DIFFUSIVE PREDATOR-PREY MODELS WITH STAGE STRUCTURE ON PREY AND BEDDINGTON-DEANGELIS FUNCTIONAL RESPONSES

SEONG LEE AND INKYUNG AHN*

Department of Mathematics, Korea University
2511, Sejong-Ro, Sejong, 30019, Korea

(Communicated by Xingfu Zou)

Abstract. In this paper, we examine a diffusive predator-prey model with Beddington-DeAngelis functional response and stage structure on prey under homogeneous Neumann boundary conditions, where the discrete time delay covers the period from the birth of immature prey to their maturity. We investigate the dynamics of their permanence and the extinction of the predator, and provide sufficient conditions for the global attractiveness and the locally asymptotical stability of the semi-trivial and coexistence equilibria.

1. Introduction. In this paper, we consider a diffusive predator-prey model with Beddington-DeAngelis functional response and stage structure on prey:

\[
\begin{align*}
\frac{\partial u_i(x,t)}{\partial t} &= bu_i(x,t) - d_i u_i(x,t) - be^{-d_i t} u_i(x,t - \tau), \\
\frac{\partial u(x,t)}{\partial t} &= D_u \Delta u(x,t) + \frac{be^{-d_i t} u(x,t - \tau) - au^2(x,t)}{1 + k_1 u(x,t) + k_2 v(x,t)}, \\
\frac{\partial v(x,t)}{\partial t} &= D_v \Delta v(x,t) + \frac{nm u(x,t)v(x,t)}{1 + k_1 u(x,t) + k_2 v(x,t)} - dv(x,t) \quad \text{in } \Omega \times (0, \infty), \\
\frac{\partial u_i}{\partial \nu} = \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} &= 0 \quad \text{on } \partial \Omega \times (0, \infty), \\
u(x,\theta) &= u_0(x) \geq 0, \quad v(x,\theta) = v_0(x) \geq 0 \quad \text{in } \Omega \times [-\tau, 0], \\
u(x,0) &\neq 0, \quad u(x,0) \neq 0 \quad \text{in } \Omega, \\
u_i(x,0) &= b \int_{-\tau}^{0} e^{d_i s} u(x,s) ds, 
\end{align*}
\]

(1.1)

where \( \Omega \) is a bounded domain in \( \mathbb{R}^N \) with smooth boundary \( \partial \Omega \), and \( u_i(x,t) \) and \( u(x,t) \) represent the density of the immature and mature prey, respectively, at time \( t \) in location \( x \). Furthermore, \( v(x,t) \) denotes the density of the mature predator, and \( D_u \) and \( D_v \) are the diffusion coefficients of the mature prey and mature predator, respectively. Moreover, \( \partial / \partial \nu \) denotes the outward normal derivative on the boundary \( \partial \Omega \) of \( \Omega \). All constants are positive for their biological sense, and the time

2000 Mathematics Subject Classification. 35K40, 35K57, 92D25.

Key words and phrases. Diffusive predator-prey model, Beddington-DeAngelis functional response, time delay, stage structure on prey, locally/globally asymptotically stable.

* Corresponding author.
delay $\tau$ is the time taken for the juvenile prey to develop from birth to maturity. Finally, $b$ is the birth rate of the mature prey, $d_i$ is the mortality rate of immature prey, $n$ is the birth rate of the predator, $m(1/time)$ and $k_1(1/prey)$ describe the effects of the capture rate and handling time on the feeding rate, respectively, $k_2$ is a constant describing the magnitude of interference among predators$(1/predator)$, $e^{-d_i\tau}$ is the survival rate of each immature prey to become mature prey, $a$ is the death rate of mature prey, and $d$ is the death rate of the predator.

The following assumptions are imposed in (1.1):

(a) Immature prey have a time postponement from their birth to maturity.
(b) Young prey are raised by their parents and dependent on their nutrition. They can avoid predators by staying in their eggs, nests, or burrows, i.e., they are immobile and cannot breed.
(c) The mature predator cannot attack immature prey; they can only hunt mature prey, because the immature prey cannot move easily and are hidden in small areas. Immature prey appear significantly less than mature prey in nature.
(d) Young prey reach maturity after surviving the immature stage; if the juvenile death rate is not zero, then not all immature prey survive the juvenile stage.

In accordance with assumptions (b) and (c), there is no diffusion of juvenile prey in the first equation of (1.1). For more background information on (1.1), we refer the reader to [15, 16] and the references therein.

We also assume that the predator consumes the mature prey with the functional response of the Beddington-DeAngelis type. Furthermore, the following is assumed as a result of the continuity of solutions to (1.1):

\[ u_i(x,0) = b \int_{-\tau}^{0} e^{ds} u(x,s) ds. \]  

From the first equation in (1.1) with initial condition (1.2), we have the following formula:

\[ u_i(x,t) = b \int_{-\tau}^{0} e^{ds} u(x,t+s) ds. \]  

Hence, the immature prey density $u_i(x,t)$ is determined by the mature prey variation $u(x,t)$ that is completely determined by the second and third equations of (1.1); therefore, we mainly deal with the following subsystem:

\[
\begin{cases} 
\frac{\partial u(x,t)}{\partial t} - D_u \Delta u(x,t) = be^{-d_i\tau}u(x,t-\tau) - au^2(x,t) - \frac{mn u(x,t)v(x,t)}{1+k_1 u(x,t)+k_2 v(x,t)}, \\
\frac{\partial v(x,t)}{\partial t} - D_v \Delta v(x,t) = \frac{mn u(x,t)v(x,t)}{1+k_1 u(x,t)+k_2 v(x,t)} - dv(x,t) \quad \text{in } \Omega \times (0,\infty), \\
\frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0 \quad \text{on } \partial \Omega \times (0,\infty), \\
u(x,\theta) = u_0(x) \geq 0, \quad v(x,\theta) = v_0(x) \geq 0 \quad \text{in } \Omega \times [-\tau,0], \\
u(x,0) \neq 0, \quad v(x,0) \neq 0 \quad \text{in } \Omega.
\end{cases}
\]

For convenience, we denote

\[ r = be^{-d_i\tau}, \quad K = \frac{be^{-d_i\tau}}{a}. \]
In this paper, we focus on the following subsystem:

\[
\begin{align*}
\frac{\partial u}{\partial t} - D_u \Delta u &= ru(x,t - \tau) - \frac{ru^2}{K} - \frac{muv}{1 + k_1u + k_2v}, \\
\frac{\partial v}{\partial t} - D_v \Delta v &= \frac{nmuv}{1 + k_1u + k_2v} - dv, \\
\frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0, \\
u(x,0) \neq 0, \ v(x,0) \neq 0
\end{align*}
\]

in \(\Omega \times (0, \infty)\),

where \(x_m(\theta) > 0\) is continuous on \(-\tau \leq \theta \leq 0\), and \(x_i(0), \ x_m(0), \ y(0) > 0\). Here \(x_m\) and \(y\) represent the mature prey and predator densities, respectively, and \(x_i\) is the immature prey density. The results of the permanence, extinction of species, and global stability of equilibria were demonstrated. Liu and Beretta [15] studied a stage structured predator-prey model with a Beddington-DeAngelis-type functional response to consider the time delay between the birth and maturity of a predator. They examined the permanence of two species and showed both analytically and numerically that stability switches occur at the interior equilibrium as the maturation time delay increases. In [11, 12], the authors considered a stage structured diffusive predator-prey model with a Beddington-DeAngelis-type functional response based on the duration of time between the birth and maturity of a predator. The global existence of nonnegative solutions, permanence, global stability, local stability and Hopf bifurcation of the equilibria were demonstrated.

The main focus of this paper is to examine the asymptotic properties of the diffusive delayed predator-prey model in (1.1) with a Beddington-DeAngelis type functional response under homogeneous Neumann boundary conditions; we assume that the discrete time delay covers the period of time between the birth and maturity of immature prey. We establish threshold dynamics for the permanence and extinction of the predator. In addition, we provide sufficient conditions for the global attractiveness of the semi-trivial and coexistence equilibria. Furthermore, we demonstrate the locally asymptotical stability of (1.1) at equilibria.

The remainder of this paper is organized as follows. In Section 2, we demonstrate the global existence of nonnegative solutions, possible equilibria, and long-term behavior of time-dependent solutions to (1.5), particularly, its uniformly persistent property. In Section 3, we obtain the locally asymptotical stability at the equilibria.
In Section 4, we study the globally asymptotical stability of system (1.5) at semi-trivial and coexistent constant steady states. Finally, we give a brief biological interpretation of our results in Section 5.

2. Permanence. In this section, we examine the global existence and persistence of solutions to (1.5) by using persistence theory [7] and a comparison argument.

We begin with the following existence theorem:

**Theorem 2.1.** For any nonnegative nontrivial initial functions, the system (1.5) has a unique global solution \((u, v)\) in \(C(\Omega \times [0, \infty))\) such that \((0, 0) \leq (u, v) \leq (M_1, M_2)\) in \(\Omega \times [0, \infty)\), where

\[
M_1 = \max \left\{ \|u_0(x)\|_\infty, \frac{be^{-d\tau}}{a} \right\},
\]

\[
M_2 = \max \left\{ \|v_0(x)\|_\infty, \frac{M_1(nm - dk_1) - d}{dk_2} \right\}.
\]

The above theorem can be proven using the upper-lower solution method [21] since the reaction terms in (1.5) satisfy the Lipschitz conditions in a bounded set; thus, we omit its proof.

Observe that system (1.5) has the zero and nonnegative equilibria \(E_0 = (0, 0)\) and \(E_1 = (K, 0)\); the positive equilibrium \(E^* = (u^*, v^*)\) of (1.5) is the unique solution to the following system:

\[
\begin{cases}
ru(1 - (1/K)u) - \frac{muv}{1 + k_1u + k_2v} = 0, \\
\frac{nmu}{1 + k_1u + k_2v} - dv = 0.
\end{cases}
\]  

(2.1)

Define

\[
\Re_0 := \frac{nmK}{d(1 + k_1K)} = \frac{nmb}{d(\alpha e^{d\tau} + k_1b)},
\]  

(2.2)

where \(r\) and \(K\) are defined in (1.4).

If \(\Re_0 > 1\), then (2.1) has a unique positive constant steady state \(E^* = (u^*, v^*)\). In particular, it can be found that

\[
\begin{aligned}
\frac{u^*}{B} &= \frac{B + \sqrt{B^2 + 4C}}{2} \quad \text{and} \quad v^* = \frac{nru^*}{d}(1 - \frac{u^*}{K}),
\end{aligned}
\]  

(2.3)

where

\[
B = \frac{K(dk_1 - nm + nrk_2)}{nrk_2}, \quad C = \frac{dK}{nrk_2}.
\]  

(2.4)

The following lemma [14] will be used in the remainder of this paper.

**Lemma 2.2.** Let \(u \in C(\Omega \times [0, \infty)) \cap C^{2,1}(\Omega \times (0, \infty))\) and be a nonnegative nontrivial solution to the following scalar problem:

\[
\begin{cases}
\frac{\partial u}{\partial t} - D\Delta u = Bu(x, t - \tau) \pm A_1u(x, t) - A_2u^2(x, t) & \text{in } \Omega \times (0, \infty), \\
\frac{\partial u}{\partial \nu} = 0 & \text{on } \partial \Omega \times (0, \infty), \\
u(x, t) = \phi(x, t) \geq 0 & \text{in } \Omega \times [-\tau, 0],
\end{cases}
\]

where \(A_1 \geq 0\) and \(B, A_2, \tau > 0\). (i) If \(B \pm A_1 > 0\), then \(u \to (B \pm A_1)/A_2\) as \(t \to +\infty\) uniformly on \(\Omega\). (ii) If \(B \pm A_1 < 0\), then \(u \to 0\) as \(t \to +\infty\) uniformly on \(\Omega\).
Next, we study the asymptotic property of (1.1). We obtain the long-term behavior for any nonnegative solution \((u, v)\) of system (1.5) as \(t \to \infty\) for all \(x \in \Omega\).

**Theorem 2.3.** (i) Suppose \(\mathcal{R}_0 > 1\). Then the nonnegative solution \((u, v)\) of system (1.5) satisfies

\[
\limsup_{t \to \infty} (u(x, t), v(x, t)) \leq \left( K, \frac{(nm - dk_1)K - d}{dk_2} \right) \quad \text{in} \quad \overline{\Omega}.
\]

(ii) Suppose \(rk_2 > m\) and \(nmA/(1 + k_1A) > d\). Then the nonnegative solution \((u, v)\) of system (1.5) satisfies

\[
\liminf_{t \to \infty} (u(x, t), v(x, t)) \geq \left( A, \frac{(nm - dk_1)A - d}{dk_2} \right) \quad \text{in} \quad \overline{\Omega},
\]

where \(A := K(1 - (m/rk_2))\).

**Proof.** It suffices to prove (i) since (ii) follows a similar argument.

First, note that \(\limsup_{t \to \infty} u(x, t) \leq K\) in \(\overline{\Omega}\) follows from the comparison argument of parabolic problems and Lemma 2.2 since \(ru(x, t - \tau) - \frac{nmv}{1 + k_1u + k_2v} \leq ru(x, t - \tau) - \frac{Ku^2}{1 + k_1u + k_2v} \in \Omega \times [0, \infty)\). Thus, for an arbitrary positive constant \(\epsilon\), there exists \(T_1 \in (0, \infty)\) such that \(u(x, t) \leq K + \epsilon\) in \(\overline{\Omega} \times [T_1, \infty)\). Using this result and the comparison argument of parabolic problems, for an arbitrary positive \(\epsilon\), there exists \(T_2 \in [T_1, \infty)\) such that

\[
v(x, t) \leq \frac{(nm - dk_1)K - d}{dk_2} + \epsilon^* \quad \text{in} \quad \overline{\Omega} \times [T_2, \infty),
\]

where \(\epsilon^* = \epsilon((nm - dk_1)/dk_2) + \epsilon\), since

\[
\frac{nmv}{1 + k_1u + k_2v} - dv \leq \frac{nm(K + \epsilon)v}{1 + k_1(K + \epsilon) + k_2v} - dv
\]

\[
= \frac{v[(nm - dk_1)K - d + \epsilon(nm - dk_1) - dk_2v]}{1 + k_1(K + \epsilon) + k_2v}
\]

in \(\Omega \times [T_1, \infty)\). Therefore, by the arbitrariness of \(\epsilon\), we obtain the desired result. \(\square\)

We now provide the uniform persistence of solutions to system (1.5). We apply persistence theory [7] to our system.

**Theorem 2.4.** If \(\mathcal{R}_0 > 1\) and \(k_2 > \frac{m}{r}\), then for given initial nonnegative functions \(u(x, \theta)\) and \(v(x, \theta)\) in \(\Omega \times [-\tau, 0]\) with \(u(x, \theta) \neq 0\) and \(v(x, \theta) \neq 0\), system (1.5) is uniformly persistent. Furthermore, (1.1) is also uniformly persistent.

**Proof.** Let \(X = C([-\tau, 0], C(\Omega, \mathbb{R}))\) with positive cone \(X^+\), and choose

\[
Y_0 = \{\psi \in X^+: \psi(x, \theta) \geq 0 \text{ in } \overline{\Omega} \times [-\tau, 0], \text{ and } \psi(x, 0) \neq 0\},
\]

\[
Y_1 = \{\psi \in X^+: \psi(x, \theta) \equiv 0 \text{ in } \overline{\Omega} \times [-\tau, 0]\}.
\]

Denote \(X^0 = \text{Int}(X^+ \times X^+).\) It follows that \(\partial X^0 = (Y_0 \times Y_1) \cup (Y_1 \times Y_0)\).

Note that system (1.5) generates a semiflow \(S(t)\) on \(X^+ \times X^+,\) and \(X^0\) and \(\partial X^0\) are invariant. As a result of Theorem 2.3, \(S(t)\) is a dissipative point in \(X^+ \times X^+\), while \(S(t): X^+ \times X^+ \to X^+ \times X^+\) is compact for each \(t > \tau\). Let \(M_0 = (0, 0)\) and \(M_1 = (K, 0)\). Then the \(\omega\)-limit sets of the semiflow \(S(t)\) on \(\partial(X^0)\), is \(\tilde{A}_0 = \{M_0, M_1\}\) because there are only two semi-trivial equilibria \(M_0\) and \(M_1\) in \(\partial X^0\) for model (1.5). The disjoint, compact and isolated invariant sets \(M_0\) and \(M_1\) cover
\(\bar{A}_0\). From the assumption that \(\mathbb{R}_0 > 1\), we can show that there exists a \(\delta\) such that for any \((u_0(x), v_0(x)) \in Y_0 \times Y_0\),
\[
\limsup_{t \to \infty} ||S(t)(u_0(x), v_0(x)) - M_i|| \geq \delta, \quad i = 0, 1.
\]

Thus, \(M_0 \cup M_1\) is an acyclic covering of \(\bar{A}_0\).

To finish the proof, we show that \(W^s(M_i) \cap (X^0) = \emptyset\), where \(W^s(M_i)\) is the stable set of \(M_i\) \((i = 0, 1)\). Suppose to the contrary that \(W^s(M_0) \cap (Y_0 \times Y_0) \neq \emptyset\). Then for a unique solution \((u, v)\) of system (1.5),
\[
\lim_{t \to \infty} u(x, t) = 0 \quad \text{and} \quad \lim_{t \to \infty} v(x, t) = 0
\]
hold uniformly in \(\overline{\Omega}\). Using the fact that for any \(\epsilon \ll 1\), there exists a \(T > 0\) such that
\[
ru(x, t - \tau) - \frac{rKu^2}{1 + k_1u + k_2v} > ru(x, t - \tau) - \frac{rKu^2}{k_2} \quad \text{in} \quad \overline{\Omega} \times [T, \infty),
\]
we obtain
\[
\frac{\partial u}{\partial t} \geq D_u \Delta u + ru(x, t - \tau) - \frac{rKu^2}{k_2}.
\]

Thus, using a comparison argument, \(u(x, t) \geq z(x, t)\) holds in \(\Omega \times [T, \infty)\), where \(z(x, t)\) is the unique solution to
\[
\begin{cases}
\frac{\partial z}{\partial t} = D_z \Delta z + rz(x, t - \tau) - \frac{rKu^2}{k_2} \quad \text{in} \quad \Omega \times [T, \infty), \\
\frac{\partial z}{\partial \nu} = 0 \quad \text{on} \quad \partial \Omega \times [T, \infty), \\
z(x, T) = u(x, T),
\end{cases}
\]
This is a contradiction since \(\lim_{t \to \infty} z(x, t) = K(1 - m/(rk_2))\) uniformly in \(\overline{\Omega}\) by Lemma 2.2. Similarly, a contradiction is reached when \(W^s(M_1) \cap (Y_0 \times Y_0) \neq \emptyset\); specifically, since \((u(x, t), v(x, t)) \rightarrow (K, 0)\) as \(t \to \infty\) uniformly in \(\overline{\Omega}\), for any given \(\epsilon \ll 1\), there exists a \(T > 0\) such that
\[
\frac{nmuv}{1 + k_1u + k_2v} - dv > \left(\frac{nmK}{1 + k_1K} - d - \epsilon\right)v = (d(\mathbb{R}_0 - 1) - \epsilon)v \quad \text{in} \quad \overline{\Omega} \times [T, \infty).
\]
Thus, we have \(W^s(M_i) \cap (Y_0 \times Y_0) = \emptyset\), \(i = 0, 1\). Therefore, according to Theorem 4.1 in [7], system (1.5) is uniformly persistent. Furthermore, Theorem 2.3 shows that \((u, v)\) is ultimately bounded; this proves the permanence of system (1.5). \(\square\)

3. Local stability of solutions. In this section, we examine the locally asymptotic stability at equilibria \(E_0 = (0, 0), E_1 = (K, 0), \) and \(E^* = (u^*, v^*)\).

Throughout the remainder of this paper, we use the following notations.

**Notation 3.1.** (i) \(0 = \mu_0 < \mu_1 < \mu_2 < \cdots \to \infty\) are the eigenvalues of \(-\Delta\) in \(\Omega\) under homogeneous Neumann boundary conditions. (ii) \(S(\mu_i)\) is the space of eigenfunctions corresponding to \(\mu_i\).

(iii) \(X_{ij} := \{c \cdot \varphi_{ij} : c \in \mathbb{R}^2\}\), where \(\{\varphi_{ij}\}\) is an orthonormal basis of \(S(\mu_i)\) for \(j = 1, \cdots, \dim S(\mu_i)\).

(iv) \(X := \{u = (u, v) \in [C^1(\Omega)]^2 : \frac{\partial u}{\partial \eta} = \frac{\partial v}{\partial \eta} = 0 \text{ on } \partial \Omega\}\); hence, \(X = \bigoplus_{i=0}^{\infty} X_i\), where \(X_i = \bigoplus_{j=1}^{\dim S(\mu_i)} X_{ij}\).
Thus, if the characteristic equation of system (1.5) at any feasible equilibrium point \( \bar{E} \) can be expressed by \( u_i = (D\Delta + F_u(\bar{E}) + F_{u_r}(\bar{E})e^{-\lambda \tau})u_i \), where

\[
F_u(\bar{E}) = \left( \frac{\partial F}{\partial u} \right)_E = \begin{pmatrix} -\frac{2r}{K}u - q_u & -q_v \\ nq_u & nq_v - d \end{pmatrix}, \quad F_{u_r}(\bar{E}) = \left( \frac{\partial F}{\partial u_r} \right)_E = \begin{pmatrix} r \\ 0 \\ 0 \end{pmatrix}
\]

and \( F = (ru(x,t - \tau) - (r/K)u^2 - q(u,v), nq(u,v) - dv) \).

For each \( i \geq 0 \), \( X_i \) is invariant under the operator \( D\Delta + F_u(\bar{E}) + F_{u_r}(\bar{E})e^{-\lambda \tau} \). Moreover, \( \lambda \) is an eigenvalue of \( D\Delta + F_u(\bar{E}) + F_{u_r}(\bar{E})e^{-\lambda \tau} \) on \( X_i \) if and only if it is an eigenvalue of the matrix \( -\mu_i D + F_u(\bar{E}) + F_{u_r}(\bar{E})e^{-\lambda \tau} \). Thus, the characteristic equation of system (1.5) at equilibrium \( \bar{E} \) takes the following form:

\[
\det(F_u(\bar{E}) + F_{u_r}(\bar{E})e^{-\lambda \tau} - \mu_i D - \lambda I) = 0. \tag{3.1}
\]

We now investigate the locally asymptotical stability of (1.5) at \( E_1 = (K,0) \).

**Theorem 3.2.** If \( \Re_0 < 1 \), i.e.,

\[
\tau > \tau_0 := \frac{1}{d_i} \ln \left( \frac{nm - dk_1}{da} \right), \tag{3.2}
\]

where \( nm - dk_1 > 0 \), then the equilibrium \( E_1 = (K,0) \) of system (1.5) is locally asymptotically stable.

**Proof.** The characteristic equation (3.1) of system (1.5) at \( E_1 \) is given by

\[
H(K,0)(\lambda) := (\lambda - re^{-\lambda \tau} + 2r + \mu_k D_u) \left( \lambda - \frac{nmK}{1 + k_1 K} + d + \mu_k D_v \right) = 0.
\]

Since \( \Re_0 < 1 \) by assumption, \( nmK/(1 + k_1 K) - d < 0 \). Thus \( \lambda = nmK/(1 + k_1 K) - d - \mu_k D_v < 0 \), which implies \( H(K,0)(\lambda) = 0 \) has at least one real negative root. Let

\[
H_1(\lambda) = \lambda - re^{-\lambda \tau} + 2r + \mu_k D_u.
\]

If \( \lambda = \alpha + i\beta \) is a root of \( H_1(\lambda) = 0 \) for \( \alpha, \beta \in \mathbb{R} \), then

\[
-2r + re^{-(\alpha + \beta i)\tau} - \mu_k D_u = \alpha + \beta i.
\]

Thus,

\[
\alpha + 2r + \mu_k D_u = re^{-\alpha \tau} \cos(\beta \tau) \quad \text{and} \quad -\beta = re^{-\alpha \tau} \sin(\beta \tau). \tag{3.3}
\]

Squaring and adding the two equations in (3.3) yields

\[
(\alpha + 2r + \mu_k D_u)^2 + \beta^2 = r^2(e^{-\alpha \tau})^2,
\]

which implies

\[
(\alpha + 2r + \mu_k D_u - re^{-\alpha \tau})(\alpha + 2r + \mu_k D_u + re^{-\alpha \tau}) \leq 0. \tag{3.4}
\]
Now, assume that $H_1(\lambda) = 0$ has a root with nonnegative real parts, i.e., $\alpha \geq 0$. It is easy to verify that $\alpha + 2r + \mu_kD_u \pm re^{-\alpha\tau} > 0$ for all $\alpha \geq 0$, which is a contradiction. Therefore, all roots of $H_1(\lambda) = 0$ have negative real parts, which completes the proof. \hfill \Box

**Remark 3.3.** If $da > (nm - dk_1)b$ when $nm > dk_1$, then the predator-free state $(\frac{b}{\tau}, 0)$ for model (1.5) with no time delay is locally asymptotically stable. Under the same assumption (i.e., $da > (nm - dk_1)b$ with $nm > dk_1$), the state $(K, 0)$ of model (1.5) is always asymptotically stable. On the contrary, if $da < (nm - dk_1)b$, then $(K, 0)$ of model (1.5) satisfying $\tau < \tau_0$ is unstable in some eigenmode. However, a large time delay $\tau$ satisfying (3.2) makes (1.5) locally asymptotically stable.

**Remark 3.4.** Note $H(0, 0)(\lambda) = (\lambda - re^{-\lambda\tau} + \mu_kD_u)(\lambda + d + \mu_kD_v) = 0$. Thus, the trivial solution $(0, 0)$ is unstable in some eigenmode since $re^{-\lambda\tau} - \mu_kD_u > 0$ for some $k > 0$.

Finally, we obtain the following theorem which provide sufficient conditions for the locally asymptotical stability of system (1.5) at $E^* = (u^*, v^*)$.

**Theorem 3.5.** Assume $\Re_0 > 1$. If

$$k_1 \geq \frac{mn}{2d} \quad \text{and} \quad k_2 \geq \min\left\{\frac{m}{\tau}, \frac{2nm^2}{d(nm - dk_1)}\right\},$$

then the positive constant equilibrium $E^*$ of system (1.5) is locally asymptotically stable.

**Proof.** We have already seen that $E^*$ exists if $\Re_0 > 1$. The characteristic equation (3.1) of system (1.5) at $E^*$ reduces to

$$H(E^*)(\lambda) := (\lambda + \frac{2r}{K}u^* + q_{uv} - re^{-\lambda\tau} + \mu_kD_u)(\lambda - nq_{uv} + d + \mu_kD_v) + nq_{uv}q_{uv} = 0. \quad (3.5)$$

When $\lambda = \alpha + \beta i$ for $\alpha, \beta \in \mathbb{R}$, if the real and imaginary parts are separated, we have

$$\begin{align*}
(2au^* + q_{uv} - re^{-\alpha\tau} \cos(\beta\tau) + \mu_kD_u + \alpha)(-nq_{uv} + d + \mu_kD_v + \alpha) \\
- \beta re^{-\alpha\tau} \sin(\beta\tau) - \beta^2 + nq_{uv}q_{uv} = 0, \\
re^{-\alpha\tau} \sin(\beta\tau)(-nq_{uv} + d + \mu_kD_v + \alpha) \\
+ \beta[2au^* + q_{uv} - re^{-\alpha\tau} \cos(\beta\tau) + \mu_kD_u + \alpha - nq_{uv} + d + \mu_kD_v + \alpha] = 0. \quad (3.6)
\end{align*}$$

For simplicity, let

$$A = 2au^* + q_{uv} + \mu_kD_u + \alpha \quad \text{and} \quad B = -nq_{uv} + d + \mu_kD_v + \alpha.$$

Squaring and adding (3.6) and (3.7) yields

$$A^2 B^2 - 2AB(\beta^2 - nq_{uv}q_{uv}) + (\beta^2 - nq_{uv}q_{uv})^2 + \beta^2(A + B)^2 = (re^{-\alpha\tau})^2(\beta^2 + B^2).$$

Thus, we obtain

$$\beta^4 + Q_1(\alpha)\beta^2 + Q_0(\alpha) = 0, \quad (3.8)$$

where

$$Q_1(\alpha) = (A + B)^2 - 2AB - 2nq_{uv}q_{uv} - (re^{-\alpha\tau})^2$$

$$= ((2au^* + q_{uv} + \mu_kD_u + 2\alpha - nq_{uv} + d + \mu_kD_v)^2$$

$$- 2(2au^* + q_{uv} + \mu_kD_u + \alpha)(-nq_{uv} + d + \mu_kD_v + \alpha) - 2nq_{uv}q_{uv}) - r^2(e^{-\alpha\tau})^2.$$
and

\[ Q_0(\alpha) = (AB)^2 + 2ABnq_*q_{v^*} + (nq_*q_{v^*})^2 - r^2(e^{-\alpha})^2B^2 \]

\[ = (2au^* + q_{u^*} + \mu_kDu + \alpha)(-nq_{v^*} + d + \mu_kDv + \alpha)^2 \]

\[ - r^2(e^{-\alpha})^2(-nq_{v^*} + d + \mu_kDv + \alpha)^2 \]

\[ + 2(2au^* + q_{u^*} + \mu_kDu + \alpha)(-nq_{v^*} + d + \mu_kDv + \alpha)(nq_{v^*}q_{u^*}) + (nq_{v^*}q_{u^*})^2. \]

Observe that

\[ Q_0(\alpha) > (-nq_{v^*} + d + \mu_kDv + \alpha)^2(2au^* + q_{u^*} + \mu_kDu + \alpha)^2 - r^2(e^{-\alpha})^2 \]

\[ = (-nq_{v^*} + d + \mu_kDv + \alpha)^2 \]

\[ \cdot (2au^* + q_{u^*} + \mu_kDu + \alpha + re^{-\alpha})(2au^* + q_{u^*} + \mu_kDu + \alpha - re^{-\alpha}) > 0. \]

The last inequality follows from the fact that using \( B = K(dk_1 - nm + nrk_2)/(nrk_2) \), where \( K = \frac{r}{a} \) from (2.4), we obtain

\[ 2au^* - re^{-\alpha} > 2aB - r = 2r \frac{dk_1 - nm + nrk_2}{nrk_2} - r = 2 \frac{dk_1 - nm}{nk_2} + r > 0 \quad (3.9) \]

by the assumptions that \( rk_2 \geq m \) and \( 2dk_1 \geq mn \).

Furthermore, observe that

\[ Q_1(\alpha) = A^2 + B^2 - 2nq_{v^*}q_{v^*} - (re^{-\alpha})^2 \]

\[ = (-nq_{v^*} + d + \mu_kDv + \alpha + \sqrt{2nq_{v^*}q_{v^*}}) \]

\[ \cdot (-nq_{v^*} + d + \mu_kDv + \alpha - \sqrt{2nq_{v^*}q_{v^*}}) \]

\[ + (2au^* + q_{u^*} + \mu_kDu + \alpha + re^{-\alpha})(2au^* + q_{u^*} + \mu_kDu + \alpha - re^{-\alpha}) > 0. \]

Here, \( (2au^* + q_{u^*} + \mu_kDu + \alpha - re^{-\alpha}) > 0 \) follows from assuming \( rk_2 \geq m \) and \( 2dk_1 \geq mn \) as the above case. \( (-nq_{v^*} + d + \mu_kDv + \alpha - \sqrt{2nq_{v^*}q_{v^*}}) > 0 \) holds if

\[ d - nq_{v^*} - \sqrt{2nq_{v^*}q_{v^*}} \geq 0. \quad (3.10) \]

Inequality (3.10) can be simplified by substituting \( u_{v^*} \) and \( q_{v^*} \) in (3.10) as follows:

\[ d - nq_{v^*} - \sqrt{2nq_{v^*}q_{v^*}} = \frac{dk_2v^*}{1 + k_1u^* + k_2v^*} - \sqrt{2n} \frac{\sqrt{mu^*(1 + k_1u^*)} \sqrt{mu^*(1 + k_2v^*)}}{(1 + k_1u^* + k_2v^*)^2} \]

\[ > \frac{(dk_2\sqrt{v^*} - \sqrt{2nm\sqrt{u^*}})(\sqrt{v^*} \sqrt{(1 + k_1u^*)(1 + k_2v^*)})}{(1 + k_1u^* + k_2v^*)^2} \geq 0. \quad (3.11) \]

The last inequality holds if and only if \( dk_2\sqrt{v^*} - \sqrt{2nm\sqrt{u^*}} \geq 0 \). Again, this inequality is equivalent to

\[ k_2^2 \geq \frac{2nm^2 u^*}{d^2 v^*}. \quad (3.13) \]

Using \( \frac{d}{\sqrt{nm - d}} \) and \( u^* > B \) from (2.4), (3.13) can be written as

\[ k_2^2 \geq \frac{2nm^2}{d(nm - dk_1)}. \quad (3.14) \]

Note that \( nm - dk_1 > 0 \) from the assumption that \( \Re_0 > 1 \). Thus, \( Q_0(\alpha) > 0 \) and \( Q_1(\alpha) > 0 \) for all \( \alpha \geq 0 \) and \( \mu_k \geq 0 \). Hence, there is no \( \beta \) satisfying (3.8) for \( \alpha \geq 0 \), which is a contradiction. Therefore all \( \alpha < 0 \), which completes the proof. \( \square \)
4. Global stability of solutions. In this section, we investigate the globally asymptotical stability of the semitrivial solution \((K, 0)\) and positive constant solution \((u^*, v^*)\).

First, we investigate the behavior of solutions to (1.5) at the semitrivial solution \(E_1 = (K, 0)\).

Theorem 4.1. If \(R_0 \leq 1\), then for given initial functions \(u(x, \theta)\) and \(v(x, \theta)\) in \(\Omega \times [-\tau, 0]\) with \(u(x, 0) \neq 0\) and \(v(x, 0) \neq 0\), the solution \((u(t), v(t))\) of system (1.5) uniformly converges to \(E_1\) on \(\Omega\) as \(t \to \infty\). Furthermore, the semitrivial uniform steady state \((B, K, 0)\) of system (1.1) is globally asymptotically stable, where \(B := (bK/d_i)(1 - e^{-d_i \tau})\).

Proof. First, we consider the case when \(R_0 < 1\). We can select a sufficiently small positive constant \(\epsilon\) such that \(\frac{nm(K + \epsilon)}{1 + k_1 (K + \epsilon)} \leq d\). Using the comparison argument of parabolic problems and Lemma 2.2, we obtain \(\limsup_{t \to \infty} u(x, t) \leq K\). Thus, there exists \(T_1 \in (0, \infty)\) such that \(u(x, t) \leq K + \epsilon\) in \(\Omega \times [T_1, \infty)\). Therefore, the second equation of (1.5) satisfies

\[
v_t - D_u \Delta v = \frac{nmuv}{1 + k_1 u + k_2 v} - dv \\
\leq v \left( \frac{nm(K + \epsilon)}{1 + k_1 (K + \epsilon)} - d \right) \leq 0 \quad \text{in} \quad \Omega \times [T_1, \infty).
\]

The comparison argument yields

\[
\lim_{t \to \infty} v(x, t) = 0 \quad \text{in} \quad \Omega.
\]

This implies that there exists \(T_2 \in [T_1, \infty)\) such that \(v(x, t) \leq \epsilon\) in \([T_2, \infty)\) which yields

\[
u_t - D_u \Delta u = ru(x, t - \tau) - \frac{r}{K} u^2 - \frac{nmuv}{1 + k_1 u + k_2 v} \\
\geq ru(x, t - \tau) - \frac{r}{K} u^2 - cmu \quad \text{in} \quad \Omega \times [T_2, \infty).
\]

Since the existence of \(T_3 \in [T_2, \infty)\) when \(u(x, t) \geq K(1 - \frac{m}{r}\epsilon) - \epsilon\) in \(\Omega \times [T_3, \infty)\) yields \(\liminf_{t \to \infty} u(x, t) \geq K\) from the arbitrariness of the small positive constant \(\epsilon\), we can apply the comparison argument once again to obtain

\[
\lim_{t \to \infty} u(x, t) = K \quad \text{in} \quad \Omega.
\]

Second, we consider the case when \(R_0 = 1\), i.e., \(\frac{nmK}{1 + k_1 K} = d\). If \(\frac{nm(K + \epsilon)}{1 + k_1 (K + \epsilon)} > d\), then

\[
v_t - D_u \Delta v = \frac{nmuv}{1 + k_1 u + k_2 v} - dv \\
\leq v \left( \frac{nm(K + \epsilon)}{1 + k_1 (K + \epsilon) + k_2 v} - d \right) \\
\leq v[\frac{nm(K + \epsilon)}{1 + k_1 (K + \epsilon)} - d\{1 + k_1 (K + \epsilon)\} - dk_2 v] \quad \text{in} \quad \Omega \times [T_1, \infty).
\]

Again, from the comparison argument,

\[
\lim_{t \to \infty} v(x, t) = 0 \quad \text{in} \quad \Omega.
\]

because there exists \(T_2 \in [T_1, \infty)\) such that \(v(x, t) \leq \frac{(nm(K + \epsilon) - d\{1 + k_1 (K + \epsilon)\})}{dk_2}\) in \([T_2, \infty)\). Using the fact that \(\frac{nmK}{1 + k_1 K} = d\) and letting \(\epsilon \to 0\) yields \(\limsup_{t \to \infty} v(x, t) \leq \)
0. Following the same argument as in the first case of this proof yields the same conclusion, i.e.,
\[
\lim_{t \to \infty} u(x, t) = K \text{ in } \Omega.
\]

Furthermore, from (1.3), it is easy to see that \( \lim_{t \to \infty} u_i(x, t) = B \) in \( \Omega \), where \( B := \frac{bK}{d_i}(1 - e^{-d_i \tau}) = \frac{bK}{d_i}(1 - e^{-d_i \tau}) \). Therefore, \( E_1 \) is globally asymptotically stable, i.e., \((K, 0)\) attracts every positive solution of system (1.5).

Next, we give a sufficient condition for the globally asymptotical stability at positive equilibrium \( E^* = (u^*, v^*) \) of system (1.5).

**Theorem 4.2.** Assume \( \Re_0 > 1 \) and \( ak_2 \geq mk_1 \). Then
\[
\lim_{t \to \infty} (u(x, t), v(x, t)) = E^* \text{ uniformly for } x \in \Omega.
\]

**Proof.** Since \( \Re_0 > 1 \), there exists a unique positive equilibrium \( E^* = (u^*, v^*) \) of system (1.5) satisfying
\[
r - \frac{r}{K} u^* - \frac{mv^*}{1 + k_1 u^* + k_2 v^*} = 0, \quad \frac{nmu^*}{1 + k_1 u^* + k_2 v^*} - d = 0.
\]

Define \( H(x) = x - \ln x - 1 \) for all \( x > 0 \). Then \( H(x) \geq 0 \) and \( H(x) = 0 \) if \( x = 1 \). Consider the Lyapunov function:
\[
W(t) = \int_{\Omega} \left( V_1(u) + C_1 V_2(v) + C_2 V_3(u) \right) dx,
\]
where
\[
V_1(u) = \int_{u}\frac{\xi - u^*}{\xi} d\xi, \quad V_2(v) = \int_{v}\frac{\eta - v^*}{\eta} d\eta, \quad V_3(u) = \int_{t-\tau}^{t} H\left(\frac{u(x,s)}{u^*}\right) ds,
\]
and
\[
C_1 = \frac{1 + k_1 u^*}{n(1 + k_2 v^*)}, \quad C_2 = ru^*.
\]

along the positive bounded solution \((u, v) \in [C(\Omega \times [-\tau, 0]; \mathbb{R}^+)]^2 \) of (1.5). Thus, \( W(t) \geq 0 \). Integrating the derivative of \( V_1 \) along the positive solution \((u, v) \) of (1.5) yields
\[
\int_{\Omega} \frac{dV_1}{dt} dx = -\int_{\Omega} \left( \frac{u - u^*}{u} \right) u_i dx
\]
\[
= -\int_{\Omega} D_u u^* \left( \frac{\nabla u^2}{u^2} \right) dx + \int_{\Omega} \left( 1 - \frac{u^*}{u} \right) (ru(x, t - \tau) - \frac{r}{K} u^2 - \frac{mu}{1 + k_1 u + k_2 v}) dx
\]
\[
= -\int_{\Omega} D_u u^* \left( \frac{\nabla u^2}{u^2} \right) dx + \int_{\Omega} \left( 1 - \frac{u^*}{u} \right) (ru(x, t - \tau) - ru - \frac{mu}{1 + k_1 u + k_2 v}) dx
\]
\[
+ \int_{\Omega} \left( 1 - \frac{u^*}{u} \right) \left( ru - \frac{r}{K} u^2 - \frac{mu}{1 + k_1 u + k_2 v} \right) dx.
\]
The last term of (4.2) can be rewritten as
\[
\int_{\Omega} \left( 1 - \frac{u^*}{u} \right) \left( ru - \frac{r}{K} u^2 - \frac{mv}{1 + k_1 u + k_2 v} \right) dx \tag{4.3}
\]
\[
= \int_{\Omega} \left( u - u^* \right) \frac{r}{K} u^* + \frac{mv}{1 + k_1 u + k_2 v} - \frac{r}{K} u - \frac{mv}{1 + k_1 u + k_2 v} dx
\]
\[
= \int_{\Omega} \left( u - u^* \right) \left[ - \frac{r}{K} (u - u^*) + \frac{m}{1 + k_1 u + k_2 v} \right] dx
\]
\[
= - \int_{\Omega} \left( u - u^* \right) \left[ \frac{r}{K} - \frac{m k_1 u^*}{(1 + k_1 u + k_2 v)(1 + k_1 u^* + k_2 v^*)} \right] dx
\]
\[
- \int_{\Omega} m (1 + k_1 u^*)(u - u^*)(v - v^*) dx.
\]
We also calculate the derivative of the second and third terms in (4.1) along the positive solution \((u, v)\) of (1.5), which yields
\[
\int_{\Omega} \frac{dV_2}{dt} dx = \int_{\Omega} \left( \frac{v - v^*}{v} \right) v dx
\]
\[
= - \int_{\Omega} d_v v^* \frac{\nabla v^2}{v^2} dx + \int_{\Omega} \left( 1 - \frac{v}{v^*} \right) \left( \frac{nmuv}{1 + k_1 u + k_2 v} - dv \right) dx \tag{4.4}
\]
\[
= - \int_{\Omega} d_v v^* \frac{\nabla v^2}{v^2} dx + \int_{\Omega} \left( v - v^* \right) \left( \frac{nmu}{1 + k_1 u + k_2 v} - \frac{nmv^*}{1 + k_1 u^* + k_2 v^*} \right) dx
\]
\[
= - \int_{\Omega} d_v v^* \frac{\nabla v^2}{v^2} dx - \int_{\Omega} \frac{nmk_2 u^*(v - v^*)^2 - nm(1 + k_2 v^*)(u - u^*)(v - v^*)}{(1 + k_1 u + k_2 v)(1 + k_1 u^* + k_2 v^*)} dx.
\]
and
\[
\int_{\Omega} \frac{dV_3}{dt} dx = \int_{\Omega} \left[ H \left( \frac{u}{u^*} \right) - H \left( \frac{u(x, t - \tau)}{u^*} \right) \right] dx
\]
\[
= \int_{\Omega} \left( \frac{u}{u^*} - \frac{u(x, t - \tau)}{u^*} \right) dx - \ln \left( \frac{u}{u(x, t - \tau)} \right) dx. \tag{4.5}
\]
Combining the results of (4.2), (4.3), (4.4), and (4.5) produces the following derivative of (4.1):
\[
\frac{dW}{dt} = \int_{\Omega} \left( \frac{dV_1}{dt} + C_1 \frac{dV_2}{dt} + C_2 \frac{dV_3}{dt} \right) dx
\]
\[
= \int_{\Omega} d_v u^* \frac{\nabla u^2}{u^2} dx + \int_{\Omega} \left( ru(x, t - \tau) - ru - ru^* \frac{u(x, t - \tau)}{u} + ru^* \right) dx
\]
\[
- \int_{\Omega} (u - u^*) \frac{r}{K} \left[ \frac{m k_1 v^*}{(1 + k_1 u + k_2 v)(1 + k_1 u^* + k_2 v^*)} \right] dx
\]
\[
- \int_{\Omega} m (1 + k_1 u^*)(u - u^*)(v - v^*) dx - \int_{\Omega} C_1 d_v v^* \frac{\nabla v^2}{v^2} dx
\]
\[
- \int_{\Omega} \left( C_1 nmk_2 u^*(v - v^*)^2 - C_1 nm(1 + k_2 v^*)(u - u^*)(v - v^*) \right) dx
\]
\[
+ \int_{\Omega} \left( C_2 \frac{u}{u^*} - \frac{u(x, t - \tau)}{u^*} - \ln \frac{u}{u(x, t - \tau)} \right) dx. \tag{4.6}
\]
Since the last term of (4.7) satisfies globally asymptotically stable provided asymptotically stable provided \( \tau \) or high juvenile prey mortality rate

\[ \tau > \frac{1}{k} \]

5. Biological interpretations. In this paper, we studied the asymptotic properties of a diffusive delayed predator-prey model with a Beddington-DeAngelis functional response under homogeneous Neumann boundary conditions. The discrete time delay was assumed to cover the time between birth and maturity of prey.

First, we obtained sufficient conditions for the permanence and extinction of predators for system (1.5). Theorem 2.4 established that predator and prey coexist permanently if

\[ \frac{nmb}{(ae^{d_1\tau} + k_1b)} > d \quad \text{and} \quad k_2 > \frac{m}{b}e^{d_1\tau}. \]

The conditions imply that the predator recruitment rate at the peak of prey abundance which is greater than its death helps the persistence of system (1.5). Furthermore, we found that large magnitude of interference among predators \( k_2 \) played a role in the persistence of system (1.5) and that its ability to satisfy the conditions was contingent upon the choice of \( \tau \).

By Theorem 4.1, the semitrivial solution \((K, 0) = (\frac{be^{-d_1\tau}}{a}, 0)\) was found to be globally asymptotically stable provided

\[ \frac{nmb}{(ae^{d_1\tau} + k_1b)} \leq d. \]

This implies that if the predator death rate \( d \) is high or if the predator birth rate \( n \) is low, the only predator may be extinct. Predators may be driven into extinction by a decreased prey carrying capacity \( K = be^{-d_1\tau} \), due to either a large prey maturation \( \tau \) or high juvenile prey morality rate \( d_1 \).

From Theorem 4.2, the coexistence equilibrium \((u^*, v^*)\) was found to be globally asymptotically stable provided

\[ \frac{nmb}{(ae^{d_1\tau} + k_1b)} > d, \quad k_2 \geq \frac{mk_1}{a}. \]
The conditions imply that sufficiently large mutual interference $k_2$ between predators has the ability to stabilize system (1.5).

Acknowledgements. The authors thank the anonymous referee for careful reading and valuable comments which have helped to improve the presentation of this paper. This research was supported by Basic Science Research Program through the National Research Foundation of Korea(NRF) funded by the Ministry of Science, ICT & Future Planning(NRF-2015R1A2A2A01007013).

REFERENCES

[1] R. Arditi and J. Michalski, Nonlinear food web models and their responses to increased basal productivity, in Food Webs: Integration of Patterns and Dynamics (G. A. Polis and K. O. Winemiller eds.), Chapman and Hall, London, (1995), 122–133.

[2] U. Brose, R. J. Williams and N. D. Martinez, Comment on “Foraging adaptation and the relationship between food-web complexity and stability”, Science, 301 (2003), 916b.

[3] G. Caristi, K. P. Rybakowski and T. Wessolek, Persistence and spatial patterns in a one-predator-two-prey Lotka-Volterra model with diffusion, Annali di Mathematica Pura ed Applicata, 161 (1992), 345–377.

[4] W. Chen and M. Wang, Qualitative analysis of predator-prey models with Beddington-DeAngelis functional response and diffusion, Math. Comp. Modelling, 42 (2005), 31–44.

[5] B. Drossel, P. G. Higgs and A. J. McKane, The influence of predator-prey population dynamics on the long-term evolution of food web structure, J. Theor. Biol., 208 (2001), 91–107.

[6] Y. Du and Y. Lou, Qualitative behavior of positive solutions of a predator-prey model: effects of saturation, Proc. Roy. Soc. Edinburgh Sect. A, 131 (2001), 321–349.

[7] J. K. Hale and P. Waltman, Persistence in infinite-dimensional systems, SIAM J. Math. Anal., 20 (1989), 388–395.

[8] E. E. Holmes, M. A. Lewis, J. E. Banks and R. R. Veit, Partial differential equations in ecology: spatial interactions and population dynamics, Ecology, 75 (1994), 17–29.

[9] D. Kesh, A. K. Sarkar and A. B. Roy, Persistence of two prey-one predator system with ratio-dependent predator influence, Math. Meth. Appl. Sci., 23 (2000), 347–356.

[10] W. Ko and I. Ahn, Analysis of ratio-dependent food chain model, J. Math. Anal. Appl., 335 (2007), 498–523.

[11] W. Ko and I. Ahn, Local stability and bifurcation of a general diffusive consumer-resource model with maturation delay, preprint.

[12] W. Ko, S. Liu and I. Ahn, Asymptotical behaviors of a general diffusive consumer-resource model with maturation delay, Discrete Contin. Dyn. Syst. Ser. B, 20 (2015), 1715–1733.

[13] W. Ko and K. Ryu, Qualitative analysis of a predator-prey model with Holling type II functional response incorporating a prey refuge, J. Differential Equations, 231 (2006), 534–550.

[14] Z. Lin, Time delayed parabolic system in a two-species competitive model with stage structure, J. Math. Anal. Appl., 315 (2006), 202–215.

[15] S. Liu and E. Beretta, A stage-structured predator-prey model with the Beddington-DeAngelis type, SIAM J. Appl. Math., 66 (2006), 1101–1129.

[16] S. Liu and J. Zhang, Coexistence and stability of predator-prey model with Beddington-DeAngelis functional response and stage structure, J. Math. Anal. Appl., 342 (2008), 446–460.

[17] R. M. May, Stability and complexity in model ecosystems, IEEE Transactions on Systems, Man, and Cybernetics, 6 (1976), p887.

[18] J. D. Murray, Mathematical Biology I: An Introduction, 3rd edition, Interdisciplinary Applied Mathematics, vol. 17, Springer, New York, 2002.

[19] J. D. Murray, Mathematical Biology II: Spatial Models and Biomedical Applications, 3rd edition, Interdisciplinary Applied Mathematics, vol. 18, Springer, New York, 2003.

[20] A. Okubo and S. A. Levin, Diffusion and Ecological Problems: Modern Perspectives, 2nd edition, Interdisciplinary Applied Mathematics, Springer, New York, 2001.

[21] C. V. Pao, Dynamics of nonlinear parabolic systems with time delays, J. Math. Anal. Appl., 198 (1996), 751–779.

[22] S. Ruan and X.-Q. Zhao, Persistence and extinction in two species reaction-diffusion systems with delays, J. Differential Equations, 156 (1999), 71–92.
[23] H. L. Smith, The interaction of steady state and Hopf bifurcations in a two-predator–one-prey competition model, *SIAM J. Appl. Math.*, 42 (1982), 27–43.

[24] D. Xu and X.-Q. Zhao, A nonlocal reaction-diffusion population model with stage structure, *Canad. Appl. Math. Quart.*, 11 (2003), 303–319.

[25] R. Xu, Global convergence of a predator-prey model with stage structure and spatio-temporal delay, *Discrete Contin. Dyn. Syst. Ser. B*, 5 (2011), 273–291.

[26] T. Yi and X. Zou, Map dynamics versus dynamics of associated delay reaction-diffusion equations with a Neumann condition, *Proc. R. Soc. A*, 466 (2010), 2955–2973.

Received February 2016; revised November 2016.

E-mail address: imp57@korea.ac.kr
E-mail address: ahnik@korea.ac.kr