Biomathematics: A course on some applications of dynamical systems

Two-species systems and limit cycles

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Introduction

In this chapter we will discuss the interaction between two species and how we can model it. We have already addressed this question when we discussed the case when two species compete for the same food resource. Here we will discuss models for the interaction between a predator and a pray.

Such discussions goes back to the early 20th century when a simple model used to explain what seemed like a paradox in fishing data in the Mediterranian. The solutions to that model are periodic, but unrealistic, because they are not stable. We will discuss a modification, and perhaps more realistic, of that model and discuss conditions under which the solution to this system also can be periodic, but stable. This will introduce the famous Poincaré-Bendixson theorem.

But the Poincaré-Bendixson theorem is very two-dimensional, and we will also have a look at another possibility to show that one has periodic solutions, which also applies to higher dimensions.

Lotka-Volterra equations

In the middle of the 1920th, the italian biologist Umberto D’Ancona took an interest in how different fish populations interact. Among his data was the following table, which describes what percentage of the catch in the Mediterrean consisted of predators (sharks, ray-fish, etc), which were not wanted in the catch:

<table>
<thead>
<tr>
<th>Year</th>
<th>1914</th>
<th>1915</th>
<th>1916</th>
<th>1917</th>
<th>1918</th>
<th>1919</th>
<th>1920</th>
<th>1921</th>
<th>1922</th>
<th>1923</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predators</td>
<td>11.9</td>
<td>21.4</td>
<td>22.1</td>
<td>21.2</td>
<td>36.4</td>
<td>27.3</td>
<td>16.0</td>
<td>15.9</td>
<td>14.8</td>
<td>10.7</td>
</tr>
</tbody>
</table>

What puzzled D’Ancona about these data was that there was a relative increase in predators in the catch during the period of the first world war, a time period during which the overall fishing was reduced.

His good friend, the mathematician Vito Volterra, came up with a mathematical explanation 1926. With $P$ being the concentration of predators and $N$ the concentration of prey, he proposed the following pair of differential equations

\[
\begin{align*}
N' &= rN - qNP, \\
P' &= pNP - sP.
\end{align*}
\]

This system of equations is called the Lotka-Volterra model, because it was formulated also by Lotka a few years earlier for a hypothetical chemical reaction.

To analyse the system and get Volterra’s explanation we first nondimensionalize the system: let the new time be $rt$ and introduce $u = pN/s$, $v = qP/r$ as new variables. That gives us the system

\[
\begin{align*}
u' &= u(1 - v) \quad \text{where } \alpha = \frac{s}{r}, \\
v' &= \alpha v(u - 1).
\end{align*}
\]
We see that there are three equilibrium:

\((0,0), (1,0), \text{ and } (1,1)\).

Of these only the last interest us, for obvious reasons.

The system derivative in this fourth equilibrium is \(\begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix}\), so the eigenvalues are \(\lambda = \pm i\), which means that we cannot determine if it is stable or not. This is actually for good reasons, because we can find an implicit equation for the solution by rewriting the equation as

\[
\frac{(1 - v)dv}{v} = \frac{\alpha(u - 1)du}{u},
\]

which can be integrated to \(\ln v - v = \alpha(u - \ln u) + C\). Exponentiating and we have the implicit equation

\[
ve^{-v} = Ku^{-\alpha}e^{\alpha u}.
\]

We can plot the trajectories by utilizing a trick, as illustrated in the figure below.

We see that the trajectories are closed curves around \((1,1)\), which means that the equilibrium is stable, but not asymptotically stable.

The catch reflects the average population over a year, so we want to estimate this. Assume the solution \((u(t), v(t))\) is periodic with period \(T\). If we rewrite the system as

\[
\begin{cases}
\frac{u'}{u} = 1 - v \\
\frac{v'}{v} = \alpha(1 - u)
\end{cases}
\]

and integrate over a period we get

\[
\int_0^T (1 - v(t))dt = \ln(u(T)) - \ln(u(0)) = 0, \quad \alpha \int_0^T (1 - u(t))dt = 0
\]

It follows that

\[
\frac{1}{T} \int_0^T u(t) \, dt = \frac{1}{T} \int_0^T v(t) \, dt = 1
\]
If we go back to the original variables this means that
\[ \frac{1}{T} \int_0^T N(t) \, dt = \frac{s}{p}, \quad \frac{1}{T} \int_0^T P(t) \, dt = \frac{r}{q}. \]

So far we have considered the ecological system without harvesting. If we assume that fishing removes a fraction \( \epsilon \) of all fishes, this is equivalent to replacing \( r \) with \( r - \epsilon \) and \( s \) with \( s + \epsilon \) in the original equations. The mean values are therefore
\[ \frac{s + \epsilon}{p}, \quad \frac{r - \epsilon}{q} \] respectively.

Thus we see that fishing diminishes the predator population and increases the preys. It follows that a diminished fishing level will lead to the result observed in the data.

**Another derivation of the model**

For completeness sake, let us also see how we can model the situation with a Markov process and from this derive the equations of the previous section.

Let us assume the prey are rabbits and the predator are foxes. Let \( A \) be the the area of bounded region in which these live. Foxes eat rabbits and the probability that a given rabbit will be eaten by a fox within a short period of time is proportional to the density of rabbits. Also, how many surviving offsprings the foxes have depends on how easy it is to catch rabbits, which in turn is proportional to the density of rabbits. If \( r \) is the number of foxes and \( k \) the number of rabbits, we have the following possible transitions, together with the intensity with which they occur.

<table>
<thead>
<tr>
<th>transition</th>
<th>intensity</th>
<th>explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>((k, r) \to (k + 1, r))</td>
<td>(\lambda_1 r)</td>
<td>a rabbit is born</td>
</tr>
<tr>
<td>((k, r) \to (k - 1, r))</td>
<td>((\mu_1 + b \frac{r}{A}) k)</td>
<td>a rabbit dies, either 'of it own' och by being eaten</td>
</tr>
<tr>
<td>((k, r) \to (k, r + 1))</td>
<td>((\lambda_2 + c \frac{k}{A}) r)</td>
<td>a fox is born</td>
</tr>
<tr>
<td>((k, r) \to (k, r - 1))</td>
<td>(\mu_2 r)</td>
<td>a fox dies</td>
</tr>
</tbody>
</table>

If we write \( x = (k, r) \), \( e_1 = (1, 0) \) and \( e_2 = (0, 1) \), we see that the intensity function of this can be written \( Af(x/A, \theta) \), where
\[ f(x, e_1) = \lambda_1 x_1, \quad f(x, -e_1) = (\mu_1 + bx_2) x_1, \quad f(x, e_2) = (\lambda_2 + cx_1) x_2, \quad f(x, -e_2) = \mu_2 x_2, \]
all other zero. The average intensity is therefore
\[ F(x) = (1, 0) f(x, (1, 0)) + (-1, 0) f(x, (-1, 0)) + (0, 1) f(x, (0, 1)) + (0, -1) f(x, (0, -1)) = (\lambda x_1 - (\mu_1 + bx_2) x_1, (\lambda_2 + cx_1) x_2 - \mu_2 x_2). \]

which gives the differential equations
\[
\begin{align*}
x_1'(t) &= (\lambda_1 - \lambda_2) x_1(t) - bx_1(t) x_2(t) \\
x_2'(t) &= cx_1(t) x_2(t) - (\mu_2 - \lambda_2) x_2(t).
\end{align*}
\]

Introducing some parameters and we have the Lotka-Volterra system of equations.
Two-species systems and limit cycles

Lotkas contribution - reaction kinetics

The law of mass action in chemistry means that the reaction
\[ A + B \rightarrow C \]
occurs with a rate which is proportional to the product of the the concentrations of \( A \) and \( B \):
\[ [C]'(t) = k[A](t)[B](t). \]
It is by no means a universal law; many reactions occur with rates that differ from this.

**Example 1** Consider a reaction between \( A \) and \( B \) forming a complex \( AB \), which also dissociates. Assuming the law of mass action, the reaction
\[ A + B \overset{k_1}{\rightleftharpoons} AB \]
leads to the differential equation
\[ [AB]' = k_1[A][B] - k_{-1}[AB]. \]
This is at equilibrium when the left hand side is zero, i.e. when
\[ \frac{[A][B]}{[AB]} = \frac{k_1}{k_{-1}} = K_a, \]
where \( K_a \) is called the association constant for the complex \( AB \). Note that \([A]' = -[AB]'\).

**Autoctalysis** is the process whereby a chemical is involved in its own production, like in the following theoretical reaction:
\[ A + X \overset{k_1}{\rightleftharpoons} 2X, \]
where a molecule of \( X \) combines with one of \( A \) to form two molecules of \( X \). If \( A \) is maintained at a constant concentration \( a \), the law of mass action gives the rate of reaction as
\[ x' = k_1ax - k_{-1}x^2, \]
which we see is a chemical analogue of the logistic equation. From the analysis of the latter we know that
\[ x(t) \rightarrow \frac{k_1a}{k_{-1}} \text{ as } t \rightarrow \infty. \]
Assume instead that \( X \) is also used up in the production of another chemical:
\[ A + X \overset{k_1}{\rightleftharpoons} 2X, \quad B + X \rightarrow C. \]
Keeping both $A$ and $B$ at constant concentrations $a, b$ this gives us the differential equation

$$x' = (k_1 a - b_2 b)x - k_{-1} x^2.$$ 

A quick analysis shows that if $k_1 a > k_2 b$ then

$$x(t) \to \frac{k_1 a - k_2 b}{k_{-1}} \text{ as } t \to \infty,$$

whereas when $k_1 a < k_2 b$ we have that $x(t) \to 0$ when $t \to \infty$.

**Example 2** Consider cells which react to the local concentration of a chemical $S$ by activating a gene so that the cells produce a product $G$. We assume the product is autocatalytically produced in a saturable way and that it degrades according to first-order kinetics. A rate equation for the product concentration $g$ might be

$$g' = k_1 s + \frac{k_2 g^2}{k_3 + g^2} - k_4 g.$$ 

The black graph above is the rhs when $s = 0$. There are two stable equilibria, of which $g = 0$ is one. So if we start there, we stay there. If we increase $s$ a little (lower red curve), we will end up in the lowest equilibria and as we increase $s$ only small changes in the equilibrium will occur. But as we pass the $s$ corresponding to the blue curve, the system settles at much higher levels.

This is a simple suggestion on how morphogenesis might work: let a lineage of cells experience a concentration gradient of $s$, and within each cell start the gene activation system from $g = 0$. Let the cell differentiate according to which level the gene concentration settles at. There will be two only different cell types with a clearly defined border between them.

A model with double autocatalysis was proposed by Lotka in 1920:

$$A + X \to 2X, \quad X + Y \to 2Y, \quad Y \to B.$$ 

If we write down the equations for this reaction:

$$x' = k_1 ax - k_2 xy, \quad y' = k_2 xy - k_3 y,$$

we see that this is the same system as the one Volterra derived for the predator-prey interaction.
Realistic predator-prey dynamics

The Lotka-Volterra equations

\[ N' = rN - qPN, \quad P' = pNP - sP \]

represented a first attempt of modelling a predator-prey system. However, it does not take into account any of the limitations we have previously discussed: the carrying capacity concept and the restrictions in the functional response of the predator. More realistically the prey equation should read

\[ N' = rN(1 - \frac{N}{K}) - Pg(N), \]

where \( g(N) \) is the functional response for the predator. For now we take this to be that of an invertebrate type, i.e. \( g(N) = \beta N/(D + N) \).

For the predator we use a logistic model in which the carrying capacity is proportional to the density of prey:

\[ P' = sP(1 - \alpha PN). \]

Remark Note that the assumptions mean that the predator do not really have any alternative food resource.

We now want to study the dynamics of this system and compare it to that of Lotka-Volterra's.

First we nondimensionalize: \( x = N/K, \quad y = \alpha P/K \) and \( rt \) as new time gives us

\[ x' = x(1 - x) - \frac{axy}{d + x}, \quad y' = by\left(1 - \frac{y}{x}\right), \]

where \( a = \beta/\alpha r, \quad d = D/K, \quad b = s/r \). The equilibria to this is given by the equations

\[ x = y, \quad ay = (1 - x)(d + x), \]

which is the intersection by a straight line and a parabola so placed that there is exactly one solution in the first quadrant, which we denote \((x^*, y^*)\).

To compute its stability is a tedious calculation. Suffice to say that it can be shown that the equilibrium is stable if and only if

\[ 2ab > (a - \sqrt{(1-a-d)^2 + 4d})(1 + a + d) - \sqrt{(1-a-d)^2 + 4d}). \]

So we see that for given \( a, d \), we have stability if \( b \) is large enough.

So what happens when \( b \) is small? The graph below illustrates (for \( a = 1, \quad d = 0.1 \)) what happens when we increase \( b \) from 0.1 to 0.5. For \( b \geq 0.26 \) we have a stable equilibrium, whereas when \( b < 0.26 \) the orbits approach a so-called limit cycle. In contrast to the Lotka-Volterra model this cycle is independent of starting conditions (but depends on parameters).

Why there is a limit cycle and why it is stable we will return to below.
General comments about two-species interactions

Systems describing the interaction between two species typically takes the form

\[ x' = xf(x, y), \quad y' = yg(x, y) \]

where we have that for

**competing species** an increase in one species leads to a diminished growth rate in the other:

\[ \frac{\partial f}{\partial y} < 0, \quad \frac{\partial g}{\partial x} < 0. \]

We have previously discussed the case when \( f(x, y) = 1 - x - \alpha_1 y \), \( g(x, y) = \rho(1 - y - \alpha_2 x) \).

**predator-prey systems** an increase in the number of predators \((y)\) decreases the growth of the prey, whereas an increase in prey increase the growth rate of the predators:

\[ \frac{\partial f}{\partial y} < 0, \quad \frac{\partial g}{\partial x} > 0. \]

The example above is

\[ f(x, y) = 1 - x - \frac{ay}{d + x}, \quad g(x, y) = b(1 - \frac{y}{x}). \]
An equilibrium \((x^*, y^*)\) in the interior of the first quadrant solves the equations
\[ f(x, y) = 0, \quad g(x, y) = 0. \]

There are some pseudogeometric methods that can be used to determine the stability of this from the shape of the curves, but we do not discuss those.

**Limit cycles: Poincaré-Bendixsons theorem**

Consider a general two-dimensional system:
\[ x' = F(x, y), \quad y' = G(x, y). \]

**Theorem 1**

A bounded semiorbit that does not approach any equilibrium is either a closed periodic orbit or approaches a closed periodic orbit.

We do not prove this theorem, but note that in order to apply it we need to construct a so-called trapping region which is such that on its boundary the vector field points into the region everywhere. Then no orbit can escape the region, and the theorem guarantees a limit cycle.

**Example 3** The graph below indicates (except for arrow length) the vector field for the predator-prey system:

We can note the following about the field on the border of the rectangle \(0 \leq x, y \leq 1\):
a) On the side \( x = 1 \) we have the vector \((-ay/(d + 1), by(1 - y))\) with the sign \((-+, +)\), so it points into the rectangle,

b) On the side \( y = 0 \) we have \((x(1 - x), 0)\), which point in the positive \( x\)-direction.

c) On the side \( x = 0 \) we do not have a vector field because of division with zero, but if we move it slightly to the right we get a field which almost points in the negative \( y\)-axis. We obviously cannot cross the positive \( y\)-axis.

d) On the side \( y = 1 \) the field is \((x(1 - x) - ax/(x + d), b(1 - 1/x))\) for which the second component is negative, so it points into the rectangle.

Around the steady-state point, which is unstable, we can take a small circle such that the vector field points outwards on its border. Based on these observations one can construct a proper trapping region based on which we can use Poincaré-Bendixson’s theorem to prove there is a stable limit cycle in the interior.

There are also some simple criteria that let us exclude the possibility of a limit cycle. The differential equations imply that \( dt = dx/F(x, y) = dy/G(x, y) \) and by applying Green’s formula to a simple, closed trajectory \( \gamma = \partial \Omega \) of the system, we see that for any function \( f(x, y) \)

\[
\int \int_{\Omega} \text{div}(fF, fG)(x, y) \, dx \, dy = \int_{\gamma} f(x, y)(F(x, y) \, dy - G(x, y) \, dx) = 0
\]

where

\[
\text{div}(F, G)(x, y) = \frac{\partial F}{\partial x}(x, y) + \frac{\partial G}{\partial y}(x, y).
\]

This tells us that if \( \text{div}(fF, fG) \) does not change sign in a region, there can be no periodic orbits in that region. This is called Dulac’s criterion; the special case with \( f = 1 \) is called Bendixson’s criteria for the nonexistence of a periodic limit cycle.

Remark The two-system situation differ from that of higher systems:

- The Poincaré-Bendixson’s theorem limits the possibilities for the trajectories in the phase plane: if a trajectory is confined to a closed, bounded region with no fixed points in its interior, it must approach a closed orbit.

- In three or more dimensions, however, trajectories can wander around in a bounded region without ever asymptotically approaching a fixed point or a closed orbit.

- In more than two dimensions trajectories can be attracted to what is called strange attractors, which is a complicated creature of a fractal nature.

The Hopf bifurcation

Here is another way of depicting how the long-term solution to the predator-prey system changes as we change \( b \). The graph below shows for each \( b \) (in the interval \( 0 < b < 0.4 \)) what
the limit curve looks like. We see that for larger $b$ this is a point, the stable equilibrium, but at a particular value of $b$, called the bifurcation value, this becomes larger and larger limit cycles. The actual bifurcation value is given by

$$b_c = 0.2625157....$$

What is illustrated here is an application of the Hopf bifurcation theorem which predicts the appearance of a limit cycle from a steady state, when this transits from a stable to an unstable one. In contrast to the Poincaré-Bendixson theorem above this theorem is true also for larger systems. In two dimensions the requirement is that as we vary a parameter ($b$ in the example) the eigenvalues of the system are complex valued, with zero real part and non-zero imaginary part for $b = b_c$ and such that the real part switches sign (derivative $\neq 0$) when passing $b_c$. The point is that when the steady state becomes unstable, what emerges is a (small) limit cycle.

The theorem in itself is local, but in real life we hope that what it predicts is true also on a wider scale – like in our case.

Example 4 To apply the theorem to the predator-prey system we need to compute the system derivative in the stationary point for general $b$. The eigenvalues are complex valued and their sum (i.e. twice the real part) is

$$A = x^*(−1 + \frac{ay^*}{(d + x^*)^2}) + y^*(-\frac{b}{x^*}) = -x^* + \frac{(1 - x^*)^2}{a} - b.$$ 

The derivative of this w.r.t. $b$ is $-1$ and a short computation shows that the critical value is given by

$$b_c = \frac{(1 - x^*)^2}{a} - ax^* = (1 - x^*)\frac{1 - x^* - (d + x^*)}{a}.$$
Exercises

Exercise 1 Consider the system

\[ x' = x(a_0 + a_1 x + a_2 y), \quad y' = y(b_0 + b_1 x + b_2 y). \]

Determine \( \alpha, \beta \) so that if we choose \( K(x, y) = x^\alpha y^\beta \), we have \( \text{div}(Kx, Ky) = BK \) for some constant \( B \). Use this to describe conditions on the coefficients of the system to guarantee that there are no periodic solutions. Use the result to show that the model for competing species cannot exhibit periodic solutions.

Exercise 2 Assume that a population of herbivores of density \( y \) causes changes in the vegetation on which it preys. An internal variable \( x \) reflects some physical or chemical property of the plants which undergo changes in response to herbivory (we call it plant quality), which in turn affects the fitness/survivorship of the herbivores. This would lead to a system

\[ x' = f(x, y), \quad y' = yg(x, y). \]

a) If \( f(x, y) = x(1 - x)(\alpha(1 - y) + x) \) when \( 0 \leq x \leq 1 \), show that if \( x(0) \) is in this interval, the solution will stay there.

b) Write the full model if we assume that the herbivore population undergoes a logistic growth such that the carrying capacity is proportional to current plant quality.

c) Analyse the system with phase-plane methods. Does it allow for stable limit cycles?

Exercise 3 Consider the dimensionless activator \((u)\)-inhibitor \((v)\) system represented by

\[ u' = a - bu + \frac{u^2}{v}, \quad v' = u^2 - v. \]

Show that the \((a, b)\) parameter space in which \( u \) and \( v \) may exhibit periodic behaviour is bounded by the curve \( b = 2(1 - a)^{-1} - 1 \) and sketch the domain.

Consider the modified system in which there is inhibition by \( u \). In this case \( u^2/v \) is replaced by \( u^2/(v(1 + Ku^2)) \) in the \( u \)-equation. Show that the boundary curve in \((a, b)\) space for the domain in which periodic solutions may exist is given parameterically by

\[ b = \frac{2}{u_0(1 + Ku_0^2)} - 1, \quad a = \frac{2}{(1 + Ku_0^2)^2} - u_0 - \frac{1}{1 + Ku_0^2}, \quad b \geq 0. \]

Sketch the domain and indicated how it changes as the inhibitor parameter \( K \) varies.

Answers and tips to exercises

Exercise 1 \( \alpha, \beta \) should solve the system

\[
\begin{align*}
  a_1 \alpha + b_1 \beta &= -2a_1 - b_1 \\
  a_2 \alpha + b_2 \beta &= -a_2 - 2b_2
\end{align*}
\]
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and then $B = (\alpha + 1)a_0 + (\beta + 1)b_0 \neq 0$. The determinant of the system $A = a_1b_2 - b_1a_2$, so if $A \neq 0$ and $B \neq 0$ we have no periodic orbits. For competing species we have $A = \rho(\alpha_{21} - \alpha_{12})$, $B = 2\rho(\rho\alpha_{21} - \alpha_{12})$. For Lotka-Volterra we have $A = \rho$ and $B = 0$, so it can (and does) have periodic solutions.

**Exercise 2**

a) The solution cannot traverse the lines $x = 0$ and $x = 1$.

b) We take $g(x, y) = \beta(1 - y/(Kx))$.

c) Three equilibria: $(1, 0), (0, 0)$ and $(\gamma, K\gamma)$, where $\gamma = \alpha/(\alpha K - 1)$. The first two are saddle points, the last has a system derivative which has trace $\gamma(1 - \gamma) - \beta$ and determinant $\beta\alpha(1 - \gamma)$. If $\gamma > 1$ we have a saddelpoint and when $\gamma < 1$ we have a knot. When $\beta \alpha < \gamma(1 - \gamma)$ it will be unstable and the square $0 \leq x \leq 1, 0 \leq y \leq K$ is a trapping region. Periodic solutions will then exist.

**Exercise 3** There is one equilibrium, in $(\gamma, \gamma^2)$ where $\gamma = (a + b)/b$. The system derivative has positive determinant ($= b$) and trace $2/\gamma - b - 1$. The region is the part where the trace is positive, so that the equilibrium is unstable.

For the second model $\gamma = \gamma(K)$ is the solution of the equation $a - bu - 1/(1 + Ku^2) = 0$. Now the trace of the system derivative is $-(b + 1 - 2/\gamma(1 + Ku^2))$ so the boundary of the $(a, b)$-region for which the equilibrium $(\gamma, \gamma^2)$ is unstable is parametrized by

$$u \to \left(\frac{2}{(1 + Ku^2)^2} - u + \frac{1}{1 + Ku^2}, \frac{2}{u(1 + Ku^2)^2} - 1\right).$$