Dynamics of a Lotka-Volterra type model with applications to marine phage population dynamics

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Abstract. The famous Lotka-Volterra equations play a fundamental role in the mathematical modeling of various ecological and chemical systems. A new modification of these equations has been recently suggested to model the structure of marine phage populations, which are the most abundant biological entities in the biosphere. The purpose of the paper is: (i) to make some methodical remarks concerning this modification; (ii) to discuss new types of canards which arise naturally in this context; (iii) to present results of some numerical experiments.

“Bacteria don’t die, they just phage away”
— Mark Müller, microbiologist

Introduction
A phage (short for bacteriophage) is a microscopic virus that infects bacteria. There is a huge number of varieties of phage, but in general phages only infect specific bacteria. Upon infecting bacteria, a phage will either begin to reproduce, or else it will integrate its DNA into the host bacteria. Phages are microscopic organisms. Their dimensions are typically between 24 to 200 nm, and their basic structure is shown in Figure 1.

![Figure 1. Structural overview (left), and actual picture (right) of phages](image-url)
Once a phage encounters a bacteria, it attaches itself via its tail fibres, and injects its DNA down through the base plate and into the bacteria. Some phages, once they have infected a bacteria, begin to multiply immediately, and in a short time completely destroy the bacteria, releasing more phages. Other phages simply remain dormant once they are attached to bacteria. Their DNA incorporates itself into that of the bacteria, and remains attached to it until the bacteria is weak or close to death. Once they detect a decline in the bacteria, they then become active again, and reproduce before the bacteria’s demise[2]. Phages are believed to be important in carbon cycling, with at least 25% of fixed carbon passing through them. They are also important in the absorption of $CO_2$ in the oceans.

A new modification of the classical Lotka–Volterra equations has been recently suggested to model the structure of marine phage populations. The purpose of the paper is: (i) to make some methodical remarks concerning this modification; (ii) to discuss new types of canards which arise naturally in this context; (iii) to present results of some numerical experiments. This paper addresses a wide range of readers, including biologists. Thus, we were trying to make the exposition as elementary and self contained as possible.

1. Methodical remarks on modified Lotka-Volterra equations

The classic Lotka-Volterra Equations were suggested to model population dynamics of a predator-prey system. They are [3, p.41]:

$$\dot{x} = x(\alpha - \beta y), \quad \dot{y} = y(-\gamma + \delta x),$$  \hfill (1)

where $x$ and $y$ are functions of time representing the populations of the prey and predator respectively, and $\alpha$, $\beta$, $\gamma$, and $\delta$ are positive constants which govern the strength of the interactions between the two species and amongst themselves. This system has a unique positive equilibrium $(\bar{x}, \bar{y})$ when $\dot{x} = \dot{y} = 0$, that is $\bar{x} = \gamma/\delta$, $\bar{y} = \alpha/\beta$.

From the analysis of experimental data, Hoffmann [1] proposed that for the phage-bacteria interaction the equations be modified such that a power law applies to the Lotka-Volterra equations. The modified Lotka-Volterra equations are therefore:

$$\dot{B} = B(\alpha - \beta \Phi^p), \quad \dot{\Phi} = \Phi^p(-\gamma + \delta B).$$  \hfill (2)

We will assume the inequality

$$p > 1.$$  \hfill (3)

Loosely speaking the equations (2) mean that the “effective size” of the phage population differs from its “physical size”, and this effective size is proportional to the power $p$ of the physical size. A naive explanation may be as follows: in the traditional Lotka-Volterra equations (1) and (2), it is assumed that the important meetings are when one predator meets one prey. With the power of two, which was among the best fits in the modified equations, we can hypothesize that unlike the traditional system, it is the meeting of two phages and one bacteria that are important. (Hoffmann talks about the $p=2$ being due to attraction of more hosts to the area of phage lysis but there are some papers indicating 2-3 phages actually do infect each bacterium in laboratory tests.) Correspondingly, the power $\Phi^p$ in (2) indicated that that are “hunting-teams” of $p$ phages which are effective. This sounds strange for a fractional $p$, but such ideas are not unusual in mathematics.

This system also has a the unique positive equilibrium:

$$B_* = \gamma/\delta, \quad \Phi_* = (\alpha/\beta)^{1/p}.$$  \hfill (4)

Returning to equations (2), we can look for a constant of motion for the system. We do this by dividing the first equation (2) by the second to obtain

$$(-\gamma \log B(t) + \delta B(t)) + (\alpha \Phi(t)^{1-p}/(p-1) + \beta \Phi(t)) = \text{const.}$$
for any positive solution \((B(t), \Phi(t))\) of (1). Thus
\[
W(B, \Phi) = (\gamma \log B + \delta B(t)) + \left(\alpha \Phi^{1-p}/(p - 1) + \beta \Phi\right)
\] (5)
is a conserved quantity, in other words, the first integral, for the motion of trajectories in this system. The value of the constant is determined by the initial conditions. Rewriting system (2) as
\[
\dot{B} = \alpha B(\Phi^p - \Phi^p), \quad \dot{\Phi} = \gamma(-B_* + B),
\]
we can see that the direction vector field in the strictly positive quadrant is as shown in the figure below. Since \(p > 1\), \(\lim W(B, \Phi) = \infty\) as \(B \to 0\), or \(\Phi \to 0\), or \(B \to \infty\), or \(\Phi \to \infty\),

![Figure 2. The main isoclines and direction field for system (2)](image)

the trajectories could not explode to infinity. Finally, since the restriction \(W(B) = W(B, \Phi_*)\) is strictly monotone for \(0 < B < B_*\), we conclude that all trajectories of (2) are periodic, and they orbit anti-clockwise around the equilibrium \((B_*, \Phi_*)\).

We can see now that a modified Volterra principle holds for system (2). For a classic Lotka-Volterra system (1), this principle states that the time averages of the population densities will be constant and equal to the equilibrium values, i.e.
\[
\frac{1}{T} \int_0^T x(t) \, dt = \bar{x}, \quad \frac{1}{T} \int_0^T y(t) \, dt = \bar{y},
\]
where \(x(t)\) and \(y(t)\) are the two populations, and \(T\) is the period of the solution [3, p.45-46].

For our system, we will have a slightly modified version of Volterra principle:
\[
\frac{1}{T} \int_0^T B(t) \, dt = B_*, \quad \frac{1}{T} \int_0^T \Phi(t)^p \, dt = \Phi_*^p.
\] (6)
The first relationship is the same as in standard case and it may be proved as usual. Next, we evaluate
\[
\frac{d}{dt} (\log B(t)) = \frac{dB}{B(t)} \frac{1}{T} = \alpha - \beta \Phi^p,
\]
which implies
\[ \int_0^T \frac{d}{dt} \left( \log B(t) \right) dt = \int_0^T (\alpha - \beta \Phi(t)^p) dt, \]
or
\[ \log(B(T)) - \log(B(0)) = \alpha T - \beta \int_0^T \Phi(t)^p dt. \]
Taking into account \( B(T) = B(0) \), we can write
\[ \frac{1}{T} \int_0^T \Phi(t)^p dt = \frac{\alpha}{\beta} = (\Phi^*)^p, \]
by the second of equations (4).

We now consider the case where we further modify the generalized Lotka-Volterra equations (2) to take into account competition within the species. We assume that the competition between members of the same species for food reduces population growth, but that this effect is relatively small compared to the natural growth rate. We assume therefore that the additional parameters \( \mu \) and \( \nu \) are small, and that they affect the square of the population, as in the original Lotka-Volterra equations. We note that Hoffmann says that effectively there is no food competition "food is not a limiting resource for microbes in the marine ecosystem". The analysis of the system with competition is interesting from the mathematical point of view. We will see that any, infinitesimally small competition would change drastically the pattern of longtime behaviour of system.

As we already used modified Lotka-Volterra equations with the powers \( p \) for the predators, we therefore include an exponent \( 2p \) for the predator competition term. This is consistent with our earlier hypothesis that the effective size of the phage population is measured as \( \Phi^p \). For instance, suppose that the interactions between two phages and one bacteria are important. In order for there to be a negative impact from competition, we consider the case where two teams of two phages encounter one bacteria. Each pair of phages will effectively be competing with the other for the one prey. Therefore, the competition between the phages will have a negative impact on their growth rate. Also, if pairs of phages are needed to consume each prey, then situations where there are 3 phages and one bacteria will have no role other than the usual interaction of two phages and one bacteria. Hence, we have no term with a cubic power in the corresponding competition model.

Our modified equations are therefore:
\[ \dot{B} = B \left( \alpha - \beta \Phi^p - \mu B \right), \quad \dot{\Phi} = \Phi^p \left( -\gamma + \delta B - \nu \Phi^p \right). \]
(7)

Following the same procedure as before, we seek a nontrivial equilibrium \((B_{ss}, \Phi_{ss})\) from the simultaneous equations
\[ \alpha - \beta \Phi^p - \mu B = 0, \quad -\gamma + \delta B - \nu \Phi^p = 0. \]
(8)
Therefore,
\[ B_{ss} = \frac{\beta \gamma + \nu \alpha}{\delta \beta + \nu \mu}, \quad \Phi_{ss} = \left( \frac{\alpha \delta - \mu \gamma}{\delta \beta + \nu \mu} \right)^{1/p}, \]
which clearly belongs to the positive quadrant for
\[ \alpha \delta > \mu \gamma. \]
(9)
Our next step is to test the stability of this equilibrium \((B_{**}, \Phi_{**})\) subject to the condition (9). To do this, we need to construct a Lyapunov function for the system. Recall that the smooth function \(V = V(B, \Phi)\) is a Lyapunov function in the positive quadrant for the system
\[
\dot{B} = f(B, \Phi), \quad \dot{\Phi} = g(B, \Phi),
\]
which has a unique positive equilibrium \((B_{**}, \Phi_{**})\), if the following two conditions hold:

(i) \(\dot{V}(B, \Phi) = \frac{\partial V}{\partial B} f + \frac{\partial V}{\partial \Phi} g < 0\) for \(B, \Phi > 0\), and \((B, \Phi) \neq (B_{**}, \Phi_{**})\);

(ii) \(\lim_{B \to 0} V(B, \Phi) = \infty\) as \(B \to 0\), or \(\Phi \to 0\), or \(B \to \infty\), or \(\Phi \to \infty\).

The existence of a Lyapunov function guarantees that the equilibrium \((B_{**}, \Phi_{**})\) is globally asymptotically stable in the positive quadrant.

We try to find such a Lyapunov function \(V(B, \Phi)\) for the system (7). There is no direct method for finding a Lyapunov function, so, following [3] we refer back to our simpler (non-competing) model. Recall that in equation (5) we used the function
\[
W(B, \Phi) = (-\gamma \log B + \delta B(1)) + (\alpha \Phi^{1-p}/(p-1) + \beta \Phi),
\]
which was a constant of motion for all trajectories. By (4) this function may be rewritten as
\[
W(B, \Phi) = \delta(-B_{**} \log B + B) + \beta \left( \Phi_{**}^{p} \Phi^{1-p}/(p-1) + \Phi \right).
\]
We therefore construct a trial Lyapunov function for system (7) in the same form as above, i.e. we set
\[
V(B, \Phi) = \delta(-B_{**} \log B + B) + \beta \left( \Phi_{**}^{p} \Phi^{1-p}/(p-1) + \Phi \right),
\]
which implies immediately that the function \(V\) satisfies condition (ii).

It remains to see if it satisfies condition (i). First, we calculate the partial derivatives needed:

\[
\frac{\partial V}{\partial B} = \delta \frac{B_{**}}{B} + \delta, \quad \frac{\partial V}{\partial \Phi} = -\beta \Phi_{**}^{p}/\Phi + \beta.
\]

Now, in our system we have
\[
f(B, \Phi) = B(\alpha - \beta \Phi^{p} - \mu B), \quad g(B, \Phi) = \Phi^{p}(-\gamma + \delta B - \nu \Phi^{p}).
\]
So for \(B, \Phi > 0\) we have
\[
\frac{\partial V}{\partial B} f(B, \Phi) + \frac{\partial V}{\partial \Phi} g(B, \Phi) = \delta(-B_{**} + B)(\alpha - \beta \Phi^{p} - \mu B)
\]
\[
+ \beta \left( \Phi_{**}^{p} - \Phi^{p} \right)(-\gamma + \delta B - \nu \Phi^{p}).
\]
On the other hand, from (8) we can write:
\[
\alpha = \beta \Phi_{**}^{p} + \mu B_{**}, \quad -\gamma = -\delta B_{**} + \nu \Phi_{**}^{p}.
\]
We substitute these expressions for \(\alpha\) and \(-\gamma\) into (12):
\[
\frac{\partial V}{\partial B} F(B, \Phi) + \frac{\partial V}{\partial \Phi} G(B, \Phi) = \delta(-B_{**} + B) \left( \beta (\Phi_{**}^{p} - \Phi^{p}) + \mu (B_{**} - B) \right)
\]
\[
+ \beta \left( \Phi_{**}^{p} - \Phi^{p} \right)(-\delta(B_{**} - B) + \nu (\Phi_{**}^{p} - \Phi^{p})).\]
This can be rewritten as
\[ \frac{\partial V}{\partial B} F(B, \Phi) + \frac{\partial V}{\partial \Phi} G(B, \Phi) = -\delta \mu (B - B_{**})^2 - \beta \nu (\Phi - \Phi_{**})^2, \]

which implies condition (i) immediately. We can therefore conclude that we have found the Lyapunov function for this system, and that the equilibrium at \((B_{**}, \Phi_{**})\) is globally asymptotically stable in the positive quadrant.

We can generalize equations (2) and (7) further to the form
\[ \dot{B} = F(B) (\alpha - \beta G(\Phi)), \quad \dot{\Phi} = G(\Phi) (-\gamma + \delta F(B)), \]

and to the form
\[ \dot{B} = F(B) (\alpha - \beta G(\Phi) - \mu F(B)), \quad \dot{\Phi} = G(\Phi) (-\gamma + \delta F(B) - \nu G(\Phi)), \]

where all constants are strictly positive. Here the quantities \(F(B)\) and \(G(\Phi)\) describe effective sizes of the prey and predator populations. We assume that these functions are strictly monotonic and increase from 0 to \(\infty\). Then there exists a unique positive equilibrium \((B_*, \Phi_*)\), to be defined from the equations
\[ F(B_*) = \gamma/\delta, \quad G(\Phi_*) = \alpha/\beta. \]

For equation (13) there exists a constant of motion given by
\[ W(B, \Phi) = \delta (-B_0 P(B) + B) + \beta (\Phi_0 Q(\Phi) + \Phi) \]

with
\[ P(B) = \int_{B_*}^{B} 1/F(s) \, ds, \quad Q(\Phi) = \int_{\Phi_*}^{\Phi} 1/G(s) \, ds, \]

From now on we assume additionally that
\[ F'(0), G'(0) = 0, \quad \text{and} \quad F'(\infty), G'(\infty) = \infty. \]

Then \(\lim W(B, \Phi) = -\infty\) as \(B \to 0\), or \(\Phi \to 0\), or \(B \to \infty\), or \(\Phi \to \infty\). We conclude again that all trajectories of (13) are periodic, and they orbit anti-clockwise around the equilibrium \((B_*, \Phi_*)\). The Volterra principle holds for equations (13) in the form
\[ \frac{1}{T} \int_0^T F(B(t)) \, dt = F(B_*), \quad \frac{1}{T} \int_0^T G(\Phi(t)) \, dt = G(\Phi_*), \]

where \(T\) is period of a solution \((B(t), \Phi(t))\). Equation (14) is asymptotically globally stable in the positive quadrant with the Lyapunov function
\[ V(B, \Phi) = \delta (-B_{**} P(B) + B) + \beta (\Phi_{**} Q(\Phi) + \Phi) \]

provided that \(\alpha \delta > \mu \gamma\). Here the positive equilibrium \((B_{**}, \Phi_{**})\), to be defined from the equations
\[ F(B_{**}) = \frac{\beta \gamma + \nu \alpha}{\delta \beta + \nu \mu}, \quad G(\Phi_{**}) = \frac{\alpha \delta - \mu \gamma}{\delta \beta + \nu \mu}. \]

The proof is as above with a few obvious modifications.
2. Canards and the effects of apparent disappearance in modified L-V equations

Some special solutions of singularly perturbed ordinary differential equations are called canards or duck-trajectories. These terms have been introduced by French mathematicians [7, 8, 9]. We first the reader remind in a convenient form of the corresponding definitions.

Let us consider a two-dimensional autonomous system:

\[ \dot{x} = f(x, y, \alpha), \quad \varepsilon \dot{y} = g(x, y, \alpha), \]  

where \( x, y \) are scalar functions of time, \( \varepsilon \) is a small positive parameter, and \( f, g \) are sufficiently smooth scalar functions. The set of points

\[ S_\alpha = \{(x, y) : g(x, y, \alpha) = 0\} \]

of the phase plane is called a slow curve of the system (15).

We will make the following assumptions:

1) The curve \( S_\alpha \) consists of regular points, i.e. at every point \( (x, y) \in S_\alpha \)

\[ [g_x(x, y, \alpha)]^2 + [g_y(x, y, \alpha)]^2 > 0. \]

holds.

2) Singular points, i.e. points at which \( g_y(x, y, \alpha) = 0 \), are isolated on \( S_\alpha \).

3) At any singular point the following inequality holds: \( g_{yy} \neq 0 \).

**Definition 1.** A singular point \( A \) of the slow curve \( S_\alpha \) is called a jump point [13] if

\[ \text{sgn} [g_y(A)g_x(A)f(A)] = 1. \]

Parts of \( S_\alpha \) which contain only regular points are called regular. A regular part of \( S_\alpha \), all points of which satisfy the inequality

\[ g_y(x, y, \alpha) < 0 \quad (g_y(x, y, \alpha) > 0), \]

is called attractive (repulsive).

The attractive and repulsive parts of the slow curve are zeroth order approximations of the corresponding attractive and repulsive integral manifolds. The integral manifolds are located in an \( \varepsilon \)-neighborhood of the slow curve, except for the jump points, at which existence theorems do not hold.

**Definition 2.** Trajectories which at first pass along the attractive integral manifold and then continue for a while along the repulsive integral manifold are called canards or duck-trajectories.

The existence of canards for the system (15) has been proved originally by techniques from so called non-standard analysis [7, 8, 9, 14]. A standard interpretation of the main results can be found in [6, 10, 11, 12]:

The canards and the corresponding values of the parameter \( \alpha \) allow asymptotic expansions in powers of the small parameter \( \varepsilon \). Near the slow curve the canards are exponentially close, and have the same asymptotic expansion in powers of \( \varepsilon \). An analogous assertion is true for corresponding parameter values \( \alpha \). Namely, any two values of the parameter \( \alpha \) for which canards exist, have the same asymptotic expansions, and the difference between them is given by \( \exp(-(1/\varepsilon^c)) \) where \( c \) is some positive number.

As a simple example we mention the equation

\[ \dot{x} = 1, \quad \varepsilon \dot{y} = xy + \alpha. \]  

(16)
It is clear that for $\alpha = 0$, the trajectory $y = 0$ is a canard. Moreover, for $\alpha = 0$, any trajectory of this system, namely

$$y = y_0 e^{\frac{x^2 - x_0^2}{2\varepsilon}}, \quad y(x_0) = y_0,$$

is a canard if $x_0 < 0$, and $x_0, y_0$ are values of the order $O(1)$ as $\varepsilon \to 0$. We can say that the trajectory $y = 0$ is the longest canard. Note, that this trajectory can be considered as a slow integral manifold. Note that in this case line $y = 0$ plays the role of a slow curve and of a slow integral manifold, simultaneously. It is illustrated in Fig. 3 that this line is attractive when $0 > x$ (repulsive when $0 < x$).

Figure 3. Canard.

To present an example of a periodic canard, we use polar coordinates and the system

$$\dot{\phi} = 1, \quad \varepsilon \dot{r} = r(r - 1) \sin \phi.$$

Its solution, satisfying an initial condition $r(\phi_0) = r_0$, is given by

$$r = 1 + \frac{r_0 - 1}{1 - r_0 + r_0 e^{\cos \phi_0-\cos \phi}},$$

Therefore, $r = 1$ is a canard.

Now we introduce new types of canards, which are important in the context of this article.

**Definition 3.** Trajectories which at first pass along a repulsive integral manifold and then continue for a while along an attractive integral manifold are called false canards.

To illustrate this definition, consider the following system

$$\dot{x} = 1, \quad \varepsilon \dot{y} = -xy$$

Any trajectory an with initial condition $y(x_0) = y_0$ can be represented in the form

$$y = y_0 e^{\frac{x^2 - x_0^2}{2\varepsilon}},$$

and the trajectory $y = 0$ is a false canard with the phase diagram represented by Fig. 4. It contains repulsive(attractive) part for $0 > x$ ($0 < x$).

In the above cases properties of attraction or repulsion can be viewed as exponential attraction and exponential repulsion by analogy with exponential stability. Using an analogy with the asymptotic stability, we introduce the following notion.

**Definition 4.** Trajectories which are canards but attraction and repulsion are not exponential are called feeble canards.
As an example, let us consider the following system

\[
\dot{x} = 1, \quad \varepsilon \dot{y} = xy^3
\]

which trajectory with an initial condition \( y(x_0) = y_0 \) is

\[
y = \frac{y_0}{1 + \frac{x^2 - x_0^2}{2\varepsilon} y_0^2}^{1/2}.
\]

In this case the canard \( y = 0 \) is a feeble canard, which is attractive when \( 0 > x \) (repulsive when \( 0 < x \)).

**Definition 5.** If on one side of the trajectory it looks like a canard, but on the other side it looks like a false canard, we'll say that this trajectory is a two–faced canard.

For example, the system

\[
\dot{x} = 1, \quad \varepsilon \dot{y} = xy^2
\]

whose trajectories are

\[
y = \frac{y_0}{1 + \frac{x^2 - x_0^2}{2\varepsilon} y_0^2},
\]

possesses the two–faced feeble canard \( y = 0 \).

It is easy to give more general examples of feeble canards. The system

\[
\dot{x} = 1, \quad \varepsilon \dot{y} = xy^{2k+1}, \quad k \geq 1,
\]
with the trajectories
\[
y = \frac{y_0}{1 + \frac{k(x^2 - x_0^2)}{\varepsilon y_0^{2k}}}^{1/2k}, \quad y(x_0) = y_0,
\]
has the feeble canard \( y = 0 \), and the system
\[
\dot{x} = 1, \quad \varepsilon \dot{y} = xy^{2k}, \quad k \geq 1,
\]
with trajectories
\[
y = \frac{y_0}{1 + \frac{(2k-1)(x^2 - x_0^2)}{2\varepsilon y_0^{2k-1}}}^{1/2k-1}, \quad y(x_0) = y_0,
\]
possesses the two-faced feeble canard \( y = 0 \), which is attractive for \( 0 > x, 0 < y \) and \( 0 < x, 0 > y \), and repulsive for \( 0 > x, 0 > y \).

Turning back to the modified Lotka-Volterra we consider two special cases, when one variable (\( B \) or \( \Phi \)) is faster than the other. We can use singularly perturbed differential systems for the modelling such phenomena. The biologically relevant case is “Fast Phages – Slow Bacteria”, and the corresponding system is
\[
\dot{B} = B(\alpha - \beta \Phi^p), \quad \varepsilon \dot{\Phi} = \Phi^p(-\gamma + \delta B),
\]
with \( p > 1 \).

**Proposition 1.** The trajectory \( \Phi = 0 \) is a feeble canard with the attractive part \( B < \gamma/\delta = B_* \) and the repulsive part \( B > \gamma/\delta = B_* \) for positive \( B \) and \( \Phi \).

We can observe here the effect of apparent disappearance of phages: they almost disappear for most of the time; however the phages population “explodes” for some short time intervals.
point that should be mentioned is that this feeble canard is two-faced in the cases \( p = 2, 4, 6, \ldots \), but that is irrelevant because we are interested in the behavior of our system for positive values of \( \Phi \), only.

We also discuss the relationship between minimal \( \Phi_{\min} \) and maximal \( \Phi_{\max} \) values of the variable \( \Phi \) in the case of fast phages and slow bacteria. Moreover, by technical reasons, we consider only the case \( p = 2 \) (the general case \( p > 1 \) will be discussed in another article). Then

\[
\frac{\Phi_{\max}}{\Phi_{\min}} = (1 + z) \left( 1 + z + \sqrt{2z + z^2} \right),
\]

where

\[
z = \frac{\delta}{\varepsilon \beta} \Psi \left( \frac{\alpha}{\beta}, \frac{\gamma}{\delta}, B_{\max} \right),
\]

and

\[
\Psi(u, v, w) = \frac{1}{2\sqrt{u}} [w - v + v (\ln v - \ln w)].
\]

Therefore we arrive the following statement:

**Proposition 2.** In the case of fast phages and slow bacteria the relationship

\[
\frac{\Phi_{\min}}{\Phi_{\max}} = O(\varepsilon^2), \quad \text{as} \quad \varepsilon \to 0
\]

holds.

We consider, finally, the “Fast Bacteria – Slow Phages” case with the corresponding equations

\[
\varepsilon \dot{B} = B(\alpha - \beta \Phi^p), \quad \dot{\Phi} = \Phi^p(-\gamma + \delta B).
\]

We note that this case is probably not interesting from a biological point of view.

**Proposition 3.** The trajectory \( B = 0 \) is a canard with attractive part \( \Phi > (\alpha/\beta)^{1/p} = \Phi_* \) and repulsive part \( \Phi < (\alpha/\beta)^{1/p} = \Phi_* \).

![Figure 8](image-url)

**Figure 8.** Fast microbes and slow phages.

In this case we observe an effect of *apparent disappearance* of bacteria.
3. Further numerical experiments

We consider modifying our system further to include two phage-like predators and two prey. We assume that both predators will eat either of the two prey. We acknowledge that the usual assumption for phages is that each predator is fairly prey-specific and Hoffmann is clearly talking about multiple independent cycles of predator and prey. Our numerical experiments suggest that this specificity could evolve naturally from a less specific cross-feeding system, as more branched systems are swept away in a long run by prey extinction.

The equations of our system are given by

\[
\begin{align*}
W(t) &= W(t)(a - bY(t)^2 - cZ(t)^2), \\
\dot{X}(t) &= X(t)(d - eY(t)^2 - fZ(t)^2), \\
\dot{Y}(t) &= Y(t)^2(-g + kW(t) + iX(t)), \\
\dot{Z}(t) &= Z(t)^2(-j + kW(t) + lX(t)),
\end{align*}
\]

where we have \(W(t)\) and \(X(t)\) as prey, and \(Y(t)\) and \(Z(t)\) as predators, and the parameters \(a\) to \(l\) are positive constants.

To see the qualitative behavior of the system, we can plot the four populations as functions of time. A typical plot is displayed below.

![Figure 9. Plot of populations W, X, Y, and Z versus time. The first species W(t) is represented by the black graph, the second species X(t) by the red graph, the third species Y(t) by the green graph, and the fourth species Z(t) by the blue graph.](image)

In this graph we have chosen our parameters \(a\) to \(l\) to be as follows:

\[
\begin{align*}
a &= 1, & b &= 0.1, & c &= 0.08, & d &= 1.1, & e &= 0.2, & f &= 0.09, \\
g &= 2, & h &= 0.05, & i &= 0.09, & j &= 1.5, & k &= 0.11, & l &= 0.07,
\end{align*}
\]

and our initial points and total time \(\tau\) as follows:

\[
W(0) = 10, \quad X(0) = 20, \quad Y(0) = 15, \quad Z(0) = 25, \quad \tau = 100.
\]

It is interesting to note that one the populations, namely \(Y(t)\), very rapidly dies off to zero. This is a typical behaviour. In fact, if we were to randomly select the parameters \(a\) to \(l\) and plot the results, we find that in the vast majority of cases at least one of the populations tends to die off very rapidly. This tendency to die off leads us to wonder if it is possible to have an
equilibrium with a positive population for all four species. We can test if it is possible by solving the equation
\[ \dot{W}(t) = \dot{X}(t) = \dot{Y}(t) = \dot{Z}(t) = 0. \]

Thus a possible positive equilibrium does indeed exist at the point:
\[ W_* = \frac{ij - gl}{ik - hl}, \quad X_* = \frac{hj - gk}{-ik + hl}, \quad Y_* = \sqrt{\frac{cd - af}{ce - bf}}, \quad Z_* = \sqrt{\frac{bd - ae}{-ce + bf}}. \]

Hence, if we were to choose our parameters to such that the all the coordinates above were positive, we would have a positive equilibrium for all four species.

We now look to include the effects of competition in our system. We modify equations (17) to (17) by adding competition terms. We must take into account two types of competition - competition between two of the same species, and competition between one species and another of the same type, i.e. between the two species of predators, or between the two species of prey. We do this by adding in the terms as shown below:
\[
\begin{align*}
\dot{W}(t) &= W(t)(a - bY(t)^2 - cZ(t)^2 - mX(t) - nW(t)), \\
\dot{X}(t) &= X(t)(d - eY(t)^2 - fZ(t)^2 - oW(t) - pX(t)), \\
\dot{Y}(t) &= Y(t)^2(-g + hW(t) + iX(t) - qZ(t)^2 - rY(t)^2), \\
\dot{Z}(t) &= Z(t)^2(-j + kW(t) + lX(t) - sY(t)^2 - uZ(t)^2).
\end{align*}
\]

We can now look at a numerical example of this system’s behavior. We choose the constants to be the same values as given in (3), and the initial values and time to be the same as in (3). We define the remaining constants to be:
\[ m = 0.001, \quad n = 0.002, \quad o = 0.003, \quad p = 0.001, \quad q = 0.0022, \quad r = 0.0009, \quad s = 0.0015, \quad u = 0.002. \]

We can now find a numerical solution in the same manner as before. We again use Mathematica’s NDSolve command to find interpolating functions, which we can plot as functions of time. This plot is shown below.

![Figure 10. Plot of populations W, X, Y, and Z versus time](image)

We have again kept the same colour convention as before, with \( W(t) \) coloured black, \( X(t) \) red, \( Y(t) \) green, and \( Z(t) \) blue. Notice how one species, namely \( Y(t) \), dies off very rapidly, while
a second, $X(t)$, is also dying out. This appears to mirror the results from the system without competition, that at least one species will typically die out. There is, however, a difference in the system with competition. We can see that the system does seem to be tending towards a stable equilibrium value for the populations, much like the system with only one predator and one prey. We can hypothesize that the tending towards equilibrium is a characteristic of a system with competition. Again, we can use random values of the parameters to generate plots for multiple values of the parameters. We notice that at least one species tends to die off, and that the surviving species tend towards an equilibrium. However, we must see if it is in fact possible to have a system where all four species can coexist together. We hence attempt to find a positive solution of the equations. We can do this analytically easily using Mathematica’s Solve function. By examining the results, we do indeed find that there exists a possible equilibrium where all 4 populations are non-zero, although it is a rather cumbersome formula.

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