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ASTR-GEOG Seminar
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Growth versus spreading in biological systems: from harmful algal blooms to epidemics

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Summary

- Using the simplest possible mathematical models, we will investigate the race between growth and spreading processes. The former tend to increase the density of the population of a species, while the latter tend to decrease it.

- The interplay between growth and spreading leads to a variety of phenomena, including travelling waves — when non-linear growth terms are resorted to.

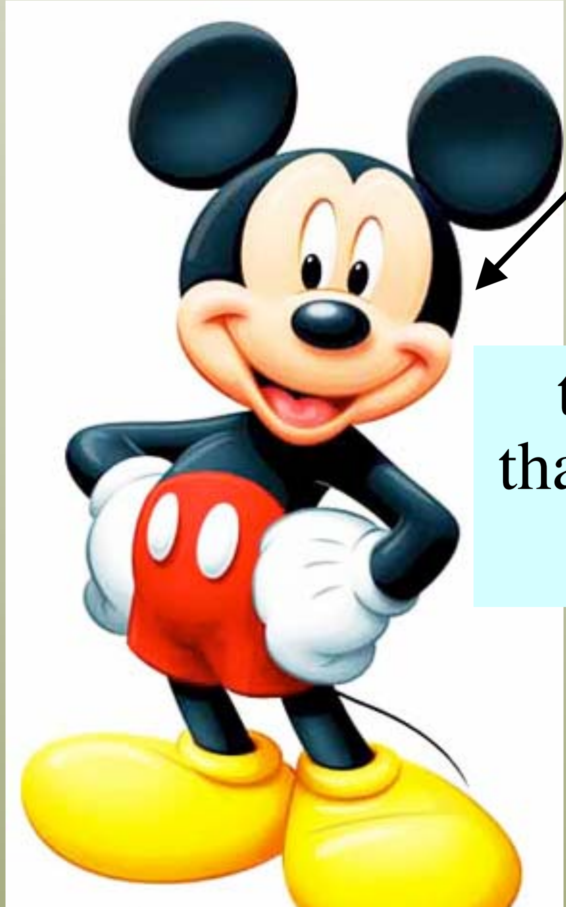
- No novel model will be presented: we will revisit some of the models developed over the last three centuries.

Contents

Introduction: two modes of spread (I)

cute rodent

not so cute rodent



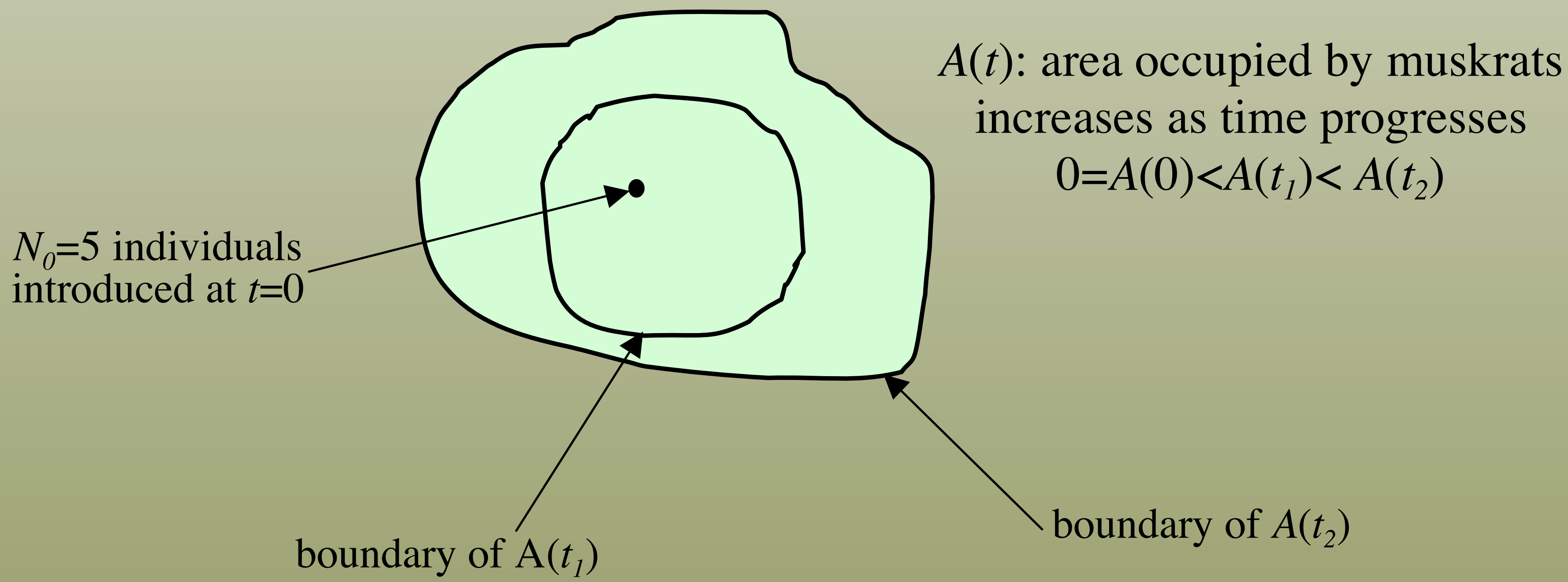
two rodents that spread over large areas

native to North America - spread everywhere
found in kids' bedrooms and theme parks
height and weight highly variable
drains parents' bank account

native to North America - introduced in Europe
found in wetlands
40-60 cm long - weight ≈ 1-1.5 kg
damages levees - hantavirus reservoir

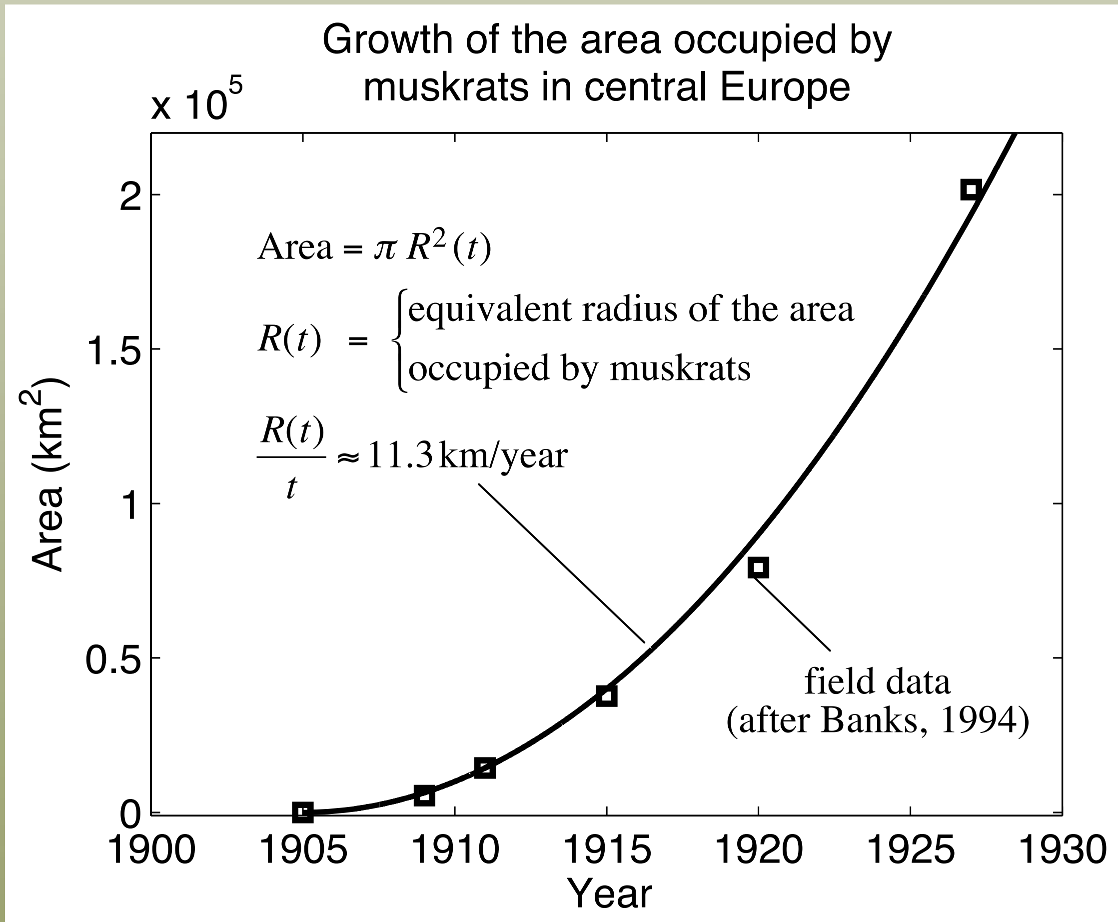
Introduction: two modes of spread (II)

• In 1905, N_0=5 muskrats were introduced in Bohemia. Then, from this point (and due to later pointwise releases), the muskrats spread over most of Eurasia.



Introduction: two modes of spread (III)

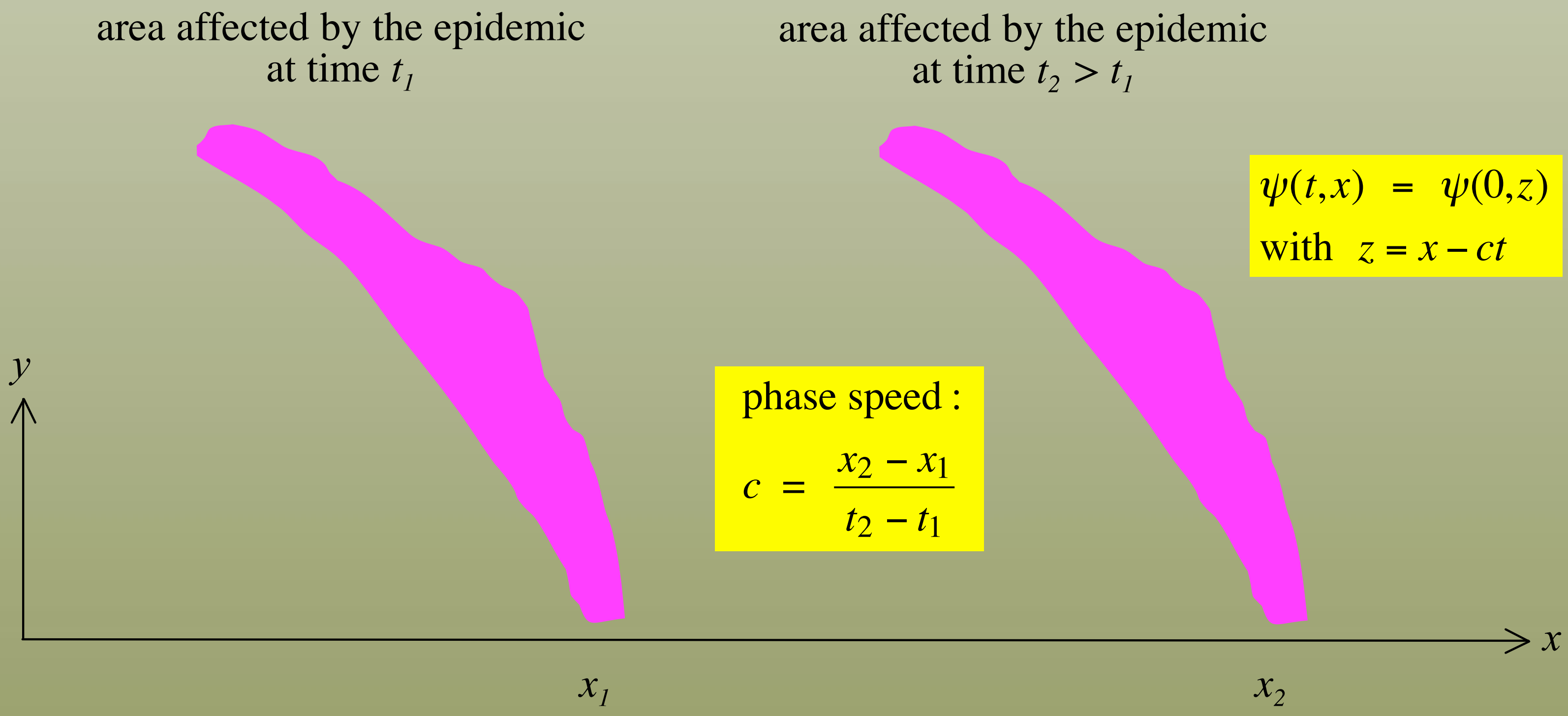
• For 2-3 decades, the area occupied by muskrats grew approximately as the square of the time elapsed since their introduction.



Introduction: two modes of spread (IV)

• There is another mode of spread: the travelling wave, in which a signal travels without being significantly altered at a speed that is approximately constant. This often applies to epidemics.

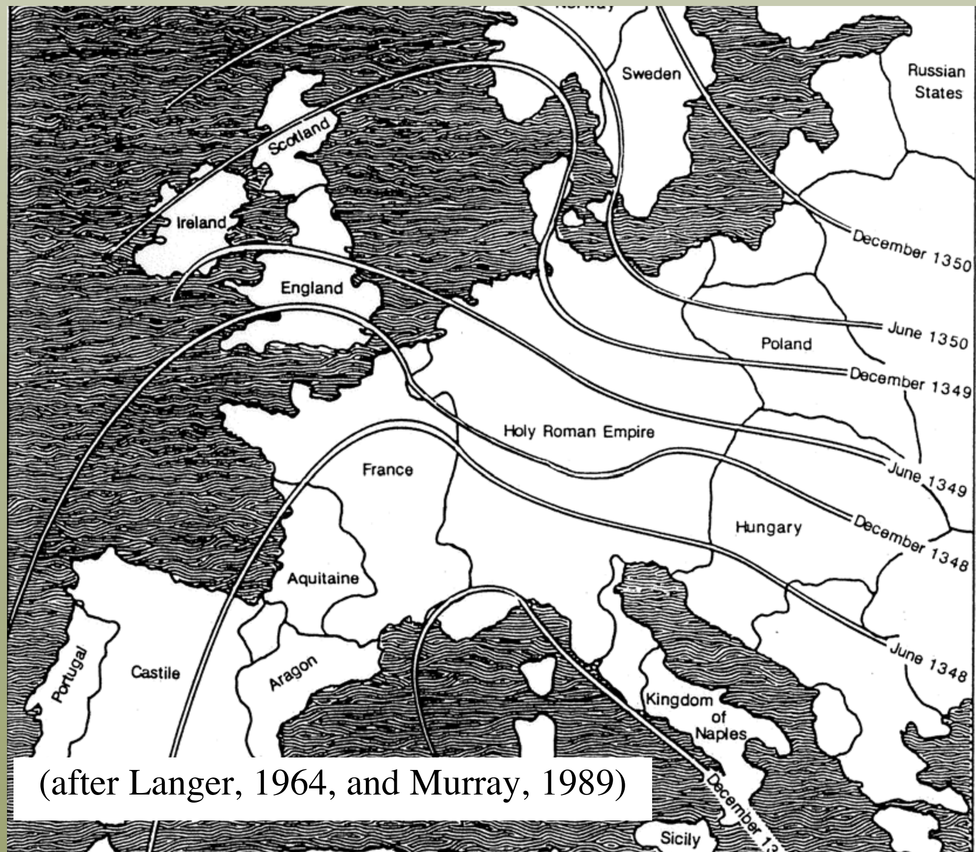
Propagation as a travelling wave



Introduction: two modes of spread (V)

• The Black Death (essentially bubonic plague) may be viewed as a wave front that travelled throughout Europe from 1347 to 1350 at a speed of 300-600 km/year, killing 1/4-1/3 of the population.

14th century miniature from the Toggenburg Bible showing victims of the Black Death



(after Langer, 1964, and Murray, 1989)

Simple models of growth (I)

• If t denotes time, the population $N(t)$ of a species obeys the ordinary differential equation (ODE):

$$\frac{dN}{dt} = \text{births} - \text{deaths} + \text{migration}$$

• Euler and Malthus (1798) suggested the simplest model:

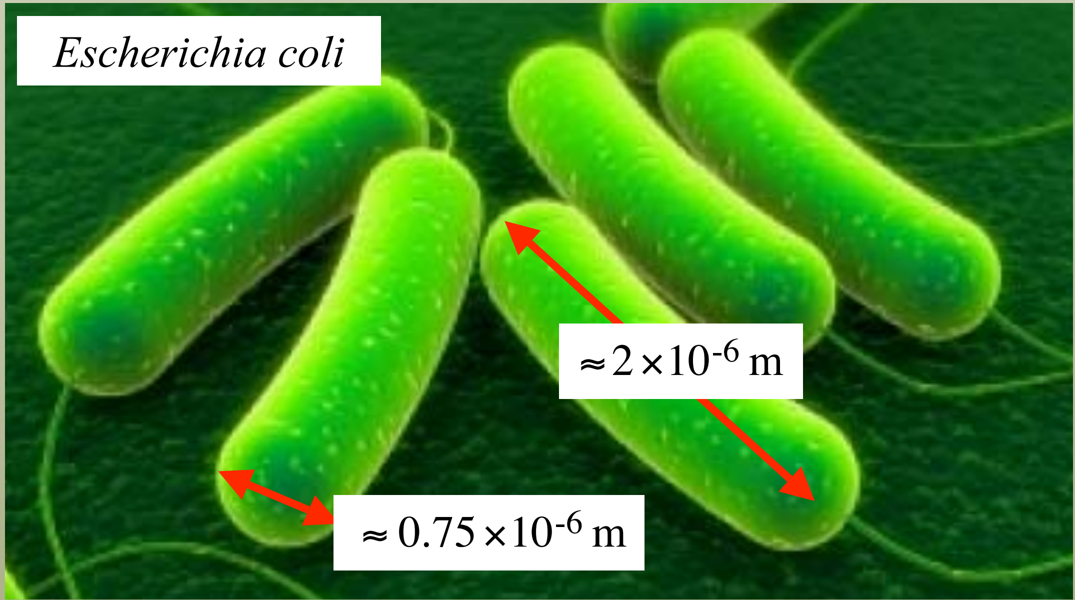
- neglect migration;
- births = βN, with β = positive constant;
- deaths = γN, with γ = positive constant.

Let $r = \beta - \gamma$ denote the net growth rate, the population evolves as

$$N(t) = N_0\, e^{rt} \quad \begin{cases} \text{population} \uparrow \text{ if } r > 0 \\ \text{population} = \text{ if } r = 0 \\ \text{population} \downarrow \text{ if } r < 0 \end{cases}$$

Simple models of growth (II)

• Exponential growth can be frightening, as is exemplified by the so-called "nightmare of Jacques Monod".



Put **one** fecal bacterium (*Escherichia coli*) in the b.428 seminar room. Their volumes are about 1.1×10^{-18} m^3 and 1.6×10^{2} m^3, respectively.

The population of *E. coli* doubles in about 20 min.

How much time does it take to fill the room with bacteria (and scare you away)?

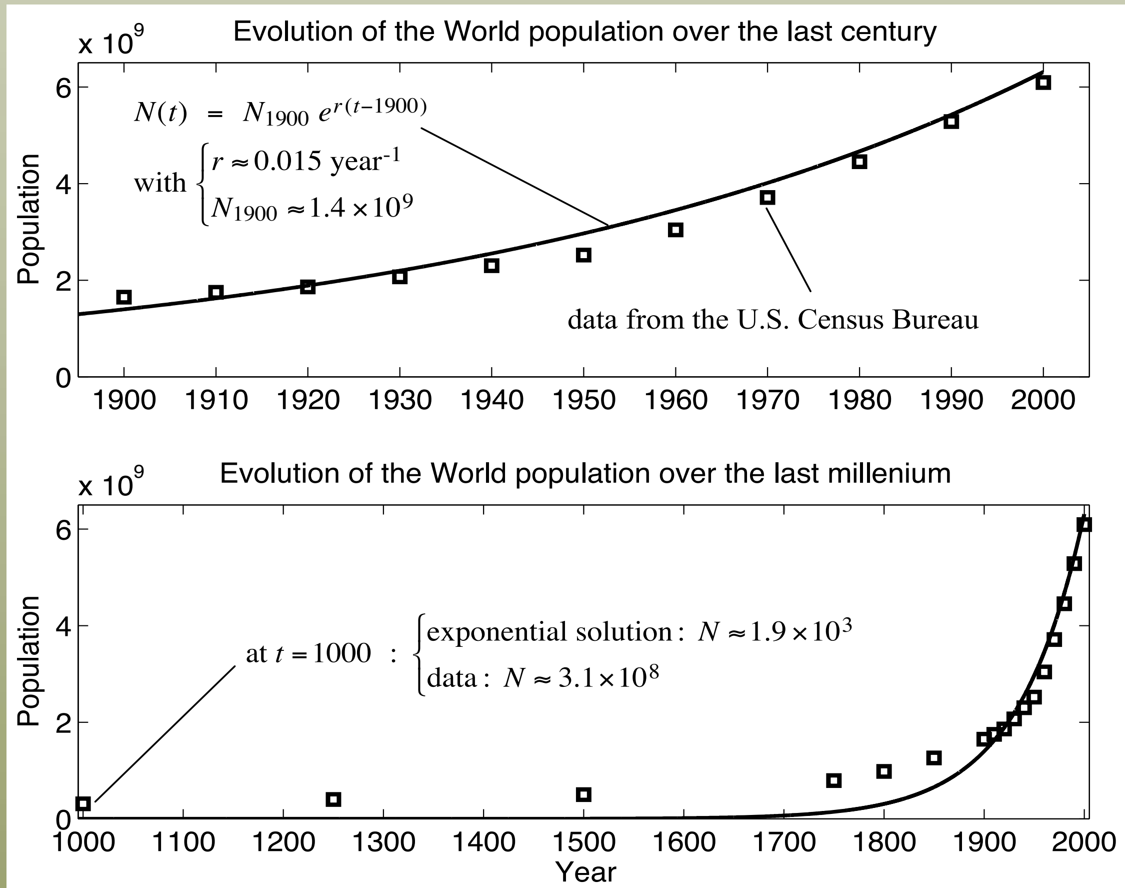
Answer: a little more than **22 hours**!

Simple models of growth (III)

• The Euler-Malthus model is unrealistic, since (among many reasons) the net growth rate r rarely remains constant. For instance, see the World population evolution:

An exponential expression is not that bad for the 20st century.

But, for the last millenium...



Simple models of growth (IV)

• Verhulst (1838, 1845) suggested a limitation to the growth rate, yielding the so-called logistic equation:

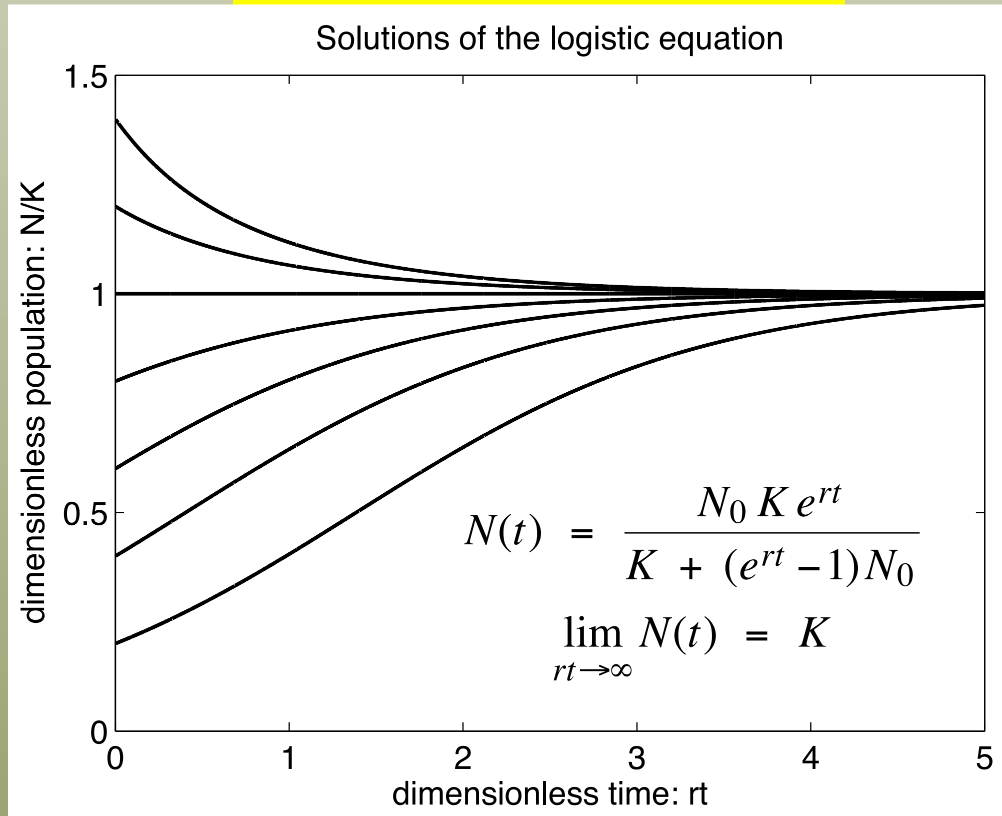
$$\frac{dN}{dt} = \underbrace{r(1 - N/K)}_{\text{growth rate}} N$$

K = carrying capacity
(sustainable population)

If $N>K$: population decreases.

If $N<K$: population increases.

Here, there is no ever-lasting exponential growth or decay.



A simple model of spreading (I)

• Consider a population of J (>>1) drunkards walking aimlessly in a random manner. Let $\xi_j(t)$ ($j = 1,2,\ldots J$) denote the position of every individual:

$$\xi_j(t+\Delta t) \;=\; \xi_j(t) \;+\; \rho_j(t) \;, \quad j = 1,2,\ldots J$$

where $\rho_j(t)$ is a (bounded) random displacement that is independent of the position, and has zero mean and constant variance, i.e.

$$\sigma_\rho^2(t) \;=\; \sum_{j=1}^{J} [\rho_j(t)]^2 \;=\; \text{constant}$$

• The center of mass does not move, i.e.

$$\bar{\xi}(t+\Delta t) \;=\; \sum_{j=1}^{J} J^{-1}\,\xi_j(t+\Delta t) \;=\; \sum_{j=1}^{J} J^{-1}\,\xi_j(t) \;=\; \bar{\xi}(t)$$

A simple model of spreading (II)

• The drunkards are spreading, i.e. the variance of their positions increases (linearly in time):

$$\sigma_\xi^2(t+\Delta t)=\sigma_\xi^2(t)+\sigma_\rho^2 \quad \Rightarrow \quad \sigma_\xi^2(t)=\sigma_\xi^2(0)+(\sigma_\rho^2/\Delta t)\,t$$

• Occasionally, the continuous (i.e. Eulerian) approach may be preferred to the previous (i.e. Lagrangian) one. Accordingly, the key variable is the population density (# individuals per unit length):

$$n(t,x) \;=\; \lim_{\Delta x\to 0} \frac{\#\ \text{individuals}\ \in [x, x+\Delta x]}{\Delta x} \;, \quad J >> 1$$

• What is the partial differential equation governing $n(t,x)$? One should have recourse to SDEs. However, the solution may be outlined by means of simple arguments.

A simple model of spreading (III)

- If the population density obeys the diffusion (or heat) equation

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2}$$

where the constant D (>0) denotes the diffusivity, the following properties hold true:

- number of individuals: $N(t) = \int_{-\infty}^{+\infty} n(t,x)\,dx = \int_{-\infty}^{+\infty} n(0,x)\,dx$;
- centre of mass: $\bar{\xi}(t) = \int_{-\infty}^{+\infty} x\,n(t,x)\,dx = \int_{-\infty}^{+\infty} x\,n(0,x)\,dx$;
- variance: $\int_{-\infty}^{+\infty} [x-\bar{\xi}]^2\,n(t,x)\,dx = \int_{-\infty}^{+\infty} [x-\bar{\xi}]^2\,n(0,x)\,dx + 2Dt$.

A simple model of spreading (IV)

• The population density and its centre of mass may be made to be equivalent in both approaches. This is trivial!

• For the width of the distribution to behave in the same way, it is necessary that

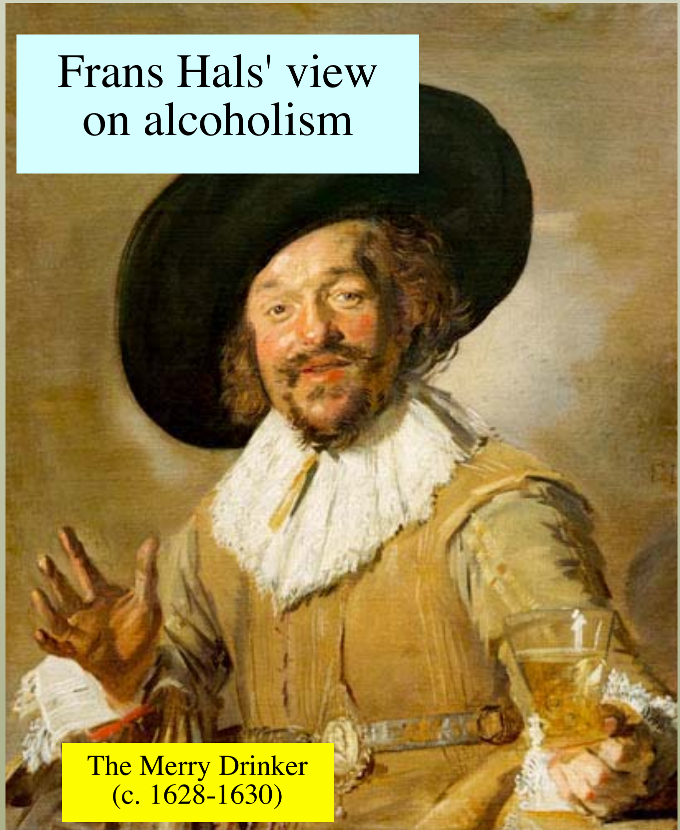
$$\sigma_\rho^2 = 2\,D\,\Delta t$$

• Example: at t=0, N_0 drunkards are released at x=0, then

$$n(t,x) = \frac{N_0\, e^{-x^2/(4Dt)}}{\sqrt{4\pi Dt}} \Rightarrow \begin{cases} \text{population}: & N_0 \\ \text{centre of mass}: & x = 0 \\ \text{variance}: & 2Dt \end{cases}$$

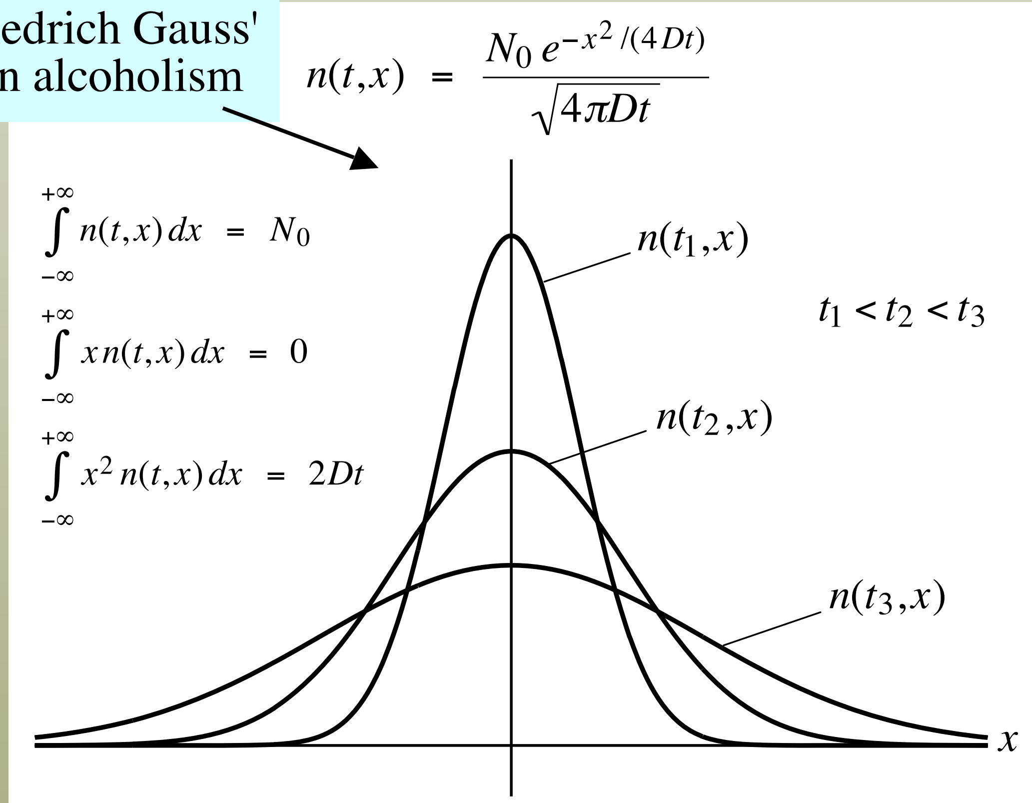
The distribution is a Gaussian, whose "width" increases in time.

A simple model of spreading (V)



The Merry Drinker
(c. 1628-1630)

Carl Friedrich Gauss' view on alcoholism



• The drunkards' speed is believed to be finite. But, the population density $n(t,x)$ is non-zero at any $t > 0$, even for large $|x|$. Is this a serious deficiency of the diffusion equation model?

A simple model of spreading (VI)

• There is no serious problem, since the number of individuals standing far away from the starting point x=0 tends to zero:

$$\text{number of individuals in the sub-domain } |x| \geq L > 0$$

$$= \int_{-\infty}^{-L} n(t,x)\,dx + \int_{L}^{+\infty} n(t,x)\,dx = \operatorname{erfc}\left(\frac{L}{\sqrt{4Dt}}\right) N_0$$

$$\sim \sqrt{\frac{4Dt}{\pi L^2}}\, e^{-L^2/(4Dt)}\, N_0 \ , \quad \frac{L}{\sqrt{4Dt}} \rightarrow \infty$$

• Determining to what measure the Lagrangian approach (random walks) and the Eulerian one (diffusion equation) are similar is not trivial, and ideally requires the use of SDEs...

• Generalizing the 1D developments to multi-dimensional problems is not that straightforward (e.g. Spivakovskaya et al. 2007).

Invasion of muskrats in Europe (I)

• Let x and y denote horizontal coordinates. If $n(t,x,y)$ is the population density of muskrats, a simple 2D model for their spread in Europe following the release at $(x,y)=(0,0)$ of N_0 individuals is:

$$\left.\begin{aligned}\frac{\partial n}{\partial t} &= rn + D\left(\frac{\partial^2 n}{\partial x^2}+\frac{\partial^2 n}{\partial y^2}\right)\\ n(0,x,y) &= \delta(\mathbf{x}-\mathbf{0})N_0\end{aligned}\right\} \Rightarrow \quad n(t,x,y) = \frac{e^{rt-|\mathbf{x}|^2/(4Dt)}}{4\pi Dt}N_0$$

with $\mathbf{x}=(x,y)$ and $|\mathbf{x}|^2 = x^2+y^2$

$$n(t,0,0)\begin{cases}\text{decreases for } 0\le t<r^{-1} \ \text{(spreading > breeding)}\\ \text{increases for } r^{-1}<t \ \text{(spreading < breeding)}\end{cases}$$

• In this model, the population density is non zero everywhere at any time $t>0$. So, how to define a (finite) area occupied by muskrats?

Invasion of muskrats in Europe (II)

• Consider the area $A(t)$ where the population density is larger than the lowest detectable level n_d (e.g. Kot 2001):

$$A(t) = 4\pi r D t^2 - 4\pi D t \log(4\pi D n_d t / N_0)$$

This expression depends on n_d, whose value is uncertain.

• Fortunately, in the long run, $A(t)$ tends to be independent of n_d and grow as t^2 as expected:

$$A(t) \sim 4\pi r D t^2 \quad , \quad rt \to \infty$$

From Banks (1994) field data: $rD \approx 2.8\,\mathrm{km}^2\ \mathrm{year}^{-2}$.

• In this model the domain of interest is assumed to be infinite. What happens in finite-size domains?

Harmful algal blooms (I)

Phaeocystis foam on a Belgian beach in May 1998 (Rousseau et al. 2006)

Red tide caused by dinoflagellates off La Jolla, California (from Wikimedia Commons)

- Under certain circumstances (e.g. excess of nutrients), the population of algae can grow rapidly in aquatic systems, resulting in adverse effects (outcompeting other species, production of neurotoxins, decrease in oxygen concentration, etc).

- Can spreading processes prevent such blooms?

Harmful algal blooms (II)

• Consider the so-called KISS model (after papers published in the 1950s by Kierstead, Slobodkin and Skellam). Assume that the conditions for growth are favourable only for $0 \le x \le L$, i.e.

$$\text{growth rate} = \begin{cases} r > 0 \text{ if } x \in [0, L] \\ r < 0 \text{ if } x \notin [0, L] \end{cases}$$

• Simplest mathematical model:

$$\begin{cases} \dfrac{\partial n}{\partial t} = rn + D\dfrac{\partial^2 n}{\partial x^2} & (r, D: \text{ positive constants}) \\ n(0,x) = n_0(x) \;,\; \left[n(t,x)\right]_{x=0,L} = 0 \end{cases}$$

The boundary conditions, though questionable, reflects the fact that the living conditions for algae are not favourable outside $[0, L]$.

Harmful algal blooms (III)

- The solution to the partial differential problem reads

$$n(t,x) = \sum_{j=1}^{\infty} a_j e^{\gamma_j t} \sin(\kappa_j x)$$

$$\begin{cases} \gamma_1 > \gamma_2 > \gamma_3 > \dots \\ \gamma_j < 0 \quad \text{for} \quad j >> 1 \end{cases}$$

$$a_j = \frac{1}{2L} \int_0^L n_0(x) \sin(\kappa_j x)\, dx \;, \quad \gamma_j = r - D\kappa_j^2 \;, \quad \kappa_j = j\pi / L$$

- The condition for a bloom to occur is $\max \gamma_j = \gamma_1 > 0$, which is equivalent to $D < rL^2 / \pi^2$ or

$$L > \pi \sqrt{\frac{D}{r}} = \text{KISS size}$$

Harmful algal blooms (IV)

• Introduce two timescales:

$$\text{timescale for growth}: \; T_g = r^{-1}$$

$$\text{timescale for spreading}: \; T_s = L^2 / (\pi^2 D)$$

Then, the condition for a bloom to occur may be rewritten as $T_g < T_s$. So, a bloom occurs if growth is faster than spreading, that transports algae out of the patch where growing conditions are favourable.

• More realistic solutions are obtained when using Robin boundary conditions (rather than Dirichlet ones), but the condition for a bloom to occur does not change fundamentally. Multi-dimensional generalization is relatively easy.

• Does a non-linear growth term (such as Verhulst's) lead to radically different solutions?

Fisher equation (I)

• The growth-spreading equation with a linear growth term (rn) considered so far has an unstable equilibrium point ($n = 0$). Travelling wave solutions are impossible.

• Now replace the linear growth term by Verhulst's non-linear expression, yielding the Fisher equation (1937):

$$\frac{\partial n}{\partial t} = r(1 - n/K)n + D\frac{\partial^2 n}{\partial x^2}$$

There are two equilibrium points: $n = 0$ (unstable) and $n = K$ (stable). This allows for the existence of travelling waves

$$n(t,x) \rightarrow n(\underbrace{x - ct}_{z})$$

where c is the phase speed.

Fisher equation (II)

- Introduce dimensionless variables:

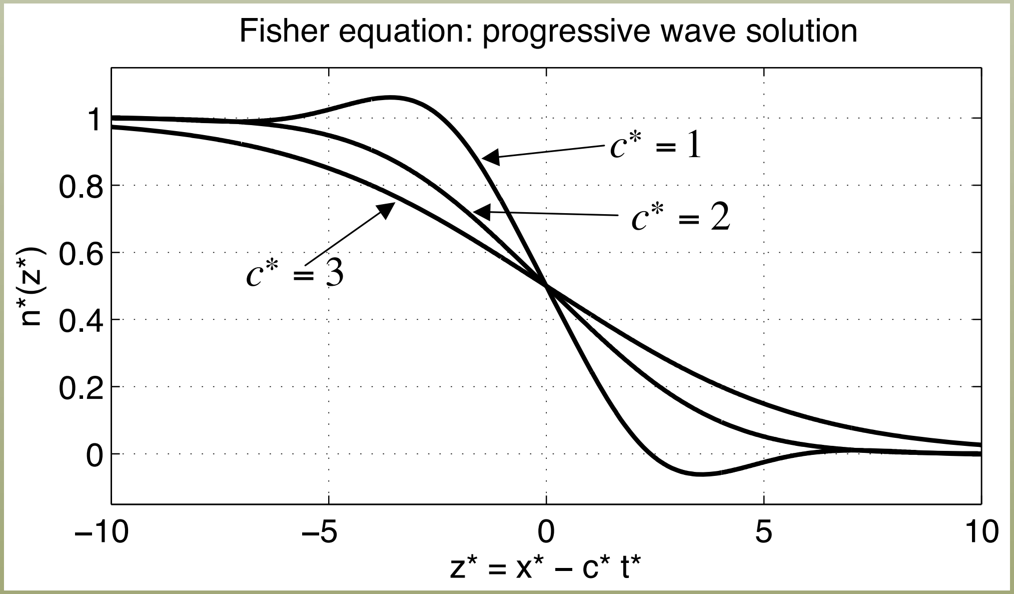
$$t^* = \frac{t}{r^{-1}}\ ,\quad x^* = \frac{x}{\sqrt{r^{-1}D}}\ ,\quad c^* = \frac{c}{\sqrt{rD}}\ ,\quad n^* = \frac{n}{K}$$

- Introduce a travelling wave solution into the Fisher equation:

$$\frac{d^2 n^*}{dz^{*2}} + c^* \frac{dn^*}{dz^*} + (1-n^*)n^* = 0$$

$n^*(-\infty) = 1$ (stable equil. pt)

$n^*(+\infty) = 0$ (unstable equil. pt)



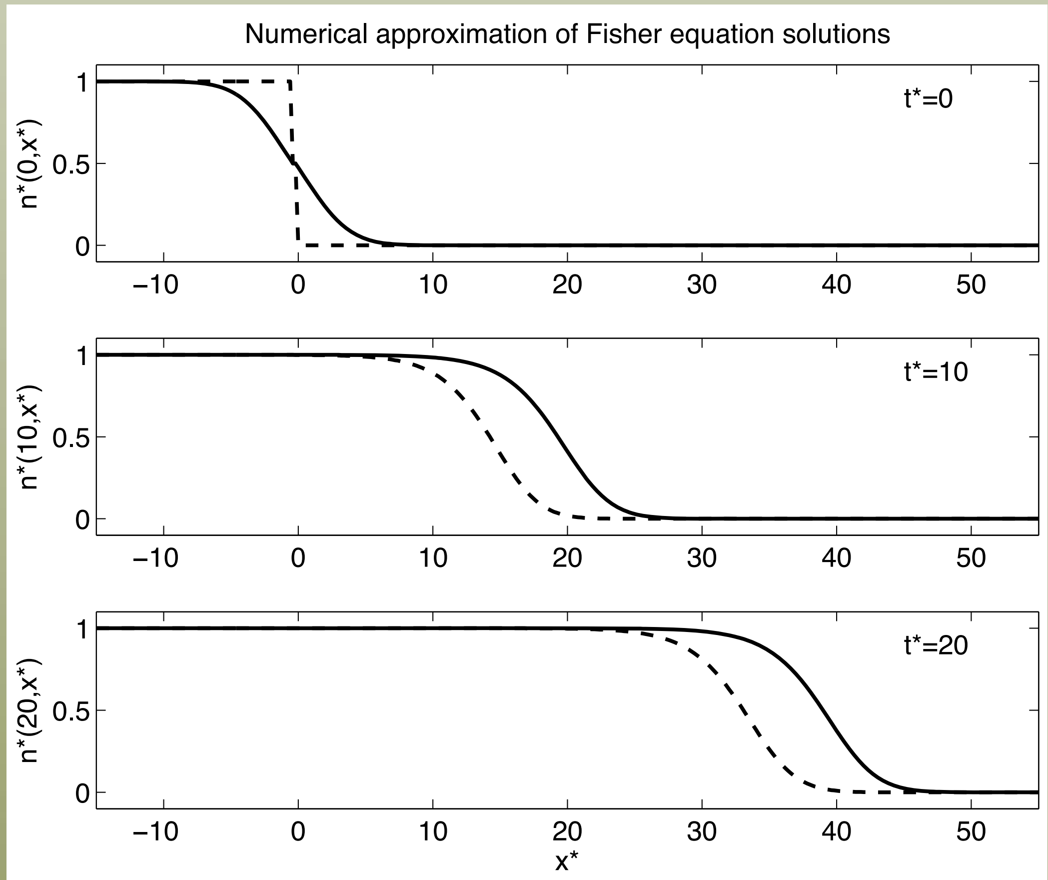
- Phase speed $c^* < 2$ is unacceptable (over/under-shootings).

Fisher equation (III)

• Irrespective of the initial profile $n^*(0,x^*)$, the solution tends to the wave that propagates with the lowest possible speed, i.e. $c^* = 2$, the phase depending on the initial value $n^*(0,x^*)$.

The dimensional phase speed corresponding to $c^* = 2$ is $c = \sqrt{4rD}$.

This is the speed at which a population governed by the Fisher equation is likely to be spreading.



A tentative model of the Black Death (I)

• In the classical SIR model (Kermack and McKendrick 1927), the population is divided into 3 classes:

- the Susceptibles: can catch the disease;
- the Infectives: have and can transmit the disease;
- the Removed class, i.e. those who have had the diseases and are recovered, immune, isolated or dead.

The incubation period is assumed to be zero.

• The original SIR model does not consider geographical spread. To do so, diffusion terms will be added.

• For a one-dimensional problem, the state variables are:

- $n_s(t,x)$: number op susceptibles per unit area;
- $n_i(t,x)$: number of infectives per unit area;
- $n_r(t,x)$: number of removed per unit area.

A tentative model of the Black Death (II)

• Governing equations:

$$\begin{cases} \dfrac{\partial n_s}{\partial t} = -r n_i n_s + D_s \dfrac{\partial^2 n_s}{\partial x^2} \\ \dfrac{\partial n_i}{\partial t} = r n_i n_s - a n_i + D_i \dfrac{\partial^2 n_i}{\partial x^2} \\ \dfrac{\partial n_r}{\partial t} = a n_i + D_r \dfrac{\partial^2 n_r}{\partial x^2} \end{cases}$$

with: *r*: positive constant related to the infection rate;
a: positive constant related to the removal rate.

Surprisingly, an epidemic will develop if there are enough ~~infectives~~ susceptibles ($n_s > n_s^{crit}$), and will decline for lack of ~~infectives~~ susceptibles ($n_s < n_s^{crit}$), where $n_s^{crit} = a / r$.

A tentative model of the Black Death (III)

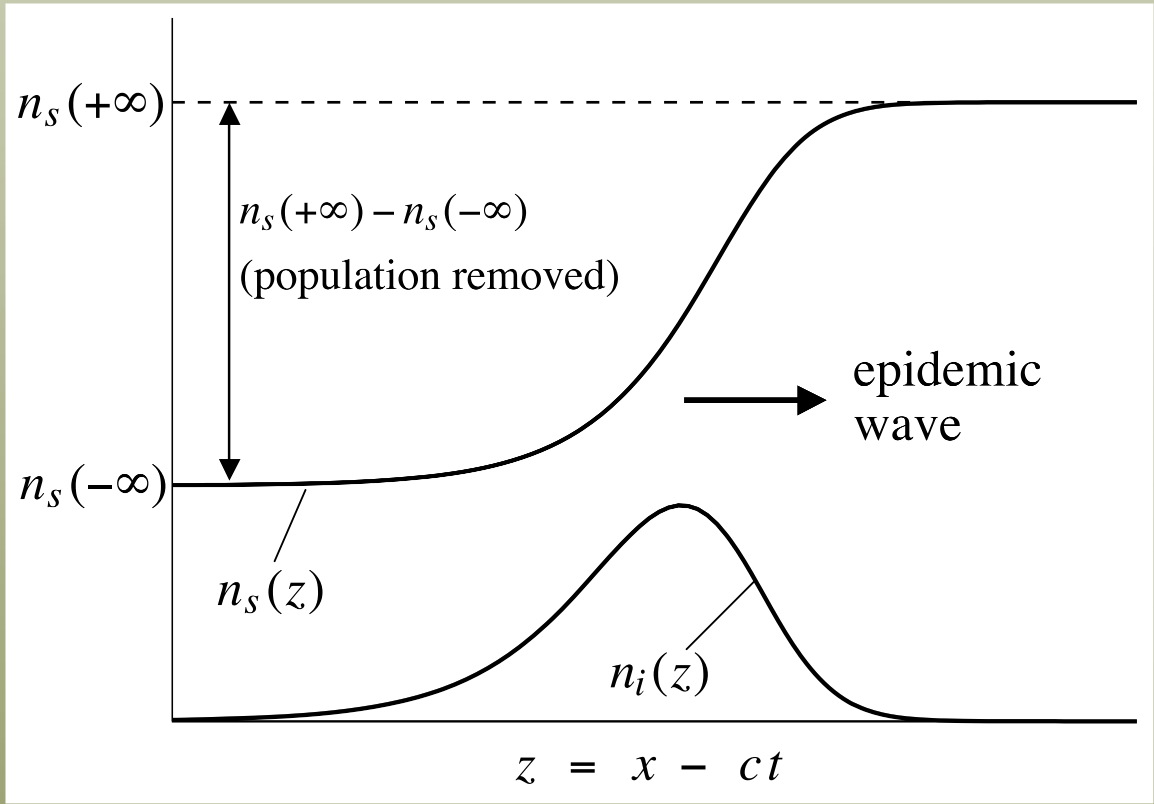
• An epidemic wave can propagate in a way that is similar to the travelling wave solution of the Fisher equation. If c is the speed of spread, look for solution of the form $n_\chi(z)$ $(\chi = s, i, r)$, with $z = x - ct$.

Fraction of the population "removed" by the epidemic:

$$\varepsilon = \frac{n_s(+\infty) - n_s(-\infty)}{n_s(+\infty)}$$

$n_s(+\infty) > n_s^{crit}$: unstable equil.

$n_s(-\infty) < n_s^{crit}$: stable equil.



A tentative model of the Black Death (IV)

• With $D_s = D = D_i$ (for simplicity), linearise the equation for the infective density in the vicinity of the epidemic front:

$$D\frac{d^2 n_i}{dz^2} + c\frac{dn_i}{dz} + rn_s(+\infty)(1-\lambda)n_i = 0$$

with $\lambda = \dfrac{n_s^{crit}}{n_s(+\infty)} = \dfrac{a}{r\,n_s(+\infty)} < 1$. Then, $n_i(z)$ is of the form

$$n_i(z) \propto \exp\left(\frac{-c \pm \sqrt{c^2 - 4Dn_s(+\infty)(1-\lambda)}}{2D}\,z\right)$$

Therefore, for a wave solution to exist, the phase speed must satisfy

$$c \geq \sqrt{4Dn_s(+\infty)(1-\lambda)} = c_{\min}$$

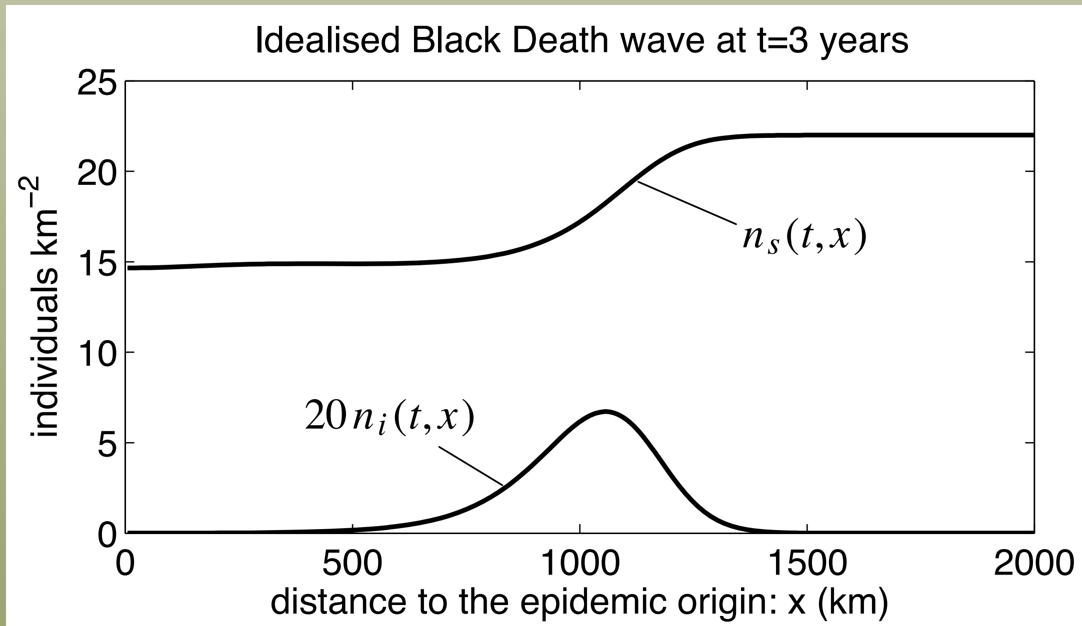
A tentative model of the Black Death (V)

- To attempt to simulate the spread of the Black Death in Europe (1347-1350), we impose (Langer 1964, Noble 1974, Murray 1989):

$$n_s(0,x) = 22\,\text{km}^{-2},\ \ c_{\min} \approx 450\,\text{km year}^{-1},\ \ a \approx 25\,\text{year}^{-1}$$

The other coefficients are calibrated so that $\varepsilon \approx 1/3$, which leads to acceptable values: $D \approx 8.7 \times 10^3\ \text{km}^2\ \text{year}^{-1}$ and $r \approx 1.4\ \text{km}^2\ \text{year}^{-1}$.

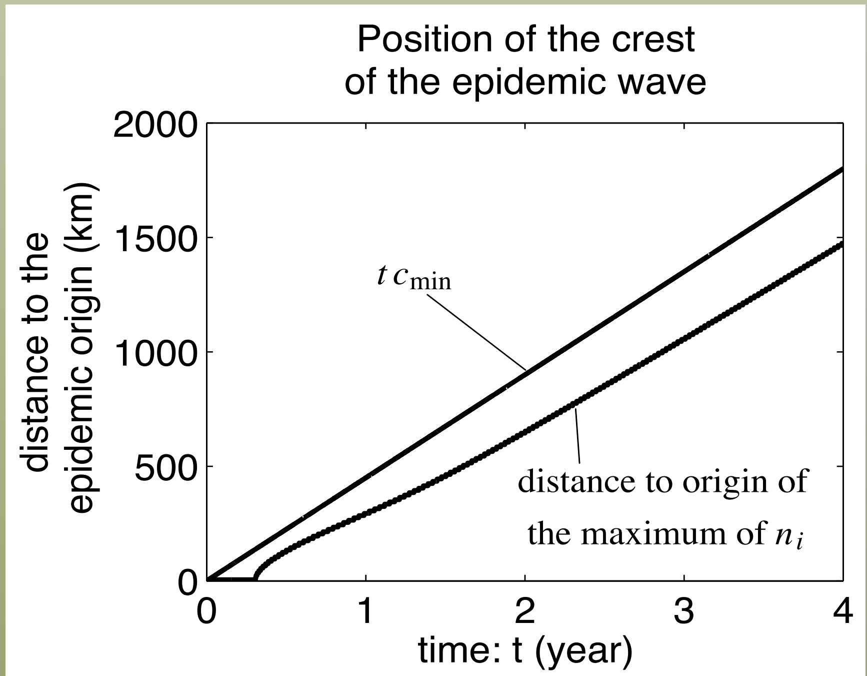
Numerical solution rather similar to Noble's (1974)



A tentative model of the Black Death (VI)

• We attempted to simulate the Black Death spread by means of a 1D model in the semi-infinite domain $0 \leq x < \infty$, the origin x=0 being the point where the epidemic was ignited (Southern Italy). At t=0, a number of infectives were released at x=0, the exact number being of little importance. No flux boundary conditions were imposed at x=0.

After the initial phase that lasted for a few months, an epidemic wave developed and spread at about the theoretical speed, i.e. c_{min}, which was prescribed to be 450 km year^{-1}.



Conclusions

• Rather simple mathematical developments based on ODEs or PDEs allowed us to gain insight into seemingly complex biological or ecological phenomena arising from the race between growth and spreading — modelled as harmonic diffusion, which may be associated with random walks.

• Growth-spreading equations may be applied to a wide variety of phenomena, of which only a few examples were given herein. Of particular interest are the progessive wave solutions allowing the latter to evolve from an unstable equilibrium value to a stable one.

• Clearly, we have adhered to the so-called *KISS principle*, also known as *Keep it simple, stupid!* (Just joking...)

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