The Evolution of Animal Grouping and Collective Motion

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COLLECTIVE
ANIMAL
BEHAVIOR

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Courtesy: Iain Couzin/BBC

Broad relevance of collective behavior

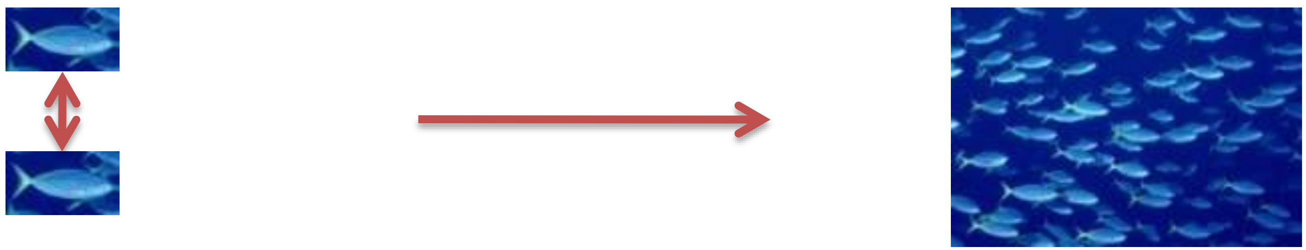
- Observed in wide range of organisms and ecological contexts
  - From bacterial (or cellular) swarms to wildebeests
- Nonequilibrium statistical mechanics of self-driven particles
- Robotics: Coordination of mobile autonomous agents
- Natural Algorithms
- Traffic Organization, Human Crowds, etc.

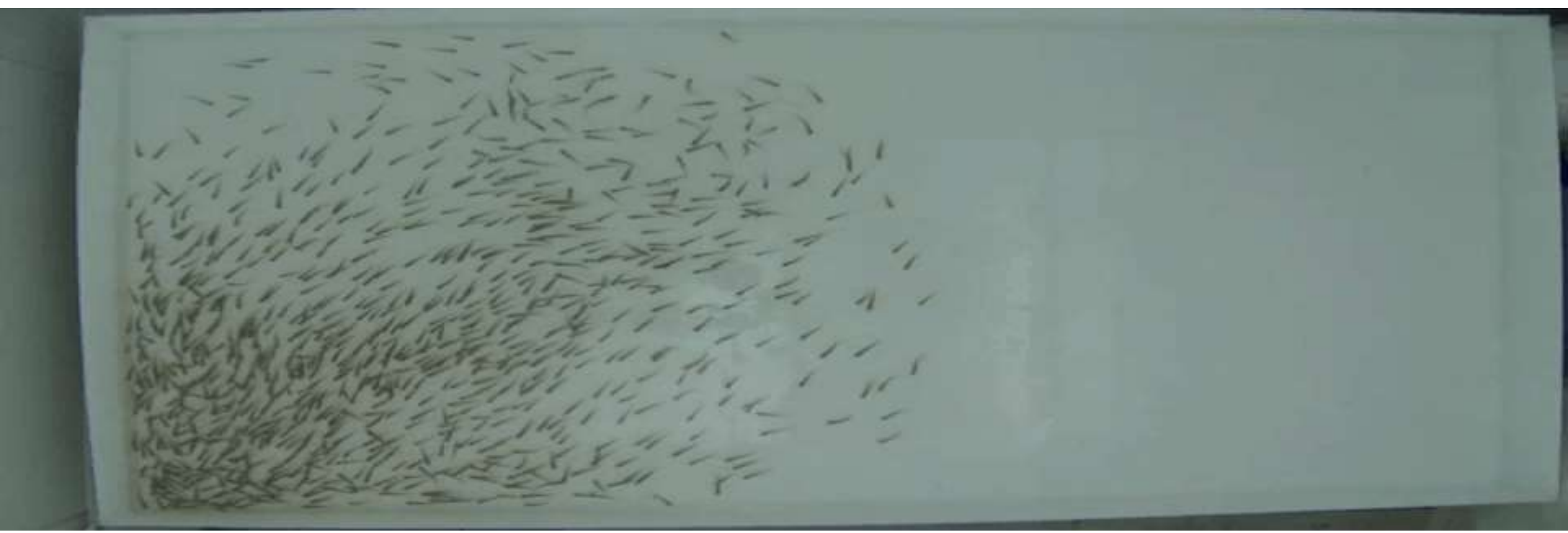
Question: Individuals to collectives

1. **How** do individual level interactions scale to collective patterns

Individual level interactions

Self-ordered collective motion



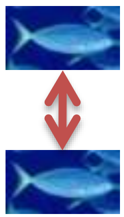


Video Courtesy: Yael Katz @ CouzinLab

Why such interactions occur?

1. **How** individual level interactions scale to collective patterns

Individual level interactions



Self-ordered collective motion

- **Local interactions can change**
  - Over relatively **long evolutionary timescales** (due to reproduction, mutation and natural selection)

2. **Why** do such interactions among individuals occur/exist in the natural world?

Image Credit: http://richardschwartz.files.wordpress.com/2010/07/fish-school.jpg

Individual versus collective benefits

- One may argue that local social interactions lead to emergent group benefits (or mutual benefits to individual members).
  - *e.g.,* Improved navigational and/or foraging ability

- But natural selection does not optimize group properties.
  - It favors individuals with higher relative-fitness, typically leading to conflict among individuals.

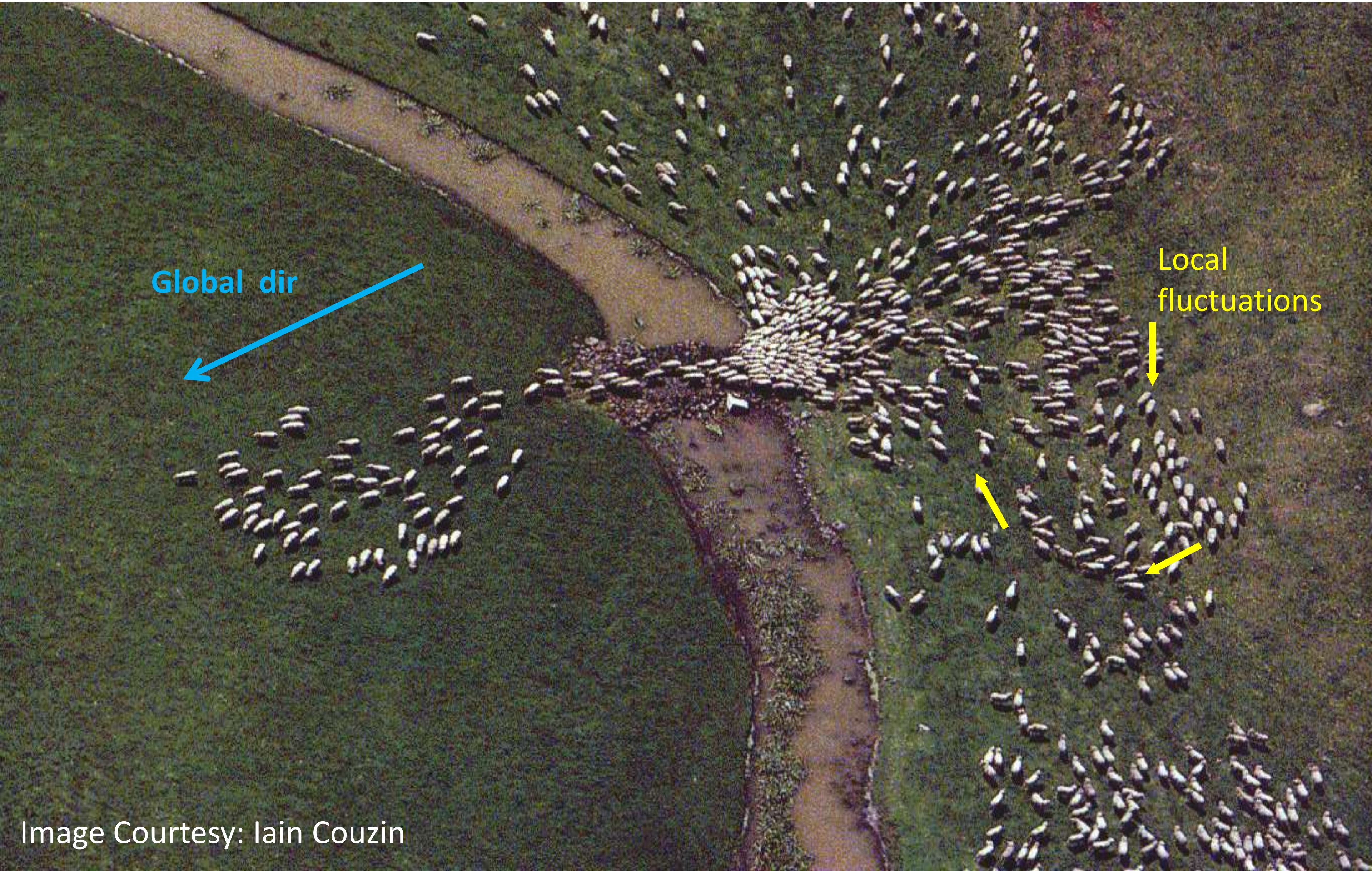
- What happens in a migratory context?

Collective motion in migratory species

- Ubiquitous phenomena: Cells to Wildebeests.
  - Involves climbing gradients (magnetic, resource, etc).
- Massive number of individuals

Image credits:
(L) Tamas Vicsek, (C) http://forces.si.edu/images/elnino/locustLarge.jpg, (R) http://www.martinwgrosnick.com/images/Wildebeest_48284F.jpg

Collective migration: hints on mechanism



A self-propelled particle model for collective migration

- We will consider following two individual traits
  - Ability to sense environmental gradient/cues
    - Geomagnetic field, resource, thermal, chemical and/or electromagnetic fields.
  - Ability to socially interact with neighbors
    - Respond to neighbors motion, *e.g.,* through visual or chemical cues.

- Given a need to migrate in a specific direction:
  - How do individuals optimize above two traits.

- Individuals (self-propelled particles) move
  - in a continuous two-dimensional space
  - with constant speed
  - update their direction of motion in discrete time steps.

Solitary migration

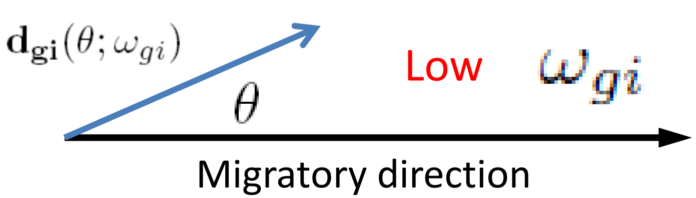
- Environment: a global migratory gradient along x-axis.

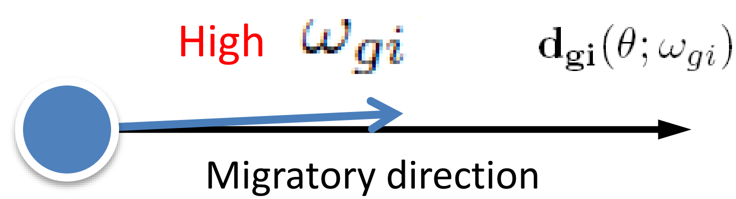
Migratory direction

- Trait 1: Gradient detection trait (ability): ω_{gi}
  - Determines how accurately an individuals find migratory direction.

$$\dot{\theta}_i = -\omega_{gi}\theta_i(t) + \sigma_g \eta_{gi}(t)$$

  - For simplicity, assume temporally uncorrelated noise.

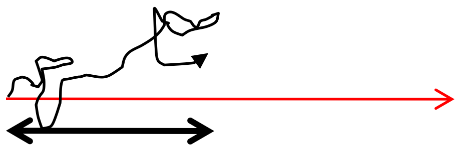




V Guttal and I D Couzin, 2010, ***PNAS,*** Vol: 107: 16172-16177 Based on Couzin *et al*, Nature, 2005

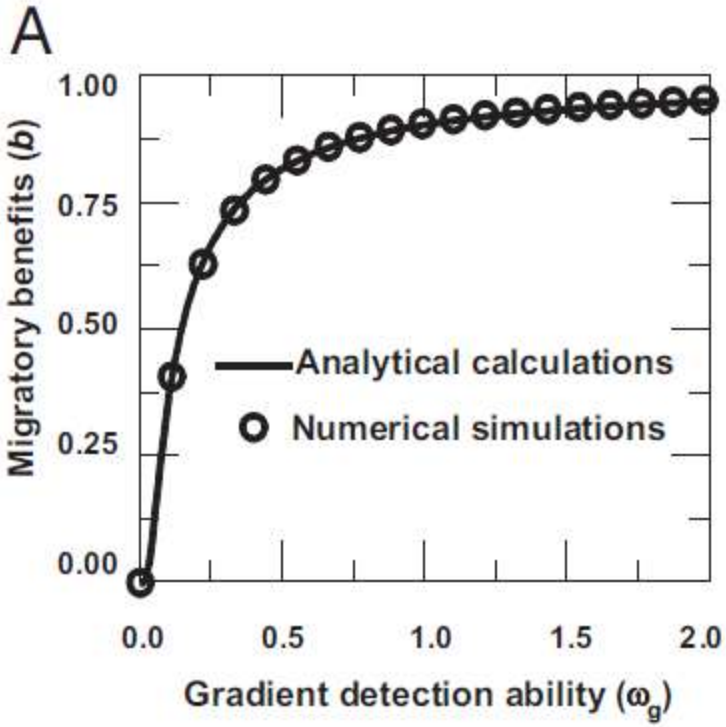
Migratory benefits

- b_i = distance moved in the direction of gradient, per unit time



$$\dot{\theta}_i = -\omega_{gi}\theta_i(t) + \sigma_g \eta_{gi}(t)$$

$$\langle b_i \rangle = \langle \cos(\theta_i(t)) \rangle = \exp[-\frac{\sigma_g^2}{4\omega_{gi}}]$$



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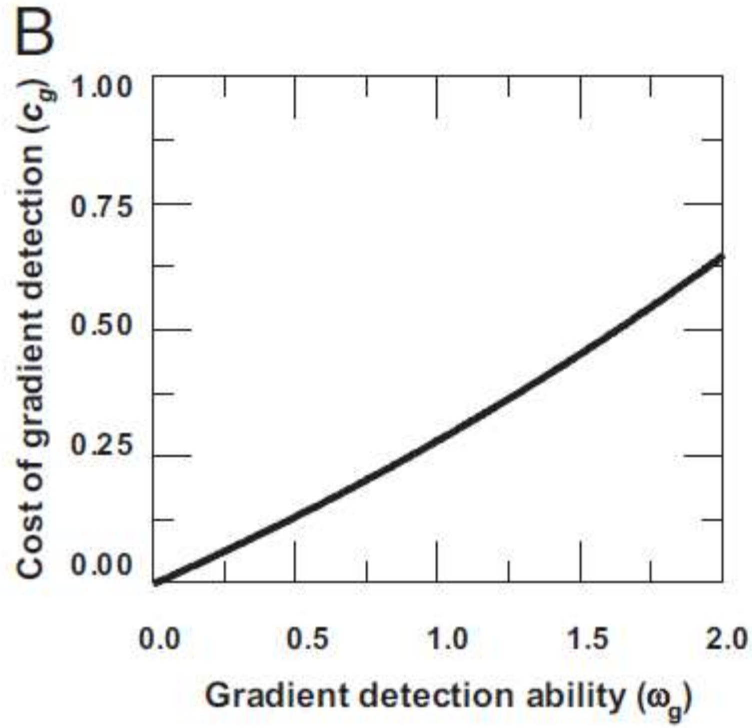
Costs of gradient detection ability

$$c_{gi} = p_g(e^{\omega_{gi}/\omega_{gc}} - 1.0)$$



Note:

- p_g has same units as migratory benefits.

- Different magnitude of costs is obtained by varying p_g

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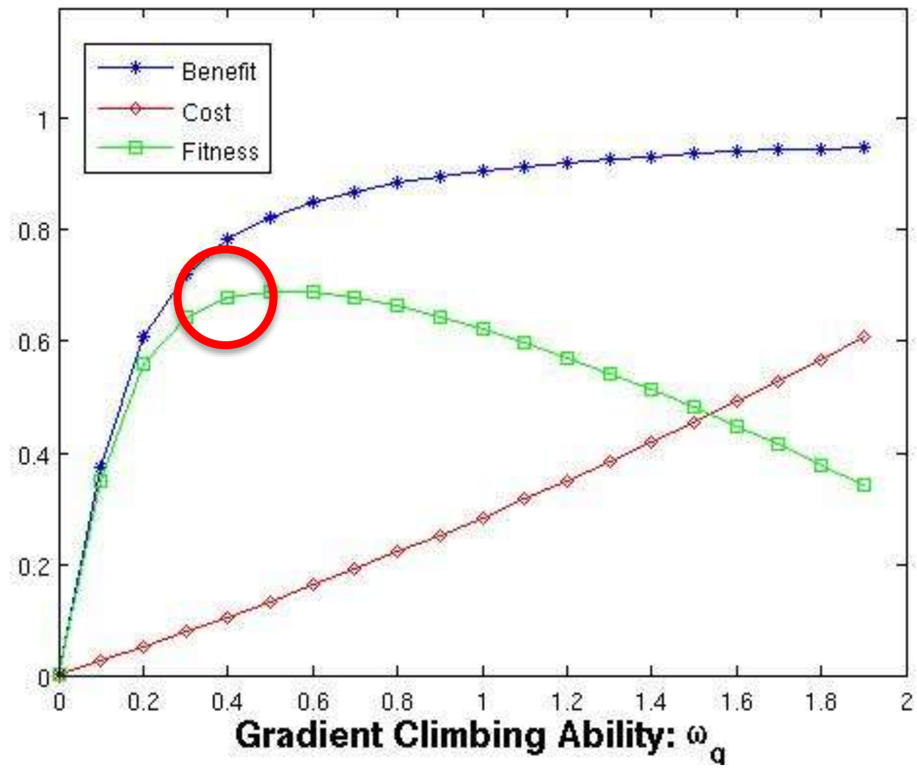
Individual migratory fitness

- Fitness (reproductive success) = Benefit – Cost.



- Solitary individual optimum.
- What if we allow flocking interactions between individuals?

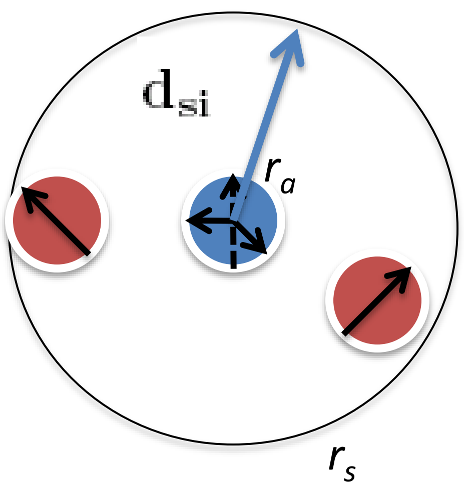
Collective motion

- Trait 2: Flocking/ Social interactions: ω_s

Denote position by $\mathbf{c}_i(t)$ and velocity by $\mathbf{v}_i(t)$

Repulsion: Avoid others within a body length r_a

Sociality: a tendency to attract towards, and align direction of travel, with neighbors within radius r_s (outer radius)



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

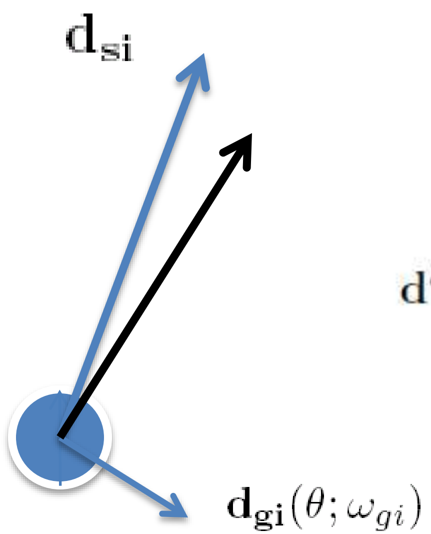
Attraction **Alignment**

V Guttal and I D Couzin, 2010, ***PNAS,*** Vol: 107: 16172-16177

Based on Couzin *et al*, Nature, 2005

Balancing two traits/tendencies

- Gradient detection trait (ability): ω_g
- Sociality trait: ω_s



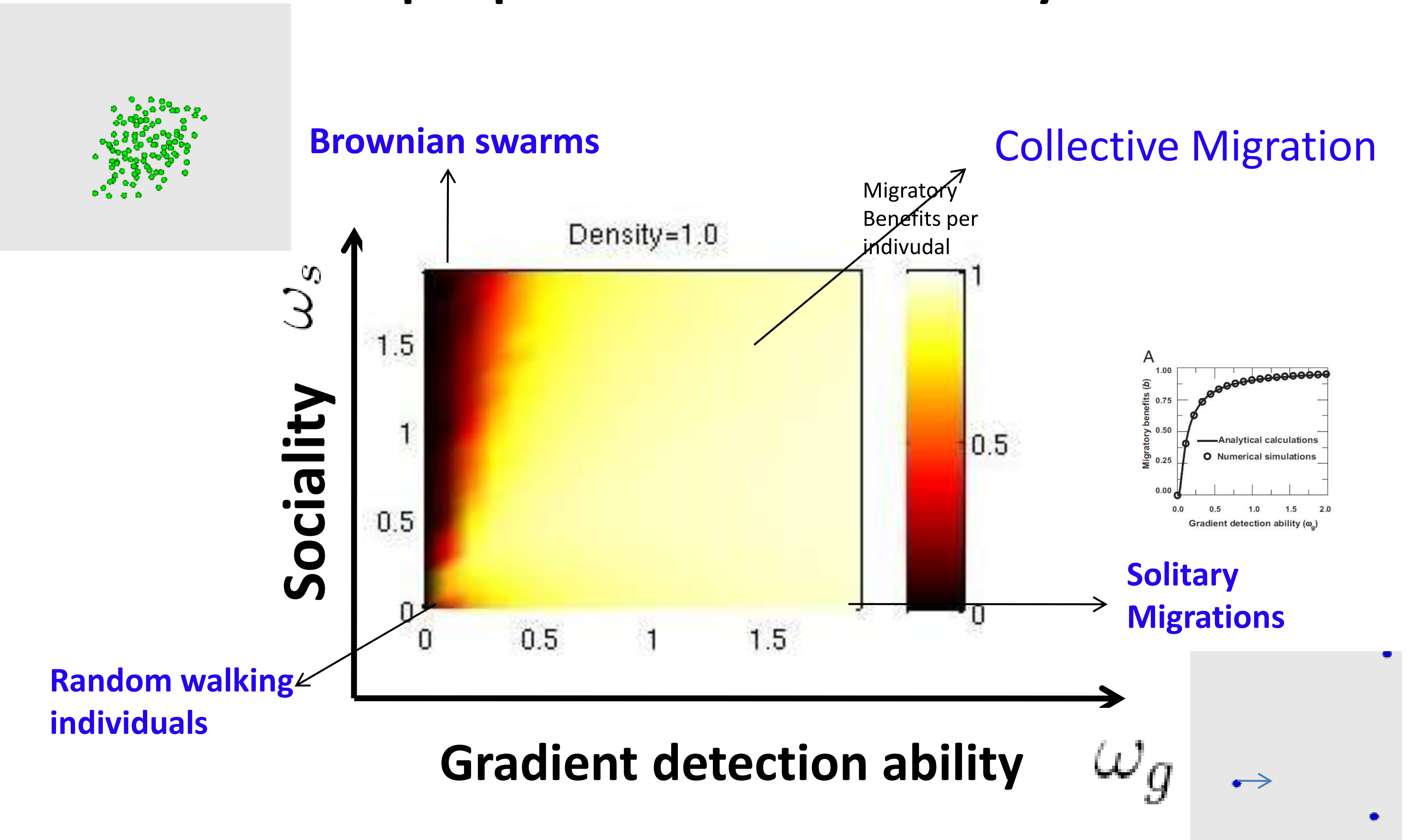
$$\mathbf{d}'_i(t+\Delta t) = \frac{\omega_{si}\hat{\mathbf{d}}_{si}(t+\Delta t) + \omega_{gi}\hat{\mathbf{d}}_{gi}(t+\Delta t) + \sigma_r\hat{\mathbf{d}}_{ri}(t+\Delta t)}{|\omega_{si}\hat{\mathbf{d}}_{si}(t+\Delta t) + \omega_{gi}\hat{\mathbf{d}}_{gi}(t+\Delta t) + \sigma_r\hat{\mathbf{d}}_{ri}(t+\Delta t)|}$$

Error in perception and/or motion

V Guttal and I D Couzin, 2010, ***PNAS,*** Vol: 107: 16172-16177

Based on Couzin *et al*, Nature, 2005

Plausible population level dynamics



Individual traits are determined by natural selection

- We do not predetermine what the individual traits in the population are.

- It is going to be determined by natural selection.

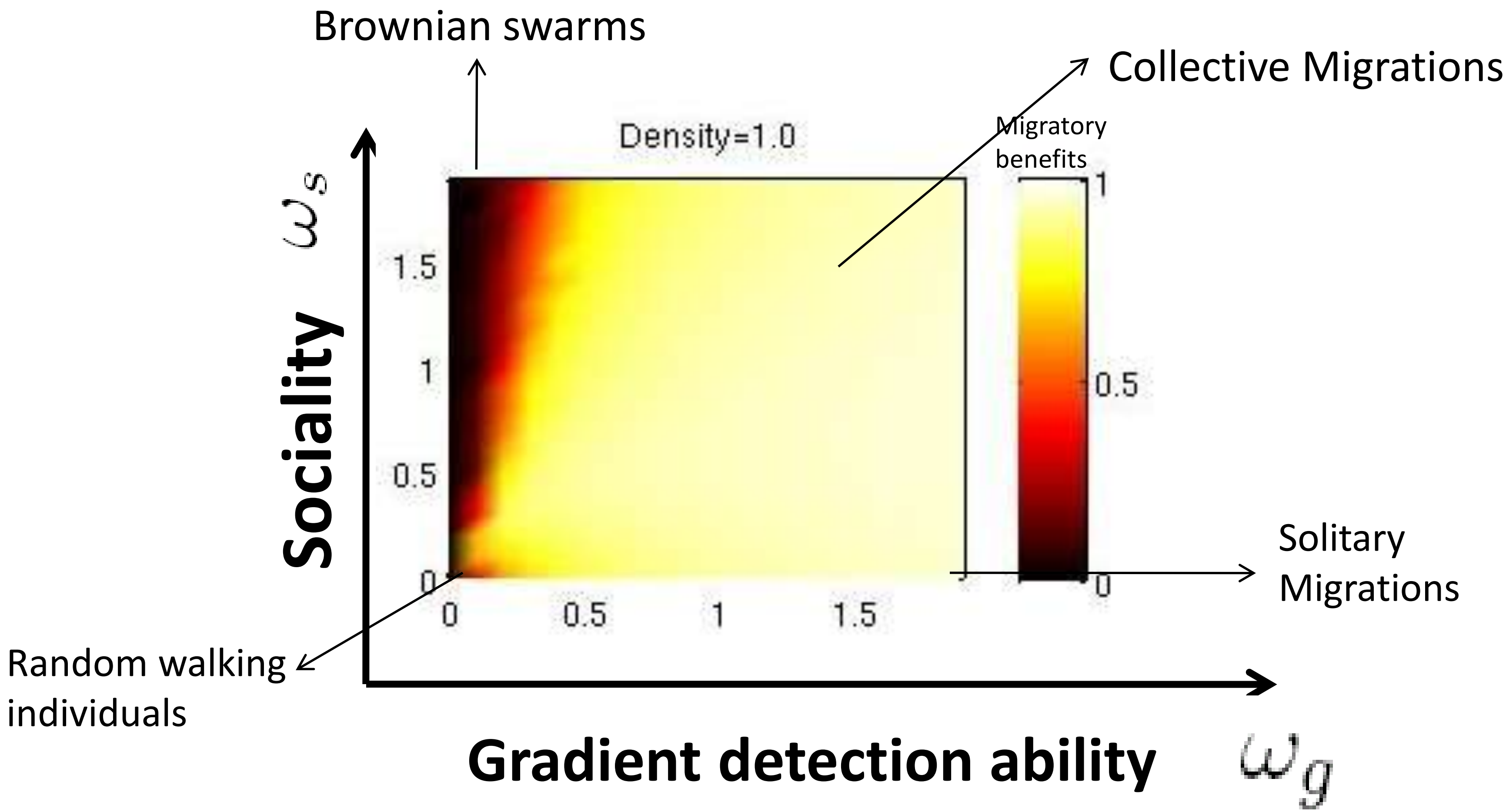
    - Individuals may possess only gradient detection ability.

    - Or only social interactions and thus, follow nearby individuals.

    - Or a combination of both.

    - Evolved populations may also be heterogeneous.

Plausible population level dynamics



- Where would evolved populations be in this parameter space?

Selection algorithm

- Start with a large homogeneous population (large sizes: 16,000 to 60,000 individuals)

- They move according to the equations of motion over one generation (averaged over several realizations) .

- Calculate Fitness:
  - Find benefit for each individual
  - Find cost of gradient detection depending on its ω_g
  - Calculate Fitness = Benefit – Cost.

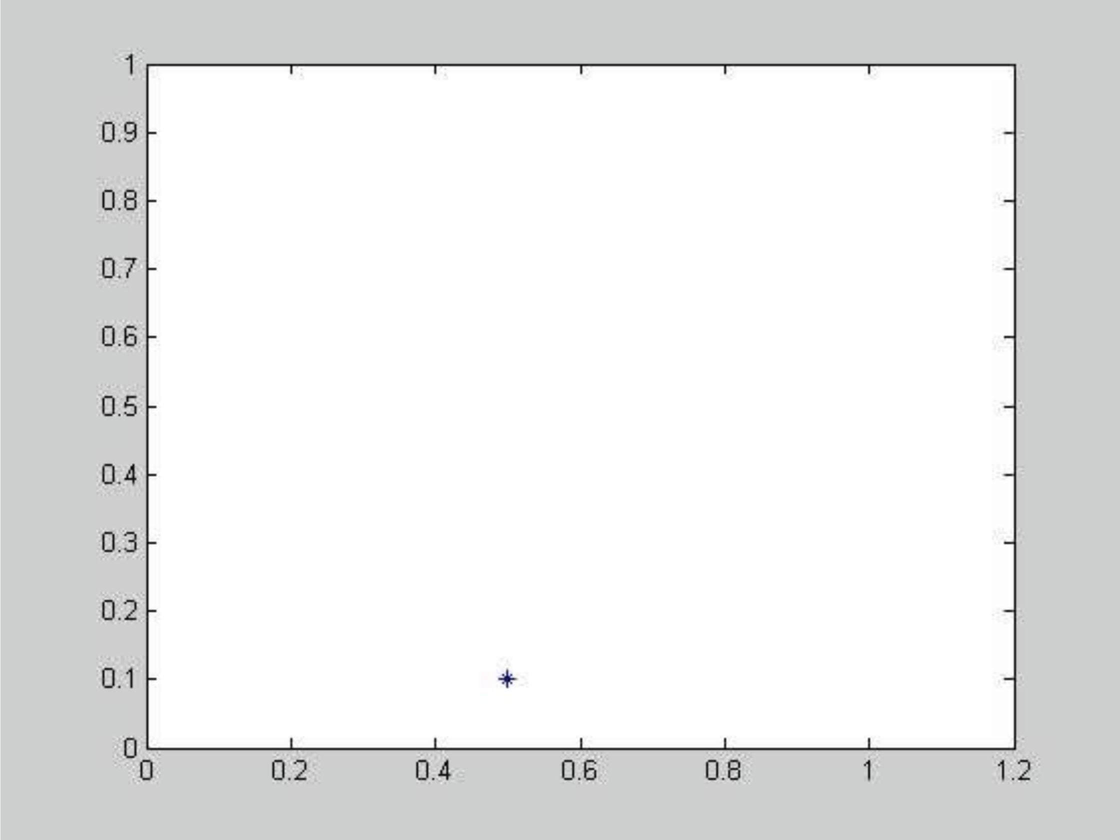
- Reproduce proportional to fitness (Roulette Wheel Selection)
  - Asexual reproduction
  - The gradient detection ability, ω_g and the sociality trait, ω_s of the parent are passed on to offspring with a small mutation.

- Repeat the process until an equilibrium of trait/phenotype distributions is reached.

Evolved strategies:

- No cost of gradient climbing:

Sociality ω_s

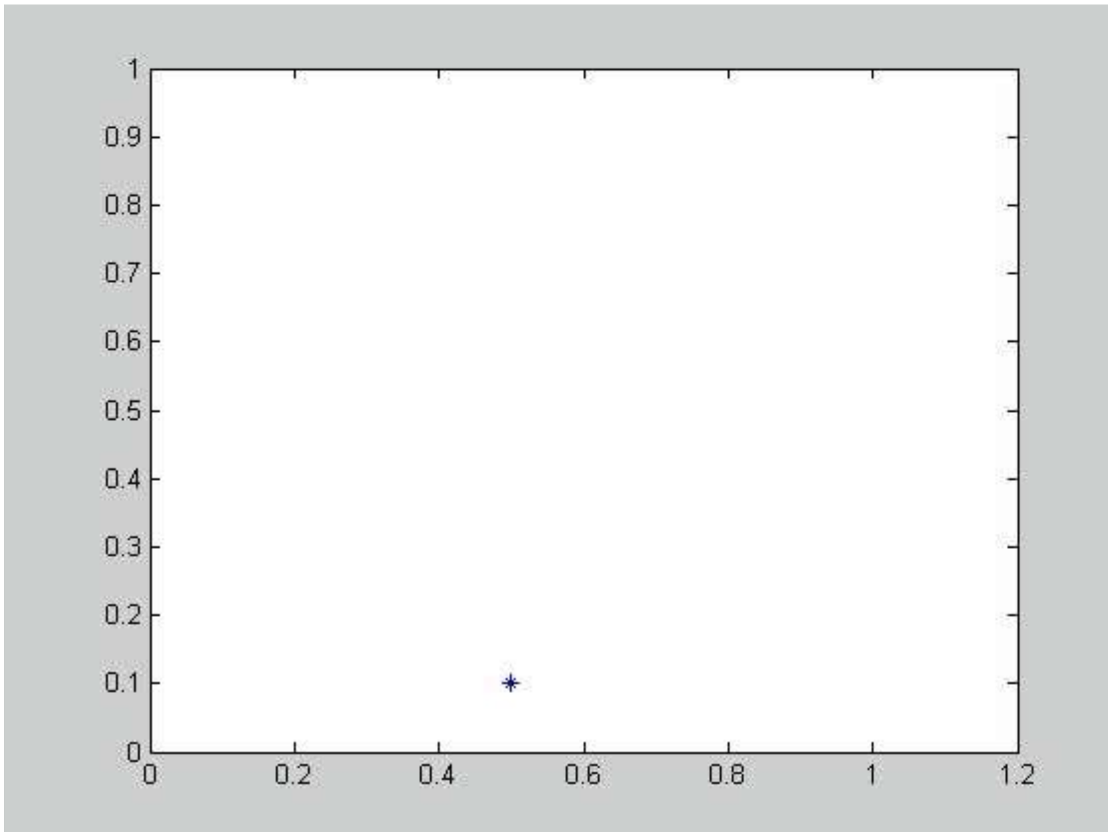


Gradient detection ability ω_g

Evolved strategies:

- Very high cost of gradient climbing:

Sociality ω_s

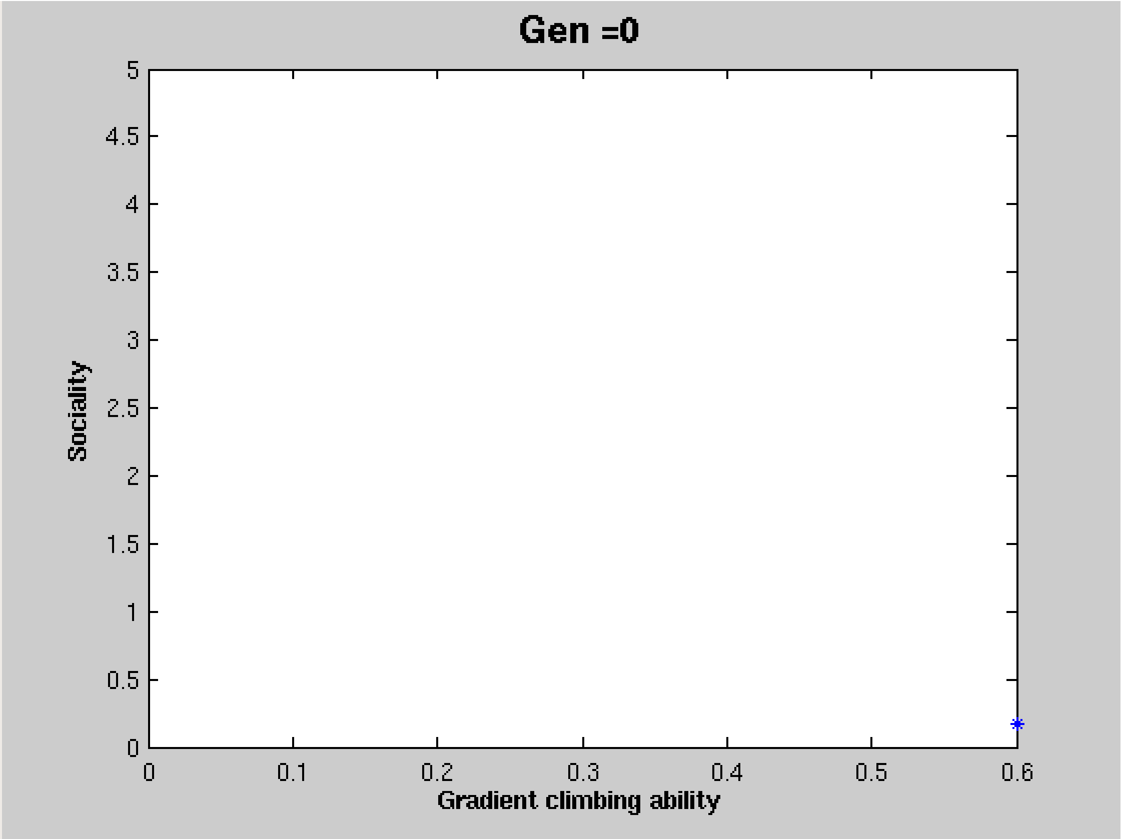


Gradient detection ability ω_g

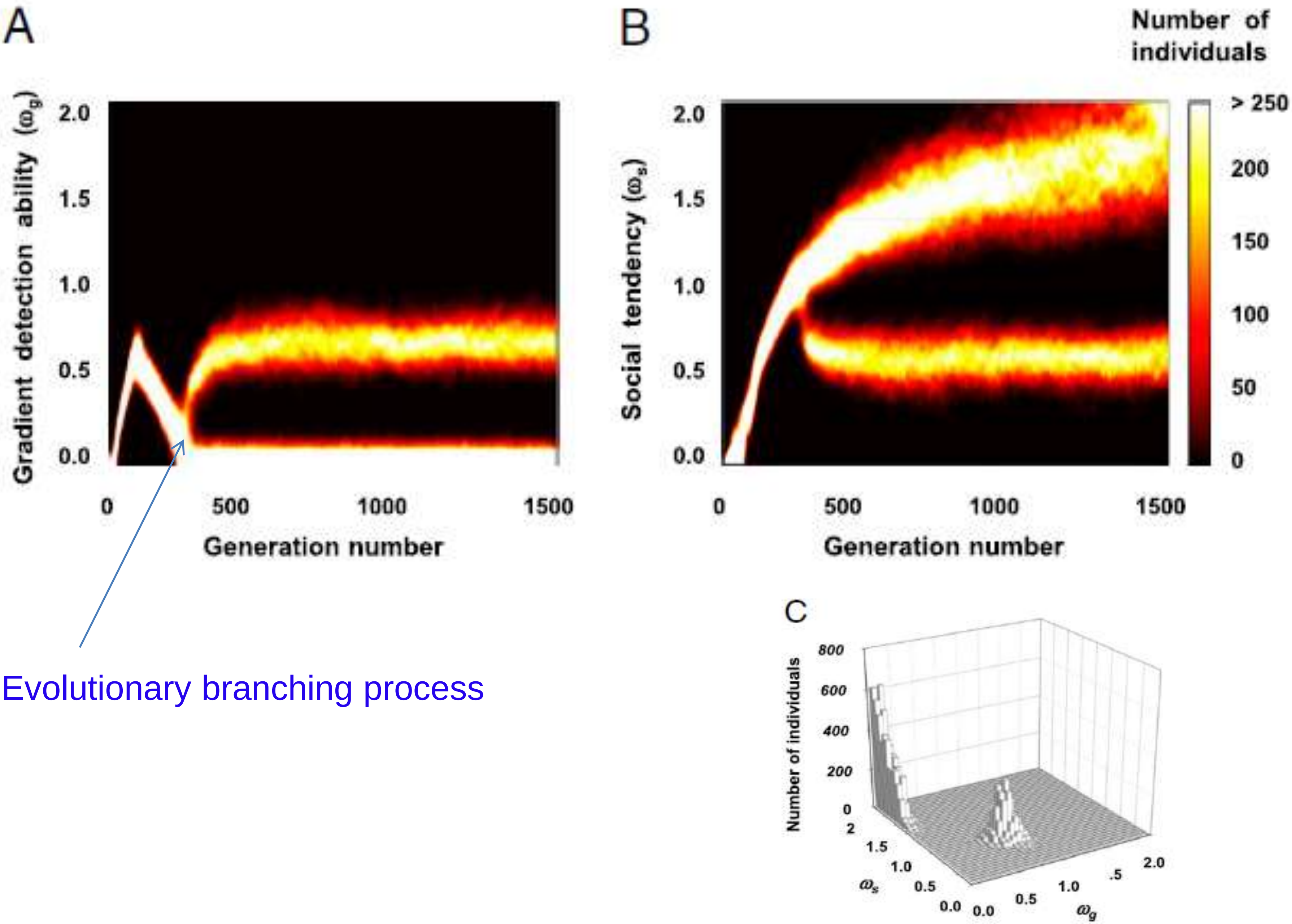
Evolved strategies:

- Intermediate cost of gradient climbing:

Sociality ω_s

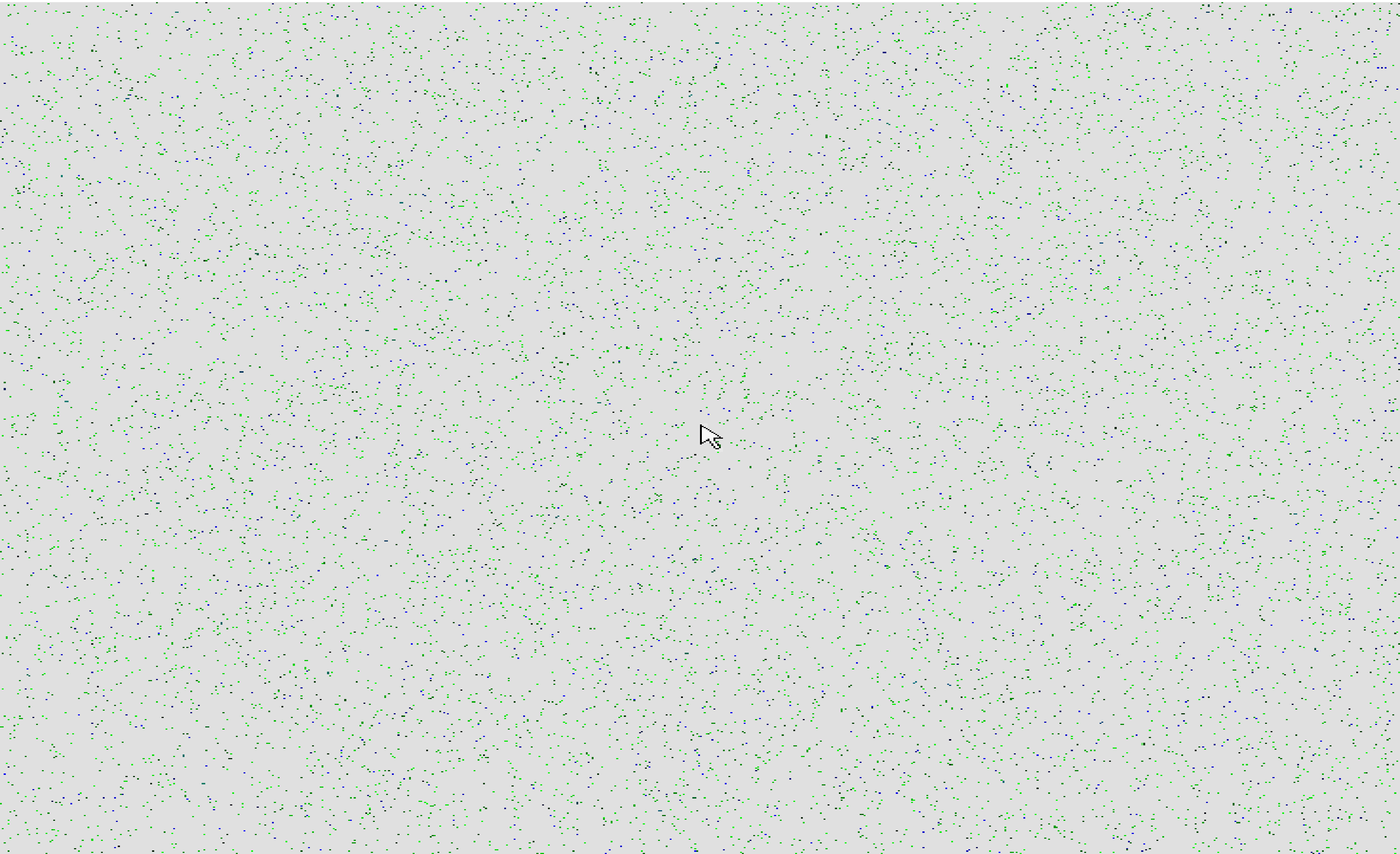


Gradient detection ability ω_g

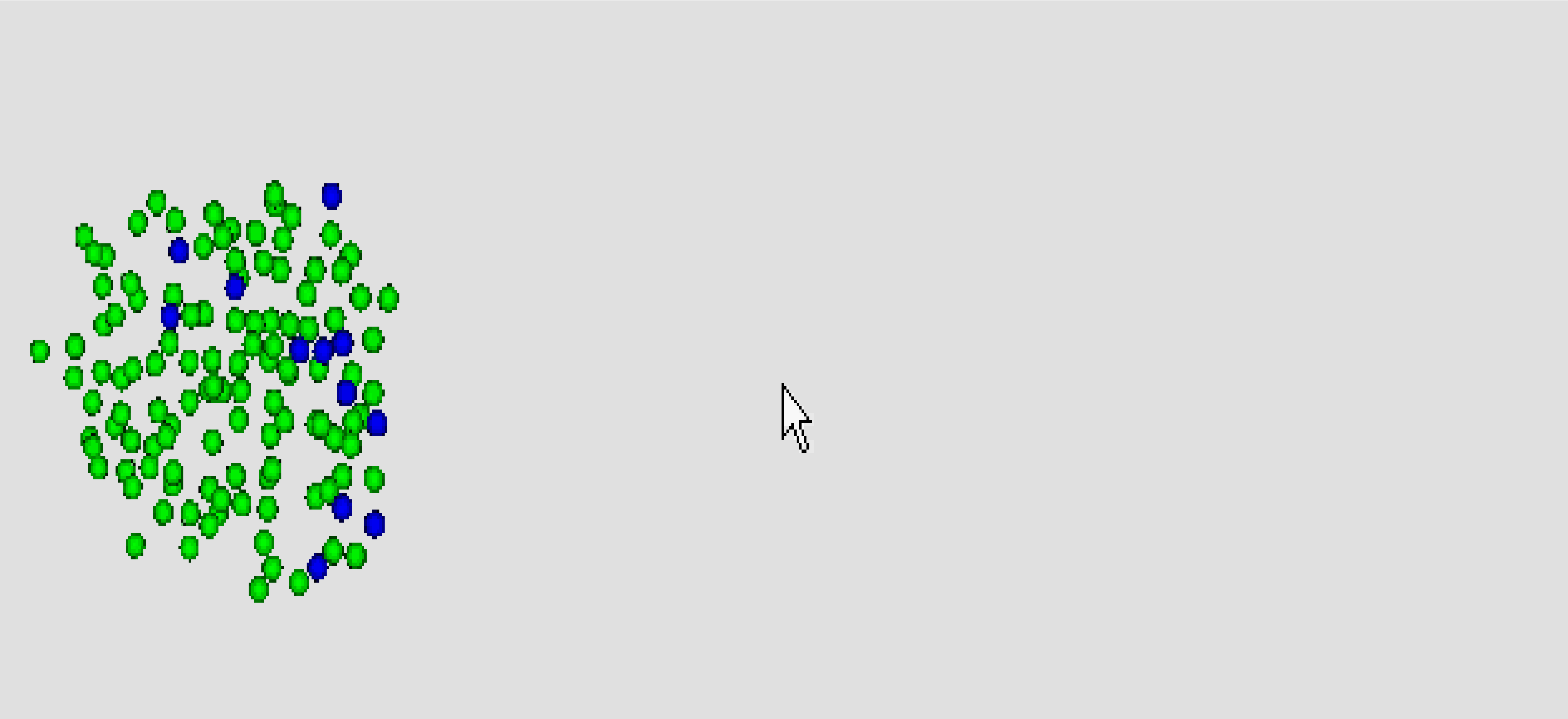


Evolutionary branching process

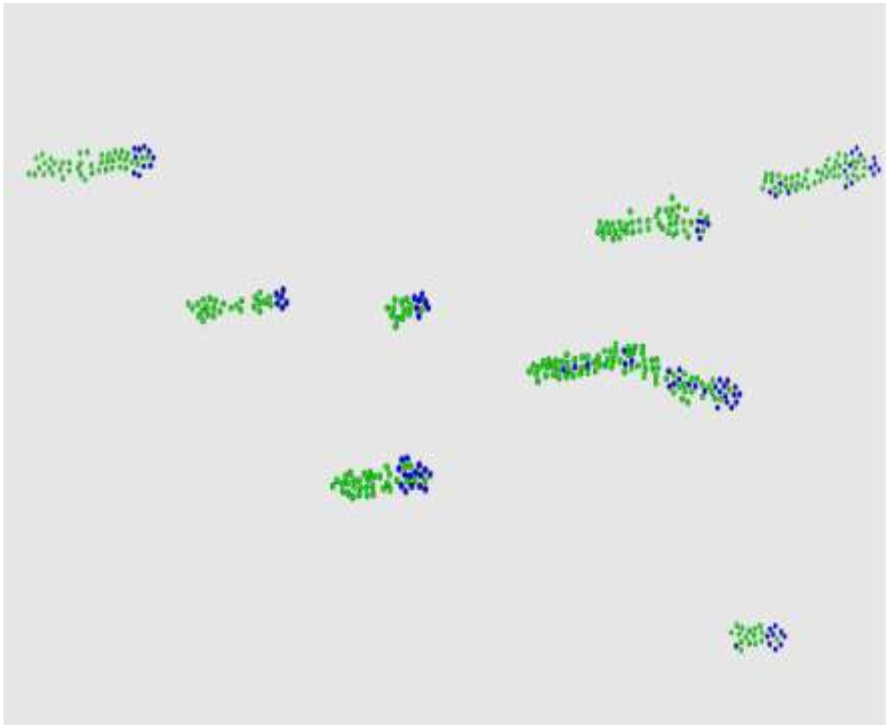
Spatiotemporal dynamics of the evolved population: 16,000 individuals using GPU (CUDA) on this laptop (realtime)



Self-sorting and collective migration



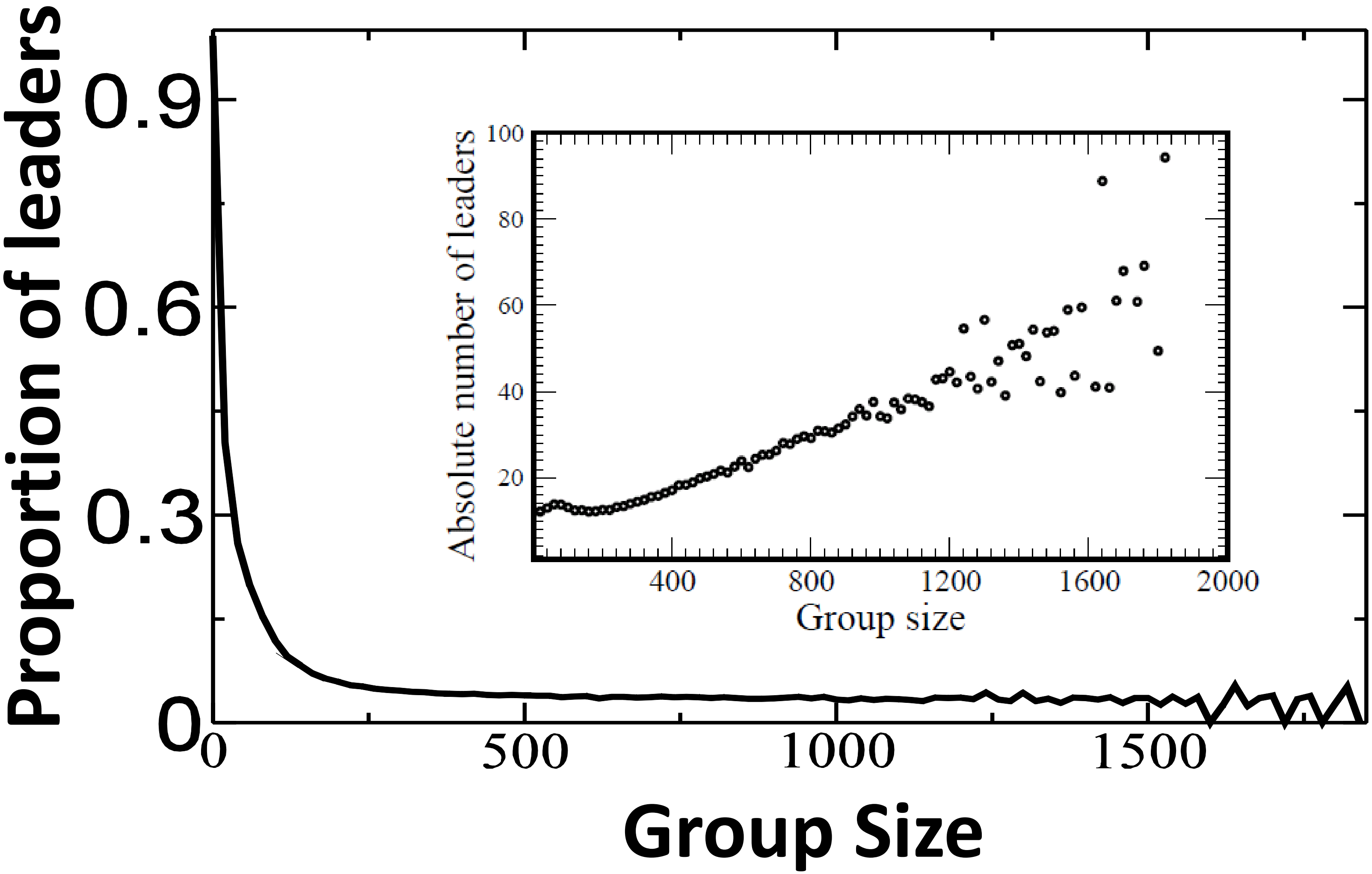
Group structure in the evolved population



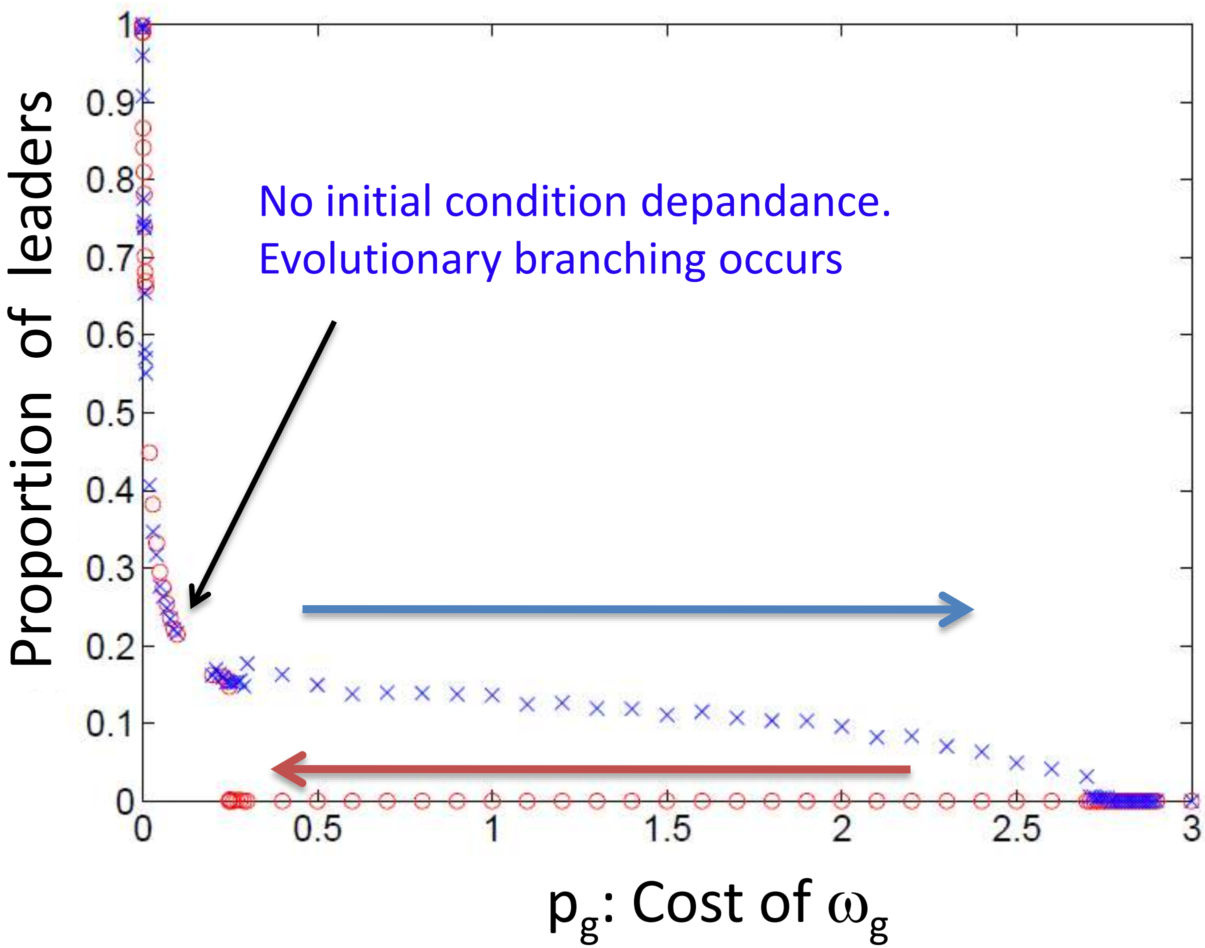
GREEN: Social individuals (high sociality but weak or no gradient detection ability)
BLUE: Leaders (high gradient climbing ability and low sociality)

Self-organize into groups with mixture populations and they collectively migrate

Group structure in the evolved population



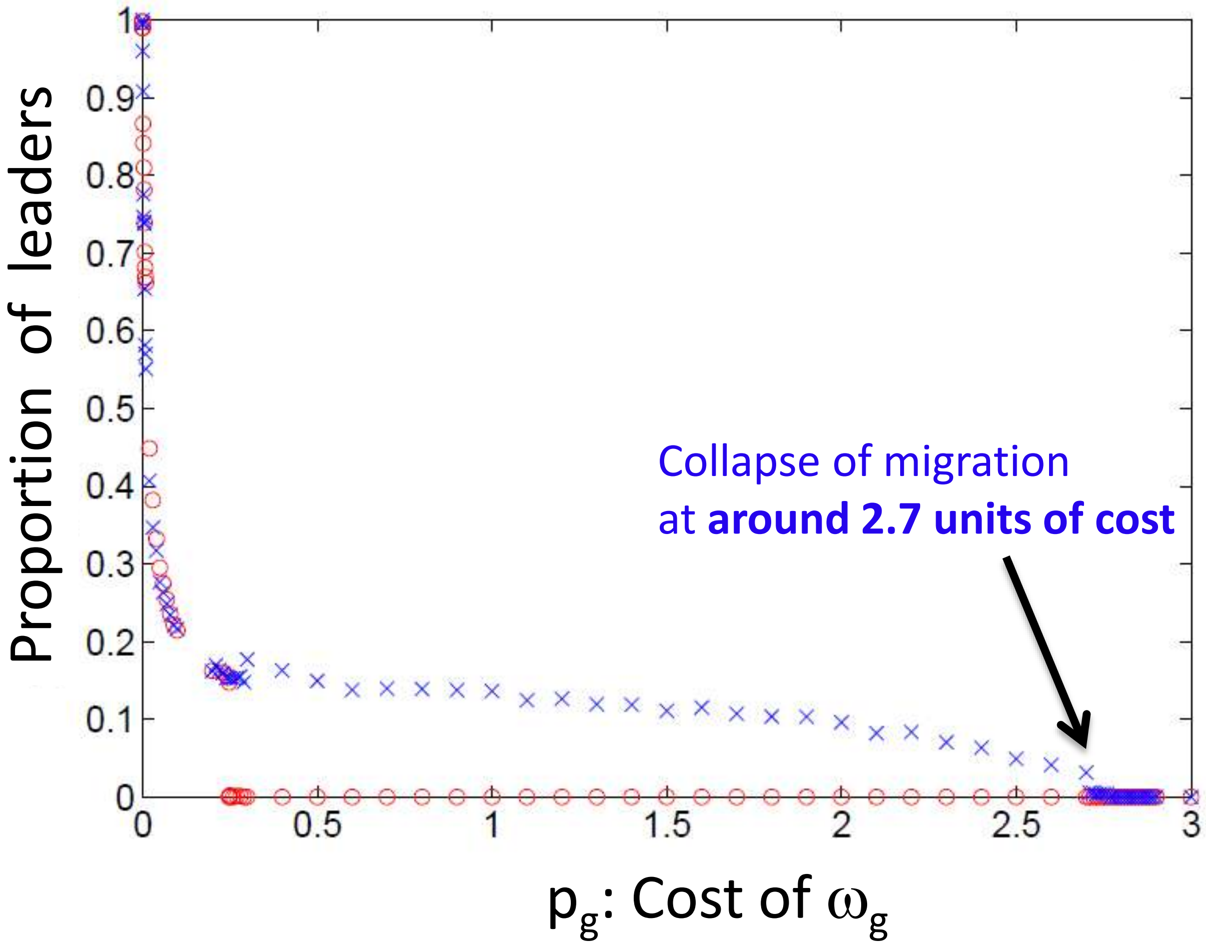
Strategies as a function of *cost of* ω_g



$$c_{gi} = p_g(e^{\omega_{gi}/\omega_{gc}} - 1.0)$$

With Yu Zou, Couzin and Kevrekidis

Solitary versus social strategies



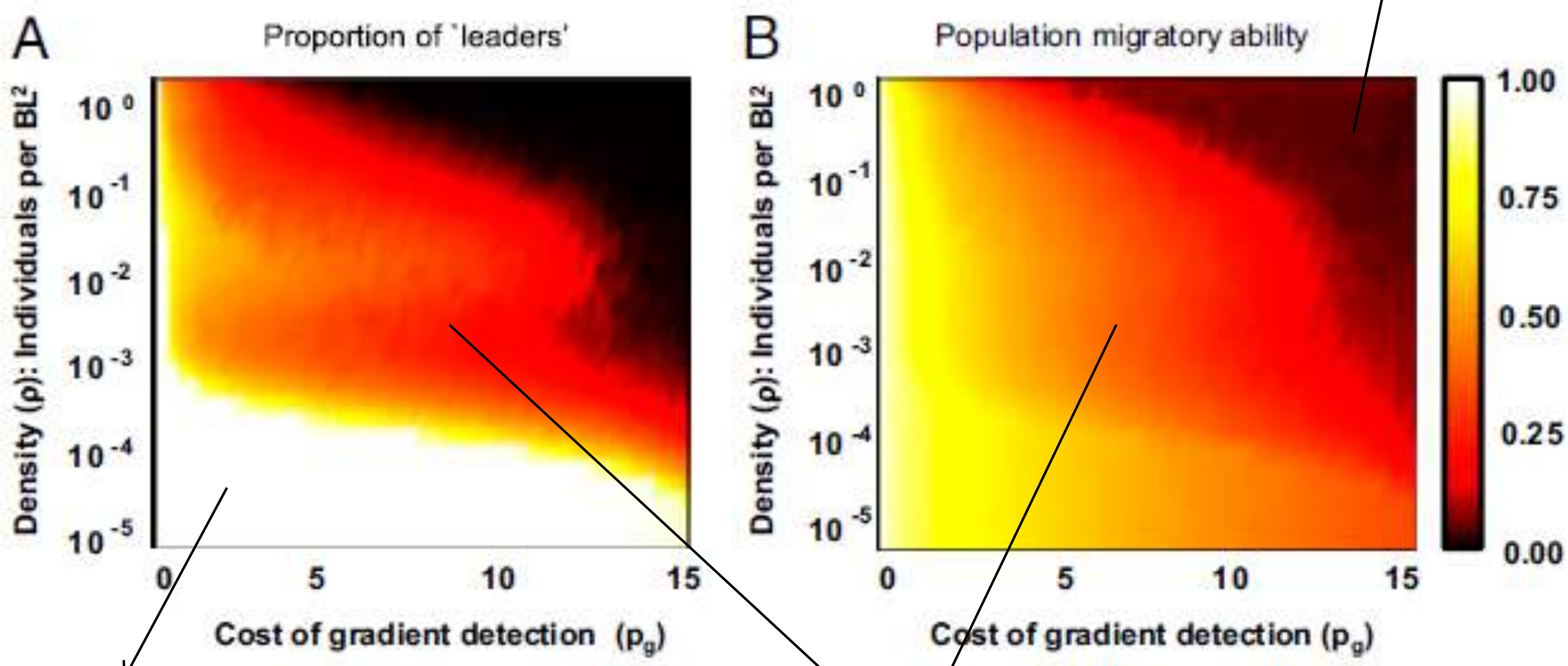
If we do not allow social Interactions:

i.e., for solitary individuals, the migration collapses **at cost approx. 18 units.**

With Yu Zou, Couzin and Kevrekidis

Phase diagram of evolved populations

Very high density and/or high cost
=> No migration



Very low density and/or low cost.
=> Individual migratory strategies

Large intermediate region
Collective migratory strategies

Role of social interactions

- It allows *exploitation* of leaders *i.e.,* those who invest in sensing environment are exploited by *social individuals* who only follow others naively.
- They both coexist as a mixed strategy, resulting in collective migration.
- In our model, evolved collective migratory populations migrate less efficiently than solitary populations.

Acknowledgements

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