New statistical tools for analyzing the structure of animal groups

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Abstract

The statistical characterization of the spatial structure of large animal groups has been very limited so far, mainly due to a lack of empirical data, especially in three dimensions (3D). Here we focus on the case of large flocks of starlings (Sturnus vulgaris) in the field. We reconstruct the 3D positions of individual birds within flocks of up to few thousands of elements. In this respect our data constitute a unique set. We perform a statistical analysis of flocks’ structure by using two quantities that are new to the field of collective animal behaviour, namely the conditional density and the pair correlation function. These tools were originally developed in the context of condensed matter theory. We explain what is the meaning of these two quantities, how to measure them in a reliable way, and why they are useful in assessing the density fluctuations and the statistical correlations across the group. We show that the border-to-centre density gradient displayed by starling flocks gives rise to an anomalous behaviour of the conditional density. We also find that the pair correlation function has a structure incompatible with a crystalline arrangement of birds. In fact, our results suggest that flocks are somewhat intermediate between the liquid and the gas phase of physical systems.

Apart from providing a coherent theoretical framework, condensed matter theory has developed some powerful tools for the quantitative study of ordering phenomena in many-particle systems. These tools may prove useful also for the study of animal groups. In this paper we wish to give an example of how fruitful this interdisciplinary approach may be. We will perform a statistical analysis of empirical 3D data of animal groups by using two classic tools of condensed matter physics, namely the conditional density and the pair correlation function. The quantitative measurements they provide are useful both to characterize in a novel way the structure of animal groups and to compare empirical data to numerical models.

1. Introduction

Group formation and coordinated motion are widespread phenomena in biology. Bird flocks are perhaps the most familiar example, because large groups of birds can be easily observed in the countryside and in urban centres, for example during their coordinated motion over the roost. Collective behaviour occurs in biological systems at various scales and in different spatial dimensions, from bacteria colonies to blood cells, insects swarms, bird flocks, fish schools and mammal herds [1–3].

Collective behaviour is a key concept also in physics. In particular, condensed matter theory has studied from a quantitative point of view collective ordering phenomena over the last 80 years [4,5]. In this context it has been rigorously proved that a system of many individual units (particles, magnetic moments, etc.) that interact only locally in space, can generate an ordered state with collective global properties. This idea represents a broader paradigm for many other disciplines. It is today a well-accepted idea, both in biology and in social sciences, that aggregations of individuals obeying only to local behavioural rules can self-organize into coordinated groups, with no need of centralized control [3].

2. Empirical observations

Our case study is represented by large flocks of European Starlings (Sturnus vulgaris). Large colonies of starlings spend the winter in Rome, Italy, where several roosting sites are located within the city urban area. Shortly before dusk starlings gather over the roost and form huge, cohesive flocks, ranging from ~100 up to ~50000 individuals. Flocks swirl over the roost, wandering in a wide, but confined area and occasionally merging to form larger groups. Attacks by peregrine falcons are frequent. In such cases, the flocks exhibit highly effective escaping manoeuvres, undergoing rapid contractions and expansions.

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Sometimes they split into two or more groups when attacked, to join together shortly after.

Our empirical observations use a trifocal technique, which is a generalization of stereo photography. The digital images were eventually processed with a novel set of algorithms based on computer vision, optimization theory and statistical mechanics. A detailed account of the empirical technique and the algorithms can be found in [6,7]. The images were collected during two seasons (winter 2005–2006, winter 2006–2007). We recorded more than 500 independent flocking events, in 80 daily sessions. Only a small percentage of these events were suitable for the algorithmic procedure, mainly because, in order to apply stereometric reconstruction, the flock must be at the same time in the field of view of all the cameras. We reconstructed 10 events during the first data-taking season and 15 in the second season. Each event consists in a series of up to 80 consecutive photographs of a single flock shot at 10 frames per second. For each instant of time we have the 3D coordinates of almost all the birds in the flock (around 90%). The flocks we have reconstructed are large, ranging from 400 to 4000 individuals.

3. Previous empirical results

The data collected during the first season have been partly analyzed in [8,9]. In this section we give a brief account of the results of the previous analysis.

3.1. Anisotropic structure and nature of the interaction

The clearest empirical indication of a non-trivial structure of flocks is the strongly anisotropic arrangement of individuals with respect to the direction of motion. Given a bird, its nearest-neighbours are more likely to be found on the sides rather than along the direction of motion. A study of how the anisotropy decays with the distance shows that each bird interacts with a fixed number (6–7) of neighbours, irrespective of their metric distances, rather than with all neighbours within a fixed radius [8]. This is in contrast with what assumed by most numerical models. Further analysis allowed us to estimate the exclusion zone around each individual, which is of the order of the wingspan (∼40 cm) and definitely smaller than the average nearest-neighbour distance, even in the densest flocks [9]. The interaction has therefore a twofold character: at short scales it has a metric nature, since the exclusion zone is a well-defined metric scale; at larger distances it has a topological nature, what matters is no longer the metric distance but the topological one. Moreover, the interaction must have a specific angular dependence (compared to the direction of motion), which is responsible for the anisotropy that we observed.

3.2. Density and packing fraction

The most obvious global characterization of a group is its density, namely the number of individuals per unit volume. Computing the density requires determining in a reliable way the volume of the aggregation. This is not trivial, because bounding box and convex hull (tools formerly used in collective animal behaviour) are very bad estimators of the volume. The technical way to define the volume of the group, as well as the method to eliminate the statistical bias introduced by the animals on the border, can be found in [7]. The analysis of [9] reveals that flocks vary very much one from the other in density, so that one cannot identify a well-defined typical value. The same variability is found in the average nearest-neighbour distance (NND), which is however always significantly larger than the size of the exclusion zone around each bird. Moreover, the local density of individuals within the group is not homogeneous: flocks are denser at the border than in the centre. Conversely, NND is smaller at the border than in the centre [9]. Birds at the border of the flock are more prone to predation than birds at the interior. Due to this, individuals on the border have the tendency to enter into the flock, where they can occupy a safer position. This tendency is stronger the closer a bird is to the border, so to create a pressure, and thus a density gradient, in the border-centre direction. This is a sort of crowded-bus-effect.

The density is not the best indicator of how packed a group is: clearly, a swarm with 100 bees/m^2 is far less packed than a flock with 100 starlings/m^2. The packing fraction is a more proper measure. It takes into account both the density and the size of the exclusion zone. We can idealize the flock as an ensemble of impenetrable spheres: each bird centre of a sphere representing the exclusion zone around it. The packing fraction, ϕ, is the ratio between the total volume physically occupied by all the spheres and the global volume of the aggregation. In formulas,

$$\phi = \frac{4}{3} \pi r_n^3,$$

where ρ is the density of the group, and r_n the size of the exclusion zone [10]. Small values of ϕ correspond to very diluted systems (gas-like), while large values to compact ones (liquid or crystals).

All the flocks we analyzed have packing fractions smaller than 0.012 [9]. This is a very small value indeed, compatible with a physical system in its gaseous phase, and more than fifty times smaller than the packing fraction of the liquid phase.

These results are somewhat puzzling: the density and packing fraction of starling flocks are very small indeed; in this respect we can say, using physical terms, that flocks are in a gaseous phase. However, unlike in a gas, correlations among individuals within a flock are very strong, giving rise to a clear anisotropy in the structure and to a striking border-to-centre density gradient. We want to investigate further this apparent paradox by using some more sophisticated tools.

3.3. New tools of analysis

We will use both the 2005–2006 and the 2006–2007 data, and look at some more complex collective features than the ones investigated so far. In particular, we shall focus on the density fluctuations and on the spatial distribution of individuals throughout the flock.

3.4. Homogeneity and density fluctuations

In a homogeneous system the density is the same, up to local fluctuations, throughout the whole system and on any scale. This means that if we consider a sphere entirely contained within the system, and compute the density in the sphere, i.e. the number of points in the sphere divided by its volume, the result is the same independent of the sphere’s size and position. Of course, there will be fluctuations, but their amplitude decreases as the sphere’s size increases; eventually, fluctuations become negligible when the sphere’s volume becomes very large. The typical example of a homogenous system is a stochastic Poisson point process, where point-particles are randomly generated in space with a given density ρ [11]. In this case, the density ρ_V within a sphere of volume V, is, on average:

$$\rho_V = \rho + \frac{\rho}{V^{1/3}}.$$

This means that if we consider many spheres of volume V, entirely contained within the system, the estimated average density will give a faithful estimate of the true density ρ, with fluctuations that decrease with the size of the spheres. Of course, the Poisson process is an extreme case, since there are no correlations whatsoever between particles. In general this is not true. In particular, we...
are interested in systems where the individual units (particles or birds) are strongly interacting. In this case we expect the local density to be influenced by the correlations present between particles. For example, if we consider a system of particles with an exclusion zone around them (a hard-core system), and we estimate the density using spheres with diameter of the order of the exclusion zone, we will find a density close to zero. However, if we consider spheres with larger size, the estimated density soon becomes independent of the spheres’ size and location, as in the Poisson case. In other words, if we observe the system on short length-scales, where the constraint due to the exclusion zone is effective, it looks rather inhomogeneous. But if we observe on larger length-scales, homogeneity is recovered. An opposite example would be a stochastic point process with short-range correlations, where particles are generated in space in clusters of a well-defined spatial extension. In this case, if we consider spheres of the order of the cluster size, the estimated density fluctuates enormously in space (depending on whether the sphere covers a cluster of particles or a void region), while the system becomes homogeneous on larger scales.

Therefore, when we say that a system is homogeneous we actually mean two things: first, that there exists a homogeneity scale (typically related to the characteristic scale of correlations), defined as the minimal size of the sphere whose density does not depend on its volume anymore; second, that we are observing the system on length-scale larger than the homogeneity scale. When these two conditions hold, it is meaningful to define the average density of the system, provided that it is estimated using a sphere’s size larger than the homogeneity scale itself. The other possibility is that a homogeneity scale cannot be defined. In this case the system is intrinsically inhomogeneous and the density depends on the scale at which we observe it. In this case defining an average density is tricky, if not meaningless. This is what happens, for example, for fractal distributions of points, where voids and structures are present at any scale [12].

3.5. The conditional density

Given the above discussion, before trying to estimate the density of a group of particles or individuals, it is important to check whether or not the system is homogeneous, and to verify that the homogeneity scale is well below the spatial extension of the aggregation. A practical and rigorous way to do that is to look at the so-called integrated conditional density \( I(r) \) [12]. This is obtained by measuring the density at various length-scales \( r \). For a homogeneous system, when \( r \) becomes larger than the homogeneity scale, the function \( I(r) \) must approach an asymptotic constant value, which is the most faithful estimate of the average density of the system.

Operationally, to compute \( I(r) \) we proceed in the following way. We consider an individual \( i \) in the group and a sphere of radius \( r \) centred in it. We then compute the density in the sphere, by counting all the individuals (excluding \( i \)) that lie within the sphere, and dividing by the volume of the sphere. We repeat for all the individuals \( i \) in the group that are acceptable as centres (see later), and we average. In formulas:

\[
I(r) = \frac{1}{n_i} \sum_{i=1}^{n_i} \frac{N_i(r)}{4/3\pi r^3},
\]

where \( N_i(r) \) is the number of points in the sphere of radius \( r \) centred in \( i \), and \( n_i \) is the number of possible centres (i.e. individuals) of the sphere. In an infinite system all the individuals in the group would be equally acceptable as centres. In finite groups however there is the problem of the border: if we consider an individual on the border or close to it, the sphere of radius \( r \) may include some empty space outside the aggregation and its density is therefore biased by such empty volume. If these individuals were considered as centres they would introduce a fictitious border-dependent bias [7]. To avoid this problem, one needs to consider as acceptable centres at scale \( r \) only those individuals for which the sphere of radius \( r \) is completely contained within the border. This method is known as ‘minus-sampling’ [11]. \( I(0) \) is called a ‘conditional’ density, because the density is estimated using as observation point one of the particles/individuals of the group.

In Fig. 1 we show the behaviour of \( I(r) \) for a first set of flocks. Each curve is computed using a single 3D reconstruction (1 instant of time of one flocking event); the various curves correspond to different independent flocks. Fig. 1 shows that for this particular set of flocks \( I(r) \) indeed reaches a constant plateau, which can be used as an estimate of the flock’s density. This is an alternative estimate of the density to the one given in the previous section. It is also more accurate because it does not need to determine the global volume of the group. The two estimates, despite being slightly different, are strongly correlated as shown in the inset of Fig. 1. The figure also shows, as previously reported, that the flocks are very heterogeneous in density, ranging from \( \rho \sim 1 \) in the densest flocks to \( \rho \sim 0.05 \) in the sparser ones.

Not only the asymptotic value, but also the shape of the conditional density can give interesting information. If we look at Fig. 1, we note that \( I(r) \) is close to zero for small \( r \), then it keeps increasing up to a broad peak, and finally reaches the asymptote. The vanishing values of the conditional density at short scales are due to the repulsion between individuals, since it is very unlikely to find more than one bird within spheres larger than the exclusion zone. As larger scales are considered, the estimated density increases and we expect it to reach a maximum when the spheres are large enough to include the first shell of neighbours of the focal bird. Indeed, the peak is located at scales of the order of the average nearest-neighbour distance. As \( r \) increases further, the homogeneity scale is overcome and \( I(r) \) saturates. The maximum scale \( r_{\text{max}} \) for which the function \( I(r) \) is defined is determined by the smallest dimension of the flock, given that the spheres of radius \( r \) must be completely included within the group. Starling flocks are rather...
thin, i.e. they have one dimension significantly smaller than the other two [9], and therefore $r_{\text{max}}$ gives a measure of the thickness of the group. The two lowest curves in Fig. 1 correspond to some of the largest flocks we analyzed (~3000 birds). On the other hand, the density is not correlated with the system size, and there are several flocks (not displayed in the figure) with low density and low values of $r_{\text{max}}$.

The function $\Gamma(r)$ can also be useful to monitor the dynamical behaviour of the aggregation during the same flocking event. In Fig. 2 we report two different cases. In the left panel the same flocking event is followed in time, each curve corresponding to the same flock at different consecutive instants (from bottom to top). In this case the flock progressively contracts, and the asymptote of the conditional density increases. During the contraction the flock becomes smaller, keeping the same proportions [9] and consequently its thickness ($r_{\text{max}}$) decreases.

From the previous analysis it may seem that flocks are homogeneous systems at large enough scales and that the function $\Gamma(r)$ has always a normal behaviour. However, this is not always the case. In Fig. 3 we report the case of four flocks where $\Gamma(r)$ keeps decreasing without reaching any constant value. In this case, either there is no homogeneity scale, or this is larger than the size of the group (these two cases are conceptually hard to distinguish). Practically speaking, it means that there are inhomogeneities in the flock, which occur at all the scales up to the system size. It is important to understand what is the origin of this inhomogeneity, and whether it is related to a peculiar spatial distribution of the birds. As already reported, previous analysis revealed that flocks are denser at the border than in the centre. This can be seen by computing the average nearest-neighbour distance as a function of the distance from the border, $r_i(d)$ (see inset in Fig. 4); in a completely homogeneous system this function must approach a constant value, while in starling flocks it keeps increasing [9] while moving towards the centre. We observe that those flocks where this

![Fig. 2. The integrated conditional density $\Gamma(r)$ is plotted for consecutive instant of times during the dynamical evolution of the same flocking event. (Left panel) The flocking event 32-06 undergoes a contraction. The numbers in the legend indicate the order in time. (Right panel) The flocking event 21-06 undergoes an expansion. The colour code is the same as in the left panel. (For interpretation of color mentioned in this figure the reader is referred to the web version of the article.)](image)

![Fig. 4. For two flocking events, we compare the behaviour of the conditional density with the one obtained for an ensemble of random points sets, generated with a radial density gradient from border to centre (see text). The curves corresponding to each event (symbols in red and blue) are obtained by averaging all the single-instant curves, after appropriate rescaling (see caption of Fig. 3). The flocking events considered are 25-08 (1300 birds, 32 instants of time) and 69-10 (1100 birds, 46 instants of time). The blue and red continuous lines correspond to the $\Gamma(r)$ computed for the random points ensemble, and are obtained by averaging over 50 independent samples. The exponent of the power law is fixed to fit the behaviour of the nearest-neighbour distance as a function of the distance from the border observed in the real flock (see inset). The decrease of $\Gamma(r)$ is very similar in real flocks and synthetic samples, apart from a different location of the peaks due to the absence of correlations in the random sets. To underline this similarity, the slope of the synthetic curves has been reported on the curves of the real flocks (dashed black lines). Inset: average nearest-neighbour distance $r_i$, as a function of the rescaled distance from the border $d_i(r_i)$, for the two considered flocking events (symbols). The continuous lines correspond to the same function computed for the ensemble of random, with an appropriate choice of the power-law exponent. For interpretation of color mentioned in this figure the reader is referred to the web version of the article.)](image)
ume with density decreasing from border to centre as a power law. The sphere is then mapped into an ellipsoid having approximately the flock’s proportions. The exponent of the distribution has been tuned to reproduce the function $r_1(d)$ of the real flock (see inset in Fig. 4). Then, the function $\Gamma(r)$ has been computed for the synthetic samples. It corresponds to the continuous lines in Fig. 4. The simulated line is consistent with the empirical data, confirming that the border-to-centre density gradient is at the same time responsible of the increasing behaviour $r_1(d)$ as well as for the anomalous decrease of $\Gamma(r)$.

Therefore, the density gradient between centre and border in starling flocks can be so large to suppress the homogeneity scale. When this happens, the ‘naïve’ density (total number of individuals over total volume) is only a very coarse estimate, whereas the full curve of the conditional density provides a more coherent description of the flock.

3.6. The pair distribution function

The conditional density gives important information on the homogeneity of the system and, as we have discussed, is influenced at short scales by the presence of correlations between individuals. There is however another two-point function, intimately related to $\Gamma(r)$, which is generally more appropriate to investigate the structure of an aggregation. This is the so-called pair distribution function $g(r)$ and it is typically used in liquid theory [13] to quantitatively characterize the degree of spatial order (gas/liquid/solid) in a system of particles. As we have seen the function $\Gamma(r)$ measures the average global density up to a distance $r$ around a given reference point/individual (the centre of the sphere). The function $g(r)$ is defined similarly, but instead of looking at the density up to scale $r$ focuses on the density exactly at distance $r$. Formally we have,
\[ g(r) = \frac{1}{4\pi r^2} \frac{1}{N_c} \sum_{j \neq i} \sum_{r} \delta(r - r_{ij}), \]

where $r_{ij}$ is the absolute distance between the centre $j$ and a neighbour $i$. Note that $g(r)$ is a distribution function (it contains a Dirac delta), meaning that to obtain a true density one needs to multiply for an appropriate spatial increment $dr$. Operationally, to compute $g(r)$ we proceed similarly to the integrated conditional density: we choose an individual $i$ and a sphere of radius $r$ around it. The sphere is acceptable only if it is completely contained within the border of the group. We then look in a small spherical shell of thickness $dr$ at the surface of the sphere and count how many birds are found within this shell. We finally divide this number by the volume of the shell $4\pi r^2 dr$. Note that to fix reasonably the ‘binning’ parameter $dr$ we need to make a trade off; if too small the resolution is high, but noise is too large (few points within the shells); if too large noise is small, but resolution is too low.

The functions $g(r)$ and $\Gamma(r)$ are directly related one to the other in the following way:
\[ \Gamma(r) = \frac{1}{4/3\pi r^3} \int_0^r g(s) 4\pi s^2 ds. \]

The function $g(r)$ is more sensitive than $\Gamma(r)$ to the detailed spatial structure of the aggregation. In a crystalline solid it exhibits very sharp peaks corresponding to the fixed distances among particles. These peaks do not decay at large values of $r$. Liquids on the other hand, unlike crystals have no long-range order. Yet, statistical correlations are still very strong: in liquids the pair correlation function has a clearly oscillating shape, with well defined peaks that flatten around the average density value for large $r$. It is zero at small scales (due to short-range repulsion between particles) and it exhibits a first very pronounced peak at the scale of the first shell of neighbours, with a few subsequent smaller peaks at the location of farther neighbours shells, whose amplitude decreases as $r$ increases. On the other hand, in a gas-like system with hard-core, only the first peak is visible, and the function decays to the density without further oscillations after this. In a Poisson point process (randomly distributed particles with no correlations – even not the hard-core) the $g(r)$ and the $\Gamma(r)$ are completely flat and constant. Since $\Gamma(r)$ is related to the integral of $g(r)$, the peak structure, if not too pronounced, can be smoothed by the integration. For this reason it is useful to look directly at the pair correlation function. On the other hand, being a differential quantify, the statistics used to compute $g(r)$ is smaller and the effect of noise is more pronounced.

In Fig. 5 we report the behaviour of $g(r)$ for various flocks at several densities (low densities in the inset). Despite the fluctuations, a structure with at least two peaks is visible. This is also true also at low densities, where however the peaks are much broader. The first thing to note is that this kind of pair correlation function is totally incompatible with any bona fide crystalline structure. The ‘crystal hypothesis’ put forward for fish schools in [14] has thus to be discarded for starling flocks. In fact, given the sparseness of the flocks, as quantified by the very low packing fraction of even the densest aggregations, one may have expected to find no structure at all, as in a gas. On the other hand, we know there are strong correlations, giving rise to a sharp anisotropy, and this does not fit the gas paradigm. The pair distribution function shows an intermediate behaviour: unlike a gas, it is not completely structureless, even though it does not show a clearly periodic liquid structure either. We believe that this is due to the fact that the interaction ruling starling flocks has a topological nature, which is completely different from the metric interaction ruling physical systems, like gas or liquids. A topological interaction is independent of the metric distance between birds, and it therefore introduces some effective long-range correlations. Whenever the density becomes very low, distant birds may still interact with a bond as strong as when they are closer. Therefore, unlike most physical systems, flocks can sustain structure and correlation in spite of very small densities and packing fractions. However, the structure is not as simple as that of a liquid, since the pair correlation function shows only two, rather weak peaks. Again, this is probably due to the topological interaction: birds have well defined mutual orientations (compare to the direction of motion), irrespective of their metric distance, so that the structure in shells, which shows off so clearly in liquids, is somewhat blurred in flocks.
4. Conclusions

In this work we have used some technical tools from liquid theory to investigate the spatial structure of starling flocks. An important remark in this respect concerns the quality of the 3D data set on which we performed our analysis. The properties we have been looking at, and in particular the two-point observables, require a large statistics to be appropriately estimated. It would have been impossible to compute in a reliable way the conditional mass or the pair correlation function in groups of a few tens of individuals. Besides, to avoid any bias due to the border of the flock, points close to the boundary have to be excluded from the statistical analysis [7], decreasing even further the statistical sample. Only thanks to the fact that our flocks are very large (from 400 to 4000 birds), we could overcome these problems.

The results of our analysis provide a more accurate characterization of the spatial structure of the groups compared to former studies. The conditional density shows that most flocks are, at large enough scales, homogeneous. In these cases the average density of the group is a meaningful concept, and it can be estimated in various ways. Yet, all flocks tend to be denser close to the border. When this border-to-centre density gradient is particularly strong, flocks appear inhomogeneous at all scales up to the system size and the average density is ill defined. The ‘naïve’ density may serve as a reference value, but it is not a rigorous estimate.

The values of density, exclusion zone and packing fraction show that all flocks we analyzed are very sparse systems. Still, a structure in space is present, as can be appreciated by looking at several observables. First of all, there is a strong anisotropy in the neighbours’ distribution, which implies a non-trivial angular dependence of the interaction between birds. Then, the pair correlation function presents at least two peaks, in correspondence of the first two shells of neighbours. This structure excludes completely any kind of crystalline structure for starling flocks. Compared to standard liquids, the structure is also quite weak, even though it is definitely more organized than in a random or gas-like system. Therefore, the pair correlation function is somewhat intermediate between a liquid and a gas. We have argued that this behaviour is linked to the topological interaction between birds.

We note that we only analyzed two-point observables that depend on the mutual distance between birds, but not on their mutual orientation. More refined quantities can be defined that also include a dependence on the angles, and would therefore be more appropriate to characterize the observed anisotropy. An example would be a pair correlation function measuring the local density at a given distance and angles from a reference bird. This function would however depend on three variables (rather than one), implying a lower statistics and larger errors. Thus, the choice of the variables and of the reference system (e.g. the preferential directions from which measuring polar and azimuthal angles) is crucial. Work in this direction is underway.

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