STABILITY ANALYSIS AND BIFURCATIONS IN A DIFFUSIVE PREDATOR-PREY SYSTEM

Leonid Braverman

Athabasca University, 1 University Drive, Athabasca, AB T9S 3A3 and
St. Mary's University College, 14500 Bannister Road SE, Calgary, AB, T2X 1Z4 Canada

Elena Braverman

Department of Mathematics and Statistics, University of Calgary
2500 University Drive NW, Calgary, AB, T2N1N4, Canada

Abstract. We consider a predator-prey system with logistic-type growth and
linear diffusion for the prey, Holling type II functional response and the nonlin-
ear diffusion $\nabla(\sigma n b \nabla b)$ for the predator, where n is the prey (nutrient) and b is
the predator (bacteria) density, respectively. This corresponds to a collective-
type behavior for predators: they spread faster when numerous enough at a
front line. We present the complete linear stability analysis for this case, discuss
some results of numerical simulations: the asymptotic behavior of the model
(with the zero Neumann boundary conditions in a 2-D domain) was similar to
the relevant Lotka-Volterra system of ordinary differential equations.

1. **Introduction.** The patterns which are formed by bacteria colonies on the sur-
face of thin agar plates were described in [4, 5]. The bacterium *Bacillus subtilis*
inoculated on a nutrient-poor solid agar exhibits fractal morphogenesis similar to
diffusion-limited aggregation (DLA), see [11, 16] also [1, 2, 3, 19, 22]. For softer
agar medium (nutrient-poor semi-solid medium) bacterium colonies tend to show
a dense-branching morphology (DBM) rather than DLA [16]. If both the nutri-
ent concentration and the agar's softness further increase, simple circular colonies
grow almost homogeneously in space [24]; this is also relevant for other bacteria
types, such as *Serratia, Salmonella, Escherichia coli* and their mutant strains, see
[20, 23] and references therein. Various mathematical models have been developed
to explain each characteristic colony pattern, such as a diffusion limited aggregation
model for DLA-like colonies [12, 19], a communication walkers model for both DLA
and DBM-like morphology [2, 3], and diffusion-reaction models [16, 24].

The reaction-diffusion system developed in [16] was also discussed in detail in [21].
The nutrient concentration n and the bacterial cells density b changed according to
the following system of equations

$$\frac{\partial n}{\partial t} = D_n \nabla^2 n - \frac{\kappa\, nb}{1 + \gamma n} \tag{1}$$

$$\frac{\partial b}{\partial t} = \nabla \cdot (D_b \nabla b) + \theta \frac{\kappa\, nb}{1 + \gamma n}, \tag{2}$$

where the diffusion coefficient was chosen as

$$D_b = \sigma nb. \tag{3}$$

Here the function $\dfrac{\kappa\,nb}{1+\gamma n}$ is the consumption rate of the nutrient by the bacteria, where k and γ are constants; $\theta\dfrac{\kappa\,nb}{1+\gamma n}$ is the growth rate of cells, where θ is a conversion factor, D_n and D_b are the diffusion coefficients of the nutrient and the bacteria cells, respectively. The choice of D_b in (3) is motivated by the experimental work [22] where the movement of bacteria was observed and it was found that the cells did not move much in the inner region where the nutrient concentration was low; on the contrary, vigorous cells movement was observed at the periphery of the colony where the nutrient level was much higher. Besides, at the outermost front of the colony, where the cell density is quite low, the cells were again fairly inactive. In [16] it was suggested that the bacterial diffusion is proportional to nb. We notice that in the analysis of (1),(2) it was usually assumed that $\gamma = 0$, see [16, 21].

However, in all abovementioned models and experiments with agar the ultimate experiment result was that the bacterial colony growth stopped, according to one of three scenarios: DLA, DBM (which is the most interesting for experimental and numerical study) and the homogeneous model when the colony grows uniformly unless all the nutrient is consumed. Here we try to model the situation of a renewable nutrient. Then the system involves two reaction-diffusion equations of a predator-prey type with a Holling Type II functional response. Diffusive predator-prey systems were extensively studied; we mention here the recent papers [6, 7, 8, 9, 10, 14, 15, 18], the monograph [26] and references therein. Usually positivity of solutions with positive initial conditions was justified, global attractivity of a unique positive equilibrium was proved, traveling waves and possible spatially inhomogeneous solutions were discussed.

However, in all above publications the diffusion term was just a Laplacian multiplied by a constant. Some works consider nonlinear diffusion in population dynamics models, see, for example, [17]. To the best of our knowledge, there are very few publications (see, for example, [13], [25] and references therein) that consider a diffusion coefficient in a Lotka-Volterra model which depends on both predator and prey densities. This form of the diffusion term was experimentally motivated [16] and can be interpreted as a collective behavior for predators whose activity increases significantly if they are numerous at a spot (together with abundant nutrient).

The paper is organized as follows. In Section 2 we reduce the number of parameters and obtain a dimensionless version of the system. We consider three nonnegative equilibria of the system (trivial, bacteria-free and coexistence) and present the complete linear stability analysis for the system with Type-II functional response in Section 3. Finally, in Section 4 we discuss results of numerical simulations.

2. **Preliminaries and dimensionless equation.** Let us denote by $n(t, x, y)$ and $b(t, x, y)$ the nutrient concentration and the density of the bacterial cells at point (x, y), respectively.

We consider the following system

$$\frac{\partial n}{\partial t} = D_n \nabla^2 n - \frac{\kappa nb}{1+\gamma n} + rn\left(1 - \frac{n}{M}\right), \tag{4}$$

$$\frac{\partial b}{\partial t} = \nabla\left(D_b \nabla b\right) + \theta\frac{\kappa nb}{1+\gamma n} - \beta b, \tag{5}$$

where r is the intrinsic nutrient growth rate, M is the carrying capacity of the environment for the nutrient (prey), β is the bacteria (predator) mortality rate, κ, θ and γ are parameters of the Holling Type II functional response, D_n is the nutrient diffusion coefficient. Following [16, 21] we assumed that the diffusion coefficient is proportional to both nutrient and bacteria densities

$$D_b = \sigma n b. \tag{6}$$

This was motivated by experiments which demonstrated that for low densities of either n or b the diffusion rate was negligible.

To obtain the dimensionless form of the system (4),(5), we introduce the following new variables:

$$n = \left(\frac{D_n}{\theta}\right)^{1/2} n^*; \; b = (\theta D_n)^{1/2} b^*; \; \gamma = \left(\frac{\theta}{D_n}\right)^{1/2} \gamma^*; \tag{7}$$

$$t = \frac{1}{\kappa(\theta D_n)^{1/2}} t^*; \; x = \left(\frac{D_n}{\theta \kappa^2}\right)^{1/4} x^*; \; y = \left(\frac{D_n}{\theta \kappa^2}\right)^{1/4} y^*; \; \beta = (D_n \theta)^{1/2} \kappa \beta^*. \tag{8}$$

After substituting these values and omitting asterisks, we obtain the dimensionless version of (4),(5)

$$\frac{\partial n}{\partial t} = \nabla^2 n - \frac{nb}{1 + \gamma n} + rn\left(1 - \frac{n}{M}\right), \tag{9}$$

$$\frac{\partial b}{\partial t} = \nabla(\sigma n b \nabla b) + \frac{nb}{1 + \gamma n} - \beta b. \tag{10}$$

3. **Equilibria: linear stability analysis.** First, let us note that the system (9),(10) has three spatially homogeneous stationary solutions $n(t, x, y) = n_0$, $b(t, x, y) = b_0$:

1. The zero equilibrium (no bacteria, no nutrient): $n_0 = 0$, $b_0 = 0$;
2. The bacteria-free equilibrium, the nutrient is at the carrying capacity level: $n_0 = M$, $b_0 = 0$;
3. Coexistence equilibrium: $n_0 = \dfrac{\beta}{1 - \beta\gamma}$, $b_0 = r\dfrac{M - \beta - Mb\gamma}{M(1 - \beta\gamma)^2}$.

Let us study the local stability of each of the three equilibria introducing spatial-temporal perturbations

$$\tilde{n}(t, x) = \tilde{n} \exp\left(\lambda t + ik_x x + ik_y y\right), \; \tilde{b}(t, x) = \tilde{b} \exp\left(\lambda t + ik_x x + ik_y y\right), \tag{11}$$

where λ is a perturbation growth rate and k_x and k_y are wave numbers. We substitute the perturbed solutions in (9),(10)

$$n(t, x, y) = n_0 + \varepsilon \tilde{n}(t, x, y), \; b(t, x, y) = b_0 + \varepsilon \tilde{b}(t, x, y), \tag{12}$$

where ε is infinitely small, and omit terms which include ε^j, $j > 1$.

3.1. **Bacteria-free equilibria.** First, consider **the zero equilibrium**. Then the linearized system has the form

$$\tilde{n}(k^2 - r + \lambda) = 0, \tag{13}$$

$$\tilde{b}(\beta + \lambda) = 0, \tag{14}$$

where $k^2 = k_x^2 + k_y^2$. The eigenvalues of the system (13),(14) are $\lambda_1 = r - k^2$, $\lambda_2 = -\beta$. Thus the system is unstable with respect to all perturbations with $k < \sqrt{r}$. Thus the zero equilibrium is absolutely unstable.

Next, consider **the bacteria-free equilibrium**. Then the linearized system has the form

$$\tilde{n}(k^2 + r + \lambda) + \tilde{b}M = 0, \tag{15}$$

$$\tilde{b}(\beta - M + \lambda) = 0. \tag{16}$$

The eigenvalues of the system are $\lambda_1 = -k^2 - r$, $\lambda_2 = \dfrac{M - \beta - M\beta\gamma}{1 + M\gamma}$. The former eigenvalue is always negative, while the latter one can be either positive or negative, depending on the relation between M and β: it is negative if $\beta > \dfrac{M}{1 + \gamma M}$ (stability) and is positive for $\beta < \dfrac{M}{1 + \gamma M}$ (instability). Thus, if the mortality rate of bacteria β exceeds the carrying capacity of the nutrient, then the bacteria-free equilibrium is locally stable. Otherwise, this equilibrium is unstable and introduction of a small number of bacteria leads to the restoration of the bacteria population rather than eventual extinction. Note that the critical value of β does not depend on the wave number k. Thus, all modes grow at the same rate at the stability threshold.

3.2. Coexistence equilibrium.
In this section we consider **the coexistence equilibrium**. First, we discuss the case $\gamma = 0$, similar to [21]:

$$\frac{\partial n}{\partial t} = \nabla^2 n - nb + rn\left(1 - \frac{n}{M}\right), \tag{17}$$

$$\frac{\partial b}{\partial t} = \nabla(\sigma nb\nabla b) + nb - \beta b. \tag{18}$$

Under this assumption, the coexistence equilibrium is possible only if

$$M > \beta. \tag{19}$$

The basic stationary solution of the system (9),(10) simplifies:

$$n_0 = \beta, \ b_0 = r(M - \beta).$$

Then the linearized system has the form

$$\tilde{n}\left(k^2 + \lambda + \frac{r\beta}{M}\right) + \tilde{b}\beta = 0, \tag{20}$$

$$\tilde{n}r\left(\frac{\beta}{M} - 1\right) + \tilde{b}\left(\lambda + \frac{k^2 r(M - \beta)\beta\sigma}{M}\right) = 0. \tag{21}$$

The characteristic equation of the system is

$$\lambda^2 + c_1\lambda + c_0 = 0,$$

where

$$c_0 = \frac{r(M - \beta)\beta(M + k^4 M\sigma + k^2 r\beta\sigma)}{M^2}, \ c_1 = \frac{r\beta + k^2(M + Mr\beta\sigma - r\beta^2\sigma)}{M}.$$

We recall that the coexistence equilibrium exists if $M > \beta$, so $c_0 > 0$, which means that the real parts of both eigenvalues have the same sign. On the other hand,

$$c_1 = \frac{r\beta}{M} + k^2 + \frac{r\beta\sigma}{M}(M - \beta) > 0,$$

consequently, both real parts (their sum is $-c_1$) are negative and under (19) the coexistence equilibrium is locally stable. The analysis of the general case $\gamma > 0$ is more complicated. Let us notice that $\gamma = 0$ means that Type II response was approximated by the linear (Type I) response.

Further, suppose that $\gamma > 0$ cannot be neglected and consider the stability of the coexistence equilibrium

$$n_0 = \frac{\beta}{1 - \beta\gamma}, \quad b_0 = -\frac{r(Mb\gamma + \beta - M)}{M(1 - \beta\gamma)^2}.$$

We recall that this equilibrium exists if the carrying capacity for the nutrient is enough to restore the bacteria population which is subject to natural mortality process: $M > \dfrac{\beta}{1 - \beta\gamma}$. Note that the product $\beta\gamma < 1$.

We apply perturbations of type (11) and substitute the perturbed solutions in (9), (10). The linearized system has a complicated form which will not be presented here; however, the characteristic equation of the system is still a quadratic equation

$$\lambda^2 + c_1\lambda + c_0 = 0, \tag{22}$$

where

$$
\begin{aligned}
c_0 &= \frac{r\,\beta\,(M\,(1 - \beta\,\gamma) - \beta)}{(1 - \beta\,\gamma)^4\,M^2} \tag{23} \\
&\quad \times \left[k^2\,r\,\beta\,\sigma\,(1 + \beta\,\gamma) + M\,(1 - \beta\,\gamma)\left((1 - \beta\,\gamma)^3 - \beta\,\gamma k^2\,r\,\sigma + k^4\,\sigma\right)\right] \\
c_1 &= \frac{r\,\beta\,(1 + \beta\,\gamma - M\,\gamma\,(1 - \beta\,\gamma))}{M\,(1 - \beta\gamma)} \tag{24} \\
&\quad - \frac{k^2\,\left(r\,\beta^2\,\sigma - M\,(1 - \beta\,\gamma)\left((1 - \beta\,\gamma)^2 + r\,\beta\,\sigma\right)\right)}{M\,(1 - \beta\,\gamma)^3}.
\end{aligned}
$$

Since the coefficients of the characteristic equation are real, then its roots are either real or a pair of a complex conjugates. Let us study the loss of stability when either one of real roots or a real part of complex roots becomes positive. In the former case at the boundary of the stability domain we have $c_0 = 0$ since the real root vanishes. In the latter case $c_1 = 0$ since both real parts vanish, while c_0 is the square of the frequence of the neutral oscillatory mode.

First we consider solutions of the equation $c_0 = 0$ with respect to M. The equation has two solutions. One of the solutions is $M_1 = \dfrac{\beta}{1 - \beta\gamma}$. Note that the coexistence equilibrium exists only for $M \geq M_1$. We will prove now that the equilibrium is locally stable for any M which is slightly greater than M_1 regardless of the values of other parameters. Introducing a small positive perturbation ξ of M which is $M = M_1 + \xi$, we expand (23), (24) into ξ powers series, keeping first nonzero terms:

$$
\begin{aligned}
c_0 &= \frac{(1 - \beta\gamma)^3 + r\,\sigma\,k^2 + \sigma\,k^2}{1 - \beta\gamma}\xi + O(\xi^2) \\
c_1 &= \left(k^2 + r\right) + O(\xi)
\end{aligned}
$$

It is easily seen that both c_0 and c_1 are positive ($\beta\gamma < 1$). Thus, roots of the characteristic equation (22) are either both negative or complex conjugate with negative real part. It means that coexistence equilibrium is locally stable as it appears at $M = M_1 = \dfrac{\beta}{1 - \beta\gamma}$.

Now we study the second solution of the equation $c_0 = 0$, which determines the boundary of the monotone instability:

$$M_2 = \frac{k^2 \, r \, \beta \, \sigma \, (1+\eta)}{(1-\eta)\left(r \, \eta \sigma \, k^2 - \sigma \, k^4 - (1-\eta)^3\right)}, \tag{25}$$

where $\eta = \beta\gamma$, $\eta < 1$. The equilibrium becomes unstable whenever $M > M_2$.

Further, we present analysis of the oscillatory mode of instability. Then in (22) $c_1 = 0$ and $c_0 \geq 0$. Solving the equation $c_1 = 0$ we obtain the expression for the carrying capacity

$$M_{osc} = \frac{r\beta[k^2\beta\sigma - (1+\eta)(1-\eta)^2]}{(1-\eta)[k^2((1-\eta)^2 + r\beta\sigma) - r\eta(1-\eta)^2]} . \tag{26}$$

It is not difficult to prove that the minimal value of M_{osc} in k is achieved when $k = 0$. Thus, uniform perturbations are the most dangerous for the loss of stability. Here

$$M_{osc,min} = \frac{\beta(1+\eta)}{\eta(1-\eta)} . \tag{27}$$

The frequency of neutral oscillation (the imaginary part of a growth rate as its real part is equal to zero) is given by the formula

$$\omega = \sqrt{\frac{r\beta(1-\eta)}{1+\eta}} . \tag{28}$$

The complete analysis of (25) is quite cumbersome because of numerous parameters, so we fix the values of some parameters for further consideration: $\sigma = 3.0$, $r = 5.0$, $\beta = 1$. Neutral curves will be represented in coordinates $M(k)$; recall that k is the wave number defining the spatial size of perturbations in (11). Analysis of the denominator of (25) shows that the positive values of M_2 are possible only for values $\eta > \eta_* \approx 0.173519$. When η slightly exceeds η_*, the monotone neutral curve $M(k)$ occupies a very narrow range of wavelengths. Note that the oscillatory mode exists for all values of $0 < \eta < 1$.

Below we present the stability map for $\eta = 0.1, 0.25, 0.5$. In the first case $\eta < \eta_*$ and thus monotone instability is impossible, in the second case the two branches (oscillatory and monotone) are separated (do not intersect) and in the third case the two instability domains merge at a certain k.

Analyzing the monotone neutral curve we can prove that its minimum exceeds the minimum of the corresponding oscillatory mode for all values of parameters. Figure 4 demonstrates the minimal critical values of the carrying capacity M for the oscillatory and the monotone modes for $r = 5$, $\beta = 1$. The oscillatory critical curve is σ-independent (we recall that σ is the diffusion coefficient) since the minimum is attained at $k = 0$ which corresponds to the diffusion-free uniform solution. In contrast to the oscillatory minimum, the short-wave monotone mode essentially depends on σ, as can be seen from Figure 4: the domain where the monotone instability domain exists becomes narrow and right-shifted as σ decreases.

The linear stability analysis demonstrated that the first bifurcation in the studied system is the long wave Hopf bifurcation for all values of parameters. Thus, spatial patterns cannot be formed near the stability threshold. If they exist, it is in the domain of parameters rather far from the critical curves.
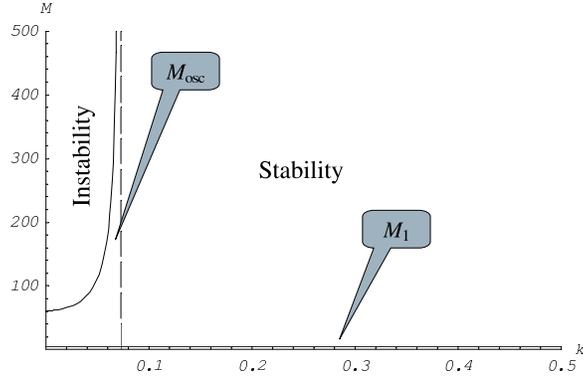
FIGURE 1. The oscillatory neutral curve for $r = 5$, $\beta = 1$, $\sigma = 3$, $\eta = 0.1 < \eta_*$
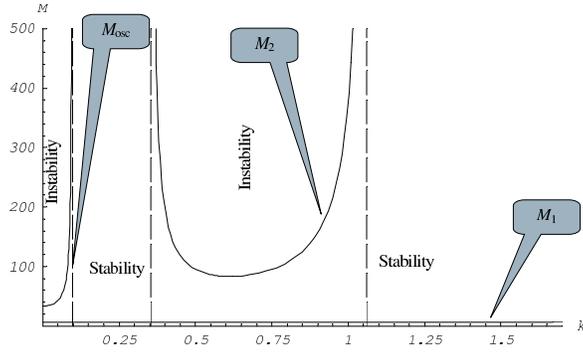

FIGURE 2. The oscillatory and monotone neutral curves for $r = 5$, $\beta = 1$, $\sigma = 3$, $\eta = 0.25 > \eta_*$ do not intersect
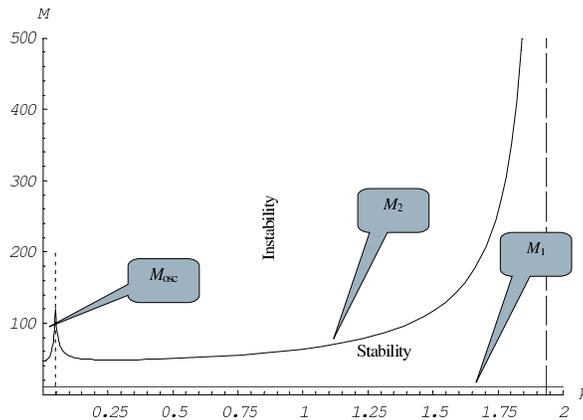

FIGURE 3. The merging oscillatory and monotone instability domains for $r = 5$, $\beta = 1$, $\sigma = 3$, $\eta = 0.5 > \eta_*$
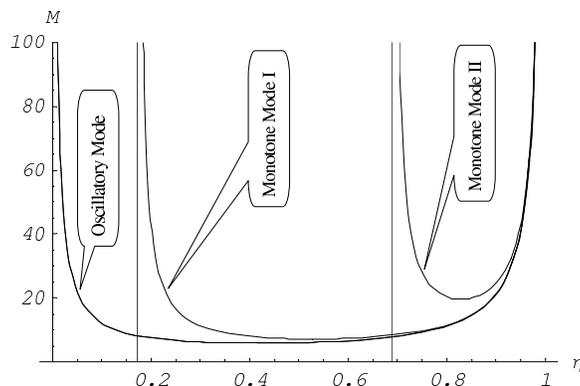
FIGURE 4. Minimal carrying capacity M as a function of η for $r = 5.0$, $\beta = 1.0$; the minimum of Oscillatory Mode is attained at $k = 0$, it is long-waved and is σ-independent; Monotone Mode I corresponds to $\sigma = 3.0$, Monotone Mode II is for $\sigma = 0.01$

4. **Discussion and numerical simulations.** In this section we present some preliminary results of direct numerical simulation for the system (9), (10) with the Neumann boundary conditions in a square domain $\Omega = [0, 1] \times [0, 1]$ for n and b

$$n_x(t, 0, y) = n_x(t, 1, y) = 0, \; n_y(t, x, 0) = n_y(t, x, 1) = 0,$$
$$b_x(t, 0, y) = b_x(t, 1, y) = 0, \; b_y(t, x, 0) = b_y(t, x, 1) = 0.$$

An explicit finite difference scheme (the first order of approximation in time and the second order in a coordinate) was applied in simulations. The stability of the scheme was verified by choosing different time steps. The results of the simulation can be summarized as follows.

1. Numerical runs confirmed the linear theory developed in the previous section.
2. Whenever the values of parameters were chosen in such a way that the relevant predator-prey system of ordinary differential equations experienced sustainable oscillations, the reaction-diffusion system (9), (10) asymptotically had spatially uniform oscillations with the same amplitudes. This fact was known for reaction-diffusion systems with the linear bifurcation term; however, nonlinear bifurcation for predators did not change the situation.

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E-mail address: `leonidb@athabascau.ca`

E-mail address: `maelena@math.ucalgary.ca`