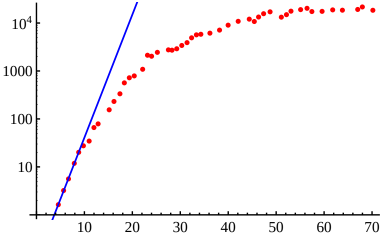
# 1.3. LOGISTIC MODEL

## 1.3.1.Definition of the model

Exponential growth is unbounded:




Exponential model:

$$N' = \alpha N$$

$\alpha$ - growth rate - constant

Idea - growth rate not constant:

$$N' = g(N)N$$

- For $N = 0,\ g(0) = \alpha$
- No growth for $N = C \rightarrow\ g(C) = 0.$
- $C$ - carrying capacity

Simplest function $g$ satisfying

$$g(0) = \alpha \quad \text{i} \quad g(C) = 0$$

is

$$g(N) = \alpha\left(1 - \frac{N}{C}\right)$$

# Logistic model:

$$N' = \alpha \left(1 - \frac{N}{C}\right) N$$

Model parameters: $\alpha$, $C$

Alternative form of the model:

$$N' = aN - bN^2$$

# Pierre Francois Verhulst

1804, Brussels, Belgium (French Empire at this time) - 1849, Brussels, Belgium

Belgian mathematician, statistician and demographist. Worked on population growth.

P.F. Verhulst (1845) Recherches mathématiques sur la loi d´accroissement de la population. Nouv. mém. de l´Académie Royale des Sci. et Belles-Lettres de Bruxelles 18:1–41.


**Verhulst model.**

Logistic model - Verhulst (1845) named the model without explanation. He plotted (*courbe logistique*) together with *courbe logarithmique* (exsponential curve)

Verhulst's logistic equation being ignored for many years until

rediscovered in year 1920. by

Raymond Pearl (1879–1940)

Lowell J. Reed (1886–1966)

Pearl, R. and L. J. Reed (1920). On the rate of growth of the population of the United States since 1870 and its mathematical representation. Proceedings of the National Academy of Sciences 6, 275–288.

Chemical chain reactions: Wilhelm Ostwald, Germany, 1883.

Statistics - logit model/transformation, logistic regression, Joseph Berkson, SAD, (1899–1982)

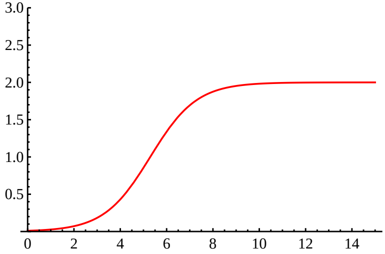
# Solving differential equation

$$N' = \alpha \left(1 - \frac{N}{C}\right) N, \quad N(0) = N_0$$

$$N(t) = \frac{1}{\frac{1}{C} + \left(\frac{1}{N_0} - \frac{1}{C}\right) \mathrm{e}^{-\alpha t}}$$

# Graph of logistic function

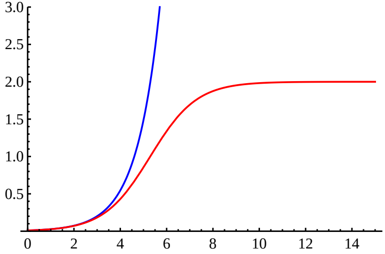
Logistic function ($\alpha = 1,\ C = 2,\ N_0 = 0.01$)



# Initial exponential growth

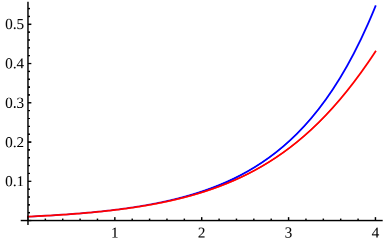
Comparison:

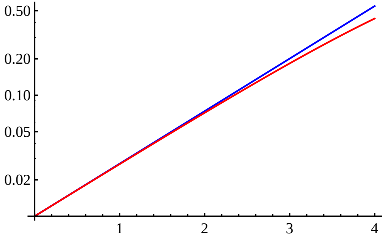
- Exponential function, $\alpha = 1,\ N_0 = 0.01$
- Logistic function, $\alpha = 1,\ C = 2,\ N_0 = 0.01$



Comparison:

- Exponential function, $\alpha = 1,\ N_0 = 0.01$
- Logistic function, $\alpha = 1,\ C = 2,\ N_0 = 0.01$

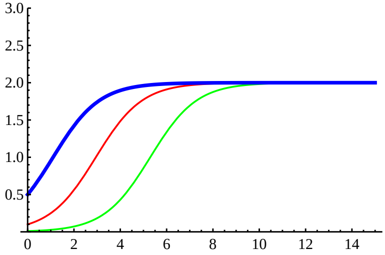


# Impact of parameter $N_0$

Logistic function, $\alpha = 1, \ C = 2$

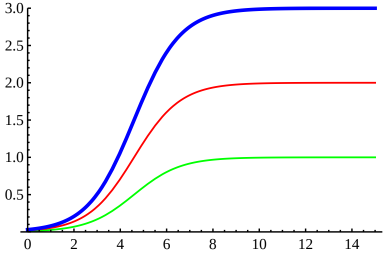
$N_0 = 0.01$ $N_0 = 0.1$ $N_0 = 0.5$



# Impact of parameter $C$

Logistic function, $\alpha = 1$

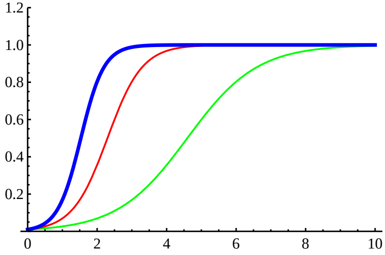
$C = 1,\ N_0 = 0.01 \quad C = 2,\ N_0 = 0.02 \quad C = 3,\ N_0 = 0.03$



# Impact of parameter $\alpha$

Logistic function, $C = 1,\ N_0 = 0.01$

$\alpha = 1$ $\alpha = 2$ $\alpha = 3$

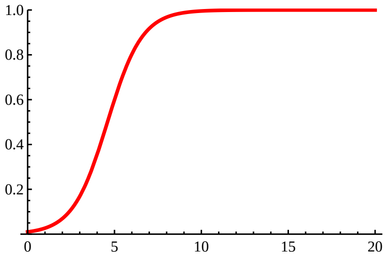


## Problem

Function $g(y) = 1 - y/C$ is not the only one satisfying conditions $g(0) = 1$ and $g(C) = 0$.
Find three different functions $g$ satisfying $g(0) = 1$ and $g(C) = 0$.

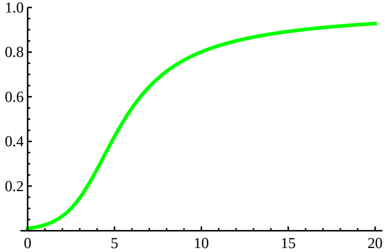
## $g(y) = 1 - y$

Model: $\quad y' = y\,(1 - y)$



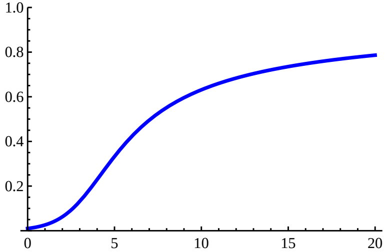
# $g(y) = (1 - y)^2$

Model: $\quad y' = y(1 - y)^2$



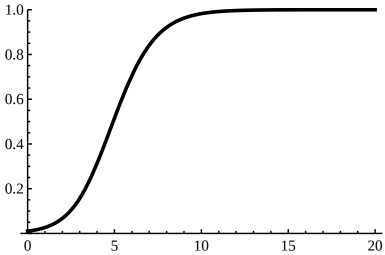
# $g(y) = (1 - y)^3$

Model: $y' = y(1-y)^3$



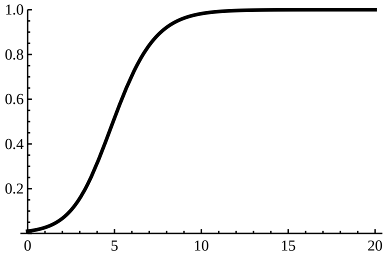
## $g(y) = \cos\left(\frac{\pi}{2}y\right)$

Model: $y' = y\cos\left(\frac{\pi}{2}y\right)$



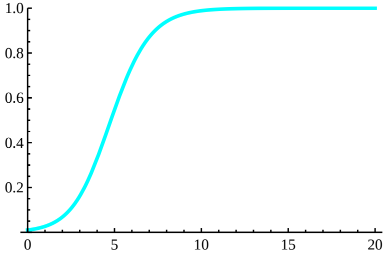
# $g(y) = \mathrm{tg}\left(\frac{\pi}{4}(1-y)\right)$

Model: $y' = y\,\mathrm{tg}\left(\frac{\pi}{4}(1-y)\right)$

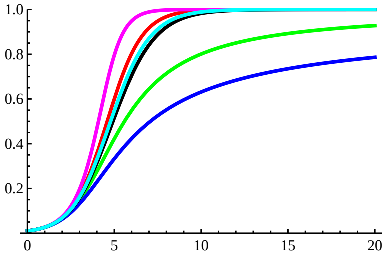


$$g(y) = \frac{\mathrm{sh}(1-y)}{\mathrm{sh}1}$$

Model: $y' = y\frac{\mathrm{sh}(1-y)}{\mathrm{sh}1}$



# Comparison.



### Problem

Obtain logistic model from the Taylor expansion of gain function using an approximation by the polynomial of third degree.

# 1.3.2. Equilibrium point.

**Definition**

For diferential equation

$$y' = f(y)$$

**equilibrium point** is a value $y^*$ such that (constant) function $y(t) = y^*$ is a solution of the differential equation.

Equilibria are sometimes called fixed points or steady states.

Note, if the solution at some time obtain value $y^*$ (come to stady state), then it remains in this state since $y(t) = y^*$ for $t \geq t_0$ is a solution of the differential equation

$$y' = f(y), \quad y(t_0) = y^*.$$

$$y(t) = y^* \quad \Rightarrow \quad y'(t) = 0 \quad \Rightarrow \quad f(y) = f(y^*) = 0$$

Equilibrium point is a zero of function $f$.

## Example

Find equilibrium points for logistic model.

**Solution.**
Logistic model:

$$y' = \alpha y \left(1 - \frac{y}{C}\right)$$

$$f(y) = \alpha y \left(1 - \frac{y}{C}\right)$$

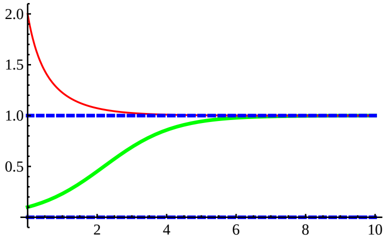
$$f(y) = 0 \quad \Rightarrow \quad \alpha y \left(1 - \frac{y}{C}\right) = 0$$

Equilibrium points:

$$y^* = 0 \quad \text{i} \quad y^* = C$$

# Equilibrium points for logistic model.

$$y' = y(1 - y)$$



# Stability of equilibrium points.

Stability of equilibrium point - after the small change, a system is returning to the equilibrium point

Globally stable equilibrium point - after every change, a system is returning to the equilibrium point

Locally stable equilibrium point - after small change, a system is returning to the equilibrium point

## Definition

Equilibrium point $y^*$ is **globally stable** if for all $y_0$ a solution of differential equation

$$y' = f(y), \quad y(t_0) = y_0$$

satisfies

$$\lim_{t \to \infty} y(t) = y^*.$$

## Definition

Equilibrium point $y^*$ is **locally stable** if there exists a neighbourhood of $y^*$ such that for all $y_0$ from this neighbourhood a solution of differential equation

$$y' = f(y), \quad y(t_0) = y_0$$

satisfies

$$\lim_{t \to \infty} y(t) = y^*.$$

## Example

Check the stability of equilibrium point in the exponential model

$$y' = -\alpha y,$$

where $\alpha > 0$.

**Solution.**

$$\begin{aligned} f(y) &= -\alpha y \\ f(y) &= 0 \quad \Rightarrow \quad -\alpha y = 0 \quad \Rightarrow \quad y = 0 \end{aligned}$$

Equilibrium point. $y^* = 0$
Solution: $y(t) = y_0 \,\mathrm{e}^{-\alpha t}$
Stability:

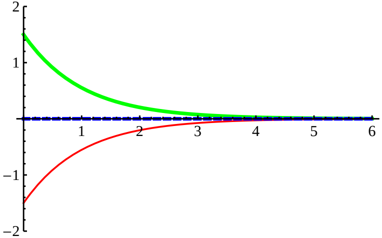
$$\lim_{t\to\infty} y(t) = \lim_{t\to\infty} y_0 \,\mathrm{e}^{-\alpha t} = 0$$

for all $y_0$.

Equilibrium point is globally stable.

Stability of the equilibrium point in the exponential model

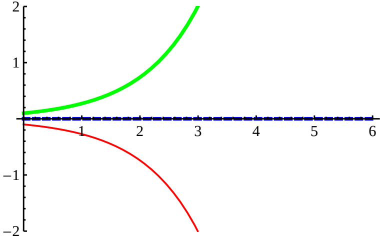
$$y' = -y$$




$y^* = 0$ je is globally stable equilibrium point.

Stability of the equilibrium point in the exponential model

$$y' = y$$




Equilibrium point $y^* = 0$ is not globally stable.

## Problem

Check the stability of equilibrium points in the logistic model.

$$y' = \alpha y\left(1-\frac{y}{C}\right),$$

where $\alpha > 0$ and $C > 0$.

**Solution.**

$$\begin{aligned} f(y) &= \alpha y\left(1-\frac{y}{C}\right) \\ f(y) &= 0 \quad \Rightarrow \quad \alpha y\left(1-\frac{y}{C}\right)=0 \quad \Rightarrow \quad y=0 \text{ ili } y=C \end{aligned}$$

Equilibrium points: $y^* = 0$ i $y^* = C$.
Solution:

$$y(t) = \frac{1}{\frac{1}{C}+\left(\frac{1}{y_0}-\frac{1}{C}\right)\mathrm{e}^{-\alpha t}}$$

Stability:

1. $y_0 > C$

$$\frac{1}{y_0} - \frac{1}{C} < 0$$

$$\frac{1}{C} + \left(\frac{1}{y_0} - \frac{1}{C}\right) \mathrm{e}^{-\alpha t} > 0$$

$$\lim_{t \to \infty} y(t) = \lim_{t \to \infty} \frac{1}{\frac{1}{C} + \left(\frac{1}{y_0} - \frac{1}{C}\right) \mathrm{e}^{-\alpha t}} = C$$

2. $0 < y_0 < C$

$$\frac{1}{y_0} - \frac{1}{C} > 0$$

$$\lim_{t\to\infty} y(t) = \lim_{t\to\infty} \frac{1}{\frac{1}{C} + \left(\frac{1}{y_0} - \frac{1}{C}\right) e^{-\alpha t}} = C$$

3. $y_0 < 0$

$$\frac{1}{y_0} - \frac{1}{C} < 0$$

Denominator is 0 for some $\bar{t} > 0$:

$$0 = \frac{1}{C} + \left(\frac{1}{y_0} - \frac{1}{C}\right) e^{-\alpha t} \quad \Rightarrow \quad \bar{t} = -\frac{1}{\alpha} \ln \frac{y_0}{y_0 - C} > 0$$

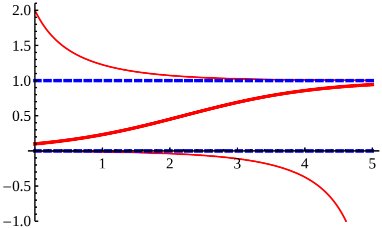
because of

$$0 < \frac{y_0}{y_0 - C} < 1.$$

Discontinuity at $\bar{t}$. Should be considered $\lim_{t\to\bar{t}} y(t) (= -\infty)$.

## Stability of equilibrium points in the logistic model

$$y' = y(1 - y)$$

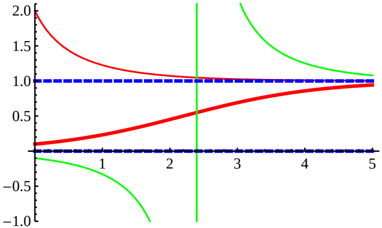



Equilibrium point $y^* = 0$ is not stable.

Equilibrium point $y^* = C = 1$ is locally stable.

## Stability of equilibrium points in the logistic model

$$y' = y(1 - y)$$




Equilibrium point $y^* = 0$ is not stable.

Equilibrium point $y^* = C = 1$ is locally stable.

For $y_0 < 0$ solution is discontinuous!

# 1.3.3. Linearisation of differential equation

Consider differential equation

$$y' = f(y), \quad y(0) = y_0.$$

What is a behaviour of the solution when we start from the point close to the equilibrium $y^*$ ($f(y^*) = 0$): $y_0 = y^* + \varepsilon$. Taylor series:

$$f(x) = \sum_{k=0}^{\infty} \frac{f^{(k)}(a)}{k!}(x-a)^k.$$

Taylor polynomial:

$$f(x) \approx f(a) + f'(a)(x-a)$$

If we start with small perturbation, we obtain a solution $y_\varepsilon$:

$$y_\varepsilon' = f(y_\varepsilon), \quad y_\varepsilon(0) = y^* + \varepsilon.$$

Define function $\varepsilon(t)$: $y_\varepsilon(t) = y^* + \varepsilon(t)$

How far is $y_\varepsilon(t)$ from $y^*$?

$$\frac{d}{dt}y_\varepsilon(t) = f(y_\varepsilon(t)), \Rightarrow$$

$$\frac{d}{dt}y_\varepsilon(t) = \frac{d}{dt}(y^* + \varepsilon(t)) = \frac{d}{dt}y^* + \frac{d}{dt}\varepsilon(t) = \frac{d}{dt}\varepsilon(t)$$

On the other hand,

$$\frac{d}{dt}y_\varepsilon(t) = f(y_\varepsilon(t)) = f(y^* + \varepsilon(t)) \approx f(y^*) + f'(y^*)\varepsilon(t) = f'(y^*)\varepsilon(t)$$

$$\Rightarrow \quad \frac{d}{dt}\varepsilon(t) = f'(y^*)\varepsilon(t)$$

Solution is exponential function.

- If $f'(y^*) > 0$ equilibrium point $y^*$ is not locally stable
- If $f'(y^*) < 0$ equilibrium point $y^*$ is locally stable

## Problem

Check the stability of equilibrium points in the logistic model.

$$y' = \alpha y \left(1 - \frac{y}{C}\right),$$

where $\alpha > 0$ and $C > 0$.

**Solution.**

$$f(y) = \alpha y \left(1 - \frac{y}{C}\right) \quad \Rightarrow \quad \text{Equilibrium points } \ y^* = 0, \ y^* = C$$

$$f'(y) = \alpha \left(1 - \frac{y}{C}\right) - \alpha \frac{y}{C}$$

$$f'(0) = \alpha > 0, \quad f'(C) = -\alpha < 0.$$

Equilibrium point 0 is not stable

Equilibrium point $C$ is stablej.

# 1.3.4. MATHEMATICA

**Example**

Using Mathematica.

File: math1.nb

**Example**

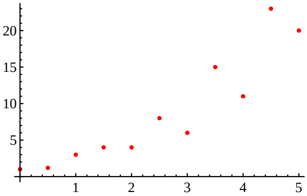
More examples.

File: math3.nb

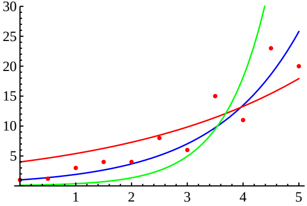
# 1.3.5. Determination of model parameters

Podaci

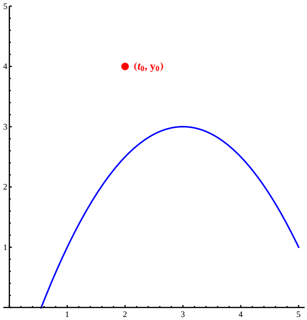
- $y_i$ - measured quantity (number of cells, volume ...) at time $t_i$
- $n$ measurements
- $(t_i, y_i), \quad i = 1, \ldots, n$



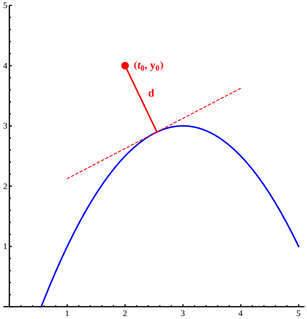
Which one is the best for description of data?



# Distance between a curve and a point.



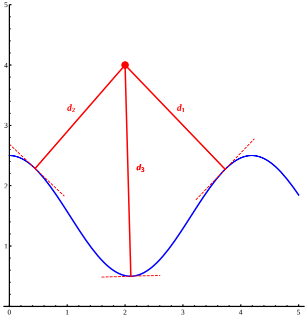
# Distance between a curve and a point.




$$d = \min_t \left[ (t - t_0)^2 + (y(t) - y_0)^2 \right]$$

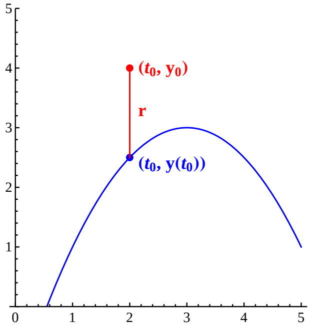
It is not easy to calculate a distance..

# Distance between a curve and a point.




Like here, for example.

# Discrepancy of a curve to the point.




- Discrepancy: $r = y(t_0) - y_0$
- Absolute discrepancy: $|y(t_0) - y_0|$
- Quadratic discrepancy: $(y(t_0) - y_0)^2$

# Discrepancy of a curve to the data.

- Data: $(t_i, y_i)$
- $n$ points
- Total quadratic discrepancy: $\sum_{i=1}^{n} (y(t_i) - y_i)^2$
- Mean quadratic discrepancy: $\frac{1}{n} \sum_{i=1}^{n} (y(t_i) - y_i)^2$

'Best' curve $\rightarrow$ curve with the least total quadratic discrepancy.

# Example: Exponential model.

$$y' = \alpha\, y, \quad y(0) = y_0$$

Solution:

$$y(t) = y_0\, \mathrm{e}^{\alpha\, t} = y(t; \alpha, y_0)$$

$y$ depends on model parameters $(\alpha, y_0)$.

Total quadratic discrepancy:

$$\Phi(\alpha, y_0) = \sum_{i=1}^{n} \left(y_0\, \mathrm{e}^{\alpha\, t_i} - y_i\right)^2$$

depends on model parameters $(\alpha, y_0)$.

'Best' curve $\quad\rightarrow\quad$ ODetermine parameters $\alpha^*, y_0^*$ such that

$$\Phi(\alpha^*, y_0^*) \leq \Phi(\alpha, y_0) \quad \forall \alpha, y_0 \ (\geq 0)$$

$(\alpha^*, y_0^*)$ is minimum point of function $\Phi$.

Determination of parameters:

$$\Phi(\alpha, y_0) = \sum_{i=1}^{n} \left(y_0 \, \mathrm{e}^{\alpha \, t_i} - y_i\right)^2 \xrightarrow{\alpha, y_0} \min$$

# Least squares method

Model

$$y' = f(y; p_1, \dots, p_k), \quad y(0) = y_0$$

$p_1, \dots, p_k, y_0$ - model parameters

Parameters are determined from the condition that they minimize functional

$$\Phi(p_1, \dots, p_k, y_0) = \sum_{i=1}^{n} (y(t_i; p_1, \dots, p_k, y_0) - y_i)^2 \xrightarrow{p_1, \dots, p_k, y_0} \min$$

This approach to the determination of model parameters is called least squares method.

Minimum of functional $\Phi$ may be obtained by use of the methods for numerical minimization.

Most popular methods are:

- Nelder-Meado simplex method
- Newton method
- gradient method
- quasi-Newton methods

## Example

Determine a constant that best describes data $(x_i, y_i),\ i = 1, \dots, n$ in the sense of least squares.

**Solution.**

Model: $y(x) = c$

Constant $c$ is determined from the condition

$$\Phi(c) = \sum_{i=1}^{n} (c - y_i)^2 \xrightarrow{c} \min$$

Point of minimum is obtained from $\Phi'(c) = 0$:

$$\Rightarrow \quad 0 = \sum_{i=1}^{n} 2(c - y_i) \quad \Rightarrow \quad 0 = \sum_{i=1}^{n} c - \sum_{i=1}^{n} y_i = nc - \sum_{i=1}^{n} y_i$$

$$\Rightarrow \quad c = \frac{1}{n} \sum_{i=1}^{n} y_i$$

**Note.** Observe that $\Phi \in C^2$:

$$\Phi(c) = \sum_{i=1}^{n} (c - y_i)^2$$

If we use absolute discrepancy, function

$$\Phi_a(c) = \sum_{i=1}^{n} |c - y_i|$$

is not differentiable.
This is the reason why mean quadratic discrepancy (i.e. least squares method) is used.

# Necessary condition for the minimum of a function of several variables.

In the case of several parameters, $\mathbf{p} = (p_1, p_2, \ldots, p_k)$, gradient is defined as

$$\nabla\Phi(\mathbf{p}) = \begin{bmatrix} \frac{\partial\Phi}{\partial p_1}(\mathbf{p}) \\ \frac{\partial\Phi}{\partial p_2}(\mathbf{p}) \\ \vdots \\ \frac{\partial\Phi}{\partial p_k}(\mathbf{p}) \end{bmatrix}$$

Necessary condition for the minimum (extrema):

$$\nabla\Phi(\mathbf{p}) = 0$$

## Problem

Find all partial derivatives for the following expressions

1. $x + y^2$
2. $ax - \dfrac{x}{a}$
3. $\sin(ax) + x\,\mathrm{e}^b$
4. $ax^y$

**Solution.**

1.

- $\dfrac{\partial}{\partial x}(x + y^2) = 1, \quad \left(\dfrac{\partial}{\partial x} y^2 = 0\right)$
- $\dfrac{\partial}{\partial y}(x + y^2) = 2y$

2.

- $\frac{\partial}{\partial x}\left(a\,x - \frac{x}{a}\right) = a - \frac{1}{a}$
- $\frac{\partial}{\partial a}\left(a\,x - \frac{x}{a}\right) = x + \frac{x}{a^2}$

3 .

- $\frac{\partial}{\partial x}\left(\sin(a\,x) + x\,\mathrm{e}^b\right) = a\cos(a\,x) + \mathrm{e}^b$
- $\frac{\partial}{\partial a}\left(\sin(a\,x) + x\,\mathrm{e}^b\right) = x\cos(a\,x)$
- $\frac{\partial}{\partial b}\left(\sin(a\,x) + x\,\mathrm{e}^b\right) = x\,\mathrm{e}^b$

4.

- $\dfrac{\partial}{\partial x}(a\,x^{y}) = a\,y\,x^{y-1} \quad \text{za } y \neq 0$
- $\dfrac{\partial}{\partial y}(a\,x^{y}) = a\,x^{y}\ln x$
- $\dfrac{\partial}{\partial a}(a\,x^{y}) = x^{y}$

## Problem

Find a linear function that best describes the data $(x_i, y_i),\ i = 1, \dots, n$.

**Solution.**

Model:

$$y(x) = a + b\,x$$

$$\Phi(a, b) = \sum_{i=1}^{n} (a + b\,x_i - y_i)^2$$

$$0 = \frac{\partial \Phi}{\partial a} = \sum_{i=1}^{n} 2(a + b\,x_i - y_i) \quad \Rightarrow \quad n\,a + b \sum_{i=1}^{n} x_i - \sum_{i=1}^{n} y_i = 0$$

$$0 = \frac{\partial \Phi}{\partial b} = \sum_{i=1}^{n} 2(a + b\,x_i - y_i)x_i \quad \Rightarrow \quad a \sum_{i=1}^{n} x_i + b \sum_{i=1}^{n} x_i^2 - \sum_{i=1}^{n} x_i y_i = 0$$

System of linear equations:

$$a + \frac{1}{n}\sum_{i=1}^{n} x_i\, b = \frac{1}{n}\sum_{i=1}^{n} y_i \quad = \quad 0$$

$$\frac{1}{n}\sum_{i=1}^{n} x_i\, a + \frac{1}{n}\sum_{i=1}^{n} x_i^2\, b = \frac{1}{n}\sum_{i=1}^{n} x_i y_i$$

**- System of normal equations**

## Problem

Find a exponential function ($y = \beta\, \mathrm{e}^{\alpha\, x}$) that best describes the data $(x_i, y_i)$, $i = 1, \ldots, n$.

**Solution.**

Model:

$$y(x) = \beta\, \mathrm{e}^{\alpha\, x}$$

$$\Phi(a, b) = \sum_{i=1}^{n} (\beta\, \mathrm{e}^{\alpha\, x_i} - y_i)^2$$

Nonlinear system of equations:

$$0 = \frac{\partial \Phi}{\partial \alpha} = \sum_{i=1}^{n} 2\, (\beta\, \mathrm{e}^{\alpha\, x_i} - y_i)\, \beta\, x_i\, \mathrm{e}^{\alpha\, x_i}$$

$$0 = \frac{\partial \Phi}{\partial \beta} = \sum_{i=1}^{n} 2\, (\beta\, \mathrm{e}^{\alpha\, x_i} - y_i)\, \mathrm{e}^{\alpha\, x_i}$$

Function $\Phi$ should be minimized by some numerical method.

In Mathematica:

- `NonlinearModelFit`
- `FindFit`
- `LinearModelFit`

- Linear least squares problem
- Nonlinear least squares problem

# Linearisation of the model.

Determine parameters on logarithmically transformed data:

$$\begin{aligned} z_i &= \ln y_i \\ z(x) &= \ln y(x) \end{aligned}$$

Now

$$\Phi = \sum_{i=1}^{n} (z(x_i) - z_i)^2 = \sum_{i=1}^{n} (\ln y(x_i) - \ln y_i)^2$$

For exponential model:

$$y(x) = \beta\, \mathrm{e}^{\alpha\, x} \quad \Rightarrow \quad z(x) = \ln \beta + \alpha\, x = b + \alpha\, x$$

- linear model

# Homework

Determine doubling time from the tumour spheroids growth data:

| Time (days) | Volume ($mm^3$) |
|---|---|
| 4.56 | 0.0016308 |
| 5.66 | 0.0032148 |
| 6.68 | 0.005614 |
| 7.89 | 0.0118598 |
| 8.81 | 0.02015 |
| 9.79 | 0.027538 |
| 10.99 | 0.034546 |
| 11.99 | 0.06608 |
| 12.86 | 0.078932 |
| 15.17 | 0.155 |

# 1.3.6. Modelling population loss

## Limited life time (death)

- Each specie lives exactly $\tau$ time units
- Species born at the time point $t - \tau$ die at the time point $t$
- Death rate at time $t$ is equal to birth rate at time $t - \tau$
- Exponential model: birth rate = $\alpha N(t)$
- growth rate = birth rate - death rate
- $N'(t) = \alpha N(t) - \alpha N(t - \tau)$
- Note, differential equation is not of the form $y' = f(t, y)$

$\rightarrow$ delayed differential equation

## Solving differential equation $N'(t) = \alpha N(t) - \alpha N(t-\tau)$

Consider solution in the form

$$N(t) = c\,\mathrm{e}^{b\,t}$$

Determine $b$ and $c$ to satisfy the differential equation.

$$cb\,\mathrm{e}^{b\,t} = \alpha c\,\mathrm{e}^{b\,t} - \alpha c\,\mathrm{e}^{b\,(t-\tau)}$$

$$\Rightarrow \quad b = \alpha - \alpha\,\mathrm{e}^{-b\tau}$$

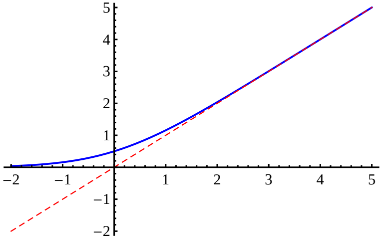
$$\Rightarrow \quad \frac{b}{1-\mathrm{e}^{-b\tau}} = \alpha \quad \Rightarrow \quad \frac{b\,\tau}{1-\mathrm{e}^{-b\tau}} = \alpha\,\tau$$

Does a solution of the nonlinear equation exist?

Consider function

$$h(x) = \frac{x}{1-\mathrm{e}^{-x}}$$

Graph of function $h$:




$h$ is strictly increasing $\Rightarrow$ bijection $\Rightarrow$ inverse function exists

$\Rightarrow$ an unique solution of equation exists: $b = h^{-1}(\alpha\tau)/\tau$

$c$ is determined from the initial condition.

Solution is an exponential function:

$$N(t) = c\,\mathrm{e}^{b\,t}$$

**Remark.** By substitution

$$w = \tau(b - \alpha),$$

nonlinear equation is transformed to

$$w\,\mathrm{e}^{w} = T.$$

Solutions of this equation defines **Lambert *W* function**.

Equation has infinite number of complex solutions.

$\Rightarrow$ A general solution of the delayed differential equation is more complex then an exponential function.

Death is modeled by $-\beta N(t)$.

For exponential model:

$$N' = \alpha N - \beta N = (\alpha - \beta)N = \bar{\alpha}N$$

Unrestricted growth + limited lifetime of species
$\Rightarrow$ exponential model

# Harvesting of population.

total increase rate = growth rate - harvesting rate

Growth without harvesting:

$$N' = f(N)$$

## Constant harvesting.

Harvesting with fixed quota.

Fixed amount of species is harvested in time unit.

$\Rightarrow$ Harvesting rate is constant. $\Rightarrow$ Harvesting rate $= K$.

Model:

$$N' = f(N) - K$$

## Example

Suppose that a growth of fish population without harvesting is described by logistic model. Let a part of fish population is harvested by the fishing with a constant rate $K$. Then, population growth with harvesting is described by

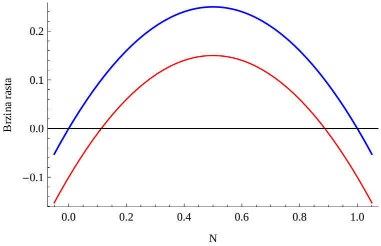
$$N' = \alpha N \left(1 - \frac{N}{C}\right) - K$$

Remark. Right side can be factorized and equation becomes

$$N' = a(b - N)(c + N)$$

# Impact of harvesting

Equilibrium points for $y' = y(1-y)$ and $y' = y(1-y) - 0.1$




What is the largest possible yield that will not decrease population size? Population size increases $\Rightarrow$

$$N' = \alpha N\left(1 - \frac{N}{C}\right) - K \geq 0.$$

Solve equation

$$\alpha N \left(1 - \frac{N}{C}\right) - K = 0$$

For a population of size $N_0$, maximal yield is

$$K_{\max} = \alpha N_0 \left(1 - \frac{N_0}{C}\right)$$

## Maximal sustainable yield

What is a largest possible yield that will not cause a total loss of population?

(Population size may decrease!)

Largest yield is possible when a population growth rate is highest.

$$N' = \alpha N \left(1 - \frac{N}{C}\right) - K$$

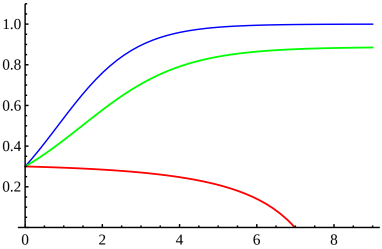
On the right side is a quadratic function; maximum is achieved for $N = \dfrac{C}{2}$

$$N' = 0 \quad \Rightarrow \quad K_{MSY} = \alpha \frac{C}{2} \left(1 - \frac{\frac{C}{2}}{C}\right) = \frac{\alpha C}{4}$$

# Constant yield

$$N' = N(1-N) - K, \quad N(0) = 0.3, \quad K_{max} = 0.21$$

$K = 0$ $\quad$ $K = 0.1$ $\quad$ $K = 0.215$

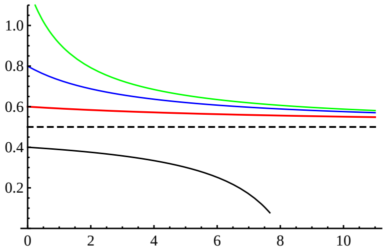



For $K > K_{max}$ population disappeared!

# Maximal sustainable yield

$$N' = N(1-N) - K_{MSY} = N(1-N) - 0.25, \quad N(0) = N_0$$

$N_0 = 1.2$ $N_0 = 0.8$ $N_0 = 0.6$ $N_0 = 0.4$




For $N_0 < \frac{C}{2} = 0.5$ population disappeared!

# Constant effort harvesting

Assumption: fish is fished with a constant effort

Limmited number of licences, ships, days on the sea, ...

Catch is proportional to the effort and population size.

$\Rightarrow$ Harvesting rate $= e\,N$.

Model:

$$N' = f(N) - e\,N$$

For logistic model

$$N' = \alpha\,N\left(1 - \frac{N}{C}\right) - e\,N$$

$$
\begin{aligned}
N' &= (\alpha - e)N - \alpha N \frac{N}{C} = \\
&= (\alpha - e)N \left(1 - \frac{N}{C(1 - e/\alpha)}\right) = \\
&= aN \left(1 - \frac{N}{\bar{C}}\right)
\end{aligned}
$$

- Logistic model.

Effects of harvesting:

- Growt rate decreases
- Carrying capacity decreases

Stable equilibrium point

$$N^* = C\left(1 - \frac{e}{\alpha}\right)$$

Harvest rate for $N = N^*$ is

$$eN^* = C\,e\left(1 - \frac{e}{\alpha}\right)$$

- Small effort $\quad\rightarrow\quad$ small catch
- Increase of effort results with the increase of a catch, but population size increases $\quad\rightarrow\quad$ smaller catch

Optimal effort (that maximizes yield):

$$e_{opt} = \frac{\alpha}{2}$$

Optimal harvest rate

$$e_{opt}N^* = \frac{C\,\alpha}{4}$$

**The same as in fixed quota!**

What is a difference between the models?

If catch size is (accidentally or intentionally) to large:

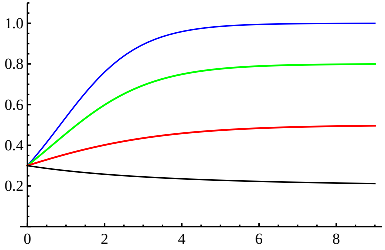
- Constant yield model - population extinction
- Constant effort mode - yield increases, but stable equilibrium remains unchanged (with smaller population)

It can be shown: in the case of an unexpected damage of a population constant effort model provides faster recovery

# Constant effort

$$N' = N(1 - N) - e\,N, \quad N(0) = 0.3$$

$e = 0$ $e = 0.2$ $e = 0.5$ $e = 0.8$



# Optimal yield

$$N' = N(1-N) - e_{opt} = N(1-N) - 0.25N, \quad N(0) = N_0$$

$N_0 = 1.2$ $N_0 = 0.7$ $N_0 = 0.3$ $N_0 = 0.1$