HIROSHIMA MATH. J.
23 (1993), 629–644

Global existence of bifurcating solutions to a two-box prey-predator model

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(Received May 8, 1992)

§ 1. Introduction

P. Waltman [1] considered the following prey-predator system:

$$(1.1)\qquad \begin{cases} \dfrac{ds(t)}{dt} = \gamma s(t)\left(1 - \dfrac{s(t)}{K}\right) - \dfrac{1}{k}\dfrac{ms(t)}{s(t) + a_1}x(t) \equiv f(s, x) \\[2ex] \dfrac{dx(t)}{dt} = \left(\dfrac{ms(t)}{s(t) + a_1} - D\right)x(t) \equiv g(s, x) \\[2ex] s(0) = s_0 > 0\,, \qquad x(0) = x_0 > 0\,, \end{cases}$$

where $x(t)$ denotes the population of the predator, $s(t)$ the population of the prey, m the maximum growth rate of the predator, D the death rate of the predater, a_1 the half-saturation constant of the predator, k the yield factor of the predator feeding on the prey, γ the intrinsic rate of increase for the prey and K the carrying capacity for the prey population. The parameters m, a_1, k, D, γ and K are all positive constants.

In this model, the prey grows logistically in the absence of predation and the predator consume prey according to a saturating functional response. It is well known that the solutions of (1.1) are positive and bounded and that the system (1.1) has three typical behaviors: (a) Dominance. When the value of carrying capacity K of prey is less than λ ($\lambda = a_1D/(m - D)$), the critical point $(K, 0)$ of (1.1) is asymptotically stable, namely in this case as $t \to \infty$ the prey grows to its limited value and predator becomes extinct. (b) Coexistence. When $\lambda < K < a_1 + 2\lambda$ the critical point (λ, x^*) ($x^* = k\gamma(a_1 + \lambda)(K - \lambda)/(mK)$) of (1.1) is asymptotically stable. (c) Periodicity. When $K > a_1 + 2\lambda$ system (1.1) has a stable periodic orbit in the first quadrant of the s-x plane (see [3], [4]).

On the other hand, the basic interest of the present paper is in the study of spatial and spatio-temporal patterns of the population densities when spatial migration effect of the two species are introduced in the model. If linear diffusions in space are assumed to represent spatial migration effects, the model would be a system of reaction-diffusion equations. The behaviors of solutions of such systems have been the main subject of a number of researchers, see [5], [6] and [7] in which the local bifurcation theoretic study and singular perturbation techniques have been used as the main tools. Even with such studies, it is still difficult to obtain a complete picture of global parametric dependency of non-uniform stationary patterns.

In this paper, therefore we take another approach. Instead of considering reaction-diffusion systems, we introduce a simple spatially discrete model with nonlinear interactions corresponding to (1.1). Our system is the following two-box prey-predator equation:

$$
\tag{1.2}
\begin{cases}
\dfrac{ds_1}{dt} = \mathrm{d_s}(s_2 - s_1) + f(s_1, x_1) \\[2ex]
\dfrac{dx_1}{dt} = \mathrm{d_x}(x_2 - x_1) + g(s_1, x_1) \\[2ex]
\dfrac{ds_2}{dt} = \mathrm{d_s}(s_1 - s_2) + f(s_2, x_2) \\[2ex]
\dfrac{dx_2}{dt} = \mathrm{d_x}(x_1 - x_2) + g(s_2, x_2) \\[2ex]
s_1(0) > 0\,, \quad s_2(0) > 0\,, \quad x_1(0) > 0\,, \quad x_2(0) > 0\,,
\end{cases}
$$

where s_i and x_i $(i = 1, 2)$ are respectively the population of the prey and the predator in the box i $(i = 1, 2)$, $\mathrm{d_s}$ and $\mathrm{d_x}$ respectively the magnitude of diffusion of the prey and the predator. The terms $\mathrm{d_s}(s_1 - s_2)$, $\mathrm{d_x}(x_1 - x_2)$, $\mathrm{d_s}(s_2 - s_1)$ and $\mathrm{d_x}(x_2 - x_1)$ represent the migration effect between the 2 boxes (see [8], [9], [10]).

Our goal is to obtain a complete global bifurcation diagram of all the non-negative equilibria of the two-box system (1.2), in which parametric dependency of the diagram is explicitly described. The organization of the paper is as follows. As the preliminary, we first denote the result on (1.1) and describe the local existence and direction of the asymmetric simple bifurcating solutions in Section 2. Section 3 is devoted to the analytical investigation of the global structure of simple bifurcating solutions. By the appropriate change of variables the problem of finding equilibria of (1.2) is reduced to solving a equation of rational expression with a real variable which will be called the θ-equation. This equation enables us to obtain a rigorous global structure of equilibria. In Section 4 we investigate numerically the stability of asymmetric bifurcating solutions. A consequence of the numerical study shows that the multiple asymmetric solutions, namely both the time periodic solution and the asymmetric equilibria are stable in a wide range of parameters.

§ 2. Local existence of bifurcating solutions from the equilibrium

We begin by stating the preliminary results for the system (1.1). We first note that the system (1.1) has three equilibrium points $P_0 = (0, 0)$, $P_1 = (K, 0)$ and $P^* = (s^*, x^*)$ where $s^* = \lambda$ and $x^* = k\gamma(\lambda + a_1)(K - \lambda)/(mK)$ with $\lambda = a_1 D/(m - D)$. The equilibrium P_0 corresponding to absence of two species persists to be a saddle point for all $K > 0$ and the equilibrium $(K, 0)$ corresponding to the existence only of the prey is stable node for $K < \lambda$ and is saddle for $K > \lambda$, so that there exists no bifurcating solutions from these points. If $K > \lambda$, the equilibrium P^* is in the interior of the first quadrant and corresponds to co-existence of both species. The linearization of system (1.1) about P^* is

$$\frac{d}{dt}\mathbf{r} = \mathbf{M}\mathbf{r}, \tag{2.1}$$

where $\mathbf{r} = (r_1, r_2)$ and

$$M = \begin{pmatrix} A & -C \\ B & 0 \end{pmatrix}$$

$$A = \frac{\gamma}{K}\left(\frac{K - 2\lambda - a_1}{\lambda + a_1}\right)\lambda,$$

$$C = \frac{1}{k}\frac{m\lambda}{\lambda + a_1},$$

$$B = \frac{a_1 k\lambda}{\lambda + a_1}\left(1 - \frac{\lambda}{K}\right).$$

The characteristic equation of M is

$$\xi^2 - A\xi + CB = 0. \tag{2.2}$$

We easily see that the equilibrium P^* is stable spiral for $K < K^* = 2\lambda + a_1$ and unstable one for $K > K^*$. It was already shown in [1] that $K = K^*$ is a nondegenerate Hopf bifurcation point and the stable periodic solution exists globally for all $K > K^*$. Hereafter we restrict our attention to the case of $K > \lambda$ and discuss what kind of solutions bifurcate from the coexistent equilibrium.

As is obviously seen, $\mathbf{x}^* = (s^*, x^*, s^*, x^*)$ is an equilibrium point of the two box system (1.2). We shall call it a symmetric equilibrium of (1.2) since the population of each species distributes equally over two boxes. Now we examine the linearized stability of equilibrium point. Let us denote J as the Jacobian matrix of the right hand side of (1.2) around the symmetric solution $\mathbf{x}^*$. We consider the eigenvalue problem.

$$\text{(2.3)} \qquad \mathbf{J}\mathbf{x} = \zeta \mathbf{x}\,,$$

where $\mathbf{x} = (t_1, y_1, t_2, y_2)$. By introducing the independent variable $\mathbf{y} = (t_+, y_+, t_-, y_-)$ with $t_\pm = t_1 \pm t_2$, $y_\pm = y_1 \pm y_2$ (2.3) is transformed into

$$\begin{pmatrix} M & 0 \\ 0 & \overline{M} \end{pmatrix} \begin{bmatrix} t_+ \\ y_+ \\ t_- \\ y_- \end{bmatrix} = \zeta \begin{bmatrix} t_+ \\ y_+ \\ t_- \\ y_- \end{bmatrix}.$$

Hence eigenvalues ζ of (2.3) are determined by the characteristic equations of M and $\overline{M}$. Since M is the linearized matrix of (1.1), we see that $K = K^*$ is a Hopf bifurcation point for the system (1.2) and the K-family of periodic solutions exist independently of d_x and d_s for $K > K^*$.

The eigenvalues of $\overline{M}$ are defined by $\eta_\pm$ roots of

$$\text{(2.4)} \qquad \eta^2 + F\eta + E = 0\,,$$

where $E = 2d_x(2d_s - A) + BC$ and $F = 2d_x + 2d_s - A$. Noting that $K > K^*$ (resp. $K \leqq K^*$) is equivalent to $A > 0$ (resp. $A \leqq 0$), we know that the real

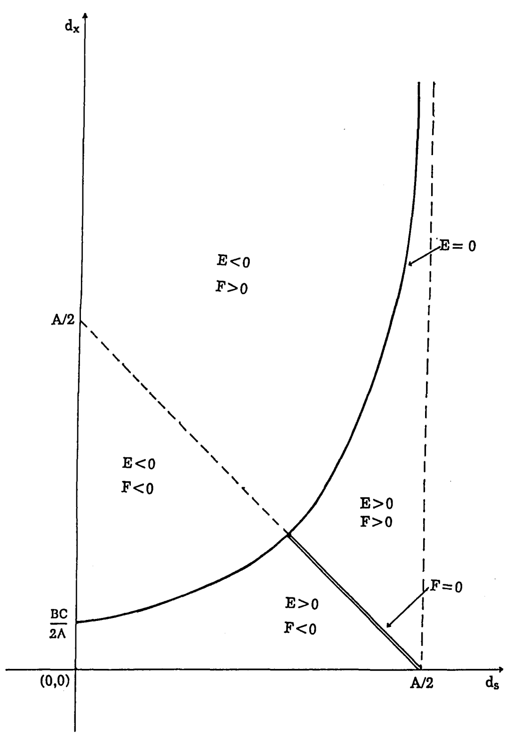

Fig. 2.1a (when $A^2 > BC$)

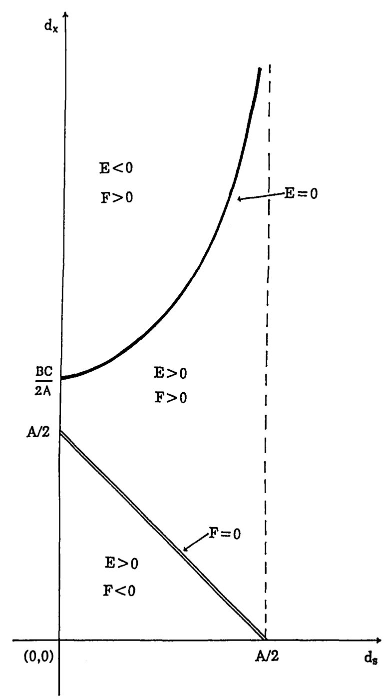

Fig. 2.1b (when $A^2 < BC$)

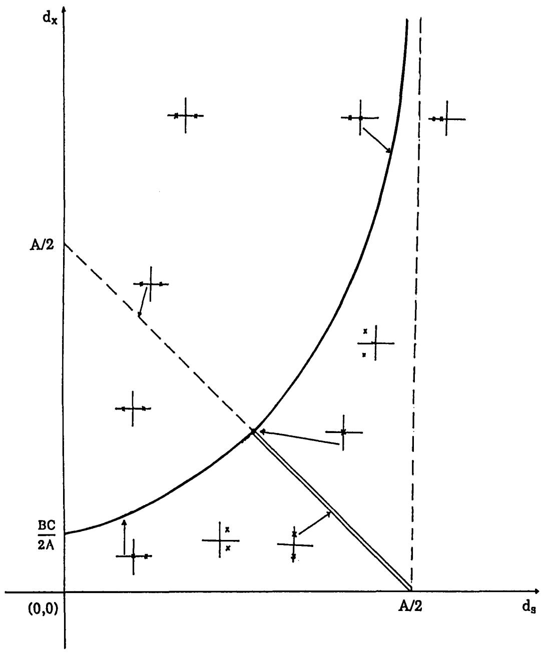

Fig. 2.2a (when $A^2 > BC$)

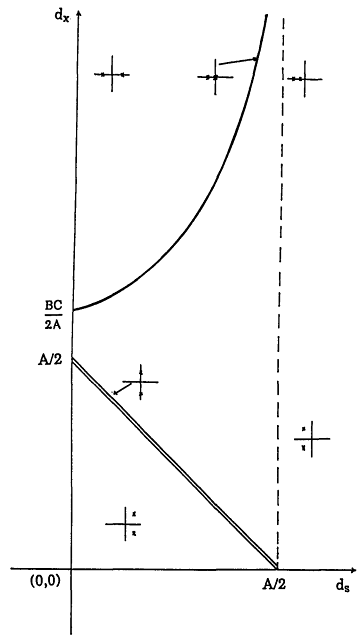

Fig. 2.2b (when $A^2 < BC$)

part of eigenvalues of M and $\overline{M}$ are all negative when $K < K^*$. Namely when $K < K^*$ the symmetric equilibrium $\mathbf{x}^*$ is stable.

Hereafter we assume that $K > K^*$ and K is fixed. The signs of E and F and the eigenvalues $\eta_\pm$ on the (d_s, d_x)-plane are shown in Figs. 2.1a 2.1b and Figs. 2.2a 2.2b.

Let

$$\Gamma_0 = \{(d_s, d_x) \in R_+^2 | E = 0\},$$

$$\tilde{\Gamma}_1 = \{(d_s, d_x) \in R_+^2 | F = 0\}.$$

If $\Gamma_0 \cap \tilde{\Gamma}_1 \neq \phi$, we put $\Gamma_1 = \{(d_s, d_x) \in \tilde{\Gamma}_1 | d_x < d_x^*, d_s > d_s^*\}$ where (d_s^*, d_x^*) is a point defined by $\Gamma_{0,1} = \Gamma_0 \cap \tilde{\Gamma}_1 \equiv \{(d_s^*, d_x^*)\}$. On the other hand, if $\Gamma_0 \cap \tilde{\Gamma}_1 = \phi$, we put $\Gamma_1 = \tilde{\Gamma}_1$.

We can easily see the following: Γ_0 is a simple bifurcation line of the symmetric equilibrium. On the Γ_0 one of the eigenvalues η is equal to zero and the eigenvector corresponding to $\eta = 0$ has the antisymmetric form ${}^t(t_1, y_1, t_2, y_2) = {}^t(t_1, y_1, -t_1, -y_1)$, since $t_+ = 0$ and $y_+ = 0$. Therefore every points of Γ_0 are symmetry-breaking bifurcation points. From the bifurcation theory we can see easily that Γ_1 is a simple Hopf bifurcation line and $\Gamma_{0,1}$ is a double critical point if it is in the interior of the first quadrant. As the consequence, we conclude the local existence of asymmetric equilibria.

Proposition 2.1. *$\Gamma_0 \neq \phi$ if and only if $K > K^*$, namely when $K > K^*$, Γ_0 is the simple bifurcation line, from which the sheet of unstable asymmetric equilibria bifurcate* (*see* [6], *Fig.* 2.3 *and Fig.* 2.4).

By simple calculation we can show the direction of bifurcating solution, that is shown by Theorem 3.1 in the next section. In the subsequent sections, we shall focus on the global existence problem of this bifurcating asymmetric solutions when d_x and d_s vary in R^2_+.

§3. Global existence of bifurcating solutions

In this section we investigate analytically the global existence of asymmetric equilibria which bifurcate from the symmetric ones in the parameter space (d_s, d_x). It is not an easy task to solve the steady state equations of (1.2) explicitely. The key of our analysis is to reduce the four coupled nonlinear equations to a single equation of rational expression which is called the θ-equation. This reduction is done in the next subsection and we discuss, in Section 3.2, the properties of the bifurcated branch of asymmetric equilibria with respect to d_s and d_x by analyzing the θ-equation.

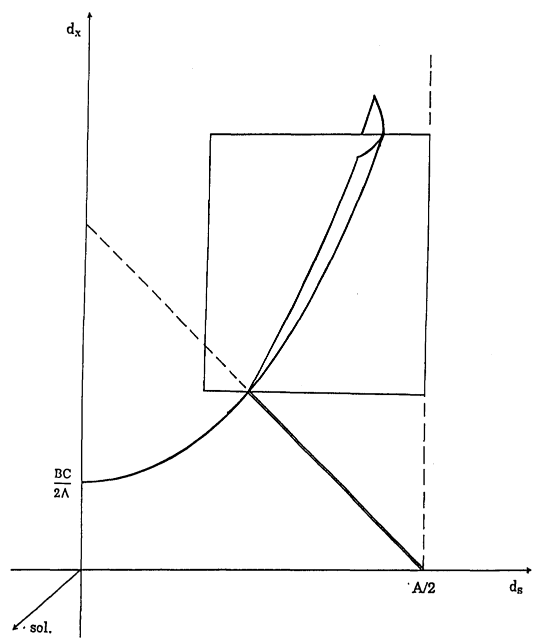

Fig. 2.3

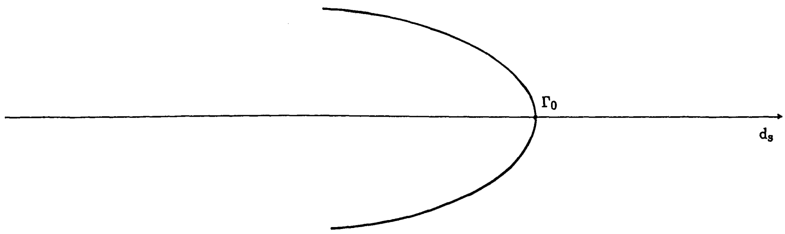

Fig. 2.4

3.1. Reduction of the steady state equations to θ-equation

Let us begin by showing our key lemma, which claims that finding any equilibria of (1.2) is equivalent to solving an equation of rational expression with a real variable.

Consider the steady state problem of the system (1.2):

$$\tag{3.1} \begin{cases} \mathrm{F}_1(s_1, x_1, s_2, \mathrm{d_s}) \equiv \mathrm{d_s}(s_2 - s_1) + f(s_1, x_1) = 0 \\ \mathrm{G}_1(s_1, x_1, x_2, \mathrm{d_x}) \equiv \mathrm{d_x}(x_2 - x_1) + g(s_1, x_1) = 0 \\ \mathrm{F}_2(s_1, s_2, x_2, \mathrm{d_s}) \equiv \mathrm{d_s}(s_1 - s_2) + f(s_2, x_2) = 0 \\ \mathrm{G}_2(x_1, s_2, x_2, \mathrm{d_x}) \equiv \mathrm{d_x}(x_1 - x_2) + g(s_2, x_2) = 0 . \end{cases}$$

Since the second and the fourth equations of (3.1) are linear in x_1 and x_2, we can rewrite them in the following form:

$$\tag{3.2} \begin{bmatrix} \dfrac{ms_1}{s_1 + a_1} - D - \mathrm{d_x} & \mathrm{d_x} \\ \mathrm{d_x} & \dfrac{ms_2}{s_2 + a_1} - D - \mathrm{d_x} \end{bmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

Let H denote the coefficient matrix of (3.2). The necessary and sufficient condition for existence of nontrivial solutions $\mathbf{x} = {}^t(x_1, x_2)$ of (3.2) is given by $\det \mathrm{H} = 0$, namely,

$$\tag{3.3} 1 = \frac{\mathrm{d_x}}{\mathrm{h}(s_1)} + \frac{\mathrm{d_x}}{\mathrm{h}(s_2)},$$

where

$$\mathrm{h}(s_i) = \frac{ms_i}{s_i + a_1} - D \qquad (i = 1, 2)\,. \tag{3.4}$$

Then x_1 and x_2 have to satisfy the relation:

$$x_2 = \left(1 - \frac{\mathrm{h}(s_1)}{\mathrm{d}_x}\right) x_1\,. \tag{3.5}$$

Let us now introduce a new parameter $\theta \in R$ in the form:

$$\frac{\mathrm{d}_x}{\mathrm{h}(s_1)} = \frac{1 - \theta^{-1}}{2}\,, \qquad \frac{\mathrm{d}_x}{\mathrm{h}(s_2)} = \frac{1 + \theta^{-1}}{2}\,, \tag{3.6}$$

where $\theta \neq 0$. It turns out that $\theta = 0$ corresponds to the case $s_1 = s_2 = s^*$ and $x_1 = x_2 = x^*$, namely the symmetric solution. From (3.6), s_1 and s_2 are expressed as the following form:

$$\begin{cases} s_1 = a_1(\alpha\theta - D)/(\beta\theta - \bar{\mathrm{C}}) \\ s_2 = a_1(\alpha\theta + D)/(\beta\theta + \bar{\mathrm{C}})\,, \end{cases} \tag{3.7}$$

where

$$\begin{cases} \alpha = 2\mathrm{d}_x + D \\ \beta = m - D - 2\mathrm{d}_x \\ \bar{\mathrm{C}} = m - D\,. \end{cases} \tag{3.8}$$

Moreover, from the relations $\mathrm{F}_1 = 0 = \mathrm{F}_2$, x_1 and x_2 are given by the functions of s_1 and s_2 as

$$\begin{cases} x_1 = \mathrm{X}_1(s_1, s_2) \equiv \dfrac{k(s_1 + a_1)}{ms_1}\left\{\mathrm{d}_s(s_2 - s_1) + \gamma\left(1 - \dfrac{s_1}{K}\right)s_1\right\} \\[2ex] x_2 = \mathrm{X}_2(s_1, s_2) \equiv \dfrac{k(s_2 + a_1)}{ms_2}\left\{\mathrm{d}_s(s_1 - s_2) + \gamma\left(1 - \dfrac{s_2}{K}\right)s_2\right\}. \end{cases} \tag{3.9}$$

The above is expressed as functions of θ through (3.7) in the form:

$$\begin{cases} x_1 = \mathrm{X}_1(s_1(\theta), s_2(\theta)) \\ x_2 = \mathrm{X}_2(s_1(\theta), s_2(\theta))\,. \end{cases} \tag{3.10}$$

Substituting (3.10) into (3.5), we obtain the equation of θ as follows:

$$F(\theta) = (\theta - 1)\mathrm{X}_2(s_1(\theta), s_2(\theta)) + (\theta + 1)\mathrm{X}_1(s_1(\theta), s_2(\theta)) = 0 \qquad (\theta \in R)\,. \tag{3.11}$$

Therefore, we reduce the problem (3.1) to finding zeroes of $F(\theta) = 0$. Conversely, it is easy to see that any zero of $F(\theta)$ gives a solution of (3.1) through (3.7) and (3.10).

The explicit form of $F(\theta)$ is given by:

$$F(\theta) = 2\frac{ka_1\gamma}{K}\frac{\theta(\theta^2-1)}{(\alpha^2\theta^2 - D^2)(\beta^2\theta^2 - \bar{C}^2)^2}\{a\theta^4 + \mathrm{b}\theta^2 + E'\} \tag{3.12}$$

where

$$\begin{cases} a = \alpha^2\beta^2\alpha' \\ \mathrm{b} = \alpha^2(\bar{\mathrm{C}}^2\alpha' - 2\beta\beta'\bar{\mathrm{C}}) - \beta^2 D^2\alpha' - \dfrac{K}{4}\mathrm{d_s d_x} mD\beta^2 \\ \mathrm{E}' = 4\dfrac{K}{\gamma}\bar{\mathrm{C}}^2\mathrm{d_s d_x} mD - D^2(\bar{\mathrm{C}}^2\alpha' - 2\beta\beta'\bar{\mathrm{C}}), \end{cases} \tag{3.13}$$

$$\begin{cases} \alpha' = K\beta - a_1\alpha \\ \beta' = K\bar{\mathrm{C}} - a_1 D. \end{cases} \tag{3.14}$$

We shall call $F(\theta) = 0$ the θ-equation.

PROPOSITION 3.1. *The problem* (3.1) *is equivalent to finding* 0 *of the θ-equation. Furthermore for any solution $\theta \in \mathrm{R}$ of $F(\theta) = 0$, (s_1, x_1, s_2, x_2) given by* (3.7)$\sim$(3.9) *is a solution of* (3.1).

Note that the function $F(\theta)$ includes the ecological parameters $\mathrm{d_s}$, $\mathrm{d_x}$ and K, but we don't denote explicitly such dependency here for the sake of simplicity.

Let us now explain the geometric meaning of the solution θ of $F(\theta) = 0$. From $F(\theta) = 0$, i.e., $(\theta - 1)x_2 + (\theta + 1)x_1 = 0$, we have the following relation:

$$\theta = \frac{x_2 - x_1}{x_2 + x_1}, \tag{3.15}$$

which implies that $x_2 = 0$ for $\theta = -1$, $x_2 = x_1$ for $\theta = 0$, and $x_1 = 0$ for $\theta = 1$. Hence, the absolute value of the parameter θ may be interpreted as the intensity of the asymmetry of solutions between the two boxes. We note that solutions of (3.11) include non-negative solutions and negative solutions as well, the latter of which has ecologically no meaning.

REMARK 3.1. Because $F(\theta)$ is an odd function of θ:

$$F(-\theta) = -F(\theta), \tag{3.16}$$

and (3.7) indicates $s_1(-\theta) = s_2(\theta)$ and $s_2(-\theta) = s_1(\theta)$, it suffices to consider the problem (3.11) in the infinite interval $\theta \geqq 0$.

3.2 Properties of the sheet of bifurcating equilibria

In this subsection, we shall study the global structure of solutions of the θ-equation in the parameter space $(\mathrm{d_s}, \mathrm{d_x}) \in \mathrm{R}^2_+$, under the assumption that K is fixed as $K > K^*$. Hence, we write $F(\theta, \mathrm{d_s}, \mathrm{d_x})$ in place of $F(\theta)$.

DEFINITION 3.1. A function $\theta_+ = \theta_+(\mathrm{d_s}, \mathrm{d_x})$: $\mathrm{R}^2_+ \to \mathrm{R}$ is said to be a *non-negative solution* of (3.11) if it satisfies (*i*) $F(\theta, \mathrm{d_s}, \mathrm{d_x}) = 0$ and (*ii*) $s_i(\theta, \mathrm{d_x}) \geqq 0$ for $i = 1, 2$, where $s_i(\theta, \mathrm{d_x})$ $(i = 1, 2)$ are defined by (3.7).

Put $\theta_1(\mathrm{d_x}) = D/\alpha$ and $\theta^*(\mathrm{d_x}) = \overline{\mathrm{C}}/\beta$. The expression (3.12) shows that for each fixed $\mathrm{d_x}$ and $\mathrm{d_s}$, $\theta = \theta_1(\mathrm{d_x})$ and $\theta = \theta^*(\mathrm{d_x})$ are the asymptotes of $F(\theta, \mathrm{d_s}, \mathrm{d_x}) = 0$ lying in the positive half plane $\theta > 0$. Let $\theta_*(\mathrm{d_x}) = \min\{\theta_1(\mathrm{d_x}), \theta^*(\mathrm{d_x})\}$. Then we have $\theta_*(\mathrm{d_x}) < 1$.

A simple calculation shows that for fixed $\mathrm{d_x}$, $s_1(\theta, \mathrm{d_x})$ is monotone decreasing function of θ (where $\theta \neq \overline{\mathrm{C}}/\beta$) and $s_2(\theta, \mathrm{d_x})$ is monotone increasing function of θ (where $\theta \neq -\overline{\mathrm{C}}/\beta$). By the following Proposition 3.2 we shall know that the region of existence of non-negative solutions is $\theta \leqq \theta_*(\mathrm{d_x})$. In this region we have $s_2 \leqq s_1$ and $s_1 \leqq \lambda$. Hence from (3.9) we have $x_1 \geqq 0$ since $K \geqq K^* = 2\lambda + a_1$, and from (3.15) we have $x_2 = -(\theta + 1)x_1/(\theta - 1) > 0$. Namely for each non-negative solution θ_+ of (3.11), equation (3.10) with $\theta = \theta_+$ gives the non-negative x_1 and x_2.

PROPOSITION 3.2 (The existence region of non-negative solutions). *For fixed* $\mathrm{d_s}$ *and* $\mathrm{d_x}$, *the existence region of non-negative solutions of* $F(\theta, \mathrm{d_s}, \mathrm{d_x}) = 0$ *is given by*: $0 < \theta_+ \leqq \theta_*(\mathrm{d_x})$.

PROOF. From (3.7), $s_1 \geqq 0$ if and only if $\theta \leqq D/\alpha = \theta_1(\mathrm{d_x})$ and $\theta \geqq \overline{\mathrm{C}}/\beta = -\theta^*(\mathrm{d_x})$. And $s_2 \geqq 0$ if and only if $\theta \geqq -D/\alpha = -\theta_1(\mathrm{d_x})$ and $\theta < -\overline{\mathrm{C}}/\beta = \theta^*(\mathrm{d_x})$. Hence when $\theta_1(\mathrm{d_x}) \leqq \theta^*(\mathrm{d_x})$, $s_1(\theta, \mathrm{d_x})$ and $s_2(\theta, \mathrm{d_x})$ are non-negative in the region $-\theta_1(\mathrm{d_x}) < \theta < \theta_1(\mathrm{d_x})$. When $\theta_1(\mathrm{d_x}) > \theta^*(\mathrm{d_x})$, $s_1(\theta, \mathrm{d_x})$ and $s_2(\theta, \mathrm{d_x})$ are non-negative in the region $-\theta^*(\mathrm{d_x}) < \theta < \theta^*(\mathrm{d_x})$. Namely when $\theta \leqq \min\{\theta_1(\mathrm{d_x}), \theta^*(\mathrm{d_x})\}$ $s_1(\theta, \mathrm{d_x})$ and $s_2(\theta, \mathrm{d_x})$ are all non-negative.

PROPOSITION 3.3 (Uniqueness and monotonicity of asymmetric solutions).
(1) *For* $(\mathrm{d_s}, \mathrm{d_x}) \in \mathrm{R}^2_+$ *such that* $0 < \mathrm{d_s} < \mathrm{A}/2 - \mathrm{CB}/(4\mathrm{d_x})$, *there exists uniquely the non-negative solution* $\theta_+ = \theta_+(\mathrm{d_s}, \mathrm{d_x})$ *of* (3.11) (*for* $\theta > 0$). *Also*, $\theta_+(\mathrm{d_s}, \mathrm{d_x})$ *is a monotone decreasing function of* $\mathrm{d_s}$ *for fixed* $\mathrm{d_x}$.
(2) *When* $\mathrm{d_s} > \mathrm{A}/2 - \mathrm{CB}/(4\mathrm{d_x})$, *non-negative solution does not exist.*

PROOF. Consider (3.12) and put $z(\theta) = a\theta^4 + \mathrm{b}\theta^2 + \mathrm{E}'$. Then we see that the roots of $F(\theta) = 0$ except 0, 1 are zeroes of $z(\theta)$. For $\mathrm{d_s} = 0$, the simple symmetry-breaking bifurcation line $\mathrm{E} = 0$ intersects with $\mathrm{d_x}$-axis at $\mathrm{BC}/2\mathrm{A} = (m - D)(K - \lambda)/2(K - 2\lambda - a_1)$ (see Figs. 2.1a, 2.1b). Since $K > K^*$ we have

$BC/2A > (m-D)/2$. Furthermore for the minimum value $BC/2A$ of the d_x on the line $E = 0$ we have $BC/2A > (m-D)/2$, so that $\beta < 0$ is satisfied for all d_x in the region $E \leqq 0$ and $a = \alpha^2\beta^2(K\beta - a_1\alpha) < 0$. This shows that $z(\theta)$ is convex with respect to θ^2.

When $E' < 0$ since $z(0) < 0$, $z(\theta_*) > 0$ and $z(\theta_{**}) < 0$ (where $\theta_{**} = \max(\theta_1, \theta^*)$ and $\theta_* = \theta_*(d_x)$), there is a unique root of $z(\theta) = 0$ in the region $(0, \theta_*)$. When $E' \geqq 0$, since $z(0) \geqq 0$ and $z(\theta_*) > 0$, there is no root in the region $(0, \theta_*)$. In fact, if there is a root in $(0, \theta_*)$, then there are 6 roots for $\theta \in R$ since $z(0) \geqq 0$, $z(\theta_*) > 0$ and $z(\theta_{**}) < 0$. This contradicts that $z(\theta)$ is the 4th order polynomial of $\theta \in R$.

After a simple calculation, we obtain that $E' > 0$ (resp. $E' < 0$) is equivalent to $E > 0$ (resp. $E < 0$). Since $E < 0$ (resp. $E > 0$) implies $d_s < A/2 - CB/(4d_x)$ (resp. $d_s > A/2 - CB/(4d_x)$), if $d_s < A/2 - CB/(4d_x)$ then θ_+ uniquely exists and if $d_s > A/2 - CB/(4d_x)$ then θ_+ does not exist.

To prove the monotonicity of asymmetric solutions, we differentiate (3.12) with respect to d_s and θ. Then we see

$$\frac{\partial}{\partial d_s} F(\theta, d_x, d_s)|_{\theta=\theta_+} > 0\,,$$

and

$$\frac{\partial}{\partial \theta} F(\theta, d_x, d_s)|_{\theta=\theta_+} > 0\,,$$

respectively. Hence we have

$$\frac{\partial\theta_+(d_x, d_s)}{\partial d_s} = -\frac{\partial F}{\partial d_s}\Big/\frac{\partial F}{\partial \theta} < 0\,.$$

This completes the proof.

PROPOSITION 3.4. *For each fixed* d_x

$$\lim_{d_s \to 0} \theta_+(d_x, d_s) = \min\{\theta_1(d_x), \Theta(d_x)\}\,, \tag{3.17}$$

where $\Theta(d_x)$ *is the solution of* $F(\theta, 0, d_x) = 0$ *satisfying* $\theta > 0$ *and* $\theta \neq 1$.

PROOF. From Proposition 3.3 and Definition 3.1, it follows for each fixed d_x that $\theta_+(d_x, d_s)$ is a monotone decreasing function of d_s and $\theta_+(d_x, d_s)$ is bounded by θ_* from above. Hence, there exists the limit θ_+^* of $\theta_+(d_x, d_s)$ as $d_s \to 0$. From Proposition 3.2 and the definition of $\theta_1(d_x)$ we have

$$0 \leqq \theta_+^* \leqq \theta_*(d_x) \leqq \theta_1(d_x)\,. \tag{3.18}$$

We shall prove (3.17) by contradiction. Assume that

(3.19) $$\theta_{+}^{*} \neq \min\{\theta_1(\mathrm{d_x}), \Theta(\mathrm{d_x})\}\,.$$

First we consider the case:

(3.20) $$\theta_1(\mathrm{d_x}) = \min\{\theta_1(\mathrm{d_x}), \Theta(\mathrm{d_x})\}\,.$$

From (3.18), (3.19) we have $\theta_{+}^{*} - \theta_1(\mathrm{d_x}) < 0$. Since $\theta_1(\mathrm{d_x})$ is the positive root of $\alpha^2\theta^2 - D^2 = 0$, from $\theta_{+}^{*} - \theta_1(\mathrm{d_x}) < 0$ we find that θ_{+}^{*} is the root of $\mathrm{z}(\theta, \mathrm{d_x}, 0) = 0$ and $\alpha^2(\theta_{+}^{*})^2 - D^2 \neq 0$. In addition, substituting (3.13) and (3.14) into (3.12) we can obtain the following form of $\mathrm{z}(\theta)$:

(3.21) $$\mathrm{z}(\theta) = (\alpha^2\theta^2 - D^2)(\beta^2\alpha'\theta^2 + \mathrm{L}) - 4K\mathrm{d_s}\mathrm{d_x}mD(\beta^2\theta^2 - \overline{\mathrm{C}}^2)/\gamma\,,$$

where $\mathrm{L} = \overline{\mathrm{C}}^2\alpha' - 2\beta\beta'\overline{\mathrm{C}}$. Taking the limit $\mathrm{d_s} \to 0$ in (3.21), we see that θ_{+}^{*} must be a solution of $\beta^2\alpha'\theta^2 + \mathrm{L} = 0$, which is just $\Theta(\mathrm{d_x})$. However this never occurs because now the case $\theta_1(\mathrm{d_x}) < \Theta(\mathrm{d_x})$ is considered.

Secondly, we consider the case $\Theta(\mathrm{d_x}) = \min\{\theta_1(\mathrm{d_x}), \Theta(\mathrm{d_x})\}$. We show that both $\theta_{+}^{*} < \Theta(\mathrm{d_x})$ and $\theta_{+}^{*} > \Theta(\mathrm{d_x})$ can not occur. First, assume that $\theta_{+}^{*} < \Theta(\mathrm{d_x})$. Then the similar argument just above leads to a contradiction. When $\theta_{+}^{*} > \Theta(\mathrm{d_x})$, for some nonzero $\mathrm{d_s} = \mathrm{d_{s_0}} > 0$ the equation $\theta_{+}(\mathrm{d_x}, \mathrm{d_{s_0}}) = \Theta(\mathrm{d_x})$ holds. Namely $\theta_{+}(\mathrm{d_x}, \mathrm{d_{s_0}})$ must be a solution of $\mathrm{z}(\theta, \mathrm{d_x}, \mathrm{d_{s_0}}) = 0$. However from $\theta_{+}(\mathrm{d_x}, \mathrm{d_{s_0}}) = \Theta(\mathrm{d_x})$ and (3.21), we get that $\theta_{+}(\mathrm{d_x}, \mathrm{d_{s_0}})$ must satisfy the following equation:

(3.22) $$4K\mathrm{d_{s_0}}\mathrm{d_x}mD(\beta^2\theta^2 - \overline{\mathrm{C}}^2)/\gamma\,|_{\theta=\theta_{+}(\mathrm{d_x}, \mathrm{d_{s_0}})} = 0\,.$$

For every $\mathrm{d_s} > 0$ the solution of (3.22) is $\theta = \theta^*(\mathrm{d_x})$ so that $\theta_{+}(\mathrm{d_x}, \mathrm{d_{s_0}}) = \theta^*(\mathrm{d_x})$. This contradicts the condition $\theta_{+}(\mathrm{d_x}, \mathrm{d_s}) < \theta^*(\mathrm{d_x})$.

From the above Propositions we have the following theorem:

THEOREM 3.1. *The asymmetric bifurcating solutions that bifurcated from the simple bifurcation line* $\mathrm{E} = 0$ *continue to exist to the limit* $\mathrm{d_s} \to 0$ *for each fixed* $\mathrm{d_x}$ *in the region* $\mathrm{E}_{-} = \{(\mathrm{d_s}, \mathrm{d_x}) \in \mathrm{R}_{+}^2 \,|\, 0 < \mathrm{d_s} < \mathrm{A}/2 - \mathrm{CB}/(4\mathrm{d_x})\}$. *The parameter* θ *by which the asymmetric bifurcating solutions are expressed is monotone decreasing about* $\mathrm{d_s}$ *and when* $\mathrm{d_s} \to 0$ *the limiting values are given by* (3.17), (*see Fig.* 3.1).

§ 4. Numerical study of global bifurcation diagram

In Section 3, we have obtained all the equilibria including non-negative and even negative ones by solving the θ-equation and shown the global existence of asymmetric solutions. The stability of the bifurcating solutions of our two box model is, of course, an important question from the biological view point. Unfortunately, the θ-equation tells us nothing about the stability,

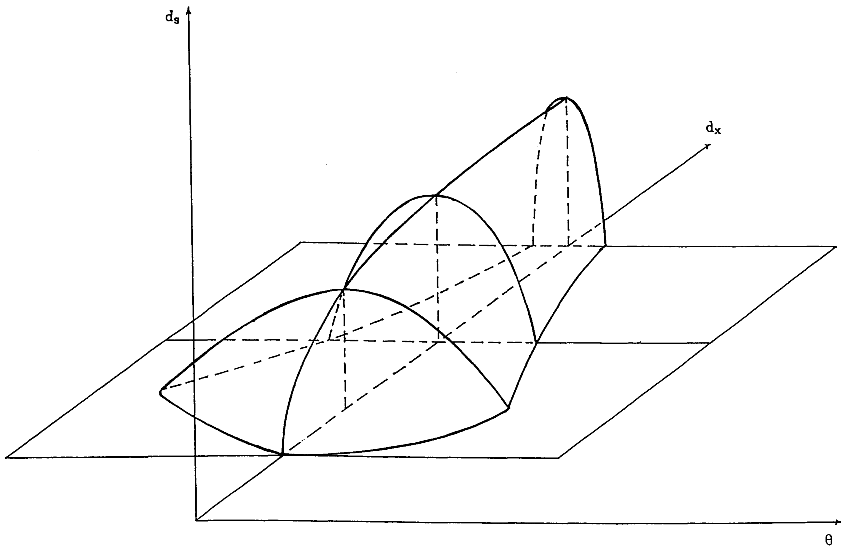

Fig. 3.1

although the local bifurcation theory furnishes us local information on it. Our question is now whether these unstable bifurcating asymmetric solutions recover their stability when the magnitude of diffusions (d_s, d_x) vary in R^2_+.

Since it is difficult to prove the global stability of asymmetric equilibria for our equation (3.1), we investigate it numerically in the parameter space $(d_s, d_x) \in R^2_+$. We vary (d_s, d_x) in $[0, A/2] \times [0, 40] \subset R^2_+$ in the form that $d_s = A/2 - 0.01i$ and $d_x = 0.1j$ with appropriate nonnegative integers i and j. For each values of (d_s, d_x), we first find zeros of $z(\theta)$ (given by (3.21)) for fixed d_s and d_x and get the asymmetric equilibria (s_1, x_1, s_2, x_2) of (3.1) using (3.7) and (3.9). Then we solve the linearized eigenvalue problem about every asymmetric equilibrium by QR method. All the numerical computation is carried for $K = 1200$, $k = 0.1$, $m = \log_e 2$, $D = (\log_e 2)/2$, $\gamma = 20 \log_e 2$, $a_1 = 100$.

Now we describe the numerical results of the linearized eigenvalue problem about the asymmetric equilibria and the symmetric trivial ones of (1.2). Fig. 4.1 shows the locations of the eigenvalues of this problem on the complex plane. According to the distribution of four eigenvalues we see that there exist the five regions (a)–(e).

region (a): The asymmetric solutions are stable, all eigenvalues have negative real part.

region (b): Asymmetric solutions are unstable, two eigenvalues have positive real part.

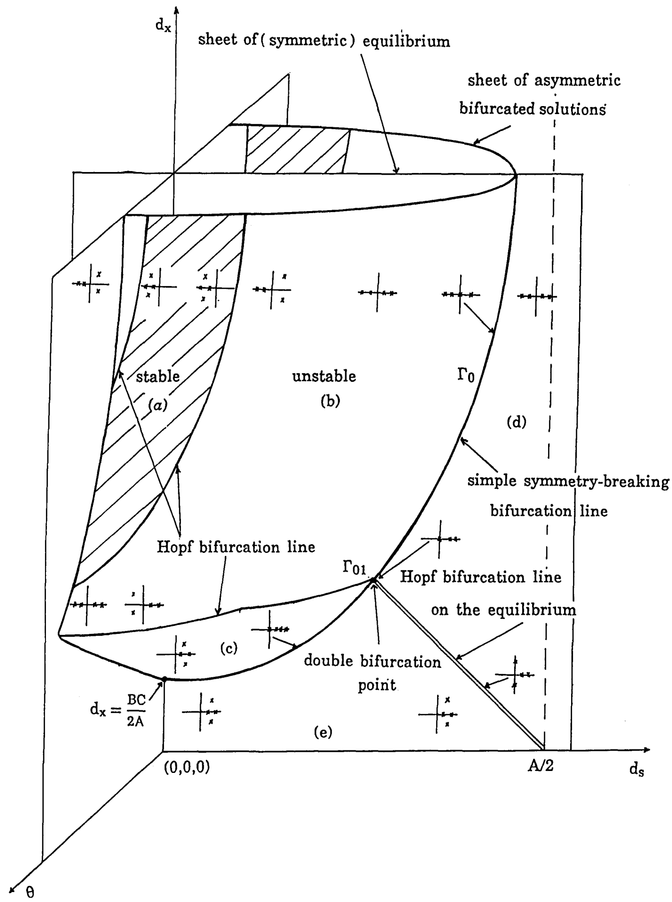

Fig. 4.1 where + represent the complex plane and x denotes the locations of the eigenvalues on the complex plane.

region (c): Asymmetric solutions are unstable, four eigenvalues have positive real part.

region (d): Asymmetric solution does not exist, the eigenvalues of symmetric equilibrium has two positive real part.

region (e) Asymmetric solution does not exist, the eigenvalues of symmetric equilibrium has four positive real part.

We give here a summary of the results. (1) These asymmetric equilibria are unstable just after bifurcating from symmetric equilibrium. This is confirmed by the local bifurcation theories. (2) For $d_x \gg 1$, when d_s decreases, Hopf bifurcation appears and the stability of asymmetric bifurcating solutions changes, and stable asymmetric bifurcating solution appears. If we decrease d_s further, Hopf bifurcation appears again and the stable asymmetric bifurcated solution loses its stability and become unstable. (3) In region $E \leqq 0$ there exists a point d^* dependent of K, d_s and other parameters, such that the asymmetric equilibria are all unstable for $d_x < d^*$.

A conclusion from Fig. 4.1 is that the bifurcating asymmetric solutions recover its stability depending on the value of $(d_s, d_x) \in R_+^2$. In fact, they are stable in the region (a) and unstable in the other region. An interesting ones is that a numerical result suggests that in the region (a) the symmetric periodic solution (which corresponding the Hopf bifurcation at the point $K > K^*$) is also stable. These two observations show that there is a multiple existence of stable solutions in the system (1.2). Namely, both the periodic solution and the asymmetric equilibria are stable in the region (a), (see [2]). In the other region symmetric periodic solutions appear.

Mathematical structure of such multiple existence is a subject of further studies.

Acknowledgements. The author wishes to thank Professors H. Fujii and Y. Hosono and Y. Nishiura of Kyoto Sangyo University for their kind discussions and continuous encouragements.

Special thanks are due Professor M. Mimura of Hiroshima University for his discussions and especially, for his kind introduction to ecological modelings.

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