

# VI Southern-Summer School on Mathematical Biology

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## Lecture V

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# Outline

## 1 Density and Diffusion



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2 Reaction-Diffusion



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- 1 Density and Diffusion
- 2 Reaction-Diffusion
- 3 Bibliography



# Space

- Up to this point, all models that we have studied assume implicitly that all individuals are in certain region of space.
- This region has been supposed not to be very important .
- We think of homogeneous regions.
- Well-mixed populations.
- **HOWEVER...**
- Individuals move, possibly generating the spatial redistribution of the population.
- And space may be heterogeneous due to several factors :
  - ▶ climate
  - ▶ soil
  - ▶ vegetation
  - ▶ composition
  - ▶ salinity....

# Density

- Let us consider a population in space.
- Let space be homogeneous. How do populations spread over space?.
- First point: we will not speak of number of individuals.
- Instead we will speak of **density** of individuals.
- The number of individuals per unit space.
- The usual notation is  $\rho(\vec{x}, t)$  for density. It is a function of time and **space**.
- In some contexts, we use the term **concentration**.



# Diffusion

- Our main hypothesis is that individuals move **randomly**.
- In some sense, they behave as molecules in a gas.
- If we look at such population from a space scale much larger than the typical scale of the movement of the individuals we will see the macroscopic phenomenon called **diffusion**.
- Particles in a gas obey Fick's law.
- We will assume the same for a population.
- **So, what's Fick's law?**



- The **Fickian diffusion law** states that:
  - ▶ The flux  $\vec{J}$  of "material" ( animals, cells,..) is proportional to to the gradient of the density of the material:

$$\vec{J} = -D\vec{\nabla}\rho \equiv -D\left(\frac{\partial\rho}{\partial x}, \frac{\partial\rho}{\partial y}\right)$$

- ▶ where we took a two-dimensional space.
- ▶ But to simplify the calculations let us consider the **one-dimensional case**:

$$J \sim -\frac{\partial\rho}{\partial x}$$



# Mass/number of individuals conservation

- Let us impose a conservation law:
  - ▶ *The rate of change in time of the quantity of individuals in a region of space is equal to the flux through the borders.*
- that is, (in one dimension,  $(x_0 - x_1)$  being the size of the region):

$$\frac{\partial}{\partial t} \int_{x_0}^{x_1} \rho(x, t) dx = J(x_0, t) - J(x_1, t)$$



# The diffusion equation

$$\frac{\partial}{\partial t} \int_{x_0}^{x_1} \rho(x, t) dx = J(x_0, t) - J(x_1, t)$$

- We can write the previous equation in a differential form:

- ▶ Take  $x_1 = x_0 + \Delta x$ .

- ▶ So that for  $\Delta x \rightarrow 0$ :

- ★  $\int_{x_0}^{x_1} \rho(x, t) dx \rightarrow \rho(x_0, t) \Delta x$

- ★  $J(x_1, t) \rightarrow J(x_0, t) + \Delta x \left( \frac{\partial J(x, t)}{\partial x} \right)_{x=x_0}$

- ▶ Which implies::

$$\frac{\partial \rho}{\partial t} \Delta x = -\Delta x \left( \frac{\partial J(x, t)}{\partial x} \right)$$

- ▶ and using Fick's law

$$\frac{\partial \rho}{\partial t} = -\frac{\partial J(x, t)}{\partial x} = D \frac{\partial^2 \rho}{\partial x^2}$$

# The diffusion equation

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

- The above equation is known as the diffusion equation.
- In two dimensions we would have:

$$\frac{\partial \rho}{\partial t} = D \nabla^2 \rho$$

where  $\nabla^2 \rho \equiv \frac{\partial^2 \rho}{\partial x^2} + \frac{\partial^2 \rho}{\partial y^2}$

- It is the same equation that describes heat diffusion if  $\rho$  is taken as temperature.
- Let us recall some facts about it.



# Diffusion Equation

- The diffusion equation is a *partial differential equation*, a **PDE**.
- It is linear, and the coefficients are constants.
- It can be solved **analytically**.

## Mathematical comment

- In order to speak of a solution of a differential equation, we need to specify supplementary conditions.
- In the case of the diffusion equation we should give an initial condition  $\rho(x, 0)$  and the values of either  $\rho(x, t)$  or  $\frac{\partial \rho(x, t)}{\partial x}$  at the borders or for  $x \rightarrow \pm\infty$ .
- To solve it analytically, means that we can find a formula connecting  $\rho(x, t)$  to  $\rho(x, 0)$ .

- There is a distinctive solution: a **Gaussian** function.
- In one dimension we have, for  $t > 0$  and  $x \in [-\infty, +\infty]$ :

$$\rho(x, t) = \frac{Q}{2(\pi Dt)^{1/2}} e^{-x^2/(4Dt)}$$

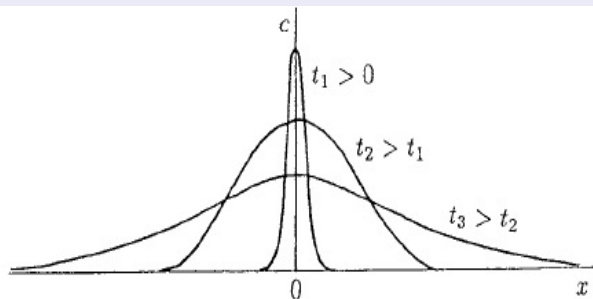
where  $Q$  is a constant.

- It is a Gaussian that "widens" with time.
- Corresponds to an initial condition concentrated in  $x = 0$ .
- Here is a plot.



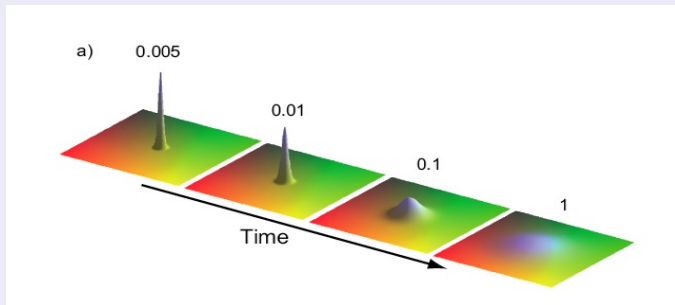
# Gauss: plots

## Solution to the 1D diffusion equation



# Gauss: 2D plot

## Solution to the 2D diffusion equation



## Let us put some biology in this lecture!

- Let us give a biological sense to all that.
- Suppose that at  $t = 0$  a population of  $N$  individuals is released at  $x = 0$ .
- After a certain amount of time we want to know the the extension occupied by the population.
- Let's be more specific: we want the extension of the region containing 95% of the population.





- Knowing the density of a population allows us to calculate the total population in a given area. In the 1D case, we have:

$$\text{Population between } -L \text{ and } L = N_L = \int_{-L}^{+L} \rho(x, t) dx.$$

- If we use the Gaussian for  $\rho(x, t)$ , perform the integral, we obtain that 95% of the population is a region of size  $2\sqrt{2Dt}$ .
- Which grows in time proportional to  $t^{1/2}$ .
- Or, at a speed which goes like  $t^{-1/2}$ . Decreasing.



# Diffusion + Growth

- The previous case corresponds to a non-growing population.
- Let us incorporate growth:

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + a\rho(x, t)$$

- Still linear.
- But, as we already learning, some saturation mechanism should become relevant for large enough populations Say:

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + a\rho(x, t) - b\rho^2(x, t)$$

# Fisher-Kolmogorov

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + a\rho(x, t) - b\rho^2(x, t)$$



Figura : Robert. A. Fisher



Figura : Andrei N. Kolmogorov

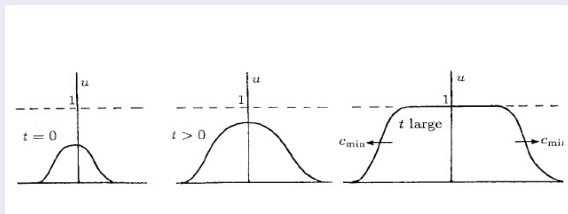
- The above equation is called Fisher-Kolmogorov equation.
- It is the simplest equation with diffusion, growth and self-regulation of a species.
- It is nonlinear.
- It is a representative of the class of “reaction-diffusion” equations.
  - ▶ This name comes from chemistry.
- The 2D version is obvious:

$$\frac{\partial \rho}{\partial t} = D \nabla^2 \rho + a\rho - b\rho^2$$

# Fisher-Kolmogorov

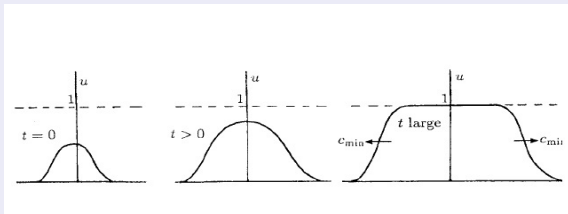
$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + a\rho(x, t) - b\rho^2(x, t)$$

- Let us again look at the problem of a population released at a point ( $x = 0$ ).
- Suppose it obeys the Fisher-Kolmogorov equation (and not anymore the simple diffusion equation).
- No explicit formula.
- But look at the plot::



# Fisher-Kolmogorov

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + a\rho(x, t) - b\rho^2(x, t)$$



- We can see that there is a wave-front. And it moves with speed  $v = 2\sqrt{aD}$ . **Constant.**
- In the case of simple diffusion the speed decreased with time.
- This pattern can be made the basis of experimental verification.
- Our observations should concentrate on the front's speed. .

- The speed does not depend on  $b$ .
- Therefore, the constant wavefront speed is not related to density dependence. The nonlinear term is there to avoid infinities.
- A equation

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + a\rho(x, t)$$

is called the Skellam equation.

# The classic example

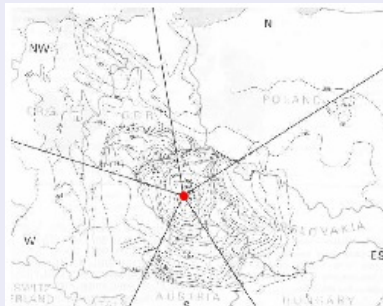
## Muskrat

- The muskrat, a species native of North-america, was introduced in Europe.
- In 1905, **five** individuals were introduced in Prague.
- Today, there are millions in Europe
- In what follow, we see the expansion of the muskrat's range around Prague over 17 years..



# Muskrat

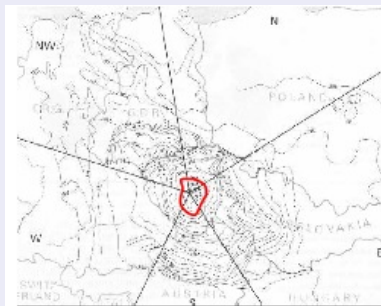
1905





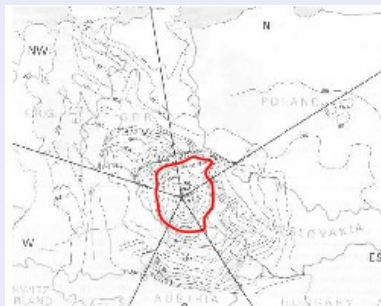
# Muskrat

1909



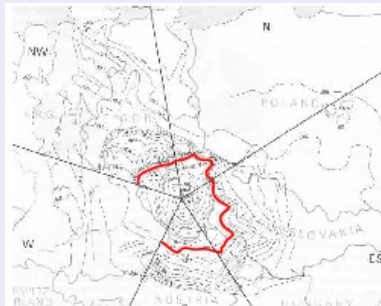
# Muskrat

1913



# Muskrat

1917



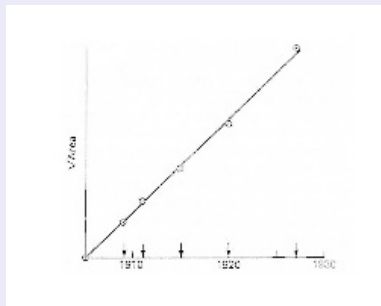
# Muskrat

1921



# Skellam !

- From these observations we can estimate the speed of invasion as a function of time.
- Here it is:



- A straight line. Constant speed. *Skellam dixit!* REJOICE!

# Micro X macro

- From the theory of the Brownian motion we can see  $D$  as the mean square displacement per unit of time.
- We could try to track individuals and calculate it .
- Beware!, it is likely that you get a **wrong value for  $D$** . Too large.
- Why?



# Home range effects

- Many species have **home ranges**.
- This comes from several factors: the need to find food, the need to find shelter .
- This slows down the diffusion process.
- In general, a mechanistic study of  $D$  is difficult. In most studies it is taken as a phenomenological constant.



## Example: Hantavirus

- In 2000, a new species of Hantavirus was discovered, being the etiological agent of a respiratory syndrome. It is fatal in up to 60% of cases
- The host is *Oligoryzomys fulvescens*. Take a look at him:



- Where you find the rat, you find the Hantavirus
- The disease "follows" the spread of the rat.



# Hantavirus II

- The diffusion of the hosts is well modeled by the usual models,.
- But  $D$  is *small*.
- *Oligoryzomys fulvescens* has a limited home-range.
- The population spreads through juvenile migrants.
- A statistically rare event.
- But determinant for the spatial redistribution of the population.
- The diffusion coefficient appearing in the equations is a proxy of all these processes.



# Bibliography

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- R.S. Cantrell e C. Cosner: *Spatial Ecology via Reaction-Diffusion Equations* (Wiley, 2003).
- A. Okubo e S.A. Levin: *Diffusion and Ecological Problems* (Springer, 2001).
- P. Turchin: *Quantitative Analysis of Movement* (Sinauer, 1998)



# Online Resources

- <http://www.ictp-saifr.org/mathbio5>
- <http://ecologia.ib.usp.br/ssmb/>

Thank you for your attention

