

## Summary of topics relevant for the final

# Mathematical techniques

Regression

Discrete time systems

Systems of ODEs

Linear systems of ODE – Brief theory

PDEs

Some elementary probability

Markov chains

# Outline

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# Regression

See Dr. Berry's notes.

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# Discrete-time systems

So far, we have seen continuous-time models, where  $t \in \mathbb{R}_+$ . Another way to model natural phenomena is by using a discrete-time formalism, that is, to consider equations of the form

$$x_{t+1} = f(x_t),$$

where  $t \in \mathbb{N}$  or  $\mathbb{Z}$ , that is,  $t$  takes values in a discrete valued (countable) set.

Time could for example be days, years, etc.

## Some mathematical analysis

Suppose we have a system in the form

$$x_{t+1} = f(x_t),$$

with initial condition given for  $t = 0$  by  $x_0$ . Then,

$$x_1 = f(x_0)$$

$$x_2 = f(x_1) = f(f(x_0)) \triangleq f^2(x_0)$$

$$\vdots$$

$$x_k = f^k(x_0).$$

The  $f^k = \underbrace{f \circ f \circ \dots \circ f}_{k \text{ times}}$  are called the *iterates* of  $f$ .

# Fixed points

## Definition 1 (Fixed point)

Let  $f$  be a function. A point  $p$  such that  $f(p) = p$  is called a *fixed point* of  $f$ .

## Theorem 2

Consider the closed interval  $I = [a, b]$ . If  $f : I \rightarrow I$  is continuous, then  $f$  has a fixed point in  $I$ .

## Theorem 3

Let  $I$  be a closed interval and  $f : I \rightarrow \mathbb{R}$  be a continuous function. If  $f(I) \supset I$ , then  $f$  has a fixed point in  $I$ .



# Periodic points

## Definition 4 (Periodic point)

Let  $f$  be a function. If there exists a point  $p$  and an integer  $n$  such that

$$f^n(p) = p, \quad \text{but} \quad f^k(p) \neq p \text{ for } k < n,$$

then  $p$  is a periodic point of  $f$  with (least) period  $n$  (or a  $n$ -periodic point of  $f$ ).

Thus,  $p$  is a  $n$ -periodic point of  $f$  iff  $p$  is a 1-periodic point of  $f^n$ .

# Stability of fixed points, of periodic points

## Theorem 5

Let  $f$  be a continuously differentiable function (that is, differentiable with continuous derivative, or  $C^1$ ), and  $p$  be a fixed point of  $f$ .

1. If  $|f'(p)| < 1$ , then there is an open interval  $\mathcal{I} \ni p$  such that  $\lim_{k \rightarrow \infty} f^k(x) = p$  for all  $x \in \mathcal{I}$ .
2. If  $|f'(p)| > 1$ , then there is an open interval  $\mathcal{I} \ni p$  such that if  $x \in \mathcal{I}$ ,  $x \neq p$ , then there exists  $k$  such that  $f^k(x) \notin \mathcal{I}$ .

## Definition 6

Suppose that  $p$  is a  $n$ -periodic point of  $f$ , with  $f \in C^1$ .

- ▶ If  $|(f^n)'(p)| < 1$ , then  $p$  is an *attracting* periodic point of  $f$ .
- ▶ If  $|(f^n)'(p)| > 1$ , then  $p$  is an *repelling* periodic point of  $f$ .

# Parametrized families of functions

Consider a system

$$x_{t+1} = f(x_t)$$

which depends on a parameter  $r$ . We write

$$x_{t+1} = f_r(x_t).$$

The function  $f_r$  is called a *parametrized family* of functions.

# Bifurcations

## Definition 7 (Bifurcation)

Let  $f_\mu$  be a parametrized family of functions. Then there is a *bifurcation* at  $\mu = \mu_0$  (or  $\mu_0$  is a bifurcation point) if there exists  $\varepsilon > 0$  such that, if  $\mu_0 - \varepsilon < a < \mu_0$  and  $\mu_0 < b < \mu_0 + \varepsilon$ , then the dynamics of  $f_a(x)$  are “different” from the dynamics of  $f_b(x)$ .

An example of “different” would be that  $f_a$  has a fixed point (that is, a 1-periodic point) and  $f_b$  has a 2-periodic point.

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# Steps of the analysis

1. Assess well-posedness of the system:
  - 1.1 Determine whether solutions exist and are unique.
  - 1.2 Determine whether solutions remain in a realistic region and are bounded.
2. Find the equilibria of the system.
3. Determine the local stability properties of the equilibria.
4. Determine the global stability properties of the equilibria (**much harder**, often not possible).

# Existence and uniqueness of solutions

## Theorem 8 (Cauchy-Lipschitz)

*Consider the equation  $x' = f(x)$ , with  $x \in \mathbb{R}^n$ , and suppose that  $f \in C^1$ . Then there exists a unique solution of  $x' = f(x)$  such that  $x(t_0) = x_0$ , where  $t_0 \in \mathbb{R}$  and  $x_0 \in \mathbb{R}^n$ , defined on the largest interval  $J \ni t_0$  on which  $f \in C^1$ .*

# Equilibria

## Definition 9 (Equilibrium point)

Consider a differential equation

$$x' = f(x), \tag{1}$$

with  $x \in \mathbb{R}^n$  and  $f : \mathbb{R}^n \rightarrow \mathbb{R}^n$ . Then  $x^*$  is an equilibrium (solution) of (1) if  $f(x^*) = 0$ .



# Linearization

Consider  $x^*$  an equilibrium of (1). For simplicity, assume here that  $x^* = 0$  (it is always possible to do this, by considering  $y = x - x^*$ ).

Taylor's theorem:

$$f(x) = Df(0)x + \frac{1}{2}D^2f(0)(x, x) + \dots,$$

where  $Df(0)$  is the Jacobian matrix of  $f$  evaluated at 0.

# What is stability?

## Definition 10 (Stable and unstable EP)

Let  $\phi_t$  be the flow of (1), assumed to be defined for all  $t \in \mathbb{R}$ . An equilibrium  $x^*$  of (1) is (locally) *stable* if for all  $\varepsilon > 0$ , there exists  $\delta > 0$  such that for all  $x \in \mathcal{N}_\delta(x^*)$  and  $t \geq 0$ , there holds

$$\phi_t(x) \in \mathcal{N}_\varepsilon(x^*).$$

The equilibrium point is *unstable* if it is not stable.

## Definition 11 (Asymptotically stable EP)

Let  $\phi_t$  be the flow of (1) is (locally) *asymptotically stable* if there exists  $\delta > 0$  such that for all  $x \in \mathcal{N}_\delta(x^*)$  and  $t \geq 0$ , there holds

$$\lim_{t \rightarrow \infty} \phi_t(x) = x^*.$$

Clearly, Asymptotically Stable  $\Rightarrow$  Stable.

# Hyperbolic EPs, sinks, sources

## Definition 12 (Sink)

An equilibrium point  $x^*$  of (1) is *hyperbolic* if none of the eigenvalues of the matrix  $Df(x^*)$  (Jacobian matrix of  $f$  evaluated at  $x^*$ ) have zero real parts.

## Definition 13 (Sink)

An equilibrium point  $x^*$  of (1) is a *sink* if all the eigenvalues of the matrix  $Df(x^*)$  have negative real parts.

## Definition 14 (Source)

An equilibrium point  $x^*$  of (1) is a *source* if all the eigenvalues of the matrix  $Df(x^*)$  have positive real parts.

## Theorem 15

If  $x^*$  is a sink of (1) and for all the eigenvalues  $\lambda_j$  of the matrix  $Df(x^*)$

$$\Re(\lambda_j) < -\alpha < 0,$$

where  $\Re(\lambda)$  denotes the real part of  $\lambda$ , then for a given  $\varepsilon > 0$ , there exists  $\delta > 0$  such that for all  $x \in \mathcal{N}_\delta(x^*)$ , the flow  $\phi_t(x)$  of (1) satisfies

$$\|\phi_t(x) - x^*\| \leq \varepsilon e^{-\alpha t}$$

for all  $t \geq 0$ .

## Theorem 16

If  $x^*$  is a stable equilibrium point of (1), no eigenvalue of  $Df(x^*)$  has positive real part.

## Phase plane analysis

- ▶ In  $\mathbb{R}^2$ , nullclines are curves.
- ▶ Nullclines are the level set 0 of the vector field. If we have

$$x_1' = f_1(x_1, x_2)$$

$$x_2' = f_2(x_1, x_2)$$

then the nullclines for  $x_1$  are the curves defined by

$$\{(x_1, x_2) \in \mathbb{R}^2 : f_1(x_1, x_2) = 0\}$$

those for  $x_2$  are

$$\{(x_1, x_2) \in \mathbb{R}^2 : f_2(x_1, x_2) = 0\}$$

- ▶ On the nullcline associated to one state variable, this state variable has zero derivative.
- ▶ Equilibria lie at the intersections of nullclines for both state variables (in  $\mathbb{R}^2$ ).

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# Linear ODEs

## Definition 17 (Linear ODE)

A *linear* ODE is a differential equation taking the form

$$\frac{d}{dt}x = A(t)x + B(t), \quad (\text{LNH})$$

where  $A(t) \in \mathcal{M}_n(\mathbb{R})$  with continuous entries,  $B(t) \in \mathbb{R}^n$  with real valued, continuous coefficients, and  $x \in \mathbb{R}^n$ . The associated IVP takes the form

$$\begin{aligned} \frac{d}{dt}x &= A(t)x + B(t) \\ x(t_0) &= x_0. \end{aligned} \quad (2)$$

# Types of systems

- ▶  $x' = A(t)x + B(t)$  is linear nonautonomous ( $A(t)$  depends on  $t$ ) nonhomogeneous (also called *affine* system).
- ▶  $x' = A(t)x$  is linear nonautonomous homogeneous.
- ▶  $x' = Ax + B$ , that is,  $A(t) \equiv A$  and  $B(t) \equiv B$ , is linear autonomous nonhomogeneous (or affine autonomous).
- ▶  $x' = Ax$  is linear autonomous homogeneous.



# Existence and uniqueness of solutions

## Theorem 18 (Existence and Uniqueness)

*Solutions to (2) exist and are unique on the whole interval over which  $A$  and  $B$  are continuous.*

*In particular, if  $A, B$  are constant, then solutions exist on  $\mathbb{R}$ .*

# Autonomous linear systems

Consider the autonomous affine system

$$\frac{d}{dt}x = Ax + B, \quad (\text{A})$$

and the associated homogeneous autonomous system

$$\frac{d}{dt}x = Ax. \quad (\text{L})$$

# Exponential of a matrix

## Definition 19 (Matrix exponential)

Let  $A \in \mathcal{M}_n(\mathbb{K})$  with  $\mathbb{K} = \mathbb{R}$  or  $\mathbb{C}$ . The *exponential* of  $A$ , denoted  $e^{At}$ , is a matrix in  $\mathcal{M}_n(\mathbb{K})$ , defined by

$$e^{At} = \mathbb{I} + \sum_{k=1}^{\infty} \frac{t^k}{k!} A^k,$$

where  $\mathbb{I}$  is the identity matrix in  $\mathcal{M}_n(\mathbb{K})$ .

# Properties of the matrix exponential

- ▶  $e^{At_1} e^{At_2} = e^{A(t_1+t_2)}$  for all  $t_1, t_2 \in \mathbb{R}$ . 1
- ▶  $Ae^{At} = e^{At}A$  for all  $t \in \mathbb{R}$ .
- ▶  $(e^{At})^{-1} = e^{-At}$  for all  $t \in \mathbb{R}$ .
- ▶ The unique solution  $\phi$  of (L) with  $\phi(t_0) = x_0$  is given by

$$\phi(t) = e^{A(t-t_0)}x_0.$$

## Computing the matrix exponential

Let  $P$  be a nonsingular matrix in  $\mathcal{M}_n(\mathbb{R})$ . We transform the IVP

$$\begin{aligned}\frac{d}{dt}x &= Ax \\ x(t_0) &= x_0\end{aligned}\tag{L-IVP}$$

using the transformation  $x = Py$  or  $y = P^{-1}x$ .

The dynamics of  $y$  is

$$\begin{aligned}y' &= (P^{-1}x)' \\ &= P^{-1}x' \\ &= P^{-1}Ax \\ &= P^{-1}APy\end{aligned}$$

The initial condition is  $y_0 = P^{-1}x_0$ .

We have thus transformed IVP (L\_IVP) into

$$\begin{aligned}\frac{d}{dt}y &= P^{-1}APy \\ y(t_0) &= P^{-1}x_0\end{aligned}\tag{L_IVP_y}$$

From the earlier result, we then know that the solution of (L\_IVP\_y) is given by

$$\psi(t) = e^{P^{-1}AP(t-t_0)}P^{-1}x_0,$$

and since  $x = Py$ , the solution to (L\_IVP) is given by

$$\phi(t) = Pe^{P^{-1}AP(t-t_0)}P^{-1}x_0.$$

So everything depends on  $P^{-1}AP$ .

## The cases

- ▶  $P^{-1}AP$  is diagonal, the solution to (L\_IVP) is given by

$$\phi(t) = P \begin{pmatrix} e^{\lambda_1 t} & & 0 \\ & \ddots & \\ 0 & & e^{\lambda_n t} \end{pmatrix} P^{-1}x_0.$$

- ▶  $P^{-1}AP$  is not diagonal, then use Jordan form (slightly more complicated).

## Theorem 20

*For all  $(t_0, x_0) \in \mathbb{R} \times \mathbb{R}^n$ , there is a unique solution  $x(t)$  to (L\_IVP) defined for all  $t \in \mathbb{R}$ . Each coordinate function of  $x(t)$  is a linear combination of functions of the form*

$$t^k e^{\alpha t} \cos(\beta t) \quad \text{and} \quad t^k e^{\alpha t} \sin(\beta t)$$

*where  $\alpha + i\beta$  is an eigenvalue of  $A$  and  $k$  is less than the algebraic multiplicity of the eigenvalue.*



# Generalized eigenvectors, nilpotent matrix

## Definition 21 (Generalized eigenvectors)

Let  $A \in \mathcal{M}_n(\mathbb{R})$ . Suppose  $\lambda$  is an eigenvalue of  $A$  with multiplicity  $m \leq n$ . Then, for  $k = 1, \dots, m$ , any nonzero solution  $v$  of

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

is called a *generalized eigenvector* of  $A$ .

## Definition 22 (Nilpotent matrix)

Let  $A \in \mathcal{M}_n(\mathbb{R})$ .  $A$  is *nilpotent* (of order  $k$ ) if  $A^j \neq 0$  for  $j = 1, \dots, k - 1$ , and  $A^k = 0$ .

# Jordan normal form

## Theorem 23 (Jordan normal form)

Let  $A \in \mathcal{M}_n(\mathbb{R})$  have eigenvalues  $\lambda_1, \dots, \lambda_n$ , repeated according to their multiplicities.

- ▶ Then there exists a basis of generalized eigenvectors for  $\mathbb{R}^n$ .
- ▶ And if  $\{v_1, \dots, v_n\}$  is any basis of generalized eigenvectors for  $\mathbb{R}^n$ , then the matrix  $P = [v_1 \cdots v_n]$  is invertible, and  $A$  can be written as

$$A = S + N,$$

where

$$P^{-1}SP = \text{diag}(\lambda_j),$$

the matrix  $N = A - S$  is nilpotent of order  $k \leq n$ , and  $S$  and  $N$  commute, i.e.,  $SN = NS$ .

## Theorem 24

*Under conditions of the Jordan normal form Theorem, the linear system  $x' = Ax$  with initial condition  $x(0) = x_0$ , has solution*

$$x(t) = P \operatorname{diag} \left( e^{\lambda_j t} \right) P^{-1} \left( \mathbb{I} + Nt + \cdots + \frac{t^k}{k!} N^k \right) x_0.$$

The result is particularly easy to apply in the following case.

## Theorem 25 (Case of an eigenvalue of multiplicity $n$ )

*Suppose that  $\lambda$  is an eigenvalue of multiplicity  $n$  of  $A \in \mathcal{M}_n(\mathbb{R})$ . Then  $S = \operatorname{diag}(\lambda)$ , and the solution of  $x' = Ax$  with initial value  $x_0$  is given by*

$$x(t) = e^{\lambda t} \left( \mathbb{I} + Nt + \cdots + \frac{t^k}{k!} N^k \right) x_0.$$

In the simplified case, we do not need the matrix  $P$  (the basis of generalized eigenvectors).

## A variation of constants formula

### Theorem 26 (Variation of constants formula)

Consider the IVP

$$x' = Ax + B(t) \quad (3a)$$

$$x(t_0) = x_0, \quad (3b)$$

where  $B : \mathbb{R} \rightarrow \mathbb{R}^n$  a smooth function on  $\mathbb{R}$ , and let  $e^{A(t-t_0)}$  be matrix exponential associated to the homogeneous system  $x' = Ax$ . Then the solution  $\phi$  of (3) is given by

$$\phi(t) = e^{A(t-t_0)}x_0 + \int_{t_0}^t e^{A(t-s)}B(s)ds. \quad (4)$$

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## Checking that a given function is solution to a PDE

Give a PDE, to check that a given function is solution to the PDE, you need to check that it satisfies the PDE.

For example, consider the wave equation

$$u_{tt} = c^2 u_{xx} \quad (5)$$

To check that

$$\xi(x, t) = F(x - ct) + G(x + ct)$$

satisfies (24), we need to compute  $\xi_{tt}$ ,  $\xi_{xx}$ , and verify that

$$\xi_{tt} = c^2 \xi_{xx}$$

By the chain rule, we have

$$\frac{\partial}{\partial t}\xi(x, t) = -cF'(x - ct) + cG'(x + ct)$$

and thus

$$\frac{\partial^2}{\partial t^2}\xi(x, t) = c^2F''(x - ct) + c^2G''(x + ct)$$

Also, by the chain rule,

$$\frac{\partial}{\partial x}\xi(x, t) = F'(x - ct) + G'(x + ct)$$

and thus

$$\frac{\partial^2}{\partial t^2}\xi(x, t) = F''(x - ct) + G''(x + ct)$$

So we have

$$\begin{aligned}\xi_{tt} &= c^2 F''(x - ct) + c^2 G''(x + ct) \\ &= c^2 (F''(x - ct) + G''(x + ct)) \\ &= c^2 \xi_{xx}\end{aligned}$$

which implies that

$$\xi(x, t) = F(x - ct) + G(x + ct)$$

satisfies (24).



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# Probability, random variable

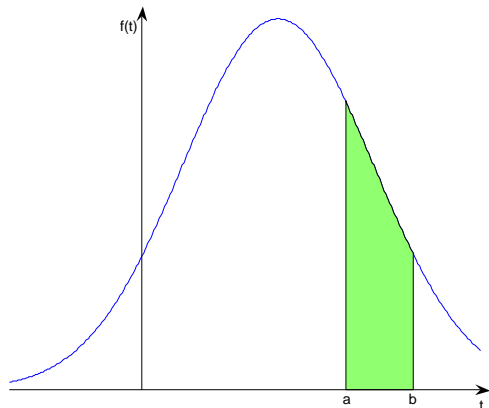
A *probability* is a function  $\mathcal{P}$ , with values in  $[0, 1]$ .

A random variable  $X$  is a variable taking random values. If the values are in a continuous space ( $\mathbb{R}, \mathbb{R}^n$ , etc.), then the variable is continuous. Otherwise ( $\mathbb{N}, \mathbb{Z}$ , etc.), the variable is discrete.

# Probability density function

Suppose  $T$  is a continuous random variable. Then it has a continuous *probability density function*,  $f$ .

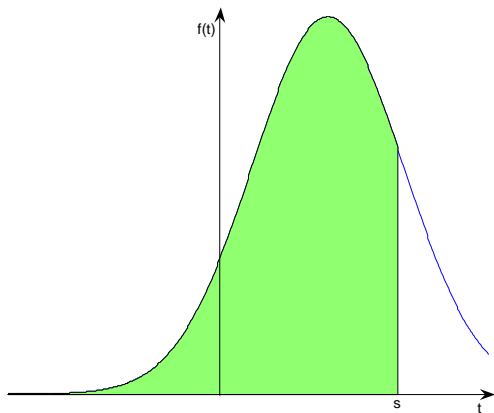
- ▶  $f \geq 0$ ,
- ▶  $\int_{-\infty}^{+\infty} f(s)ds = 1$ .
- ▶  $\mathcal{P}(a \leq T \leq b) = \int_a^b f(t)dt$ .



## Cumulative distribution function

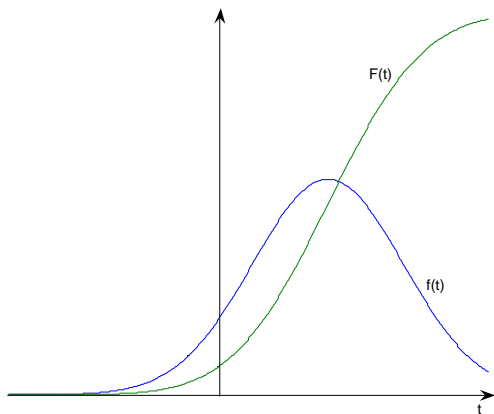
The cumulative distribution function (c.d.f.) is a function  $F(t)$  that characterizes the distribution of  $T$ , and defined by

$$F(s) = \mathcal{P}(T \leq s) = \int_{-\infty}^s f(x) dx.$$



## Properties of the c.d.f.

- ▶ Since  $f$  is a nonnegative function,  $F$  is nondecreasing.
- ▶ Since  $f$  is a probability density function,  $\int_{-\infty}^{+\infty} f(s)ds = 1$ , and thus  $\lim_{t \rightarrow \infty} F(t) = 1$ .



## Mean value

For a continuous random variable  $T$  with probability density function  $f$ , the *mean* value of  $T$ , denoted  $\bar{T}$  or  $E(T)$ , is given by

$$E(T) = \int_{-\infty}^{+\infty} tf(t)dt.$$

## Survival function

Another characterization of the distribution of the random variable  $T$  is through the *survival* (or *sojourn*) function.

The survival function of state  $S_1$  is given by

$$\mathcal{S}(t) = 1 - F(t) = \mathcal{P}(T > t) \quad (6)$$

This gives a description of the *sojourn time* of a system in a particular state (the time spent in the state).

$\mathcal{S}$  is a nonincreasing function (since  $\mathcal{S} = 1 - F$  with  $F$  a c.d.f.), and  $\mathcal{S}(0) = 1$  (since  $T$  is a positive random variable).

The *average sojourn time*  $\tau$  in state  $S_1$  is given by

$$\tau = E(T) = \int_0^{\infty} tf(t)dt$$

Assuming that  $\lim_{t \rightarrow \infty} tS(t) = 0$  (which is verified for most probability distributions),

$$\tau = \int_0^{\infty} S(t)dt$$



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Regular Markov chains

Absorbing Markov chains

We conduct an experiment with a set of  $r$  outcomes,

$$S = \{S_1, \dots, S_r\}.$$

The experiment is repeated  $n$  times (with  $n$  large, potentially infinite).

The system has no memory: the next state depends only on the present state.

The probability of  $S_j$  occurring on the next step, given that  $S_i$  occurred on the last step, is

$$p_{ij} = p(S_j|S_i).$$

# Markov chain

## Definition 27

An experiment with finite number of possible outcomes  $S_1, \dots, S_r$  is repeated. The sequence of outcomes is a *Markov chain* if there is a set of  $r^2$  numbers  $\{p_{ij}\}$  such that the conditional probability of outcome  $S_j$  on any experiment given outcome  $S_i$  on the previous experiment is  $p_{ij}$ , i.e., for  $1 \leq i, j \leq r$ ,  $n = 1, \dots$ ,

$$p_{ij} = \Pr(S_j \text{ on experiment } n + 1 | S_i \text{ on experiment } n).$$

The outcomes  $S_1, \dots, S_r$  are the *states*, and the  $p_{ij}$  are the *transition probabilities*. The matrix  $P = [p_{ij}]$  is the *transition matrix*.

## Transition matrix

The matrix

$$P = \begin{pmatrix} p_{11} & p_{12} & \cdots & p_{1r} \\ p_{21} & p_{22} & \cdots & p_{2r} \\ p_{r1} & p_{r2} & \cdots & p_{rr} \end{pmatrix}$$

has

- ▶ nonnegative entries,  $p_{ij} \geq 0$
- ▶ entries less than 1,  $p_{ij} \leq 1$
- ▶ row sum 1, which we write

$$\sum_{j=1}^r p_{ij} = 1, \quad i = 1, \dots, r$$

or, using the notation  $\mathbb{1}^T = (1, \dots, 1)$ ,

$$P\mathbb{1} = \mathbb{1}$$

## Repetition of the process

Let  $p_i(n)$  be the probability that the state  $S_i$  will occur on the  $n^{\text{th}}$  repetition of the experiment,  $1 \leq i \leq r$ . Then

$$p(n+1) = p(n)P, \quad n = 1, 2, 3, \dots \quad (7)$$

where  $p(n) = (p_1(n), p_2(n), \dots, p_r(n))$  is a (row) probability vector and  $P = (p_{ij})$  is a  $r \times r$  transition matrix,

$$P = \begin{pmatrix} p_{11} & p_{12} & \cdots & p_{1r} \\ p_{21} & p_{22} & \cdots & p_{2r} \\ p_{r1} & p_{r2} & \cdots & p_{rr} \end{pmatrix}$$

# Stochastic matrices

## Definition 28 (Stochastic matrix)

The nonnegative  $r \times r$  matrix  $M$  is *stochastic* if  $\sum_{j=1}^r a_{ij} = 1$  for all  $i = 1, 2, \dots, r$ .

## Theorem 29

*Let  $M$  be a stochastic matrix  $M$ . Then all eigenvalues  $\lambda$  of  $M$  are such that  $|\lambda| \leq 1$ . Furthermore,  $\lambda = 1$  is an eigenvalue of  $M$ .*

To see that 1 is an eigenvalue, write the definition of a stochastic matrix, i.e.,  $M$  has row sums 1. In vector form,  $M\mathbb{1} = \mathbb{1}$ . Now remember that  $\lambda$  is an eigenvalue of  $M$ , with associated eigenvector  $v$ , iff  $Mv = \lambda v$ . So, in the expression  $M\mathbb{1} = \mathbb{1}$ , we read an eigenvector,  $\mathbb{1}$ , and an eigenvalue, 1.

## Long “time” behavior

Let  $p(0)$  be the initial distribution (row) vector. Then

$$\begin{aligned}p(1) &= p(0)P \\p(2) &= p(1)P \\&= (p(0)P)P \\&= p(0)P^2\end{aligned}$$

Iterating, we get that for any  $n$ ,

$$p(n) = p(0)P^n$$

Therefore,

$$\lim_{n \rightarrow +\infty} p(n) = \lim_{n \rightarrow +\infty} p(0)P^n = p(0) \lim_{n \rightarrow +\infty} P^n$$

# Additional properties of stochastic matrices

## Theorem 30

*If  $M, N$  are stochastic matrices, then  $MN$  is a stochastic matrix.*

## Theorem 31

*If  $M$  is a stochastic matrix, then for any  $k \in \mathbb{N}$ ,  $M^k$  is a stochastic matrix.*



## Markov chains

Regular Markov chains

Absorbing Markov chains

# Regular Markov chain

## Definition 32 (Regular Markov chain)

A regular Markov chain is one in which  $P^k$  is positive for some integer  $k > 0$ , i.e.,  $P^k$  has only positive entries, no zero entries.

## Definition 33

A nonnegative matrix  $M$  is primitive if, and only if, there is an integer  $k > 0$  such that  $M^k$  is positive.

## Theorem 34

*A Markov chain is regular if, and only if, the transition matrix  $P$  is primitive.*

# Important result for regular Markov chains

## Theorem 35

If  $P$  is the transition matrix of a regular Markov chain, then

1. the powers  $P^n$  approach a stochastic matrix  $W$ ,
2. each row of  $W$  is the same (row) vector  $w = (w_1, \dots, w_r)$ ,
3. the components of  $w$  are positive.

So if the Markov chain is regular,

$$\lim_{n \rightarrow +\infty} p(n) = p(0) \lim_{n \rightarrow +\infty} P^n = p(0)W$$

## Left and right eigenvectors

Let  $M$  be an  $r \times r$  matrix,  $u, v$  be two column vectors,  $\lambda \in \mathbb{R}$ .  
Then, if

$$Mu = \lambda u,$$

$u$  is the (right) eigenvector corresponding to  $\lambda$ , and if

$$v^T M = \lambda v^T$$

then  $v$  is the left eigenvector corresponding to  $\lambda$ . Note that to a given eigenvalue there corresponds one left and one right eigenvector.

The vector  $w$  is in fact the left eigenvector corresponding to the eigenvalue 1 of  $P$ . (We already know that the (right) eigenvector corresponding to 1 is  $\mathbb{1}$ .)

To see this, remark that, if  $p(n)$  converges, then  $p(n+1) = p(n)P$ , so  $w$  is a fixed point of the system. We thus write

$$wP = w$$

and solve for  $w$ , which amounts to finding  $w$  as the left eigenvector corresponding to the eigenvalue 1.

Alternatively, we can find  $w$  as the (right) eigenvector associated to the eigenvalue 1 for the transpose of  $P$ ,

$$P^T w^T = w^T$$

Now remember that when you compute an eigenvector, you get a result that is the eigenvector, to a multiple.

So the expression you obtain for  $w$  might have to be normalized (you want a probability vector). Once you obtain  $w$ , check that the norm  $\|w\|$  defined by

$$\|w\| = w_1 + \dots + w_r$$

is equal to one. If not, use

$$\frac{w}{\|w\|}$$

## Markov chains

Regular Markov chains

Absorbing Markov chains

# Absorbing states, absorbing chains

## Definition 36

A state  $S_i$  in a Markov chain is *absorbing* if whenever it occurs on the  $n^{\text{th}}$  generation of the experiment, it then occurs on every subsequent step. In other words,  $S_i$  is absorbing if  $p_{ii} = 1$  and  $p_{ij} = 0$  for  $i \neq j$ .

## Definition 37

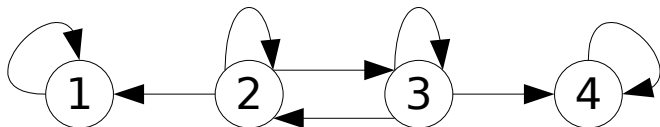
A Markov chain is said to be absorbing if it has at least one absorbing state, and if from every state it is possible to go to an absorbing state.

In an absorbing Markov chain, a state that is not absorbing is called *transient*.



## Some questions on absorbing chains

Suppose we have a chain like the following:



1. Does the process eventually reach an absorbing state?
2. Average number of times spent in a transient state, if starting in a transient state?
3. Average number of steps before entering an absorbing state?
4. Probability of being absorbed by a given absorbing state, when there are more than one, when starting in a given transient state?

# Reaching an absorbing state

Answer to question 1:

## Theorem 38

*In an absorbing Markov chain, the probability of reaching an absorbing state is 1.*

## Standard form of the transition matrix

For an absorbing chain with  $k$  absorbing states and  $r - k$  transient states, the transition matrix can be written as

$$P = \begin{pmatrix} \mathbb{I}_k & \mathbf{0} \\ R & Q \end{pmatrix}$$

with following meaning,

	Absorbing states	Transient states
Absorbing states	$\mathbb{I}_k$	$\mathbf{0}$
Transient states	$R$	$Q$

with  $\mathbb{I}_k$  the  $k \times k$  identity matrix,  $\mathbf{0}$  an  $k \times (r - k)$  matrix of zeros,  $R$  an  $(r - k) \times k$  matrix and  $Q$  an  $(r - k) \times (r - k)$  matrix.

The matrix  $\mathbb{I}_{r-k} - Q$  is invertible. Let

- ▶  $N = (\mathbb{I}_{r-k} - Q)^{-1}$  be the *fundamental matrix* of the Markov chain
- ▶  $T_i$  be the sum of the entries on row  $i$  of  $N$
- ▶  $B = NR$ .

Answers to our remaining questions:

2.  $N_{ij}$  is the average number of times the process is in the  $j$ th transient state if it starts in the  $i$ th transient state.
3.  $T_i$  is the average number of steps before the process enters an absorbing state if it starts in the  $i$ th transient state.
4.  $B_{ij}$  is the probability of eventually entering the  $j$ th absorbing state if the process starts in the  $i$ th transient state.

# Modelling topics

Single population dynamics and the logistic situation

Time of residence in a state – Exponential distribution

Epidemic models

The chemostat

Traffic flow

Shallow water waves

A simple genetic model

# Outline

## Single population dynamics and the logistic situation

The data: US census

A quadratic curve?

Population growth – Logistic equation

Qualitative analysis of the logistic ODE

The delayed logistic equation

The logistic map

Time of residence in a state – Exponential distribution

Epidemic models

The chemostat

Traffic flow

## Single population dynamics and the logistic situation

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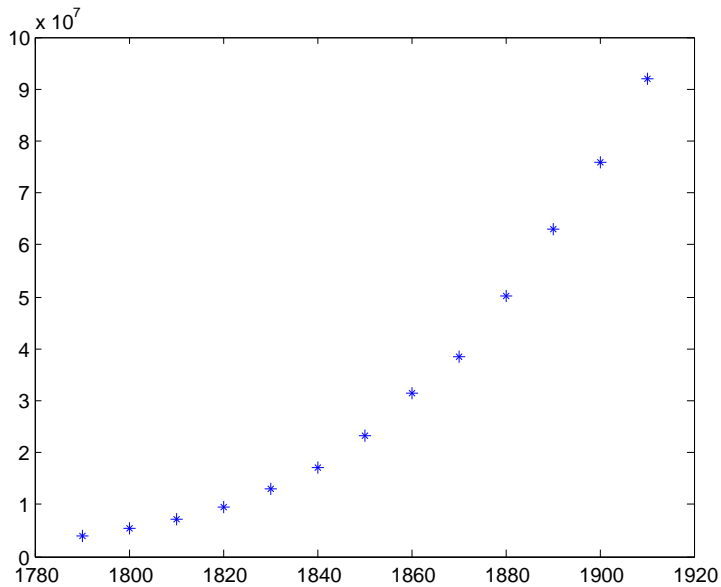
The delayed logistic equation

The logistic map

## The US population from 1790 to 1910

Year	Population (millions)	Year	Population (millions)
1790	3.929	1860	31.443
1800	5.308	1870	38.558
1810	7.240	1880	50.156
1820	9.638	1890	62.948
1830	12.866	1900	75.995
1840	17.069	1910	91.972
1850	23.192		





## Single population dynamics and the logistic situation

The data: US census

**A quadratic curve?**

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## First idea

The curve looks like a piece of a parabola. So let us fit a curve of the form

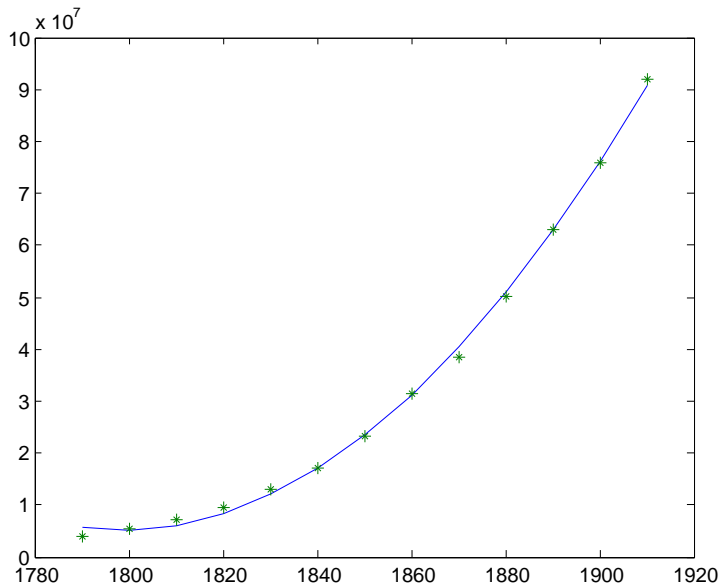
$$P(t) = a + bt + ct^2.$$

To do this, we want to minimize

$$S = \sum_{k=1}^{13} (P(t_k) - P_k)^2,$$

where  $t_k$  are the known dates,  $P_k$  are the known populations, and  $P(t_k) = a + bt_k + ct_k^2$ .

## Our first guess, in pictures



which turned out to work quite well

How does our formula do for present times?

$f(2006)$

ans = 301468584.066013

301,468,584, compared to the 298,444,215 July 2006 estimate, overestimates the population by 3,024,369, a relative error of approximately 1%.

## Single population dynamics and the logistic situation

The data: US census

A quadratic curve?

**Population growth – Logistic equation**

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# The logistic equation

The logistic curve is the solution to the ordinary differential equation

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

which is called the *logistic equation*.  $r$  is the *intrinsic growth rate*,  $K$  is the *carrying capacity*.

This equation was introduced by Pierre-François Verhulst (1804-1849), in 1844.

## Reinterpreting the logistic equation

The equation

$$N' = bN - dN - cN^2$$

is rewritten as

$$N' = (b - d)N - cN^2.$$

- ▶  $b - d$  represents the rate at which the population increases (or decreases) in the absence of competition. It is called the *intrinsic growth rate* of the population.
- ▶  $c$  is the rate of *intraspecific* competition. The prefix *intra* refers to the fact that the competition is occurring between members of the same species, that is, within the species.



## Equivalent equations

$$\begin{aligned}N' &= (b - d)N - cN^2 \\&= ((b - d) - cN)N \\&= \left(r - \frac{r}{r}cN\right)N, \quad \text{with } r = b - d \\&= rN \left(1 - \frac{c}{r}N\right) \\&= rN \left(1 - \frac{N}{K}\right),\end{aligned}$$

with

$$\frac{c}{r} = \frac{1}{K},$$

that is,  $K = r/c$ .

## Single population dynamics and the logistic situation

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**Qualitative analysis of the logistic ODE**

The delayed logistic equation

The logistic map

## Studying the logistic equation qualitatively

We study

$$N' = rN \left(1 - \frac{N}{K}\right). \quad (\text{ODE1})$$

For this, write

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

Consider the initial value problem (IVP)

$$N' = f(N), \quad N(0) = N_0 > 0. \quad (\text{IVP1})$$

- ▶  $f$  is  $C^1$  (differentiable with continuous derivative) so solutions to (IVP1) exist and are unique.

*Equilibria* of (ODE1) are points such that  $f(N) = 0$  (so that  $N' = f(N) = 0$ , meaning  $N$  does not vary). So we solve  $f(N) = 0$  for  $N$ . We find two points:

- ▶  $N = 0$
- ▶  $N = K$ .

By uniqueness of solutions to (IVP1), solutions cannot cross the lines  $N(t) = 0$  and  $N(t) = K$ .

There are several cases.

- ▶  $N = 0$  for some  $t$ , then  $N(t) = 0$  for all  $t \geq 0$ , by uniqueness of solutions.
- ▶  $N \in (0, K)$ , then  $rN > 0$  and  $N/K < 1$  so  $1 - N/K > 0$ , which implies that  $f(N) > 0$ . As a consequence,  $N(t)$  increases if  $N \in (0, K)$ .
- ▶  $N = K$ , then  $rN > 0$  but  $N/K = 1$  so  $1 - N/K = 0$ , which implies that  $f(N) = 0$ . As a consequence,  $N(t) = K$  for all  $t \geq 0$ , by uniqueness of solutions.
- ▶  $N > K$ , the  $rN > 0$  and  $N/K > 1$ , implying that  $1 - N/K < 0$  and in turn,  $f(N) < 0$ . As a consequence,  $N(t)$  decreases if  $N \in (K, +\infty)$ .

Therefore,

### Theorem 39

*Suppose that  $N_0 > 0$ . Then the solution  $N(t)$  of (IVP1) is such that*

$$\lim_{t \rightarrow \infty} N(t) = K,$$

*so that  $K$  is the number of individuals that the environment can support, the carrying capacity of the environment.*

*If  $N_0 = 0$ , then  $N(t) = 0$  for all  $t \geq 0$ .*

## Single population dynamics and the logistic situation

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**The delayed logistic equation**

The logistic map

# The delayed logistic equation

Consider the equation as

$$\frac{N'}{N} = (b - d) - cN,$$

that is, the per capita rate of growth of the population depends on the net growth rate  $b - d$ , and some density dependent inhibition  $cN$  (resulting of competition).

Suppose that instead of instantaneous inhibition, there is some delay  $\tau$  between the time the inhibiting event takes place and the moment where it affects the growth rate. (For example, two individuals fight for food, and one later dies of the injuries sustained when fighting).



## The delay logistic equation

In the of a time  $\tau$  between inhibiting event and inhibition, the equation would be written as

$$\frac{N'}{N} = (b - d) - cN(t - \tau).$$

Using the change of variables introduced earlier, this is written

$$N'(t) = rN(t) \left( 1 - \frac{N(t - \tau)}{K} \right). \quad (\text{DDE1})$$

Such an equation is called a *delay* differential equation. It is much more complicated to study than (ODE1). In fact, some things remain unknown about (DDE1).

## Delayed initial value problem

The IVP takes the form

$$\begin{aligned} N'(t) &= rN(t) \left( 1 - \frac{N(t-\tau)}{K} \right), \\ N(t) &= \phi(t) \text{ for } t \in [-\tau, 0], \end{aligned} \tag{IVP2}$$

where  $\phi(t)$  is some continuous function. Hence, initial conditions (called initial data in this case) must be specific on an interval, instead of being specified at a point, to guarantee existence and uniqueness of solutions.

We will not learn how to study this type of equation (this is graduate level mathematics). I will give a few results.

To find equilibria, remark that delay should not play a role, since  $N$  should be constant. Thus, equilibria are found by considering the equation with no delay, which is (ODE1).

### Theorem 40

*Suppose that  $r\tau < 22/7$ . Then all solutions of (IVP2) with positive initial data  $\phi(t)$  tend to  $K$ . If  $r\tau > \pi/2$ , then  $K$  is an unstable equilibrium and all solutions of (IVP2) with positive initial data  $\phi(t)$  on  $[-\tau, 0]$  are oscillatory.*

Note that there is a gray zone between  $22/7$  and  $\pi/2$ . The first part of the theorem was proved in 1945 by Wright. Although there is very strong numerical evidence that this is in fact true up to  $\pi/2$ , nobody has yet managed to prove it.

## Single population dynamics and the logistic situation

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# The logistic map

The logistic *map* is, for  $t \geq 0$ ,

$$N_{t+1} = rN_t \left(1 - \frac{N_t}{K}\right). \quad (\text{DT1})$$

To transform this into an initial value problem, we need to provide an initial condition  $N_0 \geq 0$  for  $t = 0$ .

Consider the simplified version (??),

$$x_{t+1} = rx_t(1 - x_t) \stackrel{\Delta}{=} f_r(x_t).$$

**Are solutions well defined?** Suppose  $x_0 \in [0, 1]$ , do we stay in  $[0, 1]$ ?  $f_r$  is continuous on  $[0, 1]$ , so it has a extrema on  $[0, 1]$ . We have

$$f_r'(x) = r - 2rx = r(1 - 2x),$$

which implies that  $f_r$  increases for  $x < 1/2$  and decreases for  $x > 1/2$ , reaching a maximum at  $x = 1/2$ .

$f_r(0) = f_r(1) = 0$  are the minimum values, and  $f(1/2) = r/4$  is the maximum. Thus, if we want  $x_{t+1} \in [0, 1]$  for  $x_t \in [0, 1]$ , we need to consider  $r \leq 4$ .

- ▶ Note that if  $x_0 = 0$ , then  $x_t = 0$  for all  $t \geq 1$ .
- ▶ Similarly, if  $x_0 = 1$ , then  $x_1 = 0$ , and thus  $x_t = 0$  for all  $t \geq 1$ .
- ▶ This is true for all  $t$ : if there exists  $t_k$  such that  $x_{t_k} = 1$ , then  $x_t = 0$  for all  $t \geq t_k$ .
- ▶ This last case might occur if  $r = 4$ , as we have seen.
- ▶ Also, if  $r = 0$  then  $x_t = 0$  for all  $t$ .

For these reasons, we generally consider

$$x \in (0, 1)$$

and

$$r \in (0, 4).$$

## Fixed points: existence

**Fixed points** of (??) satisfy  $x = rx(1 - x)$ , giving:

- ▶  $x = 0$ ;
- ▶  $1 = r(1 - x)$ , that is,  $p \triangleq \frac{r - 1}{r}$ .

Note that  $\lim_{r \rightarrow 0^+} p = 1 - \lim_{r \rightarrow 0^+} 1/r = -\infty$ ,  $\frac{\partial}{\partial r} p = 1/r^2 > 0$  (so  $p$  is an increasing function of  $r$ ),  $p = 0 \Leftrightarrow r = 1$  and  $\lim_{r \rightarrow \infty} p = 1$ . So we come to this first conclusion:

- ▶ 0 always is a fixed point of  $f_r$ .
- ▶ If  $0 < r < 1$ , then  $p$  takes negative values so is not relevant.
- ▶ If  $1 < r < 4$ , then  $p$  exists.



## Stability of the fixed points

**Stability** of the fixed points is determined by the (absolute) value  $f'_r$  at these fixed points. We have

$$|f'_r(0)| = r,$$

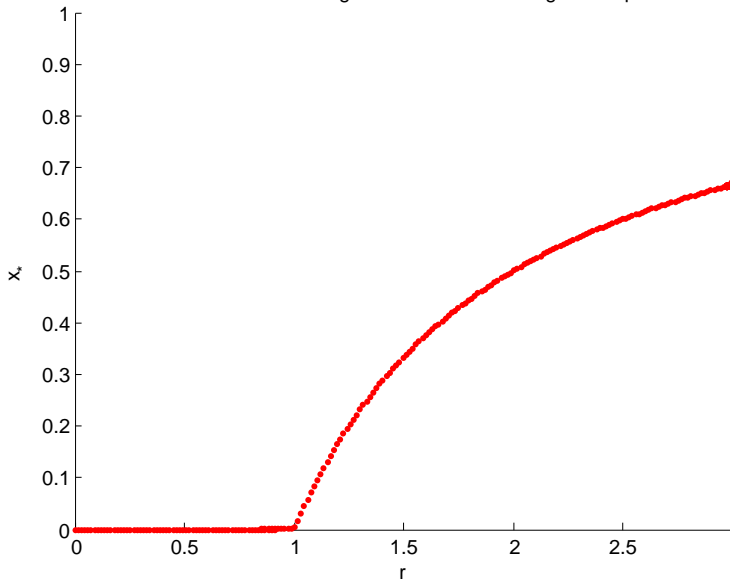
and

$$\begin{aligned} |f'_r(p)| &= \left| r - 2r \frac{r-1}{r} \right| \\ &= |r - 2(r-1)| \\ &= |2 - r| \end{aligned}$$

Therefore, we have

- ▶ if  $0 < r < 1$ , then the fixed point  $x = p$  does not exist and  $x = 0$  is attracting,
- ▶ if  $1 < r < 3$ , then  $x = 0$  is repelling, and  $x = p$  is attracting,
- ▶ if  $r > 3$ , then  $x = 0$  and  $x = p$  are repelling.

Bifurcation diagram for the discrete logistic map



## Another bifurcation

Thus the points  $r = 1$  and  $r = 3$  are bifurcation points. To see what happens when  $r > 3$ , we need to look for period 2 points.

$$\begin{aligned}f_r^2(x) &= f_r(f_r(x)) \\ &= rf_r(x)(1 - f_r(x)) \\ &= r^2x(1 - x)(1 - rx(1 - x)).\end{aligned}\tag{8}$$

0 and  $p$  are points of period 2, since a fixed point  $x^*$  of  $f$  satisfies  $f(x^*) = x^*$ , and so,  $f^2(x^*) = f(f(x^*)) = f(x^*) = x^*$ .

This helps localizing the other periodic points. Writing the fixed point equation as

$$Q(x) \triangleq f_r^2(x) - x = 0,$$

we see that, since 0 and  $p$  are fixed points of  $f_\mu^2$ , they are roots of  $Q(x)$ . Therefore,  $Q$  can be factorized as

$$Q(x) = x(x - p)(-r^3x^2 + Bx + C),$$

Substitute the value  $(r - 1)/r$  for  $p$  in  $Q$ , develop  $Q$  and (8) and equate coefficients of like powers gives

$$Q(x) = x \left( x - \frac{r-1}{r} \right) (-r^3x^2 + r^2(r+1)x - r(r+1)). \quad (9)$$

We already know that  $x = 0$  and  $x = p$  are roots of (9). So we search for roots of

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

Discriminant is

$$\begin{aligned} \Delta &= r^4(r+1)^2 - 4r^4(r+1) \\ &= r^4(r+1)(r+1-4) \\ &= r^4(r+1)(r-3). \end{aligned}$$

Therefore,  $R$  has distinct real roots if  $r > 3$ . Remark that for  $r = 3$ , the (double) root is  $p = 2/3$ . For  $r > 3$  but very close to 3, it follows from the continuity of  $R$  that the roots are close to  $2/3$ .

We use Descartes' rule of signs.

- ▶  $R$  has signed coefficients  $- + -$ , so 2 sign changes implying 0 or 2 positive real roots.
- ▶  $R(-x)$  has signed coefficients  $- - -$ , so no negative real roots.
- ▶ Since  $\Delta > 0$ , the roots are real, and thus it follows that both roots are positive.

To show that the roots are also smaller than 1, consider the change of variables  $z = x - 1$ . The polynomial  $R$  is transformed into

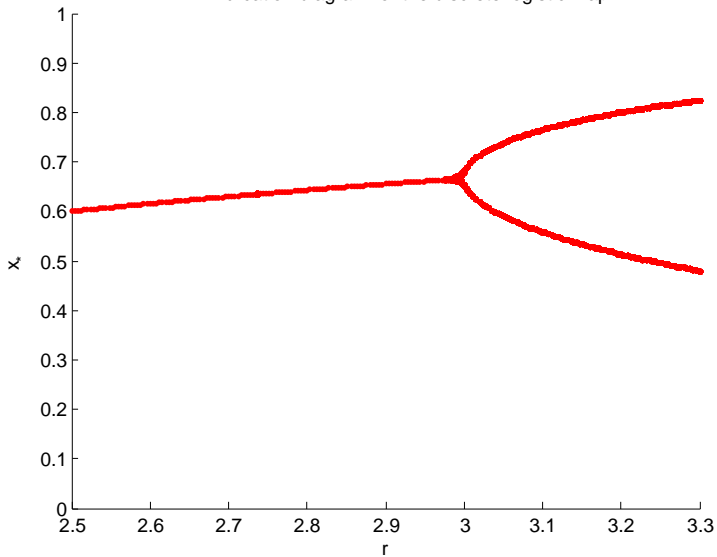
$$\begin{aligned}R_2(z) &= -r^3(z+1)^2 + r^2(r+1)(z+1) - r(r+1) \\ &= -r^3z^2 + r^2(1-r)z - r.\end{aligned}$$

For  $r > 1$ , the signed coefficients are  $- - -$ , so  $R_2$  has no root  $z > 0$ , implying in turn that  $R$  has no root  $x > 1$ .

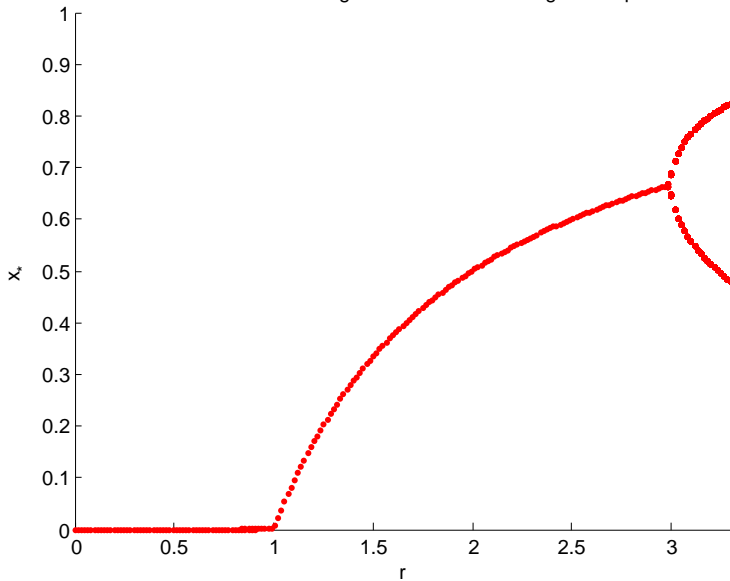
## Summing up

- ▶ If  $0 < r < 1$ , then  $x = 0$  is attracting,  $p$  does not exist and there are no period 2 points.
- ▶ At  $r = 1$ , there is a bifurcation (called a *transcritical* bifurcation).
- ▶ If  $1 < r < 3$ , then  $x = 0$  is repelling,  $p$  is attracting, and there are no period 2 points.
- ▶ At  $r = 3$ , there is another bifurcation (called a *period-doubling* bifurcation).
- ▶ For  $r > 3$ , both  $x = 0$  and  $x = p$  are repelling, and there is a period 2 point.

Bifurcation diagram for the discrete logistic map

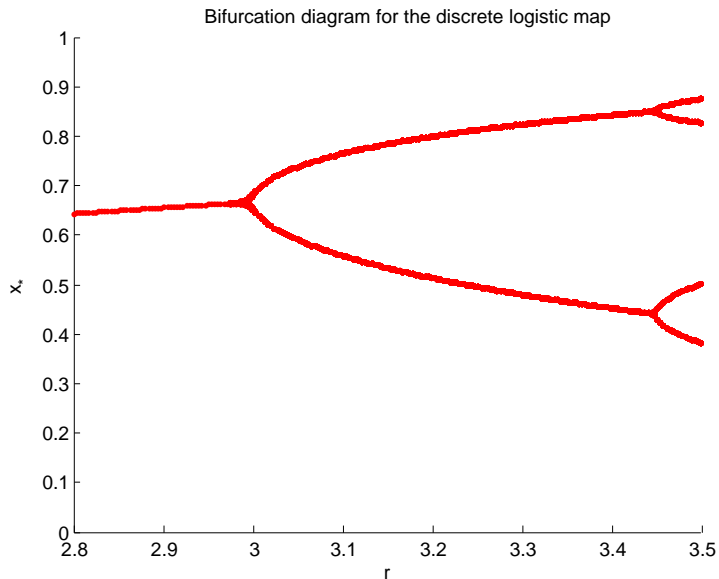


Bifurcation diagram for the discrete logistic map





## This process continues



## The period-doubling cascade to chaos

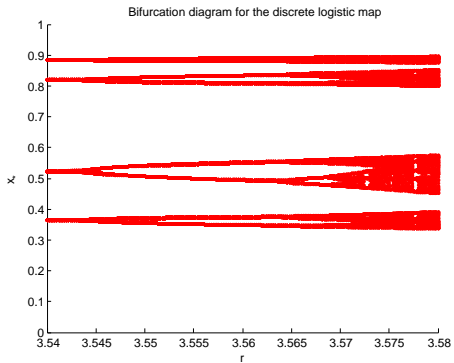
The logistic map undergoes a sequence of period doubling bifurcations, called the *period-doubling cascade*, as  $r$  increases from 3 to 4.

- ▶ Every successive bifurcation leads to a doubling of the period.
- ▶ The bifurcation points form a sequence,  $\{r_n\}$ , that has the property that

$$\lim_{n \rightarrow \infty} \frac{r_n - r_{n-1}}{r_{n+1} - r_n}$$

exists and is a constant, called the Feigenbaum constant, equal to 4.669202...

- ▶ This constant has been shown to exist in many of the maps that undergo the same type of cascade of period doubling bifurcations.



# Chaos

After a certain value of  $r$ , there are periodic points with all periods. In particular, there are periodic points of period 3.

By a theorem (called the Sarkovskii theorem), the presence of period 3 points implies the presence of points of all periods.

At this point, the system is said to be in a *chaotic regime*, or *chaotic*.

# Outline

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Time of residence in a state – Exponential distribution

A cohort model

Sojourn times in an SIS disease transmission model

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Shallow water waves

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## The exponential distribution

The random variable  $T$  has an *exponential* distribution if its probability density function takes the form

$$f(t) = \begin{cases} 0 & \text{if } t < 0, \\ \theta e^{-\theta t} & \text{if } t \geq 0, \end{cases} \quad (10)$$

with  $\theta > 0$ . Then the survival function for state  $S_1$  is of the form  $\mathcal{S}(t) = e^{-\theta t}$ , for  $t \geq 0$ , and the average sojourn time in state  $S_1$  is

$$\tau = \int_0^{\infty} e^{-\theta t} dt = \frac{1}{\theta}$$

## Time of residence in a state – Exponential distribution

A cohort model

Sojourn times in an SIS disease transmission model

## A model for a cohort with one cause of death

We consider a population consisting of individuals born at the same time (a *cohort*), for example, the same year.

We suppose

- ▶ At time  $t = 0$ , there are initially  $N_0 > 0$  individuals.
- ▶ All causes of death are compounded together.
- ▶ The time until death, for a given individual, is a random variable  $T$ , with continuous probability density distribution  $f(t)$  and survival function  $P(t)$ .



## The model

Denote  $N(t)$  the population at time  $t \geq 0$ . Then

$$N(t) = N_0 P(t). \quad (11)$$

- ▶  $N_0 P(t)$  gives the proportion of  $N_0$ , the initial population, that is still alive at time  $t$ .

## Case where $T$ is exponentially distributed

Suppose that  $T$  has an exponential distribution with mean  $1/d$  (or parameter  $d$ ),  $f(t) = de^{-dt}$ . Then the survival function is  $P(t) = e^{-dt}$ , and (11) takes the form

$$N(t) = N_0 e^{-dt}. \quad (12)$$

Now note that

$$\begin{aligned} \frac{d}{dt} N(t) &= -dN_0 e^{-dt} \\ &= -dN(t), \end{aligned}$$

with  $N(0) = N_0$ .

$\Rightarrow$  The ODE  $N' = -dN$  makes the assumption that the life expectancy at birth is exponentially distributed.

## Time of residence in a state – Exponential distribution

A cohort model

Sojourn times in an SIS disease transmission model

## An SIS model

Consider a disease that confers no immunity. In this case, individuals are either

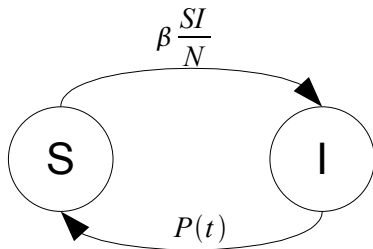
- ▶ *susceptible* to the disease, with the number of such individuals at time  $t$  denoted by  $S(t)$ ,
- ▶ or *infected* by the disease (and are also *infective* in the sense that they propagate the disease), with the number of such individuals at time  $t$  denoted by  $I(t)$ .

Assumptions:

- ▶ Individuals typically recover from the disease.
- ▶ The disease does not confer immunity.
- ▶ There is no birth or death.
- ▶ Infection is of *standard incidence* type

## A flow diagram for the model

This is the *flow diagram* of our model:



## Reducing the dimension of the problem

To formulate our model, we would in principle require an equation for  $S$  and an equation for  $I$ .

But we have

$$S(t) + I(t) = N, \text{ or equivalently, } S(t) = N - I(t).$$

$N$  is constant (equal total population at time  $t = 0$ ), so we can deduce the value of  $S(t)$ , once we know  $I(t)$ , from the equation  $S(t) = N - I(t)$ .

We only need to consider 1 equation. **Do this when possible!**  
(nonlinear systems are hard, one less equation can make a lot of difference)

## Model for infectious individuals

Integral equation for the number of infective individuals:

$$I(t) = I_0(t) + \int_0^t \beta \frac{(N - I(u))I(u)}{N} P(t - u) du \quad (13)$$

- ▶  $I_0(t)$  number of individuals who were infective at time  $t = 0$  and still are at time  $t$ .
  - ▶  $I_0(t)$  is nonnegative, nonincreasing, and such that  $\lim_{t \rightarrow \infty} I_0(t) = 0$ .
- ▶  $P(t - u)$  proportion of individuals who became infective at time  $u$  and who still are at time  $t$ .
- ▶  $\beta(N - I(u))S(u)/N$  is  $\beta S(u)I(u)/N$  with  $S(u) = N - I(u)$ , from the reduction of dimension.

## Case of an exponentially distributed time to recovery

Suppose that  $P(t)$  is such that the sojourn time in the infective state has an exponential distribution with mean  $1/\gamma$ , i.e.,  
 $P(t) = e^{-\gamma t}$ .

Then the initial condition function  $I_0(t)$  takes the form

$$I_0(t) = I_0(0)e^{-\gamma t},$$

with  $I_0(0)$  the number of infective individuals at time  $t = 0$ . This is obtained by considering the cohort of initially infectious individuals, giving a model such as (11).

Equation (13) becomes

$$I(t) = I_0(0)e^{-\gamma t} + \int_0^t \beta \frac{(N - I(u))I(u)}{N} e^{-\gamma(t-u)} du. \quad (14)$$



Taking the time derivative of (14) yields

$$I'(t) = \beta \frac{(N - I(t))I(t)}{N} - \gamma I(t),$$

which is the classical logistic type ordinary differential equation (ODE) for  $I$  in an SIS model without vital dynamics (no birth or death).

## Conclusion

- ▶ The time of sojourn in classes (compartments) plays an important role in determining the type of model that we deal with.
- ▶ All ODE models, when they use terms of the form  $k_i X$ , make the assumption that the time of sojourn in compartments is exponentially distributed.
- ▶ At the other end of the spectrum, delay differential with discrete delay make the assumption of a constant sojourn time, equal for all individuals.
  
- ▶ Both can be true sometimes.. but reality is often somewhere in between.

# Outline

Single population dynamics and the logistic situation

Time of residence in a state – Exponential distribution

## Epidemic models

- SIS model without vital dynamics

- SIR model of Kermack and McKendrick

- SIRS model with demography

The chemostat

Traffic flow

Shallow water waves

A simple genetic model

## Epidemic models

SIS model without vital dynamics

SIR model of Kermack and McKendrick

SIRS model with demography

## A SIS model

Consider a disease that confers no immunity. In this case, individuals are either

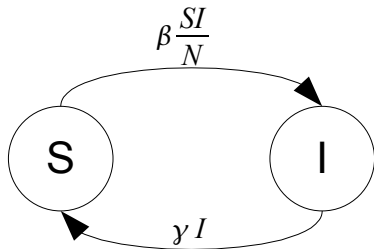
- ▶ *susceptible* to the disease, with the number of such individuals at time  $t$  denoted by  $S(t)$ ,
- ▶ or *infected* by the disease (and are also *infective* in the sense that they propagate the disease), with the number of such individuals at time  $t$  denoted by  $I(t)$ .

We want to model the evolution with time of  $S$  and  $I$  ( $t$  is omitted unless necessary).

# Hypotheses

- ▶ Individuals recover from the disease at the *per capita* rate  $\gamma$ .
- ▶ The disease does not confer immunity.
- ▶ There is no birth or death.
- ▶ Infection is of *standard incidence* type,  $\beta = SI/N$ .

## Flow diagram of the model



The evolution of  $I(t)$  is described by the following equation (see slides on *residence time*):

$$I' = \beta \frac{(N - I)I}{N} - \gamma I.$$

Develop and reorder the terms, giving

$$I' = (\beta - \gamma)I - \frac{\beta}{N}I^2 \tag{15}$$



## The basic reproduction number

Define the *basic reproduction number* (the average number of people that an infectious individual will infect, when introduced in a population of susceptibles) as

$$\mathcal{R}_0 = \frac{\beta}{\gamma}$$

We have

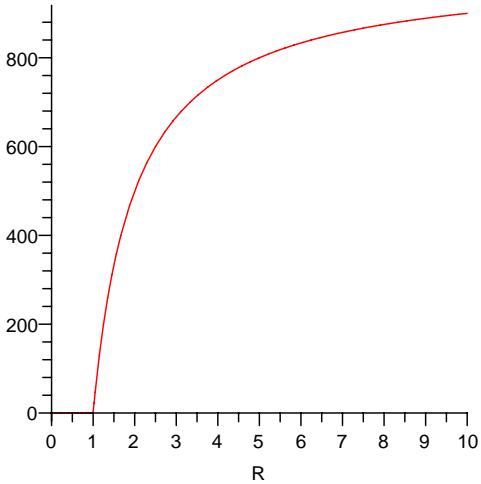
$$(\mathcal{R}_0 < 1 \Leftrightarrow (\beta - \gamma) < 0) \text{ and } (\mathcal{R}_0 > 1 \Leftrightarrow (\beta - \gamma) > 0).$$

Then

- ▶ If  $\mathcal{R}_0 < 1$ , then  $\lim_{t \rightarrow \infty} I(t) = 0$ .
- ▶ If  $\mathcal{R}_0 > 1$ , then

$$\lim_{t \rightarrow \infty} I(t) = \left(1 - \frac{1}{\mathcal{R}_0}\right) N.$$

(the case  $\mathcal{R}_0 = 1$  is usually omitted)



## Epidemic models

SIS model without vital dynamics

**SIR model of Kermack and McKendrick**

SIRS model with demography

# Kermack and McKendrick

In 1927, Kermack and McKendrick started publishing a series of papers on epidemic models. In the first of their papers, they have this model as a particular case:

$$\begin{aligned}S' &= -\beta SI \\I' &= \beta SI - \gamma I \\R' &= \gamma I\end{aligned}\tag{16}$$

## Analyzing the system

First, note (as KMK) that the total population in the system is constant. This is deduced from the fact that

$$N' = (S + I + R)' = -\beta SI + \beta SI - \gamma I + \gamma I = 0.$$

Since this is true for all values of  $t$ , we have  $N$  constant.

Let us ignore the  $R$  equation for now. We can compute

$$\frac{dI}{dS} = \frac{dI}{dt} \frac{dt}{dS} = \frac{I'}{S'} = \frac{\gamma}{\beta S} - 1$$

This gives

$$I(S) = S - \frac{\gamma}{\beta} \ln S + K,$$

which, considering the initial condition  $(S_0, I_0)$ , is,

$$I(S) = S - \frac{\gamma}{\beta} \ln S + I_0 - (S_0 - \frac{\gamma}{\beta} \ln S_0).$$

This gives a curve in the  $(S, I)$  plane.

$$I(S) = S - \frac{\gamma}{\beta} \ln S + I_0 - (S_0 - \frac{\gamma}{\beta} \ln S_0).$$

Typically, assume  $S \approx N$  and  $I > 0$  small. Let us denote  $S_\infty = \lim_{t \rightarrow \infty} S(t)$ .

We want to find the value of  $S$  when  $I \rightarrow 0$ . Then

$$I_0 - \frac{\gamma}{\beta} \ln S_0 = S_\infty - \frac{\gamma}{\beta} \ln S_\infty$$

## Epidemic models

SIS model without vital dynamics

SIR model of Kermack and McKendrick

SIRS model with demography



## The SIRS model – Assumptions (1/2)

- ▶ Like KMK, individuals are S, I or R.
- ▶ Infection is  $\beta SI$  (mass action) or  $\beta SI/N$  (proportional incidence).
- ▶ Different interpretation of the R class: R stands for “removed”, individuals who are immune to the disease following recovery.
- ▶ Recovery from the disease (movement from I class to R class) occurs at the per capita rate  $\gamma$ .  
(Time spent in I before recovery is exponentially distributed.)
- ▶ Immunity can be lost: after some time, R individuals revert back to S individuals.
- ▶ Time spent in R class before loss of immunity is exponentially distributed, with mean  $1/\nu$ .

## The SIRS model – Assumptions (2/2)

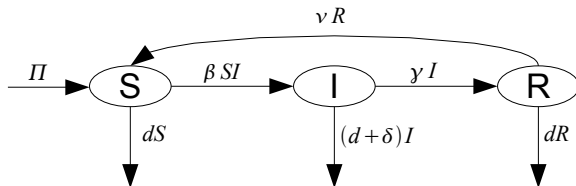
- ▶ There is birth and death of individuals:
  - ▶ No vertical transmission of the disease (mother to child) or of immunity, so all birth is into the S class.  
Birth occurs at the rate  $\Pi$ .
  - ▶ Individuals in all classes die of at the per capita rate  $d$ , i.e., the average life duration is exponentially distributed with mean  $1/d$ .
  - ▶ The disease is lethal: infected individuals are subject to additional mortality at the per capita rate  $\delta$ .

Note that birth and death can have different interpretations:

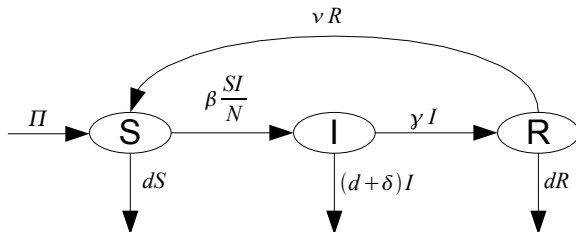
- ▶ birth and death in the classical sense,
- ▶ but also, entering the susceptible population and leaving it.

# Flow diagrams for the models

## Mass action



## Standard incidence



## SIRS model with mass action incidence

Consider the model with mass action incidence,

$$S' = \Pi + \nu R - \beta SI - dS$$

$$I' = \beta SI - (d + \delta + \gamma)I$$

$$R' = \gamma I - (d + \nu)R$$

# Outline

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Time of residence in a state – Exponential distribution

Epidemic models

**The chemostat**

Batch mode

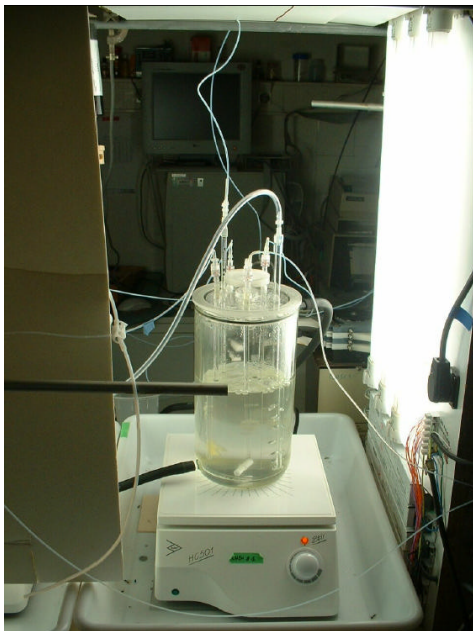
Continuous flow mode

Traffic flow

Shallow water waves

A simple genetic model

# A chemostat



The chemostat

# Principle

- ▶ One main chamber (vessel), in which some microorganisms (bacteria, plankton), typically unicellular, are put, together with liquid and nutrient.
- ▶ Contents are stirred, so nutrient and organisms are well-mixed.
- ▶ Organisms consume nutrient, grow, multiply.
- ▶ Two major modes of operation:
  - ▶ *Batch* mode: let the whole thing sit.
  - ▶ *Continuous flow* mode: there is an input of fresh water and nutrient, and an outflow the comprises water, nutrient and organisms, to keep the volume constant.

## The chemostat

Batch mode

Continuous flow mode



## Model for batch mode – No organism death

First, assume no death of organisms. Model is

$$S' = -\mu(S)x \quad (17a)$$

$$x' = \mu(S)x \quad (17b)$$

with initial conditions  $S(0) \geq 0$  and  $x(0) > 0$ , and where  $\mu(S)$  is such that

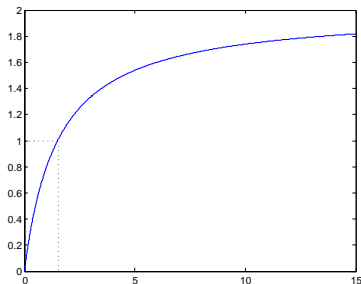
- ▶  $\mu(0) = 0$  (no substrate, no growth)
- ▶  $\mu(S) \geq 0$  for all  $S \geq 0$
- ▶  $\mu(S)$  bounded for  $S \geq 0$

# The Michaelis-Menten curve

Typical form for  $\mu(S)$  is the *Michaelis-Menten* (MM) curve,

$$\mu(S) = \mu_{max} \frac{S}{K_S + S} \quad (18)$$

- ▶  $\mu_{max}$  maximal growth rate
- ▶  $K_S$  half-saturation constant ( $\mu(K_S) = \mu_{max}/2$ ).



From now on, assume MM function.

## Equilibria

To compute the equilibria, suppose  $S' = x' = 0$ , giving

$$\mu(S)x = -\mu(S)x = 0$$

This implies  $\mu(S) = 0$  or  $x = 0$ . Note that  $\mu(S) = 0 \Leftrightarrow S = 0$ , so the system is at equilibrium if  $S = 0$  or  $x = 0$ .

This is a complicated situation, as it implies that there are lines of equilibria ( $S = 0$  and any  $x$ , and  $x = 0$  and any  $S$ ), so that the equilibria are not *isolated* (arbitrarily small neighborhoods of one equilibrium contain other equilibria), and therefore, studying the linearization is not possible.

Here, some analysis is however possible. Consider

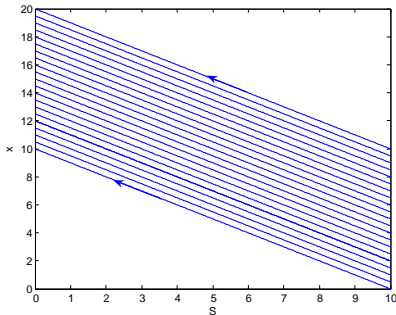
$$\frac{dx}{dS} = \frac{dx}{dt} \frac{dt}{dS} = -\frac{\mu(S)x}{\mu(S)x} = -1$$

This implies that we can find the solution

$$x(S) = C - S,$$

or, supposing the initial condition is  $(S(0), x(0)) = (S_0, x_0)$ , that is,  $x(S_0) = x_0$ ,

$$x(S) = S_0 + x_0 - S$$



## Model for batch mode – Organism death

Assume death of organisms at per capita rate  $d$ . Model is

$$S' = -\mu(S)x \quad (19a)$$

$$x' = \mu(S)x - dx \quad (19b)$$

## Equilibria

$$S' = 0 \Leftrightarrow \mu(S)x = 0$$

$$x' = 0 \Leftrightarrow (\mu(S) - d)x = 0.$$

So we have  $x = 0$  or  $\mu(S) = d$ . So  $x = 0$  and any value of  $S$ , and  $S$  such that  $\mu(S) = d$  and  $x = 0$ . One such particular value is  $(S, x) = (0, 0)$ .

This is once again a complicated situation, since there are lines of equilibria. Intuitively, most solutions will go to  $(0, 0)$ . This is indeed the case (we will not show it).

## The chemostat

Batch mode

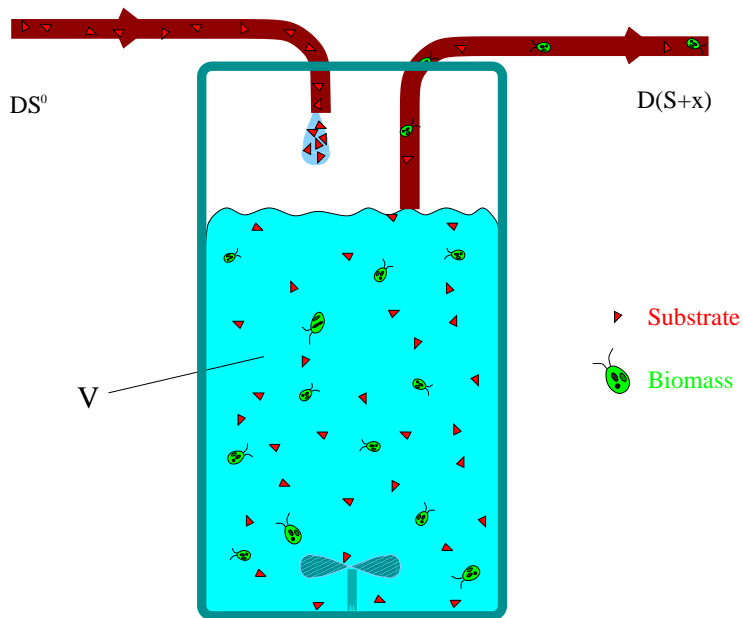
Continuous flow mode

## Modelling principles – Continuous flow mode

- ▶ Organisms (concentration denoted  $x$ ) are in the main vessel.
- ▶ Limiting substrate (concentration in the vessel denoted  $S$ ) is input (at rate  $D$  and concentration  $S^0$ ).
- ▶ There is an outflow of both nutrient and organisms (at same rate  $D$  as input).
- ▶ Homogeneous mixing.
- ▶ Residence time in device is assumed small compared to lifetime (or time to division)  $\Rightarrow$  no death considered.



# Schematic representation



## Model for continuous flow mode

Model is

$$S' = D(S^0 - S) - \mu(S)x \quad (20a)$$

$$x' = \mu(S)x - Dx \quad (20b)$$

with initial conditions  $S(0) \geq 0$  and  $x(0) \geq 0$ , and  $D, S^0 > 0$ .

# Equilibria

Existence: done in class using nullclines.

Stability: done in class using Jacobian matrix.

# Outline

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Epidemic models

The chemostat

Traffic flow

ODE model

DDE model

Shallow water waves

A simple genetic model

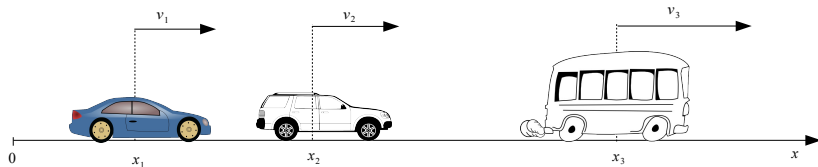
Traffic flow

ODE model

DDE model

# Hypotheses

- ▶  $N$  cars in total.
- ▶ Road is the  $x$ -axis.
- ▶  $x_n(t)$  position of the  $n$ th car at time  $t$ .
- ▶  $v_n(t) \triangleq x'_n(t)$  velocity of the  $n$ th car at time  $t$ .



- ▶ All cars start with the same initial speed  $v_0$  before time  $t = 0$ .

## Moving frame coordinates

To make computations easier, express velocity of cars in a reference frame moving at speed  $u_0$ .

Remark that here, speed=velocity, since movement is 1-dimensional.

Let

$$u_n(t) = v_n(t) - u_0.$$

Then  $u_n(t) = 0$  for  $t \leq 0$ , and  $u_n$  is the speed of the  $n$ th car in the moving frame coordinates.

## Modeling driver behavior

Assume that

- ▶ Driver adjusts his/her speed according to relative speed between his/her car and the car in front.
- ▶ This adjustment is a linear term, equal to  $\lambda$  for all drivers.

- ▶ First car: evolution of speed remains to be determined.

- ▶ Second car:

$$u'_2 = \lambda(u_1 - u_2).$$

- ▶ Third car:

$$u'_3 = \lambda(u_2 - u_3)$$

- ▶ Thus, for  $n = 1, \dots, N - 1$ ,

$$u'_{n+1} = \lambda(u_n - u_{n+1}). \quad (21)$$



This can be solved using *linear cascades*: if  $u_1(t)$  is known, then

$$u_2' = \lambda(u_1(t) - u_2)$$

is a linear first-order nonhomogeneous equation. Solution (integrating factors, or variation of constants) is

$$u_2(t) = \lambda e^{-\lambda t} \int_0^t u_1(s) e^{\lambda s} ds$$

Then use this function  $u_2(t)$  in  $u_3'$  to get  $u_3(t)$ ,

$$u_3(t) = \lambda e^{-\lambda t} \int_0^t u_2(s) e^{\lambda s} ds$$

## Example

Suppose driver of car 1 follows this function

$$u_1(t) = \alpha \sin(\omega t)$$

that is,  $\omega$ -periodic, 0 at  $t = 0$  (we want all cars to start with speed relative to the moving reference equal to 0), and with amplitude  $\alpha$ .

Then

$$u_2(t) = \frac{\lambda \alpha}{\lambda^2 + \omega^2} \left( \omega e^{-\lambda t} + \lambda \sin(\omega t) - \omega \cos(\omega t) \right).$$

When  $t \rightarrow \infty$ , first term goes to 0, we are left with a  $\omega$ -periodic term.

## Using the theory of linear systems

Consider the case of 3 cars. Let

$$X = \begin{pmatrix} u_2 \\ u_3 \end{pmatrix}$$

Then the system can be written as

$$X' = \begin{pmatrix} -\lambda & 0 \\ \lambda & -\lambda \end{pmatrix} U + \begin{pmatrix} \lambda u_1(t) \\ 0 \end{pmatrix}$$

which we write for short as  $X' = AX + B(t)$ .

The matrix  $A$  has the eigenvalue  $-\lambda$  with multiplicity 2. Its Jordan form is

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

with matrix of change of basis

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

which is such that  $P^{-1}AP = J$ .

Because  $-\lambda$  is an eigenvalue with multiplicity 2 (same as the size of the matrix), we can use the simplified theorem, and only need  $N$ .

We have

$$\begin{aligned} N &= A - S \\ &= \begin{pmatrix} -\lambda & 0 \\ \lambda & -\lambda \end{pmatrix} - \begin{pmatrix} -\lambda & 0 \\ 0 & -\lambda \end{pmatrix} \\ &= \begin{pmatrix} 0 & 0 \\ \lambda & 0 \end{pmatrix} \end{aligned}$$

Clearly,  $N^2 = 0$ , so, by the theorem in the simplified case,

$$x(t) = e^{-\lambda t} (\mathbb{I} + Nt) x_0$$

But we know that solutions are unique, and that the solution to the differential equation is given by  $x(t) = e^{At} x_0$ . This means that

$$\begin{aligned} e^{At} &= e^{-\lambda t} (\mathbb{I} + Nt) \\ &= e^{-\lambda t} \left( \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} + \begin{pmatrix} 0 & 0 \\ \lambda t & 0 \end{pmatrix} \right) \\ &= e^{-\lambda t} \begin{pmatrix} 1 & 0 \\ \lambda t & 1 \end{pmatrix} \\ &= \begin{pmatrix} e^{-\lambda t} & 0 \\ \lambda t e^{-\lambda t} & e^{-\lambda t} \end{pmatrix} \end{aligned}$$

Now notice that the solution to

$$X' = AX$$

is trivially established here, since

$$X(0) = \begin{pmatrix} u_2(0) \\ u_3(0) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix},$$

and thus

$$X(t) = e^{At}0 = 0.$$

$e^{At}$  does however play a role in the solution (fortunately), since it is involved in the variation of constants formula:

$$X(t) = e^{At}X_0 + \int_0^t e^{A(t-s)}B(s)ds$$

Let

$$\Psi(t) = \int_0^t e^{\lambda s} u_1(s) ds$$

and

$$\Phi(t) = \int_0^t s e^{\lambda s} u_1(s) ds$$

These can be computed when we choose a function  $u_1(t)$ . Then, finally, we have

$$\begin{aligned} X(t) &= \int_0^t e^{A(t-s)} B(s) ds \\ &= \begin{pmatrix} \lambda e^{-\lambda t} \Psi(t) \\ \lambda^2 e^{-\lambda t} (t\Psi(t) - \Phi(t)) \end{pmatrix} \end{aligned}$$



## Case of the $\alpha \sin(\omega t)$ driver

We set

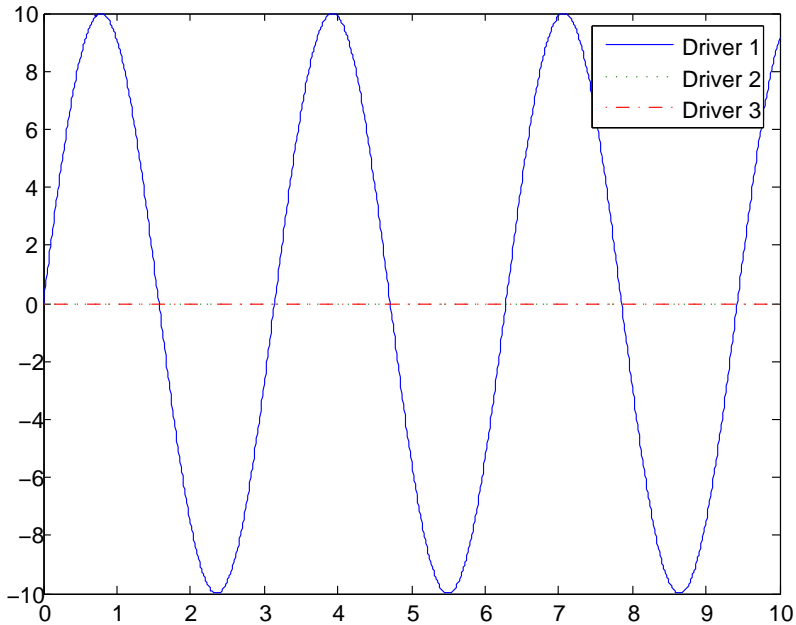
$$u_1(t) = \alpha \sin(\omega t).$$

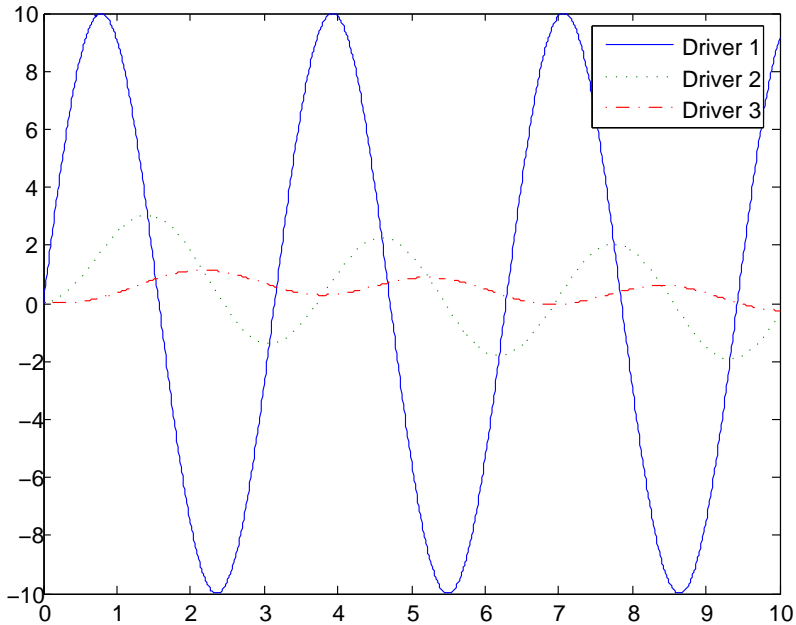
Then

$$\Psi(t) = \frac{\alpha(\omega - \omega e^{\lambda t} \cos(\omega t) + \lambda e^{\lambda t} \sin(\omega t))}{\lambda^2 + \omega^2}$$

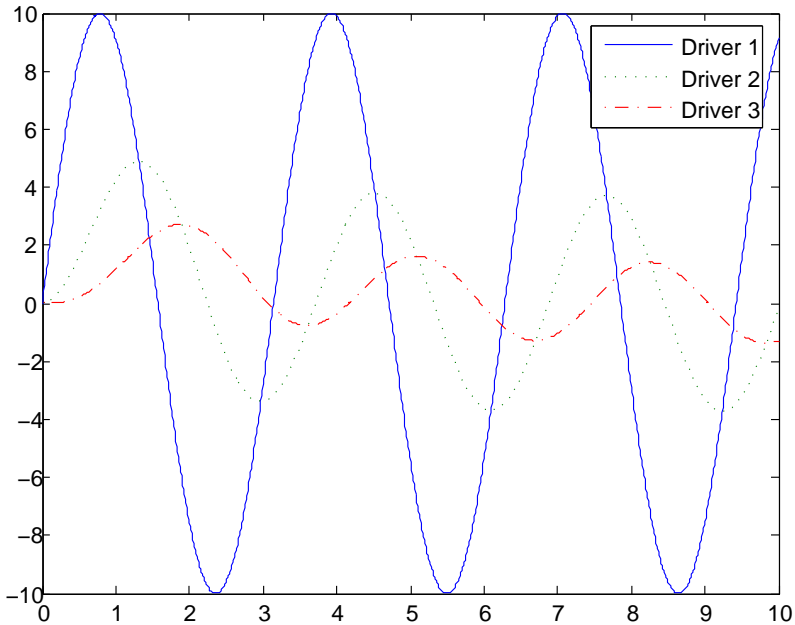
and

$$\Phi(t) = \frac{\alpha(\lambda^3 t + \lambda t \omega^2 - \lambda^2 + \omega^2) \sin(\omega t) e^{\lambda t}}{(\lambda^2 + \omega^2)^2} - \frac{\alpha \omega \cos(\omega t)(t \lambda^2 + t \omega^2 - 2\lambda) e^{\lambda t} + 2\alpha \lambda \omega}{(\lambda^2 + \omega^2)^2}$$

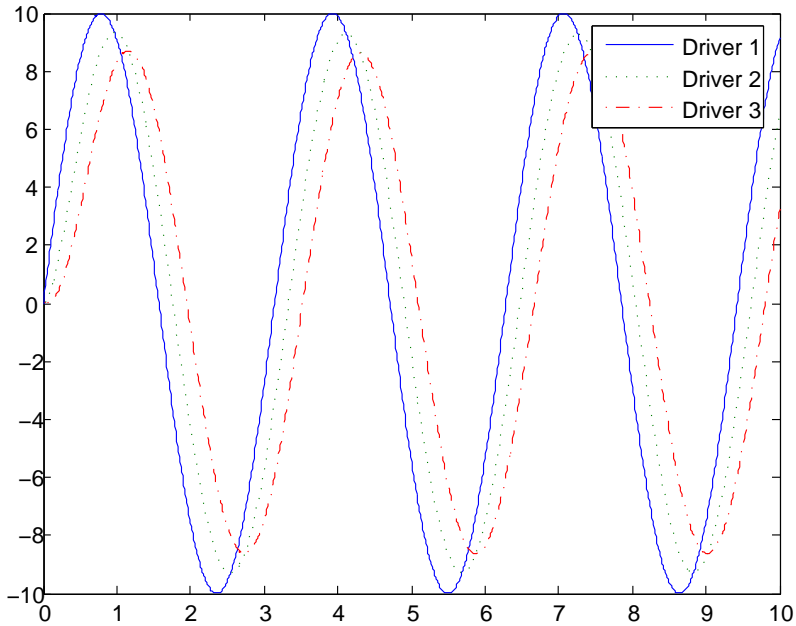




Traffic flow  $\lambda = 0.4$



Traffic flow  $\lambda = 0.8$



## Traffic flow

ODE model

DDE model

## A delayed model of traffic flow

We consider the same setting as previously, except that now, for  $t > 0$ ,

$$u'_{n+1}(t) = \lambda(u_n(t - \tau) - u_{n+1}(t - \tau)), \quad (22)$$

for  $n = 1, \dots, N - 1$ . Here,  $\tau \geq 0$  is called the *time delay* (or *time lag*), or for short, *delay* (or *lag*).

If  $\tau = 0$ , we are back to the previous model.

## Initial data

For a delay equation such as (22), the initial conditions become *initial data*. This initial data must be specified on an interval of length  $\tau$ , left of zero.

This is easy to see by looking at the terms:  $u(t - \tau)$  involves, at time  $t$ , the state of  $u$  at time  $t - \tau$ . So if  $t < \tau$ , we need to know what happened for  $t \in [-\tau, 0]$ .

So, normally, we specify initial data as

$$u_n(t) = \phi(t) \text{ for } t \in [-\tau, 0],$$

where  $\phi$  is some function, that we assume to be continuous. We assume  $u_1(t)$  is known.

Here, we assume, for  $n = 1, \dots, N$ ,

$$u_n(t) = 0, \quad t \leq (n - 1)\tau$$



## Important remark

Although (22) looks very similar to (21), you must keep in mind that it is in fact much more complicated.

- ▶ A solution to (21) is a continuous function from  $\mathbb{R}$  to  $\mathbb{R}$  (or to  $\mathbb{R}^n$  if we consider the system).
- ▶ A solution to (22) is a continuous function in the space of continuous functions.
- ▶ The space  $\mathbb{R}^n$  has dimension  $n$ . The space of continuous functions has dimension  $\infty$ .

We then computed the Laplace transform of the system, but this was not very helpful, since, after solving the problem in  $s$ -space, we were not able to transform back into the original  $t$ -space.

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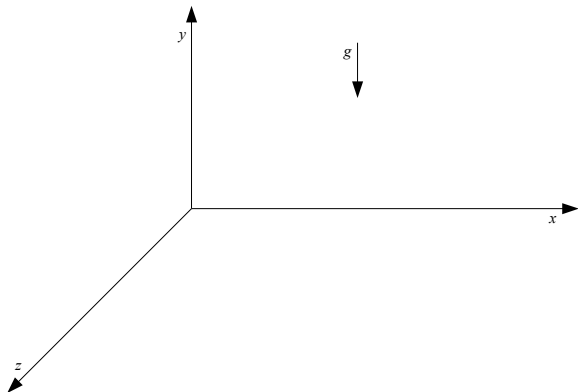
**Shallow water waves**

Traveling wave solutions

A simple genetic model

## Spatial domain

We consider the motion of a body of water that is infinite in the  $z$  direction, with or without boundary in the  $x$  direction, and the vertical direction of gravity taken as the  $y$  direction.



From now on, suppose  $z$  direction uniform (the same for all  $z$ ), so ignore  $z$  except for the sake of argument.

## The one-dimensional wave equation (1)

Following a long and complex argument, the following was derived.

The partial differential equation

$$\zeta_{tt} = c^2 \zeta_{xx} \quad (23)$$

with  $c^2 = Hg$ , is the one-dimensional wave equation. Initial conditions are given by

$$\zeta(x, 0) = h_0(x) - H \equiv \zeta_0(x)$$

$$\zeta_t(x, 0) = -Hu_x(x, 0) = -H[u_0(x)]_x \equiv \nu_0(x)$$

## The one-dimensional wave equation (2)

Things can also be expressed in terms of  $u$ . Using the same type of simplification used before for  $\zeta$ , we get

$$u_{tt} = c^2 u_{xx} \quad (24)$$

with  $c^2 = Hg$ . Initial conditions are given by

$$\begin{aligned} u(x, 0) &= u_0(x) \\ u_t(x, 0) &= -g\zeta_x(x, 0) = -g[h_0(x)]_x \equiv v_0(x) \end{aligned}$$

## Shallow water waves

### Traveling wave solutions

## Traveling wave solutions

This was obtained by d'Alembert. Consider

$$u_{tt} = c^2 u_{xx} \quad (24)$$

Note that this can be written as

$$\left( \frac{\partial}{\partial t} - c \frac{\partial}{\partial x} \right) \left( \frac{\partial}{\partial t} + c \frac{\partial}{\partial x} \right) u = 0$$

This implies that for any  $F, G$ , the sum

$$u(x, t) = F(x - ct) + G(x + ct)$$

satisfies (24).

Set

$$u(x, 0) = f(x) \quad u_t(x, 0) = g(x)$$

Then d'Alembert's formula gives

$$u(x, t) = \frac{f(x - ct) + f(x + ct)}{2} + \frac{1}{2c} \int_{x-ct}^{x+ct} g(s) ds$$



## Case of a Dirac delta initial condition

Suppose  $u_0(x) = 0$  and  $v_0(x) = \delta(x)$ , for  $-\infty < x < \infty$ , with  $\delta$  the Dirac delta,

$$\delta(x) = \begin{cases} \infty & \text{if } x = 0 \\ 0 & \text{otherwise.} \end{cases}$$

Therefore,

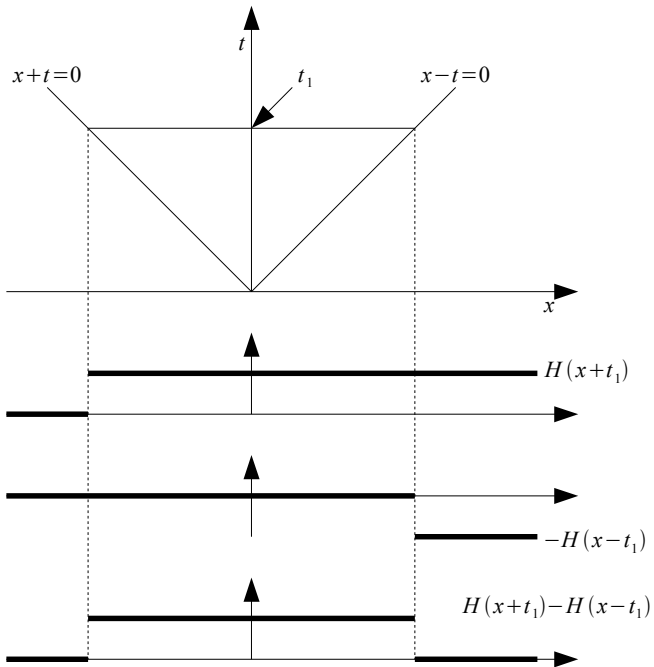
$$u(x, t) = \frac{1}{2c} \int_{x-ct}^{x+ct} \delta(z) dz = \frac{1}{2c} \{H(x + ct) - H(x - ct)\},$$

with  $H$  the Heaviside function,

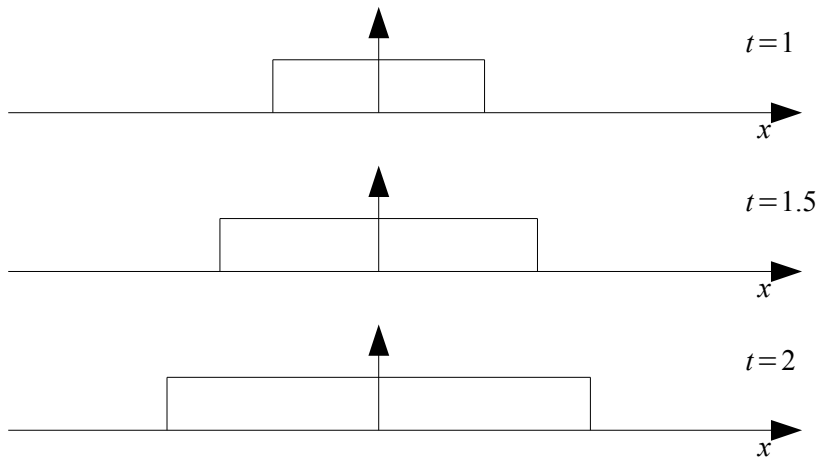
$$H(x) = \begin{cases} 0 & \text{if } x < 0 \\ 1 & \text{if } x > 0. \end{cases}$$

For simplicity, take  $c = 1$ . This gives

$$u(x, t) = \frac{1}{2} \{H(x + t) - H(x - t)\},$$



As  $t$  increases, we move further up in the top graph in  $(x, t)$ -space, resulting in a wider and wider square pulse.



# Outline

Single population dynamics and the logistic situation

Time of residence in a state – Exponential distribution

Epidemic models

The chemostat

Traffic flow

Shallow water waves

A simple genetic model

Continued matings with a  $Gg$  individual – Regular chain

Continued matings with a  $GG$  individual – Absorbing chain

## Simple Mendelian inheritance

A certain trait is determined by a specific pair of genes, each of which may be two types, say  $G$  and  $g$ .

One individual may have:

- ▶  $GG$  combination (*dominant*)
- ▶  $Gg$  or  $gG$ , considered equivalent genetically (*hybrid*)
- ▶  $gg$  combination (*recessive*)

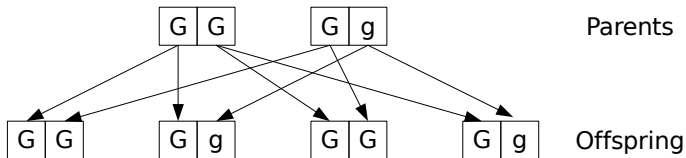
In sexual reproduction, offspring inherit one gene of the pair from each parent.

## Basic assumption of Mendelian genetics

Genes inherited from each parent are selected at random, independently of each other. This determines probability of occurrence of each type of offspring. The offspring

- ▶ of two  $GG$  parents must be  $GG$ ,
- ▶ of two  $gg$  parents must be  $gg$ ,
- ▶ of one  $GG$  and one  $gg$  parent must be  $Gg$ ,
- ▶ other cases must be examined in more detail.

## GG and Gg parents

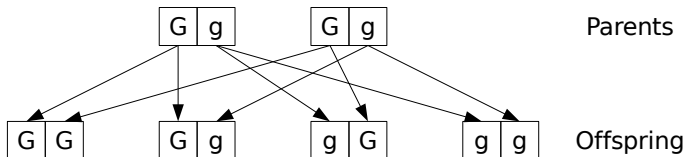


Offspring has probability

- ▶  $\frac{1}{2}$  of being  $GG$
- ▶  $\frac{1}{2}$  of being  $Gg$



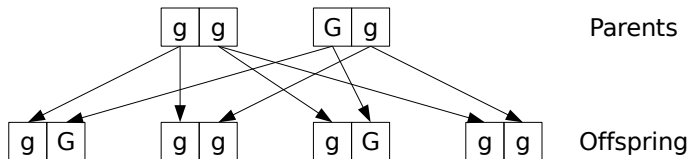
## Gg and Gg parents



Offspring has probability

- ▶  $\frac{1}{4}$  of being  $GG$
- ▶  $\frac{1}{2}$  of being  $Gg$
- ▶  $\frac{1}{4}$  of being  $gg$

## *gg* and *Gg* parents



Offspring has probability

- ▶  $\frac{1}{2}$  of being *Gg*
- ▶  $\frac{1}{2}$  of being *gg*

## A simple genetic model

Continued matings with a  $Gg$  individual – Regular chain

Continued matings with a  $GG$  individual – Absorbing chain

## Continued matings

Consider a process of continued matings.

- ▶ Start with an individual of known or unknown genetic character and mate it with a hybrid.
- ▶ Assume that there is at least one offspring; choose one of them at random and mate it with a hybrid.
- ▶ Repeat this process through a number of generations.

The genetic type of the chosen offspring in successive generations can be represented by a Markov chain, with states  $GG$ ,  $Gg$  and  $gg$ . So there are 3 possible states  $S_1 = GG$ ,  $S_2 = Gg$  and  $S_3 = gg$ .

We have

$\nearrow$	GG	Gg	gg
GG	0.5	0.5	0
Gg	0.25	0.5	0.25
gg	0	0.5	0.5

The transition probabilities are thus

$$P = \begin{pmatrix} \frac{1}{2} & \frac{1}{2} & 0 \\ \frac{1}{4} & \frac{1}{2} & \frac{1}{4} \\ 0 & \frac{1}{2} & \frac{1}{2} \end{pmatrix}$$

The Markov chain is here regular. Indeed, take the matrix  $P$ ,

$$P = \begin{pmatrix} \frac{1}{2} & \frac{1}{2} & 0 \\ \frac{1}{4} & \frac{1}{2} & \frac{1}{4} \\ 0 & \frac{1}{2} & \frac{1}{2} \end{pmatrix}$$

and compute  $P^2$ :

$$P^2 = \begin{pmatrix} \frac{3}{8} & \frac{1}{2} & \frac{1}{8} \\ \frac{1}{4} & \frac{1}{2} & \frac{1}{4} \\ \frac{1}{8} & \frac{1}{2} & \frac{3}{8} \end{pmatrix}$$

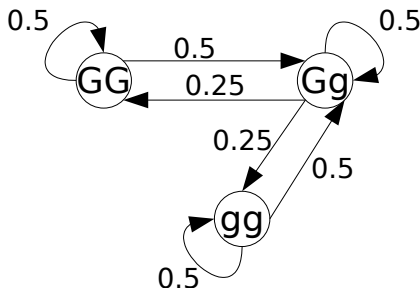
As all entries are positive,  $P$  is primitive and the Markov chain is regular.

Another way to check regularity:

### Theorem 41

*A matrix  $M$  is primitive if the associated connection graph is strongly connected, i.e., that there is a path between any pair  $(i,j)$  of states, and that there is at least one positive entry on the diagonal of  $M$ .*

This is checked directly on the transition graph



Compute the left eigenvector associated to 1 by solving

$$(w_1, w_2, w_3) \begin{pmatrix} \frac{1}{2} & \frac{1}{2} & 0 \\ \frac{1}{4} & \frac{1}{2} & \frac{1}{4} \\ 0 & \frac{1}{2} & \frac{1}{2} \end{pmatrix} = (w_1, w_2, w_3)$$

$$\frac{1}{2}w_1 + \frac{1}{4}w_2 = w_1 \quad (25a)$$

$$\frac{1}{2}w_1 + \frac{1}{2}w_2 + \frac{1}{2}w_3 = w_2 \quad (25b)$$

$$\frac{1}{4}w_2 + \frac{1}{2}w_3 = w_3 \quad (25c)$$

From (25a),  $w_1 = w_2/2$ , and from (25c),  $w_3 = w_2/2$ . Substituting these values into (25b),

$$\frac{1}{4}w_2 + \frac{1}{2}w_2 + \frac{1}{4}w_2 = w_2,$$

that is,  $w_2 = w_2$ , i.e.,  $w_2$  can take any value. So  $w = (\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$ .



## A simple genetic model

Continued matings with a  $Gg$  individual – Regular chain

Continued matings with a  $GG$  individual – Absorbing chain

## Mating with a $GG$ individual

Suppose now that we conduct the same experiment, but mate each new generation with a  $GG$  individual instead of a  $Gg$  individual.

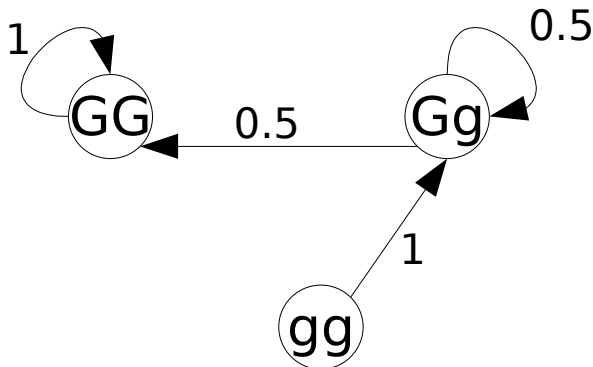
Transition table is

$\nearrow$	$GG$	$Gg$	$gg$
$GG$	1	0	0
$Gg$	0.5	0.5	0
$gg$	0	1	0

The transition probabilities are thus

$$P = \begin{pmatrix} 1 & 0 & 0 \\ \frac{1}{2} & \frac{1}{2} & 0 \\ 0 & 1 & 0 \end{pmatrix}$$

## New transition graph



Clearly:

- ▶ we leave  $gg$  after one iteration, and can never return,
- ▶ as soon as we leave  $Gg$ , we can never return,
- ▶ can never leave  $GG$  as soon as we get there.

The matrix is already in standard form,

$$P = \begin{pmatrix} 1 & 0 & 0 \\ \frac{1}{2} & \frac{1}{2} & 0 \\ 0 & 1 & 0 \end{pmatrix} = \begin{pmatrix} \mathbb{I}_1 & \mathbf{0} \\ R & Q \end{pmatrix}$$

with  $\mathbb{I}_1 = 1$ ,  $\mathbf{0} = (0 \ 0)$  and

$$R = \begin{pmatrix} \frac{1}{2} \\ 0 \end{pmatrix} \quad Q = \begin{pmatrix} \frac{1}{2} & 0 \\ 1 & 0 \end{pmatrix}$$

We have

$$\mathbb{I}_2 - Q = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} - \begin{pmatrix} \frac{1}{2} & 0 \\ 1 & 0 \end{pmatrix} = \begin{pmatrix} \frac{1}{2} & 0 \\ -1 & 1 \end{pmatrix}$$

so

$$N = (\mathbb{I}_2 - Q)^{-1} = 2 \begin{pmatrix} 1 & 0 \\ 1 & \frac{1}{2} \end{pmatrix} = \begin{pmatrix} 2 & 0 \\ 2 & 1 \end{pmatrix}$$

Then

$$T = N\mathbb{1} = \begin{pmatrix} 2 \\ 3 \end{pmatrix}$$

and

$$B = NR = \begin{pmatrix} 2 & 0 \\ 2 & 1 \end{pmatrix} \begin{pmatrix} \frac{1}{2} \\ 0 \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$$