# The Physics of Foraging: Bumblebee Flights under Predation Risk

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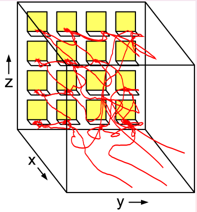
Colloquium on Complex and Biological Systems
University of Potsdam, 16 November 2012

# 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




3. **Modeling bumblebee flights**

# Part 1:

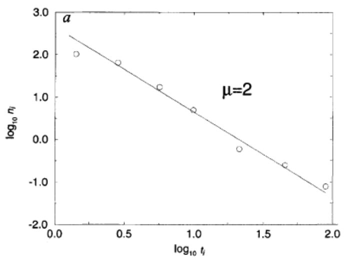
# The Physics of Foraging

# 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)

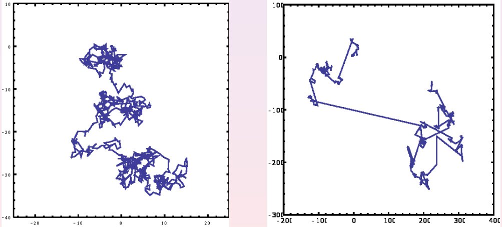
(remark: $\exists$ the more physical model of *Lévy walks*)

# 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



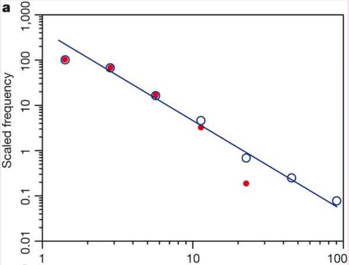

Brownian motion (left) vs. **Lévy flights** (right)

- 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):

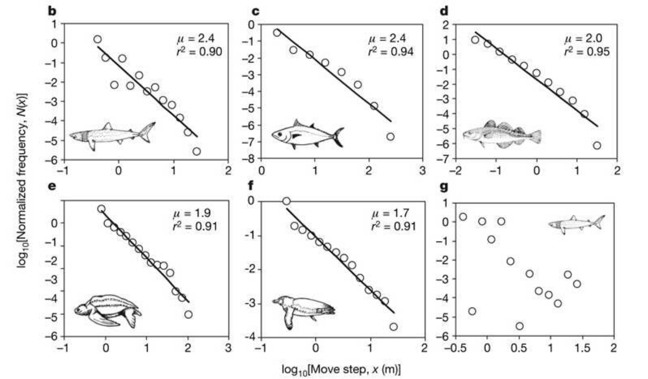



- no Lévy flights: new, more extensive data suggests (gamma distributed) stochastic process
- **but** claim that truncated Lévy flights fit yet new data Humphries et al., PNAS **109**, 7169 (2012)

# Lévy or not Lévy?

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

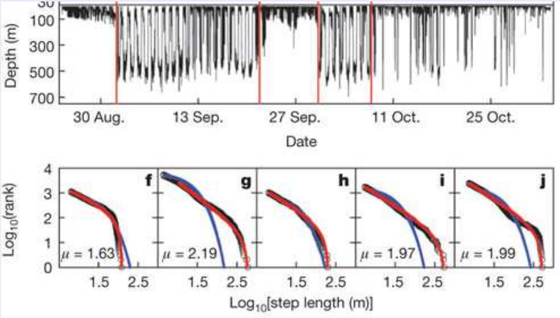
- Sims et al., Nature **451**, 1098 (2008): scaling laws of marine predator search behaviour; $> 10^6$ data points!




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

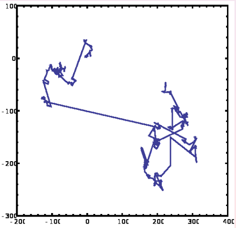
# Optimal searches: adaptive or emergent?

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

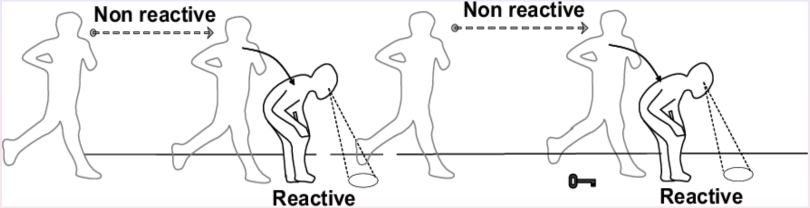
   Viswanathan et al. (1996)

   *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

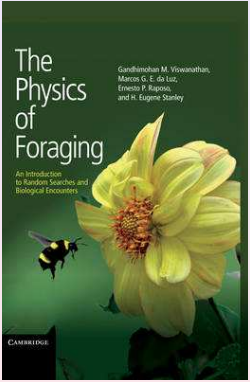



- popular account of this work in Shlesinger, Nature **443**, 281 (2006): "How to hunt a submarine?"; cf. also protein binding on DNA
- approach extended by Lomholt et al., PNAS **105**, 11055 (2008) to intermittent search with Lévy relocations for rare revisitable targets

# 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 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**

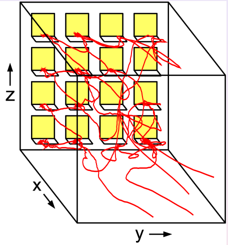
**What type of motion?**

Study bumblebee foraging in a *laboratory experiment*.

# The bumblebee experiment

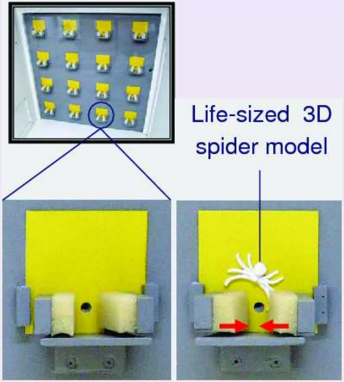
Ings, Chittka, Current Biology **18**, 1520 (2008):
**bumblebee foraging** in a cube of $\simeq$ 75cm side length

- 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**

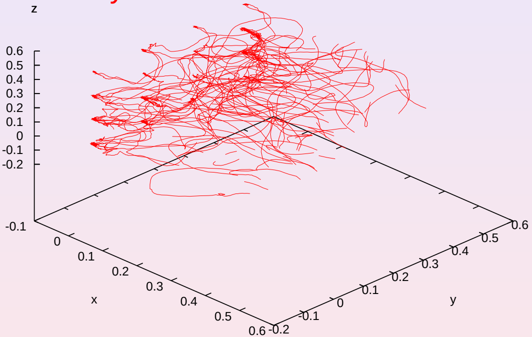
**three experimental stages:**

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

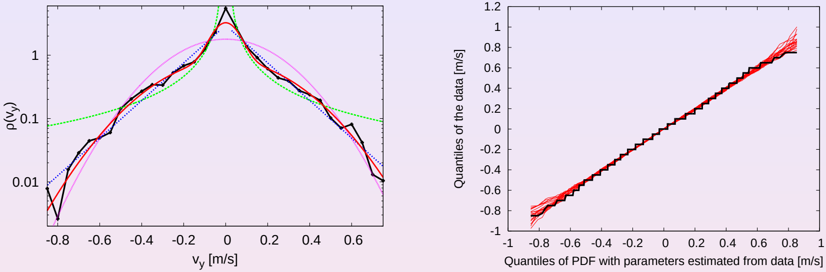
# Bumblebee experiment: two main questions

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

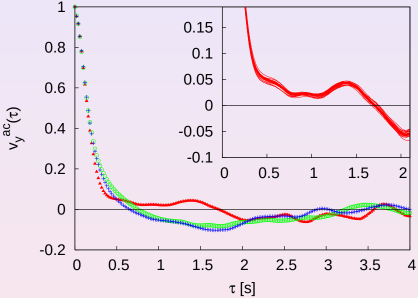
# Velocity distributions: interpretation

- **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 || 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:

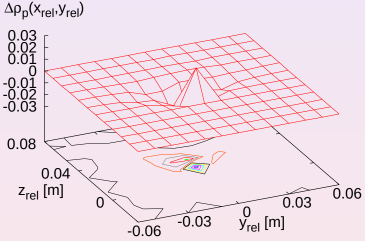



- plot: spider-free stage, predation thread, memory test
- **correlations change** from positive (spider-free) to negative (spiders)

⇒ all **changes** are in the **velocity correlations**, *not* in pdfs!

# Predator avoidance and a simple model

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

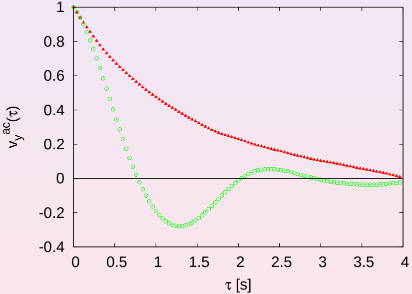



positive spike: *hovering*;
negative region: *avoidance*

modeled by Langevin equation

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

$\eta$: friction coefficient,
$\xi$: Gaussian white noise




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

# Clever bumblebees!

**Summary of Part 2:**

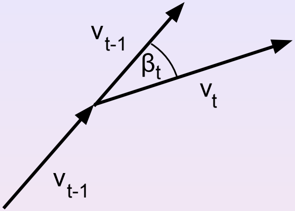
- mixture of **two Gaussian velocity distributions** reflects spatial adjustment of bumblebee dynamics to flower carpet
- all changes to predation thread are contained in the **velocity autocorrelation functions** that exhibit highly non-trivial temporal behaviour
- no problem with the **Lévy *hypothesis***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

# Part 3:

# Modeling bumblebee flights

# Reorientation (or CRW) model

describe biological movements in a plane by speed $s(t) = |v(t)|$ and turning angle $\beta$ in comoving frame:




Correlated Random Walk model

$$\beta(t) = \xi(t)\,,\; s(t) = const.$$

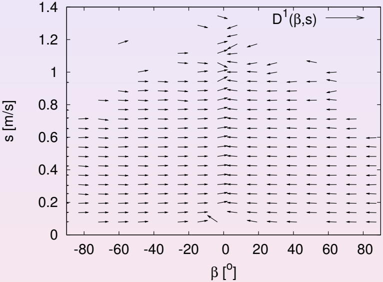
where $\xi(t)$ is typically drawn i.i.d. from a wrapped normal distribution; model captures directional biological persistence

**goal:** construct a **generalized CRW model from exp. data** for reproducing 'free' (away from flowers) bumblebee flights by using Langevin-type dynamics: drift terms plus noise

$$\begin{aligned} \frac{d\beta}{dt}(t) &= h(\beta(t), s(t)) + \tilde{\xi}(t) \\ \frac{ds}{dt}(t) &= g(\beta(t), s(t)) + \psi(t) \end{aligned}$$

# Drift coefficients: phase space dynamics

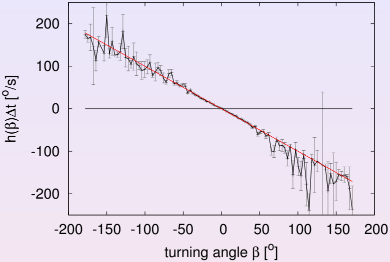
assume Markovianity for estimating **Fokker-Planck drift coefficients** $h$ and $g$; normalized drift vector field:



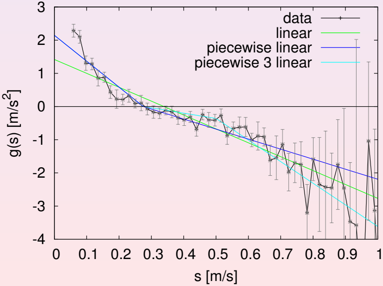

indicates that the cross-dependencies of $h(\beta(t), s(t))$ on $s$ and of $g(\beta(t), s(t))$ on $\beta$ are weak; vector field splits into

$$\begin{aligned} d\beta/dt &= h(\beta(t)) + \tilde{\xi}(t) \\ ds/dt &= g(s(t)) + \psi(t) \end{aligned}$$

# Estimation of drift terms from data




extract projection $h(\beta)$ from data:
$h(\beta) \simeq -k\beta$ with $k \approx 1/\Delta t$
integrating $d\beta/dt = h(\beta(t)) + \tilde{\xi}(t)$
wrt $\Delta t$ yields $\beta(t) = \xi(t)$



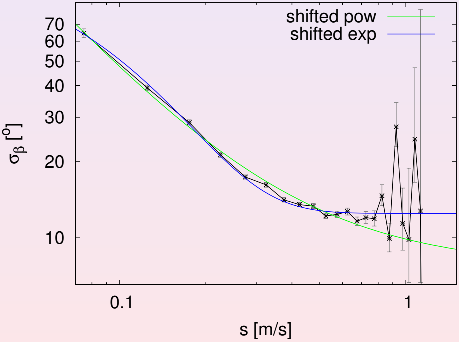

extract projection $g(s)$ from data:
$\exists$ preferred speed $s_0$; piecewise linear approximation for $g(s)$ in $ds/dt = g(s(t)) + \psi(t)$ yields

$$g(s) \approx (s - s_0) \cdot \begin{cases} -d_1, s < s_0 \\ -d_2, s \geq s_0 \end{cases}$$

with $d_1 > d_2 > 0$

# Velocity-dependent angle noise

pdf for the **turning angles** $\beta$ at each speed $s$ is approximated by a Gaussian;
however, the **variance** $\sigma_\beta$ is $s$-dependent (cf. naive reasoning):



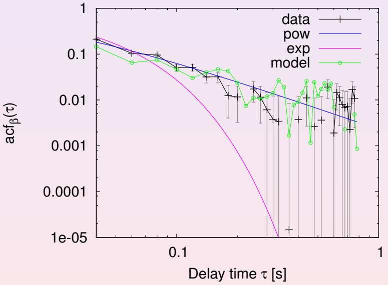

$$\beta(t) = \xi_s(t)$$

$$\xi_s(t) \sim \mathcal{N}(0, f(s(t)))$$

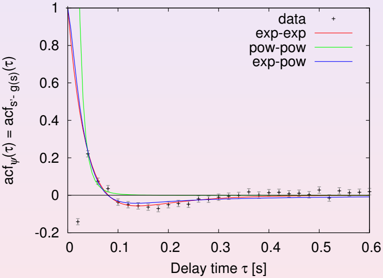
$$f(s) = c_1 e^{-c_2 s} + c_3$$

# Noise autocorrelation functions

noise $\xi_s(t)$ of turning angles $\beta$ is a steep power law:




noise of speed changes $\psi(t) = ds/dt - g(s(t))$ shows anti-correlations:




best approximated by

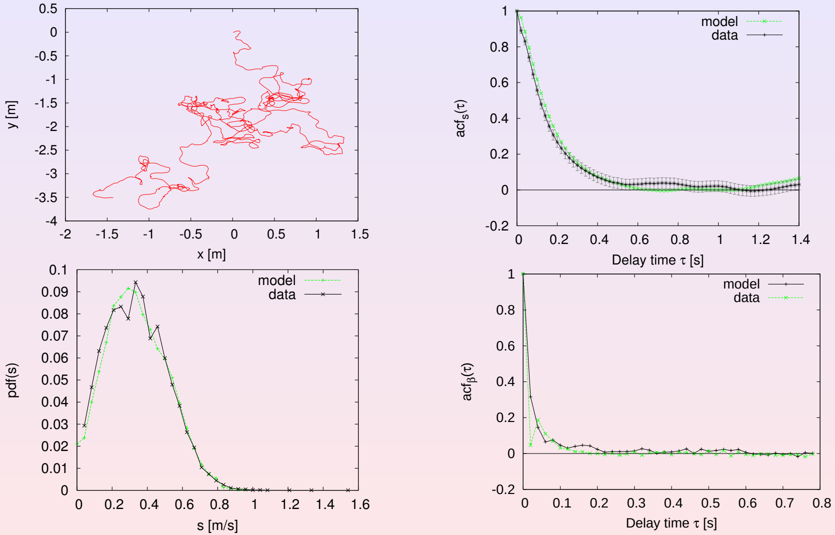
$\mathrm{acf}_\psi(t) \approx a e^{-\lambda_1 t} + (1-a) e^{-\lambda_2 t}$

# Summary: the complete model

$$\beta(t) = \xi_s(t)$$
$$\frac{ds}{dt} = g(s(t)) + \psi(t)$$

- **turning angles** $\beta$ given by power law-correlated Gaussian noise $\xi_s(t) \sim \mathcal{N}(0, \sigma_\xi(s))$ with $\sigma_\xi(s) = c_1 e^{-c_2 s} + c_3$
- piecewise linear drift $g(s)$ for **speed** $s$
- $\psi$ approximately Gaussian and anti-correlated via sum of exponentials

# Simulation and comparison to real data




good agreement given the number of approximations

# Summary

- Be careful with **(power law) paradigms** for data analysis
- **Correlation functions** can contain crucial information about interactions between forager and environment
- **Langevin-type correlated random walk model** available for bumblebee flights

**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’?)

# References

F.Lenz, T.Ings, A.V.Chechkin, L.Chittka, R.K., *Spatio-temporal dynamics of bumblebees foraging under predation risk*, Phys. Rev. Lett. **108**, 098103 (2012)

F.Lenz, A.V.Chechkin, R.K., *Constructing a stochastic model of bumblebee flights from experimental data*, under review for PLoS ONE