REMARKS ON AN APPROACH TO STUDY FLOCKING PHENOMENON IN ANIMALS

FRANCOIS GERARD
INSTITUTE FOR THEORETICAL BIOLOGY, DEPARTMENT OF BIOLOGY, PAUL SABATIER UNIVERSITY - TOULOUSE III ,118 ROUTE DE NARBONNE, 31062 TOULOUSE CEDEX 9 TÉLÉPHONE +33 (0)5 61 55 66 11 , FRANCE

Abstract. A common illustration of emergent collective behavior, in which interactions between individuals result in large-scale collective patterns, is flocking. Here, we demonstrate the straightforward derivation from field data of a quantitative microscopic theory for directional ordering in a flock. The maximum entropy model demonstrates that no free parameters are required to accurately forecast the propagation of order over whole flocks of starlings. Instead, local, pairwise interactions between birds are sufficient. In order to enhance their capacity for collective computation, it has been suggested that such collective systems should function close to a phase transition, specifically a (pseudo-)critical point. Parts of our discussion can also be found in [72]. This paper will discuss the phenomenon of flocking that animal communities exhibit in biological systems.

1. Introduction

Large animal assemblages that cooperate, including schools of fish, flocks of birds, and swarms of insects, are frequent and fascinating examples of biological self-organization. Over the past few decades, it has attracted researchers from a range of disciplines, going beyond biology. Recently, a lot of mathematicians have studied this [39], [73], [52], [53] [64], [65], [26], [75],[58], [38] as well as any references thereto. Additionally, since statistical mechanics bridges the gap between microscopic laws and macroscopic phenomena, physicists have long hoped that similar collective behaviors in biological systems may be understood in the same manner that we understand collective behavior in physics [63, 13, 51].

Although the majority of the study was aimed at understanding systems in thermal equilibrium, where a substantial body of theory supported by experiments has been solidly established, we have witnessed decades of research into self-organization and pattern production in non-equilibrium systems [27, 43], pertaining to biological systems in general as well as to animal behavior in general. Without a doubt, physics provides a robust and effective toolbox that can aid in our understanding of the complexity of the living world, even though many questions regarding non-equilibrium phase transitions remain unresolved. Theoretical investigations on the behavior of groups of animals have long relied on arbitrary (but reasonable) modeling presumptions. A interesting quality that sets living systems different from most (or all) inanimate objects is their capacity to react adaptably to changing conditions.

Key words and phrases. flocking, collective behavior, animal behaviors.

As characterized by the collective dynamics of a sizable number of interacting elements or agents that make up the complex biological system, this ability to implement functional adaptive behavior often depends on distributed information processing at multiple levels. Examples on a smaller scale include the interactions between proteins in cells [24] to neurons interacting in brains[8, 48] to the group behavior of animals and humans [61]. The parameter space in which such collective biological systems operate is large due to the complexity of individual individuals as well as the sizeable number of individuals that may make up a functional group. An important question that emerges is if some parameter combinations or parameter regions are particularly appropriate for their biological function by making their aggregate behavior in some way close to optimal. It has recently been possible to undertake model selection and directly fit the model parameters to experimental data thanks to more advanced experimental approaches. The collective dynamics at the macroscopic level will be most vulnerable, or sensitive, to minute variations in an external input at such crucial locations, according to statistical physics, where information would propagate swiftly across arbitrarily broad scales [62].

The criticality hypothesis faces a challenge in explaining how scattered systems may manage their behavior to stay in the critical region of parameter space.

Research on self-organized criticality offers one set of mechanisms for how complex systems might tune towards critical points in a self-organized way without external control, assuming a time-scale separation between the fast (relaxation) dynamics of the system and a slow driving of the system towards the critical point. It was also proposed that (self-organized) critical dynamics could account for the excess of power-law distributions in empirical data in this situation [3, 54].Self-organized criticality garnered a significant deal of scientific interest in the 1990s, with the study that went along with it focusing primarily on idealized mathematical models [47, 79]. However, there were still a lot of questions that remained unresolved about the idea, and more importantly, it was unclear whether it applied to events that happened in the real world.

Near the end of the 20th century, when scientific interest in the criticality concept began to wane, new experimental findings in the area of neurology helped to revive it. This is as a result of Beggs & Plenz's 2003 finding of crucial neuronal avalanches [7]. Since then, a number of theoretical and experimental research on the criticality hypothesis in many biological systems, including neurological systems, have been released [8, 42, 69, 67], gene-regulatory networks[5, 23], and animal group dynamics collectively [60, 15, 50, 68].Three things set apart this more recent research: 1) a closer resemblance to experimental observations; 2) an empirically motivated suggestion of mechanisms for self-tuning towards the critical point; and 3) a critique of the exclusive emphasis on the benefits of criticality in favor of the significance of adaptively managing competing trade-offs, perhaps by actively adjusting the distance to critical transitions depending on environmental context.

The discussion of flocking in biological collectives and how criticality can affect biological function will continue in this paper before we move on to possible mechanisms that could let animal collectives tune themselves in a self-organized way toward or away from critical points in the upcoming works.

2. Flocking

The emergence of order in a flock of birds serves as a natural test case for this strategy: The flock as a whole spontaneously selects a certain direction to fly out of a network of dispersed interactions among the individuals , similar to how local interactions among individual spins in a ferromagnet cause the system to spontaneously become magnetized. [4].

Vicsek and co-authors' important 1995 paper on self-propelled particles moving at constant speed v_0 and engaging with a ferromagnetic (or polar) alignment interaction provided the first theoretical analysis of flocking as a phase transition [80]. Perhaps surprisingly, this offers a hypothesis with no open parameters for the spread of directional order across the flock that is virtually complete. The reported appearance of long-range orientational order in this non-equilibrium extension of the traditional XY-model attracted a lot of attention because it seemed to go against the Mermin-Wagner principle [57, 44]. The relevant number of neighbors and the strength of the interaction are remarkably resilient across multiple flocking events; the structure of the model corresponds to pairwise interactions with a fixed number of (topological) neighbors rather than with all neighbors that are located within a certain (metric) distance.Soon after, Toner and Tu were able to demonstrate that the model's non-equilibrium property for a non-zero self-propulsion speed is what ultimately makes a difference [76, 77, 78] reasons why the Mermin-Wagner theorem is invalid. Both larger, more general effects like the existence of long-range, scale-free correlations between bird pairs and smaller, more specific effects like the nonmonotonic distance dependence of (four-point) correlations between two bird pairs are predicted by the theory. Following these initial articles, the Vicsek model transition's nature [33, 20, 2, 30], substantial study has been done on both polar and nematic interactions in models of self-propelled particles with spatially local alignment interactions [22, 66, 6, 32, 9, 35]. Whereas initially it was thought that the transformation was ongoing [80, 2], later systematic numerical simulations and theoretical investigations have demonstrated that the homogeneous ordered state is unstable with regard to longitudinal density modulations close to the critical point [33, 10, 45, 46, 30].As a result, broad, high-density bands start to develop and move through a chaotic, low-density gas-like "background." The phase transitions eventually become discontinuous as a result of the development of these spatial heterogeneities. However, substantial finite size effects frequently obscure the discontinuous nature of the transition, which is only consistently visible at very large system sizes and/or high self-propulsion speeds [21]. There is a density-order coupling, which is the underlying process causing the density instability. On average, locations with higher densities also tend to be more organized [11].

There are several different self-propelled particle flocking models, some of which even lack explicit alignment interactions [74, 34, 40, 37].However, the transition to an ordered state will resemble the one seen in the Vicsek model, including the above mentioned density-order coupling, and can be assumed to fall into the same universality class, if it can be defined, as long as the interactions are short-ranged and result in effective alignment while the system exhibits fluid-like lack of positional order. Additionally, there is a sizable class of systems that take into account self-propelled particle systems with attractive and repulsive forces that may exhibit various flocking transitions [33, 71, 29].

It has been proposed that topological distance, rather than metric distance, governs interactions between pairs of individuals based on a thorough study of experimental data gathered from 3D tracking of starling flocks [4]. As a focal individual pays attention to others if they are inside a set of nearest neighbors, regardless of their Euclidean distance, such interactions in comparable topological flocking models can likewise be long-ranged[31, 70]. The density-order coupling was thought to be disabled by the interaction's metric-free nature, eliminating the density instability and producing a continuous flocking transition [31].Recent studies on flocking models with distance-independent k-nearest-neighbor interactions, however, have demonstrated that bands emerge as a result of a weak but persistent density-order coupling [56, 70],which the presence of spatial heterogeneities can improve even further [70].

The majority of flocking models presuppose that individuals move at a constant speed. In addition to reducing model complexity, this simplifying assumption provides a clear comparison to the fixed spin amplitude in closely related statistical physics models like the Ising, Potts, or XY models. Animals traveling in groups, however, frequently demonstrate variable speed that might be affected by social interaction, necessitating the consideration of yet another level of freedom [36, 49, 16]. Scale-free velocity Variable speed models at criticality are the only ones capable of explaining correlations seen in flocks of birds [12]. Additionally, it has been demonstrated that variable speed may significantly expand and change self-organized collective activities and bring about new kinds of order-disorder transitions [36, 49].

Last but not least, recently proposed "inertial spin models" with non-dissipative couplings are based on empirical observations of highly polarized, collective turning behavior in flocks of birds [1, 17]. The inertial spin model has been shown to accurately replicate the dynamical correlations of velocities and non-exponential relaxation dynamics in contrast to the dissipative Vicsek model [18].

3. Appendix: The applicability of processing of changing phase in biology

We present parts of the discussion from our previous work for reader convenience. Animal species in particular share several fundamental characteristics with the classical statistical physics systems that gave rise to the idea of a phase transition.

However, there are also substantial discrepancies, necessitating a rigorous evaluation of the phase transition concept's applicability to herd behavior.

First, the fact that biological systems are far from equilibrium makes them fundamentally different from systems that are traditionally examined in statistical physics. Modern statistical physics has a very active research community that is focused on the theory of phase transitions in non-equilibrium situations [55, 43, 41]. There is no fundamental reason to think that the corresponding theoretical concepts do not apply to living systems, including animal groups, even though many questions remain unanswered, and this is further supported by a substantial body of literature on phase transitions in biology over the past decades [80, 14, 74, 28].

The sheer magnitude of the systems in terms of the number of constituent units is a significant distinction as well. An animal aggregation normally consists of $N \sim 10^{23}$ individuals, as opposed to a macroscopic volume of matter, which typically comprises $N \sim 10 - 10^3$ individuals. Rarely, substantially larger collectives with $\sim 10^6$ individuals are seen, usually in the context of significant migratory movements in species like pelagic fish (like sardines) or desert locusts [59], [14]. However, in statistical physics, phase transitions are only properly specified in the thermodynamic limit of infinitely massive systems. The mathematical abstraction of $N \to \infty$, although a fairly excellent approximation for the general behavior of "classical" physical matter, it is doubtful if it really describes the majority of biological systems, and animal species in particular. While accurate, this criticism does not discount the importance of criticality and phase transitions in the description of biological systems with finite sizes. The benefits of (quasi-)criticality for group animal behavior are hypothesized, but they are not predicated on the assumption of the thermodynamic limit. In finite-sized systems, a number of collective information processing variables, including correlation lengths, information transmission, and susceptibility to inputs, still reach maximum at quasi-critical points [48, 15, 62, 68].

However, through the use of renormalization techniques, the theoretical idea of universality—or universality—is inextricably related to the idea of thermodynamic limit. The creation of scaling laws and critical exponents that depend only on the basic characteristics of the system, including dimensionality and symmetry, as opposed to minute details, is predicted by universality. Only above a crucial system size may this simplified scaling behavior be seen. Unfortunately, there are significant gaps in our understanding of the nature of social interactions and fluctuations due to the complexity of animal social behavior. As a result, it seems impossible to construct even reasonable estimates of matching critical system sizes above which universal behavior in the statistical physics sense could be detected. Therefore, it is essential to use considerable caution when extrapolating universality classes from empirically observed scaling rules in small to mesoscale animal groups.

Because of these factors, we believe that classifying biological phase transitions into different universality classes is less feasible than in traditional physics-based systems, and may even be impossible. Nevertheless, the idea that a single significant set of parameters dominates group behavior close to a transition and that this can allow for a significant simplification of accurate models of specific systems is still tenable.

Boundary circumstances must be anticipated to play a non-negligible, if not a dominant, role for self-organized collective behavior due to the very tiny system sizes [19]. This would be viewed as being somewhat troublesome for many statistical physics models. But from a biological perspective, this is probably a significant or even a defining characteristic of animal collectives [25]. It becomes clear that boundaries are crucial when we consider that the core function of animal aggregates is distributed sensing of environmental cues and collective processing of this information, for example in the context of predator detection or food search. For example, in visual perception, individuals at the edge of the group will typically perceive the majority of the environmental information.

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Institute for Theoretical Biology, Department of Biology, Paul Sabatier University - Toulouse III ,118 route de Narbonne, 31062 TOULOUSE CEDEX 9 téléphone +33 (0)5 61 55 66 11

Email address: `francois.gerard@gmx.com`