

## EXISTENCE AND BIFURCATION OF STABLE EQUILIBRIUM IN TWO-PREY, ONE-PREDATOR COMMUNITIES

■ YASUHIRO TAKEUCHI

Department of Applied Mathematics,  
Faculty of Engineering,  
Shizuoka University,  
Hamamatsu 432, Japan

■ NORIHIKO ADACHI

Department of Applied Mathematics and Physics,  
Faculty of Engineering,  
Kyoto University,  
Kyoto 606, Japan

In this paper, stability of two-prey, one-predator communities is investigated by Lyapunov's direct method and Hopf's bifurcation theory. Three patterns of three-species coexistence are possible. A globally stable non-negative equilibrium exists for the system even if two competing prey species without a predator cannot coexist. The stable equilibrium bifurcates to a periodic motion with a small amplitude when the predation rate increases. It is also shown that a chaotic motion emerges from the periodic motion when one of two prey has greater competitive abilities than the other. This predator-mediated coexistence can be realized by the intimate relationship between preferences of a predator and competitive abilities of two prey.

*1. Introduction.* The relationship between complexity and stability in ecosystems is a topic of continuing interest to ecologists. In 1966 Paine discovered that predation plays an important role in species diversity (Paine, 1966). When predators were experimentally removed the system became less diverse, that is, certain benthic invertebrates and algae were led to local extinction in the marine rocky intertidal community. On the other hand, there are studies that failed to demonstrate predator-mediated coexistence or that showed an actual decrease in the number of coexisting species under the impact of predation. For details see Caswell (1978). Recent discussion on the effect of herbivores on plant diversity is found in Lubchenco (1978). She showed that the key to understanding the role of the predation might reside in the consumer prey preferences and competitive abilities of food species. When the competitively dominant species is preferred by the consumer there is a unimodal relationship between prey density and consumer density, with the highest diversity at intermediate consumer density. When

the competitively inferior species is preferred there is an inverse relationship between prey density and consumer density.

Parrish and Salla (1970) constructed a mathematical model for a two-prey, one-predator system, stimulated by Paine's observations. They showed by computer simulation that the inclusion of a predator can delay the extinction of one prey species, but they could not find a set of parametric values with which three species can coexist. Cramer and May (1972) considered the stability of the same model by perturbation methods. They gave necessary conditions for the three-species stable coexistence. The results of Cramer and May were refined by Fujii (1977). The last two papers explained mathematically the results of Paine's experiments, that is, three species converge to their coexistent state if displacements from the three-species equilibrium are sufficiently small. Fujii (1977) also suggested the existence of a stable limit cycle in three-species state space, but his proof is insufficient. Vance (1978) showed that the three-species coexistence is possible, by local stability analysis, if the predator prefers the superior competitor. Further, Vance discovered a 'quasi-cyclic' motion, which is called a spiral chaos by Gilpin (1979), by computer simulations. Recently, Hsu (1981) gave the conditions for the coexistence of two competing prey and the extinction of either prey, but he analyzed only the case where the predator can survive on either prey in the predator-prey subcommunities. Hsu also gave a numerical example of a limit cycle. None of them gave satisfactory results for the predator-mediated coexistence in the model initiated by Parrish and Salla. For a rather general family of two-dimensional competitive systems, Yodzis (1976) showed that harvesting (or predation) could alleviate competitive instabilities. He also suggested that in more complicated ecosystems with many competing species, there would be a good chance that harvesting at moderate rates would increase species diversity if one species was dominated in the unharvesting system. In this paper we intend to give the mathematical possibility of predator-mediated coexistence in consideration of the relationship between preferences of a predator and competing abilities of two prey.

The model discussed in this paper is described by the following system of differential equations:

$$\frac{d}{dt} \begin{bmatrix} x_1(t) \\ x_2(t) \\ z(t) \end{bmatrix} = \begin{bmatrix} x_1(t) (b_1 - x_1(t) - \alpha x_2(t) - \epsilon z(t)) \\ x_2(t) (b_2 - \beta x_1(t) - x_2(t) - \mu z(t)) \\ z(t) (-b_3 + d\epsilon x_1(t) + d\mu x_2(t)) \end{bmatrix}. \quad (1)$$

Here  $x_1(t)$  and  $x_2(t)$  (or  $z(t)$ ) are population sizes of prey (or predator) species,  $b_i > 0$  ( $i = 1, 2, 3$ ) are intrinsic rates of increase or decrease,  $\alpha > 0$

and  $\beta > 0$  are parameters representing competitive effects between two prey,  $\epsilon > 0$  and  $\mu > 0$  are coefficients of decrease of prey species due to predation and  $d > 0$  is equal transformation rate of predator. In (1)  $b_i$  ( $i = 1, 2, 3$ ) and  $d$  are fixed constants and  $\alpha, \beta, \epsilon$  and  $\mu$  are parameters. In general the two-prey, one-predator system will have eleven coefficients. Four of them, however, can be eliminated by scalings of time and three variables  $x_1, x_2$  and  $z$  (Hsu, 1981). System (1) is mathematically general, except for the equal transformation rate  $d$ . The relationship between stability of system (1) and competitive subsystem of two prey,

$$\frac{d}{dt} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix} = \begin{bmatrix} x_1(t) (b_1 - x_1(t) - \alpha x_2(t)) \\ x_2(t) (b_2 - \beta x_1(t) - x_2(t)) \end{bmatrix}, \tag{2}$$

is also investigated.

In Section 2 known stability conditions for a generalized Volterra system are summarized and also a new result is presented. The two-prey, one-predator system (1) is discussed in Section 3. The results are compared with biological experiments in Section 4. All the theorems of this paper are proved in the appendix.

*2. Definitions and Stability Conditions.* In this section we consider a generalized form of model (1), that is, a model called a generalized Volterra system:

$$\frac{d}{dt} x_i(t) = x_i(t) \left[ b_i - \sum_{j=1}^n a_{ij} x_j(t) \right], \quad i = 1, \dots, n, \tag{3}$$

and some known stability results with respect to the system are surveyed.

Let  $R^n$  be an  $n$ -dimensional Euclidean space and  $I$  be a subset of  $N = \{1, \dots, n\}$  such that  $x_i^* = 0$  for  $i \in I$ , where  $x^* = (x_1^*, \dots, x_n^*)^T$  is a non-negative equilibrium of (3). Further, let  $J = N - I$ . Then, correspondingly to  $x^*$ ,  $R_I^n$  is defined as follows:  $R_I^n = \{x | x_i \geq 0 \text{ for } i \in I \text{ and } x_j > 0 \text{ for } j \in J\}$ .

Since every solution that starts from an initial point in  $R_I^n$  stays in  $R_I^n$  at all future times, stability of a non-negative equilibrium of (3) is defined as follows.

*Definition 1.* A non-negative equilibrium  $x^*$  of (3) is called globally stable if and only if (i)  $x^*$  is locally stable, that is, if for any  $\epsilon > 0$  there exists a  $\delta(\epsilon)$  such that  $|x^0 - x^*| < \delta(\epsilon)$  and  $x(t) \in R_I^n$ , then  $|x(t) - x^*| < \epsilon$  for  $t \geq 0$ , and (ii) every solution converges to  $x^*$  as  $t \rightarrow +\infty$ , if  $x^0 \in R_I^n$ . Here  $x^0$  is an initial state and  $x(t)$  is the solution of (3) starting from  $x^0$ .

*Definition 2.* For an  $n \times n$  real matrix  $A$  (i)  $A \in S_w$  (or  $A \in \tilde{S}_w$ ) implies that there exists an  $n \times n$  positive definite diagonal matrix  $W$  such that  $WA + A^T W$  is positive definite (or positive semi-definite), (ii)  $A \in P$  implies that all the principal minors of  $A$  are positive ( $P$ -matrix), and (iii) if all the real parts of eigenvalues of  $A$  are negative, then  $A$  is called stable.

The following stability conditions are known and to be used in the following discussions.

**THEOREM 1** (Takeuchi and Adachi, 1980). *If  $A = (a_{ij}) \in S_w$ , then (3) has a non-negative and globally stable equilibrium for each  $b = (b_i) \in R^n$ .*

**THEOREM 2** (Takeuchi and Adachi, 1982). *If a non-negative equilibrium  $x^*$  of (3) is locally stable, then*

$$b_i - \sum_{j=1}^n a_{ij} x_j^* \leq 0, \quad i = 1, \dots, n. \quad (4)$$

**THEOREM 3** (Goh, 1978). *Suppose that there exists a non-negative equilibrium  $x^*$  of (3). Then  $x^*$  is globally stable if*

$$(i) \quad A \in \tilde{S}_w, \quad (5)$$

$$(ii) \quad b_i - \sum_{j=1}^n a_{ij} x_j^* \leq 0 \quad \text{for any } i \in I, \text{ and} \quad (6)$$

(iii) the function

$$-(x - x^*)^T (WA + A^T W) (x - x^*) + 2 \sum_{i \in I} w_i x_i \left( b_i - \sum_{j=1}^n a_{ij} x_j^* \right) \quad (7)$$

does not vanish identically along any solution of (3) except for  $x = x^*$  in  $R_+^n$ .

By Theorem 1  $A \in S_w$  ensures the existence of a non-negative globally stable equilibrium of (3) for each  $b \in R^n$ . The following example shows that there exists a non-negative and globally stable equilibrium for some  $b \in R^n$ , even if  $A \notin S_w$  or  $A \notin \tilde{S}_w$ .

*Example.* Let us consider system (3) when  $n = 2$  and

$$A = (a_{ij}) = \begin{bmatrix} 1 & 1/3 \\ a & 1 \end{bmatrix}. \quad (8)$$

This matrix does not belong to matrix class  $S_w$  or  $\bar{S}_w$  for  $a > 3$  since  $A \notin P$  for  $a > 3$  (Takeuchi *et al.*, 1978). Therefore Theorems 1 and 3 cannot be applied to this case. When  $b = (1, 2)^T, x^* = (1, 0)^T$  is an equilibrium of (3). Define for  $w_i > 0 (i = 1, 2)$

$$V = w_1(x_1 - 1 - \ln x_1) + w_2x_2; \tag{9}$$

then  $V \geq 0$  and the equality holds only for  $x = x^*$  in  $R_f^2 = \{x_1 > 0, x_2 \geq 0\}$ . Suppose that  $a > 3$ ; then the time derivative of (9) along the solution of (3) with (8) becomes

$$\frac{d}{dt} V \Big|_{(3)} = -(x_1 - 1, x_2) \begin{bmatrix} w_1 & \\ & w_2 \end{bmatrix} \begin{bmatrix} 1 & 1/3 \\ 2 & 1 \end{bmatrix} \begin{bmatrix} x_1 - 1 \\ x_2 \end{bmatrix} - (a - 2)w_2x_1x_2. \tag{10}$$

Since

$$\begin{bmatrix} 1 & 1/3 \\ 2 & 1 \end{bmatrix} \in S_w, \tag{11}$$

then

$$dV/dt \Big|_{(3)} \leq 0 \tag{12}$$

in  $R_f^2$  and the equality of (12) holds only for  $x = x^*$ . Therefore  $x^*$  is globally stable by Lyapunov's extended stability theory (LaSalle, 1960).

For fixed  $b = (1, 2)^T, x^* = (1, 0)^T$  is a globally stable equilibrium of (3), with matrix  $A$  defined by (8) for  $2 < a \leq 3$  using Theorem 3. The above example shows that  $x^* = (1, 0)^T$  is also globally stable for  $a > 3$ . The following lemma is useful in such cases and is used in Section 3.

LEMMA 1. *Suppose that matrix  $A = (a_{ij})$  of (3) belongs to class  $S_w$  and that a non-negative equilibrium  $(x^*, 0) = (x_1^*, \dots, x_p^*, 0, \dots, 0)^T$  is locally stable. Then  $(x^*, 0)$  is also a globally stable equilibrium of the following system:*

$$\frac{d}{dt} x_i(t) = x_i(t) \left( b_i - \sum_{j=1}^n \tilde{a}_{ij}x_j(t) \right), \quad i = 1, \dots, n, \tag{13}$$

where  $\tilde{A} = (\tilde{a}_{ij})$  is any matrix satisfying

$$\tilde{A} = \begin{bmatrix} A_{pp} & A_{pq} \\ \tilde{A}_{qp} & A_{qq} \end{bmatrix}, \tag{14}$$

$$\tilde{A}_{qp} \geq A_{qp}. \tag{15}$$

Lemma 1 is reasonable from a biological point of view since the  $n$ -species system (13) would have a stable state  $(x^*, 0)$  when the  $p$ -species subsystem depresses  $q$  species in (13) more strongly than in (3). It should be noted that  $A \in S_w$  (or  $A \in \tilde{S}_w$ ) does not imply  $\tilde{A} \in S_w$  (or  $\tilde{A} \in \tilde{S}_w$ ) in general.

3. *Two-prey, One-predator Models.* This section deals with the two-prey, one-predator system (1). Firstly, the boundedness of the solutions of (1) is established.

**THEOREM 4.** *All the solutions of (1) starting in  $R_{+0}^3 = \{x_i \geq 0 (i = 1, 2), z \geq 0\}$  are bounded.*

The proof of Theorem 4 is similar to that of Krikorian (1979), but his model has no competitive interactions between prey species. From the proof Theorem 4 can be easily extended to the  $n$ -prey, one-predator system ( $n \geq 3$ ) in which  $n$  prey have negative density effects.

There exist seven equilibriums for system (1), namely

(i) three-species equilibriums:  $(E_3) = (x_1^*, x_2^*, z^*)$ , where

$$x_i^* = \tilde{x}_i / |A| (i = 1, 2), \quad z^* = \tilde{z} / |A|, \tag{16}$$

$$\tilde{x}_1 = b_3\epsilon - db_2\epsilon\mu - \alpha b_3\mu + db_1\mu^2, \tag{17}$$

$$\tilde{x}_2 = db_2\epsilon^2 - db_1\epsilon\mu - b_3\beta\epsilon + b_3\mu, \tag{18}$$

$$\tilde{z} = b_3(\alpha\beta - 1) + d\mu(b_2 - \beta b_1) + d\epsilon(b_1 - \alpha b_2), \tag{19}$$

$$|A| = d(\epsilon^2 + \mu^2 - (\alpha + \beta)\epsilon\mu), \tag{20}$$

(ii) two-species equilibriums:

$$(E_{+0+}) = (b_3\epsilon, 0, db_1\epsilon - b_3) / d\epsilon^2,$$

$$(E_{0++}) = (0, b_3\mu, db_2\mu - b_3) / d\mu^2,$$

$$(E_{++0}) = (b_1 - \alpha b_2, b_2 - \beta b_1, 0) / (1 - \alpha\beta),$$

(iii) one-species equilibriums:

$$(E_{+00}) = (b_1, 0, 0),$$

$$(E_{0+0}) = (0, b_2, 0),$$

and the last one is  $(0, 0, 0)$ , which is unstable.

Conditions for non-negativity and for local stability of equilibria obtained by perturbation theory are summarized in Table I.

When no predator exists, the stability of the two-prey competitive system (2) can be concluded from Lemma 1 and Theorem 1.

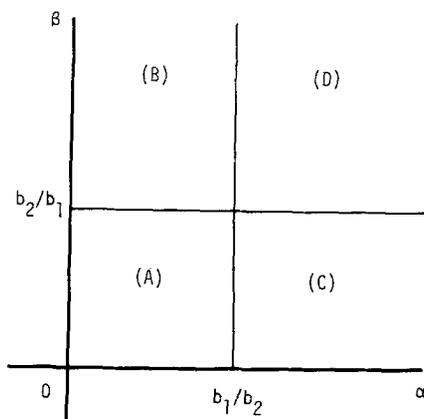


Figure 1. This figure shows the stability properties of the two-prey system (2) as a function of competitive parameters  $\alpha$  and  $\beta$ . In the region (A) positive equilibrium is globally stable; in the region (B) [or (C)] the single-species equilibrium  $(b_1, 0)$  [or  $(0, b_2)$ ] is globally stable; in the region (D)  $(b_1, 0)$  and  $(0, b_2)$  are locally stable and the trajectory converges to each one of them dependently on its initial state. See Theorem 5.

**THEOREM 5** (Figure 1). *A positive equilibrium  $(b_1 - \alpha b_2, b_2 - \beta b_1)/(1 - \alpha\beta)$  of (2) is globally stable if and only if  $\alpha < b_1/b_2$  and  $\beta < b_2/b_1$ . The  $(b_1, 0)$  [or  $(0, b_2)$ ] is globally stable if and only if  $\alpha \leq b_1/b_2$  and  $\beta \geq b_2/b_1$  (or  $\alpha \geq b_1/b_2$  and  $\beta \leq b_2/b_1$ ) and at least one of the inequalities in each pair of inequalities is strict. When  $\alpha > b_1/b_2$  and  $\beta > b_2/b_1$ ,  $(b_1, 0)$  and  $(0, b_2)$  are locally stable.*

The following lemma is useful for stability analysis of system (1).

**LEMMA 2.** *Let  $A$  be a matrix defined by*

$$A = \begin{bmatrix} 1 & \alpha & \epsilon \\ \beta & 1 & \mu \\ -d\epsilon & -d\mu & 0 \end{bmatrix}, \quad (21)$$

*then  $A$  belongs to class  $\tilde{S}_w$  if and only if  $\alpha + \beta \leq 2$ .*

TABLE I  
Existence and Local Stability Conditions for Non-negative Equilibrium Points of the Two-prey, One-predator System (1)

Equilibrium point	Non-negative conditions	Local stability conditions
$(E_3) = (x_1^*, x_2^*, z^*)$	$x_1^* \geq 0, x_2^* \geq 0, z^* \geq 0$	$a_0 = x_1^* + x_2^* > 0$ $a_1 = (1 - \alpha\beta)x_1^*x_2^* + d(\epsilon^2x_1^* + \mu^2x_2^*)z^* > 0$ $a_2 = x_1^*x_2^*z^* A  > 0$ $a_0a_1 - a_2 > 0$
$(E_{+0+})$	$\epsilon \geq b_3/(db_1)$	$\bar{x}_2 < 0$
$(E_{0++})$	$\mu \geq b_3/(db_2)$	$\bar{x}_1 < 0$
$(E_{+++})$	$(b_1 - \alpha b_2)(b_2 - \beta b_1) \geq 0$	$\alpha\beta < 1, \bar{z} < 0$
$(E_{0+0})$	always	$\alpha > b_1/b_2, \mu < b_3/(db_3)$
$(E_{+00})$	always	$\beta > b_2/b_1, \epsilon < b_3/(db_1)$
$(0, 0, 0)$	always	unstable

Here  $(E_3)$  is three-species equilibrium,  $(E_{+0+})$  and  $(E_{0++})$  are two-species equilibriums and  $(E_{+++})$  and  $(E_{+00})$  are one-species equilibriums. For details see (16)-(20) in the text.

Using Theorem 3 and Lemma 2, global stability of equilibriums of (1) can be established.

**THEOREM 6.** *Suppose that  $\alpha + \beta < 2$ .*

- (i) *If  $(E_3)$  is non-negative, then  $(E_3)$  is globally stable.*
- (ii) *If  $(E_3)$  is not non-negative, then one of  $(E_{0++}), (E_{+0+}), (E_{++0}), (E_{+00})$  or  $(E_{0+0})$  is globally stable.*

From Theorem 5, two competing species cannot coexist when  $\alpha \geq b_1/b_2$  or  $\beta \geq b_2/b_1$ . The addition of a predator feeding on two prey changes the patterns of three-species stable coexistence. Four cases, classified by the competitive abilities of two prey, are discussed.

3.1. *Case where  $\alpha < b_1/b_2$  and  $\beta < b_2/b_1$ .* We first consider the case in which the two-prey subcommunity is globally stable and stable coexistence of two prey is realized.

From Theorem 6 and non-negative conditions of equilibriums, Figure 2(a) is obtained for  $\alpha + \beta < 2$ . Figure 2(a) shows that four equilibriums can be globally stable, but three-species stable coexistence is not always possible even if  $\alpha < b_1/b_2$  and  $\beta < b_2/b_1$ .

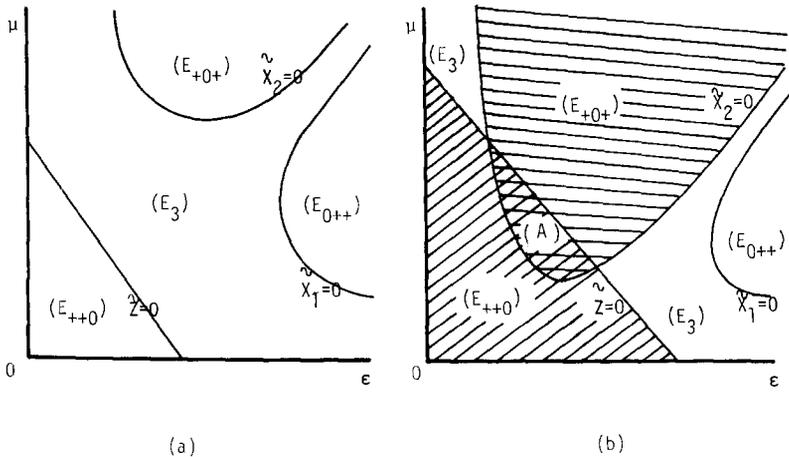


Figure 2. These figures show the stability properties of system (1) for the case  $\alpha < b_1/b_2, \beta < b_2/b_1$  when globally stable coexistence in two-prey subcommunity is possible. (a) For  $\alpha + \beta < 2$ , four equilibriums can be globally stable and three-species stable coexistence is not always possible; (b) for  $\alpha + \beta > 2$  but  $\alpha\beta < 1$ , each equilibrium is locally stable. In the region (A) the existence of non-negative  $(E_3)$  does not exclude local stability of  $(E_{+0+})$  and  $(E_{0++})$ .

See Section 3.1 for details.

Let us consider the case where  $\alpha + \beta > 2$  but  $\alpha\beta < 1$ . In region (A) of Figure 2(b) ( $E_3$ ) is non-negative but unstable. Hence non-negativity conditions of ( $E_3$ ) do not exclude in general local stability of two-species equilibrium. The global stability region in competitive parameters  $\alpha - \beta$  space of a two-prey system is reduced by addition of a predator feeding on them. Table 1 and Figure 2(b) show, however, that there exists a locally stable three-species coexistent state in this case.

3.2. Case where  $\alpha > b_1/b_2$  and  $\beta > b_2/b_1$ . For the case where the competitive interactions between two prey are greater, two prey of (2) cannot coexist by Theorem 5. Figure 3(a) and Table I conclude existence of locally stable equilibrium, similarly to the case of  $\alpha + \beta > 2$  and  $\alpha\beta < 1$ .

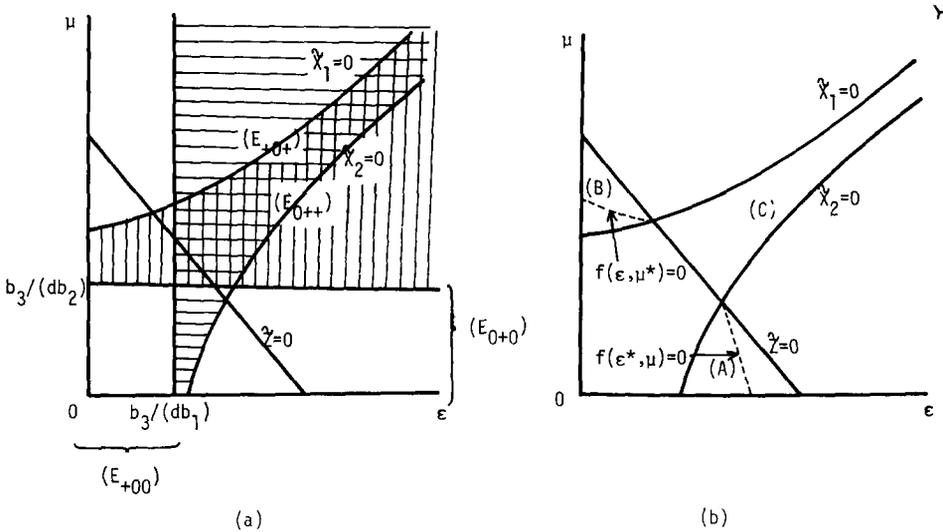


Figure 3. Figure (a) shows that there exists at least one local stable equilibrium for any  $\epsilon$  and  $\mu$  for  $\alpha > b_1/b_2$  and  $\beta > b_2/b_1$ . In the regions (A), (B) and (C) of Figure 3(b) a positive equilibrium exists. In (A) [or (B)] there exists at least one Hopf bifurcation parameter  $\epsilon^*$  (or  $\mu^*$ ) for any straight line  $\mu = \text{constant}$  (or  $\epsilon = \text{constant}$ ) if (22) is satisfied. Examples of values of  $\epsilon^*$  are given in Table II. See Theorem 7.

**THEOREM 7.** (i) In parametric region (A) [or (B)] of Figure 3(b) there exists at least one Hopf bifurcation parametric value  $\epsilon^*$  (or  $\mu^*$ ) for any  $\mu$  (or  $\epsilon$ ) fixed if

$$\frac{d}{d\epsilon}(a_0a_1 - a_2) \Big|_{\epsilon=\epsilon^*} \neq 0 \left( \text{or } \frac{d}{d\mu}(a_0a_1 - a_2) \Big|_{\mu=\mu^*} \neq 0 \right), \tag{22}$$

where

$$a_0 = x_1^* + x_2^*, \tag{23}$$

$$a_1 = (1 - \alpha\beta)x_1^*x_2^* + d(\mu^2x_2^* + \epsilon^2x_1^*)z^* \tag{24}$$

$$a_2 = x_1^*x_2^*z^*|A|. \tag{25}$$

(ii) In (C) of Figure 3(b) there exists no periodic solution of the Hopf type.

Appendix gives a stability criterion of the periodic orbits. Table II gives parametric values  $\epsilon^*$  of Hopf bifurcation in region (A) of Figure 3(b) and the values of  $H$  in the appendix. For  $\alpha = \beta = 1.5$ ,  $b_i = 1$  ( $i = 1, 2, 3$ ) and  $d = 0.5$ , the periodic solutions are locally stable. These solutions have small amplitudes at  $\epsilon > \epsilon^*$  and the periods increase with  $\epsilon$ . For larger values of  $\epsilon$  the population densities of the predator and one prey become nearly equal to zero and the periodic solution degenerates into the equilibrium  $(E_{+00})$  or  $(E_{0+0})$ .

TABLE II

Hopf Bifurcation Parametric Value  $\epsilon^*$  and the Values of Function  $H$  (A35) in the Appendix for  $b_i = 1$  ( $i = 1, 2, 3$ ),  $\alpha = \beta = 1.5$  and  $d = 0.5$

$\mu$	$\epsilon^*$	$H(\epsilon^*)$
0.138196601	3.74467490	-3176.275734
0.276393202	3.74363090	-3993.714341
0.414589803	3.74002568	-5226.346541
0.552786405	3.73359091	-7247.469273
0.690983006	3.72404025	-11018.72180
0.829179607	3.71106829	-19835.06383
0.967376208	3.69434777	-53973.75096
1.105572810	3.67352716	-13599823.77
1.243769410	3.64822684	-54482.82948

Since  $H < 0$  the bifurcation is supercritical and the periodic orbit is stable. For details see Section 3.2 in the text.

3.3. Case where  $\alpha \leq b_1/b_2$  and  $\beta \geq b_2/b_1$  (or  $\alpha \geq b_1/b_2$  and  $\beta \leq b_2/b_1$ ). Let us consider finally the case in which only one prey can survive if no predator exists. For  $\alpha + \beta < 2$  the global stability of equilibriums is concluded by Theorem 6 (Figure 4a, b). The local stability is also given in Figure 4(c) for  $\alpha\beta < 1$ . Now let us consider the case  $\alpha\beta \geq 1$ . The parametric space  $\epsilon$  and  $\mu$  is partitioned as in Figure 4(d). For any parametric values of  $\epsilon$  and  $\mu$  there exists at least one locally stable equilibrium in the cases considered in 3.1 and 3.2. But it can easily be proved that there exist parametric regions

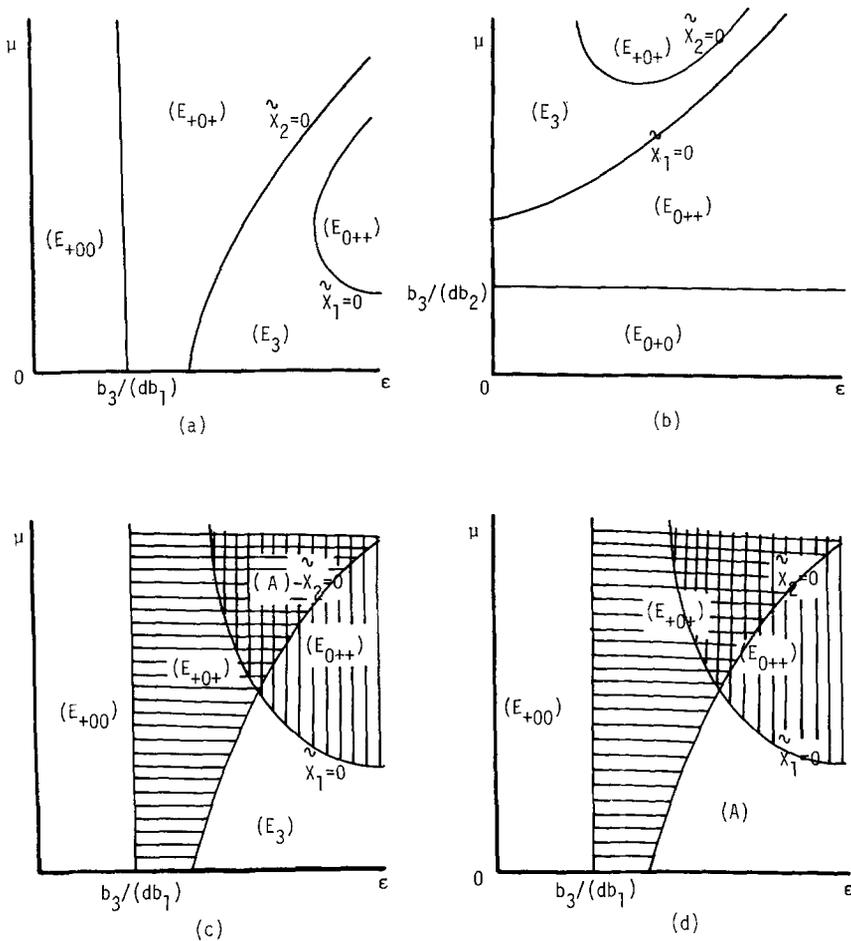


Figure 4. These figures show the stability of equilibria with respect to  $\epsilon$  and  $\mu$ . (a) Global stability for the case  $\alpha \leq b_1/b_2$ ,  $\beta \geq b_2/b_1$  and  $\alpha + \beta < 2$ ; (b) global stability for the case  $\alpha \geq b_1/b_2$ ,  $\beta \leq b_2/b_1$  and  $\alpha + \beta < 2$ ; (c) local stability for  $\alpha \leq b_1/b_2$ ,  $\beta \geq b_2/b_1$ ,  $\alpha + \beta > 2$  and  $\alpha\beta < 1$ . The existence of  $(E_3)$  does not exclude in general local stability of  $(E_{+0+})$  and  $(E_{0++})$  in region (A); (d) local stability for  $\alpha \leq b_1/b_2$ ,  $\beta \geq b_2/b_1$  and  $\alpha\beta > 1$ . In the region (A) there exist sets of parameters  $\epsilon$  and  $\mu$  with no stable equilibrium. Trajectories of (1) with parameters in this region (A) are illustrated in Figure 5. See Section 3.3 for details.

in (A) of Figure 4(d), where no locally stable equilibrium exists, since  $a_1$  (24) becomes negative as  $\epsilon \rightarrow +\infty$  in (A). Table III gives Hopf bifurcation parametric values  $\epsilon^*$  for  $\alpha = 1.0$ ,  $\beta = 1.5$ ,  $d = 0.5$  and  $b_i = 1$  ( $i = 1, 2, 3$ ). For  $\epsilon < \epsilon^*$  in (A), trajectories converge to positive equilibrium  $(E_3)$ . A periodic motion of the Hopf type appears at  $\epsilon > \epsilon^*$ , and its amplitude grows as  $\epsilon$  increases (Figure 5a). The number of peaks of the motion

TABLE III  
Hopf Bifurcation Parametric Value  $\epsilon^*$  and the Values of Function  $H$  (A35) in the Appendix for  $b_i = 1$  ( $i = 1, 2, 3$ ),  $\alpha = 1.0$ ,  $\beta = 1.5$  and  $d = 0.5$

$\mu$	$\epsilon^*$	$H(\epsilon^*)$
0.2	5.66436887	+11.19627602
0.4	5.67218172	+0.7245733785
0.6	5.66632819	-12.82129035
0.8	5.64310337	-30.21784272
1.0	5.59749821	-52.40502963
1.2	5.52229491	-80.49974008
1.4	5.40604659	-115.7490483
1.6	5.22758320	-158.8713165
1.8	4.93460777	-197.8827962

When  $H < 0$  the bifurcation is supercritical and the periodic orbit is stable. A spiral chaos emerges from the periodic orbit as  $\epsilon$  increases. When  $H > 0$  the bifurcation is subcritical and the periodic orbit is unstable. For details see Section 3.3.

in one period becomes two (Figure 5b). For further increasing of value of  $\epsilon$ , spiral chaos discovered by Vance emerges at  $\epsilon = 10$  and its cycle time increases with  $\epsilon$  (Figure 5c, d).

4. *Discussion.* Two prey species without a predator can coexist only for rather weak competition, that is, in a case where  $\alpha < b_1/b_2$  and  $\beta < b_2/b_1$ . Addition of a predator into the competitive system, however, enlarges the possibility of stable coexistence in the cases where  $\alpha \geq b_1/b_2$  or  $\beta \geq b_2/b_1$ . Three cases of coexistence are possible. The first is coexistence of three species at equilibrium for  $\alpha\beta < 1$ . Further, for  $\alpha + \beta < 2$  three species are globally stable, namely, any trajectory starting in positive initial state converges to an equilibrium. The second is stable oscillatory coexistence with a small amplitude for  $\alpha > b_1/b_2$  and  $\beta > b_2/b_1$ . The last is periodic or non-periodic coexistence for  $\alpha \geq b_1/b_2$ ,  $\beta \leq b_2/b_1$  (or  $\alpha \leq b_1/b_2$ ,  $\beta \geq b_2/b_1$ ) and  $\alpha\beta \geq 1$ . This non-periodic motion is a spiral chaos of Vance which bifurcates from a periodic motion of the Hopf type when the predation rate increases. These results enhance the validity of Paine's suggestion.

The result by Lubchenco can also be verified. Suppose that  $b_i = 1$  ( $i = 1, 2, 3$ ). Since  $\alpha < \beta$  in Figure 4 except for Figure 4(b), prey  $x_1$  is competitively superior to prey  $x_2$ . When  $\epsilon > \mu$ , that is, the predator prefers dominant prey  $x_1$ , three-species coexistence is possible. When  $\epsilon < \mu$  coexistence is impossible. Theorem 7 and Figure 3 imply, however, that an oscillatory coexistence is possible for the system with no dominant competing species if competitive interactions between prey are rather great.

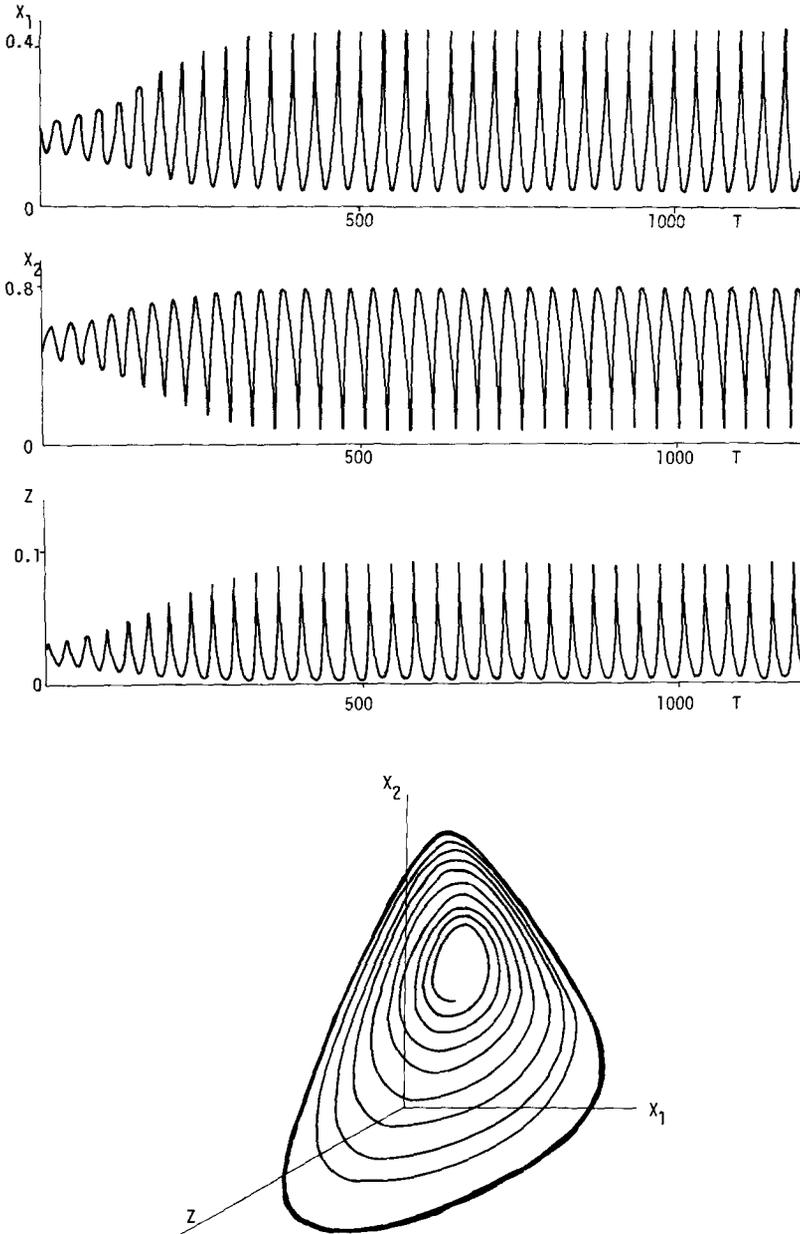


Figure 5. These figures depict one-dimensional  $x_1$ ,  $x_2$ ,  $z$  population changes with respect to time  $t$  and three-dimensional  $x_1$ ,  $x_2$ ,  $z$  population space for  $\alpha = 1.0$ ,  $\beta = 1.5$ ,  $d = 0.5$ ,  $\mu = 1.0$  and  $b_i = 1$  ( $i = 1, 2, 3$ ). The Hopf bifurcation parameter  $\epsilon^* = 5.59749821$ . (a) (above) Limit cycle with a period of about 31.25 of the Hopf type for  $\epsilon = 6$ ; (b) periodic solution with two peaks in one period for  $\epsilon = 8$ ; (c) Vance's spiral chaos for  $\epsilon = 10$ ; (d) cycle time increases compared with (c) for  $\epsilon = 13$ .

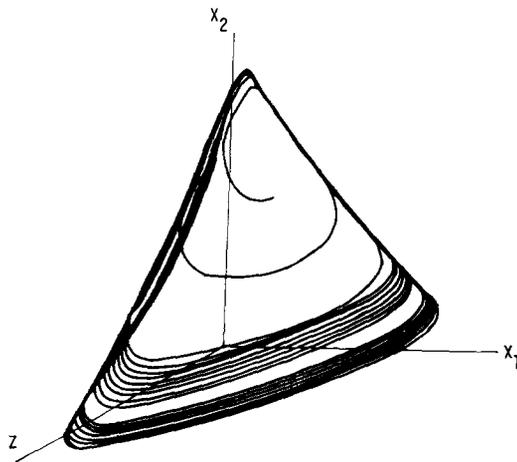
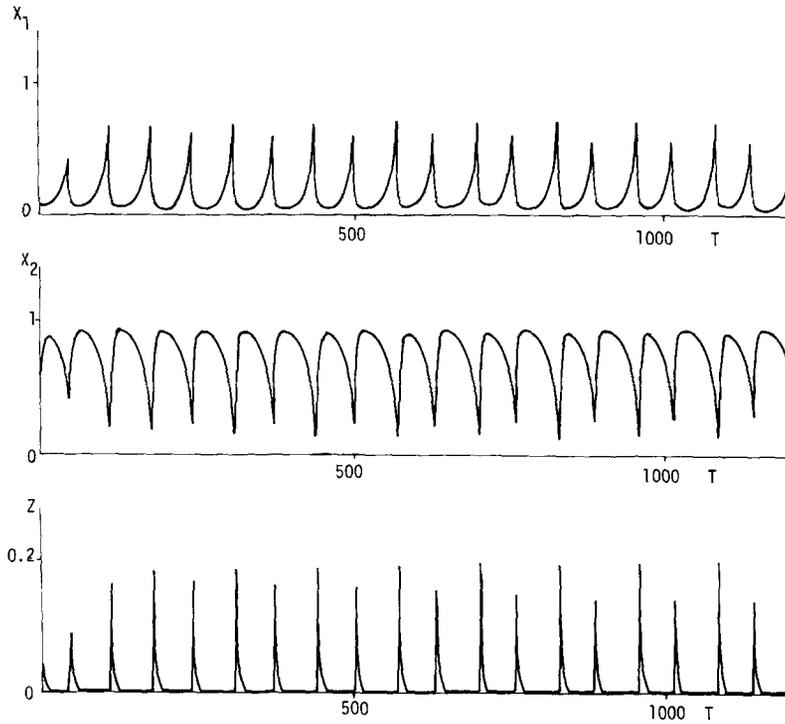


Figure 5(b)

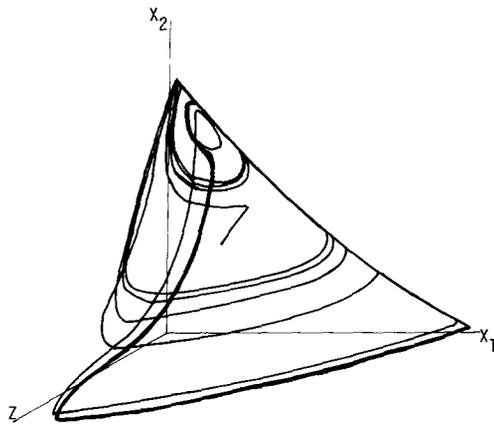
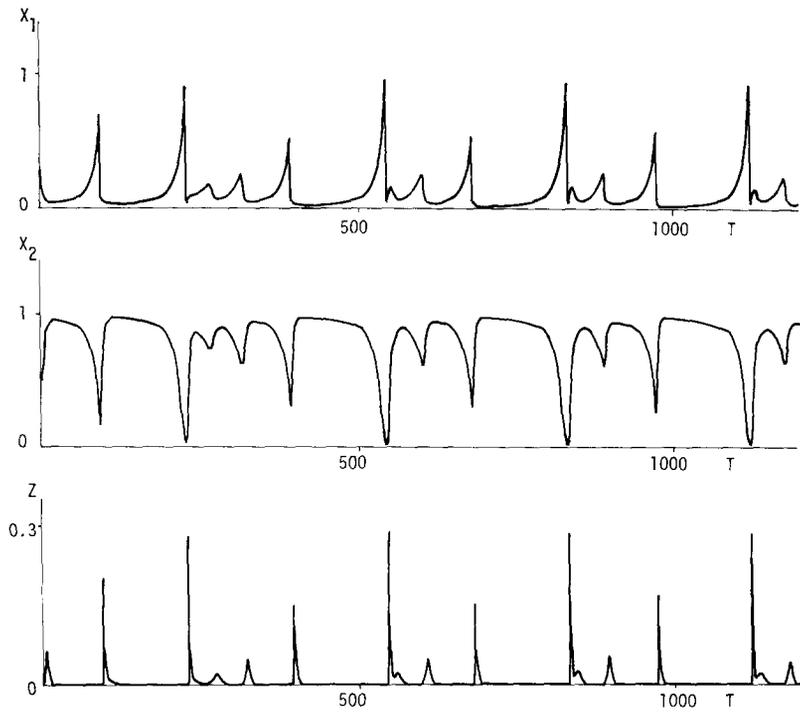


Figure 5 (c)

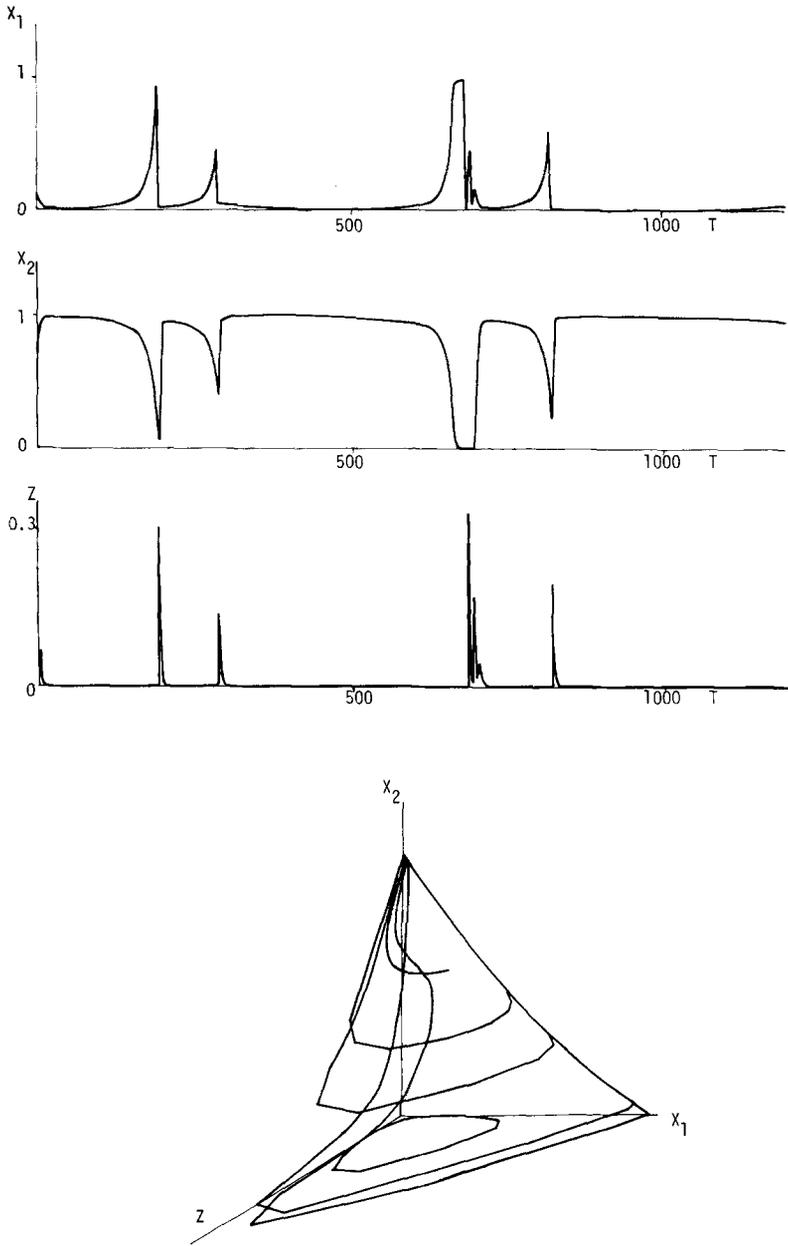


Figure 5 (d)

On the other hand, Maly's experiment (1975) showed that the addition of an alternative, less desirable prey (*Euglena*) changes only slightly the stability of a one-predator, one-prey (Rotifer *Asplanchna-Paramecium*) community. The one-predator, one-prey system is described as:

$$\frac{d}{dt} \begin{bmatrix} x_1(t) \\ z(t) \end{bmatrix} = \begin{bmatrix} x_1(t) (b_1 - x_1(t) - \epsilon z(t)) \\ z(t) (-b_3 + d\epsilon x_1(t)) \end{bmatrix}. \quad (26)$$

Similarly to the proof of Theorem 5, predator  $z$  and prey  $x_1$  cannot coexist stably if and only if

$$\epsilon \leq b_3 / (db_1). \quad (27)$$

When (27) holds and an alternative prey  $x_2$  is less desirable for a predator, that is,

$$\mu < \epsilon, \quad (28)$$

Figures 2, 3 and 4 imply that coexistence of three species is impossible. This coincides with Maly's experiments. On the other hand, if  $x_2$  is a preferable prey for  $z$ , that is,

$$\mu > \epsilon, \quad (29)$$

Figures 2(b) and 4(b) show that three-species stable coexistence is possible from (27) and (29). This seems to be reasonable from the biological point of view, but it should be noted that coexistence is impossible if  $\alpha \leq b_1/b_2$  and  $\beta \geq b_2/b_1$  (Figure 4a, b). Therefore the effect of the addition of a desirable prey into a one-prey, one-predator system is closely connected with competitive abilities of two prey species.

**5. Conclusion.** Applying Lyapunov's direct method and the Hopf bifurcation theory, the stabilizing effect of the addition of one predator into two-competing-prey communities is discussed. The presence of one predator feeding on two competing prey species increases the possibility of stable persistence even for the case where two competitors cannot coexist in a subcommunity. Three patterns of coexistence are possible mathematically: (1) coexistence at equilibrium state, (2) stable oscillatory coexistence of the Hopf type and (3) the spiral chaos of Vance. The last one is nonsense from the biological point of view since the population densities of three species become nearly equal to zero in the evolution of the system. A relationship between the existence of the periodic motion suggested by Fujii and the spiral chaos discovered by Vance is also demonstrated. The former bifurcates from a stable equilibrium by the Hopf theory and the

latter emerges from the periodic motion when the predation rate increases. It is shown that this predator-mediated coexistence can be attained by a close relationship between the preferences of a predator and the competing abilities of the prey and that the patterns of coexistence relate to the strength of the competitive interactions between the prey.

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APPENDIX

*Proof of Lemma 1.* Since  $(x^*, 0)$  is locally stable,

$$b - A \begin{bmatrix} x^* \\ 0 \end{bmatrix} \leq 0 \tag{A1}$$

is satisfied by Theorem 2. Define subsets of  $\{1, \dots, n\}$  of indices such that

$$P = \{i | x_i^* > 0\}, R = \{i | x_i^* = 0\}, Q = \{p + 1, \dots, n\} \tag{A2}$$

and function  $V(x)$  such that

$$V(x) = \sum_{i \in P} [x_i - x_i^* - x_i^* \ln(x_i/x_i^*)] w_i + \sum_{j \in R} w_j x_j + \sum_{k=1}^q \tilde{w}_k x_{p+k}, \tag{A3}$$

where  $w_i (i = 1, \dots, p), \tilde{w}_k (k = 1, \dots, q)$  are positive constant numbers. The time derivative of  $V(x)$  along a solution of (13) becomes

$$\begin{aligned} \frac{d}{dt} V(x(t)) \Big|_{(13)} &= -(x - x^*, y)^T \begin{bmatrix} W & 0 \\ 0 & \tilde{W} \end{bmatrix} \begin{bmatrix} A_{pp} & A_{pq} \\ A_{qp} & A_{qq} \end{bmatrix} \begin{bmatrix} x - x^* \\ y \end{bmatrix} \\ &\quad - y^T \tilde{W} [(A_{qp} - A_{qp})x - b_q + A_{qp}x^*] - \sum_{j \in R} w_j x_j \left( \sum_{i=1}^p a_{ij} x_i^* - b_j \right), \end{aligned} \tag{A4}$$

where  $x = (x_1, \dots, x_p)^T, y = (x_{p+1}, \dots, x_n)^T, W = \text{diag}(w_i)$  and  $\tilde{W} = \text{diag}(\tilde{w}_i)$ . Hence

$$\frac{dV(x(t))}{dt} \Big|_{(13)} \leq 0 \tag{A5}$$

in  $R_{R+Q}^n = \{(x, y) | x_i > 0 (i \in P), x_j \geq 0 (j \in R), y_k \geq 0 (k = 1, \dots, q)\}$  and the equality holds only for  $(x, y) = (x^*, 0)$  by (15), (A1) and  $A \in S_w$ . Therefore the theorem is proved by the extended Lyapunov's direct theory (LaSalle, 1960).

*Proof of Theorem 4.* Define function  $W$  such that

$$W = \sum_{i=1}^2 dx_i + z. \tag{A6}$$

The time derivative of  $W$  along a solution of (1) is described as

$$\frac{d}{dt} W(x(t), z(t)) \Big|_{(1)} = (d, d) \begin{bmatrix} b_1 - x_1 & -\alpha x_1 \\ -\beta x_2 & b_2 - x_2 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} - b_3 z. \tag{A7}$$

For any  $\lambda > 0$  the following inequality holds from (A6), (A7),  $\alpha > 0$  and  $\beta > 0$ :

$$\frac{dW}{dt} \Big|_{(1)} + \lambda W \leq \sum_{i=1}^2 d(\lambda + b_i - x_i)x_i + z(\lambda - b_3). \tag{A8}$$

For  $\lambda < b_3$  the right-hand side of (A8) is bounded above for all  $(x_1, x_2, z) \in R_{+0}^3$ . Hence

$$\frac{dW}{dt} \Big|_{(1)} + \lambda W < P, \tag{A9}$$

which results in

$$0 \leq W(x(t), z(t)) \leq P/\lambda + W(x(0), z(0))\exp(-\lambda t), \tag{A10}$$

where  $P$  is a positive constant number. By (A6) and (A10) all the components of the solution  $(x(t), z(t))$  are bounded.

*Proof of Theorem 5.* Matrix  $A(\alpha, \beta)$  of (2) belongs to  $S_w$  if and only if  $\alpha\beta < 1$  (Takeuchi *et al.*, 1978), where

$$A(\alpha, \beta) = \begin{bmatrix} 1 & \alpha \\ \beta & 1 \end{bmatrix}. \tag{A11}$$

From Theorem 1 a positive equilibrium  $(b_1 - \alpha b_2, b_2 - \beta b_1)/(1 - \alpha\beta)$  must be globally stable if  $\alpha < b_1/b_2$  and  $\beta < b_2/b_1$  (which imply  $\alpha\beta < 1$ ). Matrix  $A(\alpha, b_2/b_1)$ , satisfying  $\alpha < b_1/b_2$ , belongs to  $S_w$ . The  $(b_1, 0)$  is a locally stable equilibrium of (2) if  $\beta > b_2/b_1$ . From Lemma 1  $(b_1, 0)$  is a globally stable one of (2) with  $A(\alpha, \beta)$  satisfying  $\alpha < b_1/b_2$  and  $\beta \geq b_2/b_1$ . For  $\alpha = b_1/b_2, \beta > b_2/b_1, (b_1, 0)$  is also globally stable from Theorem 3. The other cases can be proved similarly.

*Proof of Lemma 2.* We choose  $w > 0$  such that

$$w = (d, d, 1); \tag{A12}$$

then

$$WA + A^T W = \begin{bmatrix} 2d & d(\alpha + \beta) & 0 \\ d(\alpha + \beta) & 2d & 0 \\ 0 & 0 & 0 \end{bmatrix}, \tag{A13}$$

which results in  $A \in \tilde{S}_w$ , since  $\alpha + \beta \leq 2, d > 0$ .

If there exists  $W = \text{diag}(w_i) > 0$  such that  $B = WA + A^T W$  is non-negative definite, then all the principal minors of  $B$  are non-negative. Determinants of matrices obtained by deleting the first (or second) row and column from  $B$  are non-negative if and only if

$$w_1 = w_2 = dw_3. \tag{A14}$$

The determinant of the matrix obtained by deleting the third row and column is  $4w_1w_2 - (w_1\alpha + w_2\beta)^2$ , which becomes  $w_1^2(4 - (\alpha + \beta)^2)$  from (A14). Hence  $\alpha + \beta \leq 2$ .

*Proof of Theorem 6.* Three cases ( $\alpha \leq b_1/b_2, \beta \leq b_2/b_1$ ), ( $\alpha \leq b_1/b_2, \beta \geq b_2/b_1$ ) and ( $\alpha \geq b_1/b_2, \beta \leq b_2/b_1$ ) are possible, since  $\alpha + \beta < 2$ . For each case the parameter space represented by  $\epsilon$  and  $\mu$  is divided by two hyperbolae;  $\bar{x}_1 = 0, \bar{x}_2 = 0$  and their asymptotes;  $\epsilon = b_3/(db_1), \mu = b_3/(db_2)$  and a straight line  $\bar{z} = 0$ , as shown in Figures 2(a) and 4(a, b) respectively. Equilibriums  $(E_3), (E_{+0+}), (E_{0++}), (E_{++0}), (E_{+00})$  and  $(E_{0+0})$  are non-negative in the regions indicated.

(i) From Lemma 2,  $A \in \tilde{S}_w$ . When  $(E_3)$  is non-negative equalities of (ii) in Theorem 3 hold because of the definition of  $(E_3)$ . For  $\alpha + \beta < 2$  function (7) vanishes identically along  $x_i(t) = x_i^*$  ( $i = 1, 2$ ), which results in  $x(t) = z^*$ . Hence (iii) in Theorem 3 holds. Therefore  $(E_3)$  is globally stable.

(ii) Condition  $\alpha + \beta < 2$  implies that  $|A| > 0$ , which results in  $\bar{x}_1 < 0, \bar{x}_2 < 0$  or  $\bar{z} < 0$  since  $(E_3)$  is not non-negative. Suppose that  $\bar{x}_1 < 0$ . If  $\mu \geq b_3/(db_2), (E_{0++})$  is non-negative and globally stable from  $\bar{x}_1 < 0$  and Theorem 3. If  $\mu < b_3/(db_2)$  and  $\alpha > b_1/b_2$ , then  $(E_{0+0})$  is globally stable (Figure 4b).  $(E_{+0+})$  [or  $(E_{+00})$ ] is globally stable if  $\alpha \leq b_1/b_2$  and  $\beta \leq b_2/b_1$  (or  $\alpha \leq b_1/b_2$  and  $\beta \geq b_2/b_1$ ). For the case  $\bar{z}_2 < 0$  or  $\bar{z} < 0$  the theorem can be proved similarly.

*Proof of Theorem 7.* Theorem 7 is proved by the following Hopf bifurcation theorem (Marsden and McCracken, 1976).

HOPF BIFURCATION THEOREM.

(1) Let  $X_\mu$  be a  $C^k$  ( $k \geq 5$ ) vector field on  $R^n$ . Assume that  $X_\mu(a(\mu)) = 0$  for all  $\mu$  and let the spectrum of  $dX_\mu(a(\mu))$  satisfy:

(i)  $\sigma(dX_\mu(a(\mu))) \subset \{z \mid \text{Re}z < 0\}$  for  $\mu < \mu_0$ , (A15)

(ii)  $dX_\mu(a(\mu))$  has two complex conjugate, simple eigenvalues  $\lambda(\mu), \bar{\lambda}(\bar{\mu})$  at  $\mu = \mu_0$ ,  
 (iii)  $d\text{Re}\lambda(\mu)/d\mu \big|_{\mu=\mu_0} \neq 0$ , (A16)

(iv)  $\lambda(\mu_0) \neq 0$ , (A17)

(v) the rest of  $\sigma(dX_\mu(a(\mu)))$  remains in the left-half plane bounded from the imaginary axis for  $\mu = \mu_0$ .

Here  $dX_\mu$  represents the linearized matrix of  $X_\mu$  and  $\sigma(dX_\mu)$  is the set of eigenvalues of matrix  $dX_\mu$ . Then there exists a closed orbit with a period about  $2\pi/|\lambda(\mu_0)|$ .

(2) Choose coordinates so that  $X_{\mu_0} = (X_{\mu_0}^1, X_{\mu_0}^2, X_{\mu_0}^3)$ , where  $X_{\mu_0}^1$  and  $X_{\mu_0}^2$  are those in the eigenspaces to  $\lambda(\mu_0), \bar{\lambda}(\bar{\mu}_0)$ , and  $X_{\mu_0}^3$  is one in some complementary subspace. Choose the coordinates so that

$$dX_{\mu_0}(a(\mu_0)) = \begin{bmatrix} 0 & |\lambda(\mu_0)| & 0 \\ -|\lambda(\mu_0)| & 0 & 0 \\ 0 & 0 & d_3X_{\mu_0}^3(a(\mu_0)) \end{bmatrix}. \tag{A18}$$

If the coefficient  $H$  computed by (A19) below is negative, the periodic orbits occur for  $\mu > \mu_0$  and are attracting. If it is positive, the orbits occur for  $\mu < \mu_0$  and are repelling on the center manifold.

$$\begin{aligned}
 H = & (-X_{xx}^1 X_{xy}^1 + X_{yy}^2 X_{xy}^2 + X_{xx}^2 X_{xy}^2 - X_{yy}^1 X_{xy}^1 + X_{xx}^1 X_{xx}^2 - X_{yy}^1 X_{yy}^2) / |\lambda(\mu_0)|^2 \\
 & + (F_{xx}(3X_{xz}^1 + X_{yz}^2) + F_{yy}(3X_{yz}^2 + X_{xz}^1) + 2F_{xy}(X_{yz}^1 + X_{xz}^2) \\
 & + X_{xxx}^1 + X_{yyy}^2 + X_{xyy}^1 + X_{xxy}^2) / |\lambda(\mu_0)|.
 \end{aligned}
 \tag{A19}$$

Here  $X_{xx}^i$  etc. are twice partial derivatives of  $X_\mu^i$  with respect to  $x$  at  $\mu = \mu_0$ , and

$$\begin{bmatrix} F_{xx} \\ F_{xy} \\ F_{yy} \end{bmatrix} = \Delta^{-1} \begin{bmatrix} 2|\lambda(\mu_0)|^2 + \xi^2 & -2|\lambda(\mu_0)|\xi & 2|\lambda(\mu_0)|^2 \\ |\lambda(\mu_0)|\xi & \xi^2 & -|\lambda(\mu_0)|\xi \\ 2|\lambda(\mu_0)|^2 & 2|\lambda(\mu_0)|\xi & 2|\lambda(\mu_0)|^2 + \xi^2 \end{bmatrix} \begin{bmatrix} -X_{xx}^3 \\ -X_{xy}^3 \\ -X_{yy}^3 \end{bmatrix},
 \tag{A20}$$

where

$$\xi = X_z^3 \text{ and } \Delta = \xi(\xi^2 + 4|\lambda(\mu_0)|^2).
 \tag{A21}$$

*Proof of Theorem 7.*

(i) In the parametric region (A) of Figure 3(b),

$$|A| > 0 \text{ and } (x_1^*, x_2^*, z^*) > 0,
 \tag{A22}$$

which result in

$$a_0 > 0 \text{ and } a_2 > 0.
 \tag{A23}$$

On the boundary indicated by  $\bar{X}_2 = 0$  of (A),

$$a_0 > 0, a_1 > 0 \text{ and } a_2 = 0,
 \tag{A24}$$

which imply that

$$a_0 a_1 - a_2 > 0.
 \tag{A25}$$

Similarly, on the boundary indicated by  $\bar{Z} = 0$  of (A),

$$a_0 > 0, a_1 < 0 \text{ and } a_2 = 0
 \tag{A26}$$

from  $\alpha\beta > 1$ . (A26) implies that

$$a_0 a_1 - a_2 < 0.
 \tag{A27}$$

Function  $f(\epsilon, \mu) = a_0(\epsilon, \mu)a_1(\epsilon, \mu) - a_2(\epsilon, \mu)$  is continuous. Therefore there exists at least one solution  $\epsilon^*$  for any  $\mu$  fixed in (A) such that

$$f(\epsilon^*, \mu) = 0
 \tag{A28}$$

from (A25) and (A27). The minimum value of such an  $\epsilon^*$  is denoted by  $\epsilon^*$ . From (A23) and (A28),

$$a_i(\epsilon^*) > 0, i = 1, 2, 3.
 \tag{A29}$$

(A25) and (A29) imply conditions (i), (iv) and (v); further, (A28) results in (ii) of the Hopf bifurcation theorem, where  $\mu$  and  $\mu_0$  of the conditions are replaced by  $\epsilon$  and  $\epsilon^*$  in this theorem. Condition (iii) is (22) in Theorem 7. Therefore there exists a closed orbit by the Hopf bifurcation theorem (1). In the parametric region (B) the proof can be given similarly.

(ii) In the parametric region (C),

$$|A| < 0 \text{ and } (x_1^*, x_2^*, z^*) > 0, \quad (\text{A30})$$

which result in

$$a_2 < 0. \quad (\text{A31})$$

If the matrix has pure imaginary eigenvalues, then (A31) implies that the other real eigenvalue is positive. Therefore there exists no closed orbit of the Hopf type. Hence Theorem 7 is proved.

After a very lengthy computation, we can get equations:

$$X_{xx}^i = -X_{yy}^i \quad (i = 1, 2, 3) \quad (\text{A32})$$

$$X_{xxx}^1 = X_{yyy}^2 = X_{xyy}^1 = X_{xxy}^2 = 0 \quad (\text{A33})$$

$$F_{xx} = -F_{yy}, \quad (\text{A34})$$

which imply that function  $H$  (A19) becomes

$$H = 2(F_{xx}(X_{xz}^1 - X_{yz}^2) + F_{xy}(X_{yz}^1 + X_{xz}^2)). \quad (\text{A35})$$

Hence the stability criterion of a closed orbit is established. Examples of numerical values of  $H$  are given in Tables II and III.

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