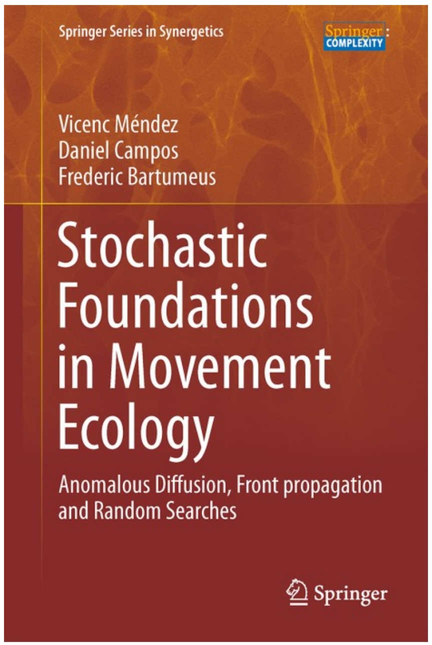
Advanced Study Group 2015:
Statistical Physics and Anomalous Dynamics of Foraging

MAX-PLANCK-GESELLSCHAFT



STOCHASTIC FOUNDATIONS IN MOVEMENT ECOLOGY III:

Mean first passage times and the exploitation-exploration tradeoff

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CSIC
*iCrea INSTITUCIÓ CATALANA DE RECERCA I ESTUDIS AVANÇATS

Stochastic Foundations in Movement Ecology III: MFPTs and the exploitation-exploration tradeoff

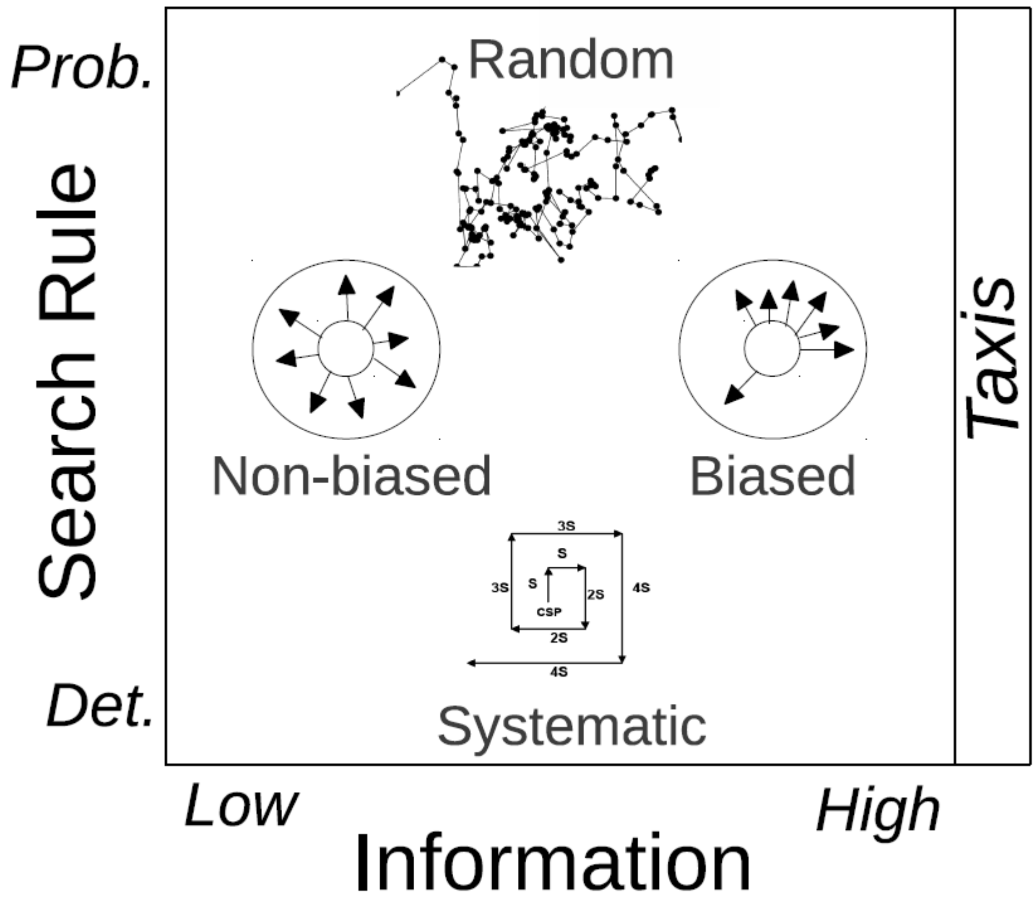
Sources:

- Raposo et al. PLoS Comput Bio (2011)
- Mendez et al. (2014) Chapter 6 and 9.
- Bartumeus et al. *PLoS ONE (*2014)
- Campos et al. *Phys. Rev. E* (2015)
- Bartumeus et al. *Ecology Letters* (submitted)
- Campos et al. (in preparation)

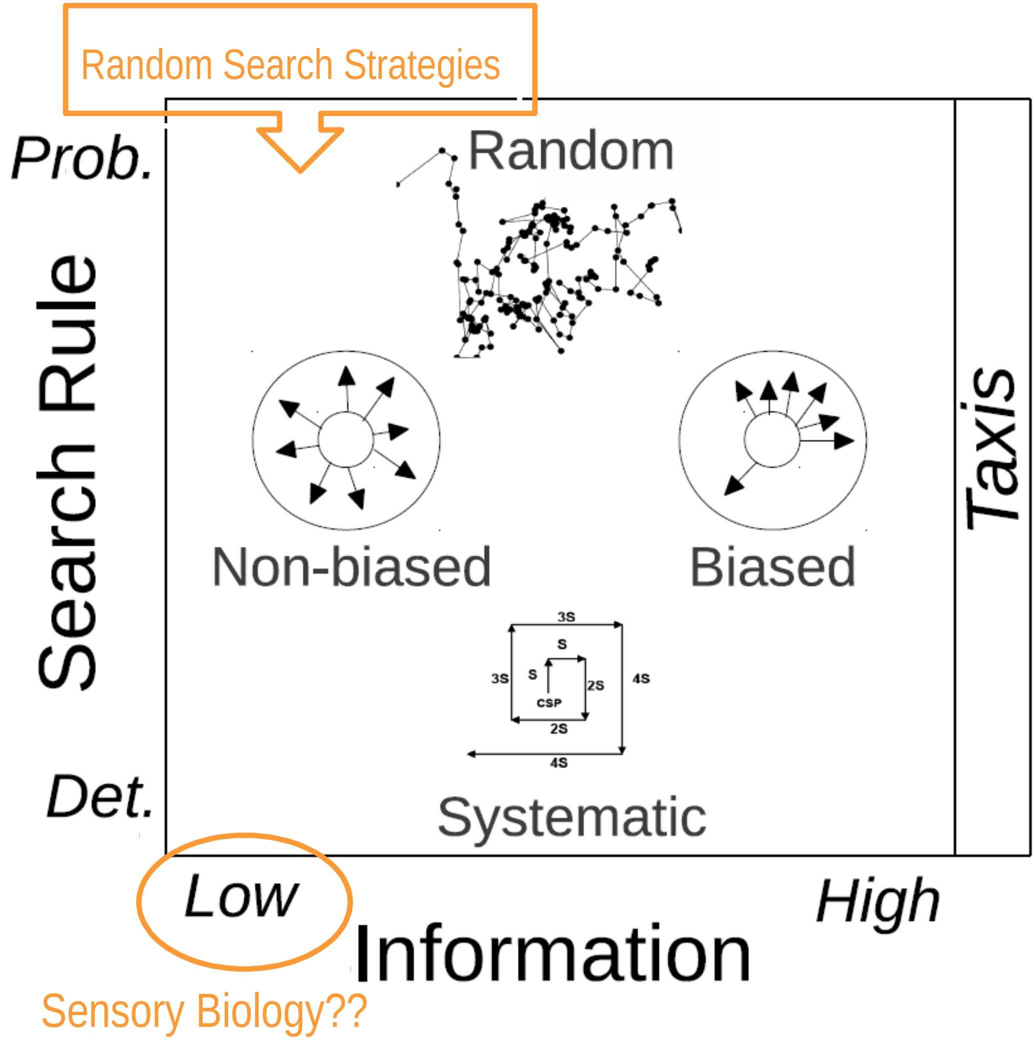
Collaborators:

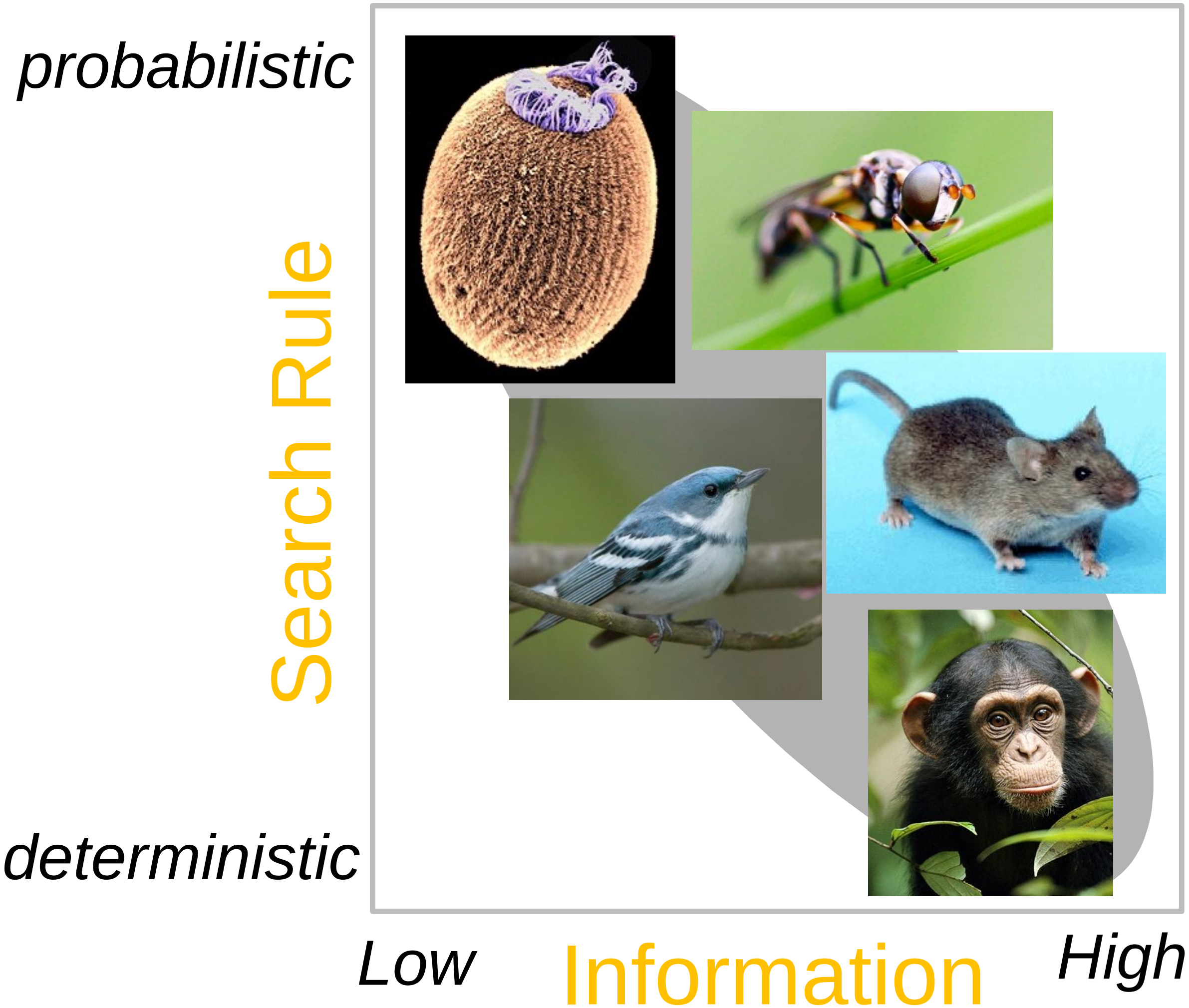
- Raposo E., da Luz M.G.E., Viswanathan G.M. (Brazil)
- Campos D., Mendez V. (Spain)

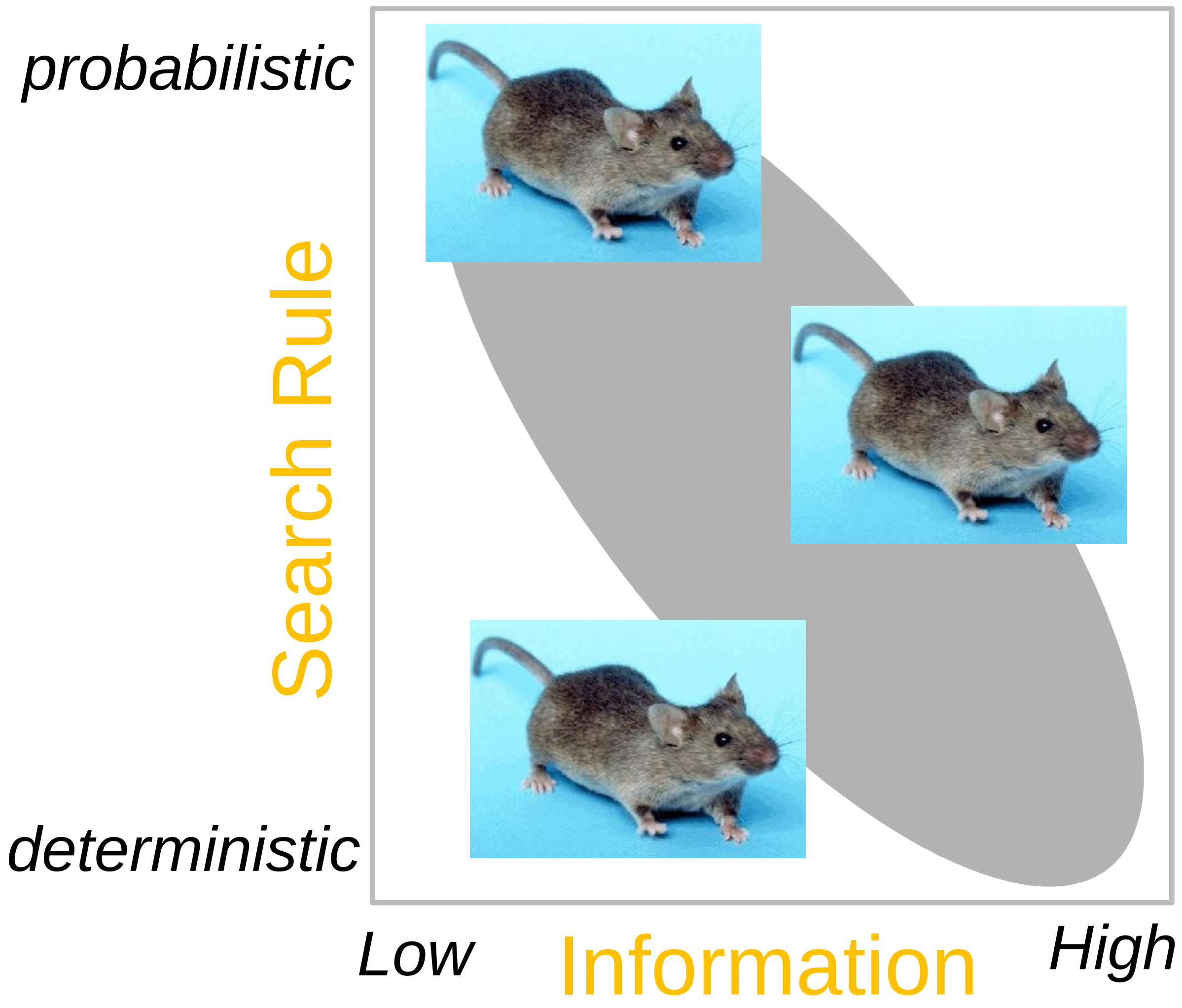
Search Strategies



Search Strategies




probabilistic
deterministic
Search Rule
Low
Information
High


probabilistic
Search Rule
deterministic
Low
Information
High

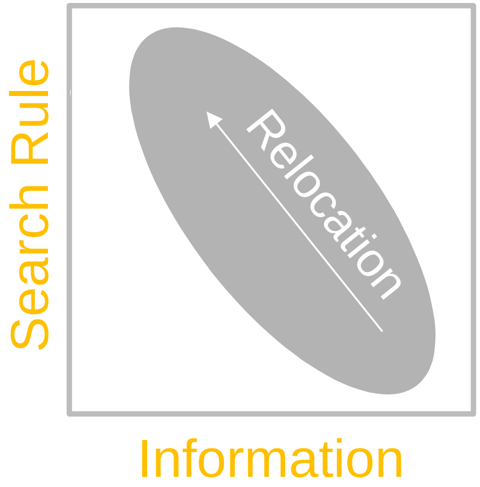
Animal Search Strategies: all types of rules

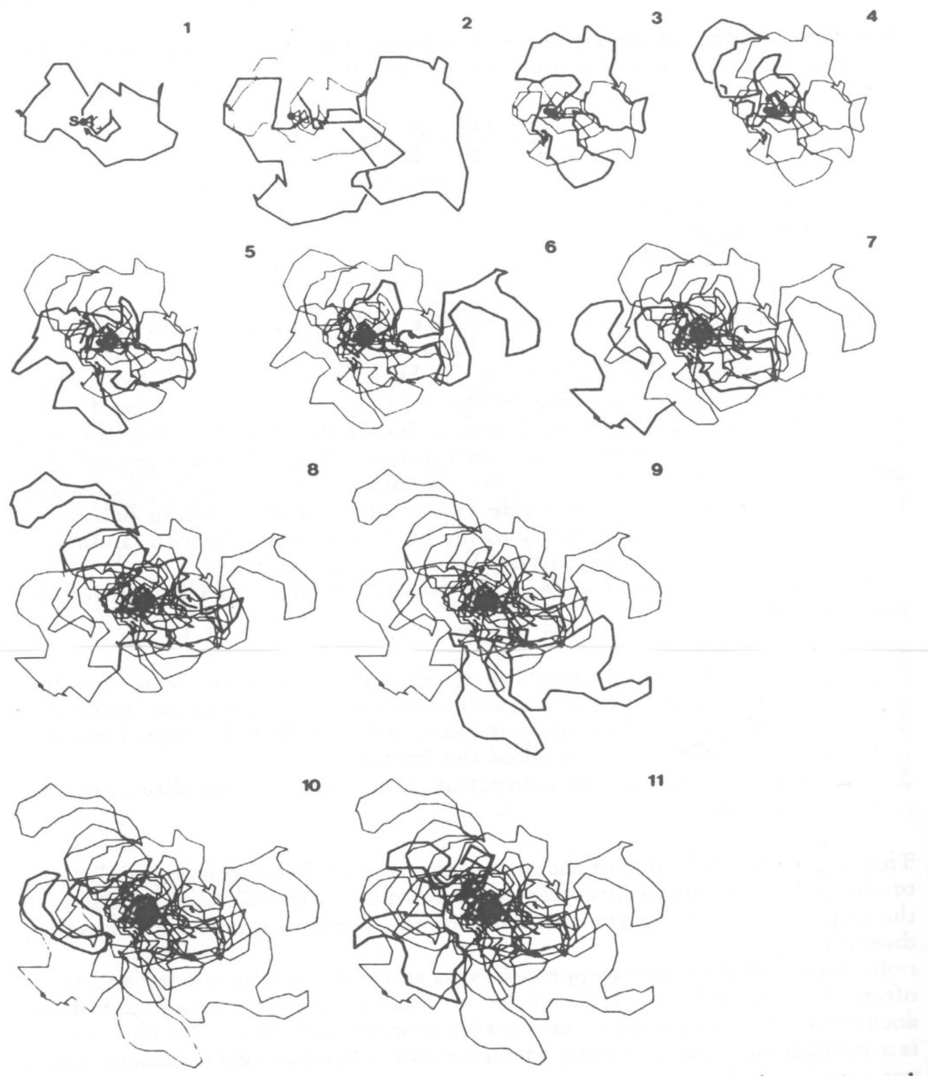
Relocation experiments

Learning, Trapline foraging

Relocation Experiments

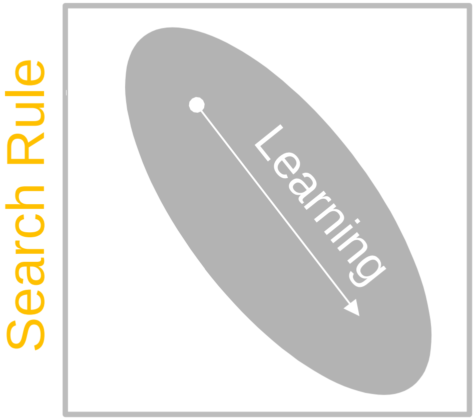
Hoffmann 1983a,b
Behav. Ecol. Sociobiol.

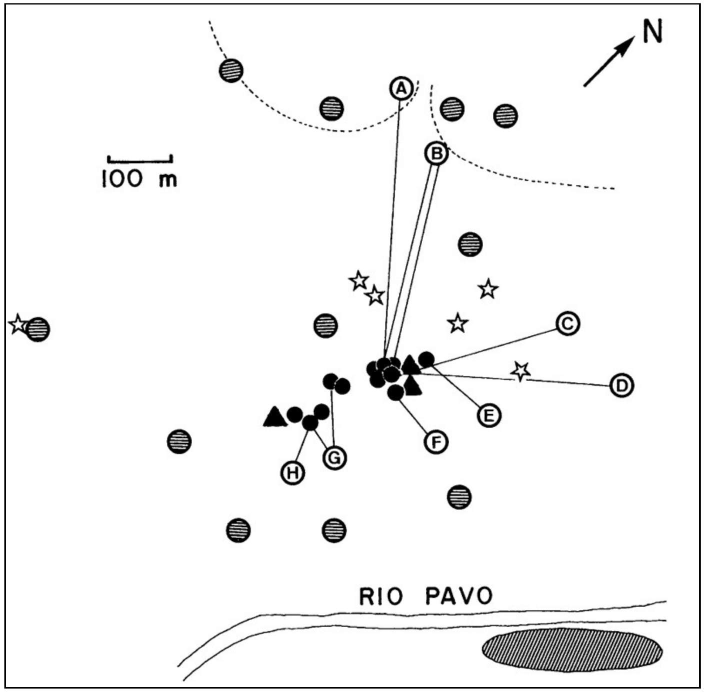


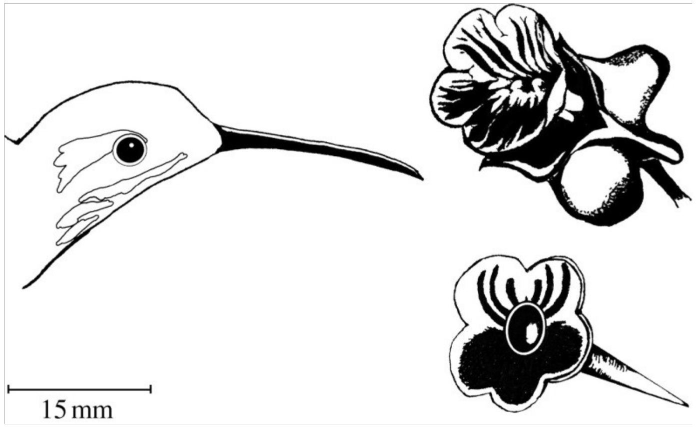


Learning Experiments

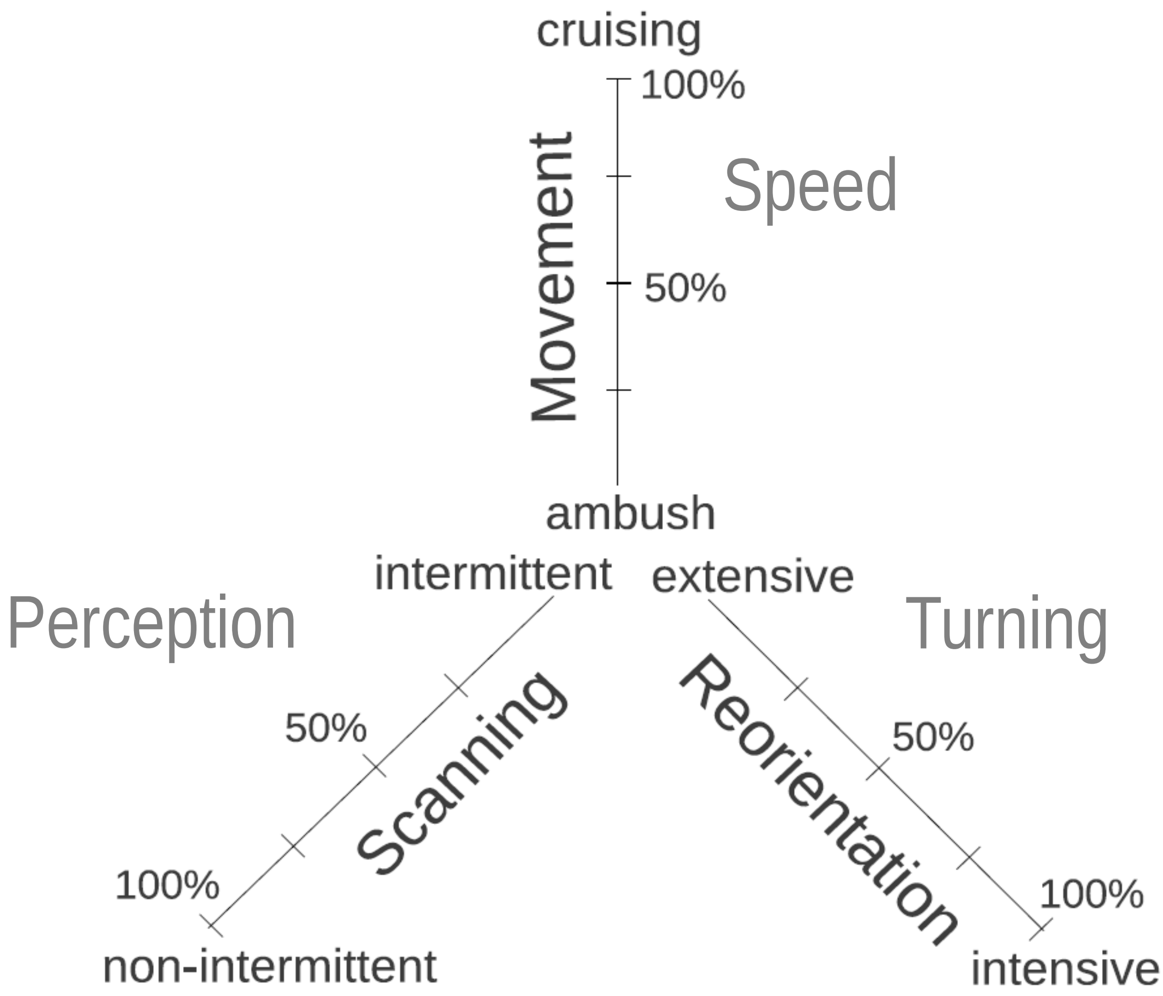
Gill 1988. Ecology.



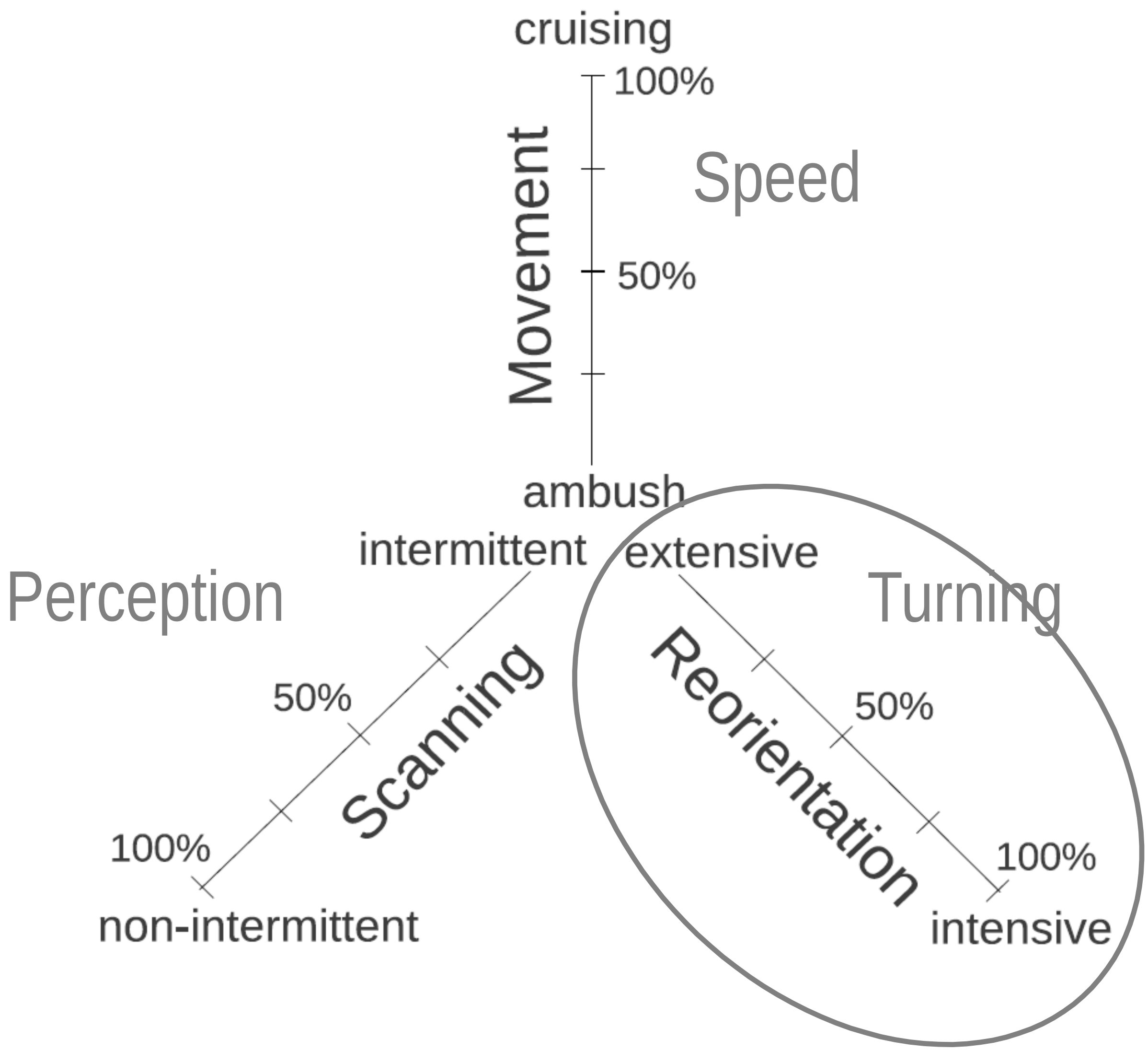




Searcher perspective

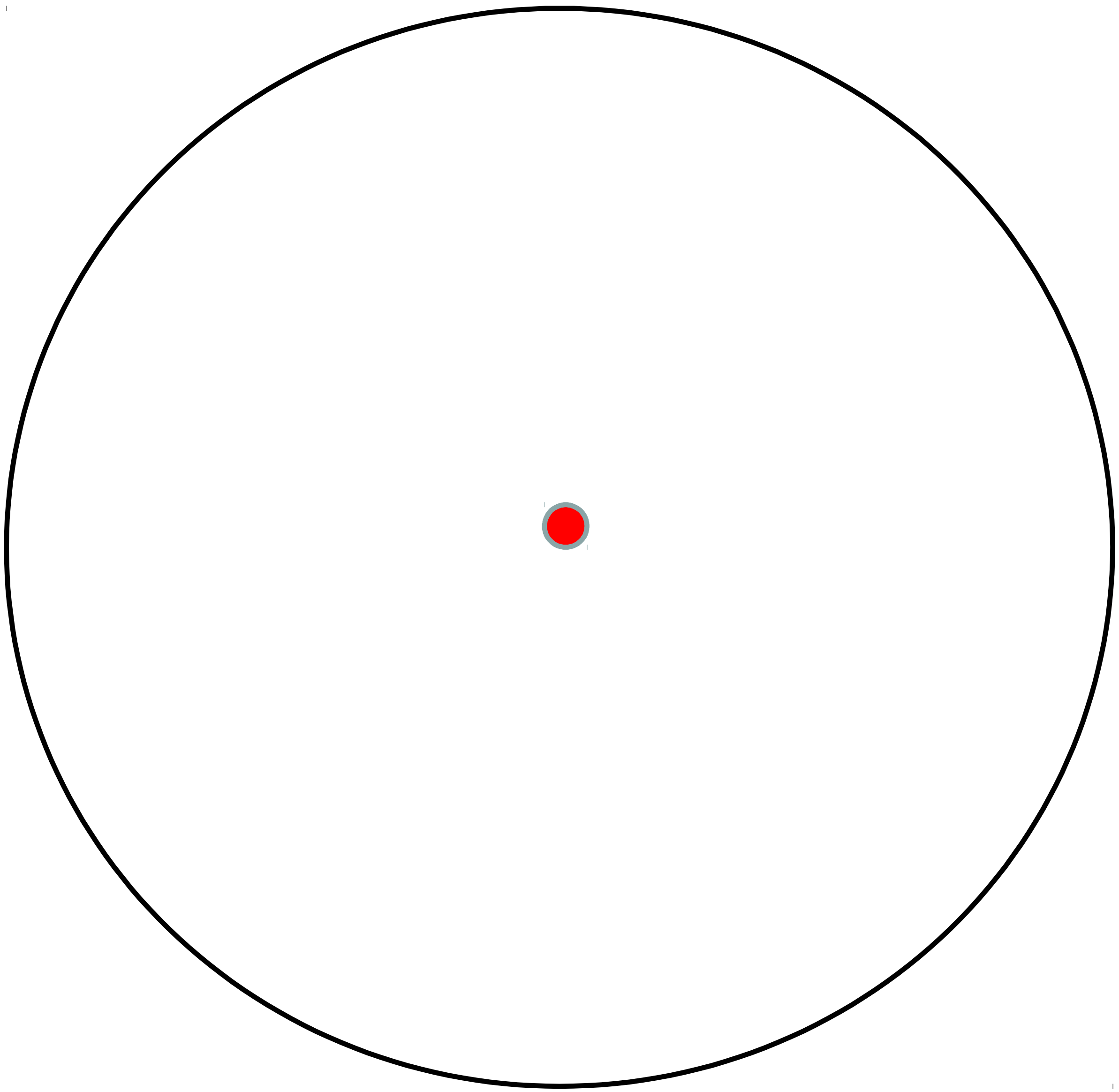


Searcher perspective

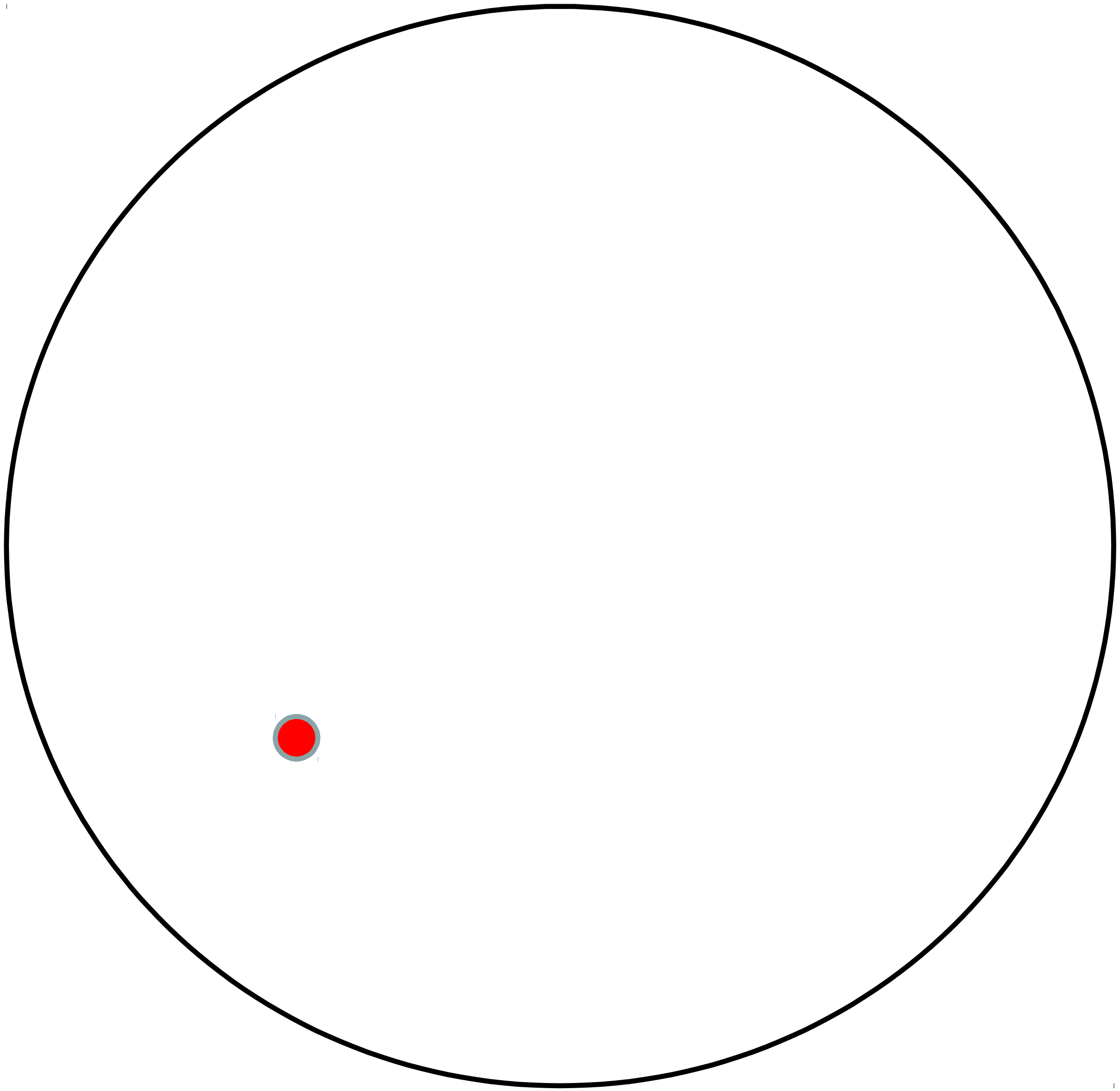


Why to turn at all?

Mean First Passage Times



Mean First Passage Times



The condition for turning

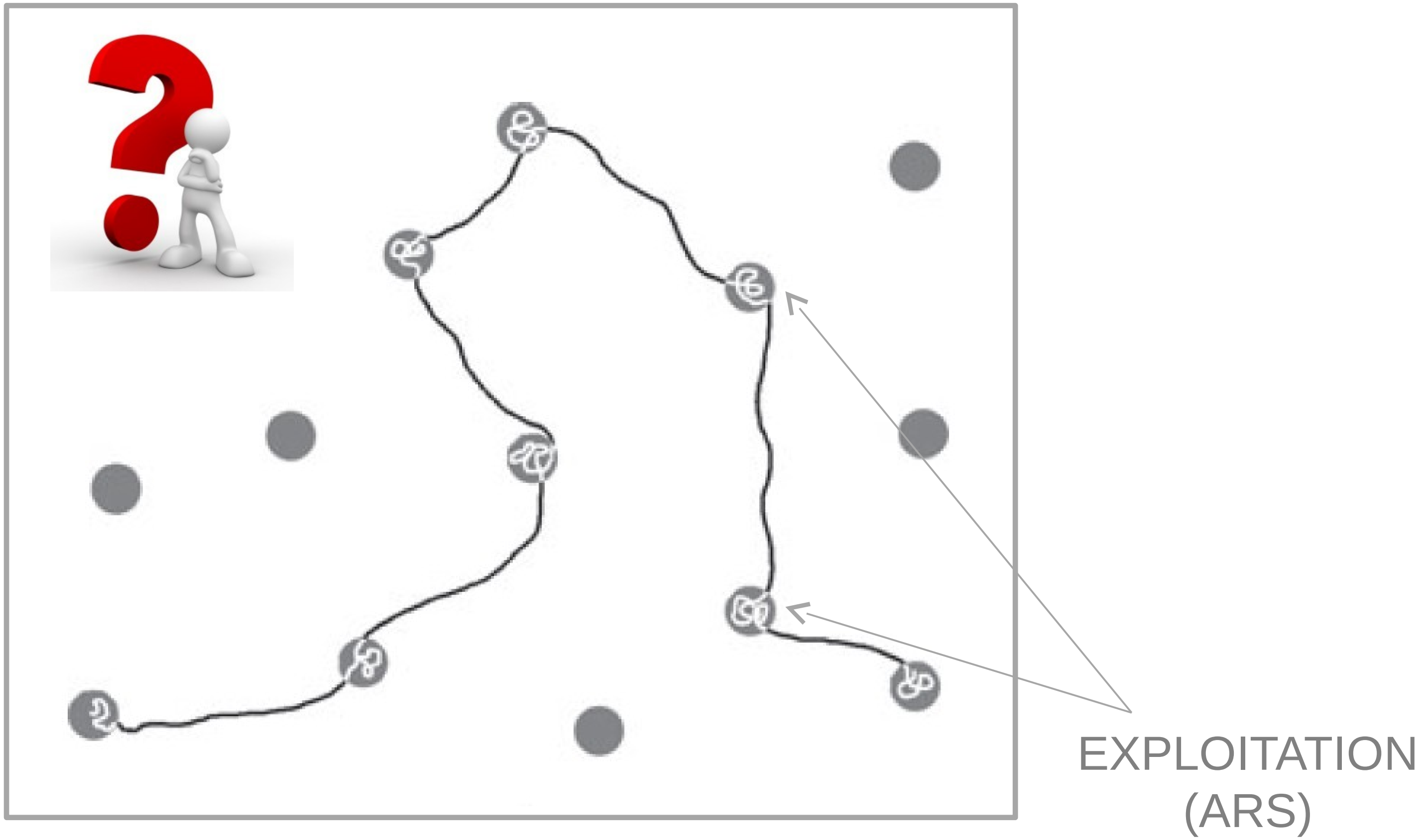
Assimetry

Heterogeneous searcher-to-target distances

Examples:

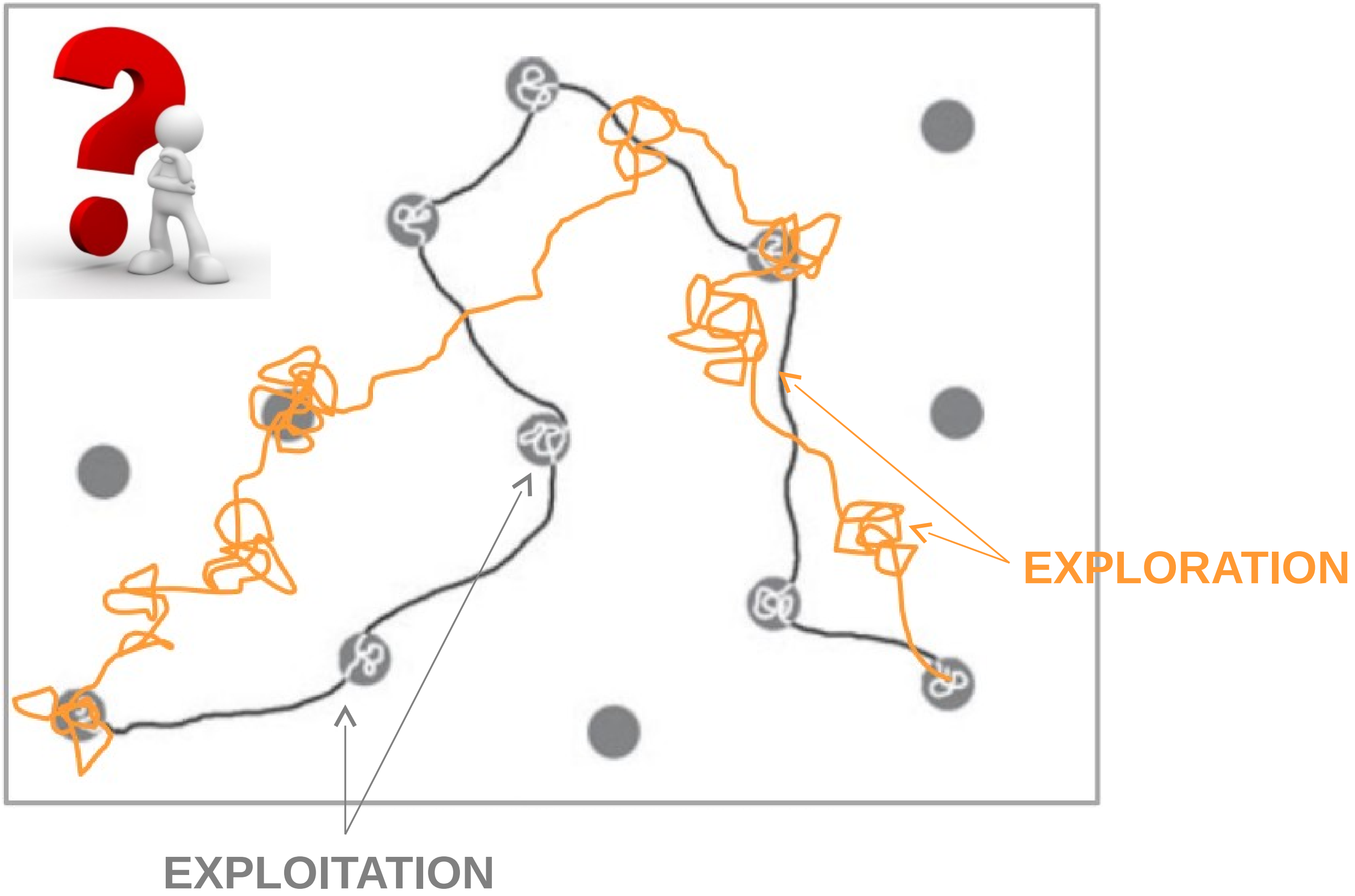
- Revisitable targets (non-destructive)
- Perception errors
- Patchy/higlhy heterogeneous landscapes

Turning behaviour as "cue"-driven



Simon Benhamou
Ecology Letters 2014 (Ideas and Perspectives)

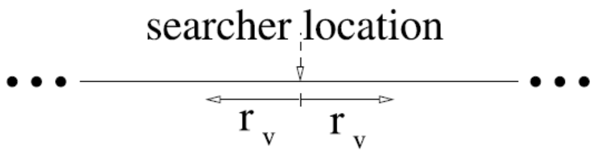
Turning behaviour as a “sampling” strategy



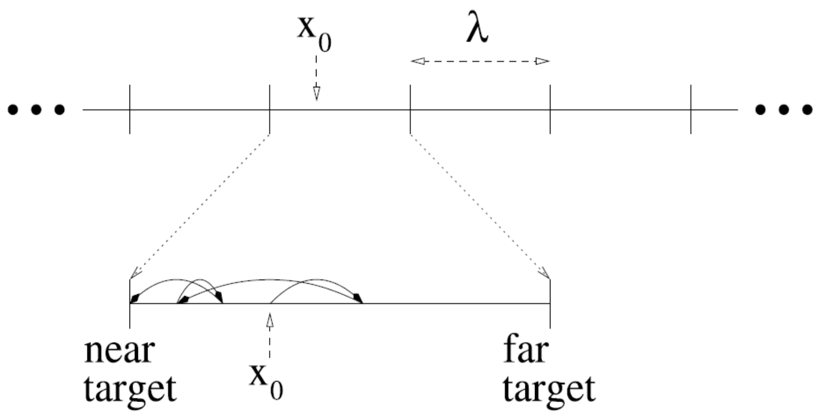
- To avoid missing nearby targets
- To improve 2D spatial coverage

Stochastic Optimal Foraging Theory

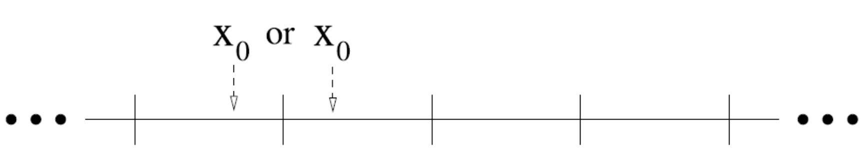
Perception:



Search process:



Back to initial conditions:



Stochastic Optimal Foraging Theory

We consider a 1D-random walker that can choose a direction (left/right) with equal probability and can take move lengths (ℓ) from a pdf $p(\ell)$

$$\int_{-\infty}^{+\infty} p(\ell)d\ell = 1, \ [p(-\ell) = p(\ell)]$$

We compute a statistical search efficiency as: $\eta = \frac{N_{\mathrm{found}}}{L_{\mathrm{tot}}}$

$$L_{\mathrm{tot}} = N_{\mathrm{found}} \langle L \rangle, \ \ \eta = \frac{1}{\langle L \rangle}$$

$$N = N_{\mathrm{found}} \langle n \rangle, \ \langle |\ell| \rangle (x_0), \ \ \eta \approx (\langle n \rangle \langle |\ell| \rangle)^{-1}$$

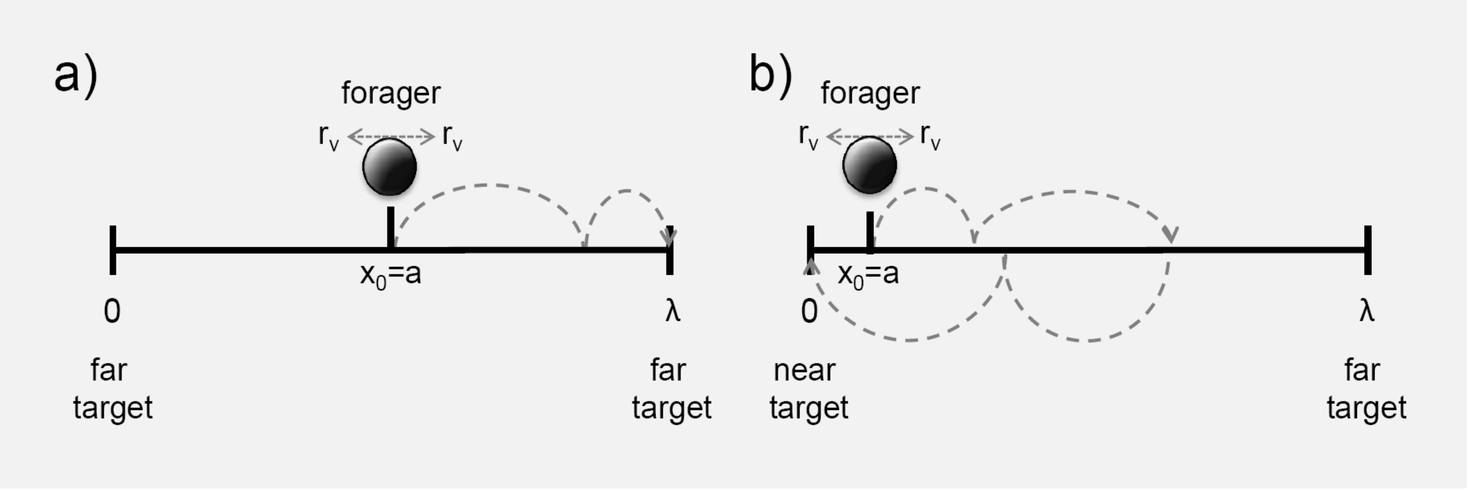
$\langle L \rangle$	average distance travelled between two targets found
$\langle n \rangle$	average number of steps between two targets found
$\langle \lvert\ell\rvert \rangle$	average step length between two targets found

Stochastic Optimal Foraging Theory

$\langle L \rangle$	average distance travelled between two targets found
$\langle n \rangle$	average number of steps between two targets found
$\langle \lvert \ell \rvert \rangle$	average step length between two targets found

These 3 quantities depend on:

- An **initial position** $(x_0 = a)$
- A **boundary condition**: the average distance between targets $(x_0 = \lambda)$



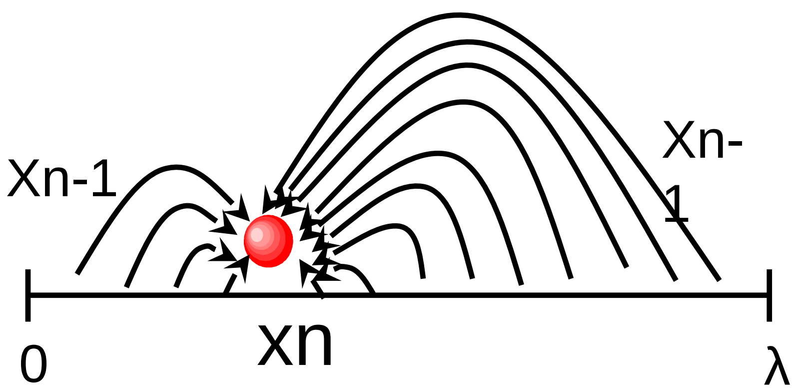
Stochastic Optimal Foraging Theory

Key concept of the calculations: a renewal approach

We note that:

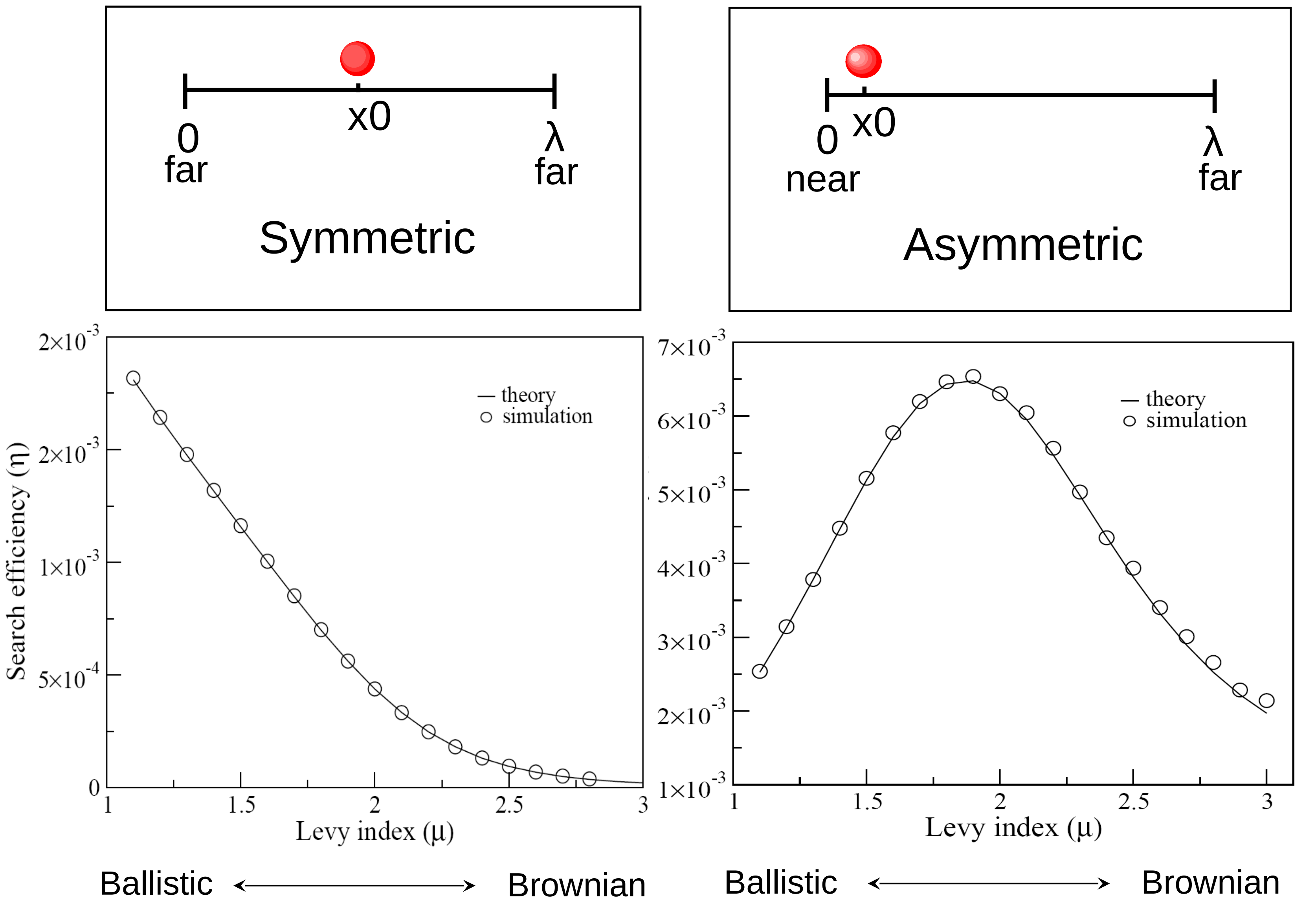
$$\rho_n(x_n) = \int_{\ell_0}^{\lambda-\ell_0} \rho_{n-1}(x_{n-1}) p(x_n - x_{n-1}) dx_{n-1} \ , \qquad \ell_0 \leq x_n \leq \lambda - \ell_0$$

The probability density for the walker to be at position xn in the interval [xn,xn+dx] after n steps can be defined as the probability density of being at the previous position xn-1 times the probability density of performing a step of length xn-xn-1. The integration accounts for all the possible previous positions xn-1 that lead to xn.



Raposo et al. PLoS Comput Bio (2011)
Bartumeus et al. *PLoS ONE* (2014)

Stochastic Optimal Foraging Theory

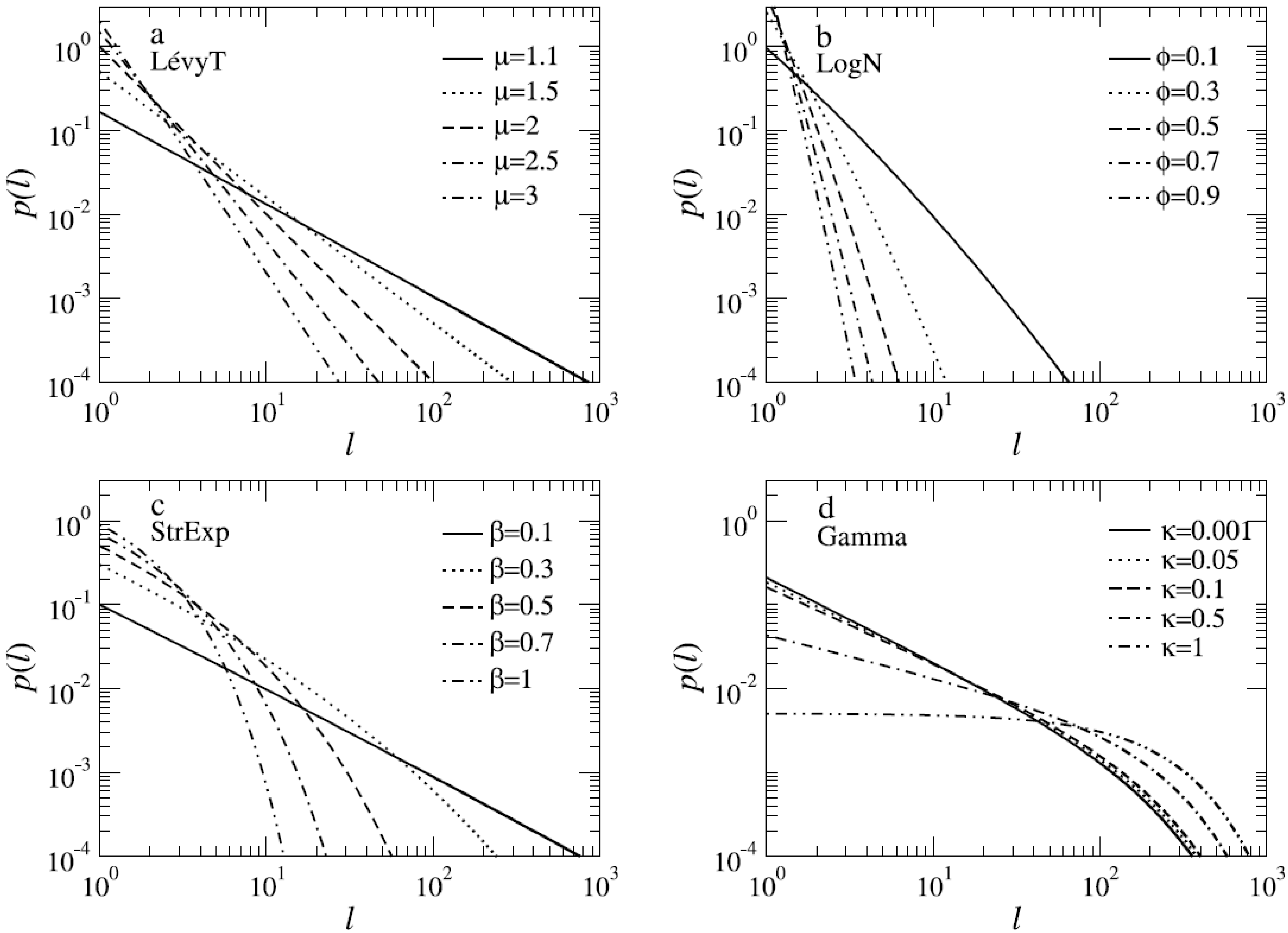


Flight distributions

Stretched exponential	$p(\ell) = \alpha\Theta(\|\ell\| - \ell_0)\|\ell\|^{\beta-1}\exp(-\phi\|\ell\|^{\beta})$
Gamma	$p(\ell) = \alpha\Theta(\|\ell\| - \ell_0)\|\ell\|^{k-1}\exp(-\beta\|\ell\|)$
Lognormal	$p(\ell) = \frac{\alpha}{\|\ell\|}\Theta(\|\ell\| - \ell_0)\exp\{-\phi[\ln(\beta\|\ell\|)]^2\}$
Power law	$p(\ell) = \alpha\frac{\Theta(\|\ell\| - \ell_0)}{\|\ell\|^{\mu}}$

where the theta function is such that $\Theta(|\ell| - \ell_0) = 0$ if $|\ell| < \ell_0$, and $\Theta(|\ell| - \ell_0) = 1$ otherwise

Flight distributions: two key parameters



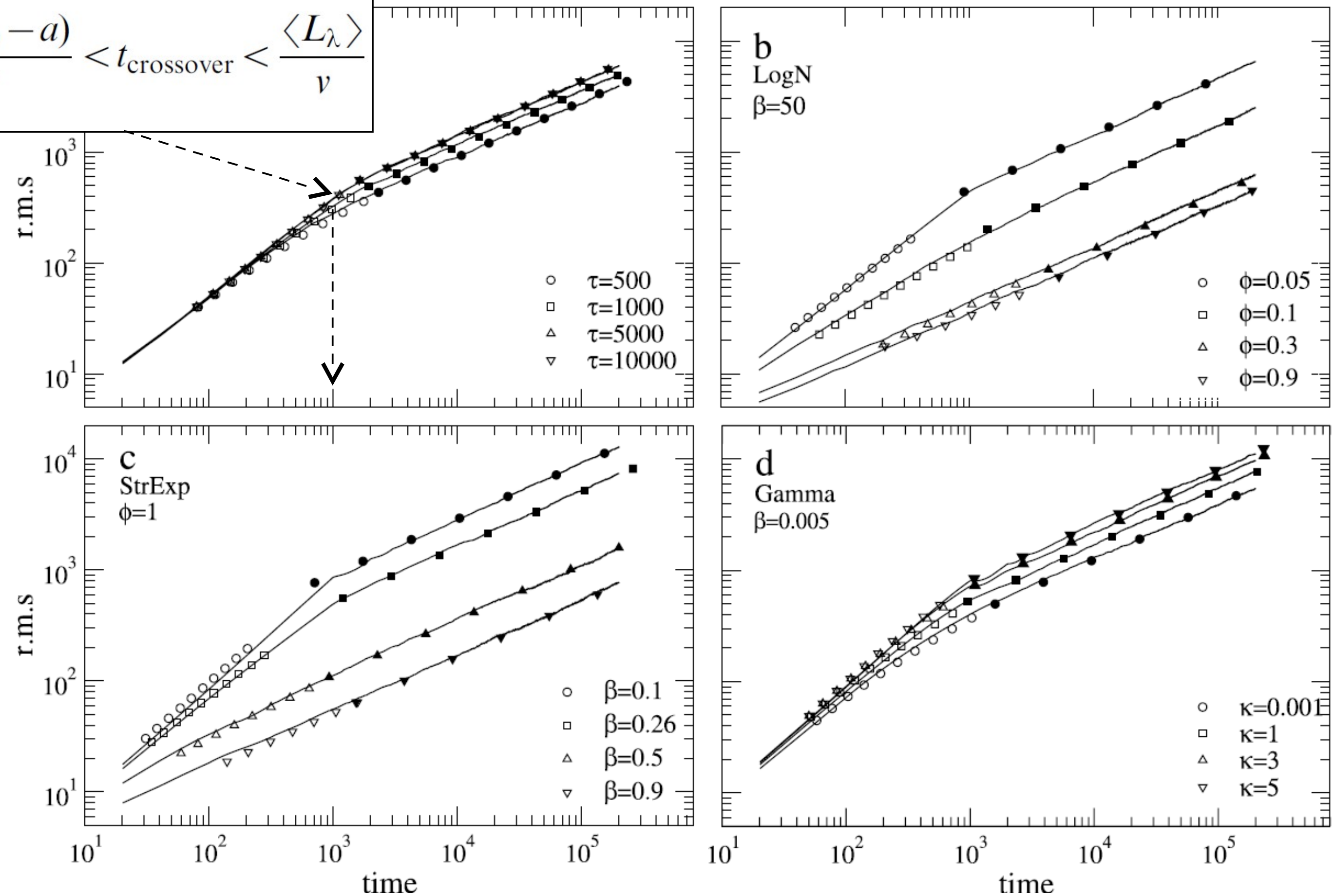
Root mean square displacement

Asymmetric condition

$$R \equiv [\langle(\Delta x)^2\rangle]^{1/2} = [\langle x^2\rangle - \langle x\rangle^2]^{1/2}$$

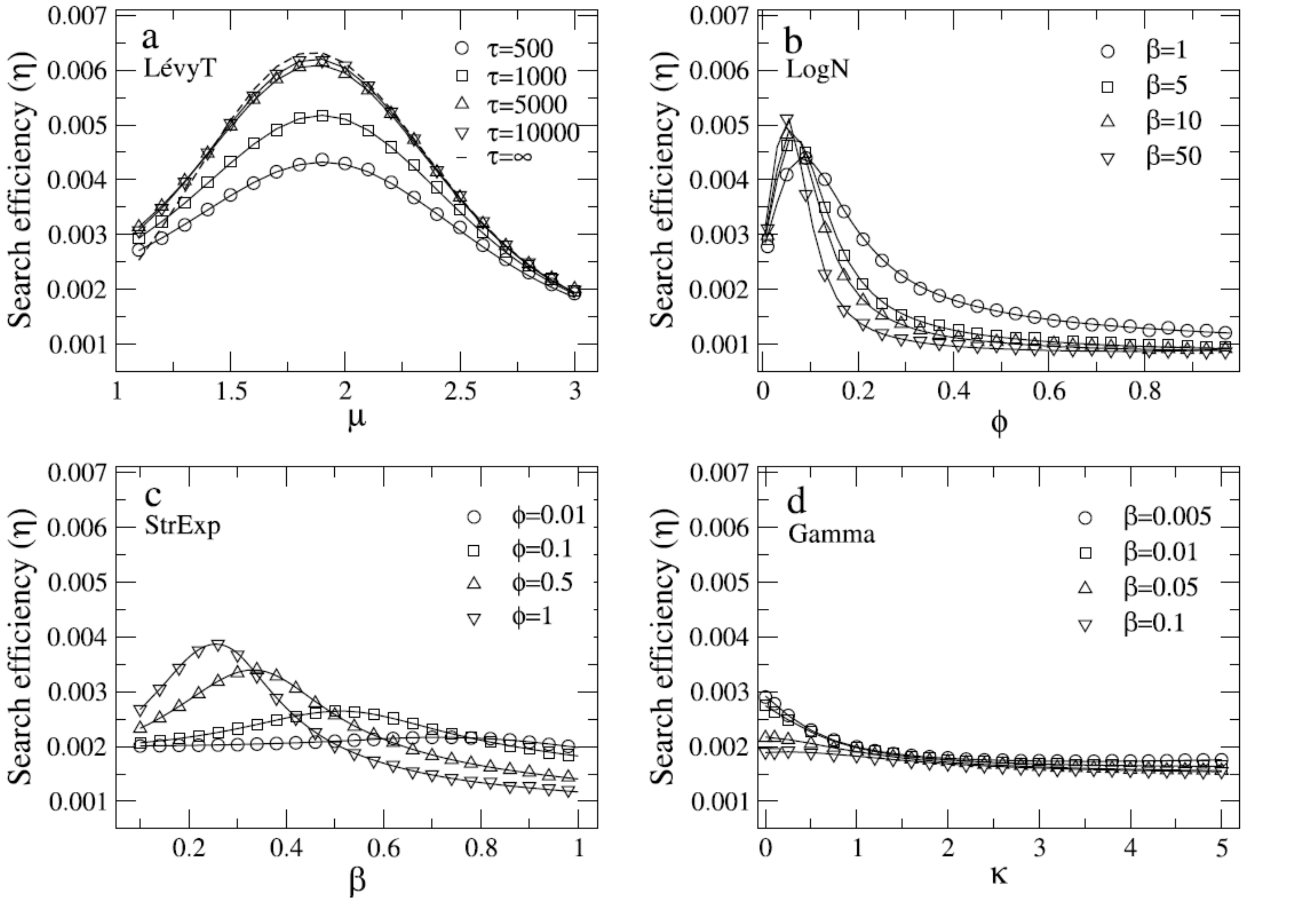
$$\begin{cases} R_{\mathrm{fpt}} = (\lambda - 2r_v)(p_0 p_\lambda)^{1/2} \\ R_{\mathrm{Brownian}} = \left(\dfrac{\lambda^2 v p_\lambda}{\langle L\rangle}\right)^{1/2} t^{1/2} \end{cases}$$

$$\frac{(\lambda - r_v - a)}{v} < t_{\mathrm{crossover}} < \frac{\langle L_\lambda\rangle}{v}$$



The Search Efficiency (1/MFPT)

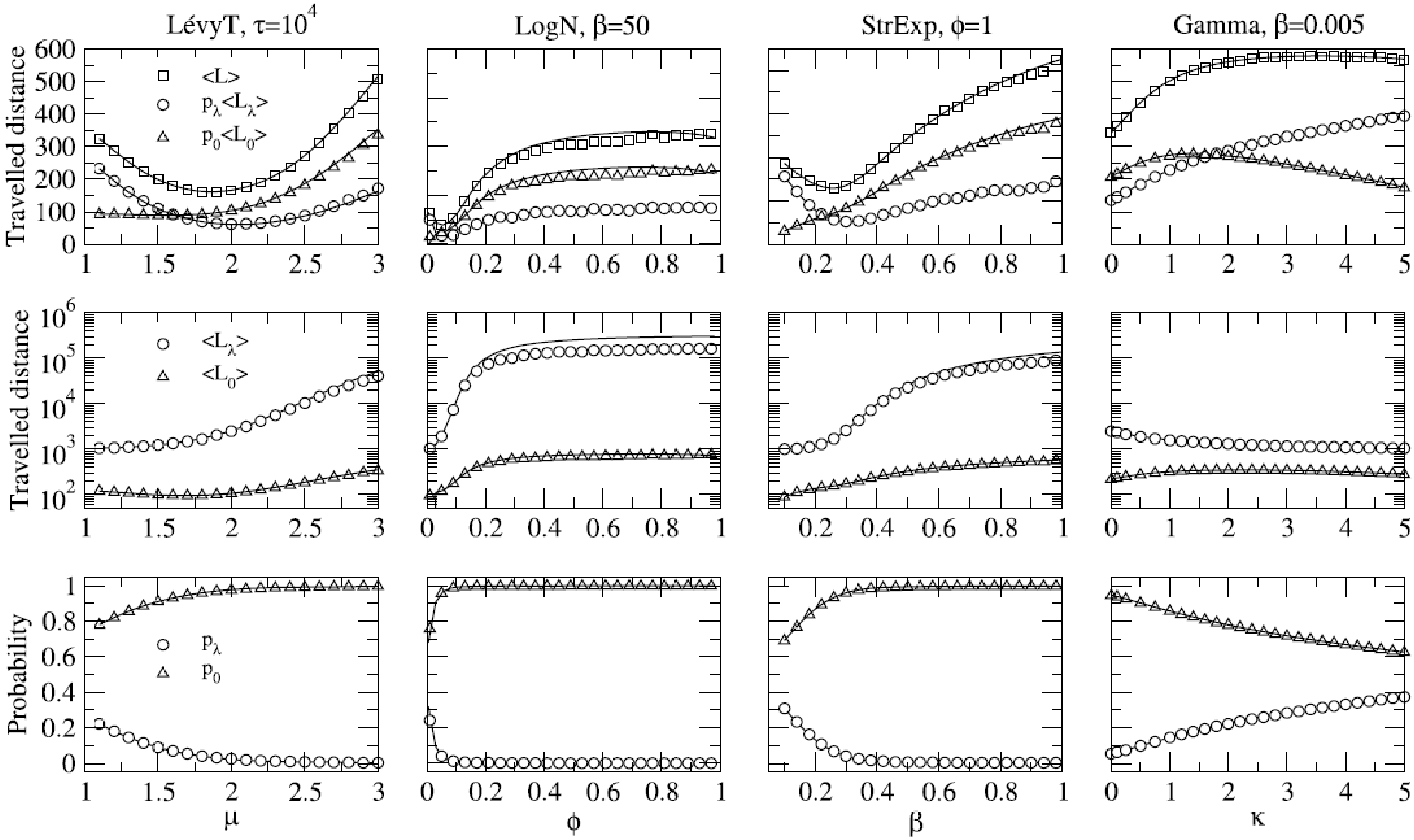
Asymmetric condition



The Search Efficiency: factorizaiton

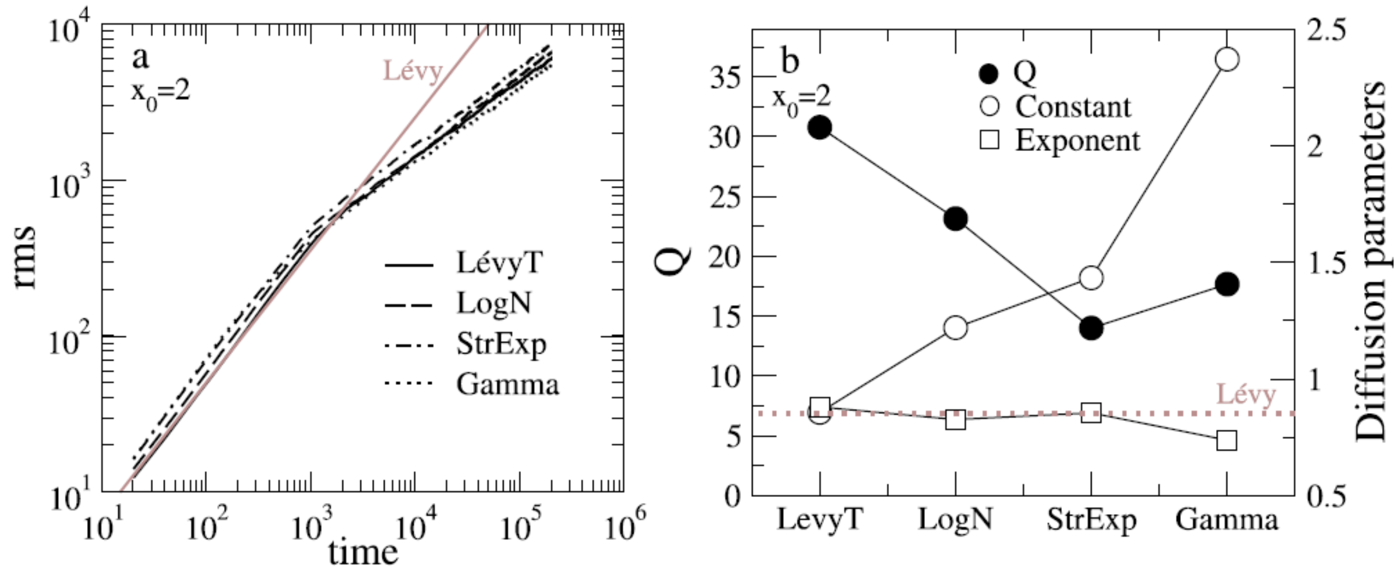
Asymmetric condition

$$\langle L \rangle = p_0 \langle L_0 \rangle + p_\lambda \langle L_\lambda \rangle$$



The Search Efficiency (1/MFPT)

Asymmetric condition

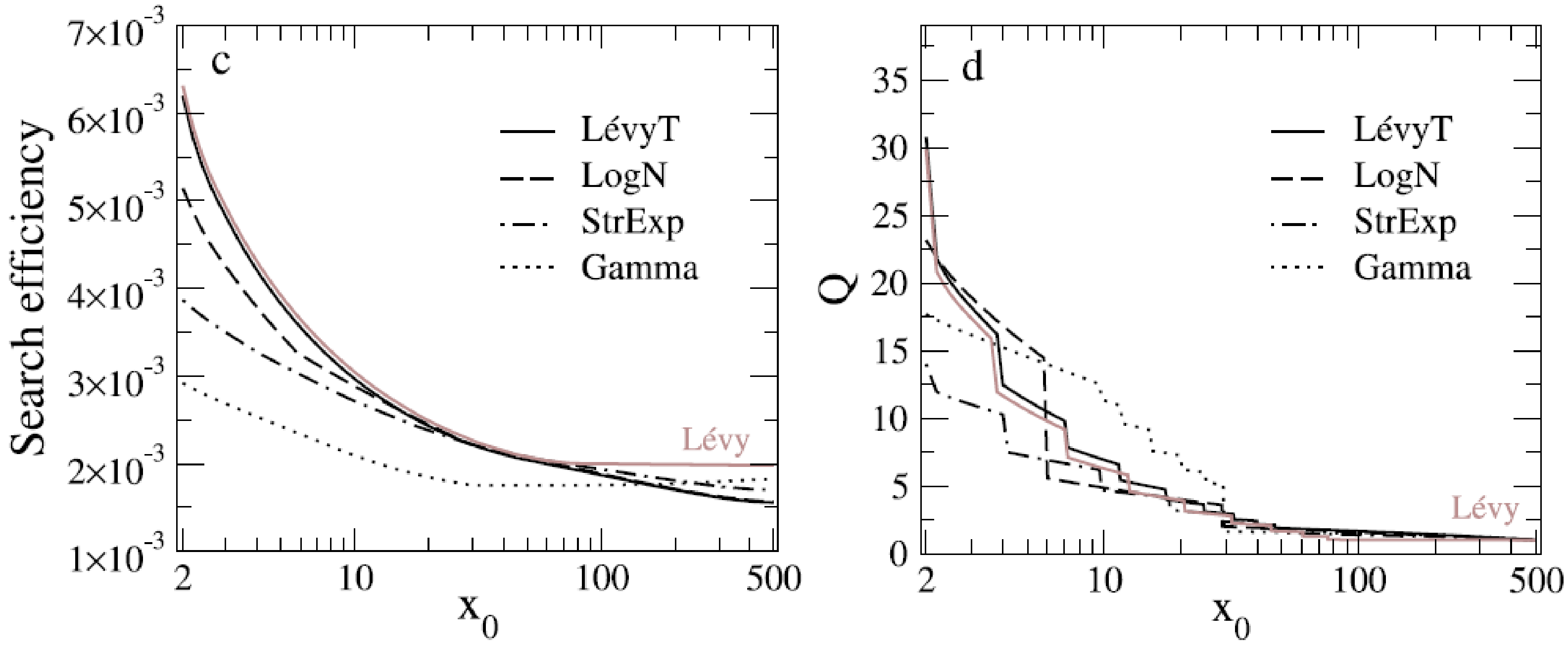


Ratio between the average numbers of encounters of the closest (first order revisit) and farthest (new and high order revisits) targets

$$Q = \frac{\langle N_0 \rangle}{\langle N_N \rangle + \langle N_H \rangle}$$

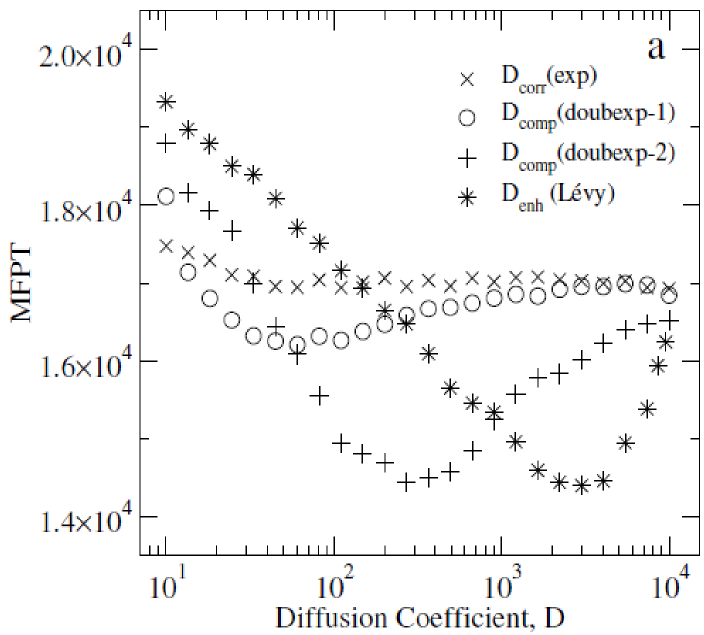
The Search Efficiency (1/MFPT)

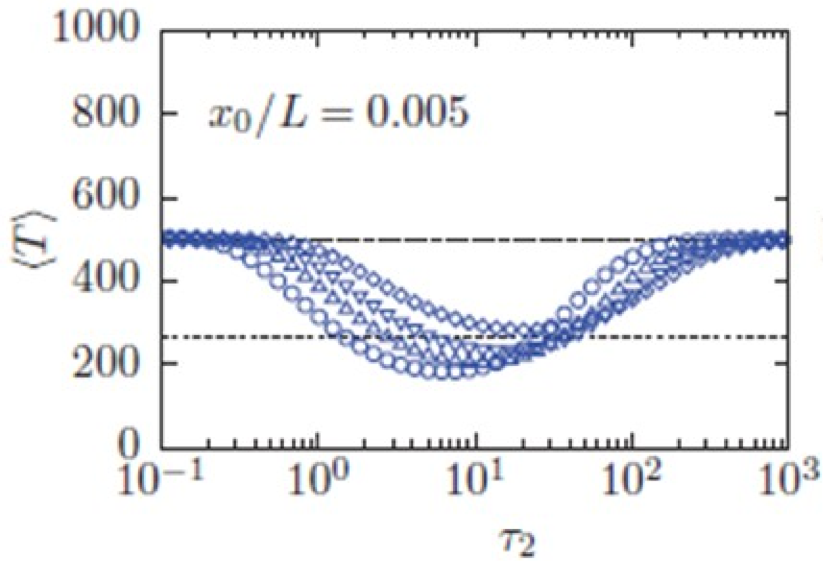
From asymetric to symetric condition…



The Search Efficiency (1/MFPT)

A mixture of scales…with the right scales….beats Levy





Why to turn at all?

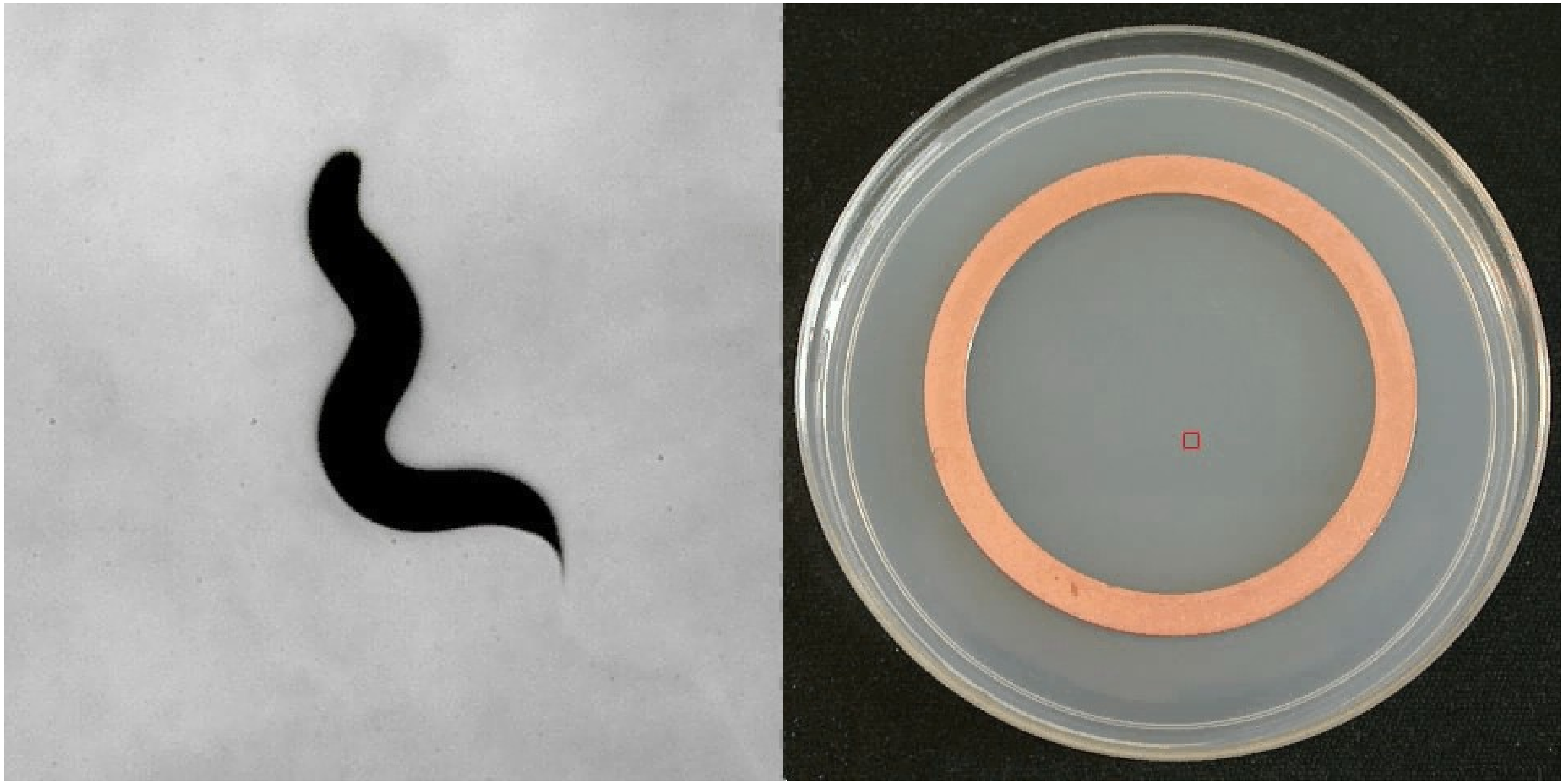
<u>To solve exploitation-exploration tradeoffs</u>

A) Reorientation behaviour (time-to-reorientation) can control movement scales.

B) If there is information about relevant landscape scales one should match reorientations to those particular scales.

C) The larger the uncertainty the larger is the number of scales needed to solve the exploitation-exploration tradeoff

Chaenorabditis elegans



> Locomotion includes crawling or swimming and they perform stereotyped turns

Omega / Reversals / Pirouettes / Pauses

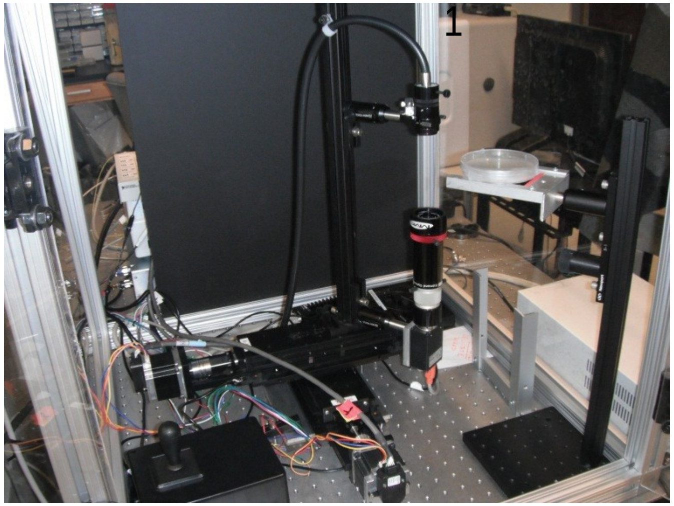
> Evidence of random movements and chemotaxis

> Mutants (sensorial and motor) and engineering genetic techniques

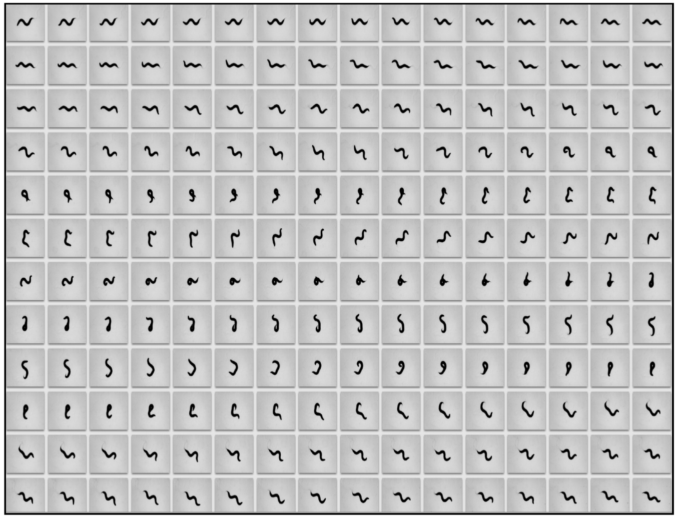
Tracking system and behavioral annotation

W.Ryu Lab. U.Toronto, Canada

4 frames sec-1



Behaviour



Turning behaviour in a random search

How to turn?

- Abruptly (reorientation)
- Smoothly (persistent curvature)

When to turn?

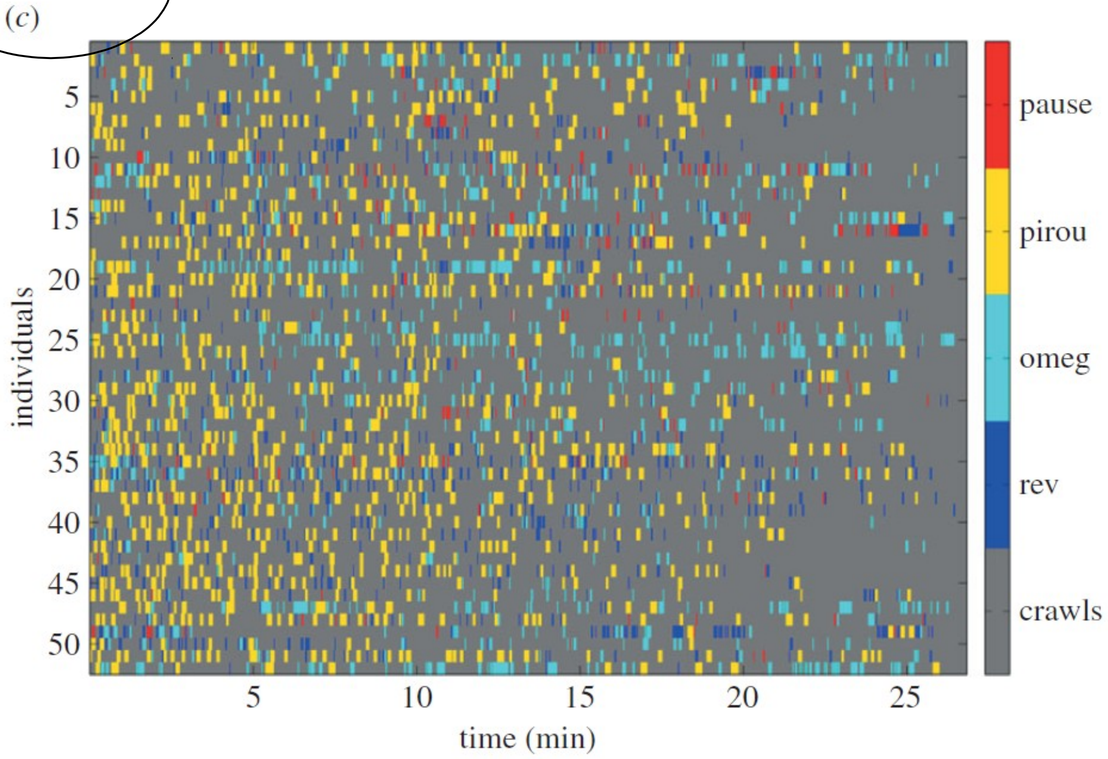
- Time between turns
- Curvature control (loops)

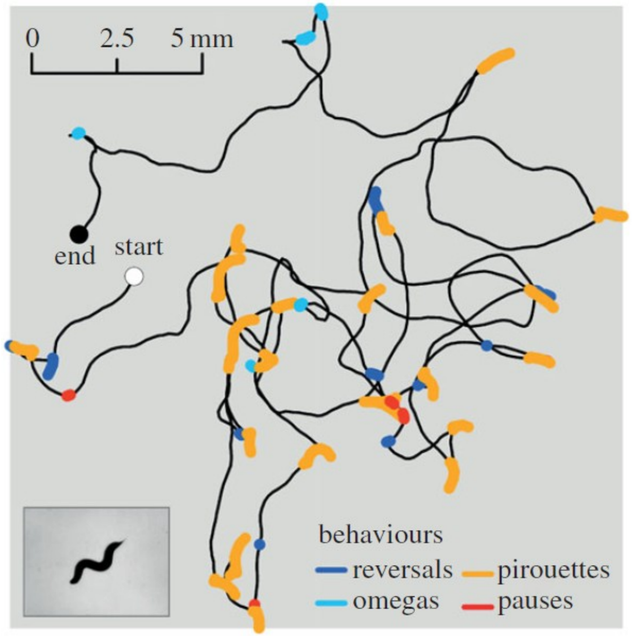
Search efficiency, space use, revisitability…

Simple relocation experiment: from food to no-food

food

No food (but no starvation). Minimal cues.



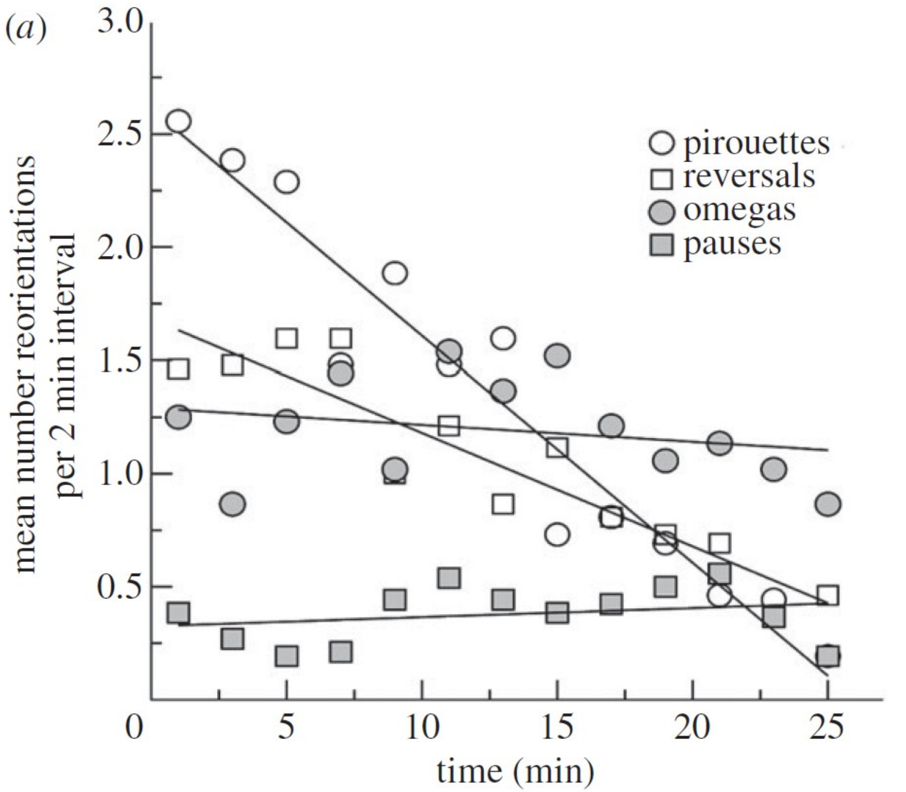


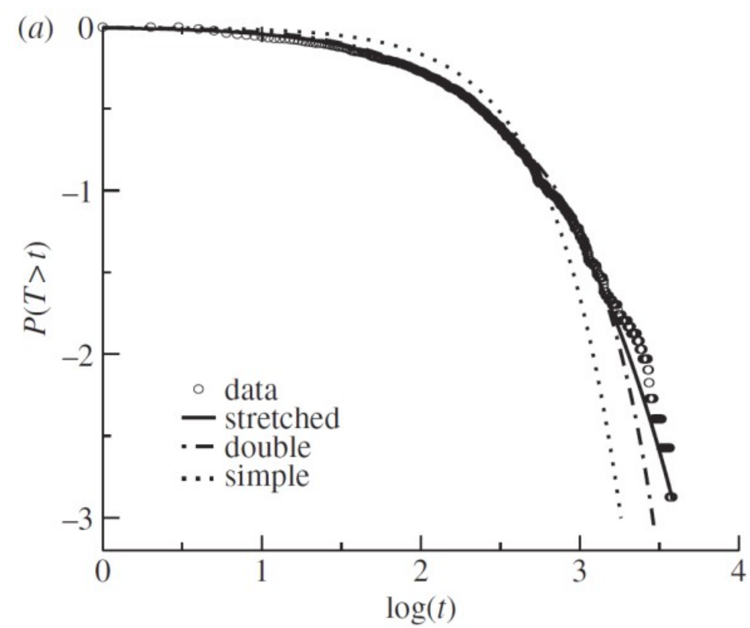
Salvador et al. (2014)
J Royal Soc Interface

Different temporal dynamics for different turn types

food

No food (but no starvation). Minimal cues.

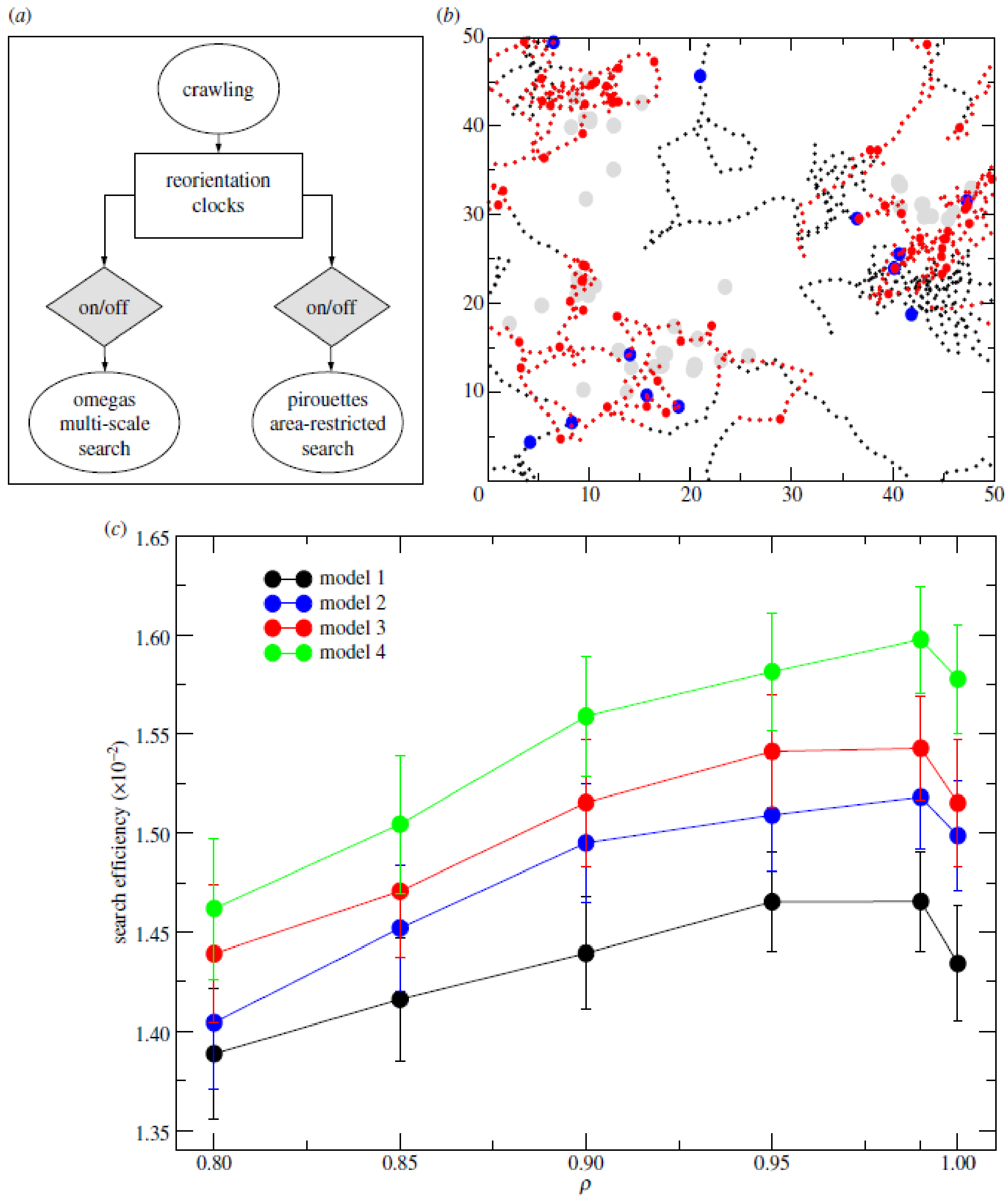




Pirouettes “food memory
Omegas ”template

Omega turns:
heavy-tail distribution

Toy model



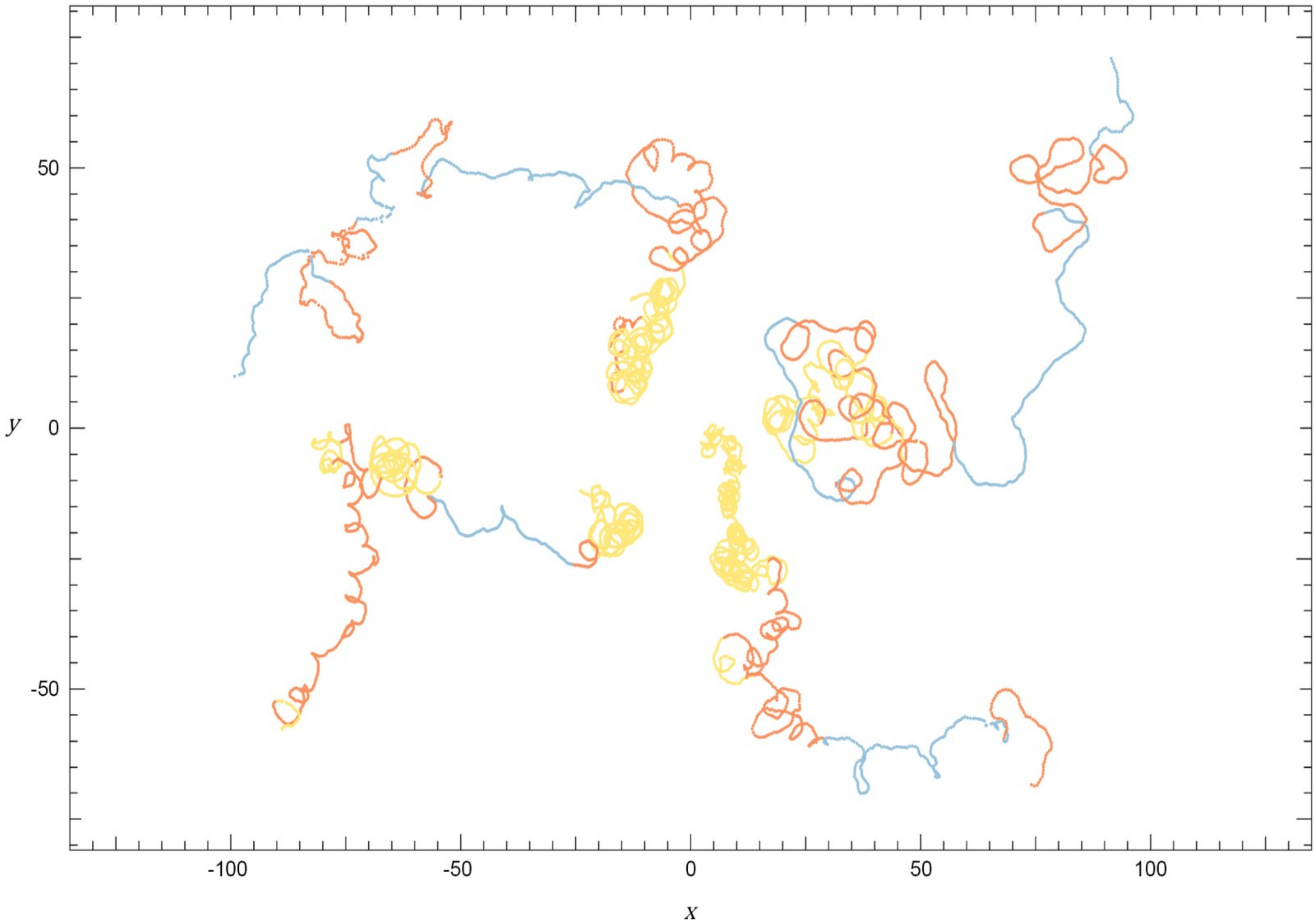
CRW + omegas + pirouettes

CRW + Exp (pirouettes)

CRW + strExp (omegas)

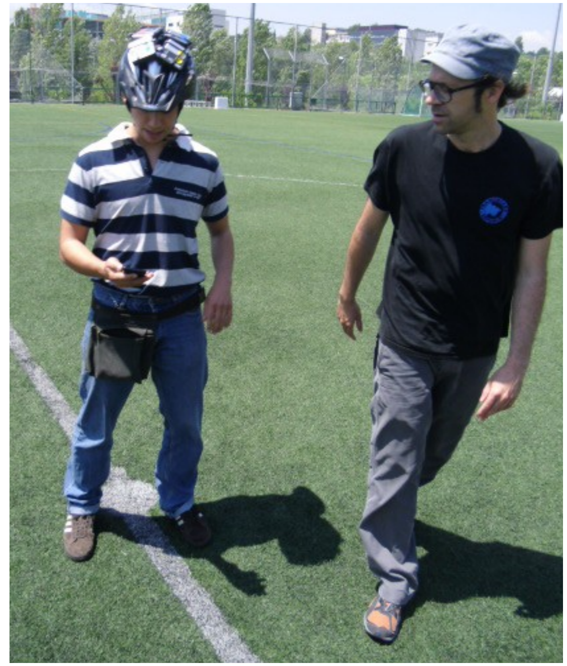
CRW

Behavioural Annotation: *Curvature*

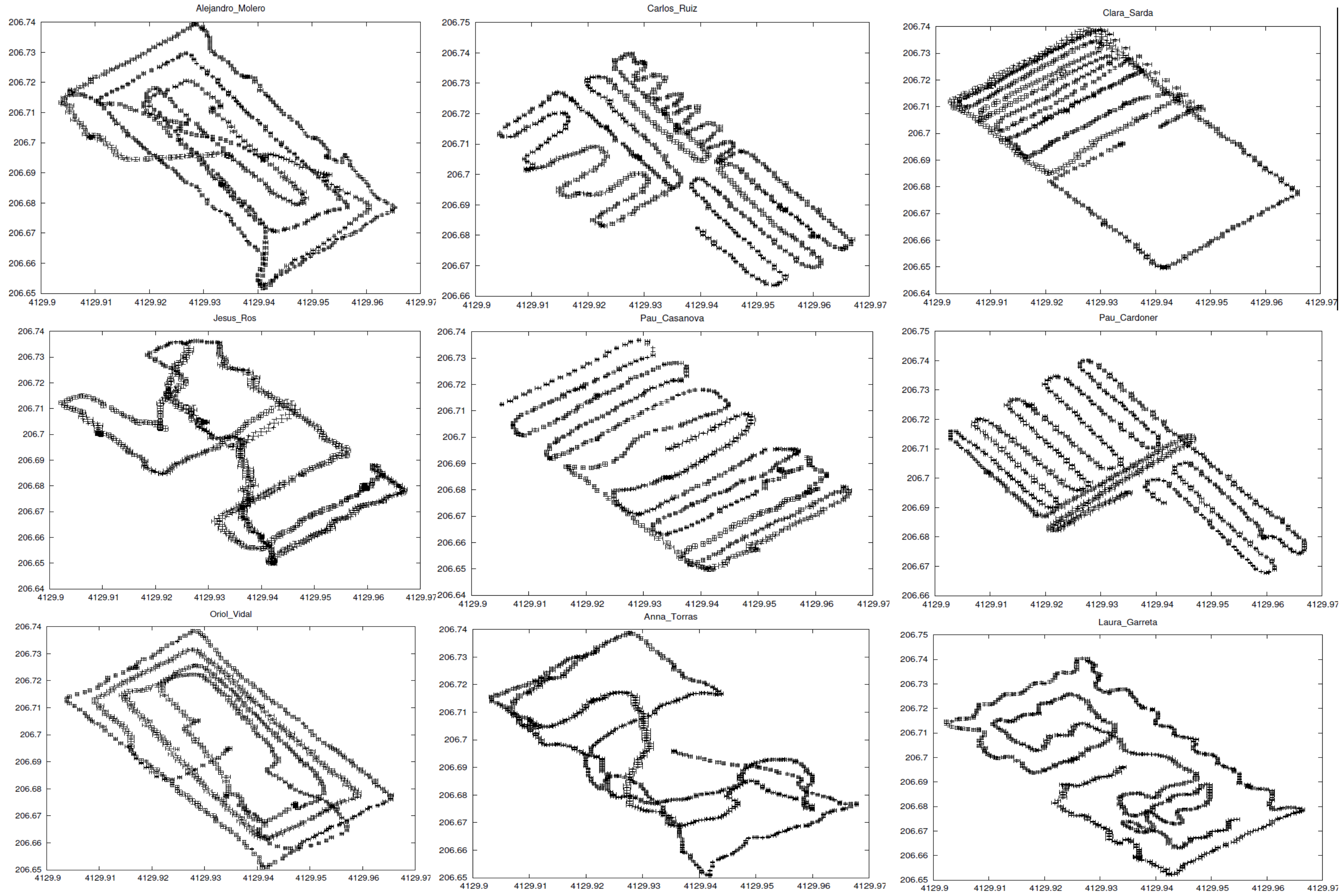


Human Search Strategies

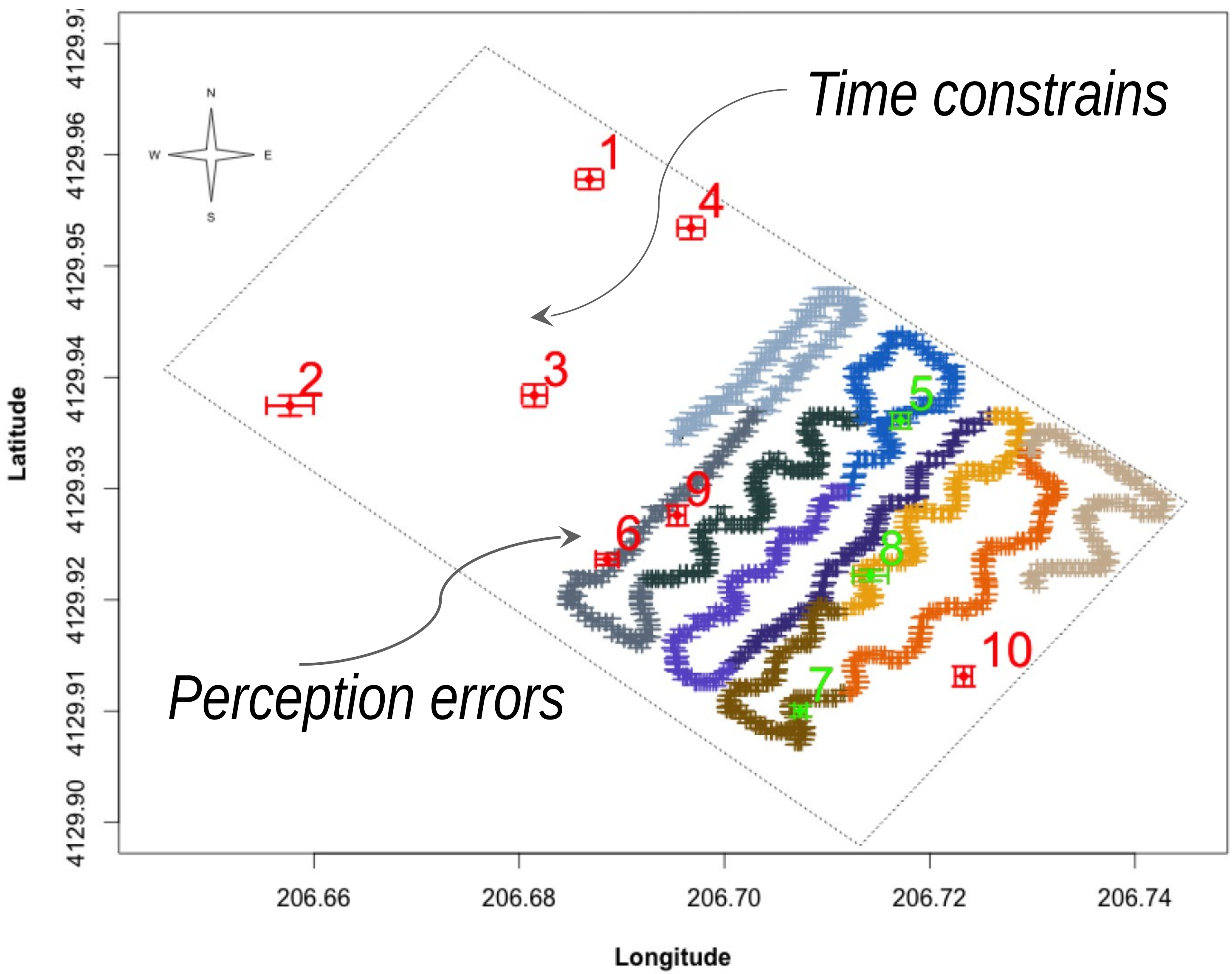
10 minutes…10 coins…of 10 cents



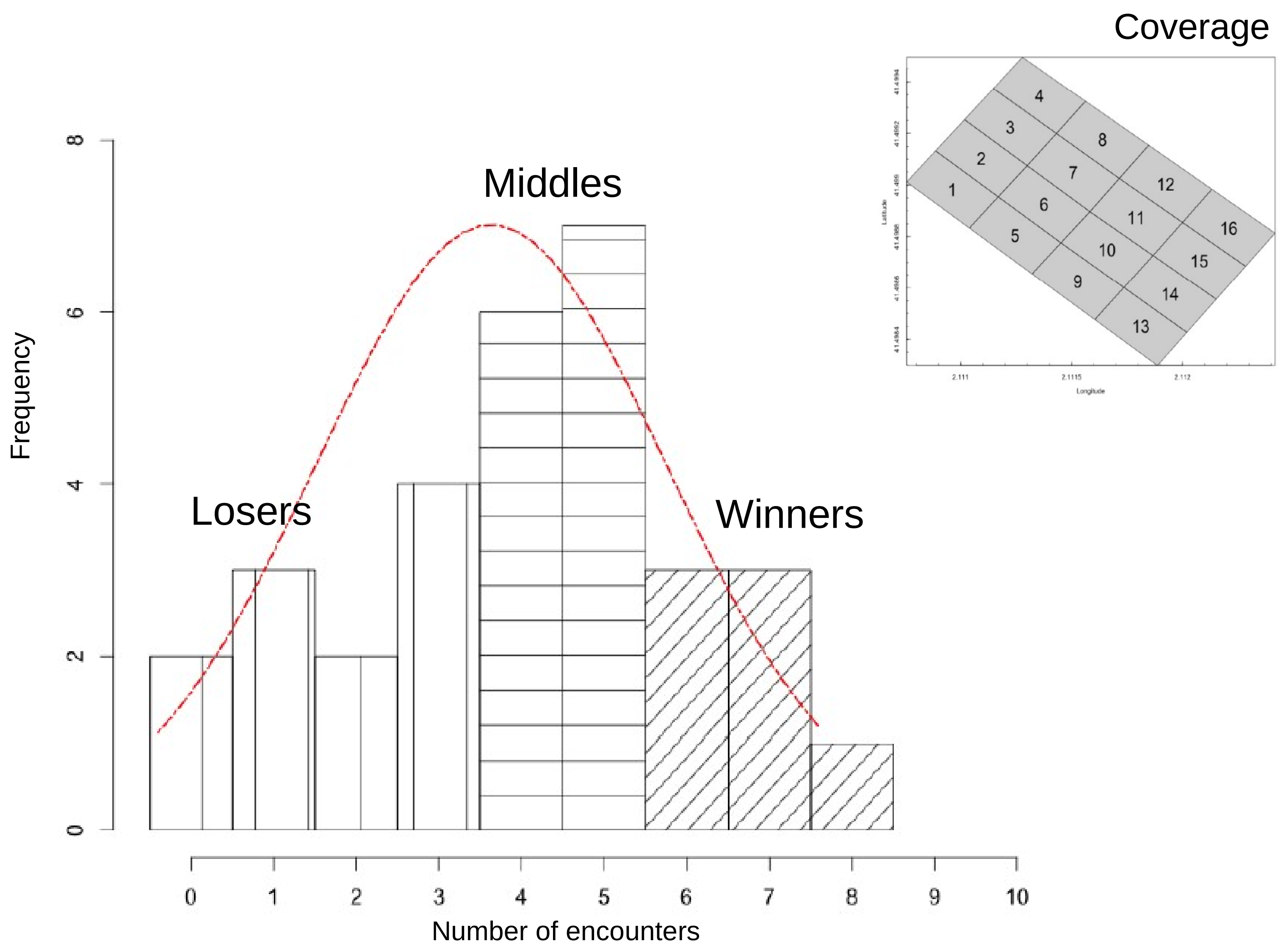
Human Search Strategies: systematic rules

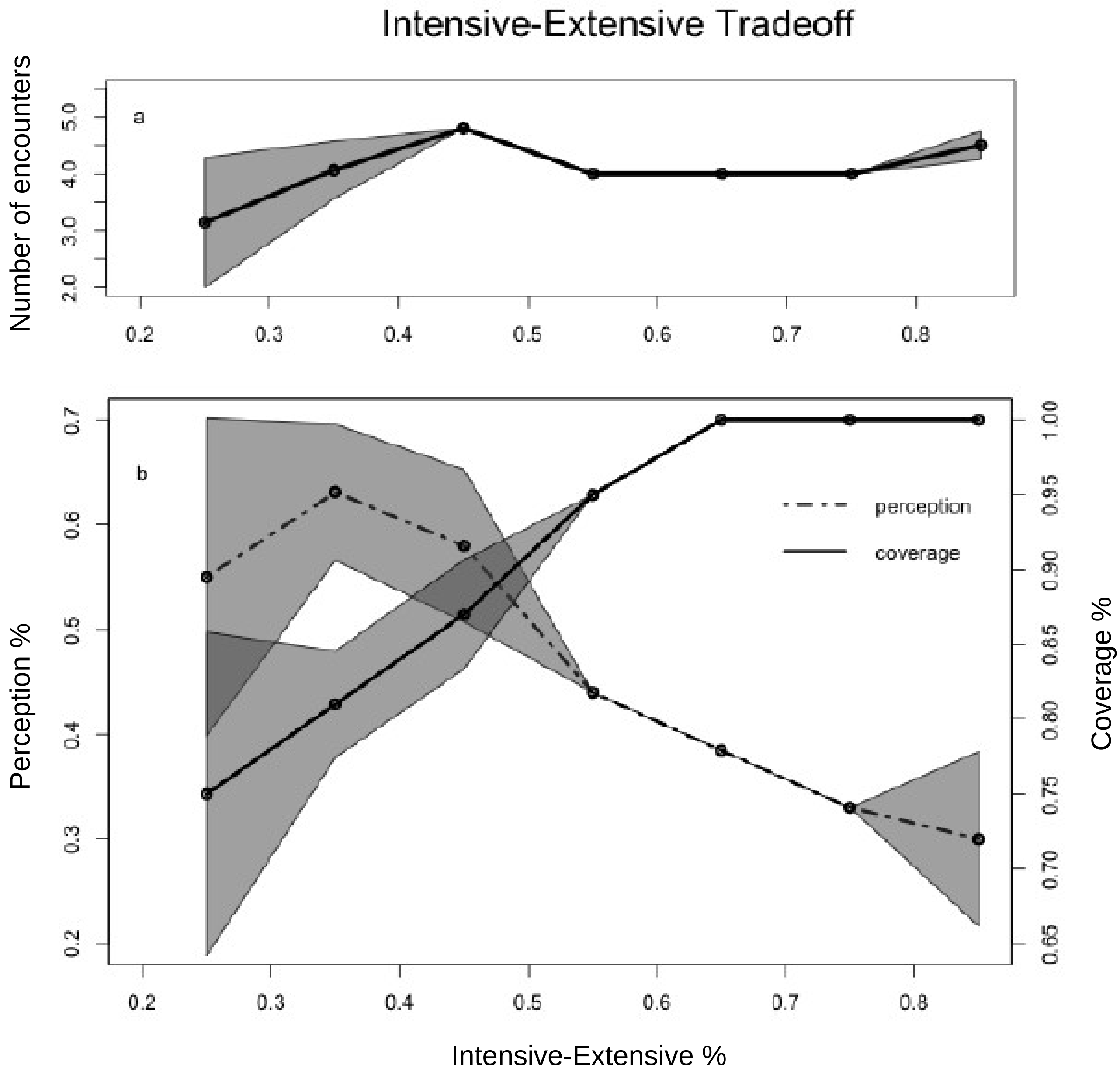


Human Search Strategies: systematic rules

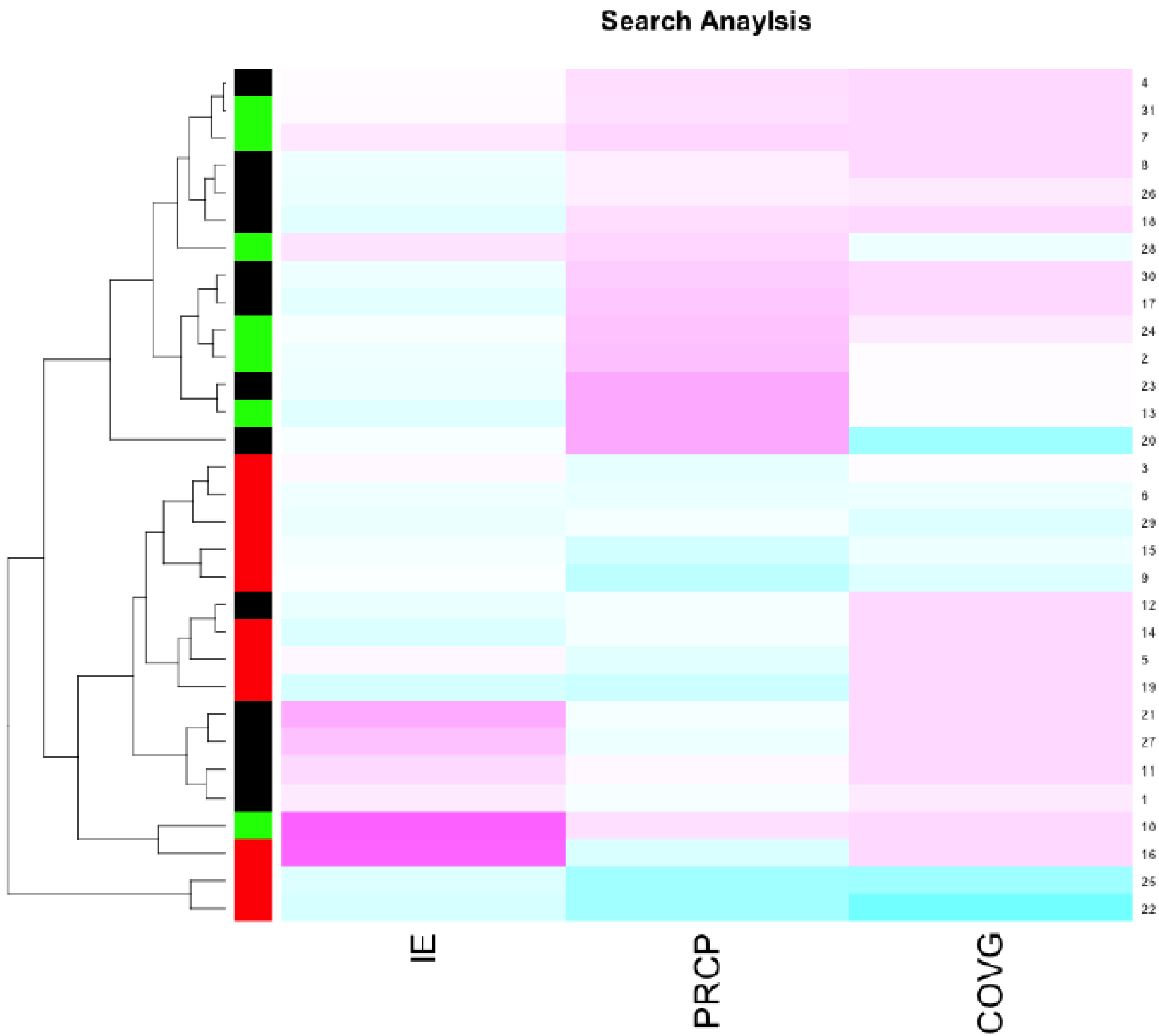


Human Search Strategies: systematic rules





Intensive-Extensive Tradeoff
Number of encounters
a
5.0
4.0
3.0
2.0
0.2
0.3
0.4
0.5
0.6
0.7
0.8
b
perception
coverage
Perception %
0.7
0.6
0.5
0.4
0.3
0.2
Coverage %
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
Intensive-Extensive %


Search Anaylsis
4
31
7
8
26
18
28
30
17
24
2
23
13
20
3
6
29
15
9
12
14
5
19
21
27
11
1
10
16
25
22
IE
PRCP
COVG

WINNERS

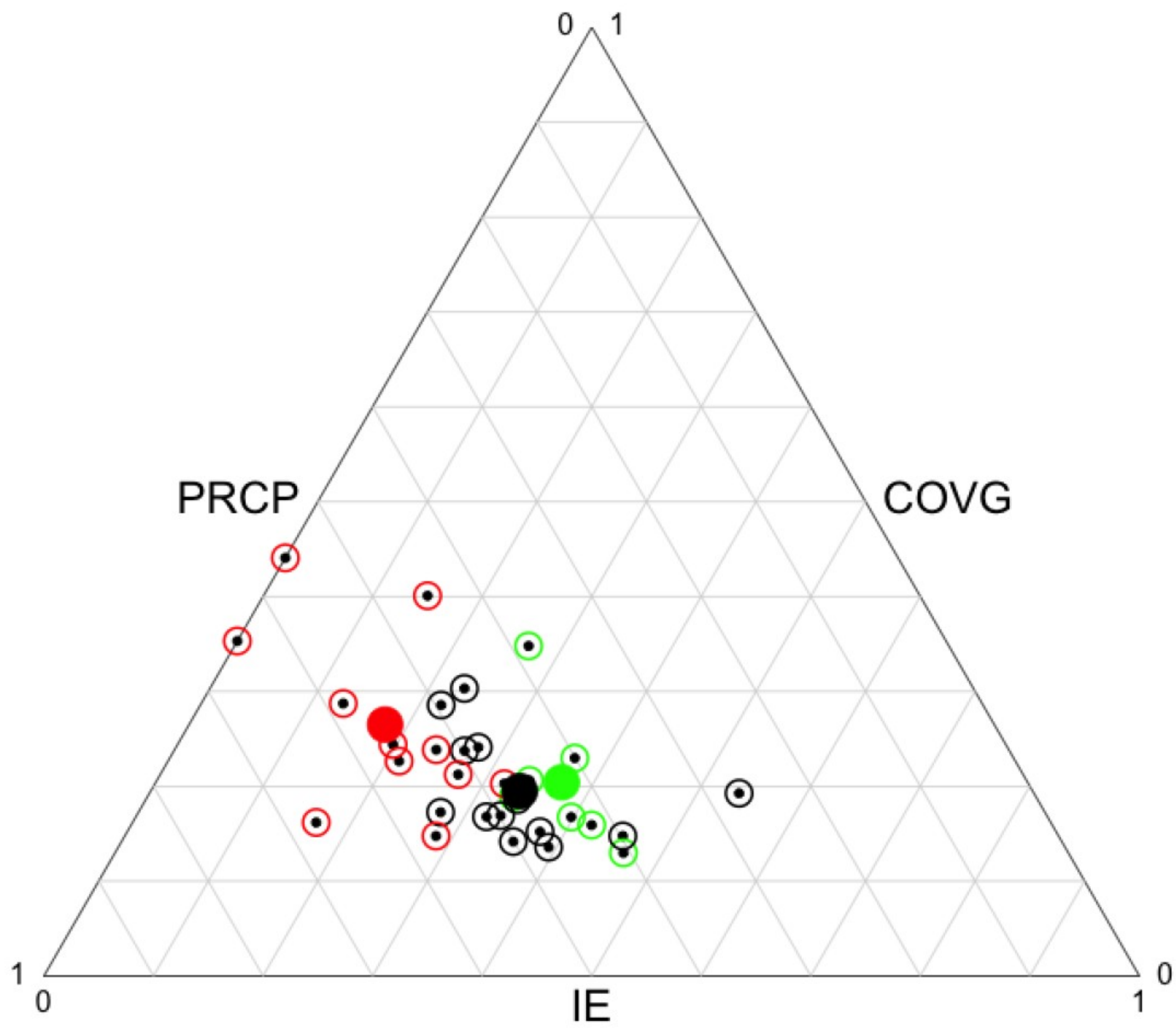
- High perception
- Medium coverage
- High Extensive

LOSERS (2 types)

- Low perception
- High coverage
- Too intensive

MIDDLES

- High perception
- Good coverage
- Extensive (ballistic)



Marco, J. Msc. (UAB, 2014)

Campos et al. 2015 (in preparation)

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THANKS

MOVOLAB