Linking animal movement, consumption and distribution

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Behavioral Ecology

Ecology is the scientific study of processes that determine the distribution and abundance of organisms in space and time. [adapted from: Elton, C.S. (1927). *Animal Ecology*. University of Chicago Press]

Behavior is the range of actions made by organisms in conjunction with themselves or their environment, which includes the other organisms around as well as the physical environment. It is the response of the organism to various stimuli or inputs. [adapted from: Wikipedia]

Behavioral ecology is the scientific study of behavioral processes that determine the distribution and abundance of organisms in space and time.

VOL. 178, NO. 2 THE AMERICAN NATURALIST AUGUST 2011

Linking Rates of Diffusion and Consumption in Relation to Resources

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Modeling consumption rate

I. **Holling's functional response**

- Movement along straight lines
- Randomly distributed resources
- No resource depletion; infinite space

Holling 1959

Resource

Handling

Consumer

Ideal gas models

I. **Holling's functional response**

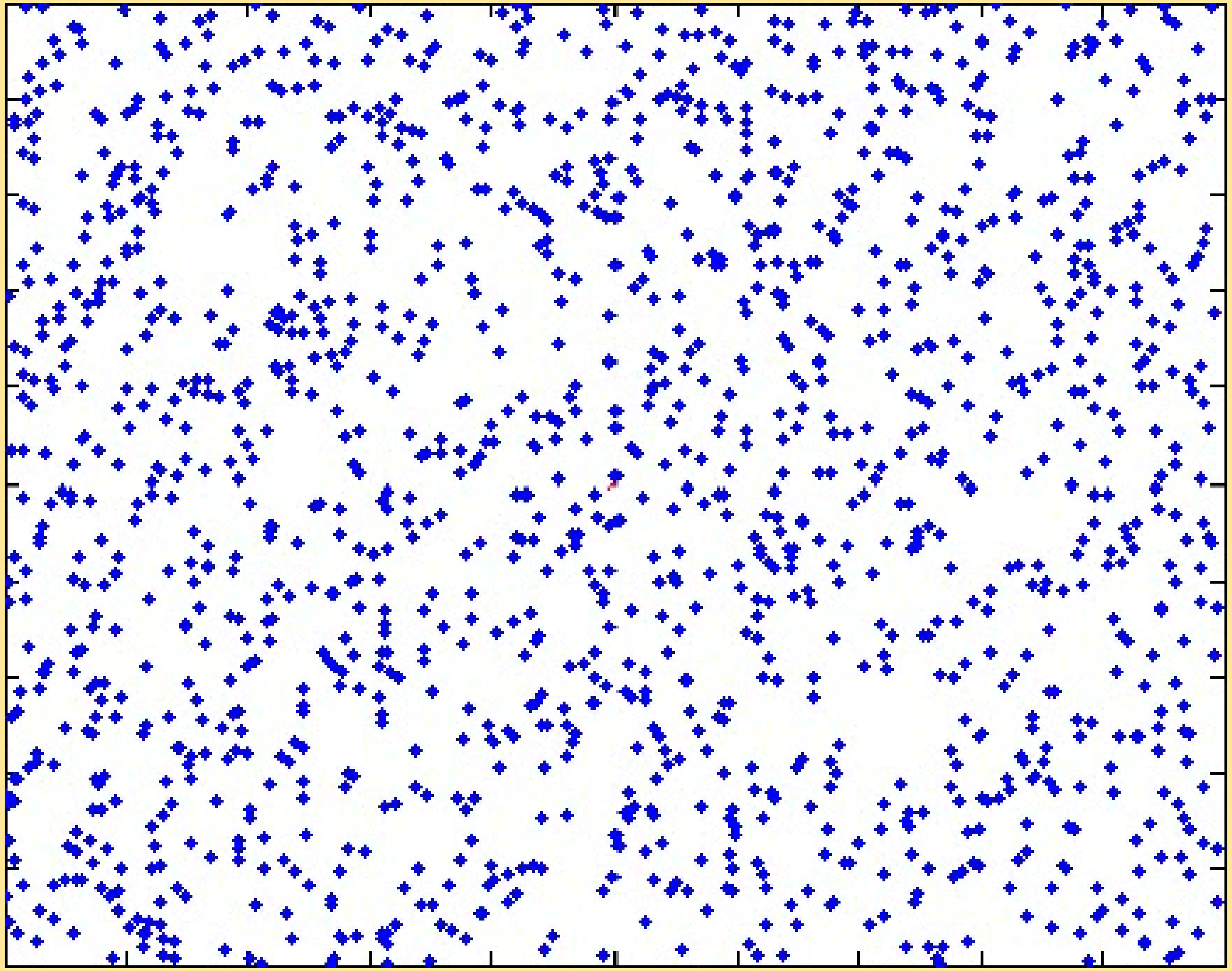
- Movement along straight lines
- Randomly distributed resources
- No resource depletion; infinite space

II. **Random walk approximation of simple diffusion**

- Movement in straight lines and random directions
- Step lengths are exponentially distributed (randomly distributed turning points)
- Infinite space

Holling 1959; Berg 1983; Hutchinson & Waser 2007

How fast do Holling’s consumers diffuse?



How fast do Holling's consumers diffuse?

- Mean step length: $E(l) = \dfrac{1}{2 \cdot \rho \cdot r}$

- Mean step duration: $E(\Delta t) = \dfrac{1}{2 \cdot \rho \cdot r \cdot s} + h$

- Mean squared displacement = $\dfrac{t}{E(\Delta t)} \cdot E(l^2) = 4 \cdot t \cdot D$

$$D = \frac{s}{4 \cdot \rho \cdot r(1 + 2 \cdot \rho \cdot r \cdot s \cdot h)}$$

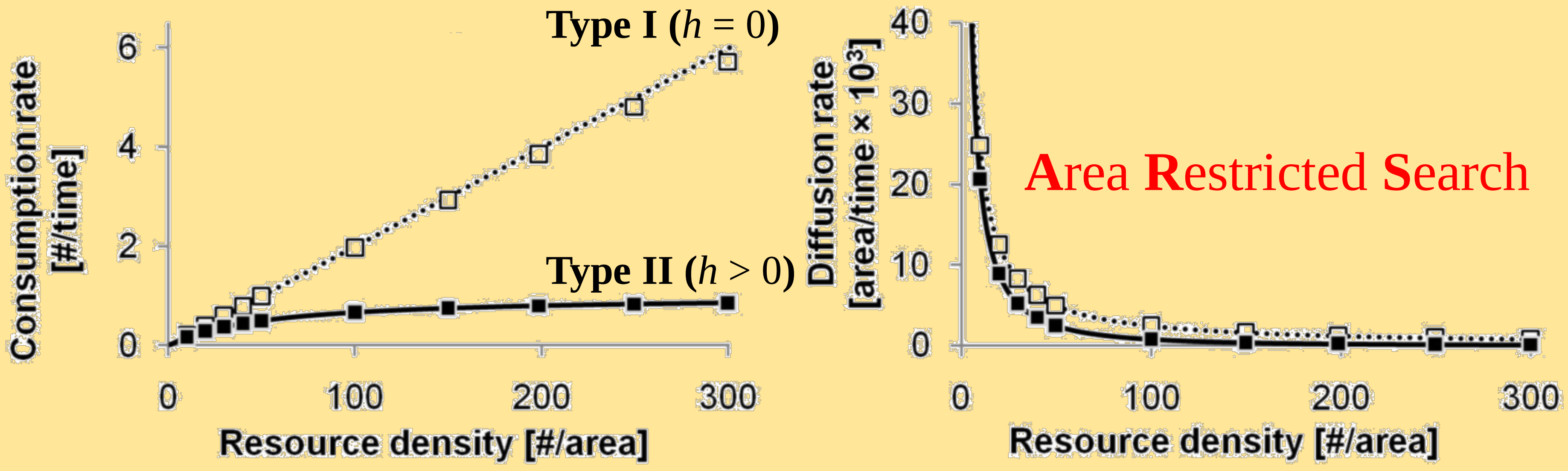
ρ= resource density
r = effective radius
s = consumer speed
h = handling time
Δt = duration
D = diffusivity

Einstein 1905; Berg 1983; Hutchinson & Waser 2007

How fast do Holling's consumers diffuse?

$$\frac{1}{E(\Delta t)} = \frac{2 \cdot r \cdot s \cdot \rho}{1 + 2 \cdot r \cdot s \cdot \rho \cdot h}$$

$$D = \frac{s}{4 \cdot \rho \cdot r\left(1 + 2 \cdot \rho \cdot r \cdot s \cdot h\right)}$$



ρ= resource density r = effective radius s = consumer speed h = handling time Δt = duration

Questions

- Can this simple *turn-at-encounter* mechanism give rise to consumer-resource spatial matching (and hence an enhanced functional response)?
- If not, what might be a minimally sufficient movement mechanism leading to spatial pattern formation?
- What might be the effects of various ecological conditions on the intensity of these emerging patterns?
- What are our theoretical expectations of consumer space-use patterns in relation to their resource distribution and dynamics?

The movement process: uncorrelated, fixed-speed, velocity-jump

- Speed, s, is constant (set to 1 spatial-units/temporal-units or l/t)
- **Background turns**: the consumer randomly chooses a new direction $[0,2\pi]$ Δt t after the last turn, where $\Delta t \sim \mathrm{Exp}(\mu)$ and μ is the background turn-rate
- **Induced turns**: the consumer randomly chooses a new direction $[0,2\pi]$ τ t after a resource encounter, where $\tau \sim \mathrm{Gamma}(k,\theta)$
- Induced turns always override previous induced turns (the clock is reset), but may or may not override background turns
- Values for k and θ are chosen so that the mode of the distribution $[\theta\cdot(k\text{-}1)]$ ranges between 0 (corresponding to *turn-at-encounter*) and 1000 t, and the coefficient of variation ($k^{-0.5}$) is either 0.5 or 0 (resulting in a delta function)

The domain and resource configuration

- Domain size Ω (=$100 \cdot 100\ l^2$)
- Domain mean resource density in the absence of depletion, ρ (=$1\ l^{-2}$)
- A circular resource patch of radius R (=5, 25 or 50 l) is situated in the middle of the domain
- Resource density outside the patch is 0
- Resources randomly occur within the patch, either homogenously, or along a density gradient ranging from $\rho(x) = 0$, at the patch boundary, to $\rho(x) = 3 \cdot \Omega \cdot (\pi \cdot R^2)^{-1}$, in the center of the domain
- The domain is wrapped around a torus

Resource encounters

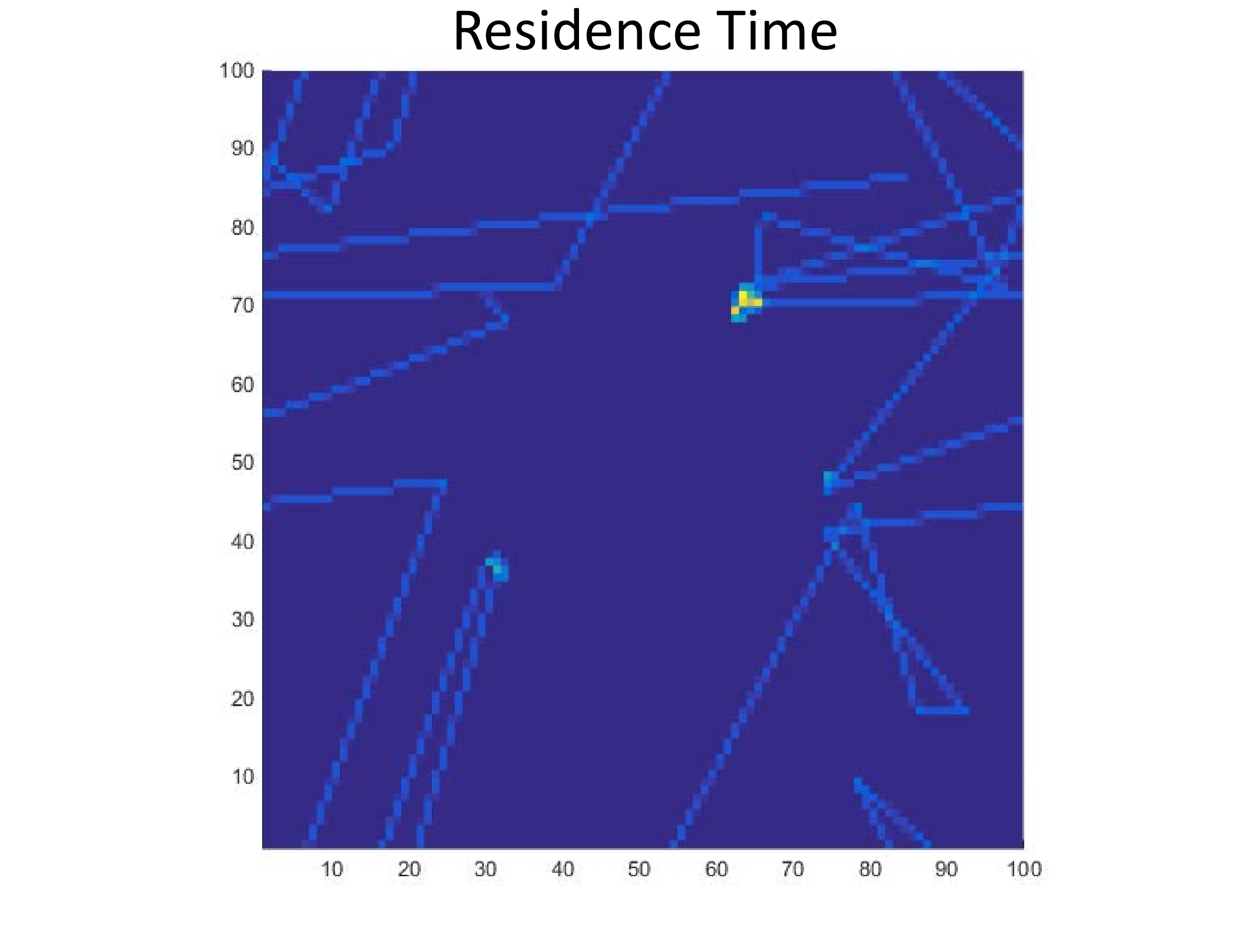
- A resource is encountered whenever its position is within an effective radius, r (= $0.5\ l$), from the consumer's path
- Once a resource is encountered it is removed (i.e., consumed) after handling-time h (= either 0 or $1\ t$), during which the consumer remains stationary
- ***Implicit Resources Scenarios*** assume that resource removal does not modify the local resource density and hence the encounter probability
- In such *Implicit Resources Scenarios*, encounter events are sampled from a non-homogenous Poisson process along the consumer's path, where the Poisson intensity at each point in space, $\lambda(x)$, is given by $\rho(x) \cdot 2 \cdot r \cdot s$

Questions

- Can a simple *turn-at-encounter* mechanism give rise to consumer-resource spatial matching (and hence an enhanced functional response)?

Results

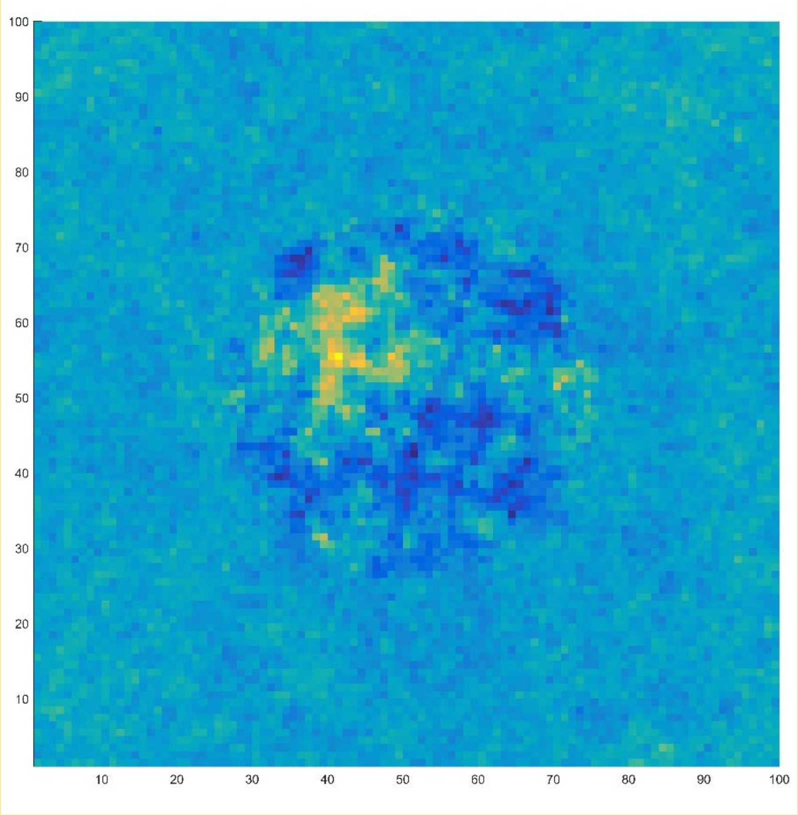
(homogenous patch, R=25, *turn at encounter*, μ=0.01, h=0)

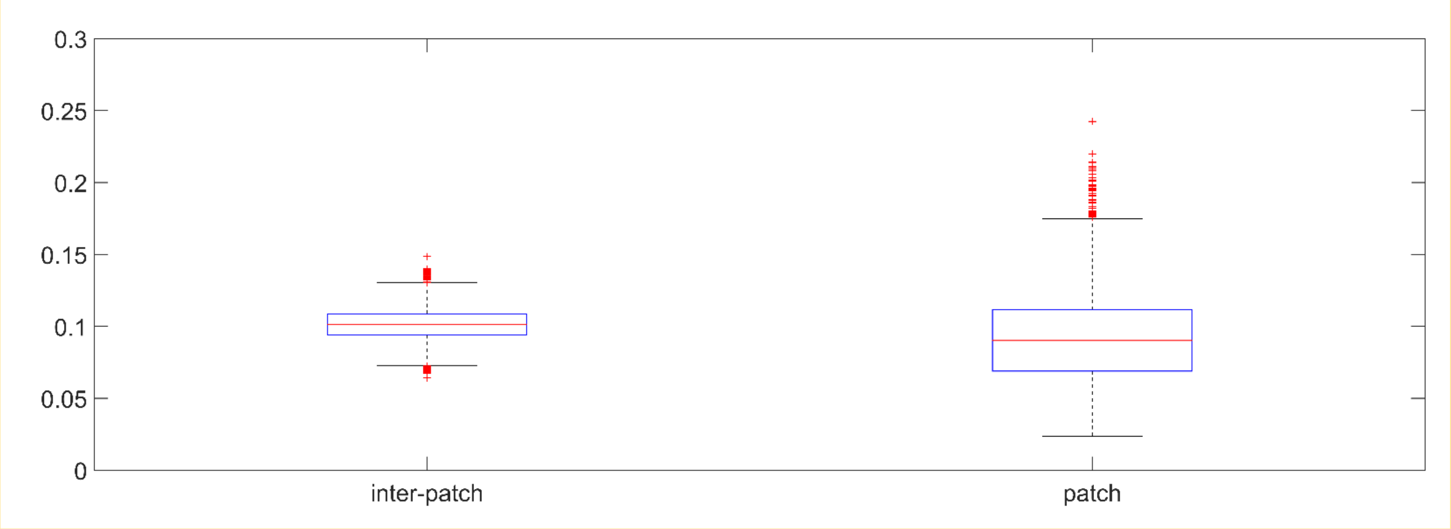


Results

(homogenous patch, R=25, *turn at encounter*, μ=0.01, h=0)

Residence Time



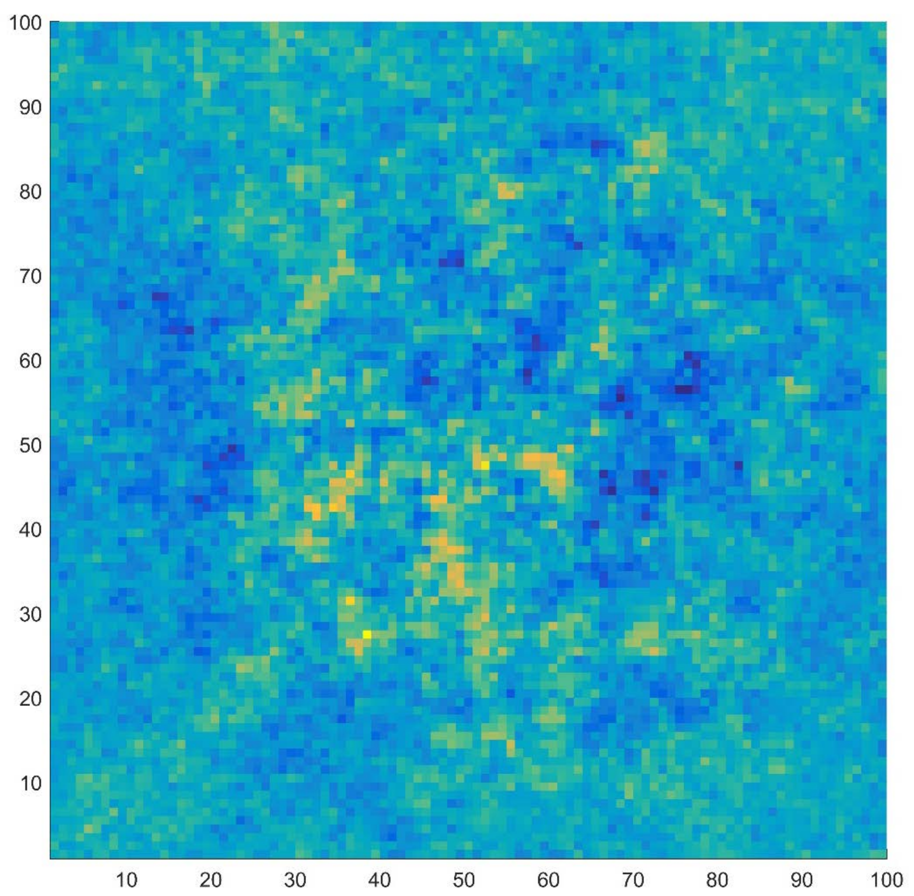


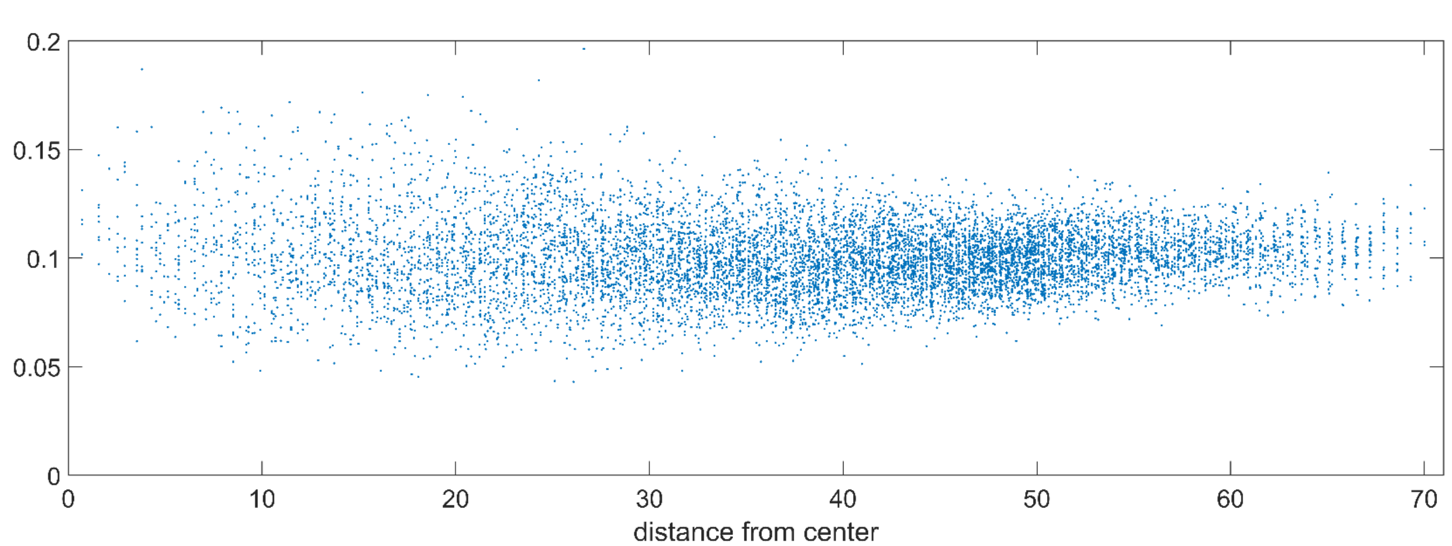
Encounter Rate = 0.97 (#/t)

Results

(conic gradient, R=50, *turn at encounter*, μ=0.01, h=0)

Residence Time





Encounter Rate = 0.99 (#/t)

Resource encounters

- ***Explicit Resources Scenario*** relax the previous assumption by explicitly simulating the resource field and updating it in real-time
- Resource density is governed by a spatiotemporally-constant per-capita mortality rate, m (=1 or $0.001\ t^{-1}$), and a spatially-dependent birth rate, $b(x)$:

$$\frac{d\rho(x,t)}{dt} = b(x) - m\rho(x,t)$$

- At steady state (and in the absence of depletion):

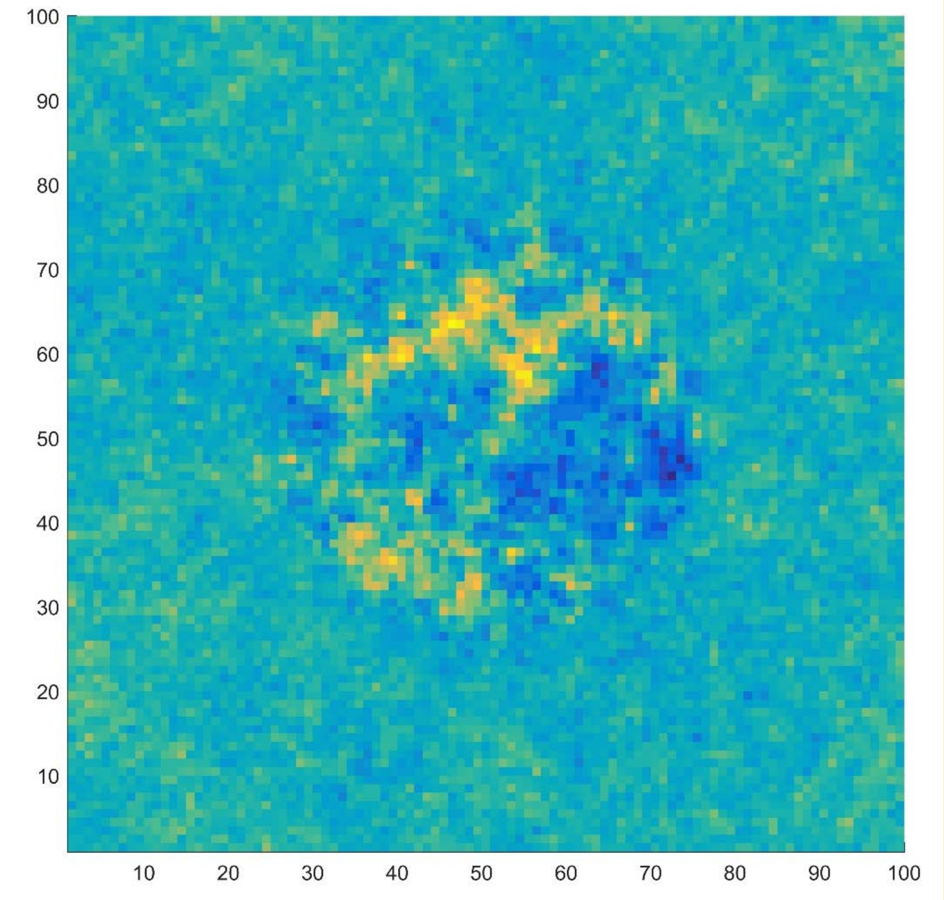
$$\frac{\int_{\Omega} \frac{b(x)}{m} dx}{\Omega} = 1$$

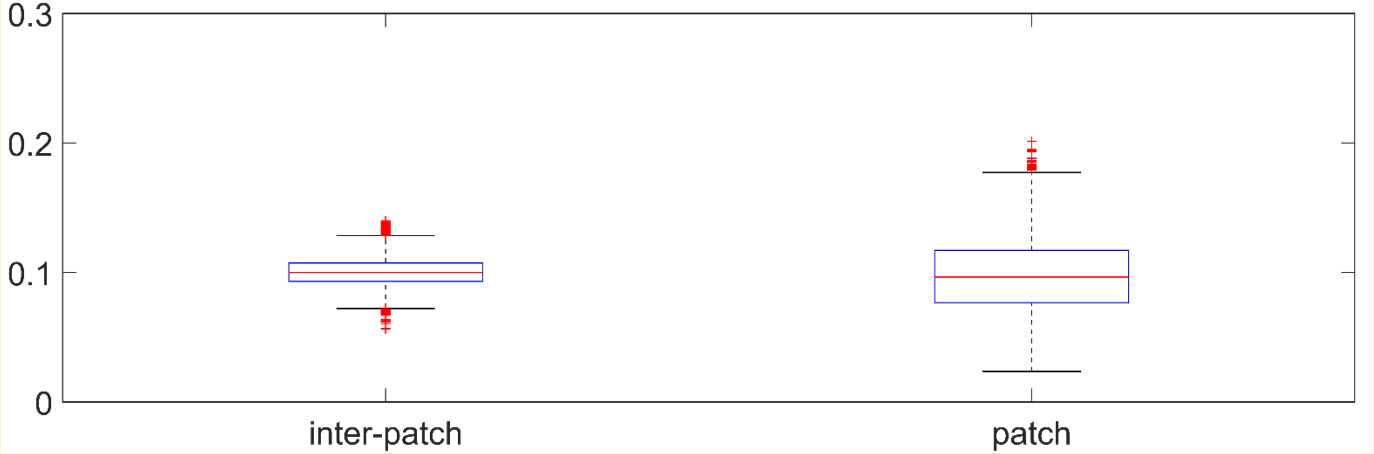
As $m \rightarrow \infty$ this process converges to the non-homogenous Poisson process used in the *Implicit Resources Scenario*

Results

(homogenous patch, R=25, *turn at encounter*, μ=0.01, h=0, m=1)

Residence Time





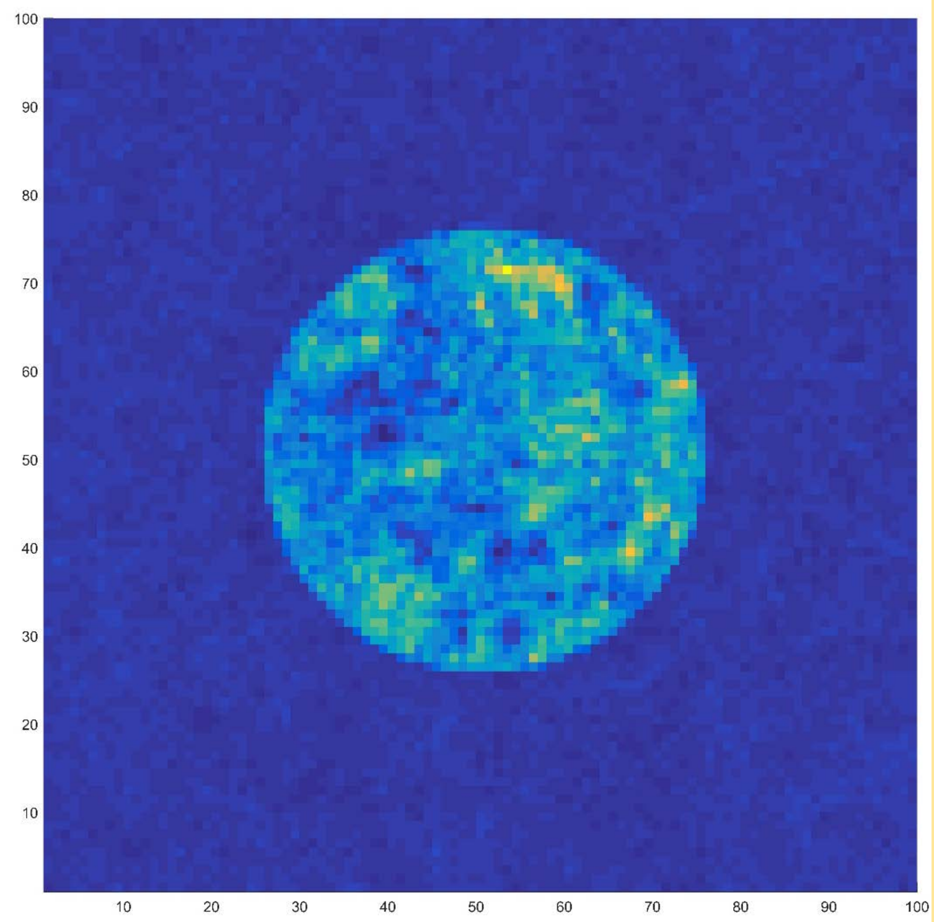
Encounter Rate = 0.63 (#/t)

(3.35 within the patch)

Results

(homogenous patch, R=25, *turn at encounter*, μ=0.01, h=1, m=1)

Residence Time



Encounter Rate = 0.46 (#/t)

(0.82 within the patch)

Turn @ Encounter

- Does not lead to consumer-resource spatial matching (beyond the trivial effect of handling time)
    - This could also be shown by deriving a steady-state solution for a transport equation model of the system
- Does lead to strong suppression of the functional response due to local depletion, even when the (domain-wide) resource renewal rate is high
- Local depletion effect may be mitigated by:
    - A substantial handling time (in relation to resource renewal rate)
    - Directional persistence in the consumer’s movement

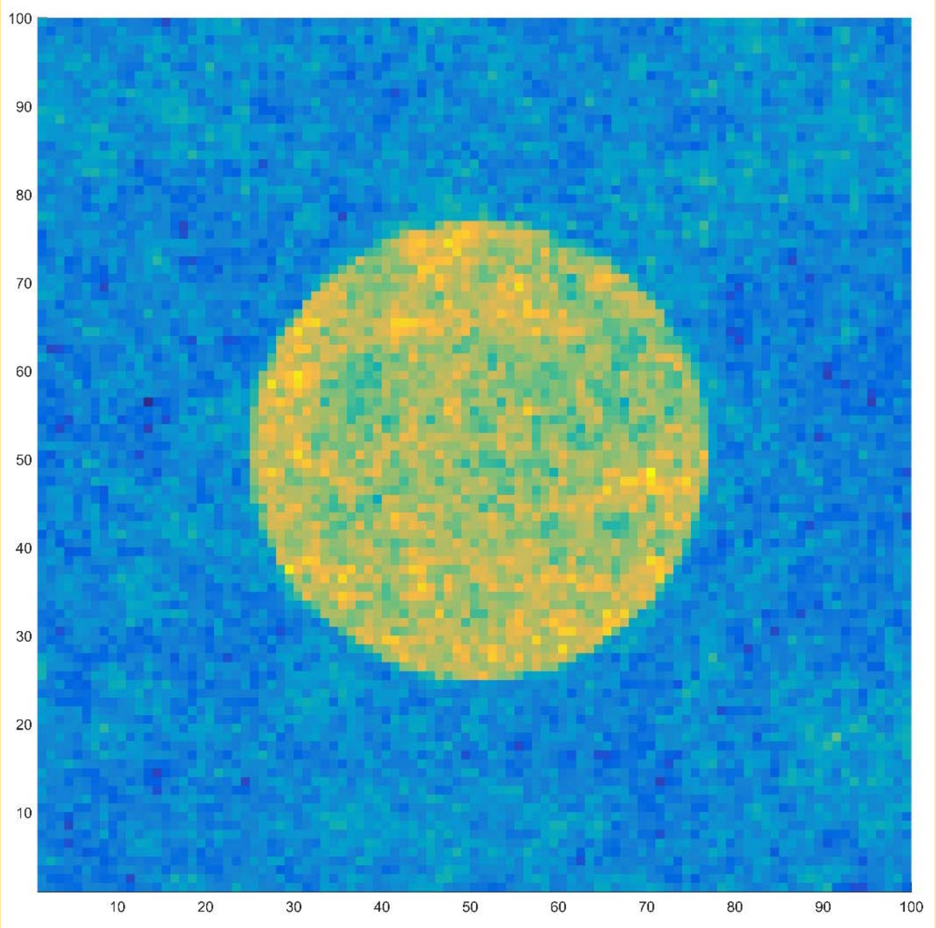
Questions

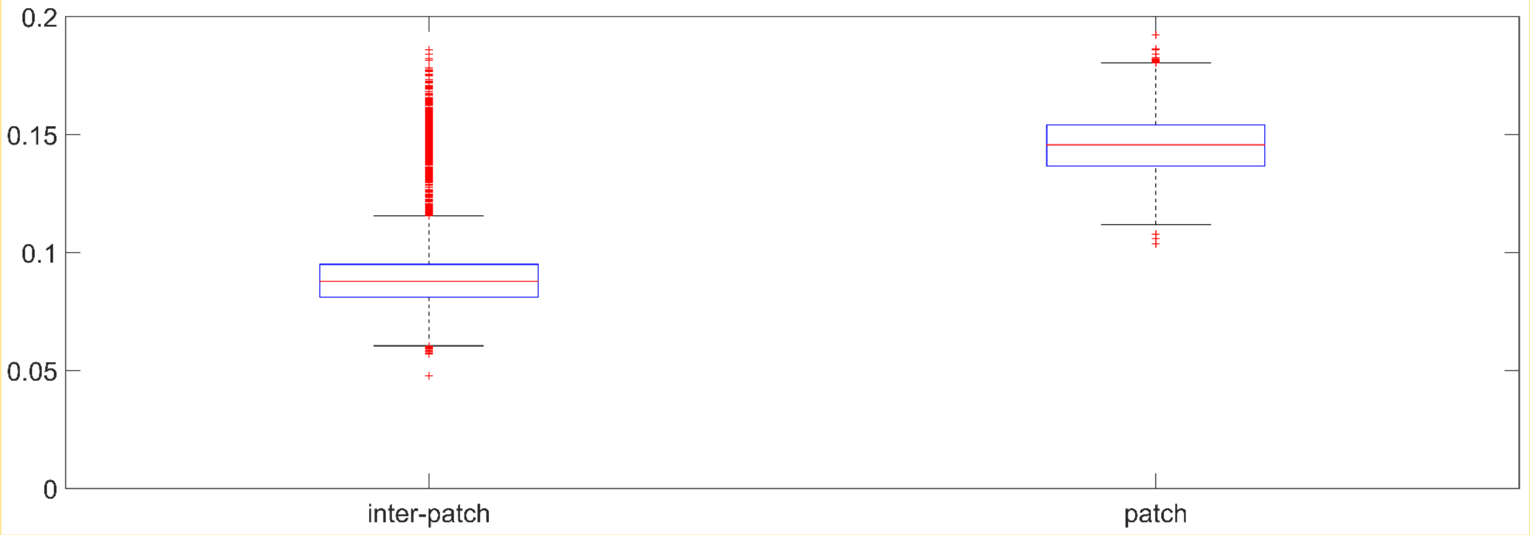
- Can this simple *turn-at-encounter* mechanism give rise to consumer-resource spatial matching (and hence an enhanced functional response)?
- If not, what might be a minimally sufficient movement mechanism leading to spatial pattern formation?

Results

(homogenous patch, R=25, turn 1 t after encounter, μ=0.01, h=0, m=1)

Residence Time





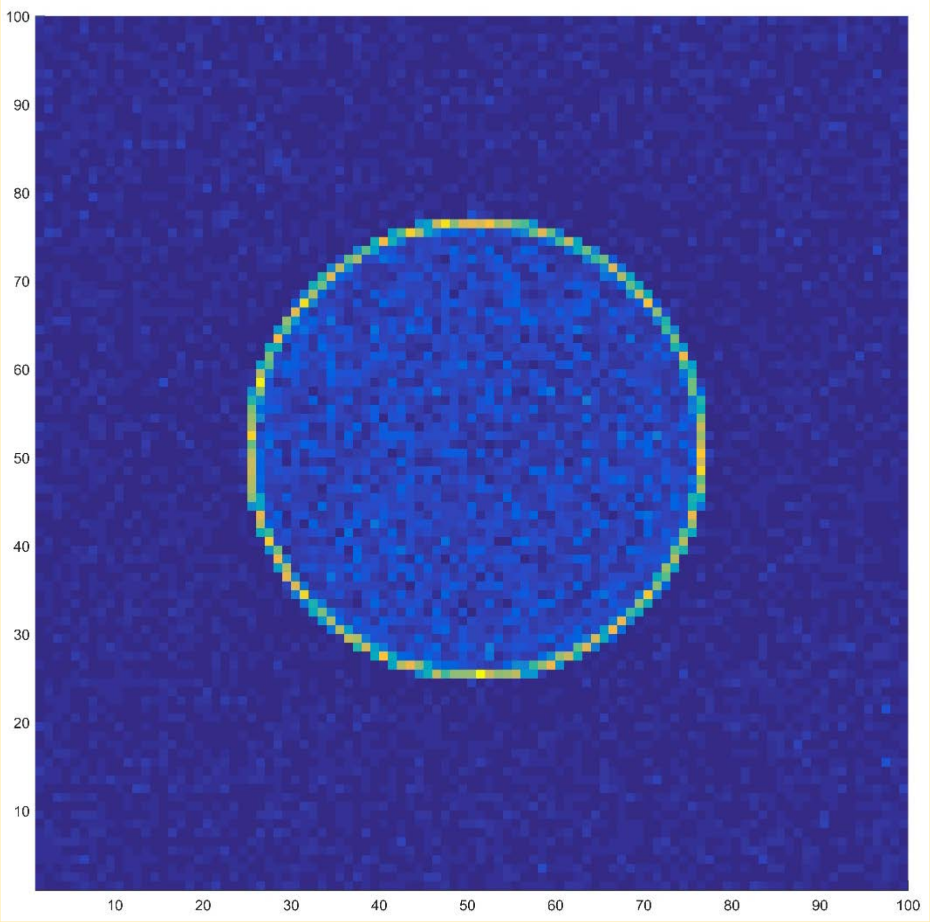
Encounter Rate = 1.45 (#/t)

(5.07 within the patch)

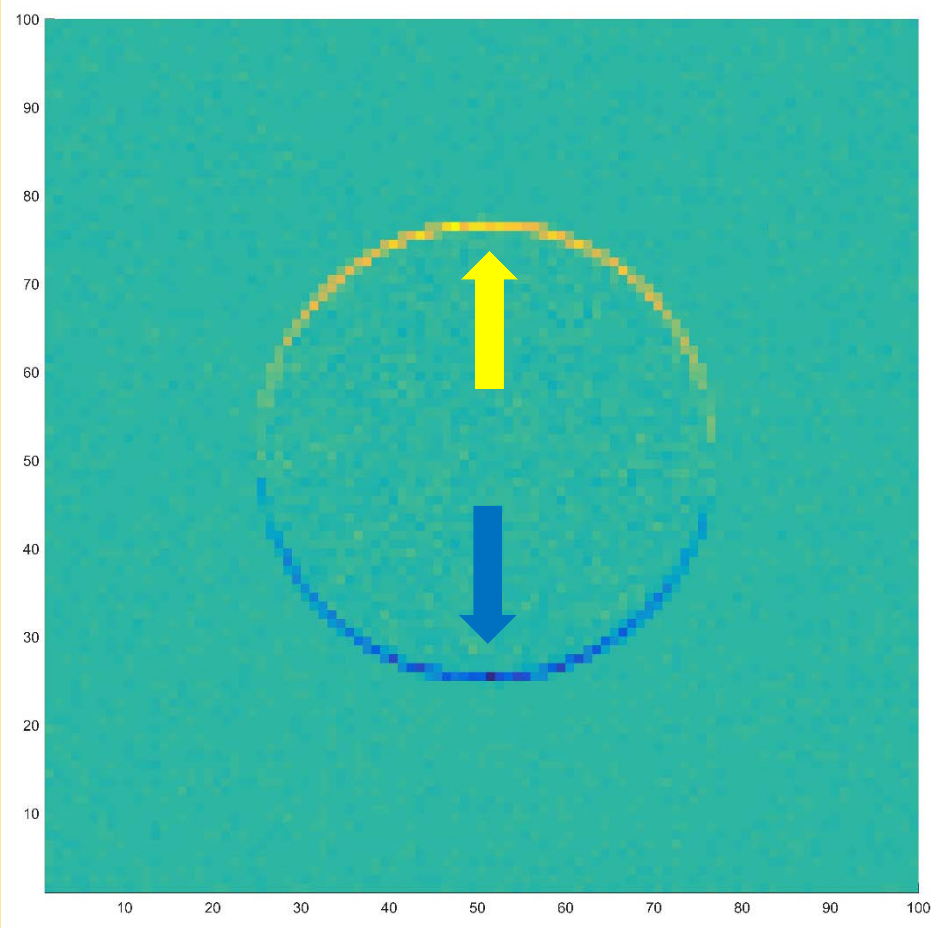
Results

(homogenous patch, R=25, turn 1 t after encounter, μ=0.01, h=0, m=1)

Turn Rate



Northing when Turning

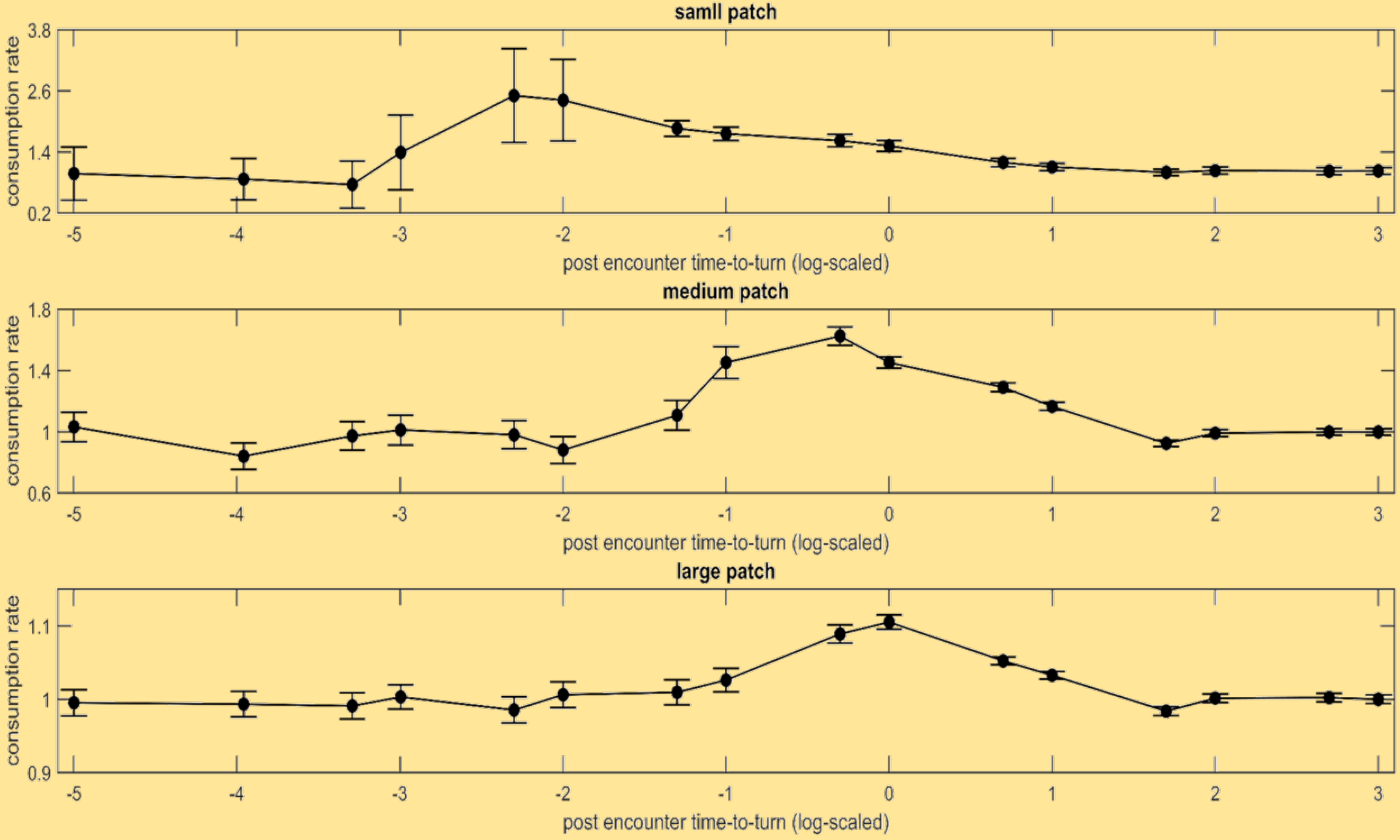


Questions

- Can this simple *turn-at-encounter* mechanism give rise to consumer-resource spatial matching (and hence an enhanced functional response)?
- If not, what might be a minimally sufficient movement mechanism leading to spatial pattern formation?
- What might be the effects of various ecological conditions on the intensity of these emerging patterns?

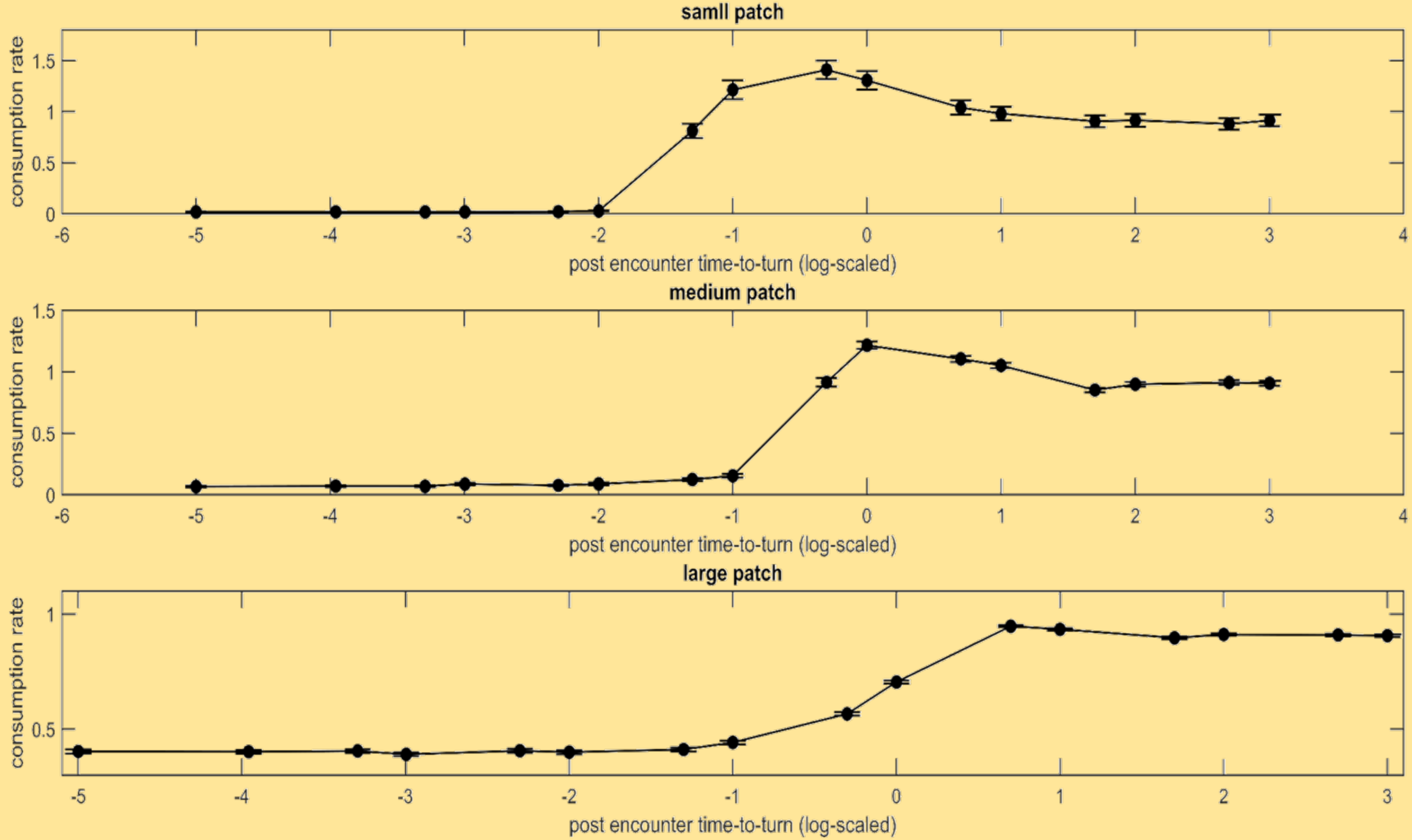
Results

(homogenous patch, R=25, μ=0.01, h=0)



Results

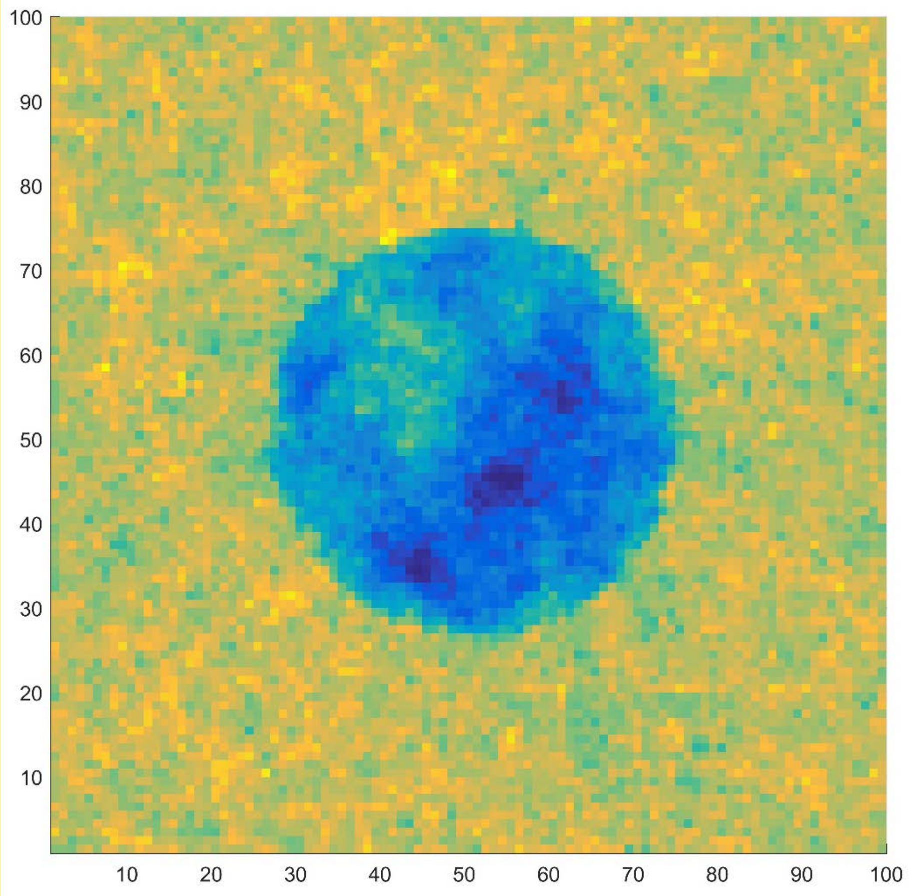
(homogenous patch, R=25, μ=0.01, h=0, m=0.001)



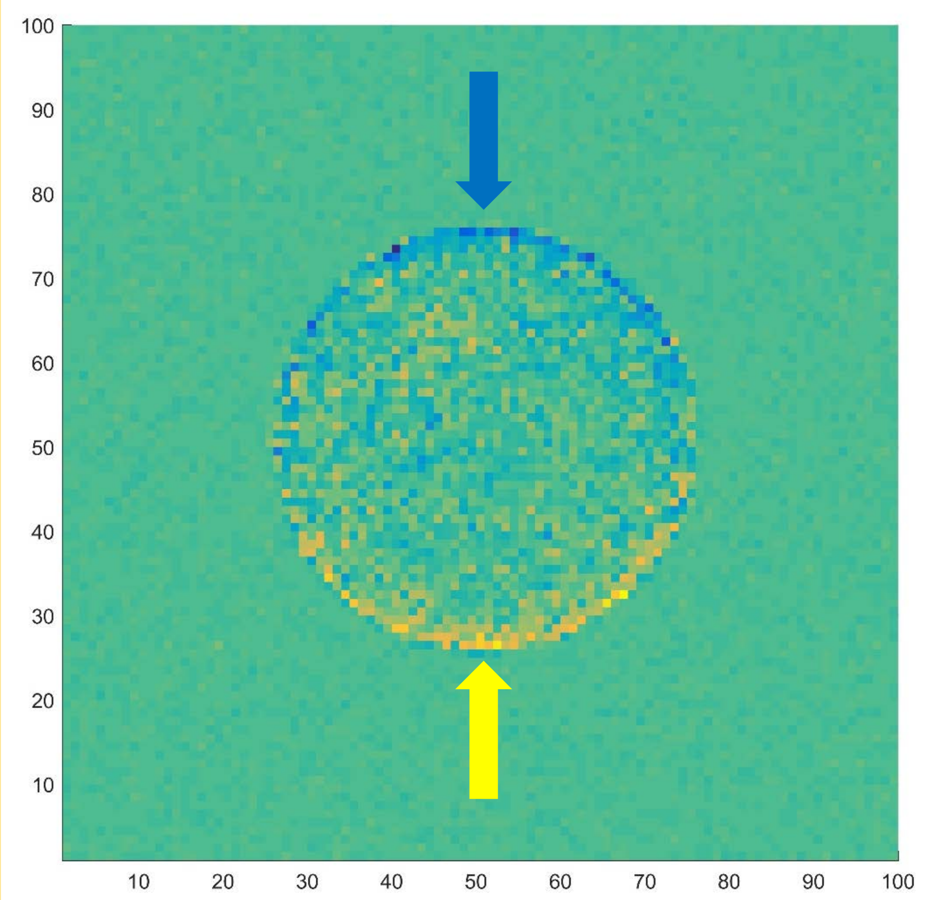
Results

(homogenous patch, R=25, turn 0.1 t after encounter, μ=0.01, h=0, m=0.001)

Residence Time



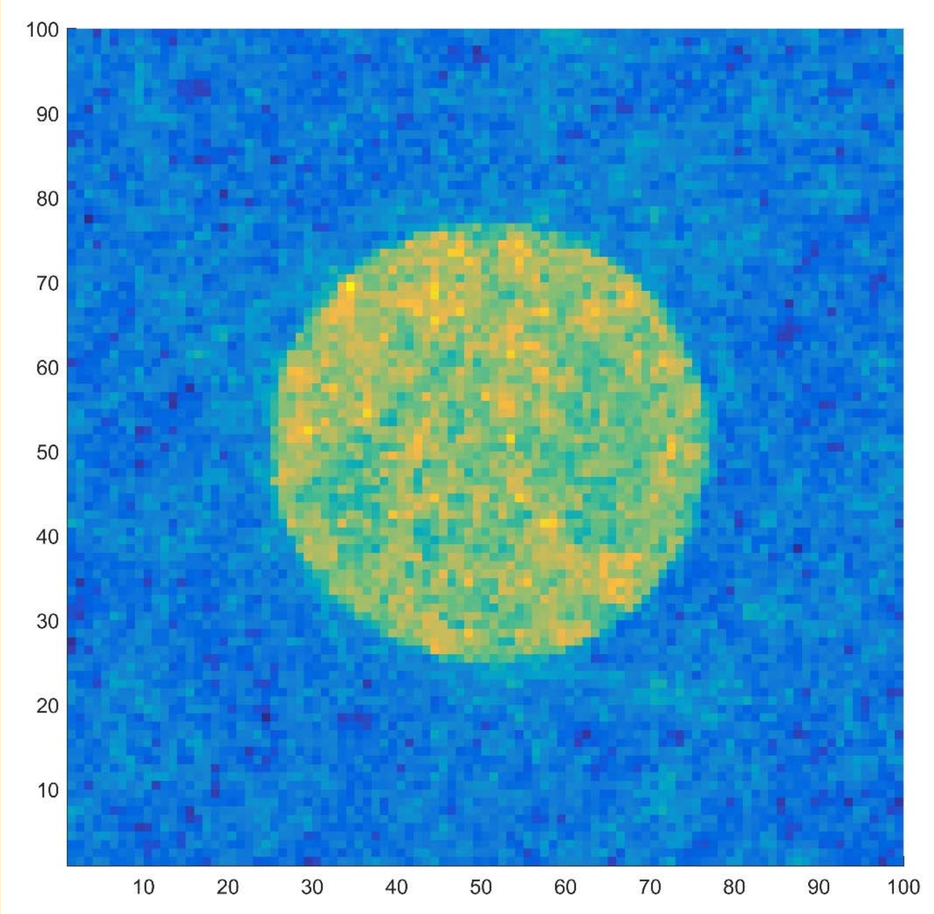
Northing when Turning



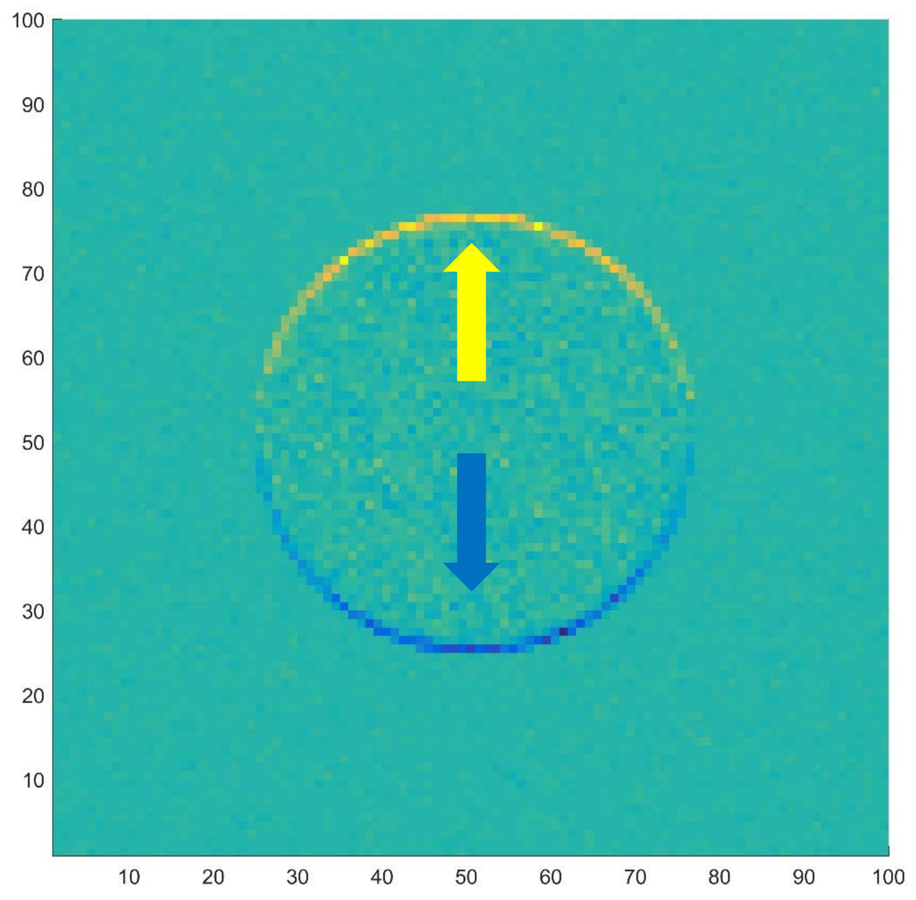
Results

(homogenous patch, R=25, turn 1 t after encounter, μ=0.01, h=0, m=0.001)

Residence Time



Northing when Turning



Conclusions

- A delayed behavioural response (= ‘spatial integration’) is needed for the emergence of consumer-resource spatial matching
- The optimal delay is a function of the resource’s spatiotemporal distribution
- Open questions:
    - Are there alternative minimalistic behavioural models?
    - Is optimal delay, and the resulting steady-state distribution, sensitive to consumer population density? Is there an ESS?
    - What are the demographic consequences?
    - Can we make general qualitative prediction as to the shape of consumer-resource relationship?

Acknowledgments

Lauréats
KILLAM
Laureates

Banting
Postdoctoral Fellowships

"About your cat, Mr. Schrödinger—I have good news and bad news."