# Spatial Ecology

$$\frac{dN}{dt} = Nr$$

*"Populační ekologie živočichů"*

Stano Pekár

**Spatial ecology** - describes changes in spatial pattern over time
  ‣ processes - colonisation / immigration and local extinction / emigration

  ‣ local populations are subject to continuous colonisation and extinction
  ‣ wildlife populations are fragmented

**Metapopulation** - a population consisting of many local populations (sub-populations) connected by migrating individuals with discrete breeding opportunities (not patchy populations)
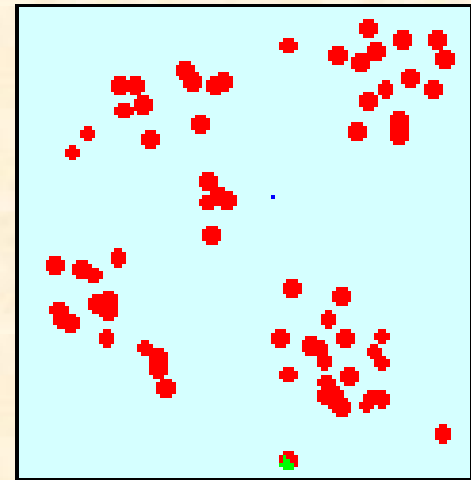
# Distribution of individuals

▶ population density changes also in space

▶ for migratory animals (salmon) seasonal movement is the dominant cause of population change

▶ movement of individuals between patches can be density-dependent

▶ distribution of individuals have three basic models:
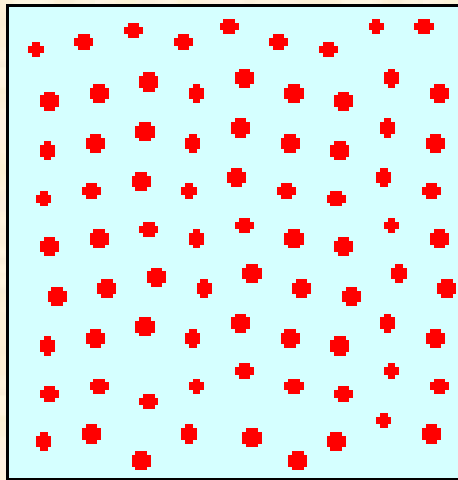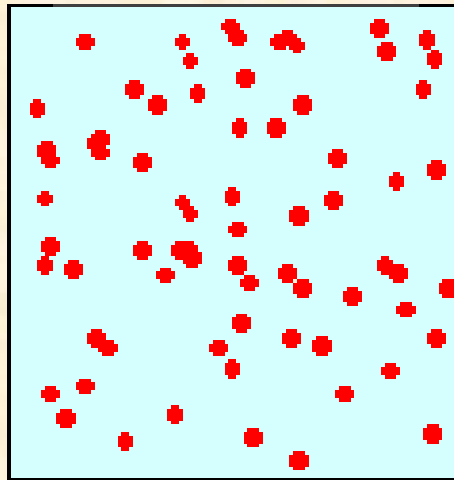


Regular        Random        Aggregated

▶ most populations in nature are aggregated (clumped)

# Regular distribution

▸ described by hypothetical discrete uniform distribution

$$P(x) = \frac{1}{n}$$

$n$ .. is number of samples
$x$ .. is category of counts (0, 1, 2, 3, 4, ...)

▸ all categories have similar probability

▸ mean:   $\mu = \dfrac{1}{2}(n+1)$

▸ variance:   $\sigma^2 = \dfrac{1}{12}(n^2 - 1)$

▸ for regular distribution:   $\boxed{\mu > \sigma^2}$

# **Random distribution**

▸ described by hypothetical Poisson distribution

$$P(x) = \frac{\mu^x e^{-\mu}}{x!}$$

$\mu$ .. is expected value of individuals
$x$ .. is category of counts (0, 1, 2, 3, 4, ...)

▸ probability of $x$ individuals at a given area usually decreases with $x$

▸ observed and expected frequencies are compared using $\chi^2$ statistics

▸ for random distribution: $\boxed{\mu = \sigma^2}$

# Aggregated distribution

▸ described by hypothetical negative binomial distribution

$$P(x) = \left(1 - \frac{\mu}{k}\right)^{-k} \frac{(k + x - 1)!}{x!(k-1)!}\left(\frac{\mu}{\mu + k}\right)^{x}$$

$\mu$ .. is expected value of individuals
$x$ .. is category of counts (0, 1, 2, 3, 4, ...)
$k$ .. degree of clumping, the smaller $k$ ($\rightarrow$0) the greater degree of clumping

▸ approximate value of $k$:  $\quad k \approx \dfrac{\mu^2}{\sigma^2 - \mu}$

▸ for aggregated:  $\boxed{\mu < \sigma^2}$

## Coefficient of dispersion (CD)

CD < 1 ... uniform distribution
CD = 1 ... random distribution
CD > 1 ... aggregated distribution

$$\boxed{CD = \frac{s^2}{\bar{x}}}$$

# Dispersal

• **Geographic range** - radius of space containing 95% of individuals

• **expansion** – increase in geographic range

• individual makes blind **random walk**

• random walk of a population undergoes **diffusion** in space

• diffusion (Brownian motion) model in 2dimensional space:

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

Elton 1958

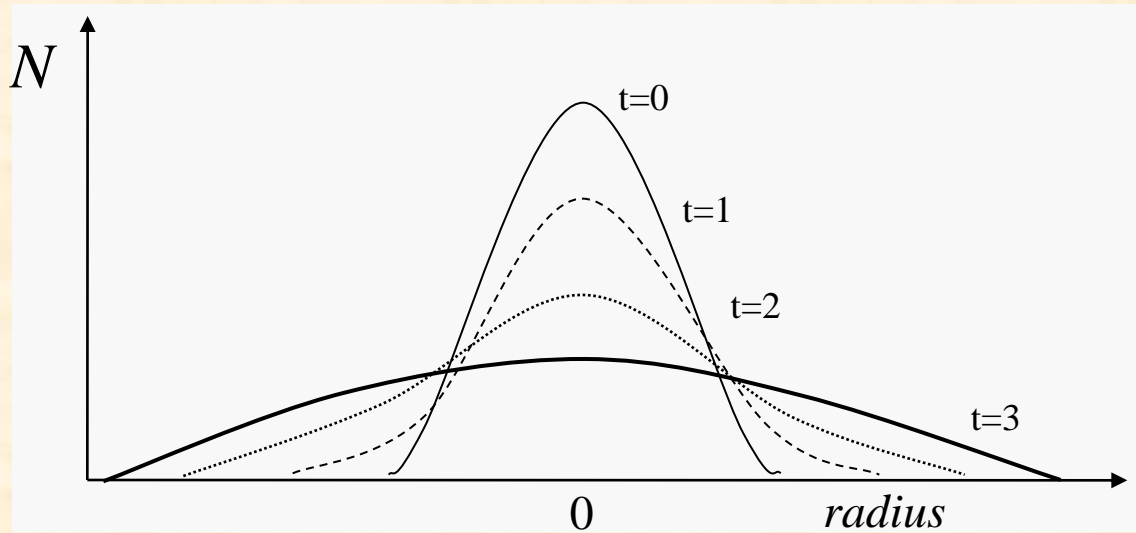- radial distance moved in a random walk is related to $\sqrt{time}$

$D$ .. diffusion coefficient (distance²/time)
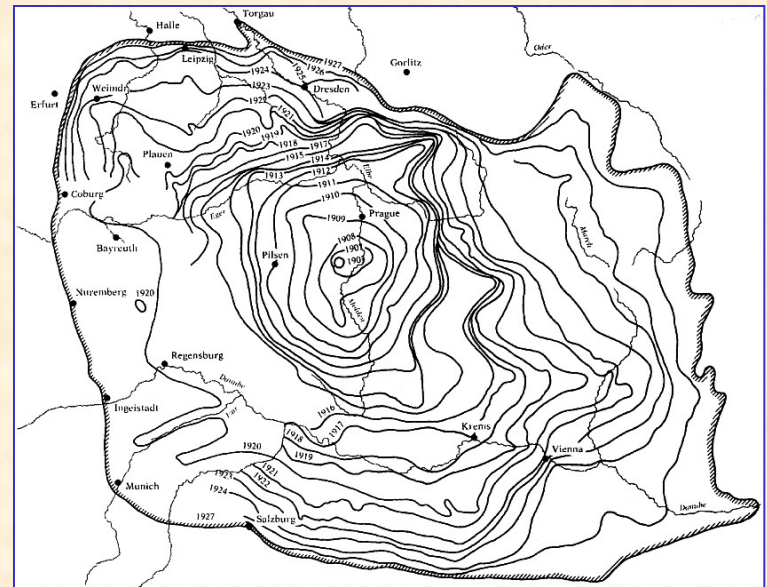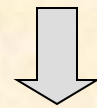


Spread of muskart in Europe

# Pure dispersal



- Diffusion model
- solved to 2dimensional Gaussian distribution

$$N(\rho, t) = \frac{N_0}{4\pi D t} \exp\left(\frac{-\rho^2}{4Dt}\right)$$

- assuming all individuals are dispersers
- range expanses linearly with time
- no reproduction

$N_0$ .. initial density

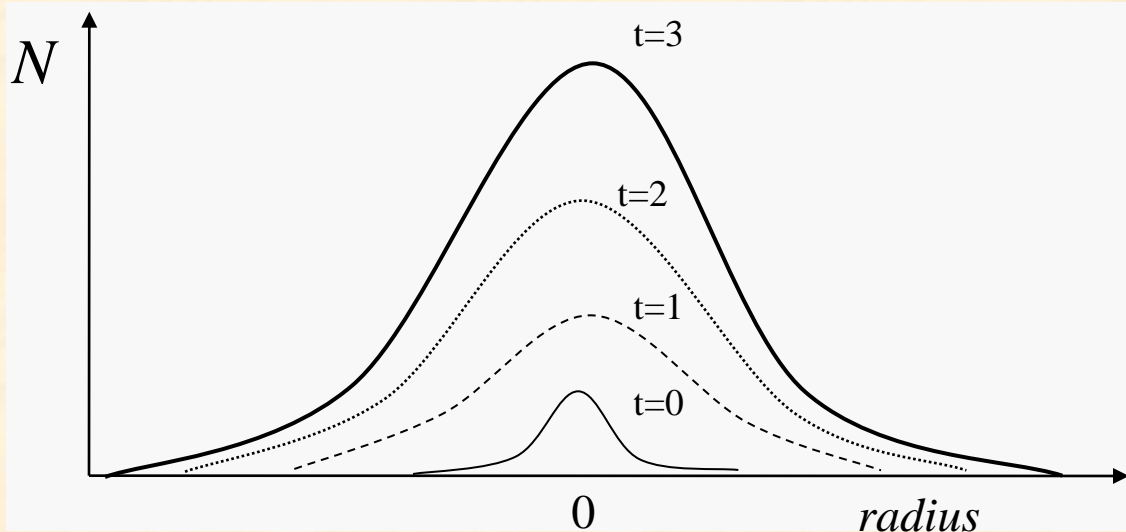$\rho$ .. radial distance from point of release (range)

$$\rho = \sqrt{4Dt}$$

$$D = \frac{\rho^2}{4t}$$

# Dispersal + population growth



• Skellam's model
- includes diffusion and exponential population growth

*r* .. intrinsic rate of increase

$$N(\rho, t) = \frac{N_0}{4\pi D t} \exp\left( rt - \frac{\rho^2}{4Dt} \right)$$

*c* - expansion rate [distance/time]

$$c = 2\sqrt{rD}$$

Skellam 1951

# Metapopulation ecology

▸ Levins (1969) distinguished between dynamics of a single population and a set of local populations which interact via individuals moving among populations

▸ Hanski (1997) developed the theory - suggested *core-satellite* model

▸ the degree of isolation may vary depending on the distance among patches



High isolation          Low isolation
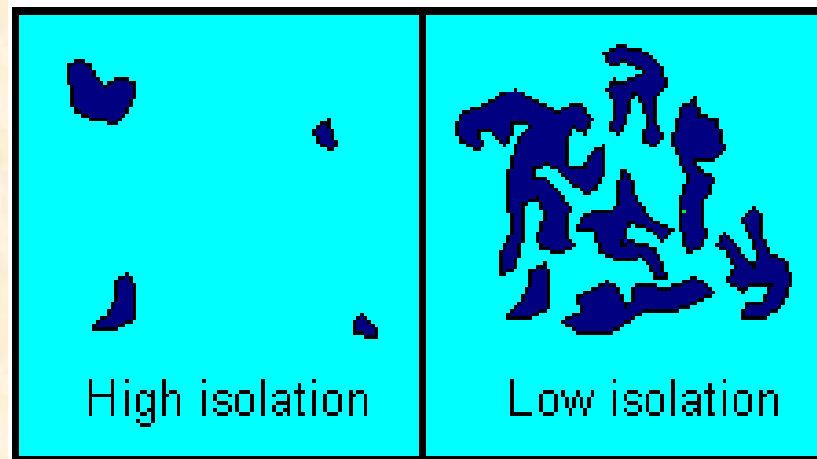
▸ unlike growth models that focus on population size, metapopulation models concern persistence of a population - ignore fate of a single sub-population and focus on fraction of sub-population sites occupied

# Levin's model

‣ assumptions

- sub-populations are identical in size, distance, resources, etc.
- extinction and colonisation are independent of $p$
- many patches are available
- natality and mortality is ignored

$p$ .. proportion of patches occupied
$m$ .. colonisation (immigration) rate - proportion of open sites colonised per unit time
$e$ .. extinction (emigration) rate - proportion of sites that become unoccupied per unit time

$$\frac{\mathrm{d}p}{\mathrm{d}t} = mp(1-p) - ep$$

Levin (1969)

▸ equilibrium is found for $\dfrac{\mathrm{d}p}{\mathrm{d}t} = 0$

$$p^* = \frac{m-e}{m} = 1 - \frac{e}{m}$$

- sub-populations will persist ($p^* > 0$) only if colonisation is larger than extinction ($m > e$)
- all patches can be occupied only if $e = 0$

- $K$ ..is fraction of patches
- defined by balance between $m$ and $e$

▸ metapopulations are found in insects, *Daphnia*, frogs, birds

▸ rescue-effect model, incidence model