Agent-Based and Continuous Models of Locust Hopper Bands: Insights Gained Through the Lens of Dynamical Systems

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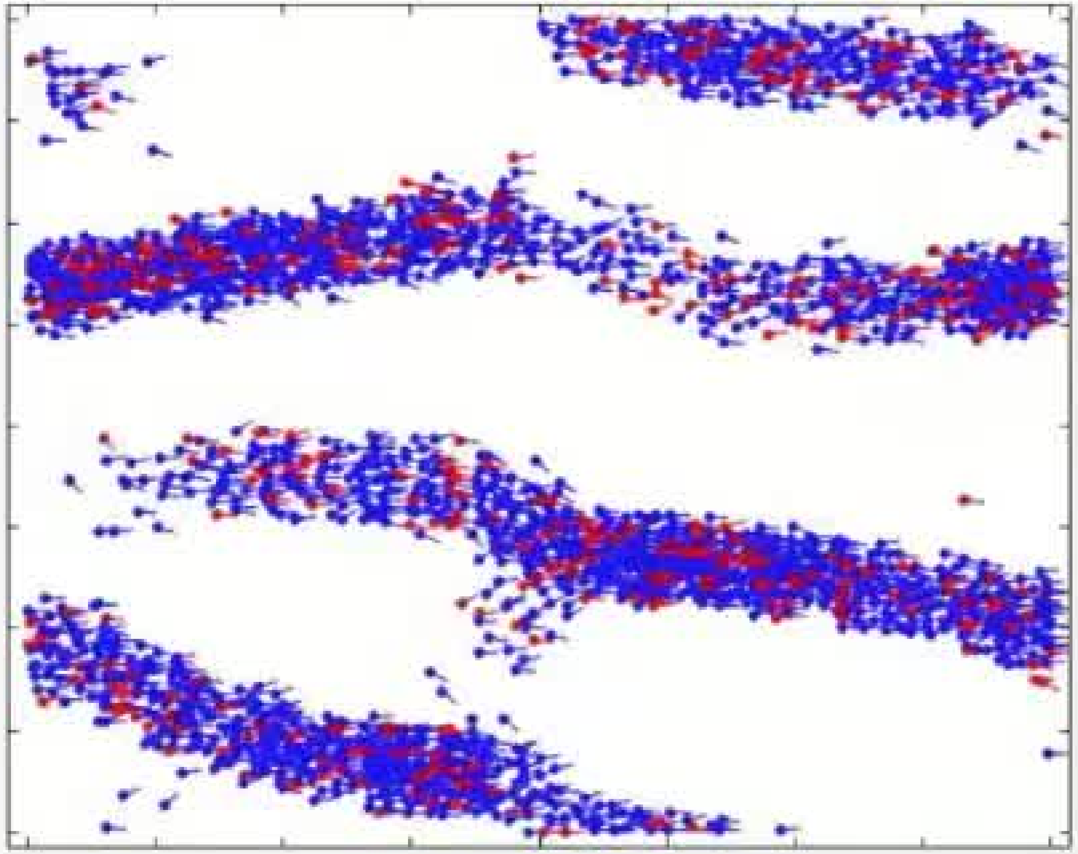

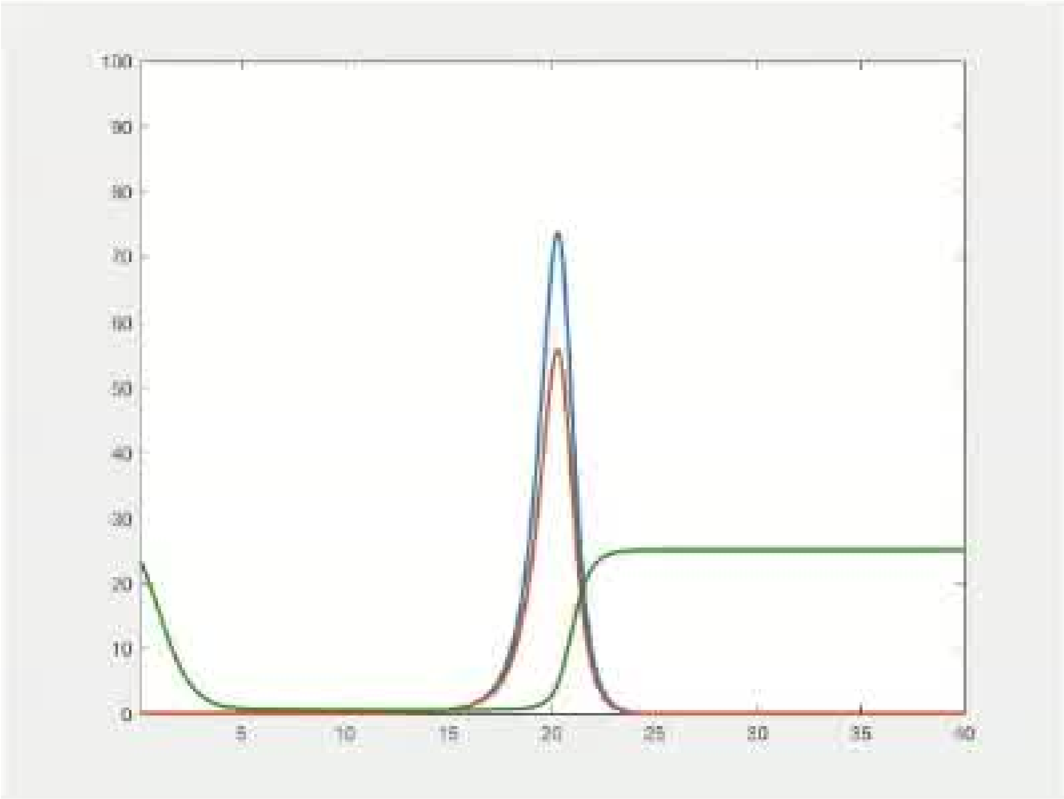

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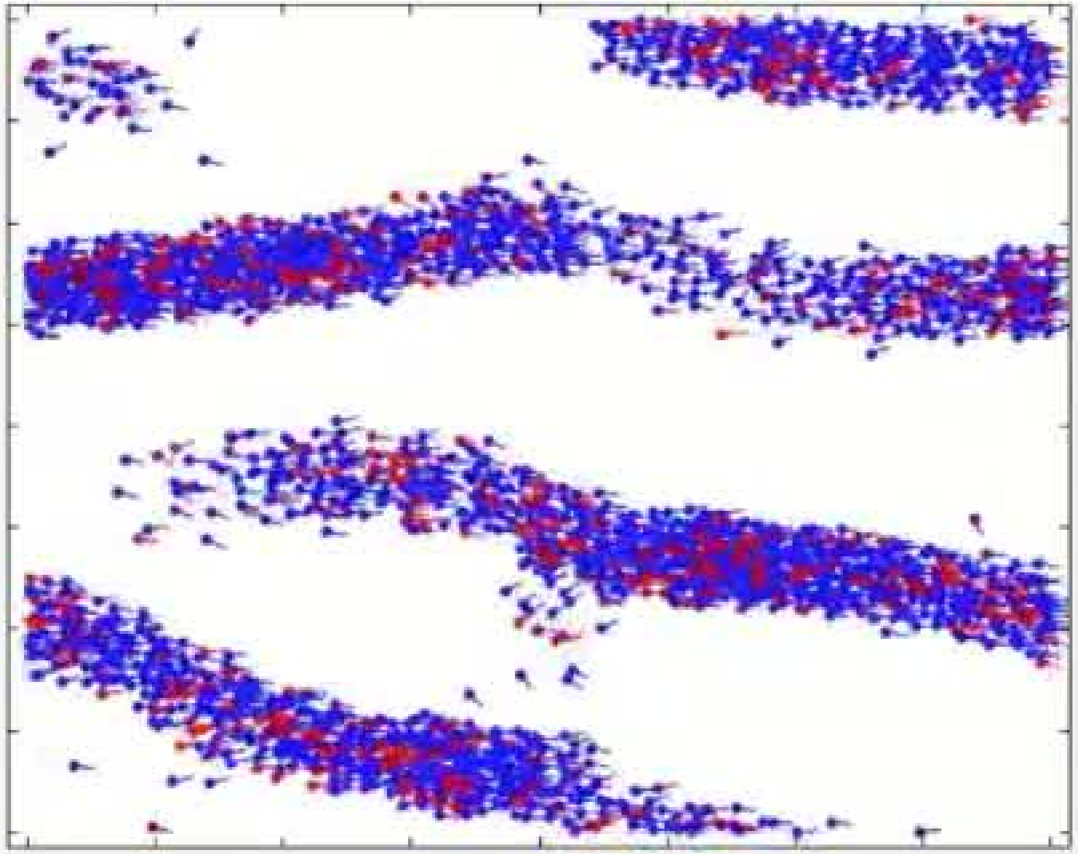

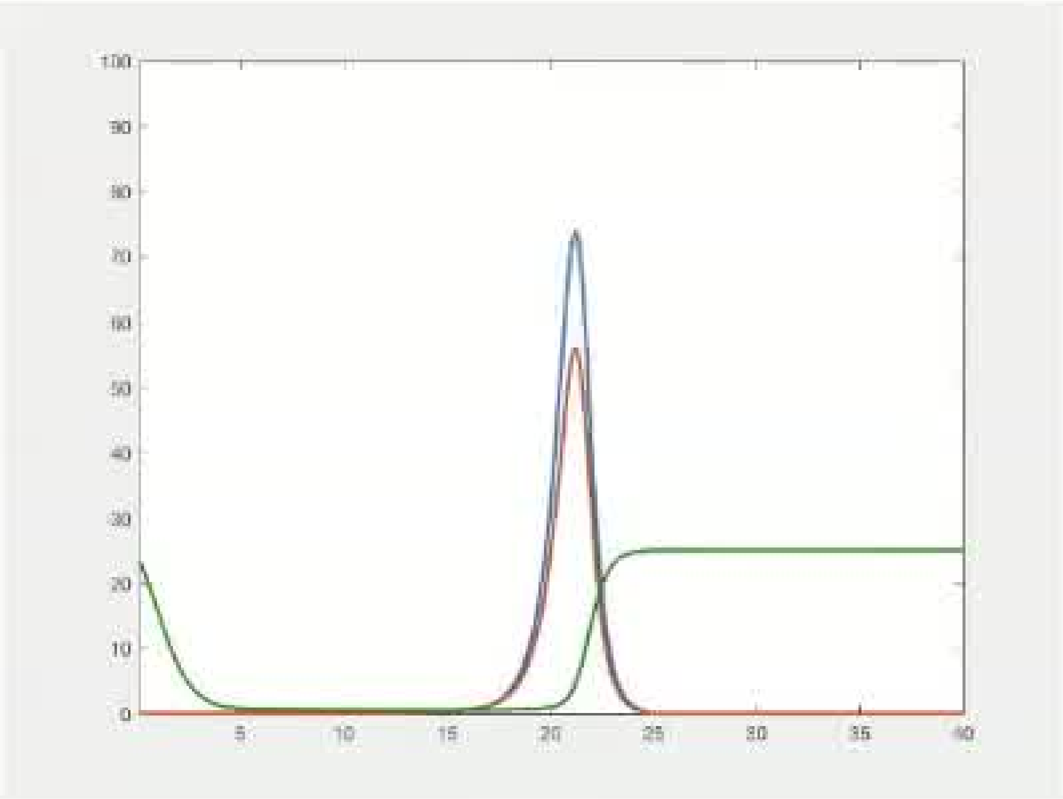

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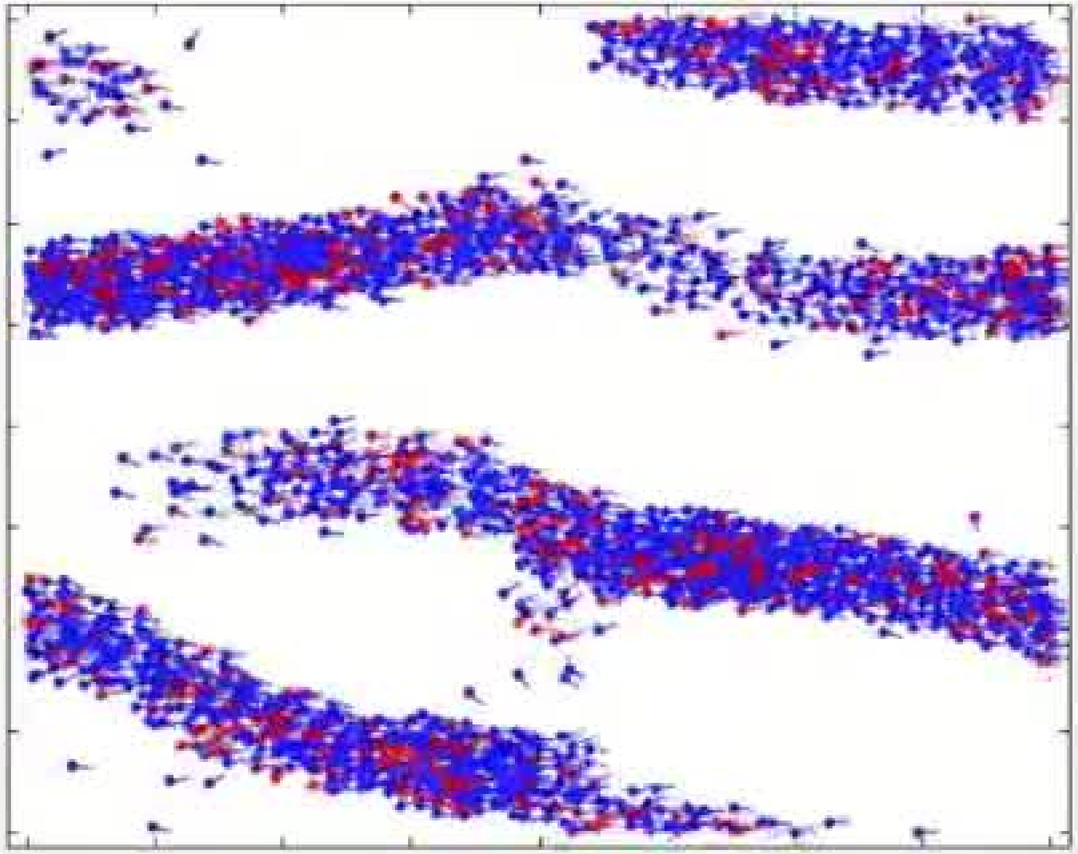

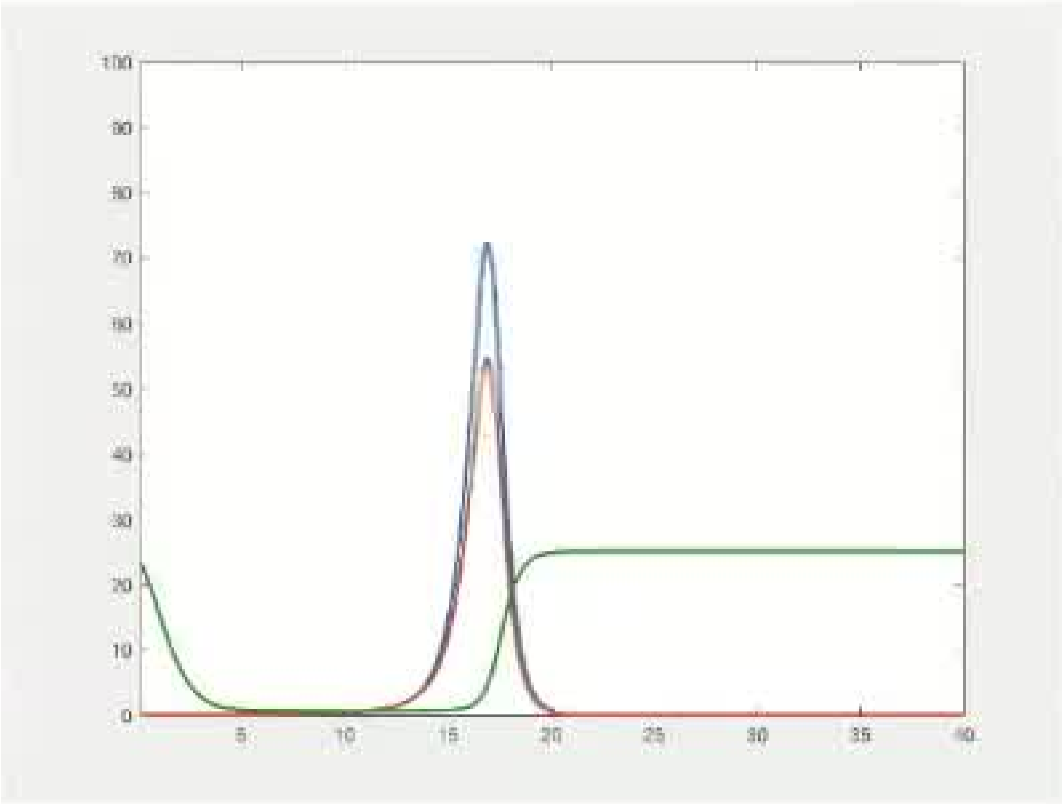

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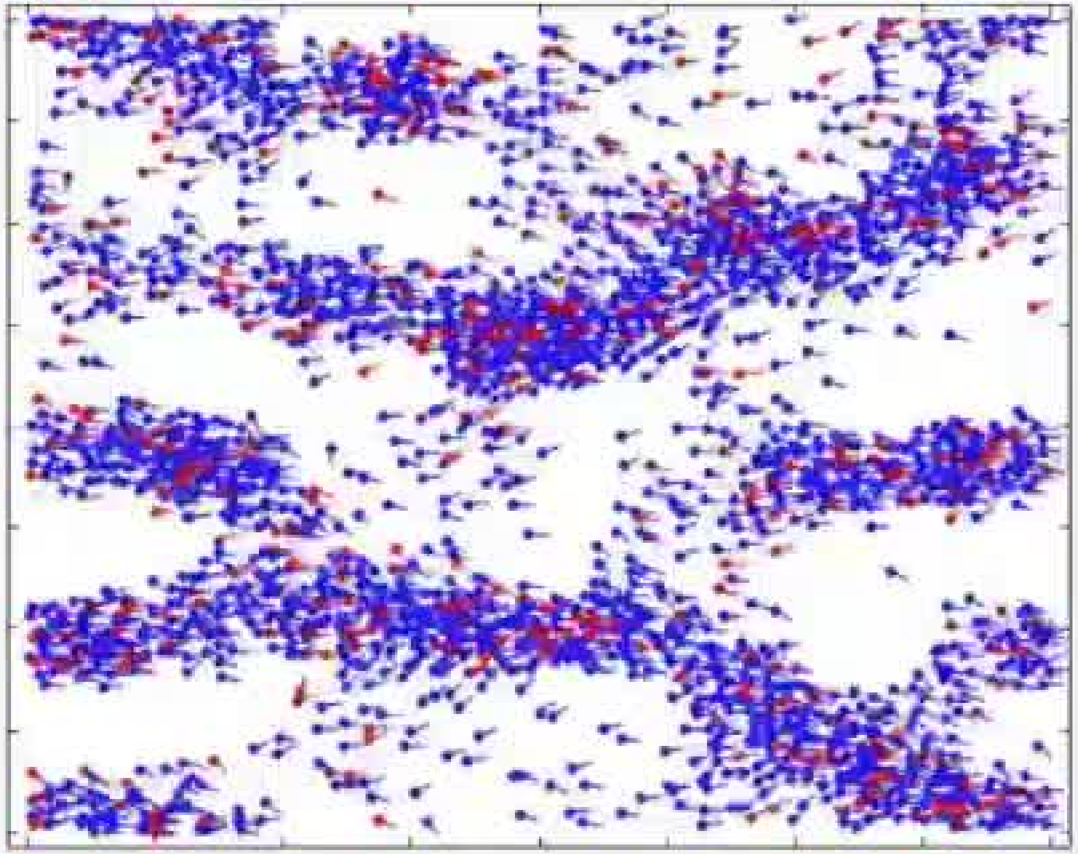

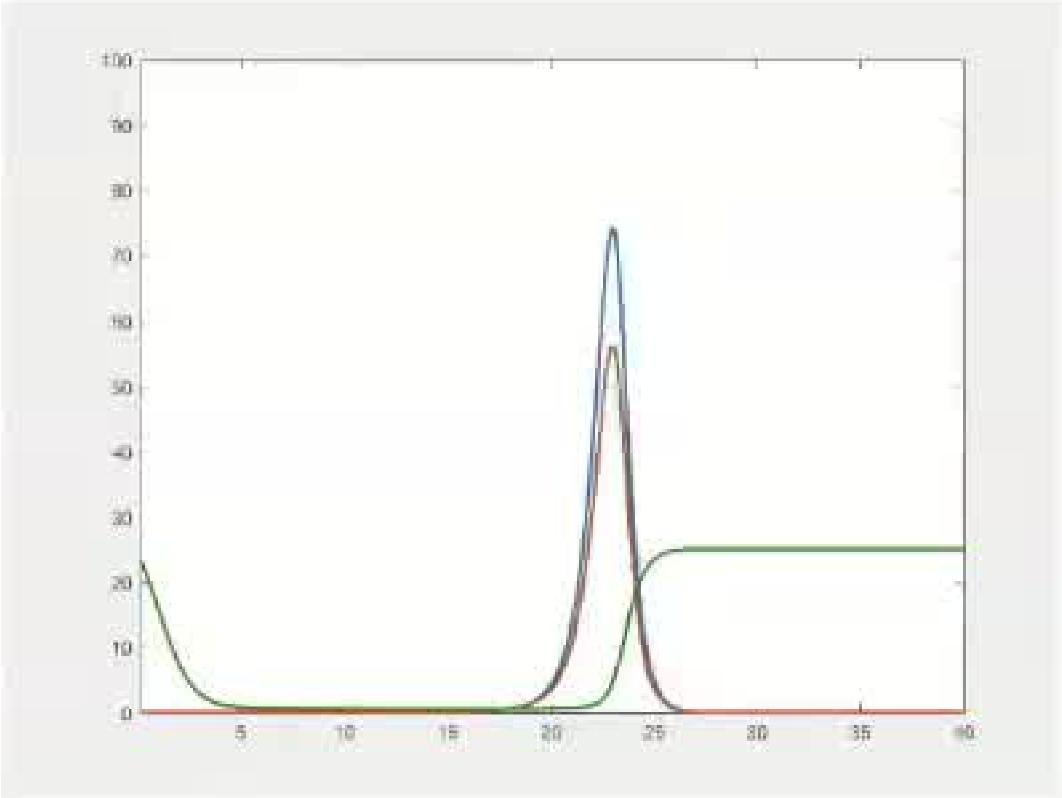

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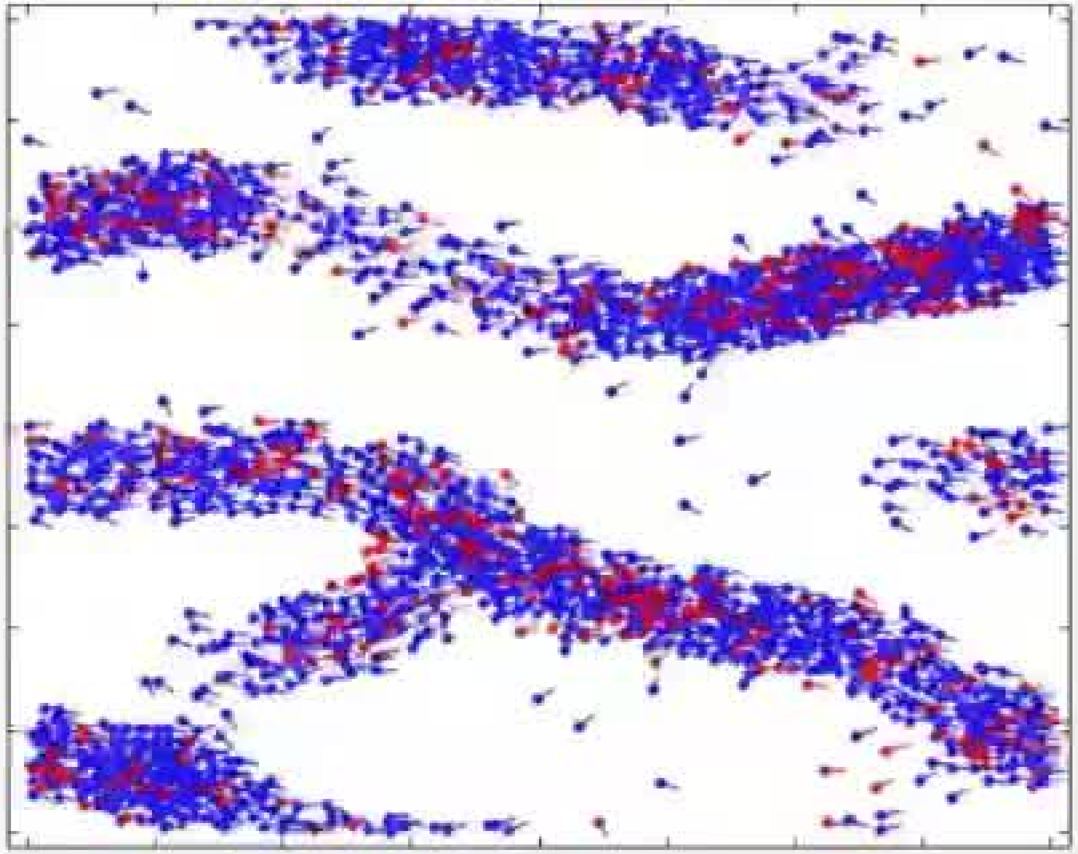

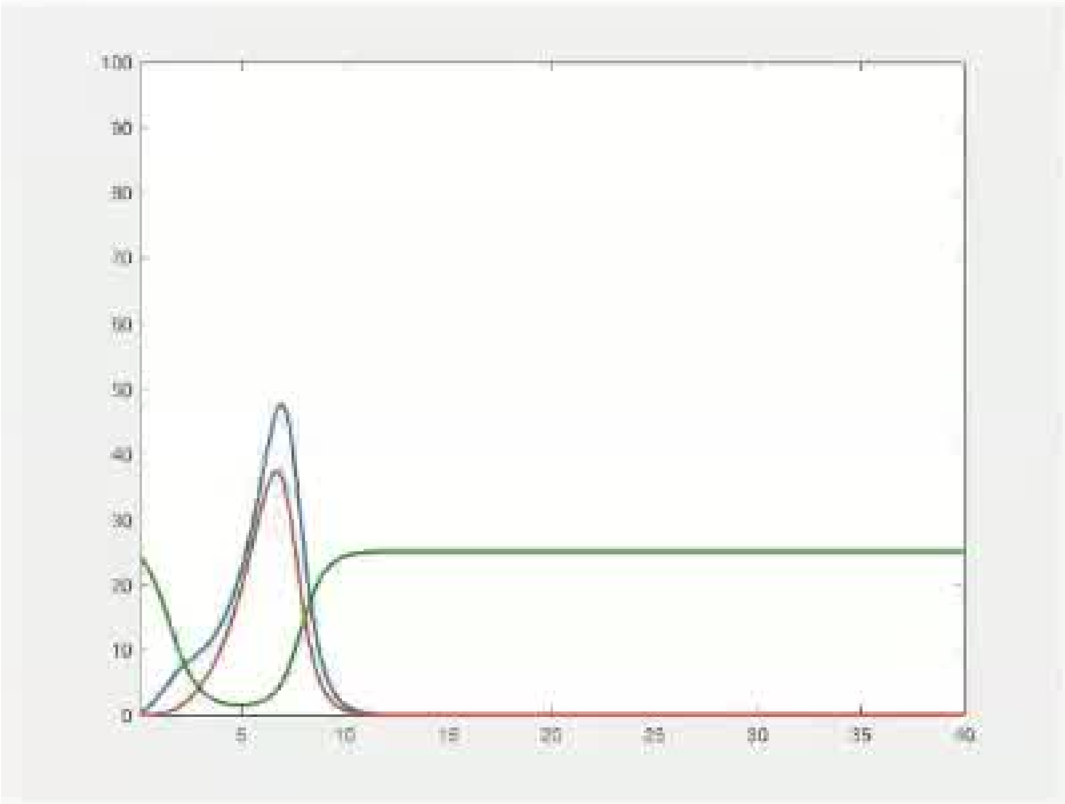

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Locust Hopper Bands

Plagues of Locusts - Wild Africa - BBC
Episode 3: Deserts. First Broadcast 11/21/2001

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Locust Hopper Bands

Columnar Structure

Desert Locust
Schistocera gregaria

Planar Front

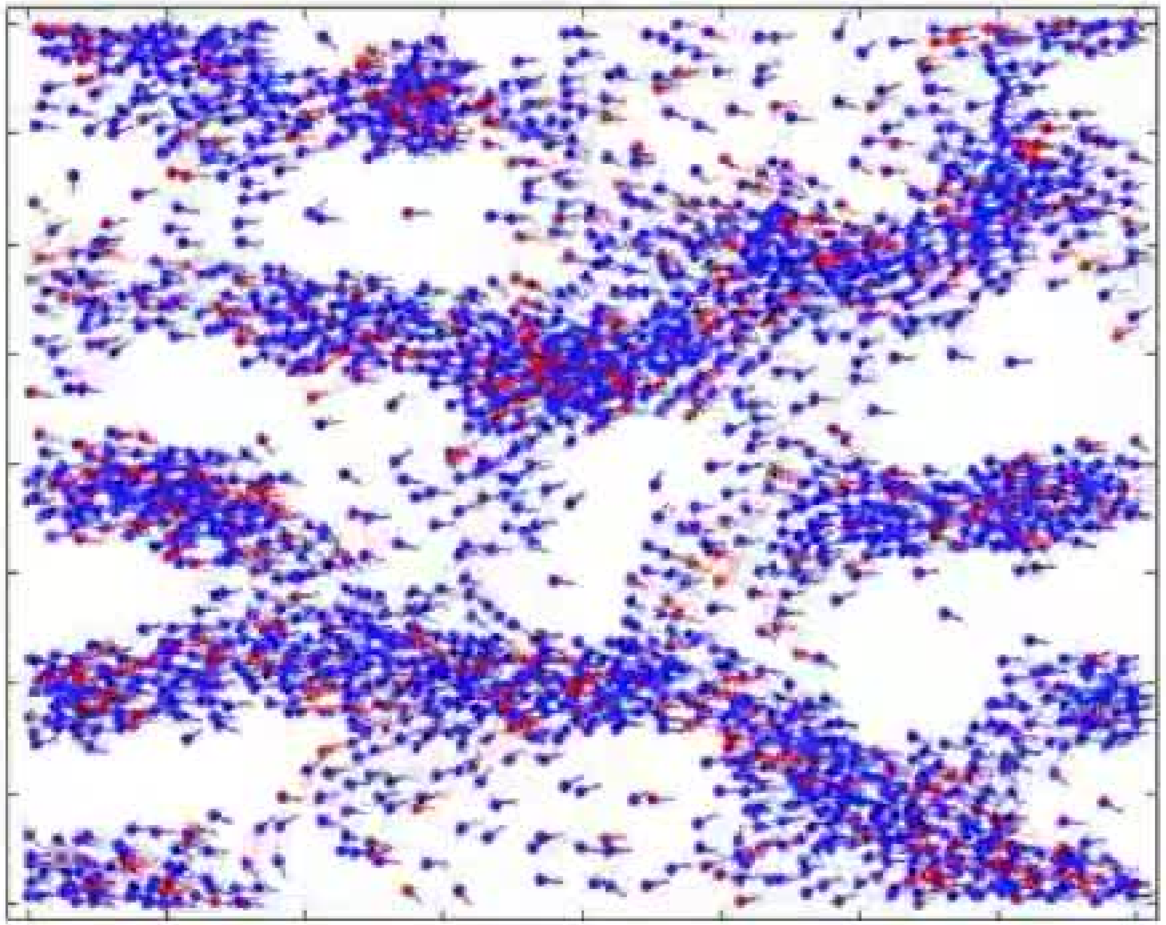
Australian Plague Locust
(Chortoicetes terminifera)

Model I: Exploring Columnar Structure

Model I: Exploring Columnar Structure

Agent- Based Model (ABM)

When Locusts Swarm
Kit Yates (Bath) & Jerome Buhl (Adelaide)
https://vimeo.com/144014400



Experiments/Observation → Agent-Based Model

Agent- Based Model (ABM)

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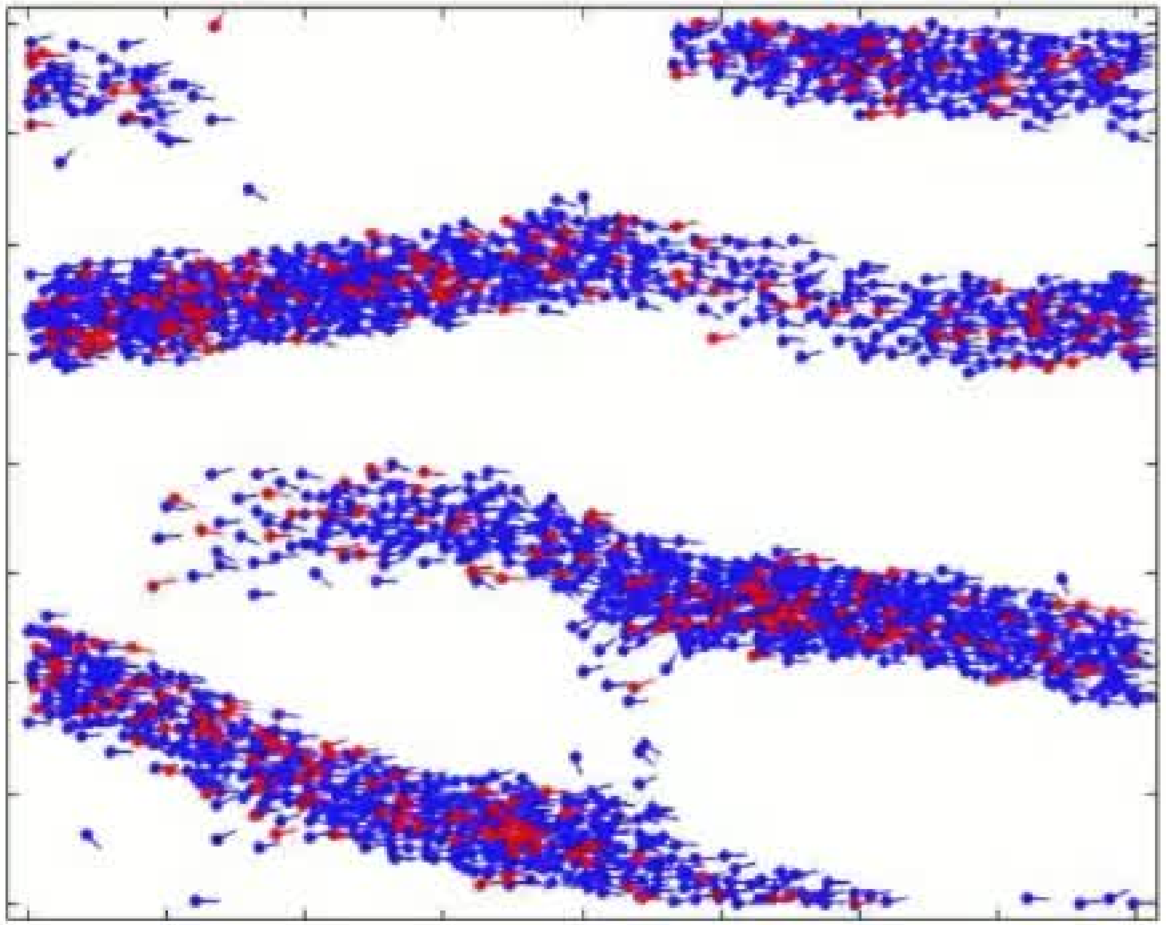
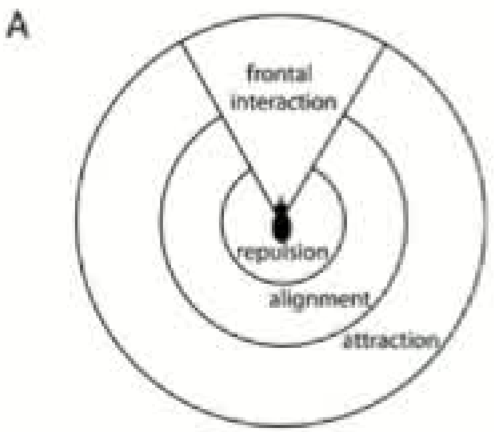
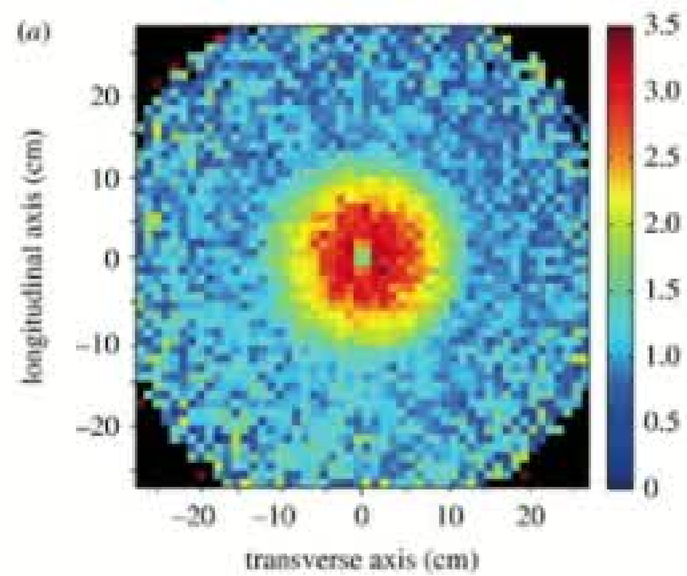


Experiments/Observation → Agent-Based Model

Locust ABM - A Selective Review



Lukeman, Li & Edelstein-Keshet (2010)



Relative density of neighbors around a focal individual.

Buhl, Sword & Simpson (2012)

Three Zone Models:

- Lukeman, R., Li, Y.-X., & Edelstein-Keshet, L. (2010). Inferring individual rules from collective behavior. Proc. Natl. Acad. Sci. USA, 107(28), 12576–12580.
- Couzin, I., Krause, J., James, R., Ruxton, G., & Franks, N. (2002). Collective memory and spatial sorting in animal groups. J. Theor. Biol., 218, 1–11.
- J. M. Miller, A. Kolpas, J. P. J. Neto, and L. F. Rossi, A continuum three-zone model for swarms, Bulletin of mathematical biology, 74 (2012), pp. 536–61.
- Aoki, I. (1982). A simulation study on the schooling mechanism in fish. Bull. Jap. Soc. Sci. Fish. 48, 1081–1088.
- Reynolds, C. W. (1987). Flocks, herds and schools: a distributed behavioral model. Comput. Graph. 21, 25–34.
- Huth, A. & Wissel, C. (1992). The simulation of the movement of fish schools. J. Theor. Biol. 156, 365–385.

Orientation Models:

- Vicsek, T., Czirók, A., Ben-Jacob, E., Cohen, I., & Shochet, O. (1995). Novel type of phase transition in a system of self-driven particles. *Physical review letters, 75*(6), 1226.
- Chaté, Hugues, et al. "Modeling collective motion: variations on the Vicsek model." *The European Physical Journal B* 64.3-4 (2008): 451-456.
- Grégoire, Guillaume, Hugues Chaté, and Yuhai Tu. "Moving and staying together without a leader." Physica D: Nonlinear Phenomena 181.3-4 (2003): 157-170.

Pause & Go Models:

- Ariel G, Ophir Y, Levi S, Ben-Jacob E and Ayali A (2014) Individuals' intermittent motion is instrumental to the formation and maintenance of swarms of marching locust nymphs. PLoS ONE 9(7): e101636.
- Nilsen, C., Paige, J., Warner, O., Mayhew, B., Sutley, R., Lam, M., Bernoff, A.J. and Topaz, C.M., 2013. Social aggregation in pea aphids: experiment and random walk modeling. PloS one, 8(12), p.e83343.

Locust ABM:

- Ariel, Gil, and Amir Ayali. "Locust collective motion and its modeling." *PLoS computational biology* 11.12 (2015): e1004522.
- Buhl, J., Gregory A. Sword, and Stephen J. Simpson. "Using field data to test locust migratory band collective movement models." Interface focus 2.6 (2012): 757-763.

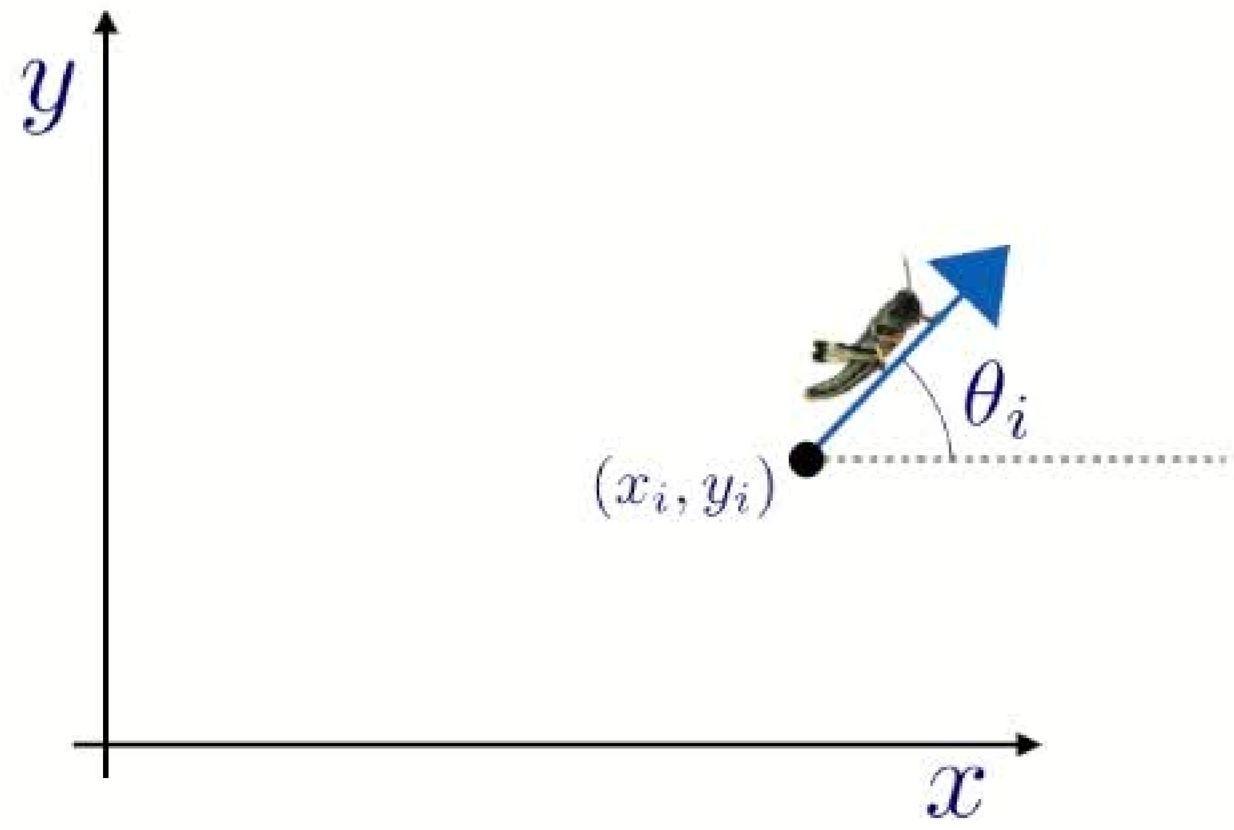
ABM: State Variables

Consider N locusts indexed by the variable $i = 1 \ldots N$

Position: $\vec{x}_i = (x_i, y_i)$ $\vec{x}_i \in \mathbb{R}^2$

Orientation: θ_i $\theta_i \in \mathbb{S}^1$

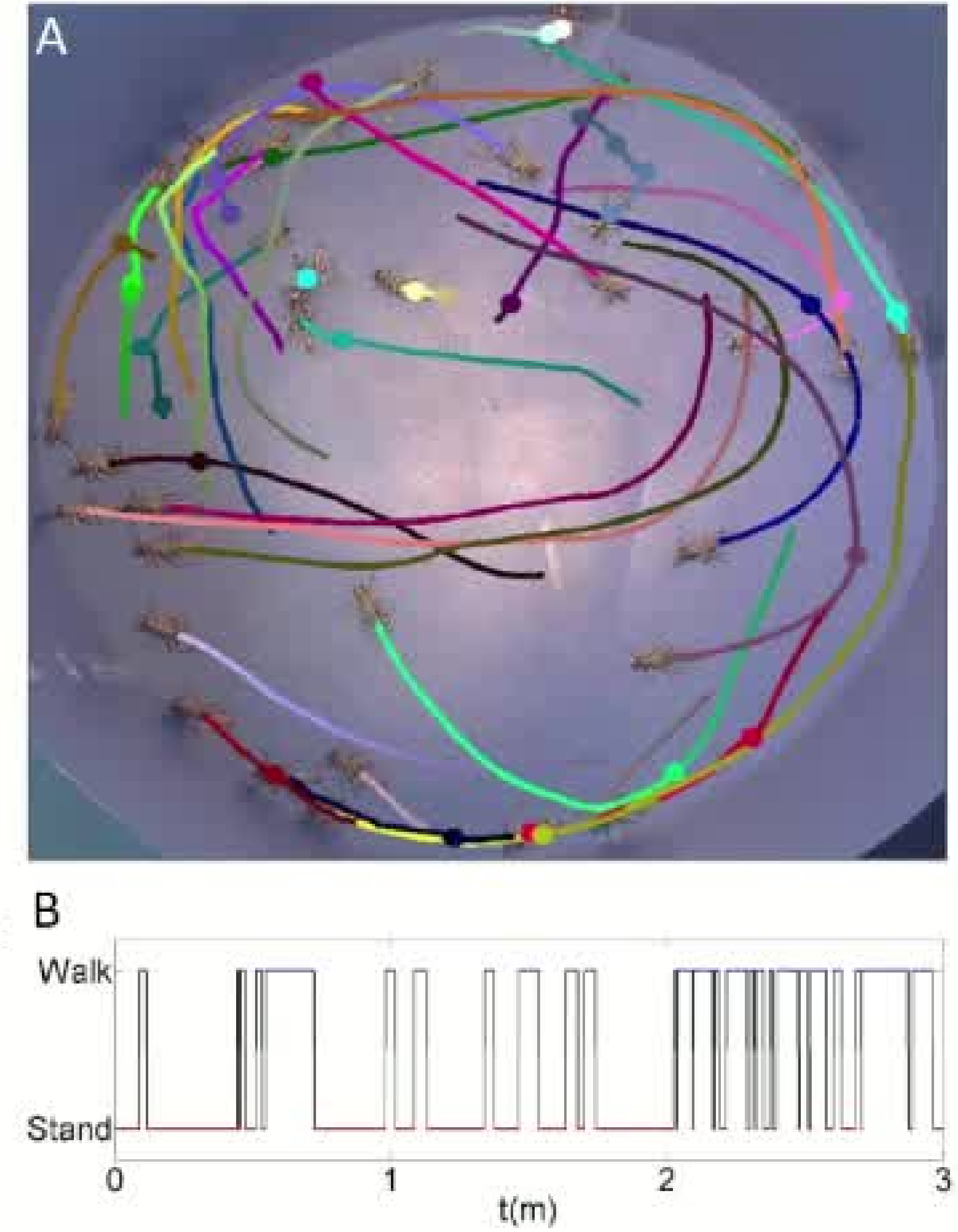
State (stationary/moving): s_i $s_i \in \{0, 1\}$



ABM: Pause/Go Motion

Motion tracking of locusts yields:

- Locusts exhibit pause/go motion.
- Pausing is more likely when a locust is blocked.
- Motion is more likely when a locust is nudged from behind.
- Locust speed is roughly constant.



Ariel, Ophir, Levi, Ben-Jacob & Ayali (2014)
Individuals' intermittent motion is instrumental to the formation and maintenance of swarms of marching locust nymphs.
PLoS ONE 9(7): e101636

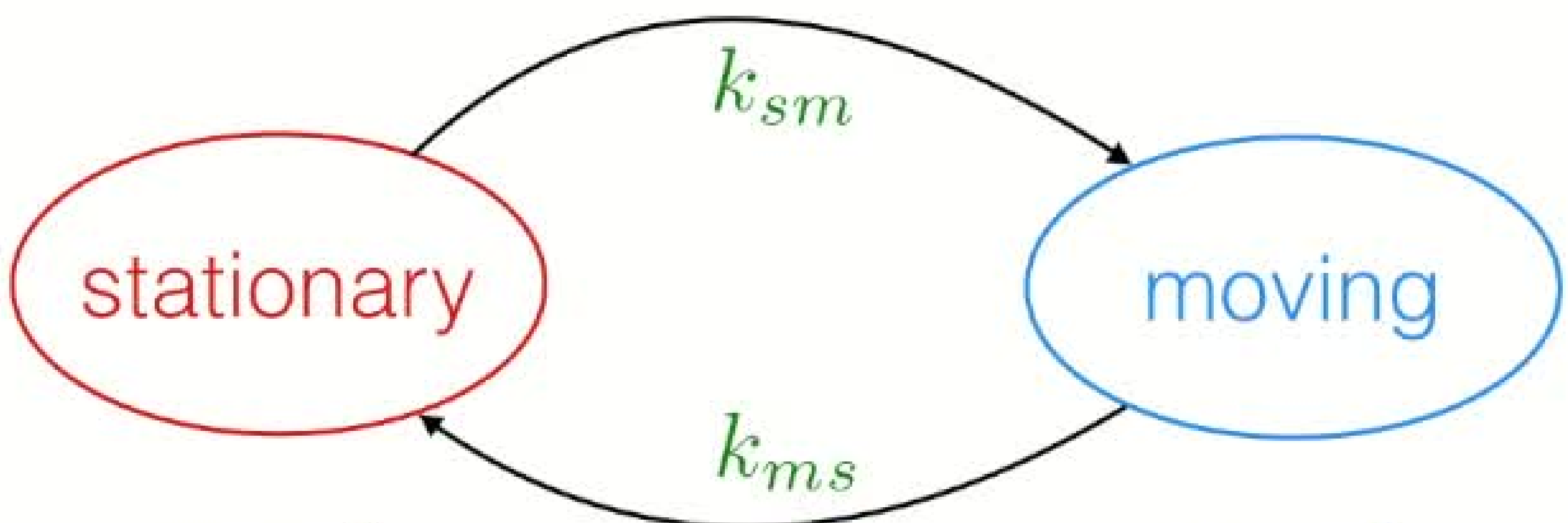
ABM: Pause/Go Motion

$$\frac{d\vec{x}_i}{dt} = s_i v \hat{u}_i(\theta_i)$$

$$\hat{u}_i(\theta_i) = \langle \cos\theta_i, \sin\theta_i \rangle$$

$$v = \text{speed (constant)}$$

Markov process for transition



$s_i = 0$

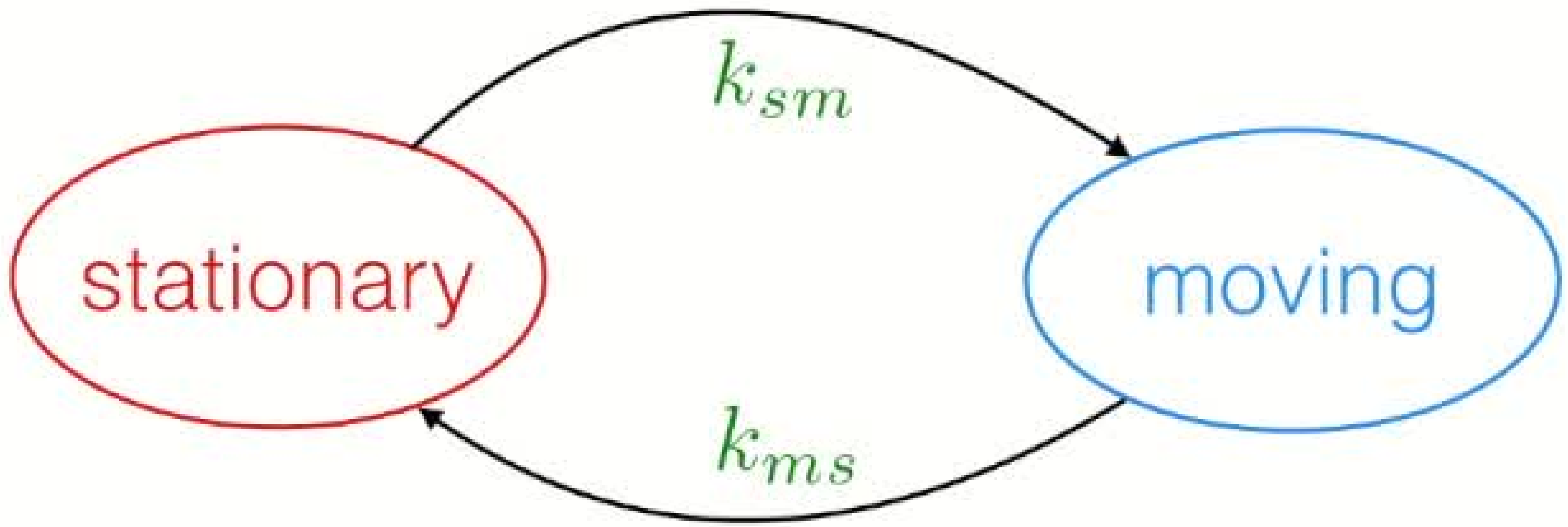
$s_i = 1$

$$\frac{d\vec{x}_i}{dt} = 0$$

$$\frac{d\vec{x}_i}{dt} = v \hat{u}_i(\theta_i)$$

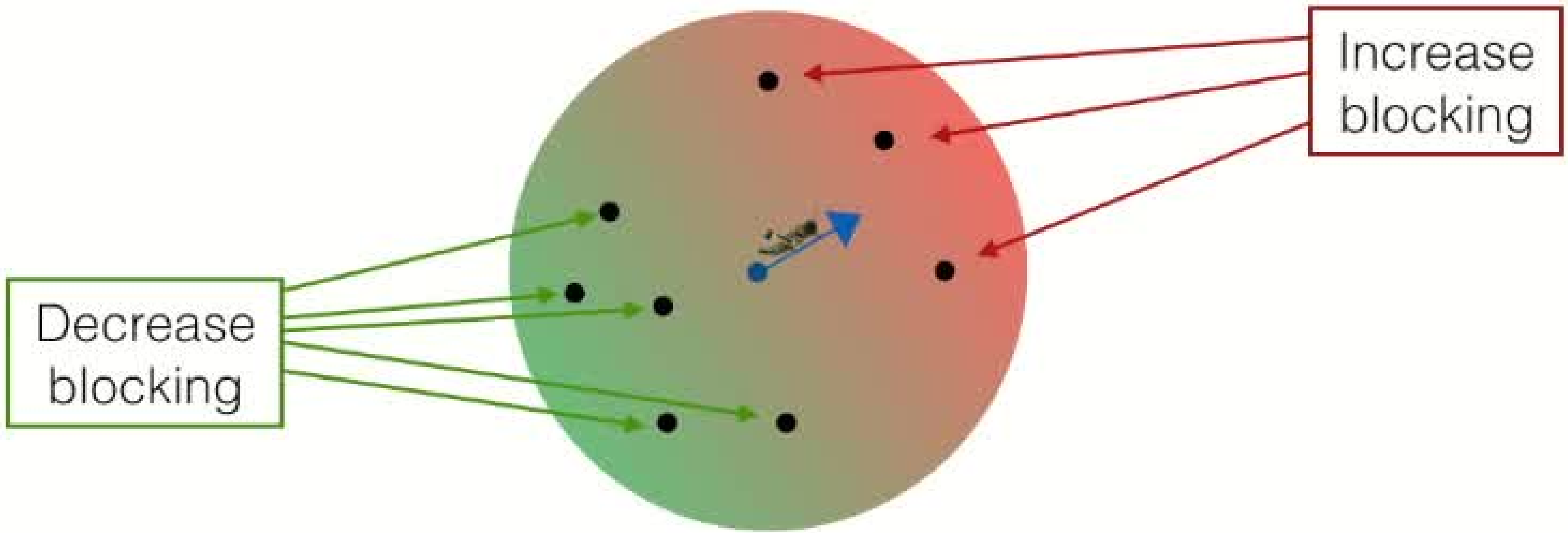
ABM: Pause/Go Motion (blocking)

Markov process for transition



$$k_{ms} = \kappa_{ms} e^{\alpha_{ms}\beta} \qquad k_{sm} = \kappa_{sm} e^{-\alpha_{sm}\beta}$$

$\beta =$ blockscore (a weighted sum of neighbors)



ABM: Orientation

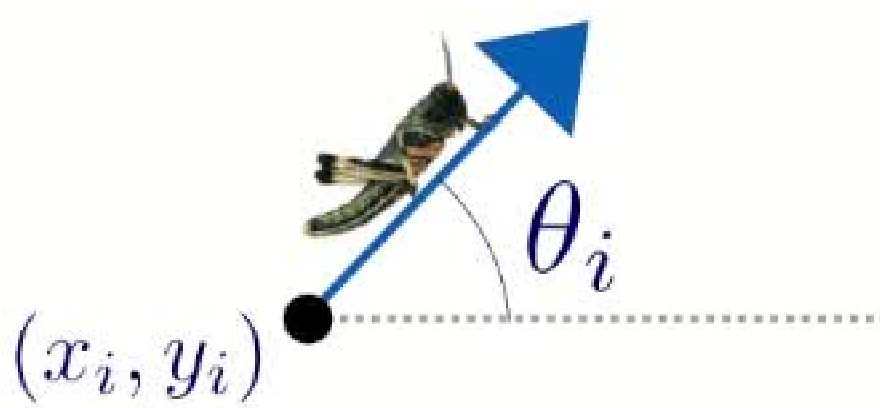
$$\frac{d\theta_i}{dt} = \omega_o + \omega_e + \omega_a + \omega_n,$$

Alignment

Environment

Attraction/Repulsion

Noise



ABM: Orientation (Alignment)

$$\frac{d\theta_i}{dt} = \omega_o + \omega_e + \omega_a + \omega_n,$$

Alignment | Environment | Attraction/ Repulsion | Noise

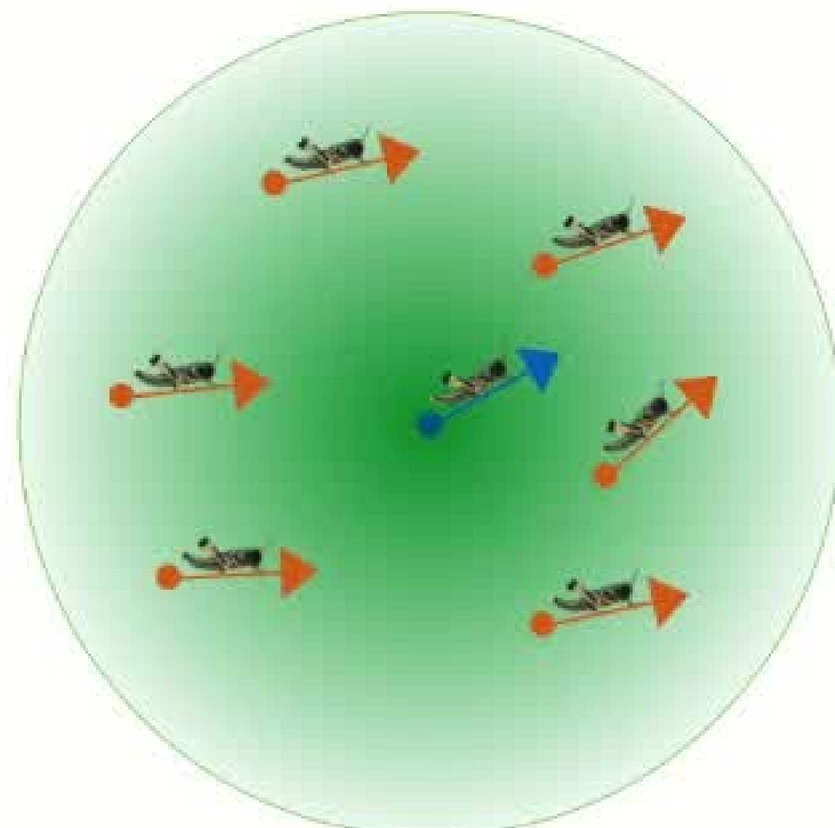
Kumamoto type coupling:

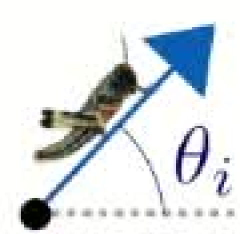
$$\omega_o = \sum_{\substack{j=1 \\ j\neq i}}^{n} c_o f_o(d_{ij}) \sin(\theta_j - \theta_i).$$

Weighted by distance, $d_{ij} = |\vec{x}_i - \vec{x}_j|$

$$f_o(d) = \begin{cases} 1 - d/\ell_o & d < \ell_o \\ 0 & d \geq \ell_o \end{cases}$$

within a finite radius, ℓ_o .





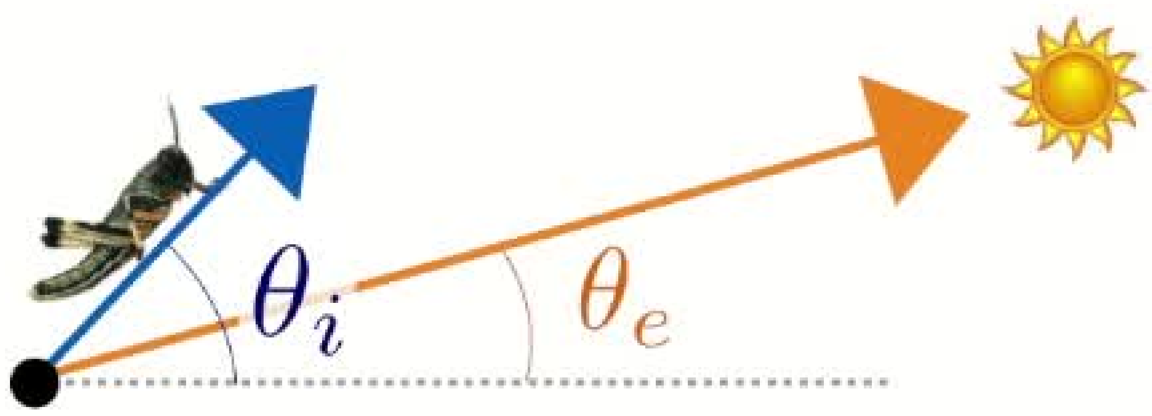
ABM: Orientation (Environment)

$$\frac{d\theta_i}{dt} = \omega_o + \omega_e + \omega_a + \omega_n,$$

Alignment | Environment | Attraction/ Repulsion | Noise

Locusts maintain a constant heading; usually downwind.

<u>Environmental bias</u>: $\omega_e = c_e \sin(\theta_e - \theta_i)$



ABM: Orientation (Attraction/Repulsion)

$$\frac{d\theta_i}{dt} = \omega_o + \omega_e + \omega_a + \omega_n,$$

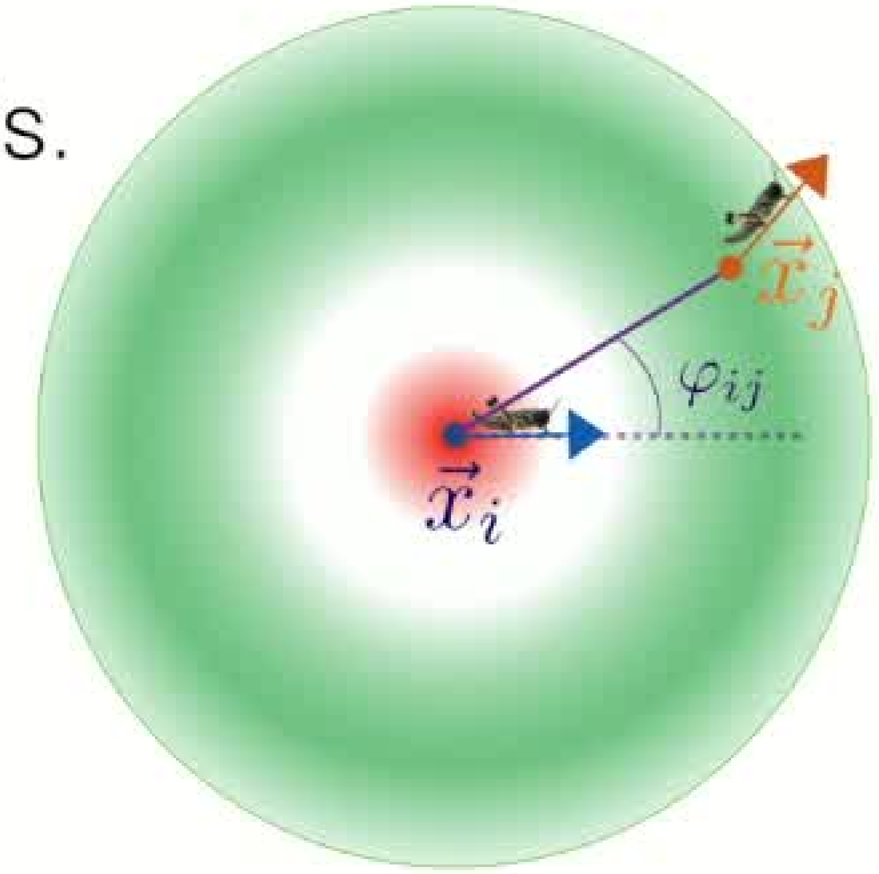
Alignment | Environment | Attraction/ Repulsion | Noise

Locust turns toward/away the weighted centroid of adjacent locusts.

$$\omega_a = \sum_{\substack{j=1 \\ j \neq i}}^{n} \left[c_r f_r(d_{ij}) - c_a f_a(d_{ij})\right] \sin(\phi_{ij}),$$

$$f_a(d) = \begin{cases} 1 - \frac{|d - l_w|}{|l_a - l_w|} & \text{for } |d - l_w| < |l_a - l_w| \\ 0 & \text{otherwise} \end{cases}$$

$$f_r(d) = \begin{cases} 1 - \frac{d}{l_r} & \text{for } d < l_r \\ 0 & \text{otherwise} \end{cases}$$

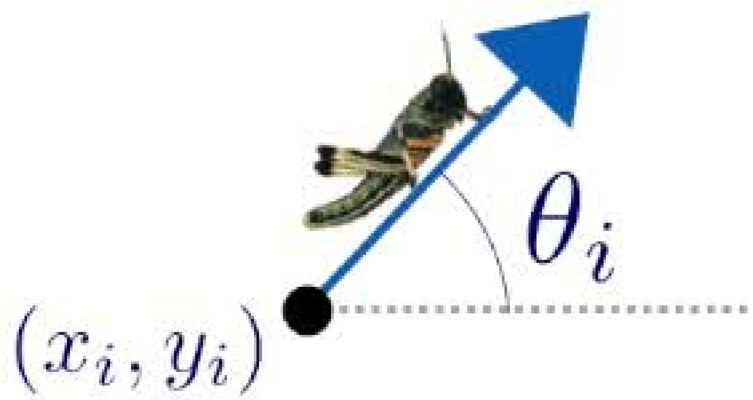


$$d_{ij} = |\vec{x}_i - \vec{x}_j|$$

ABM: Orientation (Noise)

$$\frac{d\theta_i}{dt} = \omega_o + \omega_e + \omega_a + \omega_n,$$

Alignment | Environment | Attraction/Repulsion | **Noise**



<u>White Noise</u>: $\omega_n = \sqrt{c_n}\dot{W}$

Change in $\theta_i(t)$ is normally distributed

$$\theta_i(t + \Delta t) - \theta_i(t) \sim \mathcal{N}(0, c_n \Delta t)$$

with variance $c_n \Delta t$.

ABM: Numerical Simulation

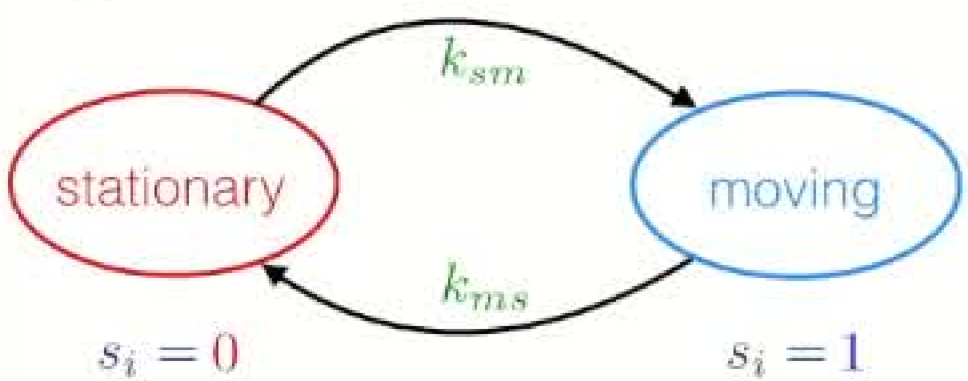
Consider $\boldsymbol{N}$ locusts indexed by the variable $\boldsymbol{i = 1 \ldots N}$

Position: $\vec{x}_i \in \mathbb{R}^2$ Orientation: $\theta_i \in \mathbb{S}^1$ State: $s_i \in \{0, 1\}$

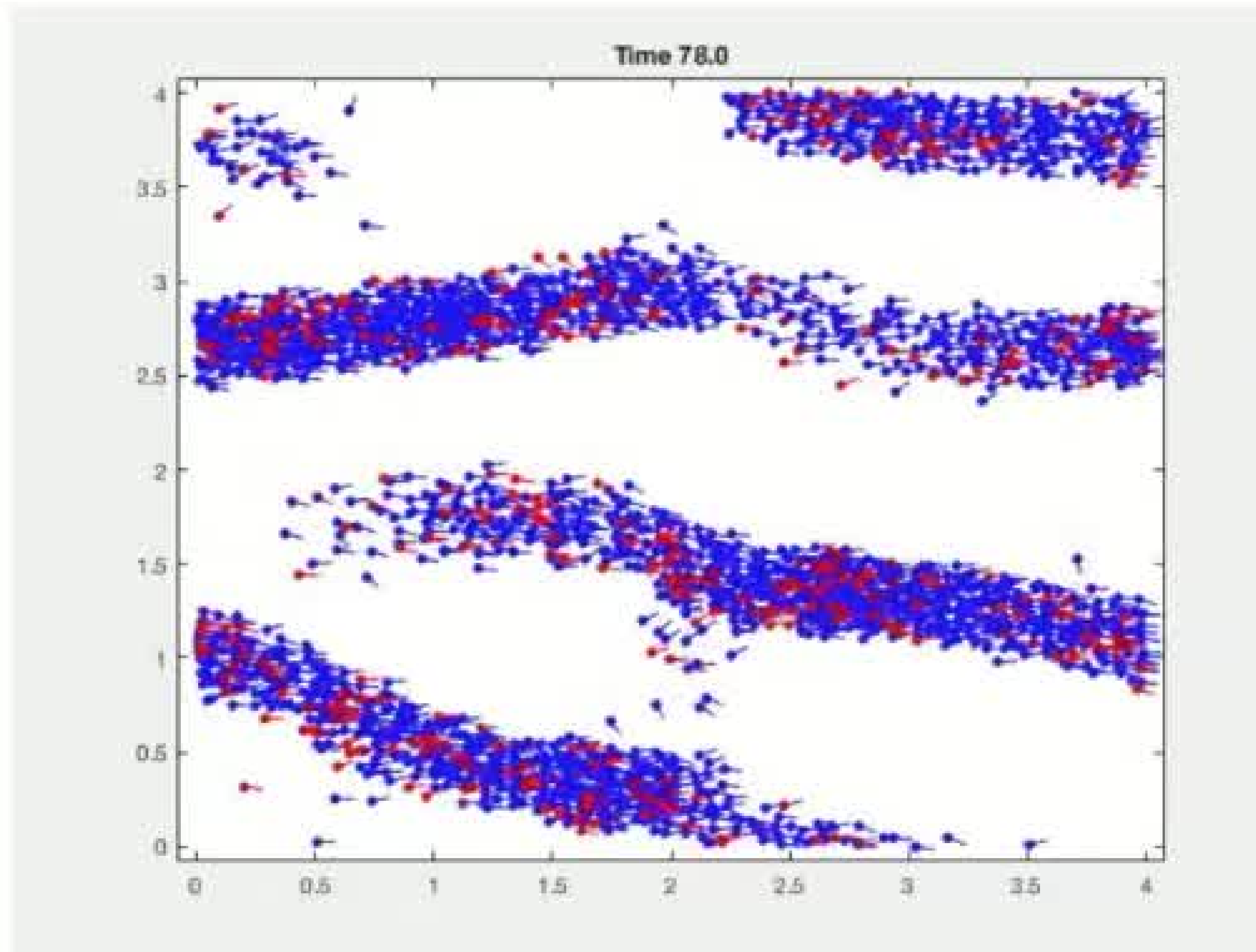
Equations of Motion

$$\frac{d\vec{x}_i}{dt} = s_i v \hat{u}_i(\theta_i)$$

$$\frac{d\theta_i}{dt} = \omega_o + \omega_e + \omega_a + \omega_n$$



Integrate with a stochastic Modified Euler Method (Honeycutt, 1992)



4000 agents

14 Parameters (estimated from experimental data)

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Consider ***N*** locusts indexed by the variable ***i = 1…N***

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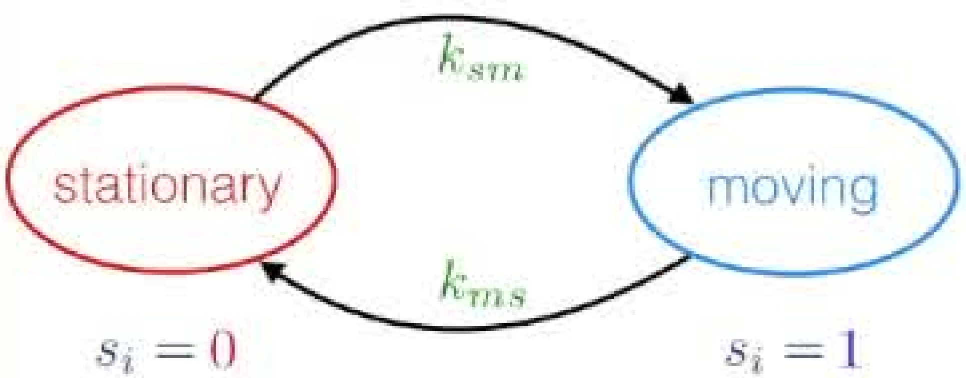

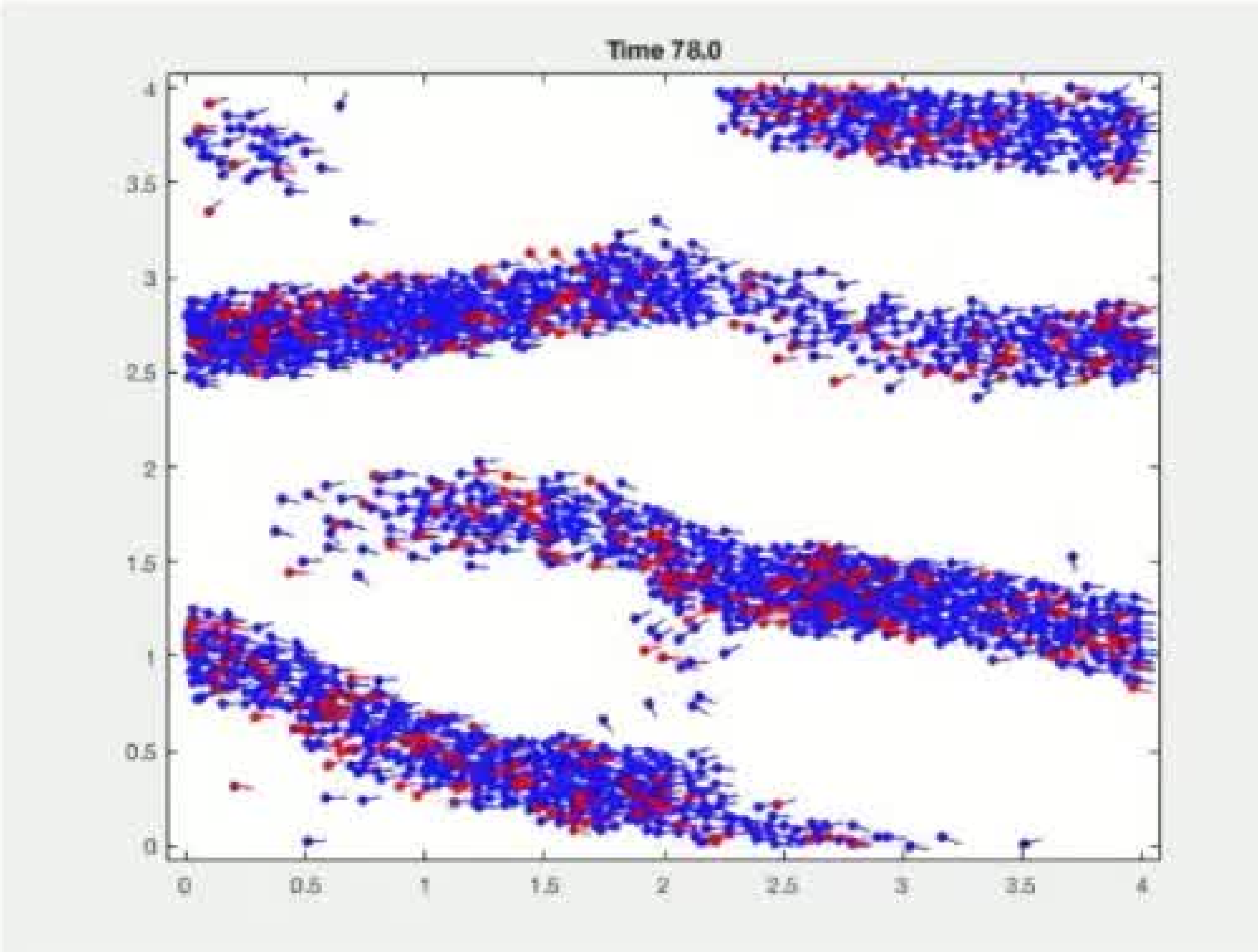

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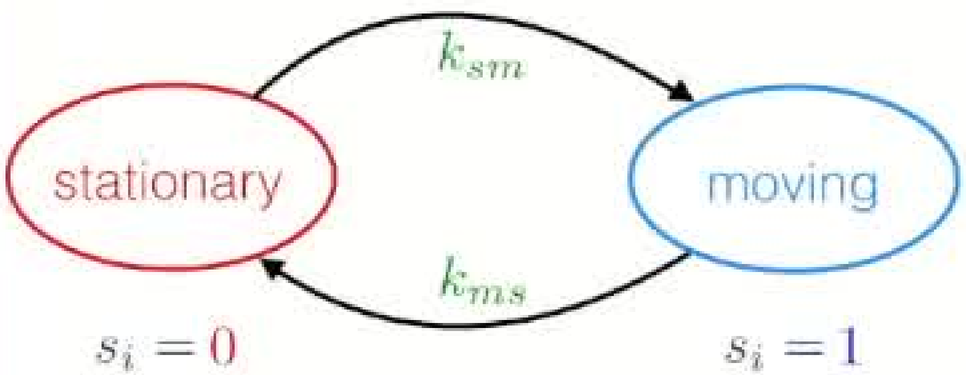

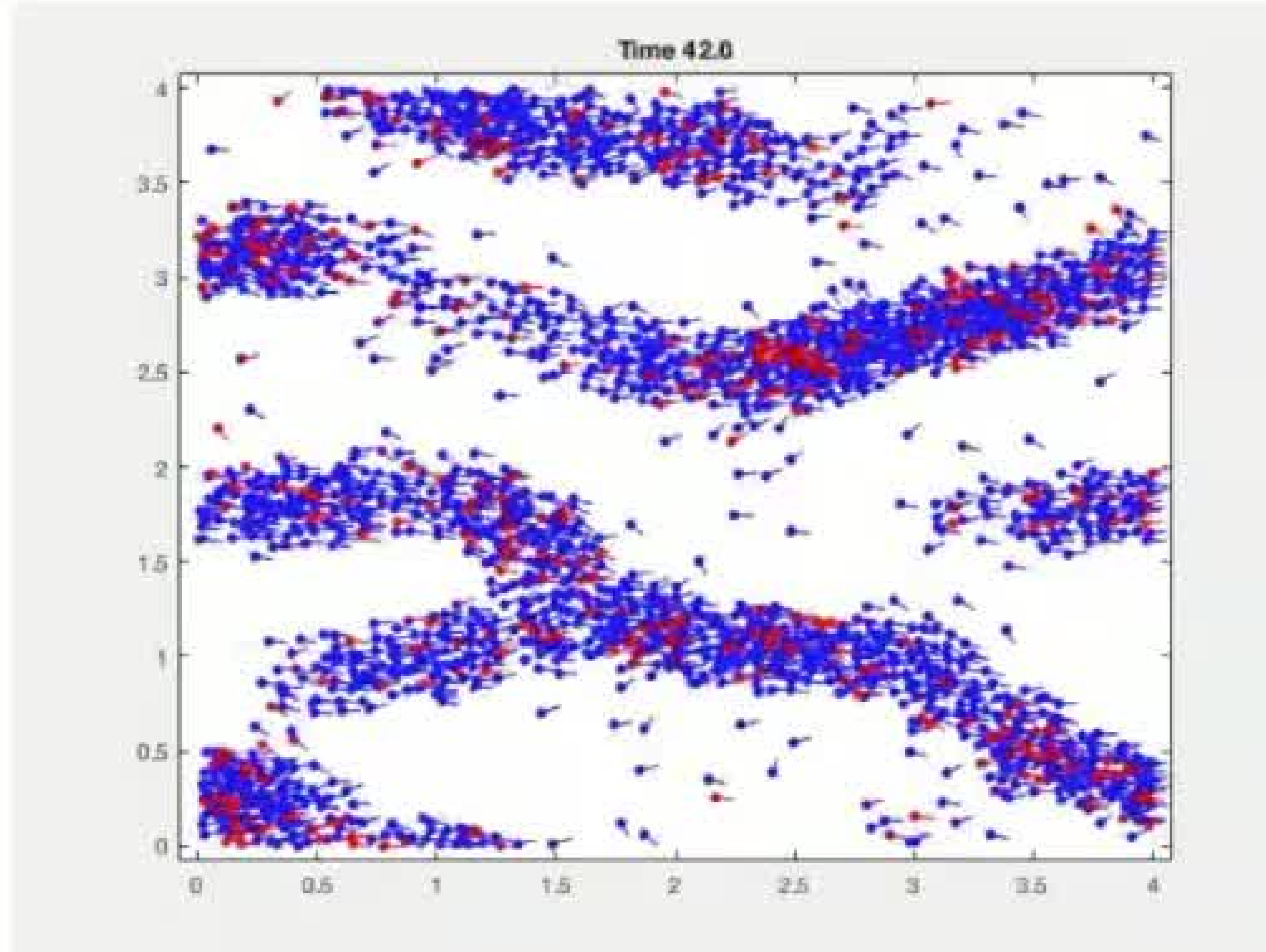

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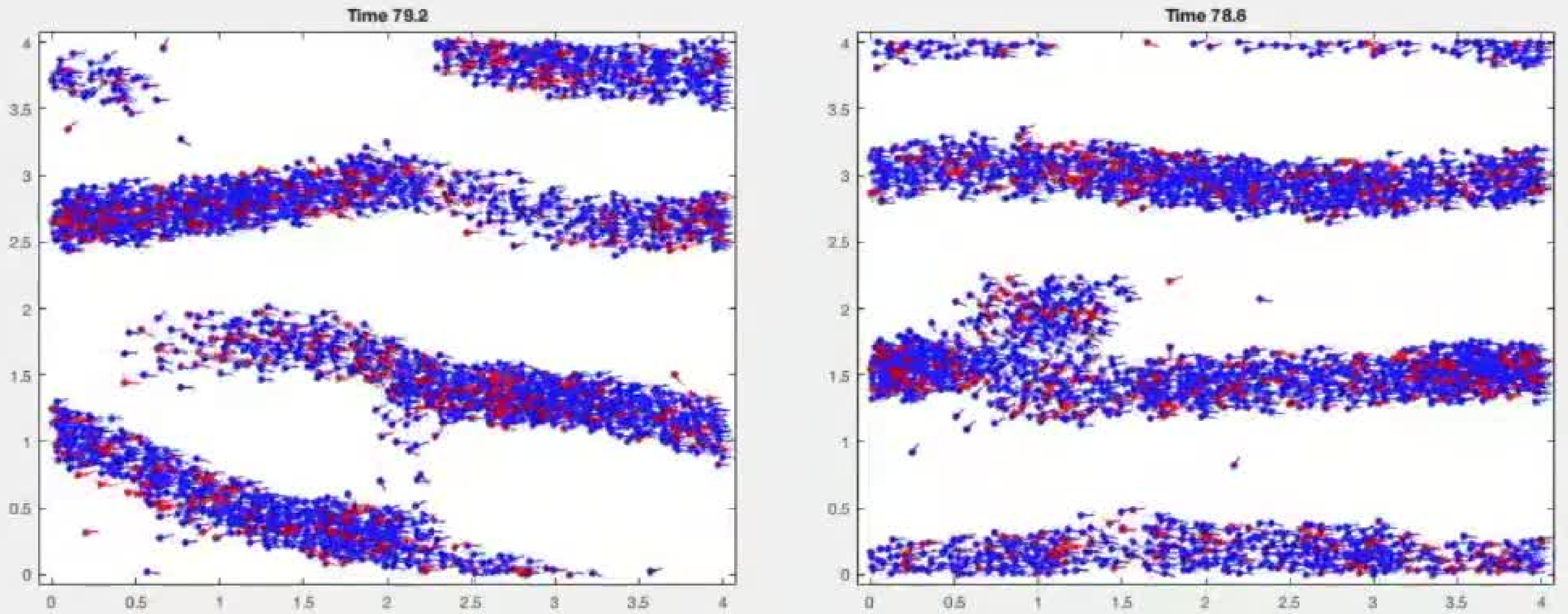
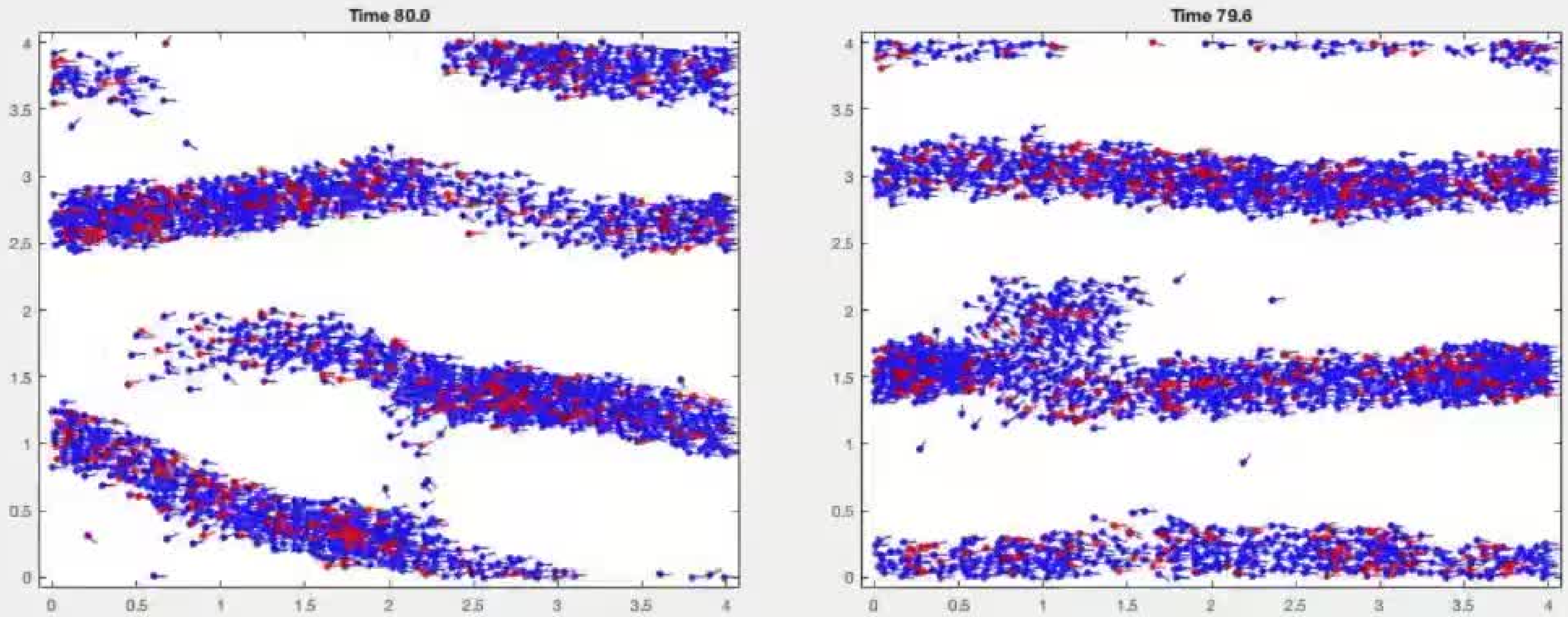
14 Parameters (estimated from experimental data)

Different Initial Conditions



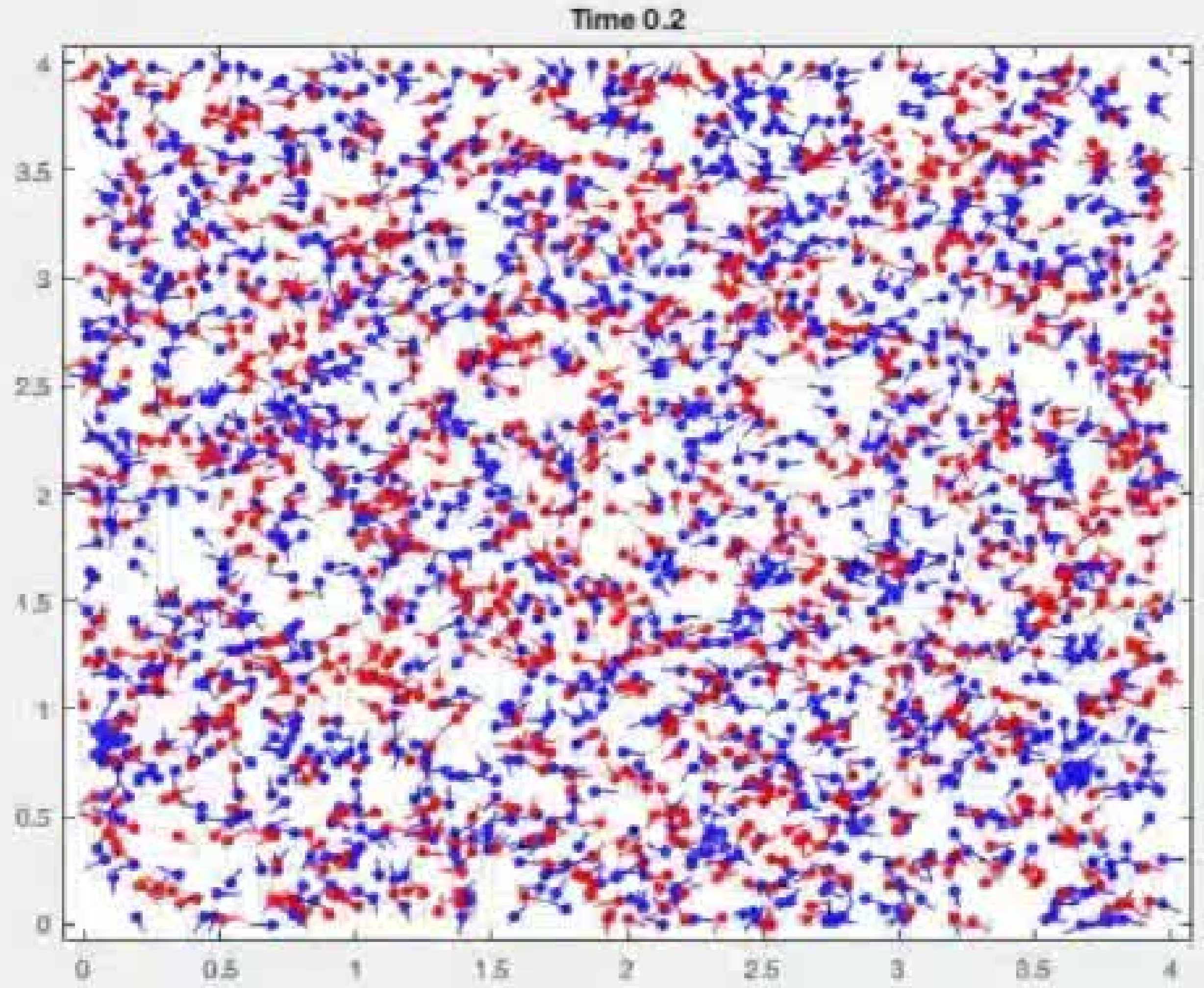
Red = Stationary
Blue = Moving

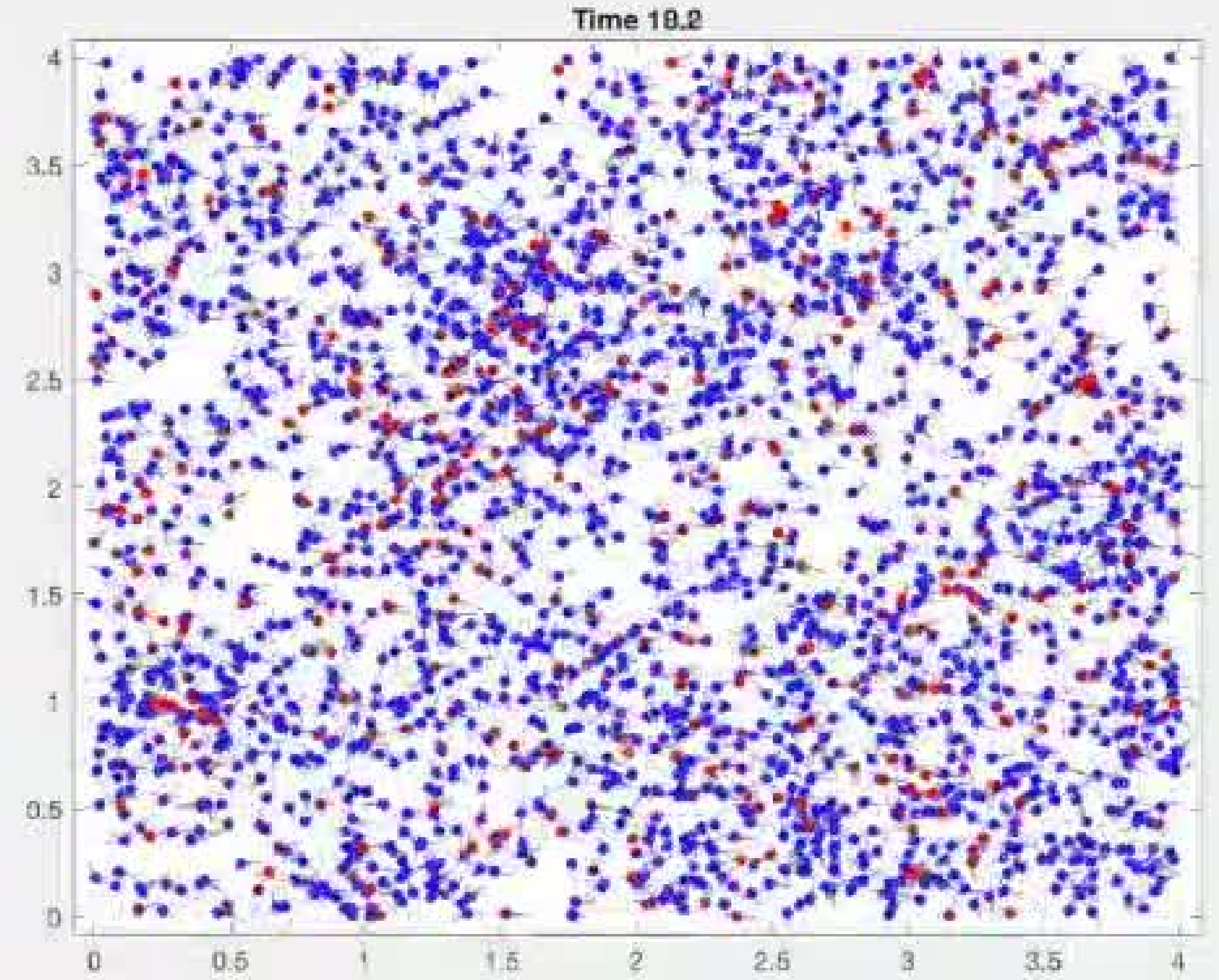
Different Initial Conditions



Red = Stationary
Blue = Moving

Alignment

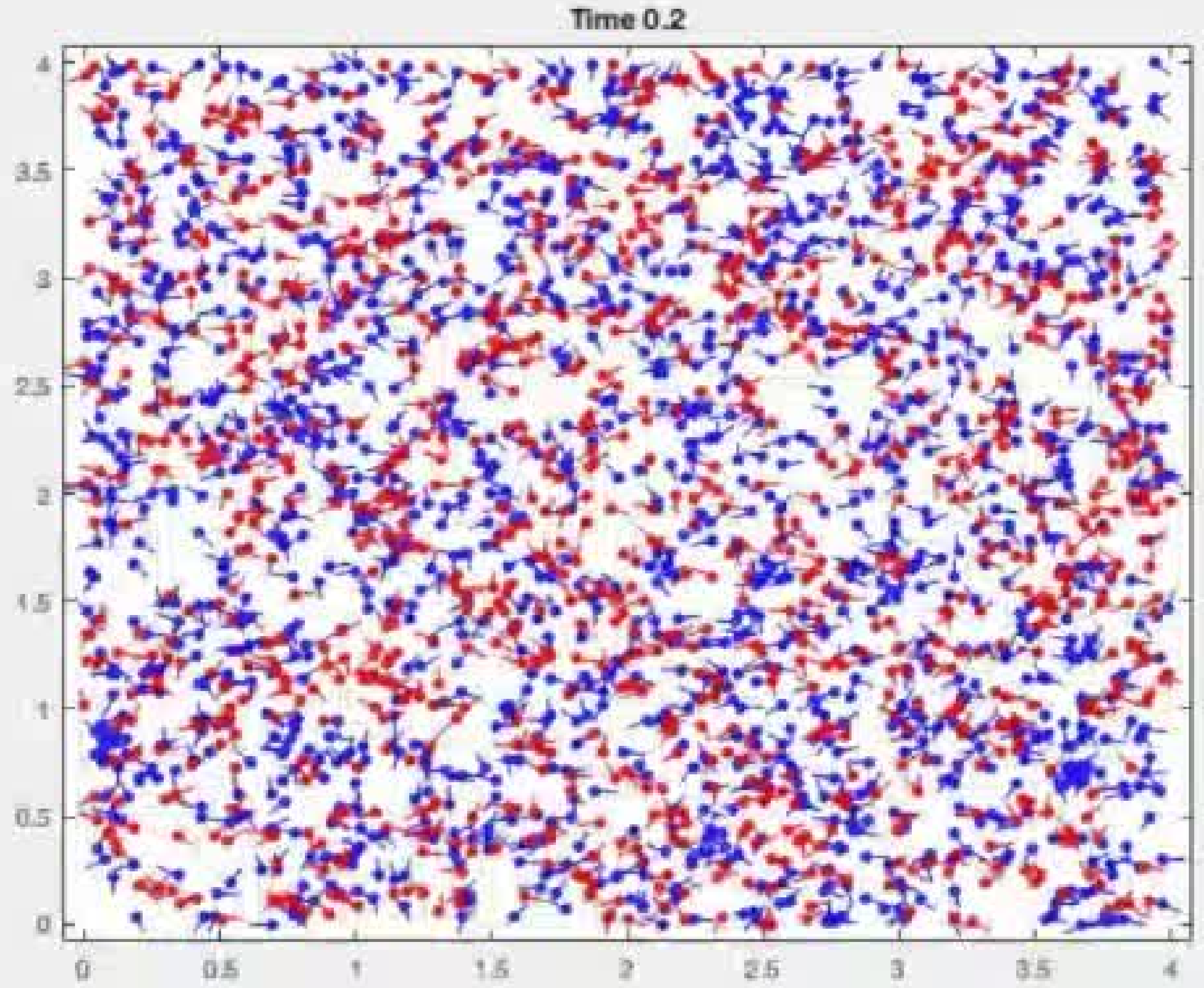


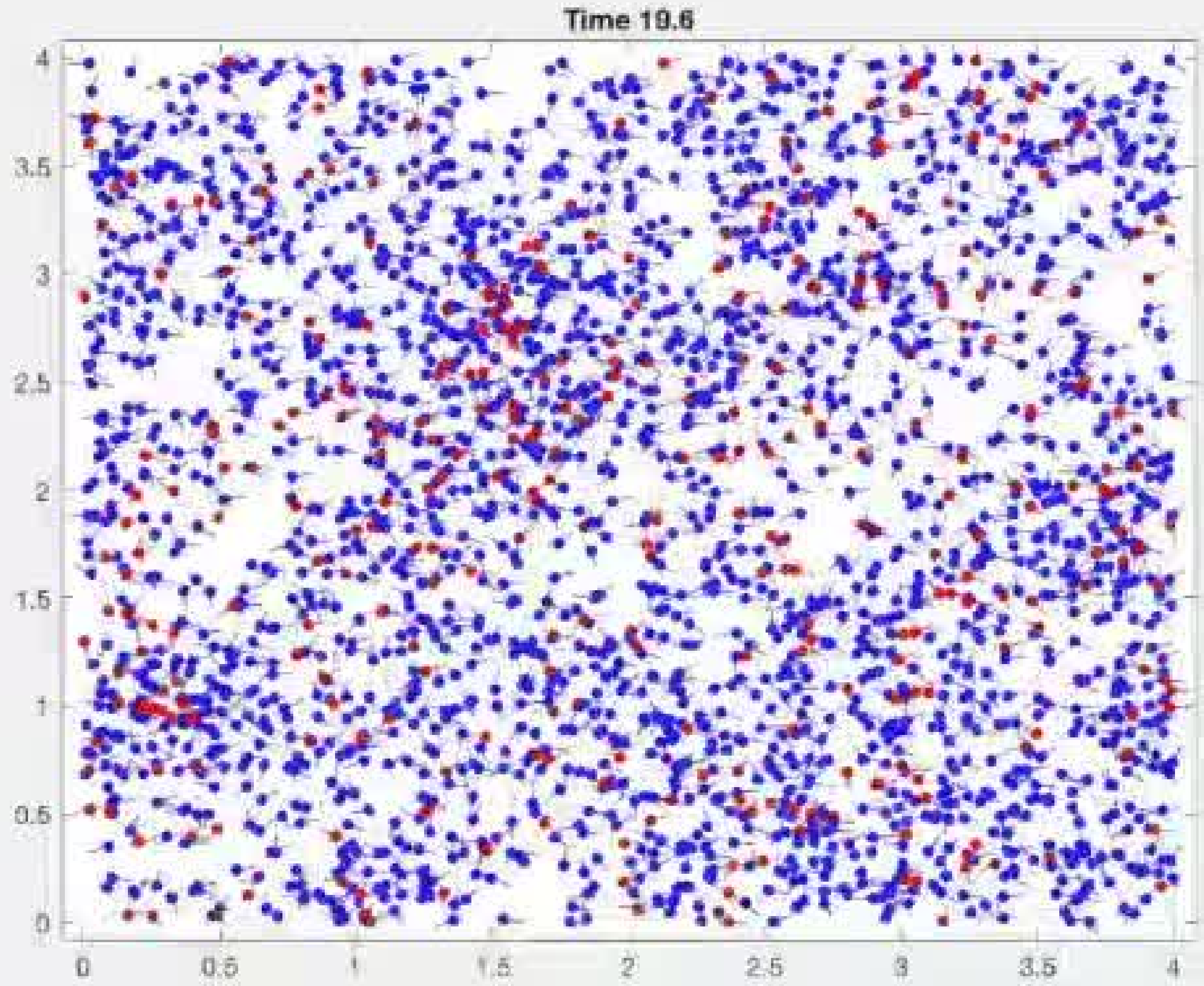


Alignment

No Alignment

Alignment

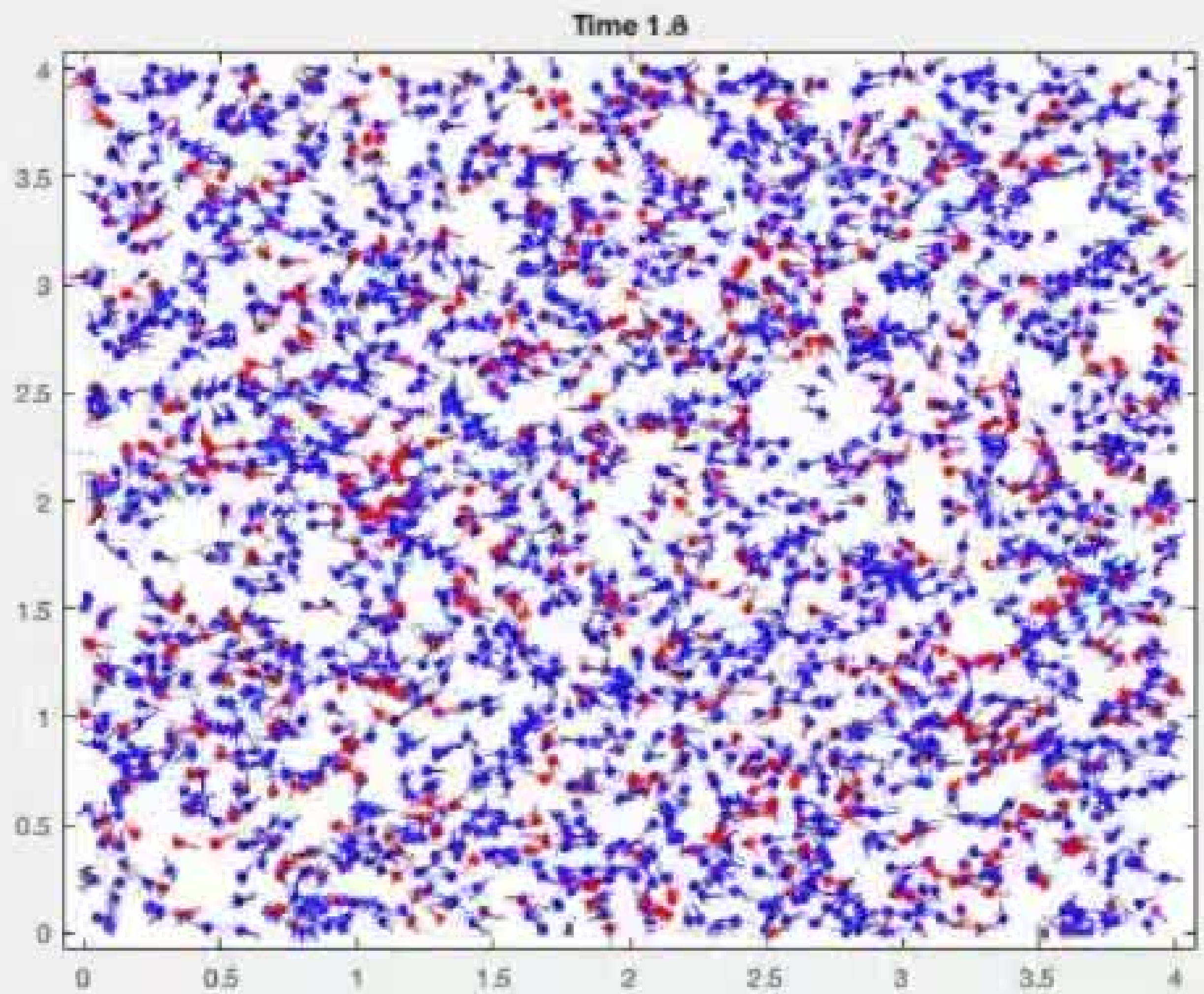


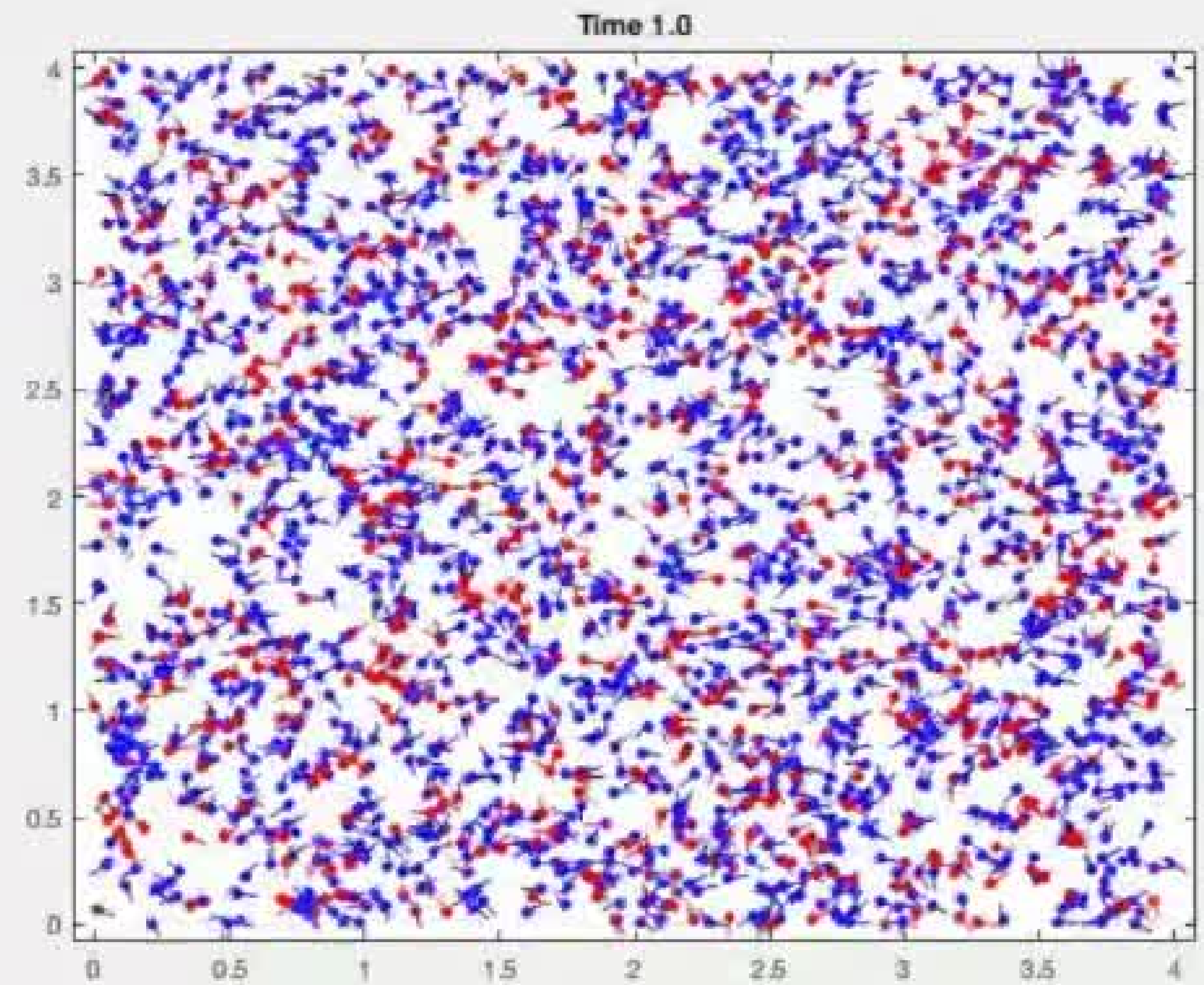


Alignment

No Alignment

Repulsion

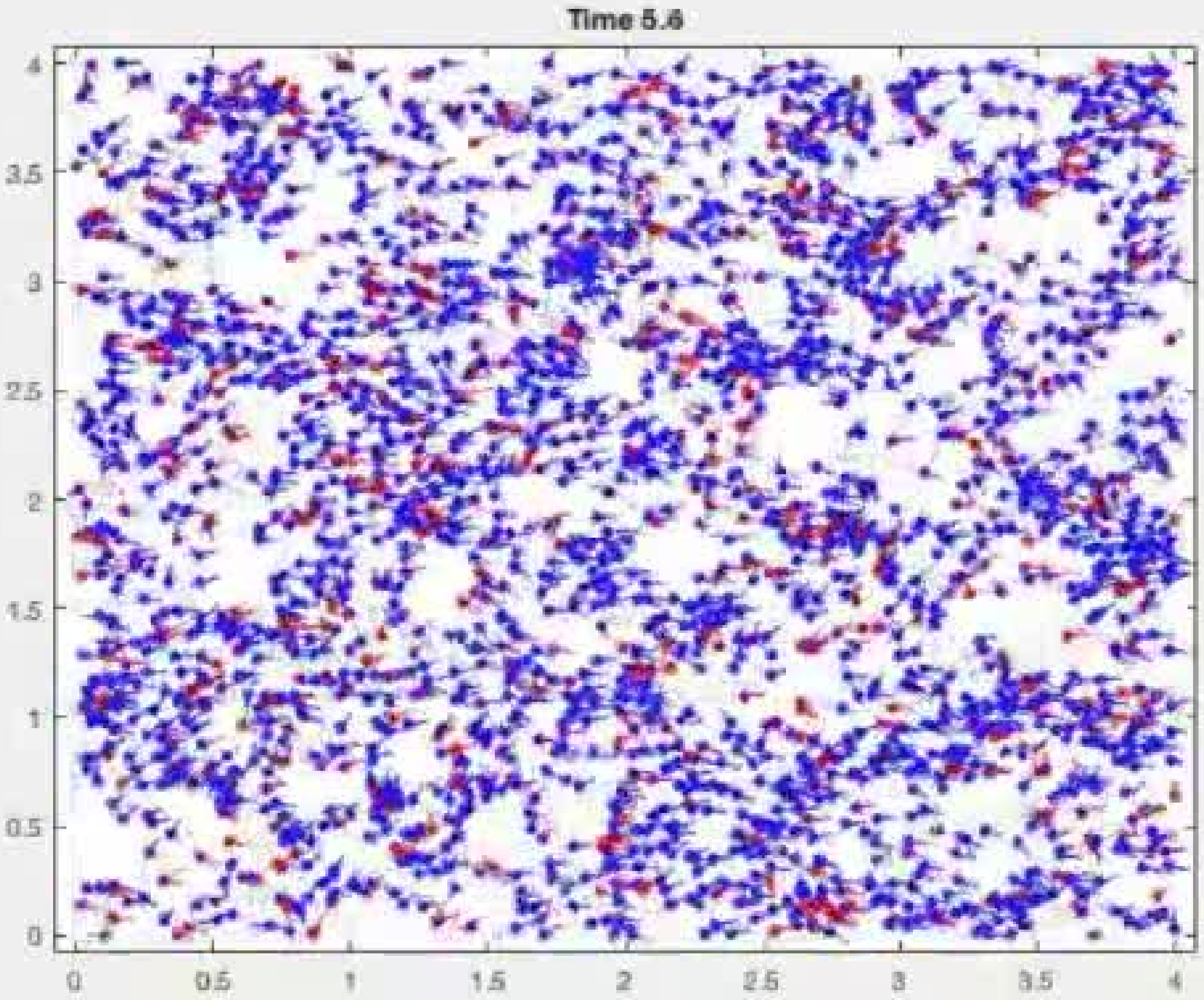




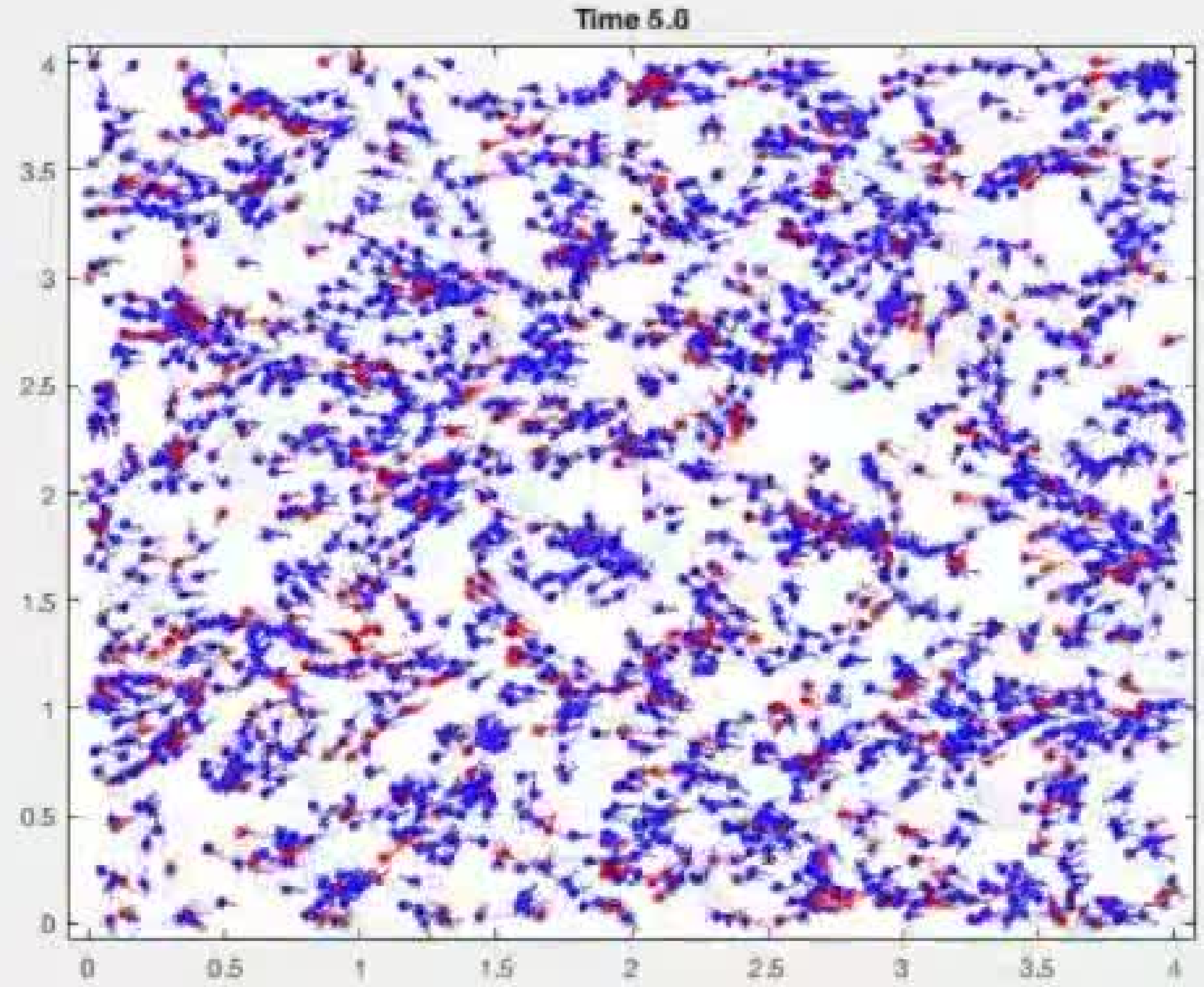
Repulsion

No Repulsion

Repulsion

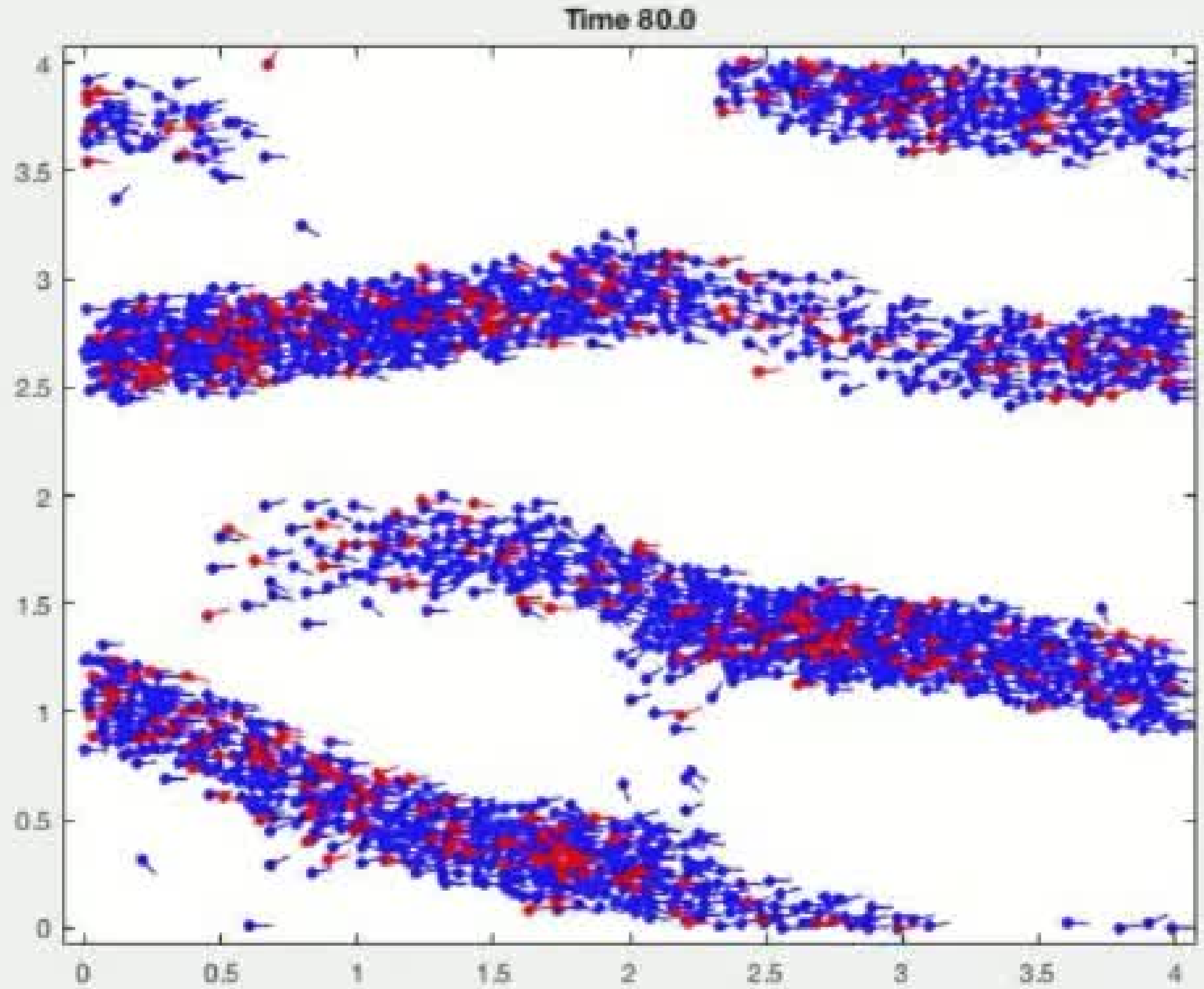


Repulsion

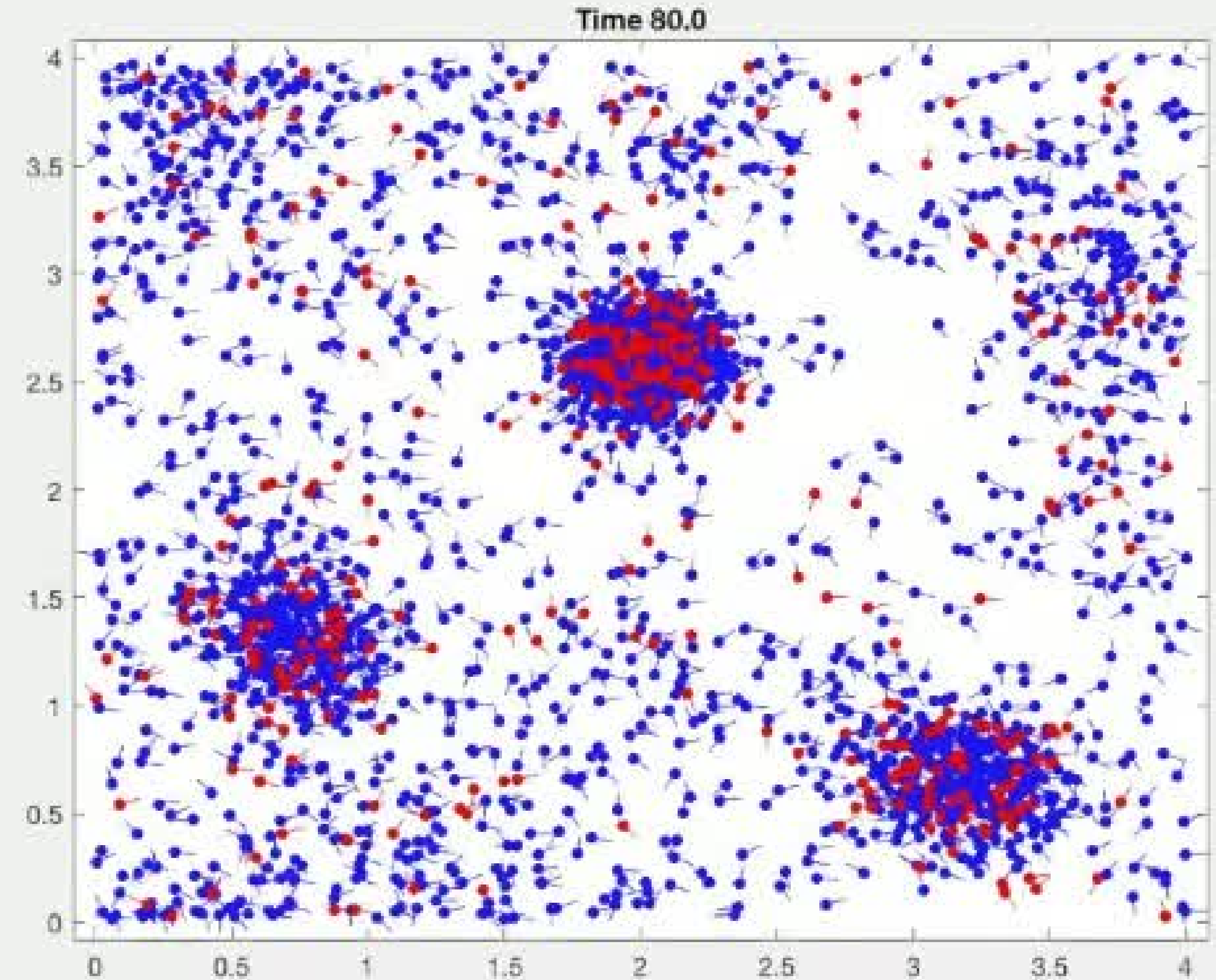


No Repulsion

Alignment

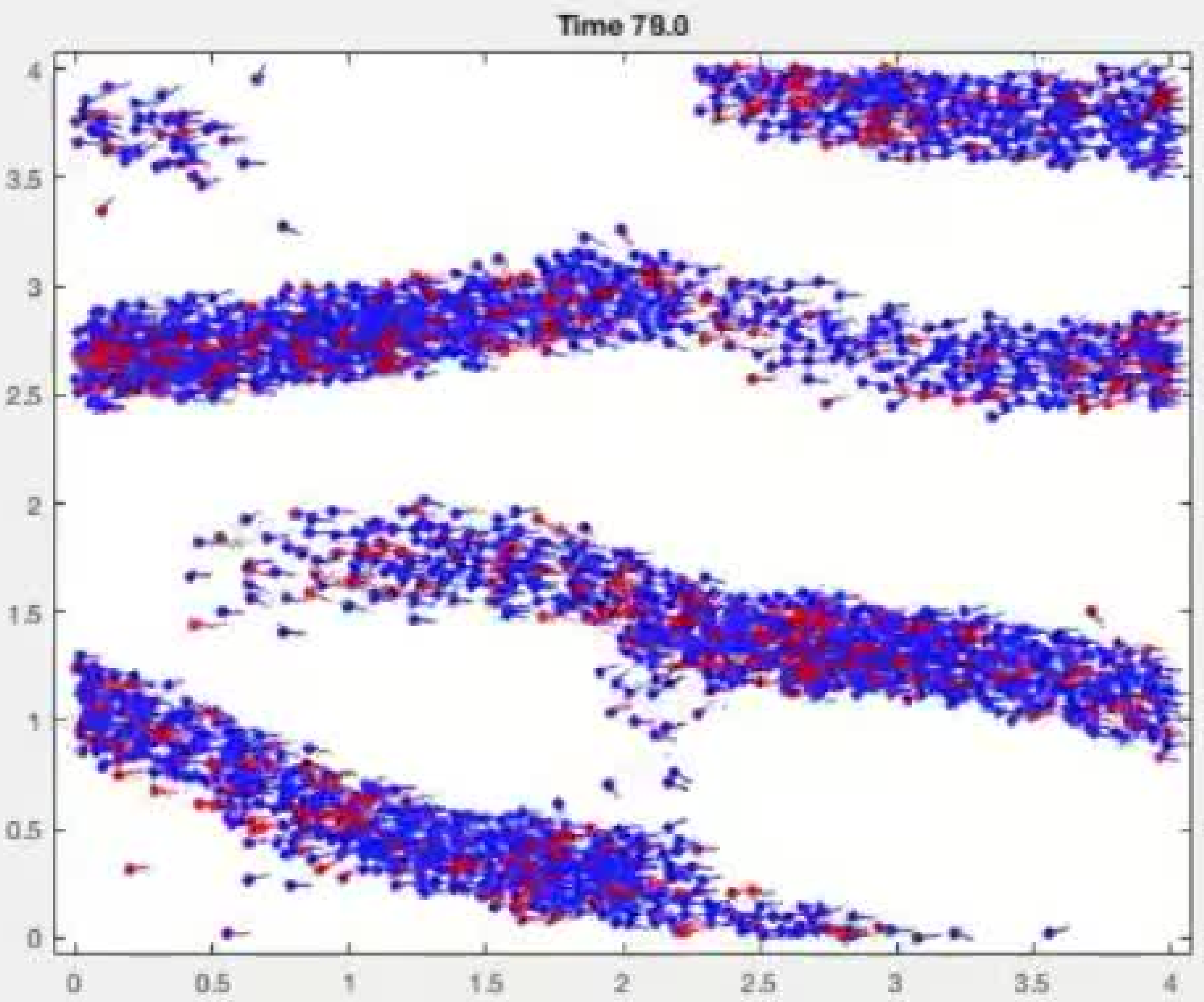


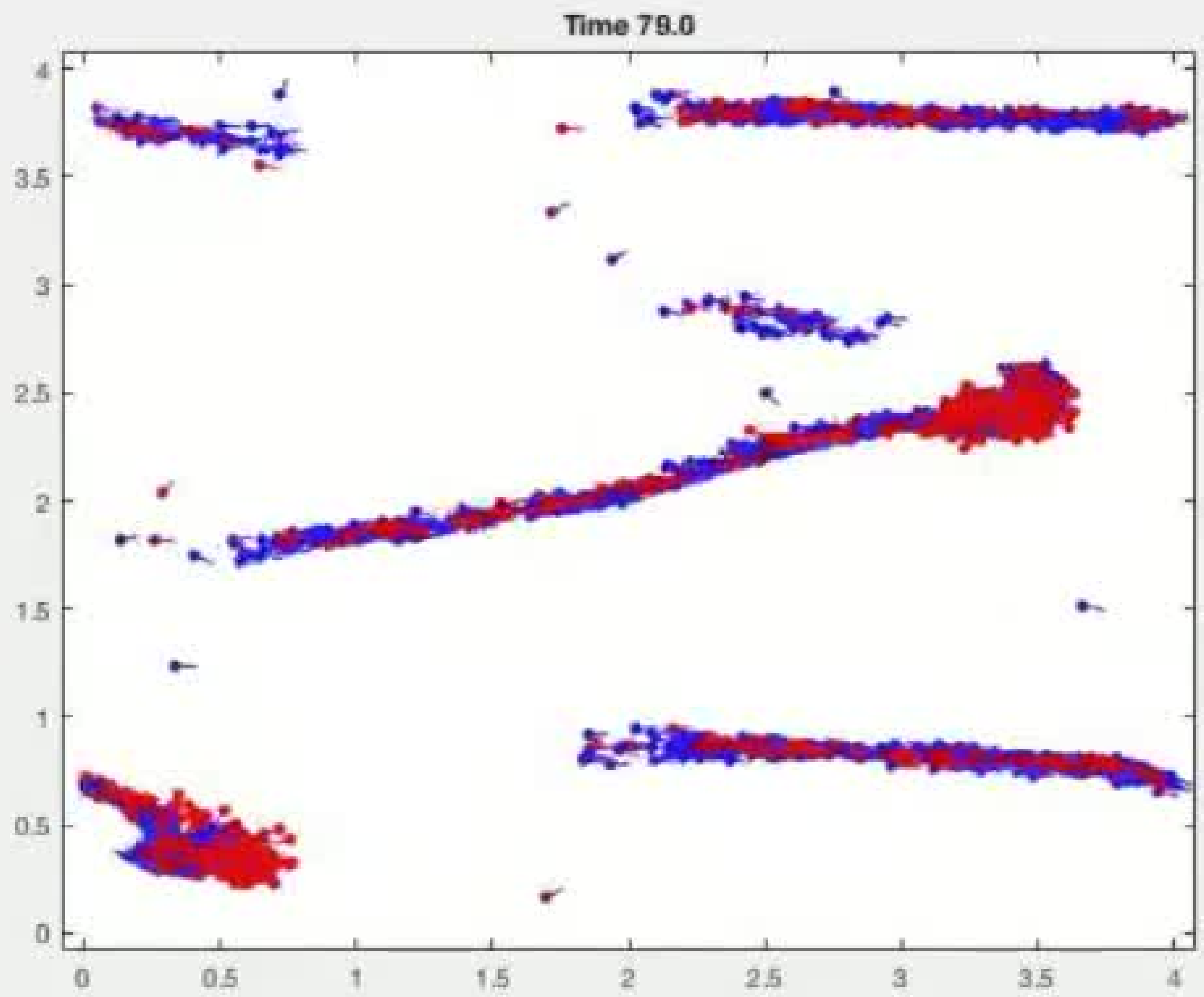
Alignment



No Alignment

Repulsion

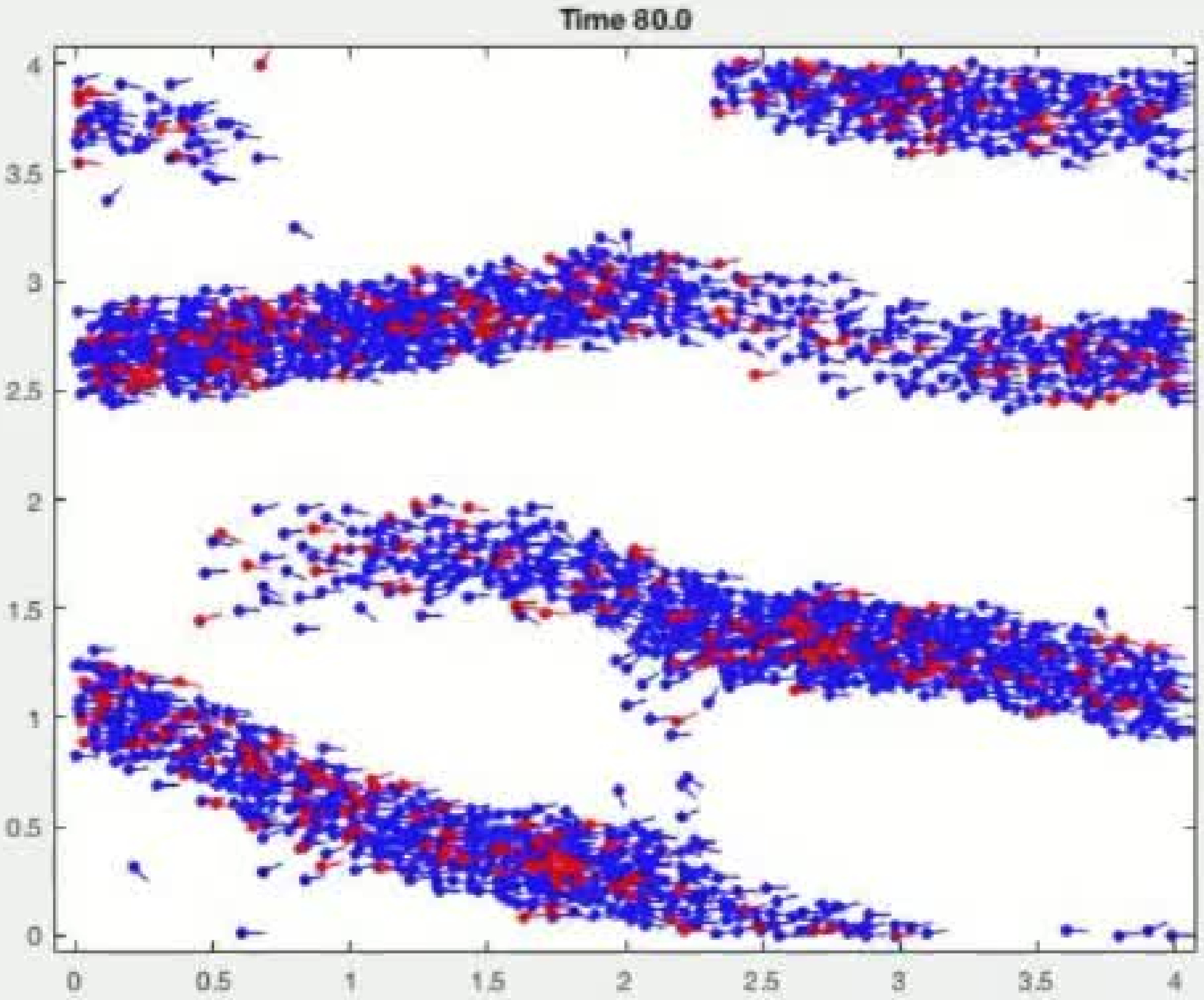




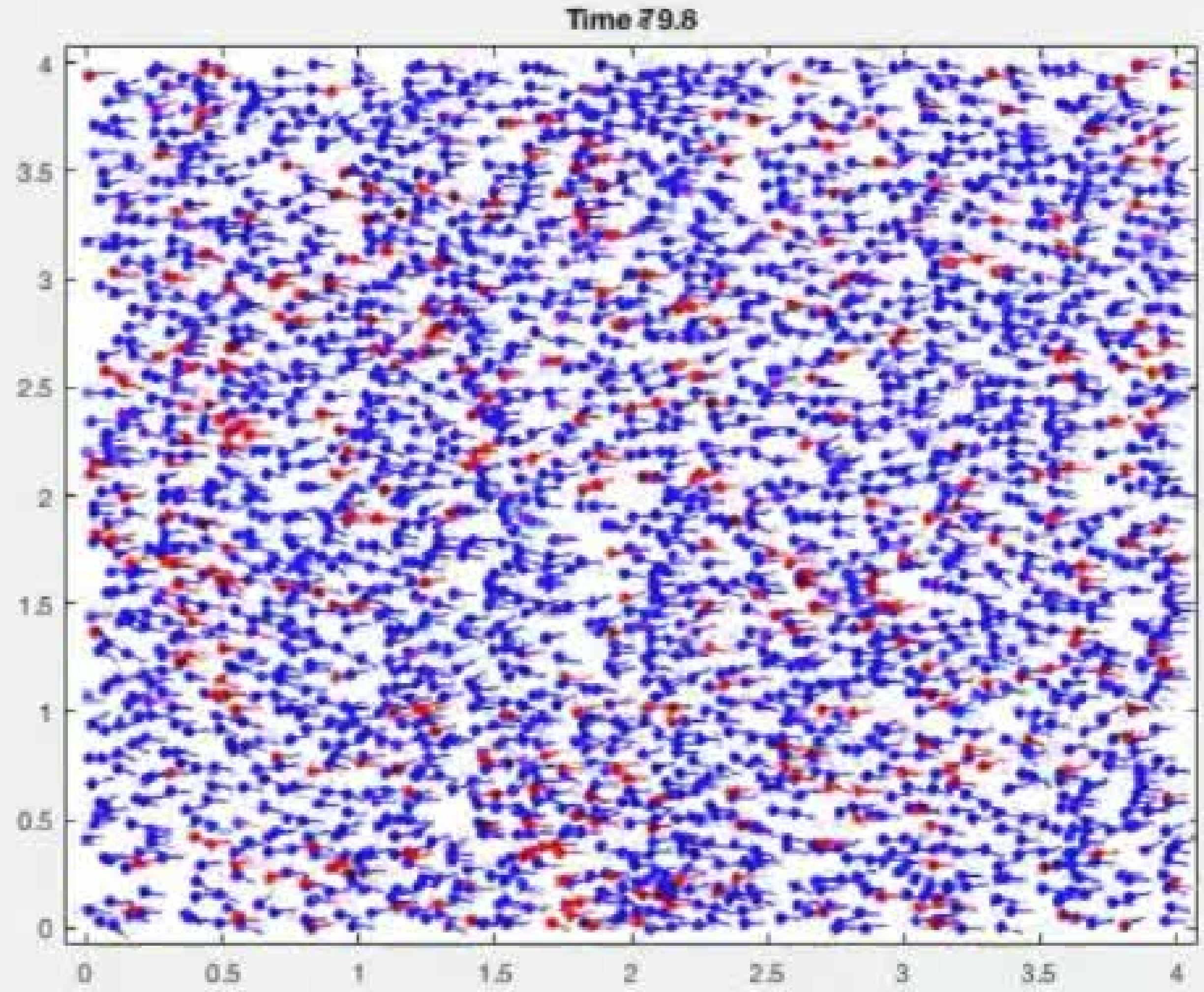
Repulsion

No Repulsion

Attraction

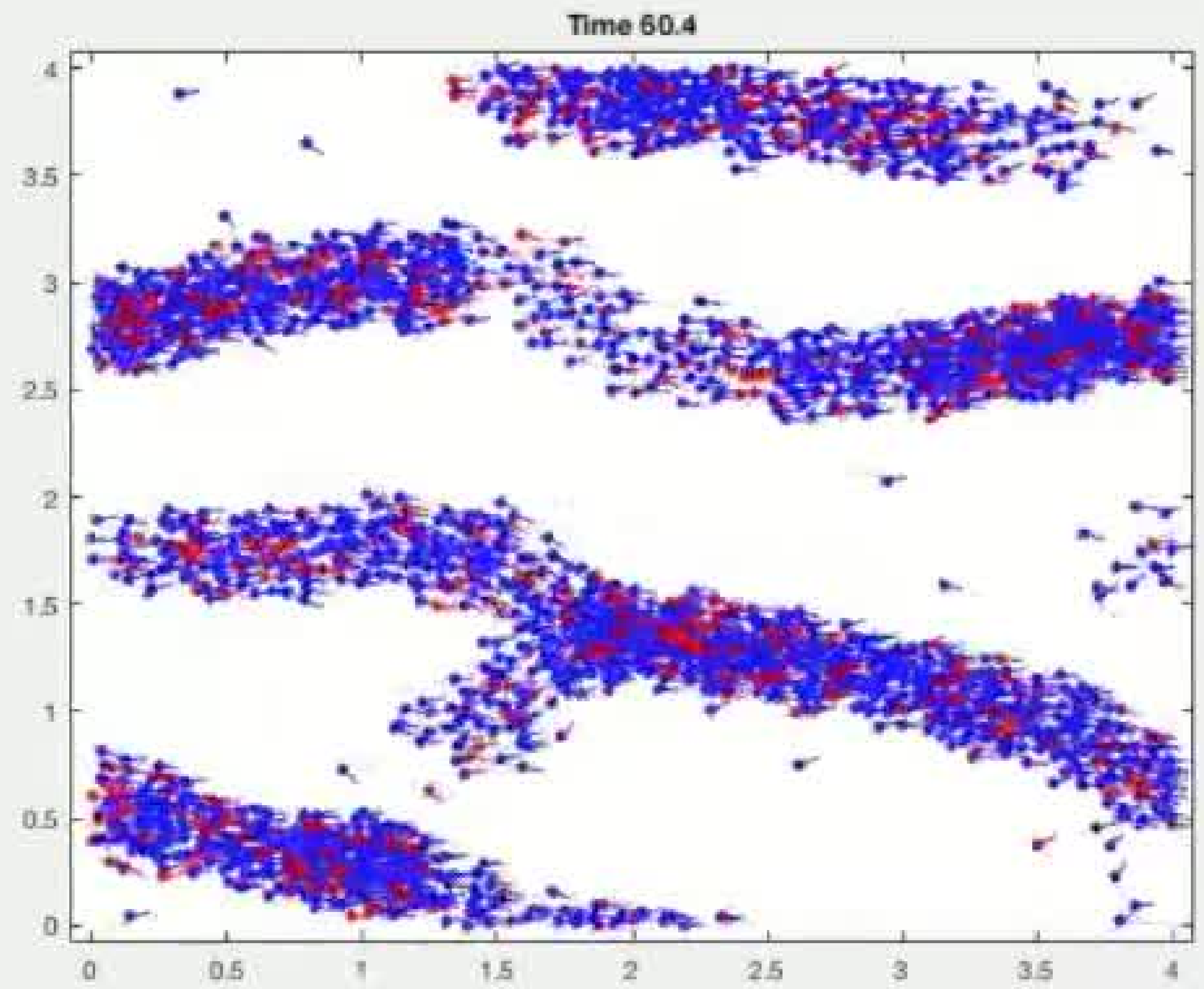


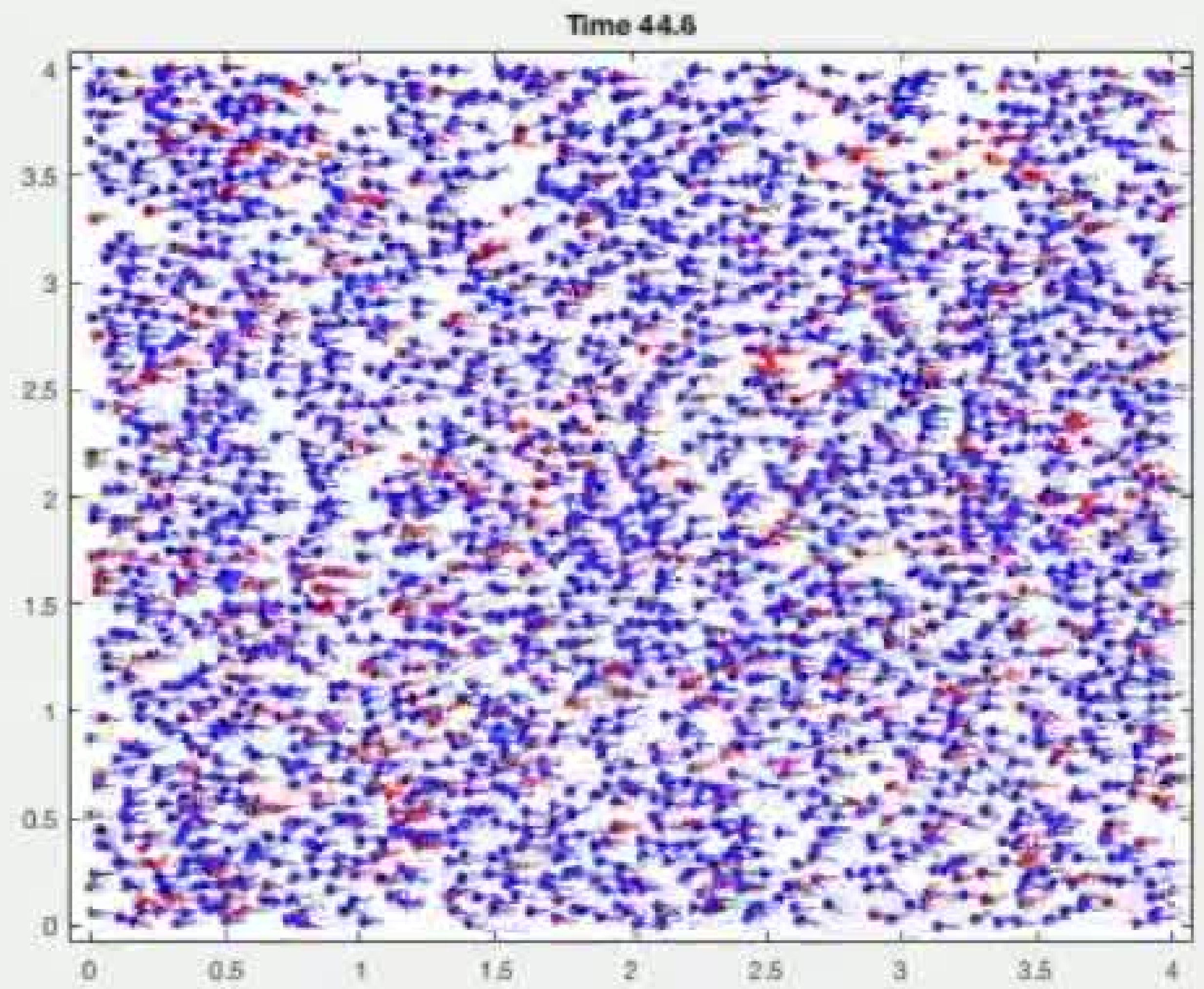
Attraction



No Attraction

Attraction/Repulsion





Can we explain the role of attraction/repulsion in creating columnar structures?

Continuum Model

$$\frac{\partial S}{\partial t} = -k_{sm}S + k_{ms}M$$

$$\frac{\partial M}{\partial t} + \nabla \cdot (\vec{v}M) = k_{sm}S - k_{ms}M$$

$$\frac{d\theta_s}{dt} = \omega_o^s + \omega_e^s + \omega_a^s$$

$$\frac{d\theta_m}{dt} + \nabla \cdot (\vec{v}\theta_m) = \omega_o^m + \omega_e^m + \omega_a^m$$

S = Density of stationary locusts
M = Density of moving locusts
θ_s = Angle of stationary locusts
θ_m = Angle of moving locusts
$\rho = S + M$ (Total density)

$$k_{sm} = \kappa_{sm} e^{-\alpha_{sm}\beta_s} \quad \beta_s = \hat{u}(\theta_s) \cdot \int_\Omega \frac{\vec{y}-\vec{x}}{|\vec{y}-\vec{x}|} f_b(|\vec{y}-\vec{x}|)\rho(\vec{y})\, d\vec{y},$$

blocking

$$\omega_o^m = c_o \int_\Omega f_o(|\vec{y}-\vec{x}|)\left[S(\vec{y})\sin\left[\theta_s(\vec{y}) - \theta_m(\vec{x})\right] + M(\vec{y})\sin\left[\theta_m(\vec{y}) - \theta_m(\vec{x})\right]\right]\, d\vec{y},$$

alignment

$$\omega_e^m = c_e \sin\left[\theta_e - \theta_m(\vec{x})\right]$$

environment

$$\omega_a^m = -c_a \widehat{\vec{u}}_\perp(\theta_m) \cdot \int_\Omega \frac{\vec{y}-\vec{x}}{|\vec{y}-\vec{x}|} f_a(|\vec{y}-\vec{x}|)\rho(\vec{y})\, d\vec{y},$$

attraction/repulsion

Steady State

$$\frac{\partial S}{\partial t} = -k_{sm}S + k_{ms}M$$
$$\frac{\partial M}{\partial t} + \nabla \cdot (\vec{v}M) = k_{sm}S - k_{ms}M$$
$$\frac{d\theta_s}{dt} = \omega_o^s + \omega_e^s + \omega_a^s$$
$$\frac{d\theta_m}{dt} + \nabla \cdot (\vec{v}\theta_m) = \omega_o^m + \omega_e^m + \omega_a^m$$

$S =$ Density of stationary locusts
$M =$ Density of moving locusts
$\theta_s =$ Angle of stationary locusts
$\theta_m =$ Angle of moving locusts
$\rho = S + M$ (Total density)

$$S(\vec{x},t) = \bar{S}, \quad M(\vec{x},t) = \bar{M}, \quad \theta(\vec{x},t) = \theta_e$$

Orientation torques vanish by symmetry

$k_{sm} = \kappa_{sm} e^{-\alpha_{sm}\beta_s}$ $\beta_s = \hat{u}(\theta_s) \cdot \int_\Omega \frac{\vec{y}-\vec{x}}{|\vec{y}-\vec{x}|} f_b(|\vec{y}-\vec{x}|)\rho(\vec{y})\, d\vec{y}$, =0 blocking

$\omega_o^m = c_o \int_\Omega f_o(|\vec{y}-\vec{x}|)\left[S(\vec{y})\sin[\theta_s(\vec{y}) - \theta_m(\vec{x})] + M(\vec{y})\sin[\theta_m(\vec{y}) - \theta_m(\vec{x})]\right] d\vec{y}$, =0 alignment

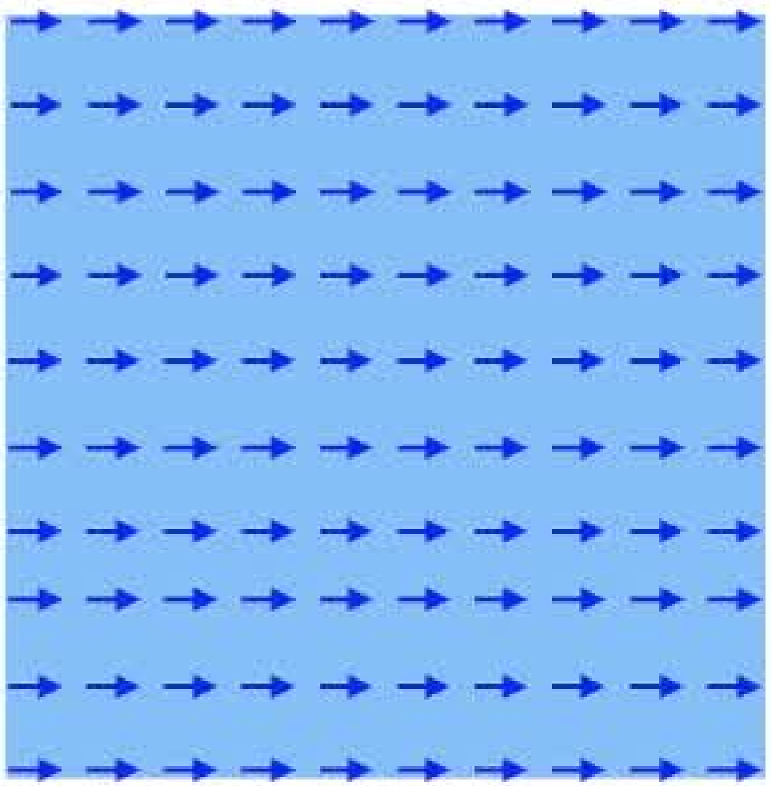
$\omega_e^m = c_e \sin[\theta_e - \theta_m(\vec{x})]$=0 environment

$\omega_a^m = -c_a \widehat{\vec{u}}_\perp(\theta_m) \cdot \int_\Omega \frac{\vec{y}-\vec{x}}{|\vec{y}-\vec{x}|} f_a(|\vec{y}-\vec{x}|)\rho(\vec{y})\, d\vec{y}$, =0 attraction/repulsion

Transverse Stability Theory

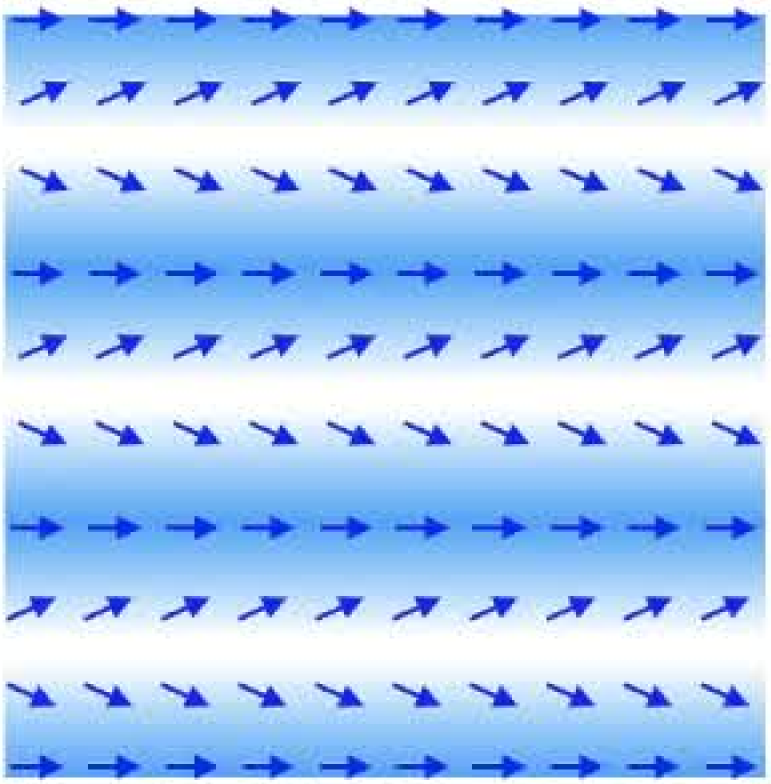
$$\begin{bmatrix} S(x,y,t) \\ M(x,y,t) \\ \theta_s(x,y,t) \\ \theta_m(x,y,t) \end{bmatrix} = \begin{bmatrix} \overline{S} \\ \overline{M} \\ 0 \\ 0 \end{bmatrix} + \varepsilon \begin{bmatrix} \widehat{S} \\ \widehat{M} \\ \widehat{\theta}_s \\ \widehat{\theta}_m \end{bmatrix} \mathrm{e}^{i\mu y + \lambda t},$$

S = Density of stationary locusts
M = Density of moving locusts
θ_s = Angle of stationary locusts
θ_m = Angle of moving locusts
$\rho = S + M$ (Total density)



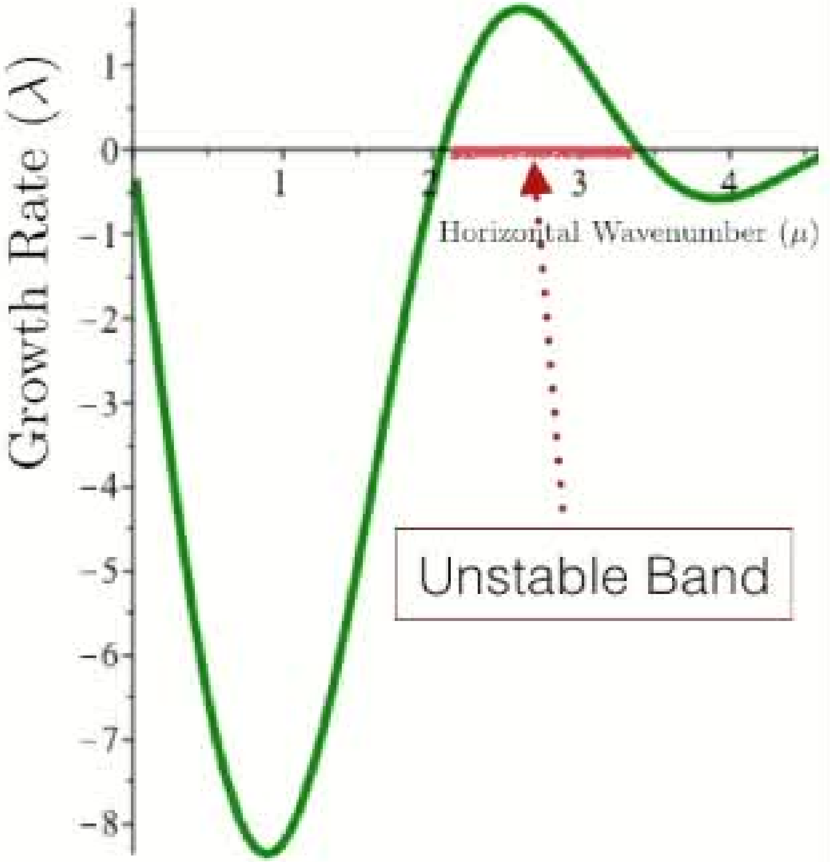
No attraction

Horizontal modulation is neutrally stable



Attraction

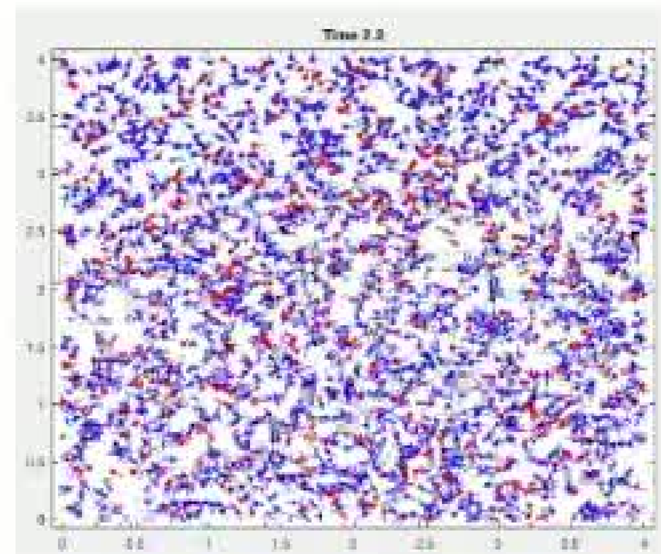
Horizontal modulation has unstable band of wavenumbers

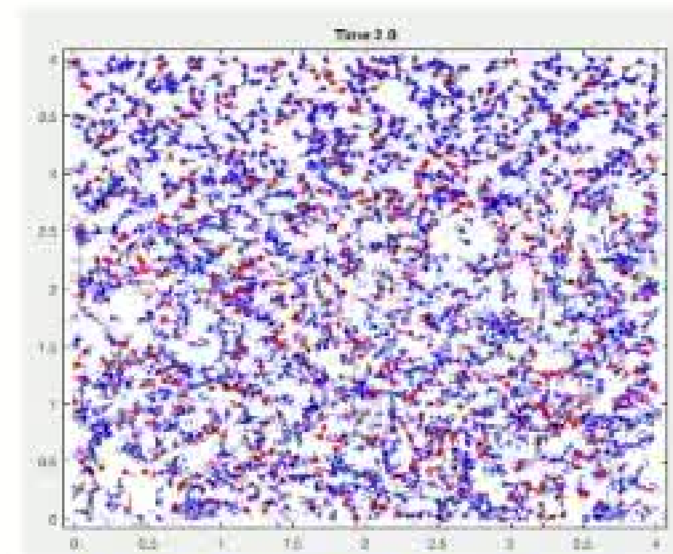


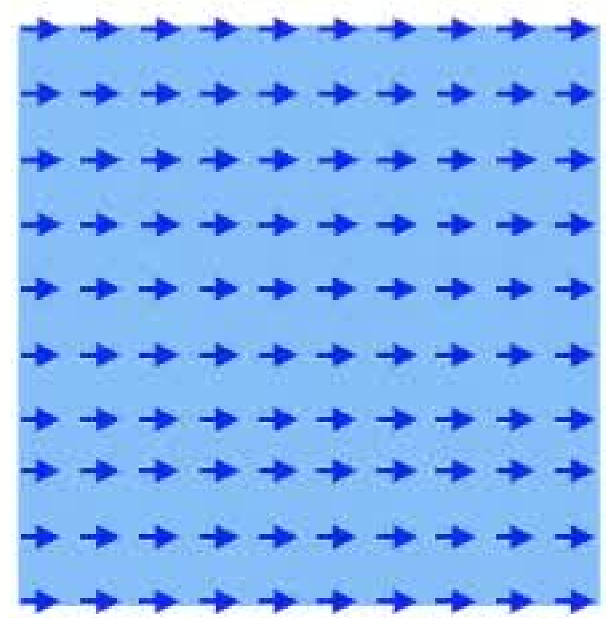
Growth Rate

Conclusions I

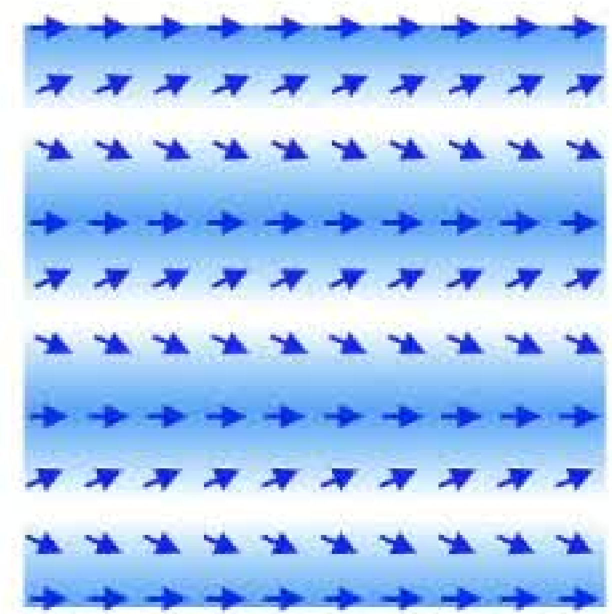
- Agent-Based Models, guided by biological observation, can capture hopper band formation.
- Homogenization yields a continuum model.
- Linear stability theory captures transition to band structured.
- Attraction and alignment are both necessary to obtain columns.







Alignment



Alignment
+ Attraction

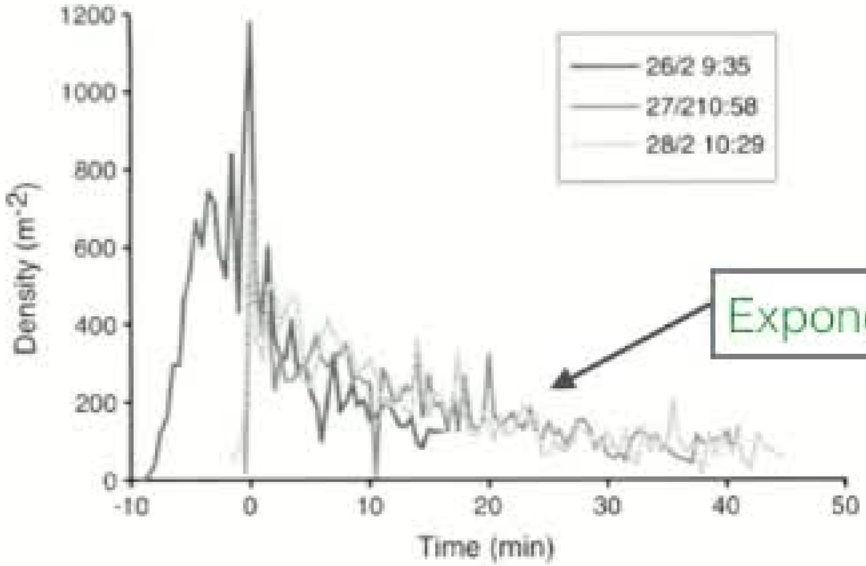
Model II: Resources, Feeding, and Planar Fronts

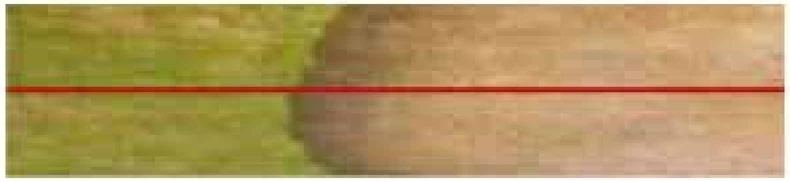
Planar fronts are observed for the Australian Plague Locust in resource rich environments

Locust Distribution in a Planar Front

Field Observation

Buhl et al 2011





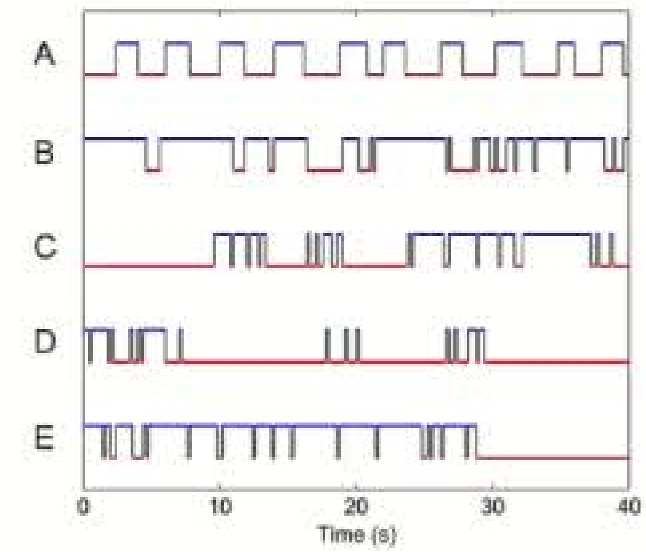
Locust density is pulse-like with a steep rising front and an exponentially decaying tail.

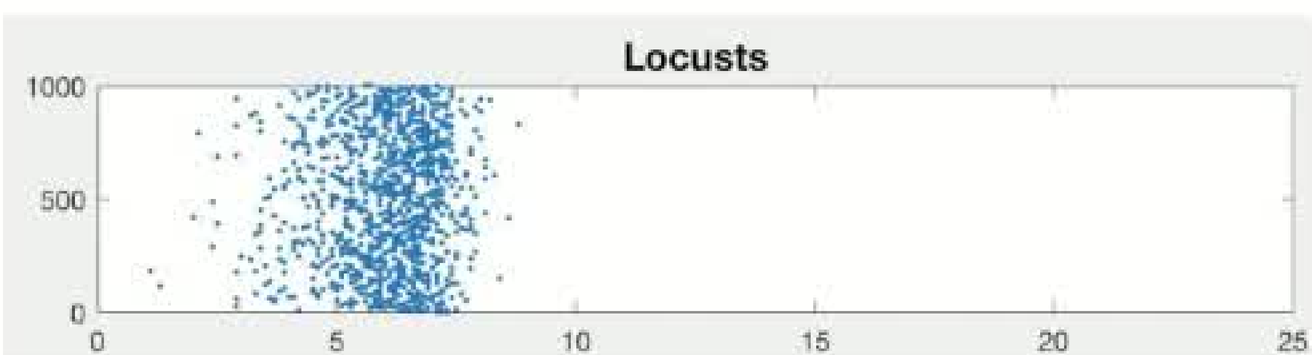
Agent- Based Model

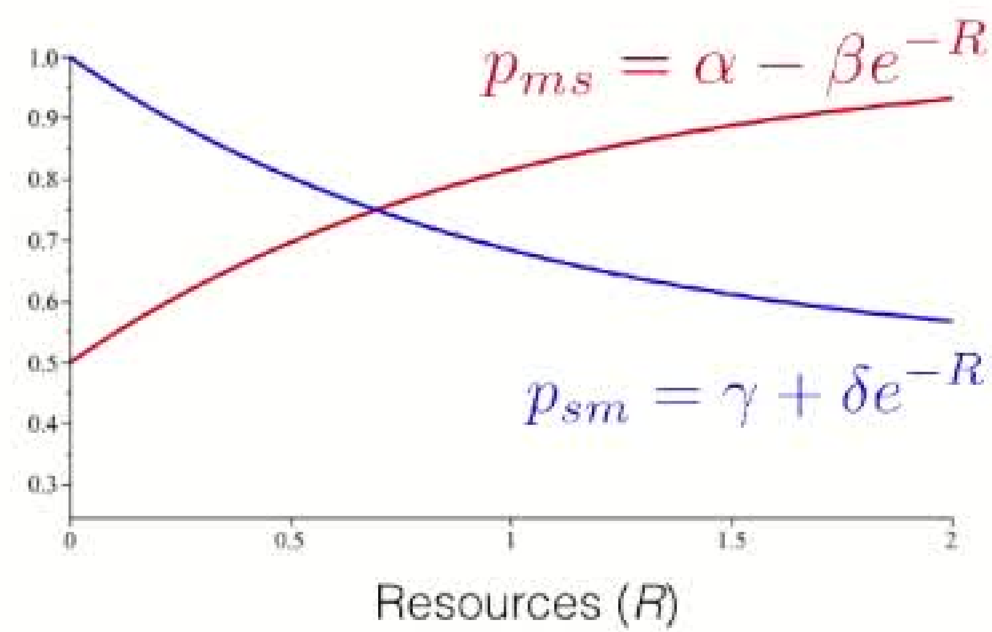
- Model is one-dimensional.
- Locusts all move in the same direction.
- Locusts stop when eating
- Transition probabilities depend on resource availability.

Lab Observation

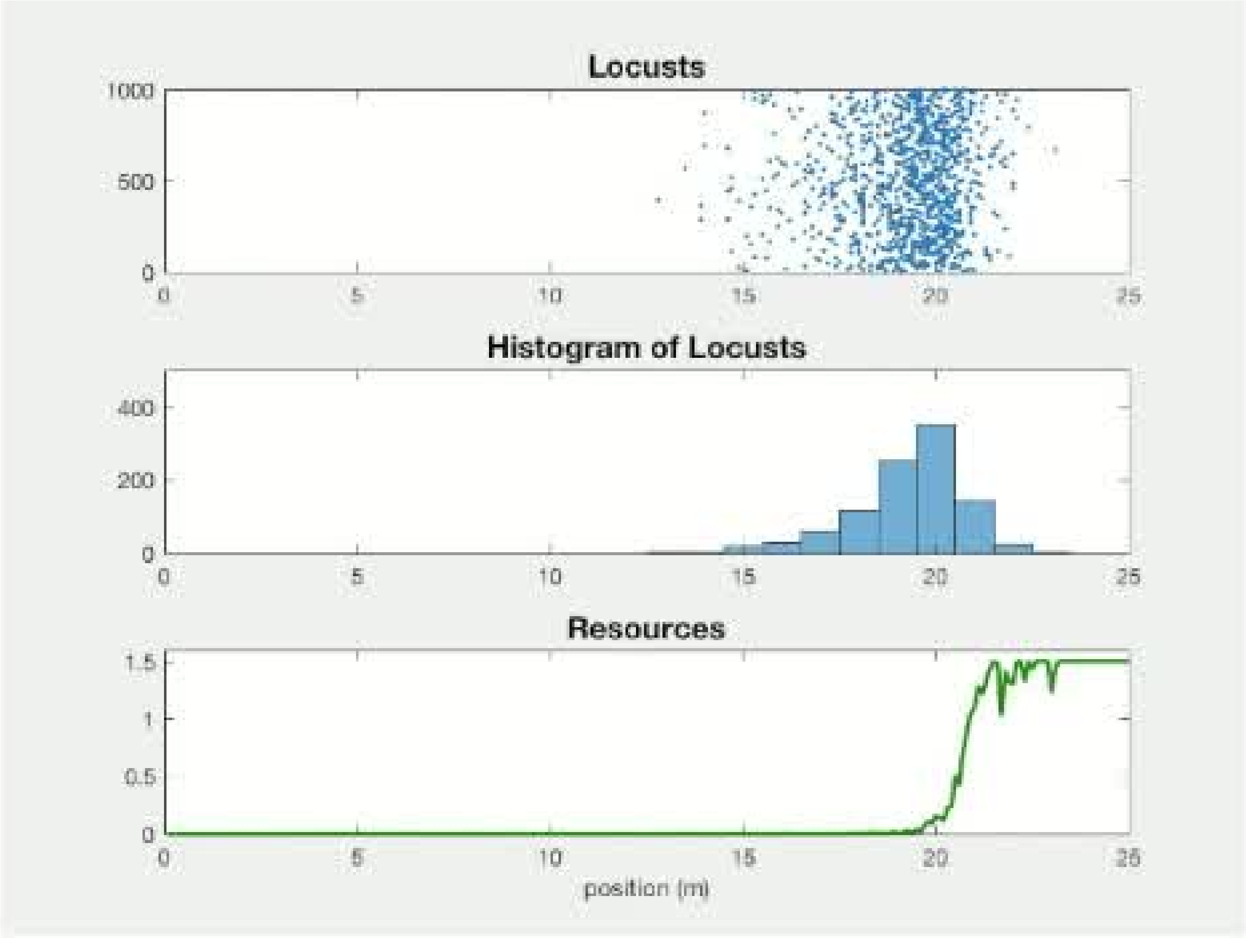
Bazazi et al 2011

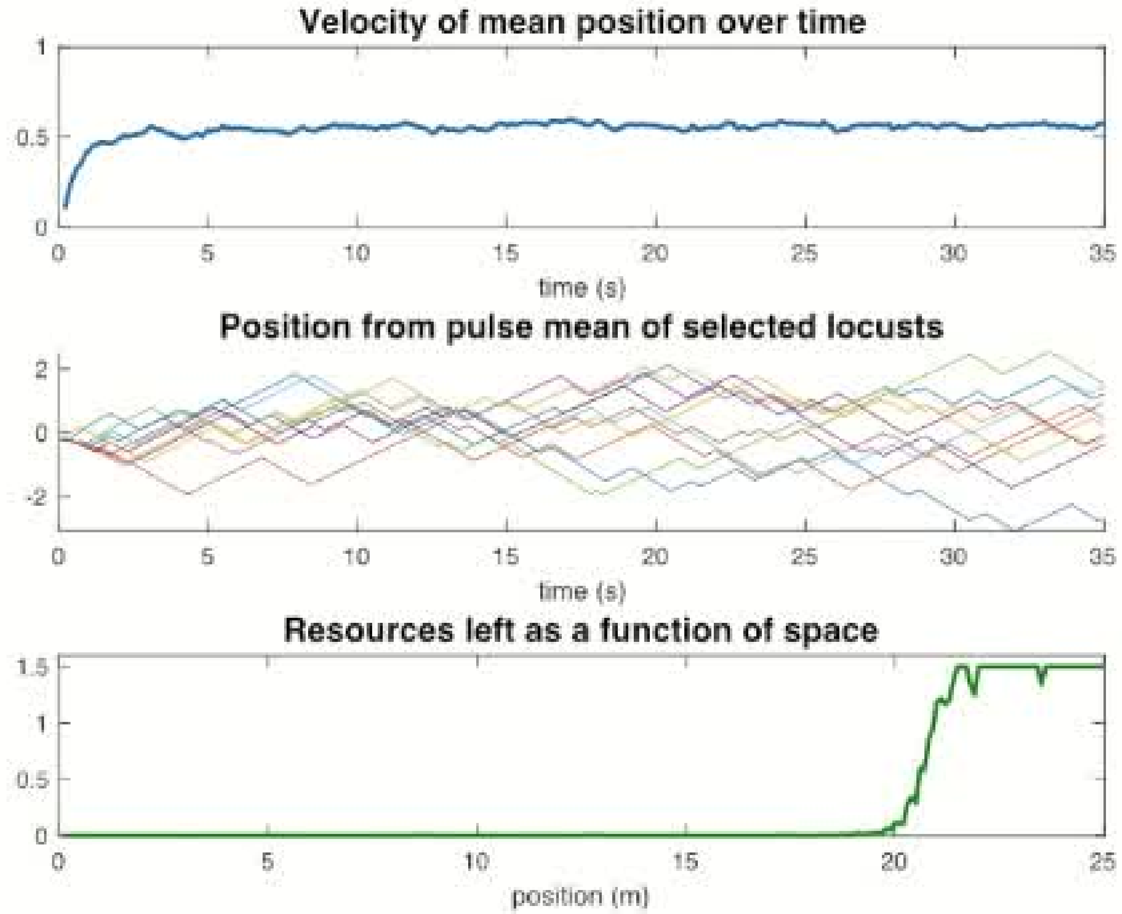






Numerics of ABM



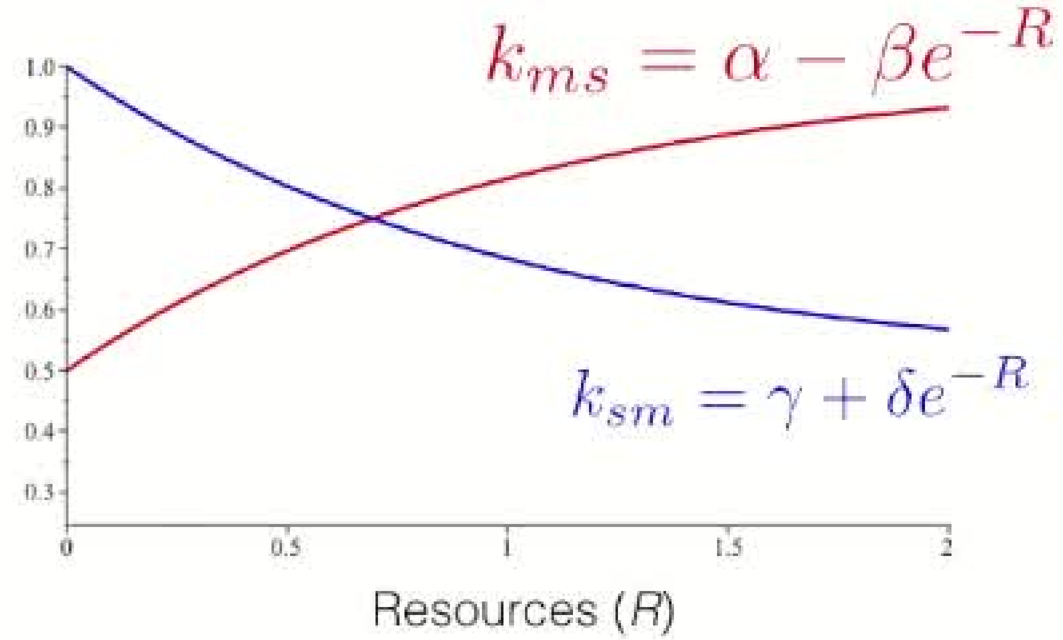


Solution quickly relaxes to a traveling wave moving with roughly constant velocity.

PDE Model

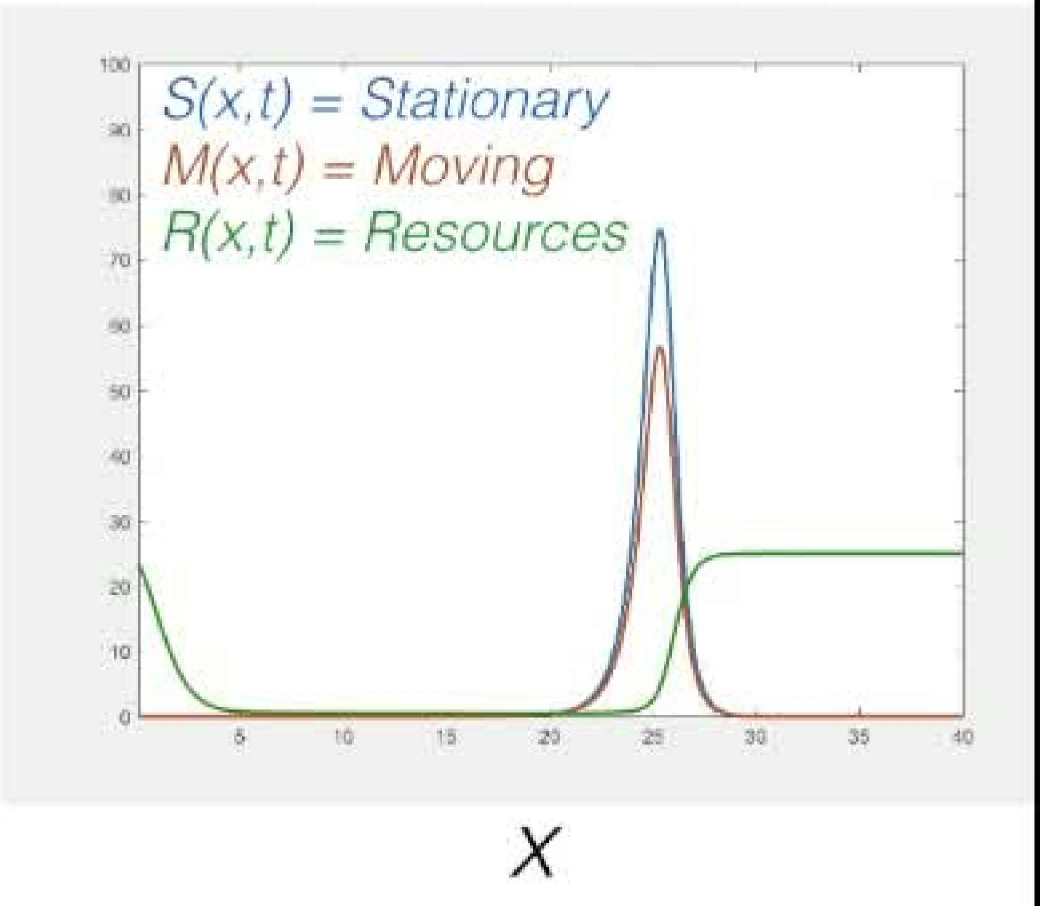
Advection - Reaction Model

$$S_t = -k_{sm}(R)\,S + k_{ms}(R)\,M$$
$$M_t + vM_x = k_{sm}(R)\,S - k_{ms}(R)\,M$$
$$R_t = -\lambda SR$$



Variables

- *S(x,t)* = Stationary locust density
- *M(x,t)* = Moving locust density
- *R(x,t)* = Resource (food) density

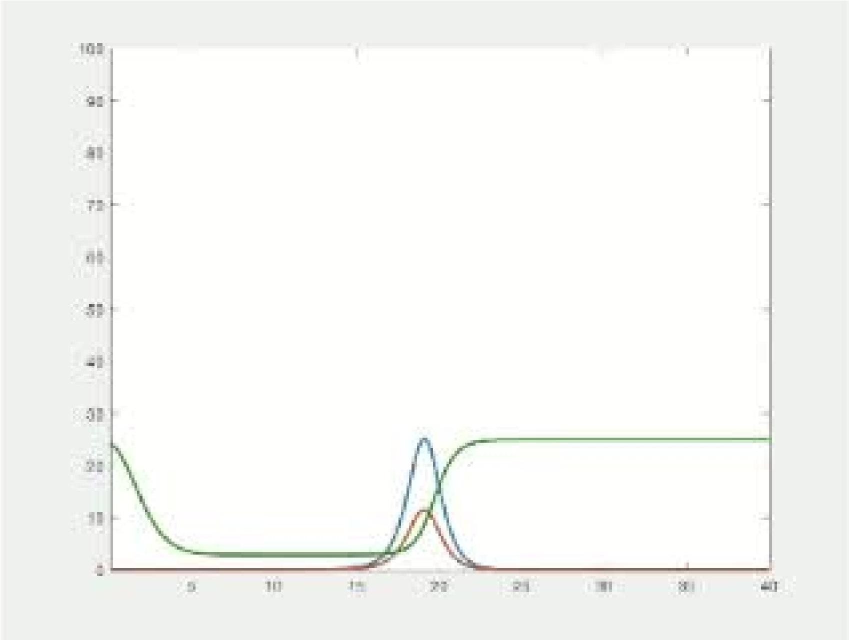


Parameters

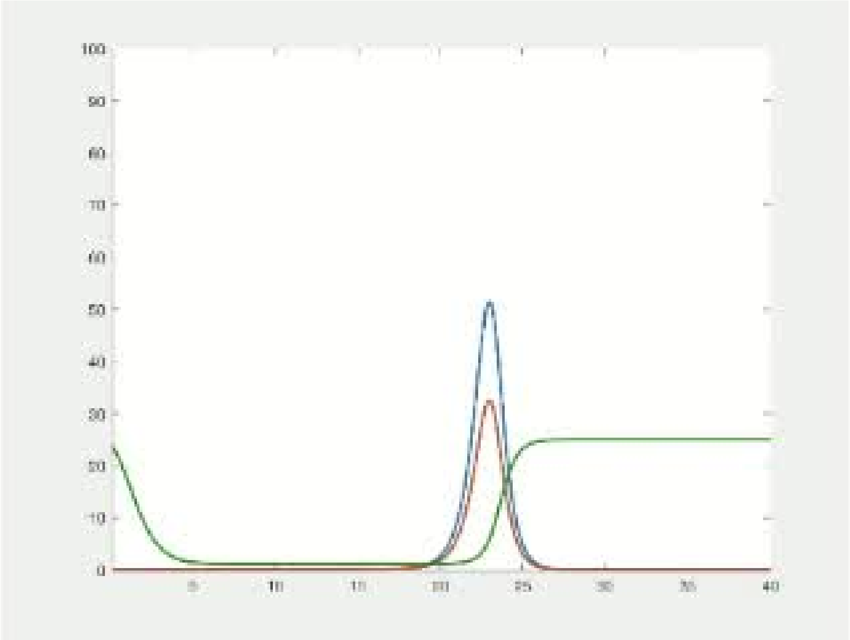
- *v*=Velocity of a moving locust
- $k_{sm}(R)$ = Stationary-to-moving transition rate
- $k_{ms}(R)$ = Moving-to-stationary transition rate
- λ = Resource consumption rate

Traveling Pulse Solution

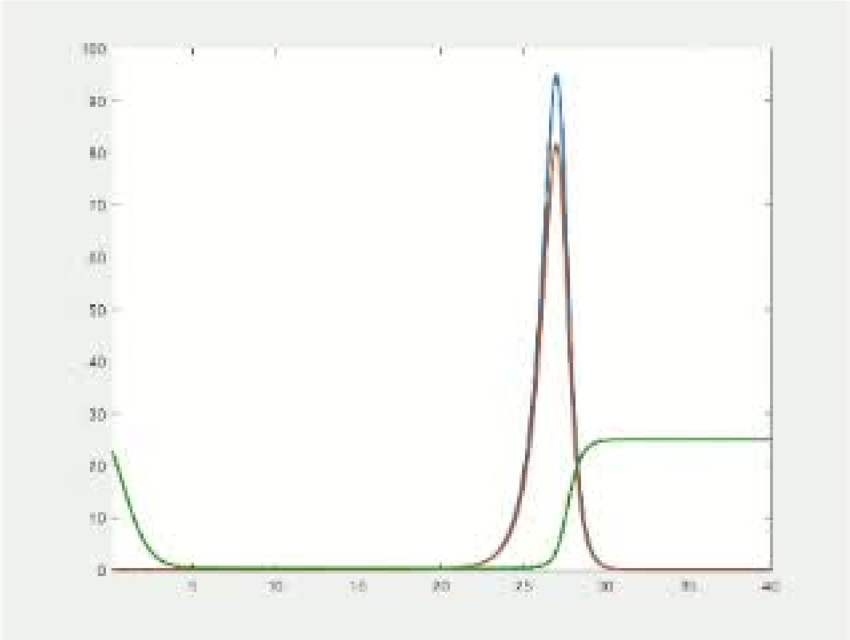
S(x,t) = Stationary
M(x,t) = Moving
R(x,t) = Resources



Mass =100



Mass =200



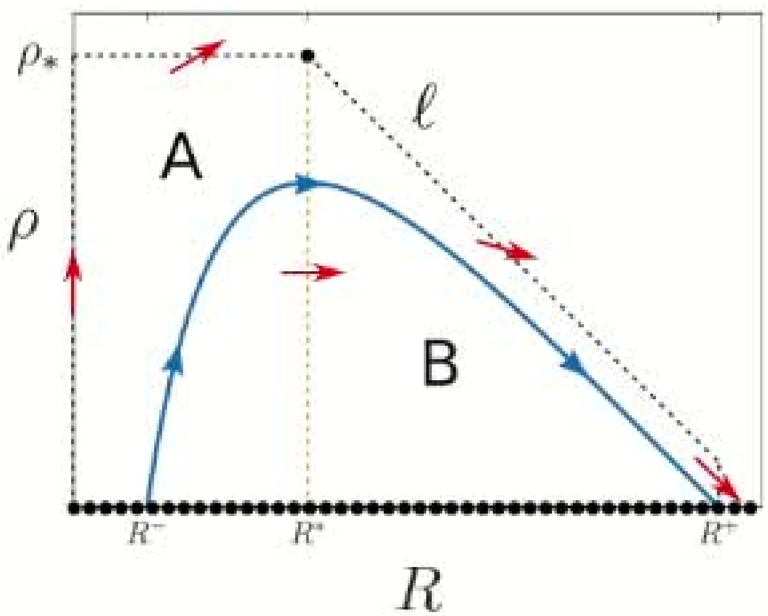
Mass =400

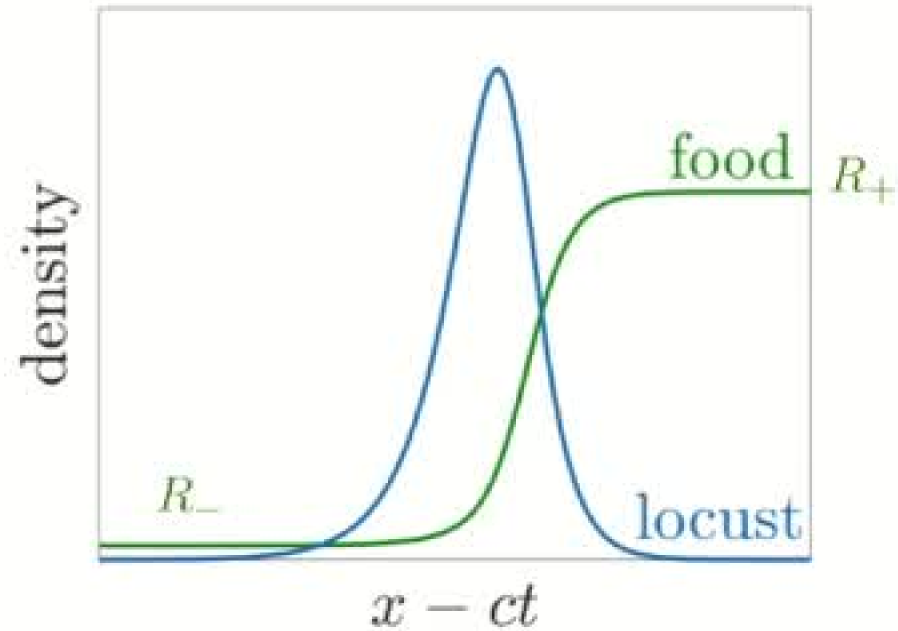
Traveling Wave Analysis

Moving reference frame $\xi = x - ct$ gives ordinary differential equation

$$R_\xi = \frac{1-c}{c}\rho R$$
$$\rho_\xi = \left(\frac{k_{sm}}{c} - \frac{k_{ms}}{1-c}\right)\rho$$

where $\rho = S + M$.

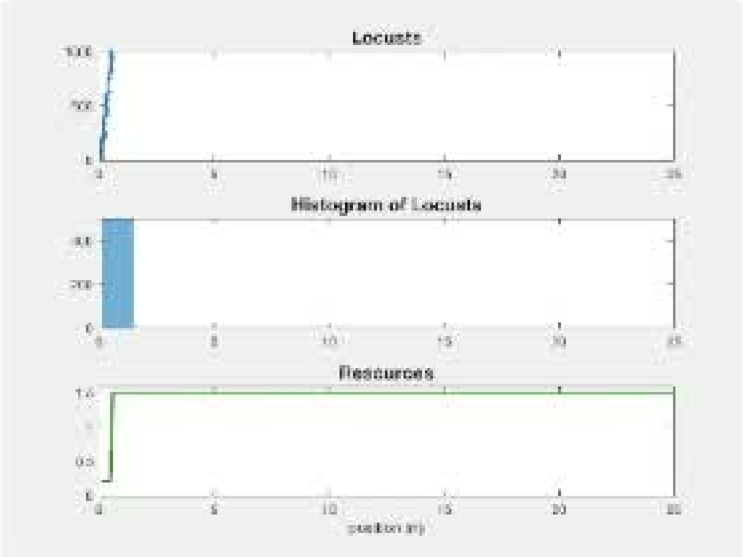


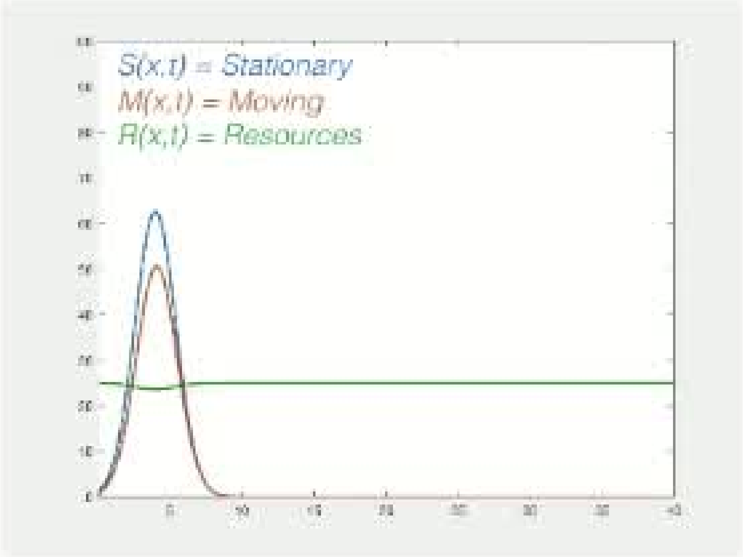


Total locust mass, M, and R_+ determine wave speed, c, and R_-

Conclusions II

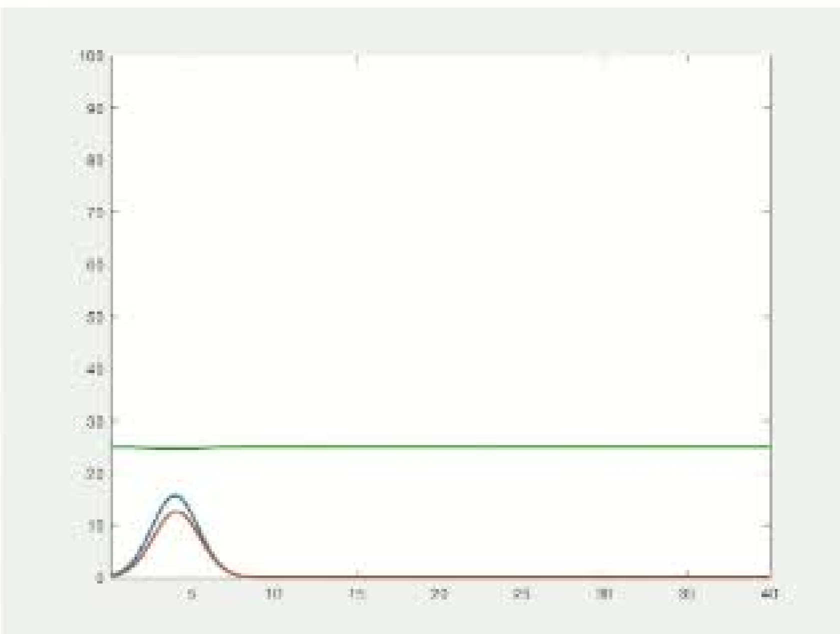
- Agent-Based Models, guided by biological observation, can capture hopper band formation.
- Homogenization yields a continuum model.
- Phase plane analysis yields a traveling pulse solution.
- Future research: Construct a 2D model that combines social interactions and foraging.



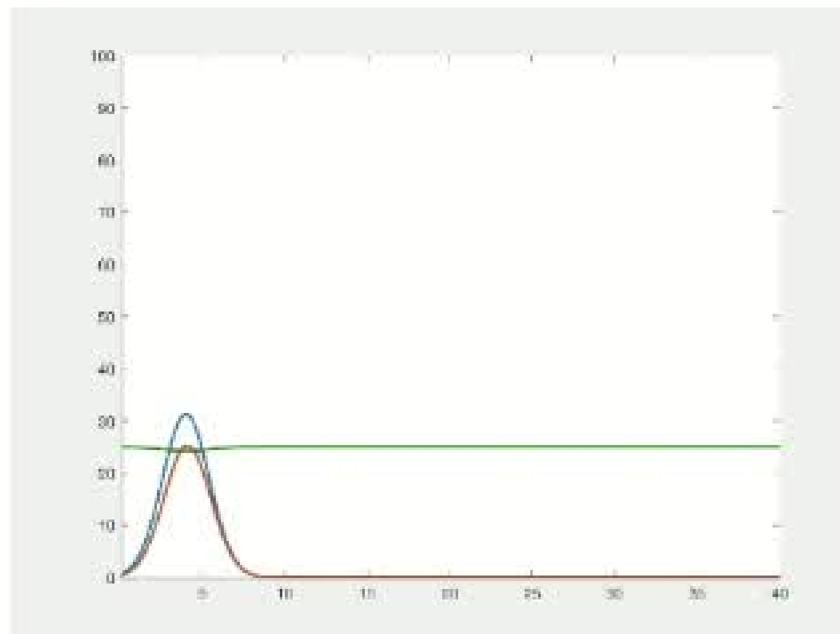


Traveling Pulse Solution

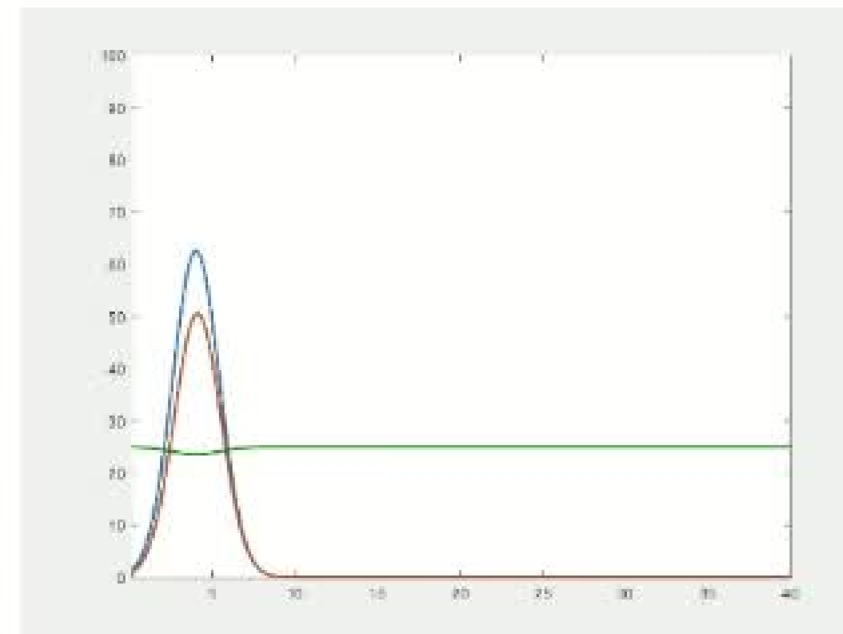
S(x,t) = Stationary
M(x,t) = Moving
R(x,t) = Resources



Mass =100



Mass =200



Mass =400