Statistical Physics and Anomalous Dynamics of Foraging

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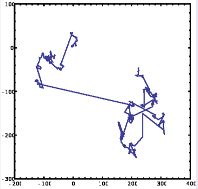
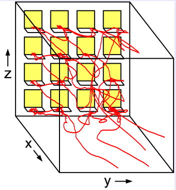
Institute of Theoretical Physics, 21 April 2016

Overview





Theme of this talk:

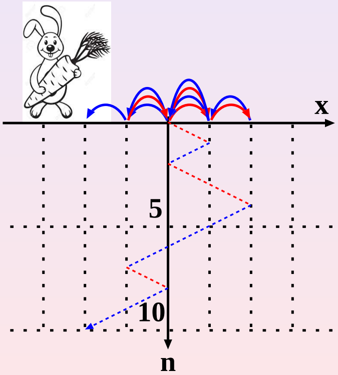
Can search for food by biological organisms be understood by mathematical modeling?

Three parts:

1. Lévy flight hypothesis: review
2. Biological data: analysis and interpretation
3. Foraging bumblebees: own research

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



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

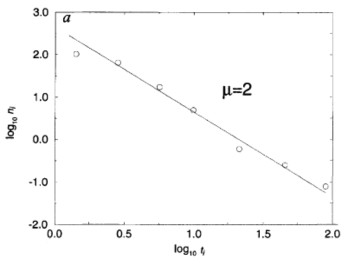
- *here:* steps of length $|\ell_n| = \ell$ to the left/right; sign determined by coin tossing
- Markov process: the steps are *uncorrelated*
- generates Gaussian distributions for x_n (central limit theorem)

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



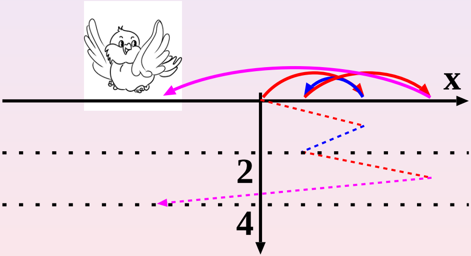
was fitted by a Lévy distribution (power law $\sim t^{-\mu}$)

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

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



- 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 $0 < \alpha < 2$)
  Gnedenko, Kolmogorov, 1949
- implying that they are scale invariant and thus self-similar
- $\rho(\ell_n)$ has 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

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

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

- Lévy walks generate anomalous (super) diffusion:

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

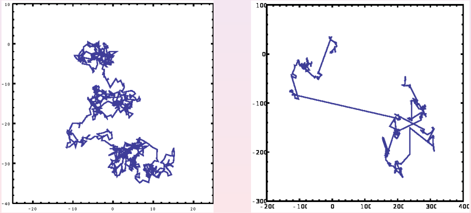
see Shlesinger at al., Nature **363**, 31 (1993) for an outline,
Zaburdaev et al., RMP **87**, 483 (2015) for details and
RK, Radons, Sokolov (Eds.), *Anomalous transport* (Wiley, 2008)

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*



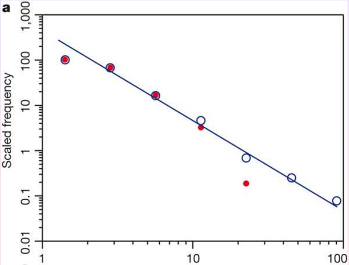
Brownian motion (left) vs. **Lévy flights** (right)

- Lévy flights also obtained for bumblebee and deer data

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):

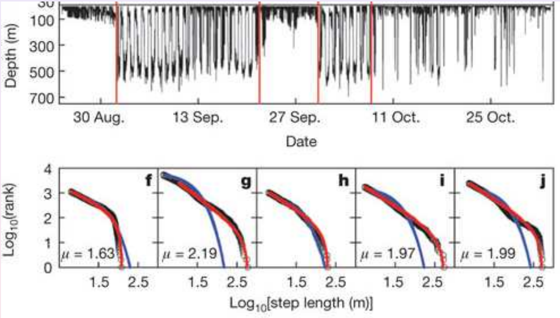


- **no Lévy flights:** new, more extensive data suggests (gamma distributed) stochastic process
- but claim that **truncated Lévy flights** fit yet new data Humphries et al., PNAS **109**, 7169 (2012)

Lévy or not Lévy?

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

- environmental context explains Lévy and Brownian movement patterns of marine predators
- but: averaged over day-night cycle, cf. oscillations!

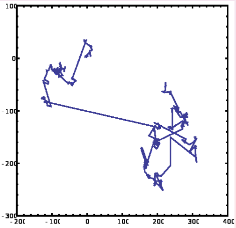
Optimal searches: adaptive or emergent?

strictly speaking **two different Lévy flight hypotheses:**

1. Lévy flights represent an (evolutionary) **adaptive** optimal search strategy

   Viswanathan et al. (1999)

   the 'conventional' Lévy flight hypothesis



2. Lévy flights **emerge** from the interaction with a scale-free food source distribution

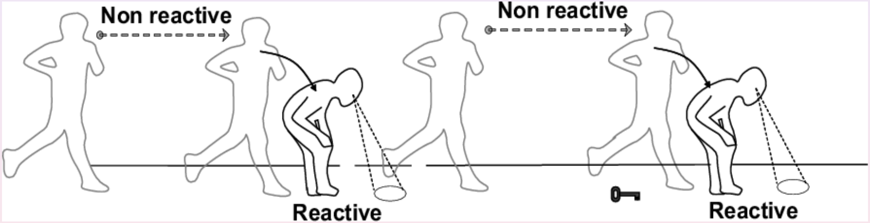
   Viswanathan et al. (1996)

   more recent reasoning

An alternative to Lévy flight search strategies

Bénichou et al., Rev. Mod. Phys. **83**, 81 (2011):

- for *non-revisitable targets* **intermittent** search strategies minimize the search time

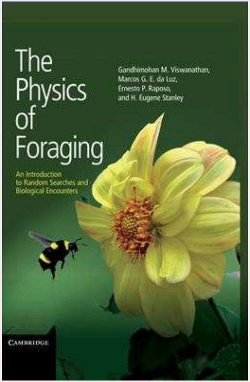


- popular account of this work in Shlesinger, Nature **443**, 281 (2006): "How to hunt a submarine?"; cf. also protein binding on DNA

In search of a mathematical foraging theory

Summary:

- two different Lévy flight hypothesis: **adaptive** and **emergent**
- scale-free Lévy flight paradigm
- problems with the data analysis
- intermittent search strategies as alternatives



Ongoing discussions:

• mussels: de Jager et al., Science (2011)

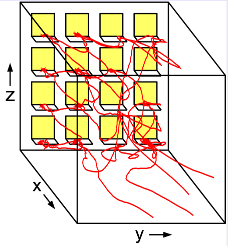
• cells perform Lévy walks: Harris et al., Nature (2012) or not: Dieterich, RK et al., PNAS (2008)

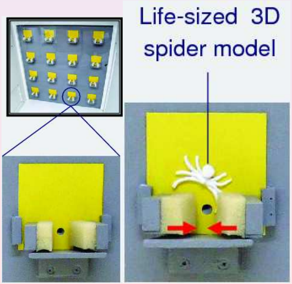
Applications:

• search algorithms for robots? Nurzaman et al. (2010)

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

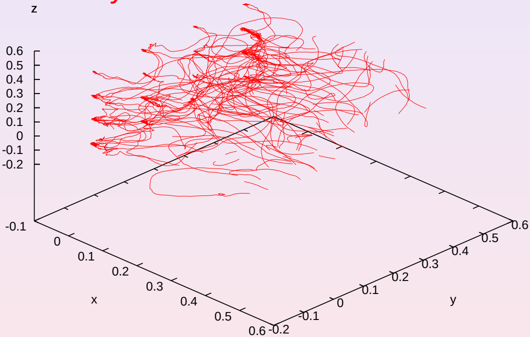
three experimental stages:

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?

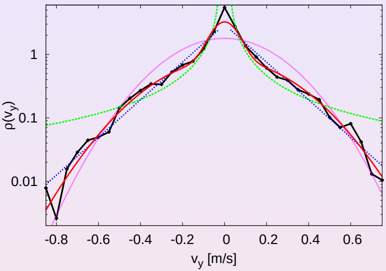


2. Are there changes of the dynamics under variation of the environmental conditions?

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

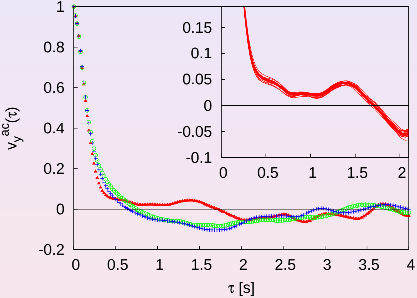


biological explanation: models spatially different flight modes near the flower vs. far away, cf. intermittent dynamics

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

Velocity autocorrelation function || to the wall

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



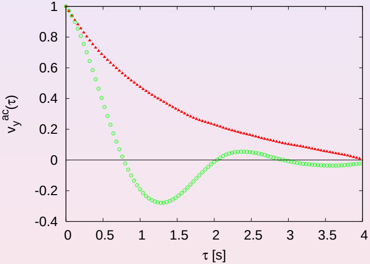
3 stages: spider-free, predation thread, memory test

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

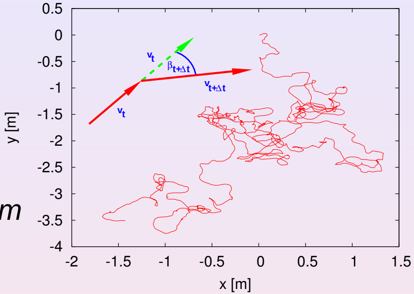
Lenz et al., PRL **108**, 098103 (2012)

Modeling free bumblebee flights

reorientation model:

describe 2d movement in comoving frame by

- speed $v(t) = const.$
- turning angle $\beta(t) = \xi(t)$ as random variable from *non-uniform pdf* modeling persistence

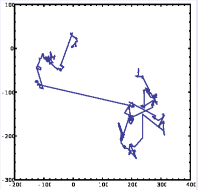


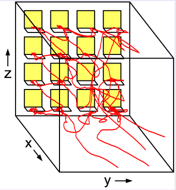
generalized model for bumblebee flights far away from flowers constructed from experimental data:

- $\beta(t) = \xi_v(t)$: power law correlated Gaussian noise
- $\frac{dv}{dt} = g(v(t)) + \psi(t)$: generalized Langevin equation with anti-correlated Gaussian noise

F.Lenz, A.V.Chechkin, RK, PLoS ONE 8, e59036 (2013)

Summary





- Be careful with (power law) paradigms for data analysis.
- Other quantities may contain crucial information about foraging; **example:** bumblebee flights under predation thread.
- **Conclusion:**
  A more general biological embedding is needed!

Statistical physics in Movement Ecology

beyond the Lévy hypothesis:

to be published

Bartumeus, Boyer, Chechkin, Giuggioli, RK, Pitchford, Watkins (2015)

Advanced Study Group

Statistical physics and anomalous dynamics of foraging

MPIPKS Dresden, July - December 2015

F.Bartumeus (Blanes, Spain), D.Boyer (UNAM, Mexico), A.V.Chechkin (Kharkov, Ukraine), L.Giuggioli (Bristol, UK), *convenor:* RK (London, UK), J.Pitchford (York, UK)

ASG webpage: http://www.mpipks-dresden.mpg.de/~asg_2015

Literature:

RK, *Extrem gesucht*, Physik Journal 14(12), 22 (2015)

RK, *Search for food of birds, fish and insects*, book chapter (preprint, 2016)