

CHAPTER 6

Conclusions

This thesis is concerned with mathematical models of co-ordinated movement of groups of similar individuals, particularly those of social animals. These types of systems are becoming increasingly important in non-biological fields, such as robotics. Mathematical modelling is a practical tool in the development of this field.

Self-organisation is the critical mechanism by which collective behaviours of these animal groups result. It has been shown in past literature (Czirók et al. 1999, Couzin et al. 2002, Janson et al. 2005) that interactions between group members, which are of repulsive, alignment and attractive natures, lead to the observed global behaviours.

Before the models for collective movement were discussed in this thesis, we introduced statistical tools in Chapter 2 for analysing samples of directional data. These tools are important because the results of the mathematical models are primarily sets of three-dimensional trajectories. Key descriptive statistics include polarisation (measuring the degree of alignment amongst group members), momentum (which measures the amount of rotation of the group) and average group direction. We also introduced statistics to measure the relative size of the group (nearest-neighbour distance and group expanse) and to measure the curvature of the path that an individual takes during the course of the simulation (net to gross displacement ratio). The spherical correlation coefficient is introduced to quantify the association between two directional samples.

We proposed the use of spherical hypothesis tests, originally formulated in Watson (1983*b*) mainly for the analysis of geological data, for analysing the samples of trajectories. The first inference test assesses whether one sample of directions can be considered as having a particular common direction. The second compares different collections of directional samples to see if they can be regarded as sharing a common average direction. The final test compares two sets of directional samples to see if they can be considered as having the same polarisation.

Part of the aim of introducing these tests is to raise awareness amongst the community of researchers interested in collective animal motion to the existence and efficiency of these techniques.

In Chapter 3, we discussed a Lagrangian self-organising model for collective movement, based on the principles from Couzin et al. (2002). The collective motion model uses repulsive, attractive and orientative interactions amongst neighbouring individuals. These interactions are modelled as a nested set of spherical volumes around each group member. An individual's reactions are in accordance with the presence of neighbours in these zones. We introduced random effects to the collective motion model, using a Fisher distribution. The direction of travel of each individual, which is initially modified according to social interactions, is perturbed by an angle drawn from this Fisher distribution.

Specific types of behaviour resulting from the collective motion model were discussed, in particular; swarm, dynamic parallel and highly parallel behaviours, these were observed by Couzin et al. (2002). These behaviours can be characterised by descriptive directional statistics from Chapter 2 (particularly, polarisation and momentum) and we use these statistics accordingly in Chapter 3. The type of behaviours resulting from the collective motion model largely depend on the relative ratios of the spherical volumes around individuals (the repulsion, alignment and attraction zones) and we showed what the consequences are for different combinations of interaction zones.

The impact of other collective motion model parameters were assessed. A decreased zone of repulsion for all individuals in the model allows individuals to move closer to one another and experience stronger alignment forces, so that aligned groups result. In contrast, Couzin et al. (2002) assigned different zones of repulsion to different individuals in their model and showed that individuals with smaller zones of repulsion move to the front of the group. An individual's ability

to change its current direction of travel is governed by the maximum turning angle. We showed that low turning angles impede this ability, resulting in swarm conditions. A conical blind volume exists behind each individual, controlling the relative number of neighbours that an individual can interact with. We have shown that with an increasing blind volume, individuals become more and more oblivious to neighbouring group members and the group behaviour changes from a cohesive parallel arrangement, to a disorganised swarm. This agrees with the results of Couzin et al. (2002), who also mention that torus behaviour is likely to result from a decreased field of perception. This is because individuals are less likely to align with the neighbours behind them. We discussed stochastic effects in the collective motion model. Variation in the stochastic effect is controlled by the concentration parameter. A decreased concentration parameter causes increased randomness and a transition from an organised group to a swarm. We showed the threshold where this occurs is when the concentration parameter is around 50. Above this threshold, individuals still retain some ability to self-organise.

Couzin et al. (2002) introduced inhomogeneous speeds to different individuals in their model and showed that speed differences explain the positioning of individuals within the group. We partitioned our individuals into two relative speed categories, fast and slower individuals. When the group is composed of a low proportion of fast individuals, the two types of individuals formed two separate distinct groups consisting of polarised individuals, these two groups orient to one another. As the ratio of fast to slow individuals increased, the two groups of faster and slower individuals ignore each another and travel in different directions. This indicates that for successful leadership or group guidance mechanisms based on speed differences, low proportions of fast moving individuals are required.

Having gained a greater understanding about the collective motion model, we were able to turn our attention to adapting this model for use in Chapter 4. We were interested in the directed motion of a group under the influence of a few select individuals who were privy to information regarding some goal. This is particularly applicable to leadership mechanisms of swarms of migrating honeybees. We have allowed a prescribed number of knowledgeable individuals (otherwise indistinguishable from the naive group members) to travel through the collective motion model, ‘pointing’ in the direction of the goal. We simulated this directed motion model and used the descriptive statistics and hypothesis tests from Chapter 2 to analyse the results.

We have two versions of the directed motion model, one where the knowledgeable individuals are present from the start of the simulation and one where the knowledgeable individuals are introduced after some delay to the already organised group. Using the tools from Chapter 2 and considering the actions of the ignorant group over time, we showed that the mechanism of ‘pointing’ knowledgeable individuals is plausible for successful guidance of the ignorant group in most of these scenarios, a conclusion also reached by Janson et al. (2005). This backs up experimental observations (Beekman et al. 2006) that the main trigger causing honeybees to organise in this way is visual. Individuals, whether in a honeybee swarm or cyberspace, are able to be guided to a pre-existing goal by a small number of individuals privy to a goal location, who ‘point’ the direction of goal to the rest of the group. This is despite these knowledgeable individuals being identical in all other respects to the naive group members.

We have shown that this mechanism is successful, even with a relatively small percentage of knowledgeable individuals present to guide the group. Janson et al. (2005) predicts that only very small ratios (1%) of knowledgeable individuals are required for successful guidance.

Both our work and Couzin et al. (2002) indicate that these small ratios are inadequate and ratios of at least 4-5% are needed. The knowledgeable individuals must move with a speed at least as large as those of the ignorant group members. Janson et al. (2005) also make this point. Our results show that speeds slightly slower than the naive members' speeds may also be effective. We show that the success of the guidance depends on the distribution of the knowledgeable individuals throughout the cross-section of the group. The successful distributions are ones where the knowledgeable individuals are distributed in some way through the middle of the group. Configurations where individuals are positioned on the periphery of the group are less effective. Errors in decision making have a large impact on ignorant individuals' abilities to react to the knowledgeable members; even small stochastic effects cause the organised state of the group to be disrupted. This suggests that randomness amongst the actions of honeybees in swarms proves to be ineffective in aiding scout bees to guide workers to a new location.

Future work to improve the directed motion model includes incorporating more complicated actions on the part of the knowledgeable individuals, by allowing them to move away from a rigid travel path (adopted in this thesis for modelling convenience) and to have the ability to travel with the ignorant group. Another improvement is to allow the individuals to have a more complex mechanism to move to the rear of the group, once they have moved past the group front. The aim of the directed motion model is to show that guidance by 'pointing' knowledgeable individuals is a plausible theory. It is hard to model this situation in all its detail and so researchers will need to assess whether the expected gains of a more complicated model are worth the effort.

Chapters 3 and 4 involve Lagrangian aggregation models based on an individual's response to discrete spherical social zones. We changed

our approach in Chapter 5 and introduced a model for collective motion based on principles from mechanics and particle physics. We reinterpreted the forces from these physical models as social forces; individuals in the model experience these social forces acting upon themselves as a force field and act accordingly. These social forces act on an individual's velocity, unlike previous models in literature (Mogilner et al. 2003).

Attraction and repulsion forces are included in the potential model. Previous literature has used this approach (Mogilner et al. (2003), Viscido et al. (2005)). We also introduced an alignment force to the model to allow individuals to orient to one another. Cohesive and alignment forces are based on gradient forces, so that individuals move along the gradient of the corresponding potential. We showed that a dissipative force prevents individuals escaping the group. Only small friction coefficients (and therefore, small dissipative forces) are required to successfully prevent escapes within the potential model.

The role parameters play in the cohesive and alignment models is investigated. The attraction and repulsion magnitudes directly contribute to the size of the groups formed. As the attraction magnitude increases, the individuals experience more attractive forces and move closer to one another, forming a cluster. Conversely, as the repulsion magnitude increases, the group becomes more diffuse because individuals tend to avoid one another. The attraction and repulsion ranges control the extent of operation of these forces. As the attraction range increases in size, attraction forces decrease exponentially and individuals tend not to be so strongly attracted to one another. Consequently, the group tends towards swarm behaviour. An increasing repulsion range causes exponentially decreased repulsion forces, attraction forces dominate in the model and clusters of individuals result.

The alignment magnitude controls the strength of the alignment effect. Lower alignment magnitudes result in a model similar to the

cohesive model, a transition to an aligned, travelling cluster appears approximately at values of 0.15-0.2 for the alignment magnitude.

Most importantly, the alignment terms are crucial to inducing the group of individuals to travel. Cohesive forces alone are not adequate. Without alignment forces, the individuals move about in a sedentary cluster.

This model, based on ideas from physics, has the most potential for future work. If the frictional force can be replaced with a suitable gradient force designed to attract individuals to the group at long range, the potential model will be able to be transformed to a Hamiltonian system. A large array of mathematical and physical theory has been developed in classical and quantum mechanics for such systems. This theory could be harnessed to advance knowledge involving this type of model for collective motion.

In this thesis, we explore the effect of social interactions between individuals co-existing in animal groups. We have found two mechanisms which allow these groups to travel as a coherent entity. In Chapter 4, we saw how a group of naive individuals can be guided in a particular direction by a number of individuals possessing knowledge of this direction. The influence of these knowledgeable individuals on the others in the group arises because they are able to transfer information as they move in a purposeful way to the goal. Naive individuals are both attracted to and aligned with these individuals, and consequently the entire group also moved towards the goal. In Chapter 5, using a different model, we showed that a group cannot travel efficiently unless the individuals align with one another. This situation is more descriptive of a fish school moving coherently, but with no clearly pre-defined travel path, through the ocean. It would be interesting to include forces in this model that are created by external cues, such as magnetic fields or chemical and biological gradients, to explore directed movements of animal groups other than honeybee swarms.