

**Modelling collective motion in animals
and
the impact of underlying social networks**

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Abstract

Nature is rich with examples of the collective motion of animal groups, such as flocks of birds or shoals of fish. The mechanisms of self-organization resulting in these spectacular phenomena have received wide attention. Individual-based models are a popular and promising approach to investigate and explain features of animal collective motion. The first part of this thesis gradually develops a novel modelling framework for the collective motion of animals and justifies it by comparison to empirical findings. Key aspects of the model are stochastic asynchronous updates and sensory zone sampling of individuals. Higher updating frequencies are related to increased levels of perceived threat and reduced stochastic effects leading to synchronisation in moving groups. Sensory zone sampling, biased according to the distance between individuals, provides a possible mechanism for the empirical finding that animals on average only interact with a fixed number of nearest neighbours.

Many group-living animals show social preferences for relatives, familiar conspecifics or individuals of similar attributes, such as size. How such preferences could affect the collective motion of animal groups has been rather unexplored. The second part of this thesis reviews previous theoretical work that combines the concepts of social networks and collective motion. Although many of the models reviewed have not been explored with ecology in mind, they present a current context in which a biologically relevant theory can be developed. The modelling framework from the first part is extended to include social connections as preferential reactions between individuals. This is used to show that the structure of social networks could influence the cohesion of groups, the spatial position of individuals within groups and the hierarchical dynamics within such groups.

This thesis aims to contribute possible mechanisms, testable hypotheses and an informed starting point for future research on how social networks could affect animal group movement.

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Additional material

Supplementary film 1: simulation with underlying social network.

Provided on compact disk with bound copy at the University of York library.

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Declaration

This submission is entirely my own work except where due acknowledgement has been given. Empirical experiments in chapter 1 were conducted in collaboration with Dr. Jolyon Faria and Prof. Jens Krause at the University of Leeds. Chapters 1 to 5 have been published in peer-reviewed journals. Each of the published chapters is presented as it appears in print and details on journals are given at the beginning of chapters.

General introduction



Figure 1: Examples for animal collective motion. Photographs by Frédérique Becker and Sebastian Bode.

Collective motion in animals

The collective motion of animals occurs in numerous different forms, many of which are familiar to us. Examples are shown in figure 1 on the previous page and include tightly bound fish shoals, flocks of birds, clouds of midges and even pedestrian crowds. The fact that more than fifty percent of fish species display synchronised movement [Parrish et al., 2002] illustrates that many group-living animals can move in aggregations of varying coordination levels. Flocks of birds flying in a line, a V-shaped formation or forming dense clusters are common sights. Perhaps it is this ubiquitousness that has resulted in the fascination of scientists from different disciplines for animal group movement phenomena. Human investigation or observation of animal collective motion can be traced back more than two-thousand years (Pliny, in Rackham [1933]) and since then, the scientific literature has grown steadily, including a wealth of theories and empirical observations, as well as anecdotes, on this topic [Bajec and Heppner, 2009].

In the widest sense, animal collective motion could be described as movement phenomena of animal aggregations. However, the examples given above already suggest that animal group movement is not easily categorised. To give an example, in fish, “schools” have been defined as polarised and synchronised groups (Pitcher et al. [1976], citing Shaw). Furthermore, definitions for flight aggregations, flight formations, flocks, herds, shoals, swarms and more exist, but despite these efforts no consensus on the naming of animal group movement phenomena has been reached in the literature [Bajec and Heppner, 2009]. Indicative of this problem is that the website “Wikipedia”, an extensive online encyclopedia, contains to date no article on the term “collective motion”, but does contain articles on subcategories of collective motion such as flocking and shoaling [Wikipedia, 2011]. It is in the sense of investigating subcategories of animal collective motion, rather than in the sense of suggesting a definitive description or explanation, that the title of this thesis is to be understood.

In addition to classifying and recording observations, two general questions have been posed, in the context of investigating the collective motion of animals: why

do groups of animals move the way they do, and how do they do it [Viscido et al., 2005, Bajec and Heppner, 2009]? Human observers tend to record attributes of the collective, such as degree of alignment, density or shape of moving animal groups and it is tempting to assign biological meaning to all such observations [Parrish et al., 2002]. Many possible reasons, such as risk dilution in the presence of predators, mating opportunities and improved ability to find food, have been offered to answer the first question [Hamilton, 1971, Parrish and Edelstein-Keshet, 1999, Krause and Ruxton, 2002, Bajec and Heppner, 2009]. Theoretical research has even investigated possible evolutionary scenarios that could explain aspects of group movement [Wood and Ackland, 2007, Wood, 2010, Torney et al., 2010]. However, nearly identical shapes to animal movement patterns can be found in systems of inanimate objects (e.g. magnets aligning, planets circling each other) which could suggest that not all that is observed actually has a direct biological reason [Parrish et al., 2002]. This thesis is predominantly concerned with the second question and attempts to suggest and test possible mechanisms underlying group movement.

According to Parrish and Edelstein-Keshet [1999], animal aggregations can be divided into two classes: self-organising ones and ones that form and move exclusively in response to external cues. The current consensus is that the collective motion of animals is a self-organising system in which the combination of individual actions result in the group behaviour we observe [Parrish and Edelstein-Keshet, 1999, Krause and Ruxton, 2002, Sumpter, 2006, Bajec and Heppner, 2009]. More specifically, the idea is that in addition to reacting to external cues, individuals react to the position and movement of other group members. Group characteristics that result from decentralised individual actions are “emergent properties” [Viscido et al., 2004] and understanding how they arise is a difficult problem (e.g. Sumpter [2006]).

Depending on the size of groups, individuals often have no knowledge of the collective, as it extends beyond their range of perception [Viscido et al., 2005, Sumpter, 2006]. Examples could be large flocks of starlings or shoals of fish in which individuals block the field of vision of others [Parrish and Edelstein-Keshet, 1999, Bal-

lerini et al., 2008]. Even creatures with comparatively limited information processing abilities, such as locusts, are capable of remarkably coordinated displays including synchronised changes in group movement direction, for example [Buhl et al., 2006]. Such observations, combined with theoretical investigations, have led researchers to suggest that animal collective motion is based on individual actions and that very simple and local behavioural rules for identical individuals could in fact account for a large variety of group movement characteristics [Parrish and Edelstein-Keshet, 1999, Sumpter, 2006, Bajec and Heppner, 2009]. An example for such a behavioural rule could be “move away from nearby individuals to avoid collisions”.

Although recent empirical advances have started to shed light on this by deriving information on individual behaviours from statistical analysis on entire groups (e.g. Yates et al. [2009], Ballerini et al. [2008]), it is still the case that researchers predominantly turn to theoretical approaches to investigate the mechanisms of animal collective motion (e.g. Conradt et al. [2009], Wood [2010], Hildenbrandt et al. [2010]). One reason for this is that the simple rules that are believed to govern individual behaviours are readily expressed in mathematical equations or “traffic rules” for individuals [Parrish and Edelstein-Keshet, 1999, Sumpter, 2006]. These representations or models of biological systems can then be used to formulate testable predictions. Modelling animal collective motion also allows researchers to compare the patterns produced by different hypothetical interaction rules to differentiate between behavioural causes and other effects [Parrish et al., 2002] - some patterns may be a direct consequence of particular behaviours, whilst others may be a product of simple biomechanics such as drag, for example. This thesis uses such a theoretical modelling approach, closely linked to empirical findings, to investigate possible mechanisms of animal collective motion.

The remainder of the introduction briefly outlines key ideas on concepts of how animal collective motion is quantified and modelled. In addition, the concept of social networks in animals is introduced.

Quantifying the collective motion of animals

An early example of quantifying the movement of animal groups is the study of fish shoals in well-lit tanks. Aoki [1980] filmed shoals of fish from above under controlled conditions and extracted time series of the positions of individual fish in two dimensions from his films (see also figure 2). Using these trajectories, Aoki analysed the speed distributions, internal structure, distribution of distances to nearest neighbours, turning events and movement correlation of individuals in his fish shoals. Each of these summary statistics is obtained by combining information on the relative position, movement direction or speed of all individuals or a subset of the group. An example for a commonly used summary statistic is the distribution of nearest neighbour distances. This is obtained by computing the distance of each individual to its closest group member and is a useful measure for the density of groups [Cavagna et al., 2008]. Aoki's comprehensive analysis includes many initial attempts of analysis techniques that are still applied to animal group movement trajectories.

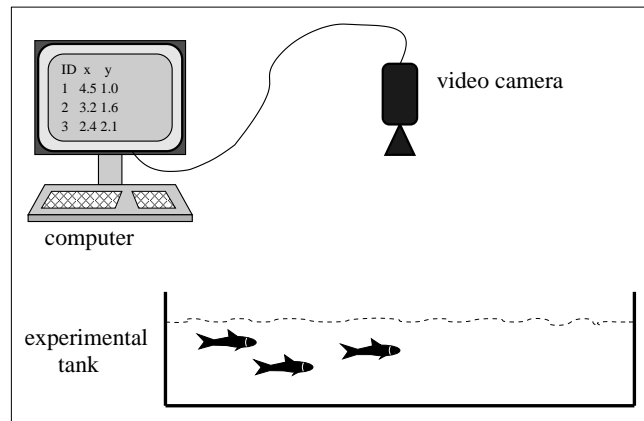


Figure 2: Example for an animal motion tracking experimental set-up. Fish are placed in a shallow experimental tank to justify analysis in two dimensions. Using a video camera placed directly above the tank, the fish movement is recorded to a computer, where time series of individual positions for individuals are extracted using motion tracking software. These trajectories can then be used in further analysis.

Filming moving groups of animals, followed by the extraction of individual tra-

jectories from the films and finally analysing these trajectories by using increasingly sophisticated approaches, has been a successful method to quantify the collective motion of animals. This approach is reasonably accessible, facilitated by the availability of motion tracking software (e.g. “SwisTrack”; Correll et al. [2006]), can be used in experimental settings (e.g. Aoki [1980], Partridge and Pitcher [1980]), natural habitats (e.g. Tien et al. [2004]) and on most grouping animals such as, fish, insects [Buhl et al., 2006] and humans [Moussaïd et al., 2010].

Beyond observing animal movement under controlled conditions, experimental manipulation has offered a useful tool to investigate possible mechanisms. Partridge and Pitcher [1980] assessed the positioning of blindfolded fish or ones with severed lateral lines to establish a sensory basis for fish schooling. Experiments with locust swarms in annular arenas revealed that the density of insects inside the arena is a driver for the frequency of switches in group movement directions [Buhl et al., 2006]. In another example, scientists waded into streams to simulate predatory attacks and measured how this affected the nearest neighbour distances and tendencies of individuals to move towards other group members [Tien et al., 2004]. Chapter 1 of this thesis makes use of different experimental conditions to alter the behaviour of individuals.

The acquisition of large datasets has made it possible to infer information on individual behaviours from group-level statistics. In a particularly striking example, Ballerini et al. [2008] used stereo-photography to reconstruct the three-dimensional positions of individual birds in flocks of starlings numbering close to three thousand individuals. Very fine details of the internal structure of these flocks, invisible to the naked eye, led to the conclusion that starlings interact with a fixed number of nearest neighbours [Ballerini et al., 2008]. Previous to this finding, the consensus had been that individuals interact with all group members within a fixed distance from them. Further work on locusts marching in an arena, as already mentioned, investigated stochastic effects in locust movement using a coarse-grained approximation of their movement [Yates et al., 2009]. Yates et al. [2009] suggested that locusts respond to

decreasing alignment of the group by increasing the randomness of their movement. The importance of this type of research is that it offers the possibility to replace theoretical speculation on interaction rules (see above) with concrete guidance for how animals interact. The group-level characteristics of Ballerini et al. [2008] and Yates et al. [2009] therefore provide a base-line to be achieved for theoretical research aiming to suggest mechanisms for animal collective motion. Chapters 2 and 3 relate the theoretical work in this thesis directly to the aforementioned findings.

In a different approach to filming animals, recent work has used GPS sensors to obtain trajectories of animals in groups. This has been used to investigate leader-follower relationships in pigeon flocks [Nagy et al., 2010] and leadership in herds of cows based on the social status of individuals [Sárová et al., 2010]. Here, this approach is not used explicitly, but in chapter 5 simulations are put in context with the results of Nagy et al. [2010].

Modelling the collective motion of animals

Three different theoretical approaches to model animal aggregations have been identified [Parrish and Edelstein-Keshet, 1999]. First, the mean-field densities of aggregations can be described using continuum equations (e.g. partial differential equations). Such models are only biologically relevant for large, dense groups without sharp discontinuities. Second, detailed equations of motion for individuals can be formulated, assigning forces and velocities to individuals. Although these models come closer in describing what individuals are doing, it is difficult to investigate them analytically and often numerical simulations or approximate solutions are presented. Third, individuals are represented directly and their movement and behaviour is simulated discretely by encoding simple rules such as “align with other group members”.

Models of the third type are often called “individual-based” models and implement responses of individuals to external cues and to the movement and positions of other group members. Typically, individual actions are modelled as a combination of biomechanical or environmental forces (e.g. drag; Cziráková et al. [1999]), attraction or

repulsion tendencies (e.g. collision avoidance; Couzin et al. [2002]), alignment or behaviour matching (e.g. velocity matching; Reynolds [1987]) and random or stochastic effects (e.g. sensory errors; Buhl et al. [2006]). Most models assume that all individuals are identical and therefore illustrate that entirely leaderless animal collective motion is possible. Furthermore, Viscido et al. [2005] suggest that movement rules should ideally be biologically realistic at the individual, group and population levels. Figure 3 illustrates the principles and patterns produced by individual-based models for collective motion.

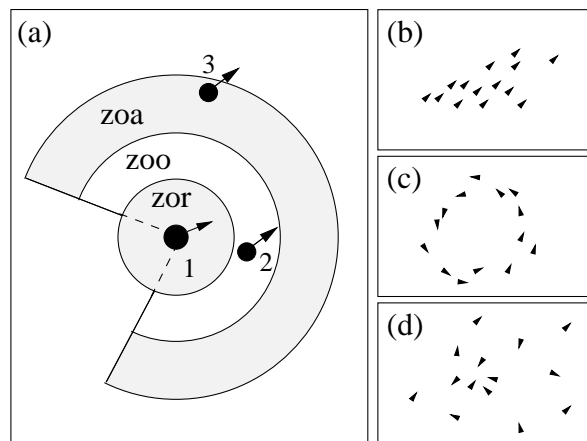


Figure 3: Example for an individual-based model for collective motion and patterns produced by it. (a) schematic illustration of three individuals (labelled 1 to 3), moving at a constant speed, showing the behavioural zones of individual 1. Each individual reacts to others by following three behavioural rules, one rule for each non-overlapping part of its behavioural zone. *zor* - zone of repulsion: “move away from other individuals to avoid collisions”. *zoo* - zone of orientation: “align with others”. For example, individual 1 has a tendency to align with individual 2. *zoa* - zone of attraction: “move towards others to maintain group cohesion”. The exact way in which the different behavioural rules combine can vary. For example, collision avoidance may override the other behaviours. Note the blind region directly behind individuals in the *zoo* and *zoa*. Varying the size of the blind region, the relative extent of the behavioural zones, or the size of stochastic effects results in different realistic patterns of moving groups. (b) highly aligned group, (c) “milling” behaviour. (d) un-aligned “swarming”. Figure inspired by findings in Couzin et al. [2002].

Individual-based models are by far the most popular and intuitive theoretical approach to animal collective motion, as they can produce realistic behaviour [Parrish and Edelstein-Keshet, 1999] and it is easy to explore the impact of varying individual behaviours [Viscido et al., 2004]. However, this hints at one of the weaknesses of such models. Many individual behaviour rules can result in realistic movement patterns and it is therefore difficult to establish which rules animals actually follow [Parrish and Edelstein-Keshet, 1999, Viscido et al., 2004, Sumpter, 2006]. While work has started towards directly inferring animal movement rules from individual trajectories (e.g. Eriksson et al. [2010]), this approach is, to date, not yet fully developed and applied. Recent advances in quantifying animal collective motion have made it possible to conduct an empirically inspired debate about mechanistic details of model formulation and to compare simulations to empirical data to a greater extent (see above). Typically, when simulations are compared to empirical data, models are not fitted to data quantitatively. Rather, a qualitative comparison of group-level characteristics is performed (e.g. Buhl et al. [2006], Yates et al. [2009]). This is the approach taken in this thesis: qualitative comparisons of individual-based models to empirical data and the development of testable hypotheses are used to demonstrate the biological relevance of the theoretical approach.

The success of individual-based models for collective motion is demonstrated by the variety of models and model analysis approaches in the literature. At times this has resulted in the complaint that the degree of replication across these studies is too low to allow for meaningful comparisons [Parrish et al., 2002]. Early biological models simulated small groups of less than fifty individuals and limited movement to two spatial dimensions (e.g. Aoki [1982], Huth and Wissel [1992]). The nature of these early studies was mostly exploratory. For example, Huth and Wissel [1992] found that, in their model, interactions of individuals with a single neighbour were insufficient to produce realistic shoaling patterns. Reynolds [1987] initiated a new application by using a model for collective motion in three dimensions for the computer animation of large animal groups. The basic idea of his model with individuals, or “boids”,

following three behavioural rules has been introduced above. Additionally, the model explicitly included features such as banking of individuals whilst turning and the impact of gravity, to create life-like animations that were subsequently used in motion pictures and computer games (see figure 4). This use of models has enjoyed popularity ever since, but the progress in this field is difficult to track as publishing innovations would have financial consequences (see also; Bajec and Heppner [2009]).

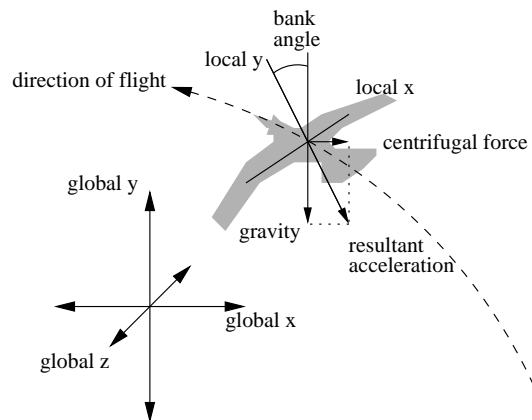


Figure 4: Adapting individual behaviours for the computer animation of collective motion. Individuals re-align their local coordinate system (defined by their body) whilst turning, to balance the combination of gravity and centrifugal force acting upon them with the uplift produced by their wings and thrust. This behaviour is called “banking” and including such aspects of bird flight in individual-based models results in a visually more convincing representation of animal collective motion than the simpler approach illustrated in figure 3. Redrawn from Reynolds [1987].

Individual-based models for collective motion gained an even wider audience when physicists adapted the idea. In substantially simplified models, individuals were essentially modelled as particles with constant velocity and an alignment behaviour subject to an error of variable size [Vicsek et al., 1995, Toner and Tu, 1995]. Simplification was taken even further by considering collective motion in one dimension [Czirók et al., 1999, O’Loan and Evans, 1999, Raymond and Evans, 2006]. Physicists were primarily interested in discovering different “phases” in collective motion and in investigating the transition between phases [Vicsek et al., 1995, Grégoire and Chaté,

2004]. These phases are analogous to different states of chemical substances, such as gaseous or liquid, and therefore describe particular characteristics of group movement. When the values of parameters in simulations are systematically varied, the patterns produced also vary and may change from one phase to another. For example, as the size of stochastic effects in the movement of individuals is increased, groups may stop displaying a highly aligned state (see figure 3b) and instead display a less organised pattern (see figure 3d). These investigations may help to place systems of “self-propelled particles” in the wider context of physics.

Models for collective motion have also been successfully used to inform and improve the control of crowd and vehicular dynamics. For example, features of escape panic have been simulated and then used to improve the design of public buildings [Helbing et al., 2000]. Most models in this field work with forces between individuals and therefore equations of motion for individuals. However, the inclusion of social interactions and the difficulty of solving these equations analytically effectively requires explicit simulation of each individual [Braun et al., 2003, Moussaïd et al., 2010]. In contrast to many biologically motivated models, the study of crowd dynamics often requires explicit consideration of limiting boundary conditions, such as walls or emergency exits of limited width [Helbing et al., 2000, Braun et al., 2003].

Another possible application for the theory of collective motion is directly linked to technological advances. Developments in electronics have meant that it has become feasible to produce and access large numbers of identical robots. This has made the design of swarms of autonomous robots a topic of research. Scientists have used models for collective motion to suggest suitable control algorithms and, more generally, to determine what conditions robot interactions have to satisfy to achieve coordinated movement (e.g. Liu et al. [2003], Tanner [2004], Lin et al. [2005], Schuresko and Cortés [2009]). Here is not the place to discuss why exactly it may be beneficial to design swarms of robots with decentralised control and it suffices to note that this concept has been embraced enthusiastically by engineers and computer scientists (e.g. Kelly and Keating [1996], Şahin et al. [2002], Jadbabaie et al. [2003], Liu et al. [2009]).

Biological applications of individual-based models for animal collective motion have become increasingly sophisticated by including blind angles in individuals' field of perception [Couzin et al., 2002], explicitly modelling the lateral line of fish (Hemelrijk and Hildenbrandt [2008]; see figure 5), accounting for the size of individuals [Hemelrijk and Kunz, 2005], including responses to obstacles (in the context of escape panic in humans Helbing et al. [2000]) and investigating leadership [Couzin et al., 2005, Conradt et al., 2009]. In a different approach, simple models are compared directly (qualitatively) to empirical data to disentangle the basic principles of animal collective motion [Buhl et al., 2006, Yates et al., 2009, Moussaïd et al., 2010].

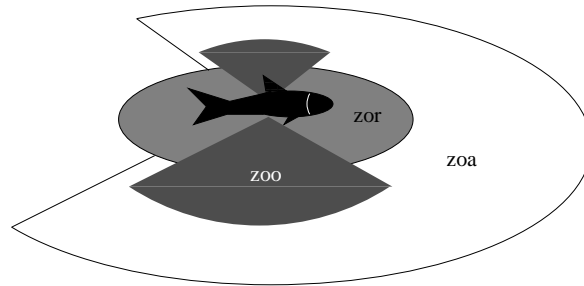


Figure 5: Illustration of model interaction zones, explicitly considering the possible influences of lateral lines in fish. Compare this to the interaction zones in figure 3. Redrawn from Hemelrijk and Kunz [2005].

The discussion above illustrates the breadth and diversity of approaches for modelling collective motion. Chapter 4 of this thesis attempts to bring together approaches from different fields to provide an informed starting point for further study.

Social networks in animals

Networks are a popular and successful tool to represent data [Newman, 2010]. In animal social networks, nodes represent individuals and edges represent connections, such as social preferences [Croft et al., 2008]. The social network approach offers one conceptual framework to study social organisation in animals at all levels (individual, dyad, group, population; Krause et al. [2007]).

Social networks are constructed by recording interactions, or affiliations, between animals [Croft et al., 2008]. For example, if one monkey grooms another, the two could be considered to have a social connection [Sueur et al., 2010]. Alternatively, in dolphins, individuals that are consistently members of the same group are often considered to have social preferences for each other [Lusseau et al., 2006, Lusseau, 2007]. The latter approach to record social associations is further explained in figure 6. Associations defined via group membership, also known as the “gambit of the group” [Whitehead and Dufault, 1999], assume all individuals within one group have social associations. Multiple observations of group membership are used to construct social networks for analysis. Therefore, these social networks represent information on the spatial association of individuals accumulated over multiple observations. Since pairs of individuals may be found in the same group more than once, these networks are either weighted, according to the number of times pair-wise associations are observed, or thresholded by only considering pair-wise associations that are observed more than a fixed number of times [Croft et al., 2008].

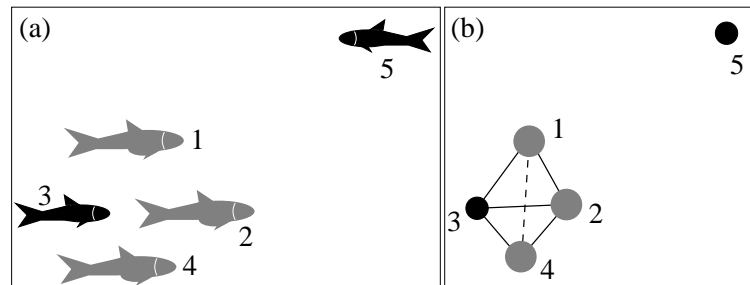


Figure 6: Constructing animal social networks from spatial associations. (a) shows a spatial configuration of five fish. Numbers assign individual IDs and colours illustrate possible differences in gender of the fish. (b) shows social associations constructed from the situation in (a). The solid lines between individuals, or nodes, in the network indicate pairs that are within a threshold distance from each other (chosen appropriately). Groups are defined as all individuals which are directly or indirectly connected by solid lines. Defining associations via group membership results in individuals 1 and 4 being connected (dashed line).

Using such methods, a network of social connections between individuals can be

assembled [Whitehead, 2008]. Once animal social networks are assembled, they can be analysed for non-random features using a large variety of analysis techniques [Croft et al., 2008, Whitehead, 2008, Newman, 2010]. Such techniques have been applied successfully to populations of fish [Croft et al., 2004], dolphins [Frère et al., 2010], buffaloes [Cross et al., 2005] and many other animals [Croft et al., 2008]. Findings of animal social network analyses include assortment by trait, such as size or sex (i.e., individuals of the same sex and similar size prefer to shoal together), behavioural assortment, preferential pairwise connections between familiar individuals, active avoidance between individuals, and key individuals that link otherwise disconnected groups [Griffiths and Magurran, 1999, Croft et al., 2004, Lusseau and Newman, 2004, Croft et al., 2005, 2009, Frère et al., 2010].

Many of the approaches in the literature to construct animal social networks rely on spatial associations of animals [Croft et al., 2008, Whitehead, 2008]. Individual or group movement is a necessary requirement for spatial proximity. Therefore, much work on animal social networks underlies the assumption that affiliations impact on, or are reflected in, the results of individual or group movement. This is investigated in the second part of this thesis. Chapter 4 makes the concept of underlying social networks explicit in the context of collective motion and reviews previous modelling work in detail. In effect, subtle differences between individuals are introduced by considering social networks underlying moving groups. While individuals may have similar physical properties, such as speed and perception range, they may differ in their position in preference networks. Chapter 5 of this thesis suggests how this could impact on aspects of animal collective motion.

This introduction to animal social networks is deliberately kept brief and the reader is referred to chapter 4, a published review article on modelling the combination of social network structures and collective motion in animals.

Thesis structure

This thesis is organised in two parts. The first part consists of three chapters and gradually develops and justifies a novel modelling framework for the collective motion of animals. This aims to create a theoretical basis that is tested against empirical evidence and is then extended to go beyond current empirical knowledge in the second part of this thesis. In chapter 1, the concept of asynchronous, stochastic updates is introduced in two dimensions. Varying update rates produce testable hypotheses and offer a possible explanation for how perceived threat increases the synchronization in collectively moving animal groups. This is subsequently tested and verified in an empirical system. Chapter 2 extends the model by including sensory zone sampling of individuals. The importance of the update rate in the model and its relatedness to commonly included stochastic errors, or noise, is illustrated. By qualitatively comparing the model to empirical data on noise terms in locust groups published elsewhere, the biological relevance of the model extension is demonstrated. In chapter 3, the modelling framework is further extended by making the sensory zone sampling of individuals dependent on distances between individuals. Simulations reproduce findings on the internal structure of starling flocks. This helps to explain the meaning of the empirical finding suggesting that on average starlings only interact with their six to seven closest neighbours.

The second part of the thesis consists of two chapters. As mentioned above, chapter 4 attempts to systematically introduce the concept of underlying social networks in the context of collective motion and reviews previous modelling work in detail. Chapter 5 takes these ideas further and produces testable predictions for how underlying social networks could impact on three aspects of animal group movement. This is achieved by the final extension of the modelling framework to include preferential updating between socially affiliated individuals.

The introduction of this thesis does not provide fine details. This is to avoid repetition, since the research in each chapter is introduced in the context of previous work in the field. Each chapter is a published manuscript and is presented as it

appears in print with supplementary information added as an appendix at the end of chapters.

Part I

A novel modelling framework for the collective motion of animals

Chapter 1

How perceived threat increases synchronization in collectively moving animal groups

Published manuscript

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Abstract

Nature is rich with many different examples of the cohesive motion of animals. Previous attempts to model collective motion have primarily focused on group behaviours of identical individuals. In contrast, we put our emphasis on modelling the contributions of different individual-level characteristics within such groups by using stochastic asynchronous updating of individual positions and orientations. Our model predicts that higher updating frequency, which we relate to perceived threat, leads to more synchronized group movement with speed and nearest-neighbour distributions becoming more uniform. Experiments with three-spined sticklebacks (*Gasterosteus aculeatus*) that were exposed to different threat levels provide strong empirical support for our predictions. Our results suggest that the behaviour of fish (at different states of agitation) can be explained by a single parameter in our model: the updating frequency. We postulate a mechanism for collective behavioural changes in different environment-induced contexts, and explain our findings with reference to confusion and oddity effects.

1.1 Introduction

The ubiquitous features observed in animal collectives have inspired researchers from a range of disciplines to describe, model, and reproduce these extraordinary displays of coordinated behaviour [Sumpter, 2006]. Most group-living animals are able to move coherently and collectively, preserving common features such as coordinated turns, maintenance of internal structures, and apparently leaderless movement. Examples include the tightly bound tori exhibited by large shoals of sardines under predation pressure [Parrish et al., 2002] and the striking pre-roosting displays of starlings [Ballerini et al., 2008]. Despite considerable research interest in group coordination there is still a significant gap between theory and experimental data. Attempts to bridge

this gap are hindered by the emergent nature of collective motion [Viscido et al., 2004] and matching modelling studies to empirical data - as, for example, in Buhl et al. [2006] and Yates et al. [2009] - remains a challenging goal in this field.

Models have been central to understanding the mechanisms behind collective animal motion [Krause and Ruxton, 2002]. Individual-based models in particular have allowed researchers to examine the emergence of different collective behaviours resulting from simple mechanisms at the level of the individual [Krause and Ruxton, 2002]. These models typically assume that identical individuals react to the position and movement of their nearest conspecifics by a combination of alignment, attraction, and repulsion [Krause and Ruxton, 2002]. Originally based on the extensive work by Aoki [1982], these simple ideas were also adopted in physics [Vicsek et al., 1995], computer science [Reynolds, 1987] and control engineering [Liu et al., 2003]. In biology the connection between the metric inter-individual distance and the subsequent behaviour has given rise to a family of models investigated computationally [Couzin et al., 2002] and tested empirically [Tien et al., 2004]. Models have been successful in shaping explanations and understanding mechanisms for different collective behaviours [Couzin et al., 2002, 2005, Hemelrijk and Hildenbrandt, 2008, Hoare et al., 2004, Viscido et al., 2005], but only at a qualitative level.

One of the earliest empirical studies to quantify individual trajectories in collective motion was performed almost three decades ago [Aoki, 1980]. In his experiments, Aoki filmed shoals of tamaroko (*Gnathopogon elongatus*) and Japanese horse mackerel (*Trachurus japonicus*) under controlled conditions and extracted time series of the positions of individual fish from his films. Aoki assembled the distribution of speeds and nearest-neighbour distance distributions of individuals within fish shoals. It is surprising that so few models incorporate these findings and no model explains them. Most modelling studies, for example, use a constant and homogeneous speed (e.g. Couzin et al. [2002]). Some studies have used Aoki's data by drawing an instantaneous speed at each time-step from an appropriate distribution [Aoki, 1982, Huth and Wissel, 1992], but they do not explain the emergence of this distribution from first

principles. In this article, we construct a model in which the speed distributions are emergent purely from the local interactions between the group members, and discuss its consequences in the context of experimental work on fish shoals.

1.2 Material and Methods

(a) Computational Model

We have developed an individual-based model of group interactions, based on local rules, that replicates the speed distributions found in Aokis and our experiments. The basis of our approach is to adopt stochastic asynchronous updating of individual fish positions and orientations; rather than using deterministic and sequential updating at each time-step, fish can react to external stimuli with a stochastic rate. The average behaviour of individuals over short time intervals then varies probabilistically. Models with asynchronous updating have been previously introduced in simple one- and two-dimensional models [O’Loan and Evans, 1999, Raymond and Evans, 2006, Samiloglu et al., 2006, Liu et al., 2003], but we believe their potential to explain empirical observations in real animals, such as effectively modelling fish speed distributions, has been overlooked.

Individuals are represented by points on the plane moving continuously in a toroidal space (a square box of side length L with periodic boundary conditions). The notation and nomenclature below follows that of Couzin et al. [2002]. Let N be the number of individuals, indexed i , with positions $\mathbf{x}_i = (x_i, y_i)$ and direction of motion θ_i . We assume that each individual reacts with an identical stochastic rate, enabling us to exploit a particle picking approach to exactly simulate the implicit underlying Master Equation of the system. The algorithmic implementation of our model contains aspects of earlier work [Couzin et al., 2002, O’Loan and Evans, 1999, Tsitsiklis et al., 1986] and proceeds as follows:

1. Choose individual j at random, where $j \in \{1, \dots, N\}$ (equal probabilities).
2. Decide which one of two behavioural rules j will follow in this step (probabilities

p and $(1 - p)$, respectively).

3. Update \mathbf{x}_j and θ_j according to the behavioural rule chosen in step (2).

N realisations of steps (1) to (3) constitute one update step of length Δt seconds. The duration of this update step corresponds to the reciprocal value of the rate at which individuals update. The output of the model is obtained by recording the positions of all individuals every $T = \lambda \Delta t$ seconds, where $\lambda \geq 1$. This is analogous to how data of animal motion is obtained empirically where individual positions and orientations are sampled according to the frame rate of video recordings [Aoki, 1980, Buhl et al., 2006]. In our simulations we keep T fixed and only vary Δt and therefore also λ .

We use purely metric behaviour rules in this implementation, based on those of Couzin et al. [2002]. We will defer commenting on the appropriateness of this approach given recent findings [Ballerini et al., 2008] until the discussion. Each individual obtains information from interaction zones - zone of repulsion (zor), zone of orientation (zoo) and zone of attraction (zoa) - which are described by concentric circles, centred on the individual, of radius r_R , r_O and r_A , respectively. Both the zoo and the zoa are punctured by a “blind angle”, α , in which individuals cannot perceive other individuals. Suppose individual j has been chosen in the algorithm described above; our first behavioural rule, which is selected with probability p , implements either alignment or repulsion. The individual tries to move away from conspecifics within its zor or aligns to conspecifics in its zoo, where, in common with other models of collective motion, repulsive motion takes precedence over alignment. The distance of j to its nearest neighbour determines the behaviour. Let $R \subseteq \{1, \dots, N\}$ be the set of individuals within the zor of j , excluding j . If $|R| \geq 1$, the desired direction of motion of j is given by

$$\theta_j^{desired} = \text{angle} \left(- \sum_{i \in R} \frac{\mathbf{r}_{ij}}{|\mathbf{r}_{ij}|} \right), \quad (1.1)$$

where $\text{angle}(\mathbf{y})$ denotes the angle the vector \mathbf{y} makes with the horizontal axis and $\mathbf{r}_{ij} = (\mathbf{x}_i - \mathbf{x}_j)$ is the vector in the direction from j to i . However, if the distance from j to its nearest neighbour is larger than r_R , then j aligns with its conspecifics. Let

$O \subseteq \{1, \dots, N\}$ be the set of individuals within the zoo of j , excluding j . If $|O| \geq 1$, the desired direction of motion of j is given by

$$\theta_j^{desired} = \frac{1}{|O|} \sum_{i \in O} \theta_i. \quad (1.2)$$

If both R and O are empty, then $\theta_j^{desired} = \theta_j$, and the individual does not deviate its direction. It executes this move with an instantaneous speed $v = v_O$.

In the alternative case we select our second behavioural rule with probability $(1 - p)$. In this case individual j gets attracted to conspecifics in its zoa and the distance \mathbf{r}_{ij} once more determines its behaviour. Let $A \subseteq \{1, \dots, N\}$ be the set of individuals within the zoa of j , excluding j . If $|A| \geq 1$, the desired direction of motion of j is given by

$$\theta_j^{desired} = \text{angle} \left(\sum_{i \in A} \frac{\mathbf{r}_{ij}}{|\mathbf{r}_{ij}|} \right). \quad (1.3)$$

Once more, if A is empty, then $\theta_j^{desired} = \theta_j$, and no deviation occurs. Subsequent movement happens at instantaneous speed $v = v_A$. Throughout this study, we choose $p = 0.5$, in agreement with previous research in which an equal weight is assigned to orientation and attraction in individuals [Couzin et al., 2002]. For both behavioural rules, once the desired direction of motion for j is calculated, the updated direction of motion, $new(\theta_j)$ is found by rotating the individual j by at most $\beta \Delta t$ from θ_j towards $\theta_j^{desired}$. Here, β denotes the maximum turning rate for individuals. Every time an individual j is updated, it is moved by v units in the updated direction

$$new(\mathbf{x}_j) = \mathbf{x}_j + v \Delta t \begin{pmatrix} \cos(new(\theta_j)) \\ \sin(new(\theta_j)) \end{pmatrix}, \quad (1.4)$$

where v is selected to be either v_O (alignment or repulsion) or v_A (attraction), as described above. The average speed of an individual, over many update steps, is consequently given by $v_{av} = pv_O + (1-p)v_A$. Parameters used in the model simulations are as follows: $N = 8$, $L = 168.73$ cm, $T = 0.04$ s, $p = 0.5$, $\alpha = 270^\circ$, $\beta = 40^\circ/\text{s}$, $v_O = 8.44$ cm/s, $v_A = 2v_O$, $r_R = 5.06$ cm, $r_O = 20.25$ cm, $r_A = 33.75$ cm, values of Δt are given in the figure legends and justified in the appendix.

In a simple stochastic implementation, all individuals would have an identical instantaneous speed, independent of the rule they follow and the behaviour of their fellow individuals. This would produce an unskewed Poisson distribution for the individual speeds (when averaged over time) that is unsupported by empirical data. The novelty of our implementation is that individuals adopt differing speeds according to the behavioural rule they follow. In such a way, we can obtain skewed distributions for the individual speeds as observed in empirical data (see below).

An inherent parameter in our model is the length of the update step Δt (in seconds). This parameter reciprocally rescales the reaction rates in the system: small values of Δt imply rapid updates, while large values of Δt imply slow updates. It is important to stress at this stage that we are not explicitly relating the size of Δt to biological or neurological reaction times of animals (but discuss the possibility of a connection later in this article). In addition, no direct physical meaning should be attached to the instantaneous positions on time-scales close to Δt . The fact that some individual might not move for one or more update steps does not imply they have stopped; rather that they are reacting more slowly to their surrounding than their fellows. At first glance it may appear that the same effect we obtain by varying Δt could be obtained by varying the speed at which individuals move. This is not the case. In our model different values of Δt do not alter the average speed at which individuals move, but they do alter the average rate at which individuals act upon information from within their sensory zones. Imposing different average speeds (i.e. changing v_A and v_O) changes the relationship between the average speed of individuals and the extent of their sensory zones.

(b) Experimental methods

We extended Aoki's experiments [Aoki, 1980] using small shoals of eight three-spined sticklebacks, *Gasterosteus aculeatus*, within an indoor circular tank of 1 m diameter. From individual movement trajectories we constructed the distributions of the indi-

vidual speeds of fish within a shoal and the distribution of the individuals' distances to their nearest shoal mates (nearest-neighbour distances). To test predictions from our model, we designed a number of new experimental treatments (table 1.1) to produce varying levels of agitation in the fish including most agitation (treatment 1), least agitation (treatment 4) and intermediate agitation levels. This allowed us to compare different model outcomes under different conditions to experimental data under parallel conditions. Evidence suggests that sticklebacks are in a greater state of agitation or excitement in higher light levels since in experiments fish of this species prefer shaded regions in tanks [Ward et al., 2008]. Fish that perceive a higher predation threat tend to use more shaded areas than fish which don't perceive the same level of threat [McCartt et al., 1997]. This suggests that they perceive a lower predation threat in shaded areas than in well-lit areas. An explanation for this could be that fish can see approaching predators which are not in shaded areas better from the shade, and that fish are less likely to be seen in shade [Helfman, 1981]. We also varied the water depth in our experimental tank. Given the white background of the tank, the fish bodies are clearly visible and thus make fish potentially conspicuous to over-head predators such as kingfishers and herons. In this situation sticklebacks show a strong tendency to move into deeper water (J. Krause 2008, unpublished data).

Table 1.1: Experimental conditions and corresponding treatments identities (IDs) from most agitation (1) to least agitation (4).

treatment ID	experimental conditions
1	shallow water (2 cm), bright light (690 lux)
2	deep water (8 cm), bright light (690 lux)
3	shallow water (2 cm), dimmed light (20 lux)
4	deep water (8 cm), dimmed light (20 lux)

1.3 Results

(a) Model output

Our model produces skewed speed distributions (in two dimensions) similar to empirical data as an emergent property of our novel update scheme (figure 1.1c,d). Individual speeds are approximated by calculating the distance covered by fish over a fixed time-step, with each time-step T comprising many multiples of Δt . This is analogous to how speed distributions are determined empirically where fish speeds are averaged over a range of video frames (see appendix; see also Aoki [1980]). The effect of varying Δt is striking: large values of Δt promote a strongly positively skewed distribution and small values reduce the skewness and give rise to speed distributions which resemble normal, or Gaussian, distributions (figure 1.1c,d). We do not claim to reproduce speed distributions of real fish quantitatively, as the influence of important factors on the speed distributions is unknown (e.g. interaction with environment). Rather, we show that our model is capable of producing similar speed distributions to the data without *a priori* assumptions or explicit addition of stochastic noise. Furthermore, our model suggests that the shape of the speed distributions can be varied by changing one parameter in our model.

From the speed and nearest neighbour distance distributions of the simulated shoals we extracted three summary statistics: the standard deviation of the speed distributions, skewness of the speed distributions, and the median of the nearest-neighbour distance distributions. Substantial changes in the summary statistics for different values of Δt are observed (figure 1.2a-c). Most prominent is the reduction in nearest neighbour distance (for a given fish this is the distance between this fish and the fish closest to it). Such a decrease in nearest neighbour distances or more compact group structures have previously been observed in empirical experiments for increasing threat or agitation levels [Tien et al., 2004, Krause, 1993, Carere et al., 2009]. The effect of Δt on the summary statistics highlights that this parameter is important for biological interpretation and is not just an invisible model implementation parameter.

We propose that values of Δt in our model correspond to states of agitation in animals. For example, low values of Δt (that is rapid updates) would correspond to high states of agitation, which might occur when animals feel threatened or at risk [Krause and Ruxton, 2002]. Our model predicts that increasing agitation makes the speed distribution of the shoal become more uniform and causes the nearest-neighbour distribution to contract. This allows us to form the following empirically testable hypothesis: the speed distributions and nearest-neighbour distributions of fish at different levels of agitation should qualitatively correspond to distributions in our model where Δt is varied appropriately. Specifically, our model predicts that:

- High states of agitation (low values Δt) should result in strongly peaked, unskewed speed distributions and a contraction of nearest-neighbour distances.
- Low states of agitation (high values of Δt) should result in well-spread distributions with positive skew and an increase in nearest-neighbour distances.

(b) Empirical Findings

Using our empirical system we confirmed previous results [Aoki, 1980] in finding long-tailed and positively skewed speed distributions (figure 1.1a,b). We then extracted the same three summary statistics from the empirical data as we did for the simulated data. To investigate the statistical significance of differences in the measurements of the summary statistics across treatments, we used a generalised linear mixed model (GLMM), taking into account the differences between shoals and the order in which the treatments were applied. In our analysis of the empirical data, we found that all three summary statistics were affected by one or more of the treatments in a statistically significant way (figure 1.2). Statistically significant differences between treatment 1 and treatments 2 and 3 (e.g. figure 1.2d,f) illustrate that water depth and light intensity can separately affect the animals' movement patterns. The lack of monotony in some of the trends is due to behavioural factors we cannot control, which are discussed in the appendix. The fact that not all of the summary statistics

show statistically significant differences between treatment 1 and treatments 2 and 3 is likely to be due to the fact that the contrast between these treatments is not large enough.

Overall, our experimental findings confirmed the predictions from our model that increasing agitation in fish makes the speed distribution of the shoal become more uniform (i.e. it decreases the distribution's standard deviation and skewness, and makes the nearest neighbour-distribution contract figure 1.2).

1.4 Discussion

This study is a combined modelling and empirical effort that has successfully predicted and reproduced emergent empirical properties of coordinated group behaviour from a model based entirely on local interactions. Our model is relatively simple and therefore provides an ideal starting point for the inclusion of individual characteristics and excitement levels into models of collective motion based on stochasticity. Our model produces novel predictions as to how group properties will alter in different behavioural contexts, and our experiments provide supporting evidence for these predictions. This reveals the importance of threat or risk levels perceived by fish for the composition of their movement trajectories and coordination. It has been suggested that fish react more quickly to shoal mates in situations of higher perceived risk or threat levels [Ward et al., 2008]. However, to our knowledge, this is the first time that the updating frequency of individuals has been modelled and tested against empirical data explicitly.

Our parameter Δt is the mean inter-update time that captures the relative frequency of updates within a given sampling time frame. It is important to emphasize that we are not making an explicit claim that this parameter is derivable from neurological information; we regard this parameter as controlling the dynamic averaging of the positional information from nearby conspecifics. The precise mechanism and quantities in our model provide an interesting avenue to be tested in further empirical research, focused on understanding the physiological interpretation of the stochastic

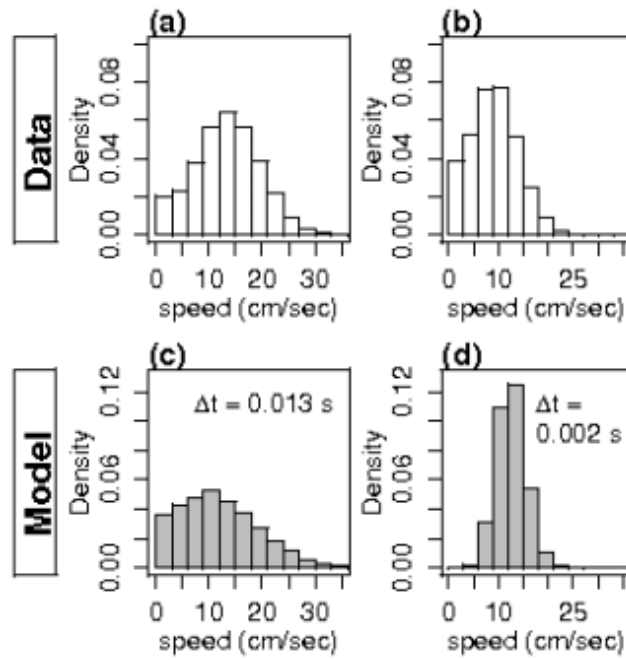


Figure 1.1: In (a) and (b) we show empirical speed distributions for two different shoals of eight fish over 10 min in identical experimental conditions (treatment 1, see table 1.1). Note how the shape of the speed distributions varies between groups. In (c) and (d) we show simulated speed distributions for different values of Δt , which illustrate the model’s capability to produce qualitatively similar speed distributions to those observed in the empirical data. To facilitate comparison, we have ensured that all histograms in this figure have area 1. Summary statistics are given for comparison: (a): mean = 13.3 ± 6.2 (s.d.) cm/s, skewness = 0.1; (b): mean = 9.1 ± 4.8 (s.d.) cm/s, skewness = 0.3; (c): mean = 12.7 ± 7.3 (s.d.) cm/s, skewness = 0.6; (d): mean = 12.7 ± 2.8 (s.d.) cm/s, skewness = 0.2. See text for details of the data analysis and the model simulations.

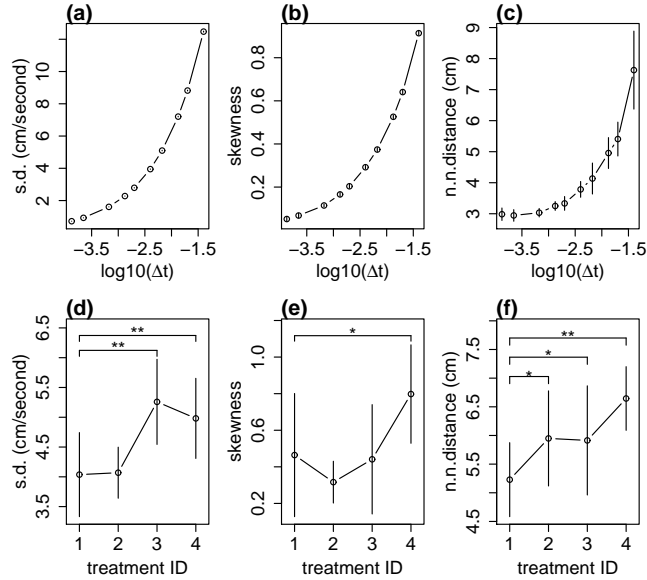


Figure 1.2: Summary statistics for a shoal of eight fish for model simulations (a-c, five replicates) and empirical data (d-f, eight replicates) for varying Δt and different treatments, respectively. The model simulations are not fitted to the data. Error bars show 1 standard deviation from the mean; in (a) and (b) the error bars are smaller than the symbols. In (a) and (b) we show the mean of the standard deviations and skewness of normalized speed distributions (to account for varying group speeds). Both these statistics, as well as (c) the mean of the median nearest-neighbour distances, increase with increasing values of Δt (note the log scale on the x-axis, Δt is measured in seconds). This trend is qualitatively replicated in the empirical data for decreasing perceived agitation levels (d-f). The effect of the treatments is analysed using a GLMM with predicting factors (categorical) treatment ID + sequential treatment order and random factor (categorical) replicate ID (see also appendix). Significant differences between treatment 1 and the other treatments are indicated with asterisks above the brackets (* $p < 0.05$, ** $p < 0.001$).

rates we find emerging from our qualitative model comparisons. The simulations presented in figures 1.1 and 1.2 use values of Δt that are significantly lower than the 0.1 s that has been previously recorded as the reaction time for fish [Partridge and Pitcher, 1980], indicating that many multiples of Δt make up a responsive reaction from the organism. The effect of reducing the step size in algorithms such as ours has previously been considered, but not in a biological context [Tsitsiklis et al., 1986].

It has recently been argued that the behavioural rules of collectively moving animals are based on the number of conspecifics each individual tracks (“topological framework”) rather than on the distance between individuals as in our model [Ballerini et al., 2008]. Some of the phenomena Ballerini and co-workers observed in their data have been reproduced in extensive simulation studies [Hildenbrandt et al., 2010] by assuming *a priori* that individuals only interact with a limited number of shoal mates. However, we suggest that this is not necessarily the only way in which the observations made in Ballerini et al. [2008] may arise in a model (see also chapter 3). Furthermore, a simple implementation of a topological framework, in which individuals only interact with a fixed number of their nearest neighbours, would not affect the emergence of speed distributions in our model. For these reasons we have continued to use a distance-based approach.

We suggest that by moving in a more coherent fashion with shoal members, an individual is able to reduce the risk of being targeted by predators as the “odd one out”, often termed the oddity effect [Krause and Ruxton, 2002]. The confusion effect - where predators find it more difficult to target an individual in a group than to target an isolated individual - is easily broken if one individual differs morphologically or behaviourally from others [Krause and Ruxton, 2002]. For example, in a threatened group where nearest-neighbour distances are generally low, an individual with a large nearest-neighbour distance will stand out from the crowd and probably be targeted by predators. This provides a mechanistic explanation for our findings: greater risk produces higher updating frequencies and higher updating frequencies produce lower oddity. Therefore, we suggest that the oddity effect could be the driving force

for the behavioural changes in different contexts and the high degree of synchrony characterizing threat-induced collective behaviours.

Finally, our method of measuring the uniformity of speed distributions and nearest-neighbour distances could provide a simple way of empirically assessing stress levels of collectively grouping animals in a remotely collectable and non-obtrusive way.

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1.5 Appendix

Theoretical methods

Justification for asynchronous updating scheme

Asynchronous updates are integral to our model. Consider a synchronous analogue of our model in which all individuals update at the same time but still choose the behavioural rule they follow at random. If $p = 0.5$ such a model will always result in symmetric distributions of individual speeds for long simulations. Such speed distributions do not have a positive skewness as observed in empirical data. Furthermore, adding a symmetric error or noise term to the desired movement of individuals in the model (as commonly done in the literature) will not result in positively skewed speed distributions for long simulations. However, if we relax the assumption that collectively moving animals align and attract on average to the same extent, that is to say, if we allow $p < 0.5$ or $p > 0.5$ in a synchronous version of our model, we can obtain skewed speed distributions. These speed distributions would be truncated

with lower value v_O and upper value v_A .

Model simulations and parameters

All simulations were initialised with random positions inside a box of side length $L = 33.75$ cm to ensure that the simulated animals were initially capable of perceiving each other. Two seconds of warm-up time were allowed before output was recorded for 4000 seconds in a toroidal box of side length $L = 168.73$ cm. The warm-up was introduced to ensure that no initial flock formation data was used in the analysis. In this study we were interested in properties of moving coherent groups and not in properties of assembling groups. Three intervals of 400 s of simulated collective motion spread evenly over the total simulation length were used for analysis. Parameters used in the model simulations: $N = 8$, $L = 168.73$ cm, $T = 0.04$ s, $p = 0.5$, $\alpha = 270^\circ$, $\beta = 40^\circ/\text{s}$, $v_O = 8.44$ cm/s, $v_A = 2v_O$, $r_R = 5.06$ cm, $r_O = 20.25$ cm, $r_A = 33.75$ cm, values of Δt are given in the figure legends. Simulations of our model resulted in stable and non-fragmented groups (see figure 1.3).

The values for parameters involving distances were chosen in such a way that they resulted in the same average group speed in the model as was observed over all of our empirical experiments which are described below. The values for the turning rate, β , and the angle of the field of perception, α , were chosen on the basis of previous extensive simulation studies [Couzin et al., 2002] with the emphasis on obtaining stable and non-fragmented groups. We chose a higher speed for attraction than for alignment and repulsion. This is an assumption justified only by the observation that individuals will predominantly get attracted to individuals in front of them (due to the blind angles in their sensory zones) and may consequently attempt to “catch up” with those individuals to maintain group cohesion.

Our model showed consistent behaviour for a wide range of speed ratios (v_A/v_O) and produced positively skewed speed distributions whilst having a variable emergent nearest neighbour distribution (see figure 1.4). Note that the trends in the summary statistics can be observed for different sizes of simulated shoals (see figure 1.5). We

speculate that the decrease of nearest neighbour distances for larger updating frequencies is a result of the reduced noise or error in the system which enables individuals to maintain high alignment when closer to each other (see also figure 1.6).

Experimental methods

Fish housing

The shoals in the investigation were drawn from a population of 160 three-spined sticklebacks (*Gasterosteus aculeatus*). None of the fish was used more than once in the experiments. The fish were collected from a wild population in Saltfleet, Lincolnshire, UK (Latitude: 53° 25' 0 N, Longitude: 0° 10' 60 E) in April 2009. The sticklebacks were roughly equal in size (TL 44 ± 5 mm s.d.) to avoid size-based biases in the experiments. The fish were housed at a University of Leeds aquarium. They were kept at $14 \pm 1^\circ\text{C}$ (s.d.), on a 12L:12D lighting regime, and fed every day at 08:00 with frozen bloodworm.

Setup

Fish were transferred to an experimental tank for observation. This tank was circular (1m diameter), had a flat base and white interior. Water in the experimental tank was $14 \pm 1^\circ\text{C}$ (s.d.), and at depth 2 cm (“shallow”) or 8 cm (“deep”). The tank was illuminated to one of two illumination levels: 20 lux (“low”) or 690 lux (“high”). The fish in the experimental tank were observed from a distance of 1m directly above the tank by a video camera (Sony Digital Handycam DCR-PC100E) with a wide angle lens, which was remotely controlled out of the visual range of the fish.

Procedure

Our experiments were conducted in July 2009 between 09:00 and 17:00. We observed eight shoals of sticklebacks, each shoal separately, using the following experimental procedure: (i) a shoal of eight fish was transferred from a holding tank to the experimental tank and left to acclimate for 10 minutes (water depth: deep; light intensity:

low.) (ii) The shoal was then subject to each treatment in order. Treatment order was generated by permutation: each treatment was applied twice at each order. Between each treatment, the fish were habituated to the conditions of the next treatment for two minutes. The four treatments differed between perceived level of excitement which was manipulated by the light intensity and the water depth of the experimental tank (see table 1.1). Every treatment lasted 10 minutes and we changed the water in the experimental tank between shoals.

Ethical Note

None of the fish were harmed in our experiments. High light intensities (690 lux) were significantly lower than the outdoor light intensity on an average day (about 30000 lux). In shallow water the fish were still capable of swimming freely.

Tracking individual fish

The video footage from our experiments was analysed with the freely available “Swis-Track” software package [Correll et al., 2006] to recover information on the position of the fish in two dimensions. Our analysis in two dimensions is justified by the shallow water depths used in the experiments which these fish often occupy in nature. Positions of fish were obtained every 0.04 seconds over intervals of at least one second. The fish positions at consecutive time points were then connected into fish tracks by using a nearest neighbour tracking approach that worked with distances between fish positions [Correll et al., 2006]. Further information can be found below. For a video of 10 minutes length we obtained fish tracks in intervals of at least one second length and over a total of at least 2.8 minutes (mean: 5.2 ± 1.8 (s.d.) minutes). The volume and statistical composition of the video fish track data was independent of the treatment, ensuring there was no bias in recovery between treatments.

Obtaining fish trajectories from fish position time series

Positions at one time step were connected to the closest positions at the next time step. This approach was justified as the distance between fish was generally larger than the distance fish moved in one or even two time steps. For the purpose of our analysis it was sufficient to assume that overlapping fish were at the same position. Erroneous fish positions produced by SwisTrack due to noise in the videos (e.g. reflections on the water, etc.) were detected by additionally considering distances between positions which were two time steps apart. Again, positions at one time step were connected to the closest position two time steps away via the closest position one time step away. If the minimal distance between fish positions across the entire shoal, either one or two time steps apart, was larger than 3.37 or 6.74 centimetres respectively (about 2.5 times the measured maximal group speed), the fish positions were considered to be wrong and were deleted from the position time series (along with all other fish positions at that time point). If the distance between fish positions two time steps apart was smaller than the distance covered over one of the two time steps this was considered to be due to an erroneous fish position. This assumption was based on the observations that the fish rarely performed very sharp turns on such a small time scale which would have allowed for an alternative explanation of such a situation. In these cases the erroneous position was replaced by averaging between the two correct positions that were two time steps apart. Less than 2 percent of the total fish positions were replaced. The resulting fish tracks were compared visually to the movement of the fish in the original videos.

Empirical speed distributions

As an approximation for the individual speeds of fish we used the distances between fish positions at two consecutive measurements or time points, following the methods of Aoki [1980]. The speed of the group (mean of individual speeds at one point in time) in the empirical data showed considerably more variation than the group speed in the simulations of our model. Since we are comparing the empirical data

to the model simulations it was necessary to “mean-normalise” the distributions of individual speeds. In the mean normalised speed distributions the group speed of the shoal at one time point was subtracted from each individual speed measurement to account for changes in the group speed. This ensured that the group speed in the mean normalised speed distributions was zero in both the empirical data and the simulated data. Figure 1.7 shows that the variation in group speed could have a noticeable impact on the distribution of individual speeds.

Note that the alignment or polarisation of the shoals was not easily obtainable in a way which is consistent with the polarisation in the model simulations because of the effect the boundary had on the movement of the shoals.

Statistical analysis

For each summary statistic (standard deviation and skewness of speed distributions, median nearest neighbour distances) one GLMM was constructed using the ‘glmmPQL’ function in the R programming environment [R Development Core Team, 2008, Venables and Ripley, 2002]. The summary statistic was the response variable and the factors (categorical) treatment ID and sequential order of treatment (irrespective of ID) were explanatory variables. Group identity was added as a random factor (categorical). For tables with p-values for the fixed effects of the GLMMs see tables 1.2, 1.3 and 1.4.

We found that the sequential order in which the treatments were applied (irrespective of treatment IDs) had a statistically significant effect on some of the summary statistics (see tables 1.2, 1.3 and 1.4). This suggests that the fish may have acclimated to the experimental conditions to some extent. Different shoals displayed different base levels for the summary statistics. These observations may explain the lack of monotony in some of the trends in figure 1.2.

Note that increasing contrasts between treatments would either make an analysis in two dimensions unjustifiable (in the case of water depth), or subject the fish to high intensities of direct light (in the case of light intensities).

Supplementary figures and tables

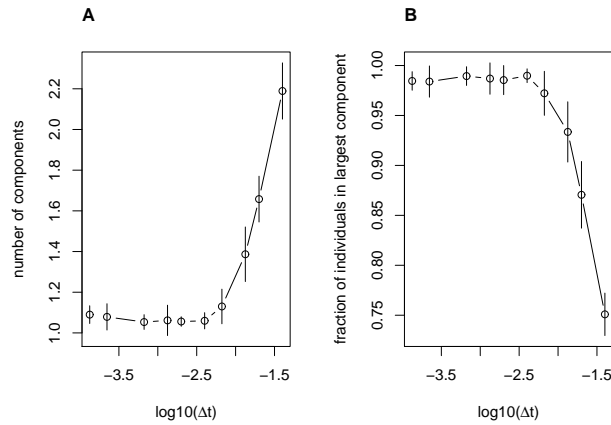


Figure 1.3: Coherence of simulated shoals. Individuals are considered to be connected if they are within r_A of each other. Components or shoals are defined as sets of individuals which are connected to each other either directly or via other individuals. Therefore, if there is one component, then all individuals are in the same shoal. In **A** we show the number of components for simulations of shoals of 8 fish. The data points are the average of the mean number of components over 1000 equally spaced sampling points during a 4000s simulation (5 replicas). Error bars show one standard deviation from the mean. Note the log scale on the x-axis (Δt measured in seconds). The average number of components is only for the largest three values of Δt substantially larger than 1. Thus, the shoals are generally very coherent. In **B** we show the average of the fraction of the total number of individuals which are within the largest component. Again, this only decreases for the three largest values of Δt and is always larger than 0.75. Therefore, on the occasion that the shoal is not entirely coherent it is only a few outliers that are not part of the shoal. This supports our observation that the simulated shoals are very coherent.

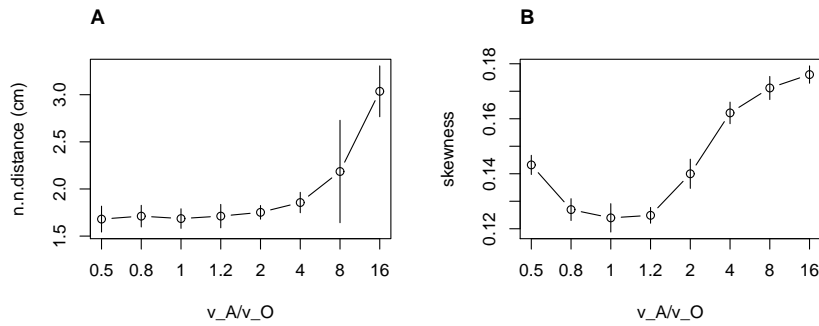


Figure 1.4: Median nearest neighbour distances (**A**) and skewness (**B**) of normalised speed distributions (normalised to account for variations in group speed) for simulated shoals of 40 individuals against the ratio of the instantaneous speed parameters, v_A/v_O . Error bars show one standard deviation from the mean (5 replicates). The nearest neighbour distances increase with increasing v_A/v_O , but remain stable over a wide range of v_A/v_O (**A**). The skewness of the speed distributions is always positive with the lowest skewness when $v_A = v_O$ (**B**). Note that the standard deviations of the speed distributions also increases with increasing v_A/v_O (not shown). Parameter values can be found in the text and $\Delta t = 0.00067$, $v_O = 8.44$ cm/s.

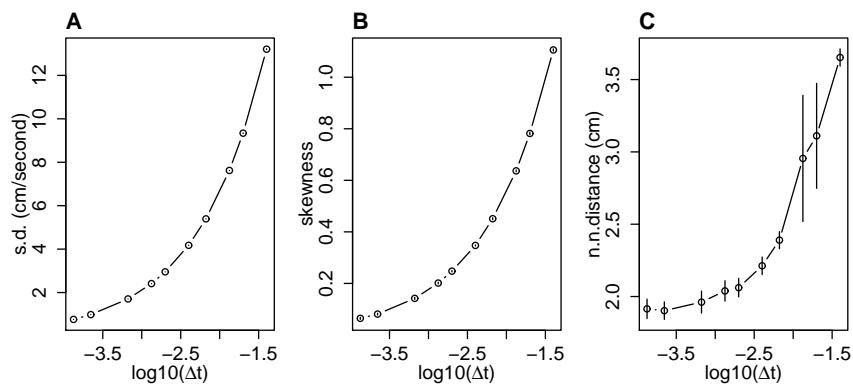


Figure 1.5: Summary statistics for a shoal of 50 fish for model simulations (5 replicates) with varying Δt . Error bars show 1 standard deviation from the mean (in **A** and **B** the error bars are smaller than the symbols). Parameter values can be found in the main text. In **A** and **B** we show the mean of the standard deviations and skewness of normalised speed distributions (to account for varying group speeds). Both these statistics, as well as the mean of the median nearest neighbour distances (**C**) increase for increasing values of Δt (note the log scale on the x-axis, Δt is measured in seconds). These trends are qualitatively the same as for the simulations of shoals of 8 fish (see figure 1.2).

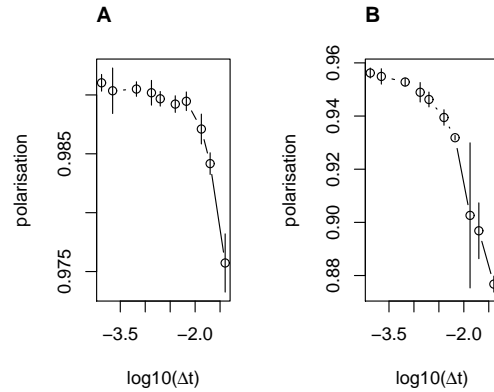


Figure 1.6: Median polarisation for simulated shoals of 8 (**A**) and 50 (**B**) individuals (5 replicates) for varying Δt . Error bars show 1 standard deviation from the mean (over replicates). Parameter values can be found in the main text. The polarisation is a measure of the alignment of the shoal. It is the length of the sum of the instantaneous unit direction vectors over all individuals divided by the number of individuals. Note how the polarisation of the shoals drops for increasing values of Δt (note the log scale on the x-axis, Δt is measured in seconds). The groups are generally very well aligned.

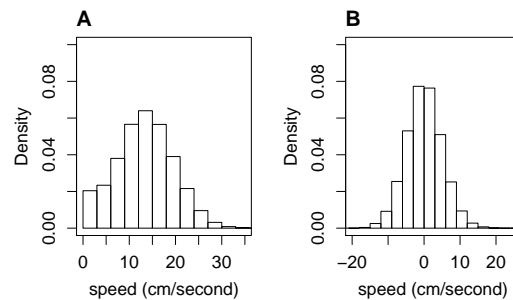


Figure 1.7: Speed distribution for a shoal of 8 fish over a 10 minute experiment under treatment 1 (**A**). In our analysis the speed distributions were mean-normalised. **B** shows the mean-normalised speed distribution for the data in **A**. For each individual speed measurement the mean speed of the entire shoal at that time was subtracted to account for changes in the group speed. Summary statistics of the two distributions are given for comparison: **A**: mean = 13.3 ± 6.2 (s.d.) cm/s, skewness = 0.1; **B**: mean = 0 ± 5 (s.d.) cm/s, skewness = 0.1.

	Value (cm/s)	DF	t-value	p-value
Intercept	4.601387	18	20.545021	<0.0001
ID 2	0.032164	18	0.164057	0.8715
ID 3	1.221405	18	6.229875	<0.0001
ID 4	0.943842	18	4.814141	0.0001
order 2	-0.503927	18	-2.570321	0.0193
order 2	-0.760083	18	-3.876863	0.0011
order 3	-0.993512	18	-5.067489	0.0001

Table 1.2: Table of p-values for treatment contrasts in the fixed effects of the GLMM for the standard deviations of empirically obtained speed distributions. The categorical factors “Treatment ID 1” and “Treatment order 1” are made into the intercept. In the first entry of the first row we can read off the intercept. The remaining six rows in the first column show differences. These comparisons are always between the intercept and the other categorical factors. The second column shows the residual degrees of freedom. As an example, treatment 4 increases the standard deviations of speed distributions by 0.943 cm/s over the intercept and this difference is significant at $p = 0.0001$. And so on. Note that the effect of treatment 4 may not be significantly different from the effect of treatment 3. The categorical factor “Treatment order” denotes the sequential order in which the treatments were applied irrespective of their treatment ID.

	Value (cm/s)	DF	t-value	p-value
Intercept	0.3841125	18	2.9853271	0.0079
ID 2	-0.1479250	18	-1.0786136	0.2950
ID 3	-0.0231125	18	-0.1685277	0.8680
ID 4	0.3335375	18	2.4320303	0.0257
order 2	0.0534125	18	0.3894639	0.7015
order 3	0.1048375	18	0.7644357	0.4545
order 4	0.1625000	18	1.1848890	0.2515

Table 1.3: Table of p-values for treatment contrasts in the fixed effects of the GLMM for the skewness of empirically obtained speed distributions. Analysis identical as for standard deviations (compare to table 1.2).

	Value (cm/s)	DF	t-value	p-value
Intercept	4.876932	18	16.115464	<0.0001
ID 2	0.719450	18	2.590028	0.0185
ID 3	0.684643	18	2.464722	0.0240
ID 4	1.416012	18	5.097658	0.0001
order 2	0.253523	18	0.912687	0.3735
order 3	0.239202	18	0.861131	0.4005
order 4	0.915746	18	3.296696	0.0040

Table 1.4: Table of p-values for treatment contrasts in the fixed effects of the GLMM for the medians of nearest neighbour distances of empirically obtained nearest-neighbour distance distributions. Analysis identical as for standard deviations (compare to table 1.2).

Chapter 2

Making noise: Emergent stochasticity in collective motion

Published manuscript

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Abstract

Individual-based models of self-propelled particles (SPPs) are a popular and promising approach to explain features of the collective motion of animal aggregations. Many models that capture some features of group motion have been suggested, but a common framework has yet to emerge. Key to all of these models is the inclusion of “noise” or stochastic errors in the individual behaviour of the SPPs. Here, we present a fully stochastic SPP model in one dimension that demonstrates a new way of introducing noise into SPP models whilst preserving emergent behaviours of previous models such as coherent groups and spontaneous direction switching. This purely individual-to-individual, local model is related to previous models in the literature and can easily be extended to higher dimensions. Its coarse-grained behaviour qualitatively reproduces recently reported locust movement data. We suggest that our approach offers an alternative to current reasoning about model construction and has the potential to offer mechanistic explanations for emergent properties of animal groups in nature.

2.1 Introduction

Modelling the collective motion of animals remains a tantalising problem for scientists of a host of different disciplines. Both visually attractive and scientifically challenging, the concept remains useful because of its applicability to both animation [Reynolds, 1987] and control systems [Liu et al., 2003, Tanner et al., 2007] as well as the fundamental ecological understanding it brings [Sumpter, 2006]. Many individual-based models have emerged in the last few decades that exploit advances in computational power to describe features seen in collective animal motion including group decision making [Couzin et al., 2005, Conradt and Roper, 2007], information flow [Sumpter et al., 2008] and response to predation [Wood and Ackland, 2007]. This article focuses

on the development of one-dimensional models that seek to describe some of the simplest observed features in collective motion. Such models are now known collectively as 1D self-propelled particle (SPP) models.

In recent years the biological relevance of these models has been demonstrated as a result of the development of novel, approximately one-dimensional, experimental systems. By constraining marching bands of locust nymphs to a specially constructed annular arena Buhl et al. [2006], and more recently Yates et al. [2009], have shown that these insects do indeed behave in a manner that is qualitatively comparable to one-dimensional SPP models. In particular, this work demonstrated that SPP models capture the spontaneous turns of the locust bands, where the entire group reverses its direction of motion without external input. It is believed that the origin of these observations lies in internal, or intrinsic, stochastic effects or “noise” which may or may not correspond to inaccuracy of the individual movements (e.g Buhl et al. [2006], Couzin et al. [2005]).

Recently, the coarse-grained behaviour of 1D SPP models has been compared to locust movement in a more systematic way. From their study Yates et al. [2009] suggested that the insects respond to a decrease of group alignment by increasing the noise in their movement. The importance of this finding is that the addition of simple noise terms is not necessarily sufficient to describe and explain collective motion in animals. However, despite its great importance the origin of this stochasticity is far from clear.

In this research we focus exclusively on a simple one-dimensional SPP model, and show how a combination of an asynchronous updating scheme and a novel implementation of particle interactions can produce a coarse-grained behaviour which reproduces findings by Yates et al. [2009] in locust movement data. The novelty of our research lies in the fact that all noise in the system emerges from the algorithmic implementation of our model rather than being added to the movement of particles. We therefore work towards explaining the origin of stochasticity in animal collective motion using our modelling approach.

First, we give an overview of selected 1D SPP models described in previous work and the results that they give. Second, we introduce our modelling approach. We then show that our model can produce stable groups and spontaneous direction switching and study the coarse-grained behaviour of our model via an equation-free approach using numerical simulations. We conclude by commenting on the potential of our modelling approach for integrating individual-level characteristics and describing motion in dimensions greater than one.

2.2 SPP Models

The first 1D SPP model simulated particles with a local aligning behaviour on a continuous line with periodic boundary conditions [Czirók et al., 1999]. In this model the individual and continuous velocities and positions are updated sequentially and simultaneously for all individuals. Particles tend to align with the average velocity of all particles within a fixed distance from them. This alignment is subject to a stochastic error in the form of uniformly distributed noise which is explicitly added to the particles' response to the average local velocity. An anti-symmetric function G is applied to the preferred velocity of individuals and introduces both propulsion and friction to the system. The individual velocities $u_i(t)$ are therefore updated as,

$$u_i(t+1) = G(\langle u(t) \rangle_i) + \xi_i, \quad (2.1)$$

where $\langle u \rangle_i$ is the local average velocity for particle i and ξ_i is a random variable with uniform probability distribution over a finite interval $[-\eta/2, \eta/2]$ [Czirók et al., 1999]. The function $G(z)$ is given by,

$$G(z) = \frac{1}{2}(z + \text{sgn}(z)), \quad (2.2)$$

which sets the average of the individual speeds in the absence of particle interactions to magnitude 1 [Czirók et al., 1999]. Analysis of the model has indicated that the average velocity of all particles undergoes a phase transition from an ordered state to a disordered state when the amplitude of the noise (η) or the particle density is varied

[Czirók et al., 1999]. Such phase transitions have also been observed for SPP models in two and three dimensions which suggests that some features of higher dimensional systems are preserved in 1D models [Vicsek et al., 1995, Chaté et al., 2008]. For certain parameter values the model exhibits a fascinating direction switching behaviour - the average velocity of all particles in the system changes sign spontaneously and on a short time scale compared to longer intervals of sustained high absolute values of the average velocity. Several variants of this scheme to introduce noise have been published [Chaté et al., 2008].

Another approach has been to implement SPP models on a one-dimensional lattice with periodic boundary conditions over which particles move with velocities $+1$ or -1 [O’Loan and Evans, 1999, Raymond and Evans, 2006]. In the first model of this type particles align with the velocity of the majority of particles around them with a given probability [O’Loan and Evans, 1999]. The magnitude of this probability is the first source of noise in the model. The second source of noise and an important aspect of the model related to this research is its asynchronous updating scheme. In each step only the position and velocity of one, randomly chosen particle are updated. Simulations of the model showed a phase transition from high to low average particle velocities for increasing sizes of the aligning probability. This is qualitatively similar to the phase transition exhibited by the model of Czirók et al. [1999].

This asynchronous 1D SPP lattice model was subsequently extended significantly by the inclusion of repulsion and attraction into the individual behaviour of the particles and the modification of the alignment behaviour [Raymond and Evans, 2006]. The authors justified their implementation of the different behaviours by showing that they correspond qualitatively to taking random samples of neighbours [Raymond and Evans, 2006]. This implementation results in two separate parameters which control the size of the error or noise in the reaction of individuals to their surrounding neighbours. One parameter controls the error arising from stochastically sampling the local group to determine the particle’s preferred direction and the other parameter introduces uncorrelated errors [Raymond and Evans, 2006].

In summary, 1D SPP models show a wealth of emergent behaviours which have increasingly been compared to real collective animal motion. The way stochastic errors have been included into such models can roughly be divided into three categories. First, adding a random variable to the preferred direction of individuals [Czirók et al., 1999]. Second, asynchronous and probabilistic updates [O’Loan and Evans, 1999, Raymond and Evans, 2006]. Third, varying the probability and accuracy with which individuals execute their behavioural rules [O’Loan and Evans, 1999, Raymond and Evans, 2006]. In the next section we will introduce our model which takes inspiration from the second and third approaches.

2.3 Modelling approach

In our model N individuals are represented by points on a continuous line and not by points on a lattice as in some of the models discussed above. The individuals, indexed i , are characterised by their position x_i and instantaneous velocity θ_i and they react to their “neighbours” which are less than a distance r_A away from them. We assume that each individual reacts with an identical stochastic rate to its surroundings. This defines an implicit master equation that in principle could be solved with a stochastic simulation algorithm [Gillespie, 1976]. Instead, we exploit the identical rates and a simple particle picking approach to simulate the the system [O’Loan and Evans, 1999]. The algorithmic implementation of our model is as follows:

1. Choose individual i at random, where $i = 1, \dots, N$ (equal probabilities, with replacement).
2. If i has neighbours, choose a neighbour k of i at random (equal probabilities for all individuals within less than r_A of i).
3. Update x_i and θ_i (based on the interaction between k and i or on previous θ_i if i has no neighbours).

N realisations of steps (1) to (3) constitute one update step of length Δt time-steps (see also figure 2.1). The duration of this update step corresponds to the reciprocal value of the algorithmic rate at which individuals update. Small values of Δt imply rapid updates, while large values of Δt imply slow updates. The output of the model is obtained by recording the positions and velocities of all individuals every $T = \lambda\Delta t$ time-steps, where $\lambda \geq 1$. This is analogous to how data of animal motion is obtained empirically where individual positions and orientations are sampled according to the frame rate of video recordings [Aoki, 1980, Buhl et al., 2006]. In our simulations we keep T fixed and only vary Δt and therefore also λ .

Suppose individual i and a neighbour k of i have been chosen in the algorithm described above. The interaction between i and k depends on the distance d between the two individuals. If $d \leq r_O < r_A$, i attempts to align with k and has desired velocity,

$$\theta_i^{desired} = G(\theta_k). \quad (2.3)$$

If $r_O < d < r_A$ individual i gets attracted to k and has desired velocity,

$$\theta_i^{desired} = G\left(\text{sgn}(x_k - x_i) \left(\frac{d - r_O}{r_A - r_O} + 1\right)\right), \quad (2.4)$$

where the fraction term in the argument is motivated by a distance rule such that at maximum distance maximal desired velocities are achieved. If i has no neighbours (there is no k such that $d < r_A$), $\theta_i^{desired}$ is given by,

$$\theta_i^{desired} = G(\theta_i). \quad (2.5)$$

The function G is given above in equation 2.2. Once $\theta_i^{desired}$ is determined, θ_i and x_i are updated according to,

$$\text{new}(\theta_i) = \theta_i + (\theta_i^{desired} - \theta_i)\Delta t, \quad (2.6)$$

$$\text{new}(x_i) = x_i + \text{new}(\theta_i)\Delta t. \quad (2.7)$$

In our model individuals react deterministically to the positions and motion of randomly selected neighbours. In previous work [Huth and Wissel, 1992], it has

been suggested that interactions with single individuals are not able to mimic the properties of animal collective motion in the same way as averaging over a number of individuals. However, viewed over time-scales larger than Δt , our algorithm is qualitatively equivalent to reacting in a noisy way to a random sample of neighbours and our results below show that our simulations are comparable to empirical data. For a more detailed discussion on the biological plausibility and interpretation of our model we refer the reader to the discussion.

The instantaneous individual speed in our model tends to be increased when particles get attracted to others (see equation 2.4). Such a dependence of the instantaneous speed on the distance between individuals has previously been used in models of collective motion for repulsion between individuals [Reynolds, 1987, Hemelrijk and Hildenbrandt, 2008]. Our assumption of higher attraction speeds is based on the hypothesis that individuals need to move faster if 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 (chapter 1).

To derive this model we use asynchronous updates similar to the ones suggested by O’Loan and Evans [1999] but we collect particle positions every T time-steps and thereby allow for different individual and average update rates in real time with an approximately continuous velocity distribution. The implementation of alignment, friction and propulsion (see $G(z)$) are inspired by Czirók et al. [1999], but our implementation of attraction is new. Our random-neighbour-picking approach has parallels to the neighbour-sampling argument Raymond and Evans [2006] invoked to justify the implementation of their behavioural rules, but we have made this sampling explicit and limited interactions in our algorithm to pairwise interactions. The effect of varying the length of update-steps in algorithms such as ours has been considered previously, but not in a biological context [Tsitsiklis et al., 1986]. The rationale behind our model is to find a set of microscopic rules that are capable of recovering empirical results.

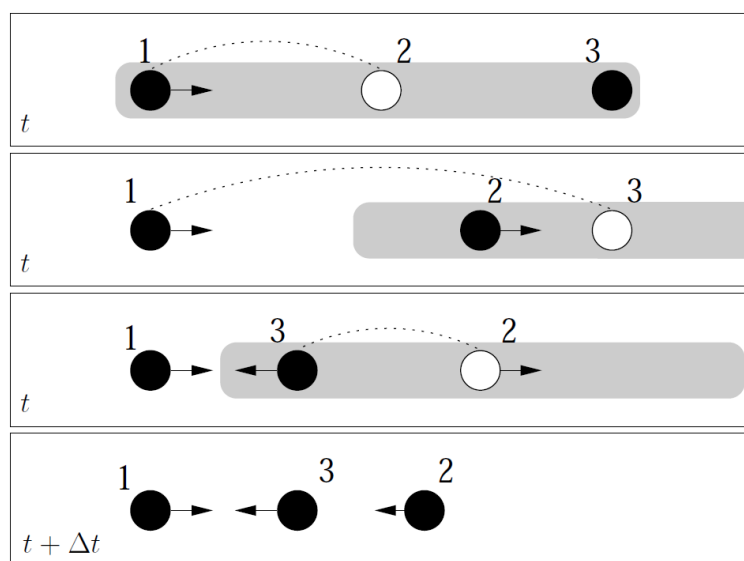


Figure 2.1: Schematic illustration of an example for one update step Δt of our model for $N = 3$ (top to bottom). The grey areas indicate the extent of r_O for updating individuals (in white) and the arrows show the direction of motion of the particles. Particles without arrows have zero instantaneous velocity. Dotted lines highlight interactions. In the first panel individual 2 is chosen and randomly picks individual 1 to interact with (alignment). In the second panel 3 is chosen and picks 1 to interact with. Since the distance between the two particles is larger than r_O , 3 gets attracted to 1. In the third panel 2 is chosen again and chooses to align to individual 3. The last panel shows the positions of 1, 2, and 3 after one update step Δt .

2.4 Model analysis

Coherence and direction switching

Here we show that our model preserves the interesting emergent behaviours previous models have found. We do not present a complete analysis of the behaviour of our model. Rather, we focus on experiments which illustrate that our model produces coherent groups in which individuals do not diffuse over long simulations and that our way of including noise results in a phase transition from an ordered to a disordered state of simulated groups for increasing noise and therefore that we are recovering previous results.

Our simulations are performed in the absence of boundary conditions. Typically, simulated collective motion is limited by periodic boundary conditions [Vicsek et al., 1995, Czirók et al., 1999, O’Loan and Evans, 1999, Raymond and Evans, 2006]. This means that individuals crossing one boundary are removed and appear at the opposite boundary which results in movement on a circle in one dimension. The advantage of this approach is that simulated groups cannot disperse in space. Boundary conditions can form a source of ambiguity in that it may not be clear in how far emergent behaviours are a result of the model or the implementation of the boundary conditions.

Initially, individuals were randomly distributed in an interval of length r_A to ensure that they were capable of perceiving at least one other particle. At the start of our simulations all individuals had velocity $\theta_i = +1$. More commonly particles are assigned random initial velocities in simulation studies [Czirók et al., 1999, O’Loan and Evans, 1999, Raymond and Evans, 2006, Buhl et al., 2006]. We chose our initial conditions to ensure that groups would not fragment within the first few time-steps of the simulations. Long simulated time intervals before recording started (typically 100,000 time-steps) ensured that no initial transitional data was used in our results.

Figure 2.2 shows that our model is capable of producing groups which remain coherent over long simulations in absence of boundary conditions. For large values of Δt (here close to T) and small values of r_A the groups tend to fragment. We show

results for two particular values of r_A for unchanged r_O to illustrate that the relative size of the former parameter can be important for the coherence of the simulated groups. Non-zero distances between individuals and their nearest neighbours in our simulations indicate that individuals do not “collapse” onto one position in coherent groups - a potential problem in deterministic simulations (figure 2.2).

In figure 2.3 we illustrate that simulated groups show spontaneous switches in direction. To do so we measure $Q = \sum_i \theta_i / N$, the average velocity of individuals. To get a feeling for how direction switches of groups can occur in our model we refer the reader to figure 2.1. In this illustration the group initially travels on average to the right hand side. After one update step is performed, the group travels on average to the left hand side. The quantity $\langle |Q| \rangle$ represents the mean over a large number of the absolute value of measurements of Q and is used to measure the order or alignment in the system. Large values indicate high order and low values low order. Our model exhibits a phase transition from an ordered state to a disordered state for increasing values of Δt (see figure 2.3a). In figure 2.4 we show two examples for the characteristic distributions of Q for our model. For low values of Δt the distribution of Q peaks at two large values of $|Q|$ which indicates that the group collectively moves in one direction with occasional and relatively quickly executed switches in direction. Higher values of Δt result in a decreased distance between the two peaks in the distribution of Q up to the point when the group does not move collectively in one direction for prolonged periods of time any more. This phase transition is captured by the sign of the skewness of the distribution of $|Q|$ which turns from negative to positive for increasing values of Δt (figure 2.4c). The time which the groups spend travelling in one direction between reversals in direction increases dramatically with decreasing Δt (see figure 2.5). This trend is qualitatively similar to findings for other SPP models in which reversal times increase for decreasing noise [O’Loan and Evans, 1999, Yates et al., 2009].

We have seen that the parameters r_A and Δt control the stability and state or phase of the simulated groups (ordered/disordered). To obtain a more complete

picture of our models' behaviour we performed a systematic scan of the $(r_A, \Delta t)$ parameter space for $N = 50$ (see figure 2.6). We used the sign of the skewness of the distribution of $|Q|$ as an indicator of the phase as the change of sign in the skewness provided a clear and easily-defined switching point (see figure 2.4c). Using the conditions for different phases established above, we divided the parameter space into three regions of distinctive model behaviours: unstable or fragmenting flocks, disordered flocks and ordered flocks. As with all stochastic simulations this phase diagram can only be understood as a an indicative approximation of the model's behaviour. In combination with our initial conditions the case $r_A = r_O$ leads to a collective which moves in one direction, but diffuses as a result of the asynchronous updating scheme. For larger r_A the groups quickly stabilise and show a distinctive divide between an ordered and a disordered phase for small and large values of Δt respectively.

In summary, we have established that our model can produce a qualitatively similar emergent behaviour to previous models. The level of noise in the system is determined by the parameters r_A and Δt . Qualitatively similar but quantitatively different phase diagrams for our model could be obtained if particles were allowed to move at instantaneous speeds larger than two (cf equation 2.4) or if they accelerated faster. The effect of N also leads to a quantitative but not a qualitative change in the behaviour of our model. Our model analysis is an illustration of principle and a more detailed investigation of the effect of different initial conditions including different measures for the stability of the group is beyond the scope of this work.

Coarse-grained behaviour

The coarse-grained behaviour of a system can often be described in terms of a small number or even single “coarse” variables. In some cases it is possible to construct a “coarse-grained” model which accurately captures the temporal development of these variables [Erban et al., 2006, Kolpas et al., 2007, Yates et al., 2009].

We adopt the approach pioneered by Yates et al. [2009] in which they study the

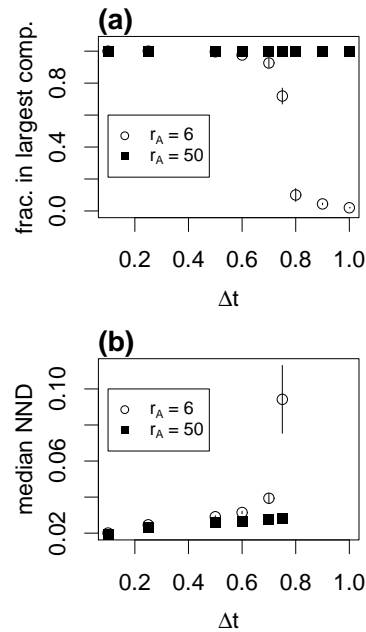


Figure 2.2: Coherence of simulated groups. Individuals within r_A of each other are considered to be connected. Components are defined as sets of individuals which are connected to each other either directly or via other individuals. If there is one component, all individuals are in the same group. (a) the fraction of the total number of individuals within the largest component. (b) the median of individual's distance to their nearest neighbour (NNDs). We show the average over 1000 equally spaced sampling points during the last 200,000 time-steps of a simulation over 300,000 time-steps (5 replicas). Error bars show one standard deviation from the mean. For larger values of Δt the groups did not maintain coherence which led to a low average proportion of individuals within the largest component. For larger r_A the groups maintained coherence over the simulation, even for large values of Δt . The NNDs increased with increasing values of Δt . For $\Delta t > 0.6$ and $r_A = 6$ the groups did not maintain cohesion over the length of the simulation which led to very large NNDs. Parameters: $N = 100$, $r_O = 5$ and $T = 1$.

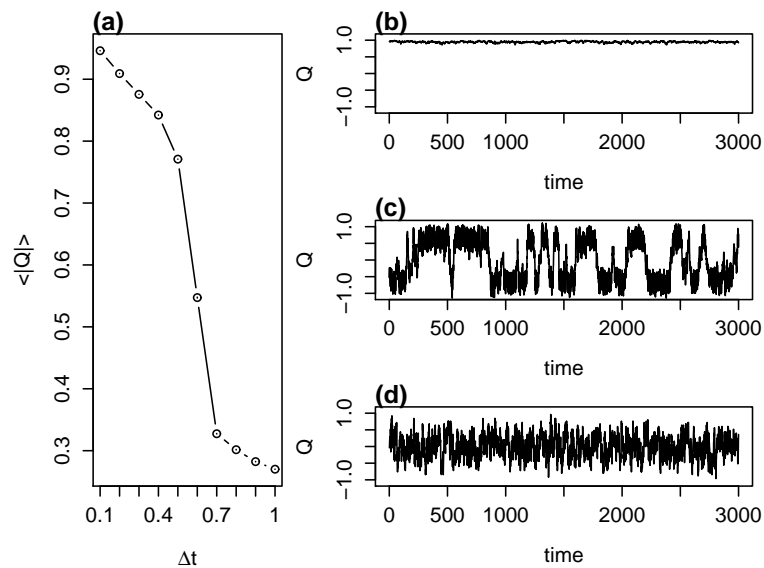


Figure 2.3: (a) $\langle |Q| \rangle$ as a function of Δt (mean over 5 replicas, error bars are smaller than the symbols). Parameters are as in figure 1 but $N = 50$ and $r_A = 50$. (b)-(d) illustrate direction switching in the simulations of our model, where $\Delta t = 0.1$ (b), $\Delta t = 0.6$ (c) and $\Delta t = 1.0$ (d). The groups remained coherent for the duration of the simulations (cf figure 2.2). Simulations lasted for 1,600,000 time-steps and output started after 100,000 time-steps.

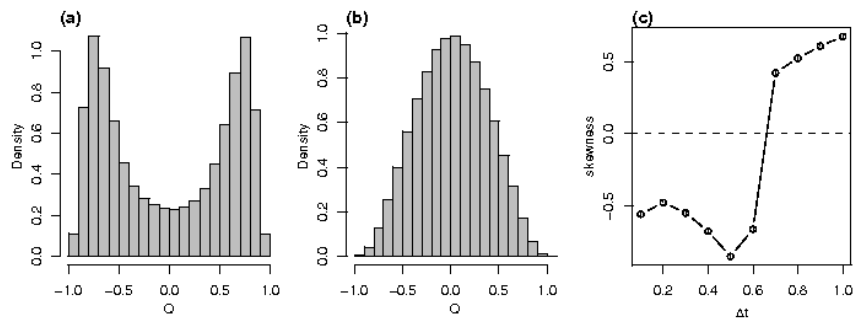


Figure 2.4: Distribution of Q for different values of Δt over 400,000 time-steps (T) at the end of 10 million time-steps. (a) $\Delta t = 0.6$, the particles switch direction occasionally and the group is mostly well aligned (high values of Q). (b) $\Delta t = 0.9$, the group is not well aligned and Q fluctuates about zero. $N = 50$, $r_A = 50$, $r_O = 5$, $T = 1$. (c) Skewness of the distribution of $|Q|$ against Δt extracted from simulations of 400,000 time-steps at the end of a 10 million time-step simulation. The sign of the skewness switches from negative to positive for increasing values of Δt . $N = 50$, $r_A = 9$, $r_O = 5$, $T = 1$.

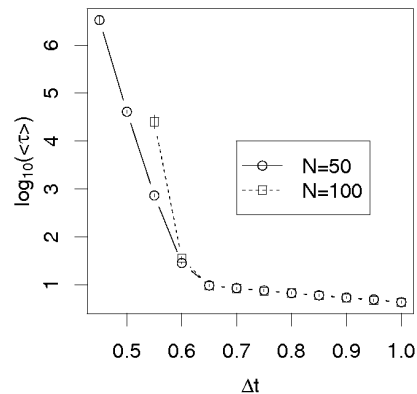


Figure 2.5: Average reversal times for simulated flocks for varying Δt . The quantity $\langle \tau \rangle$ is the average time for which $\text{sgn}(Q)$ remains unchanged. We collected 1000 values of τ for 10 replicas of each parameter combination. Error bars show one standard deviation from the mean. For smaller values of Δt the sign of Q remained unchanged over a simulation of 100 million time-steps. Note the log-scale on the y-axis. $r_A = 50$, $r_O = 5$, $T = 1$.

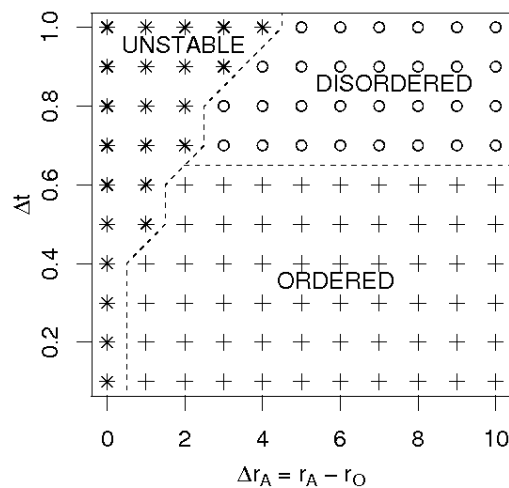


Figure 2.6: Phase diagram for simulations over 10 million time-steps. Groups were considered to be unstable if at some stage during the simulation at least one particles had no neighbours (i.e. no particles within r_A). The ordered state was defined by a negatively skewed distribution of $|Q|$. The behaviour of the model was robust over five replicates. Dashed lines are for guidance of the eye only. $N = 50$, $r_O = 5$, $T = 1$.

coarse-grained behaviour of 1D SPP models in terms of the average particle velocity Q . Yates and co-workers hypothesised that the temporal evolution of Q can be approximately described by the Fokker-Planck equation (FPE),

$$\frac{\partial f_N(Q, t)}{\partial t} = \frac{\partial^2 (D(Q)f_N)}{\partial Q^2} - \frac{\partial (F(Q)f_N)}{\partial Q}, \quad (2.8)$$

where the function $f_N(Q, t)$ is the time-dependant probability distribution for the random variable Q . $D(Q)$ and $F(Q)$ denote the diffusion and drift coefficients, respectively. These two coefficients can be interpreted as follows: the drift captures the mean rate of change of Q while the diffusion denotes the magnitude of the randomness in the evolution of Q . Since the explicit form of the FPE is not available, the drift and diffusion coefficients need to be estimated using computer simulations (for details, see Yates et al. [2009]). While it is possible to approximate interesting quantities such as the mean switching time from the estimated form of the FPE [Erban et al., 2006, Yates et al., 2009], we will limit our study to the functional form of the drift and diffusion coefficients as this provides a sufficiently detailed insight into the behaviour of Q .

When a similar technique was applied to long time-series of the alignment (Q in this case) of locust bands marching in an annular arena, the functional form of $F(Q)$ and $D(Q)$ revealed fascinating properties of the evolution of Q [Yates et al., 2009]. Previous research had shown that the locusts were highly aligned and marched in one direction for prolonged periods of time before spontaneously switching the direction of their motion within a few minutes and marching in the opposite direction [Buhl et al., 2006]. The drift coefficient estimated from this empirical data had a roughly cubic and antisymmetric shape which is consistent with particle motion in aligned states with occasional switches in direction [Yates et al., 2009]. For large positive values of Q , $F(Q)$ took large negative values, and vice-versa. This indicated that for very high average group speeds the group speed was likely to decline over time. There were three points for which $F(Q) = 0$. These corresponded to one unstable and two stable stationary points of $Q(t)$. The two stable stationary points indicate that groups of locusts had a preferred group speed which was approximately the same in

either direction. Interestingly, the diffusion coefficient had a quadratic shape with its maximum at zero alignment [Yates et al., 2009]. An equation-free analysis of a simple 1D SPP model (a variant of Cziráok’s model [Czirók et al., 1999]) indicated that the approximated diffusion coefficient for the evolution of the average particle velocity in this model was roughly constant for different values of Q , while $F(Q)$ had the same antisymmetric cubic shape as found in the locust data. Yates et al. [2009] hypothesised that the quadratic shape of $D(Q)$ for the empirical data could be a result of locusts responding to “low group alignment by increasing the noisiness of their motion”. The authors tested their hypothesis by refining their original model. In the new model the stochastic error added to the preferred direction of individuals was increased if individuals perceived a low local group alignment around them. This model produced a better fit to the empirical data and its equation-free analysis confirmed that the estimate for $D(Q)$ now had a quadratic form.

We performed an equation-free analysis on our model following the approach by Yates et al. [2009]. To facilitate a comparison to previous empirical data and models, we restricted the particles to a line of length L with periodic boundary conditions and used the same parameters as Yates and co-workers wherever possible. We found that the estimated drift coefficient for our model had a cubic shape and the diffusion coefficient a roughly quadratic shape with maximum at $Q = 0$ (see figure 2.7). The diffusion shows a noticeable increase for large values of $|Q|$. This phenomenon was not found in the empirical data [Yates et al., 2009] and is a sign that the drift coefficient affects the diffusion coefficient. In other words, the cubic drift is so pronounced or sharp that it impacts on the diffusion. For our model this effect could be explained by the fact that the groups cannot maintain high velocities as a result of the friction implemented in the function G . This cannot happen in the measurements Yates et al. [2009] made from the locust data since the absolute value of their coarse variable was bounded above by 1.

These findings indicate that our model produces a coarse-grained behaviour qualitatively similar to the coarse-grained behaviour of bands of marching locusts. The

higher noise in the evolution of Q in our simulations emerges from our model which does not assume larger stochastic errors for low values of $|Q|$. Yates and colleagues noted that the randomness in their models is not necessarily indicative of random decision making in locusts. They suggest that there may be small-scale detailed interactions between individuals which result in noise in the coarser experimental observations [Yates et al., 2009]. This is precisely what our model achieves.

2.5 Discussion

In this work we have introduced a new approach to include noise into 1D SPP models. Our approach yields a good qualitative fit to empirical data and can easily be extended to higher dimensions. It therefore suggests a mechanism whereby small-scale stochastic interactions can produce an emergent behaviour which is comparable to the coarse-grained behaviour of bands of marching locust nymphs. Our model suggests that stochasticity in animal movement could be a result of incomplete information intake (neighbour sampling) and small variations in instantaneous rates of information intake (asynchronous updates). This mechanism is parsimonious as it only relies on asynchronous updating and stochastic neighbour-sampling of individuals.

For our model it is important to maintain a clear separation between algorithmic implementation and biological interpretation. We do not claim that updates in our model translate directly into interactions between individuals. The length of update-steps, encoded in the size of Δt , does not explicitly relate to biological or neurological reaction times of animals. Furthermore, the instantaneous positions and movement of individuals on time-scales close to Δt have no direct physical meaning. We merely record the response of individuals to their surroundings averaged over multiple updates (model output every T time-steps). Therefore, it is the average behaviour of individuals in our model at time-scales larger than Δt that should be considered in a biological interpretation of our model. The importance and impact of variable update rates in our model opens up questions regarding the length of and difference between reaction and decision times in animals and their individual information processing

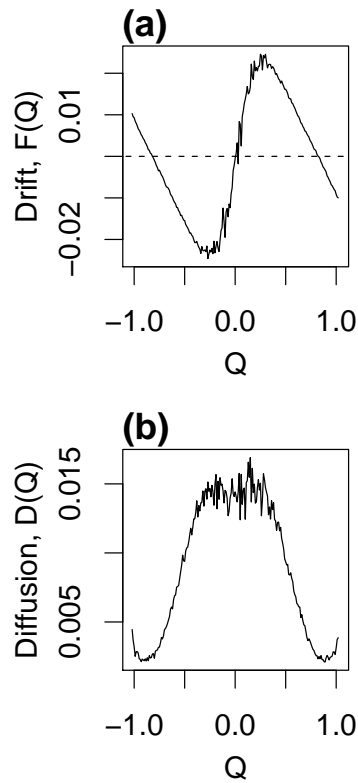


Figure 2.7: Equation-free analysis of our model. $L = 90$, $N = 30$, $r_A = 6$, $r_O = 5$, $T = 1$ and $\Delta t = 0.5$. All parameter values were chosen as close as possible to the ones by Yates and coworkers and otherwise to produce a similar coarse-grained behaviour to the locust data [Yates et al., 2009]. (a) The drift coefficient shows a characteristic antisymmetric cubic shape. (b) The diffusion coefficient has a roughly quadratic shape with maximum approximately at $Q = 0$. Notice the “ears” in $D(Q)$ for large values of $|Q|$. The estimates for drift and diffusion were obtained from long time series of model simulations in agreement with the analysis of empirical data.

capabilities.

We aim to hint at under-explored possibilities in formulating SPP models. Most SPP models implement interactions in a deterministic way and then add stochastic errors (e.g. Vicsek et al. [1995], Czirók et al. [1999]). Absence of noise terms in such models would result in accurate interactions of individuals in perfect knowledge of each other. In contrast, in our approach the algorithmic implementation of interactions itself leads to noisy interactions. We feel this is an important difference with the potential of improving our understanding of collective animal motion by suggesting possible mechanisms for seemingly imperfect or erratic animal interactions. We have previously demonstrated, for example, that an asynchronous updating scheme coupled with varied updating rates provides a mechanism that could explain both continuous speed distributions of collectively moving individuals and the way in which these distributions change in response to external stimuli (chapter 1). This work has also suggested that the length of update steps in algorithms such as the one presented here could be related to the level of threat animals perceive. The length of the update steps is one of the parameters that controls the level of noise in our model. Therefore, our model suggests a meaningful explanation and mechanism for different levels of noise in a biological system and makes testable predictions as to when and why phase transitions might occur in this system. Furthermore, a mechanism based on stochastic sampling of individual's sensory zones as in our model also offers a potential explanation for the anisotropy observed in the internal structure of large starling flocks (Ballerini et al. [2008]; see chapter 3).

SPP models commonly assume that all individuals are identical. However, this does not necessarily hold in nature. Research has begun to investigate the effect of individual features of gregarious animals onto collective behaviour [Couzin et al., 2005, Leblond and Reeb, 2006]. Our framework facilitates the inclusion of individual characteristics. One could, for example, consider different updating rates for individuals, possibly related to their individual state of agitation (chapter 1). These individual updating rates could vary over time in response to environmental stimuli or simply

the number and updating rates of neighbouring individuals. The advantage of our modelling approach, with a detailed microscopic description, is that additional features such as decision making and information transfer can be incorporated into the framework that we propose in the future.

In conclusion, we suggest that noise in models for collective motion of animals should not be considered as a necessary error to account for imperfect interactions but as an opportunity to find out more about how animals function within collective aggregations.

Acknowledgements

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Chapter 3

Limited interactions in flocks: relating model simulations to empirical data

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Abstract

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

3.1 Introduction

The mesmerizing displays of animal collective motion have received much attention from scientists [Parrish and Edelstein-Keshet, 1999, Helbing et al., 2000, Buhl et al., 2006, Sumpter, 2006]. To the casual observer, animal groups such as shoals of fish or flocks of birds often appear to show tightly bound agglomerations that change direction and shape continually and almost instantaneously. Individuals within these groups self-organize into collectives that exhibit a high degree of structure [Hemelrijk and Hildenbrandt, 2008, Cavagna et al., 2010]. How this structure emerges from the behaviour of individuals has been the main focus of research in this field.

It is now widely accepted that the movement of animal groups emerges from the interactions between many similar individuals within the group [Krause and Rux-

ton, 2002]. Highly influential individual-based models have been essential in highlighting how coordinated displays of collective motion can emerge from purely local interactions between neighbouring individuals [Vicsek et al., 1995, Reynolds, 1987, Couzin et al., 2002, Grégoire and Chaté, 2004]. These models implement simple behavioural rules for individuals; these can be loosely expressed as “get attracted to conspecifics” and “avoid collisions”. The dominant theory has been that animal interactions are based on a “metric” framework in which individuals apply these rules only to conspecifics within a fixed distance. Thus, a metric attraction rule would be “get attracted to those neighbors within the specified distance”.

A recent large-scale field study has, however, provided evidence that interactions ruling collective behavior depend on a “topological” rather than metric framework [Ballerini et al., 2008]. Using stereo-photography and multiple cameras, Ballerini *et al.* reconstructed the trajectories of individuals within large moving flocks of starlings (*Sturnus vulgaris*). They found a significant lack of nearest neighbours along the direction of motion of each individual. This only applied to the first six or seven closest neighbours on average. The distribution of directions to neighbours beyond the seventh closest was approximately uniform across an entire flock. Ballerini *et al.* interpreted the anisotropy in the flock structures as a manifestation of interactions among individuals. Since the anisotropy disappeared at a constant topological distance (sixth or seventh neighbour), irrespective of flock densities, they reasoned that interactions between collectively moving animals depend on topological rather than metric distances. Within a topological framework, an attraction rule could be “get attracted to the closest six or seven neighbours, no matter how far away they are”. In summary, the difference between the two concepts is that a topological rule limits by the number of nearest neighbours, whereas the metric rule limits by the distance between individuals. In a metric model this is most simply expressed as the number of interacting birds will change with density; by contrast in a topological framework it will not. Ballerini et al. [2008] argue that this is a key difference when it comes to explaining data.

Despite their importance, it has yet to be determined whether models adhering to either framework reproduce these findings. Here, we present an original individual-based model of collective animal motion, repeat the analysis by Ballerini et al. [2008] for the first time on model simulations and reproduce the empirical findings.

3.2 Modelling Approach

The idea in our modelling approach is to adopt a stochastic, asynchronous updating scheme that takes inspiration from previous models [Raymond and Evans, 2006, Tsitsiklis et al., 1986]. However, in contrast to these approaches we perform a weighted stochastic selection of pairs of interacting individuals, rather than using averaged responses to neighbours [Raymond and Evans, 2006] or unweighted sampling [Tsitsiklis et al., 1986]. Individuals can only react to conspecifics within their fixed spherical sensory zone, which is limited by a “blind volume”, a cone directly behind the individual [Couzin et al., 2002]. Importantly, the probability of a particular pair of individuals being selected to interact in our algorithm depends on the distance between individuals. This selection rule is the most prominent novel feature in our modelling framework. This contrasts to previous models that account for inter-individual distances by scaling contributions of neighbours to a weighted average [Grégoire and Chaté, 2004].

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

$$p_j \sim \frac{1}{d_j}. \quad (3.1)$$

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

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

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

Once a pair of interacting individuals is chosen, the focus individual reacts to its “update partner” depending on the distance between them. At close distances individuals move away from each other to avoid collisions ($d_j < r_R$), and at further distances ($r_O \leq d_j < r_A$) individuals get attracted to each other to maintain flock cohesion [Couzin et al., 2002]. At intermediate distances individuals align ($r_R \leq d_j < r_O$). The size of these behavioural zones, defined by the radii r_A , r_O and r_R remains fixed throughout the simulation. An additional feature of our model is that individuals move with differing instantaneous speeds according to how they react to their “update partner” (chapter 1). When individuals are attracted to their update partner, they move at twice the instantaneous speed than otherwise ($2v_O$ instead of v_O). Stochastic effects in our simulations are entirely generated by the internal dynamics of the algorithm.

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

frequencies. This also results in a variation of individual speeds reported previously (chapter 1). More details of our approach can be found in the appendix.

3.3 Results

Simulations of our model resulted in stable and coherent flocks with a sparseness speed ratio comparable to empirical data (see table 3.1) and non-constant speed distributions (see appendix, figure 3.3). We compared our simulated flocks with the field data presented by Ballerini et al. [2008] by following their methodology as accurately as possible (Cavagna et al. [2008]; A. Cavagna 2010 personal communication). The key observable of interest is the so-called anisotropy factor, $\gamma(n)$, which represents structural information with respect to the n th nearest neighbours. Averaged over many instances, a random spatial distribution of individuals will give rise to $\gamma(n)$ having a constant value of one-third, deviations from this value indicate structural information. Ballerini et al. [2008] observed that in the Starling flocks they were able to observe, film and analyse, $\gamma(n)$ decayed from high values to the isotropic value of one-third after a critical number, n_c , of nearest neighbours, where $n_c \approx 6.5$ [Ballerini et al., 2008]. By simulating similar numbers of birds to those filmed we are able to show that our new model is able to replicate this finding (figure 3.1). To further illuminate the nature of individual interactions in our model we repeated the tests for a topological and a metric framework as suggested by Ballerini et al. [2008], as seen in figure 3.2. To simulate flocks with different densities we varied the extent of the zone in which individuals align with conspecifics (r_O) relative to the overall extent of their sensory zone as well as the average speed at which individuals move (v_O) (table 3.1). Faced with a lack of empirical guidance on what causes different flock densities in starlings, we adopted this parsimonious approach (see also appendix). As in the empirical data we found that our simulated data supported a topological rather than a metric framework.

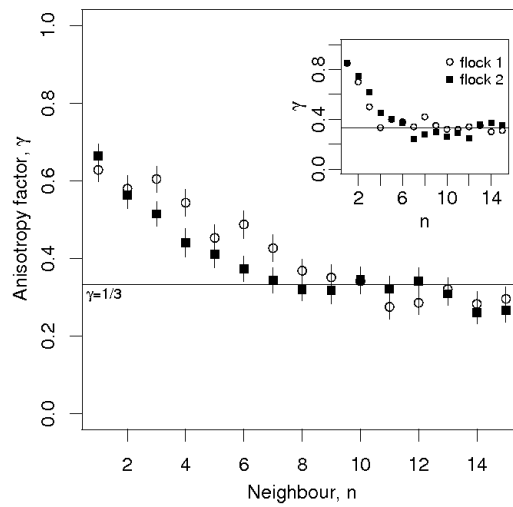


Figure 3.1: Anisotropy in two distinct model simulations (1000 individuals). The anisotropy factor γ plotted against the nearest neighbour n considered in its computation (averaged over 90 consecutive recordings). High values of this measurement quantify a lack of n th-nearest neighbours in the direction of motion averaged over all individuals in the simulated flocks. Note how $\gamma(n)$ decays with increasing n until the internal flock structure becomes isotropic ($\gamma = 1/3$). Circles correspond to simulation sim3 and solid squares correspond to simulation sim1 in table 3.1. Error bars show s.e. The inset shows the function $\gamma(n)$ for empirical data (redrawn from Ballerini et al. [2008]). Circles, flock 1; filled squares, flock 2).

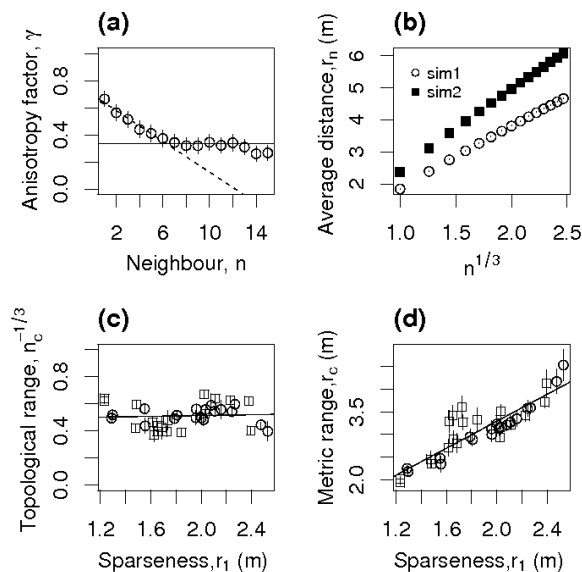


Figure 3.2: Anisotropy ranges in model simulations. Error bars show standard errors. (a) The function $\gamma(n)$ for a model simulation (averaged over 90 consecutive recordings). The topological range n_c is defined as the n -value for which a linear fit to $\gamma(n)$ in the decreasing interval intersects the value $1/3$. This is illustrated by the dashed line. On average we found $n_c = 8.81 \pm 0.749$ (s.e.m). (b) The average distance of the n th neighbour plotted against $n^{1/3}$ for two distinct model simulations (error bars smaller than symbol size). Note how $r_n \sim r_1 \times n^{1/3}$, where r_1 is the sparseness or average distance to the nearest neighbour, a good estimate for the density of flocks. This relation also implies that $r_c \sim r_1 \times n_c^{1/3}$, where r_c is the metric range (in meters) corresponding to the topological range n_c (in nearest neighbours). To test which range describes the decay of anisotropy across flocks we simulate flocks of different sparseness travelling at varying average speed. In a metric scenario r_c is constant and we therefore expect $r_1 \sim n_c^{-1/3}$, while in a topological scenario n_c should be constant and therefore we would expect to find a linear correlation between r_1 and r_c . (c) Testing for the metric scenario, no significant correlation is found between $n_c^{-1/3}$ and r_1 (Pearson's correlation test: $n=36$, $R^2=0.061$, $p=0.723$). (d) Testing for the topological scenario, we find a strong linear correlation between r_1 and r_c (Pearson's correlation test: $n=36$, $R^2=0.89$, $p < 0.00001$). The results from our model simulations are therefore in agreement with the experimental data. This plot should be compared with fig. 3 in Ballerini et al. [2008]. In panels (c) and (d), squares correspond to lower and circles to higher average speeds (see appendix).

Table 3.1: Example summary statistics and model parameters for simulations.

simulation ID	sim1	sim2	sim3	sim4
sparseness, r_1 (m)	1.84	2.38	2.53	1.30
group speed (m/s)	8.05	8.02	10.04	10.03
topological range, n_c	6.33	8.54	9.83	7.35
v_O (m/s)	8	8	10	10
r_O (m)	45	60	60	20

3.4 Discussion

We present here the first model analysis to reproduce the findings of what is currently the largest animal tracking experiment in the wild. The tracking experiment raised the importance of how only a limited number of individuals dominated the interactions [Ballerini et al., 2008]. It also led to the definition that a model with a large radius of interaction in small flock densities and a small radius of interaction in high densities should be referred to as a topological model since the number of interacting neighbours does not change as the density varies (Ballerini et al. [2008]; A. Cavagna 2010, personal communication). To date, it has not been clear how these findings arise from the local interactions between individuals within the group.

The individual behaviour in our model does not explicitly limit individual's reactions to a fixed number of closest neighbours. The overall extent of the perceptive range is the same in all simulations; but the balance between attractive and aligning behaviour is altered to achieve differing sparseness in the groups. This balance also modulates the noise in our study; recall there is no explicit addition of noise. Noise and its character are emergent from variation in update and type of interaction (chapter 2). Despite our model maintaining features from previous metric modelling frameworks, it is clear that it behaves as a topological model in the manner defined by previous work (Ballerini et al. [2008]; A. Cavagna 2010, personal communication).

The model we have constructed gives rise to emergent topological interactions con-

sistent with the most prominent large-scale empirical study to date. Our model offers a parsimonious mechanism to explain the anisotropic nature and apparent limited interactions seen in this study.

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3.5 Appendix

Supplementary methods

Full model description

In our model N individuals are represented by points in continuous three-dimensional space. Each individual obtains information from its sensory zone which is described by a sphere, centred on the individual, of radius r_A . This sphere is punctured by a blind volume, a cone directly behind the individual of interior angle $(360^\circ - \alpha)$, in which individuals cannot perceive other individuals. The individuals, indexed i , are characterised by their position \mathbf{x}_i and instantaneous velocity \mathbf{v}_i . We assume that all individuals react with an identical stochastic rate. Rather than using a Gillespie type algorithm we can therefore use a more efficient particle picking approach to exactly simulate the implicit underlying Master Equation of the system. The algorithmic implementation of our model is as follows:

1. Choose individual i at random, where $i = 1, \dots, N$ (equal probabilities, with replacement).

2. If i has neighbours (conspecifics within sensory zone of i), choose a neighbour j of i at random (probabilities depend on the distance between i and j , see below).
3. Update \mathbf{x}_i and \mathbf{v}_i (depending on the interaction between j and i or based on previous \mathbf{v}_i if i has no neighbours).

One update step of length Δt seconds consists of N realisations of steps (1) to (3). The reciprocal value of Δt is the average rate at which individuals update. Large values of Δt imply slow updates and small values of Δt imply rapid updates. The output of our model is obtained by recording the positions of individuals every $T = \lambda\Delta t$ seconds, where $\lambda \geq 1$. This is analogous to how data is obtained empirically where individual positions are sampled according to the frame rate of a camera [Ballerini et al., 2008]. For the purpose of this research we do not investigate the impact of Δt on the model behaviour but do so elsewhere. Therefore, we keep T and Δt fixed. The movement of individuals over T seconds between two separate model outputs consists therefore of the sum of λ updates on average.

The key difference between this model and previous models is that not only are neighbours (individuals within sensory zones of focus individual) with whom individuals update chosen randomly, but the probability that a particular neighbour is chosen depends on the distance between this neighbour and the updating individual. Suppose individual i has neighbours $k = 1, \dots, k_l$ which are at distances d_k from i ($0 \leq d_k < r_A$). Then individual j is chosen in step (2) above with probability,

$$p_j = \frac{1}{d_j} / \left(\sum_k \frac{1}{d_k} \right). \quad (3.2)$$

For the purpose of finding these probabilities, all d_k equal to zero are replaced with a small constant. This approach ensures that on average individual i is more likely to react to neighbours nearby.

Once individuals i and j have been chosen in the algorithm described above, they interact according to metric behavioural rules based on Couzin et al. [2002]. Let d_{ij}

be the distance between individuals i and j . If $d_{ij} < r_R$, the “repulsion radius”, i moves away from j and has desired velocity,

$$\mathbf{v}_i^{\text{desired}} = v_O \left(\frac{\mathbf{x}_i - \mathbf{x}_j}{d_{ij}} \right). \quad (3.3)$$

If $r_R \leq d_{ij} < r_O$, where r_O is the “orientation radius”, i seeks to align with individual j and consequently has desired velocity,

$$\mathbf{v}_i^{\text{desired}} = v_O \left(\frac{\mathbf{v}_j}{|\mathbf{v}_j|} \right). \quad (3.4)$$

Finally, if $r_O \leq d_{ij} < r_A$, i gets attracted to j :

$$\mathbf{v}_i^{\text{desired}} = v_A \left(\frac{\mathbf{x}_j - \mathbf{x}_i}{d_{ij}} \right). \quad (3.5)$$

Should i have no individuals within its sensory zone, it does not deviate from its direction. Note how individuals move at a different speed when getting attracted (v_A as opposed to v_O). This is based on the assumption that there exists a quantitative difference in the way animals react to conspecifics further away. Furthermore, differing speeds are required to simulate positively skewed speed distributions that have been found in empirical data [Aoki, 1980]. Throughout this work we choose $v_A = 2v_O$ assuming that attracting individuals try to “catch up” with conspecifics.

Once $\mathbf{v}_i^{\text{desired}}$ is determined, the new direction of motion for i , $new(\mathbf{v}_i)$, is determined by rotating \mathbf{v}_i towards $\mathbf{v}_i^{\text{desired}}$ by an angle of at most $\beta\Delta t$ degrees. Here β stands for the maximum turning rate of individuals. The new position of individual i is then obtained as,

$$new(\mathbf{x}_i) = \mathbf{x}_i + new(\mathbf{v}_i)\Delta t. \quad (3.6)$$

Model discussion and simulations

In our model algorithm the probability of i to choose a particular “update partner” j simply depends on the inverse of the distance d_{ij} ($p_j \sim 1/d_{ij}$). Clearly, one could imagine other dependencies between p_j and d_{ij} , possibly of the more general form $p_{ij} \sim 1/d_{ij}^c$, where c is a constant. We have not explored different values of c since

we consider our model to be an illustration of principle rather than an exhaustive parametrisation study. Likewise, we have restricted the region of the parameter space we explored by fixing $N = 1000$, $\Delta t = 0.025s$, $T = 1s$, $r_R = 1m$, $r_A = 100m$, $v_A = 2v_O$, $\beta = 120^\circ/s$ and $\alpha = 270^\circ$. Simulations lasted for 1100s, started from random initial positions and orientations inside a sphere of radius 20m and output was recorded for the last 90s. It was important to include a long warm-up time during which no model output was recorded to ensure that the simulated flocks assembled the internal structure that accurately reflected the model's emergent properties rather than the random initial conditions. For v_O we used the values 8m/s and 10m/s and for r_O we used values in the set $\{20, 25, 30, \dots, 60\}$ (in meters). We used two replicates of each parameter combination in our analysis.

Data analysis

The analysis of our simulated data followed the analysis of empirical data as closely as possible. Ballerini *et al.* developed an anisotropy factor for flocks, $\gamma(n)$, for the n th closest neighbour [Ballerini et al., 2008, Cavagna et al., 2008]. This factor quantifies the lack of nearest neighbours along the direction of motion of individuals averaged across an entire flock ($0 \leq \gamma(n) \leq 1$).

Boundary effects influence the value of $\gamma(n)$ strongly for small flocks (small N) [Cavagna et al., 2008]. Therefore, it has been recommended to find the boundary of flocks by using α -shapes and to exclude all neighbours from the analysis which are further away than the boundary is from their reference individuals (Hanisch method) [Cavagna et al., 2008]. We are using a convex hull algorithm to find the flock boundary in our analysis. The α -shapes approach has the advantage that it accounts for non-convex flocks for appropriate values of α , which regulates the allowed minimal size of concavities in the flock boundary [Cavagna et al., 2008]. Visual inspection showed that in contrast to flocks of starlings [Ballerini et al., 2008] our simulated flocks had an approximately convex boundary. We also found that the shape of our flocks was affected by a small number of outliers away from the main body of the flock (see

figure 3.3). Outliers have an effect on the boundary found by using the convex hull or the α -shapes method. However, large numbers of individuals in flocks help to smooth out any errors introduced by outliers or inaccurate boundaries. For these reasons a convex hull algorithm for the calculation of the flock boundaries was sufficient to find clear qualitative trends in the large simulated flocks in this work.

Ballerini and co-workers argued that the anisotropy in the internal structure of starling flocks is a direct result of interactions between birds and defined an interaction range n_c , given by the value of n where γ becomes $1/3$. They suggested that birds do not interact with conspecifics further than their n_c th nearest neighbour [Ballerini et al., 2008]. Specifically, n_c was found as the n value where a linear fit to the decreasing interval of $\gamma(n)$ intersects the horizontal line $\gamma = 1/3$ as in [Ballerini et al., 2008]. We automated this procedure by fitting a line to all values of $\gamma(n)$ obtained from our simulations for all $n < n_{fit}$ and a horizontal line of value $\gamma = 1/3$ to the values of $\gamma(n)$ for $n \geq n_{fit}$. The value of n_{fit} we used resulted in the smallest sum of squared residual for the corresponding fit to $\gamma(n)$. The value for n_c was then defined as the intersection between the linear part of our fit to $\gamma(n)$ and the line $\gamma = 1/3$.

Flock summary statistics

From our simulated flocks we extracted the polarisation and angular momentum, given by [Couzin et al., 2002],

$$p_{group} = \frac{1}{N} \left| \sum_{i=1}^N \mathbf{v}_i \right|, \quad (3.7)$$

$$m_{group} = \frac{1}{N} \left| \sum_{i=1}^N (\mathbf{x}_i - \mathbf{c}_{group}) \times \mathbf{v}_i \right|, \quad (3.8)$$

where $\mathbf{c}_{group} = \sum \mathbf{x}_i / N$ is the group centre. The angular momentum measures the degree of rotation of the group about the centre of the group and the polarisation the degree of alignment among individuals [Couzin et al., 2002]. High values of $0 \leq p_{group} \leq 1$ denote high levels of alignment and vice versa. Similarly, high values of $0 \leq m_{group} \leq 1$ denote a high degree of rotation about the centre of the group. The

two summary statistics presented here are commonly used to describe and identify changes in the type of collective behaviour displayed by moving groups of individuals [Couzin et al., 2002]. Since we are comparing our model to empirical data of highly aligned flocks of birds [Ballerini et al., 2008], we needed to ensure that for our choice of parameters the simulated groups always displayed the same type of collective motion.

The group speed, v_{group} , was approximated by the distance the centre of the group moved between model outputs:

$$v_{group}(t) = |\mathbf{c}_{group}(t) - \mathbf{c}_{group}(t + T)|. \quad (3.9)$$

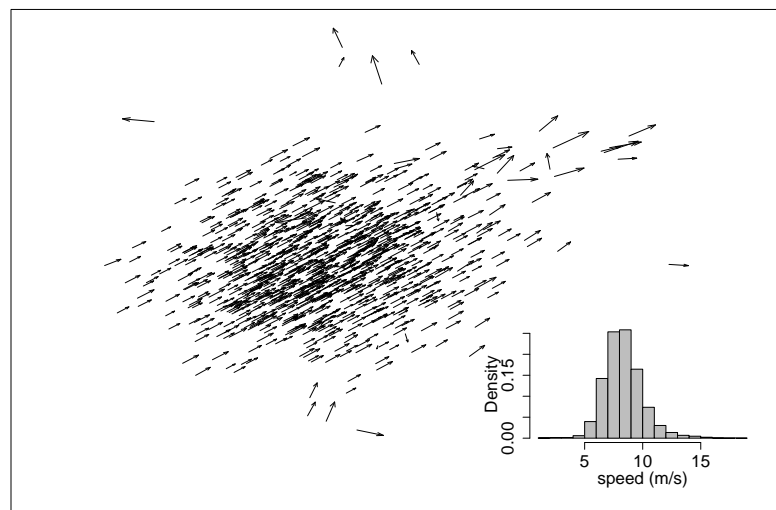


Figure 3.3: Two-dimensional projection of simulated individual velocities (approximated by the vector between two consecutive positions, 1 second apart) and distribution of individual speeds. The figure shows individual velocity vectors at one instant of time for a flock of 1,000 individuals. The length of the vectors is divided by a factor of 5 for clarity. The flock is highly aligned but some individuals leave the core of the flock temporarily. No outliers are eliminated from this picture and we confirmed that simulated flocks stay coherent over long simulation runs despite significant fluctuations at the boundary. The inset shows the distribution of individual speeds across the entire group for 20 consecutive recordings.

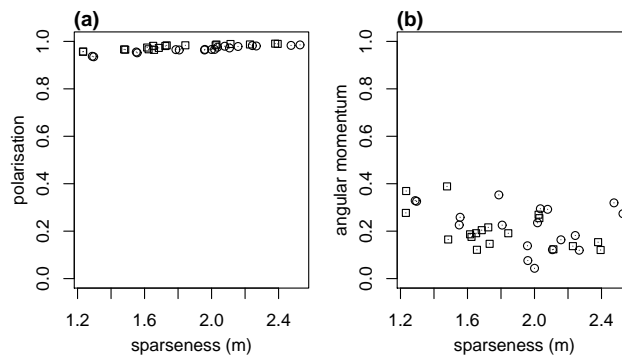


Figure 3.4: Polarisation and angular momentum plotted against sparseness for the simulated flocks used in the analysis in the main text. Error bars (standard error) are smaller than the symbol size. Squares denote simulations with $v_O = 8\text{ m/s}$ and circles simulations with $v_O = 10\text{ m/s}$. Neither of the summary statistics displays large systematic changes for different values of r_1 . This suggests that the simulated flocks displayed the same type of collective motion for all simulations.

Supplementary discussion

Empirical results indicate that the spatial shape of moving animal groups can be affected by environmental factors such as the level of predation risk [Krause and Ruxton, 2002, Couzin et al., 2002]. Simulation studies have shown that the type of collective motion can depend heavily on the extent of the sensory zones of individuals which in turn may be determined by environmental factors [Couzin et al., 2002]. Furthermore, it has been suggested that swarms may have higher frontal densities as a result of preferential attacks on the front of swarms [Hildenbrandt et al., 2010]. Potential sources for anisotropic flock structures have been identified in the body shape of animals or even the aerodynamics (or hydrodynamics) involved in collective motion. However, these possibilities have been excluded for the starling data that we use as a benchmark for our model [Ballerini et al., 2008]. As a result, our model does not account for physical aspects within animal groups such as the size and shape of individuals' bodies. In this work we do not consider the influence of environmental factors on the collective motion of individuals. The anisotropy we found in our

simulated flocks is therefore an emergent property of the behaviour of individuals.

An important aspect of the analysis by Ballerini et al. [2008] which we repeated for our simulations is to consider flocks of different densities [Ballerini et al., 2008]. In the context of simulating groups of animals it becomes important to determine the origin of the variation in density between flocks. We decided to approach this problem by varying the extent of the “zone of orientation” (r_O) of individuals and the average speed (v_O, v_A) at which individuals move. This yielded flocks with a sparseness to average group speed ratio comparable to empirical data [Ballerini et al., 2008]. However, we cannot guarantee that the behavioural differences we used are in fact the correct ones that explain different flock densities. In our model there are different ways of varying the density of simulated flocks. For example, different functions for the selection probabilities, p_j , may and varying the update frequency (Δt) does lead to different flock densities. However, this will not only affect the density of simulated flocks but also other aspects of their dynamics. Faced with a lack of empirical guidance on this issue, we chose a parsimonious approach to simulate flocks of different densities.

When we repeated the analysis described above for a different model of collective motion that is already defined in the literature [Couzin et al., 2002], we were unable to reproduce functions of $\gamma(n)$ with values significantly different from $1/3$ in the physical regime (unpublished data Bode et al. 2010; A. Cavagna 2010, personal communication). This indicates that such models may not be able to reproduce the empirical results. However, it is not clear whether this is true for all of the many different models for collective motion.

Part II

The impact of underlying social networks on the collective motion of animals

Chapter 4

Social networks and models for collective motion in animals

Published manuscript

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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.

4.1 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 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.

4.2 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 categorized 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 network¹. 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 4.1a 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

¹This definition is inspired by the use of the term “communication networks” in the modelling literature. See also introduction of chapter 5.

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 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 4.1b shows an example for such a social network in contrast to the communication network in figure 4.1a.

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 4.1

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 figure 4.2 for an illustration). In many models the communication topology at any one instant is defined by spatial proximity (recall figure 4.1a). There-

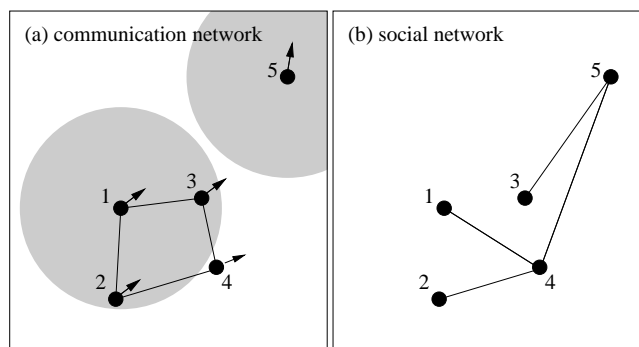


Figure 4.1: The difference between communication and social networks. The positions of individuals are marked by *black circles* with *arrows* indicating their direction of motion. Connections (edges) are marked by *black lines* between individuals. (a) Illustration of an instantaneous communication 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.

fore, 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.

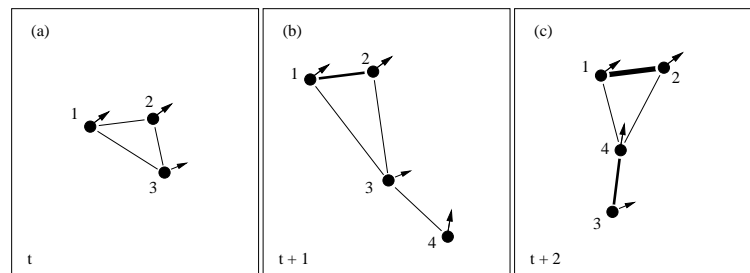


Figure 4.2: Illustration of how a social network could change over time driven by spatial proximity of individuals. Increased width of edges illustrates increased strength of social connections and the positions of individuals relative to each other are shown. Panels (a)-(c) show three consecutive instances 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 and 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 them 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.

4.3 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 explor-

Table 4.1: 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. The table lists selected details of models in the literature. * 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].

Type of interaction	Alignment only	Jadbabaie et al. [2003], Savkin [2004], Yu and Wang [2008]
	Repulsion, alignment, attraction	Tanner [2004], 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]
	m -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 *	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]

ing 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 [Buman 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 (*Loxodonta 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 naive 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 [Sárová et al., 2010]. Leader-follower relationships impose a rudimentary social network onto simulated collective motion. More gener-

ally, 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 [Qiu and Hu, 2010, Loscos et al., 2003], but have not studied the consequences of this addition.

4.4 Collective motion affecting social networks

In the section “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 (*Poecilia 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 re-assessed 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 [1997] 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 influences 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.

4.5 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 4.1). 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 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 neuro-biological perspective and one could imagine that neurological pattern recognition might yield interesting concepts. Recent work 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 (chapter 3).

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, however, this could easily be extended to include preferential interactions between socially connected animals (see chapter 5). 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 within-group structures, such as what affect the social network structure has on group formations (such as V-formations), or what affect 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 fruit-

ful. 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 section “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 has suggested how animal groups synchronise in the face of increased threat levels (chapter 1). 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.

Table 4.1: List of a number of questions of immediate interest for future research.

-
- 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?
-

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Chapter 5

The impact of social networks on animal collective motion

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Abstract

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. Counter-intuitive 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.

5.1 Introduction

Many group-living animals show social preferences for particular individuals or groups of individuals. These inter-individual preferences affect the movement of animals within groups and the movement of groups as a whole. For example, guppies (*Poecilia reticulata*) prefer to shoal with familiar conspecifics [Griffiths and Magurran, 1999], the majority of pedestrians walk in small social groups [Moussaïd et al., 2010], and group fission in macaques (*Macaca tonkeana* and *Macaca mulatta*) is strongly influenced by individual affiliations [Sueur et al., 2010].

Individual-based models have been essential in demonstrating how the collective motion of animal groups, such as flocks of birds or shoals of fish, could emerge from

simple rules and entirely local interactions between individuals (e.g. Reynolds [1987], Vicsek et al. [1995], Couzin et al. [2002], Buhl et al. [2006]). Some models have included social preferences, but the focus has been largely on pedestrian crowds (e.g. Braun et al. [2003], Moussaïd et al. [2010], Qiu and Hu [2010]). In a more general approach Hemelrijk and Kunz [2005] divided their groups into two categories: familiar and unfamiliar. Individuals were given higher social preferences for familiar individuals. Hemelrijk and Kunz 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. While the literature provides some interesting starting points there is a real need to develop this field further (see also chapter 4).

When social preferences as introduced above are present in a species that displays collective motion, it is likely that they impact on the interactions between individuals. This should in turn affect the spatio-temporal patterns that emerge from local interactions. They could, for example, determine how populations move in, split up into and form separate groups. 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.

Social preferences and interactions between moving individuals obey different time-scales. While social preferences often change slowly (e.g. familiarity, kinship), interactions between moving individuals change more frequently (e.g. collision avoidance, group cohesion). In some cases interactions between moving individuals may influence social preferences (e.g. familiarity based on spatial proximity, see chapter 4), but the impact of social links on interactions should be far more ubiquitous and strong.

Both social preferences and interactions between moving individuals can be expressed in terms of network theory [Croft et al., 2008, Whitehead, 2008, Newman, 2010]. Animals are represented by “nodes” with “edges” between them representing connections. In the context of modelling collective motion two different types of net-

works emerge from the literature for describing connections between individuals that directly affect the behaviour of animals: communication networks and social networks (chapter 4).

“Communication networks” represent the exchange of information between individuals while they are collectively moving, such as observing the spatial position of group mates. 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. 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 signaller 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 chapter 4).

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 the ability of individuals to 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]; chapter 4).

Social and communication networks are useful concepts as the network represen-

tation 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 chapter 4). In collective robotics, for example, researchers have included details of the connectivity of the communication network into robot control protocols, in an attempt to improve the coherence of robot group mobility [Schuresko and 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 why 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. Buman 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 and Hart [1992], Morrell and 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, *Columbia 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 the model of animal collective motion presented in chapter 3 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.

5.2 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 (chapter 3). 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 and 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_A , centred on the individual. This circle is punctured by a “blind angle” directly behind the individual of size $(360^\circ - \alpha)$, in which individuals cannot perceive other animals. The individuals, indexed i , are at position x_i and move at the instantaneous velocity 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 Δt seconds consists of N realisations of steps (1) to (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, Δt , 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 $T = \lambda\Delta t$ seconds,

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). Decreasing Δt 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 Δt we refer the reader to earlier publications relating to this model (chapters 1 and 2).

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 and Kunz [2005], Moussaïd et al. [2010]). The novelty of our model lies in the inclusion of social networks: the probability for choosing a particular neighbour not only depends 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 $k = 1, \dots, k_l$ 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,

$$p_j = \left(\frac{e_{ij}}{d_j} \right) / \left(\sum_k \frac{e_{ik}}{d_k} \right). \quad (5.1)$$

To avoid a singularity, we introduced a cut-off 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} 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 focus individual reacts to its “update partner” depending on the distance, d_j , between them. Only the focus 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_R , r_O and r_A [Couzin et al., 2002]. At close distances, the focus individual moves away from its update partner to avoid collisions ($d_j < r_R$) and at larger distances ($r_O \leq d_j < r_A$) it gets attracted to its update partner to maintain group cohesion [Couzin et al., 2002]. At intermediate distances the focus individual aligns with its update partner ($r_R \leq d_j < r_O$). 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. $|v_i| = 2v_O\Delta t$ instead of $v_O\Delta t$, where v_O 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 (chapter 1). The rate at which individuals turn is limited to β degrees per second. 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 entirely generated 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, we refer the reader to chapter 3. Variations of the model used in this research have demonstrated the biological relevance of our theoretical approach (chapters 1 and 2).

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 are connected by 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 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 base-line for comparison, we randomly assign strong preferences. 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 and Rényi, 1960].

Watts and 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 re-wired 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 and Strogatz, 1998]. Varying the re-wiring 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 connected to them, attaching the new node to already included nodes with strong connections by preferential attachment (“rich get richer model”; Barabási and 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_A , 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: $N = 100$, $r_R = 1$ m, $r_O = 12$ m, $r_A = 20$ m, $v_O = 3$ m/s, $v_A = 2v_O$, $\Delta t = \{0.2s, 0.1s, 0.05s\}$, $\alpha = 270^\circ$, and $\beta = 40^\circ/s$ (note that parameters have been explored elsewhere, see chapters 1-3). 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 Δt in the scenarios we use to explore the three hypotheses stated in the introduction. Varying Δt for fixed T changes the behaviour of the system. For example, low values of Δt result in more synchronized and cohesive groups than higher values of Δt (chapters 1 and 2). We utilise 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 Δt that allows for frequent group fragmentation since we are studying a fission-fusion system. Since we are only interested in non-fragmented groups in the other scenarios, we use smaller values of Δt in these simulations.

5.3 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 differ-

ent illustrative structural elements (figure 5.1). 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 and Rényi, 1960]. We simulated groups of 100 individuals.

We first measured group cohesion. To do so we use 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 assumed to be associating [Whitehead and Dufault, 1999]. Data from a number of such GoG censuses can be combined into cumulative networks that can then be analysed for non-random 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 movement) 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 one thousand 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 one thousand 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 subtracting 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 one thousand. 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 5.1 shows the GoG edge frequencies averaged over pairs with strong and weak connection in the underlying social network, for the different social network structures we imposed on groups. Figure 5.1a,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 one thousand (figure 5.1b), 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, figure 5.1c, 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 figure 5.1c, illustrates this (included in electronic submission). Preferential updating leads to spatial assortment but weakly connected individuals still interact.

The summary statistics listed in table 5.1 quantify our observations from figure 5.1

further. We examined group alignment by extracting the polarisation, $p_{group} \in [0, 1]$ from our simulated groups. High polarisation values indicate high group alignment and low polarisation 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 polarisation 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 polarisation 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 individuals 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 figure 5.1. An underlying network in which one central node is connected to all other nodes (figure 5.1) 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 vary smoothly with the difference between weak and strong connections (figure 5.5 in appendix).

Our first question was whether strong pairwise social preferences between group members always improve group cohesion. The results presented in table 5.1 show already that this is not the case. Social networks which split a group into two separate social components (see figure 5.1c) do not result in higher group cohesion than the control case without any social structure. However, we may ask whether particular social structures improve group cohesion or, more generally, what aspects of social

Table 5.1: Summary statistics for simulations with differing underlying social networks as seen in figure 5.1 (average over 10 simulations \pm standard error). Random networks are created by assigning strong connections according to the Erdős-Rényi method with edge-probability 0.1. Ten replicas for ten different random graphs and groups of 100 individuals were used.

Network	Polarisation	no. of groups	largest group /N	GoG difference
control	0.99 ± 0.0003	1.1 ± 0.01	0.99 ± 0.0002	NA
2 components	0.81 ± 0.003	1.7 ± 0.01	0.73 ± 0.003	526 ± 6
3 components	0.70 ± 0.004	2.4 ± 0.02	0.64 ± 0.004	581 ± 6
centre	0.97 ± 0.0009	1.4 ± 0.02	0.98 ± 0.001	16 ± 1
random	0.96 ± 0.002	1.7 ± 0.03	0.97 ± 0.002	10 ± 1

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 (figure 5.2). Table 5.2 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 networks. Another example is given in the appendix, where we systematically reduce the structure in underlying preference networks (figure 5.6 in appendix).

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 compare the average distance of individuals from the centre of mass (CoM) of the group ($\text{CoM} = \sum x_i/N$) to the “strong degree” (number of strong social connections) of those individuals in generated social networks. We repeated our

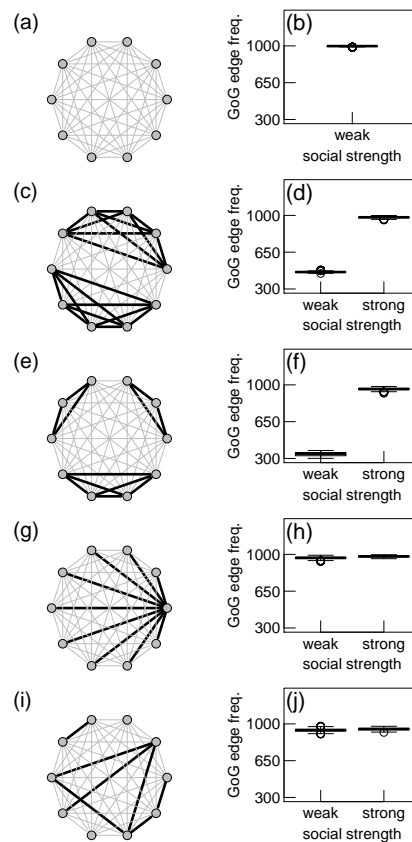


Figure 5.1: Effect of different underlying social networks on collective motion. (a,c,e,d,i) Illustrations for the underlying networks used in the simulations for $N = 10$. Strong connections are shown in thick black lines and weak connections in thin grey lines. In our simulations these networks were scaled up to $N = 100$. (b,d,f,h,j) Box-plots of the distribution of GoG edge frequencies for pairs of individuals with strong or weak social connections for one simulation with an underlying social network as the illustration in the same row (but for $N = 100$, $\Delta t = 0.2$, $T = 100$; we recorded 1000 separate output instances, T seconds apart, for each simulation). Box plots show medians and 25th and 75th percentiles; whiskers indicate 1.5 times the interquartile range and circles indicate outliers. (a) Control case, all connections have the same strength. This is equivalent to the case when all connections are strong. (c) and (e) Networks with two and three separate components, respectively. (g) Network with one well-connected individual, which has strong connections to all other nodes. (i) Random networks that are created by assigning strong connections according to the Erdős-Rényi method with edge-probability 0.1

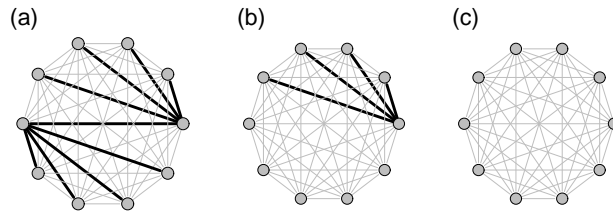


Figure 5.2: Illustration of networks with (a) two, (b) one and (c) no highly linked key individual for $N = 10$. Strong connections are shown in thick black lines and weak connections in thin grey lines. In our simulations these networks were scaled up to $N = 100$.

Table 5.2: Summary statistics for simulations with differing underlying social networks as seen in figure 5.2 (average over 10 simulations \pm standard error). Differences in summary statistics between different underlying social networks are statistically significant allowing for a Bonferroni correction for multiple comparisons (Kruskal-Wallis test; Polarisation: $H_2 = 25.8$, $P < 0.001$; no. of groups: $H_2 = 25.8$, $P < 0.001$; |largest group|/N: $H_2 = 25.1$, $P < 0.001$; GoG difference: Mann-Whitney U test, $U = 96$, $N_1 = N_2 = 10$, $P < 0.001$).

Network	Polarisation	no. of groups	largest group /N	GoG difference
2 centres	0.97 ± 0.0009	1.35 ± 0.01	0.98 ± 0.0008	12 ± 0.5
1 centre	0.98 ± 0.0007	1.2 ± 0.01	0.99 ± 0.0007	7 ± 0.7
no centre	0.99 ± 0.0003	1.1 ± 0.01	0.99 ± 0.0002	NA

analysis for the three most commonly used approaches to generate network structure randomisations: Erdős-Rényi random networks [Erdős and Rényi, 1960], small-world networks [Watts and Strogatz, 1998], and networks with skewed degree distributions [Barabási and Albert, 1999]. Figure 5.3 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 group mates 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 use the methods described by [Nagy et al., 2010]. For each individual, we examined if it turned before or after the average of the group. To do so we computed the cross-correlation $C_{ij}(\delta t)$ between the time series of movement directions (recorded every $T = 0.2$ seconds) for pairs of individuals (i, j) , shifting the time series of individual j by δt seconds (therefore $C_{ij}(\delta t) = C_{ji}(-\delta t)$). The value of δt for which $C_{ij}(\delta t)$ reaches its maximum value was 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

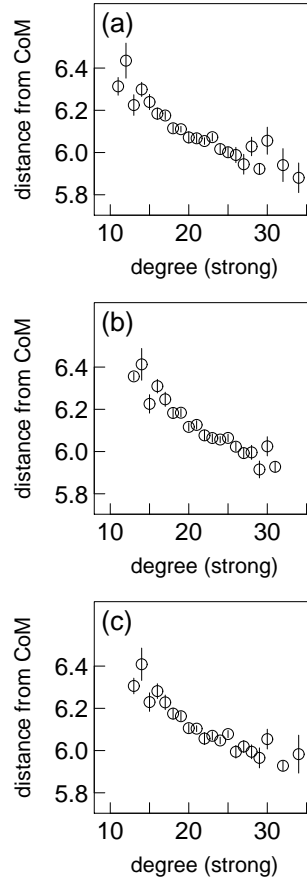


Figure 5.3: Average distance from the centre of mass (CoM) of simulated groups against the degree within a randomly generated underlying social network. To create the strong connections randomly we used the Erdős-Rényi method (a), the Watts-Strogatz method (b) and the scale-free method (c). We ensured that the total number of strong connections included in networks was on average equal for the different networks. The average over at least 2 and at most 50 simulations is shown (not all random networks contained nodes with certain very large or small degrees); error bars show standard errors. We used $N = 100$, $\Delta t = 0.1$ s, $T = 100$ and recorded 1000 separate output instances, T seconds apart, for each simulation, Only instances when groups were coherent were included in the analysis. Average fraction of times groups in output where coherent over 50 simulations \pm standard error: (a) 0.86 ± 0.0031 ; (b) 0.84 ± 0.0039 ; (c) 0.81 ± 0.0039 .

maximal value of $C_{ij}(\delta t)$ was above the threshold $C_{min} = 0.98$. To find the delay between the turns of individual i and the rest of the flock, we computed $C_i(\delta t)$ by averaging $C_{ij}(\delta t)$ over all individuals j (excluding $j = i$). Again, the value of δt for which $C_i(\delta t)$ reaches its maximum value was the delay between individuals 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 only include instances when the flock forms one cohesive group (as defined in section “Group cohesion (hypothesis 1)”) in our analysis. We computed the flock delay separately for 50 simulations and report the average. For pairwise delays we compute the average of the function $C_{ij}(\delta t)$ over 50 simulations and use 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 (figure 5.4a). 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 figure 5.4b). 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 (figure 5.4b). 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_{min}) pairwise delays is instructive (figure 5.4c). 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 figure 5.1g (figure 5.7 in appendix). 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 figure 5.4 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 $T = 0.2$ seconds. The flock delays and pairwise delays we do find are therefore stochastic effects (as the comparison to 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 (figure 5.4b,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 figure 5.4b,c in a

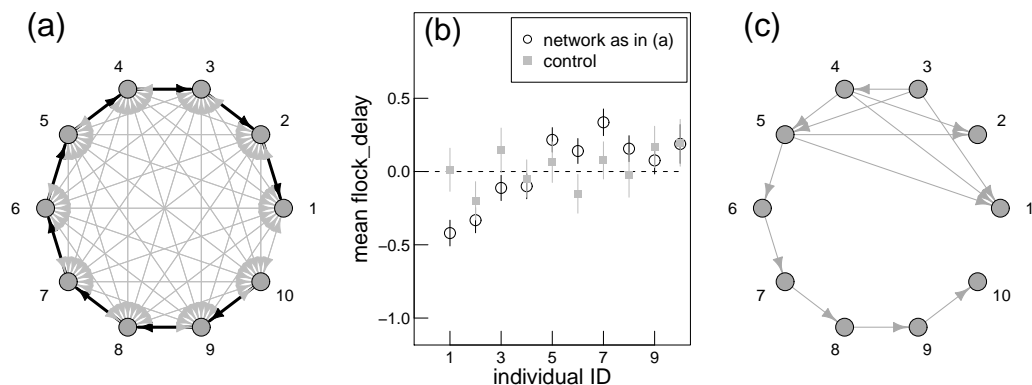


Figure 5.4: Group dynamics for a given underlying preference network. (a) Underlying network of social preferences. Strong preferences are shown in thick black lines and weak preferences in thin grey lines. Numbers denote individual IDs. (b) Mean flock delays for each individual averaged over 50 simulations. 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 standard errors. (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 greater than zero. $N = 10$, $T = 0.2$ s, $\Delta t = 0.05$ s. We recorded 5000 output instances, T seconds apart, for each simulation. Only instances when groups were coherent were included in the analysis. This was more than ninety percent of the time for control groups and more than seventy percent of the time for groups with underlying social network.

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.

5.4 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 is often obtained by using the “gambit of the group” 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 figure 5.1) 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-scaled 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 and Ruxton [2002], Morrell and Romey [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 rela-

tions 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 (see also discussion of chapter 4). We have deliberately focussed on simple illustrative networks to use as conceptual examples. However, we have demonstrated some counter-intuitive 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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5.5 Appendix

Supplementary film 1: The video file can be found in the electronic submission. This film contains a 1000 second segment of an animation showing the movement of a group of 100 individuals. The underlying social preference network divides the group into two compartments, as depicted in figure 5.1c. The different social subunits are shown in red and black. The animation starts from random initial conditions and shows that preferential updating leads to spatial assortment (individuals of the same colour tend to move in the same groups). However, interactions between weakly linked individuals still occur, as is illustrated, for example, by black individuals joining red groups. Parameter values are the same as in the main text, but $T = 1$ s.

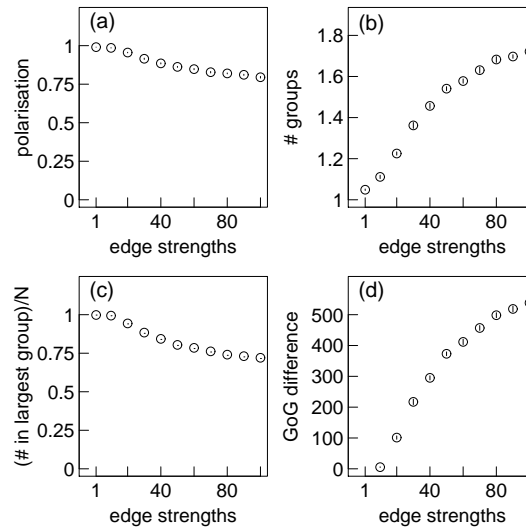


Figure 5.5: The effect of the strength of strong connections in the case of an underlying social network with 2 separate components (compare to figure 5.1c in the main text). (a) Polarisation, (b) number of groups, (c) number of individuals in the largest group divided by the overall number of individuals, 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 standard errors. $N = 100$, $\Delta t = 0.2$ s, $T = 100$ s.

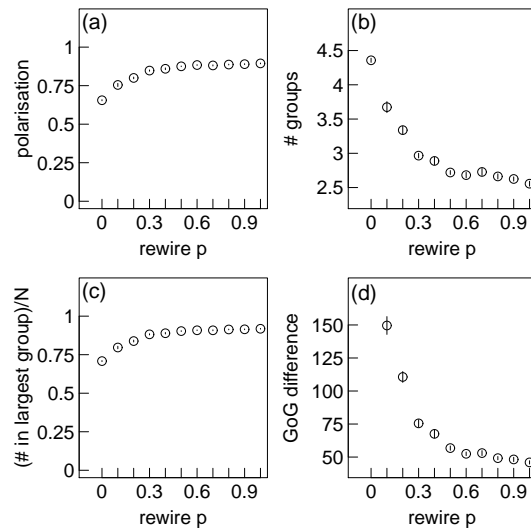


Figure 5.6: The effect of increasingly random small-world networks on collective motion. (a) Polarisation, (b) number of groups, (c) number of individuals in the largest group divided by the overall number of individuals, and (d) the GoG difference (see text for details). The re-wiring probability gradually increased, starting from a regular ring lattice with average degree = 4. With increasing re-wiring probability the original structure gets more and more diluted and the cohesion of the group increases. The average over 10 simulations is shown, error bars show standard errors. $N = 100$, $\Delta t = 0.2$ s, $T = 100$ s.

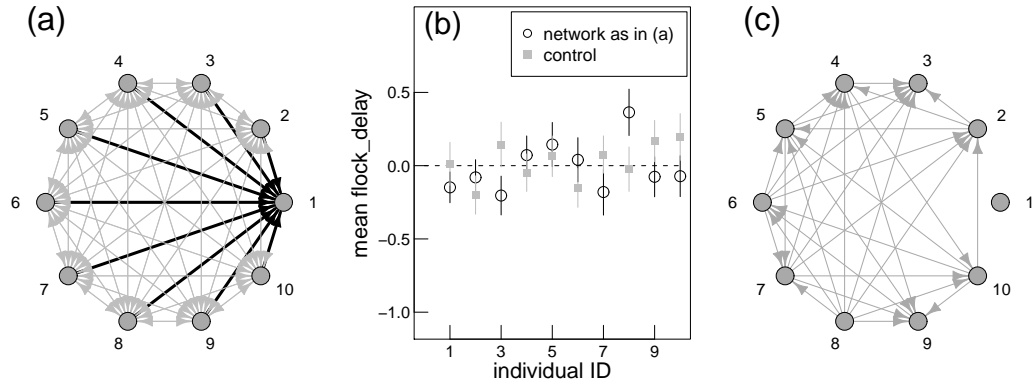


Figure 5.7: Group dynamics for a given underlying preference network. (a) Underlying network of social preferences. Strong connections are shown in thick black lines and weak connections in thin grey lines. Numbers denote individual IDs. (b) Mean flock delays for each individual over 50 simulations. 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 standard errors. (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 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. $N = 10$, $T = 0.2$ s, $\Delta t = 0.05$ s, $C_{min} = 0.98$. We recorded 5000 output instances, T seconds apart, for each simulation. Only instances when groups were coherent were included in the analysis. This was more than ninety percent of the time for control groups and for groups with underlying social network.

Discussion

Conclusions

Although predominantly a theoretical approach, this thesis has employed empirical investigation (chapter 1) and attempted to interpret and synthesise previous work from different disciplines to provide an informed starting point for future investigation of biological systems (chapter 4). Overall, this research aims to contribute in three ways to the understanding of animal collective motion.

First, the development of a novel modelling framework was used to suggest possible mechanisms for existing empirical knowledge. Chapter 1 initially set out to obtain realistic speed distributions for simulated groups without assuming them a priori. This was approached by using asynchronous and stochastic updates and eventually led to the suggestion that update rates, or the frequency at which individuals react to their environment, could explain changes at the group level in response to increased perceived threat. Chapter 2 extended the concept of asynchronous and stochastic updates by implementing individuals that sample the information, contained in their field of perception, at a given rate. Results suggested that this mechanism could explain stochastic effects in animal group movement, such as abrupt changes in the group movement direction. This could provide an explanation for the finding of Yates et al. [2009] that locusts increase the randomness of their movement at low group alignment. In chapter 3, the sensory zone sampling of individuals was further extended to include a distance-dependent bias. Interactions between individuals close to each other were more likely than interactions between individuals that were further apart. This revised mechanism reproduced findings on starling flocks suggesting that on average individual birds interact with a fixed number of nearest neighbours (“topological interactions”; Ballerini et al. [2008]). Thereby, the model sheds light on a potential misinterpretation of the empirical findings. It is not necessary to explicitly limit the number of interacting neighbours to a fixed number for a mechanistic explanation. Instead, variable relative sizes of interaction zones, in combination with a distance-dependent bias in interactions, can result, on average, in topological interactions. Chapter 5 suggested preferential updates as one possible mechanism for how

underlying social networks could be expressed in interactions between individuals. Results show that while this could be a mechanism for hierarchical group dynamics similar to the ones found by Nagy et al. [2010] in pigeons, the underlying social network may be reflected in unexpected ways in the group dynamics. In conclusion, the research in this thesis has suggested a number of mechanisms for different aspects of animal group movement.

The second way in which this thesis aims to contribute to research on animal collective motion is by formulating testable hypotheses. Based on the assumption that update rates of individuals are connected to perceived levels of threat, simulations in chapter 1 predicted that collectively moving groups synchronise and become denser when the perceived threat level increases. These predictions were subsequently tested and confirmed in empirical experiments. Chapter 5 presented detailed hypotheses regarding three aspects of group movement. Simulations were used to illustrate how underlying social networks could impact on the cohesion of groups, the positioning of individuals within groups, and on the hierarchical dynamics within groups. The predictions made are simple and could, in principle, be tested in biological systems with equipment that is readily available. However, the most intuitive way to test the hypotheses requires knowledge of underlying social networks in animal groups. Two out of the three predictions relate to spatial positioning of individuals and this is unfortunately what is often used to construct animal social networks in the first place [Croft et al., 2008, Whitehead, 2008]. Therefore, testing the impact of underlying social networks on animal collective motion is a topic that requires further work (see “Future work” section below). In summary, this work has suggested a number of testable hypotheses for animal group movement phenomena.

Finally, the third way this research aims to contribute to the understanding of animal collective motion is to provide an informed starting point for future research on how underlying social networks could affect group movement. Chapter 4 reviewed the modelling literature on this topic. The aim was to create a conceptual framework and terminology, as well as an introduction to previous theoretical work. In chapter

5 these concepts were put into action by simulating the possible impact of underlying social networks on aspects of animal group movement. The difficulties for empirical tests on this topic have briefly been discussed in the last paragraph. This caveat provides an incentive for initially approaching the impact of social networks on animal collective motion in theoretical work. An improved theoretical understanding of the problem may in the future provide guidance or inspiration for empirical investigation. In this sense, the second part of this thesis provides an informed starting point for further work on the impact of underlying social networks on group movement.

Although the findings and mechanisms in this thesis are often presented in the context of empirical data on specific animal species, the models are general and may be useful in further investigations into the collective motion of other species. The fact that it has been possible to investigate completely different aspects of animal group movement in one, two, and three spatial dimensions simply by extending one conceptual modelling framework supports this notion. Furthermore, the modelling approach has opened up a number of questions for further investigation (see also next section). However, I do not wish to suggest that the modelling framework could be the basis for a universal theory covering all aspects of animal collective motion. Many changes would be necessary to obtain certain features of pedestrian movement, as presented in Moussaïd et al. [2010], for example. In addition, the sensory basis for group movement may vary substantially across different species. For example, the lateral line in fish may influence alignment behaviours (Partridge and Pitcher [1980], Hemelrijk and Hildenbrandt [2008]; see also introduction), while birds may predominantly rely on vision [Ballerini et al., 2008]. The modelling framework presented here generalises sensing abilities and it is not clear whether this is adequate to describe collective motion across species.

In conclusion, agreeing with the approach put forward by Sumpter [2006], we have proceeded on a case-by-case basis to further the understanding of collectively moving animals. The rationale of our modelling approach was to capture generic features,

without attempting to model particular species. Therefore, we have not attempted to fit our models to data - they were not designed to produce meaningful quantitative predictions. Gradually extending the model allowed comparison to previous models at the early stages and highlighted the effect of and reason for each extension. The fact that our modelling framework has produced biologically relevant results across species and spatial dimensions may suggest that there are some basic properties of animal collective motion that are represented in our model, but it does not imply this.

Future work

This section summarises questions that arise immediately from the research in this thesis and additionally suggests avenues for future research leading on from approaches developed here.

An integral part of the modelling framework, developed in chapters 1-3 and 5, is the method of variable update rates and the sampling of information from the sensory zone of individuals. The biological interpretation of these mechanisms has been discussed to some extent above. Here, this is made more explicit.

We have stressed repeatedly that one update step in the model has no direct physical meaning, and that it is the average over a number of update steps that needs to be considered. This can be interpreted as individuals reacting to a dynamic average of information from within their sensory zone. The actions of individuals are subject to stochastic effects which arise from incomplete sampling of their sensory zone and fluctuations in the rate at which they obtain this information. These mechanisms could be investigated with regards to physiological or behavioural properties of animals. For example, in starlings, it has been suggested that vision is the predominant sensory input to achieve flocking (e.g. Ballerini et al. [2008]). It has long been possible to track the movement of human eyes or individual parts of the human body (e.g. Duchowski [2007]). This can be scaled down to allow applications on small and

fast moving animals [Plotkin et al., 2008]. By tracking the eye movements and/or head movements of individual birds in response to visual, possibly simulated, stimuli similar to what they might experience in a flocking situation, it could be tested how birds scan their environment. For example, akin to what we suggest, animals could obtain information by randomly scanning their visual range. Alternatively, information acquisition in animals could be biased in some way or systematic (e.g. scanning of sensory zone could follow a fixed routine).

In chapter 1, we noted that the individual update rates in our simulations are considerably lower than the 0.1 seconds suggested previously (Partridge and Pitcher [1980], cited in e.g. Couzin et al. [2002, 2005]). While this discrepancy is partially mitigated by the fact that we consider averages over update steps, it nevertheless raises the question of how quickly animals can obtain and process sensory information. In general, we might expect that mechanistic properties of the nervous system of animals impose an upper bound for the speed of information intake. Experiments in humans and monkeys suggest, for example, that animals can process complex patterns such as human faces that are presented to them at frequencies of over seventy images per second [Keysers et al., 2001]. Considering that in the fourteen milliseconds between images, neurons can typically produce at most one spike, this is remarkable [Keysers et al., 2001]. In addition, this finding is rather reassuring when considering individual recognition in collectively moving groups, as we have in chapter 5. Further work on the speed at which individuals can detect moving objects could help to establish the limits of data-processing speed in collectively moving animals.

Some modelling studies have distinguished between different individuals in animal collective motion (e.g. Couzin et al. [2005], Hemelrijk and Kunz [2005], Conradt et al. [2009]). However, most theoretical work assumes that individuals are virtually identical [Parrish et al., 2002, Viscido et al., 2005]. Work on animals, that at a first glance may not be distinguishable, such as certain types of fish, suggests that this assumption may be too simplistic. For example, Croft et al. [2009] and Piyapong et al. [2010] investigated personality in guppies. Underlying social networks aside,

the model presented here offers an intuitive and novel way of introducing variation across individuals. Throughout this thesis we assume that all individuals update on average at the same rate. Relaxing this assumption would allow for variable update rates across the simulated groups which could be related to perceived threat levels of individuals (chapter 1) or even personality (e.g. “shy” or “bold” individuals). Furthermore, allowing individual update rates to vary over time, possibly in response to other group members, could be useful to study the propagation of behavioural responses through moving animal groups. For example, if a predator attacked one side of a large group, it may take some time until the entire group not only responds to the threat, but also alters its behavioural state accordingly. This could be detected in localised differences between movement characteristics, such as synchrony of movement or nearest-neighbour distance, across the entire group.

In chapter 4, possible avenues for further work on the effect of underlying social networks on animal collective motion were presented. It is not necessary to repeat this discussion here. Rather, additional aspects leading on from considering social networks in the context of animal movement will be introduced.

The results in chapter 5 illustrate that leadership, in the sense of hierarchical dynamics, based purely on social preferences, is in theory possible. Leadership in animal collective motion has received considerable attention and some of this work has been reviewed in chapter 4 (e.g. Couzin et al. [2005], Conradt et al. [2009], Nagy et al. [2010], Sárová et al. [2010]). In general, the mechanisms and origins of leadership in animals have increasingly been studied [King et al., 2009, Torney et al., 2010]. The specific mechanistic question our work begins to address is: to what extent, and how, is leadership in moving animal groups facilitated by social networks. One anonymous reviewer for chapter 5 commented specifically on the sentence at the start of this paragraph. We were advised that if we wanted to discuss leadership, we should explain how leadership would translate into one of our social networks. The suggestion in the comment was that to model a group with one leader, we should have

implemented a social network in which all individuals have a strong preference for the leader but the leader has no preference whatsoever, and therefore no connection to any other group member. This scenario may be regarded as being paradigmatic for leadership: the leader ignores others in its actions, while the rest of the group follows the leader. However, this is only one possible scenario for socially mediated leadership. One could argue that the scenario in the appendix of chapter 5 is just as intuitive: everyone pays attention to the leader, while the leader spreads its attention equally across the group. This example illustrates that there can be different intuitions about the mechanisms of leadership.

Ultimately, these considerations prompt further questions: how to define leadership in animals, and how leadership could arise in animals. Our model in chapter 5 might be a useful tool to investigate different possible mechanisms, and measurements, for leadership in moving animal groups. The first question that would need to be addressed is how to measure leadership. Hierarchical dynamics are one way of measuring leadership, spatial positioning within groups may be another way. Different measurements could be interpreted as different definitions for leadership. Mechanisms could include physical, motivational or knowledge-based differences between individuals, as well as differences in the position of individuals within underlying social networks [King et al., 2009]. In animal groups a combination of the aforementioned mechanisms may be at work. Simulating different mechanisms separately, or in combination, would provide a useful baseline for comparison with empirical data.

The impact of the environment on the movement of animal groups has been modelled to some extent. For example, Wood and Ackland [2007] introduce food items for foraging swarms, Liu et al. [2008] consider nutrient profiles, and Reynolds [1987] include obstacle avoidance in individual behaviours. Hemelrijk et al. [2010] include interactions of fish with tank boundaries in their model but they do not investigate the correctness of the assumed interactions using their empirical data. Overall, it is noticeable that most studies on animal collective motion are conducted in homogeneous environments with no barriers or other features affecting the movement of

individuals. In particular, interactions of individuals or groups with obstacles such as tank boundaries are rarely investigated. However, in studying animal social networks, and therefore spatial associations of individuals, the impact of interactions with the environments may become important. Consider, for example, the construction of a social network in animals that depend on localised food sources. If spatial associations in groups of such animals were to be sampled, the result could be a network reflecting which animals feed together rather than which animals have social preferences for each other. Individuals at localised food sources may even compete, resulting in strong individuals competing at high quality food sources, irrespective of their social preferences. In a different example, consider a population of fish living in two ponds that are connected by a narrow stream. Social preferences in a random sample from the entire population may show a clear separation into two subgroups that could be entirely due to low mixing between the sub-populations in the two ponds. These conceptual examples demonstrate that there is a need to consider the impact of the environment on animal movement in the context of social networks.

Closing remarks

From biologists, via physicists, to computer scientists and engineers, a large and diverse group of scientists continues to study, and take inspiration from, animal collective motion. The future for this subject seems to be bright, not only for further scientific investigation, but also for applications in different contexts. Already, applications for the theory of collective motion have been found in pedestrian flow control and the prevention of crowd disasters (e.g. Helbing et al. [2007]). Within the next decade, the first fully functional swarms of robots may operate outside laboratory environments. In biology, smaller and better tracking devices are likely to result in an increase in data and thereby knowledge of biological systems. This may ultimately enable scientists to make specific and detailed recommendations on conservation policies and pest control, for example.

Finally, I would like to express my hope that the research presented here will

inspire further investigation. In particular, I believe that the ubiquitousness of both animal social networks and collective motion merits the study of both topics in combination.

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