Nonlinear Systems: Predator–Prey Models

Assumptions  Two species, one feeding on the other

1. Prey population \( x(t) \); Predator population \( y(t) \)

2. If no predators, prey population grows at natural rate: for some constant \( a > 0 \),
\[
\frac{dx}{dt} = ax \quad \Rightarrow \quad x(t) = x_0e^{at}
\]

3. In no prey, predator population declines at natural rate: for some constant \( b > 0 \)
\[
\frac{dy}{dt} = -by \quad \Rightarrow \quad y(t) = y_0e^{-bt}
\]

4. When populations interact, predator population increases and prey population decreases at rates proportional to the frequency of interaction \( xy \)

Resulting model: for some positive constants \( a, b, p, q, \)
\[
\frac{dx}{dt} = ax - pxy \quad \frac{dy}{dt} = qxy - by
\]

This is a famous non-linear system of equations known as the Lotka-Volterra equations. The system has numerous applications to biology, economics, medicine, etc.

There are two critical points \((0, 0)\) and \((\frac{b}{q}, \frac{a}{p})\)

In the usual way, we analyze the types of the critical points. First compute the Jacobian:
\[
J = \begin{pmatrix}
a - py & -px \\
qy & qx - b
\end{pmatrix}
\]

Critical point \((0, 0)\)  The Jacobian is \(J(0, 0) = \begin{pmatrix} a & 0 \\
0 & -b \end{pmatrix}\) and has linearization
\[
\frac{du}{dt} = au \quad \frac{dv}{dt} = -bv
\]

Since \(a > 0 > -b\) we have a saddle point. Moreover, the eigenvectors of the Jacobian are \(\begin{pmatrix} 1 \\ 0 \end{pmatrix}\) and \(\begin{pmatrix} 0 \\ 1 \end{pmatrix}\) (for eigenvalues \(a, -b\) respectively). Since we are only interested in positive populations, we obtain the following phase-portrait for the linearized system.

The original non-linear system will also have a saddle point at the origin, oriented in the same manner.
Critical point \((\frac{b}{q}, \frac{a}{p})\) The Jacobian is \(J(\frac{b}{q}, \frac{a}{p}) = \begin{pmatrix} 0 & -\frac{bp}{q} \\ \frac{aq}{p} & 0 \end{pmatrix}\) and has linearization

\[
\frac{du}{dt} = -\frac{bp}{q} v \quad \frac{dv}{dt} = \frac{aq}{p} u
\]

The eigenvalues are solutions to \(\lambda^2 + ab = 0 \iff \lambda = \pm i\sqrt{ab}\). Since \(a, b > 0\) these are pure imaginary. The linearization therefore has a stable center. The original non-linear system has a center, or a spiral sink/source at \((\frac{b}{q}, \frac{a}{p})\). Which is it?

In this situation we can actually solve the original system implicitly:

\[
\frac{dy}{dx} = \frac{dy/\text{d}t}{dx/\text{d}t} = \frac{(qx - b)y}{x(a - py)}
\]

is a separable equation which, when integrated, yields the implicit curve

\[
a \ln y + b \ln x = qx + py + C
\]

where \(C\) is the constant of integration. For each choice of constant \(C\), the trajectory is an implicit curve which is a level set of the function

\[
F(x, y) = a \ln y + b \ln x - qx - py
\]

If we had a spiral sink or source, then the critical point \((\frac{b}{q}, \frac{a}{p})\) would lie on many of these level sets. But then \(F(\frac{b}{q}, \frac{a}{p})\) would have to have many values, which makes no sense, since \(F\) is continuous at \((\frac{b}{q}, \frac{a}{p})\). The non-linear system therefore has a stable center.

For any positive initial populations, predator–prey populations oscillate

Trajectories make periodic orbits around \((\frac{b}{q}, \frac{a}{p})\)

Cannot calculate period exactly: need numerical method to approximate solutions as functions of \(t\)

Consider what is happening when the point \((x, y)\) is in each of the four labelled regions:

1. Predator population low \(\implies\) prey grows
2. High prey population \(\implies\) more food \(\implies\) predator population increases
3. High predator population eats prey \(\implies\) prey population decreases
4. Low prey population \(\implies\) less food \(\implies\) predators decrease: back to 1
More complex models — non-examinable

Competing species Assume that the populations $x(t)$ and $y(t)$ satisfy:

1. Independent of each other, both populations follow a logistic model:

$$\frac{dx}{dt} = kx(M - x) \quad \frac{dy}{dt} = ly(N - y)$$

2. Competition for resources: when the populations interact, each population exerts downward pressure on the other. We obtain a non-linear system as follows:

$$\frac{dx}{dt} = kx(M - x) - pxy \quad \frac{dy}{dt} = ly(N - y) - qxy$$

where $k, l, M, N, p, q > 0$

The system has four critical points $(0, 0), (M, 0), (0, N)$ and, provided $kl \neq pq$,

$$(x^*, y^*) = \left(\frac{l(kM - pN)}{kl - pq}, \frac{k(IN - qM)}{kl - pq}\right)$$

Analysis of Critical Points $(0, 0)$ indicate extinction of both species, while $(M, 0)$ and $(0, N)$ indicate extinction of one or the other.

We compute the Jacobian: $J = \begin{pmatrix} kM - 2kx - py & -px \\ -qy & lN - qx - 2ly \end{pmatrix}$. At each of the four critical points this evaluates as follows, and we state the eigenvalues. Assuming none of the eigenvalues are zero, we can identify the types of critical point.

<table>
<thead>
<tr>
<th>Critical Point</th>
<th>Jacobian</th>
<th>Eigenvalues</th>
<th>Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>$(0, 0)$</td>
<td>$\begin{pmatrix} kM &amp; 0 \ 0 &amp; lN \end{pmatrix}$</td>
<td>$kM, lN$</td>
<td>Nodal source</td>
</tr>
<tr>
<td>$(M, 0)$</td>
<td>$\begin{pmatrix} -kM &amp; -pM \ 0 &amp; lN - qM \end{pmatrix}$</td>
<td>$-kM, lN - qM$</td>
<td>Sink or saddle</td>
</tr>
<tr>
<td>$(0, N)$</td>
<td>$\begin{pmatrix} kM - pN &amp; 0 \ -qN &amp; -lN \end{pmatrix}$</td>
<td>$kM - pN, -lN$</td>
<td>Sink or saddle</td>
</tr>
<tr>
<td>$(x^<em>, y^</em>)$</td>
<td>$\begin{pmatrix} -kx^* &amp; -px^* \ -qy^* &amp; -ly^* \end{pmatrix}$</td>
<td>$-kx^* - ly^* \pm \sqrt{(kx^* - ly^*)^2 + 4pqx^<em>y^</em>}$</td>
<td>See below…</td>
</tr>
</tbody>
</table>

The type of critical point at $(x^*, y^*)$ depends on several considerations, mostly the quadrant of the plane in which it lies. We treat each separately.

$(x^*, y^*)$ in third quadrant Thus $x^*, y^* < 0$. This is impossible by inspection of the expressions for $x^*, y^*$ and the fact that all constants are positive.

$^1$M, N are the stable populations of each species in the absence of the other, and k, l are the respective growth rates.
\((x^*, y^*)\) in second or fourth quadrant

\(x^*, y^*\) have opposite signs. In such a case \((x^*, y^*)\) is not physically significant (negative populations are meaningless).

One of \((M, 0)\) and \((0, N)\) is a saddle and the other is a sink: one of the populations out-competes the other and the latter goes extinct.

In the case drawn, \((M, 0)\) is a saddle, and \((N, 0)\) is a sink: population \(x\) goes extinct. If \((x^*, y^*)\) were in the fourth quadrant, the situation would be reversed.

\((x^*, y^*)\) in first quadrant with \(kl > pq\)

If \(k, l\) are large, both populations have a strong negative effect on their own growth.

If \(p, q\) are large, both populations have a strong negative effect on each others’ growth.

If \(kl > pq\), then self-inhibition dominates over the effects of competition.

In this case both \((M, 0)\) and \((0, N)\) are saddle points.

Both eigenvalues at \((x^*, y^*)\) are negative and we have a sink.

Populations approach a stable equilibrium at \((x^*, y^*)\).

Populations compete for resources, but the effects are balances: species can coexist.

\((x^*, y^*)\) in first quadrant with \(kl < pq\)

Competition dominates over self-inhibition.

In this case both \((M, 0)\) and \((0, N)\) are sinks.

Eigenvalues at \((x^*, y^*)\) have opposite signs indicating a saddle.

One of the populations will go extinct, dependent on initial conditions.

Degenerate situations (where \(kl = pq\), etc) are a little more complicated, but the above cover almost all possibilities.
Co-operation

A similar model involves letting \( p, q < 0 \): populations are now boosted by each others’ presence.

If \( p, q < 0 \) are small then the benefits provided by the other populations are small. We expect stable populations \( x^* > M \) and \( y^* > N \).

Here both \((M, 0)\) and \((0, N)\) are saddles, and \((x^*, y^*)\) is a nodal sink in the first quadrant.

We could also have \( p, q < 0 \) large, in which case \((x^*, y^*)\) is not in the first quadrant and we would have a population explosion!