Mathematics of Dispersal:
When Being Different Becomes Important

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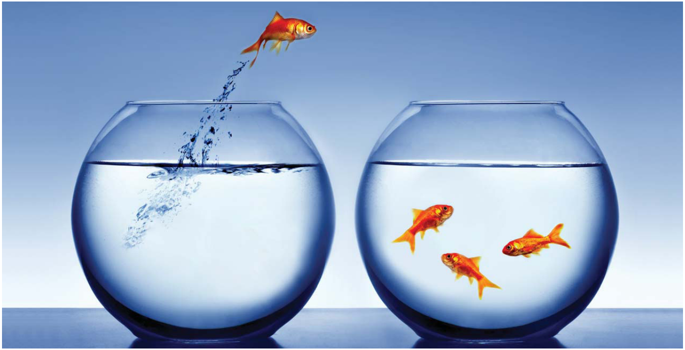
Dispersal in ecology

Dispersal is **redistribution** of a given population **in space** due to motion of its individuals.



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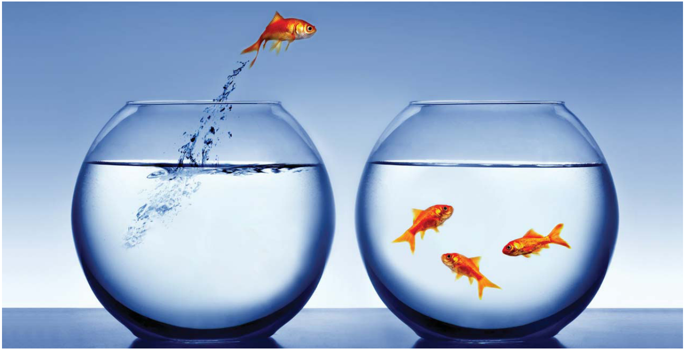

Dispersal arises as a result of interplay between **numerous factors** such as individual movement, animal behavior, population density effects, landscape structure, etc.

Importance of dispersal

Dispersal is the factor that makes ecology essentially spatial.

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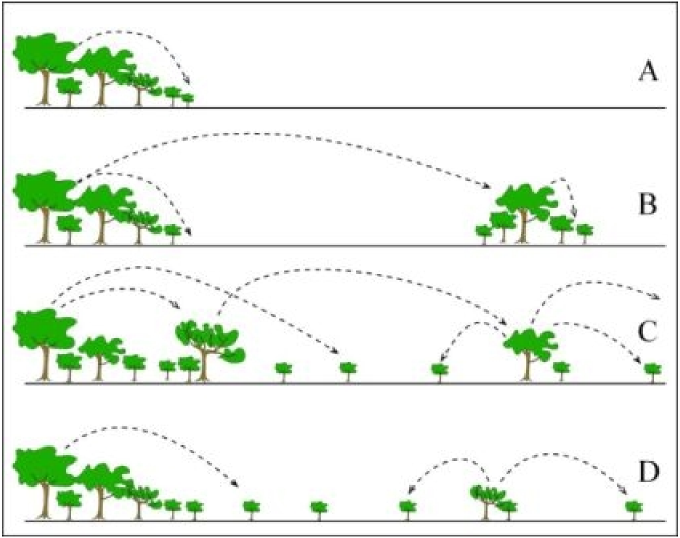
The dynamics of spatial and non-spatial systems is often qualitatively different, hence the understanding of dispersal patterns is crucial for the understanding of ecological dynamics.

Dispersal of a population takes place through movement of its individuals: hence the importance of the microscale!

Dispersal occurs in a **continuous space** as well as in fragmented environment:



The focus of the talk is on the **dispersal kernels**.

Let us start with the 1D case.

Definition. Consider a single individual (e.g. seed or animal) released at a position x' at time $t = 0$. The probability density to find it at a new position x (after some dispersal time t) is called the dispersal kernel, say $k(x, x', t)$.

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In a uniform space, the probability depends on the distance $|x - x'|$ between the initial and final positions rather than on x and x' separately, so that $k(x, x', t) \to \tilde{k}(|x - x'|, t)$ (omitting tildes later on the sake of notation's simplicity)

In an unbounded space, and neglecting mortality in transport, we observe that

$$\int_{-\infty}^{\infty} k(|x - x'|, t)dx = \int_{-\infty}^{\infty} k(|x - x'|, t)dx' = 1.$$

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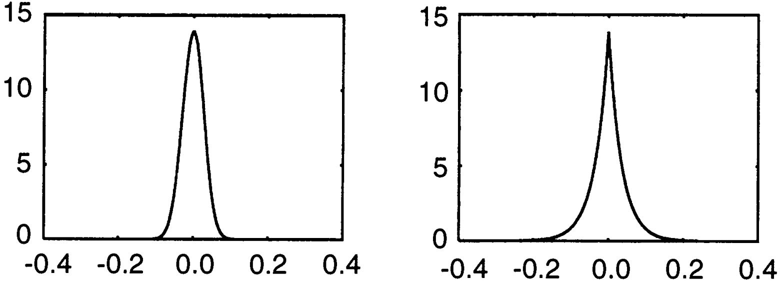
What is the **rate of decay** in the population density at large distances, i.e. for large x?

Examples of dispersal kernels



Left: the Gaussian (normal) distribution, right: “back-to-back exponential” distribution.

The tails of the curves are different.

The rate of spread of invading species is higher for a **fatter tail**.

Problems & questions

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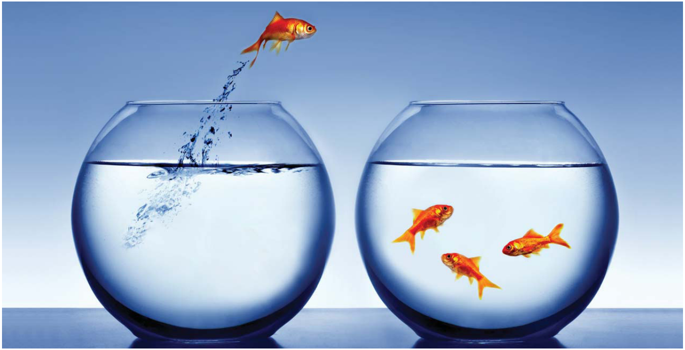
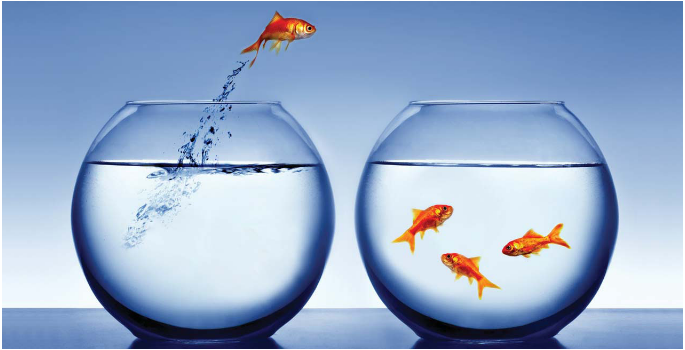
The answer is – **not necessarily**,

as the individual differences can have the same effect on the dispersal kernel



An **intuitive explanation**: a stronger fish can jump further!



An **intuitive explanation**: a stronger fish can jump further!

Important remark: The tail of the population density arises because of the movement of the individuals, hence the importance of the microscale.

Plan of the talk

- Introduction
- Part I: Fat Tails in Population Dispersal
    - Dispersal kernel and its tail
    - A concept of “statistically structured population”
    - Fat-tailed Brownian diffusion in the structured population
- Part II: Individual Movement and its Tails
    - Steps, angles and bouts
    - Peculiarities of bouts duration
    - Effect of the statistical structure
- Conclusions

Part I: Dispersal in a Population

Diffusion as a paradigm

Let $n(\mathbf{r}, t)$ is the population density at position $\mathbf{r} = (x, y)$ and time t. How will it evolve in time?

Assuming the environment is homogeneous and isotropic,

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

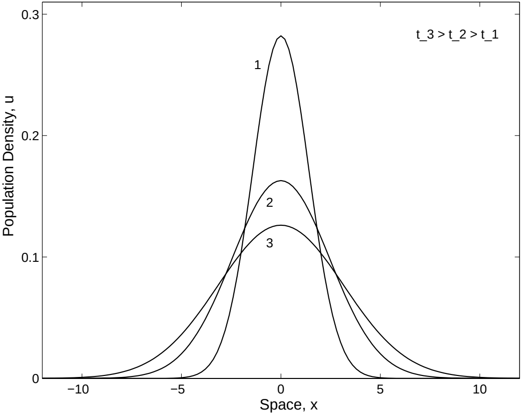
where D is the diffusion coefficient.

Density distribution after a point-source release at time $t = 0$:

$$n(\mathbf{r}, t) = \frac{N_0}{4\pi Dt} \exp\left(-\frac{r^2}{4Dt}\right) , \qquad r = |\mathbf{r}| \, .$$

Diffusion as a paradigm

$$\frac{\partial u(x,t)}{\partial t} = D\frac{\partial^2 u(x,t)}{\partial x^2} \ .$$



The large-distance asymptotics: $u(x,t) \sim exp(-\text{Const}\cdot x^2)$

Diffusion as a paradigm – a trouble

Therefore, the standard diffusion approach predicts the Gaussian-like asymptotical rate of decay in the population density – a ‘thin tail’:

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The trouble is that the experimental data often show the rate of decay at large distances remarkably lower than that of the Gaussian tail, such as exponential:

$$n(r,t) \sim \exp\left(-br\right),$$

or even power law:

$$n(r,t) \sim r^{-\gamma}.$$

How can we deal with these ‘fat tails’?

An alternative, kernel-based approach

An alternative approach:

$$n(\mathbf{r},t)=\int_{\mathbf{R}^2}K(|\mathbf{r}-\mathbf{r}'|,t)n(\mathbf{r}',0)d\mathbf{r}' \ ,$$

where the dispersal kernel $K(\xi)$ gives the probability density to find a given individual at distance ξ from the point of its release.

With the Gaussian kernel $K\sim \exp[-(\mathbf{r}-\mathbf{r}')^2/(4Dt)]$, the kernel-based approach is equivalent to the diffusion equation.

However, the kernel must not necessarily be Gaussian.

Statistically structured population

Observation 1: The fundamental solution of the diffusion equation implies that dispersal can be quantified by a single parameter D, hence assuming that all individuals are identical in their dispersive abilities.

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Observation 2: In reality, they are not identical due to inherent statistical variations.

Consider the diffusivity distribution function $\phi(D)$:

- $dn_D = N_0\phi(D)dD$ gives the fraction of the population which diffusivity lies between D and $D + dD$.
- $\int_0^\infty \phi(D)dD = 1$.

Then, in the case of a point-source release,

$$dn_D(r,t) = \frac{N_0\phi(D)dD}{4\pi Dt}\exp\left(-\frac{r^2}{4Dt}\right).$$

What is measurable in field studies is the total population density:

$$n(r,t) = \int dn_D(r,t) = \int_0^\infty \frac{N_0\phi(D)dD}{4\pi Dt}\exp\left(-\frac{r^2}{4Dt}\right).$$

One can expect that, after the integration, the large-distance asymptotics will be different from the Gaussian one.

However, what may be the properties of $\phi(D)$?

Test-case IV

Let us consider

$$\phi(D) = A_1 \exp\left[-\left(\frac{D - D_0}{\mu}\right)^2\right], \qquad \mu \ll D_0 \ ,$$

where D_0 and μ are parameters with obvious meaning.

After integration, we obtain that, for any given t and large r,

$$u(r,t) \sim r^{-2/3} \exp\left[-\frac{3r^{4/3}}{4(\mu t)^{2/3}}\right] .$$

which is clearly different from the Gaussian asymptotics, having a fatter tail.

Test-case III

To take into account that D is non-negative, let us consider

$$\phi(D) = \tilde{A}_1 D^k \exp\left[-\left(\frac{D}{\mu}\right)^2\right],$$

k is a parameter.

After integration, we obtain that, for any given t and large r,

$$u(r,t) \sim r^{2(k-1)/3} \exp\left[-\frac{3r^{4/3}}{4(\mu t)^{2/3}}\right].$$

Therefore, once again, the tail is fatter than the Gaussian one.

Test-case II

Let us now consider the case when $\phi(D)$ decays exponentially at large D. Specifically, we consider

$$\phi(D) = A_2 D^\beta \exp\left(-\frac{D}{\nu}\right),$$

ν and β are parameters.

After integration, we obtain the large distance asymptotics:

$$n(r,t) \sim r^{\beta-\frac{1}{2}} \exp\left(-\frac{r}{\sqrt{\nu t}}\right) \ ,$$

which is obviously a fat tail.

Test-case I

Let $\phi(D)$ now show a power-law decay, $\phi(D) \sim D^{-\gamma}$ for large D.

To keep the model analytically tractable, we assume that

$$\phi(D) = A_3 D^{-\gamma} \exp\left(-\frac{\alpha}{D}\right),$$

where α and γ are parameters.

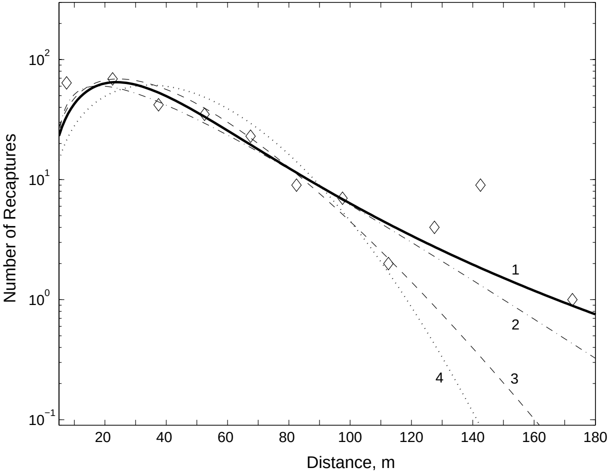
After integration,

$$n(x,t) = C(\alpha,\gamma,t)\left(\alpha + \frac{r^2}{t}\right)^{-\gamma},$$

so that, for any given t and large r, we obtain a power-law:

$$n(x,t) \sim r^{-2\gamma}.$$

Comparison with field data



(Brakefield, 1982: experiment with butterflies)

A mechanistic model for $\phi(D)$

Observation: Diffusivity is not a “first-hand” parameter but rather a function of some basic parameters:

$$D = D(\mu, \ell, \tau, \ldots) \ ,$$

Then, even if the distribution for each of $\mu, \ell, \tau, \ldots$ is normal, the distribution for D can be different.

A microscopic analysis of Brownian motion leads to

$$D = \frac{l^2}{2\tau} = \frac{v^2\tau}{2} \ .$$

Example 1: In some cases, v was shown to be described by a Maxwell-type distribution (Okubo & Chiang, 1974).

For $\phi(D)$ we then obtain a distribution with an exponential tail.

Example 2: However, if we assume that the step length is fixed and τ is distributed normally,

$$\psi(\tau) = \frac{1}{\sqrt{\pi}\delta\tau} \exp\left[-\left(\frac{\tau - \tau_0}{\delta\tau}\right)^2\right],$$

then, since $D \sim 1/\tau$, we obtain

$$\phi(D) = \frac{l^2}{2\sqrt{\pi}\delta\tau D^2} \exp\left[-\frac{1}{(\delta\tau)^2}\left(\frac{l^2}{2D} - \tau_0\right)^2\right],$$

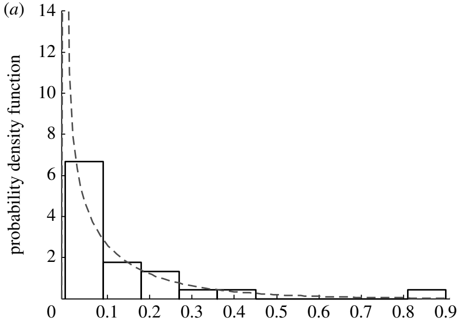
so that the large-D asymptotics is a power law:

$$\phi(D) \simeq \frac{l^2}{2\sqrt{\pi}\delta\tau D^2} \exp\left[-\left(\frac{\tau_0}{\delta\tau}\right)^2\right] \sim D^{-2} \,.$$

Laboratory data on $\phi(D)$

Data on the diffusivity distribution are scarce.

Experiment with nematodes (Hapca et al., 2009):



$\phi(D) \sim D^{-\gamma} \exp\left(-\frac{D}{\nu}\right)$, which is consistent with our analysis

Effects of finiteness

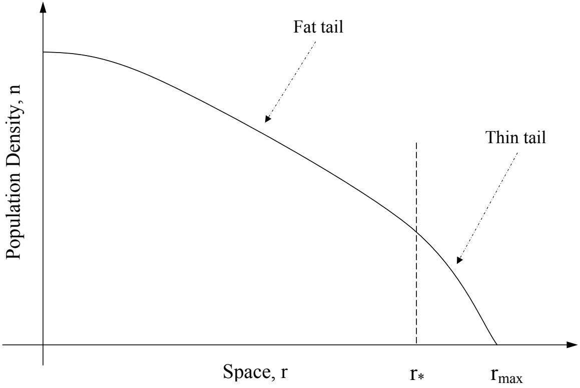
In reality, diffusivity is bounded,

$$0 < D < D_* \ ,$$

where $D_* < \infty$ is a parameter specific for the given species.

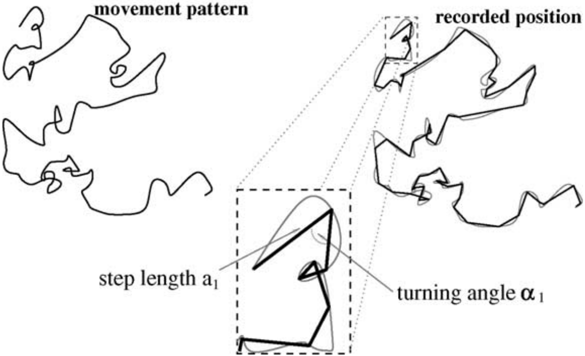
Effects of finiteness (contd.)

Our model predicts a critical distance, $r_* \sim t^{1/2}$:



Part II: Dispersal of Individuals

We assume that a curvilinear path can be mapped into a broken line (e.g. due to discreteness of observations):

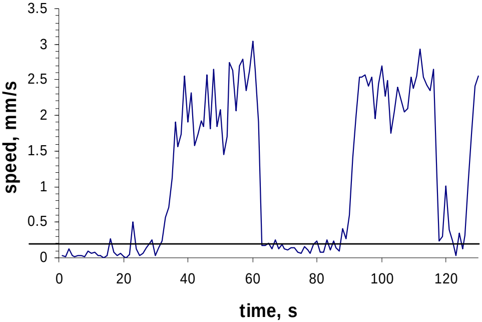


(from Jopp & Reuter, 2005)

Is the individual movement deterministic or random?

Movement along a broken line can be quantified by distribution of steps and turning angles but this is not enough.

Movement is usually split into periods of motion (or fast displacement), aka bouts, and rest (or slow displacement):



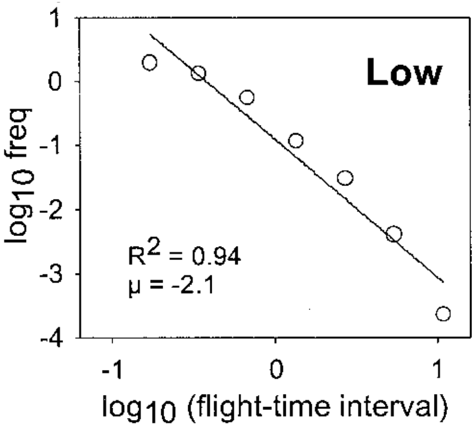
(from Mashanova, 2008)

Determinants of the individual path

Therefore, a complete microscopic description of the individual movement should include probability distributions of steps, turning angles, bouts and periods of rest (as well as cross-correlations between them).

In the below, we focus on the distributions of bouts.

An Inspiring Example: Zooplankton Movement



(from Bartumeus et al., 2003)

Main Assumptions

Our analysis is based on the following assumptions:

1. There exists an ideal distribution of the bout duration, which applies to a system of absolutely identical individuals dispersing in a homogeneous environment under stationary deterministic conditions;
2. In a real system, the ideal distribution is masked by the population's heterogeneity, i.e. by the statistical variation of individual traits.

Outline of the Theory

Let $\phi(\tau, \alpha)$ is the ideal probability distribution of bout duration. In a population of identical individuals, α is a parameter.

Taking into account the individual differences (i.e. the statistical structure of the population), α is not a parameter but a random variable with a certain distribution $\psi(\alpha)$.

Therefore, the observed probability distribution function of bout duration is

$$\Phi(\tau) = \int_{\alpha_{min}}^{\alpha_{max}} \phi(\tau, \alpha)\psi(\alpha) d\alpha \ .$$

We emphasize that α should be distributed over a finite domain,

$$0 < \alpha_{min} \le \alpha \le \alpha_{max} < \infty \ .$$

Outline of the Theory (contd.)

However, what are $\phi(\tau, \alpha)$ and $\psi(\alpha)$?

Outline of the Theory (contd.)

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We postulate that an individual stops its movement when it perceive a “signal” from its environment (e.g. noise, a fluctuation in temperature, etc.). If we assume that the arrival of these signals follows Poisson process, the waiting times between two signals is exponentially distributed:

$$\phi(\tau, \alpha) = \alpha \, \mathrm{exp}(-\alpha\tau) \ ,$$

where $\alpha = 1/ < \tau >$.

Outline of the Theory (contd.)

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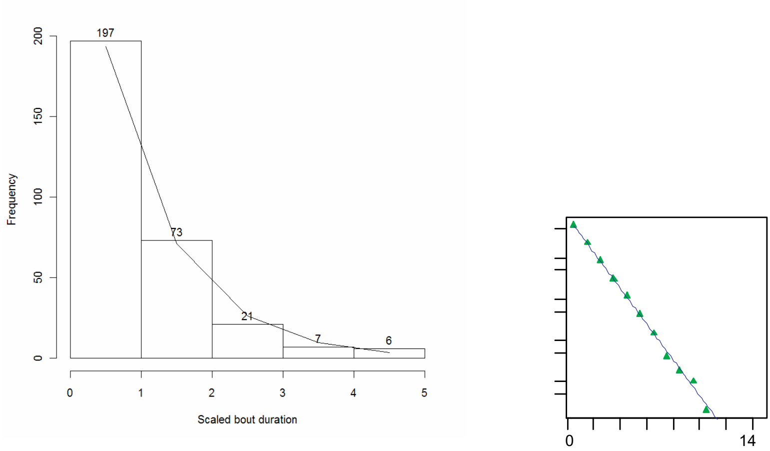
where $\alpha = 1/ < \tau >$.

It can also be regarded as the Boltzmann distribution.

A glance at the data



The frequency of the scaled bout duration in usual (left) and semi-logarithmic (right) coordinates.

Outline of the Theory (contd.)

Remarkably, whatever $\psi(\alpha)$ is, the bouts distribution function

$$\Phi(\tau) = \int_{\alpha_{min}}^{\alpha_{max}} \alpha\psi(\alpha)e^{-\alpha\tau}d\alpha$$

has different asymptotics for small and large τ:

for $\tau \ll 1/\alpha_{max}$, $\quad \Phi(\tau) \approx <\alpha> - <\alpha^2> \tau$,

for $\tau \gg 1/\alpha_{min}$, $\quad \Phi(\tau) \simeq \alpha_{min}\psi(\alpha_{min}) \cdot \frac{1}{\tau}\, e^{-\alpha_{min}\tau}$.

Outline of the Theory (contd.)

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or

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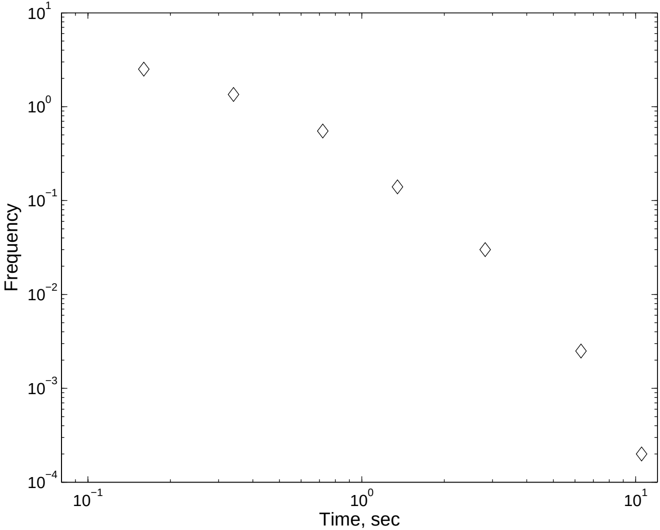
or perhaps

$$\psi(\alpha) = \mathit{Const} \cdot \alpha^{\gamma} \exp\left(-b\alpha^{\beta}\right) \ ,$$

where $\gamma, \ \beta$ and *b* are parameters and *Const* ensures that

$$\int_{\alpha_{min}}^{\alpha_{max}} \psi d\alpha = 1 \ .$$

Comparison With Zooplankton Data



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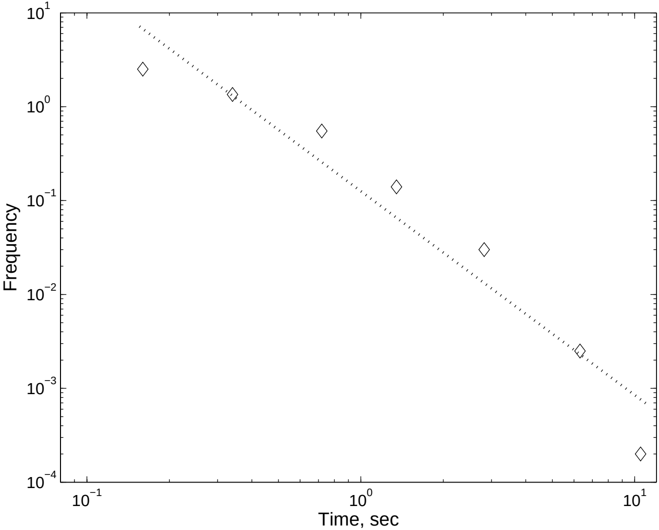

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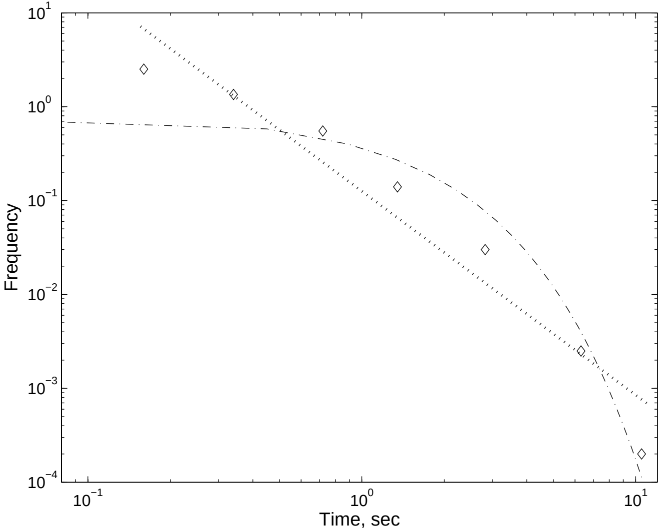

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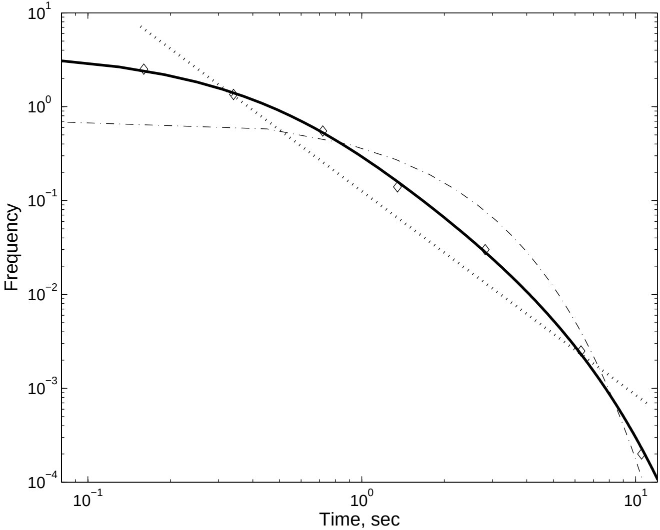

Insight into the Statistical Structure

The choice of $\psi(\alpha)$ is yet hypothetical.

What sort of information can we extract from detailed, highly resolved data?

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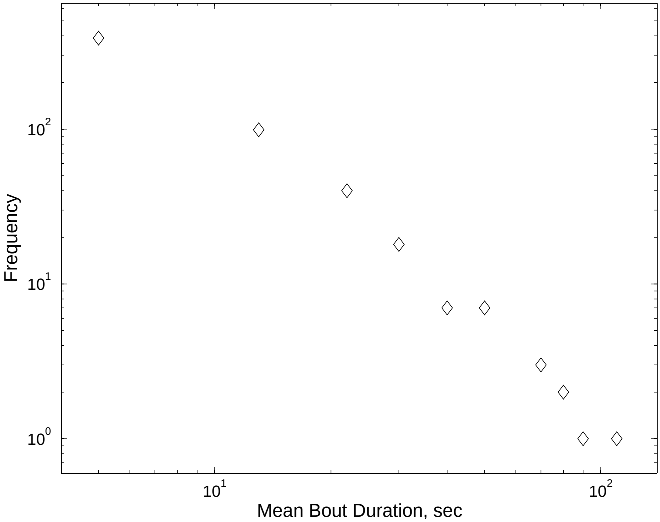
Laboratory experiment on aphids (Mashanova, 2008; Mashanova et al., 2009)

Experiment on Aphids



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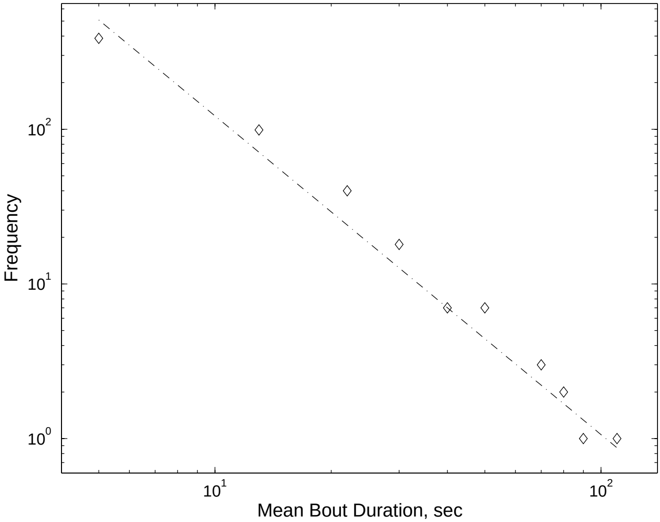

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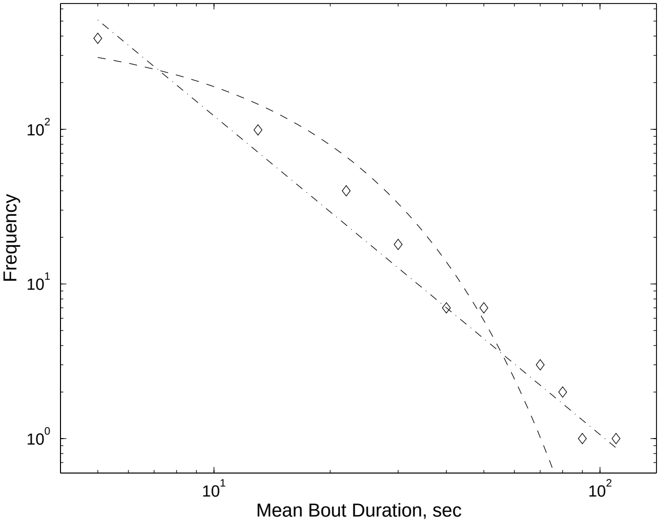

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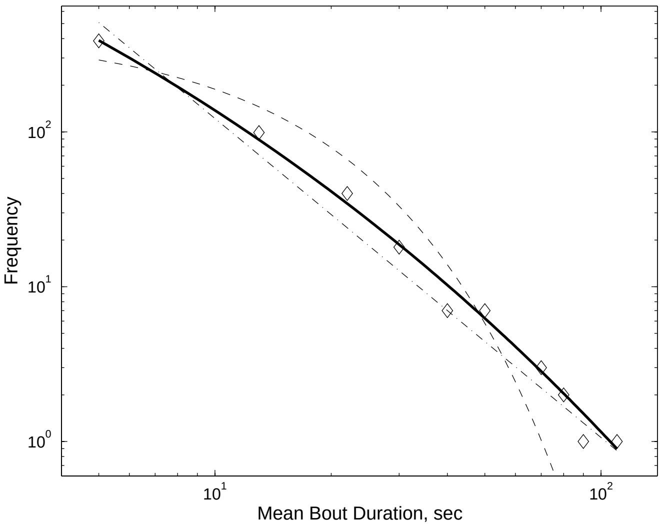


Data Fitting

Power law ($R^2 = 0.881$):

$$f(\tau) \sim < \tau >^{-\chi} \quad \text{with} \;\; \chi = 2.06 \; ;$$

Exponential ($R^2 = 0.907$):

$$f(\tau) \sim \exp(-\omega < \tau >) \quad \text{with} \;\; \omega = 0.087 \; ;$$

Fractional exponential ($R^2 = 0.999$):

$$f(\tau) \sim \exp(-b < \tau >^{\beta}) \quad \text{with} \;\; b = 4.74 \;\; \text{and} \;\; \beta = 0.21 \; .$$

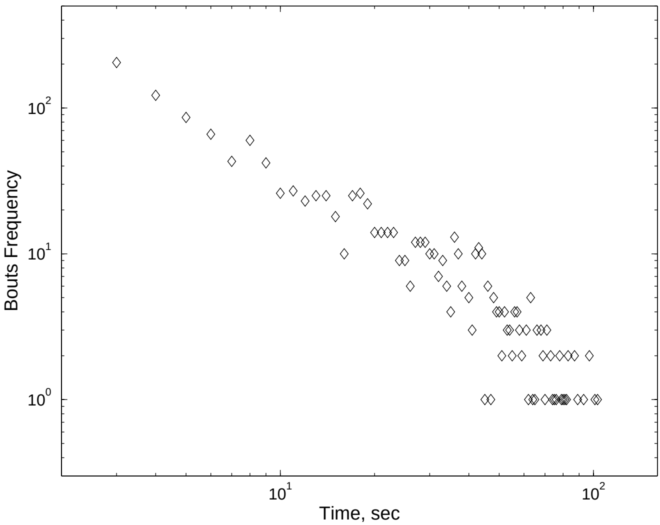
Probability Calculus

$$\alpha = \frac{1}{<\tau>} \text{ or } <\tau> = 1/\alpha \,, \quad \text{thus} \quad \psi(\alpha) = f(\tau(\alpha)) \left| \frac{d\tau}{d\alpha} \right| \,.$$

Thus, for the different best fittings we obtain:

$$\begin{aligned}
\psi(\alpha) &\sim \alpha^{\chi-2} \,, \\
\psi(\alpha) &\sim \alpha^{-2} \exp\left(-\frac{\omega}{\alpha}\right) , \\
\psi(\alpha) &\sim \alpha^{-2} \exp\left(-b\alpha^{-\beta}\right) .
\end{aligned}$$

Experiment on Aphids (contd.)



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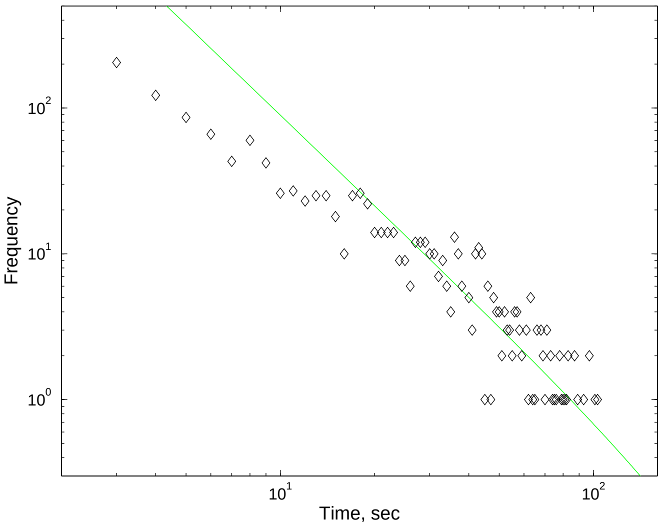

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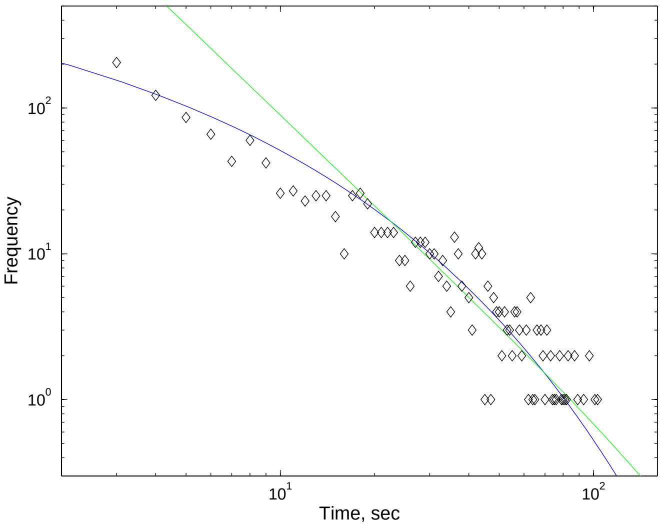

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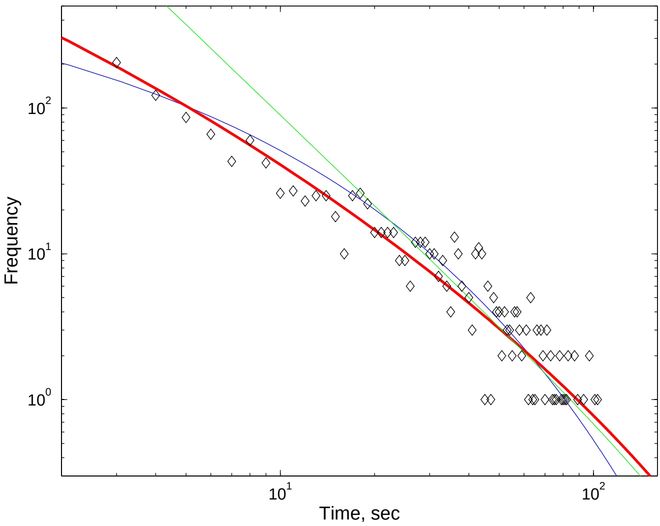

Conclusions

- Fat dispersal tails of the population density do not necessarily mean any kind of a “superdiffusive” movement

- Fat dispersal tails can appear as a result of random walk (Brownian diffusion) in statistically structured population, i.e. a population of non-identical individuals

- Our approach predicts that fat tails are an “intermediate asymptotics.” The thin Gaussian tail should re-appear on the spatial scales larger than a certain critical distance

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- The same approach works on the “microscale” of individual animal movement

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Thank you