The Physics of Foraging: Bumblebee Flights under Predation Risk

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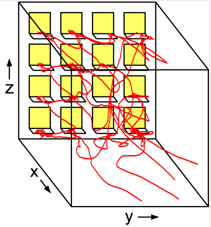
Outline

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:

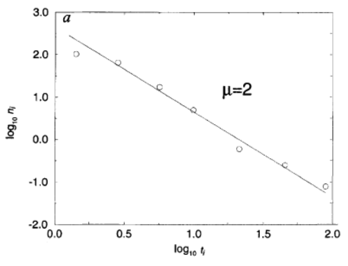
The Physics of Foraging

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
- with probability distribution function of flight lengths exhibiting power law tails, $\rho(\ell) \simeq \ell^{-1-\alpha}$, $0 < \alpha < 2$;
- 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)

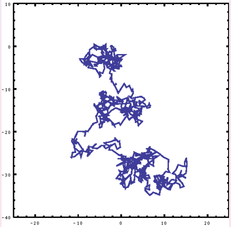
(remark: $\exists$ the more physical model of *Lévy walks*)

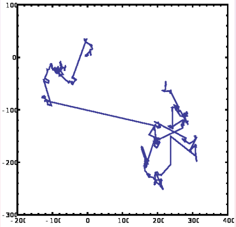
Optimizing the success of random searches

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:**

  Lèvy flights provide an *optimal search strategy* for *sparsely, randomly distributed, revisitable* targets





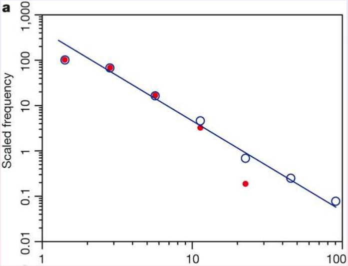
Brownian motion (left) vs. **Lévy flights** (right)

- 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):

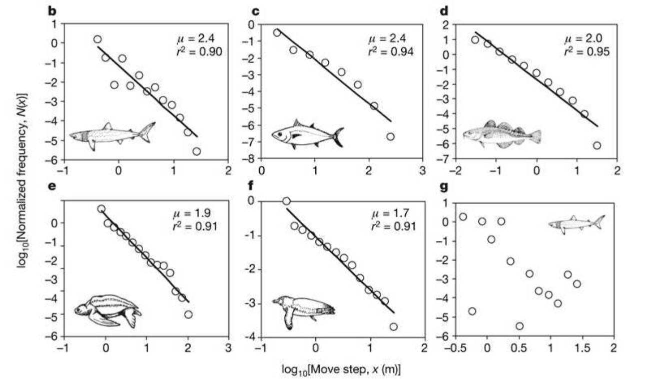


- Lévy flight behavior clearly ruled out: On the basis of new, more precise data some other (gamma distributed) stochastic process revealed
- refined data analysis yields no evidence for Lévy flights in bumblebee and deer data either

Lévy or not Lévy?

Lévy **paradigm**: Look for *power law tails* in pdf's!

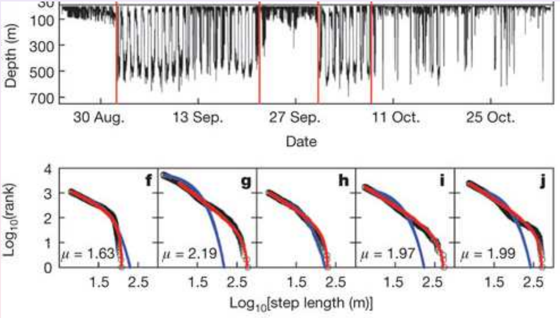
- Sims et al., Nature **451**, 1098 (2008): scaling laws of marine predator search behaviour; $> 10^6$ data points!



- 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!



blue: exponential; red: truncated power law

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

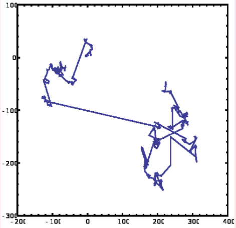
Optimal searches: adaptive or emergent?

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

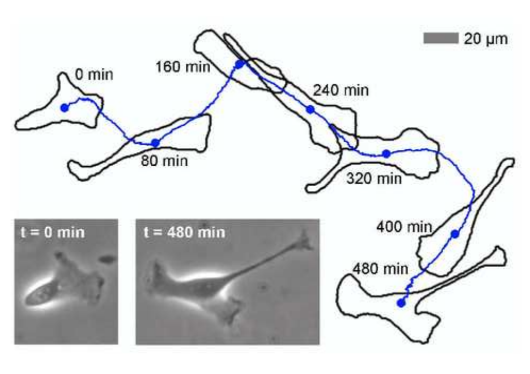
   Viswanathan et al. (1996)

   more recent reasoning

Biological cell migration: further trouble

suggested by Reynolds (Physica A, 2009) that biological cells also perform Lévy dynamics

single biological cell crawling on a substrate; trajectory recorded with a video camera (Dieterich et al., PNAS, 2008)



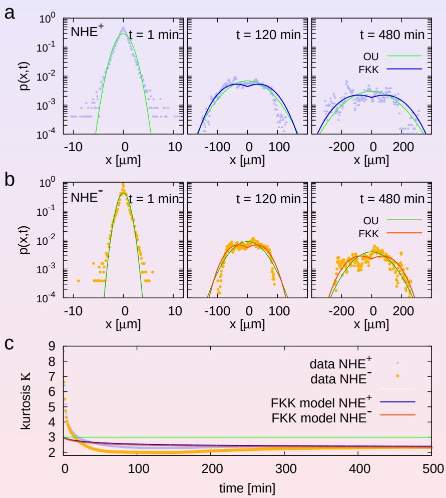
Position distribution function for cell migration

- **two types:** wildtype and deficient one
- $P(x,t) \rightarrow$ Gaussian $(t \rightarrow \infty)$ and kurtosis

$$\kappa(t) := \frac{<x^4(t)>}{<x^2(t)>^2} \rightarrow 3 \; (t \rightarrow \infty)$$

for Brownian motion (green lines, in 1d)

- **other solid lines:** fits from our model
- **also extracted:** mean square displacement, velocity autocorrelation fct.

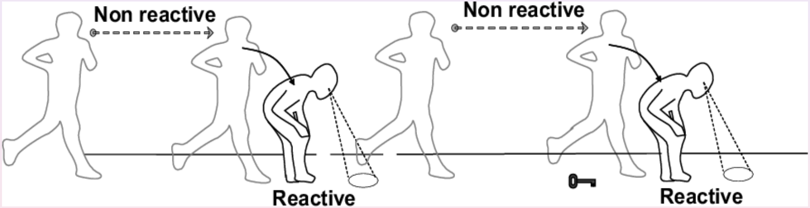


$\Rightarrow$ crossover from peaked to broad **non-Gaussian distributions**

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

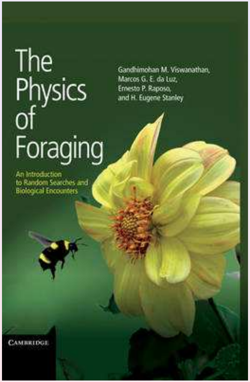


- popular account of this work in Shlesinger, Nature **443**, 281 (2006): “How to hunt a submarine?”
- cf. also protein binding on DNA

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
- different dynamics on **different time scales** and intermittent search strategies



Part 2:

Bumblebee Flights under Predation Risk

Motivation

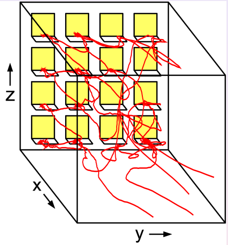
find food (nectar, pollen) in complex landscapes

try to avoid **predators**

The bumblebee experiment

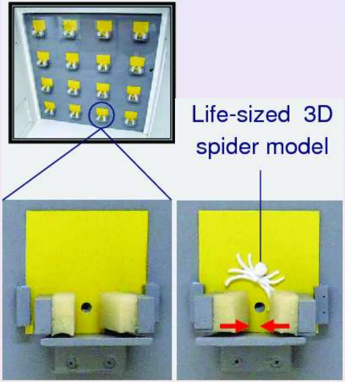
Ings, Chittka, Current Biology **18**, 1520 (2008):
bumblebee foraging in a cube of $\simeq$ 75cm side length

- 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

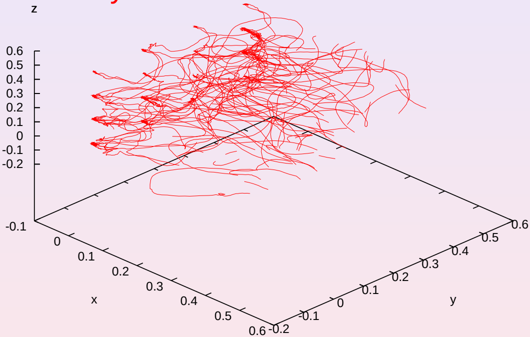
movie

- **two types** of artificial **spiders:** white (easily visible) and yellow (cryptic)
- **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

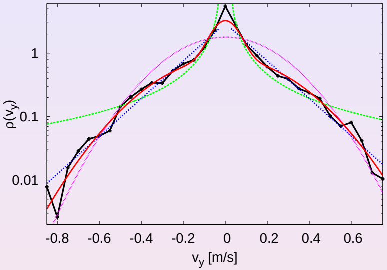
Bumblebee experiment: two main questions

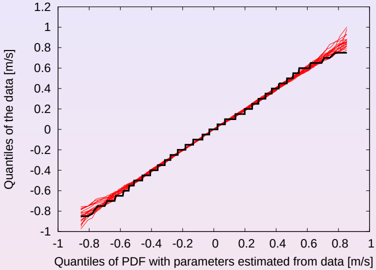
1. What type of motion do the bumblebees perform in terms of stochastic dynamics?



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

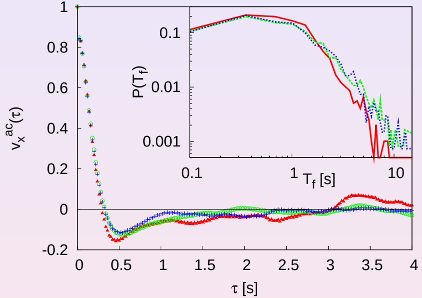
Velocity distributions: interpretation

- **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 pdf's

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

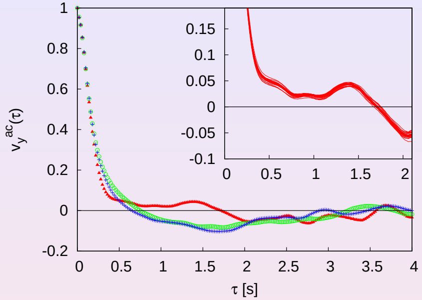
Velocity autocorrelation function ⊥ to the wall

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



- plot: spider-free stage, predation thread, memory test
- ∃ **anti-correlations** for $\tau \simeq 0.5$: bees return to flowers
- only small **quantitative changes** under predation thread, cf. shift of minimum in $V_x^{AC}(\tau)$ and changes in pdf of flight times (inset): more flights with long durations

Velocity autocorrelation function $\|$ to the wall



- plot: spider-free stage, predation thread, memory test
- $\exists$ **profound qualitative change** of correlations from positive for spider-free to negative in case of spiders
- resampling of data (inset) confirms existence of positive correlations

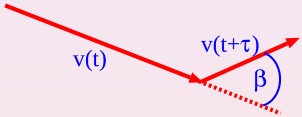
$\Rightarrow$ all **changes** are in the **velocity correlations**, *not* the pdf's!

Mathematical modeling of bumblebee flights

- trivial modeling of data via **overdamped Langevin eq.**:
  $$\mathbf{v} = \chi_{\mathsf{fz}}(\mathbf{r})\xi_1(t) + (1 - \chi_{\mathsf{fz}}(\mathbf{r}))\xi_2(t)$$
  with chararacteristic function of feeding zone χ_{fz} and Gaussian noise ξ_i , $i = 1, 2$ *correlated* according to velocity correlation of data: **non-Brownian motion**

- advanced modeling via **Langevin eq. in comoving frame**:

$$\dot{\beta} = -\gamma\beta + \xi_v(t)$$
$$\dot{v} = g(v) + \xi(t)$$



with nonlinear drift term $g(v)$, noise $\xi_v(t), \xi(t)$ and noise correlations to be determined from data (work in progress): generalized *correlated random walk model*

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 pdf's
- bumblebees exhibit strongly non-Brownian motion: modeling by **generalized Langevin dynamics**

Conclusion

suggestion: replace the fundamental question

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

by

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

(Is nature necessarily 'simple'?)

reference:

F.Lenz, T.Ings, A.V.Chechkin, L.Chittka, R.Klages, *Spatio-temporal dynamics of bumblebees foraging under predation risk*, arXiv:1108.1278 (2011)

nb: pdf-file of the talk available on homepage RK