

The Statistical Mechanics of Collective Animal Behavior

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1. COLLECTIVE BEHAVIOR

Collective animal behavior or the collective motion of organisms refers to the large-scale dynamics of grouped organic matter moving collectively in their environment. Collective behavior of massive groups of organic substances can be observed at many lengths scales, including but not limited to, bacterial colonies, flocks of migrating birds, swarms of insects, and crowds of people [1]. Explanations of such behavior under the perspective of evolutionary biology typically revolve around the advantages for collectively moving in groups or whether organisms instinctively choose to follow the leader in large packs [2]; however, employing the perspective of statistical mechanics can lead to a greater understanding of the physical laws governing the motion. Focusing on the underlying features of collective behavior with models from statistical physics can yield new insights into its qualitative aspects and quantitative backing, albeit at limited approximations. For instance, consider how swarms of insects react strongly to visual stimuli without paying attention to the random motions of each of its constituents [3]. Trying to construct a physical model in such a situation fails to capture any form of coherent structure or pattern necessary for a rigorous theory. Theorizing and experimenting on generalized collective behavior environments is possible, and the large amounts of individuals undergoing collective motion make statistical mechanics a useful tool in these simpler situations.

A particular theory of interest is the Vicsek model of collective motion, where a continuous kinetic phase transition exists for groups of organisms moving collectively on a two-dimensional plane with a fixed number of parameters [4]. The Vicsek model's relative simplicity allowed it to be extended to more advanced studies with a great deal of experimen-

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tal backing, yet it also came with indications of the theory's limitations. Although a separate idea involving entropy maximization overcomes the limited scope and applicability of the Vicsek model, Vicsek's theory was widely applicable and fundamental in understanding the dynamics of collective animal behavior.

2. THE VICSEK MODEL

The Vicsek model utilizes a singular rule regarding the velocity of particles in a two-dimensional setting to study the collective behavior of a large particle system not in equilibrium. At some given time step, a particle driven at a constant absolute velocity takes on the average direction of motion of particles in a circle of radius r about the aforementioned particle's center, including the addition of a random noise component [4]. Similar to the Ising model of ferromagnetic materials, the average velocities of the group of "organisms" align in a common direction of motion, like ferromagnetic interactions causing the spin of particles to align in the same direction [4]. In a system of N organisms, the i th organism's position change from $t \rightarrow t + 1$ was given by

$$\mathbf{x}_i(t + 1) = \mathbf{x}_i(t) + \mathbf{v}_i(t)\Delta t \quad (1)$$

where $\mathbf{v}_i(t)$ was the velocity of the i th organism at time t . In Eq. 1, the velocity of the particle at the next time step was given by the absolute value v , ($|\mathbf{v}_i(t + 1)| = v$), with an angle $\theta(t + 1)$ [4]. Additionally, this new angle can be determined from

$$\theta(t + 1) = \langle \theta(t) \rangle_r + \Delta\theta \quad (2)$$

where $\langle \theta(t) \rangle_r$ represents the average angle of the resultant velocities of all organisms inside a circle of radius r , and $\Delta\theta$ is the noise term (η) given from the uniform probability interval $[-\eta/2, \eta/2]$ chosen at random. Note that $\langle \theta(t) \rangle_r = \arctan[\langle \sin(\theta(t)) \rangle_r / \langle \cos(\theta(t)) \rangle_r]$. See Fig. 1 in Appendix A for visualization of Vicsek model and corresponding equations. Comprising the bulk of the Vicsek model, Eqs. 1,2 were used in simulations involving $N = 300$ particle-like organisms with three free parameters; η , v , and $\rho = N/L^2$, (L equalling the length of simulation plane) [4]. In the case of large density and a relatively small noise component, the organisms moved in the same collectively determined direction [4]. This kinetic

phase transition arises from the organisms being driven by a constant absolute velocity,

$$v_a = \frac{1}{Nv} \left| \sum_{i=0}^N \mathbf{v}_i \right| \quad (3)$$

where the net momentum of all organism collisions is not conserved [4]. For an entirely random distribution of organism velocities, Eq. 3 approaches zero, yet whenever the velocities of the organisms are all ordered in the same direction Eq. 3 tends towards 1 ($v_a \simeq 1$). Treating v_a as an order parameter of 1 in the simulations, η was decreased at a fixed ρ , and a kinetic phase transition from disordered to ordered collective motion was observed [4]. An analog between the kinetic phase transition and a substance's continuous phase transition can be made in the thermodynamic limit, as Eq. 3 becomes proportional to $[\eta_c(\rho) - \eta]^\beta$ and $[\rho - \rho_c(\eta)]^\delta$. β and δ are the critical exponents and $\eta_c(\rho)$ and $\rho_c(\eta)$ are the critical noise and density as L increases to infinity [4]. For the simulations conducted by Vicsek et al., β and δ were calculated to be 0.45 ± 0.07 and 0.35 ± 0.06 , respectively, with uncertainties based upon the propagation of error with v_a , $\eta_c(\rho)$, $\rho_c(\eta)$. It was shown that β and δ for a phase diagram of disordered ferromagnets were within the error bars of the Vicsek model values, hinting at an association between the kinetic phase transition of collective animal behavior and ferromagnetic materials at critical temperatures [4]. With proper modifications and theoretical treatment, the Vicsek model proved it had the capability to apply statistical mechanical models to the motion of self-driven organisms while analyzing quantitative aspects of their collective behavior.

3. APPLICATIONS OF THE VICSEK MODEL TO COLLECTIVE BEHAVIOR

The Vicsek model was used to show that flocks consisting of thousands of starlings were characterized more by the topological distance between its members as opposed to the metric distance [5]. Topological distance in this setting refers to the number of individuals in a neighborhood around a singular starling, whereas metric distance implies that the flocks orient themselves based upon the distance between its members entirely. It was observed with simulation and starling flock data that only topological distance interactions were able to produce results similar to the actual flock [5]. Converting Eqs. 1, 2 of the Vicsek model into topologically equivalent ones, with each organism having a fixed number of neighbors n_c , simulations involving a predator "attacking" the flock were conducted. With the topological

alterations in place, the highest probable outcome of the predator attack was that the flock stayed together, which is identical to how starling flocks react in their environment [5]. Although simulations were performed in the two-dimensional space characteristic of the Vicsek model, Ballerini et al. posit that similar results could be achieved in three dimensions despite difficulties regarding the increase in degrees of freedom. Nevertheless, the Vicsek model was a significant asset to the study which helped explain new aspects of collective animal behavior.

Flocks of starlings possess the unique characteristic of having a standard order parameter of approximately 0.97 [3], yet not all groupings share this extremely ordered characteristic. The collective motion of midges lack order, but simultaneously exhibit correlation between its members [3]. Specifically, the Vicsek model provided an accurate collective motion description of swarms where correlation referred to the extent at which the i th midge's behavior was related to the j th midge [3]. Additionally, the susceptibility, collective response to an external perturbation, for midge swarms was calculated by

$$Q(r) = \frac{1}{N} \sum_{i \neq j}^N \delta \vec{\varphi}_i \cdot \delta \vec{\varphi}_j \theta(r - r_{ij}) \quad (4)$$

where $\theta(r - r_{ij})$ is the Heaviside function taking values of 1 for $r_{ij} \leq r$ or 0 otherwise [3]. Moreover, a rescaled Eq. 1, ($x \equiv r_1/\lambda$) inside a metric perception distance λ allowed for the characterization of the transition between a disordered collective phase (high x) to an ordered collective phase (low x) [3]. An ordering transition at x_c was shown to cause the maximum of Eq. 4, ($\chi \equiv Q(r_0)$), to blow up near x_c by the relation $\chi \sim \frac{1}{(x-x_c)^\gamma}$ [3]. Three-dimensional Vicsek model data was fit to the previous expression with a γ of 1.5 ± 0.1 , and point of transition $x_c = 0.434$ [3]. The relatively small order parameter, correlation, and susceptibility of Eq. 4 established by the Vicsek model have striking similarities to the collective behavior of natural midge swarms [3]. Despite Attansai et al. utilizing the Vicsek model metrically, contrary to Ballerini et al.'s topological version, it was observed that disorder and correlation can coexist in systems exhibiting collective motion near their ordering transition.

4. LIMITATIONS OF THE VICSEK MODEL

Originally, the Vicsek model predicted a continuous, second-order kinetic phase transition as η decreased at a constant ρ , but considering the addition of "vectorial noise" changes the transition to a discontinuous, first-order kinetic phase transition. Errors made in subsequent angle calculations from a particularly noisy environment introduce vectorial noise, as opposed to the formerly assumed perfect "angular noise" of collective motion interactions [1]. Consequentially, in certain large enough systems, the Vicsek model breaks down, and the previously smooth (with normalization) Eq. 3 jumps instantaneously to zero as η is decreased [1]. Even with a variety of simulations at different group sizes, it was shown that the continuous kinetic phase transition occurred only from finite population size effects at low density [1].

Ordered collective phase dynamics, transversely extending bands of organisms, traveling at the center of mass velocity v has been shown to arise directly from the discontinuous phase transition unaccounted for in the original literature of Vicsek et al [2]. Boundary conditions of the simulation plane must be considered in their creation, but typically the shortest length L_b of the rectangular plane is more impactful towards collective organism bands propagating [2]. Quantitatively, the collectively organized bands are described by the local order parameter,

$$\varphi_l(\vec{x}, t) = \frac{1}{v} |\langle \vec{v}_i(t) \rangle_{\vec{r}_i \in V(x)}| \quad (5)$$

which is analogous to Eq. 3 for \vec{r}_i in a domain $V(x)$ [2]. Additional averaging of longitudinal and perpendicular density profiles for the phase fully characterize sharp kinks in the density and order parameter profile phase plots [2]. For low levels of the noise parameter η , the bands or sheets of organisms vanish as Vicsek's model predicted originally; however, the significantly strong density fluctuations were not considered as a hallmark of the model [2]. A continuous transition with the inclusion of propagating bands does exist, yet it is believed that the specific boundary conditions of the simulation have too much of a component in the results [2]. Nevertheless, collective phase dynamics exhibited from a transverse sheet of high organism density were not an intended consequence of the Vicsek model at large population size.

Many modifications of the Vicsek model were discussed in the current and former sections, and every new addition holds to the same general theme of the theory. The Vicsek model

has immense power as a simple, theoretical backbone for a number of experimentally specific situations. Taking the model for the complete explanation and attempting to garner accurate empirical results often misses the mark, even contradictory in some instances. Furthermore, the Vicsek model was designed as a two-dimensional rectangle of length L instead of a three-dimensional cube, where macroscopic organisms of the animal kingdom lie. Only upon the inclusion of a new detail, idea, or principle the Vicsek model will then produce the results observed in reality. Overall, the theory's biggest weakness is its constricting initial assumptions and conditions, but the model is still flexible enough to contribute in collective animal behavior research.

5. BEYOND VICSEK

A more modern formalism, coined maximum entropy theory, intends to apply statistical mechanical methods to biological systems in the hopes of understanding and predicting real data at a greater degree than the Vicsek model. Upon defining a set of variables that could represent the members of a flock, $\{x_1, x_2, \dots, x_N\} \equiv \mathbf{x}$, a number of equations of state can be defined for said \mathbf{x} [6]. The entropy at which the system of organisms must maximize is the Shannon entropy,

$$S[P] = - \sum_{\mathbf{x}} P(\mathbf{x}) \ln P(\mathbf{x}) \quad (6)$$

where $P(\mathbf{x})$ is a random probability distribution of \mathbf{x} [6]. The supposed constrained optimization problem of having the experimental probability distribution be normalized can be solved using Lagrange multipliers. A optimized Eq. 6 in terms of some set of parameters $\{\lambda_\nu\}$ is,

$$S[P; \{\lambda_\nu\}] = - \langle \log P(\mathbf{x}) \rangle_{\text{exp}} \quad (7)$$

and $\langle \log P(\mathbf{x}) \rangle_{\text{exp}}$ is the likelihood that the entropy maximization model generates observed experimental data [6]. Analogously with statistical mechanics, if a system has states \mathbf{x} with energy $\epsilon(\mathbf{x})$, the probability distribution at thermal equilibrium is given by $P(\mathbf{x}) = \frac{1}{Z(\beta)} e^{-\beta \epsilon(\mathbf{x})}$, and $Z(\beta)$ is the partition function $\sum_{\mathbf{x}} e^{-\beta \epsilon(\mathbf{x})}$ of $\beta = 1/k_B T$. Choosing $\mathbf{x} = \{\vec{s}_i\}$, state function of correlation $f_\mu(\mathbf{x}) = \vec{s}_i \cdot \vec{s}_j$, and parameters $-J_{ij}$, the principle equation of

the maximum entropy model,

$$P(\{\vec{s}_i\}) = \frac{1}{Z(J_{ij})} \exp \left[\frac{1}{2} \sum_{i=1}^N \sum_{j=1}^N J_{ij} \vec{s}_i \cdot \vec{s}_j \right] \quad (8)$$

where J_{ij} is adjusted so the correlation function imparts experimental results ($\langle \vec{s}_i \cdot \vec{s}_j \rangle_P = \langle \vec{s}_i \cdot \vec{s}_j \rangle_{\text{exp}}$) [6]. Note that Eq. 8 is identical to the Heisenberg model of magnets, where spins \vec{s}_i, \vec{s}_j interact with correlation strength J_{ij} at thermal equilibrium $k_B T = 1$ [6]. For a flock of particular focus, the system relaxes towards Langevin dynamics,

$$\frac{d\vec{s}_i}{dt} = -\frac{\partial H}{\partial \vec{s}_i} + \vec{\eta}_i(t) = \sum_{j=1}^N J_{ij} \vec{s}_j + \vec{\eta}_i(t) \quad (9)$$

where $\vec{\eta}_i(t)$ is a noise term driving members of the flock [6]. Solving Eq. 9 for individual trajectories $\vec{s}_i(t)$ gives a sample of the i th member out of the entire distribution of Eq. 8, and J_{ij} is the strength of the fictitious force that attempts to align the i th bird along the direction of the j th bird [6].

6. EXPERIMENTAL EVIDENCE OF MAXIMUM ENTROPY THEORY

The simplest form of interaction that simultaneously matches starling flock behavior while maintaining a correlation independent of a bird's identity is when $J_{ij} = J$ in Eq. 8 [6]. If each i th member interacts with the j th at an equivalent magnitude J , with the same amount of neighbors n_c in radius r_c , then Eq. 8 simplifies to

$$P(\{\vec{s}_i\}) = \frac{1}{Z(J, n_c)} \exp \left[\frac{J}{2} \sum_{i=1}^N \sum_{j \in n_c^i} \vec{s}_i \cdot \vec{s}_j \right] \quad (10)$$

where $j \in n_c^i$ is the j th bird apart of the n_c neighbors of the i th [6]. Accordingly, the average value of correlation for every pair of starlings is given by,

$$C_{int} \approx \frac{1}{N} \sum_{i=1}^N \frac{1}{n_c} \sum_{j \in n_c^i} \vec{s}_i \cdot \vec{s}_j \quad (11)$$

and note that Eqs. 10, 11 satisfy the entropy maximization principles previously discussed [6]. Eq. 11 was used at every instance of time to observe the maximum entropy value of both n_c and J . Corroboration of Ballerini et al.'s claim that topological distance is more significant in starling flocks than metric distance between its members was also achieved [6]. Moreover, the

mechanistic interpretation of starling flocks, governed by Eq. 9, were tested via simulation in Vicsek-like modeling conditions in reference to the maximum entropy model. The results initially showed over estimation of n_c , yet proper calibration allowed for a n_c of 7.8 which holds agreement with other studies utilizing completely different methods [6].

Bialek et al. demonstrated that the minimal model of entropy maximization could establish a complete theory on directional order of collective animal motion without the usage of free parameters, among detailed qualitative traits of starling flocks in their natural environment. The maximum entropy model allowed for the prediction of collective animal behavior of groups possessing thousands of members, as opposed to Vicsek's model consisting of hundreds. This new approach takes inspiration from the Vicsek model and builds upon it with the possibility of formulating an entire statistical mechanical model of collective animal behavior [6]. The velocities of starlings must be connected with their changing positions with a more accurate trajectory measurement to make a complete theory, yet entropy maximization approach to collective animal behavior has the potential to do just that. Additional development of the Vicsek and entropy maximization model should help connect statistical mechanics and collective animal behavior further while improving our understanding of the underlying dynamical components of self driven organic life.

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Appendix A: Auxiliary material

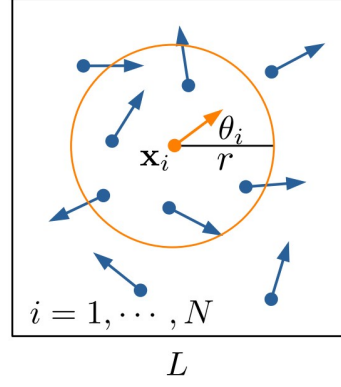


FIG. 1: Visualization of Vicsek model with a orange circle representing the i th organism's neighborhood (radius r) inside simulation square partition of length L [7].