Statistical Physics and Anomalous Dynamics of Foraging

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

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

- 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 $0 < \alpha < 2$)
  
  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
  \[ t_n = v \ell_n, \ |v| = \text{const.} \]
  to complete a step; yields finite moments and finite velocities in contrast to Lévy flights

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

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


- 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:

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*

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

\[ V_{y}^{AC}(\tau) = \frac{\langle (v_{y}(t) - \mu)(v_{y}(t + \tau) - \mu) \rangle}{\sigma^2} \]

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

**model:** Langevin equation

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

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

result: velocity correlations with repulsive interaction \( U \)

bumblebee - spider off / on

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

all changes are in the flight correlations, *not* in the pdfs
Modeling free bumblebee flights

**reorientation model:**
describe 2d movement in comoving frame by
- speed \( v(t) = \text{const.} \)
- 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

Be careful with (power law) paradigms for data analysis.

Other quantities may contain crucial information about foraging; example: bumblebee flights under predation threat.

Conclusion:
A more general biological embedding is needed!
beyond the Lévy hypothesis:

to be published

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

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