The self-organised dynamics of shape and internal structure of flocks of starlings

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Beautiful collective movements

Youtube

'Dancing' above the sleeping site

Individual behaviour?

- Telepathy (Selous, 1931)
- Selforganisation
  - Interactions of starlings are local, 7 neighbours (Ballerini *et al* 2008)

How can we learn more about this?

‚Understanding by building‘

Pfeifer and Scheier 1999

Rules of local interaction

Self-organization

Complex patterns of the group

Hypotheses for empirical studies

Start with model of fish schools

Shape of flocks

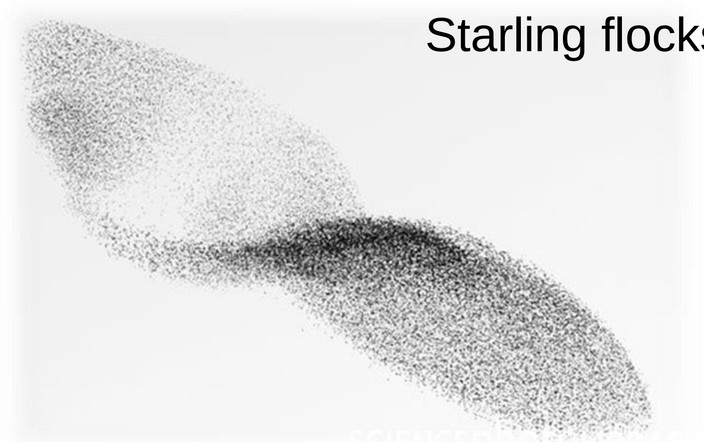
Fish schools:
usually oblong in shape

Pitcher 1967

Bird flocks:
All shapes

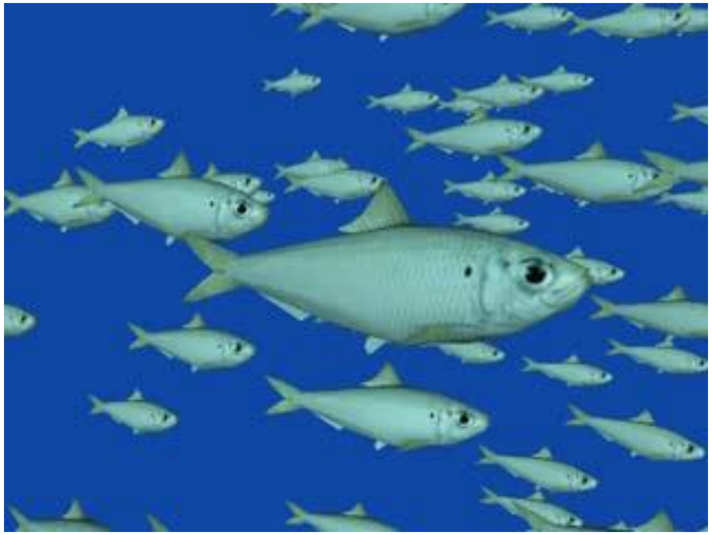
Carere *et al* 2009

Starling flocks



Model of fish school

Hemelrijk & Hildenbrandt, 2008, *Ethology*



Individuals move and interact with neighbours:

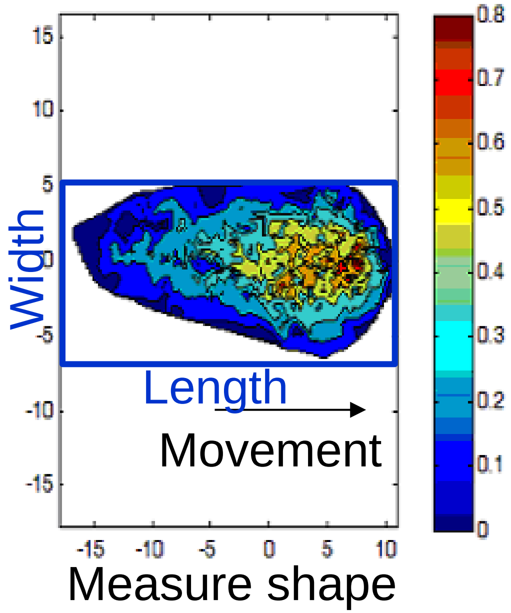
- attraction
- alignment
- avoidance:
  - through slowing down (Katz et al 2011; Herbert-Read et al 2011)

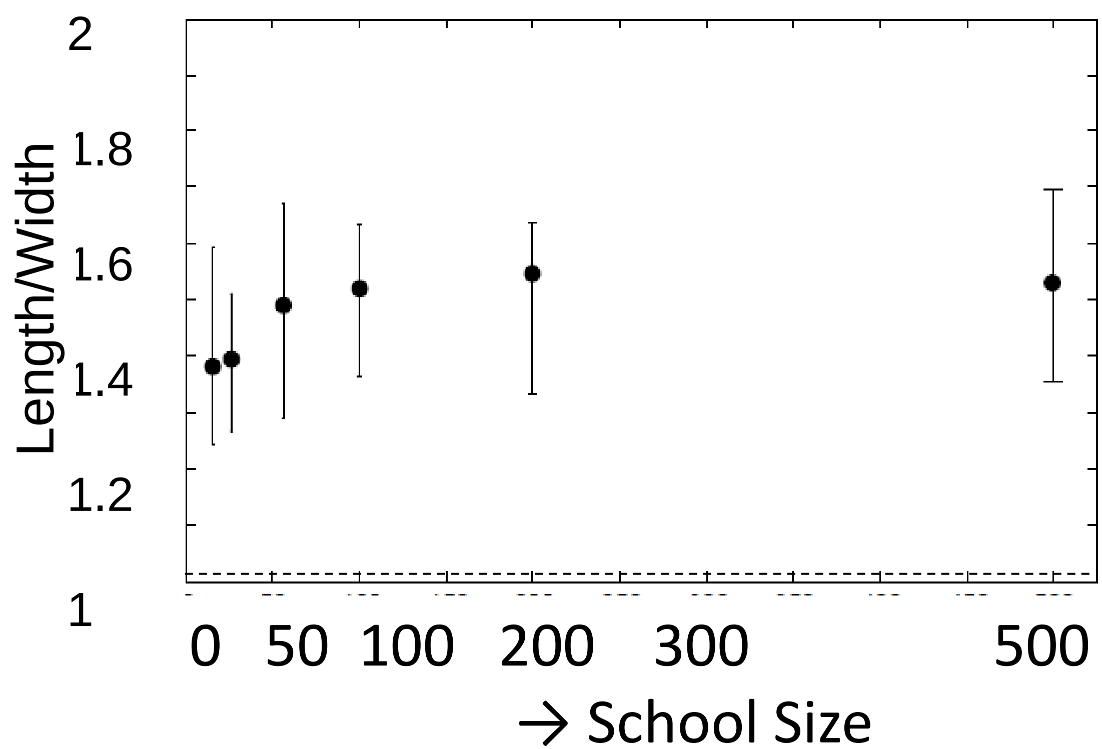
Moving schools emerge,

With shape that is oblong!

Oblong shape

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



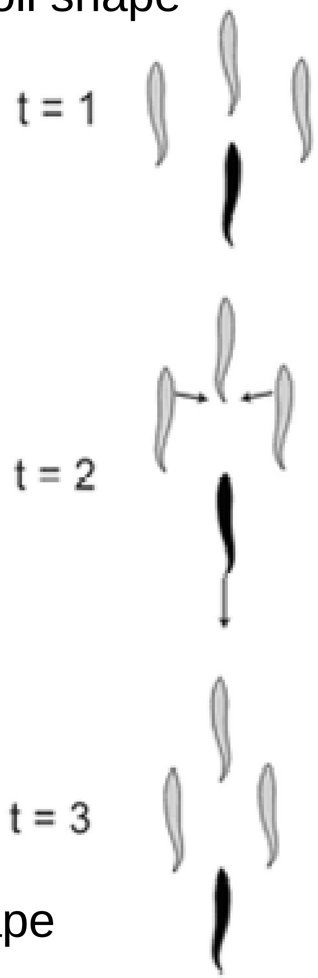


Two and three dimensional models, several group sizes, two cruise speeds, two body sizes, group compositions

as a side - effect

Causation of oblong shape

Circular or boll shape



Oblong shape

by coordinating and slowing down to avoid collisions!

Denser schools are more oblong

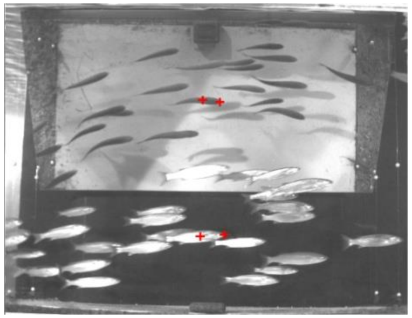
Larger schools are denser

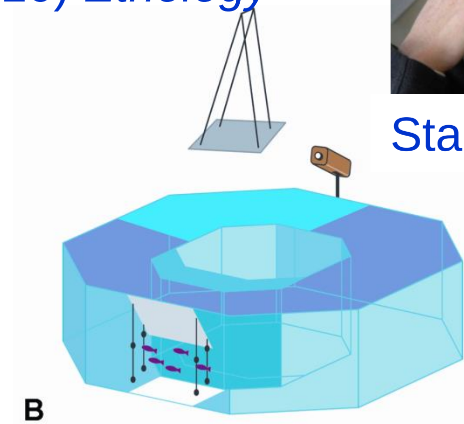
Predictions for empirical data

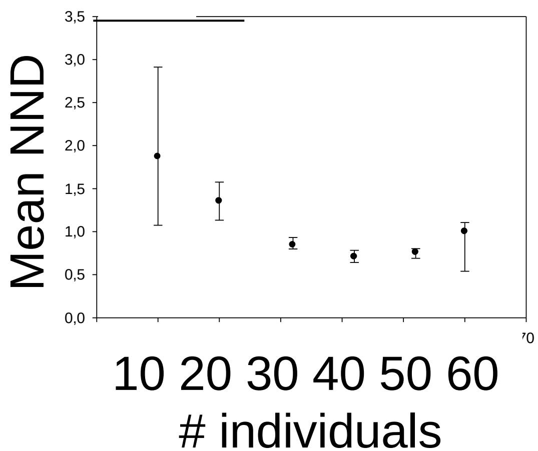
Empirical data of Mullets

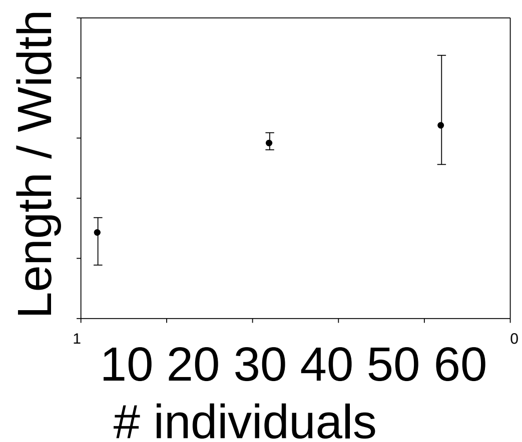
Hemelrijk, Reinders, Hildenbrandt, Stamhuis (2010) *Ethology*

Stamhuis









Corresponds to the patterns of the model!

Fish schools are oblong due to coordination while avoiding collisions

Question

What behaviour causes variation in shape in bird flocks?

Complex shapes of starling flocks

Youtube

Our model of starling flocks, StarDisPlay

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

Hildenbrandt

Flocking model with:

1. local coordination (attraction, alignment, avoidance)
2. attraction to the site for sleeping (roost) (Carere et al 2009)
3. simplified aerodynamics of flying (Norberg, 1990)
4. few interaction partners (6.5) (Ballerini et al 2008)

$F_{steering}$ (items 1–2)

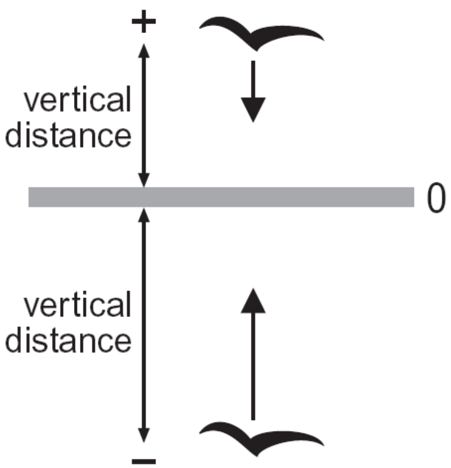
F_{flight} (items 2–3)

also in fish model (item 1)

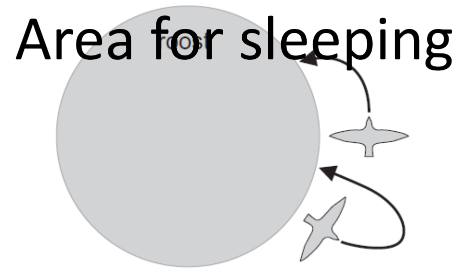
specific to birds, especially starlings (items 2–4)

Stay over the site for sleeping

Vertical attraction



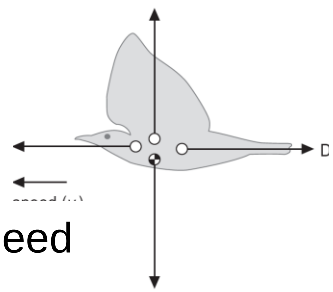
Horizontal attraction



$$F_{Steering_i} = F_{Social_i} + F_{Roost_i}$$

Flying by Fixed Wing Aerodynamics

Balanced constant level flight



Lift and drag

$$L = \frac{v^2}{v_0^2} L_0 = \frac{v^2}{v_0^2} mg \qquad D = \frac{C_D}{C_L} L$$

Flight force

$$\boldsymbol{F}_{\mathrm{Flight}_i} = \left(\boldsymbol{L}_i + \boldsymbol{D}_i + \boldsymbol{T}_0 + \mathrm{m}\boldsymbol{g} \right)$$

Update

Acceleration, *a(t)*

Velocity $\mathbf{v}_i\left(t+\Delta t\right) = \mathbf{v}_i\left(t\right) + \underbrace{\frac{1}{m}\left(\boldsymbol{F}_{steering_i}(t) + \boldsymbol{F}_{Flight_i}(t)\right)}_{a(t)} \cdot \Delta t$

Location $\mathbf{r}_i\left(t+\Delta t\right) = \mathbf{r}_i\left(t\right) + \mathbf{v}_i\left(t+\Delta t\right) \cdot \Delta t$

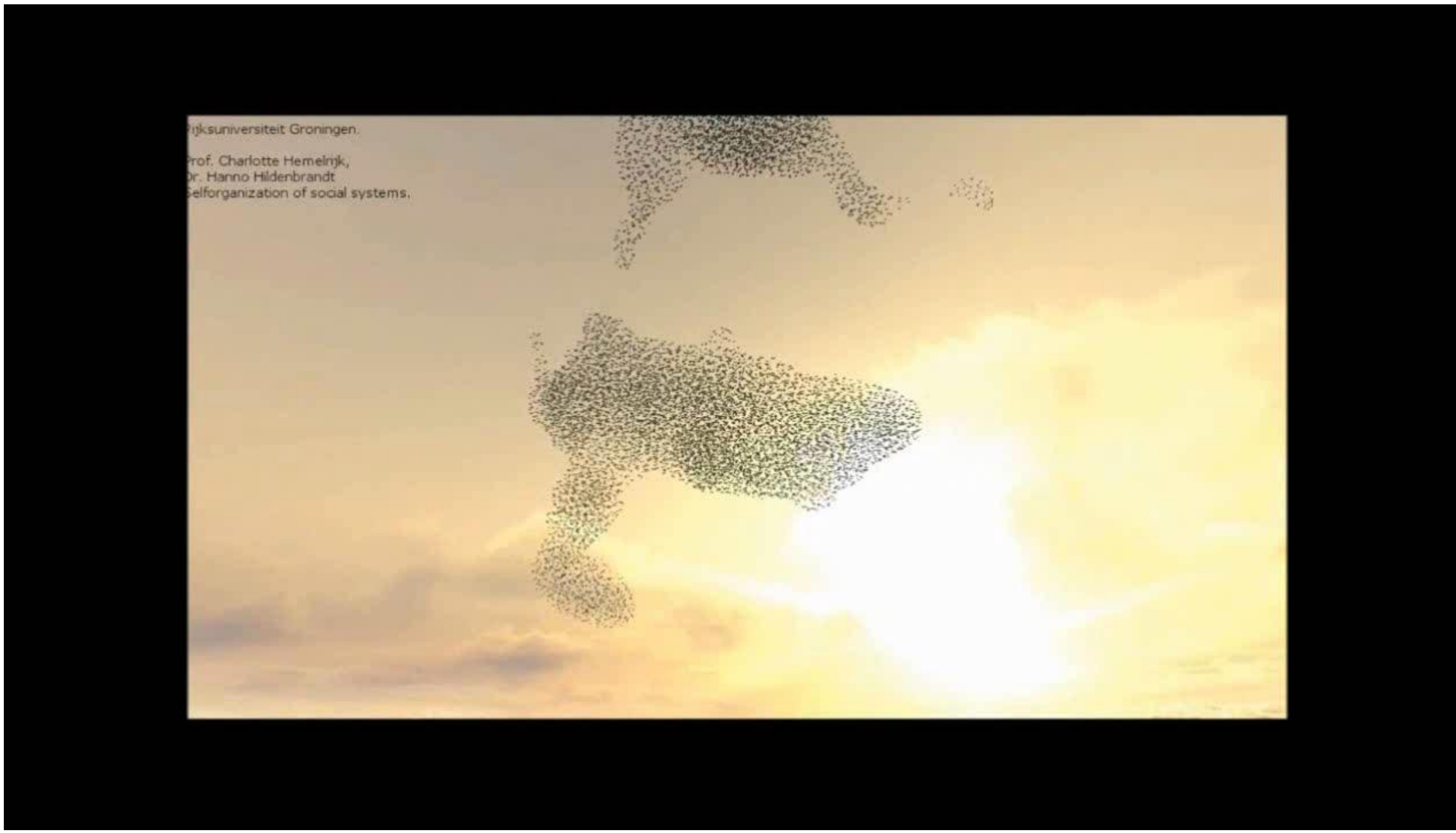
Parameters from starlings

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

Parameter	Description	Default value
Δu	Reaction time	50 -70 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	Number of interaction partners	6.5
r_h	Radius of max. separation (“hard sphere”)	0.2 m
R_{Roost}	Radius fo Roosting Area	150 m

Model of large flock size, 20.000 individuals

Hemelrijk, Hildenbrandt, 2011, 2012, PLOS ONE, InterfaceFocus



Resembles empirical data in
shape, orientation, internal structure, but volume is too small

Causes of variation of flock shape

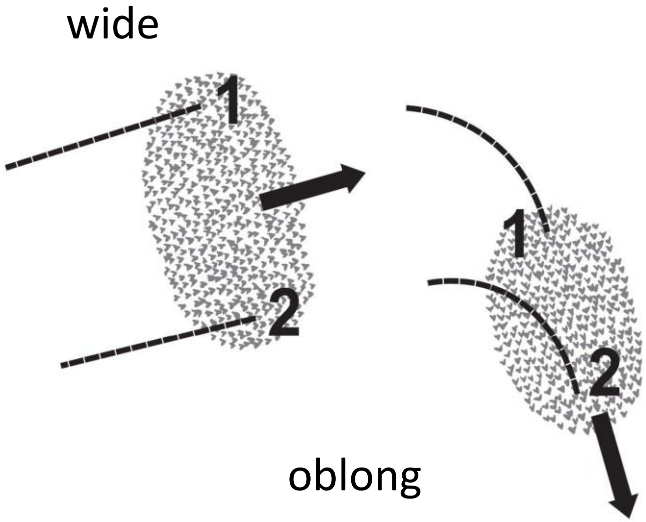
Hemelrijk & Hildenbrandt, 2011, PlosOne; 2012, Interface Focus

- Flying behaviour
- Asynchrony of behaviour in large flocks

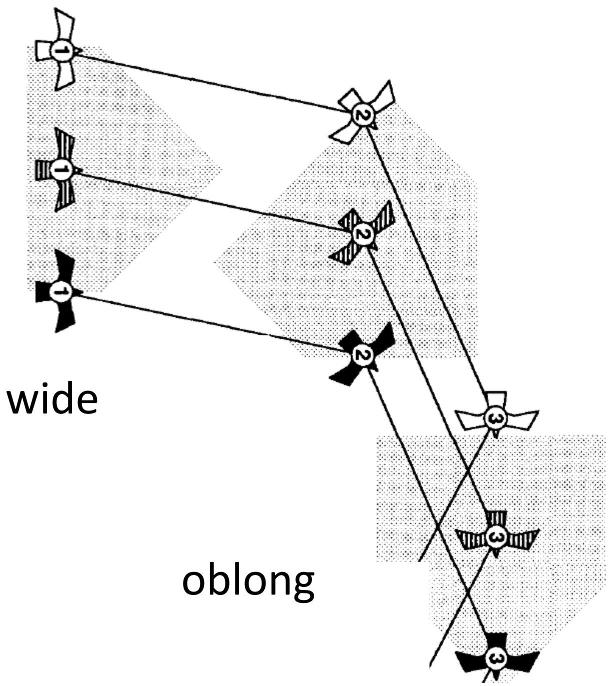
Biophysics of flight: Low variability of speed

Hemelrijk & Hildenbrandt, 2011, PlosOne

Model StarDisplay



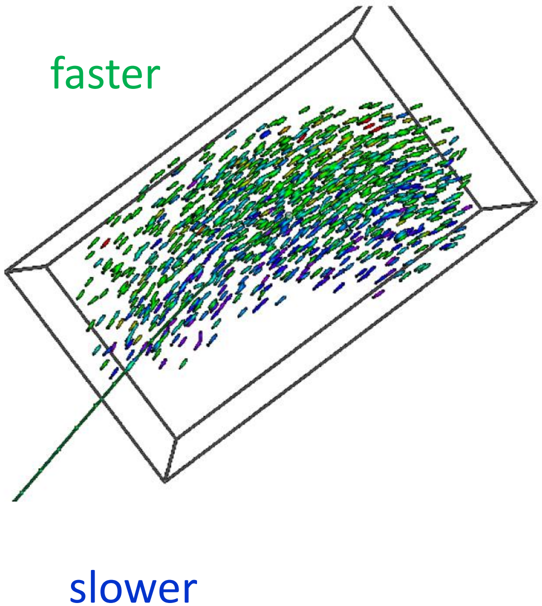
Rock doves (Pomeroy & Heppner, 1992)

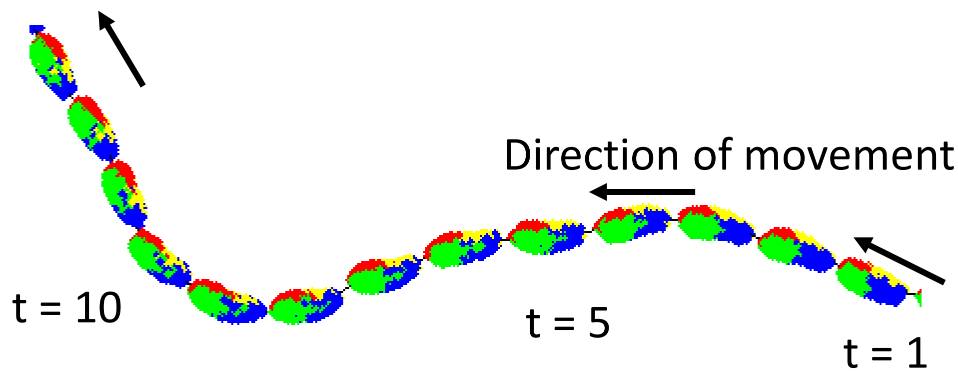


causes change of flock-shape for each turning

Adjustable speed causes oblong shape during turns in **fish schools**

Hemelrijk & Hildenbrandt, 2011, PlosOne





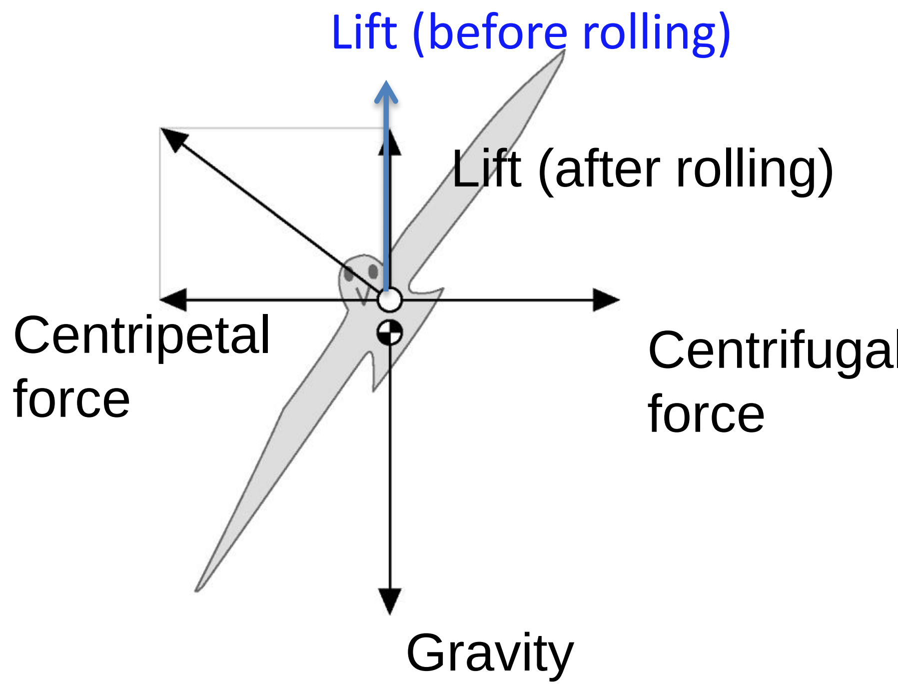
Prediction for empirical study of fish

Biophysics: Rolling while turning!

Hildenbrandt, Carere, Hemelrijk, 2010, Behav Eco

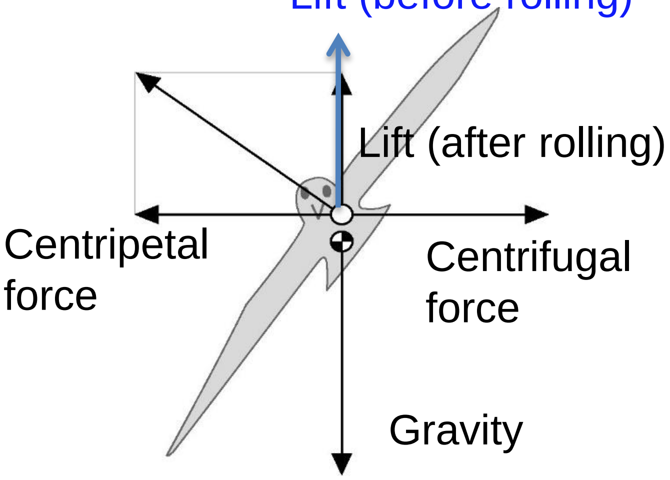
Flying:10 m/s = 36 km/h

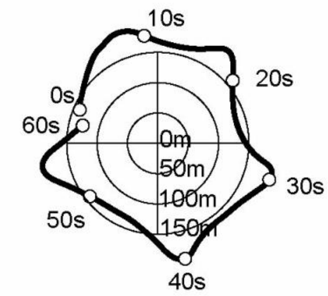
Spreeuwen



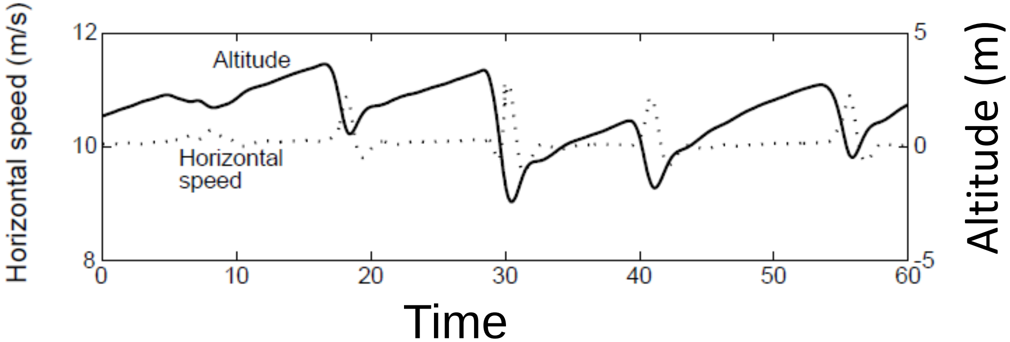
Banking while turning

Biophysics: rolling while turning

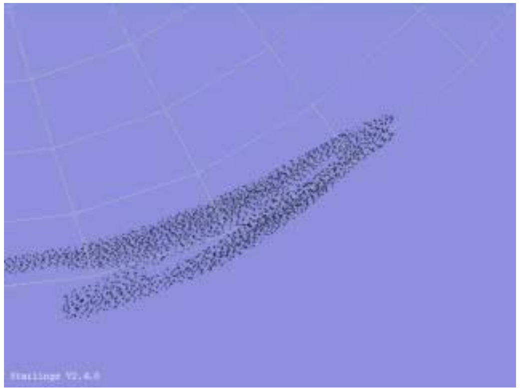




Rolling induces variability of altitude



Model without rolling:

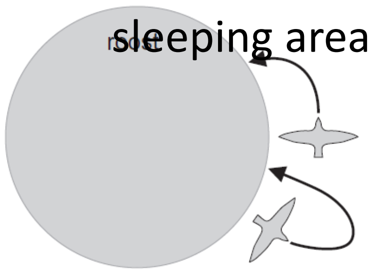


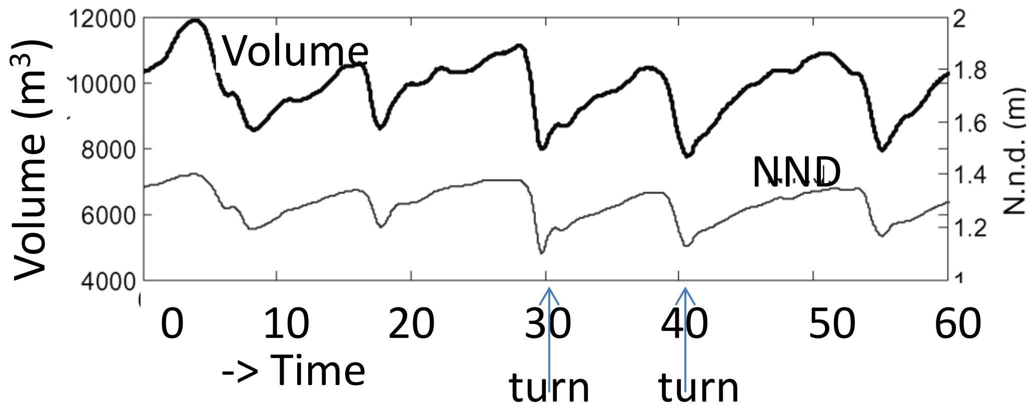
Loss of altitude during turns in Rock Doves and Steppe Eagles (Pomeroy & Heppner 1992; Gillies et al 2008)

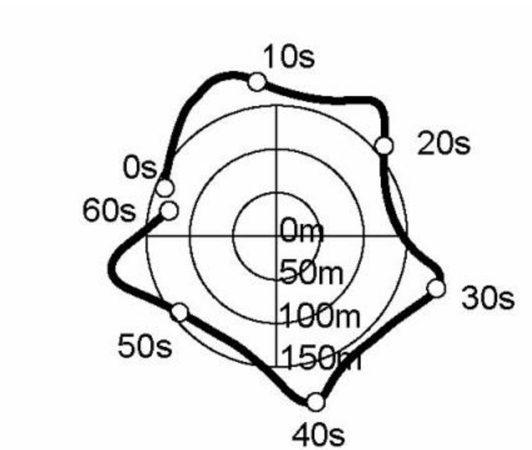
Shape changes in the vertical direction

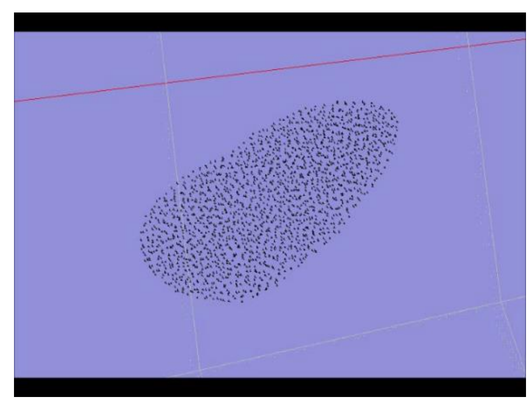
Asynchrony

Asynchrony (large flocks): heterogenous environment







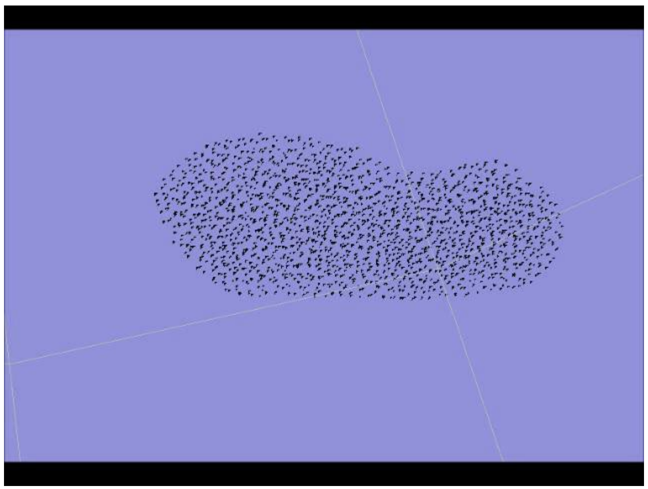


N = 2000

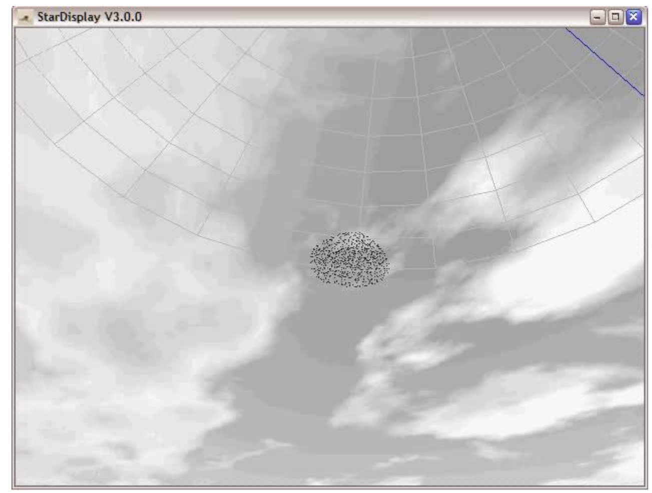
Shape changes due to frontal individuals turning earlier
Resembles Rock doves (Pomeroy and Heppner,1992)

Asynchrony: low # interaction partners (6-7)

6-7 neighbours interaction partners



High number of interaction partners (50):

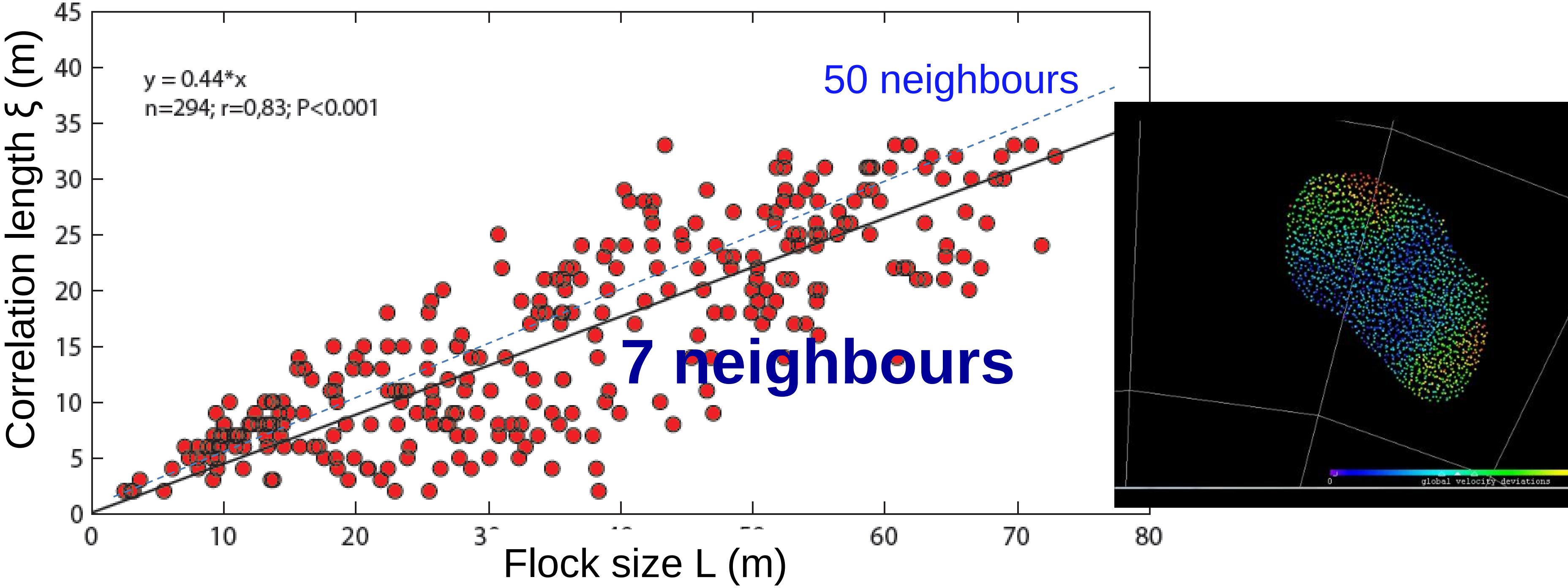


- more static volume

causes variable shape due to local interaction, weaker synchronisation

Asynchrony: flock size

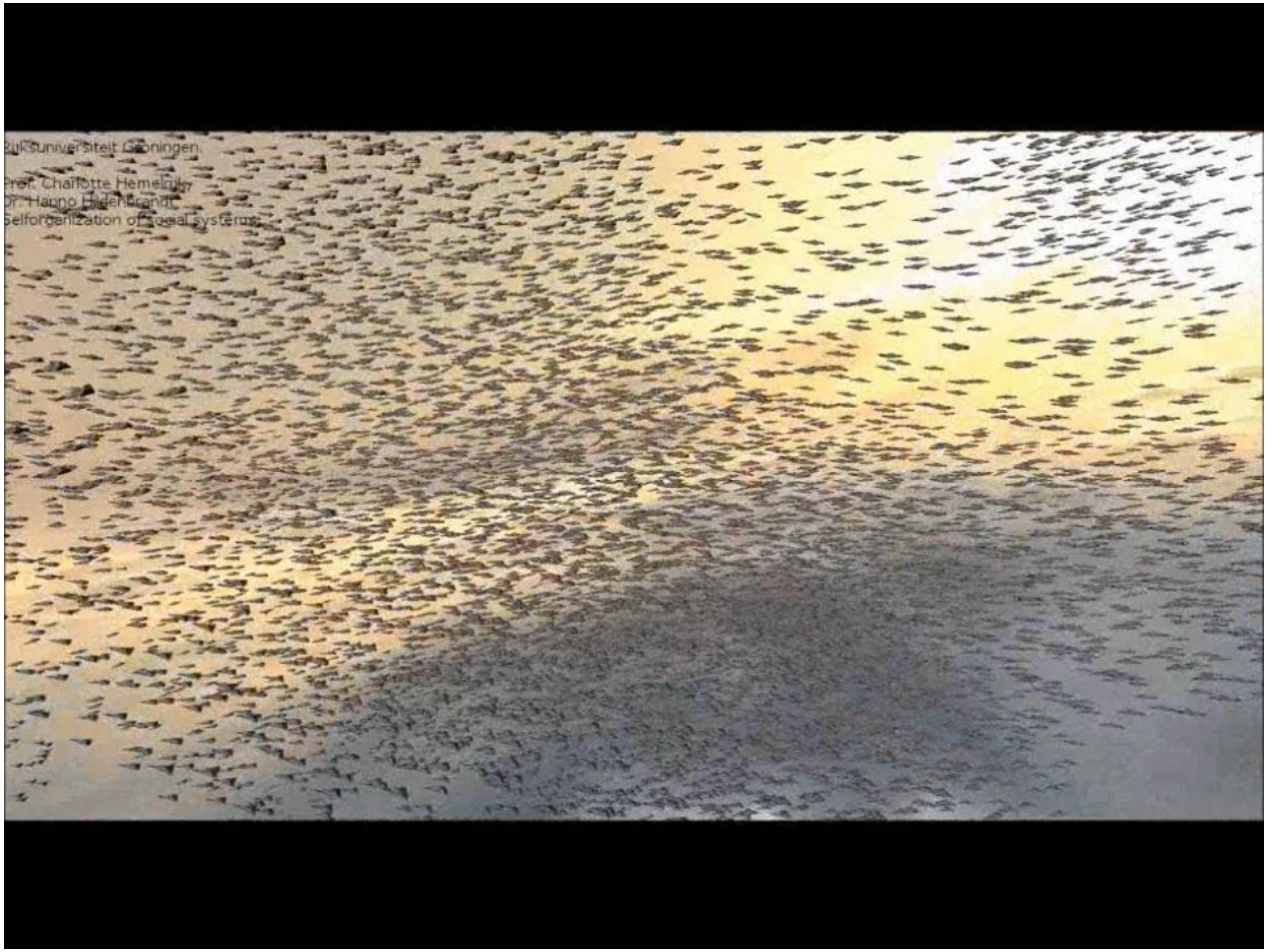
Deviation of Velocity



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

Larger sub flocks differ in direction more -> flock shape is more variable

Very large flock of 20.000 individuals



Formation of sub groups and pseudopodia

Variation of shapes of flocks in birds

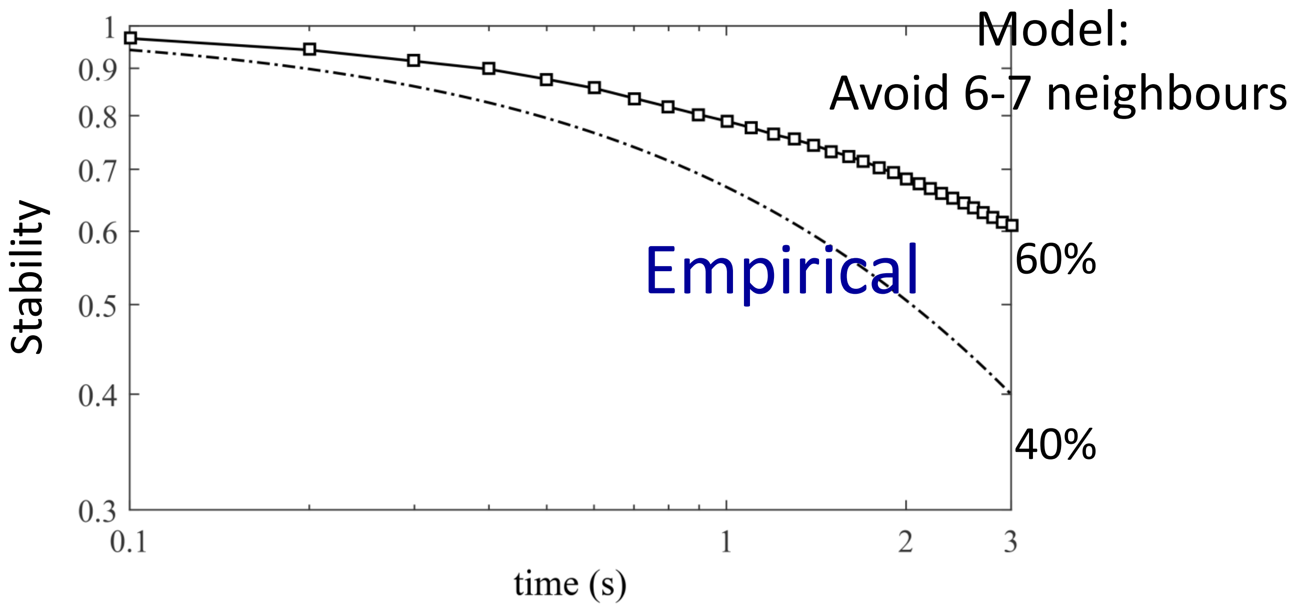
arises from

- Physical constraints of flying behaviour:
  - Banking while turning (-> loss of altitude)
  - Low variation in speed (-> changes of shape during turning)
- Asynchrony in a flock:
  - Heterogenous environment (returning to sleeping site)
  - Coordinating with only few neighbours
  - Large flocks
- Many more causes .... to be detected!

Internal motion in flock

Hemelrijk and Hildenbrandt, 2015, PlosOne

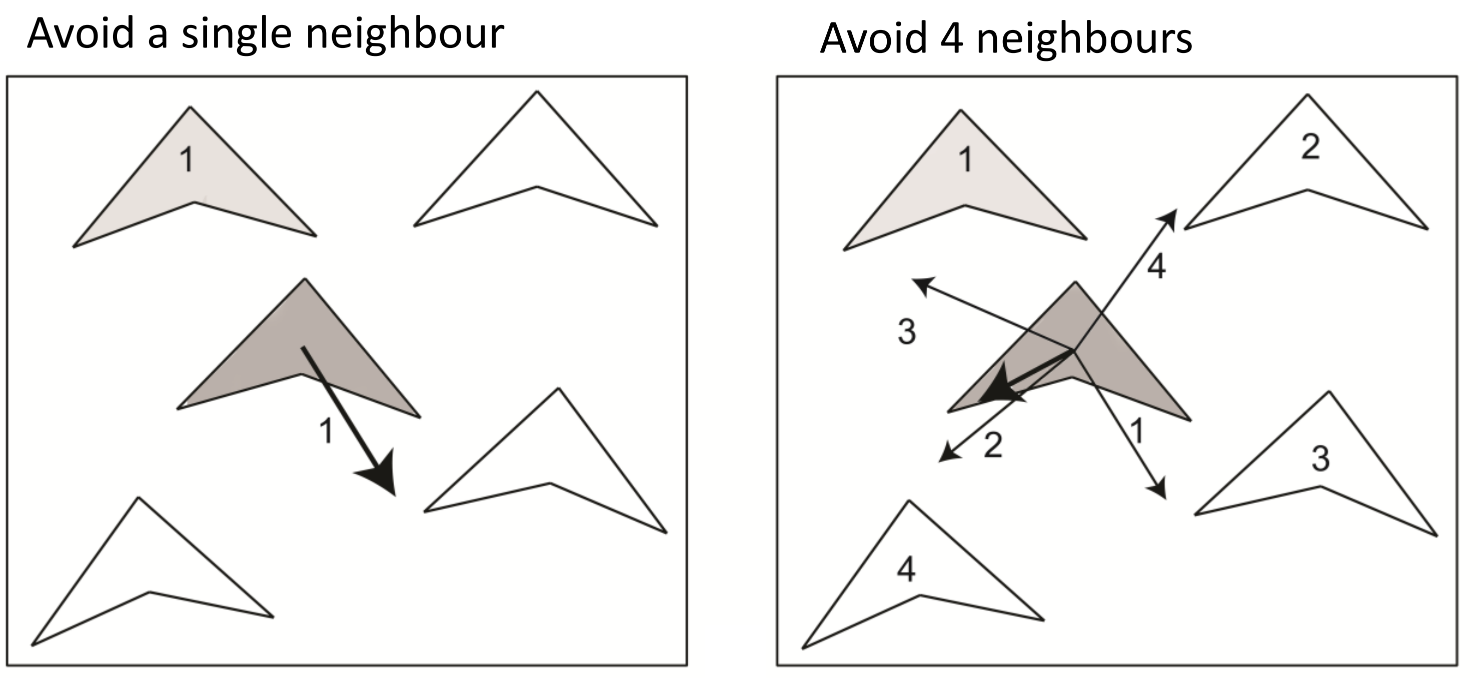
Recently empirical: stability of neighbours, % of the neighbours that are the same over time (Cavagna *et al* 2013)



In model too stable (also volume too small, remember)

Avoid only their closest neighbour ?

Avoid single, closest neighbour
(instead of seven)

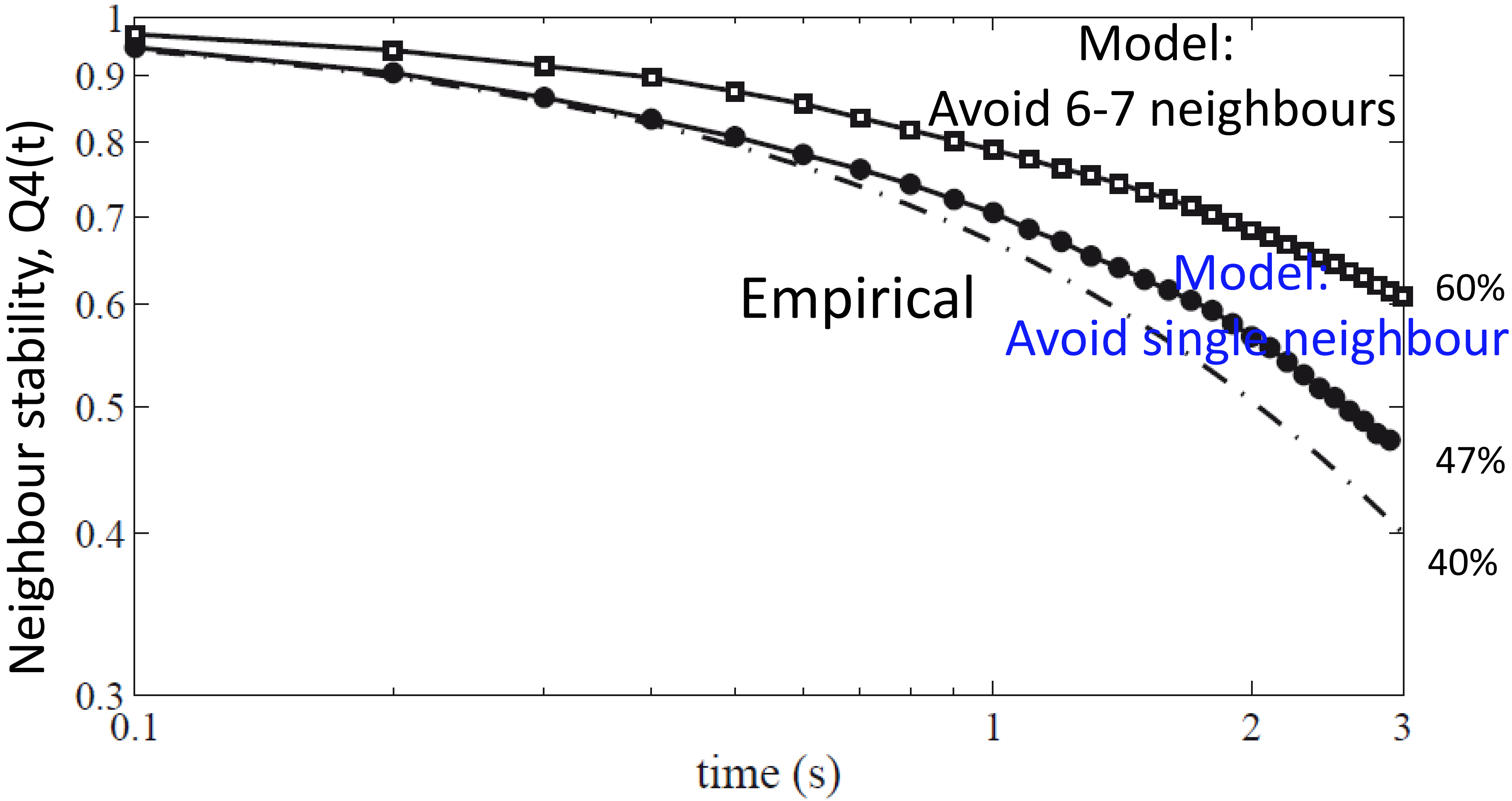


Avoidance movements are greater

Stability and volume ?

Neighbour stability

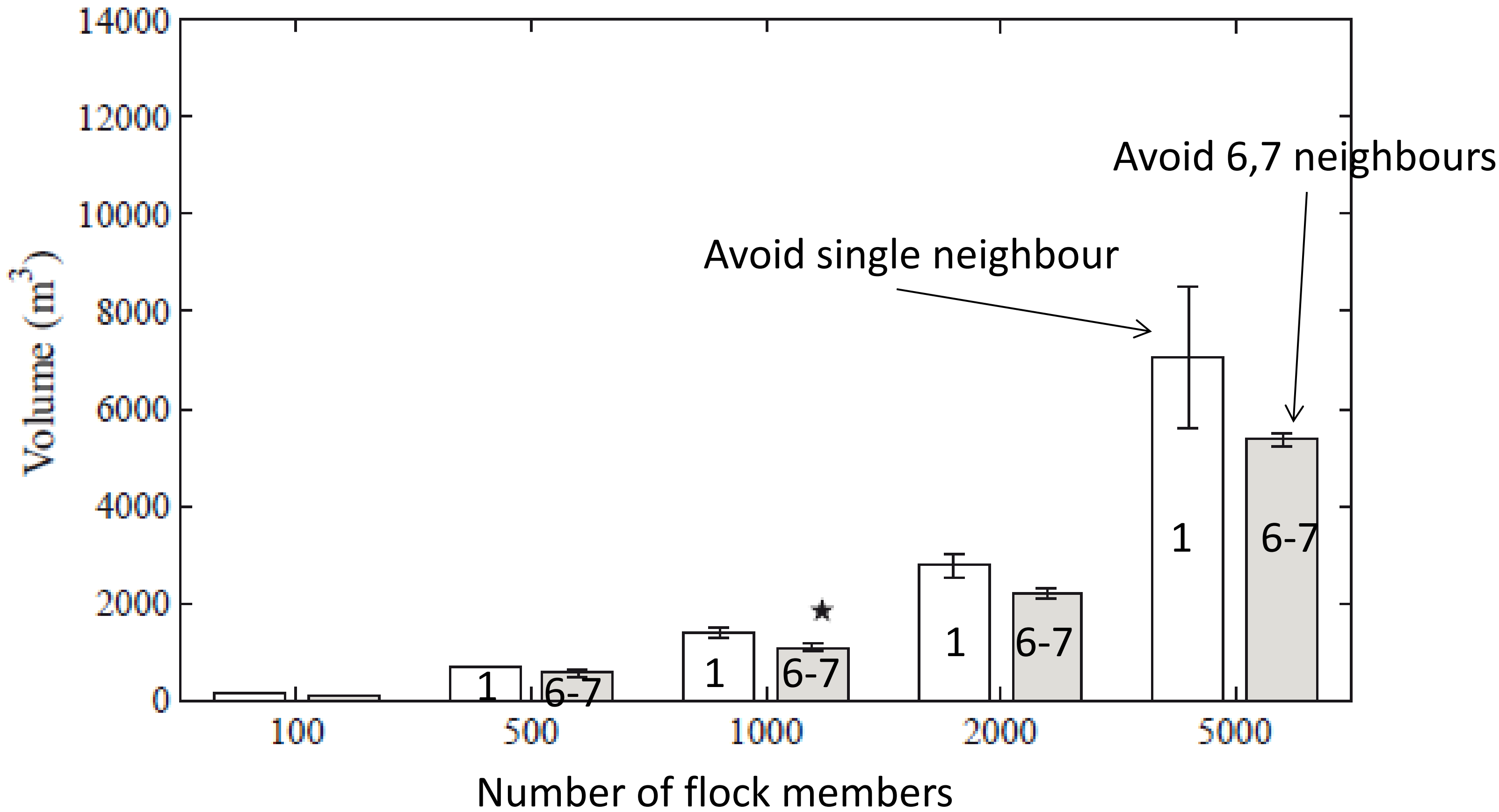
% of the neighbours that are the same over time



Avoid single neighbour -> less stability

What effect on volume?

Volume of flock



increases if avoid single, closest neighbour -> resembles empirical data better

Number of interaction partners and behaviour

For avoidance of collisions, there are fewer interaction partners than for attraction and alignment

Flock: reduction of capture success of predator

Procaccini *et al* 2011, Animal Behaviour

Agitation wave in starling flock:
moves away from predator, reduces capture rate

Flocks are too far away from us to observe details of behaviour

What individual behaviour underlies this collective behaviour?

Agitation waves

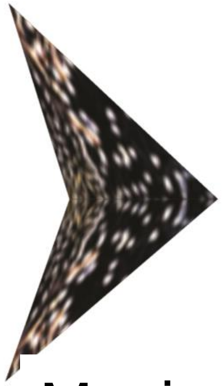
- 'Wave of orientation'
  - In dunlins (Pott 1984), white belly, brown back
  - In anchovies (Radakov 1973; Gerlotto *et al*. 2006a) silvery belly, dark back
- 'Density wave' in herring (Axelsen et al. 2001)

What escape manoeuvre is used by starlings?

In model-starlings

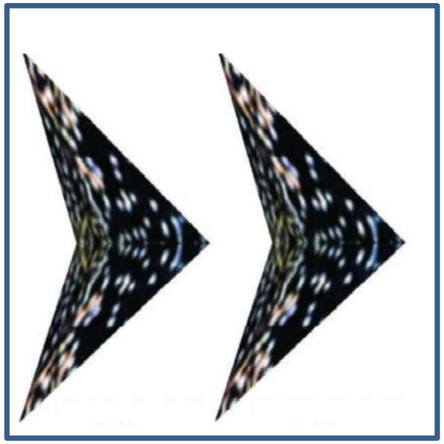
Zig-manoeuvre

Speed-up-manoeuvre



Maximal

Minimal projected area



Change in visible wing surface:
Orientation wave

Moving closer:
Density wave

Study in model, StarDisplay

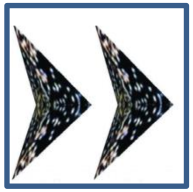
Hemelrijk, van Zuidam, Hildenbrandt, 2015, Beh Eco and SocioBio

Extensions to Stardisplay:

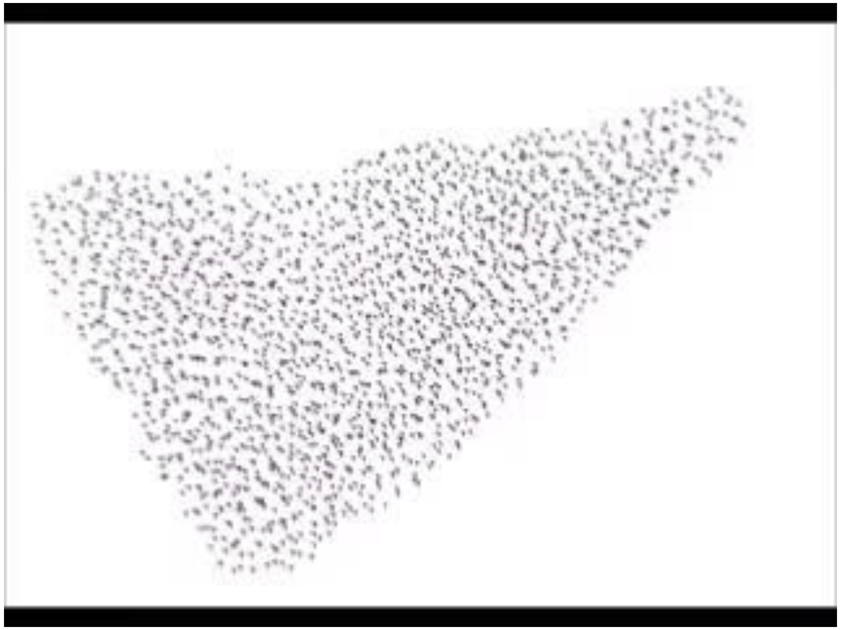
- Predator attack: escape manoeuvre
- Repetition of escape manoeuvre by neighbours
- Two escape manoeuvres
  - Speeding-up-forward into the flock (-> density wave)
  - A ‘Zig’ like escape (-> orientation wave)

Repeated speeding up manoeuvre

(Potts, 1984; Kastberger *et al* 2008)

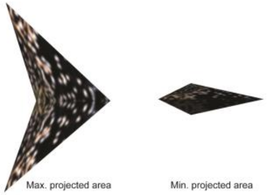


attack →

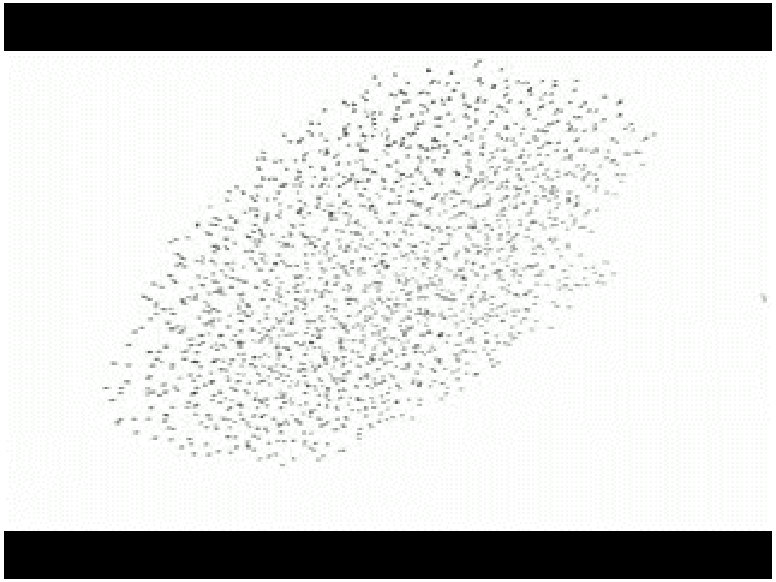


Density wave is not visible as a dark band

Repeated Zig (Rolling)



Computational model



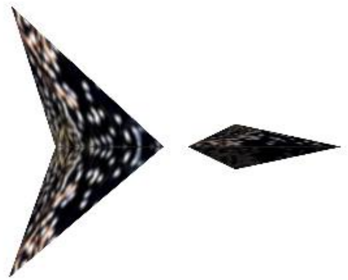
Observable orientation wave (due to great difference in surface)

Agitation wave is an orientation wave rather than density wave

Also effects of density?

Hemelrijk, van Zuidam, Hildenbrandt, 2015, Beh Eco and SocioBio

Take out effects of orientation wave:



Maximal and Minimal
projected area
Zig-manoeuvre

Starlings as balls in model

Always same projected area
Independent or orientation

In case of balls only wave of density (no of orientation) is observable

Wave of orientation: also due to density?

‘bird- shaped’ individuals

‘ball - shaped’

No wave

Agitation wave is merely orientation wave, like in dunlins and anschovies

Speed of the agitation wave

- Empirically on average 13.5 m/s (Procacini *et al* 2011)
  - Similar to cruise speed of starling (10 m/s) and to speed of falcon (11-15 m/s)
- Anticipation over large distance? Not needed
  - wave speed for transmission to nearest neighbour: = average NND / latency to react : thus 1.1m / 0.076s = 14.5 m/s

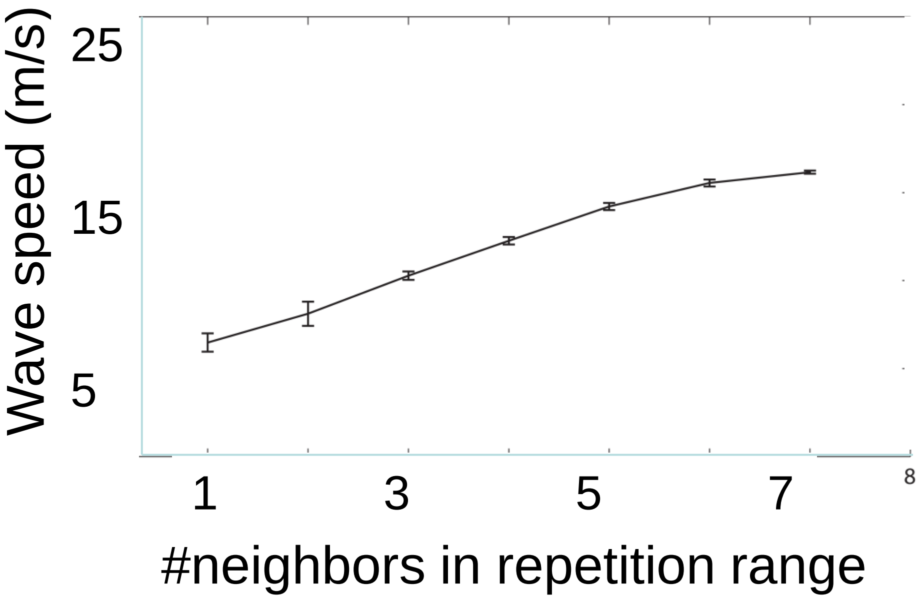
⬇

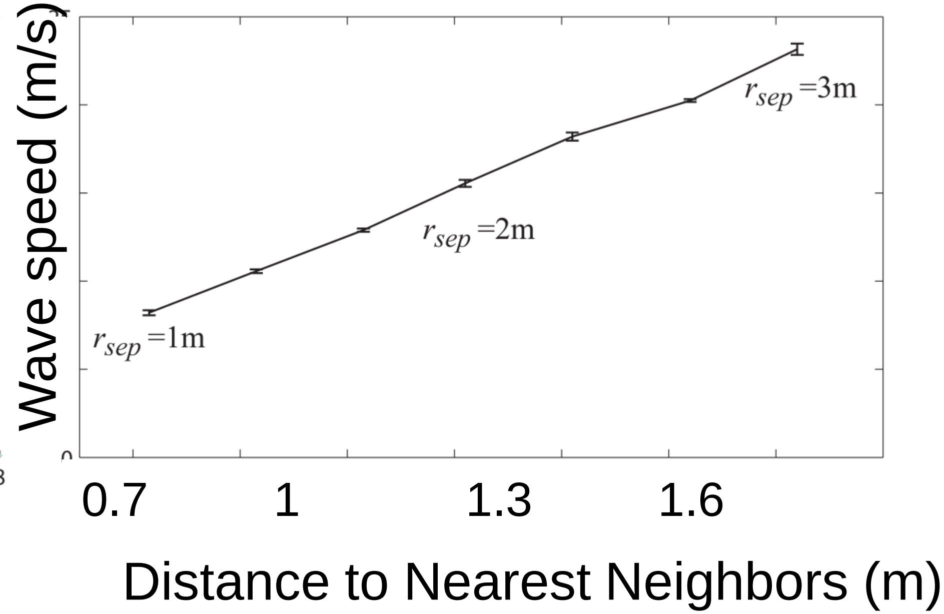
Empirical speed of wave 2-25m/s

Reproduce in model?

Speed of wave

Hemelrijk, van Zuidam, Hildenbrandt, 2015, PlosOne



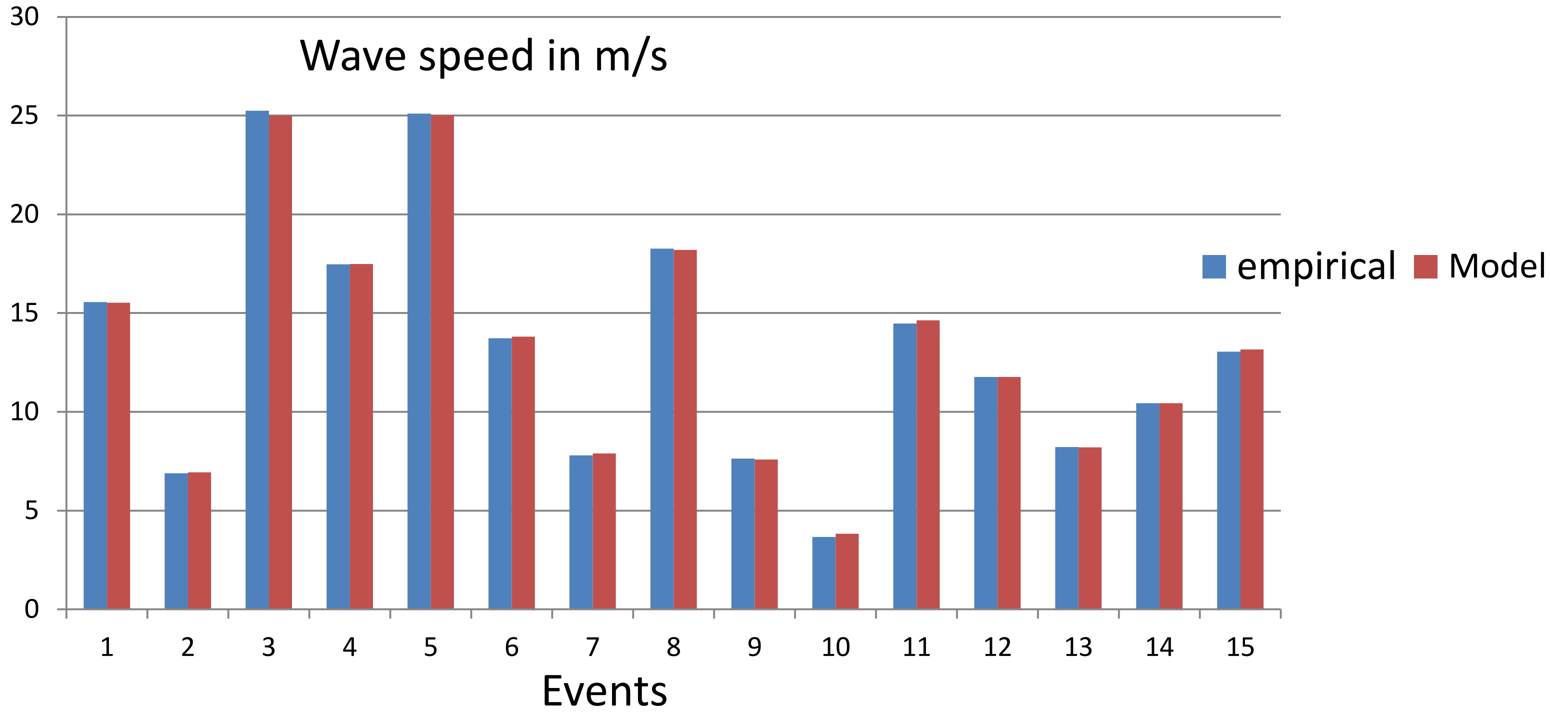


Larger number of neighbours to repeat from - > higher speed

Lower density -> faster wave

Wave speed: Model and empirical

(empirical Proccacini et al 2011, model Hemelrijk et al 2015, BESC)



For repetition range between 2-7 neighbours (without long-range anticipation) and NND between 0.71 m – 1.93m

Summary
wave of agitation in starling flocks

Individual behaviour

- Zig like behaviour -> large change in visible wing surface
- Long-range antipation is not needed, local transmittion to 2-7 closest neighbours suffices -> empirical wave speed

Hypotheses for empirical data

‚Understanding by building'

Pfeifer and Scheier 1999

Rules of local interaction

Self-organization

Complex patterns of the group

Hypotheses for empirical studies

Thanks

- Collaborators
  - Hanno Hildenbrandt (scientific programmer)
  - Claudio Carere (empirical data)
  - Lars van Zuidam (master student)
- Grants
  - Startup money Rosalind Frankin Fellowship
  - StarFlag European Framework
  - NWO pilot money
  - Gratama Foundation

Predator attacks