Statistical Physics and Anomalous Dynamics of Foraging

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The main theme of this talk

analyse **foraging movement patterns**

Understand **foraging movement patterns** of biological organisms in terms of **stochastic processes**.

1. **Lévy flight foraging hypothesis**: overview
2. **biological data**: analysis and interpretation
3. **foraging bumblebees**
4. **cell migration**
Karl Pearson (1906): model movements of biological organisms by a **random walk** in one dimension: position $x_n$ at discrete time step $n$

- $x_{n+1} = x_n + \ell_n$
- *here*: steps of length $|\ell_n| = \ell$ to the left/right; sign determined by coin tossing
- **Markov process**: the steps are **uncorrelated**
- generates **Gaussian distributions** for $x_n$ (central limit theorem)
Lévy flight search patterns of wandering albatrosses

famous paper by Viswanathan et al., Nature 381, 413 (1996):

for albatrosses foraging in the South Atlantic the flight times were recorded

the histogram of flight times was fitted by a Lévy distribution (power law \( \sim t^{-\mu} \))

assuming that the velocity is constant yields a power law step length distribution contradicting Pearson’s hypothesis
What are Lévy flights?

A random walk generating **Lévy flights**:

\[ x_{n+1} = x_n + \ell_n \]

with \( \ell_n \) drawn from a Lévy \( \alpha \)-stable distribution

\[ \rho(\ell_n) \sim |\ell_n|^{-1-\alpha} (|\ell_n| \gg 1), \quad 0 < \alpha < 2 \]

P. Lévy (1925ff)

- **fat tails**: larger probability for long jumps than for a Gaussian!
Properties of Lévy flights in a nutshell

- a Markov process (*no memory*)
- which obeys a generalized central limit theorem if the Lévy distributions are $\alpha$-stable (for $0 < \alpha \leq 2$) by Gnedenko, Kolmogorov (1949)
- implying that $\rho(\ell_n)$ and $\rho(x_n)$ are scale invariant and thus self-similar
- for $\alpha \leq 2$ $\rho(x_n)$ and $\rho(\ell_n)$ have infinite variance
  \[ \langle \ell_n^2 \rangle = \int_{-\infty}^{\infty} d\ell_n \rho(\ell_n)\ell_n^2 = \infty \]
- Lévy flights have arbitrarily large velocities, as $v_n = \ell_n/1$
Lévy walks

cure the problem of infinite moments and velocities:

- a Lévy walker spends a time
  \[ t_n = \ell_n / v, \quad |v| = \text{const}. \]
  to complete a step; yields finite moments and finite velocities in contrast to Lévy flights

- Lévy walks generate anomalous (super) diffusion:
  \[ \langle x^2 \rangle \sim t^\gamma (t \to \infty) \text{ with } \gamma > 1 \]

Zaburdaev et al., Rev. Mod. Phys. 87, 483 (2015)
RK, Radons, Sokolov (Eds.), Anomalous transport (Wiley, 2008)
another paper by Viswanathan et al., Nature 401, 911 (1999):

- question posed about "best statistical strategy to adapt in order to search efficiently for randomly located objects"
- random walk model leads to Lévy flight hypothesis:

Lévy flights provide an optimal search strategy for sparse, randomly distributed, immobile, revisitatable targets in unbounded domains

Brownian motion (left) vs. Lévy flights (right)
Revisiting Lévy flight search patterns


- **Viswanathan et al. results** revisited by **correcting old data**
  (Buchanan, Nature **453**, 714, 2008):

- **no Lévy flights**: new, more extensive data suggests (gamma distributed) stochastic process
- but claim that **truncated Lévy flights** fit yet new data
  Humphries et al., PNAS **109**, 7169 (2012)
Lévy Paradigm: Look for power law tails in pdfs

Humphries et al., Nature 465, 1066 (2010): blue shark data

- blue: exponential; red: truncated power law
- velocity pdfs extracted, *not* the jump pdfs of Lévy walks
- environment explains Lévy vs. Brownian movement
- data averaged over day-night cycle, cf. oscillations
Two different Lévy Flight Hypotheses

Bartumeus, Boyer, Chechkin, Giuggioli, RK, Pitchford, Watkins (tbp)
apply the **Movement Ecology Paradigm** to analyse foraging movement data:

Bartumeus, Boyer, Chechkin, Giuggioli, RK, Pitchford, Watkins (tbp)
Foraging bumblebees: the experiment

- tracking of **bumblebee flights** in the lab: foraging in an artificial carpet of **flowers with or without spiders**
- **no test** of the Lévy hypothesis but work inspired by the **paradigm**

three experimental stages:

1. spider-free foraging
2. foraging under predation risk
3. memory test 1 day later

**safe** and **dangerous** flowers

Ings, Chittka (2008)
Bumblebee experiment: two main questions

1. **What type of motion** do the bumblebees perform in terms of stochastic dynamics?

2. **Are there changes of the dynamics under variation of the environmental conditions?**
experimental **probability density** (pdf) of bumblebee $v_y$-velocities without spiders (bold black)

**best fit:** mixture of 2 Gaussians, cp. to exponential, power law, single Gaussian

**biological explanation:** models spatially different flight modes near the flower vs. far away, cf. intermittent dynamics

**big surprise:** no difference in pdf’s between different stages under variation of environmental conditions!
Velocity autocorrelation function \( \| \) to the wall

**model:** Langevin equation

\[
\frac{dv_y(t)}{dt} = -\eta v_y(t) - \frac{\partial U}{\partial y}(y(t)) + \xi(t)
\]

\( \eta \): friction, \( \xi \): Gauss. white noise

3 stages: spider-free, predation thread, memory test

all changes are in the flight correlations, *not* in the pdfs

**result:** velocity correlations with repulsive interaction \( U \)
bumblebee - spider off / on

Lenz, RK et al., PRL (2012)
Biological cell migration

Dieterich, RK et al., PNAS (2008)

single MDCK-F (Madin-Darby canine kidney) cell crawling on a substrate: Brownian motion?

two cell types: wild \((NHE^+)\) and NHE-deficient \((NHE^-)\)
Mean square displacement

- \( \text{msd}(t) := \langle [x(t) - x(0)]^2 \rangle \sim t^\beta \) with \( \beta \to 2 \) \((t \to 0)\) and \( \beta \to 1 \) \((t \to \infty)\) for Brownian motion; \( \beta(t) = d \ln \text{msd}(t)/d \ln t \)

anomalous diffusion if \( \beta \neq 1 \) \((t \to \infty)\); here: superdiffusion
Velocity autocorrelation function

- $v_{ac}(t) := \langle v(t) \cdot v(0) \rangle \sim \exp(-\kappa t)$ for Brownian motion
- fits with same parameter values as $msd(t)$

crossover from **stretched exponential** to **power law**
**Position distribution function**

- \( P(x, t) \rightarrow \text{Gaussian (} t \rightarrow \infty \text{)} \) and kurtosis
  \[ \kappa(t) := \frac{\langle x^4(t) \rangle}{\langle x^2(t) \rangle^2} \rightarrow 3 \ (t \rightarrow \infty) \]
  for Brownian motion (green lines, in 1d)

- other solid lines: fits from our model; parameter values as before

**note:** model needs to be amended to explain short-time distributions

crossover from peaked to broad non-Gaussian distributions
The model

- **Fractional Klein-Kramers equation** ([Barkai, Silbey, 2000]):

\[
\frac{\partial P}{\partial t} = -\frac{\partial}{\partial x} [vP] + \frac{\partial^{1-\alpha}}{\partial t^{1-\alpha}} \kappa \left[ \frac{\partial}{\partial v} v + v_{th}^2 \frac{\partial^2}{\partial v^2} \right] P
\]

with probability distribution \( P = P(x, v, t) \), damping term \( \kappa \), thermal velocity \( v_{th}^2 = kT/m \) and Riemann-Liouville fractional derivative of order \( 1 - \alpha \)

for \( \alpha = 1 \) Langevin’s theory of Brownian motion recovered

- **analytical solutions** for \( msd(t) \) and \( P(x, t) \) can be obtained in terms of special functions ([Barkai, Silbey, 2000; Schneider, Wyss, 1989])

- model generates **anomalous dynamics different from Lévy walks**: no relation to Lévy hypothesis
Be careful with (power law) paradigms for data analysis.

A profound biological embedding is needed to better understand foraging, cf. Movement Ecology Paradigm

Much work to be done to test other types of anomalous stochastic processes for modeling foraging problems.
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  http://www.mipipks-dresden.mpg.de/~asg_2015

- **cell migration**: P.Dieterich (TU Dresden), R.Preuss (Garching), A.Schwab (U.Münster)

- **bumblebee flights**: F.Lenz, T.Ings, L.Chittka (all QMUL), A.V.Chechkin (Kharkov)

**Literature**: RK, *Search for food of birds, fish and insects*, book chapter in: A.Bunde et al. (Eds.), *Diffusive Spreading in Nature, Technology and Society*, p.49 (Springer, 2018); available on my homepage