



## Empirical investigation of starling flocks: a benchmark study in collective animal behaviour

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Bird flocking is a striking example of collective animal behaviour. A vivid illustration of this phenomenon is provided by the aerial display of vast flocks of starlings gathering at dusk over the roost and swirling with extraordinary spatial coherence. Both the evolutionary justification and the mechanistic laws of flocking are poorly understood, arguably because of a lack of data on large flocks. Here, we report a quantitative study of aerial display. We measured the individual three-dimensional positions in compact flocks of up to 2700 birds. We investigated the main features of the flock as a whole (shape, movement, density and structure) and we discuss these as emergent attributes of the grouping phenomenon. Flocks were relatively thin, of various sizes, but constant proportions. They tended to slide parallel to the ground and, during turns, their orientation changed with respect to the direction of motion. Individual birds kept a minimum distance from each other that was comparable to their wing span. The density within the aggregations was nonhomogeneous, as birds were packed more tightly at the border than the centre of the flock. These results constitute the first set of large-scale data on three-dimensional animal aggregations. Current models and theories of collective animal behaviour can now be tested against these data.

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The aerial display of large flocks of birds is a stunning example of collective behaviour in animal aggregations (Emlen 1952). A paradigmatic case is provided by European starlings, *Sturnus vulgaris* (Feare 1984). These birds can be observed in many cities, where they establish their roosting

sites. Shortly before sunset, starlings return to their roost and, prior to retiring for the night, they form sharp-bordered flocks, ranging from a few hundred to tens of thousands of birds, which wheel and turn over the roosting site until darkness falls. Flocks show strong spatial coherence and are capable of fast, highly synchronized manoeuvres, either spontaneously, or as a response to predator attacks. Many features of bird flocking are present in other instances of collective animal behaviour. Fish schools, mammal herds and insect swarms represent other examples of animal aggregations that have fascinated biologists for many years (Gueron et al. 1996; Parrish & Edelstein-Keshet 1999; Krause & Ruxton 2002; Couzin & Krause 2003). Like starlings, individuals of these other taxa form cohesive groups that are able to sustain remarkable coordination and adaptability.

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Diverse instances of collective behaviour are found in many different fields of science, from the spontaneous ordering of magnetic moments in physics (e.g. Cardy 1996), the coordination of an ensemble of artificial agents with distributed intelligence in robotics (Cao et al. 1997; Jadbabaie et al. 2003), the emergence of herding behaviour in financial markets in economics (Cont & Bouchaud 2000), to the synchronized clapping in a concert hall (Neda et al. 2000; Michard & Bouchaud 2005) or the Mexican wave in a stadium (Farkas et al. 2002). In all these examples, collective behaviour emerges as the result of the local interactions between the individual units, without the need for centralized coordination. The tendency of each agent to imitate its neighbours (allelomimesis), can, by itself, produce a global collective state. Whenever this happens, we are in the presence of self-organized collective behaviour.

Although self-organization is undoubtedly a general and robust mechanism, its universality is an open issue. In physics, for example, universality is a well-defined concept: the same model and theory can be used to describe quantitatively very different physical systems, provided that they all share the same fundamental symmetries. The situation is more complicated in biology because the individuals that form a group are much more complex than particles or spins. For example, although fish schools and bird flocks behave similarly, certain collective patterns are present in one case and not in the other (Krause & Ruxton 2002). At some level, the specificities of the individuals and of the environment must make a difference. Therefore, in view of the highly interdisciplinary nature of self-organized collective behaviour, it is important to distinguish the general from the specific.

Models play a crucial role in this respect. Indeed, it was modelling exercises that revealed the general principles of how collective behaviour can emerge from self-organization. When it comes to modelling real instances of collective behaviour, however, we need to be more detailed. In this case, models must specify the minimal rules necessary to reproduce the empirical observations, so that we can distinguish between general phenomena and those specific to the system.

The field of collective animal behaviour boasts a wealth of models (Aoki 1982; Reynolds 1987; Heppner & Grenader 1990; Huth & Wissel 1992; Vicsek et al. 1995; Couzin et al. 2002; Inada & Kawachi 2002; Kunz & Hemelrijk 2003; Gregoire & Chaté 2004). Some of these were developed for fish schools, some for bird flocks, and some with a nonspecific biological target. In all cases, however, the models agree on three general behavioural rules: move in the same direction as your neighbours; remain close to them; avoid collisions. These rules are modelled using three distinct contributions to the interactions among the individuals, that is, alignment of velocities, attraction and short-range repulsion. In all cases, the models produce cohesive aggregations that look qualitatively similar to natural cases. However, each model has its own way of implementing the rules, dictated by the differing opinions as to which are the relevant mechanisms and by the different biological targets (e.g. fish versus birds). Of course, selection among different models can be achieved only by comparing their results with empirical evidence. Only empirical

observations can tell us whether or not the collective properties of a model are in quantitative agreement with the natural case. Moreover, the feedback between models and empirical data must confirm whether or not a certain rule is truly necessary to reproduce a specific biological feature.

Empirical data, then, are necessary both as a crucial input of the modelling approach and as a quantitative guideline for answering more fundamental questions about groups, their global features and biological function (see e.g. Parrish & Hammer 1997). Unfortunately, 3D data on even moderately large groups of animals are hard to obtain, and quantitative empirical data are scarce and limited to small groups (a few tens of individuals). Testing of the models has therefore been sporadic so far. At the same time, speculation on the microscopic origin and biological function of collective behaviour has outgrown empirical groundwork.

Empirical 3D studies on fishes have been done in laboratory tanks (Cullen et al. 1965; Partridge 1980; Partridge et al. 1980; Van Long et al. 1985; Tien et al. 2004). Data for birds, on the other hand, have been obtained in field observations (Miller & Stephen 1966; van Tets 1966; Major & Dill 1978; Pomeroy & Heppner 1992; Budgey 1998). These studies, however, have two major limitations: the number of individuals is small (limited to a few tens of individuals) and the group arrangements are loose, at variance with the huge, highly cohesive groups characteristic of collective behaviour. Both these drawbacks stem from a single technical problem: to reconstruct the 3D position of an object, all optical techniques (stereometry, orthogonal method, shadow method) require different images to be placed in correspondence (i.e. to be matched, Fig. 1a, b; Osborn 1997; Hartley & Zisserman 2003). For large and compact sets of featureless points, this problem is so severe that it has been suggested that these techniques are fundamentally inadequate to handle 3D biological aggregations (Aloimonos & Rosenfeld 1991).

Using statistical physics, optimization theory and computer vision techniques, we have managed to solve the correspondence problem. We developed an experimental technique capable of reconstructing the individual 3D positions in cohesive aggregations of several thousands of animals in the field (Cavagna et al. 2008a). We used this technique to collect quantitative empirical data on large flocks of starlings during aerial display. In this paper, we present quantitative and systematic data on the two main attributes of the groups: global properties (shape, size, orientation and movement) and internal structure (density profile and distribution of neighbours). Our aim in doing so is two-fold.

(1) We wish to provide a detailed analysis of the mechanistic laws of flocking, at the global and structural levels. This enables us to set a new experimental benchmark for testing existing models of self-organized collective behaviour.

(2) We wish to characterize the attributes of flocks as emergent properties of the grouping phenomenon. To this end, we attempt to place our results in the context of the biological function of grouping, individual fitness consequences, interaction with the environment and mutual interaction between individuals.

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