Topic 3
Hierarchy formation 2

Biologically Inspired Systems

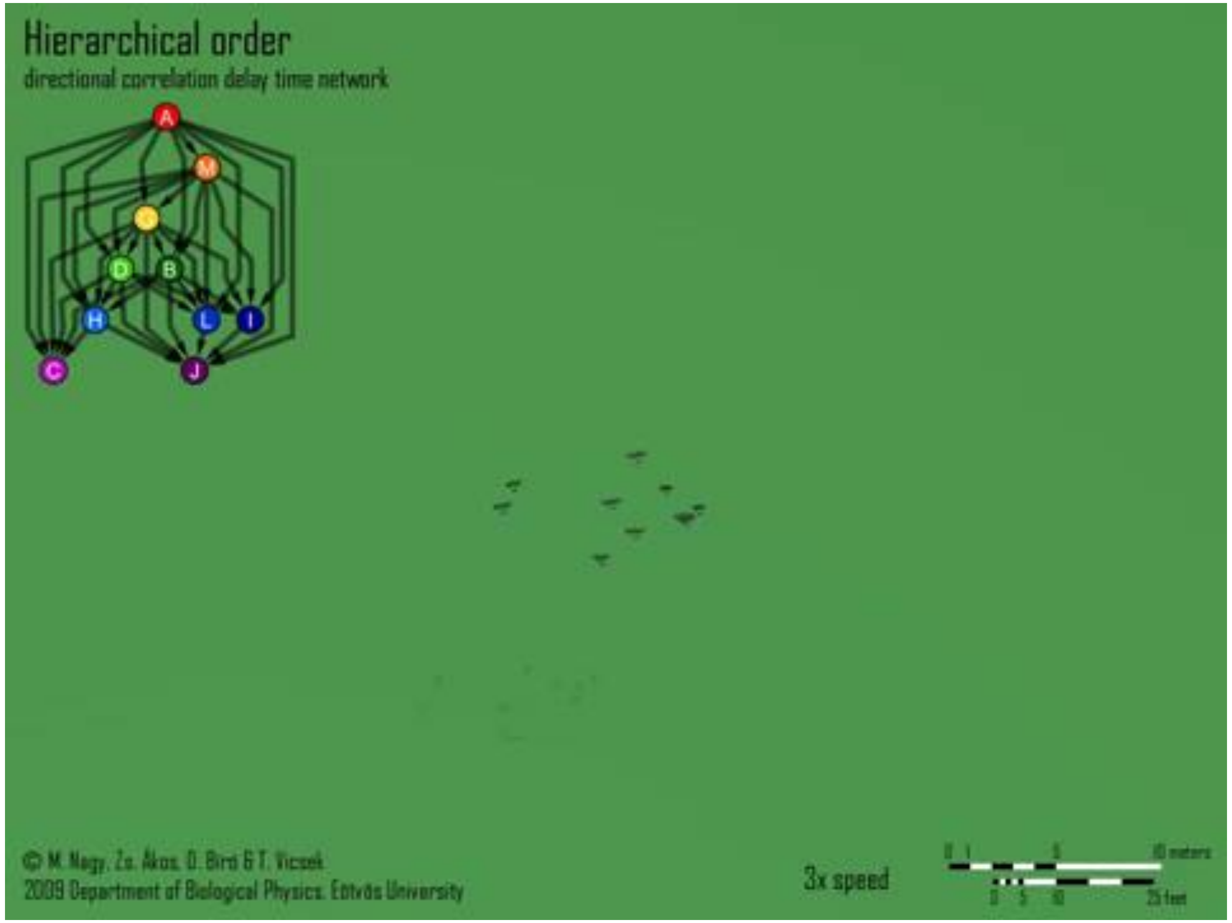
Lecture 3-4

Sept 22, 29, 2021

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”)



Trajectories of a flock of nine pigeons during a homing flight

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

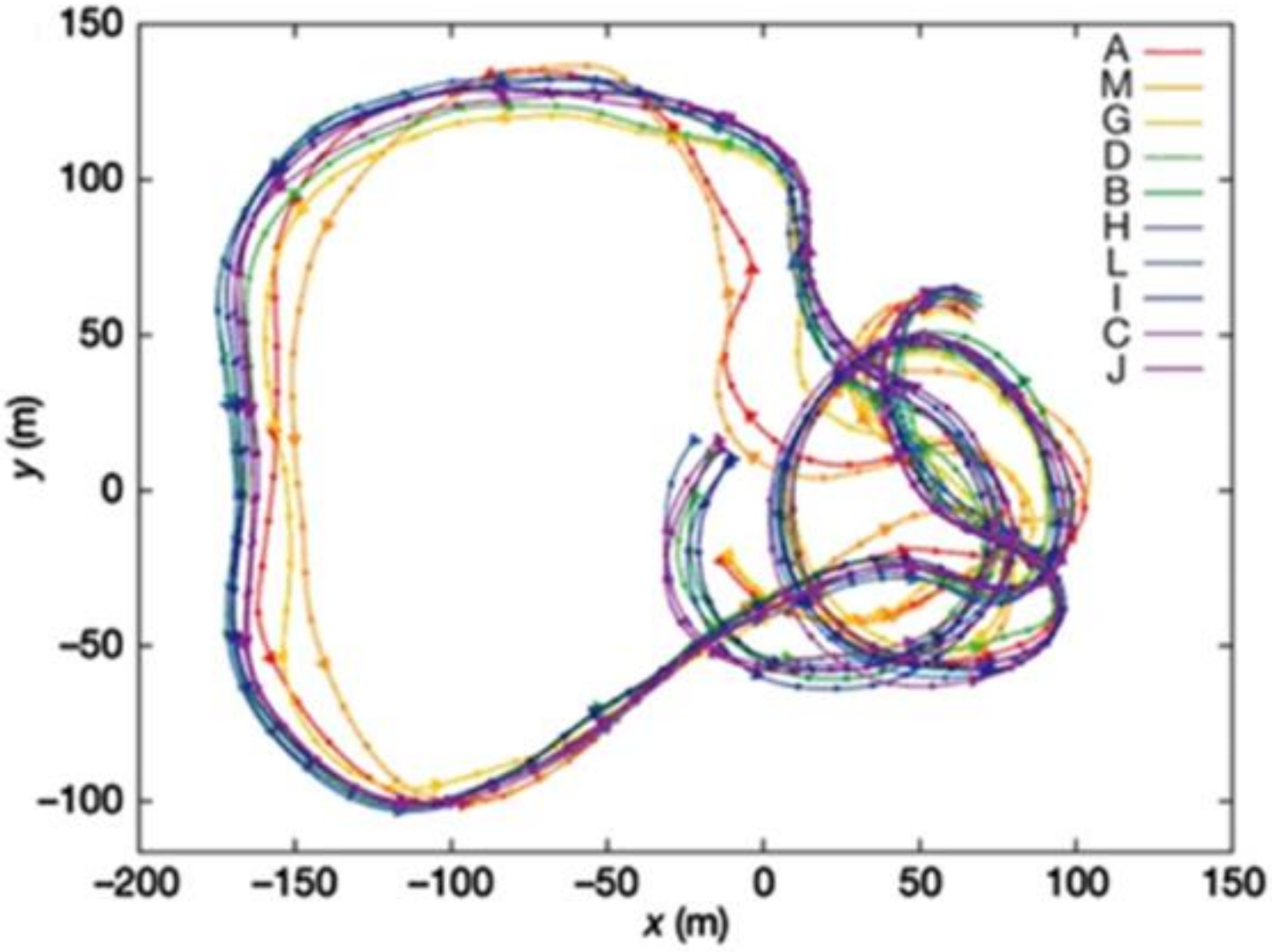
Analysis

- 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.

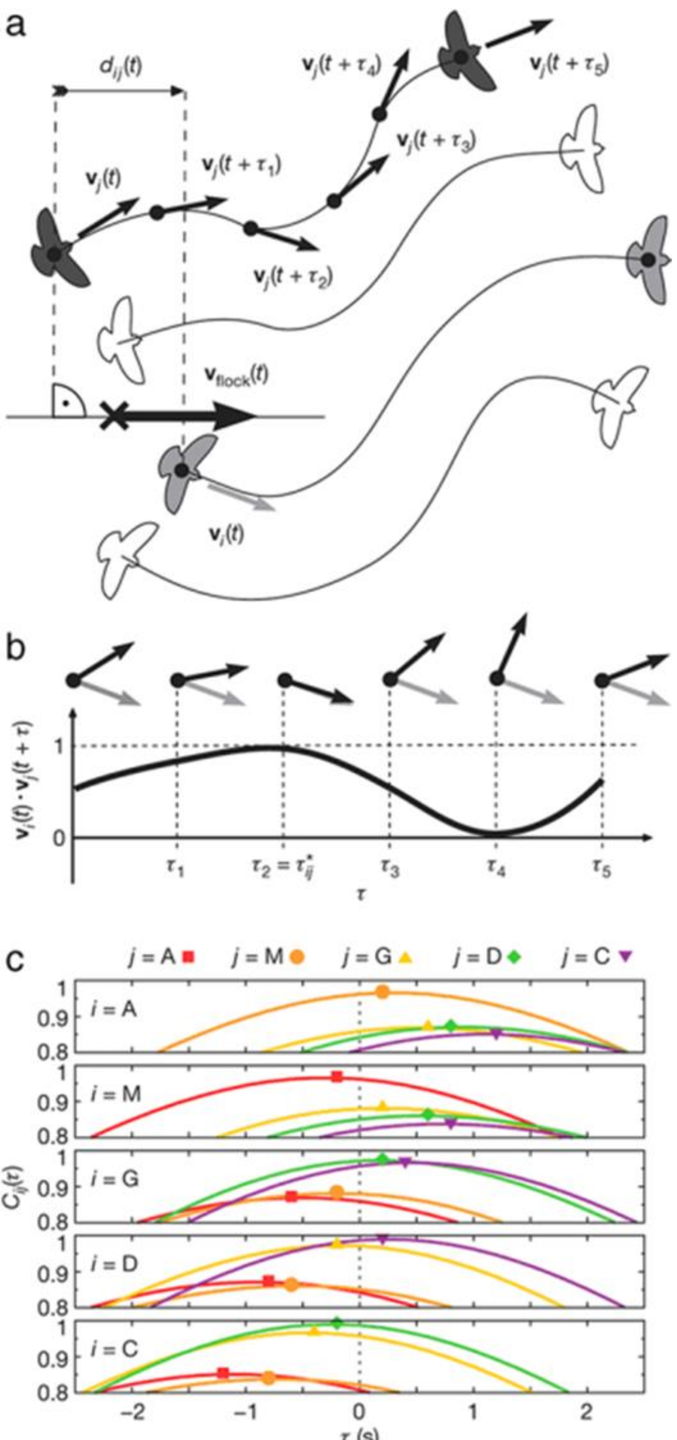
This was quantified by determining the directional correlation delay time (τ^*_{ij}) (measured in seconds) from the maximum value of the directional correlation function

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

brackets: time average for each pair of birds i, j



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.



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

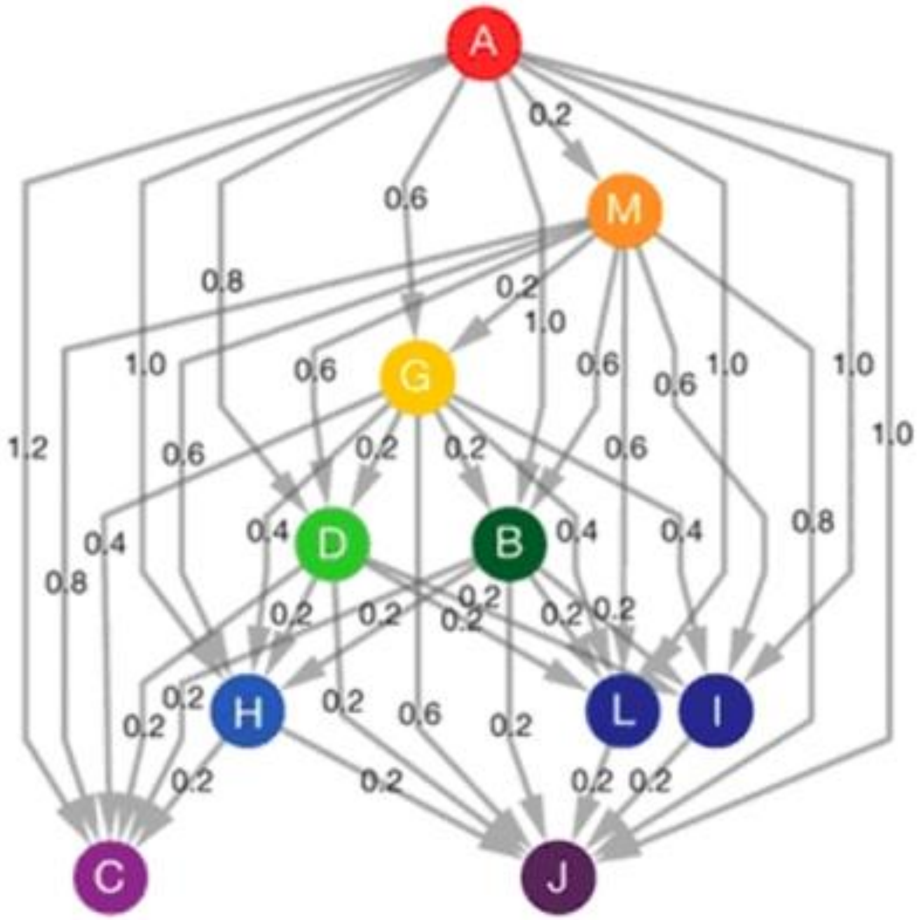
- Visualization of scalar product of the normalized velocity of bird i at time t and that of bird j at time $t+\tau$. In this example bird j is following bird i with correlation time ${\tau_{ij}}^*$.

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 $C_{min} = 0.5$.

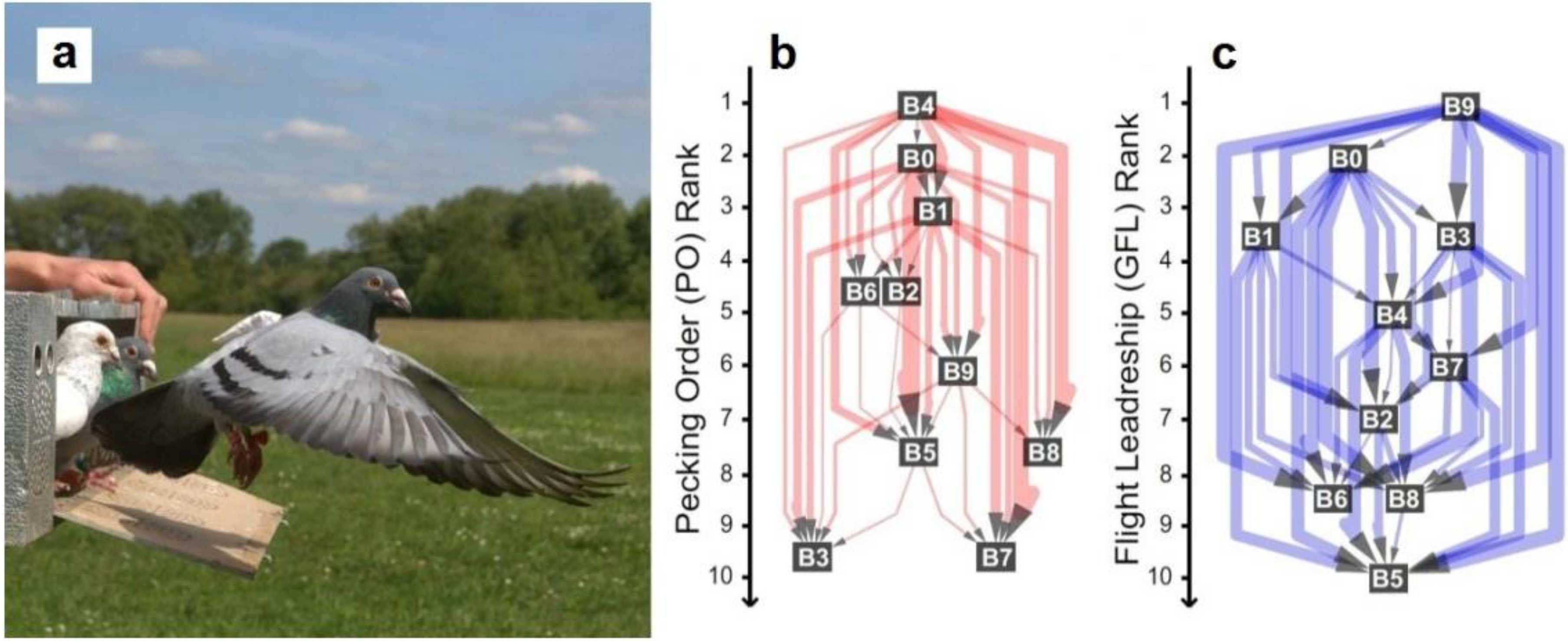


Leadership vs. dominance - a systematic study
Do dominant individuals lead?

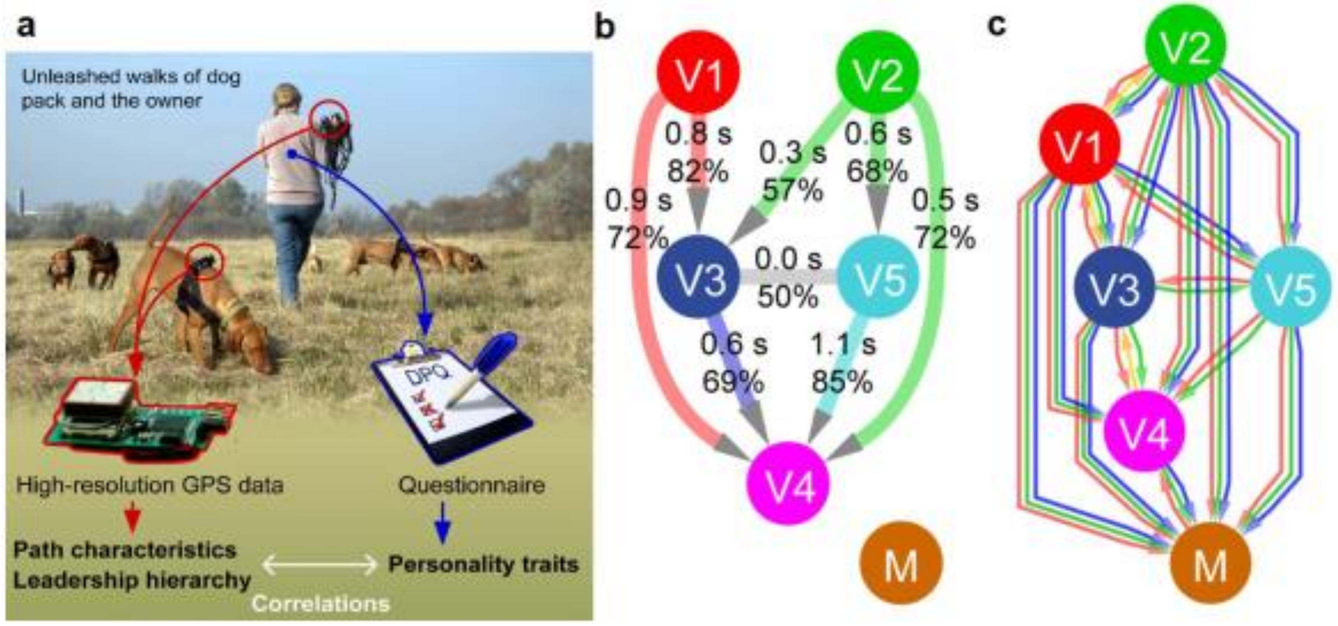
- Flock of 10 pigeons
- L-F hierarchy was determined based on the directional correlation function analysis
- Dominance hierarchy was also determined (in the same group), based on computer-vision methods
- The first automated analysis of dominance relationships
- Both structure is clearly hierarchical

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



- 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.

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.

“How much” knowledge is enough?

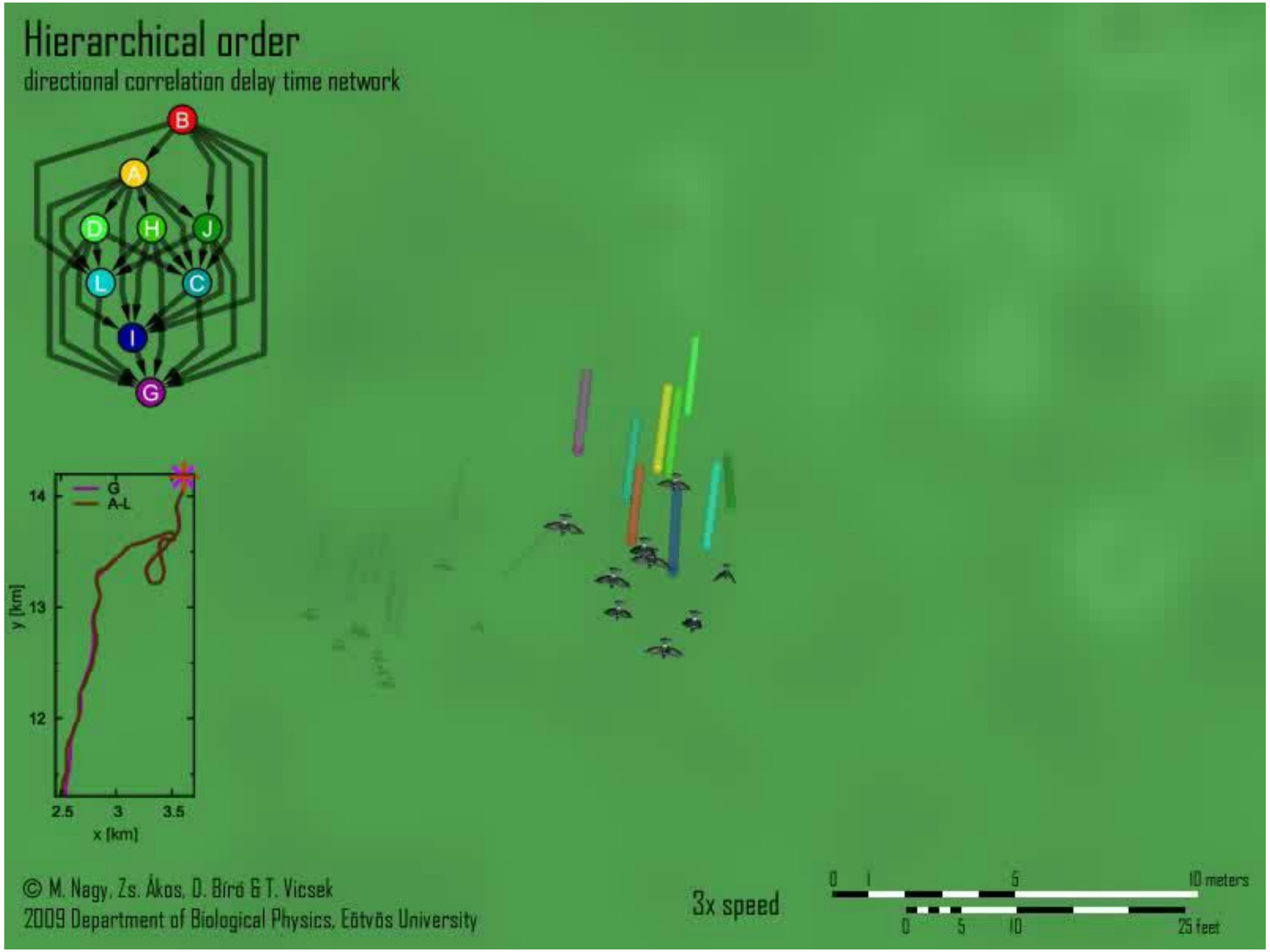
•*high resolution GPS data*

•*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:

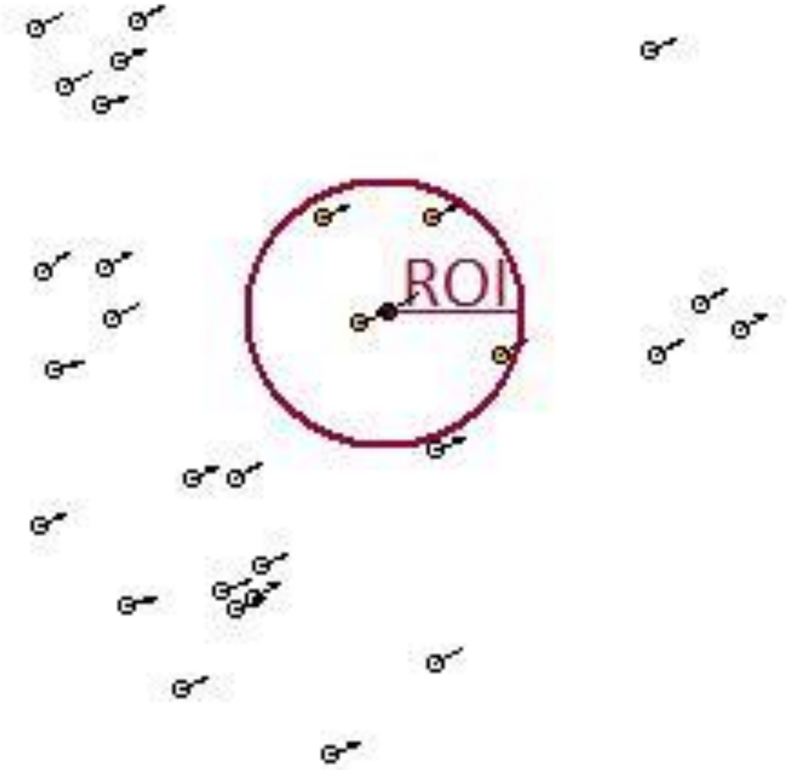
- Given a flock of boids and a pre-defined target
- The flock has to reach the target (together) in the shortest possible way
- The units interact with each other
- The average knowledge is restricted

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

New direction depends on:

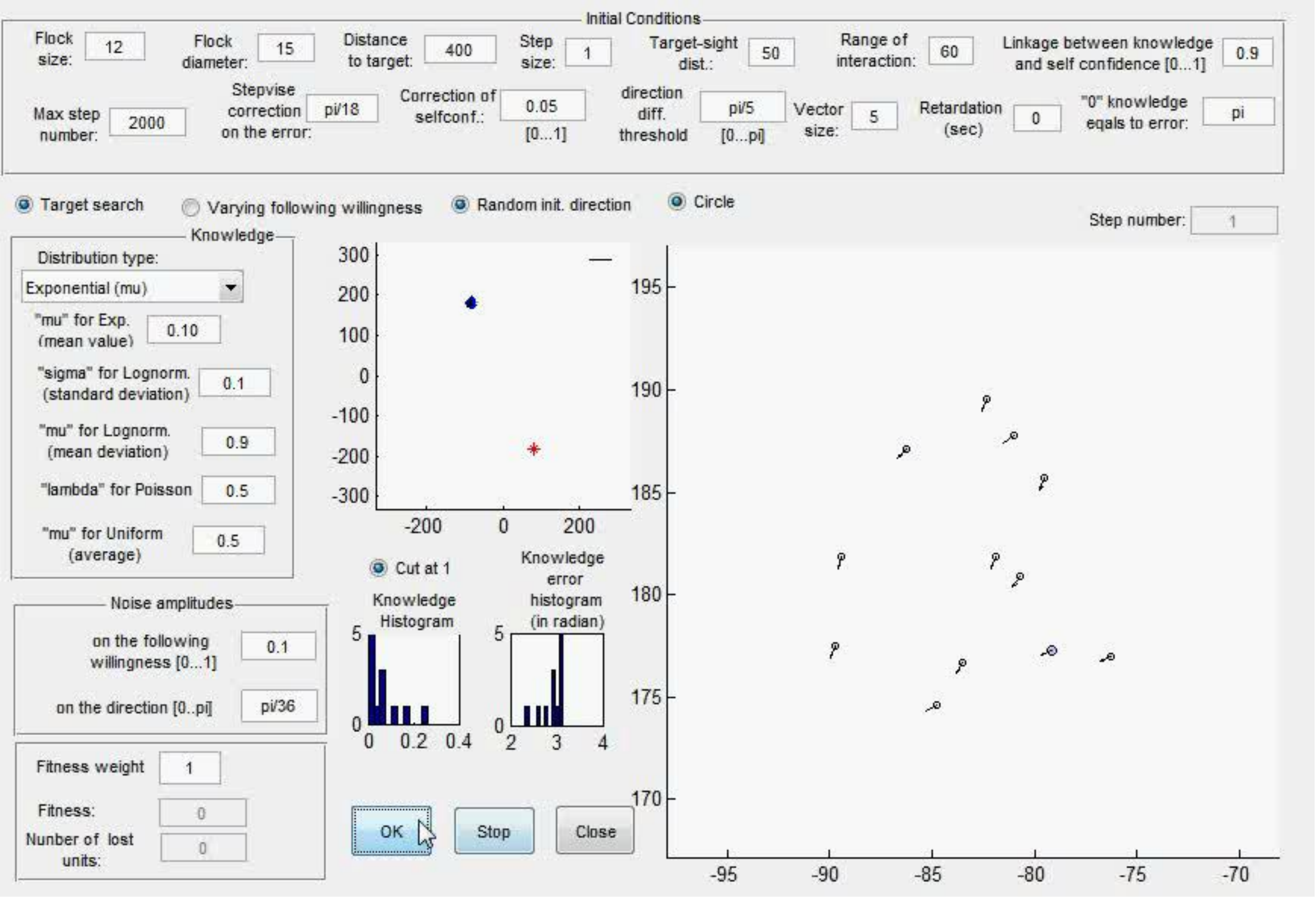
1. The average direction of neighbors (units within the "Range of Interaction, ROI") $\langle \vartheta_j^t \rangle_R$
2. Own estimation $\theta_i^t + \eta_i^t$
3. Noise ξ_i^t

(Discrete time, constant speed magnitude)



$$\vartheta_i^{t+1} = (1 - \lambda_i)(\theta_i^{t+1} + \eta_i^{t+1}) \oplus \lambda_i \left\langle \vartheta_j^t \right\rangle_R \oplus \xi_i^{t+1}$$

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
$\left\langle \vartheta_j^t \right\rangle_R$: the average direction of the boids j being within the range of interaction, R of boid i at time-step t

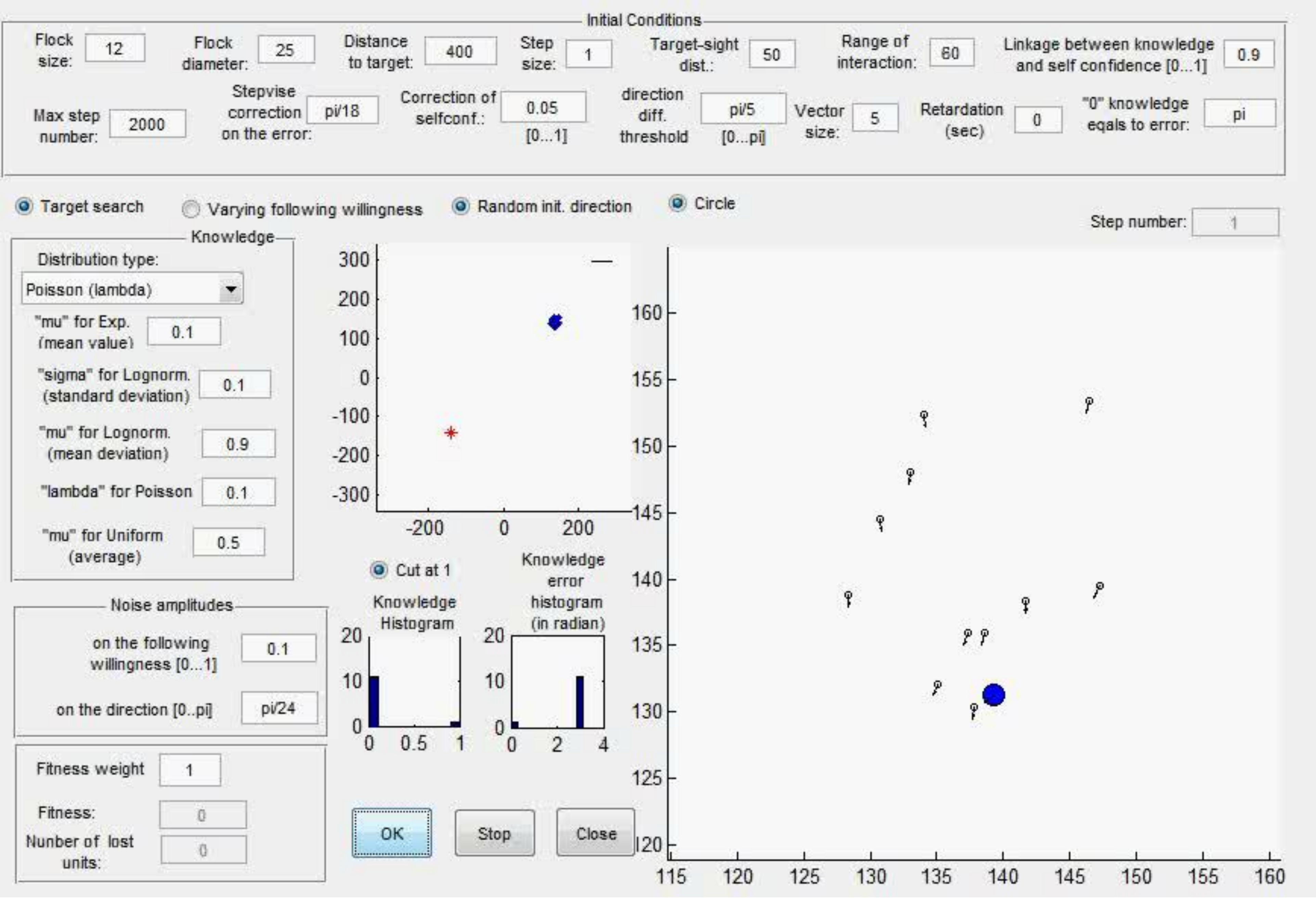


Flock size = 12,

Exponential knowledge distribution,

μ=0.1,

coded in MatLab.

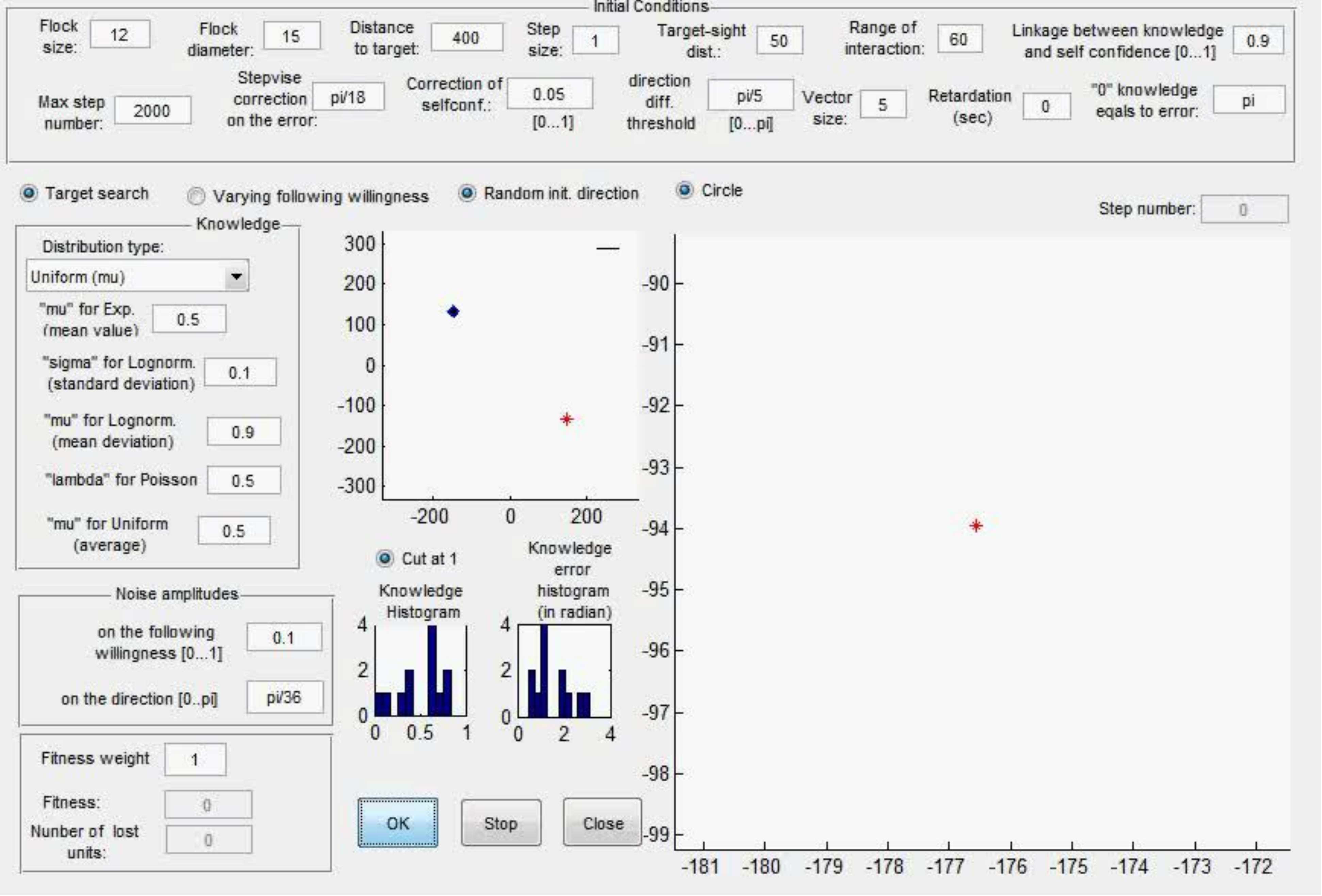


Flock size = 12,

“Two-valued” knowledge distribution,

μ=0.1,

coded in MatLab.

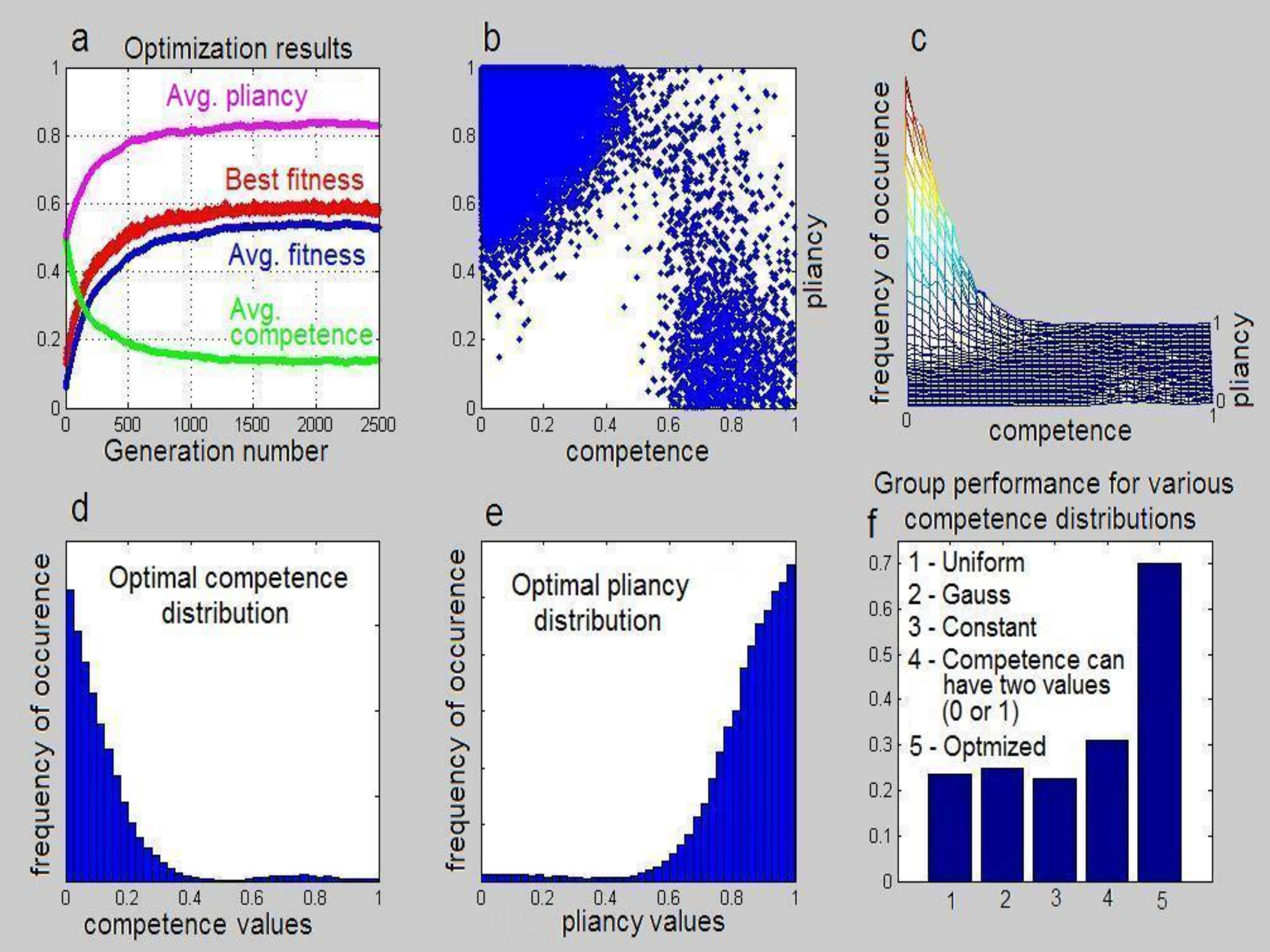


Flock size = 12,

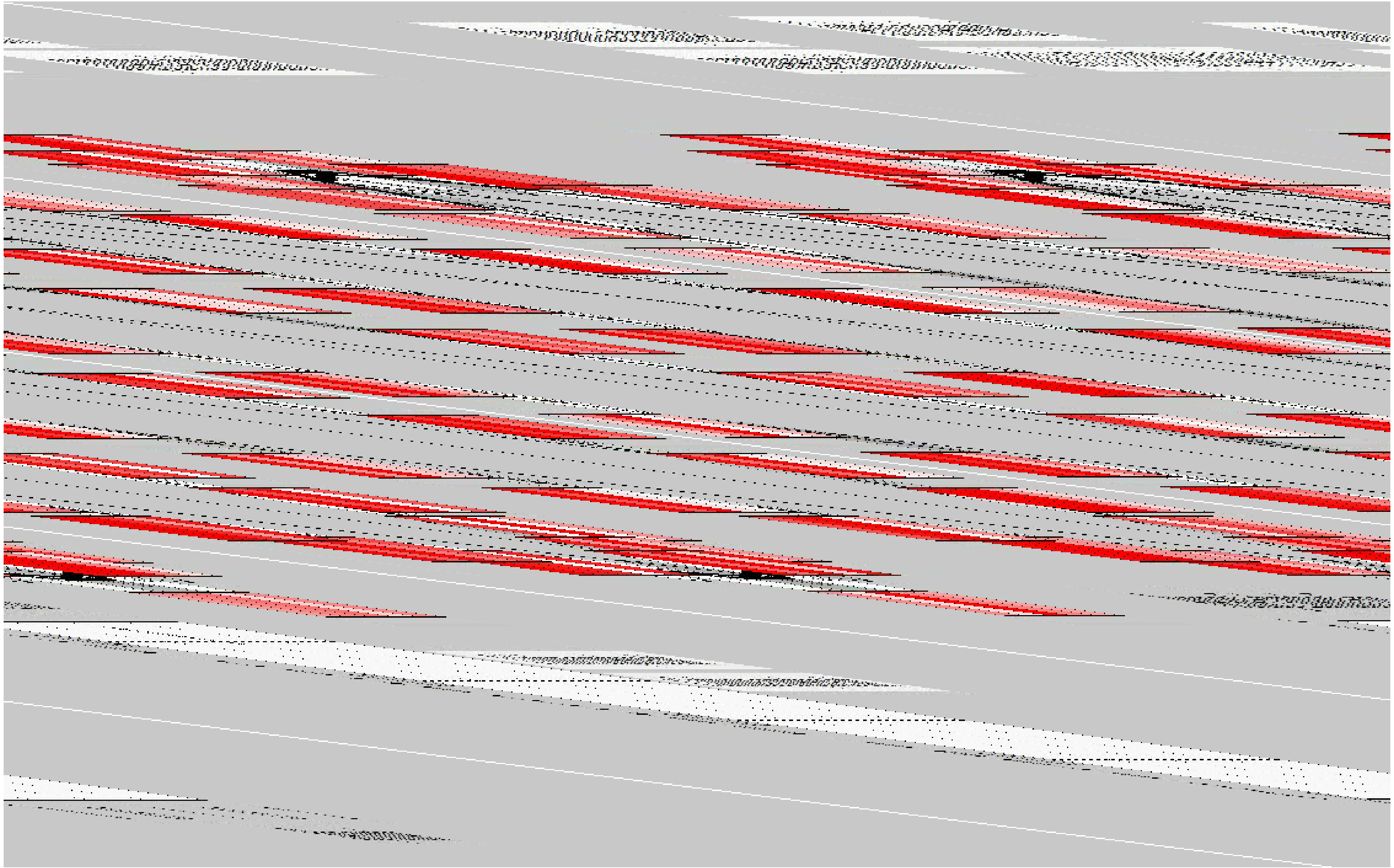
Uniform knowledge distribution,

μ=0.5,

coded in MatLab.


a
Optimization results
Avg. pliancy
Best fitness
Avg. fitness
Avg. competence
Generation number
b
competence
pliancy
c
frequency of occurence
competence
pliancy
d
Optimal competence distribution
frequency of occurence
competence values
e
Optimal pliancy distribution
frequency of occurence
pliancy values
Group performance for various competence distributions
f
1 - Uniform
2 - Gauss
3 - Constant
4 - Competence can have two values (0 or 1)
5 - Optmized

Sequence guessing game on a Small-World NW



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

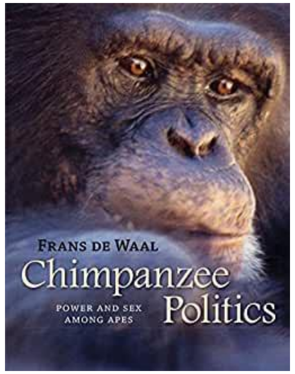
- The way knowledge is distributed has a huge effect

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

Hierarchy in humans

Dominance hierarchy

- A mechanism is needed to reduce the level of aggression triggered by the competition
- Regulate access to resources.
- The mechanism is simple: higher ranked individuals have primacy compared to their lower level mates.
- As one advances in the evolutionary tree, the structure of the dominance hierarchy gets more and more pronounced and complex, accompanied by more and more sophisticated strategies by which individuals try to get higher and higher ranks.
- Chimpanzees (few decades ago believed to be solely human):
    - coalition formation
    - manipulation
    - exchange of social favors
    - adaptation of rational strategies
- Obvious advantage: less fight



Dominance hierarchy in humans

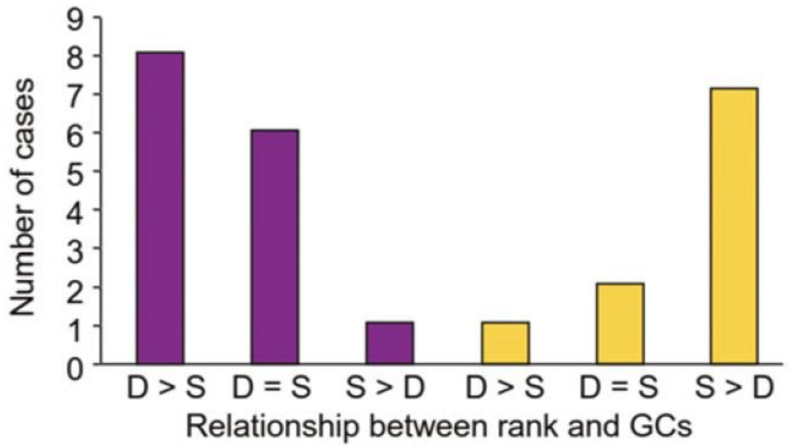
- Pretty much is known about the way it works in the animal world.
- Well-defined hormones and brain structures
- From a physiological point of view: the mechanisms determining the rank of an individual are very similar between mammals (incl. primates and humans)
  - Testosterone: (the principal male 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)



Human vs. non-human groups

- Groups of animals are **genetically open**, and over a period of time, a significant part of the group migrates or changes, so that **group identity independent of individuals does not develop**.

- anatomically modern humans appeared ~200,000 years ago
- ~120,000 – 50,000 years ago: “cognitive revolution”

- Human groups are characterized by
  - a decline in individual competition and
  - an increase in competition between groups (Bohem 1997).

- An **autonomous group entity**, independent of individuals and individuals, emerges as a new level of social organization, whose own interests are able to overshadow the individual interests of group members. (*history begins*)

- People living in human-like groups are characterized by the following genetically based species-specific traits:
  - 1. They like to participate in joint actions,
  - 2. They like to make common constructs (abstract, material, social),
  - 3. They form and accept common beliefs,
  - 4. They are loyal to their group and the group in order to push their own interests into the background, they even sacrifice their lives for the group.

Abstract way of thinking and more tightly connected groups go hand in hand (positive feedback loop)

(Vilmos Csányi)

Hierarchy in humans

- ~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
- Transition from small scale communities to large-scale societies?

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

Large-scale human hierarchies: from small goups to ultrasocieties

Problem:

- What enforced the transition from small, genetically related cooperative H-G groups to huge anonymous, hierarchically organized societies, typically organized as states, "ultrasocieties"?

  small, „traditional" HG societies: kin selection + reciprocal altruism

  Only 10-12,000 years ago (vs. 200,000 y)

- Neolithic transition

- Dunbar Number

Turchin et al, War, space, and the evolution of Old World complex societies, PNAS, 2013

Existing theories

- Many theories, but non of them completely satisfactory
- Mostly anthropological, historical approaches (qualitative)
- Quantitative approaches are rare (but existent)
  – a field of science in its infancy

- Mostly agent-based models:
  - Barceló and Castillo (eds) 2016: Simulating Prehistoric and Ancient Worlds (Computational Social Sciences). Springer, Cham, Switzerland
  - Grinin and Korotayev (eds) 2014: History & Mathematics: Trends and Cycles. Uchitel, Volgograd
  - Pumain and Reuillon 2017: Urban Dynamics and Simulation Models (Lecture Notes in Morphogenesis). Springer, Cham, Switzerland
- AB models combined with game theory
  - Boix 2015, Political Order and Inequality. Cambridge Univ. Press, New Jersey
  - Greif 2006. Institutions and the Path to the Modern Economy: Lessons from Medieval Trade. Cambridge Univ. Press, New York
- The book by Turchin (2003) Historical Dynamics: Why States Rise and Fall. Princeton Univ. Press, New Jersey - offers one of the deepest analysis

Premise: Costly institutions that enabled large human groups to function without splitting up evolved as a result of :

1. Warfare
2. Multilevel selection

Warfare intensity depends on

- the spread of historically attested military technologies (e.g., chariots and cavalry) and
- geographic factors (e.g., rugged landscape).

Multilevel selection:

- group selection „on the top of” individual selection

Simplified train of thought

- **Small H-G societies:** Throughout most of human history, people lived in small-scale, mostly egalitarian societies.
- **Warfare over resources:** These tribes often engaged in warfare with each other, over various resources.
- **Selfishness vs. Group behavior:** Although selfish behavior can be beneficial for the individuals within a group, when groups intensively compete with each other (for example, during warfare), those groups that have more cooperative and less selfish members have the advantage. Thus, human societies are subject **to multilevel selection**.

The effects of warfare on social evolution:

- Groups become internally more cohesive
- Technological progress, including military and organizational applications
- „God always favors the big battalions" (Napoleon / Turenne) → **Enlargement of group sizes**

The **capacity of the human brain** has its limits,

- it cannot handle social relations in detail among more than around 150 people (Dunbar number).
- → there is a limit to the size of egalitarian, face-to-face human groups.

Simplified train of thought – cont.

Pressure on the group size to grow $\leftrightarrow$ Dunbar no.

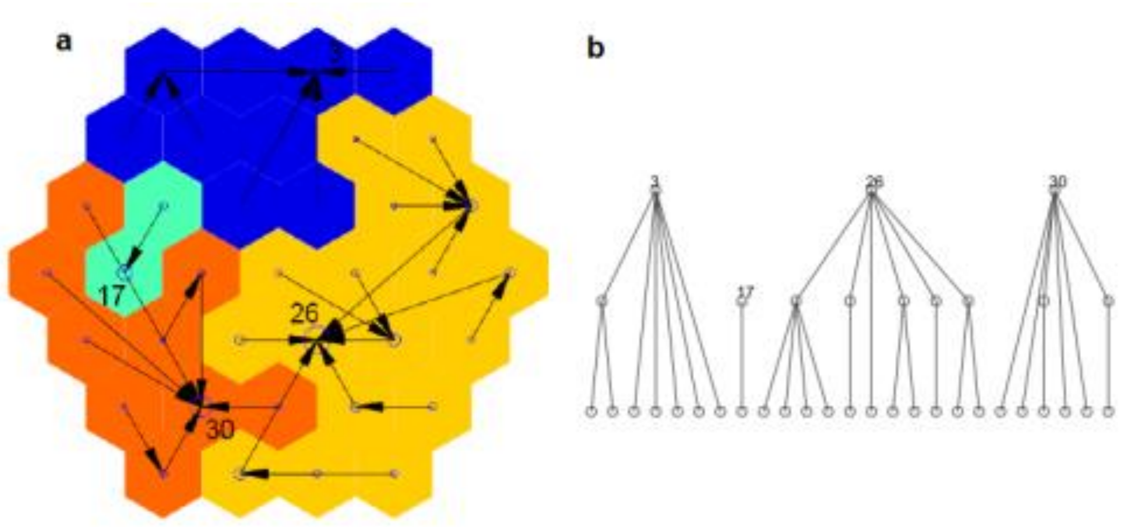
Assumption: the evolutionary response to this dilemma:

1. the ability to demarcate group membership based on cultural traits (language, dialect, clothing, etc.)
2. hierarchical organization, allowing group sizes to grow basically ad infinitum

Each element within a given level of a strictly hierarchical system needs to have, at most, n+1 connections: n :„span of control”; +1: its superior

Turchin-model:

- Nodes stand for a political entity (e.g., villages)
- Numerical experiments with AB model:
  - The modelled area is divided into hexagonal cells (autonomous local communities ,,„villages”)
  - Each of these villages are characterized by:
    - **a base-line resource level**, accounting for the heterogeneous environment, defining the productive/demographic potential of the region (a tunable parameter)
    - **actual resource level**, the base-line resource level minus the costs of the various actions in which the given community participates



A system of 37 communities organizing themselves into four polities.
The numbers in the hexagons mark the chief communities.

a. Spatial view.
b. The hierarchical structure

The Turchin-model in detail:

- Polities are organized in a hierarchical way
- Subordinate communities pay „tribute”to their superiors (a fixed portion of their total resources) → the total resource level of a community =

  = base resource level - tribute + the tribute it receives from its subordinates

- Polities may engage in warfare
  - Rebel
  - Conquest
  - Being attacked

Probability of warfare

A polity will attack its weakest neighbor if

i. it estimates that the attack will be successful

ii. it is ready to pay the corresponding costs and

iii. it is not too devastated from previous wars.

Quantitatively, the probability of an attack is:

$$A_{ij} = P_{ij} \cdot e^{-\beta c_{ij}} \cdot \frac{F_i}{F_{i,0}}$$

$P_{i,j}$: the probability of success

(an attack by community *i* on community *j*)

$$P_{ij} = \frac{F_i^a}{F_i^a + F_j^a}$$

F_i : the power of polity *i*

$F_{i,0}$: the maximum possible power of polity *i*

a : is the „success probability exponent”

$c_{i,j}$: cost of warfare

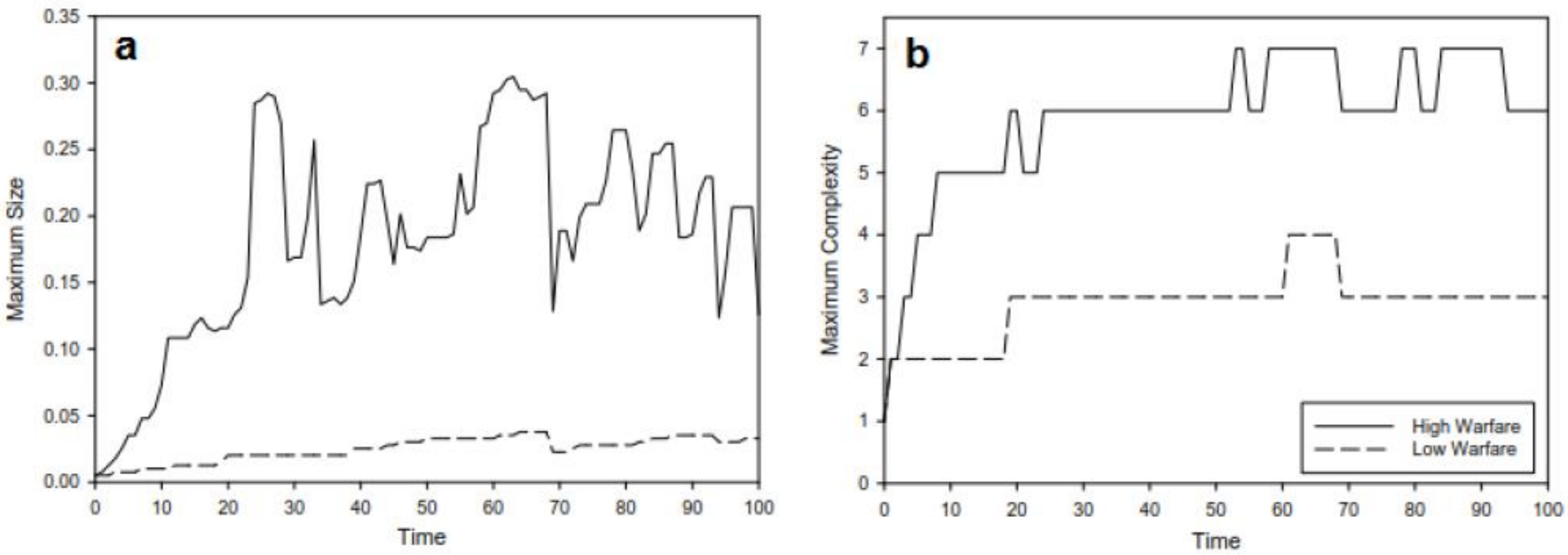
β : parameter

The Turchin-model in detail:

- Each time step is considered to be a year.
- Each year, the chief community decides whether to launch an attack on its weakest neighbor.
- If it decides to go to war:
  - it first attempts to conquer the bordering communities, followed by a series of „battles", until it either suffers a defeat or the chief community of the victim polity falls.
  - Annexing the conquered communities may require restructuring the hierarchical organization of the winner polity (the number of max. subordinates is a parameter varying between 4 and 10)
  - the direct subordinates of the aggressor chief community might decide to **secede** if they estimate that the attack will be unsuccessful.

    → spatial separation from the master state, together with all the subordinate communities of the rebelling village

Results



(a) The size and
(b) the hierarchical complexity of the polities under low and high pressure of war.

Intense warfare results in larger and more complex polities.

Provides a fission-fusion cycle reminiscent of the dynamics characterising early states of humans.

The model with realistic historical data

- A **more detailed version**
- **Afroeurasian** landmass divided into **a grid of 100 × 100-km squares**
- **Grid cells are characterized** by existence of agriculture, biome (e.g., desert), and elevation
- **At the beginning of the simulation**, each agricultural square is inhabited by an **independent polity**
- Cells adjacent to the steppe are **"seeded" with military technology** (MilTech) traits, which gradually diffuse out to the rest of the landmass
- Each cell is inhabited by a community that has a "**cultural genome**," a vector taking values of 1 or 0, depending on whether an ultrasocial trait is present.
    - such traits are costly: the probability of losing it is big, thus, in the absence of other evolutionary forces, they are present in the landscape at a very low frequency. The force that favors their spread is warfare
- Agricultural cells can conquer other such squares, building multicell polities. **The probability of winning** depends on relative powers, determined by the **polity size** (number of cells) and the average **number of ultrasocial traits**.
- The losing cell may copy the cultural genome of the victor.

causal chain: spread of military technologies → intensification of warfare → evolution of ultrasocial traits → rise of large-scale societies

Data

- polities that controlled territories greater than ~100,000 km^2 between 1,500 BCE and 1,500 CE
- on the Afroeurasian landmass
- by taking 100-year time windows, *imperial density maps* indicating the frequency and distribution of large-scale societies
- 7,941 empirical points

- predicting where and when the largest-scale complex societies arise
- hotspots appear in Mesopotamia, Egypt, and North China
- near the steppe frontier, where MilTech diffuse first, tipping the selection in favor of ultrasocial traits