On stationary researchers looking at moving animals

STATIONARITY AND SCALES IN ANIMAL MOVEMENTS

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PATTERN

OR

PROCESS ?

Real World vs. World Models

Serastruma lujae
(small ant)

Initial recording
(video 25 i/s)

Rediscretization
with a constant
step length (1.5 cm)

This is not a path

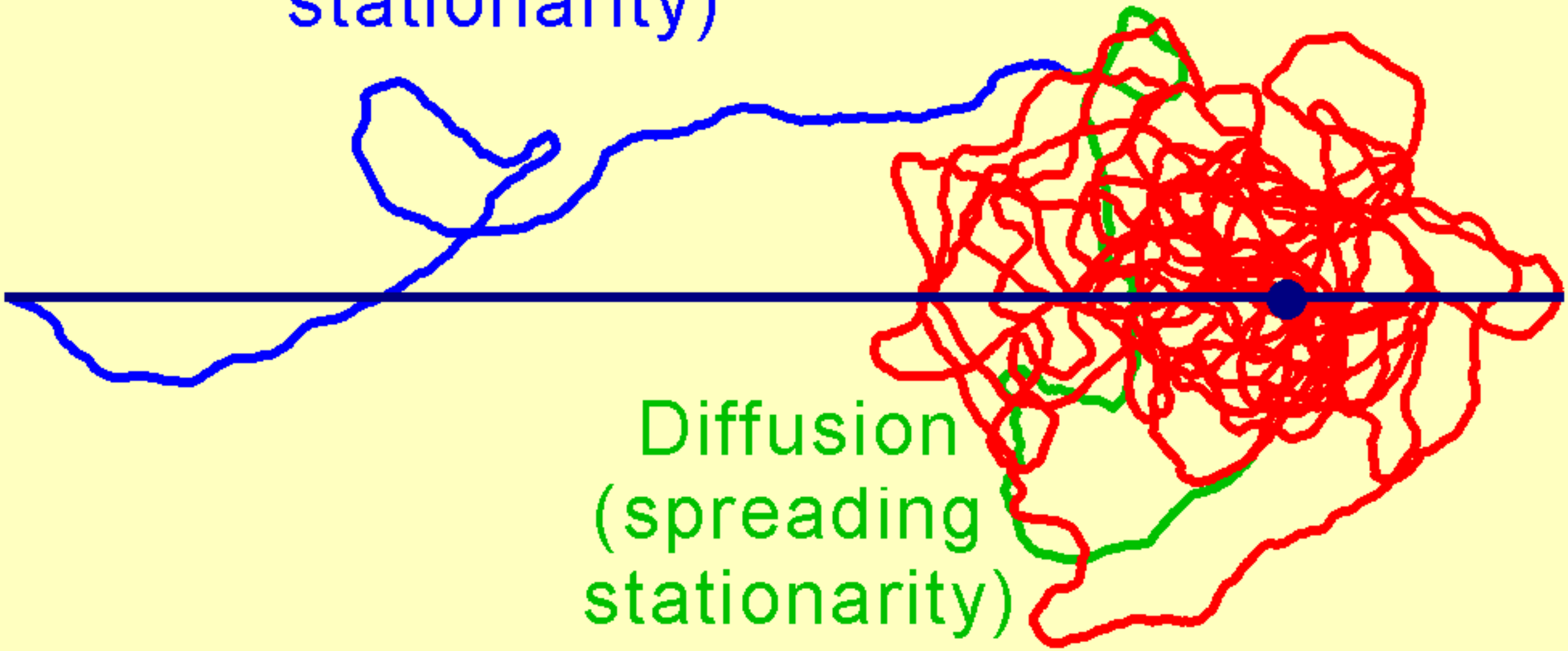
Movement Process => Pattern (path) => Path representation

inference

Various patterns generated by ... a single process

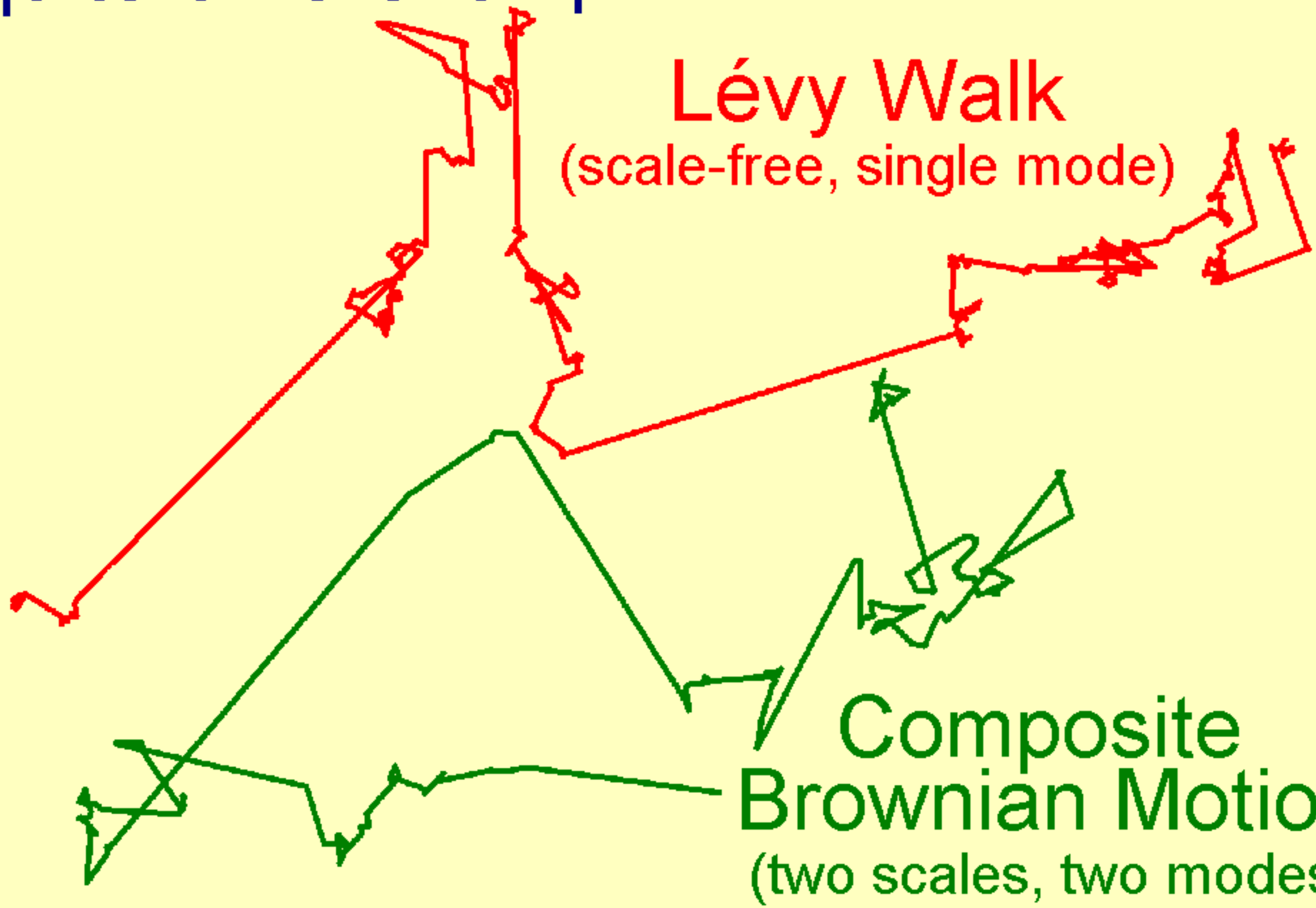
Advection (direction stationarity)

Search-loops (location stationarity)



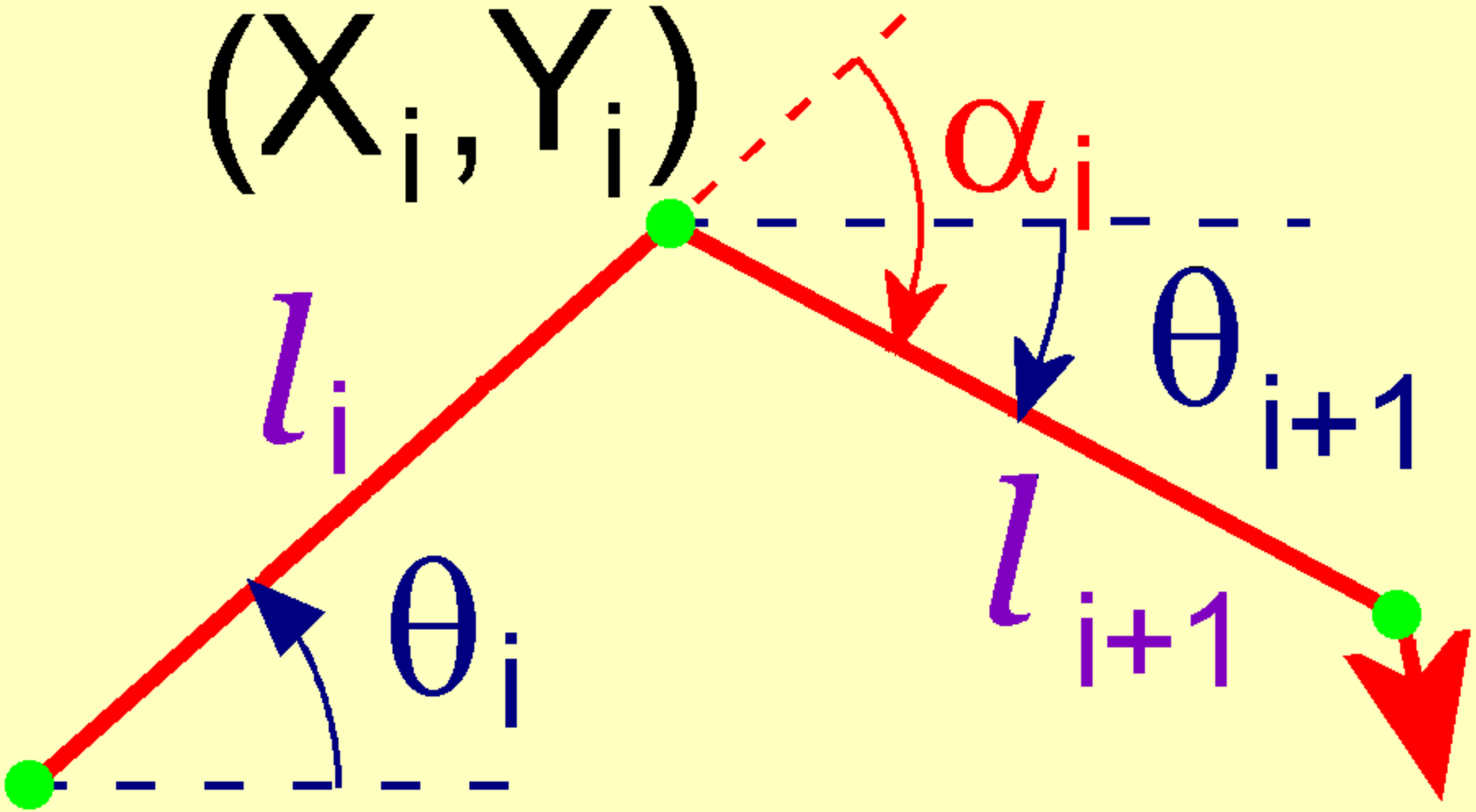
Diffusion (spreading stationarity)

Similar patterns generated by ...
quite different processes



Benhamou, Ecology 2007

Sampling issue:
key path variables depend on the sampled locations in a complex way



key path variables (steps, turning angles) are just mathematical tools to represent animal paths in a tractable way

For a given scale and behavioural mode, key path parameters are:

- persistence (inertia): local directional bias
- goal attractiveness: global directional bias
- stochasticy level

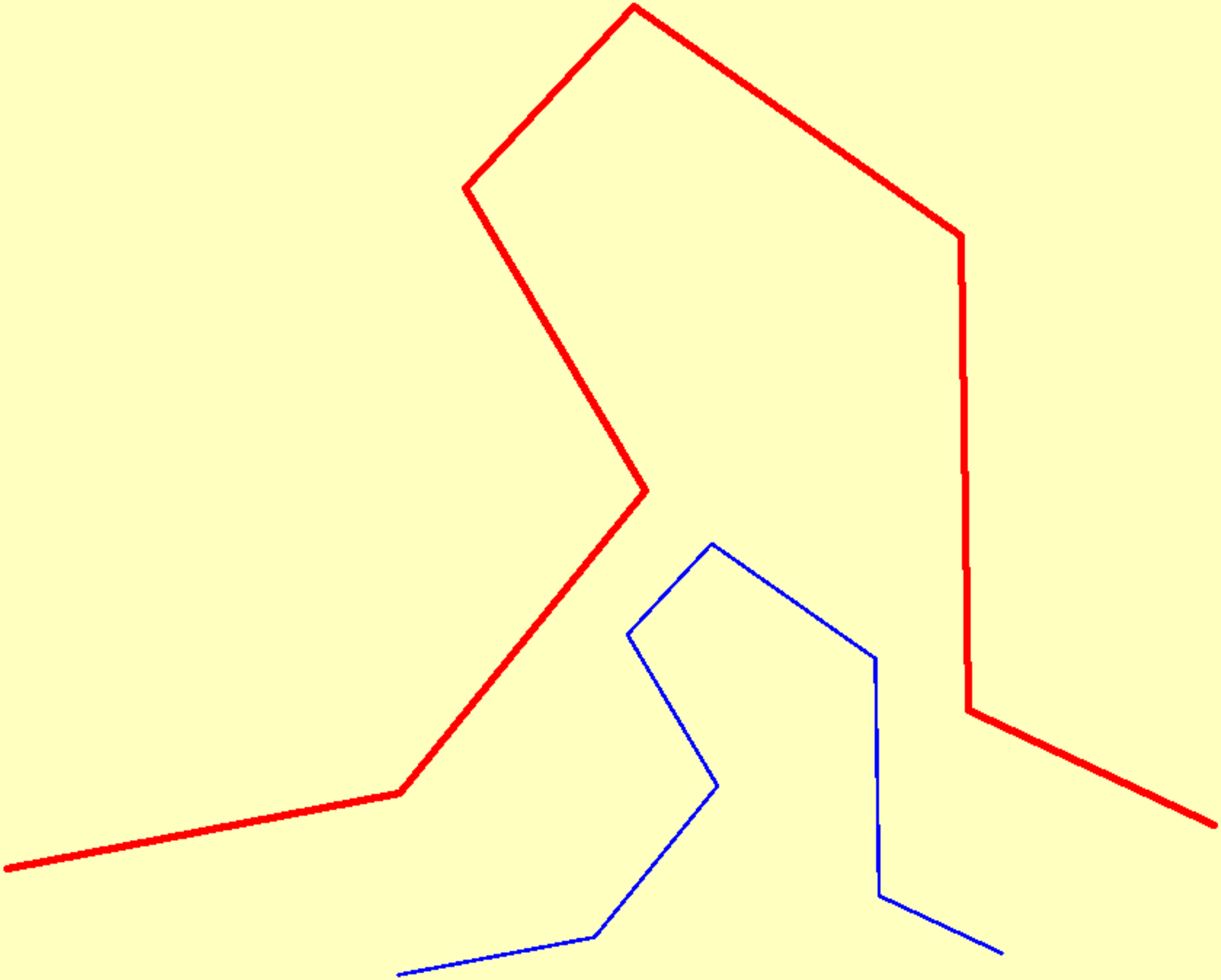
=> Modelling animal paths as

Multi-scale and multi-mode

Biased Correlated Random Walks

STATIONARITY AND OBSERVATION SCALES

"Scaling" effect

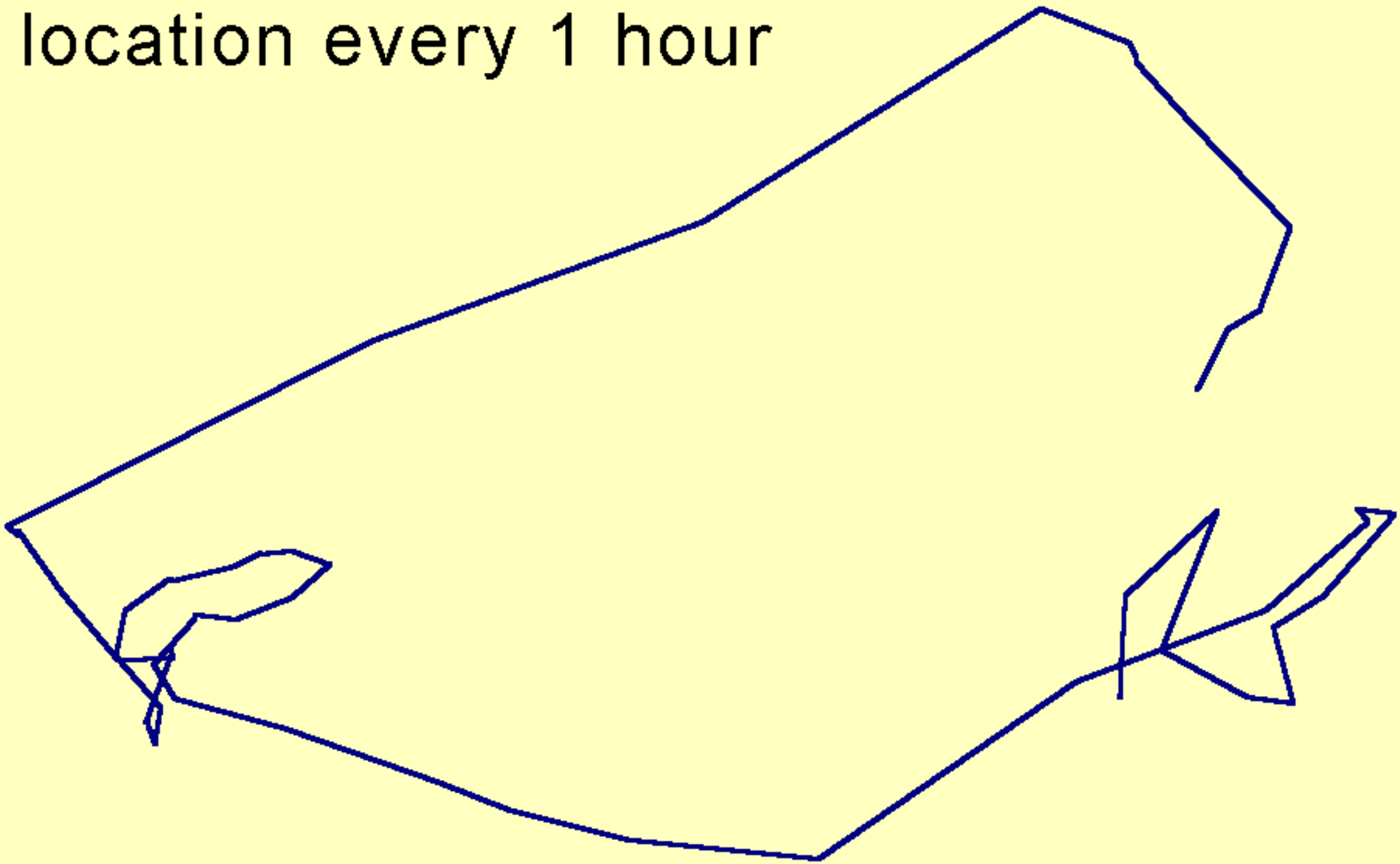


African buffalo
3-day tracking (30 km)
A location every 5 min.

"Sampling" effect

African buffalo
3-day tracking (30 km)
A location every 1 hour

"Sampling" effect

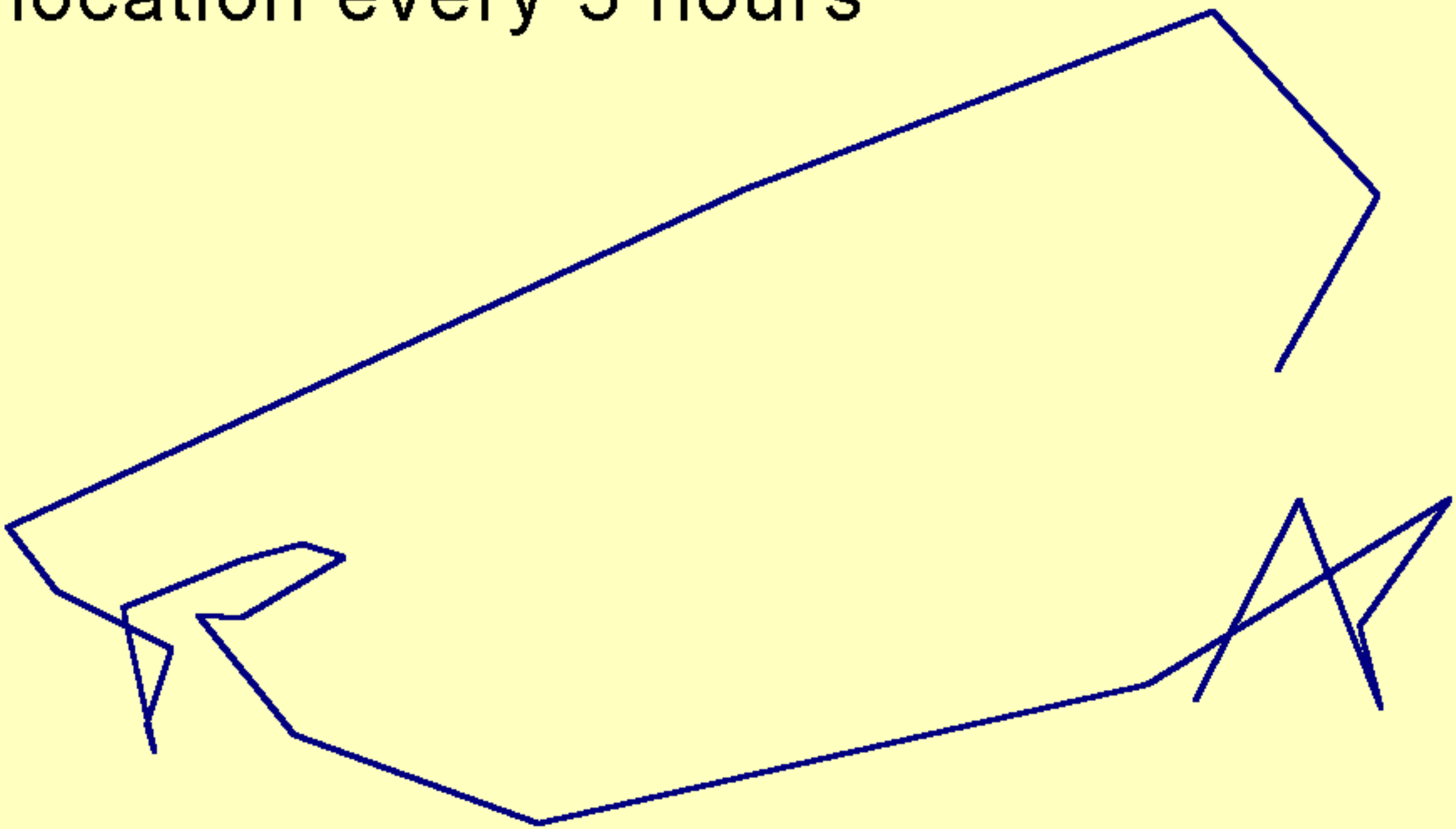


African buffalo

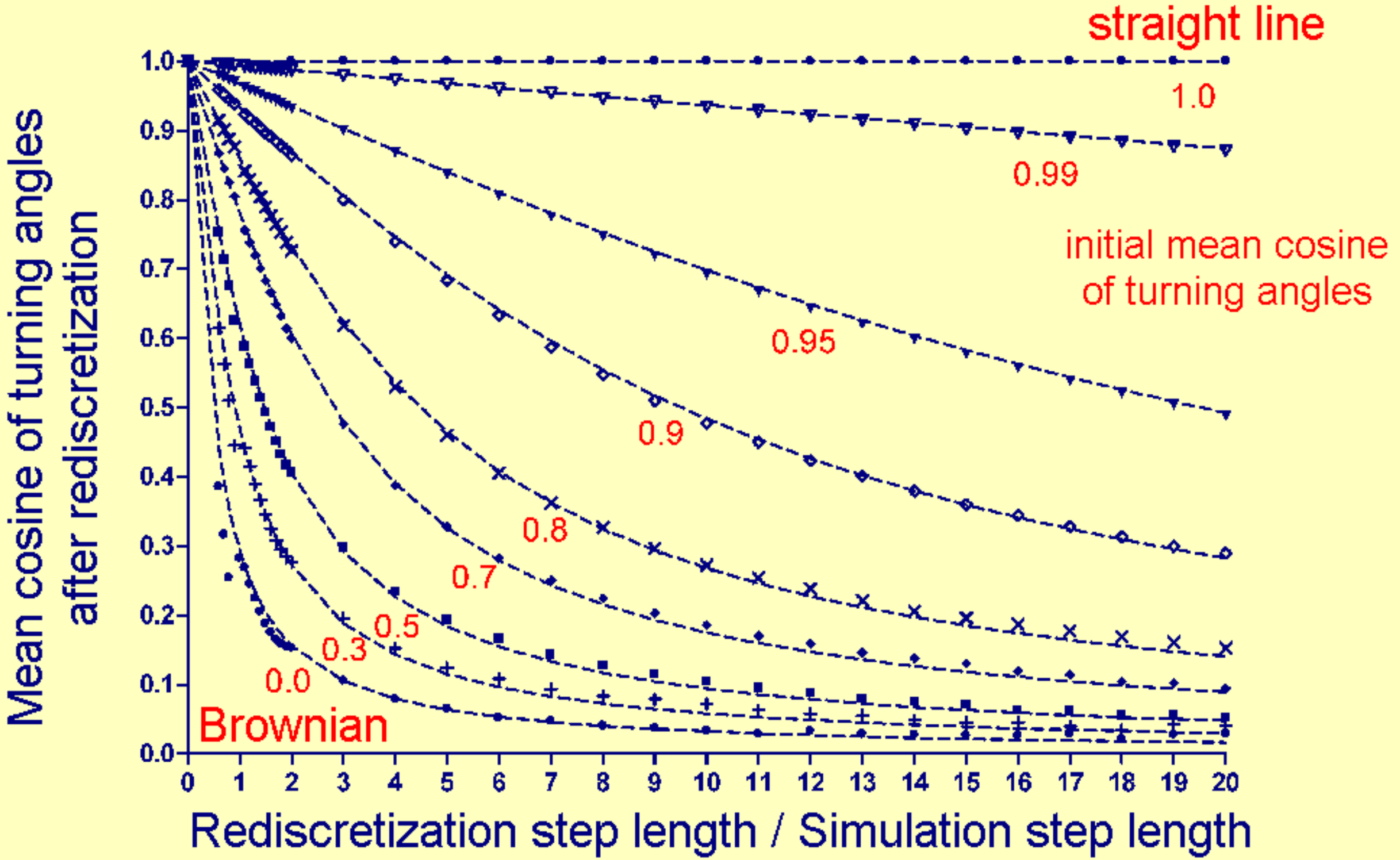
3-day tracking (30 km)

A location every 3 hours

"Sampling" effect



Quantification of homogeneous search paths: Integrating turning angles and step length distributions

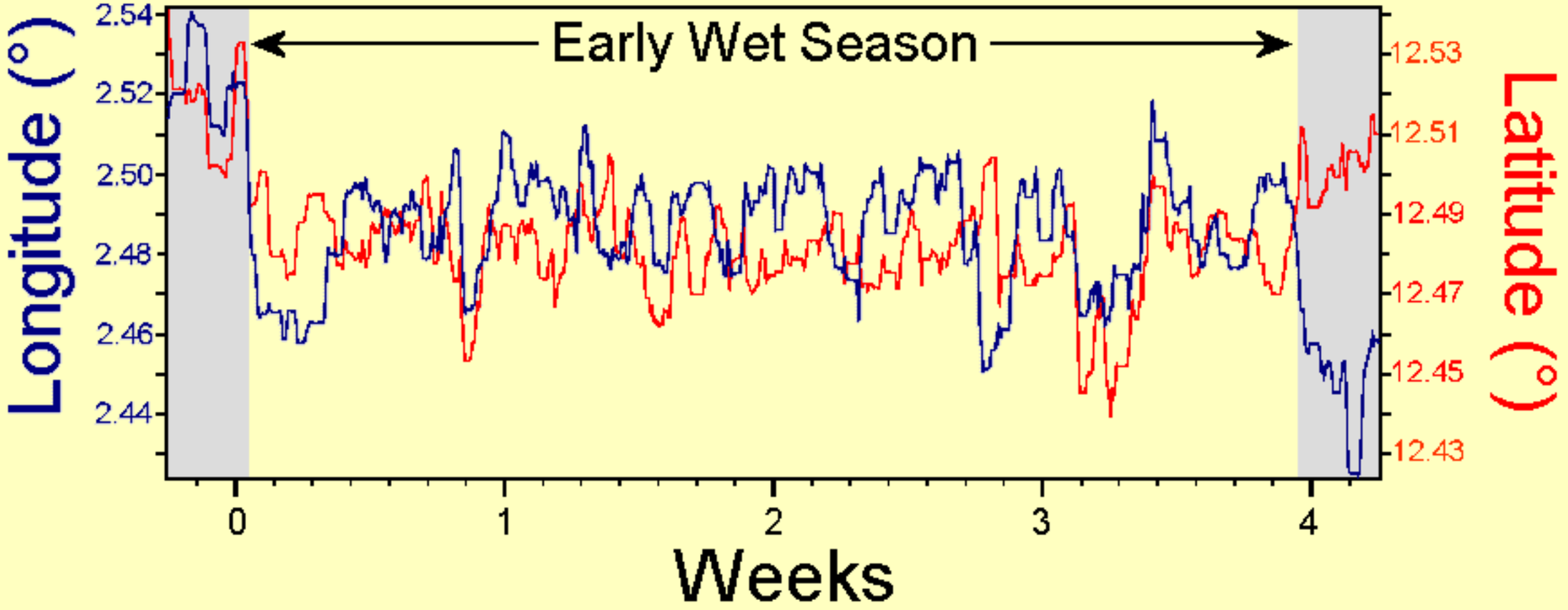


Benhamou, J. Theor. Biol. 2004

STATIONARITY AND BIOLOGICAL SCALES

STATIONARITY: A SCALE-DEPENDENT CONCEPT

Movements of a GPS-tracked African buffalo in early wet season in the W Park, Niger (1 location every 30 min.)



Benhamou, PLoS One 2011

African buffalo

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

3 km

D=
450m²/min

Preferences

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

Drift Speed

R	17
G	10
A	11
P	6

m/min

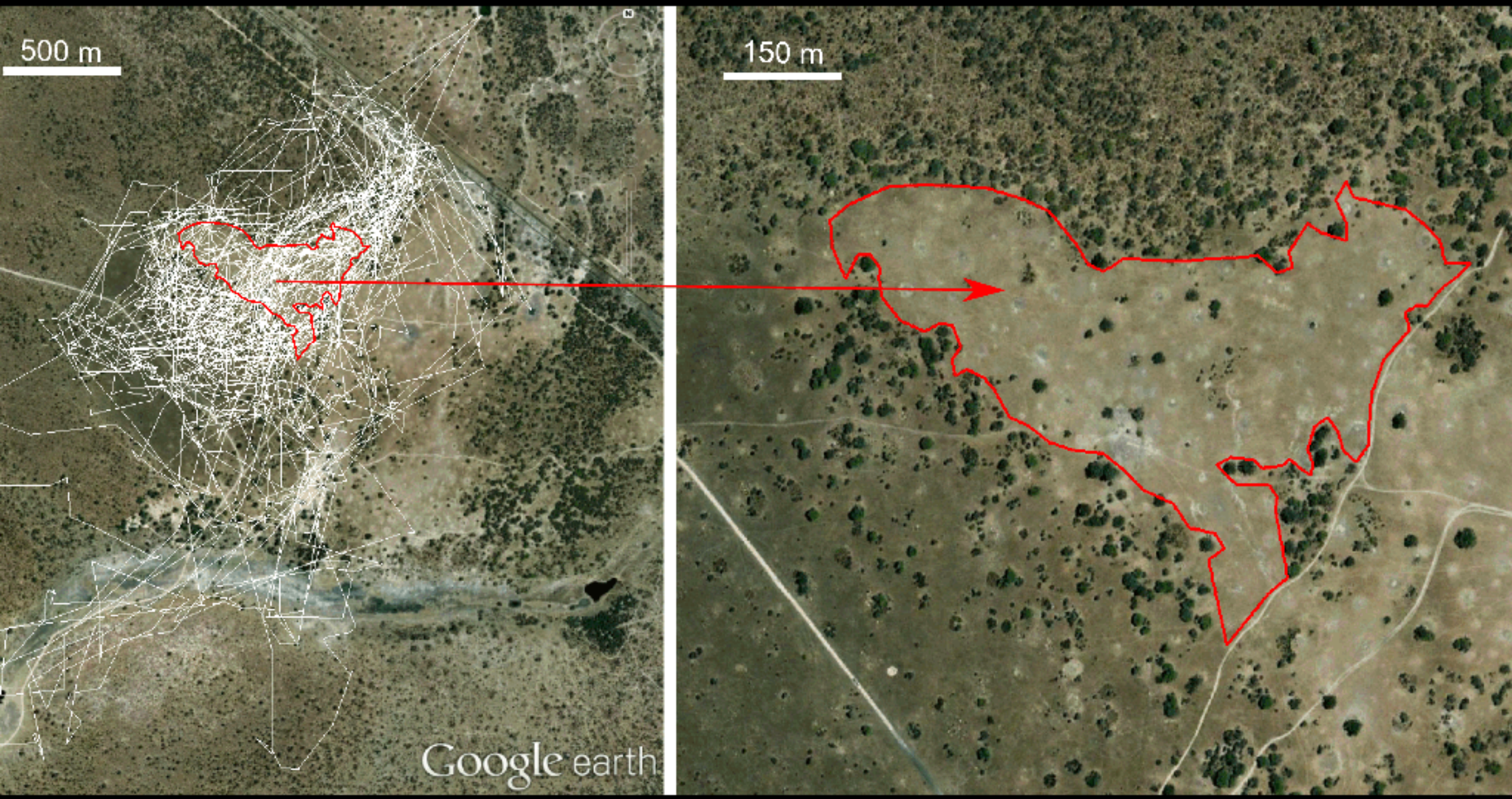
Benhamou,
PLoS One
2011

Benhamou & Riotte-Lambert
Ecol. Model. 2012

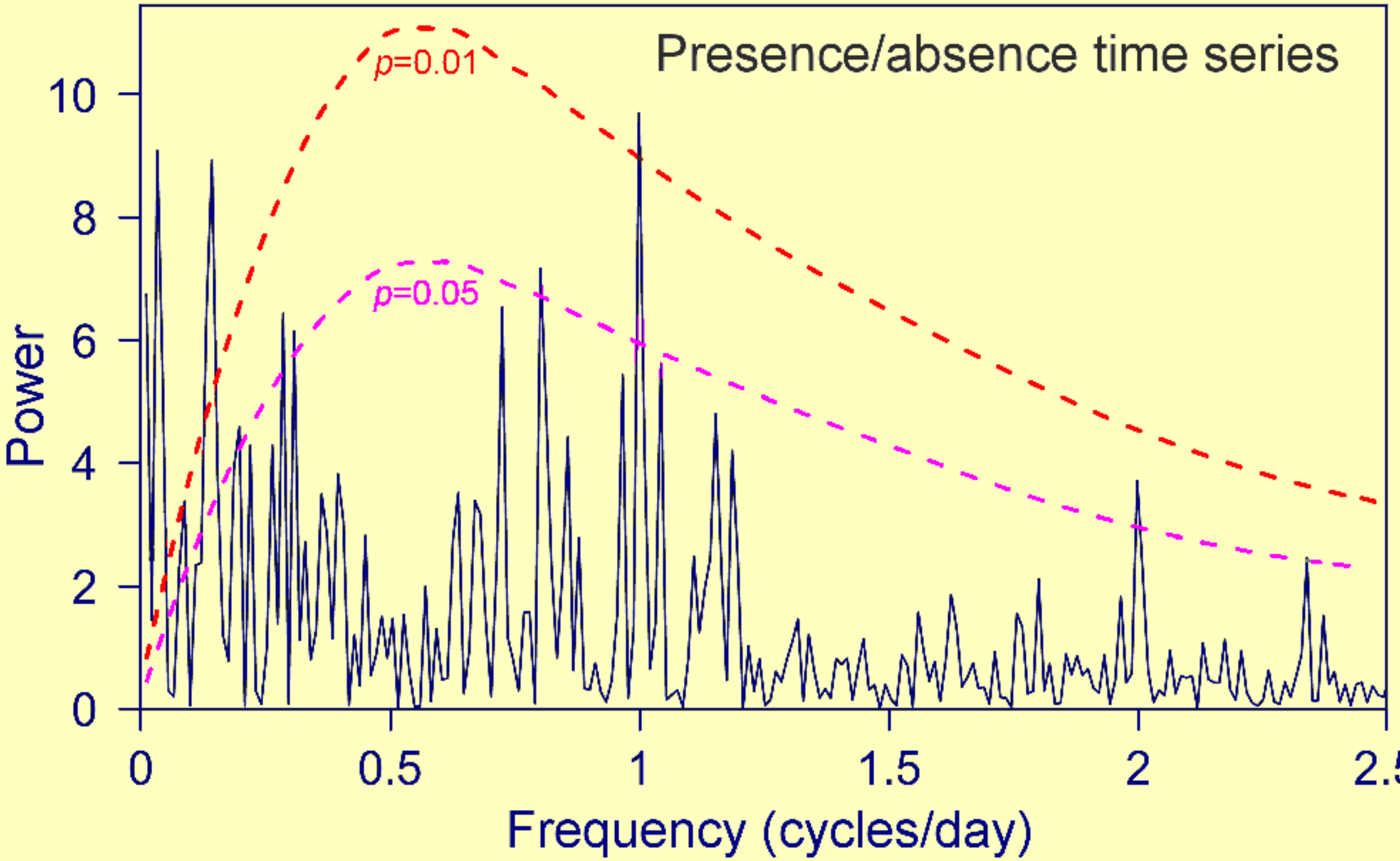
30
25
20
15
10
5

Intensity Distribution

Recursion Distribution



Riotte-Lambert et al., in press



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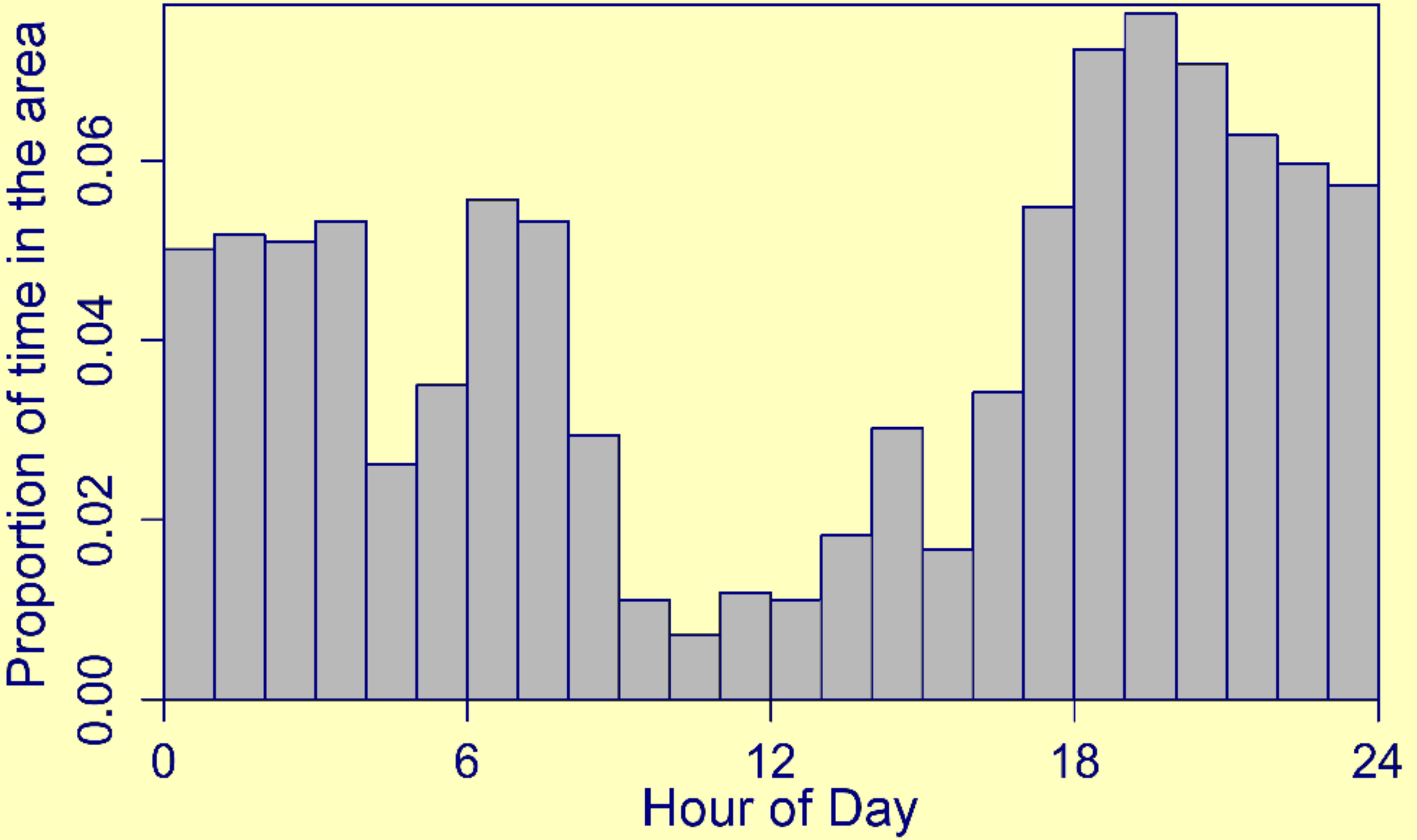

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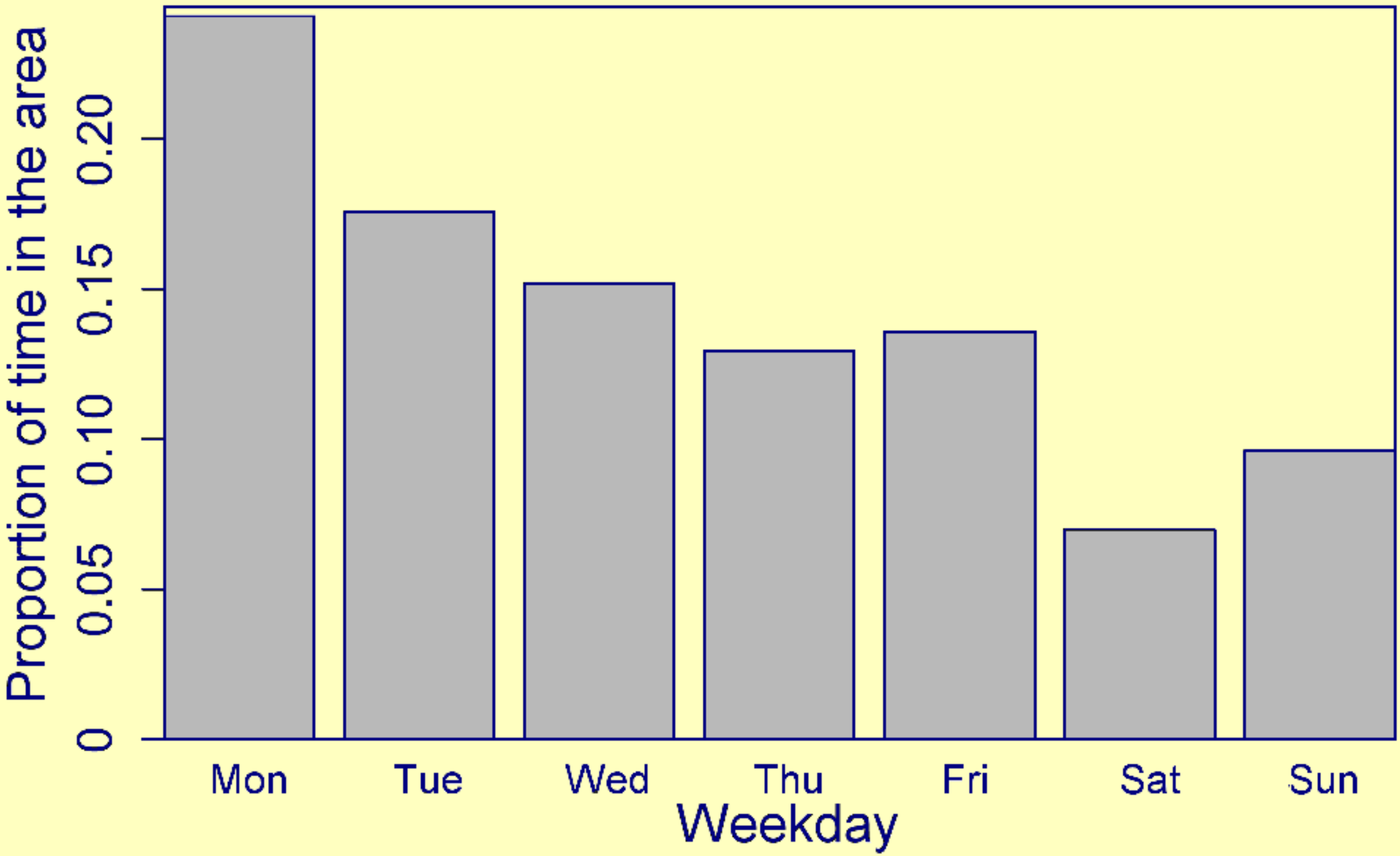
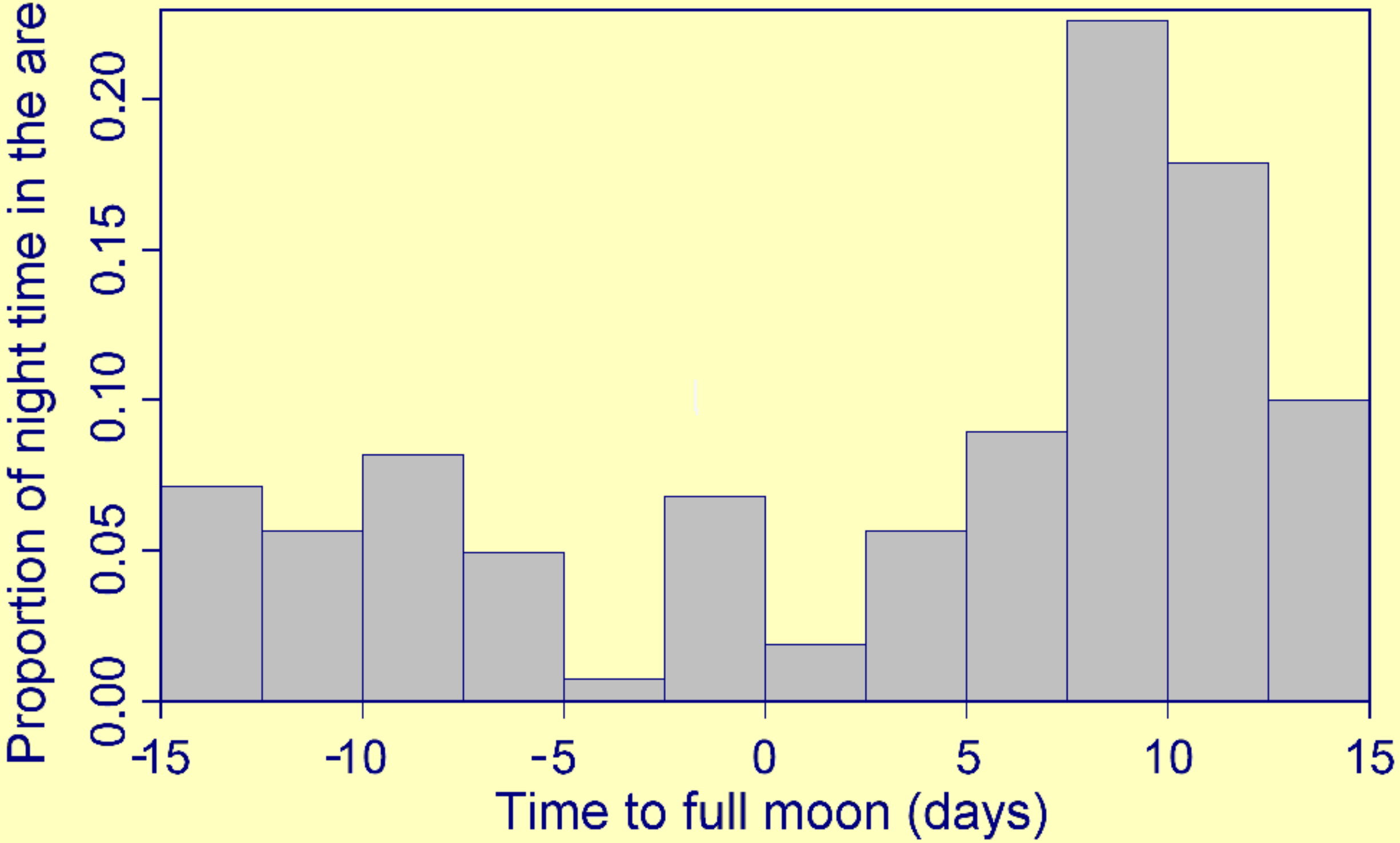


Riotte-Lambert et al., in press



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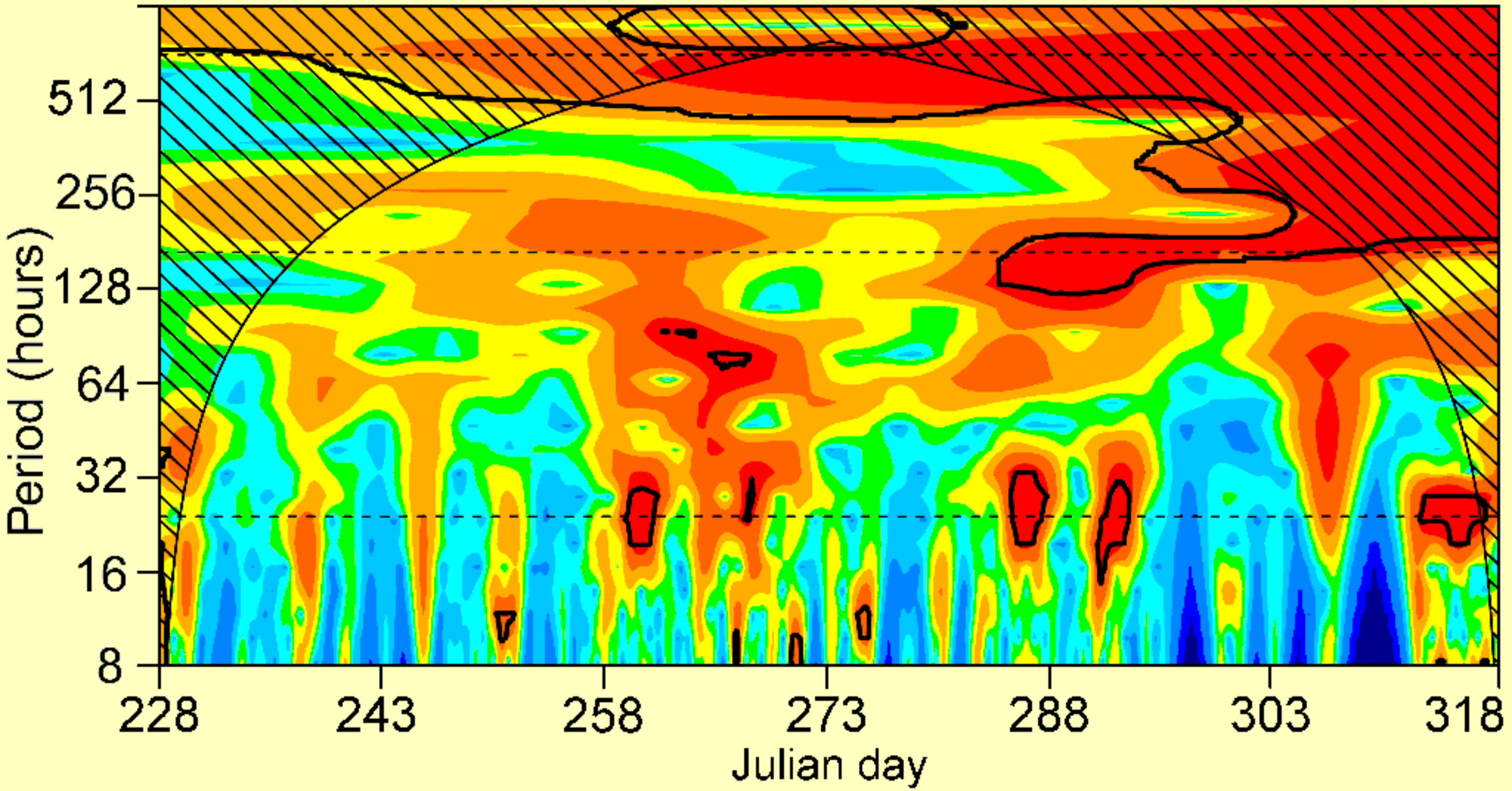

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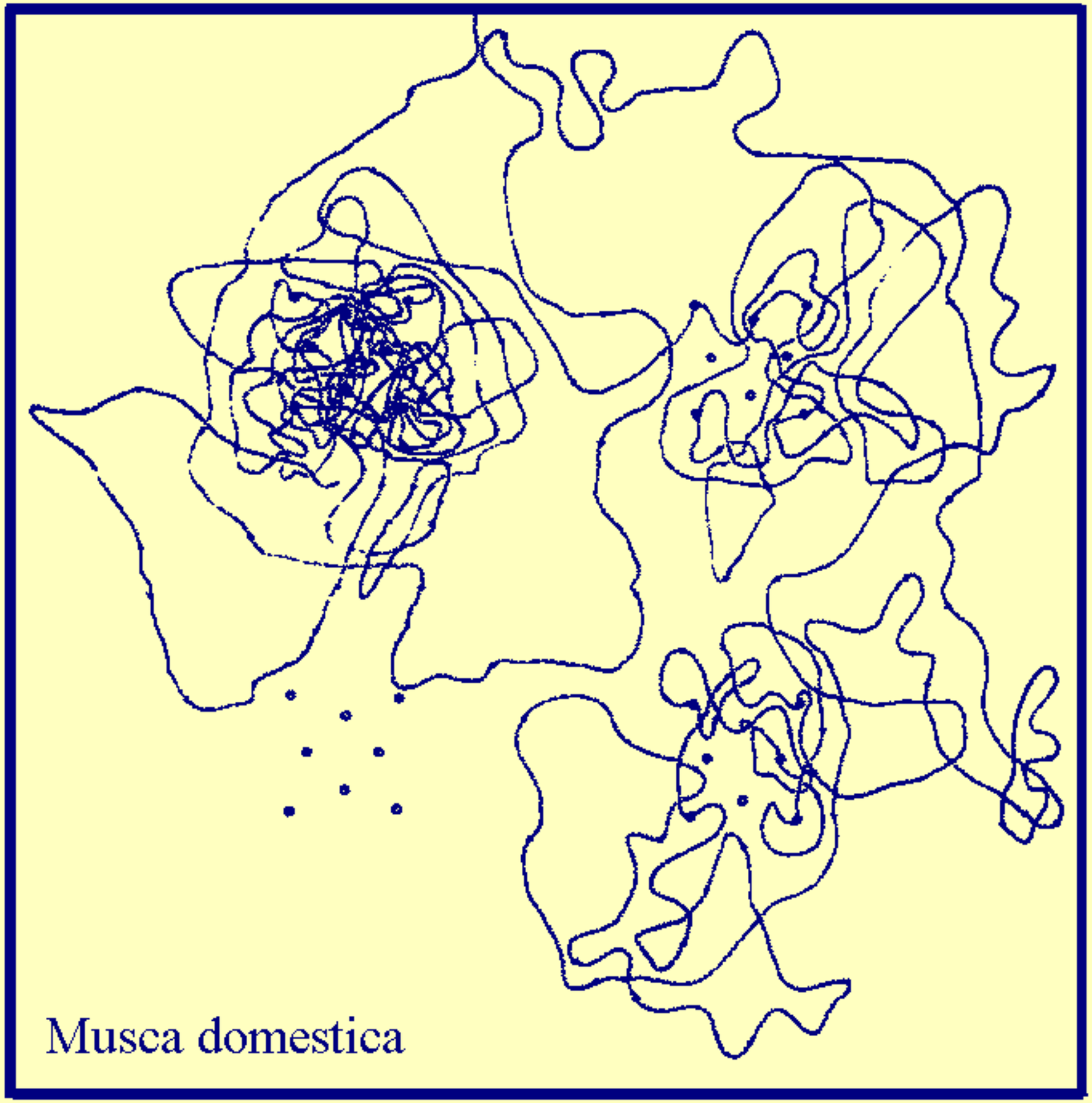
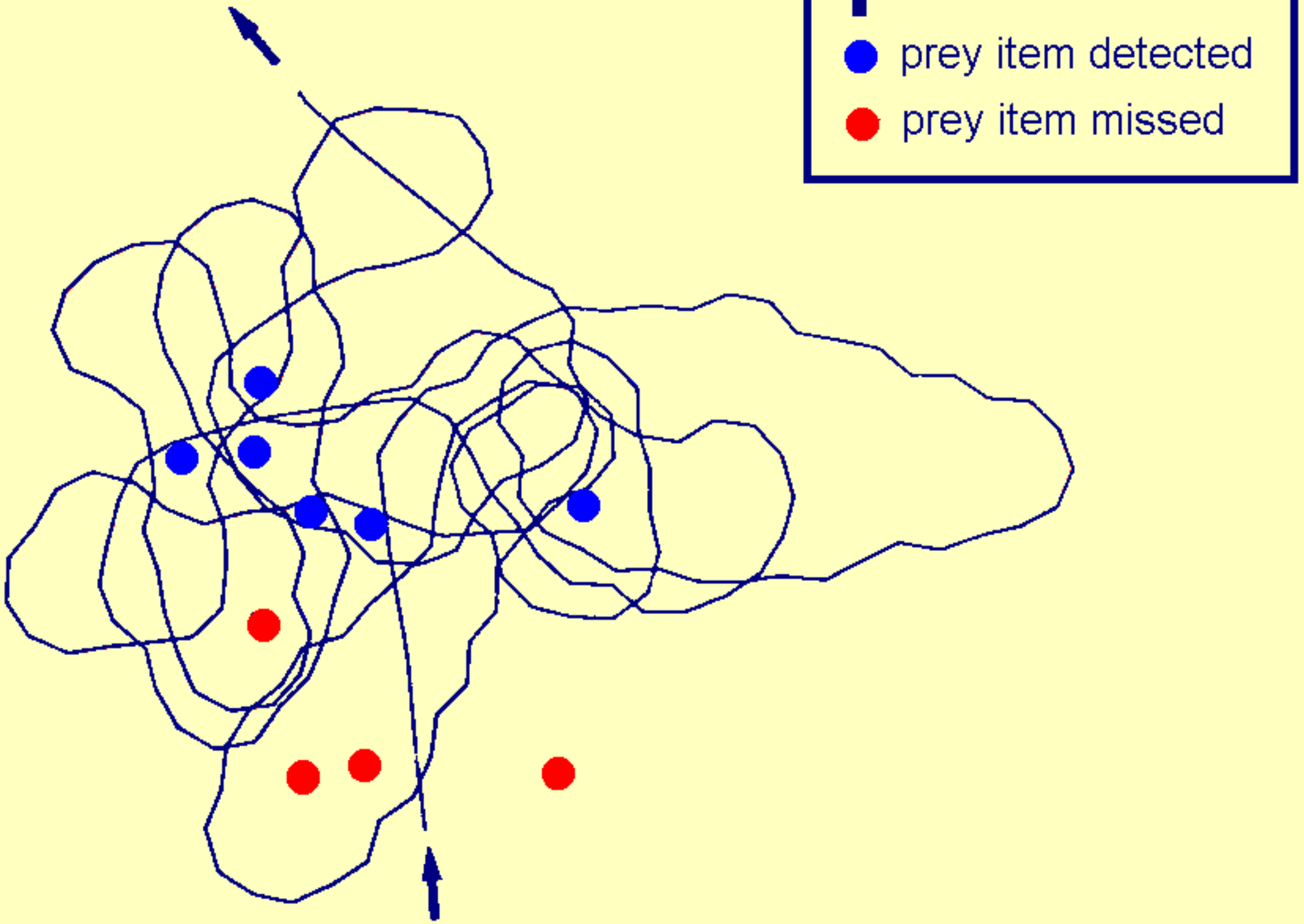


Murdie & Hassel 1973



Benhamou, *Anim. Behav.* 1994

EVIDENCE FOR SCALE-SPECIFIC MOVEMENT PROCESSES

EVIDENCE FOR SCALE-SPECIFIC NAVIGATION PROCESSES

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

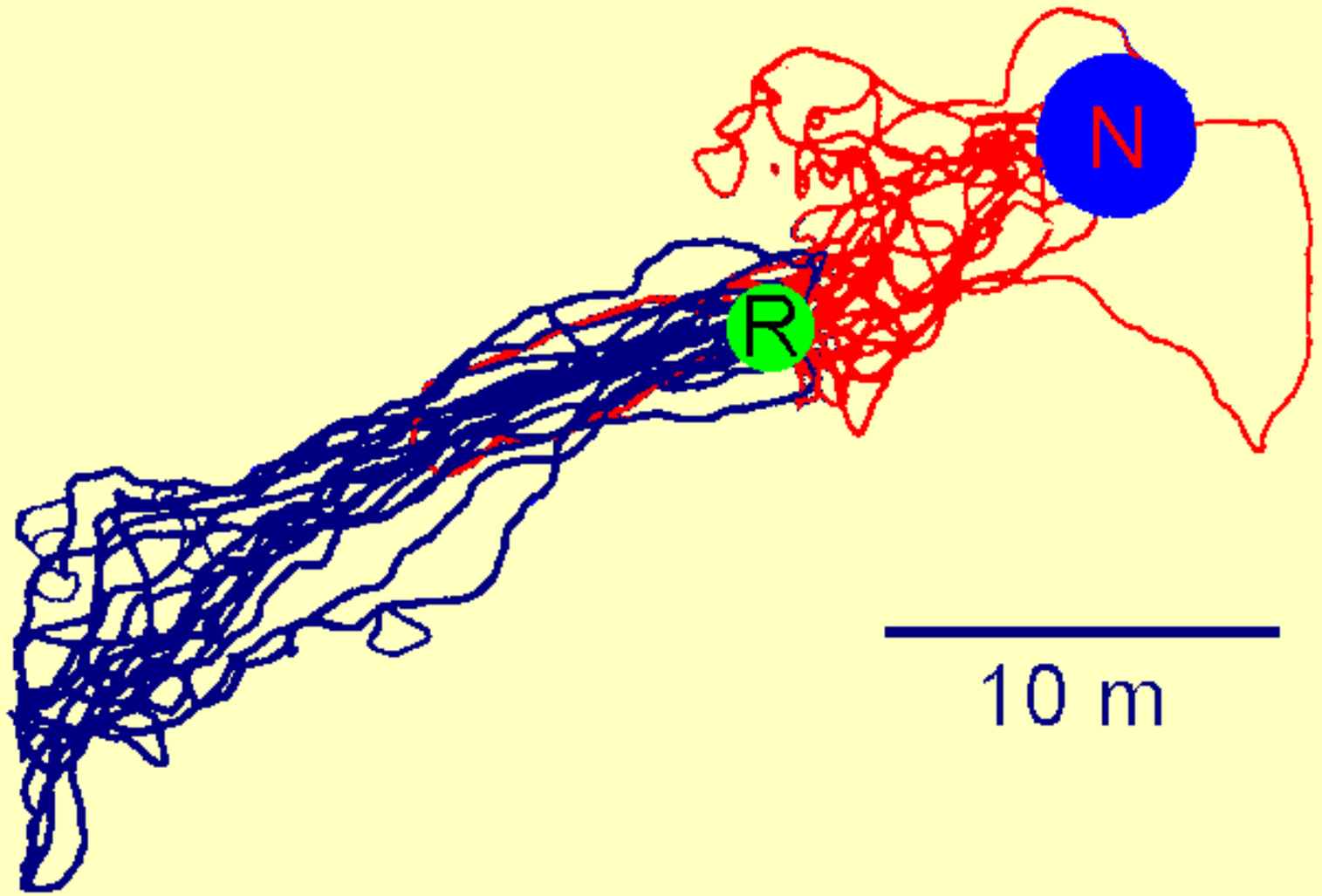
Cataglyphis fortis

Out: 592.1 m, 18.8 min
In: 140.5 m, 6.5 min

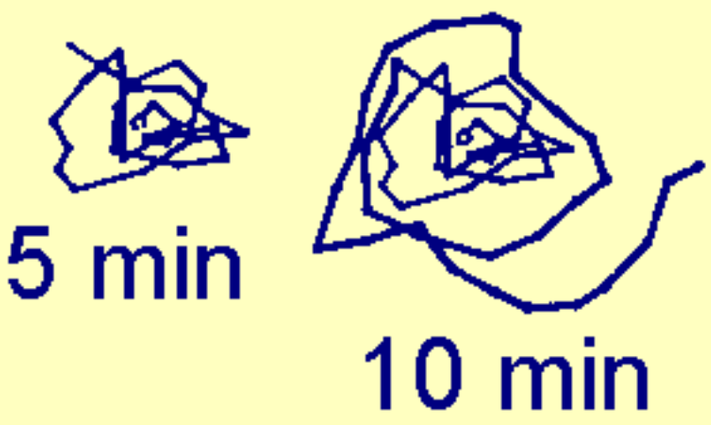
Wehner & Wehner 1990

Cataglyphis fortis

F



Wehner *et al.* 1996



Wehner & Wehner 1986

EVIDENCE FOR SCALE-SPECIFIC FORAGING PROCESSES

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

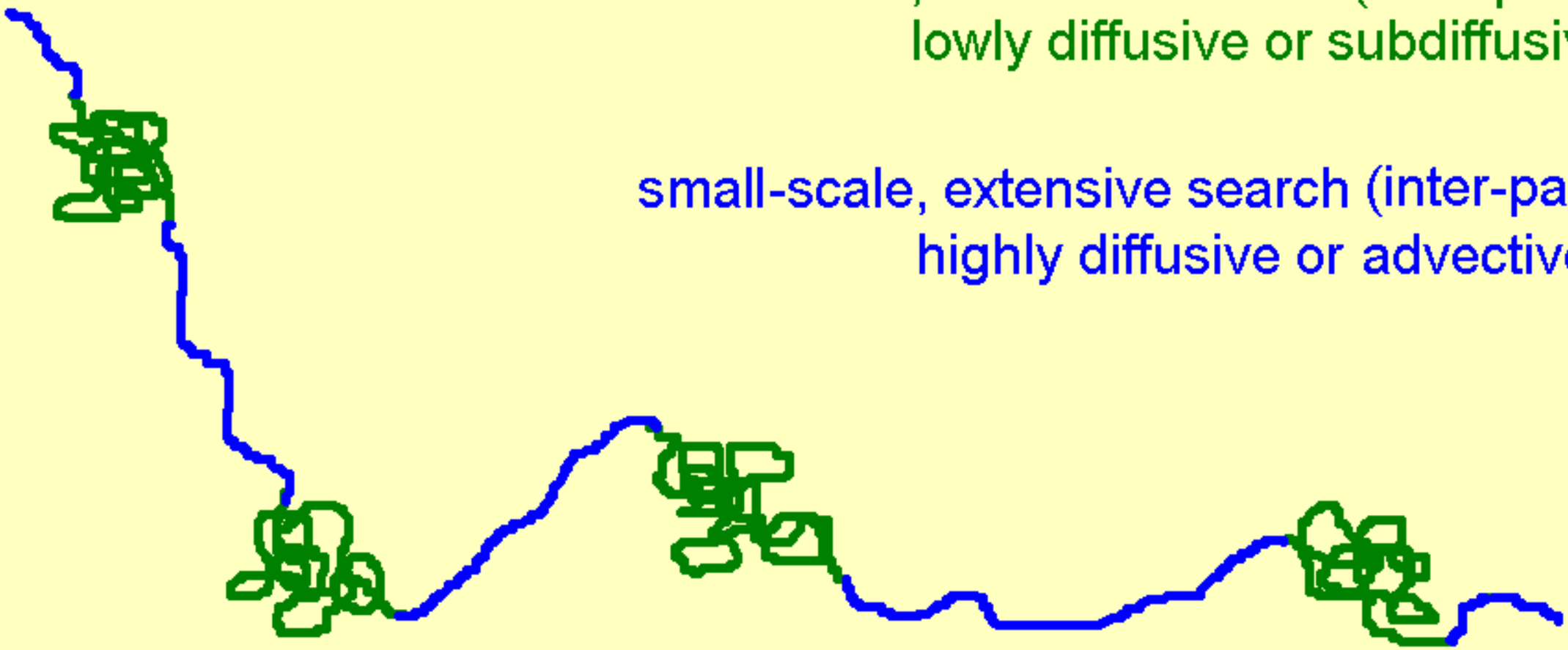
These scales may be partly coupled and are used simultaneously

Do not confound movement modes (or states) and scales

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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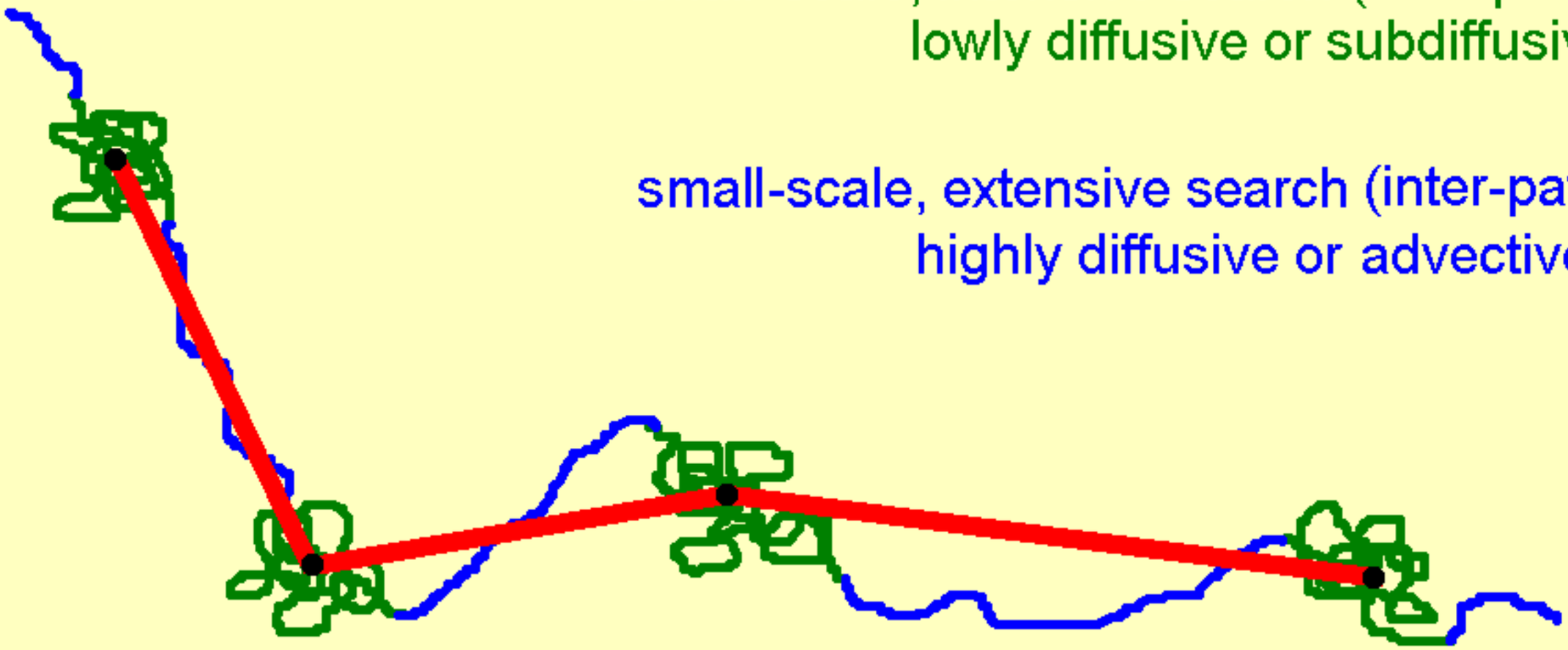
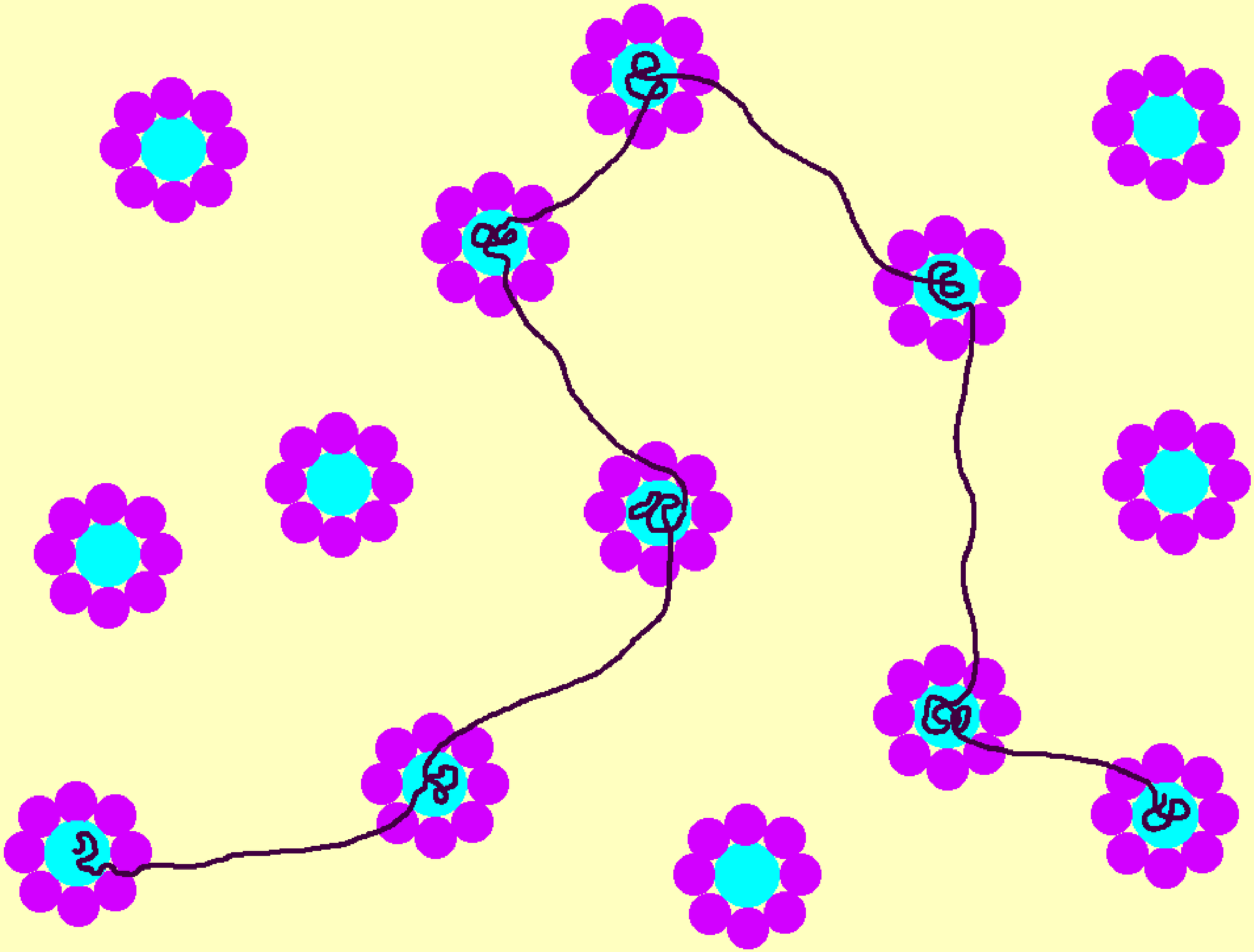


large-scale movement (sequence of visited patches):

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

AN IDEAL CASE FOR STUDYING MULTI-SCALE FORAGING MOVEMENTS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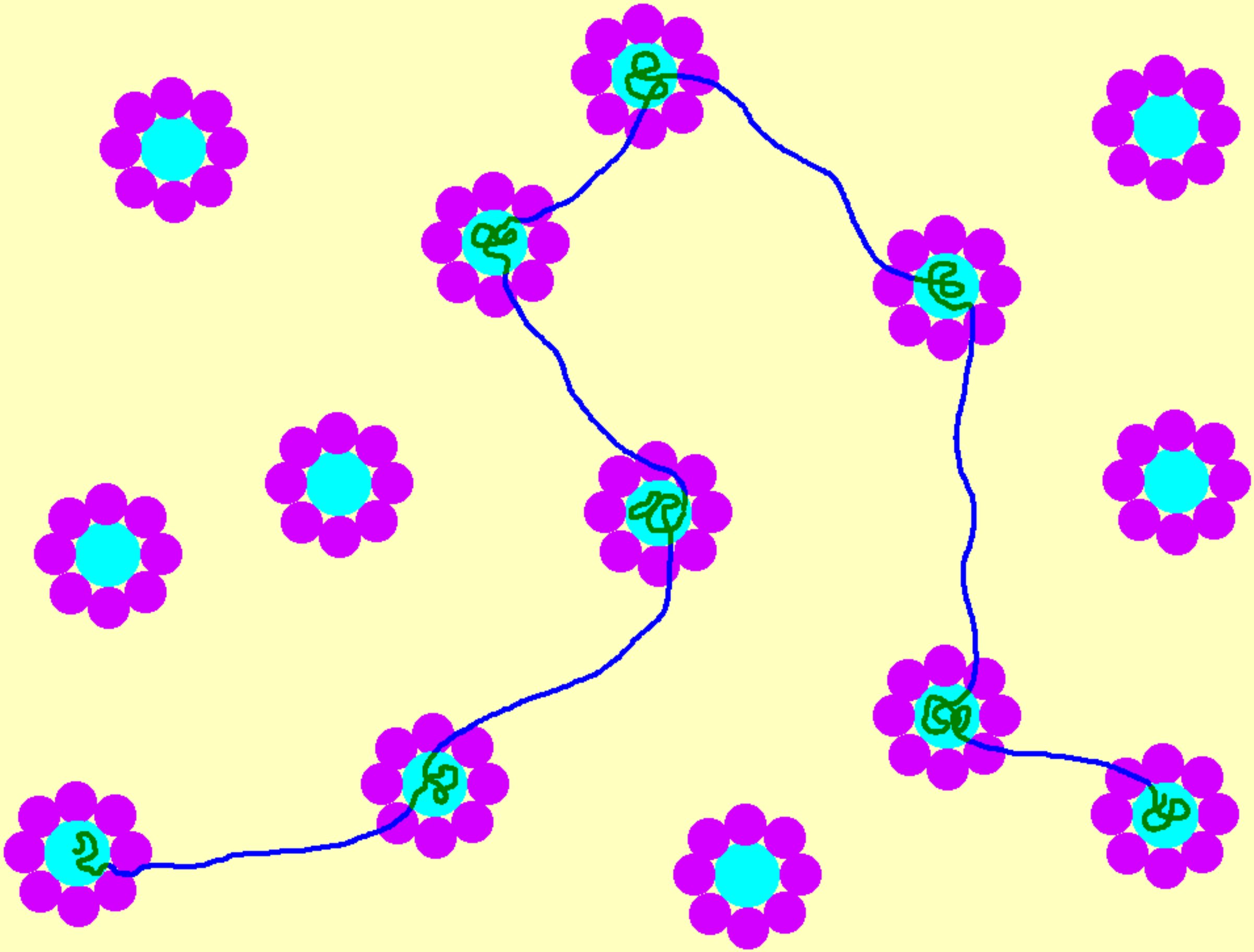
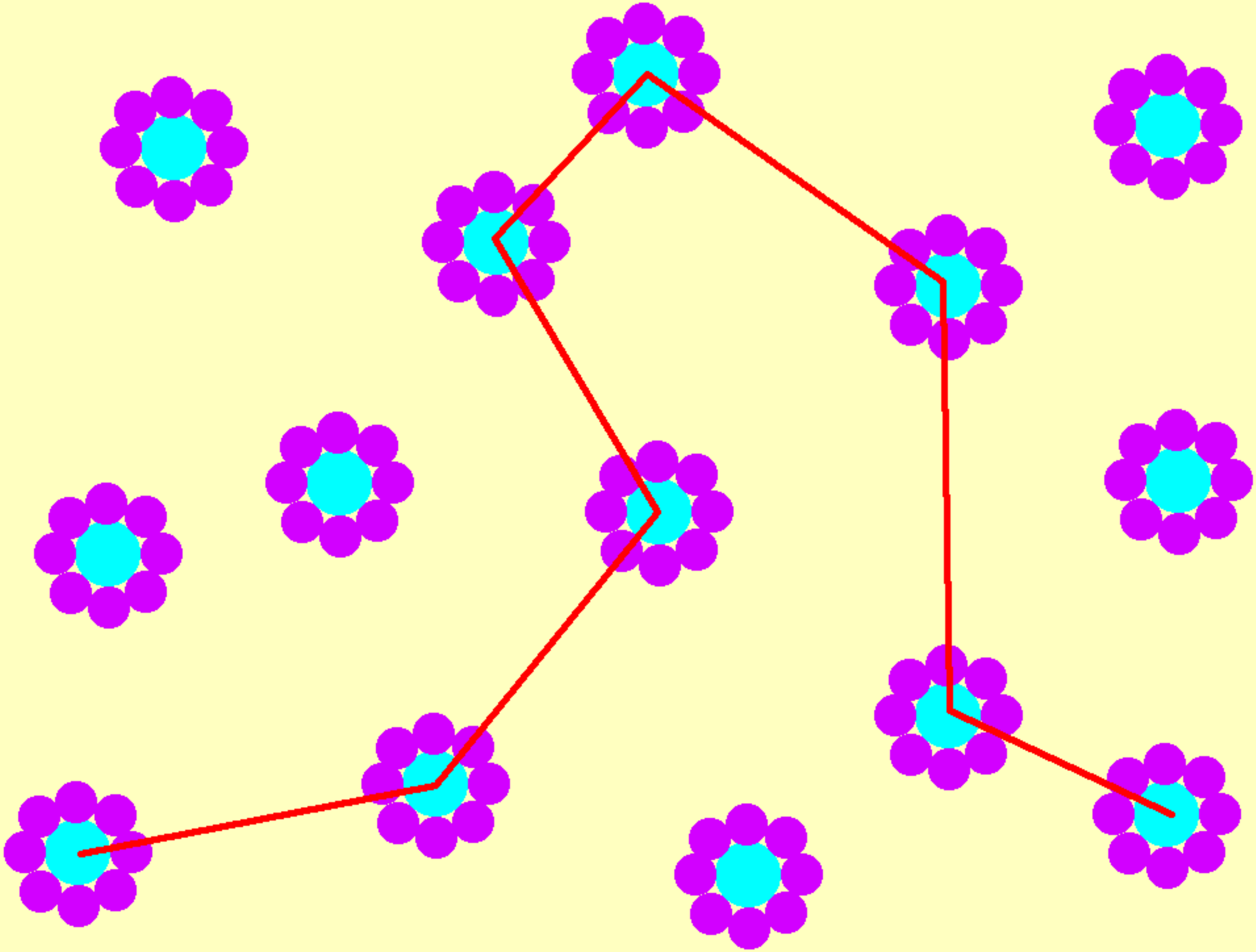
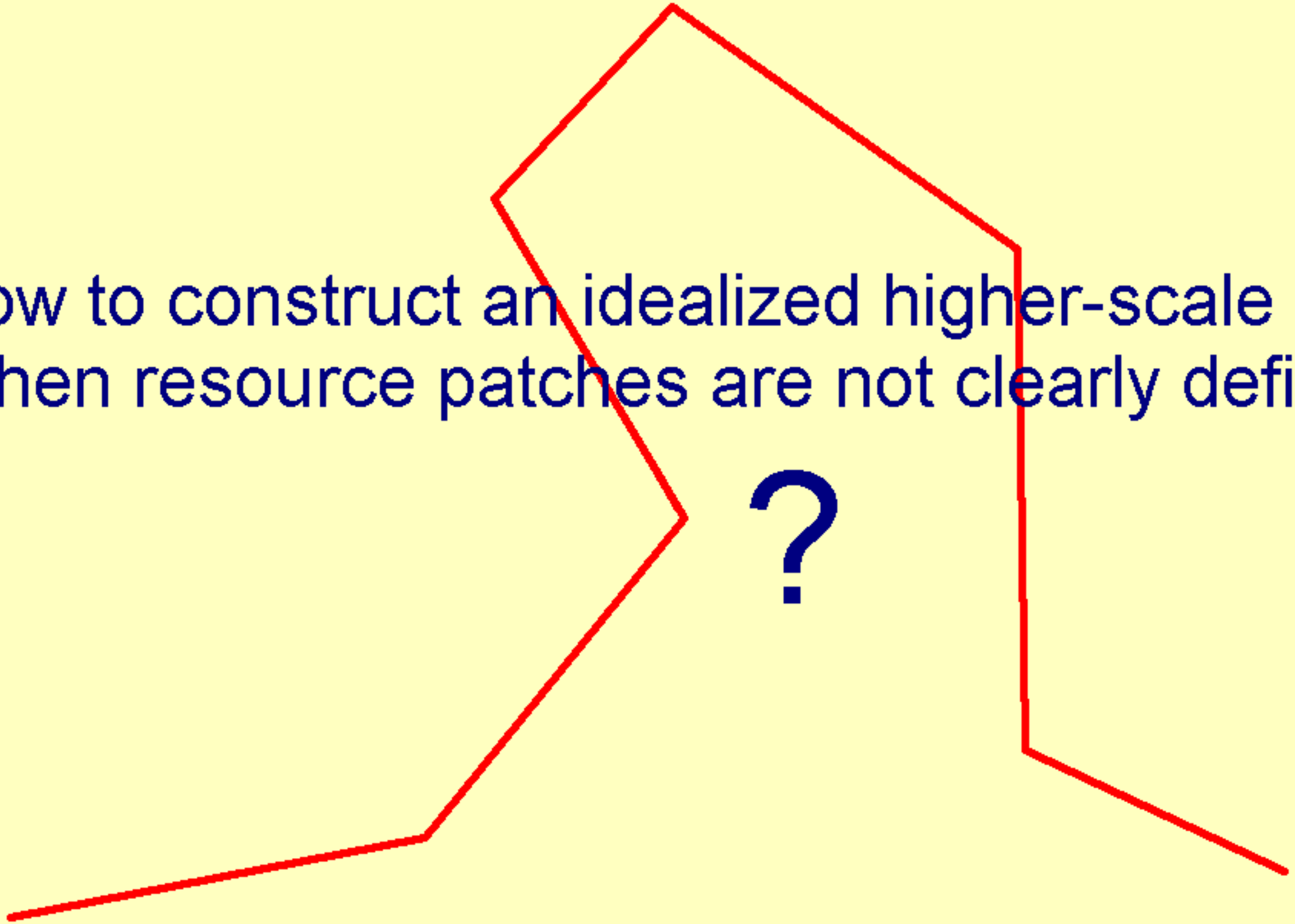


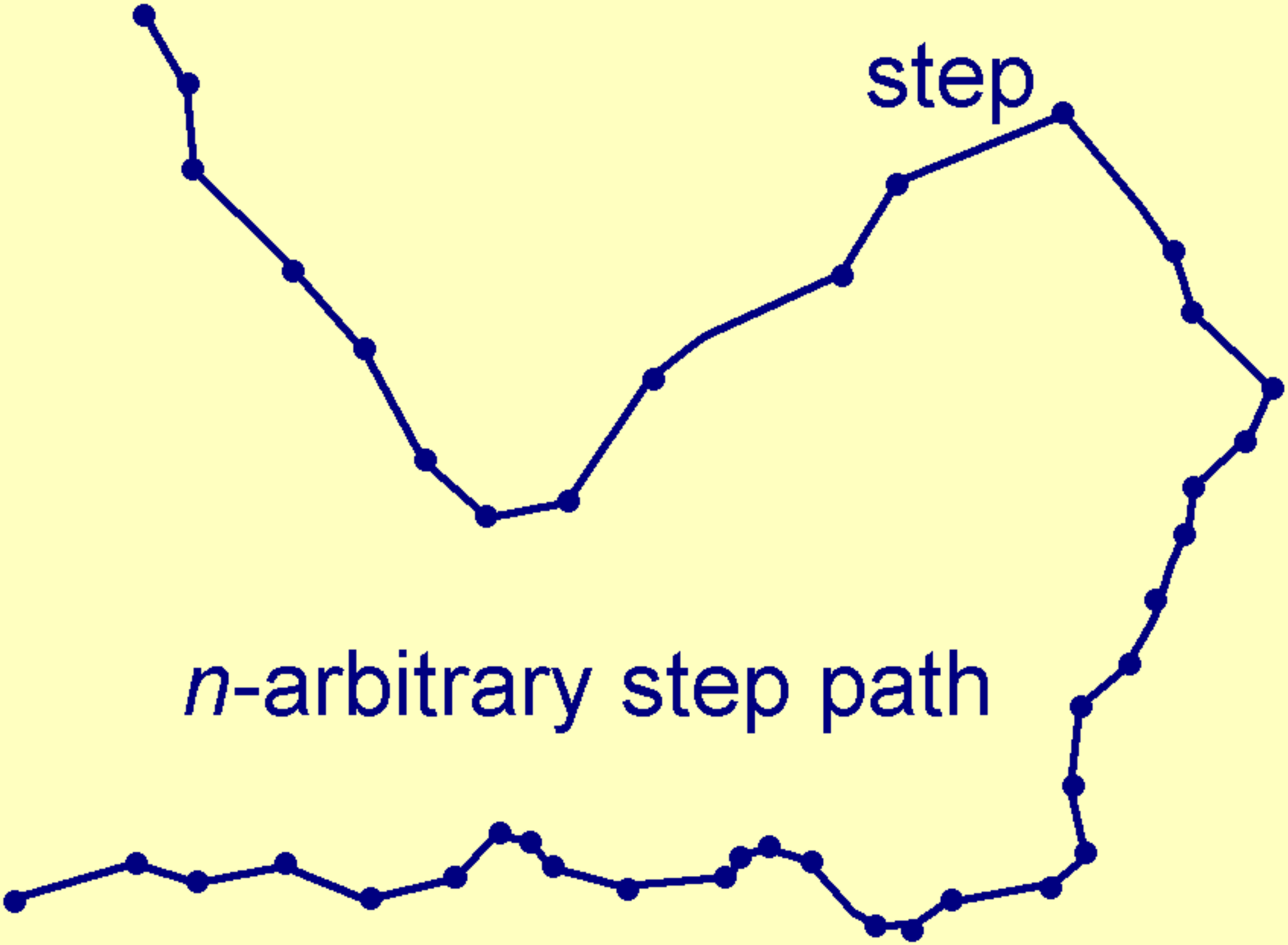


How to construct an idealized higher-scale path when resource patches are not clearly defined



STATISTICS AS AN ECOLOGICAL TRAP

A naive way to construct an idealized path



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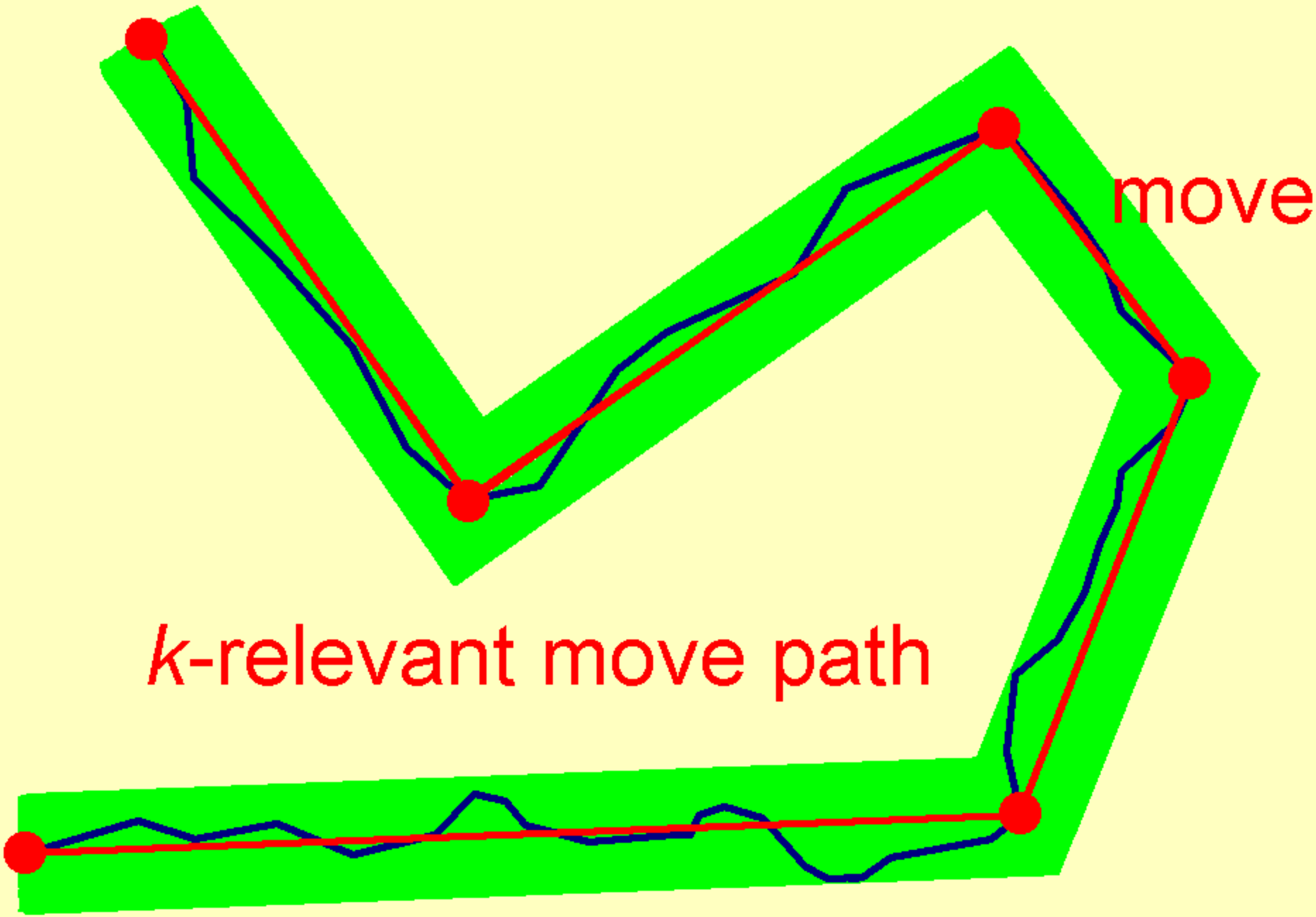
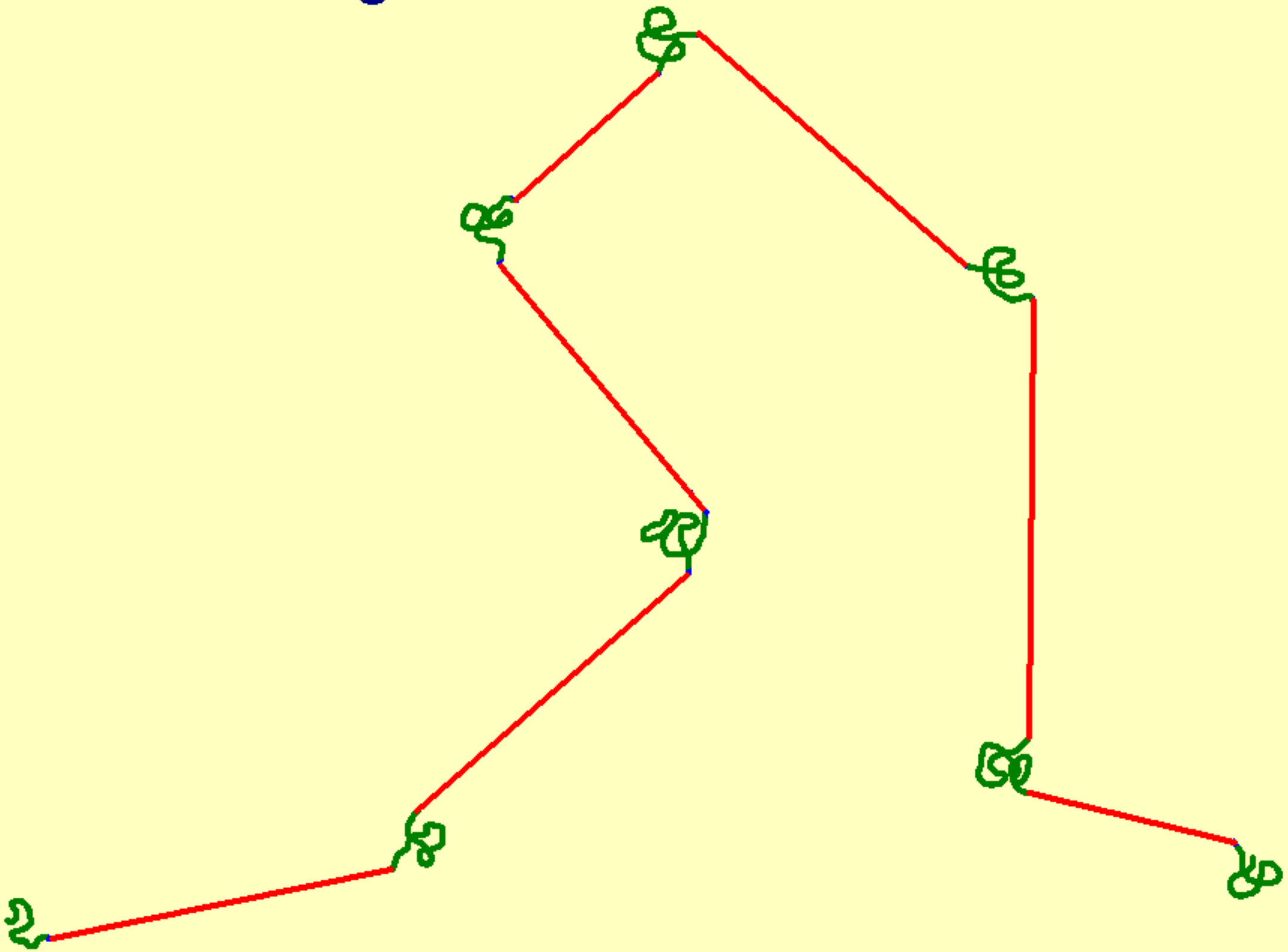
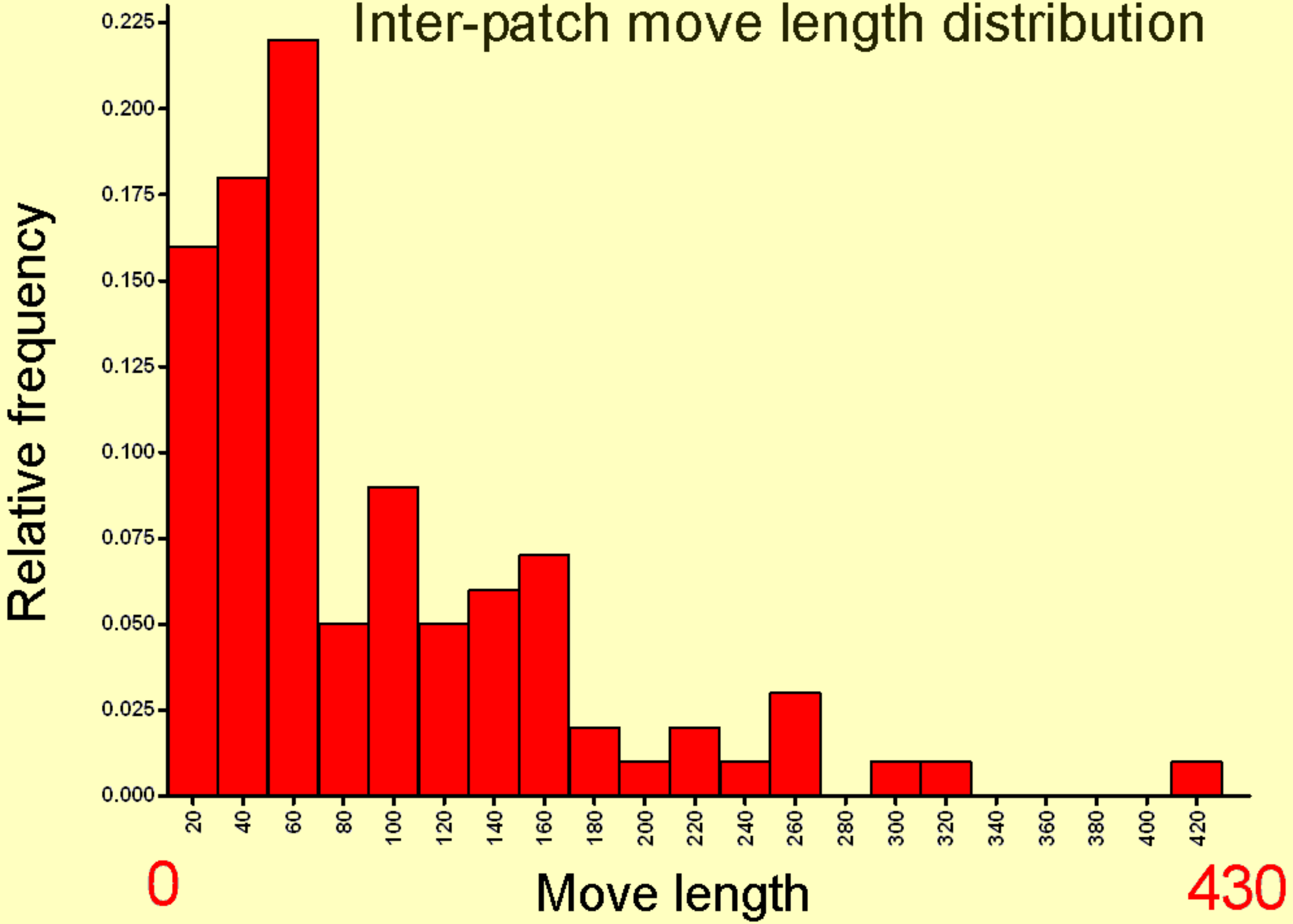


=> a strange two-mode two-scale mixture

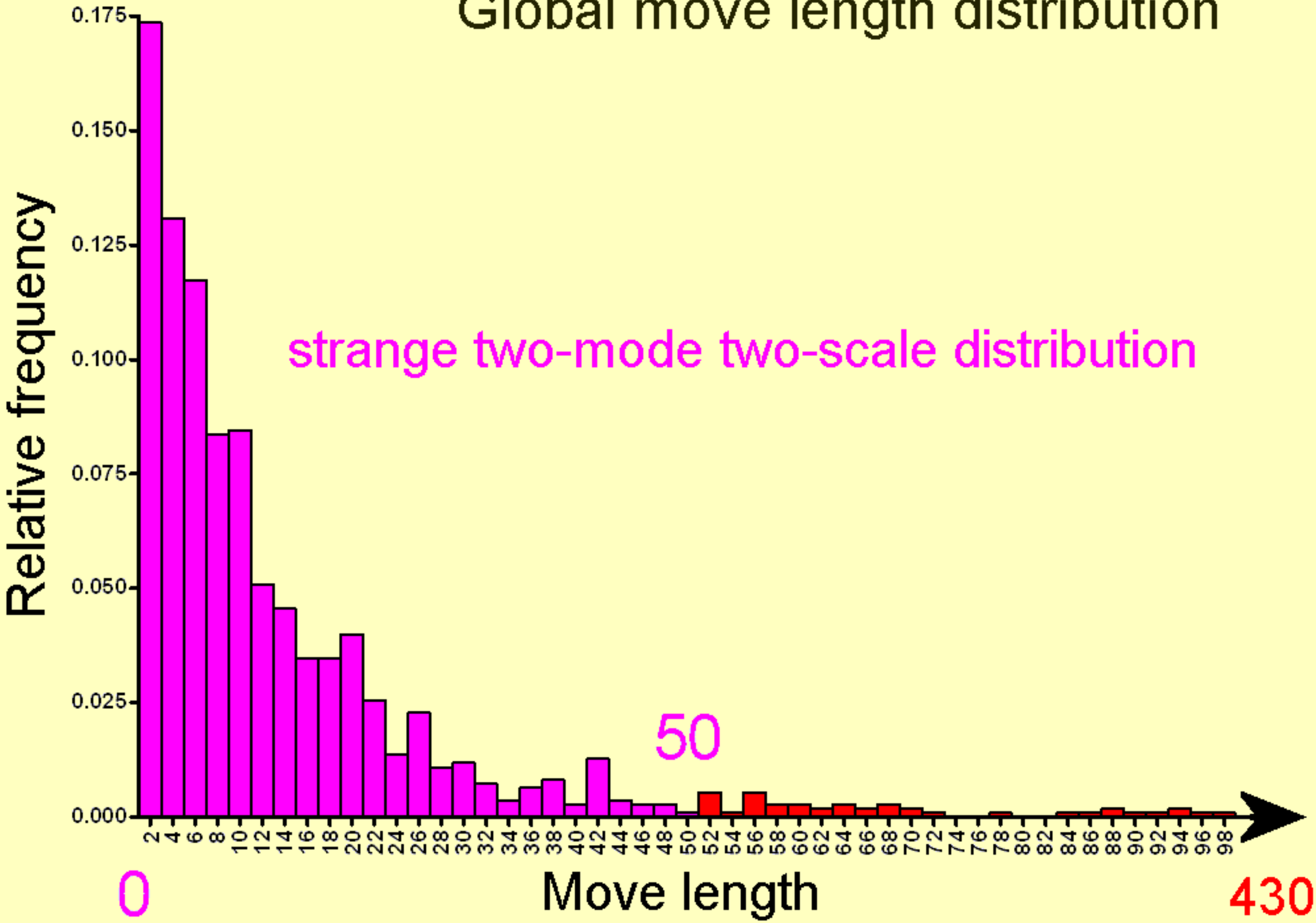


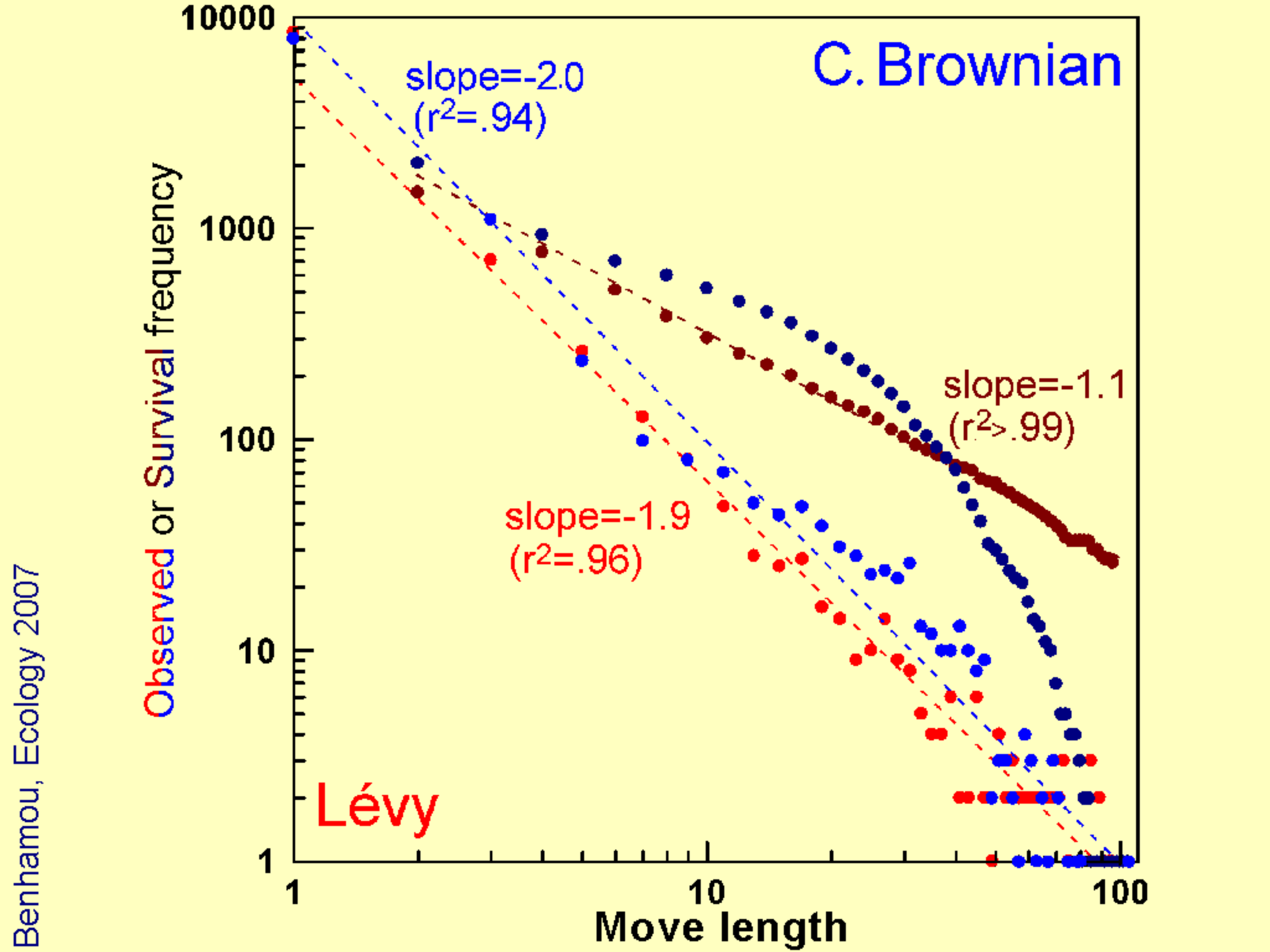
Intra-patch move length distribution

Inter-patch move length distribution



Global move length distribution




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

Step length (MRW) or 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

MRW

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

STATISTICAL (PATTERN)

Vs.

BIOLOGICAL (PROCESS)

MOVEMENT MODELS

Statistic / Mixed / Biological Approaches

General statitistical models (GLMMs, GAMs)
Model selection (AIC, BIC)
Resource Selection (Probability) Function
Lévy Walks / Fractional Brownian Motion
Location-based Kernel Density Estimation

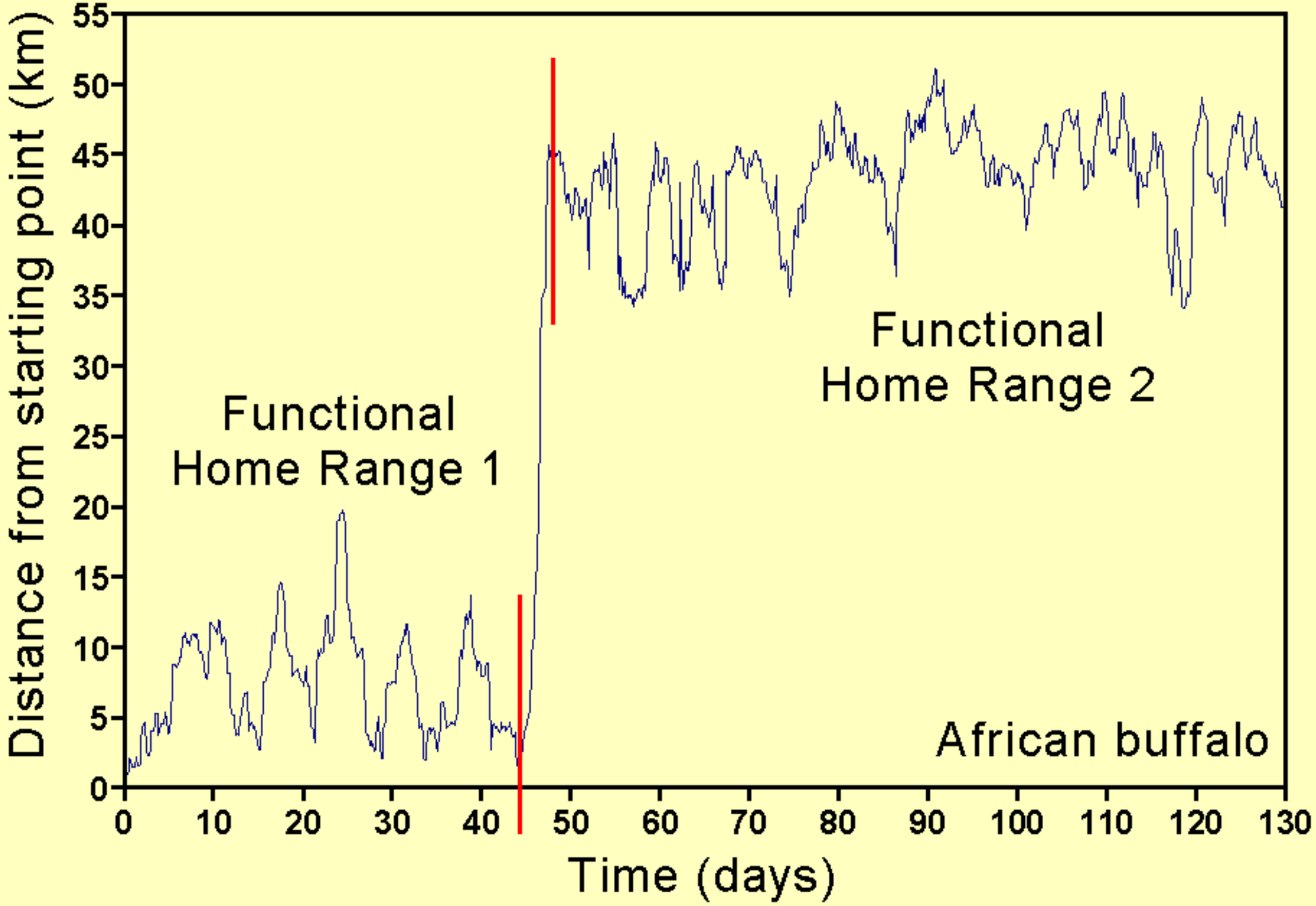
- - - - - - - - - - -

Composite Random Walks
Movement-based Kernel Density Estimation

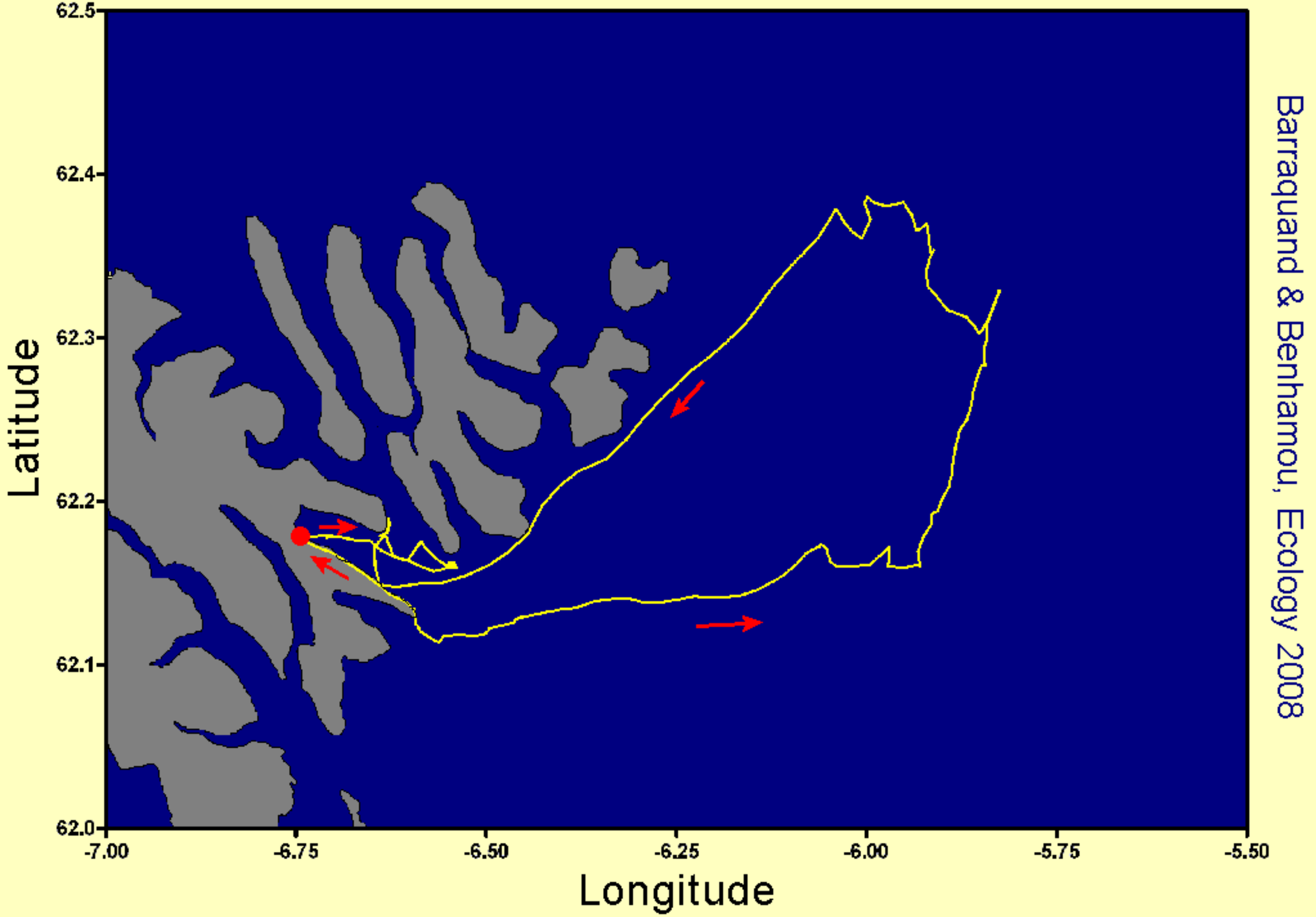
- - - - - - - - - - -

Modelling: Multiscale Multimode BCRW
Analysis:
+ State Space / Hidden Markov Models
+ Segmentation / Clustering

Location-based segmentation

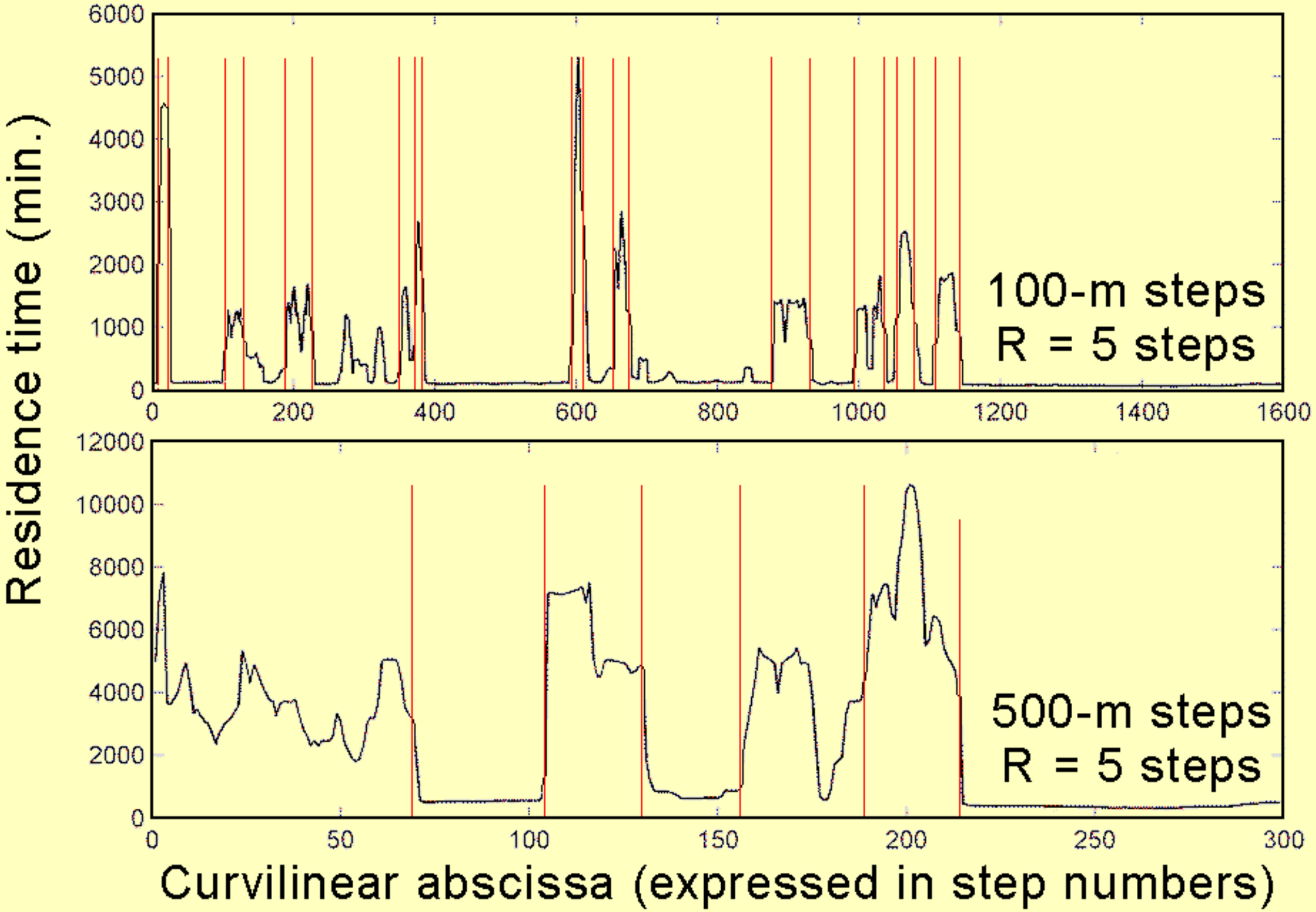


Northern fulmar



Residence time-based segmentation

Northern fulmar



Barraquand & Benhamou, Ecology 2008

CONCLUSION AND PERSPECTIVES

Scale does matter

Animals use movement processes as key tools to adapt to scale-specific features of their environments. Scale-free measures (e.g. apparent fractal dimension) are usually not biologically relevant movement parameters. Scale-free random walks (e.g. Lévy walks) may sometimes be an easy means to represent multi-scale movement patterns but they are certainly not a reliable means to model movement processes.

Next challenges in animal movement studies:

(1) identifying the various environmental scales at which an animal specifically reacts (i.e. biologically relevant scales), and …

(2) determining to which extent theses various scales are coupled or uncoupled (i.e. how a given scale affects other ones).

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(2) determining to which extent theses various scales are coupled or uncoupled (i.e. how a given scale affects other ones).

Biologically relevant scales are those for which key process parameters are stationary

Eloge de la lenteur

"Assurons-nous bien du fait, avant que de nous inquiéter de la cause. Il est vrai que cette méthode est bien lente pour la plupart des gens qui courent naturellement à la cause, et passent par-dessus la vérité du fait ; mais enfin éviterons-nous le ridicule d'avoir trouvé la cause de ce qui n'est point."

Fontenelle, 1687
Histoire des oracles

THAT'S ALL FOLKS

...thanks