Random walks with memory and animal movement

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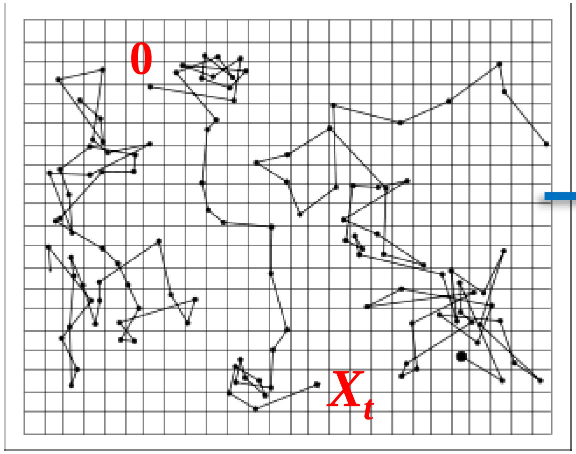
Single particle tracking

Jean Perrin (1909)

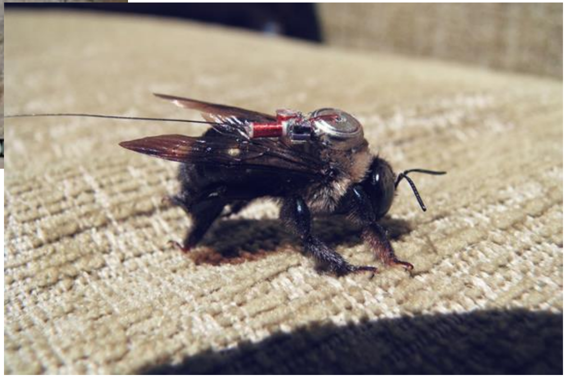


Brownian motion or "normal" diffusion, a basic transport mechanism in physics.

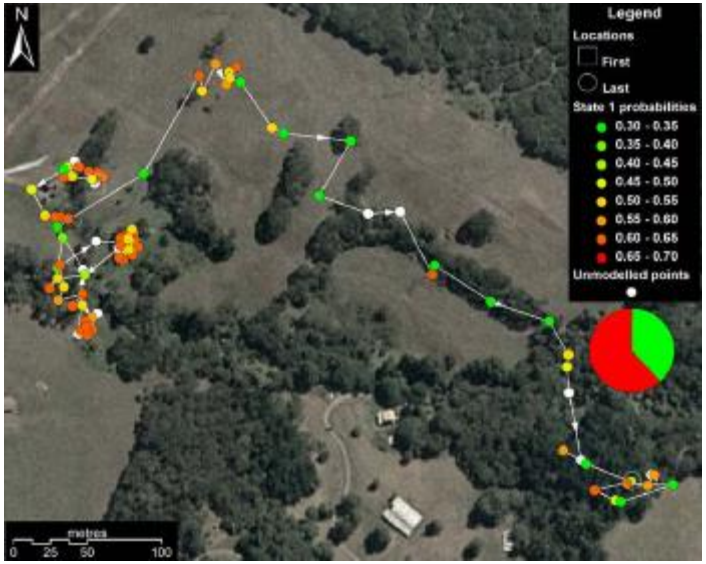
$$\langle X_t^2 \rangle = 2Dt$$

Gaussian distribution for X_t .

(CLT: sums of i.i.d. random variables.)

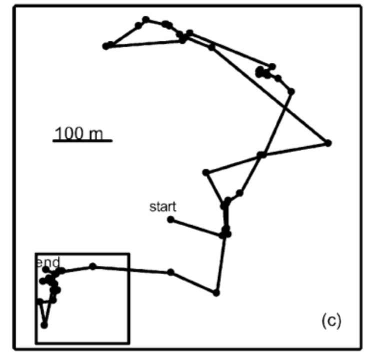


Rodents



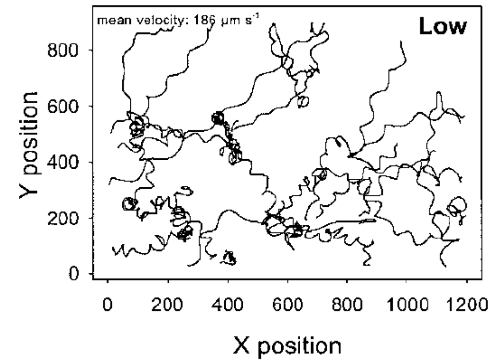
Postlethwaite & Dennis, Plos ONE, 2013

Spider monkeys



Ramos-Fernández *et al.*, *BES* 2004

Microzooplankton



Bartumeus *et al.*, *PNAS* 2003

- **(Correlated) random walks** Turchin, 1998; Codling *et al.* JRS Interface 2008…
- **Mixtures of random walks** Morales *et al. Ecology* , 2004.
- **Lévy walks, flights** $p_{\text{step}}(l) \sim l^{-(1+\mu)}$ Viswanathan *et al. Nature,* 1999.

…

- **But : Real animals have cognitive capacities and make movement decisions based on experience (long range memory).**

- **For survival, animals must process and keep information on environemental features. In particular if the environment is not so unpredictable (e.g. , herbivores, frugivorous primates, and even seabirds).**

- **Modeling memory (spatial and temporal) in animal movement: requires to extend the RW formalism . Computional simulation models are very helpful.**

- **Few mathematical results are known on RW with memory.**

ECOLOGY LETTERS

Ecology Letters, (2013) **16**: 1316–1329 doi: 10.1111/ele.12165

REVIEW AND SYNTHESIS

Spatial memory and animal movement

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Abstract

Memory is critical to understanding animal movement but has proven challenging to study. Advances in animal tracking technology, theoretical movement models and cognitive sciences have facilitated research in each of these fields, but also created a need for synthetic examination of the linkages between memory and animal movement. Here, we draw together research from several disciplines to understand the relationship between animal memory and movement processes. First, we frame the problem in terms of the characteristics, costs and benefits of memory as outlined in psychology and neuroscience. Next, we provide an overview of the theories and conceptual frameworks that have emerged from behavioural ecology and animal cognition. Third, we turn to movement ecology and summarise recent, rapid developments in the types and quantities of available movement data, and in the statistical measures applicable to such data. Fourth, we discuss the advantages and interrelationships of diverse modelling approaches that have been used to explore the memory–movement interface. Finally, we outline key research challenges for the memory and movement communities, focusing on data needs and mathematical and computational challenges. We conclude with a roadmap for future work in this area, outlining axes along which focused research should yield rapid progress.

Keywords

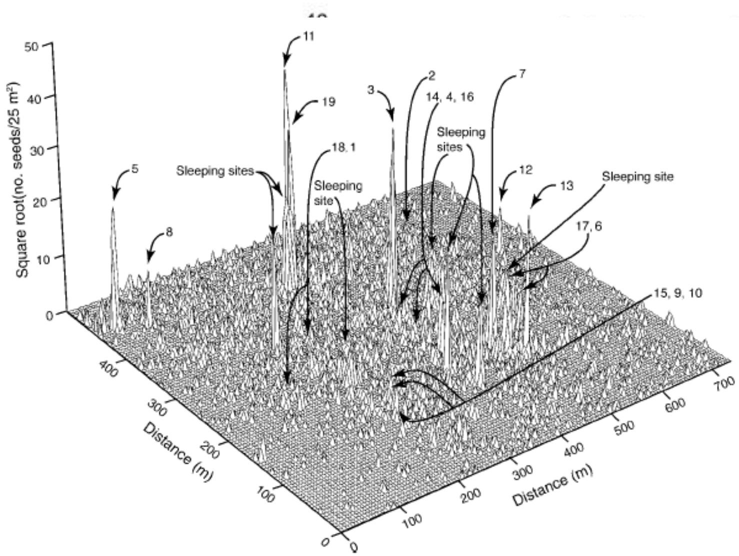
Animal spatial cognition, attribute memory, cognitive maps, movement ecology, orientation tasks, return points, spatial memory, systematic searches.

Ecology Letters (2013) **16**: 1316–1329

Observations that are not compatible with standard RW-like models:

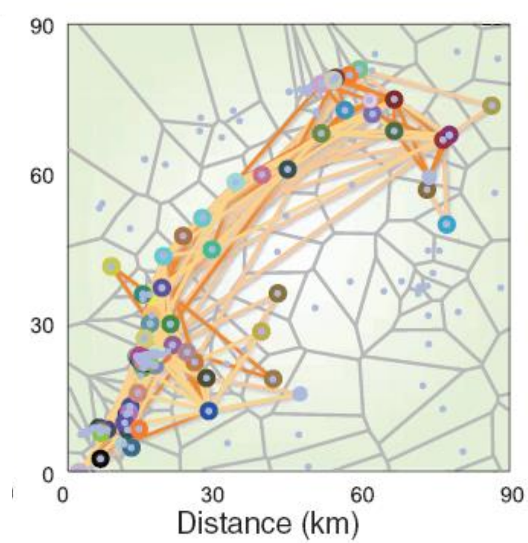
- **High recurrence.**
- **Home range; very slow diffusion.**
- **Non-uniform occupation of space: few "hotspots", many sites visited only occasionally.**
- **Routines.**

Russo *et al. Ecology,* 2006



spider monkeys

Song *et al. Science* 2010



Cell-phone users

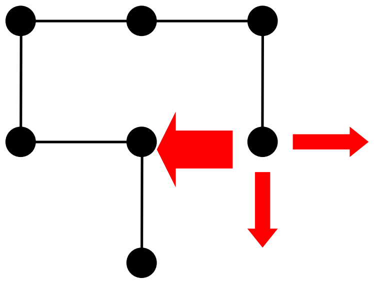
Questions

- Can we infer memory use from movement data?
- Effects of long range recurrent memory on trajectories?
  Anomalous diffusion ?
- Properties of the memory used by animals (memory kernels)?
- For which environments is memory useful? (Spatial structure and dynamics.)
- Should memory decay over time? Is forgetting advantageous for adaptation?

Path dependent random walks and related processes:

- RW with repeated increments (Elephant W) Schutz & Trimper, *PRE* 2004; Cressoni *et al., PRL* 2007.

- Re-inforced RW :



Davis, *Probab. Theor. Rel.. Field.* 1990
Othmer & Stevens, *SIAM J. Appl. Math.* 1997

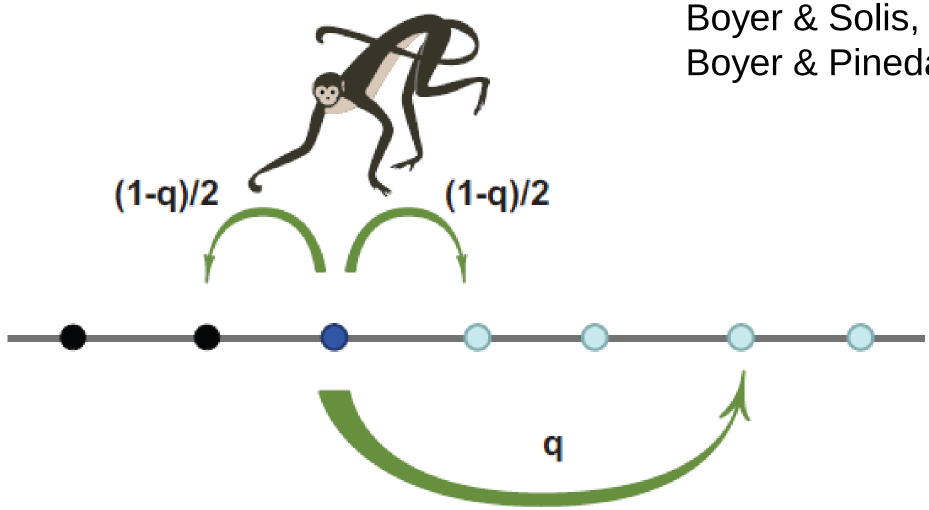
- Bold or "scared" RW (1d) Serva, *PRE* 2013.

- RW with re-locations to visited sites. Gautestad & Mysterud, *Am. Nat.* 2005; *Ecol. Complex.* 2006.

(RW with stochastic resetting to the origin
Evans & Majumdar , *PRL*, 2011 **)**

A Toy Model

Boyer & Solis, *Phys. Rev. Lett.*, 2014
Boyer & Pineda, arXiv 2015.



A walker starts at the origin *n*=0 at *t* = 0. Time and space are discrete.
At each time-step:

- **With probability 1–q : take a random walk step to a nearest neighbor.**

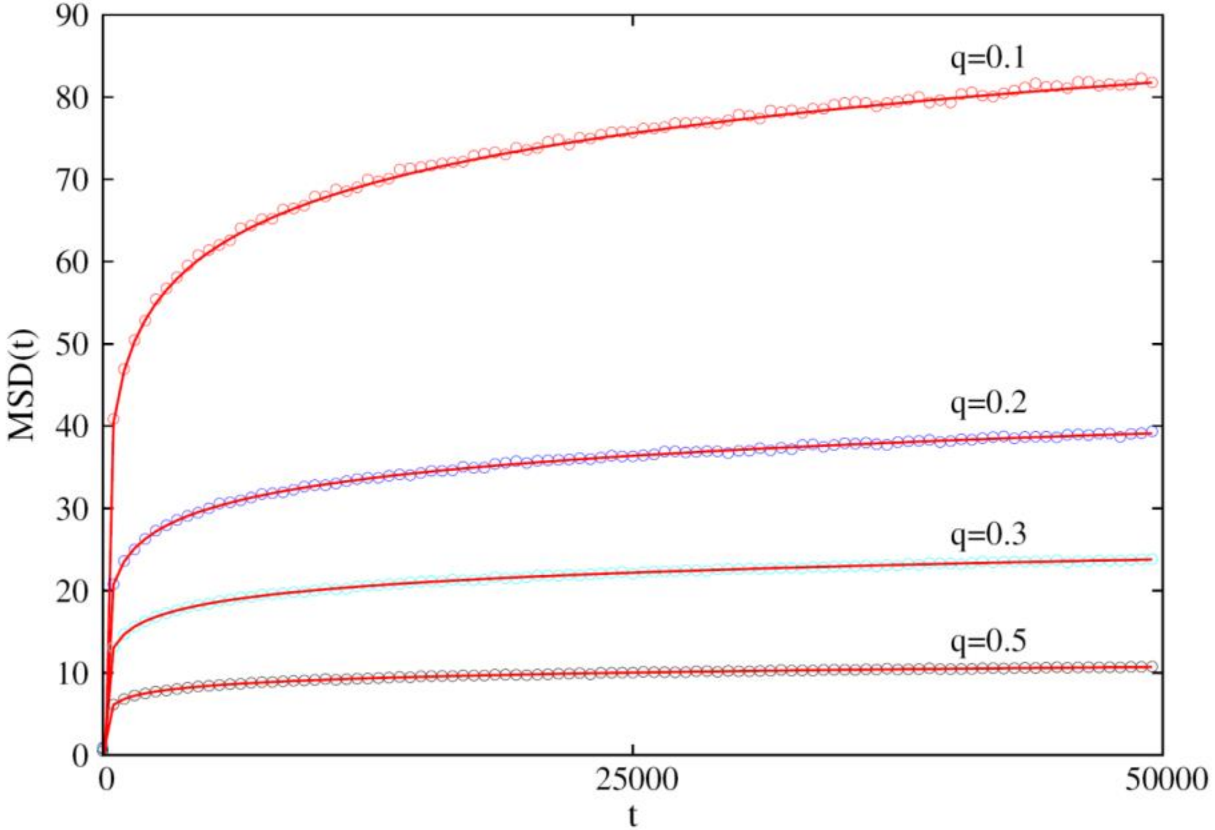
- **With probability q : relocate directly to a site visited in the past, such that**

Probability of choosing sitio *i* $\propto$ # of visits recieved by *i* during [0,t]

Memory induces anomalous diffusion:

Mean squared displacement:

$$\langle X_t^2 \rangle \equiv \sum_{n=-\infty}^{\infty} n^2 P(n,t)$$



Master equation :

$$P(n,t+1) = \frac{1-q}{2} P(n-1,t) + \frac{1-q}{2} P(n+1,t) + \frac{q}{t+1} \sum_{t'=0}^{t} P(n,t')$$

$$\longrightarrow \langle X_{t+1}^2 \rangle = (1-q)\left[1 + \langle X_t^2 \rangle\right] + \frac{q}{t+1} \sum_{t'=0}^{t} \langle X_{t'}^2 \rangle$$

Exact results:

- $$\langle X_t^2 \rangle = \frac{1-q}{q} \sum_{k=1}^{t} \frac{1-(1-q)^k}{k}$$

  $$\langle X_t^2 \rangle \simeq \frac{1-q}{q} \left[\ln(qt) + \gamma\right], \qquad t \gg 1 \qquad \gamma = 0.5772...$$

- **Scaling law:** $$P(n,t) \to \frac{1}{\sqrt{\langle X_t^2 \rangle}}\, g\left(\frac{n}{\sqrt{\langle X_t^2 \rangle}}\right)$$

Gaussian

Generalization: jumps not necessarily to nearest neighbor sites

$$P(n,t+1) = (1-q)\sum_{\ell=-\infty}^{\infty} p(\ell)P(n-\ell,t) + \frac{q}{t+1}\sum_{t'=0}^{t} P(n,t')$$

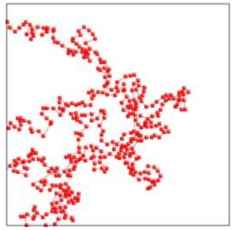
o: $$\widetilde{P}(k,t+1) = (1-q)\tilde{p}(k)\widetilde{P}(k,t) + \frac{q}{t+1}\sum_{t'=0}^{t}\widetilde{P}(k,t')$$ **(Fourier)**

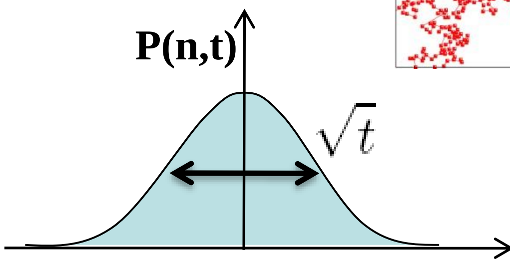
$q = 0$	$q \neq 0$
$P(k,t) = \tilde{p}(k)^t = e^{\ln[\tilde{p}(k)]t}$	$P(k,t) \simeq t^{-a(k)} = e^{-a(k)\ln t}$
Central Limit Theorem	$a(k) = (1-q)\dfrac{1-\tilde{p}(k)}{1-(1-q)\tilde{p}(k)}$

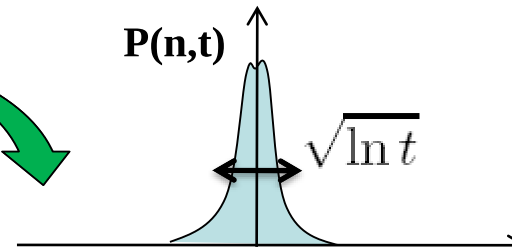
Markov | **No-Markov**

Gauss: $\langle \ell^2 \rangle < \infty$

$\tilde{p}(k) = 1 - ck^2 + \ldots$



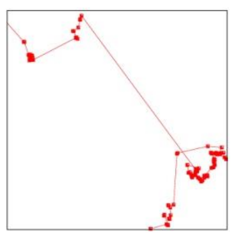


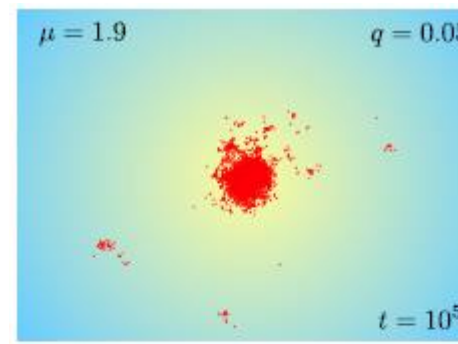


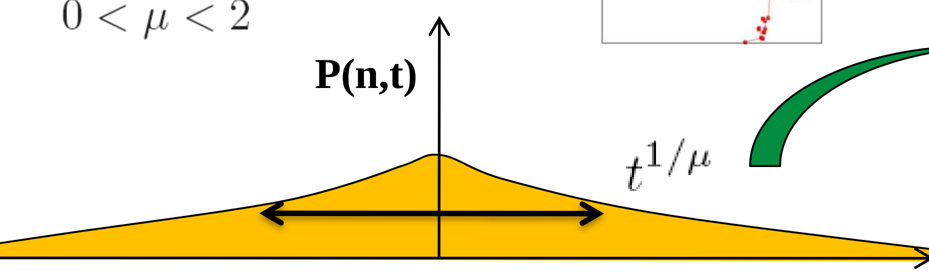
Lévy: $\langle \ell^2 \rangle = \infty$

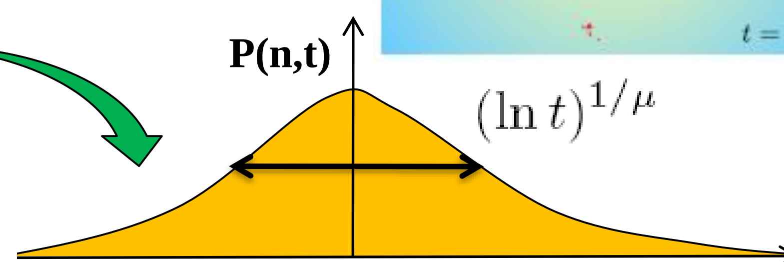
$\tilde{p}(k) = 1 - c \mid k \mid^{\mu} + \ldots$

$0 < \mu < 2$

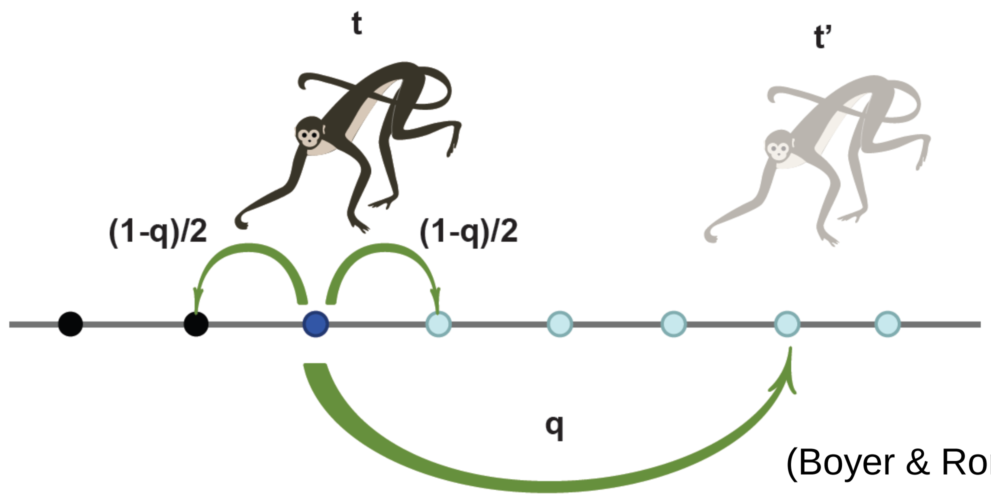




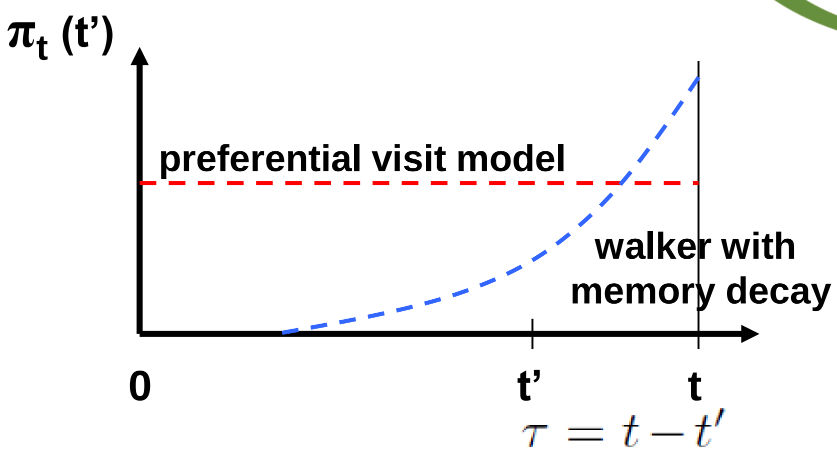




Generalization to memory kernels with decay



(Boyer & Romo, *Phys. Rev. E* 2014)



$$\pi_t(t') \propto F(t-t')$$

$$F(t-t') = (t-t'+1)^{-\beta}, \quad 0 \le t' \le t$$

$$\widetilde{P}(k,t+1) = (1-q)\tilde{p}(k)\widetilde{P}(k,t) + q\sum_{t'=0}^{t} \pi_t(t')\widetilde{P}(k,t')$$

Behavior of the Mean Square Displacement

anomalous diffusion
(sub-diffusion)

normal diffusion

$$\left(\frac{1-q}{q(1-\beta)\int_0^1 du\,\frac{-\ln u}{(1-u)^\beta}}\right)\ln t$$

$$\left(\frac{(1-q)\zeta(\beta)}{q\int_0^1 du\,\frac{1-u^{\beta-1}}{(1-u)^\beta}}\right) t^{\beta-1}$$

$$\left(\frac{1-q}{1+q\langle\tau\rangle_\infty}\right) t$$

GAUSSIAN (PRESERVED)

NON-GAUSSIAN

GAUSSIAN (CLT)

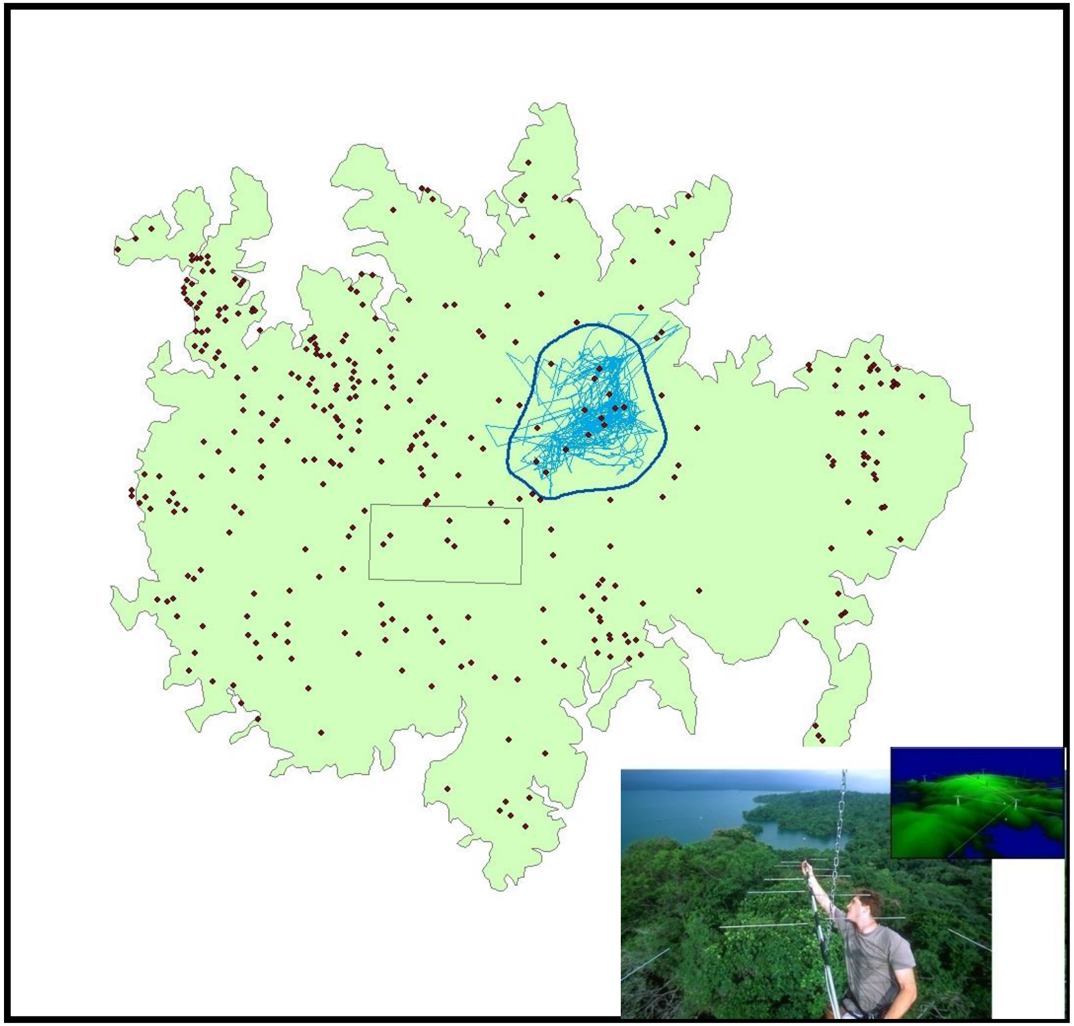
$-\infty$ 0 1 2

β

Preferential visit model

Stochastic reseting to the origin
(Evans & Majumdar) (EXPONENTIAL)

Capuchin monkeys



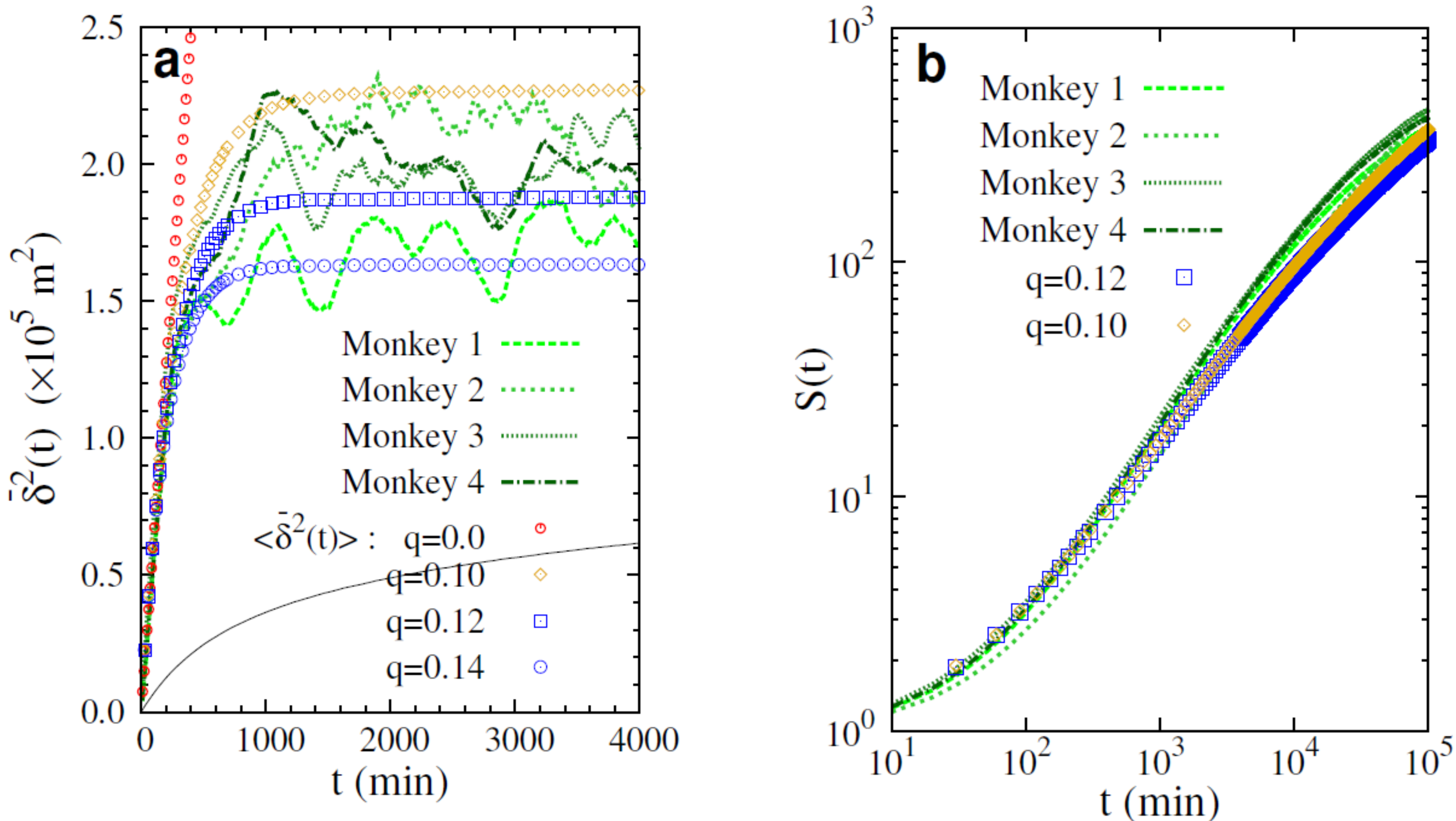
Barro Colorado Island, Panama,
radio-frequency telemetry ,
1 position every 10 min during 6 months,
4 individuals.

Analysis: space discretization in
50×50 m cells.

Crofoot *et al. PNAS,* 2008

Boyer, Crofoot, Walsh, *J. R. Soc. Interface,* 2011.

Time-averaged mean square displacements **Number of distinct visited sites**



Cell size: 50m*50m.
Time step: 30 min.

(Boyer & Solis, *Phys. Rev. Lett.*, 2014)

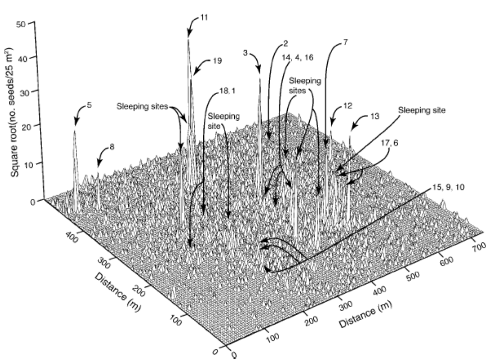
q **≈ 0.12 o $q/\Delta t$=0.004 min^{-1}**
describes well capuchin monkey data.

Intermitente use of memory, with drastic consequences on diffusion from time scales of 2-3 h.

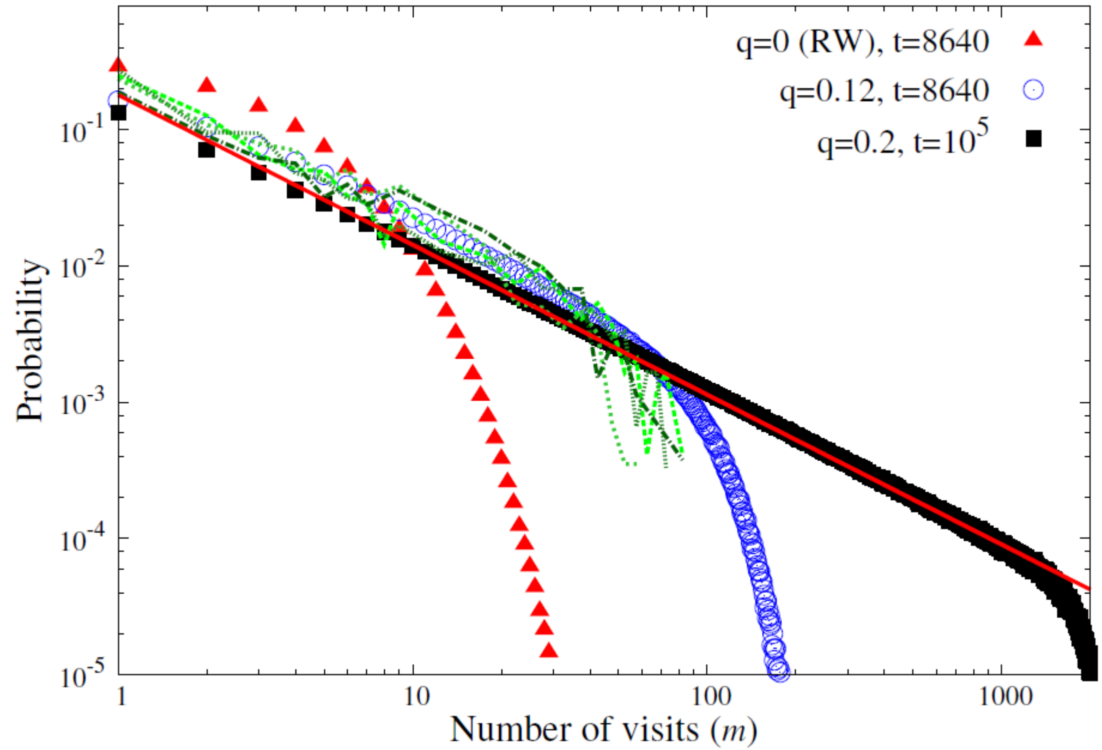
Rich-get-richer principle and power-law distributions

Probability that a randomly chosen visited site has been visited exactly *m* times:

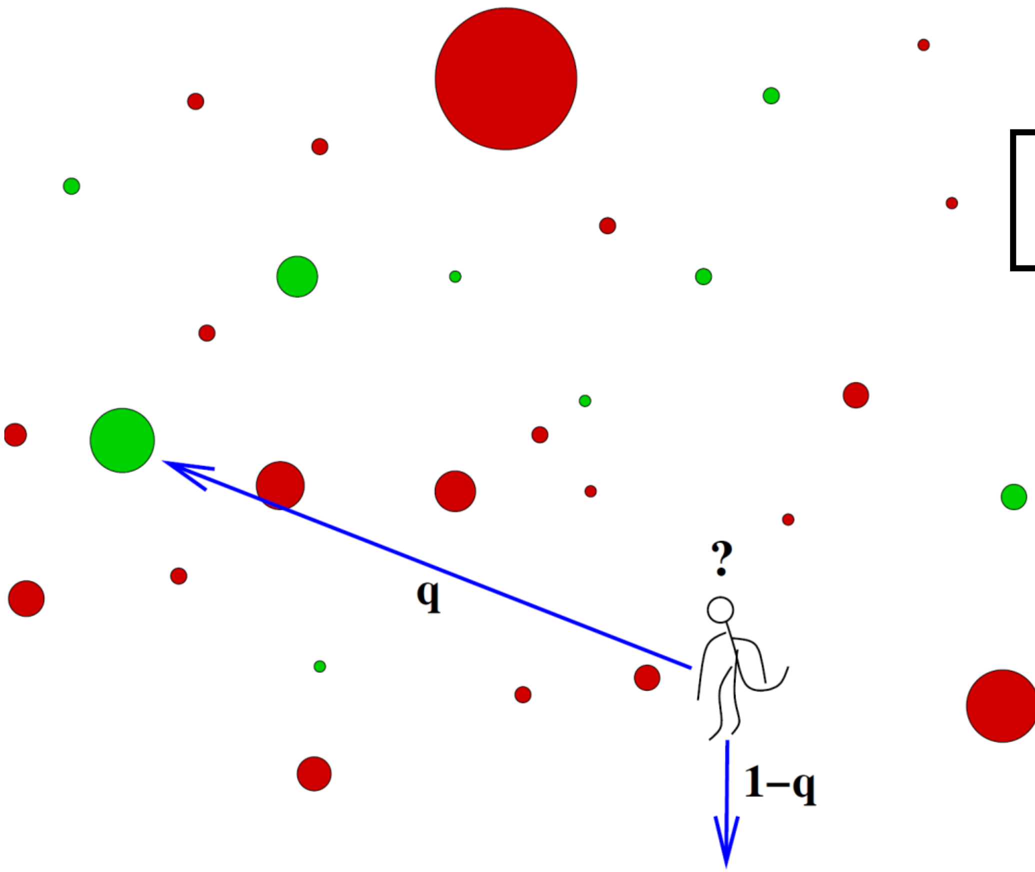
$P^{(v)}(m) \approx C\, m^{-\beta}$**, independently of *q*.**



Russo *et al. Ecology,* 2006



Beyond the toy model



chance + memory
(random search) (exploitation)

Standard modeling: Getz & Saltz, *PNAS*, 2008; Boyer & Walsh, *Phil. Trans. A,* 2010; Bonnell *et al.*, *Ecol. Model.*, 2010….

Optimization problem: many possible movement choice at a given time. Evaluate payoff of each possibility. Choose the best.

Precise. Rational.

Requires at lot of computation.

Often assumes that animal have "perfect" mental maps.

A less standard approach:

No explicit mental map of resources.

Memorize some reasonable amount of information (not perfectly).

Little computation at each decision .

Still fairly good foraging efficiency ?

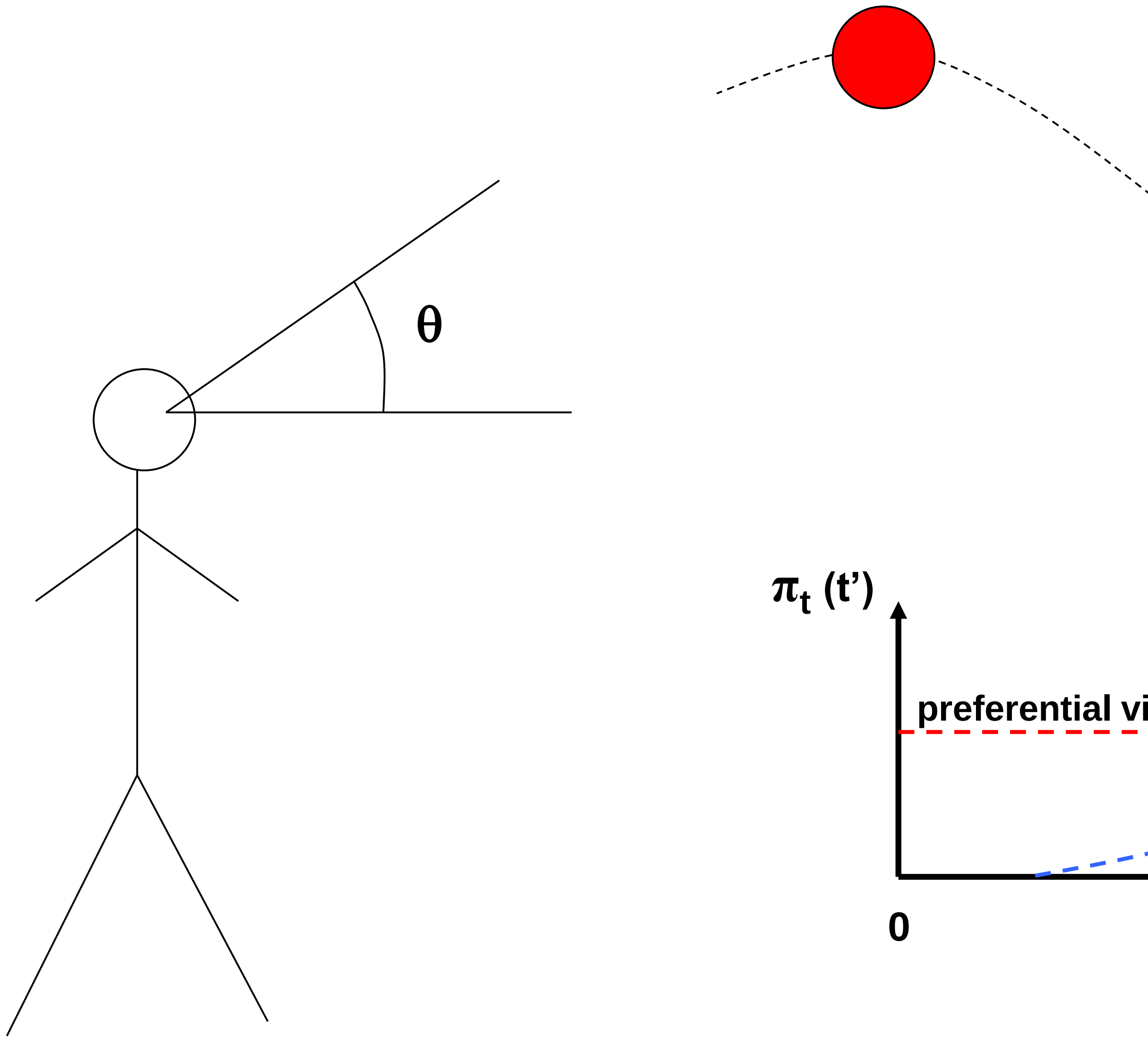
In the psychology literature: (Dijksterhuis *et al.*, *Science* 2006)

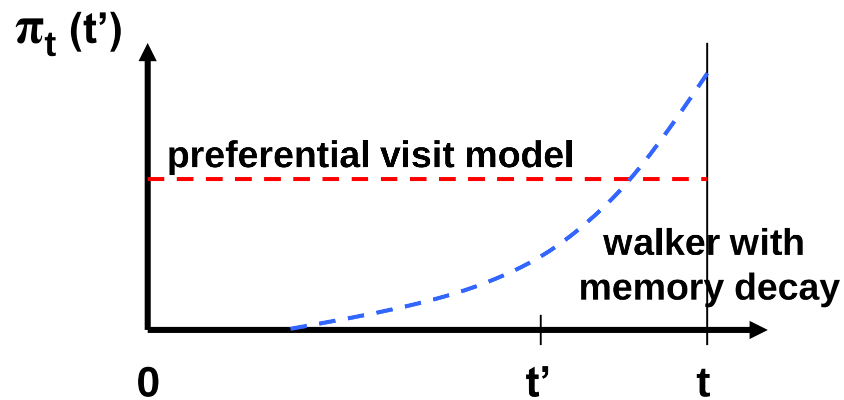
In front of simple problems, conscious decisions are easy to take.

**But for complex problems, people tend to take decisions
with the "guts" rather than rational computing.
"Deliberation-without-attention" hypothesis (≠ conscious deliberation).**

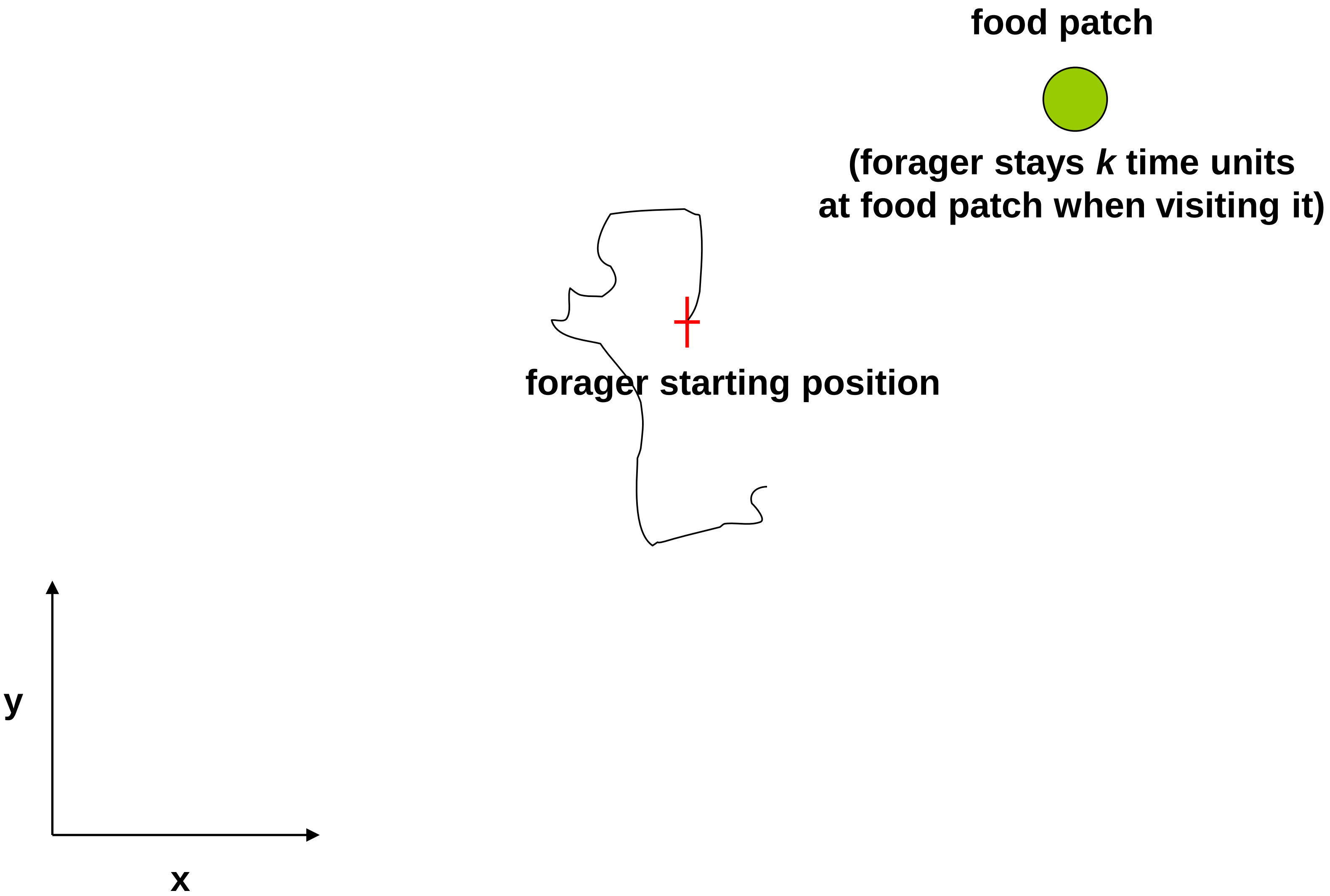
Heuristic models

(Guy Théraulaz)

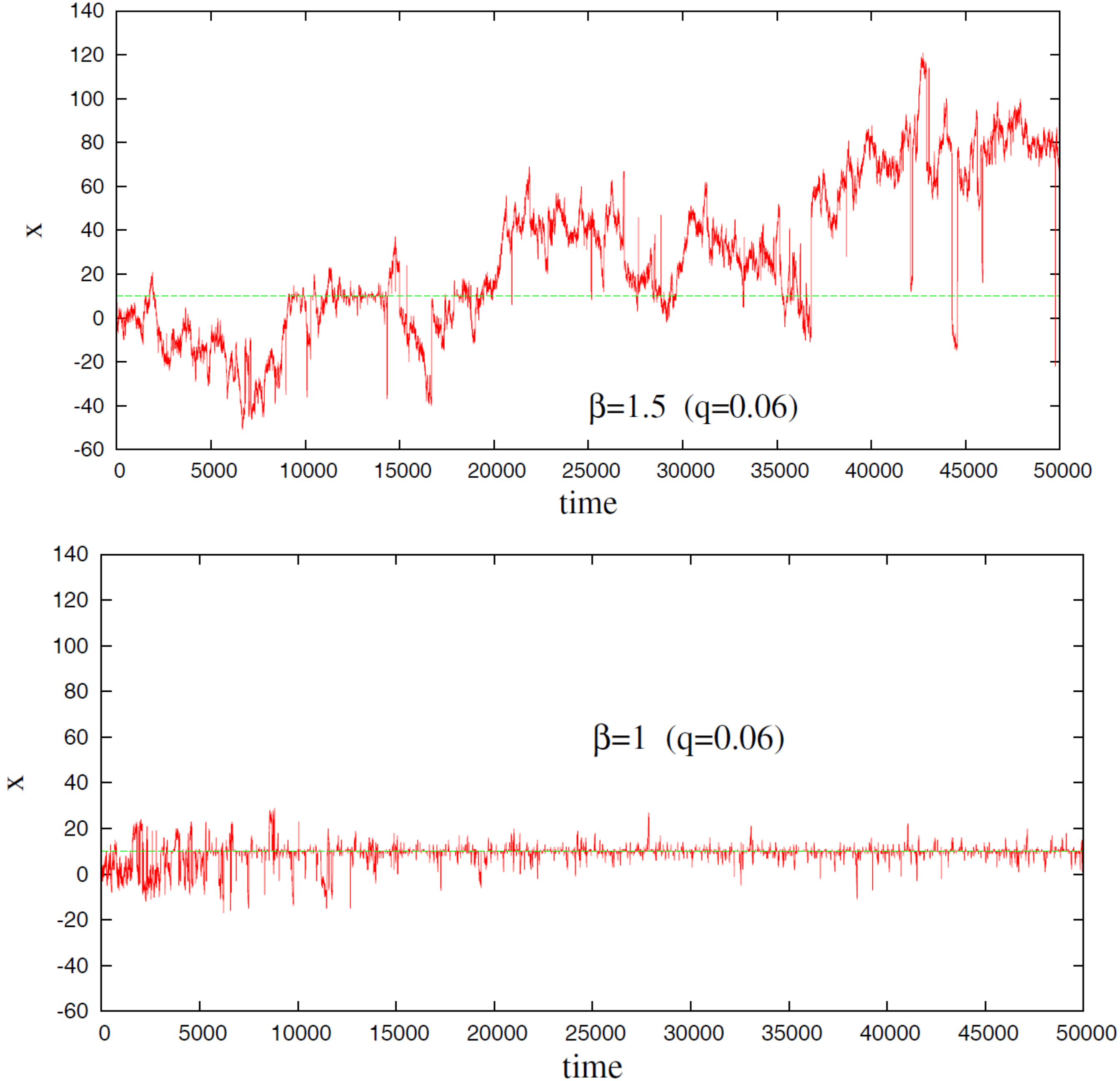




Experiment #1:

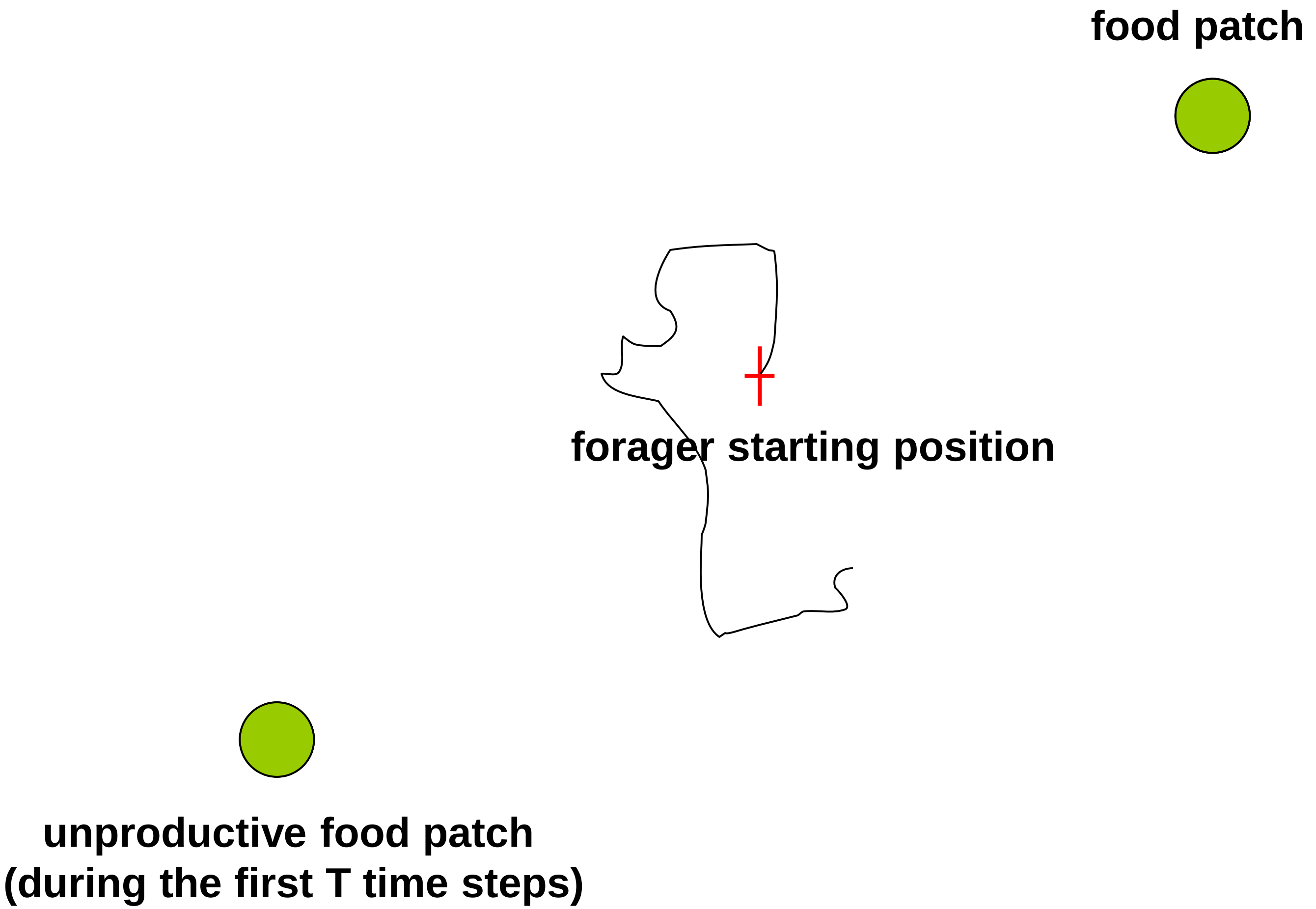


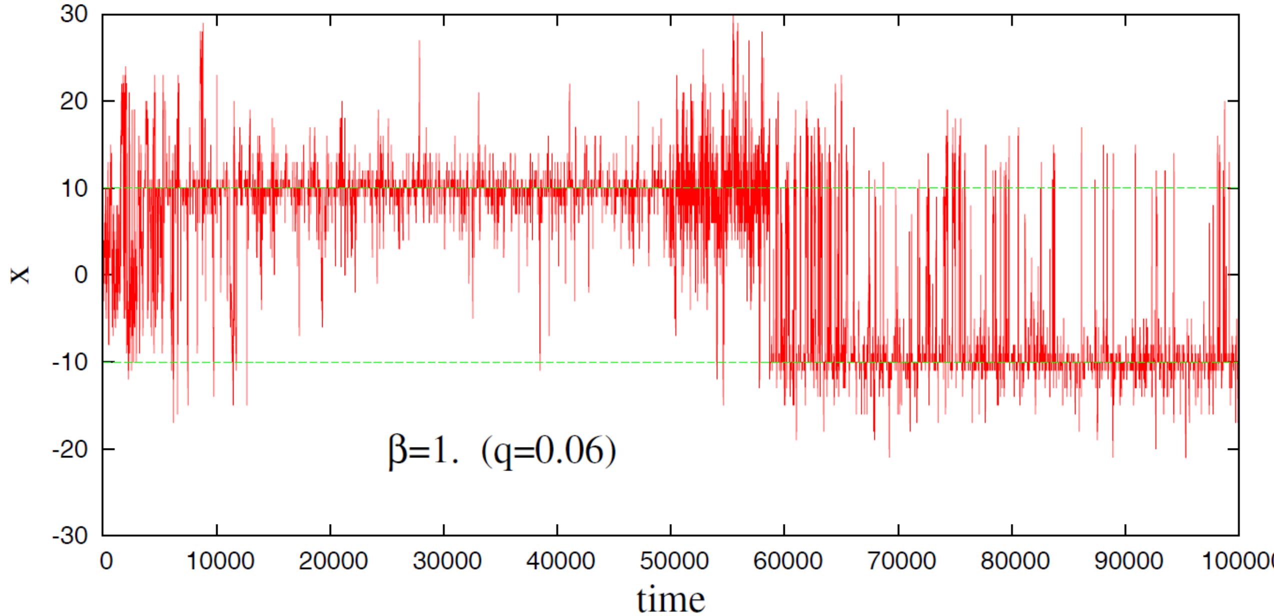
k=50



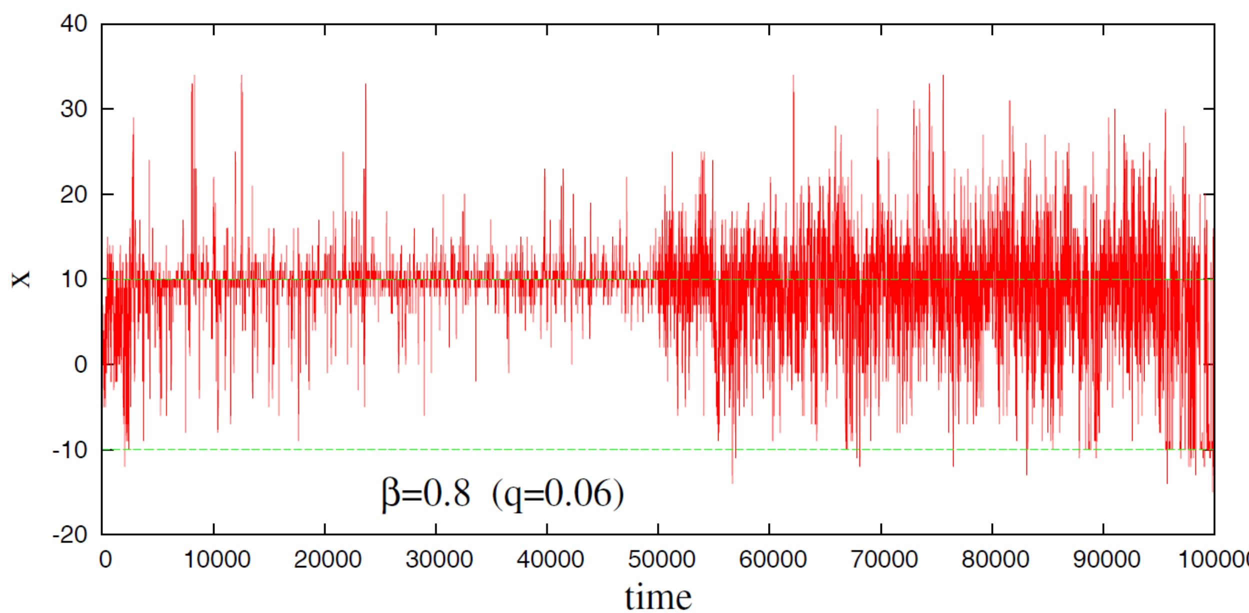
β=1.5 (q=0.06)
β=1 (q=0.06)
x
time
140
120
100
80
60
40
20
0
-20
-40
-60
0
5000
10000
15000
20000
25000
30000
35000
40000
45000
50000

Experiment #2:



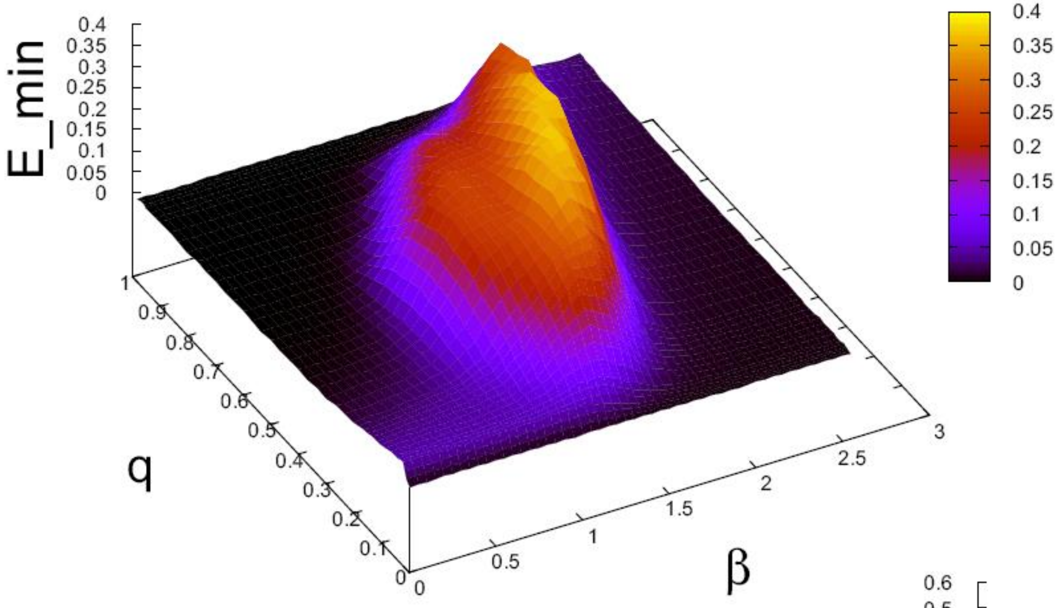


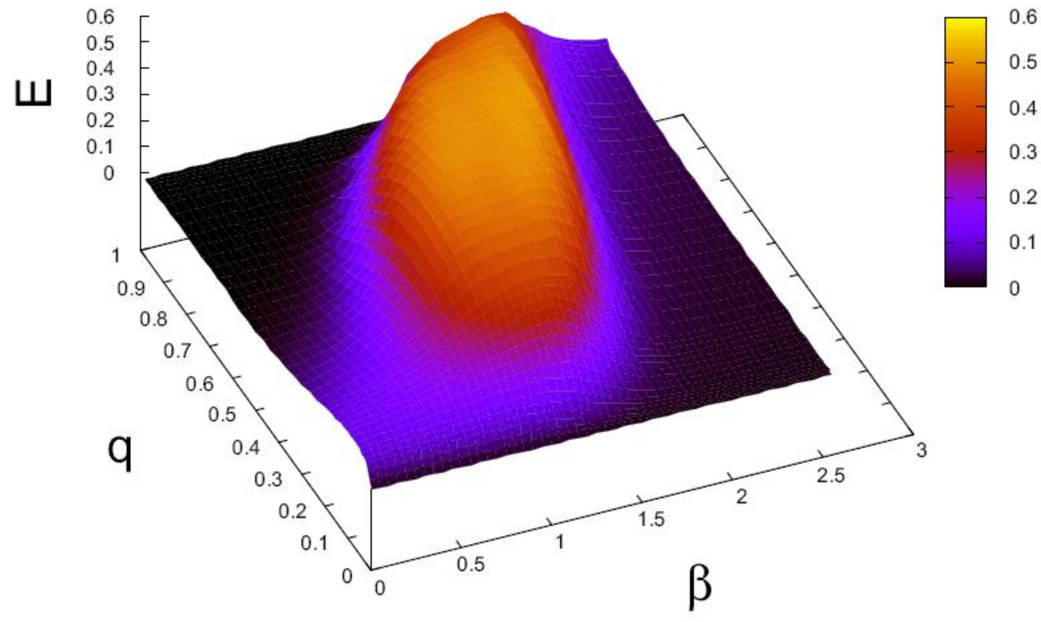
x
time
β=1. (q=0.06)



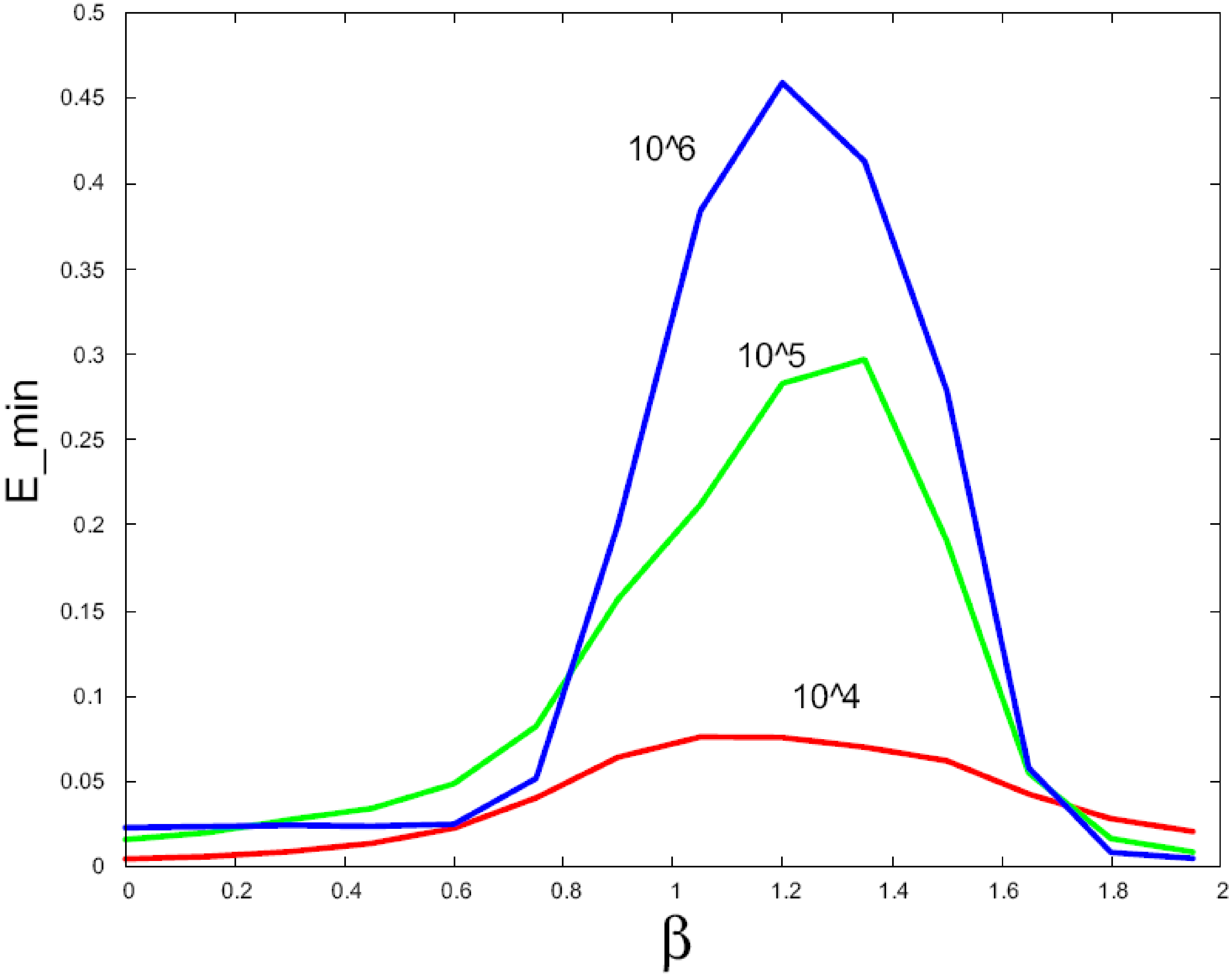
x
time
β=0.8 (q=0.06)

Memory with power-law decay

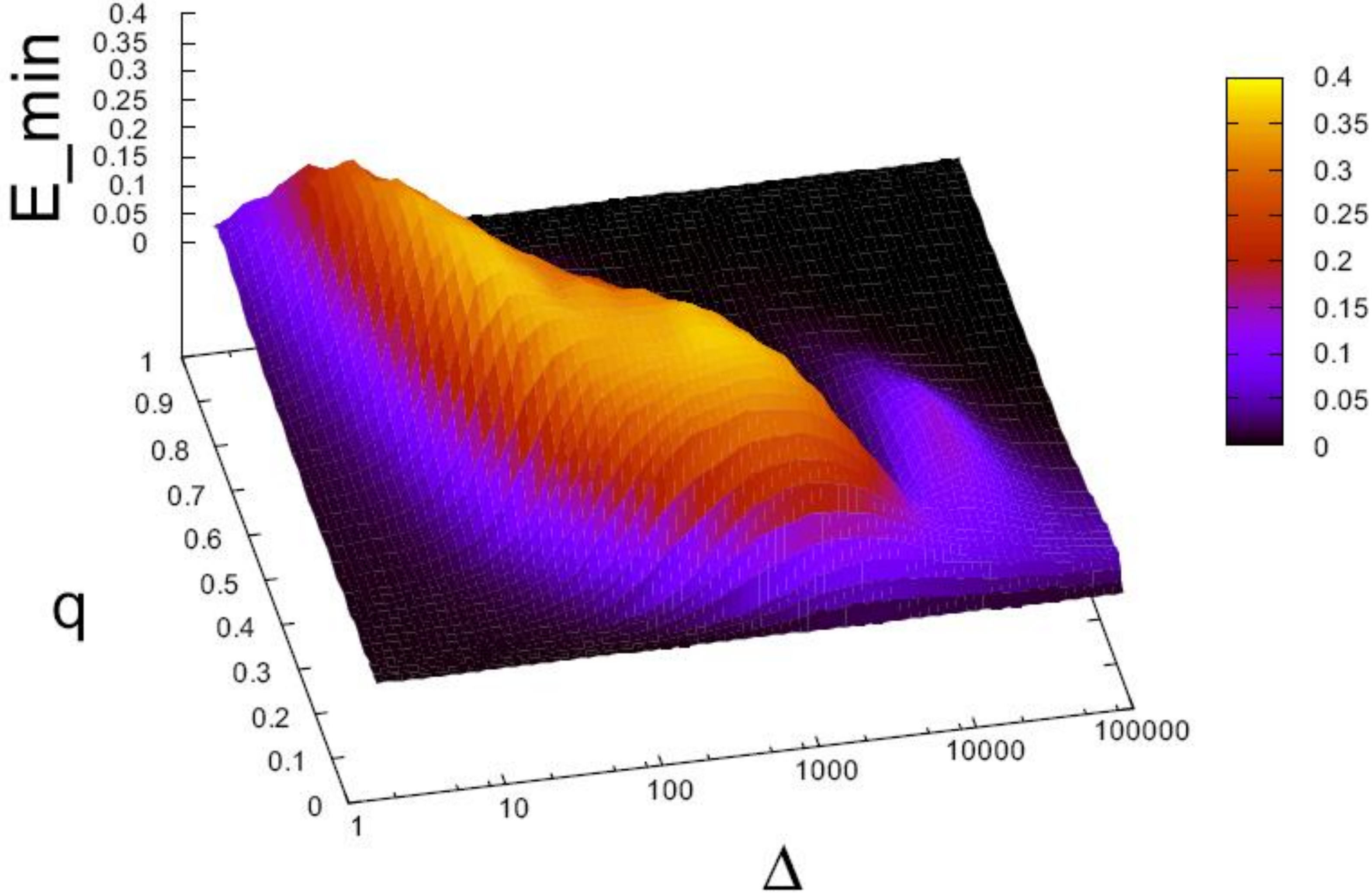




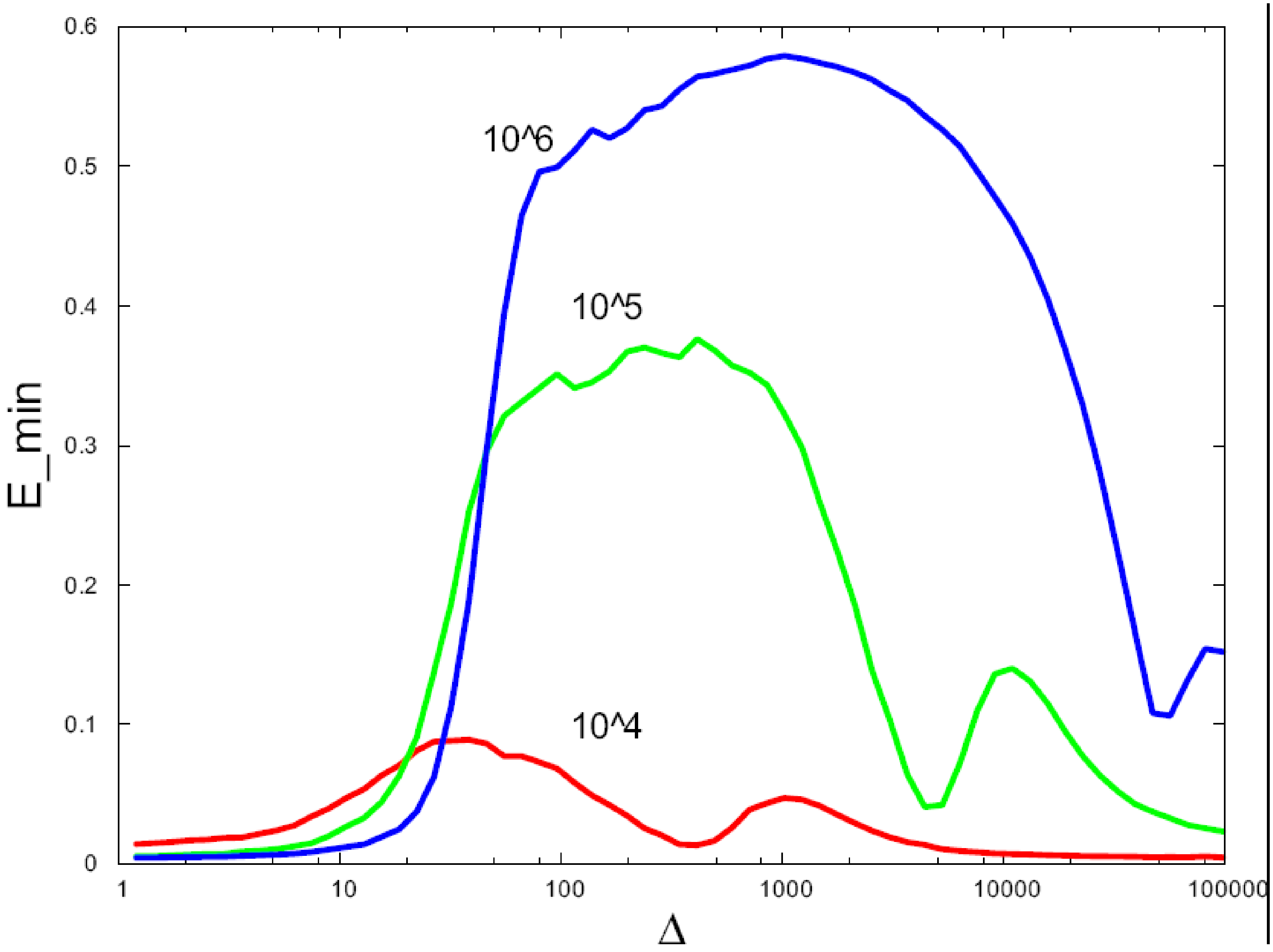
Dependence on the duration of the food patch



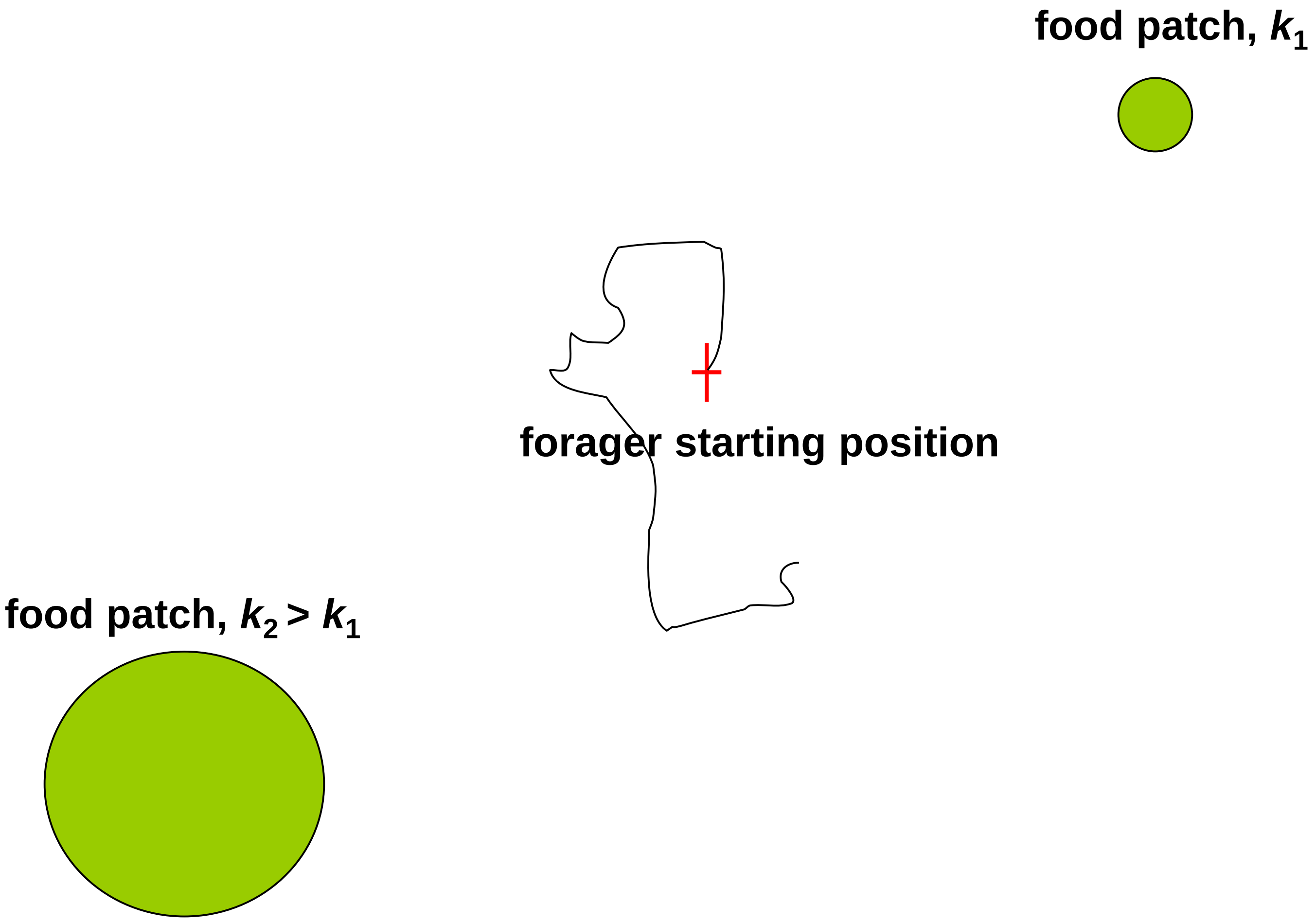
Memory with exponential decay

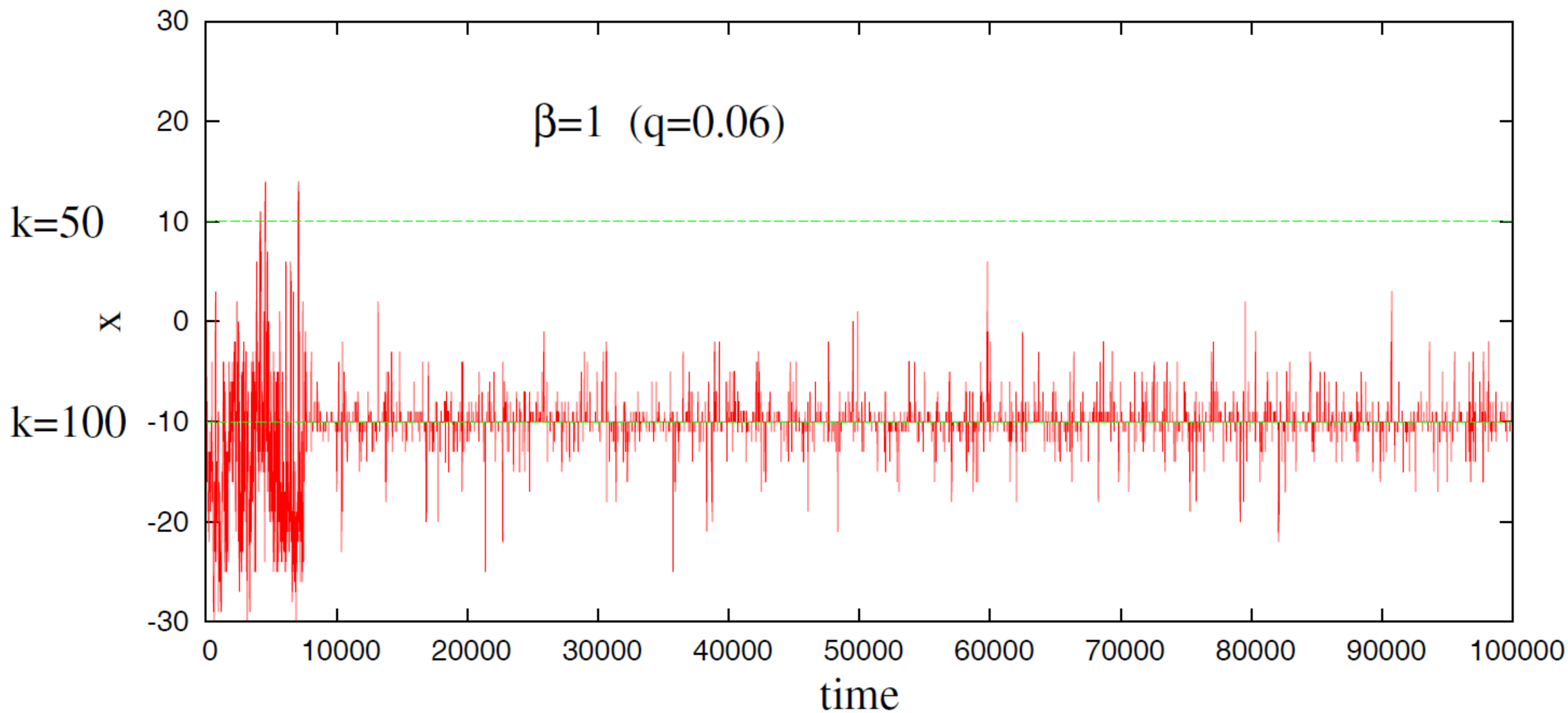


Dependence on the duration of the food patch



Experiment #3:




β=1 (q=0.06)
k=50
k=100
x
time
30
20
10
0
-10
-20
-30
0
10000
20000
30000
40000
50000
60000
70000
80000
90000
100000

Resource patch exploitation (repeated visits).

Resource patch selection (fruiting status/size).

Abandon unproductive resource patch.

Patrolling ("checking" state of formerly exploited patches).

Distance discounting.

Deal with a wide spectrum of patch temporal scales.

…

Validation with field data? Bayesian methods?

(see Merkel, Fortin, Morales, *Eco. Lett.* 2014)

Thanks to…

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Luis Martínez (UNAM)

Peter Walsh (Cambridge)
Meg Crofoot (Princeton/UC Davis)

Gabriel Ramos-Fernández (IPN-Oaxaca)

Conclusions

- **Nuevos resultados sobre procesos estócasticos con memoria de largo alcance:**

  Extención del teorema límite central: Gaussianas más allá del movimiento browniano,
  distribuciones de Lévy más allá de los vuelos de Lévy.

  Dináminca logarítmica.

  Acuerdo con datos de campo.

  A estudiar: Tiempos de primer paso; funciones de respuesta…
  Aplicaciones a ambientes heterogéneos.
  Métodos más sofisticados de análisis de trayectorias reales (infer. Bayesiana).

- **¿Efectos de los comportamientos individuales en fenómenos colectivo o a grandes escalas?**

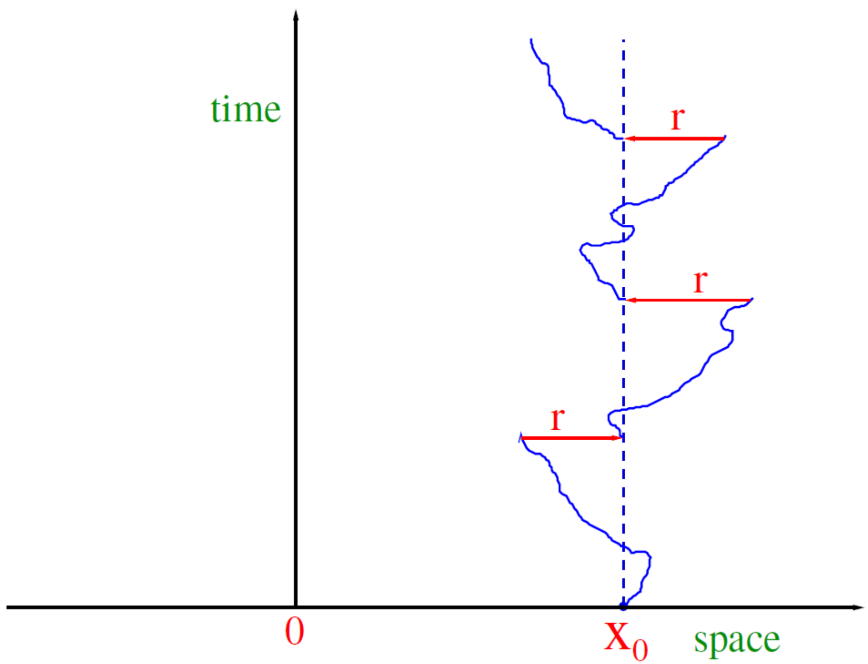
  Problemas de tráfico.

  Propagación de enfermedades.

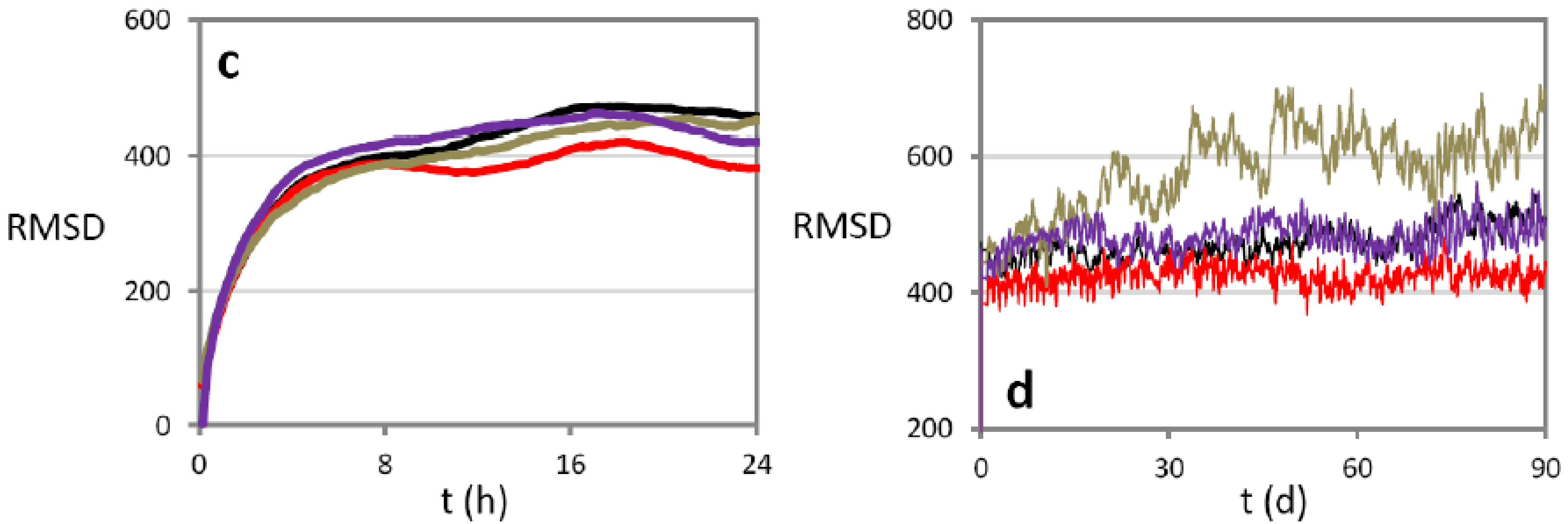
  Redes de contactos, interacción social.

Diffusion with Stochastic Resetting

Martin R. Evans[1,2] and Satya N. Majumdar[2]



Difusión muy lenta por animales



Boyer, Crofoot, Walsh, *J. R. Soc. Interface,* 2011.

Gaussians emerge here because:

Random movement (diffusion) *marginally* overcomes recurrent memory (confinement).

[by marginal we mean that fluctuations grow slower than t^{α}, as a log typically.]

Consequence of Gaussianity: effective Fokker-Planck equation for *P*:

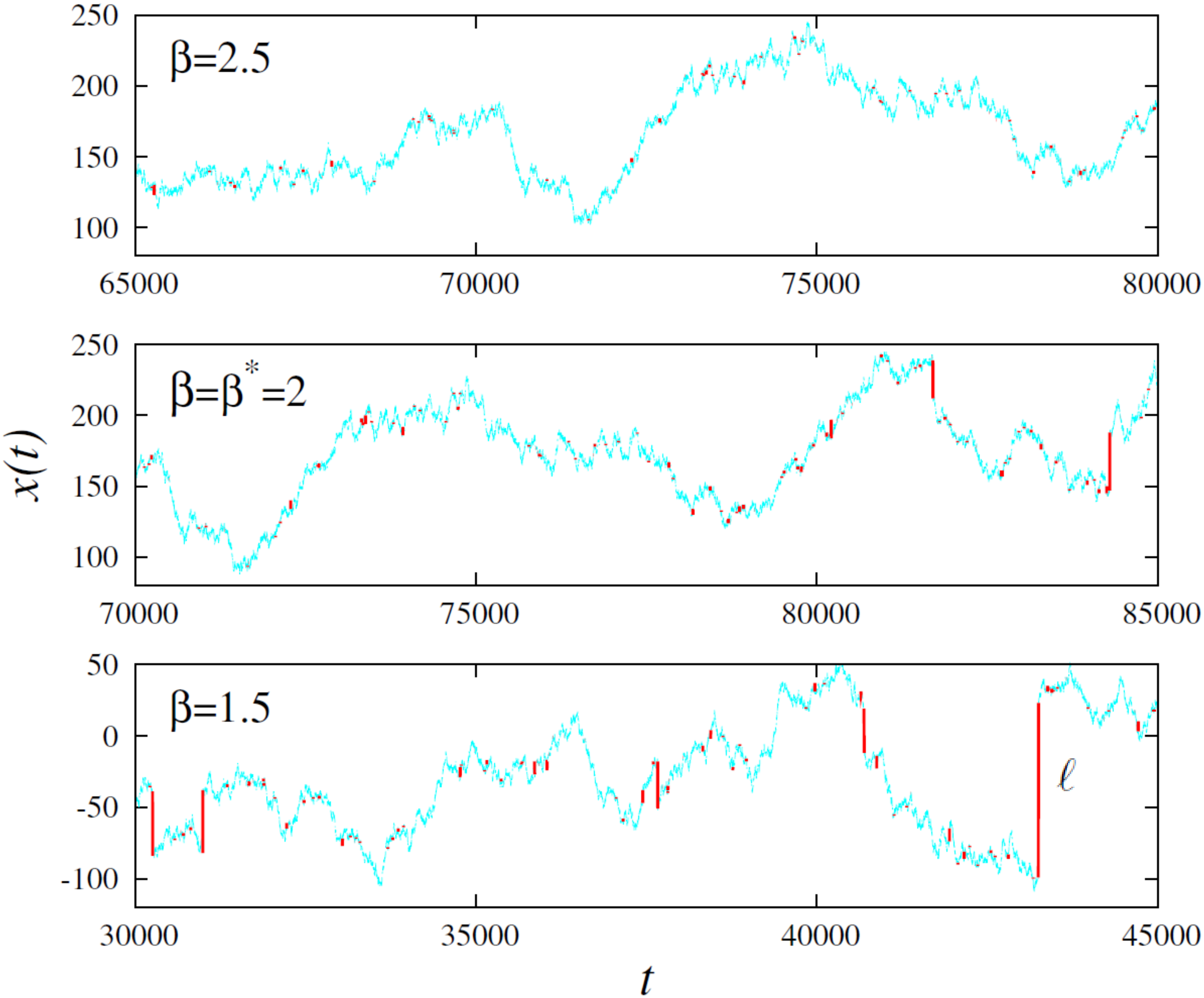
$$\frac{\partial P}{\partial t} \simeq \frac{1-q}{2qt}\,\frac{\partial^2 P}{\partial x^2}$$

But

The Gaussian saling regime is extremely long to settle,
not observable in simulations:

$$\frac{a_p}{a_{p-1}}(t) = (2p-1)\left(1+\frac{c_p}{\ln t}\right) + O((\ln t)^{-2})$$

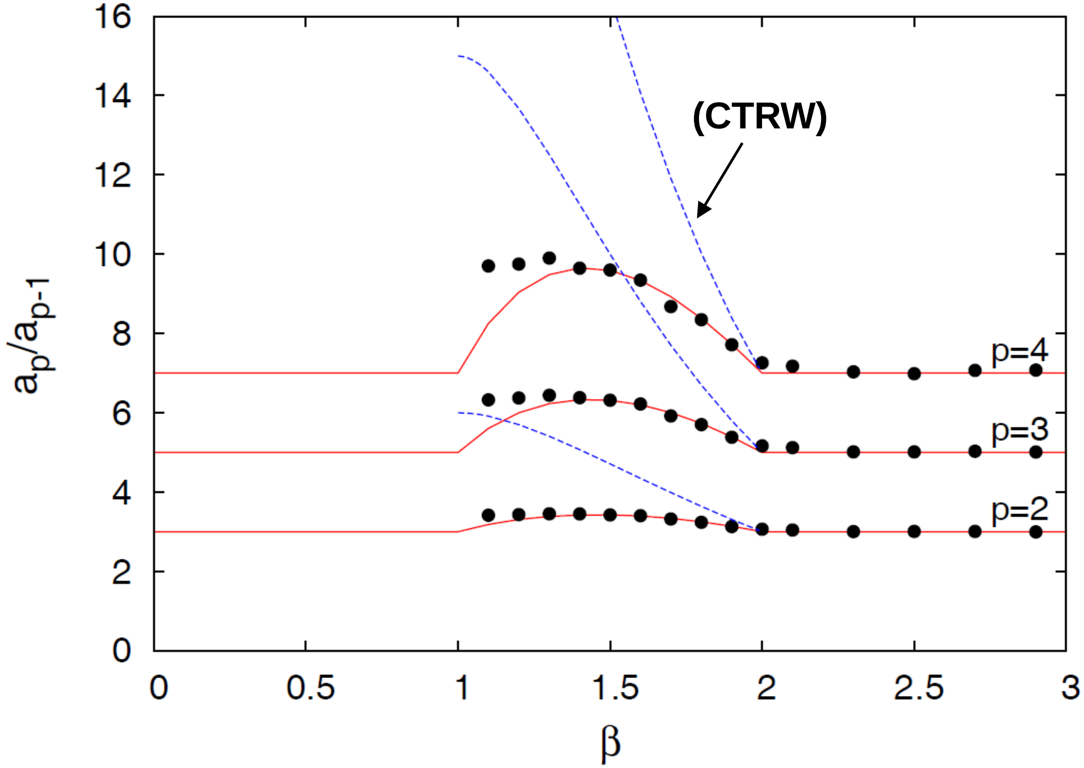
OK at t=10^{100} but not at 10^{9}.



β=2.5
β=β*=2
β=1.5
ℓ
x(t)
t
250
200
150
100
65000
70000
75000
80000
85000
50
0
-50
-100
30000
35000
40000
45000

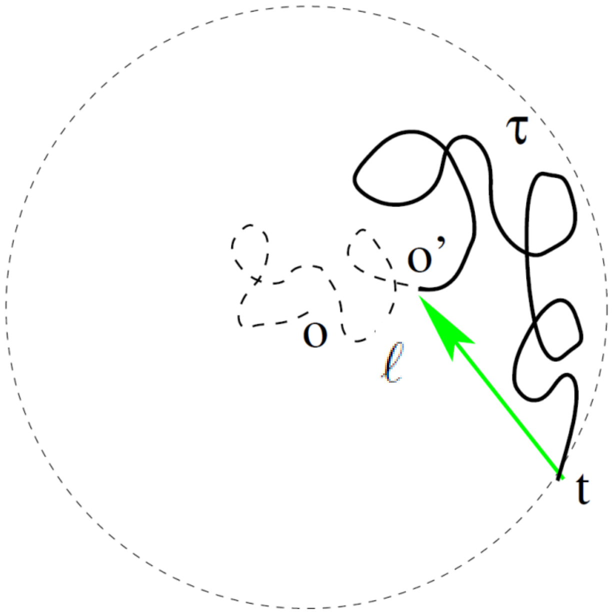
Case 1 < β < 2:

$$\frac{a_p}{a_{p-1}} = (2p-1)\frac{p\mathcal{I}_1(\beta)}{\mathcal{I}_p(\beta)} \quad \textbf{with} \quad \mathcal{I}_p(\beta) = \int_0^1 du \frac{1-u^{p(\beta-1)}}{(1-u)^{-\beta}}$$



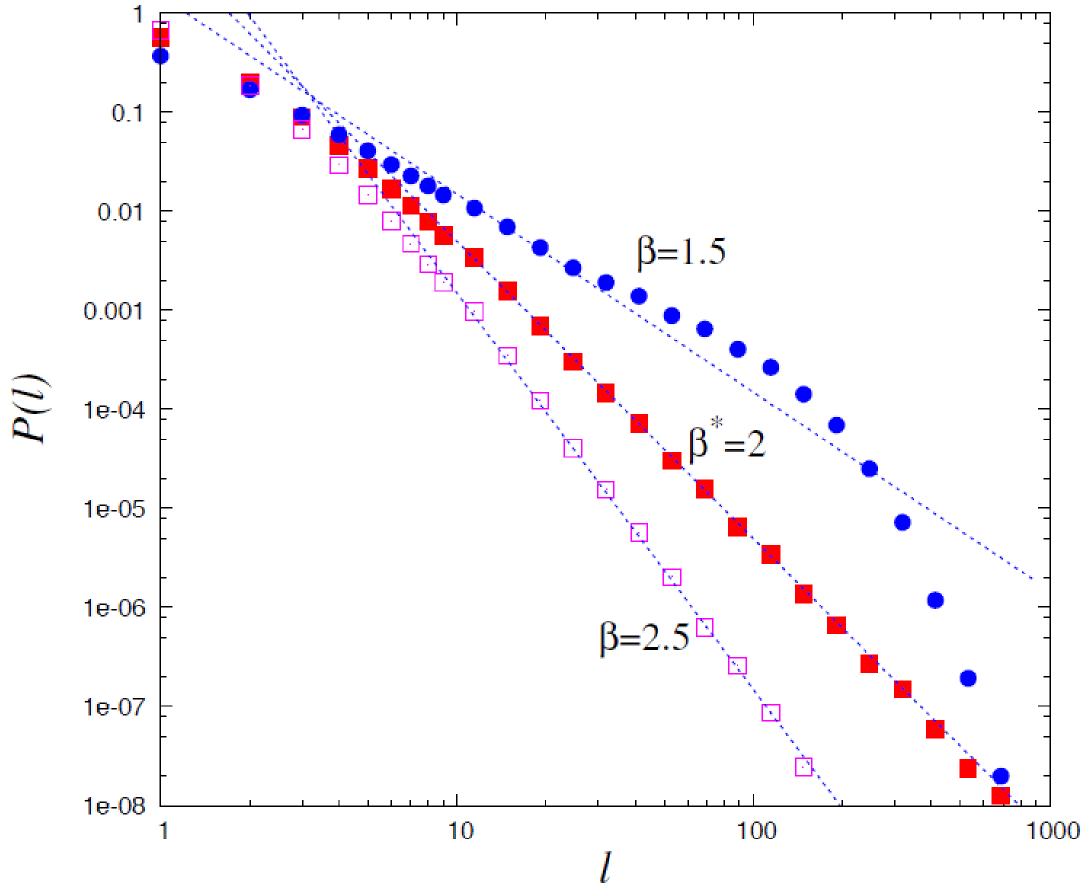
$$g(x) \propto e^{-b_\mu |x|^{\delta_\mu}}, \quad |x| \gg 1$$

Seems to be a new universality class, not related to a known subdiffusive process (e.g., Continuous Time RW).



$$\ell \sim [M_2(\tau)]^{1/2} \sim \tau^{1/2}$$

$$\Rightarrow P(\ell) \sim \ell^{-(2\beta-1)} \sim \ell^{-3}$$



Lévy-like step length distribution at $\beta = 2$.

"Lévy flights" at the onset of subdiffusion.