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Research Article

Traveling Waves in a Diffusive Predator-Prey Model Incorporating a Prey Refuge

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We establish the existence of traveling wave solutions and small amplitude traveling wave train solutions for a reaction-diffusion system based on a predator-prey model incorporating a prey refuge. By using the shooting argument, invariant manifold theory, and the Hopf bifurcation theorem, we analyze the dynamic behavior of this model in the three-dimensional phase space. Numerical results are also presented to illustrate the theoretical results.

1. Introduction

In mathematical biology, one interesting and dominant theme is the dynamic relationship between predators and their prey [1–3]. Predator-prey models have been studied mathematically since the pioneering work of Lotka and Volterra. In recent years, Leslie-Gower model [4, 5], an important predator-prey model, has been extensively modified and studied by many authors [6–11]. A modified Leslie-Gower predator-prey model is read as

$$\begin{aligned} \frac{\mathrm{d}H}{\mathrm{d}t} &= H(r - aH) - \frac{\beta_1 HP}{b + H}, \\ \frac{\mathrm{d}P}{\mathrm{d}t} &= P\left(d - \frac{\beta_2 P}{b + H}\right), \end{aligned} \tag{1}$$

where function values H and P represent prey and predator population densities, respectively, at any time t. The model parameters r, a, b, β_1, β_2, and d are positive constants. r describes the growth rate of prey H. a measures the strength of competition among individuals of species H. b measures the extent to which environment provides protection to prey H. d is the growth rate of predators P. β_1 is the maximum value of per capita reduction of H due to P. β_2 has a similar meaning to β_1.

As the authors of [6] said, we live in a spatial world, and spatial component of ecological interaction has been identified as an important factor in how ecological communities are shaped. Mite predator-prey interactions often exhibit spatial refugia, which means the prey received some degree of protection from predation and reduces the chance of extinction due to predation [6, 9–15]. A great deal of researches on the effects of prey refuges on the population dynamic has been studied. Kar [12] indicated that the increasing refuge can increase prey densities and lead to population outbreaks. Chen et al. [9] showed that the prey refuge could greatly influence the densities of both prey and predator species, while it has no influence on the species' persistence property. In [13–15] it was obtained that the refuges protecting a constant number of prey have a stronger stabilizing effect on population dynamic than the refuges protecting a constant proportion of prey.

On the other hand, the existence of traveling solutions has been wildly studied by many researchers [16–24]. A traveling wave solution is a spatial translation invariant solution of differential equations with spatial-diffusion. Dunbar [16] proved the existence of traveling wave solutions of diffusive Lotka-Volterra and used the methods of a shooting argument and a Lyapunov function. Zhang [19] showed the existence of traveling wave solutions in a modified vector-disease model by using the geometric singular perturbation theory. Hou and Leung [20] used the method of upper-lower solutions to prove the existence of traveling solutions of a competitive reaction-diffusive system. Ahmad et al. [21, 22] used only functional analysis, without constructing a Lyapunov function, to prove the existence of such solutions for a class of reaction-diffusion equations. Huang et al. [23] and Li and Wu [24] used Dunbar' method to study the existence of traveling solutions of diffusive predator-prey models with Holling type-II and Holling type-III, respectively.

In this paper, based on the above discussion, we are interested in the existence of traveling wave solutions of a reaction-diffusion Leslie-Gower-type model incorporating a prey refuge, which is modified from model (1). Taking $P^{*} = \beta_1 P$, $\beta = \beta_2/\beta_1$ and dropping the stars on P, we will extend model (1) by incorporating a prey refuge into the following system:

$$\begin{aligned}\frac{\partial H}{\partial t} &= D_1 \Delta H + H(r - aH) - \frac{(1-m)HP}{b+(1-m)H},\\ \frac{\partial P}{\partial t} &= D_2 \Delta P + P\left(d - \frac{\beta P}{b+(1-m)H}\right),\end{aligned} \tag{2}$$

where $\Delta = \nabla^2 = (\partial^2/\partial x^2 + \partial^2/\partial y^2)$ is the usual Laplacian operator in two-dimensional space. D_1 and D_2 are the diffusion coefficients of prey and predator, respectively. $m \in [0,1)$ is constant. mH is a refuge protecting of the prey, which means $(1-m)H$ of prey available to the predator. To ensure system (2) has a positive equilibrium point, we require that $r > d(1-m)$. Obviously, system (2) has four equilibrium points:

$$E_0(0,0), \quad E_1\left(\frac{r}{a}, 0\right), \quad E_2\left(0, \frac{ab}{\beta}\right), \quad E(H^*, P^*), \tag{3}$$

where

$$\begin{aligned}H^* &= \frac{dm - d + \beta r}{a\beta},\\ P^* &= \frac{abd\beta + (dm - d + \beta r)(1-m)d}{a\beta^2}\\ &= \frac{d(b + (1-m)H^*)}{\beta}.\end{aligned} \tag{4}$$

The equilibrium point E_0 corresponds to absence of both species, E_1 corresponds to the prey at the environment carrying capacity in the absence of the predator, E_2 means the extinct of prey, and E corresponds to coexistence of the two species. From [6], we know E_0 and E_1 are two saddle points and E is globally asymptotical stable when $dH^*(1-m)^3 < ad\beta(b+(1-m)H^*)$, which indicates that system (2) may have traveling waves.

For mathematical simplicity, we assume that $D_1 = 0$ (considered as the D_1 is sufficient small which indicates the prey disperse very slowly relative to the mobile herbivore predator [16]). Then system (2) can be converted to the system:

$$\begin{aligned}\frac{\partial H}{\partial t} &= H(r - aH) - \frac{(1-m)HP}{b+(1-m)H},\\ \frac{\partial P}{\partial t} &= D\Delta P + P\left(d - \frac{\beta P}{b+(1-m)H}\right).\end{aligned} \tag{5}$$

We will establish the existence of traveling wave solutions and small amplitude traveling wave train solutions of this system. The method used here is a shooting argument in $\mathbb{R}^3$ together with a Lyapunov function, LaSalle's invariant principle, and Hopf bifurcation theorem.

Remark that although the methods we use to prove the existence are similar to these in [16, 23, 24], there are several differences. For one thing, it is a different model, a modified Leslie-Gower model incorporating a prey refuge. For the other thing, we construct a different Wazewski set W and a new Lyapunov function [25–27].

The rest of the paper is organized as follows. In Section 2, main results on the existence of traveling wave solutions and small amplitude wave train solutions are stated. In Section 3, we give the proofs of the main results. In Section 4, some numerical results are presented.

2. Main Results

A traveling wave solution is a spatial translation invariant solution. In order to establish the existence of traveling wave solutions of system (5), we assume the system has a solution of the special form $H(x,t) = H(x+ct)$, $P(x,t) = P(x+ct)$, where parameter $c(> 0)$ is the wave speed. Substituting $H(x,t) = H(s)$, $P(x,t) = P(s)$, $s = x + ct$ into (5), the corresponding wave equations become

$$\begin{aligned}cH' &= H(r - aH) - \frac{(1-m)HP}{b+(1-m)H},\\ cP' &= DP'' + P\left(d - \frac{\beta P}{b+(1-m)H}\right).\end{aligned} \tag{6}$$

Here ($'$) denotes the differentiation with respect to the traveling wave variable s. Due to ecological motivation, we require that the traveling wave solutions H and P are nonnegative and satisfying the following boundary conditions:

$$\begin{aligned}H(-\infty) &= \frac{r}{a}, \qquad H(+\infty) = H^*,\\ P(-\infty) &= 0, \qquad P(+\infty) = P^*.\end{aligned} \tag{7}$$

Rewrite the system (6) as a system of first order equation in $\mathbb{R}^3$:

$$\begin{aligned}H' &= \frac{1}{c}H(r - aH) - \frac{1}{c}\frac{(1-m)HP}{b+(1-m)H},\\ P' &= U,\\ U' &= \frac{c}{D}U - \frac{1}{D}P\left(d - \frac{\beta P}{b+(1-m)H}\right).\end{aligned} \tag{8}$$

Lemma 1. *Let $f(H) = (r - aH)(b + (1-m)H) - (1-m)P^*$, and then $f(H^*) = 0$ and $f(H) = 0$ has two real roots when $r > ((d(1-m))/\beta)$ (i.e., $br - (1-m)P^* > 0$). Furthermore, the following results hold:*

(a) *if $0 < H < H^*$, then $f(H) > 0$;*

(b) *if $H > H^*$, then $f(H) < 0$.*

Now we state the main results as follows.

Theorem 2. *(i) If $0 < c < \sqrt{4Dd}$, then there are no nonnegative solutions of system* (8) *satisfying the boundary conditions* (7).

(ii) If $c > \sqrt{4Dd}$, $r > ((d(1-m))/\beta)$, then there are nonnegative solutions of system (8) *satisfying the boundary conditions* (7), *which correspond to traveling wave solutions of system* (5).

Theorem 3. *Let $P(\lambda) = \lambda^3 - (M/c + c/D)\lambda^2 + ((M-d)/D)\lambda - (adH^*/cD) = 0$, where $M = -aH^* + ((1-m)^2 H^* d^2/\beta^2 P^*)$.*

(a) *If $P(\lambda)_{maximum} < 0$, then H, P spreads to the positive equilibrium point (H^*, P^*) nonmonotonously for traveling wave variable s.*

(b) *If $P(\lambda)_{maximum} \geq 0$, then H, P spreads to the positive equilibrium point (H^*, P^*) monotonously for traveling wave variable s.*

Theorem 4. *Let $p = M - d$ and $q = adH^*$. If*

$$\max\left\{(1-m), \frac{d(1-m)}{r}\right\} < \beta < \frac{abd(1-m)^2}{(r(1-m) + (3/2)ab)^2}, \tag{9}$$

then, as the parameter β crosses the bifurcation curve $c^2 = D[q/p - p - d]$ at β_0 in the (β, c)-parameter plane, system (8) *undergoes a Hopf bifurcation to a small amplitude periodic solution at the equilibrium point $(H^*, P^*, 0)$, which corresponds to a small amplitude traveling wave train solution of system* (5).

3. Proofs of the Main Results

3.1. Proof of Theorem 2. In this section, we subdivide the proof into several Sections 3.1.1–3.1.4 for convenience. In Section 3.1.1, we recall some notations used throughout this section and state the well-known Wazewski Theorem. Section 3.1.2 contains a Wazewski set W and the exit set W^-. In Section 3.1.3, the behavior of trajectories on the strongly unstable manifold at $((r/a), 0, 0)$ is presented by some technical lemmas. In Section 3.1.4, we finish the proof of existence of traveling wave solutions by constructing a Lyapunov function.

3.1.1. Recall the Wazewski Theorem [16, 17]. Consider the differential equation:

$$\frac{\mathrm{d}y}{\mathrm{d}s} = f(y), \quad y \in \mathbb{R}^{\mathbb{N}}, \tag{10}$$

where $f : \mathbb{R}^{\mathbb{N}} \to \mathbb{R}^{\mathbb{N}}$ is a continuous function and satisfying a Lipschitz condition. Let $y(0, y_0)$ be the unique solution of (10) satisfying $y(0, y_0) = y_0$. For convenience, set $y(s, y_0) = y_0 \cdot s$. Let $U \cdot S$ be the set of points $y_0 \cdot s$, where $y_0 \in U$ and $s \in S$.

Given $W \subseteq \mathbb{R}^{\mathbb{N}}$, define

$$W^- = \{y_0 \in W : \forall s > 0,\ y_0 \cdot [0, s) \not\subseteq W\}. \tag{11}$$

W^- is called the immediate exit set of W. Given $\Sigma \subseteq W$, let

$$\Sigma^0 = \{y_0 \in \Sigma : \exists s_0 = s_0(y_0) \text{ such that } y_0 \cdot s_0 \notin W\}. \tag{12}$$

For $y_0 \in \Sigma^0$, define

$$T(y_0) = \sup\{s : y_0 \cdot [0, s) \subseteq W\}. \tag{13}$$

$T(y_0)$ is called *an exit time*. Note that $y_0 \cdot T(y_0) \in W^-$ and $T(y_0) = 0$ if and only if $y_0 \in W^-$. The notation $\mathrm{cl}(W)$ denotes the closure of W.

Lemma 5. *Suppose that*

(i) *if $y_0 \in \Sigma$ and $y_0 \cdot [0, s] \subseteq \mathrm{cl}(W)$, then $y_0 \cdot [0, s] \subseteq W$;*

(ii) *if $y_0 \in \Sigma$, $y_0 \cdot s \in W$ and $y_0 \cdot s \notin W^-$, then there is an open set V_s about $y_0 \cdot s$ disjoint from W^-;*

(iii) *$\Sigma = \Sigma^0$, Σ is a compact set and intersects a trajectory of* (10) *only once. Then the mapping $F(y_0) = y_0 \cdot T(y_0)$ is a homeomorphism from Σ to its image on W^-.*

A set $W \subseteq \mathbb{R}^{\mathbb{N}}$ satisfying the conditions (i) and (ii) is called a Wazewski set.

3.1.2. Construct W and W^-. Evaluating the Jacobin of system (8) at the equilibrium $E_1((r/a), 0, 0)$ gives

$$J(E_1) = \begin{pmatrix} -\dfrac{r}{c} & -\dfrac{(1-m)r}{c(ab + (1-m)r)} & 0 \\ 0 & 0 & 1 \\ 0 & -\dfrac{d}{D} & \dfrac{c}{D} \end{pmatrix}. \tag{14}$$

The corresponding eigenvalues of (14) are

$$\begin{aligned} \lambda_1 &= -\frac{r}{c}, \\ \lambda_2 &= \frac{c/D - \sqrt{c^2/D^2 - 4d/D}}{2}, \\ \lambda_3 &= \frac{c/D + \sqrt{c^2/D^2 - 4d/D}}{2}. \end{aligned} \tag{15}$$

If $0 < c < \sqrt{4Dd}$, then λ_2 and λ_3 are a pair of complex conjugate eigenvalues with positive real part. By Theorems 6.1 and 6.2 in [25], there exists a 2-dimensional unstable manifold based at $((r/a), 0, 0)$, the point is a spiral point on this unstable manifold, and the trajectory approaching $((r/a), 0, 0)$ as $s \to -\infty$ must have $P(s) < 0$ for some s. This violates the requirement that the traveling wave solution must be nonnegative. So the first part of Theorem 2 is proved.

We only need to account for the case $c > \sqrt{4Dd}$ in the following. It is obvious that $\lambda_1 < 0 < \lambda_2 < \lambda_3$, the eigenvectors $\mathbf{x}_1, \mathbf{x}_2, \mathbf{x}_3$ associated with $\lambda_1, \lambda_2, \lambda_3$, respectively, are

$$\mathbf{x}_i = \left(-1, p\left(\lambda_i\right), \lambda_i p\left(\lambda_i\right)\right), \quad i = 1, 2, 3, \tag{16}$$

where $p(\lambda_i) = ((c(ab + (1-m)r))/((1-m)r)) \cdot (\lambda_i + r/c)$. Applying Theorems 6.1 and 6.2 in [25], we get a one-dimension strongest unstable manifold $\mathbf{u}_1$ tangent to $\mathbf{x}_3$ at $((r/a), 0, 0)$ and a two-dimension strongly unstable manifold $\mathbf{u}_2$ tangent to the span of $\mathbf{x}_2, \mathbf{x}_3$ at point $((r/a), 0, 0)$. In a small neighborhood of $((r/a), 0, 0)$, points on $\mathbf{u}_1$ are parametrically represented by a function $f_1(m)$ ($\mathbb{R}^1 \to \mathbb{R}^2$):

$$f_1(m) = \left(\frac{r}{a}, 0, 0\right)^T + m\mathbf{x}_3 + o\left(|m|\right), \tag{17}$$

and points on $\mathbf{u}_2$ also could be represented by a function $f_2(m)$ ($\mathbb{R}^2 \to \mathbb{R}^3$):

$$f_2(m) = \left(\frac{r}{a}, 0, 0\right)^T + m\mathbf{x}_3 + n\mathbf{x}_2 + o\left(|m| + |n|\right). \tag{18}$$

Obviously, $\mathbf{u}_1 \subseteq \mathbf{u}_2$.

The motivation and method of constructing the Wazewski set W are similar to that in Dunbar [17]: it will be the complement of two blocks of $\mathbb{R}^3$ and the two blocks are chosen so that U' has the same sign as U. Thus, solutions would not have $U \to 0$ as $s \to \infty$ when entering these blocks. In this paper, the Wazewski set W is defined as follows:

$$W = \mathbb{R}^3 \setminus (T \cup Q), \tag{19}$$

where

$$\begin{gathered} T = \left\{(H, P, U) : U > 0,\ H < H^*,\ P > P^*\right\}, \\ Q = \left\{(H, P, U) : U < 0,\ H > H^*,\ P < P^*\right\}. \end{gathered} \tag{20}$$

Note that $T \cap Q = \varnothing$ and W is a closed set. We obtain

$$\begin{gathered} \partial W = \partial T \cup \partial Q, \\ W^- = \partial W \setminus \left(J \cup \left\{\left(H^*, P^*, U^*\right)\right\}\right), \end{gathered} \tag{21}$$

where

$$J = \left\{(H, P, U) : H \geq H^*,\ P \leq 0,\ U = 0\right\}. \tag{22}$$

Obviously, W^- is not a connected set. Actually, one component of W^- is $\partial P \setminus \{(H^*, P^*, U^*)\}$ and the other is $\partial Q \setminus (J \cup \{(H^*, P^*, U^*)\})$.

As the details of proving that W^- is the set described above are tedious, we just prove the portion ∂Q of ∂W to show why the set J must be excluded from ∂W to W^-.

(1) $H = H^*, P < P^*, U < 0$. Then we have

$$\begin{aligned} H' &= \frac{H}{c}\left(r - aH - \frac{(1-m)P}{b + (1-m)H}\right)_{H=H^*, P<P^*} \\ &> \frac{H^*}{c}\left(r - aH^* - \frac{(1-m)P^*}{b + (1-m)H^*}\right) = 0. \end{aligned} \tag{23}$$

Then the trajectory enters Q.

(2) $H > H^*, P = P^*, U < 0$. Then

$$P' = U < 0. \tag{24}$$

Thus, P is decreasingly entering Q.

(3) $H > H^*, P < P^*, U = 0$. Then

$$U' = \frac{P}{D}\left(\frac{\beta P}{b + (1-m)H} - d\right). \tag{25}$$

(i) $0 < P < P^*$, and thus $\beta P/(b + (1-m)H) - d < \beta P^*/(b + (1-m)H^*) - d = 0$ and the trajectory enters the Q.

(ii) $P < 0$, then $U' > 0$. This implies $H > H^*$, $P < P^*$, $U > 0$. The trajectory does not enter T and Q.

(iii) $P = 0$, and then $U' = P' = 0$, $U'' = P'' = 0$; furthermore, $U^{(n)} = P^{(n)} = 0$. This implies the trajectory does not enter the inner of Q.

(4) $H = H^*, P = P^*, U = 0$. This is a singular point not in the immediate exit set.

(5) $H = H^*, P = P^*, U < 0$. Then $P' = U < 0$, $H' = 0$ and

$$H'' = \frac{H^*}{c}\left(-\frac{(1-m)U}{b + (1-m)H^*}\right) < 0, \tag{26}$$

which implies P and H both decrease. The trajectory enters Q.

(6) $H > H^*, P = P^*, U = 0$. Then

$$\begin{gathered} U' = \frac{1}{D}\left(cU - P\left(d - \frac{\beta P}{b + (1-m)H}\right)\right)_{H>H^*, P=P^*, U=0} < 0, \\ P' = U = 0, \qquad P'' = U' < 0. \end{gathered} \tag{27}$$

Hence, the trajectory enters Q.

(7) $H = H^*, P < P^*, U = 0$. Then

$$\begin{aligned} H' &= \frac{H}{c}\left(r - aH - \frac{(1-m)P}{b + (1-m)H}\right)_{H=H^*, P<P^*} \\ &= \frac{H^*}{c}\left(r - aH^* - \frac{(1-m)P}{b + (1-m)H^*}\right) \\ &> \frac{H^*}{c}\left(r - aH^* - \frac{(1-m)P^*}{b + (1-m)H^*}\right) = 0. \end{aligned} \tag{28}$$

(i) $P < 0$, and then $U' > 0$. This implies $H > H^*$, $P < P^*$, $U > 0$. The trajectory does not enter P and Q.

(ii) $P = 0$, and then $U^{(n)} = P^{(n)} = 0$, $(n = 1, 2, \ldots)$. This implies the trajectory does not enter the inner of Q.

(iii) $0 < P < P^*$, and then

$$\begin{aligned} U' &= \frac{1}{D}\left(cU - P\left(d - \frac{\beta P}{b + (1-m)H}\right)\right)_{H=H^*, U=0} \\ &= \frac{1}{D}\left(-P\left(d - \frac{\beta P}{b + (1-m)H^*}\right)\right) \\ &< \frac{1}{D}\left(-P^*\left(d - \frac{\beta P^*}{b + (1-m)H^*}\right)\right) = 0. \end{aligned} \tag{29}$$

Hence, it implies $H > H^*$, $P < P^*$, $U < 0$, which ensures the trajectory enters the Q.

Based on the above analysis, $J = \{(H, P, U) : H \geq H^*, P \leq 0, U = 0\}$ and $(H^*, P^*, 0)$ must be excluded from ∂W to W^-.

3.1.3. Construct the Set Σ. We need to construct the set Σ before using Lemma 5. By a series of lemmas (Lemmas 5–9), we obtain set Σ will be an arc of a sufficient small circle surrounding $((r/a), 0, 0)$ on the unstable manifold $\mathbf{u}_2$. Furthermore, one endpoint of the arc is the intersection of the circle with the strongly unstable manifold $\mathbf{u}_1$, and the other endpoint is the intersection of the circle with the plane defined by $U = 0$. Lemmas also show that the first endpoint is carried by the strongly unstable manifold into T while the other is carried into P.

We take a notation $\Omega_1 = \{(H, P, U) : H \leq (r/a), P \geq 0, U \geq 0\}$.

Lemma 6. *Let $c > \sqrt{4Dd}$. Any solutions of (8) having a point s_0 such that $0 < H(s_0)$, $P(s_0) > 0$, and $U(s_0) > (c/2D)P(s_0)$ will have $P(s) > 0$ and $U(s) > (c/2D)P(s)$ for all $s > s_0$. This is particularly true for trajectories on the branch of strongly unstable manifold $\mathbf{u}_1$ in the octant Ω_1.*

Proof. Take $s_0 = 0$ without loss of generality. Suppose, on the contrary, that there exists an $s > 0$ such that $U(s) < (c/2D)P(s)$. Let

$$s_1 = \inf\left\{s > 0 : U(s) \leq \frac{c}{2D}P(s)\right\}. \tag{30}$$

For $0 \leq s \leq s_1$, $P'(s) = U(s) \geq (c/2D)P(s)$ and $P(0) > 0$, so $P(s_1) > 0$. Also $U(s_1) = (c/2D)P(s_1)$ and $U(s) > (c/2D)P(s)$ for $0 \leq s < s_1$. Thus $(c/2D)P'(s_1) \geq U'(s_1)$ (i.e., $U'(s_1) - (c/2D)P'(s_1) \leq 0$). Then, from (8), we have

$$\left(\frac{c}{D}U - \frac{P}{D}\left(d - \frac{\beta P}{b + (1-m)H}\right) - \frac{c}{2D}U\right)_{s_1} \leq 0. \tag{31}$$

Then

$$\begin{aligned} &\frac{c}{2D}U(s_1) - \frac{d}{D}P(s_1) \\ &\quad \leq \frac{c}{2D}U(s_1) - \frac{1}{D}P(s_1)\left(d - \frac{\beta P(s_1)}{b + (1-m)H(s_1)}\right) \leq 0. \end{aligned} \tag{32}$$

Since $U(s_1) = (c/2D)P(s_1)$, we have $c^2 \leq 4Dd$.

It must be the case that $0 < H(s_1) < (r/a)$. The plane defined by $U = 0$ is an invariant manifold, so $H(s_1) > 0$ is obvious. We just verify that $H(s_1) < (r/a)$. If this is not true, then there exists $0 < s_2 \leq s_1$ such that $H(s_2) = (r/a)$ and $H'(s_2) \geq 0$. But then

$$\begin{aligned} 0 \leq H'(s_2) &= \left(\frac{1}{c}H(r - aH) - \frac{1}{c}\frac{(1-m)HP}{b + (1-m)H}\right)_{s=s_2} \\ &= -\frac{1}{c}\frac{(1-m)HP}{b + (1-m)H}\Big|_{s=s_2} < 0, \end{aligned} \tag{33}$$

so $0 < H(s_1) < (r/a)$ for $0 \leq s \leq s_1$. So $c^2 \leq 4Dd$, which is a contradiction. Thus $U(s) > (c/2D)P(s)$ for all $s > 0$. Then also $P(s) > 0$ for all $s > 0$.

A trajectory on the branch of the strongly unstable manifold $\mathbf{u}_1$ in the octant Ω_1 approaches $((r/a), 0, 0)$ tangent to $\mathbf{x}_3$. From subset B, the second and third components of this tangent vector satisfy $U = \lambda_3 P$. Thus there exists a point s_0 on the trajectory whose components satisfy $0 < H(s_0) < (r/a)$, $P(s_0) > 0$, and $U(s_0) = \lambda_3 P(s_0) > (c/2D)P(s_0)$. This completes the proof. □

Lemma 7. *Assume that $c > \sqrt{4Dd}$; then a trajectory on the portion of the strongly unstable manifold $\mathbf{u}_1$ in the octant Ω_1 must satisfy*

$$P(s) \geq -\left(H(s) - \frac{r}{a}\right)\left(\frac{c(ab + (1-m)r)}{(1-m)r}\frac{c^2 + 2Dr}{2Dc}\right), \tag{34}$$

for all s.

Proof. A trajectory on the portion of the strongly unstable manifold $\mathbf{u}_1$ in the octant Ω_1 could be written as $P(s) = -p(\lambda_3)(H(s) - r/a)$, where

$$\begin{aligned} p(\lambda_3) &= \frac{c(ab + (1-m)r)}{(1-m)r}\left(\lambda_3 + \frac{r}{c}\right) \\ &= \frac{c(ab + (1-m)r)}{(1-m)r} \\ &\quad \times \left(\frac{c/D + \sqrt{c^2/D^2 - 4d/D}}{2} + \frac{r}{c}\right) \\ &> \frac{c(ab + (1-m)r)}{(1-m)r}\frac{c^2 + 2Dr}{2Dc}. \end{aligned} \tag{35}$$

□

Lemma 8. *Let $l > (c/D)$ be a fixed number. A solutions of (8) having a point s_0 such that $0 < H(s_0) < (r/a)$, $P(s_0) > 0$, and $U(s_0) < lP(s_0)$ will have $U(s) < lP(s)$ for all $s > s_0$ such that $P(s) > 0$. In particular, this is true for trajectories on branch of the strongly unstable manifold $\mathbf{u}_1$ in the octant Ω_1.*

The proof is similar to that of Lemma 6, so it is omitted.

Lemma 9. *If a solution of (8) has a point, taking to $s = 0$ without loss of generality, such that $H(0) < (r/a)$, $0 < P(0) < -((c(ab + (1-m)r))/(aH^*(1-m)))(l + (r/c))(H(s) - (r/a))$,* *and* $U(0) < lP(0)$*, then for all* $s > 0$*, as long as* $H(s) > H^*$*,* $P(s) > 0$ *the trajectory must have that* $P(s) < -(c(ab+(1-m)r)/aH^*(1-m))(l+(r/c))(H(s)-(r/a))$*. In particular, this is true for a trajectory on the branch of the strongly unstable manifold* $\mathbf{u}_1$ *in the octant* Ω_1*.*

Proof. We first prove that $H(s) < (r/a)$ for all $s > 0$ such that $P(s) > 0$. If this is not true, then there exists a first time $s_1 > 0$ such that $H(s) = (r/a)$, $H'(s_1) \geq 0$ and $P(s_1) > 0$. But then,

$$0 \leq H'(s_1) = \left(\frac{1}{c}H(r-aH) - \frac{1}{c}\frac{(1-m)HP}{b+(1-m)H}\right)_{s=s_1} < 0. \tag{36}$$

This is a contradiction. Thus $H(s) < (r/a)$ for all $s > 0$ such that $P(s) > 0$.

Now we show that $P(s) < -A_0(H(s)-(r/a))$ for all $s > 0$ as long as $H(s) > H^*$ and $P(s) > 0$. Let $A_0 = (c(ab+(1-m)r)/aH^*(1-m))(l+(r/c))$. Suppose on the contrary that there exists a first time s_2 such that $H(s_2) > H^*$, $P(s_2) > 0$, but $P(s_2) = -A_0(H(s_2)-(r/a))$. Then $P'(s_2) \geq -A_0(H'(s_2))$. By Lemma 8, $U(s) < lP(s)$ for all $s > s_0$ such that $P(s) > 0$. Then

$$\begin{aligned} lP(s_2) &\geq U(s_2) = P'(s_2) \geq -A_0\left(H'(s_2)\right) \\ &= -A_0\frac{H}{c}\left(r - aH - \frac{(1-m)P}{b+(1-m)H}\right)_{s=s_2}. \end{aligned} \tag{37}$$

For $P(s_2) = -A_0(H(s_2)-(r/a))$ and $H^* < H(s_2) < (r/a)$, we have

$$\begin{aligned} l &\geq \frac{-A_0(H/c)(r-aH-((1-m)P)/(b+(1-m)H))_{s=s_2}}{-A_0(H(s_2)-(r/a))} \\ &= -\frac{1}{c}\left(\frac{A_0H(r-aH)}{-A_0(H-(r/a))} - \frac{(1-m)P}{b+(1-m)H}\cdot\frac{A_0H}{P}\right)_{s=s_2} \\ &= -\frac{1}{c}\left(aH - \frac{A_0(1-m)H}{b+(1-m)H}\right)_{s=s_2} \\ &> \frac{1}{c}\left(\frac{A_0(1-m)H^*}{b+(1-m)(r/a)} - r\right) \\ &= \frac{aA_0(1-m)H^*}{c(ab+(1-m)r)} - \frac{r}{c} \\ &= l, \end{aligned} \tag{38}$$

which is a contradiction. This completes the proof. □

Now combine all the results of Lemmas 6–9 to follow the trajectory of a solution of (8) on the strongly unstable manifold $\mathbf{u}_1$. Let

$$\begin{aligned} \mathscr{R} = \Big\{&(H,P,U) : H^* < H < \frac{r}{a}, \\ &-\frac{c(ab+(1-m)r)}{(1-m)r}\cdot\frac{c^2+2dr}{2dc}\left(H-\frac{r}{a}\right) < P \\ &< -\frac{c(ab+(1-m)r)}{aH^*(1-m)}\left(l+\frac{r}{c}\right)\left(H-\frac{r}{a}\right), \\ &\frac{c}{2D}P < U < lP\Big\}. \end{aligned} \tag{39}$$

Then the trajectory of a solution of (8) on the strongly unstable manifold $\mathbf{u}_1$ is contained in $\mathscr{R}$. Since $0 < m < 1$, we obtain

$$\begin{aligned} P &\geq -\frac{c(ab+(1-m)r)}{(1-m)r}\cdot\frac{c^2+2Dr}{2Dc}\left(H-\frac{r}{a}\right) \\ &= \left(\frac{r}{a}-H\right)\cdot\frac{c(ab+(1-m)r)}{(1-m)r}\cdot\left(\frac{c}{2D}+\frac{r}{c}\right) \\ &\geq \left(\frac{r}{a}-H\right)\cdot\frac{c(ab+(1-m)r)}{(1-m)r}\cdot\frac{r}{c} \\ &= (r-aH)\frac{b+(1-m)(r/a)}{(1-m)} \\ &> (r-aH)\frac{b+(1-m)H}{(1-m)}. \end{aligned} \tag{40}$$

This shows the region $\mathscr{R}$ lies in the region defined by $H > 0$ and $P > (r-aH)(b+(1-m)H/(1-m))$. Then, on the strongly unstable manifold $\mathbf{u}_1$, $H' = H((r-aH)-((1-m)P/b+(1-m)H)) < 0$. So, for a solution of (8) on $\mathbf{u}_1$, $H(s)$ decreases until $H(s_0) = H^*$ for some finite s_0. And at the time s_0, we have

$$P > (r-aH^*)\frac{b+(1-m)H^*}{(1-m)} = \frac{d(b+(1-m)H^*)}{\beta} = P^*. \tag{41}$$

Thus the trajectory of this solution hits ∂W on the face $H = H^*$, $P > P^*$, and $U > 0$. Therefore, the vector field shows that the solution of (8) on $\mathbf{u}_1$ enters the region T at some finite time.

Lemma 10. *In a sufficient small neighborhood of* $((r/a),0,0)$ *the two-dimensional unstable manifold* $\mathbf{u}_2$ *intersects the plane defined by* $U = 0$ *in a smooth* $\mathscr{C}^1$ *curve* Γ*, given by* $P = \mathscr{M}(H)$*,* $U = 0$*, where*

$$\begin{aligned} P &= \mathscr{M}(H) \\ &= -\frac{\lambda_3 p(\lambda_3)}{\lambda_2 p(\lambda_2)}\left(H-\frac{r}{a}\right) \\ &= -\frac{\lambda_3(r+c\lambda_3)}{\lambda_2(r+c\lambda_2)}\left(H-\frac{r}{a}\right). \end{aligned} \tag{42}$$

Proof. The proof is similar to Lemma 5 in [16] and is omitted. □

Remark 11. The portion of the curve Γ is in the region $H < (r/a)$. Obviously, the P component of points along the curve Γ satisfies $P > 0$ from Lemma 10. From the direction of the vector filed on the quarter plane, $H > H^*$, $P > 0$, and $U = 0$, any trajectory passing through a point of Γ near $((r/a), 0, 0)$ will immediately enter the region Q.

Now, we place a sufficiently small circle about $((r/a), 0, 0)$ on the two-dimensional unstable manifold $\mathbf{u}_2$. The circle is contained in the neighborhood of $((r/a), 0, 0)$ given in Lemma 10 and satisfies the conditions of Lemmas 6–9. Then the circle intersects the curve Γ. Define Σ to be arc of this circle contained in the octant Ω_1 whose endpoints are the intersections of the circle with $\mathbf{u}_1$ and the curve Γ.

3.1.4. Proof of (ii) of Theorem 2. In this section, we firstly use Lemma 5 to produce a trajectory which remains in the region W. Second, we construct a Lyapunov function to demonstrate that the trajectory approaches $(H^*, P^*, 0)$. For simplicity, we denote $N = \{(H, P, U) : P = U = 0\}$, $L = \{(H, P, U) : H = 0\}$.

Lemma 12. *There exists a point $y^* \in \Sigma$ such that the solution $y(s, y^*) = (H_1(s), P_1(s), U_1(s))$ of* (8) *remains in the region W for all s.*

Proof. It is obvious that the set W is closed satisfying the (i) of Lemma 5. Before using Lemma 5 to prove this conclusion, we also need to check the conditions (ii) and (iii) of it. Suppose $y_0 \in \Sigma$, $s < T(y_0)$, $y(s, y_0) \in W \setminus W^-$. Then $y(s, y_0) \in \operatorname{int} W \cup J$. As $s < T(y_0)$, we easily verify that

$$y(s, y_0) \notin \{(H, P, U) : H \geq H^*,\ P < 0,\ U = 0\}. \tag{43}$$

Moreover, as N is an invariant manifold,

$$y(s, y_0) \notin \{(H, P, U) : H \geq H^*,\ P = 0,\ U = 0\}. \tag{44}$$

Thus $y(s, y_0) \in \operatorname{int} W$ and there exists an open set V around $y(s, y_0)$ disjoint from ∂W. So (ii) of Lemma 5 is satisfied.

From the previous 5 lemmas, we know that the image of one endpoint of Σ lies in the portion $\partial T \setminus \{(H^*, P^*, 0)\}$ of W^-; and the image of the other endpoint is in the component $\partial Q \setminus (J \cup \{(H^*, P^*, 0)\})$ of W^-. Thus Σ is compact, intersects any trajectory of (8) only once, and is simple connected. If $\Sigma = \Sigma^0$, then F would be a homeomorphism of the connected set Σ to its image in the disconnected set W^-. This is impossible. So $\Sigma \neq \Sigma^0$. Thus there exists some point y^* such that $y(s, y^*) \in W$ for all s. □

Lemma 13. *The solution $y(s, y^*)$ remains in the region*

$$\Omega = \left\{ (H, P, U) : 0 < H < \frac{r}{a}, 0 < P < k(H), -\frac{\beta P^2}{cb} < U < lP \right\}, \tag{45}$$

for all s, where

$$k(H) = \begin{cases} -\dfrac{c(ab + (1-m)r)}{aH^*(1-m)} \left(l + \dfrac{r}{c}\right)\left(H - \dfrac{r}{a}\right), & H^* < H < \dfrac{r}{a}, \\ -\dfrac{c(ab + (1-m)r)}{aH^*(1-m)} \left(l + \dfrac{r}{c}\right)\left(H^* - \dfrac{r}{a}\right), & 0 < H^* \leq H^*. \end{cases} \tag{46}$$

Proof. Firstly, $y(s, y^*)$ must have $H_1(s) > 0$ for all s, as L is an invariant manifold.

Secondly, we prove $P_1(s) > 0$. If it is not true, then $y(s, y^*)$ enters region $N_1 = \{(H, P, U) : P < 0\}$. Let $s_1 = \inf\{s : y(s, y^*) \in N_1\}$. Then $P_1(s_1) = 0$ and $P_1'(s_1) \leq 0$, so $U_1(s_1) \leq 0$. As N is an invariant manifold, $U_1(s_1) < 0$. And $H_1(s_1) < H^*$ for $y(s, y^*) \notin Q$. From (8), $H_1'(s_1) > 0$, which means $H_1(s)$ is increasing for $s > s_1$. Then the solution enters

$$N_2 = \{(H, P, U) : H_1(s_1) < H < H^*,\ P < 0,\ U < 0\}. \tag{47}$$

Obviously, in N_2, $P' = U < 0$, so $P_1(s)$ is decreasing. Thus, we have

$$H_1'(s) \geq \frac{1}{c} \min\{H_1(s_1)(r - aH_1(s_1)), H^*(r - aH^*)\}. \tag{48}$$

So $H_1(s)$ increases to H^* in the finite time s_2; that is, $H_2(s) = H^*$. Then also $P_1(s_2) < 0$, $U_1(s_2) < 0$. So $y(s, y^*)$ enter Q. This is a contradiction. Therefore, $P_1(s) > 0$ for all time.

By Lemma 9, we know

$$P_1 < -\frac{c(ab + (1-m)r)}{aH^*(1-m)} \left(l + \frac{r}{c}\right)\left(H_1 - \frac{r}{a}\right), \quad \text{for } H^* < H_1 \leq \frac{r}{a}. \tag{49}$$

As $P_1(s) > 0$, so $H_1(s) < (r/a)$ for all s.

Suppose, on the contrary, there exists s such that $P_1(s) \geq -A_0(H^* - (r/a))$ for $0 < H_1 \leq H^*$, where $A_0 = (c(ab + (1-m)r)/aH^*(1-m))(l + r/c)$. Take

$$s_2 = \inf\left\{s : P_1(s) \geq -A_0\left(H^* - \frac{r}{a}\right)\right\}. \tag{50}$$

Then $H_1(s_2) \leq H^*$, $P_1(s_2) > P^*$, and $U_1(s_2) = P_1'(s_2) \geq 0$. Then either $y(s, y^*) \in T$ or $y(s, y^*)$ immediately enter T, which is impossible. So $P_1(s) \leq -A_0(H^* - (r/a))$ for $0 < H_1 \leq H^*$.

At last, we prove $-(\beta P_1^2/cb) < U_1 < lP_1$. $U_1 < lP_1$ is obvious. Because a trajectory starting on Σ approaches $((r/a), 0, 0)$ tangent to $\mathbf{x}_2$ or $\mathbf{x}_3$ has $U = \lambda_2 P$ or $U = \lambda_3 P$. Since $\lambda_2, \lambda_3 < l$, from Lemma 8, we know $U_1(s) < lP_1(s)$ for all s. We only need to prove $-(\beta P_1^2/cb) < U_1$. Suppose, on the contrary, that there exists a s_3 such that $U_1(s_3) < -(\beta P_1^2(s_3)/cb) < 0$; then $U_1(s_3) < -(\beta P_1^2(s_3)/cb)$ for all $s > s_3$. If this is not true, there exists a $s_4 > s_3$ such that $U_1(s_4) = -(\beta P_1^2(s_4)/cb)$, and thus $U_1'(s_4) + (\beta P_1^2(s_4)/cb) \geq 0$. Then from (8) we have

$$\left(\frac{c}{D}U - \frac{d}{D}P + \frac{\beta P^2}{D(b+(1-m)H)} + \frac{2\beta PU}{cb}\right)_{s=s_4} \geq 0. \quad (51)$$

Then after some calculation, we obtain

$$\left(-\frac{\beta^2 P}{D}\left(\frac{1}{b} - \frac{1}{b+(1-m)H}\right) - \frac{d}{D}P - \frac{2\beta^2 P^3}{c^2 b}\right)_{s=s_4} \geq 0, \quad (52)$$

this is a contradiction. So if $U_1(s_3) < -(\beta P_1^2(s_3)/cb)$, then $U_1(s_3) < -(\beta P_1^2(s_3)/cb)$ for all $s > s_3$. Thus,

$$\begin{aligned} U_1' &= \frac{c}{D}U_1 - \frac{d}{D}P_1 + \frac{\beta P_1^2}{D(b+(1-m)H)} \\ &< -\frac{\beta P_1^2}{D}\left(\frac{1}{b} - \frac{1}{b+(1-m)H_1}\right) - \frac{d}{D}P_1 < 0, \end{aligned} \quad (53)$$

for all $s > s_3$. So $U_1(s) < U_1(s_3)$ for all $s > s_3$. Thus $P_1'(s) = U_1(s) < 0$ and bounded away from zero by $U_1(s_3)$. Therefore $P_1(s) < 0$ for some finite s, which is a contradiction. So $-(\beta P_1^2/cb) < U_1$.

This completes the proof. □

Lemma 14. *The trajectory $y(s, y^*) \to (H^*, P^*, 0)$ as $s \to -\infty$.*

Proof. Define following Lyapunov function:

$$\begin{aligned} V(H,P,U) = &\frac{dc}{D}\left[H - H^* \ln H\right] + \left[c\left(\frac{P}{D} - P^*\right) - U\right] \\ &+ P^*\left[\frac{U}{P} - \frac{c}{D}\ln\frac{P}{P^*}\right]. \end{aligned} \quad (54)$$

Then $V(H,P,U)$ is continuous and bounded below on Ω, and

$$\begin{aligned} \frac{dV}{ds} &= \frac{\partial V}{\partial H}\cdot H_t + \frac{\partial V}{\partial P}\cdot P_t + \frac{\partial V}{\partial U}\cdot U_t \\ &= \frac{dc(H-H^*)}{DH}\cdot\frac{H}{c}\left[r - aH - \frac{(1-m)P}{b+(1-m)H}\right] \\ &\quad + \left[\frac{c}{D}\left(1 - \frac{P^*}{P}\right) - \frac{P^*U}{P^2}\right]\cdot U \\ &\quad + \left(\frac{P^*}{P} - 1\right)\cdot\frac{1}{D}\left[cU + \frac{\beta P^2}{b+(1-m)H} - Pd\right] \\ &= \frac{d(H-H^*)}{D}\left[r - aH - \frac{(1-m)P}{b+(1-m)H}\right] \\ &\quad + \frac{P^*-P}{D}\left[\frac{\beta P}{b+(1-m)H} - d\right] - \frac{P^*U^2}{P^2} \\ &= \frac{d(H-H^*)}{D}\left[r - aH - \frac{(1-m)P}{b+(1-m)H}\right] - \frac{P^*U^2}{P^2} \\ &\quad + \frac{P^*-P}{D}\left[\frac{\beta P}{b+(1-m)H} - \frac{\beta P^*}{b+(1-m)H} + \frac{\beta P^*}{b+(1-m)H} - d\right] \\ &= \frac{d(H-H^*)}{D}\left[r - aH - \frac{(1-m)P}{b+(1-m)H}\right] \\ &\quad + \frac{P^*-P}{D}\left[\frac{(1-m)P^*}{b+(1-m)H} - d\right] \\ &\quad - \frac{\beta(P^*-P)^2}{D(b+(1-m)H)} - \frac{P^*U^2}{P^2} \\ &= \frac{d(H-H^*)}{D}\left[r - aH - \frac{(1-m)P}{b+(1-m)H}\right] \\ &\quad + \frac{P^*-P}{D}\cdot\frac{d(1-m)(H-H^*)}{b+(1-m)H} \\ &\quad - \frac{\beta(P^*-P)^2}{D(b+(1-m)H)} - \frac{P^*U^2}{P^2} \\ &= \frac{d(H-H^*)}{D}\left[r - aH - \frac{(1-m)P^*}{b+(1-m)H}\right] \\ &\quad - \frac{\beta(P^*-P)^2}{D(b+(1-m)H)} - \frac{P^*U^2}{P^2}, \end{aligned} \quad (55)$$

where $g(H) = f(H)/(b+(1-m)H)$ is defined. Obviously, $b+(1-m)H > 0$ in Ω and $g(H^*) = 0$. According to Lemma 1, when $r > (d(1-m)/\beta)$, the following result always holds:

$$\frac{d(H-H^*)}{D}\left[r - aH - \frac{(1-m)P^*}{b+(1-m)H}\right] \leq 0. \quad (56)$$

Therefore, the dV/ds is always nonpositive in Ω. Moreover, $dV/ds = 0$ if and only if $H = H^*$, $P = P^*$, and $U = 0$; the largest invariant subset of this segment is the single point $(H^*, P^*, 0)$. By LaSalle's Invariance Principle, $y(s, y^*) \to (H^*, P^*, 0)$ as $s \to -\infty$. This completes the proof. □

3.2. Proof of Theorem 3. The Jacobin of system (8) at the equilibrium $E(H^*, P^*, 0)$ is

$$J(E) = \begin{pmatrix} -\frac{1}{c}\left(-aH^* + \frac{(1-m)^2 H^* d^2}{\beta^2 P^*}\right) & -\frac{d(1-m)H^*}{c\beta P^*} & 0 \\ 0 & 0 & 1 \\ -\frac{d^2(1-m)}{\beta D} & -\frac{d}{D} & \frac{c}{D} \end{pmatrix}. \quad (57)$$

Let $M = -aH^* + ((1-m)^2 H^* d^2/\beta^2 P^*)$; then the corresponding characteristic equation of (57) is given by

$$P(\lambda) = \lambda^3 - \left(\frac{M}{c} + \frac{c}{D}\right)\lambda^2 + \frac{M-d}{D}\lambda - \frac{adH^*}{cD} = 0. \quad (58)$$

In order to get the sign of the roots of characteristic equation (58), we will use Routh-Hurwitz analysis [25]. The Routh-Hurwitz range of (58) is

$$\begin{array}{c|cc} \lambda^3 & a_3 = 1 & a_1 = \frac{(M-d)}{D} \\ \lambda^2 & a_2 = -\left(\frac{M}{c} + \frac{c}{D}\right) & a_0 = -\frac{adH^*}{cD} \\ \lambda^1 & b_1 & b_2 \\ \lambda^0 & c_1 & c_2 \end{array}, \quad (59)$$

where

$$\begin{aligned} b_1 &= -\frac{1}{a_2}\begin{vmatrix} a_3 & a_1 \\ a_2 & a_0 \end{vmatrix} \\ &= -\frac{1}{M/c + c/D}\begin{vmatrix} 1 & \frac{M-d}{D} \\ -\left(\frac{M}{c} + \frac{c}{D}\right) & -\frac{adH^*}{cD} \end{vmatrix} \\ &= -\frac{adH^*}{MD + c^2} + \frac{M-d}{D}, \quad (60) \\ b_2 &= -\frac{1}{a_2}\begin{vmatrix} a_3 & 0 \\ a_2 & 0 \end{vmatrix} = 0, \\ c_1 &= -\frac{1}{b_1}\begin{vmatrix} a_2 & a_0 \\ b_1 & b_2 \end{vmatrix} = a_0 = -\frac{adH^*}{cD}, \\ c_2 &= -\frac{1}{b_1}\begin{vmatrix} a_2 & 0 \\ b_1 & 0 \end{vmatrix} = 0. \end{aligned}$$

In the above range, we easily know that $a_3 > 0$, $c_1 < 0$. When $\beta > 1 - m$, (i) if $M/c + c/D < 0$ ($a_2 > 0$), then no matter the sigh of b_1, the sigh of the first arrange of (59) will change once, and the no row of (59) is full zero. So character equation (59) always has a real root and two complex roots with negative real part; (ii) if $M/c + c/D > 0$ ($a_2 < 0$), we obtain $((M - d)/D) < 0$ with $\beta > 1 - m$, and then $b_1 < 0$. Thus, the sigh of the first arrange of (59) will change once and the no row of (59) is full zero. So character equation (58) has a real root and two complex roots with negative real part.

Therefore, there is a 2-dimensional stable manifold and 1-dimensional unstable manifold based at $(H^*, P^*, 0)$ when $\beta > 1 - m$.

The differentiation of (58) is

$$P'(\lambda) = 3\lambda^2 - 2\left(\frac{M}{c} + \frac{c}{D}\right)\lambda + \frac{M-d}{D}. \quad (61)$$

Let $P'(\lambda) = 0$; then we obtain

$$\lambda_{\pm} = \frac{2(M/c + c/D) \pm \sqrt{4(M/c + c/D) - 12((M-d)/D)}}{6}. \quad (62)$$

Thus, $P(\lambda)$ get the maximum at $\lambda = \lambda_-$, $P(\lambda)$ get the minimum at $\lambda = \lambda_+$, and $P(\lambda)_{\text{minimum}} < 0$. So we just consider

$$P(\lambda)_{\text{maximum}} = \lambda_-^{\;3} - \left(\frac{M}{c} + \frac{c}{D}\right)\lambda_-^{\;2} + \frac{M-d}{D}\lambda_- - \frac{adH^*}{cD}. \quad (63)$$

If $P(\lambda)_{\text{maximum}} > 0$, (58) has two negative roots and a positive root. If $P(\lambda)_{\text{maximum}} = 0$, (58) has a negative root and a positive root. If $P(\lambda)_{\text{maximum}} < 0$, (58) has a positive root and two complex roots with negative real part. So the solution of (8) satisfying (7) spreads to the positive equilibrium $(H^*, P^*, 0)$ monotonously when $P(\lambda)_{\text{maximum}} \geq 0$, and it spreads to the positive equilibrium $(H^*, P^*, 0)$ nonmonotonously when $P(\lambda)_{\text{maximum}} < 0$.

3.3. Proof of Theorem 4. In order to prove Theorem 4, we take D, r, a, m, and d as fixed and β and c as parameters. It means we only allow the predator effectiveness to vary. We search for purely imaginary roots of the characteristic equation

$$\lambda^3 - \left(\frac{p+d}{c} + \frac{c}{D}\right)\lambda^2 + \frac{p}{D}\lambda - \frac{q}{cD} = 0, \quad (64)$$

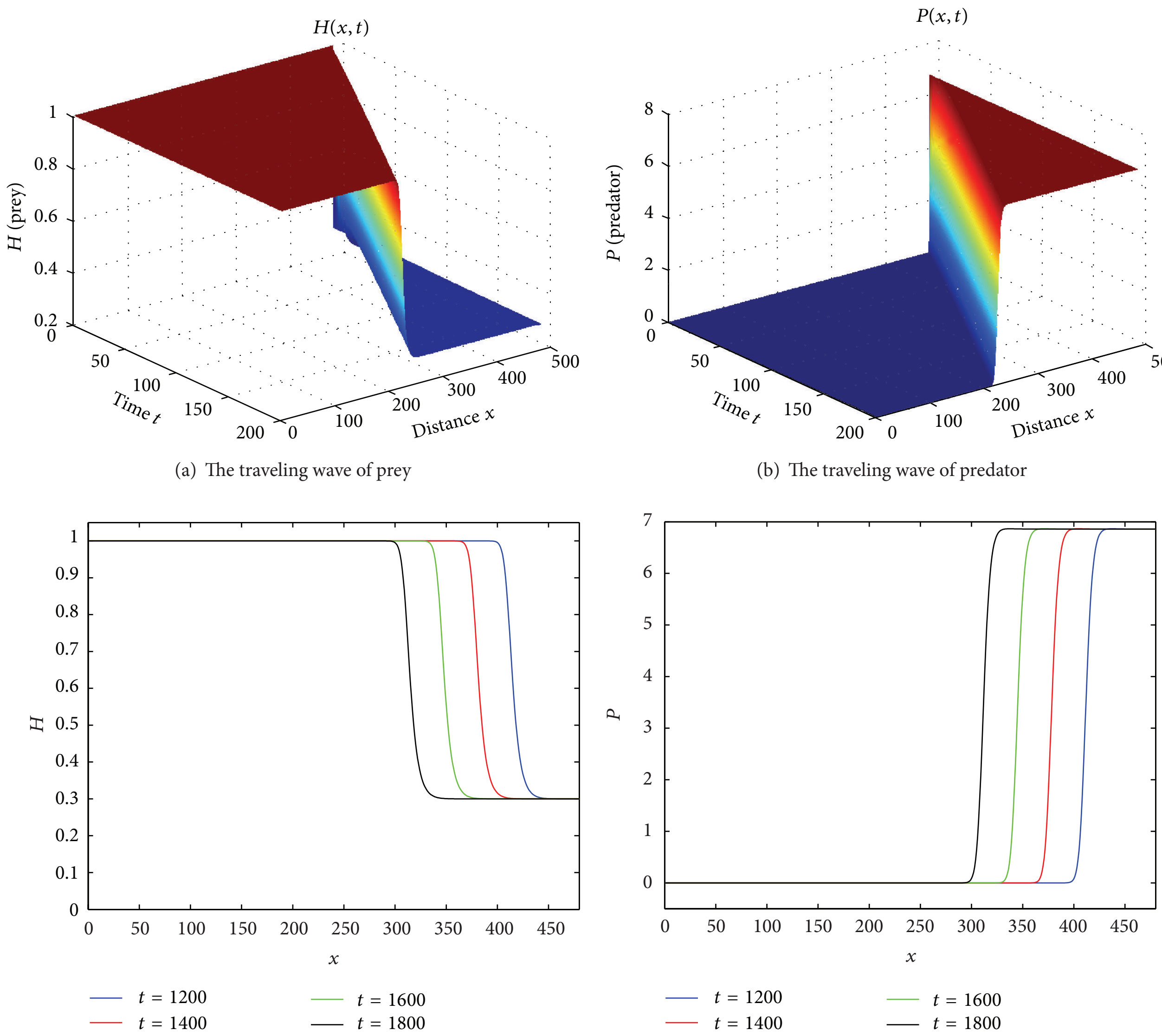
where $p = M - d$, $q = adH^*$, $M = -aH^* + ((1 - m)^2 H^* d^2/\beta^2 P^*)$, and $H^* = ((dm - d + \beta r)/a\beta)$.

It is easy to see that $p < 0$, $q > 0$ and $0 < H^* < r/a$. Substituting $\lambda = ki$ into (64) and simplifying it, we have

$$\begin{aligned} k^2 &= \frac{p}{D}, \\ k^2 &= \frac{q}{D(p+d) + c^2}. \end{aligned} \quad (65)$$

Thus, a pair of imaginary eigenvalues exists if the parameters β and c satisfy the condition

$$c^2 = D\left(\frac{q}{p} - p - d\right). \quad (66)$$



(a) The traveling wave of prey

(b) The traveling wave of predator

(c) The traveling wave of predator at different time

(d) The traveling wave of predator at different time

FIGURE 1: The traveling wave solution of system (8) from $E_1(1, 0)$ tends to $E(H^*, P^*)$ monotonously with the parameters $D = 0.8$, $r = 1$, $a = 1$, $m = 0.3$, $b = 6.65$, $d = 0.5$, and $\beta = 0.5$.

Regarding λ as a function of β and differentiating the characteristic equation (64) with respect to β, we obtain

$$\frac{d\lambda(\beta)}{d\beta} = \frac{(p'/c)\lambda^2 - (p'/D)\lambda + (q'/cD)}{3\lambda^2 - 2(((p+d)/c) + (c/D))\lambda + (p/D)}. \quad (67)$$

Here ($'$) denotes the differentiation with respect to β. Substituting $\lambda = ki$ into (66), we have

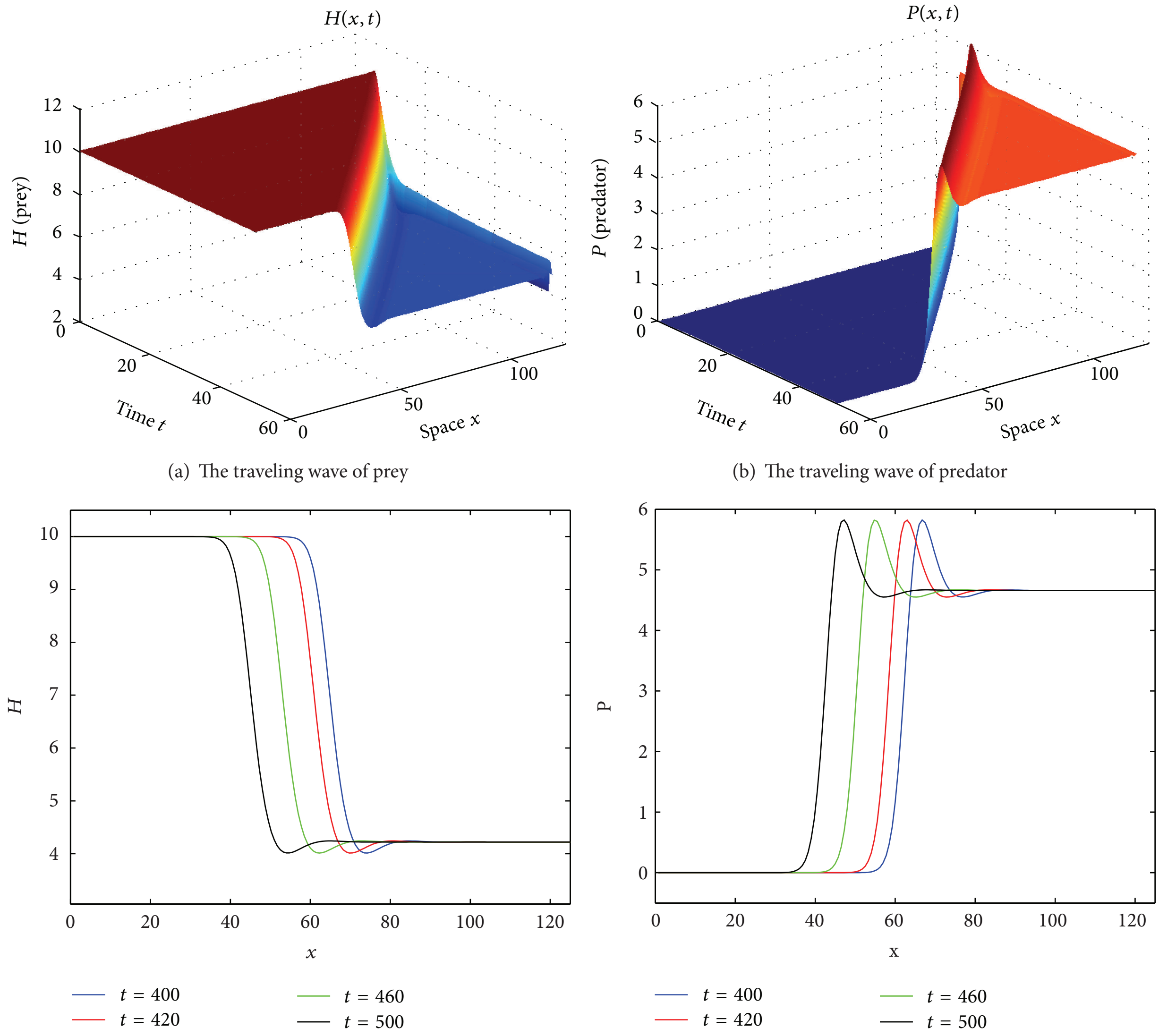
$$\frac{d\lambda(\beta)}{d\beta} = \frac{(-(p'/c)k^2 + (q'/cD)) - (p'/D)ki}{(3k^2 + (p/D)) - 2(((p+d)/c) + c/D)ki}. \quad (68)$$

After some calculation, we have that the sign of the real part of $d\lambda(\beta)/d\beta$ is determined by the sign of

$$\frac{-2}{cD}\left(pq' - p^2p' - p'q\right). \quad (69)$$

From (64), we know $(dc^2/d\beta) = (D/p^2)(pq' - p^2p' - p'q)$. Thus, it is obvious that

$$-\frac{2p^2}{cD^2}\frac{dc^2}{d\beta} = \frac{-2}{cD}\left(pq' - p^2p' - p'q\right). \quad (70)$$



(a) The traveling wave of prey

(b) The traveling wave of predator

(c) The traveling wave of predator at different time

(d) The traveling wave of predator with different time

FIGURE 2: The traveling wave solution of system (8) from $E_1(10,0)$ tends to $E(H^*, P^*)$ nonmonotonously with the parameters $D = 0.8$, $r = 1.5$, $a = 0.15$, $m = 0.35$, $b = 0.15$, $d = 1$, and $\beta = 0.75$.

So the sign of $\mathrm{Re}(d\lambda(\beta)/d\beta)$ is opposite to that of $dc^2/d\beta$. In fact, $q' = ad(H^*)'_\beta = d(1-m)/a\beta^2 > 0$, while

$$
\begin{aligned}
p' &= \{M - d\}'_\beta \\
&= \left\{-aH^* + \frac{d(1-m)^2 H^*}{\beta(b + (1-m)H^*)} - d\right\}'_\beta \\
&= -\frac{d(1-m)}{\beta^2} \\
&\quad + \left(\frac{d^2(1-m)^3}{a\beta}\left[b + (1-m)H^*\right]\right. \\
&\quad \left. - d(1-m)^2 H^* \left[b + (1-m)H^* + \frac{d(1-m)^2}{a\beta}\right]\right) \\
&\quad \times \left(\beta^2\left[b + (1-m)H^*\right]^2\right)^{-1} \\
&= d(1-m)\left\{\frac{bd(1-m)^2}{a\beta}\right. \\
&\quad \left. - \left[(1-m)^2(H^*)^2 + 3b(1-m)H^* + b^2\right]\right\}.
\end{aligned}
\tag{71}
$$

Define function $h(H^*) = (1-m)^2(H^*)^2 + 3b(1-m)H^* + b^2$, and then $h'(H^*) = 2(1-m)H^* + 3b(1-m) > 0$ if $0 < H^* < r/a$, where $(')$ denotes the differentiation with respect to H^*. So $h(H^*)$ is increasing with respect to H^*. Thus,

$$
\begin{aligned}
h(H^*) < h\left(\frac{r}{a}\right) &= \frac{(1-m)^2 r^2 + 3abr(1-m) + a^2b^2}{a^2} \\
&< \frac{((1-m)r + (3/2)ab)^2}{a^2}.
\end{aligned}
\tag{72}
$$

So if

$$\beta < \frac{abd(1-m)^2}{((1-m)r + (3/2)ab)^2}, \quad (73)$$

we have

$$\frac{bd(1-m)^2}{a\beta} - h(H^*) > 0, \quad \text{that is } p' > 0. \quad (74)$$

Then we have

$$\frac{dc^2}{d\beta} = \frac{D}{p^2}\left(pq' - p'\left(p^2 + q\right)\right) < 0. \quad (75)$$

Therefore,

$$\operatorname{Re}\left(\frac{d\lambda(\beta)}{d\beta}\right) > 0. \quad (76)$$

By the Hopf bifurcation Theorem, we obtain that when the parameter β crosses the bifurcation curve $c^2 = D((q/p) - p - d)$ at β_0 in the $\beta - c$ parameter plane, system (8) undergoes a Hopf bifurcation to a small amplitude periodic solution at the equilibrium point $(H^*, P^*, 0)$. It corresponds to a small amplitude traveling wave train solution of system (5). This completes the proof.

4. Numerical Simulations

In this section, we will give numerical examples to illustrate the results of Theorems 2 and 3. All the numerical simulations are under the Neumann boundary conditions.

Figure 1 shows that there exists traveling wave solution and it from $E_1((r/a), 0)$ tends to $E(H^*, P^*)$ monotonously. In Figure 1, we consider the following parameters $D = 0.8$, $r = 1$, $a = 1$, $m = 0.3$, $b = 6.65$, $d = 0.5$, and $\beta = 0.5$. Figure 2 shows that there exists traveling wave solution and it from $E_1((r/a), 0)$ tends to $E(H^*, P^*)$ nonmonotonously with the parameters $D = 0.8$, $r = 1.5$, $a = 0.15$, $m = 0.35$, $b = 0.15$, $d = 1$, and $\beta = 0.75$.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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