Search for Food of Birds, Fish and Insects

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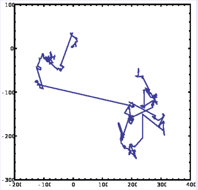
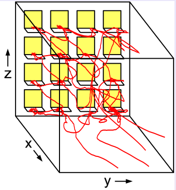
Diffusion Fundamentals VI, Technische Universität Dresden
26 August 2015

Overview





Theme of this talk:

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

Three parts:

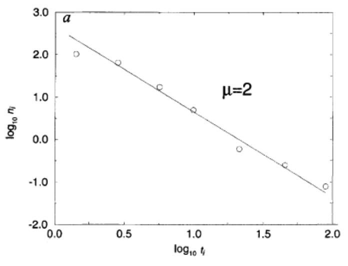
1. Lévy flight hypothesis: review
2. Biological data: analysis and interpretation
3. Foraging bumblebees: own research

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



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)

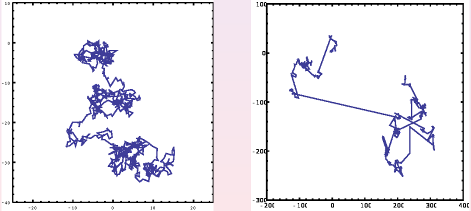
more realistic are *Lévy walks*; Zaburdaev et al., RMP **87**, 483 (2015)

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*



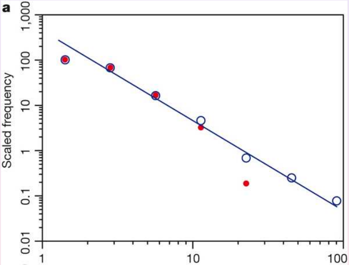
Brownian motion (left) vs. **Lévy flights** (right)

- 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):

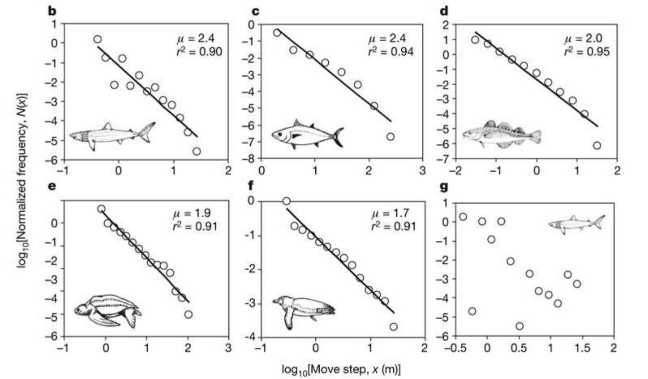


- **no Lévy flights:** new, more extensive data suggests (gamma distributed) stochastic process
- but claim that **truncated Lévy flights** fit yet new data Humphries et al., PNAS **109**, 7169 (2012) (and reply...)

Lévy or not Lévy?

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

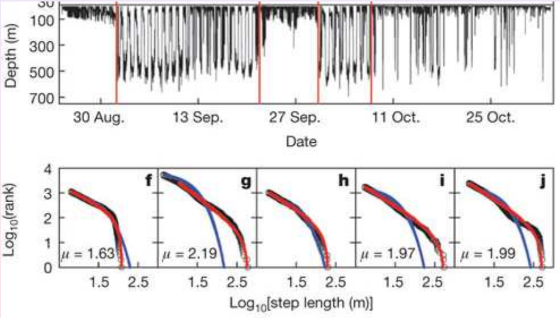
- Sims et al., Nature **451**, 1098 (2008): scaling laws of marine predator search behaviour; $> 10^6$ data points!



- 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)

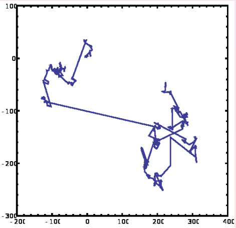
Optimal searches: adaptive or emergent?

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

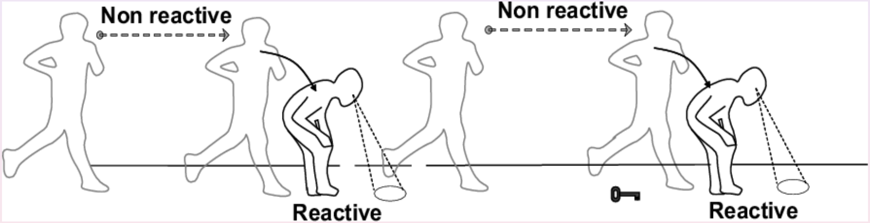
   Viswanathan et al. (1996)

   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

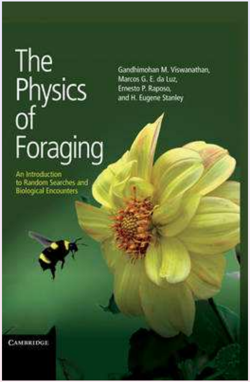


- popular account of this work in Shlesinger, Nature **443**, 281 (2006): “How to hunt a submarine?”; cf. also protein binding on DNA

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



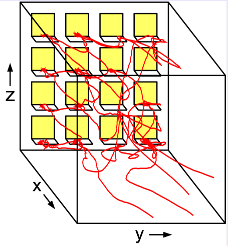
⇒ **ongoing discussions:**

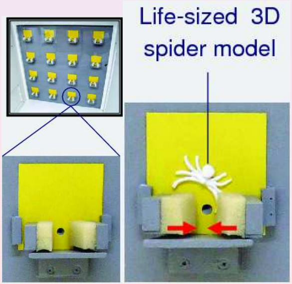
• mussels: de Jager et al., Science (2011)

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

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

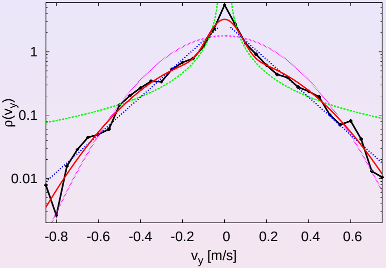
three experimental stages:

1. spider-free foraging
2. foraging under predation risk
3. memory test 1 day later

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

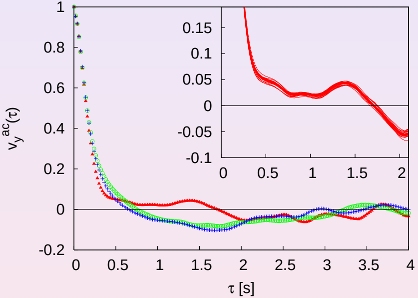


biological explanation: models spatially different flight modes near the flower vs. far away, cf. intermittent dynamics

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

Velocity autocorrelation function || to the wall

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



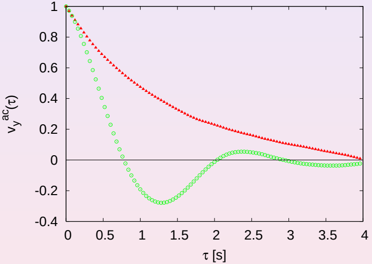
3 stages: spider-free, predation thread, memory test

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

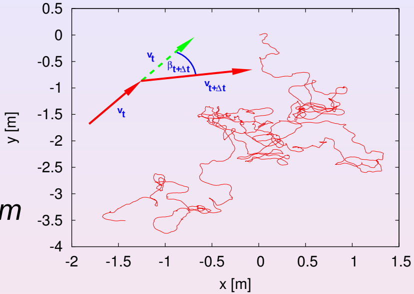
Lenz et al., PRL **108**, 098103 (2012)

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

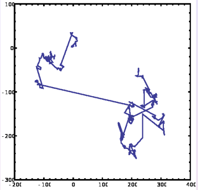


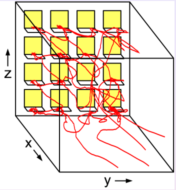
generalized model for bumblebee flights far away from flowers constructed from experimental data:

- $\beta(t) = \xi_v(t)$: 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, R.K., PLoS ONE 8, e59036 (2013)

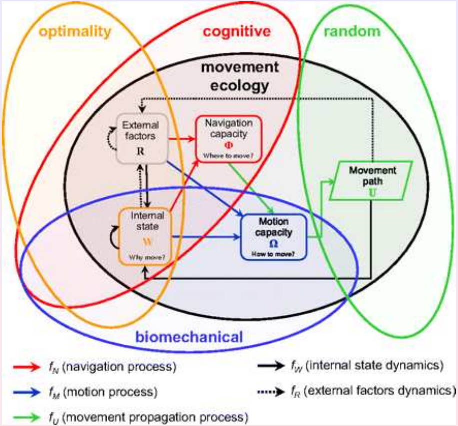
Summary





- 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!

Perspective: Movement Ecology Paradigm



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

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

Outlook: more to come...

Advanced Study Group on

Statistical physics and anomalous dynamics of foraging

MPIPKS Dresden, July - Dec. 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

Acknowledgement - bumblebee research:

joint work with F.Lenz, T.Ings, A.V.Chechkin and L.Chittka