J. Korea Soc. Math. Educ. Ser. B: Pure Appl. Math. ISSN 1226-0657
Volume 15, Number 3 (August 2008), Pages 329–342

HOPF BIFURCATION PROPERTIES OF HOLLING TYPE PREDATOR-PREY SYSTEMS

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ABSTRACT. There have been many experimental and observational evidences which indicate the predator response to prey density needs not always monotone increasing as in the classical predator-prey models in population dynamics. Holling type functional response depicts situations in which sufficiently large number of the prey species increases their ability to defend or disguise themselves from the predator. In this paper we investigated the stability and instability property for a Holling type predator-prey system of a generalized form. Hopf type bifurcation properties of the non-diffusive system and the diffusion effects on instability and bifurcation values are studied.

1. INTRODUCTION

The classical Lotka-Volterra predator-prey model in mathematical population dynamics deals with the linear reaction functions as in the following :

$$\begin{cases} u_t = u(a_1 - b_1 u - c_1 v) & \text{for } t \in (0, \infty), \\ v_t = v(a_2 + b_2 u - c_2 v) & \text{for } t \in (0, \infty), \\ u(0) = u_0 \geq 0, \quad v(0) = v_0 \geq 0. \end{cases}$$

Traditionally in many predator-prey models, the predator response to prey density is assumed to be monotone increasing. This reflects the underlying assumption that the more prey in the environment, the better off the predator. However, there have come up experimental as well as observational evidences which indicate that this assumption may not be always true. We refer the readers to Rosenzweig [16] where he considered six different mathematical models of prey-predator or parasite-host interaction and showed that sufficient enrichment or increase of the prey carrying

Received by the editors April 1, 2008. Revised July 3, 2008. Accepted July 10, 2008.
2000 *Mathematics Subject Classification.* 35K55, 35B40.
Key words and phrases. predator-prey system, diffusion pressures, Holling-type functional responses, asymptotic behaviors, Hopf type bifurcation, kinetic system, diffusive instability.
This work was supported by the Sungshin Women's University Research Grant of 2006-2007.

capacity can cause destabilization of an otherwise stable interior equilibrium. Using a truncation for the sakes of biological reality, he also integrates the equation numerically and obtains extinction of the predator.

The term *group defence* is used to describe the phenomenon whereby predation is decreased, or even prevented altogether, due to the increased ability of the prey to better defend or disguise themselves when their numbers are large enough. This phenomenon is observed in many situations. For example, it is observed that lone musk ox is easily attacked by wolves, small herds of musk ox (2-6 animals) are attacked but with rare success, but there are no successful attacks in large herds. Also large swarms of insects may be considered as another example. Large swarms of insects make individual identification difficult for their predators. When microorganisms are used for the purpose of water-decomposition of water-purification, an over abundance of prey can cause certain nutrients to be growth-limiting for the predators. By adopting Holling-type functional responses in predator-prey systems we may incorporate *group defence* with the predator-prey relationship. Since this type of functional response had first been introduced by Haldane [6] in enzymology there have been many results on Holling-type predator-prey systems. [1], [2], [3], [5], [6], [7], [8], [10], [15], [16], [17], [18], [19], [20], [21] are a few of them.

Sugie, Kohno and Miyazaki [20] investigated a necessary and sufficient conditions for the uniqueness of limit cycles of a predator-prey system of the following form :

$$(1.1) \qquad \begin{cases} u_t = ru(1-\frac{u}{k}) - \frac{u^p v}{a+u^p} & \text{for } t \in (0,\infty), \\ v_t = v(\frac{\mu u^p}{a+u^p} - D) & \text{for } t \in (0,\infty), \\ u(0) = u_0 \geq 0, \quad v(0) = v_0 \geq 0, \end{cases}$$

where the coefficients r, k, μ, D and p are positive parameters, and $\phi(u) = \frac{u^p}{a+u^p}$ represents a functional response. The parameter r is the intrinsic growth rate. k is the carrying capacity for the prey population. μ and D are the birth rate and the death rate for the predator, respectively. The predator consumes the prey with functional response $\phi(u)$. The predator converts consumed prey into new predators with efficiency μ.

When $p = 1$ or $p = 2$, the function $\phi(u)$ is often called a functional response of Holling type. If $p \leq 1$, it is said to belong to Holling type II. If $p > 1$, Holling type III. Here $\sqrt[p]{a}$ is the half-saturation constant for the predator. As an example they considered the case in which $p = 1$, $D = 1$, $\mu = 2$, $a = 1$, and $k > 3$ for system (1.1).

$$(1.2) \qquad \begin{cases} u_t = ru(1-\frac{u}{k}) - \frac{uv}{1+u} \\ v_t = v(\frac{2u}{1+u} - 1), \end{cases}$$

In this case the conditions $\mu > D$, $\lambda_1 = \frac{aD}{\mu - D} = a < k = Dk$, and $(D+\mu)\lambda_1 = 3 < Dk = k$ are all satisfied. Hence (λ_1, ν_1) is the only critical point of system (1.2) in the first quadrant. And system (1.2) has a unique stable limit cycle. If $1 < k \le 3$, then (u^*, v^*) is stable steady-state of system (1.2). The value $k^* = 3$ is the Hopf type bifurcation value of the parameter k in system (1.2).

For a prey-predator systems with Holling type IV functional response Bhattacharyya, et al. [2] obtained some results on diffusion-driven instability phenomenon. They studied the following system

$$\begin{cases} \frac{du}{d\tau} = D_1 u_{xx} + u(1 - \frac{u}{\gamma}) - \frac{uv}{(u^2/\alpha)+u+1} \\ \frac{dv}{d\tau} = D_2 v_{xx} + \frac{\beta\delta uv}{(u^2/\alpha)+u+1} - \delta v. \end{cases}$$

and proved that the instability to small perturbations may arise because of the presence of diffusion coefficients D_1 and D_2.

We investigate in this paper the stability and instability property system (1.3).

$$(1.3) \qquad \begin{cases} u_t = d_1 u_{xx} + u(a_1 - b_1 u - \frac{c_1 v}{1+qu}) & \text{in } [0,1] \times (0,\infty), \\ v_t = d_2 v_{xx} + v(a_2 + \frac{b_2 u}{1+qu}) & \text{in } [0,1] \times (0,\infty), \\ u_x(x,t) = v_x(x,t) = 0 & \text{at } x = 0, 1, \\ u(x,0) = u_0(x) \ge 0, \quad v(x,0) = v_0(x) \ge 0 & \text{in } [0,1], \end{cases}$$

where $\Omega \subset \mathbb{R}^1$ is a bounded smooth domain. The coefficients d_i, b_i, c_i $(i = 1,2)$, q, and a_1 are positive constants. Only a_2 may be nonpositive. Throughout this paper we assume that the initial functions $u_0(x)$, $v_0(x)$ are not identically zero. For details in the biological background of cross-diffusions, we refer the reader to the monograph of Okubo and Levin [14]. a_1 and a_2 are the growth rates, and $\frac{a_1}{b_1}$ is the carrying capacity of the prey species. $\frac{1}{q}$ measures the extent of protection by the environment to both species u and v. $\frac{c_1}{q}$ is the maximum value which *per capita* reduction rate of u can attain. And $\frac{b_2}{q}$ has means similarly to v for the predator species v. More explanations for the response functions of this type are found in [4], [8], [9], [10], [19] and references therein.

In order to study the asymptotic behavior of the solution to system (1.3) we first investigate its kinetic system which is the corresponding non-diffusive system. Theorem 2.1 shows the necessary conditions on the parameters a_i, b_i, c_i $(i = 1,2)$ and q for the non-diffusive system to have the unique positive steady-state $(\overline{u}, \overline{v})$. The results on the Hopf type bifurcation phenomenon for system (2.4) is shown in Theorem 2.2. For the diffusive system (1.3) the effects of diffusions are investigated. Theorem 3.1 presents the property of the diffusion coefficients that they shift the bifurcation value of the parameter q for the diffusive system (1.3) compared to the non-diffusive system (2.4). It is proved Theorem 3.2 that diffusions may cause the instability of the positive constant steady-state $(\overline{u}, \overline{v})$ under the assumptions that assures the stability of $(\overline{u}, \overline{v})$ for the non-diffusive system (2.4).

This paper consists of seven sections : Section 1. Introduction. In Section 2 we present the Hopf type bifurcation properties of the non-diffusive system (2.4). Section 3 has the results on the diffusion effects in the aspect of instability and bifurcation values.

2. HOPF BIFURCATION FOR THE KINETIC SYSTEM OF (1.3)

For system (2.4) which is the kinetic system of (1.3) :

$$\begin{cases} u_t = u(a_1 - b_1 u - \frac{c_1 v}{1+qu}) & \text{for } t \in (0,\infty), \\ v_t = v(a_2 + \frac{b_2 u}{1+qu}) & \text{for } t \in (0,\infty), \\ u(0) = u_0 \geq 0, \quad v(0) = v_0 \geq 0, \end{cases} \tag{2.4}$$

we investigate the classical Hopf bifurcation phenomenon near a positive steady-state $(\overline{u}, \overline{v})$ as q, the the reciprocal of the extent of protection by the environment of the prey passes through the values $q^*_\pm$, which satisfies the following conditions :

(H1) $\operatorname{tr} A = 0$ and $\det A > 0$ when $q = q^*_\pm$.

(H2) $\left.\frac{d(\operatorname{Re}\lambda_+)}{dq}\right|_{q=q^*_\pm} \neq 0$,

where $\lambda_+ = \frac{1}{2}\left(\operatorname{tr} A + \sqrt{(\operatorname{tr} A)^2 - 4\det A}\right)$, an eigenvalue of $A = \begin{pmatrix} \frac{df}{du} & \frac{df}{dv} \\ \frac{dg}{du} & \frac{dg}{dv} \end{pmatrix}_{(\overline{u},\overline{v})}$

with $f(u,v) = u\left(a_1 - b_1 u - \frac{c_1 v}{1+qu}\right)$ and $g(u,v) = v\left(a_2 + \frac{b_2 u}{1+qu}\right)$.

The condition (H1) provides that the eigenvalues of the matrix A are purely imaginary. If, in addition, the transversality condition (H2) is satisfied, then the Hopf bifurcation occurs at $(\overline{u}, \overline{v})$ with $q = q^*_\pm$. At such a Hopf bifurcation for q near $q^*_\pm$ small amplitude oscillations (limit cycles) exists.

System (1.3) possesses a unique positive constant steady-state $(\overline{u}, \overline{v})$ under some conditions on the parameters a_i, b_i, c_i $(i = 1, 2)$, and q. To find such conditions we have to analyze its' kinetic system (2.4). We state a result on the existence of a unique positive steady-state for system (2.4).

Theorem 2.1. *Assume that $a_2 < 0$ and $0 \leq q < -(\frac{b_1}{a_1} + \frac{b_2}{a_2})$ for system* (2.4). *Then system* (2.4) *has a unique positive steady-state $(\overline{u}, \overline{v})$, where*

(2.5) $$\overline{u} = \frac{-a_2}{a_2q + b_2}, \qquad \overline{v} = \tfrac{1}{c_1}(1 + q\overline{u})(a_1 - b_1\overline{u}) = \frac{b_2(a_1a_2q + a_1b_2 + a_2b_1)}{c_1(a_2q + b_2)^2}.$$

If $q = 0$, then $(\overline{u}, \overline{v})$ is given by

$$(\overline{u}, \overline{v}) = \left(-\frac{a_2}{b_2}, \ \frac{a_1b_2 + a_2b_1}{b_2c_1}\right).$$

Proof. A steady-state $(\overline{u}, \overline{v})$ is obtained by solving the equations

(2.6) $$(a_1 - b_1u)(1 + qu) - c_1v = 0,$$

and

(2.7) $$a_2 + \frac{b_2u}{1 + qu} = 0.$$

From (2.7) we have that

(2.8) $$\overline{u} = \frac{-a_2}{a_2q + b_2}.$$

Since $q, b_2 > 0$ in systems (1.3) and (2.4) we notice that $\overline{u} > 0$ if and only if

$$a_2 < 0 \quad \text{and} \quad 0 \le q < -\frac{b_2}{a_2}.$$

And in order to have $\overline{v} > 0$ it must hold that $\overline{u} < \frac{a_1}{b_1}$, or equivalently

$$0 \le q < -\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right).$$

Here, from the assumption $a_1, b_1 > 0$ it holds that

$$-\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right) < -\frac{b_2}{a_2}.$$

Hence we conclude that system (2.4) has a unique positive steady-state $(\overline{u}, \overline{v})$ if

$$a_2 < 0 \quad \text{and} \quad 0 \le q < -\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right).$$

from (2.6) and (2.8), it is obtained that

$$\begin{aligned}
\overline{v} &= \frac{1}{c_1}(1 + q\overline{u})(a_1 - b_1\overline{u}) \\
&= \frac{1}{c_1}\left(1 - \frac{a_2q}{a_2q + b_2}\right)\left(a_1 + \frac{a_2b_1}{a_2q + b_2}\right) \\
&= \frac{1}{c_1} \cdot \frac{b_2}{a_2q + b_2}\left(a_1 + \frac{a_2b_1}{a_2q + b_2}\right) \\
&= \frac{b_2(a_1a_2q + a_1b_2 + a_2b_1)}{c_1(a_2q + b_2)^2},
\end{aligned}$$

and if we assume that $q = 0$, then

$$\overline{u} = -\frac{a_2}{b_2} \quad \text{and} \quad \overline{v} = \frac{a_1 b_2 + a_2 b_1}{b_2 c_1}.$$

□

Theorem 2.2. *Assume that $a_2 < 0$ and $0 \le q < -(\frac{b_1}{a_1} + \frac{b_2}{a_2})$ for system (2.4). Also suppose that*

$$\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right)^2 + 4\frac{b_1 b_2}{a_1 a_2} > 0. \tag{2.9}$$

Then for system (2.4) Hopf bifurcation near $(\overline{u}, \overline{v})$ occurs at the parameter values $q = q^*_\pm$, where

$$q^*_\pm = \frac{1}{2}\left(-\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right) \pm \sqrt{\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right)^2 + 4\frac{b_1 b_2}{a_1 a_2}}\right).$$

That is, $(\overline{u}, \overline{v})$ is asymptotically stable if $0 < q < q^*_-$ or $q > q^*_+$, and unstable if $q^*_- < q < q^*_+$.

Proof. Let us denote that

$$f(u,v) = u\left(a_1 - b_1 u - \frac{c_1 v}{1 + qu}\right) = u\left(\frac{(a_1 - b_1 u)(1 + qu) - c_1 v}{1 + qu}\right)$$

and

$$g(u,v) = v\left(a_2 + \frac{b_2 u}{1 + qu}\right) = v\left(a_2 + \frac{b_2}{q} - \frac{b_2}{q^2(\frac{1}{q} + u)}\right).$$

From Theorem 2.1 we have that $\overline{u} > 0$, $\overline{v} > 0$, and

$$\overline{u} = \frac{-a_2}{a_2 q + b_2}, \qquad \overline{v} = \tfrac{1}{c_1}(1 + q\overline{u})(a_1 - b_1\overline{u}) = \frac{b_2(a_1 a_2 q + a_1 b_2 + a_2 b_1)}{c_1(a_2 q + b_2)^2}.$$

For the linear analysis write

$$x(t) = u(t) - \overline{u}, \quad y(t) = v(t) - \overline{v}$$

which on substituting into system (2.4), linearizing with small $|x|$ and $|y|$ gives

$$\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} = A \begin{pmatrix} x \\ y \end{pmatrix},$$

$$A = \begin{pmatrix} \frac{df}{du} & \frac{df}{dv} \\ \frac{dg}{du} & \frac{dg}{dv} \end{pmatrix}_{(\overline{u},\overline{v})} = \begin{pmatrix} a_1 - 2b_1\overline{u} - \frac{c_1\overline{v}(1+q\overline{u}) - c_1 q\overline{u}\overline{v}}{(1+q\overline{u})^2} & -\frac{c_1\overline{u}}{1+q\overline{u}} \\ \frac{b_2\overline{v}(1+q\overline{u}) - b_2 q\overline{u}\overline{v}}{(1+q\overline{u})^2} & a_2 + \frac{b_2\overline{u}}{1+q\overline{u}} \end{pmatrix}.$$

Using the equations $a_1 - b_1\overline{u} - \frac{c_1\overline{v}}{1+q\overline{u}} = 0$ and $a_2 + \frac{b_2\overline{u}}{1+q\overline{u}} = 0$ we may simplify the components of the community matrix A as

$$A = \begin{pmatrix} a_1 - 2b_1\overline{u} - \frac{c_1\overline{v}}{(1+q\overline{u})^2} & -\frac{c_1\overline{u}}{1+q\overline{u}} \\ \frac{b_2\overline{v}}{(1+q\overline{u})^2} & 0 \end{pmatrix}$$
$$= \begin{pmatrix} -b_1\overline{u} + \frac{c_1\overline{v}}{1+q\overline{u}} - \frac{c_1\overline{v}}{(1+q\overline{u})^2} & -\frac{c_1\overline{u}}{1+q\overline{u}} \\ \frac{b_2\overline{v}}{(1+q\overline{u})^2} & 0 \end{pmatrix}$$
$$= \begin{pmatrix} -b_1\overline{u} + \frac{c_1q\overline{u}\overline{v}}{(1+q\overline{u})^2} & -\frac{c_1\overline{u}}{1+q\overline{u}} \\ \frac{b_2\overline{v}}{(1+q\overline{u})^2} & 0 \end{pmatrix}.$$

Hence for the corresponding characteristic equation $\lambda^2 - (\operatorname{tr} A)\lambda + \det A = 0$ we find that

$$\det A = \frac{b_2c_1\overline{u}\overline{v}}{(1+q\overline{u})^3} > 0$$
$$\operatorname{tr} A = -b_1\overline{u} + \frac{c_1q\overline{u}\overline{v}}{(1+q\overline{u})^2}$$

Hence $(\overline{u}, \overline{v})$ is linearly asymptotically stable if $\operatorname{tr} A < 0$, and unstable if $\operatorname{tr} A > 0$. Thus by solving the equation $\operatorname{tr} A = 0$ we find a bifurcation parameter for system (2.4). Now, through simple computations we note that

$$\begin{aligned} \operatorname{tr} A &= -b_1\overline{u} + \frac{c_1q\overline{u}\overline{v}}{(1+q\overline{u})^2} \\ &= -b_1\overline{u} + \frac{q\overline{u}}{(1+q\overline{u})^2} \cdot (1+q\overline{u})(a_1 - b_1\overline{u}) \\ &= -b_1\overline{u} + \frac{q\overline{u}}{1+q\overline{u}} \cdot (a_1 - b_1\overline{u}) \\ &= \frac{-b_1\overline{u}(1+q\overline{u}) + q\overline{u}(a_1 - b_1\overline{u})}{(1+q\overline{u})} \\ &= \frac{\overline{u}(-2b_1q\overline{u} + a_1q - b_1)}{1+q\overline{u}} \\ &= -\frac{a_2}{b_2}(-2b_1q\overline{u} + a_1q - b_1), \end{aligned} \tag{2.10}$$

and

$$\begin{aligned} -2b_1q\overline{u} + a_1q - b_1 &= \frac{2a_2b_1q}{a_2q+b_2} + a_1q - b_1 \\ &= \frac{2a_2b_1q + (a_1q - b_1)(a_2q + b_2)}{a_2q+b_2} \\ &= \frac{2a_2b_1q + a_1a_2q^2 + (a_1b_2 - a_2b_1)q - b_1b_2}{a_2q+b_2} \\ &= \frac{a_1a_2q^2 + (a_1b_2 + a_2b_1)q - b_1b_2}{a_2q+b_2} \\ &= \frac{a_1a_2}{a_2q+b_2}\left(q^2 + (\frac{b_1}{a_1} + \frac{b_2}{a_2})q - \frac{b_1b_2}{a_1a_2}\right) \\ &= -a_1\overline{u}\left(q^2 + (\frac{b_1}{a_1} + \frac{b_2}{a_2})q - \frac{b_1b_2}{a_1a_2}\right), \end{aligned}$$

since $\overline{u} = \frac{-a_2}{a_2 q + b_2}$. Also, from the conditions $a_2 < 0$ and $0 \le q < -(\frac{b_1}{a_1} + \frac{b_2}{a_2})$ we see that

$$0 \le q^2 < -\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right) q,$$

and so

$$q^2 + \left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right) q < 0 \quad \text{and} \quad -\frac{b_1 b_2}{a_1 a_2} > 0.$$

Hence

$$\operatorname{tr} A < 0 \quad \text{if and only if} \quad q^2 + \left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right) q - \frac{b_1 b_2}{a_1 a_2} > 0,$$

and

$$\operatorname{tr} A > 0 \quad \text{if and only if} \quad q^2 + \left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right) q - \frac{b_1 b_2}{a_1 a_2} < 0.$$

Solving the equation $\operatorname{tr} A = 0$, equivalently $q^2 + (\frac{b_1}{a_1} + \frac{b_2}{a_2})q - \frac{b_1 b_2}{a_1 a_2} = 0$ we determine the bifurcation value $q^*_\pm$ for the parameter $q > 0$ as

$$q^*_\pm = \frac{1}{2}\left(-(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}) \pm \sqrt{(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2})^2 + 4\tfrac{b_1 b_2}{a_1 a_2}}\,\right). \tag{2.11}$$

under the assumption (2.9), that is, $\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right)^2 + 4\frac{b_1 b_2}{a_1 a_2} > 0$. Also the transversality condition (2.12) below has to be satisfied in order to guarantee the occurrence of the Hopf bifurcation at $q = q^*_\pm$:

$$\left.\frac{d(\operatorname{Re}\lambda_+)}{dq}\right|_{q=q^*_\pm} \neq 0, \tag{2.12}$$

where $\lambda_+ = \frac{1}{2}\left(\operatorname{tr} A + \sqrt{(\operatorname{tr} A)^2 - 4\det A}\right)$, an eigenvalue of A. Since $\det A > 0$ and $\operatorname{tr} A = 0$ at $q = q^*_\pm$, we see that $(\operatorname{tr} A)^2 - 4\det A < 0$ near $q = q^*_\pm$, and thus

$$\operatorname{Re}\lambda_+ = \tfrac{1}{2}\operatorname{tr} A.$$

Hence the transversality condition (2.12) reduces to

$$\left.\frac{d}{dq}(\operatorname{tr} A)\right|_{q=q^*_\pm} \neq 0,$$

and further to

$$\left.\frac{d}{dq}(-2b_1 q\overline{u} + a_1 q - b_1)\right|_{q=q^*_\pm} \neq 0, \tag{2.13}$$

by (2.10). Here we notice that $\frac{d\overline{u}}{dq} = \overline{u}^2$, since $\overline{u} = \frac{-a_2}{a_2 q + b_2}$, and $\frac{d\overline{u}}{dq} = \frac{(a_2)^2}{(a_2 q + b_2)^2}$. Thus we have that

$$\begin{aligned}\tfrac{d}{dq}(-2b_1 q\overline{u} + a_1 q - b_1) &= -2b_1\overline{u} - 2b_1 q\overline{u}^2 + a_1\\ &= -2b_1\overline{u}(1 + q\overline{u}) + a_1\\ &= \tfrac{2a_2 b_1 b_2}{(a_2 q + b_2)^2} + a_1.\end{aligned}$$

Hence (2.13) becomes

$$\frac{2a_2b_1b_2}{(a_2q_\pm^* + b_2)^2} + a_1 \neq 0,$$

equivalently,

$$\left(q_\pm^* + \frac{b_2}{a_2}\right)^2 + \frac{2b_1b_2}{a_1a_2} \neq 0. \tag{2.14}$$

By (2.11) the condition (2.14) is rewritten as

$$\left(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}\right)^2 + 4\tfrac{b_1b_2}{a_1a_2} \pm \left(\tfrac{b_2}{a_2} - \tfrac{b_1}{a_1}\right)\sqrt{\left(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}\right)^2 + 4\tfrac{b_1b_2}{a_1a_2}} \neq 0 \tag{2.15}$$

Since $a_2 < 0$ and a_1, b_i, c_i, $(i = 1, 2)$ are all positive constants, it trivially holds that

$$\left(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}\right)^2 + 4\tfrac{b_1b_2}{a_1a_2} - \left(\tfrac{b_2}{a_2} - \tfrac{b_1}{a_1}\right)\sqrt{\left(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}\right)^2 + 4\tfrac{b_1b_2}{a_1a_2}} \neq 0 \tag{2.16}$$

by the assumption (2.9), that is, $\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right)^2 + 4\frac{b_1b_2}{a_1a_2} > 0$.

From the following steps of computations

$$\begin{aligned}
&\left[\left(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}\right)^2 + 4\tfrac{b_1b_2}{a_1a_2}\right]^2 - \left(\tfrac{b_2}{a_2} - \tfrac{b_1}{a_1}\right)^2\left(\sqrt{\left(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}\right)^2 + 4\tfrac{b_1b_2}{a_1a_2}}\right)^2\\
&= \left[\left(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}\right)^2 + 4\tfrac{b_1b_2}{a_1a_2}\right]^2 - \left(\tfrac{b_2}{a_2} - \tfrac{b_1}{a_1}\right)^2\left[\left(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}\right)^2 + 4\tfrac{b_1b_2}{a_1a_2}\right];\\
&= \left[\left(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}\right)^2 + 4\tfrac{b_1b_2}{a_1a_2}\right]\left[\left(\tfrac{b_1}{a_1}\right)^2 + \left(\tfrac{b_2}{a_2}\right)^2 + 6\tfrac{b_1b_2}{a_1a_2} - \left(\tfrac{b_1}{a_1}\right)^2 - \left(\tfrac{b_2}{a_2}\right)^2 + 2\tfrac{b_1b_2}{a_1a_2}\right],\\
&= 8\tfrac{b_1b_2}{a_1a_2}\left[\left(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}\right)^2 + 4\tfrac{b_1b_2}{a_1a_2}\right],
\end{aligned}$$

it holds that

$$\left(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}\right)^2 + 4\tfrac{b_1b_2}{a_1a_2} + \left(\tfrac{b_2}{a_2} - \tfrac{b_1}{a_1}\right)\sqrt{\left(\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2}\right)^2 + 4\tfrac{b_1b_2}{a_1a_2}} \neq 0 \tag{2.17}$$

under the assumption (2.9). Finally (2.16) and (2.17) together prove that the transversality condition (2.15) holds.

We also see that $(\overline{u}, \overline{v})$ is asymptotically stable if $0 < q < q_-^*$ or $q > q_+^*$, and unstable if $q_-^* < q < q_+^*$, since

$$\operatorname{tr} A < 0 \qquad \text{if} \quad 0 < q < q_-^* \quad \text{or} \quad q > q_+^*,$$

and

$$\operatorname{tr} A > 0 \qquad \text{if} \quad q_-^* < q < q_+^*.$$

□

Note. By noticing that

$$\begin{aligned}\left(\tfrac{b_1}{a_1}+\tfrac{b_2}{a_2}\right)^2+4\tfrac{b_1b_2}{a_1a_2} &= \left(\tfrac{b_1}{a_1}\right)^2+\left(\tfrac{b_2}{a_2}\right)^2+6\tfrac{b_1b_2}{a_1a_2}\\ &= \left(\tfrac{b_1}{a_1}+(3+2\sqrt{2})\tfrac{b_2}{a_2}\right)\left(\tfrac{b_1}{a_1}+(3-2\sqrt{2})\tfrac{b_2}{a_2}\right)\\ &> 0.\end{aligned}$$

and using the conditions that $a_2 < 0$ and a_1, b_i, c_i, $(i = 1, 2)$ are all positive constants, we may restate the condition (2.9) in Theorem 2.2 in an equivalent form as the following :

$$0 < \tfrac{b_1}{a_1} < -(3-2\sqrt{2})\tfrac{b_2}{a_2} \quad \text{or} \quad 0 < -(3+2\sqrt{2})\tfrac{b_2}{a_2} < \tfrac{b_1}{a_1}. \tag{2.18}$$

3. THE EFFECT OF DIFFUSION TO THE STABILITY

Now we observe system (1.3) to investigate the effect of diffusion to system (2.4) about the positive constant steady-state $(\overline{u}, \overline{v})$. First, in Theorem 3.1 we observe that diffusions may cause the instability of the positive constant steady-state $(\overline{u}, \overline{v})$ under the assumptions that assures the stability of $(\overline{u}, \overline{v})$ for the non-diffusive system (2.4). The result in Theorem 3.2 shows the effect of diffusions to shift the bifurcation value of the parameter q for the diffusive system (1.3) compared to the non-diffusive system (2.4).

Theorem 3.1. *For the diffusive system* (1.3) *assume the condition* (2.9) *and that* $a_2 < 0$. *Also assume that*

$$q_-^* < q < q_+^*. \tag{3.1}$$

The positive constant steady-state $(\overline{u}, \overline{v})$ *is unstable for system* (1.3) *if*

$$\frac{d_2}{d_1} > \frac{4b_2c_1\overline{v}}{\overline{u}(1+q\overline{u})^3(b_2-\frac{c_1q\overline{v}}{(1+q\overline{u})^2})^2}. \tag{3.2}$$

Proof. In order for system (1.3) to possess the unique positive constant steady-state $(\overline{u}, \overline{v})$ the condition $0 \le q < -(\frac{b_1}{a_1}+\frac{b_2}{a_2})$ is required to hold, and it is shown from the condition (3.1) and that $0 < q_-^* < q_+^* < -(\frac{b_1}{a_1}+\frac{b_2}{a_2})$ because

$$q_\pm^* = \tfrac{1}{2}\left(-(\tfrac{b_1}{a_1}+\tfrac{b_2}{a_2}) \pm \sqrt{(\tfrac{b_1}{a_1}+\tfrac{b_2}{a_2})^2+4\tfrac{b_1b_2}{a_1a_2}}\,\right).$$

The characteristic equation of the linearization of the diffusive system (1.3) around $(\overline{u}, \overline{v})$ is given as

(3.3)
$$\lambda^2 + \left((d_1+d_2)\beta^2 + b_1\overline{u} - \tfrac{c_1 q\overline{uv}}{(1+q\overline{u})^2}\right)\lambda + \left(d_1\beta^2 + b_1\overline{u} - \tfrac{c_1 q\overline{uv}}{(1+q\overline{u})^2}\right) d_2\beta^2 + \tfrac{b_2 c_1 \overline{uv}}{(1+q\overline{u})^3} = 0,$$
where the solutions of system (1.3) of the form $u = \overline{u} + \alpha_1 e^{\lambda t}\cos\beta x$ and $v = \overline{v} + \alpha_2 e^{\lambda t}\cos\beta x$ are considered. For system (1.3) the positive constant steady-state becomes unstable if

$$K(\beta^2) = \left(d_1\beta^2 + b_1\overline{u} - \frac{c_1 q\overline{uv}}{(1+q\overline{u})^2}\right) d_2\beta^2 + \frac{b_2 c_1\overline{uv}}{(1+q\overline{u})^3} < 0. \tag{3.4}$$

By regarding K as a quadratic function in β^2
$$K(\beta^2) = d_1 d_2(\beta^2)^2 + d_2\left(b_1\overline{u} - \frac{c_1 q\overline{uv}}{(1+q\overline{u})^2}\right)\beta^2 + \frac{b_2 c_1\overline{uv}}{(1+q\overline{u})^3}$$
we find the minimum value K_{min} of the function $K(\beta^2)$. We see that K_{min} exists as

$$\begin{aligned} K_{\text{min}} &= \tfrac{b_2 c_1\overline{uv}}{(1+q\overline{u})^3} - \tfrac{d_2}{4d_1}\left(b_1\overline{u} - \tfrac{c_1 q\overline{uv}}{(1+q\overline{u})^2}\right)^2 \\ &= \overline{u}\left(\tfrac{b_2 c_1\overline{v}}{(1+q\overline{u})^3} - \tfrac{d_2\overline{u}}{4d_1}\left(b_1 - \tfrac{c_1 q\overline{v}}{(1+q\overline{u})^2}\right)^2\right), \end{aligned} \tag{3.5}$$

provided that
$$-\left(b_1\overline{u} - \frac{c_1 q\overline{uv}}{(1+q\overline{u})^2}\right) = \operatorname{tr} A > 0,$$
which is guaranteed by the condition (3.1), that is, $q_-^* < q < q_+^*$, where $q_\pm^*$ are the solutions of the equation $\operatorname{tr} A = 0$, and
$$\operatorname{tr} A = \tfrac{a_1 a_2\overline{u}}{b_2}\left(q^2 + (\tfrac{b_1}{a_1} + \tfrac{b_2}{a_2})q - \tfrac{b_1 b_2}{a_1 a_2}\right).$$
Finally we conclude that $K_{\text{min}} < 0$ if
$$\frac{d_2}{d_1} > \frac{4\frac{b_2 c_1\overline{v}}{(1+q\overline{u})^3}}{\overline{u}\left(b_2 - \frac{c_1 q\overline{v}}{(1+q\overline{u})^2}\right)^2} = \frac{4b_2 c_1\overline{v}}{\overline{u}(1+q\overline{u})^3(b_2 - \frac{c_1 q\overline{v}}{(1+q\overline{u})^2})^2}.$$

□

Theorem 3.2. *Assume that $a_2 < 0$ and the conditions (2.9), (3.1) for the diffusive system (1.3). Also assume that $d_1 \gg d_2$. Then there exits an bifurcation value $q_d^* > 0$ of the parameter q for system (1.3).*

And if condition (2.9) is also assumed, then it holds that

$$q_d^* > q_\pm^*, \tag{3.6}$$

where $q_\pm^*$ is the Hopf bifurcation value of the parameter q for the non-diffusive system (2.4) which is the kinetic system corresponding to system (1.3).

Proof. In order to find the bifurcation value of the parameter q for system (1.3) we observe $K_{\min}$ in (3.5) from the proof of Theorem 3.1 and solve the equation

$$K_{\min} = 0,$$

that is,

$$\frac{b_2 c_1 \overline{v}}{(1+q\overline{u})^3} - \frac{d_2 \overline{u}}{4d_1}\left(b_1 - \frac{c_1 q \overline{v}}{(1+q\overline{u})^2}\right)^2 = 0. \tag{3.7}$$

Equation (3.7) is reduced as

$$b_2 c_1 \overline{v}(1+q\overline{u}) - \frac{d_2 \overline{u}}{4d_1}\left(b_1(1+q\overline{u})^2 - c_1 q \overline{v}\right)^2 = 0. \tag{3.8}$$

By substituting

$$\overline{v} = \tfrac{1}{c_1}(1+q\overline{u})(a_1 - b_1\overline{u})$$

in to (3.8) we have

$$b_2(1+q\overline{u})^2(a_1 - b_1\overline{u}) - \frac{d_2\overline{u}}{4d_1}\left(b_1(1+q\overline{u})^2 - q(1+q\overline{u})(a_1 - b_1\overline{u})\right)^2 = 0,$$

and so

$$b_2(a_1 - b_1\overline{u}) - \frac{d_2\overline{u}}{4d_1}\left(b_1(1+q\overline{u}) - q(a_1 - b_1\overline{u})\right)^2 = 0. \tag{3.9}$$

Now let us substitute

$$\overline{u} = \frac{-a_2}{a_2 q + b_2}$$

into (3.9) to obtain

$$\frac{b_2(a_1a_2q + a_1b_2 + a_2b_1)}{a_2q + b_2} + \frac{a_2}{4}\left(\frac{d_2}{d_1}\right)\frac{[b_1b_2 - q(a_1a_2q + a_1b_2 + a_2b_1)]^2}{(a_2q+b_2)^3} = 0,$$

equivalently

$$b_2(a_1a_2q + a_1b_2 + a_2b_1)(a_2q+b_2)^2 + \frac{a_2}{4}\left(\frac{d_2}{d_1}\right)[[b_1b_2 - q(a_1a_2q + a_1b_2 + a_2b_1)]^2 = 0. \tag{3.10}$$

Here we observe (3.10) as an equation in the variable q and let q_d^* be the root of equation (3.10). We note that the diffusion pressures d_1 and d_2 are chosen independent of the parameters a_i, b_i, c_i $(i = 1, 2)$ and q in system (1.3). Thus when $d_1 \gg d_2$ the root of equation (3.10) q_d^* is approximated by the root of the equation

$$b_2(a_1a_2q + a_1b_2 + a_2b_1)(a_2q+b_2)^2 = 0. \tag{3.11}$$

From the assumption in the statement of the present theorem that

$$a_2 < 0 \ \text{ and } \ 0 \le q < -\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right)$$

we have

$$0 \leq q < -\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right) < -\frac{b_2}{a_2}.$$

Hence we conclude that

$$0 \leq q_d^* \approx -\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right) \tag{3.12}$$

if $d_1 \gg d_2$.

Now we remind a result in Theorem 2.2 where condition (2.9) is also assumed that

$$q_\pm^* = \frac{1}{2}\left(-\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right) \pm \sqrt{\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right)^2 + 4\frac{b_1 b_2}{a_1 a_2}}\right)$$

for the non-diffusive system (2.4) which is the corresponding kinetic system of (1.3). By noting that

$$0 < q_\pm^* < -\left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right)$$

we conclude that

$$q_d^* > q_\pm^*$$

when $d_1 \gg d_2$. □

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