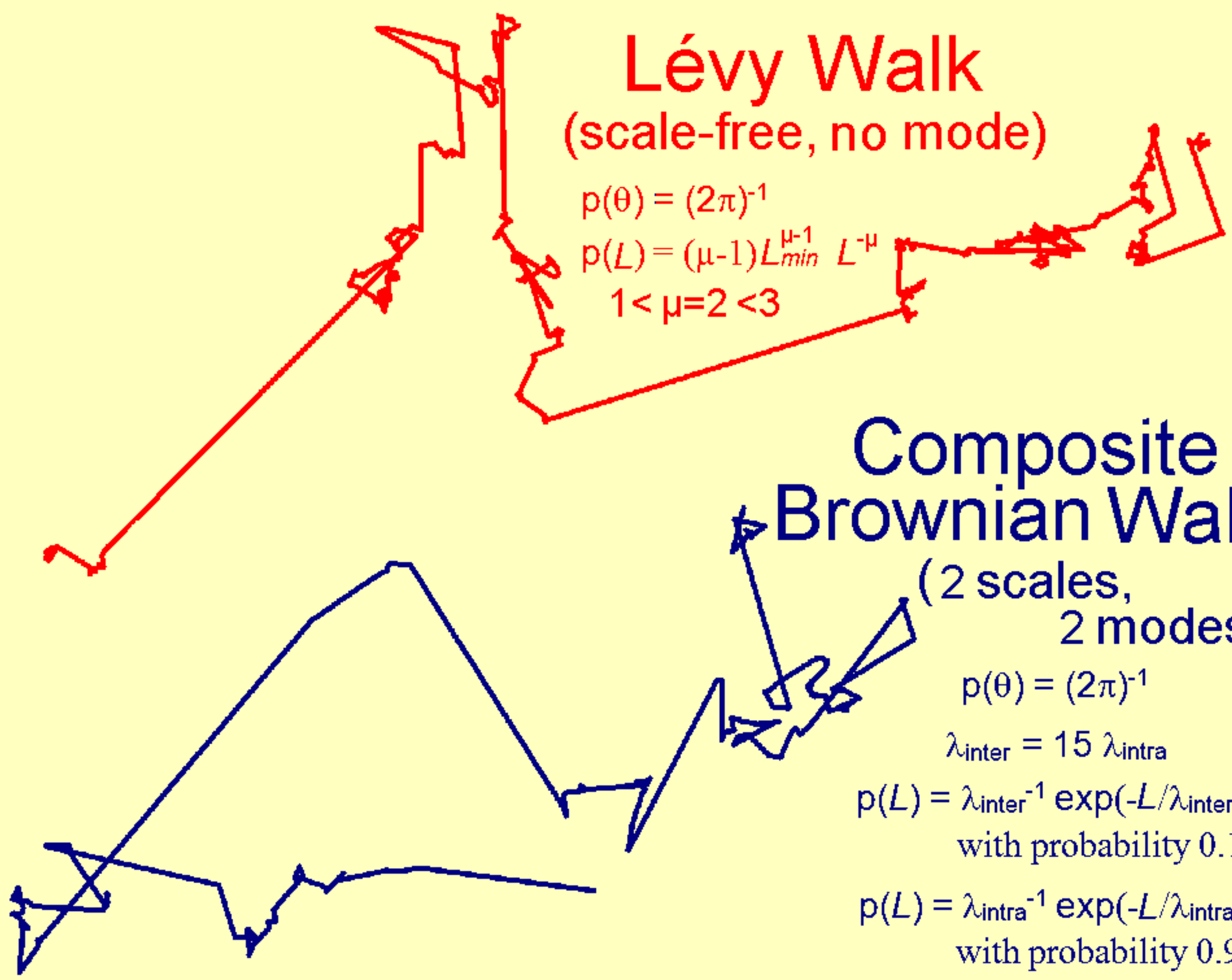
FORAGING MODES, FORAGING SCALES,

AND THE FAILURE OF THE

LEVY FORAGING HYPOTHESIS

Simon Benhamou
CEFE - CNRS Montpellier



Lévy Walk
(scale-free, no mode)

$p(\theta) = (2\pi)^{-1}$

$p(L) = (\mu\text{-}1) L_{min}^{\mu-1} L^{-\mu}$

$1 < \mu = 2 < 3$

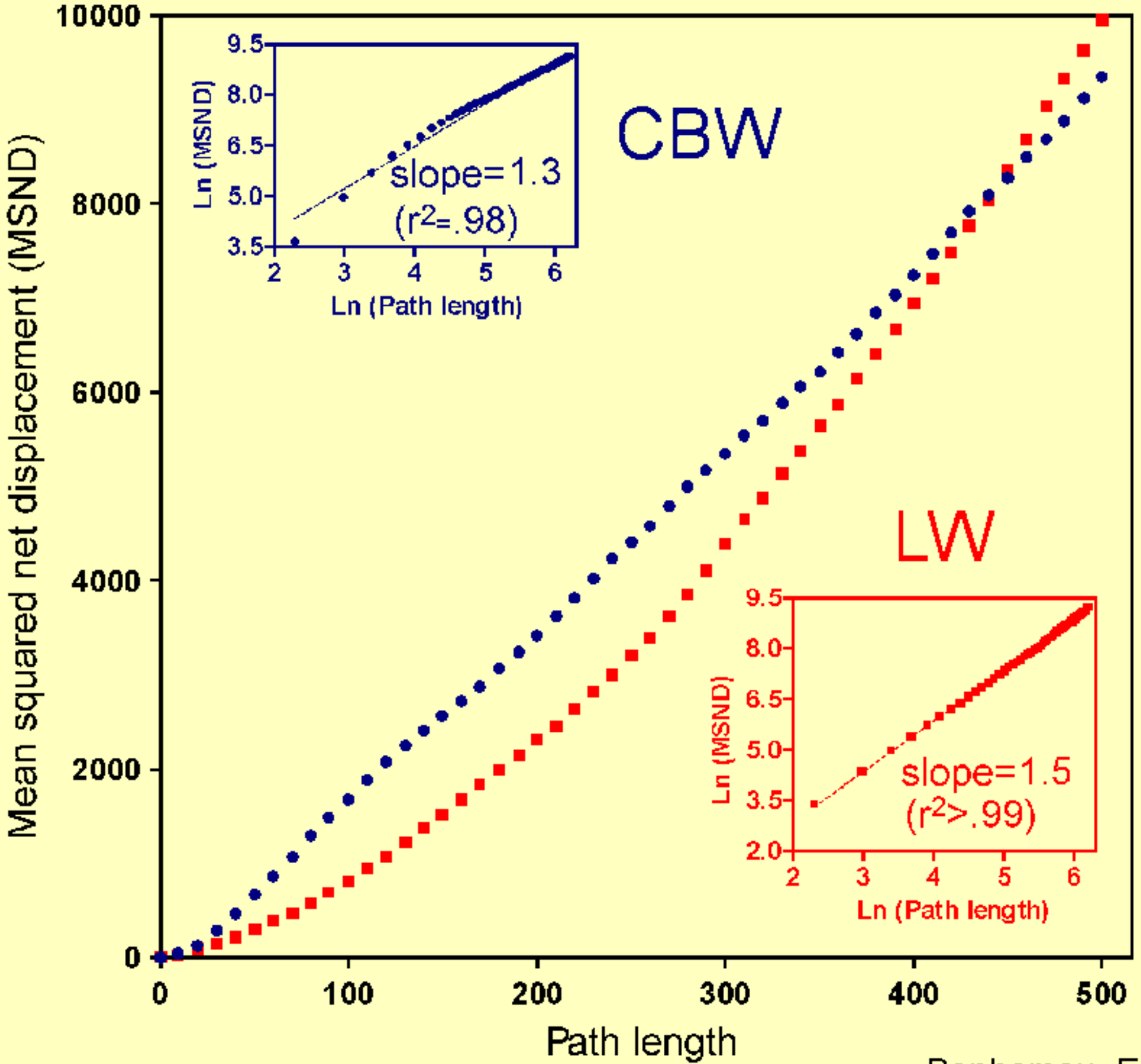
Composite Brownian Walk
(2 scales, 2 modes)

$p(\theta) = (2\pi)^{-1}$

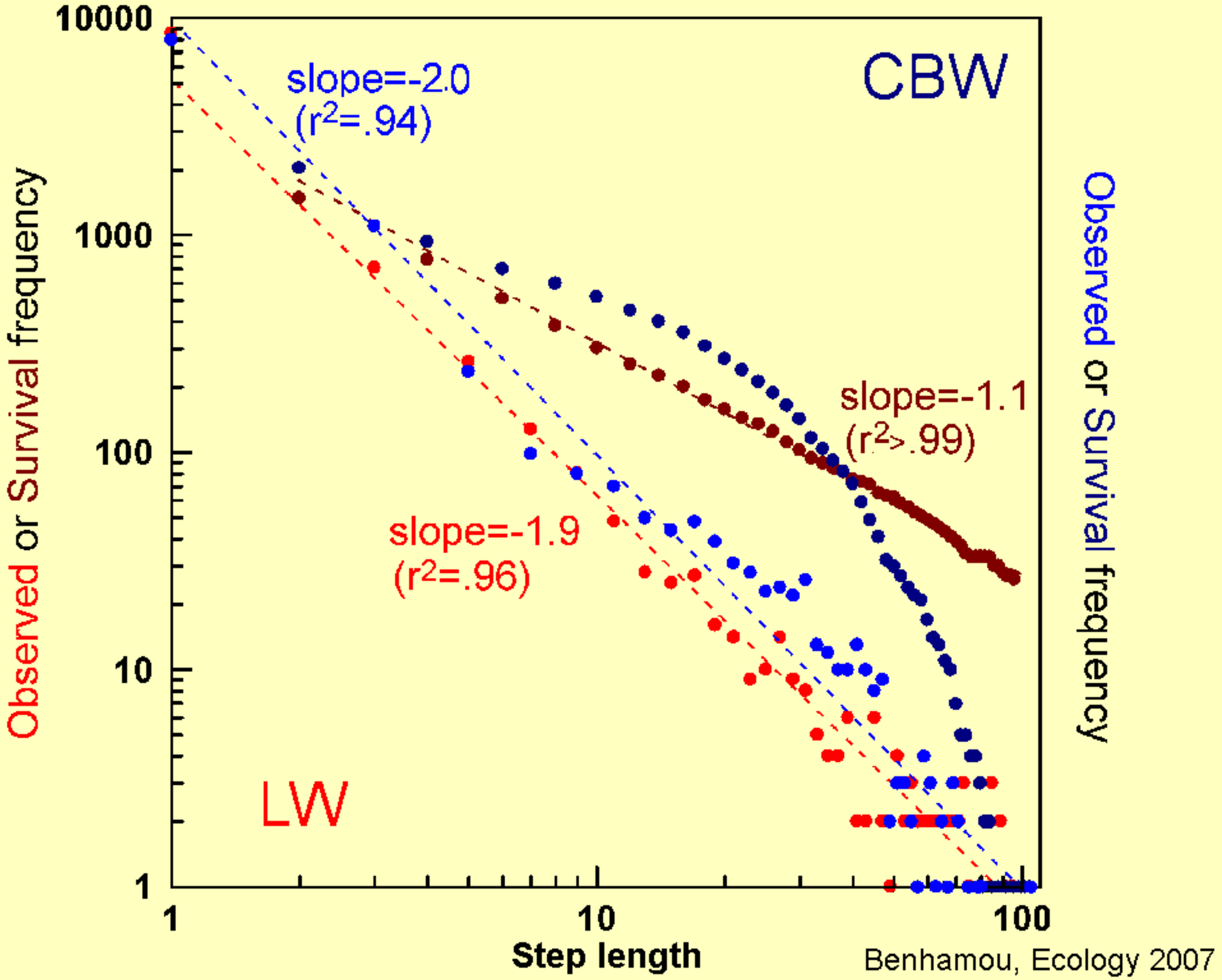
$\lambda_{inter} = 15\ \lambda_{intra}$

$p(L) = \lambda_{inter}^{-1} \exp(-L/\lambda_{inter})$
with probability 0.1

$p(L) = \lambda_{intra}^{-1} \exp(-L/\lambda_{intra})$
with probability 0.9



Benhamou, Ecology 2007



Benhamou, Ecology 2007

Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer

Nature 2007

Andrew M. Edwards[1]†, Richard A. Phillips[1], Nicholas W. Watkins[1], Mervyn P. Freeman[1], Eugene J. Murphy[1], Vsevolod Afanasyev[1], Sergey V. Buldyrev[2,3], M. G. E. da Luz[4], E. P. Raposo[5], H. Eugene Stanley[2] & Gandhimohan M. Viswanathan[6]

Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals

Ecology 2011

Andrew M. Edwards

Turn designation, sampling rate and the misidentification of power laws in movement path data using maximum likelihood estimates

Theor. Ecol. 2011

Edward A. Codling · Michael J. Plank

Incorrect Likelihood Methods Were Used to Infer Scaling Laws of Marine Predator Search Behaviour

PLoS ONE 2012

Andrew M. Edwards[1*], Mervyn P. Freeman[2], Greg A. Breed[3,4,5], Ian D. Jonsen[4,6]

Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*)

Gabriel Ramos-Fernández · José L. Mateos · Octavio Miramontes · Germinal Cocho · Hernán Larralde · Bárbara Ayala-Orozco

Behav. Ecol. Sociobiol. 2004

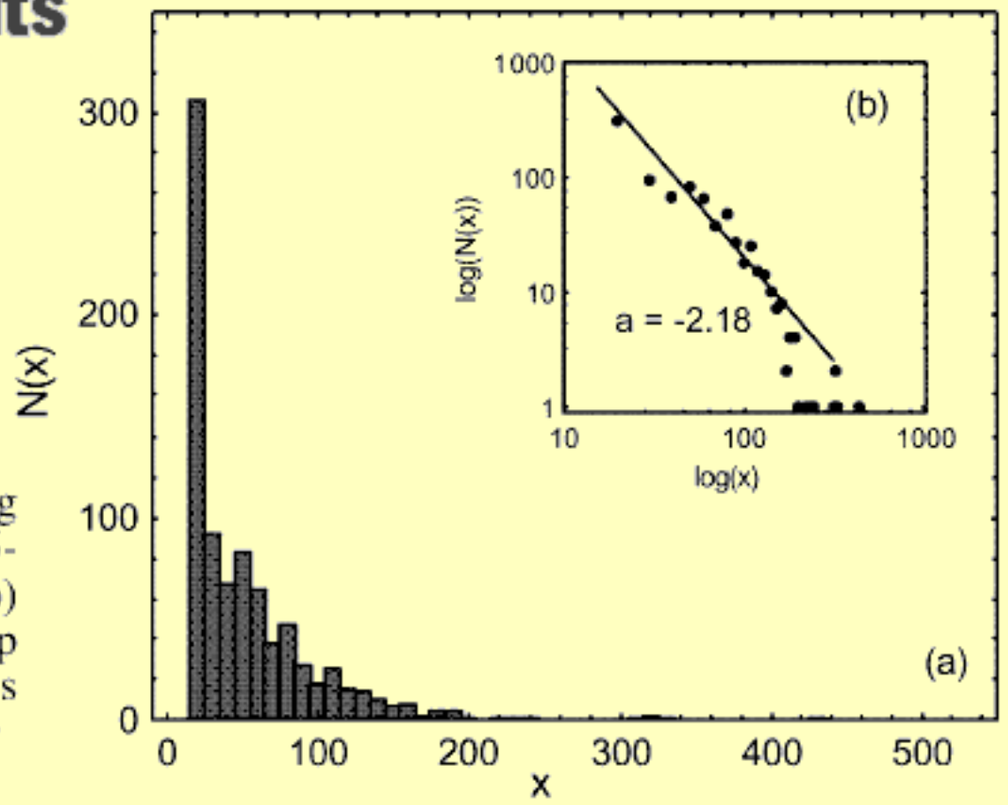


Fig. 2 a Distribution of the number of 5-min intervals $N(x)$ during which spider monkeys traveled a distance of x m. A total of 841 5-min intervals from 20 adult individuals are included. The *inset* (**b**) shows the log-log plot of the same data. A power-law relationship fits the data with r^2=0.89. The estimated value of the exponent is −2.18. The same data fitted an exponential function with r^2=0.79

Scale-free foraging by primates emerges from their interaction with a complex environment

Denis Boyer[1], Gabriel Ramos-Fernández[2,*], Octavio Miramontes[1], José L. Mateos[1], Germinal Cocho[1], Hernán Larralde[3], Humberto Ramos[1] and Fernando Rojas[4]

Proc. R. Soc. B 2006

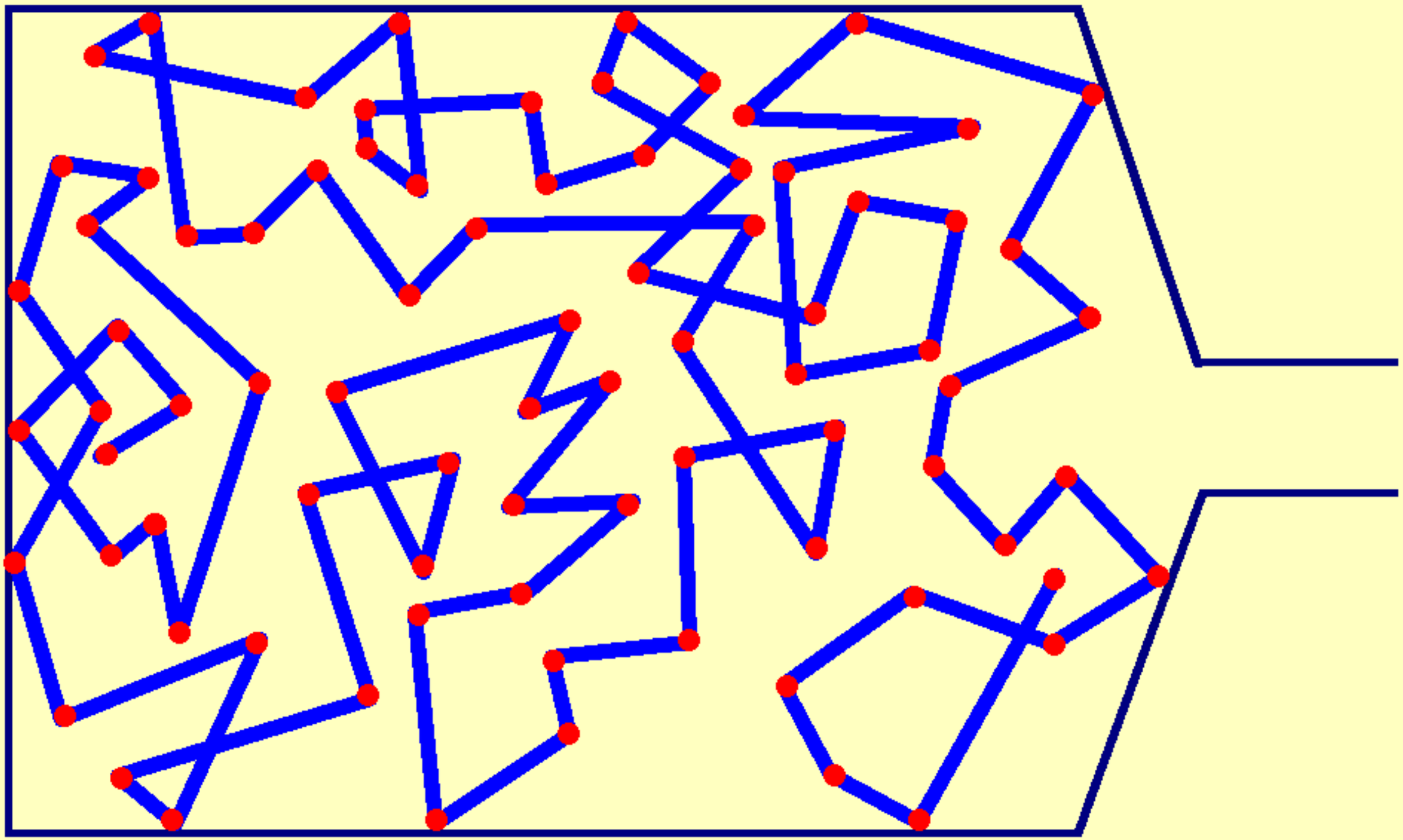
How superdiffusion gets arrested: ecological encounters explain shift from Lévy to Brownian movement

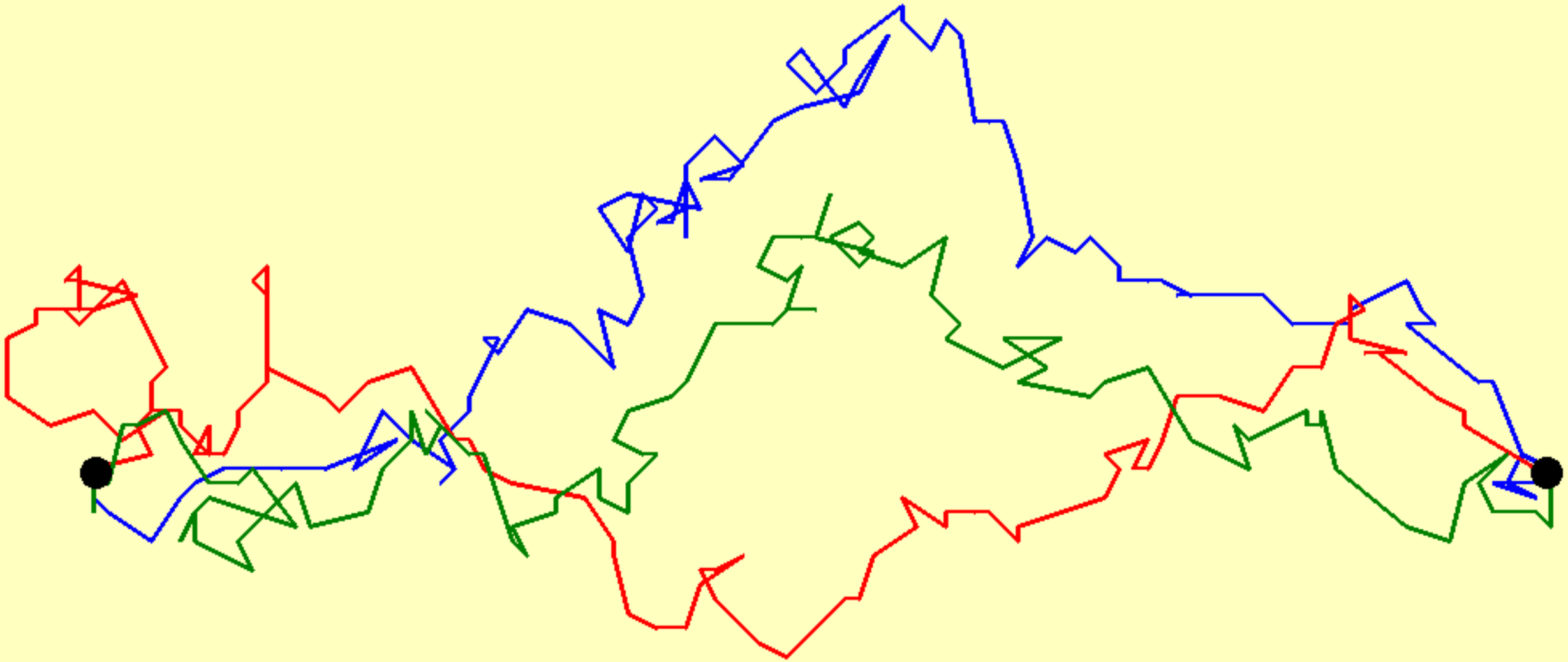
Monique de Jager[1,2,4], Frederic Bartumeus[5], Andrea Kölzsch[6,7], Franz J. Weissing[2], Geerten M. Hengeveld[6,7], Bart A. Nolet[6,7], Peter M. J. Herman[1] and Johan van de Koppel[1,3,7]

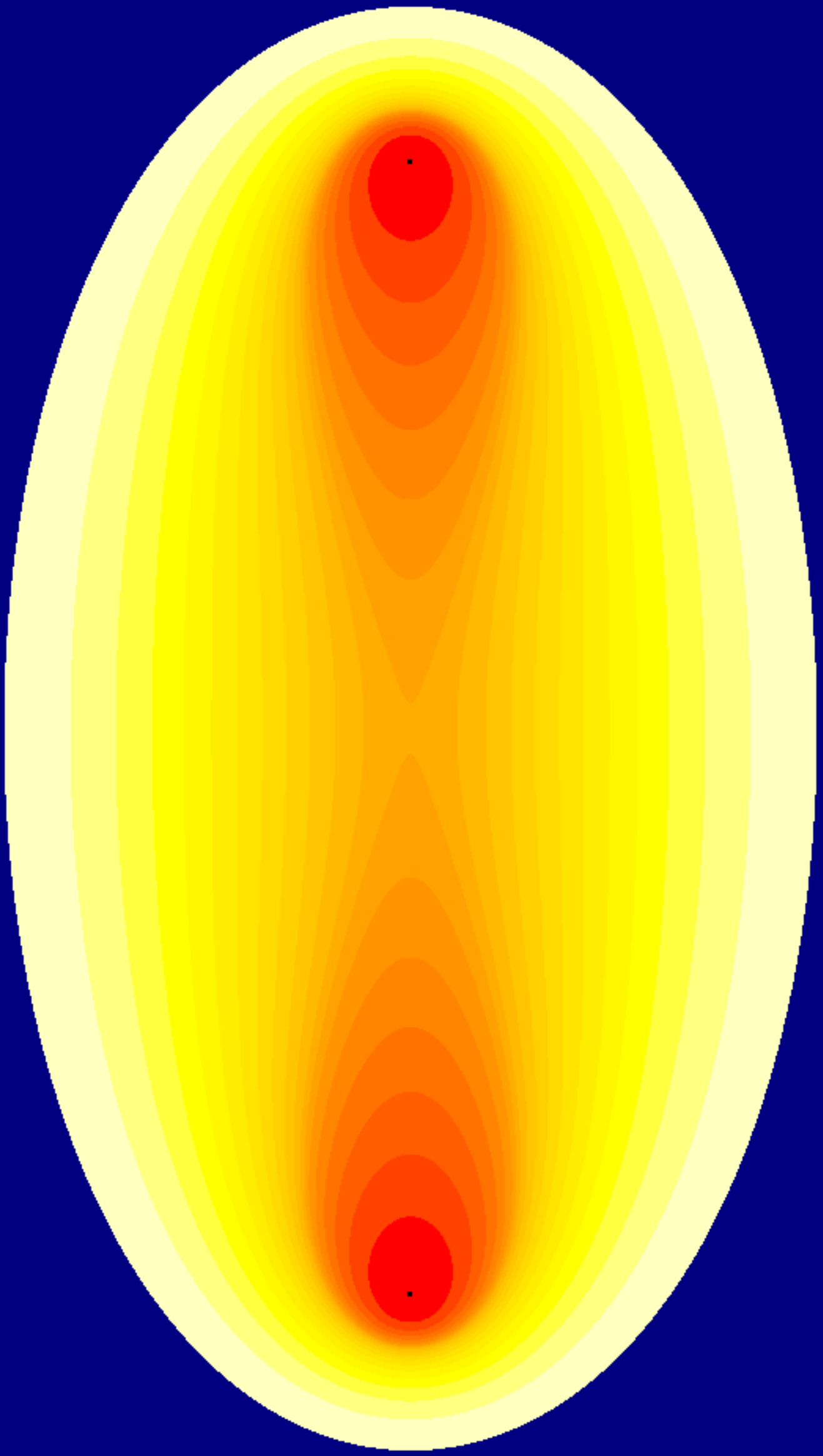
Proc. R. Soc. B 2014

Consider a gas molecule in a bottle

How many movement scales?







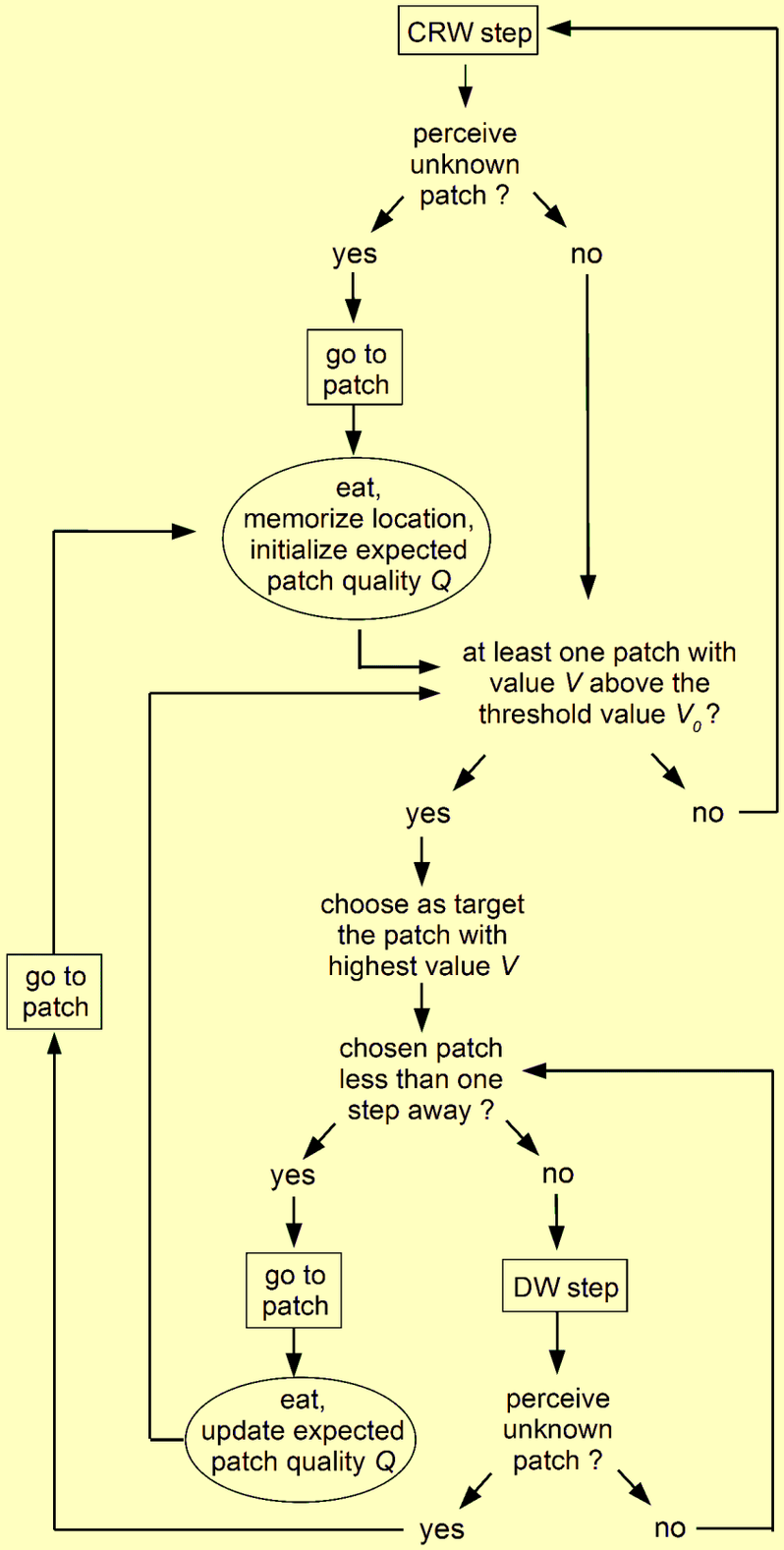
95
90
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5

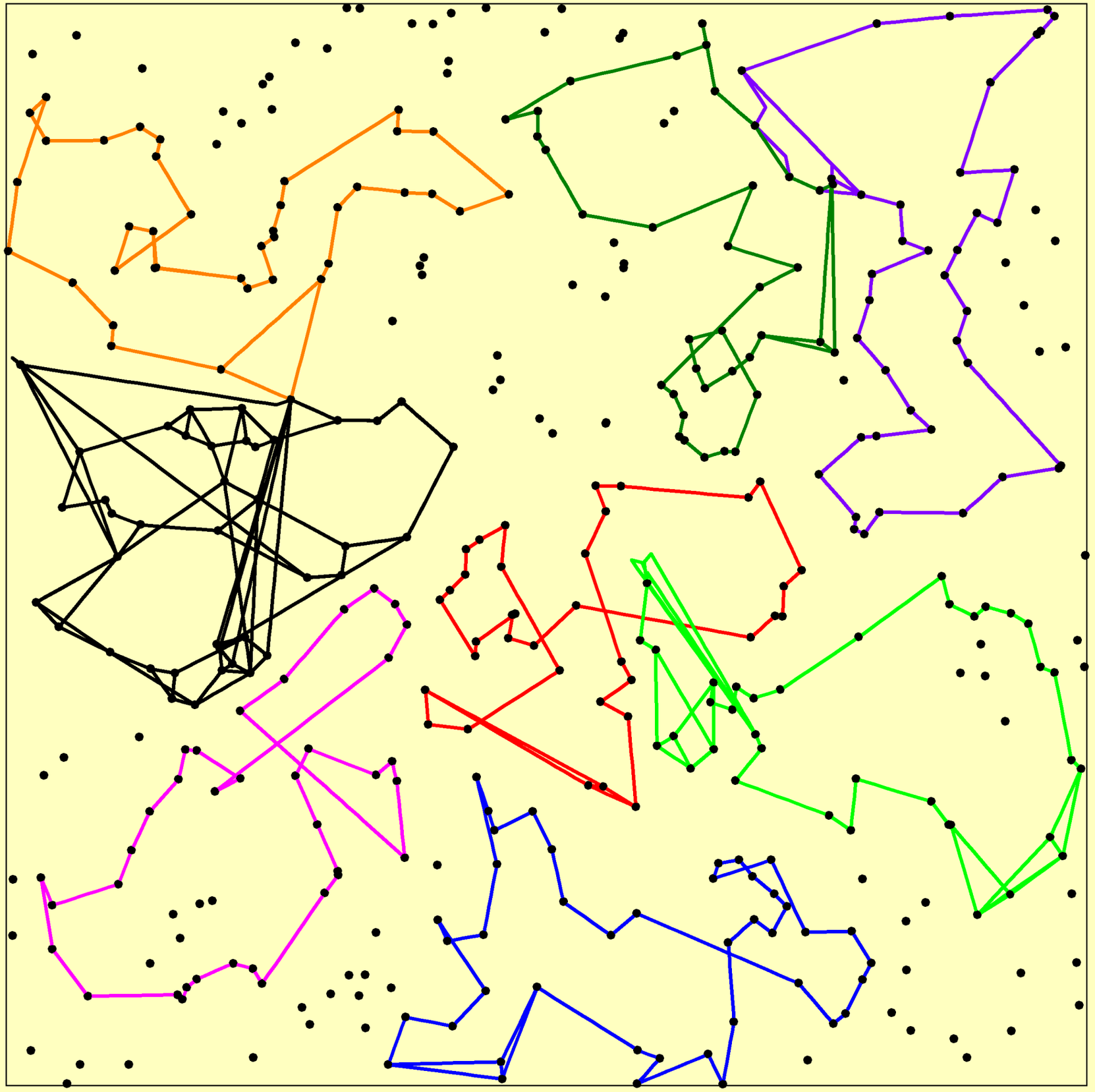
3 km

Preferences
R .07
G .14
A .21
P .57

Drift Speed
R 17
G 10
A 11
P 6
m/min

Benhamou,
PLoS One
2011





Riotte-Lambert et al., *Am. Nat.* 2015

A

B

20

15

10

5

Intake rate

90

94

91

96

93

90

94

62

Straight line

CRW

0.02

0.03

0.04

0.05

0.06

Resource renewal rate

89

71

57

6

7

8

Number of individuals

FORAGING PROCESSES
WHEN RESOURCE LOCATIONS ARE UNPREDICTABLE

Homogeneous environment

+ Poisson distribution of resource density
+ no information source
+ low empirical interest (uncommon)
+ low theoretical interest (obvious solution)

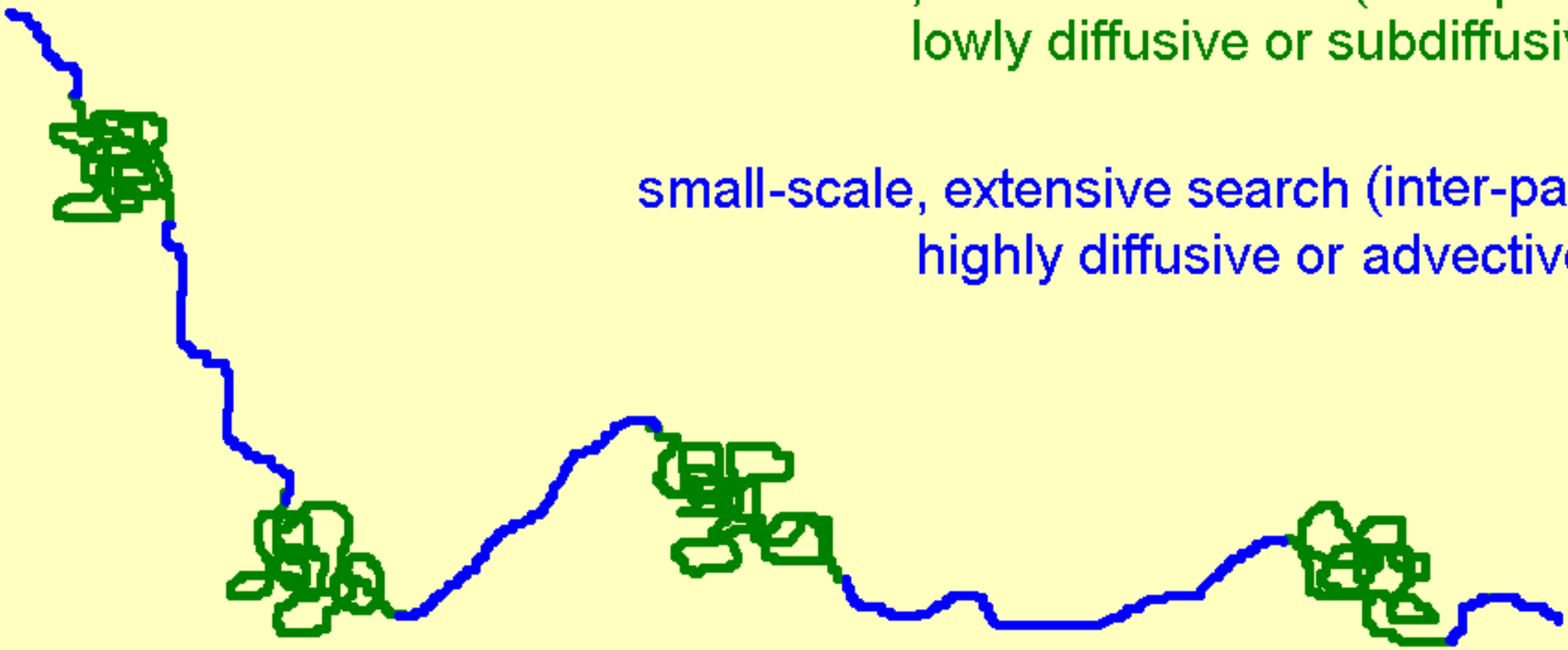
Heterogeneous environment

+ resources items are aggregated in patches
+ prey detection is an information source
+ 2 scales can be distinguished:
  - small scale: search for items within and between patches
  - large scale: patch to patch movement
+ 2 modes can be distinguished in small-scale movements
  - extensive mode or ranging (search for patches)
  - intensive mode or area-concentrated (search within patches)

Sequential search modes and simultaneous spatial scales

small-scale, intensive search (intra-patch):
lowly diffusive or subdiffusive

small-scale, extensive search (inter-patch):
highly diffusive or advective



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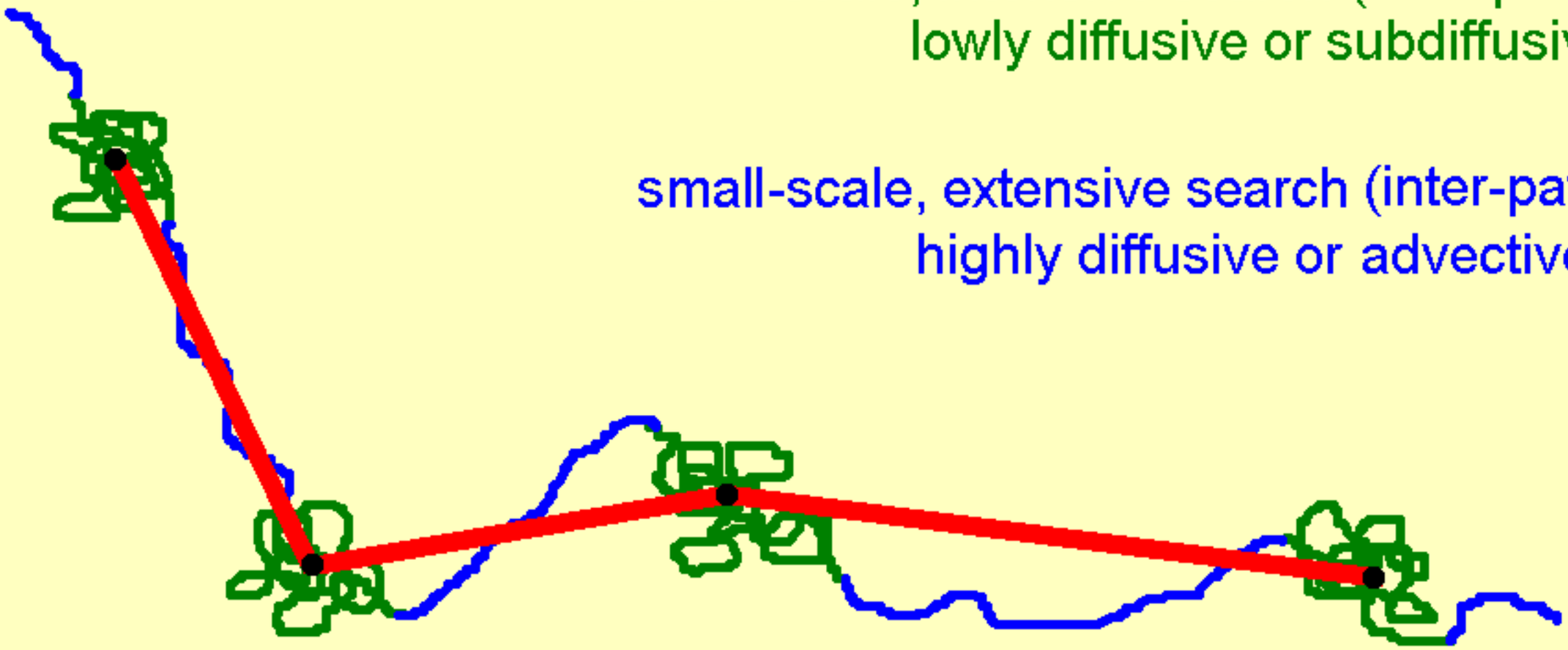
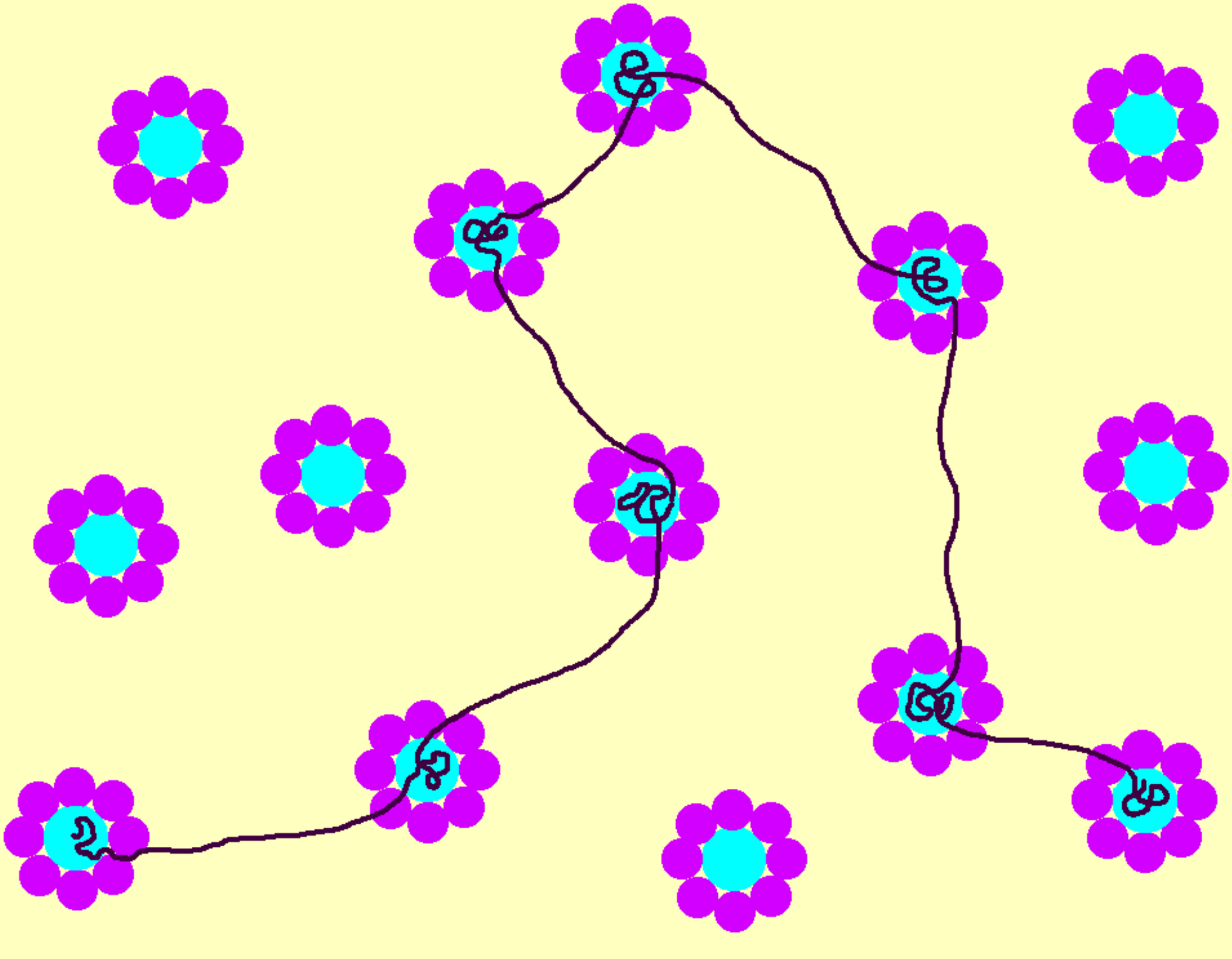
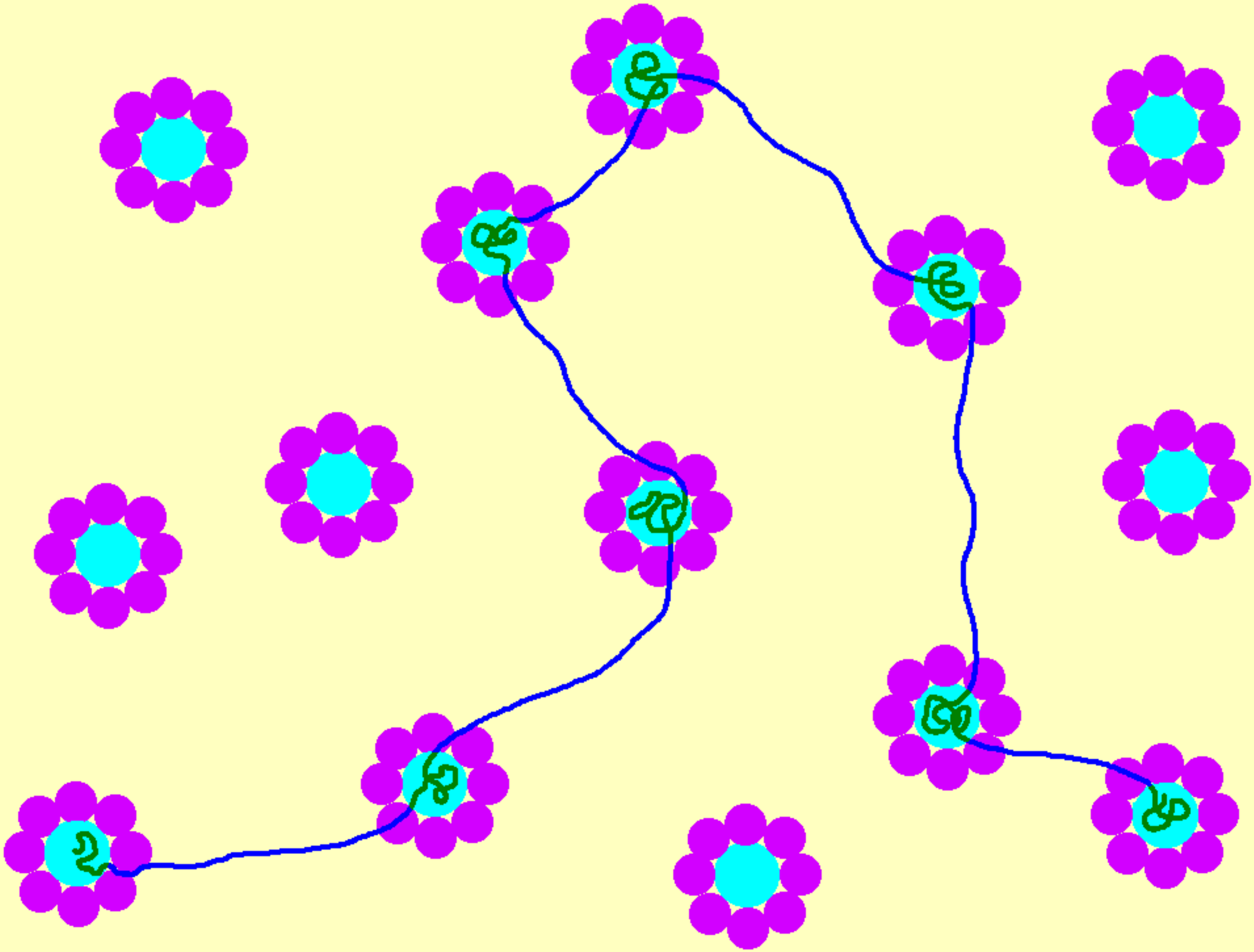
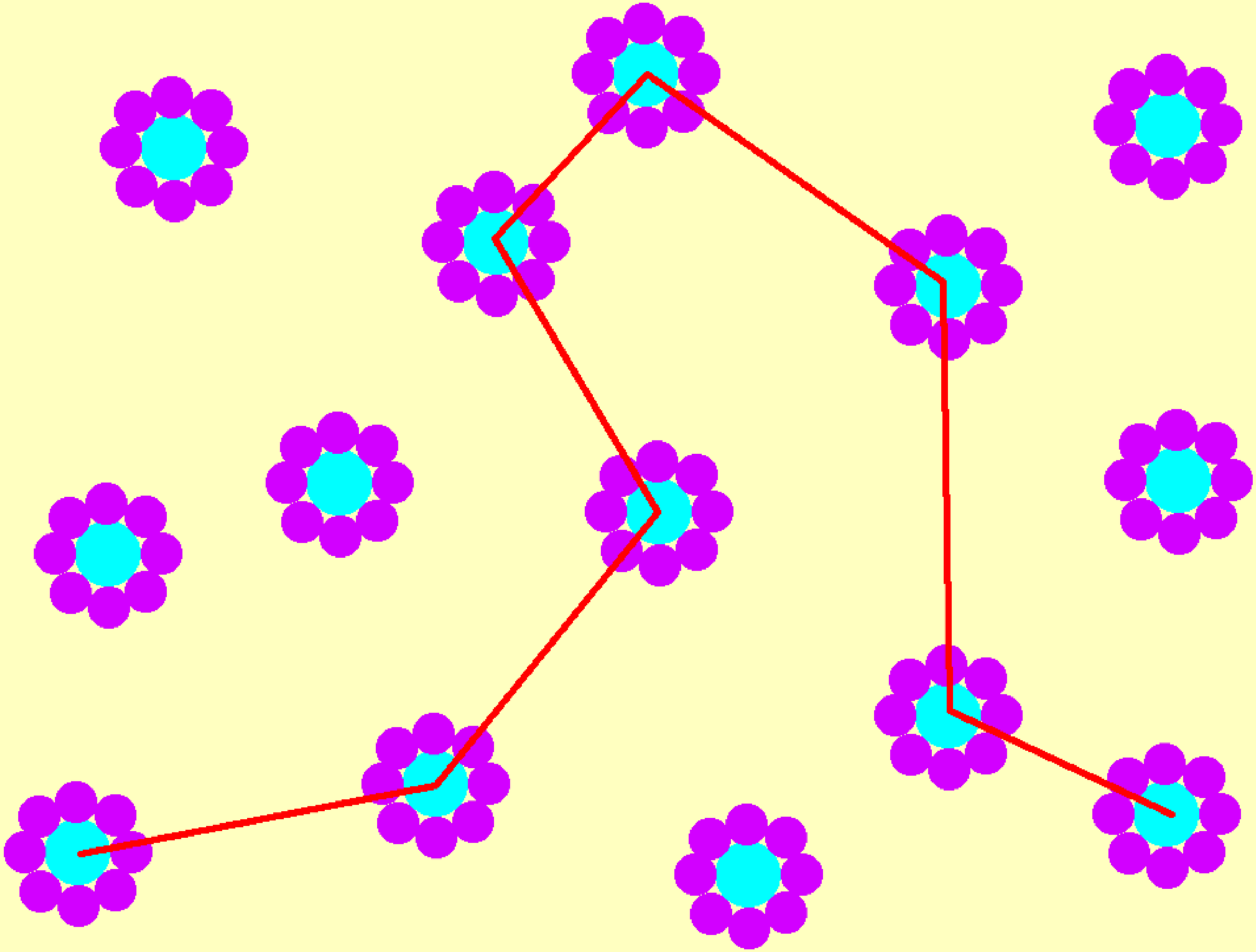


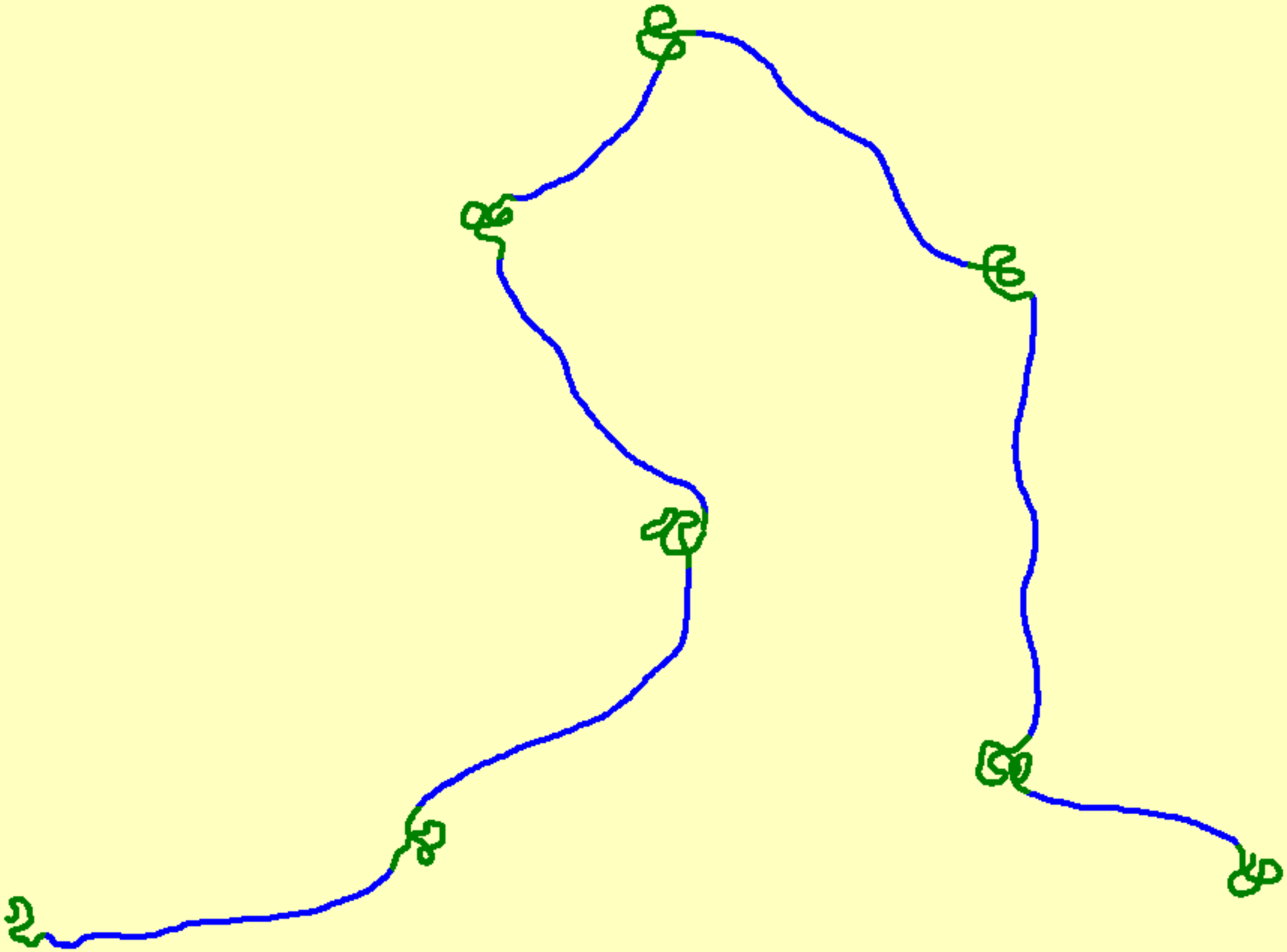
large-scale movement (sequence of visited patches):

- diffusive (random search)
- advective (migration)
- self-constrained (home range)

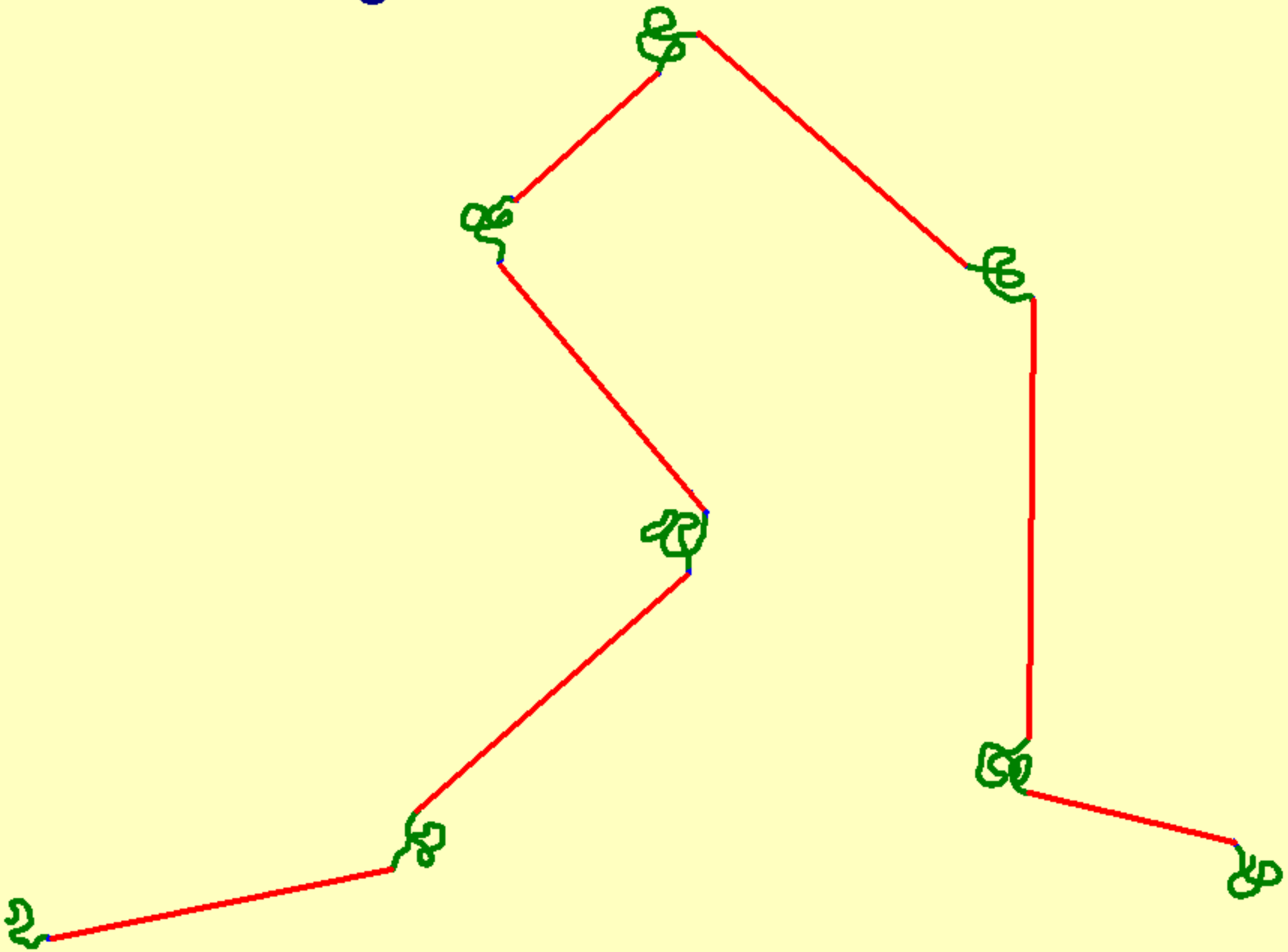




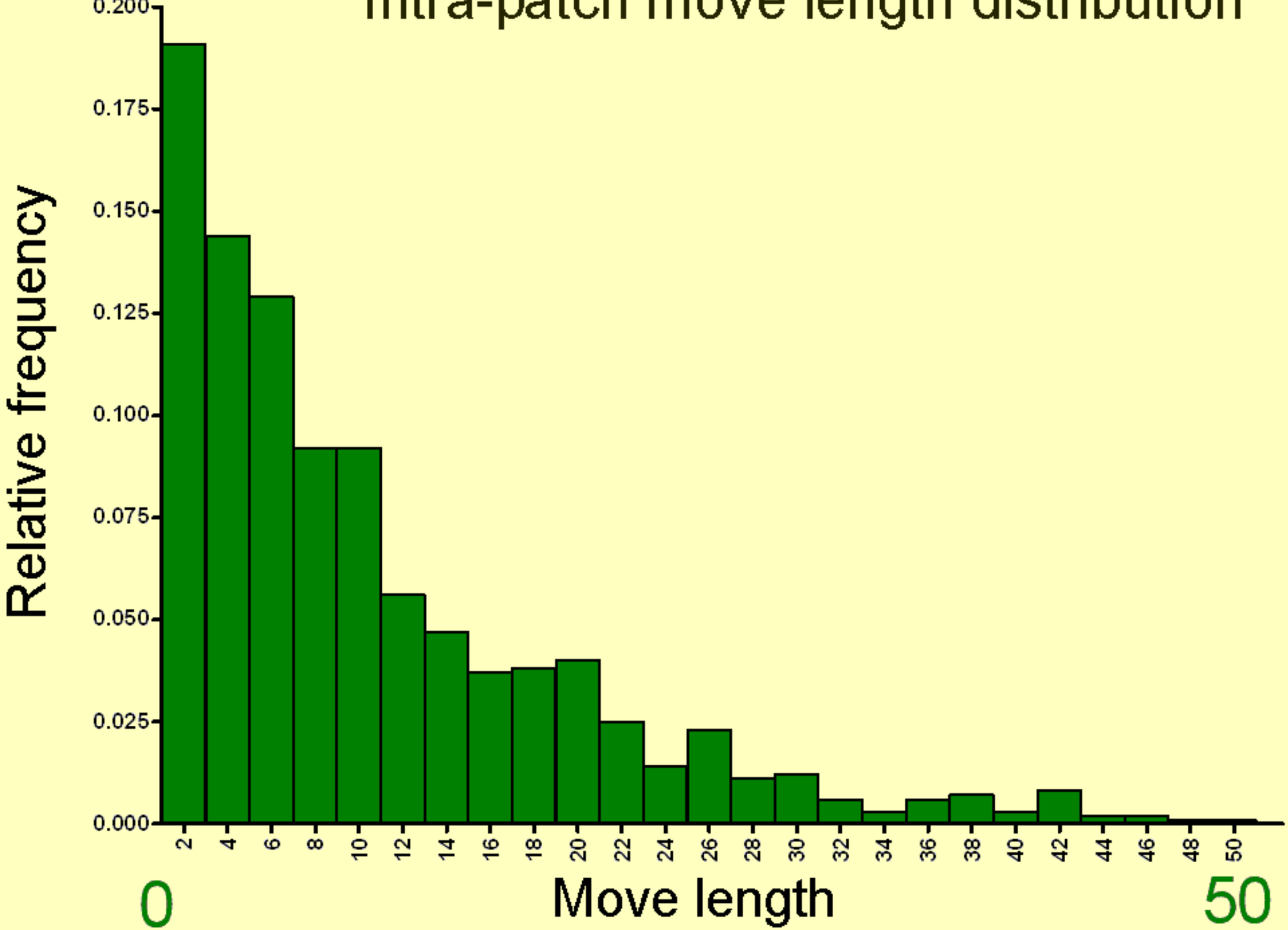




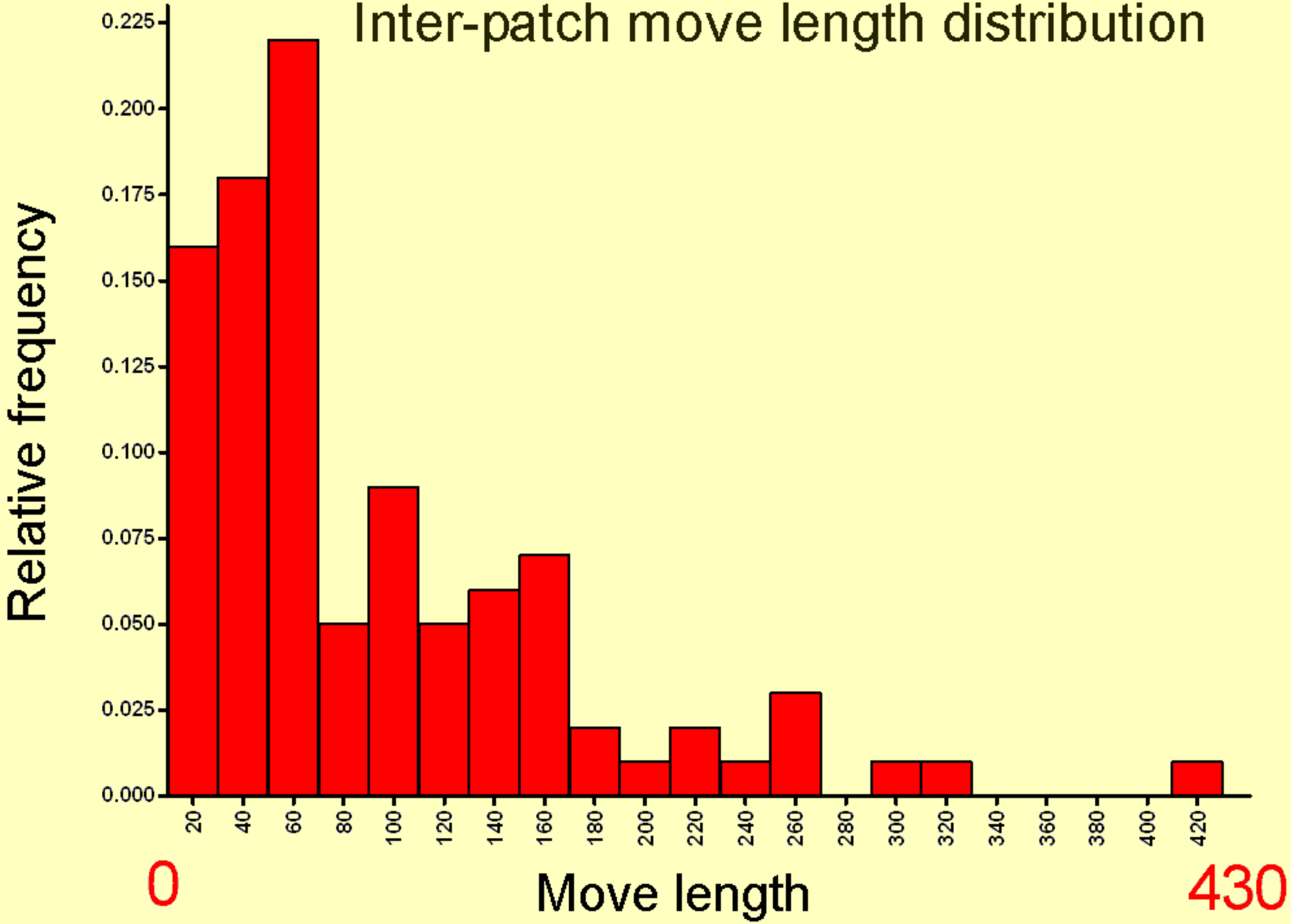
=> a strange two-mode two-scale mixture



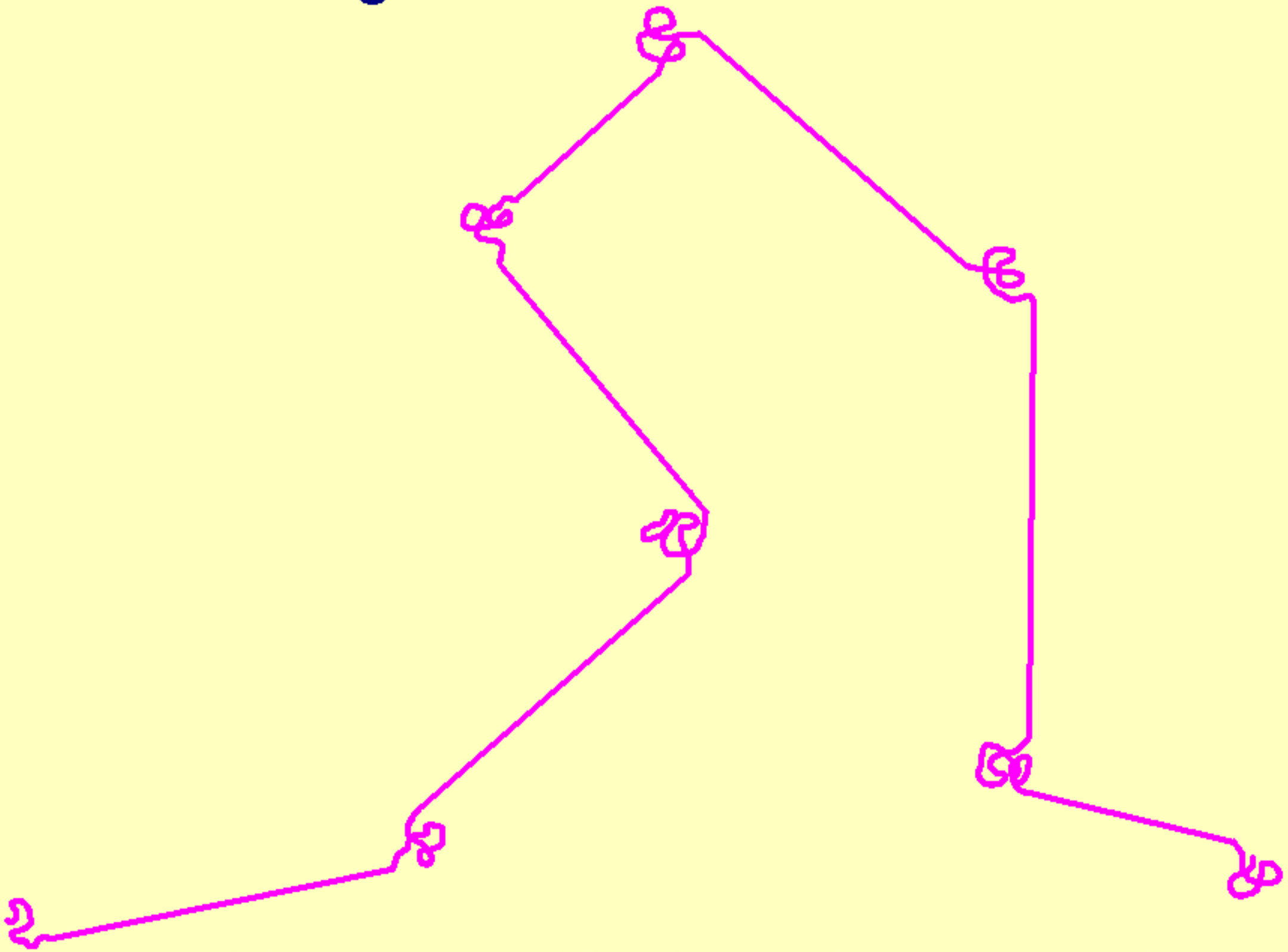
Intra-patch move length distribution



Inter-patch move length distribution

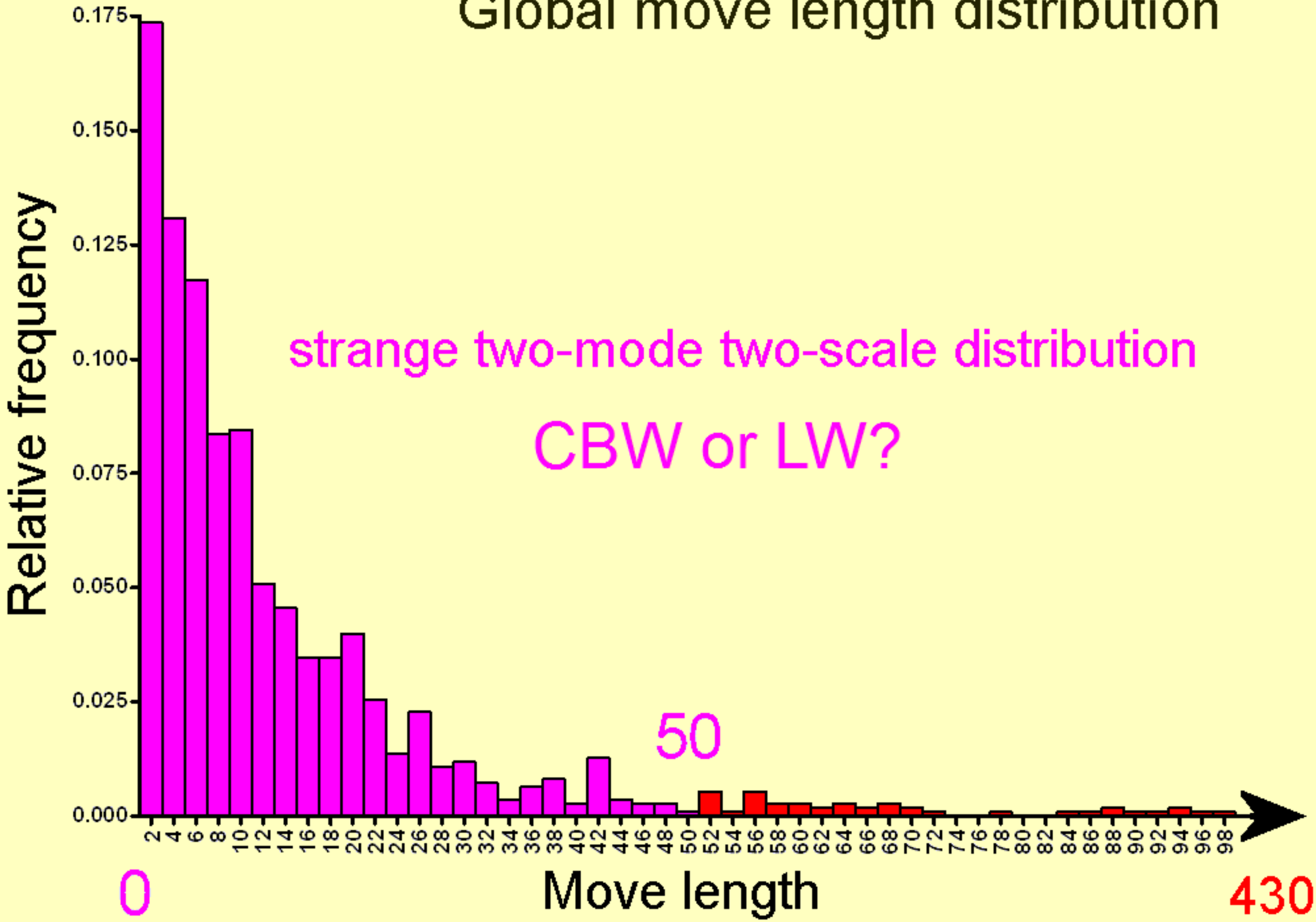


a strange two-mode two-scale mixture

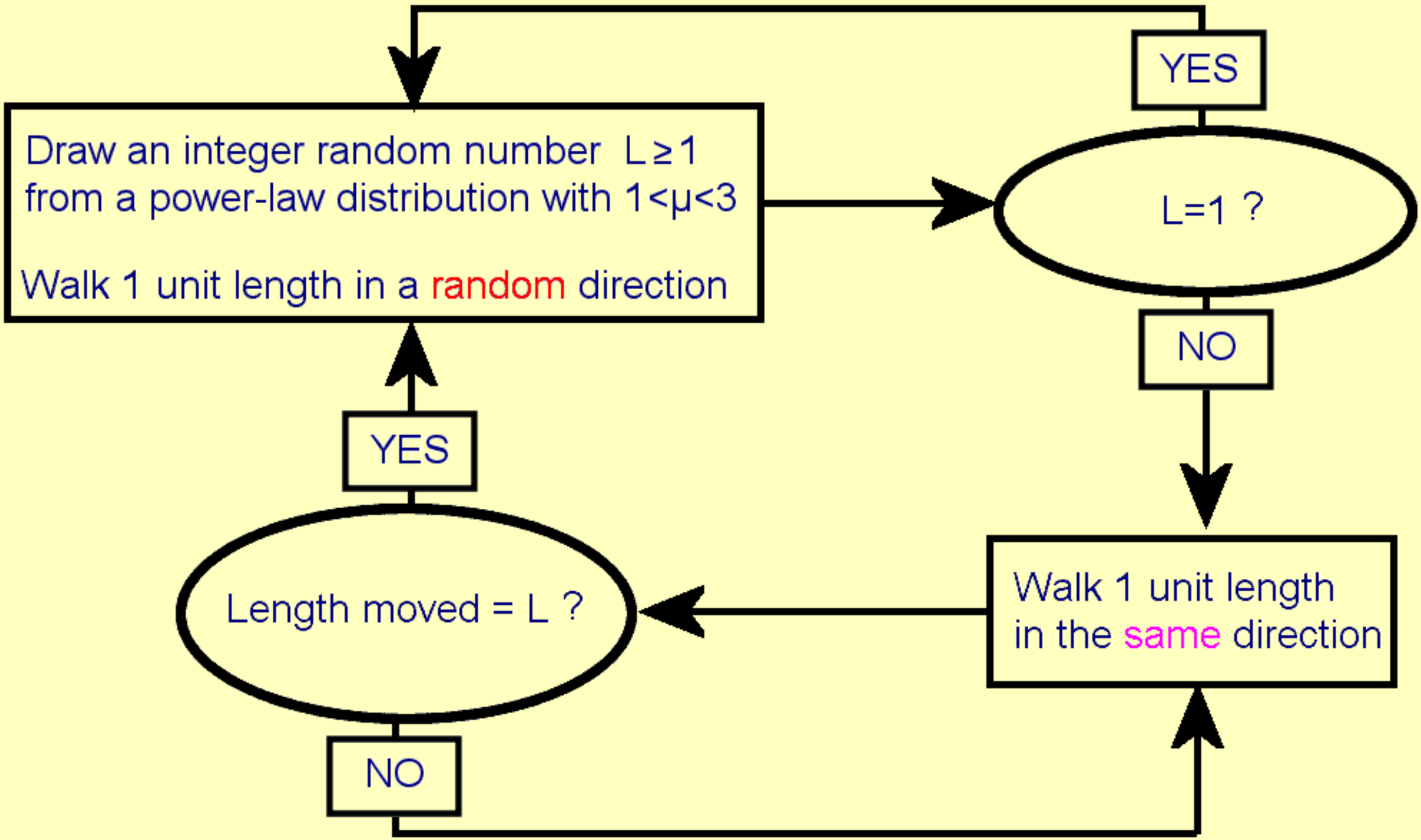


with unspecified modes or scales

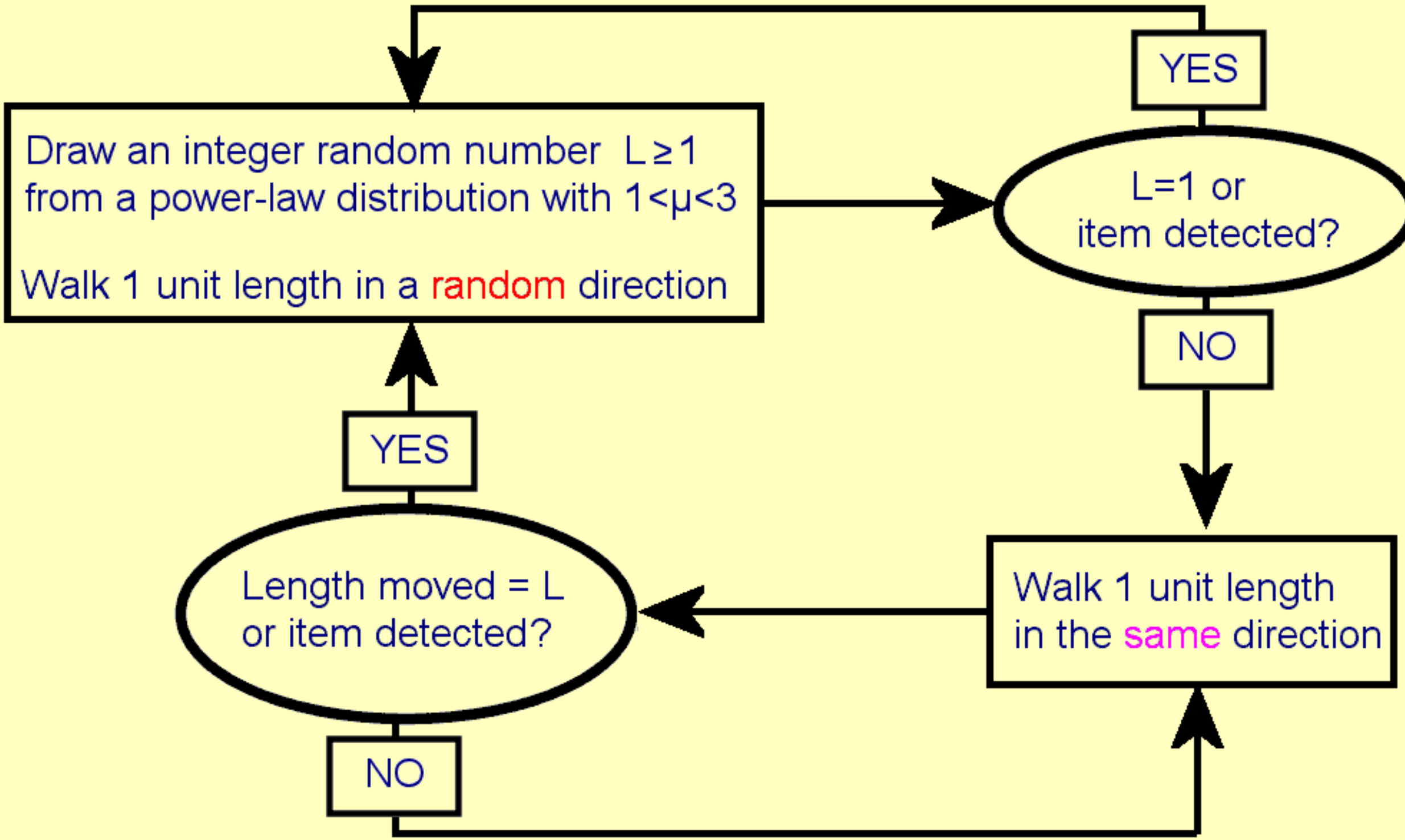
Global move length distribution



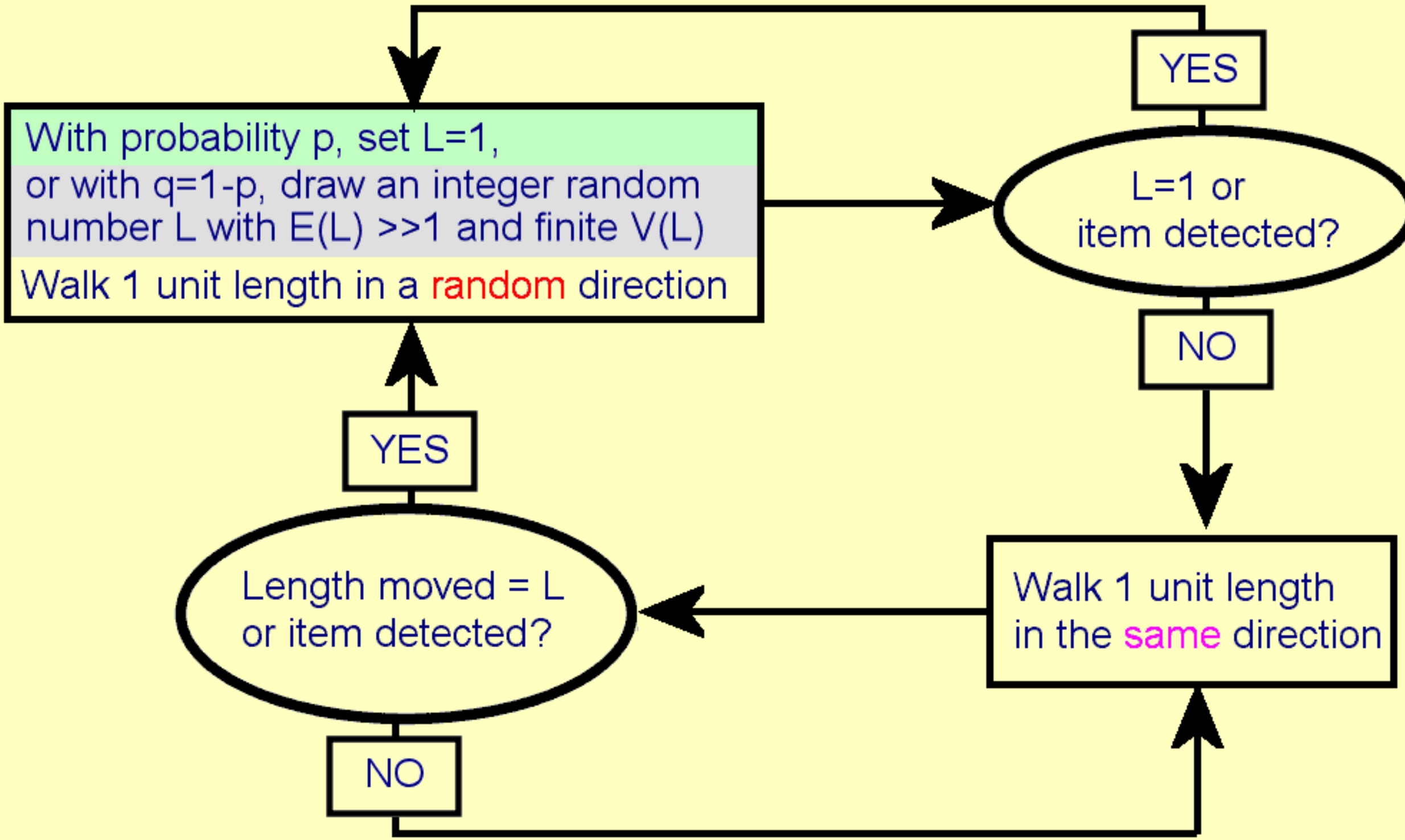
LEVY WALK


Draw an integer random number L ≥ 1
from a power-law distribution with 1<μ<3
Walk 1 unit length in a random direction
YES
L=1 ?
NO
Walk 1 unit length
in the same direction
Length moved = L ?
YES
NO

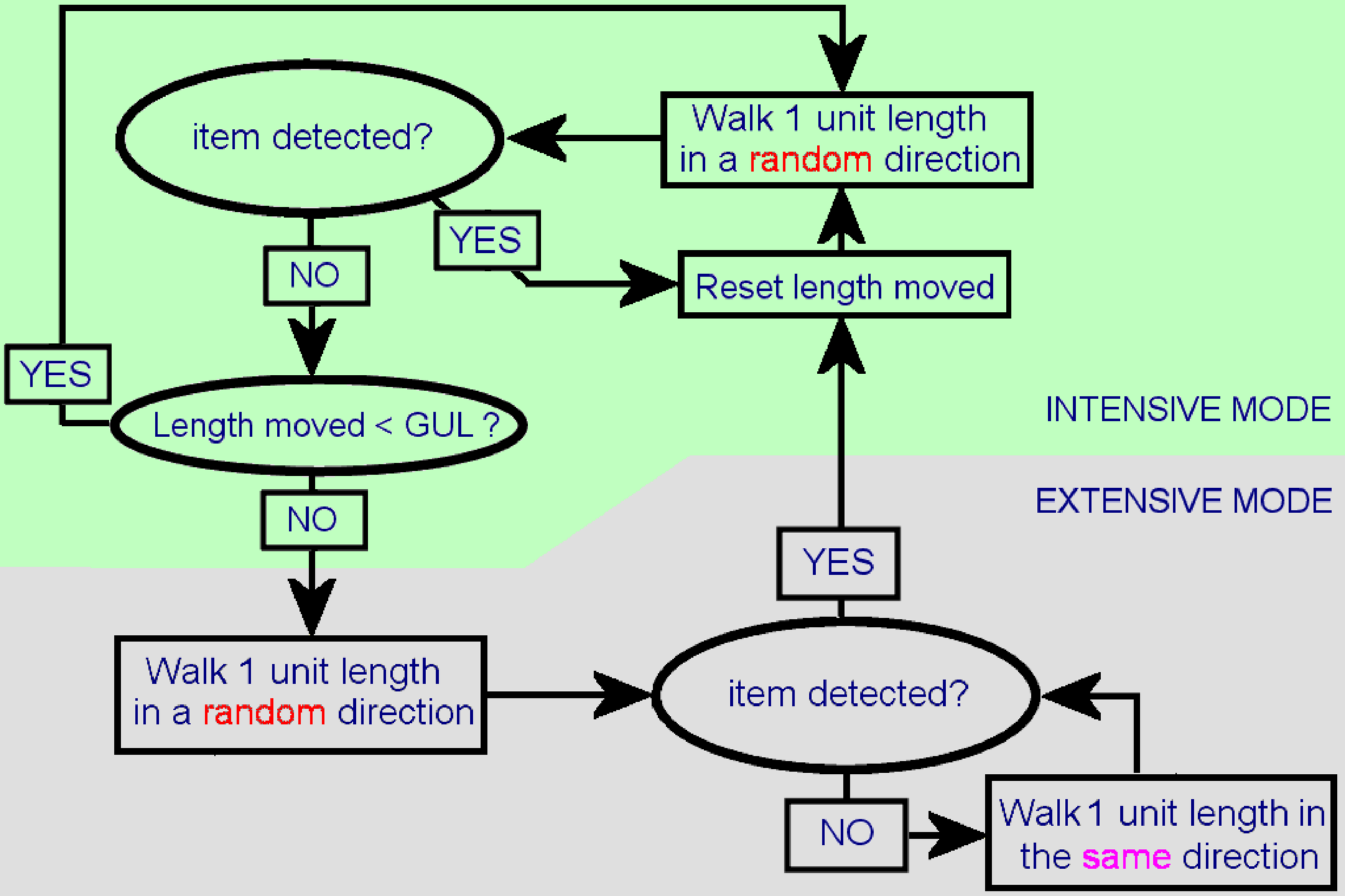
TRUNCATED LEVY WALK



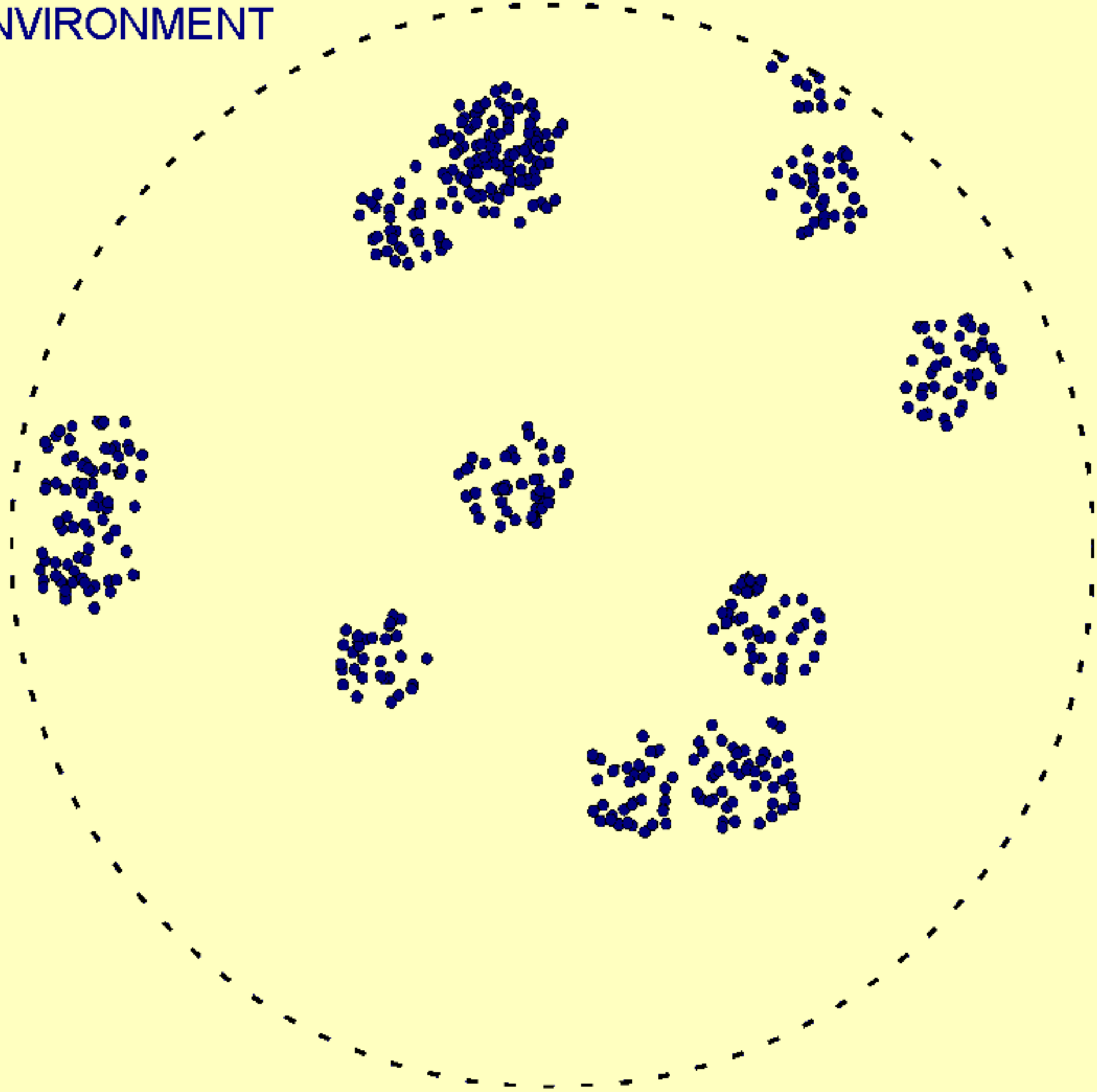
TRUNCATED COMPOSITE BROWNIAN WALK



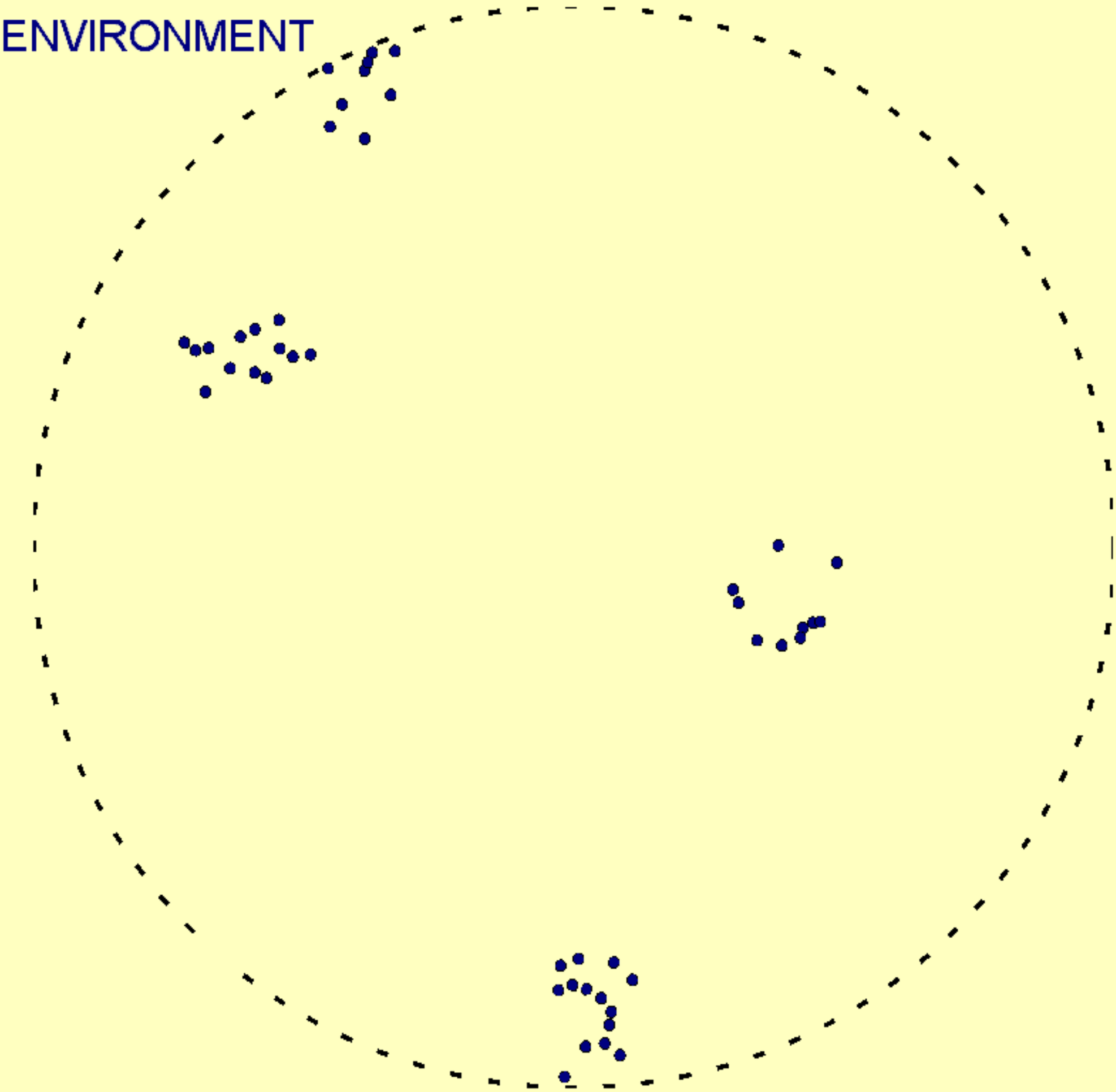
CUE-DRIVEN COMPOSITE BROWNIAN WALK

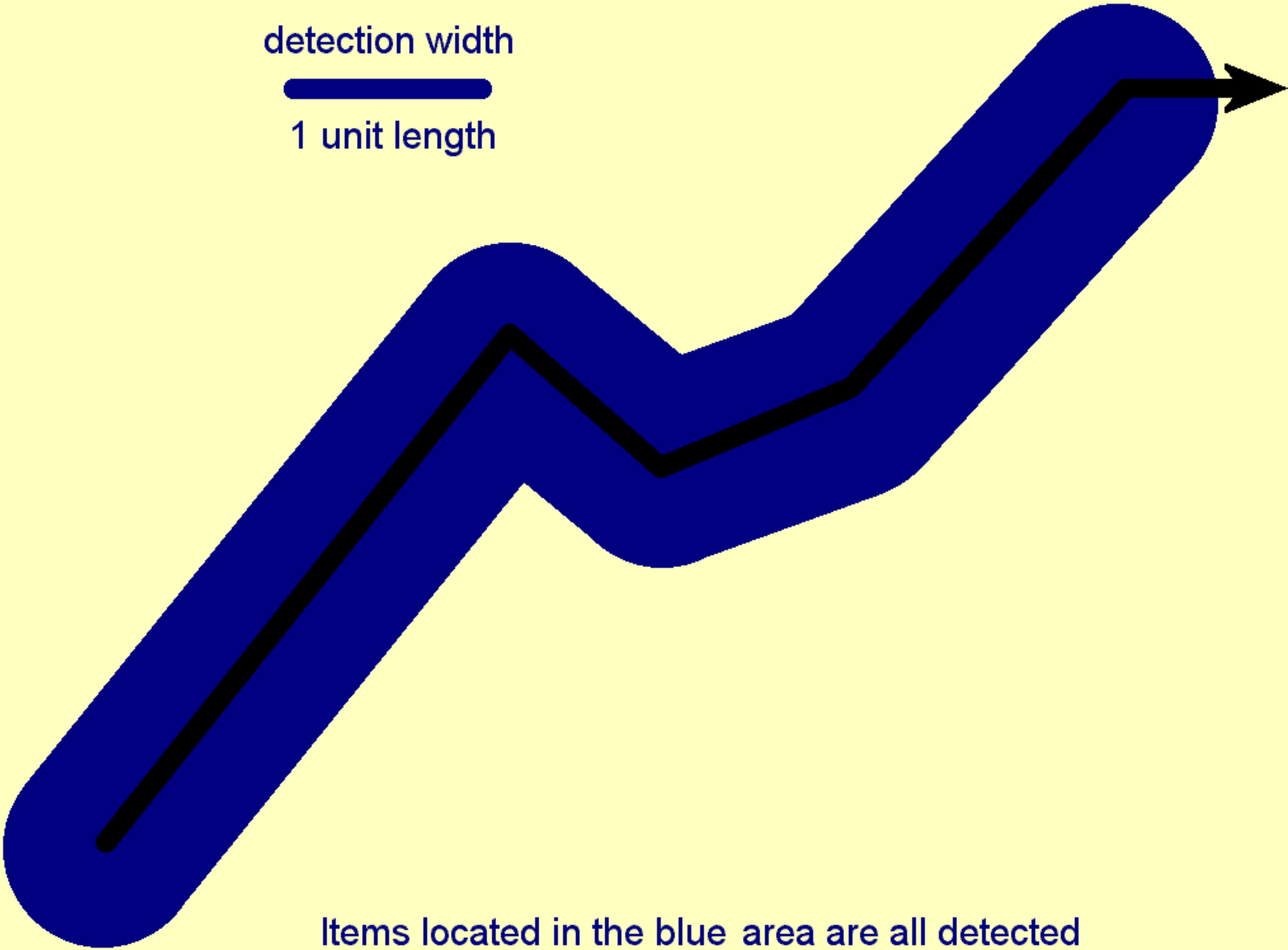


RICH ENVIRONMENT



POOR ENVIRONMENT




detection width
1 unit length
Items located in the blue area are all detected

Giving-up length (CBW)

0 10 20 30 40 50 60 70 80

1.9 1.8 1.7 1.6 1.5 1.4 1.3 1.2 1.1 1.0 0.9 0.8 0.7 0.6 0.5 0.4 0.3

Relative efficiency

PE

RE

CBW

TLW

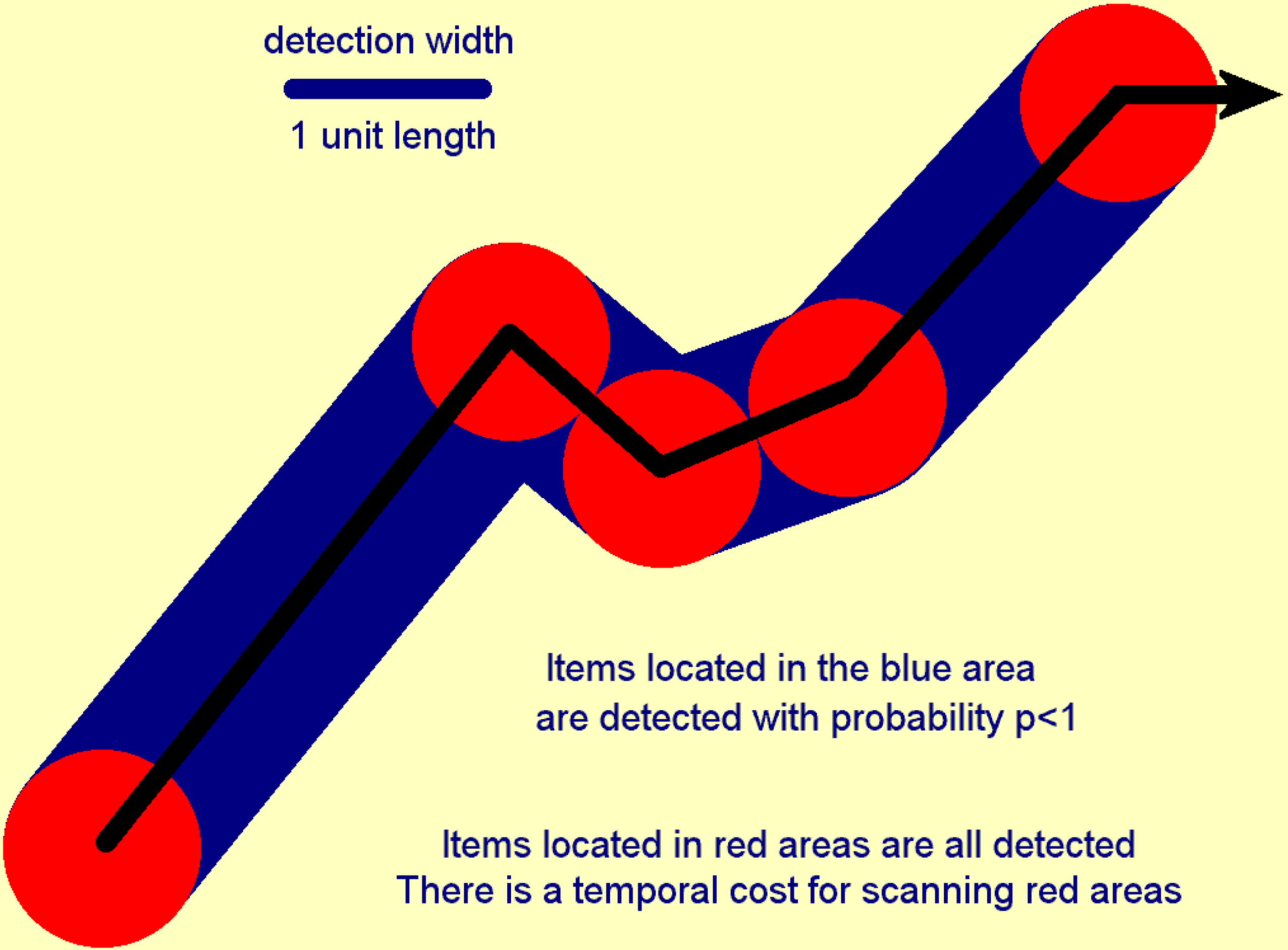
PE

RE

1.0 1.2 1.4 1.6 1.8 2.0 2.2 2.4 2.6 2.8 3.0

μ (TLW)

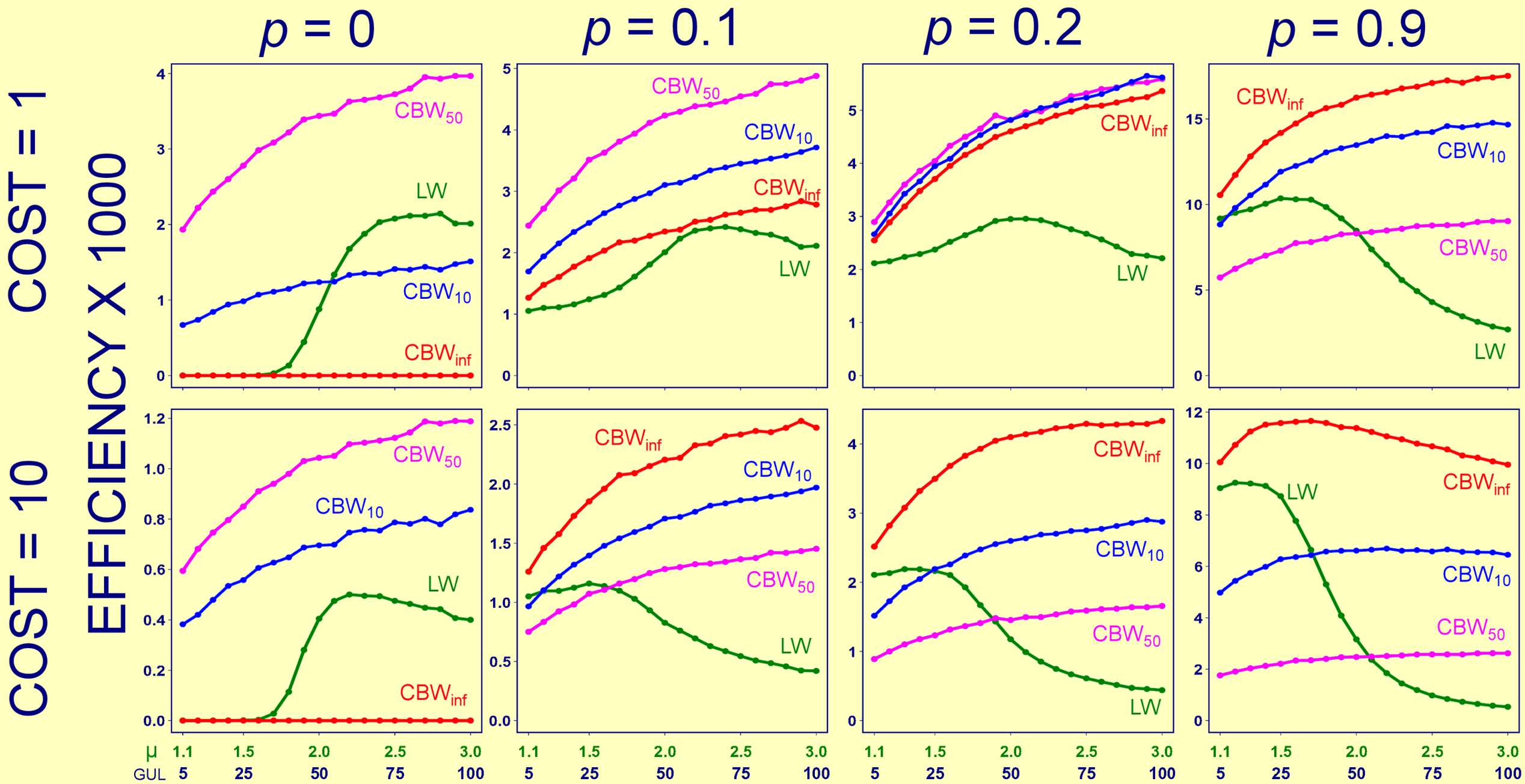
Benhamou, Ecology 2007



Items located in the blue area
are detected with probability p<1

Items located in red areas are all detected
There is a temporal cost for scanning red areas

POOR ENVIRONMENT



Benhamou & Collet, *J. Theor. Biol.*, in rev.

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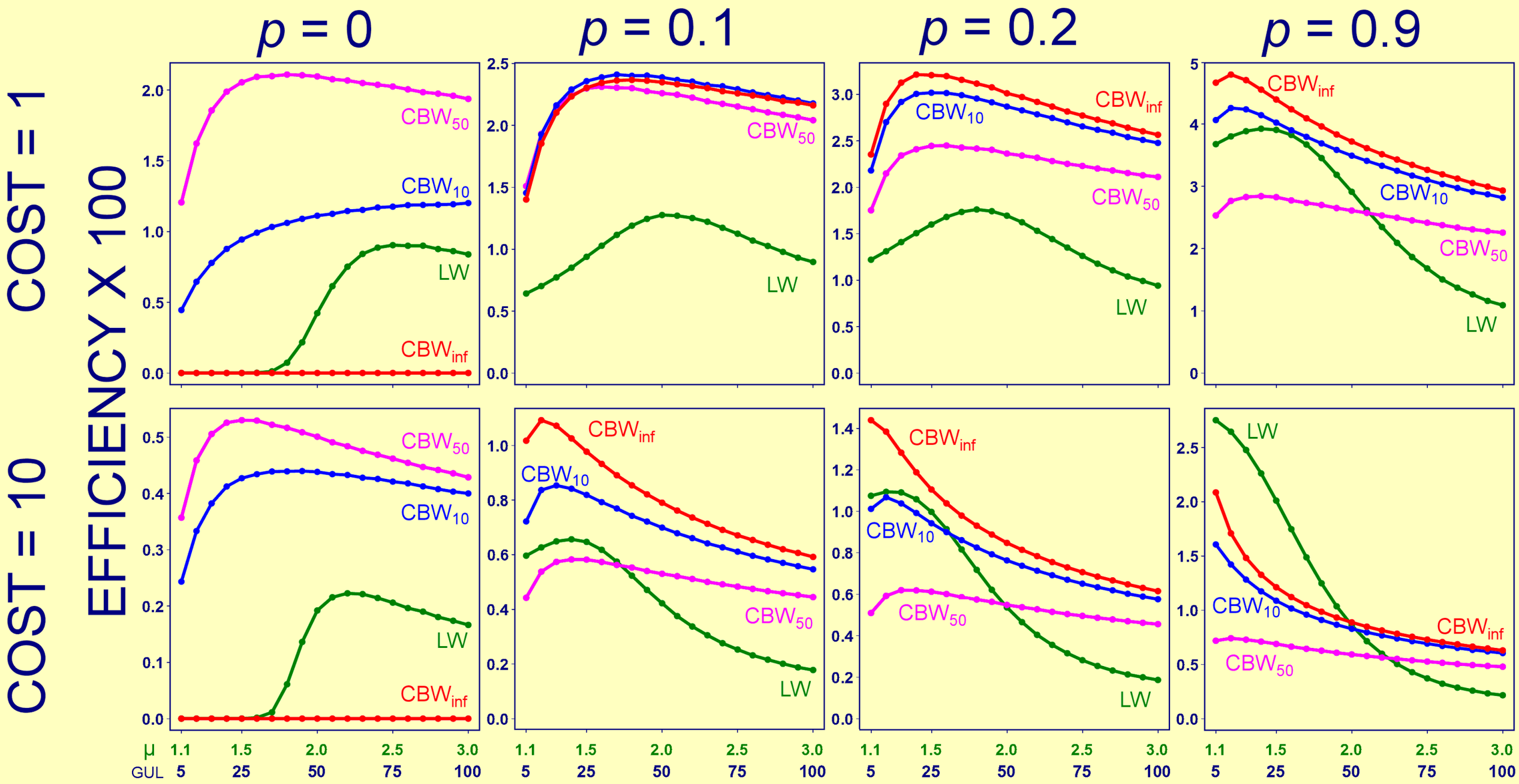

Benhamou & Collet, *J. Theor. Biol.*, in rev.

THE LEVY FORAGING HYPOTHESIS

- (Truncated) LW is the best strategy to search for prey in an unpredictable environment
- This is so because LW is superdiffusive, with fractal reorientations times.
- This is so because LW mixes relocation events (ballistic) with intensive search (diffusive)
- This is so because (truncated) LW mixes cue-driven and internally-driven reorientations

THE FACTS

- Pure LW is not efficient (but generally not considered by the LFH)
- Truncated LW with intermediate μ value is usually more efficient than SL (LW with μ=1) and mere BW (LW with μ=3)
- Truncated LW with intermediate μ value is less efficient than CBW
- Spontaneous scanning is efficient only for animals (almost) blind while moving

TAKE-HOME MESSAGE 1: THE IMPORTANCE OF ENVIRONMENTAL FEED-BACKS

- In an unpredictable but patchy environment, prey detection provides useful information

- Pure LW, SL strategy (or LW with $\mu=1$) and mere BW (or LW with $\mu>3$)
  do not use any feed-back and are unsurprisingly inefficient.

- Truncated LW uses prey detection to stop relocation, usually to shift to intensive search
  It is unsurprisingly more efficient than pure LW, SL and mere BW

- Feed-back is not rationally used in truncated LW: prey detection and length moved act similarly

- Cue-driven CBW (possibly with internally-driven scans if needed) uses the same information as truncated LW (prey detection and length moved) in a much more rational way to control locations and duration of intensive searching phases

  ⇨ Cue-driven CBW is unsurprisingly more efficient than truncated LW

  ⇨ Truncated LW is more efficient than SL (LW with $\mu=1$) or mere BW (LW with $\mu>3$)
  not because of its strange kinetics with intermediate μ values
  but because it mimics in part (in a quite irrational way) CBW behaviour

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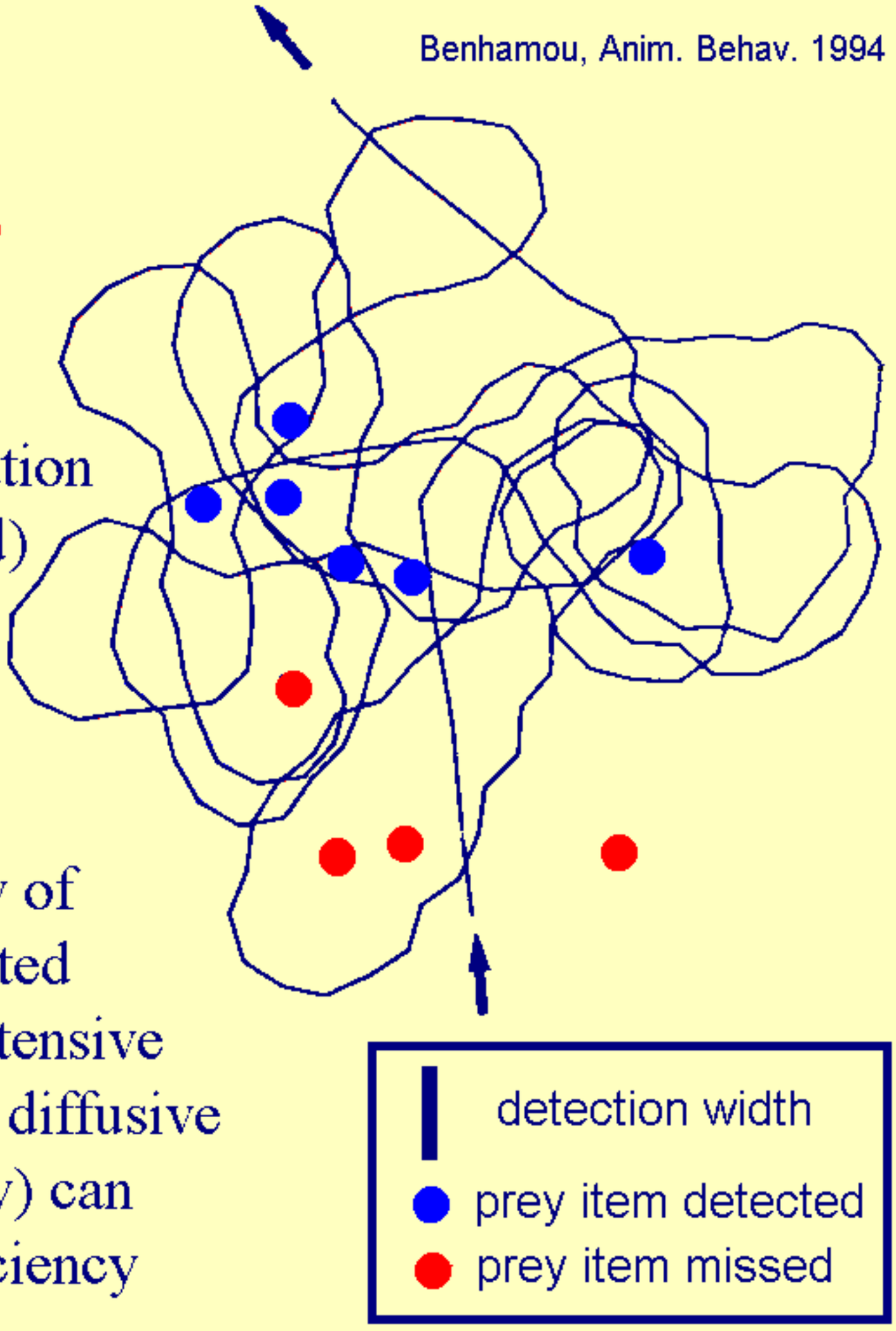
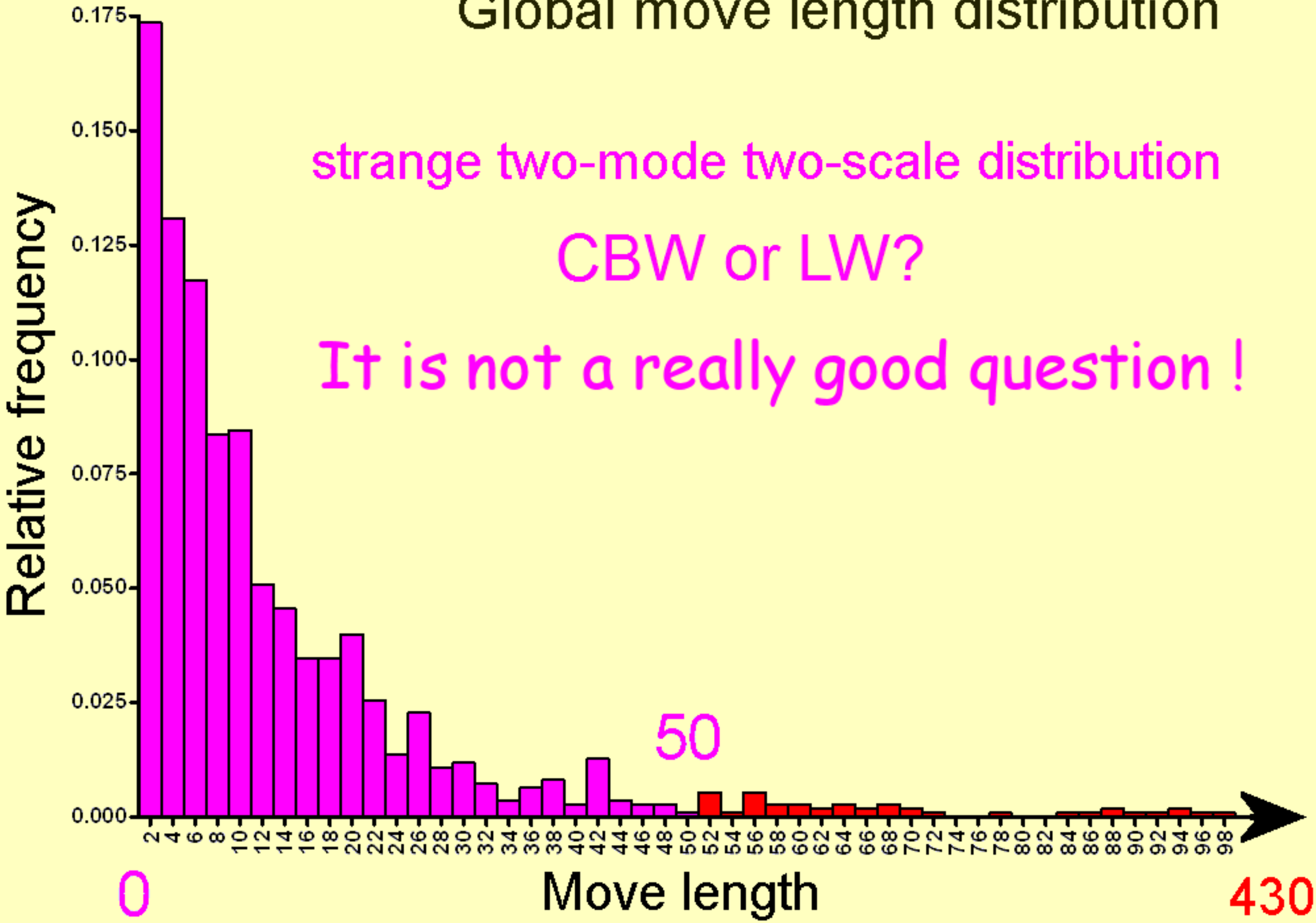
TAKE-HOME MESSAGE 2: DO NOT FORGET POSSIBLE ADDITIONAL MECHANISMS

CBW was designed as a simple alternative to LW: animals are assumed to use the same information (prey detection and length moved) and the same reorientation mechanism (purely random)

Using a simple transitory memory of the location of the last item detected to control reorientations during intensive searching (which is then no more diffusive but involves locational stationarity) can considerably improve search efficiency



Global move length distribution



strange two-mode two-scale distribution

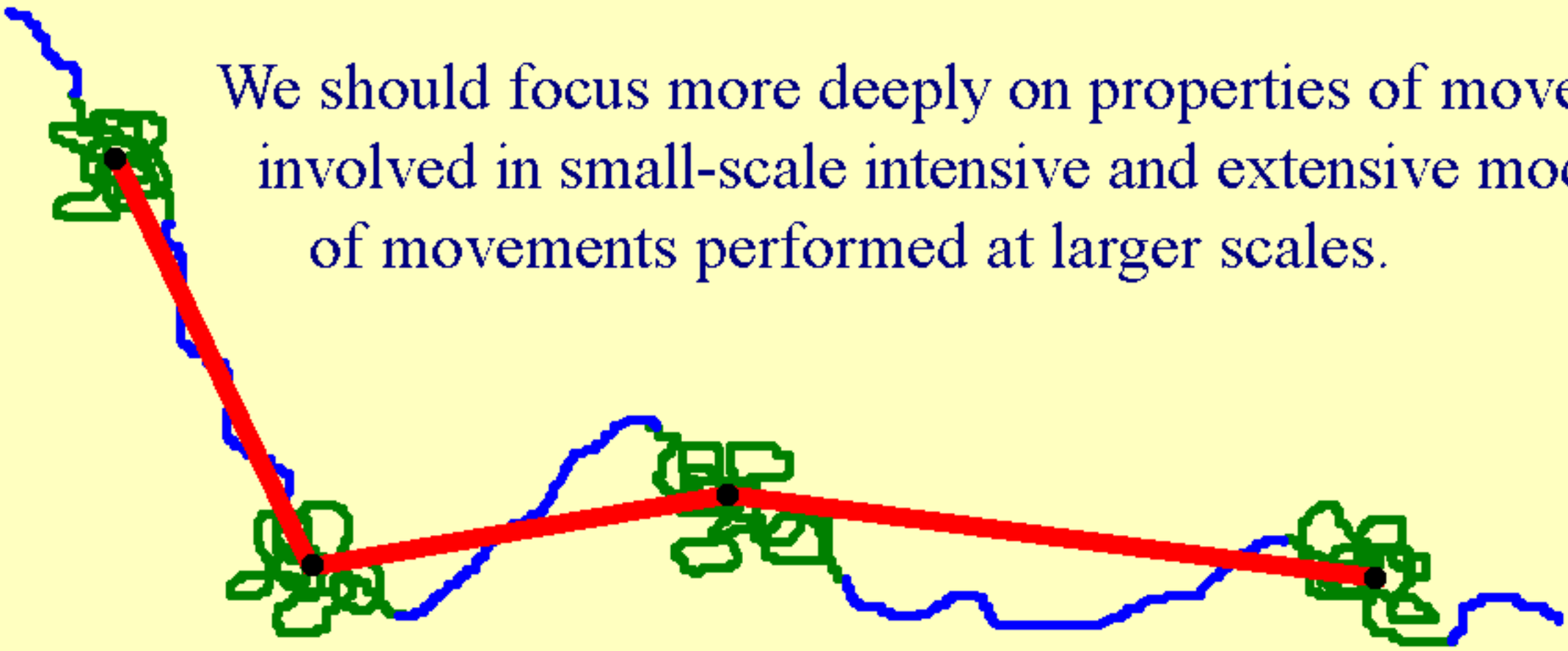
CBW or LW?

It is not a really good question !

TAKE-HOME MESSAGE 3: CONTROVERSIES ABOUT SCALE-FREE SEARCH HIDE INTERESTING QUESTIONS ABOUT MOVEMENT SCALES AND MODES

Both LW and CBW are oversimplified movement models. They can capture some key properties of efficient searching strategies but rest on a confusion about movement scales and movement modes.

We should focus more deeply on properties of movements involved in small-scale intensive and extensive modes and of movements performed at larger scales.



THAT'S ALL FOLKS

...thanks