Northeast Journal of Complex Systems (NEJCS)

Volume 4
Number 1 *Special Issue: NERCCS 2022 Papers*

Article 1

March 2022

Bistability and Switching Behavior in Moving Animal Groups

Daniel Strömbom
Lafayette College, stroembp@lafayette.edu

Stephanie Nickerson
Lafayette College, sswimnickerson@gmail.com

Catherine Futterman
Lafayette College, cfutterman@ufl.edu

Alyssa DiFazio
Lafayette College, alyssa.difazio1@gmail.com

Cameron Costello
Lafayette College, cameroncostello71@gmail.com

See next page for additional authors

Recommended Citation

Strömbom, Daniel; Nickerson, Stephanie; Futterman, Catherine; DiFazio, Alyssa; Costello, Cameron; and Tunstrøm, Kolbjørn (2022) "Bistability and Switching Behavior in Moving Animal Groups," *Northeast Journal of Complex Systems (NEJCS)*: Vol. 4 : No. 1 , Article 1.
DOI: 10.22191/nejcs/vol4/iss1/1
Available at: https://orb.binghamton.edu/nejcs/vol4/iss1/1

Bistability and Switching Behavior in Moving Animal Groups

Authors

Daniel Strömbom, Stephanie Nickerson, Catherine Futterman, Alyssa DiFazio, Cameron Costello, and Kolbjørn Tunstrøm

Bistability and Switching Behavior in Moving Animal Groups

Daniel Strömbom[1*], Stephanie Nickerson[1], Catherine Futterman[1],
Alyssa DiFazio[1], Cameron Costello[1] and Kolbjørn Tunstrøm[2]
[1] Department of Biology, Lafayette College, Easton, PA, USA
[2] Department of Physics, Chalmers University of Technology, Göteborg, Sweden.
[*] stroembp@lafayette.edu

Abstract

Moving animal groups such as schools of fish and flocks of birds frequently switch between different group structures. Standard models of collective motion have been used successfully to explain how stable groups form via local interactions between individuals, but they are typically unable to produce groups that exhibit spontaneous switching. We are only aware of one model, constructed for barred flagtail fish that are known to rely on alignment and attraction to organize their collective motion, that has been shown to generate this type of behavior in 2D (or 3D). Interestingly, another species of fish, golden shiners, do exhibit switching but have been shown to use attraction and repulsion, not alignment, to coordinate themselves in schools. Suggesting that switching may be explained by attraction and repulsion alone, without an alignment interaction. Here we introduce a model based on attraction and repulsion only and show that groups exhibiting switching similar to that observed in experiments with golden shiners emerges. We also establish that switching occur in two boundary-free extensions of the model. Our work suggests that the bistability and switching behavior observed in golden shiners and other moving animal groups may be explained via attractive and repulsive interactions alone.

1 Introduction

Moving animal groups exhibit a variety of shapes and their dynamics vary widely. Shapes include mills, tori, balls, sheets, strings, and combinations of these [1–3]. The shape or heading of a moving group may also change in response to external environmental changes, for example, predator attacks [4–6], or spontaneously in the absence of observable external stimuli, such as in starling murmurations [7] and schools of fish [8, 9].

Self-propelled particle (SPP) models are often used to investigate how group level phenomena in moving animal groups emerges from local interactions between individuals [10–17]. The individual animals are represented by particles and these particles interact with other nearby particles, typically via some combination of attraction, repulsion and alignment. Where alignment means that particles adopt the average heading of their neighboring particles. Models of this type have successfully been used to explain a range of collective phenomena observed across taxa [10, 18] and provided a theoretical understanding of how stable groups may arise from local interactions between individuals. In particular, well known stable group types like polarized groups, mills and swarms are readily produced by a large number of models [10]. However, SPP models exhibiting spontaneous switching between group types and other disruptive phenomena remain rare. While it has been shown that varying model parameters may induce switching between shapes [9, 12, 19] examples where changes occur spontaneously without parameter changes are limited. Exceptions include a number of 1D models where noise alone has been shown to drive density dependent switching between counter-clockwise and clock-wise traffic on a ring [20, 21] and noise induced switching between stationary and polarized motion on a line [22]. In 2D (or 3D) we are only aware of one model that has been shown to exhibit any type of bistability and switching [23]. This model was originally developed for the collective dynamics of barred flagtail (*Kuhlia mugil*) fish and is based on attraction and alignment, due to the fact that these fish were found to rely on these two interactions to organize their shoaling in experiments [24].

Tunstrøm et al. 2013 describe experiments with groups of 30-300 golden shiner (*Notemigonus crysoleucas*) fish that spontaneously switch between milling and polarized motion. The local interactions that golden shiners rely on to organize their schools have also been inferred from trajectory data and the authors report that attraction and repulsion are operating, but find no evidence for alignment interactions [25]. Suggesting that bistability and switching may be explained not only via a combination of attraction and alignment [23], but potentially also from attraction and repulsion alone. Establishing this would show that bistability and switching is more readily reproducible from standard local interactions than previously thought and contribute to improve our understanding of this phenomenon, and potentially other disruptive phenomena, observed in moving animal groups.

2 Model and Methods

Here we start from the attraction-repulsion model presented in [26] and remove the global attraction term. Each particle moves in the plane and updates its headings depending on the positions of its neighbors. The neighbors of a particle are all other particles within a distance of R from it. However, particles located in a blind zone behind the particle relative to the direction of travel specified by the angle β are excluded when calculating attractive forces, but included when calculating repulsive forces. We use hat notation to denote normalized vectors and bar notation to denote vectors of arbitrary length. Particle i's heading in the next time step $(t+1)$, denoted by $\hat{D}_{i,t+1}$, is a linear combination of its normalized current heading $\hat{D}_{i,t}$ in the current time step (t), the normalized direction towards the local center of mass of its neighbours excluding those in the blind zone $\hat{C}_{i,t}$, a local distance dependent repulsion term $\bar{F}_{i,t}$, and a heading noise term $\hat{\epsilon}_{i,t}$.

$$\bar{D}_{i,t+1} = d\hat{D}_{i,t} + c\hat{C}_{i,t} + r\bar{F}_{i,t} + e\hat{\epsilon}_{i,t}. \tag{1}$$

For a more detailed description of each of these terms see [26]. The parameters d, c, r and e represents the relative strength of the corresponding interaction term. Once the heading for all particles have been calculated the new position for each particle i, denoted by $\bar{P}_{i,t+1}$, is updated via the formula

$$\bar{P}_{i,t+1} = \delta \Delta t \hat{D}_{i,t}, \tag{2}$$

where δ is the speed of the particle and Δt is the time step.

First we study this model when particle motion is restricted to a bounded rectangular region to mimic the golden shiner experiments described in [9]. When a particle is not in contact with the boundary it updates its heading according to Eq 1, and when it is in contact with the boundary (i.e. its next move would take it outside the rectangular region) it adjusts its heading to be parallel to the boundary in the direction that requires the least amount of turning from its previous heading (slip boundary conditions).

Then we study adaptations of this model in two boundary-free situations. One where particles experience a weak attraction to a fixed point (roosting site model), and another where particles have a weak preference for traveling in a particular direction (migration model). The main difference between these and the model described above is that the boundaries have been removed and additional terms have been added in the heading update formula. The roosting site model contains an additional weak linear attraction to the origin (roosting site) $h\bar{H}_{i,t}$ and the heading update formula is given by

$$\bar{D}_{i,t+1} = d\hat{D}_{i,t} + c\hat{C}_{i,t} + r\bar{F}_{i,t} + h\bar{H}_{i,t} + e\hat{\epsilon}_{i,t}. \tag{3}$$

The migration model contains an additional constant migration direction term $m\hat{M}$ that is shared by all particles and a weak linear attraction term to the global center of mass of the group $gG_{i,t}$. The migration direction term is given by $\hat{M} =$

$[1/\sqrt{2}, 1/\sqrt{2}]$ and the heading update formula becomes

$$\bar{D}_{i,t+1} = d\hat{D}_{i,t} + c\hat{C}_{i,t} + r\bar{F}_{i,t} + g\bar{G}_{i,t} + m\hat{M} + e\hat{\epsilon}_{i,t}. \tag{4}$$

2.1 Measures

To quantify the group structures present in the simulations we use the same two group level measures as in [9]. The polarization

$$O_p = \frac{1}{N}\left|\sum_{i=1}^{N} \hat{D}_{i,t}\right|,$$

where N is the total number of particles and $\hat{D}_{i,t}$ is the current heading of particle i. The rotation (or normalized angular momentum)

$$O_r = \frac{1}{N}\left|\sum_{i=1}^{N} \hat{D}_{i,t} \times \hat{V}_{i,t}\right|,$$

where $\hat{V}_{i,t}$ is the normalized vector from the center of mass of all particles towards particle i. Polarized groups will exhibit high O_p and low O_r, whereas milling groups will exhibit low O_p and high O_r. More specifically, in an idealized polarized group $O_p = 1$ and $O_r = 0$, and in an idealized milling group $O_p = 0$ and $O_r = 1$.

2.2 Simulations

Mimicking the experiments in [9] we performed simulations for each of the group sizes 30, 70, 150 and 300 in a bounded region of size 105×60 units of length. Each simulation was 252000 time steps long, which is equal to 3360 units of time with time step 1/75, and we identify the unit of time with one second making both simulations and the experiments in [9] 56 minutes long to facilitate comparison of the two. For each group size four replicates were performed, and at the start of each simulation each particle was assigned a random heading and a random position in near the center of the bounded region. Motivated by the findings in [26] the parameters used here were $d = c = r = 1$, $\beta = \pi$, $e = 1/5$, $R = 6$, $\delta = 10$, $\Delta t = 1/75$. For the migration and roost site models we ran three 100000 time step (or 22 minutes) long simulations each for group sizes 30, 70, 150 and 300. The parameters used were identical to those used in the bounded region with $h = 0.0025$ added in the roost site simulations and $m = 0.0001$ and $g = 0.0025$ added in the migration simulations. On each time step in all simulation, after a 2000 time step warm up period, we collected the positions and headings of the particles so that the polarization O_p and rotation O_r of the collective of particles could be calculated subsequently.

2.3 Analysis

To analyze the simulations in the bounded region we followed [9] and created a density plot over a 30×30 grid by pooling all recorded (O_p,O_r) values over all four replicates for each group size. We also calculate a 10 second rolling average of the O_p and O_r measurement over 67500 time steps (15 minutes) for each group size to display the time evolution of these measures in simulations. To analyze the simulations from the roosting and migration model we followed the same approach as in the bounded region except that we only included the (O_p,O_r)-value from particles in the largest subgroup present at a given time in the simulation. This was done to reduce noise in the measures induced by the group split and merge behavior that is common in the roosting site simulations and, to a lesser degree, in the migration simulations. The largest subgroup was defined to be the largest connected component in the interaction network defined by the adjacency matrix A where $A(i, j) = 1$ if particles i and j are within a distance of R from each other and $A(i, j) = 0$ otherwise. See the Supplementary Information section for how to access the code required to perform simulations and analysis to replicate all results in this manuscript.

3 Results

The bistability and switching behavior generated by the model share several features with the golden shiner data (See Fig. 1). Figures 1AB shows the two types of groups that emerge in the simulations, polarized groups (A) and milling groups (B), and for all group sizes we observe switches between these two group types. Figures 1CD shows the time evolution of the order parameters over 15 minutes in the simulations (Fig. 1C) and in the experiments (Fig. 1D) with 30, 70, 150 and 300 particles/fish. We observe several switches back and forth between milling and polarized motion in both the experiments and the simulations. See Supplementary Movies 1-4 for examples of this switching behavior in simulations, and Video S1-S4 in [9] for switches in the golden shiner experiments. Figures 1EF shows density plots of the (O_p, O_r) values in the experiments (Fig. 1F) and in the corresponding simulations (Fig. 1E). We note that the amount of polarized motion relative to milling decreases with group size in both experiments and simulations.

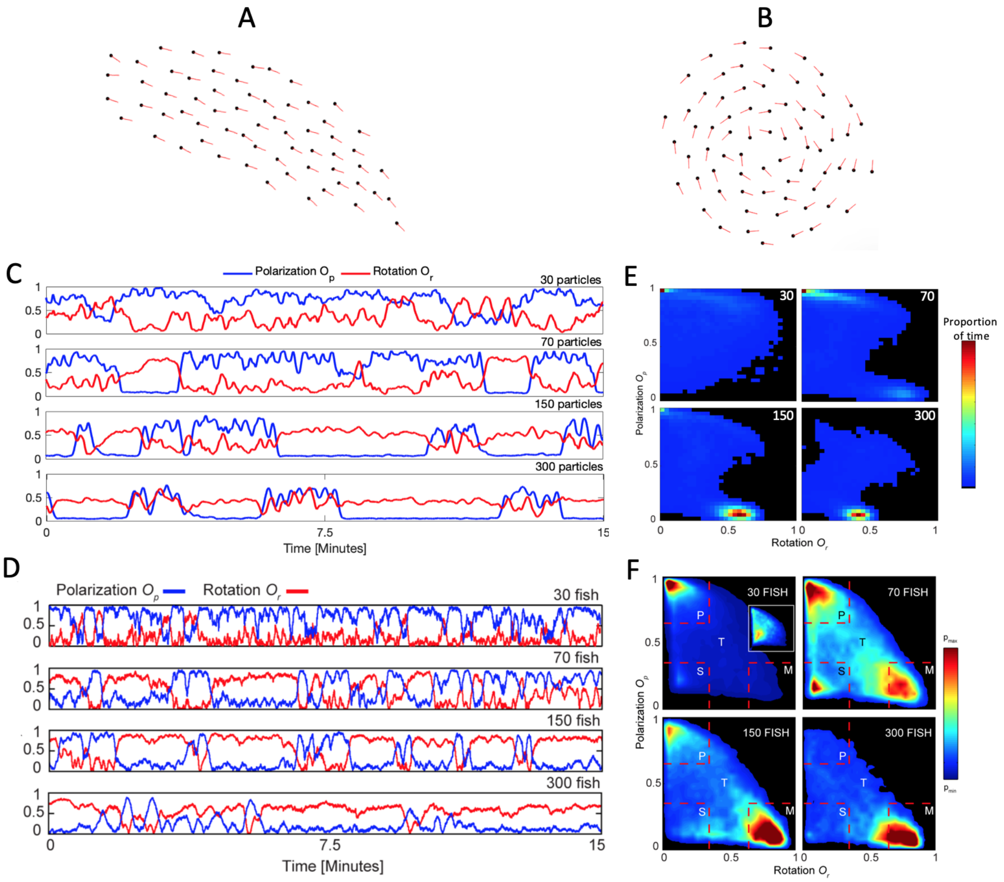

Figure 1: Bistability and switching in the experiments and simulations. (AB) Snaphots of a polarized group (A) and a mill (B) from a simulation. Black dots represent the particle positions and the red rods indicate the current heading of the particles. Note that in a polarized group (A) the polarization measure O_p will be high and the rotation measure O_r low, whereas a mill will have O_r high and O_p low. (C) Time evolution of the order parameters in simulations. (D) Time evolution of the order parameters in the experiments. In both experiments and simulations there are switches between polarized motion (O_p large and O_r small) and milling (O_p small and O_r large) and the proportion of milling seems to increase with group size. (E) Density plots of the order parameters in simulations. (F) Density plots of the order parameters in simulations. In both the experiments and simulations the group of 30 fish/particles spend almost all of its time in a polarized state (O_p large and O_r small), the group of 300 fish/particles spend almost all of its time in a rotating state (O_p small and O_r large), and the intermediate groups (70 and 150) show clear evidence of bistability with a significant amount of time spent in a polarized state and in a milling state. Panels (D) and (F) are from [9] (Tunstrøm et al. CC-BY). The P, S, and M markings in (F) illustrate the regions considered to correspond to polarized, swarm, and mill configurations, respectively, and the inset in the 30 fish panel shows the result when fish are moving in an arena 1/10 the size of the original. See [9] for details.

Groups exhibiting bistability and switching is generated in both the roosting site model and the migration model (Fig. 2). In the migration model simulations (Fig. 2AC) we note that while switches do occur they are rare in the smaller groups that spend almost all of the time in a polarized state, and only in the largest group of 300 particles does clear bistability between milling and polarized motion emerge. In the roost site simulations (Fig. 2BD) we see that while there are switches in the 30 and 70 particle groups (Fig. 2B) clear bistability is only observed in the group of 150 particles (Fig. 2D). Similarly, while we see that weak switching behavior do take place in the large 300 particle group (Fig. 2B) it does not reach more than intermediate polarization values before returning to milling and the density plot (Fig. 2D) confirms that the 300 particle groups in the roosting site model spend almost all their time in the milling state.

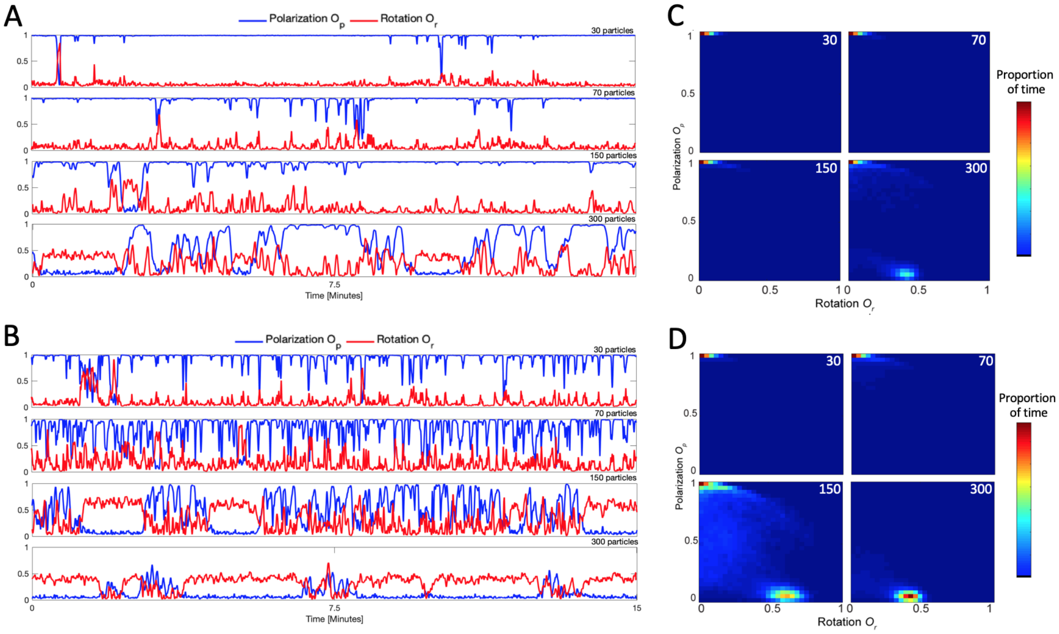

Figure 2: Bistability and switching in the migration and roost site simulations. (AC) Time evolution (A) and density plots (C) of the order parameters in simulations of the migration model. (A) shows that there are, at least brief, switches for all group sizes, but only for the largest group of 300 particles is bistability apparent in (C). (BD) Time evolution (B) and density plots (D) of the order parameters in simulations of the roosting site model. (B) shows that there is switching like behavior for all group sizes, but only for the group of 150 particles is there clear bistability in (D).

4 Discussion

Despite the fact that moving animal groups frequently switch between group types, the main theoretical tool (SPP models) used to explain how stable groups form have rarely been shown to generate such switches or other disruptive phenomena. Suggesting that our understanding of these phenomena, and thus collective motion in general, is incomplete. The only model in 2D or 3D that we are aware of that has been shown to generate bistability and switching is a model for barred flagtail fish that rely on attraction and alignment for their collective motion. However, golden shiner fish also exhibit bistability and switching, but this species has been shown to rely on attraction and repulsion, not alignment, to coordinate their schools. Suggesting that bistability and switching might be reproduced using only attraction and repulsion, excluding alignment. Here we implemented an attraction-repulsion only model to investigate.

Our finding that attraction and repulsion alone are sufficient to produce bistability and switching in a bounded region similar to that observed in the golden shiner experiments [9] is important not only because it provides an explanation for this phenomenon in golden shiners and potentially other animals that do not rely on alignment, but also because it adds another dimension to the finding that the full set of standard interactions (attraction, repulsion and alignment) are not required to generate bistability and switching. Attraction and alignment is sufficient in [23] and attraction and repulsion is sufficient here. This is potentially interesting in relation to the ongoing discussion regarding the role of alignment interactions in collective motion [15,17,27]. We now know of several mechanisms that can induce polarized collection motion in combination with repulsion and/or attraction without explicit alignment interactions, for example, burst-and-glide [17], asynchrony [27], anticipation [28,29] and asymmetric interactions [15,30,31]. This suggests that it may be possible to replace the alignment in [23] by a lower-level combination of alignment-free interactions and one, or more, polarization inducing mechanisms. Given that it already contains attraction, a blind zone, and asynchrony via stochasticity, we speculate that it might be re-parameterized into an alignment-free model that is still able to generate bistability and switching. Work in this direction could contribute to the identification of a minimal set of interactions and drivers required to generate bistability and switching, and potentially other disruptive phenomena, in animal groups beyond the two species of fish mentioned here. In addition, given that some authors have argued that using explicit alignment to explain collective phenomena in many animals may be problematic [15, 17, 26–28] an explanation for disruptive phenomena that does not rely on this interaction may be preferable in some cases.

We also show that groups exhibiting switching and bistability emerge in two boundary-free versions of our model and thereby establish that boundary interactions are not required to generate this type of behavior. In particular, the 300 particle group in the migration model simulations shows frequent switching between milling and polarized motion (Fig. 2A) and the corresponding density plot (Fig. 2C) confirms that there is indeed proper bistability in this case. Similarly, the 150 particle group confirms that there is frequent switching (Fig. 2B) and that proper bistability emerges (Fig. 2D) in the in the roost site model. Interestingly, both of these boundary-free models show the same trend as the bounded region model (Fig. 1AC) and the data (Fig. 1BD) in that polarization relative to milling tend to decrease with group size. Suggesting that this is a generic feature of the model and possibly in golden shiner schools and other natural systems.

During most of their history it was not known whether groups exhibiting bistability and switching could be generated using SPP models. Some authors even suggested that they might not be able to because the perturbations required to propagate through a group to give rise to such a distruptive phenomenon would be dampened out by the averaging of interactions that takes place in most SPP models [25], or by the alignment interactions included in many models [26]. Our work here combined with [23] shows that not only can disruptive phenomena like switching be generated using models of this type, it is readily produced in different models. This leads us to suspect that the capacity of SPP models with standard interactions to generate disruptive phenomena may have been underestimated, and that pursing this further might yield a new wave of SPP model work that may be as successful in providing explanations for disruptive phenomena exhibited by moving animal groups as traditional SPP approaches have been in explaining the emergence of stable groups.

Supplementary Materials

Movies showing simulations for all group sizes may be found here
https://www.youtube.com/playlist?list=PLqRVmqerj1FXCN3GtQ6cHTelq2LHdtCTP.
All the code needed to replicate the results in this manuscript may be found here
https://github.com/danielstrombom/bistability

References

[1] Shaw E. Schooling fishes: the school, a truly egalitarian form of organization in which all members of the group are alike in influence, offers substantial benefits to its participants. American Scientist. 1978;66(2):166–175.

[2] Newlands NK. Shoaling dynamics and abundance estimation: Atlantic bluefin tuna (Thunnus thynnus). University of British Columbia; 2002.

[3] Heppner FH. Avian flight formations. Bird-Banding. 1974;45(2):160–169.

[4] Procaccini A, Orlandi A, Cavagna A, Giardina I, Zoratto F, Santucci D, et al. Propagating waves in starling, Sturnus vulgaris, flocks under predation. Animal behaviour. 2011;82(4):759–765.

[5] Herbert-Read JE, Buhl J, Hu F, Ward AJ, Sumpter DJ. Initiation and spread of escape waves within animal groups. Royal Society open science. 2015;2(4):140355.

[6] Romenskyy M, Herbert-Read JE, Ioannou CC, Szorkovszky A, Ward AJ, Sumpter DJ. Quantifying the structure and dynamics of fish shoals under predation threat in three dimensions. Behavioral Ecology. 2020;31(2):311–321.

[7] King AJ, Sumpter DJ. Murmurations. Current Biology. 2012;22(4):R112–R114.

[8] Lecheval V, Jiang L, Tichit P, Sire C, Hemelrijk CK, Theraulaz G. Social conformity and propagation of information in collective U-turns of fish schools. Proceedings of the Royal Society B: Biological Sciences. 2018;285(1877):20180251.

[9] Tunstrøm K, Katz Y, Ioannou CC, Huepe C, Lutz MJ, Couzin ID. Collective states, multistability and transitional behavior in schooling fish. PLoS Comput Biol. 2013;9(2):e1002915.

[10] Vicsek T, Zafeiris A. Collective motion. Physics Reports. 2012;517:71–140.

[11] Vicsek T, Czirók A, Ben-Jacob E, Cohen I, Shochet O. Novel type of phase transition in a system of self-driven particles. Physical review letters. 1995;75(6):1226.

[12] Couzin ID, Krause J, James R, Ruxton GD, Franks NR. Collective memory and spatial sorting in animal groups. J Theor Biol. 2002;218:1–11.

[13] Strömbom D. Collective motion from local attraction. J Theor Biol. 2011;283:145–151.

[14] Romanczuk P, Schimansky-Geier L. Swarming and pattern formation due to selective attraction and repulsion. Interface focus. 2012;2(6):746–756.

[15] Barberis L, Peruani F. Large-scale patterns in a minimal cognitive flocking model: incidental leaders, nematic patterns, and aggregates. Physical review letters. 2016;117(24):248001.

[16] Romenskyy M, Herbert-Read JE, Ward AJ, Sumpter DJ. Body size affects the strength of social interactions and spatial organization of a schooling fish (Pseudomugil signifer). Open Science. 2017;4(4):161056.

[17] Strömbom D, Tulevech G. Attraction vs. Alignment as Drivers of Collective Motion. Front Appl Math Stat. 2022;(7:717523).

[18] Ward A, Webster M. Sociality: the behaviour of group-living animals. Springer; 2016.

[19] Paley DA, Leonard NE, Sepulchre R, Couzin ID. Spatial models of bistability in biological collectives. In: Decision and Control, 2007 46th IEEE Conference on. IEEE; 2007. p. 4851–4856.

[20] Buhl J, Sumpter DJ, Couzin ID, Hale JJ, Despland E, Miller ER, et al. From disorder to order in marching locusts. Science. 2006;312(5778):1402–1406.

[21] Yates CA, Erban R, Escudero C, Couzin ID, Buhl J, Kevrekidis IG, et al. Inherent noise can facilitate coherence in collective swarm motion. Proceedings of the National Academy of Sciences. 2009;106(14):5464–5469.

[22] Kolpas A, Moehlis J, Kevrekidis IG. Coarse-grained analysis of stochasticity-induced switching between collective motion states. Proceedings of the National Academy of Sciences. 2007;104(14):5931–5935.

[23] Calovi DS, Lopez U, Ngo S, Sire C, Chaté H, Theraulaz G. Swarming, schooling, milling: phase diagram of a data-driven fish school model. New journal of Physics. 2014;16(1):015026.

[24] Gautrais J, Ginelli F, Fournier R, Blanco S, Soria M, Chaté H, et al. Deciphering interactions in moving animal groups. Plos computational biology. 2012;8(9):e1002678.

[25] Katz Y, Tunstrøm K, Ioannou CC, Huepe C, Couzin ID. Inferring the structure and dynamics of interactions in schooling fish. Proceedings of the National Academy of Sciences. 2011;108(46):18720–18725.

[26] Strömbom D, Siljestam M, Park J, Sumpter DJ. The shape and dynamics of local attraction. The European Physical Journal Special Topics. 2015;224(17-18):3311–3323.

[27] Strömbom D, Hassan T, Hunter Greis W, Antia A. Asynchrony induces polarization in attraction-based models of collective motion. Royal Society open science. 2019;6(4):190381.

[28] Strömbom D, Antia A. Anticipation Induces Polarized Collective Motion in Attraction Based Models. Northeast Journal of Complex Systems (NEJCS). 2021;3(1):Article2.

[29] Murakami H, Niizato T, Gunji YP. Emergence of a coherent and cohesive swarm based on mutual anticipation. Scientific Reports. 2017;7.

[30] Romanczuk P, Couzin ID, Schimansky-Geier L. Collective motion due to individual escape and pursuit response. Physical Review Letters. 2009;102(1):010602.

[31] Peruani F. Hydrodynamic equations for flocking models without velocity alignment. Journal of the Physical Society of Japan. 2017;86(10):101010.