Search strategies and adaptation in Drosophila larvae

Jimena Berni
University of Sussex

Neuroloco 22 UCSB
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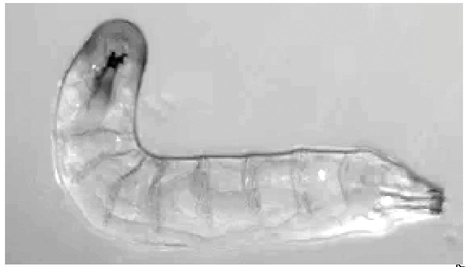
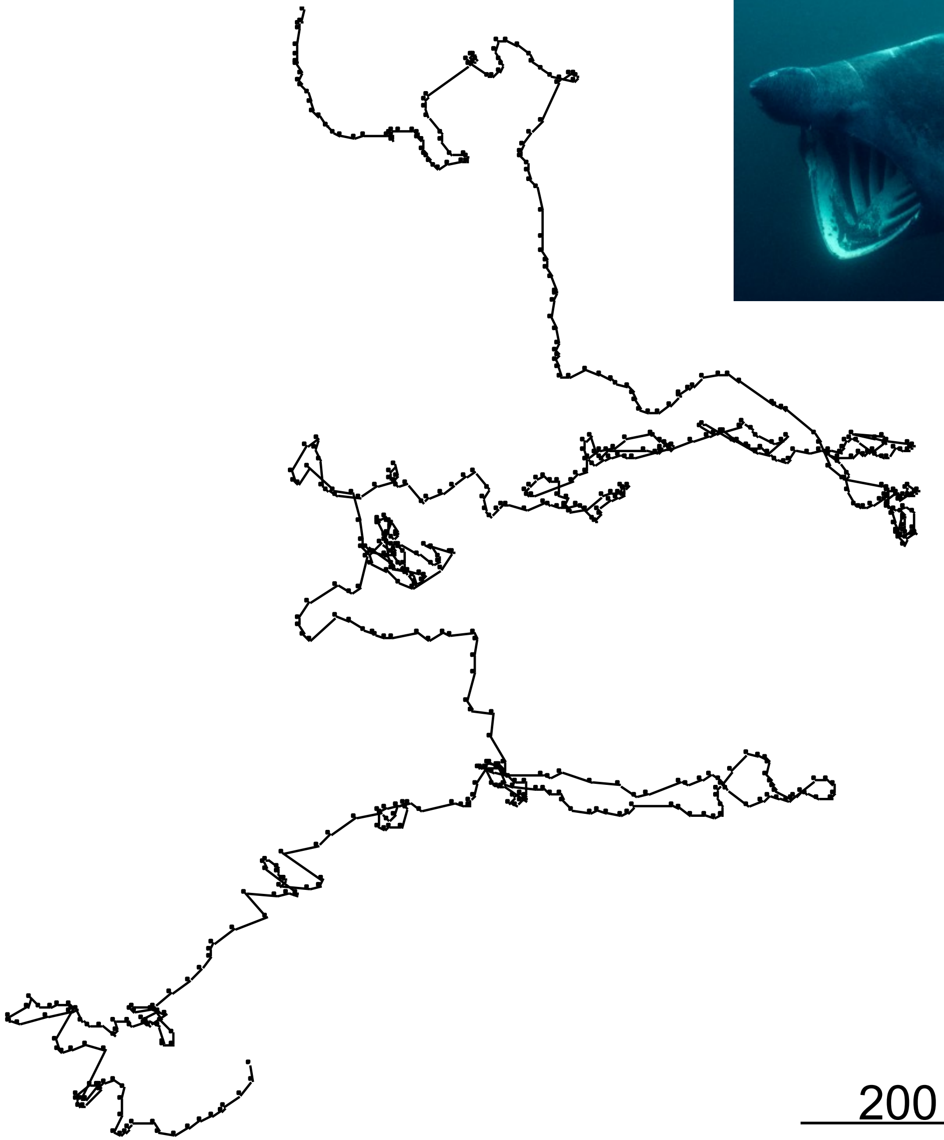
The challenge of finding and exploiting food in a changing environment

And when there are no clues or cues?

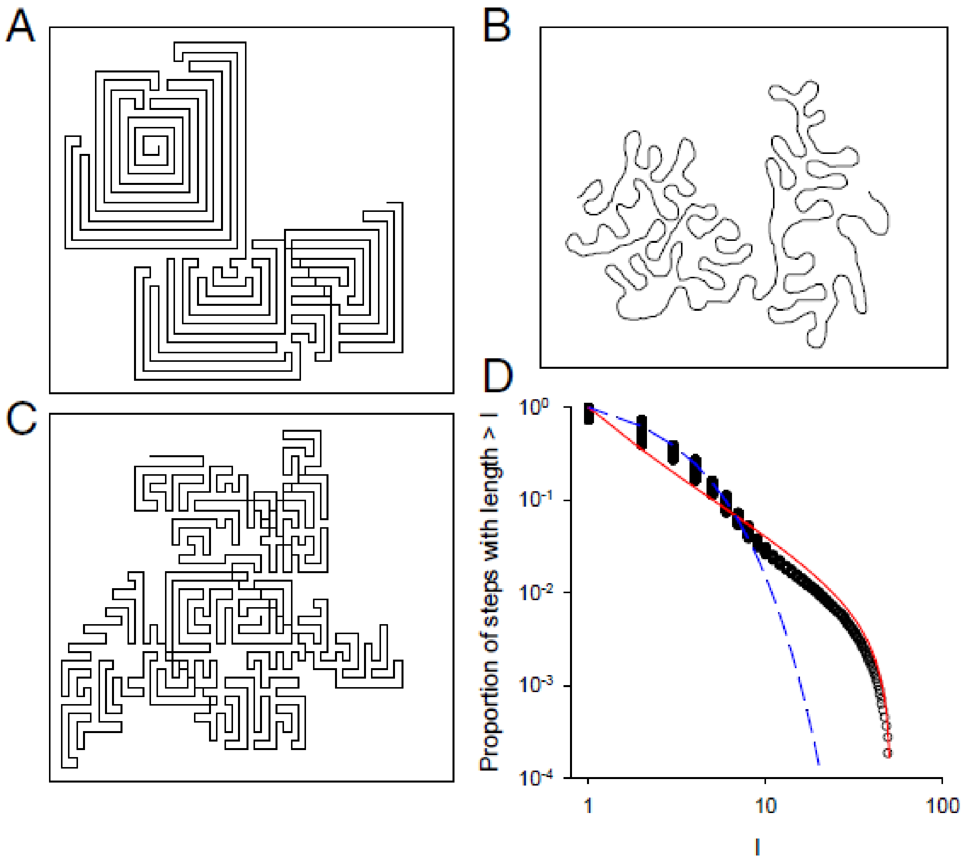
Animals explore alternating straight runs and turns





Random walks are widespread in the animal kingdom

Random walks in trace fossils



Sims et al. PNAS 2014

Cretaceous *Cosmorhaphe*

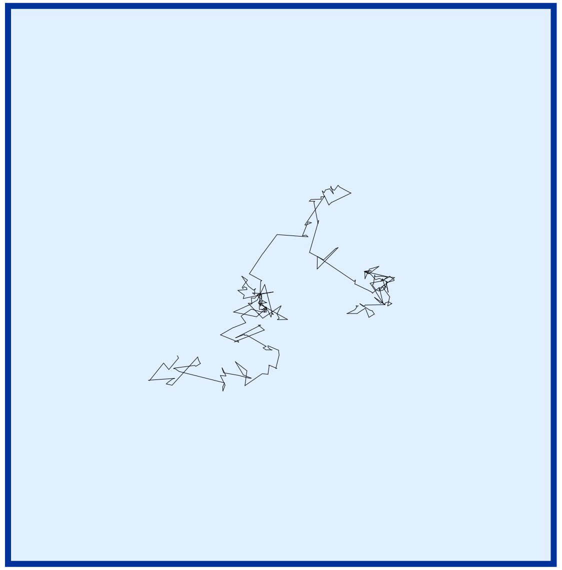
Self avoiding random walk plus random obstructions (rocks or food gaps or innate cueing)

emerges as Lévy-like movement pattern

Different types of random walks

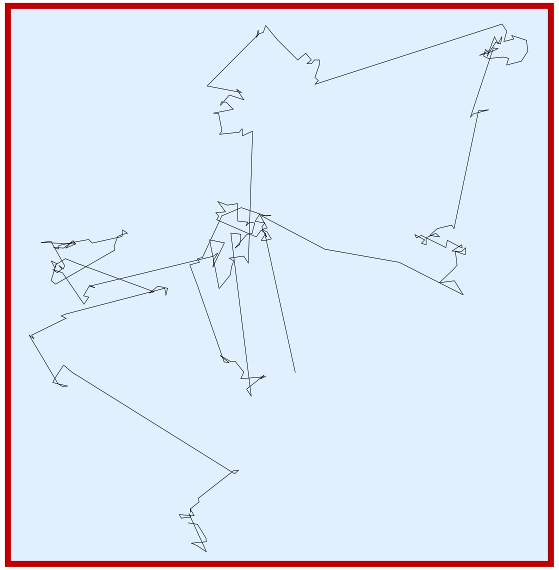
Brownian

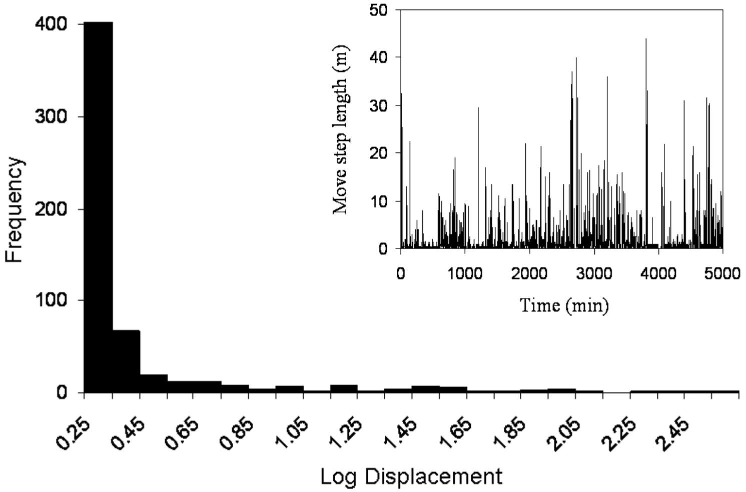
Normally diffusive (exponential)

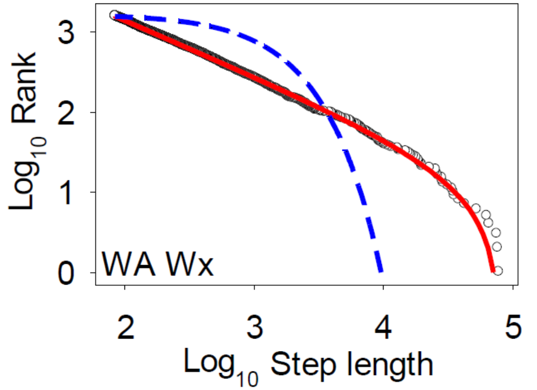


Lévy walk

Superdiffusive (power law)







Exponential

Truncated power law
(Lévy walk)

How might chances be maximised when knowledge is incomplete?

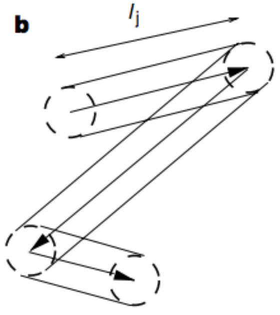
A model of random searches

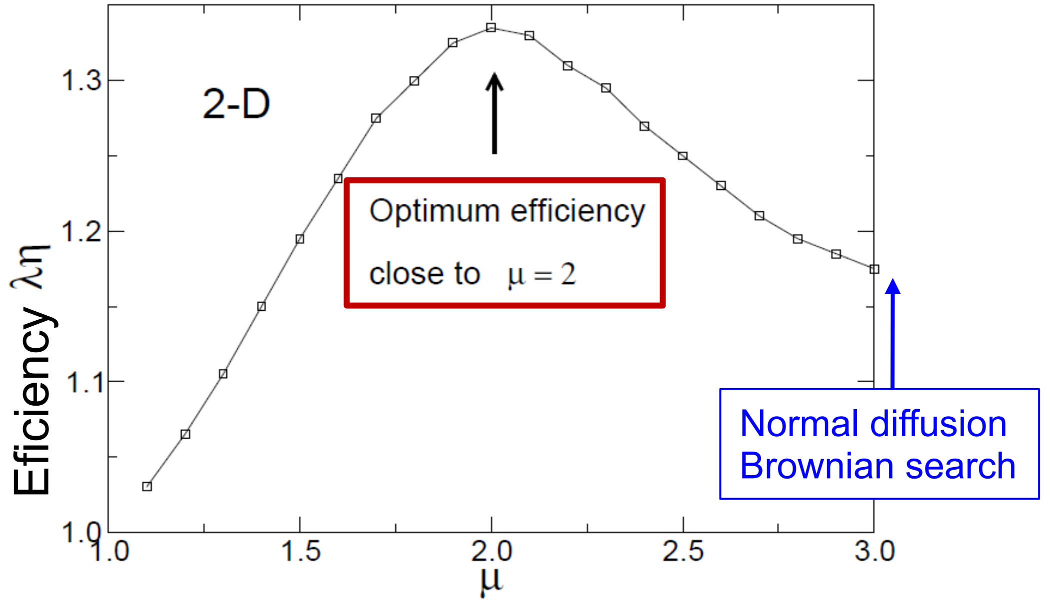
Specialized random walk (the so-called Pareto-Lévy distribution)

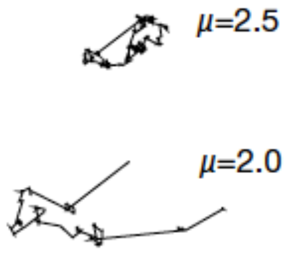
$$P(l_j) \sim l_j^{-\mu}$$

with $1 < \mu \leq 3$

where l_j is the flight length (move step length), μ the power law exponent

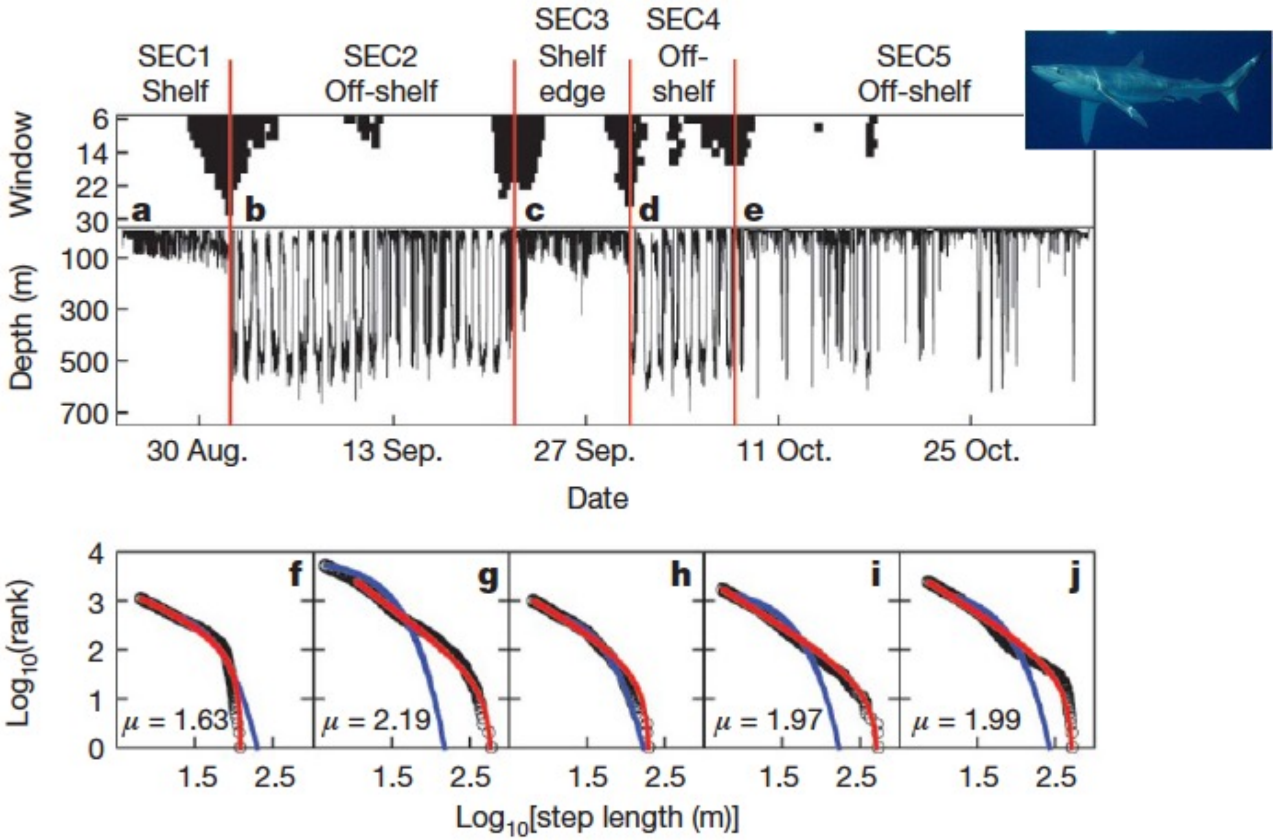


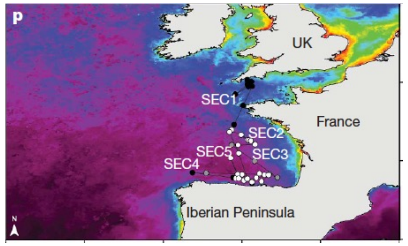


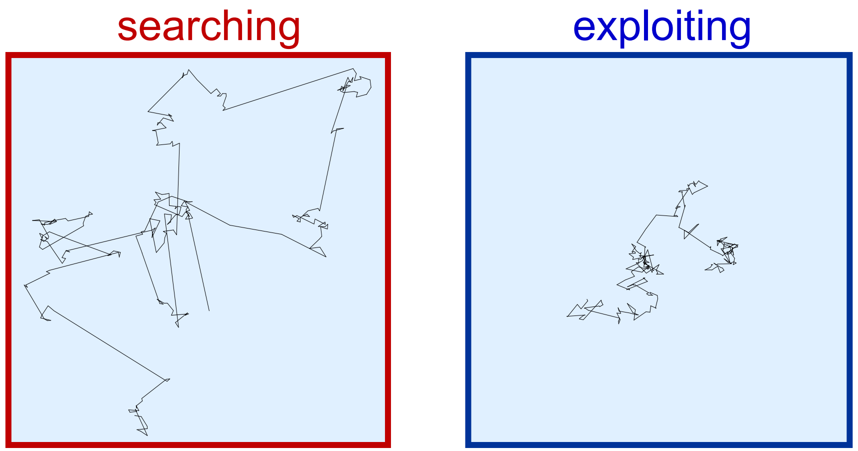


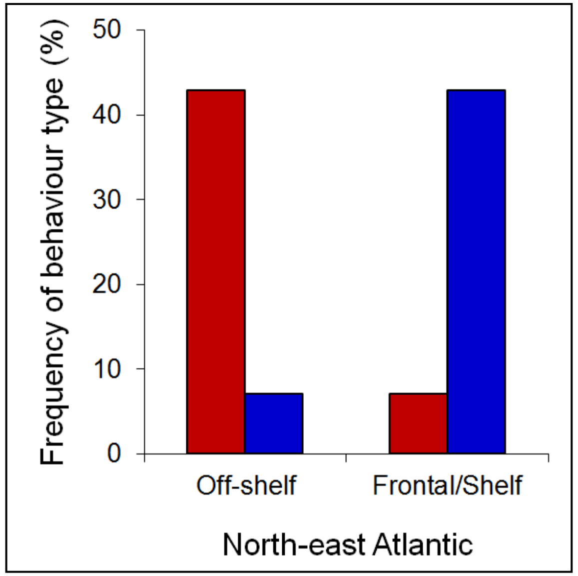
From: GM Viswanathan *et al.* (1999) Optimizing the success of random searches. *Nature* 401: 911-914

Different strategy linked to environmental context









Humphries et al., Sims *Nature* (2010)

What are the generative mechanisms?

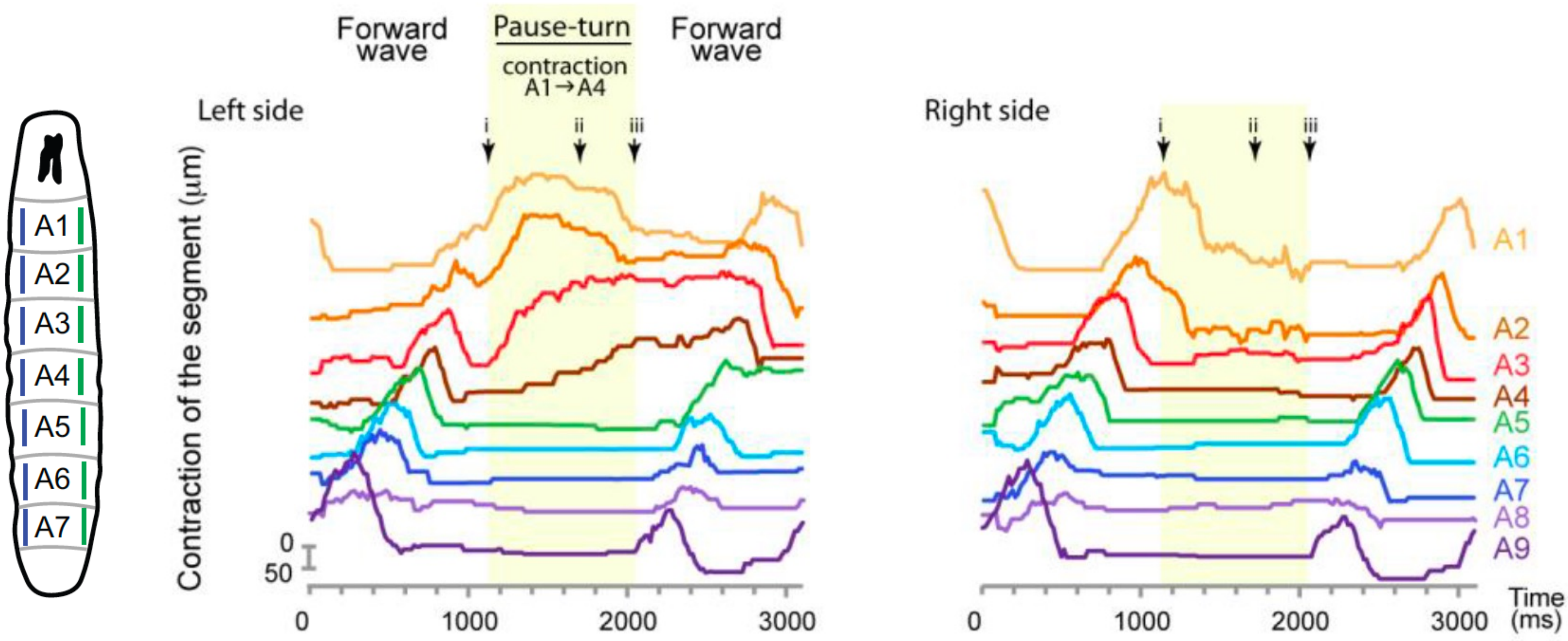
If movement patterns resembling Lévy walks are so widespread among diverse animals, how are they generated?

Intrinsic Hypothesis: it arises from endogenous neuronal activity resulting that can adapt to different resource distributions.

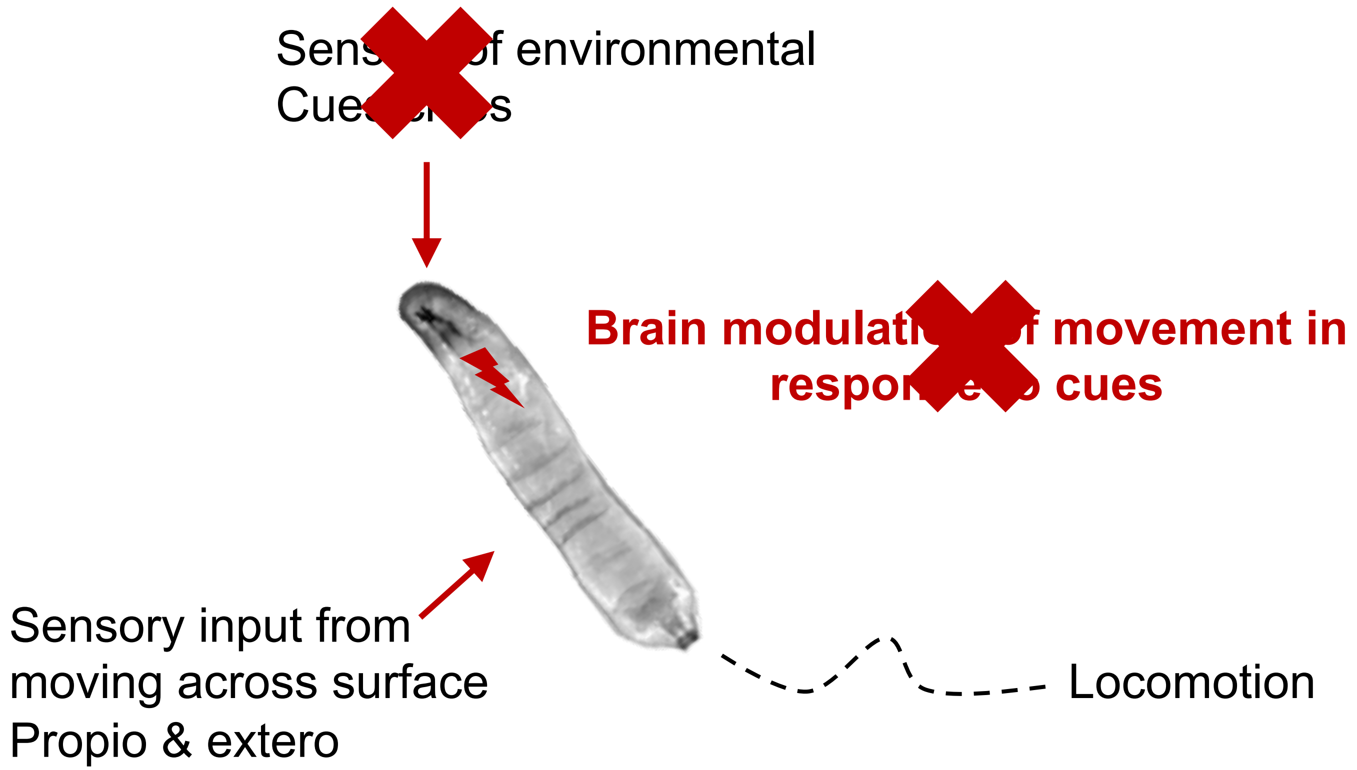
Extrinsic Hypothesis: sensory interactions of animals moving in simple, straight line paths in fractal environments, for example, power-law distributions of resource patches, give rise to Lévy patterns as an emergent phenomena

Drosophila larvae executes a search routine, which consists of crawls and pause turns

Motor patterns during crawl and turn

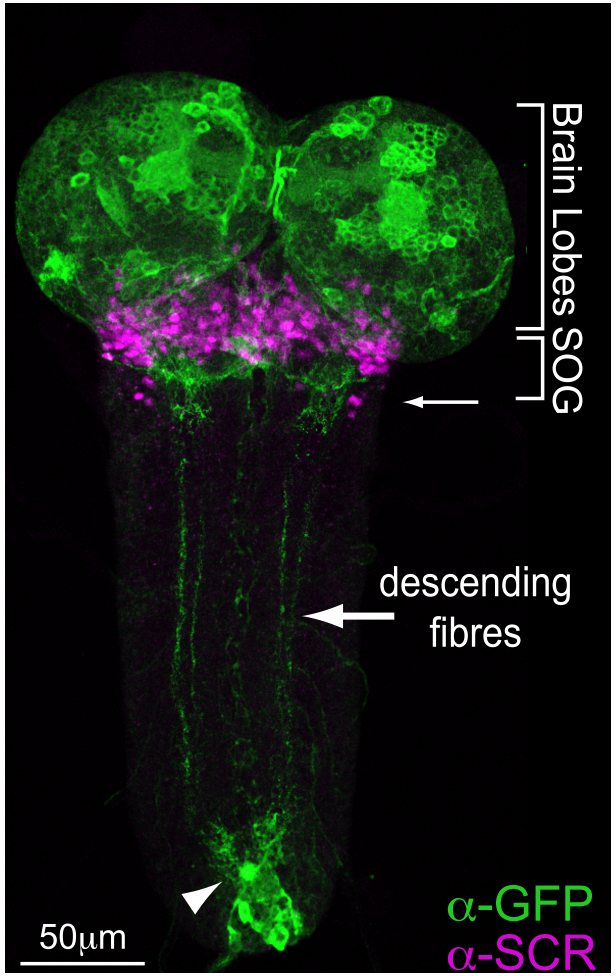


Hypothesis: LW-like movements arise from endogenous neurophysiological processes



Neuronal activity can be manipulated in distinct regions of the nervous system

Brain lobes (BL-gal4)



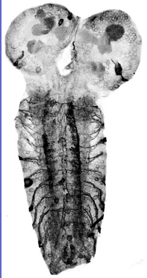
elav-GAL4, *tsh*-GAL80;
cha3.3-GAL80, UAS-mCD8-GFP

Panneural (*elav*-Gal4)

elav-GAL4/ UAS-mCD8-GFP

Berni et al., *Curr Biol. 2012*

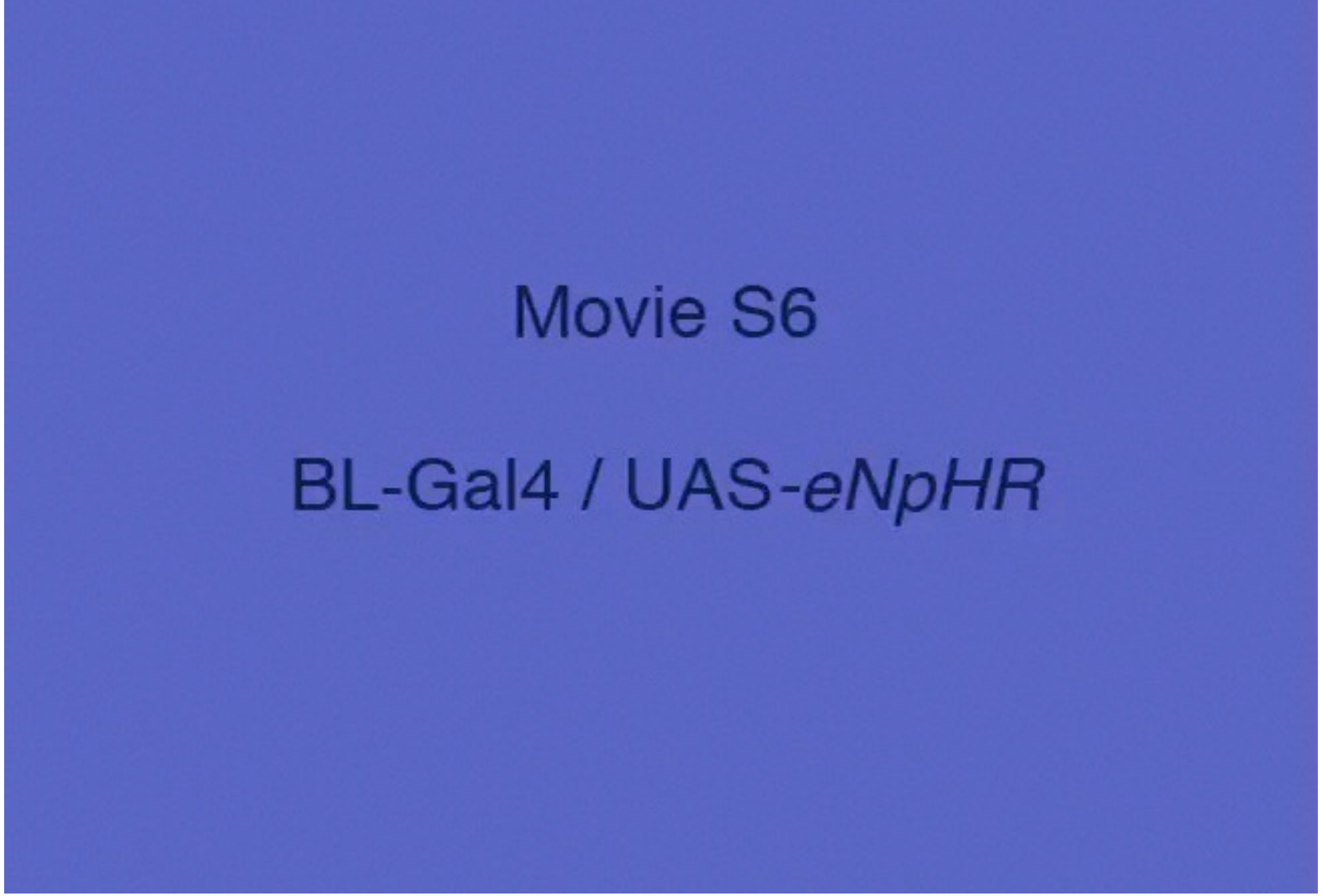
Effect of blocking neuronal activity in entire nervous system

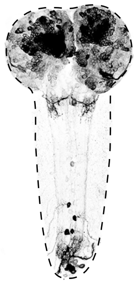


Berni et al., *Curr Biol. 2012*

Exploration is autonomously generated by the thoracic and abdominal neuromeres

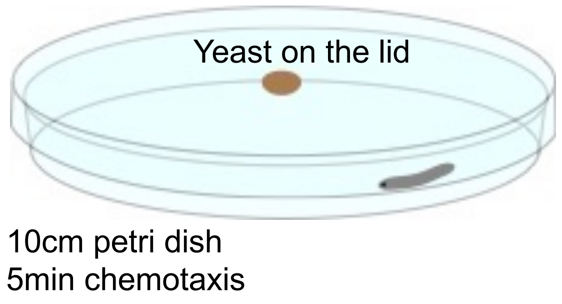
Optogenetics: using *halorhodopsin*

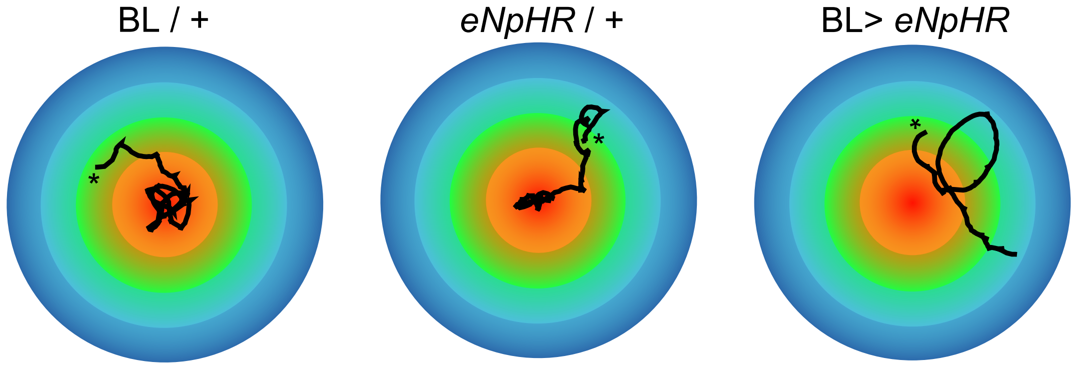


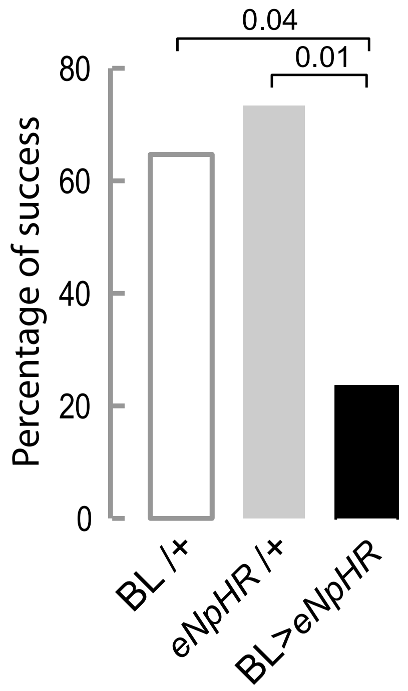


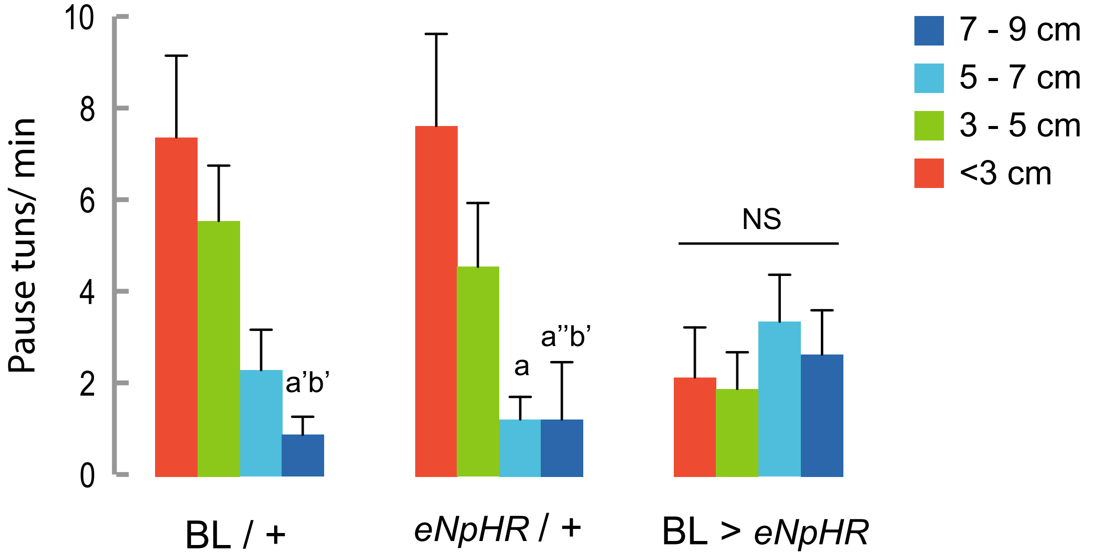
Berni et al., *Curr Biol. 2012*

Chemotaxis is affected when brain activity is blocked by ***Halorhodopsin***



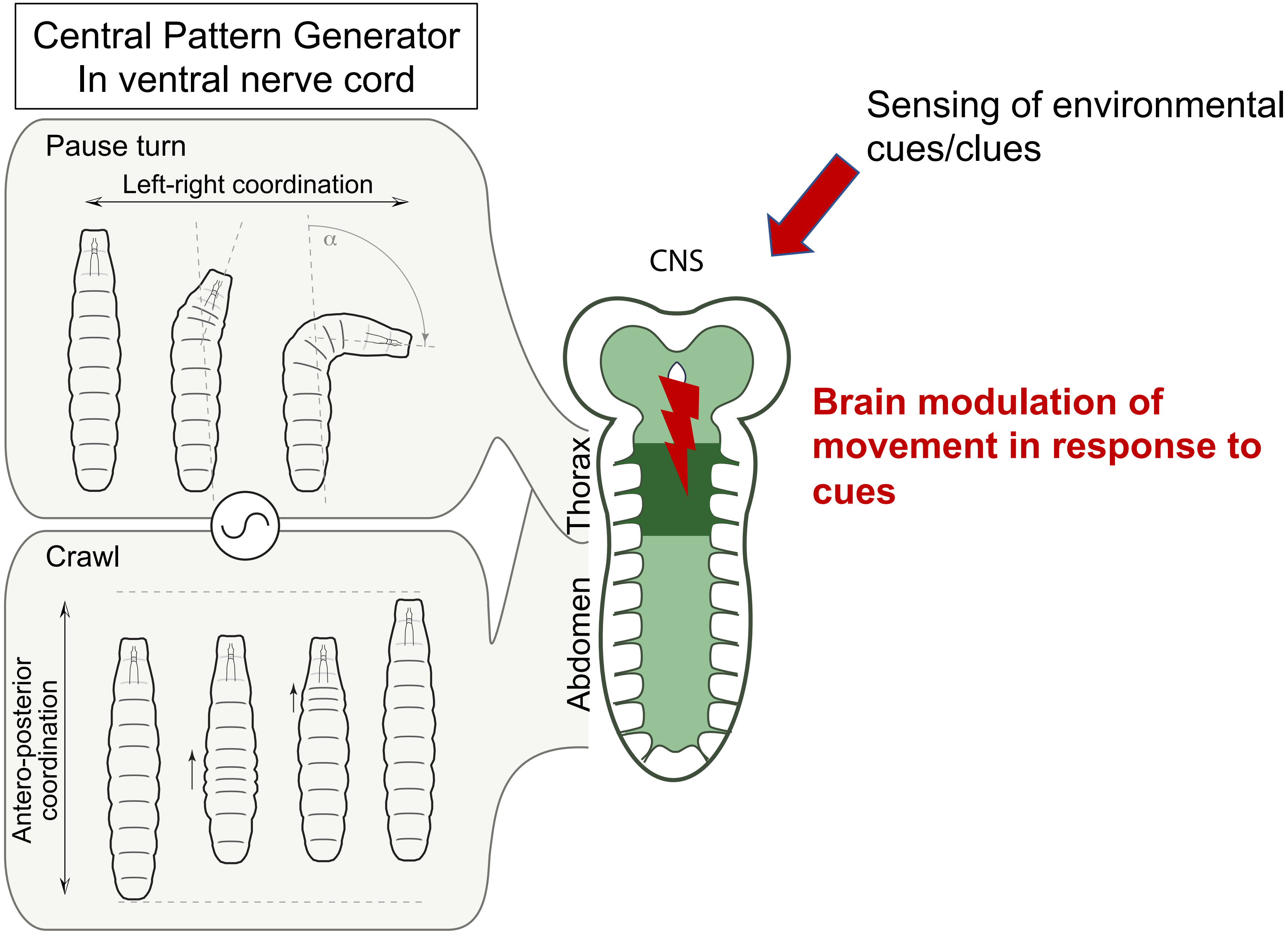




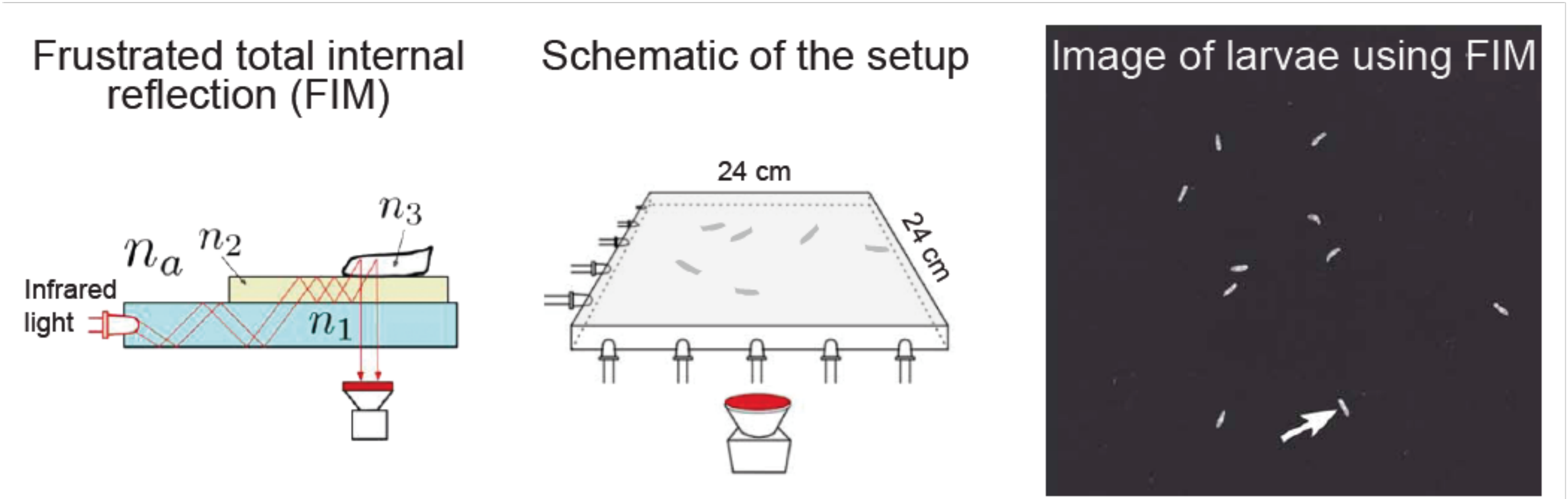


Berni et al., *Curr Biol. 2012*

Circuitry for exploration



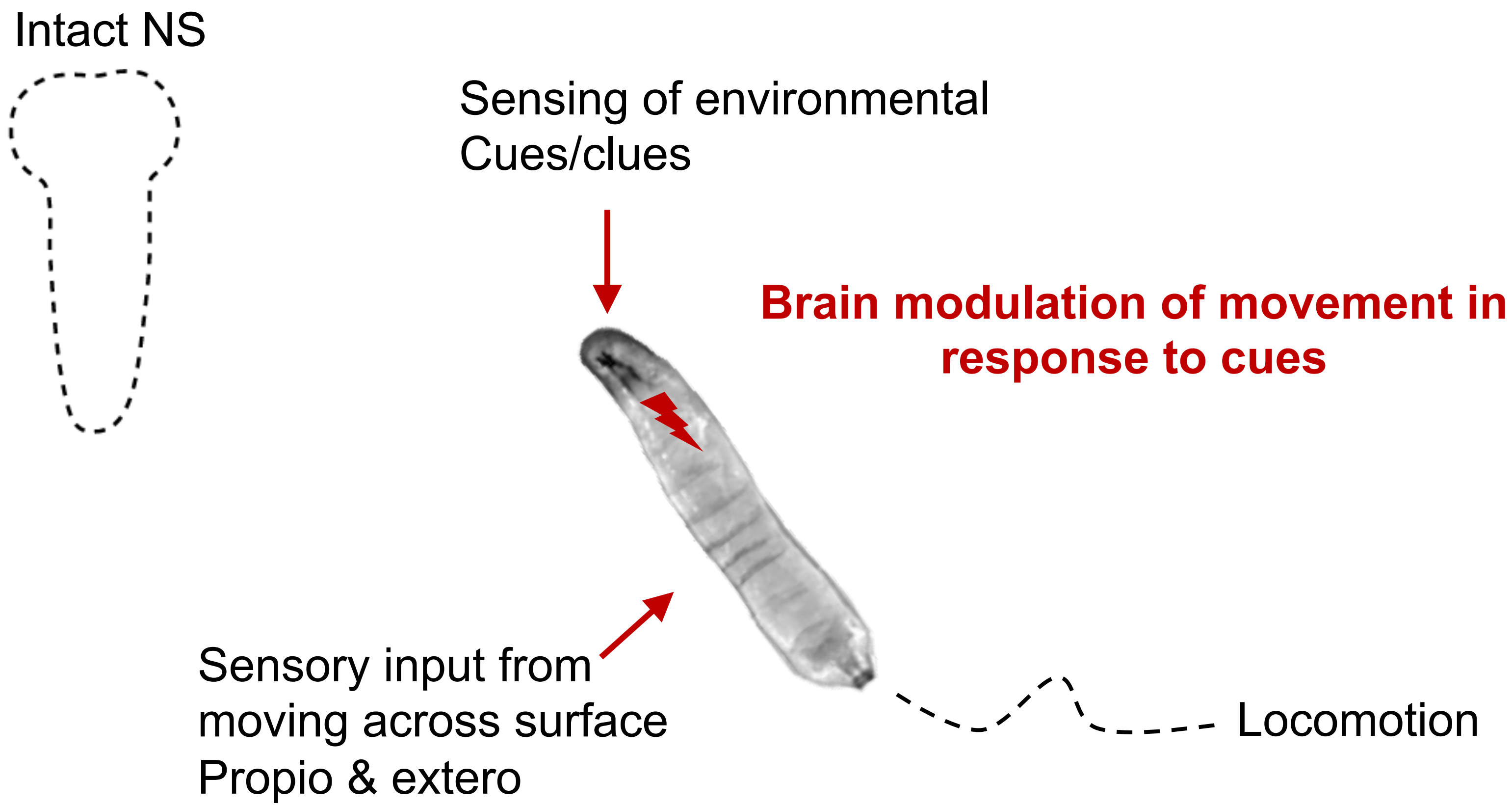
The experimental method to test the Lévy walk generative hypothesis



Modified from Risse et al. 2012

- Long recordings (50 min) – 10 larvae per experiment – 3 replicates
- Large spatial scale (240 x 240 mm^2 arenas compare to larva 2.3 mm)
- Recordings infrared light
- Stable temperature

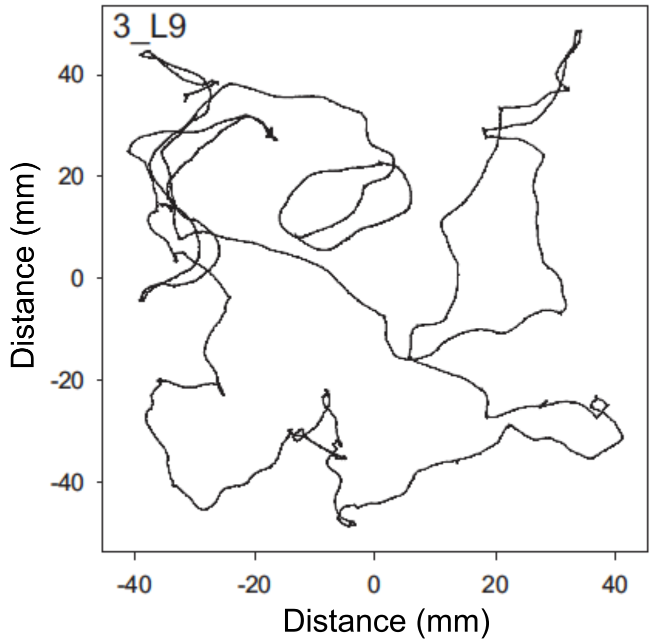
Hypothesis: LW-like movements arise from endogenous neurophysiological processes



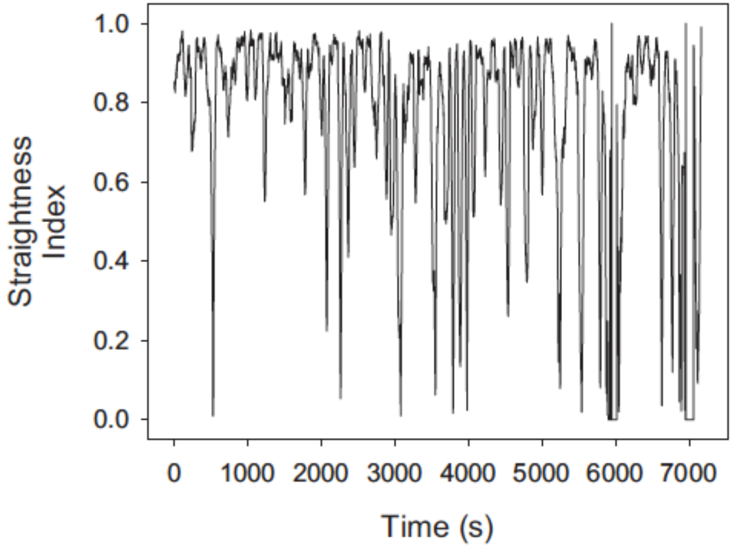
Exploration strategy in an environment with minimal external cues

Control larva (shi / + 22 ^{o}C)

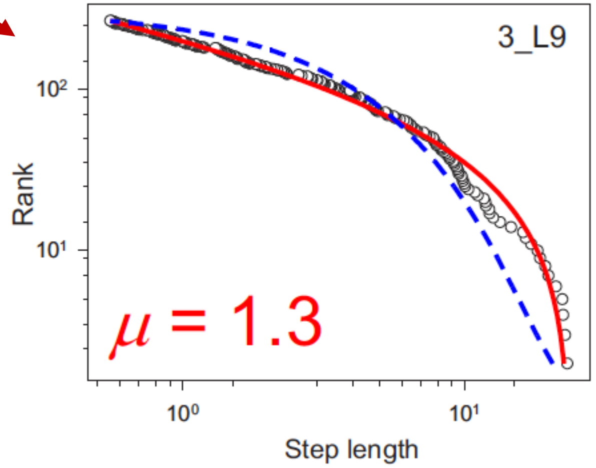
Trajectory



Tortuosity



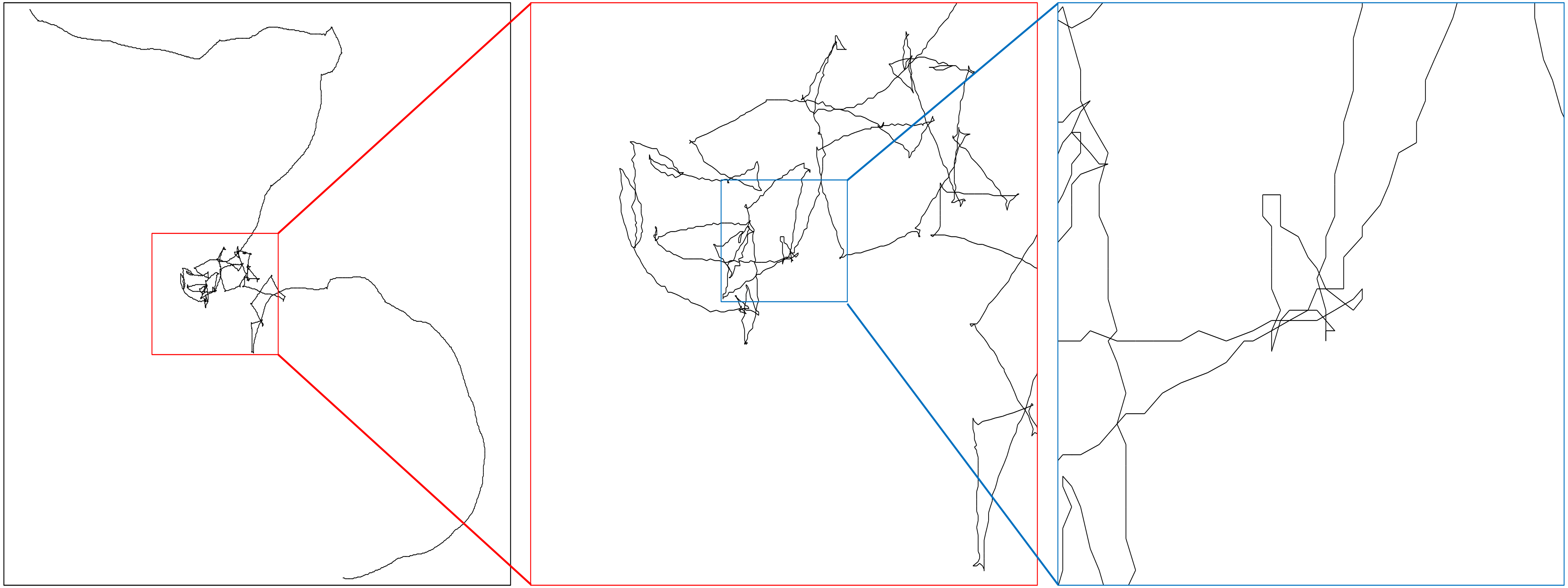
Model Fitting



Sims,,,Berni, Elife 2019

Complex path at several scales, reminiscent of self-similar fractal patterns – Levy walk is the signature of a fractal

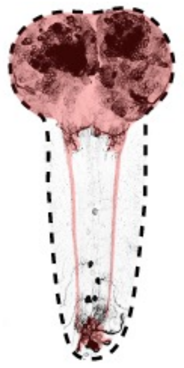
Control larva (BL / + 33 ^{o}C)

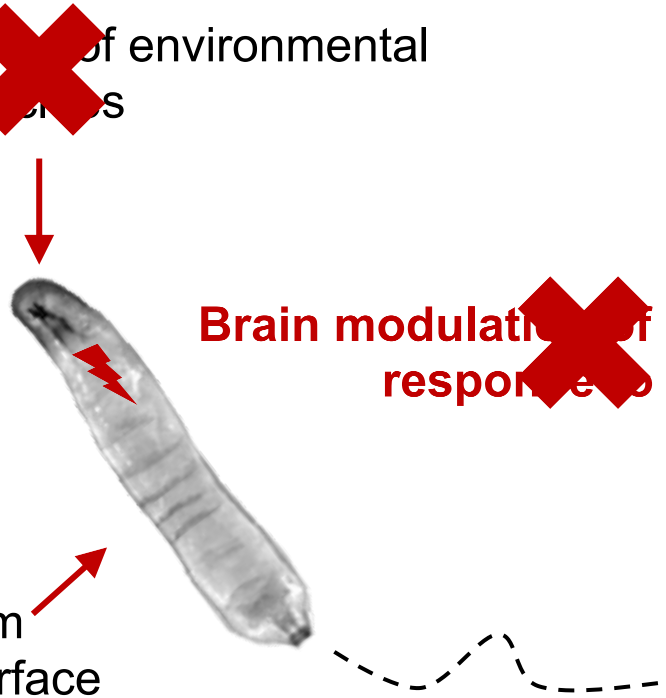


Sims,,,Berni, Elife 2019

Hypothesis: LW-like movements arise from endogenous neurophysiological processes

Blocked brain
with thermogenetics





Sens… of environmental
Cue… s

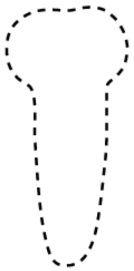
Brain modulati… f movement in respon… cues

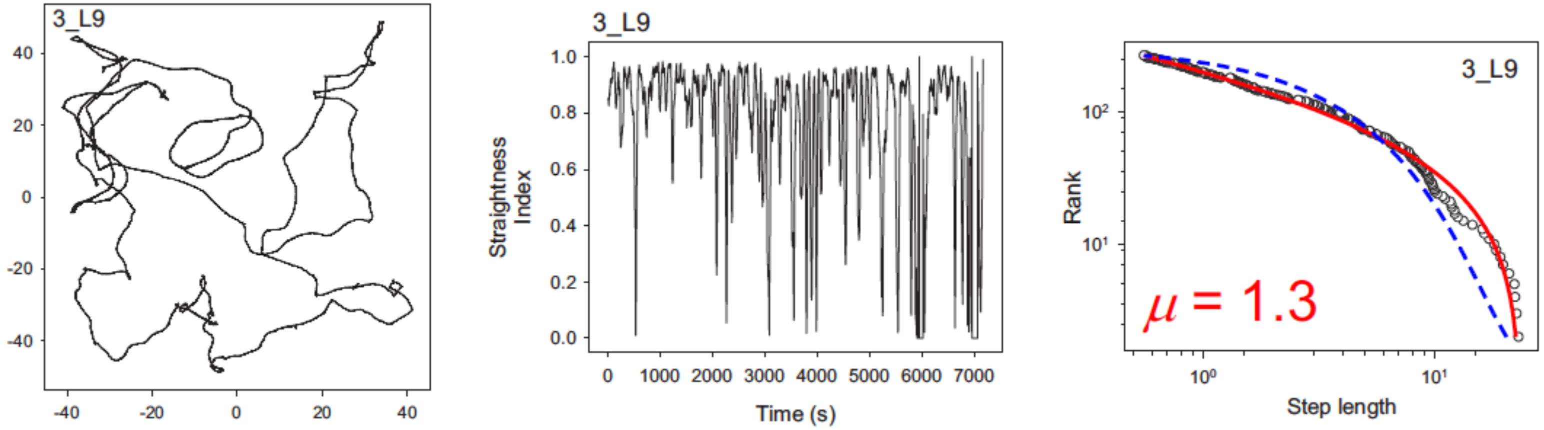
Sensory input from
moving across surface
Propio & extero

Locomotion

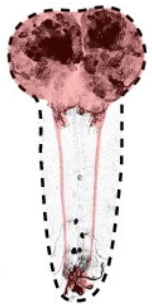
Long-term movements resembling Lévy walks consistent in BL > *shi*^{ts} larva

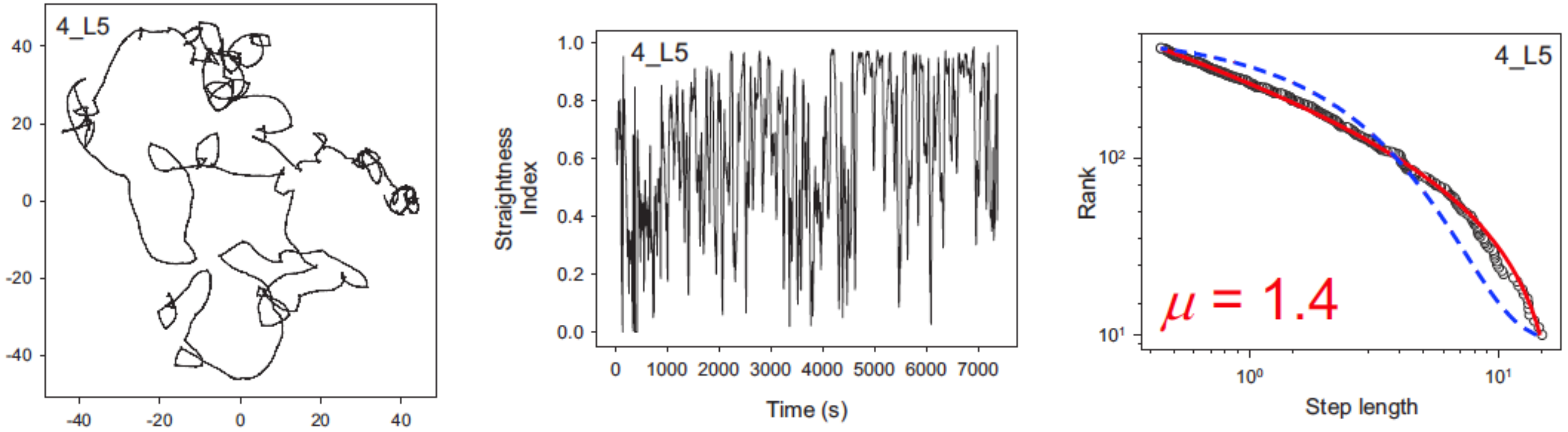
Shi/+





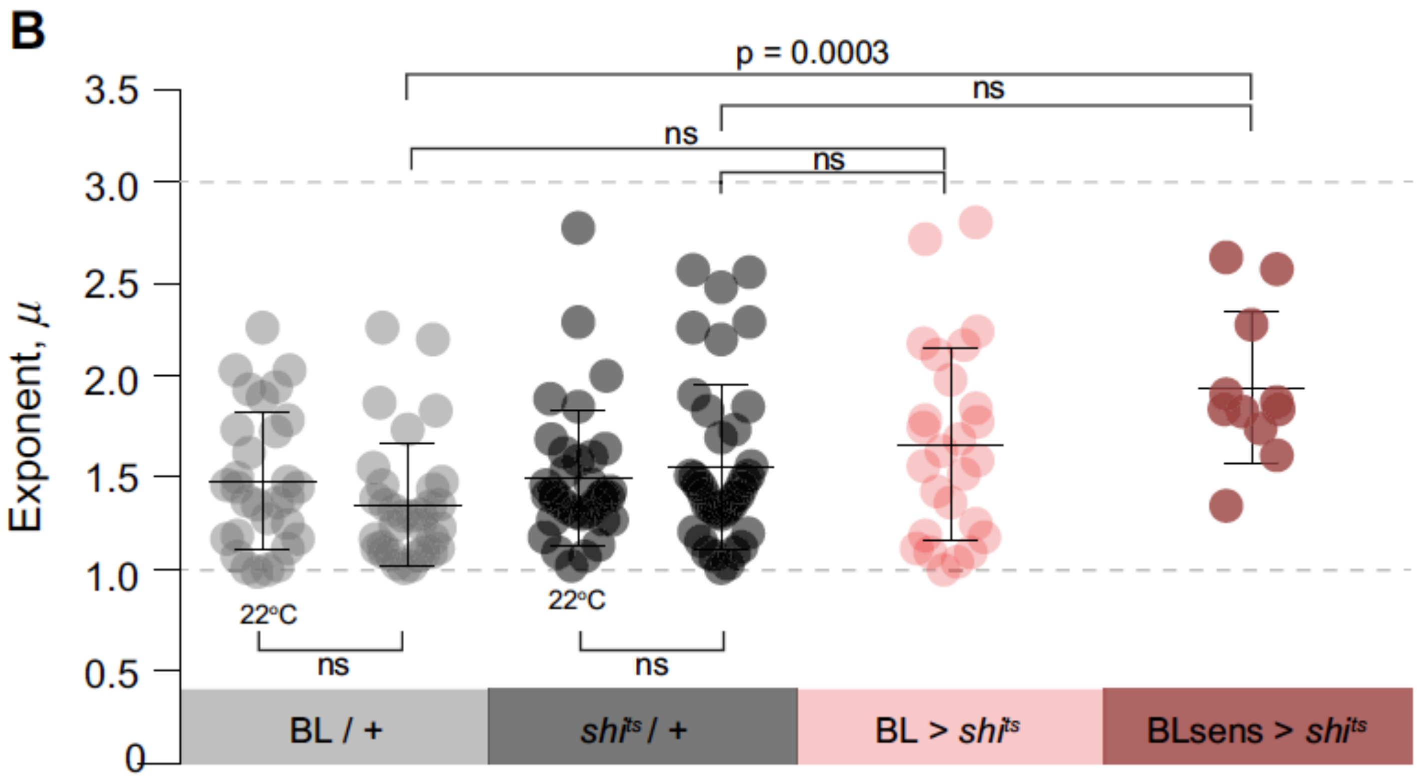
BL > shi





Sims,,,Berni, Elife 2019

Summary data of truncated power law exponents across treatments



Sims,,,Berni, Elife 2019

Results summary

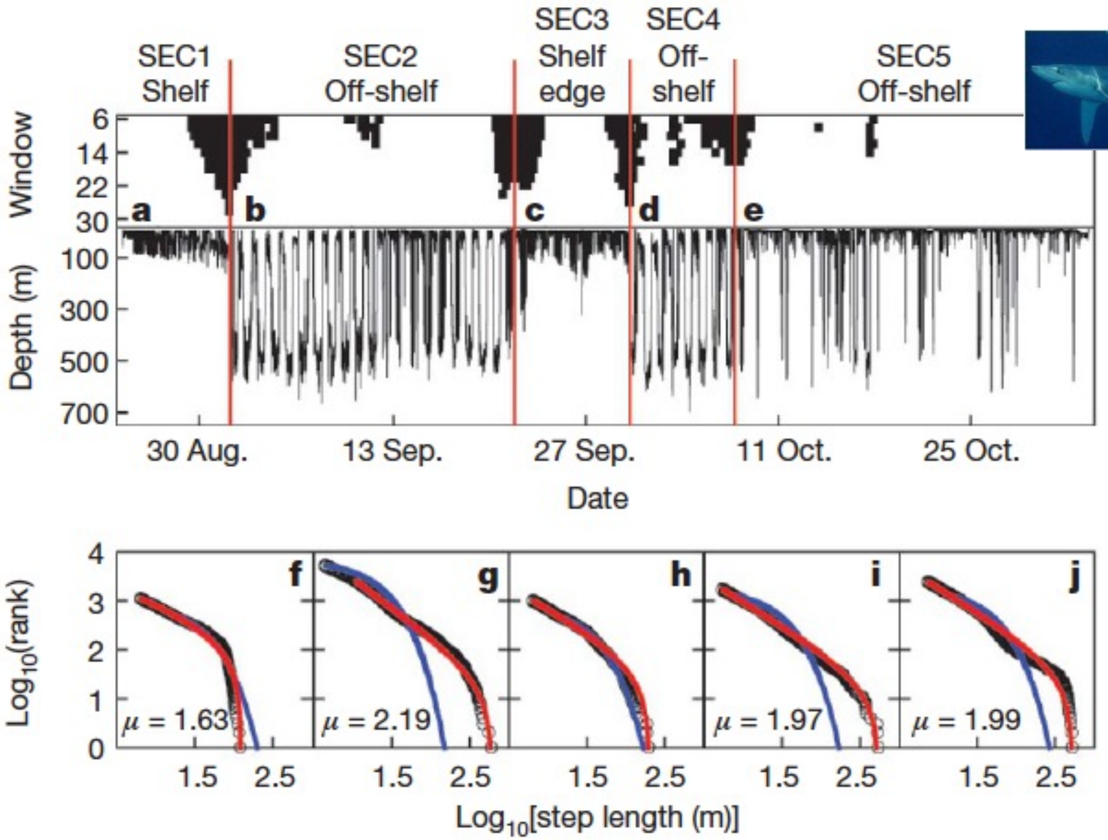
- A free running programme for exploration operates independently of the brain
- The brain modulates the exploratory routine in response to environmental cues

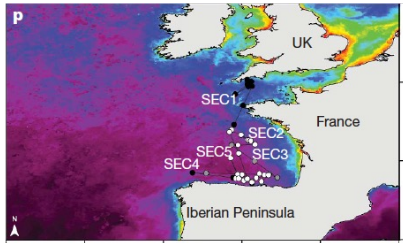
- Control larvae show movement patterns resembling LW in simple environment with minimal sensory inputs (visual, olfactory, gustatory)

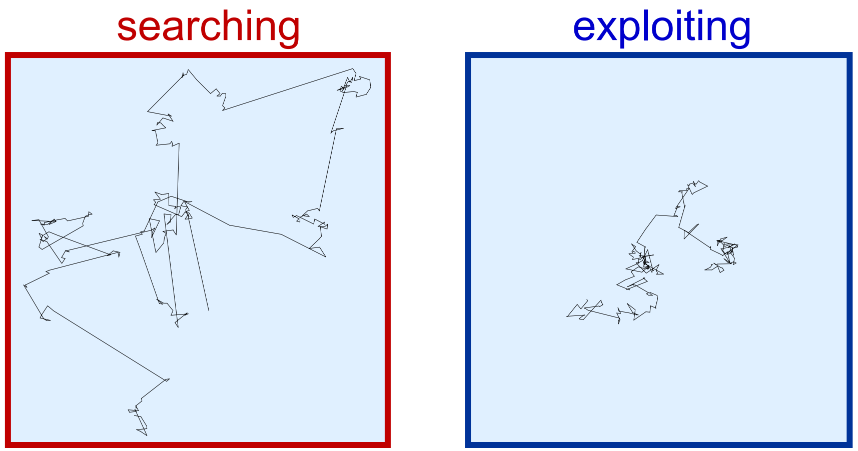
- LW-like movement pattern is a routine independent of sensory processing by the brain or the sensory system.

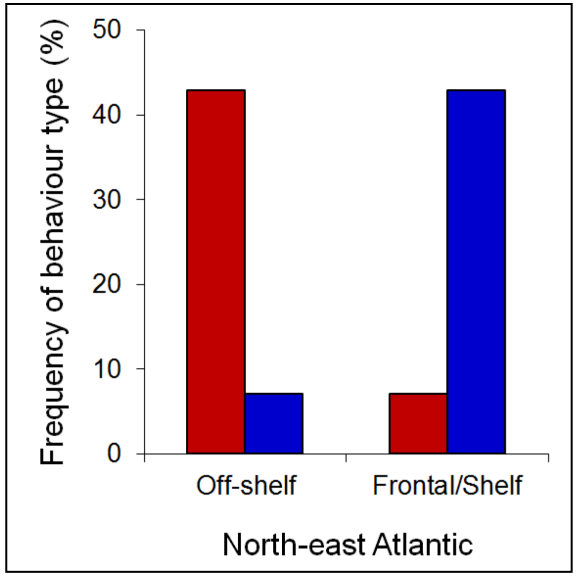
- Supports Hypothesis that such patterns arise from autonomous neuronal activity of the central pattern generators located in the ventral nerve cord.

Different strategy linked to environmental context



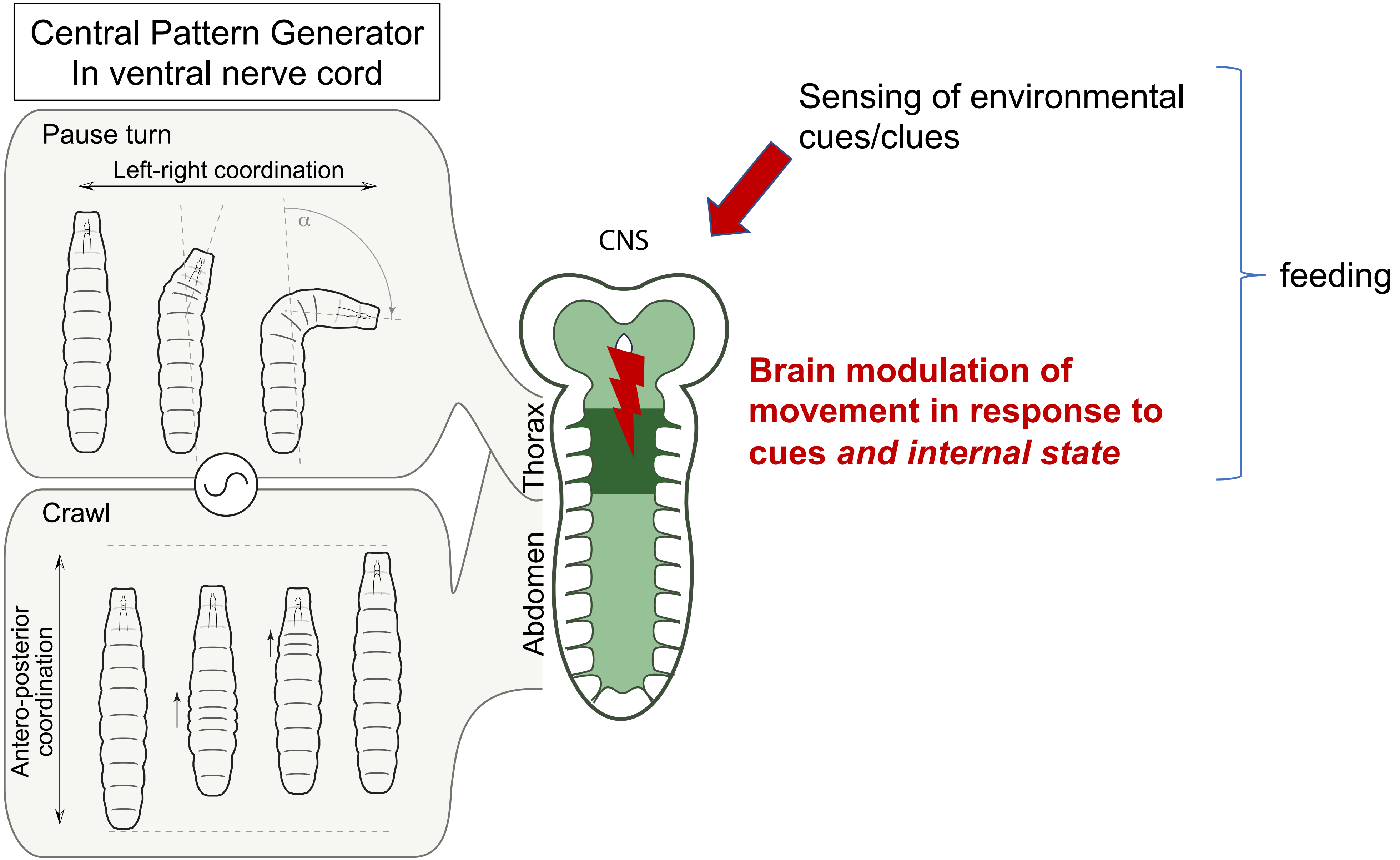






Humphries et al., Sims *Nature* (2010)

Circuitry for exploration



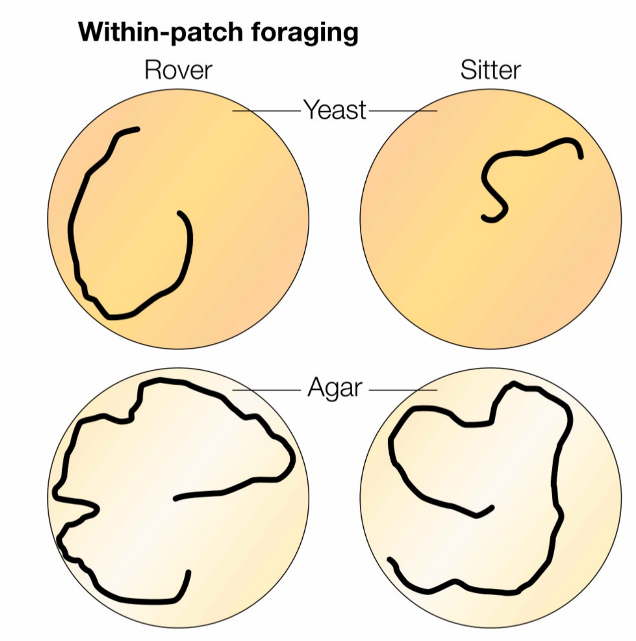
Questions

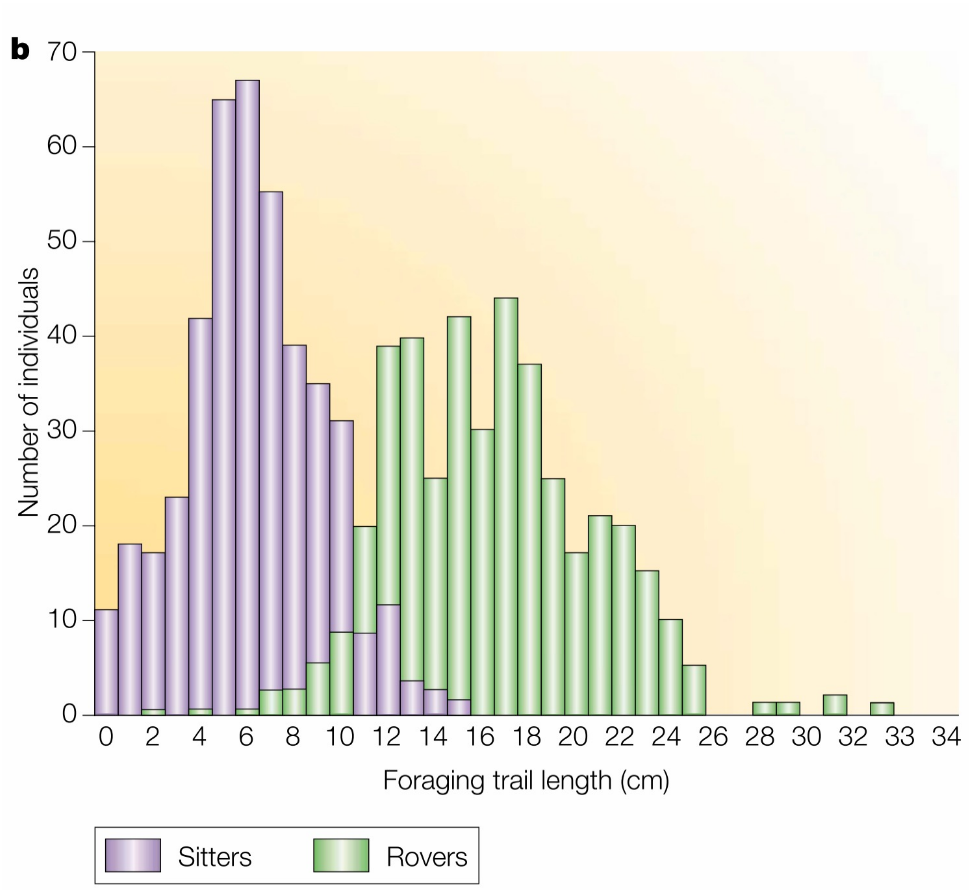
If animals adapt their foraging to the environment How is this achieved?

How is foraging modulated in response to different distribution and quality of resources?

Can genetic polymorphisms in the population confer an advantage in particular conditions?

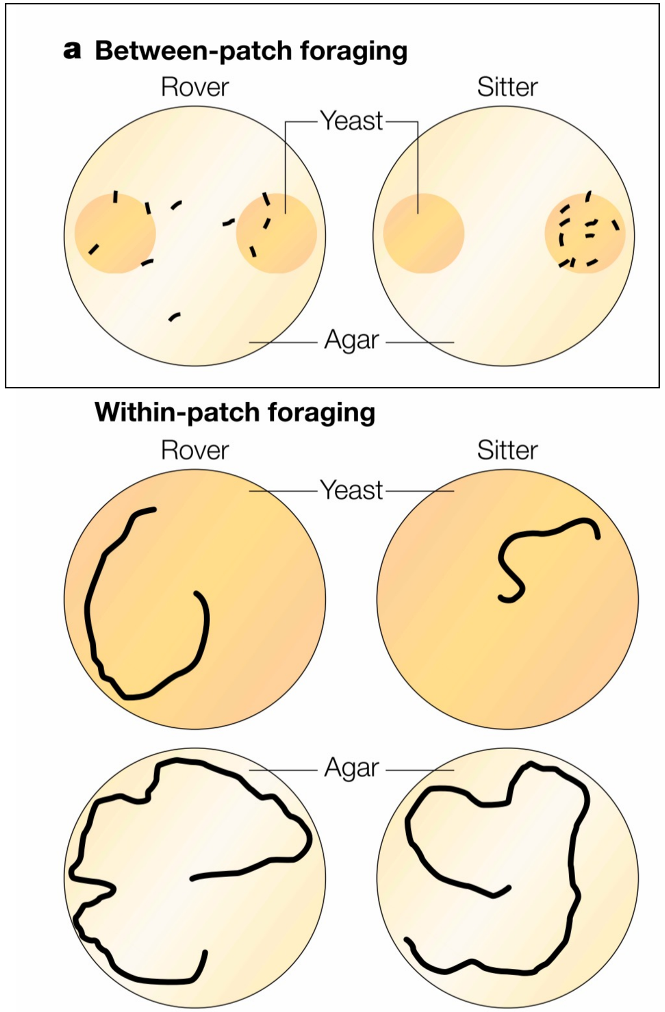
Drosophila foraging dimorphism: rovers *vs.* sitters

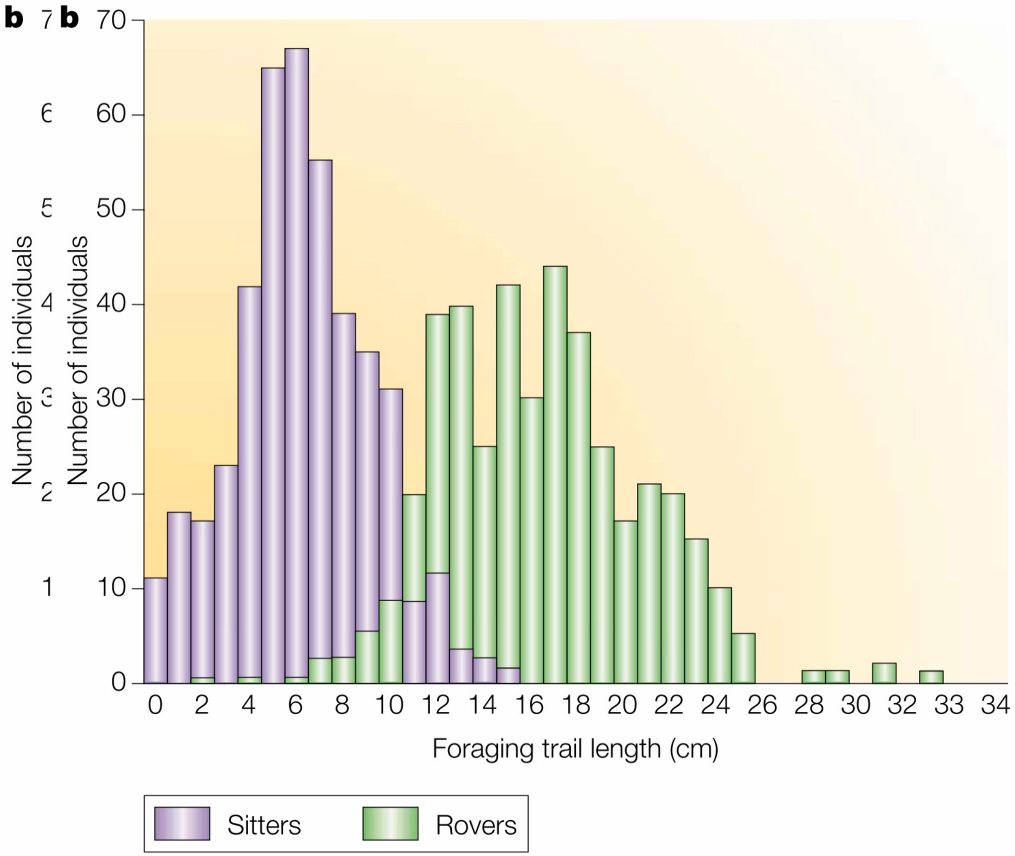




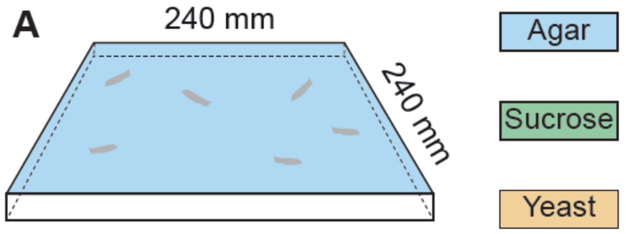
Drosophila foraging polymorphism: rovers *vs.* sitters

Hypothesis!

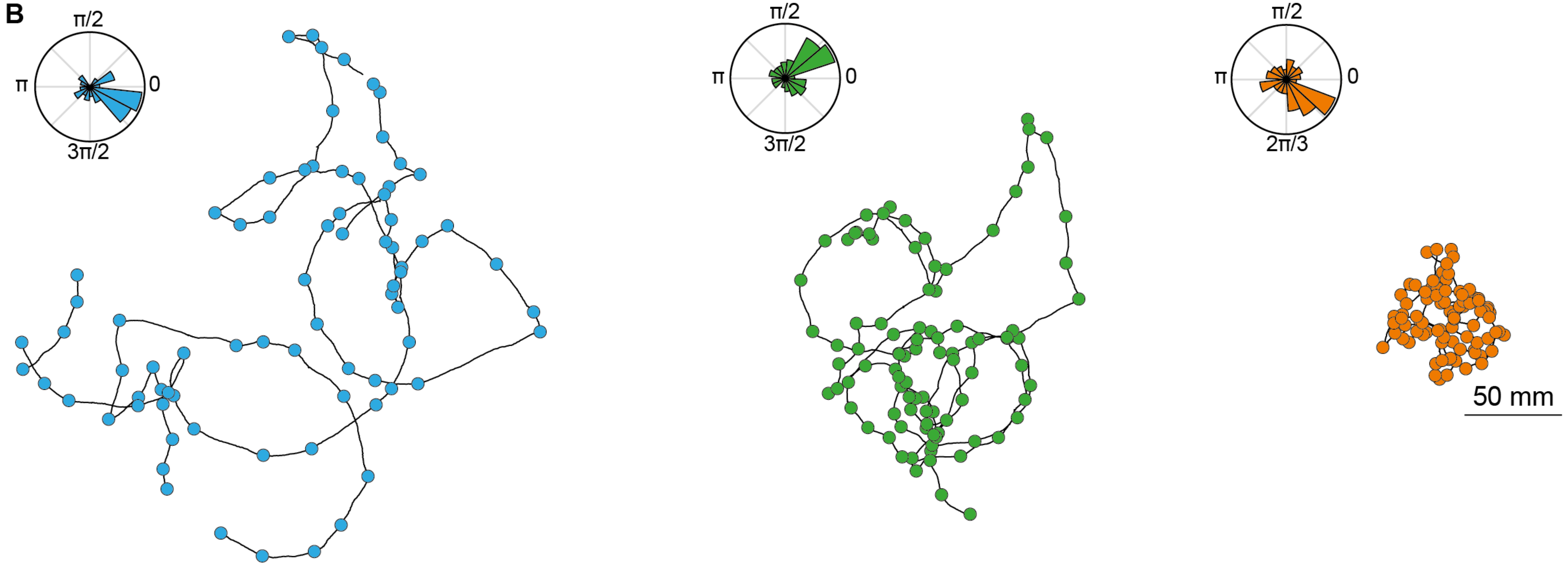




Exploratory behavior in different substrates



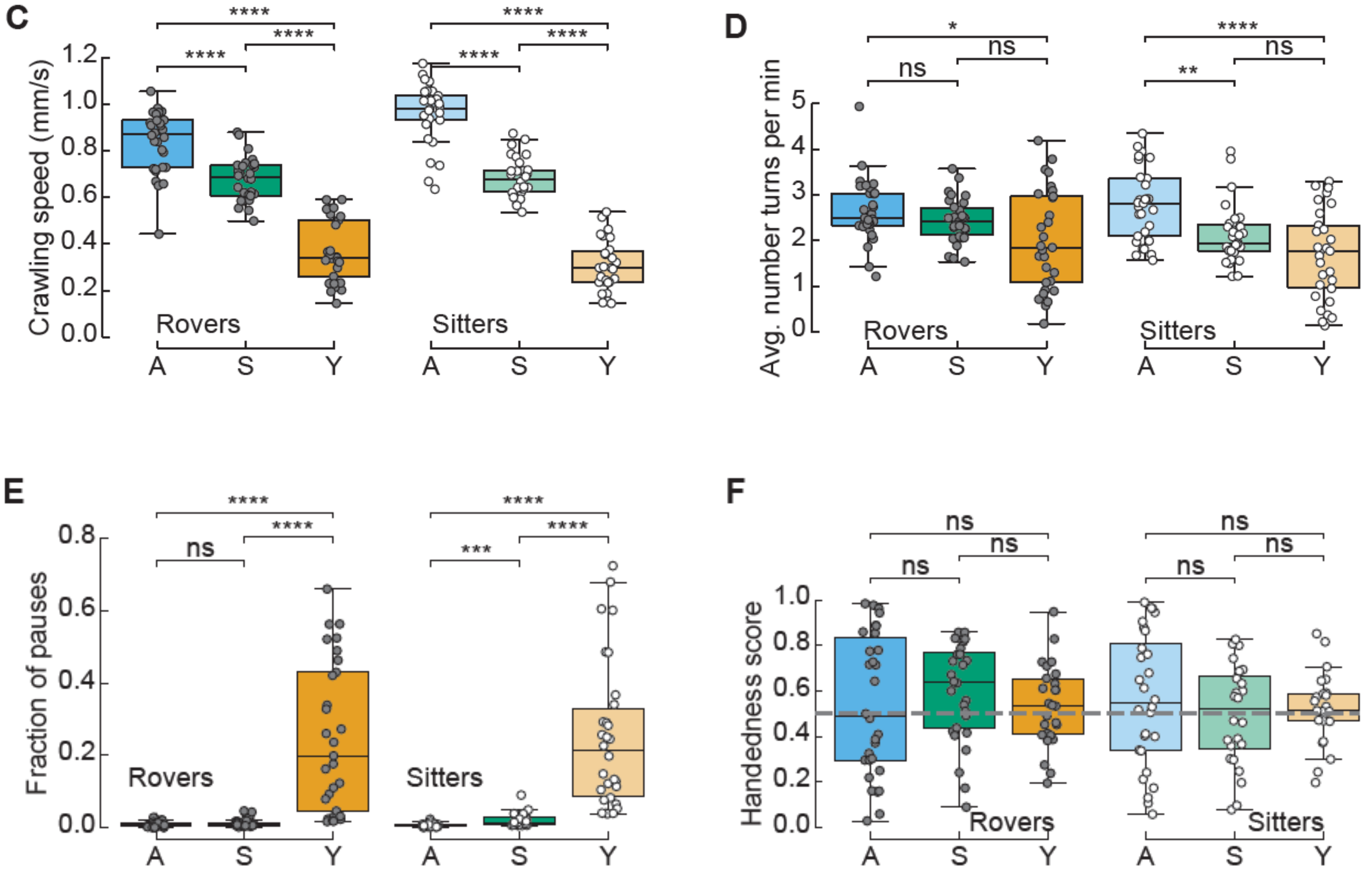
Exploratory trajectories with identified turning points



Wosniack et al., under revision

Behavioral elements that adapt in different food substrates

- Overall **reduction of crawling speeds** in food
- **More pauses** triggered in yeast substrate
- **Less frequent turns** in food substrate

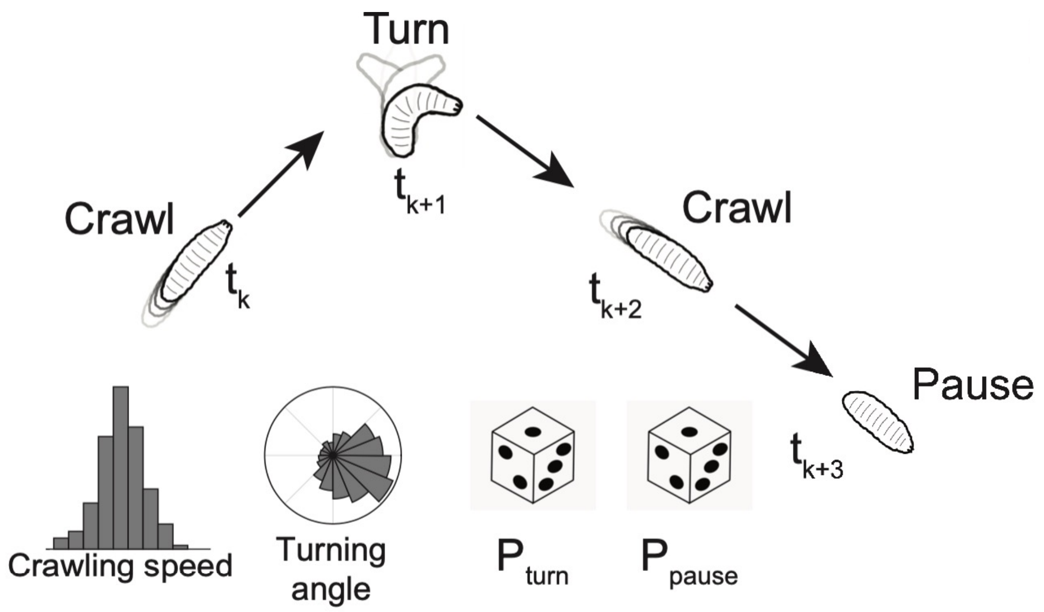


Agar

Sucrose

Yeast

A phenomenological model of crawling in different substrates



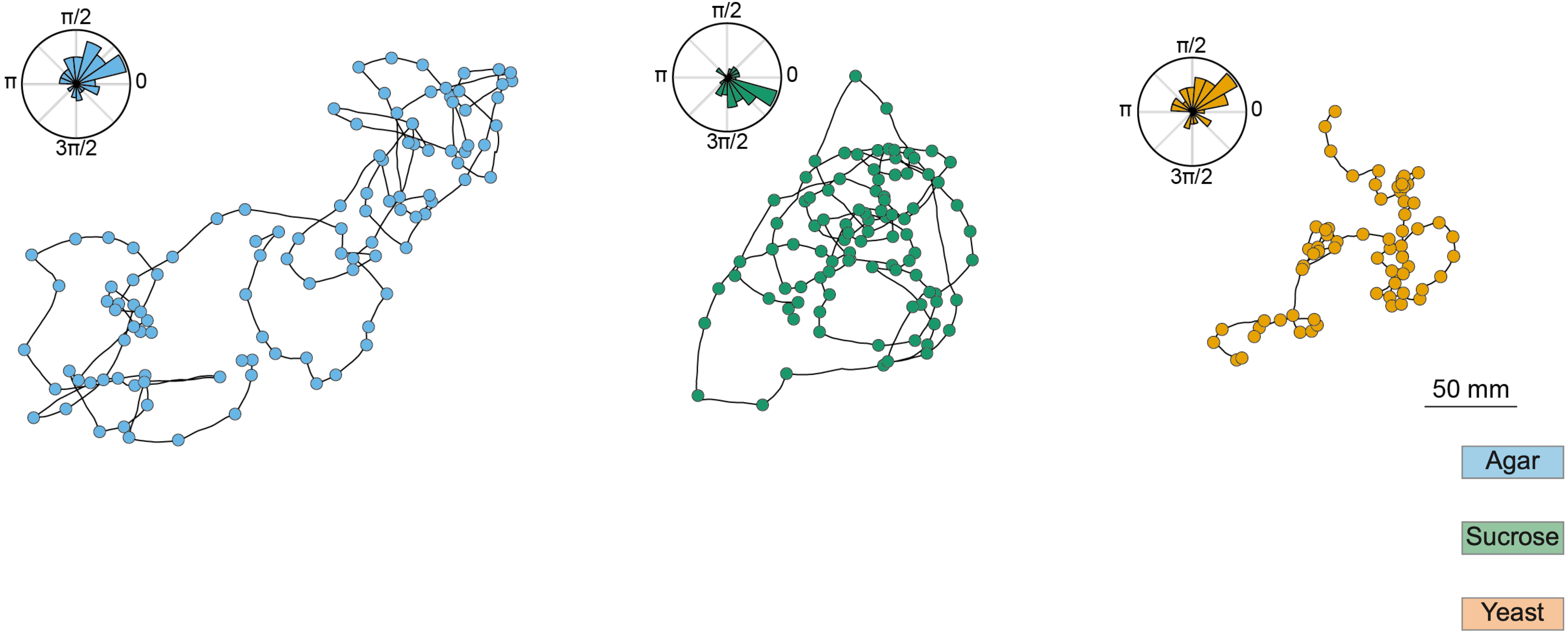
At each time step, the simulated larva either (all distributions sampled from the data):

1. Crawls with crawling speed sampled from distribution

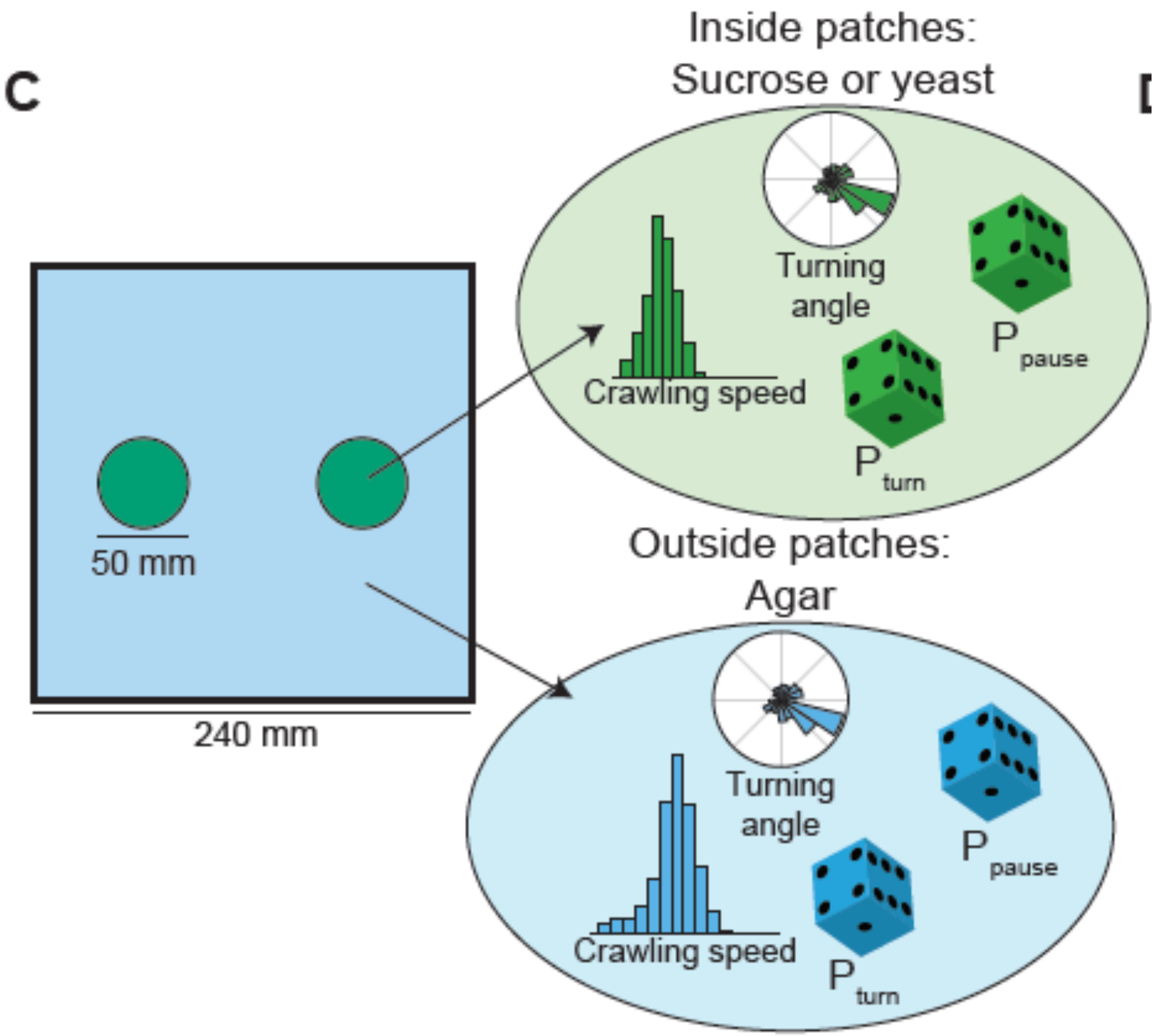
2. Turns a turning angle θ that follows a von Mises distribution with a probability P_{turn}

3. Pauses with probability P_{pause}

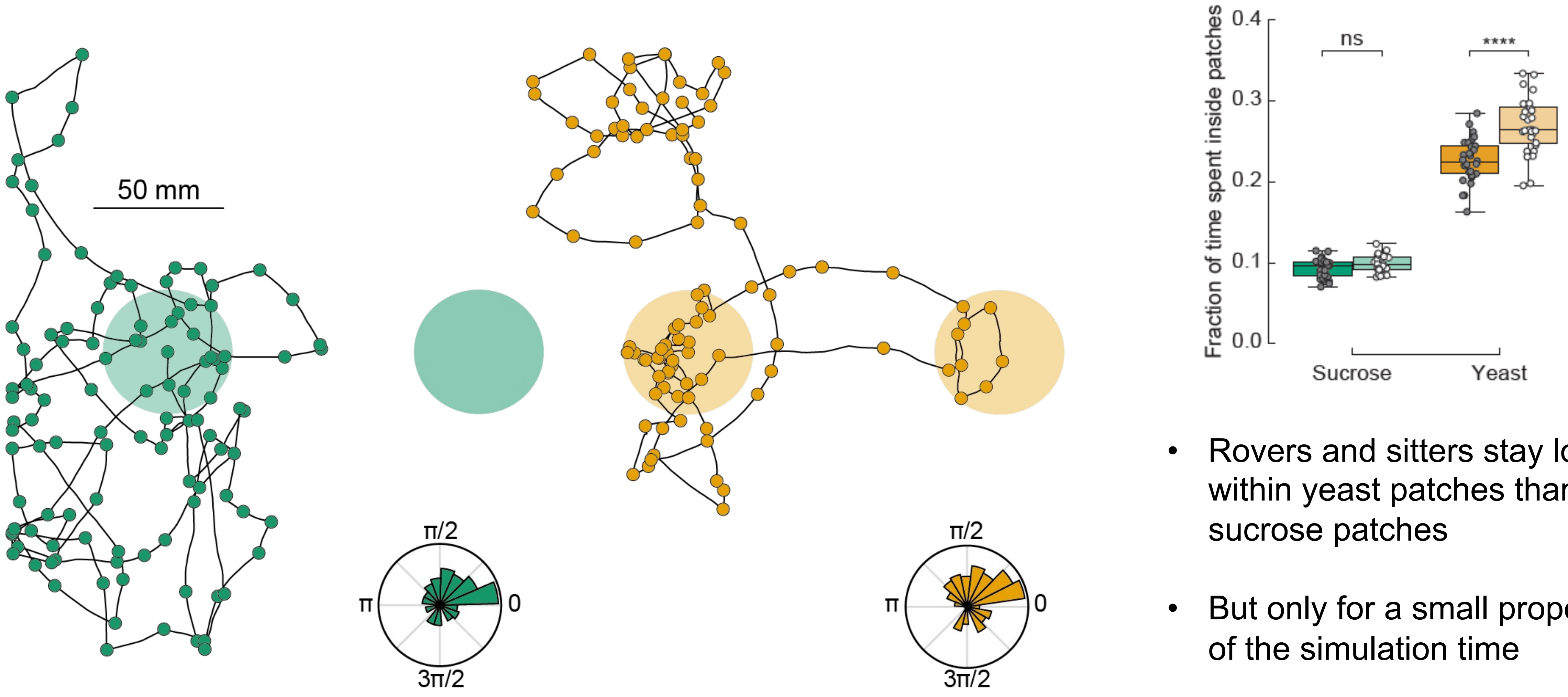
Sample trajectories generated by the model in the different substrates



Model trajectories in patchy substrates

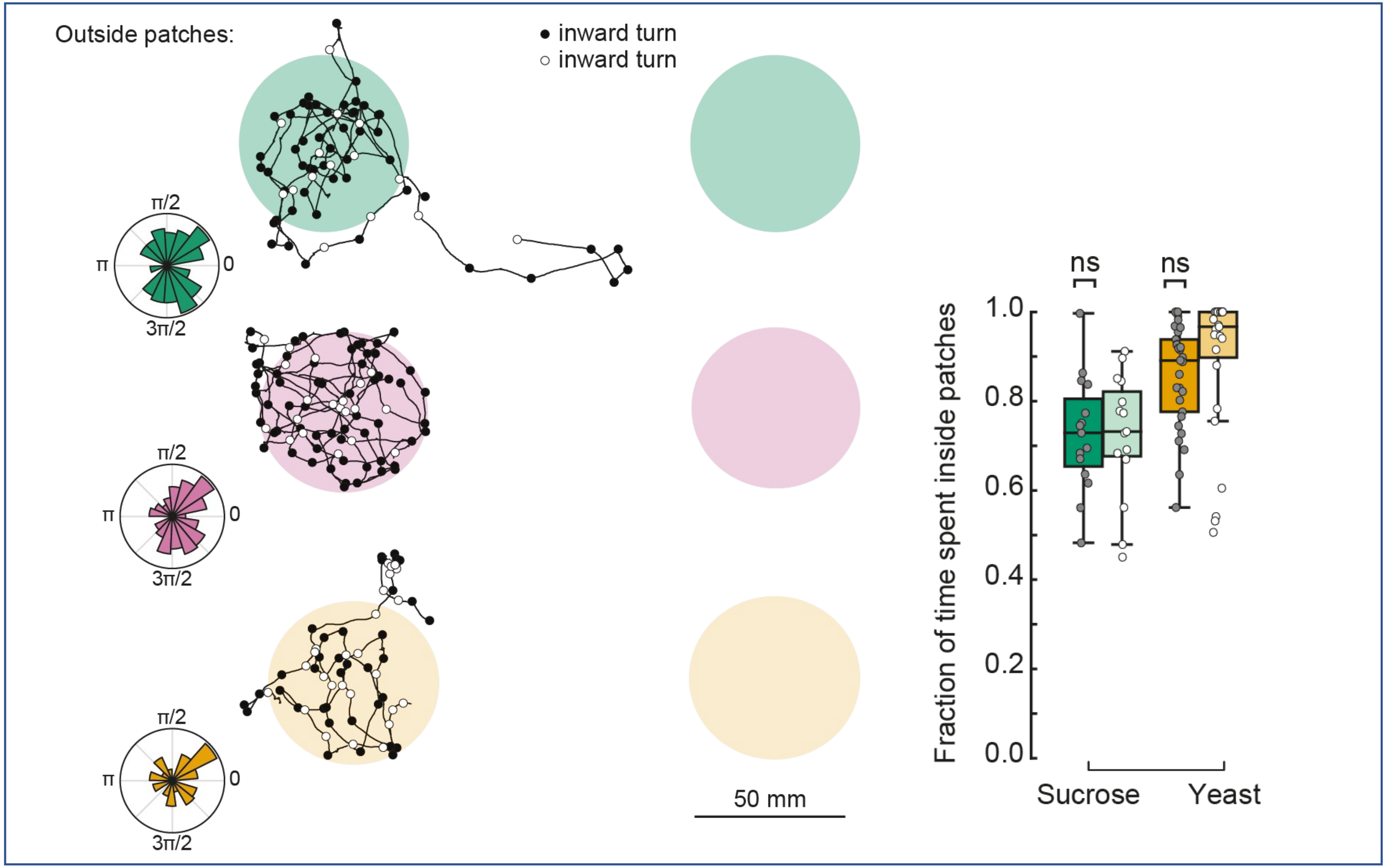


Sample trajectories generated by the model in 2 patches substrates



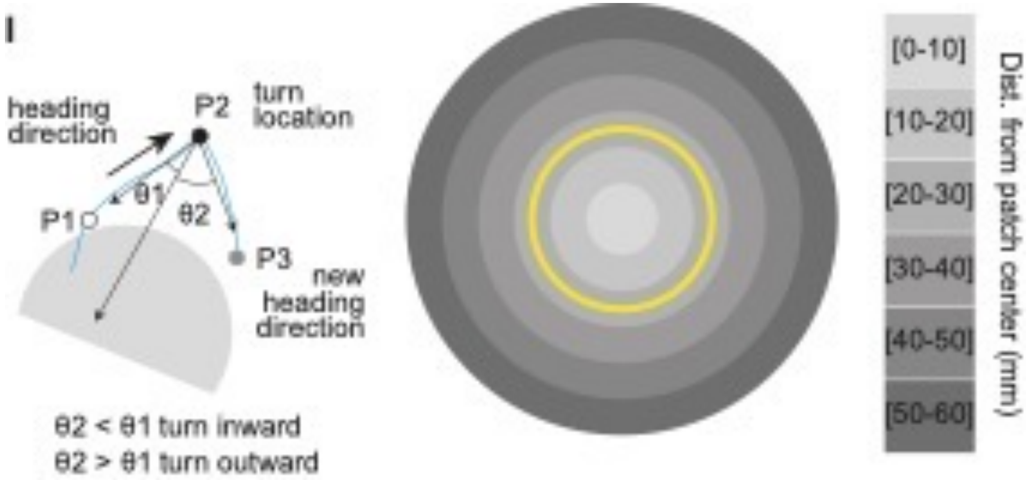
- Rovers and sitters stay longer within yeast patches than sucrose patches
- But only for a small proportion of the simulation time
- Sitters stay longer in yeast patches

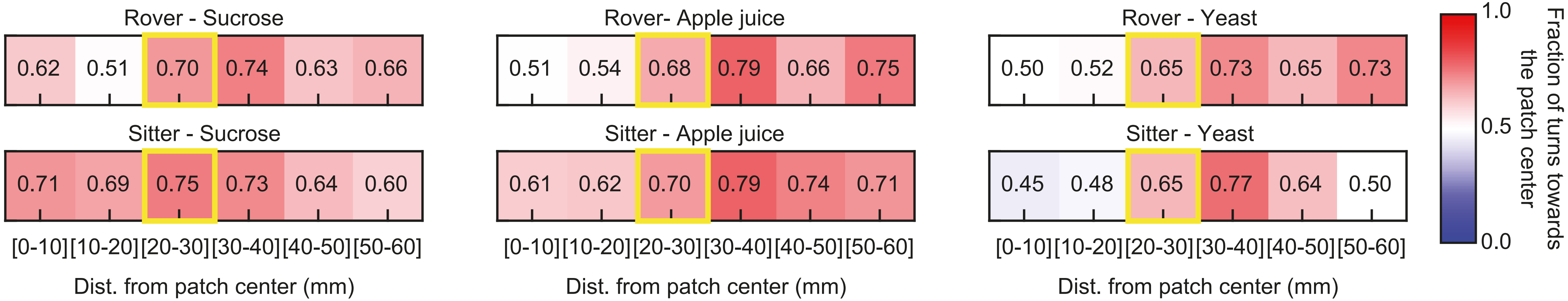
Experiments with patchy substrates



- What element of the behavior in patchy substrates is not captured by our model?

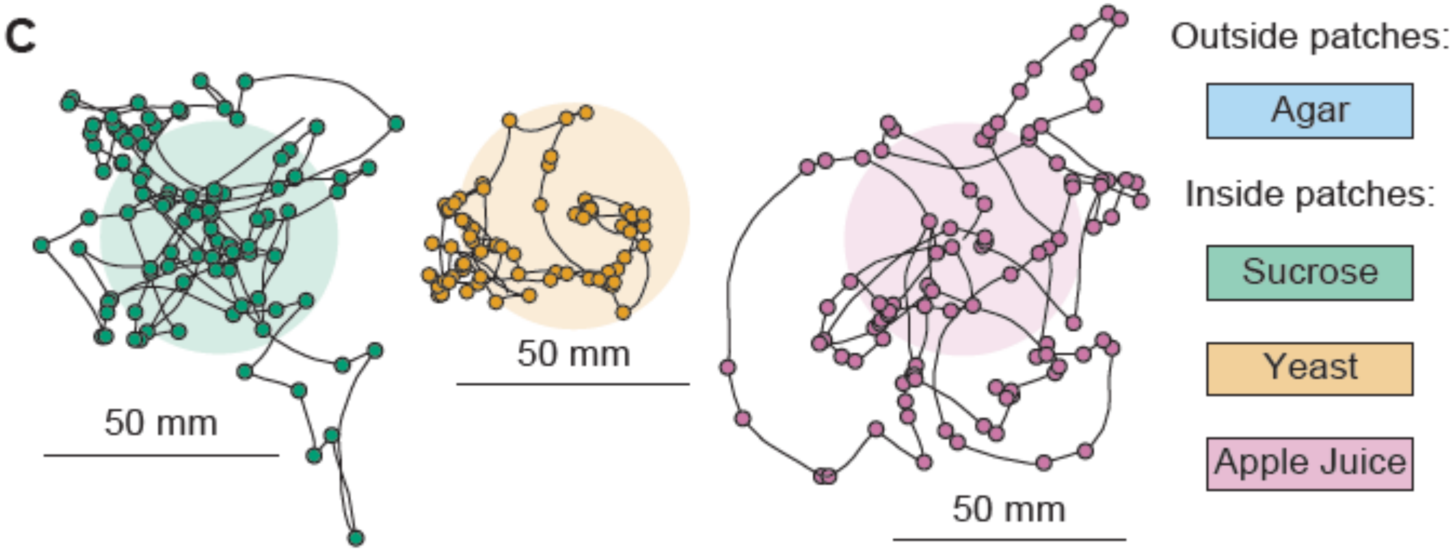
Larvae have higher probability to turn inwards the patch at the border



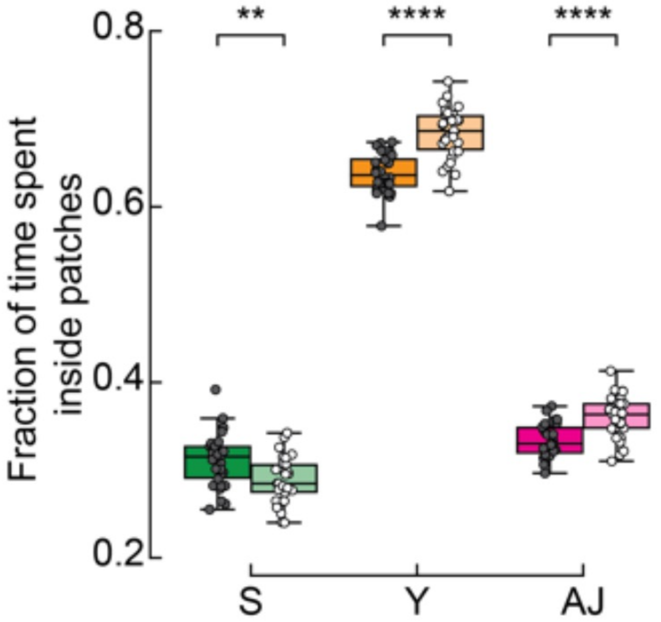


Including higher inward turn probability in the model

- More realistic larval trajectories

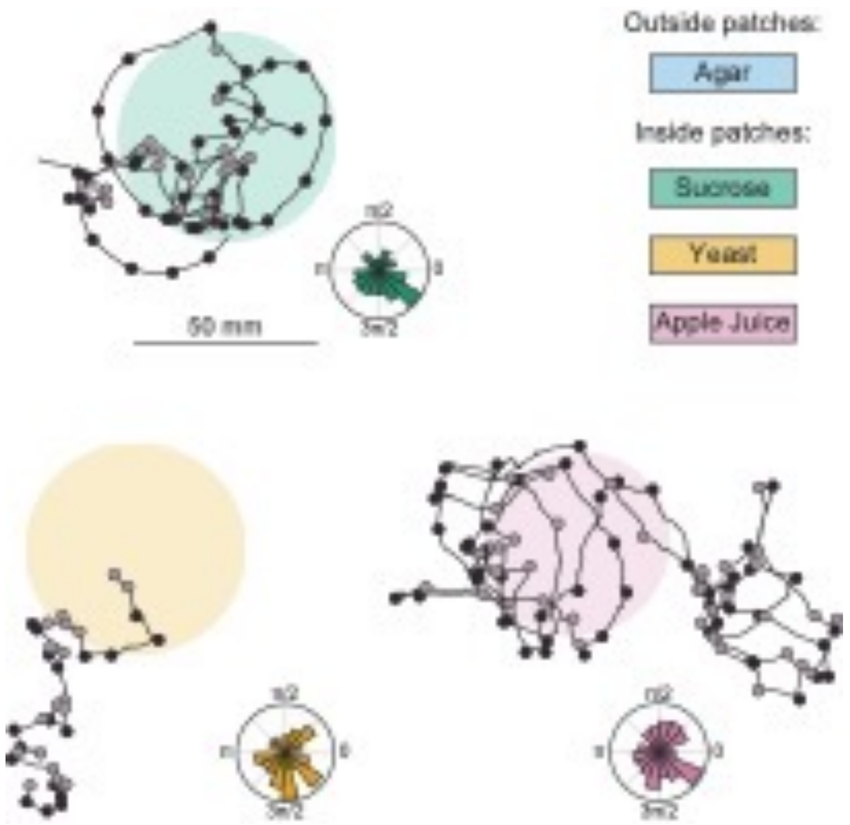


- Higher residence times compatible with experimental observations

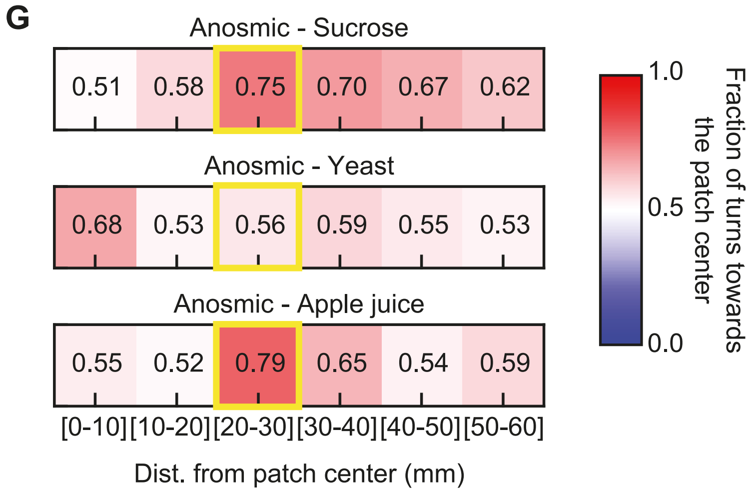


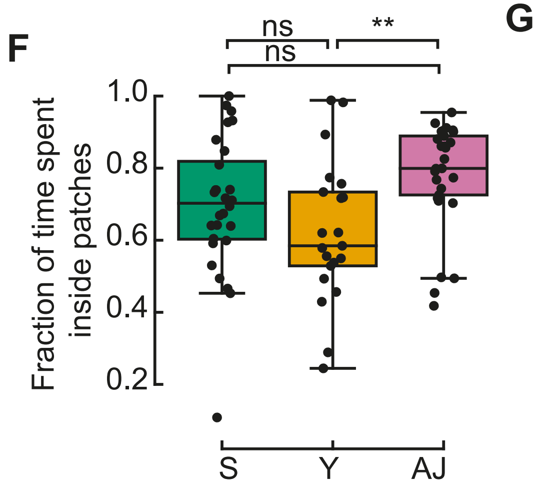
Is olfaction sole responsible for the reorientation mechanism?

- Experiments with mutant larvae (anosmic)



- Anosmic larvae increase their residence time within sucrose patches by turning inwards the patch center (not for yeast)



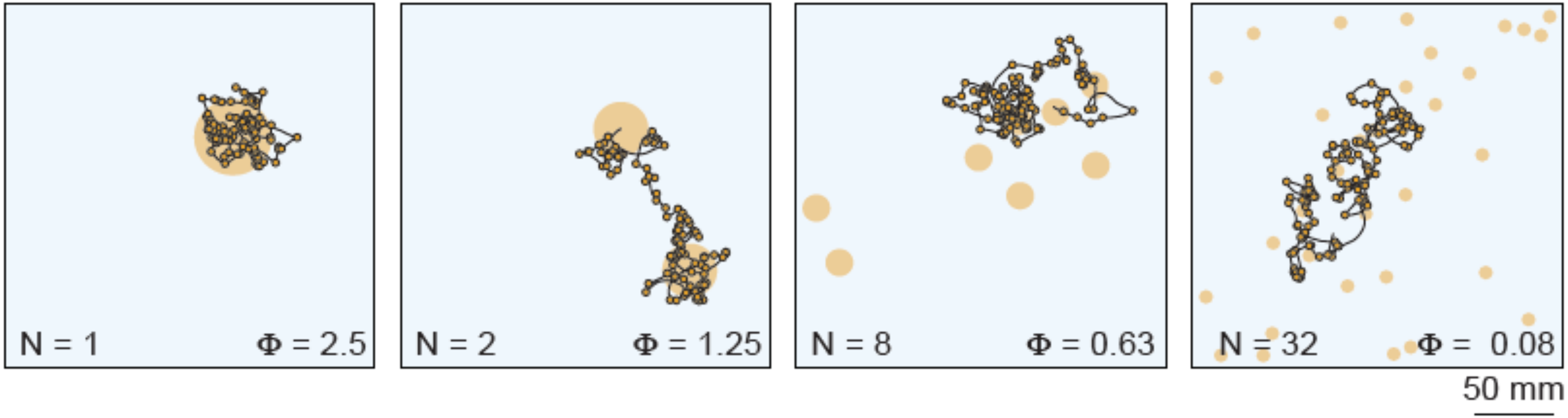


Results summary

- Characterized larval exploratory behavior in different homogeneous/patchy substrates
- Designed a model to investigate exploration in heterogeneous (patchy) environments
- **Food quality controls** the **travelled distance** by modulating crawling speed and frequency of pauses and turns.
- **Food distribution**, and in particular the food-no food interphase, controls turning behaviour, stimulating turns towards the food when reaching the patch border and **increasing the proportion of time spent within patches of food**.
- Small effect of foraging polymorphism

In silico experiment: How does the foraging strategy changes when resources are fragmented?

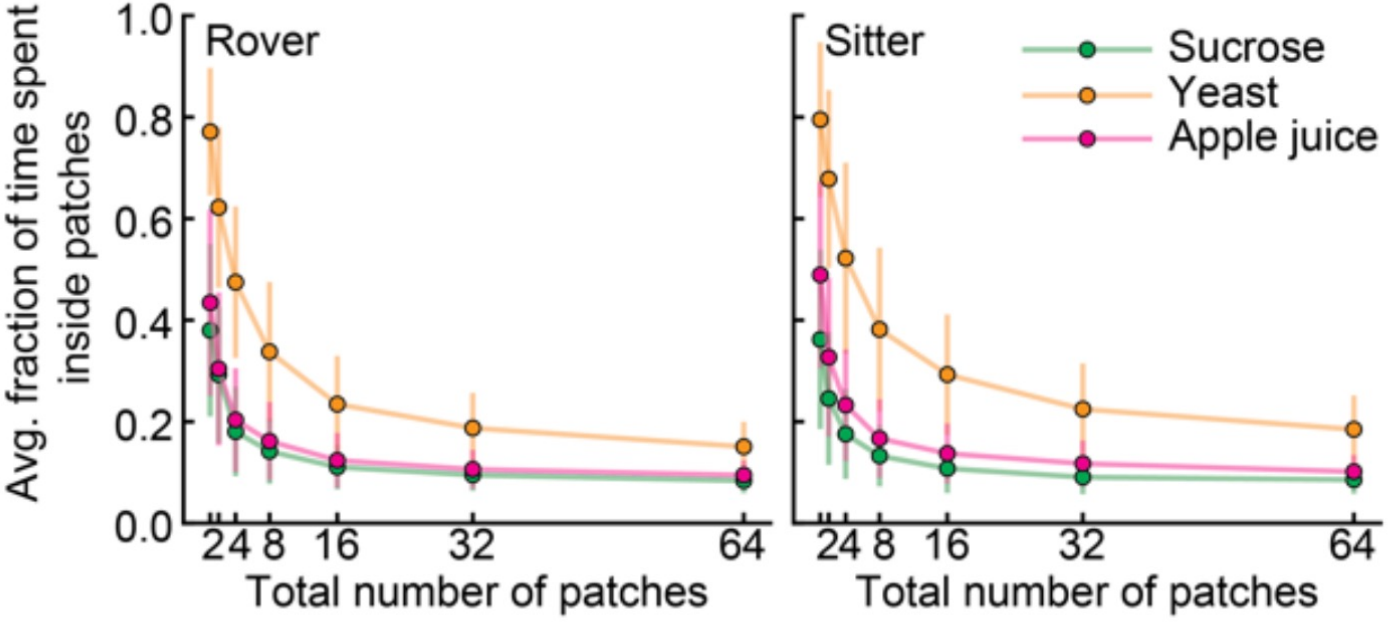
- Test the efficiency when the food resources are more fragmented
- Kept fixed food surface area and distributed it into N patches

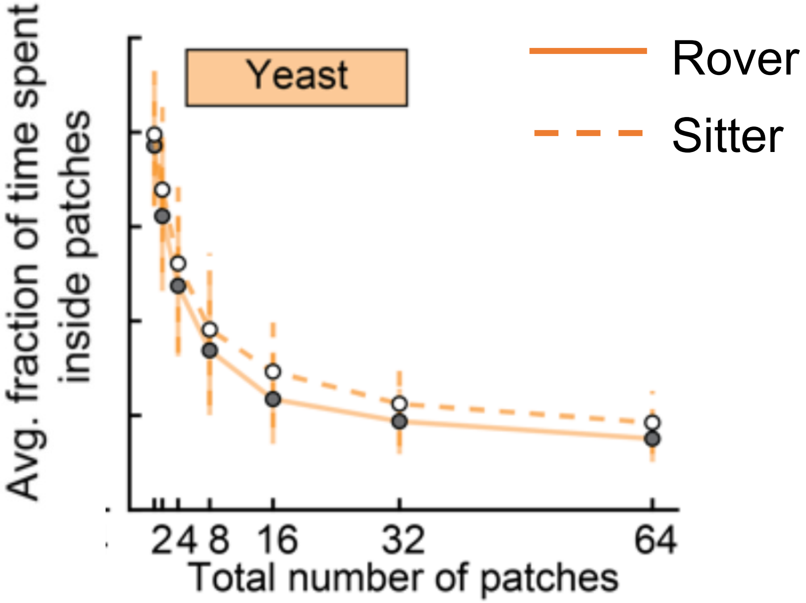


Further fragmentation

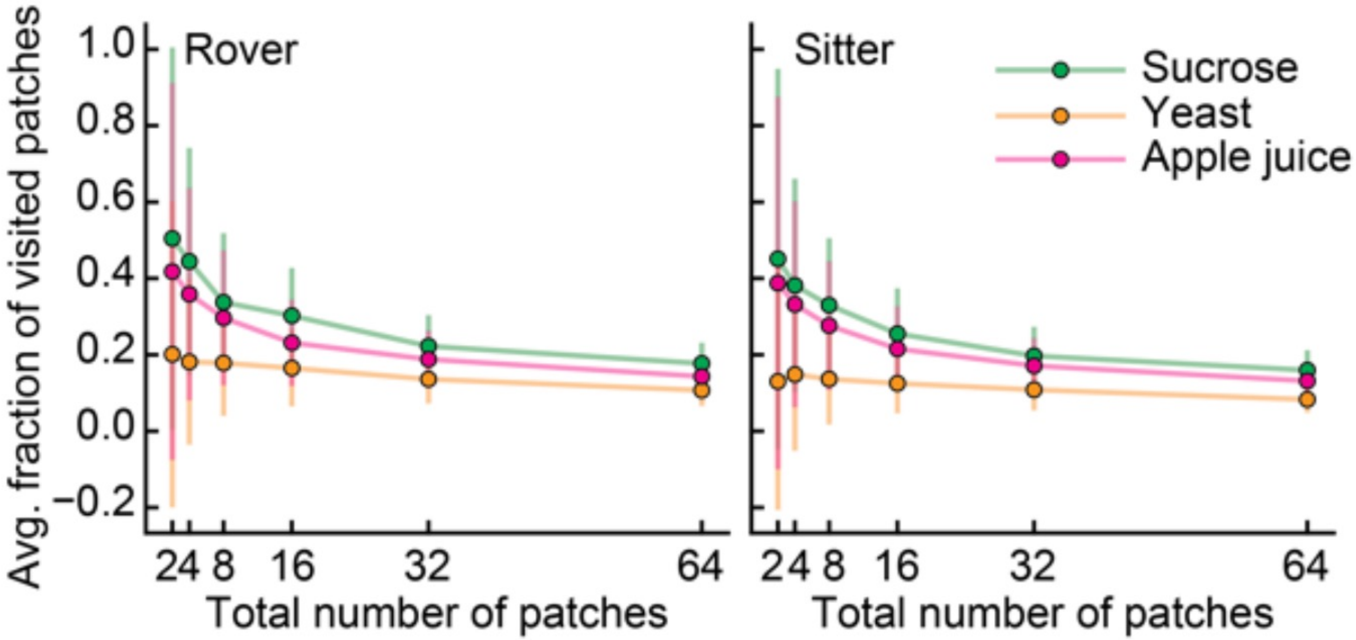
- Further fragmentation → less time within patches.
- Increase the time spent within more nutritious patches

- Sitter larvae remain "slightly" longer than rover within yeast patches

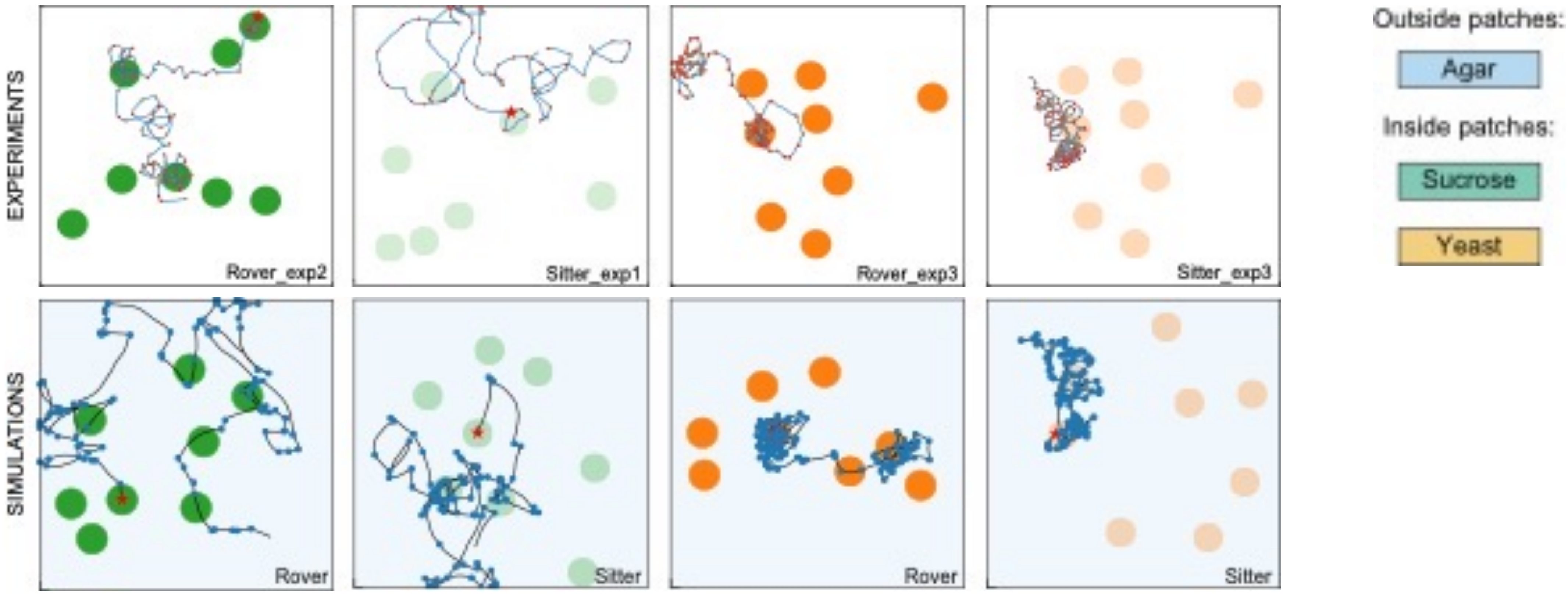




More patches are visited when the food quality is lower

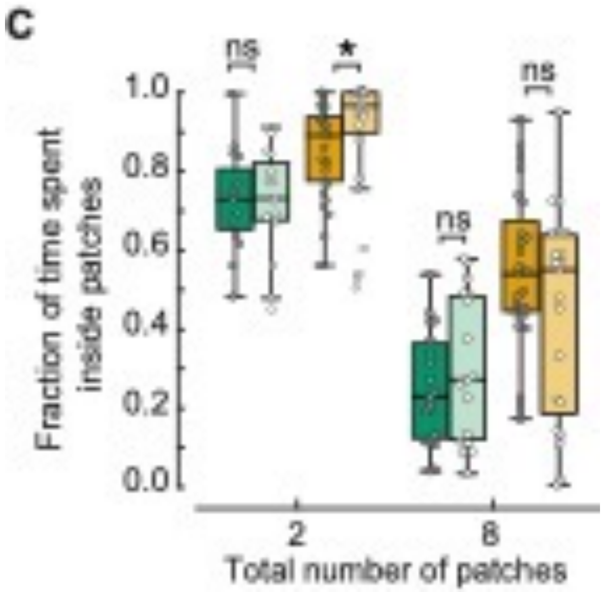


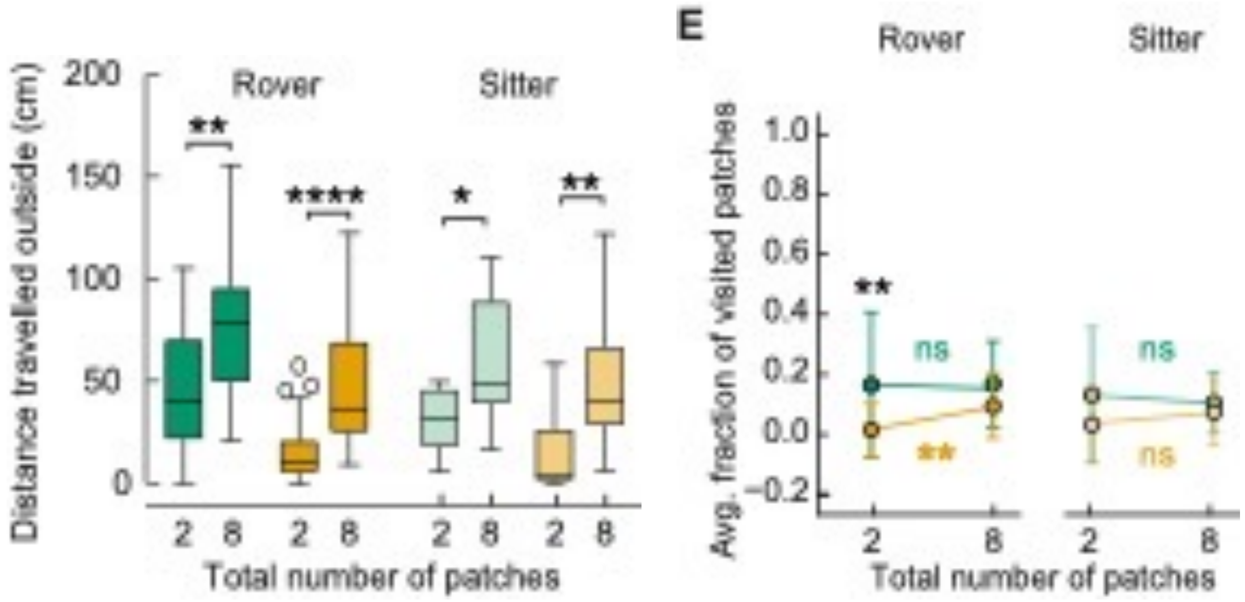
Testing the predictions



Larvae experience a trade-off between exploitation and exploration

Dark colour rover
Light colour sitter





- Larvae increase the time spent within more nutritious patches
- Larvae enhance exploration when food quality is low, but do not find more patches at this time scale.

Results summary

- when food is fragmented larvae experience a **trade-off between exploitation and exploration**
    - Larvae increase the time spent within more nutritious patches
    - Larvae enhance exploration when food quality is low

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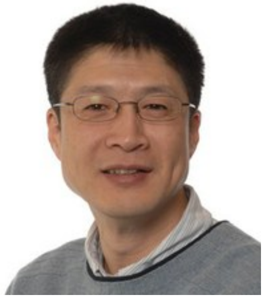

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