Biomathematics:
A course on some applications of dynamical systems

Linear system models in discrete time

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Introduction

A dynamical system in discrete time is essentially a recursion formula $u_{n+1} = f(u_n)$ where $n = 0, 1, \ldots$. Here $u_n$ might be vectors. In an ecological context we might want to count the number of foxes and rabbits every year, in which case we have system where $u_n$ has two components, one for the number of foxes and one for the number of rabbits. Since foxes eat rabbits their numbers will affect the size of the rabbit population. Reversely the rabbit population will affect the fox population, to an extent that depends on what alternative food resources the foxes have. The function $f$ describes how the populations affect each other in producing next years populations.

Such a recursion formula is linear if $f(u) = Au$ for some matrix $A$. This type of systems is extremely important, partly because the abundant number of applications and partly because in order to understand nonlinear systems we need to investigates linear approximations close to the equilibria. This motivates why we start our investigations of systems with linear ones in discrete time.

Linear 2×2-systems

We start by recalling how we solve a linear system of the form

$$\begin{align*}
x_{n+1} &= a_{11}x_n + a_{12}y_n \\
y_{n+1} &= a_{21}x_n + a_{22}y_n.
\end{align*}$$

With the notations

$$u_n = \begin{pmatrix} x_n \\ y_n \end{pmatrix}, \quad A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix},$$

we can write this as a matrix equation

$$u_{n+1} = Au_n.$$

We call the matrix $A$ the system matrix.

Had this been an one-dimensional equation ($A$ and $u_n$ real numbers) the solution would have been

$$u_n = A^n u_0.$$

This remains true for systems, except that now $A^n$ is a power of $A$.

Example 1 If

$$A = \begin{pmatrix} 7 & 4 \\ -8 & -5 \end{pmatrix}, \quad u_0 = \begin{pmatrix} 2 \\ -1 \end{pmatrix},$$

the solution to the recursion formula $u_{n+1} = Au_n$ is given by

$$u_n = \begin{pmatrix} 7 & 4 \\ -8 & -5 \end{pmatrix}^n \begin{pmatrix} 2 \\ -1 \end{pmatrix}.$$
But this is not very helpful – it does not tell us how the solution actually looks like for a general \( n \). In order to understand this we turn to linear algebra.

Assume that \( A \) has an eigenvalue \( \lambda \) with corresponding eigenvector \( v \):

\[
Av = \lambda v.
\]

If we choose that eigenvector as start vector, \( u_0 = v \), we see that

\[
u_1 = Av = \lambda v, \quad \Rightarrow \quad u_2 = Au_1 = \lambda Av = \lambda^2 v, \quad \Rightarrow \quad u_3 = Au_2 = \lambda^2 Av = \lambda^3 v
\]

etc, so that

\[
u_n = \lambda^n v.
\]

This very special start value therefore gives a simple solution: the ratio between the components does not change, but the components are multiplied by the same number \( \lambda \).

In many cases the general case is only marginally more complicated.

**Example 2** The matrix in the last example have the eigenvalues \( \lambda_1 = 3 \) and \( \lambda_2 = -1 \), with corresponding eigenvectors \( v_1 = (1, -1) \) respektive \( v_2 = (1, -2) \). These are linearly independent, so we can determine constants \( c_1 \) and \( c_2 \) such that \( u_0 = c_1v_1 + c_2v_2 \), i.e.

\[
\begin{pmatrix} 2 \\ -1 \end{pmatrix} = c_1 \begin{pmatrix} 1 \\ -1 \end{pmatrix} + c_2 \begin{pmatrix} 1 \\ -2 \end{pmatrix}.
\]

This system of equations has the solution \( c_1 = 3, \ c_2 = -1 \), so that

\[
u_0 = 3v_1 - v_2.
\]

From this it follows that

\[
u_1 = Au_0 = 3Av_1 - Av_2 = 3(3v_1) - (-1)v_2,
\]

\[
u_2 = Au_1 = 3^2Av_1 - (-1)Av_2 = 3^3v_1 - (-1)^2v_2
\]

etc. The general formula is

\[
u_n = 3^{n+1}v_1 - (-1)^nv_2.
\]

Explicitly,

\[
\begin{pmatrix} x_n \\ y_n \end{pmatrix} = 3^{n+1} \begin{pmatrix} 1 \\ -1 \end{pmatrix} - (-1)^n \begin{pmatrix} 1 \\ -2 \end{pmatrix} = \begin{pmatrix} 3^{n+1} - (-1)^n \\ -3^{n+1} + 2(-1)^n \end{pmatrix}.
\]

There are two ways to graphically illustrate the solution to a \( 2 \times 2 \)-system:

a) We plot two polygon curves, one with corners in \( (n, x_n) \) and one with corners in \( (n, y_n) \).

b) We can plot the points \( u_n = (x_n, y_n) \) and connect them with straight lines. This plot is called a phase portrait.
For a general discussion about $2 \times 2$-systems, we recall that such a system has two (not necessarily distinct and possibly complex) eigenvalues. These are obtained by determining the zeros of the characteristic polynomial

$$p_A(\lambda) = \det(\lambda I - A) = \lambda^2 - (\text{Tr}A)\lambda + \det A,$$

where $\text{Tr}A$ is the trace $A$, i.e. the sum of the diagonal elements, and $\det A$ is its determinant. Call the eigenvalues $\lambda_1$ och $\lambda_2$. If these are distinct there are two corresponding (possibly complex) eigenvectors $v_1$ and $v_2$ such that

$$Av_i = \lambda_i v_i, \quad i = 1, 2.$$

These must be linearly independent. Assume to the contrary that there are two constants $c_1, c_2$ such that $c_1 v_1 + c_2 v_2 = 0$. In such a case we have

$$0 = (\lambda_1 I - A)(c_1 v_1 + c_2 v_2) = c_1(\lambda_1 I - A)v_1 + c_2(\lambda_1 I - A)v_2 = c_2(\lambda_1 - \lambda_2)v_2$$

which is only possible if $c_2 = 0$, and then it follows that $c_1 = 0$. In the following we will take a closer look at the two most important cases.

**Two different real eigenvalues**

In this case $v_1$ and $v_2$ constitute a basis for $\mathbb{R}^2$ and we can write

$$u_n = A^n u_0 = c_1 \lambda_1^n v_1 + c_2 \lambda_2^n v_2,$$

where $c_1, c_2$ are real numbers, chosen so that $c_1 v_1 + c_2 v_2 = u_0$.

If we look at the system in the eigenvector basis it has the matrix

$$A = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix},$$

so we have two independent equations with solutions $x_k = c_1 \lambda_1^k$, $y_k = c_2 \lambda_2^k$. This implies that $|y_k|/|c_2| = |x_k|/|c_1|^{\alpha}$, där $\alpha = (\ln |\lambda_2|)/(\ln |\lambda_1|)$. The orbits are therefore given by an equation $|y| = C|x|^{\alpha}$. These orbits resembles hyperbolas if $\alpha < 0$ but parabolas if $\alpha > 0$. In the former case the origin is called a saddle point, in the latter a knot. Note that $\alpha < 0$ means that one of the eigenvalues is $> 1$ and one is $< 1$ to its absolute value. When $\alpha > 0$ the eigenvalues are on the same side of 1.
Complex eigenvalues

If one eigenvalue is complex, both are complex and complex conjugates. This is because the characteristic polynomial is real. If one of them is $\lambda = \alpha + i\beta$, the other is $\bar{\lambda} = \alpha - i\beta$. It is then possible to choose a basis in the plane so that the system matrix is

$$A = \begin{pmatrix} \alpha & -\beta \\ \beta & \alpha \end{pmatrix}.$$  

In relation to this basis it is then a good idea to work with complex number, i.e. write $u_n = x_n + iy_n$. We then have that $u_{n+1} = \lambda u_n$, and if we write $\lambda = \rho e^{i\theta}$ in polar form, this has the solution

$$u_n = \rho^n e^{in\theta}u_0.$$  

It means that the orbit follows a logarithmic spiral. The orbit approaches the origin if $\rho = |\lambda| < 1$, but moves away from the origin if $\rho > 1$. If $\rho = 1$ the orbits move on circles with the origin as center.

Remark The remaining case, only a single real eigenvalue, but this case is usually less important to understand; it mainly appear in transition phases.

An important consequence of what has been discussed is that if $|\lambda_i| < 1$ for both eigenvalues, we have that $u_n \to 0$ as $n \to \infty$, whereas if some $|\lambda_i| > 1$ we have in general that $|u_n| \to \infty$. In the former case the origin is an asymptotically stable equilibrium to the dynamical system, in the second it is unstable. Geometrically the dynamical system is stable if both eigenvalues lies within the unit circle in the complex plane.

Whether the origin is stable or not can be read off from the characteristic equation. Let $A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$ be an arbitrary 2×2-matrix with characteristic polynomial

$$p_A(\lambda) = \lambda^2 - (\text{Tr} A)\lambda + \det A.$$  

The following observation is left as an exercise to prove.

Lemma 1 All eigenvalues to $A$ lies within the unit circle if and only if

$$\det A < 1, \quad \text{and} \quad |\text{Tr} A| < 1 + \det A.$$  

Moreover, the eigenvalues are real if and only if $4\det A \leq (\text{Tr} A)^2$.

The lemma is graphically illustrated in the picture below.
A point in the yellow region gives us a saddle point, whereas a point in the grey region gives us a spiral. The rest, the white regions, gives us knots. Only points within the blue triangle makes the origin a stable equilibrium.

For larger systems the situation is similar. A brief summary is as follows. We can divide $\mathbb{R}^n$ into a direct sum of three subspaces. If $A$ can be diagonalized we order the eigenvalues after the size of their absolute value, so that $|\lambda_j| < 1$ for $1 \leq j \leq p$, $|\lambda_j| = 1$ for $p < j < q$ and $|\lambda_j| > 1$ when $q \leq j \leq n$. The first $p$ eigenvectors define a linear subspace $W^s$, the next group defines $W^c$ and the final group defines $W^u$. This gives a decomposition

$$\mathbb{R}^n = W^s \oplus W^c \oplus W^u,$$

where a vector $u_0$ in $W^s$ defines a sequence $u_n$ which is such that $u_n \to 0$ as $n \to \infty$ and a start value $u_0$ in $W^u$ defines a solution that is such that $u_n \to 0$ as $n \to -\infty$. We call $W^s$ the stable subspace, $W^u$ the unstable subspace. $W^c$ is called the central subspace.

We will mainly be interested in situation when there is no central subspace.

**Definition 1**

A matrix $A$ is said to be hyperbolic if no eigenvalues lies on the unit circle.

**Positive matrices**

In applications in biology and economics it is mostly matrices with non-negative elements that are of interest. In particular their dominant eigenvalue and associated eigenvector. There is a useful theorem addressing this situation - the Perron-Frobenius theorem. It is convenient to use the notation $A \geq 0$ for a matrix in which all $a_{ij} \geq 0$, whereas $A > 0$ means that $a_{ij} > 0$.

Since we consider dynamical systems, i.e. recursion formulas $x_{n+1} = Ax_n$, it is convenient to think about the system as a process in which we jump between different states. If we denote these states $E_1, \ldots, E_m$ we interpret $x(n)_i$ as the value of some entity when we are in state $E_i$ at time $n$ and the element $a_{ij}$ describes how this entity $x$ changes when we move from $E_j$ to $E_i$. 
Example 3 Divide an butterfly population into age classes: \( E_1 = \text{worm}, E_2 = \text{pupae} \) and \( E_3 = \text{adult butterfly} \). At each point in time we measure the number of butterflies in each state, so that \( x(n)_1 \) is the number of worms in generation \( n \) etc. The matrix \( A = (a_{ij}) \) describes how the number of individuals in the the coming state depends on the number of individuals in the present state. We can e.g. have \( x(n+1)_2 = fx(n)_1 + (1 - g)x(n)_2 \) where \( f \) is the fraction that is expected to pupate and \( g \) the fraction of puppae that become adults at the next census.

Example 4 The bacteria *Salmonella typhimurium* can be divided into two groups, the wild type and the mutant type. The wild type produce the amino acid histidine and is denoted His\(^+\), which the mutants can’t, and therefore are denoted His\(^-\). Let \( \mu \) be the probability that the gene that produces histidine mutates so that it cannot produce histidine, whereas \( \nu \) is the probability for the reverse mutation. If \( p_1(n) \) denote the proportion in generation \( n \) of the wild type His\(^+\) and \( p_2(n) = 1 - p_1(n) \) denote the proportion of the mutant type, His\(^-\), we have that

\[
\begin{align*}
  p_1(n+1) &= (1 - \mu)p_1(n) + \nu p_2(n) \\
  p_2(n+1) &= \mu p_1(n) + (1 - \nu)p_2(n).
\end{align*}
\]

Before we formulate our main result about non-negative matrices we need two nonrelated definitions.

**Definition 2**

a) A non-negative matrix \( A \) such that there is a positive integer \( k \) such that \( A^k \) is positive is said to be primitive.

b) The largest value of \( |\lambda| \) when \( \lambda \) is an eigenvalue to a matrix \( A \) is call its spectral radius and denoted \( \rho(A) \).

**Theorem 1: Perron**

If \( A \) is a primitive matrix, \( \rho(A) \) is a simple eigenvalue to \( A \) and all other eigenvalues are such that \( |\lambda| < \rho(A) \). Also, the eigenspace to \( \rho(A) \) is one-dimensional and spanned by a positive eigenvector.

**Remark** If we normalize the positive eigenvector \( v = (v_1, \ldots, v_n) \) so that \( \sum_k v_k = 1 \) it is called the Perron vector for \( A \). It will be important in the coming discussion.

The important consequence for us is that if \( v \) is the Perron vector to \( \rho(A) \) we have that

\[ A^n u_0 \approx c_1 \rho(A)^n v \]

where the relative error goes exponentially fast to zero. Independent of \( u_0 \) the size of the population grows as a geometric sequence with ratio \( \rho(A) \) and the distribution of what we measure between the different states is given by the Perron vector.
What does a non-negative matrix that is not primitive look like? An example is given by so-called reducible matrices.

**Definition 3**

A matrix \( A \) is said to be reducible if we can reorder the states so that it takes the form

\[
\begin{pmatrix}
A_{11} & A_{12} \\
0 & A_{22}
\end{pmatrix}
\]

where \( A_{11} \) and \( A_{12} \) are quadratic matrices. A matrix that is not reducible is said to be irreducible. En matris som inte är reducibel sägs vara irreducibel.

**Remark** The matrices that are primitive are therefore irreducible. It is possible to generalize Perron’s theorem to irreducible, non-negative, matrices. This is the Perron-Frobenius theorem.

We now intend to use this theory on some important biological examples.

### About the age distribution in a population

In this section we will discuss a generalisation of Malhus’ model \( u_{n+1} = ru_n \) in which we take into account the age distribution within the population.

Assume that we every \( T^{th} \) year make a census (\( T \) do not need to be an integer). At each occasion we divide the population into age groups according to

<table>
<thead>
<tr>
<th>age group</th>
<th>years old</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>between 0 and ( T )</td>
</tr>
<tr>
<td>2</td>
<td>between ( T ) and ( 2T )</td>
</tr>
<tr>
<td>( \vdots )</td>
<td>( \vdots )</td>
</tr>
<tr>
<td>( m )</td>
<td>between ( (m-1)T ) and ( mT )</td>
</tr>
</tbody>
</table>

The state of the population is given by the number of females in the different age groups, so if we let \( x_i \) = the number of females in age group \( i \), we can summarise the state of the population at a particular time point in an \( m \)-vector

\[
u = \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_m \end{pmatrix}.
\]

To describe how the state changes between two census we let \( u \) be the \( m \)-vector above and \( v \) the corresponding vector at the next census. The component of \( v \) are denoted \( y_1, \ldots, y_m \). Let

\[p_i = \text{be the probability that a female in age group } i \text{ survives to next census (is then in age group } i+1)\].
\( f_i = \) the average number of female offsprings to a given female in age group \( i \) (which are registered in age group 1 at the next census).

From this we obtain the following equations

\[
\begin{align*}
y_1 &= f_1 x_1 + f_2 x_2 + \ldots + f_m x_m \\
y_2 &= p_1 x_1 \\
y_3 &= p_2 x_2 \\
\vdots \\
y_m &= p_{m-1} x_{m-1}
\end{align*}
\]

The system matrix is

\[
A = \begin{pmatrix}
f_1 & f_2 & \ldots & f_{m-1} & f_m \\
p_1 & 0 & \ldots & 0 & 0 \\
p_1 & p_2 & \ldots & 0 & 0 \\
\vdots & \vdots & \ddots & \vdots & \vdots \\
0 & 0 & \ldots & p_{m-1} & 0
\end{pmatrix}.
\]

This is called Leslie’s model and the matrix \( A \) is called the populations reproduction matrix. The Perron vector describes in this case the asymptotic age distribution.

To illustrate we consider the following example.

**Example 5** Consider an animal population which we divide the females into three age classes: 0-1 år (puppies), 1-2 år (yearlings) och 2-3 år (adults); no animal lives longer than 3 years. Assume that half of the puppies grow up to be yearlings in a year, whereas 2/3 of these become adult. We also assume that on average the puppies have 0.4 offsprings per year, the yearlings 5 offsprings per year and the adults 3 offsprings per year. This is summarized in the following reproduction matrix

\[
A = \begin{pmatrix}
0.5 & 5 & 3 \\
0.5 & 0 & 0 \\
0 & \frac{2}{3} & 0
\end{pmatrix}.
\]

This matrix has the eigenvalues \(-1, -0.5, 2\), and the last of these has the non-negative eigenvector \( v_1 = (12, 3, 1) \). It follows that the population grows exponentially as \( 2^n \) and asymptotically stabilizes the age groups in the relation 12 : 3 : 1.

With many age groups it is often a good idea to merge some of them. If we want to formulate a dynamical system which describes the size of the age classes of a human population every year we need more than 100 age classes. A simpler model would divide the female population into three age groups: children (age 0–14 years), fertile women (age 15–39) and older (40 years or older). Assume girls is only born by mothers in the middle age group and that the three groups have survival probabilities (average over group) \( p_1, p_2, p_3 \). Let \( u_n = (x_n, y_n, z_n) \) be the number of females in each age group after \( n \) years. To get \( u_{n+1} \) from this we need (as before) to know the number born during this
year, but we also get a contribution of $\frac{14}{15}$ from the children population, the fraction that are still children, and of these the fraction $p_1$ survives. This means that

$$x_{n+1} = by_n + \frac{14}{15}p_1x_n,$$

where $b$ is the reproduction intensity for fertile women. In an analogous way we have that

$$y_{n+1} = \frac{1}{15}p_1x_n + \frac{24}{25}p_2y_n \quad \text{and} \quad z_{n+1} = \frac{1}{25}p_2y_n + p_3z_n.$$

### Example 6

If offspring is born only to mothers in the highest age class the reproduction matrix is not primitive. As an example, consider the Atlantic Salmon, which dies after it has reproduced in the river they were born in. Let us describe them with 3 age classes and the reproduction matrix

$$A = \begin{pmatrix} 0 & 0 & b \\ p_1 & 0 & 0 \\ 0 & p_2 & 0 \end{pmatrix}.$$ 

Then the characteristic polynomial is $p_A(\lambda) = \lambda^3 - bp_1p_2$, for which the zeroes are

$$\lambda_i = \xi^{i\pi/3}\sqrt{bp_1p_2}, \quad i = 0, 1, 2, \quad \xi = e^{2\pi i/3}.$$

We see that this is an example of a Leslie model in which the reproduction matrix is not primitive (but it is irreducible). The corresponding eigenvectors are $v_0 = (1, p_1/\lambda_1, p_1p_2/\lambda_1^2)$. We have that $\lambda_2 = \bar{\lambda}_1$ and $v_2 = \bar{v}_1$, so the general solution is given by

$$\lambda_0^n(c_0v_0 + c_1\xi^n v_1 + \bar{c}_1\bar{\xi}^n \bar{v}_1) = \lambda_0^n(c_0v_0 + 2 \text{Re}(c_1\xi^n v_1)).$$

This is a 3-periodic solution.

### Regular Markov chains

Assume we conduct an experiment for which we have the following list of possible outcomes:

$$E_1, E_2, \ldots, E_m.$$

We repeat this experiment over and over again and assume that the probability of an outcome in one experiment depends on the outcome of the previous experiment, but no earlier one. This assumption means that we have a Markov chain.

Let $p_i(n)$ denote the probability that we get the outcome $E_i$ in experiment $n$. We must have one of the possible outcomes, so we have that

$$\sum_{i=1}^m p_i(n) = 1.$$
for all $n$. We assume that we know the so-called transition probabilities
\[ p_{ij} = P(E_i \mid E_j), \]
i.e. the probability that we go from outcome $E_j$ to outcome $E_i$, given that the previous one was $E_j$. Again one outcome must occur, so for all $j$ we have that
\[ \sum_{i=1}^{m} p_{ij} = 1. \]

If we introduce the transition matrix
\[ P = (p_{ij}) \]
this means that the sum of probabilities in each column is one. This implies that if $e = (1, 1, \ldots, 1)$ is the row vector of 1:s, we have that
\[ eP = e. \]

We also introduce the column vector
\[ p(n) = (p_1(n), \ldots, p_m(n)) \]
which is such that
\[ p(n + 1) = Pp(n). \]
Explicitly this means that $p_i(n + 1) = \sum_j p_{ij}p_j(n)$, i.e.
\[ P(E_i \text{ in } (n + 1) \text{ step}) = \sum_{j=1}^{m} P(E_i \mid E_j)P(E_j \text{ in } n^{th} \text{ step}) \]
which is the theorem of total probability.

The main question for Markov chains is what happens after a long time (for large $n$). Is there an equilibrium distribution (called an asymptotic distribution)? In order to understand what we can expect we assume first that the transition matrix $P$ has $m$ different eigenvalues $\lambda_1, \ldots, \lambda_m$ with eigenvectors $v_1, \ldots, v_m$, so that
\[ p(n) = \sum_{i=1}^{m} a_k \lambda_k^n v_k. \]
Since the elements in $p(n)$ are probabilities we must have $|\lambda_k| \leq 1$ and since $e$ was a left eigenvector with eigenvalue 1 there is at least one (right) eigenvector with that eigenvalue (because $\det(P - E) = \det(P^{t} - E)$).

By a regular Markov chain we mean one for which the transition matrix is primitive. For such a Markov chain Perrons theorem tells us that the equation
\[ P\pi = \pi \]
has precisely one Perron vector, and that
\[ P^n v_0 \to \pi \quad \text{as} \quad n \to \infty, \]
independent of which start distribution we have. The Perron vector is called the stationary distribution of the regular Markov chain.
Example 7 The simplest, non-trivial, case of the above is a Markov chain with two states $E_1$ and $E_2$. Its transition matrix takes the form

$$P = \begin{pmatrix} 1 - a & b \\ a & 1 - b \end{pmatrix}.$$ 

The solution to the equation system $P\pi = \pi$ is

$$\pi = \left( \frac{b}{a + b}, \frac{a}{a + b} \right)$$

and the characteristic equation is $\lambda^2 - (2 - a - b)\lambda + 1 - a - b = 0$, which shows that the eigenvalues are 1 and $1 - a - b$. An eigenvector of the latter is $v_2 = (1, -1)$.

Any start vector can be written

$$\pi_0 = (c, 1 - c) = \pi + (c - \frac{b}{a + b})v_2,$$

so it follows, with $C = c - b/(a + b)$, that

$$P^n\pi_0 = \pi + C(1 - a - b)^n v_2 \rightarrow \pi \quad \text{when} \quad n \rightarrow \infty.$$ 

Here we have used that $|1 - a - b| < 1$.

Absorbing Markov chains

Assume we have a Markov chain with at least one state, call it $E_j$, which is such that if we are in it at some point in time, we will remain there forever. Such a state is called an absorbing state and for it the transition probability $p_{jj} = 1$. Since the column sum is one, and all entries are non-negative, this means that all the other entries in that column is zero. A Markov chain is absorbing if it contains at least one absorbing state and that it is possible to reach an absorbing state from each state (not necessarily in one step).

It is intuitively clear (and therefore not proved here) that for an absorbing Markov chain we will eventually end up in one of the absorbing states. If there is more than one absorbing state we want to find the probability for each of them that we end up in it. Superficially this looks simple – compute the eigenvalues etc. The technical problem is that an absorbing Markov chain with more than one absorbing state has an eigenvalue one which is a multiple zero to the characteristic polynomial.

The transition matrix for an absorbing Markov chain takes the form

$$P = \begin{pmatrix} I & S \\ 0 & R \end{pmatrix}$$

and with easily identified notations we have that

$$p(n + 1) = p(n) + Sq(n), \quad q(n + 1) = Rq(n).$$

Here all eigenvalues of $R$ must be $< 1$ for the simple reason that it is part of the definition that we with certainty will leave the non-absorbing states at some time, so that $q(n) \rightarrow 0$. 
when \( n \to \infty \). We therefore have that
\[
p(n + 1) = p(n) + SR^n q(0),
\]
which implies that
\[
p(n) = p(0) + S(I + R + R^2 + \ldots + R^{n-1})q(0) = p(0) + S(I - R)^{-1}(I - R^n)q(0).
\]
Consequently
\[
\lim_{n \to \infty} p(n) = p(0) + S(I - R)^{-1}q(0).
\]

**Remark** The matrix \((I - R)^{-1}\) has a meaning. Let \( N \) be the matrix whose \( ij \)th element is the expected value for the number of times the Markov chain is in \( E_i \) given that we start in \( E_j \), for non-absorbing states. We then have that
\[
N = (I - R)^{-1}.
\]
To see this, we observe that
\[
P^n = \begin{pmatrix} I & ? \\ 0 & R^n \end{pmatrix}
\]
which shows that \((R^n)_{ij}\) is the probability of being in \( E_i \) after \( n \) steps if one starts in \( E_j \). The expected value is therefore
\[
N_{ij} = \sum_{n=0}^{\infty} 1 \cdot (R^n)_{ij}.
\]

**Example 8** The Hardy-Weinberg law in genetics says that the expected distribution of different genotypes is the same from generation to generation. But that is the expected value, corresponding to an infinite population. What happens in a finite population, where chance may play a role?

In order to investigate this we assume we have a population with \( N \) individuals, a number constant over generations. As before these \( N \) individuals define a gene pool of \( 2N \) genes and let \( x_n \) denote the number of \( A \)-genes in the \( n \)th generation. Let \( p_n = x_n/(2N) \) be the frequency of \( A \)-alleles in the gene pool. We then have that
\[
x_{n+1} \in \text{Bin}(2N, p_n)
\]

In order to transform this into a Markov chain we introduce the \( 2N + 1 \) states
\[
E_k = \text{there are precisely } k \text{ } A\text{-genes in the population.}
\]
This defines a Markov chain with transition probabilities
\[
p_{ij} = P(x_{n+1} = i \mid x_n = j) = \binom{2N}{i} \binom{j}{2N} \left( \frac{2N - j}{2N} \right)^{2N-i}.
\]
Here we have $p_{00} = p_{2N,2N} = 1$, which means that the states $E_0$ and $E_{2N}$ are absorbing. Which is obvious, since there is only one allele in the population!

The first observation we now make is that

$$E(p_{n+1} \mid p_n) = p_n, \quad V(p_{n+1} \mid p_n) = \frac{p_n(1 - p_n)}{2N}.$$  

As already mentioned Hardy Weinberg’s law corresponds to the extreme case $N = \infty$: then the variance is zero and $p_n$ does not change with generations.

For a finite population the situation is different. Even if the average allele fraction is constant between generations there is a random variation with a variance that is inversely proportional to the size of the population. This variation in the allele frequency is called genetic drift.

The conclusion from the discussion is that since the states $E_0$ and $E_{2N}$ are absorbing, only one allele will remain in the population after a sufficiently long period of time, and the genetic variation decreases. A somewhat surprising result since we att the same time expect that the frequency of the alleles are stable over generations. But this is a slow process. In order to see this in a direct way, let $q_n$ be the probability that an offspring is a heterozygote to parents in generation $n$. That is the probability that we sample both alleles when we choose two chromosomes at random without replacement, i.e.

$$q_n = \frac{x_n}{2N} \cdot \frac{2N - x_n}{2N - 1} = \frac{2N}{2N - 1} p_n(1 - p_n).$$  

A short calculation then shows that

$$E(q_n) = (1 - \frac{1}{2N}) E(q_{n-1}).$$  

The heterogeneity therefore disappear like a geometric series with ratio $(1 - 1/(2N))$, which is very close to 1 when $N$ is large. But in a small population we expect the genetic variation to decrease with an observable speed.

The only remaining question is which allele will survive. That depends on the frequency of the $A$-allele at start, and since we know that we end up in a homozygote state, the probability that this is $A$ is $x_0/(2N)$.

The model in the previous example is called the Fisher-Wright model and its main consequence is that one of the genes will disappear with time. This phenomena is called random genetic drift.

If we add selection and mutations to the model the situation becomes more complicated. With selection we shall replace the conditional expected value $E(x_{n+1} \mid x_n)$ in the example with

$$P_n = \frac{r x_n^2 + s x_n (2N - x_n)}{r x_n^2 + 2 s x_n (2N - x_n) + (2N - x_n)^2}.$$  

If we in addition have mutations $A \rightarrow a$ with probability $\mu$ and $a \rightarrow A$ with $\nu$ this expected value becomes

$$(1 - \mu) P_n + \nu (1 - P_n).$$
This model is far too complex to analyse with the methods above. We will return to it later.

**Exercises**

**Exercise 1** In the year 1202 Fibonacci posed the following well-known problem: suppose a newly-born pair of rabbits, one male, one female, are put in a field. Rabbits are able to mate at the age of one month so that at the end of its second month a female can produce another pair of rabbits. Suppose that our rabbits never die and that the female always produces one new pair (one male, one female) every month from the second month on. How many pairs will there be in one year?

Solve this problem by introducing two age classes for the rabbits (young and adult) and write down the corresponding Leslie model. What is the growth rate of the population and which is the stable age distribution?

**Exercise 2** Bevisa Lemma 1.

**Exercise 3** Show that for a Leslie matrix we have that

a) the characteristic polynomial is \( p_n(\lambda) = \lambda^n - f_1\lambda^{n-1} - f_2p_1\lambda^{n-2} - f_3p_1p_2\lambda^{n-3} - \cdots - f_np_1\cdots p_{n-1} \).

b) There is precisely one positive, real, eigenvalue to the matrix.

c) That the eigenvector to the eigenvalue \( \lambda \) is given by

\[ v = t(1, p_1/\lambda, p_1p_2/\lambda^2, \ldots, p_1p_2\cdots p_{n-1}/\lambda^{n-1}). \]

**Exercise 4** Gray seal fecundity and survival rates are shown in the table below:

<table>
<thead>
<tr>
<th>Age</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>5+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fecundity</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.08</td>
<td>0.28</td>
<td>0.42</td>
<td></td>
</tr>
<tr>
<td>Survival</td>
<td>0.657</td>
<td>0.930</td>
<td>0.930</td>
<td>0.930</td>
<td>0.935</td>
<td>0.935</td>
<td>0</td>
</tr>
</tbody>
</table>

Decide what will happen to the population with time. Which age distribution will it have?

**Exercise 5** In the circulatory system, the red blood cells (RBCs) are constantly being destroyed and replaced. Since these cells carry oxygen throughout the body, their number must be maintained at some fixed level. Assume that the spleen filters out and destroys a certain fraction \( f \) of the cells daily and that the bone marrow produces a number proportional (\( \gamma \)) to the number lost on the previous day.

a) Explain the equations

\[ R_{n+1} = (1 - f)R_n + M_n \quad M_{n+1} = \gamma f R_n. \]

b) Determine the eigenvalues and decide what is needed in order to keep the total number of red blood cells constant.

c) Describe the behaviour of the solution \( R_n \).

**Exercise 6** Derive Equation (1).
Answers to exercises

Exercise 1 The Leslie-matrix is \( \begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix} \). The growth rate is \( \frac{\sqrt{5}+1}{2} \) and the age distribution \( \frac{1}{3+\sqrt{5}}(1 + \sqrt{5}, 2) \).

Exercise 2

Exercise 3  a) You might e.g. expand along the first column

b) Write \( p_n(\lambda) = \lambda^n(1 - f(\lambda)) \), where \( f(\lambda) \) becomes a polynomial in \( 1/\lambda \) with only positive coefficient.

Exercise 4 This is a MATLAB mission: the only real eigenvalue is 0.8586, so the population dies out. The stable age distribution is

\[
\left( 0.1498, 0.1146, 0.1241, 0.1345, 0.1457, 0.1586, 0.1727 \right)
\]
(normalised so that the sum is one).

Exercise 5 The eigenvalues are

\[
\lambda_{\pm} = \frac{1}{2}(1 - f \pm \sqrt{(1 - f)^2 + 4\gamma f})
\]

and the larger of these is one when \( \gamma = 1 \). In that case the other is \(-f\) and the general solution, which has the form \( R_n = A\lambda_+^n + B\lambda_-^n = A + B(-f)^n \to A \) as \( n \to \infty \), since \( 0 < f < 1 \).

Exercise 6 Use that \( E(p_n^2|p_{n-1}) = V(p_n|p_{n-1}) + E(p_n|p_{n-1})^2 \).