Convective instability  
in a diffusive predator–prey system

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Abstract. It is well known that biological pattern formation is the Turing mechanism, in  
which a homogeneous steady state is destabilized by the addition of diffusion, though  
it is stable in the kinetic ODEs. However, steady states that are unstable in the kinetic  
ODEs are rarely mentioned. This paper concerns a reaction diffusion advection system  
under Neumann boundary conditions, where steady states that are unstable in the ki-  
netic ODEs. Our results provide a stabilization strategy for the same steady state, the  
combination of large advection rate and small diffusion rate can stabilize the homoge-  
neous equilibrium. Moreover, we investigate the existence and stability of nonconstant  
positive steady states to the system through rigorous bifurcation analysis.

Keywords: diffusion, advection, predator–prey, instability.

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1 Introduction

The central player in mathematical biology models is the stability of steady states. It is well  
known that biological pattern formation is the Turing mechanism, in which a homogeneous  
steady state that is stable in the kinetic ODEs is destabilised by the addition of diffusion terms.  
However, steady states that are unstable in the kinetic ODEs are almost never mentioned. As  
a result, there is a widespread assumption that unstable steady states are not biologically  
significant as PDE solutions.

The objective of this paper is to explain how diffusion and advection can turn an unstable  
steady state of kinetic ODEs to a stable one, to illustrate their implications for PDE models  
of biological systems. For that purpose, we investigate the spatially extended Rosenzweig–
MacArthur model for predator–prey interaction in river, which was proposed in [3]:

\[
\begin{align*}
P_t &= d_1(P_{xx} - \alpha P_x) + P \left(1 - P - \frac{mN}{a + P}\right), \quad (0, L) \times (0, +\infty), \\
N_t &= N_{xx} - \alpha N_x - dN + \frac{mPN}{a + P}, \quad (0, L) \times (0, +\infty), \\
P_x(0, t) = P_x(L, t) = N_x(0, t) = N_x(L, t) = 0, \quad t > 0, \\
P(x, 0) = P_0(x) \geq 0, N(x, 0) = N_0(x) \geq 0, \quad x \in (0, L),
\end{align*}
\]

(1.1)

where \(P(x, t)\) and \(N(x, t)\) denote predator and prey densities, which depend on space \(x\) and time \(t\). Here, and throughout this paper, we restrict attention to one space dimension \((0, L)\), though our analysis carries over to multi-dimensions. Most predator–prey studies do not include advection terms, advection of this type arises naturally in river-based predator–prey systems [3] and \(\alpha\) is the convective rate of unidirectional flow. The parameter \(d_1\) is the random diffusion rate of the prey and the random diffusion rate of the predator is rescaled to 1. The prey consumption rate per predator is an increasing saturating function of the prey density with Holling type II form: \(m\) reflects how quickly the consumption rate saturates as prey density increases, \(a\) is the density of prey necessary to achieve one half the rate. \(d\) is the death rate of the predator, also see [9].

Here the zero Neumann boundary conditions correspond to a long river in which the downstream boundary has little influence, see e.g., [3, 7]. For the same parameter values as used ODEs, the stability of constant steady states does not change in diffusive systems under zero Neumann boundary conditions, see e.g., [12]. We will find a distinguished result for the reaction-diffusion-advection system (1.1): the coexistence steady state of (1.1) becomes stable for large advection rates though it is unstable for the corresponding diffusive system.

Over the past few decades, reaction-diffusion systems have been widely applied and extensively studied to model the spatial-temporal predator–prey dynamics, which can greatly explain the invasion of a prey by predators (e.g., [8]). For the spatial model with advection, there are some recent related works to understand how the diffusion and advection jointly effect population persist over large temporal scales and resist washout in such environment [5,6,13]. Our purpose is to investigate the stabilization effect of advection.

In Section 2, we perform linear stability of the unique equilibrium \((P^*, N^*)\) with respect to (1.1). Our results in Theorem 2.4 indicate that advection and diffusion stabilize the homogeneous equilibrium when the advection is large and diffusion is small, while it still destabilizes predator–prey interactions when the advection is small. This extends the work of [9]. Section 3 is devoted to the steady state bifurcation analysis of (1.1) which establishes the existence of its nonconstant steady states, with advection rate \(\alpha\) being the bifurcation parameter, see Theorem 3.2.

## 2 Linearized stability driven by advection

The system (1.1) has three non-negative constant equilibrium solution \((0, 0), (1, 0), (P^*, N^*)\), where

\[
(P^*, N^*) = \left(\frac{ad}{m - d}, \frac{(a + P^*)(1 - P^*)}{m}\right).
\]
Lemma 2.2. The following statements hold:

1. when \( P^* \geq 1 \), \((1,0)\) is globally asymptotically stable, see \([4]\);
2. when \( 1 - a < P^* < 1 \), \((P^*, N^*)\) is globally asymptotically stable, see \([4]\);
3. \( P^* = \frac{1-a}{2} \) is the unique bifurcation point where a Hopf bifurcation occurs, and the Hopf bifurcation is supercritical and backward;
4. when \( 0 < P^* < \frac{1-a}{2} \), \((P^*, N^*)\) is unstable and there is a globally asymptotically stable periodic orbit, see \([11]\);
5. when \( \frac{1-a}{2} < P^* < 1 \), then (2.1) has no closed orbits in the first quadrant and the positive equilibrium \((P^*, N^*)\) is globally asymptotically stable in the first quadrant, see \([11]\).

Based on this, we always assume that the constants satisfy \(0 < a < 1, P^* > 0\) and \(N^* > 0\) throughout the paper. Following the same process of Theorem 2.1 in \([12]\), we have the existence of solution and a priori bound of the solution to the dynamical equation (1.1).

Lemma 2.2. The following statements hold:

(a) If \( P_0(x) \geq 0 (\neq 0), N_0(x) \geq 0 (\neq 0)\), then (1.1) has a unique solution \((P(x,t), N(x,t))\) such that \(P(x,t) > 0, N(x,t) > 0\) for \(t \in (0, \infty)\) and \(x \in [0,L]\);

(b) For any solution \((P(x,t), N(x,t))\) of (1.1),

\[
\limsup_{t \to +\infty} P(x,t) \leq 1, \quad \int_0^L N(x,t)dx \leq \left( 1 + \frac{(a+1)L}{4d} \right).
\]

Moreover, there exists \(C > 0\) such that

\[
\limsup_{t \to +\infty} N(x,t) \leq C,
\]

where \(C\) is independent of \(P_0, N_0, d_1, a\). If \(d_1 = 1\), then \(N(x,t) \leq \left( 1 + \frac{(a+1)L}{4d} \right)\) for all \(t > 0, x \in [0,L]\).

In the following, we investigate the effect of diffusion and advection on the stability of \((P^*, N^*)\). For the convenience, we denote

\[
\begin{cases}
  f(P,N) = P \left( 1 - P - \frac{mN}{a + P} \right), \\
  g(P,N) = -dN + \frac{mPN}{a + P}.
\end{cases}
\]

Then the linearization of (1.1) at \((P^*, N^*)\) can be expressed by:

\[
\begin{pmatrix}
  \phi_t \\
  \psi_t
\end{pmatrix} = L(\alpha) \begin{pmatrix}
  \phi \\
  \psi
\end{pmatrix} := D \begin{pmatrix}
  \phi_{xx} - \alpha \phi_x \\
  \psi_{xx} - \alpha \psi_x
\end{pmatrix} + J_{(P,N)} \begin{pmatrix}
  \phi \\
  \psi
\end{pmatrix} \tag{2.2}
\]
with domain $X = \{(\phi, \psi) \in H^2((0, L)) \times H^2((0, L)) : \phi_x = \psi_x = 0, x = 0, L\}$, where

$$D = \begin{pmatrix} d_1 & 0 \\ 0 & 1 \end{pmatrix}, \quad I_{(P, N)} = \begin{pmatrix} f_P & f_N \\ g_P & g_N \end{pmatrix},$$

and

$$f_P = \frac{P^* (1 - a - 2P^*)}{(a + P^*)}, \quad f_N = -\frac{mP^*}{(a + P^*)},$$

$$g_P = \frac{a(1 - P^*)}{(a + P^*)}, \quad g_N = 0.$$

From Theorem 5.1.1 of [2], it is known that if all the eigenvalues of the operator $L$ have negative real parts, then $(P^*, N^*)$ is asymptotically stable, otherwise, $(P^*, N^*)$ is unstable.

Thus $\lambda$ is an eigenvalue of $L$ if and only if $\lambda$ is an eigenvalue of the matrix $I_k = -\mu_k D + I_{(P, N)}$ for some $k \geq 0$, where $\mu_k (k = 0, 1, 2, \ldots)$ is the $k$th eigenvalue of the following eigenvalue problem:

$$\begin{cases} 
\phi_{xx} - \alpha \phi_x = -\mu_k \phi, & x \in (0, L), \\
\phi_x(0) = \phi_x(L) = 0. 
\end{cases} \quad (2.3)$$

Since $x \in (0, L)$, we can directly calculate the eigenvalue $\mu_k$ and eigenfunction $\phi_k(x)$ as following:

$$\begin{aligned}
\mu_k &= \left(\frac{k\pi}{L}\right)^2 + \frac{\alpha^2}{4}, \quad k = 0, 1, 2, \ldots, \\
\phi_k(x) &= \alpha e^{\frac{\alpha x}{2}} \cos \left(\frac{k\pi x}{L}\right) + \frac{2k\pi}{L} e^{\frac{\alpha x}{2}} \sin \left(\frac{k\pi x}{L}\right), \quad k = 0, 1, 2, \ldots 
\end{aligned} \quad (2.4)$$

So the stability is reduced to consider the characteristic equation

$$\lambda^2 - \text{Trace}(J_k) \lambda + \text{Det}(J_k) = 0, \quad k = 0, 1, 2, \ldots \quad (2.5)$$

with

$$\text{Trace}(J_k) = -(d_1 + 1)\mu_k + f_P + g_N := -(d_1 + 1)\mu_k + \text{Trace}(J),$$

$$\text{Det}(J_k) = d_1 \mu_k^2 - (d_1 g_N + f_P) \mu_k + f_P g_N - f_N g_P := d_1 \mu_k^2 - (d_1 g_N + f_P) \mu_k + \text{Det}(J). \quad (2.6)$$

We take $\alpha$ as the main bifurcation parameter to observe its effect on the local stability $(P^*, N^*)$. First of all, we list four conditions for the sake of following discussion.

(A1) $f_P^2 + 4d_1 f_N g_P < 0,$

(A2) $f_P^2 + 4d_1 f_N g_P > 0,$

(A3) $d_1 \mu_0^2 - f_P \mu_0 - f_N g_P \leq 0,$

(A4) $d_1 \mu_0^2 - f_P \mu_0 - f_N g_P > 0.$

**Theorem 2.3.** Suppose $P^* \geq \frac{1-a}{2}$. Then $(P^*, N^*)$ is always locally asymptotically stable for any advection rate $\alpha > 0$.

**Proof.** It can find that $f_P \leq 0$ when $P^* \geq \frac{1-a}{2}$. Thus $\text{Trace}(J_k) < 0$ and $\text{Det}(J_k) > 0$ for all $k = 0, 1, 2, \ldots$, which implies the desired results. \qed
**Theorem 2.4.** Suppose \( P^* < \frac{1-a}{2} \).

1. If \(-(d_1 + 1)\mu_0 + f_P > 0\), then \((P^*, N^*)\) is unstable.

2. If there is some \( k \geq 0 \) such that \(-(d_1 + 1)\mu_k + f_P = 0\), then system \((1.1)\) generates a heterogeneous Hopf bifurcation solutions at \((P^*, N^*)\) provided either \((A1)\) holds or \((A2), (A4)\) and \(\mu_0 > \frac{f_P}{2}\) holds.

3. If \(-(d_1 + 1)\mu_0 + f_P < 0\), then \((P^*, N^*)\) is locally asymptotically stable provided either \((A1)\) holds or \((A2), (A4)\) and \(\mu_0 > \frac{f_P}{2}\) holds; and \((P^*, N^*)\) is unstable provided \((A3)\) holds.

**Proof.** It just notices that \(\text{Det}(J_k) > 0\) for all \( k = 0, 1, 2, \ldots \) if either \((A1)\) or \((A2)\) holds; and \(\text{Det}(J_0) < 0\) if \((A3)\) holds.  

**Remark 2.5.** Theorem 2.3 and Theorem 2.4 imply that the advection rate \(\alpha\) makes \((P^*, N^*)\) more stable compared with that for the corresponding ODE system in Lemma 2.1. The periodic solution bifurcating from \((P^*, N^*)\) will disappear when introducing the advection and diffusion; Moreover under the same condition that \((P^*, N^*)\) is unstable for \((2.1)\), there is newborn homogeneous/heterogeneous Hopf bifurcation solutions at \((P^*, N^*)\) or \((P^*, N^*)\) even becomes stable for small diffusion rate \(d_1\) or large advection rate \(\alpha\).

## 3 Existence of non-constant positive steady state

In this section we show that when \((P^*, N^*)\) is unstable, there exist positive non-constant steady state solutions of \((1.1)\). In order to show that we use bifurcation theory to prove the existence of positive non-constant steady state solutions. The bifurcations can be shown with parameter \(\alpha_k(\mu_k)\) as shown in Theorem 2.4. From the relation given in \((2.6)\), we define the potential bifurcation points:

\[
a^2_{k,\pm} = \frac{2f_P \pm 2\sqrt{f_P^2 + 4d_1f_Ng_P}}{d_1} - 4\left(\frac{k\pi}{L}\right)^2, \quad k = 0, 1, 2, \ldots
\]

We have the following properties of \(a_{k,\pm}\):

**Lemma 3.1.** Assume that \((A2)\) holds. Then

1. \(\lim_{k \to \infty} a_{k,\pm} = -\infty\);

2. Both \(a_{k,+}\) and \(a_{k,-}\) are monotonically decreasing with respect to \(k\), there exists \(m, n\) such that \(a_{0,+} \geq a_{1,+} \cdots \geq a_{m,+} \geq 0\) and \(a_{0,-} \geq a_{1,-} \cdots \geq a_{m,-} \geq 0\).

**Theorem 3.2.** Assume that \((A2)\) holds. Let \(a_{k,\pm}\) be defined as in \((3.1)\) such that \(a_{i,+} \neq a_{j,-}\) for any \(0 \leq i \leq m\) and \(0 \leq j \leq n\). Then

1. Near \((a_{i,\pm}, P^*, N^*)\), the set of positive non-constant steady state solutions of \((1.1)\) is a smooth curve \(\Sigma_i = \{(a_i(s), P_i(s), N_i(s)) : s \in (-\epsilon, \epsilon)\}\), where where \(P_i(s) = P^* + sa_i \phi_i(x) + s^2 \psi_{1,i}(s) + O(s^3), N_i(s) = N^* + sb_i \phi_i(x) + s^2 \psi_{2,i}(s) + O(s^3)\) for some smooth functions \(\psi_{1,i}, \psi_{2,i}\) such that \(a_i(s) = a_{i,\pm} + O(s)\) and \(\psi_{1,i}(0) = \psi_{2,i}(0) = 0\); Here \((a_i, b_i)\) satisfies

\[
L(a_i)(a_i, b_i)^T \phi_i(x) = (0, 0)^T.
\]
2. The smooth curve $\Sigma_i$ in part (1) is contained in a connected component $C_i$ of $\Gamma$, which is the closure of the set of positive non-constant steady state solutions of (1.1), and either $C_i$ is unbounded or $C_i$ contains another $(\alpha_{i, \pm}, P^*, N^*)$ with $\alpha_{i, \pm} \neq \alpha_{j, \pm}$.

Proof. The existence and uniqueness of $\alpha_{i, \pm}$ follows from discussions above. Then the local bifurcation result follows the bifurcation theorem in [1], and it is an application of a more general result Theorem 4.3 in [10].

Define a nonlinear mapping

$$F(\alpha, P, N) = \left( \begin{array}{c} d_1(P_{xx} - \alpha P_x) + f(P, N) \\ N_{xx} - \alpha N_x + g(P, N) \end{array} \right)$$

with domain $V = \{(\alpha, P, N) : 0 < \alpha < \alpha_{0, +}, (P, N) \in X \times X\}$, where $X = \{\omega \in H^2((0, L)) : \omega''(0) = \omega''(L) = 0\}$. Then $F(\alpha, P, N) = 0$ is equivalent to the steady state system of (1.1):

$$\begin{cases} d_1(P_{xx} - \alpha P_x) + P \left( 1 - \frac{mN}{a + P} \right) = 0, & x \in (0, L), \\ N_{xx} - \alpha N_x - dN + \frac{mPN}{a + P} = 0, & x \in (0, L), \\ P_x(0) = P_x(L) = N_x(0) = N_x(L) = 0. \end{cases}$$

(3.2)

It is observed that $F(\alpha, P, N) = 0$ for all $\alpha > 0$. For any $(\alpha, P^*, N^*) \in V$, the The Fréchet derivative of $F$ is given by

$$D_{(P, N)}F(\alpha, P^*, N^*)(P, N) = \left( \begin{array}{c} d_1(P_{xx} - \alpha P_x) + f_P P + f_N N \\ N_{xx} - \alpha N_x + g_P P + g_N N \end{array} \right).$$

Then $D_{(P, N)}F(\alpha_{i, \pm}, P^*, N^*)(P, N)$ is a Fredholm operator with index zero by Corollary 2.11 in [10].

We show that the conditions for Theorem 4.3 in [10] are satisfied in several steps.

Step 1. $\dim N(D_{(P, N)}F(\alpha_{i, \pm}, P^*, N^*)) = 1$.

From the definition of $\alpha_{i, \pm}$, it is easy to verify that $\det(f_i) = 0$, hence zero is an eigenvalue of $f_i$ with an eigenvector $(a_{i, 1}, b_{i, 1}) = (g_P, d_1 \mu_i)$, then $V_i = \{g_P, d_1 \mu_i\}$ is a vector space, thus one has $N(D_{(P, N)}F(\alpha_{i, \pm}, P^*, N^*)) = \text{span}\{V_i\}$ which is one-dimensional. Note that we also have that $\text{codim} R(D_{(P, N)}F(\alpha_{i, \pm}, P^*, N^*)) = 1$ as $D_{(P, N)}F(\alpha_{i, \pm}, P^*, N^*)$ is Fredholm with index zero.

Step 2. $D_{(P, N)}F(\alpha_{i, \pm}, P^*, N^*)(V_i) \not\subseteq R(D_{(P, N)}F(\alpha_{i, \pm}, P^*, N^*))$.

It is easy to see that an eigenvector of $L^* (\alpha_{i, \pm})$ corresponding to zero eigenvalue is $V_i^* = (a_{i, 1}^*, b_{i, 1}^*) = (-\mu_i + f_P g_P)\phi_i(x)$, where $L^* (\alpha_{i, \pm})$ is the adjoint matrix of $-L(\alpha_{i, \pm})$. If $(h_1, h_2) \in R(D_{(P, N)}F(\alpha_{i, \pm}, P^*, N^*))$, then there exists $(\phi_1, \phi_2)$ such that $D_{(P, N)}F(\alpha_{i, \pm}, P^*, N^*)(\phi_1, \phi_2)^T = -L(\alpha_{i, \pm})(\phi_1, \phi_2)^T = (h_1, h_2)^T$. Thus

$$\int_0^L \left( a_{i, 1}^* h_1 + b_{i, 1}^* h_2 \right) \phi_i(x) dx = 0.$$

It is noticed that $D_{(P, N)}F(\alpha_{i, \pm}, P^*, N^*)(V_i) = (0, \mu_i b_{i, 1} \phi_i(x))^T$, and

$$\int_0^L a_{i, 1}^* \cdot 0 + b_{i, 1}^* \cdot (-\mu_i b_{i, 1} \phi_i(x)) dx = \int_0^L d_1 \mu_i^2 g_P \phi_i^2(x) dx > 0.$$
Thus \( D_{(P,N)}F(\alpha_{i,\pm}, P^*, N^*)/(V_i) \notin R(D_{(P,N)}F(\alpha_{i,\pm}, P^*, N^*)) \).

Step 3. It is noticed that \( \{(\alpha, P^*, N^*) : 0 < \alpha < \alpha_{0,\pm}\} \) is a line of trivial solutions for \( F = 0 \), thus Theorem 4.3 in [10] can be applied to each continuum \( C_i \) bifurcated from \( (\alpha_{i,\pm}, P^*, N^*) \). The solutions of (3.2) on \( C_i \) near the bifurcation point are apparently positive. For each continuum \( C_i \), either \( \bar{C}_i \) contains another \( (\alpha_{j,\pm}, P^*, N^*) \) or \( C_i \) is not compact. (Here we do not make an extinction between the solutions of (3.2) and \( F = 0 \) as they are essentially same, hence we use \( C_i \) for solution continuum for both equations.) Therefore, either \( C_i \) is unbounded or \( C_i \) contains another \( (\alpha_{j,\pm}, P^*, N^*) \) with \( \alpha_{i,\pm} \neq \alpha_{j,\pm} \).

\[ \square \]

4 Conclusions and numerical simulations

It is a general result that a steady state that is unstable as a solution of the kinetic ODEs is also unstable as a PDE solution on a finite domain under zero Neumann conditions [12]. Our results in Theorem 2.4 indicate that the combination of advection and diffusion can stabilize the homogeneous equilibrium. For the constant steady state that are unstable in the kinetic ODEs, it becomes stable when the advection is large and diffusion is small, while it keeps instability when the advection is small. Moreover, we obtain non-constant steady states by bifurcation theory when the constant steady state is unstable. These results extend the work of [9]. Our analysis and methods are also suitable for higher dimensional systems, we can obtain the concrete bifurcation value in one dimensional interval. From a theoretical point of view, this paper introduces a new class of reaction-diffusion models with advection, which may be of independent interest.

Consider system (3.2) and fix \( d = 0.5, m = 1, a = 0.6 \). Then \( P^* > \frac{1-a}{2} \). Lemma 2.1 says that \( (P^*, N^*) = (0.6, 0.48) \) is locally asymptotically stable for any \( d_1 > 0 \) and \( \alpha = 0 \), and Theorem 2.3 shows that \( (P^*, N^*) = (0.6, 0.48) \) keeps stable for \( \alpha > 0 \), see Figure 4.1.

![Figure 4.1](image1.png)

Figure 4.1: (Left): \( d_1 = 1, \alpha = 0 \), and \( (P^*, N^*) \) is locally asymptotically stable; (Right): \( d_1 = 1, \alpha = 10 \), and \( (P^*, N^*) \) is still locally asymptotically stable, the same initial value \( (P_0, N_0) = (0.56, 0.4) \).

Fix \( d = 0.5, m = 1, a = 0.33 \). Lemma 2.1 says that (3.2) has a homogeneous Hopf bifurcation solution at \( (P^*, N^*) = (0.33, 0.44) \) for any \( d_1 > 0 \) and \( \alpha = 0 \), while Theorem 2.3 shows that the homogeneous periodic solutions disappears for \( \alpha > 0 \), see Figure 4.2.

Fix \( d = 0.5, m = 1, a = 0.32 \). Lemma 2.1 says that \( (P^*, N^*) = (0.32, 0.44) \) is unstable for any \( d_1 > 0 \) and \( \alpha = 0 \), while Theorem 2.3 shows that \( (P^*, N^*) = (0.32, 0.44) \) becomes stable for large \( d_1 > 0 \) and large \( \alpha > 0 \), see Figure 4.3.
Figure 4.2: (Left): $d_1 = 1, \alpha = 0$, and (3.2) has a homogeneous Hopf bifurcation solution at $(P^*, N^*)$; (Right): $d_1 = 0.3, \alpha = 1$, and the periodic solution disappears, the same initial value $(P_0, N_0) = (0.33, 0.4)$.

Figure 4.3: (Left): $d_1 = 1, \alpha = 0$, and $(P^*, N^*)$ is unstable; (Right): $d_1 = 1500, \alpha = 1$, and $(P^*, N^*)$ becomes locally asymptotically stable, the same initial value $(P_0, N_0) = (0.3, 0.4)$.

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