

A Tale of Two Tails: The Impact of Statistical Structure

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Introduction: What it is all about

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Consider a **point-source release** at $t = 0$ a number N of individuals of a certain species.

For any $t > 0$, we describe their distribution in space by the population density $u(\mathbf{r}, t)$.

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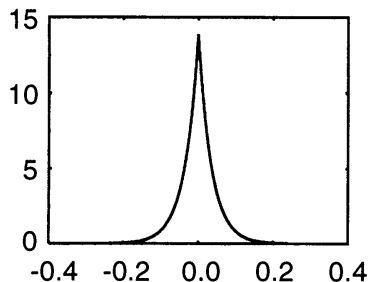
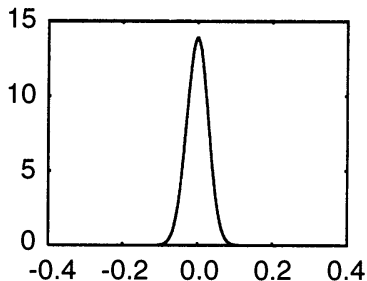
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Consider a **point-source release** at $t = 0$ a number N of individuals of a certain species.

For any $t > 0$, we describe their distribution in space by the population density $u(\mathbf{r}, t)$.

What is the **rate of decay** in the population density at large distances, i.e. for large $r = |\mathbf{r}|$?

Examples



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.

Introduction (contd.)

It has been a long story...

Skellam, J.G. (1951): Random dispersal in theoretical populations. *Biometrika* 38, 196-218.

Kot, M., Lewis, M.A. & van der Driessche, P. (1996): Dispersal data and the spread of invading organisms. *Ecology* 77, 2027-2042.

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Lewis, M.A. (1996): [A tale of two tails](#): the mathematical links between dispersal, patchiness and variability in biological invasion. *ECMTB* 3, Heidelberg, 1996.

Problems & questions

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The answer is **no**.

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,

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

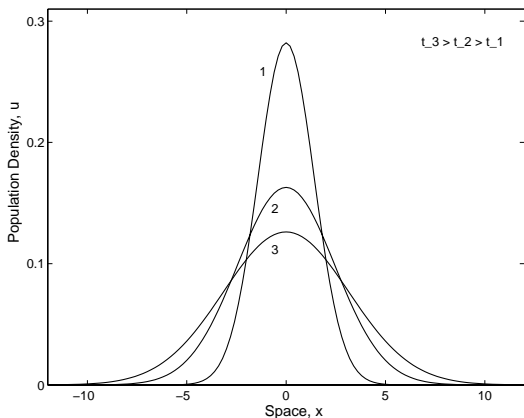
where D is the diffusion coefficient.

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

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

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:

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

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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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.

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 III

Let us consider

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

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 IIIa

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.

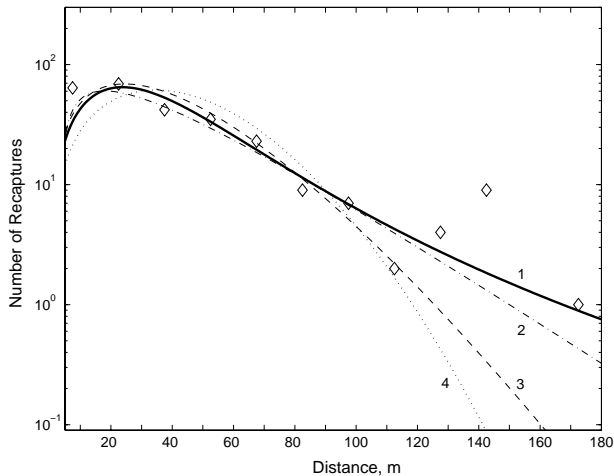
After integration,

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

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:

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

Then, even if the distribution for each of μ, ℓ, τ, \dots 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

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

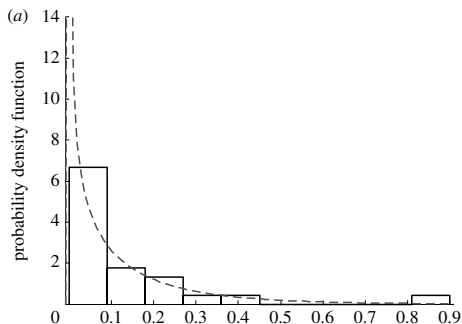
so that the **large- D asymptotics** is a power law:

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

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

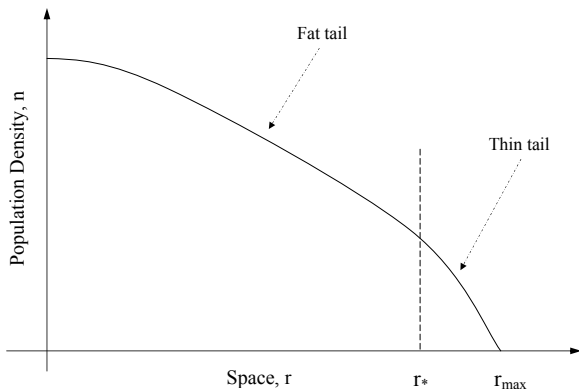
In reality, diffusivity is **bounded**,

$$0 < D < D_* ,$$

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

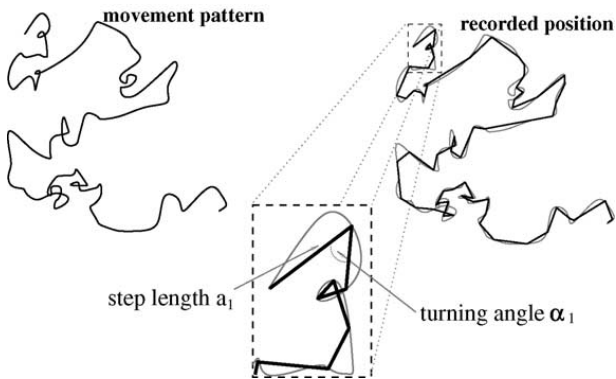
Effects of finiteness (contd.)

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



Part II: Dispersal of Individuals

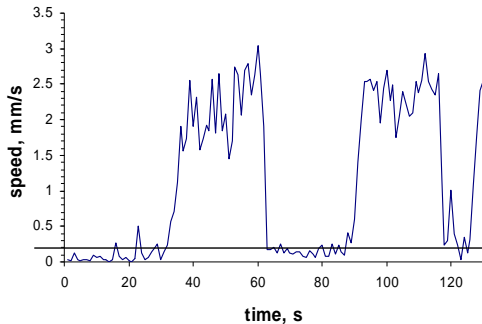
We assume that a curvilinear path can be mapped into a broken line (e.g. due to discreteness of observations):



(from Jopp & Reuter, 2005)

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) and rest (or slow displacement):



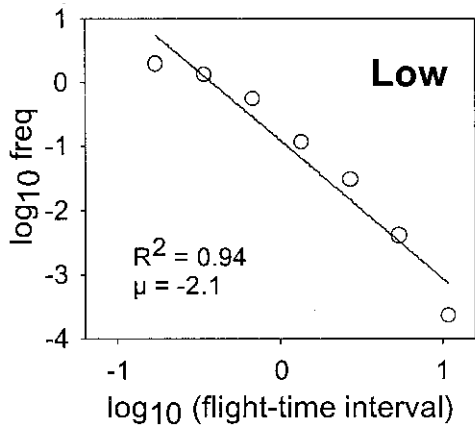
(from Mashanova, 2008)

Determinants of the individual path

Therefore, a complete microscopic description of the individual movement should include 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,

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

Outline of the Theory (contd.)

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

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We postulate that an individual stops its movement when it perceives 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**:

$$\phi(\tau, \alpha) = \alpha \exp(-\alpha\tau) ,$$

where $\alpha = 1 / \langle \tau \rangle$.

Outline of the Theory (contd.)

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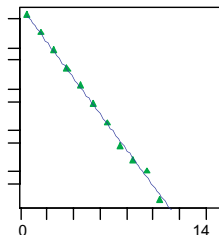
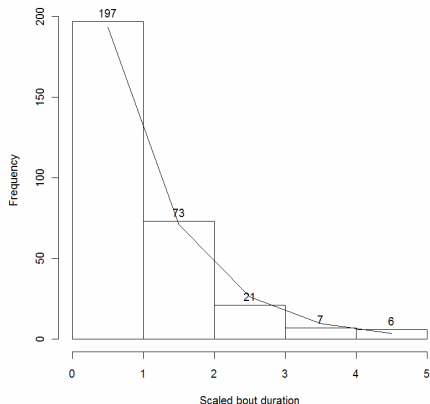
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$$\phi(\tau, \alpha) = \alpha \exp(-\alpha\tau) ,$$

where $\alpha = 1 / \langle \tau \rangle$.

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 :

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

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

Outline of the Theory (contd.)

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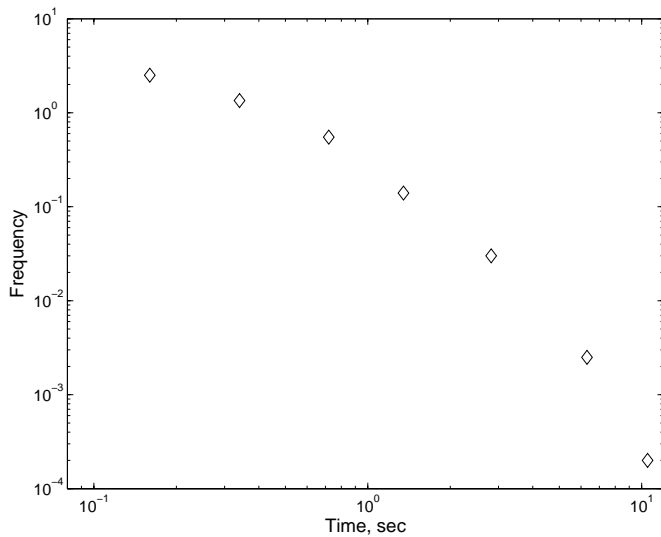
or perhaps

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

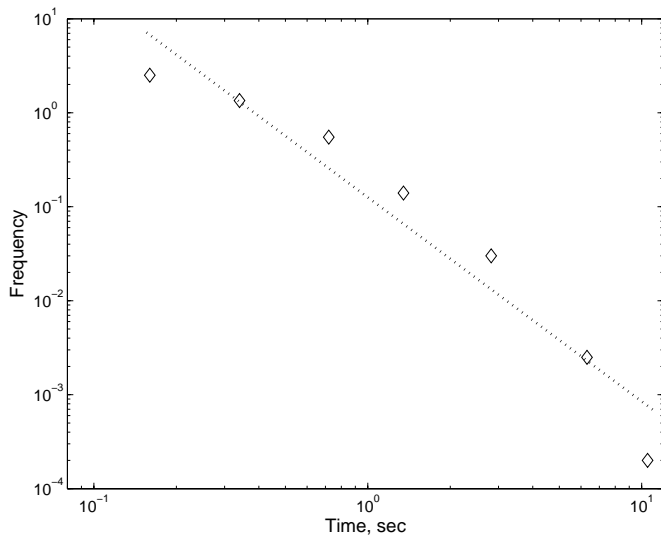
where γ , β and b are parameters and *Const* ensures that

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

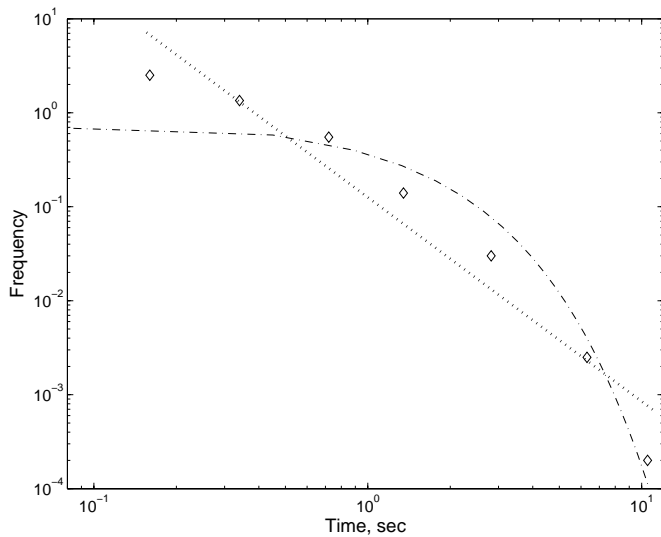
Comparison With Zooplankton Data



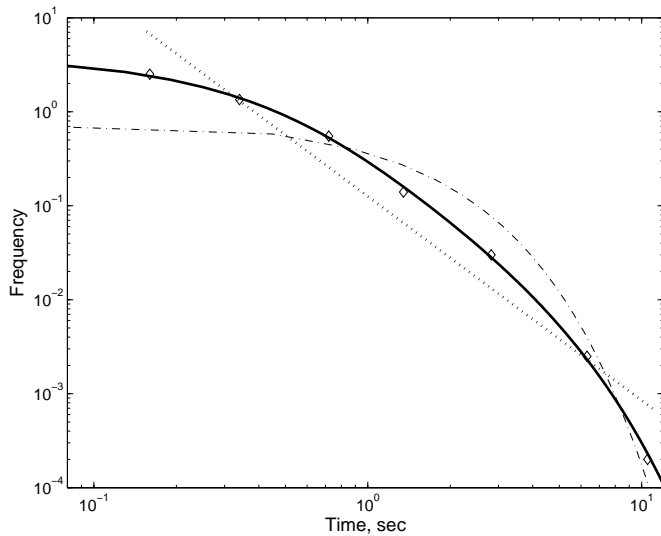
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Insight into the Statistical Structure

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

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

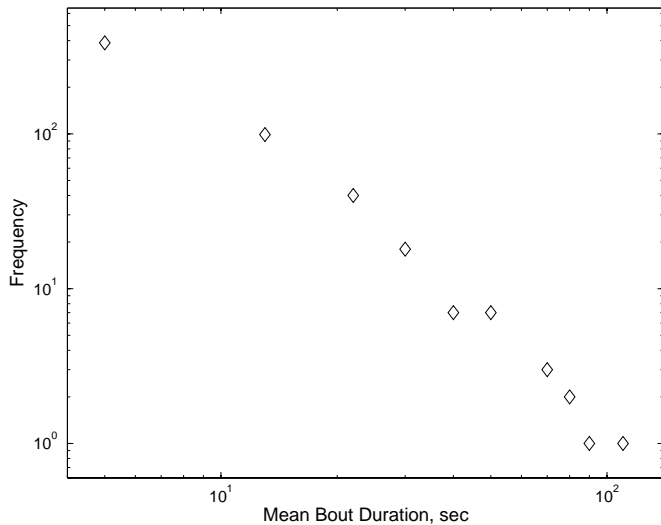
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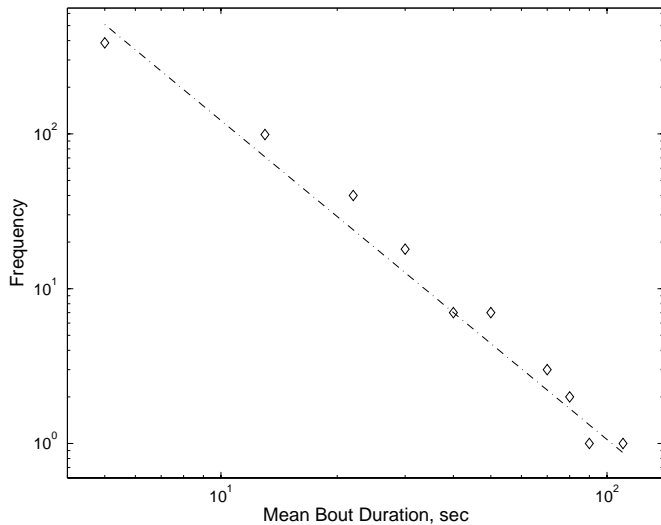
What sort of information can we extract from **detailed, highly resolved data**?

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

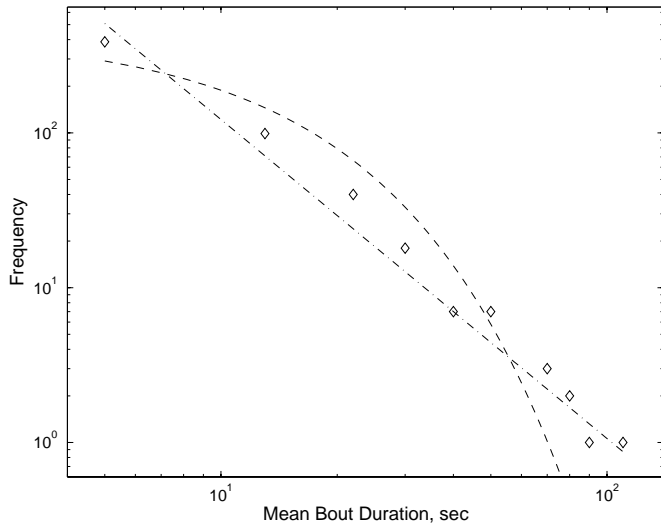
Experiment on Aphids



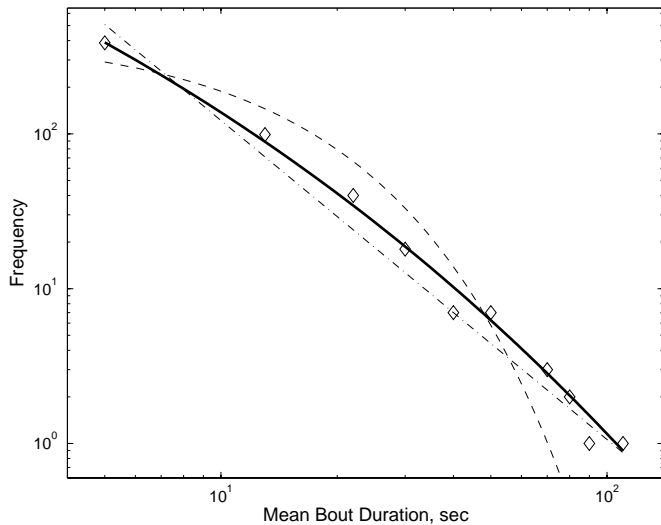
Experiment on Aphids



Experiment on Aphids



Experiment on Aphids



Data Fitting

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

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

Exponential ($R^2 = 0.907$):

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

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

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

Probability Calculus

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

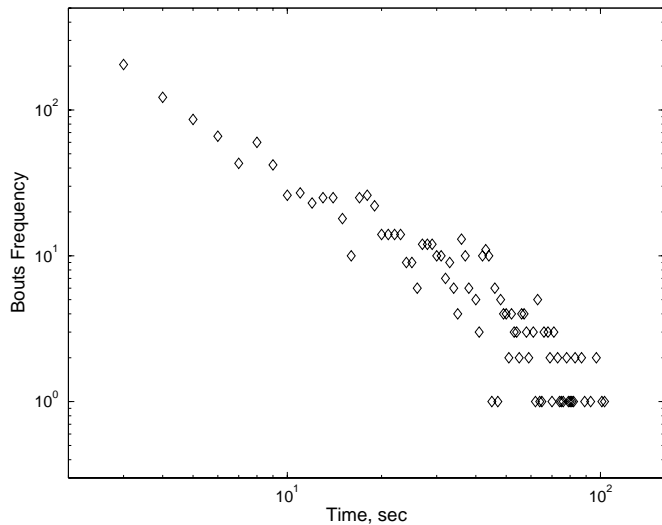
Thus, for the different best fittings we obtain:

$$\psi(\alpha) \sim \alpha^{x-2},$$

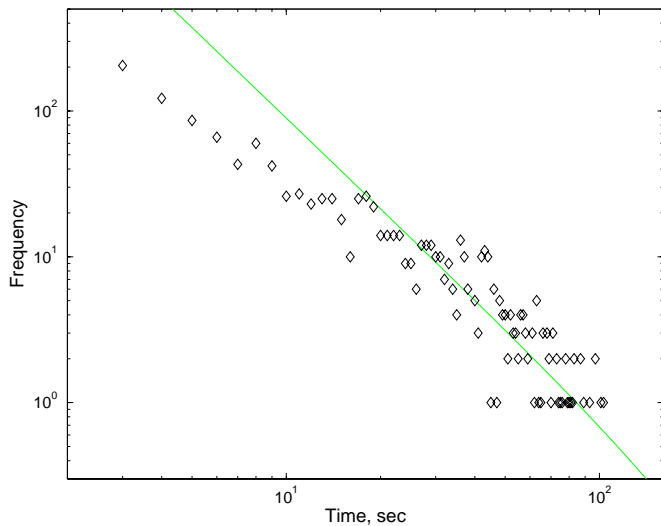
$$\psi(\alpha) \sim \alpha^{-2} \exp\left(-\frac{\omega}{\alpha}\right),$$

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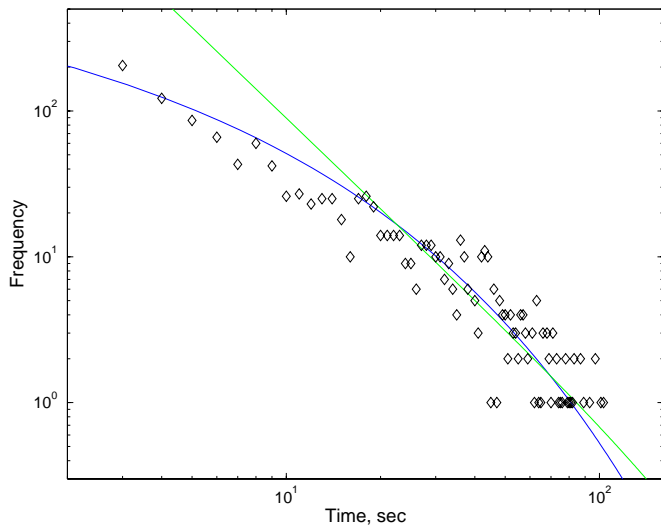
Experiment on Aphids (contd.)



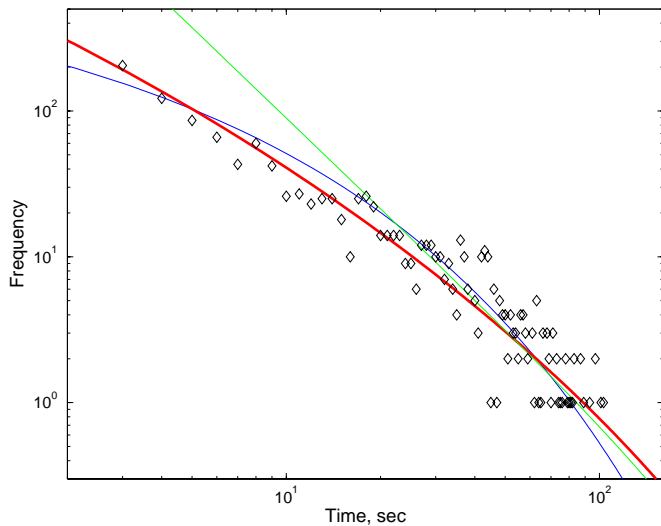
Experiment on Aphids (contd.)



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Experiment on Aphids (contd.)



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

Thanks to:

- Alla Mashanova (Royal Holloway)
- Vincent Jansen (Royal Holloway)
- Andrew Morozov (Leicester)

References

Petrovskii, S.V. & Morozov, A.Y. (2009) Dispersal in a statistically structured population: Fat tails revisited. *American Naturalist* **173**, 278-289.

Petrovskii, S.V., Mashanova, A. & Jansen, V.A.A. (2011) Variation in individual walking behavior creates the impression of a Lévy flight. *PNAS*, in press, 10.1073/pnas.1015208108

Thank you!

Open Questions & Future Work

- What **particular processes** determine the properties of the statistical structure; in particular, **how to calculate** $\psi(\alpha)$ theoretically?
- **To include** into considerations other aspects of the individual movement (such as the distributions of **steps**, **turning angles** etc.) in order to reveal the effect of individual variations on these factors and on MSD
- **Evolutionary aspects**