Age-structured population models - from Fibonacci to McKendrick-von Foerster models

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Unstructured models.

If we take the census of adults in a population in fixed time interval, then it is natural to describe the population as the sequence of numbers

$$P(0), P(1), \dots, P(k)$$

where $P(k)$ is the number of adults in the k-th breeding season. This approach makes sense if, e.g., the population has well defined breeding seasons.

The simplest assumption to make is that there is a functional dependence between subsequent generations

$$P(n+1) = r(P(n))P(n), \quad n = 0, 1, \dots, \tag{1}$$

where $r(P(n))$ is the (density dependent) net growth rate. The case of (1) is

$$P(n+1) = rP(n), \quad n = 0, 1, \dots, \tag{2}$$

The exponential (or Malthusian) equation (2) describes well population which are completely homogeneous, with characteristics of the environment and individual members constant over time.

More specifically, :

- Each member of the population produces on average the same number of offspring;
- Each member has an equal chance of dying (or surviving) before the next breeding season;
- The ratio of females to males remains the same in each breeding season.

We also assume

- Age differences between members of the population can be ignored;
- The population is isolated - there is no immigration or emigration.

The net growth rate is given as

$$r = 1 + \beta - \mu.$$

Here β is an average (constant) number of offspring each member of the population gives birth to each season; it is called the per-capita birth rate. The constant μ is the probability that an individual will die before the next breeding season and is called the per-capita death rate.

Thus, (2) can be written as

$$P(k+1) = P(k) + \beta P(k) - \mu P(k), \tag{3}$$

which expresses the basic principle of population modelling in discrete time:

> *The number of individuals in the $k+1$th census equals the population in the kth census + the total number of births in the population between the censuses − the total number of deaths in the population between the censuses.*

Changes due to migrations can be incorporated, but the structure of the equation may not persist — e.g., immigration not necessarily is proportional to the total population.

Clearly,

$$P(k) = r^k P(0), \qquad k = 0, 1, 2 \dots \tag{4}$$

and if $r < 1$, then the population decreases towards extinction, but with $r > 1$ it grows indefinitely. Such behaviour over long periods of time is not observed in any population so it is clear that the model is over-simplified and requires corrections. However, it is usually valid over short time intervals and can bring some demographical insights.

The death rate μ and the average lifespan of an individual

The average lifespan L is the expected duration of life, which is

$$L = \sum_{k=1}^{\infty} kp(k),$$

where $p(k)$ the probability that an individual, born at $k = 0$ dies exactly at age k.

How to find it?

First, we find the probability that an individual, born at $k = 0$, is alive at age k. In order to be alive at time k, it had to be alive at time $k - 1$ and could not die between $k - 1$ and k. Assuming that the probability of dying is constant in time and using the conditional probability formula we arrive at

$$\pi(k) = (1 - \mu)\pi(k - 1), \qquad p(0) = 1,$$

that is,

$$\pi(k) = (1 - \mu)^k. \tag{5}$$

To find L, we observe that to die at age k an individual must be alive at age $k-1$ and die in the interval $(k-1,k]$ which occurs with probability $\mu p(k-1)=\mu(1-\mu)^{k-1}$. It also can be explained as follows: after the first year a proportion μ of the population dies and $1-\mu$ survives, then after the second year a proportion μ of them die; that is $\mu(1-\mu)$ fraction of the initial population lives exactly 2 years and $(1-\mu)^2$ survives the second birthday, etc.

Thus, the average life span is found to be

$$L = \mu \sum_{k=1}^{\infty} k(1-\mu)^{k-1} = -\mu \frac{d}{d\mu} \frac{1-\mu}{1-(1-\mu)} = \frac{1}{\mu},$$

where we used

$$\sum_{k=1}^{\infty} k z^{k-1} = \frac{d}{dz} \sum_{k=1}^{\infty} z^k = \frac{d}{dz} \frac{z}{1-z}$$

for $z = 1 - \mu$.

Introducing structure.

The Malthusian model clearly is hugely oversimplified and its improvements may go into many directions. One could stay with global aggregated description and but introduce variable and and nonlinear coefficients. Another option is to consider a relevant internal structure of the population. This could be age and related with it differentiation in birth and death rates. Other possibilities include size or geographical structure which also may impact on death and birth rates. Let us start with revisiting the classical Fibonacci's problem of rabbits.

Fibonacci's rabbits. In his famous book, *Liber abaci*, published in 1202, Leonardo de Pisa, called Fibonacci, formulated the following problem:

> *A certain man put a pair of rabbits in a place surrounded on all sides by a wall. How many rabbits can be produced from that pair in a year if it is supposed that every month each pair begets a new pair which from the second month on becomes productive?*

To fix attention, we assume that we take monthly census just after the births for this month take place and the rabbits were newly born at the beginning of the experiment. Usually the problem is modelled as the initial value problem for a second order difference equation

$$v(k+2) = v(k+1) + v(k), \quad v(0) = 1\,, v(1) = 1. \tag{6}$$

Example 1

It is clear that (6) as a model describing a population of rabbits is oversimplified: rabbits do not die, they are always fertile as soon as they are mature, etc. However, there are biological phenomena for which (6) provides an exact fit. One of them is family tree of honeybees. Honeybees live in colonies and one of the unusual features of them is that not every bee has two parents. First, in any colony there is one special female called the queen. Further, there are worker bees who are female but they produce no eggs. Finally, there are drones, who are male and do no work, but fertilize the queen's eggs.

Example 2

Drones are borne from the queen's unfertilised eggs and thus they have a mother but no father. The females are born when the queen has mated with a male and so have two parents.

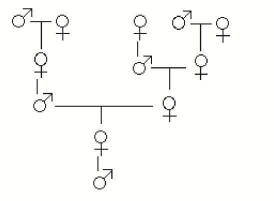


Figure: The family tree of a drone

We see that the number of ancestors kth generations earlier exactly satisfies (6).

Matrix description. Fibonacci model is an example of an age-structured population model: in this particular case each month the population is represented by two classes of rabbits, adults $v_1(k)$ and juveniles $v_0(k)$. Thus the state of the population is described by the vector

$$\boldsymbol{v}(k) = \left(\begin{array}{c} v_0(k) \\ v_1(k) \end{array} \right).$$

Since the number of juvenile (one-month old) pairs in month $k+1$ is equal to the number of adults in the month k and the number of adults is the number of adults from the previous month and the number of juveniles from the previous month (who became adults), we obtain

$$\begin{aligned} v_0(k+1) &= v_1(k), \\ v_1(k+1) &= v_1(k) + v_0(k), \end{aligned}$$

or, in a more compact form,

$$\mathbf{v}(k+1) = \mathcal{L}\mathbf{v}(k) := \begin{pmatrix} 0 & 1 \\ 1 & 1 \end{pmatrix} \mathbf{v}(k). \tag{7}$$

The solution can be found by iterations

$$\mathbf{v}(k+1) = \mathcal{L}\mathbf{v}(k) = \mathcal{L}^{k+1}\mathbf{v}(0).$$

Leslie matrices. How do we generalize this? Assume that

- we are tracking only females and not pairs,
- the census is taken immediately after the reproductive period (the length of which is negligible),
- there is an oldest age class n,
- no individual can stay in any age class for more than one time period (which is **not** the case for Fibonacci rabbits, where we allowed adults to stay adults forever).

We introduce

- the year-to-year survival probability s_i,
- the age dependent maternity function m_i.

Thus, say, in the kth breeding season, we have $v_i(k)$ individuals of age i, s_i of them survive to the $(k+1)$th breeding season, that is, to age $i+1$, and produce on average

$$f_i v_i(k) := m_{i+1} s_i v_i(k)$$

offspring (f_i is the effective birth rate of age i individuals).

In this case, the evolution of the population can be described by the difference system

$$\mathbf{v}(k+1) = \mathcal{L}\mathbf{v}(k),$$

where $\mathcal{L}$ is the $n \times n$ matrix

$$\mathcal{L} := \begin{pmatrix} f_0 & f_1 & \cdots & f_{n-2} & f_{n-1} \\ s_0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & \cdots & 0 & 0 \\ \vdots & \vdots & \dots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-2} & 0 \end{pmatrix}. \tag{8}$$

The matrix of the form (8) is referred to as a *Leslie matrix*.

A generalization of the Leslie matrix can be obtained by assuming that a fraction τ_i of i-th population stays in the same population. This gives the matrix

$$\mathcal{L} := \begin{pmatrix} f_0+\tau_0 & f_1 & \cdots & f_{n-2} & f_{n-1} \\ s_0 & \tau_1 & \cdots & 0 & 0 \\ 0 & s_1 & \cdots & 0 & 0 \\ \vdots & \vdots & \dots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-2} & \tau_{n-1} \end{pmatrix}, \tag{9}$$

Such matrices are called *Usher matrices*. We note that the matrix of the Fibonacci process is an Usher matrix.

In most cases $f_i \neq 0$ only if $\alpha \leq i \leq \beta$, where $[\alpha, \beta]$ is the fertile period. For example, for a typical mammal population we have three stages: immature (pre-breeding), breeding and post-breeding. If we perform census every year, then naturally a fraction of each class remains in the same class. Thus, the transition matrix in this case is given by

$$\mathcal{L} := \begin{pmatrix} \tau_0 & f_1 & 0 \\ s_0 & \tau_1 & 0 \\ 0 & s_1 & \tau_2 \end{pmatrix}. \tag{10}$$

On the other hand, in many insect populations, reproduction occurs only in the final stage of life and in such a case $f_i = 0$ unless $i = n$.

Projection matrices. Leslie matrices fit into a more general mathematical structure describing evolution of populations divided into states, or subpopulations, not necessarily related to age. Matrices resulting from such a modelling, that is, describing changes of a structured populations from one generation to another due to migrations between structural states and (generalized) birth processes are called *projection, or transition, matrices*.

For example, we can consider

- clusters of cells divided into classes with respect to their size,
- cancer cells divided into classes based on the number of copies of a particular gene responsible for its drug resistance,
- or a population divided into subpopulations depending on the geographical patch they occupy in a particular moment of time.

Let us suppose we have n states. Each individual in a given state j contributes on average, say, a_{ij} individuals to state i (in a unit time). Typically, this is due to a state j individual:

- migrating to i-th subpopulation with probability p_{ij};
- contributing to a birth of an individual in i-th subpopulation with probability b_{ij};
- dying with probability d_j, that is, surviving with probability $1 - d_j$.

Other choices and interpretations are, however, also possible.

For instance, if we consider size structured population of clusters of cells divided into subpopulations according to their size i, a j-cluster can split into several smaller clusters, contributing thus to the 'births' of clusters in subpopulations indexed by $i < j$. Hence, here a_{ij} are non-negative but otherwise arbitrary numbers, satisfying only $a_{ij} = 0$ for $i \geq j$.

In general, denoting, as before, by $v_i(k)$ the number of individuals at time k in state i, with $\boldsymbol{v}(k) = (v_1(k), \ldots, v_n(k))$, we have

$$\boldsymbol{v}(k+1) = \mathcal{A}\,\boldsymbol{v}(k), \tag{11}$$

where

$$\mathcal{A} := \begin{pmatrix} a_{11} & a_{12} & \cdots & a_{1\,n-1} & a_{1n} \\ a_{21} & a_{22} & \cdots & a_{2\,n-1} & a_{2n} \\ \vdots & \vdots & \cdots & \vdots & \vdots \\ a_{n1} & a_{n2} & \cdots & a_{n\,n-1} & a_{nn} \end{pmatrix}. \tag{12}$$

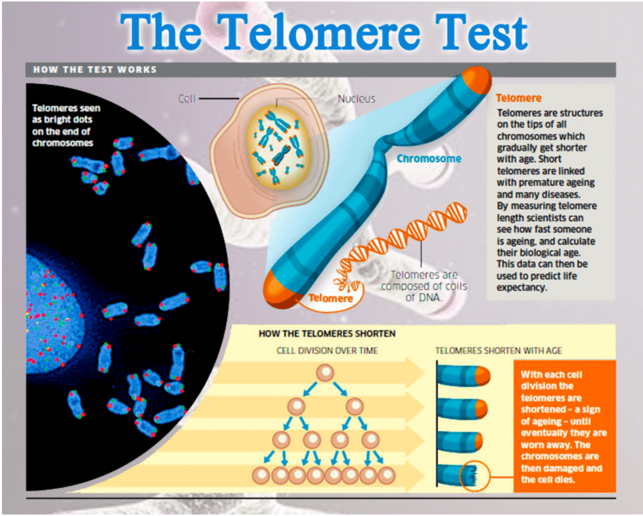
Thus

$$\boldsymbol{v}_k = \mathcal{A}^k \mathring{\boldsymbol{v}},$$

where $\mathring{\boldsymbol{v}}$ is the initial distribution of the population between the subpopulations.

Example 3

Any chromosome ends with a *telomer* which protects it agains damage during the DNA replication process. Recurring divisions of cells can shorten the length of telomers and this process is considered to be responsible for cell's aging. If telomer is too short, the cell cannot divide which explains why many cell types can undergo only a finite number of divisions. Let us consider a simplified model of telomer shortening. The length of a telomer is a natural number from 0 to n, so cells with telomer of length i are in subpopulation i. A cell from subpopulation i can die with probability μ_i and divide (into 2 daughters).



Telomeres seen as bright dots on the end of chromosomes

Telomeres are composed of coils of DNA.

Telomere

Telomeres are structures on the tips of all chromosomes which gradually get shorter with age. Short telomeres are linked with premature ageing and many diseases. By measuring telomere length scientists can see how fast someone is ageing, and calculate their biological age. This data can then be used to predict life expectancy.

With each cell division the telomeres are shortened – a sign of ageing – until eventually they are worn away. The chromosomes are then damaged and the cell dies.

Figure: Shortening of telomers

Example 4

Any daughter can have a telomer of length i with probability a_i and of length $i-1$ with probability $1-a_i$. Cells of 0 length telomer cannot divide and thus will die some time later. To find coefficients of the transition matrix, we see that the average production of offspring with telomer of length i by a parent of the same class is

$$2a_i^2 + 2a_i(1-a_i) = 2a_i,$$

(2 daughters with telomer of length i produced with probability a_i^2 and 1 daughter with telomer of length $i-1$ produced with probability $2a_i(1-a_i)$).

Example 5

Similarly, average production of daughters with length $i-1$ telomer is $2(1-a_i)$. However, to have offspring, the cell must have survived from one census to another which happens with probability $1-\mu_i$. Hence, defining $r_i = 2a_i(1-\mu_i)$ and $d_i = 2(1-a_i)(1-\mu_i)$, we have

$$\mathcal{A} := \begin{pmatrix} 0 & d_1 & 0 & \cdots & 0 \\ 0 & r_1 & d_2 & \cdots & 0 \\ \vdots & \vdots & \vdots & \dots & \vdots \\ 0 & 0 & 0 & \cdots & r_n \end{pmatrix}. \tag{13}$$

Markov matrices. A particular version of (12) is obtained when we assume that the total population has constant size so that no individual dies and no new individual can appear, so that the only changes occur due to migration between states. In other words, $b_{ij} = d_j = 0$ for any $1 \leq i, j \leq n$ and thus $a_{ij} = p_{ij}$ is the fraction of the j-th subpopulation which, on average, moves to the i-th subpopulation or, using a probabilistic language, the probabilities of such a migration.

Then, in addition to the constraint $p_{ij} \geq 0$, we must have $p_{ij} \leq 1$ and, since the total number of individuals contributed by the state j to all other states must equal the number of individuals in this state, we must have

$$v_j = \sum_{1 \leq i \leq n} p_{ij} v_j.$$

This implies

$$\sum_{1 \leq i \leq n} p_{ij} = 1,$$

which is the expression of the law of total probability, that is, of the fact that each individual must be in one of the n states at any time.

Matrices of this form are called *Markov matrices*.

We can check that, indeed, this condition ensures that the size of the population is constant. Indeed, the size of the population at time k is $N(k) = v_1(k) + \ldots + v_n(k)$ so that

$$
\begin{aligned}
N(k+1) &= \sum_{1\leq i\leq n} v_i(k+1) = \sum_{1\leq i\leq n} \left(\sum_{1\leq j\leq n} p_{ij} v_j(k) \right) \\
&= \sum_{1\leq j\leq n} v_j(k) \left(\sum_{1\leq i\leq n} p_{ij} \right) = \sum_{1\leq j\leq n} v_j(k) = N(k).
\end{aligned}
$$

Long time behaviour of structured population models.

The main interest in population theory is to determine the long time structure of the population.

Before we embark on mathematical analysis, let us consider two numerical examples which indicate what we should expect from the models. Let us consider a population divided into three classes, evolution of which is modelled by the Leslie matrix

$$\mathscr{L} = \begin{pmatrix} 2 & 1 & 1 \\ 0.5 & 0 & 0 \\ 0 & 0.4 & 0 \end{pmatrix}, \tag{14}$$

so that the population $\boldsymbol{v} = (v_1, v_2, v_3)$ evolves according to

$$\boldsymbol{v}(k+1) = \mathcal{L}\,\boldsymbol{v}(k), \quad k = 0, 1, 2\ldots,$$

with $\boldsymbol{v}(0) =: \mathring{\boldsymbol{v}}$, or

$$\boldsymbol{v}(k) = \mathcal{L}^k \mathring{\boldsymbol{v}}.$$

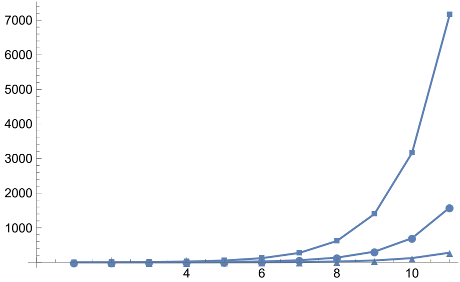


Figure: Evolution of $v_1(k)$ (squares), $v_2(k)$ (circles) and $v_3(k)$ (triangles) for the initial distribution $\mathring{\boldsymbol{v}} = (1, 0, 3)$ and $k = 1, \ldots, 10$.

We observe that each component grows very fast with k.

However, if we compare growth of $v_1(k)$ with $v_2(k)$ and of $v_2(k)$ with $v_3(k)$ we see that the ratios stabilize quickly around 4.5 in the first case and around 5.62 in the second case.

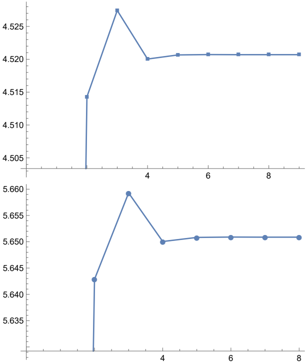


Figure: Evolution of $v_1(k)/v_2(k)$ (top) and $v_2(k)/v_3(k)$ (bottom) for the initial distribution $\mathring{\boldsymbol{v}} = (1, 0, 3)$ and $k = 1, \dots, 10$.

This suggests that there is a scalar function $f(k)$ and a vector $\boldsymbol{e}$ (here $\boldsymbol{e} = (e_1, e_2, e_3) = (25.29, 5.62, 1)$) such that for large k

$$\boldsymbol{v}(k) \approx f(k)\boldsymbol{e}(\mathring{\boldsymbol{v}}). \tag{15}$$

Let us consider another initial condition, say, $\mathring{\boldsymbol{v}} = (2, 1, 4)$ and do the same comparison.

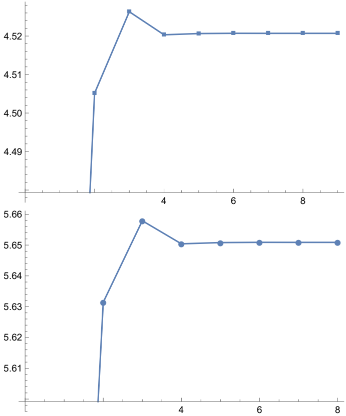


Figure: Evolution of $v_1(k)/v_2(k)$ (top) and $v_2(k)/v_3(k)$ (bottom) for the initial distribution $\mathring{\boldsymbol{v}} = (2, 1, 4)$ and $k = 1, \ldots, 10$.

It turns out that the ratios stabilize at the same level, which further suggest that $\boldsymbol{e}$ does not depend on the initial condition so that (78) can be refined to

$$\boldsymbol{v}(k) \approx f_1(k) g(\mathring{\boldsymbol{v}})\boldsymbol{e}, \quad k \to \infty, \tag{16}$$

where g is a linear function. Anticipating the development of the theory, it can be proved that $f_1(k) = \lambda_m^k$ where λ is the largest eigenvalue of $\mathcal{L}$, $\boldsymbol{e}$ is the eigenvector corresponding to λ_m and $g(\boldsymbol{x}) = \langle \boldsymbol{g}, \boldsymbol{x} \rangle$, with $\boldsymbol{g}$ being the eigenvector of the transpose matrix corresponding to λ_m.

In our case, $\lambda_m \approx 2.26035$ and the ratios $v_i(k)/\lambda_m^k$ stabilize as seen below.

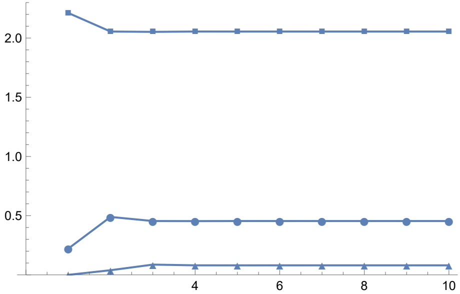


Figure: Evolution of $v_1(k)/\lambda_m^k$ (squares), $v_2(k)/\lambda_m^k$ (circles)and $v_3(k)/\lambda_m^k$ (triangles) for the initial distribution $\mathring{\boldsymbol{v}} = (1, 0, 3)$ and $k = 1, \dots, 10$.

The situation in which the structure of the population after long time does not depend on the initial condition but only on the intrinsic properties of the model (here the leading eigenvalue) is called the *asynchronous exponential growth (AEG)* property.

Unfortunately, not all Leslie matrices enjoy this property.

Consider now a Leslie matrix given by

$$\mathcal{L} = \begin{pmatrix} 0 & 0 & 3 \\ 0.5 & 0 & 0 \\ 0 & 0.4 & 0 \end{pmatrix}$$

and a population evolving according to

$$\boldsymbol{v}(k) = \mathcal{L}^k \mathring{\boldsymbol{v}}$$

with $\mathring{\boldsymbol{v}} = (2, 3, 4)$.

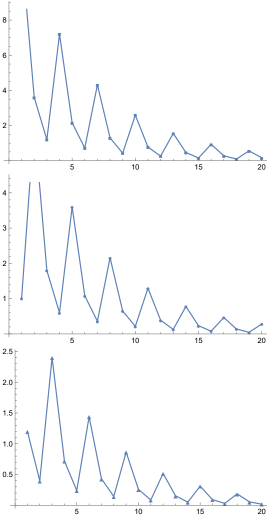


Figure: Evolution of $v_1(k)$ (top) and $v_2(k)$ (middle) and $v_3(k)$ (bottom) for the initial distribution $\mathring{\boldsymbol{v}} = (2, 3, 4)$ and $k = 1, \ldots, 20$.

The picture is completely different from that obtained before. We observe some pattern, the ratios, however, do not tend to a fixed limit but oscillate, as shown below.

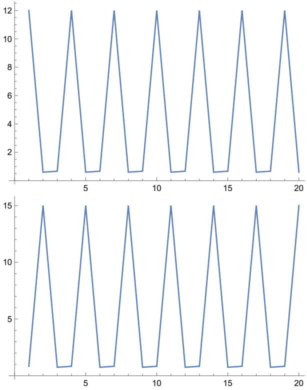


Figure: Evolution of $v_1(k)/v_2(k)$ (top) and $v_2(k)/v_3(k)$ (bottom) for the initial distribution $\overset{\circ}{\boldsymbol{v}} = (2, 3, 4)$ and $k = 1, \ldots, 20$.

This also can be explained using the eigenvalues. Indeed, the eigenvalues are given by $\lambda_1 = 0.843433, \lambda_2 = -0.421716 + 0.730434i, \lambda_2 = -0.421716 - 0.730434i$ and we can check that $|\lambda_1| = |\lambda_2| = |\lambda_3| = 0.843433$ and thus we do not have the dominant eigenvalue.

The question we will try to answer in the next lecture is what features of the population are responsible for such behaviour.

Spectral properties of a matrix and Perron–Frobenius theory.

We are interested in solving

$$\boldsymbol{x}(k+1) = \mathscr{A}\boldsymbol{x}(k), \quad \boldsymbol{x}(0) = \mathring{\boldsymbol{x}} \tag{17}$$

where $\mathscr{A}$ is an $n \times n$ matrix $\mathscr{A} = \{a_{ij}\}_{1\leq i,j\leq n}$, that is

$$\mathscr{A} = \begin{pmatrix} a_{11} & \dots & a_{1n} \\ \vdots & & \vdots \\ a_{n1} & \dots & a_{nn} \end{pmatrix},$$

and $\boldsymbol{x}(k) = (x_1(k), \dots, x_n(k))$.

The solution to (17) is given by

$$\boldsymbol{x}(k) = \mathscr{A}^k \mathring{\boldsymbol{x}}, \quad k = 1, 2, \dots. \tag{18}$$

It is rather difficult to give an explicit form of $\mathscr{A}^k$.

Since $\mathbb{R}^n$ is n-dimensional, it is enough to find n linearly independent vectors $\boldsymbol{v^i}$, $i = 1, \ldots, n$, for which $\mathcal{A}^k \boldsymbol{v^i}$ can be easily evaluated. Assume for a moment that such vectors have been found. Then, for arbitrary $\mathring{\boldsymbol{x}} \in \mathbb{R}^n$ we can find constants $c_1, \ldots, c_n$ such that

$$\mathring{\boldsymbol{x}} = c_1 \boldsymbol{v^1} + \ldots + c_n \boldsymbol{v^n}.$$

Precisely, let $\mathcal{V}$ be the matrix having vectors $\boldsymbol{v^i}$ as its columns

$$\mathcal{V} = \begin{pmatrix} | & \ldots & | \\ \boldsymbol{v^1} & \ldots & \boldsymbol{v^n} \\ | & \ldots & | \end{pmatrix}. \tag{19}$$

Note, that $\mathcal{V}$ is invertible as the vectors $\boldsymbol{v^i}$ are linearly independent. Denoting $\boldsymbol{c} = (c_1, \ldots, c_n)$, we obtain

$$\boldsymbol{c} = \mathcal{V}^{-1}\mathring{\boldsymbol{x}}. \tag{20}$$

Thus, for an arbitrary $\mathring{\boldsymbol{x}}$ we have

$$\mathcal{A}^n\mathring{\boldsymbol{x}} = \mathcal{A}^n(c_1\boldsymbol{v^1} + \ldots + c_2\boldsymbol{v^n}) = c_1\mathcal{A}^n\boldsymbol{v^1} + \ldots + c_k\mathcal{A}^n\boldsymbol{v^n}. \tag{21}$$

Now, if we denote by

$$\mathcal{A}_k = \begin{pmatrix} | & \dots & | \\ \mathcal{A}^k \boldsymbol{v^1} & \dots & \mathcal{A}^k \boldsymbol{v^n} \\ | & \dots & | \end{pmatrix}, \tag{22}$$

then

$$\mathcal{A}^k \mathring{\boldsymbol{x}} = \mathcal{A}_n \boldsymbol{c} = \mathcal{A}_k \mathcal{V}^{-1} \mathring{\boldsymbol{x}}. \tag{23}$$

Hence, the problem is to find linearly independent vectors $\boldsymbol{v^i}$, $i = 1, \dots, n$, on which the powers of $\mathcal{A}$ can be easily evaluated.

We shall use eigenvalues and eigenvectors for this purpose. Firstly, note that if $\boldsymbol{v}^{\mathbf{1}}$ is an eigenvector of $\mathcal{A}$ corresponding to an eigenvalue λ_1, that is, $\mathcal{A}\boldsymbol{v}^{\mathbf{1}} = \lambda_1 \boldsymbol{v}^{\mathbf{1}}$, then, by induction,

$$\mathcal{A}^k \boldsymbol{v}^{\mathbf{1}} = \lambda_1^k \boldsymbol{v}^{\mathbf{1}}.$$

Therefore, if we have n linearly independent eigenvectors $\boldsymbol{v}^{\mathbf{1}}, \ldots, \boldsymbol{v}^{\boldsymbol{n}}$ corresponding to eigenvalues $\lambda_1, \ldots, \lambda_n$ (not necessarily distinct), then from (21) we obtain

$$\mathcal{A}^k \mathring{\boldsymbol{x}} = c_1 \lambda_1^k \boldsymbol{v}^{\mathbf{1}} + \ldots + c_n \lambda_n^k \boldsymbol{v}^{\boldsymbol{n}}.$$

with $c_1, \ldots, c_n$ given by (20),

or

$$\mathcal{A}^k \mathring{\boldsymbol{x}} = \begin{pmatrix} | & \dots & | \\ \lambda_1^k \boldsymbol{v^1} & \dots & \lambda_n^k \boldsymbol{v^n} \\ | & \dots & | \end{pmatrix} \mathcal{V}^{-1} \mathring{\boldsymbol{x}}. \tag{24}$$

What to do, if we do not have sufficiently many eigenvectors?

Eigenvalues, eigenvectors and associated eigenvectors.

Let $\mathscr{A}$ be an $n \times n$ matrix. We say that a number λ (real or complex) is an *eigenvalue* of $\mathscr{A}$ is there exist a non-zero solution of the equation

$$\mathscr{A}\boldsymbol{v} = \lambda \boldsymbol{v}. \tag{25}$$

Such a solution is called an *eigenvector* of $\mathscr{A}$. Eq. (25) is equivalent to the homogeneous system $(\mathscr{A} - \lambda\mathscr{I})\boldsymbol{v} = \mathbf{0}$, thus λ is an eigenvalue of $\mathscr{A}$ if and only if the determinant of $\mathscr{A}$ satisfies

$$p_{\mathscr{A}}(\lambda) = det(\mathscr{A} - \lambda\mathscr{I}) = \begin{vmatrix} a_{11}-\lambda & \dots & a_{1n} \\ \vdots & & \vdots \\ a_{n1} & \dots & a_{nn}-\lambda \end{vmatrix} = 0. \tag{26}$$

$p_{\mathcal{A}}(\lambda)$ is called the *characteristic polynomial* of the matrix $\mathcal{A}$ that factorizes into

$$p_{\mathcal{A}}(\lambda) = (\lambda_1 - \lambda)^{n_1} \cdot \ldots \cdot (\lambda_k - \lambda)^{n_k}, \tag{27}$$

with $n_1 + \ldots + n_k = n$. Thus, eigenvalues are the roots of the characteristic polynomial of $\mathcal{A}$. The set of eigenvalues of $\mathcal{A}$ is called the spectrum of $\mathcal{A}$ and denoted $\sigma(\mathcal{A})$.

- The exponent n_i appearing in the factorization (27) is called the *algebraic multiplicity* of λ_i.
- To each eigenvalue λ_i there corresponds an eigenvector $\boldsymbol{v^i}$.
- The eigenvectors corresponding to distinct eigenvalues are linearly independent.

The set of all eigenvectors belonging to λ_i is a linear subspace (eigenspace), whose dimension is called the geometric multiplicity of λ_i.

In general, the algebraic and geometric multiplicities are different with geometric multiplicity being at most equal to the algebraic one. Thus, in particular, if λ_i is a single root of the characteristic polynomial, then the eigenspace corresponding to λ_i is one-dimensional.

If the geometric multiplicities of eigenvalues add up to n, that is, if we have n linearly independent eigenvectors, then these eigenvectors form a basis for $\mathbb{R}^n$. In particular, this happens if all eigenvalues are single roots of the characteristic polynomial.

If this is not the case, then we do not have sufficiently many eigenvectors to span $\mathbb{R}^n$ and if we need a basis for $\mathbb{R}^n$, then we have to find additional linearly independent vectors on which $\mathcal{A}^k$ can be easily evaluated. We employ the following procedure.

Let λ_i has algebraic multiplicity n_i and let

$$(\mathcal{A} - \lambda_i \mathcal{I})\boldsymbol{v} = 0$$

have only $\nu_i < n_i$ linearly independent eigenvectors. Then we consider the equation

$$(\mathcal{A} - \lambda_i \mathcal{I})^2 \boldsymbol{v} = 0.$$

All eigenvectors solve this equation, but there is at least one more independent solution so that we have at least $\nu_i + 1$ independent vectors (note that these new vectors are no longer eigenvectors).

If the number of independent solutions is still less than n_i, then we consider

$$(\mathcal{A} - \lambda_i \mathcal{I})^k \boldsymbol{v} = 0,$$

for $k > 2$ until we get a sufficient number of linearly independent solutions.

The process must stop at $k = n_i$. Vectors $\boldsymbol{v}$ obtained in this way for a given λ_i are called *generalized* or *associated eigenvectors* corresponding to λ_i and they span an n_i dimensional subspace called the *associated eigenspace* belonging to λ_i, denoted hereafter by E_{λ_i}.

Let us return to the system

$$\boldsymbol{x}(k+1) = \mathcal{A}\boldsymbol{x}(k), \quad \boldsymbol{x}(0) = \mathring{\boldsymbol{x}}.$$

We take as $\boldsymbol{v}$ the collection of all eigenvectors and associated eigenvectors of $\mathcal{A}$. If $\boldsymbol{v^i}$ is an eigenvector belonging to λ^i, then $\mathcal{A}^k\boldsymbol{v^i} = \lambda_i^k\boldsymbol{v^i}$.

Let $\boldsymbol{v^j}$ be an associated eigenvector found as a solution to $(\mathcal{A} - \lambda_i\mathcal{I})^{\nu_j}\boldsymbol{v^j} = \mathbf{0}$ with $\nu_j \leq n_i$.

Then, using the binomial expansion, for $k > \nu_j$ we find

$$\begin{aligned}
\mathcal{A}^k \boldsymbol{v^j} &= (\lambda_i \mathcal{I} + \mathcal{A} - \lambda_i \mathcal{I})^k \boldsymbol{v^j} = \sum_{r=0}^{k} \lambda_i^{k-r} \begin{pmatrix} k \\ r \end{pmatrix} (\mathcal{A} - \lambda_i \mathcal{I})^r \boldsymbol{v^j} \\
&= \Big(\lambda_i^k \mathcal{I} + k\lambda_i^{k-1} (\mathcal{A} - \lambda_i \mathcal{I}) + \dots \\
&\quad + \frac{k!}{(\nu_j - 1)!(k - \nu_j + 1)!} \lambda_i^{k-\nu_j+1} (\mathcal{A} - \lambda_i \mathcal{I})^{\nu_j - 1} \Big) \boldsymbol{v^j} \\
&= \lambda_i^k \boldsymbol{p}_{\lambda_i}(k, \boldsymbol{v^i}), \qquad (28)
\end{aligned}$$

where $\boldsymbol{p}_{\lambda_i}(k, \boldsymbol{v^i})$ is a polynomial in k of degree smaller than n_i with vector coefficients depending on $\boldsymbol{v^i}$, λ_i and $\mathcal{A}$.

Since

$$\boldsymbol{x} = c_1 \boldsymbol{v}^{\boldsymbol{1}} + \ldots + c_n \boldsymbol{v}^{\boldsymbol{n}},$$

that is,

$$\boldsymbol{c} = \boldsymbol{c}(\boldsymbol{x}) = \mathcal{V}^{-1}\boldsymbol{x}, \qquad (29)$$

by (28), we have

$$\mathcal{A}^k \boldsymbol{x} = \sum_{\lambda \in \sigma(\mathcal{A})} \lambda^k \boldsymbol{p}_\lambda(k, \boldsymbol{c}(\boldsymbol{x})), \qquad (30)$$

where $\boldsymbol{p}_\lambda$ are polynomials in k of degree strictly smaller than the algebraic multiplicity of λ, and with vector coefficients being linear combinations of eigenvectors and associated eigenvectors corresponding to λ and the coordinates of $\boldsymbol{c}(\boldsymbol{x})$.

Returning to our main problem, that is, to the long time behaviour of the iterates $\mathscr{A}^k$ then, from (30), we see that it is determined by λ_m^k possibly multiplied by a polynomial of degree smaller than the algebraic multiplicity of λ_m, where λ_m is the eigenvalue of the largest absolute value.

The situation observed for the Leslie matrix (14) corresponds to the situation when there is a real positive simple eigenvalue λ_m satisfying $\lambda_m > |\lambda|$ for any other eigenvalue λ. Such an eigenvalue is called the *principal* or *dominant* eigenvalue. In such a case, for any initial condition $\boldsymbol{x}$ we have

$$\mathcal{A}^k \boldsymbol{x} \approx c_m(\boldsymbol{x})\lambda_m^k \boldsymbol{v}^{\boldsymbol{m}}$$

for large k, provided $c_m(\boldsymbol{x}) \neq 0$. In such a case the vector $\boldsymbol{v}^{\boldsymbol{m}}$ is called the *stable age structure*.

An important question is to determine c_m. Clearly, $c_m(\boldsymbol{x})$ is given by (29), but this involves knowing all eigenvectors and associated eigenvectors of $\mathscr{A}$ and thus is not particularly handy. Here we shall describe a simpler method.

Let us recall that the transposed matrix $\mathcal{A}^T$ satisfies

$$\langle \mathcal{A}^T \boldsymbol{x}^*, \boldsymbol{y} \rangle = \langle \boldsymbol{x}^*, \mathcal{A} \boldsymbol{y} \rangle$$

where $\langle \boldsymbol{x}^*, \boldsymbol{y} \rangle = \sum_{i=1}^{n} x_i^* y_i$. Matrices $\mathcal{A}$ and $\mathcal{A}^T$ have the same eigenvalues and, though eigenvectors and associated eigenvectors are different (unless $\mathcal{A}$ is symmetric), the structure of the generalized eigenspaces corresponding to the same eigenvalue is identical.

Theorem 6

Let E_λ and $E^*_{\lambda^*}$ be generalized eigenspaces of, respectively, $\mathcal{A}$ and $\mathcal{A}^T$, corresponding to different eigenvalues: $\lambda \neq \lambda^*$. If $\boldsymbol{v}^* \in E^*_{\lambda^*}$ and $\boldsymbol{v} \in E_\lambda$, then

$$\langle \boldsymbol{v}^*, \boldsymbol{v} \rangle = 0. \tag{31}$$

Thus, given

$$\boldsymbol{x} = c_1 \boldsymbol{v}^{\boldsymbol{1}} + \ldots + c_n \boldsymbol{v}^{\boldsymbol{n}},$$

we obtain

$$c_m = \frac{\langle \boldsymbol{x}, \hat{\boldsymbol{v}}^{\boldsymbol{m}} \rangle}{\langle \boldsymbol{v}^{\boldsymbol{m}}, \hat{\boldsymbol{v}}^{\boldsymbol{m}} \rangle},$$

where $\mathscr{A}^T \boldsymbol{v}^{\boldsymbol{m}} = \lambda_m \boldsymbol{v}^{\boldsymbol{m}}$.

Summarizing, to determine a long time behaviour of a population described by $\boldsymbol{x}(k+1) = \mathcal{A}\boldsymbol{x}$,

- Find the dominant eigenvalue λ_m of $\mathcal{A}$ (if it exists);
- Find the eigenvectors $\boldsymbol{v^m}$ of $\mathcal{A}$ and $\boldsymbol{\hat{v}^m}$ belonging to λ_m;
- The long time behaviour of the population is then described by

$$\mathcal{A}^k\boldsymbol{x} \approx \lambda_m^k \frac{\langle \boldsymbol{\hat{v}^m}, \boldsymbol{x}\rangle}{\langle \boldsymbol{v^m}, \boldsymbol{\hat{v}^m}\rangle}\boldsymbol{v^m} \tag{32}$$

for large k, provided $\langle \boldsymbol{\hat{v}^m}, \boldsymbol{x}\rangle \neq 0$.

Example 7

Returning to Fibonacci rabbits, the eigenvalues of $\mathcal{L}$ are

$$\lambda_{1,2} = r_{\pm} = \frac{1 \pm \sqrt{5}}{2}$$

and clearly, $\lambda_1 = \frac{1+\sqrt{5}}{2}$ is the dominant eigenvalue. An eigenvector associated with this eigenvalue is $\boldsymbol{v}^{\mathbf{1}} = (1, \lambda_1) = \left(1, \frac{\sqrt{5}+1}{2}\right)$ and this gives the stable age structure. Moreover, the matrix $\mathcal{L}$ is symmetric and thus the eigenvectors of $\mathcal{L}^T$ are the same as of $\mathcal{L}$. Thus

$$\boldsymbol{v}(k) = \begin{pmatrix} v_0(k) \\ v_1(k) \end{pmatrix} \approx C_1 r_+^k \begin{pmatrix} 1 \\ \frac{\sqrt{5}+1}{2} \end{pmatrix},$$

Example 8

where

$$C_1 = \frac{2\left(v_1(0)\frac{\sqrt{5}+1}{2} + v_0(0)\right)}{5+\sqrt{5}}$$

as $\langle \boldsymbol{v^1}, \boldsymbol{v^1} \rangle = (5+\sqrt{5})/2$.

Taking, for instance, the initial condition discussed for (14):

$v_1(0) = 0, v_0(0) = 1$, we find $C_1 = 2/(5+\sqrt{5})$ and if we like to estimate the growth of the whole population, we have

$$y(k) = v_1(k) + v_0(k) \approx \frac{2}{5+\sqrt{5}}\left(\frac{\sqrt{5}+1}{2} + 1\right) r_+^k$$
$$= \frac{1+\sqrt{5}}{2\sqrt{5}} r_+^k.$$

Frobenius-Perron theorem.

The question what matrices with nonnegative entries give rise to such a behaviour is much more delicate and requires invoking the Frobenius-Perron theorem which will be discussed next.

To make further progress, we have to formalize a number of statements made in the previous sections and, in particular, the meaning of the approximate equality (32). For this, we have to set the problem in an appropriate mathematical framework.

Positive dynamical systems. First, we note that in the context of population theory, if a given equation is to describe evolution of a population; that is, if the solution is the population size or density, then solutions emanating from non-negative data must stay non-negative. Thus we have to extend the notion of positivity to vectors. We say that a vector $\boldsymbol{x} = (x_1, \ldots, x_n)$ is non-negative, (resp. positive), if for all $i = 1, \ldots, n$, $x_i \geq 0$, (resp. $x_i > 0$). We denote these as $\boldsymbol{x} \geq 0$, (resp. $\boldsymbol{x} > 0$) and define

$$X_+ = \{\boldsymbol{x} \in \mathbb{R}^n;\ \boldsymbol{x} \geq 0\}.$$

Similar convention is applied to matrices.

It is easy to prove that

Proposition 1

The solution $\mathbf{x}(k)$ *of*

$$\mathbf{x}(k+1) = \mathcal{A}\mathbf{x}(k), \quad \mathbf{x}(0) = \mathring{\mathbf{x}}$$

satisfies $\mathbf{x}(k) \geq 0$ *for any* $k = 1, \ldots,$ *for arbitrary* $\mathring{\mathbf{x}} \geq 0$ *if and only if* $\mathcal{A} \geq 0$.

The sequence $(\mathcal{A}^k)_{k\geq 1}$ is a dynamical system in the state space $X = \mathbb{R}^n$ (and in X_+ if $\mathcal{A} \geq 0$). Essentially, (32) is a statement about the limit of $\mathcal{A}^k \mathring{\boldsymbol{x}}$ as $k \to \infty$, so we must introduce a metric structure on X. To make the metric consistent with the linear structure of $\mathbb{R}^n$, it is typically defined by a norm, that is, a functional $\|\cdot\| : X \to \mathbb{R}_+$ satisfying, for any $\boldsymbol{x}, \boldsymbol{y} \in X, \alpha \in \mathbb{R}$,

$$\|\boldsymbol{x}\| = 0 \quad \text{iff} \quad \boldsymbol{x} = 0, \qquad \|\alpha \boldsymbol{x}\| = |\alpha|\|\boldsymbol{x}\|, \qquad \|\boldsymbol{x}+\boldsymbol{y}\| \leq \|\boldsymbol{x}\|+\|\boldsymbol{y}\|.$$

There is a variety of norms in $\mathbb{R}^n$ (all defining the same topology), the most common being the Euclidean metric.

However, bearing in mind the interpretation of our problems in which $\boldsymbol{x}(k) = (x_1(k), \ldots, x_n(k))$ defines the distribution of a population among the states, we see that the most natural norm is

$$\|\boldsymbol{x}\| = \sum_{i=1}^{n} |x_i| \tag{33}$$

which, for $\boldsymbol{x} \geq 0$, simplifies to

$$\|\boldsymbol{x}\| = \sum_{i=1}^{n} x_i \tag{34}$$

and which is the total population of the ensemble.

Since we want $\mathcal{A}$ to act from X to X with the same way of measuring distances, we should have

$$\|\mathcal{A}\boldsymbol{x}\| = \sum_{i=1}^{n}\left|\sum_{j=1}^{n} a_{ij}x_j\right| \leq \sum_{j=1}^{n}|x_j|\sum_{i=1}^{n}|a_{ij}| \leq \|\boldsymbol{x}\| \max_{1\leq j\leq n}\sum_{i=1}^{n}|a_{ij}|$$

$$=: \|\mathcal{A}\|\|\boldsymbol{x}\|$$

where

$$\|\mathcal{A}\| = \max_{1\leq j\leq n}\sum_{i=1}^{n}|a_{ij}|$$

is called the norm of the matrix/operator $\mathcal{A}$.

Further, the spectral radius of $\mathcal{A}$ is defined as

$$r(A) = \sup_{\lambda\in\sigma(\mathcal{A})}|\lambda|. \qquad (35)$$

Classification of projection matrices. Let $\mathscr{A} \geq 0$. The long time behaviour of $(\mathscr{A}^k)_{k\geq 1}$ is fully determined by whether $\mathscr{A}$ is a primitive irreducible, imprimitive irreducible or a reducible matrix.

For a matrix $\mathscr{A} = (a_{ij})_{1\leq i,j\leq n}$, we say that there is:

- an *arc* from i to j if $a_{ij} > 0$,
- a *path* from i to j if there is a sequence of arcs starting from i and ending in j in which the endpoint of each arc (apart from the last) is the beginning of the subsequent arc; *loop* is a path from i to itself.

We say that a non-negative matrix is *irreducible* if, for each i and j, there is a path from i to j. Otherwise, we say that it is *reducible*.

To formulate an equivalent, but more algebraic, condition, we introduce some notation. We write

$$\mathcal{A}^k = (a_{ij}^{(k)})_{1\leq i,j\leq n},$$

where

$$a_{ij}^{(k)} = \sum_{1\leq i_r\leq n, r=1,\ldots,k-1} a_{ii_1}a_{i_1i_2}\cdot\ldots\cdot a_{i_{k-1}j}.$$

If some $a_{ii_1}a_{i_1i_2}\cdot\ldots\cdot a_{i_{k-1}j}\neq 0$, then there is a path starting from j and passing through $i_{k-1},\ldots,i_1$ to i. Since the matrix elements are nonnegative, for $a_{ij}^{(k)}$ to be non-zero it is enough that there exists at least one such path. Thus, $\mathcal{A}$ is irreducible if for each pair (i,j) there is k such that $a_{ij}^{(k)}>0$.

An equivalent definition of reducibility is that $\mathscr{A}$ is reducible if, by simultaneous permutation of rows and columns, it can be brought to the form

$$\begin{pmatrix} \mathscr{A} & \mathbf{0} \\ \mathscr{B} & \mathscr{C} \end{pmatrix}$$

where $\mathscr{A}$ and $\mathscr{C}$ are square matrices.

In terms of age-structured population dynamics, a matrix is irreducible if each stage i can contribute to any other stage j. E.g., the Usher matrix

$$\begin{pmatrix} 0 & 0 & 1 & | & 0 \\ 1 & 0 & 0 & | & 0 \\ 0 & 1 & 0 & | & 0 \\ - & - & - & - & - \\ 0 & 0 & 1 & | & 1 \end{pmatrix}$$

is reducible as the last state cannot contribute to any state other than itself and fertility is concentrated in only one state.

Irreducible matrices are subdivided into two further classes. An irreducible matrix $\mathscr{A}$ is called *primitive* if

$$\mathscr{A}^k > 0,$$

otherwise it is called *imprimitive*.

Note the difference between irreducibility and primitivity. For irreducibility we require that for each (i, j) there is k such that $a_{ij}^{(k)} > 0$ but for primitivity there must be k such that $a_{ij}^{(k)} > 0$ for all (i, j).

In population dynamics, if a population has a single reproductive stage, then its projection matrix is imprimitive. E.g., the matrix

$$\mathscr{A} = \begin{pmatrix} 0 & 0 & 1 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix}$$

describing a semelparous population is imprimitive. In fact

$$\mathscr{A}^2 = \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \end{pmatrix}, \quad \mathscr{A}^3 = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}.$$

In particular, $\mathscr{A}^4 = \mathscr{A}$ — another defining feature of imprimitive matrices.

Theorem 9 (Perron-Frobenius)

Let $\mathcal{A}$ be a nonnegative matrix.

1. There exists a real nonnegative eigenvalue $\lambda_m = r(\mathcal{A})$ such that $\lambda_m \geq |\lambda|$ for any $\lambda \in \sigma(\mathcal{A})$. There is an eigenvector (called the Perron eigenvector) belonging to λ_m which is real and nonnegative.

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2. If, in addition, $\mathcal{A}$ is irreducible, then λ_m is simple and strictly positive, $\lambda_m \geq |\lambda|$ for $\lambda \in \sigma(\mathcal{A})$. The eigenvector belonging to λ_m may be chosen to be strictly positive.

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2. If, in addition, $\mathcal{A}$ is irreducible, then λ_m is simple and strictly positive, $\lambda_m \geq |\lambda|$ for $\lambda \in \sigma(\mathcal{A})$. The eigenvector belonging to λ_m may be chosen to be strictly positive.

(i)If $\mathcal{A}$ is additionally primitive, then $\lambda_m > |\lambda|$;

(ii) If $\mathcal{A}$ is imprimitive, then there are $d-1$ (d is called the imprimitivity index) eigenvalues $\lambda_j = \lambda_m e^{2\pi i \frac{j}{d}}, j = 1, \ldots, j-1$, with $\lambda_m = |\lambda_j|$.

Let us apply the Perron-Frobenius theorem in the population context. Suppose that our population is divided into n age (or other) classes and the state of the population is given by the vector $\boldsymbol{x} = (x_1, \ldots, x_n)$ giving the number of individuals (or density) in each class. Let $\mathring{\boldsymbol{x}} \geq 0$ denote the initial distribution of the population among the classes. Then

$$\boldsymbol{x}(k) = \mathcal{A}^k \mathring{\boldsymbol{x}}$$

is the distribution after k periods and

$$P(k, \mathring{\boldsymbol{x}}) = \|\mathcal{A}^k \mathring{\boldsymbol{x}}\| = \sum_{i=1}^{n} (\mathcal{A}^k \mathring{\boldsymbol{x}})_i = \sum_{i=1}^{n} x_i(k) = \|\boldsymbol{x}(k)\|$$

is the total population at time k evolving from the initial distribution $\mathring{\boldsymbol{x}}$.

If $\mathscr{A}$ is nonnegative, irreducible or primitive, then the transpose $\mathscr{A}^T$ has the same property.

Let $r := \lambda_m$ be the dominant eigenvalue of both matrices and $\boldsymbol{v}$ and $\hat{\boldsymbol{v}}$ be the corresponding strictly positive eigenvectors of, respectively, $\mathscr{A}$ and $\mathscr{A}^T$, belonging to λ_m. We normalize $\boldsymbol{v}$ so that $\|\boldsymbol{v}\| = 1$ and $\hat{\boldsymbol{v}}$ so that $\langle \hat{\boldsymbol{v}}, \boldsymbol{v} \rangle = 1$.

Combining the Perron-Frobenius theorem with the spectral decomposition we arrive at the following result.

Theorem 10 (Fundamental Theorem of Demography)

Suppose that the projection matrix $\mathcal{A}$ is irreducible and primitive and let r be the strictly positive dominant eigenvalue of $\mathcal{A}$, $\boldsymbol{v}$ the strictly positive eigenvector of $\mathcal{A}$ and $\hat{\boldsymbol{v}}$ strictly positive eigenvector of $\mathcal{A}^T$ corresponding to r. Then, for any $\boldsymbol{x}_0 \geq 0$,

(a) $\mathcal{A}$ has the AEG property

$$\lim_{k\to\infty} r^{-k}\mathcal{A}^k\boldsymbol{x}_0 = \langle \hat{\boldsymbol{v}}, \boldsymbol{x}_0\rangle \boldsymbol{v}. \tag{36}$$

(b)

$$\lim_{k\to\infty} \frac{\boldsymbol{x}(k)}{P(k,\boldsymbol{x}_0)} = \frac{\mathcal{A}^k\boldsymbol{x}_0}{P(k,\boldsymbol{x}_0)} = \boldsymbol{v}. \tag{37}$$

Theorem 10

(c) If $r < 1$

$$\lim_{k\to\infty} P(k, \boldsymbol{x}_0) = 0,$$

and

$$\lim_{k\to\infty} P(k, \boldsymbol{x}_0) = \infty$$

if $r > 1$.

Back to Leslie matrices. Let us consider the Leslie matrix

$$\mathcal{L} := \begin{pmatrix} f_0 & f_1 & \cdots & f_{n-2} & f_{n-1} \\ s_0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ldots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-2} & 0 \end{pmatrix}, \tag{38}$$

and find under what conditions the population described by $\mathcal{L}$ exhibits asynchronous exponential growth.

Irreducibility.

• First we observe that for irreducibility we need all $s_i \neq 0, 0 \leq i \leq n-2$. Indeed, if for some i the coefficient $s_i = 0$, then there would be no path from $k \leq i$ to $k > i$. In other words, there would be no way of reaching the age $k > i$.

- Assuming the above, $\mathscr{L}$ is irreducible if and only if $f_{n-1} > 0$.

Clearly, if $f_{n-1} = 0$, then there is no communication from class $n-1$ to any other class and thus $\mathscr{L}$ is reducible.

Now, let $f_{n-1} > 0$ and pick a (i, j). If $j < i$, then there is a path $(j, j+1)$...$(i-1, i)$ ensured by the survival coefficients $s_j, s_{j+1}, \ldots s_{i-1}$. If $j \geq i$, then the survival coefficients ensure that we reach the last class $n-1$. Since $f_{n-1} > 0$, we reach class 0 and arrive at i by aging.

Primitivity.

Let us first assume that $f_j > 0$ for $j = 0, \dots, n-1$, that is, that any age group is capable of reproduction. Let us consider arbitrary initial state j. Then there is an arc between j and 0 ($a_{0j} = f_j > 0$) and then from state 0 one can reach any state i in exactly i steps ($s_0 s_1 \cdot \ldots \cdot s_{i-1}$). Thus, there is a path joining j and i of length $i+1$, which still depends on the target state. However, there is an arc from 0 to itself, so we can wait at 0 for any number of steps. In particular we can wait for $n-(i+1)$ steps so that j can be connected with i in n steps. In other words

$$s_{i-1} \cdot \cdots \cdot s_1 s_0 f_0 \cdot \ldots \cdot f_0 f_j > 0,$$

where f_0 occurs $n-(i+1)$ times. Hence $\mathcal{L}^n > 0$.

For instance, for (14),

$$\mathcal{L} = \begin{pmatrix} 2 & 1 & 1 \\ 0.5 & 0 & 0 \\ 0 & 0.4 & 0 \end{pmatrix},$$

we have

$$\mathcal{L}^2 = \begin{pmatrix} 4.5 & 2.4 & 2 \\ 1 & 0.5 & 0.5 \\ 0.2 & 0 & 0 \end{pmatrix}, \quad \mathcal{L}^3 = \begin{pmatrix} 10.2 & 5.3 & 4.5 \\ 2.25 & 1.2 & 1 \\ 0.4 & 0.2 & 0.2 \end{pmatrix},$$

so $\mathcal{L}^3 > 0$ and $\mathcal{L}$ is primitive.

The above assumption is too strong — typically young individuals cannot reproduce. We will strengthen this result. For this, we need the characteristic equation for $\mathcal{L}$. Rather unusually, we begin with the eigenvector equation.

$$\mathcal{L}\boldsymbol{v} = \begin{pmatrix} f_0 & f_1 & \cdots & f_{n-2} & f_{n-1} \\ s_0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ldots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-2} & 0 \end{pmatrix} \begin{pmatrix} v_0 \\ v_1 \\ v_2 \\ \vdots \\ v_{n-1} \end{pmatrix} = \lambda \begin{pmatrix} v_0 \\ v_1 \\ v_2 \\ \vdots \\ v_{n-1} \end{pmatrix}.$$

The equations from the second row down read

$$s_0 v_0 = \lambda v_1, \quad s_1 v_1 = \lambda v_2, \quad \ldots, \quad s_{n-2} v_{n-2} = \lambda v_{n-1}.$$

Taking $v_0 = 1$, we obtain

$$v_1 = \frac{s_0}{\lambda}, \quad v_2 = \frac{s_0 s_1}{\lambda^2}, \quad \dots v_{n-1} = \frac{s_0 s_1 \dots s_{n-2}}{\lambda^{n-1}}.$$

Now, the first row gives the equation

$$\lambda = \left(f_0 + \frac{f_1 s_0}{\lambda} + \frac{f_2 s_0 s_1}{\lambda^2} + \dots + \frac{f_{n-1} s_0 s_1 \dots s_{n-2}}{\lambda^{n-1}} \right).$$

We use $s_i = l_{i+1}/l_i$ where l_i is probability of survival till the $i + 1$st reproductive cycle from birth (thus s_i is conditional probability of survival to the next reproductive cycle if one survived till i from birth) and $f_i = m_{i+1} s_i$ to rewrite the above as

$$1 = \left(\frac{m_1 l_1}{\lambda} + \frac{m_2 l_2}{\lambda^2} + \frac{m_3 l_3}{\lambda^3} + \dots + \frac{m_n l_n}{\lambda^n} \right),$$

where we used $l_0 = 1$. This equation is called the discrete Euler-Lotka equation.

We show $\mathscr{L}$ is imprimtive if and only if the maternity function is periodic, that is, if the greatest common divisor of ages of positive reproduction, called the period, is greater than 1. For instance, the sequence m_2, m_4, m_6 has period 2. In particular, the period is equal to the imprimitivity index.

Suppose that r and

$$\lambda_j = re^{i\theta}, \quad \theta \neq 2\pi n,$$

are roots to

$$\psi(\lambda) = \sum_{k=1}^{n} \lambda^{-k} m_k l_k = 1. \tag{39}$$

Then

$$\sum_{k=1}^{n} r^{-k}e^{-ik\theta}l_k m_k = 1 \qquad (40)$$

or, taking real and imaginary parts,

$$\begin{aligned}\sum_{k=1}^{n} r^{-k}\cos(k\theta)l_k m_k &= 1, &(41)\\ \sum_{k=1}^{n} r^{-k}\sin(k\theta)l_k m_k &= 0. &(42)\end{aligned}$$

If m_k is periodic, then the only nonzero terms correspond to multiples of d, $m_{k_1 d}, m_{k_2 d}, m_{k_3 d}, \ldots$. Taking $\theta_j = 2\pi j/d$, $j = 0, 1, \ldots, d-1$, we see $\cos k_l d\theta_j = 1$, $\sin k_l d\theta_j = 0$ and so, if the above equations are satisfied by r, they are also satisfied by any $\lambda_j = re^{i\theta_j}$.

If m_k is aperiodic, with $m_{k_i} \neq 0$, $i \in I \subset \{1, \ldots, n\}$, then there is no $\theta \neq 0$ for which $\cos k_i\theta = 1$ for all k_i. Indeed, otherwise there is $\theta \in (0, 2\pi)$ such that

$$\cos k_1\theta = 1.$$

This implies

$$\theta = 2\pi \frac{p}{k_1} = 2\pi \frac{j}{d},$$

where $p < k_1$ is an integer and j and d are relatively prime integers, so that $0 < j \leq d - 1$ (note that if $j = 0$, then $\theta = 0$). But then, for arbitrary $i \in I$,

$$k_i\theta = k_i \frac{2\pi j}{d} = 2\pi p_i$$

for some integer p_i.

Thus

$$k_i = p_i \frac{d}{j}.$$

However, k_i is an integer and j and d are relatively prime so that p_i must be divisible by j. Hence

$$k_i = r_i d$$

for some integer r_i, $i \in I$. Thus, any k_i is an integer multiple of d.

Thus, whatever θ, for some k we must have $\cos k\theta < 1$. But then, if (41) was satisfied, we would have

$$\sum_{k=1}^{n} r^{-k} l_k m_k > 1,$$

which contradicts the fact that r is a solution to (39), that is,

$$\sum_{k=1}^{n} r^{-k} l_k m_k = 1.$$

Reducible case.

Let us consider a more complicated case where the fertility is restricted to some interval $[n_1, n_2]$, that is, when $f_j > 0$ for $j \in [n_1, n_2]$. As we noted earlier, if $n_2 < n$, the matrix cannot be irreducible as there is no communication between postreproductive stages and the reproductive ones. Consequently, if we start only with individuals in postreproductive age, the population will die out in finite time. Nevertheless, if $n_1 < n_2$, then the population still displays asynchronous exponential growth, albeit with a slight modification, as explained below.

To analyse this model, we note that since we cannot move from stages with $j > n_2$ to earlier stages, the part of the population with $j \leq n_2$ evolves independently from postreproductive part (but feeds into it). Assume that $n_1 < n_2$ and introduce the restricted matrix

$$\tilde{\mathcal{L}} = \begin{pmatrix} f_0 & f_1 & \cdots & f_{n_2-1} & f_{n_2} \\ s_0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ldots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n_2-1} & 0 \end{pmatrix}$$

and the matrix providing (one-way) link from reproductive to postreproductive stages is given by

$$\mathcal{R} = \begin{pmatrix} 0 & \cdots & s_{n_2} & 0 & \cdots & 0 & 0 \\ \vdots & \cdots & \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & \cdots & 0 & 0 & \cdots & s_{n-2} & 0 \end{pmatrix}$$

For the matrix $\tilde{\mathcal{L}}$, $f_{n_2} > 0$ and $f_{n_2-1} > 0$, so the maternity function is not periodic and $\tilde{\mathcal{L}}$ is primitive. Thus, we can use (32), so that there is $r > 0$ and (normalized) vectors $\boldsymbol{v} = (v_0, \ldots v_{n_2})$ and $\hat{\boldsymbol{v}} = (\hat{v}_0, \ldots \hat{v}_{n_2})$ such that $\tilde{\mathcal{L}}\boldsymbol{v} = r\boldsymbol{v}$ and

$$\lim_{k\to\infty} r^{-k}\boldsymbol{v}(k+1) = \lim_{k\to\infty} r^{-k}\tilde{\mathcal{L}}^k\mathring{\boldsymbol{v}} = \boldsymbol{v}\langle\hat{\boldsymbol{v}}, \mathring{\boldsymbol{v}}\rangle, \quad 0 \le \mathring{\boldsymbol{v}} \in \mathbb{R}^{n_2}. \quad (43)$$

For $n_2 \leq j < n, k \geq 0$, we have $v_{j+1}(k+1) = s_j v_j(k)$. Hence, starting from $v_{n_2}(k)$ we get $v_{n_2+i}(k+i) = c_i v_{n_2}(k)$, where $c_i = s_{n_2+i-1} \cdot \ldots \cdot s_{n_2}$, as long as $i \leq n - n_2 - 1$. So

$$\lim_{k\to\infty} r^{-k} v_{n_2+i}(k+i) = c_i v_{n_2} \langle \hat{\boldsymbol{v}}, \mathring{\boldsymbol{v}} \rangle, \quad 0 \leq \mathring{\boldsymbol{v}} \in \mathbb{R}^{n_2},$$

and hence, changing $k+i$ into k

$$\lim_{k\to\infty} r^{-k} v_{n_2+i}(k) = c_i r^{-i} v_{n_2} \langle \hat{\boldsymbol{v}}, \mathring{\boldsymbol{v}} \rangle, \quad 0 \leq \mathring{\boldsymbol{v}} \in \mathbb{R}^{n_2},$$

for any $i = 1, \ldots, n - n_2 - 1$.

Hence, we see that the formula (32) is satisfied if we take

$$\begin{aligned}\boldsymbol{v} &= (v_0, \ldots v_{n_2}, c_1 r^{-1} v_{n_2}, \ldots, c_{n-n_2-1} r^{-(n-n_2-1)} v_{n_2})\\ \hat{\boldsymbol{v}} &= (\hat{v}_0, \ldots, \hat{v}_{n_2}, 0, \ldots, 0).\end{aligned}$$

Finally, we observe that if only one f_j is positive (semelparous population), then we do not have asynchronous exponential growth. Indeed, in this case starting from initial population in one class we will have a cohort of individuals in the same age group moving through the system.

Further applications.

Example 11

The Northern Spotted Owl has the following characteristics:

$$m_k = \begin{cases} 0 & \text{for} \quad k < 3, \\ 0.24 & \text{for} \quad k \geq 3, \end{cases}$$

$l_3 = 0.0722$ and $P = l_{k+1}/l_k = 0.942$ for $k \geq 3$ hence, in principle, we have infinitely many reproductive classes. Denoting $m_3 = m$ for $k \geq 3$, we have

$$\begin{aligned} 1 &= \sum_{k=3}^{\infty} \lambda^{-k} l_k m_k = \frac{l_3 m}{\lambda^3} + \frac{l_3 P m}{\lambda^4} + \frac{l_3 P^2 m}{\lambda^5} + \dots \\ &= \frac{l_3 m}{\lambda^3} \sum_{k=0}^{\infty} \left(\frac{P}{\lambda}\right)^k = \frac{l_3 m}{\lambda^3} \frac{1}{1 - P/\lambda}, \end{aligned}$$

Example 12

which can be re-written as

$$\lambda^3 - P\lambda^2 - l_3 m = 0.$$

Using, say, *Mathematica*, we get $\{\lambda \to 0.960772\}, \{\lambda \to -0.00938594 + 0.133968i\}$ and $\{\lambda \to -0.00938594 - 0.133968i\}$. We note the complex roots are not the roots of the original equation as for them $P/|\lambda| > 1$ and the series would be divergent. So, $\lambda = 0.960772$ is the only root outside $|\lambda| = P$.

Example 13

The dominant real eigenvalue gives an indication of the rate of growth for large times of the population. The characteristic equation can be used to find out how sensitive this parameter is with respect to environmental changes. The dominant eigenvalue can be thought of as a function of the parameters P, l_3, m determined implicitly through the equation

$$\lambda^3(P, l_3, m) - P\lambda^2(P, l_3, m) - l_3 m = 0.$$

Sensitivity of a function with respect to a parameter is given by the value of the partial derivative of the function with respect to this parameter. In this case we can find the derivatives differentiating the above equation implicitly.

Example 14

Thus,

$$3\lambda^2\frac{\partial\lambda}{\partial P} - \lambda^2 - P2\lambda\frac{\partial\lambda}{\partial P} = 0$$

or

$$\frac{\partial\lambda}{\partial P} = \frac{\lambda^2}{3\lambda^2 - 2P\lambda}$$

which, evaluated at $P = 0.942$ and $\lambda = 0.96$, gives

$$\frac{\partial\lambda}{\partial P} = 0.962.$$

In the same way,

$$\frac{\partial\lambda}{\partial l_3} = 0.254, \qquad \frac{\partial\lambda}{\partial m} = 0.075.$$

Example 15

We see that the growth rate of the population is most sensitive to the changes in adult annual survival rate, less to the survival rate to the breeding stage, and lastly to the average reproductive rate.

Example 16

Consider semelparous reproduction defined by

$$m_k = \begin{cases} 0 & \text{for} \quad k = 1, \\ 0 & \text{for} \quad k = 2, \\ 6 & \text{for} \quad k = 3, \end{cases}$$

and

$$l_k = \begin{cases} 1 & \text{for} \quad k = 1, \\ 1/2 & \text{for} \quad k = 2, \\ 1/6 & \text{for} \quad k = 3. \end{cases}$$

Example 17

The Euler-Lotka equation reduces to

$$\frac{1}{\lambda^3} = 1$$

so that

$$\lambda_0 = 1, \lambda_{1,2} = -\frac{1}{2} \pm \frac{\sqrt{3}}{2} i,$$

with all roots of modulus 1. This means that we have periodic population.

Example 18

However, if we introduce immature reproduction

$$m_k = \begin{cases} 1/4 & \text{for} \quad k = 1, \\ 0 & \text{for} \quad k = 2, \\ 6 & \text{for} \quad k = 3, \end{cases}$$

and

$$l_k = \begin{cases} 1 & \text{for} \quad k = 1, \\ 1/2 & \text{for} \quad k = 2, \\ 1/6 & \text{for} \quad k = 3, \end{cases}$$

Example 19

we have aperiodic maternity function and the Euler-Lotka equation is

$$\frac{1}{4}\frac{1}{\lambda}+\frac{1}{\lambda^3}=0,$$

yielding $\lambda_0 = 1.09$, $\lambda_{1,2} = -0.42 \pm 0.86i$ with $|\lambda_{1,2}| = 0.957$.

Hence, the single positive root is dominant.

McKendrick–von Foerster model.

From discrete Leslie model to continuous McKendrick–von Foerster model. In the classical Leslie model the census is taken in equal intervals taken, for convenience, to be also a unit of time. If the time between censuses and the length of each age class are, instead, taken to be $h > 0$ then, starting from some time t the Leslie model would take the form

$$\begin{pmatrix} x_0(t+h) \\ x_h(t+h) \\ x_{2h}(t+h) \\ \vdots \\ x_{(n-1)h}(t+h) \end{pmatrix}$$

$$= \begin{pmatrix} f_0(h) & f_h(h) & \cdots & f_{(n-2)h}(h) & f_{(n-1)h}(h) \\ s_0(h) & 0 & \cdots & 0 & 0 \\ 0 & s_h(h) & \cdots & 0 & 0 \\ \vdots & \vdots & \ldots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{(n-2)h}(h) & 0 \end{pmatrix} \begin{pmatrix} x_0(t) \\ x_h(t) \\ x_{2h}(t) \\ \vdots \\ x_{(n-1)h}(t) \end{pmatrix}. \tag{44}$$

The maximal age of individuals $\omega = nh$ is thus divided into n age intervals $[0, h), [h, 2h) \ldots [(n-1)h, nh)$ with the convention that if the age a of an individual is in $[kh, (k+1)h)$, it is considered to be kh. In this definition, as in the discrete case, nobody actually lives till ω. Thus, $x_a(t)$ denotes the number of individuals of age a, $s_a = l_{a+h}/l_a$ is the probability of survival to the age of $a + h$ conditioned upon surviving up to age a with $l_0 = 1$ and $f_a = m_{a+h}s_h$ is the effective fecundity with m_{a+h} being the average fertility of females of age $a + h$. We note that $1 - s_a$ is the number of individuals who do not survive from a to $a + h$.

We make the following assumptions and notation: for any $a \geq 0$

$$\lim_{h\to 0^+} s_a(h) = s_a(0) = 1, \tag{45}$$

$$\lim_{h\to 0^+} \frac{1 - s_a(h)}{h} = \mu(a), \tag{46}$$

$$\lim_{h\to 0^+} \frac{f_a(h)}{h} = \beta(a). \tag{47}$$

To explain these assumptions, we note that

- the probability of survival over a very short period of time should be close to 1, as in Eq. (45),
- if the death rate μ is constant, then the probability of surviving over a short time interval h approximately is $s_a(h) = 1 - \mu h$ for any a and thus the limit in Eq. (46) can serve as a more general definition of the age dependant death rate,
- if the average number of births per female over a unit time is a constant β, then the number of births over h will be βh and the last equation gives the general definition of the age dependent birth rate which, moreover, is independent of the survival rate by Eq. (45).

Finally, we assume that there is a density function $p(a, t)$

$$x_a(t) = \int\limits_a^{a+h} p(\alpha, t) d\alpha. \tag{48}$$

We are going to derive a differential equation for p. Consider a fixed age $a = ih > 0$. From (44) we see that

$$x_{a+h}(t+h) = s_a(h) x_a(t), \qquad a = 0, h, \ldots, (n-2)h. \tag{49}$$

Using (48),

$$x_{a+h}(t+h) = \int\limits_{a+h}^{a+2h} p(\alpha, t+h) d\alpha = \int\limits_a^{a+h} p(\alpha + h, t+h) d\alpha.$$

Thus (49) can be written as

$$\int_a^{a+h} p(\alpha + h, t + h) d\alpha = s_a(h) \int_a^{a+h} p(\alpha, t) d\alpha.$$

We re-write it as

$$\frac{1}{h}\left(\int_a^{a+h} p(\alpha + h, t + h) d\alpha - \int_a^{a+h} p(\alpha, t) d\alpha\right)$$
$$= -\frac{1 - s_a(h)}{h} \int_a^{a+h} p(\alpha, t) d\alpha.$$

Assuming that the directional derivative

$$Dp(a,t) = \lim_{h\to 0^+} \frac{p(a+h,t+h) - p(a,t)}{h}$$

exists, under some technical assumptions we can pass to the limit above, arriving, by (46), at

$$Dp(a,t) = -\mu(a)p(a,t), \qquad a > 0, t > 0.$$

Assuming that the partial derivatives $\partial_t p, \partial_a p$ at (a,t) exist, we can further transform the last equation to

$$\partial_t p(a,t) + \partial_a p(a,t) = -\mu(a)p(a,t), \qquad a > 0, t > 0.$$

This is the most commonly used form of the equation for p though, as we shall see later, not the best for its analysis and, in fact, false in many cases.

Now consider the class of neonates in the Leslie formulation:

$$x_0(t+h) = \sum_{j=0}^{n-1} f_{jh} x_{jh}(t),$$

which can be rewritten as

$$\frac{1}{h} x_0(t+h) = \sum_{j=0}^{n-1} \frac{1}{h} f_{jh}(h) \frac{1}{h} x_{jh}(t) h.$$

Now, if p is continuous and f is differentiable at 0, then

$$\frac{1}{h} x_{jh}(t) = \frac{1}{h} \int\limits_{jh}^{(j+1)h} p(\alpha, t) d\alpha = p(jh + \theta_j h), \quad \frac{f_{jh}(h)}{h} = \beta(jh + \theta_j' h).$$

for some $0 < \theta_j, \theta_j' < 1$.

Thus

$$p(\theta_j h, t) = \sum_{j=0}^{n-1} p(jh + \theta_j h)\beta(jh + \theta_j' h)h.$$

If we further assume that β is a continuous function, then the right hand side is the Riemann sum and we can pass to the limit as $h \to 0^+$ getting

$$p(0, t) = \int\limits_0^\omega \beta(\alpha)p(\alpha, t)d\alpha.$$

Thus, we have the classical formulation of the McKendrick–von Foerster model

$$\begin{aligned} \partial_t p(a,t) + \partial_a p(a,t) &= -\mu(a)p(a,t), \qquad a>0, t>0, && (50)\\ p(0,t) &= \int\limits_0^{\omega} \beta(\alpha)p(\alpha,t)d\alpha, t>0, && (51)\\ p(a,0) &= p_0(a), && (52) \end{aligned}$$

where the last equation provides the initial distribution of the population.

If $\omega < +\infty$, then we have to ensure that $p(a, t) = 0$ for $t \geq 0, a \geq \omega$, which can be done either by imposing an additional boundary condition on p, or by introducing assumptions on the coefficients which ensure that no individual survives beyond ω. If $\omega = \infty$ then, instead of such an additional condition, we impose some requirements on the behaviour of the solution at ∞, e.g., that they are integrable over $[0, \infty)$.

Linear constant coefficient case. Before we embark on more advanced analysis of (50)–(52), let us get a taste of the structure of the problem by solving the simplest case with $\mu(a) = \mu$ and $\beta(a) = \beta$:

$$\partial_t p(a,t) + \partial_a p(a,t) = -\mu p(a,t). \tag{53}$$

coupled with the boundary condition

$$p(0,t) = \beta \int\limits_0^\infty p(a,t)da,$$

and the initial condition

$$p(a,0) = \mathring{p}(a),$$

First, let us simplify the equation (53) by introducing the integrating factor

$$\partial_t(e^{\mu a}p(a,t)) = -\partial_a(e^{\mu a}p(a,t))$$

and denote $u(a,t) = e^{\mu a}p(a,t)$. Then

$$u(0,t) = p(0,t) = \beta\int\limits_0^\infty e^{-\mu a}u(a,t)da$$

with $u(a,0) = e^{\mu a}\mathring{p}(a) =: \mathring{u}(a)$. Now, if we knew $\psi(t) = u(0,t)$, then

$$u(a,t) = \begin{cases} \mathring{u}(a-t), & t < a, \\ \psi(t-a), & a < t. \end{cases} \qquad (54)$$

The boundary condition can be rewritten as

$$\begin{aligned}
\psi(t) &= \beta \int_0^\infty e^{-\mu a} u(a,t)da \\
&= \beta \int_0^t e^{-\mu a}\psi(t-a)da + \beta \int_t^\infty e^{-\mu a}\mathring{u}(a-t)da \\
&= \beta e^{-\mu t} \int_0^t e^{\mu\sigma}\psi(\sigma)d\sigma + \beta e^{-\mu t}\int_0^\infty e^{-\mu r}\mathring{u}(r)dr
\end{aligned}$$

which, upon denoting $\phi(t) = \psi(t)e^{\mu t}$ and using the original initial value, can be written as

$$\phi(t) = \beta \int_0^t \phi(\sigma)d\sigma + \beta \int_0^\infty \mathring{n}(r)dr. \qquad (55)$$

Now, if we differentiate both sides, we get

$$\phi' = \beta\phi,$$

which is just a first order linear equation. Letting $t = 0$ in (55), we obtain the initial value for ϕ: $\phi(0) = \beta \int\limits_0^\infty \mathring{p}(r)dr$. Then

$$\phi(t) = \beta e^{\beta t} \int\limits_0^\infty \mathring{p}(r)dr$$

and

$$\psi(t) = \beta e^{(\beta-\mu)t} \int\limits_0^\infty \mathring{p}(r)dr.$$

Then

$$p(a,t) = e^{-\mu a}u(a,t) = e^{-\mu t}\begin{cases} \mathring{p}(a-t), & t<a, \\ \beta e^{\beta(t-a)}\int\limits_0^\infty \mathring{p}(r)dr, & a<t. \end{cases}$$

Observe that

$$\lim_{a\to t^+} p(a,t) = \mathring{p}(0)$$

and

$$\lim_{a\to t^-} p(a,t) = \beta\int\limits_0^\infty \mathring{p}(r)dr,$$

so that the solution is continuous, let alone differentiable, only if the initial condition satisfies the following compatibility condition

$$\mathring{p}(0) = \beta\int\limits_0^\infty \mathring{p}(r)dr. \tag{56}$$

Thus, as we noted earlier, we must be very careful with using (50)-(52) in the differential form and interpreting the solution.

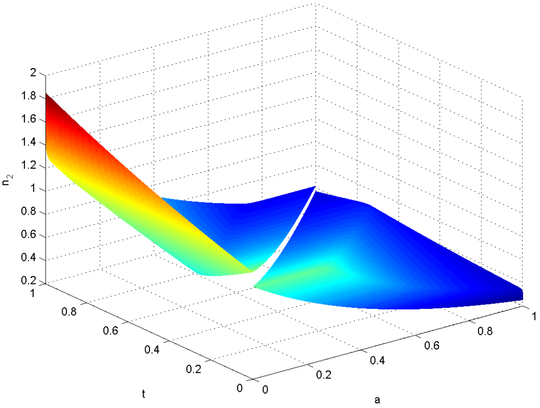

Figure: Discontinuity of the population density $p(a,t)$.

General linear McKendrick-von Foerster problem. The ideas used to solve the McKendrick-von Foerster case in the constant coefficient case can be also used in more general situations but, unfortunately, the resulting integral equation (55) cannot be explicitly solved. Before, however, we discuss the solvability of more general cases, let us introduce certain functions related to (50)-(52), which are relevant to the population dynamics.

Consider again the general McKendrick problem

$$\begin{aligned}
&\partial_t p(a,t) + \partial_a p(a,t) = -\mu(a)p(a,t)\\
&p(0,t) = \int\limits_0^\omega \beta(\alpha)p(\alpha,t)d\alpha,\\
&p(a,0) = \mathring{p}(a).
\end{aligned}$$

We recall that $\beta(a)$ is the *age specific fertility* which can be defined as the number of newborns, in one time unit, coming from a single individual whose age is in the small time age interval $[a, a + da)$. So, the number of births coming from all individuals in the population aged between a_1 and a_2 in a one time unit is

$$\int\limits_{a_1}^{a_2} \beta(\alpha)p(\alpha, t)da$$

and we can define the *total birth rate* as

$$B(t) = \int\limits_{0}^{\omega} \beta(\alpha)p(\alpha, t)da$$

which gives the total number of newborns in a unit time (ω is the maximum age in the population).

Let us consider the death rate $\mu(a)$, which is average number of deaths per unit of population aged a. We can relate $\mu(a)$ to a number of vital characteristics of the population. Similarly to the discrete case, we introduce the *survival probability* $S(a)$ as the proportion of the initial population surviving to age a. We can relate μ and S by the following argument.

Consider a population beginning with $\mathring{p}$ individuals of age 0. Then $\mathring{p}(a)S(a)(= p(a))$ is the average number of individuals that survived to age a. The decline in the population over a short age period $[a, a + da]$ is $\mathring{p}(a)S(a) - \mathring{p}(a)S(a + da)$. On the other hand, this decline can only be attributed to deaths: if the death rate is μ, then in this age interval we will have approximately $\mathring{p}(a)S(a)\mu(a)da$ deaths. Equating and passing to the limit as $da \to 0$ yields

$$\frac{dS}{da} = -S\mu$$

or

$$S(a) = S(0)e^{-\int\limits_0^a \mu(\sigma)d\sigma} = e^{-\int\limits_0^a \mu(\sigma)d\sigma},$$

since the probability of surviving to age 0 is 1.

We note that if no individuals can survive beyond ω, we must have $S(\omega) = 0$ or, equivalently,

$$\int_0^{\omega} \mu(\sigma) d\sigma = \infty. \tag{57}$$

These considerations can be used to find the average life span of individuals in the population. In fact, the average life span is the mean value of the length of life in the population, which can be expressed as

$$L = \int_0^\omega a p(a) da,$$

where $p(a)$ is the probability (density) of an individual dying at age a. We approximate the integral as the Riemann sum

$$L \approx \sum_i a_i p(a_i) \Delta a_i$$

where $p(a_i)$ is the probability that an individual survived till the age a_i and died at this age.

Thus

$$p(a_i) = S(a_i)\mu(a_i).$$

We note that $S(a)\mu(a)$ is, indeed, a probability density. Thus

$$L = \int\limits_0^\omega a\mu(a)e^{-\int\limits_0^a \mu(s)ds}da = -\int\limits_0^\omega a\frac{d}{da}e^{-\int\limits_0^a \mu(s)ds}da = \int\limits_0^\omega S(a)da$$

where we used integration by parts and $S(\omega) = 0$.

Further, we introduce

$$K(a) = \beta(a)S(a) \tag{58}$$

which is called the *maternity function* and describes the rate of birth relative to the surviving fraction of the population and is the continuous equivalent to the coefficients $f_0, f_1, \ldots, f_{n-1}$. Further, we define

$$R = \int\limits_0^\omega \beta(a)S(a)da \tag{59}$$

and call it the *net reproduction rate* of the population. It is the expected number of offspring produced by an individual during her life.

Solution of general McKendrick-von Foerster model. One of the easiest way of analysing the general model

$$\begin{aligned} &\partial_t p(a,t) + \partial_a p(a,t) = -\mu(a)p(a,t) \\ &p(0,t) = \int\limits_0^{\omega} \beta(a)p(a,t)da, \\ &p(a,0) = \mathring{p}(a), \end{aligned} \tag{60}$$

is to reduce it to an integral equation in the same way as for the constant coefficient case, though the technicalities are slightly more involved due to age dependence of the mortality and maternity functions.

First, we simplify (60) by introducing the integrating factor

$$\partial_t \left(e^{\int\limits_0^a \mu(\sigma)d\sigma} p(a,t) \right) = -\partial_a \left(e^{\int\limits_0^a \mu(\sigma)d\sigma} p(a,t) \right) \qquad (61)$$

and denote $u(a,t) = e^{\int\limits_0^a \mu(\sigma)d\sigma} p(a,t)$. Then

$$u(0,t) = p(0,t) = \int\limits_0^\omega \beta(a) e^{-\int\limits_0^a \mu(\sigma)d\sigma} u(a,t)da = \int\limits_0^\omega K(a)u(a,t)da,$$

where we recognized that the kernel in the integral above is the maternity function introduced in (58).

Further, $u(a,0) = e^{\int\limits_0^a \mu(s)ds} \mathring{p}(a) =: \mathring{u}(a)$. Also, the right hand side defines the total birth rate $B(t)$.

Now, if we knew $B(t) = u(0,t)$, then

$$u(a,t) = \begin{cases} \mathring{u}(a-t), & t < a, \\ B(t-a), & a < t. \end{cases} \tag{62}$$

The boundary condition can be rewritten as

$$\begin{aligned} B(t) &= \int\limits_0^\infty \beta(a) e^{-\int\limits_0^a \mu(\sigma)d\sigma} u(a,t)da \\ &= \int\limits_0^t \beta(a) e^{-\int\limits_0^a \mu(\sigma)d\sigma} B(t-a)da + \int\limits_t^\infty \beta(a) e^{-\int\limits_0^a \mu(\sigma)d\sigma} \mathring{u}(a-t)da \\ &= \int\limits_0^t K(t-a)B(a)da + \int\limits_0^\infty \beta(a+t) e^{-\int\limits_0^{a+t} \mu(\sigma)d\sigma} e^{\int\limits_0^a \mu(s)ds} \mathring{p}(a)da, \end{aligned}$$

where to shorten notation we extended coefficients by zero beyond $a = \omega$.

Summarizing, we arrived at the integral equation for the total birth rate

$$B(t) = \int_0^t K(t-a)B(a)da + G(t) \tag{63}$$

where

$$G(t) = \int_0^\infty \beta(a+t)\frac{S(a+t)}{S(a)}\mathring{p}(a)da, \tag{64}$$

is a known function.

Explicitly, we have

$$\begin{aligned} B(t) &= \int_0^t K(t-a)B(a)da + \int_0^{\omega-t} \beta(a+t)\frac{S(a+t)}{S(a)}\mathring{p}(a)da \\ &= \int_0^t K(t-a)B(a)da + \int_t^{\omega} \beta(a)\frac{S(a)}{S(a-t)}\mathring{p}(a-t)da, \quad (65) \end{aligned}$$

for $0 \leq t \leq \omega$, and

$$B(t) = \int_0^{\omega} K(t-a)B(a)da \quad (66)$$

for $t > \omega$.

This equation cannot be solved explicitly and we have to use more abstract approach. For this we have to introduce a proper mathematical framework. As in the discrete case, the natural norm will be

$$\|p\|_1 = \int_0^{\omega} |p(\alpha)| d\alpha$$

which in the current context, with $p \geq 0$ being the density of the population distribution with respect to age, is the total population. Thus, the state space is the space $X_0 = L_1([0, \omega))$ of Lebesgue integrable functions on $[0, \omega)$.

Since we are dealing with functions of two variables, we often consider $(a,t) \to p(a,t)$ as a function $t \to u(t,\cdot)$, that is, for each t the value of this function is a function with argument a. For such functions, we consider the space $C([0,T], L_1([0,\omega]))$ of $L_1([0,\omega])$-valued continuous functions. For functions f bounded on $[0,\omega]$ we introduce $\|f\|_\infty = \sup_{0\leq a\leq\omega}|f(a)|$.

We make the following assumptions.

(i)

$$\beta \geq 0 \text{ is bounded on } [0, \omega], \tag{67}$$

(ii)

$$0 \leq \mu \in L_1([0, \omega']) \text{ for any } \omega' < \omega \tag{68}$$

with

$$\int_0^\omega \mu(\alpha) d\alpha = \infty, \tag{69}$$

(iii)

$$0 \leq \mathring{p} \in L_1([0, \omega]). \tag{70}$$

Now, if (67)-(70) are satisfied, then we can show that K is a non-negative bounded function which is zero for $t \geq \omega$ and G is a continuous function which also is zero for $t \geq \omega$. If, additionally

$$\mathring{p} \in W^{1,1}([0,\omega]) \quad \text{and} \quad \mu\mathring{p} \in L_1([0,\omega]), \tag{71}$$

(here by W_1^1 we denote the Sobolev space of functions from L_1 with generalized derivatives in L_1), then G is differentiable with bounded derivative. Indeed, let us look at G for $t < \omega$

$$G(t) = \int\limits_t^\omega \beta(a)\frac{S(a)}{S(a-t)}\mathring{p}(a-t)da = \int\limits_t^\omega \beta(a)e^{-\int\limits_{a-t}^{a}\mu(s)ds}\mathring{p}(a-t)da$$

If we formally differentiate using the Leibnitz rule, we get

$$\begin{aligned} G'(t) &= -\beta(t)S(t)\mathring{p}(0) + \int\limits_t^{\omega} \beta(a) e^{-\int\limits_{a-t}^{a} \mu(s)ds} \mu(a-t)\mathring{p}(a-t)da \\ &+ \int\limits_t^{\omega} \beta(a) e^{-\int\limits_{a-t}^{a} \mu(s)ds} \mu(a-t)\mathring{p}'(a-t)da \end{aligned}$$

so we see that for existence of the integrals we need integrability of $\mu\mathring{p}$ and differentiability of $\mathring{p}$. Then we can prove the main result

Theorem 20

If (67)-(70) are satisfied, then (63) has a unique continuous and nonnegative solution. If, additionally, (71) is satisfied that B then B is differentiable with B' bounded on bounded intervals.

Proof.

We define iterates

$$\begin{array}{rcl} B_0(t) & = & G(t), \\ B^{k+1}(t) & = & G(t) + \int\limits_0^t K(t-s)B^k(s)ds. \end{array} \qquad (72)$$

Take $T > 0$. Then, for any $t \in [0, T]$ we have

$$|B^1(t) - B^0(t)| = \int\limits_0^t |K(t-s)F(s)|ds \leq tK_mF_m$$

where $K_m = \sup_{0\leq t\leq T} |K(s)|$ and $L_m = \sup_{0\leq t\leq T} |F(s)|$. Then

$$|B^2(t) - B^1(t)| \leq K_m \int\limits_0^t |B^1(s) - B^0(s)|ds \leq \frac{K_m^2F_m}{2}t^2$$

and, by induction,

$$|B^{k+1}(t)-B^k(t)| \leq K_m \int\limits_0^t |B^k(s)-B^{k-1}(s)|ds \leq \frac{K_m^{k+1}F_m}{(k+1)!}t^{k+1}. \tag{73}$$

Further

$$\lim_{k\to\infty} B^{k+1}(t) = G(t) + \lim_{k\to\infty}\sum_{i=0}^{k}(B^{i+1}(t)-B^i(t))$$

with

$$\begin{aligned}\sup_{0\leq t\leq T}\left|\sum_{i=0}^{k}(B^{i+1}(t)-B^i(t))\right| &\leq \sum_{i=0}^{k}\sup_{0\leq t\leq T}\left|B^{i+1}(t)-B^i(t)\right| \\ &\leq F_m\sum_{i=0}^{k}\frac{(TK_m)^{k+1}}{(k+1)!}.\end{aligned}$$

The series on the right hand side converges to $F_m e^{TK_m}$ and thus $(B^k(t))_{k\geq 0}$ converges uniformly to a continuous solution B of (63). Uniqueness follows by the Gronwall inequality.

If, in addition, (71) is satisfied, then B^k can be differentiated with respect to t and the functions

$$V^k := \frac{d}{dt}B^k$$

satisfy the recurrence

$$V^{k+1}(t) = F'(t) + K(t)F(0) + \int\limits_0^t K(t-s)V^k(s)ds,$$

which converges uniformly to some continuous function V which, by the theorem of uniform convergence of derivatives, must be the derivative of B. □

Once we have B, we can recover p by (90) and back substitution

$$p(a,t) = e^{-\int\limits_0^a \mu(\sigma)d\sigma} u(a,t) = \begin{cases} \frac{S(a)}{S(a-t)}\mathring{p}(a-t), & t < a, \\ S(a)B(t-a), & a < t. \end{cases} \tag{74}$$

Thus, if (71) is satisfied in addition to (67)-(70), then it is easy to see that p defined above satisfies the equation (50) everywhere except the line $a = t$. Along this line we have, as before,

$$\lim_{a\to t^+} p(a,t) = S(0)\mathring{p}(0) = \mathring{p}(0)$$

and

$$\lim_{a\to t^-} p(a,t) = S(0)B(0) = \int\limits_0^\omega \beta(a)\mathring{p}(a)da.$$

To ensure at least continuity of the solution we need to assume the compatibility condition

$$\mathring{p}(0) = \int_0^\omega \beta(a)\mathring{p}(a)da. \tag{75}$$

We note that if a function is continuous at a point and differentiable in both one sided neighbourhoods, then it is a Lipschitz function and it is in fact differentiable almost everywhere (in the sense that the function can be recovered from its derivative). On the other hand, if a function has a jump at a point, then its derivative at this point is of a Dirac delta type. Thus, we can state that if (75) is satisfied, then the solution is continuous and satisfies (50) almost everywhere.

If we do not assume (75) then we can still claim that the solution satisfies

$$\begin{aligned} Dn(a,t) &= \lim_{h\to 0^+} \frac{p(a+h,t+h)-p(a,t)}{h} \\ &= -\mu(a)p(a,t),\ a>0, t>0. \end{aligned}$$

Furthermore, both the birth rate B and the solution p itself grow at most at an exponential rate. Consider again (63)

$$B(t) = \int\limits_0^t K(t-a)B(a)da + G(t),$$

with G given by (64),

$$S(a) = e^{-\int\limits_0^a \mu(\sigma)d\sigma},$$

and $K(a) = \beta(a)S(a)$, we see that $K(t) \leq \|\beta\|_\infty$ and $G(t) \leq \|\beta\|_\infty \|\mathring{p}\|_1$ so that

$$B(t) \le \max_{0\le a\le\omega}\beta(a)\int\limits_0^t B(s)ds + \max_{0\le a\le\omega}\beta(a)\int\limits_0^\omega \mathring{p}(s)ds$$

$$=: \|\beta\|_\infty \int\limits_0^t B(s)ds + \|\beta\|_\infty\|\mathring{p}\|_1,$$

which, by Gronwall's inequality, yields

$$B(t) \le \|\beta\|_\infty\|\mathring{p}\|_1 e^{t\|\beta\|_\infty}. \tag{76}$$

This gives the estimate for p:

$$\begin{aligned}\|p(\cdot,t)\|_1 &\leq \int\limits_0^t B(t-s)S(s)ds + \int\limits_t^\infty \frac{S(s)}{S(s-t)}\mathring{p}(s-t)ds \\ &\leq \|\beta\|_\infty \|\mathring{p}\|_1 \left(\int\limits_0^t e^{(t-s)\|\beta\|_\infty} ds + 1\right),\end{aligned}$$

where we used $S(s)/S(s-t) \leq 1$. Then, by integration

$$\|p(\cdot,t)\|_1 \leq \|\mathring{p}\|_1 + \|\mathring{p}\|_1 e^{t\|\beta\|_\infty}(1 - e^{-t\|\beta\|_\infty}) = \|\mathring{p}\|_1 e^{t\|\beta\|_\infty}. \quad (77)$$

Long time behaviour of the solution – the constant coefficients case. Consider again the constant coefficient problem

$$\begin{aligned} &\partial_t p(a,t) + \partial_a p(a,t) = -\mu p(a,t) \\ &p(0,t) = \beta \int\limits_0^\infty p(a,t)da, \\ &p(a,0) = \mathring{p}(a) \end{aligned}$$

with the solution

$$p(a,t) = e^{-\mu t} \begin{cases} \mathring{p}(a-t), & t < a, \\ \beta e^{\beta(t-a)} \int\limits_0^\infty \mathring{p}(r)dr, & a < t \end{cases}$$

and ask what happens with the population as $t \to \infty$.

Clearly, for large t we can consider only the second part of the solution

$$p(a,t) = \beta P_0 e^{-\beta a} e^{t(\beta-\mu)}, \quad a < t,$$

where $P_0 = \int\limits_0^{\infty} \mathring{p}(r)dr$. Denote by $r = \beta - \mu$ the net growth rate. We see that if $r = 0$, we have

$$p(a,t) = \beta P_0 e^{-\mu a}, \quad a < t,$$

and one can surmise that

$$p(a,t) \approx \beta P_0 e^{-\beta a},$$

for large t and all $a > 0$.

If we assume that $\mathring{p}$ is bounded, this can be easily checked. Indeed

$$p(a,t) = \begin{cases} e^{-\mu t}\mathring{p}(a-t), & t < a, \\ \beta e^{-\mu a} P_0, & a < t \end{cases}$$

$$= \beta e^{-\mu a} P_0 + \begin{cases} -\beta e^{-\mu a} P_0 + e^{-\mu t}\mathring{p}(a-t), & t < a, \\ 0, & a < t \end{cases}$$

and, since for $t < a$, $e^{-\mu a} < e^{-\mu t}$, we have

$$|-\beta e^{-\mu a} P_0 + e^{-\mu t}\mathring{p}(a-t)| \leq C e^{-\mu t}$$

where $C = \max\{\beta P_0, \sup|\mathring{p}|\}$. In other words

$$p(a,t) = \beta e^{-\mu a} P_0 + O(e^{-\mu t}). \tag{78}$$

So we see that for large t the solution has the shape of $\beta e^{-\mu a}$, independent of the initial data, multiplied by the scalar P_0. Thus, the shape of the solution is practically not affected by the initial age distribution. In other words, the age distribution of the population after long time is the same independently of the initial age distribution.

Even if $r \neq 0$, we can write

$$e^{-rt} p(a,t) = \beta P_0 e^{-\beta a}, \quad a < t,$$

and, as before,

$$e^{-rt}p(a,t) = \begin{cases} e^{-\beta t}\mathring{p}(a-t), & t < a, \\ \beta e^{-\beta a}P_0, & a < t, \end{cases}$$

$$= \beta e^{-\mu a}P_0 + \begin{cases} -\beta e^{-\beta a}P_0 + e^{-\beta t}\mathring{p}(a-t), & t < a, \\ 0, & a < t, \end{cases}$$

and, since for $t < a$, $e^{-\beta a} < e^{-\beta t}$, we have

$$|-\beta e^{-\beta a}P_0 + e^{-\beta t}\mathring{p}(a-t)| \leq Ce^{-\beta t}$$

where $C = \max\{\beta P_0, \|\mathring{p}\|_\infty\}$.

In other words

$$p(a,t) = P_0 e^{rt} \beta e^{-\beta a} + O(e^{-\mu t}). \tag{79}$$

where we used $e^{rt}e^{-\beta t} = e^{-\mu t}$. Hence, the population is described by the Malthusian part $P_0 e^{rt}$, which is independent of the age profile of the population, multiplied by the age profile $\beta e^{-\beta a}$. The profile is called the *stable age distribution* and we recognize the *asynchronous exponential growth property*. In what follows we shall prove that this property holds for general McKendrick-von Foerster model.

However, before we move to more general models, we provide another way of deriving the stable age distribution. Let us consider the eigenvalue problem for (53)

$$\begin{aligned} \lambda p(a) + p'(a) &= -\mu p(a) \\ p(0) &= \beta \int\limits_0^\infty p(a)da. \end{aligned} \tag{80}$$

The first equation is a linear equation with the general solution

$$p(a) = Ce^{-(\mu+\lambda)a}$$

while the nonlocal initial condition yields

$$1 = \beta \int\limits_0^\infty e^{-(\mu+\lambda)a}da$$

where we cancelled the constant C.

This is an example of the Lotka renewal equation. In our case, we solve it explicitly. Integration gives

$$1 = \frac{\beta}{\mu + \lambda} \tag{81}$$

or

$$\lambda = \beta - \mu = r$$

and

$$p(a) = Ce^{-\beta a}.$$

So, the unique eigenvalue of (85) is (in this case) precisely the net growth rate. This eigenvalue is simple and the corresponding eigenvector is the stable age distribution. As we shall see, this is not a coincidence.

Long time behaviour–general case. By (76), we can apply the Laplace transform to analyse (63). The Laplace transform of an exponentially bounded integrable function f is defined by

$$\hat{f}(\lambda) = (\mathcal{L}f)(\lambda) = \int\limits_0^\infty e^{-\lambda t} f(t)dt,$$

and $\hat{f}$ is defined and analytic in a right half-plane (determined by the rate of growth of f) of the complex plane $\mathbb{C}$. In the case of B, (76) shows that $\hat{B}(\lambda)$ is analytic in $\Re\lambda > \|m\|_\infty$. For our applications it is also important to note that if the f is only non-zero over a finite interval $[a, b]$, then its Laplace transform is defined and analytic everywhere in $\mathbb{C}$. Such functions are called entire.

Moreover, we also use $\hat{f}(\lambda) \to 0$ as $|\lambda| \to \infty$ in any closed strip contained in the domain of analyticity of $\hat{f}$.

We use the property of the Laplace transform that the convolution is transformed into the algebraic product of transforms; that is, for the convolution

$$(f * g)(t) = \int\limits_0^t f(t-s)g(s)ds = \int\limits_0^t f(s)g(t-s)ds,$$

using the definition of the Laplace transform and changing the order of integration, we obtain

$$[\mathcal{L}(f * g)](\lambda) = (\mathcal{L}f)(\lambda) \cdot (\mathcal{L}g)(\lambda). \tag{82}$$

With this result, (63) yields

$$\hat{B}(\lambda) = \hat{B}(\lambda)\hat{K}(\lambda) + \hat{G}(\lambda). \tag{83}$$

Hence,

$$\hat{B}(\lambda) = \frac{\hat{G}(\lambda)}{1 - \hat{K}(\lambda)} = \hat{G}(\lambda) + \frac{\hat{G}(\lambda)\hat{K}(\lambda)}{1 - \hat{K}(\lambda)} \tag{84}$$

As we noted above, $\hat{G}$ is an entire function so the only singularities of $\hat{B}$ are due to zeroes of $1 - \hat{K}$. Since $\hat{K}$ is an entire function, these zeroes are isolated of finite order (thus giving rise to poles of $\hat{B}$ and with no finite accumulation point).

However, there may be infinitely many of them and this requires some care with handling the inverse. We know that if $\hat{f}$ is the Laplace transform of a continuous function f, then

$$f(t) = \frac{1}{2\pi i}\int\limits_{c-i\infty}^{c+i\infty} e^{\lambda t}\hat{f}(\lambda)d\lambda$$

where we integrate along a line in the domain of analyticity of $\hat{f}$.

Let us look closer at the equation

$$\hat{K}(\lambda) = 1, \tag{85}$$

or, explicitly,

$$\int\limits_0^\infty \beta(a)e^{-\lambda a-\int\limits_0^a \mu(\sigma)d\sigma} da = 1, \quad \lambda \in \mathbb{C}. \tag{86}$$

Remark 1

We observe that (86) is a continuous copy of the discrete renewal equation (39) if one replaces λ of the latter by e^{λ}. However, as we shall see below, continuous case does not admit any cyclic behaviour.

Theorem 21

Equation (85) has exactly one real root, $\lambda = \lambda_0$*, of algebraic multiplicity 1. All other roots* λ_j *of (85) occur as complex conjugates (real root is its own conjugate). Moreover,* $\Re\lambda_j < \lambda_0$ *for any* j*, there could be only denumerable number of them and, in each strip* $a < \Re\lambda < b$*, there is at most a finite number of them.*

Proof.

We introduce the real function

$$\psi(\lambda) = \int\limits_0^\infty e^{-\lambda a} K(a)da$$

for $\lambda \in \mathbb{R}$. We note that this function is well defined on $\mathbb{R}$ since K is non zero only on a finite interval. Also, because of this, it is continuous and differentiable, see Remark 2 below. Then

$$\begin{aligned} \lim_{\lambda\to-\infty} \psi(\lambda) &= \infty, \\ \lim_{\lambda\to\infty} \psi(\lambda) &= 0. \end{aligned}$$

Moreover,

$$\begin{aligned} \psi'(\lambda) &= -\int\limits_{\alpha}^{\beta} ae^{-\lambda a}K(a)da < 0, \\ \psi''(\lambda) &= \int\limits_{\alpha}^{\beta} a^2e^{-\lambda a}K(a)da > 0, \end{aligned}$$

so that ψ is strictly decreasing and concave up function. Since it is continuous, it takes on every positive value exactly once. Thus, in particular, there is exactly one real value λ_* satisfying (85).

Suppose $\lambda = u + iv$ is a root of (85). Then

$$1 = \int\limits_0^\infty e^{-va}(\cos(-ua) + i\sin(-ua))K(a)da$$

and, taking the real and imaginary part,

$$\begin{aligned}\int\limits_0^\infty e^{-va}K(a)\cos ua\,da &= 1,\\ \int\limits_0^\infty e^{-va}K(a)\sin ua\,da &= 0.\end{aligned}$$

We observe that these two equations are invariant under the change $v \to -v$ so that $\bar{\lambda} = u - iv$ also satisfies (85).

To prove the second part, we note that, since the variable a is continuous, there must be a range of a, say, $[\alpha, \beta]$ over which $\cos ua < 1$. Thus,

$$\int_0^\infty e^{-va}K(a)da > \int_0^\infty e^{-va}K(a)\cos ua\, da = 1.$$

However

$$\int_\alpha^\beta e^{-\lambda_* a}K(a)da = 1,$$

and direct comparison of these two integrals yields $\lambda_* > v = \Re\lambda$.

The last part follows from the fact that since $\hat{K} - 1$ is an entire function, in each bounded set there can be only finitely many zeros of it, by the principle of isolated zeros. Thus, there could be no more than denumerable amount of them in $\mathbb{C}$. Finally, since $\hat{K} \to 0$ as $|\lambda| \to \infty$ in any strip, we also see that there can be only finitely many of them in any vertical strip. $\square$

Remark 2

In the proof above, the continuity of ψ *is a consequence of the boundeness of the support of definition of* K*. In general, if we allow* K *to be nonzero on* $[0,\infty)$*, then the above statement is not true. Consider* $K(a) = c(1+a^2)^{-1}$ *with* $c < 2/\pi$*. Then*

$$\psi(\lambda) = c\int\limits_0^\infty \frac{e^{-\lambda a}}{1+a^2}da$$

then $\psi(\lambda) < 1$ *for* $\lambda \geq 0$ *but* $\psi(\lambda) = \infty$ *for* $\lambda < 0$ *and* $\psi(\lambda) < 1$ *for all* $\lambda \geq 0$ *and Eq. (85) has no real solution.*

Remark 3

In general, if $\omega = \infty$, one has to prove that the range of ψ contains 1. For instance, in the constant coefficient case, ψ is given by (81)

$$\psi(\lambda) = \frac{m}{\lambda + \mu}$$

and though it is discontinuous at $\lambda = -\mu$, its range for $\lambda \in (-\mu, \infty)$ is $\mathbb{R}$ and the argument holds.

Observe that the function ψ crosses the a axis at

$$R := \psi(0) = \int_0^\infty K(a)da \tag{87}$$

which is precisely the net reproductive rate. R must exceed 1 for λ_* to be positive, $R = 1$ if and only if $\lambda_* = 0$ and, finally, $R < 1$ if and only if $\lambda_* < 0$.

Next we shall show that the sign of λ_* indeed determines the long time behaviour of the population.

Let us consider the second term in the last formula of (84)

$$\hat{H}(\lambda) := \frac{\hat{G}(\lambda)\hat{K}(\lambda)}{1-\hat{K}(\lambda)}.$$

We noted that $\hat{G}(\lambda)$ and $\hat{K}(\lambda)$ tend to zero as $|\lambda| \to \infty$ in any half plane $\Re\lambda > \delta$, $\delta \in \mathbb{R}$. Furthermore, on any line $\{\sigma + iy;\ y \in \mathbb{R}\}$ which does not meet any root of (85), we have $\inf_{y\in\mathbb{R}} |1-\hat{K}(\sigma+iy)| > 0$ and

$$\int\limits_{-\infty}^{\infty} \left| \frac{\hat{G}(\sigma+iy)\hat{K}(\sigma+iy)}{1-\hat{K}(\sigma+iy)} \right| dy < \infty. \tag{88}$$

This follows from the fact that any finitely supported function, multiplied by $e^{-\sigma t}$ is an L_2 function and thus its Laplace transform, treated as the Fourier transform, is in L_2 with respect to y. Then the result follows from the Plancherel theorem.

Inverting $\hat{H}(\lambda)$ we have

$$H(t) = \frac{1}{2\pi i}\int\limits_{\sigma-i\infty}^{\sigma+i\infty} \frac{\hat{G}(\sigma+iy)\hat{K}(\sigma+iy)}{1-\hat{K}(\sigma+iy)} e^{(\sigma+iy)t}dy$$

for any $\sigma > \lambda_*$. Hence

$$B(t) = G(t) + H(t).$$

To estimate $H(t)$ we note that, by properties of $\hat{H}$, we can shift the line of integration to $\{\sigma_1 + iy;\ y \in \mathbb{R}\}$ where $\Re\lambda_1 < \sigma_1 < \lambda_*$ and λ_1 is the eigenvalue with the largest real part less than λ_*.

Then the Cauchy theorem gives

$$H(t) = H_1(t) + H_2(t)$$

where

$$H_1(t) = res_{\lambda=\lambda_*} \frac{e^{\lambda t}\hat{G}(\lambda)\hat{K}(\lambda)}{1-\hat{K}(\lambda)} = \lim_{\lambda\to\lambda_*}(\lambda - \lambda_*)\frac{e^{\lambda t}\hat{G}(\lambda)\hat{K}(\lambda)}{1-\hat{K}(\lambda)} = B_0 e^{\lambda_* t},$$

with

$$B_0 = \frac{\int\limits_0^\infty e^{-\lambda_* a}G(a)da}{\int\limits_0^\infty ae^{-\lambda_* a}K(a)da}$$

and

$$H_2(t) = \frac{1}{2\pi i}\int\limits_{\sigma_1 - i\infty}^{\sigma_1 + i\infty} \frac{\hat{G}(\sigma_1+iy)\hat{K}(\sigma_1+iy)}{1-\hat{K}(\sigma_1+iy)}e^{(\sigma_1+iy)t}dy.$$

The function H_2 satisfies the estimate

$$|H_2(t)| \leq \frac{e^{\sigma_1 t}}{2\pi} \int\limits_{\sigma_1 - i\infty}^{\sigma_1 + i\infty} \left| \frac{\hat{G}(\sigma_1 + iy)\hat{K}(\sigma_1 + iy)}{1 - \hat{K}(\sigma_1 + iy)} \right| dy = B_1 e^{\sigma_1 t}.$$

Here B_1 is a constant. Thus, we arrived at the representation

$$B(t) = e^{\lambda_* t} B_0 + G(t) + e^{\sigma_1 t} B_1.$$

However, remembering that $G(t) = 0$ for $t \geq 0$, we can write

$$B(t) = B_0 e^{\lambda_* t} \left(1 + \frac{e^{-\lambda_* t} G(t)}{B_0} + e^{(\sigma_1 - \lambda_*)t} \frac{B_1}{B_0} \right) = B_0 e^{\lambda_* t} \left(1 + \Omega(t) \right) \tag{89}$$

where $\Omega(t) \to 0$ as $t \to \infty$, provided $B_0 \neq 0$.

Now, $B_0 = 0$ if and only if $G(t) = 0$ for all $t \geq 0$ but then, from uniqueness, $B(t) = 0$ for all t.

Let us interpret this condition. We have

$$0 = G(t) = \int_0^\infty \beta(a+t)\frac{S(a+t)}{S(a)}\mathring{p}(a)da$$

which, by positivity of $\mathring{p}$, is possible only if

$$\beta(a+t)\mathring{p}(a) = 0$$

for $a \in [0, \omega]$ and $t \geq 0$. This occurs only if the support of β is to the left of the support of $\mathring{p}$ (as the support of $\beta(\cdot + t)$ moves to the left as t increases). In other words, this case occurs only if the original population is too old to become fertile.

In this case

$$p(a,t) = \begin{cases} \mathring{p}(a-t)\frac{S(a)}{S(a-t)}, & t < a, \\ 0, & a < t. \end{cases} \tag{90}$$

Otherwise, we can write

$$p(a,t) = \begin{cases} \mathring{p}(a-t)\frac{S(a)}{S(a-t)}, & t < a, \\ B_0 e^{\lambda_*(t-a)}\left(1+\Omega(t-a)\right)S(a), & a < t. \end{cases} \tag{91}$$

Now, in the case $\omega < +\infty$ we see that for $t \geq \omega$ we have

$$p(a,t) = B_0 e^{\lambda_*(t-a)}\left(1 + \Omega(t-a)\right)S(a)$$

and we identify the stable age distribution

$$p_\infty(a) = e^{-\lambda_* a - \int\limits_0^a \mu(s)ds}.$$

so that

$$\lim_{t\to\infty} e^{-\lambda_* t} p(a,t) = e^{-\lambda_* a - \int\limits_0^a \mu(s)ds}$$

on $[0,\omega]$ (provided the supports of $\mathring{p}$ and β meet).

Finally, we noted in (87) that $\lambda_* > 0$, $\lambda_* = 0$ and $\lambda_* < 0$ if and only if, respectively, $R > 1, R = 1$ and $R < 1$. Thus, the population is growing if $R > 1$, it is stable if $R = 1$ and it decays if $R < 1$ (again if supports of $\mathring{p}$ and β meet), in accordance with the interpretation of the parameter R.

Age-structured population model

Standard SIR model. Here the population as homogeneous apart from the differences due to the disease. Then, for the description of the epidemics the population is divided into three main classes: susceptibles (individuals who are not sick and can be infected), infectives (individuals who have the disease and can infect others) and removed (individuals who were infective but recovered and are now immune, dead or isolated). Depending on the disease, other classes can be introduces to cater e.g., for the latent period of the disease. We denote by $S(t), I(t), R(t)$ the number of individuals in the classes above.

By

$$S(t) + I(t) + R(t) = N(t)$$

we denote the total population size. In many models it is assumed that the population size is constant disregarding thus vital dynamics such as births and deaths. Thus, the total population is a conserved quantity and the relevant conservation law can be written as

$$\begin{aligned} S' &= -\lambda S + \delta I, \\ I' &= \lambda S - (\gamma + \delta) I, \\ R' &= \gamma I \end{aligned} \tag{92}$$

with $S(0) = S_0, I(0) = I_0, R(0) = R_0$ and $S_0 + I_0 + R_0 = N$.

The parameter λ is the force of infection, δ is the recovery rate and γ is the recovery/removal rate. While δ and γ are usually taken to be constant, the force of infection requires a constitutive law. The simplest is the law of mass action

$$\lambda = c\phi\frac{I}{N}, \tag{93}$$

where c is the contact rate (the number of contacts that a single individual has with other individuals in the population per unit time), ϕ is the infectiveness; that is, the probability that a contact with an infective will result in infection and I/N is the probability that the contacted individual is infective. In what follows we shall denote $k = c\phi/N$.

There are many other assumptions underlying this model: that the population is homogenous, that no multiple infections are possible, that an infected individual immediately become infective, etc. Concerning the nature of the disease the basic distinction is between those which are not lethal and do not impart immunity (influenza, common cold) and those which could be caught only once (leading to death or immunity) such as measles or AIDS. In the first case, $\gamma = 0$ and the model is referred to as an SIS model and in the second $\delta = 0$ and the model is called an SIR model.

In many cases the rate of infection significantly varies with age and thus it is important to consider the age structure of the population. Thus we expect the interaction of the vital dynamics and the infection mechanism to produce a nontrivial behaviour. To introduce the model we note again that, in absence of the disease, the age-dependent density of the population $n(a, t)$ would be the solution of the linear model introduced in (50)–(52). However, because of the epidemics, the population is partitioned into the three classes: susceptibles, infectives and removed, represented by their respective age densities $s(a, t), i(a, t)$ and $r(a, t)$.

Now, if we look at the population of susceptibles, than we see that it is losing individuals at the rate $\lambda(a,t)s(a,t)$ and gaining at the rate $\delta(a)i(a,t)$, where we have taken into account that the infection force and the cure rate are age dependent. Similarly, the source terms for the other two classes are given by the (age dependent) terms of the (92) model.

This leads to the system

$$\begin{aligned}
\partial_t s(a,t) + \partial_a s(a,t) + \mu(a)s(a,t) &= -\lambda(a,t)s(a,t) + \delta(a)i(a,t),\\
\partial_t i(a,t) + \partial_a i(a,t) + \mu(a)i(a,t) &= \lambda(a,t)s(a,t)\\
&\quad - (\delta(a) + \gamma(a))i(a,t),\\
\partial_t r(a,t) + \partial_a r(a,t) + \mu(a)r(a,t) &= \gamma(a)i(a,t), \qquad (94)
\end{aligned}$$

with boundary conditions

$$\begin{aligned} s(0,t) &= \int_0^{\omega} \beta(a)(s(a,t)+(1-q)i(a,t)+(1-w)r(a,t))da, \\ i(0,t) &= q\int_0^{\omega} \beta(a)i(a,t)da, \\ r(0,t) &= w\int_0^{\omega} \beta(a)r(a,t)da, \end{aligned} \tag{95}$$

where $q \in [0,1]$ and $w \in [0,1]$ are the vertical transmission coefficients of infectiveness and immunity, respectively. The system is complemented by initial conditions $s(a,0) = s_0(a), i(a,0) = i_0(a)$ and $r(a,0) = r_0(a)$.

We remark that here we assumed that the death and birth coefficients are not significantly affected by the disease. In particular, if we assume that the solution of (94) exists in such a way that all terms are separately well defined, then adding the equations together we obtain that the total population density $p(a,t) = s(a,t) + i(a,t) + r(a,t)$ satisfies

$$\begin{aligned}
\partial_t p(a,t) + \partial_a p(a,t) + \mu(a)p(a,t) &= 0, \\
p(0,t) &= \int\limits_0^\omega \beta(a)p(a,t)da, \\
p(a,0) &= p_0(a) = s_0(a) + i_0(a) + r_0(a),
\end{aligned}$$

that is, the disease does not change the global picture of the evolution of the population, as expected from the model.

Solvability of the SIR/SIS system with age structure.

Let us recall the system

$$\begin{aligned}\partial_t s(a,t)+\partial_a s(a,t)+\mu(a)s(a,t) &= -\lambda(a,t)s(a,t)+\delta(a)i(a,t),\\ \partial_t i(a,t)+\partial_a i(a,t)+\mu(a)i(a,t) &= \lambda(a,t)s(a,t)\\ &\quad -(\delta(a)+\gamma(a))i(a,t),\\ \partial_t r(a,t)+\partial_a r(a,t)+\mu(a)r(a,t) &= \gamma(a)i(a,t) \qquad (97)\end{aligned}$$

with the boundary conditions

$$
\begin{aligned}
s(0,t) &= \int_0^\omega \beta(a)(s(a,t)+(1-q)i(a,t)+(1-w)r(a,t))da,\\
i(0,t) &= q\int_0^\omega \beta(a)i(a,t)da, \quad r(0,t) = w\int_0^\omega \beta(a)r(a,t)da, \qquad (98)
\end{aligned}
$$

where $q \in [0,1]$ and $w \in [0,1]$ are the vertical transmission coefficients of infectiveness and immunity, respectively, and the initial conditions

$$
s(a,0) = s_0(a), \quad i(a,0) = i_0(a), \quad r(a,0) = r_0(a). \qquad (99)
$$

To deal with solvability of this system we have to provide a more general framework for the original McKendrick problem.

Solution of the McKendrick-von Foerster problem as a semidynamical system. We considered the problem

$$\begin{aligned} &\partial_t n(a,t) + \partial_a n(a,t) = -\mu(a)n(a,t) \\ &n(0,t) = \int\limits_0^{\omega} \beta(a)n(a,t)da, \\ &n(a,0) = n_0(a) \end{aligned} \tag{100}$$

and proved that, under assumptions (67)–(70), it has a solution

$$p(a,t) = \begin{cases} \frac{S(a)}{S(a-t)} n_0(a-t), & t < a, \\ S(a)B(t-a), & a < t, \end{cases} \tag{101}$$

where B is the solution of the Volterra equation

$$\begin{aligned} B(t) &= \int_0^t K(t-a)B(a)da + \int_0^{\omega-t} \beta(a+t)\frac{S(a+t)}{S(a)}n_0(a)da \\ &= \int_0^t K(t-a)B(a)da + \int_t^{\omega} \beta(a)\frac{S(a)}{S(a-t)}n_0(a-t)da \end{aligned} \tag{102}$$

for $0 \leq t \leq \omega$ and

$$B(t) = \int_0^{\omega} K(t-a)B(a)da \tag{103}$$

for $t > \omega$. The solution satisfies the estimate

$$\|p(\cdot,t)\|_{L_1([0,\omega])} \leq \|p_0\|_{L_1([0,\omega])}e^{t\|\beta\|_\infty}. \tag{104}$$

Unique solvability of (100) in the sense of formula (101) allows for the dynamical systems approach to the problem. This amounts to looking at the solution not through individual trajectories but more globally, as a family of mappings of the state space into itself, parametrized by time. Let us recall that our state space is $X = L_1([0,\omega])$ of all population densities with finite total population. Then, for any $p_0 \in X$ we define

$$[T(t)p_0](a) = p(a,t) \tag{105}$$

where n is the solution defined by (101). From (104) we see that $(T(t))_{t\geq 0}$ is a family of linear bounded operators on X with at most exponential growth in time.

The previous results show that $(T(t))_{t\geq 0}$ is a strongly continuous (semi)dynamical system, or a strongly continuous semigroup, that is, it is a family of bounded linear operators satisfying, for any $x \in X$,

1. $T(t+\tau)x = T(t)T(\tau)x, \quad t, \tau \geq 0;$
2. $T(0)x = x;$
3. $\lim\limits_{t\to 0^+} T(t)x = x.$

An important role is played by an operator A, called the generator of the semigroup $(T(t))_{t\geq 0}$, defined by the formula

$$Ax = \lim_{h\to 0^+} \frac{T(h)x - x}{h}, \tag{106}$$

whenever the limit exists in X.

The set of such $x \in X$ is called the domain of A and denoted by $D(A)$. Typically A is unbounded and $D(A) \neq X$. It follows that if $x_0 \in D(A)$, then $t \to x(t, x_0) = T(t)x_0$ is differentiable, $T(t)x_0 \in D(A)$ for all $t \geq 0$ and

$$\frac{d}{dt}x(t, x_0) = Ax(t, x_0), \qquad x(0, x_0) = x_0, \tag{107}$$

that is, $(T(t))_{t\geq 0}$ gives solutions to the Cauchy problem (107) and $x(t, x_0)$ is the semiflow associated with this equation due to the semigroup property.

In the case of the McKendrick-von Foerster problem, it can be proved that $A = -\partial_a - \mu$ with

$$D(A) = \{p \in W_1^1([0,\omega]);\ \mu p \in L_1([0,\omega]), p(0) = \int\limits_0^\omega \beta(a)p(a)da\}.$$

Finally we note the following fact which will be of importance in the analysis of nonlinear problems.

Proposition 2

Under assumptions (67)–(70), if p_0 is bounded, then $p(a,t)$ is bounded on $[0,\omega] \times [0,T]$ for any $0 \leq T < \infty$.

Epidemiological system – linear part. We first look at its linear part

$$\begin{aligned} \partial_t s(a,t) + \partial_a s(a,t) + \mu(a)s(a,t) - \delta(a)i(a,t) &= 0, \\ \partial_t i(a,t) + \partial_a i(a,t) + \mu(a)i(a,t) + (\delta(a)+\gamma(a))i(a,t) &= 0, \\ \partial_t r(a,t) + \partial_a r(a,t) + \mu(a)r(a,t) - \gamma(a)i(a,t) &= 0, \end{aligned}$$

with the boundary conditions

$$\begin{aligned} s(0,t) &= \int_0^\omega \beta(a)(s(a,t) + (1-q)i(a,t) + (1-w)r(a,t))da, \\ i(0,t) &= q\int_0^\omega \beta(a)i(a,t)da, \quad r(0,t) = w\int_0^\omega \beta(a)r(a,t)da, \end{aligned}$$

and the initial conditions

$$s(a,0) = s_0(a), \quad i(a,0) = i_0(a), \quad r(a,0) = r_0(a). \qquad (108)$$

The problem is an example of a more general vector McKendrick system

$$\partial_t \boldsymbol{p} = \mathcal{S}\boldsymbol{p} + \mathcal{M}\boldsymbol{p}, \tag{109}$$

$$\boldsymbol{p}(t,a) = (p_1(a,t), \ldots, p_N(a,t))$$

and $p_i(a,t)$ is the population density at time t of individuals in patch i and being of age a (here $\boldsymbol{p} = (s, i, r)$). Further,

$$\mathcal{S}\boldsymbol{p} = -\partial_a \boldsymbol{p} = (-\partial_a p_1, \ldots, -\partial_a p_N) \tag{110}$$

describes aging, $\mathcal{M}(a) = (\mu_{ij}(a))_{1\leq i,j\leq N}$ is the mortality/projection matrix.

In our case

$$\begin{aligned} m &= \begin{pmatrix} -\mu & \delta & 0 \\ 0 & -(\mu+\delta+\gamma) & 0 \\ 0 & \gamma & -\mu \end{pmatrix} \\ &= \begin{pmatrix} -\mu & 0 & 0 \\ 0 & -\mu & 0 \\ 0 & 0 & -\mu \end{pmatrix} + \begin{pmatrix} 0 & \delta & 0 \\ 0 & -(\delta+\gamma) & 0 \\ 0 & \gamma & 0 \end{pmatrix} \end{aligned} \tag{111}$$

where the first matrix describes death, which is an intrapatch phenomenon, and the second refers to migrations between patches and is thus a Kolmogorov matrix.

Similarly, we assume that

$$\mathcal{M} = \mathrm{diag}\{-\mu_1, \ldots, -\mu_N\} + \mathcal{Q}$$

where $\mathcal{Q}$ is a Kolmogorov matrix, that is, it is positive off-diagonal and the sum of entries in each column is 0. This structure has important consequences as far as the asymptotic properties are concerned.

This system is supplemented by the McKendrick boundary condition

$$\boldsymbol{p}(t, 0) = [\mathcal{B}\boldsymbol{p}](t) = \int\limits_0^\infty B(a)\boldsymbol{p}(a, t)da, \qquad (112)$$

where γ denotes the operator of taking the trace at $a = 0$ and $B(a) = \{\beta_{ij}(a)\}_{1\leq i,j\leq N}$ is the fertility matrix.

We note that births may be interpatch phenomena; in our case

$$B = \begin{pmatrix} \beta & \beta(1-q) & \beta(1-w) \\ 0 & \beta q & 0 \\ 0 & 0 & \beta w \end{pmatrix}. \tag{113}$$

The initial condition is given by

$$\boldsymbol{p}|_{t=0} = \boldsymbol{p}(0,a) = \mathring{\boldsymbol{p}}(a). \tag{114}$$

The natural phase space for the problem is $X = L_1([0,\omega],\mathbb{R}^N)$. We denote by X_+ the subset of X consisting of vectors which are coordinate-wise nonnegative almost everywhere. Further, $X_\infty = L_\infty([0,\omega],\mathbb{R}^N)$.

We mimic the scalar case approach. Let us denote by $\mathcal{V}_{\mathcal{M}}(a,b)$ the fundamental solution matrix of the equation $\boldsymbol{z}'_a(a) = \mathcal{M}(a)\boldsymbol{z}(a)$; that is, $\boldsymbol{z}(a) = \mathcal{V}_{\mathcal{M}}(a)\boldsymbol{z}_0$ satisfies the above equation with $\boldsymbol{z}(b) = \boldsymbol{z}_0$ ($\mathcal{V}_{\mathcal{M}}$ plays the role of the integrating factor in the scalar case). Since the columns of $\mathcal{V}_{\mathcal{M}}(a,0)$ are linearly independent for any a, the inverse $\mathcal{V}_{\mathcal{M}}^{-1}(a,0)$ always exists and thus $\mathcal{V}_{\mathcal{M}}(a,b) = \mathcal{V}_{\mathcal{M}}(a,0)\mathcal{V}_{\mathcal{M}}^{-1}(b,0)$.

With this, we can write the solution to (109)-(112) as

$$\boldsymbol{p}(a,t)=\begin{cases}\mathcal{V}_{m}(a,a-t)\mathring{\boldsymbol{p}}, & a>t,\\ (\mathcal{V}_{m}(a,0)\boldsymbol{\psi})(t-a) & a<t,\end{cases} \tag{115}$$

where $\boldsymbol{\psi}$ satisfies the Volterra equation

$$\boldsymbol{\psi}(t)=\int\limits_{0}^{t}(B(a)\mathcal{V}_{m}(a,0)\boldsymbol{\psi})(t-a)da+\int\limits_{t}^{\infty}B(a)\mathcal{V}_{m}(a,a-t)\mathring{\boldsymbol{p}}(a-t)da.$$

Let us define by $\mathcal{A}$ the realization of $-diag\{\partial_a\} - \mathcal{M}$ on the domain

$$D_A = \{\boldsymbol{p} \in (W^{1,1}(\mathbb{R}_+))^N, \boldsymbol{p}(0) = \mathcal{B}\boldsymbol{p}\}.$$

Then we can prove

Theorem 22

$\mathcal{A}$ generates a strongly continuous semigroup $\{\mathcal{T}(t)\}_{t\geq 0}$ such that

$$||\mathcal{T}(t)|| \leq e^{(\bar{b}-\underline{m})t},$$

where $\bar{b} := \sup_{a\in\mathbb{R}_+} ||B(a)||$ and $\underline{m} := \inf_{j,a} \mu_j(a)$. Furthermore, if $\mathring{\boldsymbol{p}} \in X_+$, then $\boldsymbol{p}(t,\cdot) \in X_+$ and if $\mathring{\boldsymbol{p}} \in X_\infty \cap X_1$, then $\boldsymbol{p}(t,\cdot) \in X_\infty \cap X_1$.

The nonlinear system. With the notation of the previous section, the problem (97)–(99) can be written in compact form

$$\begin{aligned} \partial_t \boldsymbol{p} &= \mathcal{A}\boldsymbol{p} + \mathfrak{F}(\boldsymbol{p}), \quad t > 0, \\ \boldsymbol{p}|_{a=0} &= \mathcal{B}\boldsymbol{p}, \\ \boldsymbol{p}|_{t=0} &= \mathring{\boldsymbol{p}}, \end{aligned} \tag{116}$$

where $\boldsymbol{p} = (s, i, r)$, $\mathcal{A} = \mathcal{S} + \mathcal{M}$ with $\mathcal{S}$ and $\mathcal{M}$ defined by (110) and (111).

Further, $\mathscr{B}$ is defined by (113) and $\mathfrak{F}$ is the nonlinear perturbation

$$\mathfrak{F}((s,i,r)) = \begin{pmatrix} -\lambda & 0 & 0 \\ \lambda & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} s \\ i \\ r \end{pmatrix}, \tag{117}$$

where the force of infection depends on the solution through the formula

$$\lambda(a,t) = K_0(a)i(a,t) + \int\limits_0^{\omega} K(a,s)i(s,t)ds, \tag{118}$$

where $K_0(a)$ and $K(a,s)$ are known functions.

How to deal with such problems? First we note that the boundary condition is really a part of the definition of the domain of $\mathscr{A}$ and thus, if we find a solution to (116), then it must satisfy $u \in D_A$ and automatically satisfies the boundary condition. Thus, for a time being we shall ignore it.

The main idea is to use the fact that we can solve the linear version of (116)

$$\begin{aligned} \partial_t \boldsymbol{u} &= \mathscr{A}\boldsymbol{u} + \boldsymbol{f}(t), \quad t > 0, \\ \boldsymbol{u}|_{t=0} &= \mathring{\boldsymbol{u}}, \end{aligned} \tag{119}$$

where $\boldsymbol{f}$ is a given function, and the solution is given by the Duhamel formula

$$\boldsymbol{u}(t) \;\;=\;\; \mathcal{T}(t)\mathring{\boldsymbol{u}} + \int\limits_0^t \mathcal{T}(t-s)\boldsymbol{f}(s)ds.$$

So, if we knew the solution $\boldsymbol{p}$ to (116), then it would be given by

$$\boldsymbol{p}(t) = \mathcal{T}(t)\mathring{\boldsymbol{p}} + \int\limits_0^t \mathcal{T}(t-s)\mathfrak{F}(\boldsymbol{p}(s))ds. \qquad (120)$$

Even if we do not know the solution, then (120) offers a simplification of (116) by not involving the unbounded operator $\mathcal{A}$. Of course, a solution to (120) is not necessarily a solution to (116) but at least it seems to be step in right direction in the sense that any continuous solution to (116) must be a solution to (120).

The problem (120) can be solved by Picard's iterations, similar to (72)

$$\begin{aligned} \boldsymbol{p}_0(t) &= \mathring{\boldsymbol{p}}, \\ \boldsymbol{p}_{k+1}(t) &= \mathscr{T}(t)\mathring{\boldsymbol{p}} + \int\limits_0^t \mathscr{T}(t-s)\mathfrak{F}(\boldsymbol{p}_k(s))ds, \end{aligned} \qquad (121)$$

however, handling the nonlinearity $\mathfrak{F}$ requires more care.

First, let us assume that $\mathfrak{F}$ satisfies the global Lipschitz condition on X, that is, there is $L > 0$ such that for any $\boldsymbol{u}, \boldsymbol{v} \in X$

$$\|\mathfrak{F}(\boldsymbol{u}) - \mathfrak{F}(\boldsymbol{v})\|_X \leq L\|\boldsymbol{u} - \boldsymbol{v}\|. \qquad (122)$$

Let us denote by $Y = C([t_0, T], X)$ the space of continuous functions $[t_0, T] \ni t \to \boldsymbol{u}(t) \in X$, where $-\infty < t_0 < T < \infty$. We define the norm in Y by

$$\|\boldsymbol{u}(\cdot)\|_Y = \sup_{t\in[t_0,T]} \|\boldsymbol{u}(t)\|_X.$$

Then, returning to (121) we obtain, for any $t \in [0, T]$,

$$\begin{aligned} \|\boldsymbol{p}_{k+1}(t) - \boldsymbol{p}_k(t)\|_X &\leq \int\limits_0^t \|\mathscr{T}(t-s)(\mathfrak{F}(\boldsymbol{p}_k(s)) - \mathfrak{F}(\boldsymbol{p}_{k-1}(s)))\|_X ds \\ &\leq Me^{\omega T} Lt \|\boldsymbol{p}_k - \boldsymbol{p}_{k-1}\|_Y, \end{aligned} \tag{123}$$

which, by induction as in (73), yields

$$\sup_{t\in[0,T]} \|\boldsymbol{p}_{k+1}(t) - \boldsymbol{p}_k(t)\|_X \leq \frac{(Me^{\omega T}L)^k}{k!}\|\boldsymbol{p}_1 - \mathring{\boldsymbol{p}}\|_Y$$

and, as in the linear case, this shows that $(\boldsymbol{p}_k)_{k\in\mathbb{N}}$ converges to a continuous solution to (120) defined on the whole interval $[0, T]$ for any $T < \infty$. Such solutions are called global.

If we consider another solution $\boldsymbol{v}$ to (120) with the initial condition $\mathring{\boldsymbol{v}}$, then

$$\|\boldsymbol{p}(t)-\boldsymbol{v}(t)\|_X \leq Me^{\omega T}\|\mathring{\boldsymbol{p}}-\mathring{\boldsymbol{v}}\|_X + \int\limits_0^t \|\mathcal{T}(t-s)(\mathfrak{F}(\boldsymbol{p}(s))-\mathfrak{F}(\boldsymbol{v}(s)))\|_X ds$$

$$\leq Me^{\omega T}\|\mathring{\boldsymbol{p}}-\mathring{\boldsymbol{v}}\|_X + Me^{\omega T}L\int\limits_0^t \|\boldsymbol{p}(s)-\boldsymbol{v}(s)\|_X ds$$

and Gronwall's inequality gives

$$\|\boldsymbol{p}(t)-\boldsymbol{v}(t)\|_X \leq Me^{\omega T}e^{MLTe^{\omega T}}\|\mathring{\boldsymbol{p}}-\mathring{\boldsymbol{v}}\|_X, \quad 0 \leq t \leq T,$$

so that we obtain that the solution is (Lipschitz) continuous with respect to the initial data and is unique (by putting $\mathring{\boldsymbol{p}} = \mathring{\boldsymbol{v}}$).

However, it is easy to see that even for a simple nonlinearities such as $\mathfrak{F}(u) = u^2$ we have

$$|\mathfrak{F}(u) - \mathfrak{F}(v)| = |(u+v)||u-v|$$

and thus $\mathfrak{F}$ is Lipschitz continuous as long as we restrict u and v to satisfy $|u|, |v| \leq K$ for some constant K. Thus, a quadratic nonlinearity is Lipschitz continuous, but not globally, as the Lipschitz constant depends on bounds for u and v. Functions like this are called locally Lipschitz.

Precisely, $\mathfrak{F}$ is said to satisfy a local Lipschitz condition on X if for any $c > 0$ there is $L = L_c$ such that

$$\|\mathfrak{F}(\boldsymbol{u}) - \mathfrak{F}(\boldsymbol{v})\|_X \leq L_c\|\boldsymbol{u} - \boldsymbol{v}\|_X, \tag{124}$$

whenever $\|u\|_X, \|v\|_X \leq c$.

In such a case we cannot use directly (123), as the constant L changes with the iterates and can grow to infinity. We can, however, use the same argument if we make sure beforehand that all the iterates will stay in a fixed bounded set of X. We can prove the following result.

Theorem 23

Let $\mathfrak{F} : X \to X$ be a locally Lipschitz function. If $\mathscr{A}$ is the generator of a semigroup $(\mathscr{T}(t))_{t\geq 0}$, then for every $\mathring{\boldsymbol{p}} \in X$ and every $t_0 \in \mathbb{R}$ there is $t_{max} > t_0$, such that the Cauchy problem

$$\begin{aligned} \partial_t \boldsymbol{p} &= \mathscr{A}\boldsymbol{p} + \mathfrak{F}(\boldsymbol{p}), \quad t > 0, \\ \boldsymbol{p}|_{t=t_0} &= \mathring{\boldsymbol{p}}, \end{aligned} \tag{125}$$

has a unique mild solution $\boldsymbol{p}$ on $[t_0, t_{max})$. Moreover, if $t_{max} < \infty$, then

$$\lim_{t\to t_{max}} \|\boldsymbol{p}(t)\|_X = \infty.$$

The above theorem does not address the question whether our mild solution is the solution to (125), that is, whether it can be differentiated and whether it belongs to D_A and thus satisfies the boundary conditions. We only note here that for $\boldsymbol{p}$ to be a classical solution to (125) it suffices that $\mathring{\boldsymbol{n}} \in D_A$ and $\boldsymbol{p} \to \mathfrak{F}(\boldsymbol{p})$ be continuously differentiable.

Let us return to the epidemiological problem (116) with $\mathfrak{F}$ given by (117)–(118). Our state space is $X = L_1([0,\infty))^3 = L_1([0,\infty), \mathbb{R}^3)$ and

$$\|\boldsymbol{p}\|_X = \|(s,i,r)\|_X = \|s\|_{L_1([0,\infty))} + \|i\|_{L_1([0,\infty))} + \|r\|_{L_1([0,\infty))}.$$

To simplify discussion, we only consider the intercohort infection and disregard r.

Then

$$\mathfrak{F}(\boldsymbol{p}_1) - \mathfrak{F}(\boldsymbol{p}_2) =$$

$$\begin{pmatrix} -\int\limits_0^\infty K i_1 da & 0 \\ \int\limits_0^\infty K i_1 da & 0 \end{pmatrix} \begin{pmatrix} s_1 \\ i_1 \end{pmatrix} - \begin{pmatrix} -\int\limits_0^\infty K i_2 da & 0 \\ \int\limits_0^\infty K i_2 da & 0 \end{pmatrix} \begin{pmatrix} s_2 \\ i_2 \end{pmatrix}$$

$$= \begin{pmatrix} -s_1 \int\limits_0^\infty K i_1 da + s_2 \int\limits_0^\infty K i_2 da \\ s_1 \int\limits_0^\infty K i_1 da - s_2 \int\limits_0^\infty K i_2 da \end{pmatrix}.$$

It is now easy to see that $\mathfrak{F}$ is locally Lipschitz continuous as

$$
\begin{aligned}
&\|\mathfrak{F}(\boldsymbol{p}_1)-\mathfrak{F}(\boldsymbol{p}_2)\|_X\\
&\leq 2\int\limits_0^\infty \left| s_1(a)\int\limits_0^\infty K(\alpha)i_1(\alpha)d\alpha - s_2(a)\int\limits_0^\infty K(\alpha)i_2(\alpha)d\alpha\right| da\\
&\leq 2\left(\int\limits_0^\infty |s_1(a)-s_2(a)|\int\limits_0^\infty K(\alpha)|i_1(\alpha)|d\alpha da\right.\\
&\quad\left.+\int\limits_0^\infty |s_2(a)|\int\limits_0^\infty K(\alpha)|i_1(\alpha)-i_2(\alpha)|d\alpha da\right) \leq C\|(s_1-s_2, i_1-i_2)\|_X,
\end{aligned}
$$

where $C = 2\sup_{a\in\mathbb{R}_+} K(a)\max\{\|i_1\|_{L_1([0,\infty))}, \|s_2\|_{L_1([0,\infty))}\}$. Hence, the problem has a unique solution defined at least on some interval $[0,\delta]$.

We note that the case with intracohort infection the situation is slightly different as the product *is* of two integrable functions not necessarily is integrable. However, from Proposition 2, we know that if $\mathring{s}, \mathring{i} \in X_{1,\infty} := L_1([0,\infty)) \cap L_\infty([0,\infty))$, then the solution also is in this space and so is the product $i \cdot s$.

$$\|\mathfrak{F}(\boldsymbol{p}_1) - \mathfrak{F}(\boldsymbol{p}_2)\|_{X_{1,\infty}} \leq 2 \int\limits_0^\infty |K(a)(i_1(a)s_1(a) - s_2(a)i_2(a))|\, da$$

$$\leq 2 \sup_{a\in\mathbb{R}_+} K(a) \int\limits_0^\infty (|s_1(a) - s_2(a)||i_1(a)|da + |s_2(a)||i_1(a) - i_2(a)|)\, da$$

$$\leq C\|(s_1 - s_2, i_1 - i_2)\|_{X_{1,\infty}},$$

for appropriate C and, as above, there exists a mild solution to (116) on some interval $[0, \delta]$.

Can this solution be extended to $[0,\infty)$? We observe that if $i, s \geq 0$ then in, say, intercohort case,

$$\|\boldsymbol{p}(t)\|_X = \int\limits_0^\infty (|i(a,t)| + |s(a,t)|)da = \int\limits_0^\infty (i(a,t) + s(a,t))da$$

$$= \int\limits_0^\infty p(a,t)da,$$

where p is the solution of the equation obtained by adding together (94)–(95). Since we know that p exists for all t, $\|\boldsymbol{p}(t)\|_X$ would be bounded for any finite t and thus would be extendable to $[0,\infty)$.

If we look at the iterates (121), we see that, since $\mathring{\boldsymbol{p}} \geq 0$ and the linear semigroup $(\mathcal{T}(t))_{t\geq 0}$ preserves positivity, the iterates, and thus the solution, will be positive if $\mathfrak{F}(\boldsymbol{u}) \geq 0$ for $\boldsymbol{u} \geq 0$. However, clearly $\mathfrak{F}$ is not positive.

To solve this problem, we observe that the iterations in Theorem 23 are performed on a fixed ball in X (or $X_{1,\infty}$). This means that in the iterations we can always assume that the argument $\boldsymbol{p}$ of $\mathfrak{F}$ satisfies $\|\boldsymbol{p}\| \leq C$ with respective norm, for some constant C.

Then we observe that the problem (125) is equivalent to

$$\partial_t \boldsymbol{p} = (\mathscr{A}\boldsymbol{p} - \omega\boldsymbol{p}) + (\omega\boldsymbol{p} + \mathfrak{F}(\boldsymbol{p})) = \mathscr{A}_\omega\boldsymbol{p} + \mathfrak{F}_\omega(\boldsymbol{p})$$

for any $\omega \in \mathbb{R}$. It is easy to see that the semigroup generated by $\mathscr{A}_\omega$ is $(\mathscr{T}_\omega(t))_{t\geq 0} = \{e^{-\omega t}\mathscr{T}(t)\}_{t\geq 0}$. The semigroup $(\mathscr{T}_\omega(t))_{t\geq 0}$ also preserves positivity. Therefore $\boldsymbol{p}$ is the mild solution to

$$\boldsymbol{p}(t) = \mathscr{T}_\omega(t)\mathring{\boldsymbol{p}} + \int_0^t \mathscr{T}_\omega(t-s)\mathfrak{F}_\lambda(\boldsymbol{p}(s))\,ds, \quad 0 \leq t < \delta. \tag{126}$$

In our case we have

$$\begin{aligned}\mathfrak{F}_\omega(\boldsymbol{n}) &= \begin{pmatrix} -\int\limits_0^\infty K(a)i(a)da & 0 \\ \int\limits_0^\infty K(a)i(a)da & 0 \end{pmatrix}\begin{pmatrix} s \\ i \end{pmatrix} + \omega\begin{pmatrix} s \\ i \end{pmatrix} \\ & \begin{pmatrix} -s(a)\int\limits_0^\infty K(a)i(a)da + \omega s(a) \\ s(a)\int\limits_0^\infty K(a)i(a)da + \omega i(a) \end{pmatrix},\end{aligned}$$

and we see that if we take $\omega > C\sup_{a\in\mathbb{R}_+} K(a)$, then $\mathfrak{F}_\omega(\boldsymbol{n}) \geq 0$ for any $\boldsymbol{p} \geq 0$ satisfying $\|\boldsymbol{p}\| \leq C$. Thus all iterates are nonnegative and thus the solution is nonnegative. By the earlier argument, we have global solvability of the age structured epidemiological problem.