Bioinspired systems

Hierarchy formation II: Dominance vs leadership hierarchies in animal groups, hierarchy in humans

11/6/2024

Dominance hierarchy

- Solitary vs. social lifestyles
- If the ratio of advantages/disadvantages is higher, then the given animals will knit into groups
- A mechanism is needed to reduce the level of aggression triggered by the competition within the group
- Regulate access to resources.
- The mechanism is simple: higher ranked individuals have primacy compared to their lower-level mates.
- Advantage: less fight

Dominance hierarchy

- Pretty much is known about the way it works in the animal world.
- Well-defined hormones, brain structures, neuroendocrine, genetic, and environmental influences
- From a physiological point of view: the mechanisms determining the rank of an individual are very similar between mammals (incl. primates and humans)
- Hormonal regulation
  - Testosterone: (the principal male sex hormone)
    - level in the blood indicates the rank
    - The level of the testosterone hormone and the inclination towards behaving dominantly form a positive feedback loop, as one intensifies the other.
  - Cortisol:
    - linked to stress, plays an opposing role.
    - Subordinate animals often have higher baseline cortisol levels, reflecting the stress of a lower position in the hierarchy.
    - Prolonged stress can lead to immune suppression and health issues, further solidifying their lower status.

Physiological background of dominance hierarchy in the animal world

Neurotransmitters

- **Serotonin**: The role of serotonin in social behavior and dominance is especially evident in animals like fish, crustaceans, and primates. High serotonin levels are often linked to stable, dominant individuals, whereas lower levels are found in subordinates. Changes in serotonin can influence confidence, social assertiveness, and responses to challenges, all of which are important for maintaining or changing social rank.
- **Dopamine**: This neurotransmitter is associated with motivation, reward, and social interactions. High-ranking individuals may experience increased dopamine release in response to social rewards, reinforcing behaviors that sustain their dominant status.

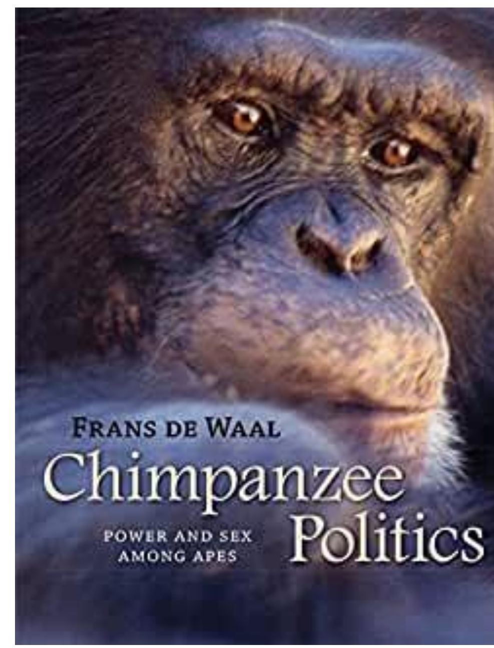
Brain Structure and Function

- Dominant and subordinate animals often display differences in brain regions involved in social cognition, stress response, and aggression.
- **Amygdala**: This region, which processes emotions and aggression, can be more reactive in dominant animals, helping them to assert or defend their rank.
- **Prefrontal Cortex**: Higher-ranking animals may have more developed prefrontal regions, which help with impulse control and decision-making in social contexts.
- **Hypothalamus**: The hypothalamus plays a crucial role in the hormonal regulation of aggression and stress responses, helping mediate hierarchical behaviors.

Genetic and Epigenetic Factors

Dominance hierarchy

- 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



Leadership in motion

The relation of collective motion to collective decision making

- If the group is to stay together, individuals constantly have to make decisions regarding
  - When and where to forage, to rest
  - How to defend themselves from predators
  - How to navigate towards a distant targets
  - Etc.
- Cost/benefit ratio (from the viewpoint of the members)
  - Preferred outcome usually differs (information, experience, inner state, etc.)
  - "consensus cost": cost paid by the animal who foregoes its preferred behavior in order to defer to the common decision

First studies – two basic types

Despotic system

- One or a few individual decides
- This can increase the efficiency

Egalitarian / democratic

- Members contribute to the outcome about the same degree
- Smaller average consensus cost

- In nature, both types have been observed
- Sometimes mixed (alternating according to the circumstances)
  - Pairs of pigeons, GPS (2006)
    - Small conflict over the preferred direction: consensus (average)
    - Above a certain threshold: one of them becomes the leader or they split up
  - Similar observations: Wild baboons, GPS (2015)
    - They follow the majority of the “initiators” (those starting off in a certain direction). (And not the dominant individuals)
    - If two groups of initiators (with similar size) heading in different directions:
      - If the angle is less than ~90° → the animals compromise
      - Big angle: they choose one direction over the other (randomly)

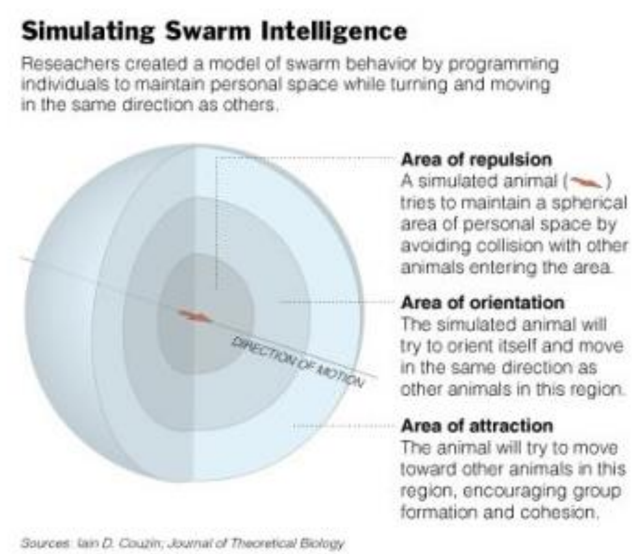
Models for leadership

- 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:

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



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

[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:

→ The desired direction:

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

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

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

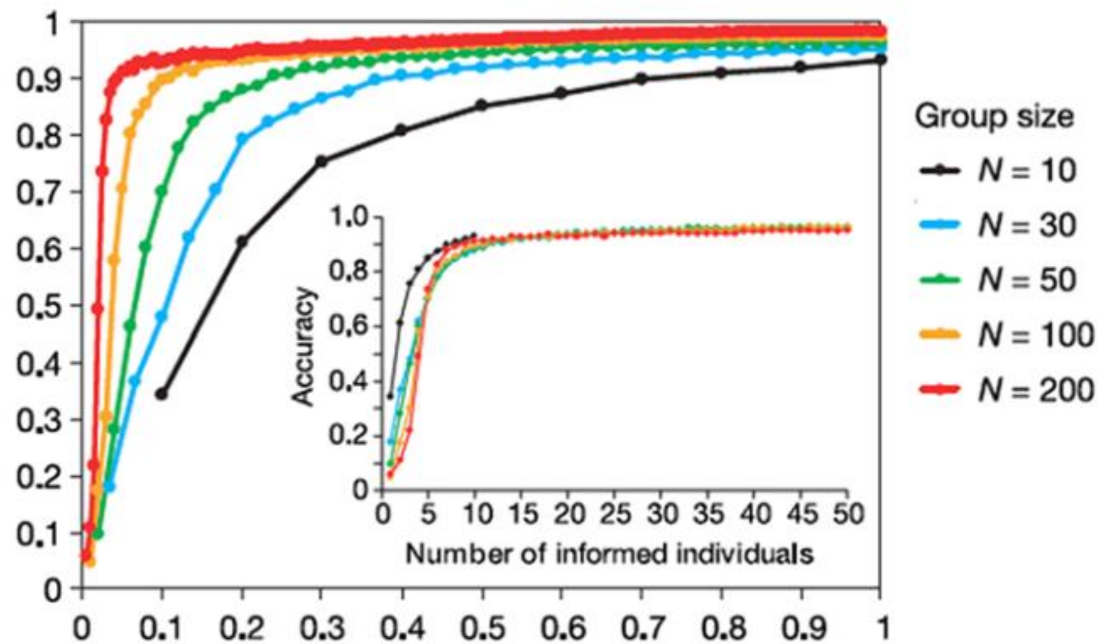
$$\vec{d}_i(t+\Delta t) = \frac{\hat{d}_i(t+\Delta t) + \omega\vec{g}_i}{\left|\hat{d}_i(t+\Delta t) + \omega\vec{g}_i\right|}$$

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



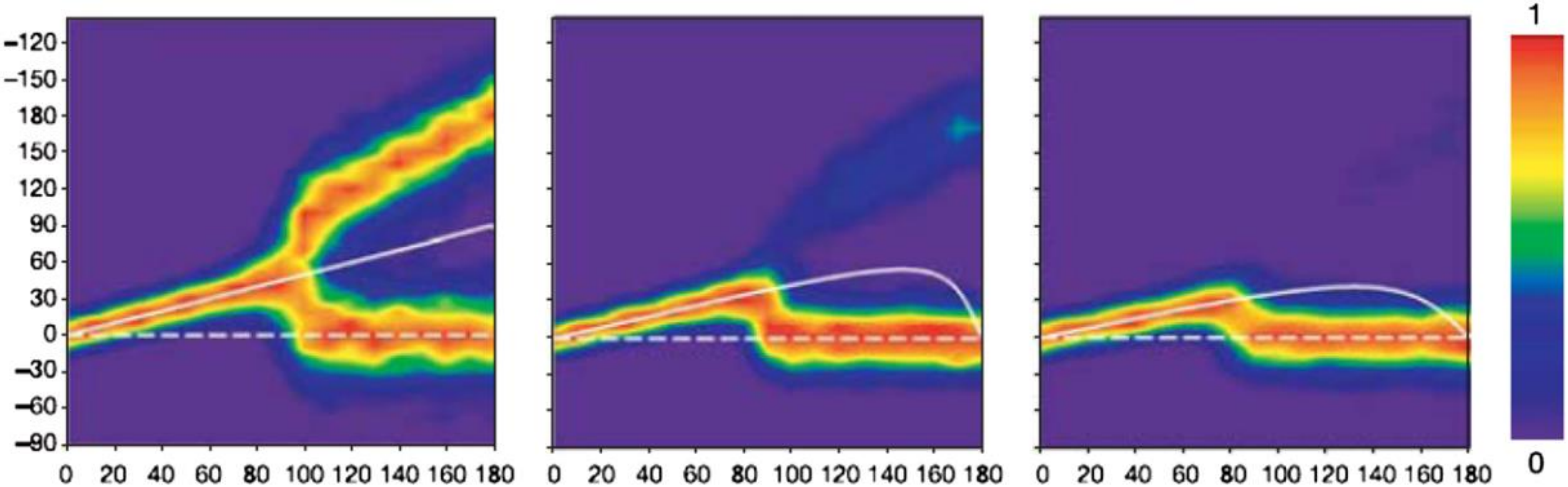
Conflicting preferences

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.

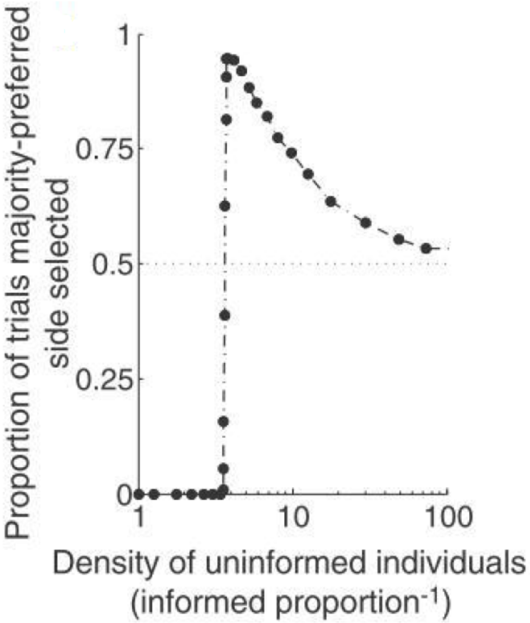
The role of uninformed individuals – simulations vs. experiments

- **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"

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

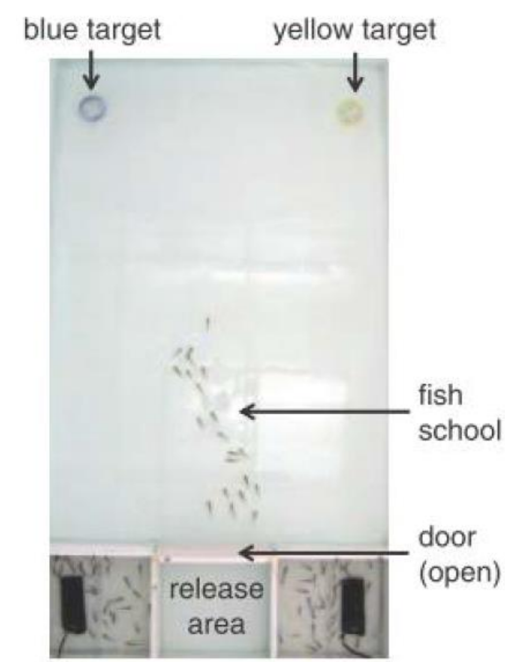
  - If all individuals are biased:
    - If the strength of the majority preference (ω_1) is equal to or stronger than the minority preference (ω_2), the group has a high probability of reaching the majority-preferred target.
    - Increasing ω_2 (beyond ω_1) can result in the minority gaining control
  - 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. ($\omega_{minority} > \omega_{majority}$)

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" $>$ ω_{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



Experimental set-up

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

Lessons

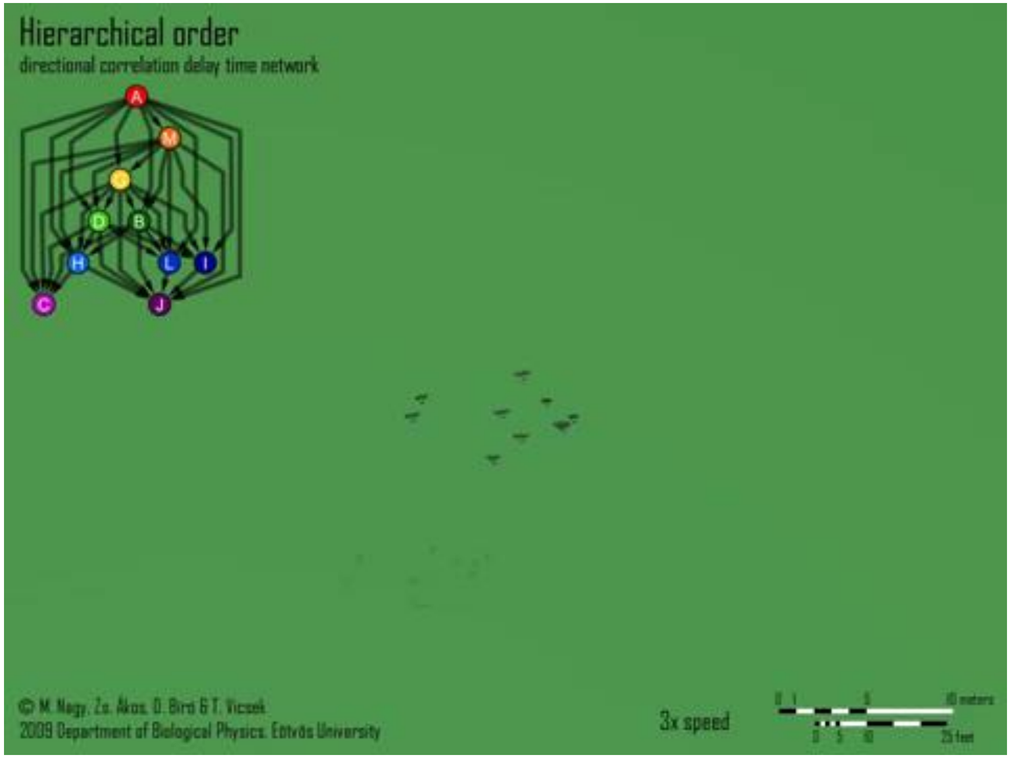
- Leadership might emerge from the differences of the level of information possessed by the group members

- 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

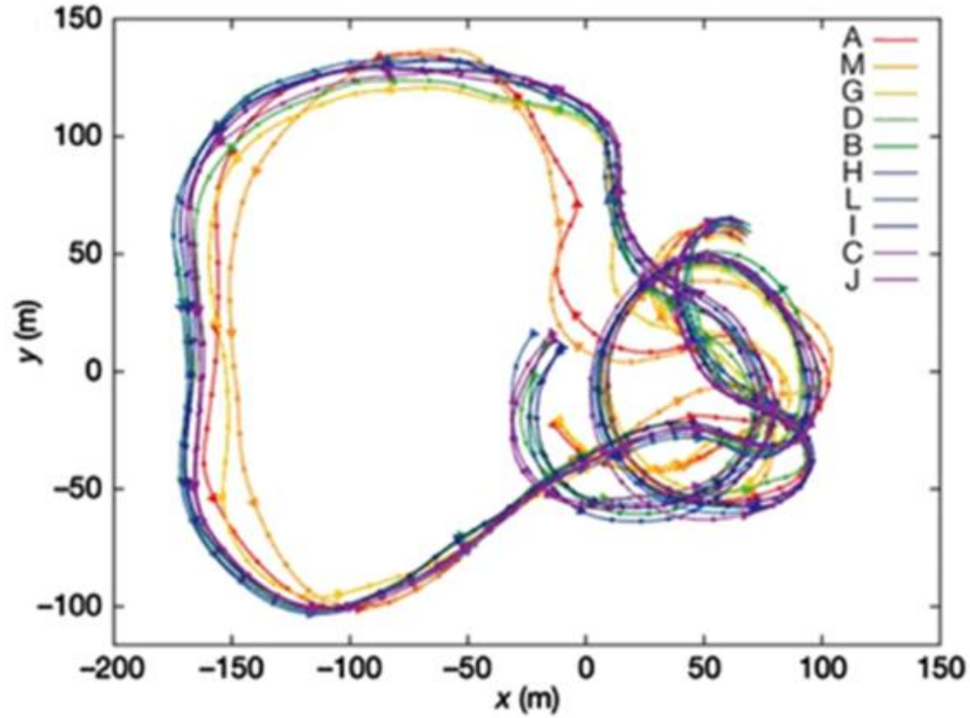
Trajectories of a flock of nine pigeons during a homing flight

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.

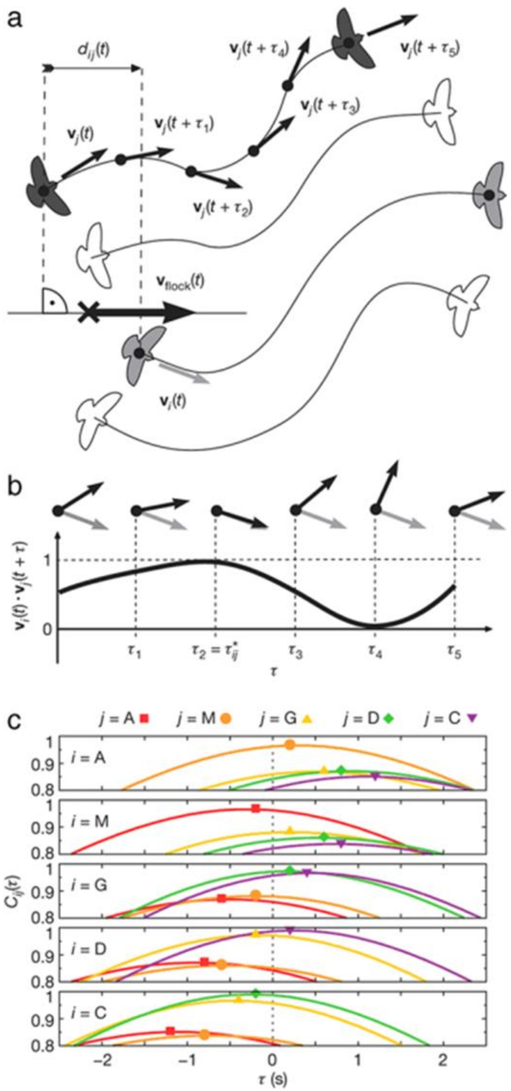


2-minute segment from a free flight performed by a flock of ten pigeons in the vicinity of the loft. The smaller and the larger dots indicate every 1s and 5s, respectively. Each path begins near the center of the plot. Letters refer to bird identity.

This was quantified by determining the directional correlation delay time ($\tau^*{}_{ij}$) (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



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

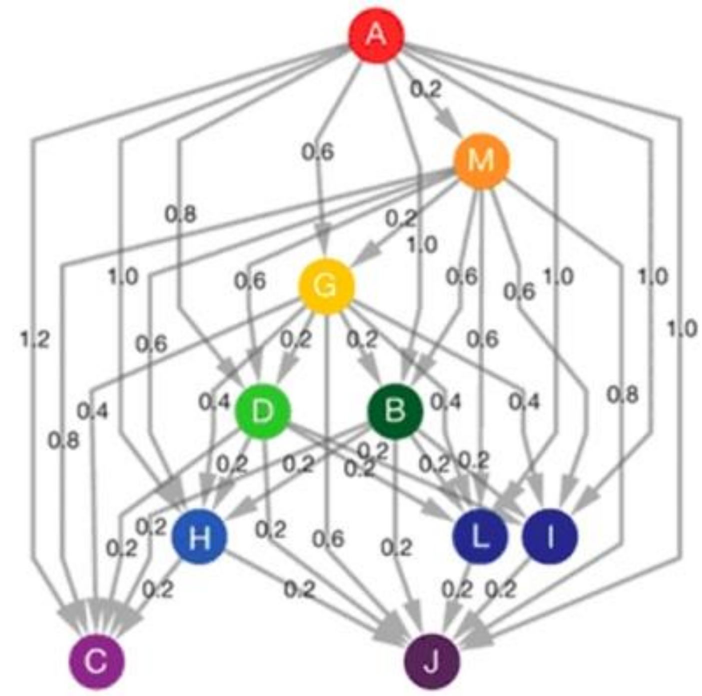
- The directional correlation function $C_{ij}(\tau)$ during the flock flight. For more transparency only the data of birds A, M, G, D and C (in the order of hierarchy for that flight) are shown. The solid symbols indicate the maximum value of the correlation function, ${\tau_{ij}}^*$.
- These ${\tau_{ij}}^*$ 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 $C_{min} = 0.5$.

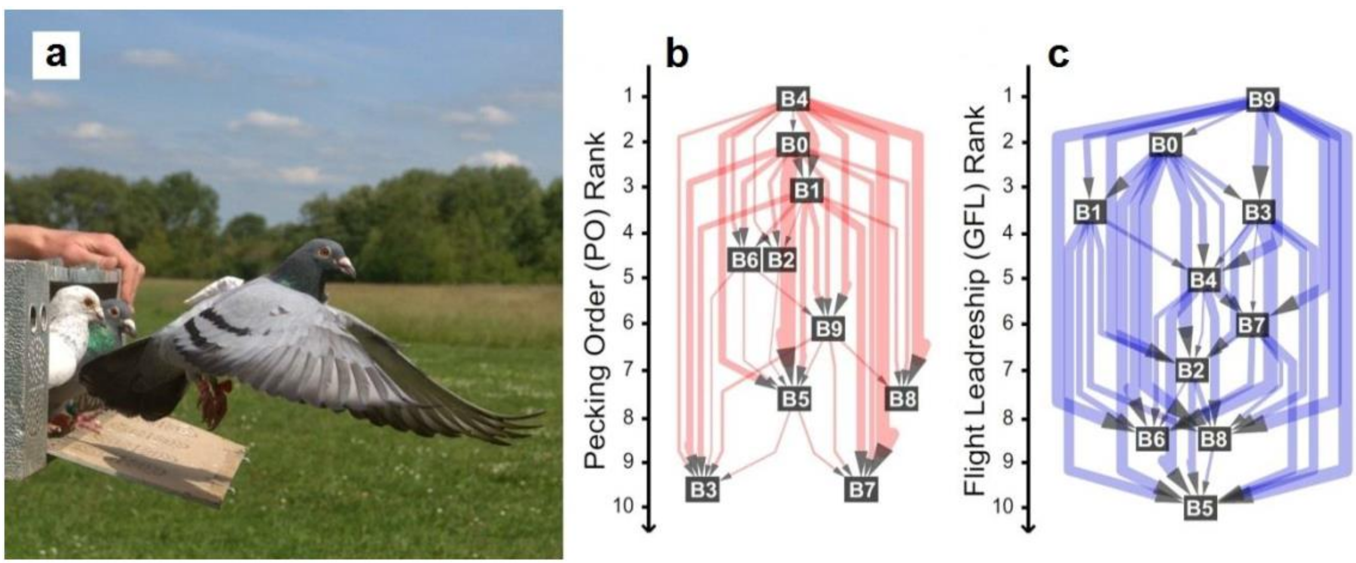


Leadership vs. dominance - a systematic study
Do dominant individuals lead?

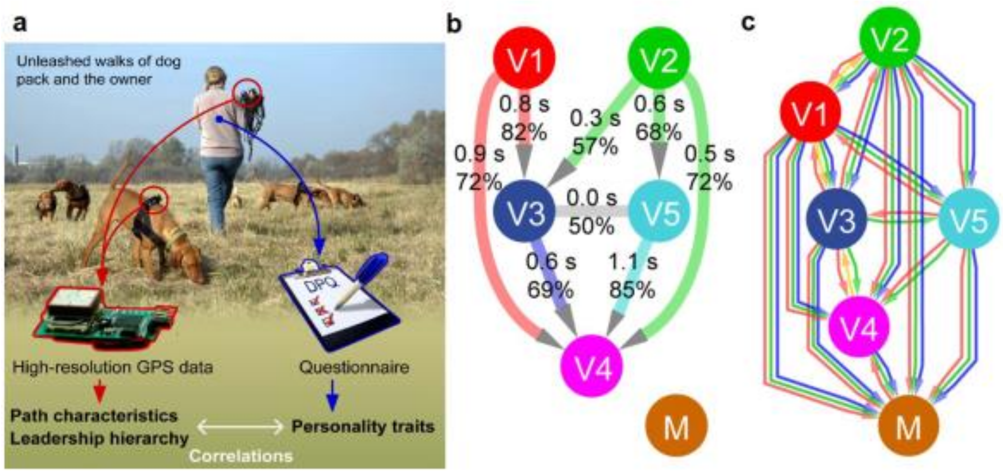
- Flock of 10 pigeons
- L-F hierarchy was determined based on the directional correlation function analysis
- Dominance hierarchy was also determined (in the same group), based on computer-vision methods
- The first automated analysis of dominance relationships
- Both structure is clearly hierarchical

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?

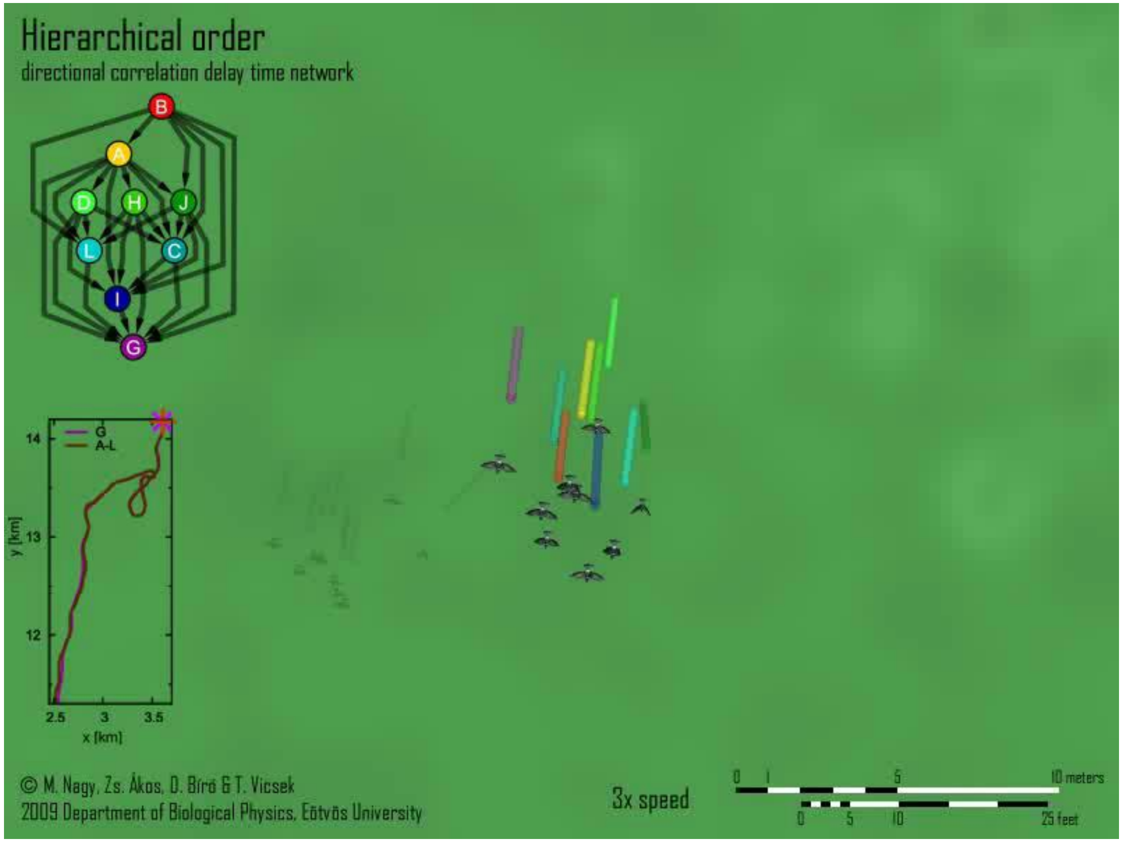
•*high resolution GPS data*

•*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:

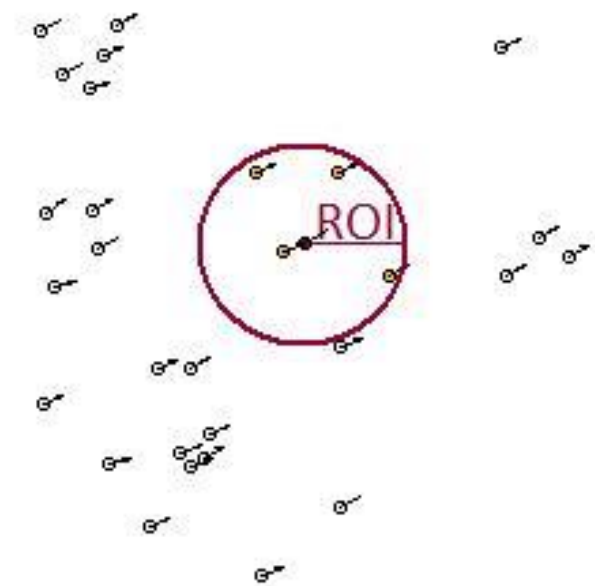
- Given a flock of boids and a pre-defined target
- The flock has to reach the target (together) in the shortest possible way
- The units interact with each other
- The average knowledge is restricted

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:

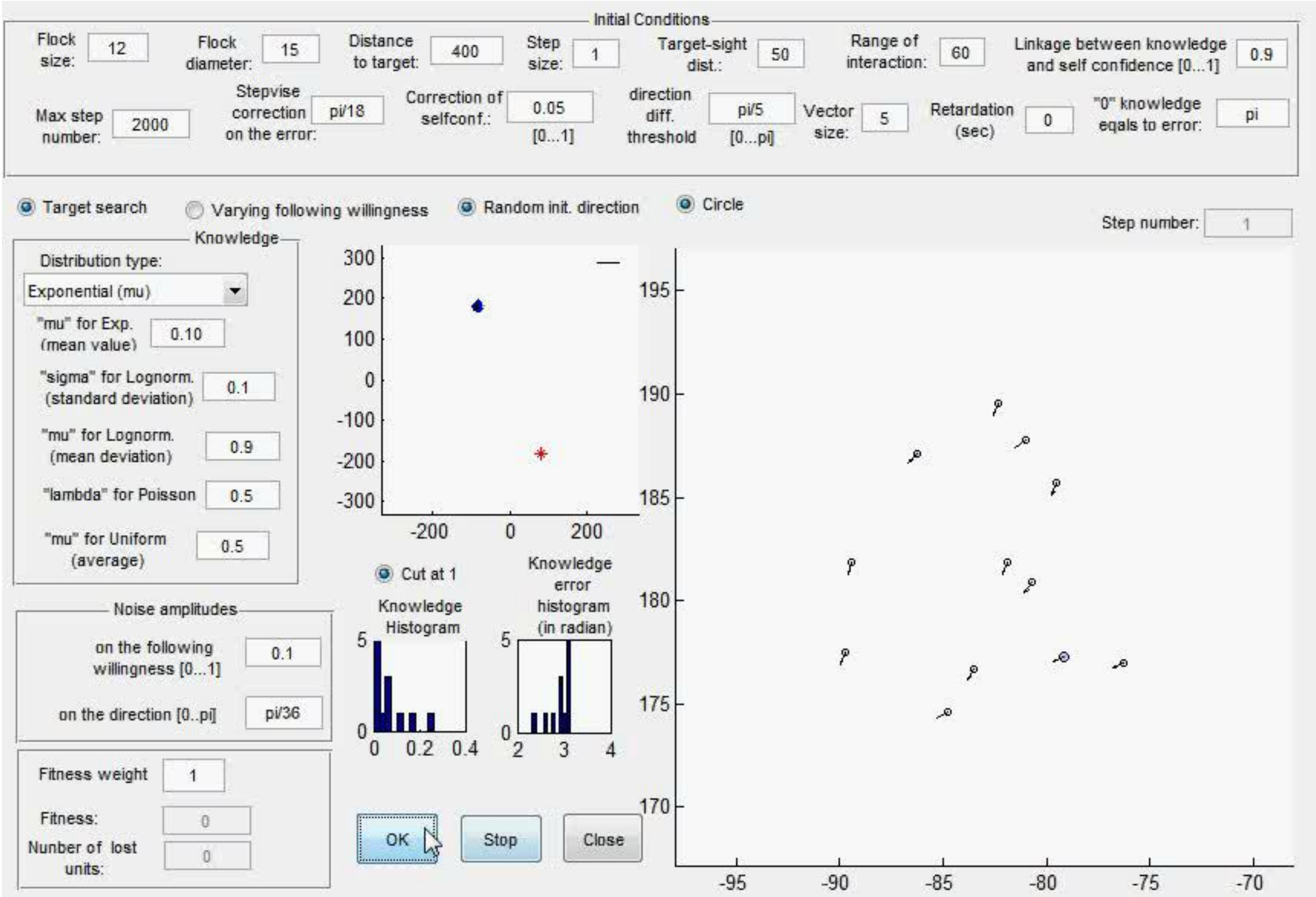
1. The average direction of neighbors (units within the "Range of Interaction, ROI") $\langle \vartheta_j^t \rangle_R$
2. Own estimation $\theta_i^t + \eta_i^t$
3. Noise ξ_i^t

(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

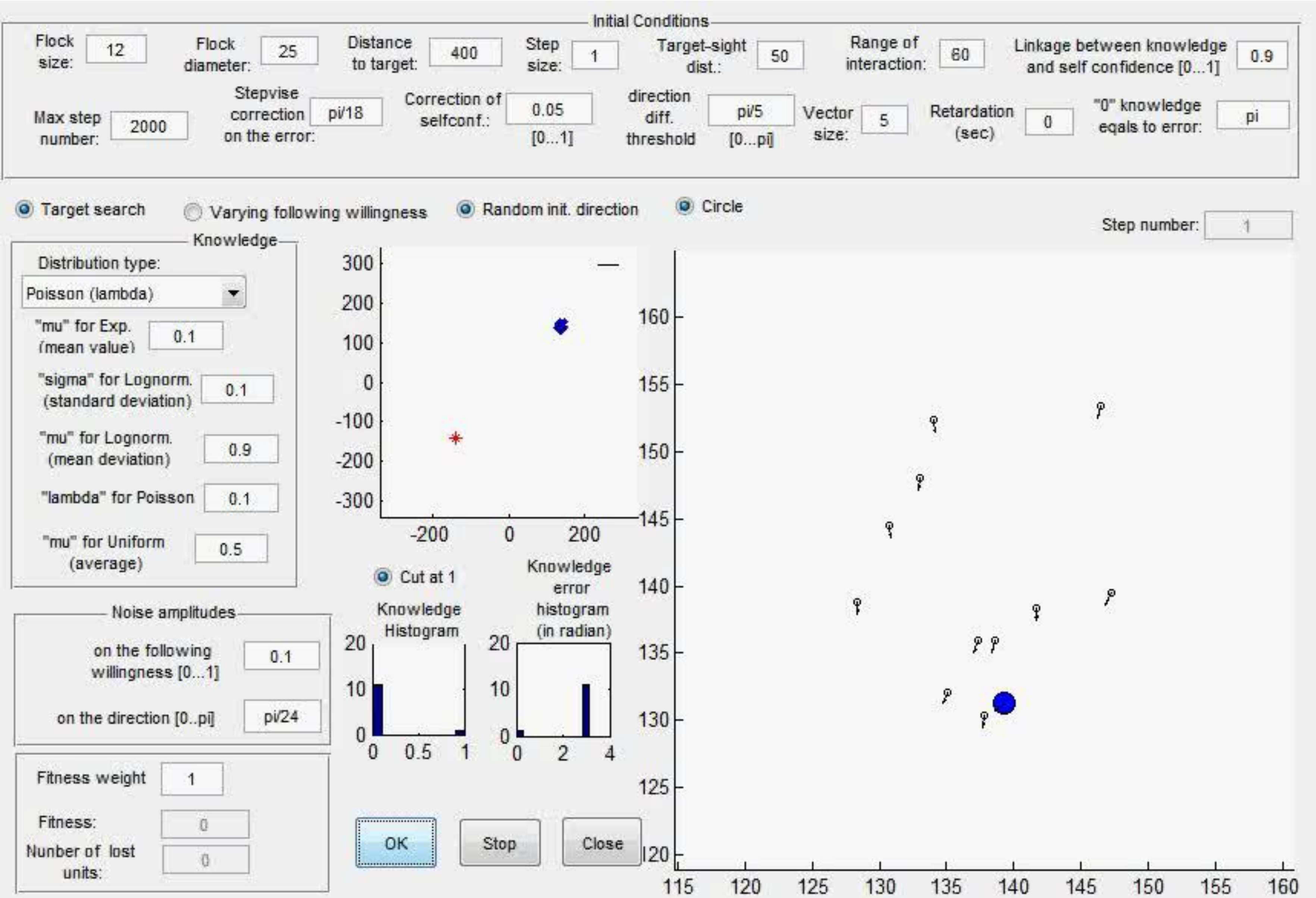


Flock size = 12,

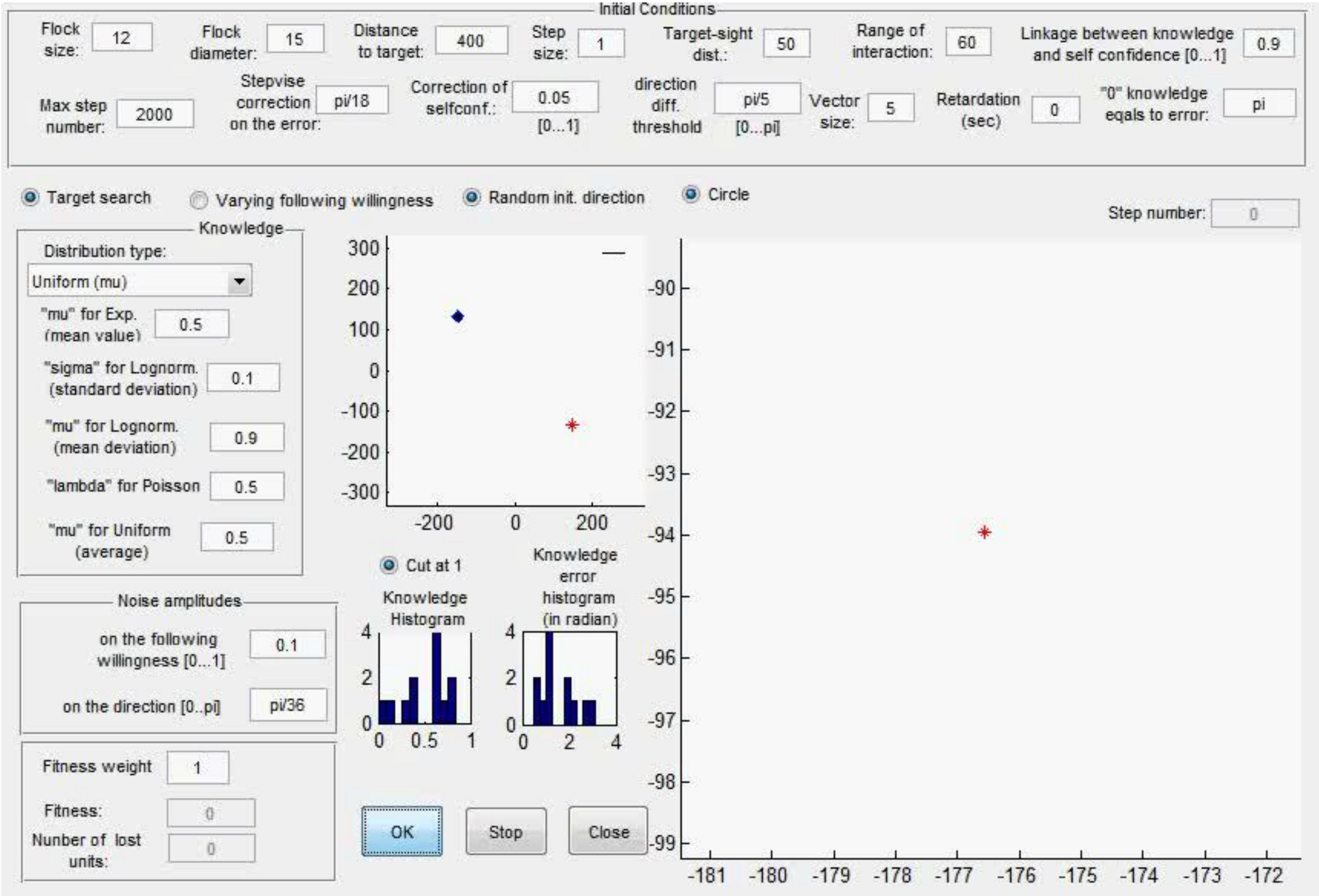
Exponential knowledge distribution,

μ=0.1,

coded in MatLab.

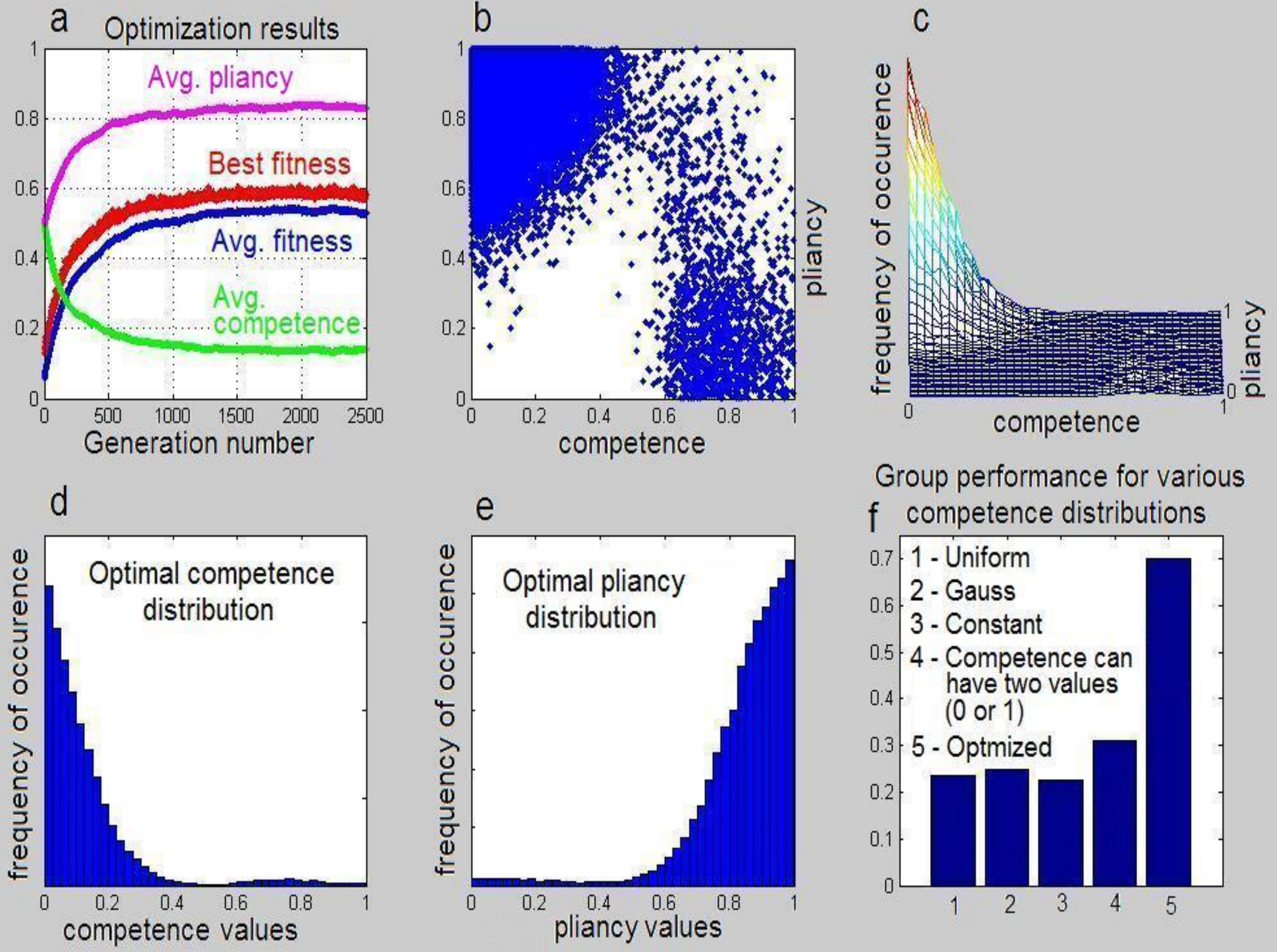


size = 12,
-valued”
edge
ution,
,
in MatLab.



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
f
Group performance for various competence distributions
1 - Uniform
2 - Gauss
3 - Constant
4 - Competence can have two values (0 or 1)
5 - Optmized

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

Sequence guessing game on a Small-World NW