

Collective Motion of Animals: Recent Findings From Field Study and Model Experiments

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Abstract

Collective motion is ubiquitous in nature on all scales, from flocking birds, schooling fishes, to swarming bacteria. Traditionally, understanding of such phenomena is achieved through modeling and simulation. Recently, with advanced imaging techniques and particle tracking algorithms, spatiotemporal data of large quantity of individuals inside a group become available from field studies. From detailed analysis of these data, interactions between individuals are unveiled, which differ largely from previous assumptions. Meanwhile, model experiments on artificial system are performed to controllably study the collective motion. In this review, I will summarize key results from these recent findings, along with simulations that incorporate these new ingredients.

Introduction

Collective motion of animals is one of the most spectacular scenes in the nature. Common examples include a flock of homing birds, a school of swirling fish, or a 10 meter trail of ants. These group behaviors emerge spontaneously from interacting individuals, providing the most vivid examples of emergent phenomena.

This interests scientists for long time. The first group of people studying such phenomena are biologists, who used to provide functional explanations. From this point of view, the collective motion of animals gives individuals inside the flock (the word "flock" will be used in this paper to generally refer to a group of collectively moving objects) many evolutionary advantages, such as better protection from predators, higher chance of finding food, and more mating opportunities [1].

But such explanation does not allow quantitative description, and hence prediction on the flocking behavior. So here comes the physicists, who are mechanistic in nature. The question they raise are: How individuals interact with each other inside a flock? How the individual-individual interaction gives rise to a global phenomena? What are the parameters that control such behaviors? After the seminal model proposed by Vicsek [2], numerous simulation works are done to reveal the origin of collective motion. Indeed, by making analogy with what we learned in equilibrium statistical mechanics, such models can successfully reproduce the abrupt, phase-transition-like dependence of group behavior on key parameters, such as population density or external pressure.

Yet the two communities seem to rarely communicate, until recently. The problem for the physical model is that the interaction one put into the simulation does not represent what really happens in nature. Different interactions could often result in the same collective behavior, making it difficult to differentiate which one is better. On the other hand, the biology community is mainly hampered by technical difficulties in tracking large quantities of animals, with sufficient resolution, size, and time to allow statistical analysis. Thanks to the rapid development in imaging technologies and algorithms for particle tracking, significant progress has been made these years. Several important findings, which will be the focus of this review, come out from the collaborative efforts of biologists and physicists on analyzing these new data.

This paper is structured as follows: first, a very brief review is given on Vicsek's self-propelling particle (SPP) model and its variations, to give readers a theoretical background. Then, major findings from quantitative field studies will be discussed in detail. Next, man-made experimental models, which are designed to mimic the natural system but with much larger control, will be reviewed. A brief summary and perspective is given at the end.

Models

In the classic simulation paper of SSP model [2], Vicsek *et al.* used a very simple rule to mimic the animal behavior in the flock: at each time step a particle will assume a velocity, with constant magnitude v_0 but orientation determined by the average direction of motion of its neighboring particles within a radius R , plus a random perturbation η :

$$\vec{v}_i(t+1) = v_0 \frac{\langle \vec{v}_j(t) \rangle_R}{|\langle \vec{v}_j(t) \rangle_R|} + \eta; \quad \vec{x}_i(t+1) = \vec{x}_i(t) + \vec{v}_i(t+1)$$

This rule captures the essence of flocking behavior: individuals tend to align with each other in the flock. The cut-off radius R reflects the limited sensing ability of the individual. The random noise reflects the inaccuracy of the animals in determining the surrounding information or making adjustment to the information. The two key parameter here are ρ , individual density, and η . Using the absolute value of averaged normalized velocity $\frac{1}{Nv_0} \left| \sum_{i=1}^N \vec{v}_i \right|$ as the order parameter, the simple Vicsek model predicts a second-order phase transition in such system in 2D. In the ordered phase, particles move coherently in the same, randomly selected direction, similar to the flocking phenomena.

The simplicity of the Vicsek model belies the rich phenomena it can generate. Since the first publication, many variations on the original rule have been tested. Interested readers are directed to a comprehensive review written by Vicsek [3]. A noticeable (and justified) trend in recent simulations is to incorporate more biologically relevant potentials. For example, inspired by the cannibal behavior in some mass migrating insects (locust and cricket, for example [4]), Romanczuk *et al.* recently studied the noncollaborative but collective motion due to individual escape and pursuit response [5]. As seen in Figure 1, the "pursuit interaction" tends to make system more heterogeneous, and collective moving groups emerge regardless of the density. In contrast, the "escape interaction" homogenizes the system and results in a second-order phase transition. The pursuit + escape case shows a mixed behavior, where flocks can spontaneously divide and reunion. The behavior of natural flock should lie between the two extremes: for cannibal animals, the escape interaction would dominate, whereas for nonaggressive individuals with limited sensory abilities, the pursuit (following) behavior will dominate.

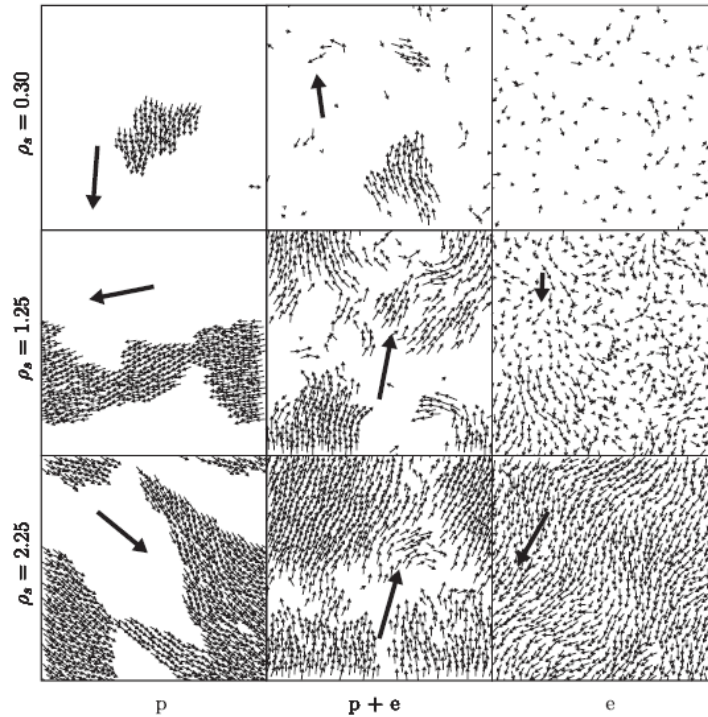


Figure 1. Typical spatial configuration for pursuit-only (p), pursuit + escape (p + e), and escape-only (e) interaction at different particle density in simulation. Large arrows indicated the mean migration direction and speed.

Another development is to take into account the shape anisotropy of the animals. The simplest case is rod, which can be polar (move in one direction) or nonpolar (move in either direction) [6]. Surprisingly, the two motions result in completely different collective phenomena, which will be detailed in later session.

However, if these studies are aimed at describing the real behavior of flocking animals instead of presenting an interesting cause of their own, the most serious problem still lies in the legitimacy of the interaction one uses in the simulation. For example, in order to introduce cohesion, an exponential or power law attraction towards the group center of mass is usually introduced, which cannot be obviously justified. If one considers the sensory anisotropy of typical animals, the isotropic alignment rules is not a good description either. Even for simple bacteria that interact passively, mimicking it with a polar rod is not enough, because they experience hydrodynamic interactions instead of just hard core repulsion [7]. Hence, to truly reflect the agent-agent interaction in nature, real measurement has to be done, as discussed in the next session.

Field Study

The field study of flocking behavior remains qualitative for a long time, due to the difficulty in data acquisition. First, imaging is not easy in many situations. For example, large scale tracking of fish schools, which is perhaps the most economically important task in the field, becomes possible only recently [8]. Second, to reconstruct trajectories of thousands of fast moving objects in 3D with sufficient long time represents a major difficulty in computer programming, and currently, it is still impossible to do it with satisfactory accuracy.

It might be argued that one could construct the bird-bird or fish-fish interaction by studying the behaviors of two isolated individuals. But this is not true. Animals behave differently when separated or inside a group. For example, locust remain solitary (noninteracting) if the whole group does not pass the critical density to a devastating gregarious state [9]. Study also shows that behavior observed in small groups cannot be simply extended to larger groups. Stated otherwise, the agent-agent interaction might not be rooted in the individual, but only manifest itself in the flocking state. Therefore, one has to infer the interaction rules from observation and measurement of real flocks. This situation is analogous to reconstruct a potential of mean force in a dense suspension of colloidal particles, where hydrodynamics and caging effect make the interaction nonadditive. Only by reconstructing the real agent-agent interaction could we correctly model the animal behavior.

An important breakthrough is made in 2008 by StarFlag, a team composed of many European biologists, statistical physicists, and computer scientists [10]. They used stereo photograph to record the motion of flocks of up to 2600 European Starlings, and reconstructed the 3D position of individual birds in the flock. The sample size is almost two orders of magnitude of previous studies. At that time, tracking of individual trajectory is not achieved so bird-bird interaction can only be inferred from static distribution (see Figure 2 for a snapshot).

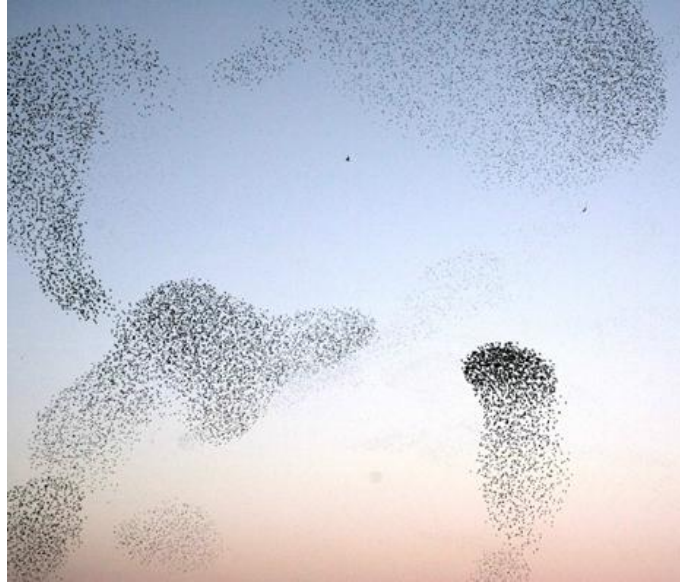


Figure 2. A typical example of starling aerial display, taken from [10]. Various flocks, ranging from several hundreds to thousands birds, wheel and turn above the roosting site.

The question they addressed in the first paper is how flocks maintain strong and robust cohesion. In simulations, it is usually done by putting an attraction that decays with some characteristic length scale. This is not true in nature, as they showed: the interaction depends on topological rather than metric distance. In other words, two birds 5m away interact as strongly as 1m away, provided that they are nearest neighbors, topologically.

To prove this, first they plotted radial distribution of flocks, much like what one did in liquid theories. Strong anisotropy was observed: there is striking lack of nearest neighbors along the direction of motion. The starlings seem to try to avoid collision with other starlings, which happens easiest along the direction of motion. Then, they mapped the decay of the anisotropy as a function of distance. The decay curve is different in flocks with different density; but if one rescaled it with topological distance, they fall on the same curve, with a cutoff distance of 6-7 neighbors. This cutoff value, as speculated, is a compromise between the bird's high sensory ability and its low information processing ability.

Why topological-distance-dependence? By simulation, the team showed that flocks with this dependence are more robust towards outside perturbation, typically the presence of predators. As can be seen from Figure 3, topological-distance-dependent flock remains as single cluster after the approaching of a predator; even if it does split, the cluster reforms behind the predator. On the contrary, the metric counterpart will split to leave a few solitary individuals, which are vulnerable to predators. This finding also rules out some of the common explanations on flocking behavior based on aerodynamics, which are not consistent with the topological dependence.

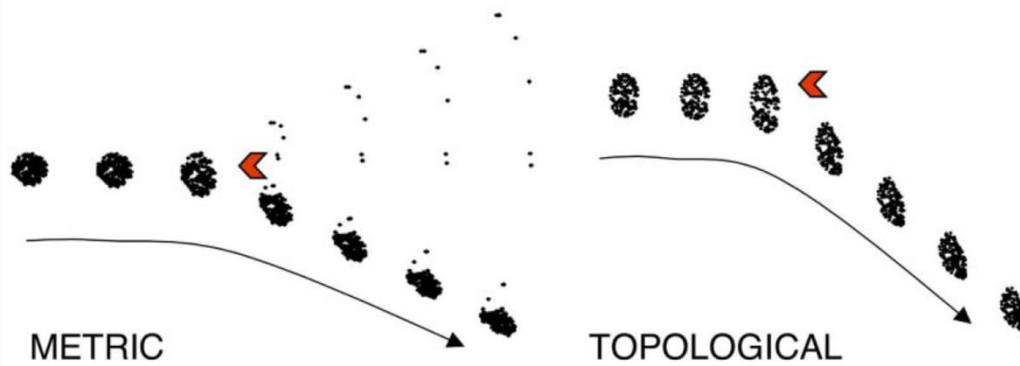


Figure 3. Simulation on the response towards predators of different kinds of flocks. Red arrows represents the approaching predator.

Subsequent simulation of the topological variation of Vicsek model showed qualitative difference with previous models [11]. There is no true long range order with this dependence; also no density segregation because local density and local order are no longer coupled. These results show the importance of the correct input to model animal behaviors, and leave other assumptions in traditional SPP models also questionable.

The next major step they take [12] is to answer this question: what point in the phase space is the flock state? The technology advance that makes this possible is a dynamical matching technique that allows them to reconstruct birds trajectories to certain accuracy. The order parameter, defined the same way as in Vicsek model, is very high, as expected from Figure 4A. Then, they calculated the correlation of fluctuation of velocity from the mean (Figure 4B), as a function of distance. The correlation length is, surprisingly, not a constant, but depends on the size of the flock. This means the correlation is essentially scale-free, and the asymptotic correlation function is a power law, with very low exponent.

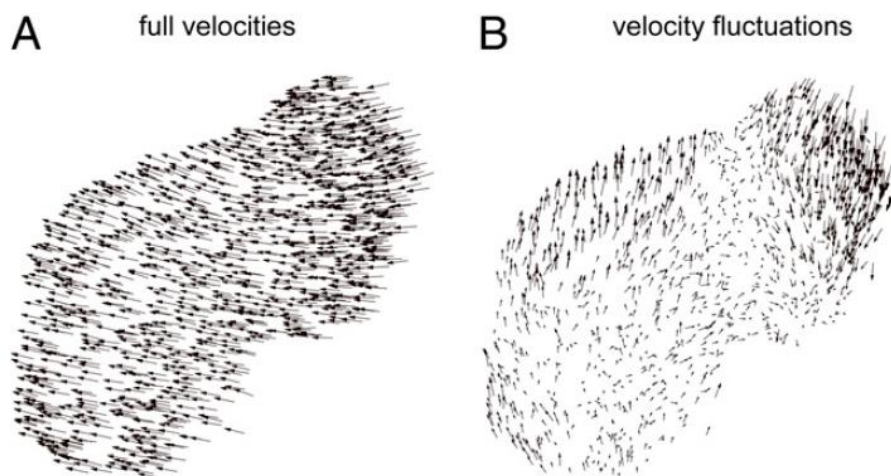


Figure 4. (A) 2D projection of the velocities of the individual birds within a starling flock at a fixed instant of time. (B) 2D projection of the individual velocity fluctuations in the same flock at the same time.

In analogy with phase-transition theories, they suggest that flocks maintain themselves at the critical state, where a power law decay of correlation is most often seen. In this state, information (velocity fluctuation) of one individual is easily transmitted to all individuals inside the flock, maximizing the response of the flock towards possible external perturbation (the appearance of a predator or a food source). Indeed, from a functional point of view, they argued that what a collectively moving animal group trying to maximize is not order, but response. In this respect, it is easy to understand the observation: at the critical point, the susceptibility of a system is at maximum, while order would keep increasing even after passing the critical point. Similar observation is also made in neural networks [13], so it remains to be explored whether this is just a coincidence or a general rule in nature. It is interesting to observe how the system really responds to a perturbation, such as a falcon. Indeed, qualitative observations have been made on how a collective group responds to predators, such as a fish school to a sea lion [14]. Quantitative measurement should give us deeper understanding at this point.

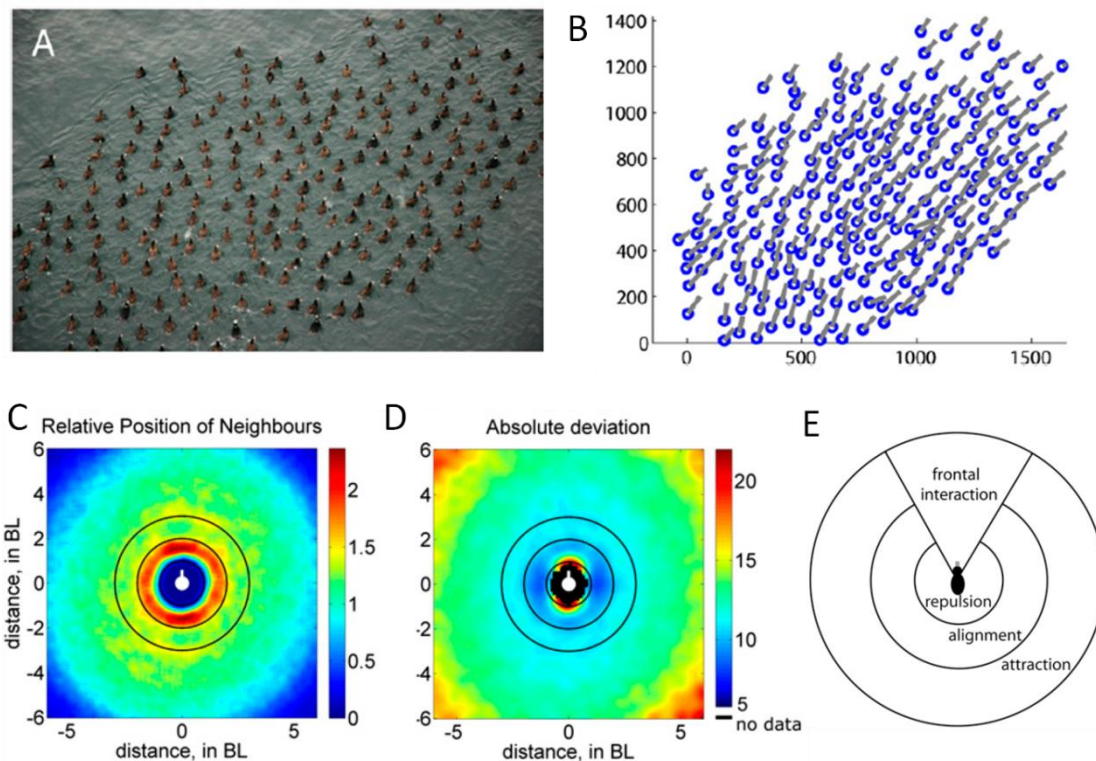


Figure 5. (A) A typical flock of surf scoter moving on the water surface. (B) The same group of duck, after tracking and correction for perspective and transformation to "real" positions. Blue circles represent the position of individual ducks. Gray lines represent their velocities. (C) Density maps for position (C) and orientation (D) of neighbors relative to a typical individual. (E) Schematics of the different interaction zones inferred by matching models to data.

In the same spirit, Lukeman *et al.* recently reconstructed in detail the interaction among collectively swimming surf scoters (Figure 5) [15]. In the extracted radial distribution and angular distribution (Figure 5C and 5D), one can clearly identify three zones: a short-range strongly repulsive zone, an intermediate-range alignment zone, and a long-range weakly attractive zone (Figure 5E). The first zone acts to prevent ducks from colliding, the second zone

aligns the ducks so that the group moves in the same direction, and the final one provides the cohesive force. Both the first and second zone are highly anisotropic: probability of finding a nearest neighbor in the first shell is higher along the direction of motion, which is just the opposite of the results observed in Starlings. Here, the duck is trying to follow the one in front it closely, possibly to take hydrodynamic advantage. The collision problem is less severe for this slowly moving creature, and it is partially solved by the coupling between position and orientation: alignment in the second zone is stronger for ducks left or right to each other than from the front or behind. The authors then went on to perform simulations and proved that, in order to reproduce the observed distribution, one has to incorporate all these three zones.

These recent findings gave us much deeper understanding of the inter-agent interaction in natural flocking system. Yet, interactions seem to vary from species to species, so as more and more studies are made, one might be soon lost in the sea of different interactions. Hence, in modeling, one has to find a compromise between oversimplification and including too many details, which ultimately fails to capture the essence of the diverse collective phenomena.

An inherent difficulty in field study is the inability to change key parameters. But in some cases, such parameter would simultaneously evolve as a response to external condition. For example, in a recent paper, Makris *et al.* reported a convincing study on the vast oceanic fish shoals formation [16].

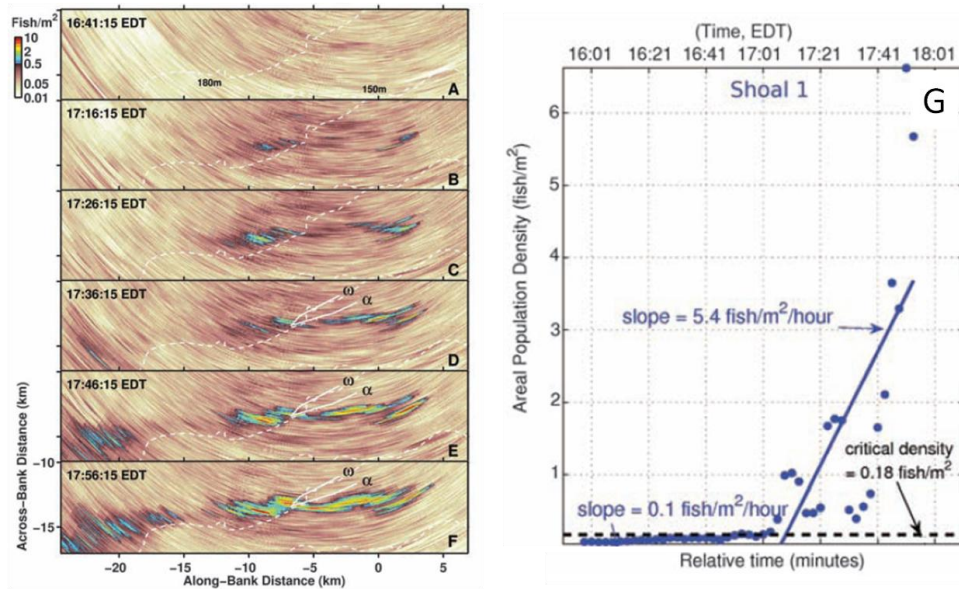


Figure 6. (A-F) Sequence of instantaneous OAWRS density images just before the sunset. (G) Mean areal population density versus time for a shoal of herring.

Using a new technique called Ocean Acoustic Waveguide Remote Sensing (OAWRS) [8], they are able to instantaneously image and continuously monitor the oceanic fish population over tens of thousands of km². Triggered by the reduction in light level, the density of Atlantic herring will initially increase homogeneously and gradually. Once it reaches a critical density of 0.18 fish/m², the fish population density starts to increase dramatically. First, several regions of very high density form (Figure 6B), similar to the nucleation process in a liquid-solid phase transition. Then, these nuclei grow by propagating horizontally outwards as a convergence wave emanating from them. The speed of the wave is much faster than the individual herring's speed, much like

acoustic waves in a medium of variable density. Once the vast shoal formed, it assumes the normal collective behavior, moving slowly towards the spawning grounds, with a velocity same as the individual herring. The kinetics of the phase transition observed here, as well as the real response of a collective group towards changing parameter, opens a new avenue in the field study.

So far, whether in simulation or field study, we assume that all group members are equal. However, each group member can, in reality, influence the group behavior with different weight, the extreme case being having a leader. To quantify such nonequality, the Vicsek group recently used light-weighted GPS to track the homing flight of a group of 10 pigeons [17]. Here, a leading event is defined when the bird i 's direction is copied by bird j at a later time. By calculating the directional correlation delay time τ^*_{ij} , obtained from the peak of $C_{ij}(\tau) = \langle \vec{v}_i(t) \cdot \vec{v}_j(t + \tau) \rangle$ for each pair of birds, they mapped out the hierarchical structure of the pigeon group (Figure 7B).

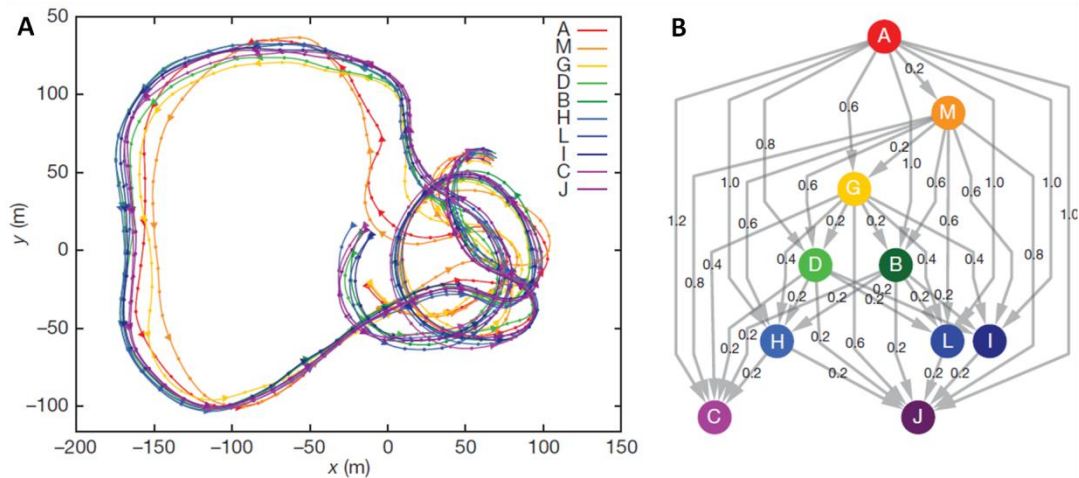


Figure 7. (A) 2-min segment from a free flight performed by a flock of ten pigeons. Letters refer to bird identity. (B) Hierarchical network of the flock for flight in A. For each pair, the directed edge points from the leader to the follower; values correspond to τ^*_{ij} of that pair (second).

The fact that there is no directed loop inside the hierarchical network means that pigeons at different levels contribute nonequally to the group dynamics. By taking out individual pigeons and measure their solo flying ability, they found out that the pigeon at the top of the network, usually also in the front of the flock in space, is also the most experienced flyer.

Whether such a hierarchy also exists in large flocks is an open question. If true, it casts doubt on the egalitarian model prevalently used in the simulation and interpretation of field study data. Nevertheless, it can shed light on many other interesting phenomena inside a group, such as how a group reaches consensus, etc.

The available data on the collective dynamics of natural animal groups are still scarce. But with the evolving technology and closer collaboration between biologists and physicists, it is conceivable that there will be growing numbers of such studies, which would help us to have a more realistic picture of the natural collective motion than produced by simulation.

Model Experiments

Parallel to the efforts of quantifying natural group dynamics, experimental physicists are trying to approach the problem in a different way. As stated previously, in natural system, key parameters are difficult to tune. This is not true if one can produce an artificial system that mimics the collective motion in the nature. In this spirit, much work has been done to make artificial self-propelling particles. The most popular method is to use millimeter-sized particles sandwiched between two vertically vibrating plane. For example, see Figure 8A for a system consisting 2820 rod-like particles (Narayan *et al.* [18]). In the active state, a single particle will have random motion due to frequent collisions with the floor and ceiling of the cell. In this study, particles are elongated, apolar rods, inspired by the shape of many living bacteria.

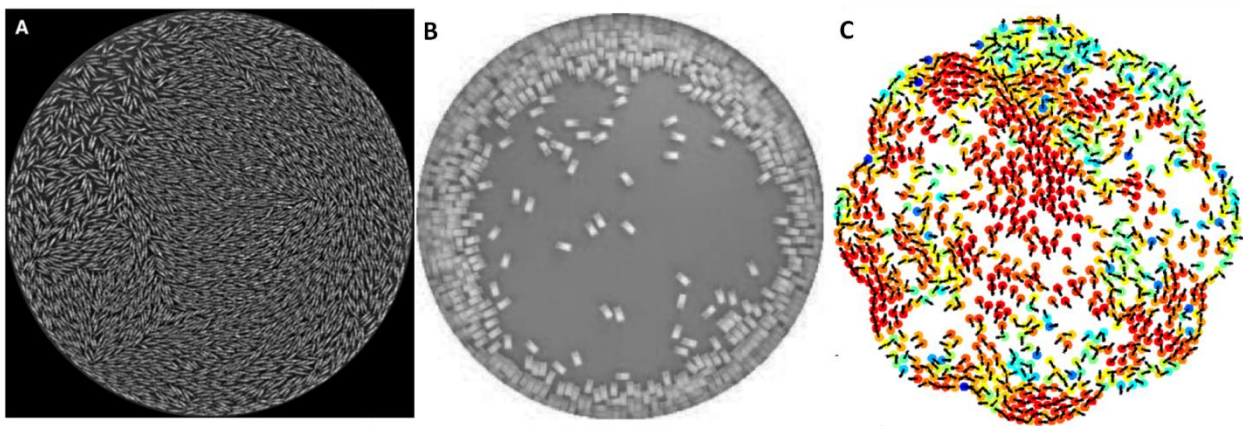


Figure 8. (A) A snapshot of active, apolar rods on vibrating plane described in [18].(B) A snapshot of active, polar rods described in [19]. (C) A snapshot of vibrated polar disks described in [20]. Black arrows indicate the intrinsic polarity of the disk. Color is coded for the degree of local alignment.

The most important finding here is that the system shows giant number fluctuations. In the central limit theorem, the average number of particles in a subsystem N and the standard deviation ΔN , should have this relationship $\Delta N / \sqrt{N} = \text{constant}$. However, in this nonequilibrium system, ΔN scales with N , which signifies much higher probability of finding giant fluctuations. Meanwhile, such giant fluctuations are extremely long-lived, decaying logarithmically in time as opposed to t^{-1} dependence in the diffusively relaxing density fluctuations.

The microscopic origin of the giant fluctuations lies in way two rods collide. After collision, particles are more likely to move along their axis than transverse to it, and this dynamic anisotropy can persist even to the scale of mean free time between collisions.

This study reveals the sensitivity of the collective dynamics to the details of the colliding event. Later, Kudrolli *et al.* study the collective motion of polar rods with a preferred direction of motion [19]. The result is qualitatively different. Not only is the giant number fluctuation absent, but also, particles tend to cluster around the boundary of the experimental wells (Figure 8B).

However, changing the shape of the particle to disk resumes the large scale collective motion and the giant number fluctuations (Figure 8C). In a clever design, Deseigne *et al.* made self-

propelled disks with a preferred direction [20]. In this case, alignment due to shape anisotropy is eliminated. The alignment effect now comes purely from the self-propulsion and hard core repulsion, when two particles collide.

Though growing in numbers, there are several inherent problems in these studies. First, boundary effects are strong and unavoidable. Second, the way the particles interact with each other, usually only through hard core collision, is far from the reality in the nature. As seen in the previous session, animals intentionally keep a distance away from each other so collision seldom happens, and alignment is achieved through other long range effects. Finally, jamming effect would gradually set in when the volume fraction increases further. Hence, while interesting as a new emergent field, such artificial system is unlikely to yield result that can help us to understand the animal collective motion.

There is also effort in more biologically related settings, for example, see [21]. They use extracted F-actin propelled by motor proteins on planar geometry. Due to the small scale of the agent compared to the system size, boundary effect is significantly attenuated. The flexibility of the actin filament is another feature that differs from previous artificial system. As a function of filament density, they observed transition from disordered phase, to continuously moving bands, and to homogeneous moving clusters. By incorporating more biologically relevant parameters, while keeping the system trackable and controllable, one may find a way to study the collective animal motions in laboratory. Note that there are many literatures on the collective bacteria behavior on the laboratory scale (for example, see [22]), which I do not have space to address here.

Conclusion and Perspective

The limited examples given here just give one a flavor of this growing field. Our understanding about collective motion is greatly enhanced through numerous simulation works, since the original SPP model. Now, with the trend of shifting from qualitative observation to quantitative measurement in life science, more and more accurate spatiotemporal data of animal behaviors are available. This presents an excellent opportunity for statistical physicists.

There are many possible directions one can explore in the future: first, more data of position and velocities (and maybe other features) of collectively moving agents should be obtained, in order to generate large enough database. Second, by comparing and extracting the common behaviors among different species, one may start to refine the existing model to a more realistic, but still general one for the biological system. The grand goal is to test whether there are some simple laws underlying all the collective behavior observed in the nature. Third, the difference between the agents, and the network property of the flock, should be studied further, with the interesting question of decision making process inside a group. Finally, if we really understand these rules, we are much closer to design artificial intelligence, be it robots or small self-driven particles, that can mimic the collective group behavior, the most noticeable example being human society.

References

- [1] D. J. T. Sumpter, *Curr. Bio.* **19**, R325 (2009).
- [2] T. Vicsek, A. Czirok, E. Ben-Jacob, I. Cohen, O. Shochet, *Phys. Rev. Lett.*, **75**, 1226 (1995).

- [3] For a comprehensive review <http://hal.elte.hu/~vicsek/papers/RMP-tv-az-as-submitted.pdf>
- [4] S. J. Simpson, G. A. Sword, P. D. Lorch, I. D. Couzin, *Proc. Nat. Acad. Sci.* **103**, 4152 (2006).
- [5] P. Romanczuk, I. D. Couzin, L. Schimansky-Geier, *Phys. Rev. Lett.*, **102**, 010602 (2009).
- [6] H. Chaté, F. Ginelli, R. Montagne, *Phys. Rev. Lett.*, **96**, 180602 (2006).
- [7] A. Baskaran, M. C. Marchetti, *Proc. Nat. Acad. Sci.* **106**, 15567 (2009).
- [8] N. C. Makris, P. Ratilal, D. T. Symonds, S. Jagannathan, S. Lee, R. W. Nero, *Science*, **311**, 660 (2006).
- [9] J. Buhl, D. J. T. Sumpter, I. D. Couzin, J. J. Hale, E. Despland, E. R. Miller, S. J. Simpson, *Science*, **312**, 1402 (2006).
- [10] M. Ballerini, N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini, M. Viale, V. Zdravkovic, *Proc. Nat. Acad. Sci.* **105**, 1232 (2008).
- [11] F. Ginelli, H. Chaté, *Phys. Rev. Lett.*, **105**, 168103 (2006).
- [12] A. Cavagna, A. Cimarelli, I. Giardina, G. Parisi, R. Santagati, F. Stefanini, M. Viale, *Proc. Nat. Acad. Sci.* **107**, 11865 (2010).
- [13] V. M. Eguiluz, D. R. Chialvo, G. A. Cecchi, M. Baliki, A. V. Apkarian, *Phys. Rev. Lett.*, **94**, 018102 (2005).
- [14] F. Gerlotto, S. Bertrand, N. Bez, M. Gutierrez, J. Mari, *ICES J. Mar. Sci.*, **63**, 1405 (2006).
- [15] R. Lukeman, Y.-X. Li, L. Edelstein-Keshet, *Proc. Nat. Acad. Sci.* **107**, 12576 (2010).
- [16] N. C. Makris, P. Ratilal, D. T. Symonds, S. Jagannathan, Z. Gong, M. Andrews, I. Bertatos, O. R. Godo, R. W. Nero, J. M. Jech, *Science*, **323**, 1734 (2009).
- [17] M. Nagy, Z. Akos, D. Biro, T. Vicsek, *Nature*, **464**, 890 (2010).
- [18] V. Narayan, S. Ramaswamy, N. Menon, *Science*, **317**, 105 (2007).
- [19] A. Kudrolli, G. Lumay, D. Volfson, V. S. Tsimring, *Phys. Rev. Lett.*, **100**, 058001 (2010).
- [20] J. Deseigne, O. Dauchot, H. Chaté, *Phys. Rev. Lett.*, **105**, 098001 (2010).
- [21] V. Schaller, C. Weber, C. Semmrich, E. Frey, A. R. Bausch, *Nature*, **467**, 73 (2010).
- [22] D. B. Kearns, *Nat. Rev. Microbiol.*, **8**, 634 (2010).