cycle in Theorem 1 approaches the origin in the characteristic direction $\theta = \arctan((\kappa - \alpha - \beta)/(\alpha + \beta - 1))$, and the topological structure of the origin consists of a hyperbolic sector and a parabolic sector; see Figure 3.

2.2. Limit cycles near the heteroclinic bifurcation. We have used Melnikov’s method to show the persistence of the heteroclinic cycle of the integrable system (2.13) when $\epsilon = 0$ under the perturbation described by (2.22). This method can also be used to study the survival of each periodic cycle in (2.13) under an appropriate perturbation (see section 7.5 of Guckenheimer and Holmes [11] and section 4.7

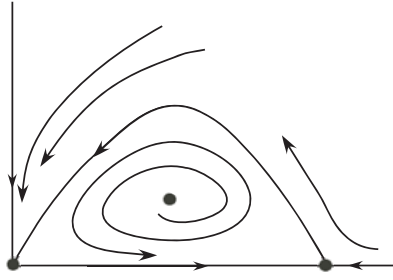


FIG. 3. Dynamics of system (2.1) when a stable heteroclinic cycle exists.

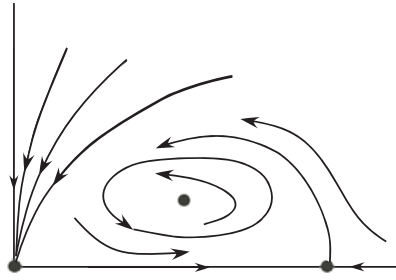


FIG. 4. Dynamics of system (2.1) when $0 < \nu_2 < \frac{6\beta}{(4-\beta)(2-\beta)^2}$, $\beta < 1$, and κ is given by (2.25).

of Chow, Li, and Wang [9]). Let Γ_γ be a periodic cycle in Figure 1 that represents the level curves of F_1 ; then this cycle survives in system (2.1) if

$$(2.25) \quad \kappa = \beta + \frac{\beta}{2-\beta}\alpha + \nu_2\alpha^2 + O(\alpha^3)$$

with

$$(2.26) \quad \nu_2 = -\frac{\int \int_{\text{int}\Gamma_\gamma} [(a-b-1)x^{a-1}y^b + (b-a)x^ay^b] dx dy}{\int \int_{\text{int}\Gamma_\gamma} bx^{a-1}y^{b-1} dx dy},$$

where $\text{int}\Gamma_\gamma$ denotes the region bounded by Γ_γ . In (2.26), ν_2 represents the solution of $M(\nu_2) = 0$, where $M(\nu_2)$ is given by (2.16) with Γ_0 replaced by Γ_γ . We first study small cycles near the equilibrium. As Γ_γ shrinks to the equilibrium $(\bar{x}, \bar{y}) = (\frac{(1-\beta)\alpha}{2-\beta}, \frac{\alpha}{2-\beta})$, the right-hand side of (2.26) approaches $-\frac{(a-b-1)\bar{x}^{a-1}\bar{y}^b + (b-a)\bar{x}^a\bar{y}^b}{b\bar{x}^{a-1}\bar{y}^{b-1}} = 0 + O(\alpha)$, which shows $\nu_2 = 0$ in (2.25). In this case, standard Hopf bifurcation analysis shows that a supercritical Hopf bifurcation occurs in (2.1). Since (2.25) implies the condition (2.9) in [15], Theorem 2.7 in [15] shows that system (2.1) has at most one limit cycle. Due to this fact and continuity, as Γ_γ moves from a circle near the equilibrium to a circle near the heteroclinic cycle, ν_2 increases from a number near 0 to a number near $\frac{6\beta}{(4-\beta)(2-\beta)^2}$. This shows that as ν_2 increases from 0 to $\frac{6\beta}{(4-\beta)(2-\beta)^2}$, system (2.1) has a unique limit cycle whose size increases from 0 to the size of the heteroclinic cycle.

One can easily check that condition (2.25) and the assumption $\beta < 1$ imply (2.24). Using Theorem 2.3 and Theorem 2.5 of Xiao and Ruan [22] and the properties associated with the heteroclinic cycle discussed above, we depict the dynamics of (2.1) before and after the heteroclinic bifurcation occurs as in Figures 4 and 5.

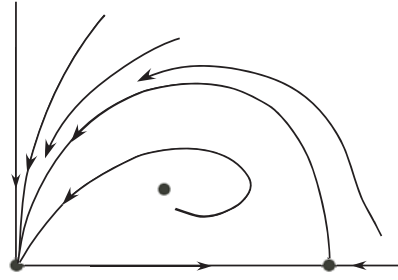


FIG. 5. Dynamics of system (2.1) when $\nu_2 > \frac{6\beta}{(4-\beta)(2-\beta)^2}$, $\beta < 1$, and κ is given by (2.25).

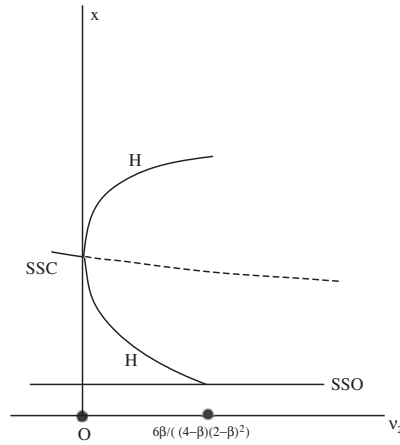


FIG. 6. Bifurcation diagram of the prey population.

2.3. Interpretation of the theoretical results. Based on the above results, the bifurcation diagram of the prey population x of system (2.1) is depicted in Figure 6. (The bifurcation diagram of the predator population y is similar.) 0 is the first critical value for ν_2 at which the Hopf bifurcation occurs. If ν_2 is slightly less than 0 , both prey and predator populations either tend to the origin (solid line labeled SSO), becoming extinct eventually, or tend toward a stable coexistence equilibrium (solid line labeled SSC), depending on the initial values. If ν_2 is greater than 0 , both prey and predator populations either tend toward the origin or tend to a limit cycle (solid line labeled H). In this case, the coexistence equilibrium (dashed line) is unstable. The Hopf bifurcation marks a critical condition at which the coexistence equilibrium becomes unstable and the prey and predator populations near the equilibrium starts oscillating periodically. If ν_2 increases from 0 to $\frac{6\beta}{(4-\beta)(2-\beta)^2}$, the amplitude of the oscillating population becomes larger. $\frac{6\beta}{(4-\beta)(2-\beta)^2}$ is the second critical value for ν_2 at which heteroclinic bifurcation occurs. It represents the collision of a large stable limit cycle with the origin. If ν_2 is slightly greater than $\frac{6\beta}{(4-\beta)(2-\beta)^2}$, the limit cycle attractor does not exist anymore, and both prey and predator populations become “unconditionally extinct”; i.e., the origin attracts all solutions (except the coexistence equilibrium solution). Thus starting in the oscillating state, a small increase in ν_2 may lead to a shift to the attractor—the origin. This heteroclinic bifurcation leading to the collapse of large oscillations of populations and extinction of populations is usually

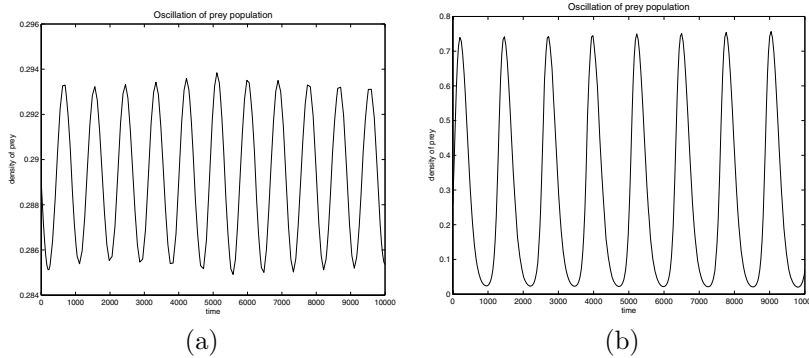


FIG. 7. *Small and large periodic oscillations of prey population.* (a) $\nu_2 = 0.2$, (b) $\nu_2 = 0.54$.

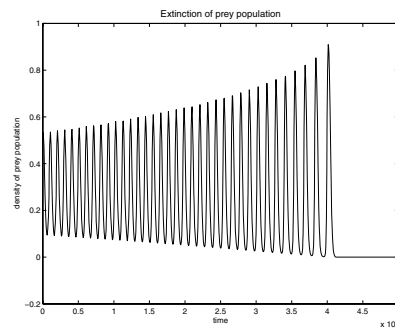


FIG. 8. *Extinction of prey population accompanied with oscillations when $\nu_2 = 0.56$.*

called a “catastrophic bifurcation” (Rinaldi and Scheffer [18]).

We carry out numerical simulations to demonstrate the dynamics of (2.1) described in the bifurcation diagram of Figure 6. We choose $\beta = 0.6$ and $\alpha = 0.02$ (a relatively small number). In this case $\frac{6\beta}{(4-\beta)(2-\beta)^2} = 0.5402$. Figure 7 shows periodic oscillations of the prey population when $\nu_2 = 0.2$ and $\nu_2 = 0.54$. Note that the amplitude of the periodic solution for $\nu_2 = 0.54$ is large, whereas the amplitude of the periodic solution for $\nu_2 = 0.2$ is very small. Figure 8 shows extinction of the population accompanied with oscillations when $\nu_2 = 0.56$, which is slightly greater than the critical value near 0.5402

Recall that α , β , and κ in terms of the parameters in the original system (1.1) are given by

$$\alpha = \frac{rm}{c}, \quad \beta = \frac{dm}{c}, \quad \kappa = \frac{fm}{c}.$$

Our assumption $\beta < 1$ implies $dm < c$. This shows that the capturing rate is relatively large. We fix $\frac{m}{c}$ so that if the prey intrinsic growth rate r is small, then α is small. We rewrite (2.25) in the form that the maximal predator growth rate f is a function of other parameters in (1.1) for small r . The resulting expression can then be used to study the dynamics of (1.1) including the Hopf bifurcation and heteroclinic bifurcation by varying f , based on the dynamics of the equivalent system (2.1). One can see that for relatively large c and f both predator and prey populations become extinct.

3. Concluding remarks. We have rigorously established the existence of a heteroclinic bifurcation and studied the related dynamics for the Michaelis–Menten-type ratio-dependent system by using Melnikov’s method. This method is often used to obtain “small” heteroclinic cycles or limit cycles in studying local bifurcations (see Guckenheimer and Holmes [11], Wiggins [21], and Chow, Li, and Wang [9]). The heteroclinic cycle described in Lemma 1 is such a small heteroclinic cycle near the origin. However, the heteroclinic cycle described in Theorem 1 that connects the origin and the equilibrium $(1, 0)$ is not a small one. This is essentially due to the variable change $x \rightarrow x/\alpha$ for small α that we have used, which together with other variable changes converts the former heteroclinic cycle into the latter one.

Our results show that near the Hopf bifurcation, depending on the initial conditions, populations of predators and prey either coexist or become extinct. These features have not been described by early prey-dependent predator-prey systems. The heteroclinic bifurcation triggers a shift from the state of periodic coexistence of populations to the state of extinction of both populations, resulting in a “catastrophe” to the predator-prey system.

Rinaldi and Scheffer [18] gave many interesting bifurcation examples in ecological models. They pointed out that a heteroclinic bifurcation is due to the collision of a stable limit cycle and a unstable saddle equilibrium. This is similar to what happens in system (1.1). However, the origin, an unstable point involved in the heteroclinic bifurcation for (1.1), is always an attractor. It is very interesting to note that the heteroclinic bifurcation results in the global attractivity of the origin.

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REFERENCES

- [1] H. R. AKCAKAYA, *Population cycles of mammals: Evidence for a ratio-dependent predation hypothesis*, Ecol. Monogr., 62 (1992), pp. 119–142.
- [2] R. ARDITI AND H. R. AKCAKAYA, *Underestimation of mutual interference of predators*, Oecologia (Berlin), 83 (1990), pp. 358–361.
- [3] R. ARDITI AND A. A. BERRYMAN, *The biological control paradox*, Trends Ecol. Evolution, 6 (1991), p. 32.
- [4] R. ARDITI AND L. R. GINZBURG, *Coupling in predator-prey dynamics: Ratio-dependence*, J. Theoret. Biol., 139 (1989), pp. 311–326.
- [5] R. ARDITI, L. R. GINZBURG, AND H. R. AKCAKAYA, *Variation in plankton densities among lakes: A case of ratio-dependent models*, Amer. Naturalist, 138 (1991), pp. 1287–1296.
- [6] J. R. BEDDINGTON, *Mutual interference between parasites or predators and its effect on searching efficiency*, J. Animal Ecol., 44 (1975), pp. 331–340.
- [7] F. BEREZOVSKAYA, G. KAREV, AND R. ARDITI, *Parametric analysis of the ratio-dependent predator-prey model*, J. Math. Biol., 43 (2001), pp. 221–246.
- [8] A. A. BERRYMAN, *The origins and evolution of predator-prey theory*, Ecol., 73 (1992), pp. 1530–1535.
- [9] S.-N. CHOW, C. LI, AND D. WANG, *Normal Forms and Bifurcation of Planar Vector Fields*, Cambridge University Press, New York, 1994.
- [10] D. L. DEANGELIS, R. A. GOLDSTEIN, AND R. V. O’NEILL, *A model for trophic interactions*, Ecol., 56 (1975), pp. 881–892.
- [11] J. GUCKENHEIMER AND P. HOLMES, *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields*, Springer-Verlag, New York, 1983.
- [12] A. P. GUTIERREZ, *The physiological basis of ratio-dependent predator-prey theory: A metabolic pool model of Nicholson’s blowflies as an example*, Ecol., 73 (1992), pp. 1552–1563.
- [13] N. G. HAIRSTON, F. E. SMITH, AND L. B. SLOBODKIN, *Community structure, population control and competition*, Amer. Naturalist, 94 (1960), pp. 421–425.

- [14] C. B. HUFFAKER, *Experimental studies on predation: Dispersion factors and predator-prey oscillations*, *Hilgardia*, 27 (1958), pp. 343–383.
- [15] S.-B. HSU, T.-W. HWANG, AND Y. KUANG, *Global analysis of the Michaelis–Menten type ratio-dependent predator-prey system*, *J. Math. Biol.*, 42 (2001), pp. 489–506.
- [16] Y. KUANG AND E. BERETTA, *Global qualitative analysis of a ratio-dependent predator-prey system*, *J. Math. Biol.*, 36 (1998), pp. 389–406.
- [17] L. S. LUCKINBILL, *Coexistence in laboratory populations of Paramecium aurelia and its predator Didinium nasutum*, *Ecol.*, 54 (1973), pp. 1320–1327.
- [18] S. RINALDI AND M. SCHEFFER, *Geometric analysis of ecological models with slow and fast processes*, *Ecosystems*, 3 (2000), pp. 507–521.
- [19] M. L. ROSENZWEIG, *Paradox of enrichment: Destabilization of exploitation systems in ecological time*, *Science*, 171 (1969), pp. 385–387.
- [20] Y. TANG AND W. ZHANG, *Heteroclinic bifurcation in a ratio-dependent predator-prey system*, *J. Math. Biol.*, 50 (2005), pp. 699–712.
- [21] S. WIGGINS, *Introduction to Applied Nonlinear Dynamical Systems and Chaos*, Springer-Verlag, New York, 2003.
- [22] D. XIAO AND S. RUAN, *Global dynamics of a ratio-dependent predator-prey system*, *J. Math. Biol.*, 43 (2001), pp. 268–290.