Statistical Physics and Anomalous Dynamics of Foraging

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Models in Population Dynamics, Ecology and Evolution

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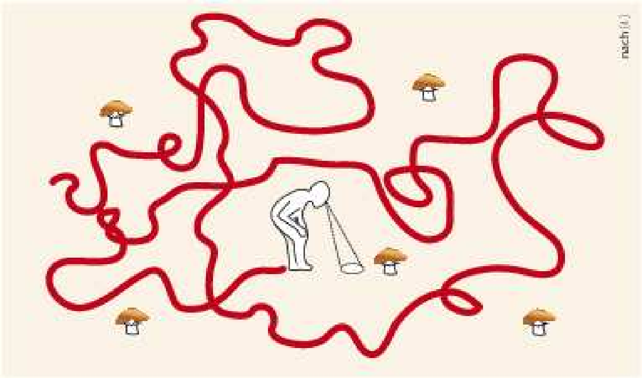
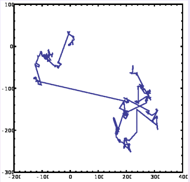
The main theme of this talk

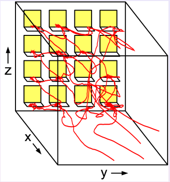
analyse **foraging movement patterns**

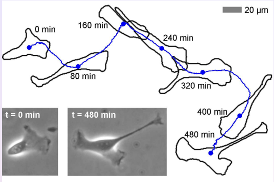


from: Chupeau et al., Nature Physics (2015)
News & Views in: RK, Physik Journal (2015) (in German)

Outline of this talk





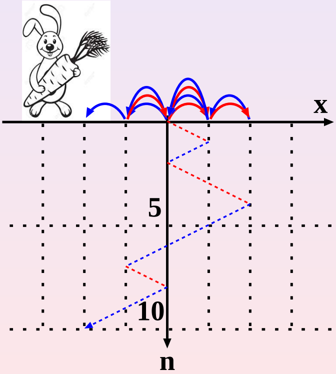


Understand **foraging movement patterns** of biological organisms in terms of **stochastic processes.**

1. Lévy flight foraging hypothesis: overview
2. biological data: analysis and interpretation
3. foraging bumblebees
4. cell migration

A mathematical theory of random migration

Karl Pearson (1906):
model movements of biological organisms by a **random walk** in one dimension: position x_n at discrete time step n



$$x_{n+1} = x_n + \ell_n$$

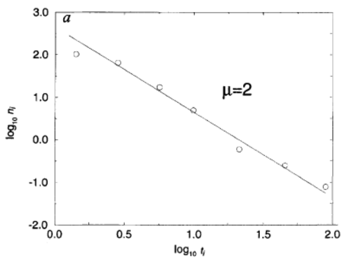
- *here:* steps of length $|\ell_n| = \ell$ to the left/right; sign determined by coin tossing
- Markov process: the steps are *uncorrelated*
- generates Gaussian distributions for x_n (central limit theorem)

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

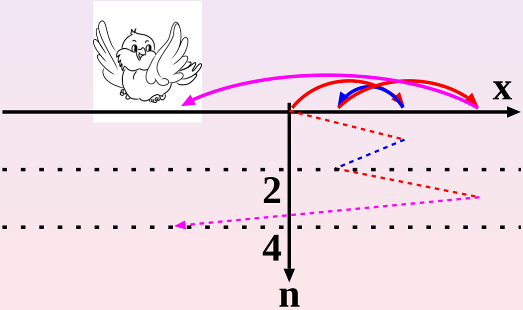
What are Lévy flights?

a random walk generating **Lévy flights**:

$x_{n+1} = x_n + \ell_n$ with ℓ_n drawn from a Lévy α-stable distribution

$$\rho(\ell_n) \sim |\ell_n|^{-1-\alpha} \; (|\ell_n| \gg 1) \; , \; 0 < \alpha < 2$$

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 α-stable (for $0 < \alpha \leq 2$)
  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

$$t_n = \ell_n / v \;,\; |v| = const.$$

  to complete a step; yields finite moments and finite velocities in contrast to Lévy flights

- Lévy walks generate anomalous (super) diffusion:

$$\langle x^2 \rangle \sim t^\gamma \; (t \to \infty) \text{ with } \gamma > 1$$

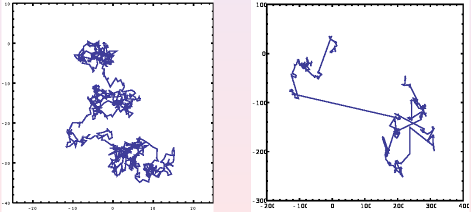
Zaburdaev et al., Rev.Mod.Phys. **87**, 483 (2015)
RK, Radons, Sokolov (Eds.), *Anomalous transport* (Wiley, 2008)

Optimizing the success of random searches

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, revisitable targets in unbounded domains*

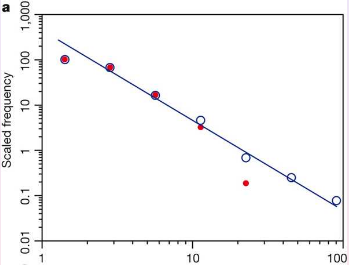


Brownian motion (left) vs. **Lévy flights** (right)

Revisiting Lévy flight search patterns

Edwards et al., Nature **449**, 1044 (2007):

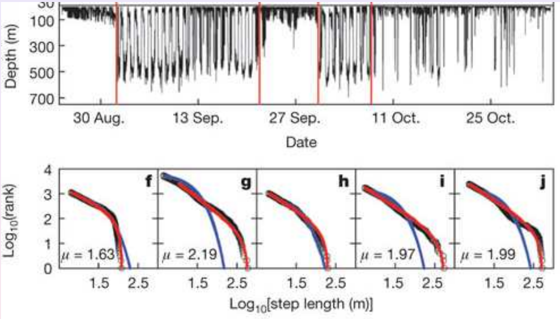
- Viswanathan et al. results revisited by correcting old data (Buchanan, Nature **453**, 714, 2008):



- **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)

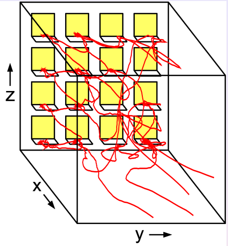
Beyond the Lévy Flight Foraging Hypothesis

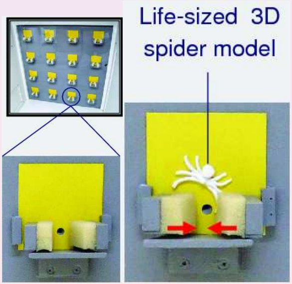
apply the Movement Ecology Paradigm to analyse foraging movement data:

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*





safe and **dangerous** flowers

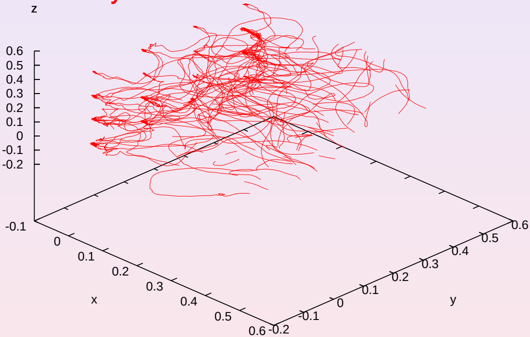
three experimental stages:

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

Ings, Chittka (2008)

Bumblebee experiment: two main questions

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

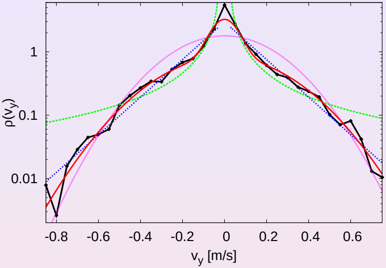


2. Are there changes of the dynamics under variation of the environmental conditions?

Flight velocity distributions

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

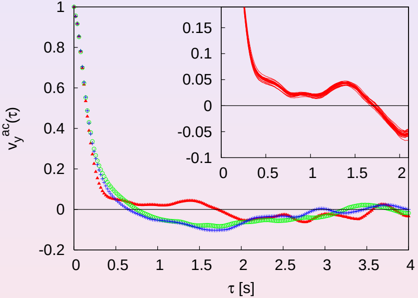


biological explanation: models spatially different flight modes near the flower vs. far away, cf. intermittent dynamics

big surprise: no difference in pdf's between different stages under variation of environmental conditions!

Velocity autocorrelation function || to the wall

$$V_y^{AC}(\tau) = \frac{\langle (v_y(t)-\mu)(v_y(t+\tau)-\mu)\rangle}{\sigma^2}$$



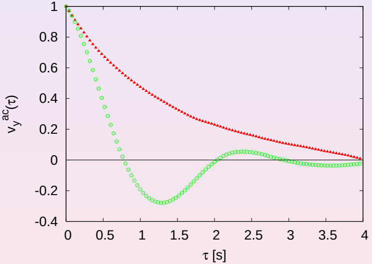
3 stages: spider-free, predation thread, memory test

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

model: Langevin equation

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

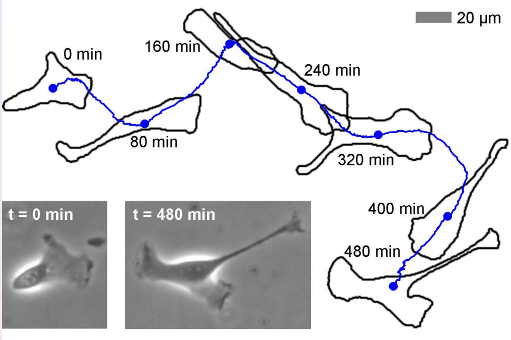
η: friction, ξ: Gauss. white noise



result: velocity correlations with repulsive interaction U bumblebee - spider off / on

Lenz, RK et al., PRL (2012)

Biological cell migration



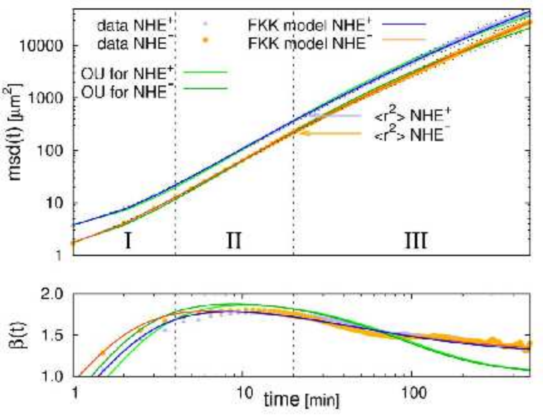
Dieterich, RK et al., PNAS (2008)

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

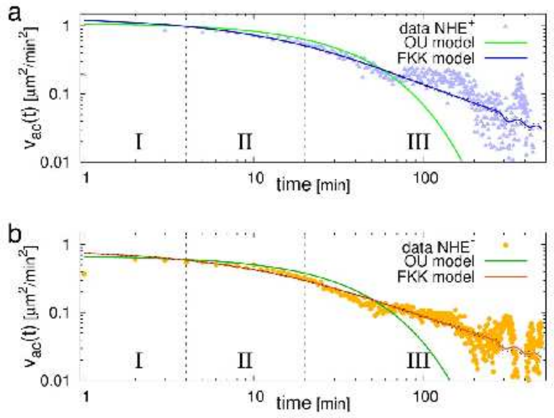
- $msd(t) := \langle [\mathbf{x}(t) - \mathbf{x}(0)]^2 \rangle \sim t^\beta$ with $\beta \to 2$ $(t \to 0)$ and $\beta \to 1$ $(t \to \infty)$ for Brownian motion; $\beta(t) = d \ln msd(t) / d \ln t$



anomalous diffusion if $\beta \neq 1$ $(t \to \infty)$; here: **superdiffusion**

Velocity autocorrelation function

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



crossover from **stretched exponential to power law**

Position distribution function

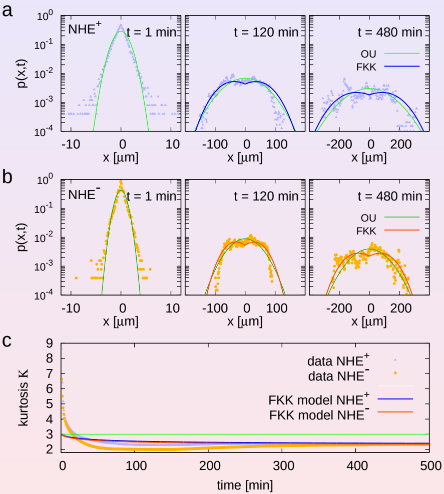
- $P(x,t) \to$ Gaussian $(t \to \infty)$ and kurtosis

$$\kappa(t) := \frac{\langle x^4(t)\rangle}{\langle x^2(t)\rangle^2} \to 3 \ (t \to \infty)$$

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):

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

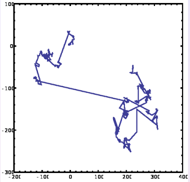
with probability distribution $P = P(x, v, t)$, damping term κ, thermal velocity $v_{th}^2 = kT/m$ and Riemann-Liouville fractional derivative of order $1-\alpha$

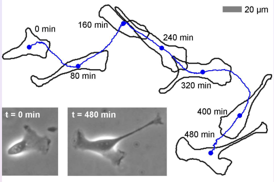
for $\alpha = 1$ Langevin's theory of Brownian motion recovered

- **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

Summary





- 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.

Acknowledgements and reference

- **Lévy Flight Hypothesis:** *Advanced Study Group* on Statistical physics and anomalous dynamics of foraging, MPIPKS Dresden (2015); F.Bartumeus (Blanes), D.Boyer (UNAM), A.V.Chechkin (Kharkov), L.Giuggioli (Bristol), *convenor:* RK (London), J.Pitchford (York) http://www.mpipks-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