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COMMENTARIES

The STARFLAG handbook on collective animal behaviour: 1. Empirical methods

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The first speculations about collective animal behaviour date back to the observations of Pliny on flocks of starlings (translated by Rackham 1933). His remarks were necessarily qualitative, although reasonable too. Most of the hypotheses formulated almost 2000 years later were based on equally qualitative observations (Selous 1931; Emlen 1952). At times, the study of collective animal behaviour has been complemented by analogies with instances of collective behaviour in other fields of science, prominently physics (Radokov 1973). However, in the absence of any quantitative empirical insight, attempts to address the fundamental issues of collective behaviour rapidly became speculative.

It was only in the mid 1960s that the first empirical studies of collective animal behaviour in three dimensions led to some quantitative results. Cullen et al. (1965) studied small groups of up to 10 fish in a tank using the shadow method for three-dimensional (3D) reconstruction. The same technique was later used to study groups of up to 30 fish (Pitcher & Partridge 1979; Partridge 1980; Partridge et al. 1980). For the first time it was possible to measure interesting quantities, such as the average nearest-neighbour distance between individuals and their angular distribution. Several other studies of fish groups have been carried out since (see, for example, Van Long et al. 1985), although always with small groups.

Empirical 3D data for birds have been harder to come by, because working in the field imposes serious constraints on accuracy. The first studies (Sugg 1965; van Tets 1966) focused on two-dimensional estimates of flock densities using a single photograph technique. Major & Dill (1978), using stereometry, reconstructed the 3D positions of individual birds in small flocks of dunlins, *Calidris alpina*, and starlings, *Sturnus vulgaris* (on average 55 individuals per flock). Subsequently, Pomeroy & Heppner (1992) managed to reconstruct the trajectories of individuals in flocks of up to 11 pigeons, *Columba livia*, using the orthogonal method, and the dynamics of turns was unveiled for the first time. Ikawa et al. (1994) studied swarms of up to 20 mosquitoes in the field, and recorded the nearest-neighbour distance.

The time span over which these empirical investigations occurred and the small numbers of animals considered illustrate the difficulty of obtaining high-quality 3D data. Even the most recent studies, such as that by Budgey (1998), could only reconstruct the positions of a maximum of 61 lapwings, *Vanellus vanellus*, basically using the same technology as Major & Dill (1978) used. Compared to the advances in most experimental fields of science, the situation in 3D studies of collective animal behaviour is somewhat disappointing. The number of animals in all these studies is very low compared to natural conditions, where groups can range up to thousands, or even hundreds of thousands of individuals. As we note in our companion paper (Cavagna et al. in this issue), analysing small groups

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has some serious drawbacks, related to the preponderance of border effects. Moreover, compactness of the groups in all these analysed cases has been poor, owing to the technical difficulties of dealing with packed groups of animals.

Notwithstanding these criticisms, the first generation of empirical studies (1970–2000) was essential to establish the field of collective animal behaviour on a firm basis and their value should not be underestimated. They gave a first realistic perception of the structure of animal groups and their dynamic properties. Moreover, the experimental techniques were sound. Although there was a need for them to be refined and developed, to produce more substantial results, the evidence suggests that the direction taken by these studies was the right one.

However, in the last 20 years the main focus of the community has shifted to a different target, leading to a drastic reduction in the number of empirical investigations and of 3D field studies in particular. With the advent of large computers, the field of collective behaviour has been dominated by numerical models (Sakai 1973; Aoki 1982; Reynolds 1987; Heppner & Grenander 1990; Huth & Wissel 1992; Vicsek et al. 1995; Gregoire & Chaté 2004). Of course, models are extremely useful. The fundamental rules of a model can be kept under complete control, so that it is possible to understand clearly the connection between a certain phenomenon (the model's output) and the biological rules causing it (the model's input). It is mainly thanks to models that we now understand how collective behaviour may emerge as the consequence of self-organization, without the need for centralized coordination of individuals.

Although models can complement empirical investigation, they cannot replace it. Apart from some general issues that can be assessed on the basis of purely qualitative observations (e.g. the emergence or not of collective behaviour), a model's outcome should always be compared with empirical data. Without this essential 'ground truthing', models can proliferate in an uncontrolled fashion and, as a by-product, so does the number of different theoretical frameworks. Selecting the right model, and deciding the correct hypothesis, becomes merely a matter of taste, or guesswork, in the absence of real data.

Like Davis (1980), we believe that, within the field of collective animal behaviour, speculation has outgrown empirical groundwork. As we show in this paper, new tools from statistical physics and computer vision can now help to solve the major outstanding problems of 3D reconstruction, and so allow a much needed return to empirical data collection. Using such tools, we managed to reconstruct, for the first time, the 3D positions of several thousand individual birds in cohesive flocks under natural conditions (Ballerini et al. 2008a, in this issue). Compared to previous empirical studies, which considered a few tens of loosely organized animals, this is an advance of two orders of magnitude in the empirical study of collective animal behaviour. This result has been achieved in the context of STARFLAG (starlings in flight: understanding the patterns of animal group movement), a project financed by the European Commission in the context of the sixth framework programme. Within STARFLAG, biologists, physicists and computer scientists joined forces to study collective animal behaviour, with both an empirical and a theoretical approach. We report here the main methods developed by STARFLAG to obtain empirical 3D data of animal groups.

The key to achieving the STARFLAG results was the solution of the correspondence, or matching, problem. This has been the most serious bottleneck of all former empirical studies. When using any 3D technique, one must place into correspondence different images of the same animal. For example, in stereometry, one has two images of the group taken from two different points of view. To make a 3D reconstruction, one must take a given animal's image on one photograph and identify the corresponding image on the other photograph (Osborn 1997). The matching problem is particularly severe when there are many similar animals positioned very close to each other, which, unfortunately, is typical in natural flocks. Until now, no computer algorithm has been able to do this automatically, and thus the matching was done by hand. Clearly, this severely limited the number of animals and the density of the groups that could be studied. STARFLAG solved this problem by using a blend of statistical physics, computer vision and mathematics.

Some of the techniques used by STARFLAG may be unfamiliar to scientists working in the field of animal behaviour. In this paper, we explain all these techniques and provide the necessary tools to reproduce our results, illustrating our points using the 3D empirical study of STARFLAG. The paper is divided into two main parts. First, we explain how to set up an apparatus for the 3D reconstruction of large, cohesive and potentially distant animal groups. Our method is stereometry, so we also give a brief reminder of this technique. The second part of the paper explains how to transform a set of stereoscopic images into a list of individual 3D coordinates of the animals within the group. Here, our solution to the correspondence problem plays a major role. This part of the paper is, therefore, the most technical, as it was heavily inspired by statistical physics, but it is also the most innovative part of the entire work. Details of how to analyse 3D data sets are given in our companion paper (Cavagna et al. in this issue) where the techniques described can be applied to the results of numerical models, in addition to empirical data.

Setting up the Apparatus

We begin this section with a discussion of digital imaging, in particular the problems that arise when working with commercial, nonmetric cameras. We then introduce some basic notions of stereometry, and show how a careful analysis of the required experimental accuracy fixes most of the technical parameters of the apparatus, such as the distance between the cameras and the necessary alignment. Finally, we deal with the synchronization problems of standard commercial cameras, and how these can affect measurement accuracy.

The 3D reconstruction of animal groups can be made at two levels: the global and the individual. At the global