

CHAPTER 1

Introduction

“The purpose of models is not to fit the data but to sharpen the questions.”
Samuel Karlin, (1923-).
11th R. A. Fisher Memorial Lecture, Royal Society 20, April 1983.

Issues that are relevant to the collective movement of animal aggregations are discussed (both of a biological and mathematical nature). Previous work in the area and other related literature are reviewed.

1.1. General animal behaviour and movement

Collective behaviour of animal groups has long since engaged humankind's imagination. This is reflected in the descriptive names given to groups of specific animals; a murder of crows, a pride of lions, an ostentation of peacocks and a gaggle of geese, for example.

Aggregative behaviour occurs in a diverse range of animals, on different physical scales. Small and uncomplicated entities (such as bacteria) form groups, as do larger animals (such as dolphins and whales) who tend to form groups with complex social structures. Animals form groups of various sizes. At one end of the scale, African army ant colonies (*Dorylus (Anomma) nigricans*) raid in swarms composed of millions of workers. Conversely, killer whales (*Orcinus orca*) tend to hunt in pods of smaller numbers. Between these extremes, lie the more common social animal groups - herds, swarms, flocks and schools (ungulates, insects, birds and fish, respectively).

In this thesis, we shall consider swarms, flocks and schools. All these groups have one property in common; these groups consist of individuals that interact with their neighbouring members in three-dimensions, yet those same individuals only contribute by a small amount to overall group dynamics. The numerous social interactions that bind individuals to one another within these groups are of particular interest.

Animals form groups for numerous reasons. A large group offers protection from predators, because living in larger numbers lowers the chances of being caught. In addition, large groups can perform organised evasive manoeuvres to outwit a predator. These evasive actions include groups splitting up instantaneously into individuals, or forming tightly-knit ball shaped clusters. Both are designed to confuse a predator's senses. Highly coherent, aligned arrangements of individuals offer obvious aerodynamic or hydrodynamic advantages when travelling over large distances, which result in energy savings for the

group members. Other advantages of living in groups include socialising, convenience in mating and more efficient foraging (Parrish & Edelstein-Keshet 1999, Krause & Ruxton 2002).

The behavioural interactions of individuals within congregations may be classified in two ways. Firstly, an individual may have short range reactions that modify their situation relative to their neighbours. Secondly, behavioural responses that may not improve the individual's situation relative to its immediate neighbours, but contribute to group-level characteristics. These will benefit the individual by benefiting the group as a whole.

In the remainder of this section, we will discuss the animal groups most relevant to the work presented in this thesis, honeybee swarms and fish schools.

1.1.1. Honeybee movement and swarming. Honeybees (*Apis mellifera*) live in one of the most highly ordered type of societies within the insect world.

A typical honey bee colony consists of approximately 25,000 adult female worker bees, 1000 or more male drones and a single queen. Drone bees are male and are only used for mating, whilst the tasks of the female worker bees are varied. They include building the honeycomb, cleaning the colony, feeding the queen and drones, guarding the hive, rearing the young, and collecting food. Eventually workers take on the role of scouts and search for food sources or, occasionally, new hive locations.

The ability of individual bees to communicate is essential to maintaining the honeybees complex society. Honeybees communicate amongst one another in a variety of ways. Pheromones are a key method of communication within the colony. The queen uses a variety of pheromones to inhibit the development of workers and the production

of new queens, to attract drones during mating, to control the onset of swarms and to control the nurse bees that look after her. Workers use pheromones as alarm signals and to aid recruitment. Auditory cues are also employed in communication amongst workers, via vibrating wing muscles (Gould & Gould 1988). Visual cues also play a role in the communication process, notably during flight (Beekman, Fathke & Seeley 2006) and in the waggle dance (von Frisch 1967).

Honeybees communicate information about food sources and, of particular relevance for this thesis, prospective nest sites to other members of the colony using the waggle dance (Seeley 1995). The waggle dance consists of a series of waggle runs, followed by a semi-circular return. The direction of the waggle run is related to the gravitational axis and the sun's position relative to the direction of the point of interest. The duration of the waggle run is correlated with the distance from the hive to the point of interest. The duration of this dance is also correlated with the quality of the new home site. There are other factors of the dance also associated with quality. This information is used by the dance-following bees when searching for the advertised area. The more vigorous and longer the dance, the more followers it attracts (de Vries & Biesmeijer 1988).

Honeybee colonies reproduce collectively by splitting into two parts. Half of the colony of bees leaves the hive and settles in a temporary cluster, while scout bees search for a suitable place for the colonies' new home. If a scout finds an appropriate nest site, she returns to the swarm and tries to recruit other scouts to visit the site, communicating the location and quality of the new site with the waggle dance. Eventually one site is selected as the most promising and the scouts stimulate the rest of the swarm group to flight and guide the group to the new home (Seeley 1998, Seeley & Buhrman 1999, Myerscough 2003, Donahoe, Lewis & Schneider 2003, Passino & Seeley 2006).

Of particular interest to researchers is the process that these scouts use to guide the swarm to the new nest site. In a swarm of approximately 10,000 bees, approximately 5% are scout bees and these scout bees are responsible for guiding the migrating swarm toward the new home (Seeley, Morse & Visscher 1979). The rest of the swarm members are ignorant of the whereabouts of the new home.

One possible mechanism for swarm guidance is for the scouts to fly continuously through the swarm, with their flight paths aligned toward the direction of the new home. This suggested mechanism follows observations that some bees fly rapidly through the swarm, ‘pointing’ in the direction of the new home (Lindauer 1971, Janson, Middendorf & Beekman 2005, Beekman et al. 2006).

1.1.2. Fish schooling. There are more than 4000 species of pelagic fishes that form groups, called schools. Given that large numbers of fish species congregate, this suggests that schooling offers considerable evolutionary advantages when compared to solitary behaviour.

Fishes form schools for various reasons (Stöcker 1999), albeit with less complex societies than those of the honeybee. Most school forming fish are small in physical size and are identical physically. Swimming in a school reduces the probability of an individual being caught by a predator. Predators find it difficult to single out an individual from the school, due to quickly moving, small, identical neighbours. If the predator succeeds in isolating a single food item, movement from other potential prey close by can distract the predator. Aggregation allows the school collectively to perform a variety of evasive tactics to confuse and avoid a predator. Swimming in a school also can result in significant energy savings, due to hydrodynamical advantages of streamlining. There are also social advantages to schooling, such as increased chances of finding a mate. Foraging is made easier. Schooling fish can

more easily adjust foraging behaviour in response to changes in availability of food sources and scarceness of food items. With more sensory organs involved in searching, the likelihood of finding food sources is increased.

Examples of coordinated behaviour in schools include various elaborate patterns (Parrish, Viscido & Grünbaum 2002). Fish may split apart simultaneously from the group (termed *flash expansion* or *explosive* behaviour in literature). Schools may form hourglass shapes, ball shapes and fountain patterns (where the school splits up around a predator and can regroup once safe), all designed to confuse predators. However, the predators themselves may employ schooling tactics to facilitate the process of catching prey; for example, several predators may cooperatively herd the school.

People have long been fascinated by the beauty and complexity generated by the coordination of fish within schools. Parr (1927) and a more extensive study by Breder (1951) are amongst the first to study the structure of these fish schools. The latter study of Breder (1951) investigated in detail the responses to the structure of the school from both internal and external stimuli. The particular relevance of this paper is that it was one of the first to suggest that internal responses within the fish school could be simplified as attraction and repulsion behaviours. Many models of collective behaviour (including the models presented in this thesis) use these two behavioural responses as a basis for interactions between group members.

Partridge (1982) investigated the maintenance of the structure of schools. The author discovered that the schooling fish maintained their position within the school by use of vision and the lateral line (an organ in each fish sensitive to vibrations in the water). The paper discusses the structure of the school as varying in a probabilistic sense, and not being fixed as a regular geometrical structure. Partridge (1982)

also postulated that the school structure results from each fish applying simple behavioural rules, attraction and repulsion (Breder 1951), coupled with a preferred distance and orientation to neighbours (an alignment behaviour). We also incorporate alignment interactions in the mathematical models presented in this thesis.

1.2. Mathematical modelling of biological systems

Biological processes represent a rich and diverse area of application for mathematics. No matter how varied the types of mathematical models, they have a common agenda of providing insights into biological phenomena, either in a predictive or explanatory sense.

Theoretical models provide an interface between the reality of a situation and theories of how that situation arises. Researchers gain insights by understanding and manipulating theoretical models.

Mathematical models are an alternative to real life experimentation. They are designed not to supplant biological experiments, but to complement them. Models can be advantageous in certain circumstances where there are constraints on experimentation. These constraints can include logistics, finances and ethics. Mathematical modelling can either reduce, or even sidestep these issues. Indeed, within the context of this thesis, we shall see that there is a lack of real data concerning movements of animal groups of large sizes, mostly due to practical constraints. We generate artificial data from our mathematical models and use this data to assess the validity of certain real-life hypotheses. Models help overcome this shortfall by allowing researchers to perform tests or observations that would otherwise be impossible. Most importantly, models provide total control of the system under examination and allow researchers to manipulate the system in ways that may be disastrous or impossible in real experiments.

Turchin (1998) discusses essential procedures in the formation of a mathematical model to describe biological phenomena, although the ideas also hold true generally for non-biological mathematical models. The first step in developing a mathematical model is typically creating a formal statement of the problem under investigation. This allows the identification of unknown areas, usually in terms of various functions and parameters. Once the model is formulated, researchers can quantitatively test the theory by manipulating the model. This provides a feedback mechanism, whereby researchers can modify the background theory. Once the model is deemed suitable, the model can be used to forecast or predict changes in the biological system.

What type of theoretical models are available to model biological behaviour? The two most obvious categories of models are deterministic and stochastic (Turchin 1998). Animals tend to have irregular elements to their movements. Even if we assumed these animals acted strictly upon environmental cues and in conformity with behavioural rules, researchers cannot have complete knowledge of the deterministic rules governing individuals. Therefore, it makes sense to model systems with a stochastic component that encapsulates information that researchers are either unaware of, or consider to be insignificant. When it is impractical or inaccurate to model such systems deterministically, a parsimonious probabilistic model may be a better approach.

Mathematical models may be classed as either Eulerian or Lagrangian. A Lagrangian approach focuses upon individuals coordinates (positions and velocities) within the system. An Eulerian approach adopts a more holistic approach, in that it considers the density of a population over space at a particular time. Traditionally, Eulerian models have been favoured, as they lead to well-studied partial differential equations (Okubo 1980). Eulerian approaches are well suited for movements of large groups (bacteria, some insects, etc), but are

less suitable for movements of animal groups consisting of relatively small numbers of individuals. The Eulerian approach does not lend itself easily to incorporating social interactions (Couzin & Krause 2003). Lagrangian approaches are currently gaining favour, as they allow researchers to specifically incorporate the social forces that individuals within a system are subject to. The drawback in Lagrangian modelling lies in its individualistic nature. Little general theoretical progress is made with these models, because it is difficult to compare different Lagrangian models devised for different systems (Turchin 1998).

Simulation modelling has recently become of interest to researchers as a tool for studying animal movement. Examples include Couzin, Krause, James, Ruxton & Franks (2002), Couzin, Krause, Franks & Levin (2005) and Janson et al. (2005). Simulation within the context of this thesis, is defined as the creation of an artificial world that is constructed ‘in silico’, using computer programmes to represent biological processes under study (Peck 2004). Simulation models can be properly investigated with the same experimental and statistical techniques that are used to analyse real biological phenomena. Designing a proper simulation requires researchers to closely represent the biological system being studied, handle the higher dimensionality of the parameter space and conduct a sensitivity analysis to determine how the model parameters affect the entire system. By performing large scale simulations statistical properties and dynamics can be investigated. If sufficient simulations are obtained, the resulting behaviour can be determined effectively free from sampling error.

Unlike traditional statistical models, it is not always possible to fit simulation models to real data. Instead, simulation models tend to incorporate information from previous studies during the construction phase. Simulations enable researchers to gain insights into future data gathering, explore hypotheses that would be difficult to test otherwise

and provide information about relationships within the system that is represented by the model (Peck 2004).

1.2.1. Mathematical modelling of animal movement. Modelling animal movement has interested mathematical biologists since the early twentieth century, see eg. Lord Rayleigh (1919). The dynamics of social animal aggregations has been examined more extensively from the late 1970s.

Early models focus on the dynamics of movement governed by the Newtonian equations of motion. In particular, the second law can be interpreted as mass multiplied by the acceleration of an individual is equal to the total force exerted on that organism by environmental and behavioural factors (Okubo 1986, Warburton & Lazarus 1991, Niwa 1994, Grünbaum & Okubo 1994, Niwa 1996). Typical forces affecting individuals include locomotory, social (attraction, repulsion and alignment), environmental and forces that vary randomly in time or are randomly oriented or are not attributable to known mechanisms. Most of these forces tend to be dependent on the distance separating individuals and the relative orientation of individuals to one another. An alternative approach to Newtonian mechanics and Hamiltonian formulations is to model individuals within aggregations with individual components that either maintain constant forward motion during discrete time intervals, or take discrete spatial steps, see eg. Huth & Wissel (1992) and Couzin et al. (2002).

Individuals within a group are subjected to external stimuli in their daily lives (usually of an environmental or a predatory nature), which causes the group to react as a whole to this stimuli. Beecham & Farnsworth (1999) formulate a model for animal groups that incorporates external effects of resource availability and predation risk, in addition to social forces, and use this model to explain animal spacing within a group.

An Eulerian framework for social animal aggregations leads to a spatial-temporal distribution of animal density. The change in animal density is modelled as the density flux at a certain point in space and time in a population of individuals, who respond to neighbours in an individual-centred domain according to some behavioural algorithm. The derivation of many Eulerian models is via the Fokker-Planck equation (Okubo 1986, Grünbaum & Okubo 1994). This stochastic differential equation (also known as the Kolmogorov Forward equation) describes the time evolution of the probability density function of the position and velocity of a particle, see eg. Balescu (1975). Alternative approaches to the Fokker-Planck equation include casting animal movement in the guise of an advection-diffusion-reaction equation (Shigesada & Teramoto 1978, Okubo 1980, Mimura & Yamaguti 1982, Dal Passo & de Mottoni 1984). Turchin (1989) considers models where individuals undergo random walks that have bias towards neighbours, leading to a diffusion-type equation. This approach assumes that individuals do indeed undergo random motion and is difficult to incorporate inter-individual interactions.

Another viable approach is to transform the population distribution from a Lagrangian model to an Eulerian equation (Grünbaum 1994, Flierl, Grünbaum, Levin & Olsen 1999, Mogilner & Edelstein-Keshet 1999). Most Eulerian descriptions are based on heuristic interpretations of Lagrangian algorithms. The Fokker-Planck approximation is commonly used, by relating the distribution of distances travelled by individuals to terms in the stochastic differential equation (Flierl et al. 1999, Okubo & Levin 2001). Grünbaum (1994) derives a non-linear partial integro-differential equation, by assuming that the individuals in a Lagrangian model are distributed as a Poisson point process.

Collective motion in a biological system can be interpreted as a multiparticle physical system. Models of ferromagnetism lend themselves as models of collective motion, ferromagnetic interactions can be interpreted as social interactions. Vicsek, Czirók, Ben-Jacob, Cohen & Shochet (1995), Albano (1996) and Czirók, Barabási & Vicsek (1999) present examples of this type of model. While the first two papers consider two-dimensional models and the latter one-dimensional, these models all consider the motion of self-propelled particles, which orient themselves according to the average direction of a local neighbourhood. Albano (1996) extended the model by Vicsek et al. (1995) with the addition of birth and death terms, thereby modelling population dynamics. All these papers observe transitions from disorganised states to organised ones, where individuals are aligned with one another. We employ orientation within local fields as part of a three-dimensional model in Chapter 5 and observe transitions through these states.

While the Fokker-Planck equation arose in response to Eulerian descriptions, stochastic differential equations (SDE's) by themselves provide an alternative approach to modelling collective motion. Alt (1995) examined desert crustaceans displaced from their homes, and their attempts to relocate their homes. The author used a SDE to model the angular turning rates of individuals in his model. He concluded his results showed that crustaceans need only use their instantaneous linear and angular velocities, coupled with their expected position further along their ideal path, to successfully relocate their home.

Brillinger, Preisler, Ager, Kie & Stewart (2002) and Bengtsson, Rydén, Öhrn & Wiktorsson (2002) use vector SDE's to model wildlife motion. The former paper models motion in three-dimensions, on the surface of a sphere and within a plane. Bengtsson et al. (2002) discusses four related SDE's, all based on a plane where individuals are constrained to move within a circle, using reflective boundaries. Both

papers use drift terms in their SDE's to model social forces of attraction and repulsion. Bengtsson et al. (2002) include synchronised diffusion terms, designed to model alignments of individuals. This is not a feature of the models in Brillinger et al. (2002), as the authors are dealing with animals that are solitary by nature. We will include distinct alignment terms in our models, particularly in Chapter 5. Bengtsson et al. (2002) include social and anti-social terms to model switches between gregarious and solitary states amongst the insects that they model.

Both articles use statistical methods to estimate parameters in their models, and in the case of Bengtsson et al. (2002), assess the best fitting model to their data. Brillinger et al. (2002) have access to data on the movements of elk within forests, while Bengtsson et al. (2002) examine the movement of soil-living insects within a jar. Unfortunately, we do not have the luxury of real data available for the models presented in this thesis and can't estimate model parameters from data. Wiktorsson, Rydén & Bengtsson (2004) follow up their previously discussed model (Bengtsson et al. 2002) by using a bi-variate autoregressive model with a reflective boundary to model the movements of soil-living insects.

The mathematical models discussed thus far are generally formulated for two-dimensional movement, which is an adequate assumption for herds moving on land. Fish schools, insect swarms and bird flocks move and interact in three dimensions. The assumption for these groups that interactions in one particular dimension are negligible (and therefore rescaling to two or one dimensions) is not so easily justified. By reducing the number of dimensions in the model, the individuals in the group will have effectively less neighbours to interact with. Models with interactions in three dimensions are biologically more realistic for our situation. In the past, higher-dimensional models have been restricted due to the available computing technology. With current advances in technology, this barrier is now negligible.

Reynolds (1987) was the first author to simulate the motion of flocks and schools within three-dimensional space. The author showed how local interactions between individuals can lead to realistic collective behaviour. Reynolds (1987) used a simulation model based on behavioural rules, physical laws and environmental interactions, to produce polarised non-colliding aggregative behaviour. The author concluded this led to realistic ‘flock-like’ motion.

Couzin et al. (2002) considered aggregative animals in three dimensions. The authors use a Lagrangian model based on social forces, which are derived from ideas of papers such as Reynolds (1987), Czirók et al. (1999), Huth & Wissel (1992) and others. Couzin et al. (2002) assume that individuals within a group are subject to simple local behavioural rules of attraction, alignment and repulsion, dependent on an individual’s relative position and velocity in the group. Errors in an individual’s decision-making are simulated by introducing stochastic effects to the model. The effects of the individuals’ reactions are cumulative and lead to realistic group behaviour, depending on certain parameters of the model. The authors demonstrate that their model retains a form of collective memory, where the previous history of the group structure influences the current formation (despite no group members having a complete personal knowledge of that history).

In order to model traffic flow of army ants (*Eciton burchelli*), Couzin & Franks (2003) use a two-dimensional variant of Couzin et al. (2002) with two types of repulsion zone, one based on visual stimulus and the other on touch. Instead of using attraction and alignment forces, the individuals in their model respond to a pheromone stimulus. Couzin & Franks (2003) show that ant trails formations can be maintained by local repulsive interactions and a desire to follow the pheromone concentration to a goal.

Couzin et al. (2005) extend the model in Couzin et al. (2002) to investigate mechanisms for directed motion of large aggregations by a small number of group members, who are privy to information regarding the location of some goal. The authors demonstrate that the knowledgeable members are able to influence the travel paths of the ignorant individuals without transferring information by explicit signalling or complex mechanisms. Guidance arises purely from the information difference. Their simulation indicates that informed and naive individuals need not differentiate between one another, and no inherent differences amongst individuals in the group are required to explain leadership (except for the possession of information regarding the whereabouts of the goal).

Parallel work into directed motion of aggregations has been conducted by Janson et al. (2005), who base the rules of interaction in their Lagrangian model on similar behavioural rules to those used by Couzin et al. (2002). Janson et al. (2005) allow their knowledgeable group members to move through the group, repeatedly flying in the direction of the goal. The authors compare the relative velocities of the knowledgeable and naive members and find the informed members only need to fly with a speed marginally greater than the ignorant mass, to successfully guide the group. The proportion of knowledgeable members required for adequate guidance is shown to be relatively low.

1.3. The how, where and why of self-organisation

In a heuristic sense, a system is considered ‘self-organising’ if it becomes more organised, without external influences assisting the process. A more precise definition can be found in Camazine, Deneubourg, Franks, Sneyd, Theraulaz & Bonabeau (2001). Initially, the authors

define the term ‘pattern’. A pattern is a particular, organised arrangement of objects in space or time. The pattern is a property emerging from the internal dynamics of the system, rather than one being imposed by an external ordering influence.

Self-organisation is a process whereby the pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of the system. Moreover, the rules specifying interactions among the systems’ components are executed using only local information, without any reference to the global pattern (Camazine et al. 2001).

Even with a full knowledge of the components of the system and the interactions between these components, the pattern resulting from self-organisation cannot be deduced, implying that there is something more complicated than simple additive interactions occurring (Anderson 2002) and that nonlinear effects may be important.

The beauty of self-organisation theory lies in its simplicity. Complex group behaviour may be produced by relatively simple interactions among group members (Couzin & Krause 2003). The challenge is to try to understand how the individual components of the system interact to produce complex patterns. The multiplicity of interactions that characterise self-organising systems show that such systems are dynamic and require continual interactions amongst the lower-level components to produce and maintain structure.

Biological systems that use self-organisation usually have a large number of individuals, and these individuals lack either the computational or communicational ability (or both) needed to implement centralised control. Individuals in self-organised systems need not have a low intelligence. The individual’s society may simply lack an extensive communication network that is required to maintain some form of centralised control (Seeley 2002).

Self-organisation requires several dynamical mechanisms in order to be effective. Positive feedback is one requirement. This can manifest in recruitment and reinforcement. Recruitment to a food source is a positive feedback that relies on trail laying and trail following in some ant species, or dances in honeybees (Camazine et al. 2001, Beekman, Sumpter & Ratnieks 2001, Beekman, Sumpter, Seraphides & Ratnieks 2004). Negative feedback may be required to counterbalance excesses of positive feedback and stabilise the overall system. It may take the form of exhaustion, saturation or competition. Randomness is often crucial, as it enables the discovery of new solutions and can act as the initial condition for new structures to be created (Bonabeau, Theraulez, Deneubourg, Aron & Camazine 1997).

There are alternatives to self-organisation for organising a biological system. Camazine et al. (2001) propose four other mechanisms for group organisation. A leader can direct the actions of the group, providing each individual with instructions on how to contribute to the overall pattern. The group may use a blueprint, a compact representation of the spatial and temporal relationships of the pattern. Each member of the group may have access to a recipe, a set of sequential instructions that precisely specify the spatial and temporal actions of an individual's contribution to the whole pattern. Finally, a template may be employed, a guide or mould that specifies the end result or goal and strongly directs the pattern formation (Cox & Blanchard 2000). It is also possible for animal groups to employ combinations of these methods.

So why should self-organisation be sometimes preferred over these alternative means of pattern formation in biological systems? Self-organisation may occur because a system is unable to evolve mechanisms of communication and computation to support the other four options (Seeley 2002). Self-organising systems can also arise because they

are more flexible to positive changes and robust to negative changes, than systems using the alternative methods.

Self-organisation is not necessarily always the best way of coordinating components in a system. With no central authority, the self-organising system is prone to opposing actions amongst its members, as they respond to different local conditions. Needless redundancies can arise, due to these unchecked actions (Seeley 2002).

The concept of self-organisation dates back to the mid twentieth century (Sumpter 2006). Self-organisation was first used in physics and chemistry to explain how microscopic processes can give rise to macroscopic structures in complex systems. Chemists are interested in building evermore complex molecules. Self-organisation may be the most realistic process to create these molecules (Lehn 2002*a*, Lehn 2002*b*). Self-organisation has been suggested for the mechanism that is responsible for initiating life on the planet (Burger 2003). Some works of popular fiction have used self-organisation in their plot (Fabi 1998, Crichton 2002). Self-organisation has also been used by biologists to describe group phenomena (Gerhard & Kirshner 1997, Maini & Othmer 2000, Camazine et al. 2001, Couzin & Krause 2003). Recent research suggests that this concept can be extended to ethology (study of animal behaviour) and that it provides a concise description of a wide range of complicated phenomena in animals (Bonabeau et al. 1997, Holland & Melhuish 1999, Kube & Bonabeau 2000) and humans (Sumpter 2006).

There are similarities between self-organising biological systems and artificial systems that interest roboticists (Arkin 1998, Wilson, Melhuish & Sendova-Franks 2004). In the field of behaviour-based robotics, studies of animal behaviour are of particular interest. Aggregative animal behaviour interests researchers who are concerned with the coordination and control of multi-agent robot teams (Muhammad &

Egerstedt 2003). A multi-agent team consists of identical individual robots that have limited sensory capacity of their own, much like the individual animals in aggregations. Lewis & Bekey (1992) discuss the possibility of using groups of nanorobots governed by a self-organising process to remove cancer cells from the human brain.

Vaughan, Sumpter, Henderson, Frost & Cameron (2000) provide a particularly relevant example of roboticists employing self-organising behaviour. The authors use the idea of a sheepdog shepherding a flock of ducks as their motivation to test a model of flocking behaviour. Vaughan et al. (2000) constructed a mobile robot to take the place of the sheepdog and tested this robot dog on real and artificial ducks. The authors postulated that simple rules of attraction and repulsion, similar to the behavioural rules in Couzin et al. (2002), would be adequate to simulate the real system. The robot dog was able to successfully guide the real and artificial flocks to a predetermined goal. The authors conclude that behavioural simulations (of flocking behaviour) are useful design tools for engineering problems.

Conversely, robot models have been effective (as an alternative to computer simulation) for investigating collective animal behaviour (Webb 2000). The rules that simple autonomous robot systems obey give biologists insights into interactions occurring in the natural processes and systems under their study. Whilst robot experiments may be more complex to simulate (compared with mathematical models), they can offer insights from a practical point of view (Webb 2000).

Biological organisms have often been used as a base for designing solutions to engineering problems. Self-organisation is useful in exploring human behaviour in crowds, where traffic flow results from interactions between pedestrians (Couzin & Krause 2003). Emergency situations, such as evacuations, benefit from mathematical models of collective motion. Helbing, Farkas & Vicsek (2000*a*) and Helbing, Farkas & Vicsek (2000*b*) studied collective models where individuals have restricted

information and respond to the motion of their neighbours. The authors found that increases in stochasticity and individual velocities (understandable in a psychological sense in panicked situations) result in longer evacuation times. This is useful information for engineers and those responsible for designing buildings and public areas.

1.4. Overview of thesis

This thesis is designed to formulate and examine mathematical models of mass movements of self-organising groups, consisting of similar individuals. In particular, we apply these models to explain behaviour amongst social insects, especially the common honeybee (*Apis mellifera*) beloved by apiarists and consumers of honey alike.

As part of this study, we will be interested in evaluating data in the form of a set of directions in space. Chapter 2 presents relevant statistical tools for the analysis of directional data. These include various descriptive statistics and hypothesis tests. These tools will be used in subsequent chapters to analyse the results of models of collective behaviour.

During the course of Chapter 3, a model of self-organising aggregative behaviour is formulated to explain movements of animal groups *en masse*. This model is based on Couzin et al. (2002). The behaviour of individuals within this model results from numerous repulsive, attractive and alignment interactions. Various aspects of the simulation of this model will be investigated using some of the statistical tools of Chapter 2 and the role of the model's parameters will be considered.

The model discussed in Chapter 3 will be adapted in Chapter 4 to explore the mechanism of honeybee swarm migration. Certain individuals with prior knowledge of a goal position will be shown to influence the other members of the group and guide them to this goal. This

section will rely on the directional tests developed in Chapter 2 to assess the ability of the knowledgeable individuals to influence the group members to make a beeline for the goal. Parts of Chapters 2 and 4 are closely based on Merrifield, Myerscough & Weber (2006).

The penultimate chapter involves a second model for aggregative behaviour. A different approach is adopted, which uses concepts from physical theory. Social forces are modelled on ideas from the theory of the behaviour of particles in gases and plasmas. While repulsive and attractive social forces have been considered in previous literature, the implementation of an alignment force and the requirement for a dissipative force are innovative. Chapter 5 involves formulating and simulating this physical model.

Appendix A contains definitions of selected symbols used throughout this thesis and Appendix B contains selected proofs. During this thesis, descriptive comments and terms are used to describe the behaviour of individuals in the models. These terms are merely a convenience and should not be read as implying ‘consciousness’ of decisions.