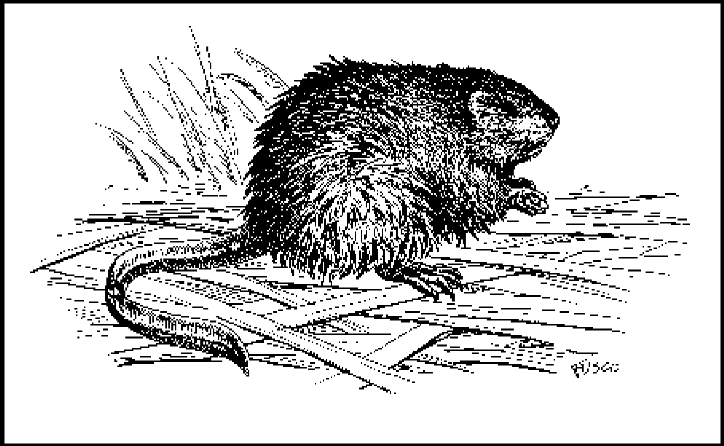
Biological Invasions: From Critters to Mathematics



Tom Robbins

Department of Mathematics

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Outline

- Biology background

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- Historical example

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- Historical example
- Model for terrestrial plant species

Biological Invasions?

- What are biological invasions?
  - A biological invasion is the introduction and spread of an exotic species within an ecosystem.

Biological Invasions?

- What are biological invasions?
  - A biological invasion is the introduction and spread of an exotic species within an ecosystem.
- Why are biological invasions important?
  - Economic impact ($100 billion by 1991)
  - Contribute to the loss of biodiversity
  - Are a threat to endangered species

Example of Loss in Biodiversity

European zebra mussel (*Dreissena polymorpha*)

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- Competes with the native crustaceans
- Decline in native crustaceans $\longrightarrow$ decline in the native fish population

Conceptual Framework

- Arrival and Establishment
  - Most invasions fail!
  - Invasion (or propagule) pressure is important
  - All communities are invasible

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  - All communities are invasible
- Spread
- Equilibrium and effects
  - Most invaders have only minor consequences
  - Few have disastrous consequences!

Establishment of Invasive Species

- How do biological invasions become established?

Natural or man-made disturbance in an ecosystem

Establishment of Invasive Species

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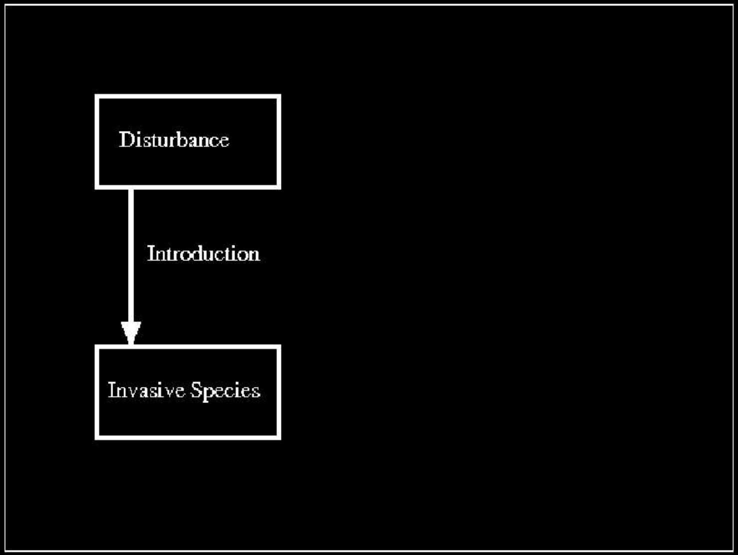

Introduction of an exotic species

Establishment of Invasive Species

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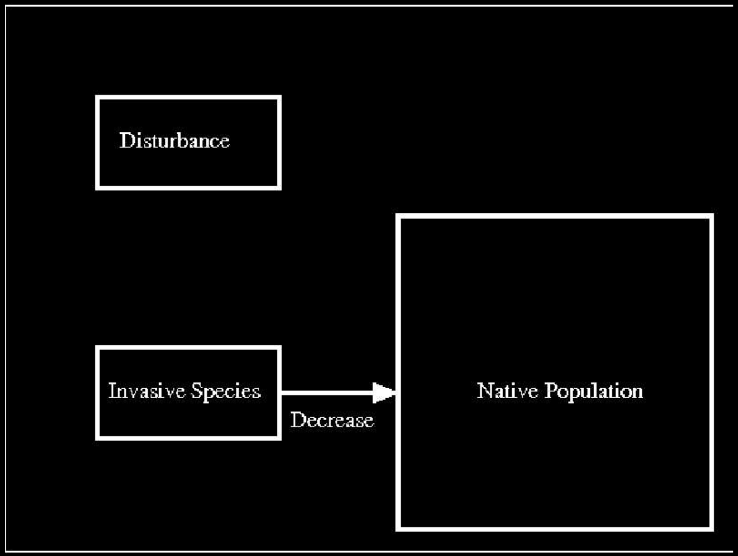

Decrease in the native species by
- Direct competition for resources
- Indirectly by external predation

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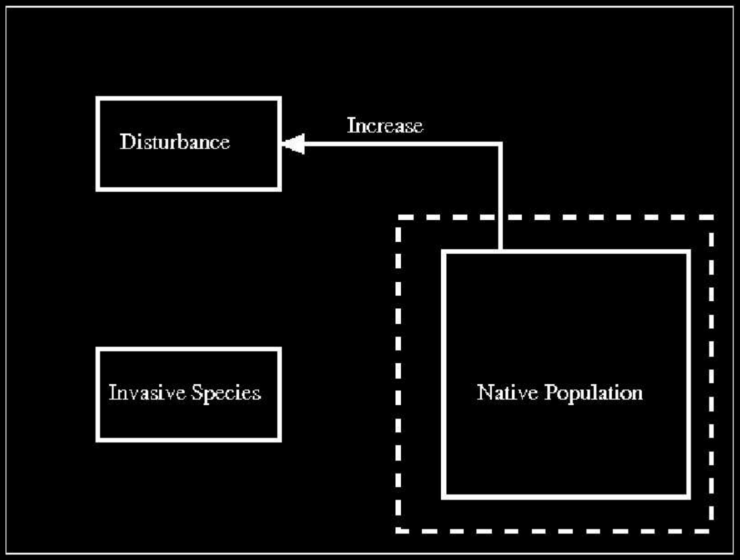
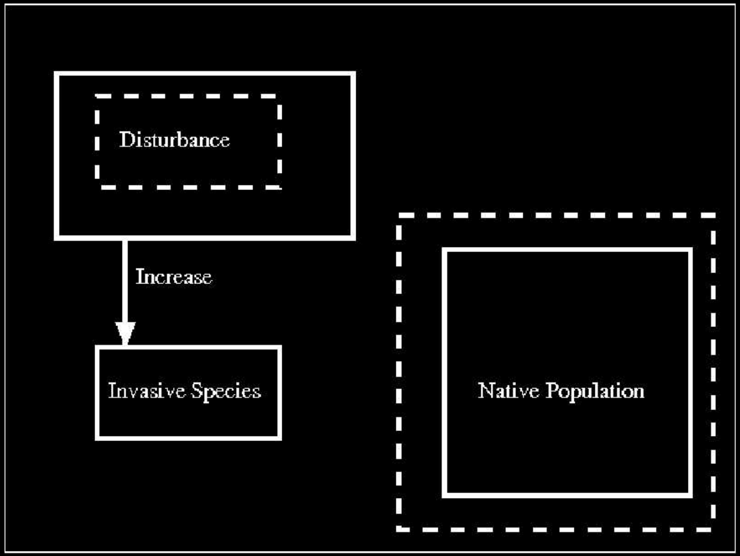


Increase in the disturbed habitat

Establishment of Invasive Species

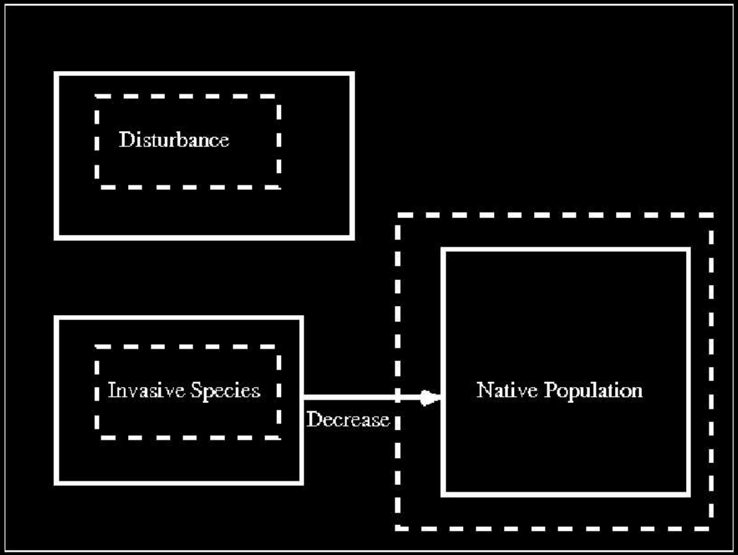
- How do biological invasions become established?



Increase in resources for the exotic

Establishment of Invasive Species

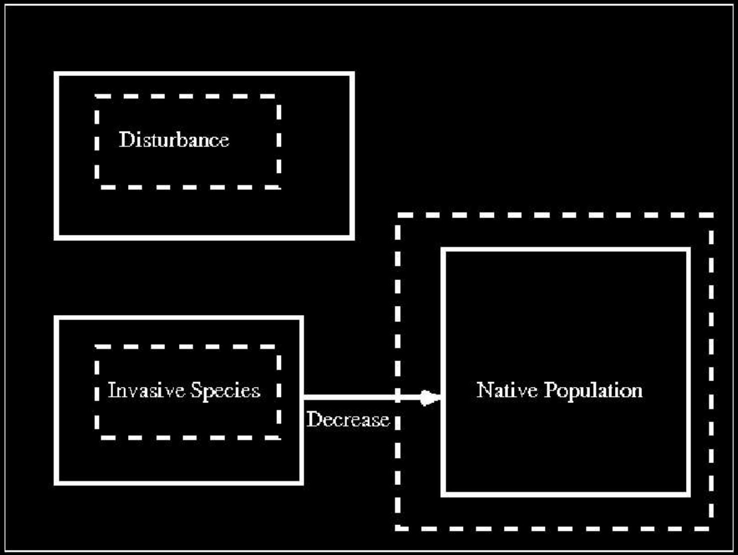
- How do biological invasions become established?



Further decrease in the native population

Establishment of Invasive Species

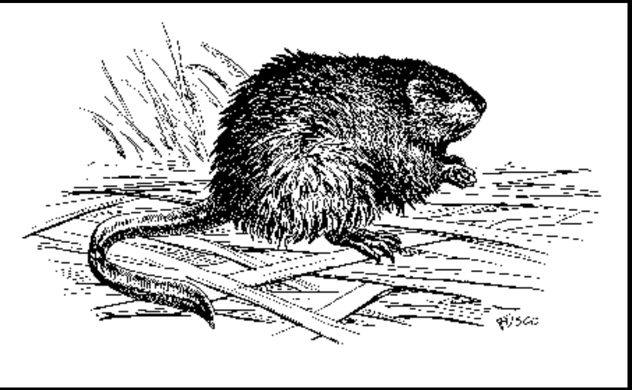
- How do biological invasions become established?



Dispersal ability is a governing factor!

Muskrat Invasion

North American muskrat (*Ondatra zibethica*)



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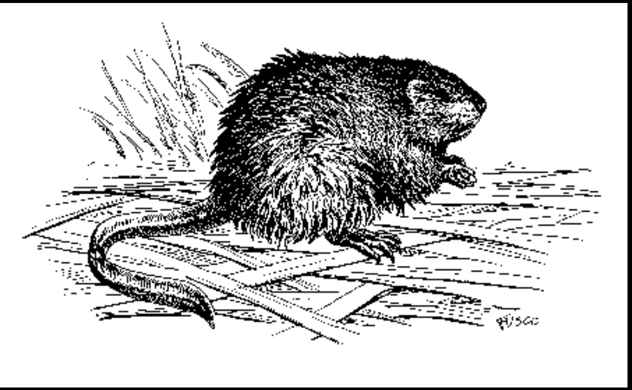

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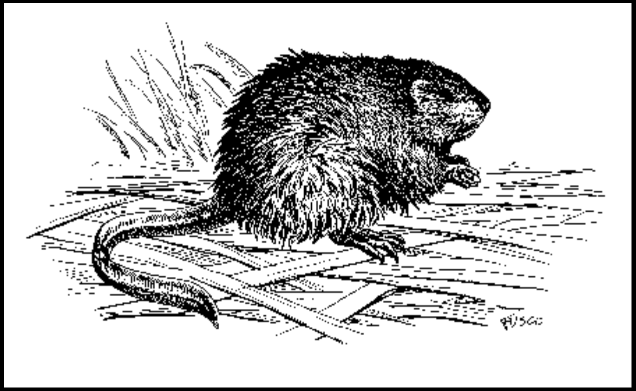

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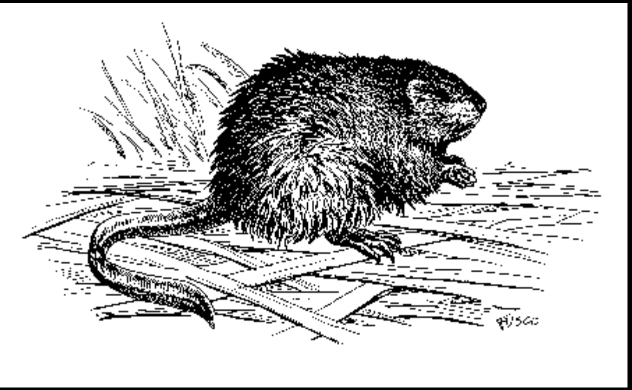
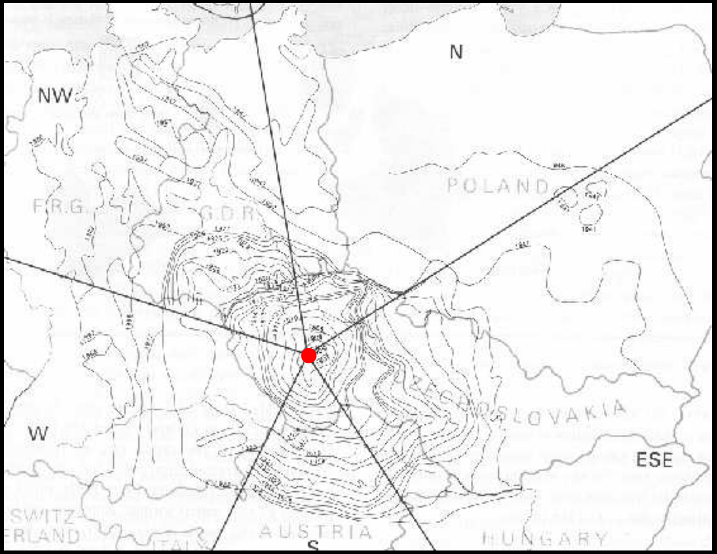


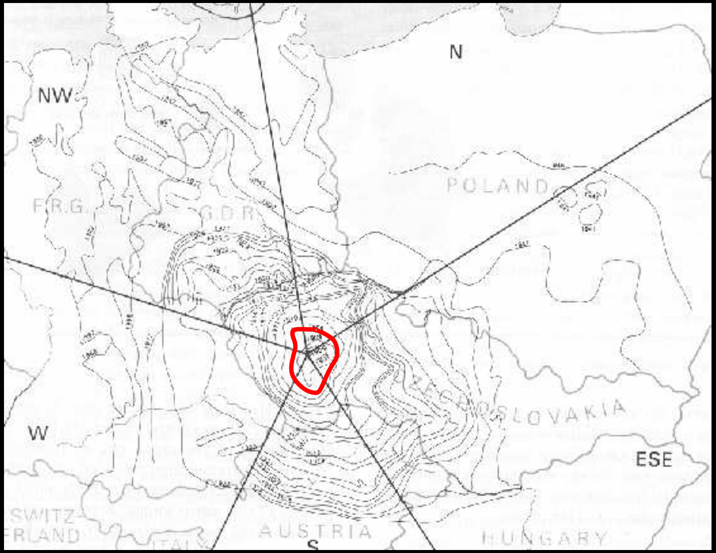
- Brought to Europe for fur-breeding in early 1900’s
- In 1905, five muskrats were released near Prague
- Spread and reproduced (with other escaped groups), inhabiting the entire continent in 50 years
- Today, they number many millions

Spread of North American Muskrat



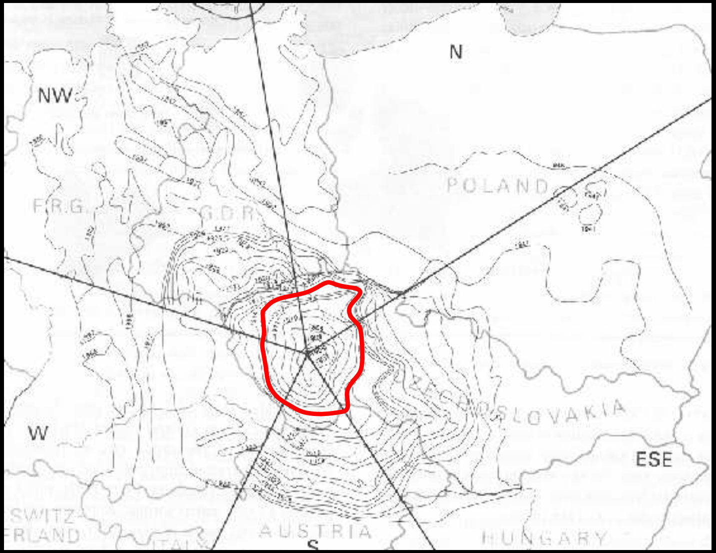
$t = 1905$ (initial introduction)

Spread of North American Muskrat



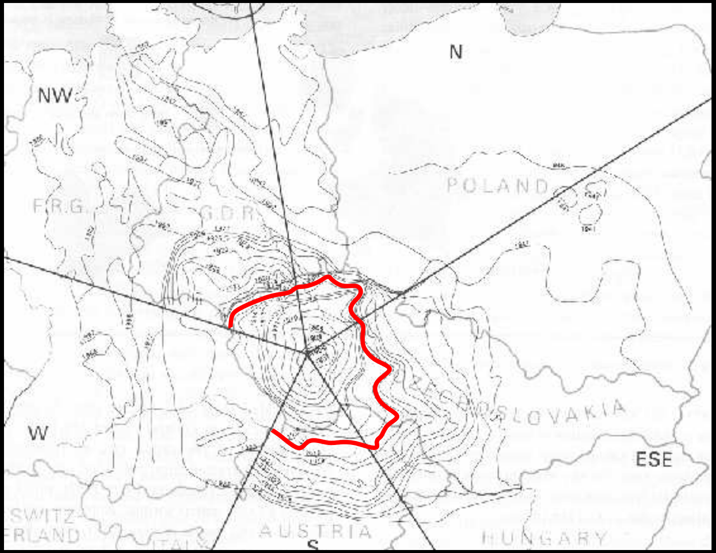
$$t = 1909$$

Spread of North American Muskrat



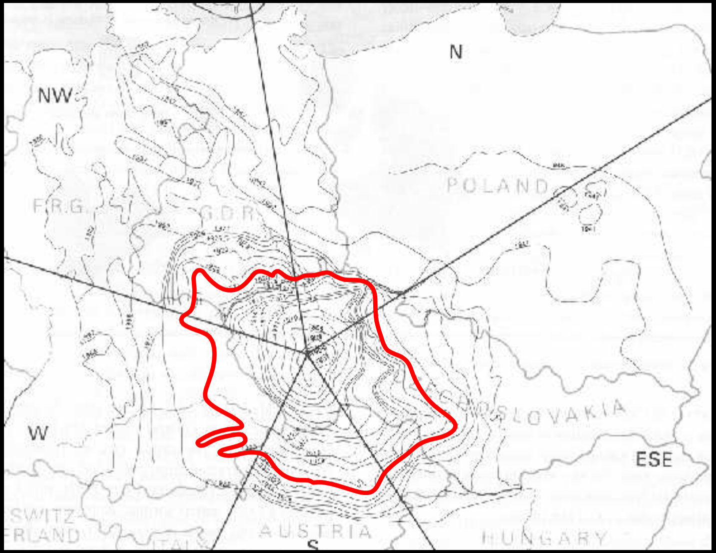
$$t = 1913$$

Spread of North American Muskrat



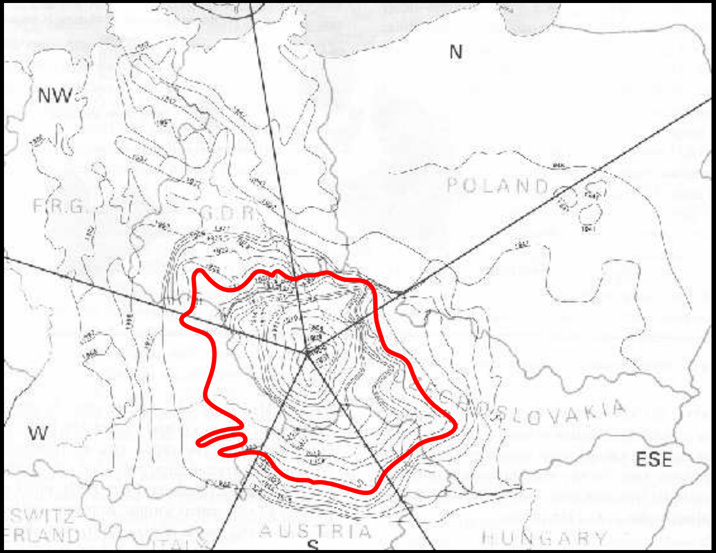
$$t = 1917$$

Spread of North American Muskrat



$$t = 1921$$

Spread of North American Muskrat



$$t = 1921$$

- Skellam's Model:
  - Individuals disperse and reproduce continuously
  - Movement is a random diffusion process
  - Population growth is Malthusian

Skellam's Model

$$\frac{\partial n}{\partial t} = D\left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2}\right) + r_0 n$$

where

- n is the population density
- D is the diffusion constant
- r_0 is the intrinsic rate of growth

Skellam's Model

$$\frac{\partial n}{\partial t} = D\left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2}\right) + r_0 n$$

ODE, exponential growth

where

- n is the population density
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Skellam's Model

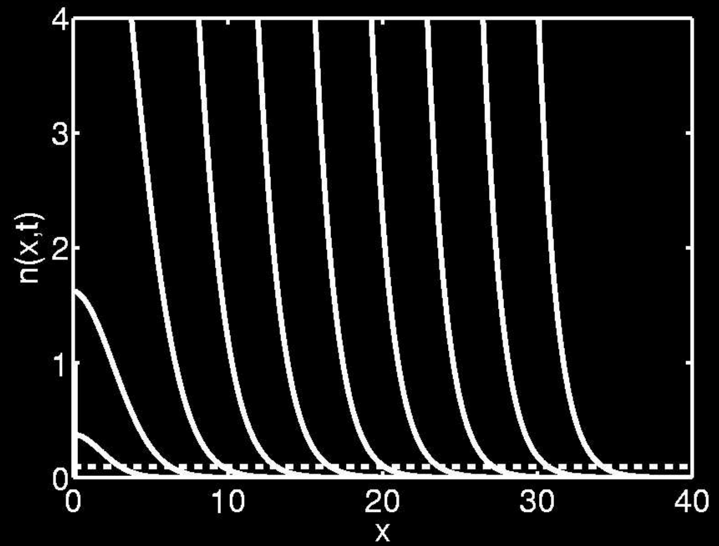
$$\frac{\partial n}{\partial t} = D\left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2}\right) + r_0 n$$

Spatial Movement (similar to heat flow)

where

- n is the population density
- D is the diffusion constant
- r_0 is the intrinsic rate of growth

Skellam Solution

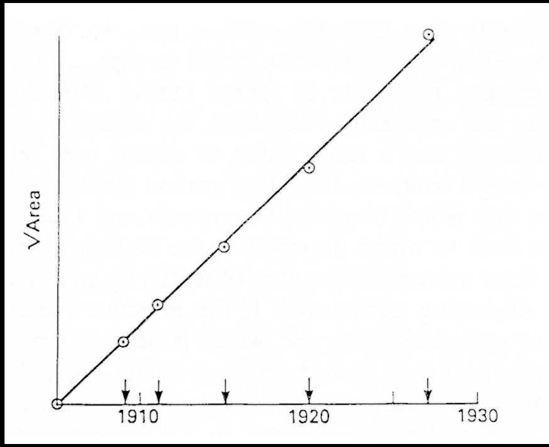


$$n(x,t) = \frac{n_0}{4\pi D t} \exp\{r_0 t - \frac{r^2}{4Dt}\}$$

where

- $n(x,0) = n_0 \delta(x)$
- $r^2 = x^2 + y^2$, radial distance

Skellam Analysis



- Predicted the area of invasion from the model

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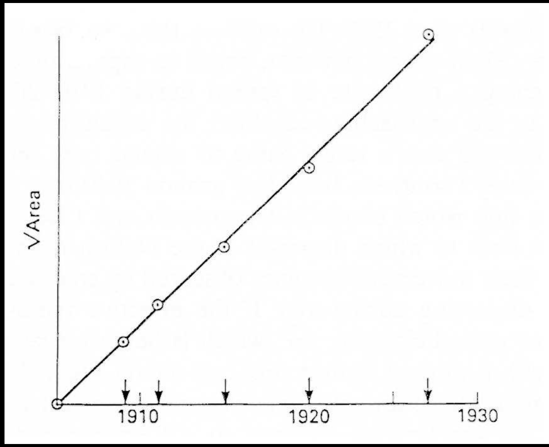

- Predicted the area of invasion from the model
- Estimated the area from the Ulbrich map

Skellam Model

- Growth and dispersal are continuous

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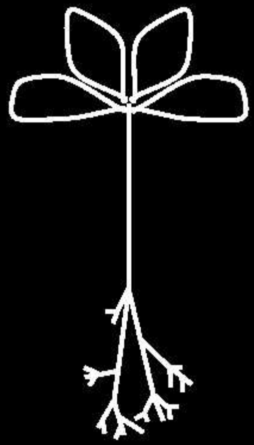
- Movement is a random diffusion process

Biological model: terrestrial plant species



- Infinite, one-dimensional environment

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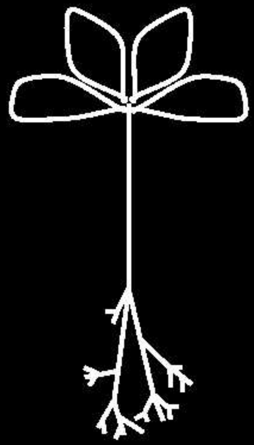

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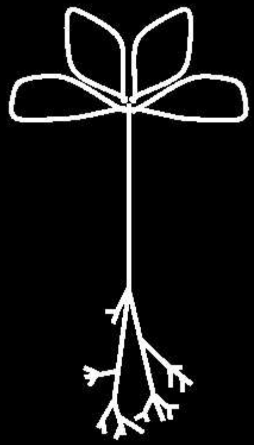


- Infinite, one-dimensional environment
- Assume that growth and dispersal occur in distinct, nonoverlapping stages
- Plant survival is limited to one cycle, with nonoverlapping generations

Mathematical model

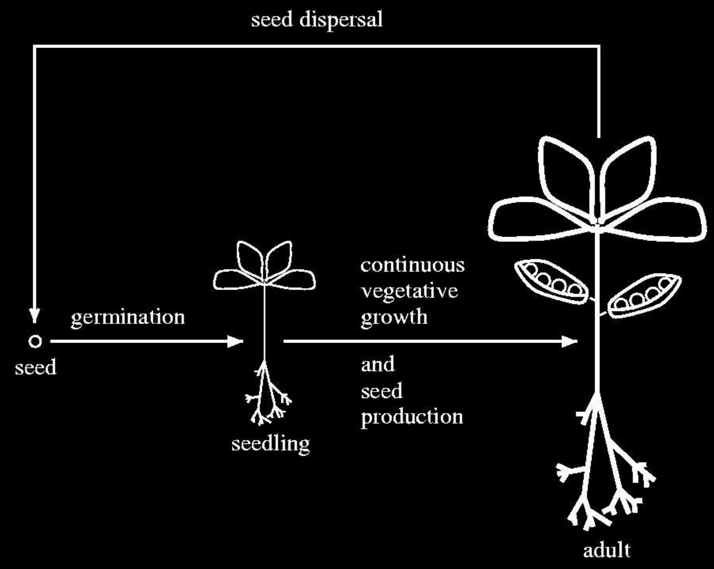
Integrodifference equation (IDE) model for the population density

$$N_{\tau+1}(x) = \int_{-\infty}^{+\infty} f(N_\tau(y); y) k(x, y) dy$$

where

- $N_\tau(x)$ is the population density
- f is the nonlinear growth function
- $k(x, y)$ dispersal kernel

Growth Function



$$N_{\tau+\frac{1}{2}}(x) = f(N_\tau(x); x)$$

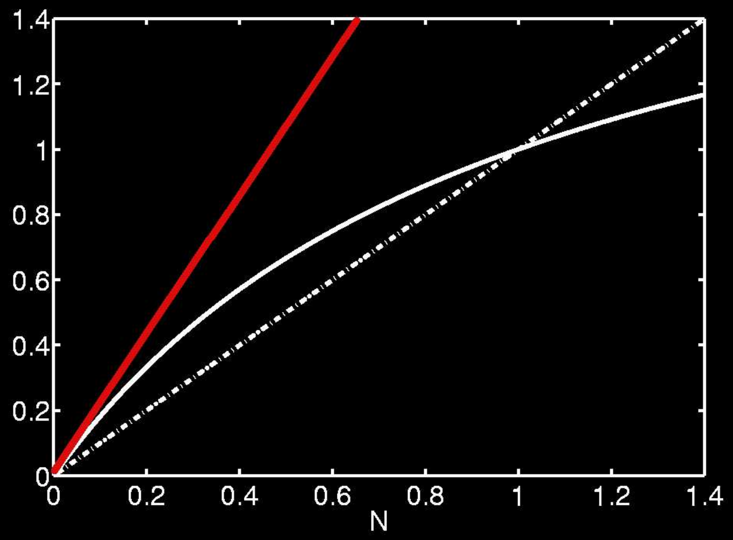
- $N_\tau(x)$ is the seed density at the start of generation τ
- $N_{\tau+\frac{1}{2}}(x)$ is the seed density at the end of generation τ before dispersal

Growth Function example

Beverton-Holt stock-recruitment curve

$$f(N) = \frac{r_0 N}{1 + [(r_0 - 1)N]}$$

where r_0 is the per capita reproductive ratio



$$r_0 = 2.0$$

Dispersal Kernel

- $k(x,y)$ is a pdf for a seed released from a location y being deposited at a location x

$$\int_{-\infty}^{+\infty} k(x,y)dx = 1$$

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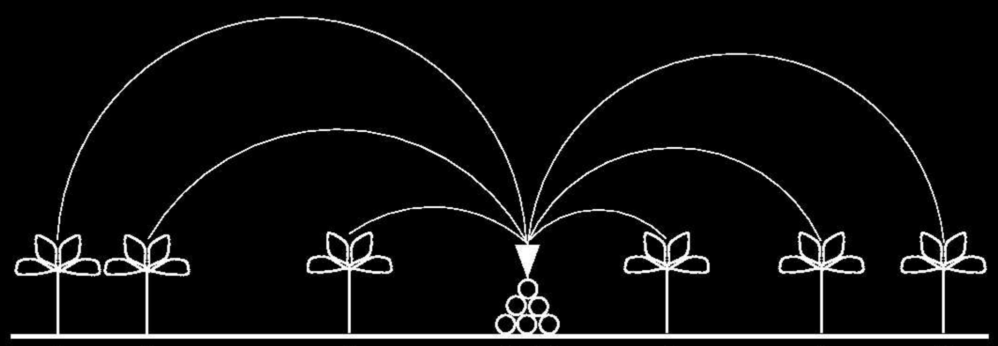
- The IDE is the sum of all seeds dispersed to x

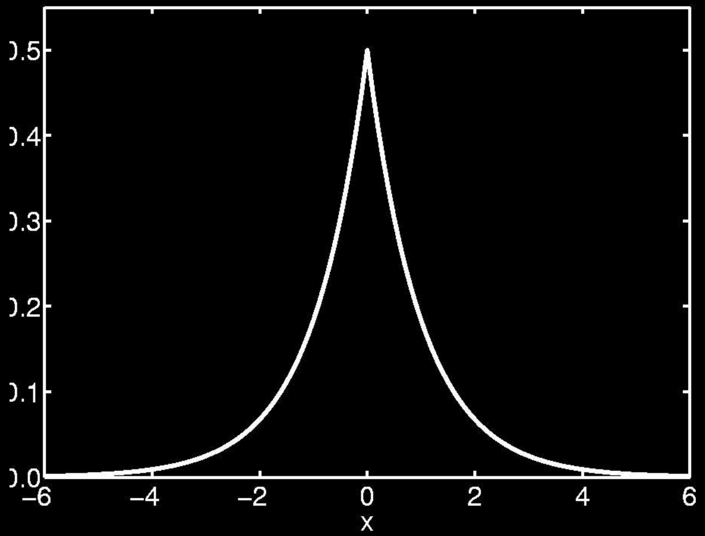
$$\int_{-\infty}^{+\infty} N_{\tau+\frac{1}{2}}(y)k(x, y)dy$$



Laplace Dispersal Kernel

The dispersal kernel is given by the Laplace distribution

$$k(x-y) = \sqrt{\frac{a}{4D}} \exp\left\{ -\sqrt{\frac{a}{D}} |x-y| \right\}$$



$D = 1$ and $a = 1$

Homogeneous Environment

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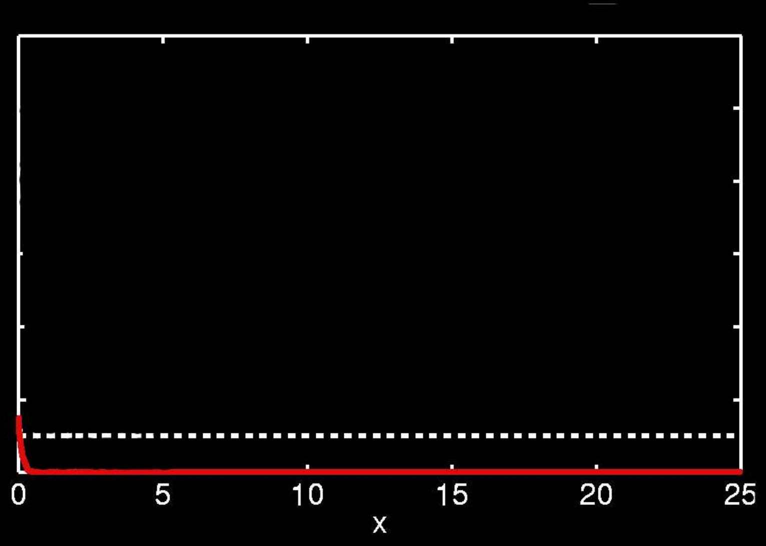
- The IDE model reduces to the convolution integral

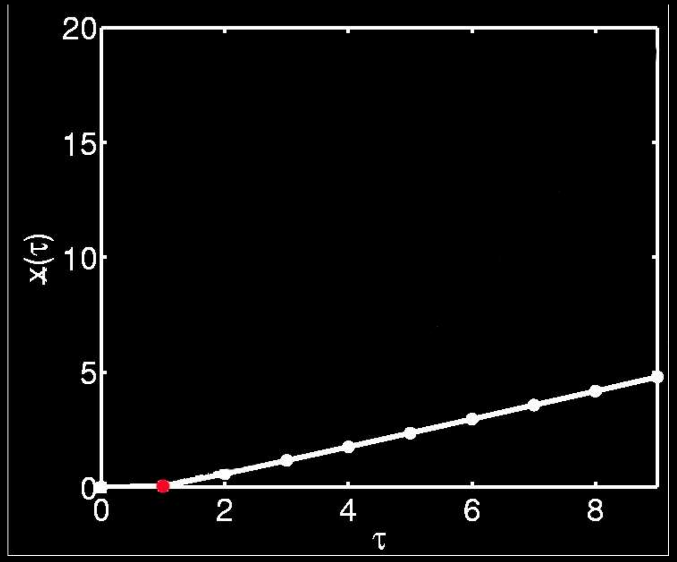
$$N_{\tau+1}(x) = \int_{-\infty}^{+\infty} f(N_\tau(y))k(x-y)dy$$

Traveling Wave Solution

The solution of the IDE approaches a traveling wave (TW) for the initial population density

$$N_0(x) = \delta(x)$$





$r_0 = 6$, $D = 1$ and $a = 10$

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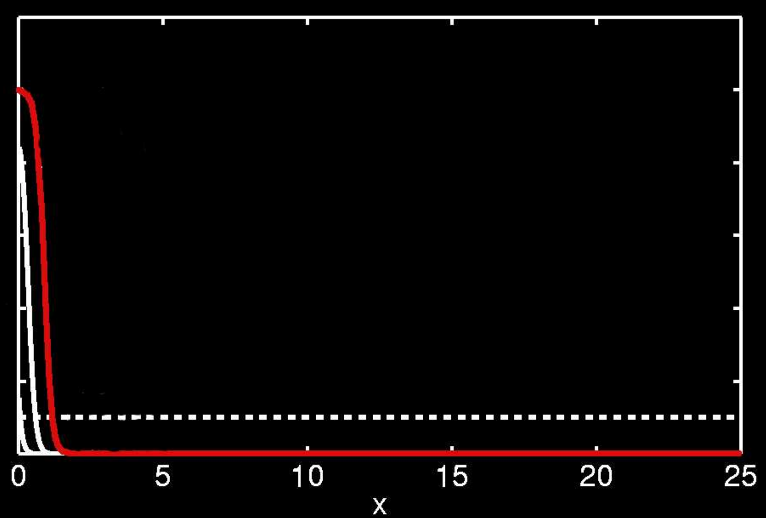

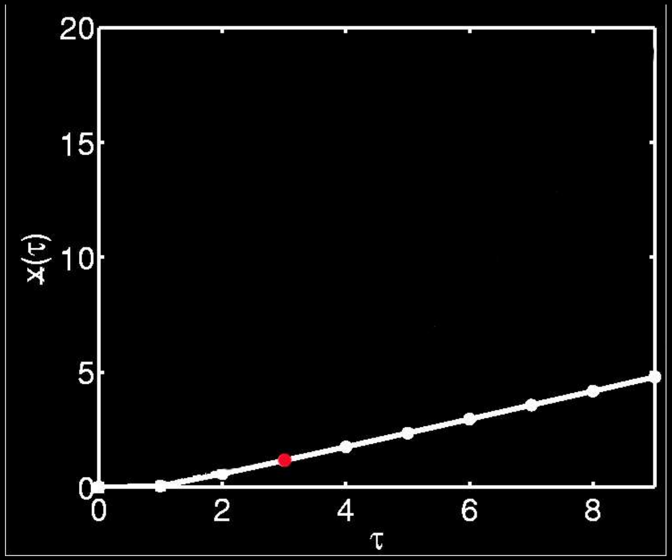

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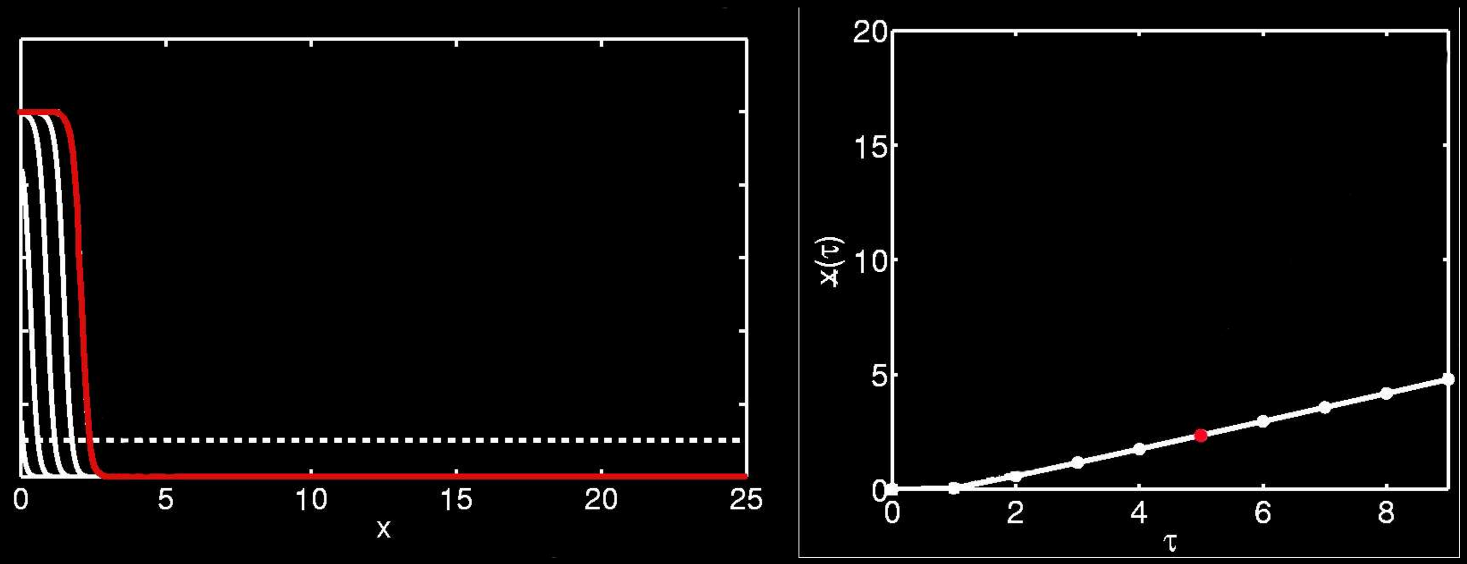

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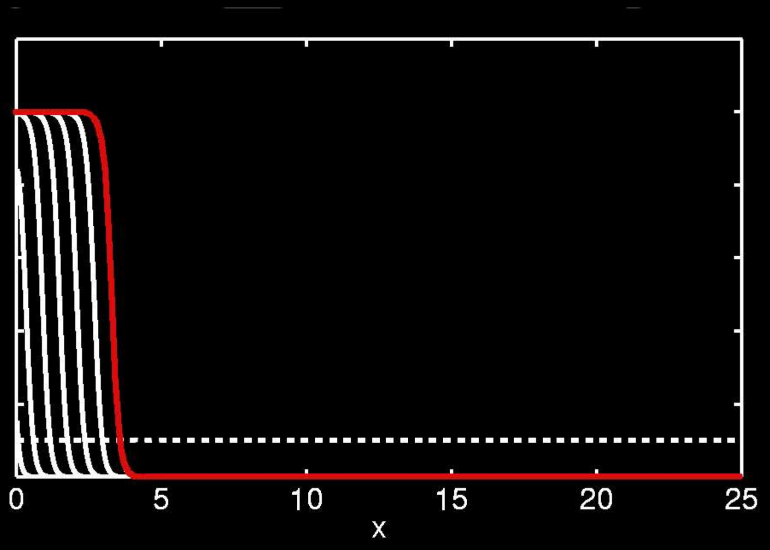

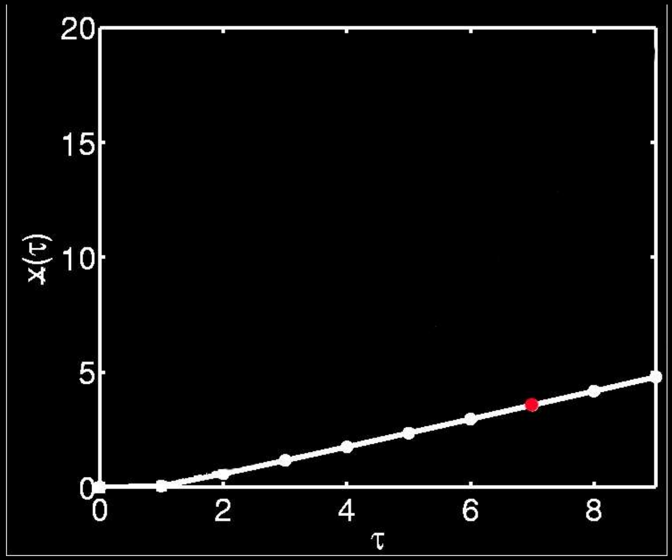

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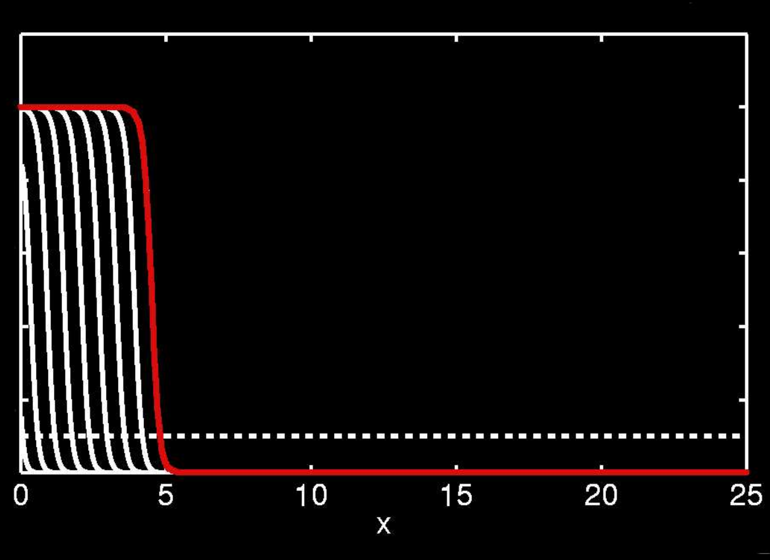

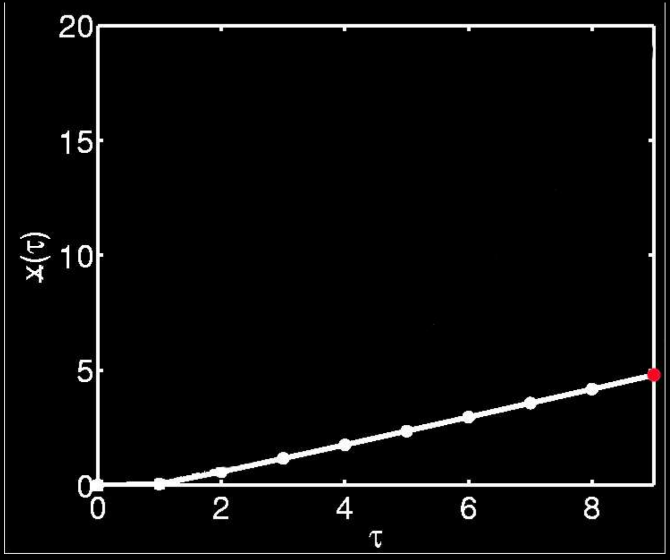

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- The asymptotic rate of spread is given by

$$c^* = \min_{0<s} \left[\frac{1}{s} \ln \left(r_0 U(s) \right) \right]$$

[Weinberger - 1982]

Dispersion Relation

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- TW ansatz: near the leading edge of the wave

$$N_\tau(x) \propto e^{-sx}$$

  for $s > 0$.

Dispersion Relation

- From this assumption

$$e^{-sx}e^{sc} = r_0 \int_{-\infty}^{+\infty} k(x-y)e^{-sy}dy.$$

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- Solving for c as a function of s

$$c(s) = \frac{1}{s}\ln\left(r_0 U(s)\right).$$

[Kot *et al*. - 1996]

Laplace Kernel Dispersion Relation

- The moment generating function

$$U(s) = \int_{-\infty}^{+\infty} \sqrt{\frac{a}{4D}} \exp\left\{-\sqrt{\frac{a}{D}}|u|\right\} e^{su} du = \frac{a}{D}\left[\frac{1}{a/D - s^2}\right]$$

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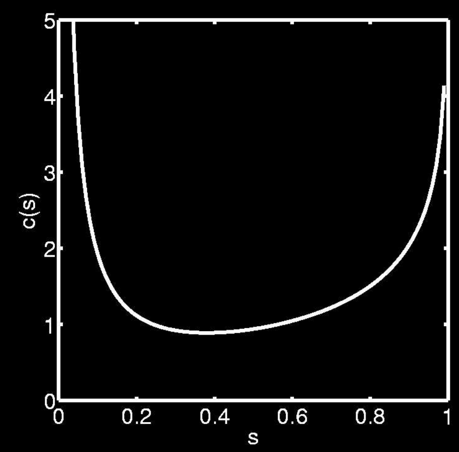
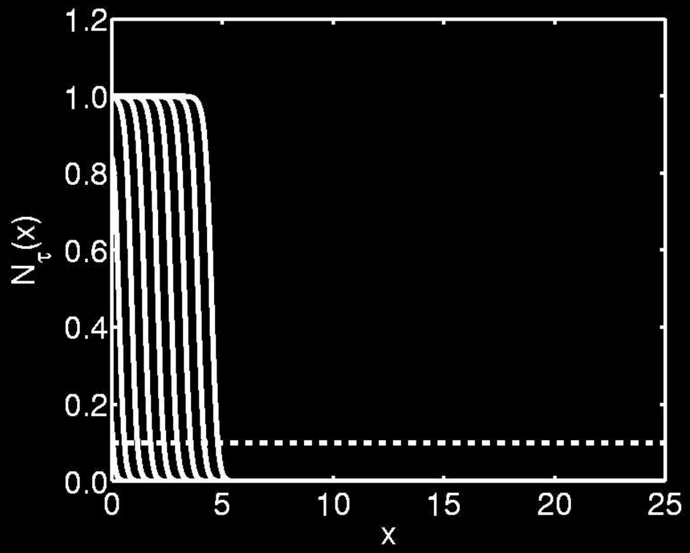
- The dispersion relation

$$c(s) = \frac{1}{s} \ln\left\{r_0 \frac{a}{D}\left[\frac{1}{a/D - s^2}\right]\right\}$$



Laplace Kernel Traveling Wave



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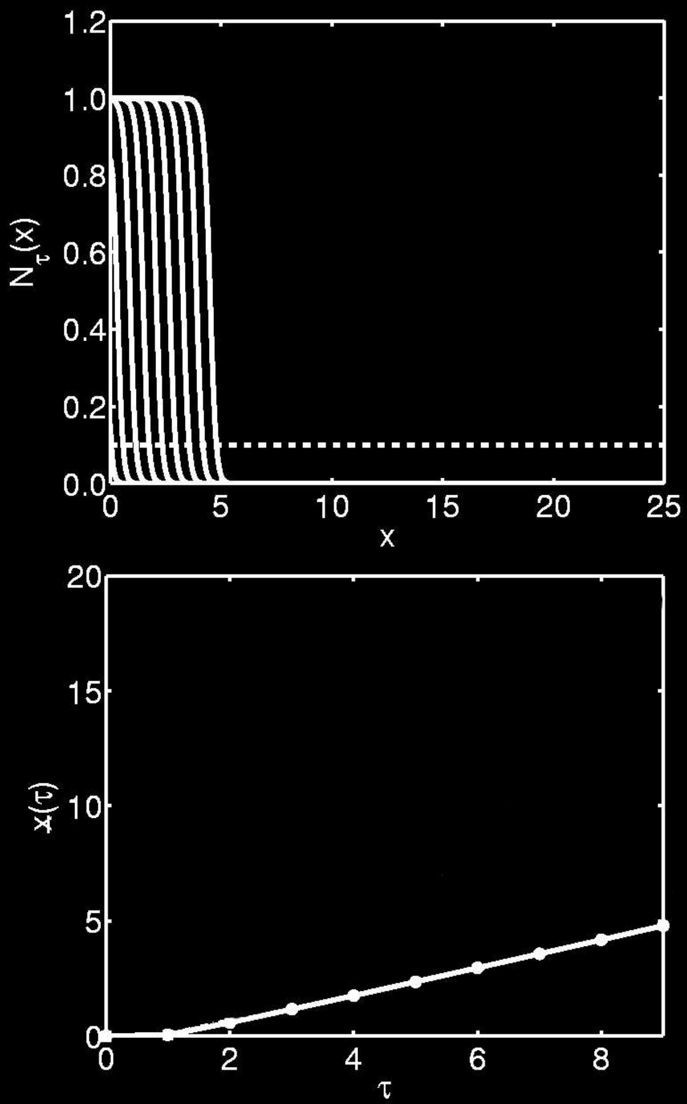
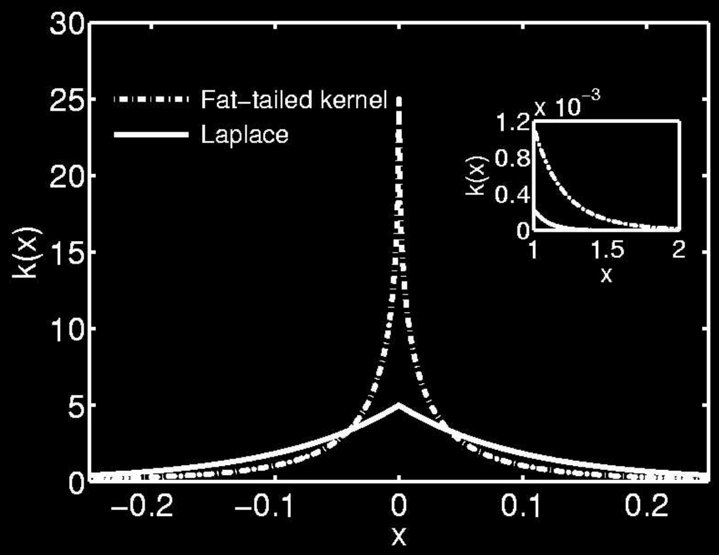


Fat-tail vs. Laplace Kernel



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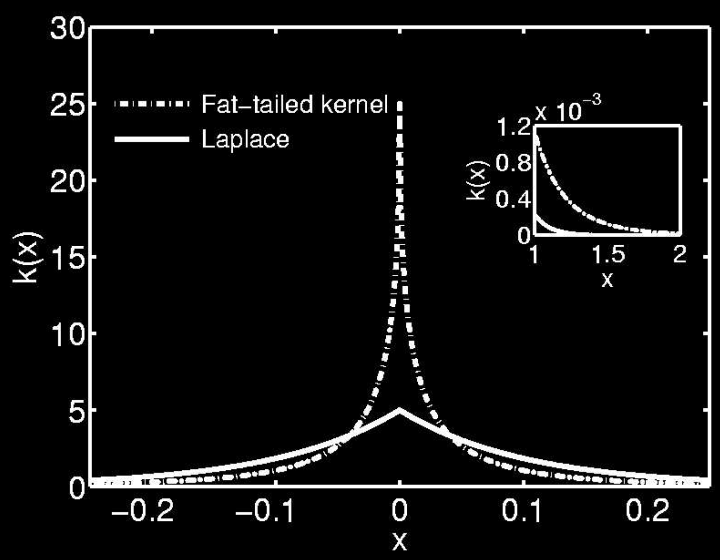

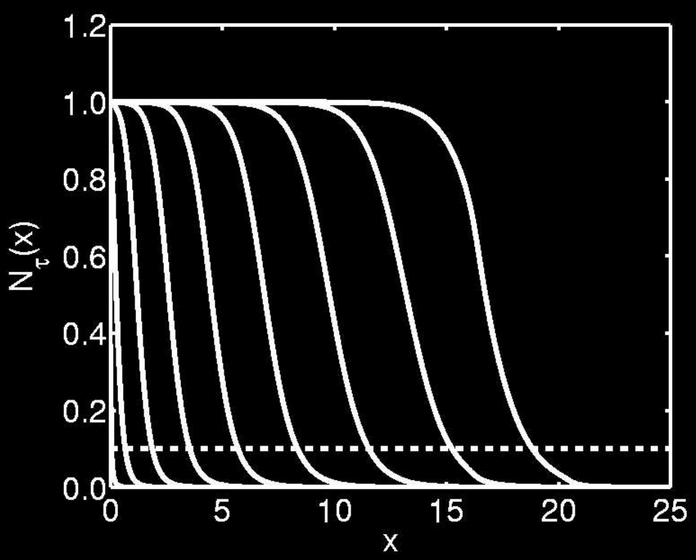

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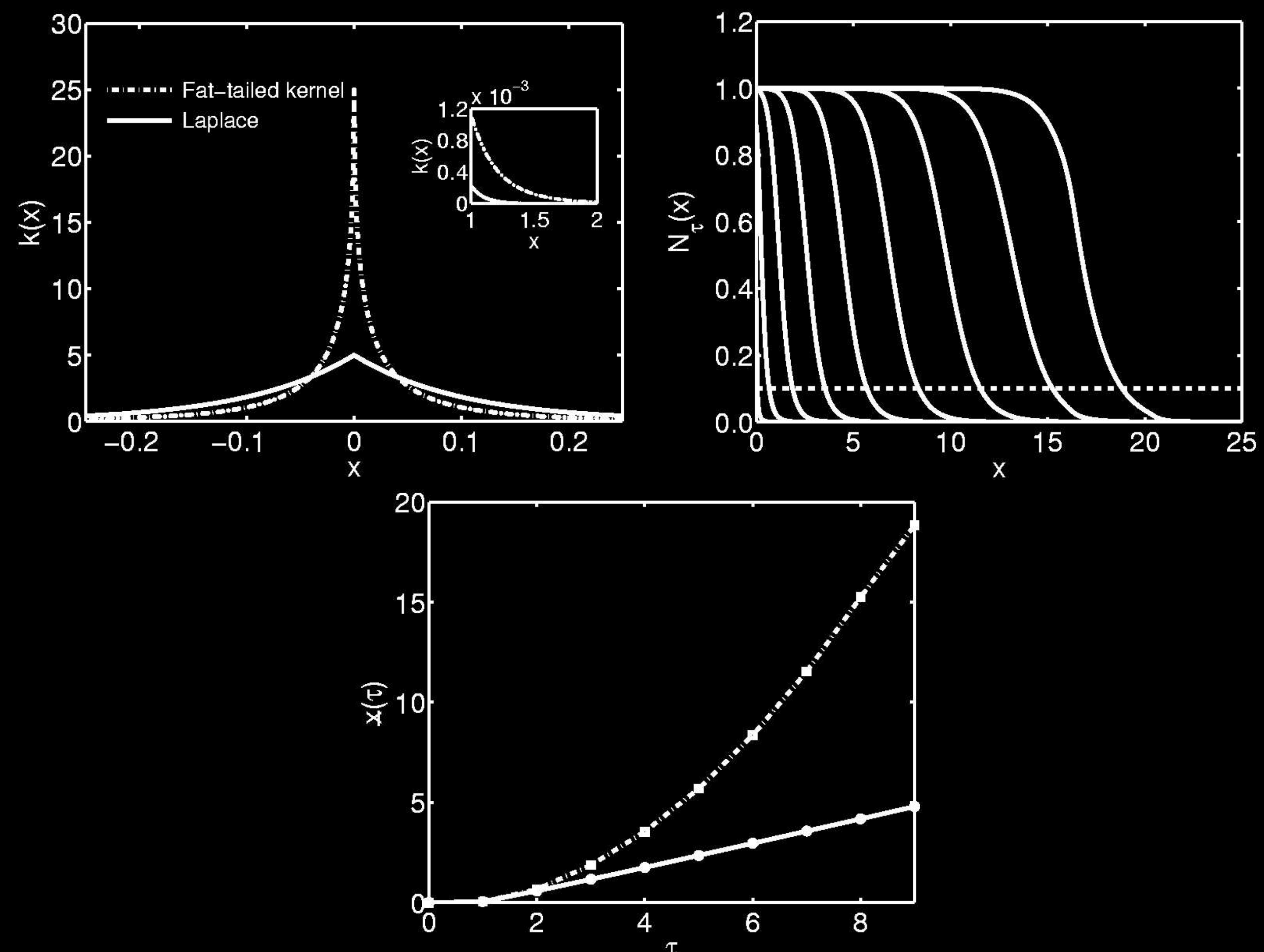

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