Statistical Physics and Anomalous Dynamics of Foraging

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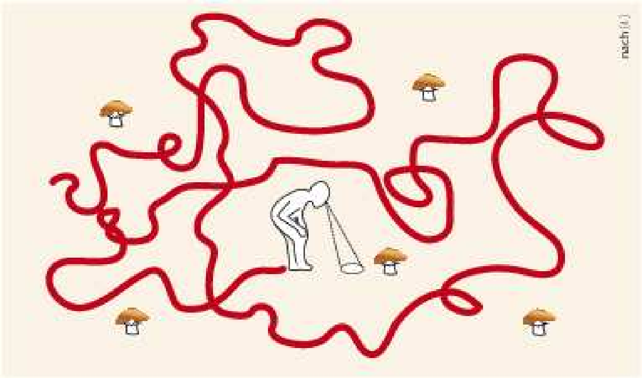
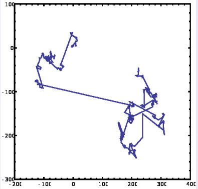
4th Workshop on Fractional Calculus, probability and Non-Local Operators: Applications and Recent Developments; BCAM, 24 November 2016

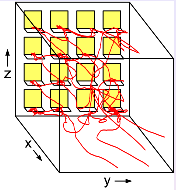
The problem



from: Chupeau, Nature Physics (2015)

Outline of my talk





Theme of this talk:

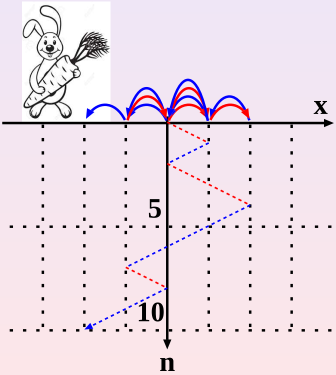
Can search for food by biological organisms be understood by mathematical modeling?

Three parts:

1. Lévy flight hypothesis: review
2. Biological data: analysis and interpretation
3. Stochastic modeling: fractional calculus and non-local operators

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



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

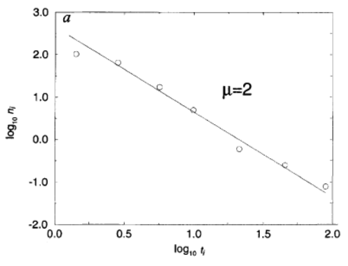
- *here:* steps of length $|\ell_n| = \ell$ to the left/right; sign determined by coin tossing
- Markov process: the steps are *uncorrelated*
- generates Gaussian distributions for x_n (central limit theorem)

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 $\sim t^{-\mu}$)

- may be due to the food distribution on the ocean surface being scale invariant: **Lévy Environmental Hypothesis**

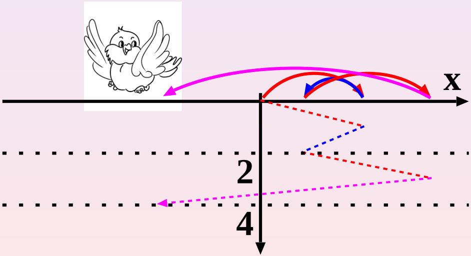
What are Lévy flights?

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 $0 < \alpha < 2$)

  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 $v_n = \ell_n / 1$
- position pdf given by the fractional diffusion equation

$$\frac{\partial f(x,t)}{\partial t} = K_\alpha \frac{\partial^\alpha f(x,t)}{\partial |x|^\alpha}$$

  with Riesz fract. derivative $\sim -|k|^\alpha f(k,t)$ in Fourier space

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

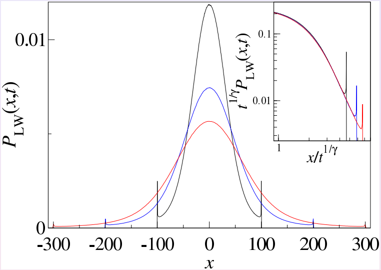
- Lévy walks generate anomalous (super) diffusion:

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

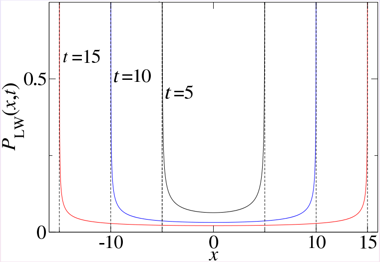
see Shlesinger at al., Nature **363**, 31 (1993) for an outline; RK, Radons, Sokolov (Eds.), *Anomalous transport* (Wiley, 2008)

Position distribution functions for Lévy walks

$1 < \alpha < 2$



$0 < \alpha < 1$



Zaburdaev et al., RMP **87**, 483 (2015)

topic of very recent research:

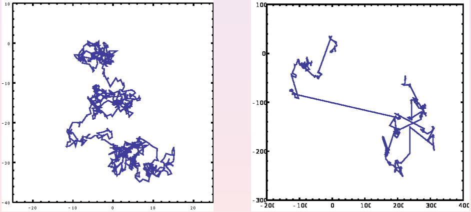
- derivation of an integrodifferential wave equation for a Lévy walk: Fedotov, PRE (2016)
- analytical formulas for densities of multidimensional Lévy walks: Magdziarz, Zorawik, PRE (2016)

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*



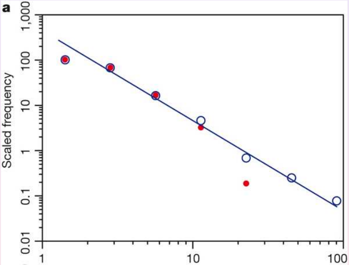
Brownian motion (left) vs. **Lévy flights** (right)

- yields the *second* **Lévy Foraging Hypothesis**

Revisiting Lévy flight search patterns

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

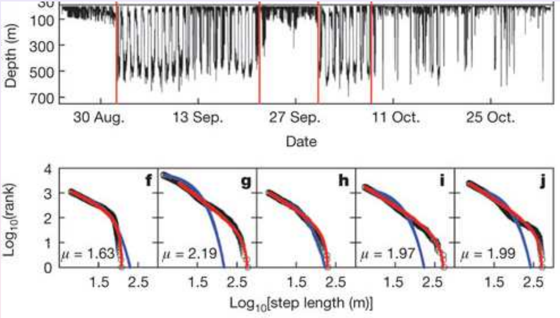
- Viswanathan et al. results revisited by correcting old data (Buchanan, Nature **453**, 714, 2008):



- **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

Summary: two different Lévy Flight Hypotheses

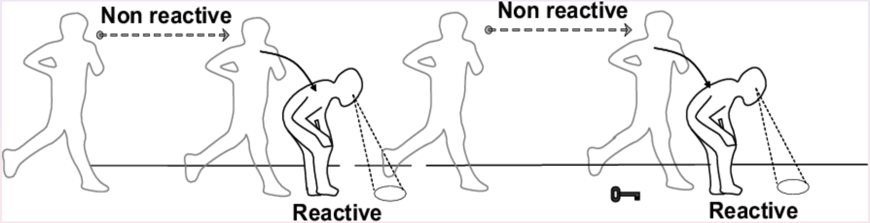
to be published

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

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

Beyond the Lévy Flight Hypothesis

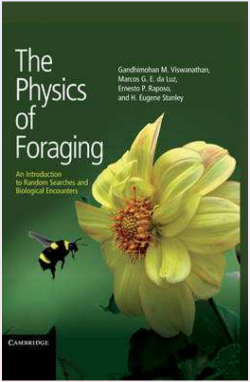
to be published

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

In search of a mathematical foraging theory

Summary:

- scale-free Lévy flight paradigm
- problems with the data analysis
- two Lévy Flight Hypotheses: **adaptive** and **emergent**
- intermittent search as an alternative
- need to go beyond the Lévy Flight Hypotheses



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)

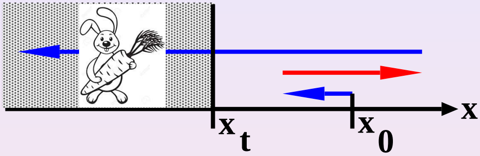
Applications:

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

Searching for a single target

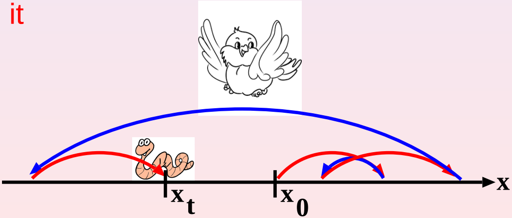
two basic types of foraging (James et al., 2010):

1. **cruise forager:** detects a target while moving



first passage problem

2. **saltaltory forager:** only detects a target when landing on it / next to it



first arrival problem

First passage and first arrival: solutions

1. **Brownian motion:**

   $$\varrho_{FP}(t) \sim t^{-3/2} \sim \varrho_{FA}(t)$$

   Sparre-Andersen Theorem (1954)

2. **Lévy flights:**

   $\varrho_{FP}(t) \sim t^{-3/2}$ (Chechkin et al., 2003; numerics only)

   $\varrho_{FA}(t) = 0 \ (0 < \alpha \leq 1)$; $\varrho_{FA}(t) \sim t^{-2+1/\alpha} \ (1 < \alpha < 2)$

   (Palyulin et al., 2014)

3. **Lévy walks:**

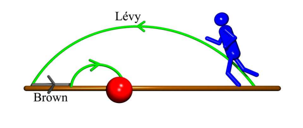
   $\varrho_{FP}(t) \sim t^{-1-\alpha/2} \ (0 < \alpha \leq 1)$; $\varrho_{FP}(t) \sim t^{-3/2} \ (1 < \alpha < 2)$

   (numerics: Korabel, Barkai (2011); analytically: Artuso et al., 2014)

   $\varrho_{FA}(t)$: the same as for Lévy flights, cf. simulations

   (Blackburn et al., 2016)

Combined Lévy-Brownian motion search



- intermittency modeled by the fractional diffusion equation

$$\frac{\partial f(x,t)}{\partial t} = K_\alpha \frac{\partial^\alpha f(x,t)}{\partial |x|^\alpha} + K_B \frac{\partial^2 f(x,t)}{\partial x^2}$$

with Riesz fractional derivative (see before)

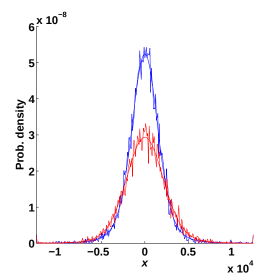
- define search reliability by cumulative probability P of reaching a target: $P = \lim_{s\to 0} \int_0^\infty \varrho_{FA}(t) \exp(-st) dt$
- **result:** Brownian motion regularizes Lévy search, $0 < P < 1$ for $0 < \alpha < 1$
- define and calculate search efficiency by

$$\varepsilon = \langle \text{visited \# targets}/\text{\# steps} \rangle \simeq \langle 1/t \rangle = \int_0^\infty \varrho_{FA}(s) ds$$

Palyulin et al., JPA, 2016

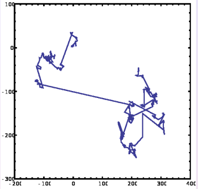
Deriving Lévy-Brownian motion from a Lévy walk

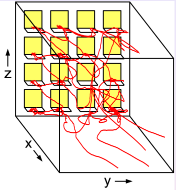
- model short-range *n*-dim correlated Lévy walks by a fractional Klein-Kramers equation (Friedrich et al., 2006)
- for $1 < \alpha < 2$ derive system of moment equations combined with a Cattaneo truncation scheme
- leads to the same fractional diffusion equation in the long time limit as seen before
- *however:*



Taylor-King et al., PRE, 2016

Summary





- Be careful with (power law) paradigms for data analysis.
- A more general biological embedding is needed to better understand foraging.
- Much work to be done to apply other types of anomalous stochastic processes for modeling foraging problems.

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