Nonlocal models of biological aggregations: Asymptotic dynamics and exotic equilibria

Chad M. Topaz
Dept. of Mathematics, Statistics, and Computer Science
Macalester College

DMS-0740484, DMS-1009633

How can one equation cause so much f***ing trouble?

Chad M. Topaz
Dept. of Mathematics, Statistics,
and Computer Science
Macalester College

DMS-0740484, DMS-1009633

Background

Aggregations display coordinated movement.

Parrish & Keshet, Nature, 1999

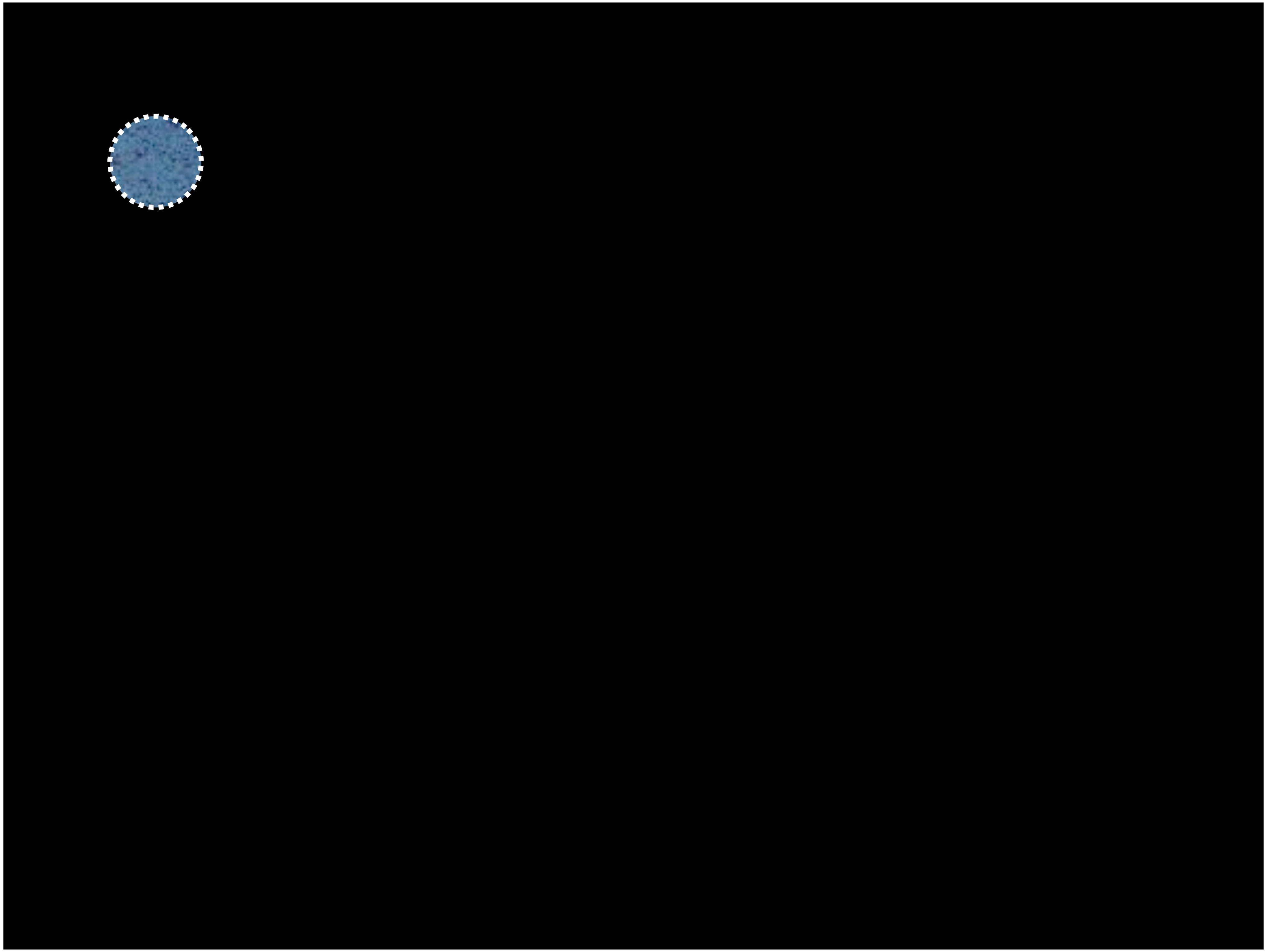
Aggregations propagate without a leader.

Dorset Wildlife Trust

Aggregations consist of socially interacting organisms.

UNFAO

Aggregations may consist of socially interacting organisms.



UNFAO

Many aggregations have sharp boundaries, constant density.

Plate 3. Wildebeest massing in a grazing front on the Serengeti Plains. March 1973.

Sinclair, 1977

Aggregations have impacts at long spatiotemporal scales.

“Social behaviors [that] on short time and space scales lead to the formation and maintenance of groups… lead at larger time and space scales to differences in spatial distributions of populations and rates of encounter and interaction with populations of predators, prey, competitors and pathogens… At the largest time and space scales, aggregation has profound consequences for ecosystem dynamics and for evolution of behavioral, morphological, and life history traits.”

--Okubo, Keshet, Grunbaum,“The dynamics of animal grouping” in *Diffusion and Ecological Problems*, Springer (2001)

What is this talk really about?

$$\rho_t + \nabla \cdot (\mathbf{v}\rho) = 0, \qquad \mathbf{v} = -\nabla Q * \rho - \nabla F$$

population density

velocity

social potential (endogenous)

external potential (exogenous)

Biological question:
How are individual behaviors and group behavior connected?

Mathematical question:
How do Q, F affect the macroscopic behavior of solutions?

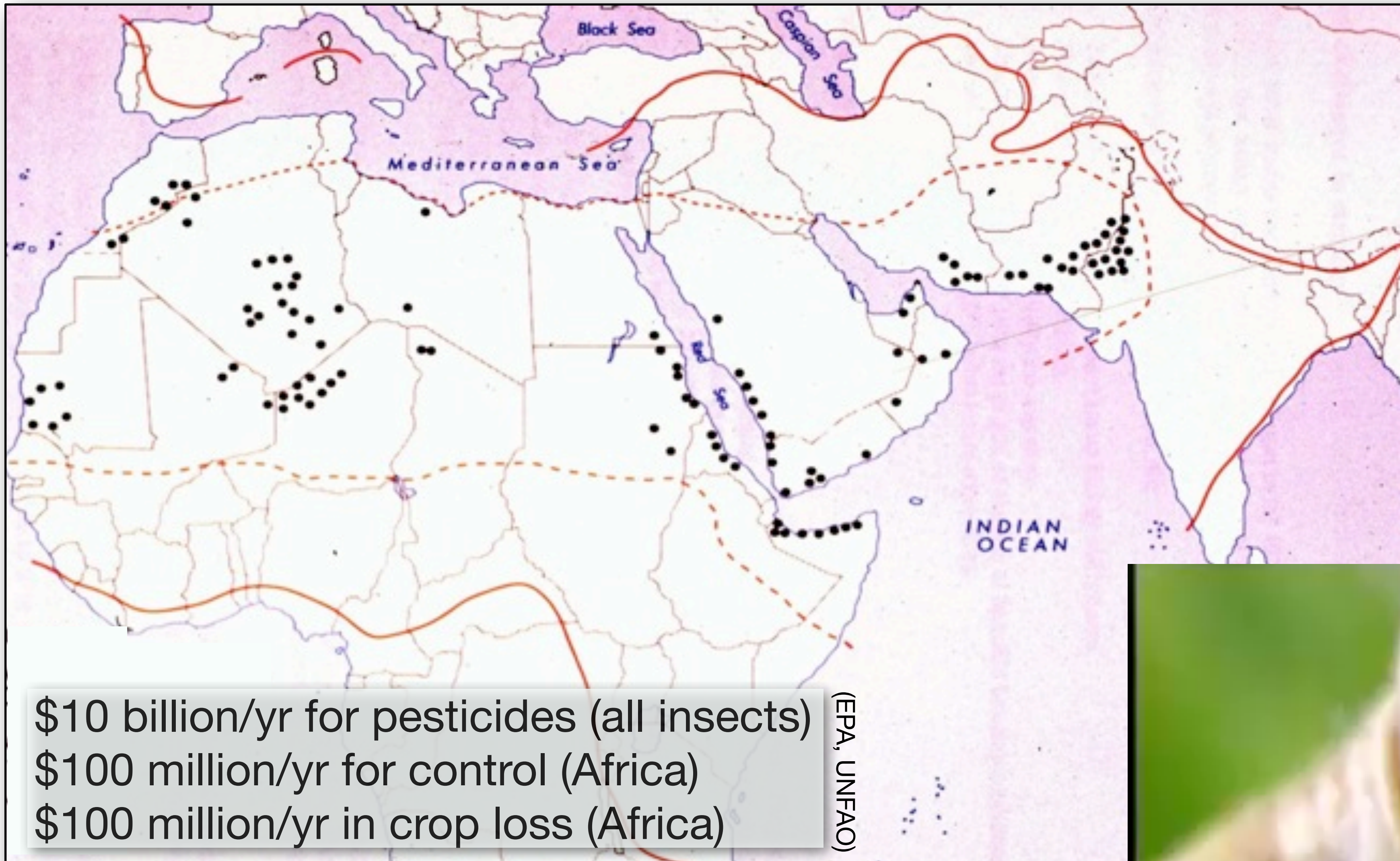
Selected, (very) abbreviated background

$$\rho_t + \nabla \cdot (\mathbf{v}\rho) = 0, \qquad \mathbf{v} = -\nabla Q * \rho - \nabla F$$

Well-posedness, blow-up in various dimensions (F=0, mostly for simple Q)	• Bodnar & Velasquez • Bertozzi, Brandman, Carrillo, Huang, Garnett, Laurent, Rosado, Slepcev...	Collapse when Q is pointy, attractive at short distances
Well-posedness, steady states in R^n (attractive/repulsive Q, F=0)	• Fetecau, Huang, Kolokolnikov	Uniform density inside a ball
Stability (F ≠ 0)	• Raoul • Fellner & Raoul	Sums of δ-masses can be stable even for Q that are repulsive at short distances
Asymptotic behavior (in 1-d, for fairly general Q, F = 0)	• Leverentz, Topaz & Bernoff	Spreading, blow-up, or compactly-supported steady state
Equilibria (in 1-d, for fairly general Q, F ≠ 0)	• Bernoff & Topaz	Steady states with compact support and possibly δ-concentrations

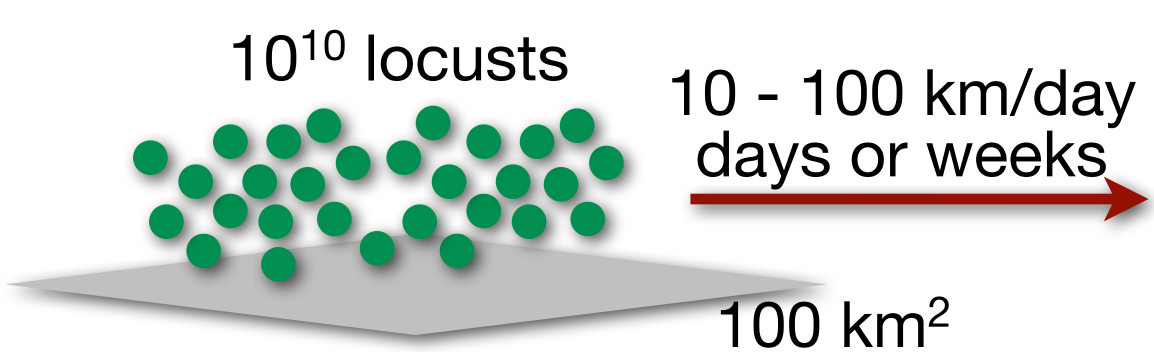
Motivation

Desert locusts form giant, destructive swarms.



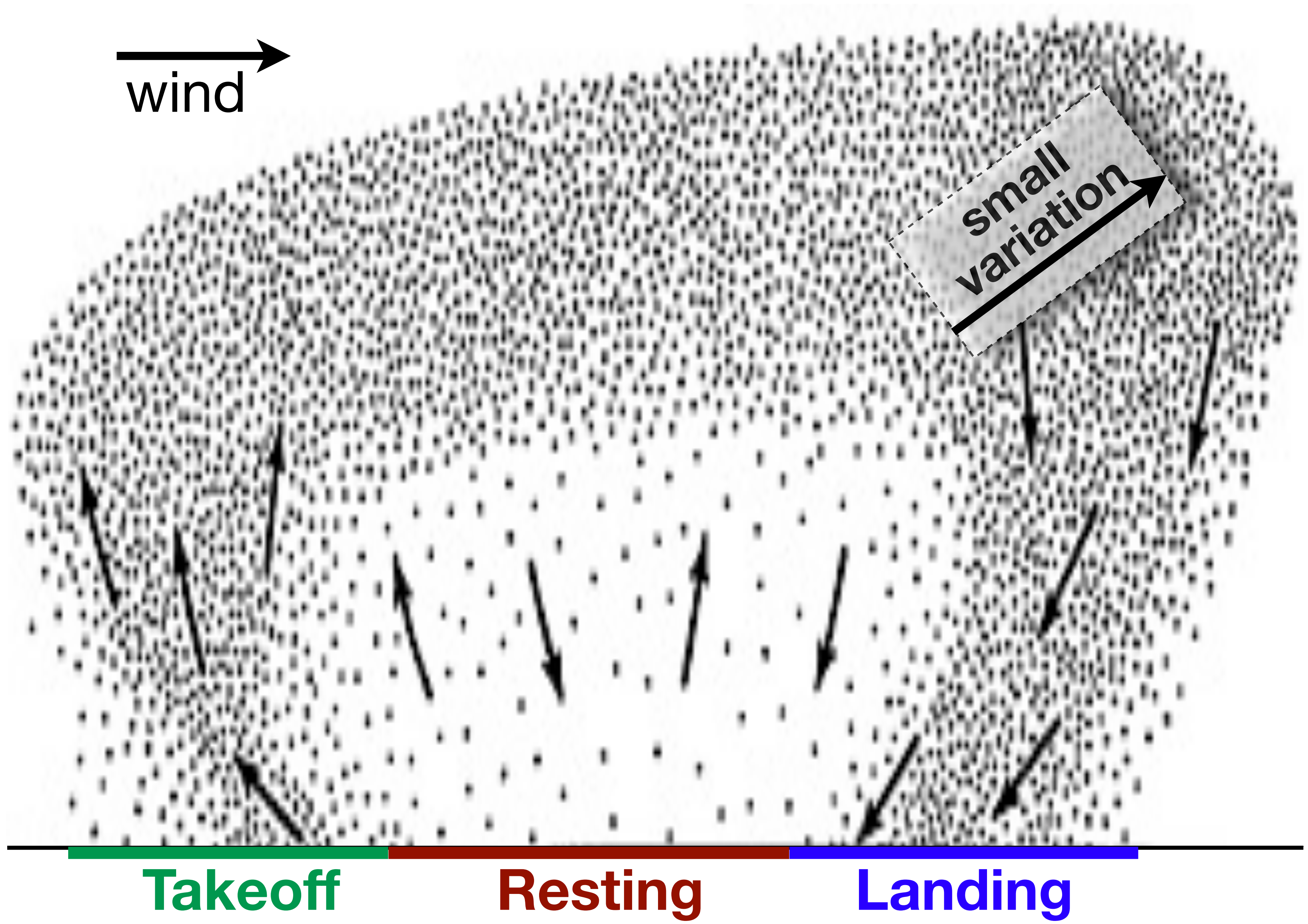
$10 billion/yr for pesticides (all insects)
$100 million/yr for control (Africa)
$100 million/yr in crop loss (Africa)

(EPA, UNFAO)



National Geographic,
“A Perfect Swarm”

Migrating locust swarms travel with a rolling motion.



Uvarov, Grasshoppers & Locusts (1977)

Meet Sheldon and Wyatt

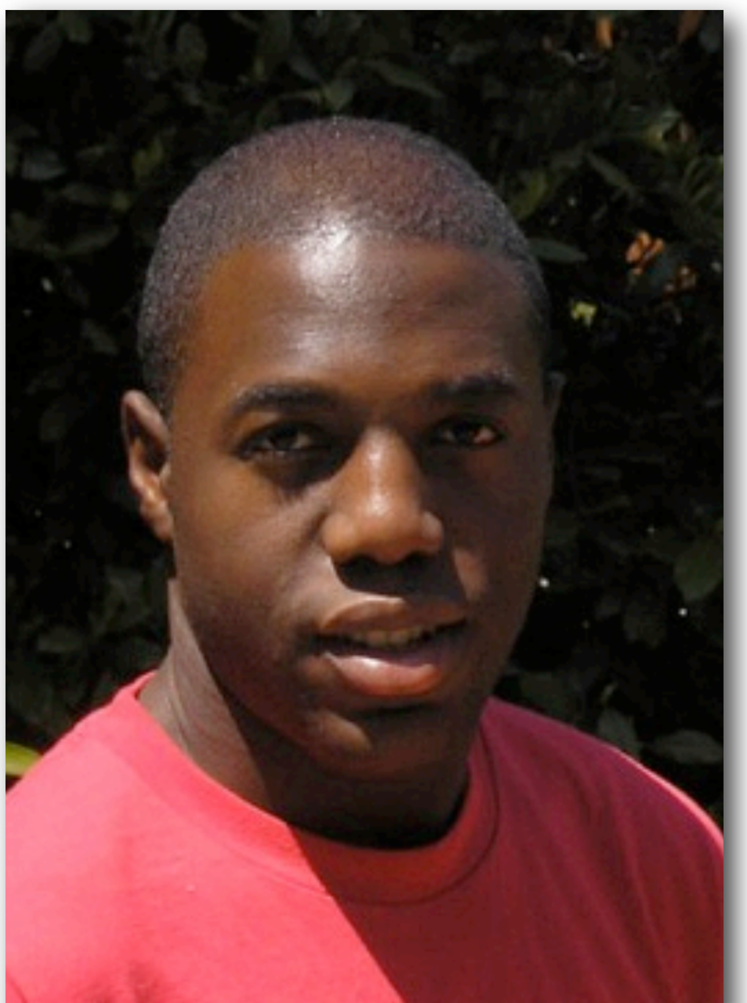
Eur. Phys. J. Special Topics **157**, 93–109 (2008)

DOI: 10.1140/epjst/e2008-00633-y

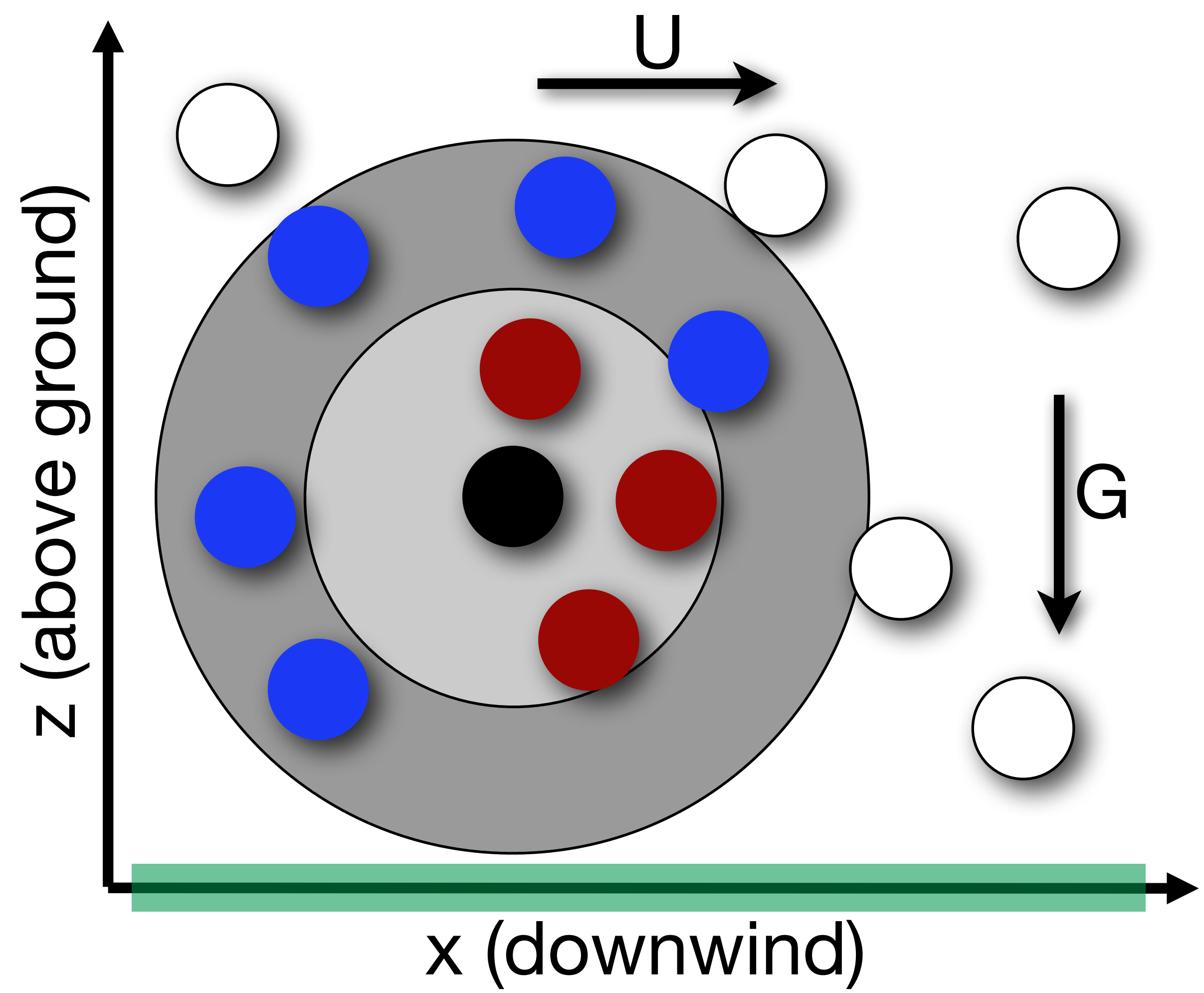
THE EUROPEAN PHYSICAL JOURNAL SPECIAL TOPICS

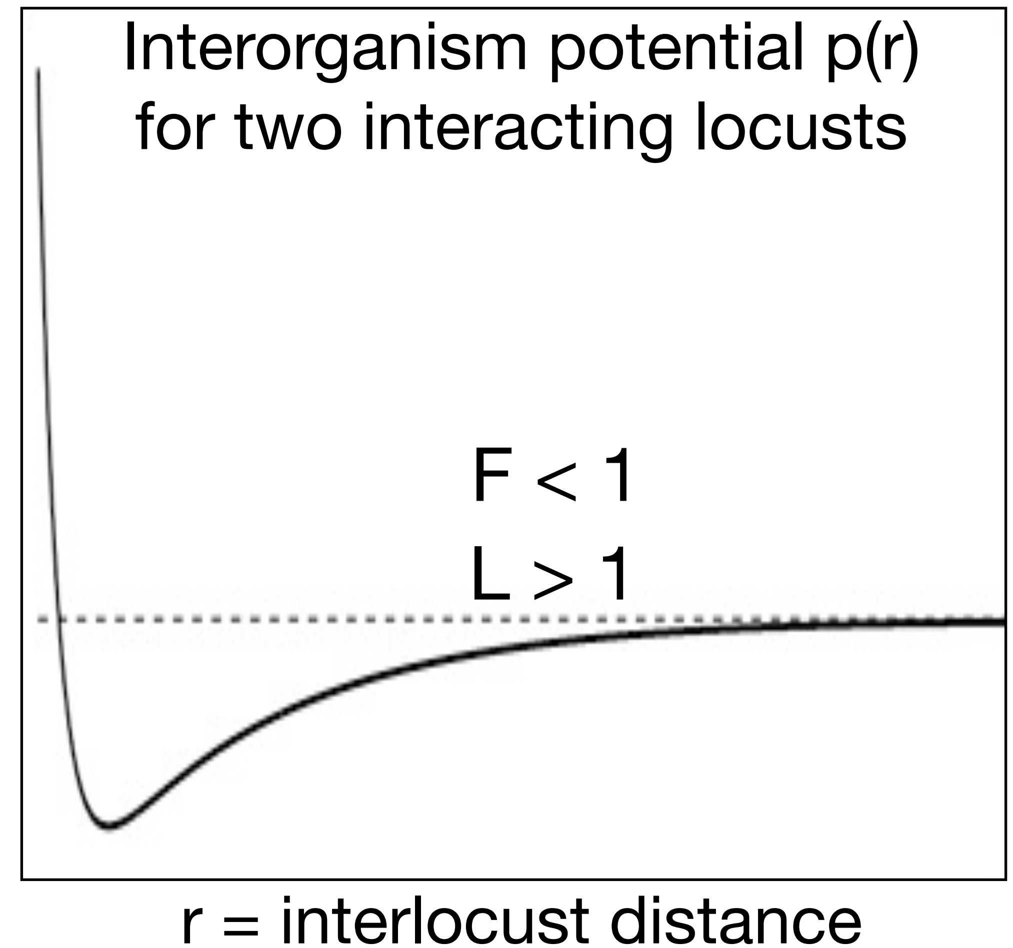
A model for rolling swarms of locusts

C.M. Topaz[1,a], A.J. Bernoff[2,], S. Logan[3,b], and W. Toolson[2,c]



We built a discrete, 2-d model for locust swarms.

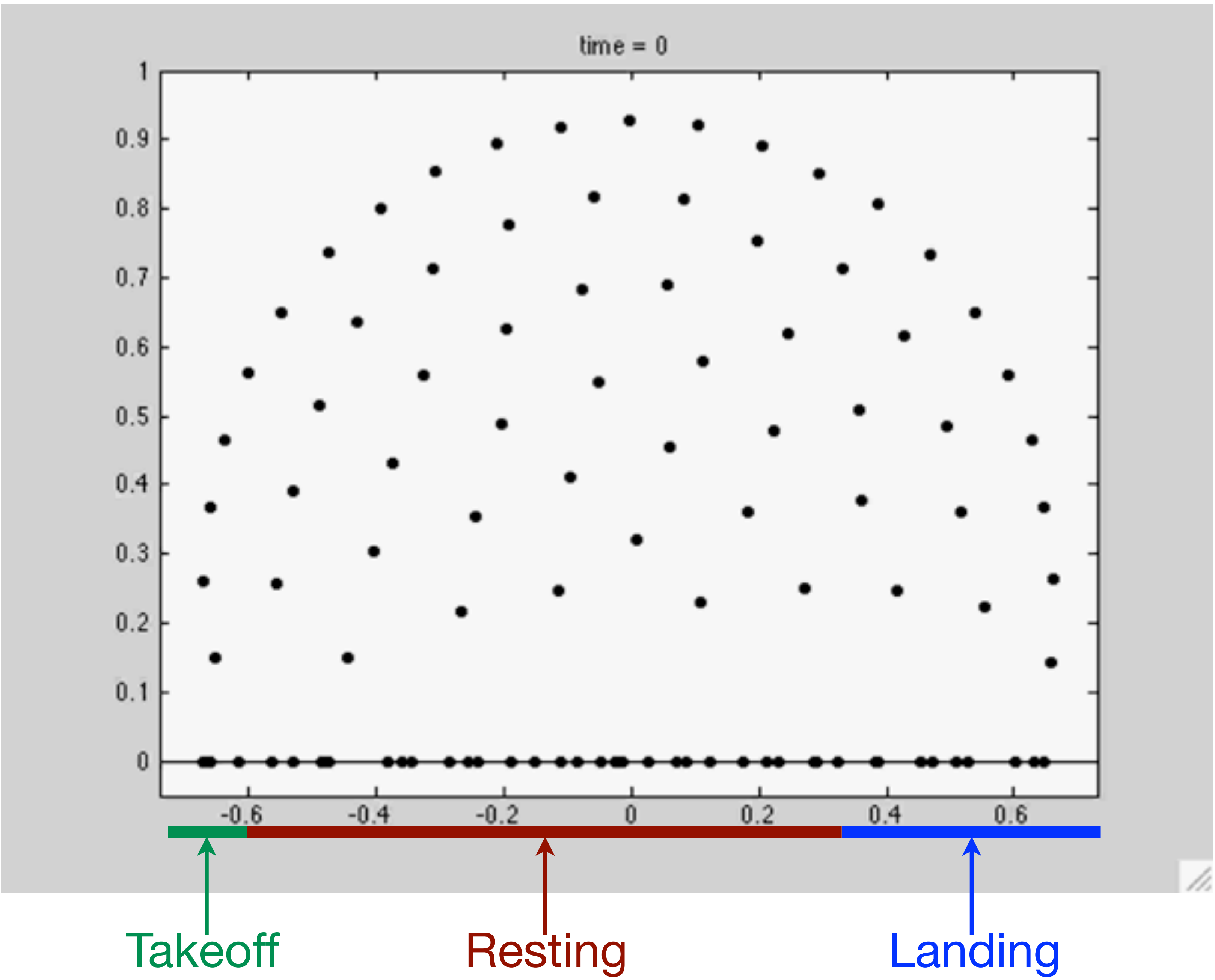


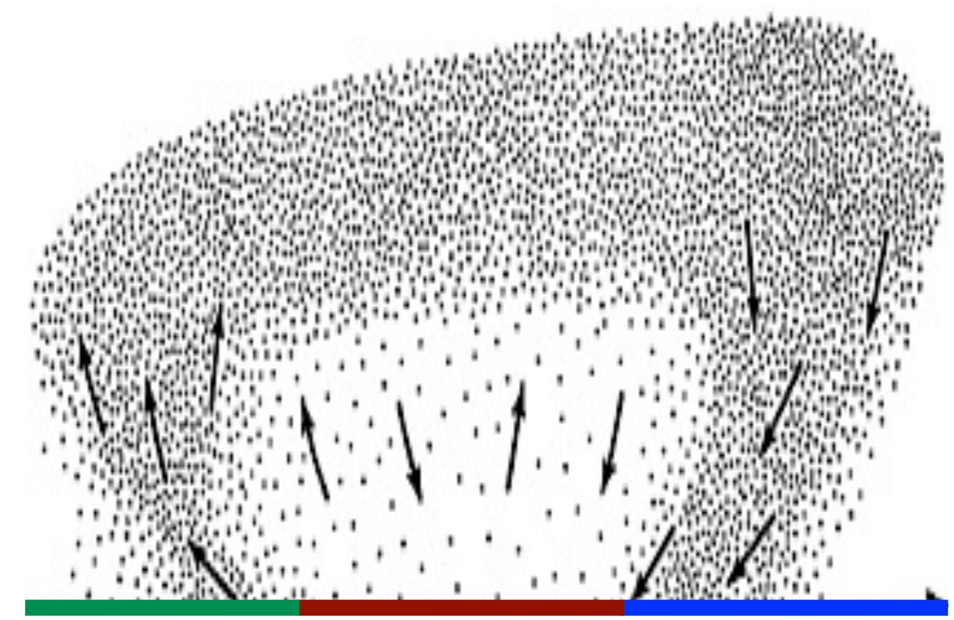


$$\dot{\vec{x}}_i = \left(\sum_{j=1}^{N} \frac{dp}{dr}(|\vec{r}_{ij}|) \frac{\vec{r}_{ij}}{|\vec{r}_{ij}|} \right) - G\hat{e}_z + U\hat{e}_x, \quad p(r) = -FLe^{-r/L} + e^{-r}, \quad \vec{r}_{ij} = \vec{x}_j - \vec{x}_i$$

interactions gravity wind

In some parameter regimes, the model forms rolling swarms similar to those observed in nature.





Uvarov, Grasshoppers & Locusts (1977)

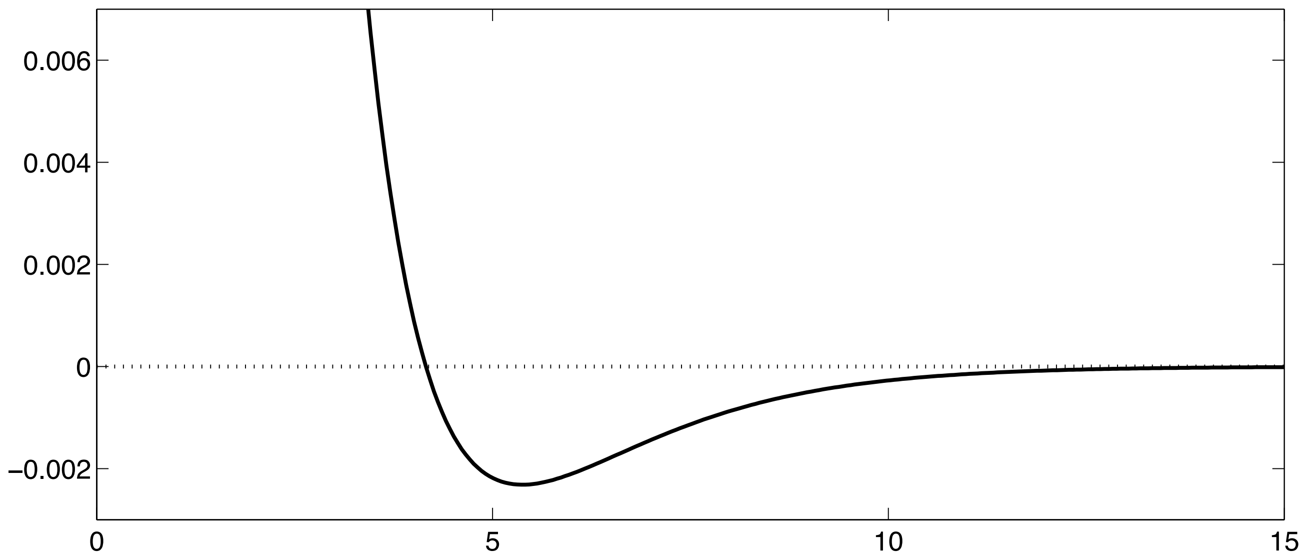
Asymptotic Dynamics

Pairwise social forces that differ only quantitatively can produce qualitatively different aggregate behaviors.

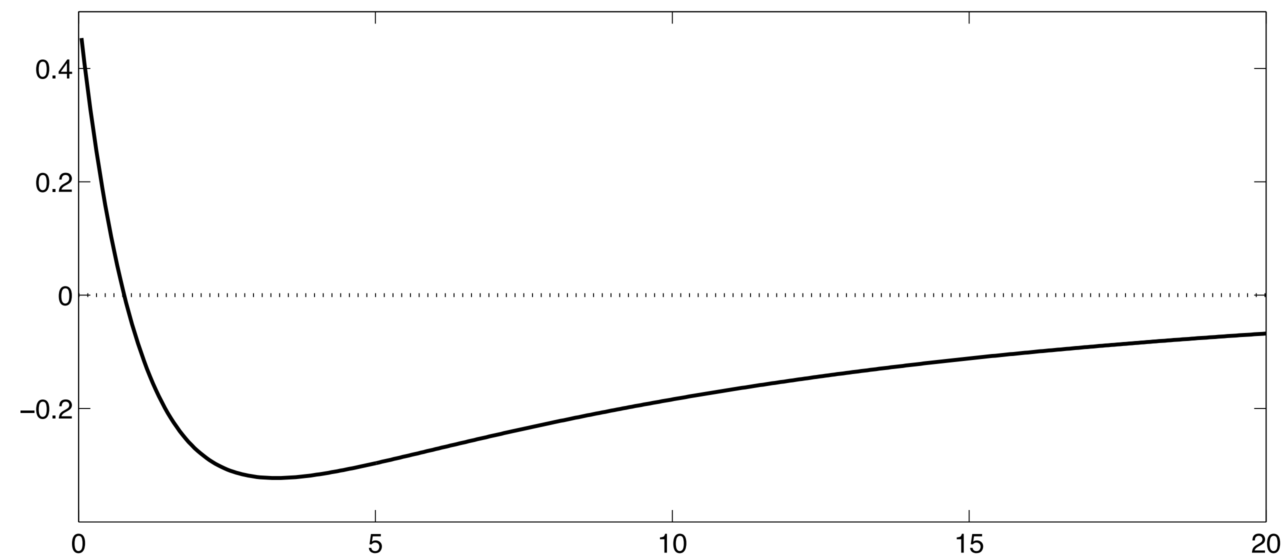
$$\dot{\mathbf{x}}_i = -\nabla_i E_{fs}, \quad E_{fs} = \frac{1}{2}\sum_{i=1}^{N}\sum_{j=1}^{N} p(r_{ij}), \quad p(r) = -FL\mathrm{e}^{-r/L} + \mathrm{e}^{-r}$$

Pairwise social forces that differ only quantitatively can produce qualitatively different aggregate behaviors.

$$-0.25e^{-|x|/1.5} + e^{-|x|}$$

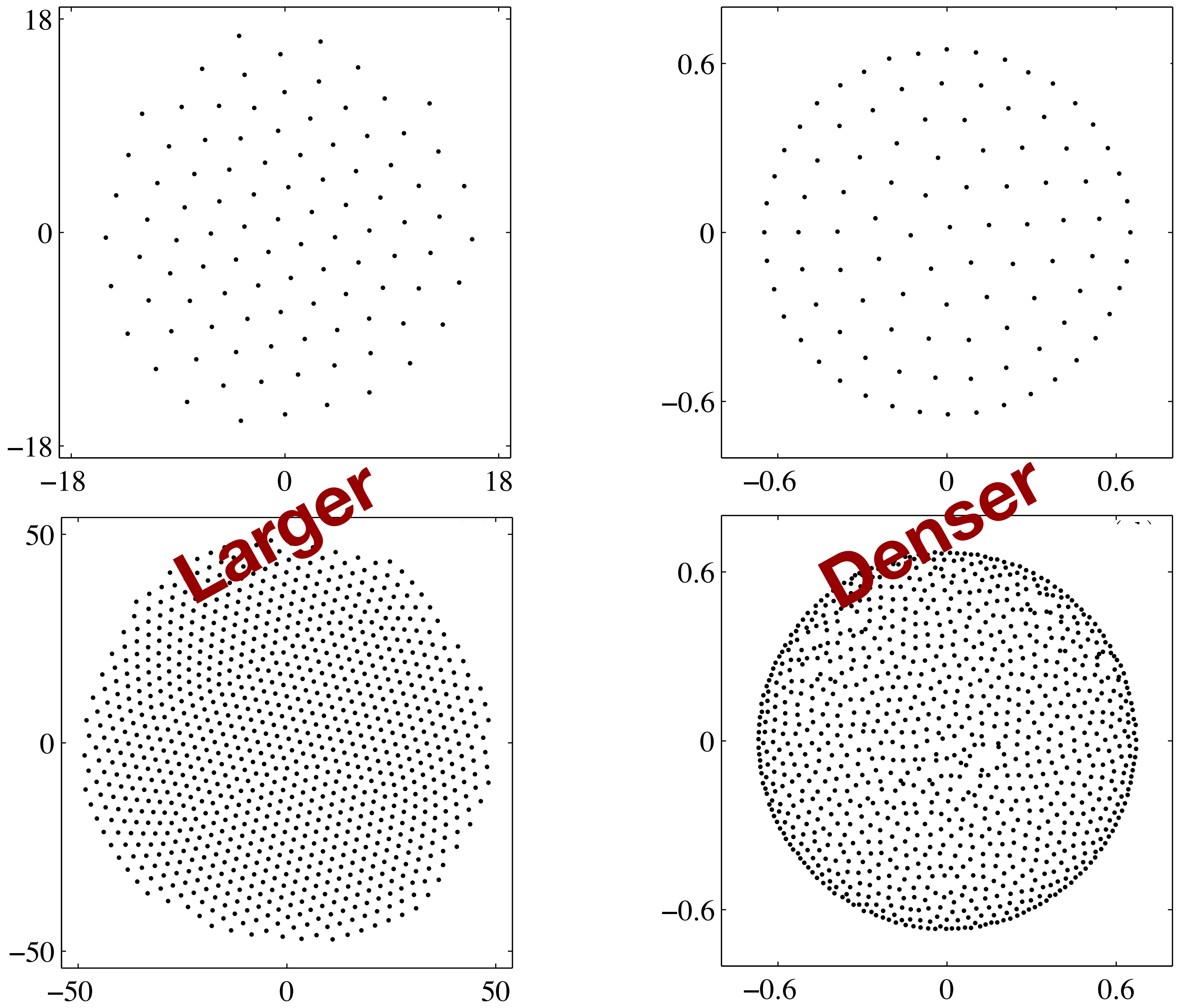


$$-0.5e^{-|x|/10} + e^{-|x|}$$



Pairwise social forces that differ only quantitatively can produce qualitatively different aggregate behaviors.

$-0.25e^{-|x|/1.5} + e^{-|x|}$ $\quad$ $-0.5e^{-|x|/10} + e^{-|x|}$



N = 100

N = 1000

Modelers use a variety of functional forms to describe pairwise social forces.

Attraction	**Repulsion**	**Reference**
a/x^m	r/x^n	Breder (1954)
$a, \ x_0 < x < x_1$	$r(x - x_0)$	Sakai (1973)
a	r/x^2	Breder (1954), Niwa (1994)
$a/x^2, \ x \geq x_0$	r/x^3	Beecham & Farnsworth (1999)
ae^{-x^2/x_a}	re^{-x^2/x_r}	Mogilner & Keshet (1999)
$ae^{-\|x\|/x_a}$	$re^{-\|x\|/x_r}$	Various

What properties of the social interaction function really matter in determining the asymptotic behavior?

SIAM J. APPLIED DYNAMICAL SYSTEMS
Vol. 8, No. 3

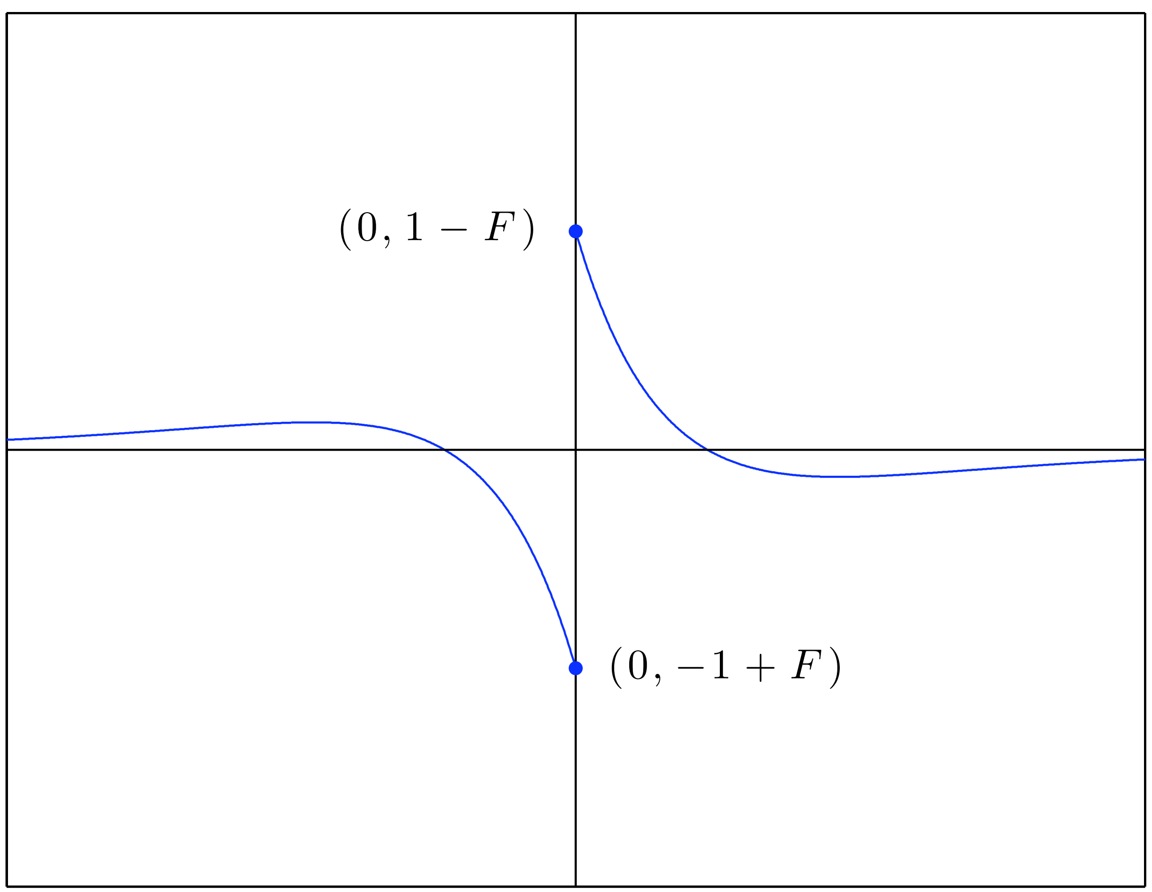
Asymptotic Dynamics of Attractive-Repulsive Swarms*

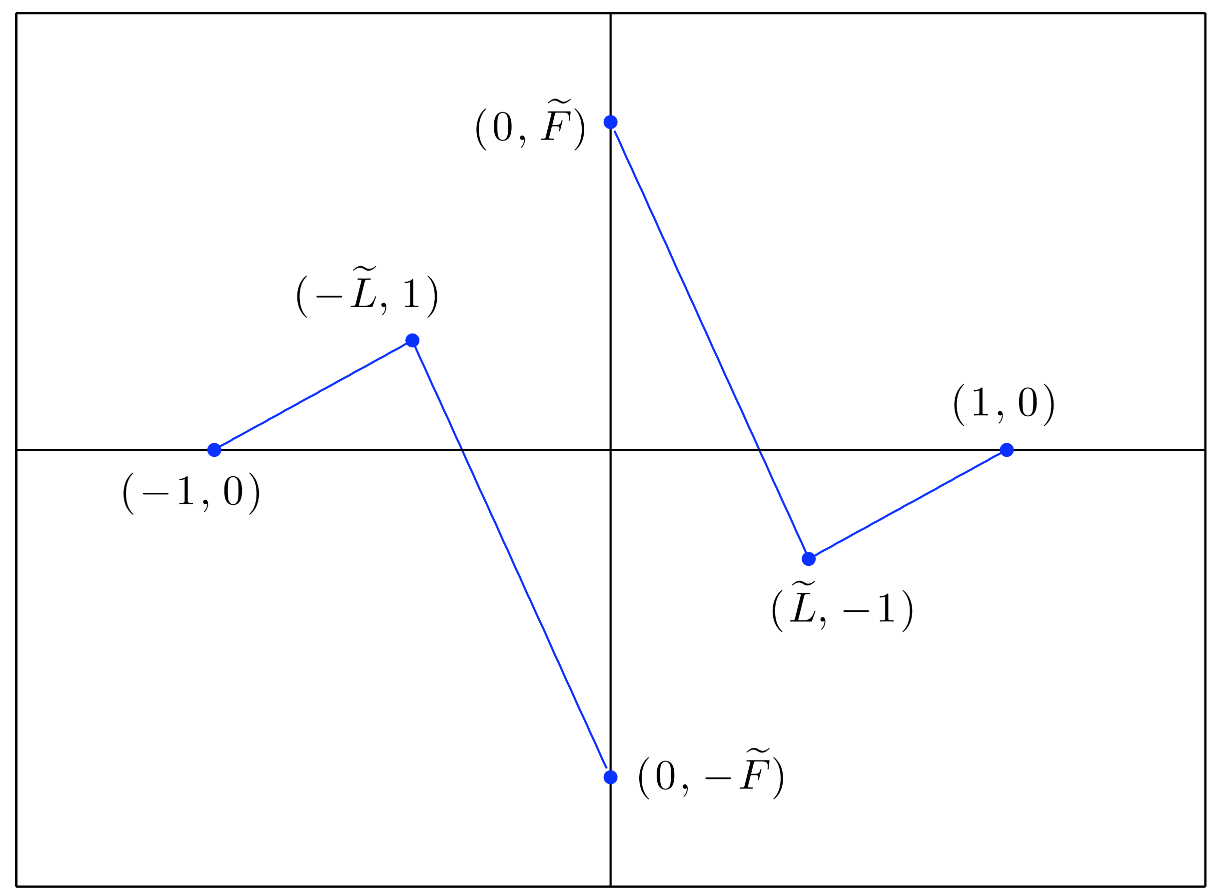
Andrew J. Leverentz[†], Chad M. Topaz[‡], and Andrew J. Bernoff[†]

We construct a minimal continuum model to investigate how long-time behavior depends on social forces.

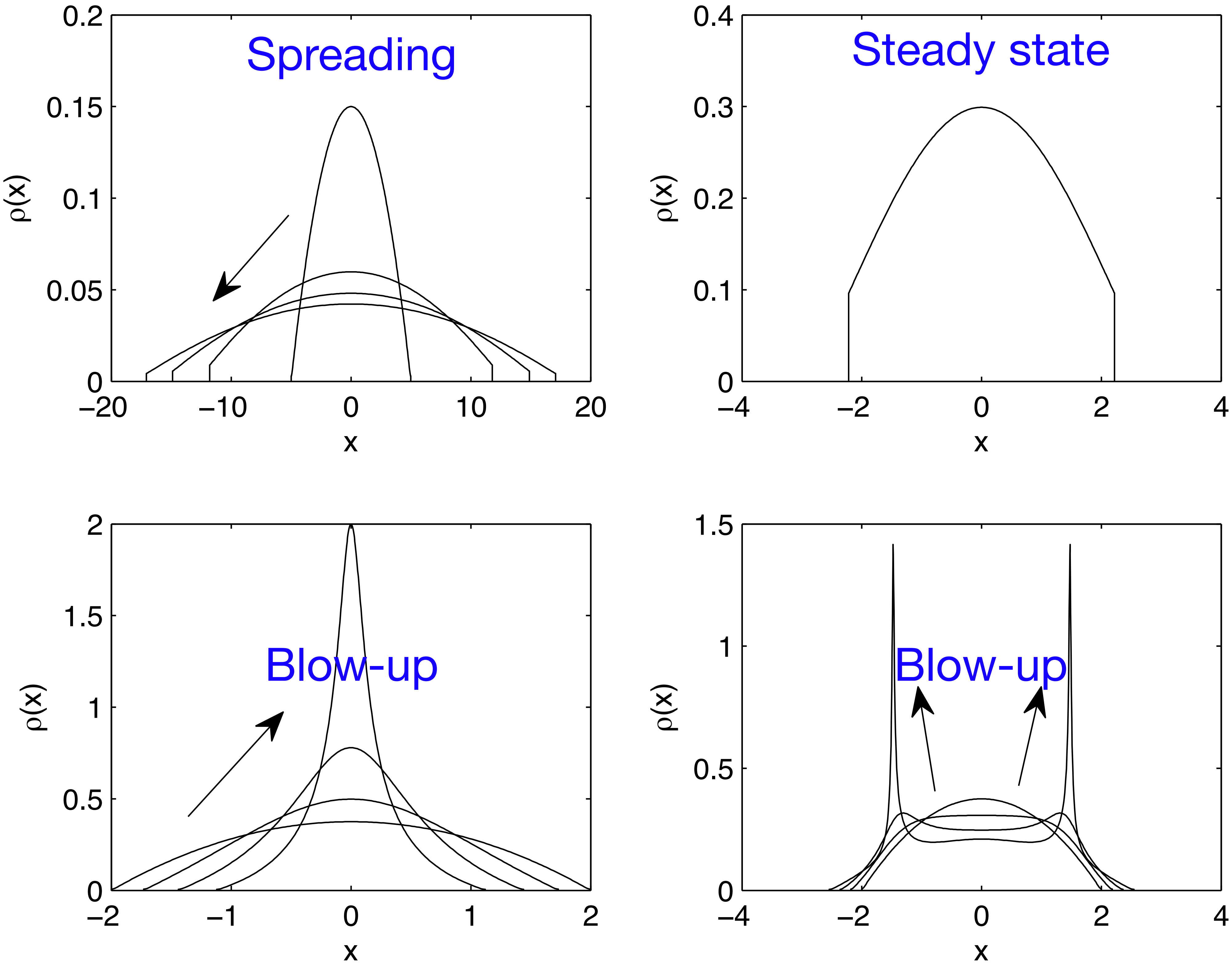
$$\rho_t + (\rho v)_x = 0$$
$$v = -\nabla Q * \rho = q * \rho$$

- Odd
- Finite first moment
- Cont. & piecewise diff. (x ≠ 0)
- Jump discontinuity (x = 0)
- Crosses zero for exactly one |x|





The swarm can asymptotically spread, reach a finite steady state, or contract.



Qualitative asymptotic behavior depends on two parameters directly computable from social force function.

$$\rho_t = \kappa(\rho^2)_{xx}, \qquad \kappa = \frac{1}{2}\int_{-\infty}^{\infty} xq(x)\,dx$$

Long wave limit:
Porous medium

$\kappa > 0$	long waves spread
$\kappa < 0$	long waves contract

Qualitative asymptotic behavior depends on two parameters directly computable from social force function.

$$\psi_t + 2\beta\psi\psi_x = 0, \quad \frac{d\psi}{dx} = \rho, \quad \beta = q(0^+)$$

Short wave limit:
Burgers

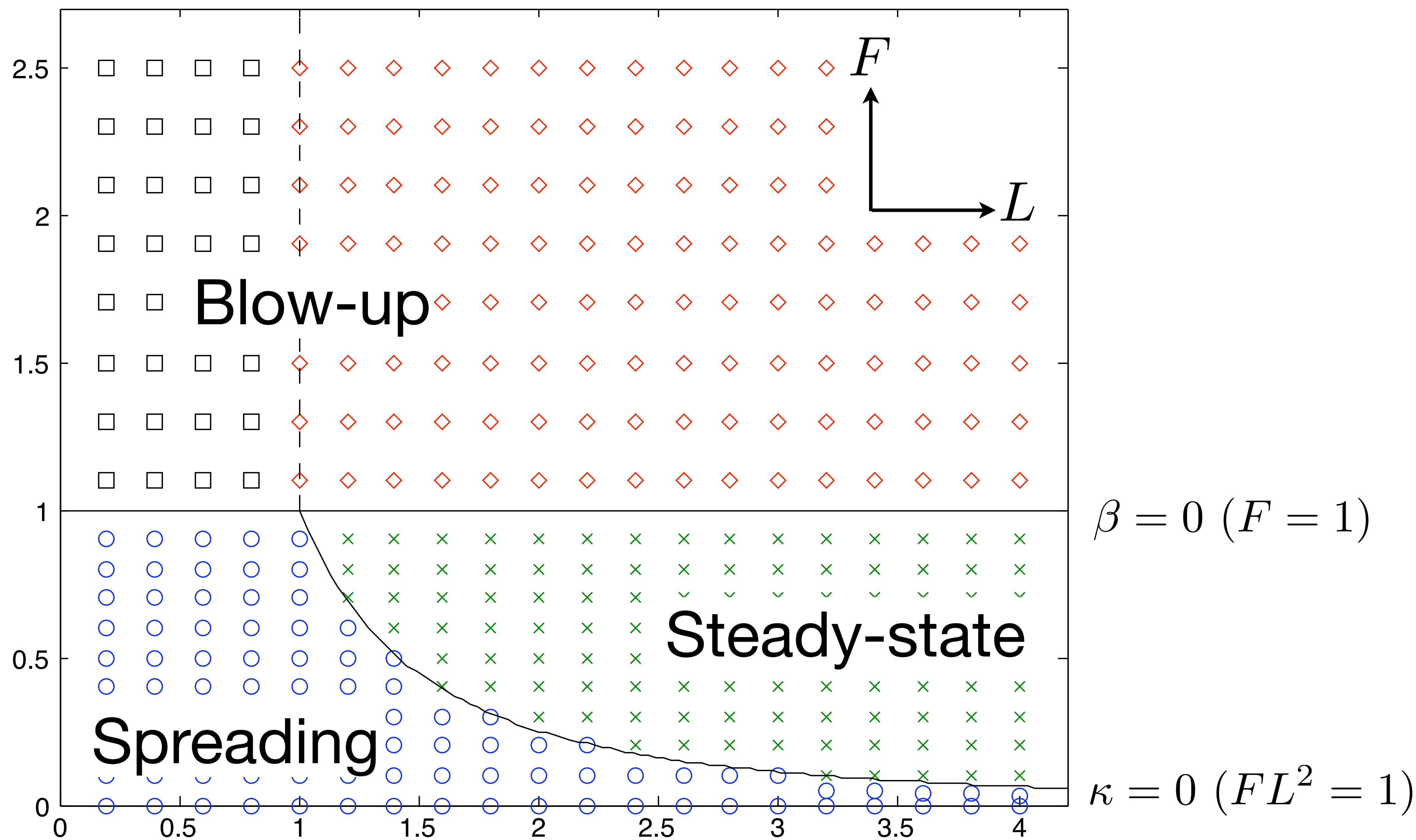
$\beta > 0$	$\beta < 0$
short waves spread	short waves contract

Qualitative asymptotic behavior depends on two parameters directly computable from social force function.

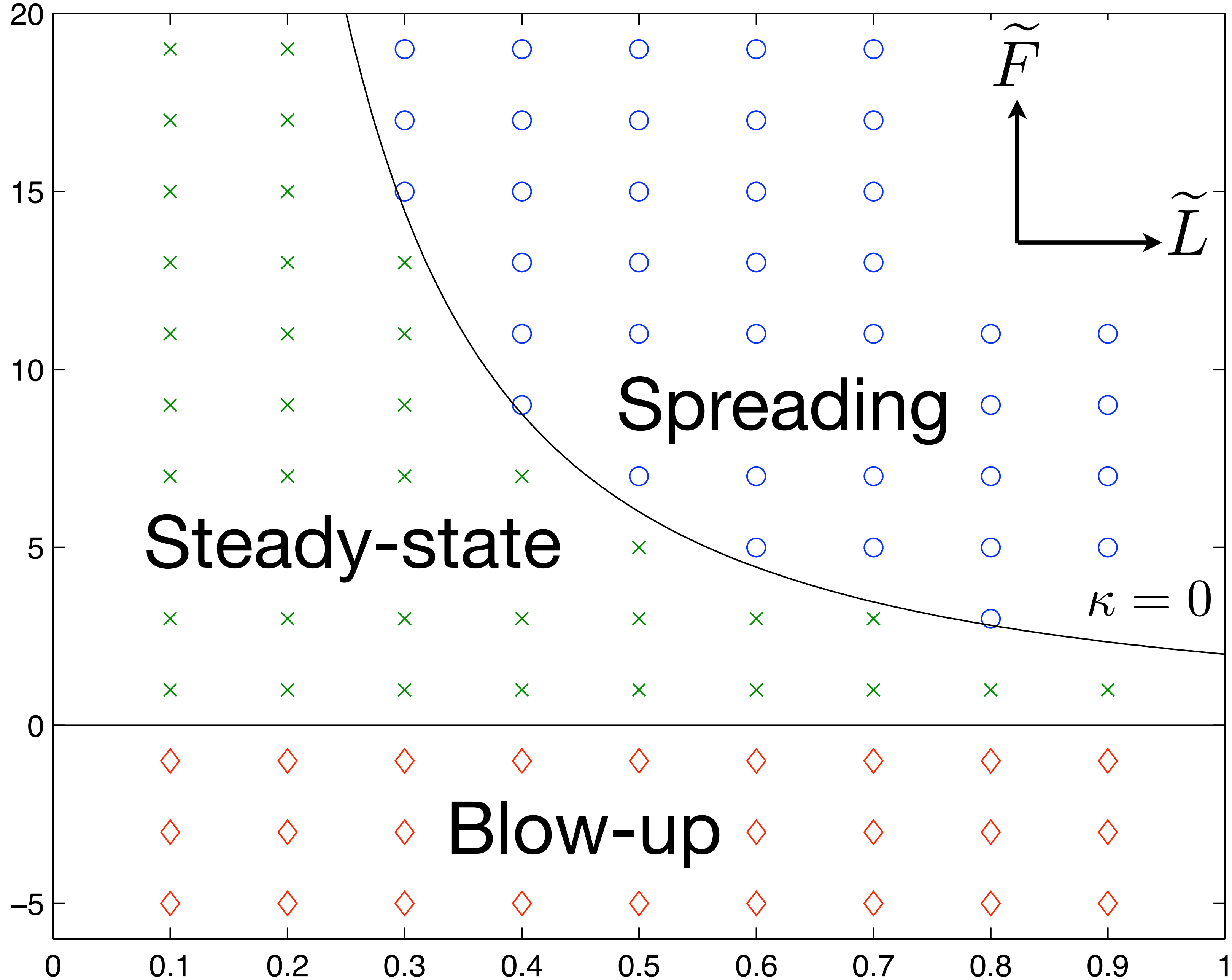
	$\beta > 0$	$\beta < 0$
$\kappa > 0$	long waves spread short waves spread SPREADING ☠	long waves spread short waves contract BLOW-UP
$\kappa < 0$	long waves contract short waves spread STEADY STATE	long waves contract short waves contract BLOW-UP

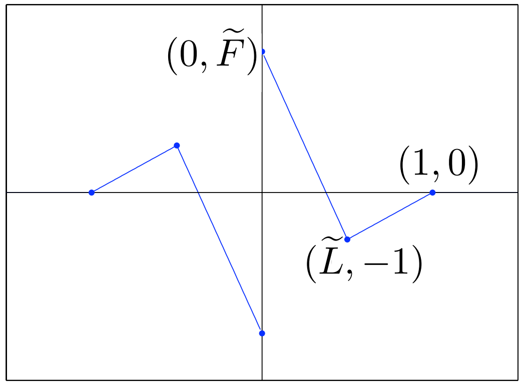
Theory agrees with asymptotic behavior seen in numerical simulations of the full model.

$$q = \mathrm{sgn}(x)\left(-Fe^{-|x|/L} + e^{-|x|}\right)$$



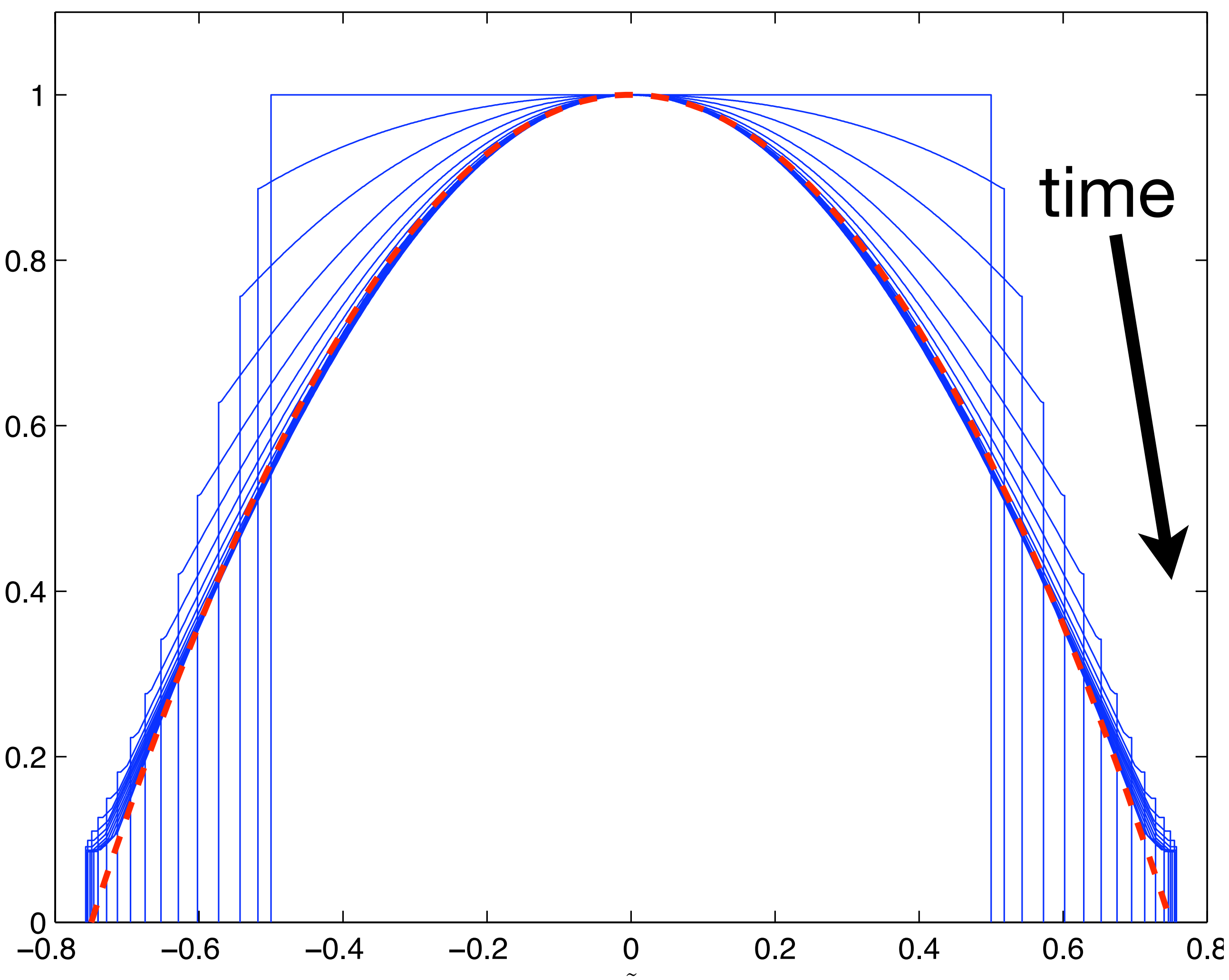
Theory agrees with asymptotic behavior seen in numerical simulations of the full model.



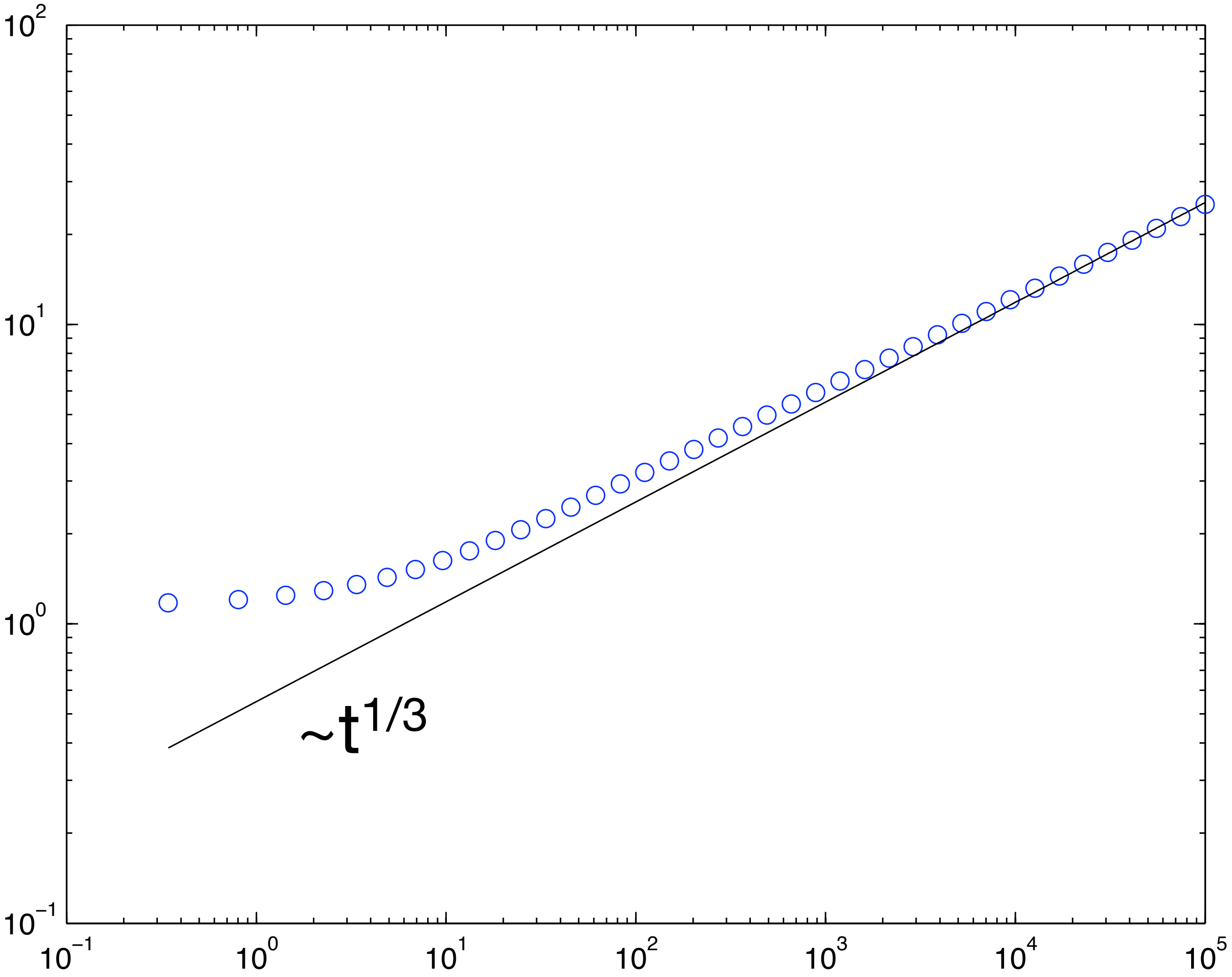


In the spreading regime, the solution asymptotically approaches Barenblatt's self-similar profile.

Rescaled density profile

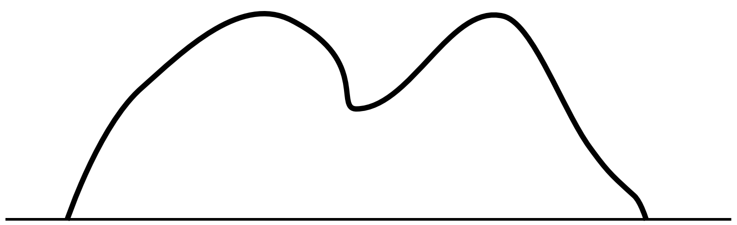


RMS width vs. time



Also: Density, slope, and speed of "traveling wave" at edge

In the blow-up regime, an analytical upper bound for blow-up time agrees with numerical simulations.

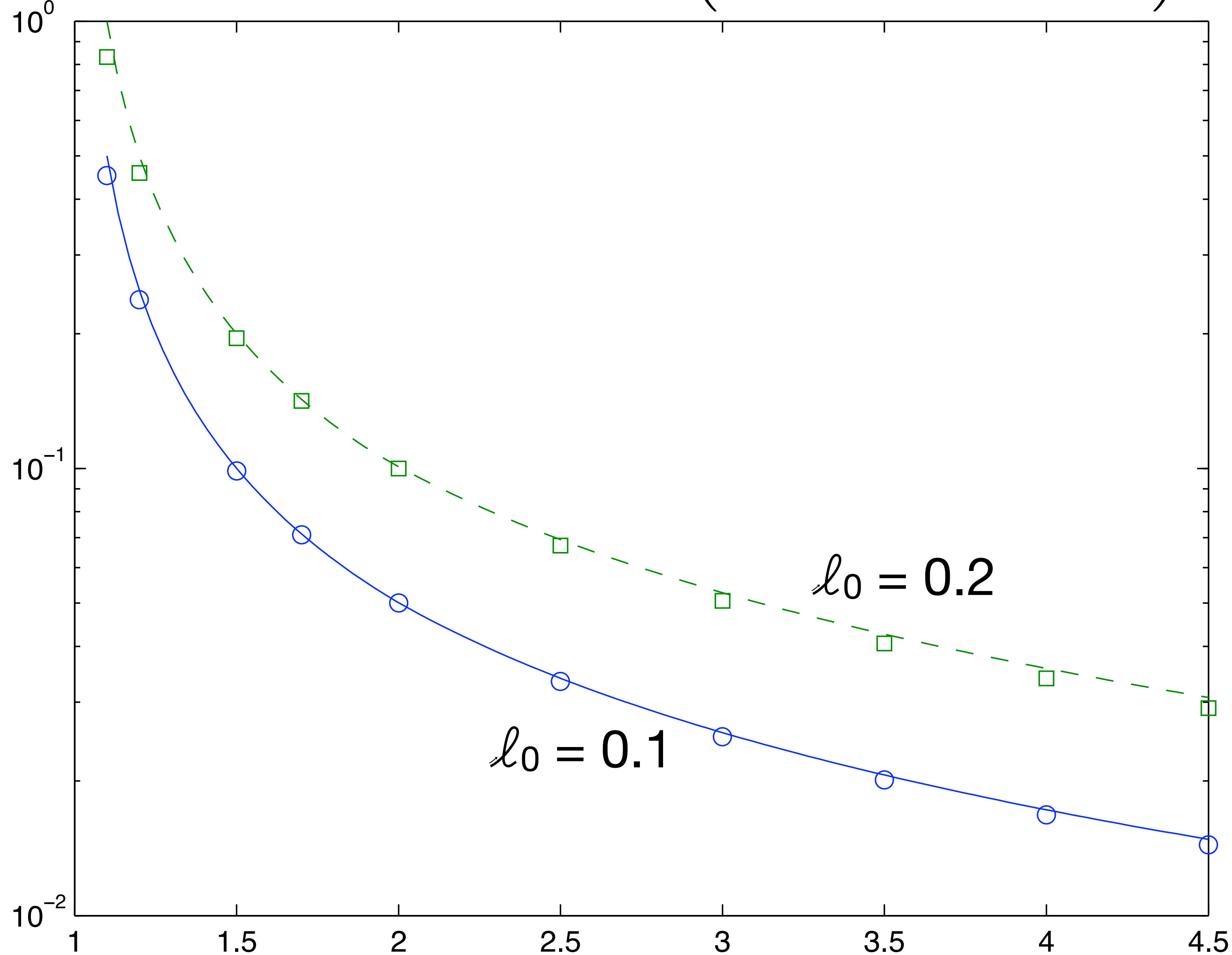


Initial length ℓ_0

Mass M

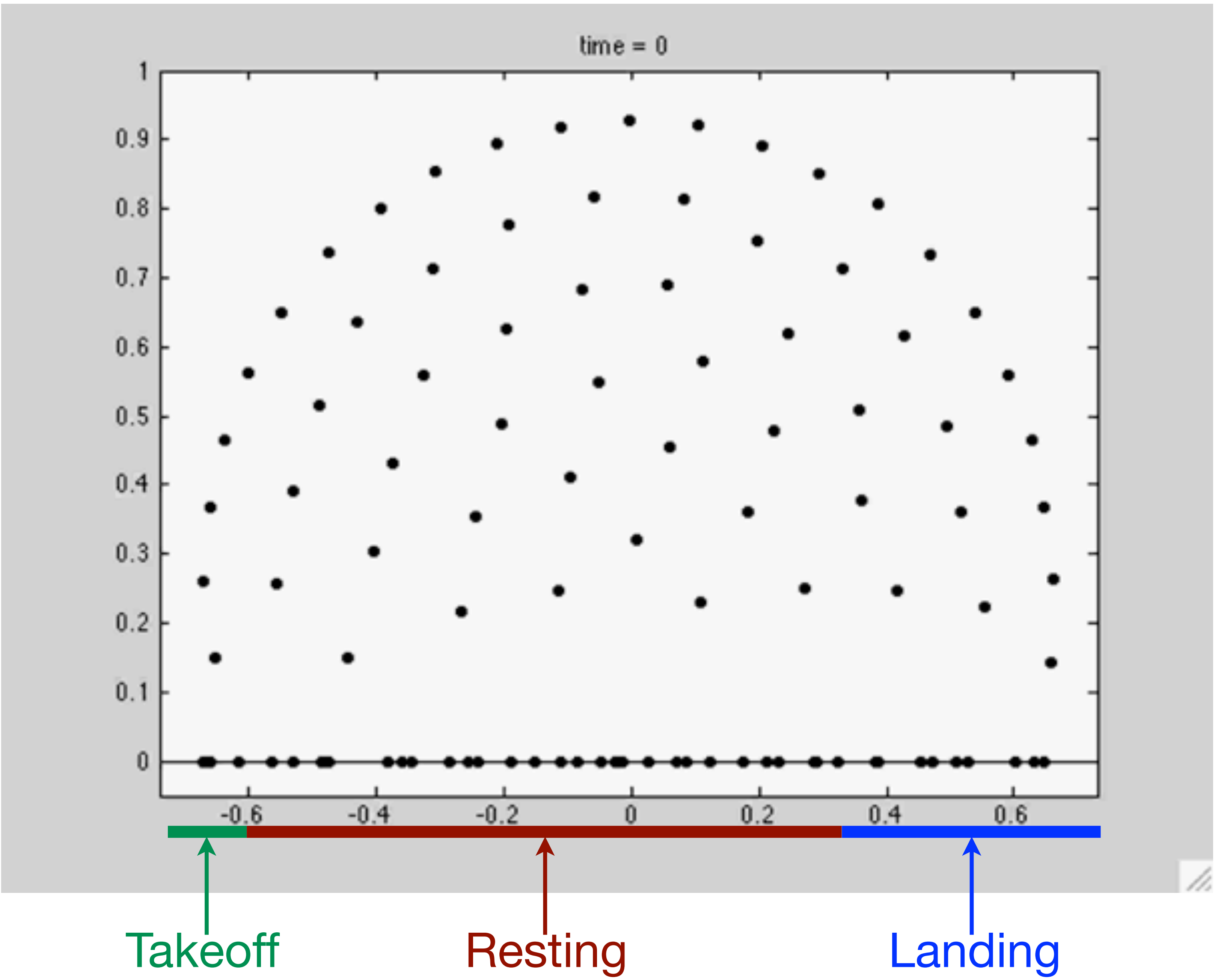
$$t^* \leq \frac{\ell_0}{2M}\left\{\min_{0<x<\ell_0}|q(x)|\right\}^{-1}$$

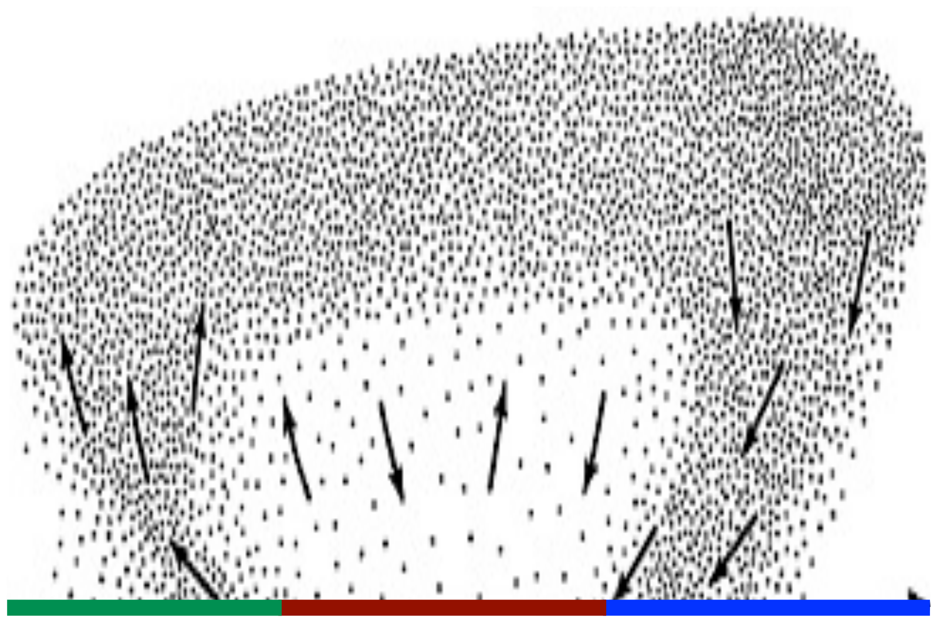
t* vs. F with $q = \mathrm{sgn}(x)\left(-Fe^{-|x|/2} + e^{-|x|}\right)$



Swarm Equilibria

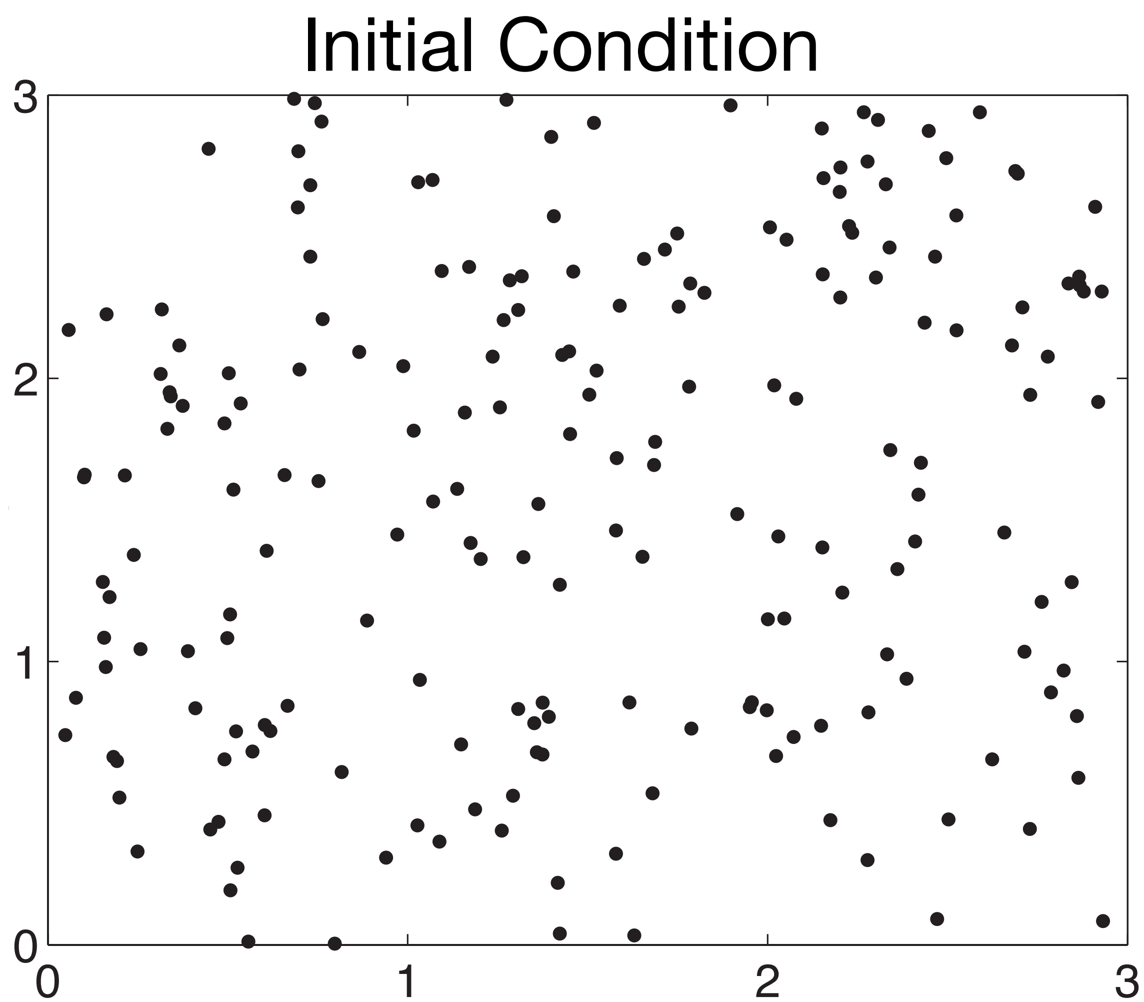
The gap in the locust swarm is crucial, allowing for rolling migration in the presence of wind.

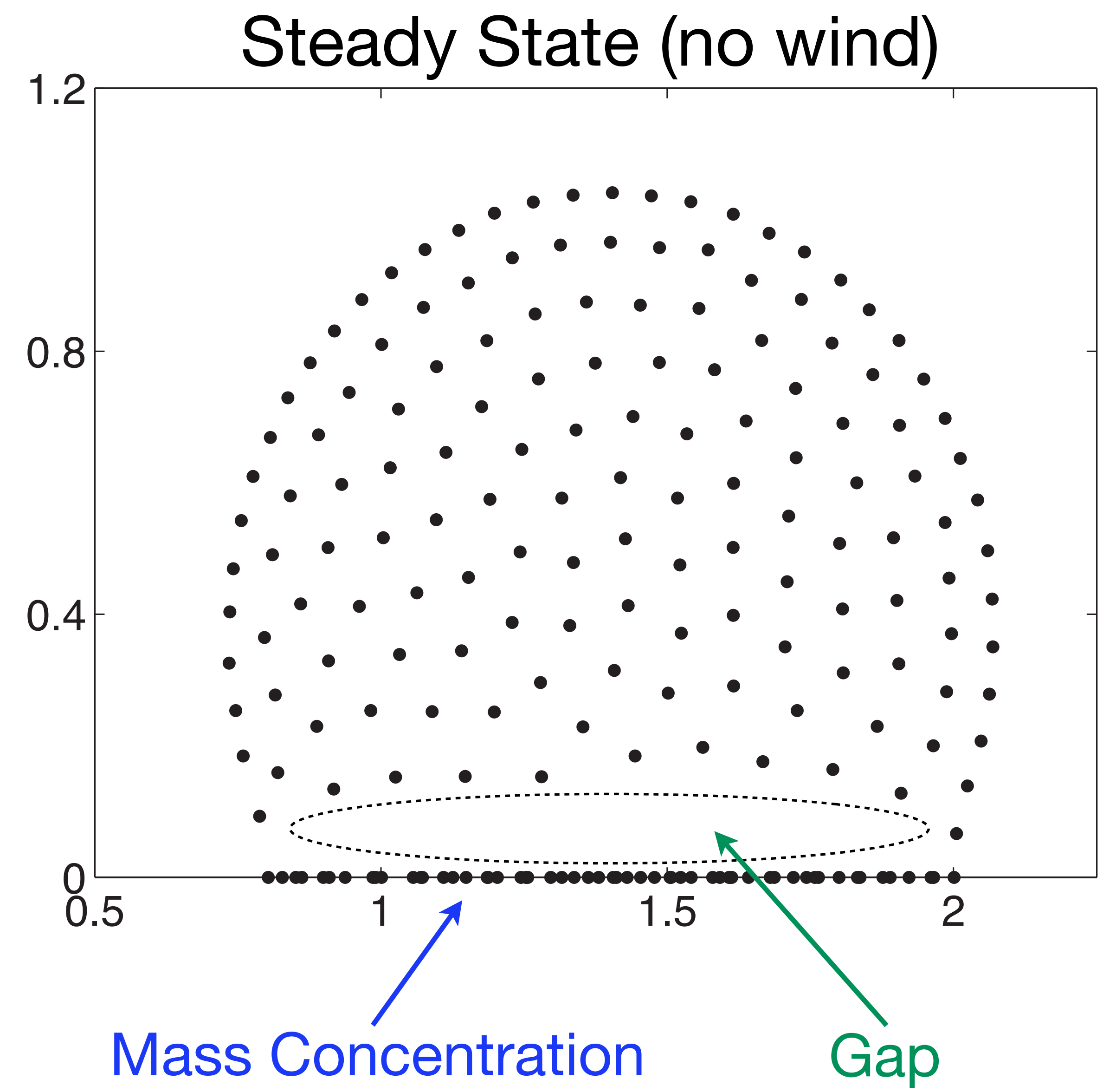




Uvarov, Grasshoppers & Locusts (1977)

Some solutions contain a gap and a mass concentration at the boundary.



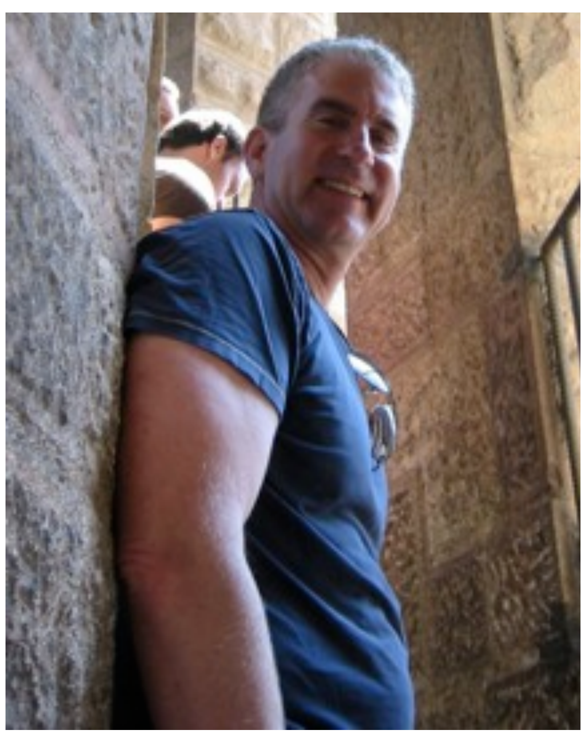


We have calculated some swarm equilibria in 1-d.

SIAM J. APPLIED DYNAMICAL SYSTEMS
Vol. 10, No. 1, pp. 212–250

A Primer of Swarm Equilibria*

Andrew J. Bernoff† and Chad M. Topaz‡



How can we study equilibrium swarms analytically?

Dynamics: $$\frac{dx_i}{dt} = \mathcal{V}_i(x_1, \ldots, x_N)$$ $$0 = \rho_t + (\rho V)_x$$

Velocity: $$\mathcal{V}_i(x_1, \ldots, x_N) = \sum_{\substack{j=1 \\ j \neq i}}^{N} q(x_i - x_j) + f(x_i)$$ $$V = \int_\Omega q(x-y)\rho(y)\,dy + f(x)$$

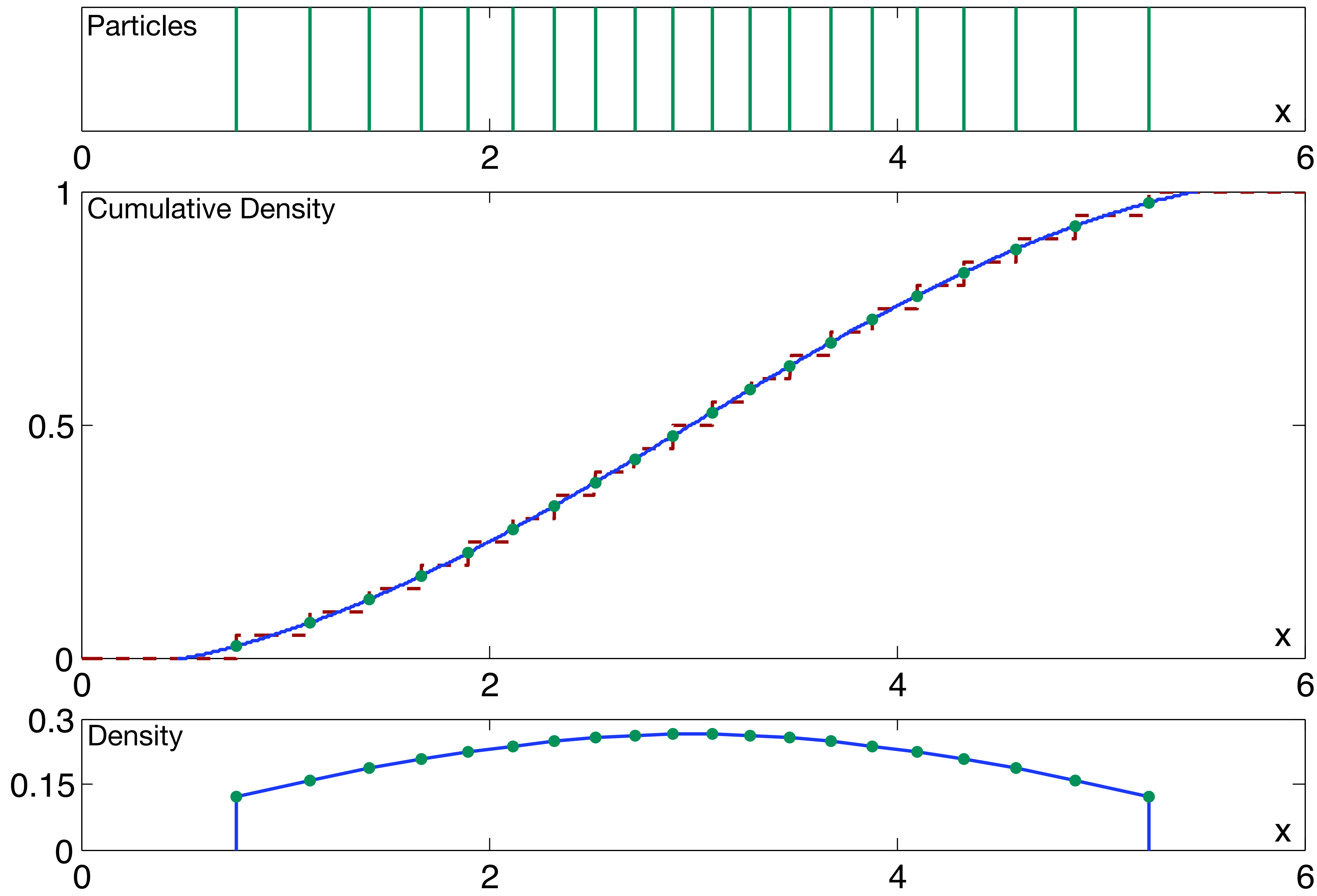
Energy: $$\mathcal{W}(x_1, \ldots, x_N) = \frac{1}{2}\sum_{i=1}^{N}\sum_{\substack{j=1 \\ i \neq j}}^{N} Q(x_i - x_j) + \sum_{k=1}^{N} F(x_k)$$ $$W = \frac{1}{2}\int_\Omega\int_\Omega \rho(x)Q(x-y)\rho(y)\,dx\,dy + \int_\Omega F(x)\rho(x)\,dx$$

ρ = Population Density

Q = Social Interaction Potential

F = External Potential

There is a convenient correspondence between discrete and continuum solutions.



Equilibrium solutions and their stability follow from analysis of the continuum energy.

Energy: $$W[\rho] = \frac{1}{2}\int_\Omega\int_\Omega \rho(x)\rho(y)Q(x-y)\,dx\,dy + \int_\Omega F(x)\rho(x)\,dx$$

Endogenous

Exogenous

Equilibrium:
(First Variation)

$$\int_{\Omega_{\bar\rho}} Q(x-y)\bar\rho(y)\,dy + F(x) = \lambda \quad \text{for } x \in \Omega_{\bar\rho}$$

Support

Constant energy
felt by test mass

Local Minimizer: $$\Lambda(x) \equiv \int_{\Omega_{\bar\rho}} Q(x-y)\bar\rho(y)\,dy + F(x) \geq \lambda \quad \text{for } x \in {\Omega_{\bar\rho}}^c$$

Global Minimizer:
(Second Variation)

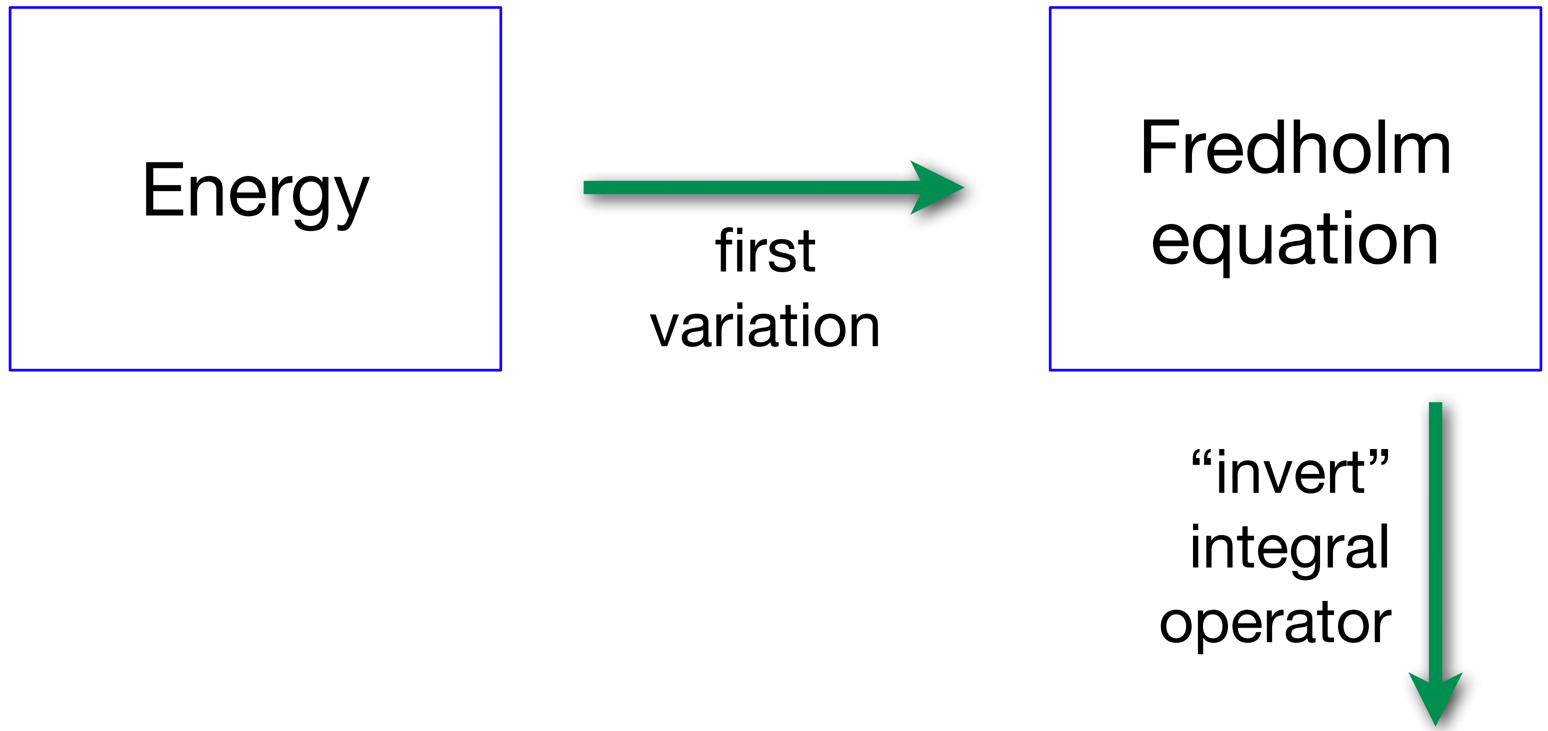
Hard(er)

We can find analytical solutions to the continuum problem.

$$\boxed{\text{Energy}} \xrightarrow[\text{variation}]{\text{first}} \boxed{\text{Fredholm equation}}$$

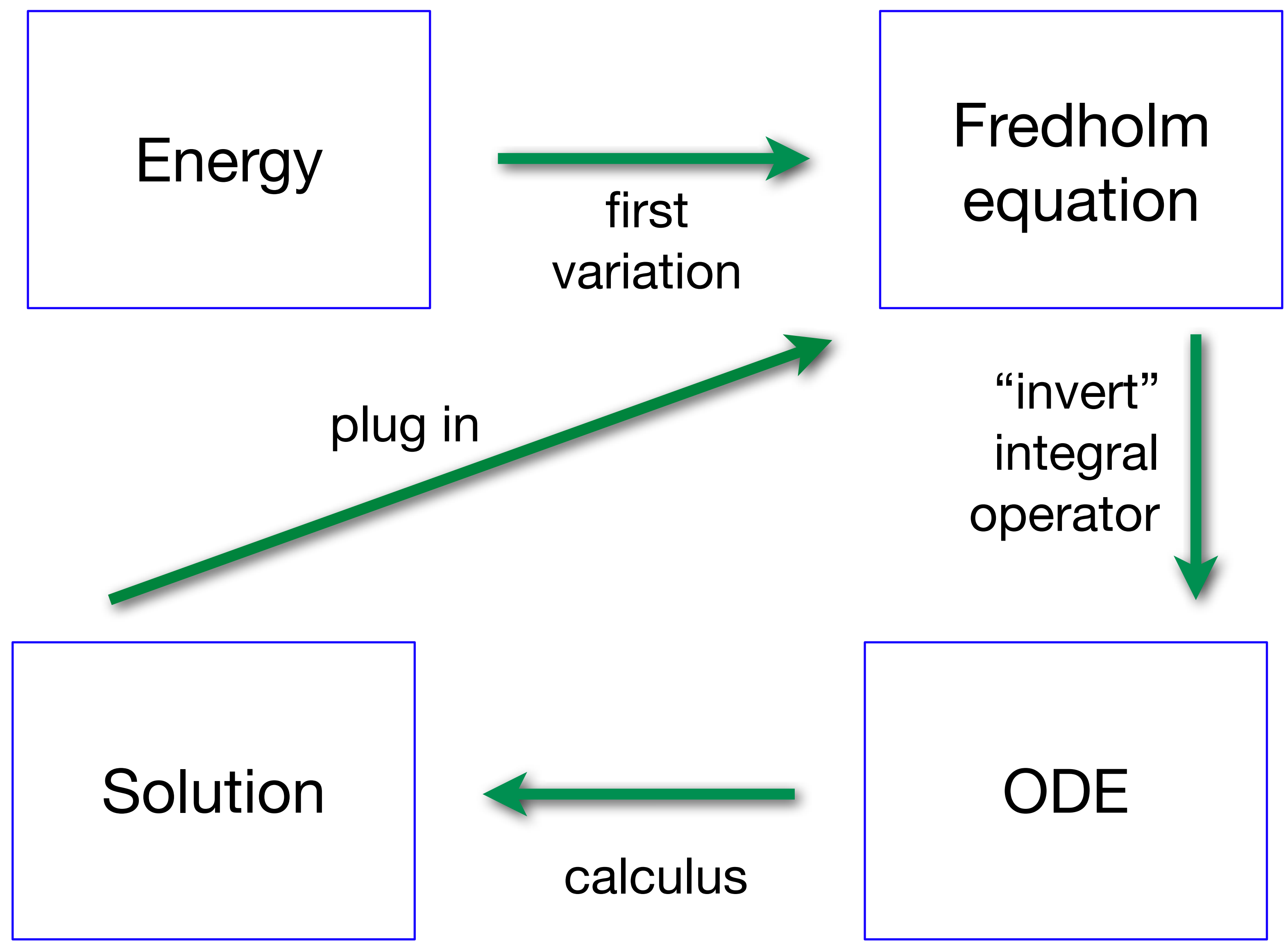
$$\int_{\alpha}^{\beta} Q(x-y)\rho(y)\,dy = \lambda - F(x), \qquad \int_{\alpha}^{\beta} \rho(x)\,dx = M$$

We can find analytical solutions to the continuum problem.



$$Q(x) = -GL\mathrm{e}^{-|x|/L} + \mathrm{e}^{-|x|} \to (\partial_{xx} - 1)(L^2\partial_{xx} - 1)$$

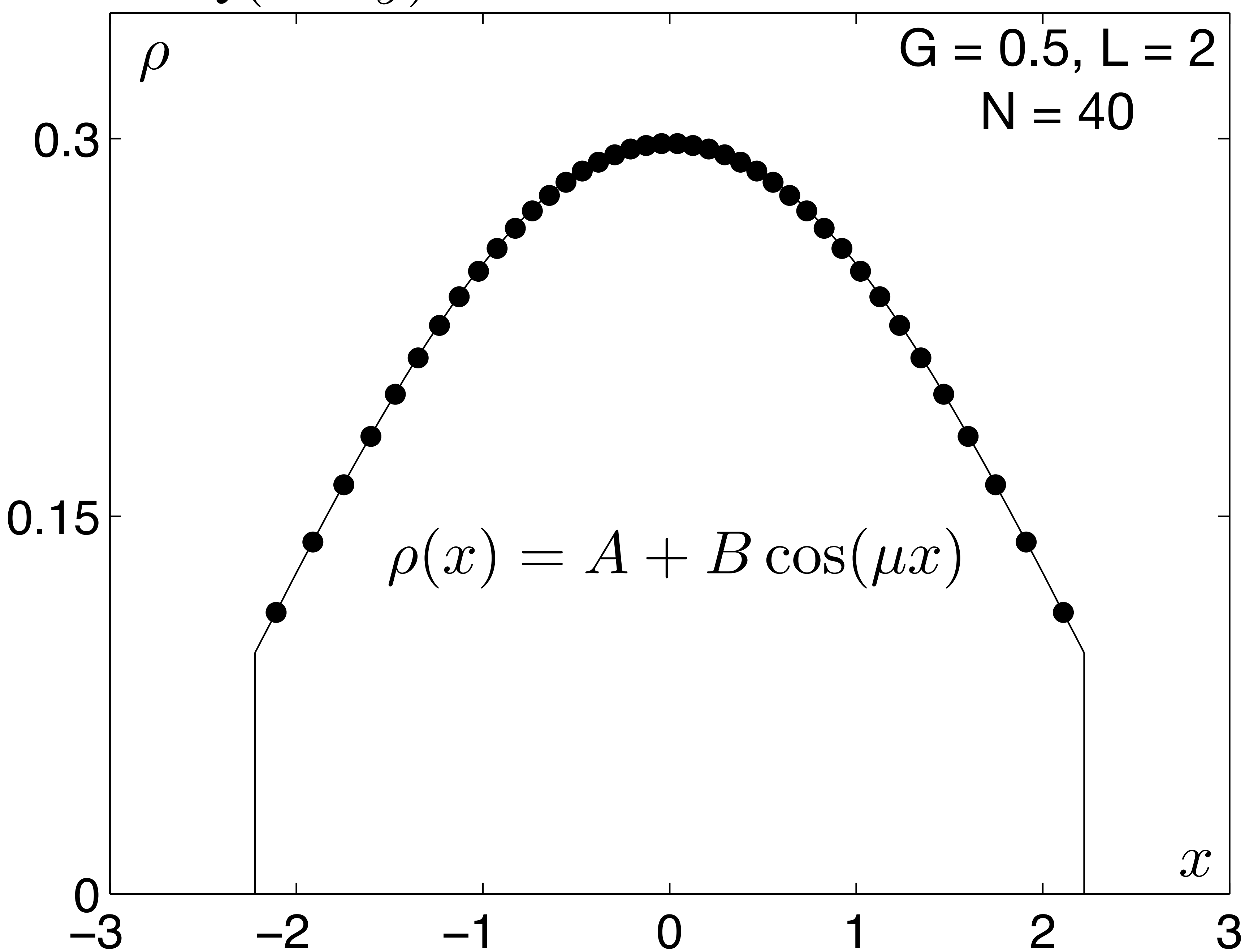
We can find analytical solutions to the continuum problem.



$$2L^2(G-1)\rho_{xx} - 2(GL^2-1)\rho = (\partial_{xx}-1)(L^2\partial_{xx}-1)[\lambda - F(x)]$$

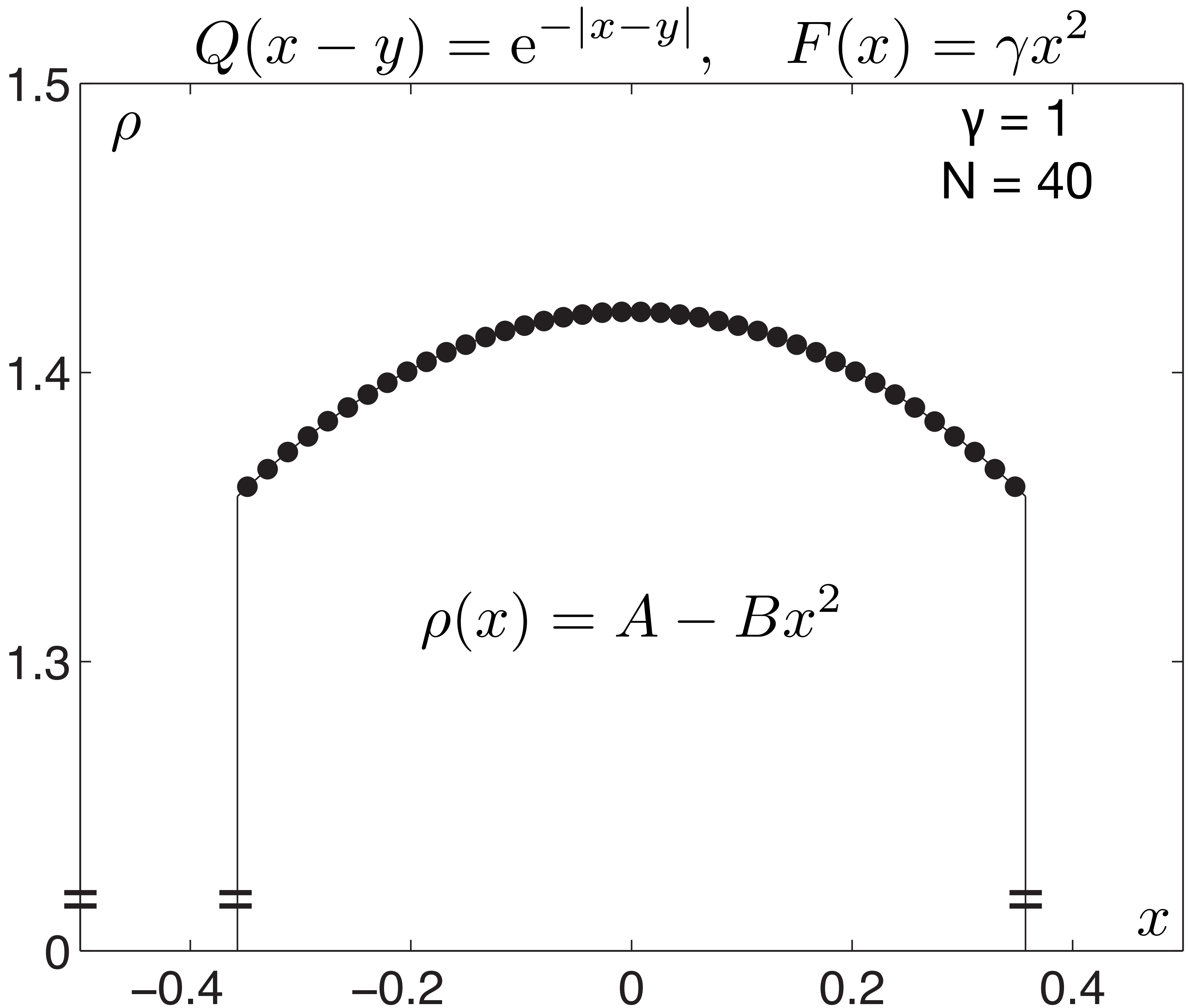
Attractive-repulsive interactions with no external force can yield compactly supported solutions.

$$Q(x-y) = -GL\mathrm{e}^{-|x-y|/L} + \mathrm{e}^{-|x-y|}$$



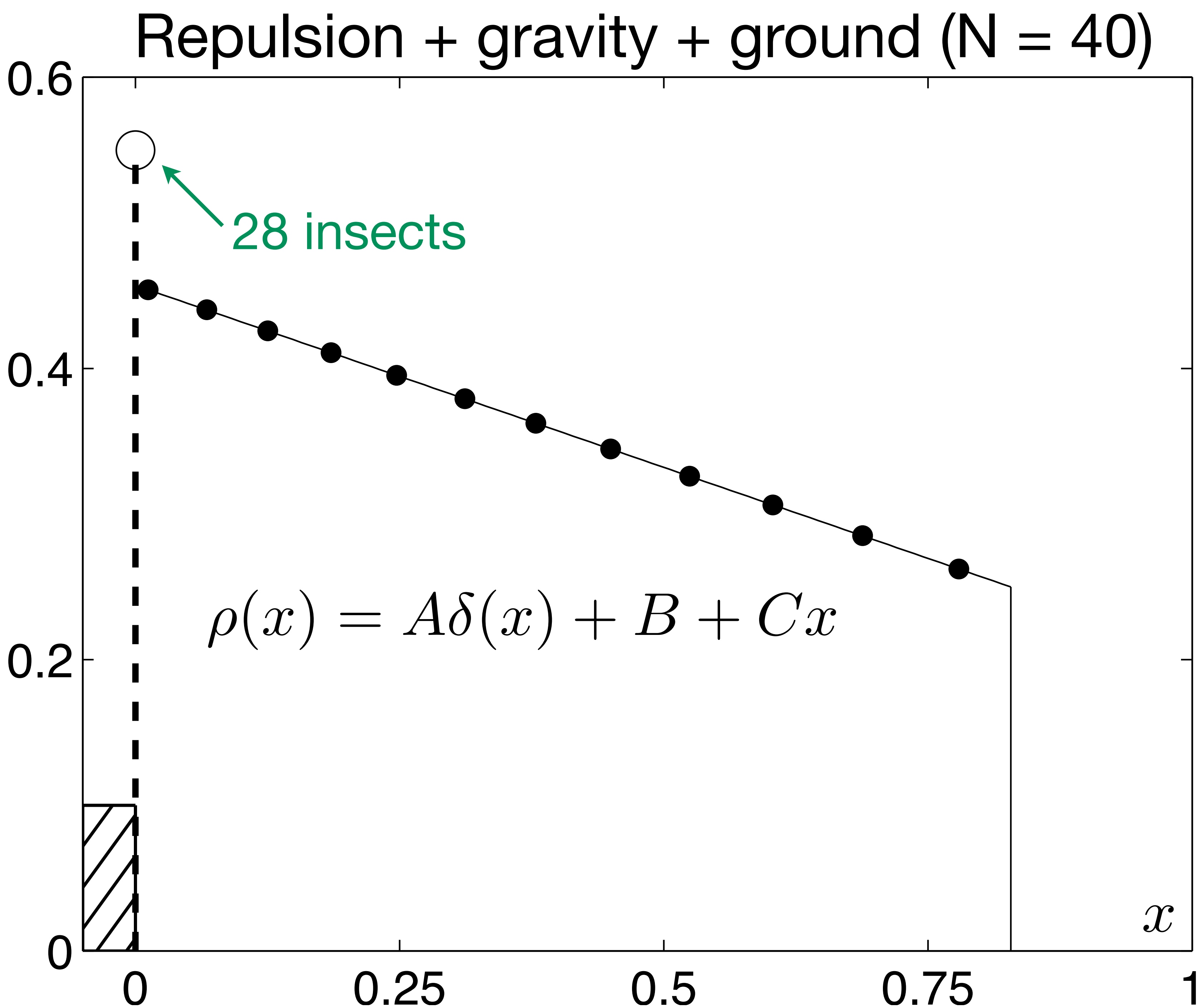
(Local Minimizer)

Repulsive interactions with a quadratic potential also yield compactly supported groups.



(Global Minimizer)

Repulsion in the presence of gravity and a boundary yield a classical component and a mass concentration.



No Gap
(Global Minimizer)

The dimensionality of the repulsive potential matters.

Quasi 2-d potential:

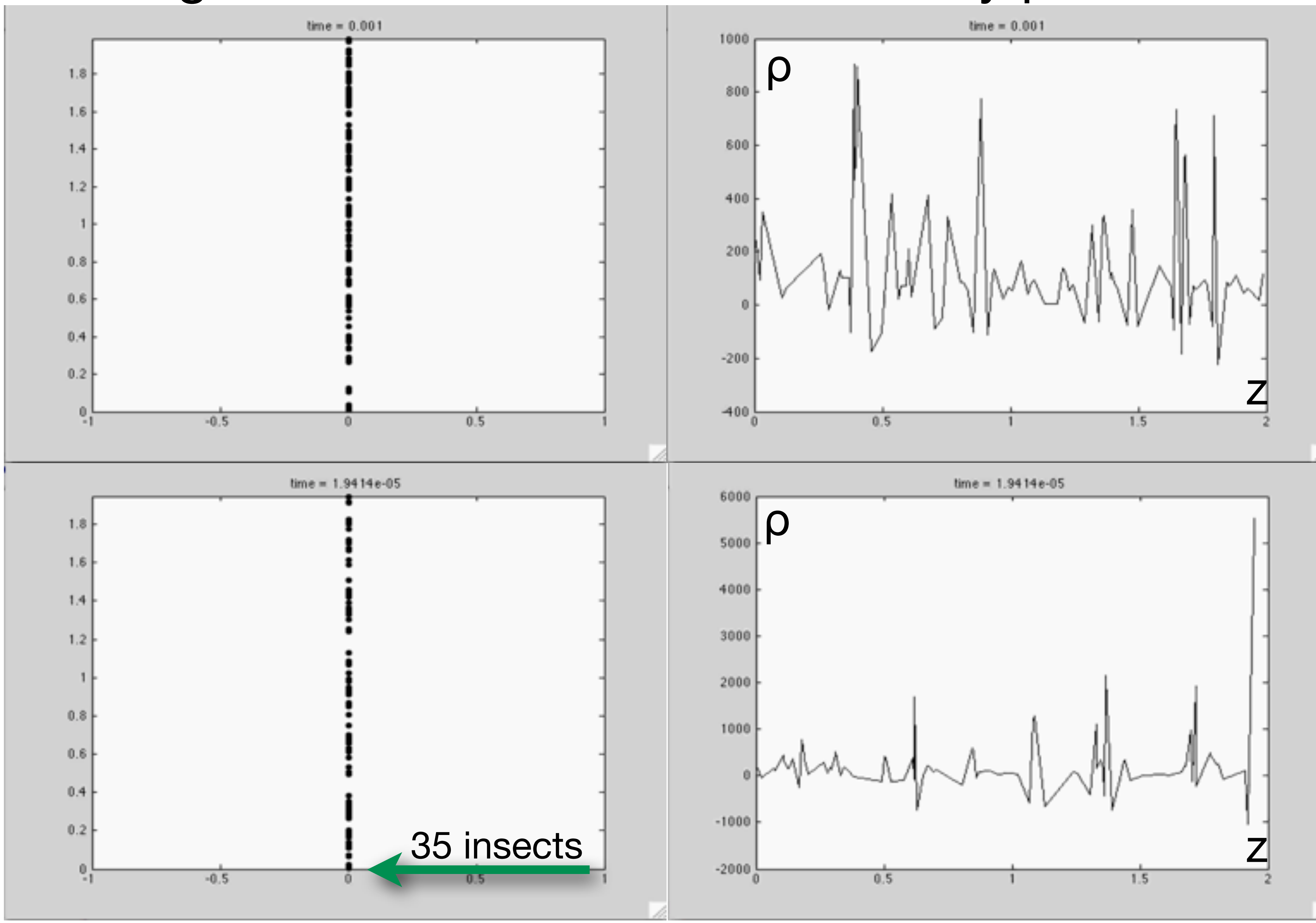
$$V(x) = \int_{-\infty}^{\infty} \mathrm{e}^{-\sqrt{x^2+y^2}}\, dy$$

Quasi-2d potential yields a mass concentration, a classical swarm, and a gap separating the components.

Organism column | Density profile

1-D

Quasi 2-D



In conclusion...

$$\rho_t + \nabla \cdot (\mathbf{v}\rho) = 0, \qquad \mathbf{v} = -\nabla Q * \rho - \nabla F$$

- For F = 0 (endogenous forces only), asymptotic dynamics depend on -∇Q via first moment and jump size at origin
- For F ≠ 0 (endogenous and exogenous forces), the model agrees with (even small N) discrete systems, and has a variational formulation from which we find exact solutions, typically with features such as jump discontinuities and concentrations.

Bonus Track

Meet two locusts.

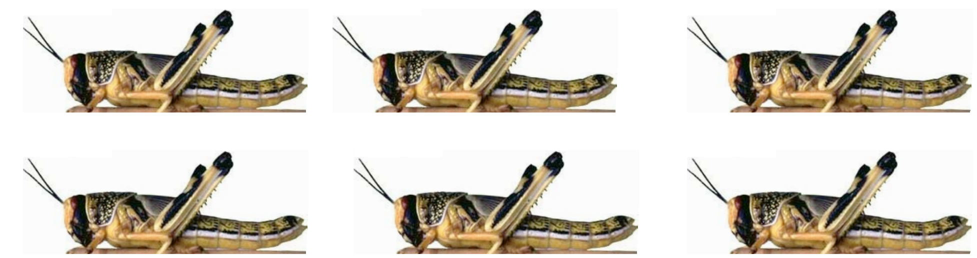
Heredity
Maturity
(Environment)

Color
Size
Body composition
Fecundity
Respiration

Locust A

Locust B

These are two “phases” of the same locust species.

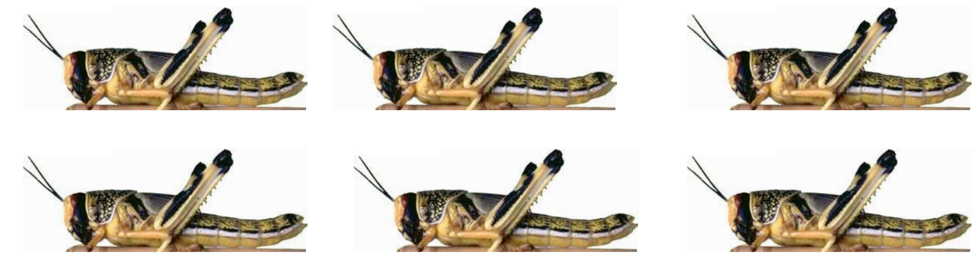


Behavior

Solitary

Gregarious

These are two “phases” of the same locust species.



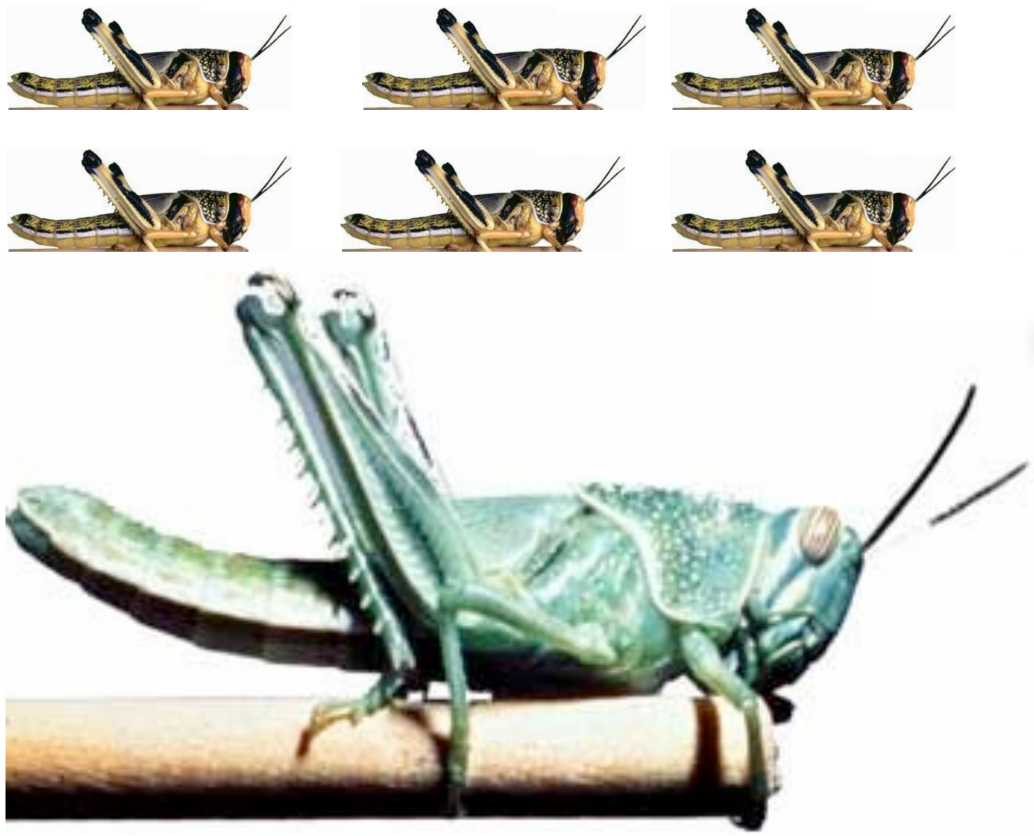
Behavior

Solitary

4 hours

Gregarious

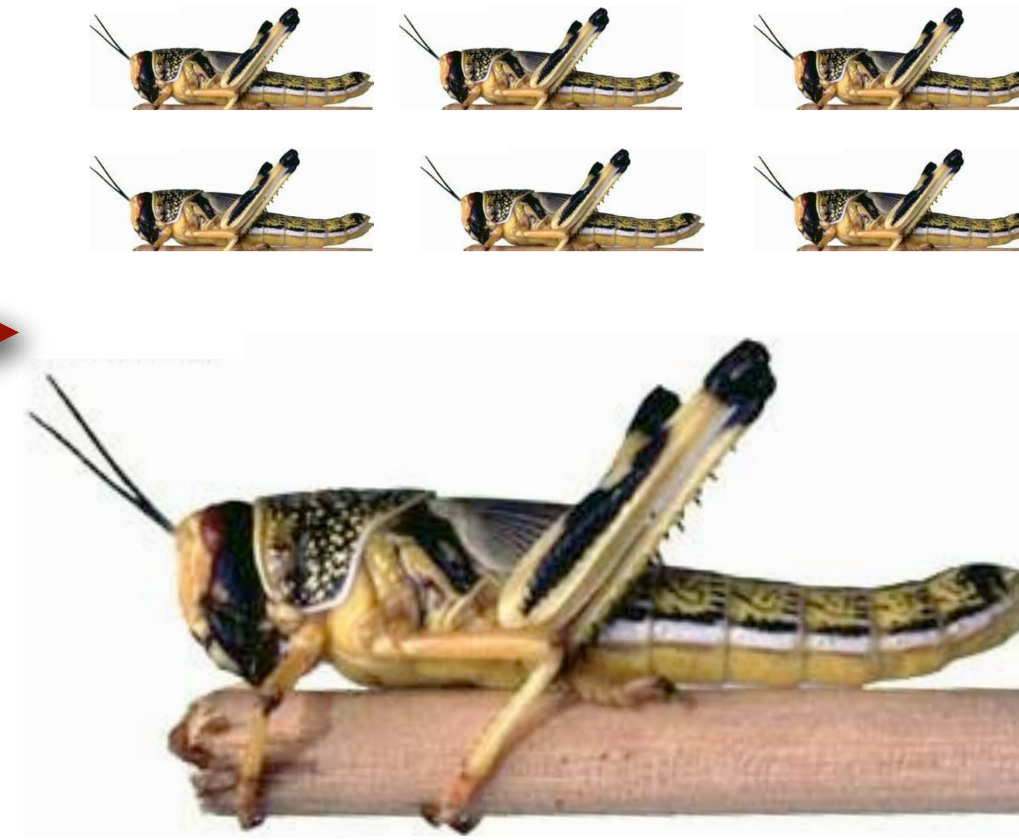
These are two “phases” of the same locust species.



Solitary

4 hours

Behavior

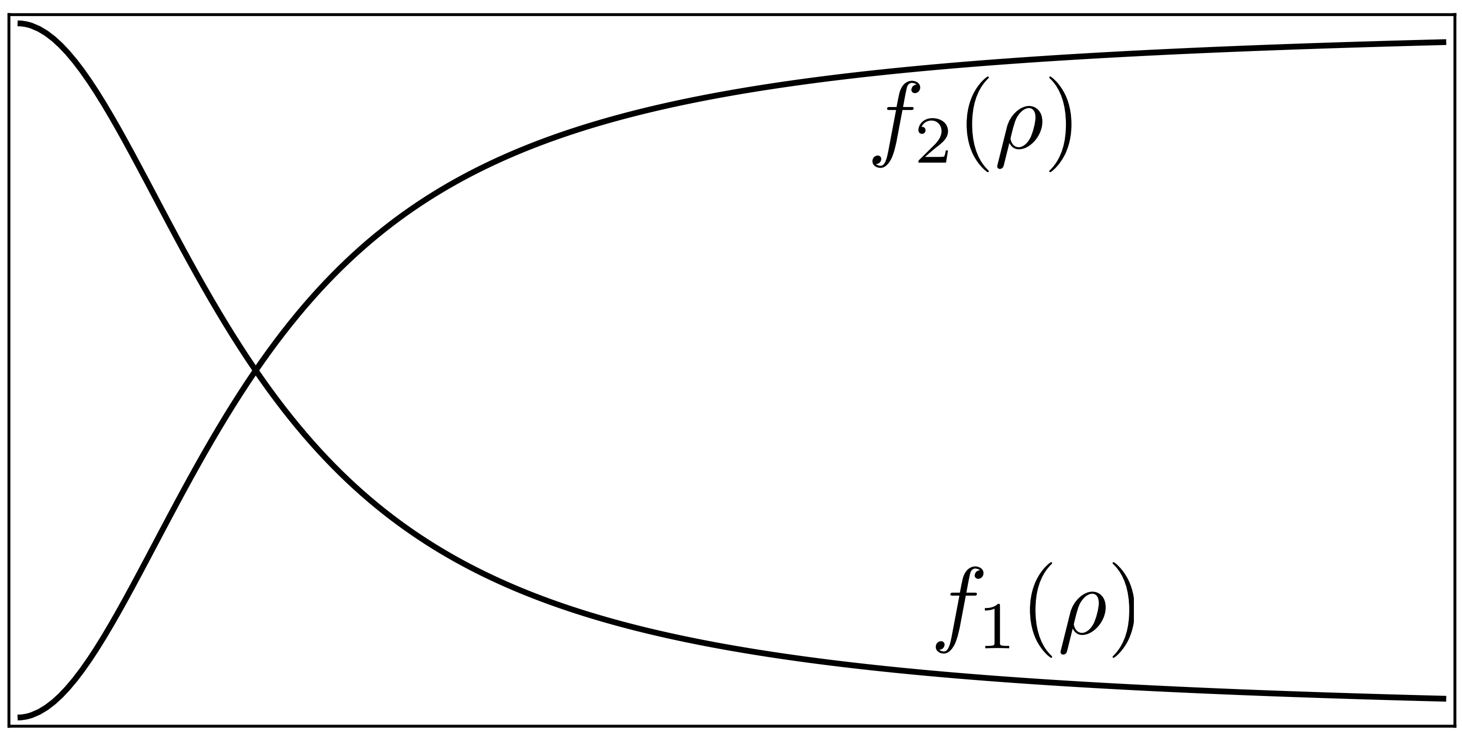


Gregarious

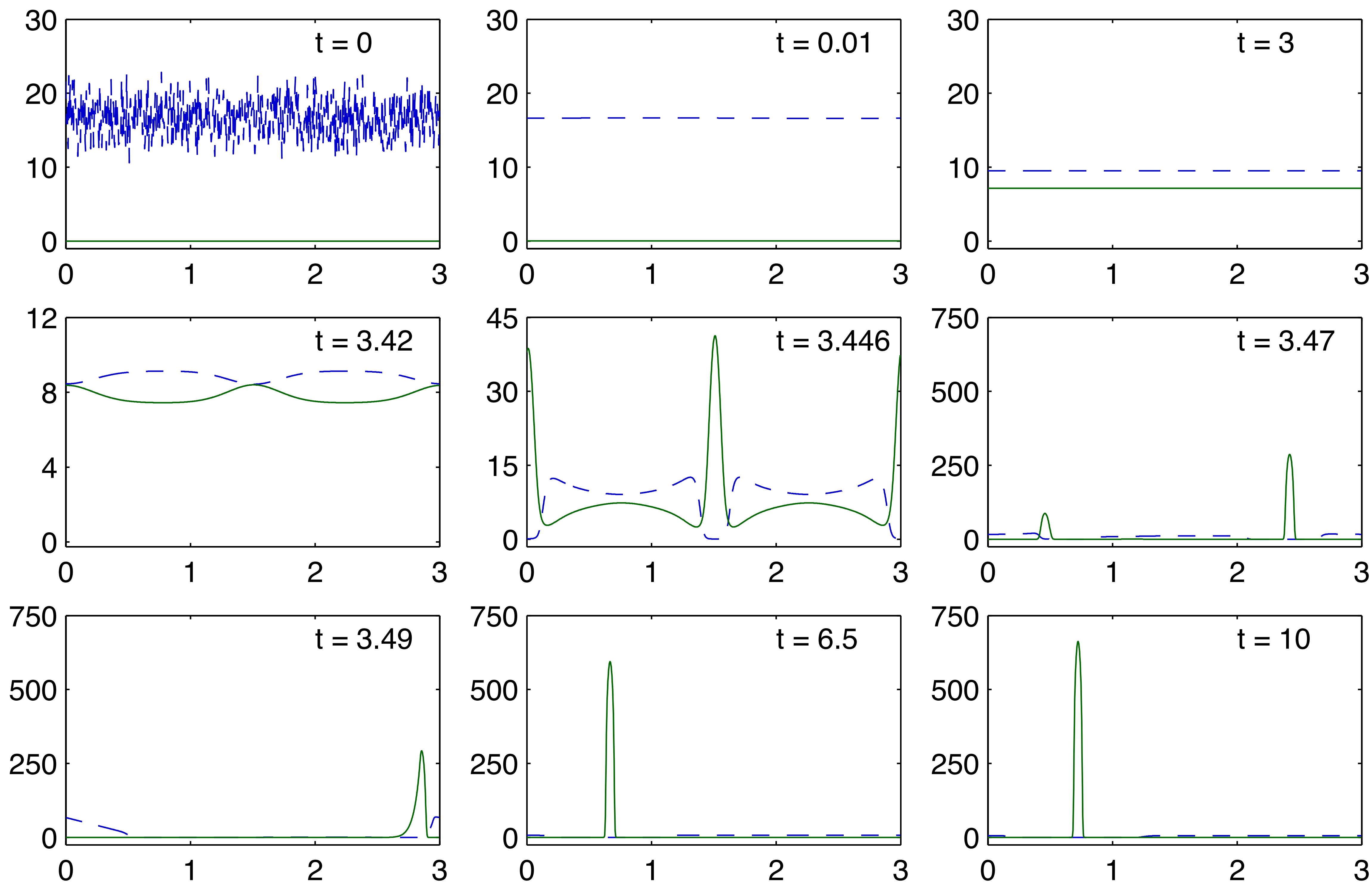
We model locust phase change with two-phase aggregation equations including reaction terms.

Topaz, D'Orsogna, Edelstein-Keshet, Bernoff (2012, preprint)

$$\dot{s} + \nabla \cdot (\mathbf{v}_s s) = -f_2(\rho)s + f_1(\rho)g$$
$$\dot{g} + \nabla \cdot (\mathbf{v}_g g) = \quad f_2(\rho)s - f_1(\rho)g$$
$$\mathbf{v}_s = -\nabla(Q_s * \rho), \quad \mathbf{v}_g = -\nabla(Q_g * \rho)$$



Above a critical total density, aggregations form.



Spatially-homogeneous and spatially-segregated model reductions approximate the bulk dynamics.

$$
\begin{aligned}
\dot{s} + \nabla \cdot (\vec{v}_s s) &= -f_2(\rho)s + f_1(\rho)g \\
\dot{g} + \nabla \cdot (\vec{v}_g g) &= \quad f_2(\rho)s - f_1(\rho)g
\end{aligned}
$$

Spatially-homogeneous and spatially-segregated model reductions approximate the bulk dynamics.

$$\begin{aligned}\dot{s} + \nabla \cdot (\vec{v}_s s) &= -f_2(\rho)s + f_1(\rho)g \\ \dot{g} + \nabla \cdot (\vec{v}_g g) &= \quad f_2(\rho)s - f_1(\rho)g\end{aligned}$$

$\downarrow$ spatially homogeneous

$$\begin{aligned}\dot{s} + \nabla \cdot (\vec{v}_s s) &= -f_2(\rho)s + f_1(\rho)g \\ \dot{g} + \nabla \cdot (\vec{v}_g g) &= \quad f_2(\rho)s - f_1(\rho)g\end{aligned}$$

Spatially-homogeneous and spatially-segregated model reductions approximate the bulk dynamics.

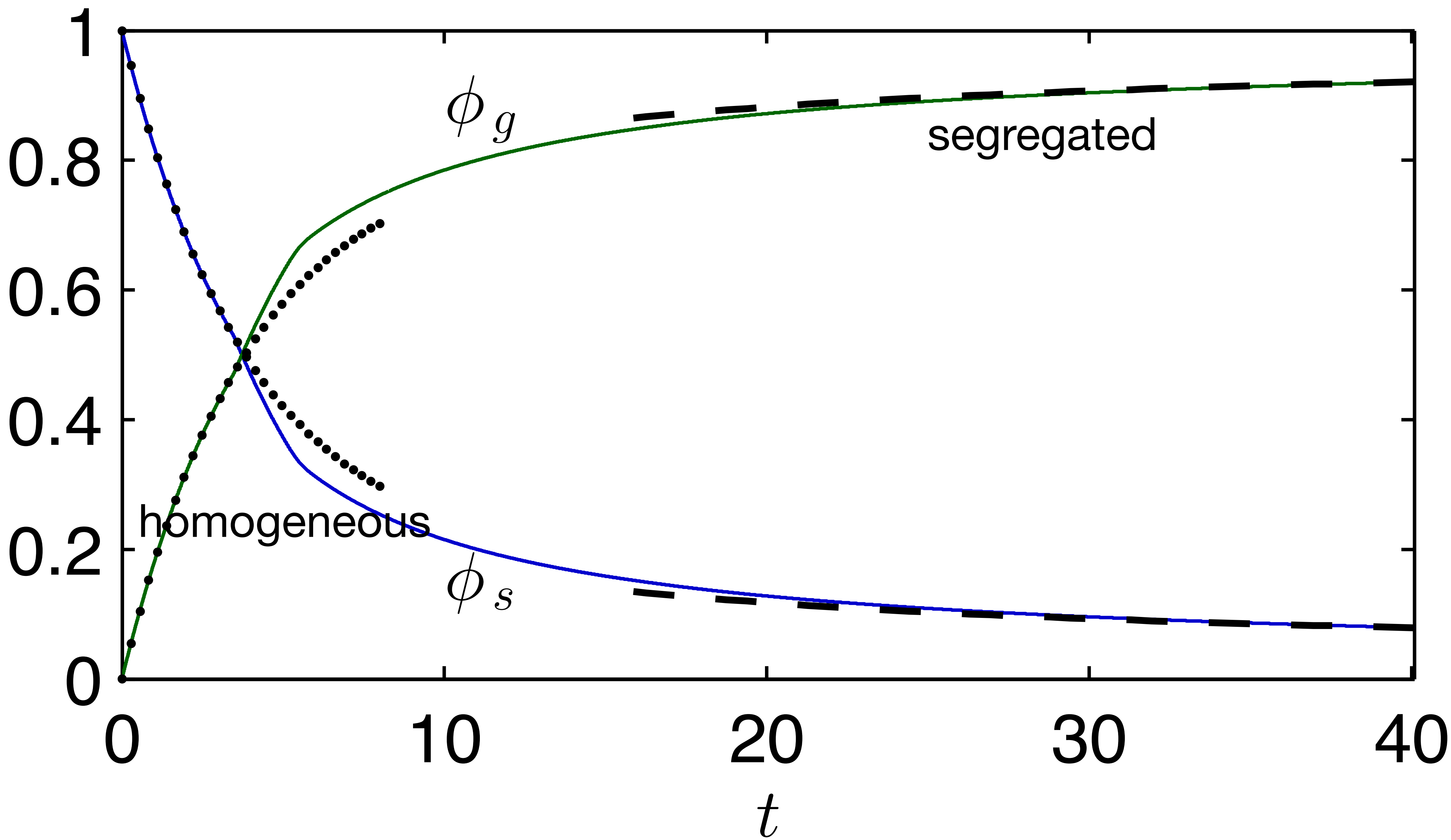
$$\begin{aligned} \dot{s} + \nabla \cdot (\vec{v}_s s) &= -f_2(\rho)s + f_1(\rho)g \\ \dot{g} + \nabla \cdot (\vec{v}_g g) &= \quad f_2(\rho)s - f_1(\rho)g \end{aligned}$$

$$\Big\downarrow \text{ spatially segregated}$$

$$\dot{\phi}_s = -\dot{\phi}_g = -\frac{c_1\phi_s^3}{1+c_2\phi_s^2} + \frac{c_3\phi_g}{1+c_4\phi_g^2}$$

soliatry/gregarious fraction

Spatially-homogeneous and spatially-segregated model reductions approximate the bulk dynamics.



Some open analytical problems

For the dynamic problem:

- Rigorous proof of convergence to the Barenblatt solution?

For swarm equilibria:

- What is a global minimizer for Morse (and other) potentials?
- When are global minimizers global attractors?
- Rates of convergence to attractors?

For the two-phase (locust) problem:

- Proof of (and convergence to) spatially segregated state?

The End