Towards an Understanding of Criticality in Living Systems

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This paper investigates the surprising prevalence of near-criticality in nature. The motivation for this paper stems from experimental observations of apparent criticality in living systems. Namely, the statistical models designed to describe natural collective behavior are often tuned to the critical point of the underlying model. I will present and discuss the experimental evidence that supports the above claim.

Introduction

Biological systems are generally too complex to model in every detail. Therefore our understanding of such systems, from networks of neurons to flocks of birds, have mostly been acquired through statistical modeling [1]. For example, the Ising model can be fitted to explain the correlating firing of neurons in a retinal neural network [2]. The disordered Potts model can describe the distribution of amino acids that code the B cell receptor proteins of zebrafish [3]. A Heisenberg-like model can be used to model the scale-free correlation observe in a flock of birds [4,5]. Interestingly, all aforementioned models share a peculiar feature. Specifically, the inferred/fitted model parameters are tuned close to the critical point of the model. Critical points occupy a space of measure zero in the space of possible model parameters. Therefore the observed criticality is surprising. In addition, physical systems tuned to the critical point have unusual properties such as divergent correlation length and divergent susceptibility to external perturbation. If criticality is indeed a general property of living system, then we may draw inspirations from the easily observable macroscopic world to inform our theories of microscopic systems. Further, the origin of such criticality is of fundamental and perhaps philosophical importance. A bird flock that responds maximally to the intrusion of a predator is more likely to survive than one that does not. One may even ask the question: "Is criticality a result of evolution?" [6].

While the prospect of living systems being naturally tuned to criticality is tantalizing, it is important to note the potential objections to such a theory. The first objection is that living systems may not be well-modeled by equilibrium statistical mechanics. Grinstein et. al. [7] noted in 1990 that "self-organized criticality" is a generic property of non-equilibrium noisy dynamics. Namely, any system described by deterministic dynamics with a conservation law will exhibit self-organized criticality upon the introduction of noise. More explicitly, if an equilibrium statistical model is fitted to describe a system governed by non-equilibrium noisy dynamics, the resultant model will generically be tuned to the critical point. To convincingly establish the criticality of the system in question, one must provide proof of criticality independent of the statistical model in use. The second objection is related to the model fitting procedure itself. Mastromatteo et. al. [8] suggested that models inferred from maximally informative experiments are more likely to be tuned to the critical point than not. A maximally informative experiment gather data optimally to distinguish one statistical model from another. However, Mastromatteo et. al. showed that "… the measure of the distinguishable distributions in a parametric family of models is directly related to

the susceptibility of the corresponding model" [8]. In other words, statistically inferred model parameters tend to be clustered near the critical point. Thus the inferred parameters cannot be used as conclusive proof of criticality. Direct experimental measurement of the model parameters is preferred. The third objection is the existence of long-range interaction. Long-range interaction can trivially generate apparent scale-free correlation [9], which can be mistakenly interpreted as a signature of criticality. A satisfactory proof of criticality using scale-free correlation must establish the absence of long-range interaction. The fourth and final object, to my knowledge, is that scale-free correlation can arise when a continuous symmetry is broken. In other words, the Goldstone theorem provides a trivial route to scale-free correlation without the need for the system to be tuned to the critical point.

There is no question that criticality is prevalent in the statistical models of living systems. However, the question remains: "Is the observed criticality a fundamental law of nature or an artifact of man-made experiment and theory?" With this question in mind, I will present recent exploration of natural swarms and flocks, where all aforementioned objections have been addressed to some degree. The method section will introduce relevant experimental and theoretical methods including: 3D tracking, the Vicsek model of swarms, and the maximum entropy approach. The result and discussion section will summarize recent experiments and statistical models of natural swarms and flocks, including the works of Cavagna et. al. [4,10], Bialek et. al. [5,11], and Attanasi et. al. [12]. Finally, I will briefly summarize the lessons learned and possible future directions.

Methods

The discovery of criticality in living systems is heavily driven by technological advances. In particular, the ability to track the behavior of large groups of living systems at real time has been invaluable. Large system sizes help avoid rare events which may spoil the generalizability of research conclusions. Further, large amounts of data are needed to construct of statistically significant models. The most significant recent advancement, in the study of natural swarms and flocks, is the success of the STARFLAG program (starlings in flight: understanding the patterns of animal group movement) [13,14]. The authors developed an array of cameras with a trifocal setup as shown in Figure 1 to solve the matching problem. The matching problem is the problem of identifying the same bird in two sets of cameras in a stereoscopic setup. A simple stereoscopic setup of a left and a right camera, similar to the left and right eyes, cannot easily reconstruct the 3D trajectories of individual birds in a large flock. The difficulty lies in the conflicting requirement of the 3D reconstruction problem and the matching problem. The two cameras should be well separated to triangulate the spatial coordinates of a bird. However, the matching problem becomes more difficult as the views of the two cameras become vastly different. The STARFLAG team solved this problem by placing a third set of cameras close to the right camera. The new camera helps solve the matching problem with the right camera. Then the combined information of the two right cameras make the matching problem with the left camera easier to solve. Finally, the left and right images can be combined to reconstruct the 3D trajectories of individual birds in a flock. It is interesting to note that one purpose of a flock flock may be to increase the difficulty of the matching and 3D reconstruction problems. Namely, a predator cannot easily identify and track the movement of an individual bird in a flock. The confusion caused to the predator is what protects

the flock. Regardless of interpretation, the STARFLAG program gave experimentalists access to the real-time dynamics of flocks of birds. These data opened the gateway to rigorous analysis of the complex behavior of natural swarms and flocks.
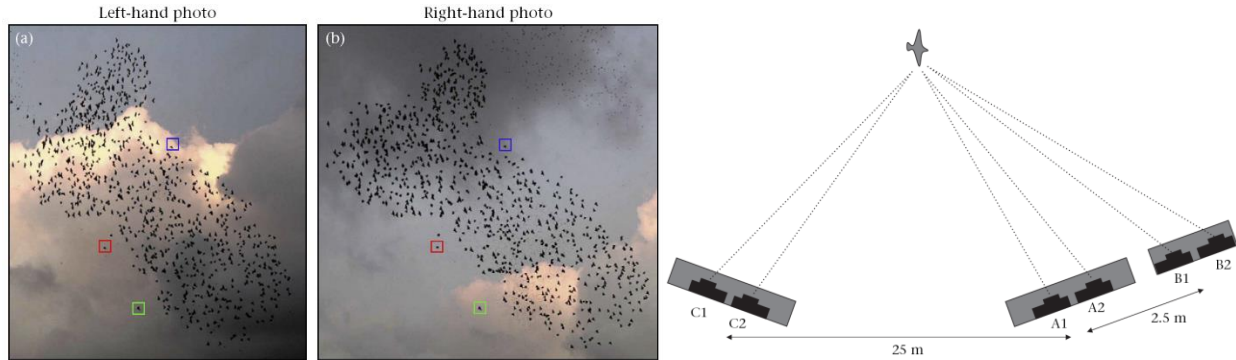

Figure 1 The matching problem in bird tracking is solved by a trifocal setup [13].

The raw experimental data collected in the STARFLAG program cannot be trivially interpreted. Therefore theoretical models are often used to assign physical interpretation to experimental data. In the traditional modeling approach, one constructs a statistical model using physical intuition and simplifying assumptions. The model parameters are often chosen to have well-defined physical meaning for easy interpretation. One such example is the Vicsek model for the swarming to flocking transition [15].

The Vicsek model is a remarkably simple model that uses microscopic rules to describe a collection of self-driven particles [15]. The model implements a simple rule of velocity alignment. Namely, "… *at each time step a given particle driven with a constant absolute velocity assumes the average direction of motion of the particles in its neighborhood of radius r with some random perturbation added.*" [15] There are three free parameters for a given system size $\eta, \rho,$ and v, where v is the distance a particle makes between two updates, η is the magnitude of the noise, and ρ is the density of the particles. This model was shown to exhibit a kinetic phase transition from no particle transport to finite net transport. The transition spontaneously breaks rotational symmetry and is analogous to the swarming-flocking transition in nature. The order parameter for the kinetic phase transition is the absolute value of the average normalized velocity

$$v_a = \frac{1}{Nv}\left|\sum_{i=1}^{N}\vec{v}_i\right|.$$

A phase transition from no transport to net transport can be driven either by decreasing noise at constant density or increasing density at constant noise as shown in Figure 2. The phase with no particle transport can be compared with the behavior of natural swarms, whereas the phase with particle transport is analogous to the behavior of flocks.
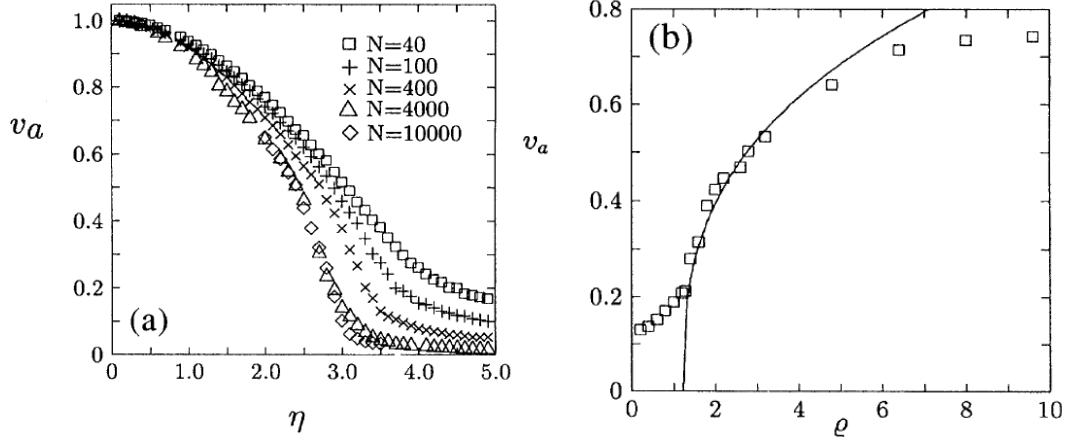
Figure 2 Swarm (low v_a) to flock (high v_a) transition in the Vicsek model, where v_a is the averaged normalized velocity of the entire swarm/flock [15].

While simple models such as the Vicsek model are easy to interpret, biases may be introduced by modeling assumptions. In general, if one failed to introduce an essential piece of physics in the model, or made an invalid assumption, then the resultant model would be inaccurate. Futher, it can be tricky to disentangle distinct properties of the physical system from intrinsic properties of the assumed model. The maximum entropy approach is an alternative procedure to construct a statistical model directly from experimental data in a manner that is relatively minimal and assumption-free. The goal of a maximum entropy is to reproduce given experimental correlations with the most random/least structured model. In the maximum entropy approach, one finds a model distribution of random variables $\vec{\sigma}$ that maximizes the Shannon entropy

$$S[P_m] = -\sum_{\sigma} P_m(\sigma) \log P_m(\sigma).$$

The model distribution $P_m(\sigma)$ is also required to satisfy the experimentally observed correlations of the system being modeled

$$\langle O_a(\sigma) \rangle_m = \langle O_a(\sigma) \rangle_r.$$

The explicit form of the model can be constructed by the method of Lagrange multipliers

$$P_m(\sigma) = \frac{1}{Z} \exp \sum_a \beta_a O_a(\sigma).$$

Finding the unique set of Lagrange multipliers that satisfy all constraints is a difficult problem known as the "inverse problem". Fortunately approximate methods exist to solve the inverse problem efficiently.

Results and Discussion

Cavagna et. al. tracked the 3D trajectories of individual starlings in 24 flocks, each consisting of a few hundred to a few thousand starlings [4]. The full velocities of each starling $\vec{v}_i$ was recorded,

as shown in Figure 3A. The full velocities were used to calculate the center of mass velocity of the entire flock. Velocity fluctuations $\vec{u}_i = \vec{v}_i - \frac{1}{N}\sum_{k=1}^{N} \vec{v}_k$ were then obtained by subtracting the flock velocity from the full velocities, as shown in Figure 3B.

Figure 3 Velocities and Velocity Fluctuation of Individual Starlings in a Flock [4].

The correlation function for velocity fluctuation was defined as

$$C(r) = \frac{1}{c_0} \frac{\sum_{ij} \vec{u}_i \cdot \vec{u}_j \delta(r - r_{ij})}{\sum_{ij} \delta(r - r_{ij})},$$

where $\delta(r - r_{ij})$ is a smoothed Dirac δ-function which picks our pairs of birds at separation r. c_0 is chosen such that $C(0) = 1$. The correlation length was defined as the distance at which $C(r)$ decays to zero as shown in Figure 4A and B.
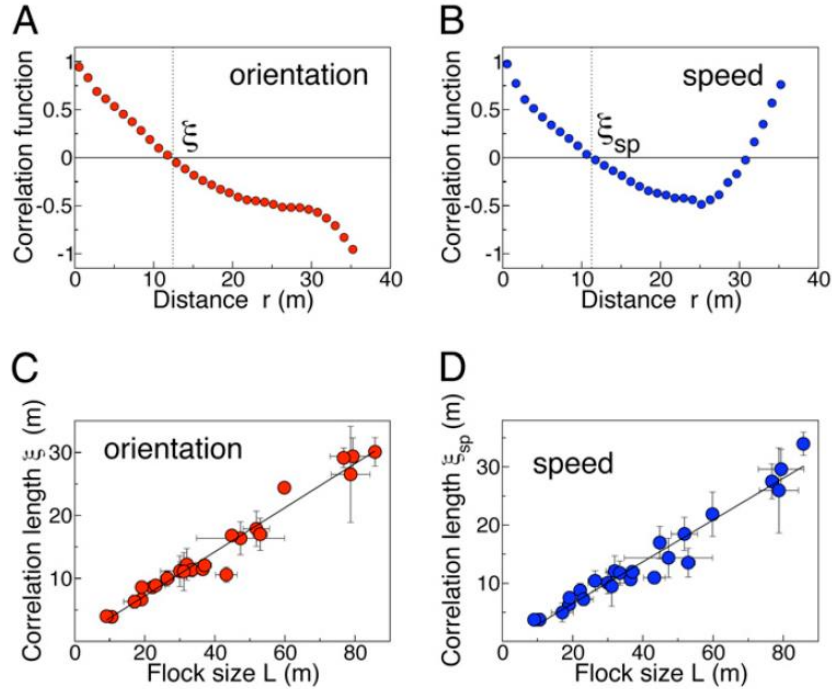

Figure 4 Correlation lengths for the orientation and magnitude of the velocity fluctuations [4].

The correlation length of velocity fluctuation can be seen to scale with the size of the flock in Figure 4C and D. This linear finite-size scaling of the correlation length $\xi(bL) = b\xi(L)$ implies that the correlation function has a special scaling form. Starting from the generic scaling form $C(r) = \frac{1}{\xi^\gamma} g(\frac{r}{\xi})$, where $g(x)$ is a dimensionless scaling function, we see that the finite-size scaling of the correlation function $C(r; L) = b^\gamma C(br; bL)$. By choosing $b = \frac{1}{r}$, we obtain

$$C(r; L) = \frac{1}{r^\gamma} f\left(\frac{r}{L}\right).$$

The above scaling form is considered scale-free because the only length scale that enters the equation is the size of the system L. The separation between neighboring birds, for example, is irrelevant. If this scale-free form holds for arbitrary flock sizes, then the asymptotic correlation function at infinite system size $C_\infty(r)$ decays as a power law $C_\infty(r) \sim \frac{1}{r^\gamma}$. The authors extracted γ as the slope of the correlation function versus flock size $C'(x \equiv r\xi^{-1} = 1) = \frac{1}{\xi^\gamma} g'(1) \sim -\frac{1}{\xi^\gamma} \sim -\frac{1}{L^\gamma}$. The fitted value of γ is statistically consistent with zero. In addition, the data for the correlation function in reduced units $x \equiv \frac{r}{\xi}$ collapsed well onto the same scaling function as shown in Figure 5. The derivative of the correlation function is shown in the inset. The slope of the derivative, marked with a red line in the inset, is an estimate of γ. The small value of γ indicates that the correlation function barely decays. Small γ implies that the correlation of velocity fluctuation of birds 100m apart is about as strong as that of birds 1m apart. The long-range correlation observed in both the orientation and speed of birds far apart allows the flock to act as one mind to external perturbation such as the intrusion of a predator. The authors noted that scale-free correlation in the "soft" degree of freedom (orientation) may be attributed to broken rotational symmetry by Goldstone theorem [4]. However, the scale-free correlation in the "stiff" degree of freedom (speed) must be due to some other mechanism. The authors suggested that the flock may be tuned to a critical point with maximal susceptibility [4].
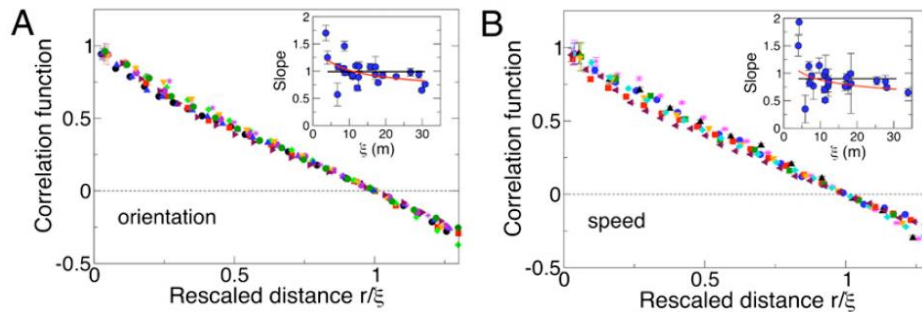

Figure 5 Data collapse for the correlation function of velocity fluctuations [4].

What is the microscopic origin of the observed scale-free correlation? Follow-up theoretical and experimental studies were performed to address this question. Intuitively, one may expect a bird to align the orientation and magnitude of its velocity to those of neighboring birds in order to maintain the cohesion of the flock. Such preference for alignment is analogous to the behavior of

a collection of spins in the equilibrium statistical mechanics context. Bialek et. al. exploited the connection between bird flock and spins rather literally [5,11]. They used the maximal entropy method to determine a Heisenberg-like statistical model for flocks of starlings. The statistical model was designed to be minimal. The assumed model allow each bird to interact with n_c of its neighbor with strength J. n_c and J are the only adjustable parameters

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

where $\vec{s}_i$ is the velocity fluctuation of bird i. The fitted model was able to explain the experimentally observed scale-free correlation as shown in Figure 6A. More interestingly, the fitted interaction range n_c is independent of the flock size as shown in Figure 6B.
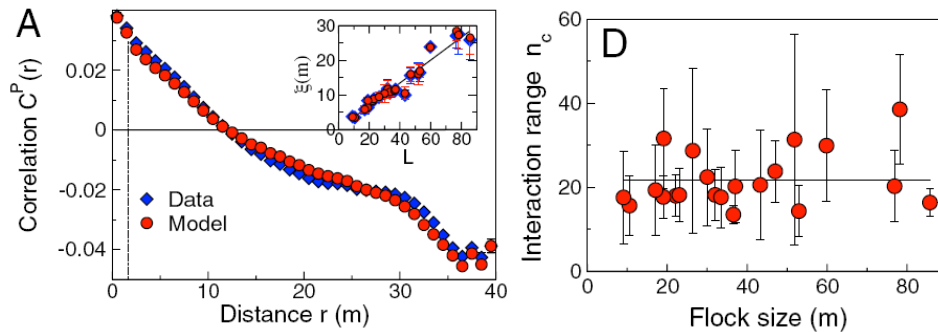

Figure 6 Correlation of velocity fluctuation from maximum entropy model and experiment [5].

The constant scaling of the interaction range with system size implies that each bird interacts strongly with a fixed number of neighbors regardless of their separations. This is an interesting and non-intuitive prediction. A follow-up study introduced a more complicated model [11]

$$P(\{\vec{v}_i\}) = \frac{1}{Z(J,n_c)} exp\left[-\frac{J}{4v_0^2}\sum_{ij=1}^{N}\left|\vec{v}_i - \vec{v}_j\right|^2 + \frac{\mu}{v_0}\sum_{i=1}^{N}v_i - \frac{g}{2v_0^2}\sum_{i=1}^{N}v_i^2\right].$$

Using the above model, Bialek et. al. showed that the model parameters inferred from experimental data were tuned to the critical point [11]. Taking the observation literally, the authors suggested that individuals in a block may change the way they interact with neighbors to achieve maximum flock cohesion. The claim that birds change their behavior to tune its parent flock to criticality is intriguing. However, criticisms of such a claim exist in the literature. An obvious objection to the above approach is that the non-equilibrium behavior of flocking cannot be captured by equilibrium statistical mechanics. For instance, the neighbors of a bird will change over the course of a flocking event. The change of neighbors is not captured by the Heisenberg-like models. Remarkably, Mora et. al. showed that the conclusions of Bialek et. al. [5,11] held up even when dynamical changes were incorporated into the model [16]. Assuming that equilibrium statistical mechanics can capture non-equilibrium systems, there are still at least three major questions that need to be answered before the claim of self-organized criticality can be established: Is the apparent self-

organized criticality a trivial manifestation of a noisy non-equilibrium dynamics in an equilibrium model [7]? Is the observed criticality a trivial result of long-range interaction [9]? Is the maximum entropy method biased towards critical models [8]?

The first two questions were addressed by Attanasi et. al. [12] and Cavagna et. al. [10], respectively. Attanasi et. al. tracked the 3D trajectories of midge swarms. They used experimental data to construct a Vicsek model. The density model parameter was directly measured as well as inferred. The data collected for the swarming insects were identical to those of the starling flocks. Namely, the velocities of individual insect in the swarm were recorded, and the correlation of velocity fluctuations were measured. The authors defined the dimensionless velocity fluctuation $\delta\vec{\phi}_i = \delta\vec{v}_i / \sqrt{\left(\frac{1}{N}\right)\sum_k (\delta\vec{v}_k)^2}$, where $\delta\vec{v}_i$ is the same velocity fluctuation as $\vec{u}_i$ defined in [4]. The correlation function of velocity fluctuation was defined to be

$$C(r) = \frac{\sum_{i\neq j}^{N} \delta\vec{\phi}_i \cdot \delta\vec{\phi}_j \delta(r - r_{ij})}{\sum_{i\neq j}^{N} \delta(r - r_{ij})}.$$

The point where the correlation function first reaches zero was taken to be the correlation length ξ. The integrated correlation was taken to be a proxy of susceptibility

$$\chi = \frac{1}{N} \sum_{i\neq j}^{N} \delta\vec{\phi}_i \cdot \delta\vec{\phi}_j \theta(r_0 - r_{ij}).$$

In addition to correlation and susceptibility, an additional order parameter was introduced

$$x = r_1/\lambda,$$

where r_1 is the nearest neighbor distance and λ is the range of interaction. x is related to the density parameter in the Vicsek model. By measuring this parameter directly, the authors addressed the criticism of possible bias in inferred model parameter [8]. The range of interaction for midges was chosen to be their average body length l, because the interaction between midges was assumed to be acoustic. All three order parameters ξ, χ, and x were directly measured as well as inferred from experimental data. The results from both approaches show striking resemblance as demonstrated by Figure 7. More importantly, the density order parameter x was found to adjust with the swarm size to keep the Vicsek model near the swarming-flocking transition critical point. This observation established that the insect swarm exhibits self-organized criticality. The direct measurement of the order parameter x ruled out the trivial explanation of Grinstein et. al. [7]. The authors offered two possible explanation for the observed self-organized criticality. The first is that insects adjust their behavior according to the size of the swarm in order to maximize the correlation length in the system. Namely x is adjusted at constant N. The second explanation is that insects with similar behavioral pattern swarm together until the size of the swarm has grown to a critical value. Namely N is adjusted at constant x. Both explanations are consistent with experiment. Detailed study of the behavior of individual insect will be needed to distinguish the two possibilities.
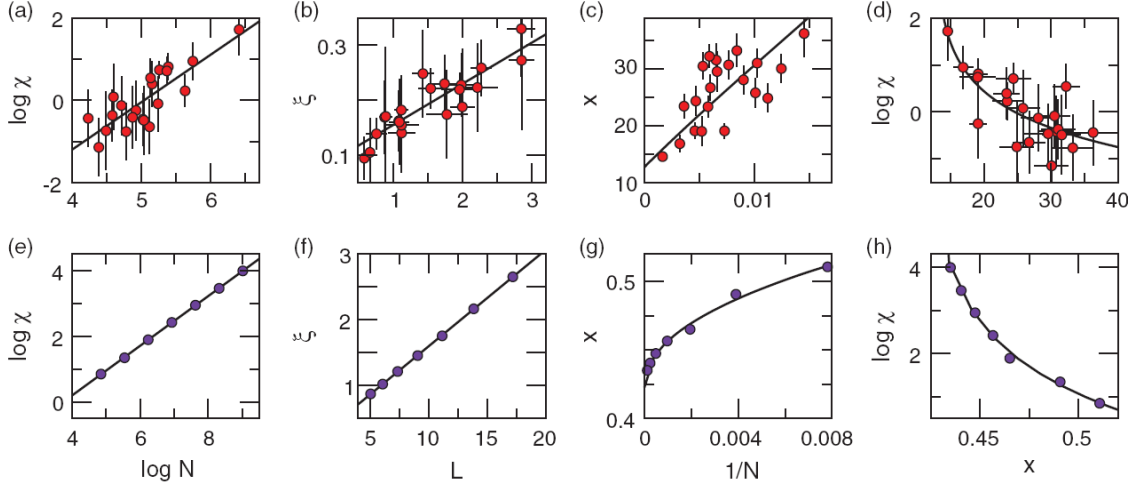
Figure 7 Finite-size scaling of natural swarm compared with critical scaling of the corresponding Vicsek model. The parameters of the Vicsek model were inferred from data. [12]

Finally, in the work of Cavagna et. al. [10], the authors used the maximum entropy approach to extract the range of interaction directly from experimental data instead of building a short-range interaction into the model. They considered the orientation of individual birds $\vec{s}_i \equiv \vec{v}_i/|\vec{v}_i|$ and constructed a minimal model with alignment interaction $J(n)$ that depend on the topological distance n between birds. The authors used the topological distance rather than the metric distance between birds because it simplifies the normalization of the two-point correlation function of orientations $\langle \vec{s}_i \cdot \vec{s}_j \rangle$. Maximum entropy was used to construct a statistical model that reproduced the experimental two-point correlation function. The resultant alignment interaction was shown to have a much shorter range than the correlation function as shown in Figure 8. This observation directly addressed the criticism that long-range correlation in starling flocks may have been trivially created by long-range interaction [9].
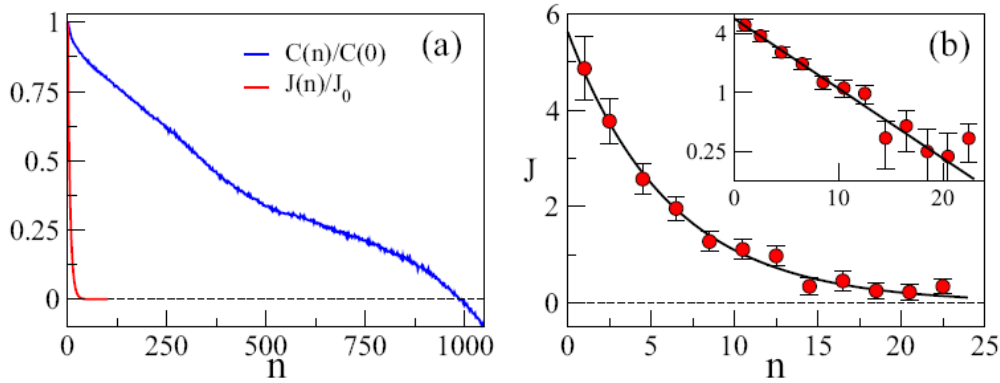

Figure 8 Maximum entropy model of flock velocity fluctuation resulted in short-range alignment interaction J(n), but long-range correlation C(n), where n is the topological distance between neighbors [10].

In summary, many criticisms have been raised and addressed since the pioneering work of the STARFLAG team, which demonstrated the existence of scale-free correlation in starling flocks

and raised the possibility of self-organized criticality [4]. Criticism of the existence of self-organized criticality lead to the direct experimental measurement of model parameter that convincingly demonstrated the critical nature of insect swarms [12]. Criticism of trivial scale-free correlation lead to novel theoretical modeling approach which directly inferred the range of interaction from experimental data [10]. Mounting evidence now demonstrates that natural swarms and flocks indeed exhibit peculiar cohesion analogous to equilibrium systems tuned to the critical point. The observed critical behavior is not an artifact of the theoretical modeling approach.

While the critical nature of insect swarm was convincingly established, the postulate of Bialek et. al. [1] that many biological systems exhibit critical behavior is far from verified. As evident from the study of natural swarms and flocks, inferred equilibrium statistical model by itself is not sufficient to establish self-organized criticality in living systems. Each proposed biological system, such as neural networks and family of amino acid sequences, need to be studied in detail. On the experimental side, techniques to directly track the real-time dynamics of large collections of living systems can acquire the most convincing evidence regarding the nature of the system. If enough details can be collected, then one can solve the "forward problem" of building macroscopic observation through microscopic rules rather than the "inverse problem" of constructing microscopic rules from macroscopic observations. Conclusions from the "forward problem" tend to be less ambiguous than those from the "inverse problem". As an example, Attanasi et. al. directly measured how the information of the turning of one bird is propagated through a flock [17]. The measurements convincingly established the almost lossless transmission of information through the flock, which directly supported the existence of scale-free correlation in starling flocks. On the theoretical side, the regime of validity of various modeling approaches need to be clearly defined to make convincing predictions. In particular, the objection of "Is the maximum entropy method biased to produce critical models?" [8] has yet to be satisfactorily addressed. One way to make progress is to construct a maximum entropy model of a system which does not exhibit critical behavior. If the inferred model is still tuned to criticality, then maximum entropy models cannot be used as a signature of self-organized criticality. One particularly interesting system to model is a colony of bacteria, where both scale-free correlation [18] and sub-critical long-range correlation [19,20] have been observed.

In conclusion, self-organized criticality has been convincingly demonstrated in natural swarms and flocks. However, it remains a question whether criticality is a fundamental property of living systems. The continuing advances in both experimental techniques and theoretical modeling approaches will enable us to explore the possibility of critical behavior of increasingly complex biological systems. By studying these biological systems, we can gain insight into the fundamental natures of critical behavior at the macroscopic scale as well as make connection with basic statistical mechanics.

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