Some Causes of the Variable Shape of Flocks of Birds
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Abstract
Flocks of birds are highly variable in shape in all contexts (while travelling, avoiding predation, wheeling above the roost). Particularly amazing in this respect are the aerial displays of huge flocks of starlings (Sturnus vulgaris) above the sleeping site at dawn. The causes of this variability are hardly known, however. Here we hypothesise that variability of shape increases when there are larger local differences in movement behaviour in the flock. We investigate this hypothesis with the help of a model of the self-organisation of travelling groups, called StarDisplay, since such a model has also increased our understanding of what causes the oblong shape of schools of fish. The flocking patterns in the model prove to resemble those of real birds, in particular of starlings and rock doves. As to shape, we measure the relative proportions of the flock in several ways, which either depend on the direction of movement or do not. We confirm that flock shape is usually more variable when local differences in movement in the flock are larger. This happens when a) flock size is larger, b) interacting partners are fewer, c) the flock turnings are stronger, and d) individuals roll into the turn. In contrast to our expectations, when variability of speed in the flock is higher, flock shape and the positions of members in the flock are more static. We explain this and indicate the adaptive value of low variability of speed and spatial restriction of interaction and develop testable hypotheses.

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Introduction
The beautiful coordination in flocks of birds has raised scientific interest since ages in both laymen and scientists [1,2,3,4,5]. Flocks of birds have great variation in shape: often different flocks have different shapes and a single flock changes its shape over time [1,5,6]. Extreme changes in shape and density of flocks occur during the aerial displays of thousands of starlings at dusk. For instance, sometimes during turning the flock may change in relative proportions, density and volume [7,8], whereas at other times the shape of a flock may remain intact while only changing its orientation relative to the movement direction [4]. Further, during turning individuals may reposition their location within a flock in an amazing way [1,4,5,8]. This variability of shape differs markedly from what is described for schools of fish. Schools of fish are usually oblong in the movement direction [9,10,11]. However, under specific conditions, shapes of schools of fish are variable too, for instance, when a school is very large, and also when it is attacked by a predator. Very large schools have been described to be amorphous and to comprise extensions at the border, so-called pseudopodia, and sparse areas in the interior, called vacuoles, as if they consist of subgroups that move in somewhat different directions [12]. Similarly, in our model of very large schools (comprising up till 10.000 individuals) in which individuals have a limited view because it is blocked by those that are closest around them, shape appears more variable than in other models. This is due to the occurrence of subgroups with different movement directions in the school (Kunz and Hemelrijk, under review). Further, when being under attack of a predator, the shape of schools may become highly diverse. The shapes that emerge are for instance coined as ‘bend’, ‘flash expansion’, ‘herd’, ‘split’, and ‘hour glass’ [13]. Computer models of such attacks show that this diversity arises from the local differences of prey behaviour in the flock [14,15]. These depend on the prey’s distance to the predator: Individuals close to the predator are avoiding it, while those further away from the predator are coordinating with the other school members. In conclusion it seems that the variability of school shape may arise from local differences in movement behaviour, thus, from reduced synchronisation of the school of fish.

Since it is very difficult to study empirically [16] whether local differences in behaviour lead to a greater variation of shapes of flocks of birds, we will study it in a model of self-organised travelling groups, because such models have helped to create a better understanding of travelling groups in many aspects, such as their alignment [17,18,19] and direction choice [20,21] and, most importantly, also their shape. They show, for instance, that shape of a group of fish and birds changes when it is under attack of a predator [14,15,22], that shape of fish schools depends on the synchronisation of spawning tendency [23], and on density and school size [24,25,26].

Our models of fish schools have shown that the commonly observed oblong shape in the movement direction emerges as a side-effect of coordination and slowing down to avoid collisions [24,27,28]. The elongated shape emerges, for all school sizes, in models in two dimensions or three, when individuals move at slow speed or fast and when a single school comprises individuals of a single body size or of two sizes. Furthermore, in our models of fish schools, schools appear to be more oblong the greater the number of individuals they include. We have confirmed these patterns in
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Methods

The Model

The behaviour of each individual in StarDisplay is based on its cruise speed, its social environment (i.e. the position and heading of its nearby neighbours), its attraction to the roost and the simplified aerodynamics of flight which includes banking while turning [26]. Following other studies [2,24,33], we model social coordination in terms of (social) forces. Because flying implies movement in all directions, our model is three dimensional. We built the model in SI units and choose real parameter values where available (Tab. 1).

Details of behavioural rules

Each individual is characterised by its mass, m, its speed, v, and its location, p. Its orientation in space is given by its local coordinate system \( (e_x, e_y, e_z) \). Following the model by Reynolds [2], its orientation is indicated by its forward direction, \( e_x \), its sideward direction, \( e_y \), and its upward direction, \( e_z \), which changes by rotating around these three principal axes (roll, pitch and yaw) (Fig. 1).

As to its speed, a force, \( f_{si} \), (Equ. 1) brings an individual back to its cruise speed \( v_0 \) after it has deviated from it [24].

\[
f_{si} = \frac{m}{\tau} (v_0 - v) + C_2 e_x, \quad \text{Speed control} \tag{1}
\]

where \( \tau \) represents the relaxation time, \( m \) is the mass of the individual \( i \) and \( v_0 \) its cruise speed, \( v \) is its speed, and \( e_x \) its forward direction.

To make each individual interact with a specific constant number of its closest neighbours (i.e. topological range), each individual \( i \) in the model adjusts its metric interaction range, \( R_i(t) \) [24] following Equ. 2.3.

\[
R_i(t + \Delta t) = (1 - s) R_i(t) + s \left( R_{\text{max}} - R_i(t) \right) \frac{|N_i(t)|}{n_i} \tag{2}
\]

Adaptive interaction range

\[
N_i(t) = \{ j \in N_i; d_j \leq R_i(t); j \neq i \} \tag{3}
\]

Neighbourhood of an individual

where \( \Delta t \) is the reaction time, \( s \) is an interpolation factor, \( R_{\text{max}} \) is the maximal metric interaction range, \( N_i(t) \) is the neighbourhood of individual \( i \) at time \( t \), i.e. the set of neighbours of an individual \( i \) which is composed of \( |N_i(t)| \) neighbours from the total flock, \( n_i \) is the fixed number of topological interaction partners it strives to have and \( d_j \) is the distance between individual \( i \) and \( j \) given by \( ||p_i - p_j|| \) where \( p_j \) gives the position of an individual \( j \). Thus, the radius of interaction at the next step in reaction-time, \( R_i(t + \Delta t) \), increases whenever the number of interaction partners \( |N_i(t)| \) is smaller than the targeted number \( n_i \), and it is decreased if it is larger than that; it remains as before if \( |N_i(t)| \) equals \( n_i \). Here \( R_i \) can neither decrease below the hard sphere in which individuals are maximally avoiding each other \( r_h \) (Eq. 4, Fig. 2) nor increase beyond \( R_{\text{max}} \). \( s \), the interpolation factor, determines the step-size of the changes and thus, the variance of the number of actual influential neighbours.

As to separation, individual \( i \) is led by a force \( f_{si} \) to move in the opposite direction of the average direction of the locations of the \( |N_i(t)| \) others in its neighbourhood (Fig. 2). Following others [14,39], we have omitted the blind angle at the back (Eq. 4 and see Parameterization & Experiments). We gave individuals a hard sphere with radius \( r_h \) as mentioned above, in which they avoid each other maximally (Eq. 4). Outside the hard sphere, but inside the radius of separation \( r_{sep} \), the degree of avoidance of others decreases with the distance to the neighbour following a halved Gaussian, g(x), with \( \sigma \) the standard deviation of the Gaussian set so that at the border of the separation zone the force is almost zero, \( g(r_{sep}) = 0.01 \) (Eq. 4).

\[
f_{si} = -\frac{w_i}{|N_i(t)|} \sum_{i \in N_i(t)} g(d_{ij}) d_{ij}; \tag{4}
\]

\[
g(d_{ij}) = \begin{cases} 1 & ; d_{ij} \leq r_h \\ \exp \left( -\frac{(d_{ij} - r_h)^2}{\sigma^2} \right) & ; d_{ij} > r_h \end{cases}
\]

Separation
Here, $|N_i(t)|$ is the number of individuals in the neighbourhood of interaction (Equ. 3) and $d_{ij}$ is the distance from individual $i$ to individual $j$. The direction from individual $i$ to individual $j$ is specified by the unit vector $\mathbf{d}_{ij} = (\mathbf{p}_j - \mathbf{p}_i)/\|\mathbf{p}_j - \mathbf{p}_i\|$ and $\omega_s$ is the weighting factor for separation (Equ. 5).

As to cohesion, individual $i$ is attracted by a force $f_{ci}$ to the direction of the centre of mass (i.e. the average $x, y, z$ position) of the group of $|N_i(t)|$ individuals located in its topological neighbourhood, but not in its blind angle, in a way similar to models of others [27,28,33,34,35]. Here, $\omega_c$ is the weighing factor for cohesion (Equ. 5, Tab. 1). Within the radius of the hard sphere $r_{\text{sep}}$, we ignore cohesion with others (Equ. 5). To represent fear of predators [36] and build a sharp boundary of the flock [4], we make individuals cohere more strongly when they are at the border of the flock than in its interior by multiplying the force of cohesion by a factor indicating the degree to which an individual is peripheral (Equ. 5, 7). This factor, called ‘centrality’ in the group, $C_i(t)$, we calculate as the length of the average vector of the direction of all its neighbours $N_{N_i}(t)$ relative to the individual $i$, [37]. A high value indicates that the individual is peripheral; a lower value indicates that it is located more in the centre of the group. The ‘neighbouring’ individuals are all $|N_{N_i}(t)|$ individuals in a radius of twice the actual perceptual distance of the individual $i$ (Equ. 7).

Here, $D_t$ and $T_0$ are calculated by equation 16 by inserting $v_0$ for $v_i$. For more details on parametrization, see our previous study 26. Hildenbrandt H, Carere C, Hemelrijk CK (2010) Self-organized aerial displays of thousands of starlings: a model. Behavioral Ecology 21: 1349–1359 doi:10.1093/beheco/arq1149.

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force, attracted, Fig. 2BC). Interaction neighbours (the same neighbours as to whom it is
Ci
~
(15)
Reduced neighbourhood

\( f_{i} = C_{i}(t) \frac{w_{z}}{|N_{i}(t)|} \sum_{j \in N_{i}(t)} X_{j} \)  \( X_{j} = \begin{cases} 0; d_{j} \leq r_{h} \\ 1; d_{j} > r_{h} \end{cases} \) Cohesion (5)

\( N_{i}^{j}(t) = \{ j \in N_{i}(t); j \text{ not in the 'blind angle' of } i \} \)

As regards its alignment behaviour (Equ. 8), individual \( i \) feels a force, \( f_{ai} \), to align with the average forward direction of its \( N_{i}^{j}(t) \) interaction neighbours (the same neighbours as to whom it is attracted, Fig. 2BC).

\( f_{ai} = w_{ai} \left( \sum_{j \in N_{i}^{j}(t)} \epsilon_{nj} - \epsilon_{ni} \right) / \left( \sum_{j \in N_{i}^{j}(t)} \epsilon_{nj} - \epsilon_{ni} \right) \) Alignment (8)

Here, \( \epsilon_{nj} \) and \( \epsilon_{ni} \) are the vectors indicating the forward direction

of individuals direction of individuals \( i \) and \( j \) and \( w_{ai} \) is the fixed weighting factor for alignment (Tab. 1).

The 'social force' is the sum of these three forces (Equ. 9).

\[ \mathbf{F}_{\text{Social}} = f_{ti} + f_{ai} + f_{ej} \] Social force (9)

Individuals fly at a similar height above the sleeping site like real starlings [7], because we made them experience both in a horizontal and vertical direction a force of attraction \( f_{\text{Roost}} \) to the 'roosting area' (Equ. 10, 11, 12, Fig. 3). The strength of the horizontal attraction, \( f_{\text{RoostH}} \), is greater, the more radially it moves away from the roost; it is weaker if it is already returning (Fig. 3A). The strength is calculated using the dot product, i.e. the angle between the forward direction of individual \( i \), \( \epsilon_{ni} \), and the horizontal outward-pointing normal \( \mathbf{n} \) of the boundary. The range of the result \([-1..1]\) is transformed to \([0..1]\) by halving the dot product and summing it with a 1/2. The actual direction of the horizontal attraction force to the roost is given by \( \epsilon_{ni} \) which is the individual's lateral direction. The sign in Equ. 11 is chosen to reduce the outward heading. The actual direction of the horizontal attraction force is given by \( \epsilon_{ni} \) which is the individual's lateral direction. Vertical attraction, \( f_{\text{RoostV}} \), is proportional to the vertical distance from the preferred height \( z_{0} \) above the roost (arbitrarily called the zero level, Fig. 3B). Here \( z \) is the vertical unit vector.

\[ f_{\text{RoostH}} = f_{\text{RoostHi}} + f_{\text{RoostVj}} \] Roost attraction (10)

\[ f_{\text{RoostHi}} = \pm w_{\text{RoostH}} \left( \frac{1}{2} + \frac{1}{2} (\epsilon_{ni} \cdot \mathbf{n}) \right) \epsilon_{ni} \] Horizontal (11)

\[ f_{\text{RoostVj}} = -w_{\text{RoostV}} (\rho_{vg} z_{0}) \cdot z; \quad z = (0,0,1)^{T} \] Vertical (12)

The random force indicates unspecified stochastic influences (Equ. 13) with \( \xi \) being a random unit vector from a uniform distribution and \( w_{a} \) being a fixed scaling factor. The sum of the social force, the forces that control speed and ranging and the random force is labeled as 'steering force' (Equ. 14).

\[ f_{ej} = w_{ai} \xi \] Random force (13)

\[ \mathbf{F}_{\text{Steering}} = \mathbf{F}_{\text{Social}} + f_{ti} + f_{\text{RoostH}} + f_{\text{RoostVj}} \] Steering force (14)

Physics of flight in the model follows the standard equations of fixed wing aerodynamics which link the lift \( L \), the drag \( D \) and the thrust \( T \) produced by a bird to attain its current speed \( v \) (Equ. 15a, Fig. 4):

\[ L = \frac{1}{2} \rho S v^{2} C_{L}; \quad D = \frac{1}{2} \rho S v^{2} C_{D} \] Lift and drag (15a)

\[ L_{0} = \frac{1}{2} \rho S v_{0}^{2} C_{L}; \quad D_{0} = \frac{1}{2} \rho S v_{0}^{2} C_{D} \] Lift and drag at cruise speed \( v_{0} \)

\[ = T_{0} \] (15b)

\[ L_{i} = \frac{v_{i}^{2}}{v_{0}^{2}} L_{0} = \frac{v_{i}^{2}}{v_{0}^{2}} mg; \quad D_{i} = \frac{C_{D}}{C_{L}} L_{i} = \frac{C_{D} v_{i}^{2}}{C_{L} v_{0}^{2}} mg \] Simplified lift and drag (15c)
where \( \rho \) is the density of the air and \( S \) represents the wing area of the bird (of identical size for all birds). The quotient of \( C_L \) and \( C_D \) of the dimensionless lift and drag coefficients in the model is fixed, resembling the almost fixed ratio in reality [29]. When a bird is flying horizontally while maintaining a constant cruise speed \( v_0 \) its lift balances its weight \( mg \) (mass times gravity) and its thrust balances its drag (Equ. 15b, Fig. 4A). Division of \( L \) by \( L_0 \) and of \( D \) by \( L \) in Equ. 15ab yields Equ. 15c in which the lift and the drag only depend on the actual speed.

Gravity is directed towards the global ‘down’ direction, \( g = (0, 0, -g) \), the lift upwards operates towards the local ‘up’ direction \( e_z \) of the bird and the drag is pointing in the direction opposite to its actual ‘forward’ direction \( e_x \) (Fig. 4). Thus, the flight forces are:

\[
F_{\text{Flight}} = (L_i + D_i + T_0 + mg); \quad L_i = L \cdot e_x; \quad D_i = -D \cdot e_x; \quad T_0 = T \cdot e_z
\]

(16)

Real birds roll into the turn in order to make turns [30]. Because in the absence of external influence we assume that birds ‘intend’ to fly with their wings at a horizontal level in order to move straight forward, we give the model-birds a tendency to roll back. To represent banked turns (Fig. 4B), we first calculate the degree to which individuals want to turn, i.e. their lateral acceleration, \( a_l \), which is exerted by the steering force. Banking implies that the individual rolls around its forward axis in the direction of its lateral acceleration, \( a_l \). The lateral acceleration follows the first law of Newton (\( F = m \cdot a \)),

\[
a_{l} = \left( \frac{F_{\text{Steering},i} \cdot e_y}{m} \right) e_y
\]

Lateral acceleration

(17)

\[\tan \beta_{in} \| a_{l} \| \Delta t \quad \text{Roll in}\]

(18)

\[\tan \beta_{out} = w_{\beta_{out}} \sin(\beta) \Delta t \quad \text{Roll out}\]

(19)

where \( \beta_i \) is the actual banking angle, \( w_{\beta_{in}} \) and \( w_{\beta_{out}} \), respectively are the weights for rolling in and out the curve of turning, \( \Delta t \) is the update time and \( \beta_{in} \) and \( \beta_{out} \) are the angles over which an individual intends to move inwards and outwards. The tendency to roll into the turn increases with the strength of the tendency to turn sideways, which is due to the urge to coordinate with its
topological neighbours and to stay above the roost (Equ. 18, Fig. 4B). Once an individual has banked in the model, its tendency to roll back to the horizontal is proportional to its actual banking angle (Equ. 19). The actual banking angle (Equ. 20) is the sum of the current angle and the tendencies to roll-in and to roll-out. The ratio of \( \frac{w_{\text{in}}}{w_{\text{out}}} \) determines the roll rate. Note that by banking the individual creates a centripetal force at the cost of lift (Fig. 4B). Consequently it temporarily tends to move downwards.

After summing the forces of steering and flying, we use Euler integration to calculate the position and velocity at the end of each time-step \( \Delta t \):

\[
v_i(t + \Delta t) = v_i(t) + \frac{1}{m} (F_{\text{Steering}}(t) + F_{\text{Flights}}(t)) \Delta t
\]

\[
p_i(t + \Delta t) = p_i(t) + v_i(t + \Delta t) \cdot \Delta t
\]

where \( v_i \) is the velocity of individual \( i \), \( m \) its mass, \( p_i \) its location, and \( \Delta t \) is the update time. For the default values, see table 1.

**Parameterization and Experiments**

We have used the parameterization to realistic data of birds, especially of starlings, from our earlier version of StarDisplay (Tab. 1) [26]. To study the effects of locality of interaction we performed several experiments in the model [38], that concern 1) the group size, 2) the number of influential neighbours (i.e. topological range), 3) the attraction to the roost, 4) the banking and have similar deviations in their velocity. We calculate the correlation length in three steps as was done for real starlings [40]. First, the deviation \( u_i \) of the velocity of each group member \( i \) of that of the centre of gravity is calculated (Equ. 23)

\[
 u_i = \bar{v} - v_i \quad \text{Deviation from flock velocity} \quad (23)
\]

Here, \( v_i \) is the velocity of individual \( i \), \( \bar{v} \) is the velocity of the centre of gravity. Further, the correlation function of the deviations of velocity among all individuals \( C(d) \) measures the average inner product of the deviations of velocity between individuals at distance \( d \) (Equ. 24):

\[
 C(d) = \frac{1}{N} \sum_{i

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Figure 5. Measuring of shape. Two ways of measuring shape. Left: Measurement of \( I_3/I_2 \) based on PCA analysis. Right: measuring of elongation, \( L/W \), length in the movement direction and width orthogonally to it. Birds fly from left to right, flock is shown from above.

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\[ C(d) = \frac{1}{c_0} \sum_{ij} \mathbf{u}_i \mathbf{u}_j \delta(d - d_{ij}) \]  
Correlation function \( (24) \)

Here, \( \delta(d - d_{ij}) \) is a smoothed Dirac \( \delta \)-function, \( d_{ij} \) is the distance between two birds and \( c_0 \) is a scaling factor such that \( C(0) \approx 1 \). High values of \( C(d) \) indicate strong correlations in velocity among all flock members at a certain distance. As is typical in flocks the values of the correlation are greater for short distances and become negative for large distances. The correlation length \( \xi \) is the distance among birds for which the correlation function is zero. This value reflects the average size of the correlated domains (i.e. the size of the coordinating subgroups).

Polarization is measured globally and locally. Polarization is measured as:

\[ \Phi_i = \frac{1}{|N_i|} \sum_{j \in N_i} \frac{\mathbf{v}_i \cdot \mathbf{v}_j}{||\mathbf{v}_i|| \, ||\mathbf{v}_j||} \]  
Local polarization \( (25) \)

\[ \Phi_i' = \frac{1}{|N_k|} \sum_{j \in N_k} \frac{\mathbf{v}_i \cdot \mathbf{v}}{||\mathbf{v}_i|| \, ||\mathbf{v}||} \]  
Global polarization \( (26) \)

Here, \( N_i \) is the set of individuals in the local neighborhood of individual \( i \) (Eq. 4), \( N_k \) is the set of \( |N_k| \) individuals in the flock, \( \mathbf{v}_i \)

is the velocity of individual \( i \) and \( \mathbf{v} \) is the velocity of the flock, i.e. the average velocity of its members. Since polarization is based on the dot product of unit vectors it ranges between 0 and 1. Higher values indicate stronger polarization, i.e. higher alignment in the flock.

The average degree of banking is the average over all flock members of the angle between the wings and the horizontal plane.

**Results**

In the model sharp turns in the trajectory of a flock arise because individuals that are outside the sleeping site are attracted back to it (Fig. 3, Fig. 6A). The turning involves banking (Fig. 6B) and whereas this hardly affects the thickness of the flock, \( I_1 \) (Fig. 6C), it strongly distorts the aspect ratio, particularly of the longest over the shortest dimension, \( I_3/I_1 \) (Fig. 6D) and the volume of the flock (Fig. 6E) (and the average distance to the nearest neighbour; data available on request).

In line with our hypothesis that variability of shape increases when individuals in a flock are less synchronised, higher variability of shape occurs a) when flock size is larger, b) when the number of interaction partners is smaller, c) when the flock turns more strongly, d) when individuals roll into a turn versus when they do not, but, in contrast to our hypothesis, variability of shape decreases when the variability of speed is higher.

The shape of large flocks is more variable than that of small ones, because individuals at different locations in the flock are more likely...
to differ in velocity (Movie S2). In larger groups larger sub-flocks form, as reflected in the longer correlation length of the deviation of the velocity from the average (i.e. a scale free correlation, Fig. 7AB). These sub-flocks are not only larger but also more diverse in their movement direction. This becomes clear from the decrease of the global polarisation with flock size, while the local polarisation remains the same (Fig. 7C). Consequently, the variability of behaviour is higher in larger flocks. Besides, in large flocks some individuals bank to return to the roost sooner than others, and consequently turn and lose height earlier than others (Movie S3). By

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**Figure 7. Deviation from average heading and velocity.** Deviation from the average of heading and velocity among individuals in the flock. A) Scale free correlation between correlation length of deviation of velocity from that of the centre of gravity versus length of the flock for default values (flock length is measured by the largest distance (in m) between two individuals in the flock); B) Corresponding snapshots of flocks true to scale. From left to right: N = 200 and L $< 20$ m, N = 2000 and L $< 50$ m. C) Polarisation (global and local) versus number of individuals in the flock for default parameters and high number of interaction partners (i.e. 50), N = flock size, lines (continuous and striped) indicate local polarization, points indicate global polarization (fat dots: default parameters, stars: 50 interaction partners).

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subsequently meeting those above the roost that are still flying outwards, the flock changes shape (aspect ratio) and volume (Fig. 6DE). When the total flock is smaller (N = 200 instead of N = 2000), the shape is more static (Fig. 6DE, movie S4) because a) interactions are more global and b) individuals experience more often the same environment (above or outside the roost).

Similarly, when they have fewer interaction partners, different flock members are more prone to behave differently, because they react to different local environments (Movie S3). When they have more interaction partners synchronisation is stronger which can be seen from two facts (Movie S5). First, the sub-flocks are larger, which is apparent from the stronger increase of the correlation length with the flock size when individuals interact with more neighbours (i.e. with 50 neighbours the slope of the regression line is 0.79 whereas with 6.5 interacting neighbours it is 0.44) and second, their movement direction is less diverse. This is apparent from the stronger local and global polarisation (Fig. 7C, Global polarisation: Wilcoxon matched-pairs signed ranks test, N = 6, TAU = 0, P<0.05 two-tailed; Local polarisation, Mann-Whitney U test, N=200, z = 9.90, P<0.0001***). Thus, the number of sub-flocks is lower, and their diversity of movement direction is lower and therefore the variability of shape of the flock is less than when there are fewer interaction partners (Fig. 6DE, movie S5 vs S3).

Strong turning happens when individuals fly outside the roost. In large flocks with few interaction partners strong turning induces more variability of shape than moving above the roost with only mild turns (Movie S6). Strong turning, compression of volume of the flock and changes in altitude (26) happen only if individuals roll into the turn. The changes in altitude are a consequence of a temporary reduction of effective lift at the cost of the generation of a centripetal force. If individuals cannot roll, they only turn mildly, remain at the same altitude and the shape of the flock is oblong and continuously bends along the outer edge of the sleeping site (Movie S7). This shape does not resemble real flocks of starlings, because it lacks vertical movement and it is static.

Even if we completely omit the force that causes individuals to return to cruise speed (equation 1) it appears possible to increase the variability of speed only marginally from a coefficient of variation of 0.01 to 0.015. This is probably a consequence of the stabilising effect of aerodynamic forces. This increase in speed variability is too small to result in qualitative differences in variability of shape when making sharp turns over the roost. However, when flock members are turning only mildly while flying above the roost, even this small increase of the variability of speed causes flocks of almost all group sizes to become more oblong in the movement direction than at lower variability of speed (Fig. 8A).

Besides, at a low variability of speed the shape of flocks of different sizes appears to be more oblong in other directions than in the movement direction (I3/I1 > L/W, Fig. 8B). The angle between the movement direction and the longest dimension I3 appears to be diverse (Fig. 8C). This diversity of angles is a consequence of the low adjustment of speed, which during turns makes different individuals follow a path of equal length and curvature. Thus they change their movement direction relative to the shape of the flock. This automatically implies that the flock changes its shape relative to the movement direction, e.g. before a sharp turn of 90 degrees, the flock shape is wide and after the turn, it is oblong (Fig. 8D) and it implies that they swap their location in the flock (e.g. before the turn, individual 1 is located at the left, after the turn it is located at the rear).

Because we can increase variability of speed over a larger range in our fish model [24] than in our bird model, we verify effects of adjustment of speed in our fish model. Upon increasing the parameter $\tau$ for the adjustment of speed from 0.03 to 0.34 (Equ. 1) the coefficient of variance of speed increases over a larger range than in our bird model, from 0.05 till 0.20 (whereas in the bird

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**Figure 8. Flock shape and orientation.** A) High and low variability of speed (respectively $\tau = \infty$, $\tau = 1$), flock size and degree to which the flock is oblong. B) Oblong in any direction I3/I1 and oblong in movement direction L/W versus number of individuals in the flock. C) Distribution of angles between the movement direction of the flock and its longest dimension I3 for flock size of 2000 individuals. D) The turning of a flock (view from above). Flock shape changes relative to the movement direction (from wide to oblong), individuals 1 and 2 follow paths of the same length and their location changes in the flock.

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model from 0.01 to 0.015). This results in an increase of the elongation of the shape of the school in the movement direction from being about 1.1 as long as wide to almost 3.5 times (Fig. 9A). Interestingly, in the fish model at parameters, where the coefficient of variance of speed is relatively high, even during turning the shape of the school remains oblong (Fig. 9B; for colour version, Supplementary material, figure S1). This arises, because individuals in the inner corner automatically slow down to avoid collisions and in the outer corner they speed up to remain close to others (Fig. 9C, S2). Consequently, when turning, individuals stick to approximately the same location in the school (indicated in different grey shades, Fig. 9B, S2). At extreme low variability of speed, like in our bird model, during turning school-shape changes its orientation and individuals swap position (Fig. 9D, S3).

**Discussion**

We show that local variability of behaviour in a group generally leads to more variable flock-shape, but not in cases of local variability of speed. Instead, high variability of speed results in an oblong shape that is permanently oriented in the movement direction. Remarkably, a lower variability of speed, thus, a stronger synchronisation of the flock-members (as is apparent from the stronger scale free correlation between subgroup size and flock size, from the stronger global and local polarisation and the smaller changes of volume during turns). Similarly, when in a model of predation on fish schools prey-individuals interact with more neighbours while evading attacks of a predator, the shape of their schools becomes less diverse than when interacting with fewer partners [15].

Turning has a big impact on the variability of shape. Turning in the model resembles descriptions of turning of real flocks, for instance, of rock doves in several aspects [8]. This concerns the temporary changes of volume of the flock and its loss of altitude during a turn, see Fig. 6C of our earlier work [26], the frequently occurring change in orientation of the flock and the repositioning of individuals as shown by Pomeroy and Heppner for rock doves in their Fig. 4B and 5 [8]. Large changes in volume arise only when flocks are large and individuals interact with few neighbours, because in this case individuals sometimes experience different environments (above and outside the roost), which desynchronises the model from 0.01 to 0.015). This results in an increase of the elongation of the shape of the school in the movement direction from being about 1.1 as long as wide to almost 3.5 times (Fig. 9A). Interestingly, in the fish model at parameters, where the coefficient of variance of speed is relatively high, even during turning the shape of the school remains oblong (Fig. 9B; for colour version, Supplementary material, figure S1). This arises, because individuals in the inner corner automatically slow down to avoid collisions and in the outer corner they speed up to remain close to others (Fig. 9C, S2). Consequently, when turning, individuals stick to approximately the same location in the school (indicated in different grey shades, Fig. 9B, S2). At extreme low variability of speed, like in our bird model, during turning school-shape changes its orientation and individuals swap position (Fig. 9D, S3).

**Figure 9. Fish schools.** Shape of fish schools [24]. A) Elongation \((L/W)\) and coefficient of variation of speed in fish model and StarDisplay. Circles: fish school, Triangles: StarDisplay. B) Series of snapshots (with fixed time interval) of a school of 600 individuals indicating the initial location of individuals (at right side at front, at front left side, right side at back, left at back) by four grey-colours. C) Snapshot of school during turning in fish model with extremely high variability of speed (\(\tau = 0.4\)). Individuals in inner corner automatically slow down and in the outer corner they speed up. Darker grey indicates faster movement. The school is oblong. D) Snapshot of school during turning in fish model with extremely low variability of speed (\(\tau = 0.02\)). The school is no longer oblong, but approximately as long as wide. For a color version of Fig. 9BCD, see Supplementary material, respectively, Figs. S1, S2, S3.

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 behaviour in the flock. Rolling into a turn is essential for creating both the reduction in volume and the loss in altitude in our model. The loss of altitude is a consequence of the reduced lift that individuals experience when banking. Without banking, the shape of the bird flock resembles that of a fish school, since it is very elongated in the movement direction (Movie S7). Together these traits (large flock size, few interaction neighbours and rolling into a turn) cause the great variability of shape. 

Change of shape during turning and repositioning of individuals are a consequence of low variability of speed. Repositioning has been observed in several species, such as dunlins [5], pewits [1], rock doves [8] and starlings [4]. Repositioning of individuals in the flock arises, because all individuals follow an equal path length during a turn, as show for rock doves [8]. Low variability of speed causes the change of orientation of the flock and the repositioning of individuals, as is shown in our fish model, because these traits are absent when variability of speed is high (Fig. 9). Here, when adjustability is high, due to the close proximity in the inner corner of the turn individuals slow down and in the outer corner, due to the large inter-individual distances, they speed up. Consequently, during a turn the shape of the school is maintained and individuals stay at approximately the same location in the school. This can be seen in Fig. 9B in which we gave individuals different grey-shades depending on their location in the group in the initial snapshot: they appear to be faithful to approximately the same location, left, front et cetera during the whole series of snapshots (for colour-version see Supplementary material, S1). The permanency of shape during turning due to high variability of speed extends our former theory about the causation of the oblong shape of fish schools to include turning behaviour [25]. This theory implies that the group shape becomes more oblong due to frequent slowing down by its members in order to avoid collisions [24,25,27,28]. Our finding that in StarDisplay variability of speed is accompanied also by elongation of the flock in the movement direction, suggests that if their speed could deviate from cruise speed more, this mechanism of elongation would work for birds also. Since shape of fish-schools is more oblong than that of bird flocks, we hypothesise that the variability of speed of birds is lower than that of fish.

There may be several biological advantages to locality of interaction and low variability of speed. Locality of interaction may result in greater variability of behaviour among individuals in a flock. This may confuse predators and reduce their success at catching of prey. Low variability of speed, may confuse predators also through the accompanying repositioning of flock members during turns, the so-called ‘crossing paths’ [8,41]. Further, it may be advantageous by saving of energy through elimination of acceleration and for avoiding collisions by preventing collisions from front to back [26] (Hemelrijk & Hildenbrandt in prep). Collision avoidance may be more important for birds than for fish, because collisions are more dangerous for birds, because their movement is faster and the viscosity of their medium is lower.

Despite its usefulness, our model has shortcomings. First, of such complex animals as birds, it concerns merely their movement behaviour in relation to the position and heading of others and of the roost, while using a simple model of flying behaviour, ignoring e.g. flapping flight. It ignores any behaviour related to other motivations, such as nutritional [42], reproductive [23] or motivations to avoid a predator [15]. It also ignores environmental disturbances, e.g. by physical forces, such as wind. Thus, in nature, there will definitely be additional reasons that cause flock shape to be variable beyond those that we consider in this paper. Indeed, in the model the variability of shape of, for instance, small flocks of 200 birds is below that observed in real flocks in nature.

A number of the explanations generated by our model can be used as testable hypotheses for empirical data, not only of birds but also of other animals moving in groups. Testable hypotheses from the present investigation concern effects of locality of interaction and variability of speed (Table 2). Particularly in the light of the great effort and difficulties of collecting empirical data of three dimensional positions of animal groups [25] and particularly of flocks of birds [6,16], such model-based hypotheses are valuable.

### Supporting Information

**Figure S1**
(TIF)

**Figure S2**
(TIF)

**Figure S3**
(TIF)

**Movie S1 Measurement of school shape.** This movie shows a bounding box around the flock in black. Its dimensions are calculated with the PCA. The the shortest dimension is the height.
The flock is clearly asymmetrical or oblong. Simultaneously the movie shows the bounding box for measuring the degree to which the flock is elongated in the movement direction (white).

**WMV**

**Movie S2 Deviation of global velocity.** This movie shows how clusters of coordinating individuals with similar deviation of velocity come and go. Blue indicates no deviation from velocity of center of gravity, red indicates maximal deviation.

**WMV**

**Movie S3 A turning flock of 2000 individuals.** This movie shows a flock of 2000 individuals under default parameters above the sleeping site. The shape compresses and changes when the flock turns at the border of the sleeping site.

**WMV**

**Movie S4 A turning flock of 2000 individuals.** This movie shows a flock of 200 individuals under default parameters above the sleeping site the shape hardly changes when the flock turns at the border of the sleeping site.

**WMV**

**Movie S5 A turning flock with individuals interacting with 50 interaction partners.** This movie shows a flock of 2000 individuals in which the individuals interact with their 50 closest neighbours. Consequently, the volume is small, the distance to the nearest neighbours is short and the shape is constant.

**WMV**

**Movie S6 Flying above roost with mild turns.** A flock of 2000 individuals (at default parameters) moves approximately straightforward. The shape hardly changes.

**WMV**

**Movie S7 Without banking.** This movie shows a flock of 2000 individuals in which the individuals do not bank while turning. Consequently, a flock emerges that is oblong and moves along the circular border of the sleeping site.

**WMV**

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**Author Contributions**

Performed the experiments: CKH HH. Analyzed the data: CKH HH. Contributed reagents/materials/analysis tools: CKH HH. Wrote the paper: CKH. Software development: HH.

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