Hierarchy
Part II

The statistical physics of biological systems

Lecture 3

Sept 28, 2020

A short reminder

- Last lecture we have seen:
  - Definition of hierarchy: control of behavior (characteristics)
  - Types of hierarchy:
    1. Order hierarchy
    2. Containment (Nested/Embedded hierarchy)
       i. Subsumptive containment hierarchy (taxonomic)
       ii. Compositional containment hierarchy (level h.)
    3. Flow (or control) hierarchy
  - Measures (circles, Random walk, GRC)
  - Dominance hierarchy
  - Models for leadership (with preferred directions)

Models for leadership

- Extension of the "Couzin model"

- No individual recognition, no signaling mechanism

- Non-informed individuals: are not required to know how many and which individuals has information

- Vice versa: Informed individuals are not required to know anything about the information-level of their mates and that how the quality of their information was compared to that of others.

The model:

- Rule 1: highest priority
    - Individuals attempt to maintain a certain distance among themselves by turning away from those neighbors j which are within a certain distance towards the opposite direction:

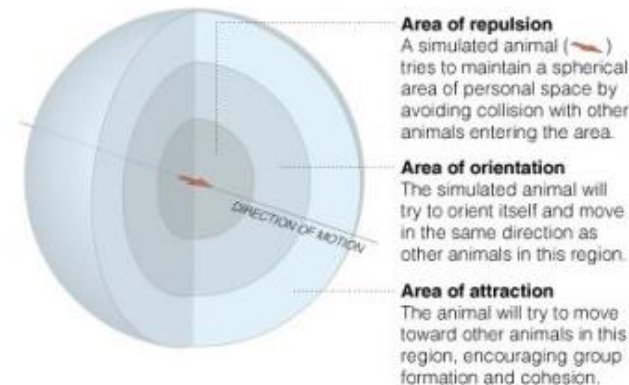$$\vec{d}_i(t + \Delta t) = -\sum_{j \neq i} \frac{\vec{r}_j(t) - \vec{r}_i(t)}{|\vec{r}_j(t) - \vec{r}_i(t)|}$$

$\vec{d}_i$: desired direction of individual i

$\vec{r}_i$: position of particle i

$\vec{v}_i$: direction of unit i

Simulating Swarm Intelligence

Researchers created a model of swarm behavior by programming individuals to maintain personal space while turning and moving in the same direction as others.

Area of repulsion
A simulated animal (➤) tries to maintain a spherical area of personal space by avoiding collision with other animals entering the area.

Area of orientation
The simulated animal will try to orient itself and move in the same direction as other animals in this region.

Area of attraction
The animal will try to move toward other animals in this region, encouraging group formation and cohesion.

Sources: Iain D. Couzin; Journal of Theoretical Biology

[Couzin, I.D., Krause, J., Franks, N.R., Levin, S.A., 2005. Effective leadership and decision-making in animal groups on the move. Nature 433, 513–516.]

Models for leadership

The model (cont):

- Rule 2

If there are no mates within the range of repulsion, than the individual will attempt to align with those neighbors j, which are within the range of alignment:

$\rightarrow$ The desired direction:

$$\vec{d}_i(t + \Delta t) = -\sum_{j \neq i} \frac{\vec{r}_j(t) - \vec{r}_i(t)}{|\vec{r}_j(t) - \vec{r}_i(t)|} + \sum_{j \neq i} \frac{\vec{v}_j(t)}{|\vec{v}_j(t)|}$$

$\vec{d}_i$: desired direction of individual i
$\vec{r}_i$: position of particle i
$\vec{v}_i$: direction of unit i

- Corresponding unit vector: $\hat{d}_i(t) = \vec{d}_i(t)/|\vec{d}_i(t)|$

- Introducing "influence": a portion of the group (p) is given information/motivation about a preferred direction, described by the (unit) vector $\vec{g}$.

- The rest of the group does not have directional preference.

Informed individuals balance their
- social alignment $\hat{d}_i(t)$ (the unit vector of $\vec{d}_i(t+\Delta t) = -\sum_{j\neq i}\frac{\vec{r}_j(t)-\vec{r}_i(t)}{|\vec{r}_j(t)-\vec{r}_i(t)|} + \sum_{j\neq i}\frac{\vec{v}_j(t)}{|\vec{v}_j(t)|}$) and
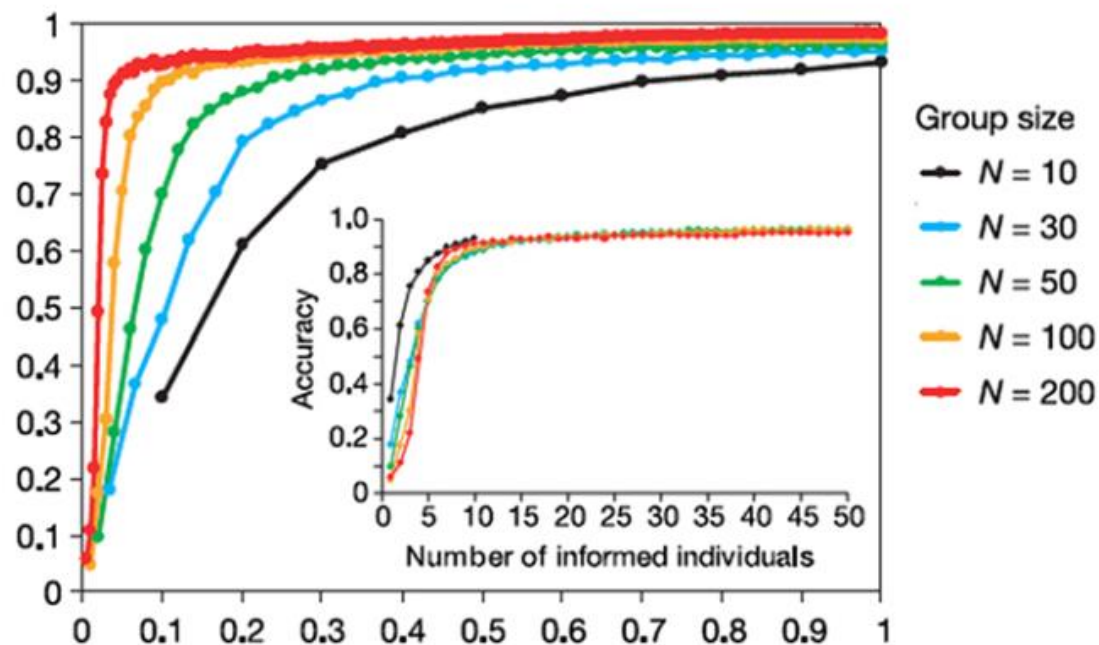- preferred direction $\vec{g}_i$

with the weighting factor ω:

$$\vec{d}_i(t+\Delta t) = \frac{\hat{d}_i(t+\Delta t) + \omega\vec{g}_i}{|\hat{d}_i(t+\Delta t) + \omega\vec{g}_i|}$$

- ω can exceed 1: the individual is influenced more by its own preferences than by its mates

- "Accuracy" of the group: normalized angular deviation of the group direction around the preferred direction $\vec{g}_i$

Results:

- for fixed group size, the accuracy increases asymptotically as the portion p of the informed members increases

  (…that is…)

- the larger the group, the smaller the portion of informed members is needed, in order to guide the group towards a preferred direction

Group size
- $N = 10$
- $N = 30$
- $N = 50$
- $N = 100$
- $N = 200$

Conflicting preferences

Informed individuals might differ in their preferred direction

1. If the number of individuals preferring one or another direction is equal: the group direction depends on the degree to which the preferred directions differ
   - If it is small: the group will go in the average preferred direction of all informed individuals
   - If it is big: individuals select randomly one or another preferred direction

2. If the number of informed individuals preferring a given direction increases
   - the entire group will go into the direction preferred by the majority (even if that majority is small)

Collective group direction when two groups of informed individuals differ in their preferences - model results

$$n_1 = n_2 = 5$$

$$n_1 = 6$$
$$n_2 = 5$$

$$n_1 = 6$$
$$n_2 = 4$$
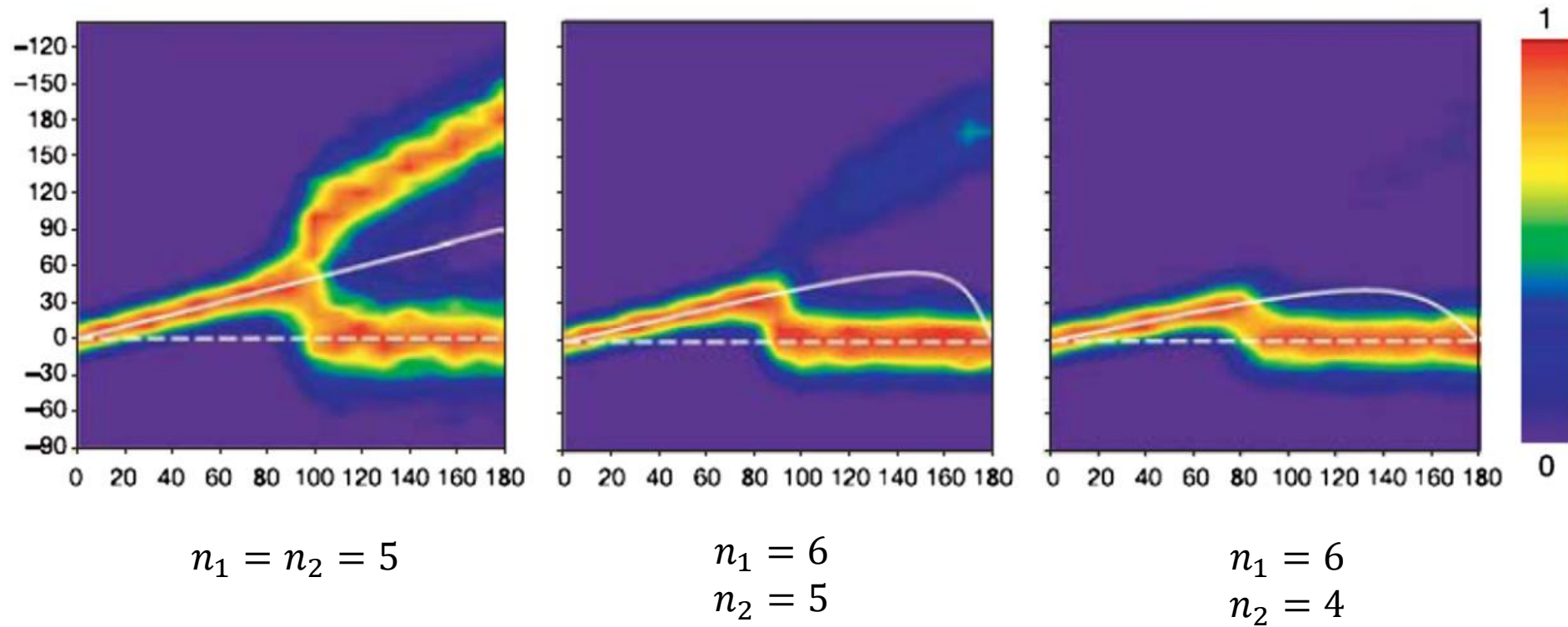
- Vertical axis: the degree of the most probable group motion.
- The first group (consisting of n_1 informed individuals) prefers the direction characterized by 0 degrees (dashed line),
- The second group (consisting of n_2 informed individuals) prefers a direction between 0 and 180 degrees (horizontal axis)

- Solid white lines are for reference only, representing the direction of the average vector of all informed individuals
- The group consists of 100 individuals altogether

Source: Couzin, I.D., Krause, J., Franks, N.R., Levin, S.A., 2005. Effective leadership and decision-making in animal groups on the move. Nature 433, 513–516.

The influence of the weighting ω of preferred direction

- Informed individuals balance their social alignment $\hat{d}_i(t)$ and preferred direction $\vec{g}_i$ with the weighting factor ω:

$$\vec{d}_i(t + \Delta t) = \frac{\hat{d}_i(t + \Delta t) + \omega\vec{g}_i}{\left|\hat{d}_i(t + \Delta t) + \omega\vec{g}_i\right|}$$

- ω can exceed 1: the individual is influenced more by its own preferences than by its mates

- Black circles: The accuracy of the group motion

- Red triangles: probability of group fragmentation

- N=50 individuals, *p*: proportion of the informed individuals
  - (a): $p = 0.02$ (1 individual)
  - (b): $p = 0.1$ (5 individuals)
  - (c): $p = 0.2$ (10 individuals)
  - (d): $p = 0.5$ (25 individuals)

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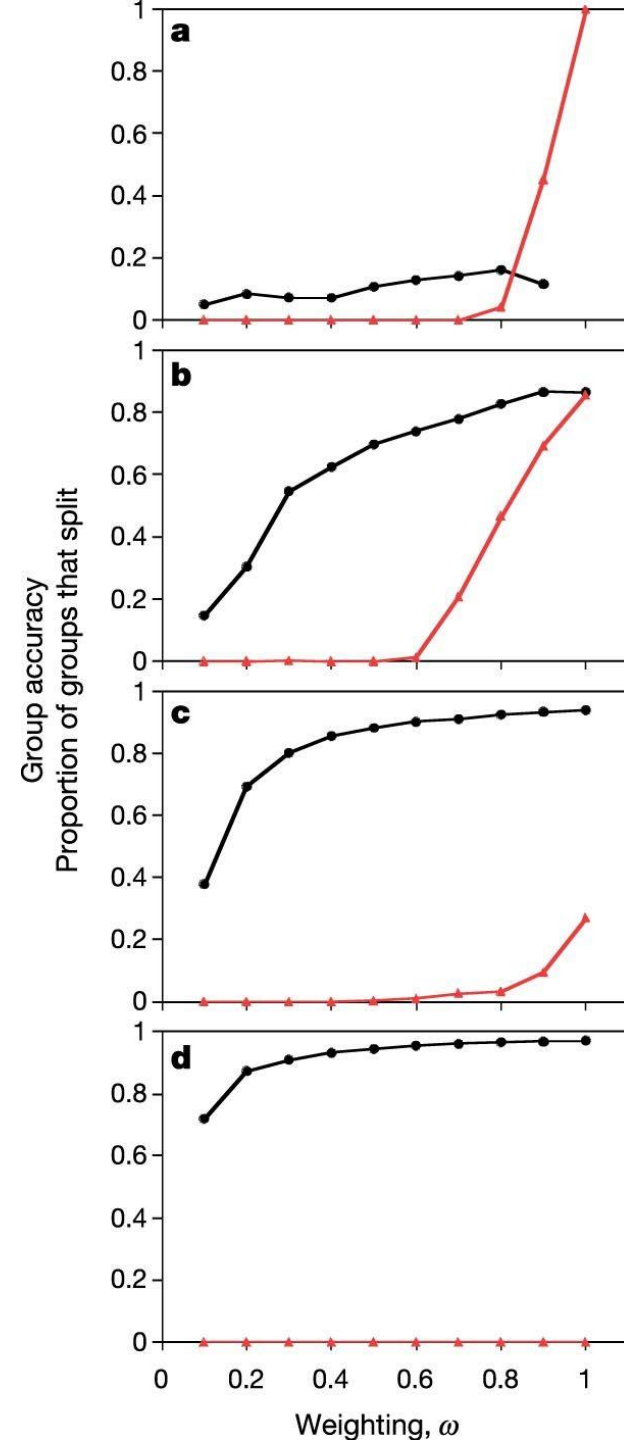
Co-released birds and previous recapitulated routes
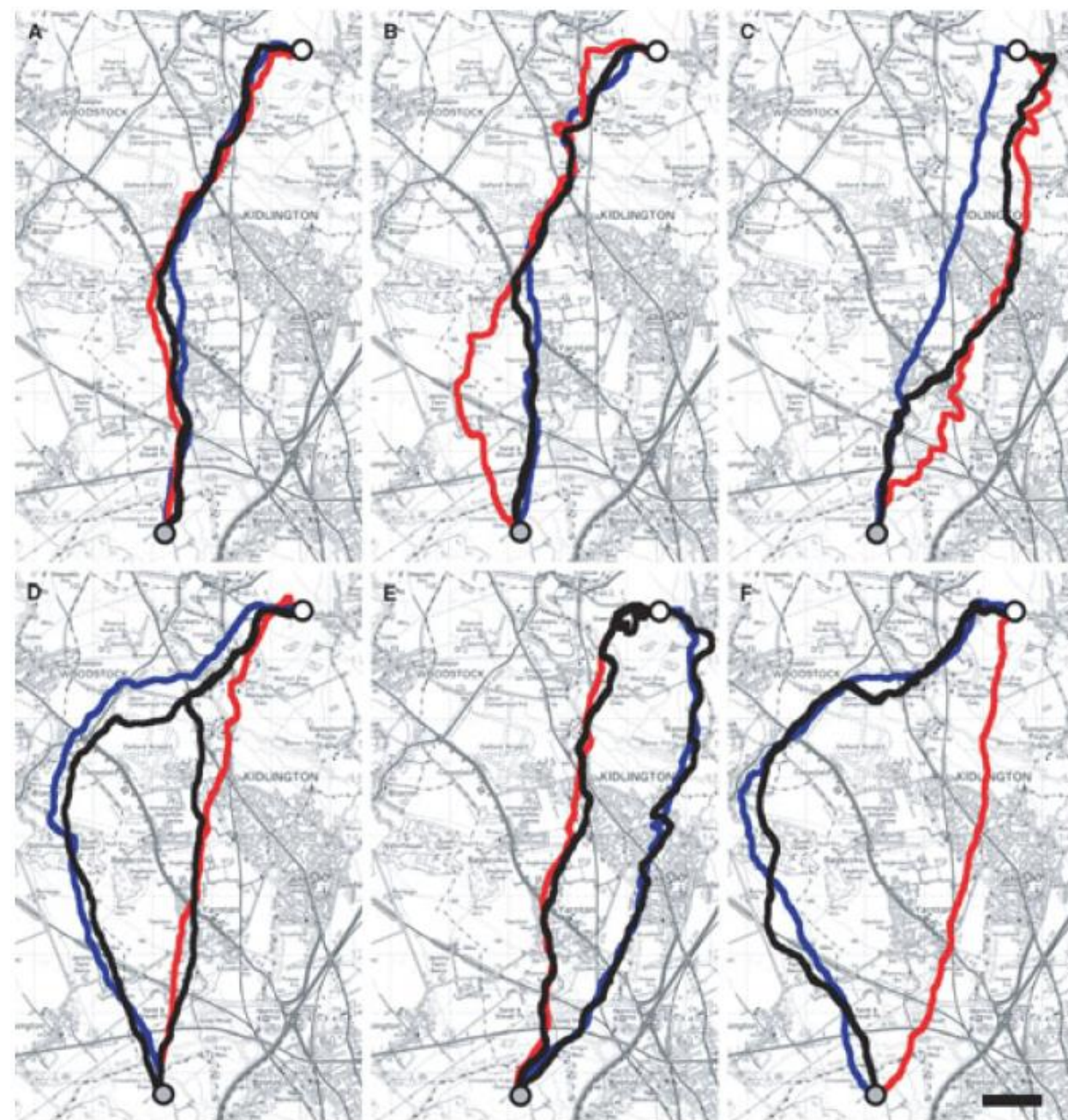
- Black lines show the flight paths of birds released together.
- Blue and red lines show the previous, stably recapitulated routes of the two individuals comprising the pair.
- (A) Birds remained in a pair throughout the flight, sometimes taking the average route.
- (B) Birds remain in a pair, initially taking an average route, then taking one of the previously established routes.
- (C) Birds remain in a pair and switch between routes.
- (D) Birds initially take a shared, average route, then split and return to their previous routes.
- (E) Birds split at release and fly along their previous routes.
- (F) Birds fly along one of the two previous routes

Further elaboration of the model: introducing the "social importance factor"

- h: strength of the effect of a given individual on the group movement
- higher h implies bigger influence
- varies with each agent

$$\vec{d}_i(t + \Delta t) = -\sum_{j \neq i} h_j \frac{\vec{r}_j(t) - \vec{r}_i(t)}{\left| \vec{r}_j(t) - \vec{r}_i(t) \right|} + \sum_{j \neq i} h_j \frac{\vec{v}_j(t)}{\left| \vec{v}_j(t) \right|}$$

Freeman, R., Biro, D., 2009. Modelling group navigation: dominance and democracy in homing pigeons. The Journal of Navigation 62, 33–40.

The role of uninformed individuals – simulations vs. experiments

- **Question**: under what conditions can a self-interested and strongly opinionated minority exert its influence on group movement decisions?

- Simulations:
  - Based on the "Couzin model"

$$\vec{d_i}(t + \Delta t) = \frac{\hat{d_i}(t + \Delta t) + \omega \vec{g_i}}{\left|\hat{d_i}(t + \Delta t) + \omega \vec{g_i}\right|}$$

  - If all individuals are biased:
    - If the strength of the majority preference (ω_1) is equal to or stronger than the minority preference (ω_2), the group has a high probability of reaching the majority-preferred target.
    - Increasing ω_2 (beyond ω_1) can result in the minority gaining control
  - If there are uninformed individuals ($\omega_3 \approx 0$):
    - (most animal groups are like this)
    - Adding uninformed individuals tends to return control spontaneously to the numerical majority
    - this effect reaches a maximum and then begins to slowly diminish, and eventually, noise will dominate
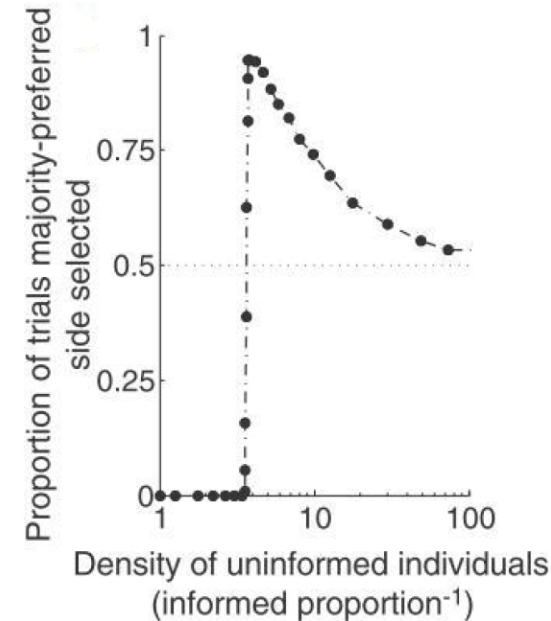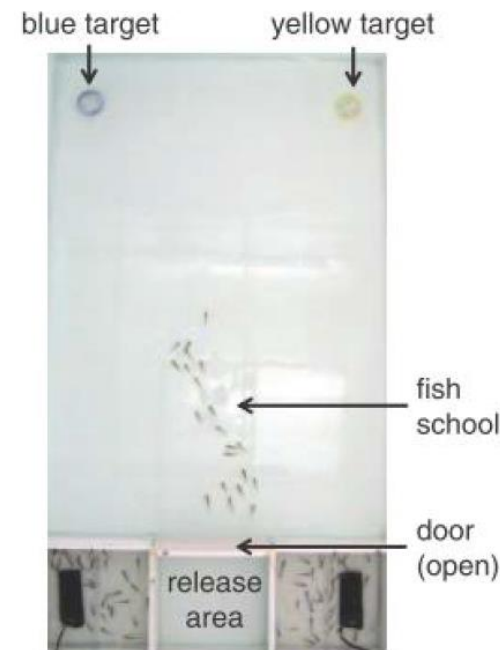

A sharp transition from a minority- to majority-controlled outcome in the model as the density of uninformed individuals is increased.

($\omega_{minority} > \omega_{majority}$)

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Experiment

- golden shiners
- two groups of initiators (with sizes N_1 and N_2) with different preferred directions (blue and yellow target)
- some did not have direction preference
- $N_1 > N_2$ ($N_1 = 6$ and $N_2 = 5$)
- Among the trained fish, ω_{yellow} is "by nature" $> \omega_{blue}$
- Simulations predict a large effect for a relatively small number of naïve individuals; $N_3 = 0, 5, 10$.
- When all individuals exhibit a preference ($N_3 = 0$) then the minority N_2 dictates the consensus (even though the fish trained to the blue target are more numerous).
- When untrained individuals are present, they increasingly return control to the numerical majority N_1.
- If individuals with the stronger preference were also in the numerical majority: the majority was more likely to win (72% of trials overall), and the presence of uninformed individuals had no effect

blue target   yellow target

fish school

door (open)

release area

Experimental set-up

Couzin et al, 2011, Uninformed individuals promote democratic consensus in animal groups. Science, 334(6062):1578-80
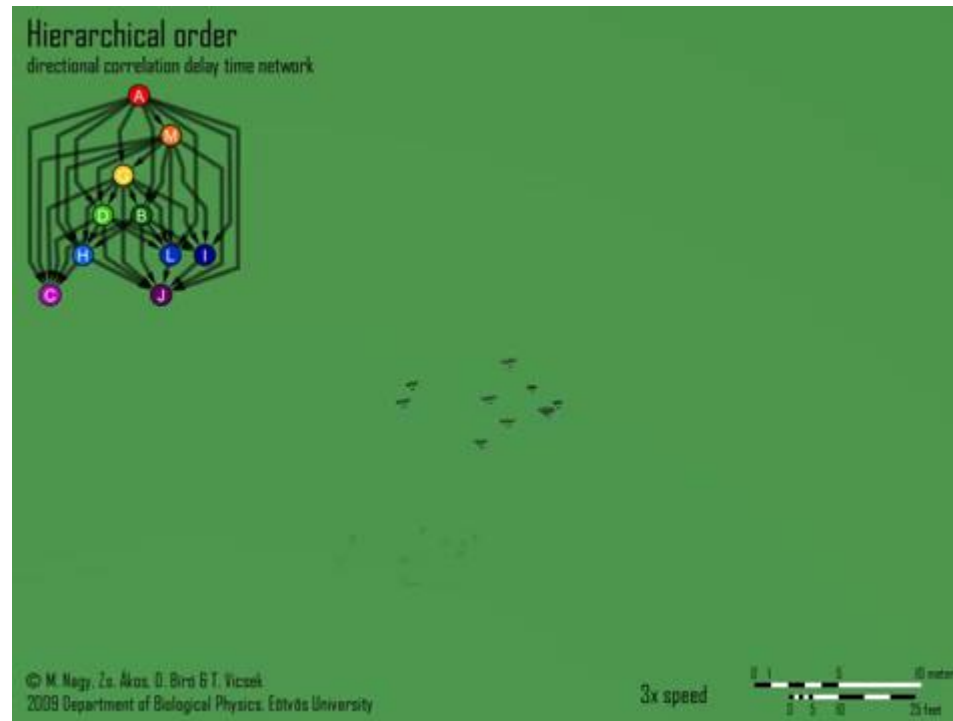
Lessons

- Leadership might emerge from the differences of the level of information possessed by the group members

- information can be pertinent → leadership can be transient and transferable too

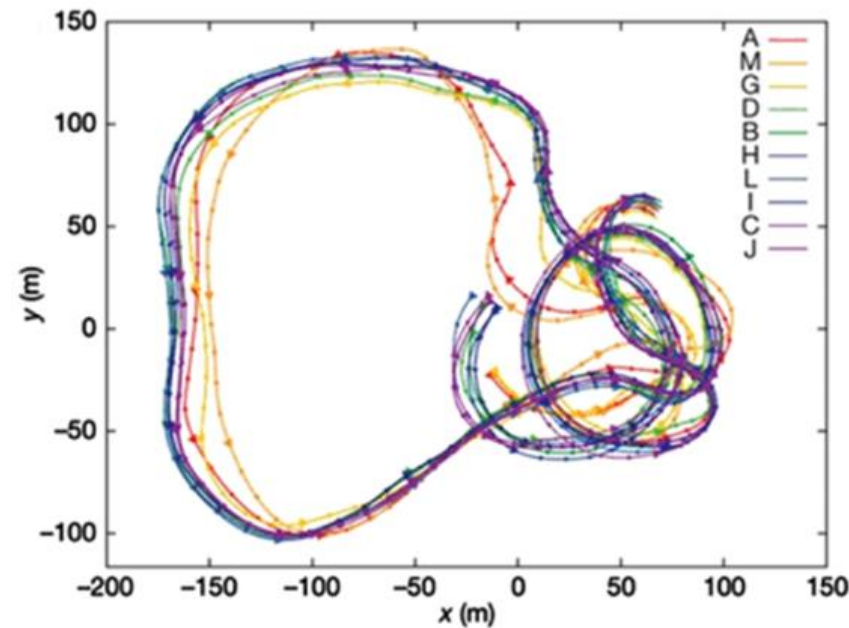# Experiments with homing pigeons

- 10 homing pigeons flying in flocks

- high-precision lightweight GPS

- Two kind of flights were recorded:

1. spontaneous flights near the home loft ("free flights") and

2. during homing following displacement to distances of approximately 15 km from the loft ("homing flights")

Nagy M, Ákos Zs, Bíró D, Vicsek T: *Hierarchical group dynamics in pigeon flocks*, Nature **464**, 890–893, 2010

Hierarchical order
directional correlation delay time network

© M. Nagy, Zs. Ákos, D. Bíró & T. Vicsek
2009 Department of Biological Physics, Eötvös University

3x speed

Trajectories of a flock of nine pigeons during a homing flight

Analysis

2-minute segment from a free flight performed by a flock of ten pigeons in the vicinity of the loft. The smaller and the larger dots indicate every 1s and 5s, respectively. Each path begins near the center of the plot. Letters refer to bird identity.

- **Goal**: to find out how homing pigeons navigate collectively (leadership hierarchy)
  - The *influence* of the birds' behavior on its fellow flock members and on the flock

- → temporal relationship between the bird's flight direction and those of others

- "**Leading event**": when a bird's direction of motion was "copied" by another bird, delayed in time.

This was quantified by determining the directional correlation delay time (τ^*_{ij}) (measured in seconds) from the maximum value of the directional correlation function

$$C_{ij}(\tau) = \left\langle \vec{v_i}(t) \cdot \vec{v_j}(t + \tau) \right\rangle$$

brackets: time average for each pair of birds i, j
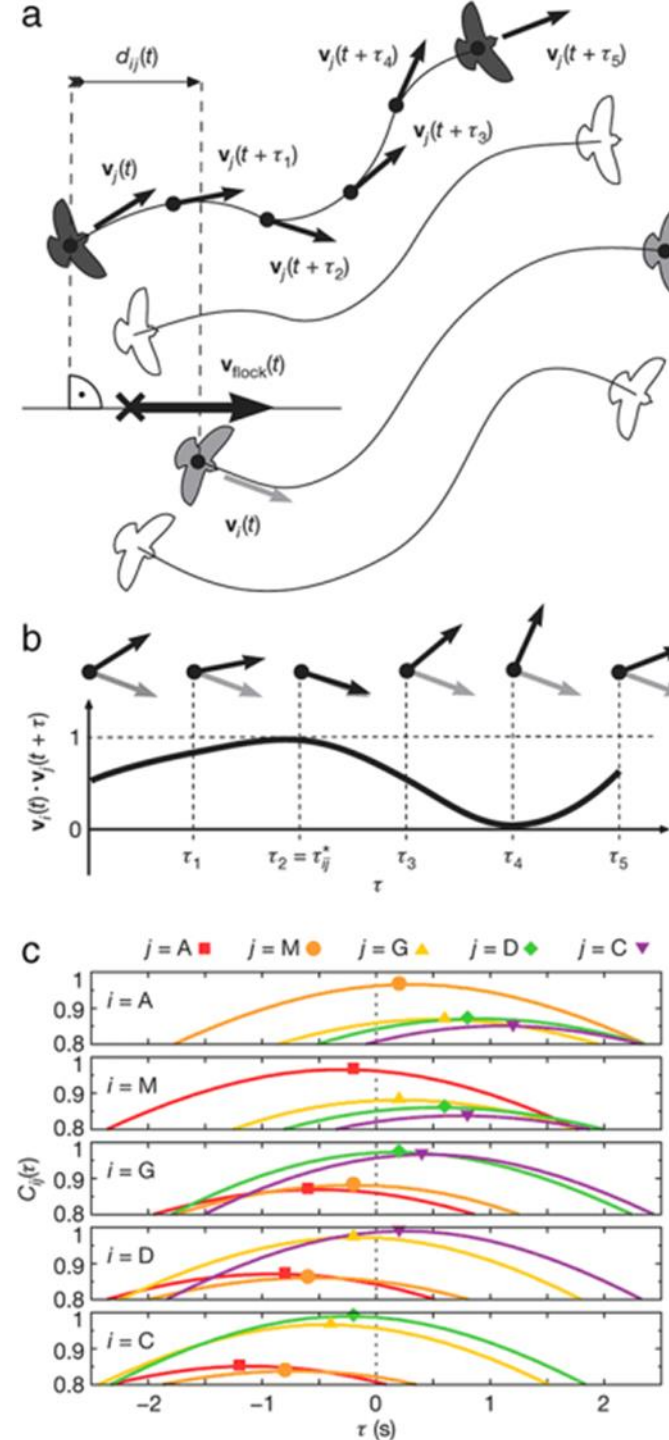
Yielding the directional correlation function

a

- light grey: bird i

- dark grey: bird j

- For each pair ($i \neq j$) the directional correlation function is

$$C_{ij}(\tau) = \langle \vec{v_i}(t) \cdot \vec{v_j}(t+\tau) \rangle$$

- The arrows show the direction of motion, $\vec{v_i}(t)$

b

- Visualization of scalar product of the normalized velocity of bird i at time t and that of bird j at time $t+\tau$. In this example bird j is following bird i with correlation time $\tau_{ij}{}^*$.

c

- The directional correlation function $C_{ij}(\tau)$ during the flock flight. For more transparency only the data of birds A, M, G, D and C (in the order of hierarchy for that flight) are shown. The solid symbols indicate the maximum value of the correlation function, $\tau_{ij}{}^*$.

- These $\tau_{ij}{}^*$ values were used to compose the directional leader-follower networks.

Hierarchical leadership network generated for a single flock flight

- The directed edge points from the leader to the follower (i.e., the average directional correlation delay time for that pair, $\overline{\tau_{ij}}$, is positive);

- Values on edges show the time delay (in seconds) in the two birds' motion.

- For pairs of birds not connected by edges directionality could not be resolved at $C_{min} = 0.5$.
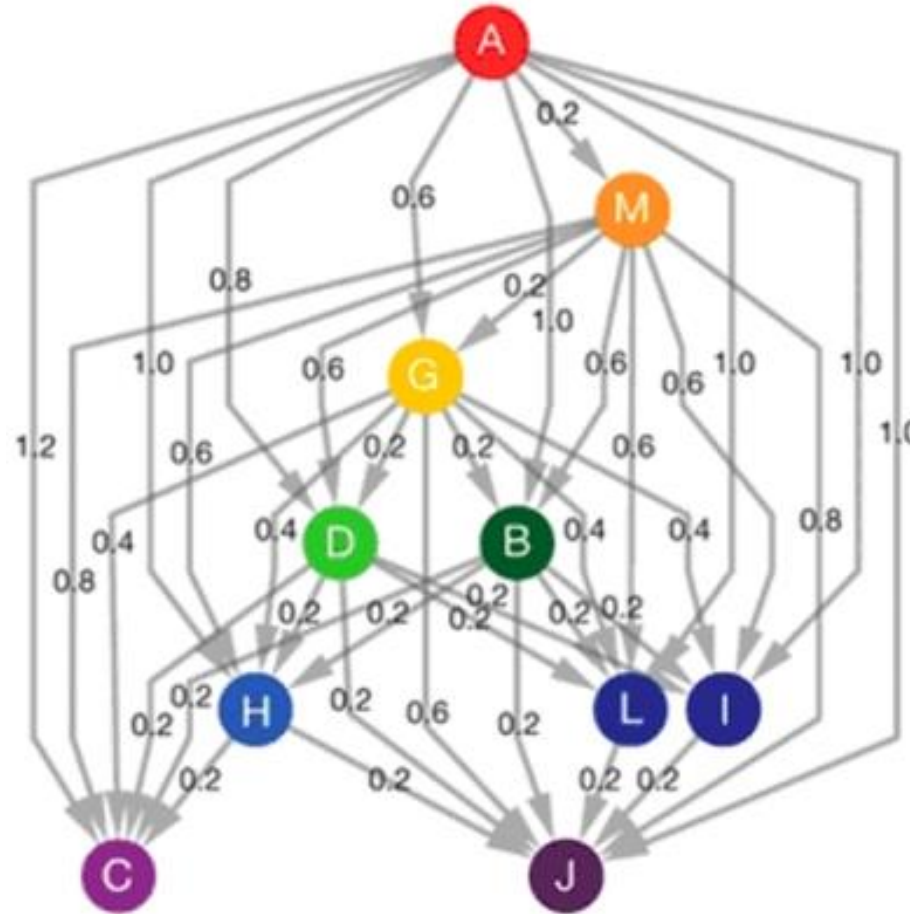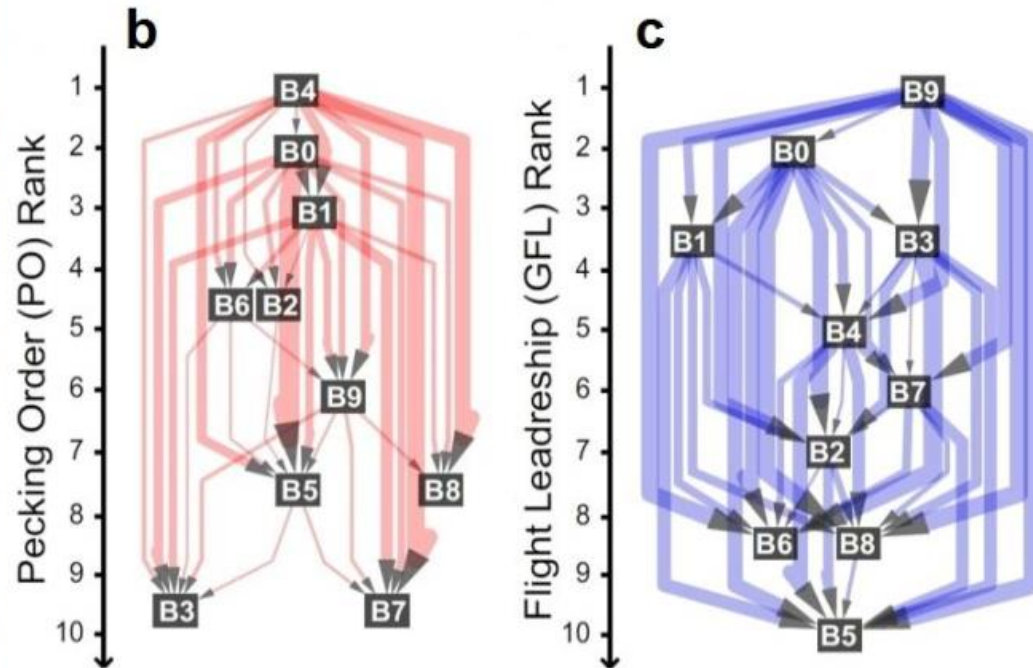
Leadership vs. dominance - a systematic study
Do dominant individuals lead?

- Flock of 10 pigeons

- L-F hierarchy was determined based on the directional correlation function analysis

- Dominance hierarchy was also determined (in the same group), based on computer-vision methods

- The first automated analysis of dominance relationships

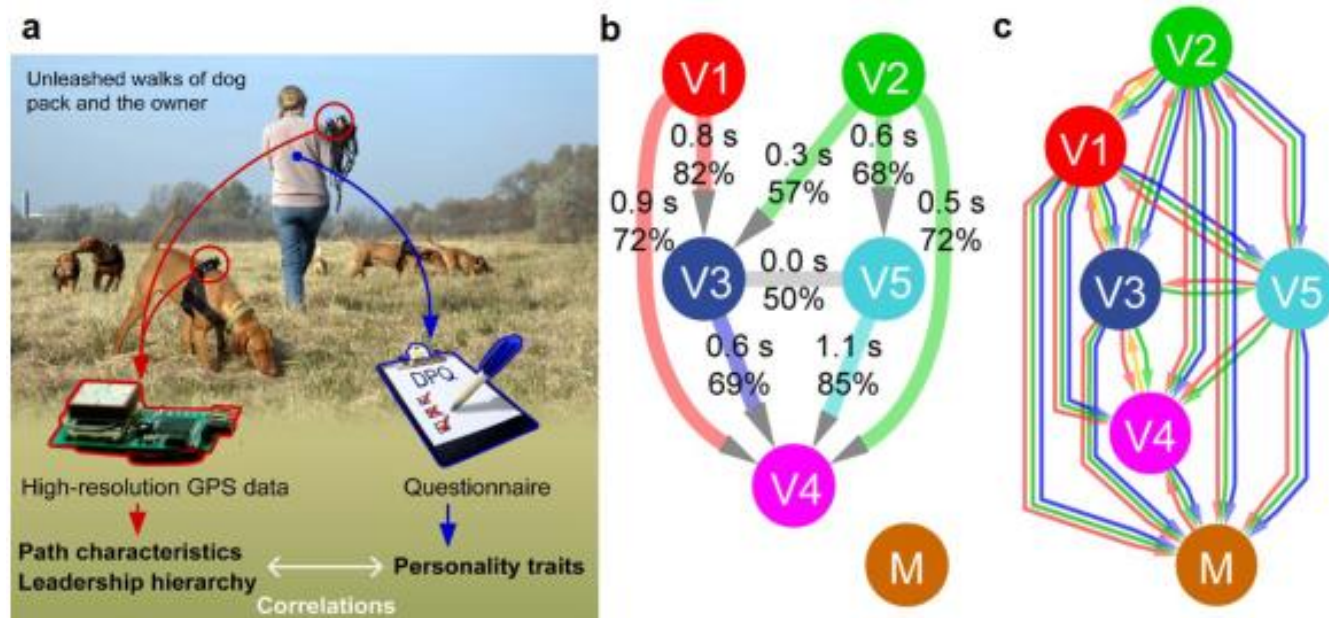- Both structure is clearly hierarchical

© 2012 M. Nagy[1,2], G. Vásárhelyi[1], B. Pettit[2], I. Roberts-Mariani[2], T. Vicsek[1] and D. Biro[2]
[1] COLLMOT Research Project, Department of Biological Physics, Eotvos University
[2] OxNav Research Group, Department of Zoology, University of Oxford

FQ Feeding-Queuing
Automatically identified interactions
Feeding
Queuing

Leadership vs. dominance – Results

- Dominance and leadership hierarchies are independent of each other!
- They can coexist within the same group without any kind of conflict: when it comes to collective travel those will lead the group who have better navigation skills (or information, etc.) and when it comes to feeding, mating, etc., dominance will decide.
- Hierarchy is context-dependent!

Dominance vs. leadership hierarchy in dogs

a)
Unleashed walks of dog pack and the owner

High-resolution GPS data → Path characteristics, Leadership hierarchy

Questionnaire → Personality traits

Correlations

b) Leader-follower hierarchy

- The basis of creating the L-F NW was the directional delay time analysis
- The directed links: point from the leader towards the follower.
- Characteristic delay times are shown on the arrows (upper values).
- Lower values indicate the portion that the leader of that pair was actually leading.

c) Dominance network of the dogs

- derived from a questionnaire.
- The arrows point from the dominant individual towards the subordinate.
- The colors represent the context of the dominance:
    - red: barking,
    - orange: licking the mouth,
    - green: eating
    - blue: fighting.

- 6 dogs, belonging to the same household
- GPS logs during more than a dozen 30- to 40-minute unleashed walks, accompanied by their owner
- All the dogs were "Vizsla", except for the one marked with "M", which was a mixed-breed. This dog did not participate in the vizsla-network.

# "How much" knowledge is enough?

- *high resolution GPS data*

- *hierarchy* of their *leading-following behavior*

- Why do an individual follow an other?

- The ones that are being followed are simply more self-willed or they are better informed?

- How accurate knowledge is needed to reach the target? Etc.

Hierarchical group dynamics in pigeon flocks, M. Nagy et al. *Nature* **464**, 890-893 2010
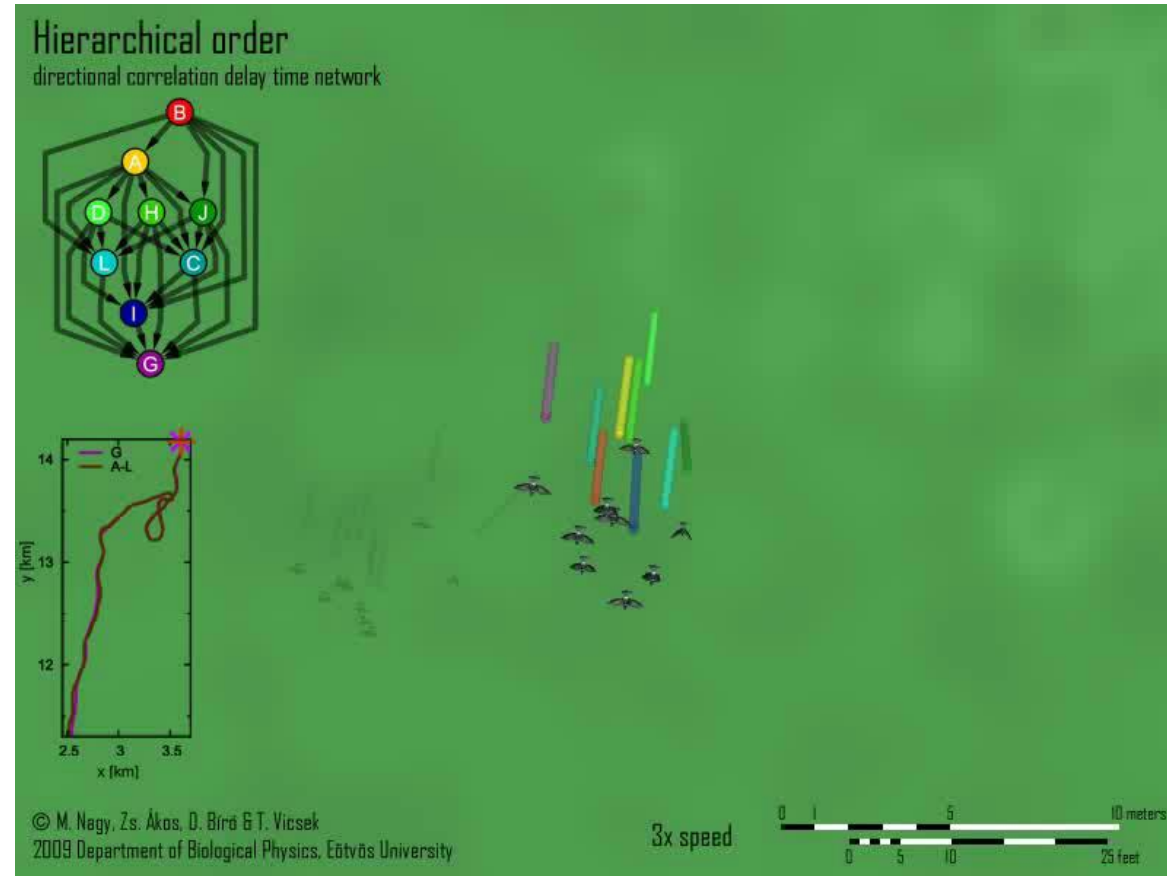
Formulating the problem:

- Given a flock of boids and a pre-defined target
- The flock has to reach the target (together) in the shortest possible way
- The units interact with each other
- The average knowledge is restricted

Question: how to distribute the available amount of knowledge among the group members in order to achieve the best group-performance?

Target

Starting point
+

New direction depends on:

1. The average direction of neighbors (units within the "Range of Interaction, ROI") $\langle \vartheta_j^t \rangle_R$

2. Own estimation $\theta_i^t + \eta_i^t$

3. Noise ξ_i^t

(Discrete time, constant speed magnitude)

$$\vartheta_i^{t+1} = (1 - \lambda_i)(\theta_i^{t+1} + \eta_i^{t+1}) \oplus \lambda_i \langle \vartheta_j^t \rangle_R \oplus \xi_i^{t+1}$$
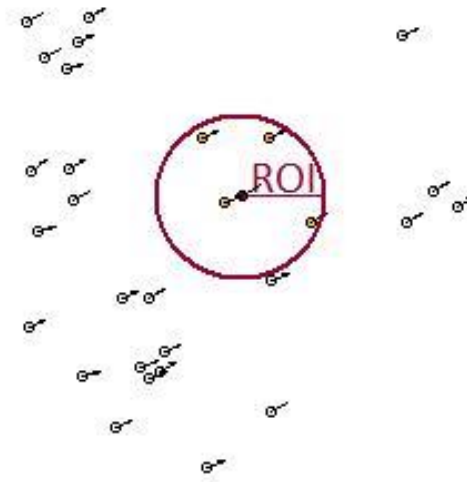
λ_i : a parameter expressing how disposed boid i is to follow others. "Pliancy"

ϑ_i^t : the direction of boid i at time-step t

θ_i^t : the proper direction from boid i towards the target at time-step t

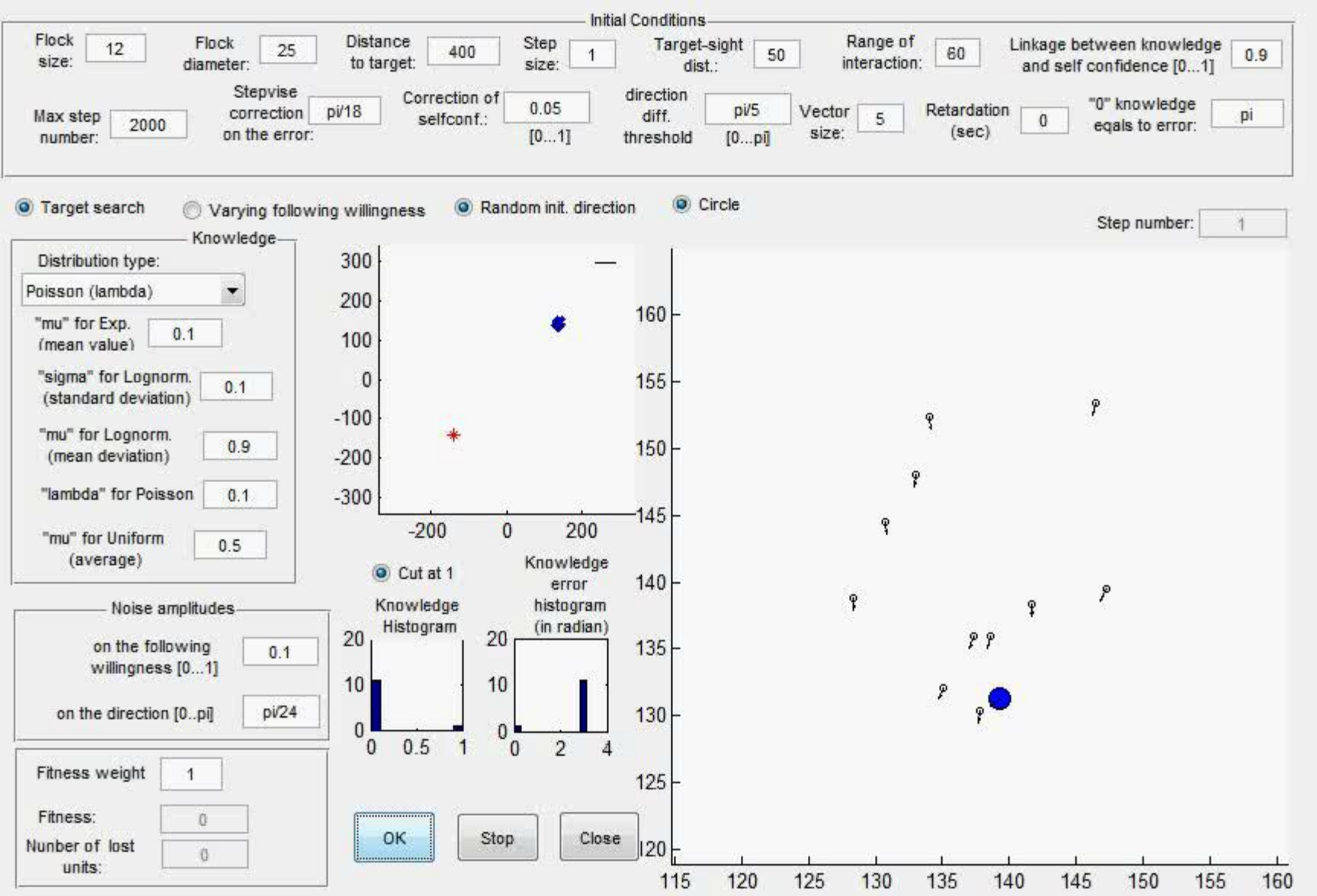η_i^t : the actual estimation error of boid i at time-step t

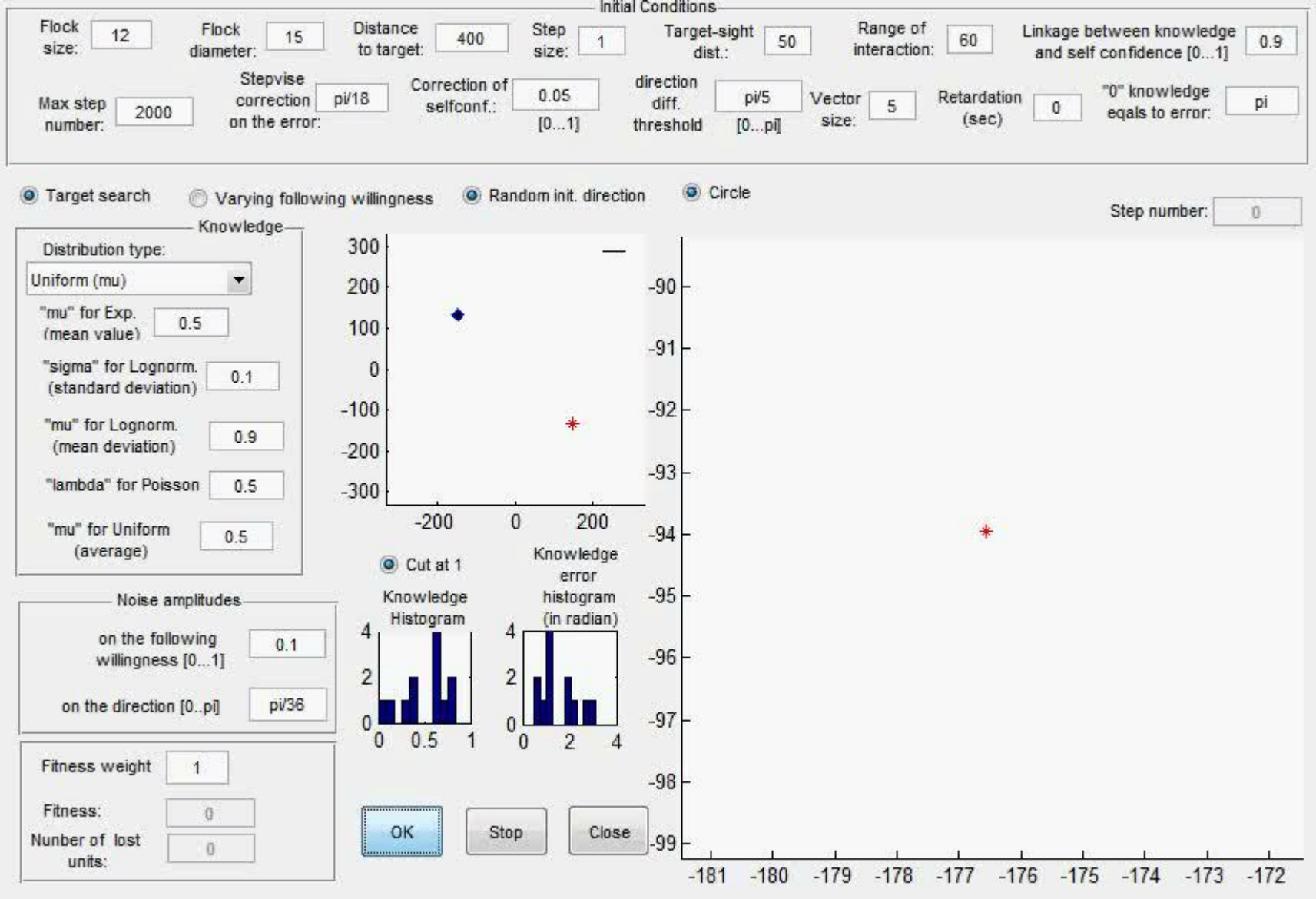ξ_i^t : random noise. $|\xi_i^t| \leq \Xi$ where Ξ is the noise amplitude.

$\oplus$: direction–summation

$\langle \vartheta_j^t \rangle_R$: the average direction of the boids j being within the range of interaction, R of boid i at time-step t
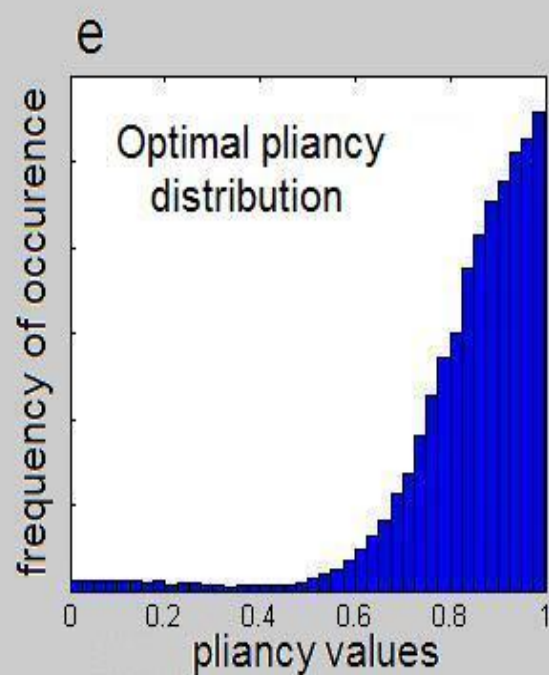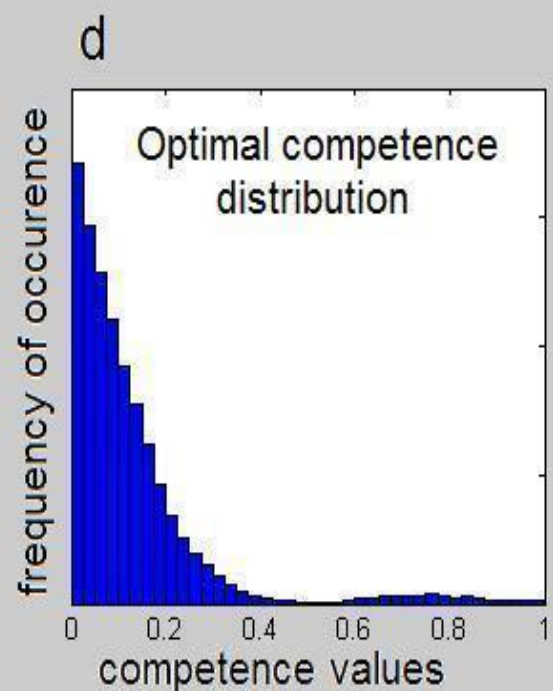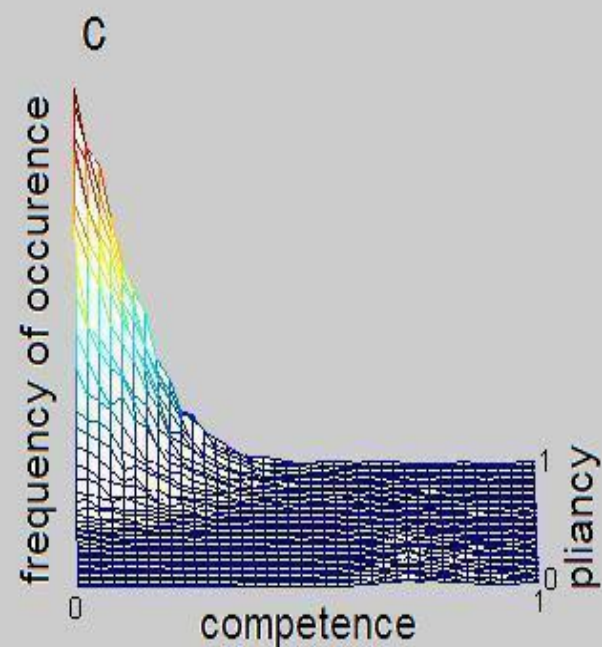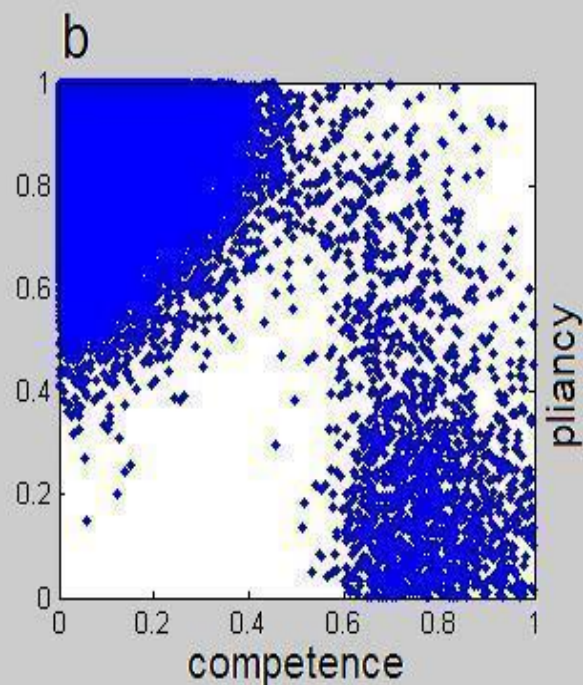
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Flock size = 12, Exponential knowledge distribution, µ=0.1, coded in MatLab.

Flock size = 12, "Two-valued" knowledge distribution, μ=0.1, coded in MatLab.

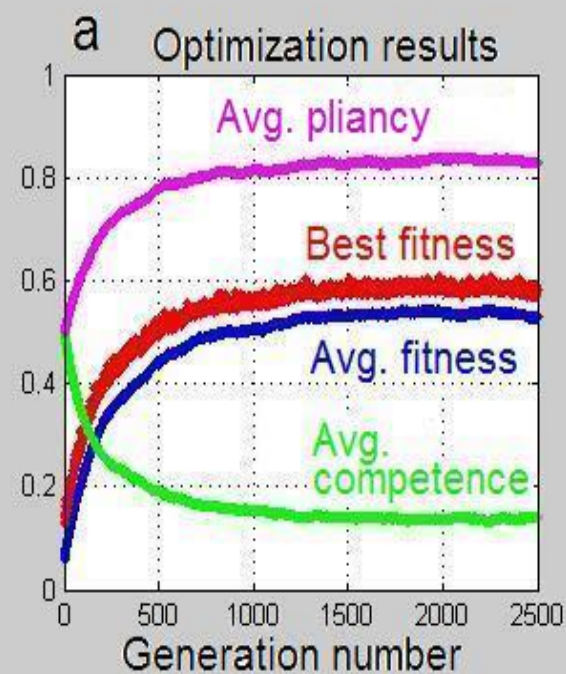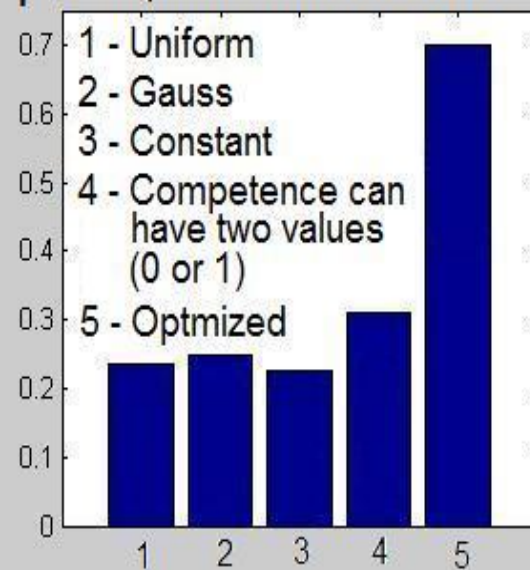Flock size = 12, Uniform knowledge distribution, μ=0.5, coded in MatLab.
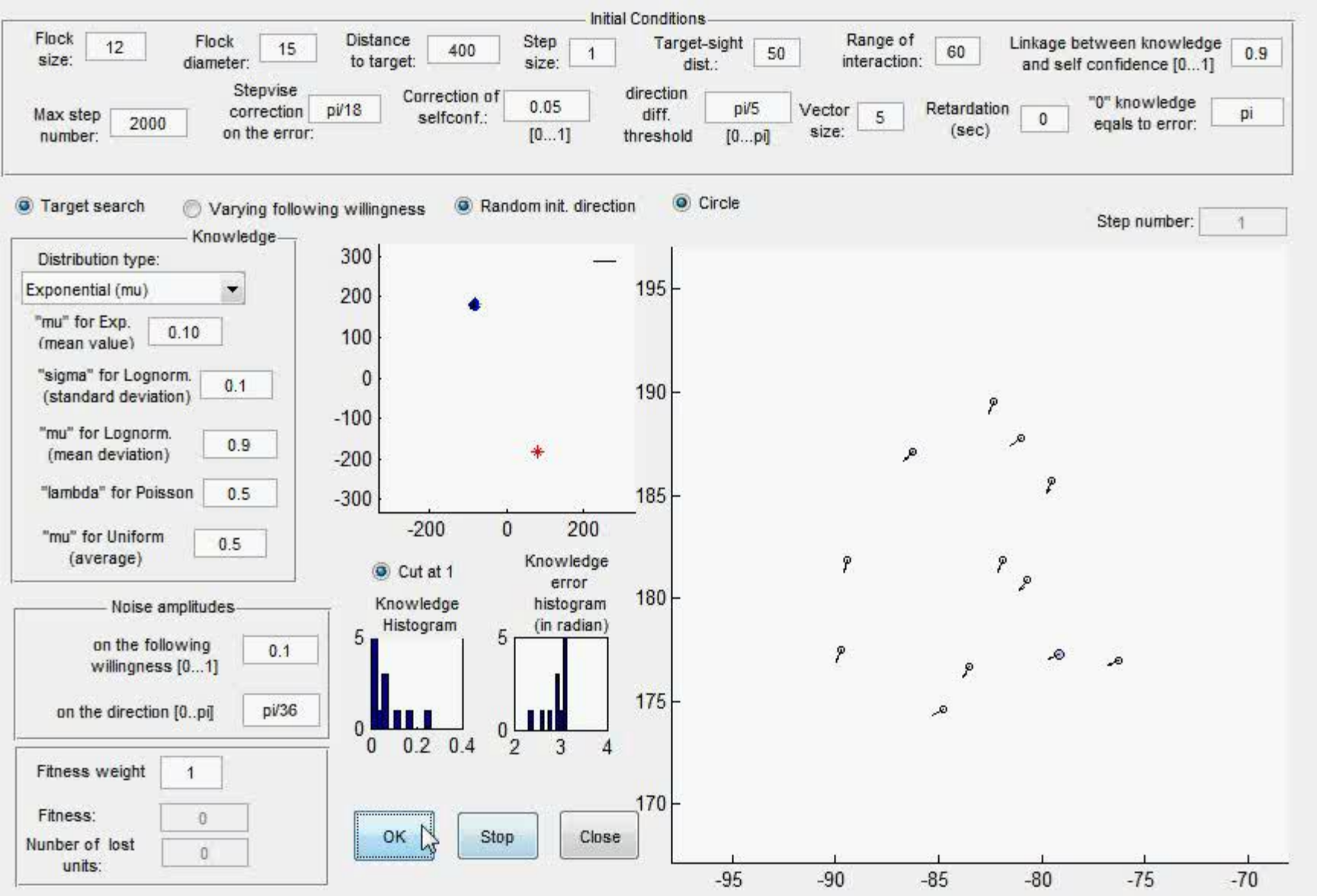
Conclusions of the simulations:

- The *average* knowledge level can be surprisingly small
    - the individual estimations are very imprecise,
    - the knowledge value of most boids can be zero or near-to zero

- The way knowledge is distributed has a huge effect

- It helps, if
    - the units pay attention for their neighbors' movement
    - the pliancy and the knowledge values are inversely related

a Optimization results

Avg. pliancy
Best fitness
Avg. fitness
Avg. competence

Generation number

b

pliancy

competence

c

frequency of occurence

pliancy

competence

d

frequency of occurence

Optimal competence distribution

competence values

e

frequency of occurence

Optimal pliancy distribution

pliancy values

f Group performance for various competence distributions

1 - Uniform
2 - Gauss
3 - Constant
4 - Competence can have two values (0 or 1)
5 - Optmized

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Dominance hierarchy in humans

- Pretty much is known about the way it works in the animal world.

- Well-defined hormones and brain structures

- From a physiological point of view: the mechanisms determining the rank of an individual are very similar between mammals (incl. primates and humans)

    - Testosterone: (the principal male sex hormone)

        - level in the blood indicates the rank

        - In humans as well:

            - Experiments: tennis players, medical students

        - The level of the testosterone hormone and the inclination towards behaving dominantly form a positive feedback loop, as one intensifies the other.

Dominance hierarchy in humans

- Glucocorticoid steroid hormone ("stress hormone"):
  - Not entirely clear picture (contradictory findings)
  - original view: subordinate individuals must be exposed to a much higher level of stress
  - Some measurements revealed the opposite
  - Some other: glucocorticoid secretion is stronger in lower-ranking individuals in general, from which the only exception is the alpha male at the very top, whose cortisol level is the highest in the whole group
  - the correlation between the level of stress hormone and high rank was found to be the strongest during periods of social instability
  - The observed differences might be due to the variations in the social organizations of different species and populations
    - in species, in which cooperative breeding is common, rank and stress hormone level are in direct proportion
    - in other species, they are in inverse proportion

    (this is one explanation)
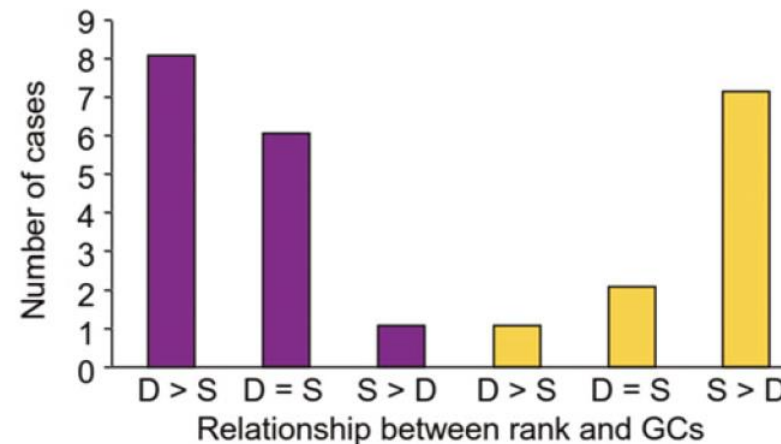
Hierarchy in humans

- Biological heritages: dominance hierarchy (anatomically modern humans appeared ~200,000 years ago, same principles than other primates)
- ~120,000 – 50,000 years ago: "cognitive revolution"
  - new way of social self-organization:
    - formal roles (chieftain, king, pharaoh, colonel, etc.)
      - social ranks are independent of the actual individuals occupying them
      - positions can be organized into any kind of hierarchical system (including egalitarianism)
    - creating and following social rules
      - Support and reinforce the social structure

Dominance hierarchy	Cultural hierarchy
• Genetically coded → Restricted variability: the basic features are the same within one species. • Controlled mainly by hormones (testosterone, stress hormones, etc.) → Mostly instinctive • Its main purpose is to minimise the inner-group aggression by determining access to common resources	• Culturally coded → Can take *any* form, from strict dictatorship to complete egalitarianism • Controlled mainly by the Neocortex → Mostly conscious • Its main purpose is to harmonize the behaviour of the group members via political power

Hierarchy in humans