Scientific Computing I

Module 3: Population Modelling – Continuous Models

Michael Bader

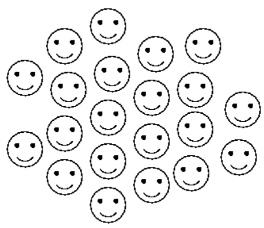
Lehrstuhl Informatik V

Winter 2005/2006

Part I

ODE Models

Discrete vs. Contiuous Models



$$\frac{dp}{dt} = F(p, t, \dots)$$

$$p(t) = ?$$

discrete model: $p(t) \in \mathbb{N}$ individuals

continuous model: $p : \mathbb{R} \to \mathbb{R}, p(t) = ?$

Advantage:

- easier(?) type of mathematical problem: differential equations, calculus
- analytical solutions available(?)

Model of Maltus (1798)

Only one species:

1. birth rate γ (number of births per time interval) proportional to size of population
2. death rate δ proportional to size of population
3. thus: constant growth (or decay) rate: $r = \gamma - \delta$

Modelling:

- constant growth rate

$$\frac{dp}{dt} = r \cdot p$$

- growth within a time interval

$$p(t + \delta t) = p(t) + r \cdot p(t) \cdot \delta t$$

Model of Maltus – Differential Equation

Written as an ordinary differential equation:

$$\dot{p}(t) = r \cdot p(t)$$

Requires initial condition (population at start)

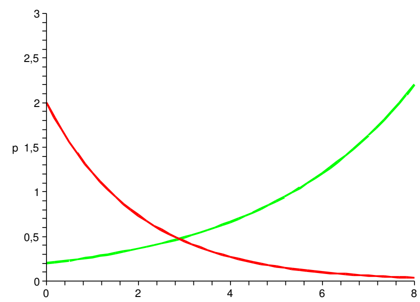
$$p(0) = p_0$$

Analytical solution:

$$p(t) = p_0 e^{rt}$$

Model of Maltus – Solutions

The model of maltus describes exponential growth or decay of a population:



Model of Verhulst (19th century)

Objective:

- model populations that approach saturation value

Assumptions:

- growth/death rate depend on population size; assume linear dependency:

$$g(t) = g_0 - g_1 \cdot p(t) \qquad d(t) = d_0 + d_1 \cdot p(t)$$

- leads to differential equation:

$$\dot{p}(t) = g(t) - d(t) = \underbrace{(g_0 - d_0)}_{=:\alpha} - \underbrace{(g_1 + d_1)}_{=:\beta} p(t)$$

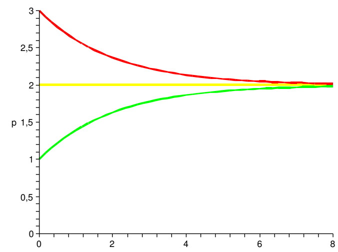
Model of Verhulst – Saturation

- solve initial value problem:

$$\dot{p}(t) = \alpha - \beta p(t), \qquad p(0) = p_0$$

- solution:

$$p(t) = p_\infty + e^{-\beta t}(p_0 - p_\infty), \qquad p_\infty = \frac{\alpha}{\beta}$$



Model of Verhulst – Logistic Growth

- saturation model does no longer model exponential growth
- let growth/death rate decrease linearly with time
- but keep growth/death rate proportinal to population size
- leads to differential equation:

$$\dot{p}(t) = (\alpha - \beta p(t))\, p(t)$$

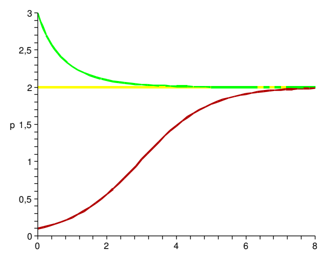
Logistic Growth

- other formulation

$$\dot{p}(t) = \alpha \left(1 - \frac{p(t)}{\beta}\right) p(t)$$

- solution:

$$p(t) = \frac{\beta}{(1 - e^{-\alpha t}) + \frac{\beta}{p_0} e^{-\alpha t}}$$

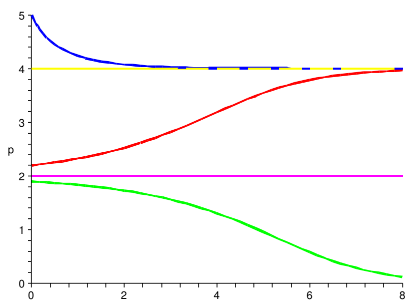


Logistic Growth with Threshold

- extended version of Verhulst's model:

$$\dot{p}(t) = \alpha \left(1 - \frac{p(t)}{\beta}\right)\left(1 - \frac{p(t)}{\delta}\right) p(t)$$

- solutions ($\beta = 2, \delta = 4$):



Example – The Passenger Pigeon

- beginning of the 19th century, estimated population in North America: four billion
- hunting diminished its number below a critical threshold (late 1880s)
- The last passenger pigeon died on September, 1st 1914.

Part II

More Than One Species – Systems of ODE

A Linear Model

- similar to Verhulst's saturation model
- additional growth term proportional to other species
- leads to system of differential equations:

$$\begin{aligned}\dot{p}(t) &= b_1 + a_{11}p(t) + a_{12}q(t)\\ \dot{q}(t) &= b_2 + a_{21}p(t) + a_{22}q(t)\end{aligned}$$

- typically:
    - $b_1 > 0, b_2 > 0$ (growth term)
    - $a_{11} < 0, a_{22} < 0$ (saturation)
    - a_{12}, a_{21}?

First Example: Arms Race

- armament of two (hostile) countries
- our suspicion: $a_{12} > 0$, $a_{21} > 0$

Observation:

- long-time behaviour depends on size of parameters
- steady-state solutions exist
- solutions exist that show unlimited growth

Second Example: Competition

- two species sharing a common natural habitat
- competition: $a_{12} < 0$, $a_{21} < 0$

Observation:

- long-time behaviour depends on size of parameters
- steady-state solutions exist
- some scenarios are physically incorrect! (negative population size)

A Non-Linear Model

- similar to Verhulst's logistic growth model
- additional growth term proportional to other species
- leads to system of differential equations:

$$\begin{aligned}\dot{p}(t) &= (b_1 + a_{11}p(t) + a_{12}q(t))\,p(t)\\ \dot{q}(t) &= (b_2 + a_{21}p(t) + a_{22}q(t))\,q(t)\end{aligned}$$

- typically:
    - $b_1 > 0, b_2 > 0$ (growth term)
    - $a_{11} < 0, a_{22} < 0$ (saturation)
    - a_{12}, a_{21}?

The Non-Linear Competition Model

- two species sharing a common natural habitat
- competition: $a_{12} < 0$, $a_{21} < 0$

Possible Scenarios:

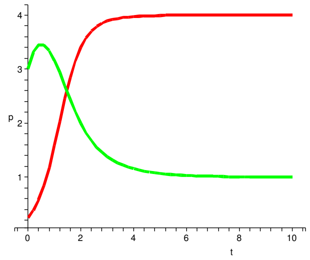
- steady-state
- one species dies out (extinction)
- no obvious nonsense

Competition – Steady State

- system of differential equations:

$$\begin{aligned}\dot{p}(t) &= \left(\tfrac{5}{2}+\tfrac{\sqrt{3}}{24}-\tfrac{5}{8}p(t)-\tfrac{\sqrt{3}}{24}q(t)\right)p(t)\\ \dot{q}(t) &= \left(\tfrac{7}{8}+\tfrac{3\sqrt{3}}{2}-\tfrac{3\sqrt{3}}{8}p(t)-\tfrac{7}{8}q(t)\right)q(t)\end{aligned}$$

- solution for $p_0 = \frac{1}{4}$, $q_0 = 3$:

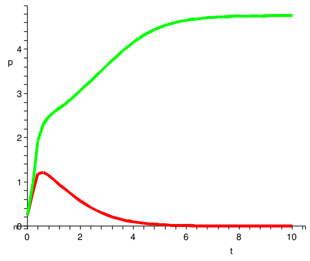


Competition – Extinction

- system of differential equations:

$$\begin{aligned}\dot{p}(t) &= \left(\tfrac{71}{8}-\tfrac{23}{12}p(t)-\tfrac{25}{12}q(t)\right)p(t)\\ \dot{q}(t) &= \left(\tfrac{73}{8}-\tfrac{25}{12}p(t)-\tfrac{23}{12}q(t)\right)q(t)\end{aligned}$$

- solution for $p_0 = \frac{1}{4}$, $q_0 = \frac{1}{4}$:



Predator-Prey

- two species: predator p and prey q
- predator eats prey: $a_{12} > 0$
- prey is eaten by predator: $a_{21} < 0$

Possible Scenarios:

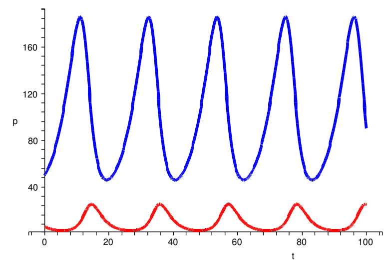
- stable oscillations
- one species dies out (what happens with the other, then?)

Predator-Prey by Lotka & Volterra

- system of differential equations:

$$\begin{aligned}\dot{p}(t) &= \left(-\tfrac{1}{2}+\tfrac{1}{200}q(t)\right)p(t)\\ \dot{q}(t) &= \left(\tfrac{1}{5}-\tfrac{1}{50}p(t)\right)q(t)\end{aligned}$$

- solution for $p_0 = 6$, $q_0 = 50$:



Open Questions

Methods to Analyse a Given Model?

- predict approximate solution or shape of solution?
- predict possible steady states?
- predict critical points?
  (species on edge of extiction?)

Methods to Improve Modeling?

- predict failure of the model?
- tune parameters to model a specific situation?

Scientific Computing I

Module 3: Population Modelling – Continuous Models (Part III)

Michael Bader

Lehrstuhl Informatik V

Winter 2005/2006

Analysing the Slope of a Solution

Example: Model of Maltus

$$\dot{p}(t) = \alpha p(t)$$

- for a sensible solution: $p(t) > 0$
- α decides slope of solution:
  - $\alpha > 0$: growing population (accelerated growth)
  - $\alpha < 0$: receding population (decelerated reduction)

Points of Equilibrium

Example: Model of Verhulst (saturation)

$$\dot{p}(t) = \alpha - \beta p(t)$$

- equilibrium: $\dot{p}(t) = 0$
- only, if $p(t) = \frac{\alpha}{\beta}$

Example: Logistic Growth

$$\dot{p}(t) = \alpha \left(1 - \frac{p(t)}{\beta}\right) p(t)$$

- constant solution, if $p(t) = \beta$ or $p(t) = 0$

Critical Points

Observation on Logistic Growth:

- constant solution $p(t) = \beta$, if $p(0) = \beta$
- constant solution $p(t) = 0$, if $p(0) = 0$
- equilibrium at $p = \beta$ is reached for nearly all initial conditions
  $\Rightarrow$ *attractive* (stable) equilibrium
- equilibrium at $p = 0$ is not reached for any other initial conditions ("repulsive")
  $\Rightarrow$ unstable equilibrium

Critical Points – Derivatives

Examine derivatives:

- critical point $p = \bar{p}$
- attractive equilibrium (asymptotically stable):

$$\begin{array}{lll} \dot{p} < 0 & \text{for} & p = \bar{p} + \varepsilon \\ \dot{p} > 0 & \text{for} & p = \bar{p} - \varepsilon \end{array}$$

- unstable equilibrium:

$$\begin{array}{lll} \dot{p} > 0 & \text{for} & p = \bar{p} + \varepsilon \\ \dot{p} < 0 & \text{for} & p = \bar{p} - \varepsilon \end{array}$$

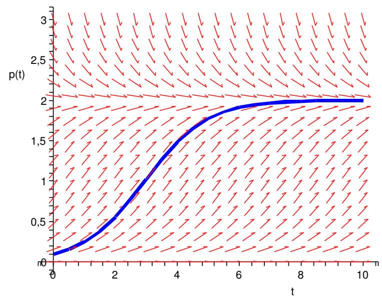
- otherwise: saddle point

Direction Field

plot derivatives vs. time and size of population:

Example: Logistic Growth

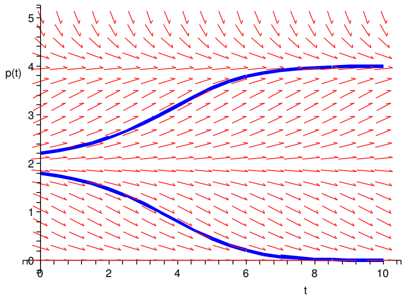
$$\dot{p}(t) = \alpha \left(1 - \frac{p(t)}{\beta}\right) p(t)$$



Direction Field (2)

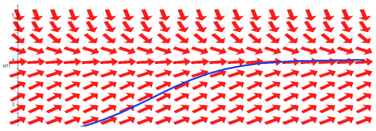
Example: Logistic Growth with Threshold

$$\dot{p}(t) = \alpha\left(1 - \frac{p(t)}{\beta}\right)\left(1 - \frac{p(t)}{\delta}\right)p(t)$$

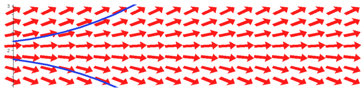


Identifying Critical Points

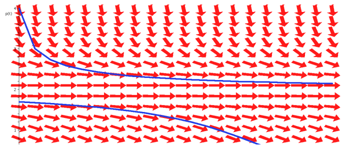
- attractive equilibrium:



- unstable equilibrium



- saddle point



Critical Points in 2D

Example: Arms Race

- system of differential equations
- equilibrium: $\dot{p} = 0$, $\dot{q} = 0$

$$\begin{aligned} \dot{p}(t) &= b_1 + a_{11}p(t) + a_{12}q(t) = 0 \\ \dot{q}(t) &= b_2 + a_{21}p(t) + a_{22}q(t) = 0 \end{aligned}$$

- solution of a linear system of equations:

$$\begin{aligned} a_{11}p(t) + a_{12}q(t) &= -b_1 \\ a_{21}p(t) + a_{22}q(t) &= -b_2 \end{aligned}$$

- in most cases one critical point
- critical line, if system matrix is singular

Direction Field for a System of ODE

- example: 2D system of differential equations:

$$\begin{aligned} \dot{p}(t) &= b_1 + a_{11}p(t) + a_{12}q(t) \\ \dot{q}(t) &= b_2 + a_{21}p(t) + a_{22}q(t) \end{aligned}$$

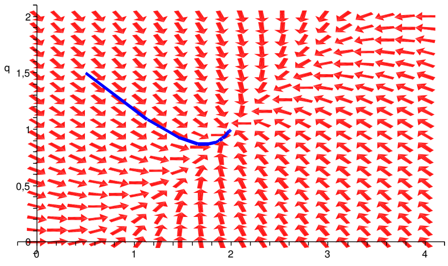
- natural exension: 3D plot: t vs. p vs. q
- 1D direction field for p vs. t or q vs. t not sufficient: what values to chose for q (or p resp.)?
- but: stationary problem $\Rightarrow$ independent of t
- thus: plot directions depending on p and q

2D Direction Field – Arms Race

- system of differential equations:

$$\begin{aligned} \dot{p}(t) &= \tfrac{3}{2} - p(t) + \tfrac{1}{2}q(t) \\ \dot{q}(t) &= 0 + \tfrac{1}{2}p(t) - q(t) \end{aligned}$$

- direction field – with critical point at $(2,1)$:

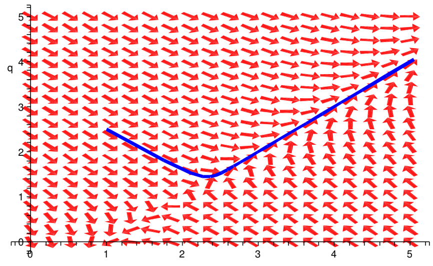


Arms Race – unlimited growth

- system of differential equations:

$$\begin{aligned} \dot{p}(t) &= \tfrac{1}{2} - \tfrac{3}{4}p(t) + q(t) \\ \dot{q}(t) &= -\tfrac{5}{4} + p(t) - \tfrac{3}{4}q(t) \end{aligned}$$

- direction field – with critical point at $(2,1)$:

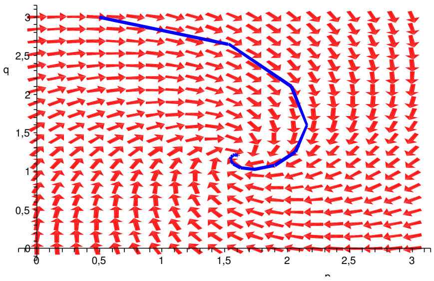


Arms race – the peaceful neighbour

- system of differential equations:

$$\begin{aligned}\dot{p}(t) &= 0 - \tfrac{3}{4}p(t) + q(t)\\ \dot{q}(t) &= \tfrac{5}{2} - p(t) - \tfrac{3}{4}q(t)\end{aligned}$$

- direction field – with critical point at $\left(\frac{8}{5}, \frac{6}{5}\right)$:

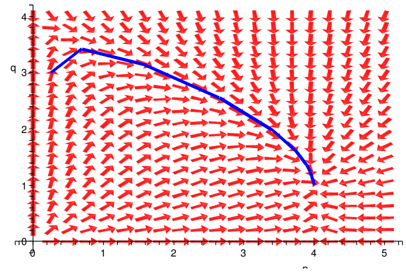


Nonlinear System – Competition

- system of differential equations:

$$\begin{aligned}\dot{p}(t) &= \left(\tfrac{5}{2} + \tfrac{\sqrt{3}}{24} - \tfrac{5}{8}p(t) - \tfrac{\sqrt{3}}{24}q(t)\right)p(t)\\ \dot{q}(t) &= \left(\tfrac{7}{8} + \tfrac{3\sqrt{3}}{2} - \tfrac{3\sqrt{3}}{8}p(t) - \tfrac{7}{8}q(t)\right)q(t)\end{aligned}$$

- direction field – critical points at $(4, 1), \ldots$:

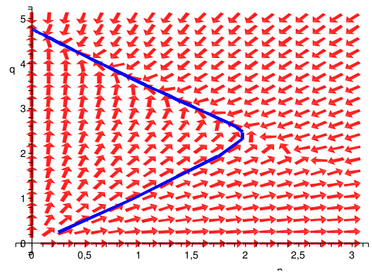


Nonlinear System – Extinction

- system of differential equations:

$$\begin{aligned}\dot{p}(t) &= \left(\tfrac{71}{8} - \tfrac{23}{12}p(t) - \tfrac{25}{12}q(t)\right)p(t)\\ \dot{q}(t) &= \left(\tfrac{73}{8} - \tfrac{25}{12}p(t) - \tfrac{23}{12}q(t)\right)q(t)\end{aligned}$$

- critical points at $(0, 4.76\ldots), (4.63\ldots, 0), \ldots$:

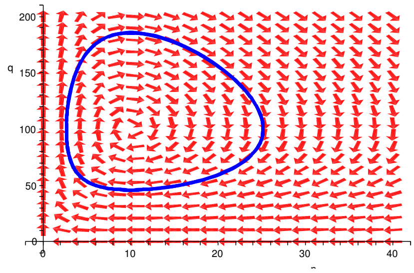


Lotka & Volterra

- system of differential equations:

$$\begin{aligned}\dot{p}(t) &= \left(-\tfrac{1}{2} + \tfrac{1}{200}q(t)\right)p(t)\\ \dot{q}(t) &= \left(\tfrac{1}{5} - \tfrac{1}{50}p(t)\right)q(t)\end{aligned}$$

- direction field – with critical point at $(10, 100)$:



2D Critical Points – Summary

Different types of critical points in 2D:

- attractive/stable equilibrium
  (arms race – steady state)
- unstable equilibrium
- saddle point (arms race – unlimited growth)
- attractive "spiral point" ("peaceful neighbour")
- unstable "spiral point"
- centre of "rotation" (Lotka-Volterra)

$\Rightarrow$ How to discriminate between these types?

Homogeneous Systems of ODE

Homogeneous System in matrix-vector-notation:

$$\dot{\mathbf{x}} = \mathbf{A}\mathbf{x}$$

- $\mathbf{x} : \mathbb{R} \to \mathbb{R}^n$, $\mathbf{A} \in \mathbb{R}^{n \times n}$
- example: $\mathbf{x}(t) = (p(t), q(t))$

Solutions:

- let $\mathbf{x}_\lambda$ be an eigenvector: $\mathbf{A}\mathbf{x}_\lambda = \lambda \mathbf{x}_\lambda$
- then $\mathbf{x}_\lambda e^{\lambda t}$ is a solution:

$$\mathbf{A}\mathbf{x}_\lambda e^{\lambda t} = \lambda \mathbf{x}_\lambda e^{\lambda t} = \frac{d}{dt}\left(\mathbf{x}_\lambda e^{\lambda t}\right) \qquad \text{q.e.d.}$$

Eigenvectors and Eigenvalues

Corollaries:

- the solutions of the homogeneous system $\dot{\mathbf{x}} = \mathbf{A}\mathbf{x}$ are linear combinations of the respective eigen-solutions:

$$\mathbf{x}_{\mathbf{hom}}(t) = \sum_{\lambda} a_\lambda \mathbf{x}_\lambda e^{\lambda t}, \qquad a_\lambda \in \mathbb{R}$$

- the solutions of the inhomogeneous system $\dot{\mathbf{x}} = \mathbf{A}\mathbf{x} + \mathbf{b}$ are

$$\mathbf{x}(t) = -\mathbf{A}^{-1} b + \mathbf{x}_{\mathbf{hom}}(t)$$

- observation: $\mathbf{x_c} = -\mathbf{A}^{-1} b$ is a critical point!

Eigenvalues and Critical Points

- the ODE system $\dot{\mathbf{x}} = \mathbf{A}\mathbf{x} + \mathbf{b}$ is solved by

$$\mathbf{x}(t) = \mathbf{x_c} + \sum_{\lambda} a_\lambda \mathbf{x}_\lambda e^{\lambda t}$$

- $\mathbf{x_c}$ attractive equilibrium,

$$\lim_{x \to \infty} \mathbf{x}(t) = \mathbf{x_c},$$

only if $e^{\lambda t} \to 0$ for all eigenvalues λ

- $\lambda \in \mathbb{R} \Rightarrow \lambda < 0$
- $\lambda = \mu + i\nu \Rightarrow \mu < 0$ ($e^{i\nu t} = \cos \nu t + i \sin \nu t$)

Stability of Linear Systems

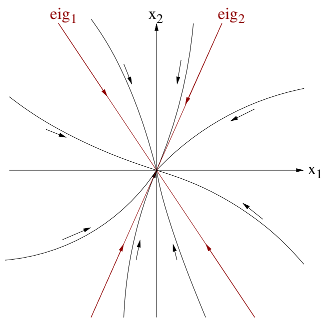
Overview:

eigenval. ($\lambda_j = \mu_j + i\nu_j$)	critical point	stability
real, all $\lambda < 0$	node	stable, attr.
real, all $\lambda > 0$	node	unstable
real, $\lambda_k > 0, \lambda_l < 0$	saddle point	unstable
complex, all $\mu < 0$	spiral point	stable, attr.
complex, all $\mu > 0$	spiral point	unstable
complex, all $\mu = 0$	centre	stable

Stability of 2D Systems

Real Eigenvalues:

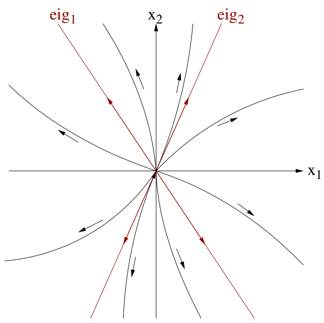
- $\lambda_1 < 0$, $\lambda_2 < 0$, attractive equilibrium



Stability of 2D Systems

Real Eigenvalues:

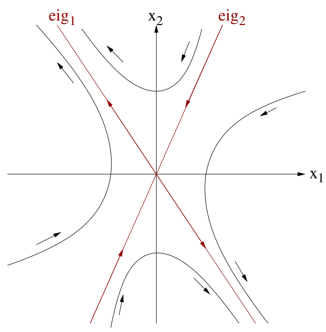
- $\lambda_1 > 0$, $\lambda_2 > 0$, unstable equilibrium



Stability of 2D Systems

Real Eigenvalues:

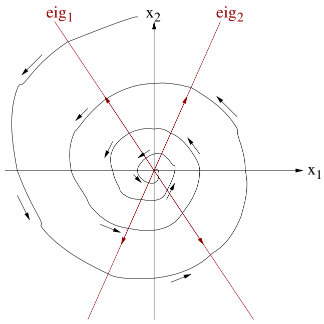
- $\lambda_1 > 0$, $\lambda_2 < 0$, saddle point



Stability of 2D Systems

Complex Eigenvalues:

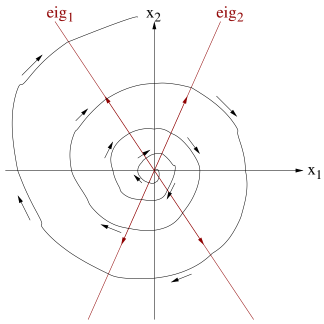
- $\mu_1 < 0$, $\mu_2 < 0$, spiral point (asympt. stable)



Stability of 2D Systems

Complex Eigenvalues:

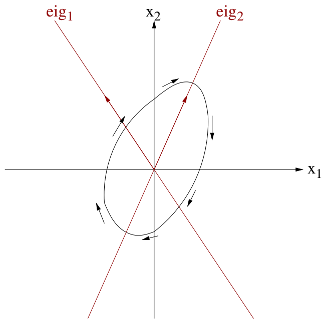
- $\mu_1 > 0$, $\mu_2 > 0$, spiral point (unstable)



Stability of 2D Systems

Complex Eigenvalues:

- $\mu_1 = \mu_2 = 0$, centre of oscillation



Stability of Non-Linear Systems

- 2D system of ODE:

$$\dot{\mathbf{x}}(t) = f(\mathbf{x}(t)),$$

  $f : \mathbb{R}^n \to \mathbb{R}^n$ nonlinear
- critical point at $\mathbf{x_c}$: $f(\mathbf{x_c}(t)) = 0$
- for analysis of critical points: linearization

$$\dot{\mathbf{x}} = f(\mathbf{x}) \approx \underbrace{f(t, \mathbf{x_c})}_{=0} + \mathbf{J_f}(\mathbf{x_c})(\mathbf{x} - \mathbf{x_c})$$

- examine eigenvalues of $\mathbf{J_f}(\mathbf{x_c})$