Random dispersal in a predator-prey-parasite model

Abstract.

1 Introduction

An intermediate host is a host that harbors the parasite only for a short transition period of time, during which some developmental stage may be completed. On the other hand, a definitive host is a host in which the parasite reaches maturity and reproduces within the host.

2 A deterministic predator-prey-parasite model

Similar to the model studied in [11], it is assumed that the parasite under consideration is a microparasite so that the parasite population is not explicitly modeled in the interaction. There are only two interacting species prey and predator in the model. Individuals in each species are classified as either infected or uninfected. Let x_1 and x_2 denote the uninfected and infected prey populations respectively, and y_1 and y_2 be the corresponding predators. The prey population in the absence of the predator and the parasite is modeled by a simple logistic equation with per capita growth rate r and carrying capacity $1/q$. It is assumed that the infected prey does not reproduce.

We use a simple Holling type I functional response, and let e denote the predator conversion rate. Since infected prey may increase its likelihood of being preyed upon due to the disease, we let θ_1 denote the factor that affects the predator-prey interaction. The predator preys on both infected and uninfected prey indiscriminately when $\theta_1 = 1$. If $\theta_1 < 1$, then the infected prey has a less chance of being captured. The infected prey will be more likely to be preyed upon if $\theta_1 > 1$. The natural death rates of the infected prey and predator are denoted by d_1 and d_2 respectively. The disease related mortality rates of the prey and predator populations are denoted by α_1 and α_2, respectively. These parameters are assumed to be constants.

Disease can be transmitted in two ways. An uninfected prey will become infected if it makes contact with an infected predator. Similarly, an uninfected predator will become infected if it contacts with an infected prey.

A simple mass action is used to model the force of infection between uninfected prey and infected predator with $\beta > 0$ being the contact rate. In this model, we also assume that the infected predator may be less competitive in catching the prey and let θ_2, $0 < \theta_2 \le 1$, denote the fraction of competitiveness. The infected predator has the same efficiency as an uninfected predator in catching the prey if $\theta_2 = 1$. Otherwise, the infected predator is less competitive. Under these biological assumptions, the model takes the following form:

$$\begin{cases} \dfrac{dx_1}{dt} = rx_1(1 - qx_1) - \delta x_1(y_1 + \theta_2 y_2) - \beta x_1 y_2 \\ \dfrac{dx_2}{dt} = \beta x_1 y_2 - (d_1 + \alpha_1)x_2 - \delta\theta_1 x_2(y_1 + \theta_2 y_2) \\ \dfrac{dy_1}{dt} = e\delta x_1 y_1 - \delta\theta_1 x_2 y_1 - d_2 y_1 \\ \dfrac{dy_2}{dt} = \delta\theta_1 x_2 y_1 - (d_2 + \alpha_2)y_2 \\ x_i(0) \ge 0,\ y_i(0) \ge 0, i = 1, 2, \end{cases} \tag{2.1}$$

where all the parameters are positive with $0 < e \le 1$ and $0 < \theta_2 \le 1$. For simplicity, we let

$$\gamma = d_1 + \alpha_1 \text{ and } \hat{\gamma} = d_2 + \alpha_2. \tag{2.2}$$

System (2.1) along with a parallel continuous-time Markov chain model were studied in [11] when $\theta_2 = 1$. It is illustrated in [11] via numerical simulations that the system with $\theta_2 = 1$ has a unique positive periodic solution when the interior steady state of the deterministic model loses its stability. There are no complicated dynamical behavior such as quasi-periodic solutions or chaos exhibited in the system when $\theta_2 = 1$.

Let $\mathbb{R}_+ = \{x \in \mathbb{R} : x \ge 0\}$ and $\mathbb{R}^4_+ = \{(x_1, x_2, y_1, y_2) \in \mathbb{R}^4 : x_i \ge 0,\ y_i \ge 0,\ i = 1, 2\}$. The following standard analysis (c.f. [14]) shows that model (2.1) is biologically sound.

Lemma 2.1 *Solutions of (2.1) exist for $t > 0$, remain nonnegative, and are bounded.*

Proof. Since $x_1'|_{x_1=0} = y_1'|_{y_1=0} = 0$ and $x_2'|_{x_2=0} \ge 0$ and $y_2'|_{y_2=0} \ge 0$, solutions of (2.1) remain nonnegative on the domain for which they are defined. Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be a solution of (2.1). Suppose that the solution exists on $[0, t_0)$, where $t_0 < \infty$. Since $x_1' \le rx_1(1 - qx_1)$, there exists $M > 0$ such that $rx_1(t)(2 - qx_1(t)) \le M$ for $t \in [0, t_0)$. Let $X = x_1 + x_2 + y_1/e + y_2$. Then $X' \le M - m_0 X$, where $m_0 = \min\{r, \gamma, d_2\} > 0$. It follows that $X(t)$ is bounded on $[0, t_0)$ and thus the solution is bounded on $[0, t_0)$. Therefore, the solution can be extended to be defined on $[0, \infty)$ with $\limsup_{t\to\infty} X(t) \leq \dfrac{M}{m_0}$. ■

In the absence of the parasite, system (2.1) reduces to the following classical Lotka-Volterra predator-prey model with logistic growth in the prey

$$\begin{cases} x_1' = rx_1(1 - qx_1) - \delta x_1 y_1 \\ y_1' = (e\delta x_1 - d_2)y_1. \end{cases} \tag{2.3}$$

It is known that the interior steady state $(\bar{x}_1, \bar{y}_1)$ exists if $e\delta > qd_2$, where

$$\bar{x}_1 = \frac{d_2}{e\delta} \text{ and } \bar{y}_1 = \frac{r}{\delta}(1 - q\bar{x}_1), \tag{2.4}$$

and $(\bar{x}_1, \bar{y}_1)$ is globally asymptotically stable in $\{(x_1, y_1) \in \mathbb{R}_+^2 : x_1, y_1 > 0\}$. Therefore, in the absence of the parasite, the predator and prey populations can coexist as a stable interior equilibrium if $e\delta > qd_2$. On the other hand if $e\delta < qd_2$, then the predator population y_1 goes extinct and the prey population x_1 will stabilize at the carrying capacity level $1/q$ if $x_1(0) > 0$.

System (2.1) always has two steady states $E_0 = (0, 0, 0, 0)$ and $E_1 = (1/q, 0, 0, 0)$ which are independent of the parameters θ_i, $i = 1, 2$. The Jacobian matrix of system (2.1) evaluated at E_0 and E_1 are given by

$$J(E_0) = \begin{pmatrix} r & 0 & 0 & 0 \\ 0 & -\gamma & 0 & 0 \\ 0 & 0 & -d_2 & 0 \\ 0 & 0 & 0 & -(d_2 + \alpha_2) \end{pmatrix} \tag{2.5}$$

and

$$J(E_1) = \begin{pmatrix} -r & 0 & -\delta/q & -(\delta\theta_2 + \beta)/q \\ 0 & -\gamma & 0 & \beta/q \\ 0 & 0 & \dfrac{e\delta}{q} - d_2 & 0 \\ 0 & 0 & 0 & -(d_2 + \alpha_2) \end{pmatrix}, \tag{2.6}$$

respectively. We see that E_0 is always unstable and E_1 is locally asymptotically stable if $e\delta < d_2 q$ and unstable if $e\delta > d_2 q$. It can be easily shown that E_1 is globally asymptotically stable whenever it is locally asymptotically stable. The proof of the following lemma is similar to [11, Lemma 2.2] and is omitted.

Lemma 2.2 *If $e\delta < d_2 q$, then $E_1 = (1/q, 0, 0, 0)$ is globally asymptotically stable in $\{(x_1, x_2, y_1, y_2) \in \mathbb{R}_+^4 : x_1 > 0\}$.*

We now assume $e\delta > d_2 q$ for the remaining discussion. Then E_1 is unstable and (2.1) has another boundary steady state $E_2 = (\bar{x}_1, 0, \bar{y}_1, 0)$, where $(\bar{x}_1, \bar{y}_1)$ is given in (2.4). The Jacobian matrix evaluated at E_2 has the form

$$J(E_2) = \begin{pmatrix} -rq\bar{x}_1 & 0 & -\delta\bar{x}_1 & -(\delta\theta_2 + \beta)\bar{x}_1 \\ 0 & -\gamma - \delta\theta_1\bar{y}_1 & 0 & \beta\bar{x}_1 \\ e\delta\bar{y}_1 & -\delta\theta_1\bar{y}_1 & 0 & 0 \\ 0 & \delta\theta_1\bar{y}_1 & 0 & -(d_2 + \alpha_2) \end{pmatrix}, \tag{2.7}$$

which is similar to the following matrix:

$$\begin{pmatrix} -rq\bar{x}_1 & -\delta\bar{x}_1 & 0 & -(\delta\theta_2 + \beta)\bar{x}_1 \\ e\delta\bar{y}_1 & 0 & -\delta\theta_1\bar{y}_1 & 0 \\ 0 & 0 & -\gamma - \delta\theta_1\bar{y}_1 & \beta\bar{x}_1 \\ 0 & 0 & \delta\theta_1\bar{y}_1 & -(d_2 + \alpha_2) \end{pmatrix}.$$

Let J_1 and J_2 denote the upper-left and lower-right 2×2 submatrices of the above matrix, respectively. It follows that E_2 is locally asymptotically stable if $det J_2 > 0$, i.e., if

$$(\gamma + \delta\theta_1\bar{y}_1)(d_2 + \alpha_2) - \frac{\beta\theta_1}{e} d_2\bar{y}_1 > 0. \tag{2.8}$$

Since (2.8) holds if $\bar{y}_1 > 0$ is small, E_2 is locally asymptotically stable when E_1 just losses its stability. Define

$$R_0 = \frac{\beta\theta_1 d_2\bar{y}_1}{e(\gamma + \delta\theta_1\bar{y}_1)(d_2 + \alpha_2)}. \tag{2.9}$$

Then (2.8) is equivalent to $R_0 < 1$. The following result provides a sufficient condition for E_2 to be globally asymptotically stable. The proof is similar to the proof of Lemma 2.3 in [11] and is therefore omitted.

Lemma 2.3 *Let $e\delta > qd_2$. Then $E_2 = (\bar{x}_1, 0, \bar{y}_1, 0)$ is globally asymptotically stable in $\{(x_1, x_2, y_1, y_2) \in \mathbb{R}^4_+ : x_1 > 0, y_1 > 0\}$ if $d_2 + \alpha_2 > \frac{\beta}{q}$.*

Observe that the sufficient condition $d_2 + \alpha_2 > \frac{\beta}{q}$ given in Lemma 2.3 holds if the disease induced mortality α_2 of the infected predator is large. In this case the infection is too lethal and the disease cannot persist in the populations.

Since $tr^2(J_2) - 4det(J_2) = (\gamma + \delta\theta_1\bar{y}_1 - (d_2 + \alpha_2))^2 + 4\frac{\theta_1\beta d_2}{e}\bar{y}_1 > 0$, E_2 cannot lose its stability through a Hopf bifurcation. We shall study the existence of a coexisting steady state. Let (x_1, x_2, y_1, y_2) denote a positive equilibrium. A straightforward calculation shows that the x_1-component must satisfy

$$\frac{d_2}{e\delta} < x_1 < 1/q \tag{2.10}$$

and

$$Ax_1^2 + Bx_1 + C = 0, \tag{2.11}$$

where

$$\begin{aligned} A &= \theta_1 rq(\beta - \theta_2 e\delta) \\ B &= \theta_1 rq\,(\theta_2 d_2 - (d_2 + \alpha_2)) + \gamma e(\delta\theta_2 + \beta) - \theta_1 r(\beta - \theta_2 e\delta) \\ C &= \gamma(d_2 + \alpha_2) - \gamma(\delta\theta_2 + \beta)d_2/\delta - \theta_1 r(\theta_2 d_2 - (d_2 + \alpha_2)). \end{aligned}$$

If x_1^* satisfies (2.10) and (2.11), then the other components of the steady states are given by

$$\begin{aligned} x_2^* &= \frac{e\delta x_1^* - d_2}{\delta\theta_1} \\ y_2^* &= \frac{\theta_1 r x_2^*(1 - qx_1^*)}{d_2 + \alpha_2 + \delta\theta_1\theta_2 x_2^* + \theta_1\beta x_2^*} \\ y_1^* &= \frac{(d_2 + \alpha_2)y_2^*}{\delta\theta_1 x_2^*}, \end{aligned}$$

which are positive by (2.10). Consequently, the number of interior steady states of (2.1) and the number of solutions of (2.11) that satisfying (2.10) are the same.

Let $f(x) = Ax^2 + Bx + C$. The following theorem shows that the system is uniformly persistent and has a unique interior steady state if E_2 is unstable, and system (2.1) has no interior steady state if E_2 is locally asymptotically stable.

Theorem 2.4 *Let $e\delta > qd_2$. Then (2.1) has no interior steady state if $R_0 < 1$ and (2.1) has a unique interior steady state $E^* = (x_1^*, x_2^*, y_1^*, y_2^*)$ if $R_0 > 1$. Moreover, system (2.1) is uniformly persistent if $R_0 > 1$.*

Proof. Observe that

$$f(1/q) = \gamma(d_2 + \alpha_2) - \gamma(\delta\theta_2 + \beta)(d_2/\delta - e/q) > 0$$

and

$$f(\frac{d_2}{e\delta}) = \gamma(d_2 + \alpha_2) + \theta_1 r(d_2 + \alpha_2) - \frac{\theta_1 rqd_2(d_2 + \alpha_2)}{e\delta} - \frac{\theta_1 r\beta d_2}{e\delta} + \frac{\theta_1 rq\beta d_2^2}{e^2\delta^2}.$$

Substituting the expression of $\bar{y}_1$ in (2.4) into the left hand side of (2.8), it can be shown that the left hand side of (2.8) is $f(\frac{d_2}{e\delta})$ given above. Thus $R_0 < 1$ if and only if $f(\frac{d_2}{e\delta}) > 0$.

Suppose $R_0 < 1$. Then $f(1/q) > 0$ and $f(\frac{d_2}{e\delta}) > 0$. If f is concave down, then it is clear that $f(x) = 0$ has no solutions satisfying (2.10). Suppose f is concave up, i.e., $A > 0$. We fix A and B. Then there is no solution satisfying (2.10) if $C < 0$. If $C = 0$, then $f(x) = 0$ has a unique nonzero solution $-\frac{B}{A}$ which is positive if $B < 0$. It is clear that this unique positive solution is less than $\frac{d_2}{e\delta}$ and thus (2.1) has no interior steady states. If $C > 0$, then $f(x) = 0$ has two positive real solutions if $B < 0$ and $B^2 - 4AC > 0$. In this case we have $\frac{-B - \sqrt{B^2 - 4AC}}{2A} < -\frac{B}{2A} < \frac{d_2}{2e\delta}$ and $\frac{-B + \sqrt{B^2 - 4AC}}{2A} < -\frac{B}{A} < \frac{d_2}{e\delta}$. Therefore, system (2.1) has no interior steady state.

On the other hand, if $R_0 > 1$, then $f(\frac{d_2}{e\delta}) < 0$. It is easy to see that $A \leq 0$ is impossible to occur. Indeed, if $A \leq 0$, then since $0 < \theta_2 \leq 1$ and $\beta \leq \theta_2 e\delta$, the left hand side of (2.8) is greater than or equal to $(\gamma + \delta\theta_1\bar{y}_1)(d_2 + \alpha_2) - \theta_1\theta_2\delta d_2\bar{y}_1 > 0$ and we obtain a contradiction. Therefore $A > 0$ and f is concave up. It is then clear that (2.11) has a unique solution satisfying (2.10). It remains to prove uniform persistence of (2.1). This is done by looking at the boundary dynamics of (2.1). From the Jacobian matrix $J(E_0)$ given in (2.5) we see that the stable manifold of E_0 lies on the $x_2y_1y_2$-hyperplane and the unstable manifold of E_0 lies on the x_1-axis. The stable manifold of E_1 from $J(E_1)$ given in (2.6) can be seen to be spanned by the vectors $(1, 0, 0, 0)^T$, $(0, 1, 0, 0)^T$ and $(x_1, x_2, y_1, y_2)^T$, where T denotes the transpose and $(x_1, x_2, y_1, y_2)^T$ is an eigenvector of $J(E_1)$ with respect to $-(d_2 + \alpha_2)$. A direct calculation shows that we can choose $y_1 = 0$. Hence the stable manifold of E_1 lies on the $x_1x_2y_2$-hyperplane. On the other hand, an eigenvector $(x_1, x_2, y_1, y_2)^T$ of $J(E_1)$ with respect to $\frac{e\delta}{q} - d_2 > 0$ can be chosen as $x_2 = y_2 = 0$, $y_1 = 1$ and $x_1 = \frac{\delta}{q(d_2 - r - \frac{e\delta}{q})} < 0$. Therefore, the unstable manifold of E_1 lies outside of the interior of $\mathbb{R}^4_+$.

We proceed to study the stable and unstable manifolds of E_2. The eigenvalues of $J(E_2)$ are $\lambda_i^{\pm} = \dfrac{trJ_i \pm \sqrt{tr^2J_i - 4detJ_i}}{2}$, $i = 1, 2$, where $\lambda_2^+ > 0$. An eigenvector $(x_1, x_2, y_1, y_2)^T$ associated with λ_2^+ can be chosen so that $y_1 < 0$ and thus the unstable manifold of E_2 lies outside of $\mathbb{R}_+^4$. Furthermore, a straightforward calculation shows that an eigenvector $(x_1, x_2, y_1, y_2)^T$ of $\lambda_2^- < 0$ can be chosen with $y_2 < 0$, i.e., the stable manifold of E_2 also lies outside of $\mathbb{R}_+^4$. Therefore the boundary dynamics of (2.1) is acyclic with acyclic covering $\{E_0, E_1, E_2\}$. Since each of the stable set of E_i does not intersect with the interior of $\mathbb{R}_+^4$, the system is uniformly persistent by [3]. ■

Notice $x_1^* > \bar{x}_1$ by (2.10), and $y_1^* = \dfrac{r(1-qx_1^*)}{\delta} - \dfrac{\beta y_2^*}{\delta} - \theta_2 y_2^* < \dfrac{r(1-q\bar{x}_1)}{\delta} = \bar{y}_1$. Therefore, the uninfected predator has a smaller population size and the uninfected prey has a larger population size in the coexisting steady state where infected populations are present. This is probably because infection causes prey to be easier to be preyed upon so that the predator concentrates more on the infected prey and the uninfected prey can thus survive better. The linearization of (2.1) at E^* yields the following Jacobian matrix

$$J(E^*) = \begin{pmatrix} -rqx_1^* & 0 & -\delta x_1^* & -\delta\theta_2 x_1^* - \beta x_1^* \\ \beta y_2^* & -\gamma - \delta\theta_1(y_1^* + \theta_2 y_2^*) & -\delta\theta_1 x_2^* & \beta x_1^* - \delta\theta_1\theta_2 x_2^* \\ e\delta y_1^* & -\delta\theta_1 y_1^* & 0 & 0 \\ 0 & \delta\theta_1 y_1^* & \delta\theta_1 x_2^* & -\hat{\gamma} \end{pmatrix} \tag{2.12}$$

The characteristic polynomial $P(\lambda)$ of $J(E^*)$ is

$$P(\lambda) = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4, \tag{2.13}$$

where

$$\begin{aligned}
a_1 &= rqx_1 + \delta\theta_1(y_1 + \theta_2 y_2) + \gamma \\
a_2 &= \delta(e\delta - \beta\theta_1 + rq\theta_1)x_1y_1 + rq\delta\theta_1\theta_2 x_1 y_2 + \delta^2\theta_1^2(\theta_2 - 1)x_2y_1 \\
&+ rq(\gamma + \hat{\gamma})x_1 + \delta\theta_1\hat{\gamma}y_1 + \delta\theta_1\theta_2\gamma y_2 + \gamma\hat{\gamma} \\
a_3 &= -\delta^3\theta_1^3\theta_2 x_2^2 y_1 + e\delta^3\theta_1 x_1 y_1^2 + \delta^2\theta_1\left(\theta_1\beta + e\beta - \theta_1 rq(1-\theta_2)\right)x_1x_2y_1 \\
&+ -rq\delta\theta_1\beta x_1^2 y_1 + \left(\beta\delta\theta_1(\beta + \delta(\theta_2 - 1)) + e\delta^3\theta_1\theta_2\right)x_1y_1y_2 \\
&+ \left(e\delta^2\hat{\gamma} + \delta(e\delta\gamma + rq\theta_1 d_2)\right)x_1y_1 - \delta^2\theta_1^2\gamma x_2 y_1 + rq\delta\theta_1\theta_2\hat{\gamma}x_1y_2 + r\gamma q d_2 + \alpha_2 x_1 \\
a_4 &= (rq\delta^2\theta_1^2 y_1 x_2 \beta - e\delta^3 {y_1}^2\theta_1\beta){x_1}^2 \\
&+ (-rq\delta^3\theta_1^3 y_1 {x_2}^2\theta_2 + (e\delta^4 {y_1}^2\theta_1^2\theta_2 + ((-\beta^2\delta^2\theta_1^2 - \beta\delta^3\theta_1^2\theta_2 \\
&+ e\delta^3\theta_1^2\theta_2\beta + e\delta^4\theta_1^2\theta_2^2)y_2 - rq\delta^2\theta_1^2\gamma + e\delta^3\gamma\theta_1\theta_2)y_1)x_2 + e\delta^3\theta_1\gamma {y_1}^2 \\
&+ ((-\beta\delta^2\theta_1 d_2 - \beta\delta^2\theta_1\alpha_2 + e\delta^3\theta_1\theta_2\gamma y_2 + e\delta^2\gamma d_2 e\delta^2\gamma\alpha_2 y_1)x_1
\end{aligned}$$

with x_i^* dented by x_i and y_i^* denoted by y_i, $1 \le i \le 2$, for simplicity. Since coefficients of $P(\lambda)$ involve complex expressions, it is not easy to study local stability of E^* analytically using linearization technique. In the following we first use the center manifold theory as described in [**?**, Theorem 4.1] to prove local stability of E^* when $R_0 > 1$ is close to 1. For the convenience of the reader, [**?**, Theorem 4.1] is presented in Appendix A.

Denote y_1 by x_3 and y_2 by x_4 and let $f_i(x_1, x_2, x_3, x_4)$, $i = 1, \cdots, 4$, be the right hand side of (2.1). The Jacobian matrix of (2.1) evaluated at E_2, $J(E_2)$, is given in (2.7). Let $\theta_{1c} > 0$ denote the value of θ_1 for which $R_0 = 1$, i.e.,

$$\theta_{1c} = \frac{e\gamma(d_2 + \alpha_2)}{\bar{y}_1(\beta d_2 - e\delta(d_2 + \alpha_2))}, \tag{2.14}$$

where it is implicitly assumed that $\beta d_2 > e\delta(d_2 + \alpha_2)$. At $\theta_1 = \theta_{1c}$, we have $R_0 = 1$ and $det(J_2) = 0$. Therefore, $J(E_2)$ has 0 as a simple eigenvalue and the rest of the eigenvalues have negative real parts when $\theta_1 = \theta_{1c}$. Within scalar multiplications, the right eigenvector $w = (w_1 \ w_2 \ w_3 \ w_4)^T$ of $J(E_2)$ with respect to 0 has components

$$w_1 = 1, \ w_2 = \frac{e}{\theta_{1c}}, \ w_3 = \frac{-rq - (\delta\theta_2 + \beta)w_4}{\delta}, \ w_4 = \frac{(\gamma + \delta\theta_{1c}\bar{y}_1)w_2}{\beta\bar{x}_1}$$

while the components of the left eigenvector $v = (v_1 \ v_2 \ v_3 \ v_4)$ needed to be chosen so that $v \cdot w = 1$, $v_2 > 0$, and $v_4 > 0$ [15]. A simple calculation yields

$$v_1 = 0, \ v_2 = \frac{-(d_2 + \alpha_2)}{\Delta}, \ v_3 = 0, \ v_4 = \frac{-\beta\bar{x}_1}{\Delta},$$

where

$$\Delta = -\left((d_2 + \alpha_2) + (\gamma + \delta\theta_{1c}\bar{y}_1)\right) w_2 < 0.$$

The local bifurcation of E_2 at $\theta_1 = \theta_{1c}$ depends on the signs of a and b, where

$$a = \sum_{i,j,k=1}^{4} v_k w_i w_j \frac{\partial^2 f_k}{\partial x_i \partial x_j}(E_2)$$

and

$$b = \sum_{i,k=1}^{4} v_k w_i \frac{\partial^2 f_k}{\partial x_i \partial \theta_1}(E_2),$$

with θ_1 evaluated at θ_{1c}. The bifurcation is to the right and the interior steady state E^* is locally asymptotically stable for $\theta_1 > \theta_{1c}$ and close to θ_{1c} if $a < 0$ and $b > 0$ [**?**, Theorem 4.1].

Toward this end, the nonzero partial derivatives of f_i with respect to the state variables and the parameter θ_1 evaluated at E_2 with $\theta = \theta_{1c}$ are given by

$$
\begin{array}{lll}
\dfrac{\partial^2 f_1}{\partial x_1^2} = -2rq, & \dfrac{\partial^2 f_1}{\partial x_1 \partial x_3} = -\delta, & \dfrac{\partial^2 f_1}{\partial x_1 \partial x_4} = -\delta\theta_2 - \beta, \\
\dfrac{\partial^2 f_2}{\partial x_1 \partial x_4} = \beta, & \dfrac{\partial^2 f_2}{\partial x_2 \partial x_3} = -\delta\theta_{1c}, & \dfrac{\partial^2 f_2}{\partial x_2 \partial x_4} = -\delta\theta_{1c}\theta_2, \\
\dfrac{\partial^2 f_3}{\partial x_1 \partial x_3} = e\delta, & \dfrac{\partial^2 f_3}{\partial x_2 \partial x_3} = -\delta\theta_{1c}, & \dfrac{\partial^2 f_4}{\partial x_2 \partial x_3} = \delta\theta_{1c}, \\
\dfrac{\partial^2 f_2}{\partial x_2 \partial \theta_1} = -\delta\bar{y}_1, & \dfrac{\partial^2 f_3}{\partial x_2 \partial \theta_1} = -\delta\bar{y}_1, & \dfrac{\partial^2 f_4}{\partial x_2 \partial \theta_1} = \delta\bar{y}_1.
\end{array}
$$

By continuity, $\dfrac{\partial^2 f_i}{\partial x_j \partial x_k} = \dfrac{\partial^2 f_i}{\partial x_k \partial x_j}$ for all $1 \leq i, j, k \leq 4$. As a consequence,

$$
\begin{aligned}
b &= v_2 w_2 \frac{\partial^2 f_2}{\partial x_2 \partial \theta_1} + v_4 w_2 \frac{\partial^2 f_4}{\partial x_2 \partial \theta_1} \\
&= \delta\bar{y}_1 w_2 (v_4 - v_2) \\
&= -\frac{\delta\bar{y}_1}{e\delta\Delta} w_2 (\beta d_2 - e\delta(d_2 + \alpha_2)) > 0,
\end{aligned}
$$

and

$$
\begin{aligned}
a &= 2(v_2 w_1 w_4 \frac{\partial^2 f_2}{\partial x_1 \partial x_4} + v_2 w_2 w_3 \frac{\partial^2 f_2}{\partial x_2 \partial x_3} + v_2 w_2 w_4 \frac{\partial^2 f_2}{\partial x_2 \partial x_4} + v_4 w_2 w_3 \frac{\partial^2 f_4}{\partial x_2 \partial x_3}) \\
&= \frac{2}{\Delta} \left(\theta_2 \delta\bar{y}_1 (\beta - e\delta) + (\beta\bar{x}_1 - (d_2 + \alpha_2))(rq + \frac{e\delta(\delta\theta_2 + \beta)\bar{y}_1}{d_2 + \alpha_2}) \right) \\
&< 0
\end{aligned}
$$

since $\beta d_2 > e\delta(d_2 + \alpha_2)$. We conclude from the center manifold theory that the bifurcation at $\theta_1 = \theta_{1c}$ is to the right and hence the interior steady state E^* is locally asymptotically stable when $\theta_1 > \theta_{1c}$ is close to θ_{1c}. We summarize below.

Lemma 2.5 *Let $e\delta > d_2 q$ and $R_0 > 1$. Then (2.1) has a unique interior steady state E^*. Moreover, E^* is locally asymptotically stable if $R_0 > 1$ is sufficiently close to* 1.

Notice that θ_{1c} given in (2.14) is independent of θ_2. To study (2.1) further, we choose parameter values so that $e\delta > qd_2$ and $R_0 > 1$:

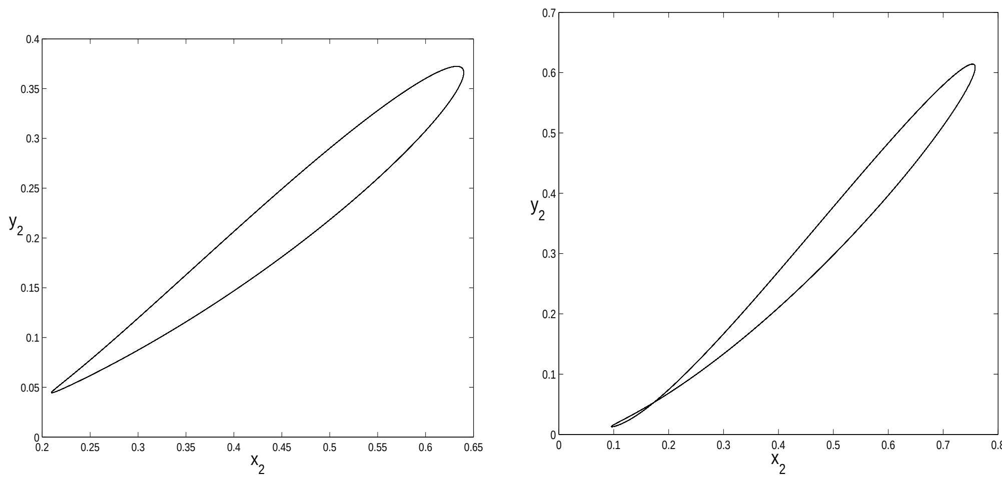
$$q = 0.2,\ \beta = 2.0,\ \gamma = 0.7,\ \delta = 0.38,\ \alpha_2 = 0.5,\ d_2 = 0.3,\ e = 1,\ r = 0.7.$$

Then $\theta_{1c} = 1.21959$. When $\theta_1 = \theta_2 = 1$, there is no interior steady state by Theorem 2.4 and our simulations suggest that the boundary steady state E_2 is globally asymptotically stable. We then increase θ_1 to $\theta_1 = 1.5 > \theta_{1c} = 1.21959$ and keep $\theta_2 = 1$. We have $R_0 = 1.189165 > 1$ so that E_2 is unstable and there exists a unique interior steady state E^* by Theorem 2.4. Simulations using several randomly chosen positive initial conditions all converge to E^* for this set of parameter values. We then increase θ_1 to $\theta_1 = 1.8$ and use $\theta_2 = 1$. In this case, simulations with randomly chosen positive initial conditions converge to the interior steady state $E^* = (x_1^*, x_2^*, y_1^*, y_2^*)$ with $x_2^* = 0.3618$ and $y_2^* = 0.1381$. When θ_2 decreases to $\theta_2 = 0.01$, then E^* becomes unstable and there exists a positive periodic solution which seems to be locally asymptotically attracting according to the simulations. Figure 1(a) plots x_2-y_2 components of the periodic solution. The same dynamical behavior occurs as we decrease θ_2 further to $\theta_2 = 0.001$ and also increase θ_1 to $\theta_1 = 2.8$. The $x_2 y_2$ projection of the positive periodic solution is given in Figure 1(b). From this numerical study we see that a decrease of the parameter value θ_2 can make the population interaction more unstable.

Although not present in this study, simulations of many different randomly chosen positive initial conditions with different values of θ_1 and θ_2 do seem converge to the positive periodic solution. Moreover, as we increase θ_1, the values of θ_2 for which a positive periodic solution appears seem become larger. We conclude from this numerical study that system (2.1) also has no complicated dynamical behavior as in the case when $\theta_2 = 1$. This is expected if θ_2 remains close to 1 by the previous study in [11] along with continuous dependence of solutions on parameters. However, we tested the system for small θ_2.

3 A predator-prey-parasite model with diffusion

In this section we will study the impact of dispersal upon the interaction of infected and uninfected prey and predator. We assume that individuals of both infected and uninfected populations of prey and predator can disperse randomly. For simplicity, the spatial domain is one dimensional with $0 \leq x \leq l$, and the diffusion coefficients for the uninfected and infected prey and predator are denoted by D_i, $1 \leq i \leq 4$, respectively. These parameters are assumed to be independent of time, space and populations. Since we can always re-scale our independent and dependent variables, we will assume $l = 1$ for convenience. Let $N_i(x,t)$ and $P_i(x,t)$, $i = 1, 2$, be the population densities of uninfected and infected prey and predator at time t and location



(a) (b)

Figure 1: The plots provide the x_2 and y_2 components of the positive periodic solution when $\theta_1 = 1.8$, $\theta_2 = 0.01$ in (a) and $\theta_1 = 2.8$, $\theta_2 = 0.001$ in (b).

x, respectively. The model is given below:

$$\begin{aligned}
\frac{\partial N_1}{\partial t} &= rN_1(1-qN_1) - \delta N_1(P_1+\theta_2 P_2) - \beta N_1 P_2 + D_1\frac{\partial^2 N_1}{\partial x^2} \\
\frac{\partial N_2}{\partial t} &= \beta N_1 P_2 - (d_1+\alpha_1)N_2 - \delta\theta_1 N_2(P_1+\theta_2 P_2) + D_2\frac{\partial^2 N_2}{\partial x^2} \\
\frac{\partial P_1}{\partial t} &= e\delta N_1 P_1 - \delta\theta_1 N_2 P_1 - d_2 N_1 + D_3\frac{\partial^2 P_1}{\partial x^2} \\
\frac{\partial P_2}{\partial t} &= \delta\theta_1 N_2 P_1 - (d_2+\alpha_2)P_2 + D_4\frac{\partial^2 P_2}{\partial x^2} \\
N_i(x,0) &= \psi_i(x),\ P_i(x,0) = \varphi_i(x),\ 0<x<1,\ 1\le i\le 2,
\end{aligned} \tag{3.1}$$

where parameters $r, q, \delta, \beta, \theta_1, \theta_2, \gamma, d_2, \alpha_2$ have the same biological meanings as in the previous model (2.1), $D_i > 0$, and ψ_i and φ_i are bounded continuous functions on $[0,1]$, $1 \le i \le 2$.

We shall study the effects of diffusion upon stability of the homogeneous steady state solutions. In particular, we assume $e\delta > qd_2$ and $R_0 > 1$ so that the spatially homogeneous system (2.1) has a unique interior steady state $E^* = (x_1^*, P_2^*, y_1^*, y_2^*)$. Let $\mathbf{D}$ denote the diagonal matrix $diag(D_1, D_2, D_3, D_4)$. Let $\phi_1 = N_1 - x_1^*$, $\phi_2 = N_2 - x_2^*$, $\phi_3 = P_1 - y_1^*$, $\phi_4 = P_2 - y_2^*$ and $\Phi = (\phi_1, \phi_2, \phi_3, \phi_4)^T$. The linearization of the reaction-diffusion system

(3.1) about E^* yields the following linear system

$$\Phi_t = \mathbf{D}\Phi_{xx} + J(E^*)\Phi, \tag{3.2}$$

where $J(E^*)$ is given by (2.11). Suppose a solution of (3.2) is of the form

$$\Phi = (v_1, v_2, v_3, v_4)^T e^{ikx+\lambda t},$$

where $i = \sqrt{-1}$, λ is an eigenvalue, and k is a wave number. A simple calculation yields

$$\left(J(E^*) - k^2 D - \lambda I\right)(v_1, v_2, v_3, v_4)^T = 0.$$

In order for a nontrivial solution to exist, it is necessary that

$$det(J(E^*) - k^2\mathbf{D} - \lambda I) = 0.$$

The resulting characteristic equation has the form

$$Q(\lambda) = \lambda^4 + b_1(k^2)\lambda^3 + b_2(k^2)\lambda^2 + b_3(k^2)\lambda + b_4(k^2) = 0, \tag{3.3}$$

where coefficients b_i, $i = 1, \cdots, 4$, are much more complicated than those a_i, $i = 1, \cdots, 4$, given in $P(\lambda)$ for the spatial homogeneous model (2.1). However, $b_i(0) = a_i$ for $1 \le i \le 4$.

We next study (3.1) numerically. We choose the same parameter values as in the homogeneous system (2.1):

$$q = 0.2,\ \beta = 2.0,\ \gamma = 0.7,\ \delta = 0.38,\ \alpha_2 = 0.5,\ d_2 = 0.3,\ e = 1,\ r = 0.7.$$

Then $\theta_{1c} = 1.21959$. Let

We plot the maximum real parts of the zeros of $Q(\lambda)$ against k^2 in Figure 3(a), where it can be seen that the maximum real part of the eigenvalues remain below -0.03 for k^2 large. Although it is not presented in this manuscript, the simulation was run for k^2 up to 10000. We then increase D_1 and D_2 to 10 and 50 respectively and even larger to test for diffusion driven instability. The same numerical result is obtained. Therefore for these parameter values where the homogeneous steady state is locally asymptotically stable, there is no Turing instability observed in (3.1). We now change θ_1 to 60 and $\theta_2 = 0.003$. Notice from Figure 1 we see that the homogeneous steady state is unstable. When $D_1 = 20$ and $D_2 = 80$, the maximum real part of the eigenvalues is about 0.0203 when $k^2 = 0$ as can be seen from Figure 1. However, as we increase k^2 up to 1 then the maximum real part of the eigenvalue decreases to negative and then increases when k^2 is larger than 1. However, the maximum real part of the eigenvalues remains negative. The same numerical result is obtained if we increase D_1 and D_2 up to few hundreds. We conclude that diffusion can stabilize the homogeneous steady state.

4 Discussion

A Appendix

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