

**NOTES ON
A Short Course
and Introduction
to Dynamical Systems
in Biomathematics**

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1 Simple one-dimensional dynamical systems — birth/death and migration processes, lo- gistic equation.

Generally, in our course we will talk about two main types of dynamical systems: continuous and discrete. Our study will be based on the well known biological models. We start from a very simple example — modelling of a birth process.

1.1 Linear models of birth/death and migration pro- cesses.

Let $N(t)$ denotes the density of some population at time t . We want to construct as simple as possible mathematical model that can predict the density $N(t + \Delta t)$, where $\Delta t > 0$ is a length of time interval we are interested in. Assume that

- an environment is very favourable for our species, i.e. there is enough food and place for every individual,
- all individuals are the same, we are not able to distinguish between them,
- a birth process is uniform and there is no death in the interval $[t, t + \Delta t)$,

- each individual divides (has children) every σ time units, the number of children per each individual and each birth moment is the same (equal to λ).

Then

$$N(t + \Delta t) = \text{number of parents} + \text{number of children},$$

i.e.,

$$N(t + \Delta t) = N(t) + \lambda \frac{\Delta t}{\sigma} N(t),$$

where the term $\frac{\Delta t}{\sigma}$ describes the number of birth moments for every individual in the interval $[t, t + \Delta t)$.

Finally, we obtain the equation

$$N(t + \Delta t) = \left(1 + \lambda \frac{\Delta t}{\sigma}\right) N(t). \quad (1)$$

Now, using Eq.(1) we build two dynamical systems — discrete and continuous. The discrete one is almost ready. Assume that the time interval has the length of one unit. Then $\Delta t = 1$. Using the notation of sequence theory we get

$$N_{t+1} = r_d N_t, \text{ with } N_t = N(t) \text{ and } r_d = 1 + \frac{\lambda}{\sigma}. \quad (2)$$

We obtain so-called recurrent formula defining the sequence (N_t) (recurrence means that we calculate the next term of the sequence knowing the previous term). This sequence describes the birth process with constant birth rate r_d in the language of discrete dynamical systems. "Discrete" means that the time is measured in discrete time moments, namely, t is a natural number ($t \in \mathbf{N}$). We are not interested in other time moments between t and $t + 1$.

On the other hand, we can build the continuous model. Let rewrite Eq.(1) in the following way

$$\frac{N(t + \Delta t) - N(t)}{\Delta t} = \frac{\lambda}{\sigma} N(t).$$

Now, we should remind that, for every function f with real values, the ratio

$$\frac{f(t + \Delta t) - f(t)}{\Delta t}$$

is called the difference quotient and if there exists a limit of this ratio as an increment Δt tends to 0, then it is called the derivative of f at the point

t . The derivative describes instantaneous (local) changes of the function. We write $\frac{df}{dt}$ or \dot{f} to underline that it is the derivative with respect to time (normally, $f'(x)$ is used, for the function of real variable x).

Hence, for $\Delta t \rightarrow 0$, we obtain

$$\dot{N}(t) = r_c N(t), \quad \text{with } r_c = \frac{\lambda}{\sigma}. \quad (3)$$

It is so-called ordinary differential equation (ODE) that tells us about the changes of population at every time t . If we know the solution, we also know the behaviour of population at every time. Therefore, such a model is called "continuous" because the time is continuous in it.

We compare these two models. The discrete version, i.e. Eq.(2) is the geometric sequence (this is a sequence with a constant ratio $\frac{x_{n+1}}{x_n}$, for every $n \in \mathbf{N}$) with common ratio

$$\frac{N_{t+1}}{N_t} = r_d > 1.$$

Therefore, such a sequence is always increasing (the next term is greater than the previous one). It is easy to see that if $N_0 = 0$, then $N_t = 0$, for every t . If there are no parents, there are no children. Assume that $N_0 > 0$. The sequence is unbounded in such a case. If not, then it is increasing and bounded and therefore, it has a limit. Let \bar{N} denotes this limit. We have

$$\bar{N} = \lim_{t \rightarrow +\infty} N_t = \lim_{t \rightarrow +\infty} N_{t+1},$$

because (N_t) and (N_{t+1}) are the same sequences except of the first term — (N_t) starts from N_0 while (N_{t+1}) starts from N_1 . Therefore, from Eq.(2) we obtain $\bar{N} = r_d \bar{N}$. This means that either $\bar{N} = 0$ or $r_d = 1$. Our sequence is increasing. Thus, $\bar{N} > N_0 > 0$ and $r_d > 1$, from the definition. It contradicts the assumption that the sequence is bounded and we have already proved that

$$\lim_{t \rightarrow +\infty} N_t = +\infty.$$

On the other hand, knowing the recurrent formula we are sometimes able to calculate so-called general term of the sequence. At the beginning we try to calculate several terms of the sequence starting from arbitrary N_0 . We see that

$$N_1 = r_d N_0, \quad N_2 = r_d N_1 = r_d^2 N_0, \quad N_3 = r_d^3 N_0,$$

and so on. Hence, we postulate that $N_t = r_d^t N_0$, for every $t \in \mathbf{N}$. This formula should be proved using the principle of mathematical induction. We have three steps of this method.

1. We check the formula for $t = 0$.

Checking: For $t = 0$ we obtain $N_0 = r_d^0 N_0$ that is true.

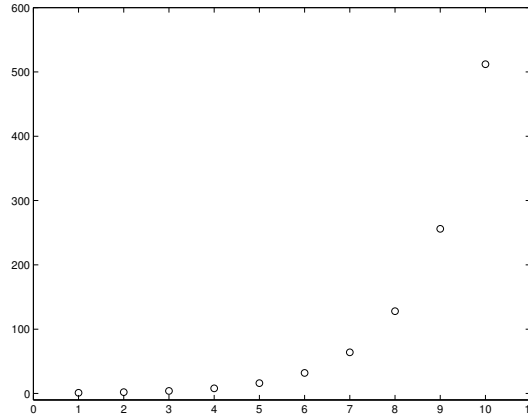
2. We assume this formula for some $t = k$ and postulate a thesis for $t = k + 1$.

Assumption: $N_k = r_d^k N_0$.

Thesis: $N_{k+1} = r_d^{k+1} N_0$.

3. We prove Thesis.

Proof: From the recurrent formula we have $N_{k+1} = r_d N_k$. Next, using Assumption we obtain $N_{k+1} = r_d N_k = r_d (r_d^k N_0) = r_d^{k+1} N_0$ which proves Thesis.



An example of solution to Eq.(2).

Now, we focus on the continuous model, i.e. Eq.(3). We want to find a function $N(t)$ with the derivative proportional to itself. We see that the function identical to 0 ($N(t) \equiv 0$) satisfies the equation. If $N(t) > 0$, we can rewrite Eq.(3) in the form

$$\frac{\dot{N}}{N} = r_c.$$

Now, we make a substitution

$$\ln N(t) = f(t),$$

for some differentiable function f . Calculating derivatives of both sides with respect to t we obtain

$$\frac{\dot{N}(t)}{N(t)} = \dot{f}(t).$$

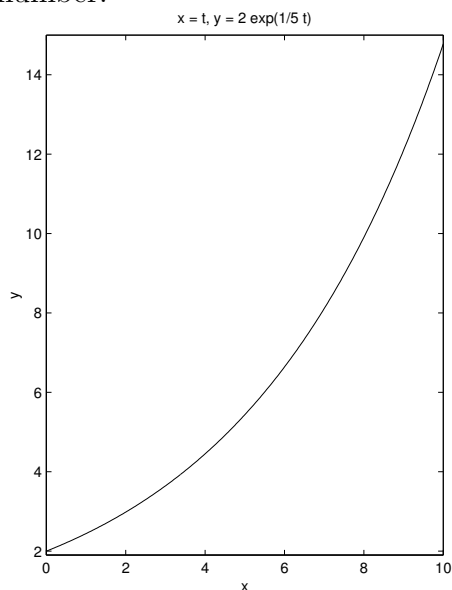
Therefore, $\dot{f}(t) = r_c$ and the function f has constant derivative. This means that this function is linear, i.e.

$$f(t) = r_c t + c, \quad \text{where } c = \text{const.}$$

Hence, $\ln N(t) = r_c t + c$ and finally,

$$N(t) = C e^{r_c t}, \quad C = e^c > 0,$$

where e is the Euler number.



An example of solution to Eq.(3).

We see that the solution to our model Eq.(3) is exponential with positive exponent $r_c t$, for $t > 0$ and therefore, it grows to infinity with increasing t .

Summing up — for the birth process there is no qualitative difference between the behaviour of solutions to continuous and discrete models. The only difference (quantitative, obviously) is the birth rate. For the continuous model this rate r_c is simply positive, while for the discrete one it should be greater than 1 to describe this process. If we fix $r_c > 0$, then we can find $r_d > 1$ such that both solutions to discrete and continuous models are the same at $t \in \mathbf{N}$. Namely, $r_d = e^{r_c}$. Due to identity $e^{r_c t} = (e^{r_c})^t$ we obtain $e^{r_c t} = r_d^t$, for every t and this means that the solutions with the same initial value N_0 are the same, for $t \in \mathbf{N}$.

Similarly, we can model parallel processes of birth and death to obtain equations of the form

$$N_{t+1} = (r_d - s_d)N_t \quad \text{or} \quad \dot{N} = (r_c - s_c)N,$$

where s_d and s_c are death rates.

In the discrete case we have $s_d \leq 1$ because the number of dead individuals cannot be greater than the number of all individuals. Therefore, the net growth rate of population $\alpha_d = r_d - s_d > 0$ and the number of individuals increases for $\alpha_d > 1$, it is constant for $\alpha_d = 1$ and decreases for $\alpha_d < 1$. In the last case we have common ratio $\alpha_d \in (0, 1)$ and then the geometric sequence is decreasing to 0.

In the continuous case the net growth rate $\alpha_c \in \mathbf{R}$. If it is positive, the number of individuals grows, if it is equal to 0, the number is constant, for $\alpha_c < 0$ this number decreases to 0.

In the same way we study processes of migrations. In the easiest case we assume that the number of migrating individuals is constant in time. Then we obtain

$$N_{t+1} = \alpha_d N_t + \beta \quad \text{or} \quad \dot{N} = \alpha_c N + \beta,$$

with $\beta \in \mathbf{R}$ describing constant migration.

For such a models the behaviour of solutions is also similar in both cases. The reason of this similarity lies in the linearity of these models. In the examples above we have used two equations

$$N_{t+1} = F(N_t) \quad \text{or} \quad \dot{N}(t) = F(N(t)),$$

where the right-hand side of equations (i.e. F) is linear. For non-linear models the differences can be large.

1.2 Logistic equation.

As an example of non-linear model we study the famous logistic (Verhulst) equation. We start with the continuous version because it is much simpler. How to construct this model? In the previous considered case we have assumed that the birth rate does not depend on external conditions and it is constant independently on the number of individuals. In the logistic model it is assumed that individuals compete for environmental resources such as food, place and so on. Therefore, if the number of individuals is large, they

are not able to spend the same amount of energy for reproduction as in the case of small population. Consider the ratio $\frac{\dot{N}}{N}$ which describes the local (in time) changes of population per one individual. In the birth process it is constant. In the logistic equation it depends on the number of individuals and it is a decreasing function of this number. The simplest form of such a function is linear. Therefore,

$$\frac{\dot{N}}{N} = r - bN,$$

where the coefficient $b > 0$ describes the magnitude of competition. Rewriting this equation in the form

$$\dot{N} = rN \left(1 - \frac{b}{r}N \right)$$

and defining $K = \frac{r}{b}$ we obtain

$$\dot{N} = rN \left(1 - \frac{N}{K} \right), \tag{4}$$

the well know logistic equation.

To study the behaviour of solutions of one ODE (as the logistic equation Eq.(4)) we can either find its solutions (if it is possible) or study its phase portrait. We use both methods to compare results.

Consider ODE of the form

$$\dot{x} = F(x)$$

with $F : \mathbf{R} \rightarrow \mathbf{R}$ continuously differentiable (this assumption guaranties the existence and uniqueness of solutions and we will talk about it later).

Finding solutions. At the beginning we assume that $F(x) \neq 0$, for every $x \in \mathbf{R}$. We "technically" treat the derivative $\dot{x} = \frac{dx}{dt}$ as the ratio of two separate terms dx and dt and write our equation in the following integral form

$$\int \frac{dx}{F(x)} = \int dt.$$

If we are able to find a function G such that $\frac{dG}{dx} = \frac{1}{F(x)}$ (as we have found for Eq.(3)), then we have

$$\int dG = \int dt$$

and therefore, $G(x(t)) = t + C$, with some constant C . Next, if G is invertible, then $x(t) = G^{-1}(t + C)$. This method is called the separation of variables and can be used also for ODEs of the form $\dot{x} = F_1(x)F_2(t)$, for which we obtain the integral equation $\int \frac{dx}{F_1(x)} = \int F_2(t)dt$.

If the function F has some number of zeros, e.g. let x_1, \dots, x_n be zeros of F , then for each x_i , $i = 1, \dots, n$, we have $F(x_i) = 0$ independently on t and therefore, $x(t) \equiv x_i$ are constant (stationary) solutions to our equation. Zeros of F are often called critical points or steady (stationary) states of the system.

Practically, in the case of Eq.(4) we obtain

$$\int \frac{dN}{N(r - bN)} = \int dt$$

under the assumption that $N \neq 0$ and $N \neq K$. We can decompose the ratio $\frac{1}{N(r - bN)}$ into so-called simple quotients (simple quotient is such a quotient that cannot be decomposed into simplest quotients with denominators possessing real zeros), i.e. we find constants A and B such that

$$\frac{1}{N(r - bN)} = \frac{A}{N} + \frac{B}{r - bN}.$$

Taking the right-hand side into the common denominator we get

$$\frac{1}{N(r - bN)} = \frac{Ar - AbN + BN}{N(r - bN)}$$

and comparing numerators we find that $Ar = 1$ and $B - Ab = 0$. Hence, $A = \frac{1}{r}$ and $B = \frac{1}{K}$. Finally, the integral form reads as

$$\int \frac{dN}{rN} - \int \frac{dN}{r(N - K)} = \int dt.$$

Normally, we want to find a solution $N(t)$ for some initial value $N(0) = N_0 > 0$. In such a case we calculate definite integrals from 0 to t with respect to time and from N_0 to $N(t)$ with respect to N . Therefore, we have

$$\int_{N_0}^{N(t)} \frac{dN}{rN} - \int_{N_0}^{N(t)} \frac{dN}{r(N - K)} = \int_0^t dt.$$

The primitive function for $\frac{1}{N-D}$ is equal to $\ln |N - D|$, for a constant $D \in \mathbf{R}$. Hence,

$$\int_{N_0}^{N(t)} \frac{dN}{rN} = \frac{1}{r} (\ln |N(t)| - \ln |N_0|) = \frac{1}{r} \ln \left| \frac{N(t)}{N_0} \right|$$

and similarly,

$$\int_{N_0}^{N(t)} \frac{dN}{r(N - K)} = \frac{1}{r} (\ln |N(t) - K| - \ln |N_0 - K|) = \frac{1}{r} \ln \left| \frac{N(t) - K}{N_0 - K} \right|.$$

In our case $N = 0$ and $N = K$ are constant solutions to Eq.(4) and all solutions are unique. Therefore, the solution with $N_0 > 0$ is positive (it cannot cross $N = 0$) and the solution with $N_0 > K$ stays in the same region $N > K$. This means that we can neglect both absolute values to obtain

$$\frac{1}{r} \left(\ln \frac{N(t)}{N_0} - \ln \frac{N(t) - K}{N_0 - K} \right) = t,$$

and next

$$\ln \frac{N(t)(N_0 - K)}{N_0(N(t) - K)} = rt.$$

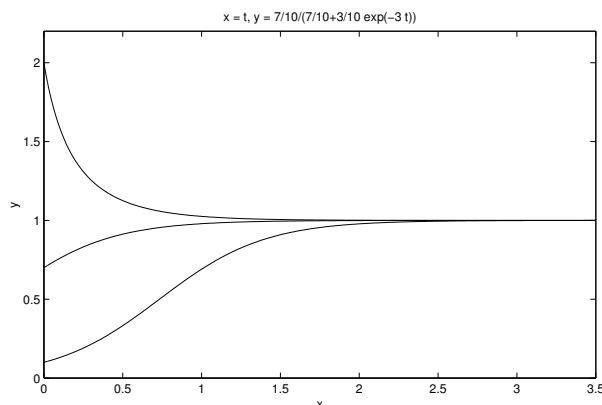
Taking the exponent we get

$$\frac{N(t)(N_0 - K)}{N_0(N(t) - K)} = e^{rt}$$

and finally, calculating $N(t)$ we find that

$$N(t) = \frac{K}{1 + \left(\frac{K}{N_0} - 1 \right) e^{-rt}}. \tag{5}$$

This is the explicit formula for every solution with positive N_0 . We see that $N(t) \rightarrow K$ as $t \rightarrow +\infty$. We have just obtained a surprising result — Formula (5) is true not only for non-constant solutions but also for the solution $N \equiv K$ (we've assumed $N \neq K$!). Moreover, if we rewrite it in the form $N(t) = \frac{N_0 K}{N_0 + (K - N_0) e^{-rt}}$, then it is true, for every solution with $N_0 \geq 0$. It occurs that this situation is rather usual for the separation of variables' method — obtained formulae give us more information than we've expected.



Solutions to Eq.(4) for different initial values.

Studying the phase portrait. In this method we draw the graph of $F(x)$ that describes the right-hand side of equation. This graph shows the dependence between x and $\dot{x} = F(x)$. The co-ordinates are x and \dot{x} on this graph.

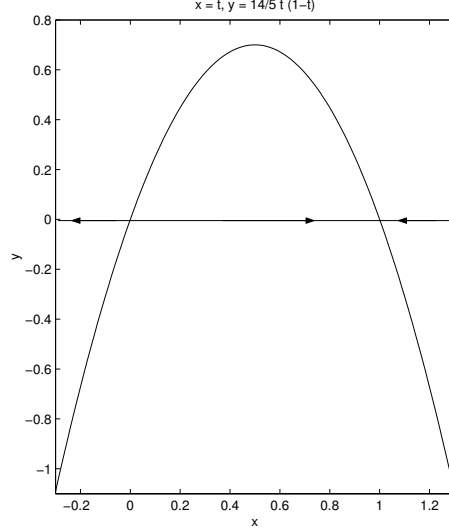
Let $x_1 < \dots < x_n$ be zeros of F . We know that each of x_i , $i = 1, \dots, n$, is a constant solution to our equation. Every solution is unique. Therefore, if $x_0 \in (x_i, x_{i+1})$, then the solution for this initial value stays in the same region (x_i, x_{i+1}) .

In every interval (x_i, x_{i+1}) the function F is either positive or negative. Assume that it is positive. This means that $\dot{x} > 0$ in this region and the solution $x(t)$ is increasing. Therefore, $x(t)$ is increasing and bounded that means it has a finite limit. Consequently, $F(x(t))$ also has a finite limit. But $F(x) = \dot{x}$ and hence, \dot{x} has the same limit. It is obvious that \dot{x} must tend to 0 (if not, then the growth of $x(t)$ is linear and $x(t)$ crosses x_{i+1}). This means that $F(x(t)) \rightarrow 0$ and finally, $x(t) \rightarrow x_{i+1}$. Similarly, if $F(x)$ is negative in (x_i, x_{i+1}) , then $x(t)$ is decreasing and $x(t) \rightarrow x_i$.

If $x_0 < x_1$ and $F(x)$ is negative in this region, then $x(t)$ decreases but it has no limit, because there is no point for which $F(x) \rightarrow 0$ there. Hence, $x(t)$ decreases to $-\infty$. If F is positive, then $x(t)$ increases to x_1 . On the opposite side, for $x_0 > x_n$, if F is positive, then $x(t)$ increases to $+\infty$, if it is negative, then $x(t)$ decreases to x_n .

At the end we complete the graph with the arrows situated in the x -axis directed from the left to the right-hand side in the regions where F is positive and in opposite direction where F is negative. Such a graph with the arrows we call the phase portrait (for one dimensional continuous dynamical

system).



Phase portrait for Eq.(4).

For the logistic equation Eq.(4) we have $F(x) = rx \left(1 - \frac{x}{K}\right)$ and we are interested in the domain $[0, +\infty)$. F is a parabola with zeros at $x = 0$ and $x = K$ and the vertex at $x = \frac{K}{2}$. Hence, $x = 0$ and $x = K$ are constant solutions. $F(x) > 0$ for $x \in (0, K)$ and $F(x) < 0$ for $x > K$. This means that the solution with $x_0 \in (0, K)$ is increasing and tends to K with $t \rightarrow +\infty$, while for $x_0 > K$ the solution decreases to K . Therefore, for every $x_0 > 0$ the solution tends to K and this result is the same as obtained previously. We complete our analysis finding regions of convexity/concavity and possible points of inflection. We start from the calculation of the second derivative $\ddot{x}(t)$. We know that $\dot{x} = rx \left(1 - \frac{x}{K}\right)$ and hence,

$$\ddot{x} = r\dot{x} - 2bx\dot{x} = r\dot{x} \left(1 - 2\frac{x}{K}\right).$$

We are looking for such a point that $\ddot{x} = 0$. Therefore, $x = \frac{K}{2}$ or $\dot{x} = 0$ (i.e. $x = 0$ or $x = K$). The only interesting point is $x = \frac{K}{2}$ because $x = 0$ and $x = K$ are constant solutions so, they are not the points of inflection. If $x \in (0, \frac{K}{2})$, then $\ddot{x} > 0$ and the solution is convex, if $x \in (\frac{K}{2}, K)$, then $\ddot{x} < 0$ and this implies concavity of solutions. This means that if there exists a point \bar{t} such that $x(\bar{t}) = \frac{K}{2}$, then this is the point of inflection for $x(t)$. Because solutions increase in the region $(0, K)$, then such a point exists only if $x_0 < \frac{K}{2}$. Hence, for $x_0 \in (0, \frac{K}{2})$ the solution has well-know S-shape, it is

convex at the beginning and changes its behaviour when reaches the value $x = \frac{K}{2}$ (it increases very fast — almost exponentially — at the beginning and much slower for large t). This type of S-shape curve is also called the logistic curve. If $x_0 \in [\frac{K}{2}, K)$, then the solution increases but it is concave and its growth is slow. If $x_0 > K$, then the solution is decreasing and convex.

All the properties above we can also study using the explicit form of solution but it seems that the method of phase portrait is simpler and it is more general because it can be used even if we are not able to calculate solutions explicitly.

Now, we turn to the discrete case. How to obtain discrete version of Eq.(4)? We use the inverse method to those for the birth process — instead of the derivative \dot{N} we write the difference quotient for $N(t)$ and then the approximation has the form

$$\frac{N(t + \Delta t) - N(t)}{\Delta t} = rN(t) \left(1 - \frac{N(t)}{K} \right).$$

Taking $\Delta t = 1$ and writing $N(t) = N_t$ we obtain

$$N_{t+1} = \tilde{r}N_t(1 - \tilde{b}N_t), \text{ with } \tilde{r} = r + 1, \text{ and } \tilde{b} = \frac{r}{K(r + 1)}.$$

Substituting $x_t = \tilde{b}N_t$ we get

$$x_{t+1} = \tilde{r}x_t(1 - x_t)$$

which means that it is one-parameter model. We write r instead \tilde{r} , for simplicity. Therefore, we study the sequence

$$x_{n+1} = rx_n(1 - x_n) \tag{6}$$

which is the well-known discrete logistic equation. Our sequence is the iteration of the function $F(x) = rx(1 - x)$. From the biological point of view we want to have $x_n \geq 0$ for every n . It is obvious that if $x_0 = 0$ or $x_0 = 1$, then $x_n = 0$ for every $n \geq 1$. Let $x \in [0, 1]$ and we are looking for parameter values such that $F(x) \in [0, 1]$. $F(x)$ is a parabola with zeros at $x = 0$ and $x = 1$ and maximum at $x = \frac{1}{2}$. The maximal value is $F(\frac{1}{2}) = \frac{r}{4}$. Hence, if $0 \leq r \leq 4$, then $F(x) \leq 1$ for $x \in [0, 1]$. On the other hand, the parameter r should describe the birth process, as in the continuous case. This implies

$r > 1$. From the mathematical point of view it is not necessary. Finally, the domain for the model is $[0, 1]$ and the parameter $r \in [0, 4]$. It is an example of the unit interval iteration.

For $r \in [0, 1]$, Eq.(6) describes the death process combined with the competition process so, we expect the extinction of the population. We prove it using known methods.

Analysis of the model we start from finding constant solutions. Hence, $x_{n+1} = x_n$, i.e. $x = F(x)$ (in the discrete case the constant solution is the constant point of the right-hand side of equation). For the logistic equation we have $x = rx(1 - x)$. This implies $x = 0$ or $1 = r(1 - x)$, i.e. $\bar{x} = \frac{r-1}{r}$. The solution \bar{x} is interesting for us when $\bar{x} > 0$ (it is always less than 1) which implies $r > 1$.

Therefore, for $r \in [0, 1]$ we have only one constant solution $x = 0$. For $r \in (1, 4]$ we have two constant solutions — $x = 0$ and $\bar{x} = \frac{r-1}{r}$.

Other interesting solutions are periodic solutions (or cycles). The solution (x_n) is periodic with the period $m \geq 1$ (we assume that constant solution is periodic with the period equal to 1) if $x_{n+m} = x_n$ for every $n \in \mathbf{N}$ and $x_{n+k} \neq x_n$ for $k < m$. Such a periodic solution we can express as the set $S = \{x_0, \dots, x_{m-1}\}$. If the cycle S attracts solutions from some neighbourhood of it, then we call it attractive or stable cycle. S is called repulsive (or unstable) if in any neighbourhood we can find a solution that is far from our cycle. The precise definition we will write later.

In the case of differentiable function F there is an easy method of checking stability of the cycle S . We calculate so-called multiplier of the cycle S , i.e.,

$$\mu(S) = F'(x_0) \cdots F'(x_{m-1}),$$

that is the product of derivatives at all the points $x_i \in S$.

If $|\mu(S)| < 1$, then the cycle is stable, if $|\mu(S)| > 1$, then the cycle is unstable. The case $|\mu(S)| = 1$ must be studied for every model separately. If S is a constant solution, i.e. $S = \{x_0\}$, then $\mu(x_0)$ is simply the derivative of F at this point. If S is a cycle of a period m , then each of the points from S is a constant solution for F^m , i.e. $F^m(x_i) = x_i$, $i = 0, \dots, m-1$. Studying stability of X_i as a constant solution of F^m we check the derivative $\left. \frac{d}{dx} F^m(x) \right|_{x_i}$. The iterations of F are defined recurrently, i.e. $F^m(x) = F(F^{(m-1)}(x))$. Calculating the derivative we obtain $\frac{d}{dx} (F^m(x)) = F'(F^{(m-1)}(x)) \frac{d}{dx} (F^{(m-1)}(x))$.

Finally,

$$\frac{d}{dx} (F^m(x)) = F' (F^{(m-1)}(x)) \cdot F' (F^{(m-2)}(x)) \cdots F'(F(x)) \cdot F'(x).$$

For our cycle we have $F(x_i) = x_{i+1}$, $F(x_{i+1}) = x_{i+2} = F^2(x_i)$ and so on. Therefore, the multiplier of S is equal to the product of the derivatives at each of the points from S .

Now, we calculate the derivative $F'(x) = r(1 - 2x)$. For our constant solutions we have $F'(0) = r$ and $F'(\frac{r-1}{r}) = 2 - r$.

Hence,

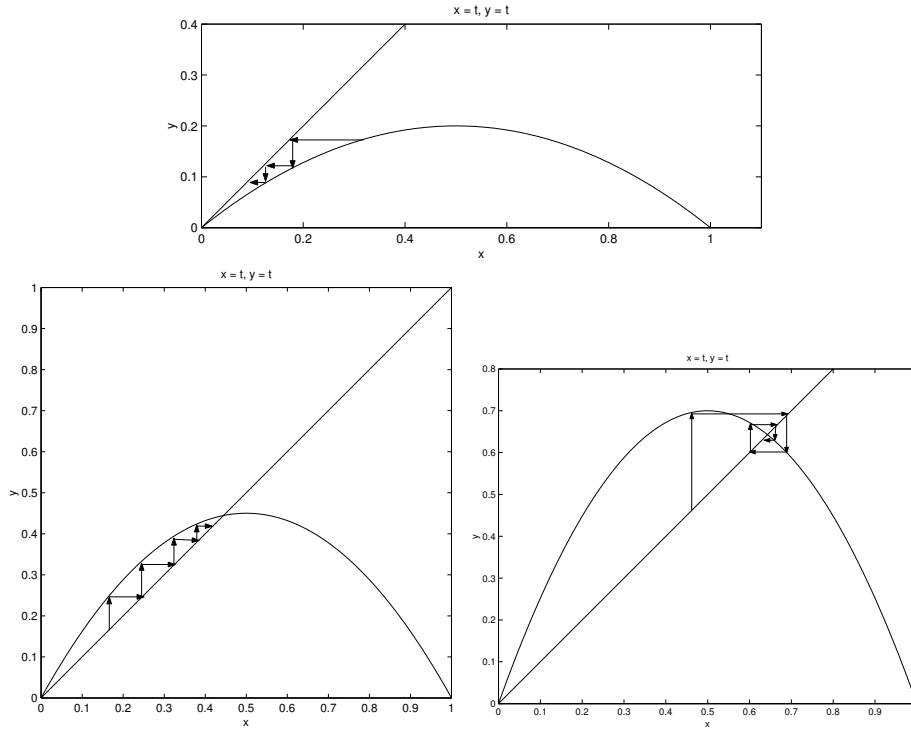
$F'(0) \in [0, 1)$ for $r \in [0, 1)$, i.e. the constant solution 0 is attractive,

$F'(0) > 1$ for $r > 1$ and then 0 is repulsive,

$F'(\bar{x}) > 1$ for $r \in [0, 1)$ and then \bar{x} is repulsive,

$F'(\bar{x}) \in (1, -1)$ for $r \in (1, 3)$ and then \bar{x} is attractive,

$F'(\bar{x}) < -1$ for $r > 3$ and then \bar{x} is repulsive.



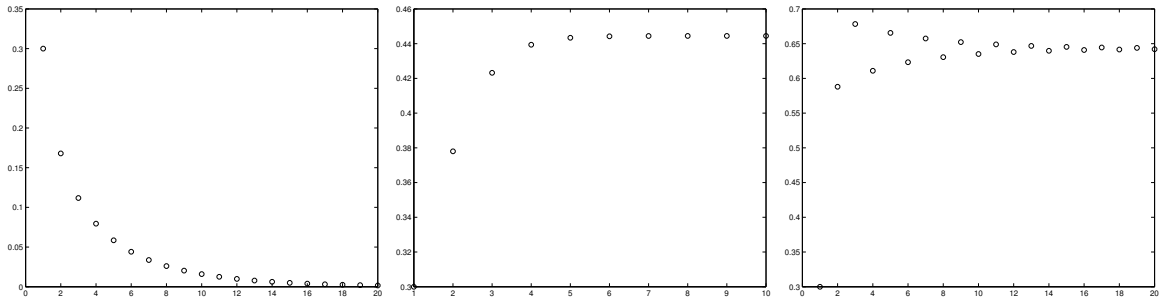
Phase portraits for Eq.(6) and different values of parameter r :
 $r < 1$ at the top, $r \in (1, 2)$ at the left and $r \in (2, 3)$ at the right.

Now, we know local stability of existing constant solutions (except the

points where $|F'| = 1$). The next step of analysis is to study global stability. The differences between local and global stability (attractivity) is the following — "local" attractivity concerns some neighbourhood of attractive solution while "global" attractivity concerns all solutions to the model, all of them are attracted by such a solution.

Assume that $r \in (0, 1]$ (the case $r = 0$ is trivial). We show that our sequence (x_n) is decreasing for $x_0 \in (0, 1)$. Hence, we want to show that $x_{n+1} < x_n$, i.e. $rx_n(1 - x_n) < x_n$. Due to positivity of x_n the last inequality is equivalent to $r(1 - x_n) < 1$ and finally, to $x_n > \frac{r-1}{r}$ which is true because $\frac{r-1}{r} \leq 0 < x_n$. This implies that $x = 0$ is globally stable.

Similarly, we show that \bar{x} is globally stable, either monotone or oscillating, for appropriate r .



Solutions to Eq.(6) for values of r corresponding to phase portraits above.

It occurs that the magnitude of μ can tell us not only about stability of periodic solution but also about monotonicity of other solutions that are attracted by it. For the constant solution, if $\mu > 0$, then the convergence is monotonic (starting from some $t \geq 0$) while for $\mu < 0$ we have monotonic subsequences that oscillate around attractive solution. Therefore, if $r \in (1, 2)$, then the convergence to \bar{x} is monotonic and if $r \in (2, 3)$, then the solutions oscillates around \bar{x} .

At $r = 3$ the solution \bar{x} loses stability. Now, there appears the periodic solution (cycle) $\bar{\bar{x}}$ with the period equal to 2 which is stable. Such a type of behaviour is called doubling period bifurcation. "Bifurcation" always means that there is a qualitative change of the solution's behaviour. Here, from the constant solution (with period 1) we obtain the periodic solution with period 2. This bifurcation occurs due to the changes of the graph of $F^2(x)$. For $r \leq 3$ this graph intersects the line $y = x$ (in $x - y$ co-ordinates) in the same points as $F(x)$, i.e. $x = 0$ and $x = \bar{x}$. For $r > 3$ there appear two new points of intersection that create the periodic solution.

We calculate our cycle as a constant solution for F^2 which is different from $x = 0$ and $x = \bar{x}$. We have

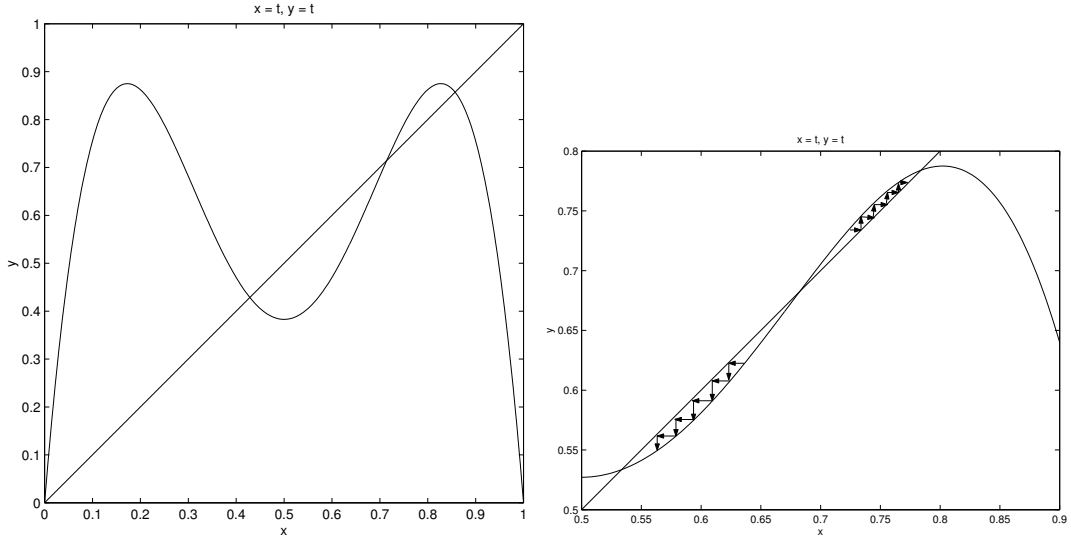
$$F^2(x) = F(rx(1-x)) = r(rx(1-x))(1-rx(1-x)) = r^2x(1-x)(1-rx+rx^2).$$

We are looking for constant solutions and hence,

$$x = r^2x(1-x)(1-rx+rx^2).$$

We are interested in $x \neq 0$. Therefore,

$$W(x) = r^3x^3 - 2r^3x^2 + r^2(r+1)x + 1 - r^2 = 0.$$



Phase portraits for Eq.(6) and $r > 3$.

We know that $\bar{x} = \frac{r-1}{r}$ is the zero of $W(x)$. Hence, we divide $W(x)$ by $x - \bar{x}$ to obtain

$$r^3x^2 - r^2(r+1)x + r(r+1) = 0.$$

Now, we can easily find zeros of the quadratic equation above. We have

$$\Delta = r^4(r+1)^2 - 4r^4(r+1) = r^4(r+1)(r-3) = r^4(r^2 - 2r - 3)$$

and hence

$$\bar{x}^1 = \frac{r+1 - \sqrt{\Delta_1}}{2r}, \quad \bar{x}^2 = \frac{r+1 + \sqrt{\Delta_1}}{2r}, \quad \text{where } \Delta_1 = r^2 - 2r - 3.$$

The set $\bar{x} = \{\bar{x}^1, \bar{x}^2\}$ forms our periodic orbit.

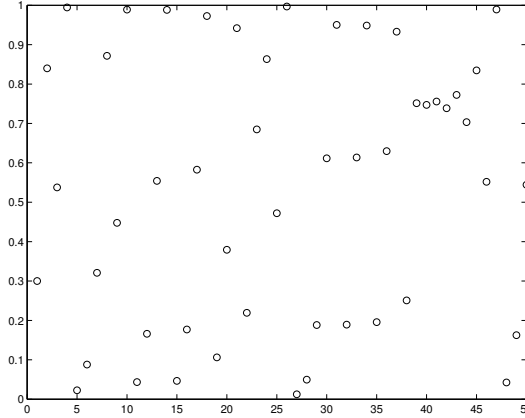
For our cycle the multiplier is equal to

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

Hence, $|\mu| < 1$ for $r \in (3, 1 + \sqrt{6})$.

In the case of periodic solution with the period 2 the magnitude of its multiplier implies that if $\mu > 0$, then the subsequences $(F^{2n}(x_0))$ and $(F^{2n+1}(x_0))$ are monotone starting from some n , one of them is increasing and the second one is decreasing. We can show that $\mu > 0$ for $r \in (3, 1 + \sqrt{5})$. If $\mu < 0$, then both of these subsequences oscillate around \bar{x}^1 and \bar{x}^2 such that the subsequences $(F^{4n}(x_0))$, $(F^{4n+1}(x_0))$, $(F^{4n+2}(x_0))$ and $(F^{4n+3}(x_0))$ are monotone.

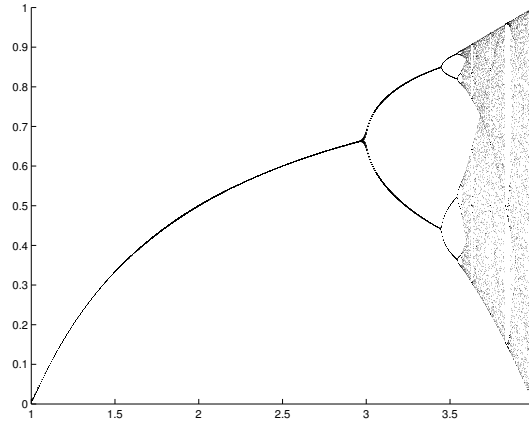
When r crosses $1 + \sqrt{6}$, the next bifurcation appears. It is the same type of bifurcation — instead of the cycle with period 2 we obtain the cycle of period 4, and so on. We do not study all bifurcations in details. There appear successively periodic orbits with periods 2^k , $3 \cdot 2^k$, $5 \cdot 2^k, \dots$, $k \in \mathbf{N}$, and finally $\dots, 7, 5, 3$ (i.e. odd numbers). The last period that appears is 3. The successive periods are connected with the so-called Sharkovski order. The first number in this order is 3. One of the consequences of the Sharkovski order is that if the function $f : [0, 1] \rightarrow [0, 1]$ has a point with the period 3 (i.e. $f^3(x) = x$ and $f(x) \neq x$, $f^2(x) \neq x$), then it has points with all periods.



Solution to Eq.(6) for $r = 4$.

For every discrete dynamical system with some parameter that can be changed we can draw so-called bifurcation diagram. This is a graph of attractive solutions depending on the parameter. For the logistic equation this

bifurcation diagram has a very interesting shape. It is a fractal. The main characteristic of fractals is a property of self-congruency. Every small piece of this diagram is the same as the whole one. It is known as the Figenbaum tree.



Figenbaum tree.

For $r = 4$ it can be shown that the behaviour of solutions to Eq.(6) is chaotic. There are many concepts of chaos. One of the most popular is those proposed by Devaney. He said that the function $f : X \rightarrow X$ (where X is the metric space with the distance function d) is chaotic when it has three properties:

- 1) topological transitivity (for every non-empty open sets $U, V \subset X$ there exists $n \in \mathbf{N}$ such that $f^n(U) \cap V \neq \emptyset$),
- 2) density of periodic points (for every $x \in X$ and its neighbourhood U_x there exists a periodic point of f that lies in U_x),
- 3) sensitivity for initial data (there exists $\delta > 0$ such that for every $x \in X$ and its neighbourhood U_x there are $y \in U_x$ and $n \geq 0$ that the inequality $d(f^n(x), f^n(y)) > \delta$ is satisfied).

This concept of chaos is called deterministic (because it is generated by deterministic equation). It occurs that in one-dimensional case where the domain of f is some interval (e.g. $[0, 1]$) the only important property is the first one. If $f : [0, 1] \rightarrow [0, 1]$ is topologically transitive, then it has dense periodic points and is sensitive for initial data. Topological transitivity (two sets lying far one from the other initially are joined by some points after some iterations) and sensitivity for initial data (points lying in a very small distance initially are far away after some iterations) measure (in some sense) irregularity of f while density of periodic solutions shows that for a large

number of points the behaviour is regular.

Coming back to the logistic function $F(x) = 4x(1 - x)$, we study the iterations of

$$G(x) = \begin{cases} 2x & \text{for } x \in \left[0, \frac{1}{2}\right] \\ 2(1 - x) & \text{for } x \in \left(\frac{1}{2}, 1\right] \end{cases} \quad (7)$$

instead of F . The functions F and G are topologically conjugate, i.e. there exists a homeomorphism (a continuous function that has a continuous inverse) $h : [0, 1] \rightarrow [0, 1]$ such that $h \circ F = G \circ h$, i.e. for every $x \in [0, 1]$ the identity $h(F(x)) = G(h(x))$ holds. This homeomorphism is $h(x) = \frac{2}{\pi} \arcsin \sqrt{x}$. Therefore, all topological properties of F and G are the same. Topological transitivity is a property of open sets. Every open set can be generated by open intervals and therefore, it is enough to show it for these intervals. The function G has a stronger property — for every open interval $I \in [0, 1]$ there exists $m > 0$ such that $G^m(I) = [0, 1]$. This property is obvious. The function G is extensive (its derivative is equal to 2 when exists, i.e. for $x \neq \frac{1}{2}$). If $\frac{1}{2} \notin I$, then the length of $G(I)$ is a double length of I . If $\frac{1}{2} \in I$, then there exists $\epsilon > 0$ such that $[0, \epsilon] \subset G(I)$. We have $G^m([0, \epsilon]) = [0, 2^m \epsilon]$ for $2^m \epsilon < 1$ and $G^m([0, \epsilon]) = [0, 1]$ for $2^m \epsilon > 1$. This implies topological transitivity of the logistic function F and this means that F is chaotic.

1.3 Exercises

1. Consider the continuous model of birth/death with migration, i.e. the equation

$$\dot{N} = \alpha_c N + \beta.$$

- a) Find a solution for every $N_0 \geq 0$ depending on α_c and β .
- b) Make an analysis of phase portraits depending on α_c and β .
- c) Explain the behaviour of solutions in terms of birth/death rates and the rate of migration.

2. Consider the discrete model of birth/death with migration, i.e. the equation

$$N_{t+1} = \alpha_d N_t + \beta.$$

- a) Find a general term of this sequence for every $N_0 \geq 0$ depending on α_d and β .
- b) Make an analysis of the behaviour of the sequence depending on α_d and β .

c) Explain the behaviour of the sequence in terms of birth/death rates and the rate of migration.

3. Compare the behaviour of solutions to the models analysed in 1 and 2.

4. Consider the discrete logistic equation, i.e.,

$$x_{n+1} = rx_n(1 - x_n).$$

a) Show that the constant solution $\bar{x} = \frac{r-1}{r}$ is globally stable (all solutions are either monotone or oscillate around \bar{x}) for $r \in [1, 3]$.

b) Find a cycle with period 2 and show that it is globally stable (the appropriate subsequences are monotone or oscillating) for appropriate $r > 3$.

c) Show that $h(x) = \frac{2}{\pi} \arcsin \sqrt{x}$ conjugates the logistic function $F(x) = 4x(1 - x)$ and $G(x) = 2x$ for $x \in [0, \frac{1}{2}]$. Explain why $G(x) = 2(1 - x)$ for $x \in (0, \frac{1}{2}]$.

2 Analysis of two-dimensional models on the background of the Poincare-Bendixon theorem.

At the beginning we study a system of two linear ODEs. It is necessary to understand the behaviour of non-linear systems that are of our main interest.

2.1 Linear two-dimensional systems.

In this subsection we focus on the analysis of linear systems of two ODEs. Such a system reads as

$$\begin{cases} \dot{x} &= ax + by \\ \dot{y} &= cx + dy \end{cases} \quad (8)$$

Not every system of the form above can have biological interpretation. One of such interpretations is the following — let x, y denote the density of immature and mature individuals of some species, respectively. Only mature individuals can reproduce. Therefore, the density of new born immature individuals is proportional to the number of mature individuals with the reproduction coefficient $b > 0$. Immature individuals mature with some coefficient of maturation $c > 0$. Individuals in both stages die. The death coefficients for mature individuals is $d < 0$ and for immature ones — $a + c \leq 0$.

The coefficient $a < 0$ describes the whole fraction of immature population that leaves this stage either due to maturation or due to death.

From the mathematical point of view we are interested in all cases of Eqs.(8), for every $a, b, c, d \in \mathbf{R}$. It occurs that in linear case the unique solution exists for every t . Looking for solutions to our system Eqs.(8) we should remember that the linearity of equations is transferred to solutions. Precisely, if $(x_1(t), y_1(t))$ and $(x_2(t), y_2(t))$ are solutions, then $x_1 + \alpha x_2, y_1 + \alpha y_2$ is also a solution for every $\alpha \in \mathbf{R}$. In fact,

$$\begin{aligned} \dot{x}_1 + \alpha \dot{x}_2 &= ax_1 + by_1 + \alpha ax_1 + \alpha by_2 = \\ &= a(x_1 + \alpha x_2) + b(y_1 + \alpha y_2) \end{aligned}$$

and similarly for the second co-ordinate of the new solution.

Therefore, solutions form a linear space. The dimension of this space is the same as the dimension of the system. Hence, for Eqs.(8) this dimension is equal to 2. To define the space of solutions we need to find two linearly independent solutions to our system. Assume that this solutions are exponential. Finally, we are looking for $(x(t), y(t)) = (x_0 e^{\lambda t}, y_0 e^{\lambda t})$ with two different values $\lambda_1 \neq \lambda_2$. Clearly, if $\lambda_1 \neq \lambda_2$, then these exponential functions are linearly independent. We check it now. Let $Ae^{\lambda_1 t} + Be^{\lambda_2 t} \equiv 0$. Choosing $t = 0$ and $t = 1$ we get

$$\begin{cases} A + B &= 0 \\ Ae^{\lambda_1} + Be^{\lambda_2} &= 0 \end{cases} .$$

Hence, $-Be^{\lambda_1} + Be^{\lambda_2} = 0$. Dividing by $B \neq 0$ we obtain $e^{\lambda_1} = e^{\lambda_2}$ which contradicts the assumption. This shows that $A = B = 0$ and $e^{\lambda_1 t}, e^{\lambda_2 t}$ are linearly independent.

Looking for exponential solutions to Eqs.(8)we obtain

$$\begin{cases} \lambda x_0 e^{\lambda t} &= ax_0 e^{\lambda t} + by_0 e^{\lambda t} \\ \lambda y_0 e^{\lambda t} &= cx_0 e^{\lambda t} + dy_0 e^{\lambda t} \end{cases} ,$$

i.e.,

$$\begin{cases} 0 &= x_0(a - \lambda) + by_0 \\ 0 &= cx_0 + y_0(d - \lambda) \end{cases} .$$

To have a non-trivial solution to the system above in the case of non-degenerated matrix $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ we need the degeneration of $\begin{pmatrix} a - \lambda & b \\ c & d - \lambda \end{pmatrix}$, i.e. $(a - \lambda)(d - \lambda) - bc = 0$.

In general case, the behaviour of solutions depends on the properties of the so-called Jacobi matrix. Let $F(x, y)$ denotes the right-hand side of Eqs.(8), i.e. $F = (F_1, F_2)$ with

$$F_1(x, y) = (ax, by), \quad F_2(x, y) = (cx, dy).$$

We calculate partial derivatives of F_1 and F_2 and form the matrix

$$dF(x, y) = \left(\begin{array}{cc} \frac{\partial F_1}{\partial x} & \frac{\partial F_1}{\partial y} \\ \frac{\partial F_2}{\partial x} & \frac{\partial F_2}{\partial y} \end{array} \right) \Big|_{(x,y)},$$

that is

$$dF(x, y) = \left(\begin{array}{cc} a & b \\ c & d \end{array} \right)$$

in our linear case. The matrix $dF(x, y)$ is called the Jacobi matrix of the function F (the system defined by the function F). In the case of two or more dimensional systems, the Jacobi matrix represents the derivative which is a linear operator (from linear algebra we know that every linear operator can be represented by a matrix and every matrix defines a linear operator).

In the case of non-degenerated Jacobi matrix we see that Eqs.(8) have only one critical point $(0, 0)$. If the system is non-homogenous, i.e.,

$$\begin{cases} \dot{x} = ax + by + \alpha \\ \dot{y} = cx + dy + \beta \end{cases},$$

then having another critical point (\bar{x}, \bar{y}) (i.e. $a\bar{x} + b\bar{y} + \alpha = 0$ and $c\bar{x} + d\bar{y} + \beta = 0$) we can translate the system such that $(0, 0)$ is the critical point for the new system. Namely, substituting $v = x - \bar{x}$ and $w = y - \bar{y}$ we obtain $\dot{v} = \dot{x} = a(v + \bar{x}) + b(w + \bar{y}) + \alpha = av + bw$, and similarly for \dot{w} . Hence, the new system is homogenous and $(0, 0)$ is the critical point. The behaviour of the system strongly depends on the character of the critical point. The definitions of stability and instability of constant solution are exactly the same as in the case of solutions to discrete dynamical systems. To check it we should calculate so-called characteristic polynomial for the system which is equal to the following determinant

$$\det(dF(0, 0) - \lambda \mathbf{I}),$$

where \mathbf{I} is the identity matrix. More precisely, if $W(\lambda)$ denotes the characteristic polynomial, then

$$W(\lambda) = \lambda^2 - (a + d)\lambda + ad - bc.$$

Hence, $W(\lambda) = \lambda^2 - \text{tr } dF \cdot \lambda + \det dF$, where $\det dF$ denotes the determinant of Jacobi matrix at the critical point (notice that for a linear case it does not depend on this point, the matrix is constant), and $\text{tr } dF$ denotes its trace.

The characteristic equation $W(\lambda) = 0$ has two complex zeros. This characteristic polynomial $W(\lambda)$ is exactly the same as this one obtained in calculation of solutions of exponential form. Zeros of this polynomial are characteristic values of the Jacobi matrix dF . Knowing the characteristic values we can simplify our system such that the right-hand side is generated by the matrix in so-called canonical form. This form depends on the characteristic values and characteristic vectors. Let λ_i , $i = 1, 2$, denotes characteristic values. Then a vector $v_i = \begin{bmatrix} v_i^1 \\ v_i^2 \end{bmatrix}$ is called the characteristic vector for the value λ_i , if $dF \cdot v_i = \lambda_i v_i$.

From now on, we focus on the systems with the simplest right-hand side in the canonical form.

1) Case $\lambda_i \in \mathbf{R}$ and $\lambda_1 \neq \lambda_2 \neq 0$ (two real different non-zero characteristic values). Eqs.(8) can be reduced to

$$\begin{cases} \dot{x} = \lambda_1 x \\ \dot{y} = \lambda_2 y \end{cases}, \quad (9)$$

with the solutions $x(t) = c_1 e^{\lambda_1 t}$, $y(t) = c_2 e^{\lambda_2 t}$. It is easy to see that if both $\lambda_i < 0$, then $(0, 0)$ attracts all solutions, while for $\lambda_i > 0$ it is repulsive. In this case the two linearly independent solutions that generate the space of solutions are of the simpler form $(0, e^{\lambda_2 t})$ and $(e^{\lambda_1 t}, 0)$. We can compare the behaviour of solutions for different λ_i in the phase portrait. It is a graph of the dependence between x and y where the dependence on the main variable t is implicitly described by the arrows which shows the direction of dynamics with increasing t . The curves that describes such a dependence in (x, y) coordinates are called orbits of the system. Due to uniqueness of solutions two orbits cannot intersect.

Hence, we are interested in the curves that create orbits in \mathbf{R}^2 . Calculating it we divide the first equation of Eqs.(9) by the second one and obtain

$$\frac{dx}{dy} = \frac{\lambda_1 x}{\lambda_2 y}, \text{ for } y \neq 0,$$

that can be solve using the separation of variables. Namely,

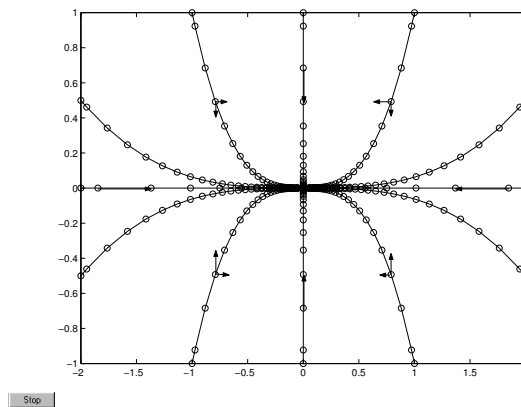
$$\lambda_2 \int \frac{dx}{x} = \lambda_1 \int \frac{dy}{y}, \quad x, y \neq 0,$$

and finally,

$$y = Cx^{\frac{\lambda_2}{\lambda_1}},$$

except the orbits for which $x \equiv 0$ or $y \equiv 0$. For $x \equiv 0$ we have the solution $(0, e^{\lambda_2 t})$, that means that y -axis forms orbits, while for $y \equiv 0$ we have $(e^{\lambda_1 t}, 0)$ and hence, x -axis forms orbits. The shape of other orbits depends on the sign and magnitude of characteristic values.

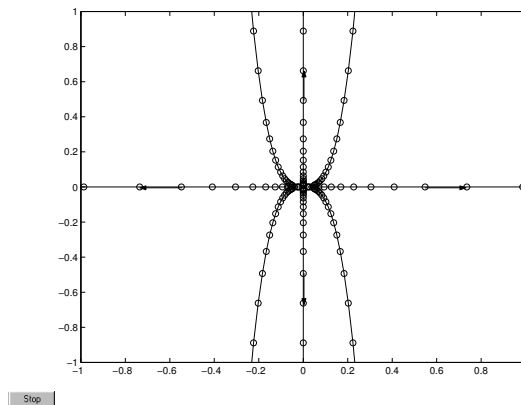
a) $\lambda_2 < \lambda_1 < 0$. The shape of orbits is parabolic, i.e. similar to the curves $y = \pm x^2$. Every solution tends to 0 as $t \rightarrow +\infty$. The origin $(0, 0)$ is called a stable node.



Phase portrait for negative characteristic values.

b) $\lambda_1 < \lambda_2 < 0$. The shape of orbits is similar to the curves $y = \pm|x|^{\frac{1}{2}}$. Every solution tends to 0 as $t \rightarrow +\infty$. The origin $(0, 0)$ is also a stable node. The phase portraits is rotated of 90 deg in comparison to Case a).

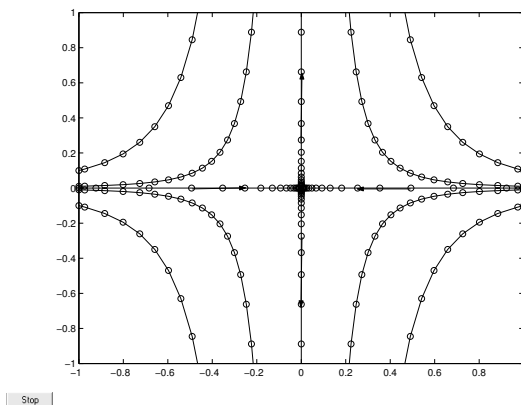
c) $\lambda_2 > \lambda_1 > 0$. The shape of orbit is the same as in Case a) but every solution is repelled from the origin. It is called an unstable node.



Phase portrait for positive characteristic values.

d) $\lambda_1 > \lambda_2 > 0$. The dependence between Cases c) and d) is exactly the same as for a) and b).

e) $\lambda_1 < 0 < \lambda_2$. The shape of orbits is hyperbolic, i.e. similar to the curves $y = \pm \frac{1}{x}$. In the x direction the solution is attracted by the origin, while in the y direction it is repelled. The origin is called a saddle. We have also two special orbits. If $y_0 = 0$, then $y(t) = 0$ for every t and $x(t) = x_0 e^{\lambda_1 t}$. Therefore, this orbit is the straight line $y = 0$ with the arrows directed into the origin. Similarly, if $x_0 = 0$, then the orbit is the straight line $x = 0$ with the arrows directed outside the origin. These lines are so-called stable and unstable manifolds, respectively (in more dimensional case we have subspaces that are attracted or repelled from the saddle that forms these manifolds).



Phase portrait for one negative and one positive characteristic values.

f) $\lambda_2 < 0 < \lambda_1$. The shape is the same as in Case e). The only difference is that x and y replace its role.

2) Case $\lambda_i \in \mathbf{R}$ and $\lambda_1 = \lambda_2 \neq 0$. If there exist two linearly independent characteristic vectors, then Eqs.(8) reduces to

$$\begin{cases} \dot{x} = \lambda_1 x \\ \dot{y} = \lambda_1 y \end{cases}, \quad (10)$$

while for only one characteristic vector we have

$$\begin{cases} \dot{x} = \lambda_1 x \\ \dot{y} = x + \lambda_1 y \end{cases}. \quad (11)$$

It is obvious that orbits for Eqs.(10) are straight lines. If $\lambda_1 < 0$, then the

origin attracts all solutions. If $\lambda_1 > 0$, then it is repulsive. It is called a star-like node.

For Eqs.(11) the solutions are equal to $x(t) = c_1 e^{\lambda_1 t}$, $y(t) = (c_2 + c_1 t) e^{\lambda_1 t}$. Calculating orbits we obtain the following ODE

$$\frac{dy}{dx} = \frac{1}{\lambda_1} + \frac{y}{x}.$$

Substituting $z = \frac{y}{x}$ we get

$$\frac{dz}{dx} = \frac{x \frac{dy}{dx} - y}{x^2}$$

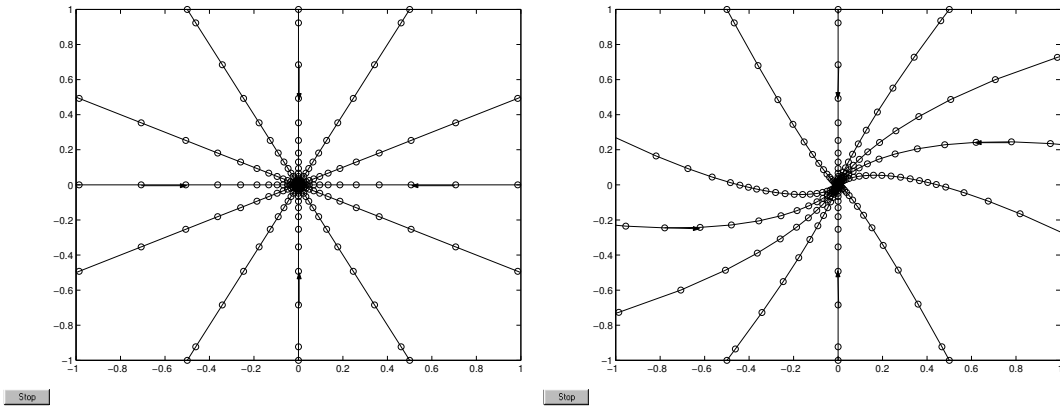
which yields

$$x \frac{dz}{dx} = \frac{dy}{dx} - z$$

and therefore,

$$x \frac{dz}{dx} = \frac{1}{\lambda_1}.$$

Hence, $\lambda_1 z + C = \ln|x|$ and finally, $y = x \left(c + \frac{1}{\lambda_1} \ln|x| \right)$. It occurs that these curves achieves its extremal values on the straight line $y = -\frac{1}{\lambda_1} x$. The origin is called degenerated node and is stable for $\lambda_1 < 0$ and unstable for the inverse inequality.



Phase portraits for negative identical characteristic values.

3) Case $\lambda_i \in \mathbf{C}$. Then $\lambda_1 = \bar{\lambda}_2$, i.e. the characteristic values are conjugate. Let $\lambda_1 = \alpha + i\beta$, where i is the imaginary unit and α, β are real and imaginary part of the characteristic values, respectively, with $\beta > 0$. Eqs.(8) can be

reduced to the following one

$$\begin{cases} \dot{x} = \alpha x - \beta y \\ \dot{y} = \beta x + \alpha y \end{cases} \quad (12)$$

We can solve Eqs.(12) using polar co-ordinates

$$x = r \cos \theta, \quad y = r \sin \theta.$$

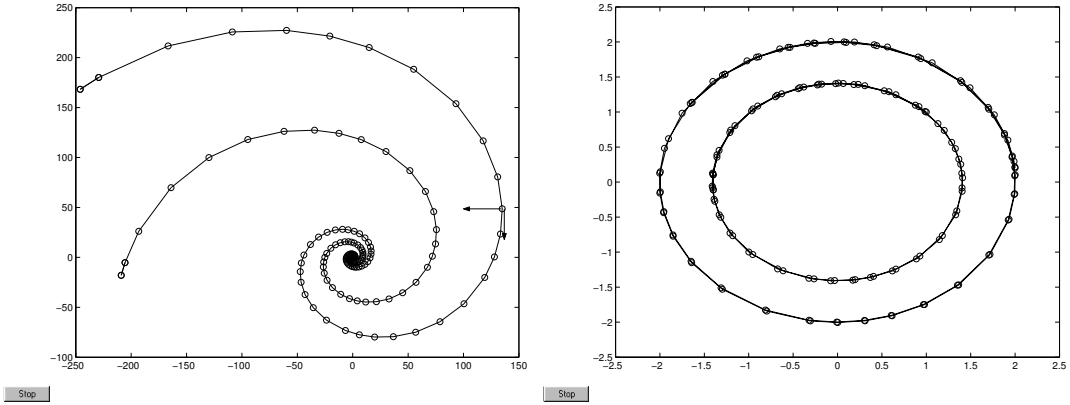
For these co-ordinates

$$\begin{cases} \dot{x} = \dot{r} \cos \theta - r \dot{\theta} \sin \theta = \alpha r \cos \theta - \beta r \sin \theta \\ \dot{y} = \dot{r} \sin \theta + r \dot{\theta} \cos \theta = \beta r \cos \theta + \alpha r \sin \theta \end{cases}.$$

Multiplying the above equations by $\cos \theta$ and $\sin \theta$, respectively we get

$$\begin{cases} \dot{r} = \alpha r \\ \dot{\theta} = \beta \end{cases},$$

with the solution $r(t) = r_0 e^{\alpha t}$, $\theta = \theta_0 + \beta t$ and orbits described by $r = C e^{\alpha \theta}$. The obtained curves encircle the origin. If $\alpha \neq 0$, then they are spirals. The origin is called a focus in this case. It is stable for $\alpha < 0$ and unstable for $\alpha > 0$. If $\alpha = 0$, then $r = \text{const}$ and orbits form circles. The origin is called a centre. In this case the origin is neither attractive nor repulsive. It is stable but in Lapunov sense (we will define it later). In this case the space of solutions is generated by $(r_0 e^{\alpha t} \cos(\theta_0 + \beta t), 0)$ and $(0, r_0 e^{\alpha t} \sin(\theta_0 + \beta t))$.



Phase portraits for complex characteristic values.

4) At least one characteristic value is equal to 0 — this case is not interesting from our point of view (we are not able to tell anything for such a system in a non-linear case).

2.2 Non-linear models.

Our study of non-linear systems we start with the description of some examples of two-dimensional continuous dynamical systems well known in biological applications. The first model is also the oldest one. It is known as Lotka-Volterra prey-predator model. It describes coexistence of two species in the environment where one of them is a predator for the second one. The same situation describes the May model. These two systems of ODE differ in the right-hand side of equations and this implies differences in the dynamics. Another situation is described by the system of competing species. We have two (or more) species that compete for the same food or other environmental resources.

1. Lotka-Volterra model. Let $V(t)$, $P(t)$ denote the density of prey and predator species, respectively. In the absence of predators, the environment is favourable for preys and this species is governed by the birth process, i.e. $\dot{V}(t) = rV(t)$, with the reproduction coefficient $r > 0$. Conversely, if there are no preys, then predators have no food and hence, they die which is described by the death process $\dot{P}(t) = -sP(t)$, with the death coefficient $s > 0$. When a predator meets a prey, then it may hunt and have a food which gives energy for life and reproduction. The number of prey-predator encounters is proportional to $V(t)P(t)$ (because it is assumed that these meetings are random). Hence, the model reads as

$$\begin{cases} \dot{V}(t) &= rV(t) - aV(t)P(t) \\ \dot{P}(t) &= -sP(t) + abV(t)P(t) \end{cases}, \quad (13)$$

where $a > 0$ is the coefficient of hunting effectiveness and $b > 0$ is the conversion coefficient (it describes how much energy one predator spends for reproduction). From the biological point of view the inequalities $a, b < 1$ should be satisfied but mathematical analysis does not depend on the magnitude of these coefficients and therefore, we do not assume additional inequalities except of positivity of all coefficients.

We also consider another prey-predator model where we assume that the environment for preys is bounded and then this species is governed by the logistic equation, i.e.,

$$\begin{cases} \dot{V}(t) &= rV(t) \left(1 - \frac{V(t)}{K}\right) - aV(t)P(t) \\ \dot{P}(t) &= -sP(t) + abV(t)P(t) \end{cases}, \quad (14)$$

where K is the carrying capacity for preys.

2. May model. We use the same notation as in the Lotka-Volterra model. In the May model it is assumed that the dynamics of both prey and predator species is governed by the logistic equation with constant carrying capacity for preys and prey-dependent carrying capacity for predators. It is also assumed that one predator cannot hunt and eat infinitely many preys that is described by so-called Michaelis-Menten function. Therefore,

$$\begin{cases} \dot{V}(t) &= r_1 V(t) \left(1 - \frac{V(t)}{K_1}\right) - a \frac{V(t)P(t)}{1+aV(t)} \\ \dot{P}(t) &= r_2 P(t) \left(1 - \frac{P(t)}{K_2 V(t)}\right) \end{cases}, \quad (15)$$

where r_1, r_2 are reproduction coefficients for preys and predators, respectively, K_1 is the carrying capacity for preys, $V(t)K_2$ is the prey-dependent carrying capacity for predators and $\frac{aV(t)}{1+aV(t)}$ is the hunting function of Michaelis-Menten type (here, the hunting function is scaled such that one predator cannot eat more than one prey due to the properties of the hunting function — it increases from 0 to 1 as V increases from 0 to $+\infty$). In the Lotka-Volterra model one predator can eat infinitely many preys (the hunting function is simply $V(t)$ for that model). The May model has not typical structure. Typically, as in the Lotka-Volterra model, the same hunting function appears in both equations.

3. Competition model. Now, we describe the situation when we have two species competing for the same food. Both species are governed by the same law — the logistic equation. The competition function has bilinear form, as in the Lotka-Volterra model — two individuals compete only when they meet and the number of meetings is random. Let $N_1(t)$ and $N_2(t)$ denote the density of the first and the second species, respectively. Hence, the model takes the form

$$\begin{cases} \dot{N}_1(t) &= r_1 N_1(t) \left(1 - \frac{N_1(t)}{K_1} - \alpha_{12} \frac{N_2(t)}{K_2}\right) \\ \dot{N}_2(t) &= r_2 N_2(t) \left(1 - \frac{N_2(t)}{K_2} - \alpha_{21} \frac{N_1(t)}{K_1}\right) \end{cases}, \quad (16)$$

where $r_i > 0$ are net reproduction rates, $K_i > 0$ are carrying capacities and α_{ij} are extra-specific competition coefficients, $i, j = 1, 2, i \neq j$.

In the literature, it can be found that two or more dimensional models with bilinear right-hand side which describes some number of competing

species coupled with prey-predator model are also called Lotka-Volterra (or Volterra-Verhulst) models.

2.2.1 Existence and uniqueness and of solutions.

As we mentioned in the previous Section, if the right-hand side of the model is continuously differentiable, then the solution exists and it is unique. We know that the Jacobi matrix (which is composed with partial derivatives of the right-hand side of ODE system) represents derivative. Therefore, if partial derivatives are continuous, then the whole derivative is continuous. Hence, it is enough to check continuity of partial derivatives.

1. For the Lotka-Volterra model we have the right-hand side of the form

$$F(V, P) = (F_1(V, P), F_2(V, P)),$$

$$F_1(V, P) = V(r - aP), \quad F_2(V, P) = P(abV - s),$$

where F_1 and F_2 are binomials (moreover, the right-hand side is bilinear, i.e. it is linear as a function of each of its both variables, separately). Hence, both these functions are defined over the whole space \mathbf{R}^2 . Due to the biological interpretation we are interested only in the first quarter $[0, +\infty)^2$.

Partial derivatives can be calculated as

$$\frac{\partial F_1}{\partial V} = r - aP, \quad \frac{\partial F_1}{\partial P} = -aV,$$

$$\frac{\partial F_2}{\partial V} = abP, \quad \frac{\partial F_2}{\partial P} = abV - s,$$

and the Jacobi matrix is

$$dF(V, P) = \begin{pmatrix} r - aP & -aV \\ abP & abV - s \end{pmatrix}.$$

These partial derivatives are linear and therefore, continuous in the whole space, obviously. Thus, for every initial $(V_0, P_0) \in [0, +\infty)^2$ there exists unique solution to Eqs.(13).

For the system with carrying capacity for preys, i.e. Eqs.(14) the only difference is that $F_1(V, P) = V \left(r - \frac{V}{K} - aP \right)$. The new F_1 is also a binomial and it has linear partial derivatives, where $\frac{\partial F_1}{\partial V} = r - 2\frac{V}{K} - aP$ and the second

partial derivative is the same as in the previous case. Hence, we have also existence and uniqueness of solutions.

2. In the case of the May model the situation is slightly different because the right-hand side of the model is not defined in the whole \mathbf{R}^2 . Let denote $G(V, P) = (G_1(V, P), G_2(V, P))$ with

$$G_1(V, P) = r_1 V \left(1 - \frac{V}{K_1} \right) - a \frac{VP}{1 + aV}, \quad G_2(V, P) = r_2 P \left(1 - \frac{P}{K_2 V} \right).$$

As the domain of G we take $(0, +\infty) \times [0, +\infty)$ (but it is defined for every (V, P) such that $V \neq 0$ and $V \neq -\frac{1}{a}$).

The Jacobi matrix for Eqs.(15) is equal to

$$dG(V, P) = \begin{pmatrix} r_1 \left(1 - \frac{2V}{K_1} \right) - \frac{aP}{(1+aV)^2} & -\frac{aV}{1+aV} \\ \frac{r_2 P^2}{K_2 V^2} & r_2 \left(1 - \frac{2P}{K_2 V} \right) \end{pmatrix}.$$

The partial derivatives of G_1 and G_2 are rational functions. Therefore, they are continuous in the regions where they are defined, i.e. for $(V, P) \in \mathbf{R}^2$ such that $V \neq -\frac{1}{a}$ and $V \neq 0$. Hence, for every initial value (V_0, P_0) such that $V_0 > 0$ and $P_0 \geq 0$ there exists unique solution to Eqs.(15).

3. For the competition model the analysis is exactly the same as for the models above. The right-hand side of the system $H(N_1, N_2) = (H_1, H_2)(N_1, N_2)$ is a binomial with the linear Jacobi matrix

$$dH(V, P) = \begin{pmatrix} r_1 \left(1 - \frac{2N_1}{K_1} - \alpha_{12} \frac{N_2}{K_2} \right) & -\alpha_{12} \frac{r_1 N_1}{K_2} \\ -\alpha_{21} \frac{r_2 N_2}{K_1} & r_2 \left(1 - \frac{2N_2}{K_2} - \alpha_{21} \frac{N_1}{K_1} \right) \end{pmatrix}.$$

Conclusions are also the same, obviously. For every non-negative initial data there exists unique solution to Eqs.(16).

2.2.2 Non-negativity of solutions.

In this subsection we study non-negativity of solution for non-negative initial data. There is no universal method for studying non-negativity of solutions but for many models it can be done in the following way — assuming that the initial data is non-negative we check the behaviour of solutions on the boundary of the region, i.e. for at least one of the variables equal to 0 (we will

use this method later when we will study phase portraits for our systems). Another method is to change the model from ODE to integral form and check non-negativity for it.

1. If $V_0 = P_0 = 0$, then we obtain the constant solution $V = P \equiv 0$. If $V_0 = 0$ and $P_0 > 0$, then $V \equiv 0$ and $P(t) = P_0 e^{-st} > 0$ is the solution and similarly, if $P_0 = 0$ and $V_0 > 0$, then $P \equiv 0$ and $V(t) = V_0 e^{rt} > 0$ is the solution. If $V_0 > 0, P_0 > 0$, then we rewrite Eq.(13) in the following integral form

$$\int_0^t \frac{\dot{V}(\xi)}{V(\xi)} d\xi = \int_0^t (r - aP(\xi)) d\xi,$$

which yields

$$|V(t)| = V_0 e^{\int_0^t (r - aP(\xi)) d\xi}.$$

Now, either $V(t) = V_0 e^{\int_0^t (r - aP(\xi)) d\xi}$ or $V(t) = -V_0 e^{\int_0^t (r - aP(\xi)) d\xi}$. But $V(0) = V_0$ so, $V(t) = V_0 e^{\int_0^t (r - aP(\xi)) d\xi} > 0$ independently on P . Similarly,

$$P(t) = P_0 e^{\int_0^t (abV(\xi) - s) d\xi} > 0,$$

independently on V . Therefore, if the initial data is non-negative, then the solution is non-negative, too. Moreover, if the initial value is positive, then the variable with this initial value is positive.

For the model with carrying capacity for preys we obtain the same under the assumption $V_0, P_0 > 0$ or $V_0 = 0$ and $P_0 > 0$. In the third case, for $V_0 > 0$ and $P_0 = 0$ we have $P \equiv 0$ and $\dot{V} = rV \left(1 - \frac{V}{K}\right)$, i.e. the logistic equation. We know that the solution to the logistic equation is positive for every positive initial value. Therefore, we conclude non-negativity.

2. and **3.** As in **1** we write the models in the integral forms and conclude that for non-negative initial data the solutions are non-negative.

2.3 Existence of solutions for every $t \geq 0$.

To have the dynamical system we need that the solution exists for every $t \geq 0$. Now, we check this property for our models with non-negative initial data.

1. Knowing that the solutions are non-negative we can approximate Eqs.(13) in the following way

$$\begin{cases} \dot{V} = rV - aVP & \leq rV \\ \dot{P} = -sP + abVP & \leq abVP \end{cases} .$$

Hence, for every fixed $\bar{t} > 0$ we have $V(t) \leq V_0 e^{r\bar{t}} := \bar{V}$ and this implies $\dot{P} \leq ab\bar{V}P$. Therefore, $P \leq P_0 e^{ab\bar{V}\bar{t}}$ which means that both variables and its derivatives are bounded at every fixed $t > 0$. It occurs that if the variable and its derivative are bounded for every fixed t , then the solution can be extended forward this point and this implies existence of solutions for every $t \geq 0$ (we will show this later).

The same approximation we have for the system with carrying capacity but for this system we can tell something more. Instead of linear approximation we can use the logistic one, i.e.,

$$\dot{V} \leq rV \left(1 - \frac{V}{K}\right).$$

This shows that the first co-ordinate of solution is not greater than the solution to the logistic equation with the same initial value V_0 . The solution to the logistic equation is always bounded — either by K (if $V_0 < K$) or by V_0 (if $V_0 > K$). Hence, the solution to our equation is also bounded by the same value as the logistic one, namely $V(t) \leq \max\{V_0, K\}$.

2. For the first equation of the May model we can use exactly the same approximation as for $V(t)$ in the Lotka-Volterra model. For the second equation the approximation is even simpler

$$\dot{P} = r_2 P \left(1 - \frac{P}{VK_2}\right) \leq r_2 P.$$

Hence, $P(t) \leq P_0 e^{r_2 t}$ and farther analysis is the same as in the previous case. Now, we can also use the logistic approximation to conclude that both variables are bounded for the May model. We have

$$\dot{V} \leq r_1 V \left(1 - \frac{V}{K_1}\right),$$

which implies $V(t) \leq \max\{V_0, K_1\}$. Let define $A := \max\{V_0, K_1\}$. Then

$$\dot{P} \leq r_2 P \left(1 - \frac{P}{AK_2}\right),$$

which is the logistic approximation with carrying capacity AK_2 . Hence, $P(t) \leq \max\{P_0, AK_2\}$.

3. The approximation is similar to **2**, namely

$$\dot{N}_i \leq r_i N_i \left(1 - \frac{N_i}{K_i}\right) \text{ for } i = 1, 2.$$

Hence, $N_i(t) \leq \max\{N_i(0), K_i\}$, $i = 1, 2$, and therefore, the solution exists and it is bounded for every $t \geq 0$.

2.3.1 Characteristic polynomials and local stability analysis.

In this subsection we study the existence and attractivity of constant solutions. We start from finding such solutions to our models. Let $F(x, y) = (F_1, F_2)(x, y)$ defines the right-hand side of studied system. Then the constant solutions are described by the system of equations

$$\begin{cases} F_1(x, y) = 0 \\ F_2(x, y) = 0 \end{cases}.$$

The single identity $F_i(x, y) = 0$, $i = 1, 2$, describes some curves in the plane. These curves are called null-clines for the i -th variable. Hence, constant solutions lie on the intersection of null-clines for different variables (we will use this terminology in the method of phase portrait).

1. For Eqs.(13) we have

$$\begin{cases} V(r - aP) = 0 \\ P(abV - s) = 0 \end{cases} \quad (17)$$

and hence, $(0, 0)$ and $(\bar{V}, \bar{P}) = \left(\frac{s}{ab}, \frac{r}{a}\right)$ are constant solutions to the Lotka-Volterra model.

For Eqs.(14) the first equation changes to

$$rV \left(1 - \frac{V}{K} - \frac{a}{r}P\right) = 0.$$

Therefore, for $P = 0$ we have either $V = 0$ or $V = K$. This implies that the third constant solution appears. It is equal to $(K, 0)$ which describes the situation in the absence of predators when preys are present in the environment. The second solution changes to

$$(\bar{V}, \bar{P}) = \left(\frac{s}{ab}, \frac{r}{a} \left(1 - \frac{s}{abK}\right)\right)$$

and it is interesting from our point of view only when $K > \frac{s}{ab}$.

2. For Eqs.(15) we obtain

$$\begin{cases} r_1 V \left(1 - \frac{V}{K_1} - \frac{aP}{1+aV} \right) = 0 \\ r_2 P \left(1 - \frac{P}{K_2 V} \right) = 0 \end{cases} \quad (18)$$

and this implies that either $P = 0$ or $P = VK_2$. Therefore, either $V = K_1$ (because $V \neq 0$) or V is the solution to the equation

$$r_1 \left(1 - \frac{V}{K_1} \right) = \frac{aVK_2}{1+aV},$$

i.e.,

$$ar_1 V^2 + (r_1 + aK_1 K_2 - ar_1 K_1)V - r_1 K_1 = 0$$

which has one positive solution $\bar{V} > 0$. Hence, we have two constant solutions $(K_1, 0)$ and $(\bar{V}, K_2 \bar{V})$.

3. Constant solutions to Eqs.(16) are described by the system of equations

$$\begin{cases} r_1 N_1 \left(1 - \frac{N_1}{K_1} - \alpha_{12} \frac{N_2}{K_2} \right) = 0 \\ r_2 N_2 \left(1 - \frac{N_2}{K_2} - \alpha_{21} \frac{N_1}{K_1} \right) = 0 \end{cases}.$$

Hence, we always have three constant solutions — the trivial one $(0, 0)$ and two semi-trivial $(K_1, 0)$, $(0, K_2)$ which describe the absence of one of the considered species. For some parameter values there exists the fourth non-trivial solution

$$(\bar{N}_1, \bar{N}_2) = \left(K_1 \frac{1 - \alpha_{12}}{1 - \alpha_{21} \alpha_{12}}, K_2 \frac{1 - \alpha_{21}}{1 - \alpha_{21} \alpha_{12}} \right).$$

This solution exists only if $\alpha_{ij} < 1$, $i, j = 1, 2$ $i \neq j$, i.e. both extra-specific competition coefficients are small, or $\alpha_{ij} > 1$, $i, j = 1, 2$ $i \neq j$, i.e. both of them are large.

The next step of our analysis is to study stability of the found solutions. Similarly to one-dimensional case, we study the derivative of the right-hand side to check stability. We calculate the characteristic polynomial

$$W(\lambda) = \left(\left(\frac{\partial F_1}{\partial x} - \lambda \right) \left(\frac{\partial F_2}{\partial y} - \lambda \right) - \frac{\partial F_1}{\partial y} \frac{\partial F_2}{\partial x} \right) \Big|_{(\bar{x}, \bar{y})}.$$

Characteristic values of W determine stability of the solution (\bar{x}, \bar{y}) :

1) if λ_i for $i = 1, 2$ are real, then

a) if $\lambda_i < 0$, then the solution is stable (it is a stable node),

b) if one of them is positive, then the solution is unstable (it is a saddle, if the second characteristic value is negative, or an unstable node, if both are positive),

2) if λ_i are complex, then they are conjugate, i.e. $\lambda_i = \Re(\lambda_i) \pm i\Im(\lambda_i)$, where $\Re(\lambda_i)$ is the real part of λ_i , $\Im(\lambda_i)$ is the imaginary part; in this case

a) if $\Re(\lambda_i) < 0$, then the solution is stable (it is a stable focus)

b) if $\Re(\lambda_i) > 0$, then the solution is unstable (it is an unstable focus).

Coming back to our systems, we obtain the following results.

1.

$$W(\lambda) = \det \begin{pmatrix} r - aP - \lambda & -aV \\ abP & abV - s - \lambda \end{pmatrix}$$

and therefore, the characteristic equation has the form

$$W(\lambda) = \lambda^2 - (r - aP + abV - s)\lambda + (r - aP)(abV - s) + a^2bVP = 0.$$

For the trivial solution we have

$$W(\lambda) = (r - \lambda)(-s - \lambda)$$

and therefore, the trivial solution is a saddle (the characteristic values are $r > 0$ and $-s < 0$).

For the non-trivial (\bar{V}, \bar{P}) we obtain

$$W(\lambda) = \lambda^2 + rs.$$

This means that the characteristic values are purely imaginary $\pm\sqrt{rs}$ and then we are not able to tell anything about stability of (\bar{V}, \bar{P}) using this method.

In the case of bounded environment

$$W(\lambda) = \det \begin{pmatrix} r \left(1 - \frac{2V}{K}\right) - aP - \lambda & -aV \\ abP & abV - s - \lambda \end{pmatrix}$$

and therefore, the characteristic equation changes to

$$W(\lambda) = \lambda^2 - \left(r \left(1 - \frac{2V}{K}\right) - aP + abV - s \right) \lambda +$$

$$+ \left(r \left(1 - \frac{2V}{K} \right) - aP \right) (abV - s) + a^2bVP = 0.$$

For the trivial solution we obtain exactly the same as above — it is a saddle.

For the semi-trivial $(K, 0)$ we have the characteristic equation of the form

$$W(\lambda) = (-r - \lambda)(abK - s - \lambda) = 0.$$

Therefore, if $abK - s < 0$, then this solution is stable (a node), while for $abK - s > 0$ it is unstable. This means that stability of semi-trivial solution to Eqs.(14) depends on the magnitude of carrying capacity K — if it is small (i.e. $K < \frac{s}{ab}$), then predators have not enough food and they die. If $K > \frac{s}{ab}$, then there exists non-trivial solution (\bar{V}, \bar{P}) and it occurs that it is stable. Namely

$$W(\lambda) = \lambda^2 + \frac{sr}{abK}\lambda + rs \left(1 - \frac{s}{abK} \right) = 0.$$

We are looking for zeros of W under the assumption $K > \frac{s}{ab}$ (when the non-trivial solution exists in biological sense). Therefore, the free term of W is positive. Hence, if its zeros are real, then they have the same sign. We also see that if the characteristic values are complex, then the real part is equal to $-\frac{sr}{2abK}$ and it is negative that guaranties stability.

The discriminant of the equation above is equal to

$$\Delta = \frac{s^2r^2}{a^2b^2K^2} - 4rs \left(1 - \frac{s}{abK} \right)$$

and it is easy to see that $\Delta > 0$ for small K , $\lim_{K \rightarrow +\infty} \Delta < 0$ and Δ is an decreasing function of K . We can check that if the characteristic values are real, then they are negative, because $\lambda_1 = \frac{1}{2} \left(-\frac{sr}{abK} - \sqrt{\Delta} \right) < 0$ and both λ_1 and λ_2 have the same sign. Hence, the non-trivial solution is stable if it exists. This means that if $K > \frac{s}{ab}$, then predators have enough food and both species survive.

2. For the May model, Eqs.(15) we have

$$W(\lambda) = \det \begin{pmatrix} r_1 \left(1 - 2\frac{V}{K_1} \right) - \frac{aP}{(1+aV)^2} - \lambda & -\frac{aV}{1+aV} \\ \frac{r_2P^2}{K_2V^2} & r_2 \left(1 - 2\frac{P}{K_2V} \right) - \lambda \end{pmatrix}.$$

For the semi-trivial solution $(K_1, 0)$ the characteristic equation is of the form

$$W(\lambda) = (-r_1 - \lambda)(r_2 - \lambda) = 0$$

and this implies that this solution is a saddle.

For the non-trivial solution $(\bar{V}, K_2\bar{V})$

$$W(\lambda) = \det \begin{pmatrix} r_1 \left(1 - 2\frac{\bar{V}}{K_1}\right) - \frac{aK_2\bar{V}}{(1+a\bar{V})^2} - \lambda & -\frac{a\bar{V}}{1+a\bar{V}} \\ r_2K_2 & -r_2 - \lambda \end{pmatrix}.$$

The free term of the binomial W is equal to the determinant of Jacobi matrix

$$\frac{ar_2K_2\bar{V}}{(1+a\bar{V})^2} + \frac{ar_2K_2\bar{V}}{1+a\bar{V}} - r_1r_2 \left(1 - \frac{2\bar{V}}{K_1}\right).$$

Due to the identity

$$r_1 \left(1 - \frac{\bar{V}}{K_1}\right) = \frac{aK_2\bar{V}}{1+a\bar{V}}$$

we obtain that the determinant has the form

$$\frac{ar_2K_2\bar{V}}{(1+a\bar{V})^2} + r_1r_2\frac{\bar{V}}{K_1} > 0.$$

In this case stability of $(\bar{V}, K_2\bar{V})$ depends on the sign of the trace of Jacobi matrix

$$r_1 \left(1 - 2\frac{\bar{V}}{K_1}\right) - \frac{aK_2\bar{V}}{(1+a\bar{V})^2} - r_2.$$

If the trace is negative, then our solution is stable. Clearly, if the discriminant of W is positive, then there are two real negative solutions, while if it is negative, then the real part of characteristic value is negative and in both cases the solution is stable (either node or focus). On the other hand, if the trace is positive, then we have inverse inequalities and the solution is unstable.

3. In the case of competing species stability depends on the magnitude of extra-specific competition. If both the coefficients are small, i.e., $\alpha_{ij} < 1$, $i, j = 1, 2$, $i \neq j$, then there is the non-trivial solution and it is stable. If both α_{ij} are large (greater than 1), then this solution also exists but it is a saddle. In this case the semi-trivial solutions $(K_1, 0)$ and $(0, K_2)$ are locally stable. Survival of the species depends on the initial conditions. If one of this coefficients is greater than 1 and the second is smaller, then this means that the extra-specific competition has large influence on one of the species and small influence on the other. This leads to the extinction of the weaker species. In this case the semi-trivial solution for the stronger species is stable.

2.3.2 Global stability analysis

In the two-dimensional case we have the Poincare-Bendixon theorem that tells us about the behaviour of solutions. This theorem implies that if the solution stays in some bounded region of \mathbf{R}^2 , then either it tends to some constant solution inside or on the boundary of this region or it tends to some closed orbit in this region (except the cases when it is a critical point or closed orbit itself). It should be noticed that if the studied solution stays in the bounded region and there is no critical point inside this region, then the solution tends to some critical point on the boundary because every closed orbit encircle some critical point. A single closed orbit is called a limit cycle. Such a limit cycle can be stable when it attracts solutions from its neighbourhood, or unstable when it is repulsive (it can be repulsive for solutions outside the cycle, inside it or from both sides).

Now, we focus on the non-existence of closed orbits for the system of ODEs with the right-hand side $F(x, y) = (F_1(x, y), F_2(x, y))$ of class C^1 (i.e. with continuous derivative). We use the Dulac-Bendixon criterion. If there exists the function $B(x, y)$ of class C^1 in the region $U \in \mathbf{R}^2$ such that the divergence of BF , i.e.,

$$Div (BF)(x, y) = \frac{\partial(BF_1)}{\partial x} + \frac{\partial(BF_2)}{\partial y}$$

is not equivalent to 0 and it does not change the sign, then there is no closed orbit in U .

Knowing this criterion and local stability of critical points we check possible existence of closed orbits for our models. Let define $B(x, y) = \frac{1}{xy}$ for $x, y > 0$.

1. For Eqs.(13) we do not know local stability of the internal critical point (\bar{V}, \bar{P}) but we can try to use the criterion. We obtain

$$Div (BF)(V, P) = \frac{\partial}{\partial V} \left(\frac{r}{P} - a \right) + \frac{\partial}{\partial P} \left(ab - \frac{s}{V} \right) = 0$$

and one of the assumptions is not satisfied. The situation is better for Eqs.(14). In this case

$$Div (BF)(V, P) = \frac{\partial}{\partial V} \left(\frac{r}{P} - \frac{rV}{KP} - a \right) + \frac{\partial}{\partial P} \left(ab - \frac{S}{v} \right) = -\frac{s}{KP} < 0$$

and this implies that there is no closed orbit in the first quarter of the plane.

3. Exactly the same we obtain for the system of competing species,

$$\begin{aligned} Div (BH)(N_1, N_2) &= \frac{\partial}{\partial N_1} \left(\frac{r_1}{N_2} - \frac{r_1 N_1}{K_1 N_2} - \frac{r_1 \alpha_{12}}{K_2} \right) + \\ &+ \frac{\partial}{\partial N_2} \left(\frac{r_2}{N_1} - \frac{r_2 N_2}{K_2 N_1} - \frac{r_2 \alpha_{21}}{K_1} \right) = -\frac{r_1}{K_1 N_2} - \frac{r_2}{K_2 N_1} < 0. \end{aligned}$$

From one of the previous Subsections we know that every solution to Eqs.(16) is bounded that implies it stays in some bounded region in $(\mathbf{R}^+)^2$. Therefore, it tends to one of the constant solutions. If only one constant solution is stable, then all other solutions tend to it. If there are two stable solutions, then the first quarter is divided into two regions that are attracted either by one or by the second stable solution.

2. It occurs that for the May model a stable limit cycle can exist. It depends on the model parameters. Using the Dulac-Bendixon criterion we see that

$$Div (BG)(V, P) = -\frac{r_1}{K_1 P} + \frac{a^2}{(1 + aV)^2} - \frac{r_2}{K_2 V^2}$$

and independently on P the inequality $Div (BG)(V, P) < \frac{a^2}{(1+aV)^2} - \frac{r_2}{K_2 V^2}$ is satisfied. Hence, $Div (BG)(V, P) < \frac{1}{V^2} - \frac{r_2}{K_2 V^2}$ and if $K_2 < r_2$, then there is no closed orbit in the first quarter. In such a case the non-trivial internal constant solution is locally stable and the Dulac-Bendixon criterion implies its global stability. If this solution is unstable, then our criterion implies the existence of at least one closed orbit and other solutions are attracted by some closed orbit. If this orbit is only one, then it is a stable limit cycle.

One of the more general methods of local and global stability analysis is the method of Lapunov functions. Let $(0, 0)$ be a constant solution to ODEs with the right-hand side F of class C^1 on U . The continuously differentiable function $L : Q \rightarrow \mathbf{R}$, $Q \subset U$ is called the Lapunov function on Q if it has the following properties:

- 1) $L(x, y) \geq 0$,
- 2) $L(x, y) = 0 \iff x = y = 0$,
- 3) if $(x(t), y(t))$ is the solution to the studied equation, then $L(x(t), y(t))$ is a non-increasing function of t , i.e.,

$$\frac{d}{dt} L(x(t)) = (\text{grad } L) \cdot F =$$

$$= \frac{\partial L}{\partial x}(x, y)F_1(x, y) + \frac{\partial L}{\partial y}(x, y)F_2(x, y) \leq 0$$

(i.e. the scalar product of the gradient of L and the function F is non-positive).

The derivative above is usually called the derivative of L along the solution to the studied equation. One of the more useful theorems tells that if there exists the Lapunov function defined over the whole domain U and $L(x(t), y(t))$ is strictly decreasing for $(x, y) \neq (0, 0)$, then the constant solution $(0, 0)$ is globally attractive, i.e. it attracts all solutions. Hence, if $(\text{grad } L) \cdot F < 0$ for $(x, y) \neq (0, 0)$, then we obtain global stability.

As an example we study Eqs.(14) in the case when non-trivial critical point exists, i.e. $K > \frac{s}{ab}$. Before finding the Lapunov function we rewrite our system in such a form that $(0, 0)$ is a critical point. Namely, let $x = V - \bar{V}$ and $y = P - \bar{P}$, where $\bar{V} = \frac{s}{ab}$ and $\bar{P} = \frac{r}{a} \left(1 - \frac{s}{abK}\right)$. Then

$$\begin{cases} \dot{x} &= r(x + \bar{V}) \left(1 - \frac{x + \bar{V}}{K} - \frac{a}{r}(y + \bar{P})\right) \\ \dot{y} &= (y + \bar{P}) (-s + ab(x + \bar{V})) \end{cases}.$$

Let define

$$L(x, y) = A \left(x - \bar{V} \ln \frac{x + \bar{V}}{\bar{V}}\right) + B \left(y - \bar{P} \ln \frac{y + \bar{P}}{\bar{P}}\right) \quad (19)$$

with positive constants A and B in the domain $\{(x, y) : x > -\bar{V}, y > -\bar{P}\}$. It is easy to see that $L(0, 0) = 0$. Calculating partial derivatives of L we obtain

$$\frac{\partial L}{\partial x} = A \left(1 - \frac{\bar{V}}{x + \bar{V}}\right) = A \frac{x}{x + \bar{V}}$$

and similarly,

$$\frac{\partial L}{\partial y} = B \frac{y}{y + \bar{P}}.$$

Hence, L has a minimum at $(0, 0)$ and therefore, L is non-negative on the whole domain. As the last condition we check the sign

$$(\text{grad } L) \cdot F(x, y) = Arx \left(1 - \frac{x + \bar{V}}{K} - \frac{a}{r}(y + \bar{P})\right) + By (ab(x + \bar{V}) - s).$$

If $A = bB$, then

$$(\text{grad } L) \cdot F(x, y) = -\frac{Ar}{K}x^2 \leq 0.$$

There appears some difficulty, because $(\text{grad } L) \cdot F(x, y) = 0$ for every (x, y) such that $x = 0$. It occurs that every point $(0, y_0)$ lying on the orbit of our equation is a point of inflection for $L(x(t), y(t))$ and $L(x, y)$ is strictly decreasing. Hence, $(0, 0)$ is globally stable. More precisely, if $\bar{t} > 0$ is such that $(x(t), y(t)) = (0, y(\bar{t}))$, $y(\bar{t}) \neq 0$, then $\dot{L}(0, y(\bar{t})) = 0$ and $\ddot{L}(0, y(\bar{t})) < 0$ which implies that $\dot{L}(x(t), y(t))$ is decreasing at this point and it is a point of inflection. Finally, (\bar{V}, \bar{P}) is globally stable for Eqs.(14) when it exists.

Using the same Lapunov function we can show global stability of non-trivial solution to Eqs.(16) in the case of local stability. Similar method can be used in the May model.

2.3.3 Phase space portraits.

The phase space for our biological models is $(\mathbf{R}^+)^2$. Drawing the phase portrait we start from finding null-clines for both variables. These null-clines divide the space into regions where each of the variables is monotonic. We represent it in the graph using appropriately directed arrows. These arrows suggest the dynamics of solutions. We complete our phase portraits by local or/and global stability analysis.

1. The null-clines for Eqs.(13) are straight lines:

$$V = 0 \text{ and } P = \frac{r}{b} \text{ for } V,$$

$$P = 0 \text{ and } V = \frac{s}{ab} \text{ for } P.$$

Inside the first quarter of \mathbf{R}^2 both variables are positive. Hence,

$$\dot{V} > 0 \iff P < \frac{r}{b}, \quad \dot{V} = 0 \iff P = \frac{r}{b}, \quad \dot{V} < 0 \iff P > \frac{r}{b}.$$

This means that V is decreasing above the null-cline and increasing under it. At the null-cline we have $\frac{dV}{dP} = 0$ and therefore, the points on the null-cline are possible extrema for orbits treated as a function $V(P)$.

Similarly, P is increasing for $V > \frac{s}{ab}$, i.e. on the right-hand side of the null-cline and decreasing for $V < \frac{s}{ab}$. The function $P(V)$ has possible extrema on the null-cline. This suggest that solutions encircle the non-trivial solution (\bar{V}, \bar{P}) but we do not know stability of it. It cannot be studied using standard methods. As we know, the trivial solution is a saddle with the stable manifold $V = 0$ and unstable one $P = 0$.

It occurs that the analysis of the simplest model is not so simple. It can be shown that all orbits inside the first quarter are closed. Calculating the equation of orbits we obtain

$$\int \frac{abV - s}{V} dV = \int \frac{r - aP}{P} dP.$$

Hence,

$$abV - \ln V^s = \ln P^r - bP + C,$$

that implies the following implicit formula

$$\frac{e^{abV}}{V^s} = c \frac{P^r}{e^{bP}}, \quad c = \text{const} > 0.$$

Let consider two auxiliary functions $x(V) = \frac{e^{abV}}{V^s}$, $y(P) = \frac{P^r}{e^{bP}}$. We have $x = cy$. Studying coupled graphs $x(y)$, $x(V)$, $y(P)$ and $V(P)/P(V)$ we see that in (V, P) co-ordinates solutions form closed orbits. Hence, (\bar{V}, \bar{P}) is a centre and therefore, the solutions are periodic.

Knowing that solutions are periodic we can tell something more. Let T denotes the period of our solution. Then $V(0) = V(T)$ and $P(0) = P(T)$. From the first equation of Eqs.(13) we obtain

$$\int_{V(0)}^{V(T)} \frac{dV}{V} = \int_0^T (r - aP) dt$$

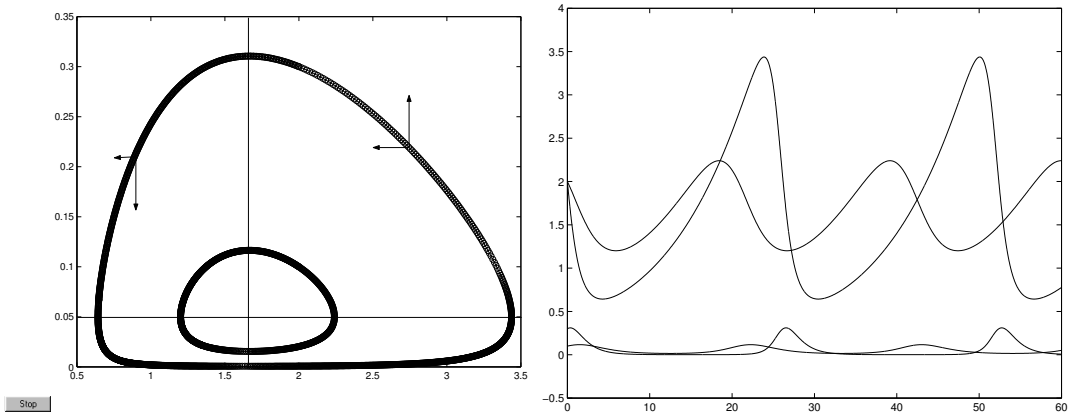
and hence, $\int_0^T P(t) dt = \frac{r}{a} T$. Dividing by the length of the period T we obtain that the mean value of \bar{P} is equal to

$$\frac{1}{T} \int_0^T P(t) dt = \frac{r}{a}.$$

Similarly, we get

$$\frac{1}{T} \int_0^T V(t) dt = \frac{s}{ab}.$$

This means that the mean value of every positive solution to Eqs.(13) is the same and equal to the non-trivial constant solution. It is so-called mean values' conservation law.



Phase portrait and solutions to Eqs.(13).

The co-ordinates of solutions to Eqs.(13) behave similarly to sine and cosine functions. They are periodic and curves are translated in a phase.

For Eqs.(14) we have two types of the phase portrait. If the non-trivial constant solution exists, then it is very similar to the previous case. The only difference is the null-cline for V . It changes to the straight line $P = \frac{x}{a} - \frac{V}{aK}$. Existence of the internal constant solution means that the null-clines for V and P intersect inside the first quarter of \mathbf{R}^2 . Positive solutions encircle (\bar{V}, \bar{P}) — it is a node or focus depending on parameters. As we know, all positive solutions are attracted by this point.

If null-clines for V and P do not intersect, then the only stable solution $(K, 0)$ is a global attractor — from the phase portrait we see that solutions stay in a bounded region of the phase space and therefore, it tends to our unique stable solution located on the boundary of this region.

2. For the May model the phase portrait suggests that solutions also stay in a bounded region and if the limit cycle exists, then it is unique and therefore, it is a stable limit cycle.

3. Similarly as in the previous cases, solutions to Eqs.(16) stay in a bounded region and it implies global stability of constant solutions if only one of them is stable. If $(K_1, 0)$ and $(0, K_2)$ are commonly stable, then the phase space is divided into the regions that are attracted either by $(K_1, 0)$ or by $(0, K_2)$. The boundary of these regions is the stable manifold of the non-trivial solution which is a saddle in this case.

2.3.4 Hopf bifurcation.

As we said earlier, bifurcation means the change of qualitative behaviour of solutions. One of such bifurcations is the Hopf one. It occurs when from a constant solution bifurcates a limit cycle which encircle this constant solution. This bifurcation is connected with the change of some parameter of the model. Such a type of behaviour we have for the May model. In the most popular case we have stable constant solution at the beginning. It loses stability for some parameter value and then a cycle appears. To have a cycle we need that this constant solution is a focus. We know that instability is connected with positive real part of characteristic value while negativity of this part implies stability. Hence, we conclude that the Hopf bifurcation can appear when the real part is equal to 0. If the characteristic values cross the imaginary axis with non-zero speed as the parameter changes, then we have the Hopf bifurcation, i.e. a limit cycle appears.

For the May model the complex characteristic values have real part equal to

$$\Re = \frac{r_1 \left(1 - 2\frac{\bar{V}}{K_1}\right) - \frac{aK_2\bar{V}}{(1+a\bar{V})^2} - r_2}{2}$$

where the numerator of this quotient is the trace of Jacobi matrix. Changing one of the parameters, e.g. r_1 we see that for very small r_1 the real part is negative while for large values of r_1 it is positive. Hence, for some \bar{r}_1 we have $\Re = 0$ and the characteristic values cross the imaginary axis from the left to the right-hand side. This implies the Hopf bifurcation.

2.4 Exercises.

1. Prepare phase portraits for the system of linear ODEs with at least one characteristic value equal to 0.
2. Compare the behaviour of solutions to the linear systems with the right-hand side in canonical and non-canonical form.
3. Prepare phase portraits for the competition, May and prey-predator with bounded environment models.
4. Check global stability for the May and competition models.

3 Some general remarks on discrete and continuous dynamical systems.

In general case the problem is analogous to considered above — we study either the behaviour of some sequence defined by a recurrent formula or the behaviour of solutions to some ODEs.

3.1 Discrete dynamical systems.

Using the term "discrete dynamical system" we mean the iteration of some continuous function F defined on some subset of \mathbf{R}^k into this subset. Namely, let F comes from $U \subset \mathbf{R}^k$ into U ($F : U \rightarrow U$) and we study the sequence

$$x_{n+1} = F(x_n).$$

Sometimes, the domain of F is closed, e.g. there is a very famous theory on the iterations of the interval $[0, 1]$. From the biological point of view, the interesting domain is \mathbf{R}^+ that can be understood either as to the open half-line $(0, +\infty)$ or the left-hand closed half-line $[0, +\infty)$. In higher dimensions we use the domain $(\mathbf{R}^+)^k$, that is the first quarter in \mathbf{R}^2 , the first octant in \mathbf{R}^3 , and so on. The domain is specified for every model separately.

The behaviour of the sequence (x_n) depends not only on the function F that defines our dynamical system but also on the first term of the sequence $x_0 \in U$. For arbitrary x_0 the set

$$\text{orb}(x_0) = \{F^n(x_0), n \in \mathbf{N}\}, \text{ where } F^n(x) = F(F^{n-1}(x)), F^0(x) = x,$$

is called the trajectory (or orbit) of the point x_0 . Sometimes, instead of the trajectory of x_0 we study so-called Cauchy problem

$$\begin{cases} x_{n+1} = F(x_n) \\ x_0 \in U \end{cases}.$$

Both formulas defines the same sequence, obviously. The difference is that in the first case we treat this sequence as the set of points.

The name and notion of "dynamical systems" is closely related with the dynamics of points from the set U under the iterations of the function F , where n is the iteration parameter. Therefore, we can also treat the system as a transformation $n \rightarrow F^n(x)$ for arbitrary $x \in U$. Every term of our

sequence is always defined and unique due to the recurrent formula that defined the system. Our main interest is to study the asymptotic behaviour of the sequence $F^n(x)$ for $x \in U$.

3.2 Continuous dynamical systems.

We do not study general class of continuous dynamical systems but only the type of it generated by ordinary differential equations of the form

$$\dot{x} = F(x), \quad F : U \rightarrow U, \quad U \subset \mathbf{R}^k. \quad (20)$$

Now, existence and uniqueness of solutions is not so obvious as in the discrete case. We should specify some properties of F . Let start with the case $k = 1$, for simplicity (definitions and theorems are similar for $k > 1$). If the function $F : U \rightarrow U$, where $U \subset \mathbf{R}$ is an open interval, is continuous, then for every $x_0 \in U$ there exists the solution to the Cauchy problem

$$\begin{cases} \dot{x}(t) &= F(x(t)) \\ x(0) &= x_0 \end{cases},$$

which means that there exists an interval I and differentiable function $x(t)$ such that $0 \in I$, $x(0) = x_0$ and $x(t)$ satisfies the equation above for every $t \in I$. The quantity x_0 is called an initial condition or value. So, continuity of the function F is sufficient for the existence of solutions but not for uniqueness. To obtain a unique solution we assume that the right-hand side of equation is a Lipschitz function.

We tell that F satisfies the Lipschitz condition if there exists some constant $L > 0$ such that for every $x, y \in U$ the inequality

$$|F(x) - F(y)| \leq L|x - y|$$

holds. For $k = 1$ the symbol $|x|$ means absolute value of x . In higher dimensions it is the standard norm (for $x = (x_1, \dots, x_k)$ we have $|x| = \sqrt{x_1^2 + \dots + x_k^2}$).

More precisely, it is enough that F is locally Lipschitz (i.e. for every point $x \in U$ there exists a neighbourhood U_x of this point where F satisfies the Lipschitz condition). Usually, in biological models the function F has continuous derivative and then the Lipschitz constant on every closed subset of U is equal to the maximal value of $|F'(x)|$. Clearly, if $y, z \in [a, b] \subset U \subset$

\mathbf{R} , then by one of the theorems of mean value there exists a point ξ between y and z such that

$$\frac{F(y) - F(z)}{y - z} = F'(\xi)$$

and the same is true for absolute values, obviously. The function $|F'(x)|$ is continuous and $[a, b]$ is a compact set. Using the theorem about continuous functions on compact sets we conclude that $|F'(x)|$ achieves its upper bound (the lower bound is 0). Therefore,

$$|F(y) - F(z)| \leq |F'(\xi)||y - z| \leq \max_{[a,b]} |F'(x)||y - z|.$$

Therefore, if F is continuously differentiable, then the solution exists and it is unique.

Now, we show that continuity is not sufficient for uniqueness of solutions. The main example of such a continuous function F for which the solution is not unique is $F(x) = x^{\frac{1}{3}}$. It is obviously continuous on \mathbf{R} as the inverse of x^3 . Consider the equation

$$\dot{x} = x^{\frac{1}{3}} \quad \text{with} \quad x(0) = 0.$$

It is obvious that $x(t) \equiv 0$ is the solution to this problem. On the other hand, for $x \neq 0$ we have

$$\frac{\dot{x}}{x^{\frac{1}{3}}} = 1.$$

Let define the auxiliary function

$$f(t) = x^{\frac{2}{3}}(t).$$

Then

$$\dot{f} = \frac{2}{3}x^{-\frac{1}{3}}\dot{x}.$$

Hence,

$$\frac{\dot{x}}{x^{\frac{1}{3}}} = \frac{3}{2}\dot{f} = 1,$$

and we obtain that $f(t)$ has constant derivative equal to $\frac{2}{3}$. Finally,

$$f(t) = \frac{2}{3}t + c$$

and therefore,

$$x(t) = \pm \left(\frac{2}{3}t + c \right)^{\frac{3}{2}}$$

is a general solution to our equation. Using the initial value $x(0) = 0$ we obtain $c = 0$. So, $x(t) = \pm \left(\frac{2}{3}t \right)^{\frac{3}{2}}$ are another solutions to our Cauchy problem for $t \geq 0$. Moreover, if we combine $x = 0$ with the calculated above general solution we obtain next solutions. How to do it? Let c be an arbitrary negative number. Then the general solution is defined for every $t \geq -c$. Taking $x(t) = 0$ for $t < -c$ and the general solution for $t \geq -c$ we obtain the solution to our problem because such a function is differentiable at $t = -c$ (has left-hand side and right-hand side derivatives equal to 0.) This is so called juncted function with a smooth junction at $t = -c$.

From now on we assume that the studied ODE has a unique solution (e.g. F has continuous derivative). To have a dynamical system we need that this solution is defined for all $t \geq 0$. If the right-hand side of equation is linear, then it is easily fulfilled. If not, then the solution can blow up. Consider the equation

$$\dot{x} = x^2 \text{ with } x(0) = x_0 \neq 0.$$

We can solve this equation using the method of variables' separation, i.e.,

$$\int \frac{dx}{x^2} = \int dt$$

and therefore, $-\frac{1}{x} = t + c$. Hence, for the initial value x_0 we obtain

$$x(t) = \frac{1}{\frac{1}{x_0} - t}.$$

This solution is not defined for $t = \frac{1}{x_0}$. It has so-called blow-up at this point. In general case, this means that the norm of solution tends to ∞ with t tending to such a point.

On the other hand, if F has continuous derivative and the solution is bounded for every arbitrary $\bar{t} \geq 0$, then it has also bounded derivative and therefore, it can be extended forward the point \bar{t} because it has a limit at this point and this limit can be treated as a new initial value. More precisely, if $\bar{x} = \lim_{t \rightarrow \bar{t}^-} x(t)$, then (\bar{t}, \bar{x}) is the new initial condition for the studied equation and the solution for this initial condition exists for some

time interval and fulfils the condition $x(\bar{t}) = \bar{x}$. The solution is unique and hence, it is the same solution defined over the longer interval. The last problem is to show that this limit exists. If not, then there are two sequences $t_{n_1} \rightarrow \bar{t}^-$ and $t_{n_2} \rightarrow \bar{t}^-$ such that the sequences $x(t_{n_1})$ and $x(t_{n_2})$ has different limits $\lim_{n_1 \rightarrow \infty} x(t_{n_1}) \neq \lim_{n_2 \rightarrow \infty} x(t_{n_2})$. Assume that $t_{n_2} > t_{n_1}$ (if not, then we can choose proper subsequences) and use the theorem of mean value on the interval $[t_{n_1}, t_{n_2}]$. Then

$$\frac{x(t_{n_2}) - x(t_{n_1})}{t_{n_2} - t_{n_1}} = \dot{x}(\tilde{t}_n), \tilde{t}_n \in [t_{n_1}, t_{n_2}].$$

If $n \rightarrow \infty$, then the right-hand side of this equality is bounded. The denominator of the left-hand side tends to 0 and the numerator tend either to some non-zero number or to infinity (if some of this sequences has limit equal to ∞). Therefore, the whole quotient tends to ∞ which contradicts this equality.

It is obvious that if the right-hand side F of Eq.(20) is bounded for every $x \in U$, then the solution and its derivative are bounded. From now on we assume that the solution to Eq.(20) is unique for every $t \geq 0$. Then we can study either the transformation from t to $x(t)$ for arbitrary x_0 , i.e. the solution to the Cauchy problem or the transformation from x_0 to $x(t)$ understood as a set of points, i.e. the trajectory (or orbit) of the point x_0 (exactly as in the discrete case). Sometimes, the solution is written as $x(t, x_0)$ to underline its dependence on both variables. Hence, we define orb $(x_0) = \{x(t, x_0), t \geq 0\} \subset U$. Similarly as in the discrete case, we are mainly interested in the asymptotic behaviour of solutions depending on the initial value x_0 . Methods of asymptotic analysis depends on the spatial dimension k . There are also some methods that can be used independently on k . One of them is the linearization method that concerns stability of constant solutions.

3.3 Stable constant solutions and linearization theorem.

Now, we are ready to explain the concept of stability. Everybody knows the physical meaning of stability. A ball situated in a valley is stable (small deviation from the stable position does not lead out of this positions, the ball comes back to it). A ball situated in a top of a mountain is unstable (every deviation leads out of this position). There is also another — more general

— notion of stability, so-called Lapunov stability. We can compare it with a ball in a plain. After a small perturbation our ball is not far from the origin but it not necessary comes back there.

Comparing this physical interpretation to the phase portraits for one-dimensional systems — if the arrows from both sides of the constant solution x_i are directed to this point, then this point is stable. Otherwise, x_i is unstable.

Hence, we tell that the constant solution \bar{x} is (Lapunov) stable, if the solution with initial value from the neighbourhood of \bar{x} stays near \bar{x} . More precisely, for every $\epsilon > 0$ there exists $\delta > 0$ such that if $|x_0 - \bar{x}| < \delta$, then $|x(t) - \bar{x}| < \epsilon$ for every $t \geq 0$, where $x(t)$ is the solution with initial value x_0 .

We tell that \bar{x} is asymptotically stable, if the solutions starting from the neighbourhood of \bar{x} tends to it with $t \rightarrow +\infty$.

Other solutions (i.e. non-constant) also can be stable. We tell that the solution $\bar{x}(t)$ with initial value \bar{x} is stable, if for every $\epsilon > 0$ there exists $\delta > 0$ such that if $|x_0 - \bar{x}| < \delta$, then $|x(t) - \bar{x}(t)| < \epsilon$ for every $t \geq 0$.

Similarly, we define stability of solutions for discrete dynamical systems — the difference is that for discrete dynamical systems $t \in \mathbf{N}$.

The more general concept is an attractor of dynamical system (both discrete and continuous). Roughly speaking, the set $V \subset U$ is an attractor of some set $W \subset U$ if for every initial value $x_0 \in W$ the solution is attracted by the points from V . This means that the distance between the solution and V tends to 0 as $t \rightarrow +\infty$, where $\text{dist}(x, Y) = \inf_{y \in Y} |x - y|$. It is not necessary that attractors of dynamical systems are solutions to these systems. There is a famous theory of so-called strange attractors connected with the theory of fractals. One of the well-known strange attractors is the Lorenz one. We will talk about it later.

The concept of stability and attractors is local, i.e. not every solution to studied system must tend to stable solution or attractor. We can also tell about global attractor and global stability. A global attractor is such a type of attractor that attracts all points from U , i.e. every solution tends to it. Similarly, some solution to our dynamical system is called globally stable, if its orbit is a global attractor.

One of the main methods of (local) stability analysis is the linearization theorem. It can be used for both discrete and continuous dynamical systems.

At the beginning we consider one-dimensional case and study stability of the constant solution $x = 0$. Let $F : U \rightarrow U$, $U \subset \mathbf{R}$ be the right-hand side of studied dynamical system (discrete or continuous) and $F(0) = 0$ (if $\bar{x} \neq 0$ is a constant solution, then we make a substitution $x \mapsto x - \bar{x}$). Assume that F can be expanded as:

$$F(x) = F'(0)x + R(x),$$

where $F'(0)x$ is the linear part of F and $R(x)$ is the non-linear one. If F has the second derivative, then $R(x) = \frac{F''(\xi)}{2}x^2$, $\xi \in (0, x)$ (or $\xi \in (x, 0)$ if $x < 0$).

The main assumption of the linearization theorem concerns the derivative $F'(0)$. We should assume that $F'(0) \neq 0$ in the continuous case or $|F'(0)| \neq 1$ in the discrete one. Why should we assume it? In the linear continuous case the solution is exponential with the exponent $F'(0)t$ and therefore, if $F'(0) = 0$, then every small perturbation (a non-linear term is such a perturbation) can change the sign of $F'(0)$ — if this sign is positive, then the solution tends to ∞ and it is unstable, while if the sign is negative, the solution tends to 0. Hence, small changes of the sign implies large changes of the behaviour of solutions. Similarly, in linear discrete case the solution is an involution function with the base $F'(0)$. Now, $|F'(0)| = 1$ is the boundary of stability region $(-1, 1)$.

We should also assume that the non-linear part is small near the point of linearization $x = 0$. Namely, $\lim_{x \rightarrow 0} \left| \frac{R(x)}{x} \right| = 0$. Then a small perturbation does not lead to large changes of the behaviour of solutions.

The linearization theorem tells that under the above assumptions the constant solution $x = 0$ is asymptotically stable if $F'(0) < 0$ for continuous case or $|F'(0)| < 1$ for discrete case and unstable otherwise. The same is true for every constant solution \bar{x} . This means that the linear part of the right hand-side decides of stability or instability. Moreover, in the continuous case we can tell something more. Namely, the shape of orbits is the same (in topological meaning) for linear and non-linear case. Hence, the character of critical points is the same in both cases.

Coming back to the logistic equation Eq.(4), we use this theorem to check stability of constant solutions $x = 0$ and $x = K$. We have $F'(x) = r - 2\frac{rx}{K}$.

For $x = 0$ we obtain $F'(0) = r$, the linear part is rx and the non-linear one $R(x) = -bx^2$. Hence, $\frac{R(x)}{x} = -bx \rightarrow 0$ as $x \rightarrow 0$ and $F'(0) \neq 0$ and we can use the theorem of linearization. Inequality $F'(0) = r > 0$ implies

instability of $x = 0$.

For $x = K$ we have $F'(K) = r(1 - 2\frac{K}{K}) = -r \neq 0$. Substituting $z = x - K$ we get $F(z) = -rz - \frac{r}{K}z^2$ so, the non-linear part $R(z) = -\frac{r}{K}z^2$ fulfils the assumption of linearization and therefore, $x = K$ is asymptotically stable due to $F'(K) < 0$.

3.3.1 Global stability.

The main method of global stability (of constant solutions) analysis is finding Lapunov functions. Let $(0, \dots, 0) \in U$ be the constant solution to Eq.(20) and $x(t) \in U$ be a solution. Assume that the right-hand side of Eq.(20) is of class C^1 on U and $U \subset \mathbf{R}^k$ is open. The continuously differentiable function $V : Q \rightarrow \mathbf{R}$, $Q \subset U$ is called the Lapunov function on Q if it has the following properties: $V(x) \geq 0$ and $V(x) = 0 \iff x = 0$, i.e. $x_1 = \dots = x_k = 0$, $V(x(t))$ is a non-increasing function of t , i.e. $\frac{d}{dt}V(x(t)) = (\text{grad } V) \cdot F \leq 0$. If Eq.(20) has a Lapunov function defined on some neighbourhood of $(0, \dots, 0)$, then the origin $(0, \dots, 0)$ is stable. Moreover, if the Lapunov function is defined over the whole domain U and $V(x(t))$ is strictly decreasing for $x \neq 0$ in the whole domain, then the origin is globally stable. Hence, if $(\text{grad } V) \cdot F < 0$ for $x \neq (0, \dots, 0)$, implies global asymptotic stability (attractivity) of the origin

Notice, that to use the theorems above we need an open domain and a critical point inside it. Nevertheless, if the critical point lies on the boundary of the open domain and $V(x(t))$ is strictly decreasing for every solution inside the domain and defined on the closure of this open domain, then the thesis also holds.

Existence of a global attractor can be also shown on the background of dissipative systems theory. We tell that the right-hand side of Eq.(20) fulfils the dissipativity condition, it there exists a function $W : U \rightarrow \mathbf{R}^+$ of class C^1 such that the scalar product

$$(\text{grad } W(x)) \cdot F(x) = \sum_{i=1}^k \frac{\partial W(x)}{\partial x_i} F_i(x) \leq C - \delta W(x)$$

satisfies the inequality above, for some positive constants C , δ and $W(x) \rightarrow +\infty$ as $|x| \rightarrow +\infty$. We see that for large values the function W has similar properties as a Lapunov function. Clearly, it is a Lapunov function in more general sense.

We tell that the system of ODEs is dissipative, if the right-hand side is dissipative. Notice, that in the literature there can be found more general concept of dissipativity connected with an existence of bounded attractive subset of the domain.

If Eq.(20) is dissipative, then all solutions are bounded. Namely,

$$\text{grad } W(x(t)) \cdot F(x(t)) = \frac{d}{dt}W(x(t)) \leq C - \delta W(x(t))$$

and hence, multiplying by $e^{\delta t}$ we get

$$\frac{d}{dt} (W(x(t))e^{\delta t}) \leq Ce^{\delta t}.$$

Integrating this inequality from 0 to t we obtain

$$W(x(t)) \leq W(x(0))e^{-\delta t} + \frac{C}{\delta} (1 - e^{-\delta t}) \leq W(x(0)) + \frac{C}{\delta}$$

which implies that $W(x(t))$ is bounded for every $t \geq 0$ and therefore, $x(t)$ is also bounded (if not, then W cannot be bounded).

Boundness of solutions for F of class C^1 implies existence for all $t \geq 0$. Hence, we can study asymptotic behaviour and attractors of Eq.(20). Notice that, if the system is dissipative, then the set $A = \{x : x \in \mathbf{R}^k, W(x) \leq 2\frac{C}{\delta}\}$ is absorbing, i.e. for every bounded set $Q \subset U$ there exists t_Q such that $x(t) \in A$ for $t \geq t_Q$, where $x(t)$ is the solution for initial value $x_0 \in Q$.

It occurs that if there exists compact absorbing set for the system with properties mentioned above, then such a system has global attractor that is connected. The exact structure of this attractor is not known, unfortunately.

Examples of Lapunov function we've given in the previous Section. Now, we try to check dissipativeness of some system. Consider Eqs.(14) with $b < 1$ and the function $W(V, P) = V + P$ for positive V, P . Both partial derivatives of W are equal to 1. Hence,

$$\begin{aligned} (\text{grad } W(V(t), P(t))) \cdot F(V(t), P(t)) &= rV \left(1 - \frac{V}{K}\right) - aVP + abVP - sP \leq \\ & rV \left(1 - \frac{V}{K}\right) - sP \end{aligned}$$

due to positivity of solutions. Let $\delta = s$ and C be a maximal value of parabola $V \left(r + s - r\frac{V}{K}\right)$. Then

$$\text{grad } W(V, P) \cdot F(V, P) \leq C - \delta W(V, P).$$

Therefore, the system is dissipative and the global attractor exists.

3.3.2 Hopf bifurcation.

As we know the Hopf bifurcation is connected with changes of some parameter. Consider ODE of the form

$$\dot{x} = F(x, \mu), \quad (21)$$

with F of class C^1 and $F(0, \mu) = 0$ for every μ . Then $x(t, \mu) \equiv 0$ is the constant solution to Eq.(21). Let μ_0 be the point of bifurcation, i.e. for $\mu < \mu_0$, the trivial solution is asymptotically stable and for $\mu > \mu_0$, it is unstable. If, for $\mu = \mu_0$, there exists a pair of characteristic values such that $\lambda_1 = \bar{\lambda}_2$, $\Re(\lambda_1)\Big|_{\mu=\mu_0} = 0$, $\frac{d}{d\mu}\Re(\lambda_1)\Big|_{\mu=\mu_0} > 0$, and other characteristic values have negative real parts, then for $\mu > \mu_0$ there exists a limit cycle with the period $T = \frac{2\pi}{\Im\lambda_1}$. Additionally, if the trivial solution is asymptotically stable for $\mu = \mu_0$, then this limit cycle is attractive.

In general case, it is not easy to study stability at the point of bifurcation. Attractivity of limit cycle can be suggested by numerical simulations. But we should be very careful and aware that it is only suggestion.

The theorem presented above is not only one that concerns the Hopf bifurcation. This bifurcation can also occur when the constant solution is unstable and gains stability at some parameter value. It is not an usual situation for biological ODEs and we do not study such types of bifurcation.

3.4 Exercises.

1. Check the assumption of the linearization theorem for all two-dimensional models presented in previous Sections.
2. Check dissipativeness of the May and competition models.

4 Three or more dimensional continuous dynamical systems.

In this section we mainly study some examples of three dimensional systems of ODE using general methods that we know from the previous Section. The main difference between two and more dimensional cases is the possible

chaotic behaviour of the system of three or more ODEs. In two-dimensional case the behaviour is regular, due to the Poincare-Bendixon theorem. However, there are many biological models with regular behaviour also in more dimensional case.

As usually, we start from the description of the models.

4. Food chain. We consider the environment with the main predator (with the concentration $P_1(t)$), the second predator ($P_0(t)$) which is a prey for the main predator, and the prey ($V(t)$) that is a food for the second predator. The model reads as

$$\begin{cases} \dot{V} &= V(a_0(1-V) - \mu_1 P_0) \\ \dot{P}_0 &= P_0(a_1(1-P_0) - \mu_2 P_1 + \eta_1 V) , \\ \dot{P}_1 &= P_1(-1 + \eta_2 P_0) \end{cases} \quad (22)$$

where the equations above was scaled to reduce the number of coefficients such that the carrying capacities for preys and second predator are equal to 1 and the death coefficient for the main predator is also 1.

5. Weather forecasting. This model was proposed by American meteorologist Lorenz in 1963 to study convection movement of air in atmosphere. He tried to prepare a long-time forecasting of the weather on the basis of the model. After many simplifications, he obtain the following system of ODEs

$$\begin{cases} \dot{x}_1(t) &= \sigma(x_2 - x_1) \\ \dot{x}_2(t) &= rx_1 - x_2 - x_1x_3 , \\ \dot{x}_3(t) &= -bx_3 + x_1x_2 \end{cases} \quad (23)$$

with σ , r describing viscosity and heat conduction of a medium, respectively, and b reflects a size of space.

4.1 Properties of the models 4 and 5.

The right-hand sides of both Eqs.(22) and (23) are polynomials of the second degree and hence, the local existence and uniqueness of solutions is obvious. Moreover, due to the form of the right-hand side of Eqs.(22), the solution is non-negative for non-negative initial data. It is not satisfied for Eqs.(23). Nevertheless, for both systems we have solutions defined for every $t \geq 0$ (for Eqs.(23) solutions are bounded, for Eqs.(22) co-ordinates V and P_0 are bounded, while the growth of P_1 is at most exponential).

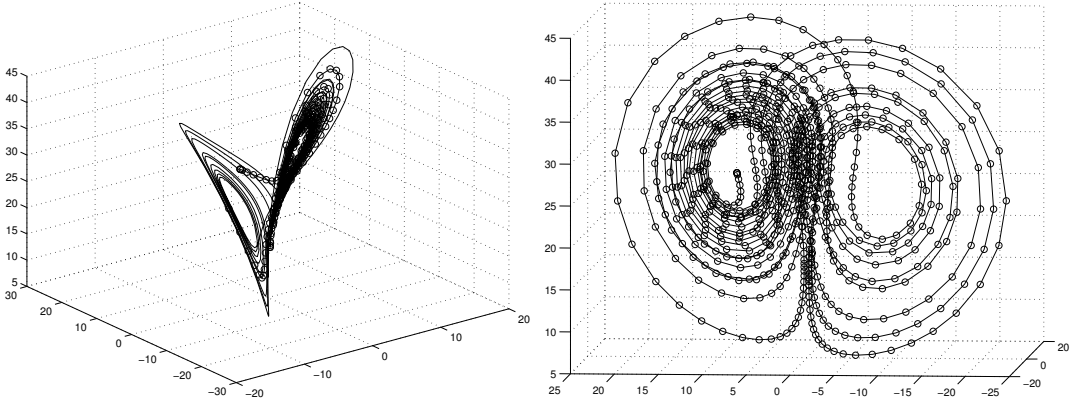
We can show the following property of Eqs.(23). Multiplying the i -th equation of the model by x_i and adding the right and left-hand sides, respectively, we obtain the following identity

$$\frac{1}{2} \frac{d}{dt} (x_1^2 + x_2^2 + (x_3 - \sigma - r)^2) = - \left(\sigma x_1^2 + x_2^2 + b \left(x_3 - \frac{\sigma}{2} - \frac{r}{2} \right)^2 \right) + b \left(\frac{\sigma}{2} + \frac{r}{2} \right)^2. \quad (24)$$

Consider the function $W(x_1, x_2, x_3) = \frac{1}{2} \frac{d}{dt} (x_1^2 + x_2^2 + (x_3 - \sigma - r)^2)$. It occurs that it is a proper function to check dissipativity of the system. Let $f(x_1, x_2, x_3)$ denote the right-hand side of Eqs.(23). Then

$$\begin{aligned} & (\text{grad } W(x_1, x_2, x_3)) \cdot f(x_1, x_2, x_3) = \\ & = \sigma x_1(x_2 - x_1) + x_2(rx_1 - x_2 - x_1x_3) + (x_3 - \sigma - r)(-bx_3 + x_1x_2) = \\ & -\sigma x_1^2 - x_2^2 - bx_3^2 + b(\sigma + r)x_3 = -\sigma x_1^2 - x_2^2 - \frac{b}{2}(x_3 - \sigma - r)^2 + \frac{b}{2}(\sigma + r)^2 - \frac{b}{2}x_3^2. \end{aligned}$$

Choosing $C = \frac{b}{2}(\sigma + r)^2$ and $\delta = \min\{\sigma, 1, \frac{b}{2}\}$ we obtain the inequality $\text{grad } W(x) \cdot f(x) \leq C - \delta W(x)$ that implies dissipativity of Eqs.(23). This means that for every parameter values the system has a global attractor. But this attractor can have a complicated structure. Consider the sphere $R_0 = \{x \in \mathbf{R}^3 : x_1^2 + x_2^2 + (x_3 - \sigma - r)^2 \leq c^2\}$, for sufficiently large c . If the ellipsoid $\{x \in \mathbf{R}^3 : \sigma x_1^2 + x_2^2 + b(x_3 - \frac{\sigma}{2} - \frac{r}{2})^2 = b(\frac{\sigma}{2} + \frac{r}{2})^2\}$ lies inside the sphere above, then the left-hand side of Eq.(24) is negative and therefore, R_0 is an invariant set for our system. Moreover, on the boundary of R_0 the right-hand side of Eq.(24) is negative. If we consider the discrete dynamical system generated by $x(n)$, for natural n , then $R_1 = x(1)(R_0)$ is the smaller set than original R_0 and so on. Let V_n denotes the volume of R_n . Then $V_n = e^{-n(\sigma+b+1)}V_0$. It is obvious that the volume of the limit set is equal to 0. This limit set is called the strange Lorenz attractor.



Lorenz attractor.

4.2 Constant solutions.

4. Let $(\bar{V}, \bar{P}_0, \bar{P}_1)$ denote the critical point. The third equation implies that $\bar{P}_1 = 0$ or $\bar{P}_0 = \frac{1}{\eta_2}$. In the case $\bar{P}_1 = 0$ we obtain up to 4 critical points: $A = (0, 0, 0)$, $B = (0, 1, 0)$ and $C = (1, 0, 0)$ exist independently on the parameters,

$$D = \left(\frac{a_1(a_0 - \mu_1)}{a_0 a_1 + \mu_1 \eta_1}, \frac{a_0(a_1 + \eta_1)}{a_0 a_1 + \mu_1 \eta_1}, 0 \right)$$

exists for $a_0 > \mu_1$. If $\bar{P}_0 = \frac{1}{\eta_2}$, then we obtain another two equilibrium states:

$$E = \left(0, \frac{1}{\eta_2}, \frac{a_1(\eta_2 - 1)}{\mu_2 \eta_2} \right) \text{ and } F = \left(\frac{a_0 \eta_2 - \mu_1}{a_0 \eta_2}, \frac{1}{\eta_2}, \frac{a_0 a_1 \eta_2 - a_0 a_1 + a_0 \eta_1 \eta_2 - \mu_1 \eta_1}{a_0 \mu_2 \eta_2} \right).$$

It is easy to check that:

- D exists if $a_0 > \mu_1$. If $a_0 = \mu_1$, then $D = B$. Hence, D bifurcates from B .
- E exists if $\eta_2 > 1$. If $\eta_2 = 1$, then $E = B$. Hence, E also bifurcates from B .
- F exists if $a_0 \eta_2 > \mu_1$ and $a_0 \eta_2 (a_1 + \eta_1) > a_0 a_1 + \eta_1 \mu_1$. Therefore, F exists if $\eta_2 > \max\left\{ \frac{\mu_1}{a_0}, \frac{a_0 a_1 + \eta_1 \mu_1}{a_0 (a_1 + \eta_1)} \right\}$.

Now we study the co-existence of D , E and F .

1. Let $\mu_1 < a_0$. Then D exists and the inequalities

$$\frac{\mu_1}{a_0} < \frac{a_0 a_1 + \eta_1 \mu_1}{a_0 (a_1 + \eta_1)} < 1$$

are satisfied. Therefore,

- if $\eta_2 < \frac{a_0 a_1 + \eta_1 \mu_1}{a_0 (a_1 + \eta_1)}$, then there are no E and F ;
- if $\eta_2 = \frac{a_0 a_1 + \eta_1 \mu_1}{a_0 (a_1 + \eta_1)}$, then there is no E and F bifurcates from D ;
- if $\eta_2 \in \left(\frac{a_0 a_1 + \eta_1 \mu_1}{a_0 (a_1 + \eta_1)}, 1 \right)$, then there is no E but F exists;
- if $\eta_2 = 1$, then F exists and E bifurcates from B ;
- if $\eta_2 > 1$, then there are all six equilibrium states.

2. Let $\mu_1 = a_0$. Then $D = B$ and D bifurcates from B . In this case $F = \left(\frac{\eta_2 - 1}{\eta_2}, \frac{1}{\eta_2}, \frac{(a_1 + \eta_1)(\eta_2 - 1)}{\eta_2 \mu_2} \right)$. Hence,
- if $\eta_2 < 1$, then there are no E and F ;
 - if $\eta_2 = 1$, then $E = F = B$. This means that E and F bifurcates from B ;
 - if $\eta_2 > 1$, then E and F exist.
3. Let $\mu_1 > a_0$. Then D does not exist. In this case the opposite inequalities

$$1 < \frac{a_0 a_1 + \eta_1 \mu_1}{a_0(a_1 + \eta_1)} < \frac{\mu_1}{a_0}$$

are fulfilled. Hence,

- if $\eta_2 < 1$, then E and F do not exist;
- if $\eta_2 = 1$, then E bifurcates from B but F does not exist;
- if $\eta_2 \in \left(1, \frac{\mu_1}{a_0} \right)$, then there is E and F does not exist;
- if $\eta_2 = \frac{\mu_1}{a_0}$, then F bifurcates from E ;
- if $\eta_2 > \frac{\mu_1}{a_0}$, then we have both E and F .

The Jacobi matrix for Eqs.(22) has the following form

$$J(V, P_0, P_1) = \begin{pmatrix} a_0(1 - 2V) - \mu_1 P_0 & -\mu_1 V & 0 \\ \eta_1 P_0 & a_1(1 - 2P_0) - \mu_2 P_1 + \eta_1 V & -\mu_2 P_0 \\ 0 & \eta_2 P_1 & \eta_2 P_0 - 1 \end{pmatrix}. \quad (25)$$

We see that if the co-ordinate $\bar{V} \neq 0$ for the stationary solution, then

$$a_0(1 - 2\bar{V}) - \mu_1 \bar{P}_0 = -a_0 \bar{V}.$$

Similarly, if $\bar{P}_0 \neq 0$, then

$$a_1(1 - 2\bar{P}_0) - \mu_2 \bar{P}_1 + \eta_1 \bar{V} = -a_1 \bar{P}_0.$$

Taking into account the formula (25) and the above equalities we obtain the following:

- A is unstable independently on the parameters (characteristic values are equal to a_0 , a_1 and -1).

- For B the characteristic polynomial is equal to $W(\lambda) = (a_0 - \mu_1 - \lambda)(-a_1 - \lambda)(\eta_2 - 1 - \lambda)$. Hence, we have stability for $a_0 < \mu_1$ and $\eta_2 < 1$ that implies the absence of E , D and F .
- For C the characteristic polynomial is equal to $W(\lambda) = (-a_0 - \lambda)(a_1 + \eta_1 - \lambda)(-1 - \lambda)$. Hence, C is always unstable.
- For E , the characteristic equation is of the form:

$$\left(\frac{a_0\eta_2 - \mu_1}{\eta_2} - \lambda \right) \left(\lambda^2 + \frac{a_1}{\eta_2}\lambda + \frac{a_1(\eta_2 - 1)}{\eta_2} \right) = 0.$$

Hence, if $\frac{a_0\eta_2 - \mu_1}{\eta_2} > 0$, then E is unstable. If E exists, then $\eta_2 > 1$ and this implies that there is no influence of the quadratic term on the stability (characteristic values are either real negative or complex with negative real part $-\frac{a_1}{2\eta_2}$). Therefore, E is stable when F does not exist.

- For D we obtain the similar formula as in the previous case:

$$\left(\frac{a_0\eta_2(a_1 + \eta_1)}{a_0a_1 + \mu_1\eta_1} - 1 - \lambda \right) (\lambda^2 + \alpha\lambda + \beta) = 0,$$

where

$$\alpha = \frac{a_0a_1(a_0 - \mu_1 + a_1 + \eta_1)}{a_0a_1 + \eta_1\mu_1} > 0 \text{ and } \beta = \frac{a_0a_1(a_0 - \mu_1)(a_1 + \eta_1)}{a_0a_1 + \mu_1\eta_1} > 0$$

when D exists. The quadratic term have no influence on the stability, once again. This means that D is stable when E and F does not exist.

- For F the Jacobi matrix has the following form:

$$J(F) = \begin{pmatrix} -\frac{a_0\eta_2 - \mu_1}{\eta_2} & -\frac{\mu_1(a_0\eta_2 - \mu_1)}{a_0\eta_2} & 0 \\ \frac{\eta_1}{\eta_2} & -\frac{a_1}{\eta_2} & -\frac{\mu_2}{\eta_2} \\ 0 & \frac{a_0a_1(\eta_2 - 1) + \eta_1(a_0\eta_2 - \mu_1)}{a_0\mu_2} & 0 \end{pmatrix}.$$

The matrix $J(F)$ has the form

$$\begin{pmatrix} -a & -b & 0 \\ c & -d & -e \\ 0 & f & 0 \end{pmatrix},$$

where $a, b, c, d, e, f > 0$ are arbitrary positive constants when F exists. The characteristic equation has the following form: $\lambda^3 + \alpha\lambda^2 + \beta\lambda + \gamma = 0$ with $\alpha = \text{tr } J(F) = a + d > 0$, $\beta = ad + bc + ef > 0$, $\gamma = \det J(F) = aef > 0$. The Routh-Hurwitz criterion implies that $\gamma < \alpha\beta$ guaranties stability. In our case the inequality $\gamma < \alpha\beta$ is easily fulfilled. Therefore, we obtain stability.

Hence, for every parameter values there exists one stable equilibrium state:

- if there is F , then it is stable;
- if there is no F but E exists, then E is stable;
- if there is no E and F but D exists, then D is stable;
- if there is no E, D and F , then B is stable.

Now, we focus on the global stability (in $(\mathbf{R}^+)^3$) of critical points. At the beginning we show that, if the inequality

$$\eta_2 > \max \left\{ \frac{\mu_1}{a_0}, \frac{a_0 a_1 + \mu_1 \eta_1}{a_0(a_1 + \eta_1)} \right\} \quad (26)$$

holds, then every solution to Eqs. (22) tends to the unique non-trivial critical point F . If Ineq. (26) is satisfied, then F exists. It is the only equilibrium with all positive co-ordinates. Substituting $x_0 = V - \bar{V}$, $x_1 = P_0 - \bar{P}_0$ and $x_2 = P_1 - \bar{P}_1$, where $F = (\bar{V}, \bar{P}_0, \bar{P}_1)$, we obtain

$$\begin{cases} \dot{x}_0 &= -(x_0 + \bar{V})(a_0 x_0 + \mu_1 x_1) \\ \dot{x}_1 &= -(x_1 + \bar{P}_0)(a_1 x_1 + \mu_2 x_2 - \eta_1 x_0) . \\ \dot{x}_2 &= (x_2 + \bar{P}_1)\eta_2 x_1 \end{cases} \quad (27)$$

We know that $V(t), P_0(t), P_1(t) > 0$ for every $t \geq 0$ and therefore, $x_0 > -\bar{V}$ and $x_i > -\bar{P}_{i-1}$ for $i = 1, 2$. Consider the standard (compare Eq.(19)) Lapunov function

$$\begin{aligned} V(x_0, x_1, x_2) &= A_0 \left(x_0 - \bar{V} \ln \frac{x_0 + \bar{V}}{\bar{V}} \right) + \\ &+ \sum_{i=1}^2 A_i \left(x_i - \bar{P}_{i-1} \ln \frac{x_i + \bar{P}_{i-1}}{\bar{P}_{i-1}} \right), \end{aligned}$$

with $A_0 = \frac{\eta_1 \eta_2}{\mu_1}$, $A_1 = \eta_2$ and $A_2 = \mu_2$ in the domain $\Omega = \{(x_0, x_1, x_2) : x_0 > -\bar{V}, x_i > -\bar{P}_{i-1}, i = 1, 2\}$.

It is easy to see that $V(x_0, x_1, x_2) \geq 0$ in Ω and $V(x_0, x_1, x_2) = 0$ iff $x_0 = x_1 = x_2 = 0$. Calculating the derivative of V in the direction of a solution to Eqs.(27) we get

$$\dot{V}(x_0, x_1, x_2) = A_0(-x_0)(a_0 x_0 + \mu_1 x_1) + A_1(-x_1)(a_1 x_1 + \mu_2 x_2 - \eta_1 x_0) + A_2 x_2 x_1 \eta_2$$

and finally,

$$\dot{V}(x_0, x_1, x_2) = -(A_0 a_0 x_0^2 + A_1 a_1 x_1^2).$$

We see that $\dot{V} \leq 0$ that implies global stability of F . To obtain global asymptotic stability we need something more. We have $\dot{V}(x_0, x_1, x_2) = 0$ for every $(x_0, x_1, x_2) = (0, 0, x_2)$. Let the point $(0, 0, x_2(\bar{t}))$ lies on the trajectory of Eqs.(27) for some $\bar{t} > 0$. Then calculating the second derivative we obtain $\ddot{V}(0, 0, x_2) = 0$. The next derivative $\ddot{V}(0, 0, x_2) = -\mu_2^2 (\bar{y}_1^F)^2 x_2^2(\bar{t}) < 0$ that shows that it is a point of inflection. Hence, V is strictly decreasing and therefore, F is globally asymptotically stable.

If F does not exist, then other equilibrium state is globally stable. As the next step we focus on the case when F does not exist but E exists. If $\mu_1 > a_0$ and $1 < \eta_2 < \frac{\mu_1}{a_0}$, then the state E is globally stable. Let $E = (0, \bar{P}_0^E, \bar{P}_1^E)$ and $x_0 = V$, $x_1 = P_0 - \bar{P}_0^E$, $x_2 = P_1 - \bar{P}_1^E$. Then Eqs.(22) take the form

$$\begin{cases} \dot{x}_0 &= x_0 (a_0(1 - x_0) - \mu_1(x_1 + \bar{P}_0^E)) \\ \dot{x}_1 &= -(x_1 + \bar{P}_0^E) (a_1 x_1 + \mu_2 x_2 - \eta_1 x_0) \\ \dot{x}_2 &= \eta_2 x_1 (x_2 + \bar{P}_1^E) \end{cases}.$$

Consider the Lapunov function

$$V(x_0, x_1, x_2) = B_0 x_0 + \sum_{i=1}^2 B_i \left(x_i - \bar{P}_{i-1}^E \ln \frac{x_i + \bar{P}_{i-1}^E}{\bar{P}_{i-1}^E} \right)$$

defined on $[0, \infty) \times (-\bar{P}_0^E, \infty) \times (-\bar{P}_1^E, \infty)$ and calculate the derivative \dot{V} (assuming $x_0 > 0$). Then

$$\begin{aligned} \dot{V} &= -B_0 (\mu_1 \bar{P}_0^E - a_0) x_0 - B_0 a_0 x_0^2 \\ &\quad - B_1 a_1 x_1^2 - B_0 \mu_1 x_0 x_1 + B_1 \eta_1 x_0 x_1 - B_1 \mu_2 x_1 x_2 + B_2 \eta_2 x_1 x_2. \end{aligned}$$

Hence, for $B_1\mu_2 = B_2\eta_2$ and $B_1\eta_1 = B_0\mu_1$ one gets $\dot{V} < 0$ for every $x_0 > 0$ under the assumption $\mu_1\bar{P}_0^E > a_0$. This implies that E is globally stable if it exists and the state F does not exist.

Similarly we show global stability of the state D under the assumption that F and E do not exist and global stability of $B = (0, 1, 0)$ for $a_0 < \mu_1$ and $\eta_2 < 1$ (when F , E and D do not exist). Appropriate Lapunov functions are

$$V_D(x_0, x_1, x_2) = \alpha_0 \left(x_0 - \bar{V}^D \ln \frac{x_0 + \bar{V}^D}{\bar{V}^D} \right) + \\ + \alpha_1 \left(x_1 - \bar{P}_0^D \ln \frac{x_1 + \bar{P}_0^D}{\bar{P}_0^D} \right) + \alpha_2 x_2$$

and

$$V_B(x_0, x_1, x_2) = \beta_0 x_0 + \beta_1 \left(x_1 - \bar{P}_0^B \ln \frac{x_1 + \bar{P}_0^B}{\bar{P}_0^B} \right) + \beta_2 x_2.$$

5. Eqs.(23) always has the trivial critical point $A = (0, 0, 0)$. For every critical point the identity $x_1 = x_2$ holds and therefore, if $x_1 = x_2 \neq 0$, then $x_3 = r - 1$ and two other critical points exists for $r > 1$, i.e. $B = (\sqrt{b(r-1)}, \sqrt{b(r-1)}, r-1)$ and $C = (-\sqrt{b(r-1)}, -\sqrt{b(r-1)}, r-1)$. The Jacobi matrix for Eqs.(23) has the form

$$J(x_1, x_2, x_3) = \begin{pmatrix} -\sigma & \sigma & 0 \\ r - x_3 & -1 & -x_1 \\ x_2 & x_1 & -b \end{pmatrix}.$$

We see that $\det(J(0, 0, 0) - \lambda \mathbf{I}) = -(\lambda - b)((\lambda + 1)(\lambda + \sigma))$. Hence,

$$\lambda^2 + (\sigma + 1)\lambda + \sigma(1 - r) = 0.$$

Therefore, for $r < 1$ the trivial solution is asymptotically stable. For $r > 1$ the origin is unstable. The points B and C are stable until r reaches the value $r_c = \frac{\sigma(\sigma+b+3)}{\sigma-b-1}$. For $r > r_c$ both of these points are unstable. This suggests that for $r > 1$ convection movement starts with every small perturbation of the origin $(0, 0, 0)$. If $1 < r < r_c$, the characteristic values are as follows: one of them is real negative, another two are complex with negative real part. If $r = r_c$ we have a Hopf bifurcation. But obtained cycles are unstable. The solution encircle the point B some times and goes to the point C . Then its encircle the point C some times and so on.

As a conclusion we can say that exactly the same methods as for Eqs.(22) can be used to study n -dimensional food chain or n -dimensional competitive system (these systems have structures like Eqs.(22) or Eqs.(16)).

4.3 Exercises.

1. Check boundness of solutions to Eqs.(22) and (23).
2. Check the identity (24).
3. Check existence and co-existence of constant solutions to Eqs.(22).
4. Use the linearization theorem to show stability or instability of constant solutions to Eqs.(22).
5. Check global stability of constant solutions D and B to Eqs.(22).
6. Check boundness of solutions to Eqs.(22) and (23).
7. Use the linearization theorem to show stability or instability of constant solutions to Eqs.(23).

5 Equations with one discrete delay.

In this section we focus on delay differential equations (DDE). As in the previous Sections, we start our study of equations with delay from the simplest case — linear equation. In the first Section we've analysed the model of birth and death process. For most of species we observe the following — the death process is immediate, while the birth process is delay comparing to the trigger of this process. Therefore, the model should have the form

$$\dot{N}(t) = rN(t - \tau) - sN(t), \quad (28)$$

where $N(t)$ denotes the density of the species, r and s are coefficients of birth and death, respectively, and $\tau > 0$ is the delay of birth.

Moreover, if we study both processes in cellular level, then they are both delay in comparison to the biochemical signals that initiate them. Hence, it is possible to consider

$$\dot{N}(t) = rN(t - \tau_1) - sN(t - \tau_2), \quad (29)$$

where τ_1, τ_2 are delays of birth (proliferation) and death (apoptosis). Normally, τ_1 and τ_2 have similar magnitude. In abnormal state, they can differ

dramatically. As an example we can consider a growth of tumour when apoptosis is blocked. It is possible to describe this situation using large values of τ_2 .

The last form of linear DDE, i.e.,

$$\dot{N}(t) = rN(t) - sN(t - \tau), \quad (30)$$

does not have clear biological interpretation, but it can be also compared to the process of tumour growth, where the delay of proliferation is very small such that we neglect it, while the delay of apoptosis is large.

Equations with one delay are much simpler to analyse than those with two or more delays. Therefore, in our study we focus on such a type of equations.

From the mathematical point of view, the simplest form of linear delay equation is

$$\dot{x}(t) = rx(t - \tau), \quad (31)$$

where x is a real variable and $r = \text{const}$ is either positive or negative.

Let $t_0 = 0$ and we want to find a solution to Eq.(31). At the point 0 we have

$$\dot{x}(0) = rx(-\tau)$$

and therefore, we should know the value $x(-\tau)$. Calculating $\dot{x}(t)$ for every $t \in [0, \tau]$ we use values of x at points from the interval $[-\tau, 0]$. Hence, the initial value for equation with delay is not a constant x_0 from the domain of right-hand side of equation but all values of x on $[-\tau, 0]$, i.e. a function $x_0 : [-\tau, 0] \rightarrow \mathbf{R}$. This is the first difference between ODE and DDE.

If we know the initial function x_0 , then we can calculate the solution on $[0, \tau]$. For $t \in [0, \tau]$ our equation reads as

$$\dot{x}(t) = rx_0(t - \tau),$$

i.e. it is the equation with known function describing the right-hand side. This equation can be easily integrated. Namely, integrating both sides of it with respect to $t \in [0, \tau]$ we obtain

$$\int_0^t \dot{x}(s)ds = r \int_0^t x_0(s - \tau)ds$$

and hence,

$$x(t) = x_0(0) + r \int_0^t x_0(s - \tau)ds.$$

Now, knowing values of x for $t \in [0, \tau]$, we can use the same method to calculate $x(t)$ for $t \in [\tau, 2\tau]$, and so on. Generally, knowing $x(t)$ for $t \in [(n-1)\tau, n\tau]$, we calculate

$$x(t) = x(n\tau) + r \int_{n\tau}^t x(s - \tau) ds,$$

for $t \in [n\tau, (n+1)\tau]$. The procedure described above is called the step method. It is easily seen that if x_0 is integrable, then $x(t)$ is properly defined for every $t \geq 0$.

The second difference between ODE and DDE is that two solutions with different initial values can intersect. Consider the following example

$$\dot{x}(t) = -x\left(t - \frac{\pi}{2}\right),$$

with

a) $x_0(t) = \sin t$,

b) $x_0(t) = 0$,

for $t \in \left[-\frac{\pi}{2}, 0\right]$.

It is obvious that in Case b) the solution is identical to 0, i.e. $x(t) = 0$ for $t \geq 0$.

In Case a) we use the step method. Let $t \in \left[0, \frac{\pi}{2}\right]$. Then

$$\dot{x}(t) = -\sin\left(t - \frac{\pi}{2}\right) = \cos t.$$

Integrating from 0 to t we obtain

$$x(t) = x_0(0) + \sin t - \sin 0 = \sin t.$$

For $t \in \left[(n-1)\frac{\pi}{2}, n\frac{\pi}{2}\right]$ we get

$$x(t) = x\left(n\frac{\pi}{2}\right) + \sin t \Big|_{n\tau}^t = \sin t.$$

Hence, $x(t) = \sin t$ for every $t \geq 0$.

It is obvious that both solutions intersect in every point $k\pi$ for $k \in \mathbf{N}$. It does not contradict uniqueness of solutions because these solutions should be considered in another space (not in \mathbf{R}). The proper space is suggested by initial data. In general case we need to have continuous initial data, i.e.

continuous function $x : [-\tau, 0] \rightarrow \mathbf{R}$. It is a Banach space (a normed linear space is called a Banach space if all Cauchy sequences are convergent; a sequence (a_n) is a Cauchy sequence if for every $\epsilon > 0$, there exists $N \in \mathbf{N}$ such that for every $n, m \geq N$ the inequality $|a_n - a_m| < \epsilon$ is satisfied). Hence, we should consider the solution $x(t)$ as a function from this space. How to do it? For every fixed $t \geq 0$ we define $x_t : [-\tau, 0] \rightarrow \mathbf{R}$ as $x_t(h) = x(t+h)$, where $x(t)$ is the solution for the initial function x_0 . This solution is continuous and hence, x_t is in our Banach space. All properties and theorems for delay equations are considered in this Banach space. This means that our equation is infinite-dimensional. This is a difficult theory and we only mention about it.

Coming back to Eq.(31) and the step method we see that the recurrent formula for finding solutions is not so easy. Even for the simplest constant initial function we obtain the polynomials of the more and more high degree on next intervals $[n\tau, (n+1)\tau]$. Consider Eq.(31) with the constant initial function $x_0 = 1$. Then for $t \in [0, \tau]$ we have $\dot{x} = r$ and therefore, $x(t) = 1 + rt$. For the second interval $t \in [\tau, 2\tau]$ we obtain the equation

$$\dot{x} = r(1 + r(t - \tau))$$

with the solution

$$\begin{aligned} x(t) &= x(\tau) + \int_{\tau}^t r(1 + r(s - \tau))ds = \\ &= 1 + r\tau + r(t - \tau) + \frac{r^2}{2}(s - \tau)\Big|_{\tau}^t = 1 + rt + \frac{r^2}{2}(t - \tau)^2 \end{aligned}$$

and so on. Hence, this formula is useful to show the existence and uniqueness of solutions, but not for calculating it. Only in special cases it is possible to find solutions analytically, in most cases we calculate it only numerically. The mathematical analysis concerns mainly local and global stability and bifurcations. As we know, changes of stability and bifurcations are connected with the changes of some parameter of the model. In this section we focus on delays. From the mathematical point of view, the delay can be treated as a parameter of the model. The only difficulty appear when delay tends to 0. In such a case we should be very careful. On the other hand, for every fixed delay $\tau > 0$, substituting $s = \frac{t}{\tau}$ we get

$$\frac{d}{ds}x = r\tau x(s - 1)$$

from Eq.(31). It is the equation with parameter τ and the delay equal to 1. The same substitution we can use for every model with delay.

This shows that we can study stability and bifurcations with respect to the magnitude of delay.

As we know, we start stability analysis from finding constant solutions. It is obvious that constant solutions for the system with positive delay are the same as for the system without delay, i.e. $\tau = 0$. Clearly, if the solution is constant, then it does not depend on t and also on $t - \tau$. Hence, the only constant solution to Eq.(31) is $x = 0$.

The behaviour of solutions and stability or instability of the trivial solution depends on the sign of r and on the magnitude of τ , for negative r . Studying stability we are looking for exponential solutions to our equations and generate the characteristic quasi-polynomial, i.e. if $x(t) = ce^{\lambda t}$, $c, \lambda \neq 0$ is a solution to Eq.(31), then

$$c\lambda e^{\lambda t} = rce^{\lambda(t-\tau)}$$

and therefore,

$$W(\lambda) = \lambda - re^{-\lambda\tau} = 0.$$

The equation above is called the characteristic or transcendental equation. Comparing to the case without delay, this methods leads to finding the characteristic polynomial. In the case with non-zero delay, zeros of $W(\lambda)$ are also called characteristic values. The difference is that there are infinitely many characteristic values in the case with $\tau > 0$. We cannot calculate all of them. We need some other methods to check when real parts of characteristic values are negative (that implies stability).

One of the useful methods of local stability analysis is so-called Mikhailov criterion. It is the general criterion for the system of delay differential equations. We present it for the case with one delay, but it can be used for arbitrary number of different delays and delay in integral form. Assume that the characteristic quasi-polynomial of the system has the form

$$W(\lambda) = P(\lambda) + Q(\lambda)e^{-\lambda\tau},$$

where P and Q are polynomials with $\deg Q < \deg P$ and the characteristic equation $W(\lambda) = 0$ has no root on the imaginary axis. We study the total change of argument of the vector $W(i\omega)$ as ω increases from 0 to $+\infty$. If this

change is equal to $\frac{\pi}{2} \deg P$, where $\deg P$ is the degree of P , then we obtain stability. Other values imply instability.

The end of the vector $W(i\omega)$ describes the curve in the complex plain. We call this curve the Mikhailov hodograph. Stability is connected with the shape of this curve. We cannot use the Mikhailov criterion, if the hodograph crosses the point $(0, 0)$. If the hodograph encircle the origin $(0, 0)$ with positive direction of the proper angle, then we have stability. As an example of the usage of this criterion we study stability for the three-dimensional system of ODEs (originally, the criterion was formulated by Mikhailov for ODEs). Hence, the characteristic polynomial has the following form

$$W(\lambda) = \lambda^3 + a\lambda^2 + b\lambda + c$$

and substituting $\lambda = i\omega$ we get

$$f_1(\omega) = \Re(W(i\omega)) = -a\omega^2 + c \text{ and } f_2(\omega) = \Im(W(i\omega)) = -\omega^3 + b\omega.$$

To study the shape of Mikhailov hodograph we need to know the behaviour of f_1 and f_2 . It depends on parameters a , b and c . The argument for $\omega = 0$ is simply 0. Hence, to obtain stability we need that the hodograph goes into the positive direction in complex plain and makes the angle $\frac{3}{2}\pi$. If $a < 0$, then f_1 is increasing. Independently on the initial behaviour of f_2 , the hodograph stays in the fourth quarter of \mathbf{R}^2 for large values of ω (precisely, for $b \leq 0$ the function f_2 is decreasing, and then the hodograph stays in this quarter for all $\omega > 0$, if $b > 0$, then f_2 achieves its maximal value at $\omega = \sqrt{\frac{b}{c}}$ and next increases). Therefore, the total change of the argument is from 0 to $-\frac{\pi}{2}$. Hence, it is equal to $-\frac{\pi}{2} \neq \frac{3\pi}{2}$. This implies instability. Similarly, if $a = 0$, then $f_1 = c$ for all $\omega \geq 0$ and the hodograph stays on the straight line $\Re = c$. It also stays in the fourth quarter for sufficiently large ω that proves instability. For $a > 0$ the function f_1 is decreasing. If $b \leq 0$, then f_2 is also decreasing, the the hodograph switches from the fourth to the third quarter of \mathbf{R}^2 for large ω . This implies that the change of argument is equal to $-\frac{\pi}{2}$ and we obtain instability. If $b > 0$, then f_2 is increasing for $\omega < \sqrt{\frac{b}{c}}$ and in this case we can obtain that the hodograph encircle the origin in positive direction. It is possible when $f_2(\omega) = 0$ for such a value of ω , for which $f_1(\omega) < 0$. This means that $-ab + c < 0$. Hence, the inequality $c < ab$ implies stability. For $c > ab$ the hodograph do not encircle the origin in positive direction and this implies instability.

Now, we use the criterion to study eq.(31).

1) Case $r > 0$. The characteristic equation is

$$\lambda = re^{-\lambda\tau}.$$

Comparing the functions $f_1(\lambda) = \lambda$ and $f_2(\lambda) = re^{-\lambda\tau}$ we see that there exists $\bar{\lambda} > 0$ such that $f_1(\bar{\lambda}) = f_2(\bar{\lambda})$, which implies that $\bar{\lambda}$ is the characteristic value with positive real part (here, $\bar{\lambda}$ is real and therefore, $\Re(\bar{\lambda}) = \bar{\lambda} > 0$). Hence, the trivial solution is unstable.

In this case we can tell something more. Assume that the initial function is positive, $x_0(t) > 0$ for $t \in [-\tau, 0]$. Then for $t \in [0, \tau]$ we obtain $\dot{x} = rx(t-\tau) > 0$ which implies that $x(t)$ is increasing and hence, positive. Using the step method we show that the solution is increasing and positive for every $t \geq 0$. This implies that the solution is increasing to ∞ . If not, then it is increasing and bounded. Hence, it has a finite limit. As for ODEs, the only possible limit is a constant solution. In our case, $x(t)$ cannot tend to 0 which means that it is unbounded. The same result we obtain under the weaker assumption that x_0 is non-negative and positive on some interval contained in $[-\tau, 0]$. On the other hand, if x_0 is negative, then $\dot{x} < 0$ and the solution $x(t)$ decreases to $-\infty$.

2) Case $r < 0$. Let $r = -a$, with $a > 0$. The characteristic equation is

$$W(\lambda) = \lambda + ae^{-\lambda\tau} = 0.$$

We study characteristic values using the Mikhailov criterion. For $\lambda = i\omega$, we have

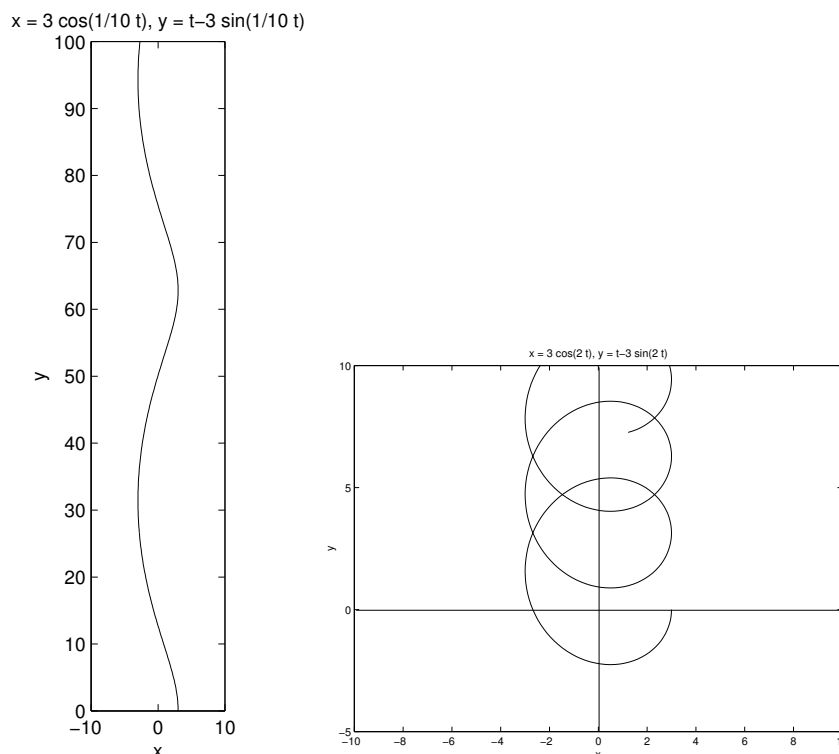
$$W(i\omega) = \Re + i\Im, \quad \Re = a \cos(\omega\tau), \quad \Im = \omega - a \sin(\omega\tau).$$

If $\tau = 0$, then $\Re = a > 0$ and $\Im = 0$ and hence, $\arg W(0) = 0$. It is the case when we have stability for the model without delay (while for the previous Case, the trivial solution is unstable for $\tau = 0$).

If $\arg W(i\omega)$ increases to $\frac{\pi}{2}$, then the Mikhailov criterion implies stability. It is obvious that \Re oscillate round 0 as a cosine function. If \Im is increasing, then the total increase of $\arg W(i\omega)$ is equal to $\frac{\pi}{2}$. The same total change we have until $\Im > 0$ for every $\omega > 0$ such that $\Re = 0$. Identity $\Re = 0$ implies $\omega\tau = \frac{\pi}{2} + k\pi$. Therefore, for fixed τ we obtain sequences $\omega_k = \frac{1}{\tau} \left(\frac{\pi}{2} + k\pi \right)$ and $\Im_k = \omega_k \pm a$. The sequence ω_k is increasing. Therefore, $\Im_k > 0$ for every $k \in \mathbf{N}$ only if $\Im_0 > 0$, i.e. $\omega_0 > a$. The last inequality is equivalent to

$$a\tau < \frac{\pi}{2}.$$

At $a\tau = \frac{\pi}{2}$ there appear a pair of purely imaginary conjugate characteristic values. It can be show that these characteristic values crosses the imaginary axis from the left to the right-hand side and therefore, the trivial solution looses stability. It is due to the positivity of derivative of the real part of these characteristic values. If τ increases, then the next pair appear. The derivative is also positive and hence, the solution cannot stay stable.



Examples of Mikhailov hodographs for stable and unstable cases.

In Case $r > 0$ we were able to show positivity of solutions with positive initial function. In this case it is not so obvious. Moreover, for every $a > 0$ we can find an initial function such that $x(\tau) < 0$ for large values of delay. Assume that $x_0(t) = C > 0$ for $t \in [-\tau, 0]$. Then $\dot{x}(t) = -aC$ for $t \in [0, \tau]$. Hence, $x(\tau) = C - aC\tau$ and if $\tau > \frac{1}{a}$, then $x(\tau) < 0$. Therefore, if r is negative, then positivity of solutions is not conserved.

It should be noticed, that we have the same result concerning stability for every model with one discrete delay. If for $\tau = 0$ we have stability, then the solution is also stable for small delays. If the solution looses stability for some value of the delay parameter, then it is unstable for every greater

delays. If for $\tau = 0$ we have instability, then the solution is unstable for small delays. It is due to continuous dependence of solutions on parameters (on the delay in our case). The dynamics of characteristic values is always such that they cross imaginary axis from the left to the right. Therefore, instability preserves for every positive values of delay.

In the case of one DDE with two or more delays or the system of at least two DDEs so-called stability switches can occur. In such a case, if purely imaginary characteristic values appear, then the dynamics in the complex plane is not necessary in the right-hand side direction. Therefore, the studied solution can loose stability at some τ_c^1 but get it back at $\tau_c^2 > \tau_c^1$ and so on.

Another problem is the Hopf bifurcation arising when the solution loses stability. We study this bifurcation with the delay as a parameter of bifurcation. It occurs that we only need to check the derivative $\frac{dx}{d\tau}(\tau_c)$, where x denotes a real part of the characteristic value and $\tau_c = \frac{\pi}{2a}$ is the threshold value of delay. Let $\lambda(\tau) = x(\tau) + iy(\tau)$ denotes a characteristic value. Then,

$$\begin{cases} x &= -ae^{-x\tau} \cos y\tau \\ y &= ae^{-x\tau} \sin y\tau. \end{cases} \quad (32)$$

Using the theorem of implicit function one calculates

$$\frac{dx}{d\tau}(\tau_c) = \frac{a^2}{\frac{\pi^2}{4} + 1},$$

which is positive. Then, the Hopf bifurcation occurs for τ_c and the nontrivial stationary solution loses stability at this point.

Similarly, we can study the more general linear equation of the form

$$\dot{x}(t) = ax(t) + bx(t - \tau), \quad (33)$$

for different non-zero values of a and b . Eqs.(28) and (30) are the examples of Eq.(33) with a and b of different signs.

To show existence and uniqueness of solutions to Eq.(33) we use the step method. Let $x_0 : [-\tau, 0] \rightarrow \mathbf{R}$ be a continuous function. For $t \in [0, \tau]$ we get

$$\dot{x}(t) = ax(t) + bx_0(t - \tau)$$

which is the linear non-homogenous equation. This type of equation can be solved using the variation of constant method. In this method we solve homogenous equation

$$\dot{x} = ax$$

and obtain the general solution of the form $x(t) = Ce^{at}$. Next, we are looking for a special solution to non-homogenous equation of the same form with $C = C(t)$, i.e. we assume that C is a function of t . Hence,

$$\dot{C}e^{at} + Ca e^{at} = aCe^{at} + bx_0(t - \tau)$$

which implies $C(t) = b \int e^{-at} x_0(t - \tau)$. The general solution to non-homogenous equation is the sum of general solution to homogenous one and this special solution found above. Using an initial value we obtain

$$x(t) = x_0(0)e^{at} + be^{at} \int_0^t e^{-as} x_0(s - \tau) ds,$$

for $t \in [0, \tau]$. This formula guaranties existence and uniqueness of solution on $[0, \tau]$. The step method implies that the solution exists and it is unique for every $t \geq 0$.

Now we focus on stability of unique constant solution $x = 0$. As we know, the most important for stability in the case of positive delay is stability for non-zero delay. Hence, if $a + b > 0$, then the trivial solution is unstable for $\tau = 0$ and it stays unstable for $\tau > 0$. Therefore, we study Eq.(33) only for $a + b < 0$. We have three cases.

1) For $a, b < 0$ we rewrite Eq.(33) in the form $\dot{x}(t) = -\alpha x(t) - \beta x(t - \tau)$ with positive α and β . The characteristic equation is $\lambda + \alpha + \beta e^{-\lambda\tau} = 0$ and

$$W(i\omega) = i\omega + \alpha + \beta \cos(\omega\tau) - i\beta \sin(\omega\tau).$$

The imaginary part is the same as for Eq.(31) and the real part is translated on α . Hence, if we compare Mikhailov hodographs, we obtain the same curve translated on α in the real direction in complex plane. This implies that if $\alpha > \beta$, then the hodograph for Eq.(33) stays in the right-hand side of the complex plane and does not encircle the origin that implies stability independently on the magnitude of delay. If $\alpha < \beta$, then there exists τ for which Eq.(33) loses stability. For this delay we have $\Re = \Im = 0$ and therefore,

$$\cos(\omega\tau) = -\frac{\alpha}{\beta} \text{ and } \omega = \beta \sin(\omega\tau).$$

Finally,

$$\tau = \frac{\arccos\left(-\frac{\alpha}{\beta}\right)}{\sqrt{\alpha^2 + \beta^2}}.$$

This implies that the trivial solution loses stability later than in the case $r < 0$ for Eq.(31).

2) For $a > 0$ and $b < 0$ we rewrite Eq.(33) in the following form $\dot{x} = ax(t) - \beta x(t - \tau)$, with $\beta > 0$. In this case we have

$$W(i\omega) = i\omega - a + \beta \cos(\omega\tau) - i\beta \sin(\omega\tau)$$

and the change of stability occurs when $\cos(\omega\tau) = \frac{a}{\beta}$. Hence, $\tau = \frac{\arccos(\frac{a}{\beta})}{\sqrt{a^2 + \beta^2}}$, that is earlier than for Eq.(31).

3) For $a < 0$ and $b > 0$, we have the real part of characteristic value equal to $-a - b \cos(\omega\tau)$ and due to the assumption $a + b < 0$ the Mikhailov hodograph stays in the right-hand side of the complex plane. Therefore, the trivial solution is stable independently on the delay.

Finally, we focus on global stability. Generally, finding Lapunov functionals for DDEs is difficult ("functional" means a real-valued function with the domain contained in some space of functions). To obtain global stability of the solution using Lapunov functionals we need something more than in the case without delay. One of the theorems about Lapunov functionals implies that if V is a Lapunov functional for DDE on some set G and M is the maximal invariant set for which the derivative of V along the solution is equal to 0, then every bounded solution with initial function $x_0 \in G$ tends to M as $t \rightarrow +\infty$.

Consider DDE of the form $\dot{x}(t) = -ax(t) + bx(t - \tau)$ with $a > |b|$ and Lapunov functional

$$V(x(t)) = \frac{1}{2} \left(x^2(t) + |b| \int_{t-\tau}^t x^2(s) ds \right). \quad (34)$$

It is easily seen that $V(x)$ is non-negative and $V(x) = 0$ only if $x(t) \equiv 0$. We can show that every solution to our equation is bounded. Clearly, if $|x_0| \leq K$, then

$$|x(t)| \leq Ke^{-at} + |b|e^{-at} \int_0^t Ke^{as} ds,$$

for $t \in [0, \tau]$. Thus, $|x(t)| \leq Ke^{-at} + K|b|e^{-at} \frac{e^{at} - 1}{a} \leq K$. Using the step method we show that $|x(t)| \leq K$ for every $t \geq 0$. Next, we calculate the derivative along a solution. The second term of the right-hand side of V is a function of upper (and lower) limits of the integral. Let $f(t) = \int_0^t g(s) ds$

be a function of upper limit for continuous function g . Then f is integrable and $\dot{f}(t) = g(t)$. Hence, calculating the derivative of V along the solution to our equation we obtain

$$\begin{aligned}\dot{V}(x(t)) &= x(t)\dot{x}(t) + \frac{|b|}{2} (x^2(t) - x^2(t - \tau)) = \\ &= -ax^2(t) + bx(t)x(t - \tau) + \frac{|b|}{2} (x^2(t) - x^2(t - \tau)).\end{aligned}$$

Next, using the identity $(x(t) \pm x(t - \tau))^2 = x^2(t) \pm 2x(t)x(t - \tau) + x^2(t - \tau)$ we get

$$\dot{V}(x(t)) = -\frac{|b|}{2} (x(t) \pm x(t - \tau))^2 - (a - |b|)x^2(t) \leq 0.$$

The maximal invariant set such that $\dot{V}(x(t)) = 0$ is the trivial solution that implies global stability of the trivial solution.

5.1 Non-linear models with delay — delay logistic equation.

In this section we study more general case — non-linear equation with one discrete delay of the form

$$\dot{x}(t) = F(x(t), x(t - \tau)) \tag{35}$$

with continuous initial function $x_0 : [-\tau, 0] \rightarrow \mathbf{R}$. As we know from the previous Section, we should study this equation in the Banach space of continuous function defined on $[-\tau, 0]$ but it is possible to analyse main properties using simpler real space and standard analytical methods. We do not treat the function F as defined on this Banach space but simply on \mathbf{R}^2 where $x(t)$ and $x(t - \tau)$ are two variables, i.e. $(x(t), x(t - \tau)) \in \mathbf{R}^2$. Hence, F is continuous if it is continuous as the function of these two variables. Differentiability of F should be studied in the sense of Frechet in Banach space but it can be reduced to differentiability in \mathbf{R}^2 and so on.

Theorems about existence and uniqueness of solutions are exactly the same as in the case of ODE. If F is a Lipschitz function (with respect to two-dimensional variable $(x(t), x(t - \tau)) \in \mathbf{R}^2$), then for every continuous initial function x_0 there exists unique solution to Eq.(35). Similarly, continuous derivative guarantees that Lipschitz conditions is locally satisfied. Hence, if

F has continuous partial derivatives with respect to $x(t)$ and $x(t - \tau)$, then there exists unique solution to Eqs.(35).

We can also use theorems of linearization, Hopf bifurcation and Lapunov functionals, as in ODE case.

5.1.1 Logistic equation.

As an example of non-linear delay equation we study the delay logistic equation. The classical form of this equation reads as

$$\dot{N}(t) = rN(t) \left(1 - \frac{N(t - \tau)}{K} \right), \quad (36)$$

with the same notation as for Eq.(4). Eq.(36) has the following biological interpretation. In the equation without delay we assume that the influence of competition on the dynamics of the described species is immediate. It is not necessary true. Consider a herbivorous species and its net reproduction per one individual. If in the previous season large number of individuals have eaten much food, then it may lead to reduction of this herbivore present season and individuals cannot spend much energy for reproduction. Therefore, the net reproduction per one individual does not depend on the present density ($N(t)$) but on the density in the previous season ($N(t - \tau)$).

The following form of the delay logistic equation was proposed to describe EAT (a kind of tumour in mice)

$$\dot{N}(t) = rN(t - \tau) \left(1 - \frac{N(t - \tau)}{K} \right), \quad (37)$$

where $N(t)$ denotes the concentration of tumour cells in a target organism, r is the net reproduction rate of tumour (which means the difference between proliferation and apoptosis) and K is the carrying capacity. Delay τ reflects the length of cell cycle.

For both models, Eqs.(36) and (37), we define an initial non-negative continuous function $N_0 : [-\tau, 0] \rightarrow \mathbf{R}^+$. Using the step method we show that the solution to Eqs.(36) and (37) is defined for every $t \geq 0$. Namely, for Eq.(36) we obtain the recurrent formula

$$N(t) = N(n\tau) e^{r \int_{(n-1)\tau}^{t-\tau} r \left(1 - \frac{N(s)}{K} \right) ds},$$

while for Eq.(37),

$$N(t) = N(n\tau) + r \int_{(n-1)\tau}^{t-\tau} N(s) \left(1 - \frac{N(s)}{K}\right) ds,$$

for $t \in [n\tau, (n+1)\tau]$ and $n \in \mathbf{N}$. The form of recurrent formula for Eq.(36) implies that the solution with non-negative initial function is non-negative. Moreover, if $N(0) > 0$, then the solution is positive. It is not true for Eq.(37). It occurs that the solution for non-negative N_0 may be negative. It can be shown that if $N_0(t) \in [0, K]$ for $t \in [-\tau, 0]$, then

1. if $r\tau > p_1$, where p_1 is the greatest root of the polynomial $W_1(x) = -\frac{1}{48}x^3 - \frac{1}{8}x^2 + \frac{1}{4}x + 1$, then there exists an initial function N_0 such that the corresponding solution to Eq.(37) has negative values;
2. if $r\tau < p_2$, where p_2 is the greatest root of the polynomial $W_2(x) = -\frac{1}{16}x^3 - \frac{1}{4}x^2 + 1$, then the corresponding solution to Eq.(37) is nonnegative.

This property of non-negativity or possible negativity of appropriate solutions is the main difference between Eq.(36) and Eq.(37). It is easy to see that if the solution to Eq.(37) is negative on some interval of the length equal to τ , then it tends to $-\infty$ as $t \rightarrow +\infty$. If this solution is non-negative, then it has similar properties as in the case of Eq.(36).

It is also possible to show that solutions to both equations are bounded above.

Now, we focus on critical points and their stability. Eqs.(36) and (37) have two stationary solutions — the trivial one and the nontrivial carrying capacity K .

We study stability using the standard linearization theorem. For the trivial solution, we assume that the solution $N(t)$ has a very small norm $|N(t)| < \epsilon$ and therefore, we neglect terms of the higher order. Hence, for Eq.(36) the linearized equation is simply $\dot{x} = rx(t)$, i.e. it is an equation without delay. The characteristic value is equal to $r > 0$. As we remember from the theory of ODE, the non-linear part should be small to use the linearization method. Here, the non-linear part is equal to $f(x(t), x(t-\tau)) = -\frac{r}{K}x(t)x(t-\tau)$. If we treat the function f as a function of two variables $x_1 = x(t)$ and $x_2 = x(t-\tau)$, then we need to show that

$$\lim_{(x_1, x_2) \rightarrow (0, 0)} \left| \frac{f(x_1, x_2)}{\sqrt{x_1^2 + x_2^2}} \right| = 0.$$

We have

$$\left| \frac{f(x_1, x_2)}{\sqrt{x_1^2 + x_2^2}} \right| = \frac{r}{K} \left| \frac{x_1 x_2}{\sqrt{x_1^2 + x_2^2}} \right|$$

and due to inequality $\pm x_1 x_2 \leq \frac{1}{2}(x_1^2 + x_2^2)$, we obtain

$$\left| \frac{f(x_1, x_2)}{\sqrt{x_1^2 + x_2^2}} \right| \leq \frac{r}{2K} \frac{x_1^2 + x_2^2}{\sqrt{x_1^2 + x_2^2}} = \frac{r}{2K} \sqrt{x_1^2 + x_2^2}$$

that tend to 0 as $(x_1, x_2) \rightarrow (0, 0)$. Hence, the linearization theorem implies instability of the trivial solution.

For Eq.(37) the linearized equation is of the form

$$\dot{x} = rx(t - \tau). \quad (38)$$

To use the linearization theorem for non-trivial solution we substitute $x(t) = N(t) - K$ and obtain the same linearized equation for both models, i.e.,

$$\dot{x} = -rx(t - \tau). \quad (39)$$

The characteristic quasi-polynomial for both Eqs.(38) and (39) has the same form

$$W(\lambda) = \lambda + be^{-\lambda\tau} = 0, \quad (40)$$

where $b = -r$ for the trivial solution to Eq.(37) and $b = r$ for the non-trivial solution to both models. We apply the analysis for linear equations from the previous Subsection. Hence, the trivial solution is unstable independently on the delay. The non-trivial solution loses stability for $r\tau = \frac{\pi}{2}$. We also know that the Hopf bifurcation occurs at $\tau = \frac{\pi}{2r}$.

5.1.2 Lapunov functionals for non-linear equations.

At the beginning of this Section we've mentioned that finding Lapunov functionals for DDEs is not easy. Now, we give an example where Lapunov functional is a combination of Eq.(19) for ODE and Eq.(34). Consider the following form of non-linear DDE

$$\dot{x}(t) = x(t) (a - bx(t) - cx(t - \tau)), \quad (41)$$

with $a, b, c > 0$ and $b > c$ and non-negative initial function such that $x_0(0) > 0$. The form of Eq.(41) implies that the solution is positive for such initial

function (as in the case of classic logistic equation, Eq.(36)). Therefore, we can estimate $\dot{x}(t) \leq x(t)(a - bx(t))$ that implies boundness of solutions for positive initial functions. It is obvious that Eq.(41) has one non-trivial critical point $x^* = \frac{a}{b+c}$ and therefore, the equation can be rewritten as

$$\dot{x}(t) = -x(t) (b(x(t) - x^*) + c(x(t - \tau) - x^*)).$$

Let define the following Lapunov functional

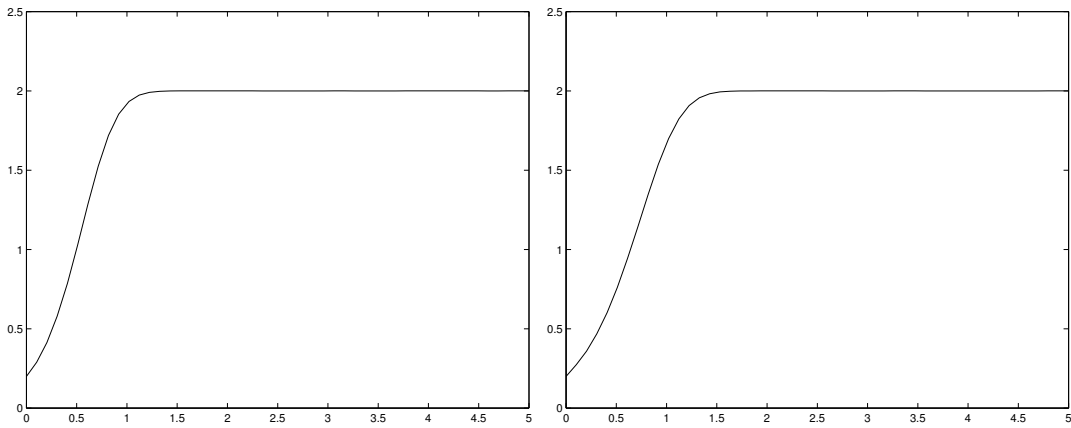
$$V(x(t)) = x(t) - x^* - x^* \ln \frac{x(t)}{x^*} + \frac{c}{2} \int_{t-\tau}^t (x(s) - x^*)^2 ds$$

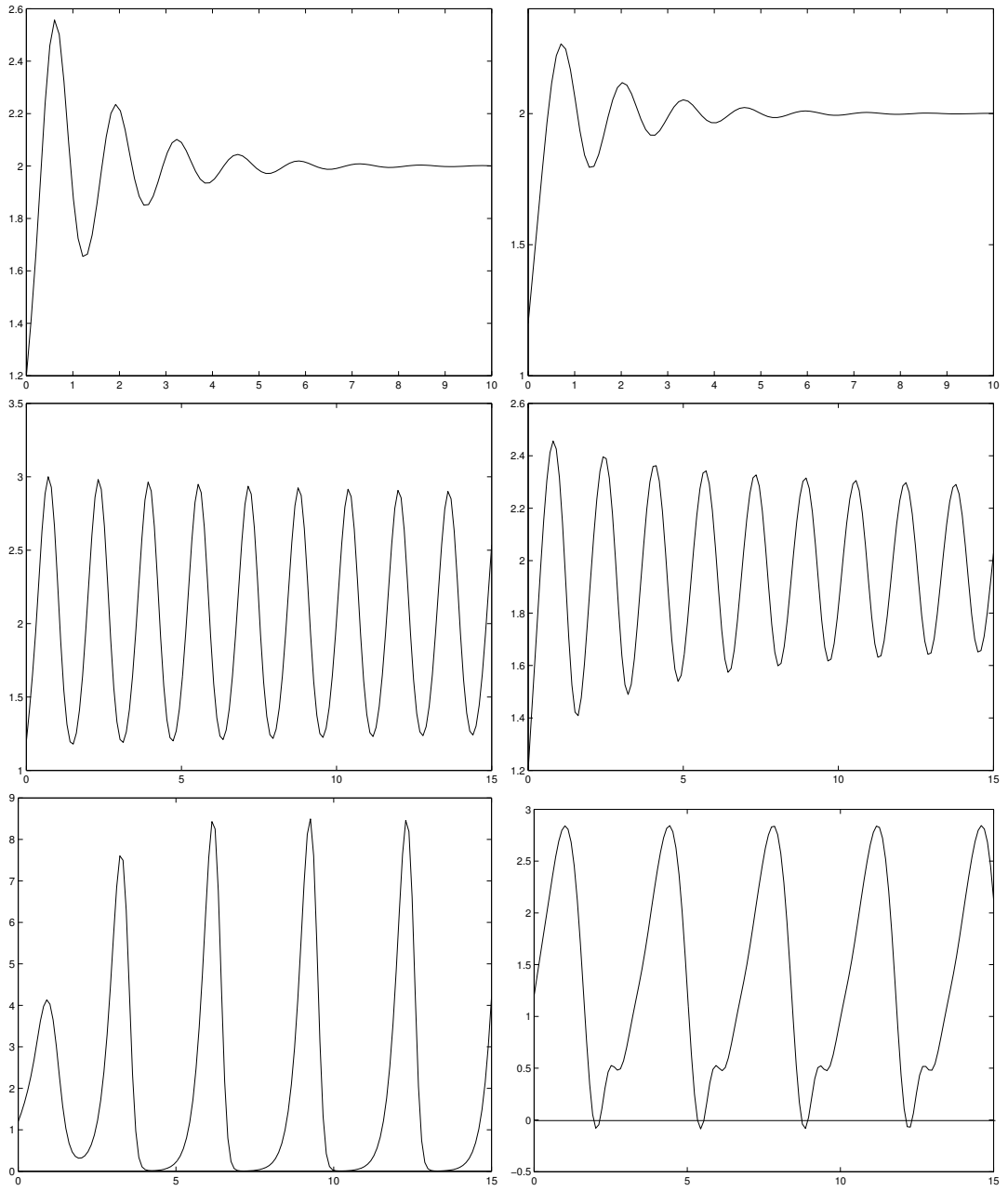
for positive $x(t)$. Hence, $V(x)$ is properly defined and $V(x(t)) \geq 0$ and $V(x(t)) = 0 \iff x(t) = x^*$.

Calculating the derivative along the solution we obtain

$$\begin{aligned} \dot{V}(x(t)) &= \dot{x}(t) - \frac{x^*}{x(t)} \dot{x}(t) + \frac{c}{2} ((x(t) - x^*)^2 - (x(t - \tau) - x^*)^2) = \\ &= -x(t) \frac{x(t) - x^*}{x(t)} (b(x(t) - x^*) + c(x(t - \tau) - x^*)) \\ &\quad + \frac{c}{2} ((x(t) - x^*)^2 - (x(t - \tau) - x^*)^2) = \\ &= -\frac{c}{2} ((x(t) - x^*) - (x(t - \tau) - x^*))^2 - (b - c)(x(t) - x^*)^2 \leq 0. \end{aligned}$$

The invariant set for which the derivative above is equal to 0 is the constant solution x^* . This implies global (in \mathbf{R}^+) stability of the non-trivial solution x^* .





Similarities and differences between solutions to Eqs.(36) and (37).

6 Appendix. Matlab files for creating figures presented above.

1. Discrete birth process.

```
function [n] = birth(n)
x=[1:n]
for
i=1:n, y(i) = any(i);
end
plot(x,y,'o k')
axis([0 11 -10 600]);
function f=any(n)
r=2;
a=1;
if n<1
f=r*any(n-1);
else
f=a;
end
```

2. Continuous birth process.

```
function birthcon
t=sym('t');
a=0.2;
c=2;
tk=10;
y=c*exp(a*t)
ezplot(t,y,[0,tk])
axis([0 10 1.9 15]);
```

3. Solutions to continuous logistic equation.

```
function logisticcon
t=sym('t');
K=1;
a=2; b=0.1; c=0.7; r=3; tk=3.5;
y1=a*K/(a+(K-a)*exp(-r*t));
ezplot(t,y1,[0,tk]); drawnow; hold on;
y2=b*K/(b+(K-b)*exp(-r*t));
```

```

ezplot(t,y2,[0,tk]); drawnow;
y3=c*K/(c+(K-c)*exp(-r*t));
ezplot(t,y3,[0,tk]); drawnow; hold off;
axis([0 3.5 0 2.2]);

```

4. Phase portrait for logistic continuous equation.

```

function logisticfaz
t=sym('t');
K=1; r=2.8; tk=1.3;
y1=r*t*(K-t)/K;
ezplot(t,y1,[-0.3,tk]);
axis([-0.3 1.3 -1.1 0.8]);

```

5. Phase portraits for discrete logistic equation.

```

function logisticfaz1
t=sym('t');
K=1; r=2.8; tk=1.1;
y1=r*t*(K-t)/K;
ezplot(t,y1,[0,tk]); drawnow; hold on;
y2=t;
ezplot(t,y2,[0,tk]); hold off;
axis([0 1 0 0.8]);

```

6. Solutions to discrete logistic equation.

```

function [n] = logisticdis1(n)
x=[1:n];
r = 4; a = 0.3; y(1) = a;
for i=2:n,
y(i) = r*y(i-1)*(1-y(i-1));
end
plot(x,y,'o r');

```

7. Phase portrait for discrete logistic equation in the case of periodic solution with period 2.

```

function logisticfaz2
t=sym('t');
r=3.5; tk=1.1;
y1=r*r*t*(1-t)*(1-r*t+r*t*t);
ezplot(t,y1,[0,tk]); drawnow; hold on;
y2=t;

```

```
ezplot(t,y2,[0,tk]); hold off;
axis([0.5 1 0.3 1]);
```

8. Fingenbaum tree.

```
function tree
END=500
hold on
for i=1:END,
r = 1 + i*(3/END); a = 0.5;
for j=1:100,
a = r*a*(1-a);
end
for j=1:100,
a = r*a*(1-a);
plot(r,a);
end;
end;
hold off
```

9. Phase portrait for linear systems of two ODEs.

```
function linear1
tspan=[0,5];
options=odeset('OutputFcn',@odephas2);
sol=ode23(@f,tspan,[0.5,1],options);
axis([-1 1 -1 1]);
hold on;
sol=ode23(@f,tspan,[2 1],options);
hold on;
sol=ode23(@f,tspan,[-0.5 -1],options);
hold on;
sol=ode23(@f,tspan,[0 1],options);
hold on;
sol=ode23(@f,tspan,[-2 0],options);
hold on;
sol=ode23(@f,tspan,[0 -1],options);
hold on;
sol=ode23(@f,tspan,[2 0],options);
hold on;
sol=ode23(@f,tspan,[-0.5 1],options);
```

```

hold on;
sol=ode23(@f,tspan,[0.5 -1],options);
hold on;
sol=ode23(@f,tspan,[-2,1],options);
hold on;
sol=ode23(@f,tspan,[-2,-1],options);
hold on;
sol=ode23(@f,tspan,[2,-1],options);
hold off;
function yp=f(t,y)
a=1; b=3; c=0.1; d=0.1;
yp=zeros(2,1);
yp(1)=-a*y(1);
yp(2)=-b*y(2);

```

10. Lotka-Volterra model.

```

function LV
tspan=[0,60];
options=odeset('AbsTol',1e-10,'RelTol',1e-7);
sol=ode23(@f,tspan,[2 0.3],options);
plot(sol.x,sol.y);
axis([0 60 -0.5 4]);
hold on;
sol=ode23(@f,tspan,[2 0.1],options);
plot(sol.x,sol.y);
hold off;
function yp=f(t,y)
a=2; b=0.3; r=0.1; s=1;
yp=zeros(2,1);
yp(1)=r*y(1)-a*y(1)*y(2);
yp(2)=-s*y(2)+a*b*y(1)*y(2);

```

11. Lorenz attractor.

```

function Lorenz
tspan=[0,20];
options=odeset('OutputFcn',@odephas3);
sol=ode23(@f,tspan,[0 8 27],options);
function yp=f(t,y)
s=10; r=28; b=8/3;

```

```

yp=zeros(3,1);
yp(1)=s*(y(2)-y(1));
yp(2)=r*y(1)-y(2)-y(1)*y(3);
yp(3)=-b*y(3)+y(1)*y(2);

```

12. Mikhailov hodographs.

```

function mikhailow
t=sym('t');
a=3; tau=5; tk=10;
x=a*cos(tau*t);
y=t-a*sin(tau*t);
ezplot(x,y,[0,tk])
axis([-10 10 -5 tk]);

```

13. Solutions to delay logistic equation.

```

function log1
tau=0.7;
tk=10;
tspan=[0,tk];
options=ddeSet('AbsTol',1e-12,'RelTol',1e-7);
sol=dde23(@f,tau,@history,tspan,options);
t=linspace(0,tk,10*tk);
y=ddeval(sol,t);
plot(t,y)
function yp=f(t,y,ytau)
r=4; K=2;
yp=r*ytau*(1-ytau/K);
function y=history(t)
y=1.2;

```