The Evolution of Animal Grouping and Collective Motion

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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

   - System of self-driven interacting particles
   - Continuum hydrodynamic description: universal macroscopic features (Ramaswamy, Toner, Tu, etc).

Video Courtesy: Yael Katz @ CouzinLab
Why such interactions occur?

1. How individual level interactions scale to collective patterns

   Individual level interactions

   ![Image of individual level interactions]

   Self-ordered collective motion

   ![Image of 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](http://forces.si.edu/images/elnino/locustLarge.jpg), (R) [http://www.martinwgrosnick.com/images/Wildebeest_48284F.jpg](http://www.martinwgrosnick.com/images/Wildebeest_48284F.jpg)
Collective migration: hints on mechanism

Image Courtesy: Iain Couzin
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.

- Trait 1: Gradient detection trait (ability): $\omega_{gi}$
  - Determines how accurately an individuals find migratory direction.
  - For simplicity, assume temporally uncorrelated noise.

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

Based on Couzin *et al*, Nature, 2005
Migratory benefits

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

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

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

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 \( p_g \)

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:** \( \omega_s \)
  
  Denote position by \( c_i(t) \) and velocity by \( v_i(t) \)

**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)

\[
    d_{si}(t + \Delta t) = \sum_{j \neq i} \frac{c_j(t) - c_i(t)}{|c_j(t) - c_i(t)|} + \sum_{j=1}^{\text{max}} \frac{v_j(t)}{|v_j(t)|}
\]

**Attraction**  
**Alignment**


Based on Couzin *et al*, Nature, 2005
Balancing two traits/tendencies

- Gradient detection trait (ability): $\omega_g$
- Sociality trait: $\omega_s$

Error in perception and/or motion


Based on Couzin *et al*, Nature, 2005
Plausible population level dynamics

Brownian swarms

Collective Migration

Random walking individuals

Sociality

Gradient detection ability

Migratory Benefits per individual

Solitary Migrations
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 \( \omega_g \)
  – Calculate Fitness = Benefit – Cost.

• Reproduce proportional to fitness (Roulette Wheel Selection)
  – Asexual reproduction
  – The gradient detection ability, \( \omega_g \) and the sociality trait, \( \omega_s \) 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:
Evolved strategies:

• Very high cost of gradient climbing:
Evolved strategies:

- Intermediate cost of gradient climbing:

\[ \text{Sociality } \omega_s \]

\[ \text{Gradient detection ability } \omega_g \]
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

![Graph showing the relationship between group size and proportion of leaders.](image)
Strategies as a function of cost of $\omega_g$

No initial condition dependence.
Evolutionary branching occurs

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

With Yu Zou, Couzin and Kevrekidis
Solitary versus social strategies

If we do not allow social Interactions:

\[ i.e., \text{for solitary individuals, the migration collapses at cost approx. 18 units.} \]

\[ \text{Collapse of migration at around 2.7 units of cost} \]

With Yu Zou, Couzin and Kevrekidis
Phase diagram of evolved populations

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

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

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.
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