# The variable shape of flocks of birds

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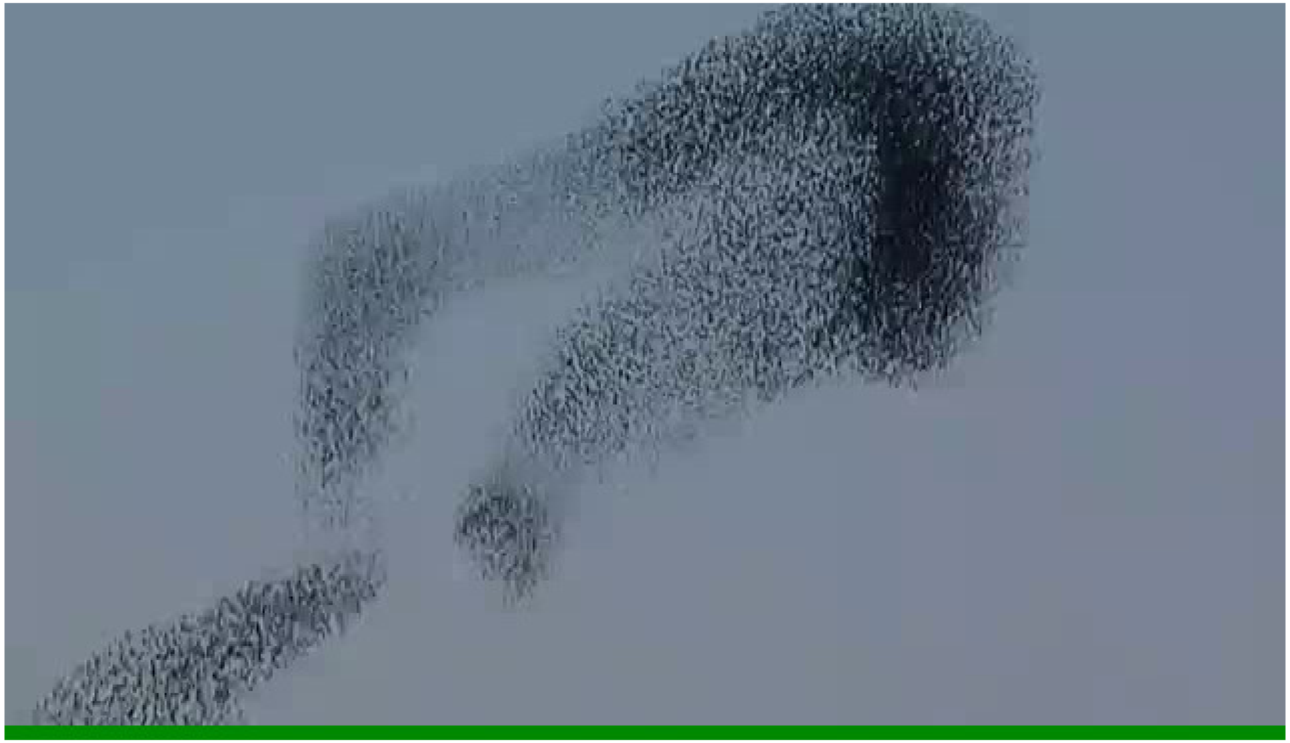
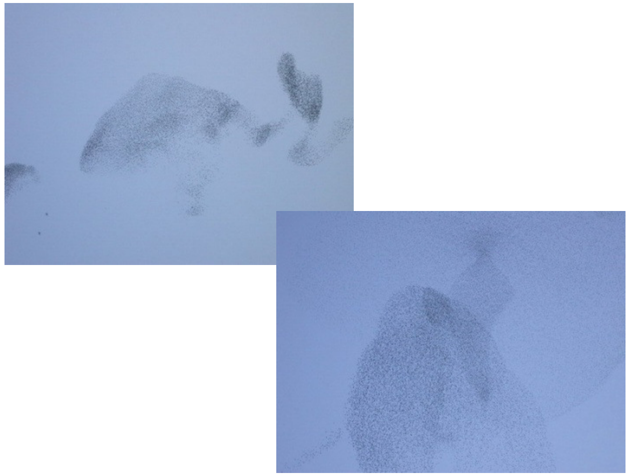
# Starlings

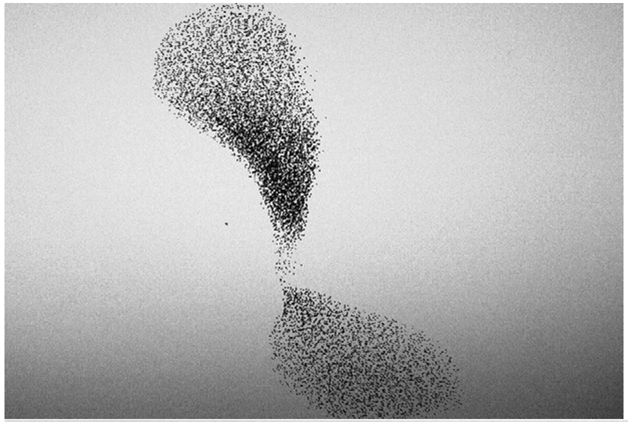


- Starling display above the roost in Utrecht: shape is highly variable (Brodie 1976, Carere et al 2009)

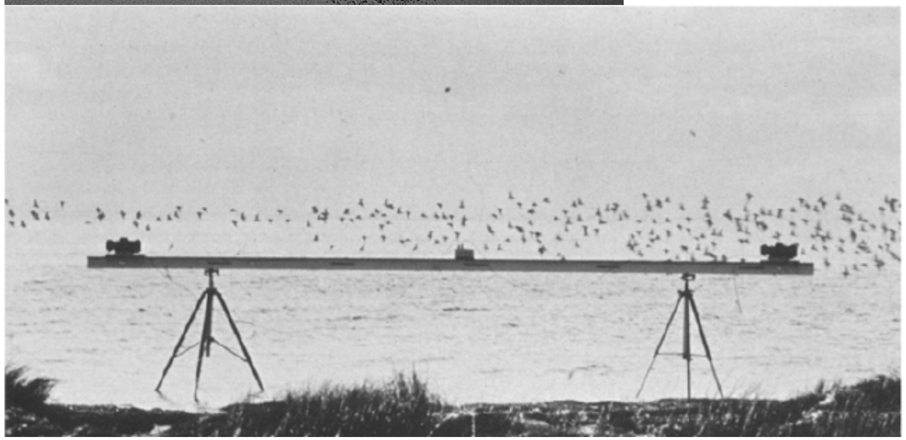
# Variable flock shape



Starlings above roost



Starlings avoiding a predator

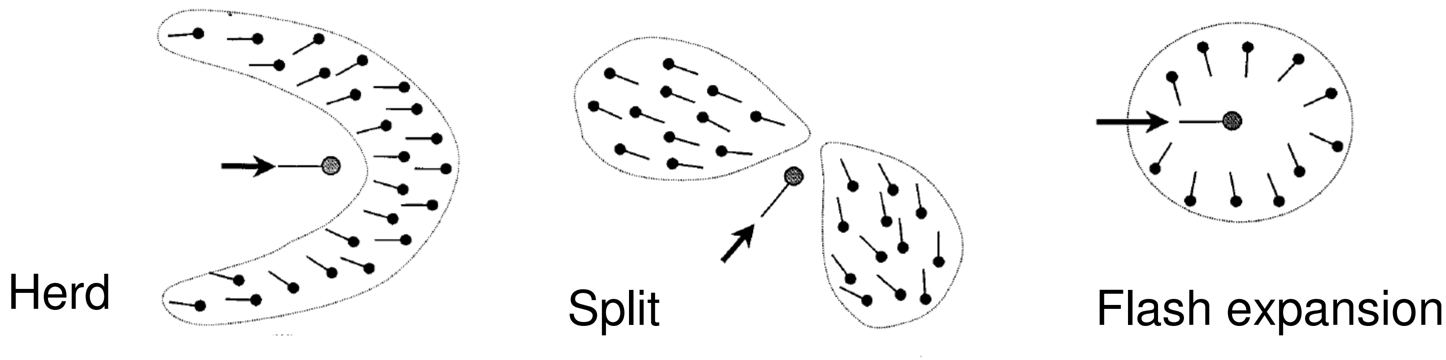


Dunlins travelling

in all contexts: ‘telepathy’ (Selous, 1930)

# Fish Schools

- Usually oblong (Pitcher 1976;Bumann et al 1997)
- But not if
  - –School is very large (Gerlotto & Paramo 2003)
  - –Attacked by a predator



# Hypothesis

More local differences in behaviour →

Shape is more variable

↓

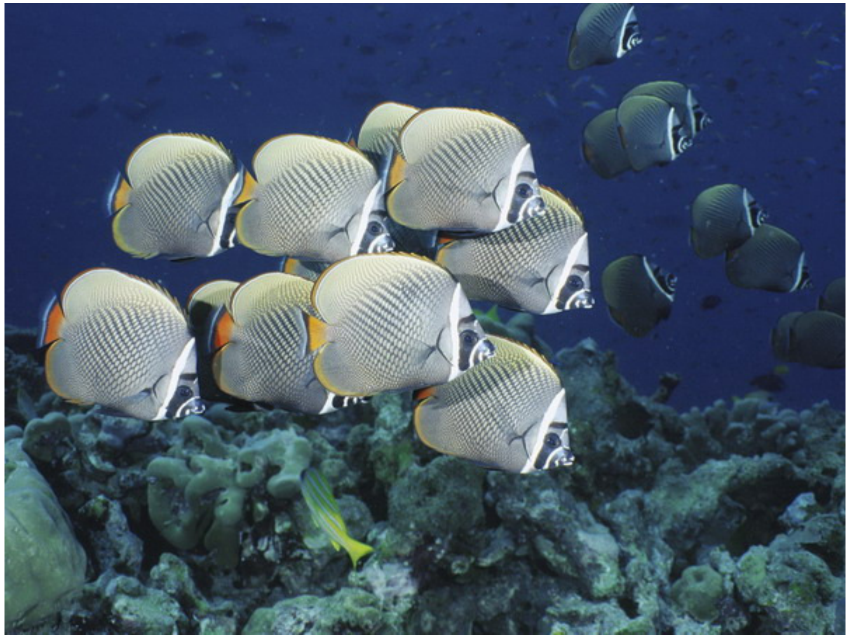
Hard to study empirically →

We study it in a model

# Model of self-organisation

Simple rules of the individual →
Complex behaviour at a group level

This talk:
– model of flocks resembling real birds
– theory of shape of schools of fish



## School shape:

Oblong

Adaptive?

- Lower detectability, because predators attack at front (Bumann, Krause, Rubenstein1997)

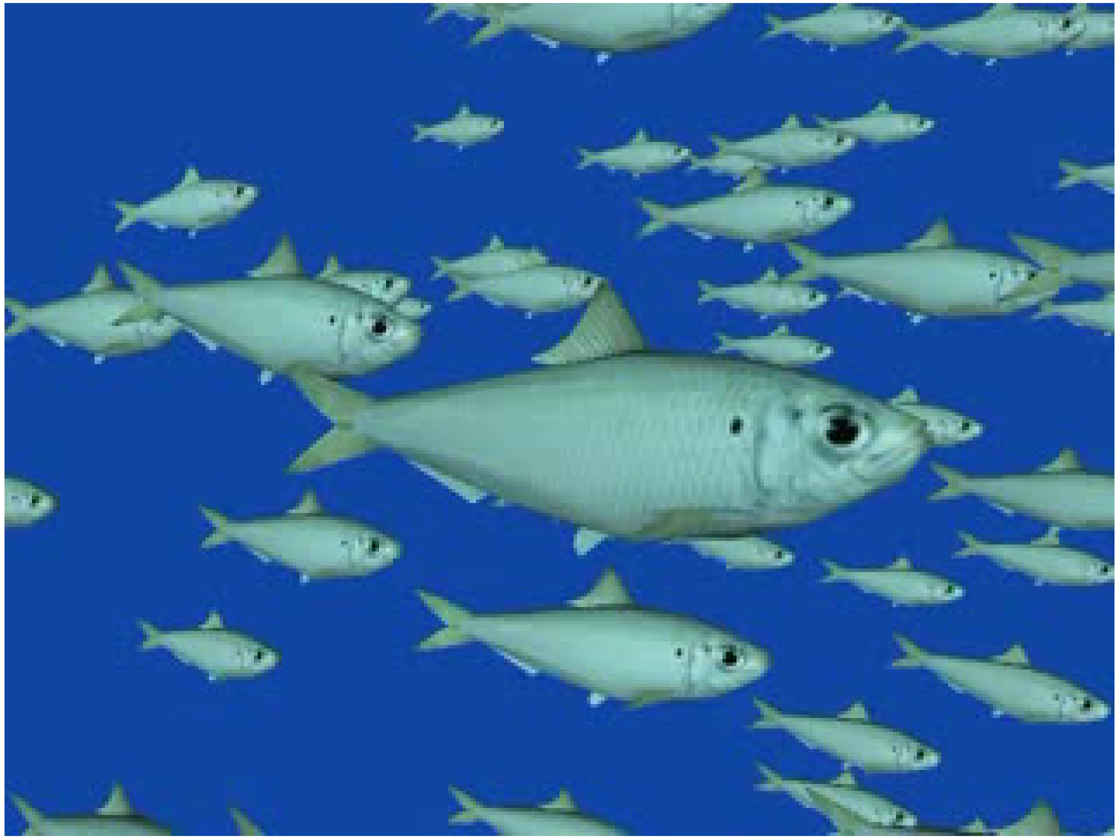
How organised ?

- Cognition or self-organisation?

(Kunz & Hemelrijk, 2003; 2005; Hemelrijk & Hildenbrandt 2008)

# Theory about oblong shape

(Kunz & Hemelrijk 2003, *Artificial Life*;Hemelrijk & Kunz 2004, *Behavioural Ecology*; Hemelrijk & Hildenbrandt, 2008, *Ethology*; Hemelrijk *et al* 2010, *Ethology*)



Computer Models are based on

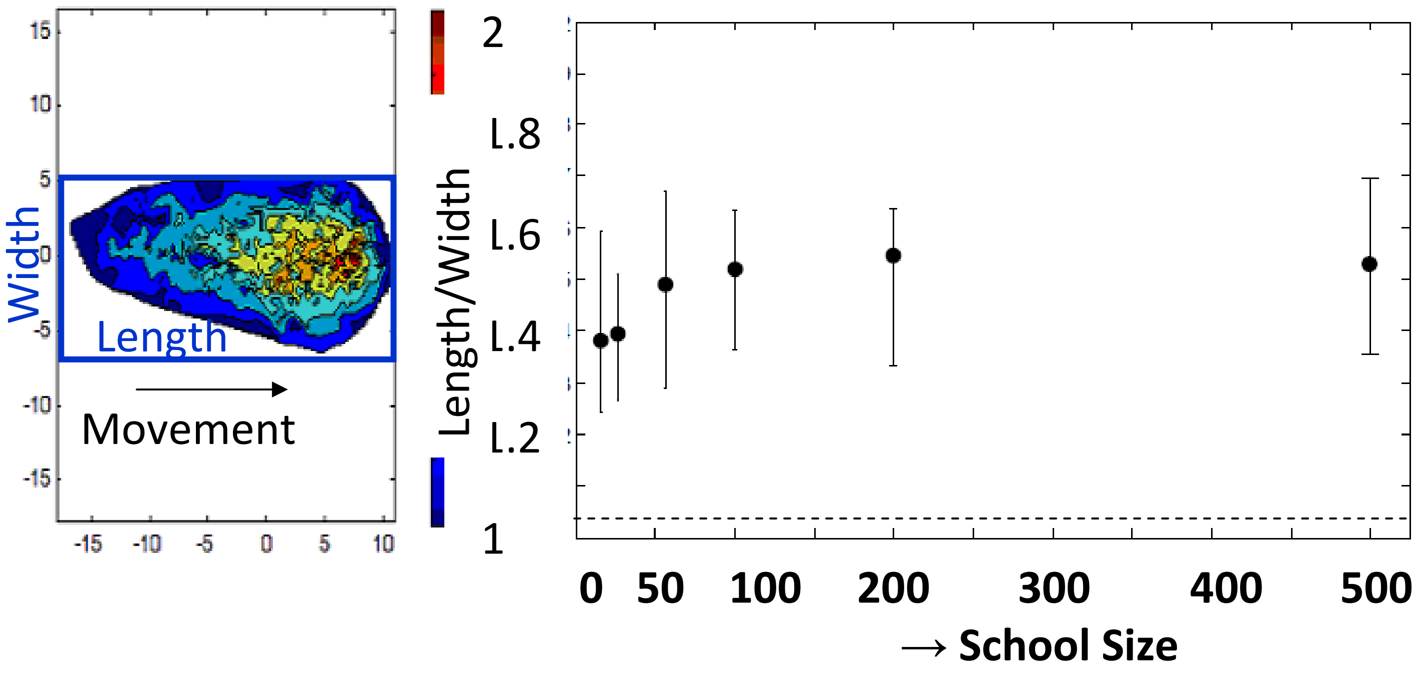
- Attraction
- Alignment
- Avoidance

$$\mathbf{F}_{\mathbf{Social}_\mathbf{i}} = \mathbf{f}_{att_\mathbf{i}} + \mathbf{f}_{ali_\mathbf{i}} + \mathbf{f}_{avo_\mathbf{i}}$$

Oblong shape by self-organisation

# Oblong Shape

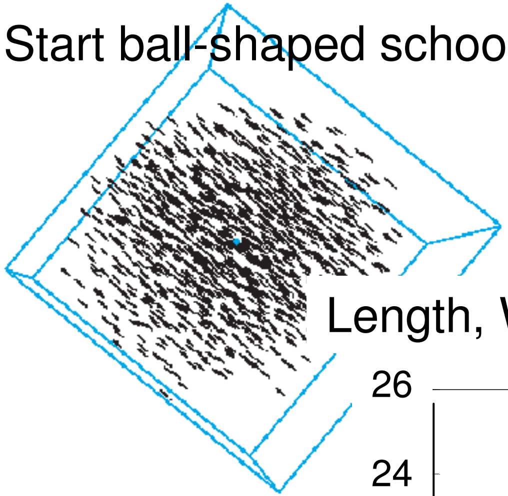
(Kunz & Hemelrijk 2003; Hemelrijk & Kunz 2004; Hemelrijk & Hildenbrandt,2008)

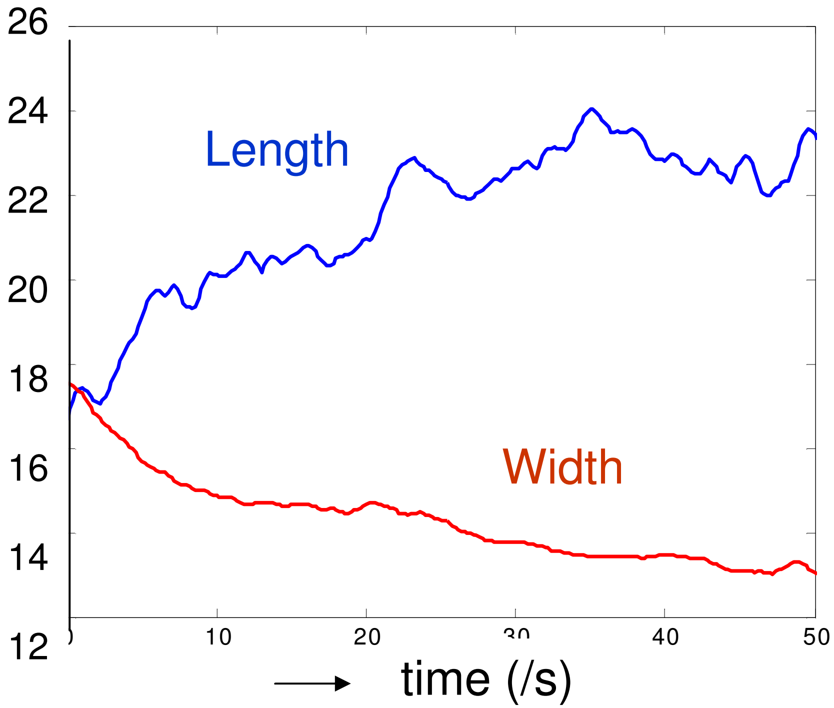


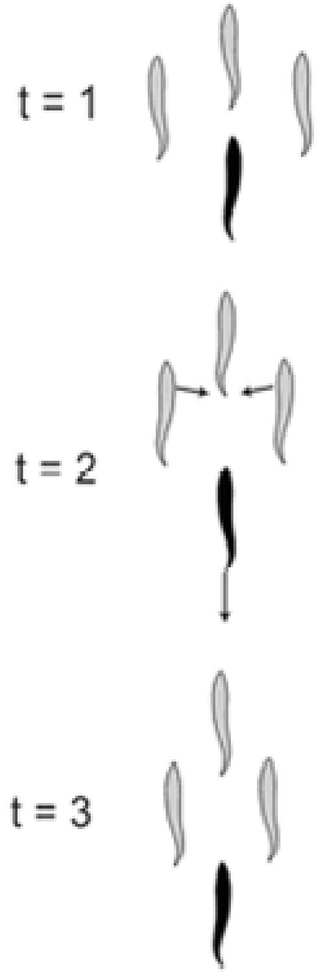

Two and three dimensional models, several group sizes, group compositions, two cruise speeds

as a side - effect

# Development of Shape



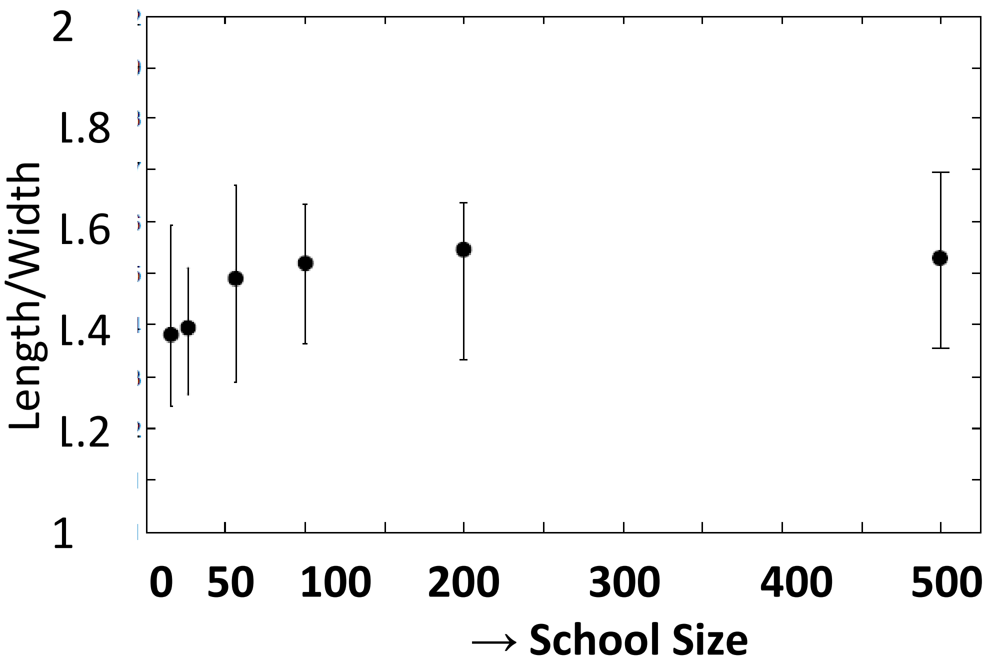



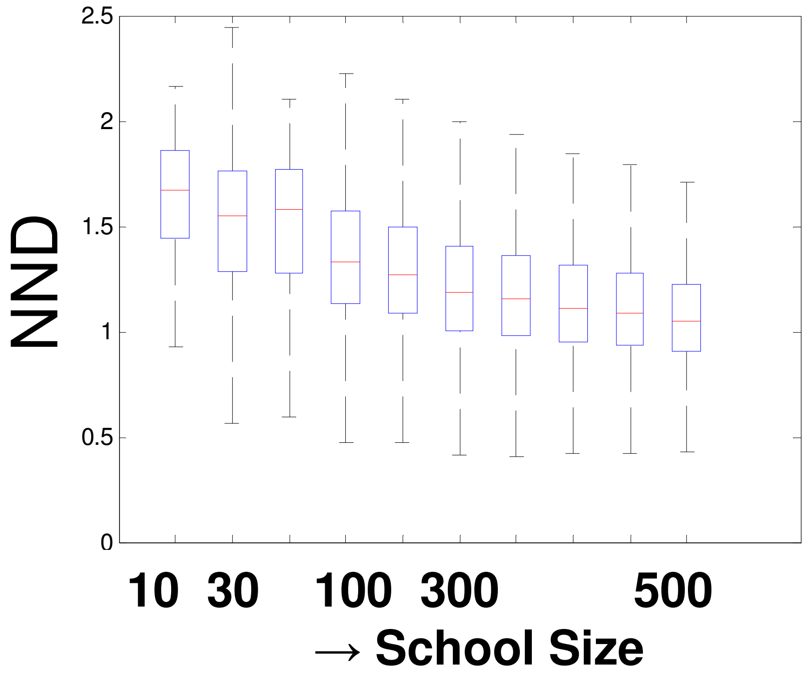




Collision Avoidance → usually Slow Down & Move Inwards → Lengthening of Swarm

# Supporting evidence

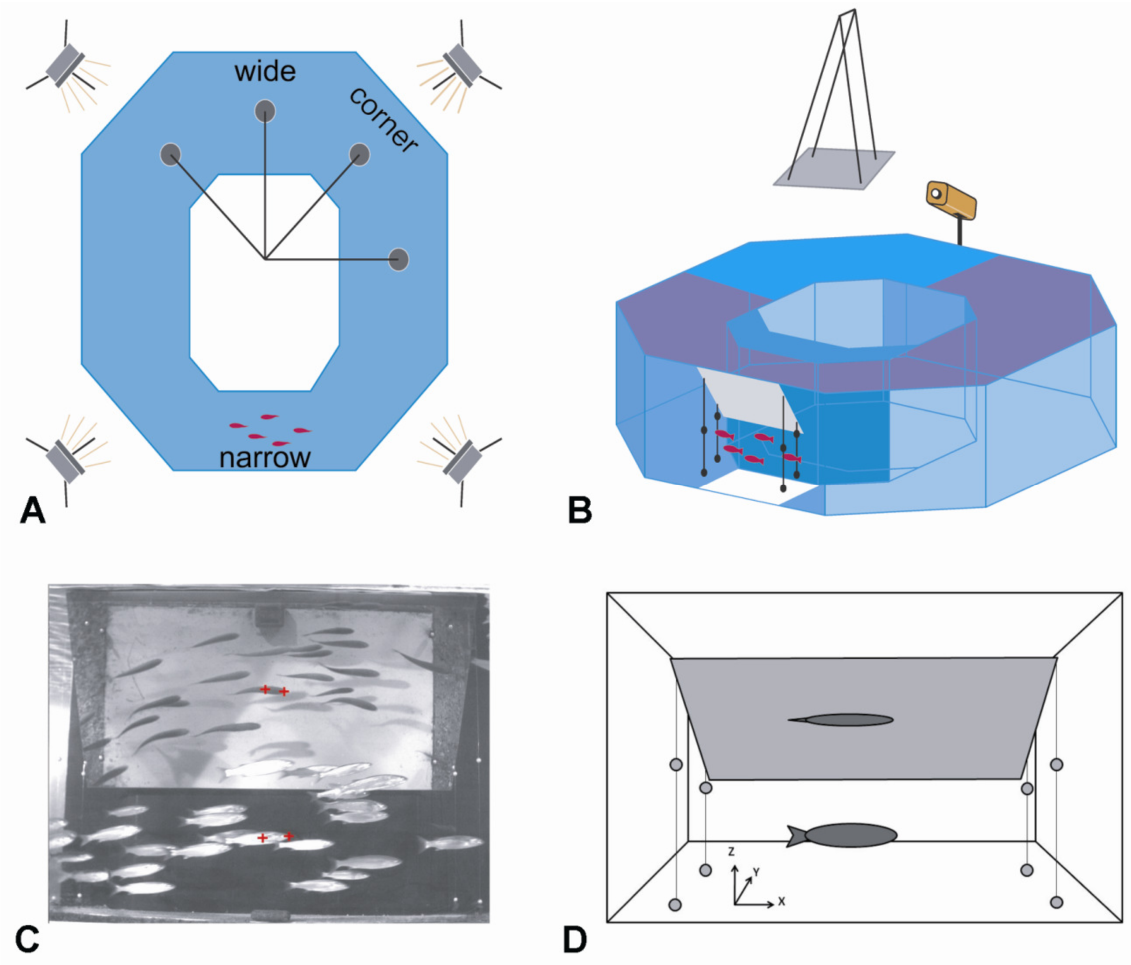
Hemelrijk & Hildenbrandt,2008; Kunz & Hemelrijk 2003




Larger schools shorter Nearest Neighbour Distance -> more frequent avoidance -> more oblong as a side-effect

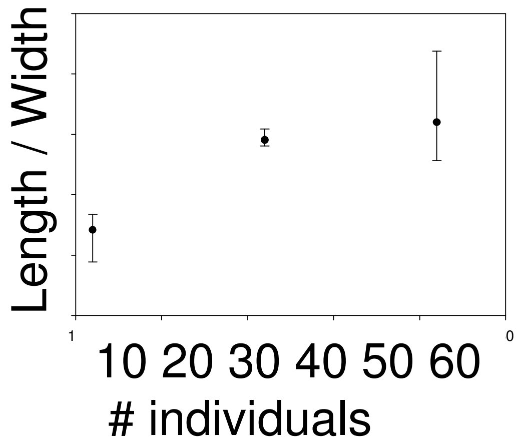
# Empirical study

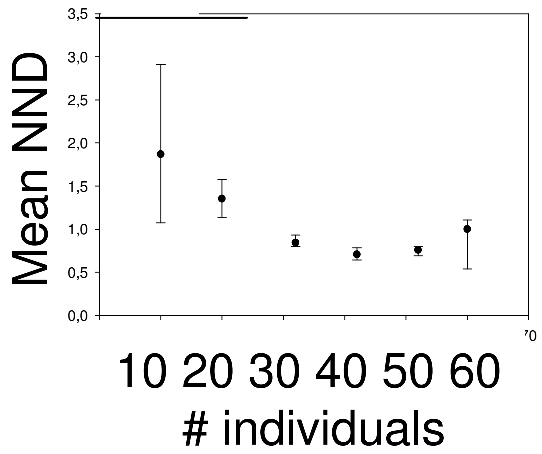



Prof. dr. Eize Stamhuis
(Marine Biology)
and students

# Empirical data of Mullets

Hemelrijk, Reinders, Hildenbrandt, Stamhuis (2010) *Ethology*




Corresponds to the patterns of the model!

# Oblong form

- Arises as a side-effect of coordination!
  – Due to falling back to avoid collision

# Our model of starling flocks, StarDisPlay

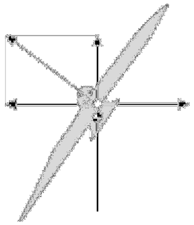
(Hildenbrandt, Carere, Hemelrijk, 2010) *Behavioural Ecology*

Flocking model with:

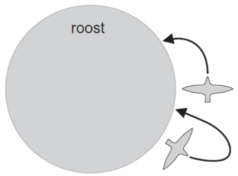
1. local coordination (attraction, alignment, avoidance)

also in fish model

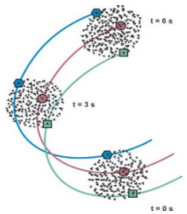
2. simplified aerodynamics of flying with banking while turning (Norberg, 1990)



3. attraction to the sleeping site (roost) (Carere et al 2009)




4. few interaction partners (6.5) (Ballerini et al 2008)
5. low speed variability



specific to starlings

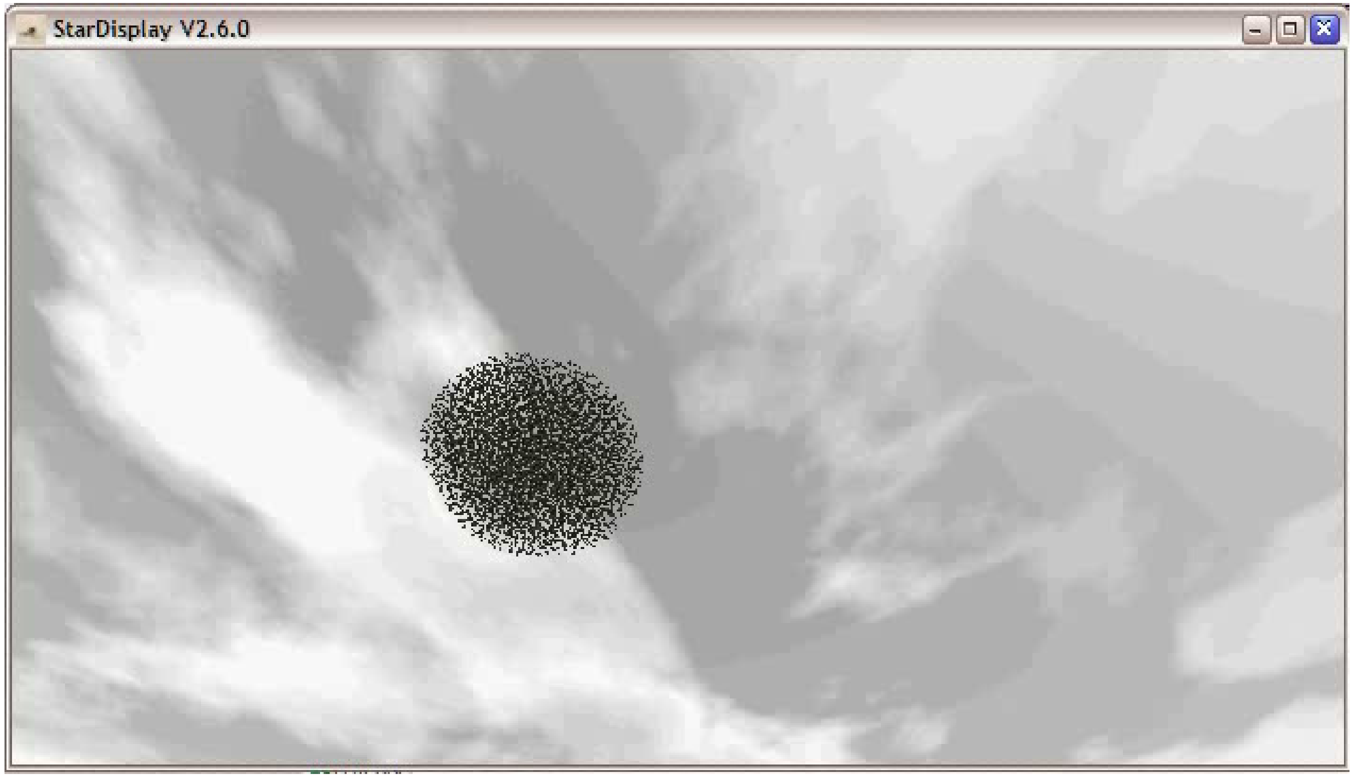
# Parameters From Starlings

| Parameter | Description | Default value |
|---|---|---|
| $\Delta u$ | Reaction time | 50 ms |
| $v_0$ | Cruise speed | 10 m/s = 36 km/h |
| $M$ | Mass | 80 g |
| $C_L/C_D$ | Lift-drag coefficient | 3.3 |
| $L_o$ | Default lift | 0.78 N |
| $D_0, T_0$ | Default drag, default thrust | 0.24 N |
| $n_c$ | Topological range (# Interaction partners) | 6.5 |
| $r_h$ | Radius of max. separation ("hard sphere") | 0.2 m |
| $R_{Roost}$ | Radius fo Roosting Area | 150 m |

# Flocking manouevres by self-organisation

(Hildenbrandt, Carere, Hemelrijk, 2010, Behavioural Ecology)

Model



# Resemblance flocks of real starlings

(Hildenbrandt, Carere, Hemelrijk, 2010, Behavioural Ecology)

To empirical data from Ballerini *et al* (2008):

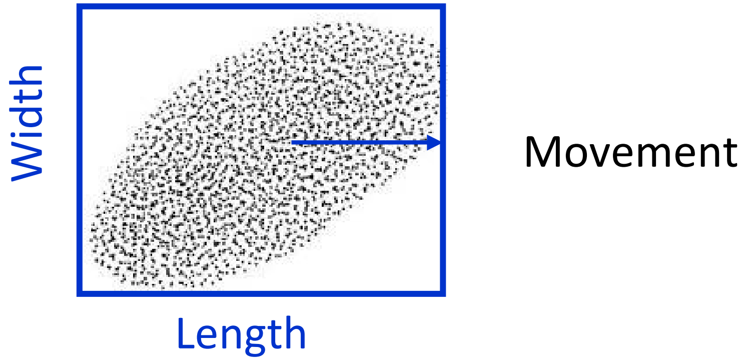
- aspect ratios of flock shapes (10 events)
- flat shape of flock
  - seldom oblong
- orientation of flock
  - parallel to bottom
  - at the same height
- distribution
  - distance and angle to nearest neighbours
  - density in front and back

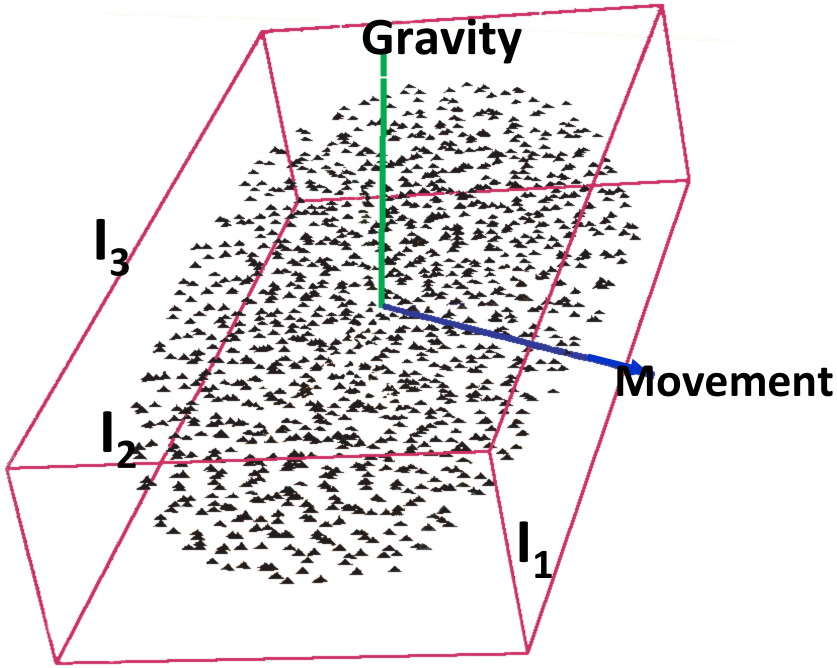
# Greater local variability

- Larger flock size
- Lower number of interaction partners
- Sharp turns related to environment
- Rolling while turning
- Higher speed variability (adjustability)

Higher variability of shape

# Measure shape of flocks



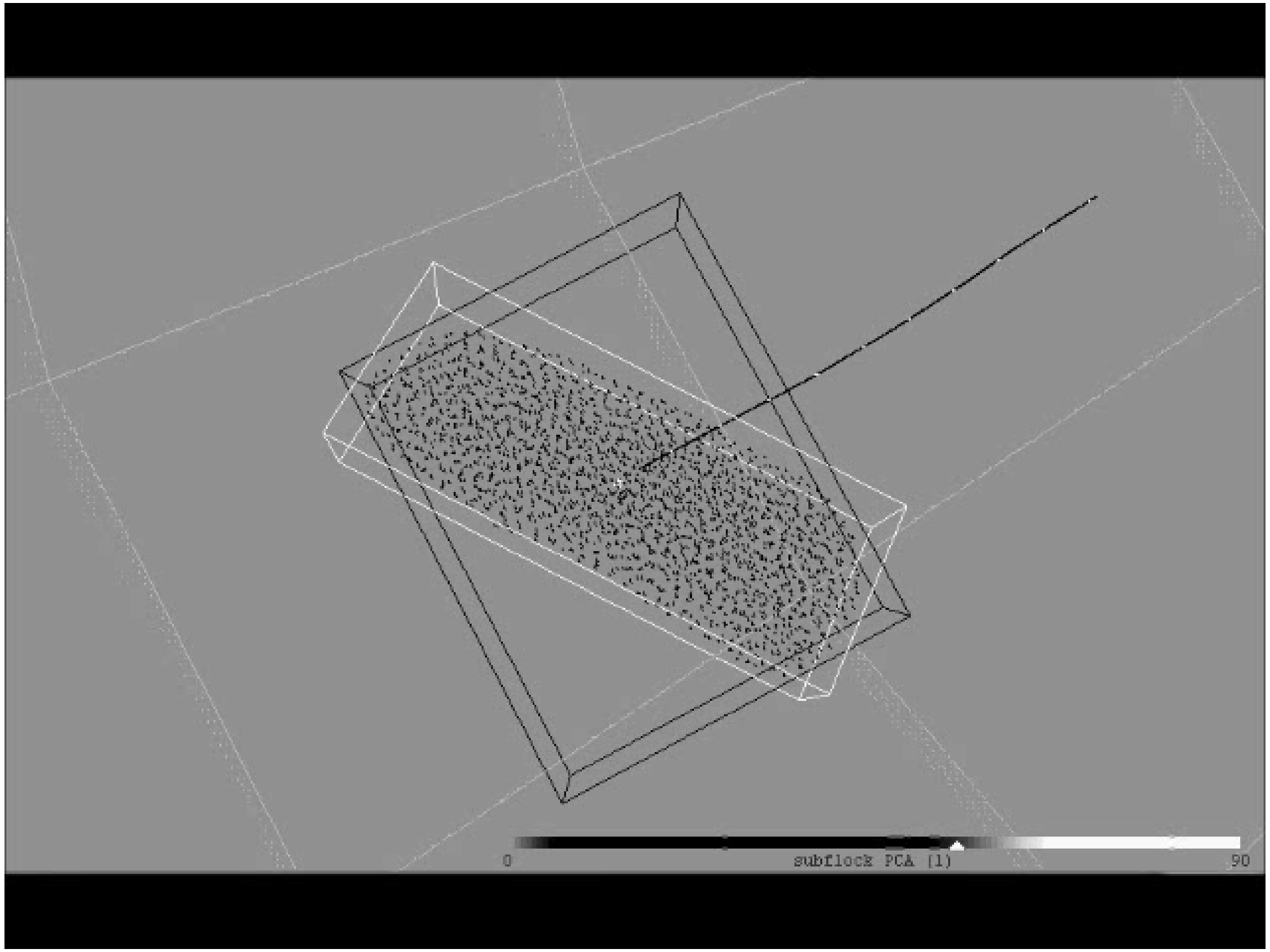




*Oblong shape* (L/W):
Paralel to movement direction

*Oblong shape*: Aspect ratios ($l_3/l_2$), ($l_3/l_1$), ($l_2/l_1$), of bounding box parallel to longest dimension

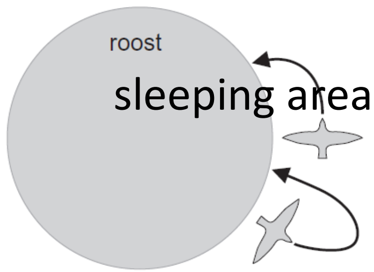
Flocks and schools are flat ($l_1$= thickness)

# Measurements

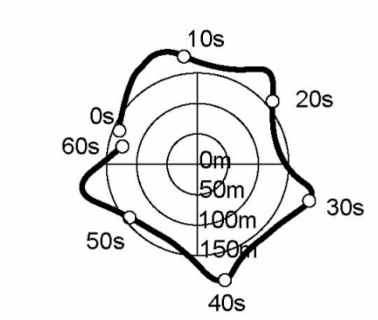


# Results

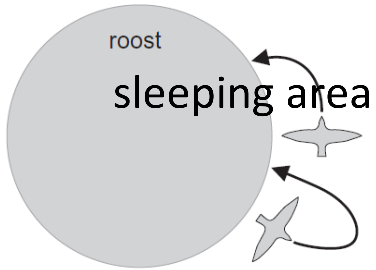
## Default situation



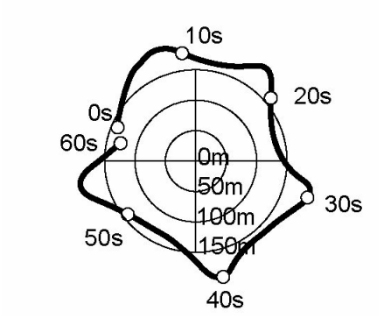

N = 2000

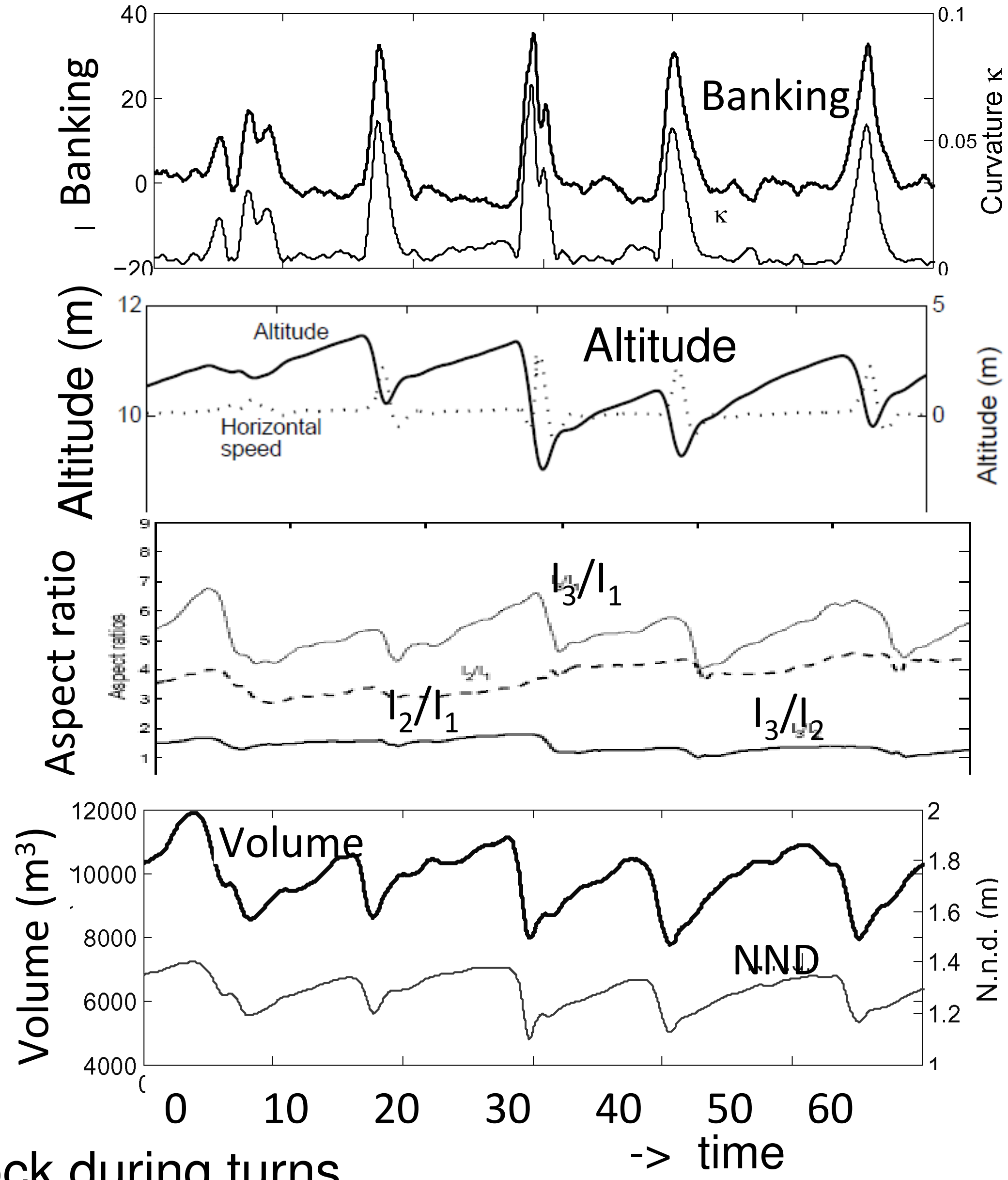


# Flying above the roost




N = 2000



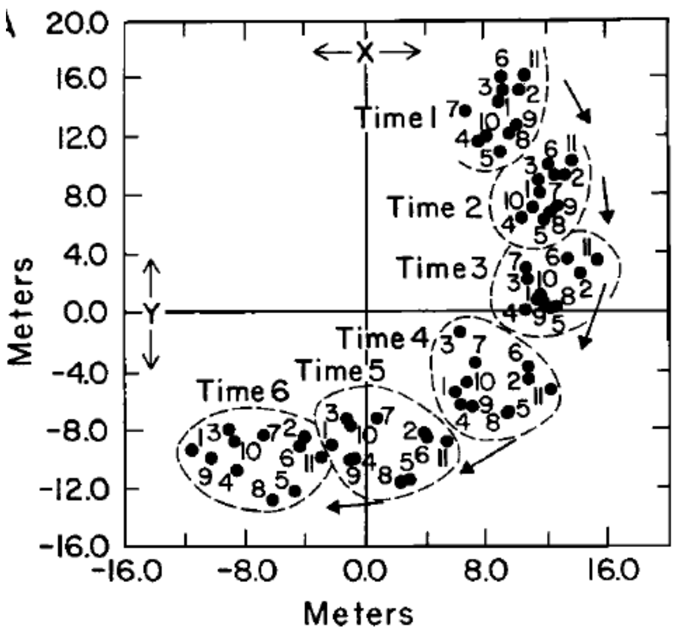

Compression in flock during turns

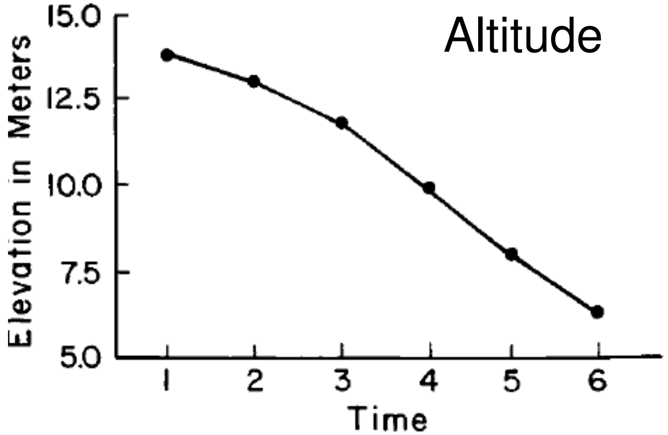
Realistic?

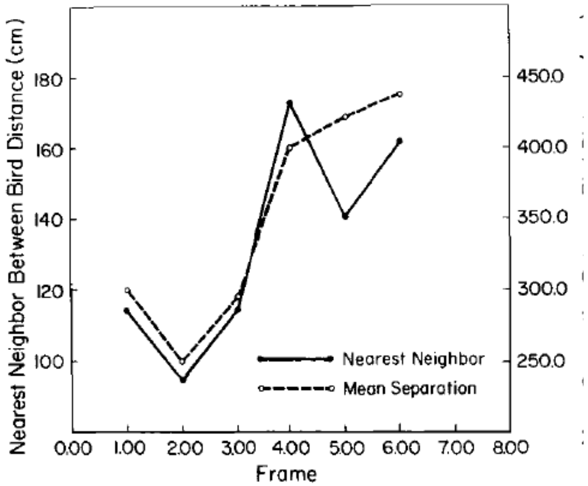
# Similar to empirical data of rock doves

Pomeroy & Heppner 1992

Turning



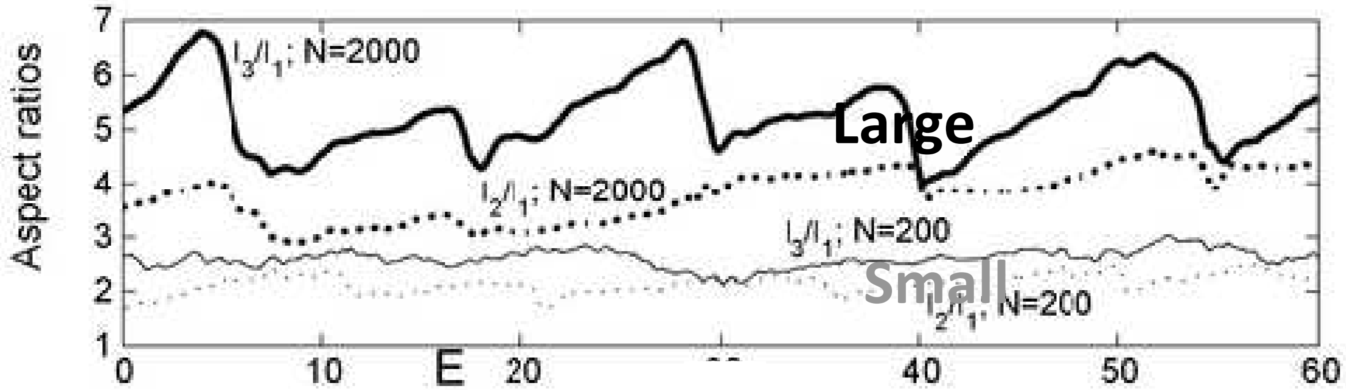

Nearest Neighbour Distance

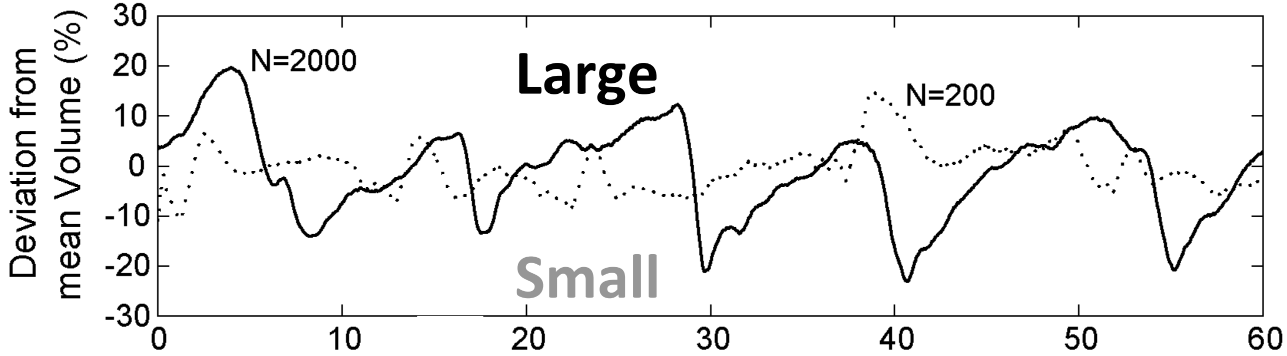
# Model Experiments

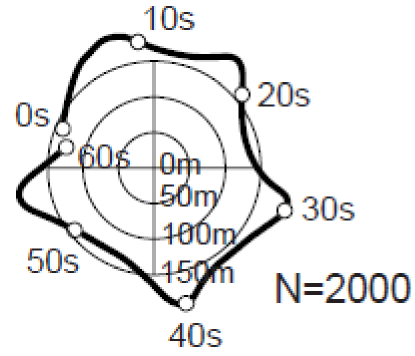
Differences among individuals in behaviour:

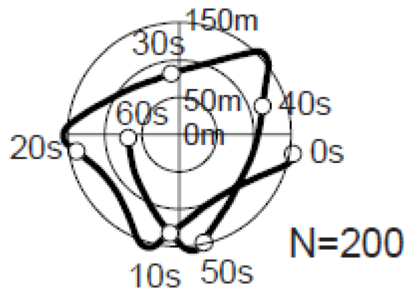
- flock size (200, 2000)
- # interaction partners (6.5, 50)
- rolling or not when turning
- turning or not
- variability of (adjustable) speed

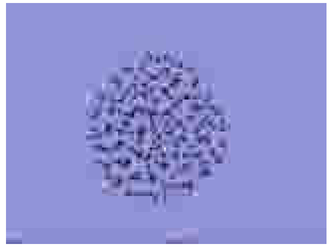
# Flock size



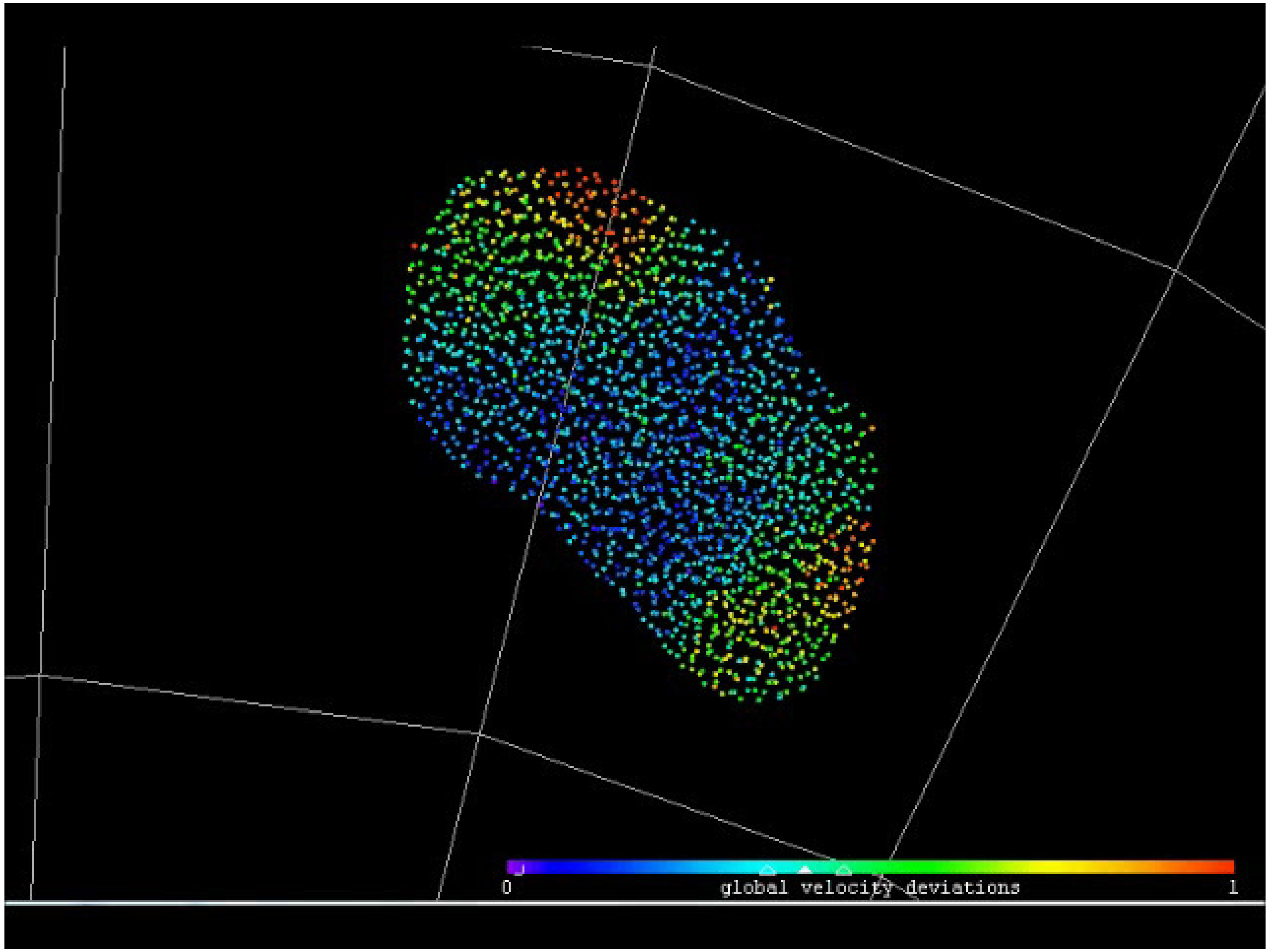



Small flocks cause relatively smaller changes in volume due to

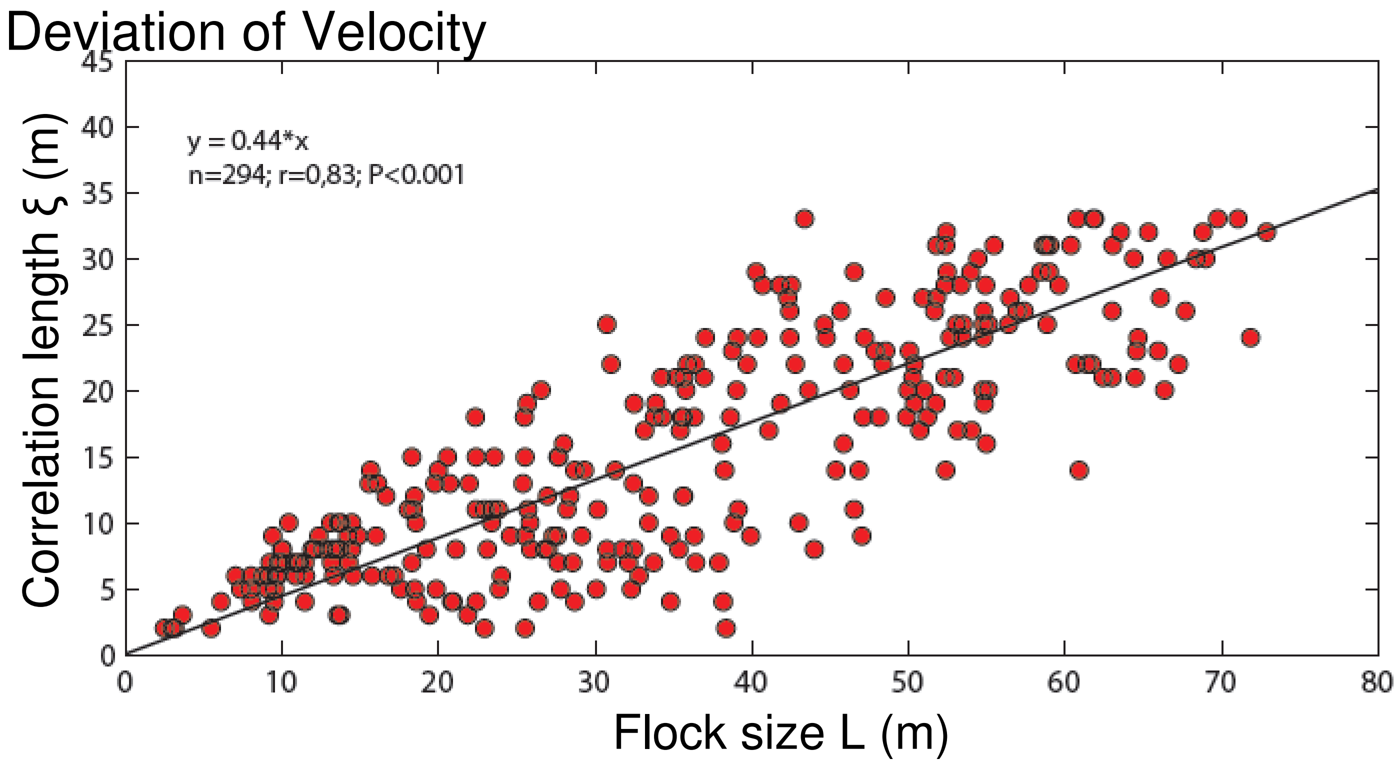
- more similar condition (above roost, or outside)
- more global interaction in flock

# Deviations of global velocity during movement approx. straightforward



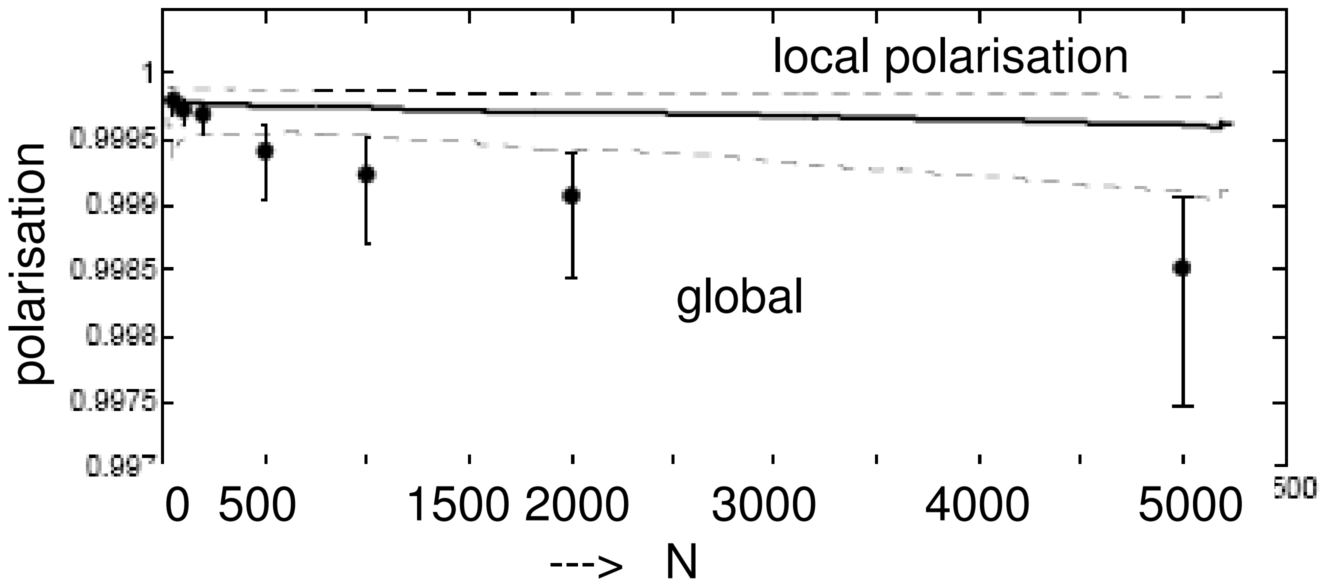

temporary sub flocks

# Larger flocks less synchronised




Larger groups have greater sub-flocks of similar speed deviation like in real starlings (Cavagna *et al* 2010)

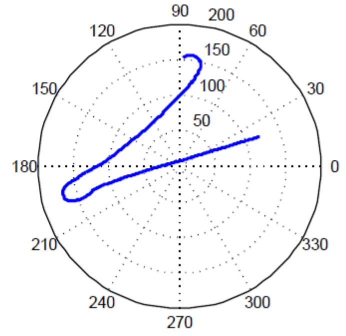
# Larger flocks: weaker global polarisation

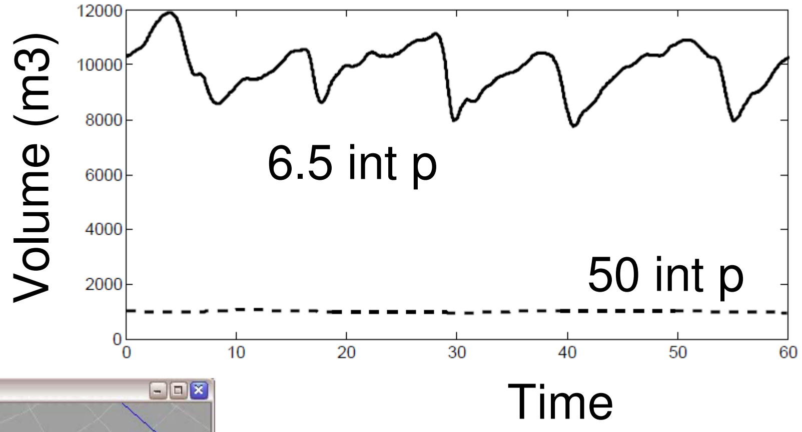


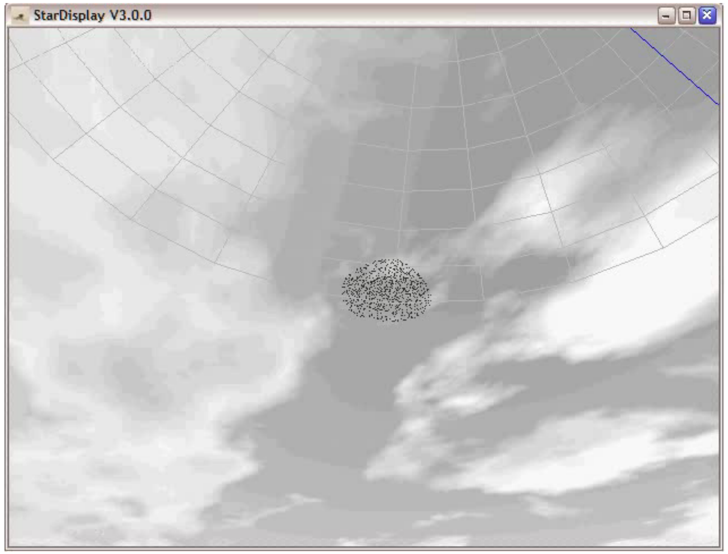

Larger sub flocks differ in direction more → flock shape is more variable

# High # interaction partners (50)

N=2000

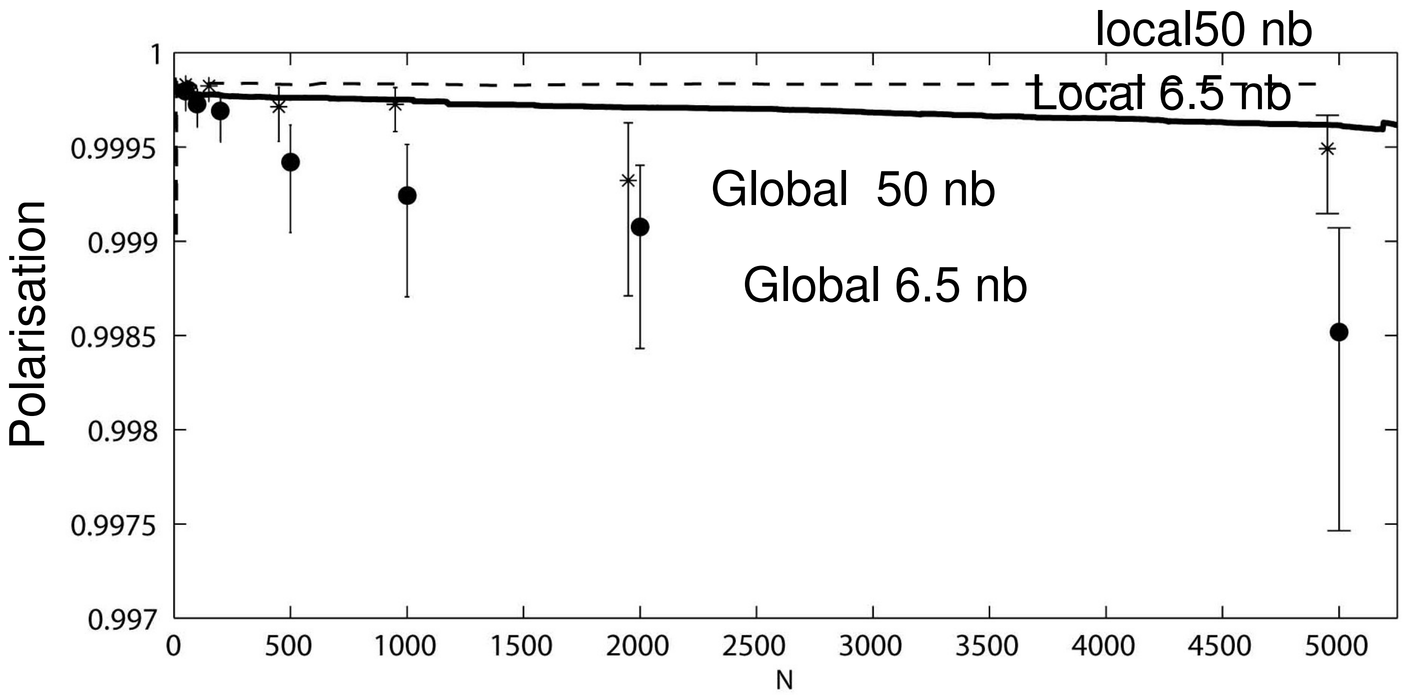


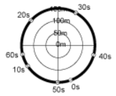

causes stable shape due to more global interaction, stronger synchronisation

# More interaction partners (50 vs 6.5)

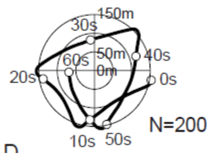



More polarised → more 'synchronised'

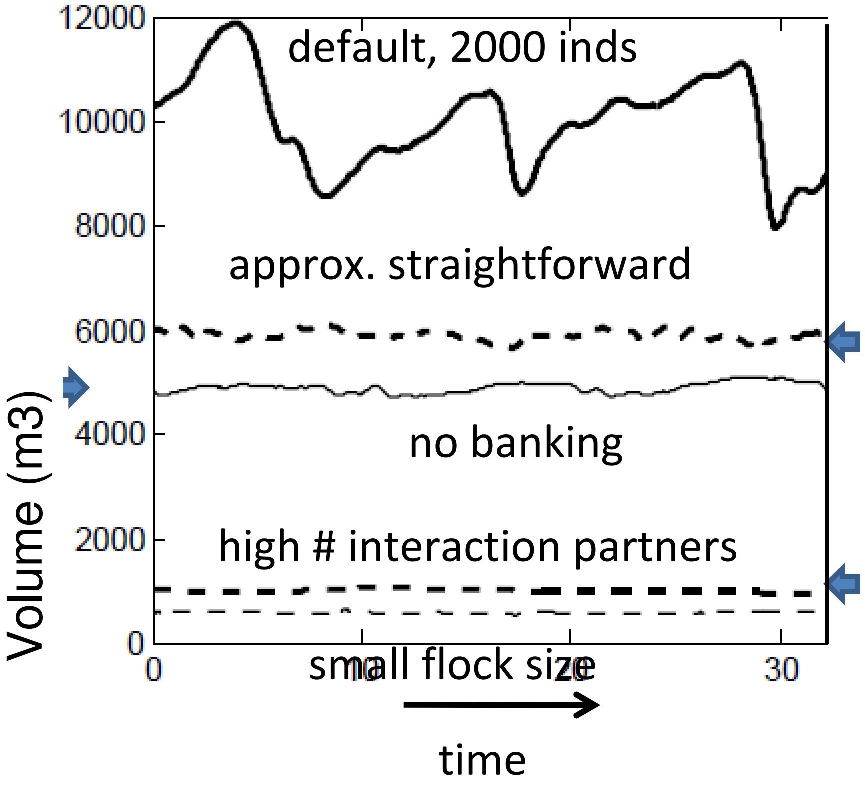
# Causes of changes of volume and shape

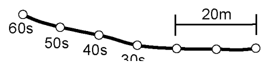


no banking

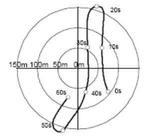



N=200



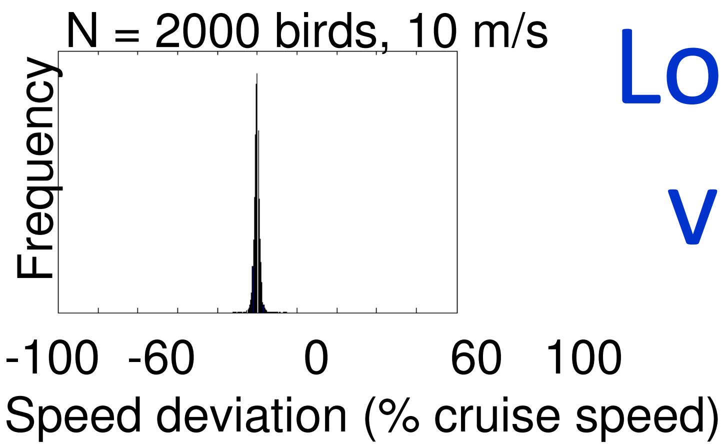




approx. straightforward



high # interact.-partners

More local differences -> more complex shape




# Low adjustability and variability of speed

Speed $v_i$, cruise speed $v_0$
Force to return to cruise speed

$$\mathrm{f}_{\tau_i} = \frac{m}{\tau}(v_0 - v_i) \cdot \mathbf{e}_{\mathbf{x}_i}$$

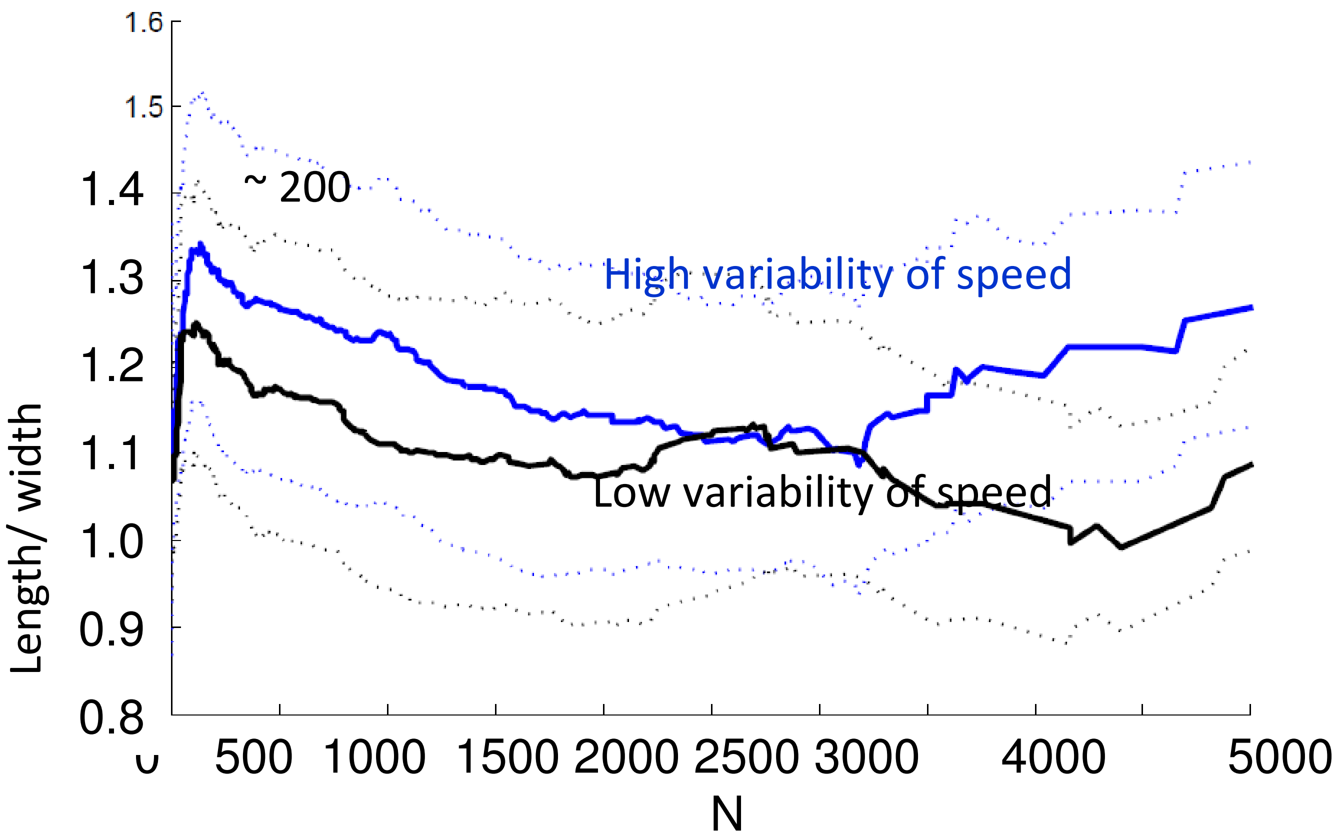
Variability of speed can hardly be increased:

From coefficient of variation 0.01 to 0.015

Aerodynamic forces stabilise the speed

No effect on variability of volume

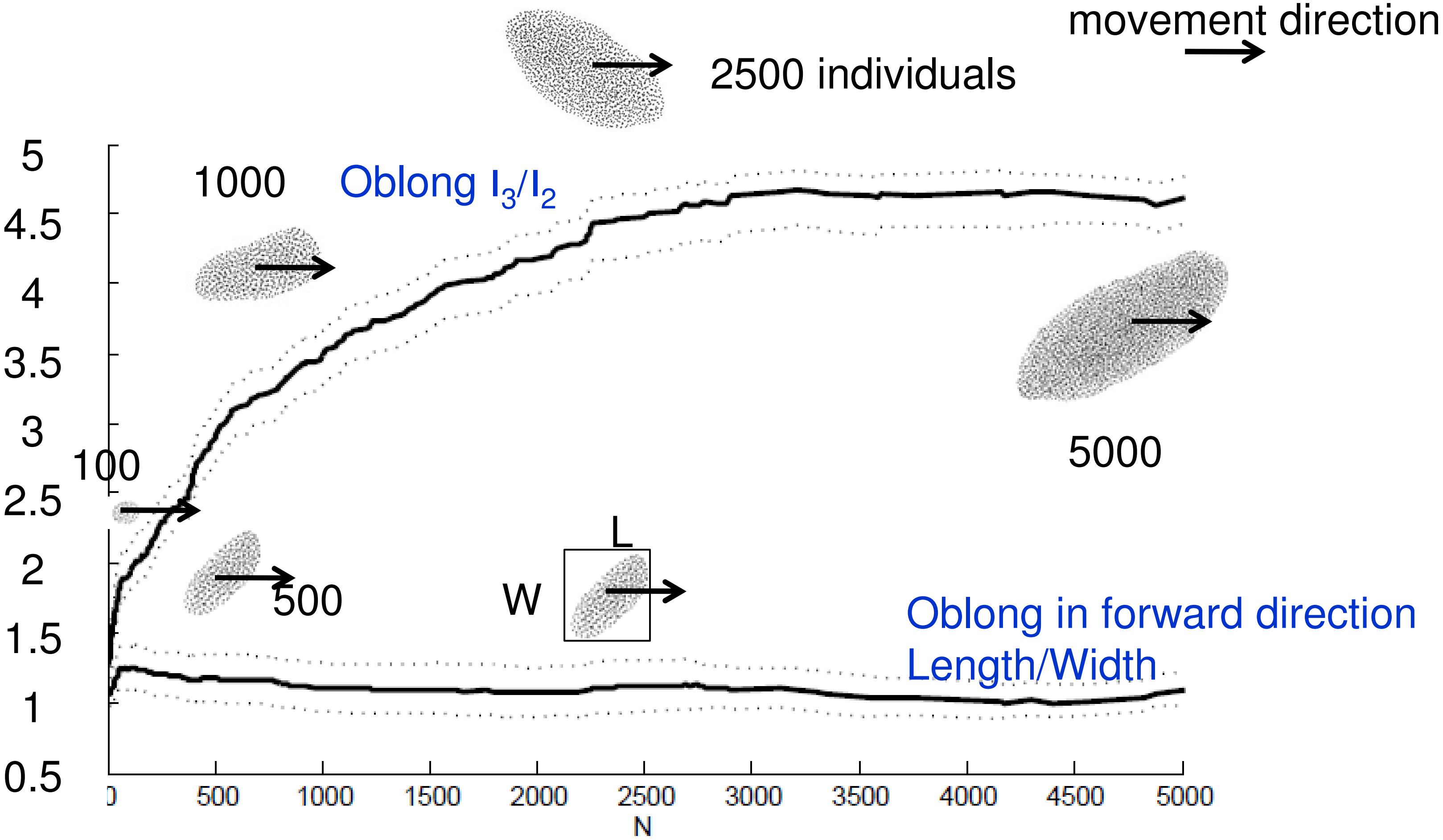
# Higher variability (adjustability) of speed




-> more oblong in movement direction

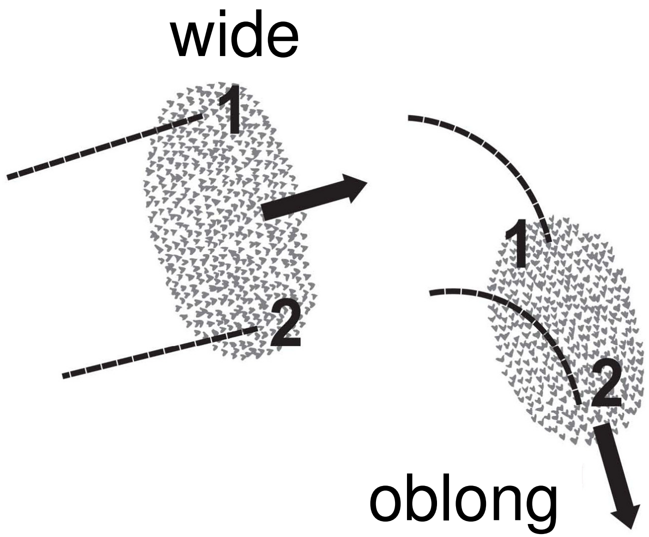
What shape ?

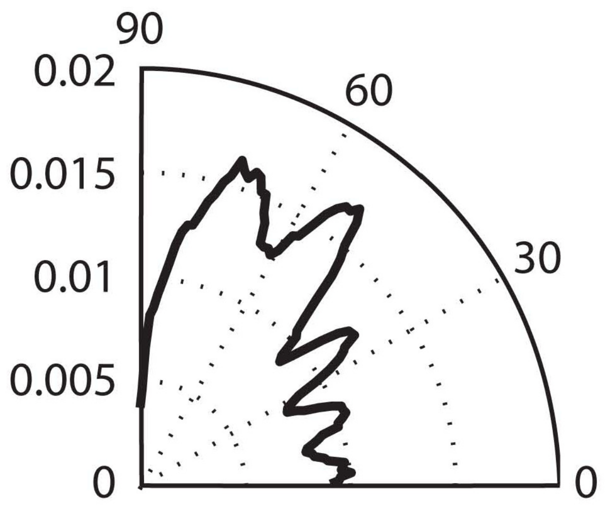
# Oblong in other directions




Why?

# Turning behaviour and low variability of speed



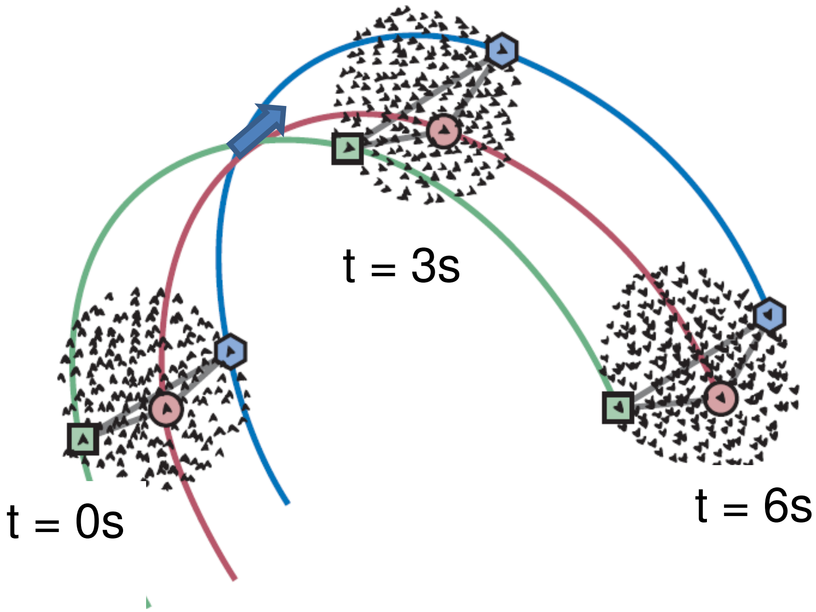

Angles of longest dimension with movement direction

causes changes in orientation of flock relative to the movement direction

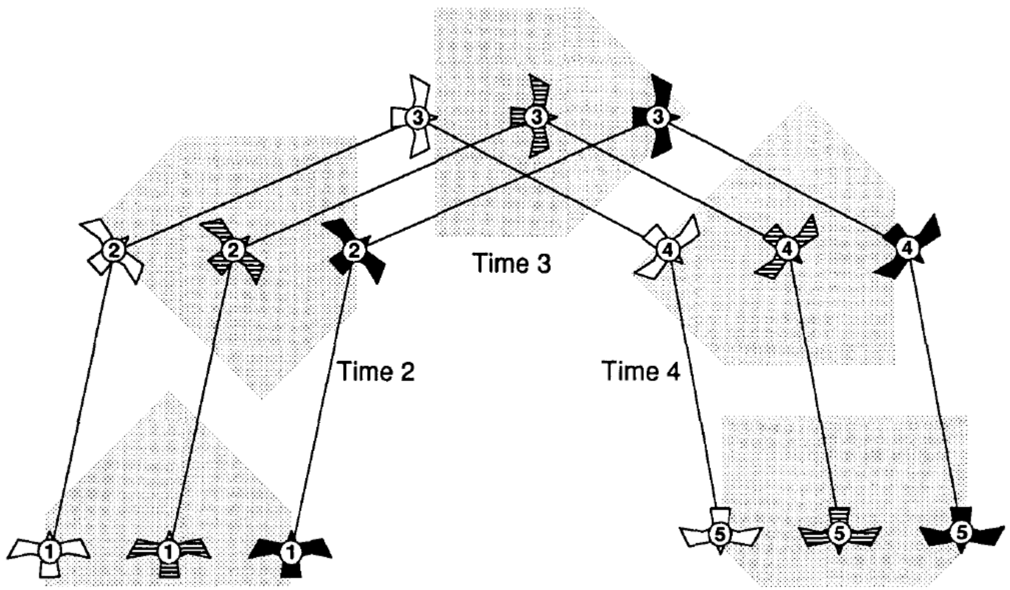
Empirical relevance? ->

# Resemblance to empirical data

(Pomeroy and Heppner 1992)




model StarDisplay



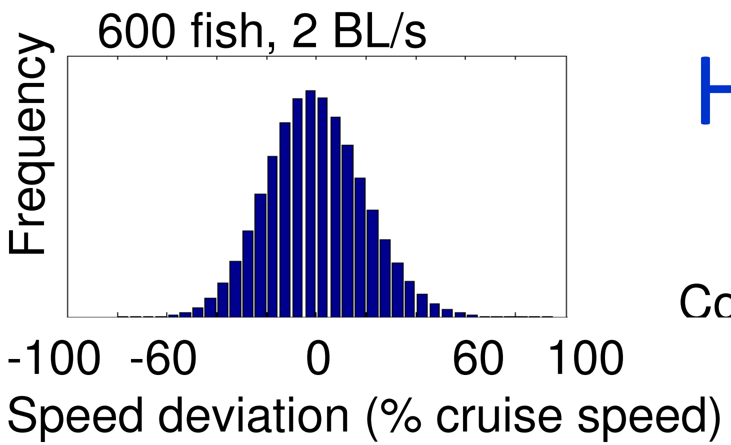

Rock doves

## ‘Repositioning’ in rock doves, dunlins and pewits

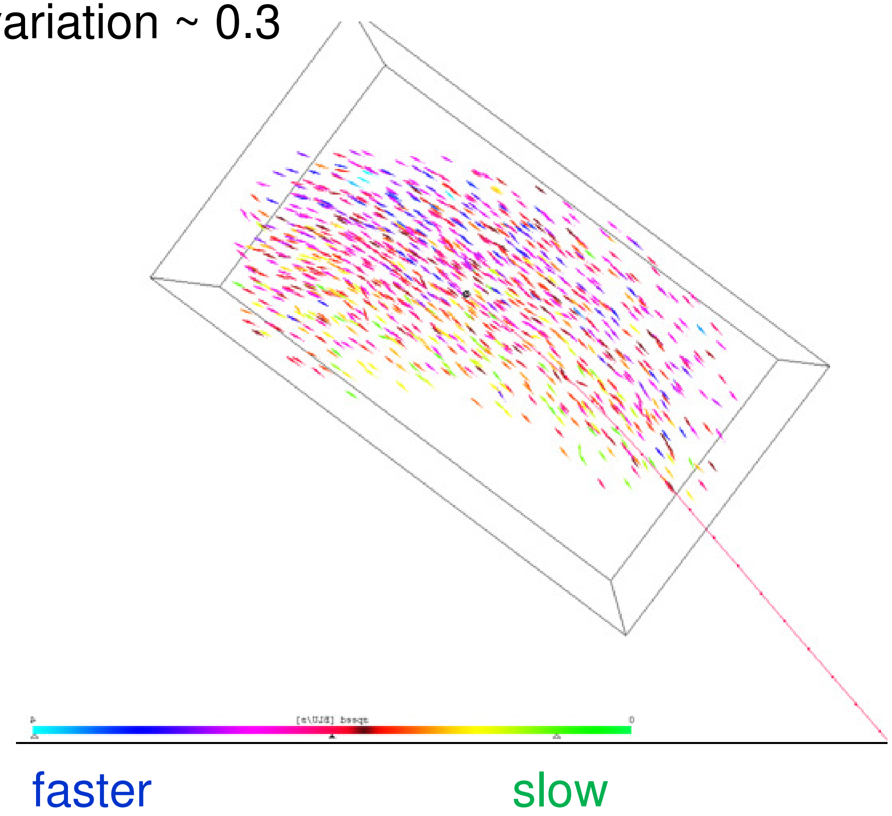
(Selous 1930; Davies 1980; Pomeroy and Heppner, 1997)

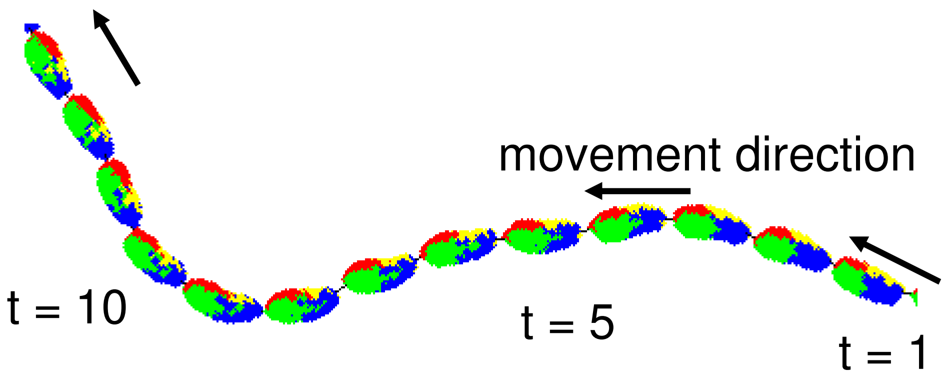
# Higher variability of speed

## Model of fish schools




Coefficent of variation ~ 0.3




Maintainenance of shape relative to the traveling direction, by automatic slowing down in inner corner

# Summary

Greater variability of shape of flocks arises from larger local differences in behaviour due to:

- larger flocks
- fewer partners for interaction
- rolling while turning
- reacting to a heterogeneous environment (sleeping site, attack by raptor)
- But **not** due to higher variability (adjustability) of speed....

# Unexpectedly

Low variability (adjustability) of speed

High variability in orientation of the shape

# Testable hypotheses

Greater locality of interaction

– in larger locks

– with fewer interacting neighbours

– in a heterogeneous versus uniform environment

– when rolling during turning

More variable shape

# Testable hypotheses

Higher variability (adjustability) of speed induces

- more oblong shape in the movement direction
- fixed locations in the group during turns

Lower variability of shape

# Testable hypotheses

Lower variability (adjustability) of speed induces

- Equal path length
- Repositioning during turns
- Change of shape relative to movement direction

Higher variability of shape

# Financial support

- European framework, StarFlag
- NWO pilot grant
- Startup grant from Rosalind Franklin Fellowship