STOCHASTIC FOUNDATIONS IN MOVEMENT ECOLOGY III:

Mean first passage times and the exploitation-exploration tradeoff

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

Sources:
• Mendez et al. (2014) Chapter 6 and 9.
• Bartumeus et al. PLoS ONE (2014)
• 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

- Prob.
- Search Rule
- Det.
- Taxis

- Systematic
- Random
- Non-biased
- Biased

Information
- Low
- High
Search Strategies

Random Search Strategies

Prob.  \[ \begin{array}{c}
\text{Search Rule} \\
\text{Det.} \\
\text{Low} \\
\text{Information} \\
\text{Sensory Biology??}
\end{array} \]
probabilistic

Search Rule

deterministic

Low

Information

High
Animal Search Strategies: all types of rules

Relocation experiments

- Reynolds et al. 2007. Ecology

Learning, Trapline foraging

Relocation Experiments

Hoffmann 1983a,b
Behav. Ecol. Sociobiol.
Learning Experiments


Search Rule

Information

RIO PAVO

100 m

15 mm
Searcher perspective

- **Movement**
  - cruising (100%)
  - ambush (50%)

- **Speed**
  - intermittent
  - extensive

- **Perception**
  - Scanning
    - non-intermittent (100%)

- **Turning**
  - Reorientation
    - intensive (100%)
Perception

Speed

Turning

Reorientation

Cruising

Non-intermittent

Intermittent

Ambush

Extensive

Intensive

Scanning

Movement

50%

100%

50%

100%

Searcher perspective
Why to turn at all?
Mean First Passage Times
Mean First Passage Times
Turning behaviour in a random search

The condition for turning

Assimetry
Heterogeneous searcher-to-target distances

Examples:
• Revisitable targets (non-destructive)
• Perception errors
• Patchy/highly 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:*
We consider a 1D-random walker that can choose a direction (left/right) with equal probability and can take move lengths $\ell$ from a pdf $p(\ell)$

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

We compute a statistical search efficiency as:

$$\eta = \frac{N_{\text{found}}}{L_{\text{tot}}}$$

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

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

\[\langle L \rangle\] average distance travelled between two targets found
\[\langle n \rangle\] average number of steps between two targets found
\[\langle |\ell| \rangle\] 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 \(x_0 = \lambda\)

<table>
<thead>
<tr>
<th>Quantity</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>(\langle L \rangle)</td>
<td>average distance travelled between two targets found</td>
</tr>
<tr>
<td>(\langle n \rangle)</td>
<td>average number of steps between two targets found</td>
</tr>
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<td>(\langle</td>
<td>\ell</td>
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![Diagram](image-url)
Key concept of the calculations: a renewal approach

We note that:

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

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

Symmetric

Asymmetric

Ballistic ← Brownian

Ballistic ← Brownian
## Flight distributions

<table>
<thead>
<tr>
<th>Distribution</th>
<th>Probability Density Function</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stretched exponential</td>
<td>$p(\ell) = \alpha \Theta(</td>
</tr>
<tr>
<td>Gamma</td>
<td>$p(\ell) = \alpha \Theta(</td>
</tr>
<tr>
<td>Lognormal</td>
<td>$p(\ell) = \frac{\alpha}{</td>
</tr>
<tr>
<td>Power law</td>
<td>$p(\ell) = \alpha \frac{\Theta(</td>
</tr>
</tbody>
</table>

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

a. LévyT

b. LogN

c. StrExp

d. Gamma
Root mean square displacement

Asymmetric condition

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

\[
\begin{cases} 
R_{\text{fpt}} = (\lambda - 2r_v)(p_0 p_{\lambda})^{1/2} \\
R_{\text{Brownian}} = \left( \frac{\lambda^2 v p_{\lambda}}{\langle L \rangle} \right)^{1/2} t^{1/2}
\end{cases}
\]
The Search Efficiency (1/MFPT)

Asymmetric condition

- **Figure a**: LévyT with different values of $\tau$.
- **Figure b**: LogN with different values of $\beta$.
- **Figure c**: StrExp with different values of $\phi$.
- **Figure d**: Gamma with different values of $\beta$. 

Graphs showing the search efficiency ($n$) as a function of various parameters.
The Search Efficiency: factorization

Asymmetric condition

\[ \langle L \rangle = p_0 \langle L_0 \rangle + p_\lambda \langle L_\lambda \rangle \]
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 asymmetric to symmetric condition…
The Search Efficiency (1/MFPT)

A mixture of scales...with the right scales....beats Levy
Why to turn at all?

To solve exploitation-exploration tradeoffs

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
Chaenorhabditis 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-
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

No food (but no starvation). Minimal cues.

Salvador et al. (2014)
J Royal Soc Interface
Different temporal dynamics for different turn types

No food (but no starvation). Minimal cues.

Pirouettes “food memory
Omegas ”template

Omega turns:
heavy-tail distribution
Toy model

(a) Toy model flowchart:
- Crawling
- Reorientation clocks
  - On/off
  - Omegas multi-scale search
  - Pirouettes area-restricted search

(b) Graphical representation:
- 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*

Diagram showing:
- **Time constraints**
- **Perception errors**
Human Search Strategies: systematic rules

- Losers
- Middles
- Winners

![Coverage Chart]

Frequency

Number of encounters
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)
THANKS