# Spatial Ecology:
## Lecture 4, Integrodifference equations

II Southern-Summer school on Mathematical Biology

# Integrodifference equations

- Diffusion models assume growth and dispersal occur at the same time.
- When reproduction and dispersal occur at discrete intervals an integrodifference equation is a more relevant formulation. E.g.
  - annual plants,
  - Many insects,
  - Migrating bird species

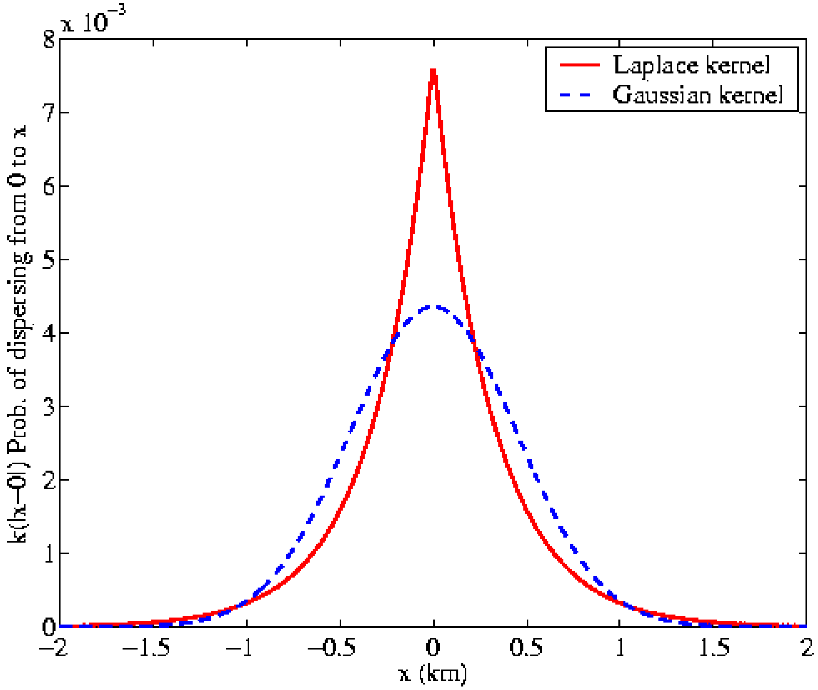
# Integrodifference equation

$N_t$ → Dynamics → $N_{t+\tau}$ → Dispersal → $N_{t+1}$

One generation (e.g.1 year)

The model:

$$N_{t+1}(x) = \int_{-\infty}^{\infty} \underbrace{K(x,y)}_{\text{Prob. of dispersing from y to x}} \underbrace{N_{t+\tau}(y)}_{\text{Dynamics}} dy$$



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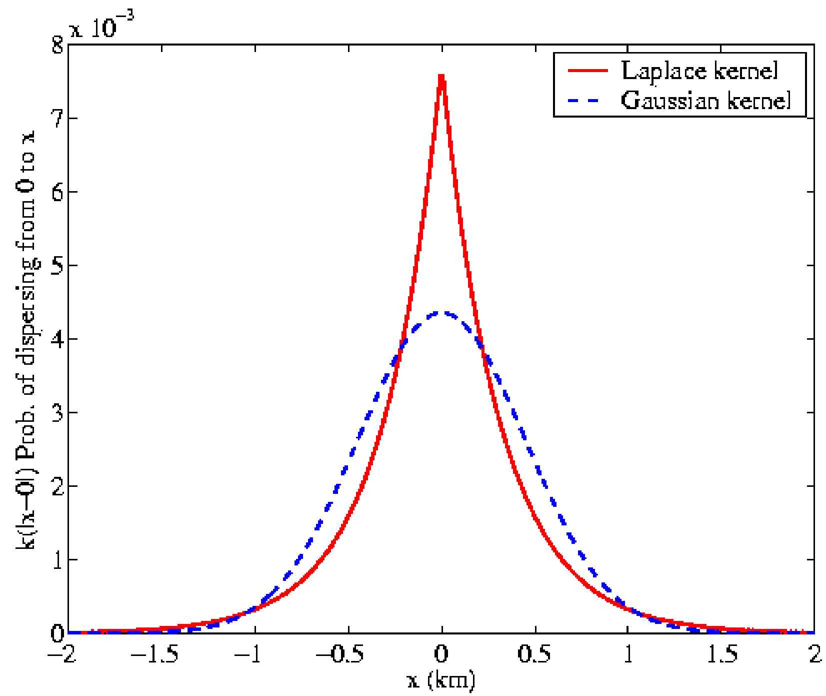



Dynamics $N_{t+\tau}(y) = f(N_t(y))$

Kernels k(x,y)=k(x-y) when dispersal depends on distance only

# Mechanistic derivation of dispersal kernels

$$u_t = Du_{xx} - \underbrace{a(t)}_{\text{Settling rate}} u, \qquad u(0,x) = \delta(x)$$

$$k(x) = \underbrace{\int_0^\infty a(t)u(x,t)dt}_{\text{Total settled}}$$

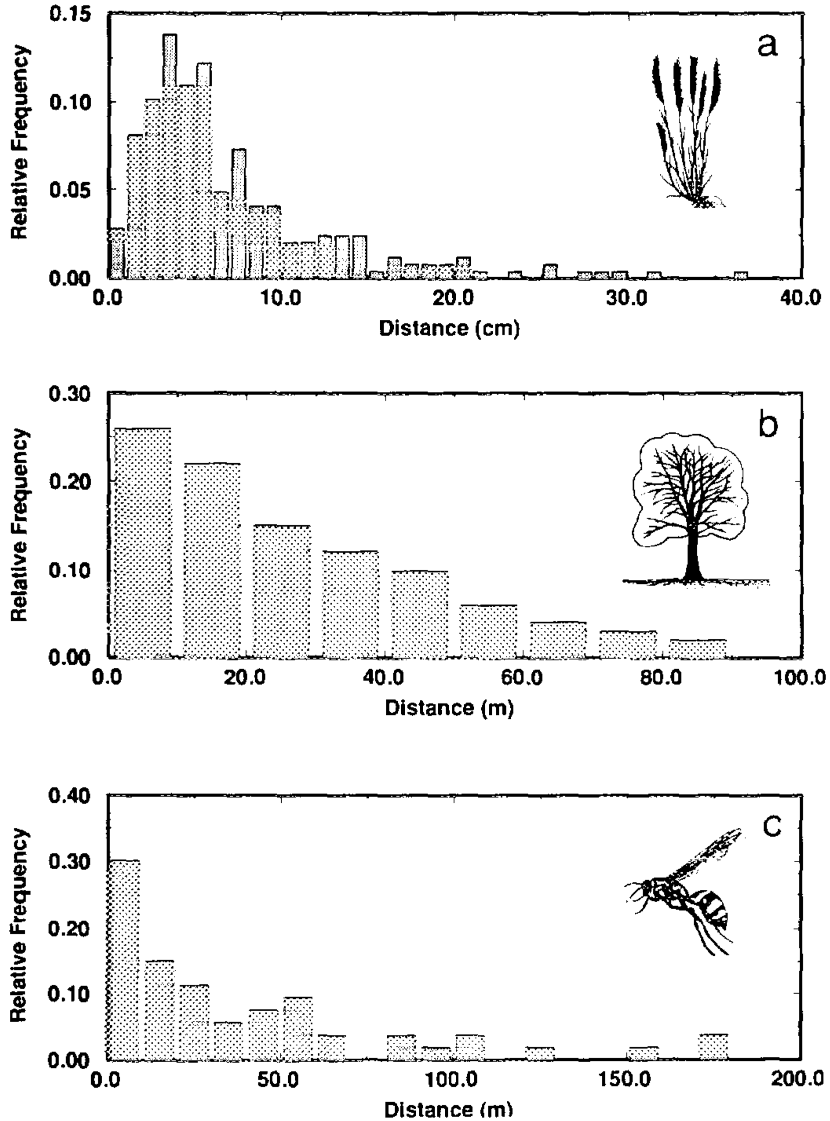
- Gaussian: a(t)=δ(t-T), stops at time T

$$k_G(x) = \frac{1}{\sqrt{4\pi DT}} \exp\left(-\frac{x^2}{4DT}\right)$$

- Laplacian: a(t)=a>0, constant settling rate

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

# Dispersal kernels from data



# Travelling wave speeds

- **Assume**
  - f is linearly bounded, f(N)<=f'(0)N (*No Allee effect*)
  - f is monotone
  - K(x) has a moment generating function (*no 'fat-tailed dispersal kernels*)
- Then we can linearly determine the asymptotic wave speed.
  - Look at behaviour near $N^*=0$ (linearise there)

$$N_{t+1}(x) = \int_{-\infty}^{+\infty} K(x,y) f(N_t(y)) dy \longrightarrow \boxed{N_{t+1}(x) = f'(0)\int_{-\infty}^{+\infty} K(x,y) N_t(y) dy}$$

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- Look for solutions at the edge of the travelling wave which decay exponentially, so $N_t(x) = \exp(-sx)$

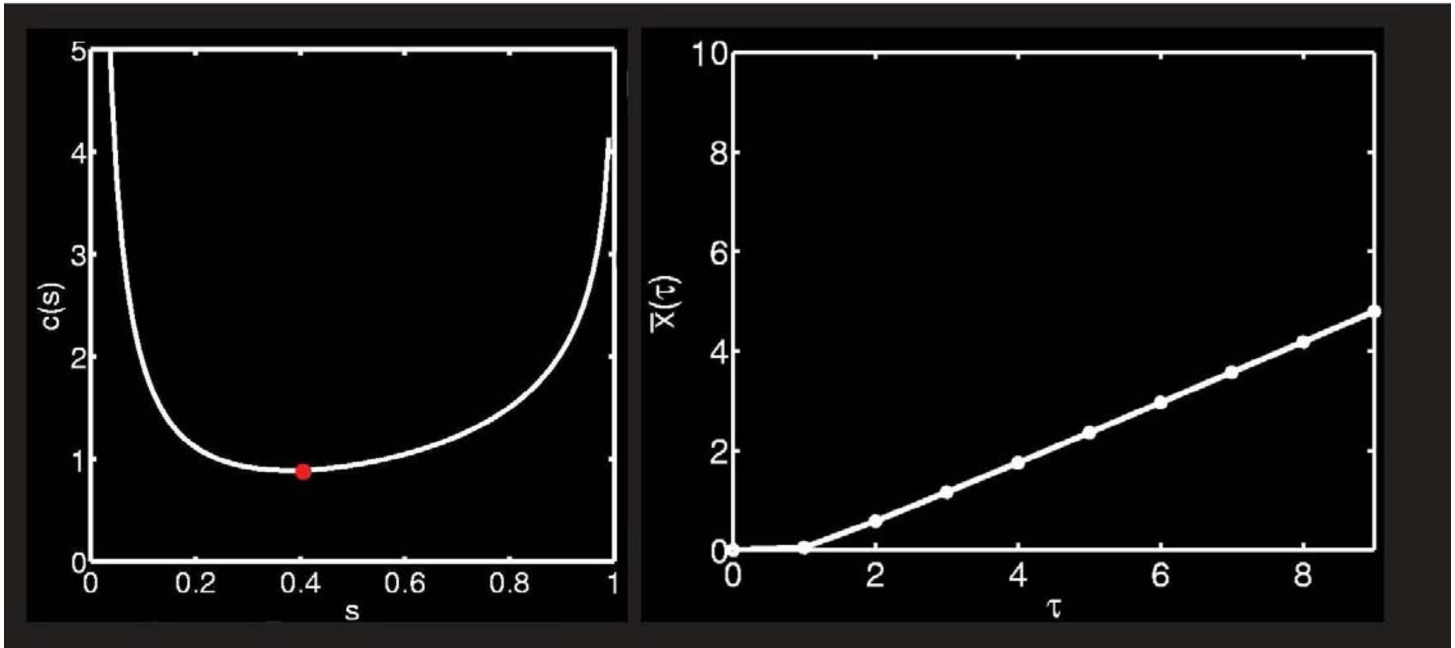
$$\exp(sc) = f'(0)\int_{-\infty}^{+\infty} K(y)\exp(sy)dy = f'(0)M(s)$$

- M(s) is the moment generating function for k(y)

# Asymptotic wave speed

- Differentiating with respect to s, and noting that initial conditions with compact support lead to a minimum speed give c*

$$c^* = \min_s \left\{ \frac{1}{s} \ln\left[ M(s) f'(0) \right] \right\}$$



# Examples of wave speeds

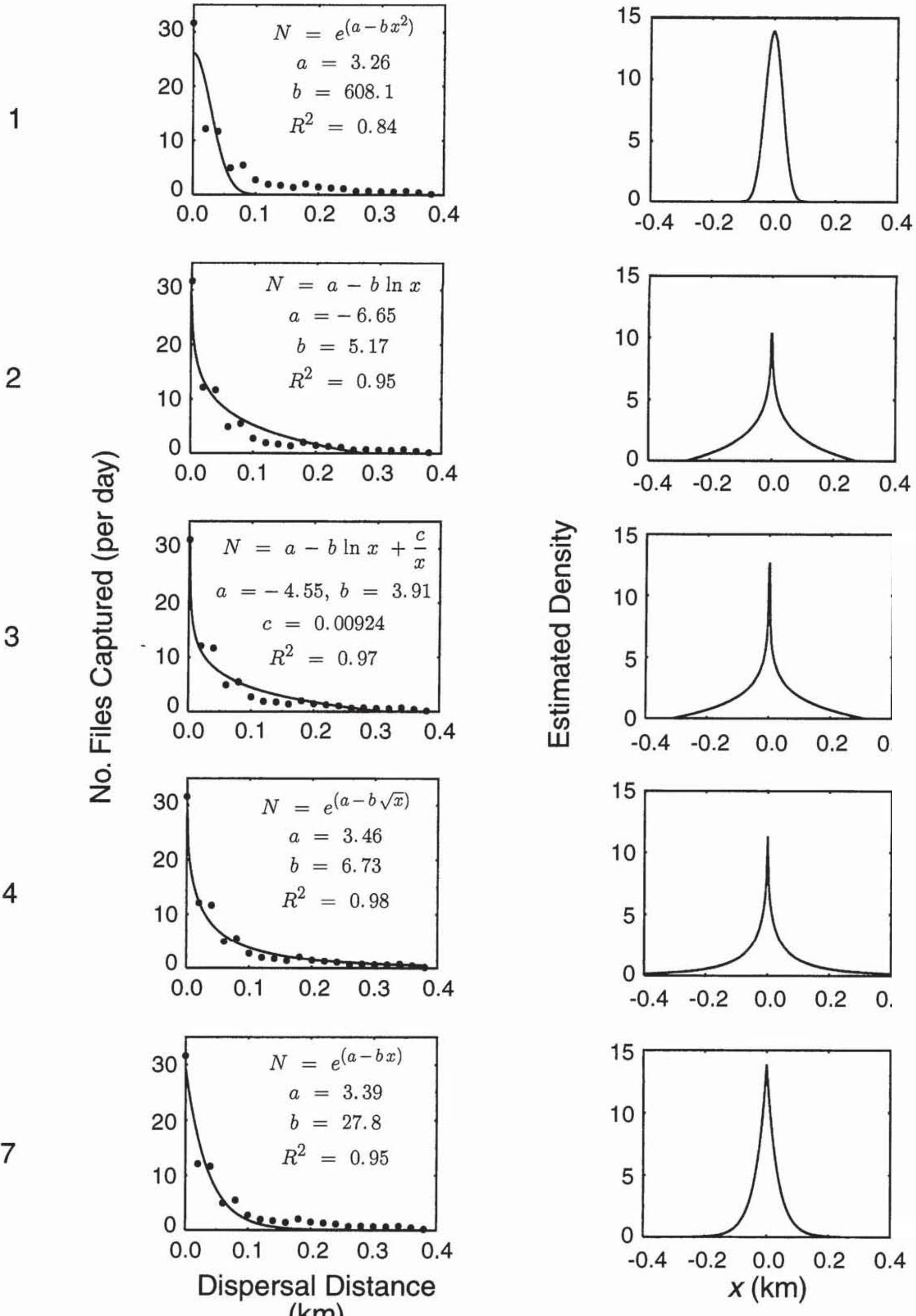
- Gaussian

$$M_G(s) = \exp(\sigma^2 s^2 / 2), \quad \text{where } \sigma^2 = 2D \qquad c = \sigma^2 \sqrt{2 \ln f'(0)}$$

  - Note if r=ln f'(0) and D=$\sigma^2$/2 then the wave speed is the same as the PDE case: $c = 2\sqrt{Dr}$
- Laplacian

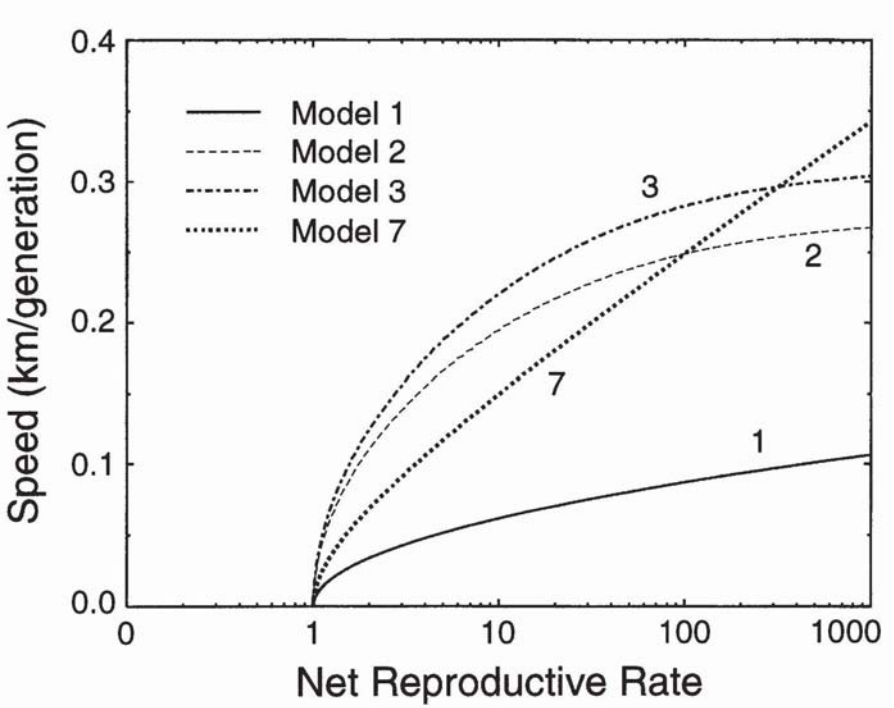
$$M_L(s) = \frac{1}{1 - \sigma^2 s^2 / 2}, \quad \text{where } \sigma^2 = 2D / a$$

- We can't find c explicitly, but since $M_L(s) >= M_G(s)$ then $c_{Laplace} > c_{Gaussian}$

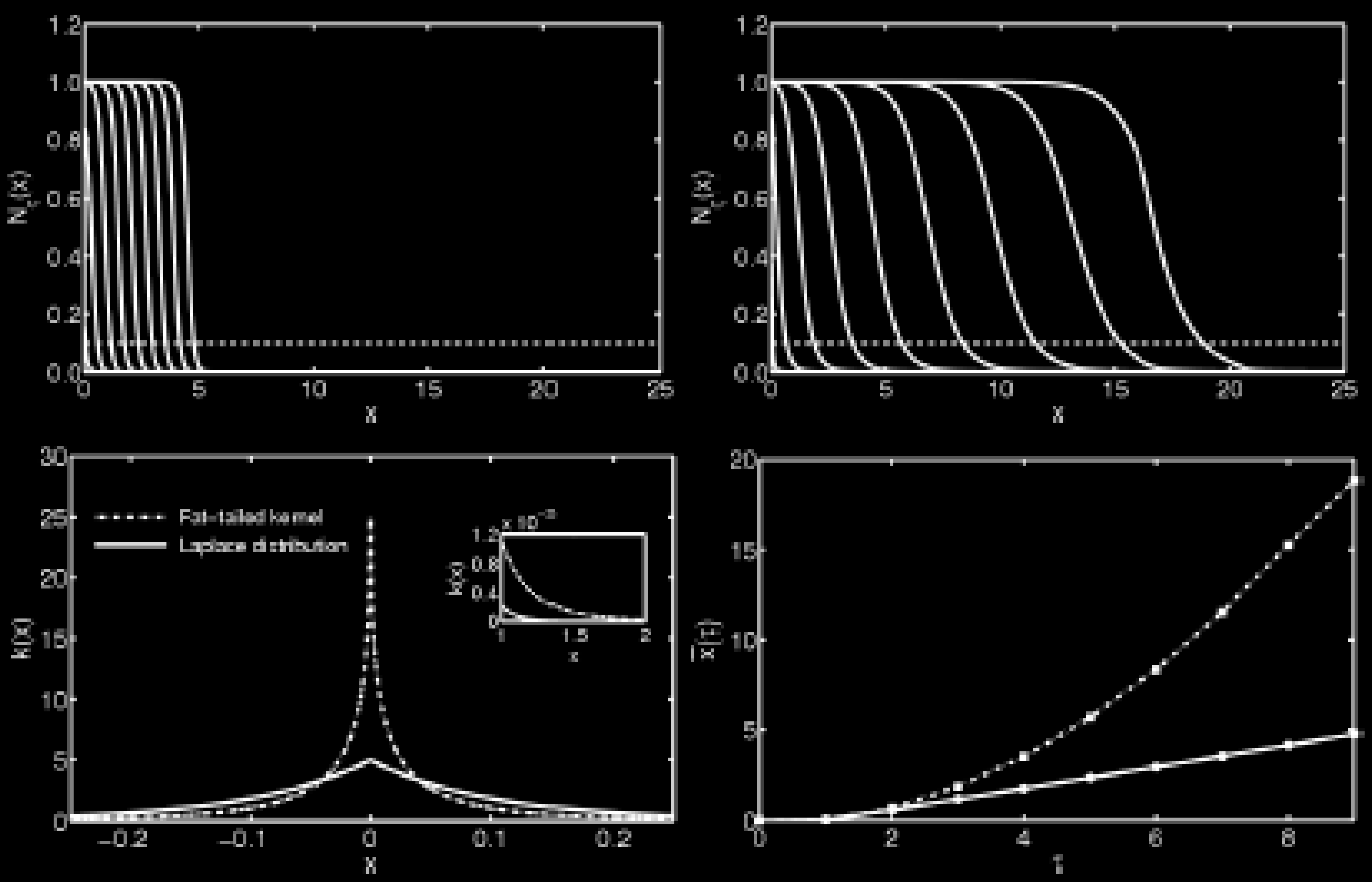




Shape of the kernel greatly affects speed.



# Fat tailed kernels



# Spatial extent

- Fat tailed kernels can give accelerating waves, we can't calculate the speed, but we can measure the spatial extent of the wave at a given time.
  - Spatial extent= distance from source where population first falls below a threshold N.

$$N_{t+1}(x) = f'(0)\int_{-\infty}^{+\infty} K(x,y)N_t(y)dy, \quad N_0(x) = N_0\delta(x)$$

- Use Fourier Transforms

$$\hat{N}_t(w) = \int_{-\infty}^{\infty} N_t(x)e^{iwx}dx, \quad N_t(x) = \int_{-\infty}^{\infty} \hat{N}_t(w)e^{iwx}dw$$

Hence, $\hat{N}_t(w) = (f'(0))^t(\hat{k}(w))^t N_0$

# Spatial extent

- In the case of the Cauchy Kernel:

$$k(x) = \frac{\beta}{\pi(\beta^2 + x^2)}, \qquad \hat{k}(w) = \exp(-\beta\,|\,w\,|)$$

- Its easy to find the inverse of the Fourier transform in this case so

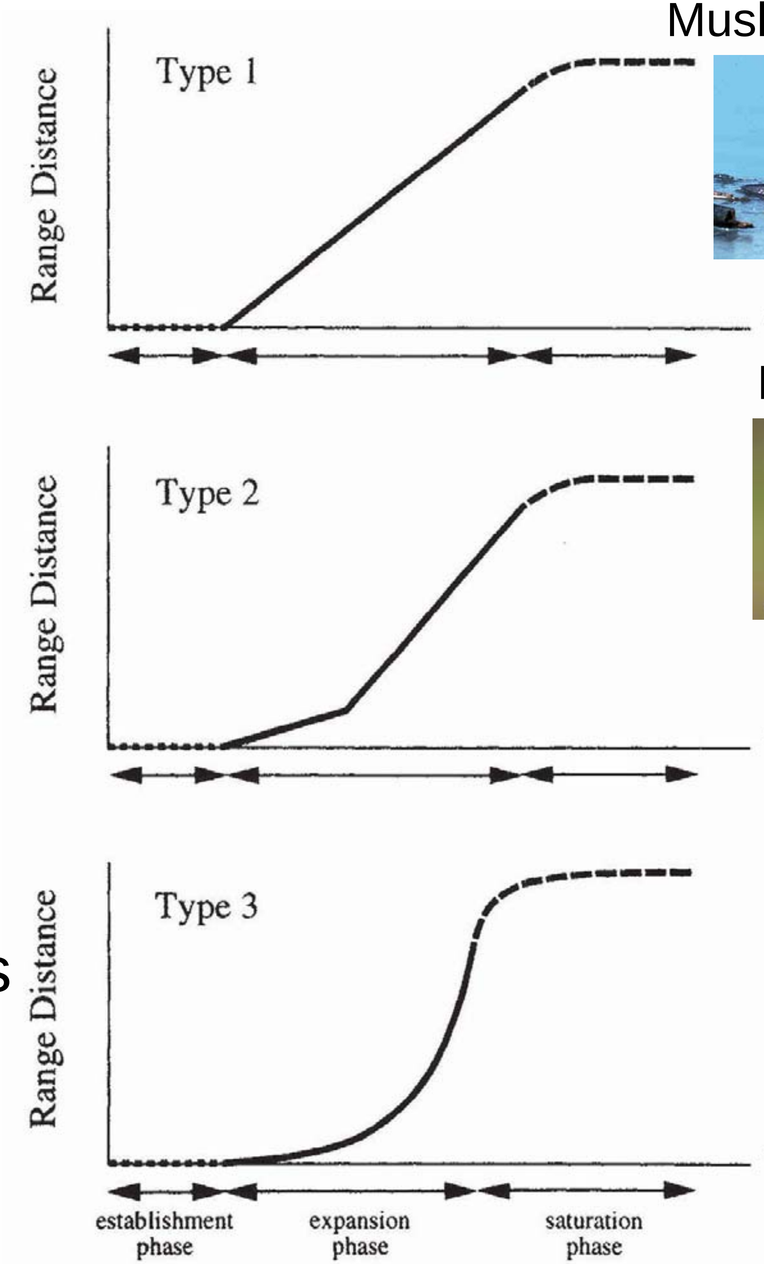
$$N_t(x) = \frac{N_0 R^t}{\pi} \frac{\beta t}{(\beta t)^2 + x^2}, \qquad x_f(t) = \sqrt{\frac{\beta t N_0 R^t}{\pi N} - (\beta t)^2}$$

- More generally

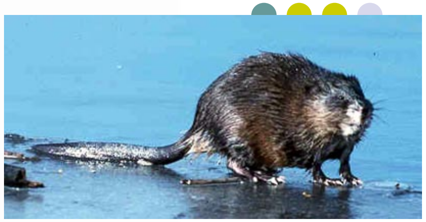
$$N_t(x) \approx N_0 R^t k(x), \qquad x_f(t) = k^{-1}\left(\frac{N}{N_0 R^t}\right), \qquad \text{provided } |x| >> 1$$

# Population spread and invasion

- Linear expansion with time
- Slow initial spread followed be linear expansion *(e.g.Allee effects)*
- Spread rate continually increases with time *(e.g long distance dispersal)*



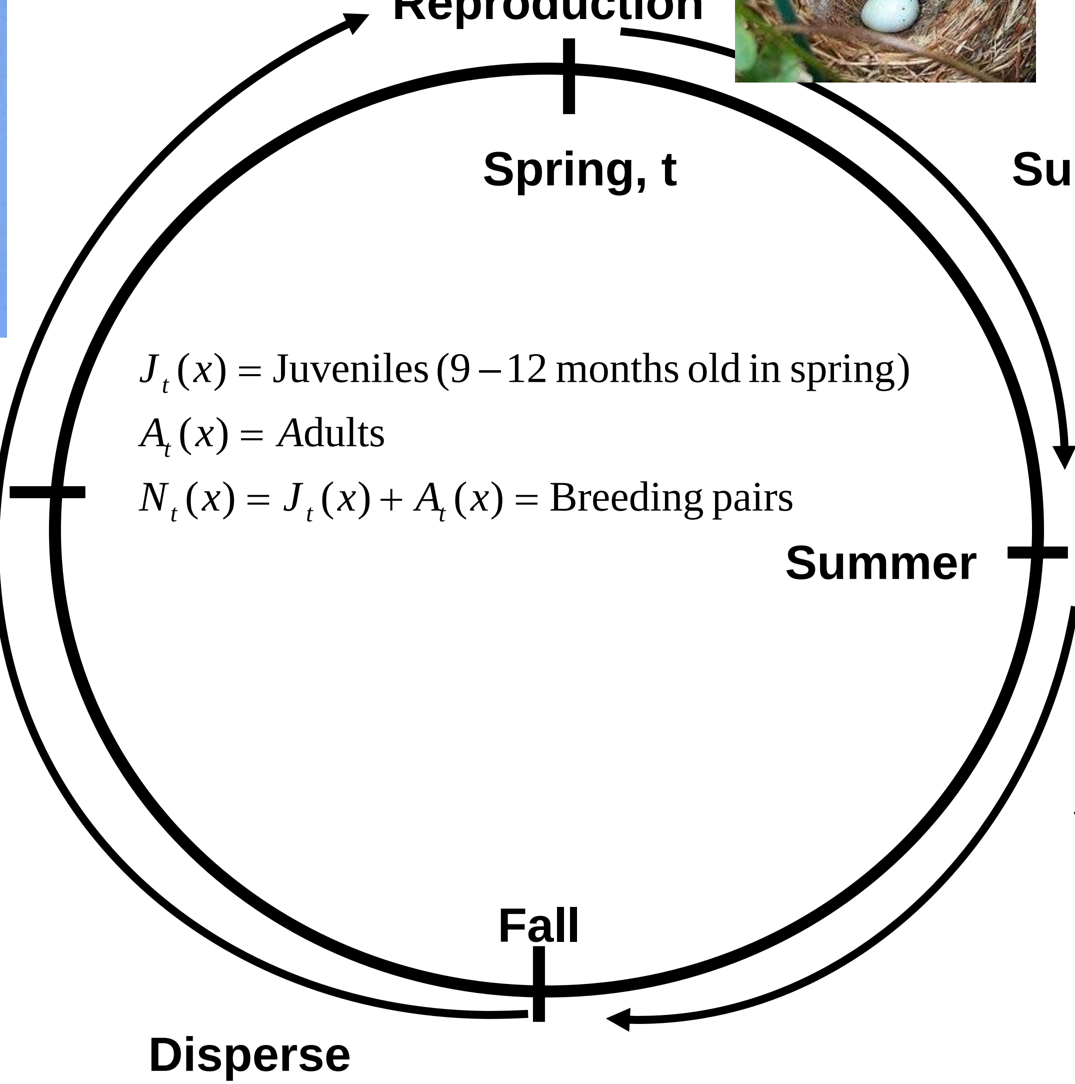

Muskrat



House finch

Cheat grass

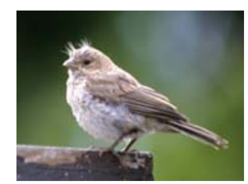
# House finch model




$$J_t(x) = \text{Juveniles (9} - \text{12 months old in spring)}$$

$$A_t(x) = \text{Adults}$$

$$N_t(x) = J_t(x) + A_t(x) = \text{Breeding pairs}$$

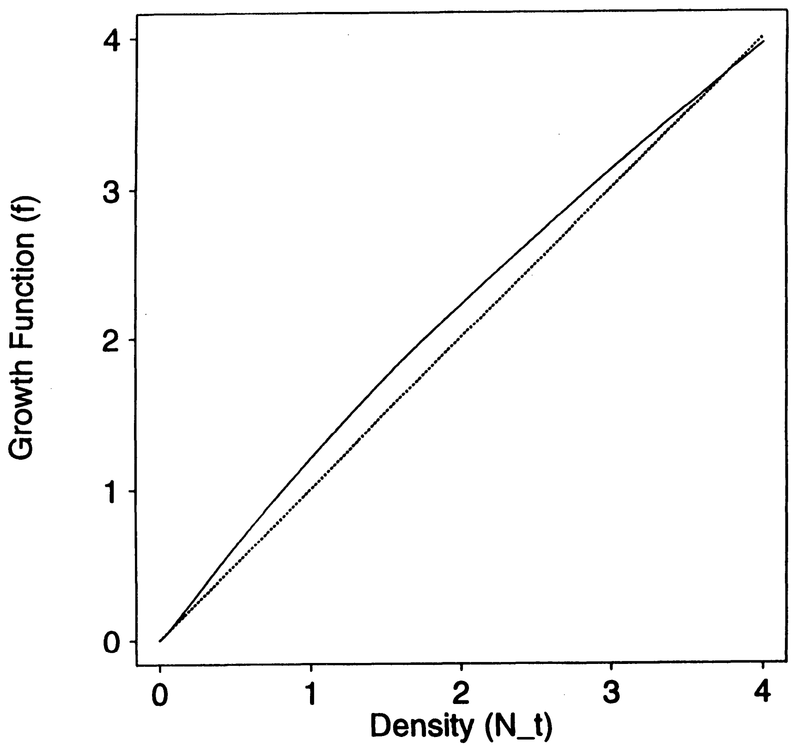


# Reproduction

- Average number of offspring produced

$$f(N_t) = \frac{cN_t^2}{4/(\sigma T) + 2N_t + N_t^2/\delta}$$

- Competition for nesting sites
- C= average number of offspring born that survive summer
- σ, rate or pair formation
- T, Time for pair formation
- δ, density of nest sites




Allee efffect!

# Dispersal

$$J_{t+1}(x) = \underbrace{(1-p_J)f(N_t)}_{\text{Non-dispersing juveniles}} + \underbrace{p_J\int_{-\infty}^{+\infty}K_J(y-x)f(N_t(y))dy}_{\text{Dispersing juveniles}}$$

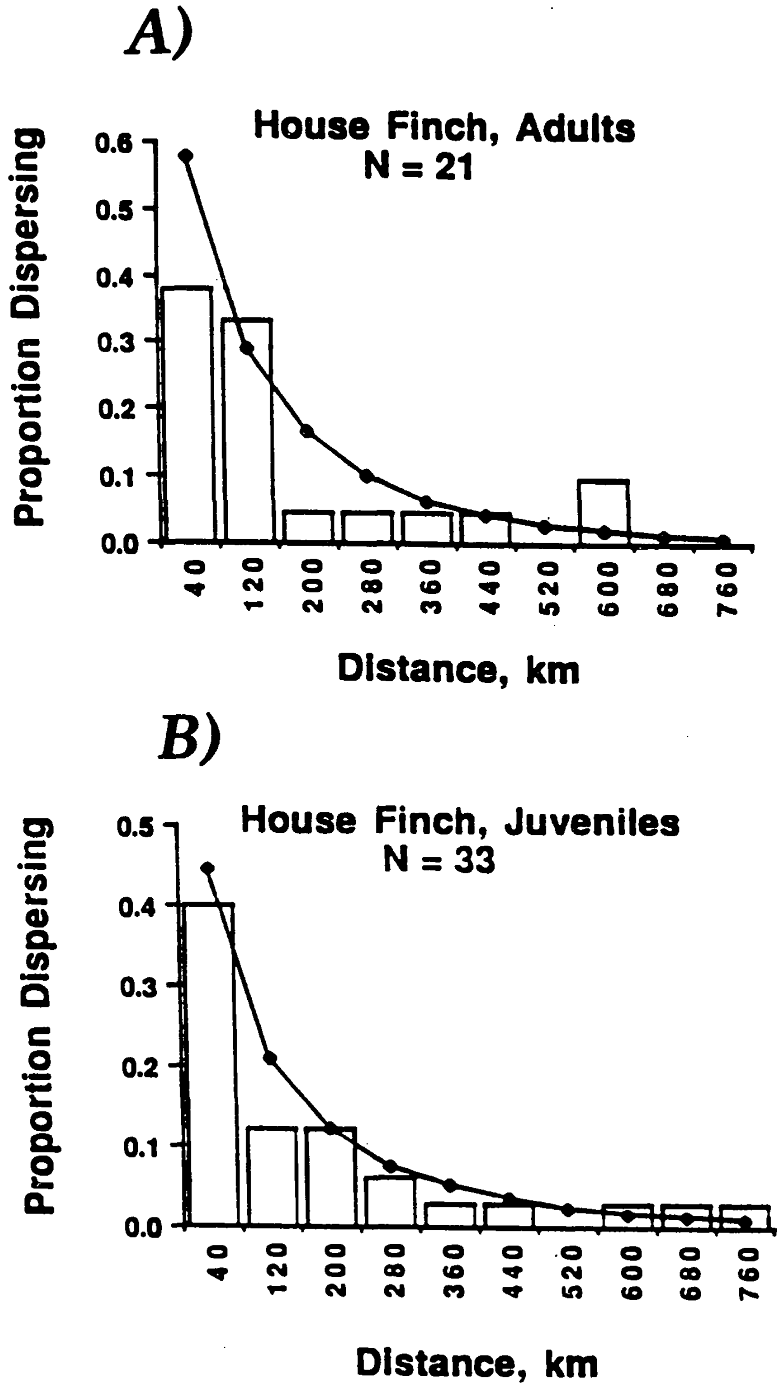

$$A_{t+1}(x) = \underbrace{s(1-p_A)f(N_t)}_{\text{Non-dispersing Adults which survive}} + \underbrace{p_A\int_{-\infty}^{+\infty}K_A(y-x)N_t(y)dy}_{\text{Dispersing adults}}$$

Add the equations together to get an equation for breeders

$$N_{t+1}(x) = (1-p_J)f(N_t) + s(1-p_A)f(N_t) + \int_{-\infty}^{+\infty}K_J(y-x)p_J f(N_t(y))dy + p_A\int_{-\infty}^{+\infty}K_A(y-x)N_t(y)dy$$

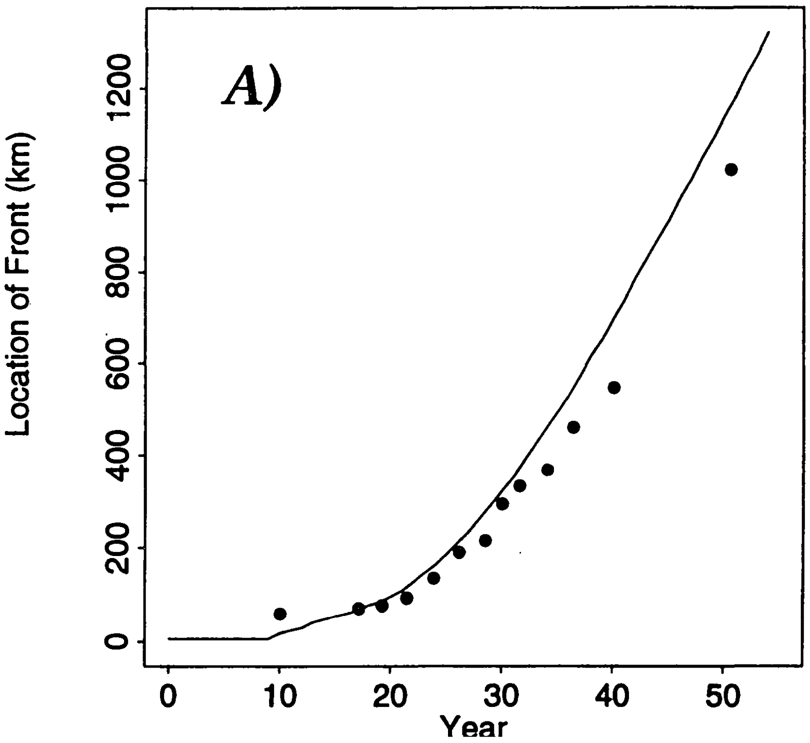
Expected density of birds
at the Christmas Bird Counts
in successive years

- Dispersal kernels



# Results: Range expansion

- Slow initial spread followed be linear expansion



# Invasion summary

- Shape of the kernel significantly affects speed.
- Travelling waves may exhibit accelerating spread if the dispersal kernels have ‘fat tails’ (not expontenially bounded)
- Populations escaping an Allee effect may termporally accelerate before achieving a constant speed

# References


- M. Kot, M.A. Lewis, P van den Driessche. (1996) Dispersal data and the spread of invading organisms, Ecology 77:2027-2042
- J.A.Powell,(2009)Spatiotemporal Models in Ecology:An Introduction to Integro-Difference Equations http://www.math.usu.edu/powell/wauclass/labs.html
- Neubert, M.G., M. Kot and M.A. Lewis, 1995. Dispersal and pattern formation in a discrete-time predator-prey model. *Theoretical Population Biology* 48: 7–43.
- R.R. Veit, M.A. Lewis(1996) Dispersal population growth and the Allee effect: Dynamics of the house finch invasion of Eastern North America, American Naturalist, 148(2), 255-274