A critical review of 'Self-organized aerial displays of thousands of starlings: a model'

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ABSTRACT

The paper we are reviewing combines theoretical mathematical models and recently acquired empirical data to create a computer model of the flocking of starlings (Sturnus vulgaris) above a roost [6]. Our review will analyse the underlying equations and show the development of our recreation of the computer model step-by-step. We found that the authors managed to replicate the complexity of this impressive collective behaviour. However, we also find their implementation of a key specific of starling behaviour, topological interaction, flawed at both a theoretical and technical level. We offer an improved implementation that avoids both of these problems.

General background

Starlings, although seen in North America as well, are a bird species native to Europe [4]. They can be found in both urban and rural settings and exhibit spectacular coordinated behaviour in their flocking events. This aerial display can be observed as the starlings return to their roosts around sunset after spending the day feeding elsewhere.

Also known as a 'murmuration', the aerial display comprises of each member of the flock moving in coordination with its group. Rules of coordination are based on separation, attraction and alignment [6]. These forces, among other complex interactions explored in this paper, lead to a phenomenon called self-organization, in which each individual mimics those around it and creates a comprehensive state of coordination with the whole flock [1].

Self-organization has been a well-explored area of research for mathematicians with the primary focus of modelling this type of behaviour as an interaction of various forces. It is not unique to one group of individuals, but is found anywhere from audiences clapping in a synchronous manner [3] to movements in schools of fish. However, there remains much speculation on modelling something so multifaceted.

For example, in this paper, one aspect of the model considers social forces. Hildenbrandt et al. offer a three-fold view of this force (investigated further in the next section), with a mention of internal motivation and decision making for each individual in the flock. This concept is not explored in greater depth in this study, but is thoroughly analyzed by one of the co-authors, Hemelrijk, in another paper: Hemelrijk argues that attraction, both positive and negative, is further specified into sexual attraction, dominance attraction and predatory response [5]. In fact, predators are a major component in other self-organization studies despite their absence in this one. Another co-author of this paper,

Carere, argues in a different study that synchronization of flight may be an anti-predatory response, as roosts are areas of high predatory traffic [2]. His argument is supported by an investigation of varying flocking patterns after a series of predatory perturbations.

Something to note, however, is that the aforementioned studies considering complex parameters in modelling self-organization are only able to gather qualitative data such as changes in flock shape. In addition to the lack of quantitative data on starling flocks, there is data lacking on starlings altogether. Hence, concepts such as evolutionary rationalization and mechanics of large flocks have an inadequate understanding. Ballerini's research team provided a major breakthrough in this area by gathering quantitative data on large starling flocks, which Hildenbrandt, Carere and Hemelrijk able to use to compare their model with. Techniques used to gather this data are elaborated in the 'Starling Data' section.

While data is gathered for large starling flocks, Hildenbrandt focuses on forces interacting on the individual level rather than the flock level. As vectors, these forces were modelled with respect to the local coordinates of the individual starlings, described in Figure 1.

Fish and the three basic social forces

The collective behaviour of shoaling in fish is similar to flocking in birds. However, the dynamics are simpler and can be effectively modelled with just three 'social forces': cohesion, separation and alignment. In the paper, the authors use the term social forces to refer to non-physical forces that encourage the animals to move in certain ways, depending on how their neighbors move. These three forces also appear prominently in flocks of starlings and so it is helpful to first

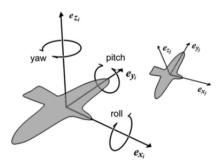


Figure 1. The three orienting axes of the starling: the vertical (yaw) axis, the forward (roll) axis, and the sideways (pitch) axis.

understand their effect in this simpler system at a conceptual level.

Cohesion is the force that encourages fish to move closer to their neighbors, creating a clustering effect. In this simplified system, each fish wants to move to a weighted average of the other fish's positions with the weighting depending on the distance to the neighbor. Thus, if a fish is within another fish's perceptual range, its position will be considered in the cohesion force. This force can be understood biologically as a desire for fish to remain close to avoid being picked off by predators.

Separation counters this and makes fish avoid other fish. In our simple model, this is shorter range force than cohesion to recognise the fact that its main purpose is to stop fish crashing into each other. Meanwhile, alignment steers fish so that they are pointing in the same direction. Again this is a short range force.

We also included the speed control equation used in the paper for this model, given by $\mathbf{f}_{\tau_i} = \frac{m}{\tau} (v_0 - v_i) \mathbf{e}_{\mathbf{x}_i}$. Importantly, v_0 is the fish's cruise speed and v_i is the fish's actual speed. Hence this equation provides a force inversely proportional to any deviation from the fish's cruise speed, resulting in fish tending toward their natural cruise speed.

Each force has a weighting associated with it, allowing the authors to experiment with different relative strengths to try to achieve a qualitative and quantitative match with the data. We created a model with the forces we have described, including sliders that allowed us to manually change the weightings of each force to investigate their effects. A notable finding is that when the ratio of cohesion to separation is high enough, the fish tend to gather in a sphere as shown in Figure 2. Furthermore, the rough size of that sphere seems to be proportional to this ratio [a) and b)]. However, after the ratio gets too low, the fish do not have a strong enough net attraction. This means a sphere cannot form and instead, the fish disappate throughout the space, as in c).

Differences of the Social Forces in Birds Cohesion

Fish can be modelled by having each individual consider all neighbors, with the weighting of the social forces inversely proportional to the distance of the neighbor. However, the paper gives birds more complicated neighborhoods.

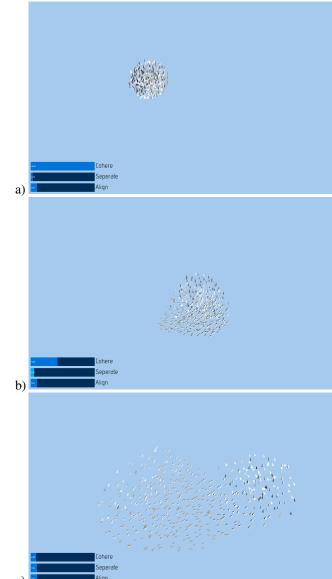


Figure 2. a),b),c) Investigating altering the ratio of cohesion to seperation in our fish computer model. Writing w_c, w_s as the cohesion and separation weightings respectively, a) has $w_c=10, w_c=0.33$; b) has $w_c=4.2, w_c=0.53$; and c) has $w_c=1, w_c=1$.

The full details for calculating N_i are given in the 'Topological Interaction' section. For now all we need to know is that N_i is the neighborhood of bird i i.e. the collection of other birds that bird i considers its neighbors. In the authors' implementation it is a sphere of radius R_i centered on bird i.

One notable thing about this paper in comparison to others in the same research area is its calculation of the neighborhood for cohesion. Most papers include a stronger force to the sides of the bird than the front, justifying this with the experimental data. Theoretically, this anisotropy in the cohesion force is due to a flying bird's field of vision being mainly directed to the sides rather than the front. An increased awareness in the lateral directions creates an increased desire to be closer to birds positioned laterally of the individual. Unusually for papers in this area, though

recognising a blind spot behind the birds, the authors apply an equal force in all other directions. They also note that within a sphere of radius r_h equal roughly to half the birds wingspan, there is no cohesion force. The outer radius R_i is discussed in the topological neighborhood section. The resulting area that the birds look for neighbors is as in Figure 3.

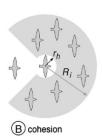


Figure 3. The neighborhood for the cohesion force

The cohesion force considers birds within only neighborhood described the The centrality facabove. tor is included to account fact that birds for on outside of the flock have the stronger desire to cothan birds on the here inwho are already close their neighbors. Equaachieves that by takthe modulus of the sum of the distances to its neigh-

(7)
$$C_i(t) = \frac{1}{|N_G(t)|} |\sum_{j \in N_G(t)} \mathbf{d_{ij}}| \text{ where } N_G = \{j \in N : \mathbf{d_{ij}} \leq 2\mathbf{R_i}, \mathbf{j} \neq \mathbf{i}\}.$$

 d_{ij} is a vector from bird i to bird j. If the bird is central in the flock, its closest neighbors should be evenly spaced around it, the vectors roughly cancel out, giving a low centrality factor. If the bird is instead on the extreme outside of the flock, its nearest neighbors will all be on one side, making the d_{ij} vectors add in the same direction and thus giving a high centrality factor making it want to cohere strongly.

Separation

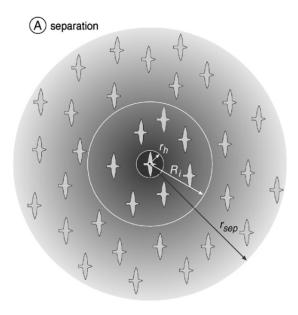


Figure 4. The neighborhood for the separation force

The separation is force is best understood by its effects within three different areas. If the neighbor is closer than $r_h = 0.2m$, there is a very strong force encouraging it to separate so this neighbor contributes significantly to the separation force. Biologically, this is to avoid a crash. If the neighbor is between $r_h = 0.2m$ and $R_{sep} = 4m$ distance, it

contributes a force given by $e^{\left(-\frac{r_{o}}{\sigma^2}\right)}$ which decreases with increasing distance, with a sigma chosen such that it reaches 0 at r_{sep} . Then past r_{sep} there is no separation force. Noting that $r_h = 0.2, r_{sep} = 4$, we can easily understand how the force changes with distance visually, in Figure 5.

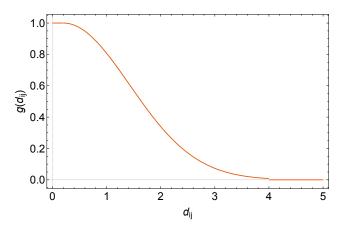


Figure 5. How the $g(d_{ij})$ term in the separation force changes with distance between neighbors d_{ij}

Note that it is possible that $R_i > r_{sep}$, in which case there may be neighbors in i's neighborhood to which i experiences no separation force. Indeed, a flock that is sparse enough so that birds are more than $r_{sep} = 4m$ from their nearest neighbors would have birds that experience no separation force and instead are only guided by the cohesion and alignment force.

Alignment

The alignment neighborhood is almost identical to the cohesion neighborhood, but without the inner sphere where the force is zero. It is also the simplest force to describe and steers the bird towards the average forward direction of its interaction neighbors. It is calculated by giving it a force in the direction of the difference between its direction and its interaction neighbors. This is calculated by looking at the normalised forward vectors for the birds.

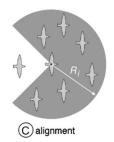


Figure 6. The alignment neighborhood

Starling Data

Data was collected on starling

flocks flying above their roost in Rome, employing a technique called 'stereo photography', in a study done by Ballerini et al. in 2008 [1]. This is a technique where photographs of the flock are taken from three different points of view, also known as the trifocal technique, and the photographed two-dimensional images are reconstructed digitally in three dimensions.

Similar to stop motion photography, photos are taken at ten

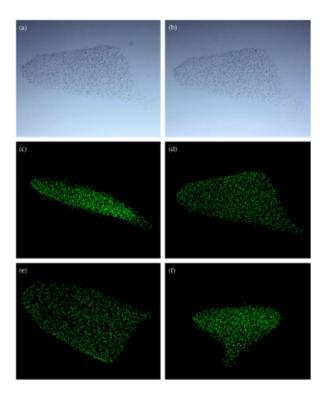


Figure 7. (Figure 1 a-f, Ballerini et al. 2008) 1a, b show a twodimensional photograph of a starling flock and 1c-f display various angles of the same flock in its three-dimensional reconstruction

frames per second, for eight seconds, giving a total of eighty photos from each angle. The distances between the cameras and the birds can be calculated and averaged, but a problem arises if the flock leaves the field of view. This is the issue that is addressed and solved by Ballerini's team with their three-dimensional reconstructions of positions and velocities of twenty-four flocking events. The number of birds in these events range from 122-4268, in a variety of flock shapes and densities. The authors of this paper use Ballerini et al.'s empirical data to compare with those generated from a model they created called StarDisplay.

Roost Force

The first notable difference between fish and birds is that whilst fish have no spatial preference within the body of water they move in, birds want to remain close to their roost.

To achieve this, the authors introduce a social force that acts in the direction of a fixed point above the roost. This is split into two equations: the vertical roost force and the horizontal roost force.

- (10) $f_{Roost_i} = f_{roostH_i} + f_{roostV_i}$
- $f_{RoostH_i} = \pm w_{RoostH} \left(\frac{1}{2} + \frac{1}{2}(e_{x_i} \cdot n)\right) e_{y_i}$ (11)
- (12) $f_{RoostV_i} = iw_{RoostV}$ (vertical distance)**z** where $z = (0, 0, 1)^T$

The vertical roost force is very simple. By setting the preferred vertical height as 0, (12) introduces a force that is linearly proportional to any deviation from this force, that always acts vertically.

The horizontal roost force is slightly more complicated and is stronger if the bird is flying away from the roost than if it is flying back to it. It acts in a lateral direction relative to the bird, encouraging it to bank [see Banking] and turn back towards the roost. The \pm sign is chosen so that this force reduces the distance the bird is travelling away from the roost.

Using the simulation of fish we previously developed, we added the roost force and some wings. Whereas the fish had to be enforced to stay within a fixed area, by adding forces that made it like there were solid walls to avoid, such as in a pond, this was no longer necessary with the introduction of the roost force as birds tend to return to a central position. The introduction of this roost force already started to generate the more complex behaviour associated with birds. [Pictures] However, qualitatively analysing the model we created at this point, it was still not possible for the flock to split into 'subflocks', a notable phenomena in real flocks. To do so, we need an extra contribution.

Topological Interaction

A major finding with the new empirical data was that starlings interact with their closest 6-7 neighbors, irrespective of the density of the flock [1]. In practice, this means that in a sparse flock, a starling will be affected by its neighbors that maybe be 20 or so metres away whilst in a dense flock it may be ignoring the movements of a bird even as close as 2 metres away. This idea that agents may react to neighbors based on a fixed number rather than distance is called topological interaction.

The equations used are:

(2)
$$R_i(t + \Delta u) = (1 - s)R_i(t) + s\left(R_{max} - R_{max} \frac{|N|_i(t)}{n_c}\right)$$

(3) $N_i(t) = \{j \in N : d_{ij} \le R_i, j \ne i\}$

(3)
$$N_i(t) = \{j \in N : d_{ij} \le R_i, j \ne i\}$$

Conceptually, we can understand these equations as implementing the interaction by imagining an invisible sphere of a certain radius R_i around each bird. If a bird is within this sphere, it is a neighbor and so affects the individual through the social forces described previously. N_c keeps track of the number of neighbors within this sphere. R_i , the adaptive interaction radius of the sphere increases or decreases so that the sphere includes the prefered number of neighbors. So if there are more than $n_c = 6.5$ neighbors in the sphere of adaptive interactive radius, it shrinks until it excludes enough birds so that it is at its prefered number. And if there are too few birds the sphere grows until it includes its preferred number.

In practice this implementation has several problems. Biologically, the equations suggest that each bird, instead of just noting the birds around it, keeps track of a seemingly arbitrary distance which it adjusts until 6 birds are within a sphere of this radius from it. This would not be a problem in itself, but the implementation also fails to actually implement the idea of topological interaction as described in the Balerini paper [1]. Technically, it means that there are possibly lengthy periods of time when birds are interacting with less than 6 or more than 7 neighbours.

We have created an implementation that avoids both of these problems. Instead of using equations (2) and (3), we found the topological neighborhood with just one equation.

Nearest neighbors of $s_i, N^*(s_i) =$ $\{s_j: \exists s_{k_1}, ..., s_{k_{(N-n_c-1)}} \text{ s.t. } |p_i - p_j| < |p_i - p_k| \text{ and } s_i \neq s_j\}$ where N is the flock size, n_c is the topological range.

Practically, we can implement this with each starling containing a list of all other birds in the flock. The starling then has a function that sorts them by the distance, choosing the closest 6-7 neighbors. This implementation avoids both problems inherent in the authors' implementation. Biologically it seems more reasonable with each bird just checking which ones are closest to it, obviously at an instinctive level, and reacting to them. More importantly it removes the need for a continually changing invisible sphere of influence that for the majority of the time, doesn't include the preferred number of neighbors. Therefore, our implementation means that each bird is always reacting with exactly 6 or 7 other birds, as in Ballerini's paper suggests starlings do [1]. Whilst it is not obvious initially how this will effect the overall simulation, as we are using an agent-based model, small changes at an agent level can produce a major change at the system level. Unfortunately, we do not have access to the authors' exact model and so we cannot do side-by-side comparisons to quantitatively and qualitatively investigate these differences.

On a technical note, as a sort takes $O(n \log n)$ in the worst case and every bird must perform this sort, we are now at an $O(n^2 \log n)$ time algorithm. The authors' implementation takes only $O(n^2)$ time, as each bird just has to check if the other birds are within a certain radius of it. However, if the primary goal is to create an accurate simulation, this slight reduction in speed should not be a problem.

Either way, implementing this interaction does a lot to create more complexity within the model, allowing break away groups as well as social forces to be passed more like a ripple effect through the flock rather than instantaneously. See Figure 8 for an example.

Physics and the Force of Flight

Although we did not implement this force in our simulation, we believe it is worth investigating the development of its model, which we will describe in this section.

The authors begin with some basic relations derived from aerodynamic laws:

- $Q = \frac{1}{2}\rho v^2$
- (2)
- $C_L = \frac{L}{QS}$ $C_D = \frac{D}{QS}$ (3)

Equation (1) describes the relation between dynamic pressure Q, air density ρ and the individual's speed ν . Equations (2) and (3) describe the lift and drag coefficients, respectively, in terms of the dynamic pressure, lift L, drag D, and wing area S. In order to generalize these expressions to a flock of starlings, Hildenbrandt's team has implemented some simplifying assumptions. This includes fixed wing dynamics, in which the birds' wings are static instead of flapping up and down, as they would naturally move. Furthermore, the air density and ratio of lift and drag coefficients are assumed to be constant, and the wing areas of all birds are assumed to be identical.

It is with these assumptions in mind that the authors are able to create a one-dimensional model given the three aerodynamic relations. They produce this model as follows:

First, the lift and drag are characterized: from (1) and (2), it follows that $L = \frac{1}{2}\rho S v^2 C_L$ and from (1) and (3), it follows that $D = \frac{1}{2} \rho S v^2 C_D$.

Second, the lift and drag are evaluated at cruise speed and actual speed. (Note: at cruise speed, lift balances weight and drag balances thrust). These relations were manipulated to obtain a one-dimensional model that only depends on actual speed.

$$L_i = \frac{{v_i}^2}{{v_0}^2} mg$$

$$D_i = \frac{C_D}{C_L} \frac{{v_i}^2}{{v_0}^2} mg$$
With this one d

With this one-dimensional model of lift and drag, the authors create a force of flight, which adds complexity to their overall model. In this sum, the bolded parameters indicate the vectors of their respective un-bolded parameters.

$$\begin{aligned} F_{flight} &= L_i + L_0 + D_i + D_0 = L_i + mg + D_i + T_0 \\ \text{In this sum,} \end{aligned}$$

 $\mathbf{L_i} = \mathbf{L_i} \cdot \mathbf{e_z}$, where E_z is the positive vertical direction

 $\mathbf{D_i} = -\mathbf{D_i} \cdot \mathbf{e_x}$, where e_x is the positive horizontal direction $T_0 = T_0 \cdot e_x$

g is the vector
$$(0,0,-g)^T$$
.

This relation is crucial to the model because it provides a time series of the starlings' position and velocity.

Banking

Banking is a naturally occurring phenomenon in bird flocks, which describes the manner in which flocks 'tilt' inwards while making a turn. It is driven by lateral acceleration, and hence, Hildenbrandt et al. argue that the magnitude of the inward banking angle, β_{in} , is relative to the magnitude of the lateral acceleration. They also include a weighting factor and a variable that represents a time step (see Figure 2[check]). Conversely, the magnitude of the outward banking angle, β_{out} , is relative to the sine of the inwards banking angle. The mathematical justification of this relationship is



Figure 8. A still from our fully-developed computer simulation, showing the complexity as subflocks emerge.

neither provided in the paper, nor can it be justified by hand.

More importantly, however, is the relationship between β_{in} and β_{out} . The authors argue that, once an individual experiences lateral acceleration and banks inward, it is not only experiencing the force of acceleration. There is a balance, as shown in Figure 9, of inward and outward forces, which contribute to the position of the starling at the end of each time step.

Incorporating banking, force of flight and steering results in an important relationship: using Euler integration gives both velocity and position at the end of each time step as seen below. (In this relation, v_i is the speed of individual i, m is its mass, p_i is its position and Δt is its updated time) $v_i(t + \Delta t) = v_i(t) + \frac{1}{2}(F_{\text{Correc}}, (t) + F_{\text{Figure}}, (t))\Delta t$

$$v_i(t + \Delta t) = v_i(t) + \frac{1}{m} (F_{Steering_i}(t) + F_{Flight_i}(t)) \Delta t$$

$$p_i(t + \Delta t) = p_i(t) + v_i(t + \Delta t) \Delta t$$

Assessing the Model

Upon setting up some initial parameters to mimic the empirical observations, the authors compare data from StarDisplay to data gathered in Table 1 of Ballerini et al. 2008 [1]. Both sets of values can be found in Table 2 of Hildenbrandt et al. 2010 [6], given here as Table 1.

Notably, this data is not generated with respect to the traditional scientific method. Instead of producing values and then comparing them with the empirical data gathered by Ballerini, Hildenbrandt et al. generate values until they look similar to the empirical data. Moreover, this model is judged both qualitatively and quantitatively in its similarity

to the empirical data.

Firstly, the flocks' shapes are characterized by their dimensions: I_1, I_2, I_3 . I_1 is the thickness, is observed to be the smallest of all three dimensions, i.e. the flock is relatively thin. Consequently, ratios of the other two dimensions are calculated with respect to thickness, and these values constitute the aspect ratios.

Secondly, the flocks' orientations are characterized by the scalar products of their orientation parameters: thickness, gravity and normalized velocity. The scalar product of I_1 and G is close to 1 in all flocks, which means that the yaw-axis (vertical axis) is parallel to the gravity vector. The scalar product of V and G is close to 0 in all flocks, which means that the velocity vector is perpendicular to the gravity vectors, i.e. birds are moving in the e_x and e_y directions for the most part. The scalar product of V and I_1 , albeit a little more variable than V and G, is also close to 0, indicating orientation of the yaw axis to be perpendicular to velocity. Its variability is the result of banking.

In this context, banking is explored as the cross product of I_1 and V (because they are perpendicular to each other and the flock is relatively "flat"). The authors argue that the degree of banking is correlated with the flock's path's curvature. During curving, the flock's shape changes; its thickness is not affected significantly, but it is compressed in other dimensions. The authors conclude that the variation in flock shape arises mostly during turning. Additionally, banking in

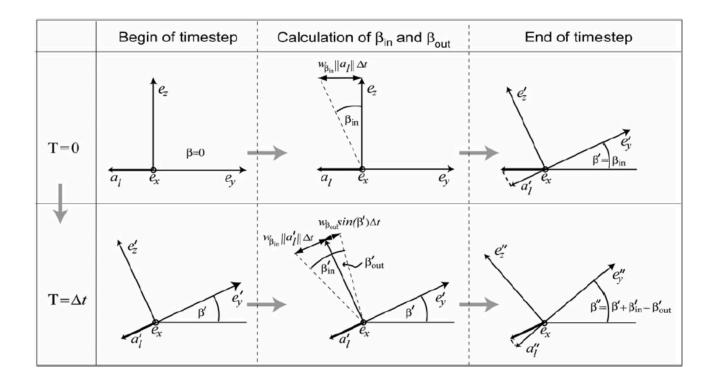


Figure 9. (Figure 3 from Hildenbrandt et al. 2010) Visualization of inward and outward banking angles and lateral acceleration for each time step

	Number of birds		Cruise speed (m/s)	Velocity (m/s)	NND (m)		Volume (m ³)	Thickness I ₁ (m)	Aspect ratios		Orientation parameters		
Flock/flocking event									I_2/I_1	I_{3}/I_{1}	$ I_1 \cdot G $	VG	V-I1
M32-06 (E32-06)	781	1.6	10.0	9.8 (9.8)	0.69 (0.68)	0.04 (0.08)	532 (930)	4.27 (5.33)	2.02 (2.97)	4.60 (4.02)	0.85 (0.89)	0.01 (0.06)	0.49 (0.20)
M28-10 (E28-10)	1246	1.75	11.0	10.8 (10.9)	0.70 (0.73)	0.1 (-0.06)	1500 (1840)	4.35 (5.21)	2.94 (3.44)	6.67 (6.93)	0.97 (0.80)	0.04 (0.09)	0.20 (0.41)
M25-11 (E25-11)	1168	2.0	9.0	8.8 (8.8)	0.78 (0.79)	0.1(-0.1)	1781 (2340)	5.87 (8.31)	2.15 (1.90)	5.40 (5.46)	0.99 (0.92)	0.03 (0.12)	0.08(0.14)
M25-10 (E25-10)	834	2.4	12.0	12.1 (12.0)	0.89 (0.87)	-0.06(0)	1609 (2057)	5.41 (6.73)	2.30 (2.65)	4.80 (4.98)	0.96 (0.99)	0.01 (0.18)	0.16 (0.18)
M21-06 (E21-06)	617	3.0	12.0	11.9 (11.6)	1.10 (1.00)	0.04(0)	2375 (2407)	6.42 (7.23)	2.18 (2.56)	4.41 (4.53)	0.99 (0.96)	0.04 (0.09)	0.01 (0.11)
M29-03 (E29-03)	448	3.0	10.1	10.2 (10.1)	1.00 (1.09)	0.04(0)	1218 (2552)	4.66 (6.21)	1.97 (3.58)	4.31 (5.96)	0.98 (0.97)	0.02 (0.27)	0.08 (0.06)
M25-08 (E25-08)	1360	4.5	11.9	11.9 (11.9)	1.26 (1.25)	0.02 (0.16)	5171 (12 646)	6.00 (11.92)	3.95 (3.32)	5.65 (5.12)	0.98 (0.95)	0.01 (0.14)	0.12 (0.12)
M17-06 (E17-06)	534	4.0	9.5	9.1 (9.2)	1.28 (1.30)	0.02(0.5)	3483 (5465)	6.46 (9.12)	2.75 (2.76)	6.10 (6.94)	0.98 (0.91)	0.03 (0.09)	0.08 (0.32)
M16-05 (E16-05)	2631	4.0	15.0	15.0 (15.0)	1.33 (1.31)	0.04(0)	17388 (28 128)	13.04 (17.14)	2.36 (2.46)	4.13 (4.07)	0.98 (0.90)	0.01 (0.19)	0.20 (0.25)
M31-01 (E31-01)	1856	5.4	6.9	7.0 (6.9)	1.54 (1.51)	0.05 (0.17)	11547 (33 487)	6.57 (19.00)	6.09 (2.44)	8.646 (4.07)	0.99 (0.95)	0.05 (0.09)	0.03 (0.13)
Statistical tests model	versus empi	rical data	(Supplementar	y Table S1)		ME1	ME8	ME7	ME2	ME3	ME6	ME4	ME5
Correlation tests (Sup-					C7			C5, C6	C3, 4	C1, C2			

Table 1. Data comparison. The values are given in pairs with the first values being the results from the simulation and the second values in brackets coming from Ballerini et al.

small flocks shows interesting phenomenon - the whole flock banks together instead of the banking beginning with an individual and following with all others.

Finally, other parameters that are measured include nearest neighbour distance (NND), flock density, volume, radius of separation, cruise speed and balance shift. Balance shift is the difference of the center of the flock's mass and the positional center of the flock, i.e. if it is above zero, most of the flock's weight occurs at the front of the flock, and vice versa if it is below zero. Both radius of separation and cruise speed are not comparable to Ballerini et al.'s data because they were not collected in the empirical setting. This links to a key point in this study's limitation: Ballerini et al. did not collect data as a time series, so changes of flock shape and density were not investigated. Rather, observations were made at a particular moment in time.

Limitations and Future Directions

One way to develop this model would be to introduce the effect of the birds having regular predators. This would presumably change the dynamics, possibly leading to an increased weighting in the cohesion force and possibly an increased weighting in the random force as birds are more fearful and more prone to sudden random movements. This would create the spontaneous large-scale movements that are noticeable in certain flocks of birds even in the absence of the usual predator.

It would also be interesting to look at introducing environmental factors such as the weather into the model.

Conclusion

To summarise, the paper is a notable contribution to a growing area of complexity science, synthesising new empirical data with a range of important recent theoretical developments in complexity science. Having analysed and recreated parts of the model StarDisplay, we recognise its ability to simulate the complexity of the collective behaviour of starling flocking. We also offer an improved implementation of topological interaction which could provide notable qualitative and quantitative differences in the accuracy of the model.

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