Summer school, CIRM, Marseille 2016

Animal movements at various scales

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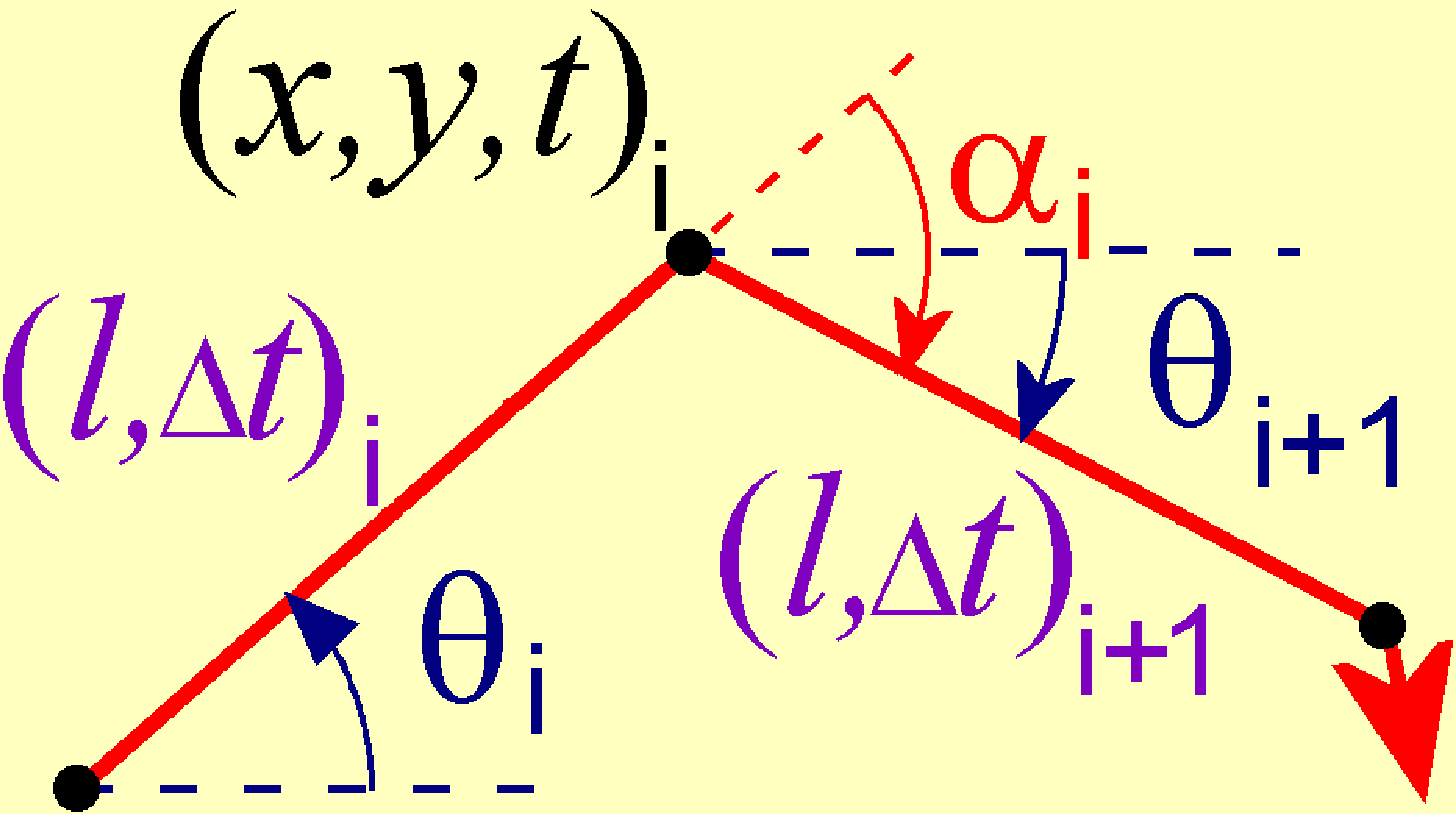
GOOD
MORNING
FOLKS

Discrete movement representation ...



... and sampling issue.

Mean Squared Net Displacement (MSND)

$$R_n^2 = \left(\sum_{j=1}^{n} l_j \cos(\theta_j)\right)^2 + \left(\sum_{j=1}^{n} l_j \sin(\theta_j)\right)^2 = \sum_{j=1}^{n} l_j^2 + 2\sum_{j=1}^{n-1}\sum_{k=j+1}^{n} l_j l_k \cos(\theta_k - \theta_j)$$

Assuming that step lengths *l* are not auto-correlated and not cross-correlated with directions θ, one gets:

$$E(R_n^2) = nE(l^2) + 2E(l)^2 \sum_{j=1}^{n-1}\sum_{k=j+1}^{n} E[\cos(\sum_{h=j}^{k-1}\alpha_h)] = nE(l^2) + 2E(l)^2 \sum_{m=1}^{n-1}(n-m)c_m$$

Example 1: *Biased Random Walk (with goal at infinity)*

$$\sum_{m=1}^{n-1}(n-m)c_m = n(n-1)c/2$$

Example 2: *Systematic square walk*

$$\sum_{m=1}^{n-1}(n-m)c_m = \frac{1 - \sin[(n+1)90°] - n}{2}$$

Example 3: *Balanced Correlated Random Walk*

$$\sum_{m=1}^{n-1}(n-m)c_m = \frac{c}{1-c}\left(n - \frac{1-c^n}{1-c}\right)$$

(Brownian motion: $c = 0$)

(Long-term dispersal: $n \to \infty$)

Benhamou, Ecology 2006

Mean Squared Net Displacement (MSND)

Balanced Correlated Random Walk

$$E(R_n^2) = nE(l^2) + E(l)^2 \frac{2c}{1-c}\left(n - \frac{1-c^n}{1-c}\right)$$

$$E(R_n^2)_a = L_n E(l)\left(\frac{1+c}{1-c} + b^2\right) = 4Dt$$

with path length $L_n = nE(l)$ and coefficient of variation of step length b $(E(l^2) = E(l)^2(1+b^2))$

Transport mean free path l^*

For a non-correlated RW (BM: $c=0$) with step length l^*

$$E(R_n^2) = L_n E(l^*)\left(1+b^2\right) \quad \Rightarrow \quad E(l^*) = \frac{1+c+b^2(1-c)}{(1+b^2)(1-c)} E(l)$$

Particular cases:

Constant step length ($b=0$) for both BM and CRW: $l^* = l(1+c)/(1-c)$

Exponential distribution ($b=1$) for both BM and CRW: $E(l^*) = E(l)/(1-c)$

How to compute the path tortuosity of random search movements?

Sinuosity index for CRW: ***S***

$$D = V/S^2$$

D: coefficient of diffusion
t: time, *V*: mean speed

$$E(R_n^2)_a = L_n E(l)\left(\frac{1-c^2-s^2}{(1-c)^2+s^2}+b^2\right) = 4Dt$$

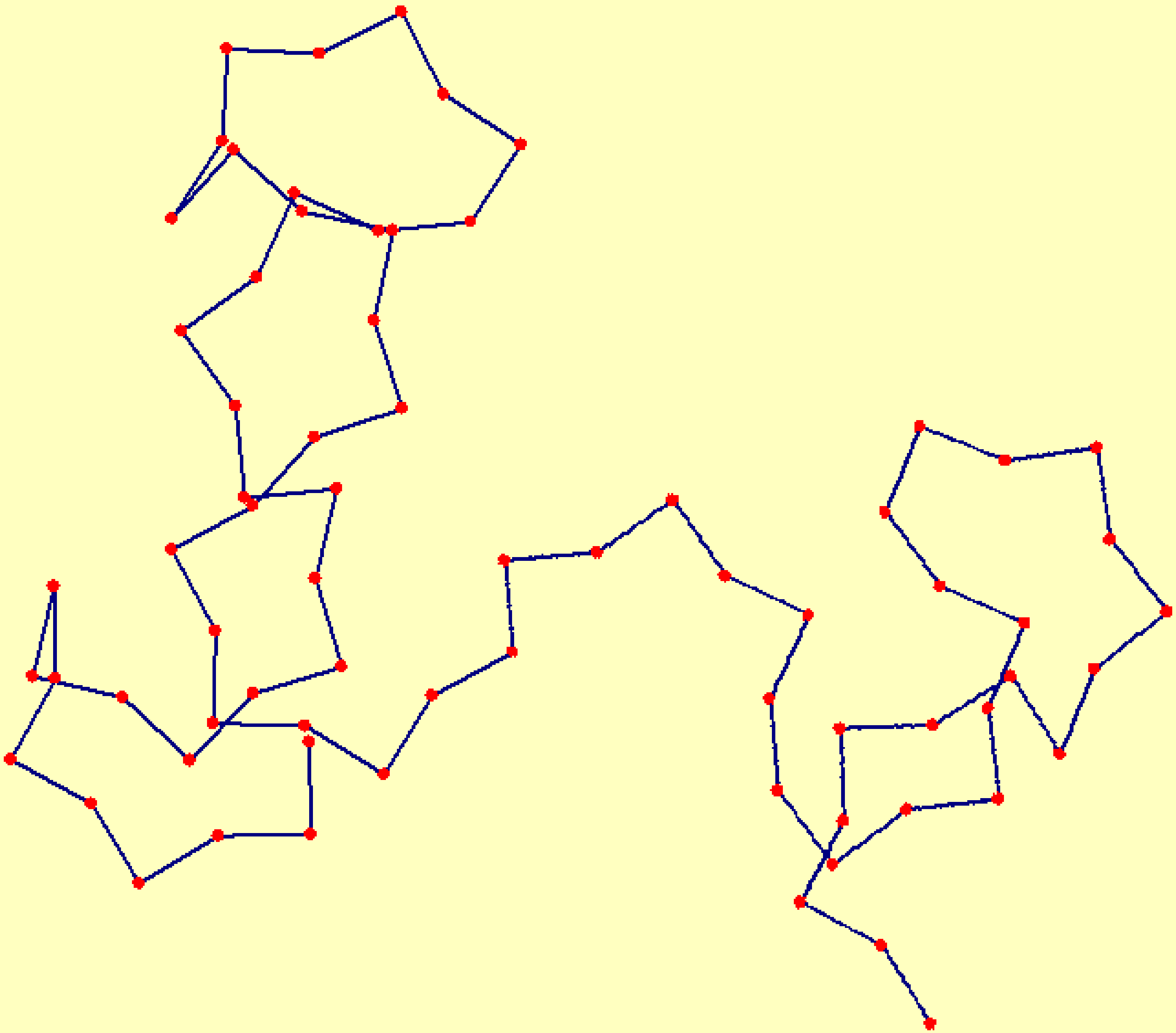
Balanced CRW:

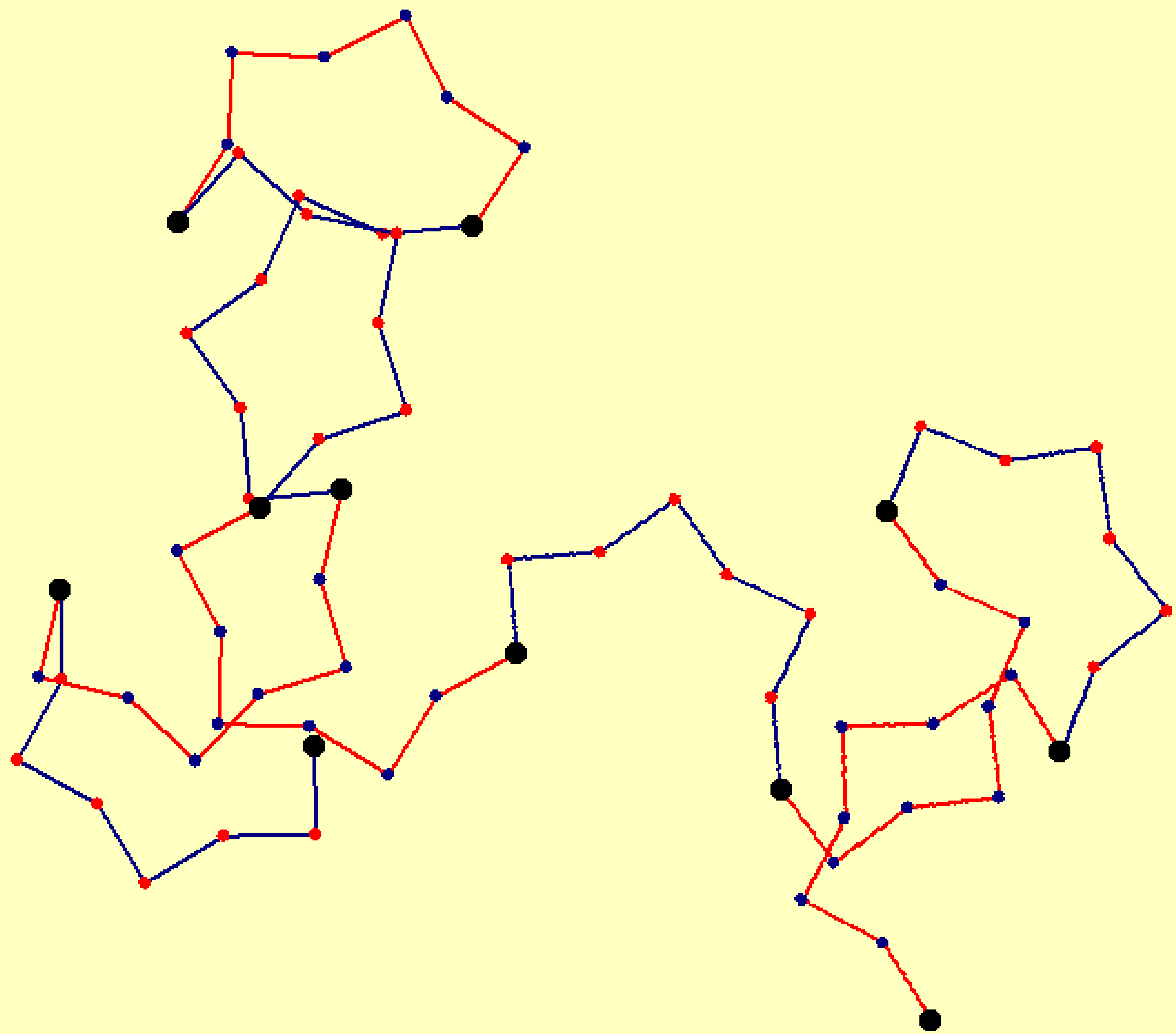
Modelling $S = 2\left[E(l)\left(\frac{1+c}{1-c}+b^2\right)\right]^{-0.5} \simeq \sigma(\alpha)/\sqrt{E(l)}$ for $c > 0.5$

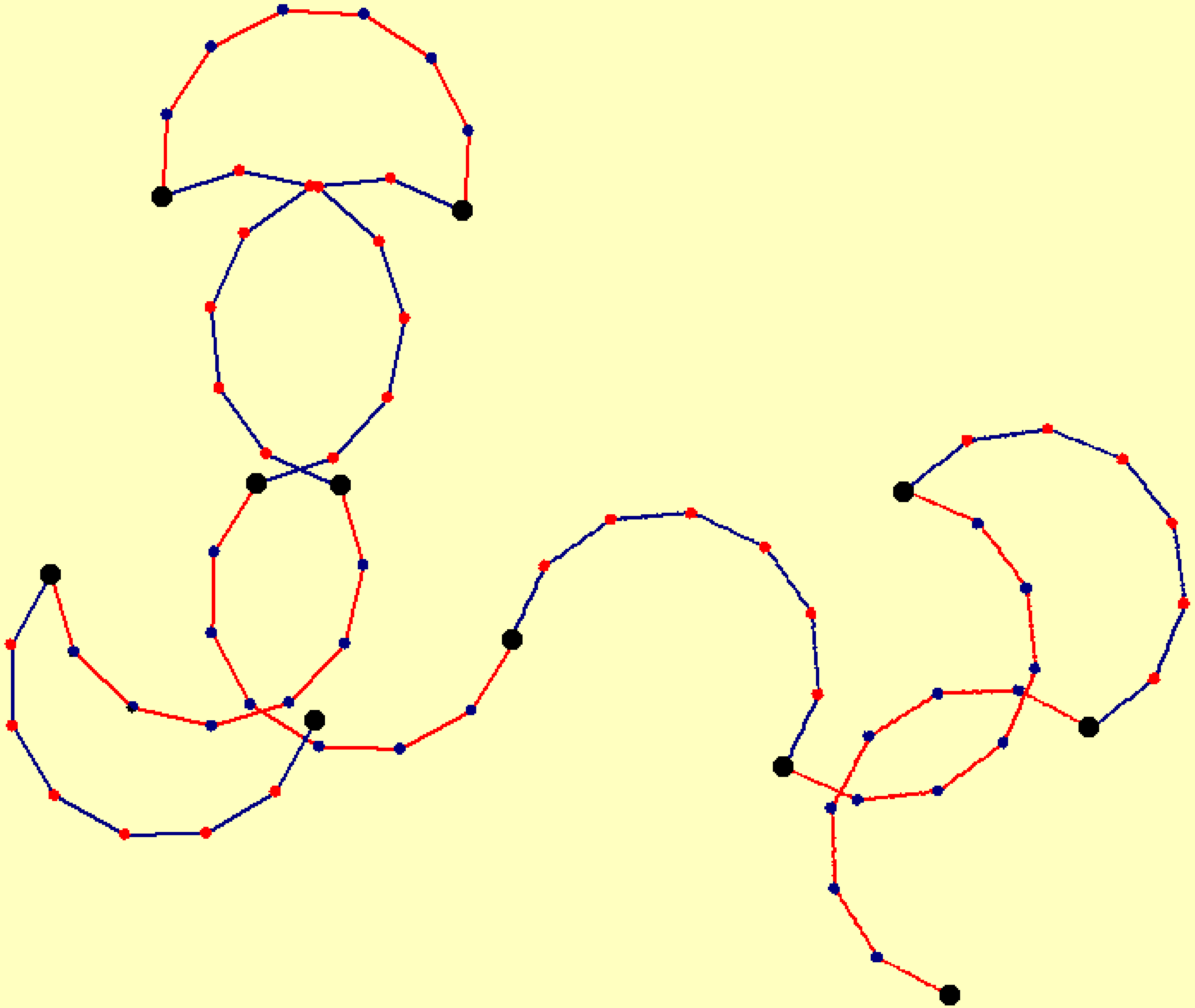
Analysis $S = \left[\frac{2}{l_r}\tan\left(\frac{\pi}{2}(1-c_r)\right)\right]^{0.5} \simeq 1.18\ \sigma(\alpha_r)/\sqrt{l_r}$ for $c > 0.5$

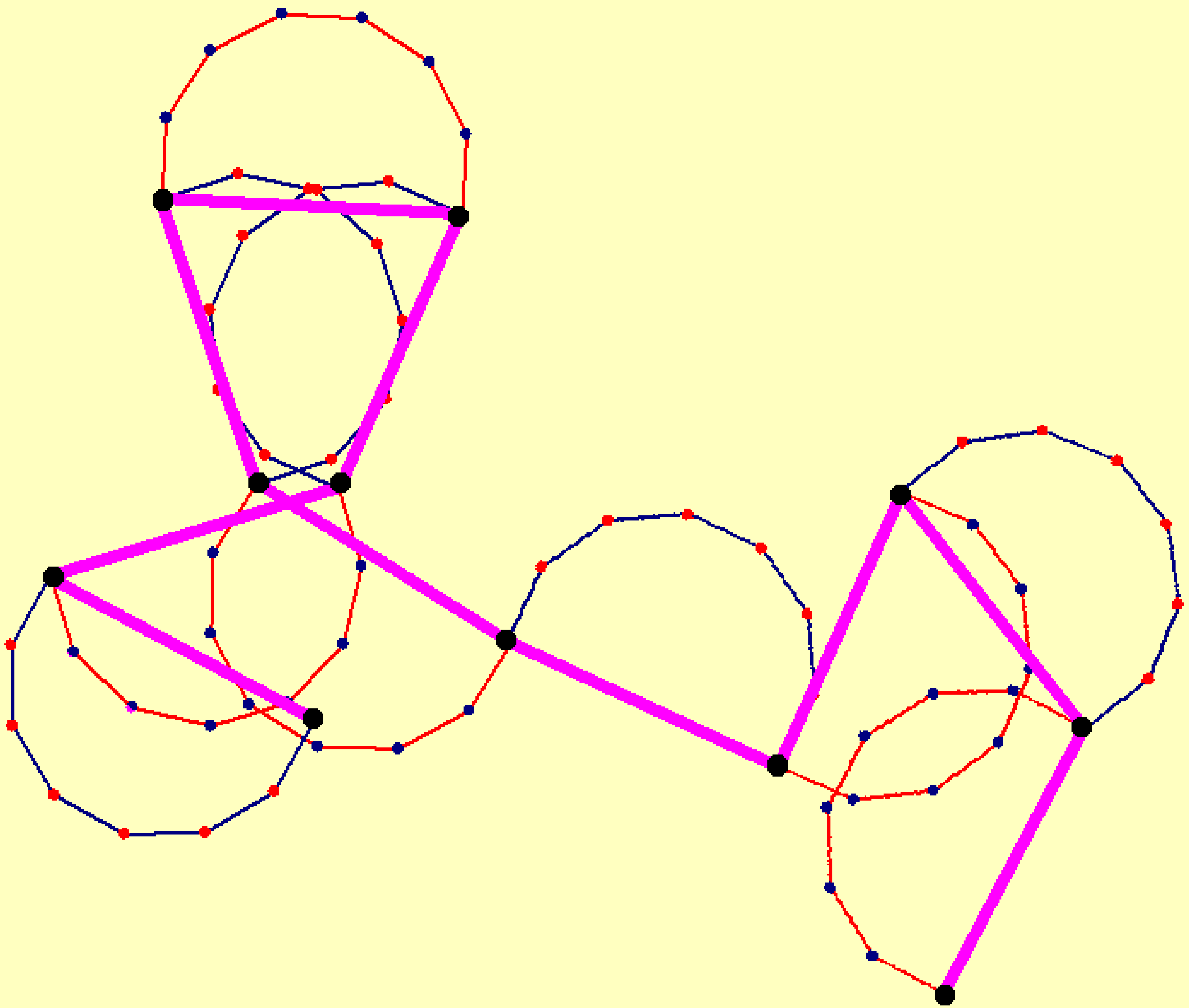
Bovet & Benhamou, J. Theor. Biol. 1988

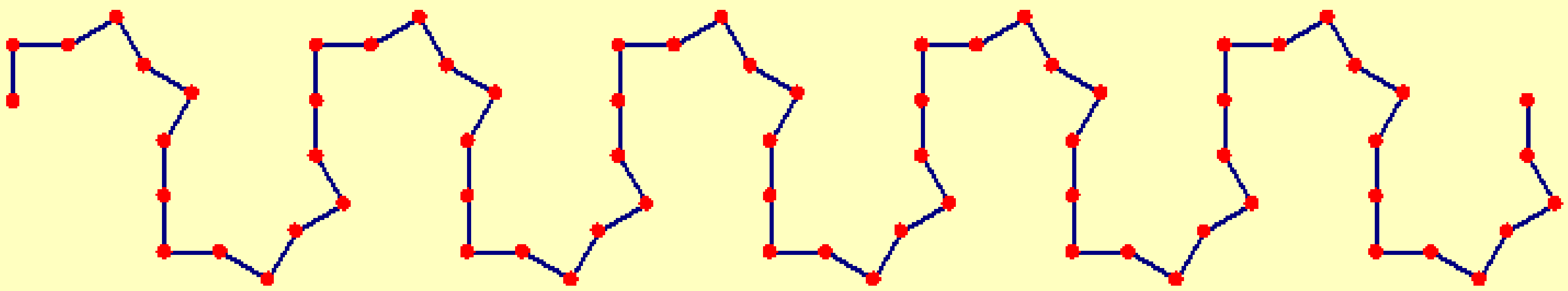
Benhamou, J. Theor. Biol. 2004 , Ecology 2006

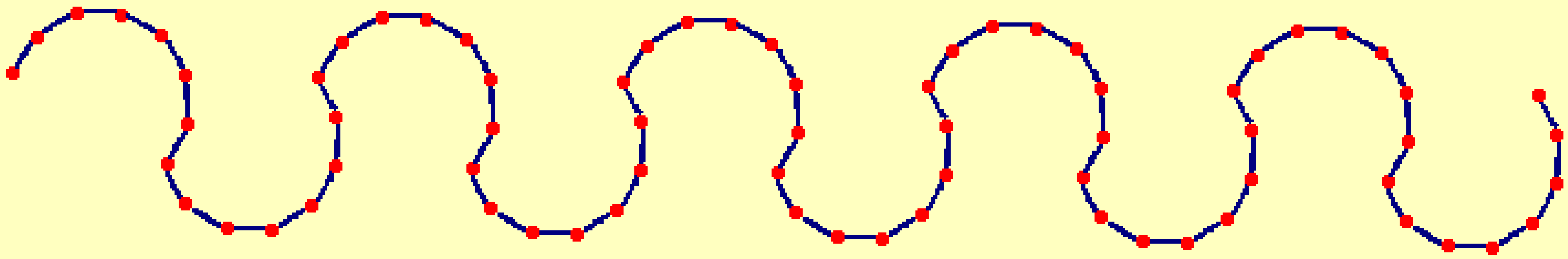


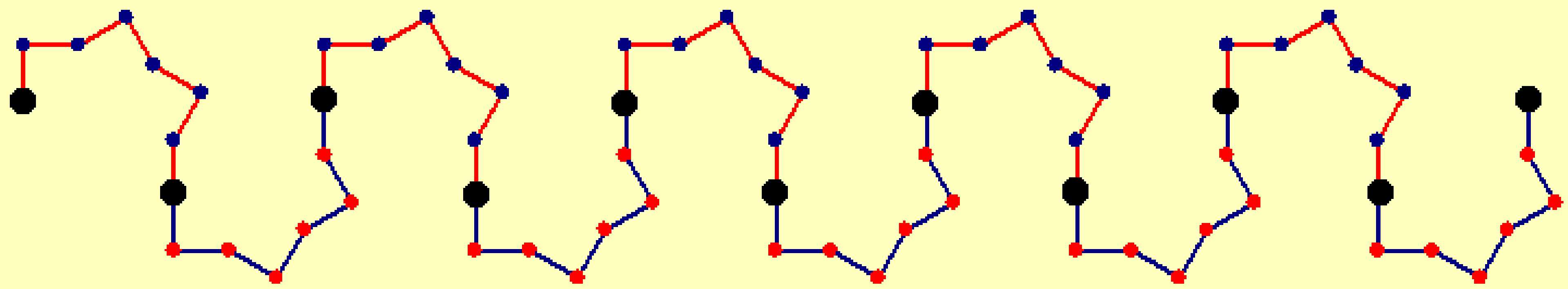
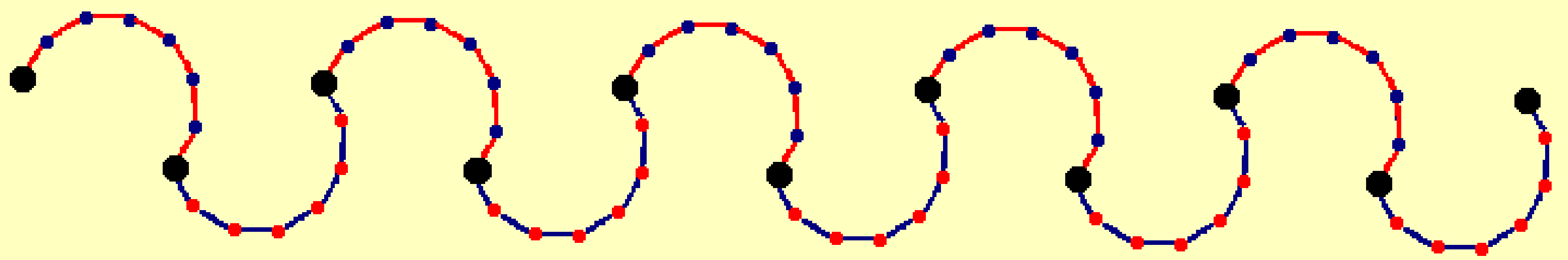


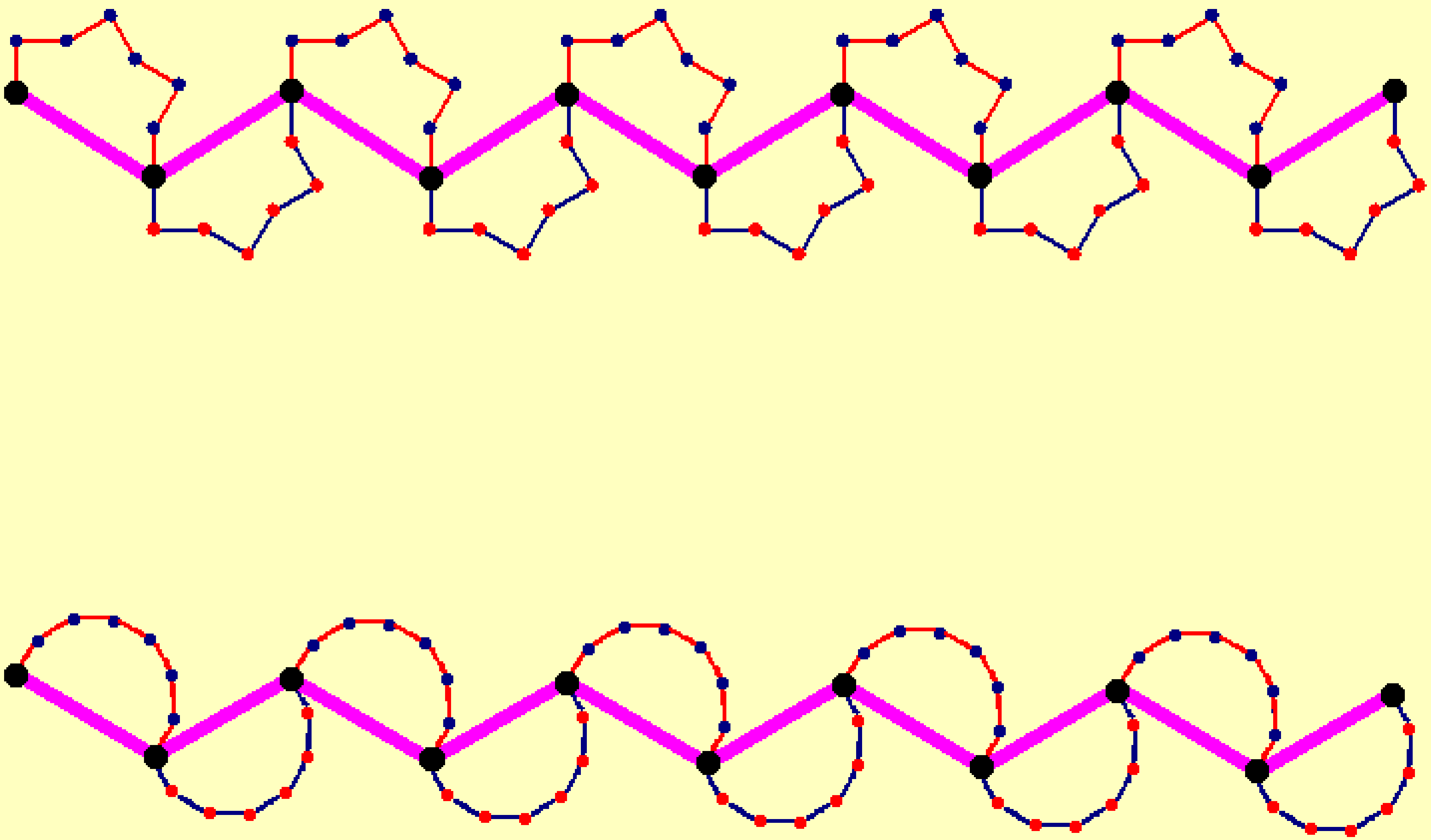










Real World vs. World Models

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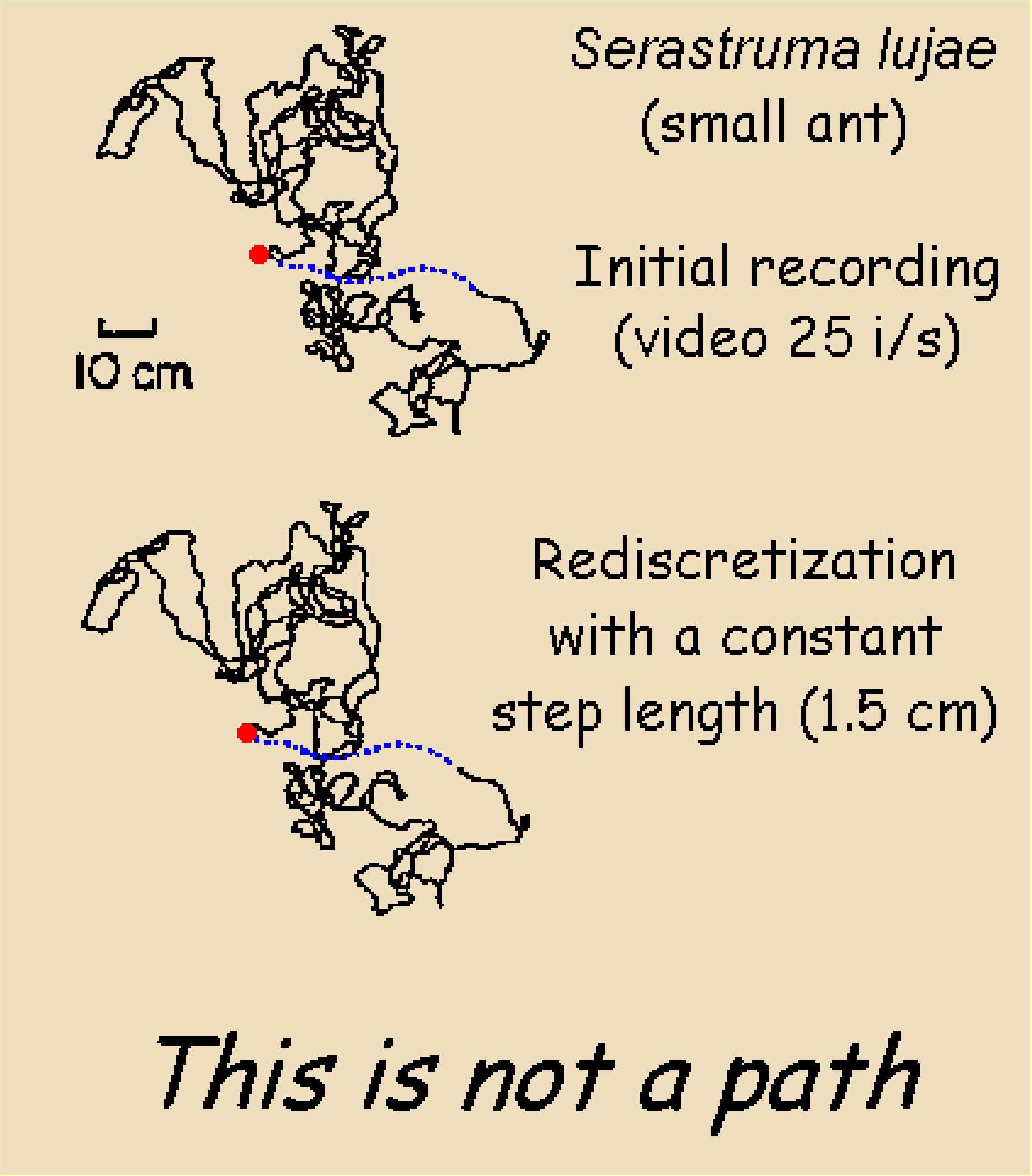

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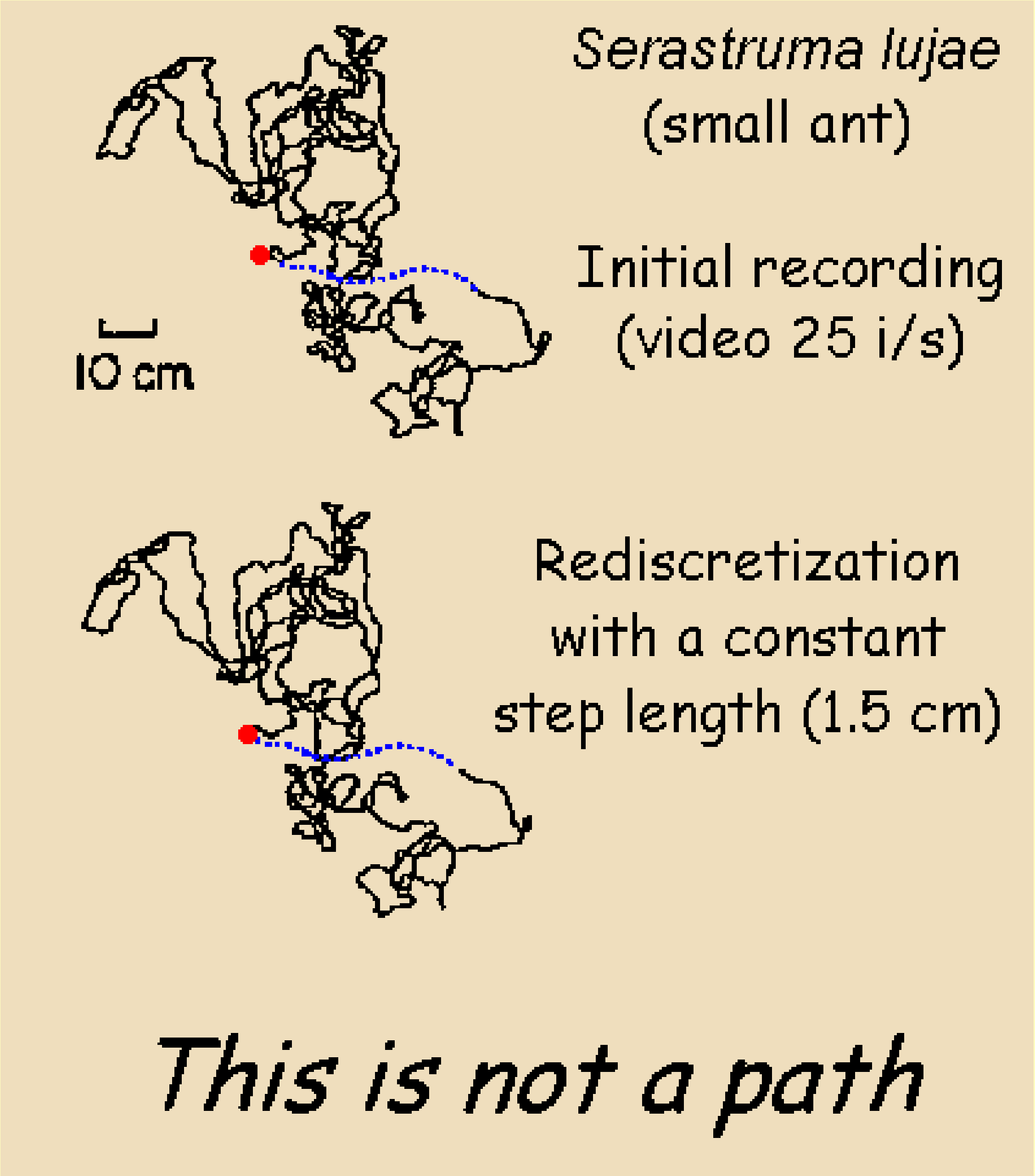
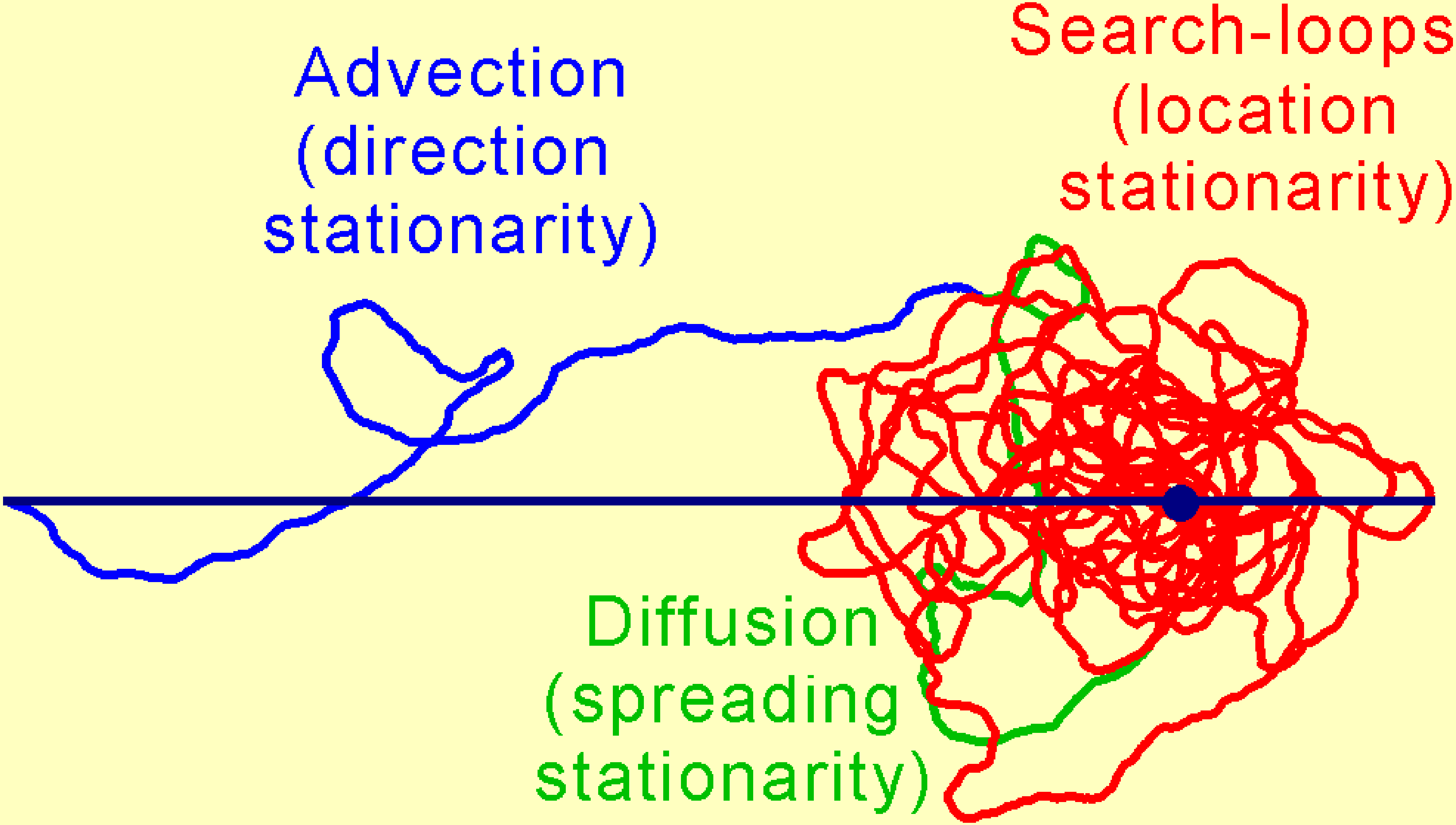


Movement Process => Pattern (path) => Path representation

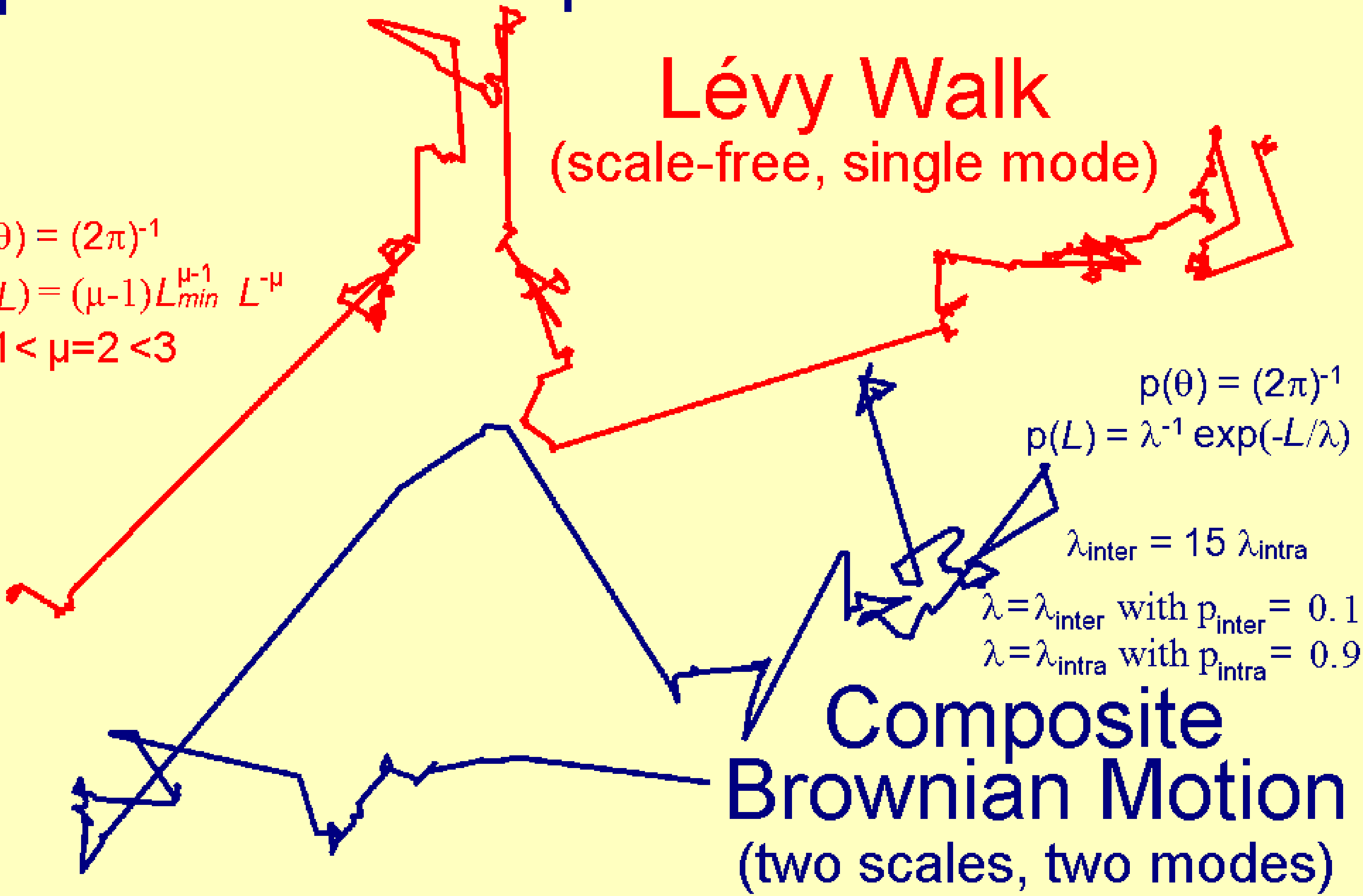
inference

Various patterns generated by ... a single process

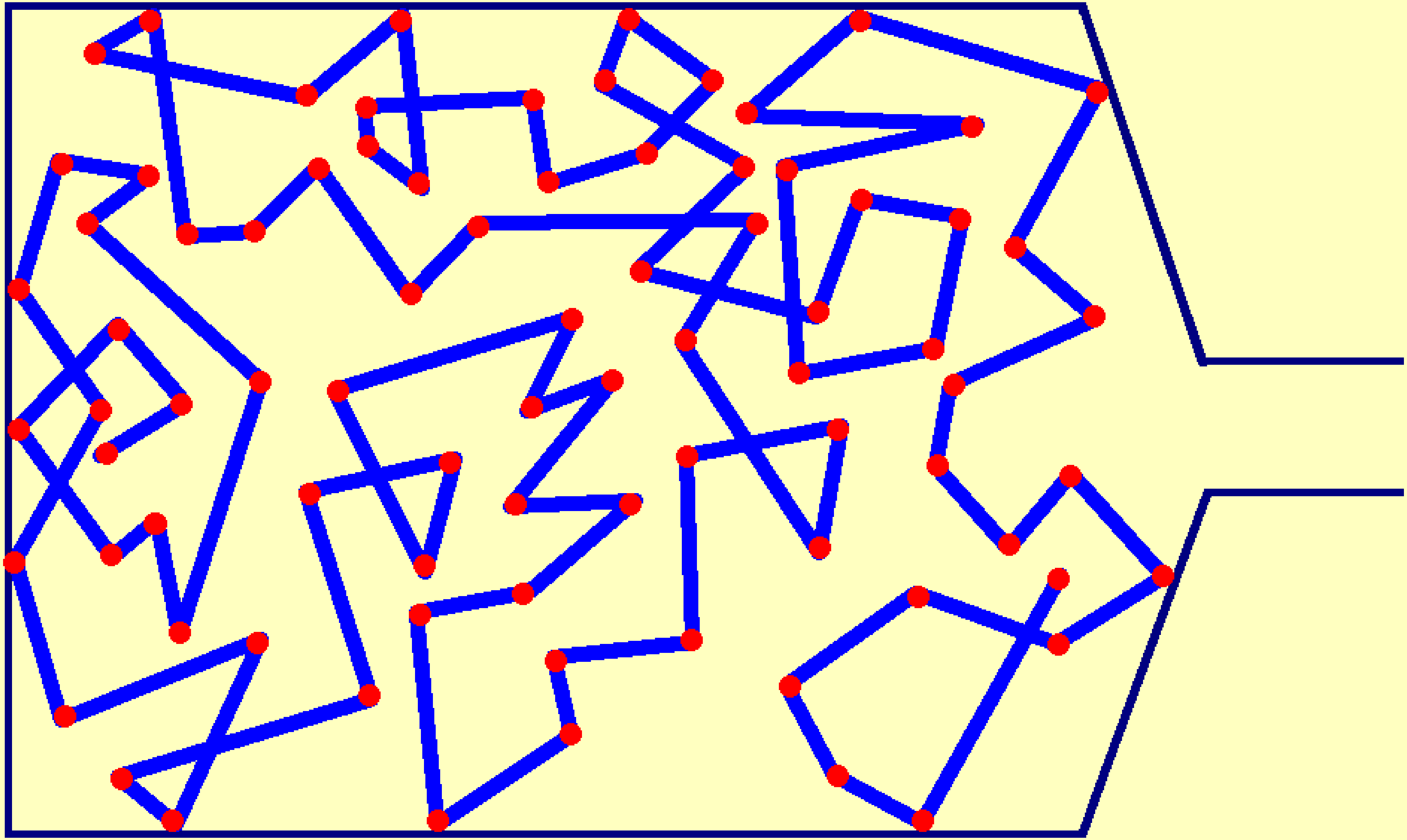


Benhamou, *Ecol. Let.* 2014

Similar patterns generated by ... quite different processes



Consider a gas molecule in a bottle
How many movement scales?



EVIDENCE FOR SPATIAL SCALE-SPECIFIC MOVEMENT PROCESSES

NAVIGATION BEHAVIOUR

Because of a trade-off between working range and accuracy, several (usually three) scales can be distinguished:

+ small scale: pinpointing the goal location
+ medium scale: navigating through a familiar environment
+ large scale: navigating through large unfamiliar environments

These scales are usually uncoupled and used sequentially

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FORAGING BEHAVIOUR

Because of the heterogeneity of the environment, at least two scales can be distinguished:

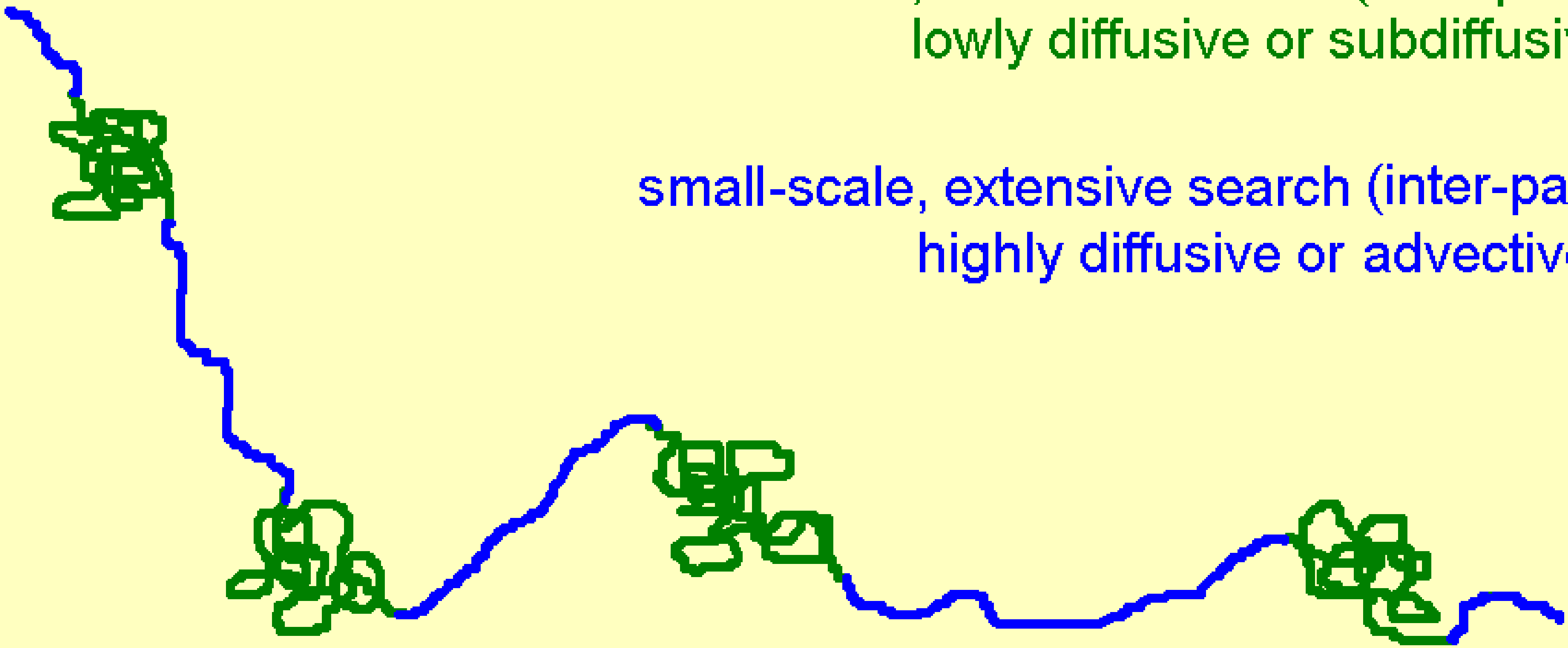
+ small scale: search for prey items between and within patches
+ large scale: patch to patch movement

These scales may be partly coupled and are used simultaneously

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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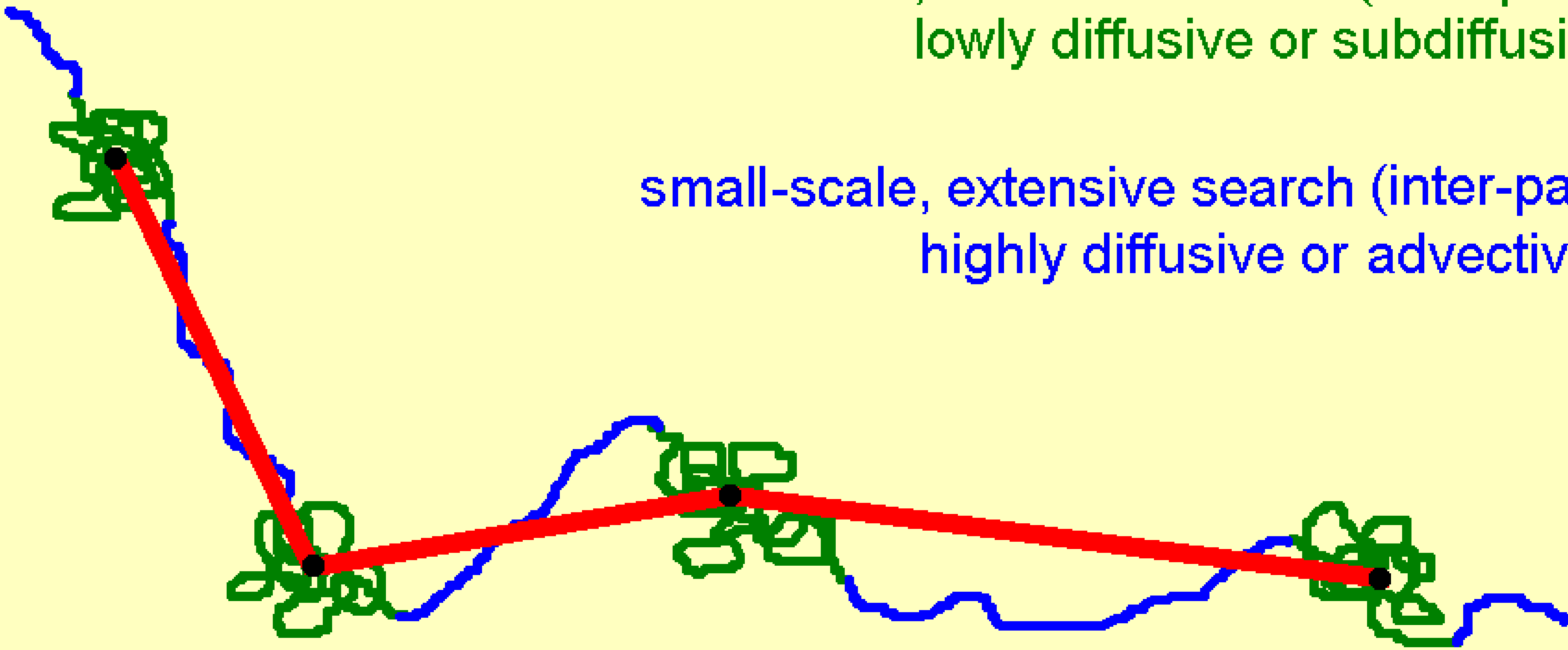
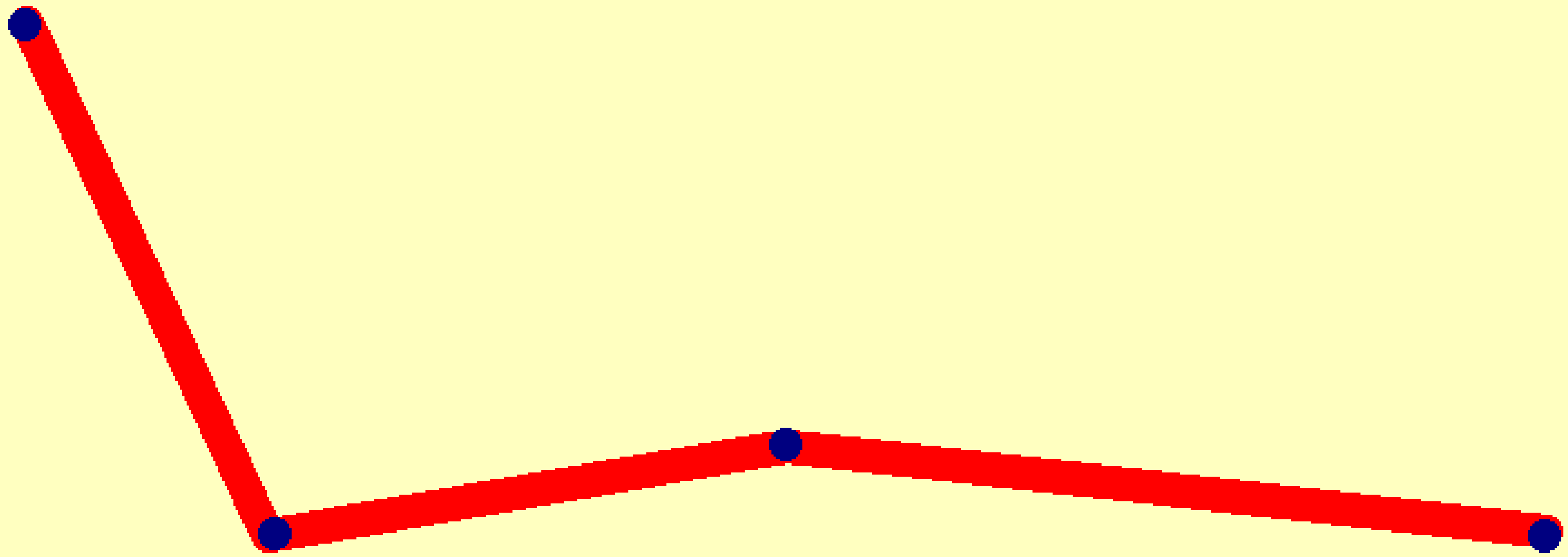
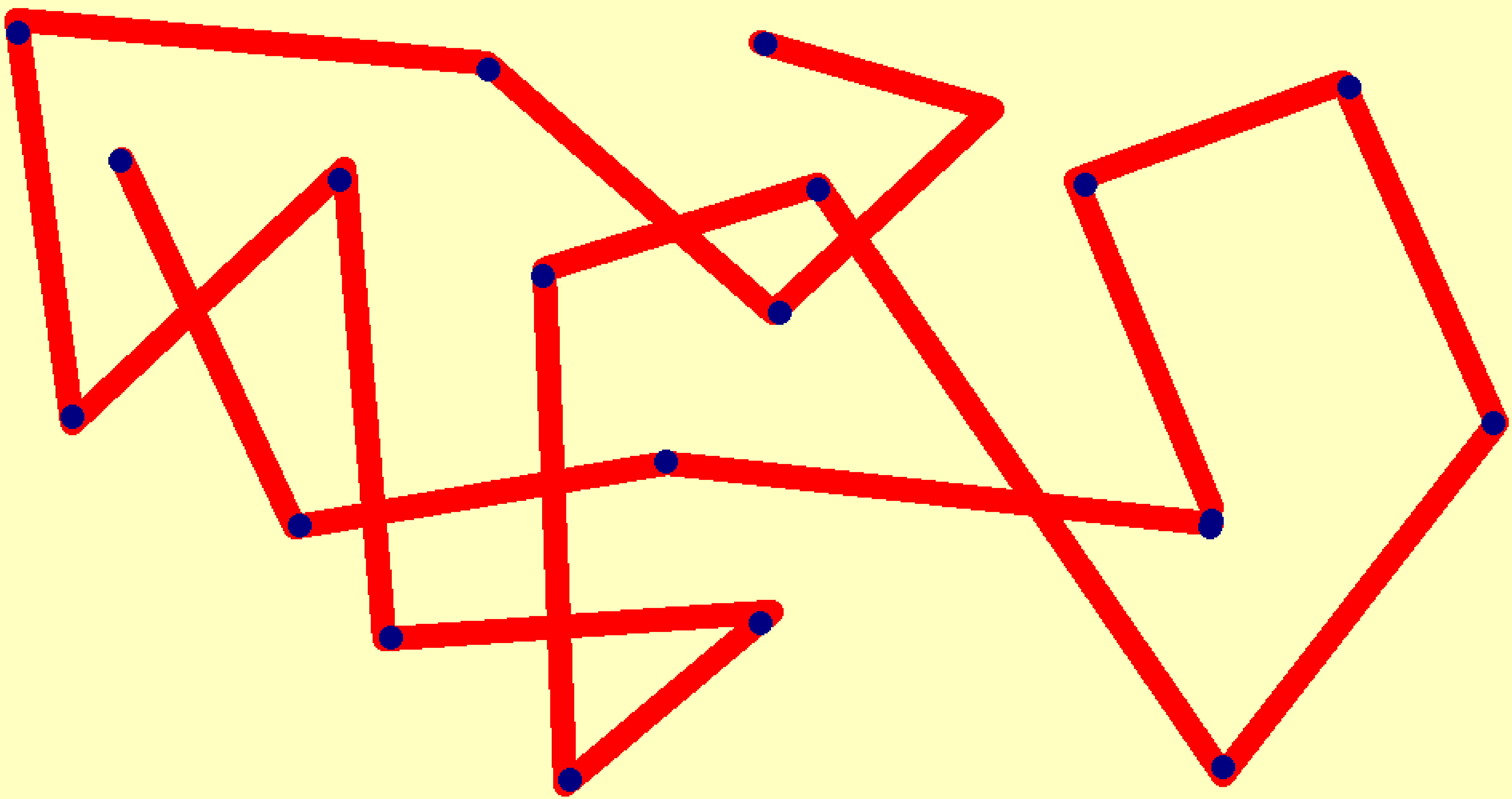


large-scale movement (sequence of visited patches):
- diffusive (random search)
- advective (migration)
- self-constrained (home range)

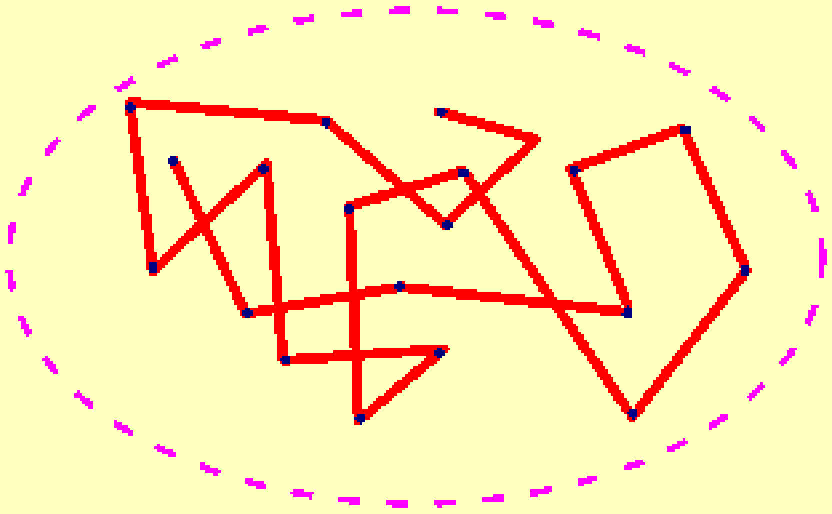
Multi-scale space-use approach



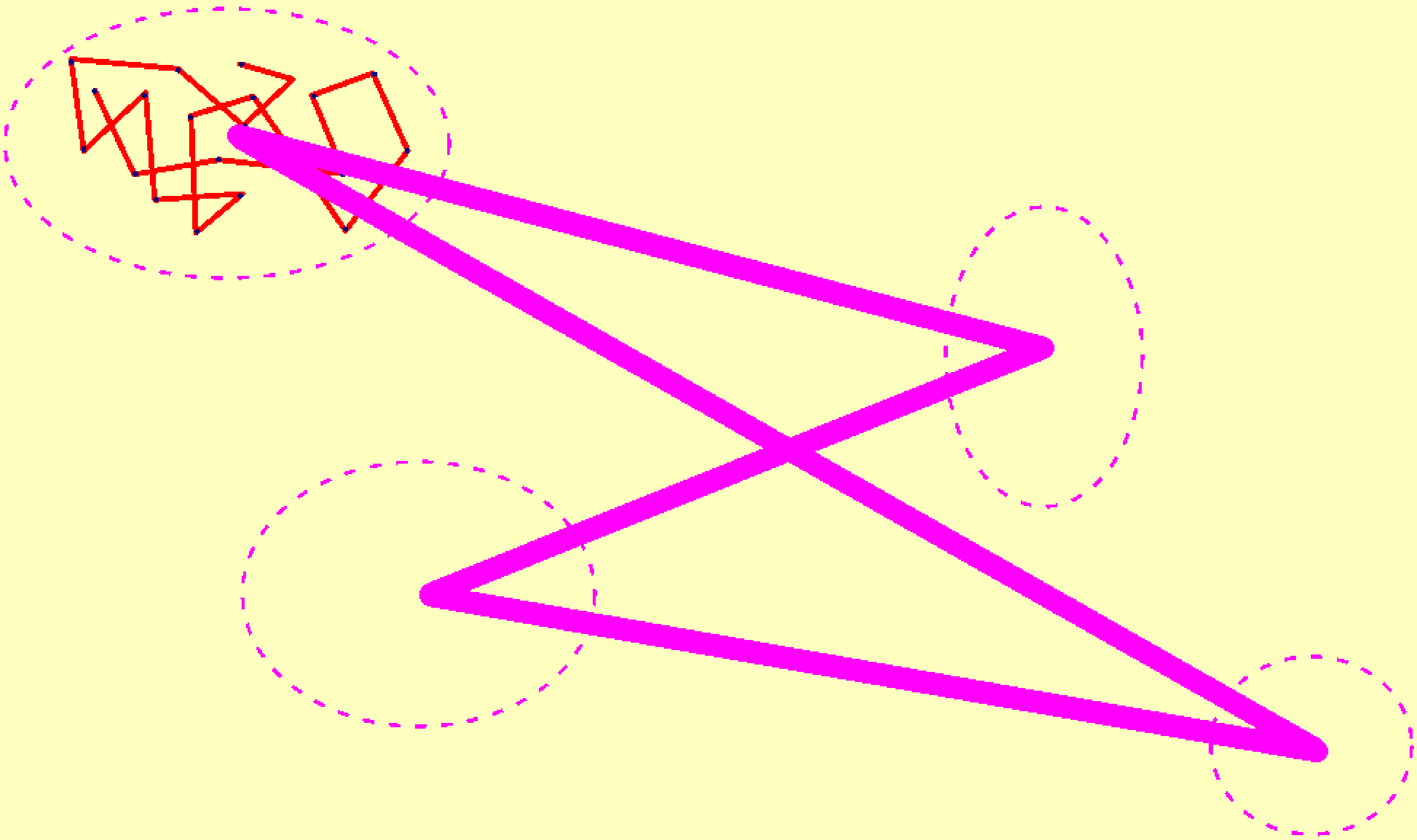
Multi-scale space-use approach



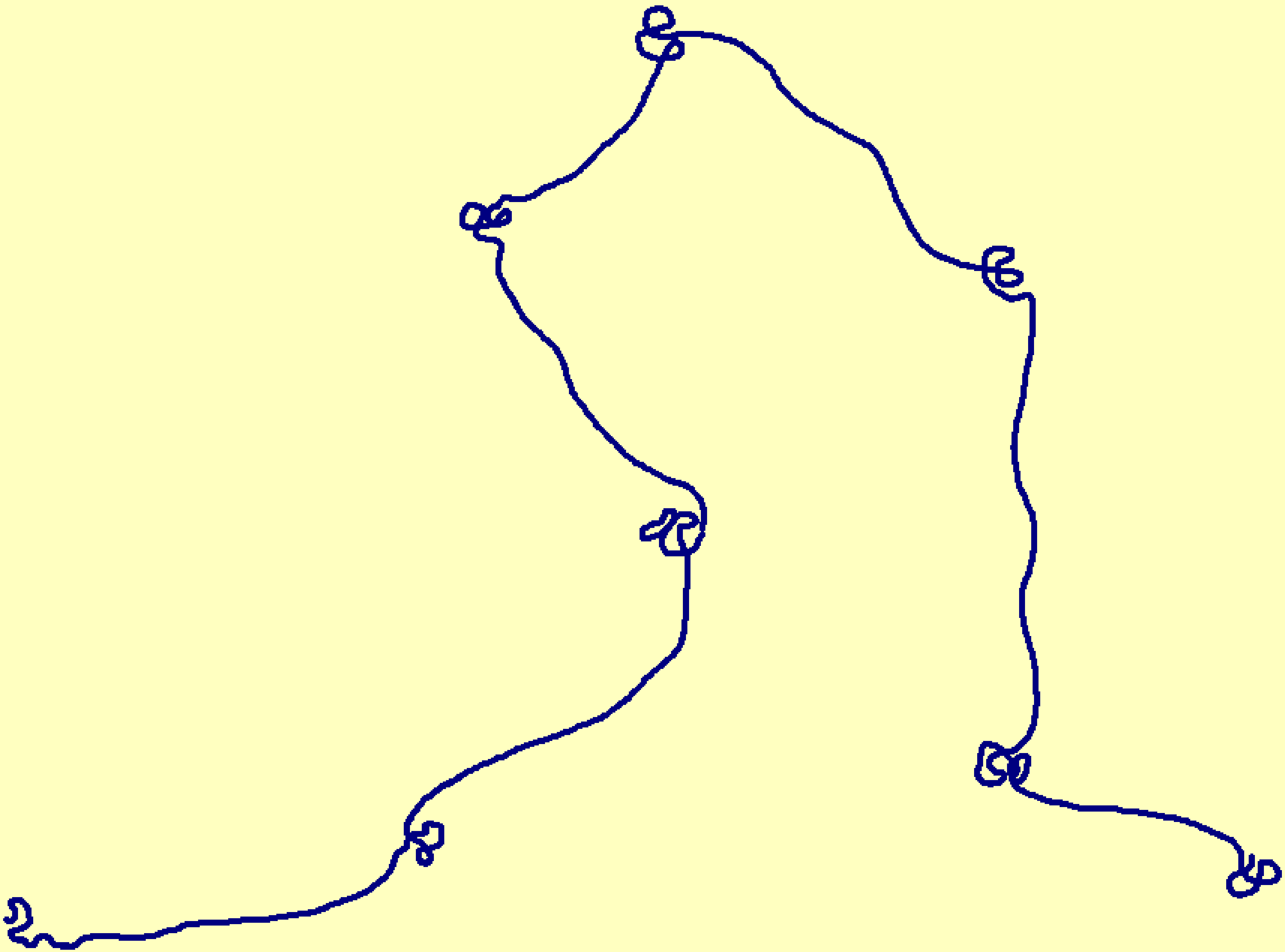
Multi-scale space-use approach

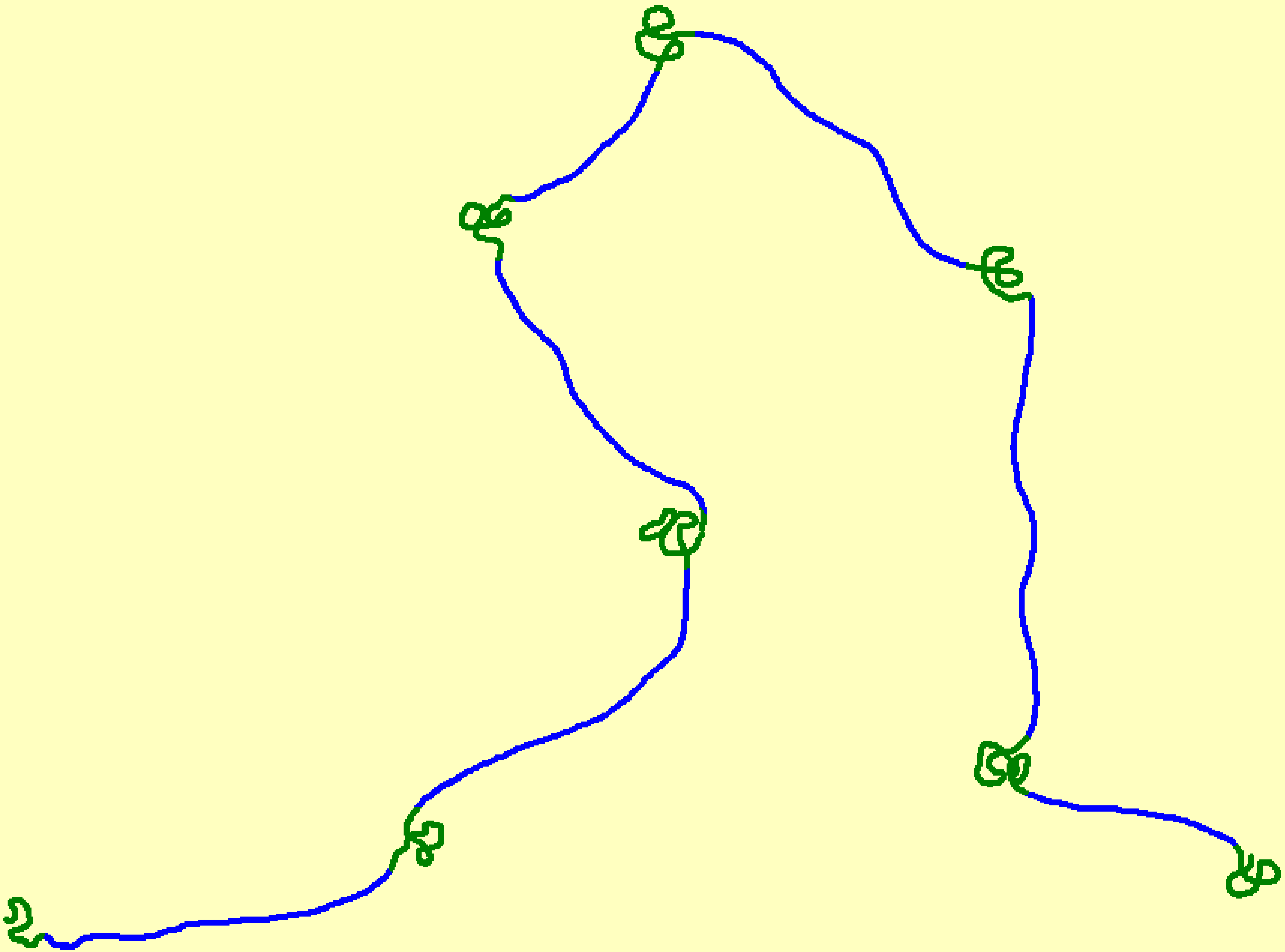


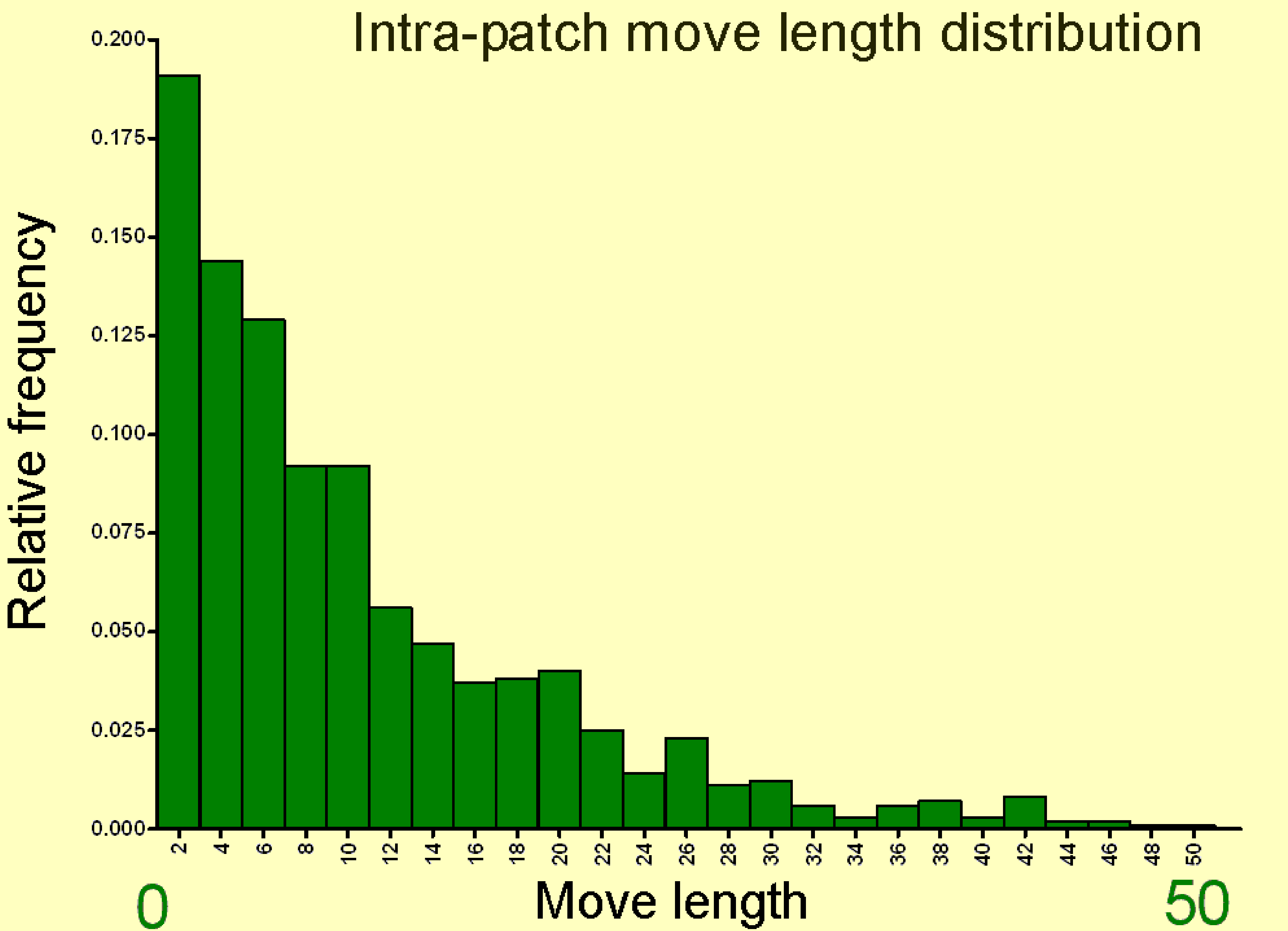
Multi-scale space-use approach



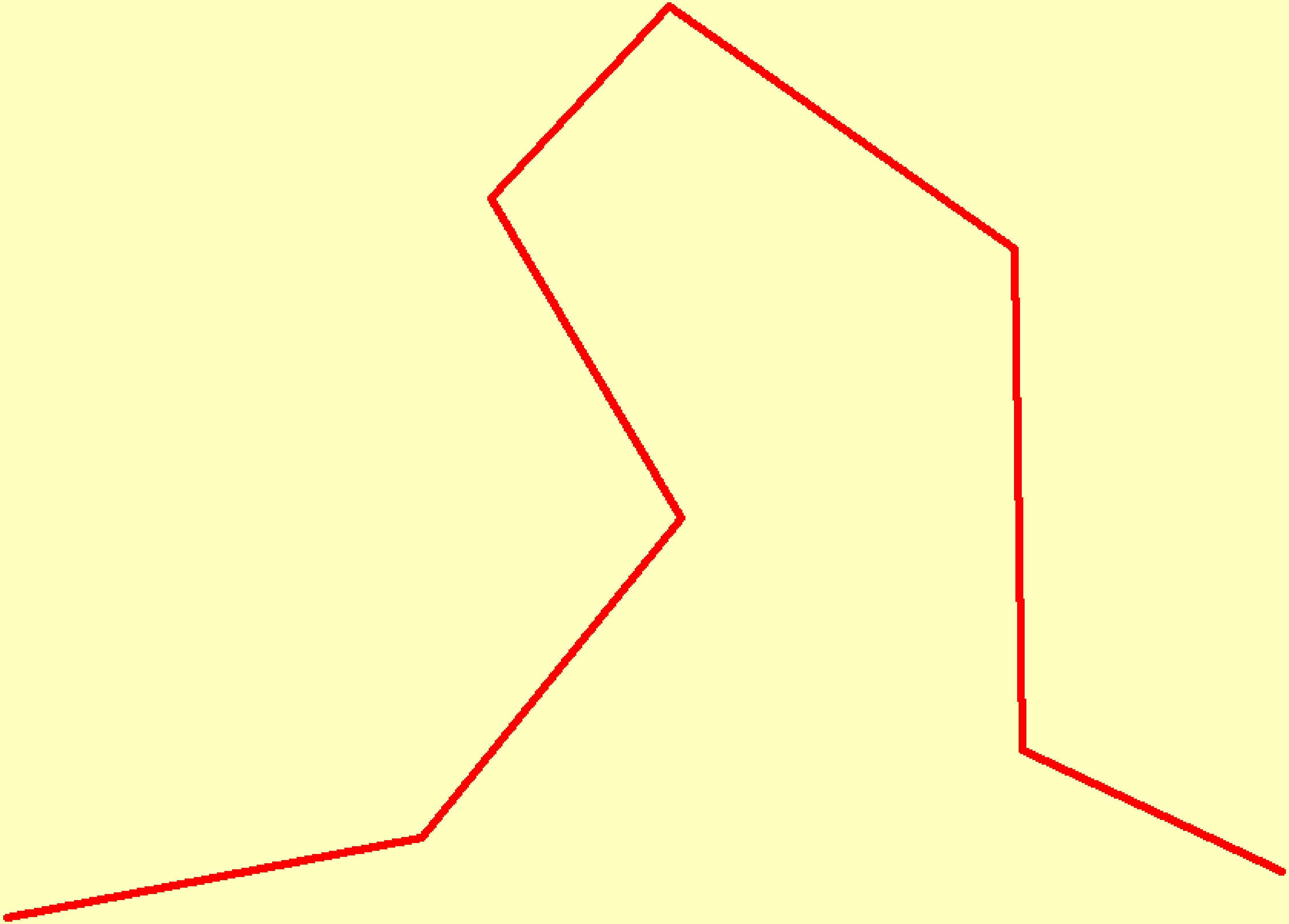
Back to basics

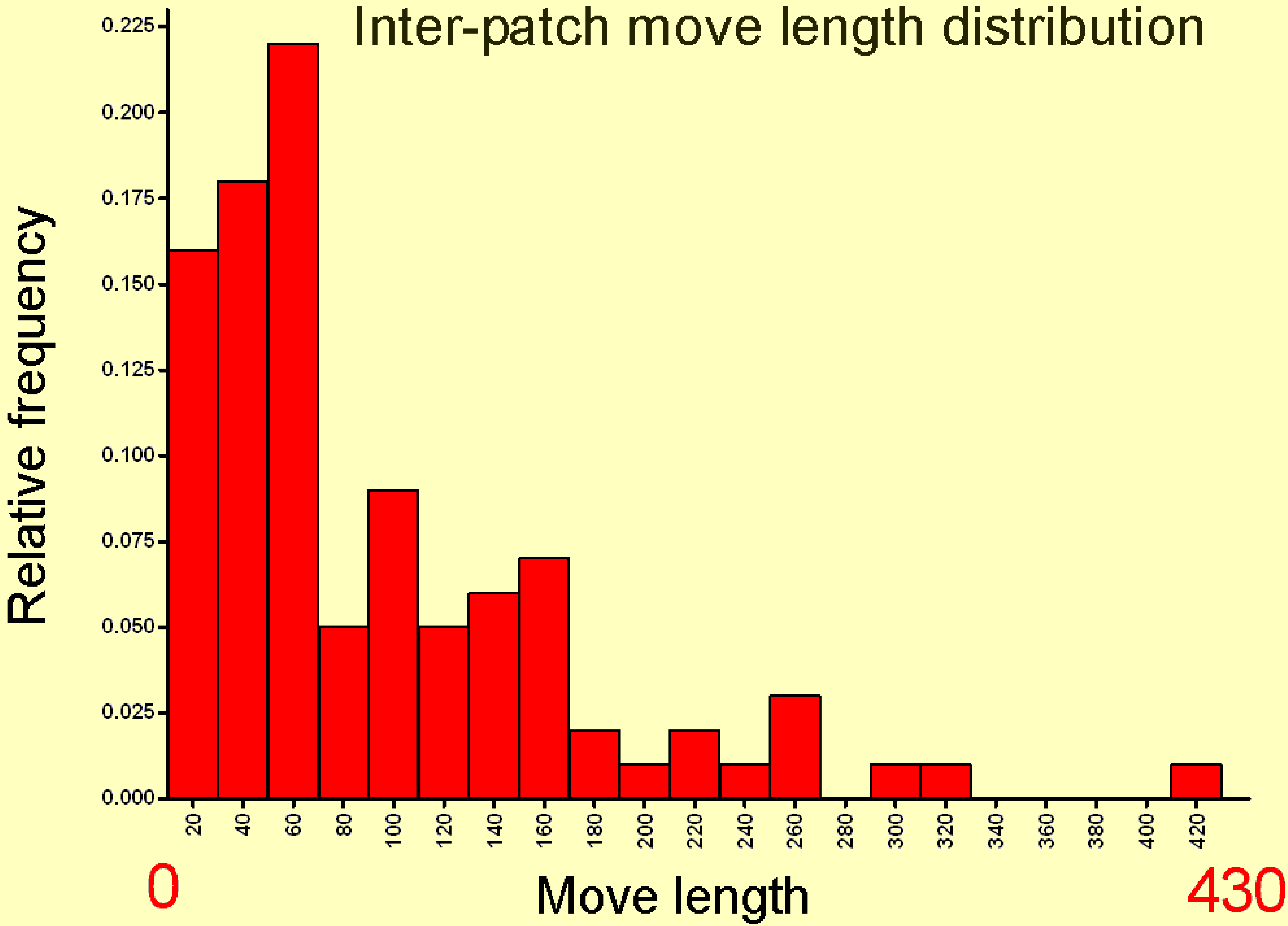




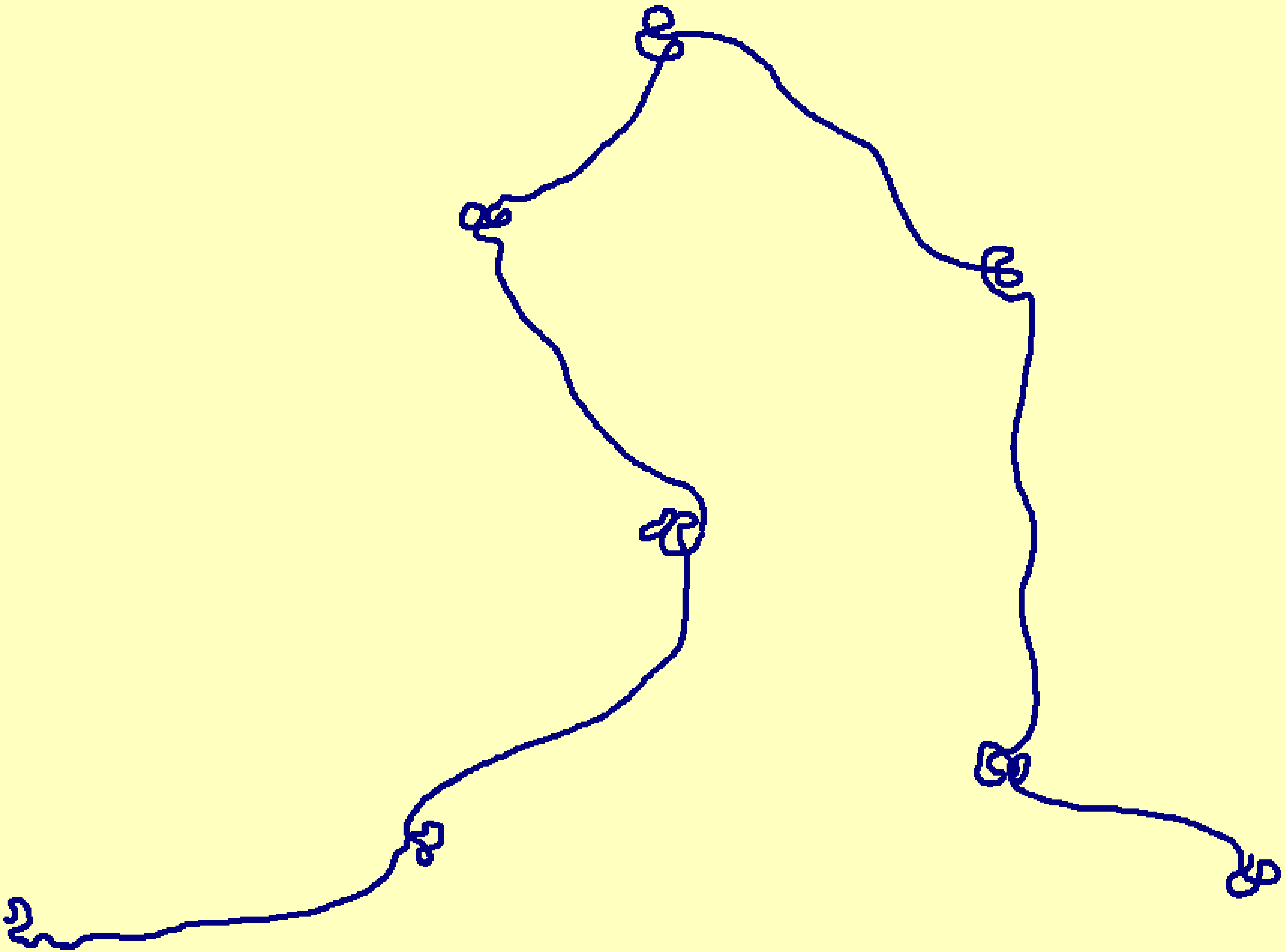


Intra-patch move length distribution
Relative frequency
0.200
0.175
0.150
0.125
0.100
0.075
0.050
0.025
0.000
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
46
48
50
Move length
0
50

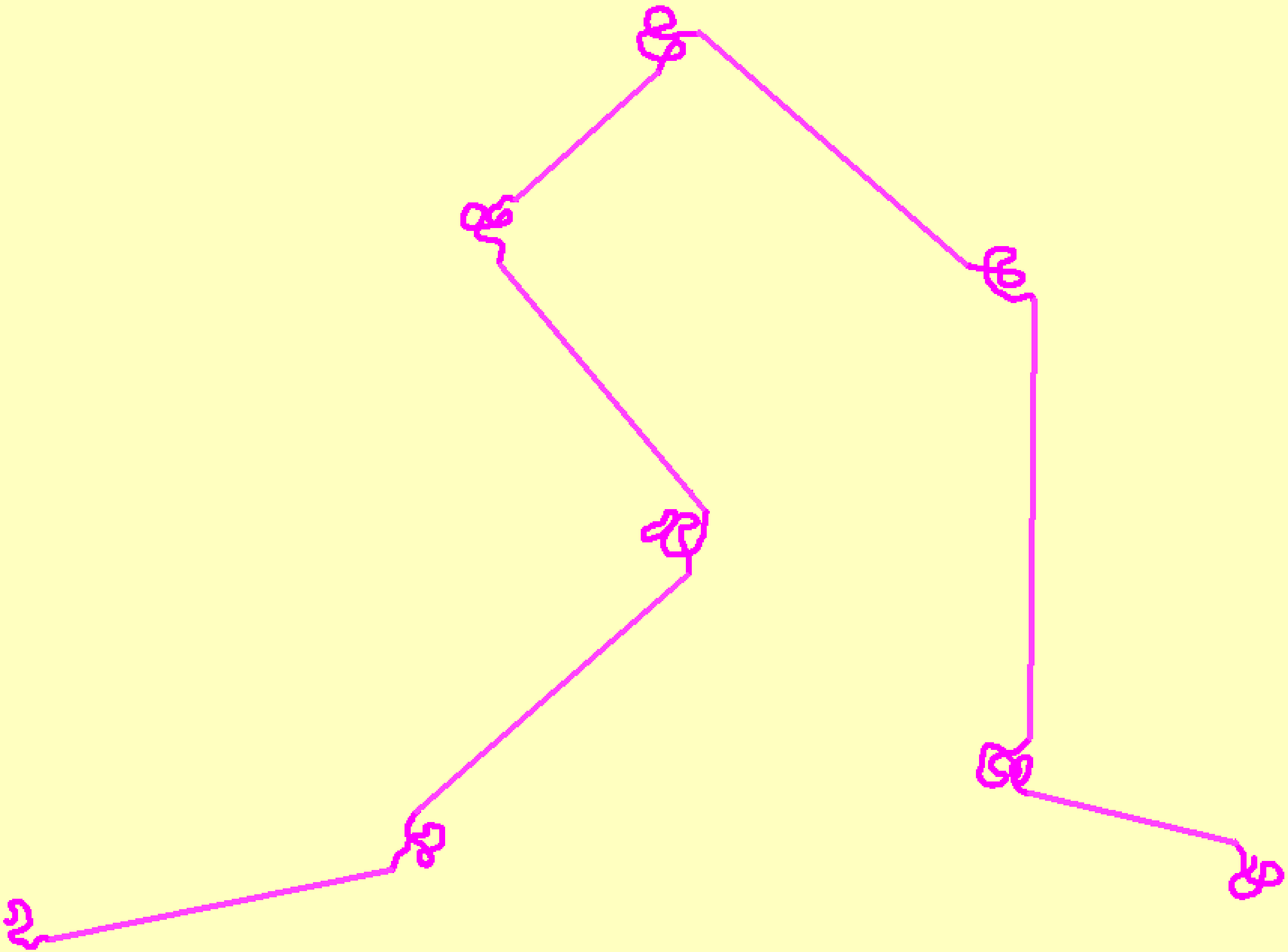



Inter-patch move length distribution
Relative frequency
0.225
0.200
0.175
0.150
0.125
0.100
0.075
0.050
0.025
0.000
20 40 60 80 100 120 140 160 180 200 220 240 260 280 300 320 340 360 380 400 420
0
Move length
430

Using the classical but naïve "significant turn" approach ...

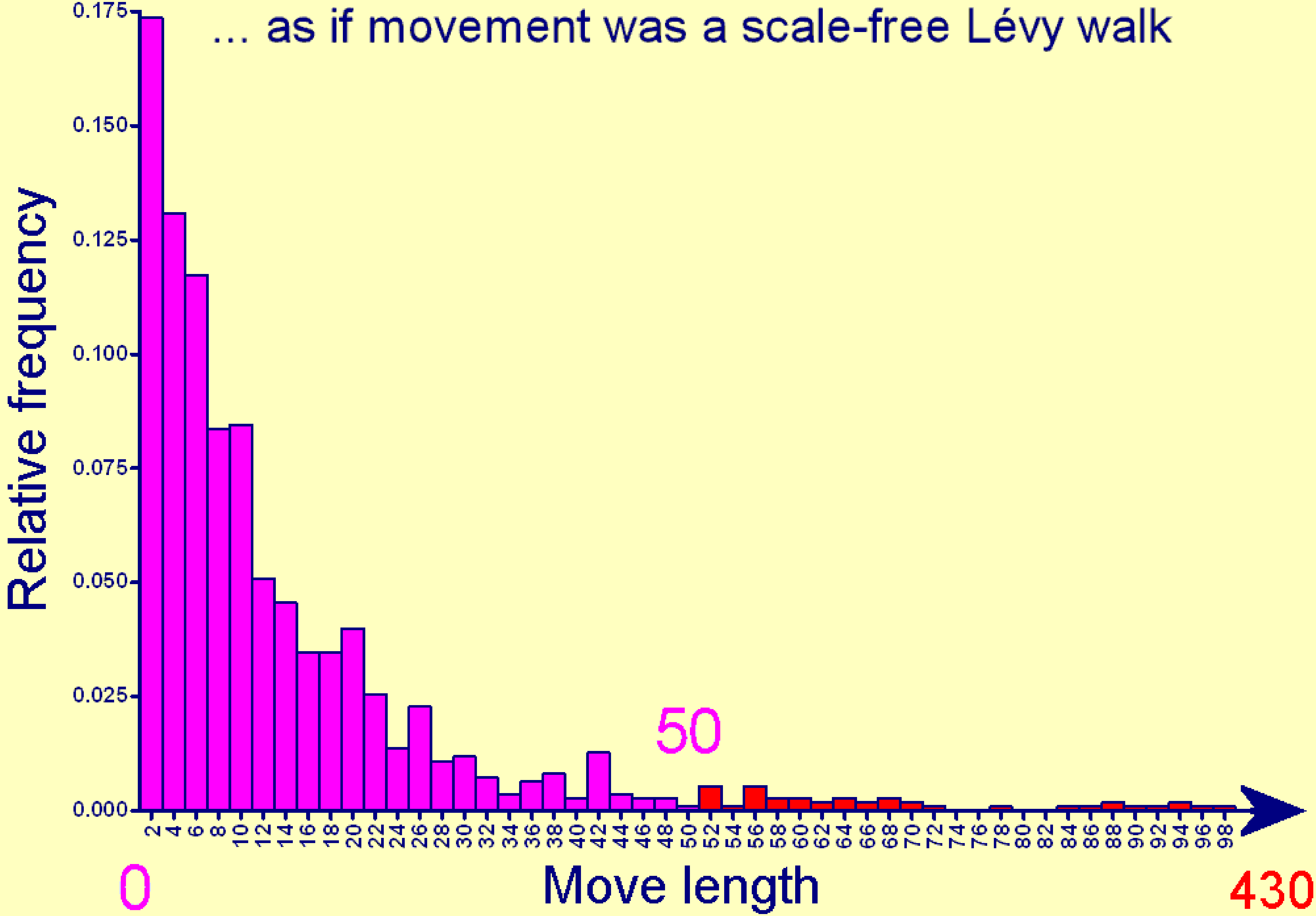


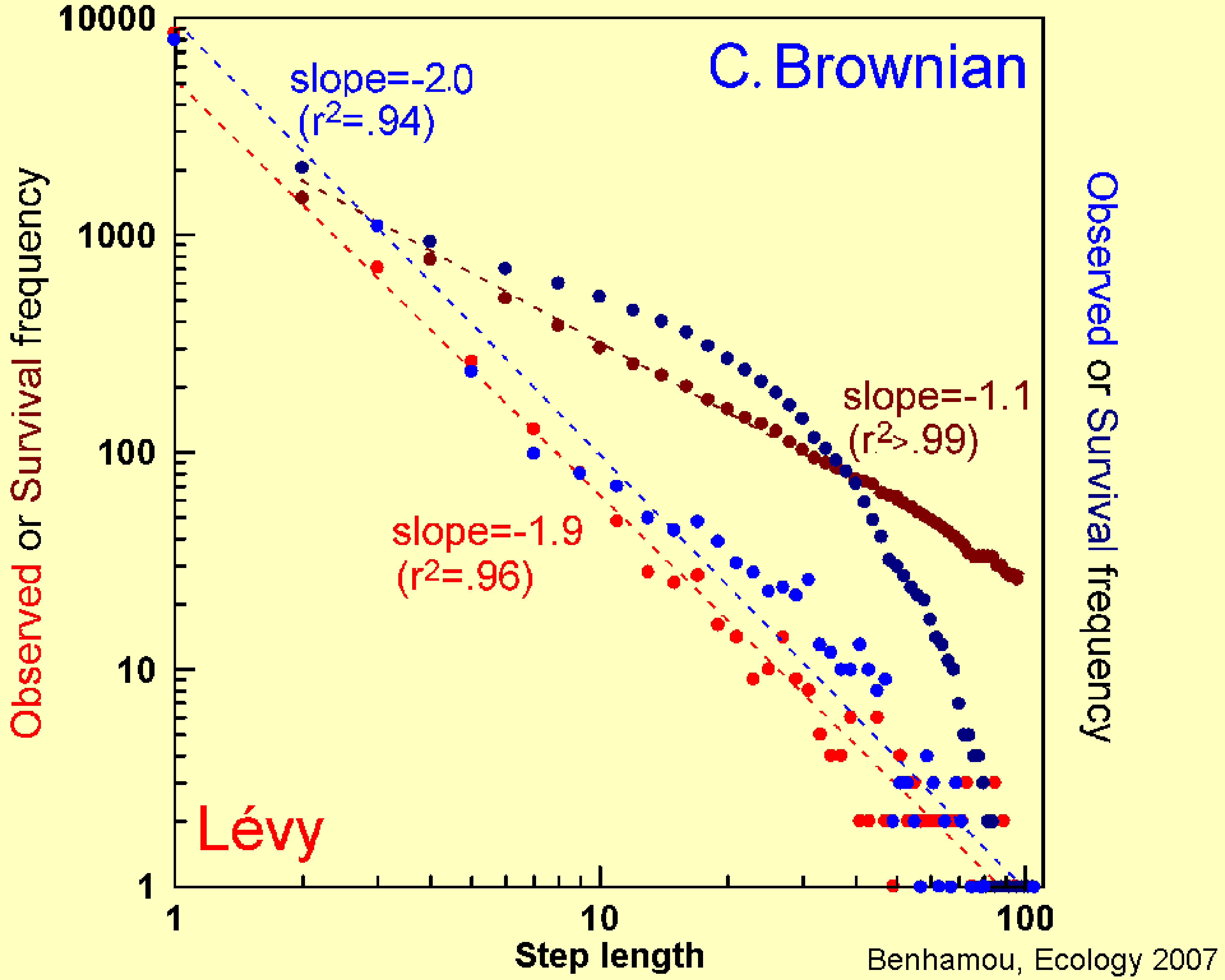
... results in a strange two-mode two-scale mixure

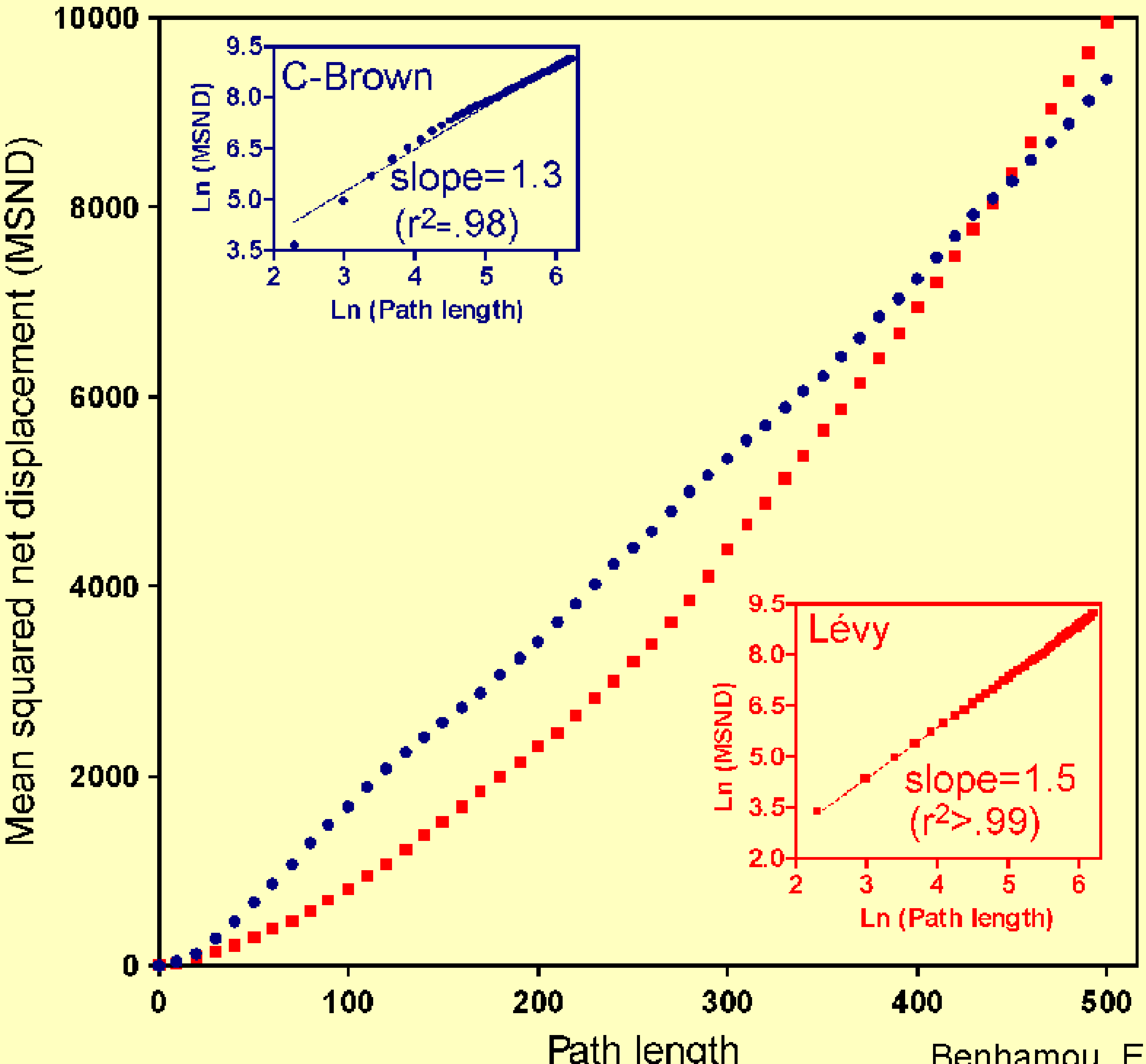


The resutling move length distribution seems to be heavy-tailed

... as if movement was a scale-free Lévy walk

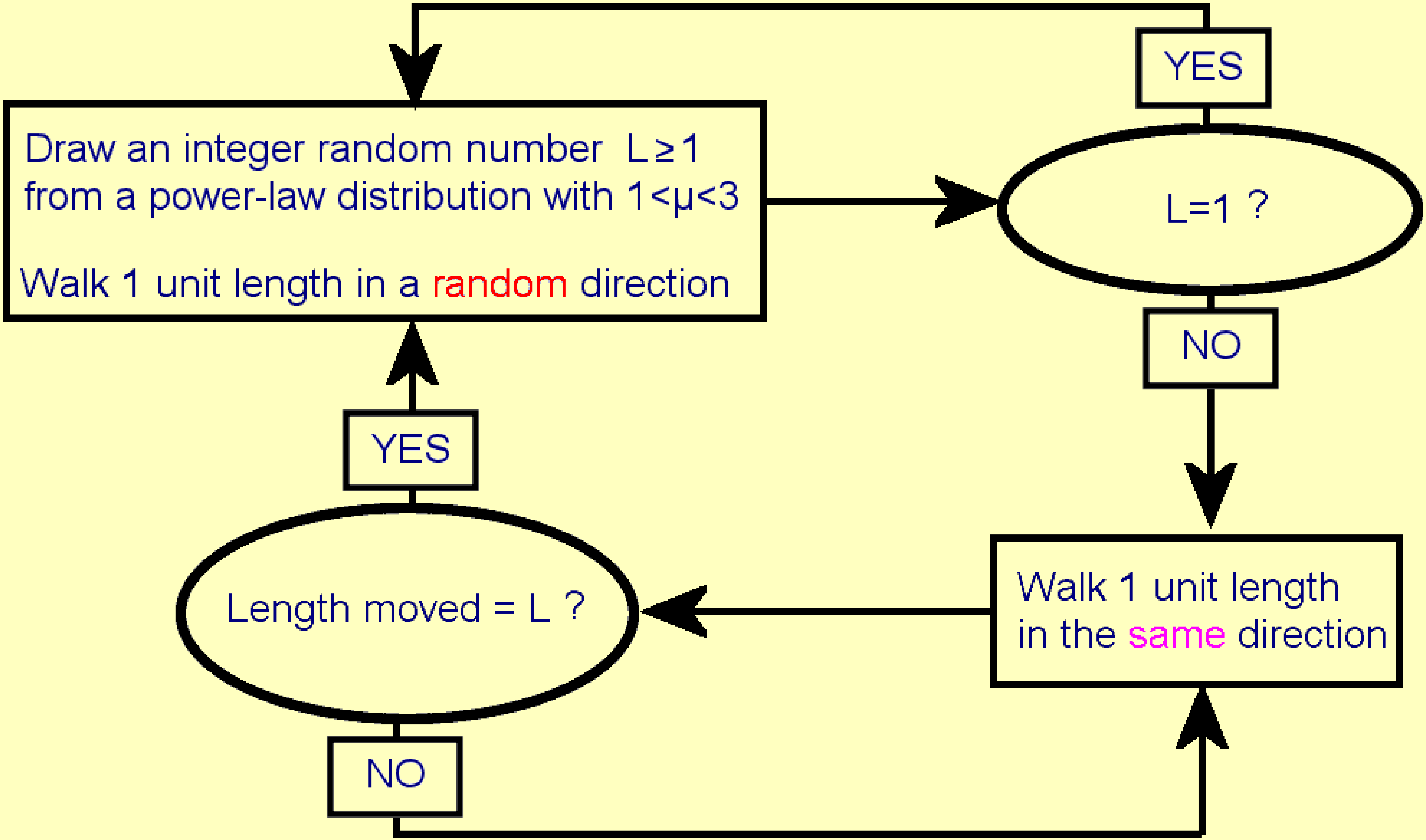



C. Brownian
Lévy
slope=-2.0
(r2=.94)
slope=-1.1
(r2>.99)
slope=-1.9
(r2=.96)
Observed or Survival frequency
Observed or Survival frequency
Step length
10000
1000
100
10
1
1
10
100
Benhamou, Ecology 2007

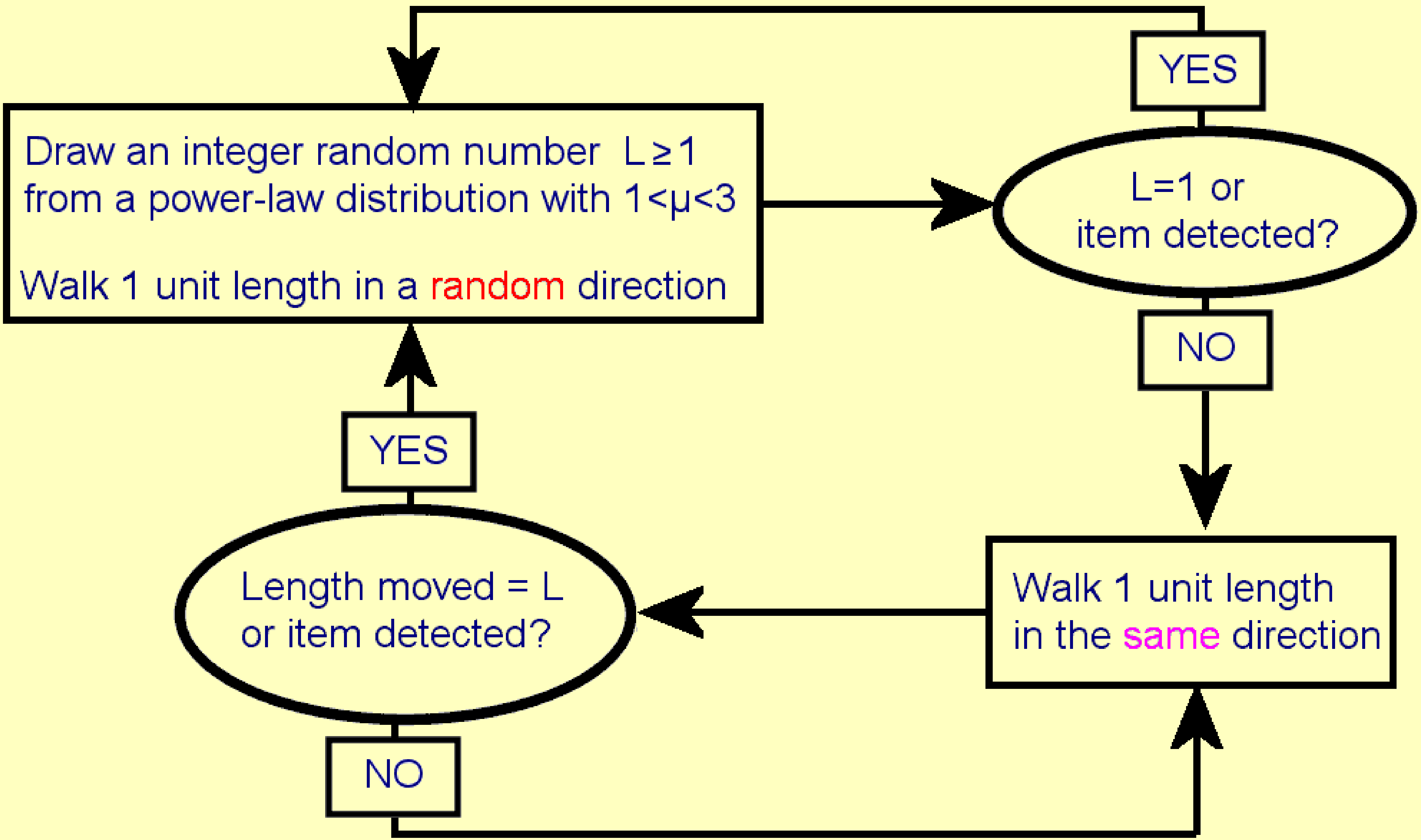


Benhamou, Ecology 2007

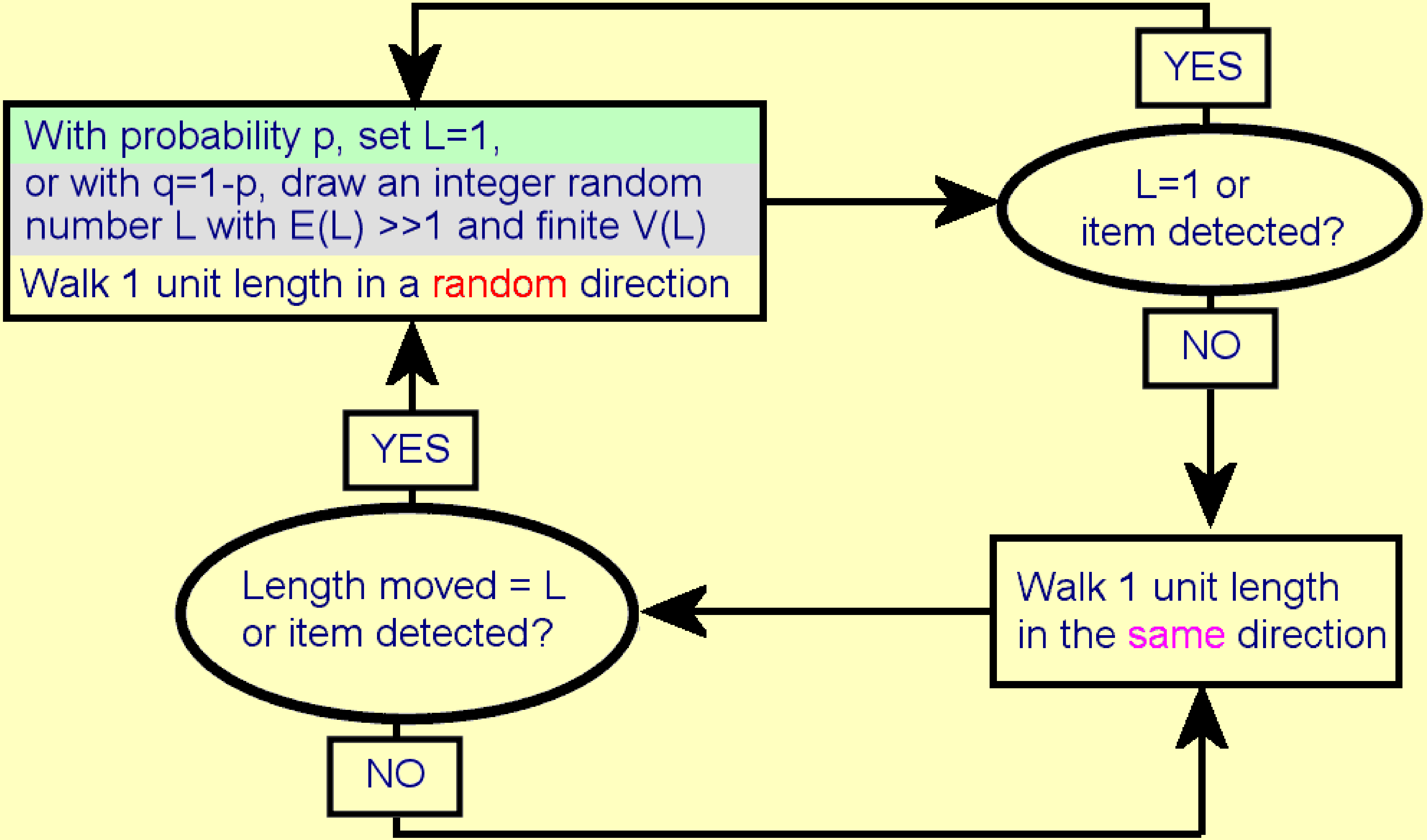
LEVY WALK


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

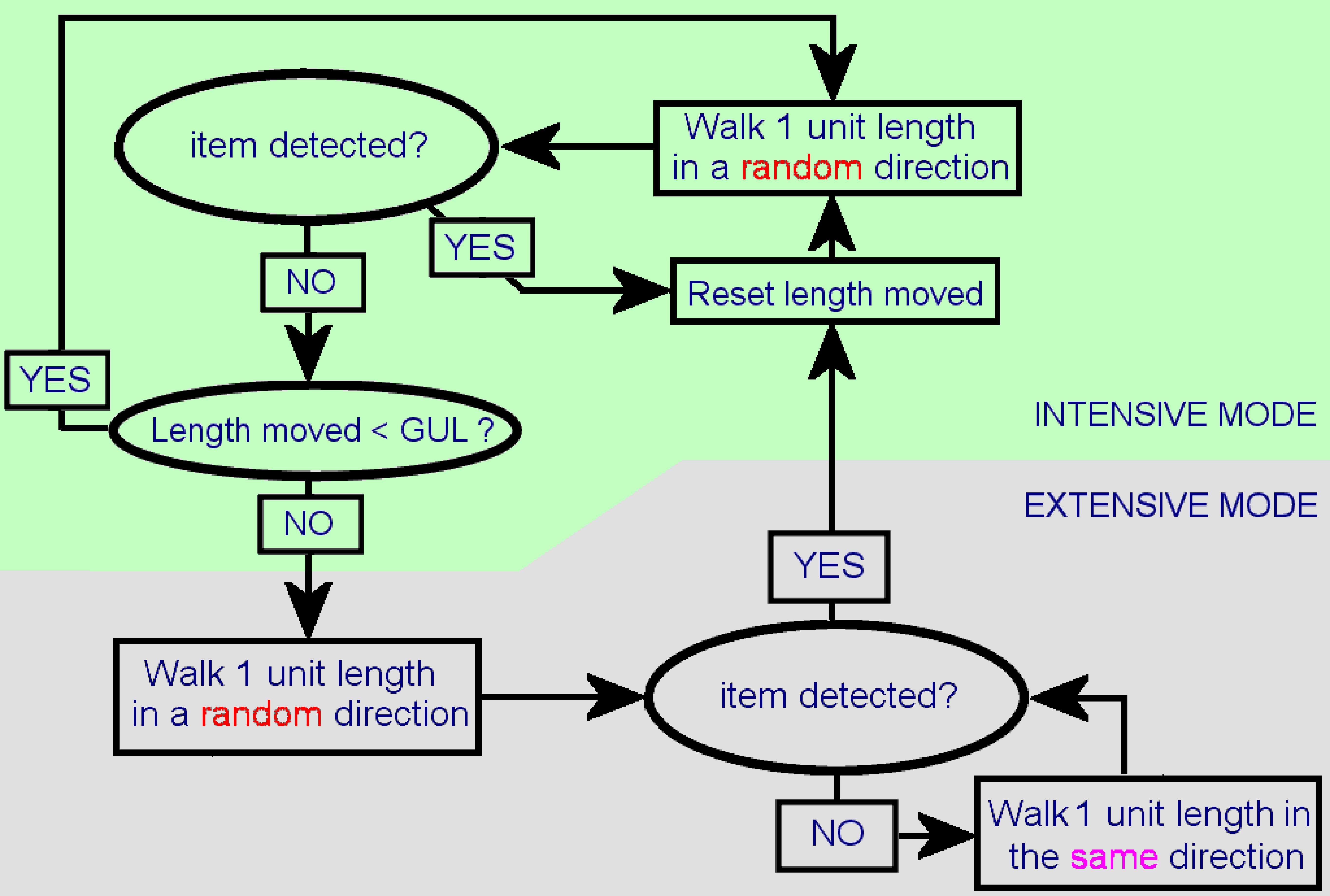
TRUNCATED LEVY WALK



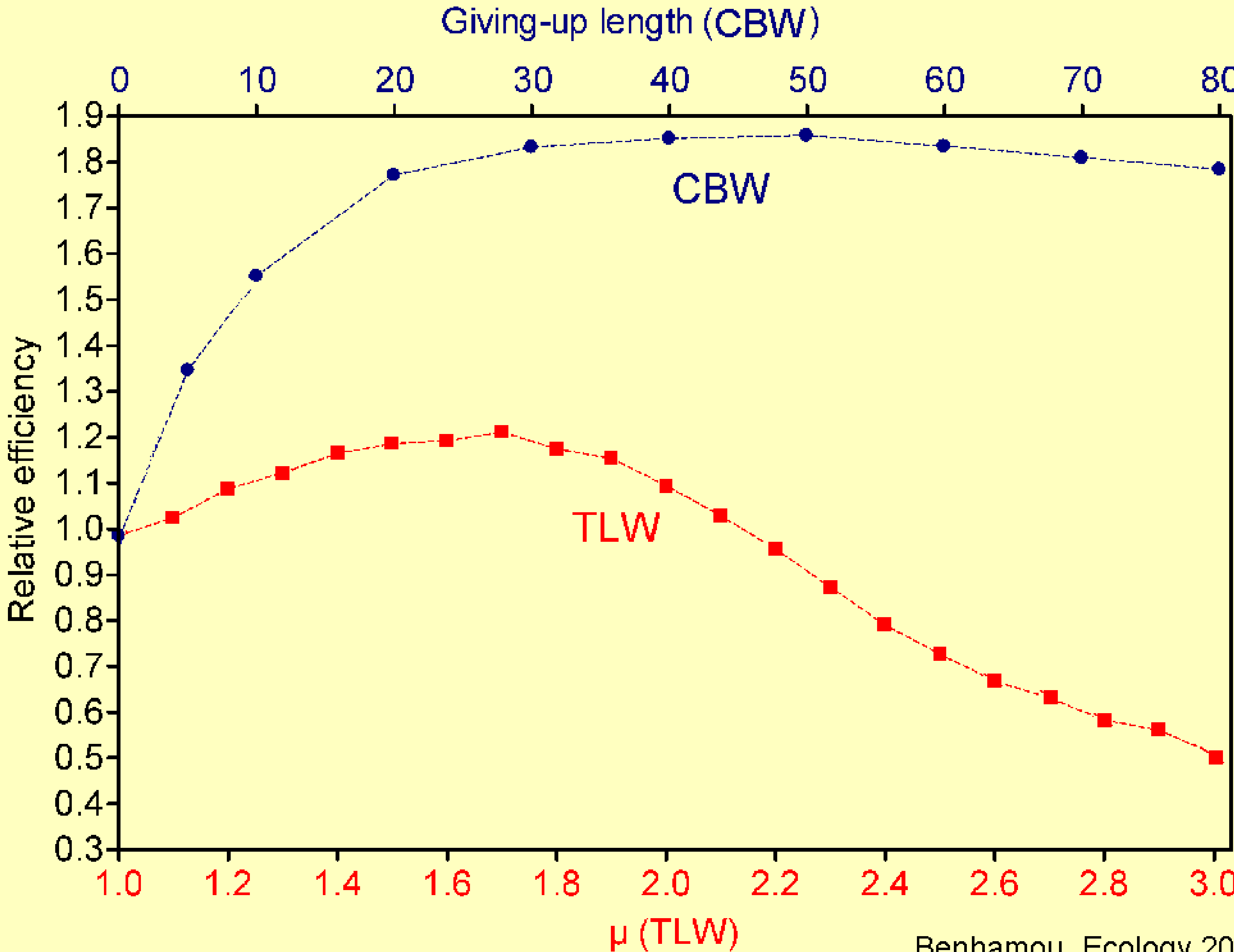
TRUNCATED COMPOSITE BROWNIAN WALK



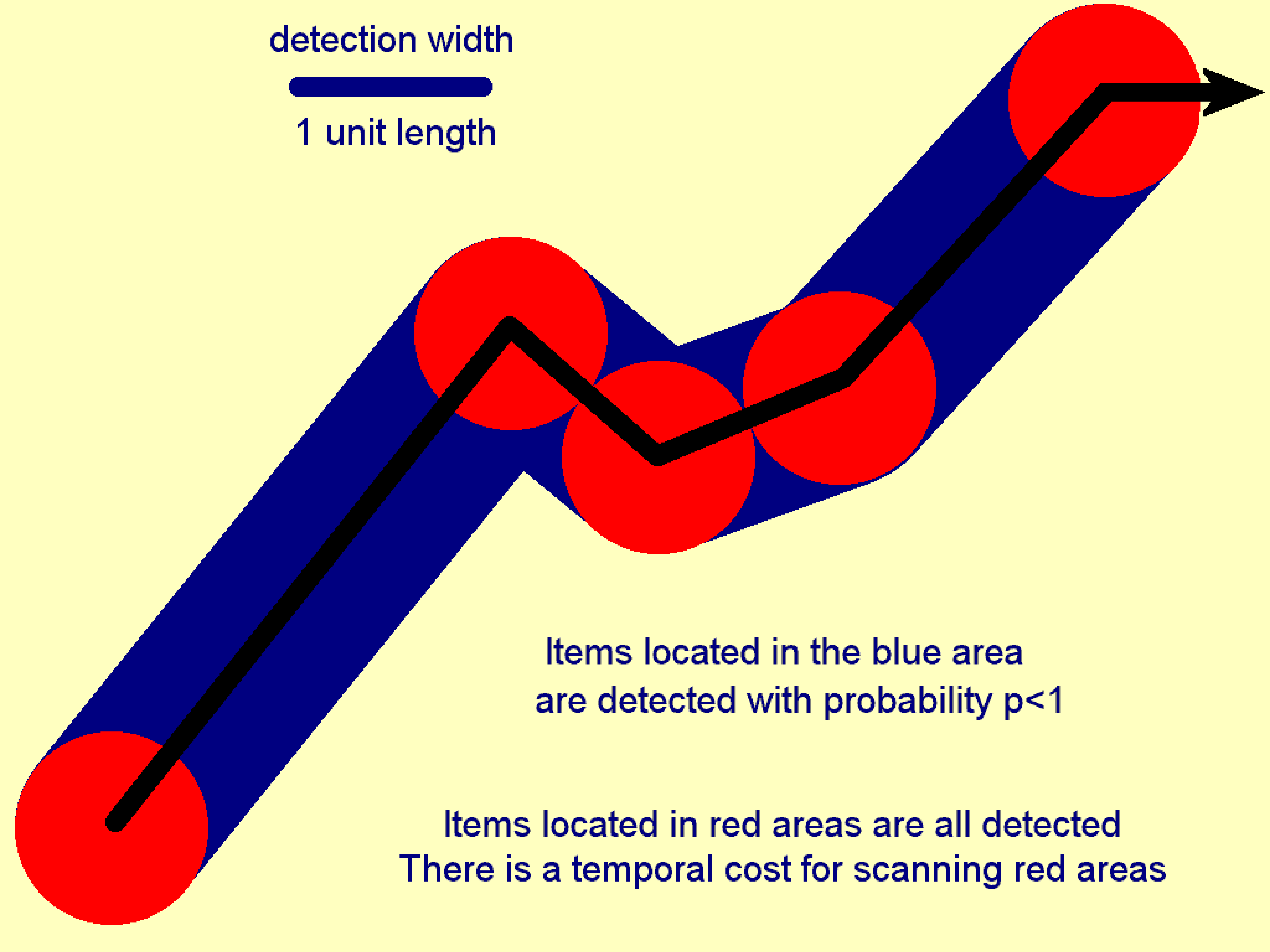
CUE-DRIVEN COMPOSITE BROWNIAN WALK

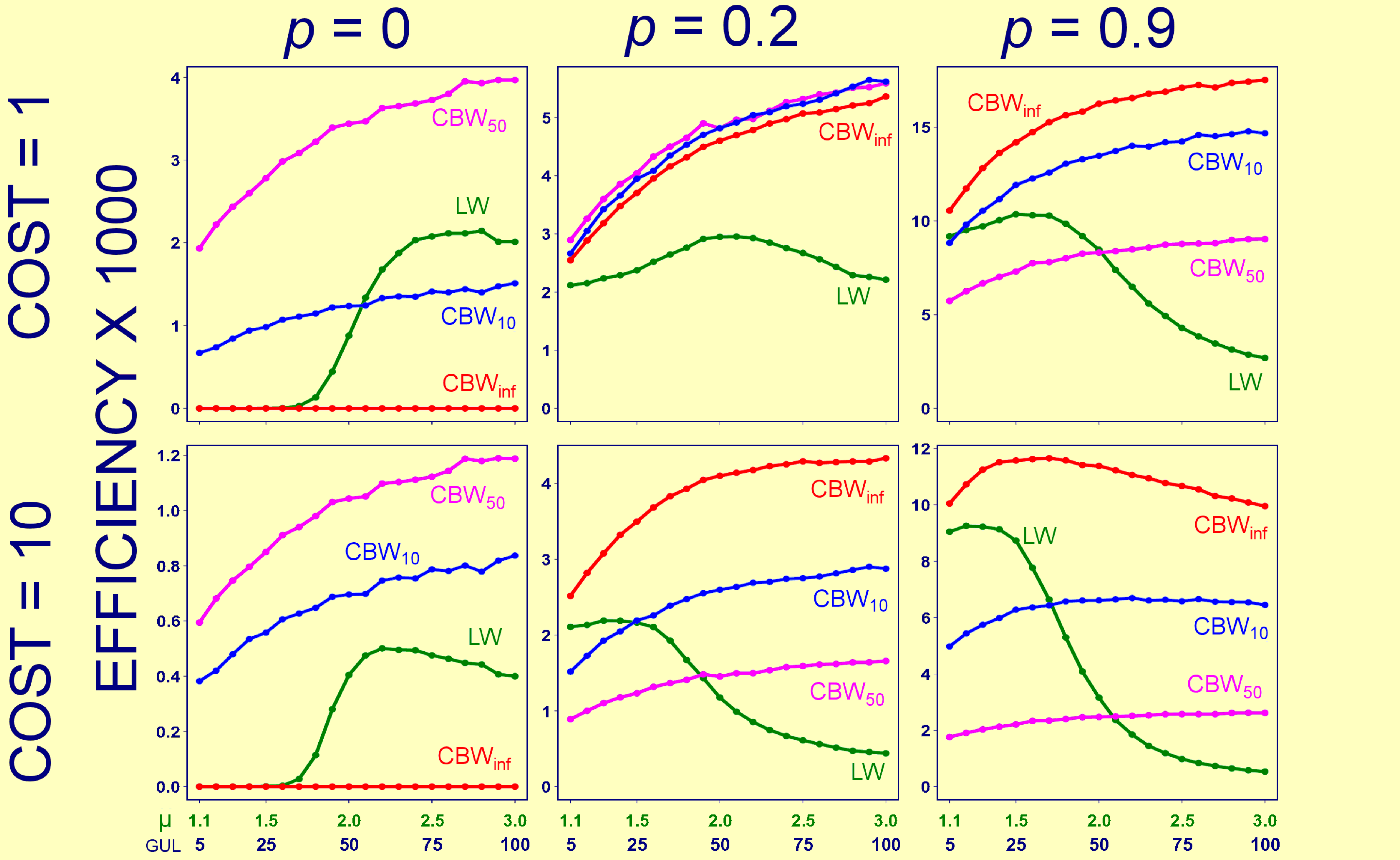



detection width
1 unit length
Items located in the blue area are all detected

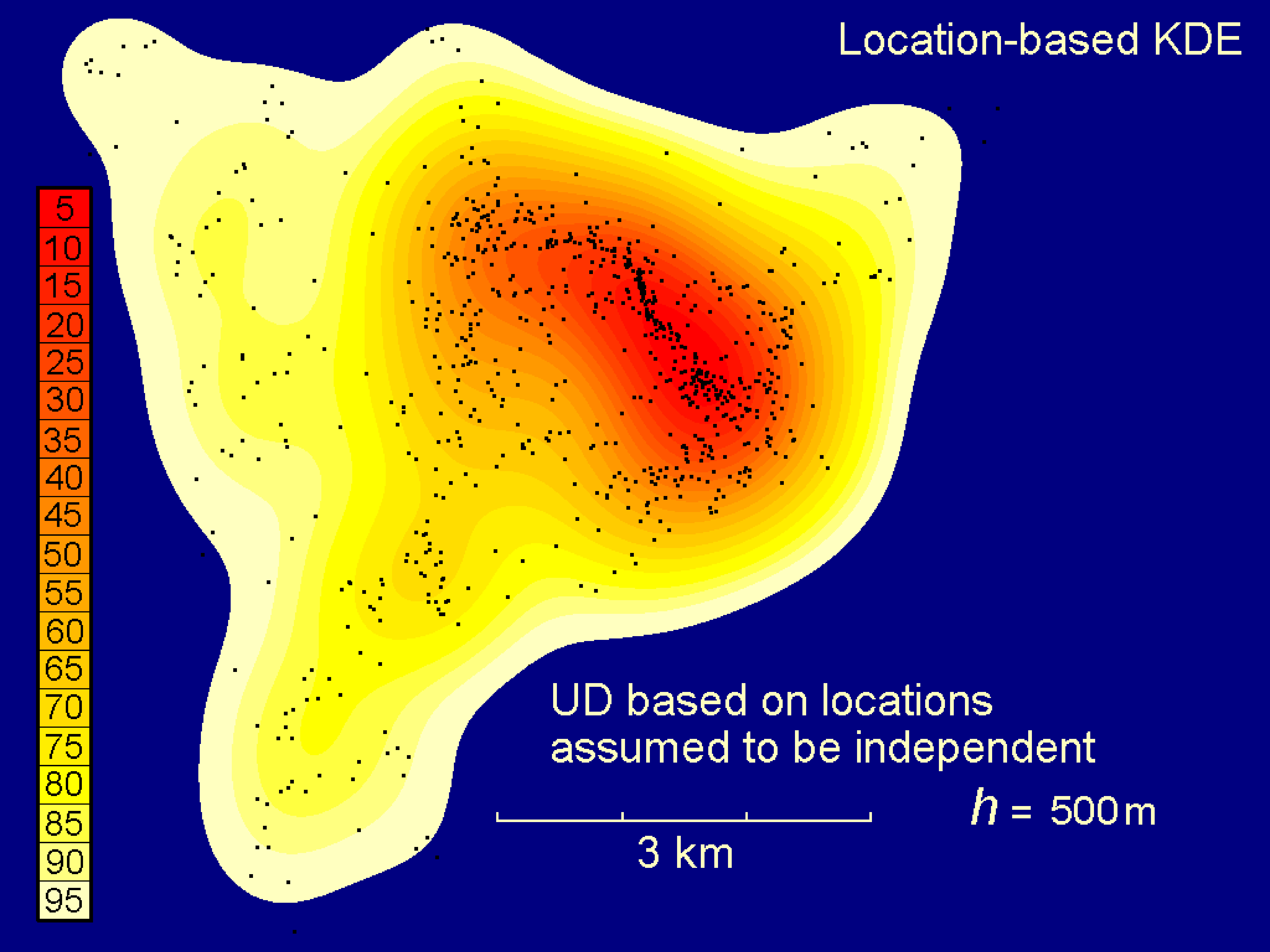


Benhamou, Ecology 2007

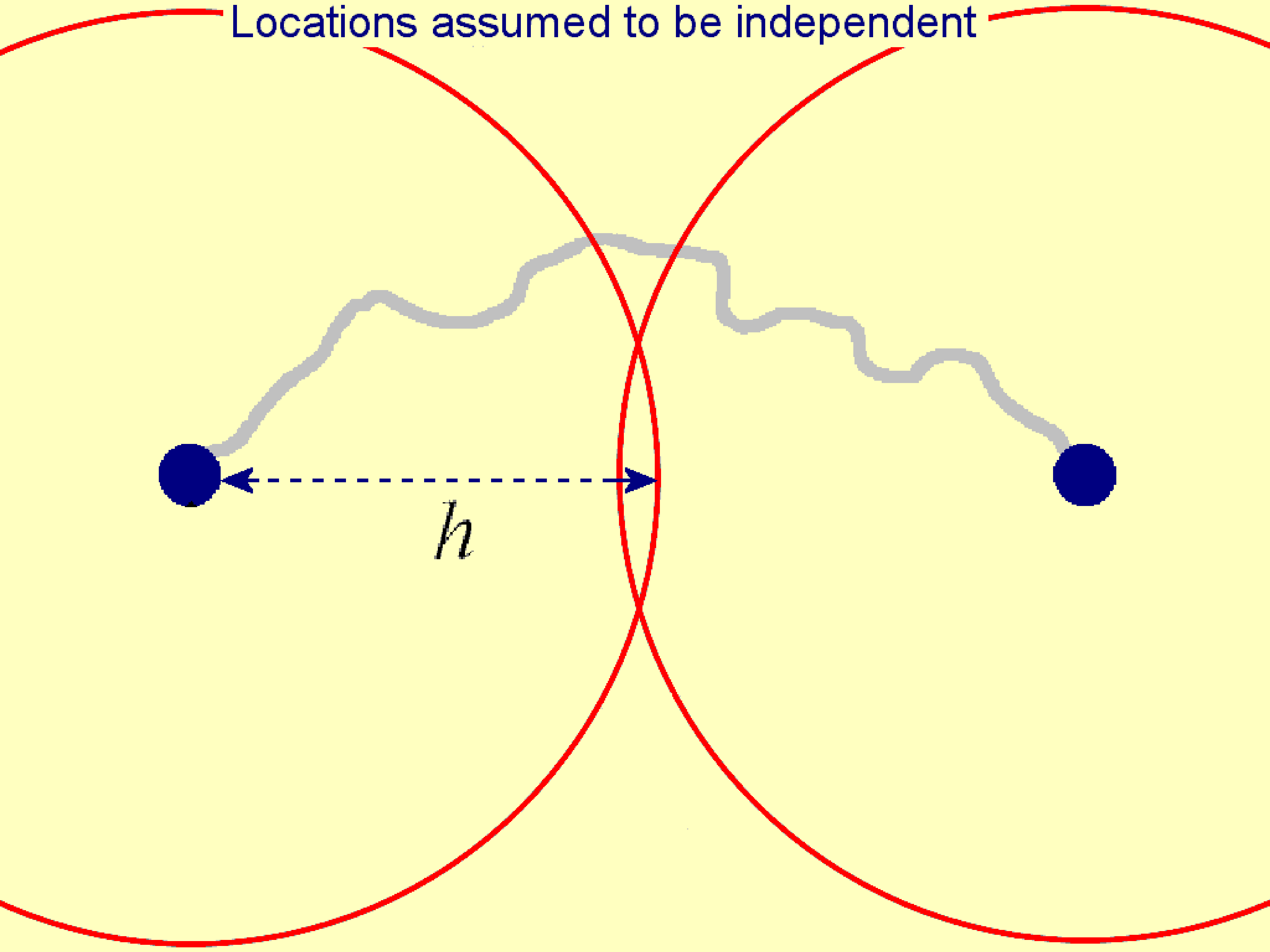

detection width
1 unit length
Items located in the blue area
are detected with probability p<1
Items located in red areas are all detected
There is a temporal cost for scanning red areas



Benhamou & Collet, *J. Theor. Biol.*, 2015

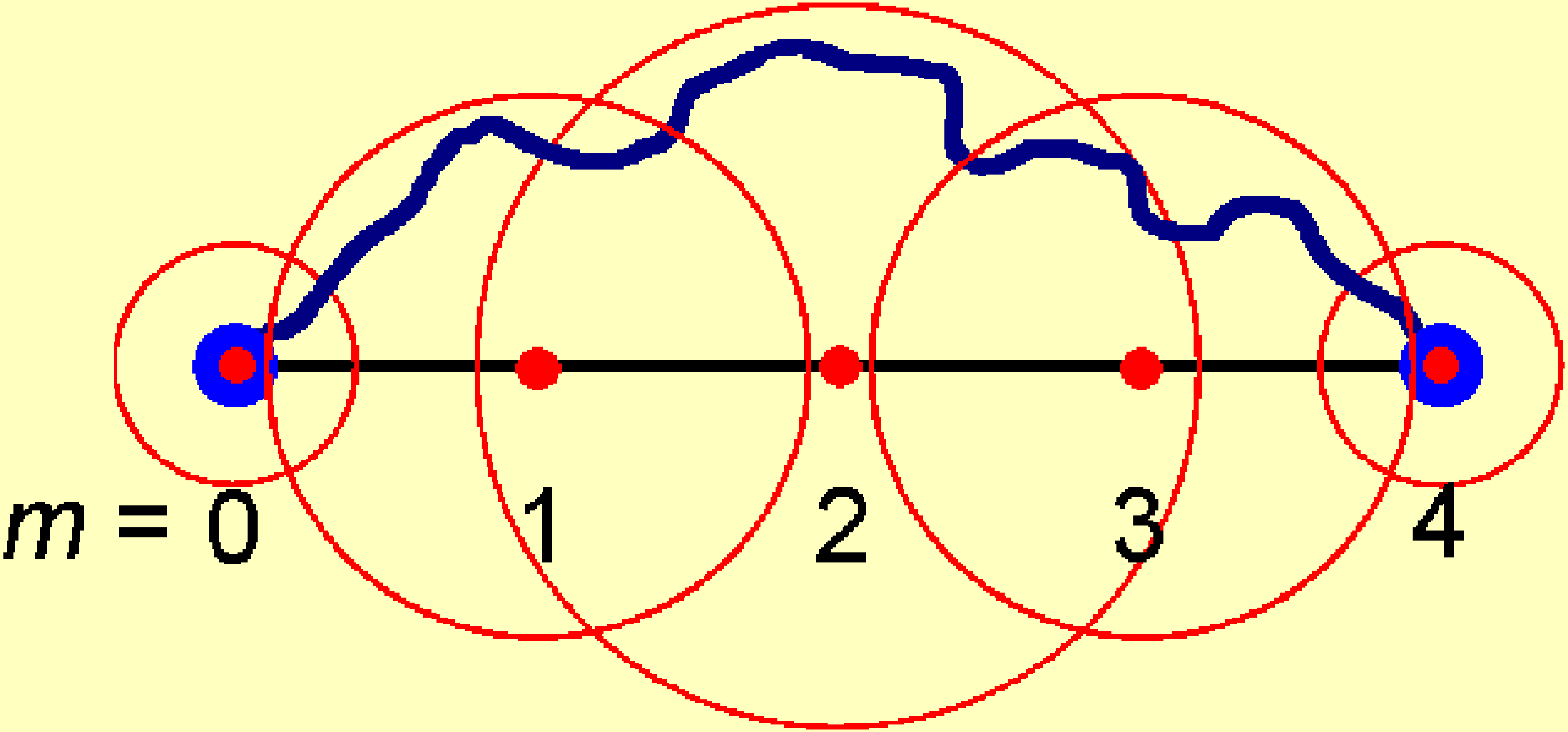


Location-based KDE
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
UD based on locations assumed to be independent
h = 500m
3 km

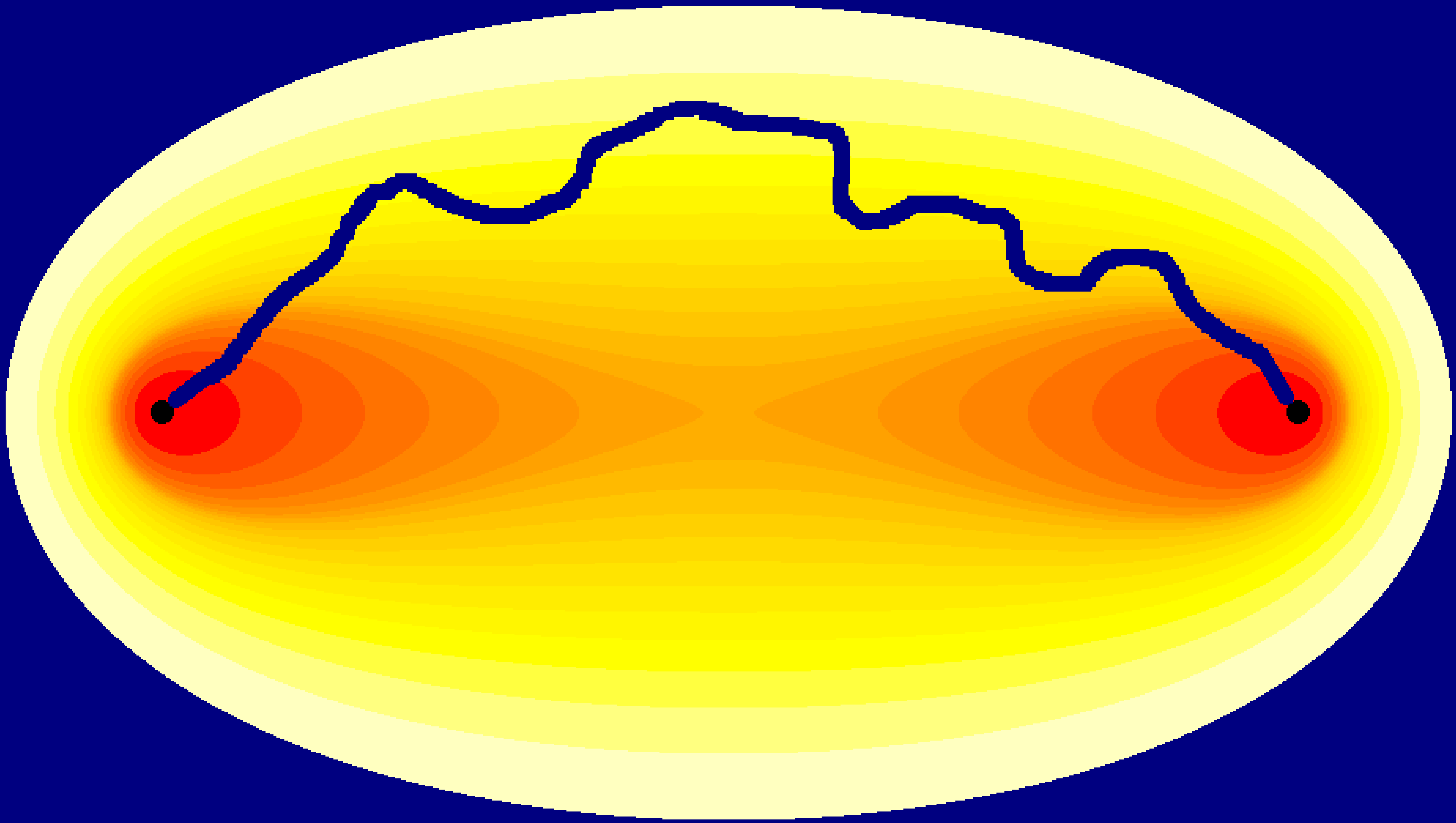

Locations assumed to be independent
h

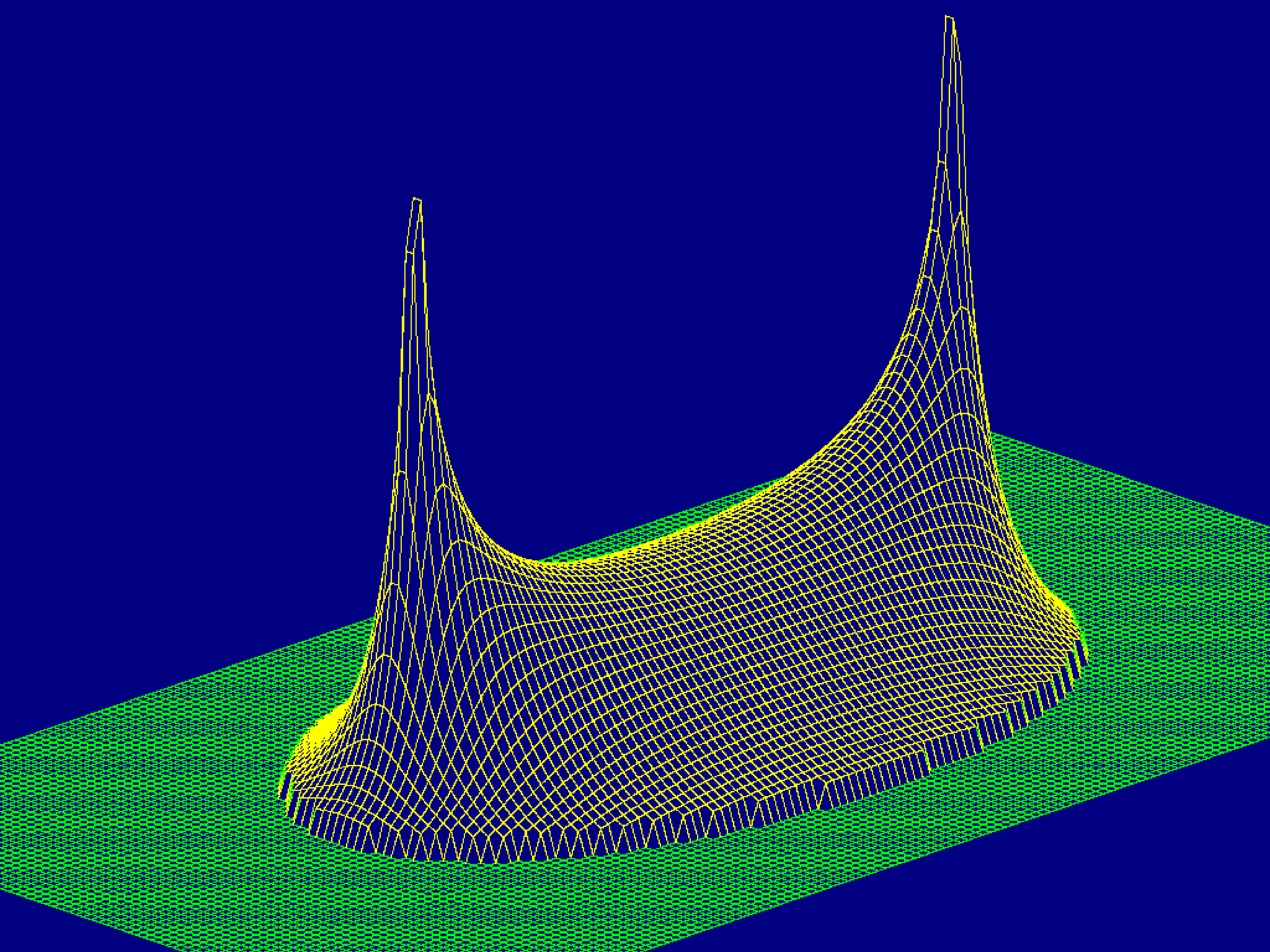
Locations interpolated with a constant activity time

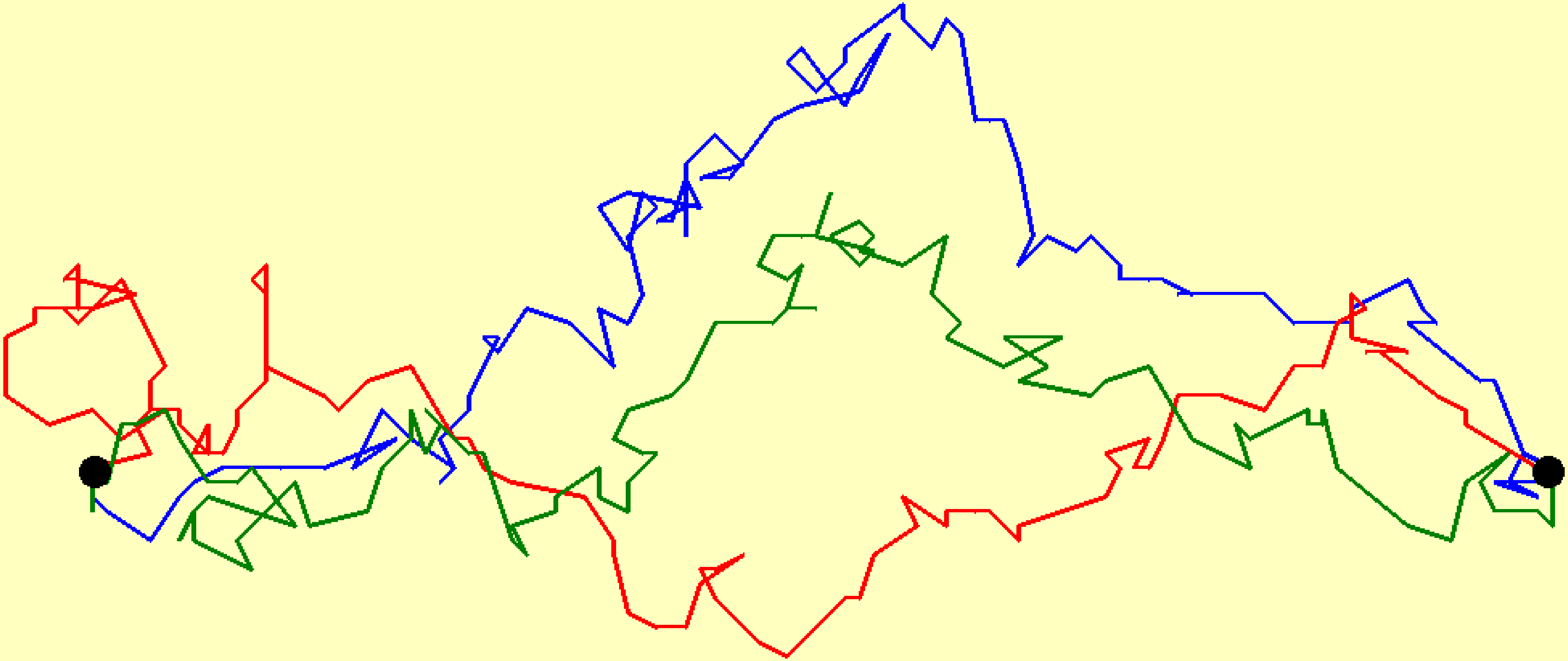
$$h^2(m) = h_{loc}^2 + 2m/n(1 - m/n)DT \qquad n = 4$$



$$u(\mathbf{z}) = \frac{1}{2\pi N} \sum_{i=1}^{N} \frac{1}{h_i^2} \exp\left[-\frac{\left\|\mathbf{z}_i - \mathbf{z}\right\|^2}{2h_i^2} \right]$$







COMPUTATION OF CONDITIONAL PROBABILITIES

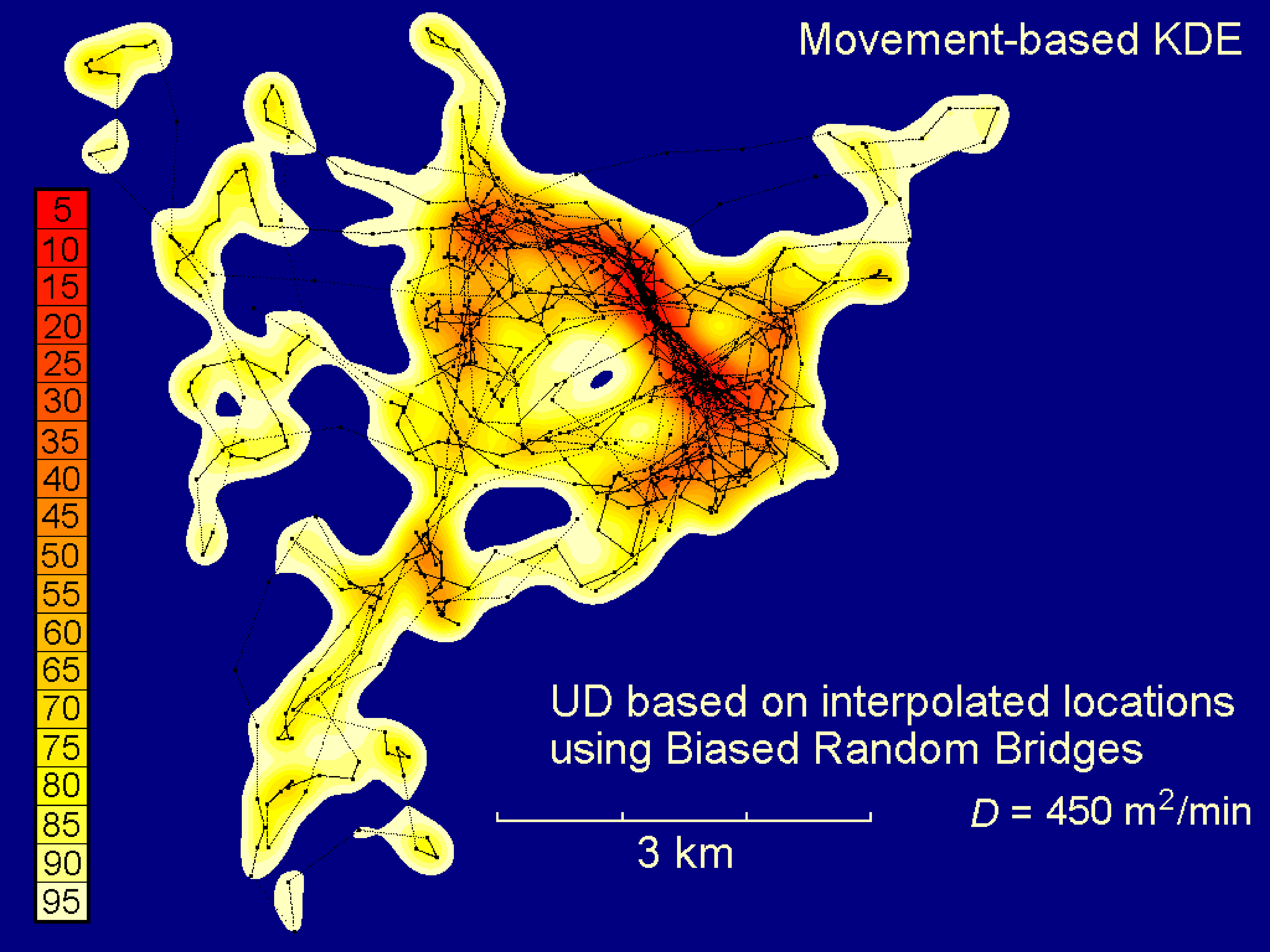
$$\text{Proba}\,(\mathbf{z}_t \mid \mathbf{z}_0, \mathbf{z}_T) = \frac{\text{Proba}\,(\mathbf{z}_t \mid \mathbf{z}_0) \times \text{Proba}\,(\mathbf{z}_T \mid \mathbf{z}_0, \mathbf{z}_t)}{\text{Proba}\,(\mathbf{z}_T \mid \mathbf{z}_0)}$$

$$\text{Proba}\,(\mathbf{z}_t \mid \mathbf{z}_0) = f_W(\mathbf{z}, t \mid \mathbf{z}_0) \sim \mathcal{N}(\mathbf{z}_0 + \mathbf{v}t, 2\mathbf{D}_{\mathbf{xy}}t)$$

$$\text{Proba}\,(\mathbf{z}_T \mid \mathbf{z}_0) = f_W(\mathbf{z}_T, T \mid \mathbf{z}_0) \sim \mathcal{N}(\mathbf{z}_0 + \mathbf{v}T, 2\mathbf{D}_{\mathbf{xy}}T)$$

$$\text{Proba}\,(\mathbf{z}_T \mid \mathbf{z}_0, \mathbf{z}_t) = f_W(\mathbf{z}_T, T-t \mid \mathbf{z}) \sim \mathcal{N}(\mathbf{z} + \mathbf{v}(T-t), 2\mathbf{D}_{\mathbf{xy}}(T-t))$$

$$\text{Proba}\,(\mathbf{z}_t \mid \mathbf{z}_0, \mathbf{z}_T) = f_B(\mathbf{z}, t \mid \mathbf{z}_0, \mathbf{z}_T) \sim \mathcal{N}(\mathbf{z}_0 + (\mathbf{z}_T - \mathbf{z}_0)t/T, 2\mathbf{D}_{\mathbf{xy}}t(1-t/T))$$



Movement-based KDE
5
10
15
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25
30
35
40
45
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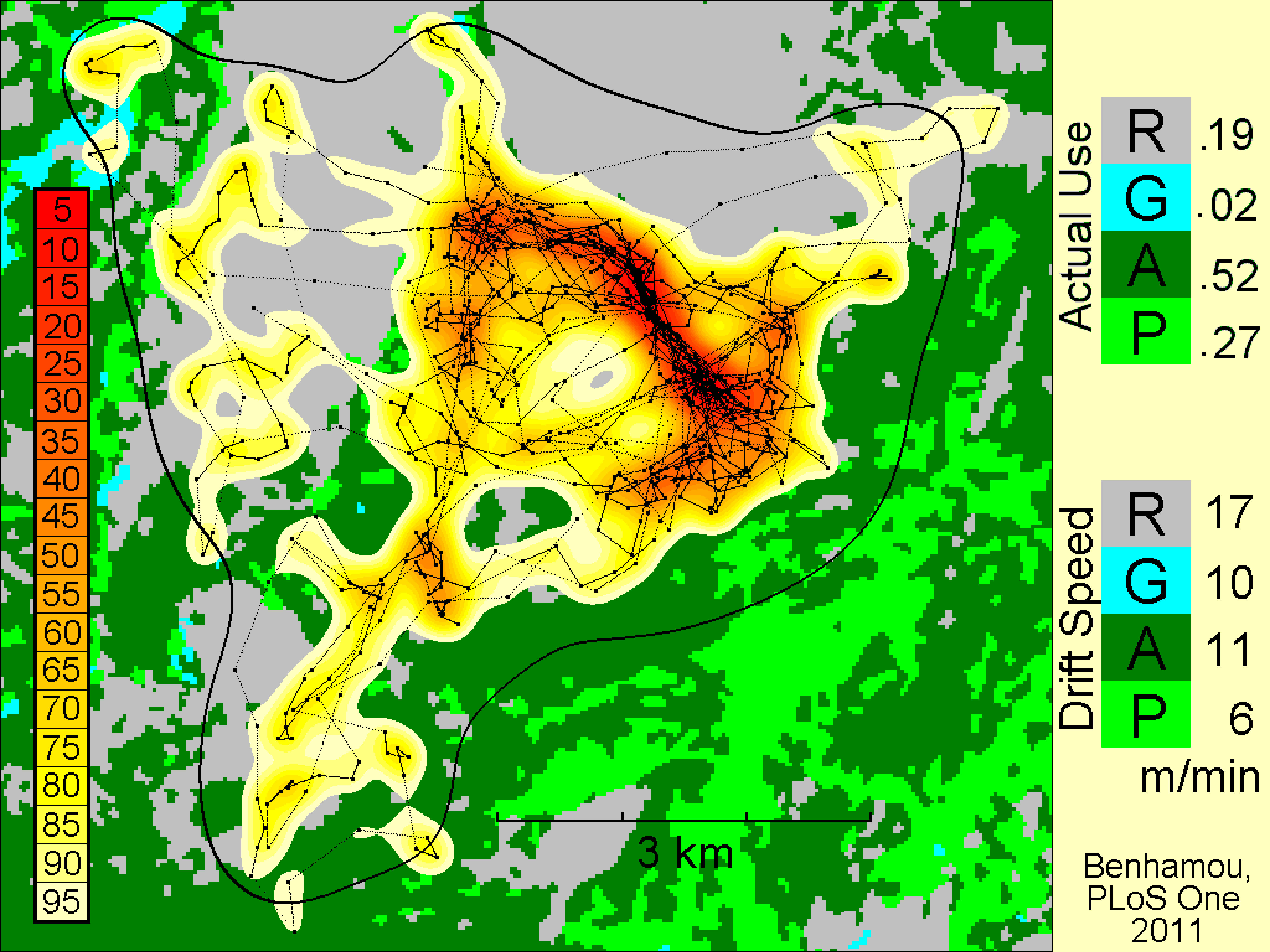
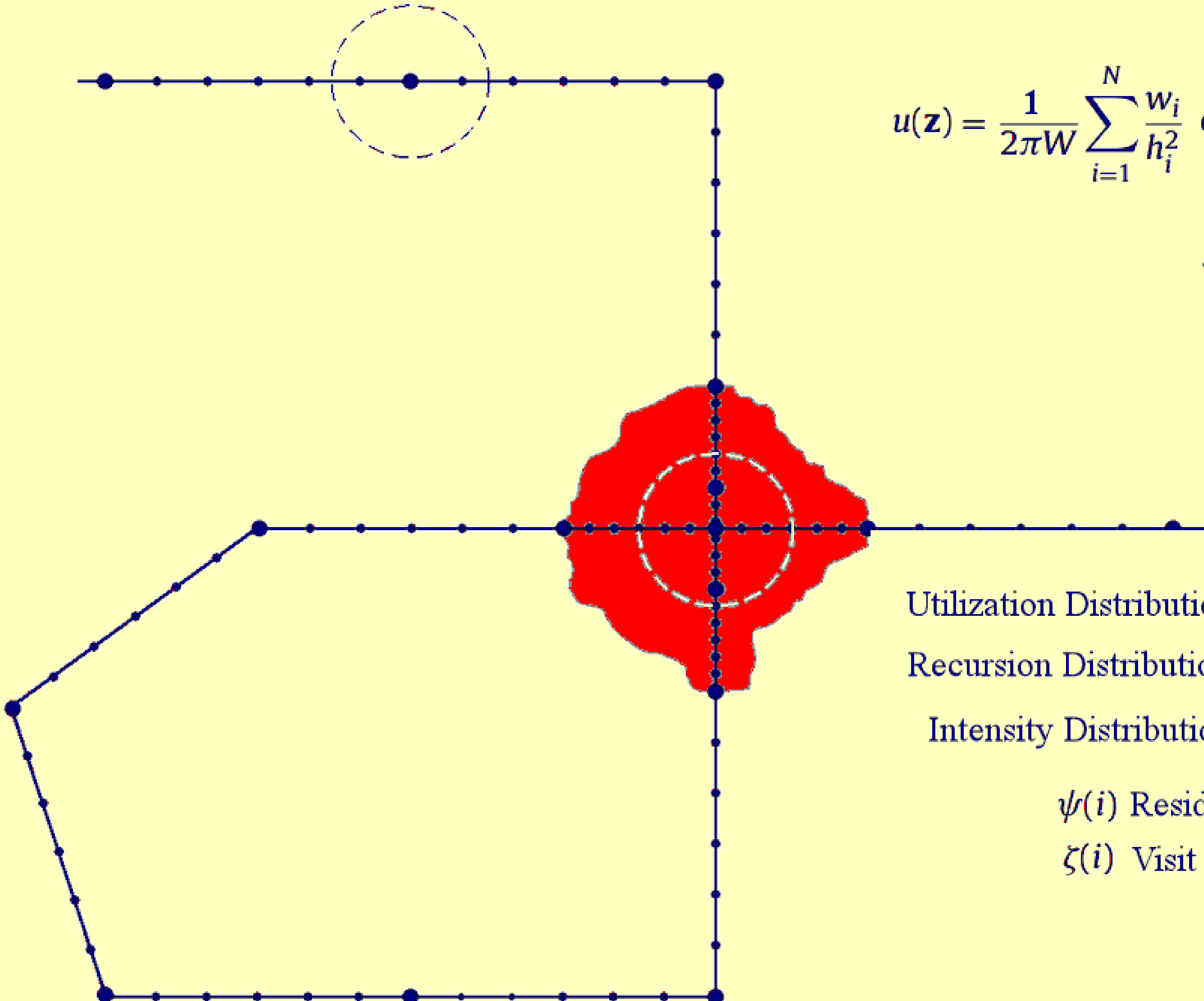
60
65
70
75
80
85
90
95
UD based on interpolated locations
using Biased Random Bridges
D = 450 m2/min
3 km



5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
3 km
Actual Use
R .19
G .02
A .52
P .27
Drift Speed
R 17
G 10
A 11
P 6
m/min
Benhamou,
PLoS One
2011



$$u(\mathbf{z}) = \frac{1}{2\pi W}\sum_{i=1}^{N}\frac{w_i}{h_i^2}\,\exp\left[-\frac{\left\|\mathbf{Z}_i - \mathbf{z}\right\|^2}{2h_i^2}\right]$$

$$\text{with}\quad W = \sum_{i=1}^{N} w_i$$

Utilization Distribution UD $w_i = 1$

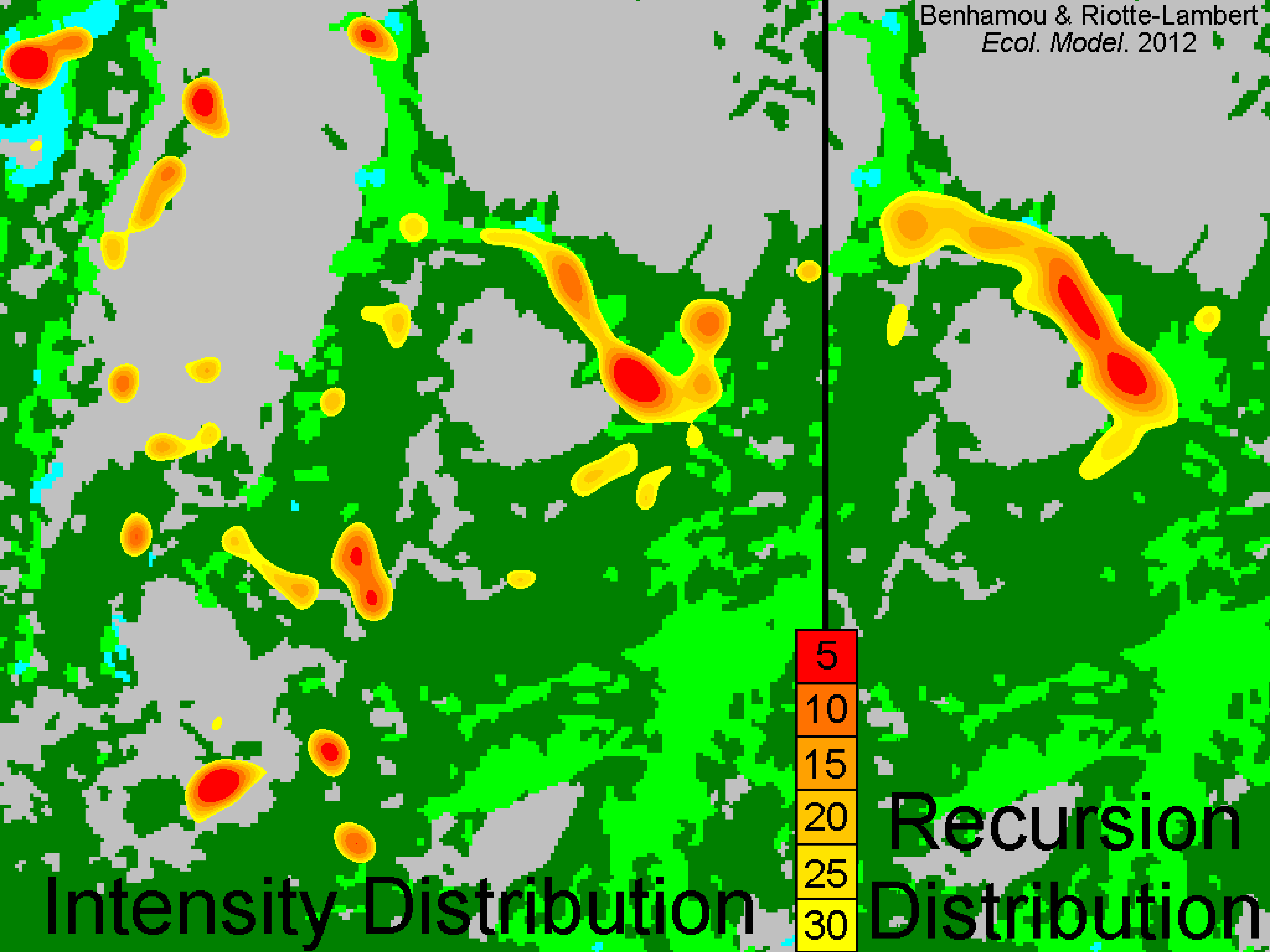
Recursion Distribution RD $w_i = 1/\psi(i)$

Intensity Distribution ID $w_i = 1/\zeta(i)$

$\psi(i)$ Residence time

$\zeta(i)$ Visit number

Benhamou & Riotte-Lambert, Ecol. Model. 2012



Benhamou & Riotte-Lambert
Ecol. Model. 2012
5
10
15
20
25
30
Intensity Distribution
Recursion Distribution

Encounter "probability" of two animals moving independently of each other

What does mean "encounter"?

- to be in the same area
- to be within a given distance of the other one

There are four situations that are worth considering:

1) At a given time and at a given place (in the same area)

2) At any time and at a given place (in the same area)

3) At a given time at any place (within a given distance)

4) At any time and at any place (within a given distance)

1) At a given time and at a given place (in the same area)

Consider a circular area Z with centre *C* and radius *R*, and 2 animals A and B

Encounter Prob. = P(A is in Z at time t) x P(B is in Z at time t)

Let the locations of A and B at any time *t* follow a circular bivariate Gaussian distribution with means $\mu_A(t)$ and $\mu_B(t)$ and standard deviations $\sigma_A(t)$ and $\sigma_B(t)$.

Let *C* be at distances $\lambda_A(t)$ of $\mu_A(t)$ and $\lambda_B(t)$ of $\mu_B(t)$

The probability density for an animal to be at distance δ of *C* is given by the Rice distribution: $f(\delta) = \delta/\sigma^2 \exp[-(\delta^2+\lambda^2)/(2\sigma^2)]\ I_0(\lambda\delta/\sigma^2)$ where I_0 is the modified Bessel function of the first kind with order zero

Probability to be in Z: $F(R) = \int_0^R f(\delta) d\delta$ (using numerical integration)

(if Z is not circular, the prob. can be estimated by computer simulations)

2) At any time and at a given place (in the same area)

Consider an area Z of any shape (not necessarily circular)

Time integration of movement to compute the UDs of the two animals
=> computation of the proportion of time spent by each animal in area Z

Encounter "prob." = PPtion of time (A in Z) x PPtion of time (B in Z)

3) At a given time at any place (within a given distance *D*)

Let the locations of A and B at any time t follow a circular bivariate Gaussian distribution with means $\mu_A(t)$ and $\mu_B(t)$ and variances $\sigma_A^2(t)$ and $\sigma_B^2(t)$.

=> the difference follows a circular bivariate Gaussian distribution with mean $\mu_\Delta(t) = \mu_A(t) - \mu_B(t)$ and variance $\sigma_\Delta^2(t) = \sigma_A^2(t) + \sigma_B^2(t)$

The probability density for an animal to be at distance δ of another animal at time *t* is given by the Rice distribution:

$$f(\delta)=\delta/\sigma_\Delta^2 \exp[-(\delta^2+||\mu_\Delta||^2)/(2\sigma_\Delta^2)]\ I_0(||\mu_\Delta||\delta/\sigma_\Delta^2)$$

Probability to be within *D* of each other:

$F(D)=\int_0^D f(\delta)d\delta$ (by numerical integration)

4) At any time and at any place (within a given distance *D*)

Compute the "difference distribution" at any time, as previously:

=> Circular bivariate Gaussian distribution

with mean $\mu_\Delta(t)$ and variance $\sigma_\Delta^2(t)$

Integrate over time (e.g. using kernel approach) => "difference UD"

Then, compute the proportion of time spent in a circular area centred on (0, 0) with radius *D*

TAKE HOME MESSAGES

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2) THE SCALE-FREE MOVEMENT APPROACH IS USUALLY MEANINGLESS
   - MULTI-SCALE MOVEMENT PATTERNS CAN LOOK LIKE SCALE-FREE
   - SCALE-FREE MOVEMENT PROCESSES ARE USUALLY POORLY EFFICIENT

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5) JOINT SPATIAL DISTRIBUTION OF 2 (OR MORE) INDIVIDUALS OPENS INTERESTING BUT TRICKY PERSPECTIVES

THAT'S
ALL
FOLKS

...thanks