The Physics of Foraging: Bumblebee Flights under Predation Risk

Friedrich Lenz[1] Thomas C. Ings[2] Lars Chittka[2]
Aleksei V. Chechkin[3] Rainer Klages[1]

[1]Queen Mary University of London, School of Mathematical Sciences

[2]Queen Mary University of London, Biological and Chemical Sciences

[3]Institute for Theoretical Physics NSC KIPT, Kharkov, Ukraine

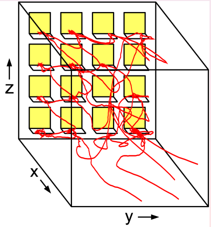
INI Colloquium Series
University and ETH Zurich, 25 October 2013

Outline

1. **The physics of foraging:**
   Can biologically relevant search strategies be identified by mathematical modeling?

- the albatross story and the Lévy flight hypothesis
- further biological data, their analysis and interpretation

2. **Bumblebees foraging under predation risk:**
   - the experiment
   - the analysis
   - the modeling



Part 1:

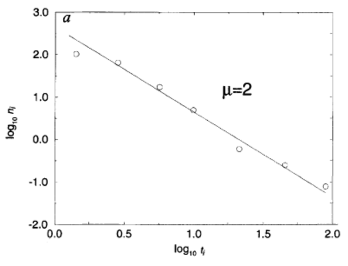
The Physics of Foraging

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)

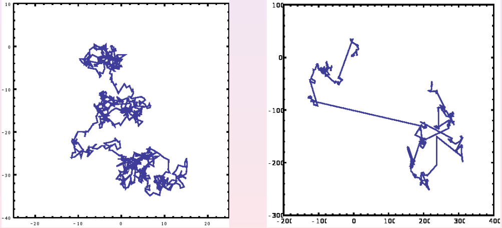
(remark: $\exists$ the more physical model of *Lévy walks*)

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



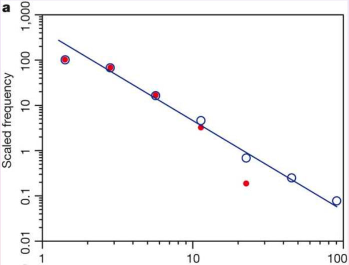
Brownian motion (left) vs. **Lévy flights** (right)

- 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):

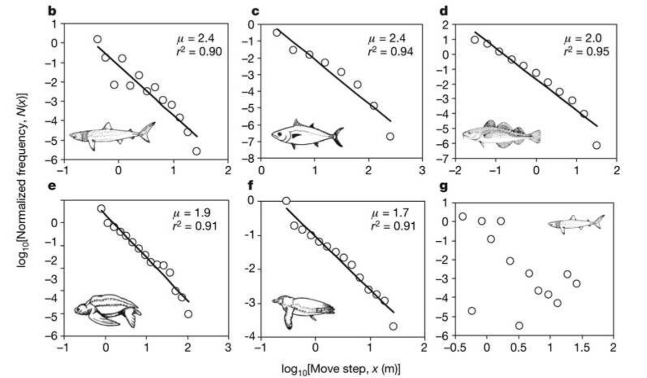


- no Lévy flights: new, more extensive data suggests (gamma distributed) stochastic process
- **but** claim that truncated Lévy flights fit yet new data Humphries et al., PNAS **109**, 7169 (2012)

Lévy or not Lévy?

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

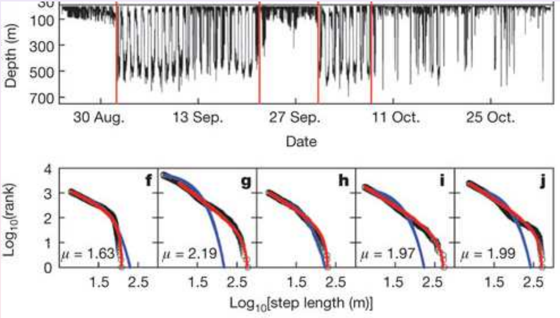
- Sims et al., Nature **451**, 1098 (2008): scaling laws of marine predator search behaviour; $> 10^6$ data points!



- 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)

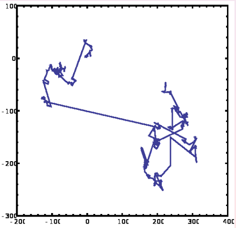
Optimal searches: adaptive or emergent?

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

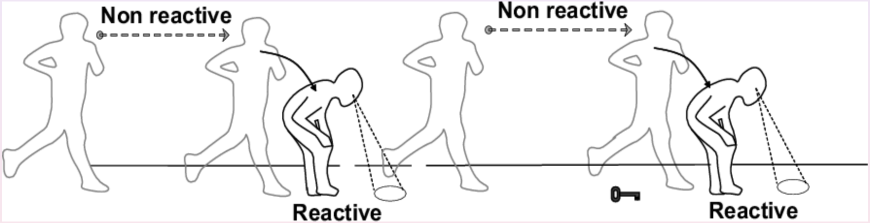
   Viswanathan et al. (1996)

   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

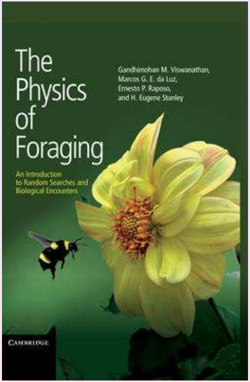


- popular account of this work in Shlesinger, Nature **443**, 281 (2006): "How to hunt a submarine?"; cf. also protein binding on DNA

In search of a mathematical foraging theory

Summary of Part 1:

- 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); biological cell migration (2008, 2012); mussels (2011); ...

Part 2:

Bumblebee Foraging under Predation Risk

Motivation: bumblebees

bumblebee foraging – two very practical problems:

1. find food (nectar, pollen) in complex landscapes

2. try to avoid **predators**

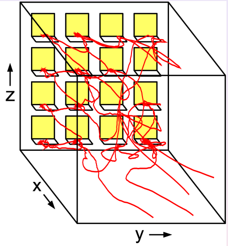
What type of motion?

Study bumblebee foraging in a *laboratory experiment*.

The bumblebee experiment

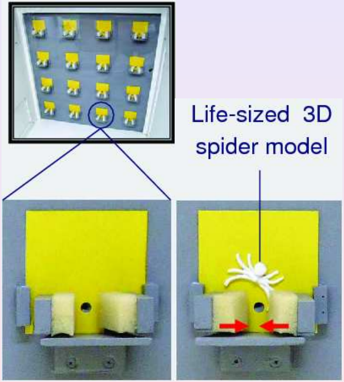
Ings, Chittka, Current Biology **18**, 1520 (2008):
bumblebee foraging in a cube of $\simeq$ 75cm side length

- artificial yellow flowers: 4x4 grid on one wall
- two cameras track the position (50fps) of a single bumblebee *(Bombus terrestris)*



- **advantages:** systematic variation of the environment; easier than tracking bumblebees on large scales
- **disadvantage:** no typical free flight of bumblebees; no test of the Lévy *hypothesis* (*but* questioning of the Lévy *paradigm*!)

Variation of the environmental conditions



safe and **dangerous**
flowers

movie

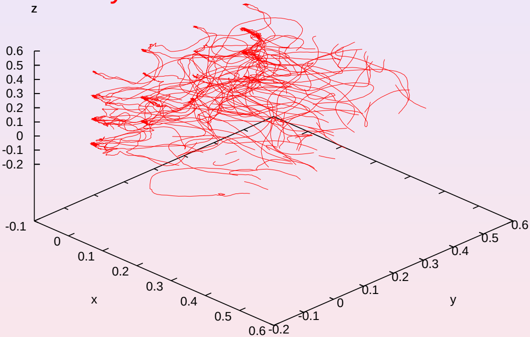
three experimental stages:

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

#bumblebees=30 , #data per bumblebee for each stage $\approx$ 7000

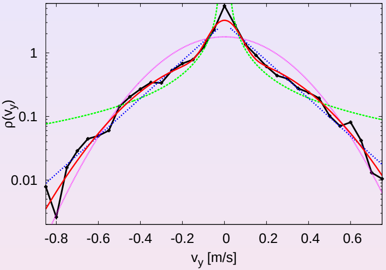
Bumblebee experiment: two main questions

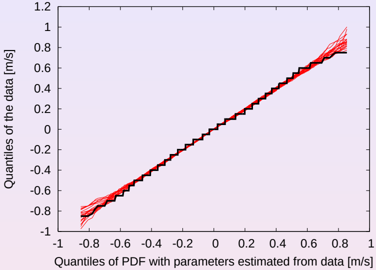
1. What type of motion do the bumblebees perform in terms of stochastic dynamics?



2. Are there changes of the dynamics under variation of the environmental conditions?

Velocity distributions: analysis





left: experimental data yielding **pdf of v_y-velocities** of a single bumblebee in the spider-free stage (black crosses) with max. likelihood fits of mixture of 2 Gaussians; exponential; power law; single Gaussian

right: **quantile-quantile plot** of a Gaussian mixture against the experimental data (black) plus surrogate data

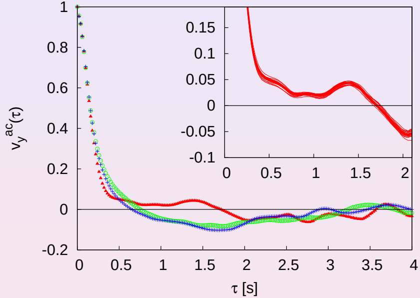
Velocity distributions: interpretation

- **best fit** to the data by a mixture of two Gaussians with different variances (verified by information criteria with resp. weights)
- **biological explanation:** models spatially different flight modes near the flower vs. far away, cf. intermittent dynamics
- no contradiction to Lévy *hypothesis*; but **Lévy *paradigm*** 'suggests': all relevant information captured by pdfs

$\Rightarrow$ **big surprise: no difference in pdfs** between different stages under variation of environmental conditions!

Velocity autocorrelation function $\parallel$ to the wall

$V_y^{AC}(\tau) = \frac{\langle (v_y(t)-\mu)(v_y(t+\tau)-\mu)\rangle}{\sigma^2}$ with average over all bees:

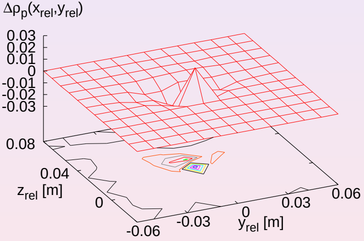


- plot: spider-free stage, predation thread, memory test
- **correlations change** from positive (spider-free) to negative (spiders)

$\Rightarrow$ $\boxed{\text{all } \textbf{changes} \text{ are in the } \textbf{velocity correlations}, \textit{not} \text{ in pdfs!}}$

Predator avoidance and a simple model

predator avoidance as difference in position pdfs spider / no spider from data:

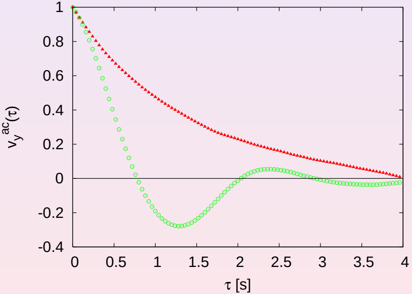


positive spike: *hovering*;
negative region: *avoidance*

modeled by Langevin equation

$$\frac{dv_y}{dt}(t) = -\eta v_y(t) - \frac{\partial U}{\partial y}(y(t)) + \xi(t)$$

η: friction coefficient,
ξ: Gaussian white noise



simulated velocity correlations with repulsive interaction potential U bumblebee - spider off / on

Clever bumblebees!

Summary of Part 2:

- mixture of **two Gaussian velocity distributions** reflects spatial adjustment of bumblebee dynamics to flower carpet
- all changes to predation thread are contained in the **velocity autocorrelation functions** that exhibit highly non-trivial temporal behaviour
- no problem with the **Lévy *hypothesis*** but with the Lévy *paradigm*, which suggests that all relevant foraging information is contained in *scale-free* pdfs
- change of correlation decay in the presence of spiders due to **experimentally extracted repulsive force** as reproduced by Langevin dynamics

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)

- **Correlation functions** can contain crucial information about interactions between forager and environment

suggestion: replace the question

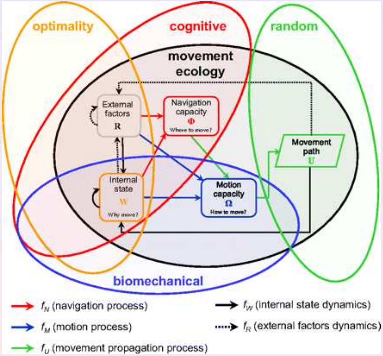
What is the mathematically **most efficient search strategy**?

by the more fundamental question

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

Outlook

Our 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.

References

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

We also have a stochastic model for *free* bumblebee flights:
F.Lenz, A.V.Chechkin, R.K., PLoS ONE 8, e59036 (2013)