Limited interactions in flocks: relating model simulations to empirical data

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The mechanism of self-organization resulting in coordinated collective motion has received wide attention from a range of scientists interested in both its technical and biological relevance. Models have been highly influential in highlighting how collective motion can be produced from purely local interactions between individuals. Typical models in this field are termed ‘metric’ because each individual only reacts to conspecifics within a fixed distance. A recent large-scale study has, however, provided evidence that interactions ruling collective behaviour occur between a fixed number of nearest neighbours (‘topological’ framework). Despite their importance in clarifying the nature of the mechanism underlying animal interactions, these findings have yet to be produced by either metric or topological models. Here, we present an original individual-based model of collective animal motion that reproduces the previous findings. Our approach bridges the current gap between previous model analysis and recent evidence, and presents a framework for further study.

**Keywords:** collective motion; topological interactions; metric interactions; anisotropy; starlings

1. INTRODUCTION

The mesmerizing displays of animal collective motion have received much attention from scientists [1–5]. To the casual observer, animal groups such as shoals of fish or flocks of birds often appear to show tightly bound agglomerations that change direction and shape continually and almost instantaneously. Individuals within these groups self-organize into collectives that exhibit a high degree of structure [6,7]. How this structure emerges from the behaviour of individuals has been the main focus of research in this field.

It is now widely accepted that the movement of animal groups emerges from the interactions between many similar individuals within the group [8]. Highly influential individual-based models have been essential in highlighting how coordinated displays of collective motion can emerge from purely local interactions between neighbouring individuals [9–12]. These models implement simple behavioural rules for individuals; these can be loosely expressed as ‘get attracted to conspecifics’ and ‘avoid collisions’. The dominant theory has been that animal interactions are based on a ‘metric’ framework in which individuals apply these rules only to conspecifics within a fixed distance. Thus, a metric attraction rule would be ‘get attracted to those neighbours within the specified distance’.

A recent large-scale field study has, however, provided evidence that interactions ruling collective behaviour depend on a ‘topological’ rather than metric framework [13]. Using stereo-photography and multiple cameras, Ballerini \textit{et al.} reconstructed the trajectories of individuals within large moving flocks of starlings (\textit{Sturnus vulgaris}). They found a significant lack of nearest neighbours along the direction of motion of each individual. This only applied to the first six or seven closest neighbours on average. The distribution of directions to neighbours beyond the seventh closest was approximately uniform across an entire flock. Ballerini \textit{et al.} interpreted the anisotropy in the flock structures as a manifestation of interactions among individuals. Since the anisotropy disappeared at a constant topological distance (sixth or seventh neighbour), irrespective of flock densities, they reasoned that interactions between collectively moving animals depend on topological rather than metric distances. Within a topological framework, an attraction rule could be ‘get attracted to the closest six or seven neighbours, no matter how far away they are’. In summary, the difference between the two concepts is that a topological rule limits by the number of nearest neighbours, whereas the metric rule limits by the distance between individuals. In a metric model, this is most simply expressed as the number of interacting birds will change with density; by contrast in a topological framework it will not. Ballerini \textit{et al.} [13] argue that this is a key difference when it comes to explaining data.

Despite their importance, it has yet to be determined whether models adhering to either framework reproduce these findings. Here, we present an original individual-based model of collective animal motion, repeat the analysis by Ballerini and co-workers [13] for the first time on model simulations and reproduce the empirical findings.

2. MODELLING APPROACH

The idea in our modelling approach is to adopt a stochastic, asynchronous updating scheme that takes inspiration from previous models [14,15]. However, in
contrast to these approaches, we perform a weighted stochastic selection of pairs of interacting individuals, rather than using averaged responses to neighbours [14] or unweighted sampling [15]. Individuals can only react to conspecifics within their fixed spherical sensory zone, which is limited by a ‘blind volume’, a cone directly behind the individual [9]. Importantly, the probability of a particular pair of individuals being selected to interact in our algorithm depends on the distance between individuals. This selection rule is the most prominent novel feature in our modelling framework. This contrasts to previous models that account for inter-individual distances by scaling contributions of neighbours to a weighted average [10].

For a reference individual, $i$, we relate the probability $p_j$ of selecting a neighbour $j$, a distance, $d_j$, away to $d_j$ by

$$p_j \sim \frac{1}{d_j^\alpha}.$$  

We introduce a cut-off for values of $d_j$ close to zero to avoid the singularity there. The distance-dependent probabilities are normalized over all individuals within the sensory zone of a reference individual. Other relations between $p_j$ and $d_j$ are of course possible, but not explored here for simplicity. The sampling approach of our algorithm leads to individuals preferentially reacting to nearby conspecifics.

In brief, our algorithm consists of three consecutive steps, a fixed number of which are performed between separate recordings of model output.

1. Choose individual $i$ at random (equal probabilities, with replacement).
2. Pick ‘update partner’ $j$ of $i$ as described above.
3. Update the position and velocity of $i$ as described below.

Once a pair of interacting individuals is chosen, the focus individual reacts to its ‘update partner’ depending on the distance between them. At close distances, individuals move away from each other to avoid collisions ($d_j < r_\text{R}$), and at further distances ($r_\text{O} \leq d_j < r_\text{A}$) individuals get attracted to each other to maintain flock cohesion [9]. At intermediate distances, individuals align ($r_\text{R} \leq d_j < r_\text{O}$). The size of these behavioural zones, defined by the radii $r_\text{A}$, $r_\text{O}$ and $r_\text{R}$, remains fixed throughout the simulation. An additional feature of our model is that individuals move with differing instantaneous speeds according to how they react to their ‘update partner’ [16]. When individuals are attracted to their update partner, they move at twice the instantaneous speed than otherwise ($2v_\text{O}$ instead of $v_\text{O}$). Stochastic effects in our simulations are entirely generated by the internal dynamics of the algorithm.

The overall behaviour of our model is akin to animal behaviour producing cohesive flocks which change direction, but the exact algorithmic update of each individual has no direct physical meaning: it is the sum of a number of updates we observe and interpret. The movement of individuals between two separate model outputs consists of an average of the sum of a number of updates (averaging over changes in instantaneous speed) and the overall effect is for each individual to compose a kinetic average of its surroundings. Our model is therefore to be understood as follows: individuals react upon information they obtain from a sampling of their (fixed) sensory zone, biased negatively with distance, at a certain frequency (fixed in this study). Individual information intake is subject to asynchronies and small variations in individual update frequencies. This also results in a variation of individual speeds reported previously [16]. More details of our approach can be found in the electronic supplementary material.

### 3. RESULTS

Simulations of our model resulted in stable and coherent flocks with a sparseness to speed ratio comparable to empirical data (table 1) and non-constant speed distributions (see electronic supplementary material, figure S1). We compared our simulated flocks with the field data presented by Ballerini et al. by following their methodology as accurately as possible ([17]; A. Cavagna 2010, personal communication). The key observable of interest is the so-called anisotropy factor, $\gamma(n)$, which represents structural information with respect to the $n$th nearest neighbours. Averaged over many instances, a random spatial distribution of individuals will give rise to $\gamma(n)$ having a constant value of one-third, deviations from this value indicate structural information. Ballerini et al. [13] observed that in the starling flocks they were able to observe, film and analyse $\gamma(n)$ decayed from high values to the isotropic value of one-third after a critical number, $n_c$, of nearest neighbours, where $n_c \approx 6.5$. By simulating similar numbers of birds to those filmed, we are able to show that our new model is able to replicate this finding (figure 1). To further illuminate the nature of individual interactions in our model, we repeated the tests for a topological and a metric framework as suggested by Ballerini and co-workers [13], as seen in figure 2. To simulate flocks with different densities, we varied the extent of the zone in which individuals align with conspecifics ($r_\text{O}$) relative to the overall.
Figure 1. Anisotropy in two distinct model simulations (1000 individuals). The anisotropy factor $\gamma$ plotted against the nearest neighbour $n$ considered in its computation (averaged over 90 consecutive recordings). High values of this measurement quantify a lack of nth-nearest neighbours in the direction of motion averaged over all individuals in the simulated flocks. Note how $\gamma(n)$ decays with increasing $n$ until the internal flock structure becomes isotropic ($\gamma = 1/3$). Circles correspond to simulation sim3 and solid squares correspond to simulation sim1 in table 1. Error bars show s.e. The inset shows the function $\gamma(n)$ for empirical data (redrawn from Ballerini et al. [13]). Circles, flock 1; filled squares, flock 2.

4. DISCUSSION

Here, we present the first model analysis to reproduce the findings of what is currently the largest animal-tracking experiment in the wild. The tracking experiment raised the importance of how only a limited number of individuals dominated the interactions [13]. It also led to the definition that a model with a large radius of interaction in small flock densities and a small radius of interaction in high densities should be referred to as a topological model since the number of interacting neighbours does not change as the density varies ([13]; A. Cavagna 2010, personal communication). To date, it has not been clear of how these findings arise from the local interactions between individuals within the group.

The individual behaviour in our model does not explicitly limit an individual’s reactions to a fixed number of closest neighbours. The overall extent of the perceptive range is the same in all simulations; but the balance between attractive and aligning behaviour is altered to achieve differing sparseness in the groups. This balance also modulates the noise in our study; recall that there is no explicit addition of noise. Noise and its character are emergent from variation in update and type of interaction [18]. Despite our model maintaining features from previous metric modelling frameworks, it is clear that it behaves as a topological model in the manner defined by previous work ([13]; A. Cavagna 2010, personal communication).

The model we have constructed gives rise to emergent topological interactions consistent with the most prominent large-scale empirical study to date. Our model offers a parsimonious mechanism to explain the anisotropic nature and apparent limited interactions seen in this study.
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