Statistical physics and anomalous dynamics of foraging

Rainer Klages

Queen Mary University of London, School of Mathematical Sciences

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Motivation

Statistical physics of foraging:

Can biologically relevant search strategies be identified by mathematical modeling?

3 parts:

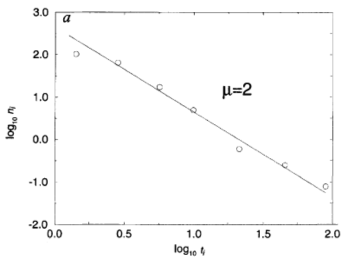
1. the albatross story and the Lévy flight hypothesis
2. biological data: analysis and interpretation
3. own research in this direction

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 distribution of flight times was fitted with a Lévy flight model (power law)



Lévy flights in a nutshell

Lévy flights have **well-defined mathematical properties**:

- a Markovian stochastic process *(no memory)*
- with probability distribution function of flight lengths exhibiting power law tails, $\rho(\ell) \sim \ell^{-1-\alpha}$, $0 < \alpha < 2$;
- it has infinite variance, $< \ell^2 >= \infty$,
- satisfies a generalized central limit theorem (Gnedenko, Kolmogorov, 1949) and
- is **scale invariant**

for an outline see, e.g., Shlesinger at al., Nature **363**, 31 (1993)

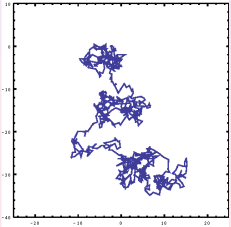
(remark: $\exists$ the more physical model of *Lévy walks*)

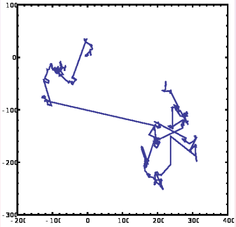
Optimizing the success of random searches

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 *sparsely, randomly distributed, revisitable* targets





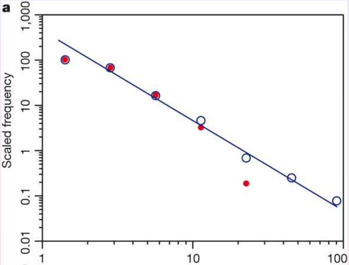
Brownian motion (left) vs. **Lévy flights** (right)

- 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):

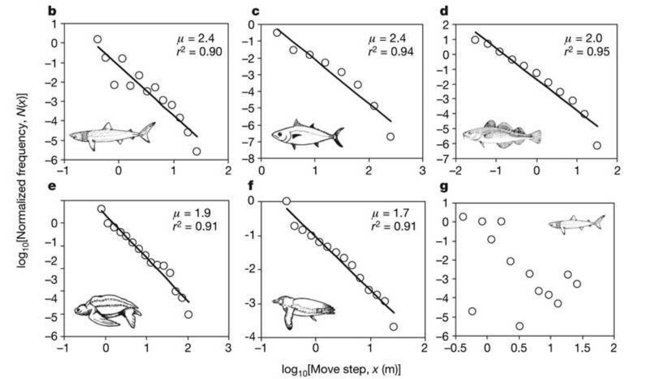


- no Lévy flights: new, more extensive data suggests (gamma distributed) stochastic process
- **but** claim that truncated Lévy flights fit yet new data Humphries et al., PNAS **109**, 7169 (2012)

Lévy or not Lévy?

Lévy **paradigm**: Look for *power law tails* in pdfs!

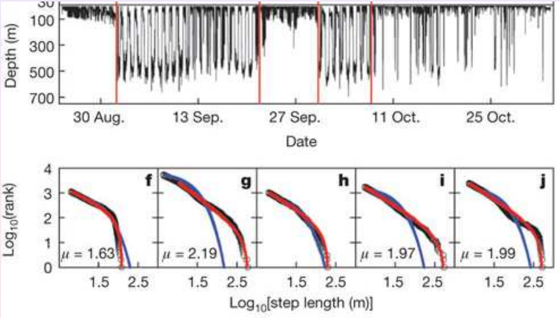
- Sims et al., Nature **451**, 1098 (2008): scaling laws of marine predator search behaviour; $> 10^6$ data points!



- prey distributions also display Lévy-like patterns...

Lévy flights induced by the environment?

- Humphries et al., Nature **465**, 1066 (2010): environmental context explains Lévy and Brownian movement patterns of marine predators; $> 10^7$ data points!; for blue shark:



blue: exponential; red: truncated power law

- **note:** $\exists$ day-night cycle, cf. oscillations; suggests to fit with two different pdfs (not done)

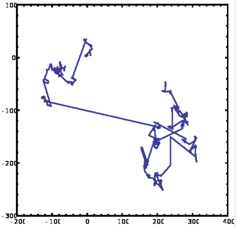
Optimal searches: adaptive or emergent?

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)

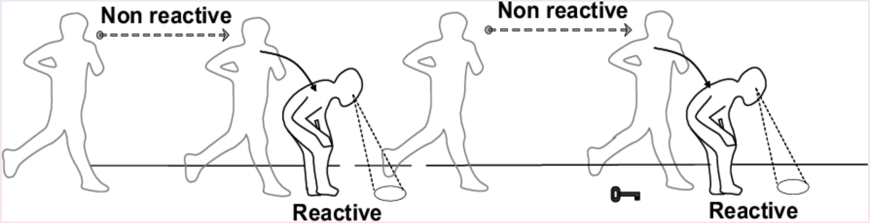
   more recent reasoning

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

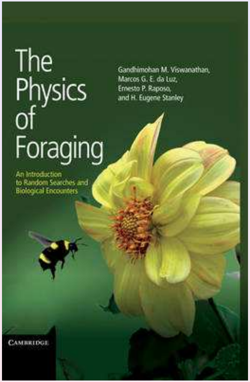


- popular account of this work in Shlesinger, Nature **443**, 281 (2006): "How to hunt a submarine?"; cf. also protein binding on DNA

In search of a mathematical foraging theory

Summary:

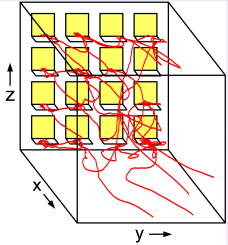
- two different Lévy flight hypothesis: **adaptive** and **emergent**
- scale-free Lévy flight paradigm
- problems with the data analysis
- intermittent search strategies as alternatives



⇒ **discussion is ongoing:** spider monkeys (2004); mussels (2011); ...

Foraging bumblebees

- tracking of **bumblebee flights** in the lab
- foraging in an artificial carpet of **flowers with or without spiders**



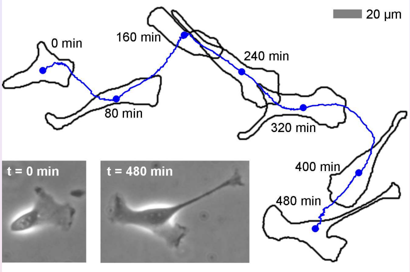
note: no test of the Lévy hypothesis but work inspired by the 'paradigm'

main result of data analysis and stochastic modeling:
no change in the **velocity pdf** under predation thread; only change in the **velocity autocorrelation function**

F.Lenz, T.Ings, A.V.Chechkin, L.Chittka, R.K., Phys. Rev. Lett. **108**, 098103 (2012)

Lévy motion of migrating cells?

single biological cell crawling on a substrate:



- T-cells perform (generalized) Lévy walks:
  T.H. Harris et al., Nature **486**, 545 (2012)
- our (earlier) finding for kidney cells:
  - for long times superdiffusion but not Lévy
  - different dynamics on different time scales instead of scale-free

Dieterich et al., PNAS **105**, 459 (2008)

Summary

- Be careful with **(power law) paradigms** for data analysis:

  '... the better fit of the complex model ... trades off with the elegance and clarity of the simpler model.' (?)

  de Jager et al., Science (2012)

- Other quantities **(correlation functions)** can contain crucial information about interactions between forager and environment

suggestion: replace the question

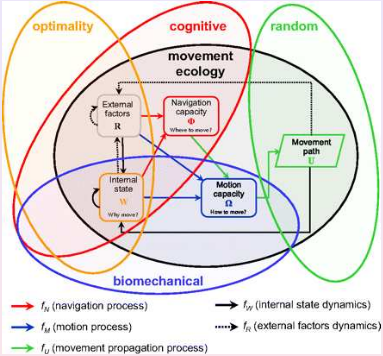
What is the mathematically **most efficient search strategy**?

by the more fundamental question

How can we **statistically quantify** changes in foraging dynamics due to **interactions with the environment**?

Outlook

This conclusion fits to the **Movement Ecology Paradigm**:



Nathan et al., PNAS **105**, 19052 (2008)

Mathematically, this suggests a state space approach

$$\mathbf{u}_{t+1} = F(\mathbf{\Omega}, \mathbf{\Phi}, \mathbf{r}_t, \mathbf{w}_t, \mathbf{u}_t)$$

for the location $\mathbf{u}_t$ of an organism at time t.