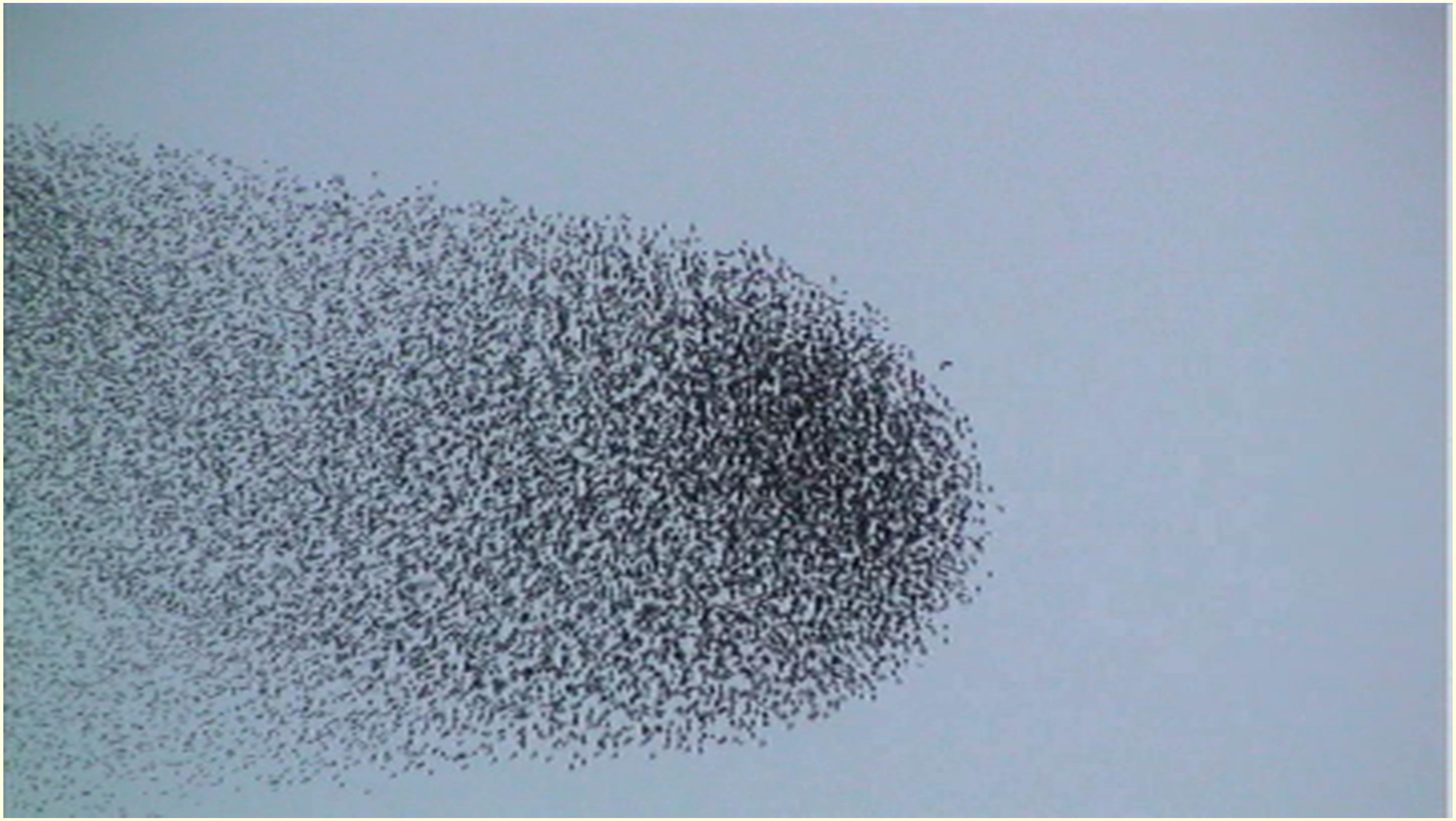
Collective motion in animal populations

Simon Levin, 2010
Trieste

Iain Couzin

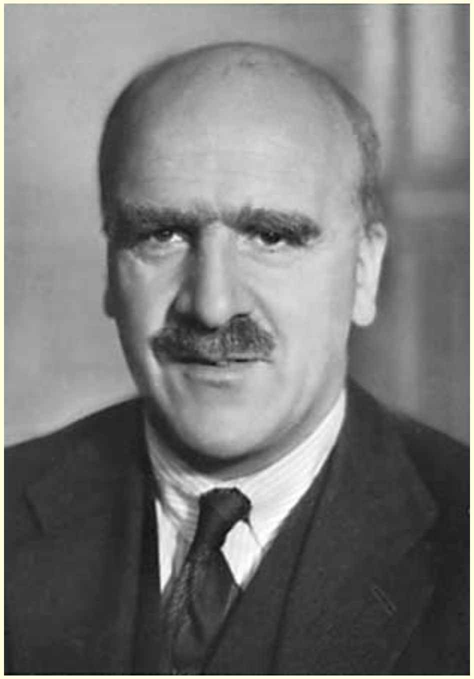
The main topic of my lecture is collective motion



But for context, it's important to start first with uncorrelated movement

Claudio Carere

There is a classic literature concerned with the modeling of animal movements

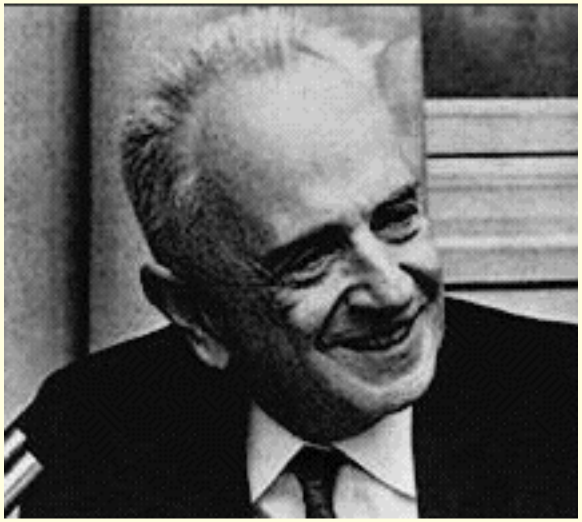


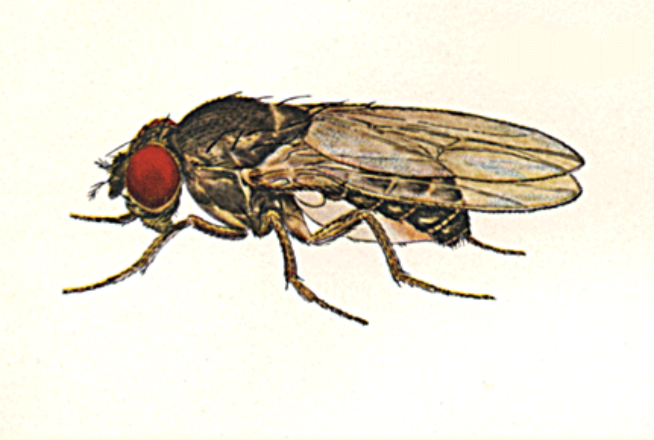
Haldane

Fisher

Wright

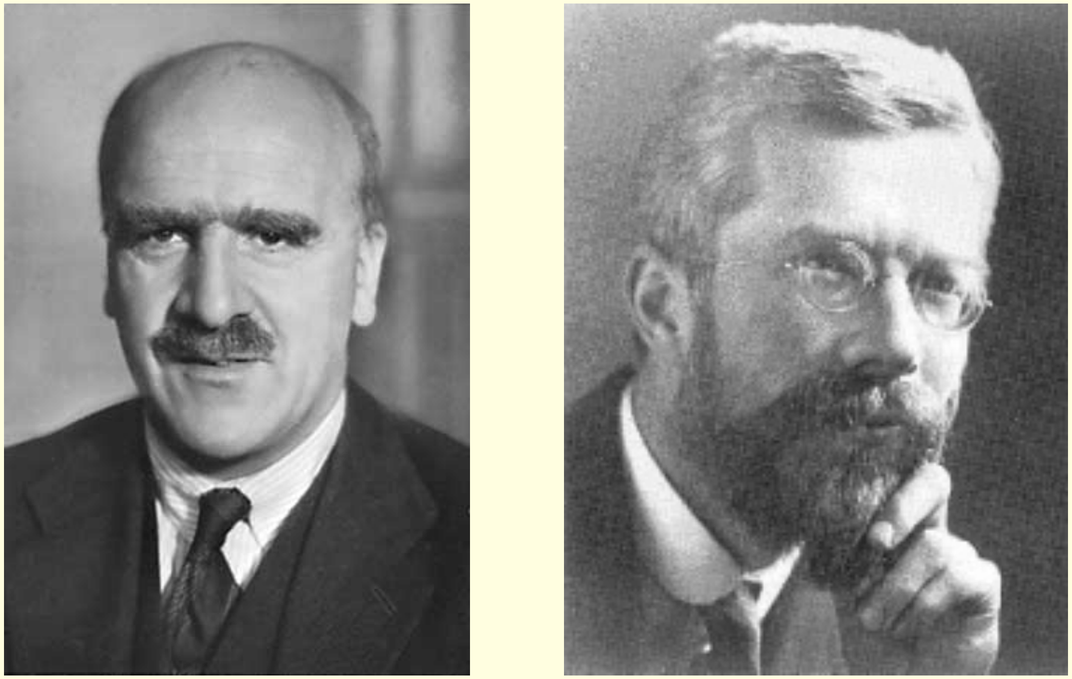
Dobzhansky and Wright dealt with the dispersal of D.pseudoobscura





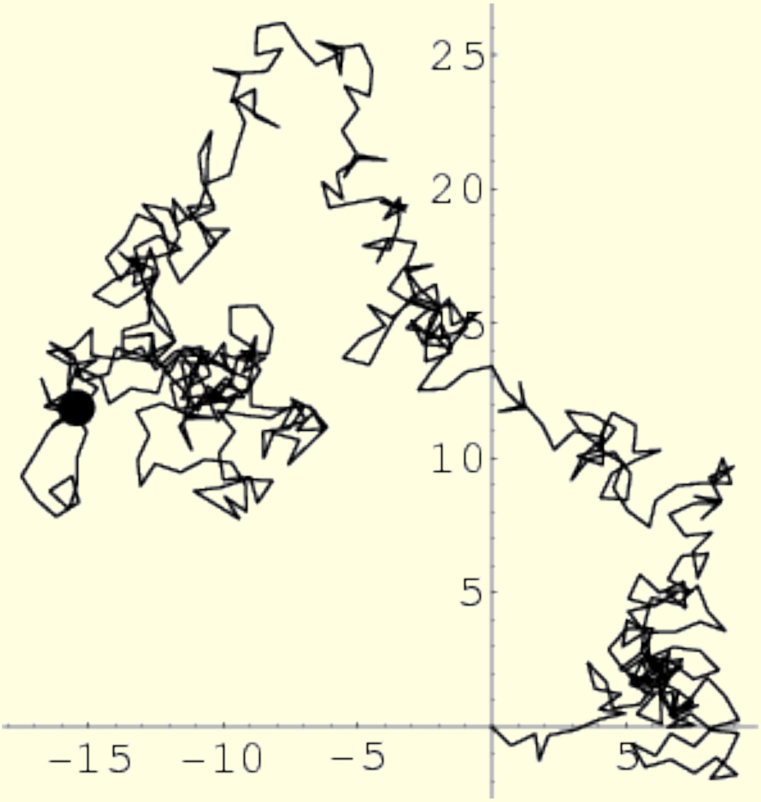
insects.eugenes.org

Haldane and Fisher



were concerned with advancing fronts and clines,

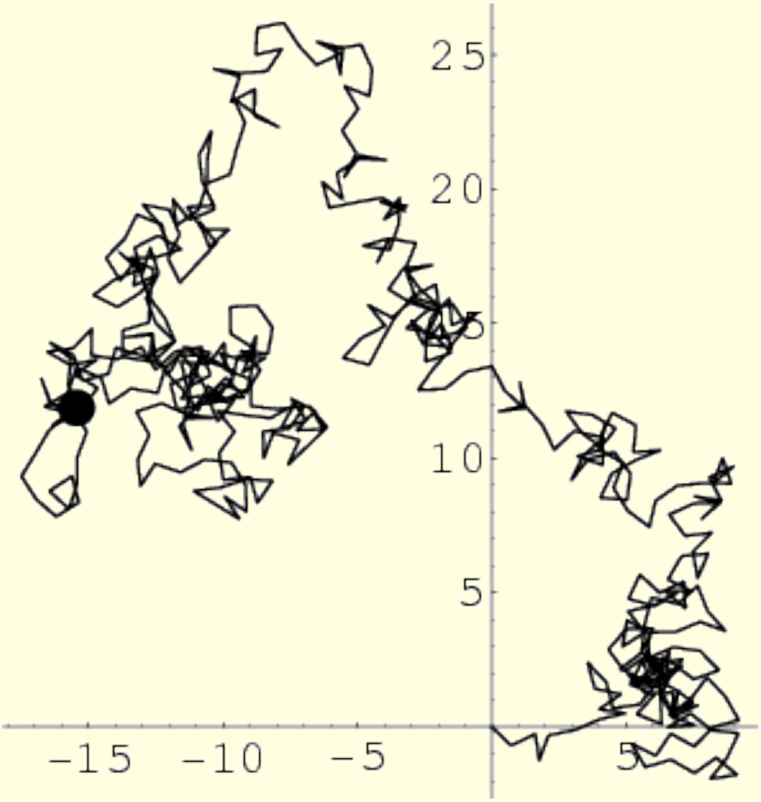
The null movement hypothesis: a random walk



$$\partial n / \partial t = D(\partial^2 n / \partial x^2 + \partial^2 n / \partial y^2)$$

mathworld.wolfram.com

The null movement hypothesis: a random walk plus growth



$$\partial n / \partial t = D(\partial^2 n / \partial x^2 + \partial^2 n / \partial y^2) + f(n)$$

mathworld.wolfram.com

Rates of advance
Fisher, Haldane, KPP

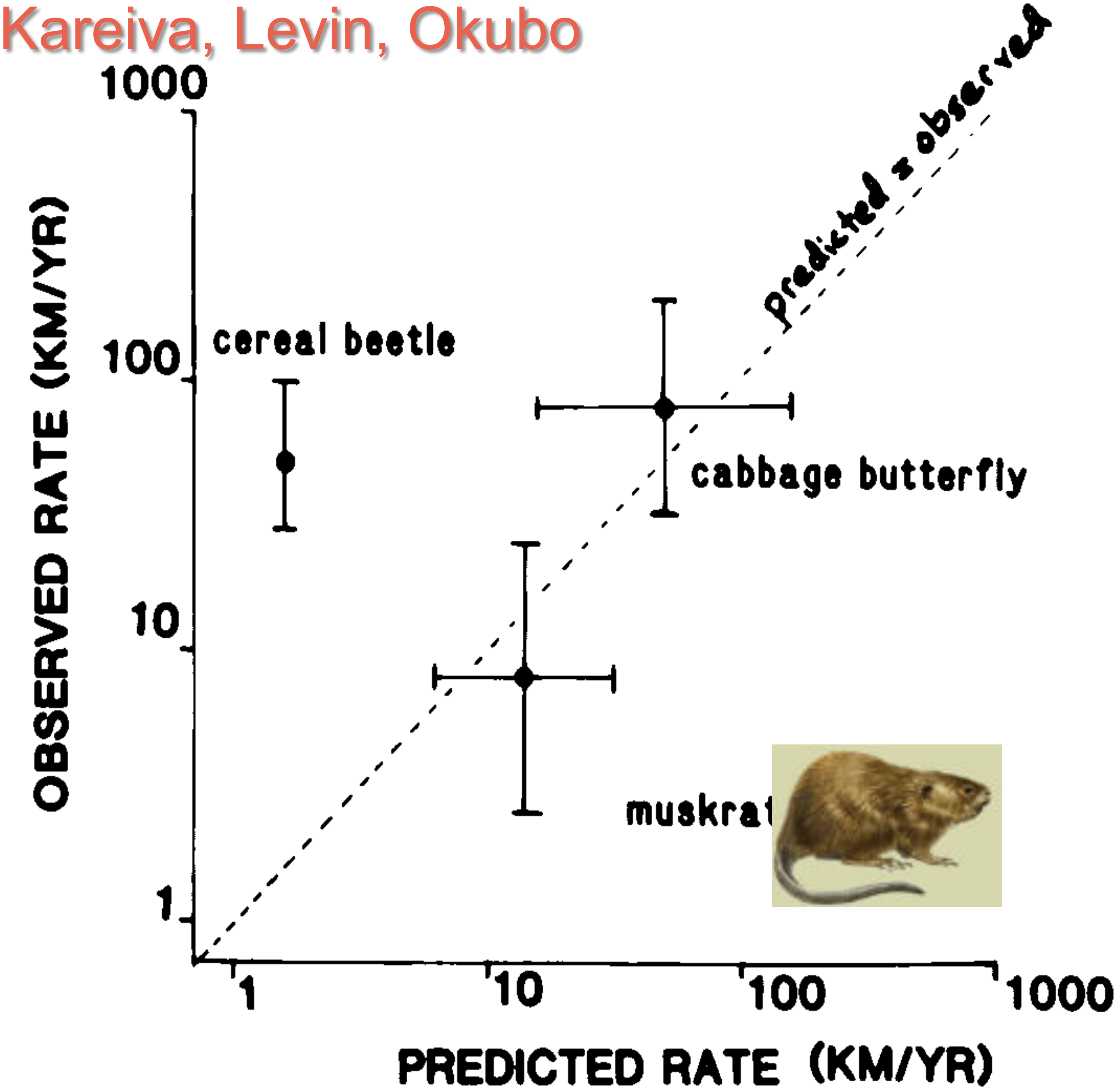
$$\partial n / \partial t = f(n) + D \partial^2 n / \partial x^2$$

Asymptotic Rate: $2\sqrt{rD}$

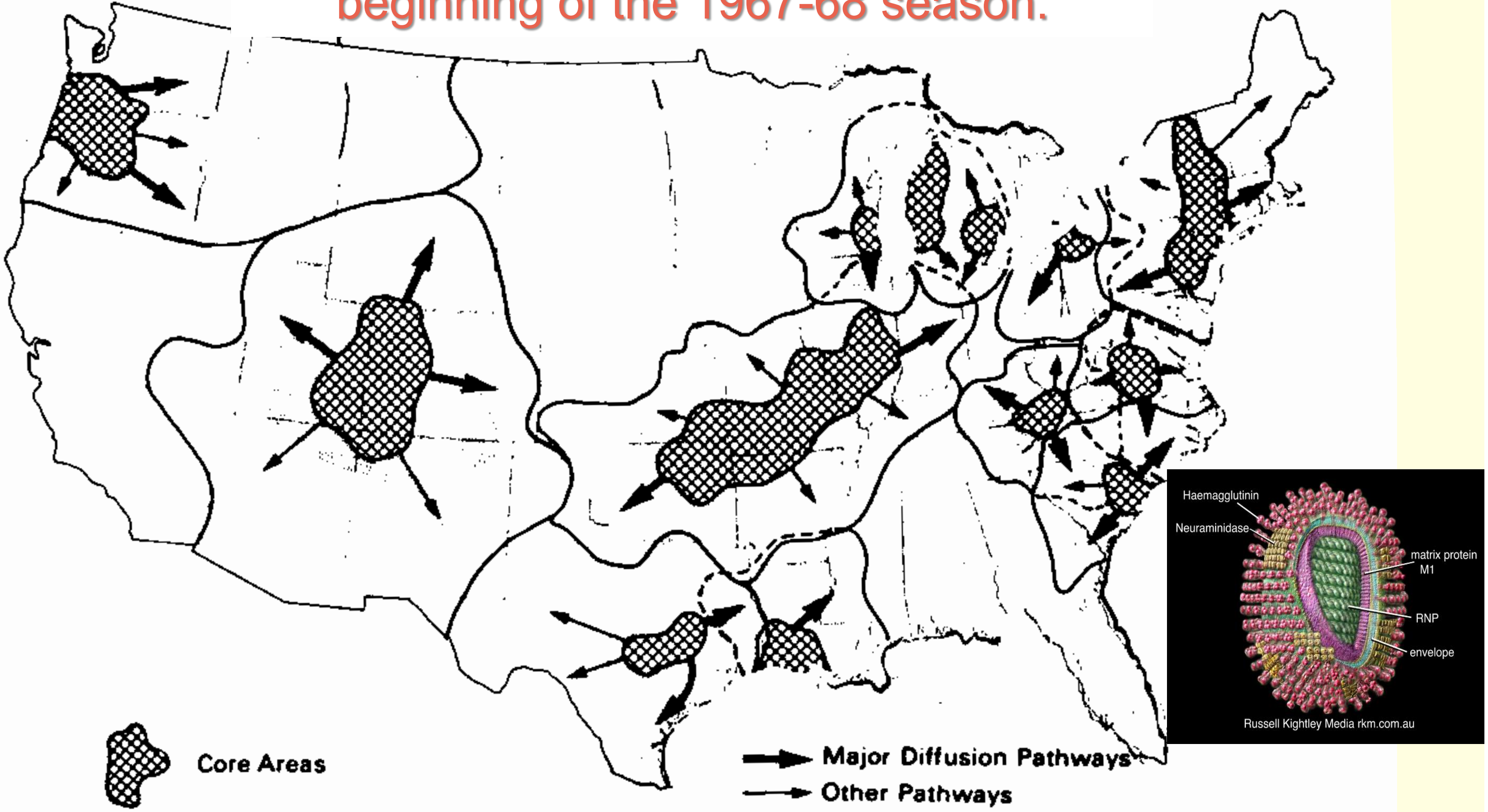
$r = f'(0)$ (intrinsic rate of natural increase)

D (diffusion coefficient)

Andow, Kareiva, Levin, Okubo



Core areas and diffusion pathways for primary outbreaks of influenza during the beginning of the 1967-68 season.



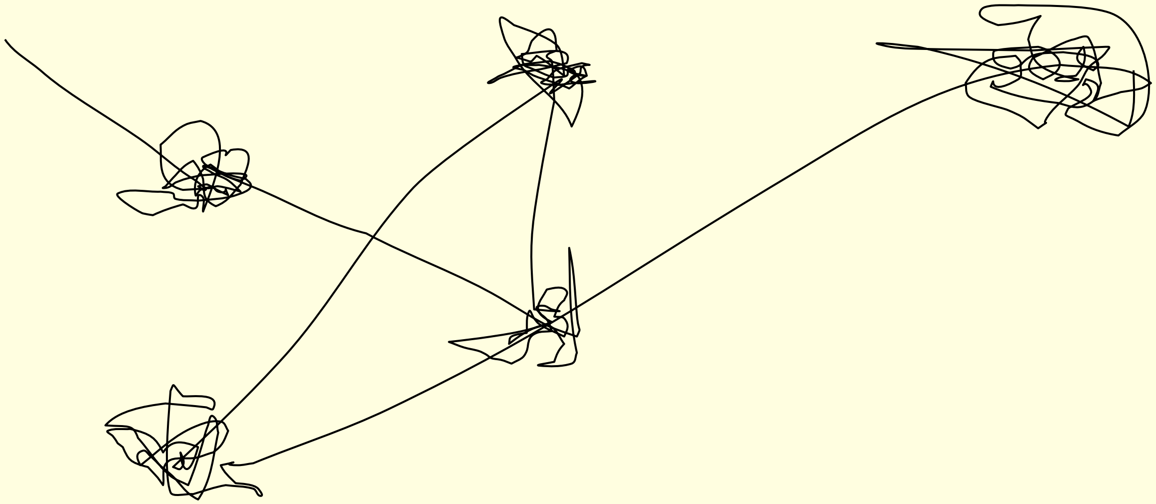
From: Influenza Models (P. Selby, ed)., MTP Press.

Other approaches to movement

- Long-distance spatial contact process
  - Integral equation
    - Skellam
    - Mollison

Other approaches to movement

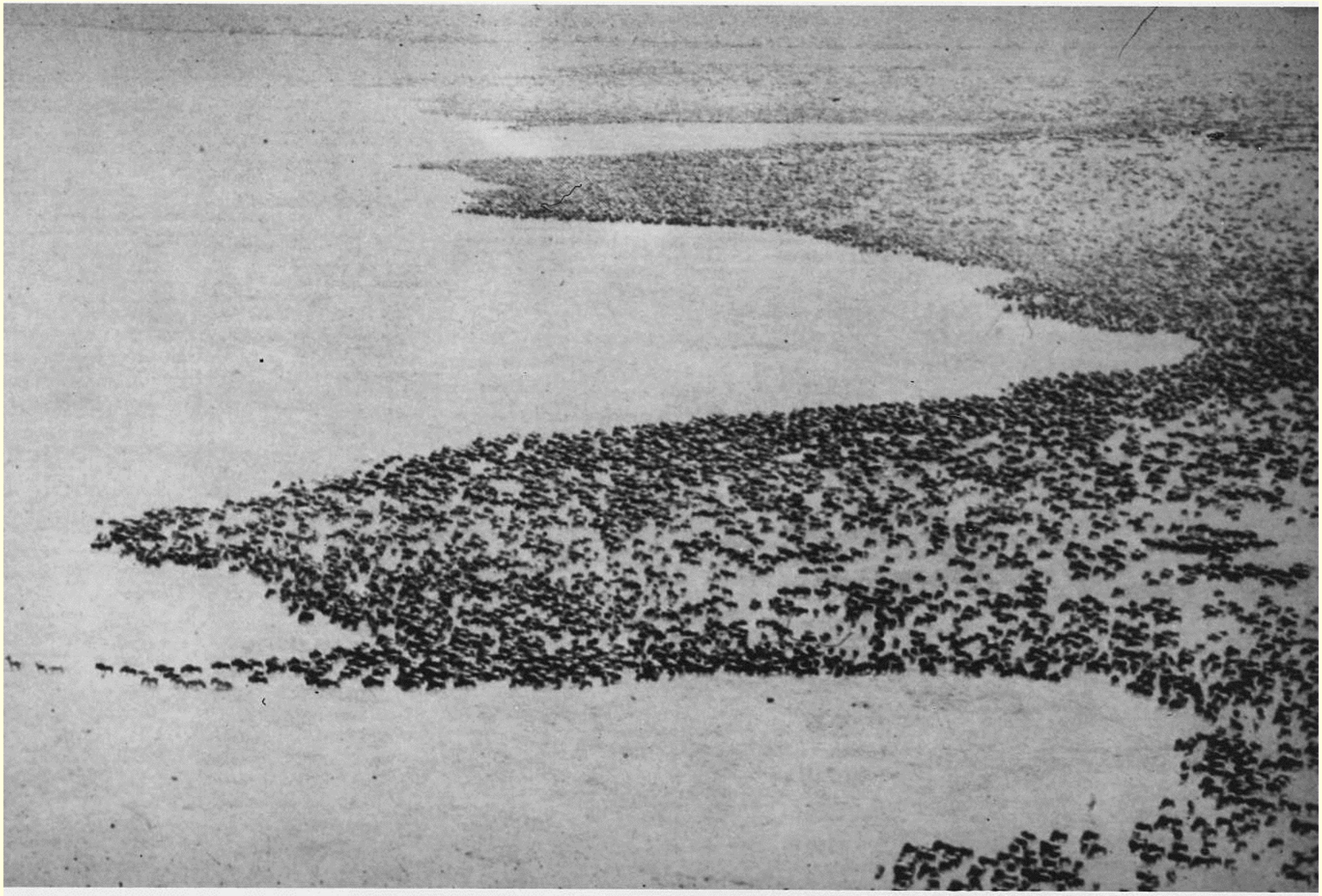
- Long-distance spatial contact process
- Anomalous diffusion
  - Variance increases as a power of time



Rates of advance are just one application of such models:

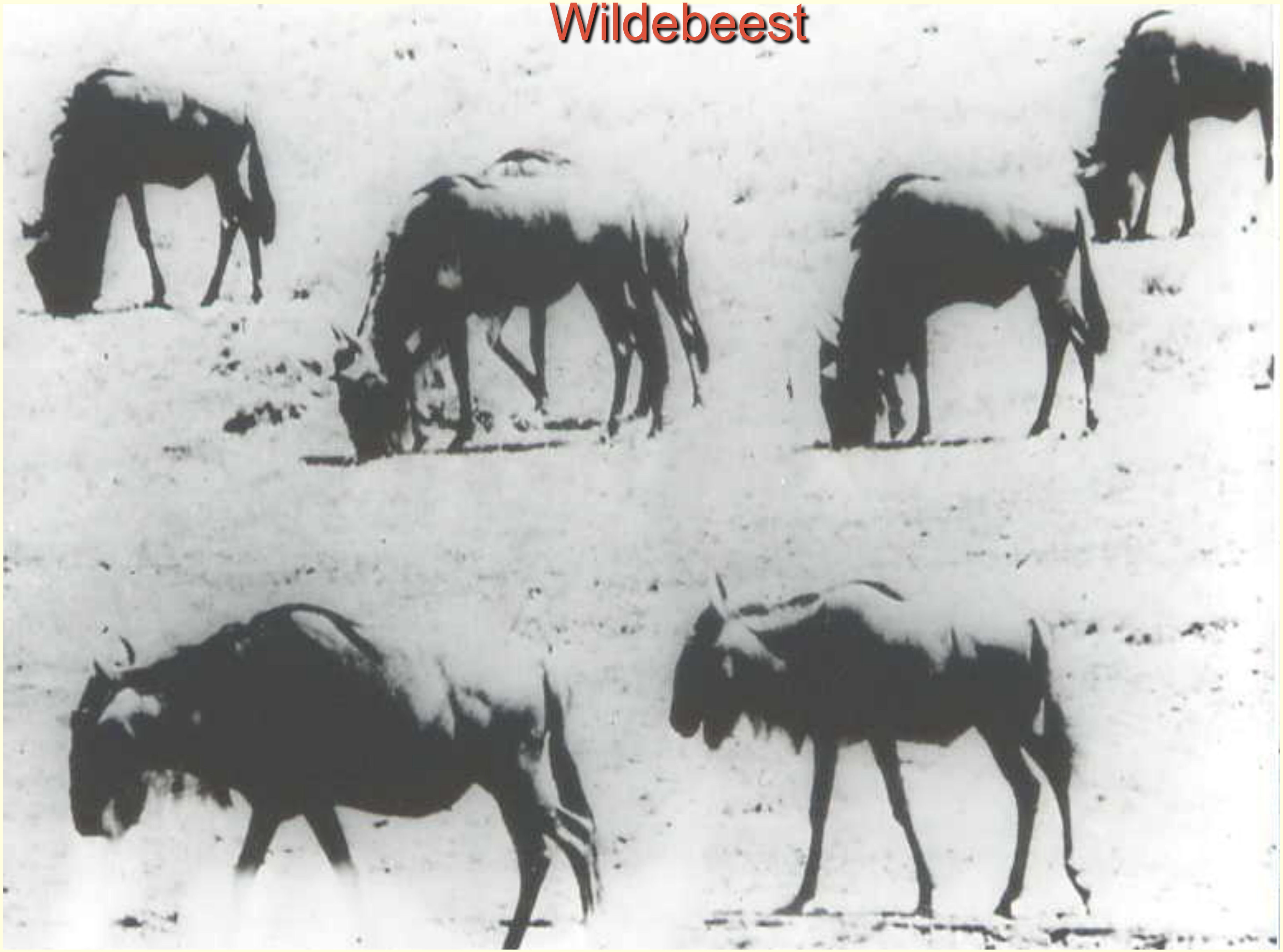
Rates of advance are just one application of such models

- Critical patch size for persistence
- Pattern formation and patchiness
- Coexistence

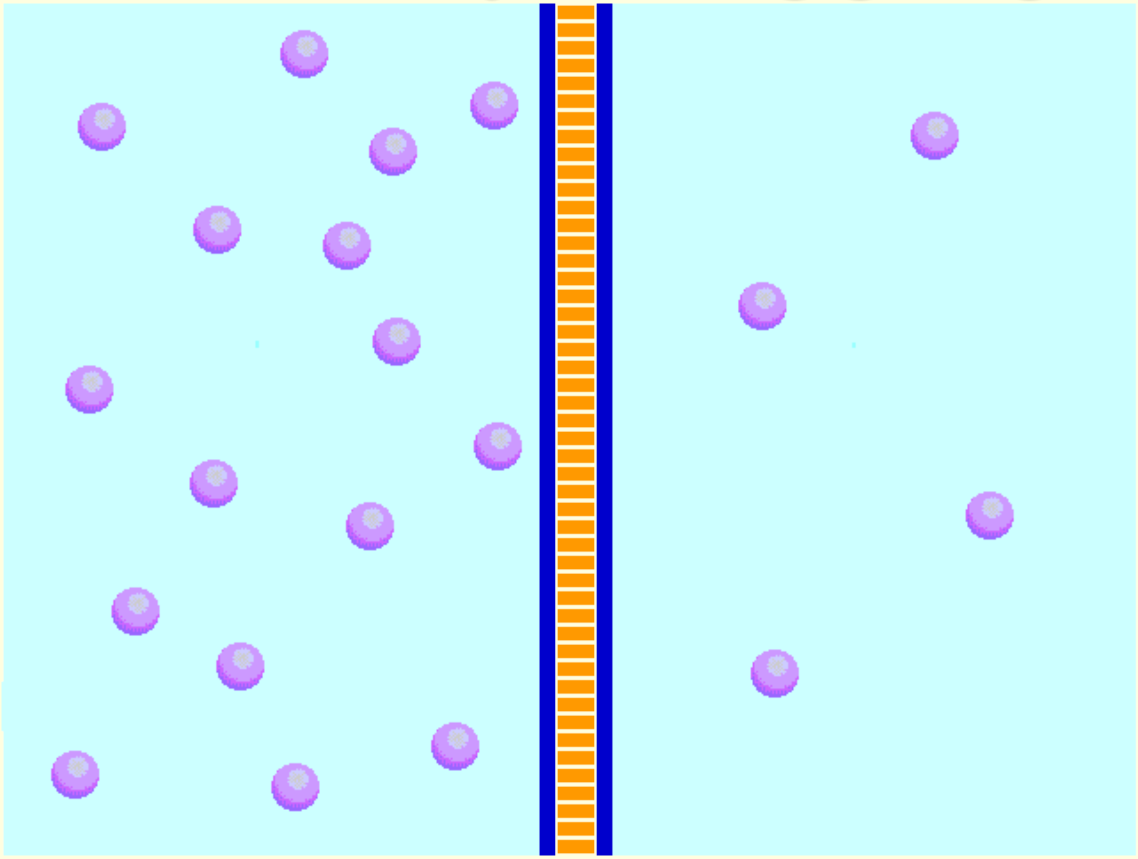


Aerial photograph of a large wildebeest herd, courtesy A.R.E. Sinclair (plate 3 from A.R.E. Sinclair, *The African Buffalo*).

Wildebeest



Diffusion alone can't explain.. it's the enemy of aggregation



www.indiana.edu

Central tendencies could lead to aggregation

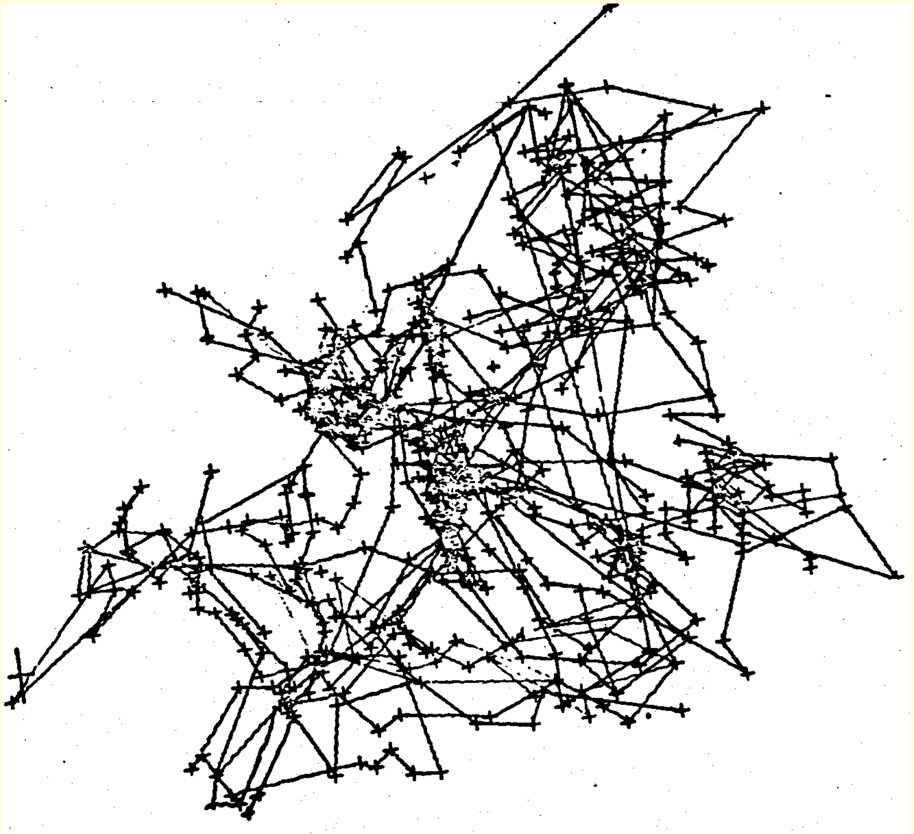
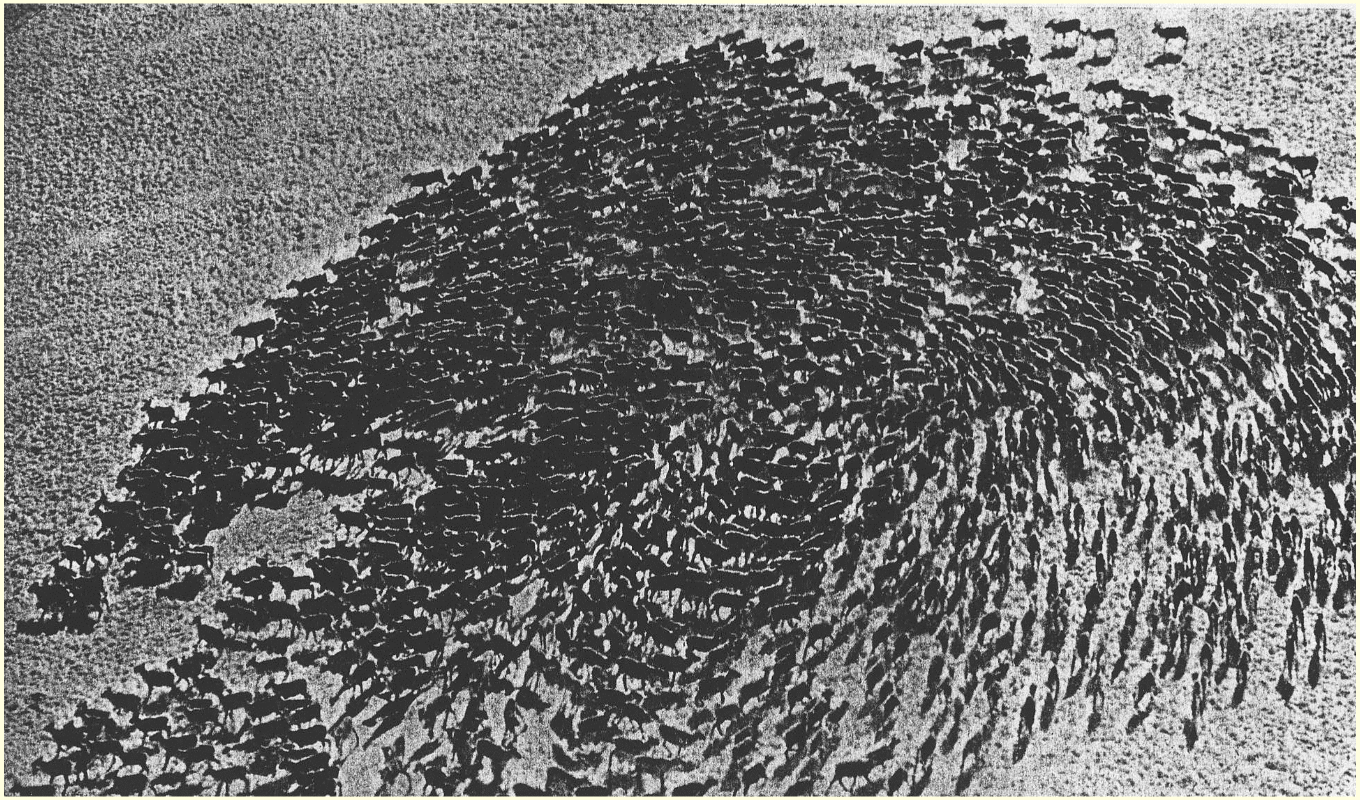


FIG. 1. An example of red fox movement as obtained from telemetry data.

But can aggregation be endogenous?

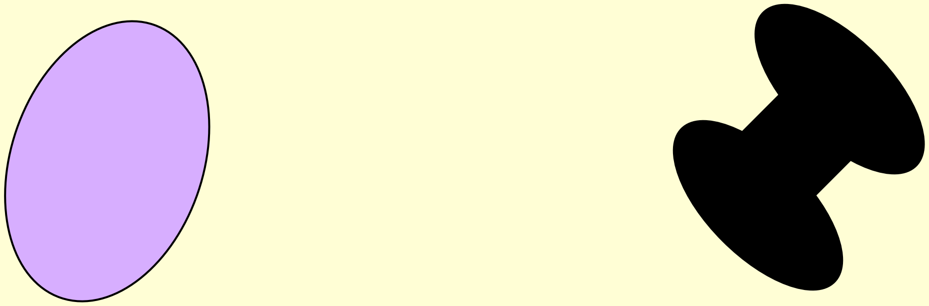
Inter-individual interactions are essential



The rde approach extends easily to coupled populations

$$\frac{\partial u}{\partial t} = F\left(u,v\right) + D_u \nabla^2 u$$

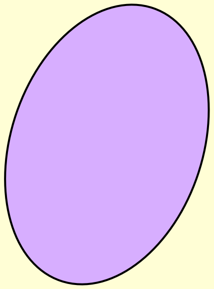
$$\frac{\partial v}{\partial t} = G\left(u,v\right) + D_v \nabla^2 v$$



With equal diffusion rates, no stable non-uniform patterns in convex environments

$$\frac{\partial u}{\partial t} = F\left(u,v\right) + D\nabla^2 u$$

$$\frac{\partial v}{\partial t} = G\left(u,v\right) + D\nabla^2 v$$

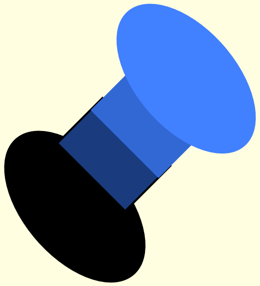


Matano

But stable non-uniform patterns are possible in non-convex regions

$$\frac{\partial u}{\partial t} = F\left(u,v\right) + D\nabla^2 u$$

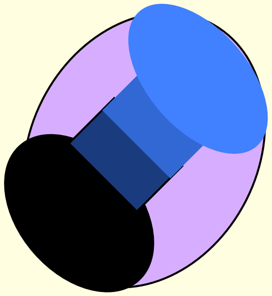
$$\frac{\partial v}{\partial t} = G\left(u,v\right) + D\nabla^2 v$$



Depending on second eigenvalue of Laplacian, with Neumann conditions

(Matano)

Spatially or density dependent diffusion can achieve the same result even in convex regions

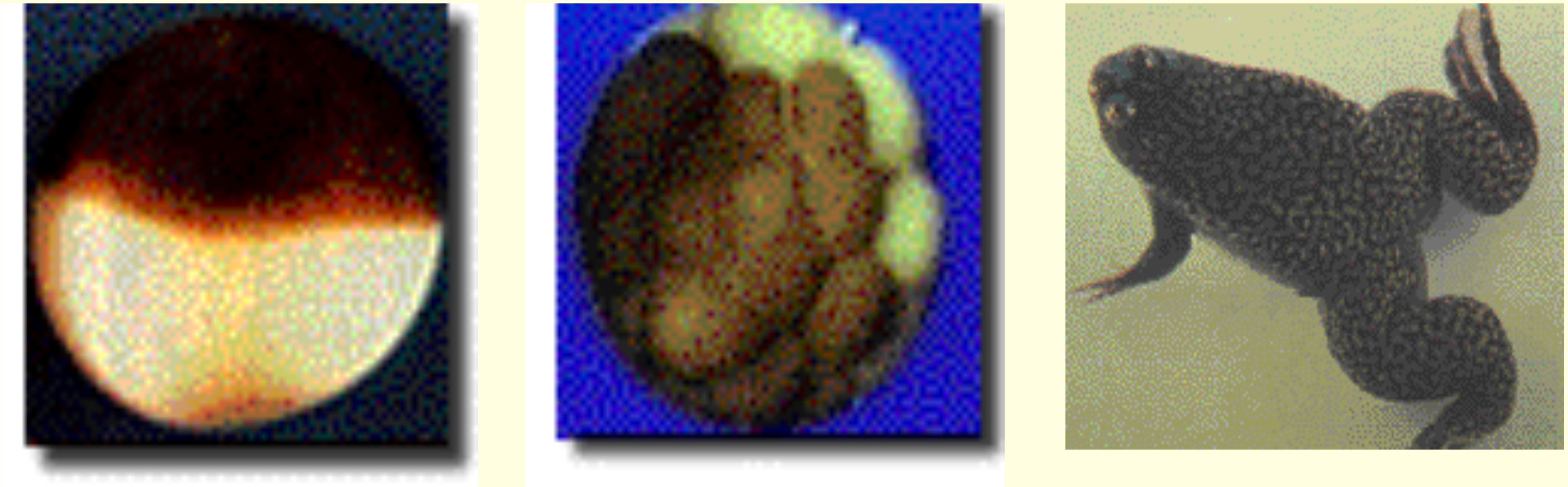


$$\frac{\partial u}{\partial t} = F\left(u,v\right) + D(*)\nabla^2 u$$

$$\frac{\partial v}{\partial t} = G\left(u,v\right) + D(*)\nabla^2 v$$

But unequal diffusion can lead to stable non-uniform patterns arise in convex environments

Animal coat patterns are the simplest of challenges for the study of development, in which highly differentiated structures self-organize from initially homogenous ensembles



http://worms.zoology.wisc.edu/frogs/mainmenu.html

Alan Turing (1912-1954)

Alan Turing posited the existence of two interacting chemicals (morphogens) in a homogeneous space

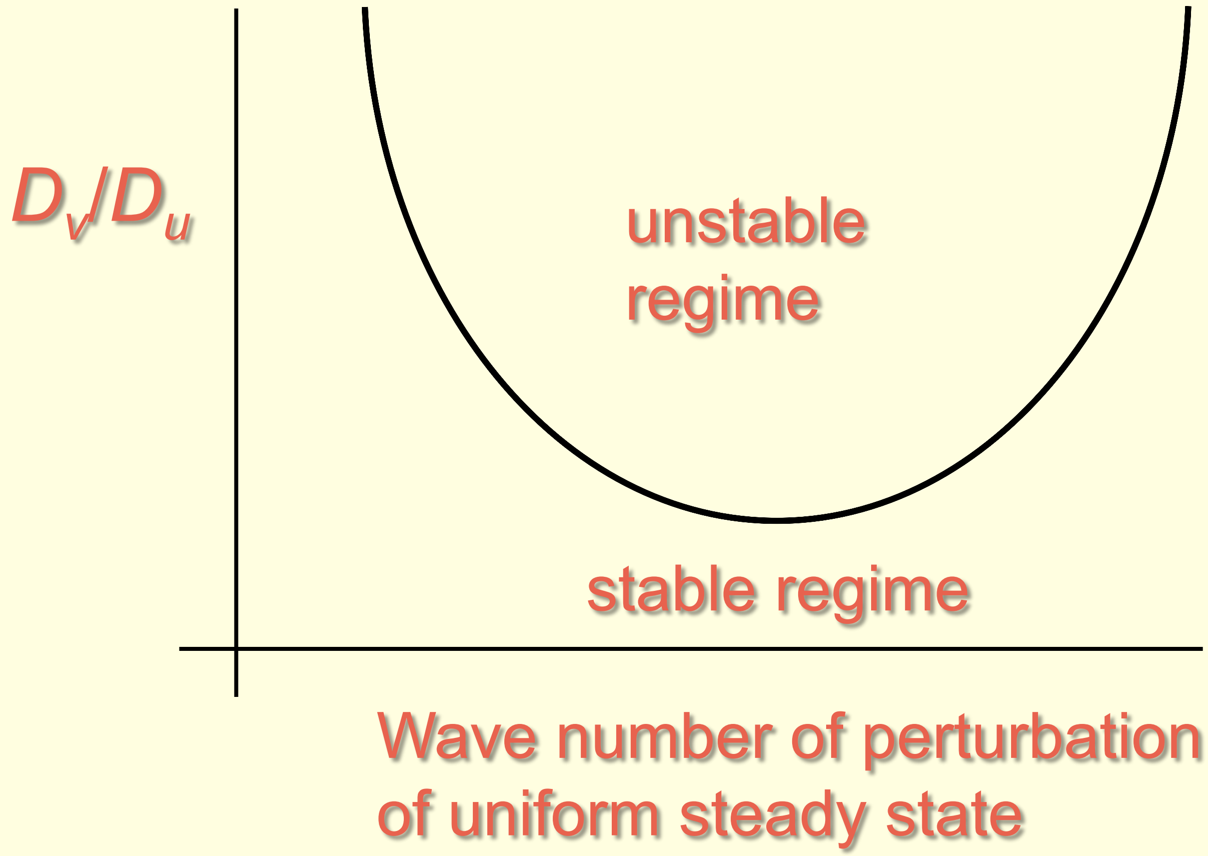
Turing instabilities:

$$\frac{\partial u}{\partial t} = F(u,v) + D_u \nabla^2 u$$

$$\frac{\partial v}{\partial t} = G(u,v) + D_v \nabla^2 v$$

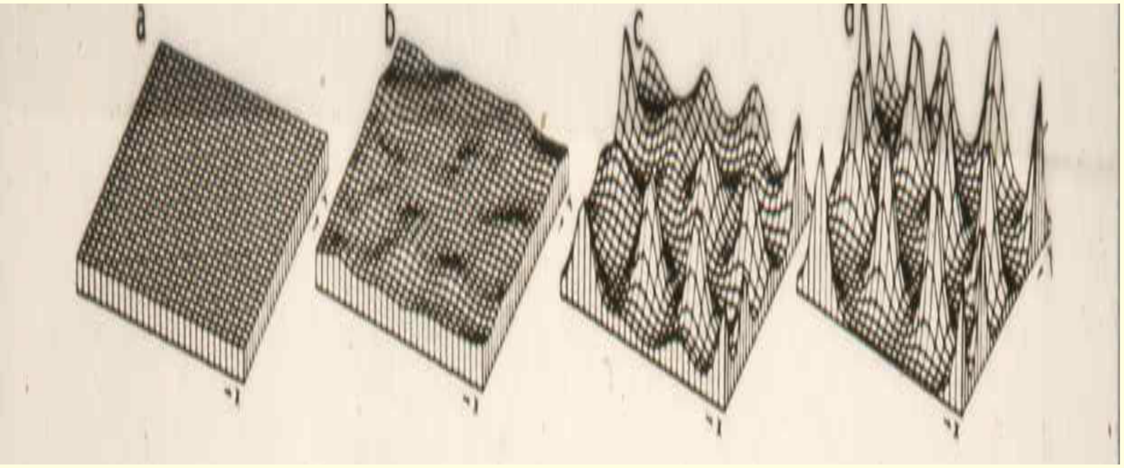
uniform states can become unstable if D_v/D_u is above some threshold.

Turing (diffusive instabilities): The linear theory



Dissipative structures

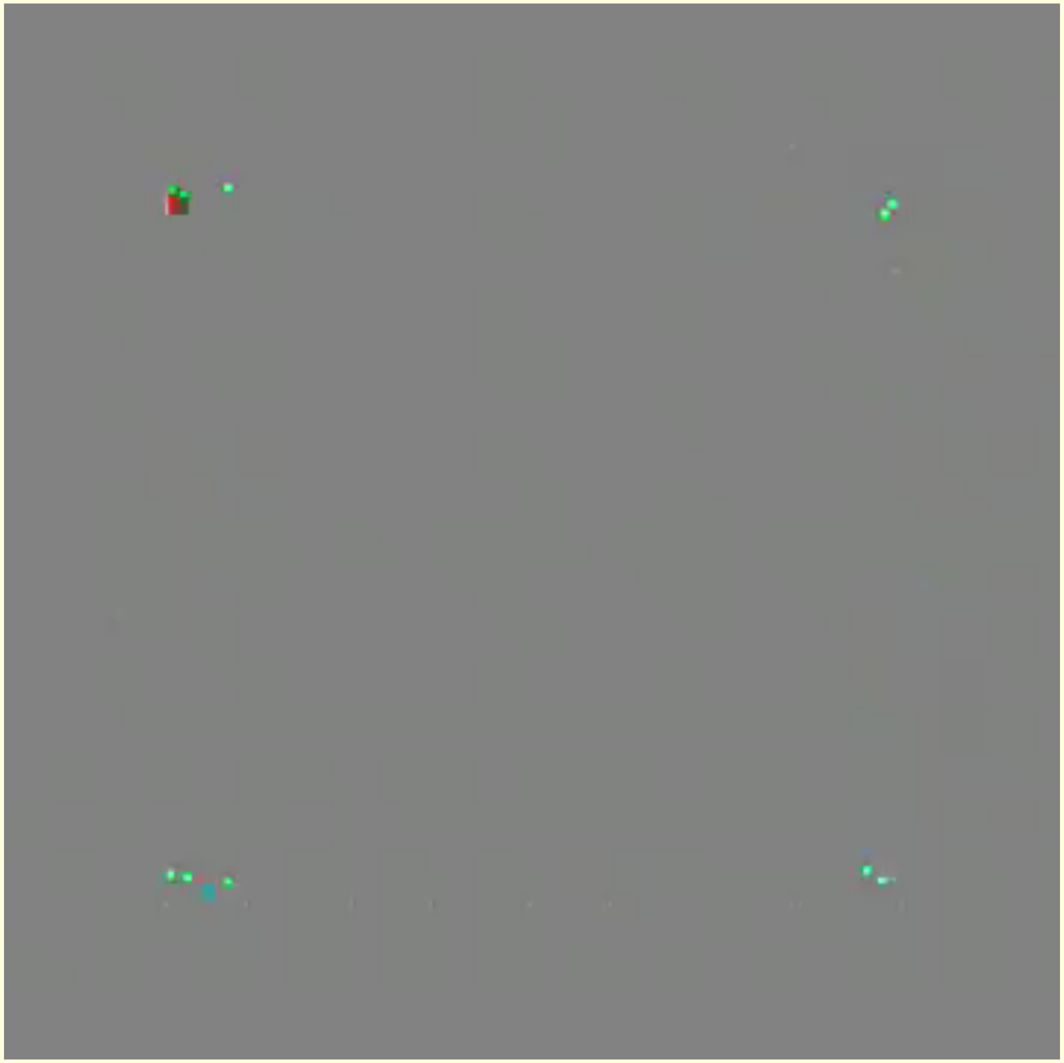
- Nonlinear theory (Segel and Levin)
- Multiple scale expansion
- Successive approximations
- *Stable non-uniform patterns can emerge*



Meinhardt

The resulting spatial pattern in the distribution of morphogens establishes pre-patterns for development

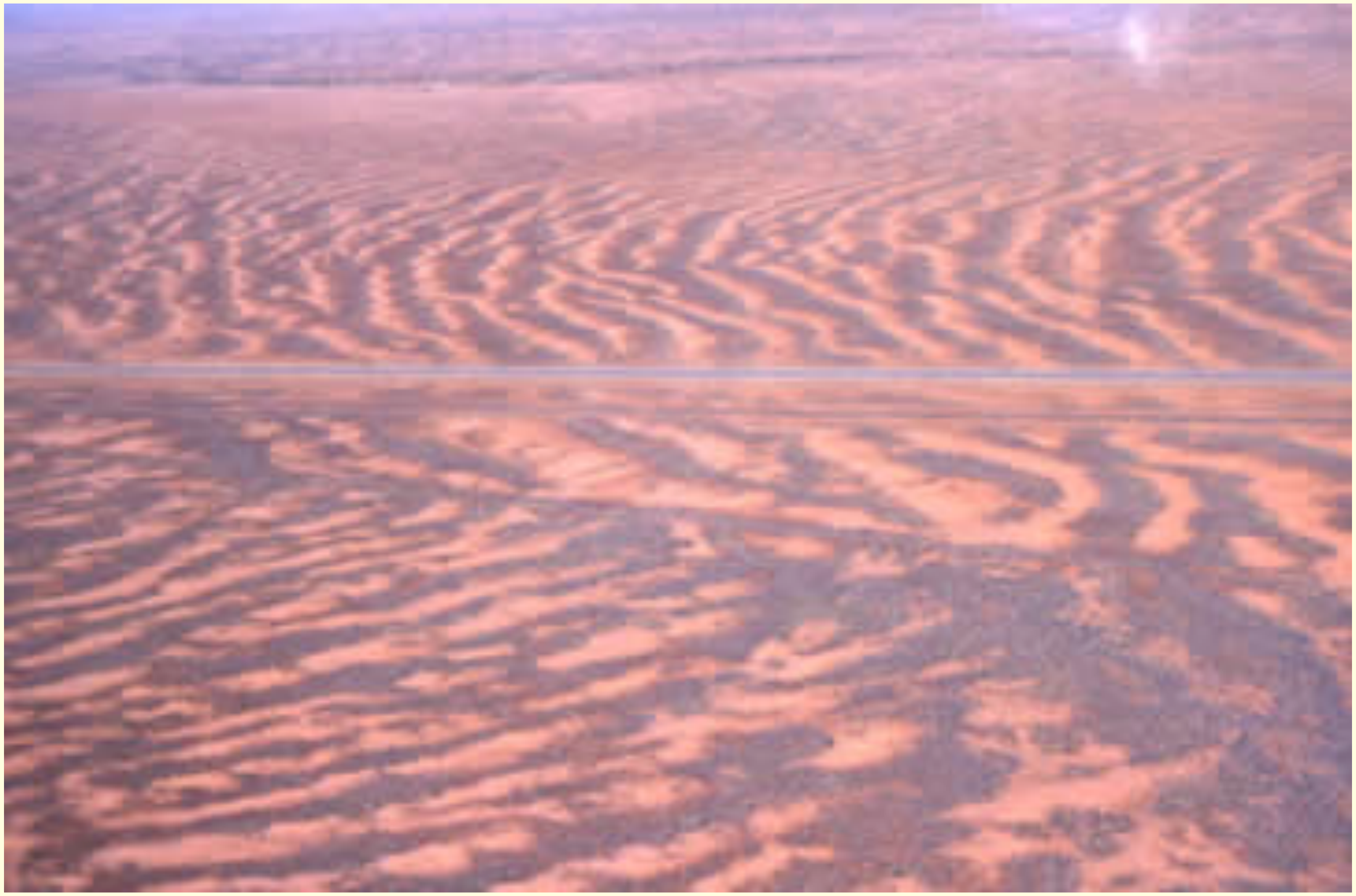
Gierer-Meinhardt patterns



Tatsuo Yanagita

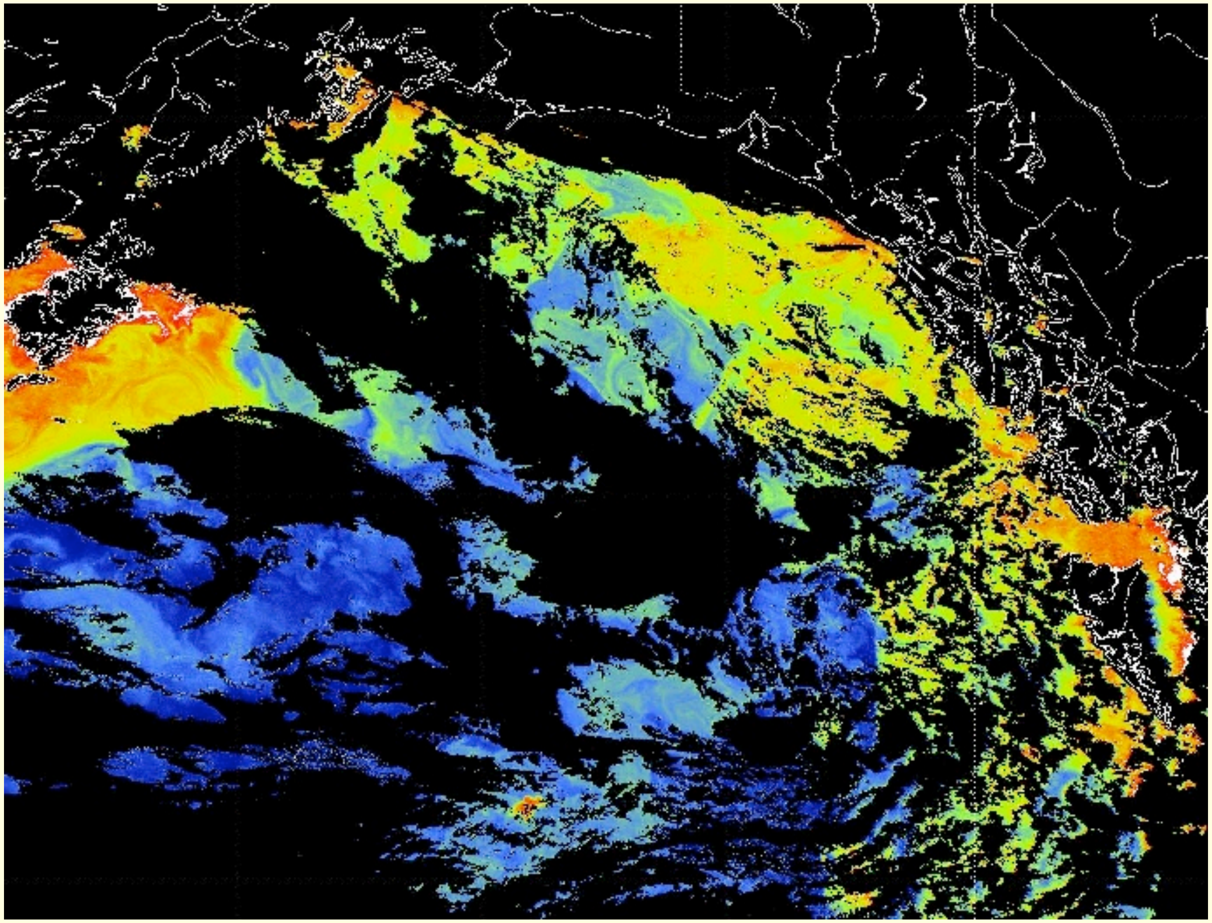
Pattern arises from balance between short-range activation long-range inhibition

Do such mechanisms underlie spatial patterns in ecology?



arts.monash.edu.au/ges/staff/ddunkerley

Plankton are patchy on almost every scale

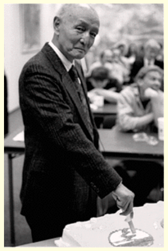


disc.sci.gsfc.nasa.gov

Could Turing apply to planktonic patchiness?

- Phytoplankton as “activators”
- Zooplankton as “inhibitors”

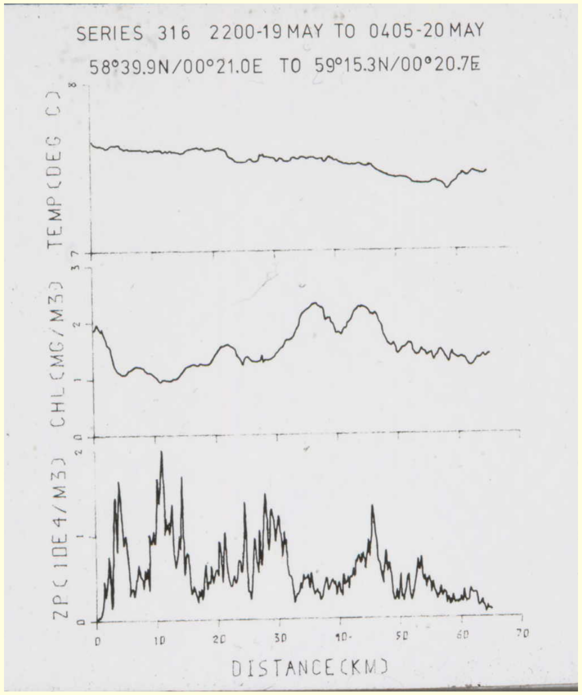
Levin and Segel, and Okubo, applied such models to aggregation of marine zooplankton, like krill



sanctuaries.noaa.gov

Didn't work

Zooplankton are more patchily distributed

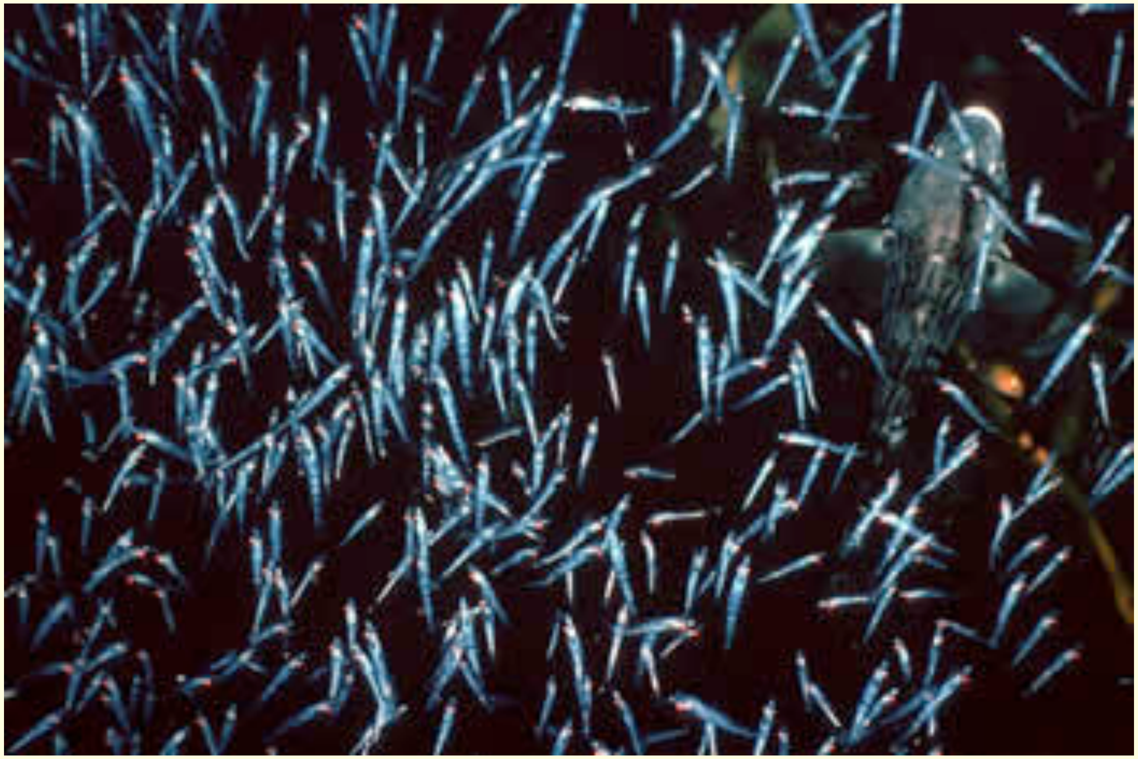


Mackas et al

Zooplankton don't move randomly, but aggregate

www.coolantarctica.com

Zooplankton don't move randomly, but aggregate



Hence, collective motion is important to these patterns

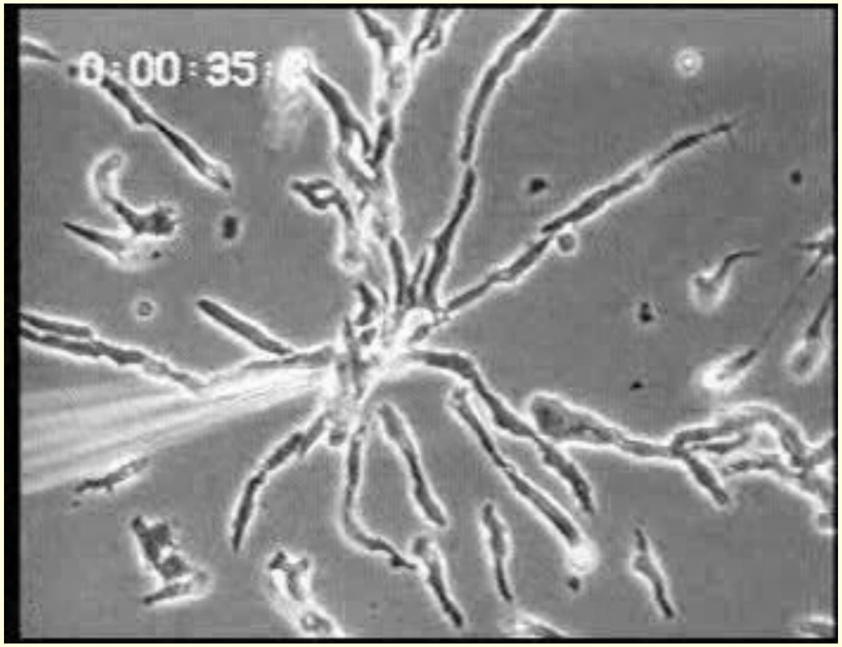
www2.le.ac.uk

Zooplankton don't move diffusively, but aggregate

www.oceanfootage.com

Aggregation has been addressed for a wide range of organisms

- Slime molds



Bonner: The social cell

Keller and Segel: Initiation of aggregation as an instability

Keller-Segel Model

$$\frac{\partial n}{\partial t} = \nabla \cdot \{\overbrace{D_n(c)\nabla n}^{\text{Random cell movement}} - \overbrace{\chi(c)n\nabla c}^{\text{Directed cell movement}}\}$$

$$\frac{\partial c}{\partial t} = \underbrace{D_c\nabla^2 c}_{\text{Chemical diffusion}} - \underbrace{n\,\delta(c)}_{\text{Chemical degradation by cells}}$$

J. Sherratt

Aggregation has been addressed for a wide range of organisms

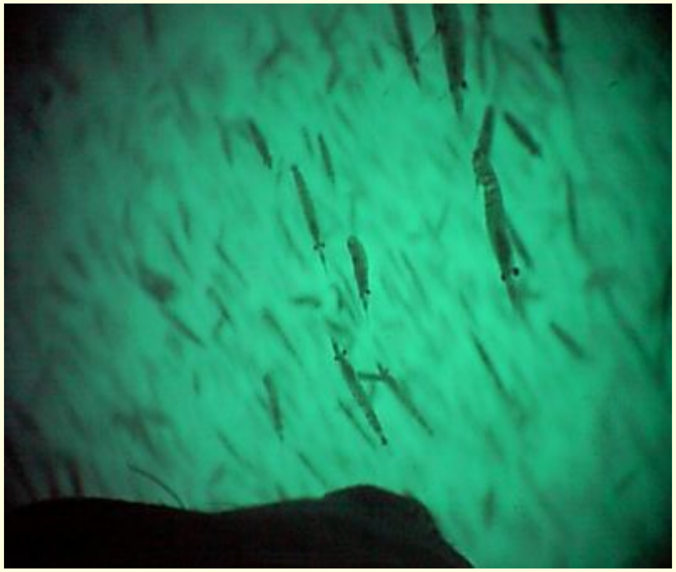
- Slime molds
- Insects

:www.abc.net.au/science/news/ stories/s266199.htm

Aggregation has been addressed for a wide range of organisms

- Slime molds
- Insects
- Krill

antarctica.org.nz/04-biology/



www.antarctica.ac.uk/.../Bird_Island/ 2000/bidir1200.html

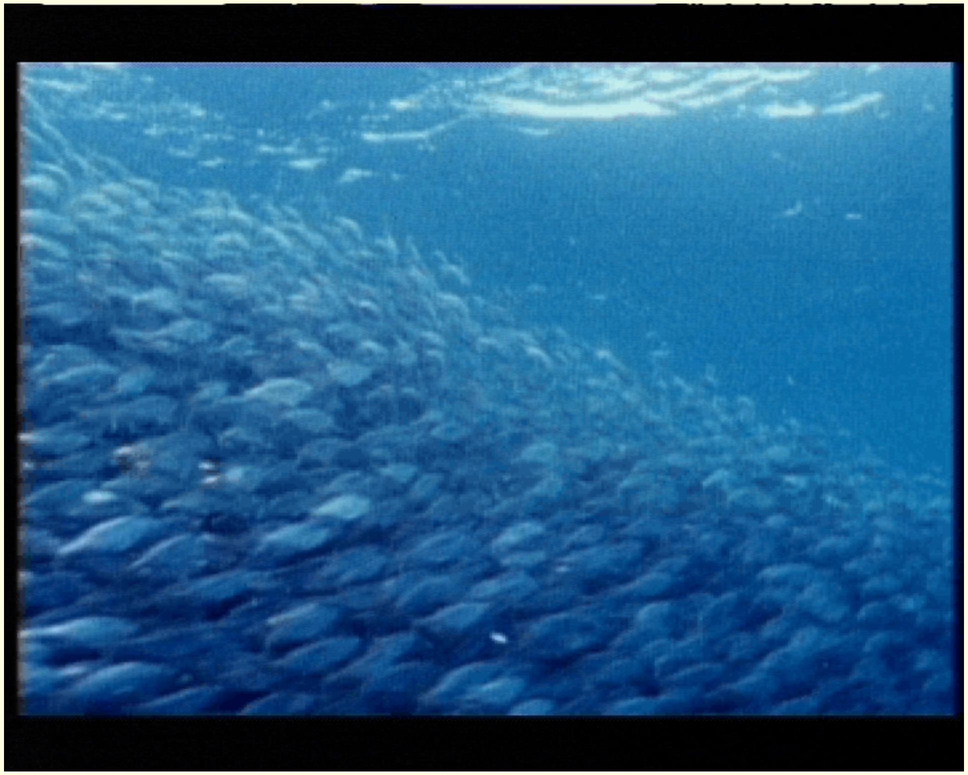
Aggregation has been addressed for a wide range of organisms

- Slime molds
- Insects
- Krill
- Birds

Carere

Aggregation has been addressed for a wide range of organisms

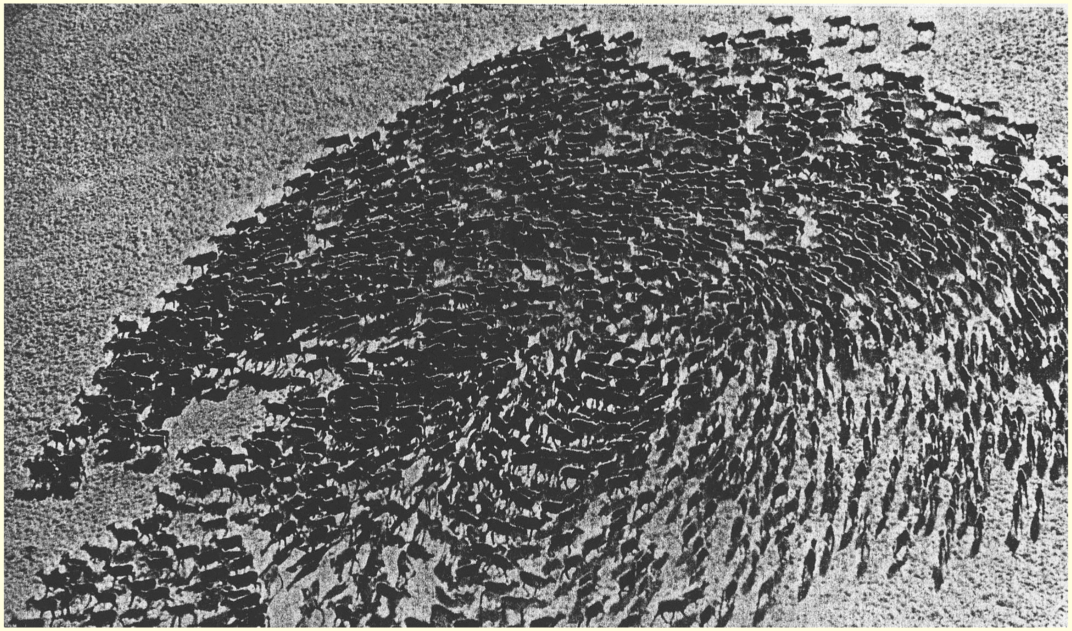
- Slime molds
- Insects
- Krill
- Birds
- Fish



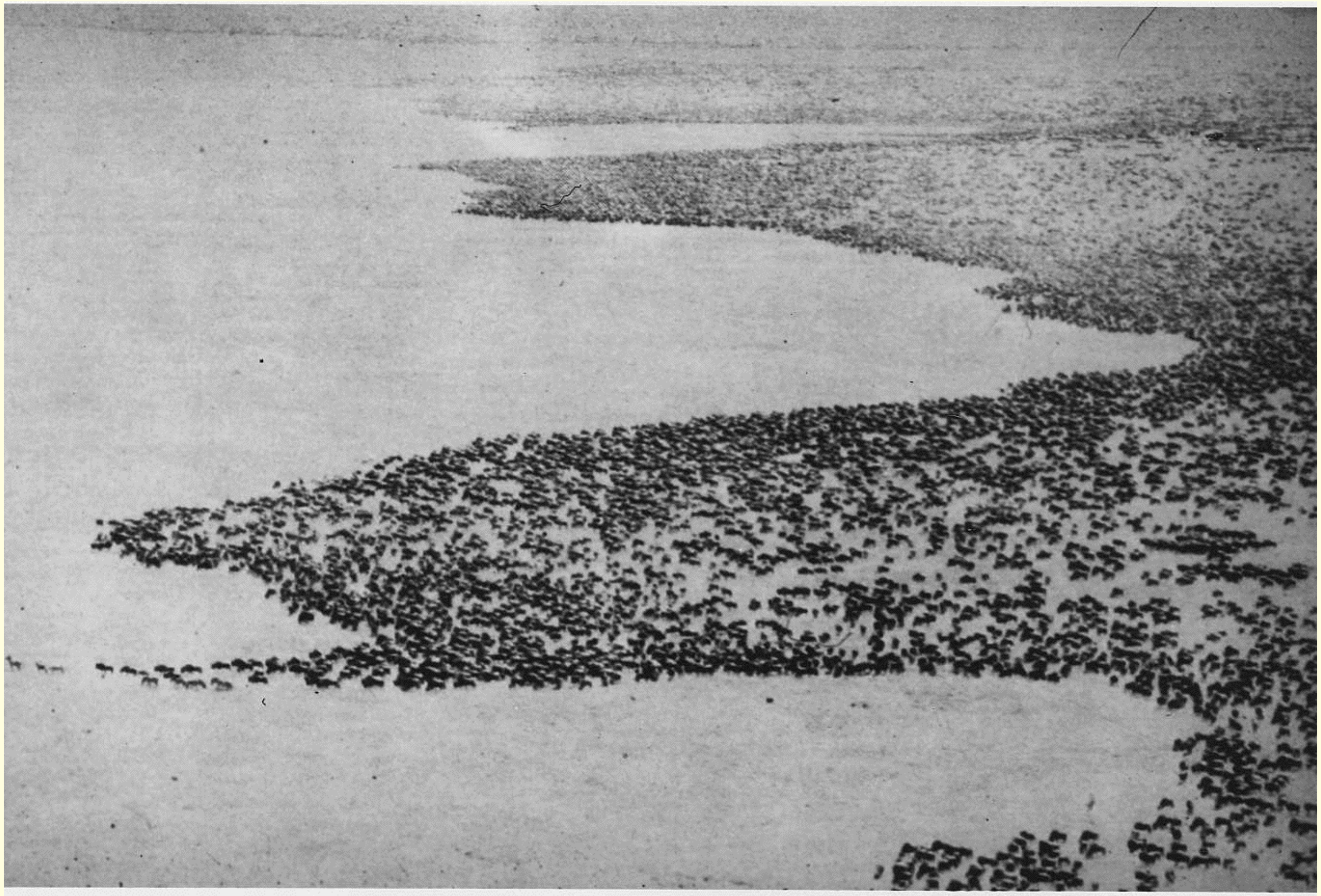
Couzin/BBC

Aggregation has been addressed for a wide range of organisms

- Slime molds
- Insects
- Krill
- Birds
- Fish
- Ungulates



Wildebeest



Aerial photograph of a large wildebeest herd, courtesy A.R.E. Sinclair (plate 3 from A.R.E. Sinclair, *The African Buffalo*).

Can such patterns arise endogenously, basically as hydrodynamic instabilities?

$$\frac{\partial P}{\partial t} + \nabla\left\{\frac{aP}{S} \; \nabla S + b\nabla P\right\} = \beta\nabla^2 P^2$$

Can such patterns arise endogenously, basically as hydrodynamic instabilities?

Again, a simple balance between short-range repulsion ("activation") and long-range attraction ("inhibition") can produce patterns

Reproducing wave-fronts (Gueron and Levin)

$$y = y(x,t)$$

$$\dot{y} = v_0(t) + F(\Delta(y))$$

$$\boxed{\Delta(y(x,t)) = \frac{1}{2\delta}\int_{x-\delta}^{x+\delta} y(s,t)\,ds - y(x,t)}$$

Observations on large mammals

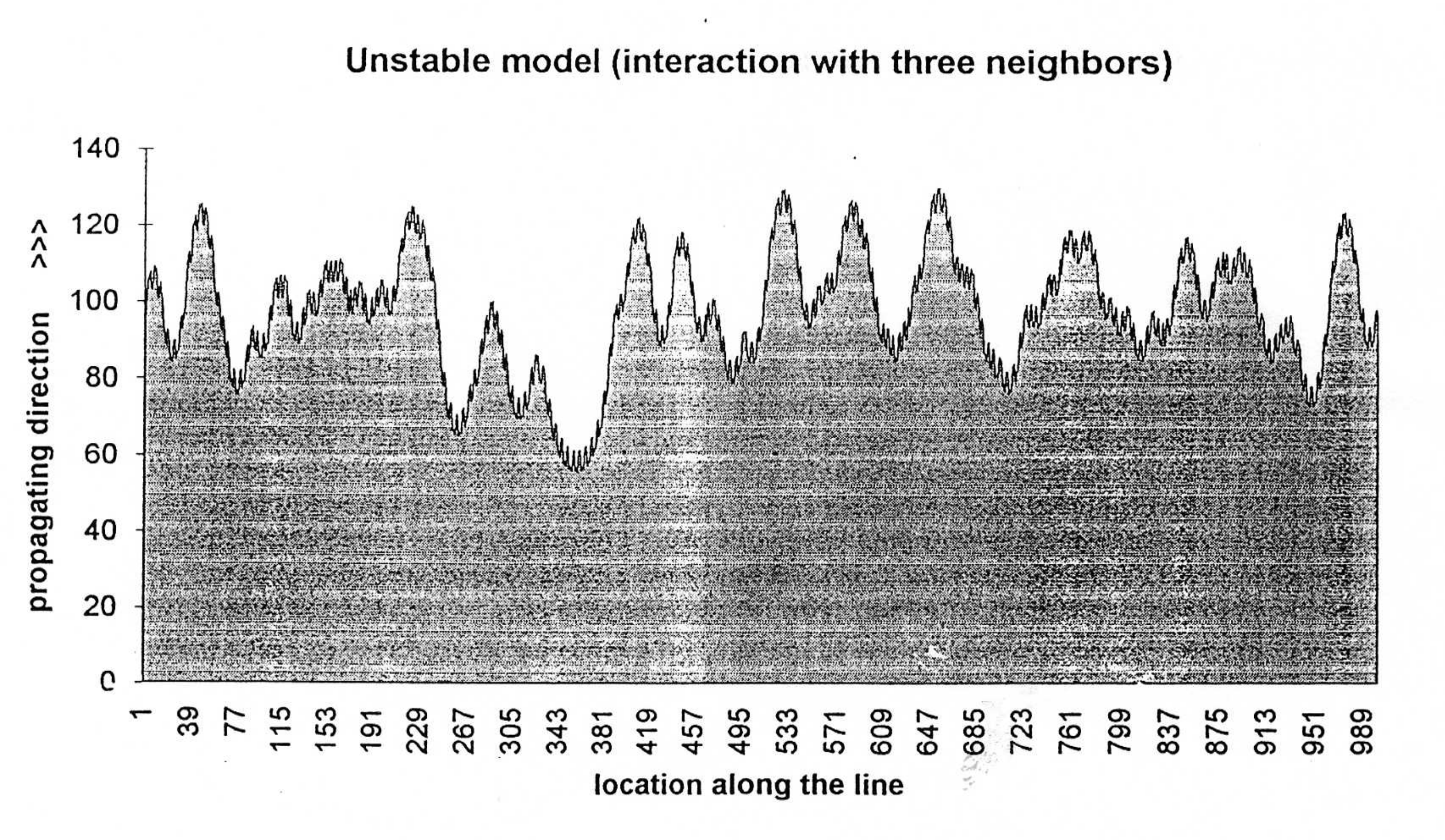
- Repulsion if others too close
- Attraction if others too far

Observations on ungulates:

- Attraction:
  - Slow down if too far ahead
  - Speed up if too far behind
- Repulsion
  - Speed up if slightly ahead
  - Slow down if slightly behind

$$\dot{y} = v_0(t) + F(\Delta(y))$$

Traveling fronts arise spontaneously



Most generally, the problem is

What is the relationship between an individual agent

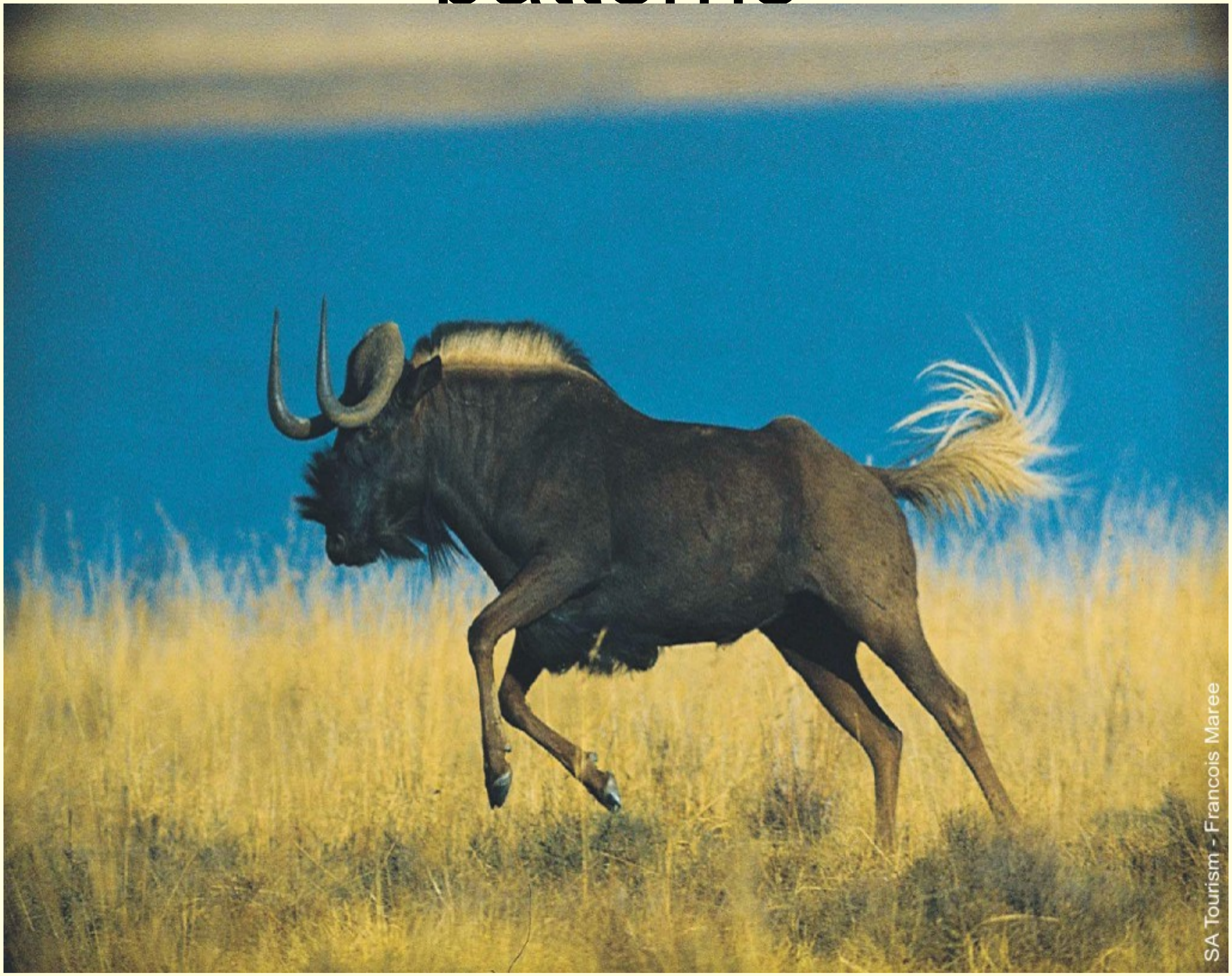
...and how it responds to its neighbors and local environment

...and the macroscopic properties of ensembles of such agents?

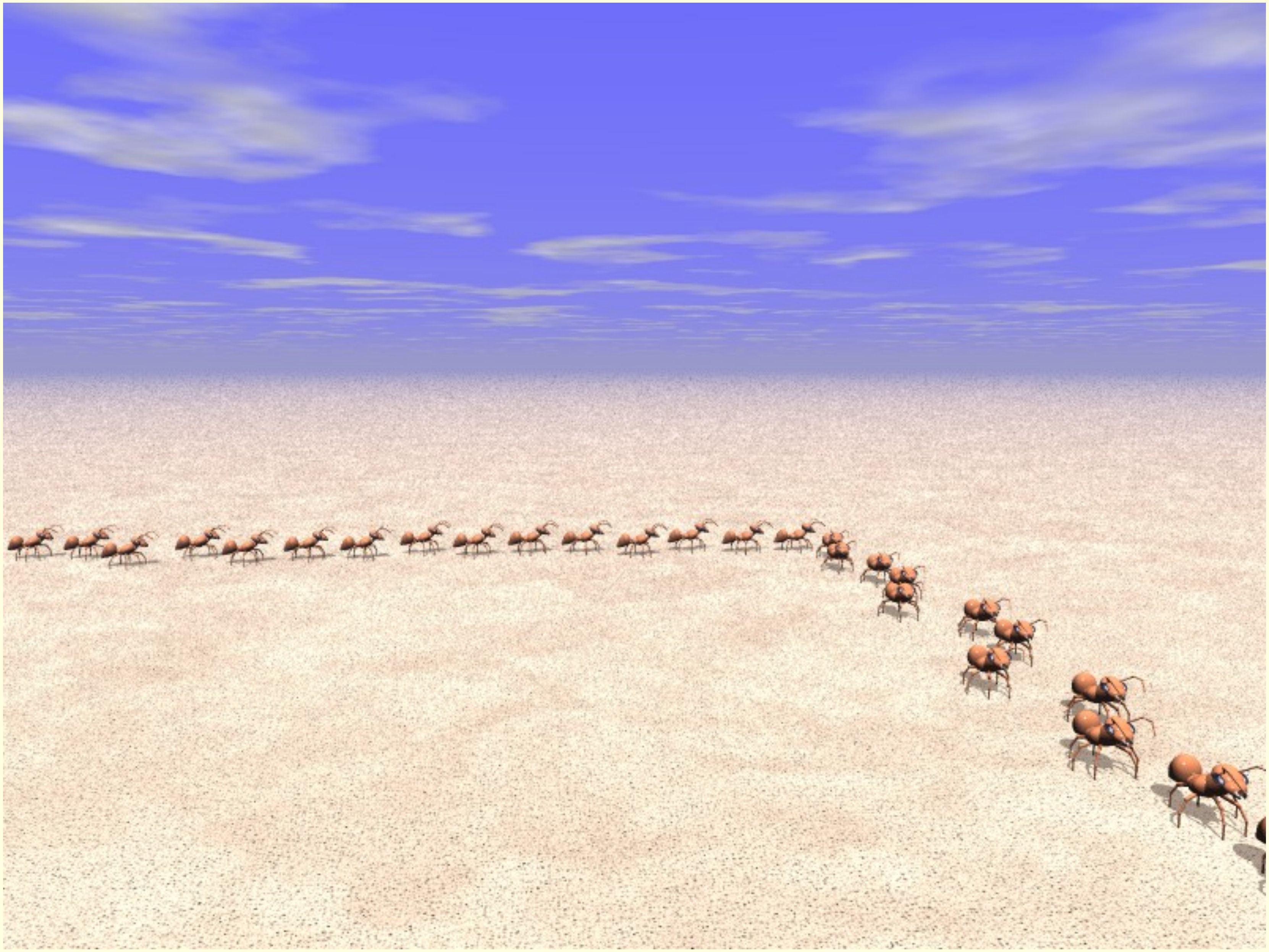
How do we relate the macroscopic patterns to the microscopic rules?

dzignsetc.bizland.com

Wildebeest show a variety of patterns


SA Tourism - Francois Maree

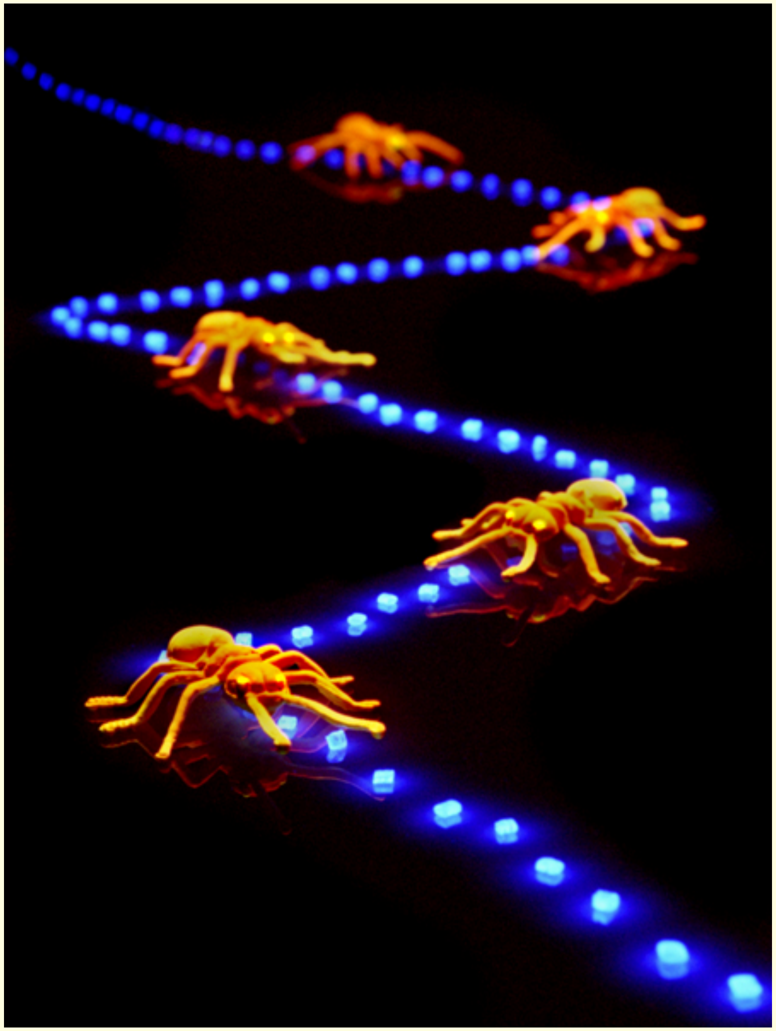
www.ribbitphotography.com

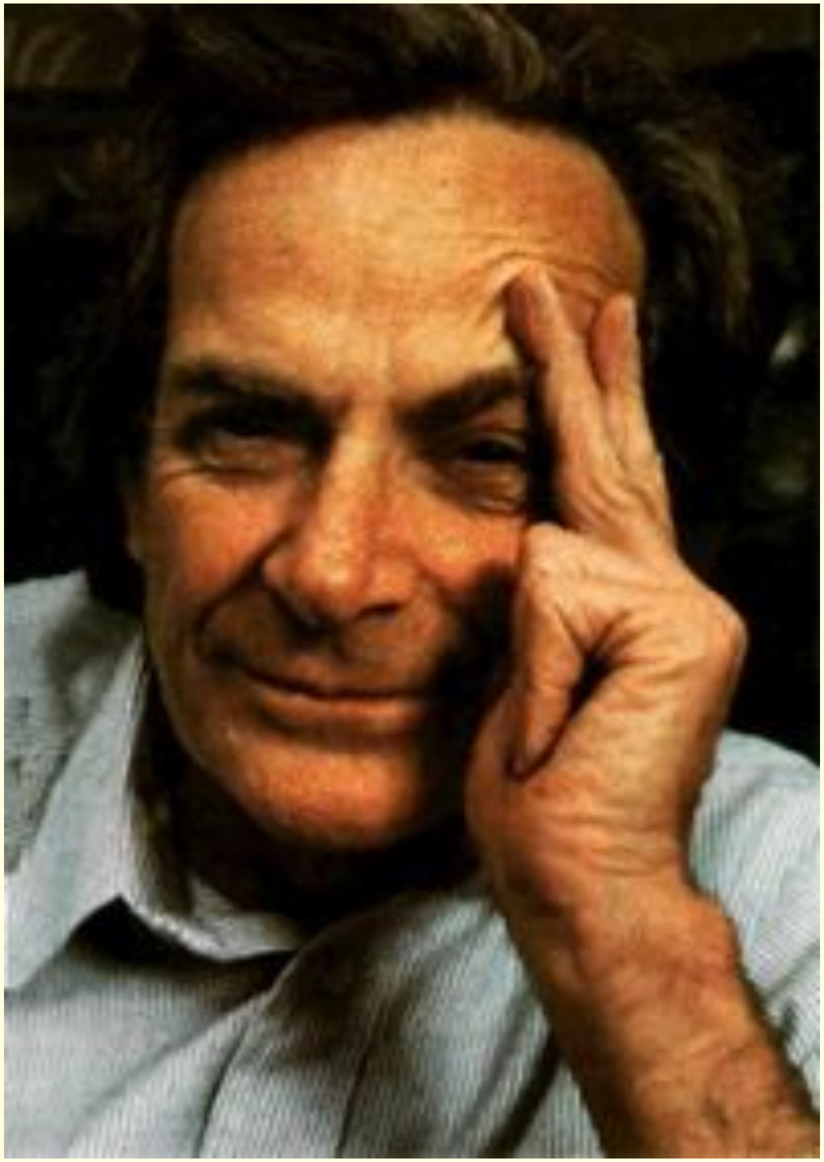


Ants

www.irtc.org

Feynman: Trail-following





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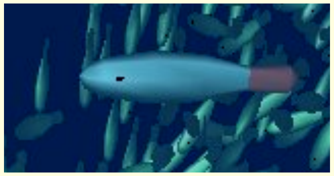
Lagrangian-Eulerian connections

- Begin from microscopic (Lagrangian) rules

$$m\ddot{x} = \underset{\text{Random}}{F_1} + \underset{\text{Directed}}{F_2} + \underset{\text{Grouping}}{F_3} + \underset{\text{Arrayal}}{F_4}$$



Flierl, Grunbaum, Levin, Olson 1999

Lagrangian/Eulerian transformation

1. Start from individual-based model, in which positions or velocities change according to specific rules.

Lagrangian/Eulerian transformation

1. Start from individual-based model, in which positions or velocities change according to specific rules.
2. Write population descriptions in terms of spatial/velocity density.

Spatial/velocity density

$$n\left(\mathrm{x},\mathrm{v},t+\delta t\right)=$$

$$\int \mathrm{dx}'\,\mathrm{dv}'\,\mathcal{P}_{\delta\mathrm{X}}\,(\mathrm{x}-\mathrm{x}'-\mathrm{v}'\,\delta t\,;\mathrm{x}',\mathrm{v}',\,t)$$

$$*\,\mathcal{P}_{\delta\mathrm{V}}\,(\mathrm{v}-\mathrm{v}'-\mathrm{a}\delta t\,;\mathrm{x}',\mathrm{v}',t)\,n\,(\mathrm{x}',\mathrm{v}',\,t)$$

$\mathcal{P}_{\delta\mathrm{X}}$ = probability particle at x´, velocity v´, time t has random jump δx = x-x´-v´δt, etc.

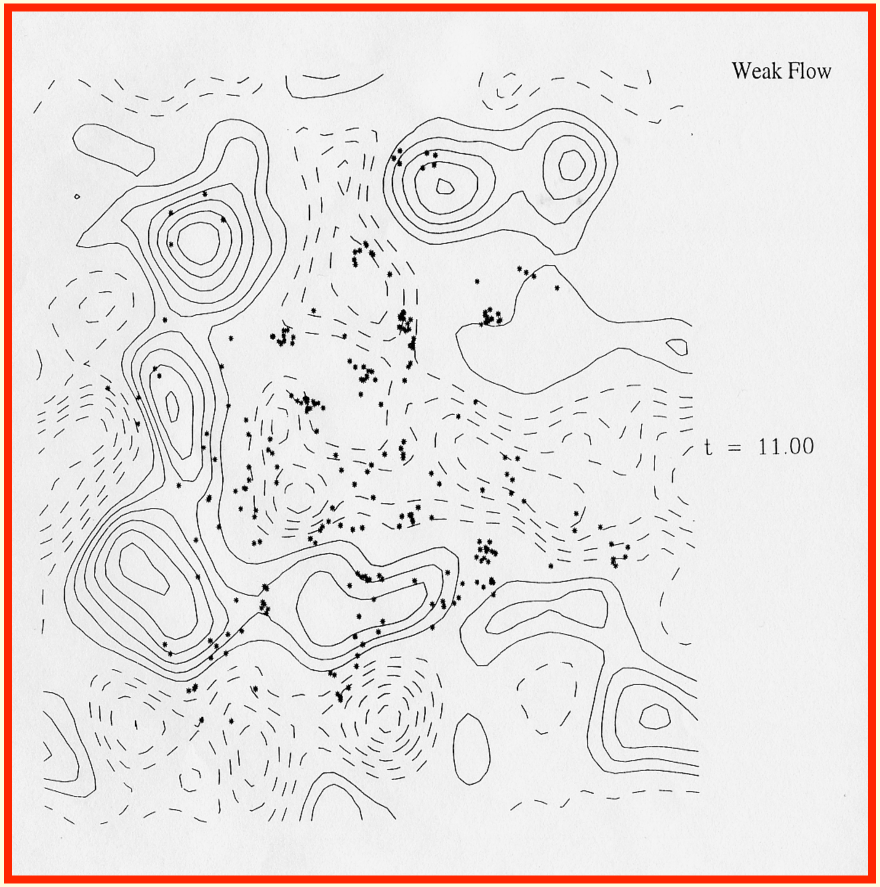
Lagrangian/Eulerian transformation

1. Start from individual-based model, in which positions or velocities change according to specific rules.
2. Write population descriptions in terms of spatial/velocity density.
3. To close system, assume something like Poisson distribution locally.

Boltzmann equation

$$
\begin{aligned}
\frac{\partial}{\partial t} n(\mathrm{x},\mathrm{v},t) = - \frac{\partial}{\partial x_i} [v_i n(\mathrm{x},\mathrm{v},t) \\
- \frac{\partial}{\partial v_i} [a_i n(\mathrm{x},\mathrm{v},t)] \\
+ \frac{1}{2} \frac{\partial^2}{\partial v_i \partial v_j} [\gamma_{ij} n(\mathrm{x},\mathrm{v},t)
\end{aligned}
$$

If closures are good, these approximations work well



If closures are not known, may be able to use equation-free methods

- Coarse-graining techniques of Kevrekidis et al. start from individual-based approaches
- “Equation-free” computation
- Circumvents explicit closure, allows microscopic simulators to perform system-level tasks directly

But real aggregations are heterogeneous assemblages of individuals

Couzin, Krause, Franks, Levin

3 February 2005

International weekly journal of science

nature

£10.00

www.nature.com/nature

Leadership by numbers

Decision making in animal groups

American prehistory
Adding flesh to the bones

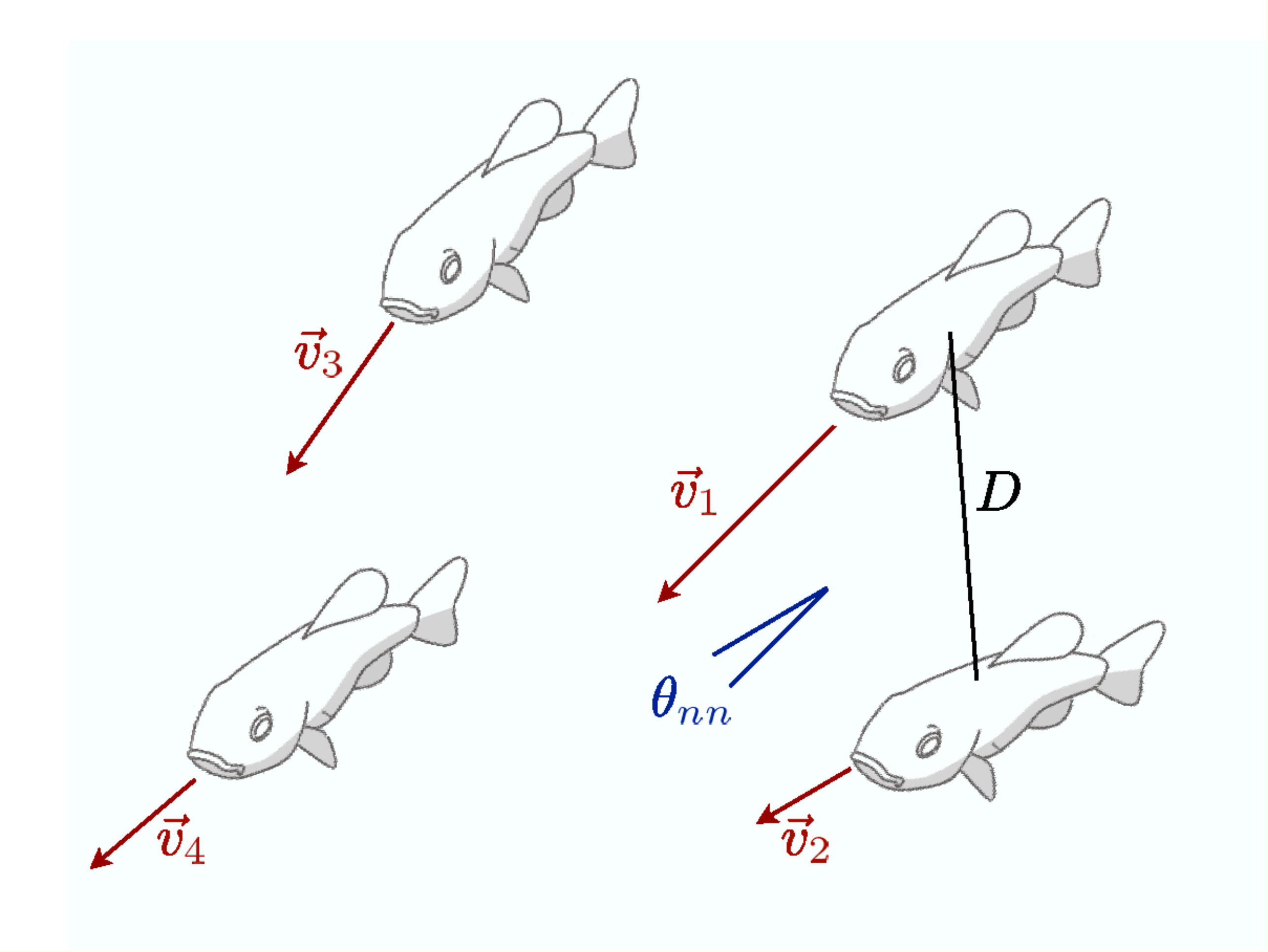
Ozone depletion
Whose methyl chloroform?

Reanalysing the genome
Genes work both ways

naturejobs the pull of new Europe

- Utilize simulations to explore these issues

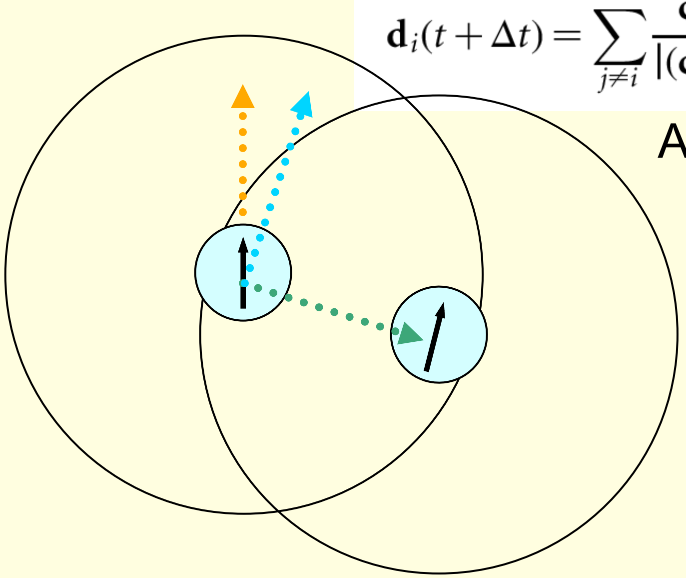
Velocity vectors



Social interactions

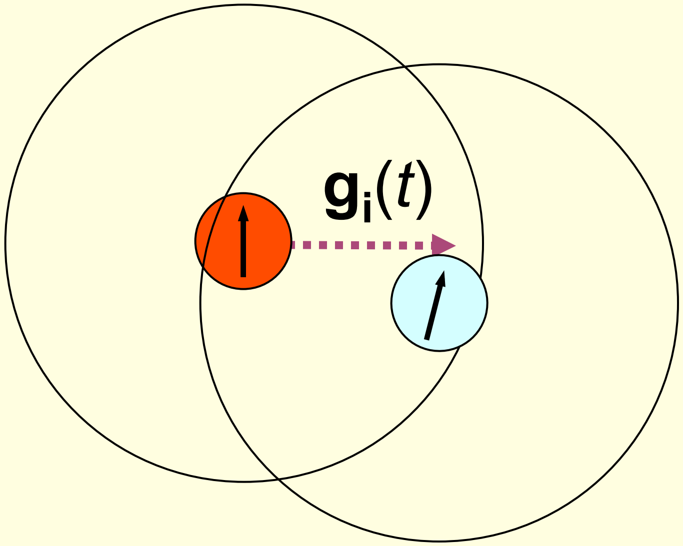
$$\mathbf{d}_i(t+\Delta t) = \sum_{j\neq i} \frac{\mathbf{c}_j(t)-\mathbf{c}_i(t)}{|(\mathbf{c}_j(t)-\mathbf{c}_i(t))|} + \sum_{j=1} \frac{\mathbf{v}_j(t)}{|\mathbf{v}_j(t)|} \qquad (2)$$

Attraction Alignment



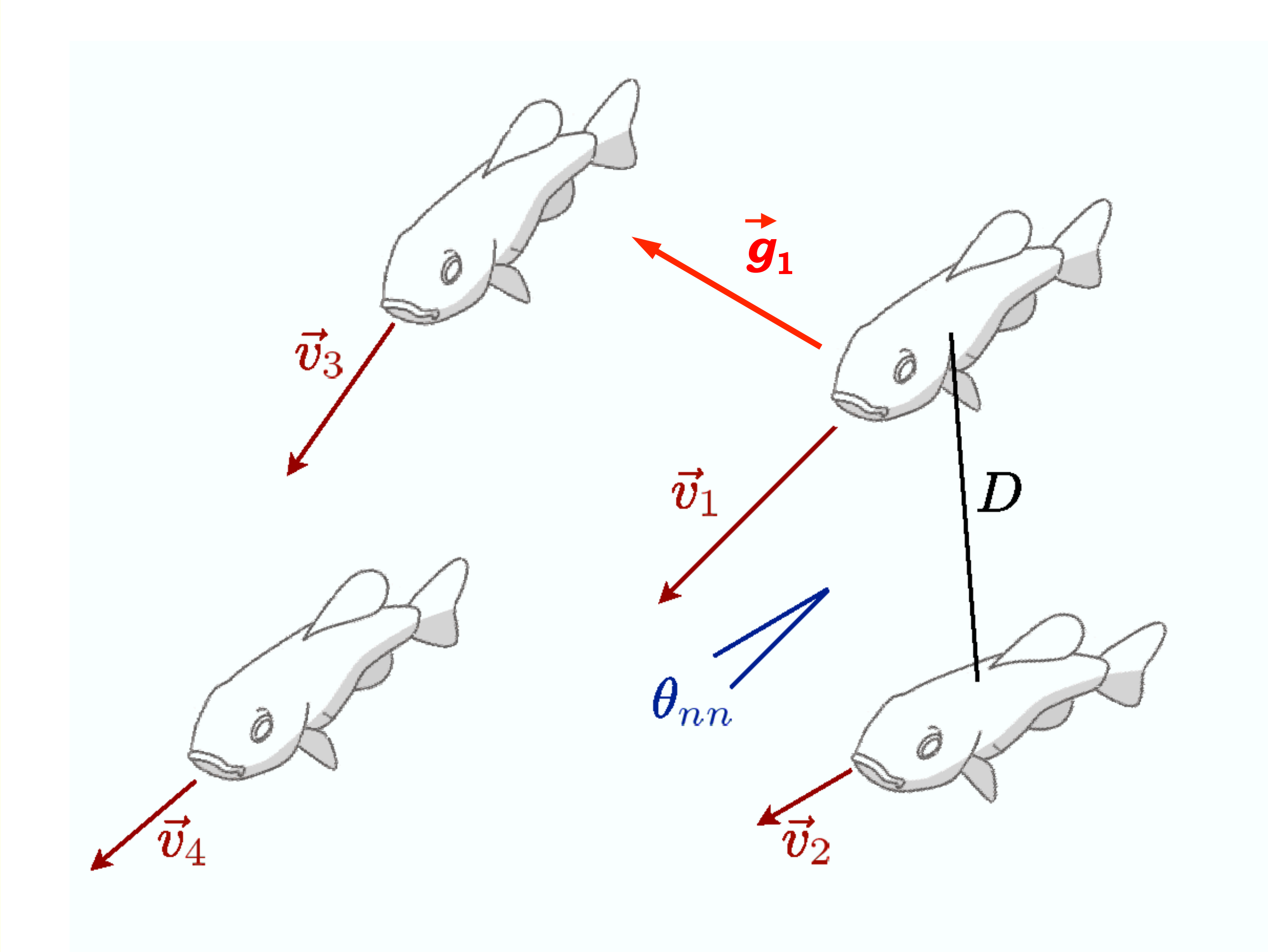
+ local repulsion

“Informed” individuals have an additional influence, here simulated as a desired direction of motion (e.g towards a resource or the direction of a section of a migration route)

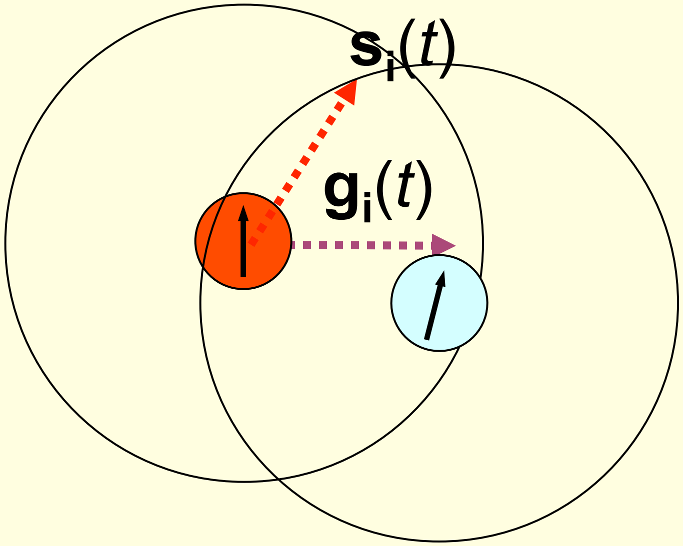


But individuals have no explicit knowledge as to who is informed and who is not.

Collective decision-making



So the direction chosen by informed individuals must reconcile these tendencies.



$$\mathbf{d}_\mathbf{i}(t+\Delta t) = \frac{\mathbf{s}_\mathbf{i}(t) + \omega\, \mathrm{g}_\mathrm{i}(t)}{|\,\mathbf{s}_\mathbf{i}(t) + \omega\, \mathrm{g}_\mathrm{i}(t)\,|}$$

Collective decision-making

1 informed individuals in group of 100.

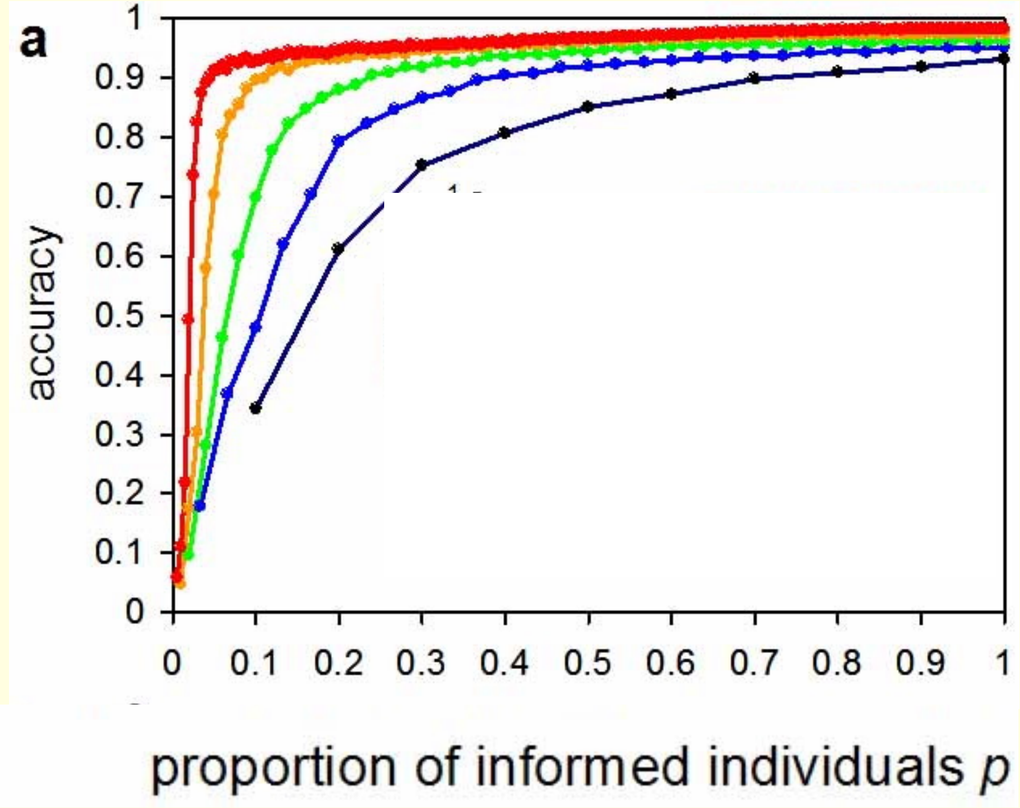
Collective decision-making

5 informed individuals in group of 100.

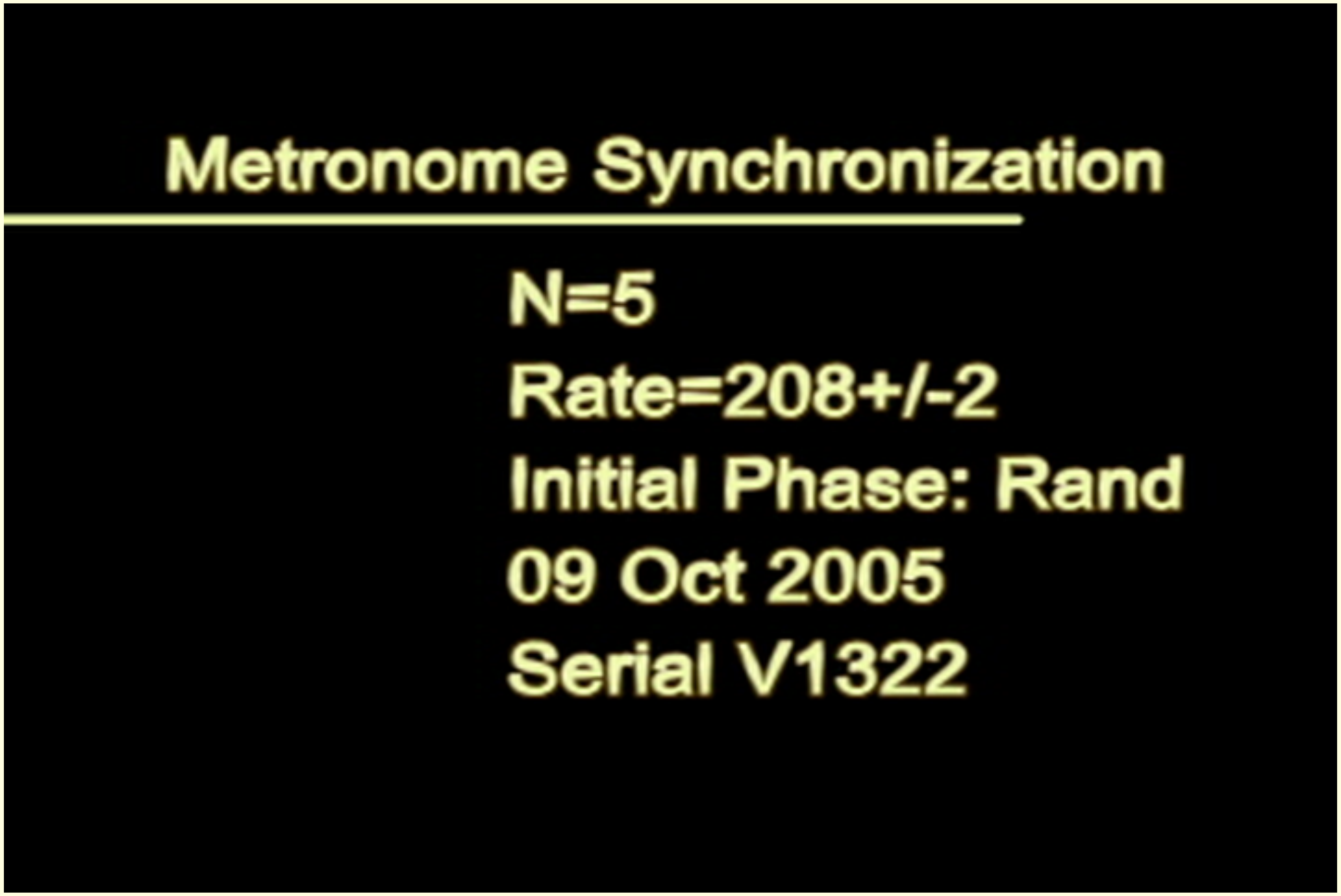
Collective decision-making

10 informed individuals in group of 100.

Animal groups may be led by a small number of individuals



Tim Buchman’s recreation of Huyghens’ experiment

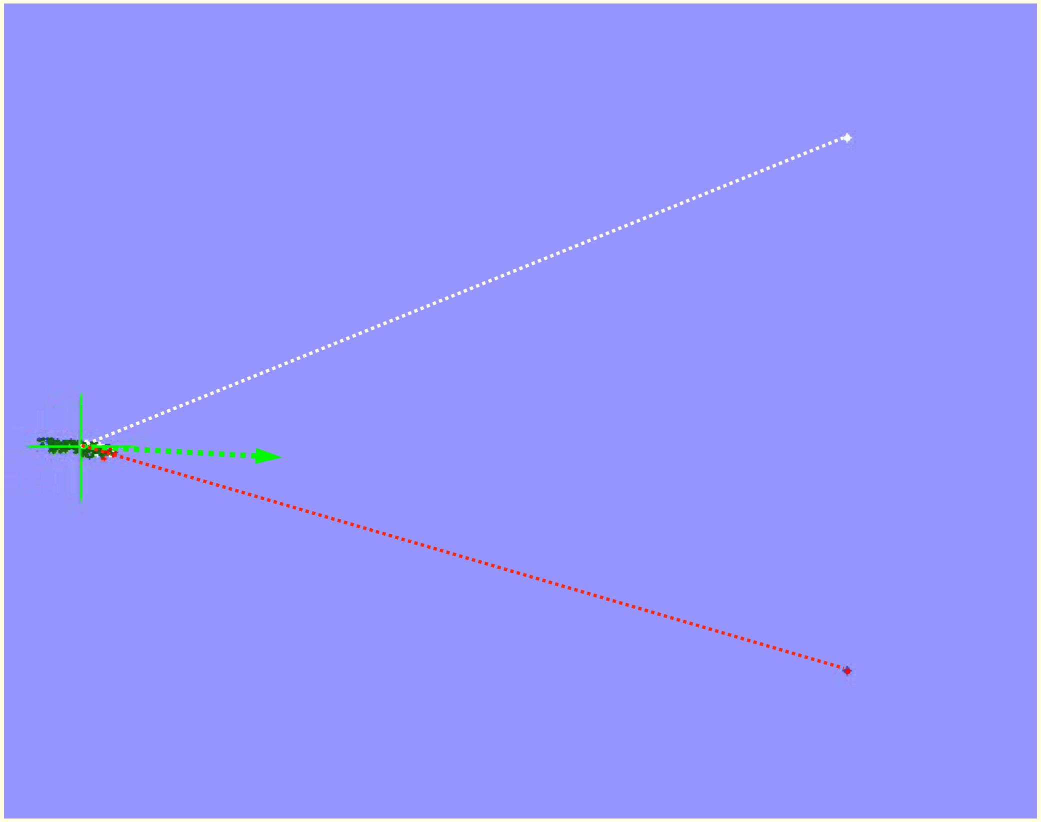


Metronome Synchronization

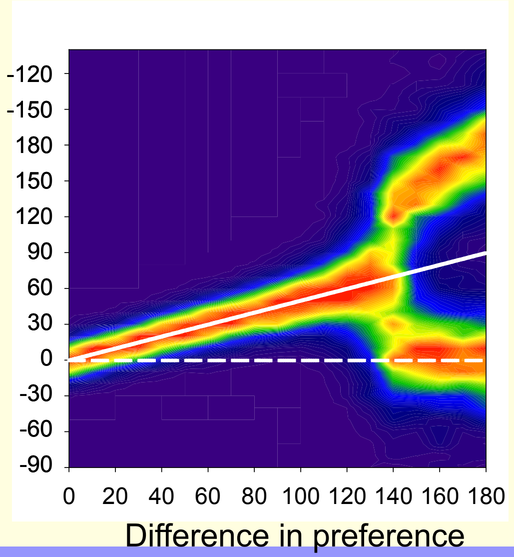
N=5
Rate=208+/-2
Initial Phase: Rand
09 Oct 2005
Serial V1322

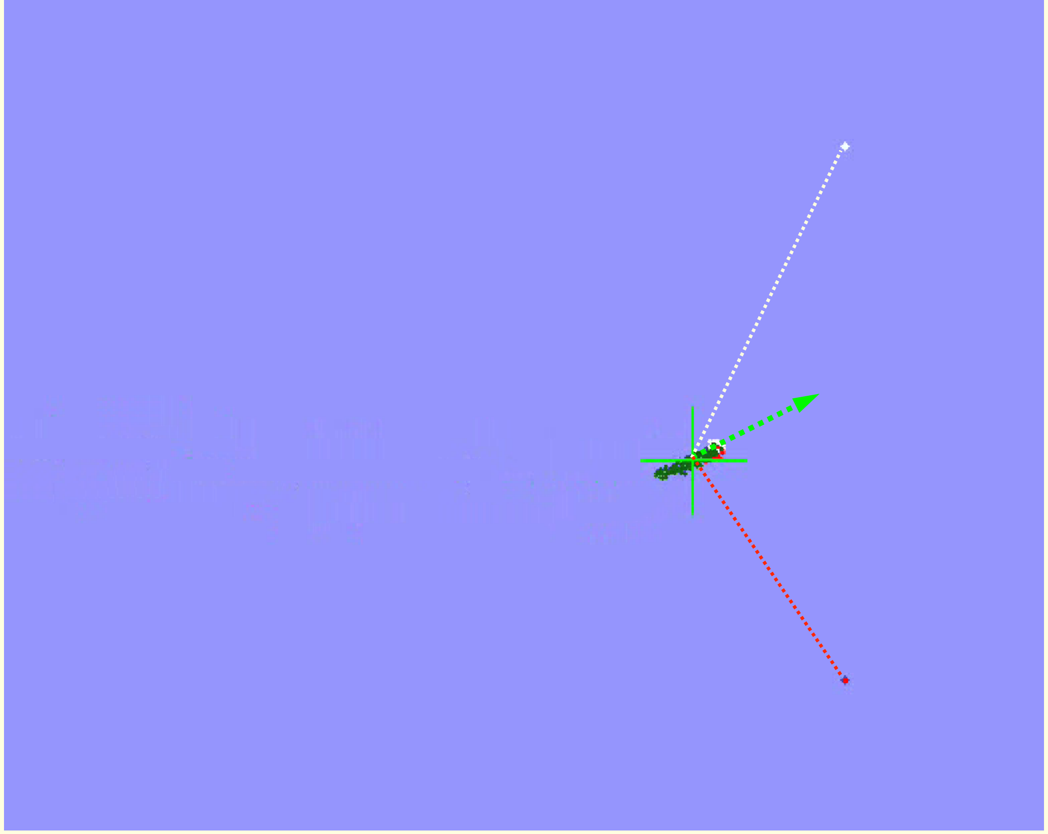
Competing preferences

Difference in preference

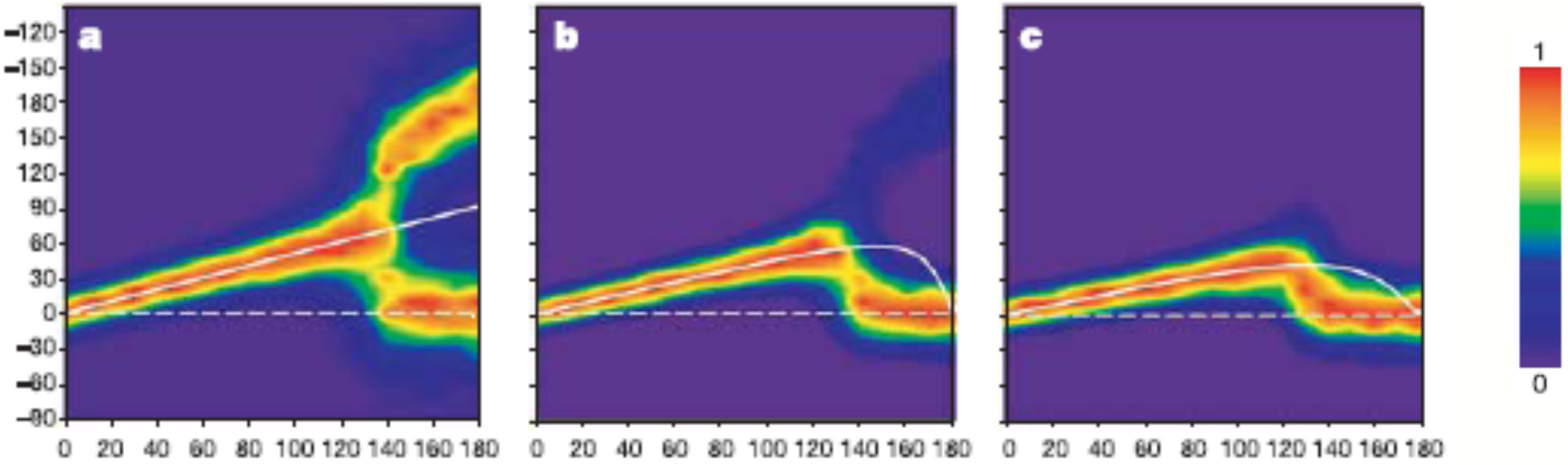


Collective decision-making

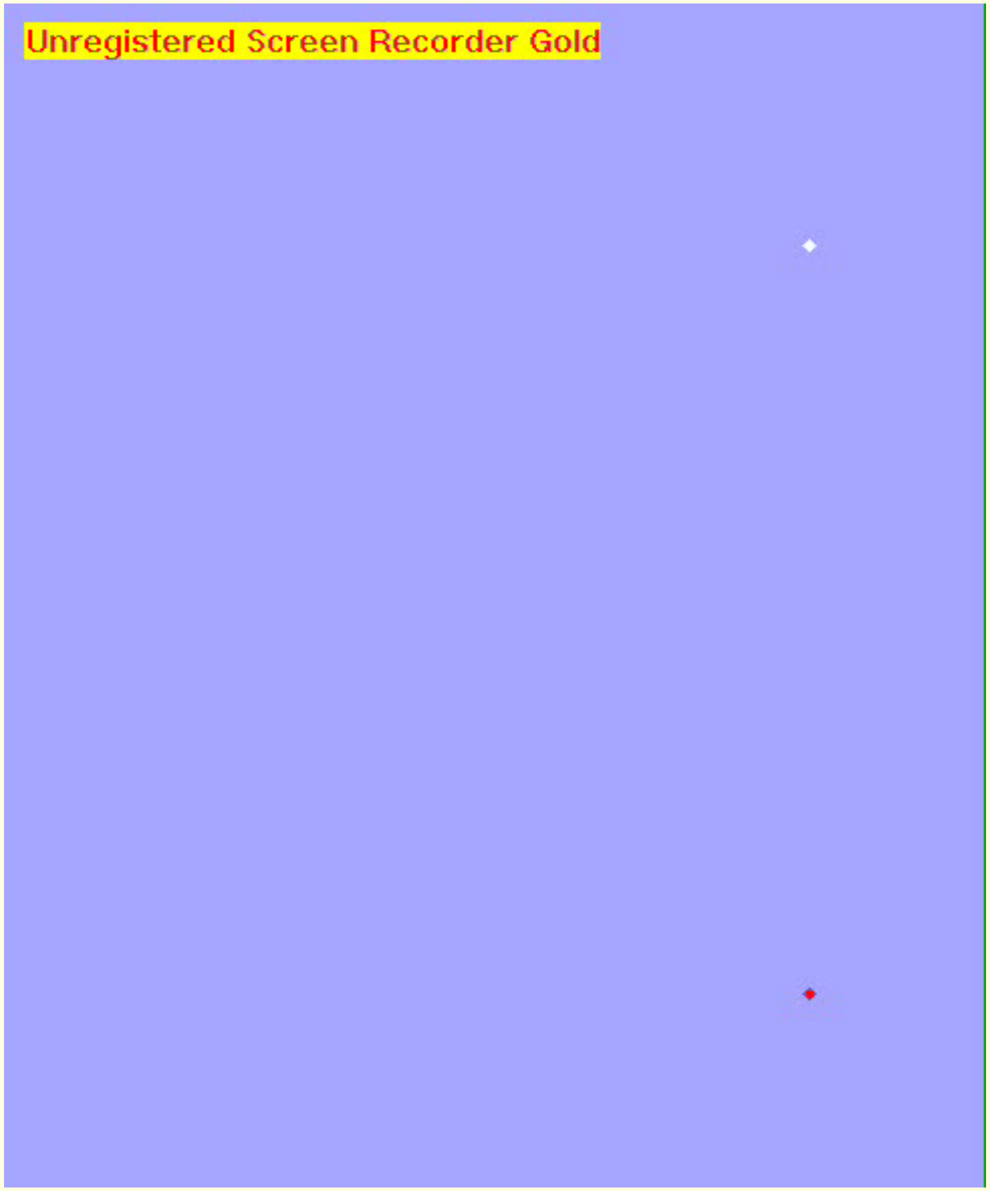


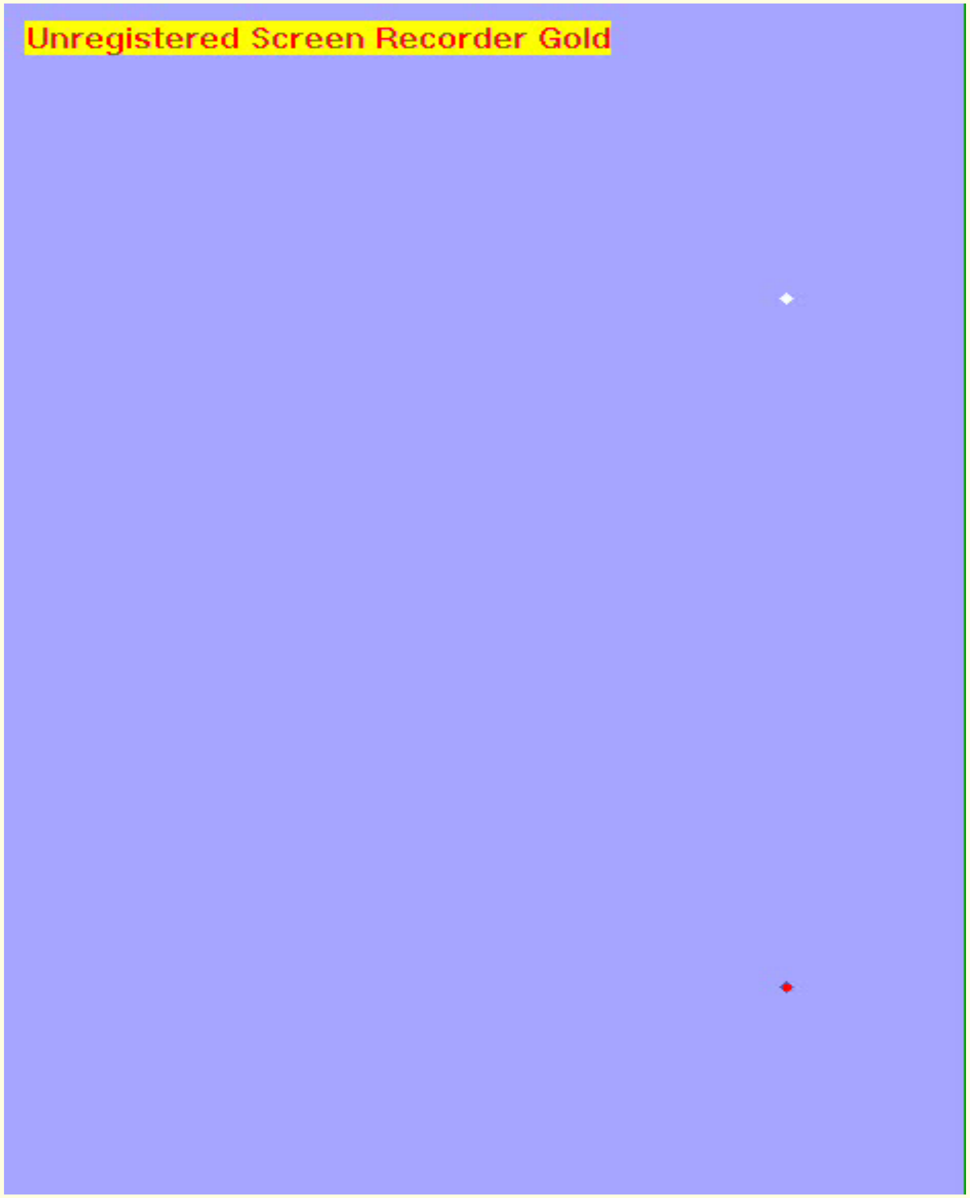


Unequal numbers of leaders



Couzin, I.D., Krause, J., Franks, N.R. and Levin, S.A. (2005) *Effective leadership and decision-making in animal groups on the move.* Nature 434, 513-516





Efforts to understand simulations

- *Leonard, Nabet*
- *Kevrekidis, Moon*
- *Couzin, Levin*
- Strong connections to control theory

Distributed, communicating robots

Naomi Leonard

A continuous multi-agent model with simple interconnections

We consider $N = N_1 + N_2 + N_3$ individuals divided into 3 subgroups.

- N_1 individuals with preferred direction $\bar{\theta}_1$
- N_2 individuals with preferred direction $\bar{\theta}_2$
- N_3 individuals with no preferred direction

These individuals are moving at constant speed in a given plane seeking to stay together.
We are only considering the dynamics of their heading.

Kuramoto model

$$\dot{\theta}_j = \sin(\bar{\theta}_1 - \theta_j) + k \sum_{l=1}^{N} \sin(\theta_l - \theta_j) \qquad j = 1, \ldots, N_1$$

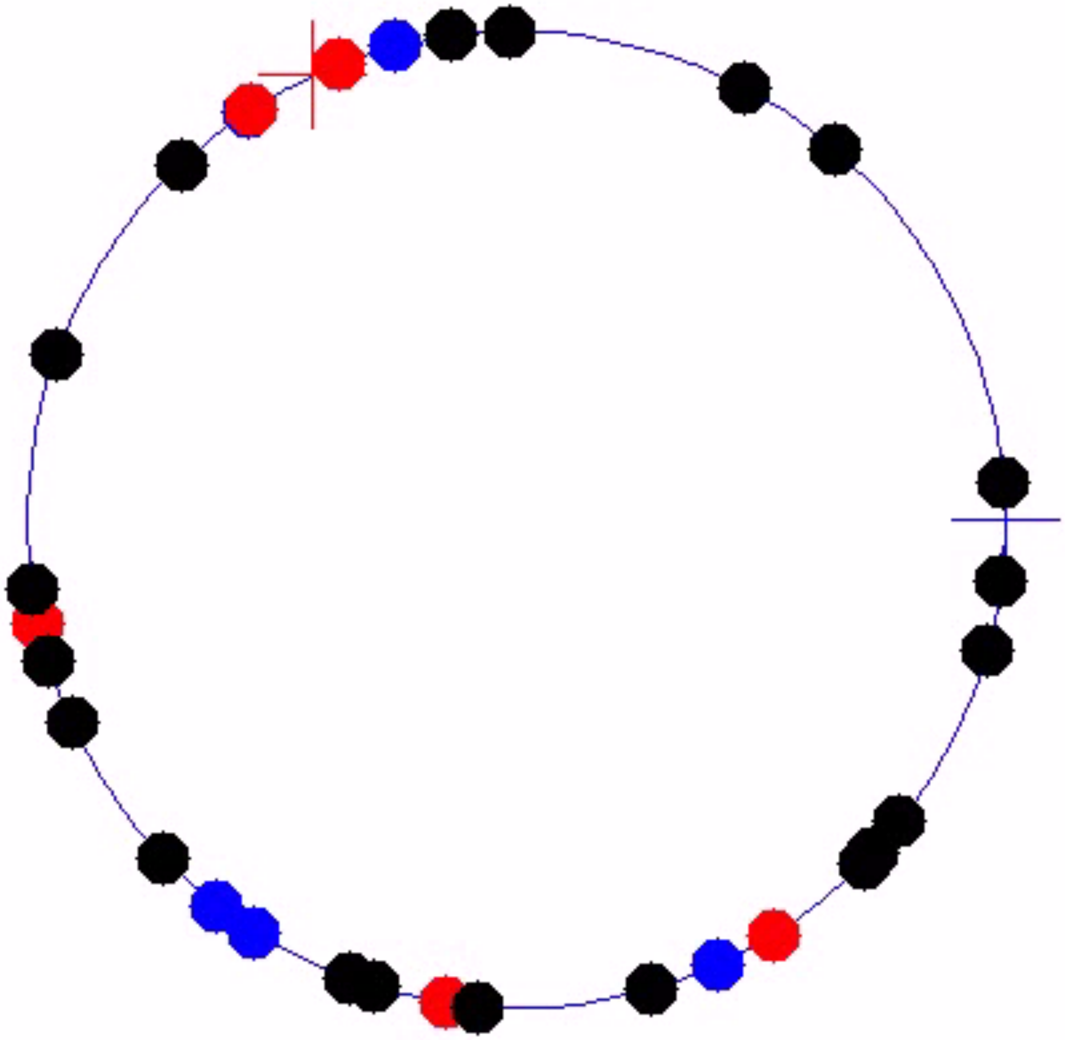
$$\dot{\theta}_j = \sin(\bar{\theta}_2 - \theta_j) + k \sum_{l=1}^{N} \sin(\theta_l - \theta_j) \qquad j = N_1 + 1, \ldots, N_1 + N_2$$

$$\dot{\theta}_j = k \sum_{l=1}^{N} \sin(\theta_l - \theta_j) \qquad j = N_1 + N_2 + 1, \ldots, N$$

Gradient system, with potential

$$V = \sum_{j\in\mathcal{N}_1} \cos(\bar{\theta}_1 - \theta_j) + \sum_{j\in\mathcal{N}_2} \cos(\bar{\theta}_2 - \theta_j) + \frac{K}{N} \sum_{l=j+1}^{N} \sum_{j=1}^{N-1} \cos(\theta_j - \theta_l)$$

So all solutions go to equilibrium

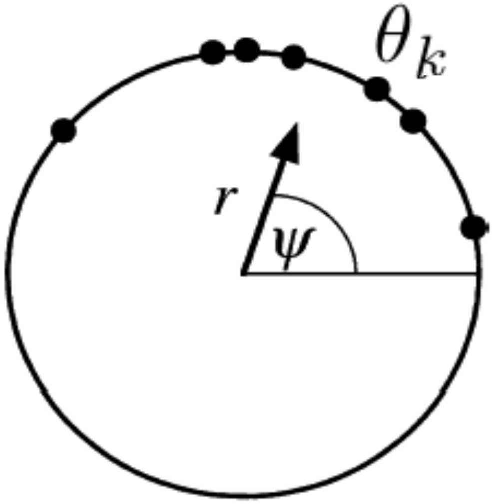


Multiple scales

Bifurcation analysis

The complex order parameter

$$p_\theta = re^{i\psi} = \sum_{j=1}^{N} e^{i\theta_j}$$



r measures the level of synchrony in the group,
ψ gives the average direction of the group.

A lump model

We write the dynamics for ψ_1, ψ_2, ψ_3 the average heading of respectively η_1, η_2 and η_3.

$$r_j e^{i\psi_j} = \frac{1}{N_j} \sum_{l \in \eta_j} e^{i\theta_l} \qquad j = 1, 2, 3$$

$$\dot{r}_j e^{i\psi_j} + i\dot{\psi}_j = \frac{1}{N_j} \sum_{l \in \eta_j} i\dot{\theta}_l e^{i\theta_l} \qquad j = 1, 2, 3.$$

During the second time scale

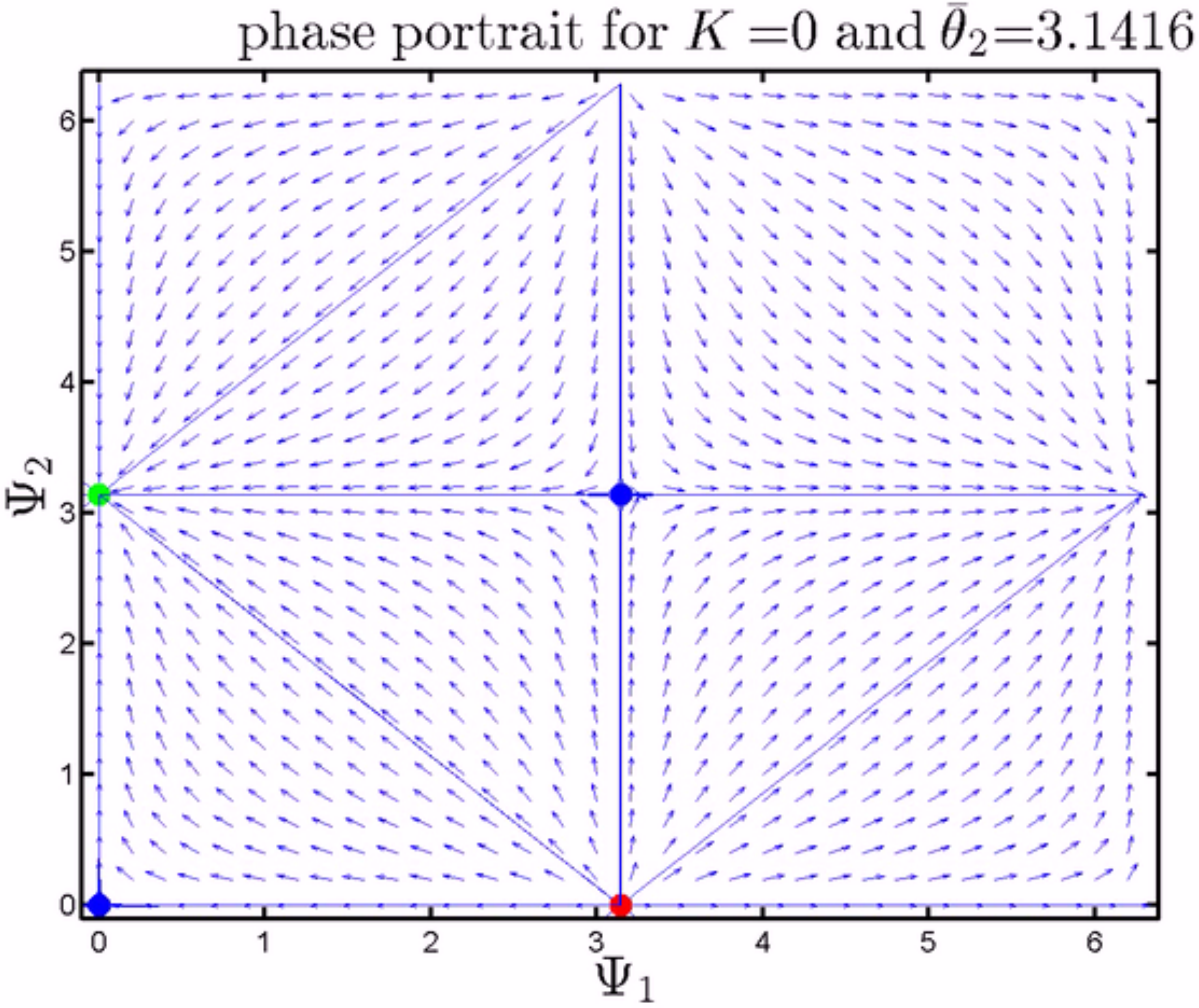
$$\begin{aligned} \theta_l &= \psi_j \\ r_j &= 1 \\ \dot{r}_j &= 0 \end{aligned}$$

Everyone in cluster has same heading

A lump model

We get for the second time scale

$$\begin{aligned}
\dot{\psi}_1 &= \sin(\bar{\theta}_1 - \psi_1) + kN_2 \sin(\psi_2 - \psi_1) + kN_3 \sin(\psi_3 - \psi_1) \\
\dot{\psi}_2 &= \sin(\bar{\theta}_2 - \psi_2) + kN_1 \sin(\psi_1 - \psi_2) + kN_3 \sin(\psi_3 - \psi_2) \\
\dot{\psi}_3 &= kN_1 \sin(\psi_1 - \psi_3) + kN_2 \sin(\psi_2 - \psi_3)
\end{aligned}$$



phase portrait for K =0 and $\bar{\theta}_2$=3.1416

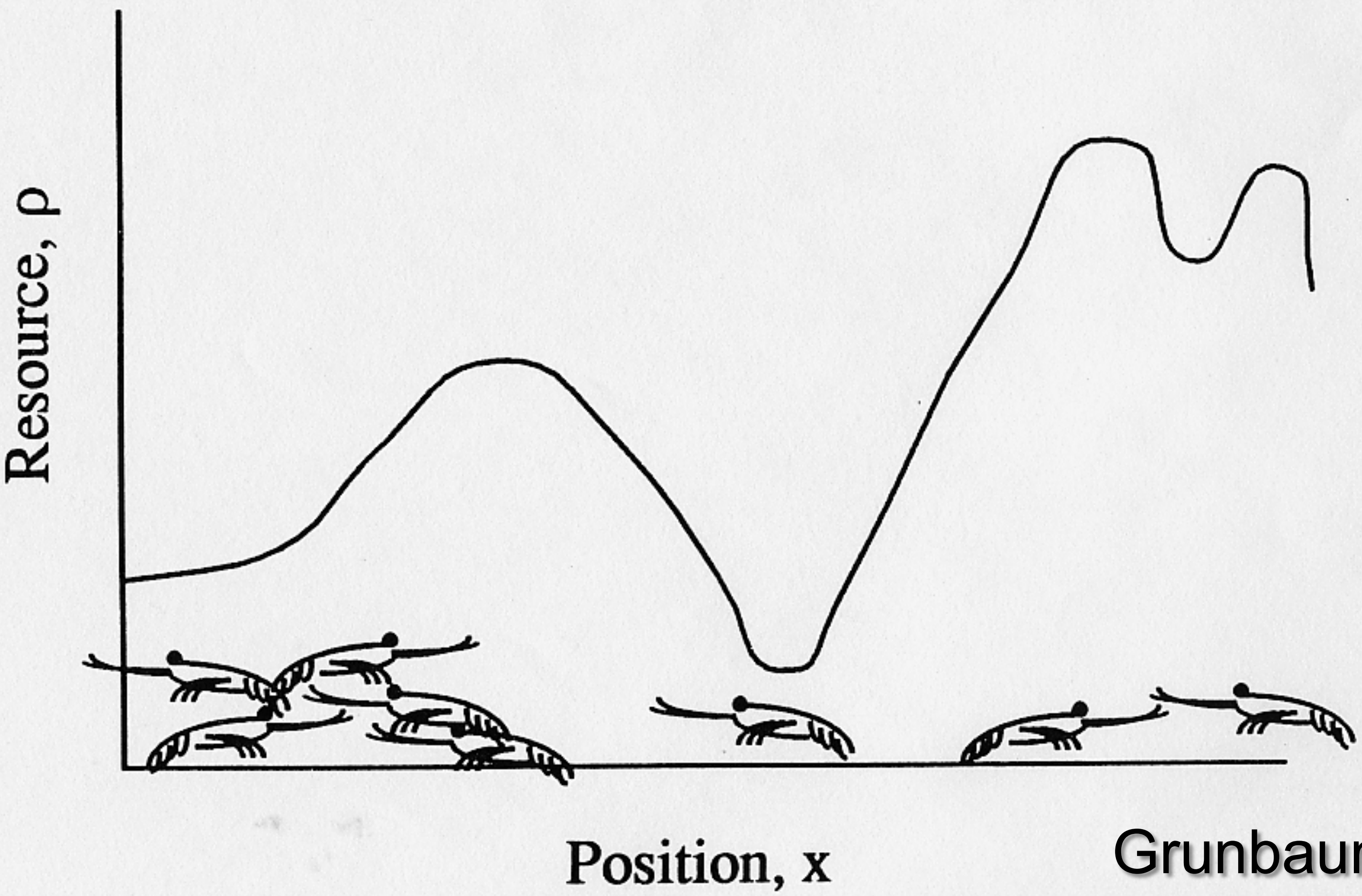
Conclusions

- Naïve individuals are crucial to consensus
- Non-spatial models miss key detail
- Multi-scale analyses also essential

That’s ecological

What strategies does evolution shape?

What is the value of information?



Searching on Resource Landscapes

Grunbaum

How does selection shape the trade-off between tracking resources and tracking other individuals?

Guttal and Couzin

- Two evolvable parameters, gradient-following and neighbor-following
- Depending on values of parameters, may evolve
  - Solitary random walk or migratory behavior
  - Aggregation
  - Fission-fusion dynamics

Evolving specialized leadership roles

- Assume reproductive fitness is dependent on following a defined migration route
- The route is not known a priori but shown by environmental cues
- Detecting these cues is costly (e.g. lost foraging time, reduced predator vigilance, energetic costs of exploration)
- Naive following of others is a low cost alternative strategy

Specialization and evolutionary branching within migratory populations
Colin Torney, Simon A. Levin & Iain D. Couzin (PNAS, to appear

Evolving specialized leadership roles

- Model fluctuating environmental signal as a stochastic process
- Individual heading θ follows mean reverting process, where θ=0 is the optimum migration direction

$$d\theta_t = -x_g \theta dt + \sigma dW_t$$

Level of investment in detecting the environmental cue

Noise term, representing fluctuations or errors in detection

- Level of investment x_g is costly but following others is free

Natural selection

- Select for highest average migration speed, minus a cost function

Evolution: In absence of social information, fitness is

$$F = \exp(-\sigma^2 / 4 x_g)$$

Mean Velocity

Quantifying the social information

- Follow Kuramoto's approach for coupled oscillators to reduce population orientations to 2 dimensional order parameter

$$\frac{1}{N}\sum_{i=1}^{N} e^{i\theta} = \int_{-\pi}^{\pi} \rho(\theta) e^{i\theta} d\theta = r e^{i\psi}$$

Average heading

Degree of ordering, *r = 0* complete disorder, *r* = 1 completely aligned

- Leads to coarse grained representation of social interactions

$$d\theta_t = -x_s(\theta - \psi)dt + \eta\sqrt{(1-r)}dW_t$$

Level of sociality

Turns toward mean population heading

Noise is decreasing function of degree of ordering

Add these together

$$d\theta_t = (x_g d\theta_g + x_s d\theta_s)/(x_g + x_s)$$

Adaptive dynamics and branching

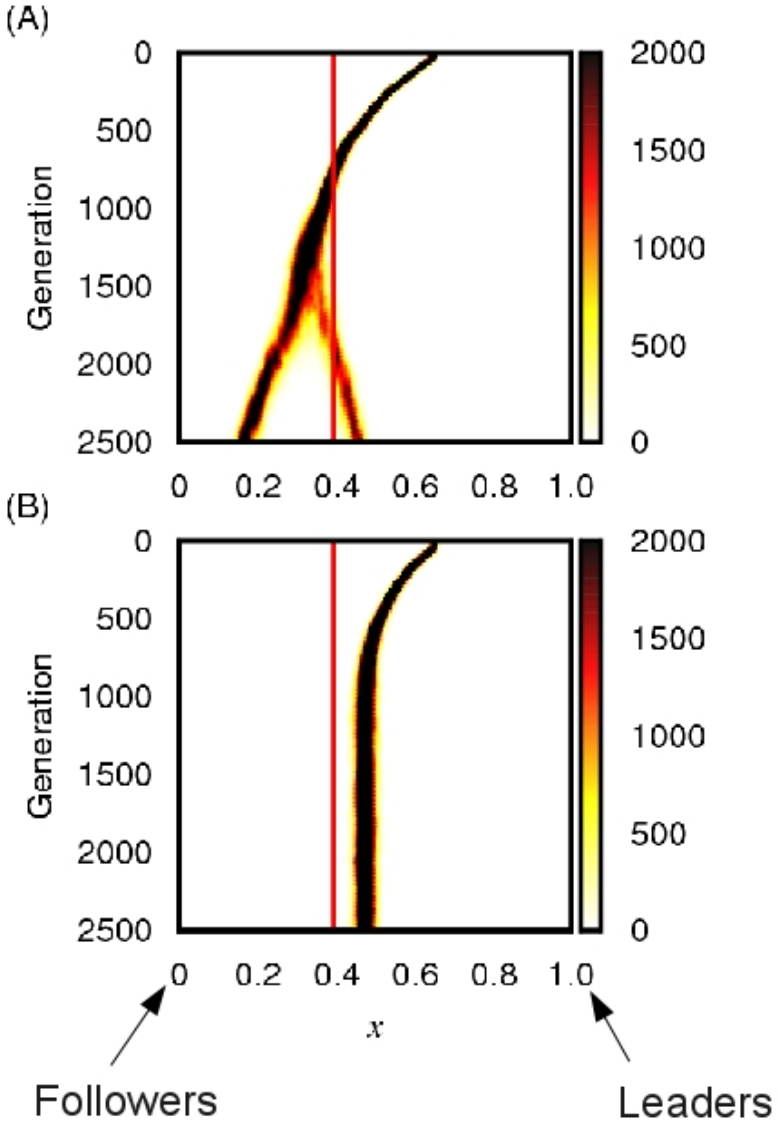
- Evolutionary change determined by differential fitness of mutant in the resident population

$$s_x(y) = F(y,x) - F(x,x)$$

- Population moves toward convergence stable solution (CSS)
- But if CSS not an evolutionary stable solution (ESS) branching will occur -

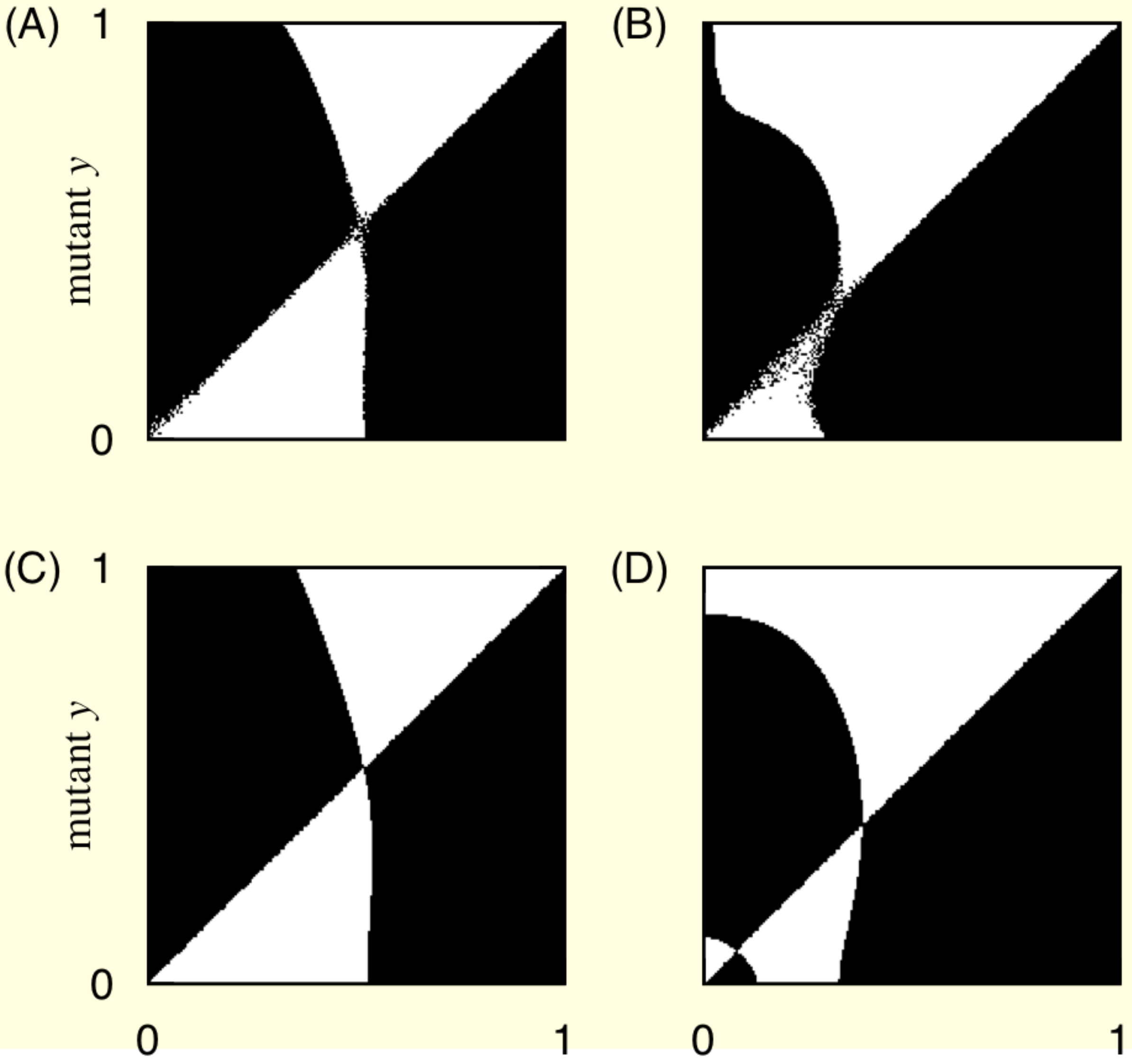
$$\left.\frac{\partial^2 F(y,x^*)}{\partial y^2}\right|_{y=x^*} > 0$$

- Branching and specialized sub-populations of leaders and followers emerge if CSS is less than critical value (red line)



Invasibility plots

Dark: Mutant can invade



Conclusions:

Collective motion is important biologically, and raises fascinating mathematical problems

- Statistical mechanics of collectives
- Multi-scale dynamics
- Game theory
- Unifying theory and experiment/ observation

Can such simplistic insights be extended to human groups?

How much does herd behavior explain?

Can we model the dynamics of social norms?

- Antibiotic use
- Energy use
- Environmental protection
- Consumption

Social norms can be good

- Charitable giving
- Systems of justice
- Moral persuasion

www.pwgsc.gc.ca

Social norms can be good *or they can be bad*

- Charitable giving
- Systems of justice
- Moral persuasion
- Caste systems
- Overconsumption

www.starlimos.de

www.weirdthings.org

Equity is a fundamental aspect of achieving sustainability

Sao Paolo

Equity can only be achieved through

- Concern for others and sense of fairness
- Social norms and international agreements that incorporate these principles

We live in a global commons, in which

- Individual agents act largely in their own self-interest

www.centerstage-musicals.com

We live in a global commons, in which

- Individual agents act largely in their own self-interest
- Social costs are not adequately accounted for

Courtesy ODOT

www.enn.com/news/enn-stories/2001

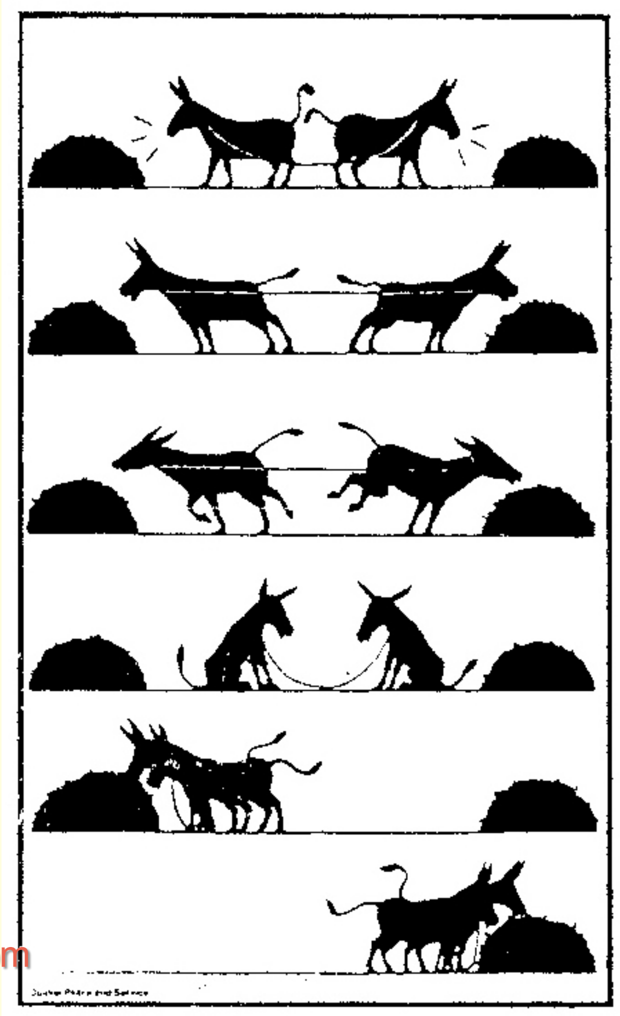
The challenge….achieving cooperation at the global level

For public goods, leads to *The Tragedy of the Commons*

Aelbert_Cuyp

William Forster Lloyd (1832)

But cooperation does arise in Nature…and in theory



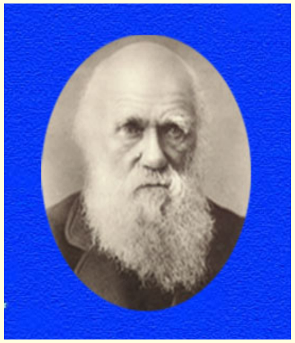
How?

peoplesgeography.files.wordpress.com

The evolution of altruism and cooperation

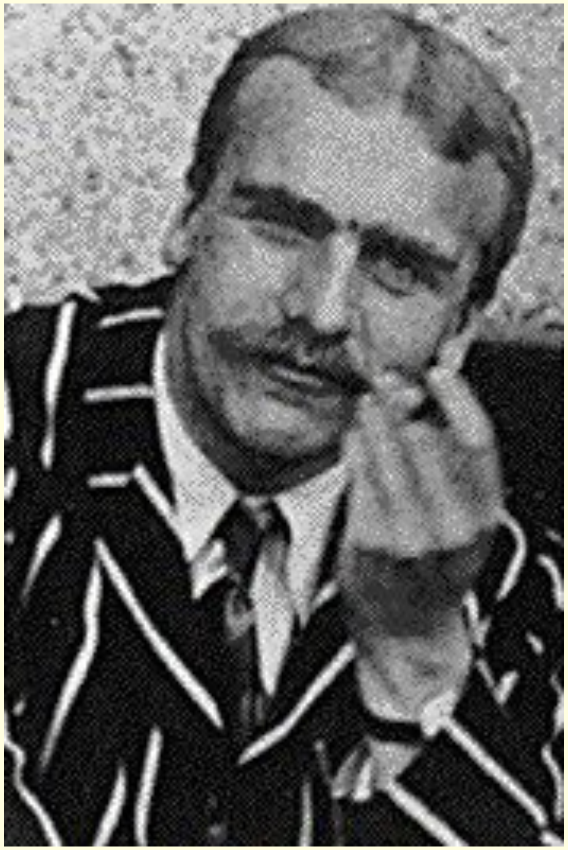
- Altruism was a puzzle for Charles Darwin

morningnoonandnight.files.wordpress.com



Delayed publication of "Origin of Species" for twenty years

Now well-understood that altruism and cooperation facilitated by close genetic relationship



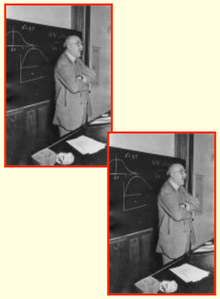
www.blackwellpublishing.com

J.B.S.Haldane

I would lay down my life for

Now well-understood that altruism and cooperation facilitated by close genetic relationship

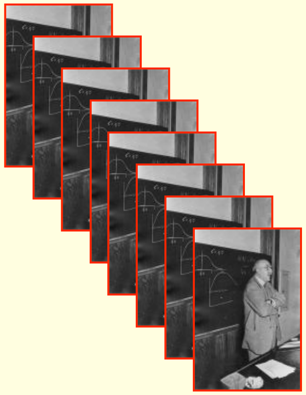
J.B.S.Haldane



Two siblings

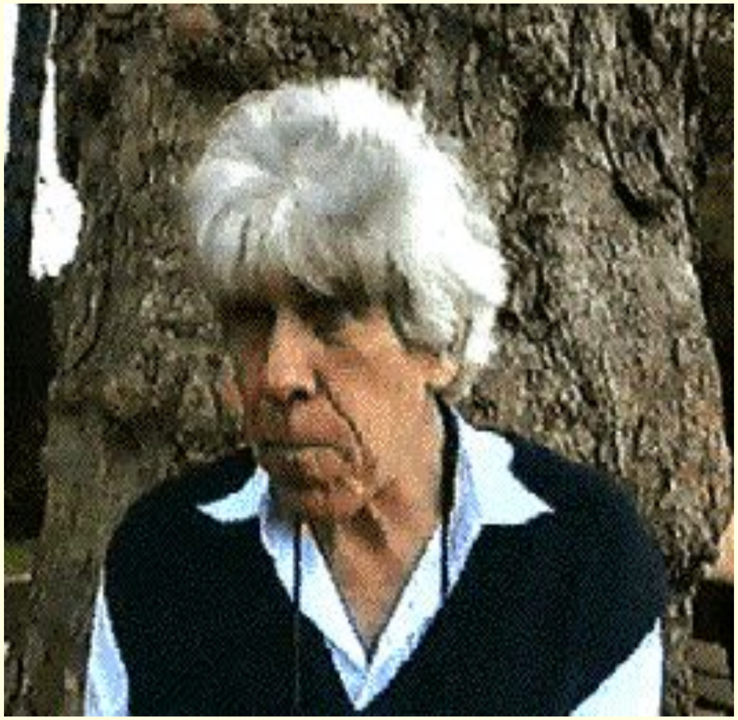
Now well-understood that altruism and cooperation facilitated by close genetic relationship

J.B.S.Haldane

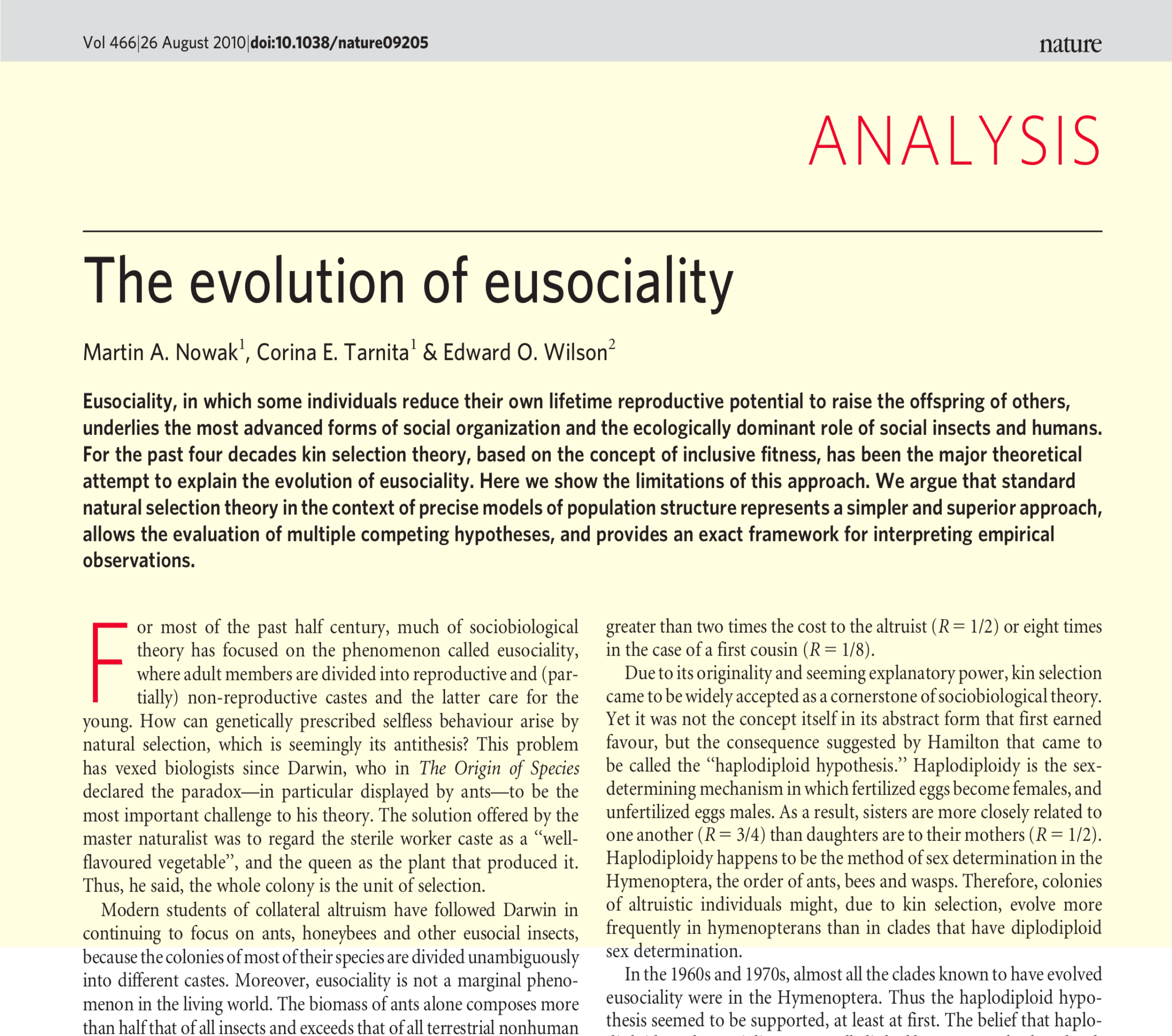


Or eight cousins

W.D.Hamilton and the social insects



Well, not as well-understood as it used to be



Vol 466|26 August 2010|**doi:10.1038/nature09205**

nature

ANALYSIS

The evolution of eusociality

Martin A. Nowak[1], Corina E. Tarnita[1] & Edward O. Wilson[2]

Eusociality, in which some individuals reduce their own lifetime reproductive potential to raise the offspring of others, underlies the most advanced forms of social organization and the ecologically dominant role of social insects and humans. For the past four decades kin selection theory, based on the concept of inclusive fitness, has been the major theoretical attempt to explain the evolution of eusociality. Here we show the limitations of this approach. We argue that standard natural selection theory in the context of precise models of population structure represents a simpler and superior approach, allows the evaluation of multiple competing hypotheses, and provides an exact framework for interpreting empirical observations.

For most of the past half century, much of sociobiological theory has focused on the phenomenon called eusociality, where adult members are divided into reproductive and (partially) non-reproductive castes and the latter care for the young. How can genetically prescribed selfless behaviour arise by natural selection, which is seemingly its antithesis? This problem has vexed biologists since Darwin, who in *The Origin of Species* declared the paradox—in particular displayed by ants—to be the most important challenge to his theory. The solution offered by the master naturalist was to regard the sterile worker caste as a "well-flavoured vegetable", and the queen as the plant that produced it. Thus, he said, the whole colony is the unit of selection.

Modern students of collateral altruism have followed Darwin in continuing to focus on ants, honeybees and other eusocial insects, because the colonies of most of their species are divided unambiguously into different castes. Moreover, eusociality is not a marginal phenomenon in the living world. The biomass of ants alone composes more than half that of all insects and exceeds that of all terrestrial nonhuman

greater than two times the cost to the altruist ($R = 1/2$) or eight times in the case of a first cousin ($R = 1/8$).

Due to its originality and seeming explanatory power, kin selection came to be widely accepted as a cornerstone of sociobiological theory. Yet it was not the concept itself in its abstract form that first earned favour, but the consequence suggested by Hamilton that came to be called the "haplodiploid hypothesis." Haplodiploidy is the sex-determining mechanism in which fertilized eggs become females, and unfertilized eggs males. As a result, sisters are more closely related to one another ($R = 3/4$) than daughters are to their mothers ($R = 1/2$). Haplodiploidy happens to be the method of sex determination in the Hymenoptera, the order of ants, bees and wasps. Therefore, colonies of altruistic individuals might, due to kin selection, evolve more frequently in hymenopterans than in clades that have diplodiploid sex determination.

In the 1960s and 1970s, almost all the clades known to have evolved eusociality were in the Hymenoptera. Thus the haplodiploid hypothesis seemed to be supported, at least at first. The belief that haplo-

Indeed, close genetic relationship not essential for cooperation

Reciprocal altruism also facilitates cooperation

media-2.web.britannica.com

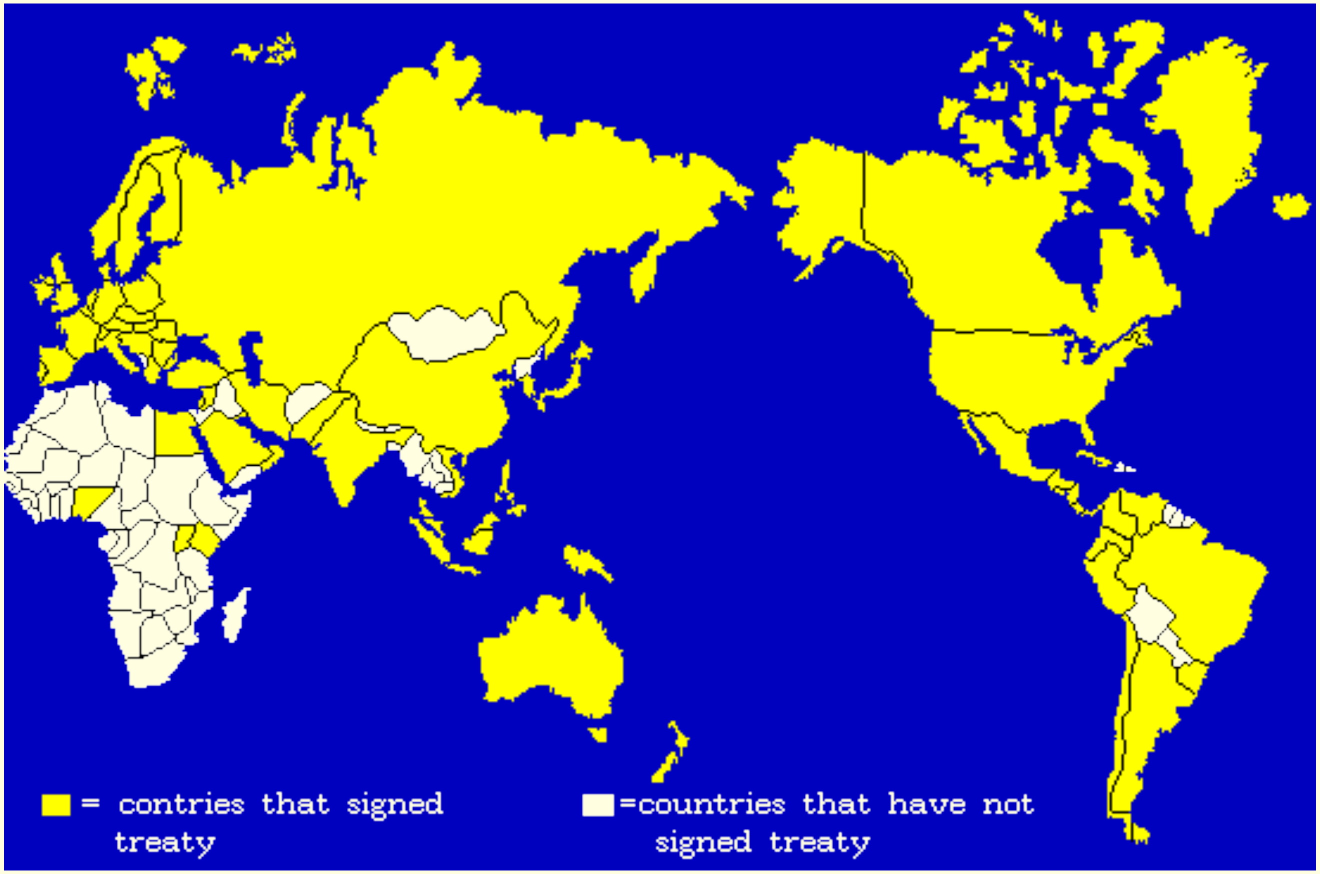
Cooperation is easily explained in small groups, with repeated interactions

blueroof.files.wordpress.com

But how is cooperation sustained in larger groups, like societies?

picdit.files.wordpress.com

And can these principles be extended to the global level?



www.purdue.edu/envirosoft

The Commons solution (Hardin)

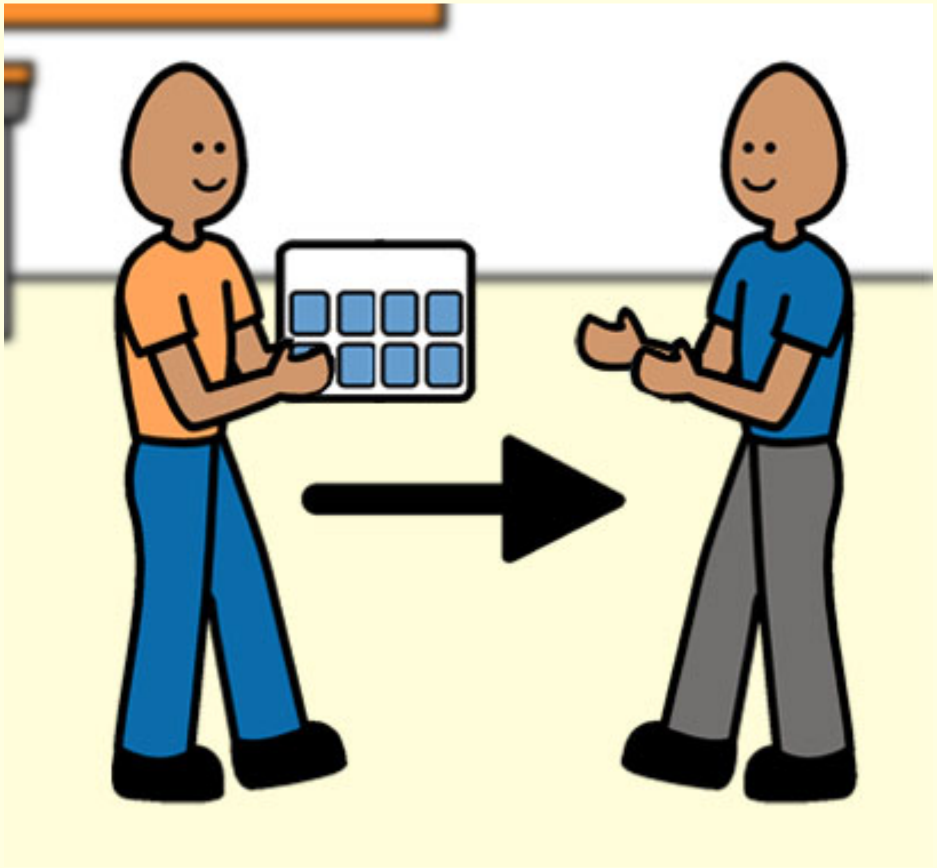
"Mutual coercion, mutually agreed upon"

http://www.physics.ohio-state.edu/~wilkins

The maintenance of cooperation in small societies depends on shared and mutually agreed-upon norms

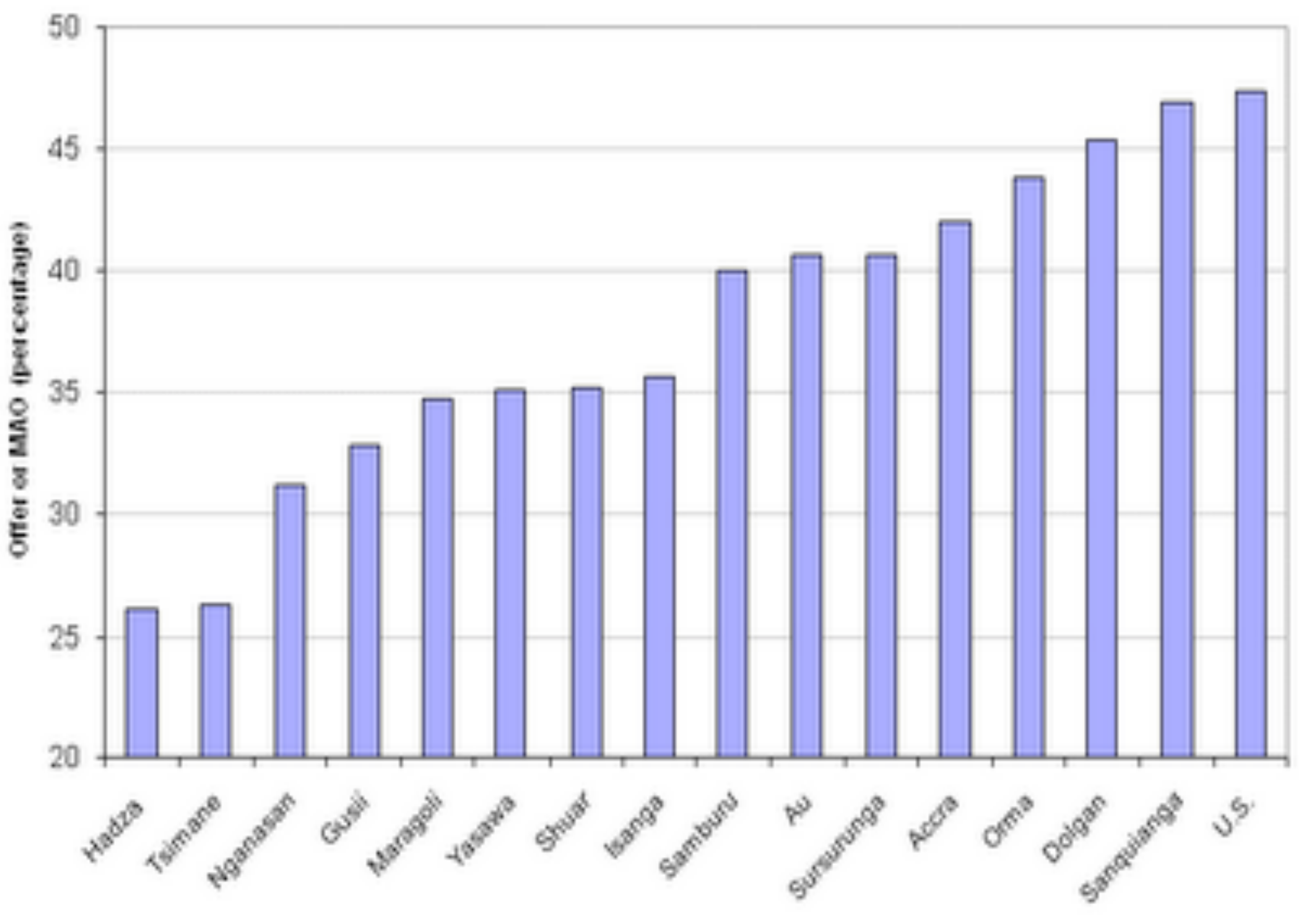
- *Elinor Ostrom, and others, have pioneered the study of how distributed management maintains the stability of common property resources, such as fisheries*

Other-regarding behavior: The Ultimatum Game



www.progressdaily.com

Henrich, J., Heine, S. J., & Norenzayan, A. (in press). The Weirdest people in the world? Behavioral and Brain Sciences.



Cultural differences

	Mean Offer	Mean Reject
US East	41	17
US West	43	9
Chile	34	7
Japan	44	20
Kenya	44	4
Spain	27	29
UK	34	24
Papua/NG	41	34

Modified from Oosterbeek et al., ideas.repec.org

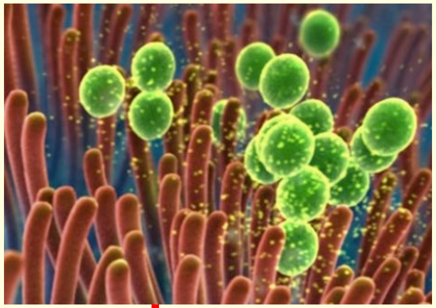
Public goods and punishment

E. Fehr

- Humans will punish others who deviate from social norms, at cost to themselves
- Punishment itself is a norm, and can evolve from repeated interactions
- How do social norms arise and spread?

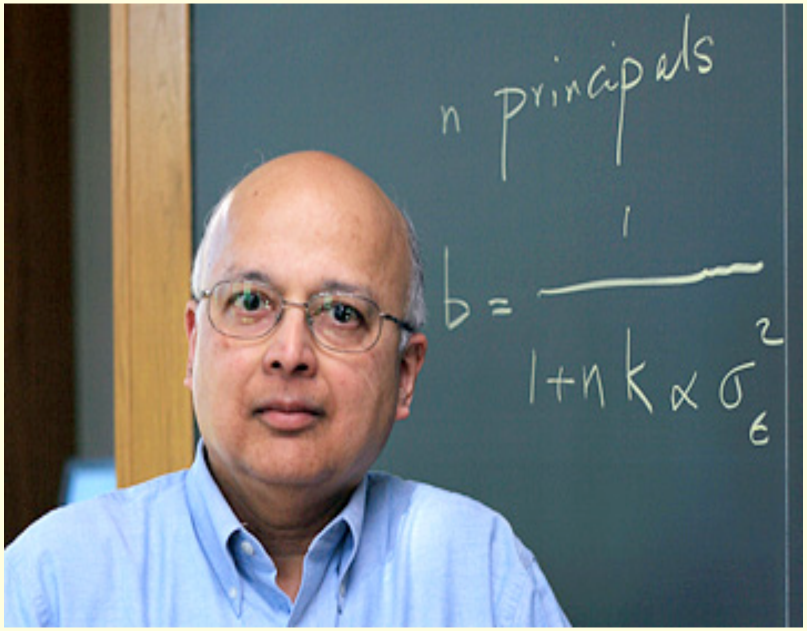
Public goods evolution in Nature

- Production of extracellular proteins
- Defenses against biofilms
- Nitrogen fixation
- Evolution of reduced resource use by plants
- Evolution of reduced predation
- Evolution of reduced virulence



http://www.treehugger.com

Why do individuals contribute to public goods?



Avinash Dixit

Dixit-Levin

Individual utility:

$$v_i = F(x_i, z_i, <z>_i)$$

x=private effort,
z=public effort,
<z>=public pool

Dixit-Levin

x=private effort,
z=public effort,

Individual utility:

$$v_i = F(x_i, z_i, < z >_i) + \sum_{k \neq i} \gamma_{ik} F(x_k, z_k, < z >_k)$$

where γ is *prosociality*, and < z > is the public pool, which benefits from local prosociality and "leakage" from other groups

Example (with Dan Rubenstein)

- Pastoralism and sharing of grazing grounds

http://www.ilri.org/ilrinews/

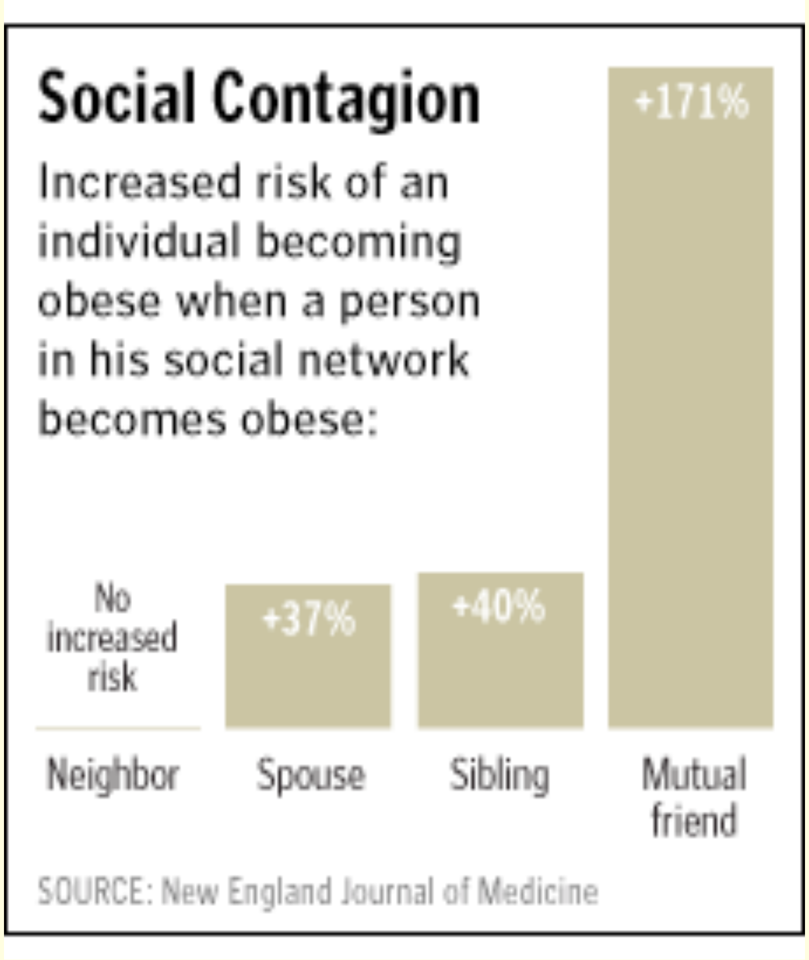
But what selects for group formation and local prosociality?

- Genetic relatedness
- Genetic tendencies for cooperation among unrelated individuals
- Penalties for defection
- Learning and imitation
- Leadership

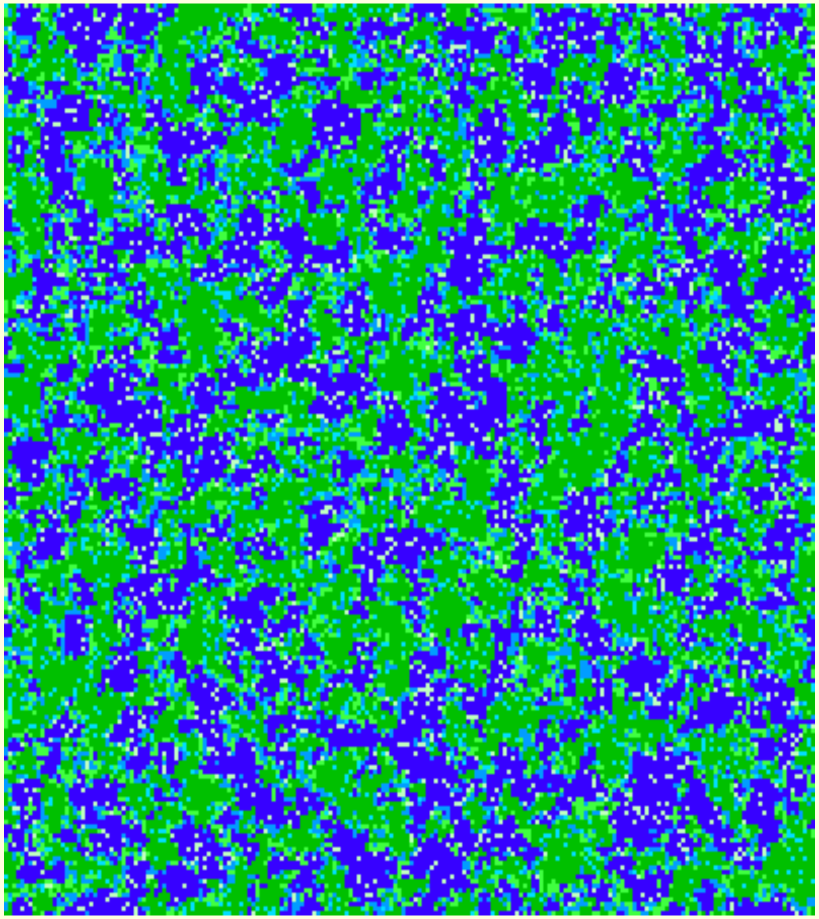
Individuals imitate others' behavior

www.pigeon.psy.tufts.edu

Social contagion and spending

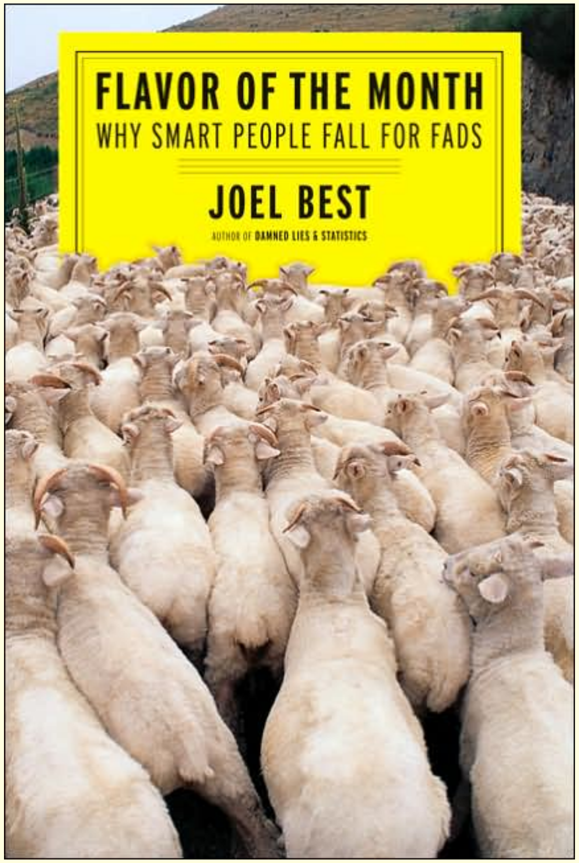


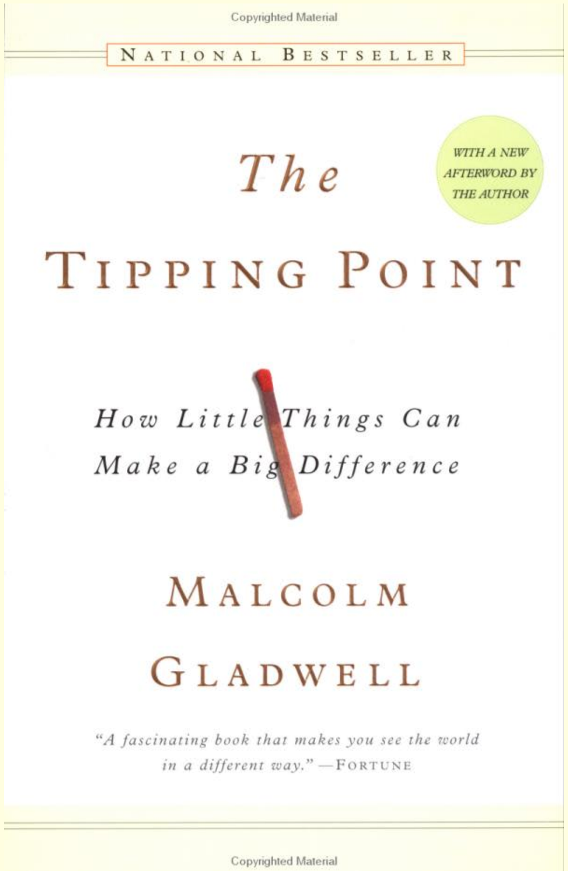
SOURCE: New England Journal of Medicine



http://socialmarketing.blogs.com Durrett and Levin 2005

Implications for social norms: Imitation can drive collective changes in human behaviors





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The

TIPPING POINT

How Little Things Can
Make a Big Difference

MALCOLM
GLADWELL

WITH A NEW AFTERWORD BY THE AUTHOR

"A fascinating book that makes you see the world in a different way." —FORTUNE

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Fundamental questions for studying dynamics of decisions

- How are individual decisions affected by the social context?
- How does the social context, including enforcement, emerge and evolve?
- How does leadership arise, and affect transitions?
- How do collectives arise, and interact with other collectives?

There has been a great deal of work on the dynamics of animal groups

Iain Couzin

But human behaviors are more complicated than those of fish

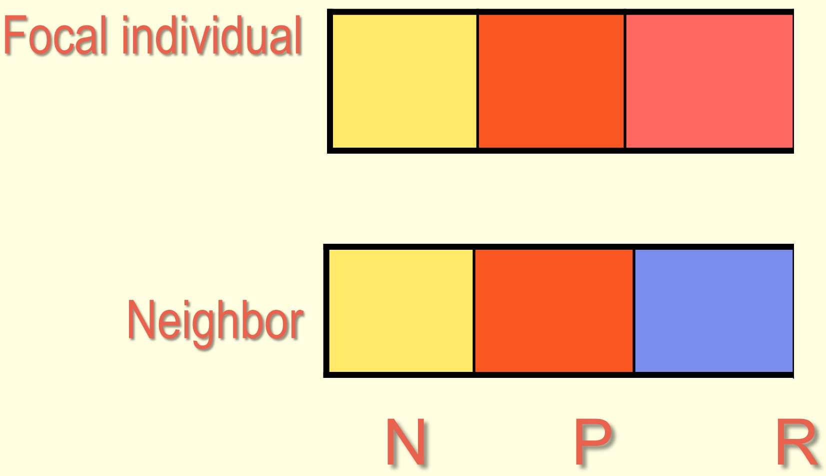
- *Imitation*
- *Responses to cues conditioned by evolution, culture, learning*
- Calculation
- Communication, at a high level

- *Can we tease these apart? How do behaviors arise and spread?*

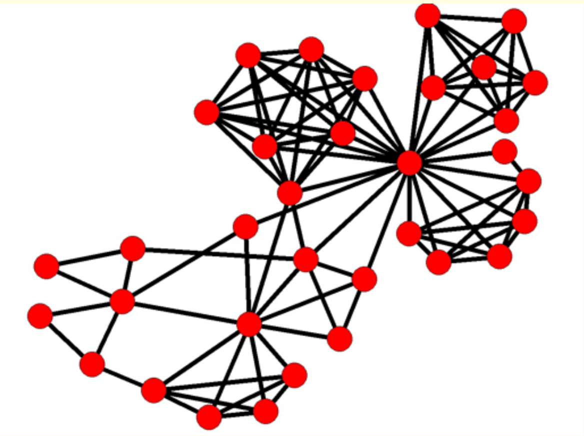
Simplest (Ising) model: Homophilous imitation

Labels

Durrett and Levin JEBO



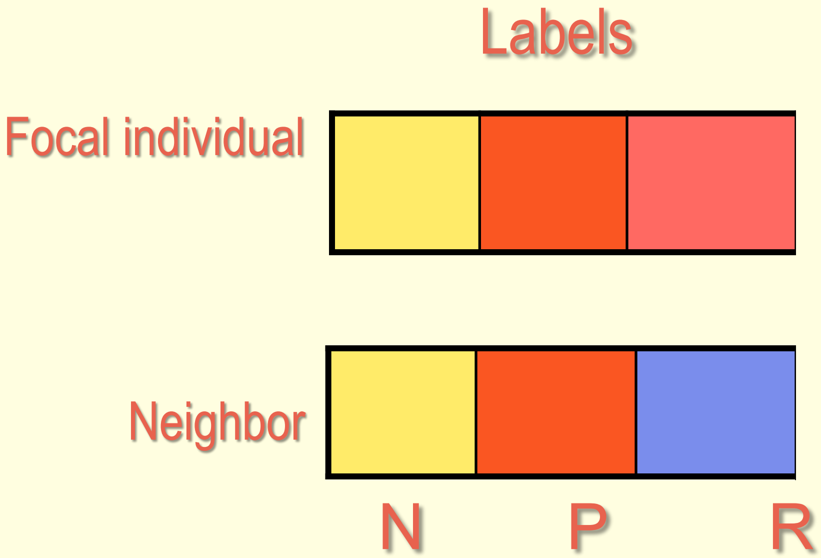
*Nationality (N)
*Political party (P)
*Religion (R)



www.news.ku.edu/MichaelVitevich

Simplest model: Homophilous imitation

Durrett and Levin, JEBO

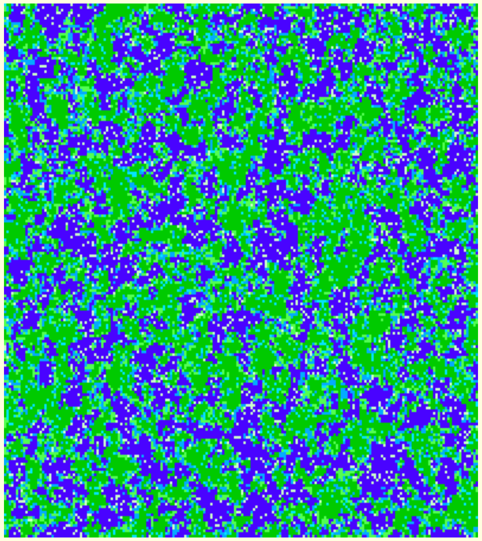

Labels

Focal individual

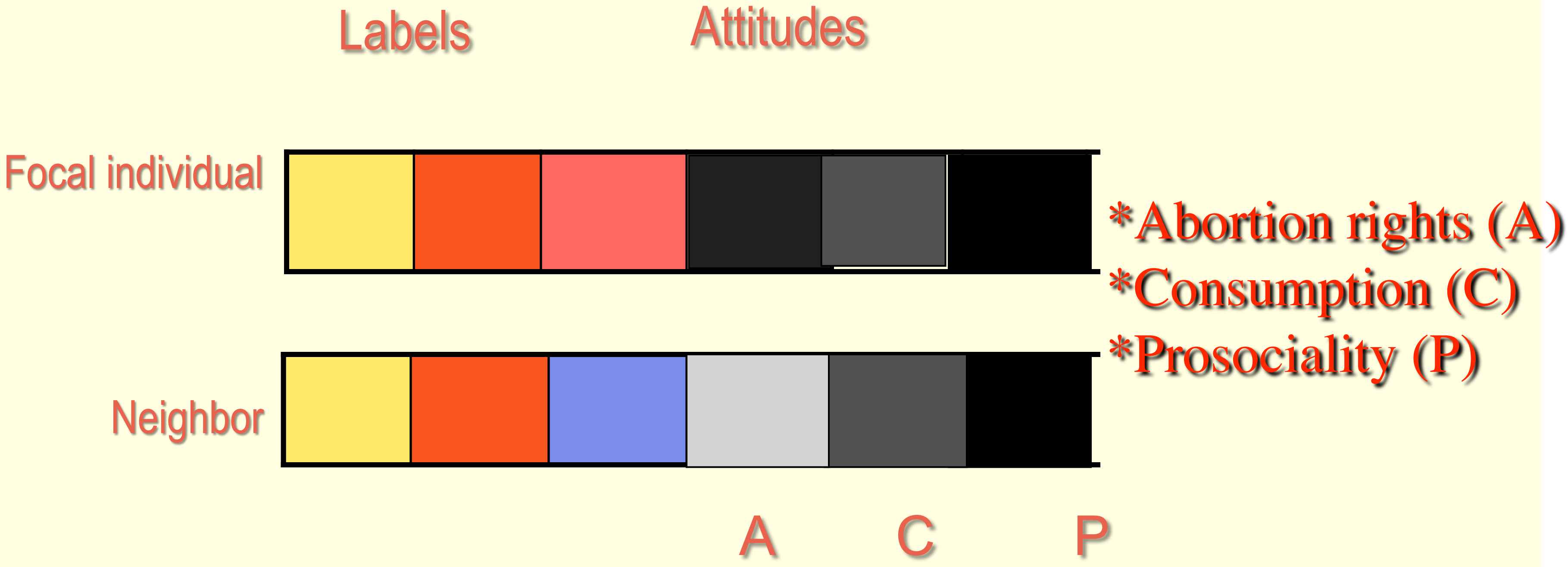
Neighbor

N P R

- *Nationality
- *Political party
- *Religion



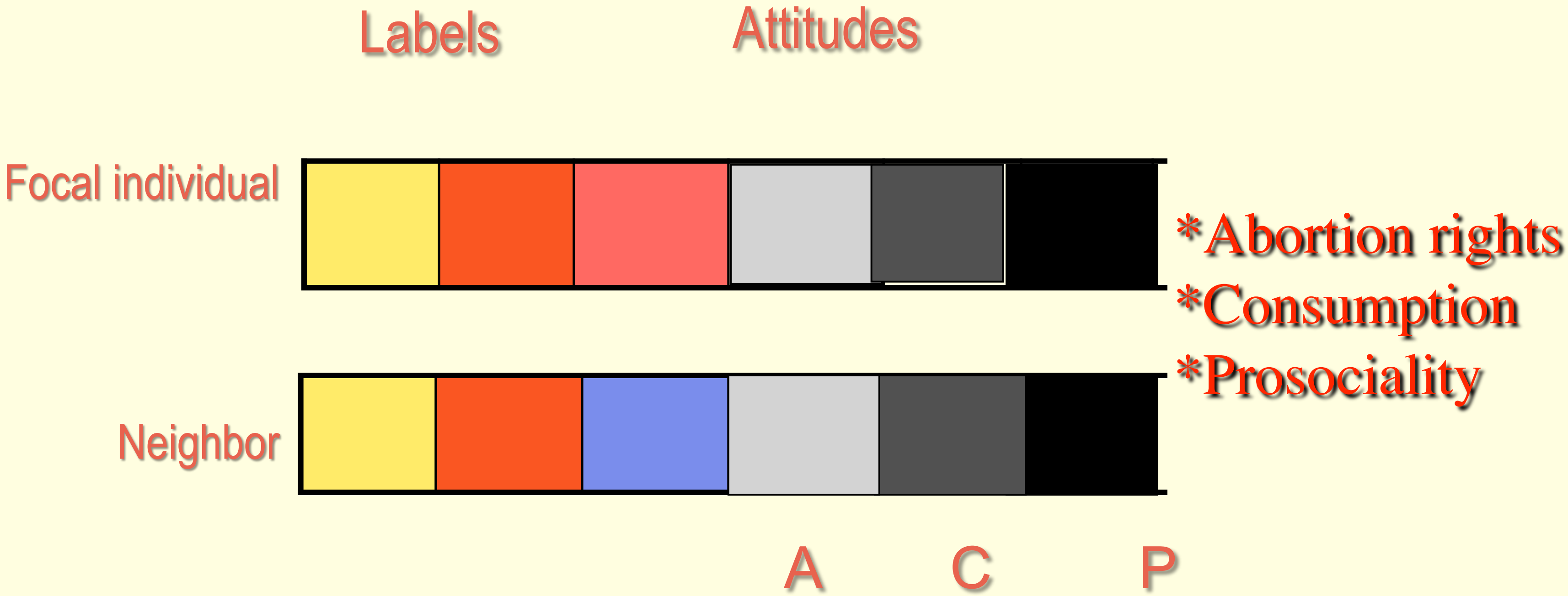
Social norms, multiple traits/opinions



*Abortion rights (A)
*Consumption (C)
*Prosociality (P)

Individuals change opinions
based
on their similarities to neighbors

Social norms, multiple traits/opinions



Labels

Attitudes

Focal individual

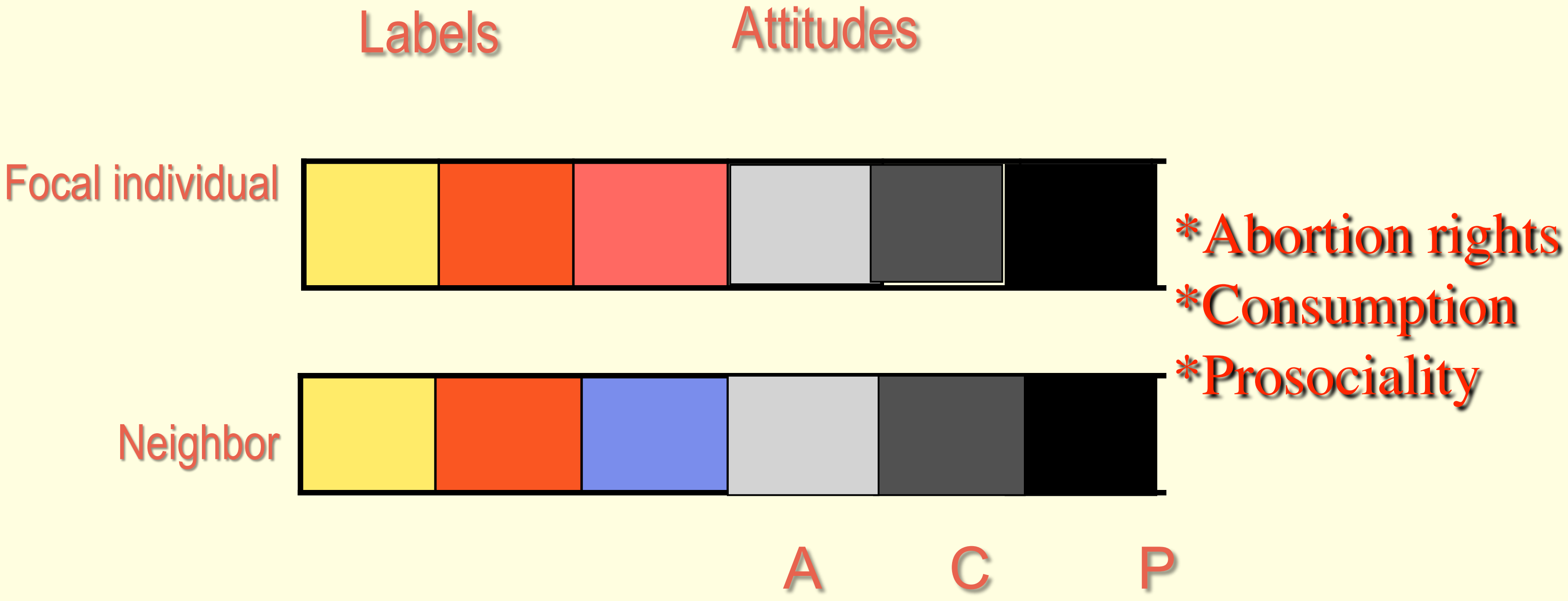
Neighbor

*Abortion rights
*Consumption
*Prosociality

A C P

Individuals change opinions
based
on their similarities to neighbors

Social norms, multiple traits/opinions



Labels

Attitudes

Focal individual

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*Abortion rights
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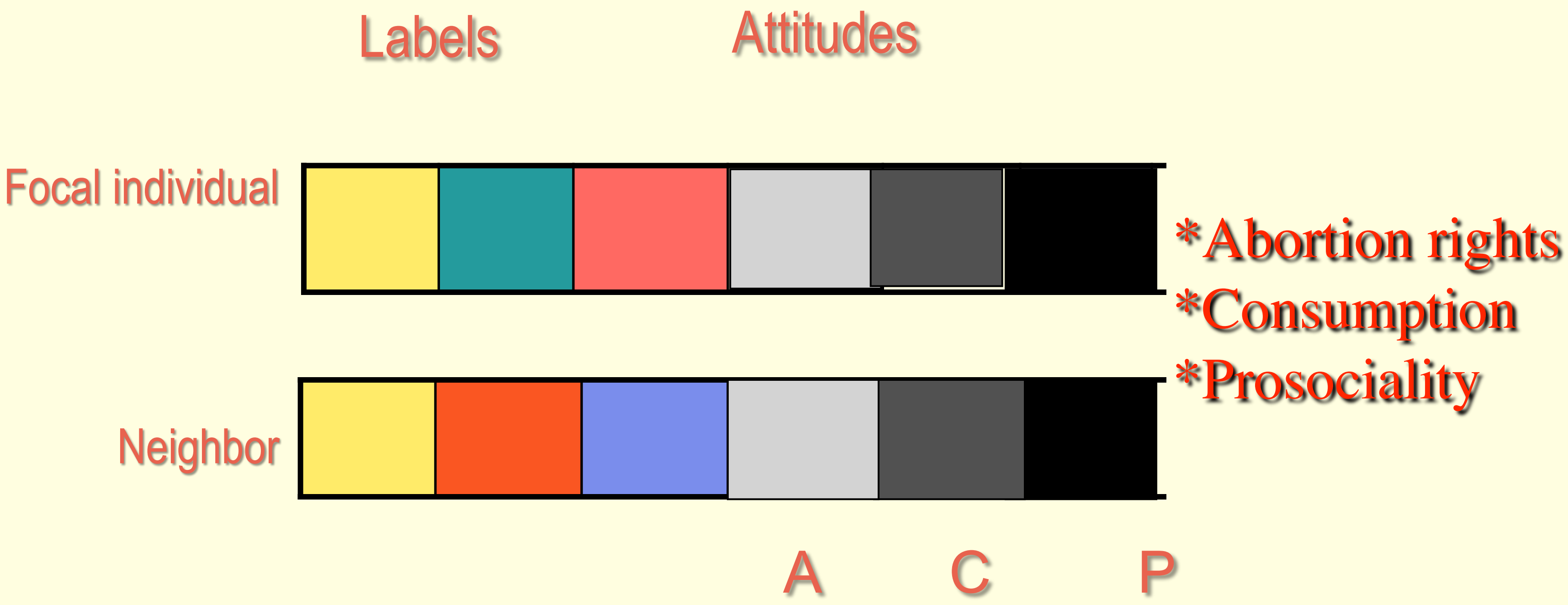
A C P

Individuals may change labels, less often, if their opinions disagree with group norms

Social norms, multiple traits/opinions



Labels

Attitudes

Focal individual

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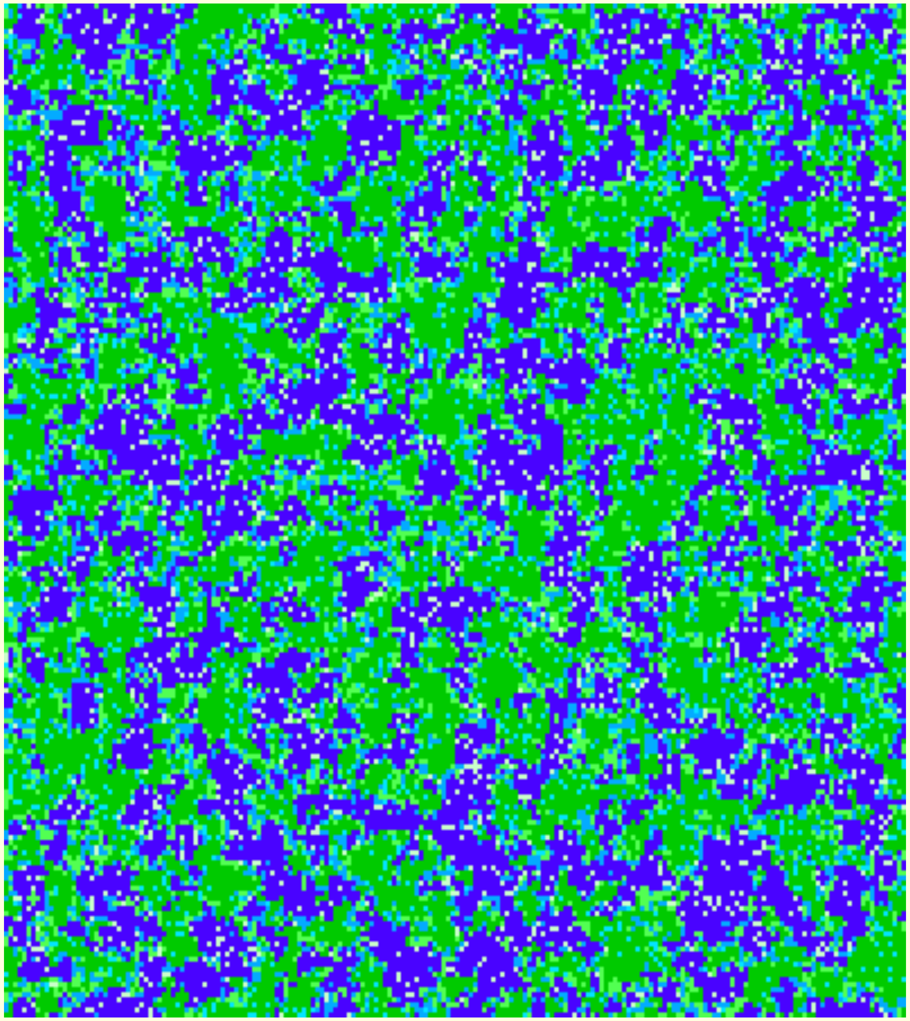
A C P

Individuals may change labels, less often, if their opinions disagree with group norms

Homophilous Imitation



Formation of cooperative groups

- Imitation alone can lead to formation of stable groups
  - Opinions and attitudes on diverse issues may get bundled as “frozen accidents”
  - Sudden shifts are possible

Formation of cooperative groups

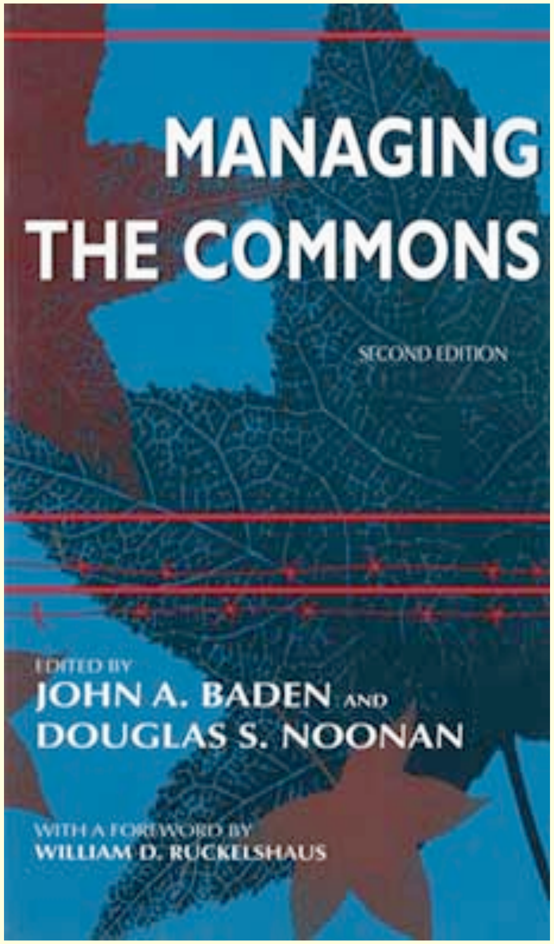
- Imitation alone can lead to formation of stable groups
- Existence of groups can produce collective benefits
  - Enforce communal norms


www.internetsensation.com

Formation of cooperative groups

- Imitation alone can lead to formation of stable groups
- Existence of groups can produce collective benefits, payoffs for membership
- Collective benefits can lead to selection for imitation, local prosociality, less inter-group mixing, intergroup conflict

These considerations influence:
Management issues



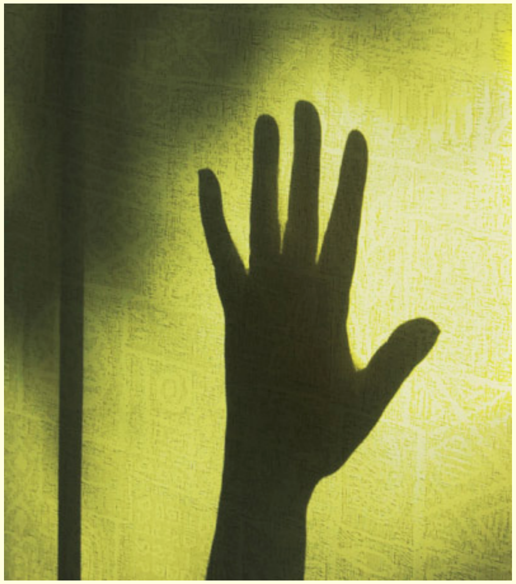
Ecological systems and socio-economic systems alike are complex adaptive systems

http://www.latinamericanstudies.org/maya

The nature of ecological and socioeconomic systems as complex adaptive systems means

- Patterns emerge from and feed back to influence (collective) individual behaviors
- Individual variation represents the capacity of systems to adapt, and to maintain robustness, but..
- Emergent patterns carry no assurance of collective good
- Management requires a balance between free-market and regulation

Adam Smith’s Invisible Hand



www.bized.co.uk

The invisible hand does not protect society

Those lessons are magnified for ecological and environmental systems

media-2.web.britannica.com

The CAS perspective also means

- In both cases, management requires a balance between free-market and regulation
- New institutions must be adaptive
  - Can adaptive features be built in?
  - Robustness
- Trust and cooperation essential
  - Key to macroscopic goals is in microscopic incentives
  - Montreal Protocol?

Can cooperation be extended to the global level?

Emergence of cooperation within groups is often for the benefit of conflict with *other* groups

Lariviere

In the global commons, there is no "other"

Understanding how to achieve international cooperation is at the core of achieving sustainability in dealing with our common enemy: environmental degradation

…so that we can achieve a sustainable future for our children and grandchildren

Thank you

Carole Levin