Content: Systems of difference equations
2.7-2.9, 3.2-3.6

Systems of difference equations

The basic principle for a system of dependent recursion equations is the same as for a single equation, if we only use matrix language. We write the problem as

\[ u_{n+1} = f(u_n) \]

where \( u_n \) is an \( n \)-vector and \( f : \mathbb{R}^n \to \mathbb{R}^n \) is usually assumed continuously differentiable. An equilibrium (or steady state) is a vector \( u^* \) such that \( u^* = f(u^*) \) and we can infer its stability from \( f \)'s derivative (jacobian) as before: write \( u_n = u^* + e_n \) and apply the linear approximation

\[ u^* + e_{n+1} \approx f(u^*) + f'(u^*)e_n \quad \Rightarrow \quad e_{n+1} = f'(u^*)e_n, \]

which is a good enough approximation as long as \( e_n \) is sufficiently small. The stability (of \( u^* \)) is determined from the eigenvalues of the matrix \( f'(u^*) \): if they all have a modulus \( k \leq 1 \), it is stable; if at least one has a modulus \( k > 1 \), it is unstable.

Example Consider, for \( r > 0 \), the system

\[
\begin{align*}
x_{n+1} &= rx_n e^{-y_n} \\
y_{n+1} &= y_n(1-e^{-x_n})
\end{align*}
\]

which has two equilibria, \( (0,0) \) and \( (1,1) \). The latter case, the additional equilibrium appears in the first quadrant, \( (x, 1/e^x) \) with \( x = 0 \), \( y = 1 \), \( x = 1/e \). The derivative of \( f \) is

\[ f'(x,y) = \begin{pmatrix} xe^{-y} & -xre^{-y} \\
1-e^{-y} & xe^{-y} \end{pmatrix}, \]

and therefore

\[ f'(0,0) = \begin{pmatrix} r & 0 \\
0 & 0 \end{pmatrix}, \quad f'(u^*) = \begin{pmatrix} \frac{1}{1+r} & \frac{-1}{1+r} \\
\frac{1}{1+r} & \frac{1}{1+r} \end{pmatrix}. \]

We see that \( y_n \) goes to zero, whereas \( x_n \) increases geometrically. (Can we prove this?)

Remark We will soon see that this system is a first attempt to model a particular biological system.

The spread of an infection in discrete time

To describe the spread of an infection in a small population, like a household, we have \( S_n, I_n, R_n \) be the number of susceptibles, infectives and removeds on day \( n \) from initiation. If the total population is \( N \), this means \( S_n + I_n + R_n = N \) for all \( n \). Let \( p \) be the probability that an encounter between a susceptible and an infective produces a new infective. We assume there is perfect mixing, so that the probability that a susceptible avoids getting infected by all \( I_n \) infectives during the sampling interval is \( q_n = (1-p)^{I_n} \). With \( a = -\ln(1-p) \) this can be written \( e^{-al_n} \) and we find that the number of susceptibles has decreased to \( S_n e^{-al_n} \). Those lost have been infected, and together with the fraction \( b \) that is still infected makes up the group of infectives on the next occasion. This justifies the system

\[ S_{n+1} = e^{-al_n}S_n, \quad I_{n+1} = S_n(1 - e^{-al_n}) + bI_n \]

is used as a discrete time model for infectious diseases.

We are now interested in two questions:

1. What are the criteria for the infection to catch on?
2. Are there susceptibles that never get the disease as a consequence of the dynamics alone?

One-step iteration shows that

\[ S_1 = S_0(1 - e^{-al_0}) + bI_0, \]

so for there to be an epidemic, i.e. \( I_1 > I_0 \), we need

\[ S_0 > \frac{(1-b)I_0}{1-e^{-al_0}} \]

We therefore a large enough population to spark an epidemic.

With \( S_0 > 0 \) we see that \( \{S_n\} \) is a decreasing sequence bounded from below, so \( S_{\infty} = \lim_{n\to\infty} S_n \) exists. Moreover, \( S_{\infty} = S_0 \exp(-a\sum_{k=0}^{n-1} l_k) \). We can note that \( R_{n+1} = R_n + (1-b)I_n \), and since \( R_0 = 0 \) we have that \( S_\infty = S_0 \exp(-al_0/(1-b)) \). Since \( R_n \leq N \) if follows that \( S_\infty \geq S_0 \exp(-aN/(1-b)) > 0 \), and consequently \( \lim_{n\to\infty} I_n = 0 \). It follows that \( S_\infty + R_\infty = N \) and therefore

\[ S_\infty = S_0 e^{-a(N-S_\infty)/(1-b)} \]
which is the equation that determines the number of individuals that never get infected. It follows that the fraction $Q = (N - S_0)/N$ that got the disease is approximately given by

$$1 - Q = e^{-rQ/S_0}, \quad r = \frac{a}{1-b}.$$  

**Host-parasitoid systems**

These two-species systems are found almost exclusively in the world of insects. Each species has a number of life-cycle stages that include eggs, larvae, pupae and adults. The parasitoid species exploits the host species as follows. An adult female parasitoid searches for a host on which to deposit its eggs (on the surface or injected). The larval parasitoids develop and grow at the expense of their host, consuming and eventually killing it before it pupates. The life cycles of the two species are thus closely intertwined:

On model for this (the Nicholson-Baily model) is built around

- $N_t$ = density of host species in generation $t$
- $P_t$ = density of parasitoid in generation $t$
- $f = f(N_t, P_t)$ fraction of host not infected
- $\lambda$ = host reproductive rate
- $c$ = average number viable eggs laid by a parasitoid on a single host

The situation is very much like the one in the previous section, so the fraction of host not infected can be modelled as $e^{-\sigma y}$. A first attempt to model the situation might then be

$$\begin{align*}
N_{t+1} &= \lambda N_t e^{-\sigma y}, \\
Y_{t+1} &= cN_t (1 - e^{-\sigma y}).
\end{align*}$$

If we introduce $x_n = \sigma N_n$, $y_n = a P_n$, the equations become

$$\begin{align*}
x_{n+1} &= \lambda x_n e^{-y_n}, \\
y_{n+1} &= c' x_n (1 - e^{-y_n}),
\end{align*}$$

which we analysed above. We saw that the host will eventually get rid of the parasitoid, which means that such systems should not exist in the real world. To be realistic we therefore need to modify it so that it under a set of circumstances will provide a stable solution with cohabitation of the two species.

How can we make it stable? One natural model improvement is to take into account a carrying capacity for the host population:

$$\lambda = \lambda(N) = e^{(1-N/K)}.$$  

With $x_n = N_n/K$, $y_n = a P_n$, this gives us the system

$$\begin{align*}
x_{n+1} &= x_n e^{(1-x_n-y_n)}, \\
y_{n+1} &= c' x_n (1 - e^{-y_n}).
\end{align*}$$

A non-zero equilibrium would be given by

$$\begin{align*}
1 = e^{(1-x)} - y, \\
y = c' x (1 - e^{-y}).
\end{align*}$$

The last equation express $c'$ as a function of $r$ and $x$, which we use as parameters.

For the analysis, $f(x, y) = (\lambda e^{1-x} - c' x (1 - e^{-y}))$ have the derivative

$$f'(x, y) = \begin{pmatrix}
1 - rx e^{1-x} - y & -x e^{1-x} - y \\
c'(1 - e^{-y}) & c' xe^{-y}
\end{pmatrix}$$

which in the origin takes the value

$$f'(0, 0) = \begin{pmatrix}
a' & 0 \\
0 & 0
\end{pmatrix},$$

which we see is unstable. In the nonzero equilibrium we have

$$f'(x, y) = \begin{pmatrix}
1 - rx e^{1-x} - y & -x e^{1-x} - y \\
c'(1 - e^{-y}) & c' xe^{-y}
\end{pmatrix}$$

which gives the characteristic equation

$$(\lambda - (1 - rx))(\lambda - \frac{r(1-x)e^{-r(1-x)}}{1 - e^{-r(1-x)}}) + r(1-x) = 0.$$  

We want to find the region in $x, r$–plane which gives two eigenvalues with modulus $< 1$.

For this we consider an equation

$$\lambda^2 - a\lambda + b = 0.$$  

An analysis (see book) shows that both its roots have modulus less than one precisely if

$$|a| < 1 + b < 2.$$  

In our case we have

$$a = \frac{1 - rx - (1-r)e^{-r(1-x)}}{1 - e^{-r(1-x)}}, \quad b = r(1-x) \frac{1 - rx e^{-r(1-x)}}{1 - e^{-r(1-x)}}$$

Using this information we can plot the boundaries on the region within which the equilibrium is stable:

**Two-year salmon: synchronisation by age structure**

Some species of Pacific salmon have a two-year life cycle. Eggs hatch in a river after spawning. After one year, the survivors are immature young, and after a year they are mature adults returning to the river ready for reproduction. After reproduction, the adults die. Let $y_n$ be the number of immature young and $a_n$ the number of reproducing adults in year $n$. It is reasonable that

$$a_{n+1} = c' y_n, \quad y_{n+1} = g(a_n)$$
where \( r \) is the fraction of young that mature into adults and \( g(a) \) describes reproduction as a function of the number of adults. A reasonable model for the latter is a Verhulst model with a predator threshold, i.e., a function of the form
\[
g(a) = \frac{ra^2}{K^2 + a^2}.
\]

First we reduce the number of parameters by introducing \( x_n = a_n/K, y_n = cy_n/K, \) giving us the equations
\[
\begin{align*}
x_{n+1} &= y_n - \frac{\mu x_n}{1 + x_n^2}, \\
y_{n+1} &= \frac{\mu x_n}{1 + x_n^2}, \quad \mu = rv/K.
\end{align*}
\]

The equilibria are easily computed to be the points \((x^*, x^*)\) for which either \( x^* = 0 \) or it solves the equation \( 1 + x^2 = \mu x \). If we call the solutions of this equation \( x_\pm \), we see that they are real and nonzero only if \( \mu > 2 \), and in that case we have that \( x_+ x_- = 1 \), \( x_+ + x_- = \mu > 2 \), which means that \( x_+ > 1 \) and \( x_- < 1 \).

The derivative of \( f(x, y) = (y, \mu x^2/(1 + x^2)) \) is
\[
f'(x, y) = \begin{pmatrix} 0 & 2\mu x/(1 + x^2) \\ 0 & -2\mu x/(1 + x^2) \end{pmatrix} \Rightarrow \lambda^2 = \frac{2\mu x}{(1 + x^2)^2},
\]
from which we see that the origin have eigenvalues zero, and therefore is stable. For the other two we have that \( \lambda^2 = 2/(1 + x^2) \) which means that \( x_+ \) is always stable and \( x_- \) is always unstable.

Because of how variables are separated in this system, we can learn more using cobwebbing techniques. This is illustrated below, where we illustrate the first step from \((x_0, y_0)\) to \((a_1, y_1)\) in the left figure.

We see that with the initial conditions chosen, the system will approach \( x_+ \), which in particular shows that this is stable. Similarly, if we move closer to the origin where the red and blue curve switch place, the iteration will instead approach the origin, which therefore also is stable. In fact, the lines through \( x_+ \) divides the first quadrant in four rectangles as illustrated in the figure. We see that if we start in I the cod will be extinct, whereas if we start in III the solution will approach \( x_- \) the balanced state.

What happens when we start in II (or II')? The graph below illustrates it:

Asymptotically we enter a two-period solution which oscillates between \((x_+, 0)\) and \((0, x_-)\): if we start in II the even-year offspring approaches \((0, x_+)\) and the odd-year offspring approaches \((x_+, 0)\). In particular, breeding adults will appear only every other year. This is called the synchronized state.

The regions I, II, III are called domains of attraction for the different asymptotic states (two equilibria, one 2-cycle).

**Exercises**

**Exercise 1** Do some numerical simulations of the Nicholson-Bailey model and graph the result. See book for guidance!

**Exercise 2** In the blood there is a steady production of \( CO_2 \) levels that results from the basal metabolic rate. \( CO_2 \) is lost by way of the lungs at a ventilation rate governed by \( CO_2 \)-sensitive chemoreceptors located in the brainstem. In a discrete time model for this we assume that breathing takes place at constant intervals and let \( C_n \) denote the amount of \( CO_2 \) in the blood on the \( n \)th breath. Let \( V_n \) be the ventilation volume (the volume inhaled and exhaled in a breath) at the same time.

1. Justify the following model:
\[
\begin{align*}
C_{n+1} &= C_n - \beta V_n C_n + m, \\
V_{n+1} &= \frac{V_{max} C_n}{K + C_n}.
\end{align*}
\]

2. Determine the equilibria and their stability.

**Exercise 3** Determine analytically the 2-cycle in the salmon model. Examine its stability.
Answers and tips

Exercise 1 The book investigates $x = 0.4$ and $r = 0.5, 2, 2.2, 2.65$. First compute $c'$ for each, and then simulate.

Exercise 2 1. The $C_n$ equation is mass balance, the $V_n$ a model which assumes that the ventilation volume is determined by the $CO_2$ level with a saturation model.
2. An advice is to rewrite the system in variables $(x_n, y_n)$ in only two parameters: $\mu = \frac{m}{K}$, $\alpha = \beta V_{max}$. There is one equilibrium $(x, y)$ where $x$ solves $x^2/(1 + x) = \mu/\alpha$ and $y = \mu/x$. Stability region in $(\mu, y)$ is $|1 - y| - 1 < y^3/\mu^2 < 1$. 