Mathematical Models in Biology

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February 5, 2009

Contents

Chapter 1

Introduction to Modelling

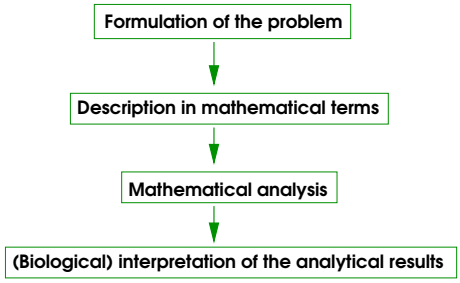
Literature: [45, 9]

Mathematical modelling is a process by which a real world problem is described by a mathematical formulation. This procedure is a kind of abstraction, that means, neither all details of single processes will be described nor all aspects concerning the problem will be included.
A main problem is to find an appropriate mathematical formulation. Then, for further studies of the model, common mathematical tools can be used or new ones are developed.

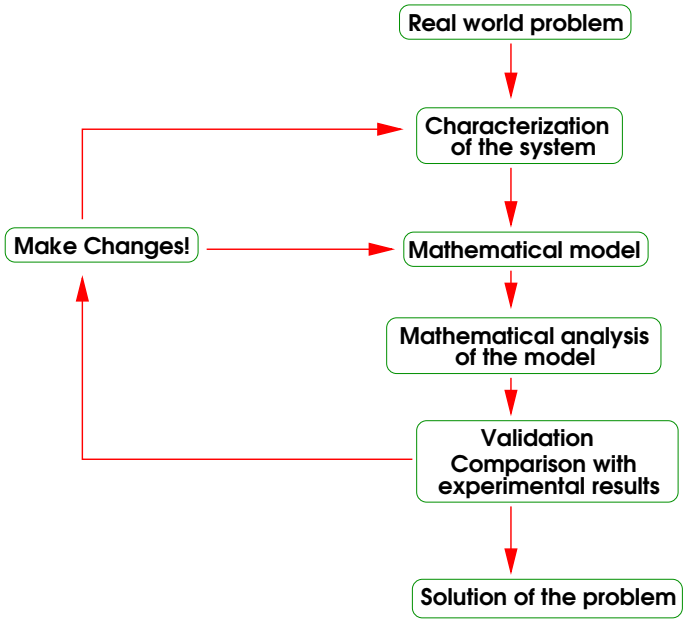
Shortly, a model should be

- as simple as possible
- as detailed as necessary

Vice versa, one mathematical formulation may be appropriate for several real-world problems, even from very different domains.



A great challenge of modelling is to bring together the abstract, mathematical formulation and concrete experimental data. The modelling process can be roughly described as follows (adapted from [45], Fig. 4.2.):



We are not able to do a lot of validation during the lecture (due to lack of time), but in practice, this step is also very important!

There are many different modelling approaches and their number is still increasing. We cannot treat all these approaches in our lecture, the goal is to gain first insight in some of the standard techniques. E.g., we will review some mathematical methods that are frequently used in mathematical biology, consider some standard models, and last, but not least have an introduction into the art of modelling.
In contrast to Bioinformatics which deals mainly with the description and structure of data, the aim of Biomathematics is to understand the underlying mechanisms and to use them for predictions. The methods which are used depend strongly on the mechanisms of biological systems. There are two ways doing Biomathematics:

Qualitative theory	Quantitative theory
Modelling of the basic mechanisms in a simple way; parameter fitting and analysis of (concrete) data doesn't greatly matter.	Here, the model of the biological system is very detailed and parameters are taken from the experiments (e.g. by data fitting). The analysis of the system is less important than to get simulations of concrete situations.
The results are qualitative. A rigorous analysis of the models is possible and the qualitative results can be compared with experimental results. Quantitative prediction of experimental results is not (main) goal of this approach.	The results are qualitative, quantitative prediction should be possible. It is important to know a lot of details about the biological system.

For the modelling itself, there are also several approaches. We will consider only a few (the most important?) ones in our lecture: One criterion concerns the stochasticity. In deterministic models, all future states can be determined (by solving), if the state of the system at a certain point in time t is known. However, if stochastic effects play a role (especially e.g. for small population sizes), stochastic models are used.

Difference Equations: The time is discrete, the state (depending on time) can be discrete or continuous. They are often used to describe seasonal events.

Ordinary Differential Equations (ODEs): Here, time and state are continuous, but ODEs only deal with (spatially) homogenous quantities. They are often used to describe the evolution of populations, as they are one of the major modelling tools. Therefore, we will look at this modelling tool in great detail.

Partial Differential Equations (PDEs): Still using continuous time, PDEs allow to consider further continuous variables like space or age.

Stochastic processes: Stochastic processes describe a completely stochastic way of modelling. They are used often in the context of small populations.

Part I

Deterministic models

In the first part of the lecture we will consider deterministic models. This means, that the dynamics does not include any chance factors; the values of the variables or their changes are predictable with certainty. In real life, there is always some uncertainty. But in many cases, this uncertainty is not significant (e.g. due to large numbers of the involved "individuals") and the system can be treated as a deterministic system.

Typically, deterministic models are in the form of

- difference equations
- ordinary differential equations
- partial differential equations

Chapter 2

Discrete Models

In this chapter, we consider populations in time-discrete models , that means, the development of the system is observed only at discrete times $t_0, t_1, t_2, \ldots$ and not in a continuous time course. We assume a fixed time interval between generations which makes sense for our purposes here. Here we do not consider spatial models, we assume to have more or less spatially homogeneous (population) densities, masses ....

2.1 Linear difference equations

Literature: [1, 12, 27, 13]

Example:

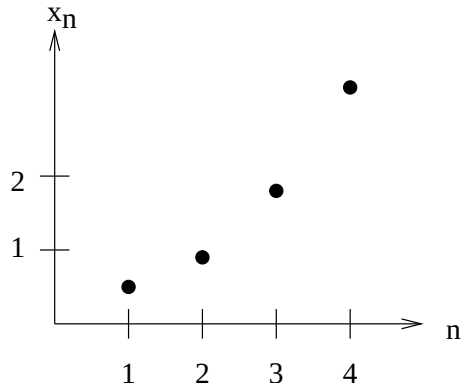
Let x_n be the population size in the n-th generation. Model assumption: Each individual has (in the average) a descendants. Then we get:

$$x_{n+1} = ax_n \qquad (a \in \mathbb{R}_+)$$

Assumption: clearly defined sequence of generations; after one generation only descendants left
This procedure can also be refined to smaller time intervals, for example of months, years, ... The equation stays to be

$$x_{n+1} = ax_n,$$

but the interpretation of the factor a is a different one: $a = 1 + \gamma - \mu$, where γ is the birth rate and μ is the death rate (per time interval, e.g. year). In this model, no age-structure of the population is included.



Generally:

$x_{n+1} = f(x_n)$ is denoted to be a difference equation of first order.

Most simple case:

Linear difference equation of first order:

$$x_{n+1} = ax_n$$

For this, an explicit solution can easily be computed:

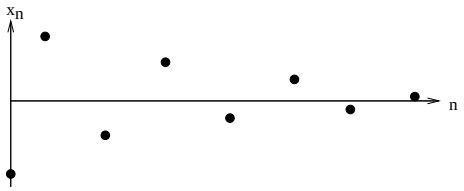
$$x_n = a^n x_0, \qquad n \geq 1.$$

x_0 is called starting value or initial value.
For most biological systems, it makes sense to assume $a > 0$. Let us first consider some properties and applications for that case:

- From $x_0 \geq 0$ we get directly $x_n \geq 0$ for all n. (This may be important for applications, as e.g. the size of a population)
- We can distinguish the following cases:
  $x_n \to 0$ for $0 < a < 1$, strictly monotone decreasing sequence, e.g. radioactive decay
  $x_n = x_0 \ \forall n$ for $a = 1$, constant sequence
  $x_n \to \infty$ for $a > 1$, strictly monotone increasing sequence, e.g. bacterial reproduction
  Problem of the model: Unlimited growth is unrealistic in the long run, the model should respect something like a "capacity of the habitat".

Further cases (not preserving positivity):

- $-1 < a < 0$: There is $x_n \to 0$, but the sequence is not monotone.



  This behaviour is called "alternating".
- $a < -1$: $x_n \to \pm\infty$, also alternating .

2.1.1 Model for an insect population

Literature: Edelstein-Keshet [12]

For this model, we do not consider the life cycle of insects in great detail, i.e. we neglect the different stages and just choose single generations as time steps in order to formulate a model for an insect population growth.
Here, the reproduction of the poplar gall aphid is considered. Adult female aphids place galls on the leaves of poplars. All descendants (of one aphid) are contained in one gall. Only a fraction will grow up to adulthood. The so-called fecundity is the capacity of producing offspring, i.e. how many descendants are "produced". It depends of course on environmental conditions, the quality of the food and the population size; the same applies for the survivorship. At the moment, we neglect these influences and assume all parameters to be constant (a quite naive model ...). The following terms are introduced:

a_n	=	Number of adult females aphids in generation n
p_n	=	Number of progeny in generation n
m	=	Fractional mortality of young aphids
f	=	Number of progeny per females aphid
r	=	Ratio of female aphids to total adult aphids

Initial condition: There are a_0 females. Now we want to write down equations which describe the sequence of the aphid population in time course. Each female produces f progeny; thus the equation reads

$$p_{n+1} = f a_n \tag{2.1}$$

Only a fraction $1 - m$ of this progeny survives to adulthood. The proportion r of these surviving individuals are females. So wet get

$$a_{n+1} = r(1 - m)p_{n+1}. \tag{2.2}$$

The two equations (2.1) and (2.2) can be combined and then yield the following difference equation:

$$a_{n+1} = fr(1-m)a_n,$$

This equation corresponds exactly to the well known homogeneous linear difference equation of first order. Thus, the solution reads

$$a_n = (fr(1-m))^n a_0,$$

for $fr(1-m) < 1$ the population will die out. The expression $fr(1-m)$ can be interpreted as the per capita number of adult females that is produced by an mother aphid.

2.1.2 Model for Red Blood Cell (RBC) Production

Literature: Edelstein-Keshet [12]

There is a continuous destruction and replacement of red blood cells in the circulatory system. Since these cells transport oxygen to the different parts of the body (which is really important), they should be kept at a fixed level. Let R_n denote the number of circulating RBCs at day n, M_n those RBCs, which are produced by the bone marrow at day n.
Assumptions for a simple model:

- There is a certain fraction of cells, which is removed daily by spleen
- There is a reproduction constant γ (the number produced per number lost)

Thus:

$$\begin{aligned} R_{n+1} &= (1-f)R_n + M_n \\ M_{n+1} &= \gamma f R_n \end{aligned}$$

Also this model can be taken together into one equation:

$$R_{n+1} = (1-f)R_n + \gamma f R_{n-1}.$$

But remark that three different time steps have to be considered in this case (it is called a second order difference equation), which makes the analysis a little bit more complicated (we will see something of that later, respectively how to treat systems).

2.2 Nonlinear difference equations

A slightly more general equation is given by

$$x_{n+1} = f(x_n),$$

which is called one-dimensional difference equation of first order. The linear difference equations from the section above can be considered as a special case. Therefore, we introduce some concepts here in a more general context.

An interesting characteristic is the existence of stationary points and their stability.

Definition 1 *$\bar{x}$ is called stationary point of the system $x_{n+1} = f(x_n)$, if*

$$\bar{x} = f(\bar{x}).$$

$\bar{x}$ is also called fixed point or steady state.

Let us consider the following non-homogeneous linear model as an example:

$$x_{n+1} = ax_n + b \qquad \text{(i.e. } f(x_n) = ax_n + b\text{)}, \tag{2.3}$$

where
a: constant reproduction rate; growth / decrease is proportional to x_n (Assumption: $a \neq 1$)
b: constant supply / removal

(Example: x_n is a fish population, a reproduction rate, b catch quota).
How is the behaviour of x_n "in the long time run", i.e., for large n ?
We look for stationary points of equation (2.3):

$$\begin{aligned} f(\bar{x}) = \bar{x} &\Leftrightarrow a\bar{x} + b = \bar{x} \\ &\Leftrightarrow b = (1-a)\bar{x} \\ &\Leftrightarrow \bar{x} = \frac{b}{1-a} \end{aligned}$$

Hence, there exists exactly one stationary state.

Definition 2 *Let $\bar{x}$ be a stationary point of the system $x_{n+1} = f(x_n)$.*
$\bar{x}$ is called locally asymptotically stable, if there exists a neighbourhood U of $\bar{x}$ such that for each starting value $x_0 \in U$ we get:

$$\lim_{n\to\infty} x_n = \bar{x}.$$

$\bar{x}$ is called unstable, if $\bar{x}$ is not (locally asymptotically) stable.

We need a practicable criterion for investigating stability of stationary points. This will be deduced in the following.

We consider a stationary point $\bar{x}$ of the difference equation $x_{n+1} = f(x_n)$. Then one is interested in the local behaviour near $\bar{x}$. For this purpose, we consider the deviation of the elements of the sequence to the stationary point $\bar{x}$:

$$z_n := x_n - \bar{x}$$

z_n has the following property:

$$\begin{aligned} z_{n+1} &= x_{n+1} - \bar{x} \\ &= f(x_n) - \bar{x} \\ &= f(\bar{x} + z_n) - \bar{x}. \end{aligned}$$

Let the function f be differentiable in $\bar{x}$, thus we get $\lim_{h\to 0} \frac{f(\bar{x}+h)-f(\bar{x})}{h} = f'(\bar{x})$ and $f(\bar{x}+h) = f(\bar{x}) + h \cdot f'(\bar{x}) + O(h^2)$. This yields:

$$\begin{aligned} z_{n+1} &= f(\bar{x} + z_n) - \bar{x} \\ &= f(\bar{x} + z_n) - f(\bar{x}) \\ &= z_n \cdot f'(\bar{x}) + O(z_n^2). \end{aligned}$$

$O(z_n^2)$ is very small and can be neglected, i.e.

$$z_{n+1} \approx z_n \cdot f'(\bar{x}),$$

which is again a linear difference equation, where we already know the criteria for stability.
Hence we have shown:

Proposition 1 *Let f be differentiable. A stationary point $\bar{x}$ of $x_{n+1} = f(x_n)$ is*

- *locally asymptotically stable, if $|f'(\bar{x})| < 1$*
- *unstable, if $|f'(\bar{x})| > 1$*

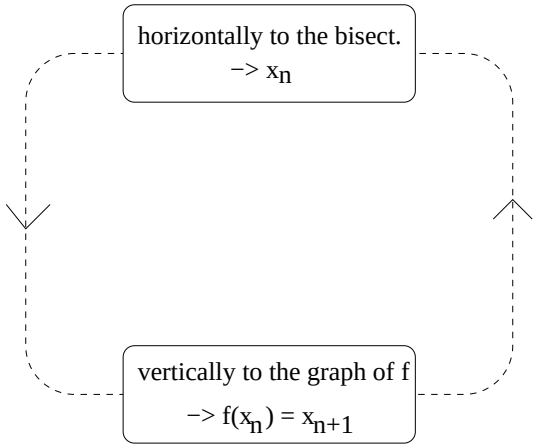
Remark: These criteria are sufficient, but not necessary!

In case of the non-homogeneous, linear system we have $f'(\bar{x}) = a$, which means that the stationary point is locally asymptotically stable if $|a| < 1$ respectively. unstable, if $|a| > 1$.

2.2.1 Graphic iteration or "cobwebbing"

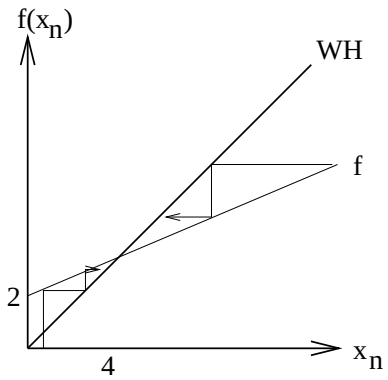
Cobwebbing is a graphical method for drawing solutions of discrete-time systems (see e.g. [1]). Furthermore, it can give an impression about the existence of stationary points and their stability. The proceeding is as follows:

- Draw the graph of f and the first bisecting line in a coordinate system. Cutting points are stationary points.
- Choose a starting value x_0 and the corresponding $f(x_0)$.
- Iteration:

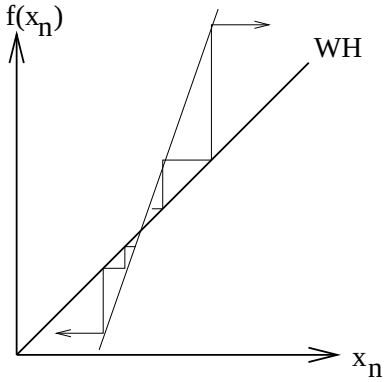


Examples

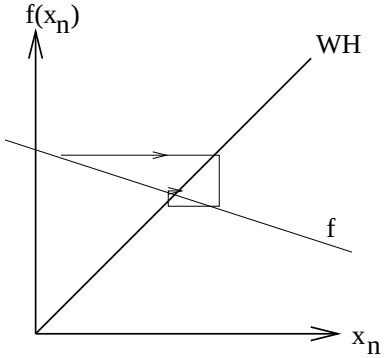
(for the non-homogeneous linear model (2.3))



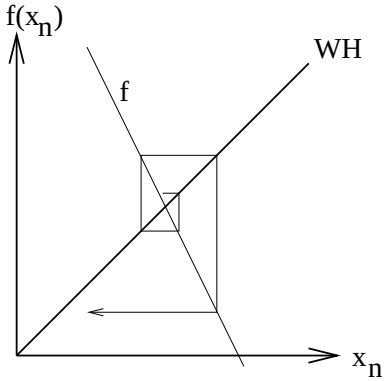
$a = \frac{1}{2}$, $b = 2$, stable



$a = 2$, $b = -4$, unstable



$a = -\frac{1}{2}$, $b = 6$, oscillatory stable



$a = -2$, $b = 12$, oscillatory unstable

2.2.2 Logistic equation

Literature: Edelstein-Keshet [12]

Problem:

The unlimited growth of a population is unrealistic, since a habitat has only a limited capacity.
The "old" linear model can be reformulated in the following way:

$$\begin{aligned} x_{n+1} &= rx_n - \mu x_n \\ &= x_n(r-\mu), \end{aligned}$$

where $r = 1 + \gamma$ is the reproduction rate.
Assumption of the model: The death rate μ is proportional to the number of individuals, $\mu(x) = dx$ (the more individuals, the higher the death rate).

$$\begin{aligned} \Rightarrow \quad x_{n+1} &= x_n(r - dx_n) \\ &= rx_n(1 - \frac{d}{r}x_n) \\ &= rx_n(1 - \frac{x_n}{K}), \end{aligned}$$

where $\frac{d}{r} = \frac{1}{K}$, K is the capacity of the habitat.
(Another "direct" possibility of interpretation: $x_{n+1} = rx_n - dx_n^2 \rightsquigarrow$ the death term growth faster for large x_n than the birth term)
The equation is simplified by measuring the population size as a portion of the maximal population:

$$x_{n+1} = rx_n(1 - x_n), \qquad \text{corresponds to } K = 1$$

Even if r is nonnegative, $\mathbb{R}_+$ is not positive invariant in general. E.g. for $x_i > 1$, x_{i+1} becomes negative. Furthermore, it is easy to see that for $r > 4$ and $x_i = \frac{1}{2}$, $x_{i+1} = \frac{r}{4}$ there show up negative values.
Thus, it makes sense to assume

$$0 \leq r \leq 4.$$

Then, the right hand side function

$$f(x) = rx(1-x) \tag{2.4}$$

maps the interval $[0, 1]$ into itself.
Determination of the fixed points (due to nonlinearity, it is possible to have several of them):

$$\begin{aligned} \bar{x} = f(\bar{x}) \quad &\Leftrightarrow \quad \bar{x} = r\bar{x}(1-\bar{x}) \\ &\Leftrightarrow \quad \bar{x}[1 - r(1-\bar{x})] = 0 \\ &\Leftrightarrow \quad \bar{x}_1 = 0 \text{ or } 1 - r(1-\bar{x}) = 0 \quad \leftrightarrow \bar{x}_2 = 1 - \frac{1}{r}. \end{aligned}$$

$\bar{x}_2$ is positive and therefore biologically relevant only for $r > 1$.

Analysis of the stability:

$f'(\bar{x}) = r - 2r\bar{x}$
For $\bar{x}_1 = 0$ we have $f'(0) = r$, i.e. stability for $0 < r < 1$ respectively unstable behaviour for $r > 1$.
For $\bar{x}_2 = 1 - \frac{1}{r}$ it holds: $f'(1 - \frac{1}{r}) = r - 2r(1 - \frac{1}{r}) = 2 - r$, i.e. it is stable for $1 < r < 3$.
Hence, there are the following cases:

$r < 1$: $\bar{x}_1 = 0$ stable, $\bar{x}_2 = 1 - \frac{1}{r} < 0$ unstable

$1 < r < 2$: $\bar{x}_1 = 0$ unstable, $\bar{x}_2 = 1 - \frac{1}{r}$ stable

$2 < r < 3$: $\bar{x}_1 = 0$ unstable, $\bar{x}_2 = 1 - \frac{1}{r}$ oscillatory stable

$r > 3$: $\bar{x}_1 = 0$ unstable, $\bar{x}_2 = 1 - \frac{1}{r}$ unstable

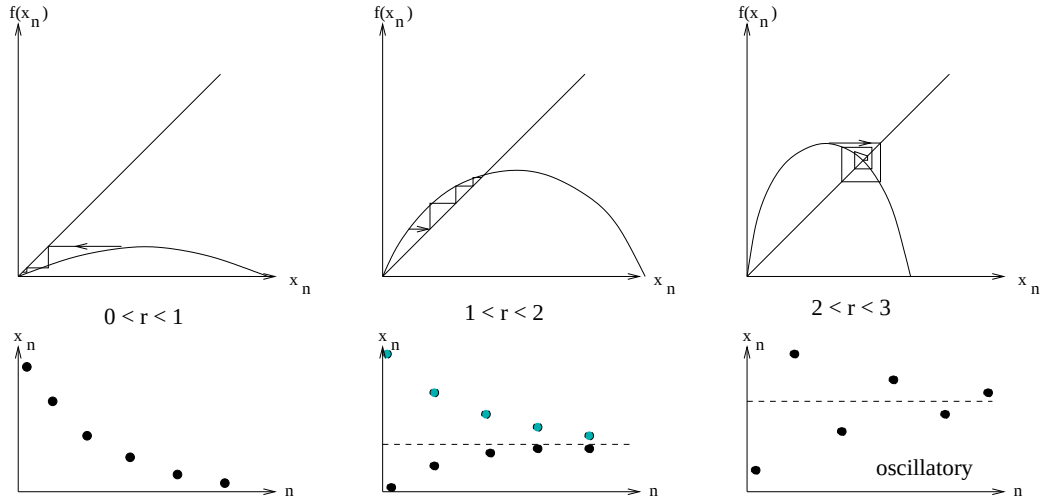
We consider the graphical iteration.

$$x_{n+1} = rx_n - rx_n^2$$

Short curve sketching:

- parabola (open down-side)

- intersecting $(0,0)$
- local maximum at $f'(x) = 0 \;\Leftrightarrow\; r - 2rx = 0 \;\Leftrightarrow\; x = \frac{1}{2},\ f(x) = \frac{r}{4}$
- intersecting $(1,0)$



Observation: At $r = 1$ $\bar{x}_1 = 0$ looses its stability (there $f'(0)$ becomes > 1), at the same time another stable stationary point appears. This phenomenon is called "transcritical bifurcation". Generally, an abrupt change of the qualitative behaviour, dependent on parameter values, is called bifurcation.

Case $r > 3$

Assertion: For $r > 3$, there are orbits of period 2 (so-called "oscillations"). These are fixed points of the function $g = f^2$, i.e. they satisfy

$$x_{n+2} = f(x_{n+1}) = x_n \text{ resp. } x_n = f(f(x_n)).$$

Obviously, fixed points of f are also fixed points of g, but not reversely. Therefore, we look for a $\bar{x}$, such that $\bar{x} = g(\bar{x})$, i.e.

$$\begin{aligned} \bar{x} &= f(f(\bar{x})) \\ &= rf(\bar{x})(1 - f(\bar{x})) \\ &= r(r\bar{x}(1-\bar{x}))(1 - r\bar{x}(1-\bar{x})) \end{aligned}$$

which can be computed. Except for the already known stationary points $\bar{x}_1 = 0$ and $\bar{x}_2 = 1 - \frac{1}{r}$ we get:

$$\bar{x}_{3,4} = \frac{-(r^3 + r^2) \pm \sqrt{(r^3 + r^2)^2 - 4(-r^3)(-r^2 - r)}}{-2r^3}$$

which are real for $r > 3$ and have the following property:

$$f(\bar{x}_3) = \bar{x}_4 \text{ and } f(\bar{x}_4) = \bar{x}_3$$

The stability of the periodic orbit of f is equivalent to the stability of the fixed point of g, hence we consider

$$\begin{aligned} g'(\bar{x}_3) &= [f(f(\bar{x}_3))]' = f'(f(\bar{x}_3)) \cdot f'(\bar{x}_3) = f'(\bar{x}_4) \cdot f'(\bar{x}_3) \\ g'(\bar{x}_4) &= f'(\bar{x}_3) \cdot f'(\bar{x}_4) \end{aligned}$$

By $f'(x) = r - 2rx$ we get:

$$\begin{aligned} g'(\bar{x}_3) &= (r - 2r\bar{x}_4)(r - 2r\bar{x}_3) \\ &= r^2(1 - 2\bar{x}_3 - 2\bar{x}_4 + 4\bar{x}_3\bar{x}_4). \end{aligned}$$

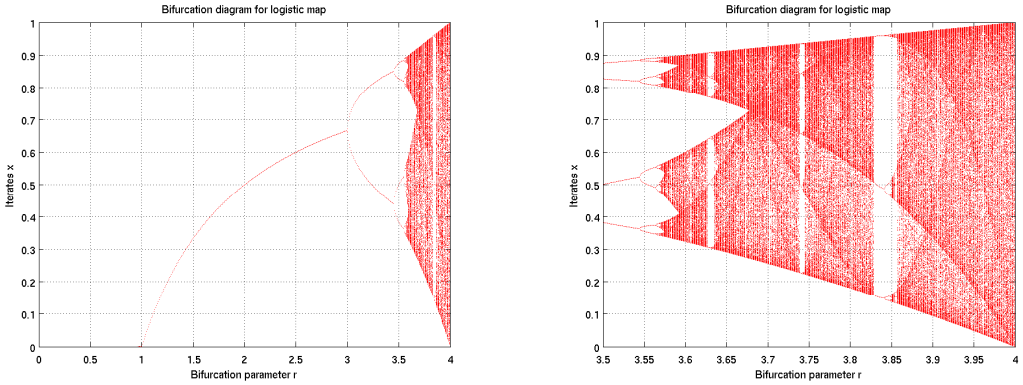
Result:

For $r > 3$, r "near" 3:	$\lvert g'(\bar{x}_3)\rvert < 1 \Rightarrow$ stable
$r = 1 + \sqrt{6}$	$g'(\bar{x}_3) = -1 \Rightarrow$ Stability is lost

For a visualisation of the different behaviour of the discrete logistic equation for different values of r, have e.g. a look on Fig. 2.9. in the book of Edelstein-Keshet [12]. And just for fun: see Fig. 2.3. in the same book.

Bifurcation diagram

For larger r (> 3) there happens so-called period-doubling (which can be computed analogously, e.g. by $h(x) = g(g(x)) = f(f(f(f(x)))) \ldots$). It can be shown that in each case the orbit with the larger period is stable (Feigenbaum). There are also orbits with other periods. We will learn something about the existence of these orbits in the next subsection.
The qualitative behaviour can be represented by a so-called bifurcation diagram. In each case, the "stable objects" will be plotted.



Creating such a diagram with the aid of a computer:

- Choose a parameter value (here it is done for r)
- Run 1000 steps of iteration (from an arbitrary starting value).
- Plot the next 1000 values (of the iteration) in the line above the chose r.
- Do the same procedure for other values of r

The discrete logistic equation, although it looks so simple, shows up chaotic behaviour for "large" values of r. This means, that e.g. for slightly altered starting conditions, it will show a quite different time course, may look like "jumping", unpredictable.
This chaotic behaviour is not caused by stochastic or random influences, it can be exactly reproduced by starting under the same conditions, as we consider here a deterministic model.
How realistic is such a chaotic behaviour, does this appear in real-world ecological systems or is this a more or less artificial finding? In reality, it is difficult to decide which influences are caused by a "deterministic chaotic behaviour" and which ones are due to stochastic influences.
The logistic equation is a nice example for a nonlinear difference equation with a parameter that influences the behaviour of the system extensive. In biological applications it is used not so often, it is more a useful "pedagogical" example. But the results and methods can be used everywhere. There are other, more realistic models, which describe the limited growth of a population. A few examples, just mentioned:

- The model of Varley, Gradwell and Hassell (1973):

  $$N_{t+1} = \frac{\lambda}{\alpha} N_t^{1-b},$$

  where $\lambda > 1$ is the reproductive rate, $1/\alpha N_t^{-b}$ denotes the fraction that survives to the reproductive adulthood.

- The model of Hassell (1975):

  $$N_{t+1} = \lambda N_t (1 + aN_t)^{-b},$$

  where λ, a, b are positive constants.

- The model of May (1975):

  $$N_{t-1} = N_t \cdot exp\left(r \cdot \left(1 - \frac{N_t}{K}\right)\right),$$

  where r and K are positive constants.

- Later, the generalised Ricker equation is introduced.

Further information about the discrete logistic equation can be found e.g. in [12, 17, 27, 10, 44].

2.2.3 Sarkovskii theorem

Following the discussion about the existence of orbits with different periods (for the logistic equation) we want to have a look for some more general results. We mention these theorems and observations without proofs (which can be found e.g. in [38], [34], [27]) The theorem of Li and Yorke deals with a more general class of maps of intervals which includes (2.4) as a special case.

Theorem 1 (Li and Yorke) *Let $f : [0,1] \to [0,1]$ be a continuous function with $f(0) = f(1) = 0$ and $f(x) > 0$ for $0 < x < 1$. Assume that the system*

$$x_{n+1} = f(x_n)$$

has an orbit of minimal period 3. That means, there are three different point x_1, x_2, x_3 with $x_2 = f(x_1)$, $x_3 = f(x_2)$ and $x_1 = f(x_3)$. Then, for each integer p there exists an orbit of minimal period p.

The assumptions of this theorem do not claim the stability of the orbit of period 3, and there is nothing said about the stability of all the other periodic orbits. In concrete cases most of these orbits seem to be unstable. Although, the theorem of Li and Yorke yields an applicable criterion for a complex dynamic.

It was shown by Smale and Williams that the discrete logistic equation has an orbit of minimal period 3 for $r = 3.83$. Hence, the assumptions of the theorem of Li and Yorke are fulfilled for this equation. By examining the equation for parameter values near $r = 3.83$, the following behaviour is found: In the parameter interval $[1, 4]$, there is a kind of "window" (α, β) (which is approximately $\alpha = 3.82$, $\beta = 3.84$) such that for all $r \in (\alpha, \beta)$ there exist a stable and an unstable orbit of period 3. At the lower end of this parameter interval, these two orbits appear by a saddle-node-bifurcation; at the upper end, the stable one shows a period doubling, creating a stable orbit of period 6.

Even though the theorem of Li and Yorke seems to be quite astonishing, it is only a special case of the theorem of Sarkovskii (dating from 1964). It is a very nice result, which depends only on the continuity of the considered function. For the formulation of this theorem we introduce a special order on the integers.

Definition 3 (Sarkovskii ordering) *The so-called Sarkovskii ordering of the natural numbers is as follows:*

$$3 \lhd 5 \lhd 7 \lhd \ldots \lhd 2 \cdot 3 \lhd 2 \cdot 5 \lhd 2 \cdot 7 \lhd \ldots \lhd 2^2 \cdot 3 \lhd 2^2 \cdot 5 \lhd \ldots \lhd 2^n \cdot 3 \lhd 2^n \cdot 5 \lhd \ldots \lhd \ldots \lhd 2^3 \lhd 2^2 \lhd 2^1 \lhd 1$$

In words: First comes the 3, then all other odds in ascending order, then all odds multiplied with 2, then all odds multiplied with the powers of 2 and so on. Finally, the pure powers of 2 are listed, in descending order.

Theorem 2 (Sarkovskii) *Let $f : \mathbb{R} \to \mathbb{R}$ be a continuous function. If the system $x_{n+1} = f(x_n)$ possesses a periodic orbit of minimal period p, and $p \lhd q$, then it also shows up a periodic orbit of minimal period q.*

The special case $p = 3$ covers the theorem of Li and Yorke. A further result is, that if there is a power of two as a period, also the lower powers of two appear as minimal periods.

There are some other nice theorems in this area, one of them we will mention, but not prove, because it is applied in the context of the Ricker model. The proof can be found e.g. in [34]. f is taken to be the right hand side of the discrete system.

Theorem 3 *Let $f : (0, \infty) \to (0, \infty)$ be continuous, and assume that f and f^2 have at most one fixed point. Then one of the following six mutually exclusive scenarios holds:*

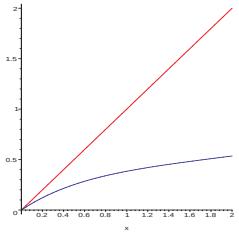
1. *All solutions tend to ∞.*
2. *All solutions converge to 0.*
3. *There exists a unique fixed point x^* of f, and all solutions converge to x^*.*
4. *There exists a unique fixed point x^* of f, and all solutions starting in $(0, x^*)$ converge to 0, while all solutions starting in (x^*, ∞) tend to ∞.*
5. *There exists a unique fixed point x^* of f, and all solutions starting in $(0, x^*)$ converge to x^* or tend to ∞ while all solutions starting in (x^*, ∞) tend to ∞.*
6. *There exists a unique fixed point x^* of f, and all solutions starting in $(0, x^*)$ converge to 0 while all solutions starting in (x^*, ∞) converge to x^* or to 0.*

2.2.4 Ricker model

Another example for a discrete population dynamics is the so-called generalised Ricker equation:

$$x_{n+1} = x_n(q + re^{-x_n}), \qquad 0 \le q < 1, \;\; r > 0. \tag{2.5}$$

Let $f(x) = x \cdot (q + re^{-x})$. If $q + r \le 1$, we have $\lim_{x\to 0} \frac{f(x)}{x} = q + r \le 1$.



Looking for fixed points of f or f^2 ($\neq 0$):

$$\begin{aligned} & x = f(x) \\ \Leftrightarrow \quad & x = x(q + re^{-x}) \\ \Leftrightarrow \quad & x = 0 \text{ or } 1 = q + re^{-x} < q + r \le 1 \end{aligned}$$

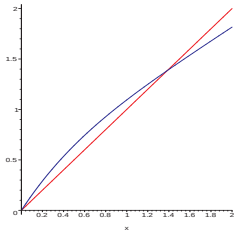
$\rightsquigarrow$ no fixed point of f (except for the 0). In the same way we get (for $x > 0$)

$$\begin{aligned} & x = f^2(x) \\ \Leftrightarrow \quad & x = x(q + re^{-x}) \cdot (q + re^{x(-q-re^{-x})}) \\ \Leftrightarrow \quad & 1 = (q + re^{-x}) \cdot \underbrace{(q + r\overbrace{e^{\overbrace{x(-q-re^{-x})}^{<0}}}^{<1})}_{<1} < 1 \end{aligned}$$

Since $\frac{f(x)}{x}$ is strictly decreasing and f and f^2 cannot have a fixed point, Theorem 3 shows that all solutions tend to zero (there remain possibilities 1 and 2, since there is no fixed point, and $f(x) < x$ gives convergence towards 0).

Case $q + r > 1$:
f has a unique fixed point $x^* > 0$, $x^* = -\ln(\frac{1-q}{r})$. Test it:

$$f(x^*) = -\ln(\frac{1-q}{r}) \cdot (q + re^{\ln(\frac{1-q}{r})}) = -\ln(\frac{1-q}{r}) \cdot 1$$



Normalise the equation (then it is more convenient to handle):
Observing $1 = q + re^{-x^*}$ yields $r = (1-q)e^{x^*}$, and thus

$$\begin{aligned} x_{n+1} &= x_n(q + re^{-x_n}) \\ &= x_n(q + (1-q)e^{x^*}e^{-x_n}) \\ &= x_n(q + (1-q)e^{x^*-x_n}). \end{aligned}$$

Putting $\rho = x^*$ and $y_n = \frac{x_n}{\rho}$, we have

$$\begin{aligned} y_{n+1} &= y_n[q + (1-q)e^{\rho(1-y_n)}] \\ &= g(y_n), \end{aligned}$$

wherein $g(y) = y[q + (1-q)e^{\rho(1-y)}]$. Now $y^* = 1$ is the unique fixed point of g.

The following proposition is stated without a proof (due to lack of time, it is easily done by some basic calculations and smaller propositions in the style of the last subsection)

Proposition 2 *Consider the generalised Ricker model (2.5) with $q + r > 1$. Let $\rho = -\ln(\frac{1-q}{r})$ be the unique fixed point of f. Then we have:*

1. *If $\rho \leq 2 + \ln(1 + \frac{2q}{1-q})$, all solutions converge to ρ.*
2. *If $\rho > \frac{2}{1-q}$, then the set of initial values, for which the solutions converge to ρ is countable. Moreover, f^2 has a positive fixed point different from ρ.*

(If $q = 0$ - when adults do not survive the reproductive period - then there is no gap between $2+\ln(1+\frac{2q}{1-q})$ and $\frac{2}{1+q}$; otherwise there is a gap growing with q).

Remark: If $\rho \in (2 + \ln(1 + \frac{2q}{1-q}), \frac{2}{1-q})$, the behaviour of the solutions is rather complicated, similar to that of the discrete logistic equation.

A "real world" application of the Ricker model:
There are data from the Skeena River Sockeye Salmon in British Columbia, Canada, (see the internet link below) and are taken as four year averages:

Year	Population (in thousands)
1908	1,098
1912	740
1916	714
1920	615
1924	706
1928	510
1932	278
1936	448
1940	528
1944	639
1948	523

Reasons, why the Ricker model was chosen, were e.g.:

- In opposite to the logistic growth model, x_n does not become negative for large populations
- Ricker's model is often used in fishery management as a more realistic updating function, which can also handle largely fluctuating populations
- The life cycle of the salmon is well-suited to be modeled by a discrete dynamical system.

The model parameters were fitted:

$$P_{n+1} = R(P_n) = 1.535P_n \exp(-0.000783P_n)$$

With these parameter values, the following simulation was done:

(figure, data and some more information taken from http://www-rohan.sdsu.edu/∼jmahaffy/courses/s00/math121/lectures/product_rule/product.html)

Result:
The Ricker model shows an equilibrium around 550 000 , this fits well to the data. The fluctuations can be explained by the influence of varying environmental parameters.

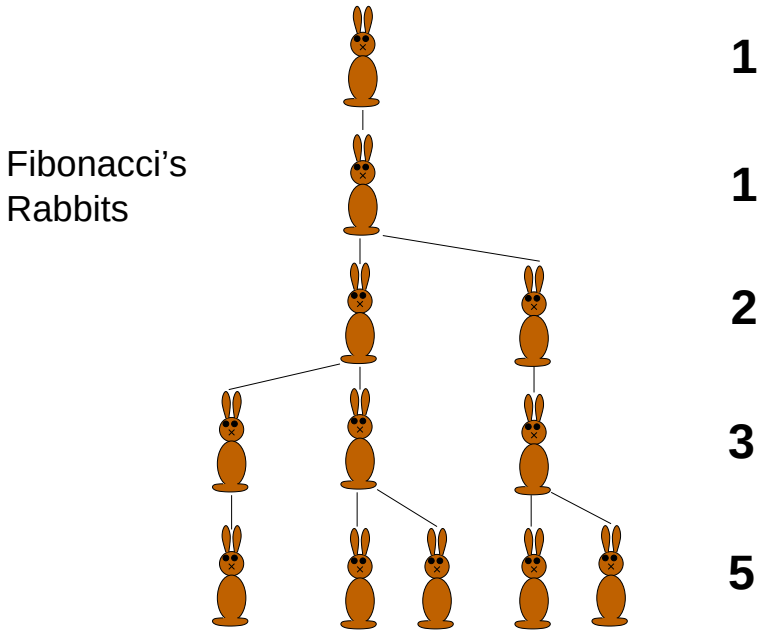
2.3 Systems of difference equations

Very nice source: http://www.mcs.surrey.ac.uk/Personal/R.Knott/Fibonacci/fibnat.html#Rabbits . Let us consider the following example:

In the year 1202, Fibonacci investigated how fast rabbits could breed in ideal circumstances. The assumptions are:

- Rabbits are able to mate at the age of one month and at the end of its second month the females can produce another pair of rabbits.
- The rabbits never die
- The females produce one new pair every month from the second month on.

This leads to the following "population dynamics":



We introduce one time step to be one month and x_n to be the number of pairs at time n.

The Fibonacci sequence is defined as follows:

$$x_{n+1} = x_n + x_{n-1}.$$

This difference equation depends on two time steps, but it can be reformulated by introducing a new variable $y_n = x_{n-1}$. This leads to the 2D system

$$\begin{aligned} x_{n+1} &= x_n + y_n \\ y_{n+1} &= x_n. \end{aligned}$$

This system depends only on one time step, but has two equations. Generally, a linear system in 2D can be written as

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

or in matrix notation

$$\begin{pmatrix} x \\ y \end{pmatrix}_{n+1} = \underbrace{\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}}_{\text{Matrix } A} \begin{pmatrix} x \\ y \end{pmatrix}_n$$

Obviously, $(\bar{x}, \bar{y}) = (0, 0)$ is a stationary state .

2.3.1 Linear systems

[38] In many cases, one is interested to know something about the behaviour of the solutions for large values of n. We try to collect here some basic facts for homogeneous linear systems. Let $u \in \mathbb{R}^m$ be a m-vector, $A \in \mathbb{R}^{m\times m}$. We consider the system

$$u_{n+1} = Au_n. \tag{2.6}$$

Then $u_n = A^n u_0$, $n = 0, 1, 2, \ldots$ is the solution of (2.6) with initial condition u_0. Let λ an eigenvalue of A with the corresponding eigenvector u, then we have $A^n u = \lambda^n u$ and $u_n = \lambda^n u_0$ satisfies the difference equation (2.6).
For u_0 being a linear combination of eigenvectors of A, $u_0 = b_1 v_1 + \ldots + b_k v_k$, ($\lambda_i$ corresponding eigenvalue of the eigenvector u_i) we get as the solution of (2.6):

$$u_n = b_1\lambda_1^n v_1 + \ldots + b_k\lambda_k^n v_k.$$

Without proof, we mention the following

Theorem 4 (Putzer algorithm) *The solution of (2.6) with initial value u_0 is*

$$u_n = A^n u_0 = \sum_{i=0}^{m-1} c_{i+1,n} M_i u_0,$$

where the M_i are given by

$$M_0 = I, \qquad M_i = (A - \lambda_i I)M_{i-1}, \qquad i = 1, \ldots, m$$

and the $c_{i,n}$ are uniquely determined by

$$\begin{pmatrix} c_{1,0} \\ \vdots \\ \vdots \\ c_{m,0} \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix} \quad \textit{and} \quad \begin{pmatrix} c_{1,n+1} \\ \vdots \\ \vdots \\ c_{m,n+1} \end{pmatrix} = \begin{pmatrix} \lambda_1 & 0 & 0 & \ldots & 0 \\ 1 & \lambda_2 & 0 & \ldots & 0 \\ 0 & 1 & \lambda_3 & \ldots & 0 \\ \vdots & \ddots & \ddots & & \vdots \\ 0 & \ldots & 0 & 1 & \lambda_m \end{pmatrix} \begin{pmatrix} c_{1,n} \\ \vdots \\ \vdots \\ c_{m,n} \end{pmatrix}. \tag{2.7}$$

For the matrix A, the spectral radius $\rho(A)$ is defined by

$$\rho(A) := max\{|\lambda| : \lambda \text{ is eigenvalue of } A\}.$$

Another nice property is given in the following theorem (also without proof here, but this could be done by using the Putzer algorithm).

Theorem 5 *Let A be a $m \times m$ matrix with $\rho(A) < 1$. Then every solution u_n of (2.6) satisfies $\lim_{n\to\infty} u_n = 0$. Moreover, if $\rho(A) < \delta < 1$, then there is a constant $C > 0$ such that*

$$\|u_n\| \le C\|u_0\|\delta^n$$

for all $n \in \mathbb{N}_0$ and any solution of (2.6).

Remark: If $\rho(A) \ge 1$, then there are solutions u_n of (2.6) which do not tend to zero for $n \to \infty$. E.g., let λ be an eigenvalue with $|\lambda| \ge 1$ and u the corresponding eigenvector, then $u_n = \lambda^n u$ is a solution of (2.6) and $\|u_n\| = |\lambda|^n\|u\|$ does not converge to zero for $n \to \infty$.

What happens, if the spectral radius reaches the 1? We mention the following theorem, without proof.

Theorem 6 *Let A be a $m \times m$ matrix with $\rho(A) \le 1$ and assume that each eigenvalue of A with $|\lambda| = 1$ is simple. Then there is a constant $C > 0$ such that*

$$\|u_n\| \le C\|u_0\|$$

for every $n \in \mathbb{N}$ and $u_0 \in \mathbb{R}^m$, where u_n is solution of (2.6).

Up to now, we considered the behaviour of solutions in general. This can be done more detailed, with respect to certain subspaces in which the solutions start.

Let λ be an eigenvalue of a $m \times m$ matrix A with multiplicity l. Then, the generalised eigenvectors of A corresponding to λ are the nonzero solutions v of

$$(A - \lambda I)^l v = 0.$$

Of course, every eigenvector of A is also a generalised eigenvector. The set of all generalised eigenvectors corresponding to λ, together with the 0-vector, is a vector space with dimension l, and is called generalised eigenspace. Obviously, if v is a generalised eigenvector, then Av is contained in the same generalised eigenspace, because A commutes with $(A - \lambda I)^l$. The intersection of any two (distinct from each other) generalised eigenspaces is the 0-vector.

Theorem 7 (The stable subspace theorem) *Let $\lambda_1, \ldots, \lambda_m$ be the eigenvalues of A (not necessarily distinct from each other) such that $\lambda_1, \ldots, \lambda_k$ are the eigenvalues with $|\lambda_i| < 1$, $i = 1, \ldots, k$. Let V be the k-dimensional space spanned by the generalised eigenvectors corresponding to $\lambda_1, \ldots \lambda_k$. If u_n is a solution of $u_{n+1} = Au_n$ with $u_0 \in V$, then $u_n \in V$ for all $n \in \mathbb{N}$ and $\lim_{n\to\infty} u_n = 0$. ($V$ is called the stable subspace).*

2.3.2 Phase plane analysis for linear systems

Here, we consider a linear two-dimensional system,

$$u_{t+1} = Au_t, \tag{2.8}$$

where u_t is a two-dimensional vector and A a real 2×2 matrix (nonsingular).

Reminder to some simple matrix operations:
Consider a matrix $A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$. A "fast formula" for the computation of the eigenvalues is

$$\lambda_{1,2} = \frac{a+d}{2} \pm \frac{1}{2}\sqrt{(a+d)^2 - 4(ad-bc)} = \frac{1}{2}tr(A) \pm \frac{1}{2}\sqrt{tr(A)^2 - 4det(A)}$$

Let λ be an eigenvalue, then the eigenvector(s) v, defined by $Av = \lambda v \leftrightarrow (A - \lambda I)v = 0$ can be computed by solving

$$\begin{aligned} (a-\lambda)v_1 + bv_2 &= 0 \\ cv_1 + (d-\lambda)v_2 &= 0 \end{aligned}$$

The so-called "real Jordan canonical form of A" is useful for our analysis.

Theorem 8 *For any real 2×2 matrix A there exists a nonsingular real matrix P such that*

$$A = PJP^{-1},$$

where J is one of the following possibilities

1. $$J = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}$$
   if A has two real (not necessarily distinct) eigenvalues λ_1, λ_2 with linearly independent eigenvectors.
2. $$J = \begin{pmatrix} \lambda & 1 \\ 0 & \lambda \end{pmatrix}$$
   if A has a single eigenvalue λ (with a single eigenvector).
3. $$J = \begin{pmatrix} \alpha & \beta \\ -\beta & \alpha \end{pmatrix}$$
   if A has a pair of complex eigenvalues $\alpha \pm i\beta$ (with non-zero imaginary part)

Proof: First case: A has real (not necessarily distinct) eigenvalues λ_1, λ_2 with the two linearly independent eigenvectors v_1, v_2. Take v_1 to be the first column vector and v_2 to be the second column vector. Then P is nonsingular, since v_1 and v_2 are linearly independent. We get

$$\begin{aligned} AP &= (Av_1 \quad Av_2) \\ &= (\lambda_1 v_1 \quad \lambda_2 v_2) \\ &= (v_1 \quad v_2) \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}, \end{aligned}$$

hence $A = PJP^{-1}$. Second case: A has one eigenvalue λ with a single independent eigenvector v. Choose a vector w in $\mathbb{R}^2$ which is independent of v. The Cayley-Hamilton-Theorem (each quadratic matrix is root of its characteristic polynom) yields

$$(A - \lambda I)(A - \lambda I)w = 0.$$

Consequently,

$$(A - \lambda I)w = cv,$$

with $c \neq 0$ (w is not an eigenvector). Let $u = c^{-1}w$ and $P = (v \quad u)$, then (due to $Au = A(c^{-1}w) = c^{-1}Aw = c^{-1}(\lambda w + cv)$)

$$\begin{aligned} AP &= (Av \quad Au) \\ &= (\lambda v \quad \lambda u + v) \\ &= (v \quad u) \begin{pmatrix} \lambda & 1 \\ 0 & \lambda \end{pmatrix}. \end{aligned}$$

Third case: Assume $\alpha \pm i\beta$ to be the eigenvalues of A, $\beta > 0$, with the corresponding eigenvectors $u + iv$, where u, v are real, independent vectors. Since

$$A(u + iv) = (\alpha + i\beta)(u + iv)$$

we have

$$\begin{aligned} Au &= \alpha u - \beta v \\ Av &= \beta u + \alpha v. \end{aligned}$$

Define $P = (u \quad v)$, then we get

$$\begin{aligned} AP &= (Au \quad Av) \\ &= (\alpha u - \beta v \quad \beta u + \alpha v) \\ &= (u \quad v) \begin{pmatrix} \alpha & \beta \\ -\beta & \alpha \end{pmatrix} \\ &= PJ \end{aligned}$$

□

If there are complex eigenvalues, i.e. the Jordan canonical form is $J = \begin{pmatrix} \alpha & \beta \\ -\beta & \alpha \end{pmatrix}$ with $\beta > 0$, choose an angle θ such that

$$\cos\theta = \frac{\alpha}{\sqrt{\alpha^2 + \beta^2}}, \quad \sin\theta = \frac{\beta}{\sqrt{\alpha^2 + \beta^2}},$$

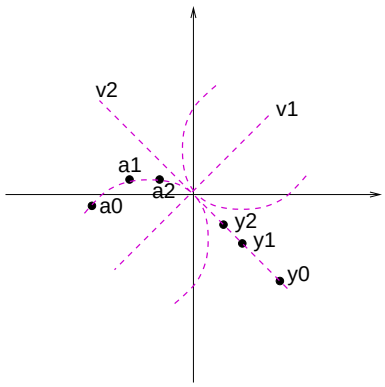
then we can write

$$J = \sqrt{\alpha^2 + \beta^2} \begin{pmatrix} \cos\theta & \sin\theta \\ -\sin\theta & \cos\theta \end{pmatrix} = |\lambda| R_\theta.$$

(R_θ is called rotation matrix)
Theorem 8 leads us to a distinction of cases for the behaviour of solutions of equation (2.8) in the phase plane.

Case 1a: $0 < \lambda_1 < \lambda_2 < 1$ (Sink)
All solutions of equation (2.8) are of the form

$$u_t = C_1 \lambda_1^t v_1 + C_2 \lambda_2^t v_2,$$

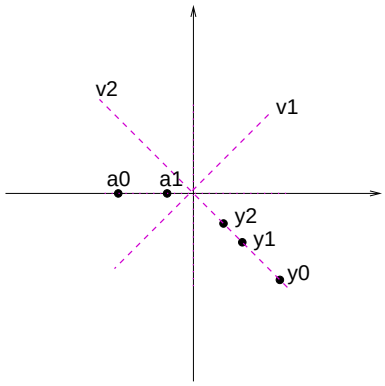


This is called a sink (or also a stable node) .
For the special cases $C_1 = 0$ respectively $C_2 = 0$, the solutions are lying on the line containing v_2 respectively v_1, otherwise the solution can be written as

$$u_t = \lambda_2^t \left(C_1 (\frac{\lambda_1}{\lambda_2})^t v_1 + C_2 v_2 \right).$$

Case 1b: $0 < \lambda < 1$

There are two possibilities:
If A has one eigenvalue with two independent eigenvectors, case 1a can be slightly modified and the figure has the form



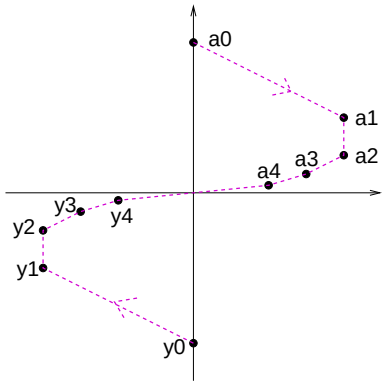
If A has a simple eigenvalue with only one independent eigenvector (and one generalised eigenvector v_2, i.e. $(A - \lambda I)^2 v_2 = 0$), i.e.

$$J = \begin{pmatrix} \lambda & 1 \\ 0 & \lambda \end{pmatrix},$$

then the solution can be written as

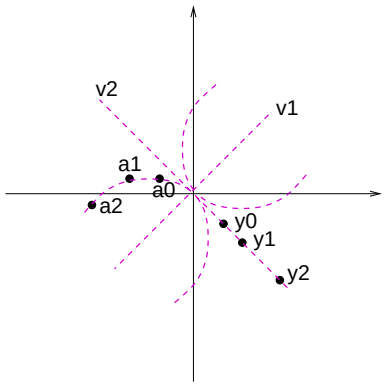
$$u_t = \begin{pmatrix} \lambda^t & t\lambda^{t-1} \\ 0 & \lambda^t \end{pmatrix} u_0.$$

For $t \to \infty$, all solutions tend to 0.



Case 2: $1 < \lambda_1 < \lambda_2$ (Source)

Similar to Case 1a, but the solutions tend away from 0 for $t \to \infty$.



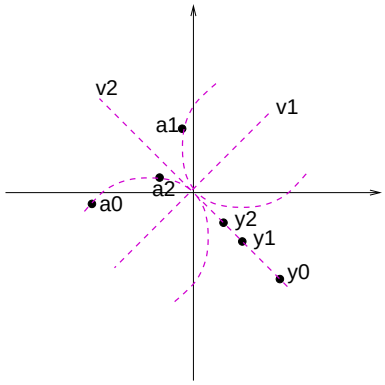
(it is also called an unstable node)

Case 3: $-1 < \lambda_1 < 0 < \lambda_2 < 1$ (Sink with reflection)

Again, it is similar to Case 1a, the solutions are described by

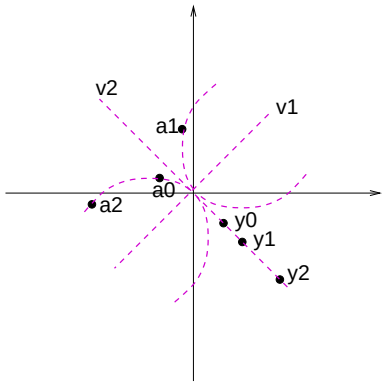
$$u_t = C_1 \lambda_1^t v_1 + C_2 \lambda_2^t v_2.$$

Since λ_1^t has alternating signs, the solutions jump between the different branches (provided that $C_1 \neq 0$)



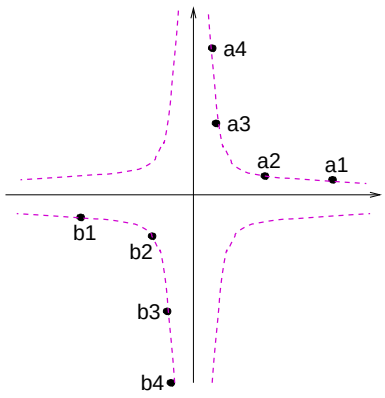
Case 4: $\lambda_1 < -1 < 1 < \lambda_2$ (Source with reflection)

Corresponding to Case 2, but jumping in the direction of v_1.



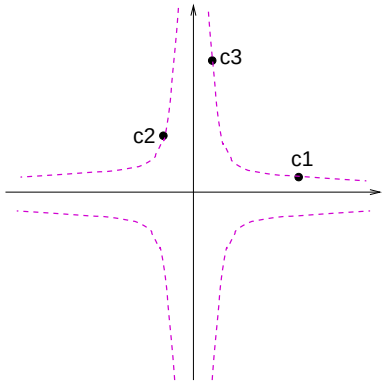
Of course, also reflection in both directions is possible ($\lambda_1, \lambda_2 < 0$).

Case 5: $0 < \lambda_1 < 1 < \lambda_2$ (saddle)



One direction (eigenvector) is stable, the other is unstable, the resulting dynamics around the origin is called a saddle.

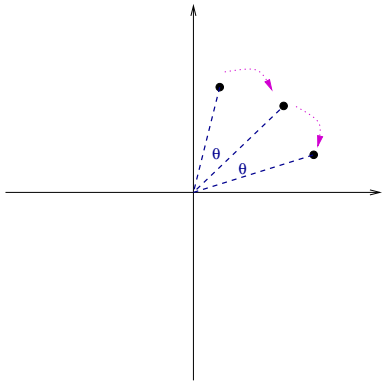
Case 6: $-1 < \lambda_1 < 0 < 1 < \lambda_2$ (saddle with reflection)



Same like case 5, but the stable direction has a negative eigenvalue, leading to jumping behaviour in that component.
Of course, this reflection could also appear in the unstable direction (exclusively or additionally).

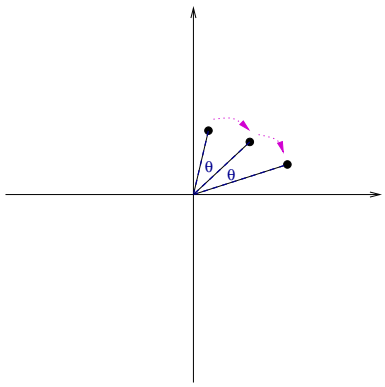
Now we consider some cases with complex eigenvalues.

Case 7: $\alpha^2 + \beta^2 = 1$ (Centre)



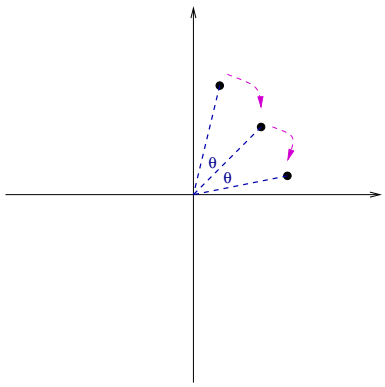
Each solution moves clockwise (with the angle θ) around a circle centred at the origin, which is called a centre.

Case 8: $\alpha^2 + \beta^2 > 1$ (unstable spiral)



Since $J = |\lambda| R_\theta$ and $|\lambda| > 1$, the solution moves away from the origin with each iteration, in clockwise direction. This creates an unstable spiral.

Case 9: $\alpha^2 + \beta^2 < 1$ (stable spiral)



Same as Case 8, but $|\lambda| < 1$, leading to a stable spiral.

2.3.3 Stability of nonlinear systems

Up to now, we only considered linear systems and their behaviour. But most of the realistic model systems are nonlinear and we need some tools how to learn something about their behaviour and the stability of equilibria.

Definition 4 *An autonomous system is given by*

$$u_{n+1} = f(u_n), \qquad n \in \mathbb{N}_0,$$

where $u_n \in \mathbb{R}^m$ *and* $f : \mathbb{R}^m \to \mathbb{R}^m$ *(or* $f : D \to D$, $D \subseteq \mathbb{R}^m$*).*

If A is a $m \times m$ matrix, then $f(x) = Ax$ is a special case.

Definition 5 *Let* $u_{n+1} = f(u_n)$ *be an autonomous system,* $f : D \to D$, $D \subseteq \mathbb{R}^m$. *A vector* $v \in D$ *is called equilibrium or steady state or stationary point or fixed point of* f*, if* $f(v) = v$ *and* $v \in D$ *is called periodic point of* f*, if* $f^p(v) = v$. p *is a period of* v.

1. *Let* $v \in D$ *be a fixed point of* f. *Then* v *is called stable, if for each* $\varepsilon > 0$ *there is* $\delta > 0$ *such that*

$$\|f^n(u) - v\| < \varepsilon \quad \text{for all } u \in D \text{ with } \|u - v\| < \delta \text{ and all } n \in \mathbb{N}_0$$

   (i.e. $f^n(U_\delta(v)) \subseteq U_\varepsilon(v)$*). If* v *is not stable, it is called unstable.*

2. *If there is, additionally to (1), a neighbourhood* $U_r(v)$ *such that* $f^n(u) \to v$ *as* $n \to \infty$ *for all* $u \in U_r(v)$*, then* v *is called asymptotically stable.*

3. *Let $w \in D$ be a periodic point of f with period $p \in \mathbb{N}$. Then w is called (asymptotically) stable, if w, $f(w), \ldots, f^{p-1}(w)$ are (asymptotically) stable fixed points of f^p.*

Remark: Intuitively, a fixed point v is stable, if points close to v do not wander far from v. If additionally all solutions starting near v converge to v, v is asymptotically stable.

Remember to the homogeneous linear systems $u_{n+1} = Au_n$: Theorem 5 yields that in this case the origin is asymptotically stable if and only if $\rho(A) < 1$. In fact, 0 is global asymptotically stable, which means that all solutions tend to 0, independent from their starting point. The weaker conditions in Theorem 6 yields that 0 is stable.

Theorem 9 *Let $u_{n+1} = f(u_n)$ be an autonomous system. Suppose $f : D \to D$, $D \subseteq \mathbb{R}^m$ open, is twice continuously differentiable in some neighbourhood of a fixed point $v \in D$. Let J be the Jacobian matrix of f, evaluated at v. Then*

1. *v is asymptotically stable if all eigenvalues of J have magnitude less than 1.*
2. *v is unstable if at least one eigenvalue of J has magnitude greater than 1.*

Remark: If $max\{|\lambda| : \lambda \text{ eigenvalue of } K\} = 1$, then we cannot give a statement about the stability of the fixed point v by that criterion; the behaviour then depends on higher order terms than linear ones.

2.3.4 Proceeding in the 2D case

Here we consider the 2D case more concrete. The system can be formulated with the variables x and y:

$$\begin{aligned} x_{n+1} &= f(x_n, y_n) \\ y_{n+1} &= g(x_n, y_n) \end{aligned} \tag{2.9}$$

Stationary states $\bar{x}$ and $\bar{y}$ satisfy

$$\begin{aligned} \bar{x} &= f(\bar{x}, \bar{y}) \\ \bar{y} &= g(\bar{x}, \bar{y}) \end{aligned}$$

We need the Jacobian matrix at a certain stationary point $(\bar{x}, \bar{y})$:

$$A = \begin{pmatrix} \frac{\partial f}{\partial x}|_{\bar{x},\bar{y}} & \frac{\partial f}{\partial y}|_{\bar{x},\bar{y}} \\ \frac{\partial g}{\partial x}|_{\bar{x},\bar{y}} & \frac{\partial g}{\partial y}|_{\bar{x},\bar{y}} \end{pmatrix}$$

The eigenvalues λ_1 and λ_2 of A yield the information about stability of the system. In some cases, it is easier to handle the following (necessary and sufficient) condition, which can be derived from the theorem above in the 2D case (first introduced by [42]):
Both eigenvalues satisfy $|\lambda_i| < 1$ and the steady state $(\bar{x}, \bar{y})$ is stable, if

$$2 > 1 + det\, A > |tr\, A|. \tag{2.10}$$

This can be easily shown:
The characteristic equation reads

$$\lambda^2 - tr\, A\, \lambda + det\, A = 0$$

and has the roots

$$\lambda_{1,2} = \frac{tr\, A \pm \sqrt{tr^2 A - 4\, det\, A}}{2}$$

In case of real roots, they are equidistant from the value $\frac{tr\, A}{2}$. Thus, first has to be checked that this midpoint lies inside the interval $(-1, 1)$:

$$-1 < \frac{tr\, A}{2} < 1 \quad \Leftrightarrow \quad |tr\, A/2| < 1.$$

Furthermore, the distance from $tr\, A/2$ to either root has to be smaller than to an endpoint of the interval, i.e.

$$1 - |tr\, A/2| > \frac{\sqrt{tr^2 A - 4\, det\, A}}{2}.$$

Squaring leads to

$$1 - |tr\, A| + \frac{tr^2 A}{4} > \frac{tr^2 A}{4} - det\, A,$$

and this yields directly

$$1 + det\, A > |tr\, A|.$$

Advantage: It is not necessary to compute explicitely the eigenvalues

2.3.5 Example: Cooperative system / Symbiosis model

A simple model for two cooperating species (that means: one species benefits from the existence of the other) looks as follows:

$$\begin{aligned} x_{n+1} &= x_n + x_n(\gamma - \mu x_n) + \alpha x_n y_n \\ y_{n+1} &= y_n + y_n(g - m y_n) + a x_n y_n \end{aligned}$$

Interpretation of the included terms:

$x_n(\gamma - \mu x_n)$, $y_n(g - m y_n)$:	Growth of the single species, with limited capacity
$\alpha x_n y_n$, $a x_n y_n$:	Symbiosis term, proportional to the own and to the "external" population size

Computation of the stationary states :
Obviously, $(\bar{x}, \bar{y}) = (0,0)$, $(\bar{x}, \bar{y}) = (\frac{\gamma}{\mu}, 0)$, $(\bar{x}, \bar{y}) = (0, \frac{g}{m})$ are stationary.
Next, we compute the coordinates of the coexistence point ($\bar{x} \neq 0, \bar{y} \neq 0$):

$$\begin{aligned} x_n(\gamma - \mu x_n) + \alpha x_n y_n &= 0 \\ y_n(g - m y_n) + a x_n y_n &= 0, \qquad \text{where } x_n, y_n \neq 0 \end{aligned}$$

$$\begin{aligned} \Leftrightarrow \qquad (\gamma - \mu x_n) + \alpha y_n &= 0 \qquad \Rightarrow \quad y_n = \frac{\gamma - \mu x_n}{-\alpha} \\ (g - m y_n) + a x_n &= 0 \qquad \text{insert here} \end{aligned}$$

$$\begin{aligned} g + \frac{m}{\alpha}(\gamma - \mu x_n) + a x_n = 0 \quad &\Leftrightarrow \quad g + \frac{m\gamma}{\alpha} + (a - \frac{m\mu}{\alpha}) x_n = 0 \\ &\Leftrightarrow \quad x_n = -\left(\frac{g + \frac{m\gamma}{\alpha}}{a - \frac{m\mu}{\alpha}} \right) = \frac{\alpha g + \gamma m}{m\mu - a\alpha}. \end{aligned}$$

Inserting this result above:

$$\begin{aligned} y_n = \frac{\gamma - \mu \frac{\alpha g + \gamma m}{m\mu - a\alpha}}{-\alpha} &= \frac{\mu}{\alpha}\left(\frac{\alpha g + \gamma m}{m\mu - a\alpha} \right) - \frac{\gamma}{\alpha}\left(\frac{m\mu - a\alpha}{m\mu - a\alpha} \right) \\ &= \frac{1}{\alpha} \frac{\mu\alpha g + \mu\gamma m - \gamma m\mu + \gamma a\alpha}{m\mu - a\alpha} \\ &= \frac{g\mu + \alpha\gamma}{m\mu - a\alpha}, \end{aligned}$$

hence we obtain for the coexistence point

$$\bar{x} = \frac{\gamma m + \alpha g}{m\mu - a\alpha} \quad \text{and} \quad \bar{y} = \frac{g\mu + a\gamma}{m\mu - a\alpha}$$

For simplification we set $\gamma, g = 1$, $\mu, m = 2$, i.e. we consider the system

$$\begin{aligned} x_{n+1} = x_n + x_n(1 - 2x_n) + \alpha x_n y_n &=: f(x_n, y_n) \\ y_{n+1} = y_n + y_n(1 - 2y_n) + a x_n y_n &=: g(x_n, y_n) \end{aligned}$$

Computation of the (general) Jacobian matrix:

$$\begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix} = \begin{pmatrix} 2 + \alpha y - 4x & \alpha x \\ a y & 2 + a x - 4y \end{pmatrix}$$

- At $(\frac{\gamma}{\mu}, 0) = (\frac{1}{2}, 0)$: $\begin{pmatrix} 0 & \frac{\alpha}{2} \\ 0 & 2+\frac{a}{2} \end{pmatrix}$
  $\Rightarrow \lambda_{1,2} = 1 + \frac{a}{4} \pm \frac{1}{2}\sqrt{(2+\frac{a}{2})^2}$, also $\lambda_1 = 2 + \frac{a}{2} > 1$ and $\lambda_2 = 0$.
  $\Rightarrow$ this point is unstable

- At $(0, \frac{g}{m}) = (0, \frac{1}{2})$: $\begin{pmatrix} 2+\frac{\alpha}{2} & 0 \\ \frac{a}{2} & 0 \end{pmatrix}$
  $\Rightarrow \lambda_{1,2} = 1 + \frac{\alpha}{4} \pm \frac{1}{2}\sqrt{(2+\frac{\alpha}{2})^2}$, also $\lambda_1 = 2 + \frac{\alpha}{2} > 1$ and $\lambda_2 = 0$.
  $\Rightarrow$ this point is unstable

- At the coexistence point $(\frac{2+\alpha}{4-a\alpha}, \frac{2+a}{4-a\alpha})$:

$$\begin{pmatrix} 2+\frac{\alpha}{4-a\alpha}(2+a) - \frac{4}{4-a\alpha}(2+\alpha) & \frac{\alpha}{4-a\alpha}(2+\alpha) \\ \frac{a}{4-a\alpha}(2+a) & 2+\frac{a}{4-a\alpha}(2+\alpha) - \frac{4}{4-a\alpha}(2+a) \end{pmatrix}$$
$$= \frac{1}{4-a\alpha}\begin{pmatrix} -a\alpha-2\alpha & \alpha(2+\alpha) \\ a(2+a) & -a\alpha-2a \end{pmatrix} = \frac{1}{4-a\alpha}\begin{pmatrix} -\alpha(2+a) & \alpha(2+\alpha) \\ a(2+a) & -a(2+\alpha) \end{pmatrix}$$

$$\begin{aligned} tr(A) &= (-2\alpha - a\alpha - 2a - a\alpha)\cdot\frac{1}{4-a\alpha} = -\frac{2}{4-a\alpha}(a+\alpha+a\alpha) \\ det(A) &= [a\alpha(2+a)(2+\alpha) - a\alpha(2+a)(2+\alpha)]\cdot\left(\frac{1}{4-a\alpha}\right)^2 = 0 \end{aligned}$$

$\Rightarrow \lambda_{1,2} = -\frac{(a+\alpha+a\alpha)}{4-a\alpha} \pm \frac{1}{2}\sqrt{\left(\frac{-2(a+\alpha+a\alpha)}{4-a\alpha}\right)^2}$
$\Rightarrow \lambda_1 = -\frac{2}{4-a\alpha}(a+\alpha+a\alpha), \quad \lambda_2 = 0$
Hence we obtain: The coexistence point is stable, if

$$|\lambda_1| < 1 \;\Leftrightarrow\; |\frac{2(a+\alpha+a\alpha)}{a\alpha-4}| < 1 \qquad \text{(depending on the parameters!)}$$

Consider the special case $a = \alpha$: $\lambda_1 = -\frac{2a}{2-a} = \frac{2a}{a-2}$

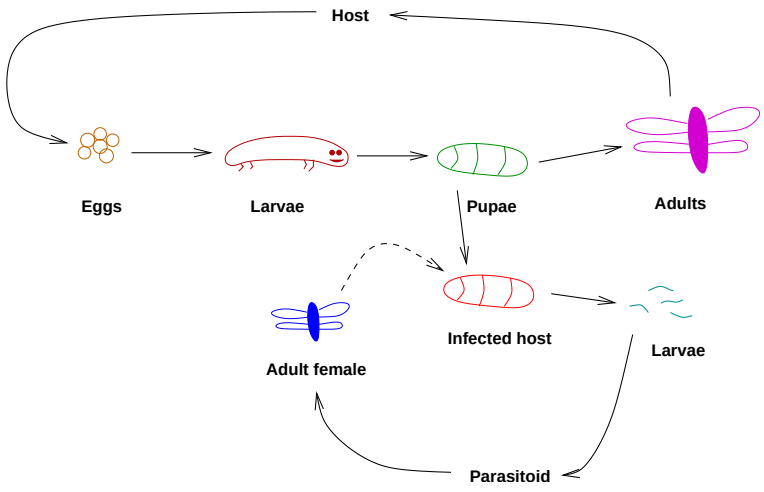
$$\begin{aligned} \lambda_1 = 1 &\;\Leftrightarrow\; \frac{2a}{a-2} = 1 \Leftrightarrow a = -2 \qquad \text{(a should be positive)} \\ \lambda_1 = -1 &\;\Leftrightarrow\; \frac{2a}{a-2} = -1 \Leftrightarrow a = \frac{2}{3} \end{aligned}$$

It follows: For $a \in [0, \frac{2}{3})$ the coexistence point is stable in this special case.

2.3.6 Example: Host-parasitoid systems

(as an example for two-species interactions, [12])

Insect populations can easily be divided into discrete generations, so it makes sense to use discrete models in this case. Here we consider a system of two insect species, both have several life-cycle stages (including eggs, larvae, pupae and adults).
The so-called parasitoid exploits the second as follows: An adult female parasitoid looks for a host, on which it can deposit its eggs (there are several possibilities to do that: attaching to the outer surface of the larvae or pupae of the host, or injection into the host's flesh). These eggs develop to larval parasitoids which grow at the expense of their host, even it is possible, that the host is killed by that. Obviously, the life-cycles of these two species are coupled somehow, see the following figure:



We assume the following properties for a simple model for this system:

1. Parasitised hosts give rise to the next generation of the parasitoid species.
2. Non-parasitised hosts give rise to the next generation of their own species.
3. The fraction of parasitised hosts depends on one or both population densities.

At the moment, we neglect natural mortality in order to put up the basic host-parasitoid model. The following definitions are used:

$$\begin{aligned} N_t &= \text{Host species density in generation t} \\ P_t &= \text{Parasitoid density in generation t} \\ f &= f(N_t, P_t) = \text{ Fraction of non-parasitised hosts} \\ \lambda &= \text{Host reproductive rate} \\ c &= \text{Average number of viable eggs that a parasitoid puts on a single host} \end{aligned}$$

By these assumptions we come to the following basic host-parasitoid model:

$$\begin{aligned} N_{t+1} &= \lambda N_t f(N_t, P_t) \\ P_{t+1} &= cN_t(1 - f(N_t, P_t)). \end{aligned}$$

One special case and famous example for such a host-parasitoid model is the Nicholson-Bailey model. They made the following assumptions:

- The encounters of host and parasitoid happen randomly, thus the number of encounters N_e is proportional to the product of their densities,

  $$N_e = aN_tP_t$$

  where a is the so-called searching efficiency of the parasitoid (this assumption is due to the so-called "law of mass action").

- The first encounter is the relevant one; further encounters do not increase or decrease the number of eggs etc.

Thus, one has to distinguish between hosts, which had no encounter, and hosts with n encounters, where $n \geq 1$. The probability of r encounters can be represented by a probability distribution which is based on the average number of encounters per unit time. Here, the Poisson distribution is the appropriate one which leads to

$$f(N_t, P_t) = p(0) = e^{-aP_t}$$

(the zero term of the Poisson distribution corresponds to the fraction without parasitoids).
This yields the Nicholson-Bailey equations:

$$\begin{aligned} N_{t+1} &= \lambda N_t e^{-aP_t} \\ P_{t+1} &= cN_t(1 - e^{-aP_t}). \end{aligned}$$

Next step is to analyse the system. Let

$$\begin{aligned} F(N,P) &= \lambda N e^{-aP} \\ G(N,P) &= cN(1-e^{-aP}). \end{aligned}$$

Stationary solutions are

- the trivial one: $N = 0$ (then in the next step, also $P = 0$ is reached, independent on the initial value)
- $\bar{N} = \lambda \bar{N} e^{-a\bar{P}}$, $\bar{P} = c\bar{N}(1-e^{-a\bar{P}})$
  $\Leftrightarrow \bar{P} = \frac{\ln \lambda}{a}$, $\bar{N} = \frac{\lambda \ln \lambda}{(\lambda-1)ac}$
  Only for $\lambda > 1$, $\bar{P}$ is positive (and biologically meaningful)

The Jacobian reads

$$\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} \frac{\partial F(\bar{N},\bar{P})}{\partial N} & \frac{\partial F(\bar{N},\bar{P})}{\partial P} \\ \frac{\partial G(\bar{N},\bar{P})}{\partial N} & \frac{\partial G(\bar{N},\bar{P})}{\partial P} \end{pmatrix} = \begin{pmatrix} \lambda e^{-a\bar{P}} & -a\lambda \bar{N} e^{-a\bar{P}} \\ c(1-e^{-a\bar{P}}) & ca\bar{N}e^{-a\bar{P}} \end{pmatrix} = \begin{pmatrix} 1 & -a\bar{N} \\ c(1-\frac{1}{\lambda}) & \frac{ca}{\lambda}\bar{N} \end{pmatrix}.$$

The trace and the determinant of this matrix are computed as follows:

$$\begin{aligned} tr\, J &= 1 + \frac{ca}{\lambda}\bar{N} = 1 + \frac{\ln \lambda}{\lambda - 1}, \\ det\, J &= \frac{ca}{\lambda}\bar{N} + ca\bar{N}(1-\frac{1}{\lambda}) = ca\bar{N} = \frac{\lambda \ln \lambda}{\lambda - 1}. \end{aligned}$$

Now, we want to show that $det\, J > 1$. Equivalently, one can show that $S(\lambda) = \lambda - 1 - \lambda \ln \lambda < 0$. This function $S(\lambda)$ has the following properties: $S(1) = 0$, $S'(\lambda) = 1 - \ln \lambda - \lambda \frac{1}{\lambda} = -\ln \lambda$. Thus, for $\lambda \geq 1$ it is $S'(\lambda) < 0$ and $S(\lambda)$ is a decreasing function of λ. Consequently, for $\lambda \geq 1$ it is $S(\lambda) < 0$ which is equivalent to $det\, J > 1$. Then, the stability condition (2.10) is violated and the equilibrium $(\bar{N}, \bar{P})$ can never be stable. This means that small deviations from the steady-state level in each case lead to diverging oscillations.

Of course, this model can be applied on real world data. This was done, e.g. for a greenhouse whitefly and its dynamics. Indeed, there was found a dynamics which fits quite well to the theoretical Nicholson-Bailey model. The plot of the dynamics can be found in [12], Figure 3.3.

Since the Nicholson-Bailey model is unstable for all parameter values, but most natural host-parasitoid system are more stable, it probably makes sense to check modifications of the model. Here, a few modifications are mentioned:

The following assumption is considered: If no parasitoids are there, the hosts population only grows to a limited density, corresponding to the carrying capacity of the environment. In the equations, this yields

$$\begin{aligned} N_{t+1} &= N_t \lambda(N_t) e^{-aP_t}, \\ P_{t+1} &= cN_t(1-e^{-aP_t}), \end{aligned}$$

where the growth rate is

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

In absence of the parasitoids, the host population grows up (or declines if $N_t > K$) until the capacity $N_t = K$. The revised model reads

$$\begin{aligned} N_{t+1} &= N_t e^{r(1-N_t/K)-aP_t} \\ P_{t+1} &= cN_t(1-e^{-aP_t}). \end{aligned}$$

This system is more complicated to discuss (e.g. it is not possible to get explicit expressions for the coexistence point $(\bar{N}, \bar{P})$), so we will not go into the details here, but Beddington et al. [4] have studied this model in detail and found that it is stable for a wide range of realistic parameter values.

Nice photographs of such host-parasitoid systems can e.g. be found in Grzimeks Tierleben [19].

2.4 Age-structured Population growth

2.4.1 Life tables

Literature: Gotelli [17]

Up to now, birth and death rates were represented as single constants, which are valid for the complete population. This assumption may be valid for "simple" organisms like bacteria, but for most of the higher developed organisms, like animals or plants, the birth and death rates depend on their age. Consequently, the age structure can strongly affect the growth of a population and it may be important, to include it into population growth models.
Therefore, the population is divided into $n+1$ different age classes:

$$[0, \Delta t[, \quad [\Delta t, 2\Delta t[, \quad \ldots, [n\Delta t, (n+1)\Delta t[$$

respectively (when we choose a "well-suited" time unit)

$$[0, 1[, \quad [1, 2[, \ldots, [k, k+1[, \ldots, [n, n+1[.$$

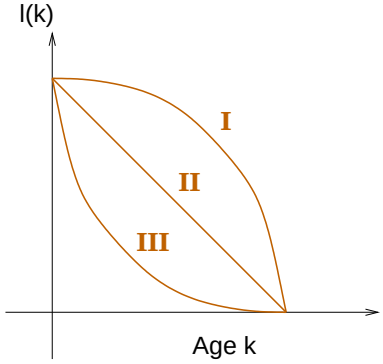
Let k denote the age class (or age). In the following, we will do some standard life table calculations, as they are often used in ecology.
First entry in such a life table are the available age classes k. After that, the actual number $S(k)$ of individuals in each age class is fixed.
The next column consists of the so-called fertility schedule, which describes the average number of offspring born by an individual of the corresponding age class. It is often denoted by $b(k)$ or $m(k)$ (birth or maternity). Being very precise, this model concerns only females and ignores the population sex ration - as long as the sex ratio is approximately 50/50, it can be justified to ignore the males. Typical fertility schedules are the so-called semelparous respectively iteroparous reproduction. In the first case, an organism reproduces only once during its life, resulting in zero entries in all but one single reproductive age (typical examples: many flowering desert plants; oceanic salmon). In the second case, the organism can reproduce repeatedly during its life (example for this kind of reproduction are birds or trees). In plant ecology, the terms "annual" respectively "perennial" are often used, describing plants which live only in a single season respectively live for more than one season. Neglecting some exceptions, most annual species behave semelparous and most perennial species are iteroparous.
In the next column, the so-called survivorship $l(k)$ is written down. It is computed from the $S(k)$ column by

$$l(k) = \frac{S(k)}{S(0)},$$

which means the proportion of those individuals that survive until the beginning of the age k - or equivalently the probability that an individual survives from birth to the beginning of age k. This quantity is monotone decreasing.
The so-called survival probability, computed by

$$g(k) = \frac{l(k+1)}{l(k)},$$

is the probability that an individual of age k survives to age $k+1$. In nature, there are three different basic types of survivorship curves, shown by a graph with $l(k)$ on the y axis and the age k on the x axis. The single points are connected to form the so-called survivorship curve.



Case I: High survivorship during young and intermediate ages, steep drop-off when approaching the maximum life span.
Examples: humans, mammals in general

Case II: The mortality rate is more or less constant throughout life.
Examples: some birds (but often with steeper mortality during the more vulnerable egg and chick stages)

Case III: Poor survivorship for young age classes, much higher survivorship for older individuals.
Examples: many insects, marine invertebrates, flowering plants (all produce a lot of descendants - eggs, larvae or seeds - , only few pass through the vulnerable stage, but then they have relatively high survivorship in later years)

Another interesting quantity is the net reproductive rate R_0. It is defined as the mean number of offspring produced per female over her lifetime and is computed by

$$R_0 = \sum_{k=0}^{n} l(k)b(k).$$

The so-called generation time G is the average age of parents of all the offspring which is produced by a single cohort (born at the same time) and is calculated by

$$G = \frac{\sum_{k=0}^{n} l(k)b(k)k}{\sum_{k=0}^{n} l(k)b(k)}.$$

Remark: Populations with relevant age structure always have a generation time greater than 1.0.
Comparing the population growth for an age-structured population to the growth rate of a standard exponential growth (or the corresponding discrete model) leads to the concept of the intrinsic rate of increase. Consider a population which grows exponentially for a time G (the generation time), then its size is

$$N_G = N_0 e^{rG} \qquad (N_0 \text{ is the starting value})$$

We have approximately

$$R_0 \approx \frac{N_G}{N_0} = e^{rG}$$

and hence, the intrinsic rate of increase is defined by

$$r = \frac{\ln(R_0)}{G}.$$

Example for a life table:

k	$S(k)$	$b(k)$	$l(k)$	$g(k)$	$l(k)b(k)$	$l(k)b(k)k$
0	500	0	1.0	0.8	0.0	0.0
1	400	2	0.8	0.5	1.6	1.6
2	200	3	0.4	0.25	1.2	2.4
3	50	1	0.1	0.0	0.1	0.3
4	0	0	0.0		0.0	0.0
					$\sum = 2.9$	$\sum = 4.3$

Remark: The data are taken by following a cohort of newborn and considered what happens to them, how they reproduce etc. $\rightsquigarrow l(0) = 1$.

This life-table yields the following results:

$$\begin{aligned} R_0 &= \sum l(k)b(k) = 2.9 \\ G &= \frac{\sum l(k)b(k)k}{\sum l(k)b(k)} = 1.483 \text{ years} \\ r &= \frac{\ln(R_0)}{G} = 0.718 \text{ individuals/(individual } \cdot \text{ year)} \end{aligned}$$

Remark: Insurances also use tables like this; but in opposite to ecology, they mainly use so-called "mortality tables". These are (roughly speaking) created by introducing "mortality probabilities", i.e. the probability that a person of age x dies before he/she reaches age $x + 1$. So, instead of a cohort as data basis, the "mortality behaviour" of a present population in a short time interval is considered.

2.4.2 Leslie model

Literature: Riede, Gotelli [48, 17]

The Leslie model describes the evolution of an age-structured population (i.e., the numbers of births and deaths depend on the actual age structure). The population growth is represented in matrix form and was introduced by the population biologist P.H. Leslie in 1945 [40].
Let $x_k(j)$ be the population size in age class k at time j, P_k: Survival factor of age class k

$$\Rightarrow \quad x_{k+1}(j+1) = P_k x_k(j) \qquad \text{for } k = 0, \ldots, n-1$$

In terms of above, P_k can be introduced as $P_k = \frac{l(k+1)}{l(k)}$ (compare $P_k \leftrightarrow g(k)$).
F_k: Number of descendants of an individual with age k per time unit (compare $F_k \leftrightarrow b(k)$)
Then the newborns at time $j+1$ are determined by

$$\Rightarrow \quad x_0(j+1) = F_0 x_0(j) + F_1 x_1(j) + \ldots + F_n x_n(j)$$

This can be written as a matrix in the following way (attention, slightly modified notation as before):

$$\vec{x}(j+1) = \begin{pmatrix} x_0(j+1) \\ x_1(j+1) \\ x_2(j+1) \\ \vdots \\ x_n(j+1) \end{pmatrix} = \underbrace{\begin{pmatrix} F_0 & F_1 & F_2 & \ldots & F_n \\ P_0 & 0 & 0 & \ldots & 0 \\ 0 & P_1 & 0 & \ldots & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \ldots & 0 & P_{n-1} & 0 \end{pmatrix}}_{\text{Leslie-Matrix L}} \begin{pmatrix} x_0(j) \\ x_1(j) \\ x_2(j) \\ \vdots \\ x_n(j) \end{pmatrix}$$

Short notation of this system:

$$\vec{x}(j+1) = L\vec{x}(j)$$

This kind of model, consisting of a system of $n+1$ difference equations, is called Leslie model (introduced 1945).

A short example with concrete numbers

- Classification into four age classes, in units of 1 million individuals
- $P_0 = \frac{3}{5}$, $P_1 = \frac{2}{5}$, $P_2 = \frac{3}{10}$
- $F_0 = 0$, $F_1 = 80$, $F_2 = 50$, $F_3 = 0$
- Given: Age distribution in year j: $\vec{x}(j) = \begin{pmatrix} 1 \\ 2 \\ 3 \\ 1 \end{pmatrix}$

  $\Rightarrow$ Age distribution in year $(j+1)$:

$$\vec{x}(j+1) = \begin{pmatrix} 0 & 80 & 50 & 0 \\ \frac{3}{5} & 0 & 0 & 0 \\ 0 & \frac{2}{5} & 0 & 0 \\ 0 & 0 & \frac{3}{10} & 0 \end{pmatrix} \begin{pmatrix} 1 \\ 2 \\ 3 \\ 1 \end{pmatrix} = \begin{pmatrix} 310 \\ \frac{3}{5} \\ \frac{4}{5} \\ \frac{9}{10} \end{pmatrix}$$

Generally, from $\vec{x}(j+1) = A\vec{x}(j)$, $j = 0, 1, 2, \ldots$ we obtain

$$\vec{x}(j) = A\vec{x}(j-1) = AA\vec{x}(j-2) = \ldots = A^j\vec{x}(0).$$

If $\vec{x}(0) = \vec{v}$ is an eigenvector of A, it follows that

$$\vec{x}(j) = \lambda^j \vec{v}.$$

Definition 6 (Convergence of vectors)

$$\lim_{j\to\infty} \vec{x}(j) = \vec{x} \;\Leftrightarrow\; \lim_{j\to\infty} x_k(j) = x_k \qquad \textit{for all } k = 1, 2, \ldots, n$$

Consider the special case 2D: The starting vector $\vec{x}(0)$ can be represented by using a basis $(\vec{v}, \vec{w})$ of eigenvectors of A (assuming its existence):

$$\vec{x}(0) = a\vec{v} + b\vec{w}, \qquad a, b \in \mathbb{R}$$

Let λ_1, λ_2 be the eigenvalues which correspond to $\vec{v}, \vec{w}$. Then we get:

$$\begin{aligned} \vec{x}(j) = A^j\vec{x}(0) &= A^j(a\vec{v} + b\vec{w}) \\ &= A^j a\vec{v} + A^j b\vec{w} \\ &= aA^j\vec{v} + bA^j\vec{w} \\ &= a\lambda_1^j\vec{v} + b\lambda_2^j\vec{w} \end{aligned}$$

Definition 7 *Let $\lambda_1 \in \mathbb{R}$.*

1. *λ_1 is called simple zero of $f(\lambda)$, if $f(\lambda) = 0$ and $f'(\lambda) \neq 0$.*
2. *λ_1 is called simple eigenvalue of A, if λ_1 is simple zero of $det(A - \lambda I)$ (characteristic polynomial).*
3. *λ_1 is called dominating eigenvalue of A, if the following conditions are satisfied:*
   (a) *λ_1 is simple eigenvalue*
   (b) *λ_1 is real and > 0*
   (c) *$\lambda_1 > |\lambda|$ for all other eigenvalues λ of A.*

Questions:

1. Are there equilibria ?
   $\Rightarrow$ this can be computed via the fixed point equation $\vec{x} = L\vec{x}$
2. Are there age distributions which stay unchanged during time course?
   Let $x(j) := \sum_{k=0}^{n} x_k(j)$ be the size of the complete population at time j. A constant age distribution means:
   $$\frac{x_k(j+1)}{x(j+1)} = \frac{x_k(j)}{x(j)} \qquad \text{for all } k, \text{ all } j$$
   $$\begin{aligned} &\Leftrightarrow \quad x_k(j+1) = \frac{x(j+1)}{x(j)} x_k(j), \qquad \text{define } \lambda := \frac{x(j+1)}{x(j)} \\ &\Leftrightarrow \quad x_k(j+1) = \lambda x_k(j) \\ &\Leftrightarrow \quad \vec{x}(j+1) = \lambda\vec{x}(j) \\ &\Leftrightarrow \quad L\vec{x}(j) = \lambda\vec{x}(j), \end{aligned}$$
   Hence, $\vec{x}(j)$ is an eigenvector of L corresponding to the eigenvalue λ.
3. Does a solution of this system approach (approximately) a constant age distribution? ?

Proposition 3 (Dominating eigenvalue) *Suppose A has a dominating eigenvalue λ_1. Let $\vec{v}$ be eigenvector, corresponding to λ_1 of A. Then, there exists an $a \in \mathbb{R}$ with*

$$\lim_{j\to\infty} \frac{\vec{x}(j)}{\lambda_1^j} = a\vec{v},$$

i.e., for large j we have $\vec{x}(j) \approx \lambda_1^j a\vec{v}$.
(assuming that $\vec{x}(0)$ can be represented as $\vec{x}(0) = a\vec{v} + b\vec{w} + \ldots$ in the basis of eigenvectors, where $a \neq 0$)

Therefore, in the long-term behaviour each age class grows with the same factor λ_j per time step.

Simple example:

$$\vec{x}(j+1) = \begin{pmatrix} 1 & 1 \\ \frac{3}{4} & 0 \end{pmatrix} \vec{x}(j)$$

The eigenvalues are computed by the characteristic polynomial:

$$det \begin{pmatrix} 1-\lambda & 1 \\ \frac{3}{4} & -\lambda \end{pmatrix} = \lambda^2 - \lambda - \frac{3}{4} = 0,$$

thus $\lambda_{1,2} = \frac{1}{2} \pm 1$, $\lambda_1 = \frac{3}{2}$, $\lambda_2 = -\frac{1}{2}$
Computation of the corresponding eigenvectors:

$$\begin{pmatrix} 1-\lambda_1 & 1 \\ \frac{3}{4} & -\lambda_1 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = 0 \quad \Leftrightarrow \quad \begin{array}{rcl} -\frac{1}{2}x_1 + x_2 & = & 0 \\ \frac{3}{4}x_1 - \frac{3}{2}x_2 & = & 0, \end{array}$$

which gives e.g. $\vec{v} = \begin{pmatrix} 2 \\ 1 \end{pmatrix}$. Analogously:

$$\begin{pmatrix} 1-\lambda_2 & 1 \\ \frac{3}{4} & -\lambda_2 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = 0 \quad \Leftrightarrow \quad \begin{array}{rcl} \frac{3}{2}x_1 + x_2 & = & 0 \\ \frac{3}{4}x_1 + \frac{1}{2}x_2 & = & 0, \end{array}$$

which gives e.g. $\vec{w} = \begin{pmatrix} -\frac{2}{3} \\ 1 \end{pmatrix}$

As starting vector we choose $\vec{x}(0) = \begin{pmatrix} 3 \\ 4 \end{pmatrix}$.
Representation in the eigenvector basis:

$$\vec{x}(0) = \frac{17}{8}\vec{v} + \frac{15}{8}\vec{w}$$

The proposition about the dominating eigenvalue yields here:

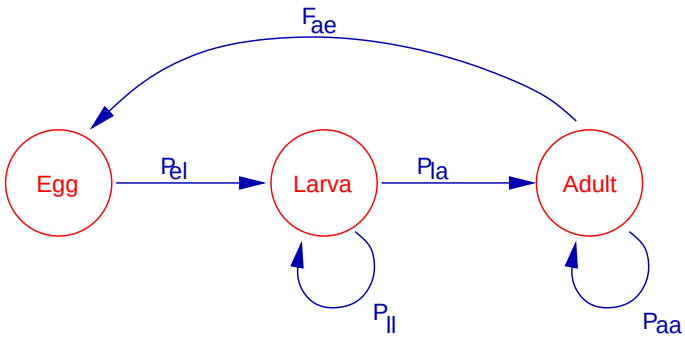
$$\vec{x}(j) \approx \left(\frac{3}{2}\right)^j \frac{17}{8}\vec{v} \qquad \text{for large } j.$$

2.4.3 Model variations

In some cases, it makes sense to choose other criteria for a classification than the age. For example, there may be organisms whose survival or reproduction depends more on the size or on the stage than on its age.
A typical example for a stage-dependent population growth are insects: egg, larval, pupal and adult stage. It is possible to modify the Leslie matrix in such a way that its rows and columns do not represent the age of an organisms but its stage (or size or ...). A transition matrix for a simplified insect life cycle (egg, larva, adult - mentioned in this order in the matrix) may look as follows:

$$\begin{pmatrix} 0 & 0 & F_{ae} \\ P_{el} & P_{ll} & 0 \\ 0 & P_{la} & P_{aa} \end{pmatrix}.$$

In the first row, the fertilities are inserted, in the other rows, you find transition probabilities between stages. In contrast to the classical Leslie matrix, it is also possible to have positive entries in the diagonal, which means, that an individual can also stay in a particular stage (in the example, larvae and adults can do this).
These life cycles can also be illustrated in so-called loop diagrams. They are created as follows: Each stage is represented by a circle, the transitions between stages are shown by arrows, marked by the transition probabilities. "Missing" arrows are interpreted to have zero entries in the corresponding transition matrix. Hence, for the example above (the insects) we get the following loop diagram:



2.4.4 Example: Demographics of the Hawaiian Green Sea Turtle

Literature: Robert's Notebook [49]

The Hawaiian green sea turtle has five states (different ages, taking different time intervals); estimated annual survivorship and estimated annual eggs laid are also given:

1. Eggs, Hatchlings (<1): 0.23; 0
2. Juveniles (1-16): 0.68; 0
3. Sub adults (17-24): 0.75; 0
4. Novice breeders (25): 0.89; 280
5. Mature breeders (26-50): 0.92; 70

The transition matrix for this five-stage model reads in general form:

$$L = \begin{pmatrix} p_1 & e_2 & e_3 & e_4 & e_5 \\ q_1 & p_2 & 0 & 0 & 0 \\ 0 & q_2 & p_3 & 0 & 0 \\ 0 & 0 & q_3 & p_4 & 0 \\ 0 & 0 & 0 & q_4 & p_5 \end{pmatrix},$$

where e_i denotes the eggs laid per female turtle, p_i the proportion of individuals that remain in stage i in the following year, and q_i the proportion of individuals that survive and move into stage $i+1$.
The following data are given:

- Stage survivor probabilities: $s = (0.23, 0.68, 0.75, 0.89, 0.92)^T$
- Stage duration in years: $d = (1, 15, 7, 1, 24)^T$
- Eggs laid per female turtle: $e = (0, 0, 0, 280, 70)^T$

Let p_i denote the proportion remaining in stage i the following year and q_i the proportion that will survive and move into stage $i+1$. The following data are given (respectively, can be computed from the given data for d and s):

- $p = (0, 0.67901, 0.71149, 0, 0.9075)^T$,
- $q = (0.23, 0.001, 0.039, 0.89, 0.013)^T$,

thus, the transition matrix L is given by

$$L = \begin{pmatrix} 0 & 0 & 0 & 280 & 70 \\ 0.23 & 0.679 & 0 & 0 & 0 \\ 0 & 0.001 & 0.711 & 0 & 0 \\ 0 & 0 & 0.039 & 0 & 0 \\ 0 & 0 & 0 & 0.89 & 0.907 \end{pmatrix}$$

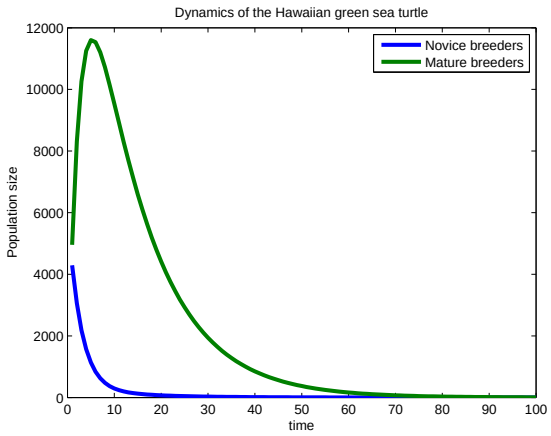
From a scientific project, the following population numbers are known:

$$P = (346000, 240000, 110000, 2000, 3500)^T$$

By iteration, we can compute the predicted numbers at later time points.
More interesting: We examine the general behaviour by mathematical analysis. The eigenvalues can be computed numerically, the result is:

$$\lambda_1 = -0.7247, \quad \lambda_2 = -0.689, \quad \lambda_3 = -0.00325, \quad \lambda_4 = -0.00014, \quad \lambda_5 = -0.00899$$

Obviously, the largest eigenvalue (i.e. the eigenvalue with the largest absolute value) has absolute value < 1, which yields that the 0 is a stable stationary state; unfortunately, the population of the turtles will die out under the given conditions.



2.4.5 Positive Matrices

Generally, positive matrices are very important in mathematical biology. So, in this subsection, we collect some interesting facts about positive matrices.
Important questions in that context are:

- Considering a system of the form

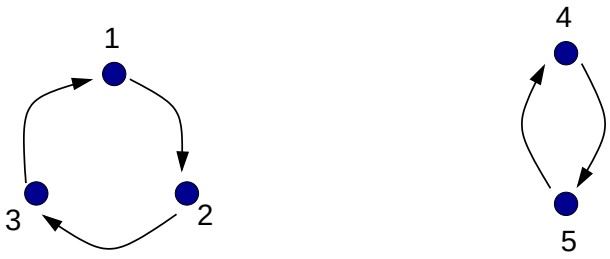
  $$y_{n+1} = Ay_n, \qquad \text{where } A_{ij} \geq 0,$$

  are there conditions such that it can be split into two independent subsystems?
- Which statements about the asymptotic behaviour can be given?

Splitting of a system

Literature: [43]

As an example, we consider the five states with transitions, as shown here:



This "object" consists of two parts which are not connected.
First, we need to know, how a graph is defined:

Definition 8 *A (directed) graph $G = (V, E)$ consists of a set of vertices V and the (directed) edges E.*

That means, the example above can be described by $V = \{1, \ldots, 5\}$, $E = \{1 \to 2, 2 \to 3, 3 \to 1, 4 \to 5, 5 \to 4\}$. Similar to the construction of loop diagrams out of a transition matrix, one can define a corresponding matrix to such a graph:

Definition 9 *An incidence matrix of the directed graph with vertices $V = \{v_1, \ldots, v_n\}$ and directed edges E is a matrix $A \in \{0,1\}^{n \times n}$, such that*

$$A_{ij} = \begin{cases} 1 & \text{if } v_i \to v_j \in E \\ 0 & \text{else} \end{cases}$$

Thus, the incidence matrix for our example looks like follows:

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

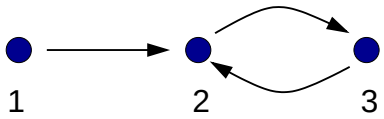
It is easy to see, that it can be split up into two independent subsystems. The concept of irreducibility considers that in a more formal way:

Definition 10 *Let A be a non-negative matrix, $\hat{A} \in \{0,1\}^{n \times n}$ is defined by*

$$\hat{A}_{i,j} = \begin{cases} 1 & \text{if } A_{i,j} > 0 \\ 0 & \text{if } A_{i,j} = 0. \end{cases}$$

$\hat{A}$ is an incidence matrix of a directed graph $G = (V, E)$, $V = \{v_1, \ldots, v_n\}$.
If the directed path is connected (i.e. for all $v_i, v_j \in V$ there is a directed path $v_i = v_{l_1} \to v_{l_2} \to \ldots \to v_{l_m} = v_j$ where $v_{l_k} \to v_{l_{k+1}} \in E$ for $k = 1, \ldots, m-1$), then A is called irreducible.

Remark: It is possible to have a graph, which is not connected, but which cannot be cut into two independent subsystems, though. Example:

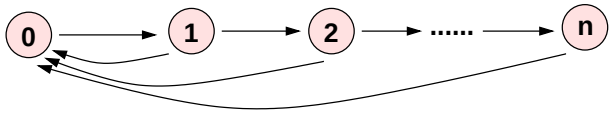


The subsystem ("subgraph"), consisting of the vertices 2 and 3, is called a trap, that means, it is connected and no edge points outwards of the subgraph. Obviously, an irreducible transition matrix corresponds to a graph which has exactly one trivial trap: the graph itself.

Proposition 4 *If $A \in \mathbb{R}^{n \times n}$ is irreducible, then it holds:*

1. *For each pair $(i, j) \in \{1, \ldots, n\}^2$, there is a number $m \in \mathbb{N}$, such that $A^m_{i,j} > 0$*
2. *$(I + A)^{n-1}$ is strictly positive.*

Considering again the example of the Leslie Matrix, the graph of the corresponding incidence matrix looks as follows:



In case of $F_{i_0} = \ldots = F_n = 0$ (which means that the elder age classes aren't fertile anymore), then the corresponding graph becomes reducible. So, these elder age classes do not influence the population dynamics (and maybe can be left out for some analyses).

Asymptotic behaviour

Here, we mention the famous theorems of Perron and Frobenius - without proofs (they can be found e.g. in [16]).

Theorem 10 (Perron) *If $A \in \mathbb{R}^{n\times n}$ is strictly positive, then the spectral radius $\rho(A)$ is a simple eigenvalue. The corresponding eigenvector is strictly positive. The absolute values of all other eigenvalues are strictly smaller than $\rho(A)$; they do not have a non-negative eigenvector.*

Theorem 11 (Frobenius) *If $A \in \mathbb{R}^{n\times n}$ is non-negative and irreducible, then the spectral radius is a simple eigenvalue with a non-negative eigenvector.*

Remark, that the Theorem of Frobenius still allows more eigenvalues with $|\lambda| = \rho(A)$. Theorem 5 (and the following theorems) is useful to apply for matrix iterations again.

Chapter 3

Continuous models I: Ordinary differential equations

3.1 Introduction

In contrast to the last chapter, we will now use continuous models, i.e. mainly models which include a continuous time course. This kind of modelling is done by differential equations. In this chapter, we consider only ordinary differential equations and systems thereof. This allows to consider only one independent variable, e.g. time, but for a lot of problems, this is sufficient. Roughly speaking, for spatial modelling we will need also partial differential models (which is done later).

Before starting with some basic theory of ODEs, we introduce a first, very simple ODE model.

Example: Spread of a rumour

In a human population of fixed size N, a rumour is distributed by word-of-mouth advertising, i.e. a member of the population comes to know about the rumour by narration of another person. Let $I(t)$ be the number of people who know already about the rumour at time t. Model assumption: Each informed person has $k > 0$ contacts per time unit with members of the population, and - very human of course :-) - tells the rumour each time. If q is the fraction of non-informed people, then each informed person has qk contacts with non-informed people. At time t, it is

$$q = \frac{N - I(t)}{N}.$$

Thus, in the very short time interval dt, each informed person had contact to

$$qk\,dt = \frac{N - I(t)}{N} k\,dt$$

to non-informed people, which corresponds to the number of newly informed persons (by this certain information source). Thus, including all informed persons at time t, there are

$$dI = I(t)\frac{N - I(t)}{N} k\,dt,$$

newly informed persons in the time interval dt, which leads to the differential equation

$$\frac{dI}{dt} = I(t)\frac{N - I(t)}{N} k.$$

This can be reformulated to

$$\frac{dI}{dt} = kI - \frac{k}{N} I^2 = \frac{k}{N} I(N - I).$$

It has exactly the form of the logistic differential equation, a very famous ODE, which we will study in detail later. Also, the solution will be determined later, here it is only mentioned to be of the form

$$I(t) = \frac{N}{1 + (N-1)e^{-kt}}.$$

If $t \to \infty$, then $I(t) \to N$, which means, that sooner or later each member of the population knows the rumour. This maybe shows that our assumptions were not too realistic ...

The appearance of the logistic differential equation is a typical example that a certain differential equation (or difference equation or whatever) may describe very different processes. So, one solution or model analysis may help for understanding the behaviour of many different models!

(this example was taken from [23])

3.2 Basics in the theory of ordinary differential equations

Literature: e.g. [23, 5]

3.2.1 Existence of solutions of ODEs

Definition 11 (ODE) *An equation $F(t, y(t), y'(t)) = 0$, which relates an unknown function $y = y(t)$ with its derivative $y'(t) = \frac{d}{dt}y(t)$, is called an ordinary differential equation (ODE) of first order, shortly $F(t, y, y') = 0$.*
Often, the explicit case in $\mathbb{R}^n$ is considered:

$$y'(t) = f(t, y), \tag{3.1}$$

where $f : G \to \mathbb{R}^n$, $G \subseteq \mathbb{R} \times \mathbb{R}^n$ domain.
In the case $n = 1$ it is called scalar.
If f does not depend explicitely on t, the ODE (3.1) is called autonomous,

$$y'(t) = f(y). \tag{3.2}$$

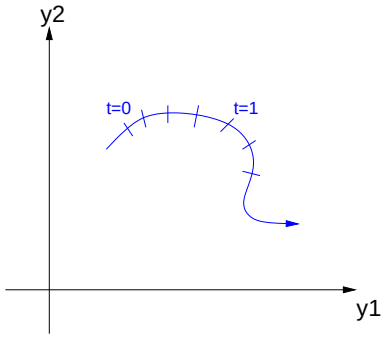
Definition 12 *A solution of equation (3.1) is a function $y : I \to \mathbb{R}^n$, where $I \neq \emptyset$, I interval and*

1. *$y \in C^1(I, \mathbb{R}^n)$ (or y out of another well-suited function space)*
2. *$graph(y) \subset G$*
3. *$y'(t) = f(t, y(t))$ for all $t \in I$.*

Initial value problem: For a given $(t_0, y_0) \in G$ find a solution $y : I \to \mathbb{R}^n$ with

$$\begin{cases} y' = f(t, y) & \text{for all } t \in I \\ y(t_0) = y_0, & t_0 \in I \end{cases} \tag{3.3}$$

Phase portrait: In the 2D case, $y(t) = (y_1(t), y_2(t))$ is plotted in a (y_1, y_2) coordinate system, the resulting curves are parametrised by t.



Also in the the 3D case a phase portrait can be drawn analogously.

Definition 13 (k-th order ODE) *(Explicit and scalar) ODEs of k-th order are equations of the form*

$$y^{(k)} = f(t, y, y', y'', \ldots, y^{(k-1)}) \text{ with } f : G \to \mathbb{R}. \tag{3.4}$$

y is called solution of (3.4), if there exists a non-empty interval $I \subseteq \mathbb{R}$ with

1. $y \in C^k(I, \mathbb{R})$
2. $\{(t, y(t), y'(t), \ldots, y^{(k-1)}(t)) | t \in I\} \subset G$
3. $y^{(k)}(t) = f(t, y(t), \ldots, y^{(k-1)}(t))$ *for all* $t \in I$.

Such an ODE of k-th order can be reduced to a system of first order by introducing additional variables:

$$\begin{cases} z_1' = z_2 \\ \vdots \\ z_{k-1}' = z_k \\ z_k' = f(t, z_1, \ldots, z_{k-1}) \end{cases} \tag{3.5}$$

If $y^{(\kappa-1)} = z_\kappa$ for $1 \leq \kappa \leq k$, then y is a solution of (3.4) if and only if z is a solution of (3.5).

Theorem 12 (Peano, 1890) *Let $f \in C(G, \mathbb{R}^n)$ and $(t_0, y_0) \in G$. Then, there exists an $\varepsilon > 0$ and a solution $y : I \to \mathbb{R}^n$ of the initial value problem (3.3) with $I = [t_0 - \varepsilon, t_0 + \varepsilon]$ and graph$(y) \subset G$.*

Definition 14 (Lipschitz continuity)

1. *f is called Lipschitz continuous in G with respect to y, if there exists a constant $L > 0$ with*

$$\|f(t, y) - f(t, z)\| \leq L\|y - z\| \quad \text{for all } (t, y), (t, z) \in G$$

2. *f is called locally Lipschitz continuous in G with respect to y (denoted as $f \in C^{0,1-}(G, \mathbb{R}^n)$), if for each $(t, y) \in G$ there exists a neighbourhood $U \subseteq G$, in which f is Lipschitz continuous with respect to y.*

Theorem 13 (Picard-Lindelöf) *Let $f \in C^{0,1-}(G, \mathbb{R}^n)$ and $(t_0, y_0) \in G$. Then, there exists an $\varepsilon > 0$ and a solution $y : I \to \mathbb{R}^n$ of the initial value problem (3.3) with $I = [t_0 - \varepsilon, t_0 + \varepsilon]$ and graph$(y) \subset G$. Furthermore, y is determined uniquely in I, i.e. for any solution $z : J \to \mathbb{R}^n$ of the initial value problem is $y|_{I \cap J} = z|_{I \cap J}$.*

If not mentioned separately, we assume $f \in C^{0,1-}(G, \mathbb{R}^n)$ in the following.

Definition 15 *A solution $y : I \to \mathbb{R}^n$ of the initial value problem (3.3) is called maximal, if there is no solution $z : J \to \mathbb{R}^n$ with $I \subset J$ and $z|_I = y$. The interval I is open: $I = (a, b)$.*

Existence of a maximal solution of the initial value problem (3.3) can be shown by the lemma of Zorn.

Proposition 5 *Let $G = \mathbb{R} \times \mathbb{R}^n$, $(t_0, y_0) \in G$. Let $y : (a, b) \to \mathbb{R}^n$ be the maximal solution of the initial value problem (3.3). If $b = \infty$, then the solution exists for all $t > t_0$ (global existence). If $b < \infty$, then we have*

$$\|y(t)\| \to \infty \quad \text{for } t \to b_-.$$

3.2.2 Solutions

There are a lot of solution formulae for special cases of initial value problems, which can be found in several books about differential equations e.g. [2, 5, 23].
Here, we mention only one such formula (without proof), which will be used several times in the following:

Variation of constants

Proposition 6 *Let $I \subseteq \mathbb{R}$ be an open interval. The initial value problem*

$$\begin{cases} y'(t) = a(t)y(t) + b(t) & \text{for } a, b : I \to \mathbb{R} \text{ continuous} \\ y(t_0) = y_0 \end{cases}$$

has a unique solution which is defined on I. The solution is given by

$$y(t) = y_0 e^{A(t)} + \int_{t_0}^{t} e^{A(t) - A(s)} b(s)\, ds, \qquad \text{where } A(t) = \int_{t_0}^{t} a(s)\, ds.$$

Why is this formula called "variation of constants", and which approach leads to this solution?
Approach:

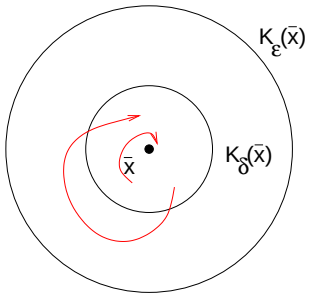
3.2.3 Stability and attractiveness

An interesting and important topic for models is the stability and attractiveness of solutions, which should be defined carefully.

Let $f \in C^{0,1-}(\mathbb{R} \times \mathbb{R}^n, \mathbb{R}^n)$, $\dot{x} = f(t,x)$, let $x(t,t_0,x_0)$ be the maximal solution with $x(t_0) = x_0$. Let $\bar{x} \in C^1([t_0,\infty), \mathbb{R}^n)$ be a fixed solution of the ODE with $\bar{x}(t_0) = \bar{x}_0$. All solutions exist globally in a neighbourhood of $\bar{x}$, for given initial data.

Definition 16 (Stability, Lyapunov) *$\bar{x}$ is called stable, if*

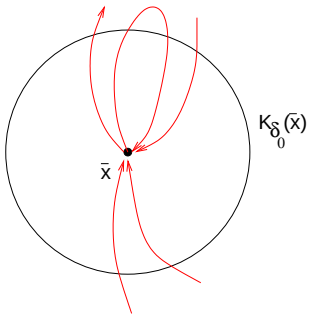
$$\forall\, t_1 \geq t_0 \;\; \forall\, \varepsilon > 0 \;\; \exists\, \delta > 0 : \;\; (\|x_0 - \bar{x}_0\| < \delta \;\; \Rightarrow \;\; \|x(t,t_1,x_0) - \bar{x}(t)\| < \varepsilon \text{ in } [t_1,\infty))$$



$\bar{x}$ is called uniformly stable, if δ does not depend on t_1 (which is always the case if f is not dependent on or periodic in t).

Definition 17 (Attractiveness) *$\bar{x}$ is called attractive, if*

$$\forall\, t_1 \geq t_0 \;\; \exists\, \delta_0 > 0 : \;\; (\|x_0 - \bar{x}_0\| < \delta_0 \;\; \Rightarrow \;\; \lim_{t\to\infty} \|x(t,t_1,x_0) - \bar{x}(t)\| = 0).$$



In this case, all solutions starting in the δ_0 neighbourhood of $\bar{x}(t_1)$ are "attracted" by $\bar{x}$. $\bar{x}$ is called attractor for that trajectory.
Domain of attraction:

$$\mathcal{A}(\bar{x}) = \{x_0 \in \mathbb{R}^n \,|\, \exists\, t_1 \geq t_0 : \;\; \lim_{t\to\infty} \|x(t,t_1,x_0) - \bar{x}(t)\| = 0\}$$

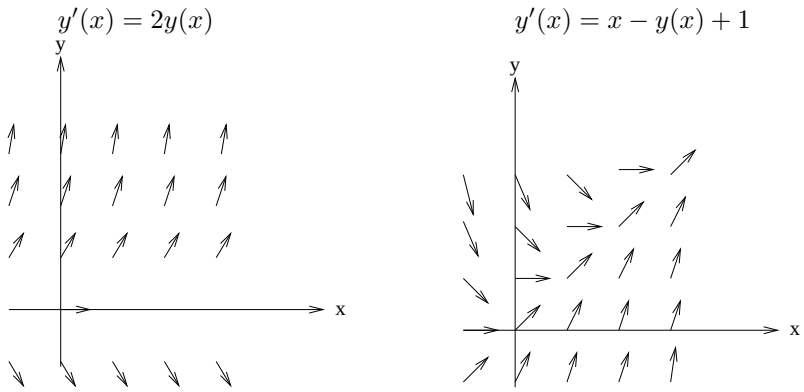
$\bar{x}$ is called uniformly attractive, if δ_0 does not depend on t_1 (which is the case if f is not dependent on or periodic in t).
$\bar{x}$ is called asymptotically stable, if $\bar{x}$ is stable and attractive.

3.2.4 The slope field in the 1D case

First, we consider the general 1D ODE

$$y'(x) = f(x,y).$$

If $y = y(x)$ is a solution curve, then $f(x,y)$ describes the direction of the tangent of this curve in (x,y) and hence the direction of the solution curve in this point.
Examples:



Very useful in this context are isoclines ("curves of same slope", also called nullclines). These are curves satisfying the equation

$$f(x, y) = \underbrace{m}_{\text{fixed}}, \qquad m \in \mathbb{R}$$

In the examples above, we have $y = \frac{m}{2}$ resp. $y = x - m + 1$
Often, the isoclines for $m = 0$ are considered (with horizontal arrows).

3.3 Growth models

3.3.1 The simplest example of ordinary differential equation: exponential growth

The simplest nontrivial ordinary differential equation is

$$\dot{x} = x.$$

The solution is well-known: $x(t) = ae^t$.
We consider a little generalisation:

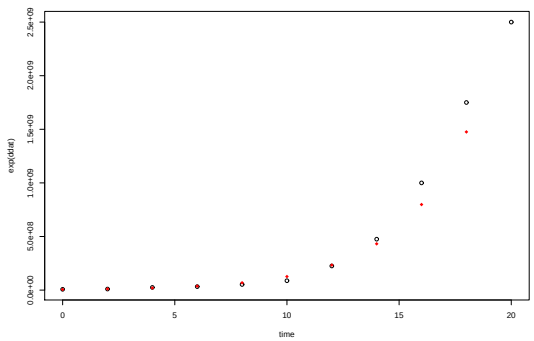
$$\dot{x} = bx.$$

Also, this solution is easy to find: $x(t) = ae^{bt}$. If $b > 0$, it is called exponential growth, if $b < 0$ it is called exponential decay. b as actual rate can also be interpreted as the difference between an underlying growth rate and an underlying death (or decay) rate. Typical examples are the growth of a population of bacteria in Petri dishes, or radioactive decay.
Is this simple model applicable for real-world examples? We consider the following data, describing the population density of some kind of E.coli Bacteria during time course:

Time	0	2	4	6	8	10
Pop. density	7.50e+06	1.00e+07	2.50e+07	3.25e+07	5.25e+07	8.75e+07
Time	12	14	16	18	20	
Pop. density 2.25e+08	4.75e+08	1.00e+09	1.75e+09	2.50e+09		

(data taken from [18])

We try to adapt the function of experimental growth to these data and get:



Fitted data shown as red bullets, experimental data in gray circles

By a fitting procedure (using a computer) we got the following parameter values: $a = 5851232$, $b = 0.3072317$. Since Malthus applied this model first (to the human population!), it is also called Malthusian growth. This model seems to describe the experimental data quite well.
But what happens for larger times? After a certain time, the capacity of the Petri dish will be reached, reducing or even stopping the population growth. This behaviour will be included in the model in the next section.
Short exercise: What is wrong with the modelling approach $x(t) = a \cdot e^{bt+c}$?

An important feature of a exponentially growing population is that is has a constant doubling time. That means that the population doubles its size after a fixed time interval (the same happens for exponential decay), see e.g. [11].
Short exercise: How is the exact relation between doubling time and growth rate?

For plots of exponentially growing population, often the so-called semilogarithmic plot is used. There, the y-axis does not show the population size but the logarithm of the population size. Advantage: The growth can be shown covering many orders of magnitude. In the semilogarithmic plot, the exponential growth curve is converted into a straight line with the growth rate as slope.

3.3.2 Verhulst equation

In the last section, it was assumed that there are unlimited resources for population growth, that means that the increase is proportional to the present population (leading to the exponential growth), or the per capita birth rate is constant and density-independent. This assumption is justified only for certain populations at the beginning of their development. To describe a more realistic situation, it is necessary to incorporate limited resources into the model. This was done by Verhulst (see e.g. [21]) by the following assumptions:

- A biotope has a capacity $K(t)$, where $K(t) > 0$ is a continuous function
- For small densities of populations, there is approximately exponential growth with an exponent $a(t)$, where $a(t) > 0$ is continuous.
- The increase $\dot{u}$ of the population density u is additionally proportional to the remaining living space ($(K - u)$ resp. $(1 - \frac{u}{K})$).

$$\Rightarrow \boxed{\dot{u}(t) = a(t)u(t)\left(1 - \frac{u(t)}{K(t)}\right)}$$

Solving the time-dependent Verhulst equation can easily be done by the so-called "trick of Riccati": We introduce a new variable $v(t) = \frac{1}{u(t)}$. W.l.o.g. let $t_0 = 0$, $v_0 = \frac{1}{u_0}$. Hence we get:

$$\begin{aligned}
\dot{v}(t) &= -\frac{\dot{u}(t)}{u^2(t)} \\
&= -\frac{a(t)u(t)(1 - \frac{u(t)}{K(t)})}{u^2(t)} \\
&= -a(t)(\frac{1}{u(t)} - \frac{1}{K(t)}) \\
&= -a(t)v(t) + \frac{a(t)}{K(t)}
\end{aligned}$$

Apply the variation of constants:

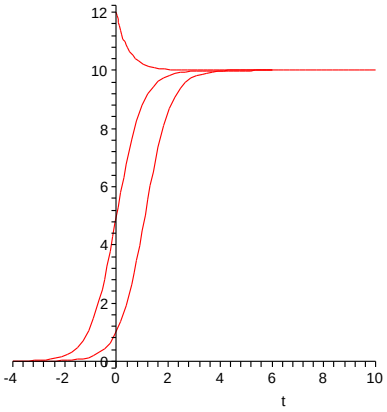
$$\Rightarrow \quad v(t) = v_0 e^{-A(t)} + \int_0^t e^{-(A(t)-A(s))} \frac{a(s)}{K(s)}\, ds, \qquad (A(t) - A(s) = \int_s^t a(\tau)\, d\tau),$$

where $A(t) = \int_{t_0}^t a(s)$. Return to the variable $u(t) = \frac{1}{v(t)}$ and we get the solution:

$$u(t) = \frac{u_0}{e^{-A(t)} + u_0 \int_0^t e^{-(A(t)-A(s))} \frac{a(s)}{K(s)}\, ds} \tag{3.6}$$

For the special case $a, K = const$ we get the following explicit solution of the time-independent Verhulst equation:

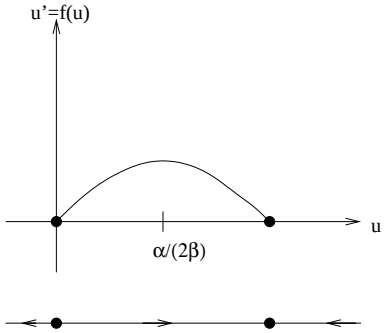
$$\begin{aligned} u(t) &= \frac{u_0}{e^{-at} + u_0 \frac{a}{K} e^{-at} \int_0^t e^{as}\, ds} \\ &= \frac{u_0}{e^{-at} + \frac{u_0}{K}(1 - e^{-at})} = \frac{u_0}{e^{-at}(1 - \frac{u_0}{K}) + \frac{u_0}{K}} = \frac{u_0 K}{e^{-at}(K - u_0) + u_0} \end{aligned}$$



Here, we can consider the stationary solutions and their behaviour. The time-independent Verhulst equation can be written in the form

$$\dot{u} = f(u) = \alpha u - \beta u^2.$$

A short insight can be gained by the following simple procedure:



Zeros of $f(u)$	stationary points
$f(u)$ positive:	Arrow to the right
$f(u)$ negative:	Arrow to the left.

Hence we get: Let $\bar{y}$ a stationary point.

$f'(\bar{y}) < 0$:	$\bar{y}$ stable stationary point
$f'(\bar{y}) > 0$:	$\bar{y}$ unstable stationary point.

Further special cases of the Verhulst equations:

1. Let the function K tend to a positive limit $\bar{K}$,

$$K(t) \to \bar{K} \quad \text{for } t \to \infty.$$

Furthermore, for the positive function a it is assumed that

$$\int_0^\infty a(t)\, dt = \infty. \tag{3.7}$$

Then, the rule of de l'Hospital yields the limit for equation (3.6) with $u_0 > 0$:

$$\lim_{t\to\infty} u(t) = \lim_{t\to\infty} \frac{e^{\int_0^t a(s)\, ds} a(t)}{\frac{a(t)}{K(t)} e^{\int_0^t a(s)\, ds}} = \bar{K}.$$

If K has a positive limit, then $u(t)$ tends to this limit (if it is positive at all). For condition (3.7) it is sufficient that a has a positive bound.
These conclusions are true in particular if $K(t) = \bar{K}$ is constant, which seems to be the biologically most relevant case. If $u_0 > 0$ and a has a positive lower bound (no further conditions), then $u(t)$ tends to $\bar{K}$.

2. The parameters are assumed to be periodic functions with period T. Assume the period to be $T = 1$, hence
$$a(t+1) = a(t), \qquad K(t+1) = K(t).$$
A solution with period 1 and initial value u_0 satisfies $u_1 = u(1) = u_0$. By formula (3.6) we get
$$u_1 = \frac{u_0}{e^{-\int_0^1 a(s)\,ds} + u_0 \int_0^1 e^{-\int_s^1 a(\tau)\,d\tau} \frac{a(s)}{K(s)}\,ds}, \tag{3.8}$$
which leads to
$$u_0 = \frac{1 - e^{\int_0^1 a(s)\,ds}}{\int_0^1 e^{-\int_s^1 a(\tau)\,d\tau} \frac{a(s)}{K(s)}\,ds}.$$
For the Verhulst equation with periodic parameters, there is exactly one periodic solution (except for $u = 0$). The right hand side of (3.8) defines a function $g : \mathbb{R} \to \mathbb{R}$ with $g(u_0) = u_1$ which has the following properties: $g(0) = 0$, $g(u_0) < u_0$ for large u_0, g is strictly monotone increasing and concave. Hence, all solutions with initial data $u_0 > 0$ converge towards the unique non-trivial periodic solution.
Assume a to be constant (just for simplification). Then the periodic solutions reads
$$u(t) = \frac{u_0}{e^{-at} + u_0 \int_0^t e^{-a(t-s)} \frac{1}{K(s)}\,ds}$$
with the initial value
$$u_0 = \frac{e^a - 1}{a \int_0^1 e^{a(1-s)} \frac{1}{K(s)}\,ds}.$$
Using this expression for u_0, we get after several steps
$$u(t) = \left(\frac{\int_0^1 e^{-a(1-s)} \frac{1}{K(s)}\,ds}{\int_0^1 e^{-a(1-s)}\,ds} e^{-at} + \frac{\int_0^t e^{-a(t-2)} \frac{1}{K(s)}\,ds}{\int_0^t e^{-a(t-s)}\,ds} (1 - e^{-at}) \right)^{-1}.$$
The limit $a \to \infty$ yields
$$u(t) = K(t).$$
That means: For a large, the population adapts fast to the changes of the capacity. For $a \to 0$ the limit is
$$u(t) = \left(\int_0^1 \frac{1}{K(s)}\,ds \right)^{-1}.$$
If the population can adapt only slowly, it stays nearly constant, at a value of the harmonic mean value of the capacity.

3.4 Some more basics of ordinary differential equations

3.4.1 Linear systems with constant coefficients

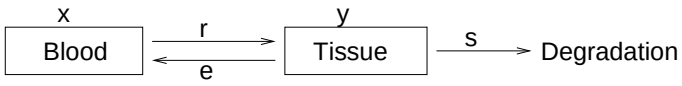
Let $A \in \mathbb{C}^{n \times n}$, we consider the linear system
$$\dot{x} = Ax \text{ in } I = \mathbb{R}. \tag{3.9}$$
We have:
$$x(t) = e^{\lambda t} a \text{ is solution of (3.9)} \;\Leftrightarrow\; a \text{ is eigenvector of } A \text{ corr. to the eigenvalue } \lambda.$$
Furthermore: If A is diagonalisable, i.e., there is a basis $\{a_1, \ldots, a_n\}$ of eigenvectors, then $\{e^{\lambda_1 t} a_1, \ldots, e^{\lambda_n t} a_n\}$ is a fundamental system of (3.9) (basis of the solution space).
If A is real and $\lambda = \mu + i\nu$ is an eigenvalue of A with eigenvector $a + ib$, then the complex solution $x(t) = e^{\lambda t}(a + ib)$ yields two real solutions by $z_1 = Re\, x$ and $z_2 = Im\, x$.
The stationary points of the system $\dot{x} = Ax$ are given by the vectors in the kernel of A. In particular, if $det\, A \neq 0$, then there is only the stationary point 0.

3.4.2 Special case: Linear 2×2 systems

Now we consider the special linear case of $A \in \mathbb{R}^{2\times 2}$, thus

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

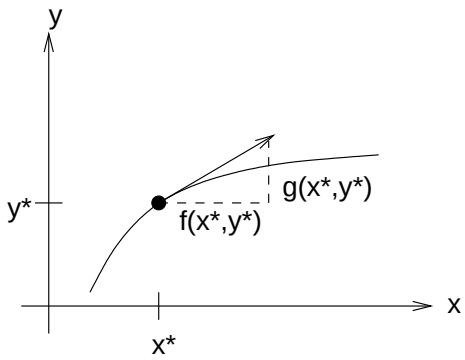
A first, very simple example for a model with two compartments comes from the pharmacokinetics (see [48]):



$x(t)$: Concentration in the blood
$y(t)$: Concentration in the tissue
E.g., one is interested in the course of concentration in the tissue, for a given initial concentration (which results from the amount of taken medicine)

$$\begin{aligned} \dot{x} &= -rx + ey \\ \dot{y} &= rx - ey - sy, \qquad\qquad r, e, s > 0 \end{aligned}$$

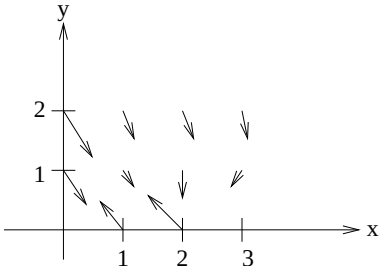
Also in the 2D case, a slope field can be used, the procedure is as follows:
Let $(x(t), y(t))$ be a solution curve of an autonomous 2D system. For each point of time t, the ODE system yields the corresponding tangent vector.



Each point (x, y) is assigned to a vector. Thereby, a rough overview about the behaviour of $\begin{pmatrix} x(t) \\ y(t) \end{pmatrix}$ is given.

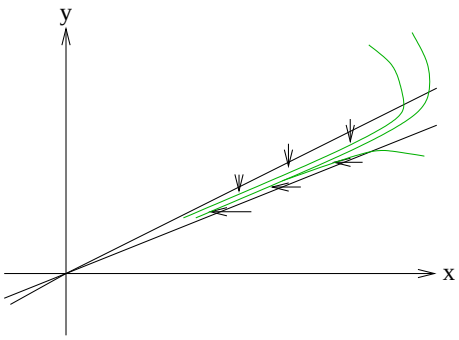
In the above mentioned example: Set $r = \frac{1}{2}$, $e = 1$, $s = \frac{1}{4}$, thus

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} -\frac{1}{2} & 1 \\ \frac{1}{2} & -\frac{5}{4} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$



Also in the 2D case, isoclines are very useful:
The curve with $\dot{x} = 0$ is called x-Nullisocline (the vectors are vertical)
The curve with $\dot{y} = 0$ is called y-Nullisocline (the vectors are horizontal)
In the example:

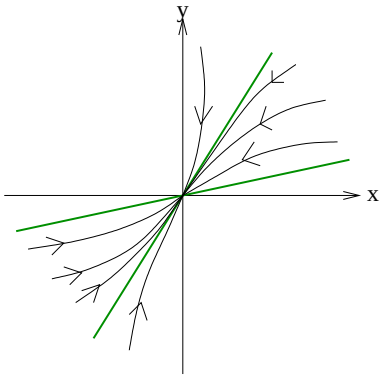
$$\begin{aligned} \dot{x} = -\frac{1}{2}x + y = 0 \quad &\Rightarrow \quad y = \frac{1}{2}x \text{ is x-Nullisocline} \\ \dot{y} = \frac{1}{2}x - \frac{5}{4}y = 0 \quad &\Rightarrow \quad y = \frac{2}{5}x \text{ is y-Nullisocline} \end{aligned}$$



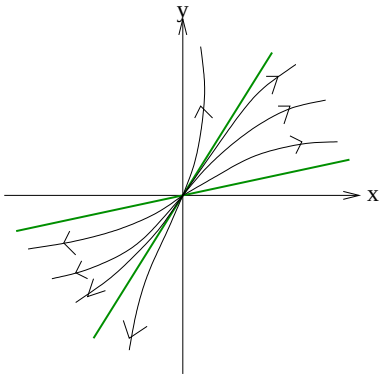
Next step is to get a kind of classification of 2D linear systems, which is often called "zoo". The qualitative dynamic behaviour (of the solution curves) depends on the eigenvalues.
Let $\lambda_1, \lambda_2 \neq 0$, $\lambda_1 \neq \lambda_2$.

Case 1 λ_1, λ_2 are real, $\lambda_1 \cdot \lambda_2 > 0$ (i.e. they have the same sign)

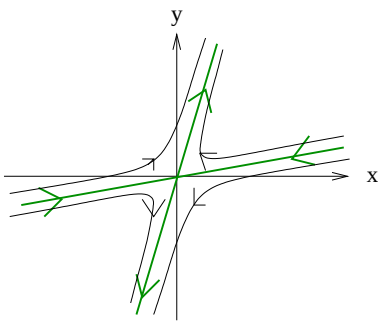
a) $\lambda_1, \lambda_2 < 0$. Then $det(A) > 0$, $tr(A) < 0$
$\Rightarrow (0,0)$ is a stable, two-tangent node.



b) $\lambda_1, \lambda_2 > 0$. Then $det(A) > 0$, $tr(A) > 0$ (compare to a) with inverse time)
$\Rightarrow (0,0)$ is an unstable, two-tangent node



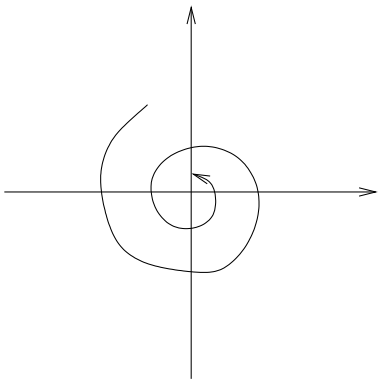
Case 2 $\lambda_1 < 0$, $\lambda_2 > 0$. Then $det(A) < 0$.
This means: There is one stable and one unstable "direction".



$\Rightarrow (0,0)$ is a saddle.

Case 3 $\lambda_1 = \bar{\lambda}_2$ with non-vanishing imaginary part, the eigenvalues are complex conjugated. Then $tr(A)^2 < 4det(A), det(A) > 0$

a) $Re(\lambda_1) = Re(\lambda_2) < 0$ ($\rightsquigarrow tr(A) < 0$)



$\Rightarrow (0,0)$ is a stable spiral.

Example: $A = \begin{pmatrix} -2 & -1 \\ 1 & -2 \end{pmatrix}$,

Eigenvalues $\lambda_{1,2} = -2 \pm i \quad A\begin{pmatrix} 1 \\ -i \end{pmatrix} = (-2+i)\begin{pmatrix} 1 \\ -i \end{pmatrix}$

Eigenvectors $v_{1,2} = \begin{pmatrix} 1 \\ \mp i \end{pmatrix} \quad A\begin{pmatrix} 1 \\ i \end{pmatrix} = (-2-i)\begin{pmatrix} 1 \\ i \end{pmatrix}$

Solutions for λ_1:

$$\begin{aligned} x(t) = e^{\lambda_1 t}\begin{pmatrix} 1 \\ -i \end{pmatrix} &= e^{(-2+i)t}\begin{pmatrix} 1 \\ -i \end{pmatrix} \\ &= e^{-2t}e^{it}\begin{pmatrix} 1 \\ -i \end{pmatrix} \\ &= e^{-2t}(\cos(t) + i\sin(t))\begin{pmatrix} 1 \\ -i \end{pmatrix} \qquad \text{(by the Euler formula)} \\ &= e^{-2t}\begin{pmatrix} \cos(t) + i\sin(t) \\ -i\cos(t) + \sin(t) \end{pmatrix} \\ &= e^{-2t}\left(\begin{pmatrix} \cos(t) \\ \sin(t) \end{pmatrix} + i\begin{pmatrix} \sin(t) \\ -\cos(t) \end{pmatrix}\right) \end{aligned}$$

Here, we are only interested in real solutions, so we use the following ansatz:

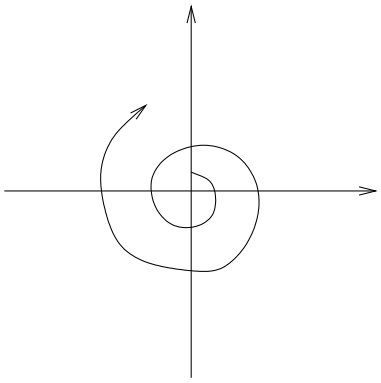
$$x(t) = e^{-2t}\begin{pmatrix} \cos(t) \\ \sin(t) \end{pmatrix}$$

Indeed,

$$\begin{aligned} \dot{x}(t) &= (-2)e^{-2t}\begin{pmatrix} \cos(t) \\ \sin(t) \end{pmatrix} + e^{-2t}\begin{pmatrix} -\sin(t) \\ \cos(t) \end{pmatrix} \qquad \text{(Product rule)} \\ &= e^{-2t}\begin{pmatrix} -2\cos(t) - \sin(t) \\ -2\sin(t) + \cos(t) \end{pmatrix} \\ &= \begin{pmatrix} -2 & -1 \\ 1 & -2 \end{pmatrix} e^{-2t}\begin{pmatrix} \cos(t) \\ \sin(t) \end{pmatrix} = Ax(t) \end{aligned}$$

□

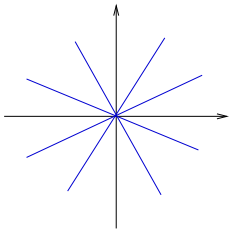
b) $Re(\lambda_1) = Re(\lambda_2) > 0$, then $tr(A) > 0$. This case is analogous to a) with inverse time.



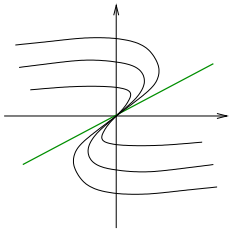
$\Rightarrow (0,0)$ is an unstable spiral.

Further cases / special cases

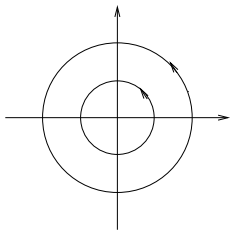
- both eigenvalues are real and equal:
  - there are two linearly independent eigenvectors
    $\Rightarrow (0,0)$ is a star (positive eigenvalues: unstable; negative eigenvalues: stable)



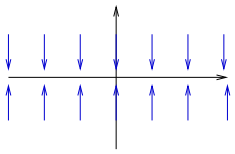
  - there is only one eigenvector (stability depending on the sign)
    $\Rightarrow (0,0)$ is a one-tangent node.



- the eigenvalues are purely imaginary
  $\Rightarrow (0,0)$ is a centre

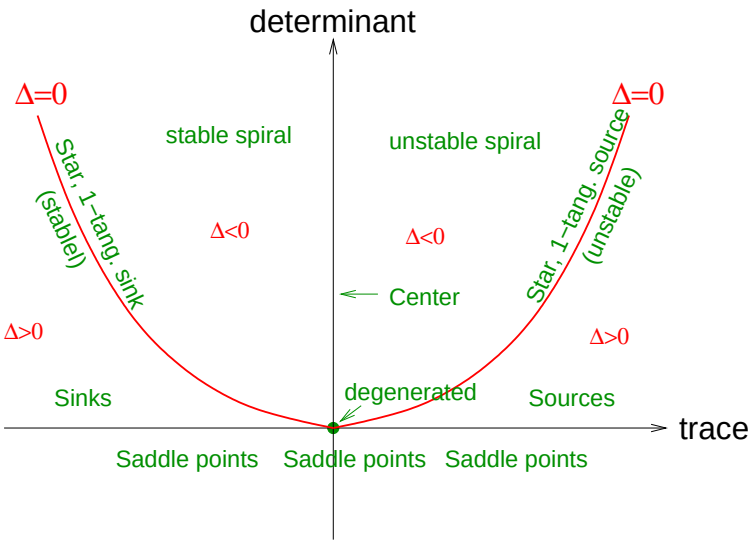


At least one eigenvalue is $= 0$: "degenerated"
Example: $\dot{x} = 0, \;\; \dot{y} = -y$



In this case, the x-axis generates a continuum of stationary states.

In summary, the so-called trace-determinant diagram (for linear 2×2 systems with constant coefficients) is very useful:



In our example: $\dot{x} = \begin{pmatrix} -\frac{1}{2} & 1 \\ \frac{1}{2} & -\frac{5}{4} \end{pmatrix} x$ we get:

$$\begin{aligned} det(A) &= \frac{5}{8} - \frac{1}{2} = \frac{1}{8} > 0 \\ tr(A) &= -\frac{1}{2} - \frac{5}{4} = -\frac{7}{4} < 0 \\ tr(A)^2 - 4det(A) &= \left(\frac{7}{4}\right)^2 - 4 \cdot \frac{1}{8} = \frac{49}{16} - \frac{8}{16} = \frac{41}{16} > 0 \end{aligned}$$

$\Rightarrow$ real eigenvalues
$\Rightarrow$ (2-tang.) sink (stable)

There is a simple criterion to decide for or against stability in a linear system:

Proposition 7 *Consider the linear case $\dot{x} = Ax$, $A \in \mathbb{C}^{n \times n}$. Let $\sigma(A)$ be the spectrum of A.*

1. *0 is asymptotically stable $\Leftrightarrow$ Re $\sigma(A) < 0$*
2. *0 is stable $\Leftrightarrow$ Re $\sigma(A) \leq 0$ and all eigenvalues λ with Re $\lambda = 0$ are semi-simple (i.e., geometric and algebraic multiplicity are the same)*
3. *If there is a $\lambda \in \sigma(A)$ with Re $\lambda > 0$, then 0 is unstable. (The reversed direction is wrong!!!)*

Remark: There is a link between stability in the discrete and in the continuous case. We can create a discrete map of a continuous system (ODE) by choosing e.g. the solution after a time interval 1 (in the given unit of time). For a linear system $\dot{x} = Ax$, we get

$$F(x) = e^A x.$$

In the continuous case the eigenvalues of A are contained in the negative half-plane of $\mathbb{C}$, the stationary point $x = 0$ is stable. Then we get

$$\sigma\{e^A \mid \lambda \in \sigma(A) \subseteq \mathbb{C}^-\} \subseteq \{|z| < 1\}$$

(cf. the stability criterion for discrete systems!).

3.5 Predator-Prey models

First, we consider the standard predator prey model, one of the most famous equations in mathematical biology [48].

Observation of d'Ancona (an italian biologist), who studied the populations of various fish species in the Adriatic Sea:

Before the first world war: The fraction of sharks at fishing in the Adriatic Sea: $\sim 11\ \%$
during " $\sim 36\ \%$
after " $\sim 11\ \%$

The complete data set looks as follows (years / percentages of predators in the fish catches in Fiume (italian port):

1914	1915	1916	1917	1918	1919	1920	1921	1922	1923
12	21	22	21	36	27	16	16	15	11

Is there a reasonable explanation for this fact? D'Ancona asked the famous Italian mathematician Vito Volterra (1860-1940), who was his father-in-law, if he could put up a mathematical model to explain that observation (there wasn't a reasonable biological/ecological explanation available).
Let x be the prey (eatable fishes), y the predators (Mediterranean sharks, skates, rays etc)
$\rightsquigarrow$ classical predator prey model, introduced by Volterra and Lotka (1925/26)

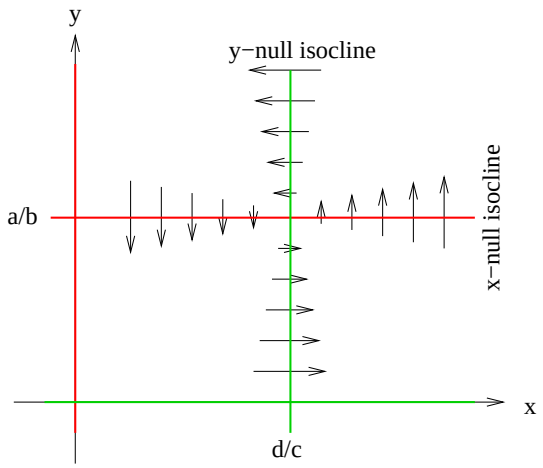
$$\begin{aligned} \dot{x} &= ax - bxy \\ \dot{y} &= -dy + cxy \qquad \text{(all parameters } > 0) \end{aligned}$$

First examination: Slope field / stationary points
We compute the stationary points in our example:

$$\dot{x} = ax - bxy = 0 \quad \Leftrightarrow \quad x = 0 \text{ or } y = \frac{a}{b} \qquad \text{drawn in red}$$

$$\dot{y} = cxy - dy = 0 \quad \Leftrightarrow \quad y = 0 \text{ or } x = \frac{d}{c} \qquad \text{drawn in green}$$

$\Rightarrow (0,0)$ and $(\frac{d}{c}, \frac{a}{b})$ are stationary points. $(\frac{d}{c}, \frac{a}{b})$ is called "coexistence point".



The next step is to look for possibilities how to analyse nonlinear systems, e.g. for stability.
Again, this can be done (or at least to attempt it) by a linearisation.
Let $(\bar{x}, \bar{y})$ be a stationary point. A perturbation is considered:

$$x = \bar{x} + u, \quad y = \bar{y} + v,$$

this yields

$$\begin{aligned} \dot{x} = (\bar{x} + u)^{\cdot} &= f(\bar{x} + u, \bar{y} + v) = f(\bar{x}, \bar{y}) + \frac{\partial f(\bar{x}, \bar{y})}{\partial x} u + \frac{\partial f(\bar{x}, \bar{y})}{\partial y} v + \dots \\ \dot{y} = (\bar{y} + v)^{\cdot} &= g(\bar{x} + u, \bar{y} + v) = \underbrace{g(\bar{x}, \bar{y})}_{=0} + \frac{\partial g(\bar{x}, \bar{y})}{\partial x} u + \frac{\partial g(\bar{x}, \bar{y})}{\partial y} v + \dots \end{aligned}$$

$\rightsquigarrow$ Approximation with linear terms:

$$\begin{aligned} \dot{u} &= \frac{\partial f}{\partial x} u + \frac{\partial f}{\partial y} v \\ \dot{v} &= \frac{\partial g}{\partial x} u + \frac{\partial g}{\partial y} v \end{aligned}$$

This can also be done more generally, for dimension n. In the frame of

$$\dot{x} = f(x), \quad f \in C^1(\mathbb{R}^n, \mathbb{R}^n), \quad f(\bar{x}) = 0, \ \ \bar{x} \in \mathbb{R}^n, \tag{3.10}$$

we consider solutions $x(t)$ of (3.10) in the neighbourhood of $\bar{x}$, $x(t) = \bar{x} + y(t)$,, then

$$\dot{y}(t) = f'(\bar{x})y(t) + o(\|y\|).$$

The corresponding linearised system is

$$\dot{z} = Az, \quad A = f'(\bar{x}) = \left(\frac{\partial f_i}{\partial x_k}(\bar{x})\right).$$

Proposition 8 (Linearisation, Stability, Perron, Lyapunov) *If the real parts of all eigenvalues of $A = f'(\bar{x})$ are negative, then $\bar{x}$ is exponentially asymptotically stable, i.e. there are constants $\delta, C, \alpha > 0$, such that $\|x(0) - \bar{x}\| < \delta$ implies*

$$\|x(t) - \bar{x}\| < Ce^{-\alpha t} \qquad \text{for } t \geq 0.$$

Addendum:
From Re $\sigma(A) \cap (0, \infty) \neq \emptyset$ it follows that $\bar{x}$ is unstable [2].

Now, the following question appears: When do linear and nonlinear model "correspond" locally?
Then answer is given by the next proposition.

Definition 18 *$\bar{x}$ is called hyperbolic, if $0 \notin$ Re $\sigma(f'(\bar{x}))$.*

Proposition 9 (Hartman & Grobman, 1964) *Let $\bar{x}$ be hyperbolic. Then, there is a neighbourhood U of $\bar{x}$ and a homeomorphism $H : U \to \mathbb{R}^n$ with $H(\bar{x}) = 0$, which maps the trajectories of $\dot{x} = f(x)$ one-to-one into trajectories of $\dot{z} = Az$, with respect to the time course.*

The same in a less formal description (in 2D):
Let $Re\,\lambda_j \neq 0$ for all j. Then all solution curves of the nonlinear system

$$\begin{aligned} \dot{x} &= f(x, y) \\ \dot{y} &= g(x, y) \end{aligned}$$

show the same qualitative behaviour at the stationary point $(\bar{x}, \bar{y})$ as those of the corresponding linear problem.

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}$$

(derivatives at $(\bar{x}, \bar{y})$)

Remark: This proposition is not valid for $Re\,\lambda = 0$, i.e. there are problems with the examination of centres and spirals.

Now we can apply this knowledge for the above mentioned simple predator prey model:
General Jacobian Matrix:

$$\begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix} = \begin{pmatrix} a - by & -bx \\ cy & cx - d \end{pmatrix}$$

- In $(0, 0)$, the Jacobian is $\begin{pmatrix} a & 0 \\ 0 & -d \end{pmatrix}$
  $\Rightarrow$ eigenvalues a, $-d$
  $\Rightarrow$ saddle point (unstable)
- In $(\frac{d}{c}, \frac{a}{b})$, the Jacobian is: $\begin{pmatrix} a - b\frac{a}{b} & -b\frac{d}{c} \\ c\frac{a}{b} & c\frac{d}{c} - d \end{pmatrix} = \begin{pmatrix} 0 & -\frac{bd}{c} \\ \frac{ca}{b} & 0 \end{pmatrix}$
  $tr = 0$, $det = \frac{abcd}{bc} = ad$, thus:

  $$\lambda_{1,2} = \frac{tr}{2} \pm \sqrt{\frac{tr^2}{4} - det} = \pm i\sqrt{ad} \qquad \text{(purely imaginary)}$$

  $\Rightarrow$ no statement about stability possible at the moment
  We do not know now, if $(\frac{d}{c}, \frac{a}{b})$ is a spiral or if there are closed trajectories (solution curves)!

Invariants of motion

An invariant of motion $E(x, y)$ satisfies the equation

$$\frac{d}{dt}E(x(t), y(t)) = \frac{\partial E}{\partial x} \cdot \dot{x} + \frac{\partial E}{\partial y} \cdot \dot{y} = 0$$

This means: The variable $E(x, y)$ does not change during time course, along a solution. Descriptive meaning: $E(x, y)$ is a kind of "mountains" over the x, y plane, $\frac{d}{dt}E(x(t), y(t)) = 0$ means that a trajectory lies on a level curve of E.
A physical interpretation would consider $E(x, y)$ to be an energy, a direct biological interpretation is more difficult, and also more difficult to find in general.

Back to the beginning: We try the following ansatz for the predator prey model:

$$E(x, y) = d \ln x - cx + a \ln y - by,$$

thus

$$\begin{aligned} \frac{d}{dt}E(x(t), y(t)) &= (\frac{d}{x} - c)(ax - bxy) + (\frac{a}{y} - b)(cxy - dy) \\ &= (d - cx)(a - by) + (a - by)(cx - d) \\ &= 0, \end{aligned}$$

which shows that the chosen $E(x, y)$ indeed is an invariant of motion for this predator prey model.

In order to determine the shape of the mountains, a fixed y is chosen and E is assumed to be a function depending only on x: $d \ln x - cx + const.$
$\Rightarrow$ derivative $\frac{d}{x} - c$, null at $x = \frac{d}{c} = \bar{x}$
second derivative $-\frac{d}{x^2} < 0 \Rightarrow E$ has a local maximum at $\bar{x}$.
Analogous steps can be done for a fixed x. This yields:

$\Rightarrow E$ is a mountain with one tip

$\Rightarrow$ The level curves are closed

$\Rightarrow$ The trajectories are closed curves

Temporal mean values of the population sizes

It can be shown:
Temporal means over one period are constant, independent from the initial point (but amplitude and periodic time are not!).
Let T be the periodic time, thus $x(T) = x(0)$, $y(T) = y(0)$. Then:

$$\frac{1}{T}\int_0^T x(t)\,dt = \bar{x} = const. \text{ and } \frac{1}{T}\int_0^T y(t)\,dt = \bar{y} = const.$$

Proof:
Generally, $\frac{d}{dt}(\ln(x)) = \frac{\dot{x}}{x} = a - by$, thus

$$\int_0^T \frac{d}{dt}(\ln(x(t)))\,dt = \int_0^T a - by(t)\,dt$$

Then, it follows that

$$\begin{aligned} 0 &= \ln(x(T)) - \ln(x(0)) \\ &= aT - b\int_0^T y(t)\,dt \end{aligned}$$

and $\frac{1}{T}\int_0^T y(t)\,dt = \frac{a}{b} = \bar{y}$, analogously the other equation can be shown.

□

Conclusion:

A non-recurring decimation of the predators does not have any influence on the mean values (otherwise, there is just another trajectory chosen, with the same mean value). The model has to include a continuous fishing in order to explain the obeyed phenomenon, e.g.:

$$\begin{aligned}\dot{x} &= ax - bxy - \varepsilon_1 x = (a-\varepsilon_1)x - bxy \\ \dot{y} &= cxy - dy - \varepsilon_2 y = -(d+\varepsilon_2)y + cxy\end{aligned}$$

(under the assumption that the crop of fishing is proportional to the fish population). Then the coordinates of the coexistence point are

$$\left(\frac{d+\varepsilon_2}{c}, \frac{a-\varepsilon_1}{b}\right)$$

more fishing ⇒ more prey, less predators
less fishing ⇒ less prey, more predators
Coming back to the question of d'Ancona, the answer is that lacking fishery (due to the first world war) lead to a higher level of predators (in the mean). After starting more fishery again, the predators assume lower levels again.

3.5.1 Improved predator prey model

$$\begin{aligned}\dot{x} &= ax\left(1 - \frac{x}{K}\right) - bxy \\ \dot{y} &= cxy - dy\end{aligned}$$

Main properties of this model:

- The prey develops according to Verhulst, if there are no predators $\dot{x} = ax(1 - \frac{x}{K})$
- The predator dies out exponentially, if there is no prey available

Problem: The model has a lot of parameters, it might make sense to reduce their number, if possible. This is done by rescaling.
Define $x = \alpha u$, $y = \beta v$, $t = \kappa\tau$, thus $\tau = \frac{t}{\kappa}$

$$\begin{aligned}\to \dot{x} &= \frac{dx}{dt} = \frac{d(\alpha u)}{dt} = \alpha\frac{du}{d\tau}\cdot\frac{d\tau}{dt} = \alpha\frac{du}{d\tau}\cdot\frac{1}{\kappa} \\ \dot{y} &= \frac{dy}{dt} = \frac{d(\beta v)}{dt} = \beta\frac{dv}{d\tau}\frac{d\tau}{dt} = \beta\frac{dv}{d\tau}\frac{1}{\kappa} \\ \to \dot{u} &= \frac{\kappa}{\alpha}[a\alpha u(1 - \frac{\alpha u}{K}) - b\alpha u\beta v] = a\kappa u(1 - \frac{\alpha u}{K}) - \kappa\beta buv \\ \dot{v} &= \frac{\kappa}{\beta}[c\alpha u\beta v - d\beta v] = \kappa c\alpha uv - \kappa dv\end{aligned}$$

Now define $\kappa = \frac{1}{a}$, $\alpha = \frac{d}{c}$, $\beta = \frac{a}{b}$

$$\begin{aligned}\to \dot{u} &= a\cdot\frac{1}{a}u(1 - \frac{\frac{d}{c}u}{K}) - \frac{1}{a}\frac{a}{b}buv = u(1 - \frac{\frac{d}{c}u}{K}) - uv \\ \dot{v} &= \frac{1}{a}c\frac{d}{c}uv - \frac{1}{a}dv = \frac{d}{a}uv - \frac{d}{a}v.\end{aligned}$$

Now introduce the new parameters $\gamma = \frac{d}{a}$, $K' = \frac{c}{d}K$ (this simplifies the notation). By habit, we write the system again in variables x and y; and for simplicity we write again K instead of K' and $\gamma = 1$ is assumed. The result of all these procedures is

$$\begin{aligned}\dot{x} &= x\left(1 - \frac{x}{K}\right) - xy \\ \dot{y} &= (x-1)y\end{aligned}$$

which just contains one parameter. So, all the reformulations are justified. There are three stationary points for the system (3.11):

$$P_0 = (0,0),\ \ P_1 = (K,0),\ \ P_2 = (1, 1 - \frac{1}{K}).$$

(Obviously, the last one does not have a biological meaning if $K < 1$)
For $K = 1$ the points P_1 and P_2 "cross each other".
Corresponding Jacobian matrix in general:

$$\begin{pmatrix} 1 - \frac{2}{K}x - y & -x \\ y & x - 1 \end{pmatrix}$$

In the stationary points we get:

- $(0,0)$: $\begin{pmatrix} 1 & 0 \\ 0 & -1 \end{pmatrix} \Rightarrow P_0$ is a saddle
- $(K,0)$: $\begin{pmatrix} -1 & -K \\ 0 & K-1 \end{pmatrix} \Rightarrow \lambda_1 = -1,\ \lambda_2 = K - 1$
  If $K > 1$, then P_1 is a saddle; if $K < 1$, P_1 is a asymptotically stable sink.
- $(1, 1 - \frac{1}{K})$: $\begin{pmatrix} -\frac{1}{K} & -1 \\ 1 - \frac{1}{K} & 0 \end{pmatrix}$
  $\Rightarrow$ trace is $-\frac{1}{K}$ (negative in each case), the determinant is $1 - \frac{1}{K}$ (changes the sign at $K = 1$)
  If $K > 1$, then P_2 is asymptotically stable.
  If $K < 1$, then P_2 is a saddle.
  It has to be checked, if there is a spiral or a sink in the first case. The eigenvalues are

$$\lambda_{1,2} = -\frac{1}{2K} \pm \frac{1}{2}\sqrt{\left(\frac{1}{K}\right)^2 - 4\left(1 - \frac{1}{K}\right)}.$$

  The discriminant is > 0 for small K, < 0 for large K.
  A change of sign happens at

$$\begin{aligned} & \left(\frac{1}{K}\right)^2 + 4\frac{1}{K} - 4 = 0 \\ \Leftrightarrow \quad & -4K^2 + 4K + 1 = 0 \\ \Leftrightarrow \quad & K_{1,2} = \frac{1}{2}(1 + \sqrt{2}) \end{aligned}$$

  If $1 < K \leq \frac{1}{2}(1 + \sqrt{2})$, then P_2 is a asymptotic stable sink (with two tangents for $K < \frac{1}{2}(1 + \sqrt{2})$ and one tangent for $K = \frac{1}{2}(1 + \sqrt{2})$).
  If $K > \frac{1}{2}(1 + \sqrt{2})$, then P_2 is a asymptotic stable spiral.

At the moment we observed only local results (which are given by the linearisation). But of course it would be very interesting to know something about the global (or at least "locally less limited" behaviour).

One possibility are the so-called Lyapunov functions [20, 25]. First we consider a Lyapunov function which is connected to a certain fixed point $\bar{x}$.

Definition 19 (Lyapunov function) *Let $\bar{x} \in \mathbb{R}^n$ be a fixed point for the ODE*

$$\dot{x} = f(x), \qquad x \in \mathbb{R}^n,\ \ f : U \to \mathbb{R}^n,\ \ U \subseteq \mathbb{R}^n,$$

(i.e. $f(\bar{x}) = 0$).
Then a function $V : W \to \mathbb{R}$ which is defined on some neighbourhood $W \subseteq U$ of $\bar{x}$ is called Lyapunov function of $\bar{x}$ in W, if

a) $V \in C^1(W, \mathbb{R})$

b) $V(\bar{x}) = 0$ and $V(x) > 0$ if $x \in W \setminus \{\bar{x}\}$

c) $\dot{V}(x) = (grad\ V(x))^* f(x) = \sum_{j=1}^n \frac{\partial V}{\partial x_j}\dot{x}_j = \sum_{j=1}^n \frac{\partial V}{\partial x_j} f_j(x) \leq 0$ for $x \in W$.

If $\dot{V}(x) < 0$ for $x \neq \bar{x}$, then V is called a strong Lyapunov function of $\bar{x}$ in W.

Remark: $\dot{V}$ is the derivative of V along solution curves of the ODE.

Theorem 14 (Lyapunov, Smale) *If $\bar{x}$ possesses a Lyapunov function V in W, then $\bar{x}$ is stable. Moreover, if V is a strong Lyapunov function there, then $\bar{x}$ is asymptotically stable, $W \subseteq \mathcal{A}(\bar{x})$.*

Proof: Let $\varepsilon > 0$, $m := \min_{\partial K_\varepsilon(\bar{x})} V > 0$. Due to property a), find a $\delta > 0$ such that $V(x) \leq \frac{m}{2}$ in $K_\delta(\bar{x})$. Consider a trajectory $x(t)$ with $x(0) \in K_\delta(\bar{x})$. Then $V(x(0)) \leq \frac{m}{2}$ and $\dot{V}(x(t)) = (\text{grad } V(x(t)))^* f(x(t)) \leq 0$. Thus, $V(x(t))$ cannot reach again the value m. Hence, $\bar{x}$ is stable.
If V is a strong Lyapunov function, then choose $K_{\delta_0}(\bar{x}) \subset W$ and define for $\alpha > 0$:

$$V_\alpha = \{x \in \bar{K}_{\delta_0} \,|\, V(x) \geq \alpha\},$$

V_α is compact. On V_α, $\dot{V}(x)$ assumes its maximum (called $v_\alpha < 0$). A trajectory which starts in V_α has to leave V_α in finite time. Hence:

$$\lim_{t\to\infty} x(t) = \bar{x}.$$

□

This idea can be transfered into a more general background. Solutions can tend not only to fixed points, but to more "extended" objects.

Definition 20 ($\alpha-$ and $\omega-$ limit set) *The $\alpha-$ (ω-) limit set $\alpha(p)$ ($\omega(p)$) of a point p is the set of all points, to which the trajectory, that starts in p, tends for $t \to -\infty$ ($t \to \infty$).*

Definition 21 (Lyapunov function II) *Consider*

$$\dot{x} = f(x).$$

$V : M \to \mathbb{R}$ is called Lyapunov function for f, if

a) $V \in C^1(M, \mathbb{R})$

b) $V \geq 0$

c) $(\text{grad } V(x))^* f(x) \leq 0$ for all $x \in M$.

Proposition 10 (LaSalle) *If V is a Lyapunov function for f in the sense of Def. 21, then*

$$\omega(p) \subseteq \{y \in M \,|\, (\text{grad } V(y))^* f(y) = 0\} =: \mathcal{V}_0$$

for each $p \in M$. Furthermore, $\omega(p)$ is contained in the largest invariant subset of $\mathcal{V}_0$.

This allows to estimate a region where solutions will tend to, even if it is not possible to compute exactly a limit set. Application of the Lyapunov functions to the predator prey model:

Consider $x > 0$, $y > 0$,

$K \geq 1$ Ansatz: $V(x, y) = x - \ln x + y - \left(1 - \frac{1}{K}\right) \ln y$
Thereby, we get:

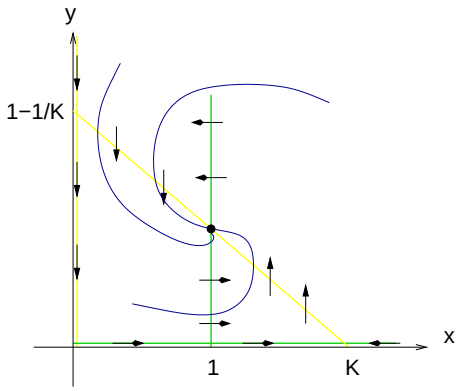
$$\begin{aligned}
\frac{d}{dt}V(x,y) &= \left(1 - \frac{1}{x}\right)\dot{x} + \left(1 - \left(1 - \frac{1}{K}\right)\frac{1}{y}\right)\dot{y} \\
&= \left(1 - \frac{1}{x}\right)\left(x\left(1 - \frac{x}{K}\right) - xy\right) + \left(1 - \left(1 - \frac{1}{K}\right)\frac{1}{y}\right)(x-1)y \\
&= (x-1)\left(1 - \frac{x}{K} - y\right) + (x-1)y - \left(1 - \frac{1}{K}\right)(x-1) \\
&= (x-1)\left(1 - \frac{x}{K}\right) - \left(1 - \frac{1}{K}\right)(x-1) \\
&= -\frac{1}{K}(x-1)^2
\end{aligned}$$

Now, the conditions for a Lyapunov function have to be checked.

1. Obviously, $V(x, y)$ is continuously differentiable for $x, y > 0$.
2. Due to $\ln x \leq x - 1$ we have $V(x, y) \geq 1$

3. $\frac{d}{dt}V(x,y) = -\frac{1}{K}(x-1)^2 \leq 0$

Obviously, here it is $\mathcal{V}_0 = \{(x,y)|\frac{d}{dt}V(x,y) = 0\} = \{(x,y)|x = 1, y > 0\}$. The largest invariant subset of $\mathcal{V}_0$ is just the point $\left(1, 1-\frac{1}{K}\right)$ (in all other points, there is $\dot{x} \neq 0 \Rightarrow$ doesn't work!)
$\Rightarrow$ all trajectories in $x > 0$, $y > 0$ converge towards the stationary point $\left(1, 1-\frac{1}{K}\right)$



$0 < K < 1$ By the Lyapunov function

$$V(x,y) = x - \ln x + y,$$

also in this case convergence towards a stationary point can be shown.

Limit $K \to \infty$ corresponds to the classical Volterra-Lotka model,

$$V(x,y) = x - \ln x + y - \ln y$$

which is here an invariant of motion $\Rightarrow$ the ω-limit set is a closed curve (already known), and corresponds to a periodic orbit.

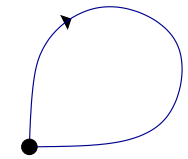
3.5.2 Existence / Exclusion of periodic orbits

After having determined the positions and the stability of stationary points, it might be interesting to know if there are also periodic orbits somewhere. There are further utilities for the existence or exclusion of certain limit sets [20, 25].

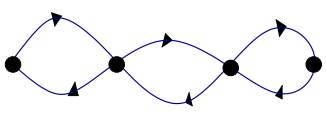
Theorem 15 (Poincare-Bendixson) *Consider a trajectory $x(t) \in \mathbb{R}^2$ (or $x(t) \in D$, where $D \subset \mathbb{R}^2$ is compact and connected, positively invariant) of the ODE $\dot{x} = f(x)$, f smooth, with only finitely many roots. If $x(t)$ is bounded, then the ω-limit set is one of the following objects:*

- *a stationary point*
- *a periodic orbit*
- *a homoclinic orbit or heteroclinic cycle.*

A homoclinic orbit is an orbit that tends to the same stationary point for $t \to \pm\infty$, while a heteroclinic orbit tends to different stationary points. A heteroclinic cycle is a closed chain of heteroclinic orbits. Somehow, a homoclinic orbit resp. a heteroclinic cycle can be interpreted as a generalisation of a periodic orbit.



homoclinic orbit

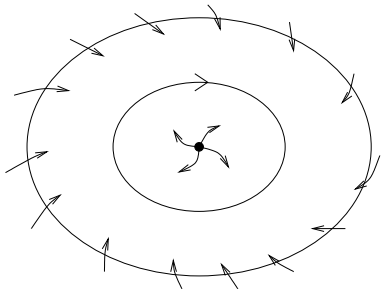


heteroclinic cycle

Direct consequence of this theorem: If there is no stationary point, there has to be a periodic orbit.

Remark: This proposition is not valid e.g. in higher dimensional spaces etc.! (Famous counterexample: The Lorenz attractor)

Example of application:



Example: The Van der Pol oscillator was first introduced to represent an electric circuit with a nonlinear element (a triode valve, with current-dependent resistance); later Balthazar van der Pol realised that the approach can be similarly used for from oscillator models of vacuum tubes respectively of the human heart; here we consider only a simplified version, as a famous example for showing the existence of limit cycles [52, 12]. The system reads:

$$\begin{aligned} \dot{x} &= y + x - \frac{x^3}{3} \\ \dot{y} &= -x \end{aligned}$$

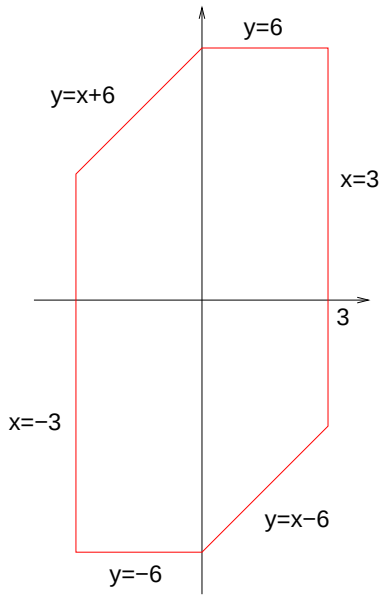
Obviously, there is only one stationary state: $(0, 0)$. The general Jacobian matrix reads

$$J = \begin{pmatrix} 1 - x^2 & 1 \\ -1 & 0 \end{pmatrix},$$

thus, in (0,0) it is

$$J(0, 0) = \begin{pmatrix} 1 & 1 \\ -1 & 0 \end{pmatrix},$$

which yields a positive trace and a positive determinant. Hence (0,0) is unstable and repels the solutions somehow.
Goal: By applying the Theorem of Poincare-Bendixson, we want to show that the system shows up periodic orbits. For that purpose, we consider the following region:



This region is used as D in the theorem; thus we need to check that the solutions cannot leave D. In order to do that, we prove, that the arrows of the vector field on the boundary point inside. Due to the symmetric region and the fact, that the equations are odd, it is sufficient to consider the following three segments of the boundary of D:

$$x = 3 \quad \text{for} \quad -3 \leq y \leq 6, \quad y = 6 \quad \text{for } 0 \leq x \leq 3, \quad y = x + 6 \quad \text{for} \quad -3 \leq x \leq 0.$$

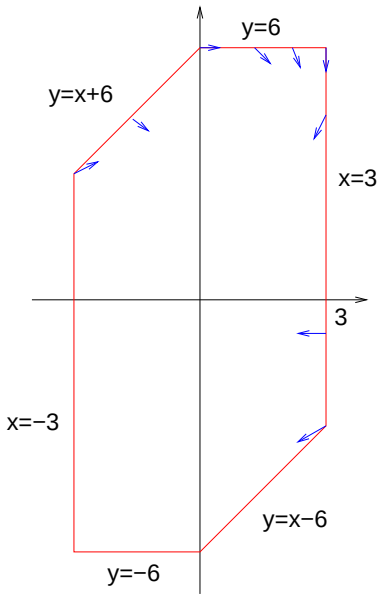
$x = 3$, $-3 \leq y \leq 6$: On that segment we find that $\dot{x} = y + x - \frac{x^3}{3} = y - 6 \leq 0$, thus the arrows point to the left.
We need to prove, that solution curves may not "escape" through one of the corners. At $(x, y) = (3, 6)$, the arrow has the direction $(0, -3)$, so it does not point outward. At $(x, y) = (3, -3)$ the arrow has the direction $(-9, -3)$ which is more "flat" than the segment $y = x - 6$, so the solution cannot escape there, too.

$y = 6$, $0 \leq x \leq 3$: On that segment we find that $\dot{y} = -x \leq 0$, thus the arrows point downwards.
The remaining corner in that case is $(0, 6)$, there the arrow points to the right, and thus, the solution cannot D leave here.

$x + 6$, $-3 \leq x \leq 0$: On that segment, we find

$$\begin{aligned} \dot{x} &= y + x - \frac{x^3}{3} = 2x + 6 - \frac{x^3}{3} > 0 \\ \dot{y} &= -x \geq 0, \end{aligned}$$

which means that the arrows point to the right and upward, but $\frac{-x}{2x+6-\frac{x^3}{3}} \leq 1$, but the slope is smaller than 1, which means inward. At the corner $(-3, 3)$, the arrow points in the direction $(9, 3)$, which is also inward.



Altogether, we have shown that D cannot be left by a solution curve. Since $(0, 0)$ is the only stationary point in D and all solutions tend away from $(0, 0)$, the only remaining possibility according to Poincare-Bendixson is the existence of a closed periodic orbit as a ω-limit set.

In some cases, the existence of closed orbits can be excluded by the so-called negative criterion of Bendixson(-Dulac) [20].

Proposition 11 (Negative criterion of Bendixson) *Let $D \subseteq \mathbb{R}^2$ be a simply connected region and $(f, g) \in C^1(D, \mathbb{R})$ with div $(f, g) = \frac{\partial f}{\partial x} + \frac{\partial g}{\partial y}$ being not identically zero and without change of sign in D. Then the system*

$$\begin{aligned} \dot{x} &= f(x, y) \\ \dot{y} &= g(x, y) \end{aligned}$$

has no closed orbits lying entirely in D.

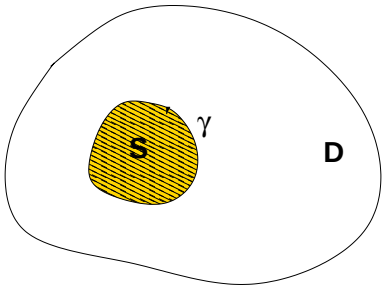
Proof: Each solution curve satisfies $\frac{dy}{dx} = \frac{g}{f}$ or, in particular

$$\int_\gamma (f(x, y)\, dy - g(x, y)\, dx) = 0$$

on any closed orbit γ. In this case, Green's theorem yields that

$$\int\int_S \left(\frac{\partial f}{\partial x} + \frac{\partial g}{\partial y}\right) dx\, dy = 0, \tag{3.11}$$

where S is the interior of γ.



If $\frac{\partial f}{\partial x} + \frac{\partial g}{\partial y} > 0$ (or < 0) holds on D, then there is no region $S \subseteq D$ such that (3.11) is true. Hence, it is not possible to have closed orbits which lie entirely in D.

□

The negative criterion of Bendixson can also be generalised; the same idea also works for the system

$$\begin{aligned} \dot{x} &= \rho(x,y) f(x,y) \\ \dot{y} &= \rho(x,y) g(x,y), \end{aligned}$$

where $\rho > 0$ is continuously differentiable.

3.6 Volterra's competition model and quasimonotone systems

Literature: Murray [44], Hirsch [24], Smale [50], Edelstein-Keshet [12], Riede [48], Gotelli [17]

Basic properties of the model:

- Two species compete for the same food (limited) - e.g. for a territory which corresponds to food resource
- Each species grows according to Verhulst and participates at the capacity of the other species.

These assumptions yield the following ODE system:

$$\begin{aligned} \dot{x}_1 &= r_1 x_1 \left(1 - \frac{x_1 + b_1 x_2}{K_1}\right) \\ \dot{x}_2 &= r_2 x_2 \left(1 - \frac{x_2 + b_2 x_1}{K_2}\right). \end{aligned}$$

K_i is the capacity of species i. b_i gives information about how strong the other species participates at the capacity of species i (it is also called the competitive effect). r_i is the birth rate of species i. In opposite to the original model of Volterra, we do not assume that $b_2 = \frac{1}{b_1}$, this allows that both species use their environment individually. If two species are similar to each other, there is approximately $b_1 = b_2 = 1$.

The isoclines lie on both coordinate axis and on two additional lines:

$\dot{x}_1 = 0$: $x_1 = 0$ or $x_1 + b_1 x_2 = K_1$

$\dot{x}_2 = 0$: $x_2 = 0$ or $b_2 x_1 + x_2 = K_2$

Thus, there are four stationary points in general:

$$P_1 = (0,0), \quad P_2 = (K_1, 0), \quad P_3 = (0, K_2), \quad P_4 = (\bar{x}_1, \bar{x}_2),$$

where

$$\bar{x}_1 = \frac{K_2 b_1 - K_1}{b_1 b_2 - 1}, \qquad \bar{x}_2 = \frac{b_2 K_1 - K_2}{b_1 b_2 - 1}.$$

Remark, that the coexistence point may be outside of the biological meaningful area, depending on the parameter values.

The general Jacobian reads

$$J(x_1, x_2) = \begin{pmatrix} r_1 - \frac{2r_1}{K_1}x_1 - \frac{r_1 b_1}{K_1}x_2 & -\frac{r_1 b_1}{K_1}x_1 \\ -\frac{r_2 b_2}{K_2}x_2 & r_2 - \frac{2r_2}{K_2}x_2 - \frac{r_2 b_2}{K_2}x_1 \end{pmatrix}$$

For $b_1 = b_2 = 1$ these isoclines are parallel. But it is possible, to have parameters b_1 and b_2 which are lying nearby, but there is still no cutting point in the positive area. This case is considered first.

Case 1: $K_2 < K_1/b_1$ **and** $K_2/b_2 < K_1$

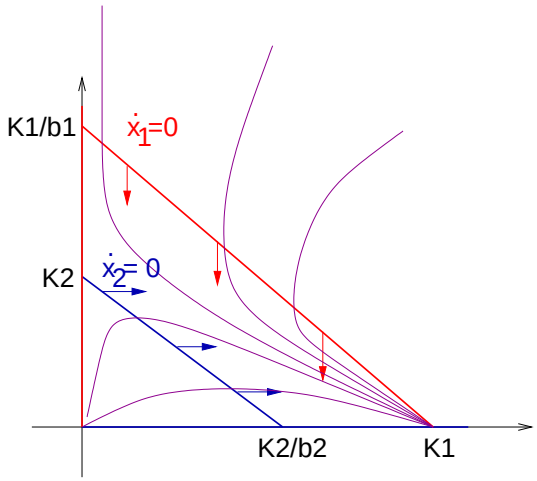
Without loss of generality, we assume $K_1 > K_2$ (i.e. we denote the population with the greater capacity to be x_1). Then, the system has three stationary points:

$$(0,0), \quad (0,K_2), \quad (K_1,0).$$

The Jacobian matrices in these stationary points are:

- $J(0,0) = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix} \rightsquigarrow (0,0)$ is an unstable node
- $J(0,K_2) = \begin{pmatrix} r_1(1 - b_1\frac{K_2}{K_1}) & 0 \\ -r_2 b_2 & -r_2 \end{pmatrix}$, hence we get as determinant $det = -r_1 r_2(1 - b_1\frac{K_2}{K_1}) < 0$ which corresponds to a saddle.
- $J(K_1,0) = \begin{pmatrix} -r_1 & -r_1 b_1 \\ 0 & r_2(1 - b_2\frac{K_1}{K_2}) \end{pmatrix}$, both eigenvalues are negative, thus $(K_1,0)$ is a stable node.

The phase portrait looks as follows:



This behaviour is also called the "exclusion principle of Volterra". It says that the population with the smaller capacity will die out, and the population with the larger capacity will tend to its equilibrium K_1 (assumed that both populations were present in the beginning).

Case 2: $K_2 > K_1/b_1$ **and** $K_1 < K_2/b_2$

Without loss of generality, we assume $K_1 > K_2$ (i.e. we denote the population with the greater capacity to be x_1). Then, the system has three stationary points:

$$(0,0), \quad (0,K_2), \quad (K_1,0).$$

The Jacobian matrices in these stationary points are:

- $J(0,0) = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix} \rightsquigarrow (0,0)$ is an unstable node

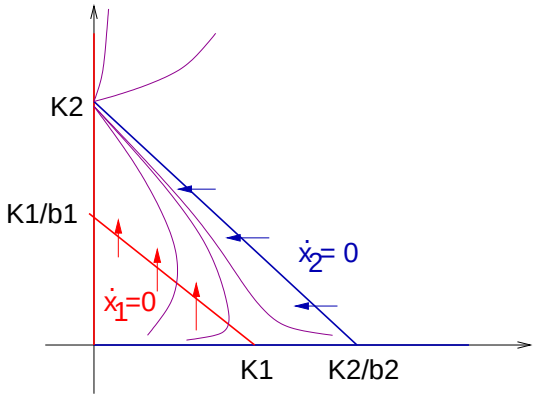
- $J(0,K_2) = \begin{pmatrix} r_1(1-b_1\frac{K_2}{K_1}) & 0 \\ -r_2 b_2 & -r_2 \end{pmatrix}$, hence we get as determinant $det = -r_1 r_2(1-b_1\frac{K_2}{K_1}) > 0$ and trace $tr = r_1\,(1-b_1K_2/K_1) - r_2 < 0$. The eigenvalues can be computed by

$$\begin{aligned} \lambda_{1,2} &= \frac{1}{2}\left(tr \pm \sqrt{tr^2 - 4det}\right) \\ &= \frac{1}{2}\left(r_1\,(1-b_1K_2/K_1) - r_r \pm \sqrt{r_1^2(1-b_1K_2/K_1)^2 + r_2^2}\right) < 0, \end{aligned}$$

  thus, both eigenvalues are negative, $(0,K_2)$ is a stable node.

- $J(K_1,0) = \begin{pmatrix} -r_1 & -r_1 b_1 \\ 0 & r_2(1-b_2\frac{K_1}{K_2}) \end{pmatrix}$, i.e. the determinant is negative and $(K_1,0)$ is a saddle.

The phase portrait looks as follows:



Also in this case, we can see the exclusion principle.

But also coexistence of both is possible!

Case 3: $K_2 < K_1/b_1$ **and** $K_2/b_2 > K_1$

Here, an coexistence point shows up, thus, there are four stationary points. The Jacobian matrices in these stationary points are:

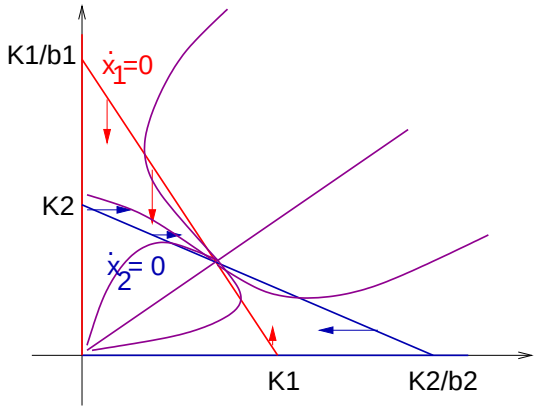
- $J(0,0) = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix} \rightsquigarrow (0,0)$ stays to be an unstable node

- $J(0,K_2) = \begin{pmatrix} r_1(1-b_1\frac{K_2}{K_1}) & 0 \\ -r_2 b_2 & -r_2 \end{pmatrix}$, hence we get as determinant $det = -r_1 r_2(1-b_1\frac{K_2}{K_1}) < 0$ which corresponds to a saddle.

- $J(K_1,0) = \begin{pmatrix} -r_1 & -r_1 b_1 \\ 0 & r_2(1-b_2\frac{K_1}{K_2}) \end{pmatrix}$, one eigenvalue is positive, the other is negative, thus $(K_1,0)$ is also a saddle.

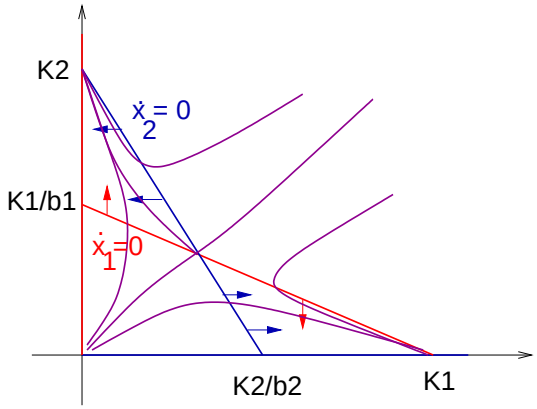
- $J(\bar{x}_1,\bar{x}_2) = \begin{pmatrix} r_1 - \frac{2r_1}{K_1}(\frac{K_2 b_1 - K_1}{b_1 b_2 - 1}) - \frac{r_1 b_1}{K_1}(\frac{b_2 K_1 - K_2}{b_1 b_2 - 1}) & -\frac{r_1 b_1}{K_1}\frac{K_2 b_1 - K_1}{b_1 b_2 - 1} \\ -\frac{r_2 b_2}{K_2}\frac{b_2 K_1 - K_2}{b_1 b_2 - 1} & r_2 - \frac{2r_2}{K_2}\frac{b_2 K_1 - K_2}{b_1 b_2 - 1} - \frac{r_2 b_2}{K_2}\frac{K_2 b_1 - K_1}{b_1 b_2 - 1} \end{pmatrix}$
  Of course, one could compute the eigenvalues of this matrix, but it is hard work. They are both negative, thus the coexistence point is a stable node.

Anyway, the behaviour of the system in this case is as follows:



Case 4: $K_2 > K_1/b_1$ **and** $K_2/b_2 < K_1$

With the same kind of examination we find the following behaviour of the solutions:



Obviously, coexistence of the species is only possible if they are not very similar. This phenomenon is called the "principle of competitive exclusion".

It makes sense to simplify a model with so many parameters. This can again be done by rescaling:

$$u_1 = \frac{x_1}{K_1}, \quad u_2 = \frac{x_2}{K_2}, \quad \tau = r_1 t, \quad \rho = \frac{r_1}{r_2}, \quad a_1 = b_1 \frac{K_2}{K_1}, \quad a_2 = b_2 \frac{K_1}{K_2}.$$

Then the system becomes

$$\begin{aligned} \frac{du_1}{d\tau} &= u_1(1 - u_1 - a_1 u_2) = f_1(u_1, u_2) \\ \frac{du_2}{d\tau} &= \rho u_2(1 - u_2 - a_2 u_1) = f_2(u_1, u_2) \end{aligned}$$

and the analysis is much easier!
Using the negative criterion of Bendixson and Dulac, it can easily be shown that no periodic orbits can exist in such a system:
Scale the system by $\frac{1}{u_1 u_2}$, which yields

$$\frac{\partial\left(\frac{1}{u_1 u_2} f_1(u_1, u_2)\right)}{\partial u_1} + \frac{\partial\left(\frac{1}{u_1 u_2} f_2(u_1, u_2)\right)}{\partial u_2} = -\frac{1}{u_2} - \frac{\rho}{u_1} < 0.$$

Concrete example for such a competitive behaviour: Let x be the population size of swarm fishes with a capacity of $K_1 = 5000$ individuals and y the population size of territorial fishes with a capacity of $K_2 = 40$ individuals. 200 swarm fishes use the same resources like one territorial fish does, thus $b_2 = 1/200 = 0.005$. One territorial fish uses the resources like 50 swarm fishes do, $b_1 = 50$. Furthermore, let $r_1 = 0.05$ and $r_2 = 0.04$. Then, the coexistence point has the coordinates $(4000, 20)$ and is a stable node.

Another nice example can be found in Edelstein-Keshet [12], Fig. 6.9., describing time courses of the

results of the model compared to real experimental data.

This kind of system belongs to the context of quasimonotone systems, which show some interesting properties.

Let $\Omega \subseteq \mathbb{R}^n$ be a convex domain, $f \in C^1(\Omega, \mathbb{R}^n)$, the ODE is of the form

$$\dot{x} = f(x), \quad x \in \Omega. \tag{3.12}$$

Definition 22 (quasimonotone) *The ODE (3.12) is called quasimonotone, if either*

$$\frac{\partial f_i}{\partial x_j} \geq 0 \quad \text{in } \Omega \text{ for } i \neq j \quad \Leftrightarrow \quad (3.12) \text{ is cooperative} \tag{3.13}$$

or

$$\frac{\partial f_i}{\partial x_j} \leq 0 \quad \text{in } \Omega \text{ for } i \neq j \quad \Leftrightarrow \quad (3.12) \text{ is competitive} \tag{3.14}$$

Remark: Quasimonotone systems were introduced already in 1930 by Max Müller and Erich Kamke; a more detailed theory was developed by Morris Hirsch in the 1980s.

Remark: $\dot{x} = f(x)$ is cooperative $\Leftrightarrow$ $\dot{x} = -f(x)$ is competitive.
Many results for one property can be obtained for the other by a time reverse, but this does not work in all cases!

In the linear case $\dot{x} = Ax$, $A \in Mat_n(\mathbb{R})$, it is

$$\begin{aligned} \text{cooperative} &\quad \Leftrightarrow \quad a_{ij} \geq 0 \text{ for } i \neq j \\ \text{competitive} &\quad \Leftrightarrow \quad a_{ij} \leq 0 \text{ for } i \neq j \end{aligned}$$

It can be easily shown:
If A is cooperative, then the system $\dot{x} = Ax$ leaves the cone $C = \mathbb{R}^n_+$ positively invariant. In more detail, for $x(t)$ and $y(t)$ being trajectories, the implication

$$x_0 \leq y_0 \quad \Rightarrow \quad x(t) \leq y(t) \qquad \text{for } t \geq 0$$

holds.
(This notation means $y \geq x \Leftrightarrow (y - x) \in \mathbb{R}^n_{0+}$)
A similar statement can also be given in the nonlinear case:

Proposition 12 *Let $\dot{x} = f(x)$ be cooperative. Let x, y be solution with $x(0) = x_0$ and $y(0) = y_0$. Then*

$$x_0 < y_0 \quad \Rightarrow \quad x(t) < y(t) \quad \text{for all } t \in [0, T]$$

(the same statement holds also for $\leq$).

Definition 23 *Two vectors are called unordered if neither $p < q$ nor $q < p$.*

Proposition 13 *Let $\dot{x} = f(x)$ be competitive.*

a) If x_0 and y_0 are unordered, $x(t)$, $y(t)$ are solutions, then also $x(t)$ and $y(t)$ are unordered.

b) Similarly: If $x(\tau)$ and x_0 are unordered, then also $x(t + \tau)$ and $x(t)$ are unordered for $t \in [0, T - \tau]$.

c) Let x,y be solutions of $\dot{x} = f(x)$ with $x_0 < y_0$. Then, if solutions exist, for $t \leq t_0$ it is

$$x(t) < y(t),$$

thus $\mathbb{R}^n_+$ is negatively (backwards) invariant.

Proposition 14 *Let $n = 2$ and $\dot{x} = f(x)$ cooperative or competitive. Let $\gamma^+(p) = \{x(t) : t \geq 0\}$ be a limited half-orbit, which is contained in Ω, then $\omega(p)$ consists only of a stationary point.*

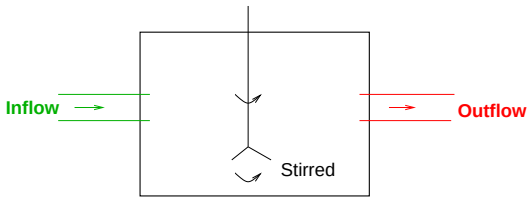
Remark: Cooperative systems in $\mathbb{R}^n$ with $n \geq 3$ can exhibit non-trivial periodic orbits (Hadeler & Glass [22])

Proposition 15 *A cooperative system $\dot{x} = f(x)$ in $\mathbb{R}^n$ with $n \geq 3$ cannot exhibit an orbitally stable periodic orbit.*

3.7 The chemostat

Literature: e.g. Smith and Waltman [51]

The chemostat is a "famous" system and often used in mathematical biology, ecology and biotechnology to investigate existing competitive systems. It is also called "Bio-reactor" or "Continuously stirred tank reactor (CSTR)". Classically, it describes the behaviour of two species, which compete for one substrate, which is renewed at a constant rate. The chemostat is a basic instrument in laboratories, e.g. for fermentation processes. The basic structure of a chemostat looks as follows:



In general, the chemostat describes a competition between n user species which live on the same substrate. The substrate is provided with a constant rate, the washing out rates of substrate and the users may be different. There are "nutrient uptake" functions to describe the exploitation of the substrate.
The substrate is denoted by s and the users by x_i, $i = 1, \dots, n$. It is assumed that the system is spatially homogeneous (i.e. "well-stirred"). The chemostat equations are (in a simplified version)

$$\begin{aligned} \dot{s} &= D(1-s) - \sum_{i=1}^{n} p_i(s) x_i \\ \dot{x}_i &= x_i(p_i(s) - D_i), \qquad i = 1, \dots, n. \end{aligned} \tag{3.15}$$

$D > 0$ is the transfer rate of the substrate and the D_i are the washing out rates of the users.
p_i, the so-called nutrient uptake functions or specific growth rates, are continuously differentiable and assumed to be monotone increasing, with $p_i(0) = 0$. The $p'(s) > 0$ (monotone increasing) says that the users really consume something (more and more) of the substrate. Additionally, it is assumed that $\lim_{s\to\infty} p(s) = p_\infty < \infty$. This means that the consumption rate per user tends to a saturation, even though substrate is present in excess. Commonly, these uptake functions $p_i(s)$ are in the form of so-called monotone Monod or Michaelis Menten functions, $p_i(s) = \frac{m_i s}{a_i + s}$, where m_i is the maximum growth rate and a_i the Michaelis Menten constant of the i-th user (will be considered in detail elsewhere).
a_i corresponds to the nutrient concentration at which $\frac{m_i s}{a_i+s}$ reaches half of its maximum m_i.
The λ_i which are uniquely determined by $p_i(\lambda_i) - D_i = 0$ are called the "break-even" concentration and can be interpreted as the minimum nutrient level required to maintain the present level of user species.
First, we consider the case $n = 1$, i.e. the system

$$\begin{aligned} \dot{s} &= D(1-s) - p(s)x \\ \dot{x} &= x(p(s) - D_1). \end{aligned} \tag{3.16}$$

Looking for stationary points:

$$\begin{aligned} \dot{x} = 0 \quad &\Leftrightarrow \quad x(p(s) - D_1) = 0 \quad \Leftrightarrow \quad x = 0 \text{ or } p(s) - D_1 = 0 \\ \dot{s} = 0 \quad &\Leftrightarrow \quad D(1-s) - p(s)x = 0. \end{aligned}$$

In the first case ($x = 0$): $D(1-s) = 0 \Leftrightarrow s = 1$, thus, there is one stationary point $(s, x) = (1, 0)$.
In the second case ($p(s) - D_1 = 0$) we need $D(1-s) - D_1 x = 0$. So, if $\bar{s}$ is the unique solution of $p(s) = D_1$ (due to the positive derivative), then it follows that $\bar{x} = \frac{D}{D_1}(1 - \bar{s})$. For having this second stationary point in $\mathbb{R}^2_+$, it is required that $0 < \bar{s} < 1$ (otherwise $\bar{x} < 0$). But if $p(1) < D_1$, then $p(s) < D_1$ for $s < 1$ (due to the monotonicity), then there no further stationary point possible in $\mathbb{R}^2_+$ and $(1, 0)$ is globally stable (which is shown below).

On the other hand, if $p(1) > D_1$, there is an additional stationary point $(\bar{s}, \bar{x})$ with $s \in (0, 1)$, $\bar{x} > 0$ where $\bar{s}$ is the unique solution of the equation $p(s) = D_1$, and $\bar{x} = \frac{D}{D_1}(1 - \bar{s})$. The (local) stability of the stationary points is considered in the following:
The Jacobian matrix of (3.16) is

$$J(s, x) = \begin{pmatrix} -D - p'(s)x & -p(s) \\ xp'(s) & p(s) - D_1 \end{pmatrix},$$

hence

$$J(1,0) = \begin{pmatrix} -D & -p(1) \\ 0 & p(1) - D_1 \end{pmatrix}.$$

If $p(1) < D_1$, then $(1,0)$ is stable. If $p(1) > D_1$, then $(1,0)$ is unstable. Furthermore, we have

$$J(\bar{s},\bar{x}) = \begin{pmatrix} -D - p'(\bar{s})\bar{x} & -p(\bar{s}) \\ \bar{x}p'(\bar{s}) & 0 \end{pmatrix}.$$

Obviously, $p(\bar{s}) > 0$ and $p'(\bar{s}) > 0$, hence the determinant is positive and the trace is negative, leading to a stable stationary point $(\bar{s},\bar{x})$ (under the assumption of its existence).
In order to exclude periodic orbits, the negative criterion of Bendixson and Dulac can be applied (the generalised version). For this, the system is transformed (for positive x) into

$$\begin{aligned} s' &= \frac{D(1-s)}{x} - p(s) \\ x' &= p(s) - D_1, \end{aligned}$$

which yields the divergence of the Jacobian

$$\mathrm{div}J = -\frac{D}{x} - p'(s) < 0$$

and the periodic orbits cannot exist due to Bendixson-Dulac.
Finally, we can show that the trajectories are bounded in $\mathbb{R}^2_+$. It is

$$\dot{(s+x)} = D - Ds - D_1 x \leq D - \delta(s+x)$$

with $\delta = \min(D, D_1)$. Hence, all trajectories in $\mathbb{R}^2_+$ reach the triangle

$$\{(s,x): \ s \geq 0,\, x \geq 0,\, s + x \leq \frac{D}{\delta}\}$$

and stay in there. The theorem of Poincare and Bendixson yields now: All solutions tent to stationary states.
If $p(1) > D_1$, then all trajectories with $x > 0$ tend to the stationary point $(\bar{s},\bar{x})$;
if $p(1) < D_1$, then all trajectories with $x < 0$ tend to the stationary point $(1,0)$.

For more than one user, the analysis of the chemostat is much more difficult. Now we consider the case $n = 2$:

$$\begin{aligned} \dot{s} &= D(1-s) - p_1(s)x_1 - p_2(s)x_2 \\ \dot{x}_1 &= x_1(p_1(s) - D_1) \\ \dot{x}_2 &= x_2(p_2(s) - D_2). \end{aligned}$$

Assume that $p_1(1) > D_1$ and $p_2(1) > D_2$, otherwise the corresponding user dies out. Then, there is a uniquely determined solution $\bar{s}_i$ of the equation $p_i(s) = D_i$. In order to exclude limit cases, we assume $\bar{s}_1 \not\equiv \bar{s}_2$. Let $\bar{s}_1 < \bar{s}_2$. Then, there are three stationary points (s, x_1, x_2):

$$E_0 : (1,0,0), \quad E_1 : (\bar{s}_1, \bar{x}_1, 0), \quad E_2 : (\bar{s}_2, 0, \bar{x}_2)$$

where $\bar{x}_i = D(1-\bar{s}_i)/p(\bar{s}_i)$. The next step is to analyse the stability. The Jacobian is

$$J = \begin{pmatrix} -D - p_1'(s)x_1 - p_2'(s)x_2 & -p_1(s) & -p_2(s) \\ p_1'(s)x_1 & p_1(s) - D_1 & 0 \\ p_2'(s)x_2 & 0 & p_2(s) - D_2 \end{pmatrix},$$

hence

$$J(E_0) = \begin{pmatrix} -D & -p_1(1) & -p_2(1) \\ 0 & p_1(1) - D_1 & 0 \\ 0 & 0 & p_2(1) - D_2 \end{pmatrix}.$$

The eigenvalues can be directly read from the matrix: $-D$, $p_1(1) - D_1 > 0$, $p_2(1) - D_2 > 0$, which yield a saddle. The stable manifold is the line $x_1 = 0$, $x_2 = 0$ (i.e. $(s,0,0)$, $s \in \mathbb{R}$). Furthermore,

$$J(E_1) = \begin{pmatrix} -D - p_1'(\bar{s}_1)\bar{x}_1 & -p_1(\bar{s}_1) & -p_2(\bar{s}_1) \\ p_1'(\bar{s}_1)x_1 & p_1(\bar{s}_1) - D_1 & 0 \\ 0 & 0 & p_2(\bar{s}_1) - D_2 \end{pmatrix}.$$

One eigenvalue is $p_2(\bar{s}_1) - D_2 < p_2(\bar{s}_2) - D_2 = 0$. The other eigenvalues can be found in the upper left 2×2 matrix, which is the matrix for the system with $x_2 \equiv 0$. For this, it was shown above, that the determinant is positive and the trace is negative. Hence, E_1 is locally stable. Finally, we consider

$$J(E_2) = \begin{pmatrix} D - p_2'(\bar{s}_2)\bar{x}_2 & -p_1(\bar{s}_2) & -p_2(\bar{s}_2) \\ 0 & p_1(\bar{s}_2) - D_1 & 0 \\ p_2'(\bar{s}_2)\bar{x}_2 & 0 & 0 \end{pmatrix}.$$

The vector $(0, 1, 0)$ is left eigenvector for the eigenvalue $p_1(\bar{s}_2) - D_1 > p_1(\bar{s}_1) - D_1 = 0$, hence E_2 is unstable. It is expected that E_1 is globally stable in the domain $s > 0$, $x_1 > 0$, $x_2 > 0$. This was shown for the special case $D = D_1 = D_2$, or for different D_i and special functions p_i. The proofs use special Lyapunov functions.

What are the biological conclusions? At first glance, we notice that there is only one user in an equilibrium. This can be seen by the fact that in general the equations $p_1(s) = D_1$ and $p_2(s) = D_2$ cannot be solved at the same time. There is again the principle of competitive exclusion . The analysis of stability shows that E_1 is stable, but not E_2. The users differ only by the inequality $\bar{s}_1 < \bar{s}_2$. Thus, the user who has the better nutrient uptake will prevail against the other one.

The first idea of a competitive exclusion principle was claimed already in 1934 by the Russian biologist Gause (for two species with similar ecology). In 1960, this first statement was precised by Hardin and called "competitive exclusion principle" (CEP). It was stated that "ecological differentiation is the necessary condition for coexistence". A later generalisation came to the result that n species cannot coexist on fewer than n resources.
In nature, there are some counterexamples, e.g. the biodiversity of many organisms in nature. A famous example "The paradox of the plankton" can be found in Hutchinson [30], 1961. Indeed, there is a discrepancy between theoretical approach and experimental observation. A lot of examinations were done, from biological and from modelling view.

3.8 Short introduction into bifurcations

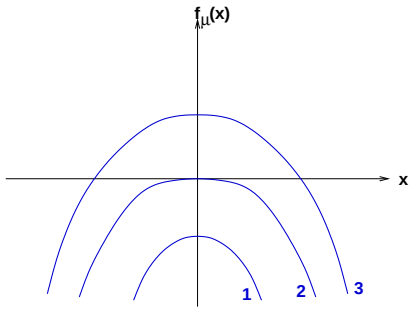
A bifurcation can shortly be defined as a sudden change of qualitative behaviour (of a dynamical system), dependent on a parameter at a certain threshold (e.g. the appearance or the disappearance of stationary points, change of stability, ...).
In the following, the bifurcation parameter is denoted by μ.

Here we introduce some elementary examples for bifurcations. Of course, this is an incomplete list, and also a lot of details are left out. More information about bifurcations can be found e.g. in [3, 20] (there also exists an English version of Arrowsmith).

Saddle-Node Bifurcation

From "nothing" there appears a saddle and a node (at least in the 2-dimensional case, the name is self-explanatory).
But first we consider a 1-dimensional example:

$$\dot{x} = \mu - x^2 =: f_\mu(x).$$



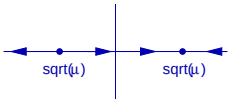
1: $\mu < 0$

There are no stationary points!

2: $\mu = 0$

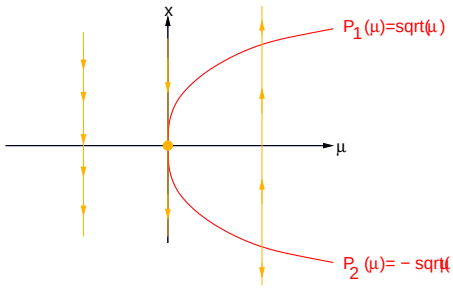
There is one stationary point, "hybrid"

3: $\mu > 0$



Two stationary points are there, one is stable, the other is unstable. Their position depends on the value of μ.

The bifurcation diagram looks as follows:

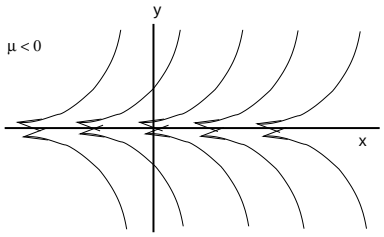


Observation: If the parameter μ varies, then for $\mu < 0$ there are no singularities, for $\mu = 0$ there is exactly one stationary point, and for $\mu > 0$ there shows up a pair of stationary points, one of them is stable, the other one is unstable.

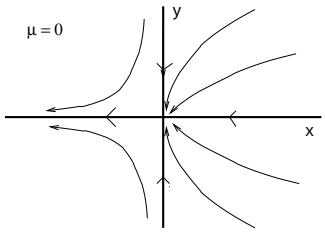
2D case:

$$\begin{cases} \dot{x} = \mu - x^2 \\ \dot{y} = -y \end{cases}$$

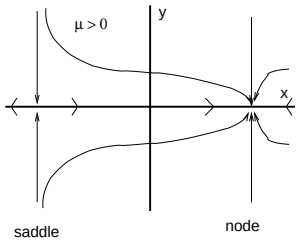
(thus, the bifurcation parameter does not concern the variable y, only x)



no stationary points



(0,0) is a saddle−node



(two stationary points)

The general Jacobian is

$$J_f(x,y) = \begin{pmatrix} -2x & 0 \\ 0 & -1 \end{pmatrix},$$

this yields for the two stationary points in the last case:

$$J_f(\sqrt{\mu},0) = \begin{pmatrix} -2\sqrt{\mu} & 0 \\ 0 & -1 \end{pmatrix}, \qquad J_f(-\sqrt{\mu},0) = \begin{pmatrix} 2\sqrt{\mu} & 0 \\ 0 & -1 \end{pmatrix}$$

Transcritical Bifurcation (Exchange of stability)

Two stationary points exchange their stability, exactly at the parameter value, where both points meet.

Again, we consider a 1D example first:

$$\dot{x} = \mu x - x^2 = x(\mu - x) = f_\mu(x).$$

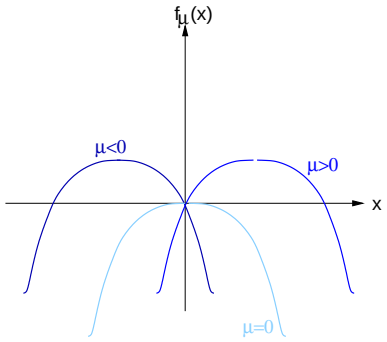
The position of the "peak" can be computed:

$$f'_\mu(x) = 0 \Leftrightarrow \mu - 2x = 0 \Leftrightarrow x = \frac{\mu}{2},$$

$$\rightsquigarrow \quad f_\mu(\frac{\mu}{2}) = \frac{\mu^2}{4},$$

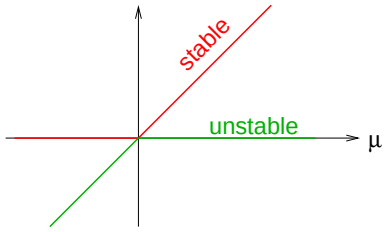
thus the peak has the coordinates $\left(\frac{\mu}{2}, \frac{\mu^2}{4}\right)$, which is on a parabola, dependent on μ).

For $\mu < 0$, 0 is stable, μ is unstable.
For $\mu = 0$, $0 = \mu$ is hybrid (unstable).
For $\mu > 0$, 0 is unstable, μ is stable.



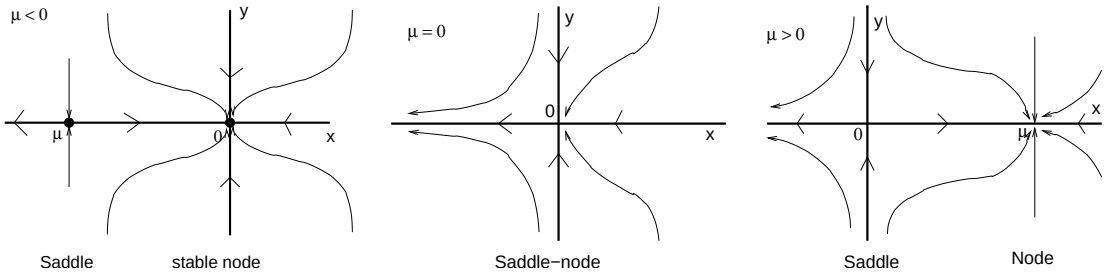
Observation: Two stationary points exchange their stability depending on the parameter μ, at the parameter value where they meet.

Bifurcation diagram:



Again, the bifurcation parameter only affects the variable x.
2D case:

$$\begin{cases} \dot{x} = \mu x - x^2 \\ \dot{y} = -y \end{cases} \qquad \rightsquigarrow \qquad J(x,y) = \begin{pmatrix} \mu - 2x & 0 \\ 0 & -1 \end{pmatrix}$$



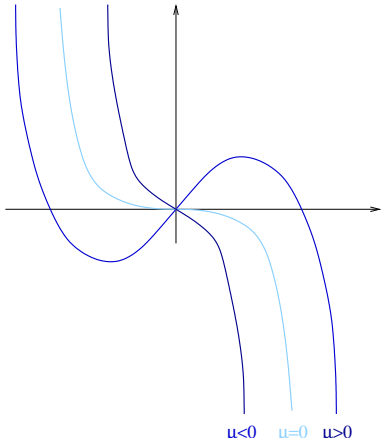
Pitchfork Bifurcation

A stationary point is stable for parameter values $\mu \leq \mu_0$, for $\mu > \mu_0$ there show up two additional

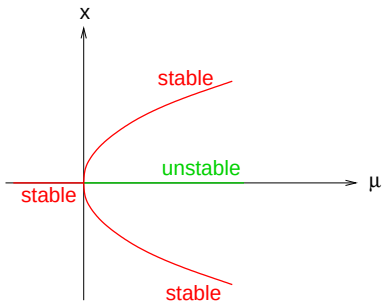
stationary points which are stable, whereas the originally stable point becomes unstable. First, we consider the 1D example

$$\begin{aligned} \dot{x} &= \mu x - x^3 = x(\mu - x^2) \\ (&= x(x+\sqrt{\mu})(x-\sqrt{\mu}) \quad \text{for } \mu \geq 0) \end{aligned}$$

For $\mu < 0$, 0 is stable and the only stationary point.
For $\mu = 0$, 0 is stable and the only stationary point.
For $\mu > 0$, 0 is unstable, $\sqrt{\mu}$ and $-\sqrt{\mu}$ are stable.



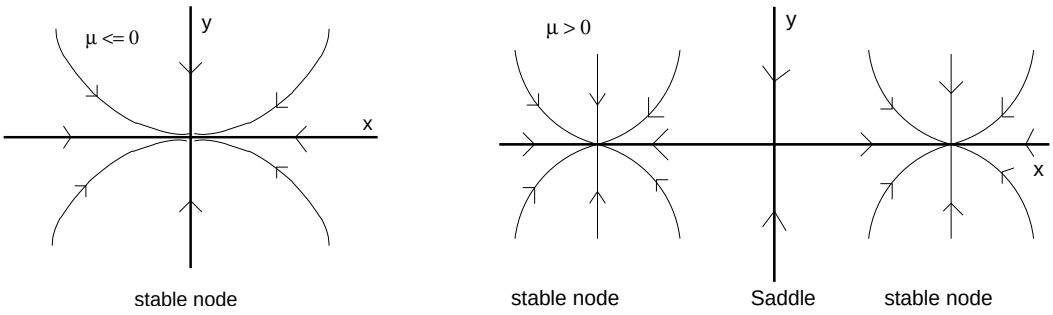
Bifurcation diagram:



(looks like a pitchfork, there the name comes from)
2D case:

$$\begin{cases} \dot{x} = \mu x - x^3 \\ \dot{y} = -y \end{cases}$$

(μ is only involved in the equation of the variable x)



Hopf Bifurcation

Roughly speaking: A stationary point looses its stability, at the same time a stable periodic orbit shows up around the stationary point. Since periodic orbits cannot show up in the (continuous!) 1D case, 2D is the simplest case allowing for such a behaviour.

a) Supercritical case:

Let $\mu \in \mathbb{R}$ and consider as an example

$$\left.\begin{aligned} \dot{x} &= -y + x(\mu - x^2 - y^2) \\ \dot{y} &= x + y(\mu - x^2 - y^2) \end{aligned}\right\} =: f_\mu(x,y)$$

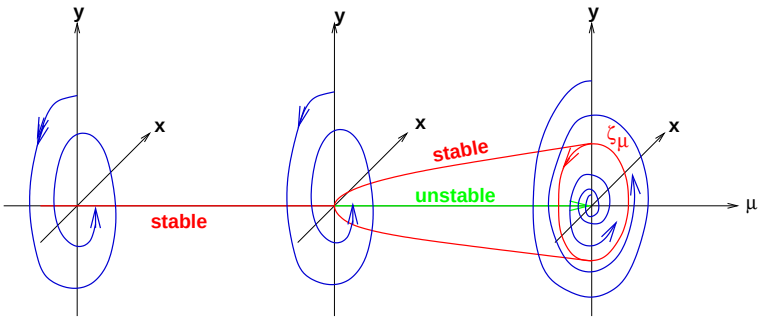
$P_0 = (0,0)$ is the only stationary point, the Jacobian matrix reads

$$J_{f,\mu}(0,0) = \begin{pmatrix} \mu & -1 \\ 1 & \mu \end{pmatrix},$$

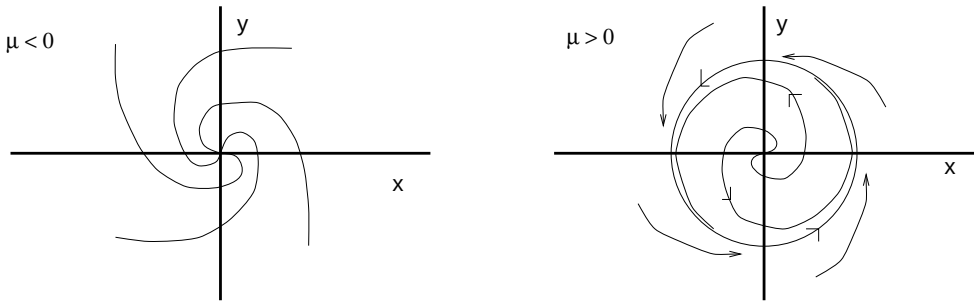
with trace $tr = 2\mu$, determinant $det = \mu^2 + 1$ and discriminant $\Delta = -4$. Introduce the Lyapunov function $V(x,y) = \frac{1}{2}(x^2 + y^2)$. Along solutions it is

$$\begin{aligned} \dot{V}(x,y) &= \frac{\partial V}{\partial x}\dot{x} + \frac{\partial V}{\partial y}\dot{y} \\ &= x(-y + x(\mu - x^2 - y^2)) + y(x + y(\mu - x^2 - y^2)) \\ &= (x^2 + y^2)(\mu - x^2 - y^2). \end{aligned}$$

If $\mu \leq 0$ then P_0 is globally asymptotically stable.
If $\mu > 0$ then P_0 is a repellor; since in $\{(x,y) \,|\, x^2 + y^2 < \mu\}$ we have $\dot{V} > 0$ for $(x,y) \neq (0,0)$. Furthermore, $\{(x,y) \,|\, x^2 + y^2 = \mu\}$ is the trace of a periodic orbit ζ_μ, because f_μ is tangential to the circle $\{(x,y) \,|\, x^2 + y^2 = \mu\} : (x,y) f_\mu(x,y) = 0$.
ζ_μ is orbitally stable, since outside of ζ_μ it is $\dot{V} < 0$, inside $\dot{V} > 0$ for $(x,y) \neq (0,0)$. (Orbital stability is a kind of generalisation of "normal stability"; the difference is that in the orbital stability, the distance between a solution and the complete orbit / trajectory / solution curve is considered - instead of comparing the positions of the solutions at a certain time point. This plays especially a role for periodic orbits, where the period may differ, even though the orbits are nearby).
For $\mu \to 0+$, ζ_μ shrinks itself to P_0.



In the phase plane, the solutions look similar to



Mathematical interpretation: While μ runs through the real numbers at $\mu = 0$, a pair of conjugate complex eigenvalues $\lambda_{1,2}(\mu) = \mu \pm i$ crosses the imaginary axis from the left halfspace to the right.

More generally: A supercritical Hopf bifurcation means that a pair of conjugate complex eigenvalues of the Jacobian of a stationary point crosses the imaginary axis from left to right at a certain parameter value μ_0. There, the stationary point looses its stability and stable periodic orbits show up (limit cycles).
Example: Predator prey model of Rosenzweig.

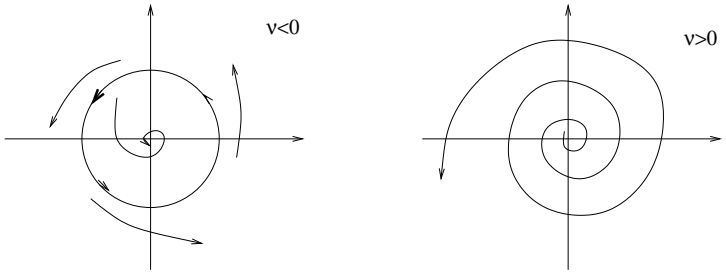
b) Subcritical case: Invert the time course and the "direction" of the parameter ($\nu := -\mu$) in the example above (supercritical case):

$$\begin{aligned} \dot{x} &= y + x(\nu + x^2 + y^2) \\ \dot{y} &= -x + y(\nu + x^2 + y^2) \end{aligned}$$

For $\nu \geq 0$ P_0 is a repellor. For $\nu < 0$ P_0 is a local attractor with

$$\{(x, y) \,|\, x^2 + y^2 < |\nu|\} = \mathcal{A}(P_0)$$

(this can be shown by the same Lyapunov function as above).
ζ_ν is a orbitally unstable periodic orbit.



In general: In the case of a subcritical Hopf Bifurcation a pair of conjugate complex eigenvalues of the Jacobian of a stationary point crosses the imaginary axis from left to right for a certain parameter value ν_0. Then the stationary point looses its stability, for $\nu < \nu_0$ there exist orbitally unstable periodic orbits which shrink themselves to the stationary point in the case of $\nu \to \nu_0-$.
(Example: Lorenz equation, see [20])

The following theorem can be applied to show the existence of periodic orbits [20]:

Theorem 16 (Hopf, 1942) *Consider the system $\dot{x} = f_\mu(x)$, $x \in \mathbb{R}^n$. Suppose, that f_{μ_0} has an equilibrium at (x_0, μ_0) with the following properties:*
The Jacobian $f'_{\mu_0}(x_0)$ has exactly one pair of purely imaginary complex eigenvalues (no other eigenvalues with zero real parts).
Then there is a (locally) smooth curve of equilibria $(x(\mu), \mu)$ with $x(\mu_0) = x_0$. The eigenvalues $\lambda(\mu)$, $\bar{\lambda}(\mu)$ of the Jacobian $f'_\mu(x(\mu))$ which are purely imaginary at $\mu = \mu_0$, depend smoothly on μ. If additionally

$$\frac{d}{d\mu}(Re\ \lambda(\mu))|_{\mu=\mu_0} =: d \neq 0,$$

then there is a unique three-dimensional so-called "centre manifold" passing through (x_0, μ_0) in $\mathbb{R}^n \times \mathbb{R}$ and a smooth system of coordinates (preserving the planes $\mu = const.$), such that the differential equation can be formulated on the surface corresponding to the eigendirections of the pair of purely imaginary eigenvalues (depending on $(x, \mu) \in \mathbb{R}^n \times \mathbb{R}$) as

$$\begin{aligned} \dot{x}_1 &= (d\mu + a(x_1^2 + x_2^2))x_1 - (\omega + c\mu + b(x_1^2 + x_2^2))x_2 + higher\ \ order\ \ terms \\ \dot{x}_2 &= (\omega + c\mu + b(x_1^2 + x_2^2))x_1 + (d\mu + a(x_1^2 + x_2^2))x_2 + higher\ \ order\ \ terms, \end{aligned}$$

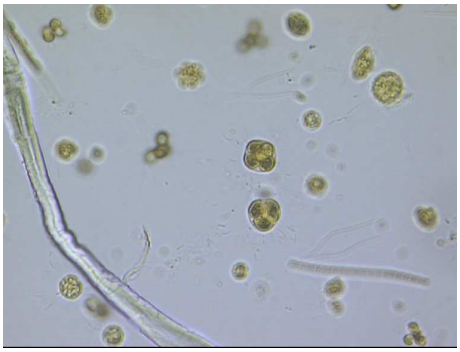
If $a \neq 0$, then there is a surface of periodic solutions in the centre manifold which has quadratic tangency with the eigenspace of $\lambda(\mu_0)$, $\bar{\lambda}(\mu_0)$ (agreeing to second order with the paraboloid $\mu = -(a/d)(x^2 + y^2)$) . If $a < 0$, then these periodic solutions are stable limit cycles, while if $a > 0$ the periodic orbits are repelling (i.e. unstable).

3.9 Ecosystems Modelling

Literature: Britton [7]

Example: We consider plankton in the ocean. It is limited by the element nitrogen (which is essential, i.e. plankton cannot grow without any nitrogen). There are two kinds of plankton:

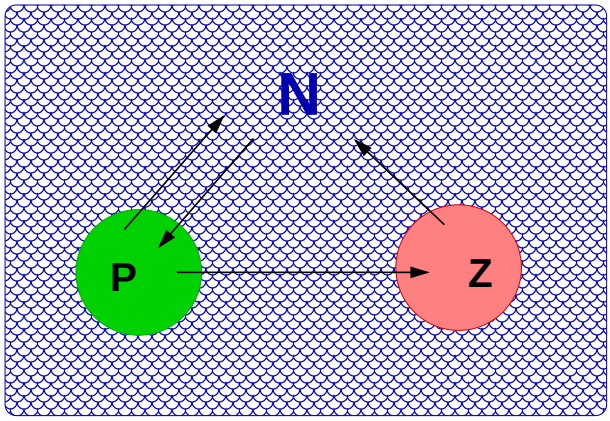
- Phytoplankton (plant plankton) : can perform photosynthesis and therefore requires essential elements
- Zooplankton (animal plankton) : they feed on phytoplankton



Assumptions for the model approach:

- Everything is well-mixed (so, we can deal with spatially independent concentrations)
- The system is closed to nitrogen
- Nitrogen can be taken up from the ocean by phytoplankton (and then is incorporated into the phytoplankton)
- Zooplankton can incorporate nitrogen by consuming phytoplankton
- Death and excretion from the plankton recycle the nitrogen to the ocean - the delaying process of decay and remineralisation is neglected here

The following notations are used: N describes the concentration of available nitrogen, P the concentration of phytoplankton, and Z the concentration of zooplankton. Remark, that we take P and Z to be in the unit of mass of nitrogen which is incorporated in the plankton per unit surface area of the ocean.



The basic model (with linear functional responses) of these processes can be formulated as follows:

$$\dot{N} = aP + bZ - cNP \tag{3.17}$$
$$\dot{P} = cNP - dPZ - aP \tag{3.18}$$
$$\dot{Z} = dPZ - bZ. \tag{3.19}$$

Obviously, these equations satisfy

$$\dot{N} + \dot{P} + \dot{Z} = 0,$$

which leads immediately to $N + P + Z = A$. This means that the nitrogen is conserved, A is the total concentration of nitrogen in the system.
We look for the stationary states of the system:

- From equation (3.19): $0 = dPZ - bZ \rightsquigarrow Z = 0$ or $P = \frac{b}{d}$
- From equation (3.18): $0 = cNP - dPZ - aP \rightsquigarrow P = 0$ or $cN - dZ - a = 0 \Rightarrow N = \frac{dZ+a}{c}$
- furthermore use the conservation equation $A = N + Z + P$.

Now we look for possible combinations which satisfy the three equations at once:

- Possibility 1: $Z = 0$ and $P = 0 \Rightarrow N = A - Z - P = A$
  $\rightsquigarrow S_0 = (A, 0, 0)$
- Possibility 2: $Z = 0$ and $N = \frac{dZ+a}{c} = \frac{a}{c}$, $P = A - Z - N = A - \frac{a}{c}$
  $\rightsquigarrow S_1(\frac{a}{c}, A - \frac{a}{c}, 0)$
- Possibility 3: $P = \frac{b}{d}$, $Z = \frac{cN-a}{d}$, $N = A - P - Z \Rightarrow Z = \frac{c(A-P-Z)-a}{d} \Rightarrow \frac{d+c}{d}Z = \frac{c}{d}(A - P) - \frac{a}{d}$
  $Z = \frac{c}{d+c}(A - \frac{b}{d} - \frac{a}{c})$, thus $N = A - \frac{b}{d} - \frac{c}{d+c}(A - \frac{b}{d} - \frac{a}{c})$
  $\rightsquigarrow S_2(A - \frac{b}{d} - \frac{c}{d+c}(A - \frac{b}{d} - \frac{a}{c}), \frac{b}{d}, \frac{c}{d+c}(A - \frac{b}{d} - \frac{a}{c}))$
  Remark: P (the coordinate of the stationary point S_2) is independent of A, this means biologically that not the phytoplankton, but only the zooplankton benefits from an increased level of nitrogen. (This is a typical behaviour in such models; species at alternate levels in the food chain may benefit from an increased supply of nutrients)

Now we want to see, how the dynamics is influenced by the parameter c. This parameter describes the uptake "rate" of nitrogen (which may depend on the season; e.g. the phytoplankton was observed to become more efficient as the season progresses, leading to an increased c).
The general Jacobian matrix reads:

$$J = \begin{pmatrix} -cP & a - cN & b \\ cP & cN - dZ - a & -dP \\ 0 & dZ & dP - b \end{pmatrix}$$

In S_0:

$$J_0 = \begin{pmatrix} 0 & a - cA & b \\ 0 & cA - a & 0 \\ 0 & 0 & -b \end{pmatrix},$$

one can directly see the eigenvalues: $\lambda_1 = 0$, $\lambda_2 = cA - a$, $\lambda_3 = -b$

In S_1:

$$J_1 = \begin{pmatrix} -cA + a & 0 & b \\ cA - a & 0 & -dA + \frac{da}{c} \\ 0 & 0 & dA - \frac{da}{c} - b \end{pmatrix},$$

the eigenvalues are determined by $(-cA + a - \lambda)(-\lambda)(dA - \frac{da}{c} - b - \lambda) = 0 \rightsquigarrow \lambda_1 = 0$, $\lambda_2 = -cA + a$, $\lambda_3 = dA - \frac{da}{c} - b$.
Int S_2:

$$J_2 = \begin{pmatrix} -\frac{cb}{d} & a - \frac{c}{c+d}[d(A - \frac{b}{d}) + a] & b \\ \frac{cb}{d} & 0 & -b \\ 0 & d(A - \frac{b}{d} - \frac{1}{c+d}[d(A - \frac{b}{d}) + a]) & 0 \end{pmatrix},$$

then eigenvalues here are $\lambda_{1,2} = -\frac{bc \pm \sqrt{b^2c^2 + 4d^2ba - 4d^2bAc + 4db^2c}}{2d}$, $\lambda_3 = 0$.
Let us look for the qualitative behaviour of the system, dependent on the actual parameter values (mainly c).

Case 1: $c < \frac{a}{A}$ There is only S_0 in the biologically relevant area. The eigenvalues of the Jacobian matrix in S_0 are ≤ 0. In S_1, the Jacobian matrix has at least one positive eigenvalue and is thus unstable. Interpretation: The nitrogen uptake is not enough to keep a phytoplankton (and furthermore a zooplankton) population alive.

Case 1/2: $c = \frac{a}{A}$ S_0 and S_1 meet at $(A, 0, 0)$. In S_0, the eigenvalue $\lambda_2 = cA - a$ crosses the 0 towards positive values (for increasing c), in S_1, the eigenvalue $\lambda_2 = -cA + a$ crosses the 0 towards negative values (and $\lambda_3 = dA - \frac{da}{c} - b < 0$ is sure), so S_0 looses its stability, becoming a saddle (if we neglect here the problem with the 0-eigenvalue), while S_1 gains stability. So we have here a transcritical bifurcation!

Case 2: $c > \frac{a}{A}$, and $c < \frac{a}{A - \frac{b}{d}}$ S_0 has at least one positive eigenvalue (in the Jacobian matrix) and thus is unstable. S_1 has all eigenvalues ≤ 0 and is taken to be stable here.
Interpretation: The nitrogen uptake is higher, allowing the existence of a non-zero phytoplankton population; but the level of the phytoplankton is still not sufficient to keep the zooplankton population on a non-zero level

Case 2/3: $c = \frac{a}{A + \frac{b}{d}}$ S_1 and S_2 meet at $(A - \frac{b}{d}, \frac{b}{d}, 0)$; the eigenvalue $\lambda_3 = dA - \frac{da}{c} - b$ of the Jacobian matrix in S_1 crosses the 0 towards positive values, thus S_1 looses stability, becoming a saddle; at the same time, the positive eigenvalue in S_2 crosses the 0 towards negative values, thus S_2 gains stability. Another transcritical bifurcation here!

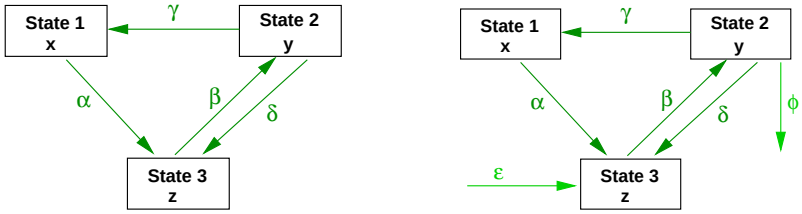
Case 3: $c > \frac{a}{A + \frac{b}{d}}$ S_0 is unstable, S_1 is unstable, S_2 has all eigenvalues ≤ 0 and thus assumed to be stable here.
Interpretation: Now the nitrogen uptake of the phytoplankton is so high that it is sufficient to keep phytoplankton and zooplankton alive.

For realistic situations / simulations thereof, it makes sense to use a c which is varying in an annual cycle. Then oscillations in plankton populations will occur (and also can be observed in the ocean).

In this example, we have already included a law of conservation (here: conservation of nitrogen). Since such conservation principles play a big role in a lot of biological (and other practical) problems, it is useful to consider such systems in greater detail. That is done in the next section.

3.10 Compartmental models

The idea of linear compartmental models is to define different states, together with a directed graph which denotes possible transitions between the states. Each edge of such a graph is equipped with a rate. If there is a connection to the "outer space" of the system (i.e. there may be an in- or outflow from the system), the system is open. Speaking in terms of a population, the total number of particles is not preserved, there may be emigration or immigration. Otherwise, the system is called closed. In the graph, this means: If there is an edge going outside (or from outside to) of the system, it is not closed.
Here two examples for linear compartmental models:



The left one (a) shows a linear compartmental model in a closed system, the right one (b) for a open system. Let x, y, z denote the the densities of the states 1, 2, 3. Then the equation for the closed system reads

$$\frac{d}{dt}\begin{pmatrix} x(t) \\ y(t) \\ z(t) \end{pmatrix} = \begin{pmatrix} -\alpha & \gamma & 0 \\ 0 & -(\gamma+\delta) & \beta \\ \alpha & \delta & -\beta \end{pmatrix} \begin{pmatrix} x(t) \\ y(t) \\ z(t) \end{pmatrix}, \qquad \begin{pmatrix} x(0) \\ y(0) \\ z(0) \end{pmatrix} = \begin{pmatrix} x_0 \\ y_0 \\ z_0 \end{pmatrix}$$

The open system (b) corresponds to the equation

$$\frac{d}{dt}\begin{pmatrix} x(t) \\ y(t) \\ z(t) \end{pmatrix} = \begin{pmatrix} -\alpha & \gamma & 0 \\ 0 & -(\gamma+\delta+\phi) & \beta \\ \alpha & \delta & -\beta \end{pmatrix} \begin{pmatrix} x(t) \\ y(t) \\ z(t) \end{pmatrix} + \begin{pmatrix} 0 \\ 0 \\ \varepsilon \end{pmatrix}, \quad \begin{pmatrix} x(0) \\ y(0) \\ z(0) \end{pmatrix} = \begin{pmatrix} x_0 \\ y_0 \\ z_0 \end{pmatrix}$$

Remark that ε is not a rate and has to be handled carefully, such that is has correctly chosen time units a.s.o.

The systems can be shortly written by

$$\dot{x} = Ax, \qquad x(0) = x_0, \text{ with } (1,1,1)A = 0, \;\; A_{ij} \geq 0 \text{ for } i \neq j.$$

Some theoretical background for this kind of systems resp. matrices.

Definition 24 (M-Matrices) *A matrix A with $A_{i,j} \geq 0$ for $i \neq j$ is called M-matrix.*

Let e_i be the i-th unit vector and $e = (1, 1, \ldots, 1)^T$ the vector with all entries being one.

Definition 25

(1) The positive cone of $\mathbb{R}^n$ is the set $\{x \in \mathbb{R}^n | \, x \geq 0\}$ where the inequality $x \geq 0$ is to interprete as $x_i \geq 0$ for each entry x_i of x.

(2) The solution-operator $S_t x_0$ of the ODE $\dot{x} = Ax$, $x(0) = x_0$ is called semigroup with generator A or fundamental system for A.

Theorem 17 *Let $A \in \mathbb{R}^{n \times n}$ be a matrix, and $S_t = e^{At}$ the semigroup induced by A on $\mathbb{R}^n$. The semigroup S_t leaves the positive cone of $\mathbb{R}^n$ invariant, if and only if A is an M-Matrix.*

Proof:
$\Rightarrow$: If A is an M-Matrix, then there is a $\lambda > 0$, such that $A + \lambda I$ is non-negative in each element. Hence, $e^{(A+\lambda I)t}$ is also non-negative. Since A and I commute, we find

$$S_t = e^{(A+\lambda I)t} e^{-\lambda t},$$

and thus S_t is a non-negative matrix (in the sense that all entries are non-negative.

$\Leftarrow$: If S_t is a semigroup with infinitesimal generator A, then

$$S_t = I + tA + \mathcal{O}(t^2).$$

Since S_t leaves the positive cone invariant, we find $e_i^T S_t e_j \geq 0$, i.e.

$$0 \leq e_i^T S_t e_j = e_i^T e_j + t e_i^T A e_j + \mathcal{O}(t^2).$$

Thus, if $i \neq j$, we find

$$0 \leq e_i^T A e_j + \mathcal{O}(t)$$

and therefore $0 \leq e_i^T A e_j$.

□

The conservation of positivity is often important in biology, thus M-matrices play a certain role. With a simple trick, it is possible to reduce the dimension of the ODE $\dot{x} = Ax$.

Proposition 16 *Let A be an M-matrix and $y(t)$ defined by*

$$\dot{y} = (I - ye^T)Ay, \qquad y(0) = y_0.$$

This ODE leaves the simplex $\mathcal{S} = \{x \in \mathbb{R}^n_+ | \, e^T x = 1\}$ invariant. Furthermore, if $x(0) \in \mathbb{R}^n_+$, $x(0) \neq 0$ and $y(0) = x(0)/e^T x(0)$, then $y(t) = x(t)/e^T x(t)$.

Proof: This proposition can be shown by a direct computation. Let $x(0) \in \mathbb{R}^n_+ \setminus \{0\}$ and consider $z(t) = x(t)/e^T x(t)$. Since A is an M-Matrix, $e^T x(t) \neq 0$, and $z(t)$ is well defined.

$$\frac{d}{dt} z(t) = \frac{d}{dt} \frac{x}{e^T x} = \frac{\frac{d}{dt} x}{e^T x} - \frac{x}{e^T x} \frac{\frac{d}{dt} e^T x}{e^T x} = \frac{Ax}{e^T x} - \frac{x}{e^T x} \frac{e^T A x}{e^T x} = Az - z e^T A z.$$

This is the equation for $y(t)$. Furthermore, let $e^T y(0) = 1$. Since

$$\frac{d}{dt}(1 - e^T y) = -\frac{d}{dt} e^T y = -e^T (I - ye^T) Ay = -(1 - e^T y)(e^T A y)$$

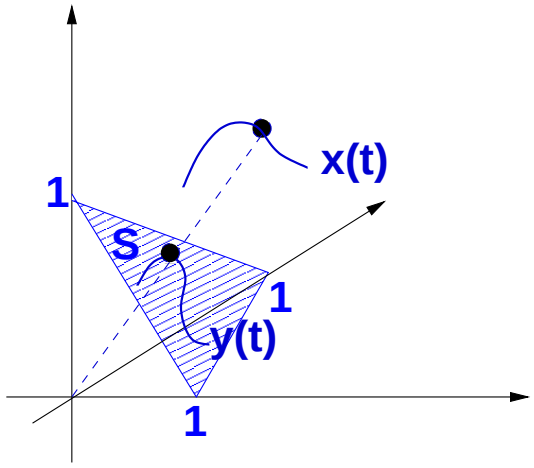
we find

$$1 - e^T y(t) = (1 - e^T y(0)) e^{-\int_0^t e^T A y(\tau) \, d\tau} = 0.$$

It follows that $\mathcal{S}$ is invariant.

□

This proposition can be interpreted that it is possible to project solutions of $\dot{x} = Ax$ into the simplex $\mathcal{S}$ by the map $T : \mathbb{R}^n_+ \setminus \{0\} \to \mathcal{S}$, $x \mapsto x/e^T x$. This projection $y(t)$ again satisfies an autonomous ODE.



The next proposition gives some insight about the stationary points of the projected system:

Proposition 17 *A stationary point of $\dot{y} = (I - ye^T)Ay$ corresponds to an eigenvector of A.*

Proof: Let u be a solution of $\dot{y} = 0$, i.e. $(I - ue^T)Au = 0$. Hence

$$Au = -(e^T Au)u,$$

i.e. u is an eigenvector with eigenvalue $-(e^T Au)$.

□

If a closed system is considered, the matrix A has the additional property that $e^T A = 0$. This has an interesting consequence:

Proposition 18 *The solution of $\dot{x} = Ax$ with $e^T A = 0$ conserves the total mass, i.e.*

$$e^T x(t) = e^T x(0).$$

3.10.1 Treatment of Hepatitis C

Literature: [47, 43]

Hepatitis C is a viral infection which is quite prevalent in the population. About 2-15 % are infected, most of them without symptoms, but they have a higher risk to develop cirrhosis and liver cancer.
Present treatment strategy: The patients get high doses of interferon-α (IFN) over a period of about one year.
Not much is known about the viral dynamics and the mechanisms of the IFN therapy, and the early time prediction about treatment success is quite poor (but would be interesting since the adverse effects are pretty serious).
Questions to a model are:

- Is it possible to gain insight into the mechanisms of interferon-α?
- Is it possible to predict the success or failure of the treatment for a certain individual short after the beginning of the treatment?
- Is it possible to enhance the treatment, if it fails?

These questions are approached in a series of articles (Neumann et al. [47]). In the figure, there are data about the decline of the virus load during the treatment with interferon-α (data of three patients). After the onset of treatment, these data show three phases:

1. Delay (1-3 hours)

2. Phase 1: sharp decrease of the total virus load ($\approx$ 2 days)
3. Phase 2: slow decrease of the total virus load (during several months)

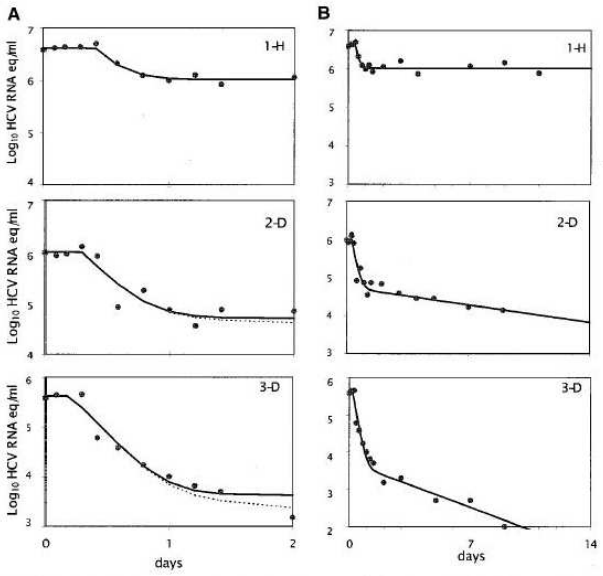
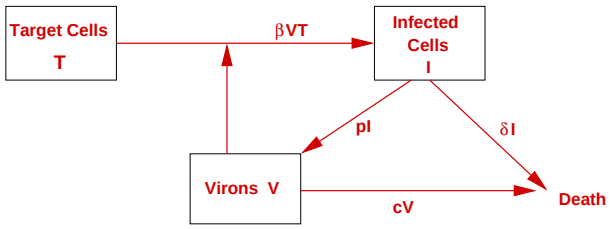


Fig. 1. HCV kinetics during the first 2 days (**A**) and the first 14 days (**B**) of IFN therapy for three representative patients receiving three different daily doses: 5 mIU (first row), 10 mIU (second row), and 15 mIU (third row). A biphasic viral decline can be observed. The first-phase slope is mainly determined by the free virion clearance rate and therapy efficacy. The second-phase slope is determined by the infected cell death rate and the efficacy and has large interpatient variation. The ratio between the viral load at day 2 and at day 0 gives a good estimate of the antiviral efficacy. On average, the slope is faster and the decrease is larger for the two higher doses (see Table 1). Solid lines in (A) are the best fit of the model to the viral load data (circles) assuming a constant level of infected cells (Eq. 4). Solid lines in (B) and dotted lines in (A) show the best fit with the full solution of the model (Eq. 5). Parameter values used are given in Table 1.

How can the rapid decline during the first day and the significantly slower rate later be explained?

Some background information: Target cells are infected by virons, free viral particles of Hepatitis C. These infected cells can be detected by the immune system and thus have a higher clearance rate. Additionally, these infected cells "produce" new virons which can infect more target cells ... This basic model has the following structure:



State of the system:

- Density of the target cells T
- Density of free virons V
- Density of infected cells I

Dynamics: The following assumption is made: The population of target cells is constant, $T(t) = T$ (only slightly influenced by infection). Since their number should be quite large, one can assume that, even if the viral infection is quite prevalent, only a small fraction of target cells is infected. This yields that the incidence (the number of newly infected cells per time unit) is proportional to the number of free virons. Additionally, the infection is assumed to be in an equilibrium when the therapy is started. The death rate of infected cells is denoted by δ. The "production" of new virons depends on the number of infected cells, thus there are pI new virons per time unit. c denotes the so-called clearance rate for free virons. Taken together, this yield the following model equations:

$$\dot{I} = \beta TV - \delta I$$
$$\dot{V} = pI - cV.$$

Assuming T to be constant, this is a linear system!
The next step is to include the effects of the therapy into the model. There are mainly two possible effects:

- The production of virons from infected cells is reduced by a fraction $(1-\varepsilon)$, thus in the model we replace p by $(1-\varepsilon)p$, where $0 \leq \varepsilon \leq 1$.
- The de novo rate of infection is reduced by a fraction $(1-\eta)$, thus in the model we replace β by $(1-\eta)\beta$, where $0 \leq \eta \leq 1$.

Before starting the therapy, it is $\varepsilon = \eta = 0$, if the therapy is initiated, it can be $\varepsilon > 0$ or $\eta > 0$ or both. The modified system reads

$$\begin{aligned} \dot{I} &= (1-\eta)\beta TV - \delta I \\ \dot{V} &= (1-\varepsilon)pI - cV. \end{aligned}$$

The effects of η and ε on the dynamics are considered, since this might help to get an idea which of the two effects can explain better the behaviour of the system (compared to the measured data).

It is important to know something about the time scales of the processes. From the experiments, the following can be extracted:

$$\begin{aligned} \delta \approx 0.1 \text{ day}^{-1} &\Leftrightarrow \text{Mean "life" time } \approx 10 \text{ days} \\ c \approx 6 \text{ day}^{-1} &\Leftrightarrow \text{Mean "life" time } \approx 4 \text{ h} \end{aligned}$$

Let us consider both possible effects, taking into account these different time scales. In the phase short after the initiation of the therapy, the first effect would cause an decrease of infected T-cells with a time scale of the magnitude of the mean life span of an infected cell, i.e. with ≈ 10 days. Thus, a rather slow and long-lasting decline of infected cells has to be expected in the initial phase, if $\eta > 0$. The second effect, leading to a smaller production rate of the virons, would induce the clearance of virons on a time scale of hours. Hence, it seems more plausible that the IFN therapy blocks the de novo production of virons (at least mainly) than that it blocks the infection itself.

In the next step, we want to study if the two different phases can also be explained mathematically, i.e. as properties of the system. Due to the considerations above, η is set to 0. For the analysis we need the eigenvalues of the corresponding matrix

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} -\delta & \beta T \\ (1-\varepsilon)p & -c \end{pmatrix}$$

The eigenvalues of this matrix are

$$\begin{aligned} \lambda_{\pm}(\varepsilon) &= \frac{1}{2}\left(-(\delta+c) \pm \sqrt{(-(\delta+c))^2 - 4(\delta c - (1-\varepsilon)p\beta T)}\right) \\ &= \frac{1}{2}\left(-(\delta+c) \pm \sqrt{(\delta-c)^2 + 4(1-\varepsilon)p\beta T}\right). \end{aligned}$$

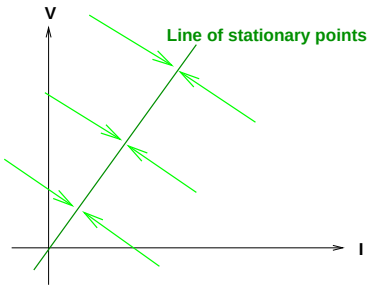
Case 1, no therapy ($\varepsilon = 0$): Here, the system is assumed to be in a locally stable, non-trivial equilibrium (with $I, V > 0$). Hence, it must be either $\lambda_+(0) = 0$ or $\lambda_-(0) = 0$ (allowing for an equation solution $\neq 0$ in a linear system only leaves the possibility of a line of stationary points, the two equations are then linear dependent on each other). The assumption of local stability leads to $\lambda_{\pm}(0) \leq 0$. Thus

$$\lambda_+(0) = 0 > \lambda_-(0).$$

The condition $\lambda_+(0) = 0$ can be solved for T (assuming such a non-trivial equilibrium, thus requires that size of T):

$$\begin{aligned} & \delta^2 - 2\delta c + c^2 + 4p\beta T = \delta^2 + 2\delta c + c^2 \\ \Leftrightarrow \quad & \delta c = p\beta T \\ \Leftrightarrow \quad & T = \frac{\delta c}{p\beta} \end{aligned}$$

This yields a continuum (i.e. a line) of stationary points (I^*, V^*), attracting all trajectories:

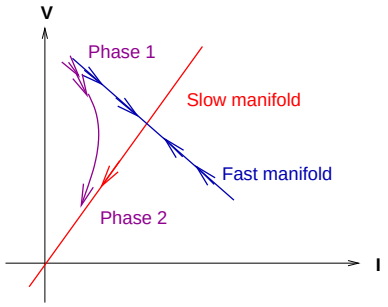


The model is somehow degenerated, because the dynamics of T is not included. If this is done, there is a unique, (locally) attracting fixed point, the system becomes nonlinear.

Case 2, with therapy: Now we suppose $0 < \varepsilon \ll 1$. Here, the explicit formula for $\lambda_\pm(\varepsilon)$ yields that

$$0 > \lambda_+(\varepsilon) \gg \lambda_-(\varepsilon).$$

(Obviously $\lambda_+(\varepsilon) < \lambda_+(0)$ for $\varepsilon > 0$) This kind of system is called "stiff" which means in our case, that there are two quite different time scales. The starting point is chosen at the stationary point on the line with stationary point for $\varepsilon = 0$. If ε gets a value larger than 0, the eigenvectors will slightly change. Along the fast manifold, which corresponds to the eigendirection for $\lambda_-(\varepsilon)$, the new slow manifold is approached, which corresponds to the eigendirection of $\lambda_+(\varepsilon)$. Remark that in the case before, this was the line of stationary points! Then, this line is followed slowly towards the unique stationary point at $(I, V) = (0, 0)$, where the infection is gone.



Thereby, the behaviour of the system with the two phases (as it can be seen in the original data) is explained very nicely! Though, the delay between the start of the IFN therapy and the start of the virus load decline is not explained by this model.
It is also possible, to get some hints what could happen when the therapy fails: If the fast decline of phase I is missing, then the reduction of the viron production rate by infected cells is insufficient. Otherwise, if the decline in phase II is very slow or even not present, then the death rate for infected cells might not be sufficiently large. So, the therapy should be modified in these directions. This gives an example, how a quite simple mathematical model can help to tailor the therapy against Hepatitis C for a given patient.

3.10.2 Epidemic models

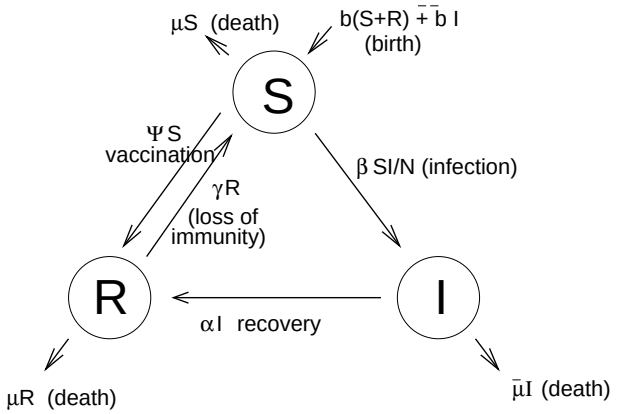
Literature: [44, 28, 12]

Another famous example for a compartmental system are epidemic models. There is a broad collection of models of this type, depending e.g. on the properties of the given disease and its pathogens. Here, we can only have a short look into this class of models, we do this for the example of the so-called SIR-model.

The total population N is divided into distinct classes, one very common possibility is to take

$$\begin{aligned} S &= \text{Susceptibles (who can catch the disease)} \\ I &= \text{Infectives (who have the disease and can transmit it to others)} \\ R &= \text{Removed/Recovered/Immunes (who cannot catch the disease)} , \end{aligned}$$

where $N = S + I + R$.



A corresponding ODE system can read as follows:

$$\begin{array}{llll} \dot{S} = -\mu S & +b(S+R)+\bar{b}I & -\beta\frac{SI}{N} & (-\Psi S)+\gamma R \\ \dot{I} = -\bar{\mu}I & & +\beta\frac{SI}{N} \quad -\alpha I & \\ \dot{R} = -\mu R & & +\alpha I & (+\Psi S)-\gamma R \end{array}$$

(the meaning of the parameters is explained in the figure above)

This model can be extended by modification of certain terms, introduction of new classes, time delay ... many possibilities!
In contrast to the Hepatitis model, we consider here also nonlinear terms.

Kermack-McKendrick epidemic model

(originally introduced by Kermack & McKendrick, [35, 36, 37])
It describes the dynamics resp. the persistence of a disease which is transferred by a direct contact of an infective with a susceptible individual. The model is well-suited to describe typical diseases which are caused by bacteria or viruses, like smallpox or measles.
Assumption: There is no population dynamics, the disease is dispersed on a much faster time scale than a time scale on which demographic changes are relevant - so this assumption is justified in most of the cases.

$$\begin{aligned} \dot{S} &= -\beta SI + \gamma R \\ \dot{I} &= \beta SI - \alpha I \\ \dot{R} &= \alpha I - \gamma R \end{aligned}$$

If α is the recovery rate, then $1/\alpha$ is the mean retention period in class I and $P(t \leq x) = e^{-\alpha x}$ is the probability that an individual which was infected at time 0 is still infected at time x (it is the survival probability; the underlying probability distribution is the exponential distribution). Such a model is classically called a SIRS-model, indicating the typical way of an individual through the different classes: A susceptible becomes infected, then recovers and (maybe after a certain time) becomes susceptible again.

Check, if the total population N stays constant:

$$\begin{aligned} \dot{N} &= \dot{S} + \dot{I} + \dot{R} \\ &= -\beta SI + \gamma R + \beta SI - \alpha I + \alpha I - \gamma R \\ &= 0 \end{aligned}$$

First, we consider the case of $\gamma = 0$, which means, that recovered individuals cannot become susceptible again (there are a lot of diseases where this seems to be the case). Then, the system separates, since the first two equations do not include R. Hence, it is sufficient to consider only the both equations

$$\begin{aligned} \dot{S} &= -\beta SI \\ \dot{I} &= \beta SI - \alpha I \end{aligned}$$

The solutions cannot be given explicitely, but it is possible to set up the equation of the trajectories, parametrised by S,

$$\frac{dI}{dS} = -1 + \frac{\alpha}{\beta}\frac{1}{S}$$

and to solve this equation explicitely:

$$I(S) - I_0 = \frac{\alpha}{\beta} \ln S - S - \left(\frac{\alpha}{\beta} \ln S_0 - S_0 \right).$$

Thus, all trajectories are concave and can be "reproduced" by a shift in direction of I (in the domain $S > 0$ and $I > 0$, which is the biologically relevant one). All points with $I = 0$ are stationary. The maximal value of the variable I is reached at $S = \frac{\alpha}{\beta}$.

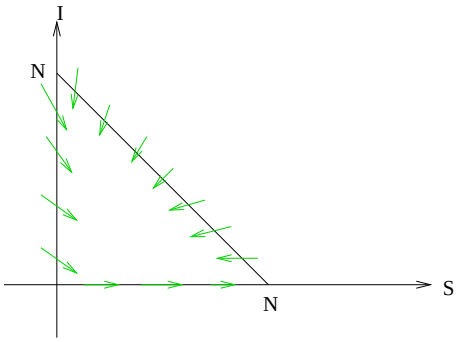
Now we come to the case of $\gamma > 0$.
The 3D system can be transformed into a 2D system by using $R = N - S - I$ (N is constant), thus

$$\begin{aligned} \dot{S} &= -\beta SI + \gamma(N - S - I) \\ \dot{I} &= \beta SI - \alpha I \end{aligned}$$

This can be easily analysed by standard methods.
In this case, the solutions are only meaningful if they run inside the triangle

$$D_N = \{(S, I) : \ S \geq 0, I \geq 0, S + I \leq N\}$$

(otherwise R had to become negative)



We have to check, if D_N stays positively invariant (i.e. no solutions can leave the domain D_N) .

$$\begin{array}{ll} S = 0, 0 \leq I \leq N: & \dot{S} = \gamma(N - I) \geq 0 \\ I = 0: & \dot{I} = 0 \\ I \geq 0, S + I = N: & (\dot{S} + \dot{I}) = -\alpha I \leq 0 \end{array}$$

Stationary points:

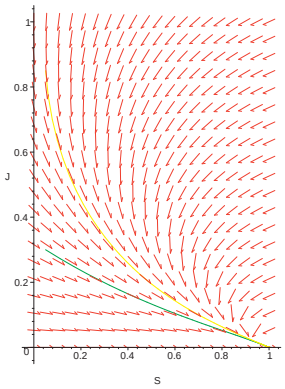
- $I = 0 \Rightarrow S = N$
  $(N, 0)$: The population consists exclusively of susceptibles.
- $I \neq 0 \Rightarrow \bar{S} = \frac{\alpha}{\beta}$, which gives (with the first equation)

$$\begin{aligned} & 0 = -\beta \frac{\alpha}{\beta} \bar{I} + \gamma(N - \frac{\alpha}{\beta} - \bar{I}) \\ \Leftrightarrow \quad & (\gamma + \alpha)\bar{I} = \gamma(N - \frac{\alpha}{\beta}) \\ \Leftrightarrow \quad & \bar{I} = \frac{\gamma}{\gamma + \alpha}(N - \frac{\alpha}{\beta}) \end{aligned}$$

  $(\bar{S}, \bar{I}) = (\frac{\alpha}{\beta}, \frac{\gamma}{\gamma+\alpha}(N - \frac{\alpha}{\beta}))$
  $\bar{I} > 0 \Leftrightarrow \frac{\alpha}{\beta} < N$ and lies then automatically in D_N. At the same time, it is $\bar{R} = \frac{\alpha}{\alpha+\gamma}(N - \frac{\alpha}{\beta})$.

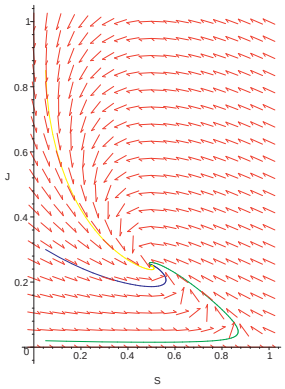
What are the consequences for the qualitative behaviour? $\rightsquigarrow$ have a look at the phase portraits:

First picture:



$(N, 0)$ is the only stationary point in D_N. It can be shown, that there is no periodic orbit, $(N, 0)$ is globally attractive in D_N.
Biological meaning: If the transmission rate β lies under the threshold $\frac{\alpha}{N}$, then the disease "dies out", independent from the starting values.

Second picture:



There exists a "endemic equilibrium" (a stationary point $(\bar{S}, \bar{I})$ in D_N).
Possible interpretation: The endemic equilibrium exists , if the product of infection rate, expected duration of the infection period and the total population size is > 1, i.e.

$$\beta \cdot \frac{1}{\alpha} \cdot N > 1$$

Next, the stability of the stationary points has to be analysed. The general Jacobian is

$$J(S, I) = \begin{pmatrix} -\beta I - \gamma & -\beta S - \gamma \\ \beta I & \beta S - \alpha \end{pmatrix},$$

at the stationary point $(N, 0)$ it is

$$J(N, 0) = \begin{pmatrix} -\gamma & -\beta N - \gamma \\ 0 & \beta N - \alpha \end{pmatrix}.$$

In the case of $\beta < \alpha/N$ both eigenvalues are negative, the point $(N, 0)$ is a stable node, thus an attractor.
In the case of $\beta > \alpha/N$, the two eigenvalues have different signs, hence it is a saddle.
At the endemic equilibrium we have

$$J(\bar{S}, \bar{I}) = \begin{pmatrix} \frac{-\gamma(\gamma+\beta N)}{\alpha+\gamma} & -(\alpha+\gamma) \\ \frac{\gamma(\beta N-\alpha)}{\alpha+\gamma} & 0 \end{pmatrix}.$$

Trace and determinant are

$$\begin{aligned} tr &= -\frac{\gamma(\gamma+\beta N)}{\alpha+\gamma} < 0 \\ det &= \gamma(\beta N - \alpha). \end{aligned}$$

Thus, the endemic equilibrium is a saddle in case of $\beta < \alpha/N$ or an attractor in the case of $\beta > \alpha/N$. It depends on α and γ, if it is a node or a spiral. The discriminant can help to decide this problem. For the discriminant, we get

$$\begin{aligned}(\beta\bar{I}+\gamma)^2 - 4\beta\bar{I}\cdot(\beta\bar{S}+\gamma) &= \beta^2\bar{I}^2 + 2\gamma\beta\bar{I} + \gamma^2 - 4\alpha\beta\bar{I} - 4\gamma\beta\bar{I} \\ &= x^2 - 2(\gamma+2\alpha)x + \gamma^2,\end{aligned}$$

where $x = \beta\bar{I} = \frac{\gamma(\beta N-\alpha)}{\alpha+\gamma}$. This polynomial has two positive nulls $x_1 < x_2$ in each case:

$$x_{1,2} = \gamma + 2\alpha \pm 4\sqrt{(\alpha+\gamma)\alpha}.$$

If β runs from α/N to ∞, then $\beta\bar{I}$ runs from 0 to ∞ and there is an interval (β_1, β_2) such that for each β in this interval, $(\bar{S}, \bar{I})$ is a spiral.

Now, periodic orbits will be excluded by the negative criterion of Bendixson.
Choose $\rho(S, I) = \frac{1}{I}$, this leads to the following system:

$$\begin{aligned}\dot{S} &= -\beta S + \gamma(\frac{N}{I} - \frac{S}{I} - 1) =: f(S, I) \\ \dot{I} &= \beta S - \alpha =: g(S, I)\end{aligned}$$

for $I > 0$. Hence:

$$\frac{\partial f}{\partial S} + \frac{\partial g}{\partial I} = -\beta - \frac{\gamma}{I} + 0 < 0$$

$\Rightarrow$ no periodic orbits in $\{(S, I)|S, I \geq 0\}$.

Following the theorem of Poincare-Bendixson, each trajectory converges towards a stationary point, which are here $(N, 0)$ or $(\bar{S}, \bar{I})$.

This yields altogether the following theorem:

Theorem 18 (Threshold theorem) *For $\beta < \frac{\alpha}{N}$ all trajectories converge to the non-infected equilibrium $(N, 0)$.*
For $\beta > \frac{\alpha}{N}$ all trajectories in D_N with $I > 0$ converge to the endemic equilibrium $(\bar{S}, \bar{I})$.

Biological interpretation: The main influencing parameter is $R_0 = \beta/\alpha$, which corresponds to the product of contact rate β and mean retention period in class I. If the size N of the total population is larger than the threshold α/β, then there exists a stable endemic equilibrium; if $N < \alpha/\beta$, then the disease cannot "survive". Remark, that the parameter γ does not have any influence on the existence of the endemic equilibrium, only on the position of it, i.e. the number of infectives in the equilibrium:

$$\bar{I} = \frac{\gamma}{\gamma+\alpha}(N - \frac{\alpha}{\beta})$$

At first glance this seems astonishing since a large value of γ means that immunes become susceptible again very fast, but indeed the number of susceptibles at the beginning of an epidemic does not depend on γ.

Concluding, we can consider the bifurcation of the stationary points at $\beta = \alpha/N$. $\bar{I}$ is interpreted as a function of β. For $\beta < \alpha/N$ $(N, 0)$ is stable and $(\bar{S}, \bar{I})$ is lying in the domain of $I < 0$. When $\beta = \alpha/N$, then $(\bar{S}, \bar{I})$ crosses $(N, 0)$ and the equilibria exchange their stability ($\rightsquigarrow$ transcritical bifurcation).

This kind of epidemic models can be easily modified and adapted to the properties of certain diseases:

- If the disease does not lead to any immunity, i.e. the individuals can become infected immediately after their recovery, one would use e.g. a SIS model.
- If the disease leads to a lifelong immunity of an recovered individual, it makes sense to use a SIR-model (which is equivalent to choose the recovery rate $\gamma = 0$)

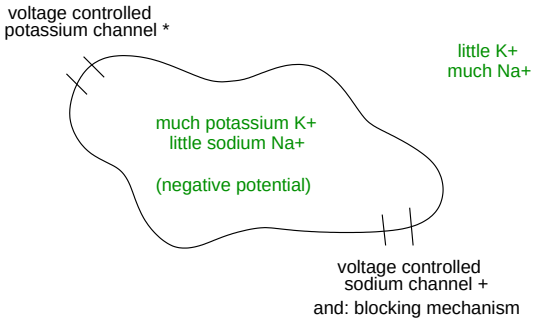
Of course, many more variations are possible.
Another very interesting topic is to introduce vaccination into these epidemic models. The aim of vaccination can be to reduce or to eliminate the disease in consideration. Several factors have to be kept in mind, costs, adverse effects, practicability ... This may lead to very different vaccination strategies.
Many realistic models are refined in such a way, that they handle e.g. different age classes (due to age-dependent contact rates for example, or a different susceptibility). These models can give very useful hints about how to choose successful vaccination strategies and how to optimise them.

3.11 The model of Fitzhugh-Nagumo

Literature: e.g. Keener [32], Scholarpedia [31]

Here, we try to learn some very basic facts about the modelling of electric signalling or firing of individual nerve cells (or neurons). A seminal work was written by Hodgkin and Huxley [26] in 1952. Their model consists of four coupled differential equations. It is quite complicated and hardly analysable (with bearable expense). Since some projections onto a plane look like the phase curves of a 2D system, it makes sense to introduce 2D systems with similar phase curves. This was done e.g. by Fitzhugh and Nagumo [15, 46], their model will be introduced later.

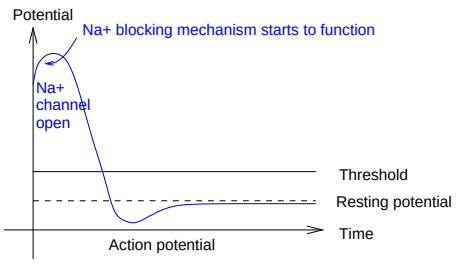
Dynamics of a neuron:
First we consider a resting neuron:



$*$: K^+ channel: opens slowly, if the potential exceeds the resting potential
$+$: Na^+ channel: opens fast, if the potential exceeds the threshold. The voltage controlled blocking mechanism blocks slowly, if the potential exceeds the resting potential.

The mechanism is as follows:
A positive (electric) burst come from the outside to the cell
$\rightsquigarrow$ the potential becomes less negative, the Na^+ channel opens
$\rightsquigarrow$ $Na+$ ions enter the cell (due to an surplus outside), the potential raises
$\rightsquigarrow$ a slow mechanism blocks the Na^+ channels, a slow mechanisms opens the K^+ channels, the build-up of positive charge in the cell is diminished.
(A nice introduction in German can be found at http://www.egback.de/skripten/12/b212-28.htm , with many links, also to pages in English)

Above the resting potential there mechanisms turn off slowly, the cycle can restart.



The model should describe the structure of an interaction of two processes:

- fast process with positive feedback

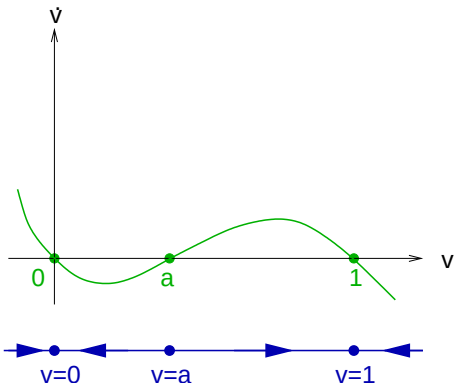
- slow process with negative feedback

To simplify matters, only those mechanisms which concern the Na^+ channel are considered (yielding less precise action potentials than with K^+ channel).

$\underline{Na^+ \text{ channel:}}$ Let v be the potential (scaled to handling mathematical values).

$$\begin{array}{lcl} v = 0 & : & \text{Resting potential} \\ v = a & : & \text{Threshold, above which the neuron fires} \\ v = 1 & : & \text{Potential during opened } Na^+ channels \end{array}$$

(without blocking mechanism)
Phase diagram:



"Suitable" equation for this behaviour:

$$\dot{v} = -v(v-a)(v-1) = f(v)$$

Check for stability:

$$\begin{array}{lcll} f'(0) & = & -a < 0 & \Rightarrow stable \\ f'(a) & = & a(1-a) > 0 & \Rightarrow unstable \\ f'(1) & = & -(1-a) < 0 & \Rightarrow stable \end{array}$$

A problem is the missing blocking mechanism. Therefore we introduce a further variable, called w, which describes the strength of the blocking mechanism. Its desired properties are:

- at $v = 0$ we have $w = 0$ (that means: no blocking)
- for $v \to 1$ w increases

First attempt: $\dot{w} = \varepsilon v$ where $\varepsilon > 0$. Unfortunately, if v stays positive over a long time period, then w can tend to ∞. Thus, an upper bound for w should exist.
Second attempt:

$$\dot{w} = \varepsilon(v - \gamma w)$$

This yields:

- at $v = 0$ we have $w \to 0$
- at $v = 1$ we have $w \to \frac{1}{\gamma}$ (equilibrium, maximum)
- for a fixed v, w tends to $\frac{v}{\gamma}$ (equilibrium)

The parameters have the following meaning:
γ influences the value of the equilibrium
ε influences the speed of response (thus ε small)

Now we come to the equations of Fitzhugh and Nagumo. There, the properties of the blocking mechanism are included:

- If w is large, then the Na^+ channels are blocked

- If the Na^+ channels are blocked, then a further entry of Na^+ ions is prevented and the cell returns to the resting potential.

Equations of Fitzhugh-Nagumo:

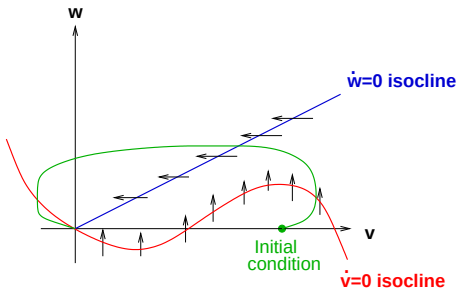
$$\dot{v} = -v(v-a)(v-1) - w$$
$$\dot{w} = \varepsilon(v - \gamma w)$$

Determination of the Null-Isoclines:

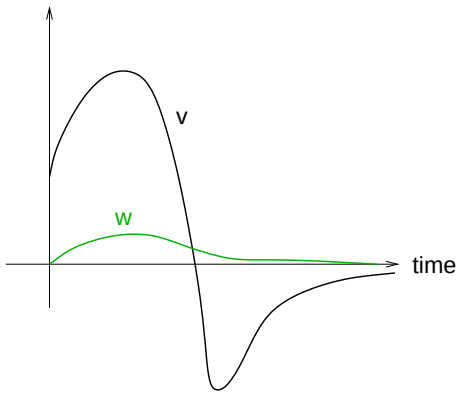
$$\dot{v} = 0 \quad \Leftrightarrow \quad w = -v(v-a)(v-1)$$
$$\dot{w} = 0 \quad \Leftrightarrow \quad w = \frac{v}{\gamma}$$

Depending on the parameters, there are generically one or three stationary points.

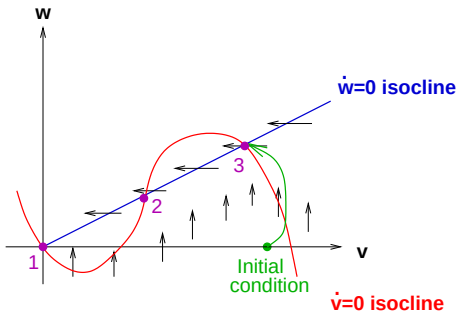
Case 1: There is only one stationary point: $(0, 0)$. In this case, the phase portrait looks as follows,



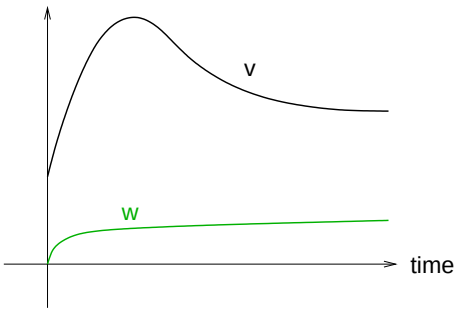
and a typical time course of the solution is



Case 2: $1/\gamma$ is small, then the phase portrait looks like



and a typical time course of the solution is



It can be shown: The stationary points 1 and 3 are stable, 2 is unstable.

Up to now, we consider only single excitations from positively charged ions. In the next step, a constant input of positive ions (i.e. an electric current I_a). w is coupled to v by a coupling constant $\delta > 0$:

$$\begin{aligned} \dot{v} &= -v(v-a)(v-1) - \delta w + I_a = v^3 + (1+a)v^2 - av - \delta w + I_a \\ \dot{w} &= \varepsilon(v - \gamma w) \end{aligned} \tag{3.20}$$

Then the Null-Isoclines are

$$\begin{aligned} \dot{v} = 0 &\quad \Leftrightarrow \quad w = (-v(v-a)(v-1) + I_a)/\delta \\ \dot{w} = 0 &\quad \Leftrightarrow \quad w = \frac{v}{\gamma} \end{aligned}$$

In order to determine the stationary points, one is lead to the nulls of the following function:

$$F(v) = v(v-1)(v-a) + \frac{\delta v}{\gamma} - I_a$$

They cannot be computed explicitely very easy, since F is a cubic function. From

$$F(v) = v^3 - (1+a)v^2 + av + \frac{\delta}{\gamma}v - I_a$$

follows

$$F'(v) = 3v^2 - 2(1+a)v + a + \frac{\delta}{\gamma}.$$

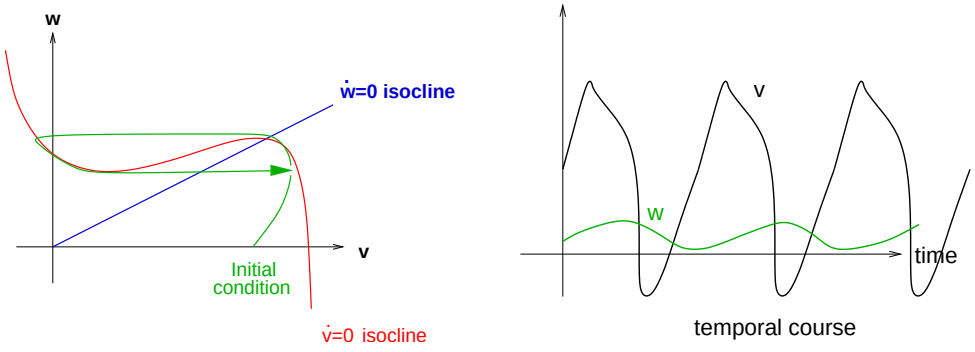
F' has the nulls

$$v_{1,2} = \frac{1}{3}(1+a) \pm \frac{1}{3}\sqrt{1 - a + a^2 - 3\delta/\gamma}.$$

In the case of

$$\frac{\delta}{\gamma} \geq \frac{1}{3}(1 - a + a^2)$$

F' has no real nulls, it is $F'(v) > 0$ for all v. Thus, F is monotone increasing and F has exactly one null v_I for each I. Then, the system (3.20) has exactly one stationary point (v_I, w_I), where $w_I = v_I/\gamma$, which corresponds to the resting position.
The phase portrait and the time course of a solution look as follows:



In the next step, the stability of the stationary point is investigated. The general Jacobian (for an arbitrary point) reads

$$J(v,w) = \begin{pmatrix} -3v^2 + 2(1+a)v - a & -\delta \\ \varepsilon & -\varepsilon\gamma \end{pmatrix}$$

Thus we get

$$\begin{aligned} tr\, J &= -3v^2 + 2(1+a)v - a - \varepsilon\gamma \\ det\, J &= (3v^2 - 2(1+a)v + a) \cdot \varepsilon\gamma + \varepsilon\delta. \end{aligned}$$

In the case of a single stationary point, $det\, J$ is positive. The eigenvalues are

$$\lambda_{1,2} = \frac{tr\, J}{2} \pm \frac{1}{2}\sqrt{(tr\, J)^2 - 4\, det\, J}$$

At places where the trace disappears, the discriminant is negative and the eigenvalues are complex conjugated. We continue with the case of one stationary point.
Obviously, the Jacobian J for fixed (v^*, w^*) does not depend directly on the Input I_a. But here, we mainly consider the Jacobian J at the stationary point (v_I, w_I) in order to determine the qualitative behaviour of the system. Since the coordinates (v_I, w_I) depend on the input I_a, also the Jacobian $J(v_I, w_I)$ indirectly does depend on I_a, thus the qualitative behaviour is influenced by I_a.
I and v_I depend monotonely of each other, thus v_I can be chosen as parameter instead of I. Then, the trace at the stationary point is given by

$$tr\, J = -3v_I^2 + 2(1+a)v_I - a - \varepsilon\gamma$$

The trace is a quadratic polynomial in v, which becomes negative for large $|v|$. The nulls of this polynomial are

$$\begin{aligned} v_{1,2} &= \frac{-(2(1+a)) \pm \sqrt{4(1+a)^2 - 12(a+\varepsilon\gamma)}}{-6} \\ &= \frac{1}{3}(1+a) \pm \frac{1}{3}\sqrt{1 - a + a^2 - 3\varepsilon\gamma}. \end{aligned}$$

There are two cases, dependent on the values of the ingoing parameters:

Case 1: If $\gamma \geq \frac{1}{3\varepsilon}(1 - a + a^2)$, then the trace never becomes positive. Then, the stationary point stays stable, independent of the value of I_a
$\rightsquigarrow$ here, the appearance of neural impulses cannot be simulated

Case 2: If $\gamma < \frac{1}{3\varepsilon}(1 - a + a^2)$, then the trace becomes positive in a range of $I_1 < I_a < I_2$. If the parameter I_a runs from $-\infty$ to $+\infty$, then at I_1, I_2, respectively there appears a Hopf bifurcation. For certain I near I_1 resp. I_2, the system exhibits periodic orbits.
The bifurcation at I_2 is biologically not relevant.
The bifurcation at I_1 is an important neuro-physiological phenomenon: If the dendritic input of a neuron exceeds a certain threshold, then the resting position looses its stability and periodic oscillations of the voltage at the membrane show up.

A simulation applet can be found at http://thevirtualheart.org/FHNindex.html

Chapter 4

Partial differential equations

4.1 Basics of Partial Differential equations

4.1.1 Why to use partial differential equations

Up to now, we mainly considered homogenous populations, concentrations etc. without any further structure like age or spatial structure. (Exceptions: Leslie model with discrete age classes, cellular automata models could include spatial phenomena).
But there are a lot effects that are based on that kind of additional structure or properties of the biological system which require the treatment of this structure: Spatially non-homogenous distribution of a population in their habitat; non-homogeneous densities of chemical substances (e.g. due to local production effects or boundary effects); influence of the age distribution of a population, diffusion and/or transport effects ...
So, in such situations a well-suited model should also cover this additional structure. Moreover, a discrete model is often not able to deal with , since the discretisation might be "artificial" and not related to the real-world problem which is considered.
In order to describe such a model in continuous variables, partial differential equations are used. The kind of partial differential equations considered here does not cover stochastic effects, though it is possible to introduce stochastic partial differential equations.

4.1.2 Short recollection of functions of several variables

We start to consider a function $V : \mathbb{R}^n \to \mathbb{R}$, $(x_1, ..., x_n) \mapsto V(x_1, ..., x_n)$.
Examples:

- The height of a mountain : $\mathbb{R}^3 \to \mathbb{R}$
- Temperature of coffee in a cup $T : \mathbb{R}^3 \to \mathbb{R}$
- Concentration of a chemical in a test tube $u : \mathbb{R}^3 \to \mathbb{R}$
- a Lyapunov function

The nabla operator is defined as

$$\vec{\nabla} = \begin{pmatrix} \frac{\partial}{\partial x_1} \\ \vdots \\ \frac{\partial}{\partial x_n} \end{pmatrix},$$

it can be applied on a scalar function $V : \mathbb{R}^n \to \mathbb{R}$, then it is called the gradient of V:

$$\vec{\nabla} V = \begin{pmatrix} \frac{\partial V}{\partial x_1} \\ \vdots \\ \frac{\partial V}{\partial x_n} \end{pmatrix}$$

The gradient (which is a vector) points always in the direction of the steepest (increasing) slope.
In the 2D case, the behaviour of a function can also be represented by a set of contours for which

$$f(x, y) = constant.$$

In the 3D case, the same can be done, there it is (not very surprisingly) called level surface; generally in n dimensions it is denoted as level set. E.g. considering a temperature field, such level surfaces are called equitherms.
Note: The gradient of f at a point is perpendicular to the level set of f at that point.
There is some importance of these level sets; e.g. the so-called level set methods are widespread numerical techniques which are based on these level sets and their properties (often used e.g. for tracking interfaces and shapes).

Next, we consider a function $\vec{f} : \mathbb{R}^n \to \mathbb{R}^n$, i.e.

$$\vec{f}(x) = \begin{pmatrix} f_1(x_1, ..., x_n) \\ \vdots \\ f_n(x_1, ..., x_n) \end{pmatrix}$$

Already well-known is the Jacobian matrix of $\vec{f}$, possible notation:

$$D\vec{f}(x) = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & \cdots & \frac{\partial f_1}{\partial x_n} \\ \vdots & & \vdots \\ \frac{\partial f_n}{\partial x_1} & \cdots & \frac{\partial f_n}{\partial x_n} \end{pmatrix}$$

The trace of the Jacobian is also denoted as divergence of $\vec{f}$:

$$div\, \vec{f} = \vec{\nabla} \cdot \vec{f} = \frac{\partial f_1}{\partial x_1} + \ldots + \frac{\partial f_n}{\partial x_n}$$

($\vec{\nabla}$ is interpreted as a vector, $\cdot$ as a scalar product).
A scalar field $\vec{\nabla} \cdot \vec{f}$ is assigned to the vector field $\vec{f}(x)$, descriptively it can be interpreted as the source field of $\vec{f}$.

A vector field $\vec{f}$ is called a gradient field, if there is a function $g(x_1, ..., x_n)$ such that

$$\vec{f} = \vec{\nabla} g$$

The construction of the function g (if $\vec{f}$ is a gradient field) can be done by partial integration, but note that g can be determined only up to some additive constant.

The Laplacian Δu of a function $u : \mathbb{R}^n \to \mathbb{R}$ is defined as

$$\Delta u(x,t) = \frac{\partial^2}{\partial x_1^2} u(x,t) + \ldots + \frac{\partial^2}{\partial x_n^2} u(x,t), \qquad x \in \mathbb{R}^n;$$

it can also be interpreted as the divergence of the gradient field $\vec{\nabla} u$ ($\vec{\nabla} u : \mathbb{R}^n \to \mathbb{R}^n$).

4.1.3 Typical formulations in the context of PDEs

Literature: e.g. [45] (very short version)

Roughly speaking, a partial differential equation involves partial derivatives (of one or more dependent variables). Each of these variables is a function of at least two independent variables.

Simplified notation: $u_t = \frac{\partial u}{\partial t}$, $u_x = \frac{\partial u}{\partial x}$, $u_{xx} = \frac{\partial^2 u}{\partial x^2}$ and so on.
Sometimes, also the notation $\partial_t u = \frac{\partial u}{\partial t}$ etc. is used.

The most simple case concerns formulations with two independent variables, e.g. x and t. Let the dependent variables be functions of the form $u(x,t)$. A general partial differential equation (shortly: PDE) for the case of one dependent variable is defined as

$$g(u, u_x, u_t, u_{xx}, u_{xt}, u_{tt}, \ldots, \theta(x,t), f(x,t)) = 0,$$

$\theta(x,t)$ corresponds to a set of parameters, $f(x,t)$ is a given function. The highest partial derivative that occurs in this equation is called the order of the PDE.

A PDE is called linear if g depends linearly on the dependent variable (e.g. u(x,t)) and its partial derivatives, otherwise it is a non-linear equation.

A linear, second-order PDE reads (fairly general)

$$au_{tt} + 2bu_{tx} + cu_{xx} + du_t + eu_x + gu = f(x,t).$$

The parameters a, b, c, d, e, g can be constants or functions of x and t (independent variables). A typical classification is done by considering

$$\Gamma(x,t) = b^2(x,t) - a(x,t)c(x,t).$$

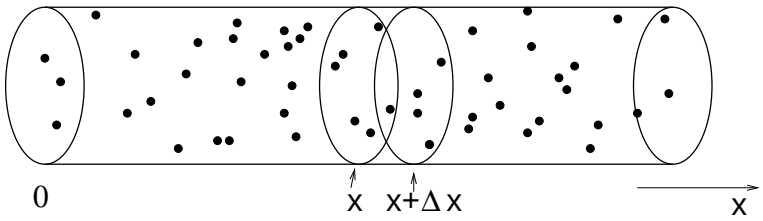
At (x,t), the equation is called

1. parabolic, if $\Gamma = 0$,
2. hyperbolic, if $\Gamma > 0$,
3. elliptic, if $\Gamma < 0$.

In case of a, b, c being constant, the equation has this property over the whole domain of the independent variables.

4.1.4 Conservation equations

Literature: [12]
The conservation equation (which exists in various forms) is one of the basic equations to describe changes in a spatial distribution and contained in very different applications.
First, we consider a special case to get a rough idea about it: the flow of particles in a tube.



The following assumptions are made:

- There is only motion in one space dimension
- The tube has a uniform cross-sectional area A

The variable x describes the position along the tube. We consider the interval between x and $x+\Delta x$. The changes in the concentration can be caused by two effects: Flow of particles into and out of the interval $(x, x+\Delta x)$ and the creation or degradation of particles (e.g. by a chemical reaction). (In principle, a pure conservation equation does not consider creation / degradation of particles - so it really conserves the particles, but here, we include already that possibility in the derivation of the basic equation). Now we can try to put up a balance equation in terms of number of particles:

Rate of change of particle population in $(x, x+\Delta x)$ per unit time
$=$ + rate of entry into $(x, x+\Delta x)$ per unit time
− rate of departure from $(x, x+\Delta x)$ per unit time
± rate of local degradation or creation per unit time

More formally, we introduce the following variables: Let $c(x,t)$ be the concentration of particles at (x,t), $J(x,t)$ the flux of particles at (x,t) (which corresponds to the number of particles that cross a unit area at x in the positive direction per unit time), and $\sigma(x,t)$ the sink resp. source density (i.e. the number particles that are created or degradated per unit volume at (x,t). Obviously, only the flux at the cross sections at x and $x+\Delta x$ changes the total population. Furthermore, let A be the cross-sectional area of the tube and ΔV the volume of the length element Δx, which is then $A\Delta x$. The corresponding equation, with the correct units, reads:

$$\frac{\partial}{\partial t}(c(x,t)A\Delta x) = J(x,t)A - J(x+\Delta x,t)A \pm \sigma(x,t)A\Delta x. \tag{4.1}$$

This equation is divided by $A\Delta x$ (constant by assumption), this yields

$$\frac{\partial c(x,t)}{\partial t} = \frac{J(x,t) - J(x+\Delta x,t)}{\Delta x} \pm \sigma(x,t). \tag{4.2}$$

Then, we obtain by taking the limit $\Delta x \to 0$:

$$\frac{\partial c(x,t)}{\partial t} = -\frac{\partial J(x,t)}{\partial x} \pm \sigma(x,t). \tag{4.3}$$

Equation (4.3) is called the one-dimensional balance equation in its basic version.
One possible generalisation is to allow the cross-sectional area of the tube to vary over space and time. In order to do that formally correct, we introduce the concentration $c(x,t)$ as a quantity such that $\int_{x_1}^{x_2} c(x,t)A(x,t)\,dx$ describes the total number of particles located within the tube in (x_1,x_2) at time t; in the same way the source density $\sigma(x,t)$ is defined by $\int_{x_1}^{x_2} \sigma(x,t)A(x,t)\,dx$ being equal to the net rate of particle creation / degradation within (x_1,x_2) at time t. Then, the integral form (also called the weak form) of the equation of balance reads

$$\frac{\partial}{\partial t}\int_{x_0}^{x_0+\Delta x} c(x,t)A(x,t)\,dx = J(x_0,t)A(x_0,t) - J(x_0+\Delta x,t)A(x_0+\Delta x,t) \pm \int_{x_0}^{x_0+\Delta x} \sigma(x,t)A(x,t)\,dx.$$

An integral mean value theorem yields that there are some locations (x_1,x_2) (where $x_0 \le x_1, x_2 \le x_0+\Delta x$) such that the following equation is satisfied:

$$\frac{\partial}{\partial t}(c(x_1,t)A(x_1,t))\Delta x = J(x_0,t)A(x_0,t) - J(x_0+\Delta x,t)A(x_0+\Delta x,t) \pm (\sigma(x_2,t)A(x_2,t))\Delta x \tag{4.4}$$

Equation (4.4) is divided by Δx and the limit $\Delta x \to 0$ is taken, so we get

$$\frac{\partial}{\partial t}(c(x_0,t)A(x_0,t)) = -\frac{\partial}{\partial x}(J(x_0,t)A(x_0,t)) \pm (\sigma(x_0,t)A(x_0,t)). \tag{4.5}$$

Remark: If $A(x_0,t)$ has a constant value $\tilde{A}$, then equation (4.5) can be divided by $\tilde{A}$ which yields again equation (4.3).

Application: Propagation of the action potential along an axon:

The action potential propagates as a signal from the cell body (also called soma) to the terminal synapses. Here, we want to set up a model which describes the transport of charge in the axial direction. The following variables and parameters are used:

x	=	distance along the axon
$q(x,t)$	=	density of charge per unit length at time t and position x
$J(x,t)$	=	flux of charged particles (also called current)
$\sigma(x,t)$	=	rate of charge entry / leave through the axon membrane

The basic equation reads:

$$\frac{\partial q}{\partial t} = -\frac{\partial J}{\partial x} + \sigma$$

The charge can be represented in the following way:

$$q(x,t) = 2\pi a C v(x,t),$$

where C is the capacitance of the axonal membrane, a the radius of the axon and v denotes the voltage across the membrane. Let I_i be the net ionic current into the axon, then σ can be described by

$$\sigma(x,t) = -2\pi a I_i.$$

Ohm's law yields that the current is proportional to the gradient of voltage and inversely proportional to the intracellular fluid resistance. Let R be the intracellular resistivity. Then, the current J can be expressed by

$$J = -\left(\frac{\pi a^2}{R}\right)\frac{\partial v}{\partial x}.$$

Taking these equations together yields

$$\frac{\partial v}{\partial t} = \frac{a}{2RC}\frac{\partial^2 v}{\partial x^2} - \frac{I_i}{C}$$

In the same way as done here in the 1D case, it is possible to derive a higher dimensional conservation equation. The main difference is that, e.g. in the 3D case, a 3D box has to be considered , adding up the flows into and out of the box in these three directions. This leads to the equation

$$\frac{\partial c}{\partial t} = -\nabla \cdot J \pm \sigma. \tag{4.6}$$

4.2 Age structure

4.2.1 Introduction of the basic model

Literature: [43, 41]

As already introduced in the discrete case, e.g. for several diseases it makes sense to consider an age-structured population, since in different age classes there might be different contact rates, different susceptibility etc.
Short repeat of the discrete approach: Let $x_k(j)$ be the population size in age class k at time t_j, where $t_j = hj$; the age class k contains the interval $[kh, (k+1)h[$. Then, the dynamics reads

$$x_k(j+1) \quad = \quad P_{k-1}x_{k-1}(j) \qquad \text{for } k > 0,$$

The survival probabilities P_k can be assumed to have a relation to a continuous death rate:

$$P_k = 1 - \mu(kh)h + \mathcal{O}(h^2),$$

where $\mu(a) \in C^0_+$. This death rate $\mu(a)$ is assumed to be equally bounded away from 0, i.e.

$$\mu(a) \geq \bar{\mu} > 0.$$

We consider now the case of $h \to 0$. $x_k(j)$ is assumed to approximate a smooth function

$$x_k(j) = u(kh, hj) + \mathcal{O}(h).$$

Using $u(a+h, t+h) = (1 - h\mu(a) + \mathcal{O}(h^2))u(a,t)$ leads to

$$\frac{u(a+h,t+h) - u(a+h,t) + u(a+h,t) - u(a,t)}{h} = (-\mu(a) + \mathcal{O}(h))u(a,t)$$

which corresponds to

$$\frac{\partial}{\partial t}u(a,t) + \frac{\partial}{\partial a}u(a,t) = -\mu(a)u(a,t)$$

in the limit $h \to 0$. This equation has the form of a transport equation ("transporting" as the aging of a population), with an additional death term. $u(a,t)\,da$ represents the number of individuals between the ages a and $a + da$ at time t and the total population at time t can be computed by

$$N(t) = \int_0^\infty u(a,t)\,da.$$

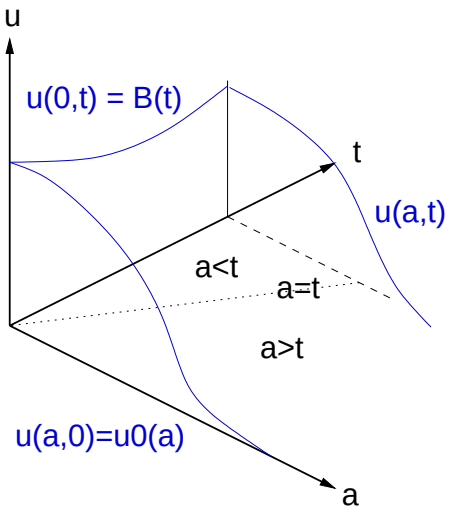
(Please note that - even though the maximum death age is finite, we only use $0 \leq a < \infty$ as age range, for simplicity)
As usual, it is necessary to introduce initial and boundary conditions. Generally, in our case they read:

$$u(a,0) = u_0(a) \qquad \text{(initial population / age structure)}$$

and

$$u(0,t) = B(t) \qquad \text{(offspring at age } a = 0\text{, time } t)$$

There is a big difference: For $a > t$, the actual age structure $u(a,t)$ is only affected by the initial population $u_0(a)$; for $a < t$ the age structure $u(a,t)$ is affected by the entire population and the births of it. This can be visualised in the following way:



As it can be seen here, the individuals move on so-called characteristics of the form $a = t+constant$ in the age-time space. So, in some sense, the model, which is also called "McKendrick-von Foerster equation", can be interpreted as a transport with speed 1, including a sink term (the mortality).
Now let us introduce suitable boundary conditions, describing the appearance of newborns. In the discrete model, the approach reads

$$x_0(j+1) \quad = \quad \sum_k F_k x_k(j),$$

where F_k denotes the expected number of births in the age interval $[kh, (k+1)h[$; obviously F_k depends on the discretisation size h. It is reasonable to assume that F_k can be derived from a rate,

$$F_k = F_k(h) = \beta(kh)h + \mathcal{O}(h^2),$$

where $\beta(a) \in C^0_+$ (the set of continuous non-negative functions). $\beta(a)$ is called the "maternity function"; it describes the average number of offspring per female of age a. In general, it is also possible to consider that maternity function time-dependent (i.e. $\beta(a,t)$), but for the moment, we neglect the time-dependence here. Further assumption: There is a maximal fertile age $\bar{a}$, i.e. $\beta(a) \neq 0$ for some $a \leq \bar{a}$, but $\beta(a) = 0$ for $a > \bar{a}$ (e.g. the "menopause").
Then

$$u(0,t) = \sum_k F_k(x_k(j) + \mathcal{O}(h)) = \sum_k h(\beta(kh)u(kh,t) + \mathcal{O}(h))$$

and

$$\lim_{h\to 0} u(0,t) = \int_0^\infty \beta(a)u(a,t)\,da.$$

Taking all together, the continuous age structured model reads

$$\frac{\partial}{\partial t}u(a,t) + \frac{\partial}{\partial a}u(a,t) \quad = \quad -\mu(a)u(a,t) \tag{4.7}$$

$$u(0,t) \quad = \quad \int_0^\infty \beta(a)u(a,t)\,da \tag{4.8}$$

$$u(a,0) \quad = \quad u_0(a), \tag{4.9}$$

where $u(a,t)$ describes the population density of age a at time t, $\beta(a)$ resp. $\mu(a)$ denote the birth resp. death rate. $u_0(a)$ is the initial condition. For μ and β the following assumptions are made:

$$\mu \in C^0_+ \quad , \qquad \mu(a) > \bar{\mu} > 0 \tag{4.10}$$

$$\beta \in C^0_+ \quad , \qquad \beta(a) = 0 \text{ for } a > \bar{a}, \;\; \beta(\cdot) \not\equiv 0 \tag{4.11}$$

Remark that (4.8) is a so-called nonlocal boundary condition since it depends on the solution of the problem.

Also in the continuous case, asymptotically exponential growth can be expected. Here, there is an infinite dimensional state space; one has to be careful with that. When considering an infinite dimensional

state space (like we have it in this case here), it is not so easy to deduce the asymptotic behaviour from the spectrum of linear operators. In most cases, only the point spectrum is considered, but also other parts of the spectrum (e.g. the essential spectrum) can play a role and are not so simple to control. Here, only the point spectrum is considered, which determines the behaviour of our systems, but keep in mind that this in not the absolute truth (and there are also examples where it is completely wrong).
It can be shown that the essential spectrum is contained in $\{z \in \mathbb{C} \,|\, Re(z) < -\bar{\mu}\}$ (a consequence of the assumptions (4.10) and (4.11)), so the stability / instability of the trivial solution is not influenced by that. Moreover, the semigroup (the solution operator) becomes eventually compact (for more details, see [53]). Some other "basics" can be found in the following propositions.

Proposition 19 *Consider the operator $L : D(L) \subset C^1 \to C^0$, with*

$$Lu = -\partial_a u(a) - \mu(a)u(a),$$

$$D(L) = C^1_{bd} = \{\phi \in C^1 \,|\, \phi(0) = \int_0^\infty \beta(a)\phi(a)\,da\}.$$

Then, the age-structured model can be written as $u_t = Lu$. The point spectrum of L is

$$\sigma_p(L) = \{\lambda \in \mathbb{C} \,|\, g(\lambda) = 1\},$$

where

$$g(\lambda) = \int_0^\infty \beta(a) e^{-\int_0^a \mu(\tau)+\lambda\,d\tau}\,da$$

and the corresponding eigenfunctions read

$$v_\lambda(a) = e^{-\int_0^a \mu(\tau)+\lambda\,d\tau}.$$

Proof: Using the ansatz

$$Lv_\lambda = \lambda v_\lambda(a)$$

leads to

$$\begin{aligned} \dot{v}_\lambda(a) &= -(\mu(a)+\lambda)v_\lambda(a) \\ v_\lambda(0) &= \int_0^\infty \beta(a)v_\lambda(a)\,da. \end{aligned}$$

(Remark: The "dot" here denotes the derivative with respect to a!)
Hence, we get $v_\lambda(a) = v_\lambda(0)e^{-\int_0^a \mu(\tau)\,d\tau - \lambda a}$ and

$$v_\lambda(0) = \int_0^\infty \beta(a)v_\lambda(0)e^{-\int_0^a \mu(\tau)+\lambda\,d\tau}\,da.$$

By definition, an eigenfunction $v_\lambda(a)$ satisfies $v_\lambda(a) \not\equiv 0$, thus the integral yields $v_\lambda(0) \neq 0$. Hence, an eigenfunction for λ can be found if and only if $g(\lambda) = 1$.

Remark 19

1. *Obviously, $g(\lambda)$ is strictly decreasing, so there is a unique real solution $\hat{\lambda}$ of the equation*

$$g(\lambda) = 1.$$

2. *Let $\lambda \in \mathbb{C}$, $g(\lambda) = 1$ and $Im(\lambda) \neq 0$. This yields:*

$$\begin{aligned} 1 &= g(\lambda) \\ &= \left| \int_0^\infty \beta(a)e^{-\int_0^a \mu(\tau)+\lambda\,d\tau}\,da \right| \\ &\leq \int_0^\infty \beta(a) \left| e^{-\int_0^a \mu(\tau)+\lambda\,d\tau} \right| da \\ &< \int_0^\infty \beta(a)e^{-\int_0^a \mu(\tau)+Re(\lambda)\,d\tau}\,da \\ &= g(Re(\lambda)). \end{aligned}$$

Since $g(\cdot)$ is strictly decreasing, it follows directly that $Re(\lambda) < \hat{\lambda}$.

The next proposition is mentioned without proof:

Proposition 20 *Let $u(a,0) > 0$ and define*

$$R_0 := g(0).$$

Assuming (4.10) and (4.11) leads to:
If $R_0 > 1$, then $\|u(a,t)\| \to \infty$. If $R_0 < 1$, then $\|u(a,t)\| \to 0$.

Remark 20 *Since $\beta(a)$ describes the birth rate and $e^{-\int_0^a \mu(\tau)\,d\tau}$ the probability to be alive at age a, R_0 can be interpreted as the average number of children of an individual:*

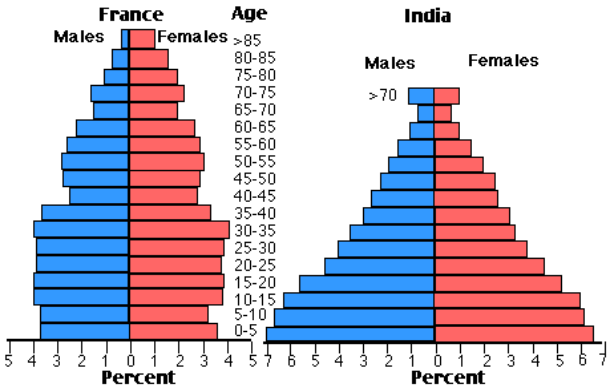
$$R_0 = \int_0^\infty \beta(a) e^{-\int_0^a \mu(\tau)\,d\tau}\,da.$$

For $R_0 > 1$, the population will tend to infinity, while for $R_0 < 1$ the population will die out. Being precise, the model concerns only females and female children, compare it to the discrete model in lecture part I.

Remark 21 *The shape of the population tends asymptotically to*

$$v_{\hat\lambda}(a) = e^{-\int_0^a \mu(\tau)\,d\tau - \hat\lambda a}.$$

For a growing population ($\hat\lambda > 0$), the shape of the population is monotone decreasing. For $\hat\lambda < 0$, one can assume for most cases that the death rate is increasing and starts with very small values for young age classes, which leads to a unimodal shape: increase up to a certain maximum, then decrease. Indeed, this behaviour can be found in data of different countries
(see e.g. http://users.rcn.com/jkimball.ma.ultranet/BiologyPages/F/France_India75.gif)



These pyramids compare the age structure of the populations of France and India in 1984

Let us consider the special case $\beta = \beta(a)$, $\mu = constant$. In this case, we can use the so-called "method of characteristics" to study the behaviour of the age-structured model. In short notation, the equation (4.7) reads

$$u_t + u_a = -\mu u, \qquad a > 0,\ \ t > 0.$$

Introducing new variables $\xi = a - t$ and $\tau = t$ yields

$$U_\tau = -\mu U, \tag{4.12}$$

where $U = U(\xi,t) = u(\xi+\tau,\tau)$ (due to $u(a,t) = U(a-t,t)$, by the chain rule $u_t = U_\xi \xi_t + U_\tau \tau_t = -U_\xi + U_\tau$ and $u_a = U_a = U_\xi \xi_a + U_\tau \tau_a = U_\xi$). The general solution of equation (4.12) reads

$$U(\xi,\tau) = C(\xi) e^{-\mu\tau}$$

(C is an arbitrary function), respectively

$$u(a,t) = C(a-t) e^{-\mu\tau}$$

using the original variables. We have to distinguish two cases in order to determine the function C.

- Case $a > t$: The solution is determined by the initial age structure:

$$\begin{aligned} u(a,0) &= C(a) = u_0(a) \\ \rightsquigarrow\ u(a,t) &= u_0(a-t)e^{-\mu t}, \quad \text{for } a > t \end{aligned}$$

- Case $a < t$: The solution is determined by the progenity:

$$u(0,t) = B(t) = C(-t)e^{-\mu t} \quad \Leftrightarrow \quad C(s) = B(-s)e^{-\mu s},$$

thus

$$u(a,t) = B(t-a)e^{-\mu a}, \quad \text{for } a < t,$$

where (according to the nonlocal boundary condition)

$$\begin{aligned} B(t) &= \int_0^\infty \beta(a)u(a,t)\,da && (4.13) \\ &= \int_0^t \beta(a)u(a,t)\,da + \int_t^\infty \beta(a)u(a,t)\,da && (4.14) \\ &= \int_0^t \beta(a)B(t-a)e^{-\mu a}\,da + \int_t^\infty \beta(a)u_0(a-t)e^{-\mu t}\,da. && (4.15) \end{aligned}$$

(4.15) is called the renewal equation, which is a linear integral equation for $B(t)$. It can be solved in special cases, but generally, numerical methods are necessary.

4.2.2 Structured predator-prey model

Literature: [41]

Let $u(a,t)$ denote the prey population, which is assumed to have a constant per capita mortality rate m. Thus, the age-time dynamics reads

$$u_t + u_a = -mu, \qquad \text{for } a > 0,\ \ t > 0.$$

As before, the initial number of prey is

$$u(a,0) = u_0(a)$$

and the total prey population

$$N(t) = \int_0^\infty u(a,t)\,da.$$

Further assumption: Only the eggs of the prey can be eaten up by the predators $P(t)$ (we neglect their age structure).
The assumption of the maternity function ($\beta(a) = \beta_0 \cdot a \cdot e^{-\gamma a}$) leads to the following equation for the offspring of the prey (the eggs):

$$B(t) = \int_0^\infty \beta_0 \cdot a \cdot e^{-\gamma a} u(a,t)\,da.$$

Since the predators only eat up eggs, only the boundary condition is affected, not the PDE for the age-time dynamics itself. Following the Lotka-Volterra predator-prey model, this leads to

$$u(0,t) = B(t) - kB(t)P(t), \qquad k \text{ const.}$$

To avoid a negative right hand side in case of a large predator population, we introduce $M(B,P) = max(B - kBP, 0)$ (as a very simple approach ...) and use

$$u(0,t) = M(B,P)$$

as boundary condition.
Again following the Lotka-Volterra model, the predator dynamics reads

$$\begin{aligned} \frac{dP}{dt} &= cBP - \delta P && (4.16) \\ P(0) &= P_0, && (4.17) \end{aligned}$$

(c: yield, δ: per capita mortality rate).
Approach: By the method of moments, we aim to obtain a system of ODEs for $N(t)$ and $P(t)$, which is simpler than the original mixed ODE-PDE system.
For that purpose, the PDE is multiplied by a function $g(a)$ (the so-called "moment function") and integrated over $0 \le a \le \infty$. The function g is required to satisfied $\lim_{a\to\infty} u(a,t)g(a) = 0$, no further restrictions. Later, we can choose certain functions g which allow us to get the desired ODEs.
Multiplying the PDE by g and integrating it (using integrations by parts) yields

$$\begin{aligned} \frac{d}{dt}\int_0^\infty g(a)u(a,t)\,da &= -\int_0^\infty g(a)u_a(a,t)\,da - m\int_0^\infty g(a)u(a,t)\,da \qquad (4.18)\\ &= M(B,P)g(0) + \int_0^\infty g'(a)u(a,t)\,da - m\int_0^\infty g(a)u(a,t)\,da. \qquad (4.19)\end{aligned}$$

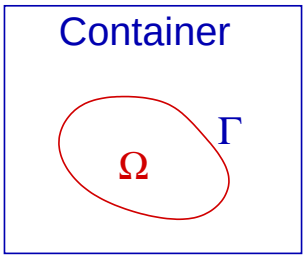
We can use now different choices for $g(a)$:

- $g(a) = 1$. Then (4.19) yields:
$$\frac{dN}{dt} = M(B,P) - mN \qquad (4.20)$$
- $g(a) = \beta(a)$. Then (4.19) yields:
$$\frac{dB}{dt} = -\gamma B + \beta_0 H - mB, \qquad (4.21)$$
where
$$H(t) = \int_0^\infty e^{-\gamma a}u(a,t)\,da.$$
H is a new variable, let us look for another equation involving H!
- $g(a) = e^{-\gamma a}$. Then (4.19) yields:
$$\frac{dH}{dt} = M(B,P) - (m+\gamma)H. \qquad (4.22)$$
Obviously, now we have a system of four ODEs for four variables. Since the equation for N decouples, it is sufficient to consider only the equations for P, B and H (4.16, 4.21, 4.22) with the initial conditions
$$\begin{aligned} P(0) &= P_0\\ B(0) &= \int_0^\infty \beta_0 a e^{-\gamma a}u_0(a)\,da\\ H(0) &= \int_0^\infty e^{-\gamma a}u_0(a)\,da.\end{aligned}$$

4.3 Spatial structure

4.3.1 Derivation of Reaction-Diffusion Equations

Consider a population which lives and moves around in a container. Its density is denoted by $u(x,t)$, the particle / individual flux by $J(x,t) \in \mathbb{R}^3$ (vector which points into the general direction of movement, $|J(x,t)|$ is proportional to the amount of particles / individuals which flow in that direction per unit time).
Let Ω be a test volume with boundary Γ:



Question: Which factors influence the change of density in Ω?

- Change by "reactions" (e.g. birth, death, interactions), $f(u(x,t))$
- Flux through Γ

This leads to the following approach:

$$\frac{d}{dt}\int_\Omega u(x,t)\,dV = \int_\Omega f(u(x,t))\,dV - \int_\Gamma J(x,t)\,dS, \tag{4.23}$$

where dV denotes the volume integral ($\mathbb{R}^n$), dS the surface integration ($\mathbb{R}^{n-1}$). For Ω a domain with boundary Γ, the divergence theorem of Gauß yields

$$\int_\Gamma J(x,t)\,dS = \int_\Omega \text{div } J(x,t)\,dV. \tag{4.24}$$

Applied on (4.23), we get

$$\int_\Omega \left(\frac{d}{dt}u - f(u) + \text{div } J\right) dV = 0.$$

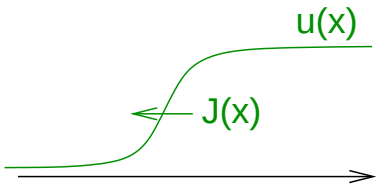
Since this equation is satisfied for all test volumes Ω, the integral can be left out, leading to

$$\frac{d}{dt}u - f(u) + \text{div } J = 0. \tag{4.25}$$

(For the case $f(u) \equiv 0$, this equation is called the first law of Fick: the connection between the time-derivative of the density and the flux when assuming conservation of mass.)
Fick's second law says that the flux has the direction of the negative gradient (of the particle distribution), i.e.

$$J = -D\nabla u \tag{4.26}$$

For better understanding, we consider a 1D example with a positive gradient of u ($\frac{\partial}{\partial x}u(x,t) > 0$):



The flux tries to equilibrate high and low levels of u, so it points to the left.
Inserting (4.26) into (4.25) yields a reaction-diffusion equation:

$$\frac{d}{dt}u = D\Delta u + f(u). \tag{4.27}$$

In the case of $f = 0$, equation (4.27) is called diffusion equation or heat equation.

4.3.2 The Fundamental solution of the Diffusion equation

Literature: e.g. [6, 39, 54]

The fundamental solution is a particular solution of the diffusion equation $u_t = \Delta u$ which can help to find other solutions by convolution and shows up typical properties of solutions of reaction-diffusion equations in general.
Consider a particle starting at the origin 0. This can be described by the δ-distribution $\delta_0(x)$. It is not a function in classical definition, but a so-called distribution; it is defined by its action on smooth functions. Let $f(x)$ be a smooth function, then $\delta_0(x)$ is defined by the following two properties:

$$\int_\mathbb{R} \delta_0(x) f(x)\,dx = f(0) \quad \text{and} \quad \int_\mathbb{R} \delta_0(x)\,dx = 1,$$

so

$$\delta_0(x) = \begin{cases} +\infty & \text{for } x = 0 \\ 0 & \text{for } x \neq 0 \end{cases}$$

Now, we consider the initial value problem for a particle, starting in 0 and diffusing in one dimension:

$$g_t = Dg_{xx}, \qquad g(x,0) = \delta_0(x), \tag{4.28}$$

the corresponding fundamental solution is

$$g(x,t) = \frac{1}{2\sqrt{\pi Dt}} e^{-\frac{x^2}{4Dt}}. \tag{4.29}$$

The initial condition in (4.28) is not continuous, but the solution (4.29) is continuous for all $t > 0$ (even infinitely often continuously differentiable); this is called the regularising property of the diffusion equation.
Initially (i.e., at $t = 0$), there is $g(x,0) = \delta_0(x) = 0$ for all $x \neq 0$, but after an arbitrary small time $t > 0$, there is $g(x,t) > 0$ for all $x \in \mathbb{R}$. So, there is a minimal chance to find the particle arbitrarily far away from its starting point, i.e. the diffusion equation allows for infinitely fast propagation.
The solution of the diffusion equation with more general initial conditions,

$$u_t = Du_{xx}, \qquad u(x,0) = f(x),$$

can be found by convolution with g:

$$u(x,t) = (f * g(\cdot,t))(x).$$

The convolution integral is given by

$$\begin{aligned} (f * g(\cdot,t))(x) &= \int_{-\infty}^{\infty} f(y)g(x-y,t)\,dy \\ &= \frac{1}{2\sqrt{\pi Dt}} \int_{-\infty}^{\infty} f(y) e^{-\frac{(x-y)^2}{4Dt}}\,dy \end{aligned}$$

4.3.3 Some basics in Biological Motion

Literature: [7, 12]
In a similar way as in section 4.1.4 (or for the reaction-diffusion equation) the conservation equation can be generally written as

$$\frac{\partial u}{\partial t} + \nabla \cdot J - f = 0 \quad \Leftrightarrow \quad \frac{\partial u}{\partial t} + div\, J - f = 0.$$

For the reaction-diffusion equation, Fick's law told us that the net flow of particles is proportional to the concentration gradient,

$$J_{diff} = -D\nabla u,$$

thus called "flux due to diffusion".
Another possibility is to consider "flux due to advection" (with velocity v). It just describes that particles are moving in the direction of v (i.e. the particles are e.g. in a moving fluid , taking this velocity and being part of the net collective motion; then v - which might depend on the spatial variables and t - is the velocity of the fluid). Obviously, the flow is proportional to the present concentration u, thus

$$J_{adv} = vu$$

(remark, that v is a vector, i.e. it has a "direction") and the so-called advection equation (with a source term) reads

$$\frac{\partial u}{\partial t} = -\nabla \cdot J_{adv} + f = -\nabla \cdot (vu) + f.$$

In 1D, it corresponds to the so-called one-dimensional transport equation

$$\frac{\partial u(x,t)}{\partial t} = -\frac{\partial}{\partial x}(v(x,t)u(x,t)).$$

Of course, in many examples advection and diffusion play a role at the same time. For describing such a situation, it is possible to combine these two types of fluxes, $J = J_{adv} + J_{diff}$, which results in the so-called advection-diffusion equation with source term:

$$\frac{\partial u}{\partial t} = -\nabla \cdot (vu) + \nabla \cdot (D\nabla u) + f.$$

Special cases:
If the flow is in a three-dimensional domain, but is only one-dimensional, in x-direction, and all dependent variables depend only on x and t, the advective velocity v and the diffusion coefficient D are constant, then the advection-diffusion equation without source term reads

$$\frac{\partial u}{\partial t} = -v\frac{\partial u}{\partial x} + D\frac{\partial^2 u}{\partial x^2}.$$

Considering a cylindrically symmetric flow (i.e. all motion in the radial direction, R), with the cylindrical polar coordinates R, ϕ, z, then the advection-diffusion equation (with constant coefficients) reads

$$\frac{\partial u}{\partial t} = -v\frac{\partial u}{\partial R} + D\frac{1}{R}\frac{\partial}{\partial R}\left(R\frac{\partial u}{\partial R}\right).$$

Similarly, for a spherically symmetric flow (spherical polar coordinates r, θ, ϕ), all motion in radial direction r and the dependent variables only dependent on r, constant coefficients, the advection-diffusion equation reads

$$\frac{\partial u}{\partial t} = -v\frac{\partial u}{\partial r} + D\frac{1}{r^2}\frac{\partial}{\partial r}\left(r^2\frac{\partial u}{\partial r}\right).$$

The proceeding is just to take the vector differential operators in the appropriate coordinate system.

4.3.4 Chemotaxis

Literature: [44, 12], Wikipedia

A lot of organisms (e.g. bacteria, but also other single-cell of multicellular organisms) are able to orient themselves and direct their movement, according to some chemical densities in their environment (e.g. towards higher nutrient levels). This kind of motion is called chemotaxis.
If the movement tends to higher concentrations of the chemical (e.g. bacteria searching for the highest concentration of food molecules), the chemotaxis is called positive. If the movement tends away from high concentration (e.g. in order to flee away from poisons), it is called negative chemotaxis.
Typical example: *Dictyostelium discoideum* (a slime mould). Single-cell amoebae move towards relatively high concentrations of cyclic-AMP (a chemical which is produced by the amoebae themselves).
For the model, we assume the presence of a so-called attractant, $a(x,t)$. The cells move up the gradient. Let $n(x,t)$ be the actual number of cells, which increases the flux of cells. This leads to the following approach for the chemotactic flux:

$$J = n\chi(a)\nabla a, \tag{4.30}$$

where $\chi(a)$ is a function which depends on the density of the attractant.
Let $f(n)$ be the growth term for the cells, this yields the general conservation equation:

$$\frac{\partial n}{\partial t} + \nabla \cdot J = f(n).$$

The flux J may consist of a "classical" diffusion-driven component (with a diffusion coefficient D of the cells) and additionally the chemotaxis flux (4.30), which leads to the following basic reaction-diffusion-chemotaxis equation

$$\frac{\partial n}{\partial t} = f(n) - \nabla \cdot n\chi(a)\nabla a + \nabla \cdot D\nabla n. \tag{4.31}$$

The attractant $a(x,t)$ itself underlies a diffusion (with diffusion coefficient D_a) and is (somehow) produced (there is a source term $g(a,n)$), so its dynamics is described by the following equation:

$$\frac{\partial a}{\partial t} = g(a,n) + \nabla \cdot D_a\nabla a.$$

Normally, it is expected that $D_a > D$.
Equation (4.31) can be generalised for describing several species by using vectors instead of scalars. $\chi(a)$ may be different for each species.
Assumption by Keller & Segel ([33]): There is a production of the attractant by the slime mould (i.e. the production is proportional to n); if there is no production, the attractant decays exponentially, thus

$$g(a,n) = hn - ka$$

In some cases, the amoebae production rate may be neglected, resulting in $f(n) = 0$.
For a simple version of the model, the chemotactic term $\chi(a)$ can be assumed to be constant (χ_0). Then, the models reads (for constant diffusion coefficients; one space dimension):

$$\begin{aligned} \frac{\partial n}{\partial t} &= D\frac{\partial^2 n}{\partial x^2} - \chi_0 \frac{\partial}{\partial x}\left(n\frac{\partial a}{\partial x}\right), \\ \frac{\partial a}{\partial t} &= hn - ka + D_a\frac{\partial^2 a}{\partial x^2} \end{aligned}$$

Of course, the behaviour of the chemotactic factor $\chi(a)$ may be different. Two examples are e.g. the so-called log law,

$$\chi(a) = \frac{\chi_0}{a},$$

and the so-called receptor law:

$$\chi(a) = \frac{\chi_0 K}{(K+a)^2},$$

where $\chi_0 > 0$ (in both examples) and $K > 0$.

Another example of taxis can be the response to a (external) force field (e.g. microorganisms, subject to gravitational force). Let Φ be the potential of a force field which acts on particles. If it leads quickly to a terminal velocity $v = \alpha\nabla\Phi$ (α constant), then the flow can be described by

$$J_{Force} = \alpha u \nabla\Phi$$

and the equation for the particle concentration reads

$$\frac{\partial u}{\partial t} = -\nabla\cdot(\alpha u\nabla\Phi) + \nabla\cdot(D\nabla u).$$

4.3.5 Steady State Equations and Transit Times

Literature: [7]

In many biological situations, a steady state is reached and it is also interesting to consider that (and not only the dynamical behaviour). Remark, that "steady state" does not mean that any fluxes have to be zero, but only that they do not change in time.
Considering the conservation equation (4.25), the steady state for this equation reads

$$-\nabla\cdot J + f = 0, \tag{4.32}$$

where J does not depend on t. Consider some special cases (always under the assumption of $f = 0$, i.e. no sources or sinks):

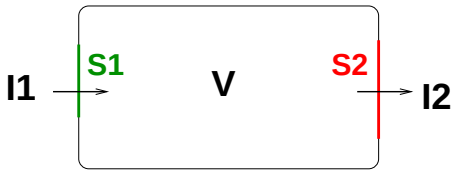
- 1D problem: $\frac{dJ}{dx} = 0, \rightsquigarrow J = C$
- cylindrically symmetric: $\frac{1}{R}\frac{d}{dR}(RJ) = 0 \rightsquigarrow J = C/R$
- radially symmetric in two dimensions: $\frac{1}{r^2}\frac{d}{dr}(r^2 J) = 0 \rightsquigarrow J = C/r^2$

where C is in each case a constant of integration.
If we have a pure diffusional flux, with a constant D, then

- 1D problem: $J = -D\frac{du}{dx}, \rightsquigarrow u = Ax + B$
- cylindrically symmetric: $J = -D\frac{du}{dR} \rightsquigarrow u = AlogR + B$
- radially symmetric in two dimensions: $J = -D\frac{du}{dr}, \rightsquigarrow u = -A/r + B$

($A = -C/D, B$ constants (of integration), determined by the boundary conditions)

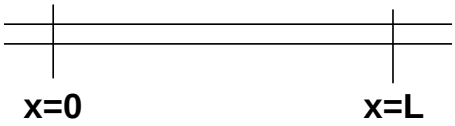
Transit time
We consider the following situation:



Particles enter a volume V via a subset S_1 (of the surface of V), and leave it again via a subset S_2. I_1 and I_2 describe the entry current respectively the exit current.
Let us consider the steady state situation, i.e. $I_1 = I_2 = I$, let N denote the number of particles in V. The transit time is defined by

$$\tau = \text{ average time for a particle to cross } V \text{ from } S_1 \to S_2 = \frac{N}{I}.$$

Example: 1D problem, constant diffusion:



Boundary conditions: $u(0) = u_0$, $u(L) = 0$.
We look for the steady state flux:

$$0 = D\frac{d^2u}{dx^2} \text{ in } (0, L),$$

the solution reads

$$u(x) = u_0\left(1 - \frac{x}{L}\right),$$

the flux is therefore

$$J = -D\frac{du}{dx} = D\frac{u_0}{L}$$

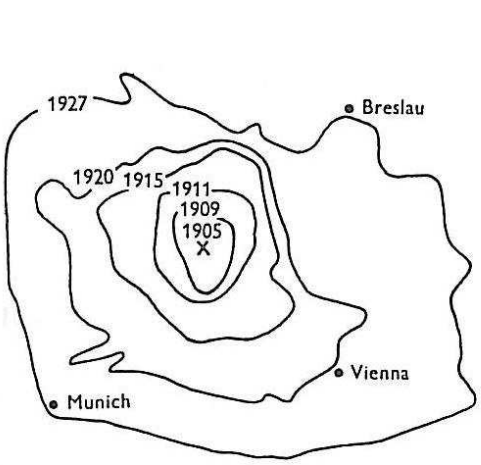
(a constant!)
The above mentioned current corresponds here to J, in the complete tube (between 0 and L) there are $N = \int_0^L u(x)\,dx = \frac{1}{2}Lu_0$ particles. Thus, the transit time from 0 to L can be computed:

$$\tau = \frac{N}{J} = \frac{\frac{1}{2}Lu_0}{D\frac{u_0}{L}} = \frac{1}{2}\frac{L^2}{D}.$$

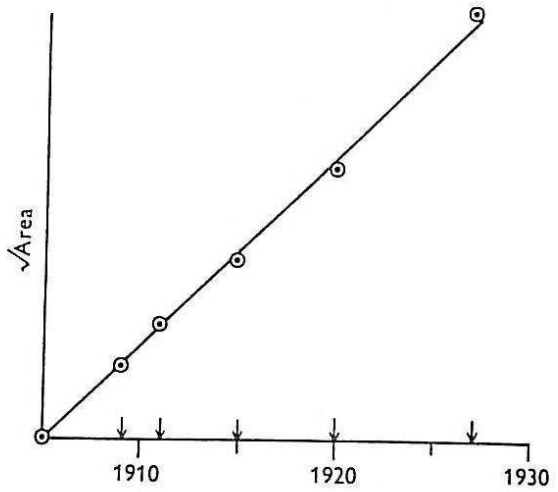
4.3.6 Spread of Muskrats

Literature: [12]

There are real biological examples for populations which spread out according to a diffusion (approximation), e.g. Skellam considered the spread of muskrats (*Ondatra zibethica*) in central Europe during 27 years (a few of them escaped in 1905 from a Bohemian landowner and by good luck, good records of the spread were done):



(a)



(b)

Figure 10.1 *Spread of muskrats over central Europe during a period of 27 years described by Skellam (1951) as a random dispersal. (a) Equipopulation contours (level curves of* $p(\mathbf{x}, t)$ *for the lowest detectable muskrat population. A graph of (area)*$^{1/2}$ *of the regions enclosed by these curves reveals linear dependence on time* t, *as predicted by the growth-dispersal model of equation (1). [From Skellam J. G. (1951). Random dispersal in theoretical populations.* Biometrika, 38, *figs. 1 and 2, p. 200. Reprinted with permission of the Biometrika Trustees.]*

(Similar conclusions were done e.g. for the spread of oak forests over Britain). The model can be put up in the following way:
Assumptions:

- continuous reproduction of the population with rate α
- the spread-out happens "randomly", corresponding to classical diffusion (we will learn something about that connection later)

Goal is to describe the density of muskrats at position x and time t, $u(x,t)$. The basic model reads

$$u_t = D\Delta u + \alpha u, \quad u(x,0) = u_0(x).$$

The initial condition should reflect, that originally, the muskrats spread from one point, so we need a point mass:

$$u_0(x) = \bar{u}_0 \delta_0(x).$$

The following proposition can be shown by a simple computation:

Proposition 21 *The solution of* $u_t = D\Delta u + \alpha u, \quad u(x,0) = u_0(x)$ *reads*

$$u(x,t) = \frac{\bar{u}_0}{2\sqrt{\pi D t}} e^{-\frac{|x|^2}{4Dt} + \alpha t}.$$

So, the model predicts that muskrats are present everywhere after an arbitrary short time (which is not too realistic), but since there is only a very small density far away, the problem can be circumvented by introducing a minimal density $\underline{u}$; "real" muskrats are observable only at locations where there density exceeds $\underline{u}$.

Proposition 22 *Let* $A(t) = \{x \,|\, u(x,t) \geq \underline{u},\, x \in \mathbb{R}^2\}$ *the domain, where the muskrats are observable. For large time, we find asymptotically:*

$$\sqrt{|A(t)|} \sim 2\sqrt{\pi \alpha D} t \quad \text{for } t \to \infty.$$

($|A(t)|$ means the area of the domain $A(t)$; $\sqrt{|A(t)|}$ is proportional to the radius).
Proof:

$$
\begin{aligned}
\underline{u} &\leq u(x,t) = \frac{\bar{u}_0}{2\sqrt{\pi D t}} e^{-\frac{|x|^2}{4Dt}+\alpha t} \\
\Leftrightarrow \quad \frac{2\sqrt{\pi D t}\underline{u}}{\bar{u}_0} &\leq e^{-\frac{|x|^2}{4Dt}+\alpha t} \\
\Leftrightarrow \quad |x|^2 &\leq 4Dt \cdot \left(\alpha t - \ln\left(\frac{2\sqrt{\pi D t}\underline{u}}{\bar{u}_0}\right)\right) = 4\alpha D t^2 \left(1 - \frac{1}{\alpha t}\ln\left(\frac{2\sqrt{\pi D t}\underline{u}}{\bar{u}_0}\right)\right)
\end{aligned}
$$

The last term vanishes for $t \to \infty$, this yields

$$|x|^2 \leq 4\alpha D t^2$$

Thus, it is asymptotically

$$|A(t)| \equiv |\{x \,|\, |x|^2 \leq 4\alpha D t^2\}| = 4\pi\alpha D t^2.$$

□

Obviously, the radius of $A(t)$ is a linear function in t, as it can be (more or less) be found by considering the data.

4.3.7 The Spruce-Budworm model and Fisher's equation

Literature: e.g. [6, 44],
some background information can be found at http://www.unbf.ca/forestry/centers/cwru/patch.htm

The spruce-budworm is a caterpillar of a moth which defoliates spruce stands in Canada.
Situation:

- epidemic spread-out
- large damages in the forest during heavy epidemics
- in the situation of large damages, the population falls onto a low, but endemic level.
- outbreaks occur in intervals of 30-40 years

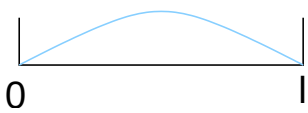
But if the woodland is small enough, it is not possible to establish a stable surviving population. So the question arises about the maximal size of a woodland which does not allow a stable settling of the budworms.
In the following, we use Fisher's equation:

$$u_t = D u_{xx} + \mu u(1-u), \tag{4.33}$$

where $u(t,x)$ describes the population density; spread-out by diffusion, including Verhulst's law of growth with saturation. (Originally, Fisher's equation was introduced for modelling the spread of an advantageous gene in a population, see [14]).

Consider a woodland in the interval $[0,l]$. For a PDE on a bounded interval, it is necessary to introduce boundary conditions. For the application considered here, it is reasonable to use homogeneous Dirichlet boundary conditions,

$$u(0,t) = 0, \quad u(l,t) = 0,$$



since outside of the woodland, the budworms cannot live; thus, there is $u = 0$.

Remark: For describing a situation in a closed box (e.g. by inserting impermeable walls), homogeneous Neumann boundary conditions would be appropriate:

$$u_x(0,t) = 0, \qquad u_x(l,t) = 0,$$

then no individual can leave the patch. Also combinations of these boundary conditions can occur, but we will neglect these possibilities for the moment.

The question about the minimal interval size to support a population has been shown to be equivalent to the question, when the trivial solution $u(x,t) = 0$ is unstable (in case of a stable $u(x,t) \equiv 0$, each solution near 0 would tend to 0 and lead to extinction), see e.g. [6].
For Fisher's equation, it is again equivalent to search for the critical domain length l^* such that a non-trivial steady state exists for $l > l^*$. We look for stationary solutions (with $u_t = 0$), thus

$$u_{xx} = -\frac{\mu}{D}u(1-u)$$

with $u(0) = 0$, $u(l) = 0$.
Introducing a new variable $v := u_x$ leads to the following ODE system:

$$\begin{aligned} u_x &= u' = v \\ v_x &= v' = -\frac{\mu}{D}u(1-u) \end{aligned}$$

(Remark here, there are derivatives with respect to x, not to time t as often usual).
The usual analysis of such an ODE-system yields:

- Stationary points $P_1 = (0,0)$, $P_2 = (1,0)$
- General Jacobian matrix: $Df(u,v) = \begin{pmatrix} 0 & 1 \\ -\frac{\mu}{D} + 2\frac{\mu}{D}u & 0 \end{pmatrix}$
- Eigenvalues of the Jacobian matrix in the stationary points:

$$\begin{aligned} Df(0,0): &\quad \begin{pmatrix} 0 & 1 \\ -\frac{\mu}{D} & 0 \end{pmatrix}, \quad \lambda_{1,2} = \pm i\sqrt{\frac{\mu}{D}} \qquad \text{centre} \\ Df(1,0): &\quad \begin{pmatrix} 0 & 1 \\ \frac{\mu}{D} & 0 \end{pmatrix}, \quad \lambda_{1,2} = \pm\sqrt{\frac{\mu}{D}} \qquad \text{saddle} \end{aligned}$$

We have to check, if also the nonlinear system has a centre in $(0,0)$ (Hartman-Grobman theorem cannot be applied).
Here, it is very useful to introduce a Hamiltonian function to check for that.
A Hamiltonian function has to satisfy

$$\frac{\partial H}{\partial v} = u' \quad \text{and} \quad \frac{\partial H}{\partial u} = -v', \tag{4.34}$$

so for solution $(u(x), v(x))$ of the original system, we get

$$\frac{d}{dx}H(u(x),v(x)) = \frac{\partial H}{\partial u}u' + \frac{\partial H}{\partial v}v' = -v'u' + u'v' = 0. \tag{4.35}$$

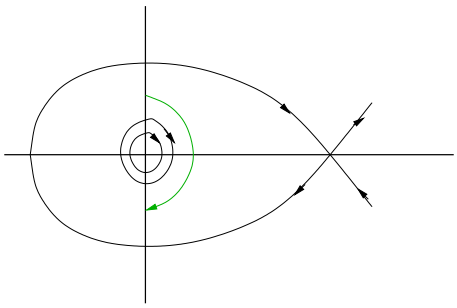
Condition (4.34) and property (4.35) are the defining properties for H to be a Hamiltonian function (of the corresponding ODE system). Obviously, (4.35) means, that H does not change along solution curves $(u(x), v(x))$, so the solution curves lie on level lines of H.
In our example, we can define a Hamiltonian function as follows:

$$H(u,v) = \frac{1}{2}v^2 + \frac{\mu}{D}\frac{u^2}{2} - \frac{\mu}{D}\frac{u^3}{3}$$

(it is easy to check, that (4.34) and (4.35) are satisfied). Certain properties of a Hamiltonian function yield, that for each bounded solution, there are only three possibilities: it is

- an equilibrium point, or
- a connection of equilibrium points, or
- a closed orbit

Now, we have to recall the boundary conditions; we look for a solution that starts in 0 ($u(0) = 0$) and connects to $u(l) = 0$, while it stays nonnegative in between. Such a solution looks as follows:



There is a unique u-axis intersection point $\bar{u}$ for each solution. If we let tend $\bar{u} \to 1$, then the solution would approach the saddle point, but very close to the saddle point, the motion becomes "more slowly" and "more slowly", i.e. $l \to \infty$ for $\bar{u} \to 1$.
Surprisingly, it is not true that $l \to 0$ for $\bar{u} \to 0$. For $\bar{u} \to 0$, we are in the range close to $(0,0)$, where mainly the linearisation influences the behaviour of the solutions. The linearisation yielded a centre at $(0,0)$ with the eigenvalues $\lambda_{1,2} = \pm i\sqrt{\frac{\mu}{D}}$, so the solution near $(0,0)$ is approximately given by

$$\begin{pmatrix} u(x) \\ v(x) \end{pmatrix} = \begin{pmatrix} c_1 \cos(\sqrt{\frac{\mu}{D}}x) \\ c_2 \sin(\sqrt{\frac{\mu}{D}}x) \end{pmatrix}.$$

Looking for a Dirichlet solution, we need a half circle starting at $x_0 = 0$, where $\pi = \sqrt{\frac{\mu}{D}}l$, thus $l = \pi\sqrt{\frac{D}{\mu}}$.
So, the critical patch size in the limit $\bar{u} \to 0$ reads $l^* = \pi\sqrt{\frac{D}{\mu}}$.

Part II

Stochastic Models

Chapter 5

Stochastic Models

Here, we consider stochastic models / stochastic processes where the outcome contains some uncertainty. They are especially useful in the context of small populations, where stochasticity and random effects play a big role. There, a probability is assigned to the different outcomes; we study, how these probabilities change in time.

There are two main types of stochasticity, concerning the dynamics of a population:

1. Environmental stochasticity: effects of temperature, rainfall, competition from other species ...
2. Demographic stochasticity: variation and uncertainty due to individuals of the population (e.g. even a population with a positive net growth rate can die out due to "bad luck"). This factor is relevant in case of small population sizes.

5.1 Some basics

5.1.1 Basic definitions

(can be found in nearly all books concerning probabilities / stochastics ...)

Definition 26 (σ-Algebra) *Let Ω be a non-empty set. $\mathcal{A}$ is called a σ-algebra, if*

- $\Omega \in \mathcal{A}$
- *From $a \in \mathcal{A}$ it follows that $\Omega \setminus a \in \mathcal{A}$.*
- *From $a_n \in \mathcal{A}$ it follows that $\bigcup_n a_n \in \mathcal{A}$.*

Definition 27 (Probability measure) *Let Ω be a non-empty set, $\mathcal{A}$ a σ-algebra. Let P be a map $P : \mathcal{A} \to [0, 1]$ with*

- $P(\{\}) = 0$
- $P(\Omega) = 1$
- $P(\bigcup_n a_n) = \sum_n P(a_n)$ *if $a_i \cap a_j = \{\}$ for $i \neq j$*

Then, P is called a probability measure.

Definition 28 (Law of conditional probability) *Let $A, B \in \mathcal{A}$ be conditional events with $P(B) > 0$ ($\mathcal{A}$ σ-algebra). Then:*

$$P(A|B) = \frac{P(A \cap B)}{P(B)}.$$

Definition 29 (Independent events) *Let $A, B \in \mathcal{A}$ be conditional events ($\mathcal{A}$ σ-algebra). A and B are independent of each other, if*

$$P(A \cap B) = P(A) \cdot P(B).$$

Theorem 22 (Bayes) *Let $A, B \in \mathcal{A}$ ($\mathcal{A}$ σ-algebra), $P(A), P(B) > 0$. Then*

$$P(A|B) = \frac{P(B|A)P(A)}{P(B)}.$$

This equation can be easily shown:

$$P(A|B) = \frac{P(A \cap B)}{P(B)} = \frac{P(A \cap B)P(A)}{P(A)P(B)} = \frac{P(B|A)P(A)}{P(B)}.$$

Let Ω be a sample space (i.e. all possible outcomes of an "experiment") with a probability measure.

Definition 30 (Random variable) *A random variable X is a map*

$$X : \Omega \to \mathbb{R}$$

such that all sets $\{\omega \in \Omega | X(\omega) \leq r\}$ are measurable for any $r \in \mathbb{R}$. Hence, $P(X \leq r)$ is well-defined.

A stochastic process is a family of random variables $\{X(t)\}$ (with a parameter t).
Random variables can be continuous or discrete (i.e., X is continuous or discrete), requiring different mathematical formalisms.

5.1.2 Some introducing examples

Example:

Let A be the final age of a cell, thus, the random variable is defined on $\mathbb{R}_0^+$. So, the probability of a cell death during the age interval (a_1, a_2), assuming that it was still alive at age $a_1 < a_2$, can be determined in the following way:

$$\begin{aligned} P(A \in (a_1, a_2) | A > a_1) &= \frac{P(A \in (a_1, a_2) \cap A > a_1)}{P(A > a_1)} \\ &= \frac{P(A \in (a_1, a_2))}{P(A > a_1)}. \end{aligned}$$

Obviously, A is a continuous random variable. The age of death can be described by a so-called probability density function $f(a)$:

$$P(a_1 \leq A < a_2) = \int_{a_1}^{a_2} f(\alpha)\, d\alpha.$$

The probability of a dead cell by age a can be described by the cumulative density function:

$$F(a) = P(A < a) = \int_0^a f(\alpha)\, d\alpha.$$

The two functions are related by $f(a) = F'(a)$.

Example: Survival of one individual

The consideration of one single individual can be interpreted as a special case of an Individual based model (IBM), which can be easily formulated , but may be difficult to analyse.
For creating a model, it is necessary to characterise the model completely:

- Characterisation of the state space
- Characterisation of the dynamics (i.e. the transitions between the steps)

Here we want to consider:

- two states: dead or alive (one individual)
- Dynamics:

  $$\text{Alive} \quad \to \quad \text{Dead} \qquad (\text{with Rate } \mu)$$

  only death is possible.

Assume that the individual is alive at age a, then the probability that it is dead at age $a + \Delta a$ can be described by

$$P(\text{dead at } a + \Delta a | \text{ alive at } a) = \mu \Delta a + o(\Delta a),$$

where $o(\cdot)$ denotes the Landau symbol , i.e. $\lim_{x \to 0} \frac{o(x)}{x} = 0$. Using a random variable A which gives the age of the individual when it dies, the same approach reads

$$P(A \in [a, a + \Delta a] | A > a) = \mu \Delta a + o(\Delta a).$$

Assume $\mu(a) \in C^0(\mathbb{R}_+)$ (the death rate μ depends on age a in general). Applying the law of conditional probability leads to

$$P(A \in [a, a + \Delta a)) = P(A > a)\mu(a)\Delta a + o(\Delta a)$$

This equation is divided by Δa:

$$\frac{P(A > a) - P(A > a + \Delta a)}{\Delta a} = P(A > a)\mu(a) + \frac{o(\Delta a)}{\Delta a}.$$

Taking the limit $\Delta a \to 0$ yields

$$\frac{d}{da} P(A > a) = -\mu(a) P(A > a), \qquad P(A > 0) = 1.$$

Hence, we get

$$P(A > a) = e^{-\int_0^a \mu(\tau)\, d\tau}.$$

The special case $\mu(a) \equiv \mu$ constant corresponds to the exponential distribution

$$P(A > a) = e^{-\mu a}.$$

Example: Individual based model: Level of small populations

We consider now a population consisting of N individuals. The random variables (for $1 \leq i \leq N$, $i \in \mathbb{N}$) are defined by

$$X_i^{(t)} = \begin{cases} 1 & \text{if individual i is alive at time t} \\ 0 & \text{if individual i is dead at time t} \end{cases}$$

(such kind of random variables with only 0 and 1 values, are also called "random characteristics"). Obviously, the total population size at time t can be gained by summing up all these $X_i(t)$:

$$Y_t = \sum_{i=1}^{N} X_i^{(t)}.$$

From above, we know that

$$P(X_i^{(a)} = 1) = e^{-\int_0^a \mu(\tau)\, d\tau}$$

(assumed that the age of all individuals is zero at time zero and we transfer our observations to the age a). Thus, Y_a is distributed according to a binomial distribution, i.e.

$$Y_a \sim Bin(N, e^{-\int_0^a \mu(\tau)\, d\tau}).$$

The expected value and the variance of the binomial distribution are well-known, we get

$$E(Y_a) = N \cdot e^{-\int_0^a \mu(\tau)\, d\tau}, \qquad Var(Y_a) = N \cdot (1 - e^{-\int_0^a \mu(\tau)\, d\tau}) \cdot e^{-\int_0^a \mu(\tau)\, d\tau}.$$

Similarly to above, we choose a small time interval Δa.
Assumption: The population consists of $k + 1$ individuals at time t resp. age a. The probability that at least one individual dies during Δa reads

$$\begin{aligned} & 1 - (1 - P(\text{death of one specific individual}))^{k+1} \\ = \;& 1 - (1 - \mu(a)\Delta a + o(\Delta a))^{k+1} \\ \approx \;& 1 - (1 - (k+1)\mu(a)\Delta a + o(\Delta a)) + o(\Delta a) \\ = \;& (k+1)\mu(a)\Delta a + o(\Delta a) \end{aligned}$$

(the probability of the death of two individuals during $[a, a+\Delta a]$ is of higher order $o(\Delta a)$. So, the probability, that exactly one individual dies, reads

$$P(Y_{a+\Delta a} = k \,|\, Y_a = k+1) = (k+1)\mu(a)\Delta a + o(\Delta a).$$

In the special case $\mu(a) \equiv \mu$ we get for $0 \leq t_1, t_2$:

$$E(Y_{a_1+a_2}) = E(Y_{a_1})e^{-\mu a_2}.$$

Similarly, for each individual, it is

$$P(A > a+b \,|\, A > a) = e^{-\mu b}$$

which does not depend on a. Such a distribution is "memoryless" which is called a Markov process.

5.2 Markov Chains

In the simplest case, a stochastic process does not have any memory; i.e. it is characterised completely by its current state, not by past states. If a stochastic process $\{X(t)\}$ is history-independent in such a way, it is called a Markov process.
Assume t to be a discrete sequence $t_1, t_2, \ldots$, a Markov process is a one-step memory process:

$$P(X(t_i) = x_1 \,|\, X(t_{i-1}) = x_2 \cap X(t_{i-2}) = x_3 \cap \ldots) = P(X(t_i) = x_1 \,|\, X(t_{i-1}) = x_2), \tag{5.1}$$

obviously with a dependency only on one step back. The x_i are contained in the set $I = \{a, b, \ldots\}$, which may be finite or infinite.
A model that tracks the progression of a Markov process from one time-step to the next is called Markov chain.

5.2.1 Some formalism of Markov chains

Short notation: $X_n := X(t_n)$. The so-called transition matrix is defined in the following way:

$$(P)_{i,j} = p_{ij} := P(X_2 = i \,|\, X_1 = j).$$

It contains all necessary information for describing the dynamics of the Markov process.
Let π_n describe the probability density in time step n, i.e.

$$\pi_n = (P(X_n = a), P(X_n = b), P(X_n = c), \ldots)^T,$$

then the following equation is satisfied:

$$P(X_{n+1} = i) = \sum_{\tilde{c} \in I} P(X_{n+1} = i \,|\, X_n = \tilde{c}) P(X_n = \tilde{c}) = e_i^T P \pi_n,$$

thus

$$\pi_{n+1} = P\pi_n.$$

This represents a deterministic, linear iterative system for the probability distribution. π_n can be interpreted in two different ways:

- We consider one individual, then it describes the probability to find it in a certain state at time step n.
- We consider an ensemble of individuals, then it describes the relative part of the total population which is in a certain state at time step n. (In that case, probabilistic interpretation is not necessary).

Definition 31 *Let $p_{i,j}^{(n)} = (P^n e_i)_j$ be the probability of being in state j after n steps, starting in state i.*

1. *A state j (which is represented by e_j) is called recurrent, if*

$$\sum_{n=0}^{\infty} p_{j,j}^{(n)} = \infty$$

and transient else.

2. *A state j is called periodic with period s, if s is the greatest common divisor of*

$$\{n \,|\, p_{j,j}^{(n)} > 0\}.$$

3. *A state j is called absorbing, if*

$$Pe_j = e_j.$$

In that case, only transitions into this state are possible and the state itself is invariant under P.

4. *A Markov chain is called irreducible, if the transition matrix is irreducible.*

Remark 23 1. *If a state is recurrent, the expected number of returns to this certain state are infinite. If the expected number of returns is finite, then it is transient (eventually, the particle leaves this state and will never return).*

2. *If the Markov chain is finite and irreducible, then all states are recurrent.*

3. *If there is an absorbing state, then the Markov chain is not recurrent.*

4. *If the Markov chain is irreducible and one state is periodic of period s, then all states are periodic with the same period.*

Theorem 24 *For a finite Markov chain, there is a non-negative, stationary distribution $\hat{\pi}$,*

$$\hat{\pi} = P\hat{\pi}$$

(which is also called invariant random measure).

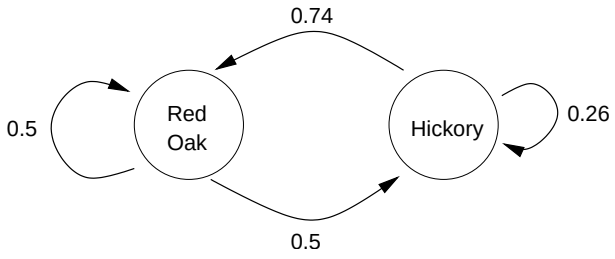
Remark 25 *For a reducible Markov chain, there may be more than one invariant random measure. If the Markov chain is not finite, there may be no invariant measure.*

5.2.2 Example: A two-tree forest ecosystem

We consider a population consisting of red oak and hickory, thus denote the sample space of possible outcomes by

$$S = \{RO, HI\}.$$

It is assumed that both trees have similar life spans. In each generation, a red oak can stay (i.e. it is replaced by another red oak) or is replaced by a hickory; similarly, a hickory stays or is replaced by a red oak. This represents a Markov process with generation index t.
The transition diagram looks as follows:



which can also be written in a transition matrix P,

$$P = \begin{pmatrix} 0.5 & 0.74 \\ 0.5 & 0.26 \end{pmatrix},$$

which means that a dying hickory is replaced by a red oak with probability 0.74 and by hickory with probability 0.26 (similarly for a red oak).
Let $u_t = \begin{pmatrix} o_t \\ h_t \end{pmatrix}$ denote the probability of red oak and of hickory at a given location (in the forest), after t generations. (Remark: in a large statistically homogeneous forest, o_t and h_t can also be interpreted as proportions).
Choosing an initial proportion u_0 (at time 0), the track of changes in the system over time is done by

applying the transition matrix P, i.e. $u_1 = Pu_0$, $u_2 = Pu_1$, ...
An equilibrium u^* of the forest is reached when

$$Pu^* = u^*,$$

thus, u^* is an eigenvector corresponding to an eigenvalue $\lambda = 1$. This eigenvector is computed by

$$(P - I)u^* = \begin{pmatrix} -0.5 & 0.74 \\ 0.5 & -0.74 \end{pmatrix} \begin{pmatrix} o^* \\ h^* \end{pmatrix} = 0,$$

the solution reads

$$\begin{pmatrix} o^* \\ h^* \end{pmatrix} = \begin{pmatrix} 0.597 \\ 0.403 \end{pmatrix}.$$

More generally, we can consider a system with n possible states. The transition probabilities $p_{i,j}$ (probability of a transition from state j to state i) are entered into the transition matrix $P = (p_{ij})$. Obviously, the matrix columns sum to 1 (if everything is well-defined), because a transition from state j to somewhere should happen with probability 1. A vector $v = (u_1, \ldots, u_n)^T$ with nonnegative entries summing to 1 is called a probability vector.
So, a general Markov model for transitions has the form of a discrete system,

$$u_{t+1} = Pu_t, \qquad \text{for a given } u_0.$$

The following theorem yields how to calculate the long-term probabilities:

Theorem 26 *Assume that some power of P has all positive entries (i.e. P is primitive). Then for any probability vector u_0 and model $u_{t+1} = Pu_t$, it is $u_t \to u^*$ for $t \to \infty$, where $Pu^* = u^*$.*

5.2.3 The Princeton forest ecosystem

Literature: Horn [29]

In an experiment, five dominant tree species in a forest were considered; especially which species replaced a dead tree, so the corresponding translational probabilities were determined:

% Saplings	RO	HI	TU	RM	BE
Red Oak	0.12	0.14	0.12	0.12	0.13
Hickory	0.12	0.05	0.08	0.28	0.27
Tulip Tree	0.12	0.10	0.10	0.05	0.08
Red Maple	0.42	0.53	0.32	0.20	0.19
Beech	0.22	0.18	0.38	0.35	0.33

Applying Theorem (26) predicts for the long-term behaviour:

$$u^* = \begin{pmatrix} \text{Red oak} \\ \text{Hickory} \\ \text{Tulip Tree} \\ \text{Red Maple} \\ \text{Beech} \end{pmatrix} = \begin{pmatrix} 0.128 \\ 0.197 \\ 0.080 \\ 0.298 \\ 0.297 \end{pmatrix}.$$

Comparison to the experimentally determined data yields good accordance.

5.2.4 Non-Markov Formulation

Literature: Murthy [45]

We consider $X(t_i)$, which does not satisfy the Markov condition (5.1), i.e. the underlying stochastic process is history-dependent. Again, t is assumed to be a discrete sequence $t_1, t_2, \ldots$. Let $X(t)$ assume the discrete values $s_1, \ldots, s_r$, i.e. $x_i \in \{s_1, \ldots, s_r\}$, $i = 1, \ldots, k+1$. Let

$$P(X(t_i) = x_1 \,|\, X(t_{i-1}) = x_2 \cap X(t_{i-2}) = x_3 \cap \ldots) = P(X(t_i) = x_1 \,|\, X(t_{i-1}) = x_2 \cap \ldots \cap X(t_{i-k}) = x_{k+1}),$$

where $k > 1$ (of course, the conditions concerning time steps with negative indices should be neglected). Thus, there is a dependency on k steps back.
It is possible to enlarge the state space in such a way that this Non-Markov formulation with r states can be transformed into a Markov formulation which is based on r^k states. For getting an idea, how this could work, we consider the following example.

Example:

Let $r = 2$ and $k = 2$, so we consider the process

$$P(X(t_i) = x_1 \,|\, X(t_{i-1}) = x_2 \cap X(t_{i-2}) = x_3), \tag{5.2}$$

where $x_1, x_2, x_3 \in \{s_1, s_2\}$. Now we define a new random variable $Y(t_i)$ in the following way:

$$Y(t_i) = \begin{cases} 1 & \text{if } X(t_i) = s_1 \text{ and } X(t_{i-1}) = s_1 \\ 2 & \text{if } X(t_i) = s_1 \text{ and } X(t_{i-1}) = s_2 \\ 3 & \text{if } X(t_i) = s_2 \text{ and } X(t_{i-1}) = s_1 \\ 4 & \text{if } X(t_i) = s_2 \text{ and } X(t_{i-1}) = s_2 \end{cases}.$$

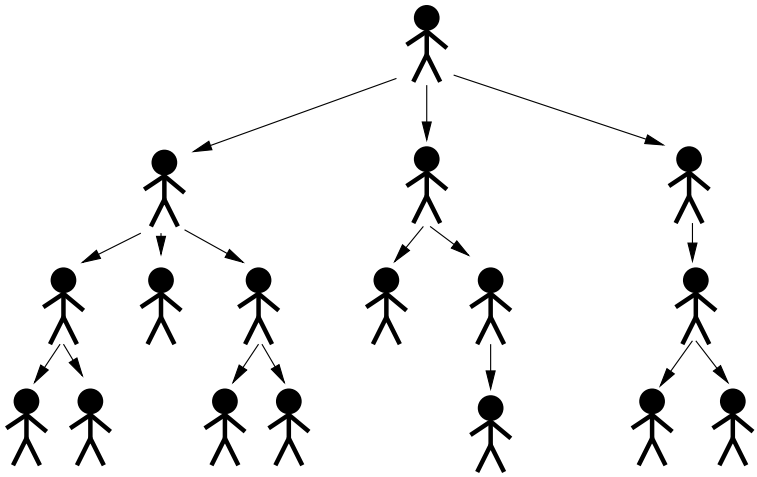
Then, we find:

$$P(Y(t_i) = k \,|\, Y(t_{i-1}) = j \cap Y(t_{i-2}) = n \ldots) = P(Y(t_i) = k \,|\, Y(t_{i-1}) = j),$$

$(k, j \in \{1, \ldots, 4\})$, which shows the property of a Markov chain.

5.3 Branching processes / Galton-Watson-Process

Originally, H.W. Watson and Francis Galton wanted to find something out about the extinction of family names. Assuming that family name inheritance was restricted only to males, an extinction of a (rare) family name could happen, even if every man had (on average) more than one son. So, they assigned probabilities $p_0, p_1, p_2, ...$ to the events that a man has $0, 1, 2., ...$ sons; then, they determined the probability for a extinction of the direct male line after r generations. There are a lot of similar stochastic problems which can be treated in the same way, so it makes sense to consider this approach in greater detail.



The so-called Galton-Watson process is a Markov process in discrete time. Basics:

- Number of available parents at time t $(t = 0, 1, 2, \ldots)$: Y_t
- At the beginning: one single parent, i.e. $Y_0 = 1$.
- After one step: number of offspring $Y_1 = X$ with probability $P(X = n) = p_n$
- Iteration: Each offspring becomes a parent (with a random number of offspring).
- Property: The conditional distribution of Y_{t+1} (for given $Y_t = m$) corresponds to the sum of m independent variables, where each of them has the same distribution as X. This is called a branching process.

For the further investigation, the introduction of the so-called generating function might be helpful:

The Generating function

We consider a discrete random variable Y (with natural number values and the probabilities $p_n = P(Y = n)$, $n = 0, 1, 2, \ldots$). The generating function is defined as

$$g(s) = \sum_{n=0}^{\infty} s^n p_n, \qquad 0 \leq s \leq 1. \tag{5.3}$$

(Sometimes, also the notation $g(s) = E(s^Y)$ is used.) Obviously, equation (5.3) converges for all $0 \leq s \leq 1$, increases in s, $g(0) = p_0$ and $g(1) = 1$.
The generating function contains all interesting information about Y. E.g., the probabilities p_n can be calculated by

$$p_n = \frac{1}{n!} \frac{d^n g}{ds^n}\bigg|_{s=0}.$$

Also the mean can be easily determined:

$$E(Y) = \sum_{n=0}^{\infty} n p_n = g'(1).$$

Furthermore, one can show: The generating function for a sum of independent random variables equals the product of the individual generating functions.

Goal: We calculate the change in the generating function for the number of parents Y_t iteratively (from one time-step to the next). So, the generating function for the number of parents at each time t can be calculated (for a given Y_0).
Assumption: Let $g(s)$, the generating function for the number of offspring, X, from a parent be given, Y_t are the (identical) parents at time step t. (E.g., for parents with 0, 1 or 2 offspring with probability $\frac{1}{3}$ for each case, the generating function reads $g(s) = \frac{1}{3} + \frac{s}{3} + \frac{s^2}{3}$.)
Assumption: The number of offspring arising from certain parents does not influence the number of offspring from other parents (in the same generation). Thus, we get the number of parents in generation $t + 1$ by just adding up,

$$Y_{t+1} = \sum_{i=1}^{Y_t} X_i$$

(X_i are independent random variables, but identically distributed with generating function $g(s)$).
From above we know: If the number of parents in generation t is $Y_t = m$, then the generating function for the number of parents in generation $t+1$ is $(g(s))^m$. The "problem" is, that we do not really "know" the number of parents in generation t, since Y_t is also a random variable. We handle that in the following way: Let $q_{tm} = P(Y_t = m)$ be the probability mass for the random variable Y_t, $h_t(s)$ the generating function for Y_t. Hence, the generating function for the number of parents in generation $t + 1$, $(g(s))^m$, has to be conditioned upon the possible values of m in generation t:

$$h_{t+1}(s) = \sum_{m=0}^{\infty} P(Y_t = m)(g(s))^m = \sum_{m=0}^{\infty} q_{tm}(g(s))^m = h_t(g(s)) = h_t \circ g(s), \tag{5.4}$$

where $\circ$ denotes a functional composition.
Let us consider a few steps in detail: At $t = 0$, there is only one single parent ($Y_0 = 1$), so there we have $h_0(s) = s$. Now we can apply formula (5.4), this yields $h_1(s) = g(s)$, then $h_2(s) = g \circ g(s)$ and so forth. Considering the example from above, we get:

$$\begin{aligned}
h_0(s) &= s \\
h_1(s) &= g(s) = \frac{1}{3} + \frac{s}{3} + \frac{s^2}{3} \\
h_2(s) &= g \circ g(s) = \frac{1}{3} + (\frac{1}{3} + \frac{s}{3} + \frac{s^2}{3})/3 + (\frac{1}{3} + \frac{s}{3} + \frac{s^2}{3})^2/3 \\
&= \frac{13}{27} + \frac{5s}{27} + \frac{6s^2}{27} + \frac{2s^3}{27} + \frac{s^4}{27}.
\end{aligned}$$

and so forth. This yields: The probabilities of 0, 1, 2, 3 or 4 parents after 2 generations is $\frac{13}{27}, \frac{5}{27}, \frac{6}{27}, \frac{2}{27}, \frac{1}{27}$, respectively. Since 0 parents is equivalent to a extinction, the probability of extinction after 2 generations

reads $\frac{13}{27}$.
Each iteration with the generating function yields

$$h_t(s) = h_{t-1} \circ g(s) = g^t(s),$$

which corresponds to a t-fold composition of the generating function $g(s)$. This iteration provides a straight-forward method for calculating $h_t(s)$. Then, this generating function can be used to calculate the expected number of parents in generation t:

$$E(Y_t) = h_t'(1) = h_{t-1}'(g(1))g'(1) = h_{t-1}'(1)g'(1) = R_0 E(Y_{t-1}),$$

where $R_0 = g'(1) = E(Y_1)$ describes the so-called reproduction ratio, hence $E(Y_t) = R_0^t$. In the following considerations, we denote the single steps/generations by n instead of t.

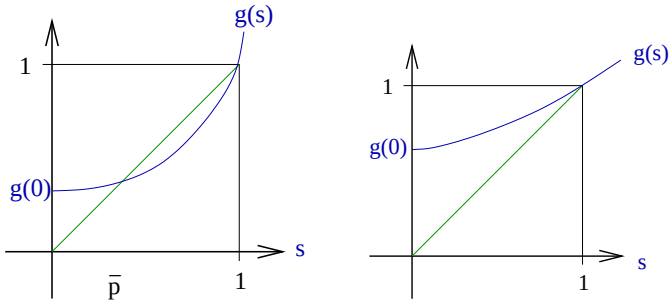
Theorem 27 *Let $g(\cdot)$ be the generating function of the random variable X. Assume $g(0) > 0$ (i.e. $P(X = 0) > 0$). If $E(X) = g'(1) > 1$, then there exists exactly one root $\bar{p}$ of $g(s) = s$ for $0 < s < 1$. If $E(X) = g'(1) \leq 1$, then define $\bar{p} := 1$. The probability of extinction is given by*

$$P(\lim_{n\to\infty} Y_n = 0) = \bar{p}.$$

Proof:
According to the definition, $g(s) = \sum_{n=0}^{\infty} s^n p_n$, $0 \leq s \leq 1$, we obtain the following properties of g:

$$\begin{aligned}
g(0) &= p_0 > 0, \\
g(1) &= \sum_{n=0}^{\infty} p_n = 1 \\
g'(s) &= \sum_{n=1}^{\infty} n \cdot s^{n-1} p_n = \sum_{n=0}^{\infty} (n+1) s^n p_{n+1} \geq 0, \\
g''(s) &= \sum_{n=1}^{\infty} (n+1) \cdot n \cdot s^{n-1} p_{n+1} = \sum_{n=0}^{\infty} (n+2)(n+1) s^n p_{n+2} \geq 0.
\end{aligned}$$

Hence, g is a monotonic increasing and convex function. There are two possibilities:



In both cases, the root $\bar{p} \in [0, 1]$ of $g(s) = s$ is unique. Now, let $q_{n0} = P(Y_n = 0)$. Then we have

$$q_{n0} = h_n(0) = h \circ h_{n-1}(0) = g(q_{n-1,0})$$

and $q_{00} = P(Y_0 = 0)$ which corresponds to a discrete, deterministic iterative system for q_{n0}. g is non-decreasing in the interval $[0, 1]$, $g(s) > s$ in $[0, \bar{p})$ and $g([0, \bar{p}]) \subset [0, \bar{p}]$, then induction yields

$$q_{n0} = g(q_{n-1,0}) \geq q_{n-1,0}, \quad q_{00} = 0 < \bar{p}, \quad q_{n0} = g(q_{n-1,0}) < \bar{p}$$

(q_{n0} is non-decreasing and bounded by $\bar{p}$, thus it converges). Furthermore, g is continuous, so it satisfies

$$g(\lim_{n\to\infty} q_{n0}) = \lim_{n\to\infty} g(q_{n0}) = \lim_{n\to\infty} q_{n0},$$

which means that the limit point corresponds to a fixed point of g, thus

$$\lim_{n\to\infty} q_{n0} = \bar{p}.$$

□

For the interpretation of that theorem, we consider two cases:

Case 1: The expected number of children is below one, then the population dies out with probability 1.

Case 2: Even if the expected number of children is greater than 1, there is still a positive probability for extinction (at least if $g(0) > 0$, then an individual can die without any offspring). In the other case, if extinction does not happen, then the population tends to infinity with probability one. (This behaviour can be reflected only in a stochastic model - a deterministic approach cannot consider realisations of extinction here).

In many examples, it is found that

$$P(\text{Extinction}) = \frac{1}{R_0} \quad \text{if } R_0 > 1.$$

5.3.1 Example: Polymerase chain reaction (PCR)

The polymerase chain reaction (PCR) is a standard technique of molecular biology: a small amount of nucleid acid (DNA or RNA), which is taken from a probe, is multiplied so that it can be detected. (The so-called DNA fingerprinting technique also relays on PCR).
In many cases, one is interested not only in the sequence of the DNA fragment, but also in the amount of these fragments, which was present in the original probe. The Quantitative PCR (QPCR) can perform that. Typically, this technique is applied in order to estimate the virus load of a patient.
The proceeding is as follows:

- Start with a small amount of single DNA strings (produced by heating the original double strings)
- Incubation in a mixture of primers (a very short piece of DNA, 6-8 nucleotides long) and nucleotides
- A primer is attached to the string
- The nucleotides subsequently attach to the end of the primes $\rightsquigarrow$ production of a double string from the single string
- Heating splits the double string, restart!

In this way, the cycle is repeated over and over again. In principle, the amount of DNA should be doubled in each step; in practice, this string replication is stochastic and probability of doubling p_d (also called amplification factor) ranges between 0.6 and 0.8. It is assumed that each string acts independent of the others (e.g. no competition, enough resources available), so it can be described by a Galton-Watson process, which $p_1 = 1 - p_d$ (no doubling happened), $p_2 = p_d$ (doubling was performed) and $p_n = 0$ for $n \neq 1, 2$. So, the corresponding generating function reads $g(s) = (1 - p_d)s + p_d s^2$.
The state for the QPCR model is Y_n which describes the number of single DNA strings in generation n. In the context of (Q)PCR, one is maybe not so interested in the probability of extinction (which would be a bad result of an experiment), but in an estimate for Y_0, the number of single DNA strings in the starting generation. This estimate should be based on given Y_n and Y_{n+1} for large n, since these values can be measured (typically, it is $10 \leq n$).
Originally, in the Galton-Watson process, a single parent at the beginning was assumed, i.e. $Y_0 = 1$. If we allow for Y_0 parents at the beginning, the analysis can be modified and yields

$$E(Y_n) = R_0^n Y_0,$$

thus, the reproductive ratio R_0 satisfies

$$R_0 = \frac{E(Y_{n+1})}{E(Y_n)}.$$

Hence, we come to the following approach for the estimator of R_0:

$$\hat{R}_0 = \frac{\hat{Y}_{n+1}}{\hat{Y}_n}$$

(the $\hat{}$ denotes an estimator).
If R_0 and n are known, then Y_0 can be computed by $Y_0 = E(Y_n)/R_0^n$. This leads us to a simple estimator for the original number of DNA strings:

$$\hat{Y}_0 = \frac{\hat{Y}_n}{\hat{R}_0^n} = \hat{Y}_n \left(\frac{\hat{Y}_{n+1}}{\hat{Y}_n} \right)^{-n} = \frac{\hat{Y}_n^{n+1}}{\hat{Y}_{n+1}^n}. \tag{5.5}$$

Since the experiment underlies stochastic influences, this estimator will provide slightly different values for $\hat{Y}_0$. In principle, it is also possible to analyse the estimator (5.5), considering confidence intervals etc., but we will not do that in this lecture here.

5.4 The Birth-Death process / Continuous time

Literature: (very general, about continuous-time stochastic processes): Capasso [8]

5.4.1 Pure Birth process

Assumption: Only birth is considered (birth rate β).
Without taking into account demographic stochasticity, a simple ODE model for the number $n(t)$ of individuals in the population at time t reads

$$\dot{n}(t) = \beta n, \qquad n(0) = n_0,$$

yielding the solution

$$n(t) = n_0 e^{\beta t}.$$

The underlying stochastic process is defined in the following way:

$$\begin{aligned} N_t &= \text{number of individuals at time } t \text{ (a random variable)} \\ p_n(t) &= P(N_t = n), \quad n = 0, 1, 2, \ldots \end{aligned}$$

For the birth event, we assume a Poisson process : For a short period of time τ, the probability of one event in τ is proportional to τ, the probability of two events is $o(\tau)$. So we get for one individual:

$$\begin{aligned} P(1 \text{ birth in } [t, t+\tau)) &= \beta\tau + o(\tau) \\ P(>1 \text{ birth in } [t, t+\tau)) &= o(\tau) \\ P(0 \text{ births in } [t, t+\tau)) &= 1 - \beta\tau + o(\tau) \end{aligned}$$

For n individuals, this leads to:

$$\begin{aligned} P(1 \text{ birth in } [t, t+\tau)) &= n\beta\tau(1-\beta\tau)^{n-1} = n\beta\tau + o(\tau) \\ P(m \text{ births in } [t, t+\tau)) &= \binom{n}{m} (\beta\tau)^m (1-\beta\tau)^{n-m} = o(\tau), \qquad m \leq n \\ P(0 \text{ birth in } [t, t+\tau)) &= 1 - n\beta\tau + o(\tau) \end{aligned}$$

A so-called master equation relates probabilities at different time steps:

$$\begin{aligned} p_n(t+\tau) &= p_{n-1}(t) \cdot P(1 \text{ birth in } [t, t+\tau)) \\ &\quad + p_n(t) \cdot P(0 \text{ births in } [t, t+\tau)) \\ &= p_{n-1}(t) \cdot (n-1)\beta\tau + p_n(t)(1 - \beta\tau n) + o(\tau) \end{aligned}$$

This equation can be rearranged and yields

$$\frac{p_n(t+\tau) - p_n(t)}{\tau} = \beta((n-1)p_{n-1}(t) - np_n(t)).$$

By considering the limit $\tau \to 0$, we can deduce an infinite ODE system from the stochastic process:

$$\frac{d}{dt} p_n(t) = \beta((n-1)p_{n-1}(t) - np_n(t)), \qquad n = n_0, n_0+1, n_0+2, \ldots,$$

where $p_{n_0-1} = 0$. The initial data describe n_0 individuals present at time $t = 0$:

$$p_n(0) = \begin{cases} 1 & \text{if } n = n_0 \\ 0 & \text{else} \end{cases} \tag{5.6}$$

Next step is to consider the behaviour of the mean $M_1 = \sum_{n=1}^{\infty} n \cdot p_n$ of the variable N_t. The differential equation for M_1 reads:

$$\begin{aligned} \frac{dM_1}{dt} &= \sum_{n=1}^{\infty} n\dot{p}_n \\ &= \sum_{n=1}^{\infty} n\beta((n-1)p_{n-1} - np_n) \\ &= \beta\sum_{n=1}^{\infty}((n-1)np_{n-1} - n^2p_n) \\ &= \beta\sum_{n=1}^{\infty}(n(n+1)p_n - n^2p_n) \\ &= \beta\sum_{n=1}^{\infty} np_n \\ &= \beta M_1 \end{aligned}$$

Initially, there is $M_1(0) = n_0$, so the solution of the ODE reads

$$M_1(t) = n_0 e^{\beta t},$$

which corresponds to the solution of the linear deterministic model. For the calculation of the variance $\sigma^2 = M_2 - M_1^2$ (where $M_2 = \sum_{n=1}^{\infty} n^2 \cdot p_n$, we first derive a differential equation for $M_2 - M_1$:

$$\begin{aligned} \frac{d(M_2 - M_1)}{dt} &= \frac{d}{dt}\sum_{n=1}^{\infty} n(n-1)p_n \\ &= \beta\sum_{n=1}^{\infty} n(n-1)\cdot((n-1)p_{n-1}(t) - np_n(t)) \\ &= \beta\sum_{n=1}^{\infty}((n+1)n^2p_n - (n-1)n^2p_n) \\ &= 2\beta\sum_{n=1}^{\infty} n^2p_n, \end{aligned}$$

which means

$$\frac{d(M_2 - M_1)}{dt} = 2\beta M_2.$$

From this equation, it follows that

$$\frac{dM_2}{dt} = 2\beta M_2 + \beta M_1.$$

This again leads to the following differential equation for the variance:

$$\begin{aligned} \frac{d\sigma^2}{dt} &= \frac{d}{dt}(M_2 - M_1^2) \\ &= \frac{dM_2}{dt} - 2M_1\frac{dM_1}{dt} \\ &= \frac{dM_2}{dt} - 2\beta M_1^2 \\ &= 2\beta M_2 + \beta M_1 - 2\beta M_1^2 \\ &= 2\beta\sigma^2 + \beta M_1. \end{aligned}$$

Initially, the variance is zero, i.e. $\sigma^2(0) = 0$ (which follows directly from the initial condition (5.6)). Then, the solution reads

$$\sigma^2(t) = n_0 e^{\beta t}(e^{\beta t} - 1).$$

Interpretation: The variance increases exponentially for large time t.

Generally, in the pure birth process, there is a zero probability that a population becomes extinct, which makes sense, since there is no death included in the model. In order to consider that, we step further to a simple birth-death process in the next subsection.

5.4.2 Birth-Death process

Here, we consider a small population (where the number of individuals at a certain (continuous) time is counted), i.e. the state of the population is described by

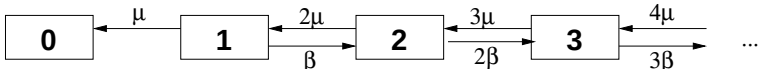
$$N_t = \#\text{ of individuals at time } t.$$

- For one individual, the birth rate reads β (Also here, we assume a Poisson process for the birth event, which means that the Poisson process counts the number of events, and - correspondingly - the time between two births is exponentially distributed with rate β).
- Similarly, the life span in exponentially distributed with rate μ, thus, the death rate is μ.

The probability of population state i at time t is defined by

$$p_i(t) = P(N_t = i).$$

The master equation (in the form of an ODE) helps to describe the time evolution of $p_i(t)$.
Let us consider the following compartmental model:



This can be described by the following ODE system:

$$\begin{aligned} \frac{d}{dt}p_0 &= \mu p_1 \\ \frac{d}{dt}p_i &= -i(\beta+\mu)p_i + (i-1)\beta p_{i-1} + (i+1)\mu p_{i+1}, \qquad \text{for } i \geq 1. \end{aligned}$$

Since these equation cannot be solved straight-forward, a possible "trick" are the generating functions . Here, they are introduced in the following way:

$$f : [0,1] \times \mathbb{R} \to \mathbb{R}_+, \quad (s,t) \mapsto f(s,t) = \sum_{i=0}^{\infty} s^i p_i(t).$$

From $f(\cdot,t)$, the $p_i(t)$ can be gained by

$$p_i(t) = \frac{1}{i!}\frac{d^i}{ds^i} f(s,t)|_{s=0}.$$

For $f(s,t)$, a PDE can be deduced - a solution of this PDE provides a solution for the $p_i(t)$. This is considered in the following proposition:

Proposition 23 *The generating function for the continuous birth-death-process is given by*

$$f(s,t) = \frac{\mu(s-1) - (\beta s - \mu)e^{-(\beta-\mu)t}}{\beta(s-1) - (\beta s - \mu)e^{-(\beta-\mu)t}},$$

where μ is the death rate and β the birth rate.

Proof:
The time-derivative of f reads:

$$\begin{aligned}
\frac{\partial}{\partial t}f(s,t) &= \sum_{i=0}^{\infty} s^i \dot{p}_i(t) \\
&= \mu p_1 + \sum_{i=1}^{\infty} s^i(-i(\beta+\mu)p_i + (i-1)\beta p_{i-1} + (i+1)\mu p_{i+1}) \\
&= \mu s^0 p_1 - (\beta+\mu)\sum_{i=1}^{\infty} i s^i p_i + \beta\sum_{i=1}^{\infty}(i-1)s^i p_{i-1} + \mu\sum_{i=1}^{\infty}(i+1)s^i p_{i+1} \\
&= -(\beta+\mu)\sum_{i=1}^{\infty} i s^i p_i + \beta\sum_{i=0}^{\infty} i s^{i+1} p_i + \mu\sum_{i=1}^{\infty} i s^{i-1} p_i \\
&= -(\beta+\mu)s\frac{\partial}{\partial s}\sum_{i=0}^{\infty} s^i p_i + \beta s^2\frac{\partial}{\partial s}\sum_{i=0}^{\infty} s^i p_i + \mu\frac{\partial}{\partial s}\sum_{i=0}^{\infty} s^i p_i \\
&= (\beta s^2 - (\beta+\mu)s + \mu)\frac{\partial}{\partial s}f(s,t) \\
&= (s-1)(\beta s - \mu)\frac{\partial}{\partial s}f(s,t).
\end{aligned}$$

If we assume that we start with only one individual (i.e. $p_1(0) = 1$ and $p_i(0) = 0$ for $i > 1$), then the corresponding initial value problem reads:

$$\begin{aligned}
\frac{\partial}{\partial t}f(s,t) &= (s-1)(\beta s - \mu)\frac{\partial}{\partial s}f(s,t) \\
f(s,0) &= s.
\end{aligned}$$

Also in the situation here, the method of characteristic curves can help to find a solution for the problem. It can be formulated in the following way: A characteristic curve $S(s,t)$ satisfies $S(s,0) = s$ and $f(s,t)$ stays constant along such a curve; this yields

$$f(S(s,t),t) = const. \quad \Rightarrow \quad f_t(S(s,t),t) + S_t(s,t)f_s = 0.$$

Thus,

$$S_t(s,t) = -\frac{f_t(S(s,t),t)}{f_s} = -(S-1)(\beta S - \mu)$$

By comparison with the PDE above, we get

$$\begin{aligned}
\dot{S}(s,t) &= -(S-1)(\beta S - \mu), \\
S(s,0) &= s \qquad \text{initial value}
\end{aligned}$$

(here, the dot denotes the time-derivative). Separation of variables yields (using expansion into partial fractions):

$$\begin{aligned}
-t = -\int_0^t d\tau &= \int_s^{S(s,t)} \frac{1}{(s'-1)(\beta s' - \mu)}\, ds' \\
&= \int_s^{S(s,t)} \frac{(\beta-\mu)^{-1}}{s'-1}\, ds' - \int_s^{S(s,t)} \frac{\beta(\beta-\mu)^{-1}}{\beta s' - \mu}\, ds' \\
&= \frac{1}{\beta-\mu}\ln\left(\frac{S(s,t)-1}{s-1}\right) - \frac{\beta}{(\beta-\mu)}\frac{1}{\beta}\ln\left(\frac{\beta S(s,t)-\mu}{\beta s - \mu}\right) \\
&= \frac{1}{\beta-\mu}\ln\left(\frac{S(s,t)-1}{\beta S(s,t)-\mu}\frac{\beta s-\mu}{s-1}\right).
\end{aligned}$$

This leads to:

$$\begin{aligned} e^{-(\beta-\mu)t} &= \frac{S(s,t)-1}{\beta S(s,t)-\mu}\frac{\beta s-\mu}{s-1} \\ \Rightarrow \qquad S(s,t)-1 &= \frac{s-1}{\beta s-\mu}e^{-(\beta-\mu)t}(\beta S(s,t)-\mu) \\ \Rightarrow \qquad S(s,t)\cdot\left(1-\beta\frac{s-1}{\beta s-\mu}e^{-(\beta-\mu)t}\right) &= 1-\mu\frac{s-1}{\beta s-\mu}e^{-(\beta-\mu)t} \\ \Rightarrow \qquad S(s,t) &= \frac{(\beta s-\mu)-\mu(s-1)e^{-(\beta-\mu)t}}{(\beta s-\mu)-\beta(s-1)e^{-(\beta-\mu)t}}, \end{aligned}$$

an explicit formula for the characteristic curves. According to the assumption, $f(S(s,t),t)$ stays constant, so we get:

$$f(S(s,t),t) = f(S(s,0),0) = f(s,0) = s = S^{-1}(s,t)$$

(the inverse function with respect to the variable s), thus (by solving the equation for $S(s,t)$ for s):

$$f(S,t) = f(S(s,t),t) = s = \frac{\mu(S-1)-(\beta S-\mu)e^{-(\beta-\mu)t}}{\beta(S-1)-(\beta S-\mu)e^{-(\beta-\mu)t}}$$

Renaming S by s yields

$$f(s,t) = \frac{\mu(s-1)-(\beta s-\mu)e^{-\beta-\mu)t}}{\beta(s-1)-(\beta s-\mu)e^{-(\beta-\mu)t}}.$$

□

Also here, in the continuous case, it is interesting to compute the probability of extinction (analogous to the Galton-Watson process).

Proposition 24 *The probability of extinction reads*

$$q = \begin{cases} \frac{\mu}{\beta} & \text{if } \beta > \mu \\ 1 & \text{if } \beta < \mu. \end{cases}$$

Proof: According to the "definition" of the extinction probability , we find

$$q = \lim_{t\to\infty} P(N_t = 0) = \lim_{t\to\infty} f(0,t) = \lim_{t\to\infty} \frac{-\mu+\mu e^{-(\beta-\mu)t}}{-\beta+\mu e^{-(\beta-\mu)t}} = \begin{cases} \frac{\mu}{\beta} & \text{if } \beta > \mu \\ 1 & \text{if } \beta < \mu. \end{cases}$$

□

The next goal is, to compare the behaviour of the continuous birth-death process (considered here) and the discrete Galton-Watson process. In order to do this, we introduce generations into the continuous birth-death process (instead of continuous time), to derive the so-called embedded Galton-Watson process. First step for this is to determine the number of children per individual (during his/her complete life-span).

Proposition 25 *Let X be the number of children of one individual. Then X is geometrically distributed, $X \sim Geom\left(\frac{\mu}{\beta+\mu}\right)$, i.e.*

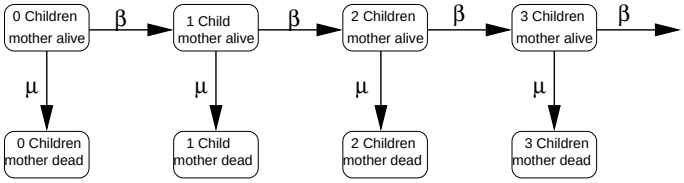
$$P(i \ \ children) = \left(\frac{\beta}{\mu+\beta}\right)^i \left(\frac{\mu}{\beta+\mu}\right).$$

Proof: We start by considering an individual born at time $t = 0$ and introduce

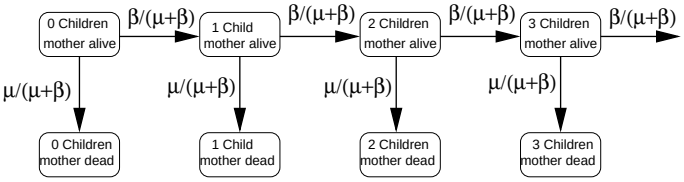
$$\begin{aligned} q_i(t) &= P(i \text{ children at time } t, \text{ mother alive }), \\ r_i(t) &= P(i \text{ children at time } t, \text{ mother dead }). \end{aligned}$$

The number of children can be described graphically in the following way:

- Time-continuous case:



- Discrete case:



What we could do: Define a generating function and solve the problem similarly to above. But since only the final numbers of children are of interest here (and not the continuous time course), we introduce transition probabilities for that purpose, i.e. the embedded discrete process . Assumed a state where the mother is alive, then there are two possible transitions, with the following transition probabilities:

$$\begin{aligned} P(i \text{ children, mother alive } \rightarrow\ i+1 \text{ children, mother alive }) &= \frac{\beta}{\beta+\mu} \\ P(i \text{ children, mother alive } \rightarrow\ i \text{ children, mother dead }) &= \frac{\mu}{\beta+\mu}. \end{aligned}$$

Let $q_{i,n}$ (resp. $p_{i,n}$) be the probability to be in the state with i children and mother alive (resp. dead) after step n, then we get

$$\begin{aligned} q_{i,n} &= \frac{\beta}{\beta+\mu} q_{i-1,n-1}, \\ p_{i,n} &= \frac{\mu}{\beta+\mu} q_{i,n-1}, \end{aligned}$$

where $q_{0,0} = 1$ and $q_{0,n} = 0$ for $n > 0$. This leads to the assertion.

□

Remark 28 *The probability of extinction for a birth-death process with birth rate β and death rate μ coincides with that of a Galton-Watson process, where the number of children of one individual is given by $X \sim Geom\left(\frac{\mu}{\beta+\mu}\right)$. It can be shown that the probability of extinction for a geometrically distributed offspring with parameter r reads*

$$q = \begin{cases} r/(1-r) & \text{if } r < 1-r \\ 1 & \text{else .} \end{cases}$$

$r = \mu/(\beta+\mu)$ leads directly to $q = \mu/\beta$ if $r < 1-r$ which is equivalent to $\beta > \mu$.

5.4.3 A model for common cold in households

We consider households, consisting of N members.

Assumption: One member catches the cold. Then, the disease can spread out (randomly) to (some of) the other members of the household.

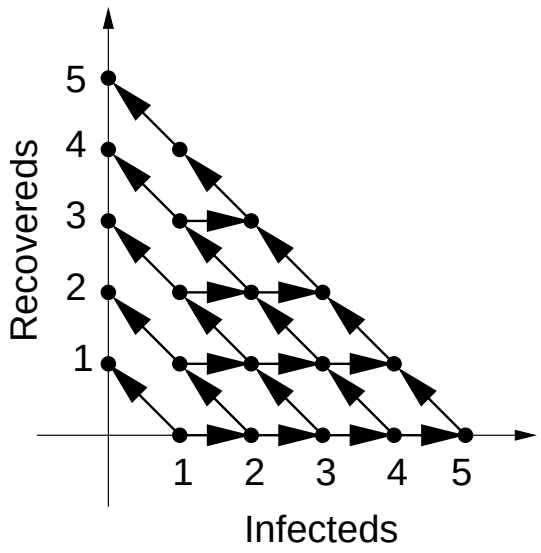
Data were collected from 181 families (consisting of 5 members). Question: How many members got the cold finally? Let F_i describe the number of households with finally i infected members.

Total number of infected members	Number of households
1	$F_1 = 112$
2	$F_2 = 35$
3	$F_3 = 17$
4	$F_4 = 11$
5	$F_5 = 6$

Goal: Put up a model which can describe more or less these numbers of infected individuals!

In some sense, the infection can be considered as a kind of "birth" and the recovery as "death", but, different to above, a linear birth-death process is not sufficient here, since there will be involved nonlinear interactions between infectives and susceptibles.

State of a household: Obviously, at each point of time, a household consists of a certain number of susceptibles, infected and recovered persons. Since the total number N is fixed, it is sufficient to characterise the state of a household by (i, r), where i denotes the number of infected and r the number of the recovered members. Then, the number of susceptibles can be computed by $N - i - r$. For a household of size $N = 5$, the following states and transitions are possible:



Dynamics: The recovery rate per individual is taken to be constant (as in the classical SIR model). Considering a transition from state (i, r) to state $(i - 1, r + 1)$ corresponds to the recovery of one of i infected persons. Hence, the recovery rate in a household is $i\alpha$. The infection rate (rate at which one susceptible individual becomes infected) is assumed to be proportional to the number of infected individuals. So, the rate for a transition from (i, r) to $(i + 1, r)$ is $\beta i(N - i - r)$.
This leads to the following model equations: Let $p_{i,r}(t)$ be the probability of the system being in state (i, r) at time t. The master equation reads:

$$\frac{dp_{i,r}(t)}{dt} = -(i\alpha + \beta i(N - i - r))p_{i,r}(t) + (i + 1)\alpha p_{i+1,r-1}(t) + (i - 1)(N - i + 1 - r)\beta p_{i-1,r}(t), \quad (5.7)$$

for $i = 0, \ldots, N$ and $r = 0, \ldots, N - i$. (Indices exceeding 0 or N are taken to be zero, for keeping the notation simple).
Initially, we assume that one person is infected and there are $N - 1$ susceptible persons, i.e.

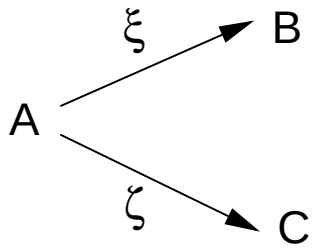
$$p_{1,0} = 1, \quad p_{i,r}(0) = 0 \quad \text{for } (i, r) \neq (1, 0).$$

For testing our model, we can compare it to the data from the table, which contain a "final size of the epidemic". How to compute such a distribution of final sizes from the master equation (5.7)?

Embedded time-discrete Markov process and final size distribution

The goal is to consider the "final" probabilities $\lim_{t\to\infty} p_{i,r}(t)$, that means the probabilities of the system being in state (i, r) if the epidemic has come to an end. In that case, no infected are present anymore (all have moved into the recovered class), so the total mass of the probability $p_{i,r}$ is contained in the states $(0, r)$, $r = 1, \ldots, 5$, all others are zero.
Of course, it is possible to simulate the system of ODEs over a long time interval with the help of a computer program, to obtain the distribution for $t \to \infty$, but there is another possibility, which is faster and more elegant: The idea is to count the "events" instead of considering the time. An event can be either an "infection" or the "recovery" of an individual. So, such an event corresponds to a transition from a state (i, r) to another state (i', r'). The number of events can be used as a new "time" variable,

which yields a discrete-time dynamical system (this is called the embedded discrete-time Markov process or the embedded Markov chain). After a finite number of iterations, a probability distribution without mass at states with $i \neq 0$ is reached.
In order to do that, the transition probabilities from state (i, r) into another state (i', r') are needed (probabilities, not rates!). If we are in state (i, r), which event will happen first, recovery or infection?
In a more abstract formulation: Rate ξ leads from state A to state B, and from state A to state C we go with rate ζ - which one is the final state?



What is the probability of moving from state A to B ($P(A \to B)$) rather than moving from state A to C ($P(A \to C)$)? Let $p_A(t)$, $p_B(t)$ and $p_C(t)$ be the probabilities of being in state A, B resp. C at time t under the assumption that at time $t = 0$, the initial state is A. Then we find the following "system":

$$\begin{aligned}
\frac{d}{dt}p_A(t) &= -(\xi+\zeta)p_A(t), \qquad p_A(0) = 1,\\
\frac{d}{dt}p_B(t) &= \xi p_A(t), \qquad p_B(0) = 0,\\
\frac{d}{dt}p_C(t) &= \zeta p_A(t), \qquad p_C(0) = 0,
\end{aligned}$$

which is a system of linear equations, its solutions reads:

$$\begin{aligned}
p_A(t) &= e^{-(\xi+\zeta)t},\\
p_B(t) &= \frac{\xi}{\xi+\zeta}\left(1 - e^{-(\xi+\zeta)t}\right),\\
p_C(t) &= \frac{\zeta}{\xi+\zeta}\left(1 - e^{-(\xi+\zeta)t}\right).
\end{aligned}$$

This yields:

$$P(A \to B) = \lim_{t\to\infty} p_B(t) = \frac{\xi}{\xi+\zeta}, \qquad P(A \to C) = \lim_{t\to\infty} p_C(t) = \frac{\zeta}{\xi+\zeta}.$$

Observation: The transition probability between two states corresponds to the rate of that transition (ξ or ζ), divided by the sum of all rates of all possible transitions starting from the first state ($\xi + \zeta$).

Returning to the problem of the cold in households, the goal is to define a corresponding discrete Markov chain: $P_{(i,r),(i',r')} = P((i, r) \to (i', r'))$ denotes the transition probability from (i, r) to (i', r'). Also here, there are two possibilities to leave a certain state (i, r): by recovery or by infection. So we get, similarly to above:

$$\begin{aligned}
P_{(i,r),(i+1,r)} &= \frac{\beta i(N-i-r)}{\beta i(N-i-r) + i\alpha}\\
&= \frac{(\beta/\alpha) i(N-i-r)}{(\beta/\alpha) i(N-i-r) + i}\\
&= \frac{R_0(N-i-r)}{R_0(N-i-r)+1},
\end{aligned}$$

for $i = 1, \ldots, N$ and $r = 0, \ldots, N - i - 1$, where $R_0 = \beta/\alpha$. In the same way, we get:

$$\begin{aligned}
P_{(i,r),(i-1,r+1)} &= \frac{\alpha i}{\beta i(N-i-r) + i\alpha}\\
&= \frac{i}{(\beta/\alpha) i(N-i-r) + i}\\
&= \frac{1}{R_0(N-i-r)+1},
\end{aligned}$$

for $i = 1, \ldots, N$ and $r = 0, \ldots, N - i$. The states $(0, r)$ are called absorbing states since they cannot be left anymore, thus

$$P_{(0,r),(0,r)} = 1 \qquad \text{for } r = 0, \ldots, N.$$

All not yet mentioned index combinations have $P_{(i,r),(i',r')} = 0$. Although the original model contains two parameters, α and β, there is only one parameter left in these equations, R_0. This reduction of parameters is possible since we can ignore the time course of the disease and are interested only in the final size of the epidemic.

The probability $q_{i,r}(n)$ to have state (i, r) after n events can be found by using the transition probabilities $P_{(i,r),(i',r')} = 0$:

$$q_{i,r}(n) = \sum_{(k,l)} P_{(k,l),(i,r)} q_{k,l}(n-1),$$

for $i, r = 1, \ldots, N$. So, this system of equations forms a discrete model for the household!
(It is possible to apply further methods, e.g. to embed this nonlinear model into a linear model)

Now we should check, if our model can reproduce the experimental data. Fortunately, there is only one parameter, R_0, so we look for an estimate for R_0.
First possibility: Parameter determination by a least-square fit (R_0 is varied until the error between the experimental data and the model prediction is "minimal") - possible to do, but let us consider the
Second possibility: We consider the probability of having exactly one infected person in a household (after the epidemic). Obviously, there is just one path from state (1,0) to state (0,1). From above, we know:

$$P_{(1,0),(0,1)} = \frac{1}{R_0(N-1)+1},$$

thus

$$R_0(N-1)+1 = \frac{1}{\text{Probability for one infected person}}$$

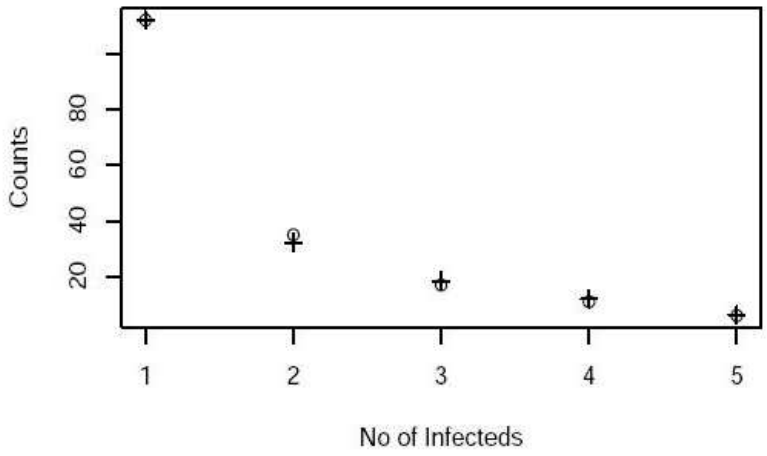
and

$$R_0 = \frac{1}{(N-1)} \cdot \left(\frac{1}{\text{Probability for one infected person}} - 1 \right).$$

An estimate for the probability for one infected person can be gained by the following idea: F_i denotes the number of households with i infected persons. Then, the probability for one infected person is $F_1/(\sum_{i=1}^{N} F_i)$, and we get

$$\hat{R}_0 = \frac{1}{(N-1)} \left(\frac{\sum_{i=1}^{N} F_i}{F_1} - 1 \right).$$

For our data, the result is $\hat{R}_0 \approx 0.154$. Then the comparison of experimental (cross) and model-predicted data (circles) - considering an ensemble of families at once - yields:



Quite good agreement!

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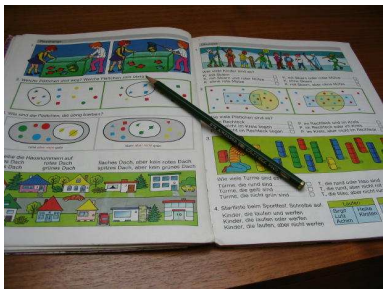

Index