

Social networks and models for collective motion in animals

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Abstract The theory of collective motion and the study of animal social networks have, each individually, received much attention. Currently, most models of collective motion do not consider social network structure. The implications for considering collective motion and social networks together are likely to be important. Social networks could determine how populations move in, split up into and form separate groups (social networks affecting collective motion). Conversely, collective movement could change the structure of social networks by creating social ties that did not exist previously and maintaining existing ties (collective motion affecting social networks). Thus, there is a need to combine the two areas of research and examine the relationship between network structure and collective motion. Here, we review different modelling approaches that combine social network structures and collective motion. Although many of these models have not been developed with ecology in mind, they present a current context in which a biologically relevant theory can

be developed. We argue that future models in ecology should take inspiration from empirical observations and consider different mechanisms of how social preferences could be expressed in collectively moving animal groups.

Keywords Social networks · Collective motion · Collective behaviour · Communication networks · Social interaction · Group behaviour

Introduction

Imagine that you and your friends are walking in a protest crowd marching through the streets. In following the crowd, you align yourself in the same direction as those around you. However, within the crowd you are more likely to move in the direction of your friends in order to stay together. Thus, your position in the crowd is related to the position of your friends, and if the crowd splits into two, your choice of which crowd to follow will also be affected by your preference to be near your friends. Everyone else is moving in the same way: they are moving with the crowd, but preferentially moving alongside their friends. From this the overall crowd structure and collective movement remains, but strong substructures exist within the group. Similar processes occur in non-human animals. Guppies (*Poecilia reticulata*), for example, are small fresh-water fish that tend to move in shoals. Frequent encounters present opportunities for individuals to move between shoals (Croft et al. 2003). Controlled experiments in which guppies were presented with a choice of shoaling with two or more conspecifics demonstrated a strong and consistent preference of guppies to shoal with individuals with whom they are familiar (Griffiths and Magurran 1999). We therefore know from experimentation, observation and personal

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experience that social ties affect movement in groups. The implications for considering collective motion and social networks together are likely to be important. Social networks could determine how populations move in, split up into and form separate groups (social networks affecting collective motion). Conversely, collective movement could change the structure of social networks by creating social ties that did not exist previously and maintaining existing ties (collective motion affecting social networks). From an evolutionary perspective, there could be fitness trade-offs for an animal between having many beneficial social ties and maintaining these ties in moving animal groups. Separately, both the theory of collective motion and social connections in animals have received a lot of attention as we will briefly describe.

Collective motion is the term used to describe the synchronised motion of groups of animals such as shoals of fish or flocks of birds that appear to behave as one body, continually changing shape and direction (Sumpter 2006). The movement of animal groups has been shown to emerge from local interactions between many neighbouring individuals within a group using rules such as (loosely expressed) ‘get attracted to nearby individuals’ (Krause and Ruxton 2002; Sumpter 2006). We can learn about behaviours governing animals by studying their collective motion, and also use similar conceptual ideas to study human crowds (Helbing et al. 2000) and to design teams of robots (Liu et al. 2003).

Social preferences between animals can be represented by networks in which nodes represent individuals and edges connections between them (Croft et al. 2008). The particular appeal of the social network approach to studying animal behaviour is that it allows the study of the social organisation of animals at all levels (individual, dyad, group, population) and for different types of interaction using one conceptual framework (Krause et al. 2007). Network analysis offers many novel techniques for examining social organisation in animals and exploring how these aspects influence individuals and groups (Whitehead 2008; Krause et al. 2009; Sih et al. 2009).

In ecology, models of collective motion typically do not consider social network structure (i.e. social preference is equal for all perceived conspecifics; e.g. Couzin et al. 2002; Hemelrijk and Hildenbrandt 2008). If ecologists are to make the move towards studying the relationship between social networks and collective motion, then models are likely to be as important as they have been for studies of collective motion alone. It is important to develop the theory in the context of research that has already been conducted, and we therefore provide a review of relevant models. Most of these models have not been developed with ecology in mind. However, they present a current context in which we can develop a biologically relevant theory of the interplay between social networks and

collective motion. We present a way forward for this type of research.

Concepts and context

Before we introduce and discuss the literature in detail, it is necessary to explain some key concepts regarding the synthesis of collective motion and social networks, and also outline the context in which ecologists are interested in this notion. First, we propose a working definition for collective motion for the purpose of our review. Second, we define the two different types of networks that are important in collective motion. Then, we briefly describe two perspectives on the effect of social networks on collective motion that are of direct interest to ecologists. Finally, we outline the different approaches with which we have categorised the relevant literature.

A working definition for collective motion

So far we have followed the typical practice and given examples and a loose definition for the collective motion of animals. However, a more specific definition will help in the context of this review. Petit and Bon (2010) suggest that collective movement corresponds to a sequence of events including a pre-departure period, initiation and subsequent group movement. This concept is appealing as it is easy to imagine how the different consecutive events affect each other. Petit and Bon (2010) remark that most models for collective movement do not adhere to the notion of consecutive events but focus on a minimalist scenario in which continually moving groups are considered. We found that this observation holds for most of the literature we review here.

While we appreciate the need for a more unifying framework of animal group movement and comment on this later on, we will restrict the focus of this review to instances of collective motion (as opposed to collective movement). We define the collective motion of animals as: *the manifestations of the locally aligned, locally synchronous and continuous movement of one or more groups of interacting individuals*. Multiple groups are included in our definition to allow for group fission and fusion processes which we believe are important in moving animal groups and interactions do not have to occur between all individuals involved. The notion of ‘groups’ in our definition implicitly suggests the concept of a coherent collection of individuals. Coherence of animal groups is often defined in terms of spatial proximity (e.g. Croft et al. 2003) and a definition in terms of communication networks may be possible but we will defer from defining group cohesion explicitly. Our definition is far from complete and somewhat vague but its main intention is to highlight the concept of continuous

group movement in contrast to the ‘stop-and-go’ dynamics defined by Petit and Bon (2010). We will base our review on this working definition but note that it is not a characterisation of collective motion.

Communication networks and social networks

Relationships, associations and interactions between individuals can be expressed in terms of network theory. Individuals are represented by ‘nodes’ with ‘edges’ between them representing connections. Edges can either take binary values (they exist or not) or weighted values (representing the strength of the connection) and they can be undirected (connection between two animals) or directed (connection from one animal to another). There are many excellent textbooks providing more information on network analysis and terminology (Croft et al. 2008; Whitehead 2008; Newman 2010). In the context of collective motion, two different types of networks emerge from the literature for describing connections between individuals that directly affect the behaviour of animals: communication networks and social networks. These two network types are related, and to avoid ambiguity we will define them in more detail.

‘Communication networks’ represent the exchange of information between individuals. If animal *A* obtains information from or about animal *B*, then *A* is connected to *B* in the corresponding communication network. Communication could consist of observing the spatial position of shoal mates, receiving olfactory cues or hearing warning calls from conspecifics. The information intake of animals is limited by their sensory capabilities. 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 and Hildenbrandt 2008). Individuals can move in and out of the sensory zones of other group members. Communication networks can therefore rapidly change over time, with each configuration of the communication topology capturing the structure of information exchange at each instant in time. Figure 1a illustrates an instant of a communication network based on the extent of the sensory zones of individuals. For simplicity, we show binary and undirected networks.

A ‘social network’ represents interaction or association preferences between all individuals. For example, if animal *A* prefers animal *B* over animal *C*, then the edge between *A* and *B* in the corresponding social network has a higher weight than the edge between *A* and *C*. In animals, this could be the preference of large guppies to shoal with other large guppies, the preference for familiar individuals or the preference of offspring for a parent rather than a stranger. Social networks are not limited by communication. They underlie a group or population and do not necessarily

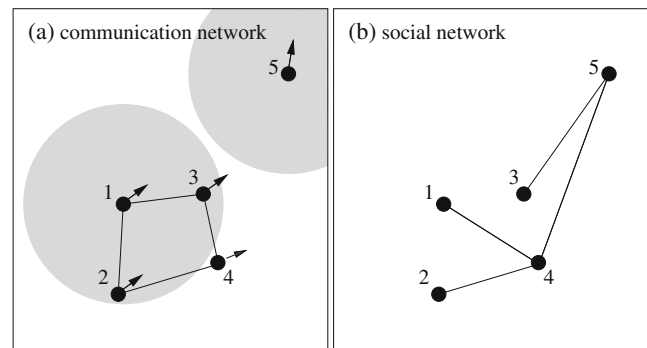


Fig. 1 The difference between communication and social networks. The positions of individuals are marked by *black circles* with *arrows* indicating their direction of motion. Connections (edges) are marked by *black lines* between individuals. **a** Illustration of an instantaneous communication network. The extent of the sensory zones for individuals 1 and 5 are marked by *grey regions*. Edges in the communication network are based on which individuals can perceive each other and can therefore exchange information. **b** Example for a social network indicating strong social preferences that could underlie the group of individuals in **a**. Note how this network contains connections between individuals 4 and 5, for example, which is not the case in the communication network in **a**. Limited perception can therefore restrict the communication network to a structure different to the underlying network of social preferences

change over time or with the movement of individuals. One way to consider social networks is to ignore weak connections and to focus on strong social preferences. Figure 1b shows an example for such a social network in contrast to the communication network in Fig. 1a.

Communication networks may or may not be equivalent to preference networks. Consider the situation when two ‘associates’ cannot perceive each other due to sensory limitations. In this case, they are not connected in the communication network but they are still connected in a social network describing their relationship. However, if all individuals can perceive each other, then a weighted communication network could express the preferences of individuals to interact with each other in the weights of its edges. These two network concepts help to organise the literature on social networks in collective motion into the different approaches that have been taken.

Population level

Researchers interested in linking the behaviour of individuals and groups to the structure of groups in animal populations have turned to network theory (Lusseau and Newman 2004; Cross et al. 2005; Lusseau et al. 2006; Lusseau 2007; Nagy et al. 2010). Social network analyses of shoaling guppies, for example, have shown small-world properties (where most nodes can be reached from every other via a small number of intermediate nodes), assortment by trait such as size or sex (i.e. individuals of the same sex and similar size prefer

to shoal together), preferential pairwise connections between familiar individuals, positive degree correlations (e.g. well-connected individuals tend to be connected to other well-connected individuals) and behavioural assortment (Griffiths and Magurran 1997; Dugatkin and Wilson 2000; Croft et al. 2003, 2004, 2005, 2009). Social networks are typically constructed from animal populations found in the wild by invoking the ‘gambit of the group’ (GoG, Whitehead and Dufault 1999; for other methods see Whitehead 2008; Krause et al. 2009). This means that associations are recorded between every pair of individuals that are members of the same collectively moving group. Data are collected for a number of GoG censuses and the cumulative network in which all recorded associations are included is then analysed for non-random features (Croft et al. 2008).

Significant fission–fusion processes, such as shoals dispersing at night and forming new groups the next day, are likely to be important in defining group composition and the network structure obtained in the way described above. However, fission–fusion events also occur frequently during shoaling due to groups splitting up and groups joining together (Croft et al. 2003). During these events, individuals may actively choose to move preferentially towards certain neighbours (e.g. those of the same sex) to whom they have a stronger social affiliation. This suggests that the composition of animal groups could be determined by social aspects not only in the initial formation of groups but also in encounters of moving groups.

Network analyses of collectively moving animal groups have shown the importance of individuals’ position in the social network. For example, Lusseau and Newman (2004) showed that the information flow in a bottlenose dolphin network was susceptible to the removal of dolphins with high betweenness (betweenness is a measure of importance of individuals in a network to the flow of information between others). One could imagine that one or a small number of individuals might link otherwise separate groups. Network analyses deal with static network representations but collective motion and the adaptability of groups might mean that the network reconfigures after the loss of individuals. Thus, it is important to bring together theories of collective motion and social networks.

Group level

Many animal groups have a distinctive, often hierarchical, underlying social network structure (Croft et al. 2008; Whitehead 2008). When moving collectively, animals obtain information through their links in the communication network, as described above. Social connections between animals may result in preferences between animals which in turn may alter their behaviour towards each other. Theoretical work has demonstrated that subtle changes in

the behaviour of individual animals, such as higher speeds (Couzin et al. 2002; Wood 2010), can impact on their spatial position within a group. From a social network perspective, we might expect that socially mediated changes in behaviour, due to individuals’ social network position, could affect the spatial position of animals within groups. We might, for example, hypothesise that well-connected individuals tend towards the centre of the group.

Recent research has used pigeons tagged with GPS transmitters to examine 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 to say 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. Individuals assuming positions higher in the hierarchy network tended to be closer to the front of the flock. This research demonstrates that different positions of animals within a collectively moving aggregate can be linked to differential roles of individuals possibly related to their position within a social network. Consequently, it will be necessary in the future to investigate to what extent underlying social structures, be they long- or short-term, impact on individual spatial positions within moving groups.

Social preferences within groups are often determined by social behaviours such as grooming and social dominance (Hemelrijk 2000). However, the discussion above suggests that social preferences may be expressed in collective motion at a more general level. In addition to distinct spatial positioning within groups, we might expect to find socially mitigated leadership, fine details in the internal structure of groups, or even particular formations. To what extent such features could be a result of underlying social preference networks is an important area of research.

Approaches in the literature

Many researchers have independently included the notion of networks into models of collective motion. We grouped the literature into three different approaches of how to consider networks in collective motion, which we briefly introduce before we discuss the associated literature in detail.

The first approach is particular to the physics and engineering literature. It can be posed as, ‘What type of communication network is necessary to achieve cohesive and aligned collective motion in a given number of independent individuals?’ It amounts to analytically deriving necessary and sufficient conditions on communication network structures (e.g. connected or containing a globally reachable node) for certain types of collective motion (e.g. cohesive, aligned). This problem is of importance for the design of efficient and robust multi-robot swarms (Liu et al.

2003). However, it is also of interest to biological models as it shows us which communication network structures are possible in collective and cohesive motion. Although progress has been made in considering communication topologies in collectively moving groups for engineering purposes, there is no agreed consensus on the requirements for a communication topology to obtain cohesive and aligned collective motion in biology. More importantly, from the perspective of this review, a direct link to social networks is missing: most of the studies do not explicitly introduce social networks with preferences between certain individuals. Weighted communication topologies may or may not (depending on the existence of non-social mechanisms) be equivalent to a weighted animal social network, in which individuals react more strongly to preferred individuals. This connection has not been made in the literature and could be explored using the types of modelling approaches we review. It might be interesting to consider future findings such as the loss of cohesion or alignment as a result of social networks in the light of the analytical work of this literature. We refer the interested reader to Table 1, which gives examples for different types of communication networks and models that have been considered.

The second approach (‘Social networks affecting collective motion’) is conceptually very different from the first one. It can be posed as, ‘Given different social or communication network structures, what can we expect from our collectively moving groups?’ In ecology, this approach would address how different social preferences (such as sex preferences in guppies, Croft et al. 2004) or

structures (such as hierarchical positions in pigeons, Nagy et al. 2010) affect collective motion. While the structure of the communication topology is still of interest, this work is predominantly motivated by social aspects of interactions. Crucially, the impact of manipulating the communication topology in response to an underlying fixed (time-invariant) social network is studied. In contrast to the first approach, the objectives in this part of the literature are not limited to investigating group cohesion and alignment.

Finally, the third approach (‘Collective motion affecting social networks’) considers how social networks can emerge and change over time as a result of different movement patterns. Unlike the second approach, there is no predefined fixed social network structure from the start. From an ecological perspective, this could be useful for studying whether social networks are based on kinship or acquired familiarity, for example. Loosely speaking, one could ask the question ‘Are an individual’s associates the types of individuals to whom it prefers to affiliate with (in an already existing social network) or are they its associates because it has developed a familiarity with them (in an emergent social network)?’ It might also be interesting to investigate whether social dominance or leadership is only expressed in collective motion, or whether it could be achieved through collective motion (Quera et al. 2010). The social preferences of individuals may change over time, perhaps due to increased familiarity with individuals, or positive or negative reactions between individuals. This could affect social network structure by increasing or decreasing the weights assigned to preferences (see Fig. 2

Table 1 A rough inventory of studies that establish ‘Conditions on networks’ and focus on necessary and sufficient conditions for cohesive and aligned collective motion in communication networks

Type of interaction	Alignment only	Jadbabaie et al. (2003); Savkin (2004); Yu and Wang (2008)
	Repulsion, alignment, attraction	Tanner et al. (2003); Shi et al. (2005); Liu et al. (2009)
	Nutrient profile+others	Liu et al. (2008)
	Fixed target+others	Tanner (2004)
Spatial dimension	Closed loops (e.g. ellipsoids)	Paley et al. (2008)
	2-dimensional	Jadbabaie et al. (2003); Sepulchre et al. (2005, 2007, 2008); Yu and Wang (2008)
	3-dimensional	Scardovi et al. (2007); Sarlette et al. (2009)
	<i>m</i> -dimensional	Liu et al. (2003); Shi et al. (2005)
Type of communication	All-to-all	Scardovi et al. (2007); Sepulchre et al. (2007)
	Time invariant ^a	Liu et al. (2003); Tanner et al. (2003); Lin et al. (2005); Li (2008); De Smet and Aeyels (2009)
Type of network	Undirected	Shi et al. (2005); Zavlanos et al. (2007)
	Directed	Saber and Murray (2003); Li (2008)
	Binary	Yu and Wang (2008)
	Weighted	Saber and Murray (2003); Li (2008); Liu et al. (2008)

The table lists selected details of models in the literature

^a A word of caution: it has been suggested that models of collective motion with time-invariant or fixed communication topology are formally not equivalent to systems with time-dependent communication topology (Toner and Tu 1995)

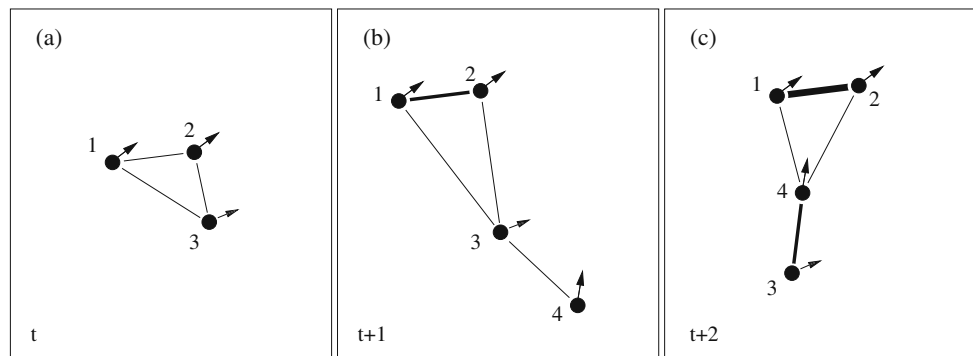


Fig. 2 Illustration of how a social network could change over time driven by spatial proximity of individuals. Increased width of edges illustrates increased strength of social connections and the positions of individuals relative to each other are shown. **a–c** Three consecutive instances of time (t , $t+1$, $t+2$). **a** Individuals 1–3 close to each other having established loose social ties. In **b**, individual 3 has moved away from 1 to 2 and another individual, 4, has appeared. 1 and 2

have strengthened their connection and 3 has established a social connection to 4. **c** The final configuration in which 3 has lost its social connection to 1 and 2 as a result of being distant from for some time. Individuals 3 and 4 and 1 and 2 have increased the strength of their social connections, and since 4 has moved towards 1 and 2 it has established connections to them

for an illustration). In many models, the communication topology at any one instant is defined by spatial proximity (recall Fig. 1a). Therefore, the instantaneous effect of changes in the social network may be small, but over time the impact can be significant.

The categories and concepts developed in the three different approaches are not mutually exclusive in biological systems. A collectively moving group might have underlying shoaling preferences (such as guppies preferentially shoaling with individuals of a similar size), but the social network can also adapt over time (such as guppies gaining familiarity with certain other individuals). In the following, we discuss the relevant literature in the light of the last two approaches—that are directly connected to social networks—in more detail.

Social networks affecting collective motion

In this section, we review models that investigate the impact of imposed networks on collective motion. Much of the work we review was not biologically motivated. We have nevertheless grouped the relevant literature into three aspects of collective motion that are directly related to the concepts we have introduced. With this, we highlight areas where previous work could be relevant and useful to biology.

Group structure and formations

Empirical studies in a wide range of group living animals have shown preferences for familiar individuals, family members or certain characteristics, and form various structures based on such preferences (Croft et al. 2008). Some field studies have even demonstrated preference for

avoidance between certain individuals (e.g. Frère et al. 2010). The evidence of such social preferences calls for theoretical work exploring possible underlying mechanisms for the spatial association within and between shoals. Further investigation is also needed to explore the extent to which movement between groups and the fragmentation of groups could be explained by underlying social networks.

Some migratory birds move in characteristic ‘V-shaped’ formations (Bajec and Heppner 2009) and detailed empirical work has revealed that collectively moving animal aggregates across a range of species show a remarkable variation in the internal structure they adopt. Starling flocks (*Sturnus vulgaris*), for example, are denser at the edges than at the core of the group (Ballerini et al. 2008) while the shoals of roach (*Rutilus rutilus*) are densest at the front (Bumann et al. 1997). It is possible that these observations could be explained simply by physical features of the animals involved or particular behaviours in response to predation pressure. However, the role of social network structure in shaping these formations needs to be explored in the context of biology.

A unified framework for imposing social networks into models of collective motion was recently suggested by Qiu and Hu (2010). They used their model to examine the role of social network structure on the formations of collectively moving human crowds. Their social network is implemented by values (connection weights w_{ij} between individuals i and j) that represent how important an individual j 's spatial position is in the calculation of individual i 's desired position. Their model allowed for two scenarios. In the first, all pairs of individuals were connected in the social network (and thus able to interact when they can perceive each other). In the second, all individuals within a group can interact, but only a limited predefined number of individuals were capable of reacting to members of other groups (these could be

considered ‘group leaders’). This framework is general and allows for the inclusion of complex preference networks. Qiu and Hu (2010) show that in their simulations the precise social structure within a group has a marked effect on the formation in which groups move, and this is reflected in the average distance of group members to the centre of the group. For example, a linear network topology (a ‘chain’ of connections) leads to a linear group formation. A network in which all followers are only connected with the group leader results in a compact formation with a low average spatial distance of group members to the centre of the group in contrast to the linear scenario. This work clearly demonstrates how group formations can be reliant on the underlying social network.

The effect of a simple social network structure on collective motion was also explored in a model for fish shoals by Hemelrijk and Kunz (2005). Individuals in the model are split into two categories: familiar and unfamiliar. In a similar manner to the previous model, the social network was implemented by values that represent how heavily an individual i weights (in terms of preference) its movement tendencies in respect to individual j (in addition to spatial distance weightings). Individuals were given higher social preferences for familiar individuals. Hemelrijk and Kunz (2005) found that individuals spatially clustered with familiar conspecifics within the group. This demonstrates that sub-structures within collectively moving groups could be explained by social networks. The spatial assortment of familiar or similar individuals within collectively moving groups has also been studied in the context of pedestrian crowds (Fridman and Kaminka 2007) and cell sorting (Belmonte et al. 2008). The precise mechanisms for the expression of individual preferences employed by these models are based on weighted behavioural responses between individuals and therefore similar to the ones presented above. Fridman and Kaminka (2007) used the quantity ‘hierarchical social entropy’ as a measure for group formation in their simulations. This measure decreases as individuals increase their spatial clustering (equalling zero if all individuals are on the same position). Hierarchical social entropy could be useful to assess the degree of structure and grouping in animal populations and in biological models.

Moussaïd et al. (2010) suggested an interesting theory specific to the movement and formations of social groups within pedestrian crowds. Importantly, they presented a model guided by a detailed empirical investigation. It was observed that more than two thirds of pedestrians moved in coherent and stable groups of two to four individuals in two pedestrian crowds of different densities and that the members of these groups were walking side by side. As pedestrian densities increased, the linear formations bent forward and adopted a V-shape. These formations and

density-dependent changes were reproduced in a ‘social force’ model in which social tendencies (and other pedestrian movement tendencies) are directly translated into forces acting on individuals. The novelty of the model by Moussaïd et al. (2010) is the consideration of the communication needs of individuals in pre-defined social groups. Group members turn their ‘gazing direction’ to be able to see their partners and move to ensure that they do not have to twist their head too much. While this model is specific to pedestrian movement, it is to date the only study comparing a model for collective motion to individual movement data whilst considering an underlying social structure. Furthermore, the empirical observations suggest that underlying social networks have a strong effect on formations of collectively moving groups. This study demonstrates the potential of comparing and informing models of collective motion and social structure with real-world data. In general, this work suggests that biologically relevant models can be developed and tested in collectively moving animals where social structure is either known or can be manipulated experimentally.

The study of the formation and requirements of ad hoc mobile networks (e.g. networks of wireless, hand-held devices) led researchers to combine aspects from social theory and collective motion in models (Musolesi et al. 2004; Borrel et al. 2009). Both studies included social preferences as fixed dyadic weights between pairs of individuals. The precise mechanisms of group behaviour are roughly similar to what has been described above. However, Borrel et al. (2009) performed an interesting analysis. The authors studied the distribution of inter-contact durations (based on spatial proximity) for random underlying networks (described by dyadic weights) and compared them to empirical data published elsewhere. They found power law distributions of inter-contact durations (with cut-offs) in their simulations that are similar to the empirical evidence. To rephrase this slightly, their random social network produced power law contact networks. They suggested that this finding was independent of the type of random social network used in their simulations. This analysis shows that the structure of an underlying social network is not necessarily reflected in the structure of contacts or, in a wider sense, communication networks. This is an important point: when we study social aspects of animal behaviour, we often record contacts between animals. The work by Borrel et al. (2009) illustrates that we have to choose carefully what aspects of the contacts or communication between animals we study if we want to infer information on the social preferences of these animals. It also demonstrates that, depending on the non-social behaviour of animals (such as a preference for larger groups, or home range constraints), observations of animal associations do not necessarily recover social preferences of animals in all cases.

While most of the work presented in this section has not been conducted with biology in mind, it presents a body of interesting approaches that include social interactions in models of collectively moving groups that could inspire biologically relevant mechanisms. Furthermore, the analysis of these models has culminated in useful measures and approaches [e.g. ‘hierarchical social entropy’ (Fridman and Kaminka 2007), distribution of contact durations (Borrel et al. 2009)] that could be usefully applied to biological systems.

Structured interactions and the efficiency of group movement

Social network structure may impact on the nature of communication between animals and this in turn could affect the overall efficiency of communication. Consider, for example, the case of a social hierarchy in which individuals predominantly pay attention to a small number of dominant individuals. Such a focus of attention could result in reduced efficiency of information transfer between subordinate individuals. If information (such as direction or the presence of a predator) does not propagate through a moving animal group with enough efficiency, the individuals within the group will suffer a fitness loss due, for example, to less efficient foraging, less efficient flying, or slower anti-predator reactions.

Motivated by the notion of small-world networks (Watts and Strogatz 1998), Buscarino et al. (2006) manipulated the communication network structure in a simple model for collective motion. The original version of the model allows individuals to react to the average orientation of all individuals within a fixed range of perception (Vicsek et al. 1995). In the adapted model, long-range interactions beyond the range of perception of individuals were introduced in a stochastic way. This led to improved alignment in the presence of stochastic effects or noise (Buscarino et al. 2006). While this work is primarily related to efficient and sufficient communication between individuals, one could imagine that underlying social preferences may forge long-range communication links that go beyond local information exchange. For example, African elephants (*Laxodonta africana*) mostly move in small social units and are capable of long-distance vocal communication with elephants in separate social units (McComb et al. 2000). The work by Buscarino et al. (2006) demonstrates that long-range communication could impact on or even facilitate the collective motion of such groups.

The theoretical work presented so far suggests that social preferences can have a profound impact on collective motion. This could be particularly important in situations where there is limited space for group movement due to a restrictive local environment. This could, for example, have heavy fitness implications for animal groups attempting to

escape from a predator. Braun et al. (2003) studied the impact of individual agents’ characteristics on evacuation efficiency. Their model simulates the escape of a group of people from a room with one door. Social ties were implemented via distance-dependent attractive forces between individuals in the same family or group within the crowd. Overall, the framework is versatile and allows the inclusion of weighted and directed connections between individuals, although the effect of this was not studied. Braun et al. (2003) found that the flow of people out of the room decreased slightly with stronger social ties and, qualitatively, that the members of predefined social groups moved closer to each other over time. The situation simulated by this model would become particularly interesting to biologists if the group represented an animal collective with a predator in pursuit. However, the effect of social networks on collective anti-predatory response has not been studied.

Leaders and followers

Leadership in moving animal groups has received a lot of attention (e.g. Couzin et al. 2005; Conradt et al. 2009). It has been argued, for example, that small groups of informed individuals can lead large groups of naïve individuals simply by moving towards their target (Couzin et al. 2005). Additionally, it has been suggested that individuals can increase their influence on group movement by adjusting their own behaviour (Conradt et al. 2009). The last two examples are possible explanations for leadership without the need for social preferences. However, recent empirical work has shown that dominant beef cows (*Bos taurus*) have more influence on herd movement than more subordinate cows (Šárová et al. 2010). Leader–follower relationships impose a rudimentary social network onto simulated collective motion. More generally, modelling socially mitigated leadership in the collective motion of animals could allow insights into the possible situations in which we can realistically expect to find leadership as a social phenomenon. The research directed at the aspects of socially mitigated leadership in collective motion is currently somewhat removed from biological systems. Some of the studies reviewed here may, however, provide a good starting point to investigate this field and further our understanding of how hierarchical social structures affect group movement.

Some analytical studies incorporate leaders into their models (Jadbabaie et al. 2003; Liu et al. 2003; Hu and Hong 2007; Consolini et al. 2008). Followers in these models have equal preferences for leaders or other followers in their interactions. It is only the behaviour of the leader that is different in that leaders do not interact with other individuals. This represents an extreme social

network structure where all individuals are socially connected, with the exception of the leaders that have only incoming (directed) social connections. Essentially, this represents a hierarchical sub-structure within the social network. The only criteria examined in this body of literature are the stability (coherence) and alignment of simulated flocks, and the necessary conditions on the communication topology to achieve the aforementioned criteria. Simulation studies have also included the concept of leadership into collective motion (Loscos et al. 2003; Qiu and Hu 2010), but have not studied the consequences of this addition.

Collective motion affecting social networks

In Group level, we have hinted at how social networks could emerge and develop as a result of collective motion and at the impact this could have. Now we develop this concept in more detail.

As we discussed in the previous section, theoretical work has suggested that faster individuals are more likely to be found at the front of groups (Couzin et al. 2002; Wood 2010) and that individual group members can increase their influence on the movement of the group by adjusting their behaviour (Conradt et al. 2009). Simple mechanisms such as the ones explored in these models may result in spatial sorting within moving animal groups and subsequently in increased familiarity between similar individuals (according to behaviour or physical properties). Effects such as increased familiarity between individuals could result in changes to the underlying social network (e.g. increased preference for familiar individuals). Empirical work on guppies (*P. reticulata*) has demonstrated that individual fish prefer to shoal with conspecifics with whom they are familiar (Griffiths and Magurran 1999). This suggests the possibility for underlying social network structures to change: as two individuals shoal together (due to any factor such as chance, home range overlap, assortment preference, etc.), they adjust their preferences to increase the chance that they will shoal in the future. Thus, a promising approach may be to investigate how the structure of moving animal groups changes over time and in space. With regards to the mechanisms of how exactly social networks may change as a result of group dynamics, inspiration could be taken from the literature on adaptive co-evolutionary networks (Gross and Blasius 2008).

The approach of ‘collective motion affecting social networks’ has been studied little. In the following, we will give examples from the literature that are intended to illustrate examples of how social networks could emerge as a result of collective motion.

An early model for crowd behaviour assigned social parameters and spatial goals to agents (Musse and

Thalmann 1997). Agents were members of groups and when they reached their spatial goal they reassessed their group membership and social parameters based on the social parameters of other agents present. Thus, their social affiliations and preferences changed over time as a result of their decisions. This led to group formation and movement between groups. Musse and Thalmann (1997) developed and explained their model in detail but their analysis of the model is only qualitative. While the impact of the particular mechanism suggested by Musse and Thalmann is not clear, their work may provide a valuable starting point to include re-assessment of group membership in animals once targets (such as e.g. waterholes or roosts) have been reached. Although this example does not fit with our definition of collective motion, it is a good example of how different social behaviours can influence and create social network structures. It is easy to see how this might translate to models of collective motion, where the behavioural characteristics of animals influence the underlying social network.

An entirely different concept was presented by Wessnitzer et al. (2001). The goal of their collective motion and decision-making model was the self-organisation of individuals into formations (e.g. a line or square). Initially, individuals did not communicate. Subsequently, one agent began to recruit other individuals for the task at hand based on distance-dependent probabilities. The way in which the communication links were assembled also depended on the task. The recruitment of individuals to the group continued until a sufficient number of agents was assembled (Wessnitzer et al. 2001). Formation control is a problem relevant to many engineering problems, and further work can be found in this literature (e.g. Şahin et al. 2002; Trianni and Dorigo 2006). The self-organisation into formations is possibly not directly related to collective motion in the classical sense (shoals of fish, flocks of birds), but the example of the defensive formations of muskoxen (*Ovibus moschatus*) illustrates that this does occur in nature and may be influenced by social preferences.

In the previous section, we discussed models of leadership. A recent study showed how leaders could emerge from local interactions between individual group members (Quera et al. 2010). This approach is based on a matrix of ‘ideal distances’ that agents ideally attempt to maintain between each other. Individuals move to minimise the difference between the actual distances to agents they can perceive and the preferred distances to these agents. The ideal distances can be viewed as weighted interaction and proximity preferences and are not static. Instead, they are updated based on a reward system in which pairs of agents predict distances between each other before moving. Good predictions are rewarded by manipulating the ideal distances and vice versa. In the analysis of the model, hierarchical leadership is defined rigorously and measures for leadership and the extent to which the group moved

together (alignment and cohesion in one quantity) are defined (Quera et al. 2010).

In summary, some interesting concepts have been developed in this field, but the direct link to animal behaviour is currently missing.

Discussion

We have seen that a myriad of models for collective motion that include communication networks or social networks into their mechanisms have been developed for a number of different reasons. However, despite the high level of interest in both social animal networks and animal collective motion in ecology, only a very small fraction of the literature is concerned with animal behaviour. Bringing together these two areas of research is the natural progression that will allow us to understand the interplay between social networks and collective motion. We suggest that this will represent an important advance in the field of animal behaviour. In the following, we present a number of questions and perspectives for future work (see also Table 2). We feel that addressing these questions and issues will greatly help our understanding of the connection of social networks and collective motion, and our understanding of the movement of animals groups in general.

Defining collective motion

At this stage, we need to revisit our working definition for collective motion. Recall that Petit and Bon (2010) defined the collective movement of animals as a sequence of events including pre-departure and initiation. It is likely that social preferences impact on such events. Fission–fusion events are thought to be the key drivers behind many network

Table 2 List of a number of questions of immediate interest for future research

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- How does the spatial positioning of animals within moving groups vary over time, flocking events and social rank?
 - Can detailed internal substructures or formations tell us something about social preferences in animals?
 - Is current data gathering that infers social networks from spatial association adequate?
 - When and where is socially mitigated leadership possible?
 - Is there a cost to maintaining social ties in collective motion?
 - Can social affiliations improve or hinder the predatory response of moving animal groups?
 - Could different social structures explain differences in collective motion between species?
 - Do aspects of collective motion result in particular social network structures in animal groups?
-

structures sampled by ecologists, and thus understanding how the social networks underlying group fission are likely to prove important for informing field ecologists (Franks et al. 2010). Research on macaques (*Macaca tonkeana* and *Macaca mulatta*), for example, suggests that mechanisms underlying group fission in group departure events are mainly influenced by individual affiliations (Sueur et al. 2010). This raises the question of whether future models for the movement of animal groups should cover a wider spectrum of behaviours than the ones included in our definition of collective motion.

For two reasons, we believe that models can continue to focus on minimalist scenarios as they have done on the past. First, extending the scope of group movement models is likely to increase their complexity (even more so than in minimalist models), as we may have to account explicitly for factors such as the environment (e.g. resources, obstacles), the internal state of individuals (e.g. food deprivation) and the time of day. Second, we tentatively suggest that the behaviour of animals varies to an extent that allows a separate treatment of different behavioural contexts. A set of minimalist models could therefore present a compartmental description of behaviour.

Characterising collective motion

There is a crucial need to characterise the movement of animal groups in a way that is appropriate to study the impact of underlying social networks. Many of the studies we review only consider summary statistics such as alignment and cohesion—measures that may be inappropriate for the problem at hand. Innovative measures such as ‘hierarchical social entropy’ (Fridman and Kaminka 2007) and the distribution of contact durations (Borrel et al. 2009) are the exception in theoretical studies. Although there is value in purely theoretical analyses, much inspiration comes from empirical work. Detailed investigations of individual animal trajectories have offered insights into the internal structure of flocks of birds (Ballerini et al. 2008) and formations within pedestrian crowds (Moussaïd et al. 2010). Another interesting approach to study group fission and fusion events at the individual level is presented by Michelena et al. (2010). They look at a mechanism for how animals form groups and split into smaller subgroups on a given food environment. While the mechanism suggested is based on differences between bold and shy individuals and therefore not on social affiliations between individuals, the approach by Michelena et al. (2010) to study individual probabilities for leaving or joining other conspecifics might be useful in the context of group fission and fusion as a result of social preferences.

While already existing work opens up new questions about the mechanisms generating them, we would like to

see this go further. Specifically, it would be interesting to see whether the positions animals occupy within groups (relative to conspecifics) are fixed or vary over time and between flocking events. Here the work by Nagy et al. (2010) on small flocks of pigeons provides an interesting starting point. Experiments could also be designed to test ideas regarding emerging or changing networks. For example, two guppies could be made familiar with each other before being added to a group. Their relative positions and orientations could then be tracked (e.g. using free tracking software such as SwisTrack; Correll et al. 2006) and researchers could investigate whether familiar individuals tend to shoal together more than they do with less familiar group members. Another option would be to track patterns of interactions of moving individuals in different groups where they are known to have different social structures. These social structures could be also related to environmental or group size constraints, or have movement limitations. Such experiments would require replication and are not without difficulties. However, we anticipate that experiments of this nature will help elucidate the role of social networks in collective motion. Although we would expect a cycle between models and empirical experiment, such empirical studies could open up questions important in their own right.

Mechanisms at the individual level

Rather than simply assuming that social preferences directly translate into attractive, repulsive or aligning tendencies—as in most of the literature we review—it may be worthwhile to consider the precise mechanisms of how this could work in animals. For example, Lemasson et al. (2009) study collective motion from a neurobiological perspective and one could imagine that neurological pattern recognition might yield interesting concepts. Recent work by Bode et al. (2010b) suggests a simple neighbour sampling approach by which individual-to-individual preferences can be modelled without a priori assuming that social connections translate into particular movement tendencies. The idea behind this concept is that animals sample information from their field of perception, rather than averaging over it (as is typically assumed). In the current implementation, animals prefer to react to nearby conspecifics (Bode et al. 2010b); however, this could easily be extended to include preferential interactions between socially connected animals. Preferential interactions can, but do not necessarily translate into attractive social forces. In a different approach, it has already been demonstrated that the communication needs of social group members could explain movement features in pedestrian crowds (Moussaïd et al. 2010).

Issues at the population level

In the introduction, we highlighted the difference between group-level and population-level perspectives. Most current animal social network data is recorded from the population-level perspective. The predominant method essentially samples instances of spatial assortment of individuals in groups. Despite rigorous approaches and careful analysis (Croft et al. 2008; Whitehead 2008; Franks et al. 2010), we do not yet know the extent to which the sampling techniques used can accurately reconstruct social preferences in moving populations in which individuals are continually switching group membership within a sampling period. Within populations, areas of interest include the fragmentation and formation (fission–fusion) of groups as a result of social interactions, the number of groups formed in limited space as a result of different social structures and the effect of boundaries on the preceding issues in limited space. These aspects are particularly important if we want to derive information on the social structure in populations from empirical observations. Careful modelling of such scenarios will provide a baseline and may even enable us to specifically suggest effective sampling protocols. From this perspective, research can address questions relating to the effect of large-scale social network structures, such as degree distributions (e.g. the distribution could be Poisson or skewed with some very well-connected individuals), average path lengths (where a high average path length could represent high rates of mixing between groups) and the network position of key individuals. The social position of individuals in a large-scale network, representing the social structure of the population, would likely represent the level to which individuals mediate between groups, in addition to local social preferences. To include large-scale social network structures in models of collective motion, networks with the desired properties can be generated and each individual allocated to a network position (i.e. a node).

Issues at the group level

In the previous sections, we have discussed the need for research to examine how social network structure might affect group formations and internal structures, efficiency of communication or group leadership. For group formations, we can address questions such as why starling flocks are denser at the edges than at the core of the group. Biologically relevant models can be developed and tested in collectively moving animals where social structure can be manipulated experimentally. This would allow researchers to examine questions related to within-group structures, such as what effect the social network structure has on group formations (such as V-formations) or what effect the social network position (e.g. well connected or poorly connected)

of an individual has on their spatial position (e.g. middle of the group or periphery of the group). One possible approach for empirical work could be to remove dominant animals from groups and to compare the collective motion of the group the situation when subordinate individuals are removed. Theoretical work on dominance interactions in stationary groups, for example, has suggested that dominant individuals take central spatial positions within groups (Hemelrijk 2000). Could this concept extend to collectively moving groups?

Examining the communication or even navigation efficiency of groups with different social network configurations will allow a link to fitness based on foraging efficiency, predator escape efficiency, etc. For example, we could ask whether a dense network structure decreases time to escape from predators or hinders the shaping of anti-predatory group formations such as torus formations. When examining group leaders, analysing the role of hierarchical social network structures could prove fruitful. Nagy et al. (2010) claim that small groups navigate more efficiently with leaders. Could this explain social hierarchies in some small groups of migrating animals?

We have suggested that movement patterns can affect social structure by allowing individuals to become familiar with others as a result of their position in a group (see ‘Leaders and followers’). To establish whether this is a plausible mechanism, studies are needed that investigate the relative positions of animals within moving groups over possibly long time scales. One mechanism for this could be the ageing of animals and the corresponding change of their physical abilities. Alternatively, varying predation pressure could impact on collective motion. Recent empirical and theoretical work by Bode et al. (2010a) has suggested how animal groups synchronise in the face of increased threat levels. This could provide a starting point to investigate the positioning of animals within groups in such situations. Alternatively, we could also imagine a complex feedback scenario. Animals with weak social ties, for example, may occupy peripheral positions in groups. On the edge of groups, they may face higher predation. As a result, predation pressure on moving animal groups may result in or even select for denser and more homogeneous social networks.

Other questions of interest

There are other general questions that could be asked of collective motion in the context of social networks. For example, it could be valuable to investigate whether there is a general cost to maintaining social ties in collective motion (e.g. ungulate parents and offspring trying to maintain proximity; Espmark 1971) and to examine the extent to which this could explain different social structures across species. Costs and benefits associated with maintaining

social ties in collectively moving animal groups will highlight fitness trade-offs for individuals that could explain why some species are and others are not sociable. Researchers are increasingly interested in the effect of ‘personality’ (behavioural syndromes) on collective motion in a shift away from the simplifying assumption of identical individuals (Croft et al. 2009; Piyapong et al. 2010). Introducing social interactions will add another aspect of individualism to the theory of collective motion, and this additional meta-level is a further step to disentangle and understand the true complexity of animal groups.

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