Statistical Physics and Anomalous Dynamics of Foraging

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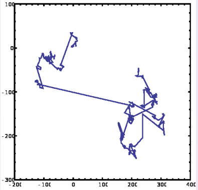
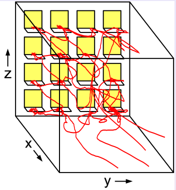
Advanced Study Group 2015 on foraging





- **Topic:** Statistical physics and anomalous dynamics of foraging
- **Team:** 1 convenor and 5 team members
- **Duration:** 6 months from July 1st until December 31st, 2015
- **Concept:** bring together a team of experts working on the chosen topic, supported by a vivid visitors programme

Motivation

Main theme:

Can biologically relevant search strategies be identified by mathematical modeling?

Four parts of this talk:

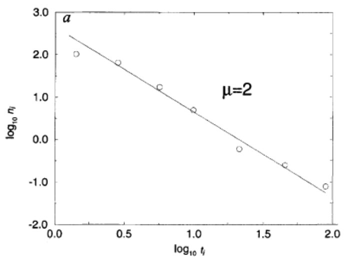
1. review the Lévy flight hypothesis
2. biological data: analysis and interpretation
3. own research: cell migration and foraging bumblebees
4. ASG: the team and key topics

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



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)

• for more details: A.V.Chechkin et al., *Introduction to the theory of Lévy flights* in: R. Klages, G.Radons, I.M.Sokolov (Eds.), *Anomalous transport* (Wiley-VCH, 2008)

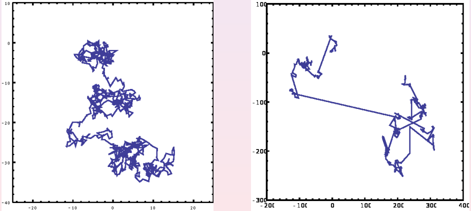
nb: $\exists$ the more physical model of *Lévy walks*; Zaburdaev et al., RMP **87**, 483 (2015)

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*



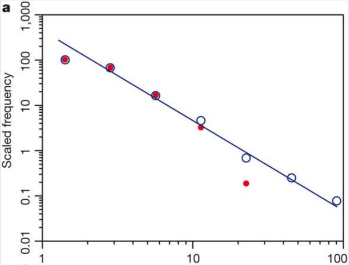
Brownian motion (left) vs. **Lévy flights** (right)

- 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):

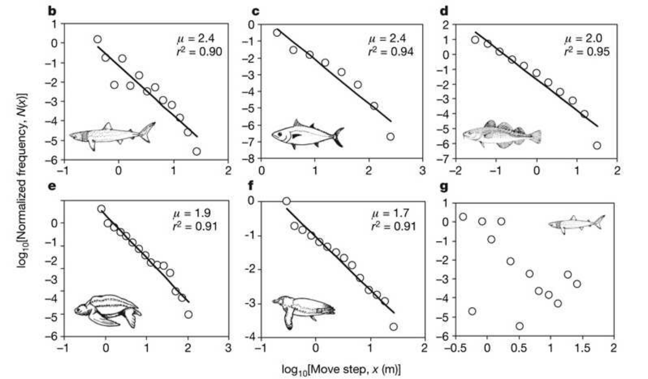


- **no Lévy flights:** new, more extensive data suggests (gamma distributed) stochastic process
- but claim that **truncated Lévy flights** fit yet new data Humphries et al., PNAS **109**, 7169 (2012) (and reply...)

Lévy or not Lévy?

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

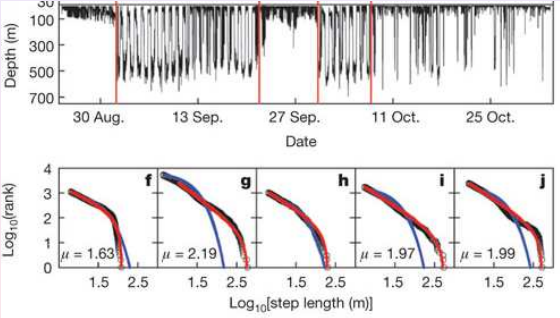
- Sims et al., Nature **451**, 1098 (2008): scaling laws of marine predator search behaviour; $> 10^6$ data points!



- 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)

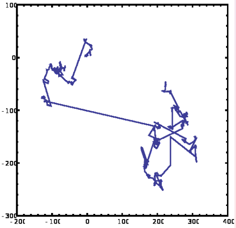
Optimal searches: adaptive or emergent?

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

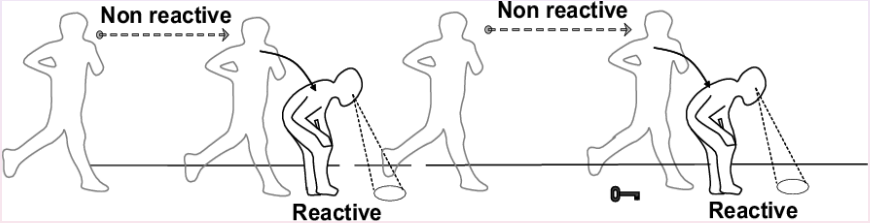
   Viswanathan et al. (1996)

   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

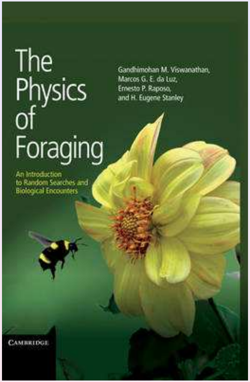


- popular account of this work in Shlesinger, Nature **443**, 281 (2006): "How to hunt a submarine?"; cf. also protein binding on DNA

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



$\Rightarrow$ **ongoing discussions:**

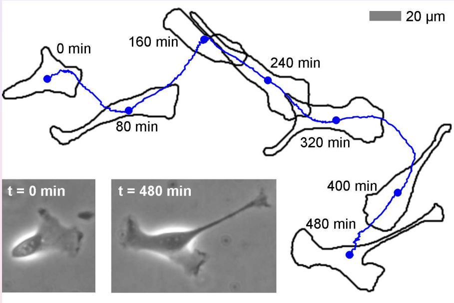
• spider monkeys: Ramos-Fernandez et al., Beh. Ecol. Sociobiol. (2004)

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

• ...

Own work: Lévy motion of migrating cells?

single biological (MDCK-F) cell crawling on a substrate:

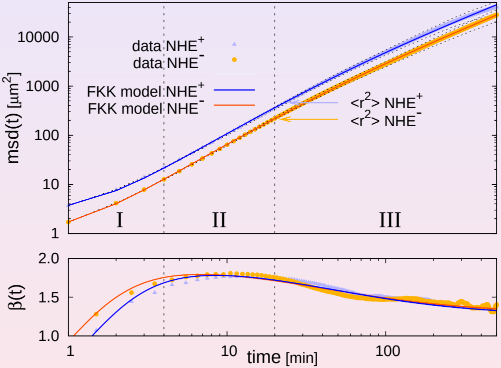


Dieterich, RK, Preuss, Schwab, PNAS **105**, 459 (2008)

two types: wildtype (NHE+) and NHE-deficient (NHE-)

Experimental results I: mean square displacement

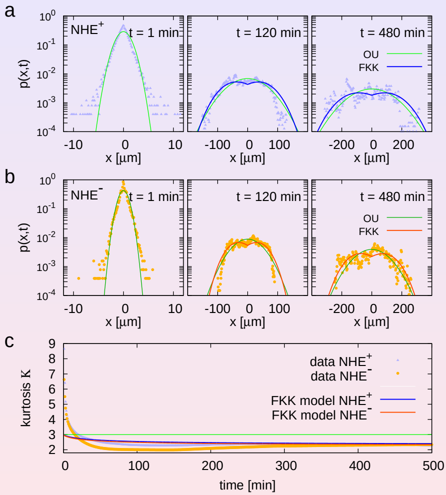
- $msd(t) :=< [\mathbf{x}(t) - \mathbf{x}(0)]^2 >\sim t^\beta$ and time dependent exponent $\beta(t) = d \ln msd(t)/d \ln t$



- different dynamics on different time scales with superdiffusion for long times; *not* scale-free!

(*solid lines:* (Bayes) fits from our model)

Experimental results II: position distribution function



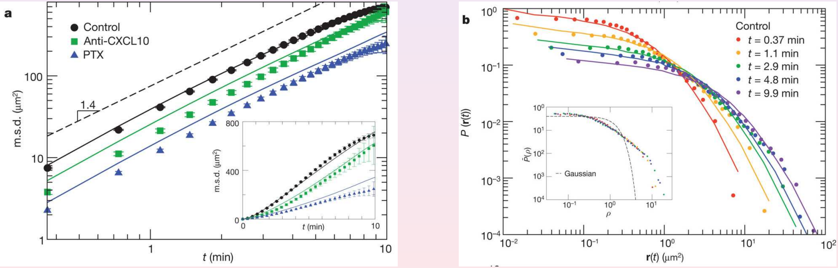
- green lines: results for Brownian motion
- *other solid lines:* fits from our model; parameter values as before

- non-Lévy distributions with different dynamics on different time scales

Generalized Lévy walks for migrating T cells

T.H. Harris et al., Nature **486**, 545 (2012):

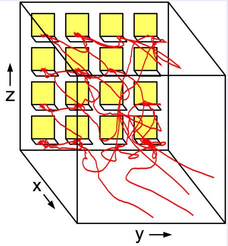
- T cell motility described by a generalized Lévy walk (Zumofen, Klafter, 1995); claim: more efficient than Brownian motion
- mean square displacement (for 3 different cell types) and position distribution function:



- microscopic justification of the model?
- pdf not Lévy: how does the result fit to the Lévy hypothesis?

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)

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)

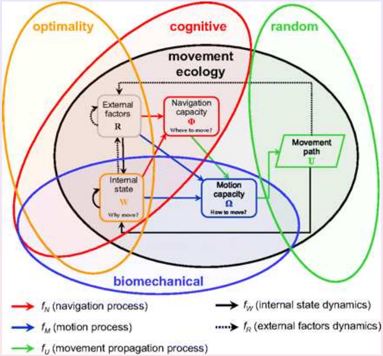
- Other quantities can contain crucial information about interactions between forager and environment (e.g., correlation functions)

- Palyulin, Chechkin, Metzler, PNAS (2014):

  'The main message from this study is that Lévy flight search and its optimization is sensitive to the exact conditions.'

Perspective

more general approach by 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.

The ASG team

- **experiments on foraging and data analysis:**
  - Frederic Bartumeus (Blanes, Spain)
  - Jon Pitchford (York, UK)
- **statistical physics applied to foraging:**
  - Denis Boyer (UNAM, Mexico)
  - Luca Giuggioli (Bristol, UK)
- **statistical physics and anomalous dynamics applied to biology:**
  - Aleksei Chechkin (Kharkov, Ukraine)
  - RK (London, UK)

Key topics and activities

1. Critically assess the Lévy hypothesis.
2. Test other types of anomalous stochastic dynamics for modeling foraging.
3. How to define optimality for foraging?
4. Assess the influence of external environmental constraints on foraging.
5. Assess the influence of internal conditions of a forager on foraging.
6. Study collective foraging.

- informal focus workshop 9-10 September 2015
- check out the ASG webpage: http://www.mpipks-dresden.mpg.de/˜asg_2015