The impact of social networks on animal collective motion

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Many group-living animals show social preferences for relatives, familiar conspecifics or individuals of similar attributes such as size, personality or sex. How such preferences could affect the collective motion of animal groups has been rather unexplored. We present a general model of collective animal motion that includes social connections as preferential reactions between individuals. Our conceptual examples illustrate the possible impact of underlying social networks on the collective motion of animals. Our approach shows that the structure of these networks could influence: (1) the cohesion of groups; (2) the spatial position of individuals within groups; and (3) the hierarchical dynamics within such groups. We argue that the position of individuals within a social network and the social network structure of populations could have important fitness implications for individual animals. Counterintuitive results from our conceptual examples show that social structures can result in unexpected group dynamics. This sharpens our understanding of the way in which collective movement can be interpreted as a result of social interactions.

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networks emerge from the literature for describing connections between individuals that directly affect the behaviour of animals: communication networks and social networks (Bode et al. 2011b). ‘Communication networks’ represent the exchange of information between individuals while they are collectively moving, such as observing the spatial position of groupmates. In models of collective motion it is often assumed that individuals can only perceive other individuals within their sensory zone, a region of fixed size around them (e.g. Couzin et al. 2002; Hemelrijk & Hildenbrandt 2008). Individuals can move in and out of the sensory zones of other group members. Communication networks can therefore change rapidly over time, with each configuration of the communication topology capturing the structure of information exchange at each instant in time. How individuals react to the information they perceive is not encoded in communication networks. In a different context, the term ‘communication network’ is commonly used to refer to the active space of a signal requiring both a sender and a receiver (McGregor 2005). In contrast, our use of the terminology is founded in the modelling literature and refers to direct information transmission (see also Bode et al. 2011b).

In a ‘social network’, connections between individuals represent social preferences with stronger connection weights representing stronger preferences. Social networks are not limited by communication or spatial positions: two individuals might share a highly weighted social network connection despite not currently being able to perceive each other or being a large distance apart. In other words, individuals that share an edge in a social network may not share an edge in a communication network at one instant of time. The existence of such underlying social networks in groups of animals requires individuals to have some kind of cognitive process (e.g. sex discrimination or individual recognition). Ecologists working on animal networks are typically interested in these social networks as they reveal patterns of social preferences (Croft et al. 2008; Bode et al. 2011b).

Social and communication networks are useful concepts as the network representation facilitates analysis of the topological structure of the connections. This permits investigation of features such as the connectivity of the group based on connections, the relative importance of nodes in the networks and many more (Croft et al. 2008; Whitehead 2008; Newman 2010). Here we investigate the relationship between the two types of networks in the context of collectively moving animal groups.

Some studies, published outside of biology, have explored the effect of communication networks on the coherence of collectively moving groups (e.g. Jadbabaie et al. 2003; Liu et al. 2003; Tanner et al. 2003; see also Bode et al. 2011b). In collective robotics, for example, researchers have included details of the connectivity of the communication network in robot control protocols, in an attempt to improve the coherence of robot group mobility (Schuresko & Cortés 2009). A focus on the effect of social networks on group coherence could have interesting implications for ecology, where many researchers are interested in fission–fusion events (in which groups break up or join together; e.g. Croft et al. 2003). This leads to our first hypothesis, which we phrase as a question. Do strong pairwise social preferences between group members always improve group cohesion? Specifically, we might ask whether groups in which all individuals have equal preferences for each other are the most coherent and stable, and whether groups with multiple separate social components are less coherent with a higher frequency of group fission events.

Another general question of interest regarding collective motion is whether different individuals occupy different positions in the group. We suggest that the location of individuals within their social network could affect their spatial position in the group. A theoretical study of dominance interactions in stationary groups has suggested that dominant animals take central positions within groups (Hemelrijk 2000). Furthermore, it has been argued that fish could be subject to varying levels of predation pressure depending on their spatial positions in shoals (e.g. Bummana et al. 1997). The above shows it has long been suggested that the spatial position of animals within groups can have significant fitness implications at the individual level (see also Hamilton 1971; Mooring & Hart 1992; Morrell & Romey 2008; Wood 2010). This leads to our second hypothesis: individuals with a lot of strong connections in the social network will be closer to the centre of the group than individuals with fewer strong connections.

Research using pigeons, Columba livia, tagged with GPS transmitters has examined group dynamics within small flocks for long- and short-distance group motion (Nagy et al. 2010). The delay between the directional choices of pairs of birds, that is the correlation between birds’ flight directions, was used to construct a directional leader—follower network that reveals a well-defined and consistent (over a number of flights) hierarchy among flock members. Nagy et al. (2010) cautiously described their findings as ‘hierarchical group dynamics’. It is unclear whether such hierarchical group dynamics could result from underlying social network structures alone. For example, physical or motivational differences between individual birds, such as preferred flying speed or the need for food could lead to leader—follower relationships that are possibly unrelated to underlying social networks. This leads to our third hypothesis that hierarchical group dynamics can arise purely from underlying social networks and that the former accurately reflect the structure of the latter. Here we extend a model of animal collective motion (Bode et al. 2011a) by adding preferential interactions between socially connected individuals. We use simple but illustrative conceptual examples to study the effect of social network structures on three different aspects of animal group movement: group coherence, individual spatial position in groups and hierarchical dynamics in groups. Specifically, we test the three hypotheses described above.

(1) Do strong pairwise social preferences between group members always improve group cohesion? (2) Individuals with a lot of strong connections in the social network will be closer to the centre of the group than individuals with fewer strong connections. (3) Hierarchical group dynamics can arise purely from underlying social networks and the former accurately reflect the structure of the latter.

METHODS

In this section we describe and justify our modelling approach and some key methods.

Model for Collective Motion

Our model extends a previously published model that reproduces large-scale empirical data (Bode et al. 2011a). The behaviour of individuals follows the commonly adapted ‘Avoidance—Alignment—Attraction’ approach in which a combination of local alignment, repulsion and attraction between individuals results in collective behaviour (Reynolds 1987; Couzin et al. 2002, 2005; Buhl et al. 2006; Hemelrijk & Hildenbrandt 2008). In our model, N individuals are represented by points in two-dimensional space. Each individual obtains information from its sensory zone, which is described by a circle of radius \( r_s \) centred on the individual. This circle is punctured by a ‘blind angle’ directly behind the individual of size \( 360°−{\alpha} \), in which individuals cannot perceive other animals. The individuals, indexed \( i \), are at position \( \mathbf{x}_i \) and move at the instantaneous velocity \( \mathbf{v}_i \). We assume that all individuals react with an identical stochastic rate to their environment. 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) If \( i \) has neighbours (conspecifics within sensory zone of \( i \)), choose a neighbour \( j \) of \( i \) at random with probability \( p_j \) (see below).
(3) Update \( x_i \) and \( v_i \), as described below.

One update step of length \( \Delta t \) consists of \( N \) realizations of steps (1)–(3). This ensures that each individual gets moved on average once per update step. The exact algorithmic update of each individual over one update step, \( \Delta t \), has no direct physical meaning. We observe the sum of a number of updates. The output of our model is obtained by recording the positions of individuals every \( T = \lambda \Delta t \), where \( \lambda \geq 1 \). Therefore, the movement of individuals between two separate model outputs consists of an average over the sum of a number of updates (averaging over changes in instantaneous velocity). Increasing \( \Delta t \) for fixed \( T \) results in the model output being composed of the average of an increasing number of shorter steps' while the average speed of individuals is constant. For more details on the effect of the parameter \( \Delta t \) see earlier publications relating to this model (Bode et al. 2010a, b).

Previous models that have considered social networks underlying collective motion have translated social preferences into attractive or aligning forces between individuals (e.g. Braun et al. 2003; Hemelrijk & Kunz 2005; Moussaid et al. 2010). The novelty of our model lies in the inclusion of social networks: the probability of choosing a particular neighbour depends not only on the distance between this neighbour and the updating individual, but also on the social preference individuals have for each other (the weight of the network connection between them). Suppose individual \( i \) has neighbours \( k = 1, \ldots, k \) which are at distances \( d_k \) from \( i \) (\( 0 \leq d_k < r_A \)). Furthermore, denote the preferences of individual \( i \) for its neighbours by \( e_{ik} \geq 0 \). Then individual \( j \) is chosen in step (2) above with probability,

\[
p_j = \left( \frac{e_{ij}}{d_j} \right) \left( \sum_k e_{ik}/d_k \right)
\]

To avoid a singularity, we introduce a cutoff for values of \( d_k \) close to zero, but in practice this is almost never activated. Our approach ensures that on average individual \( i \) is more likely to react to neighbours nearby.

By varying the preferences \( e_{ab} \) that individuals \( a \) and \( b \) have for each other across the group, the concept of 'preferential updating' between individuals is introduced. This means that an updating individual is more likely to react to the position and movement of one or a number of specific individuals as opposed to the rest of the group for a given fixed distance between individuals. Therefore, we can impose a weighted social network of preferences on the interactions within our modelling framework. To see this, note that the preferences \( e_{ab} \) denote the weighted edges (=preferences) between nodes (=individuals) \( a \) and \( b \) in a network of \( N \) nodes in total. We can consider undirected networks, where \( e_{ab} = e_{ba} \), or directed networks.

Once a pair of interacting individuals has been chosen as described above, the focal individual reacts to its 'update partner' depending on the distance, \( d_j \), between them. Only the focal individual, and not the update partner, is moved in one update. The sensory zone of individuals is divided into hierarchical interaction zones of radius \( r_0, r_2 \) and \( r_3 \) (Cousin et al. 2002). At close distances, the focal individual moves away from its update partner to avoid collisions (\( d_j < r_0 \)) and at larger distances (\( r_0 \leq d_j < r_2 \)) it gets attracted to its update partner to maintain group cohesion (Cousin et al. 2002). At intermediate distances the focal individual aligns with its update partner (\( r_2 \leq d_j < r_3 \)). Focal individuals move at different instantaneous speeds according to how they react to their update partner. When moving towards their update partner (attraction), individuals move at twice the instantaneous speed than otherwise (i.e. \( v_i = 2v_0\Delta t \) instead of \( v_0\Delta t \), where \( v_0 \) is the speed parameter in our model). Our assumption of higher attraction speeds is based on the hypothesis that individuals need to move faster when they are interacting with individuals further away (e.g. to catch up with them), but is also necessary for the recovery of realistic distributions of individual speeds (Bode et al. 2010a). The rate at which individuals turn is limited to \( \beta \) degrees/s. Therefore, the new velocity of focal individuals, \( v_i \), is obtained by turning them by at most \( \beta \Delta t \) degrees towards their preferred movement direction (e.g. directly away or towards their update partner) in one update.

Then the focal individual is moved by the vector \( v_i \), the length of which depends on the type of interaction as described above. Stochastic effects in our simulations are generated entirely by the internal dynamics of the algorithm. We do not perturb the movement directions of updating individuals by adding a random variable. For further details, including a biological interpretation of our algorithm, see Bode et al. (2011a). Variations of the model used in this research have demonstrated the biological relevance of our theoretical approach (Bode et al. 2010a, b).

**Generation of Social Network Structures**

To simplify our analysis we restrict the weights of edges in underlying social preference networks to ‘strong’ and ‘weak’ connections. If they are not linked by strong preferences, individuals in the social networks we consider have weak connections. This takes into account that individuals can react to conspecifics even if they do not have strong preferences for them, although they are more likely to react to individuals to whom they are strongly connected. Typically we set the connection weights to \( e_{ab} = 1 \) for weak connections and \( e_{ab} = 100 \) for strong connections (the ratio between these measures is the only thing that matters, and we also systematically vary this difference; see the Appendix).

Most of our analyses are performed by using simple but illustrative networks selected to explore the effect of key types of network structures. In cases where this is not appropriate, and to provide a baseline for comparison, we assign strong preferences randomly. To ensure that the method of assigning strong connections does not affect our results, we use three different approaches.

**Erdős–Rényi method**

Strong edges are independently added to the network from the set of all possible edges with a fixed probability (Erdős & Rényi 1960).

**Watts–Strogatz method**

Nodes are arranged in a ring lattice and all have identical numbers of strong edges to their immediate neighbours. These edges are then rewired independently with fixed probability without duplicating edges. This leads to the 'small-world' phenomenon in which all nodes are connected by a small number of edges (Watts & Strogatz 1998). Varying the rewiring probability leads to networks of different levels of randomness.

**Scale-free method**

To include strong connections we start with a small number of nodes, then add nodes and a fixed number of strong edges

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connected to them, attaching the new node to already included nodes with strong connections by preferential attachment (‘rich get richer model’, Barabási & Albert 1999).

Model Parameters and Simulations

Simulations of our model are performed within a toroidal box of side length \( L = 200 \) m (box with periodic boundary conditions). This is to ensure that after group fission, it is subsequently possible for groups to re-form rather than to disperse in unbounded space. Simulations started from random initial conditions within a box of side length \( r_{K} \), to ensure that individuals were aggregated initially. Parameter values were chosen to ensure that in the control case (all individuals are weakly connected) stable and coherent groups formed. Since this work is intended as an illustration of principle, we confined simulations to the parameter space given by: \( N = 100, r_{K} = 1 \) m, \( r_{O} = 12 \) m, \( r_{A} = 20 \) m, \( v_{O} = 3 \) m/s, \( v_{A} = 2v_{O}, \Delta t = [0.2, 0.1, 0.05] \) s, \( \alpha = 270^\circ \) and \( \beta = 40^\circ/s \) (note that parameters have been explored elsewhere, Bode et al. 2010a, b). When started from random initial conditions the summary statistics initially reflected transitional group formation behaviour. To avoid recording such transitional data, we introduced a warm-up time of 100 \( T \) (therefore depending on the size of \( T \)) for our simulations.

We use different values of \( \Delta t \) in the scenarios we use to explore the three hypotheses stated in the Introduction. Varying \( \Delta t \) for fixed \( T \) changes the behaviour of the system. For example, low values of \( \Delta t \) result in more synchronized and cohesive groups than higher values of \( \Delta t \) (Bode et al. 2010a, b). We utilize this feature of our model to adjust the emergent properties in simulations to suit the scenarios investigated. For our first hypothesis we choose a value of \( \Delta t \) that allows for frequent group fragmentation since we are studying a fission–fusion system. Since we are only interested in nonfragmented groups in the other scenarios, we use smaller values of \( \Delta t \) in these simulations.

RESULTS

Group Cohesion (hypothesis 1)

To explore possible effects of social network structure on group cohesion and alignment, we generated five different underlying social networks that each captures different illustrative structural elements (Fig. 1). The network structures we used were: (1) fully connected where all connections have the same strength (i.e. no structure); (2) two components; (3) three components; (4) a key individual (hub) that is strongly connected to all others; (5) randomly created strong connections (Erdős & Rényi 1960). We simulated groups of 100 individuals.

We first measured group cohesion. To do so we used the network of possible interactions between individuals for each model output we used in our analysis (snapshots/still images of group movement). Possible interactions were determined by the spatial positions of individuals. Two individuals were considered to be connected in the network of possible interactions if they were within a distance of \( r_{A} \) from each other (perceptual range). Groups were defined as distinct subsets of individuals with no connection between their respective elements (i.e. the closest distance between individuals in two separate groups is larger than \( r_{A} \)). We recorded the number of groups and the fraction of the total number of individuals belonging to the largest group in our simulations.

We also recorded the frequency for each pair of individuals to be in the same group. This measure was inspired by field ecologists who commonly use the ‘gambit of the group’ (GoG) approach. In this sampling approach, groups of animals are repeatedly observed, and all individuals within each collectively moving group are

![Figure 1. Effect of different underlying social networks on collective motion.](image)
assumed to be associating (Whitehead & Dufault 1999). Data from
a number of such GoG censuses can be combined into cumulative
networks that can then be analysed for nonrandom features and
social preferences (Croft et al. 2008). This can be thought of as
taking multiple samples of the network of possible interactions, to
reconstruct (in relative terms) the underlying social network. Here
we actually impose the social network and investigate whether it is
reflected in our GoG-inspired analysis.

For each model output (a snapshot/still image of group move-
ment) we recorded for all pairs of individuals whether they were in
the same group or not, regardless of whether they were strongly or
weakly connected in the social network. This resulted in counts
between zero and the number of model outputs we used in our
analysis (we recorded 1000 model outputs). We called these counts
‘GoG edge frequencies’. In our analysis GoG edge frequencies close
to zero indicate that individuals were rarely found in the same
group and GoG frequencies close to 1000 indicate that they were in
the same group most of the time. Since we were interested in the
impact of the imposed social network, we compared the average
GoG edge frequencies of pairs of individuals with strong and weak
social connections. We condensed this into one quantity by sub-
tracting the average GoG edge frequency for weak connections
from the one for strong connections and called this measure ‘GoG
difference’. The GoG difference takes values between zero and
1000. High GoG differences indicate that pairs with underlying
strong connections are observed more frequently in the same
group than pairs with weak underlying connections in simulations.

Figure 1 shows the GoG edge frequencies averaged over pairs
with strong and weak connections in the underlying social
network, for the different social network structures we imposed on
groups. Figure 1a, b shows the control case, in which all social
network connections have the same strength. We could therefore
only record the GoG edge frequency for one social connection
strength. This takes a value of less than 1000 (Fig. 1b), which is
explained by the fact that the group occasionally fragments in our
simulations. It is noticeable that underlying social networks that
include clear separations into distinct subunits with respect to the
strong connections (e.g. two or three components, Fig. 1c, e)
produce high GoG edge frequencies for strong connections and
significantly smaller ones for weak connections. Since the GoG edge
frequencies are defined by group membership, which in turn is
defined by spatial proximity, our modelling approach translates
social or updating preferences into spatial proximity in collective
motion in such cases. Our supplementary film, which shows the
scenario depicted in Fig. 1c, illustrates this. Preferential updating
leads to spatial assortment but weakly connected individuals still
interact.

The summary statistics listed in Table 1 quantify our observa-
tions from Fig. 2 further. We examined group alignment by

extracting the polarization, \( p_{\text{group}} \in [0, 1] \) from our simulated
groups. High polarization values indicate high group alignment and
low polarization values indicate low group alignment (Couzin et al.
2002). In the control case (no imposed social network structure),
the simulations result on average in one stable group, which is
highly aligned and contains all individuals. If the underlying social
network contains separate subunits (e.g. two or three components),
the polarization drops significantly, because on average more than
one group is formed. The groups move separately from each other,
often in different directions, which explains the reduction in the
polarization for the population as a whole. Separate groups within
the population may still be highly aligned, but we only consider
the entire population in our analysis. The average fraction of individ-
uals in the largest group also decreases as a result of more than one
separately moving group. Individuals within different subunits of
the underlying social network can still interact, which occasionally
leads to the formation of only one group. This is reflected in the
average number of groups present and the average fraction of
individuals in the largest group. The large GoG differences confirm
our observations from Fig. 2. An underlying network, in which one
central node is connected to all other nodes (Fig. 2), results in an
overall much less fragmented population. However, such a highly
structured social network still results in a higher GoG difference
than random networks, despite the fact that the random networks
we explored contained a higher number of strong connections.
These findings are not just a result of the large difference between
weak and strong connections in our simulations but they also vary
smoothly with the difference between weak and strong connec-
tions (Appendix Fig. A1).

Our first question was whether strong pairwise social prefer-
ences between group members always improve group cohesion. The
results presented in Table 1 show already that this is not the case.
Social networks that split a group into two separate social compo-
nents (see Fig. 1c) do not result in higher group cohesion than the
control case without any social structure. However, we may ask

![Figure 2](image-url) Illustration of networks with (a) two, (b) one and (c) no highly linked key individual for \( N = 10 \). Strong connections are shown in thick black lines and weak connections in thin grey lines. In our simulations these networks were scaled up to \( N = 100 \).
whether particular social structures improve group cohesion or, more generally, what aspects of social networks increase or decrease group fragmentation. We tested this by designing three social networks with two, one or no ‘key individuals’ that are linked to others by strong connections (Fig. 2). Table 2 shows that in this scenario the degree of group cohesion and alignment increased with the removal of key individuals and strong connections.

This example suggests that group cohesion benefits from homogeneous underlying preference networks. Strong pairwise preferences may therefore be detrimental to group cohesion if they break the homogeneity of the underlying preference network. Another example is given in the Appendix, where we systematically reduce the structure in underlying preference networks (Appendix Fig. A2).

**Positions within Groups (hypothesis 2)**

To test our second hypothesis, that individuals with a lot of strong connections in the social network will be closer to the centre of the group than individuals with fewer strong connections, we compared the average distance of individuals from the centre of mass (CoM) of the group (CoM = \( \Sigma x_i / N \)) to the ‘strong degree’ (number of strong social connections) of those individuals in generated social networks. We repeated our analysis for the three most commonly used approaches to generate network structure randomizations: Erdös–Rényi random networks (Erdös & Rényi 1960), small-world networks (Watts & Strogatz 1998) and networks with skewed degree distributions (Barabási & Albert 1999). Figure 3 shows that in all cases the distance from the CoM decreases as the strong degree in the underlying social network increases. This confirms our hypothesis and suggests that well-connected individuals occupy positions closer to the centre of the group, whereas individuals with fewer strong connections are on average further away from the centre of the group.

To explain this result, recall that as the number of strong social connections an individual has increases, its preferential interactions with groupmates will be biased towards a larger proportion instead of a small subset of the group (averaging over all possible spatial configurations of the group). Therefore, if the individual is situated on the periphery of the group and has many strong social preferences, its average direction of attraction will be towards the CoM of the group. If the individual is already situated close to the CoM of the group and has many strong social preferences, the attraction tendencies towards individuals on the periphery of the group will balance. These tendencies only hold if the interactions of individuals are not biased towards a small subset of the group.

**Hierarchical Group Dynamics (hypothesis 3)**

To investigate whether hierarchical group dynamics can arise purely from preference interactions, we used the methods described by Nagy et al. (2010). For each individual, we examined whether it turned before or after the average of the group. To do so, we computed the cross-correlation \( C_i(t) \) between the time series of movement directions (recorded every \( T = 0.2 \) s) for pairs of individuals \( (i,j) \), shifting the time series of individual \( j \) by \( \Delta t \) s (therefore \( C_i(t) = C_i(t + \Delta t) \)). The value of \( \Delta t \) for which \( C_i(t) \) reaches its maximum value is the delay between individuals \( i \) and \( j \). Negative values for the delay mean that the movement direction of the \( i \)th individual lags behind the one of the \( j \)th individual. We recorded this pairwise delay only if the maximal value of \( C_i(t) \) was above the threshold \( C_{max} = 0.98 \). To find the delay between the turns of individual \( i \) and the rest of the flock, we computed \( C_i(t) \) by

![Figure 3](image-url)
averaging $C_{ij}(\delta t)$ over all individuals $j$ (excluding $j = i$). Again, the value of $\delta t$ for which $C_{ij}(\delta t)$ reaches its maximum value was the delay between individual $i$ and the rest of the flock. We call this the ‘flock delay’ of individual $i$. Once more, positive values for the delay mean that the movement direction of the $i$th individual is ahead of the rest of the flock. Before we performed this analysis, we filtered the data for each simulation and included only instances when the flock formed one cohesive group (as defined in the section Group Cohesion (hypothesis 1)) in our analysis. We computed the flock delay separately for 50 simulations and we report the average. For pairwise delays we computed the average of the function $C_{ij}(\delta t)$ over 50 simulations and used this to find the pairwise delays as described above. Further details of the method can be found elsewhere (Nagy et al. 2010).

We now use directed connections in our social network (in contrast to the previous undirected networks). This allows us to model hierarchical underlying social structures. For our conceptual study we use a simple chain-like structure of strong connections in the underlying social network that helps to illustrate the many facets of how social preferences could impact on group dynamics (Fig. 4a). In our example, individual 2 preferentially interacts with individual 1, individual 3 preferentially interacts with individual 2, and so on. Individual 1 has equal preference for all individuals.

In a null scenario, without underlying social preferences, there are no systematic differences in the flock delays between individuals apart from random fluctuations (see Fig. 4b). However, given the directional structure of the underlying preference network, we might expect to find this reflected in Hierarchical Group Dynamics (hypothesis 3). Calculating the flock delays for each individual in our example shows that there are indeed differences between individuals (Fig. 4b). However, it is not animals at the front of the chain of strong preferences (individuals 1, 2, 3 and 4) that have the highest positive flock delays. In fact, they have negative flock delays and therefore appear to turn after the rest of the group. It is individuals in the middle of the chain that have the highest positive flock delays (in particular individual 7). An examination of the significant (recall $C_{\text{max}}$) pairwise delays is instructive (Fig. 4c). The back end of the structure of strong preferences is reflected in significant pairwise delays. For individuals 1 and 2 in particular, this is not the case. They turn after individuals that are behind them in the chain of strong preferences. This is because individual 1 has no interaction preferences; it therefore reacts, on average, accurately to the average of the group, which results in a delay behind the rest of the group. Individual 2 closely follows 1 and therefore also lags behind the rest of the group.

We repeated this analysis for an underlying social network similar to the one depicted in Fig. 1g (Appendix Fig. A3). For this case we found that although there were differences in the flock delays of individuals, it was difficult to establish a clear trend compared to the control case in which all preferences are equal. Again, the pairwise delays are instructive. All individuals except for individual 1 have a strong social preference for individual 1. We found no incoming or outgoing pairwise delays to individual 1. The imposed social network structure is therefore reflected in the lack of delays between individual 1 and the rest of the group. As in Fig. 4, individual 1 reacts on average accurately to the entire group. Since all other individuals closely follow 1, the entire group turns synchronously at delays that we cannot detect accurately at a resolution of model output every $T = 0.2$ s. The flock delays and pairwise delays we do find are therefore stochastic effects (as the comparison with the control case mentioned above suggests). This example is instructive as it shows that even if there is a distinctive structure of strong social preferences, this need not be reflected in hierarchical group dynamics.

The group dynamics recovered from our model simulations (Fig. 4b, c) are not as strictly hierarchical as the group dynamics found for flocks of pigeons (Nagy et al. 2010). This can be seen from the mismatch in the hierarchical sorting of individuals obtained by using flock delays or pairwise delays. However, our examples illustrate an important point. Had we found group dynamics as in Fig. 4b, c in a biological system, it is unlikely that we would have guessed the underlying network of preferences. Therefore, hierarchical group dynamics could be a result of social preferences, but it is important to observe that we cannot necessarily infer the social preferences from recorded hierarchical group dynamics.

**DISCUSSION**

We have presented a model of animal collective motion that includes social network structures. Our simulations suggest that...
social preferences could lead to spatial association of socially connected individuals and could also impact on group fission and fusion. Furthermore, our model leads to the testable predictions that animals with many social links can be found closer to the centre of moving groups. Finally, our model shows that social preferences alone could lead to hierarchical group dynamics but, more importantly, that social structure may not necessarily be reflected as expected in the group dynamics.

Current animal social network data are often obtained by using the GoG technique we described above. This method essentially samples instances of spatial assortment of individuals in groups. Despite careful approaches and analysis (Croft et al. 2008; Whitehead 2008; Franks et al. 2010) more research is needed to assess how different sampling methods can accurately reconstruct social preferences in moving populations with ongoing group fission and fusion. We have shown that for simple underlying social networks (e.g. two or three subsets of strongly linked individuals, see Fig. 1) the GoG sampling technique can be effective, but a more rigorous approach incorporating collective motion will be necessary in the future, in combination with an analysis of sampling over multiple days (after large-scale fission–fusion events: Franks et al. 2010) and within days (capturing fine-scale fission–fusion events as we do here), for example, larger populations and the effect of limited space will have to be investigated further without relying on toroidal boxes as we have done for simplicity.

The positioning of individuals within moving groups has been related to their internal state and it has been suggested that predation pressure is higher on individuals moving in particular positions, such as frontal or even central group positions (e.g. Krause & Ruxton 2002; Morrell & Romney 2008). Our simulations show that spatial positioning of individuals could also be related to their position within an underlying social network. This raises further questions considering the fitness consequences for animals that have many or few social ties. For example, we could ask whether predation pressure could result in homogeneous social networks in which all individuals have similar numbers of social ties or whether it could even result in selection against social preferences in the first place.

It has been suggested that the mechanism for the pairwise leader–follower relations found in pigeons is based on state-dependent behaviours, such as navigational knowledge or current motivation (Nagy et al. 2010). Our model demonstrates that leadership, in the sense of hierarchical dynamics based purely on social preferences, is in theory possible (although with possibly unexpected hierarchies). The notion of socially mediated leadership is supported by a study, unrelated to hierarchical dynamics in pigeons, showing that dominant beef cows, Bos taurus, have more influence on herd movement than more subordinate cows (Sárová et al. 2010). Other research suggests superior information (Couzin et al. 2005) or small changes in behaviour (Conradt et al. 2009) as possible mechanisms for leadership. We suggest that to answer questions about leadership in biological systems, all of these social, knowledge-based, behavioural or physical factors have to be considered.

Our model assumes that social preferences translate into updating preferences. This is one possible mechanism for how social affiliations may translate into behavioural responses. Another approach could be to translate social preferences directly into attractive forces between individuals. Would our findings still hold? Ultimately only further empirical data will help to answer the questions of how social affiliations translate into behavioural responses and how these affect collective motion. We suggest that in future work it will certainly be beneficial to consider other approaches in addition to ours (Bode et al. 2011b). We have deliberately focused on simple illustrative networks to use as conceptual examples. However, we have demonstrated some counterintuitive results, and our work is a step towards sharpening our understanding of how social networks could impact on three important aspects of group movement.

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Supplementary Material


References

Figure A1. The effect of the strength of strong connections in the case of an underlying social network with two separate components (compare with Fig. 1c in the main text). (a) Polarization, (b) number of groups, (c) number of individuals in the largest group divided by the overall number of individuals, and (d) the GoG difference (see text for details). The figure shows that as the strength of the strong connections is increased, the impact of the underlying social network becomes clearer. As the strength of strong connections tends to infinity one would expect that spatial proximity between weakly linked individuals is only a result of boundary conditions and stochastic effects. The average over 10 simulations is shown; error bars show SEs. \( N = 100, \Delta t = 0.2 \text{ s}, T = 100 \text{ s}. \)

Figure A2. The effect of increasingly random small-world networks on collective motion. (a) Polarization, (b) number of groups, (c) number of individuals in the largest group divided by the overall number of individuals, and (d) the GoG difference (see text for details). The rewiring probability gradually increases, starting from a regular ring lattice with average degree \( \langle k \rangle = 4 \). With increasing rewiring probability the original structure gets more diluted, and the cohesion of the group increases. The average over 10 simulations is shown; error bars show SEs. \( N = 100, \Delta t = 0.2 \text{ s}, T = 100 \text{ s}. \)
Figure A3. Group dynamics for a given underlying preference network. (a) Underlying network of social preferences. Strong connections are shown in thick black lines and weak connections in thin grey lines. Numbers denote individual IDs. (b) Mean flock delays for each individual over 50 simulations. We show the control case when all social connections have the same strength and the case for the network illustrated in (a). Error bars show SEs. (c) Pairwise delays between individuals, denoted by arrows from the leading to the following individual averaged over 50 simulations. Delay values are not given but are greater than zero. The social structure from (a) is not reflected in the pairwise delays in (c). However, the pairwise delays are consistent with the flock delays in (b). Individual 8, for example, appears to lead the flock (high positive flock delay) and also has many outgoing but no incoming links in the network of pairwise delays. The differences between individuals appear to be dominated by stochastic fluctuations and it is difficult to see a trend different from the control case. It is, in fact, the absence of any pairwise delays between individual 1 and the rest of the group that reflects the imposed social network. $N = 10$, $T = 0.2 \text{s}$, $\Delta t = 0.05 \text{s}$, $C_{\text{min}} = 0.98$. We recorded 5000 output instances, $T_s$ apart, for each simulation. Only instances when groups were coherent were included in the analysis. This was more than 90% of the time for control groups and for groups with underlying social network.