Chapter 4

An application to honeybee swarm movement

The self-organising model from Chapter 3 is used to examine a hypothesis of the mechanism of honeybee swarm migration. This section provides a good opportunity to showcase the application and convenience of the spherical tests developed in Section 2.4.

4.1. Introduction

In Chapter 3, we developed a model based on principles of self-organisation, for the general movement of non-specific animal groups. Within this chapter we shall use this collective model, coupled with the statistical tools discussed in Chapter 2, to investigate leadership of swarms of migrating honeybees.

4.1.1. Recollection of spherical theory. Recall the relevant spherical tools formulated in Chapter 2, which will be used in the course of this chapter.

We want to estimate some measure of the association between the random vectors $\mathbf{x}$ and $\mathbf{y}$ ($\mathbf{x}, \mathbf{y} \in \mathbb{R}^3$). We use the spherical correlation coefficient ($\widehat{\rho}_3$) to measure this association (discussed in detail in Section 2.2)

$$\widehat{\rho}_3 = \frac{det\left(\sum_{j=1}^{J} \mathbf{x}_{j,-}\mathbf{y}_{j,-}^T\right)}{\sqrt{det\left(\sum_{j=1}^{J} \mathbf{x}_{j,-}\mathbf{x}_{j,-}^T\right) det\left(\sum_{j=1}^{J} \mathbf{y}_{j,-}\mathbf{y}_{j,-}^T\right)}},$$

where $\mathbf{x}_{j,-}$ and $\mathbf{y}_{j,-}$ are the j-th means corrected random samples of the vectors $\mathbf{x}$ and $\mathbf{y}$, respectively ($j = 1, \ldots, J$).

We can test that a sample of vectors is from a population with particular mean direction $\boldsymbol{\mu}_0$, using Lemma 7. If the null hypothesis ($H_o : \boldsymbol{\mu} = \boldsymbol{\mu}_0$) is true, we can base a test on the result

$$\left(\frac{1 - \mathrm{E}\left(c^2\right)}{q - 1}\right)^{-1} \frac{1}{N} \left(|\mathbf{S}_N^{\perp \boldsymbol{\mu}_0}|^2\right) \xrightarrow{D} \chi^2_{q-1}$$

as $N \to \infty$. Recall that $\mathbf{S}_N^{\perp \boldsymbol{\mu}_0}$ represents the orthogonal component of the decomposition of the resultant vector onto the hypothesised direction ($\boldsymbol{\mu}_0$) and χ^2_{q-1} denotes a Chi-squared distribution with $q - 1$ degrees of freedom.

We can test the possibility of several directional samples sharing a common mean direction. Under the null hypothesis of equal mean directions, the statistic $2T$, which can be written as

$$\begin{aligned} 2T &= \sum_{k=1}^{K} w_k |\mathbf{S}_{N_k}| - |\sum_{k=1}^{K} w_k \mathbf{S}_{N_k}| \\ &\approx \sum_{k=1}^{K} |\mathbf{z}_{N_k}|^2 - |\sum_{k=1}^{K} \lambda_k^{\frac{1}{2}} \mathbf{z}_{N_k}|^2 \\ \text{where } \lambda_k &= \frac{N_k w_k \mathrm{E}(c_k)}{\sum_{k=1}^{K} N_k w_k \mathrm{E}(c_k)}, \\ \mathbf{z}_{N_k} &= \left(\frac{w_k}{N_k \mathrm{E}(c_k)} \right)^{\frac{1}{2}} \mathbf{S}_{N_k}^{\perp} \end{aligned}$$

$$\text{and } w_k = \frac{(q-1)\,\mathrm{E}(c_k)}{1-\mathrm{E}(c_k^2)},$$

is asymptotically distributed approximately as a $\chi^2_{(K-1)(q-1)}$ distribution (see Lemma 8).

We can test that two independent directional samples have the same population polarisations. For large N_1 and N_2, under the null hypothesis of equal polarisations

$$\left(\frac{\mathrm{Var}(c_1)}{N_1} + \frac{\mathrm{Var}(c_2)}{N_2} \right)^{-\frac{1}{2}} \left(\frac{|\mathbf{S}_{N_1}|}{N_1} - \frac{|\mathbf{S}_{N_2}|}{N_2} \right) \xrightarrow{D} N(0,1),$$

as N_1 and N_2 tend towards infinity. This is discussed in Lemma 9.

The simulations have inherent randomness (due to starting positions being generated by random numbers) and chaos, hence simulation results will differ between runs. Hypothesis testing is used to quantify the results from these models with some degree of confidence and to avoid the need for large numbers of memory-intensive simulation runs.

4.1.2. Introduction to honeybee swarm migration and modelling issues. Fundamentally, we are interested in the movements of a group unaware of some goal, under the influence of a few select individuals who are privy to information regarding the position of this goal. This idea has been shown to be successful, when tested experimentally by inducing the directing of fish shoals to food (Reebs 2000). The idea need not only apply in a biological context. It has applications in robotics and other such fields (Arkin 1998, Vaughan et al. 2000).

One particular situation in nature where this occurs is during honeybee swarm migration. We discussed this in Section 1.1.1.

A swarm of honeybees are guided to a pre-determined nest site by a small number of scout bees, who have prior knowledge of the location of the site (Lindauer 1955, Lindauer 1971). The informed bees are indistinguishable from the ignorant members of the swarm and are thought to guide the uninformed swarm to their new home by flying continuously through the swarm with flight paths aligned in the direction of the new home, using visual cues (Beekman et al. 2006). We shall refer to this in the text as the 'scout hypothesis'.

Janson et al. (2005) examines this possibility explicitly with a simulation model (based on the rules of avoidance, attraction and alignment) and conclude that such an option for guidance is indeed plausible. Couzin et al. (2005) also investigate by extending their model formulated in Couzin et al. (2002) to examine the phenomenon of a select few group members privy to information regarding a goal (a food source or new home, for example) guiding the majority of uninformed group members, with no particular guidance mechanism (such as 'pointing'). The informed group members in Couzin et al. (2005) move by responses to their neighbours and a desire to move towards the goal, the direction of travel is the result of a weighted vector sum of these two forces (Couzin & Franks (2003) use this approach in modelling ant trail formations). Couzin et al. (2005) is not set up to directly assess the hypothesis of 'pointing' scout bees, their model tests the mechanism of information transfer in a group of non-specific animals.

In this chapter, we modify the collective motion model from Section 3.2, which will allow us to assess whether this is a plausible mechanism for guidance. The output from this model is a set of directions for the ignorant group members. How can we tell if the knowledgeable individuals have enough impact that the ignorant group follow their path?

Statistical methods are needed to assess whether the knowledgeable individuals (the scout bees) have been able to influence the ignorant members (workers) and guide them from an arbitrary travel path to one aligned with the goal (the new nest-site). Are the uninformed individuals moving in a direction consistent with the goal and are these individuals moving in a coherent group towards this goal?

In order to answer these questions, Couzin et al. (2005) and Janson et al. (2005) have applied measures of accuracy to the results of their simulations. Neither sets of authors consider the dispersion (cohesiveness) of the group of uninformed individuals in their analysis. Janson et al. (2005) fix their goal some distance along the x-axis, away from the initial positions of the group. The authors locate the point where the group first reaches the x-coordinate of the goal and measure the distance between this point and the goal. This distance is defined as accuracy, illustrated in Figure 4.1. They also compare the length of the trajectory of the centre of the group with a direct path between the origin and goal position, to obtain a ratio indicating how linear the trajectory is.

Couzin et al. (2005) use a re-scaled angular deviation (which they refer to as 'normalised angular deviation' or NAD) of the group direction around the direction of the goal, as a measure of accuracy. This description is open to interpretation. The authors refer to Batschelet (1981), a text devoted to circular statistics, but the authors' results are directions in three-dimensions. Couzin et al. (2005) calculate the group direction as a vector extending toward the position of the centre of the group at the end of the simulation, from the position fifty timesteps beforehand and calculate the deviation of this group direction around

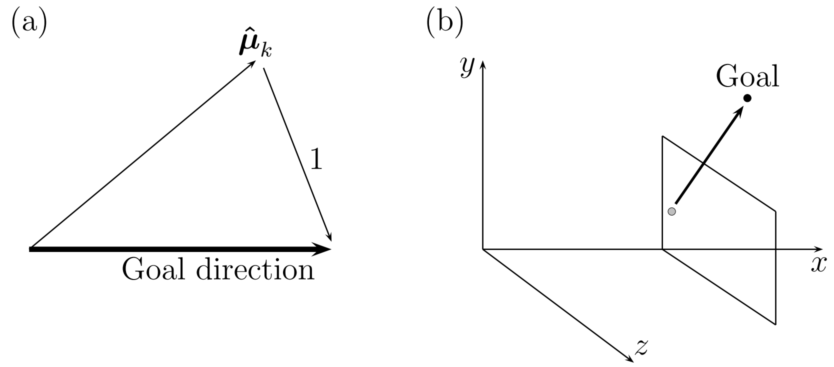

FIGURE 4.1. Measures of accuracy used to assess the quality of guidance. Diagram (a) represents accuracy, as used by Couzin et al. (2005). The vector represented by 1 is the k-th group direction around the goal direction, $\hat{\boldsymbol{\mu}}_k$ is the k-th group direction ($k = 1, \ldots, 400$). Diagram (b) shows accuracy, as used by Janson et al. (2005). The grey dot represents the position where the group enters the plane perpendicular to the goal position's x-coordinate.

the goal direction. The concept of one vector around another vector is unclear (see the diagram in Figure 4.1). Using 400 simulations, the authors calculate 400 group directions and the corresponding angular deviation of these. The closer the rescaled angular deviation is to 1, the more closely aligned the group directions are with the goal direction. By using only the group direction, information about the dispersal of the individuals within their simulations is lost.

We want to avoid possible situations where the group's direction is aligned with that of the goal by chance, due to a large dispersal (such as is found in swarm conditions, Couzin et al. (2002)). Hence, we use measures of dispersion to indicate how concentrated the vectors are around the group direction; the smaller the measure of dispersion, the more likely the individual direction vectors are to be clustered around the group average direction (indicative of a coherent group formation).

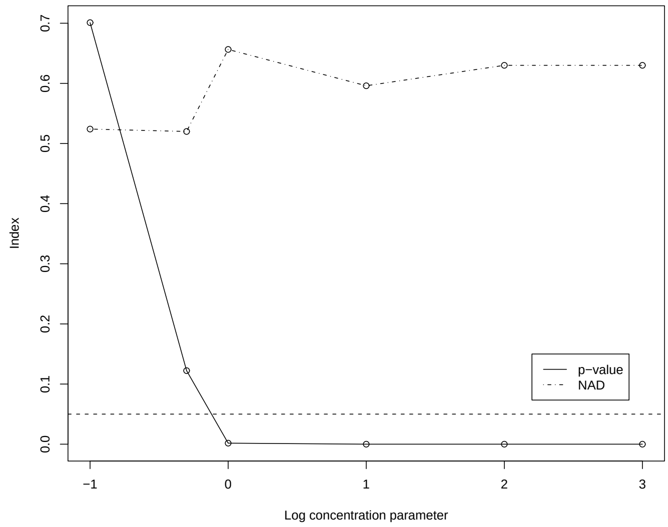

Figure 4.2. 'Normalised' angular deviation (denoted *NAD*) and p-values of a random Fisher sample, as a function of the log concentration parameter ($\log_{10} \kappa$). The polarisation of the sample increases with increasing κ. The dashed line indicates the significance level of 0.05.

To illustrate the appropriateness of spherical theory for analysing vectorial samples, we compare inference tests discussed in Section 2.4 with techniques used in previous literature. We take a random sample from a Fisher distribution (refer to Section 3.2.2) which is centred on the direction $\boldsymbol{\mu} = (.8, .42, .42)$ and test the hypothesis that the true direction could be the x-axis ($\boldsymbol{\mu}_0 = (1, 0, 0)$), using Lemma 7. The concentration parameter ($\kappa > 0$) controls the alignment of the sample vectors relative to one another. As the value of the concentration parameter increases, the distribution degenerates to a point distribution centred on the mean (in this case, the direction (.8,.42,.42)). The value of the concentration parameter is varied to compare the effect on the hypothesis test presented here and 'normalised' angular deviation measures used by Couzin et al. (2005). As the concentration parameter increases (and the sample becomes highly polarised), the hypothesis test correctly rejects the possibility of alignment with the x-axis (5% significance level). Normalised angular deviation fails to account for this change in dispersion and remains relatively invariant (Figure 4.2).

4.2. Modifications to the model of directed movement of naive groups

We base the model to test the idea of directed movement of naive groups on an adaption of the collective model discussed in the previous chapter (Section 3.2).

Let the number of knowledgeable individuals in the model be $N_{informed}$ and the number of ignorant members be $N_{ignorant} = N - N_{informed}$. The ignorant members simply follow the collective motion model discussed in Section 3.2. The informed individuals move with a given constant speed (which is at least as fast as that of the naive members) from random starting positions within the group, towards the goal. For convenience, this direction is assumed to coincide with the positive x-axis direction (see Figure 4.3). The goal is set at an arbitrarily large distance along the x-axis. Janson et al. (2005) fix the position of their goal, while Couzin et al. (2005) adopt a similar approach to ours by using a goal direction (individuals never actually reach this goal). If need be, the positions and directions of the goal can be rotated relative to one another, to incorporate any goal direction required.

To update the informed individuals position ($\mathbf{r}_{informed}(t)$) at each time step τ, we can use (3.5) again

$$\mathbf{r}_{informed}(t+\tau) = \mathbf{r}_{informed}(t) + \mathbf{v}_{informed}(t+\tau) \times \Delta_{informed}. \quad (4.1)$$

Recall, $\Delta_{informed} = \tau s_{informed}$, where $s_{informed}$ is the knowledgeable individual's speed in the direction $\mathbf{v}_{informed}(t+\tau)$. We can set the speed of the knowledgeable individuals to any level we require. The direction of travel in the next timestep of the knowledgeable individuals ($\mathbf{v}_{informed}(t+\tau)$) simplifies to $(1, 0, 0)$.

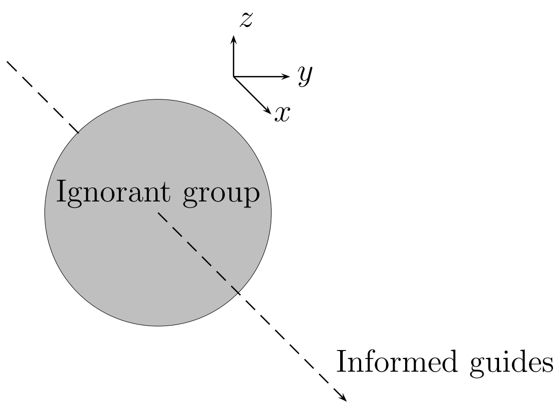

Figure 4.3. Diagram of model for investigating the scout hypothesis.

We need to introduce a condition to allow the informed individuals to move back through the group when they have gone past the naive group front. To make things as simple as possible, once the informed member has moved beyond the front of the group, that member shifts to the back of the naive group and begins to move through the naive group again. We are not concerned precisely how the individuals make this transition, nor even if it is the same individual moving through the group again. We just want to ensure that there is a steady stream of knowledgeable individuals travelling through the naive group, 'pointing' in the direction of the goal. The model aims to be a simplistic version of reality, intending to capture only the relevant information for the guidance mechanism.

Let the origin of our coordinate system coincide with the centre of the naive group. The informed members move in the x-direction, hence the location of the front of the naive group becomes the maximum of the x-coordinates of the ignorant mass. Let $\mathbf{r}_{informed,x}$ denote the x-coordinate of the knowledgeable members in question at time t and $\mathbf{r}_{group,x}(t)$ be the x-coordinate of the centre of the naive group. If the distance between the informed member's position and the centre of the naive group is larger than the distance between the centre of the naive group and the maximum x-coordinate (provided $\mathbf{r}_{informed,x}(t) - \mathbf{r}_{group,x}(t) > 0$), the informed individual is assumed to have moved beyond the limits of the naive group. If so, the informed individual is moved to a corresponding position at the rear of the naive group after a suitable delay and flies through the group again, in the direction of the goal.

Janson et al. (2005) allow informed individuals to fly through the ignorant group in a direct line, oriented between the group centre and the position of the goal. The informed individuals are assumed to be at the front of the group, once they are surrounded by 10 or less ignorant members. The informed individuals then move to the rear of the swarm and repeat their actions. Janson et al. (2005) and the work presented here assumes that only the ignorant members need react to the knowledgeable individuals. Couzin et al. (2005), in contrast, allow their informed individuals to interact with group members, as well as head in the direction of the goal. The informed members direction of travel in Couzin et al. (2005) is a weighted sum of these two resulting vectors. This means that the informed individuals need not move in a straight line through the group. Their informed individuals move with a similar speed to the ignorant group members. Couzin et al. (2005) is not set up to directly assess the hypothesis of 'pointing' scout bees, their model tests the mechanism of information transfer in a group of non-specific animals.

Both Couzin et al. (2005) and Janson et al. (2005) introduce stochastic effects, the latter with a separate stochastic term. Couzin et al. (2005) introduces randomness in two ways; a direct perturbation to the informed individuals' direction and a perturbation of the goal direction to simulate uncertainty in the coordinates of the location. The combination of these terms may unnecessarily complicate issues. We introduce only one stochastic term to perturb the direction of travel, as discussed in the previous chapter (Section 3.2.2).

How should the knowledgeable individuals be distributed within the naive group? There are a myriad of possibilities available, some illustrated in the cross-sections shown in Figure 4.4. Options include allowing the knowledgeable individuals to move one after another through the centre of the group (configuration 1). Alternatively, the informed individuals could be distributed equidistantly on the perimeter of the group (configuration 2). A compromise between these two scenarios is to distribute the individuals amongst the group (configuration 3). Beekman et al. (2006) make the observation that the scout bees appear to be flying in the top portion of the swarm, 'sandwiching' the workers between themselves and the ground. We can simulate this scenario by arbitrarily installing a reflecting barrier in lieu of the ground and forcing the knowledgeable individuals to move 'above' the group (configurations 4 and 5). We also shall see we have cause to combine configurations 1 and 2, in configuration 6. We shall discuss the consequences of these configurations later in the chapter.

Experimental evidence suggests that only a small number of knowledgeable individuals are required to guide the uninformed group. Experimental observations of honeybees indicates that 5% of the swarming bees have prior knowledge of the location (Seeley et al. 1979). We shall take this observation into account, by assigning low numbers of knowledgeable individuals (5% of the total number of individuals in the simulation, unless stated otherwise) in the model.

4.3. Results and analysis of the directed motion model

In Section 3.3, we examined the effect of model parameters on the collective motion model and the resulting types of behaviour. We can use this information to generate parallel behaviour amongst the ignorant group, with a judicious selection of parameters. We add knowledgeable individuals 'pointing' in the direction of the goal (according

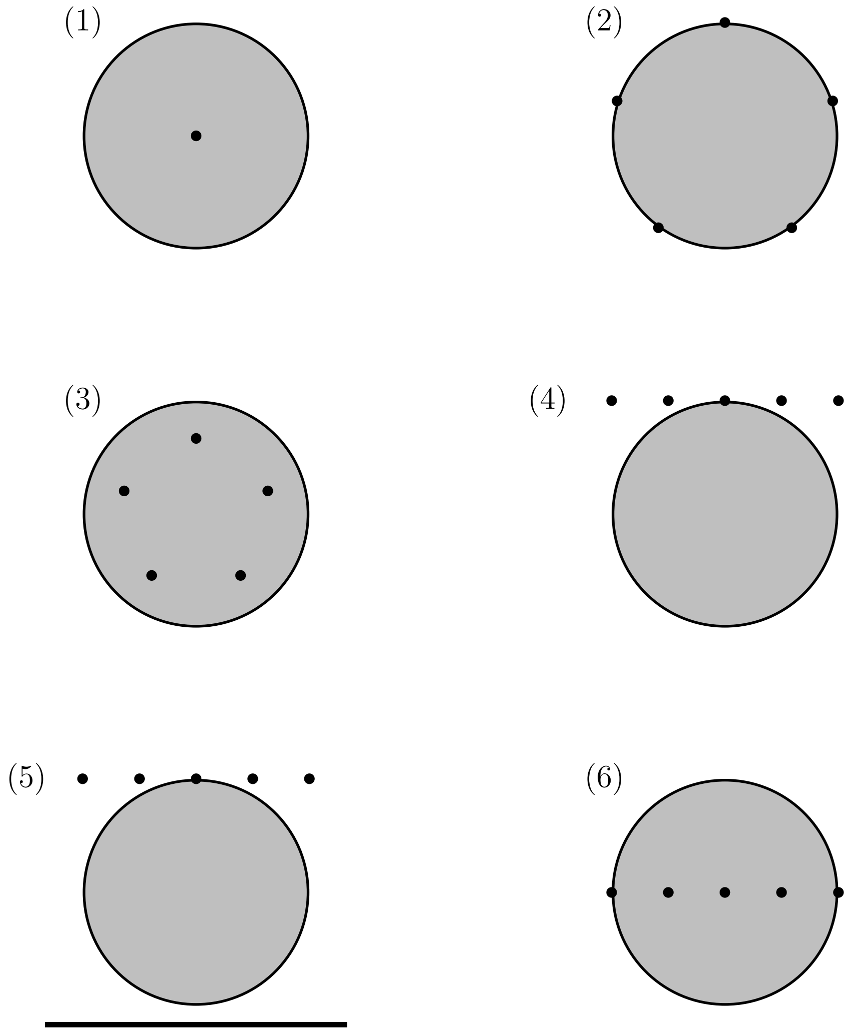

Figure 4.4. Configurations for informed individuals path within the self-organising group. The grey circle represents the cross-section of the approximate mass of ignorant group members and the dots indicate the positions of the knowledgeable members. Figure (1) is the concentrated configuration (configuration 1), (2) the configuration where individuals are dispersed along the perimeter of the group (configuration 2), (3) the configuration where the informed are dispersed within the group (configuration 3), (4) the informed are dispersed on one side of the group (configuration 4), (5) is the same as configuration 4 with a reflecting boundary (configuration 5) and (6) the configuration where the informed are distributed both on the boundary and throughout the group (configuration 6).

to Section 4.2). Unless stated otherwise, we use the following parameters: $N = 100$; $N_{informed} = 5$; $\Delta r_o = 17.5$, $\Delta r_a = 2$, $T = 200$, $\Delta r_r = 1$, $\delta = 330°$, $\gamma = 400°$/unit time (which lead to highly parallel behaviour, Figure 3.10). The simulations in this chapter are generated by MATLAB (Version 7). The statistical tests are conducted in R (Version 2.0.1). The figures are produced by MATLAB and R. A simulation of the directed motion model with 100 individuals and 2000 timesteps typically takes 2 hours to run to completion. This is substantially longer than the time taken to run the collective motion model, due to the addition of knowledgeable individuals.

We commence with a discussion and evaluation of the behaviour resulting from the model of directed motion. We shall then consider variants to this model.

4.3.1. Analysis of the directed motion model. Firstly, we discussed the setup of the directed motion model used in this section. As shown in Figure 4.4, we have several options for distributing the knowledgeable individuals throughout the mass of ignorant members. In this section, we allow for two possibilities: we allow the informed members to move through the centre of the group (configuration 1), and allow the informed members to be distributed on the perimeter of the group (configuration 2). In Section 4.3.2, we shall examine the effectiveness of all configurations.

We have a choice of the timing of the introduction of the knowledgeable individuals to the group of ordinary group members. The knowledgeable individuals can be present from the beginning of the simulation; or be introduced after a delay, once the group members have formed an organised group. Certainly, the latter option will provide strong evidence that the informed members have been able to influence the ignorant members, if the naive group can be influenced to move from an arbitrary travel path to one aligned with the goal. We investigate both options in this section.

To summarise, we shall use four variations of the directed motion model in this section. We introduce the knowledgeable individuals at the start of the simulation and after a suitable delay, and we distribute the knowledgeable individuals around the perimeter of the group and through the centre of the group. We shall consider the results of these simulations in the remainder of the section.

4.3.1.1. *Analysis of the directed motion model with no delay to the introduction of the knowledgeable members.* We shall start by assessing the directed motion model that has knowledgeable individuals present from the onset of the simulation. Final positions from these two simulations are shown in Figure 4.5, where the first column of figures are for configuration 1 and the second for configuration 2. When the informed members are concentrated through the group centre (configuration 1), it is clear that the uninformed members in the simulation are aligned in the direction of the goal (the x-axis, $\boldsymbol{\mu}_0 = (1, 0, 0)$). It is not so apparent for the second simulation (whose knowledgeable members are distributed around the group perimeter, configuration 2). We need to examine the situation more closely, both with a statistical analysis and considering the actions of the naive group over time.

We use the spherical hypothesis test of a particular group direction (Lemma 7) to assess whether the average directions of both groups in Figure 4.5 could coincide with the direction of the goal. We calculate a test statistic of 0.0004 (p-value of 0.999) for the group with configuration 1 and a test statistic of 0.0055 (p-value of 0.997) for the group with configuration 2. The p-values are larger than the significance level of 0.05. In both cases, the results from the hypothesis tests suggest no evidence against the null hypothesis (of alignment of the group in Figure 4.5 with the goal direction). These results are summarised in Table 4.1.

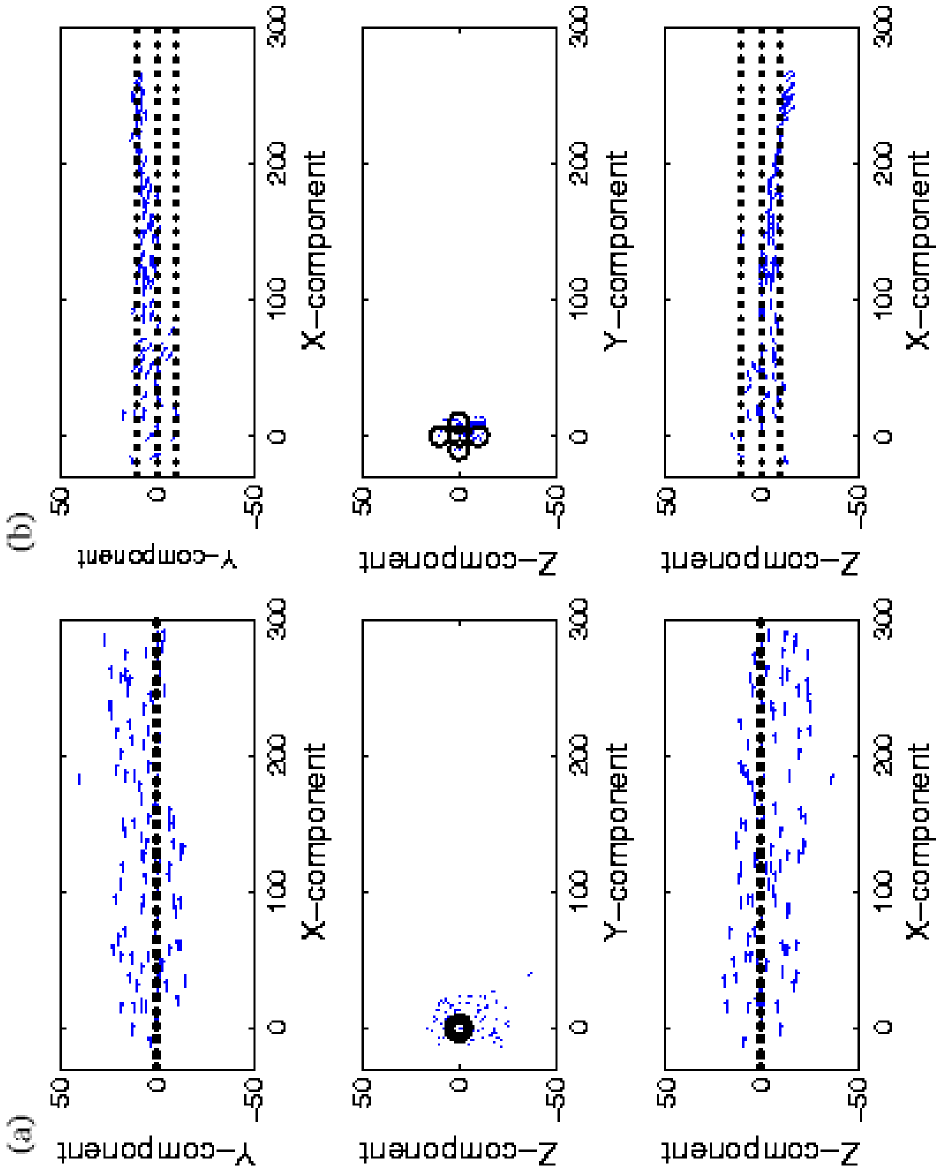

Figure 4.5. Final results of the direction model. Column (a) refers to configuration 1, column (b) to configuration 2. The knowledgeable individual's travel paths are indicated by the dashed lines and black circles, the orientation and position of the ignorant members by the arrows.

We can compare the random initial positions of the ignorant group with the final positions of these groups (Figure 4.5) for both configurations, to show there has been a significant change in the directions. We check that we can regard the samples of initial and final positions for each configuration as independent samples. The estimate of the spherical correlation ($\widehat{\rho}_3$) for configuration 1 is $6{\times}10^{-4}$ and -8×10^{-4} for the second configuration. In both cases, these estimates are small, meaning that we can effectively regard the samples of initial and final positions as independent when using the hypothesis tests.

Using Lemma 8, which tests whether two directional samples could share a common average direction, we obtain large test statistics for both configurations (5149 for configuration 1 and 5400 for configuration 2). Consequently, both p-values are below 5% and we conclude there have been significant changes in group means for both configurations.

We can also show that there has been a significant change in the group polarisation for each configuration during the simulation, using Lemma 9. Comparing the polarisations of the random initial positions with the final positions for both configuration 1 and 2, we obtain test statistics of 16.12 and 15.81, respectively (both p-values from the tests are small). This indicates that there has been a significant change in group polarisations of the two groups, during the simulations.

Using the statistical tests developed in Section 2.4, we have shown for both configurations that there has been a significant change over the course of the simulations in group directions and polarisations, and that the final directions of the individuals in both of the simulations can be regarded as aligning with the direction of the goal. However,

Table 4.1: Summary statistics for hypothesis tests of different configurations of informed individuals. Define $\boldsymbol{\mu}_k$ $(k = 1, \ldots, 6)$ as the hypothesised group direction of the k-th group. The test statistic column gives the value of the test statistic from the appropriate test. The p-value column gives the corresponding p-value.

Configuration	*Null hypothesis*	*Test statistic*	*p-value*	$\hat{\boldsymbol{\mu}}$	p_{group}
Non-delayed informed individuals					
1	$\boldsymbol{\mu_1} = (1,0,0)$	0.0004	0.999	(.999,.003, -.001)	0.999
2	$\boldsymbol{\mu_2} = (1,0,0)$	0.0055	0.997	(.984,-.150,-.093)	0.882
Delayed informed individuals					
	5 group means all equal	5963.264	small		
1	$\boldsymbol{\mu}_1 = (1,0,0)$	1.9461	0.3779	(.999,.022,-.029)	0.902
2	$\boldsymbol{\mu}_2 = (1,0,0)$	389.6532	small	(.924,.295,.242)	0.983
3	$\boldsymbol{\mu}_3 = (1,0,0)$	3.4913	0.1745	(.999,-.028,-.023)	0.939
4	$\boldsymbol{\mu}_4 = (1,0,0)$	497.9486	small	(-.571,.783,.244)	0.863
5	$\boldsymbol{\mu}_5 = (1,0,0)$ (end of simulation)	887.3989	small	(.030,.127,.991)	0.885
5	$\boldsymbol{\mu}_5 = (1,0,0)$ (at half-way point)	5.71849	0.0573	(.986,.151,.067)	0.954
6	$\boldsymbol{\mu}_6 = (1,0,0)$	5.9074	0.0521	(.998,-.044,.040)	0.931
	$\boldsymbol{\mu}_1 = \boldsymbol{\mu}_3$	5.7987	0.0551		
	$\boldsymbol{\mu}_1 = \boldsymbol{\mu}_3 = \boldsymbol{\mu}_3$	8.9407	0.0626		

it is also worthwhile considering the behaviour of descriptive statistics (defined in Section 2.2) during the simulations and we shall now do so.

Figures 4.6, 4.7 and 4.8 show how various descriptive statistics (from Section 2.2) behave over the time period of the simulation. Like Figure 4.5, these figures are split into two columns; the left columns show statistics associated with configuration 1 and the right with configuration 2. Figure 4.6 shows the movement of the centre of the groups as a function of time and demonstrates a decided drift in the direction of the goal, apparent in the y-x and z-x planes. The components of the group averages show a tendency for the group average directions (Figure 4.7) to align with the direction of the goal (in both cases, the x-components tend towards 1, while the $y-$ and $z-$components fluctuate around 0). The polarisations and momenta shown in Figure 4.8 are indicative of highly coherent cohesive groups (with low rotational movement) moving throughout the simulations. Indeed it should be, for the model parameters were selected to ensure such groups would form.

We can calculate the net to gross displacement ratios for the two groups (*NGDR*, defined in (2.9)), which measures the curvature of a path. The closer the ratio is to 1, the more linear the path. We can use this statistic to measure how straight the path of the centre of each group is (Figure 4.6). The group with configuration 1 has a mean *NGDR* value of 0.9945 and the group with configuration 2 has a mean value of 0.8427. Both of these ratios indicate that the groups as a whole have travelled in a relatively linear path. We know that from the analysis of the final positions of the ignorant members in each group, that these paths can be considered oriented towards the goal.

The analysis of the results of the directed motion models (that have knowledgeable individuals present from the beginning of the simulation) have shown that the ignorant individuals in each case have

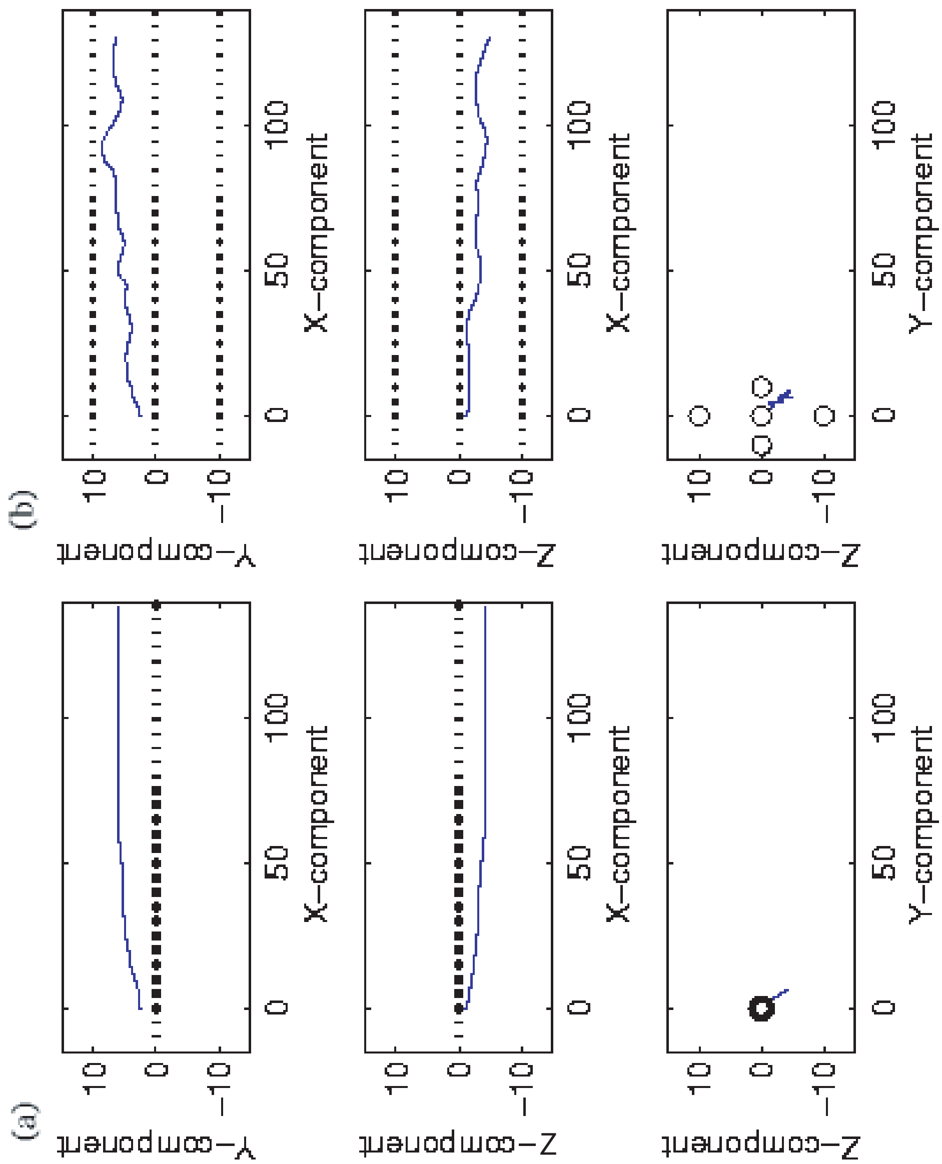

Figure 4.6. Movements of the centre of mass of the group (Equation 2.1) over time (simulations from Figure 4.5). Column (a) refers to configuration 1, column (b) to configuration 2.

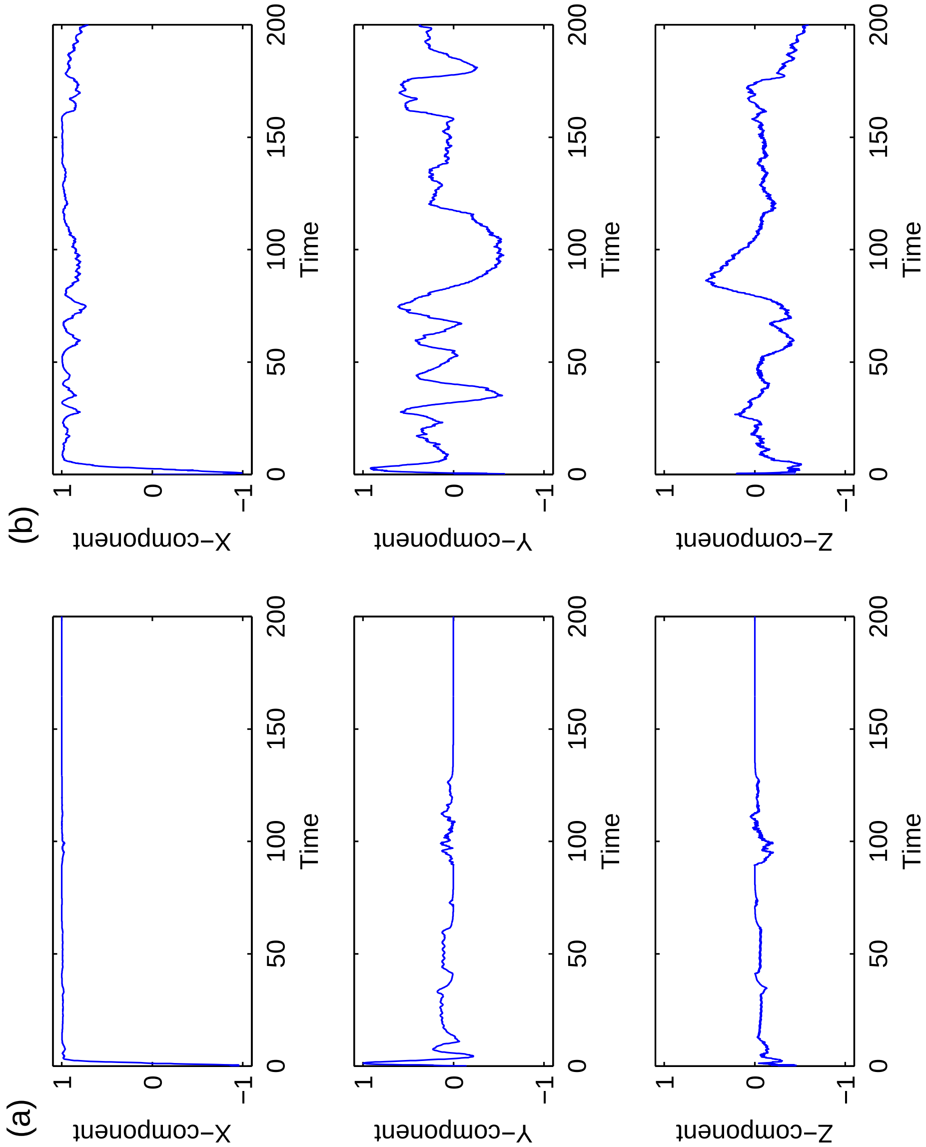

Figure 4.7. Movements of the estimated average direction of the group (Equation 2.3) over time (simulations from Figure 4.5). Column (a) refers to configuration 1, column (b) to configuration 2.

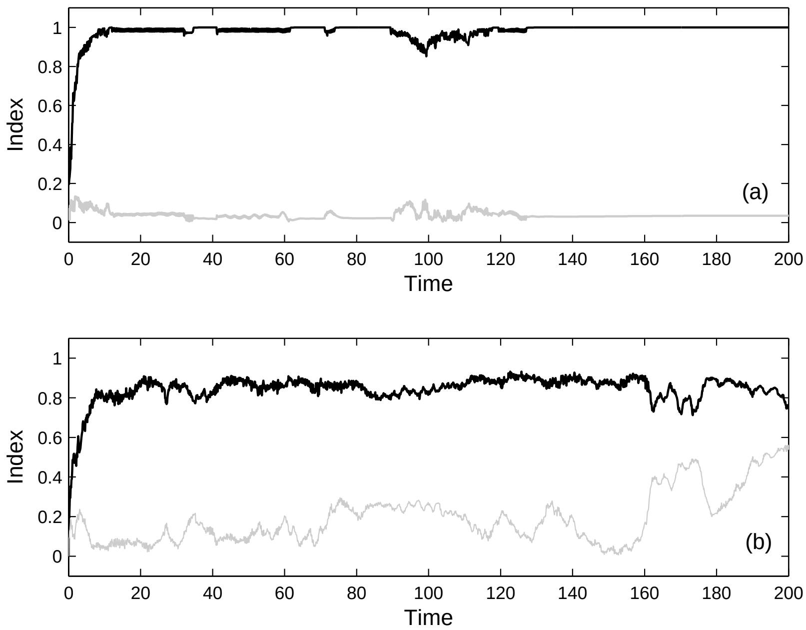

Figure 4.8. Group polarisations and angular momenta (2.4, 2.5) over time (simulations from Figure 4.5). Column (a) refers to configuration 1, column (b) to configuration 2. Black indicates polarisations, gray momenta.

formed polarised groups, travelling in a linear fashion in one direction. Moreover, this direction can be regarded as coinciding with the direction of the goal. It seems likely that the knowledgeable individuals in this scenario have influenced the ignorant individuals and caused them to align with their travel paths.

4.3.1.2. *Analysis of the directed motion model with delayed knowledgeable members.* We now perform a similar analysis to the previous section, on simulations where we allow the ignorant mass to first form an aligned group and introduce the knowledgeable individuals afterwards (at 40 simulation timesteps) to see if these individuals can influence the already organised group. The configurations of the knowledgeable individuals amongst the group are either through the group centre (configuration 1) or distributed around the perimeter (configuration 2).

Figures 4.9 and 4.10 show the behaviour of the descriptive statistics associated with both simulations (configuration 1 in Figure 4.9 and configuration 2 in Figures 4.10). We look at these figures to determine whether the ignorant members alter their behaviour to align with the knowledgeable individuals' paths.

In both simulations, some time after the knowledgeable individuals are inserted, the ignorant members travel paths have significantly altered, to be aligned with the direction of the goal. This is apparent from the pictures of the centre of the group and the spherical mean (Figures 4.9 and 4.10). The centre of group clearly changes direction once the knowledgeable individuals are introduced (at the point marked by the star in the figures), as does the spherical mean. Polarisations and momenta behave as expected for a parallel group. We calculate *NGDR*'s for the entire trajectories of individuals in the simulations, post and prior to introduction of knowledgeable individuals. Calculations of the mean *NGDR* for the centre of group's travel path yield 0.6711 for the group with configuration 1, and 0.3529 for those with configuration 2. These ratios are not as high as those simulations where there is no delay in introducing the knowledgeable individuals, because the masses in Figures 4.9 and 4.10 need to be shifted away from an arbitrary travel path first. This produces a curved path and has the effect of adding more curvature to the path, until the informed individuals have established their presence.

We can use the directional statistical tests (Section 2.4) to help answer certain key questions. Has there been a change in the direction

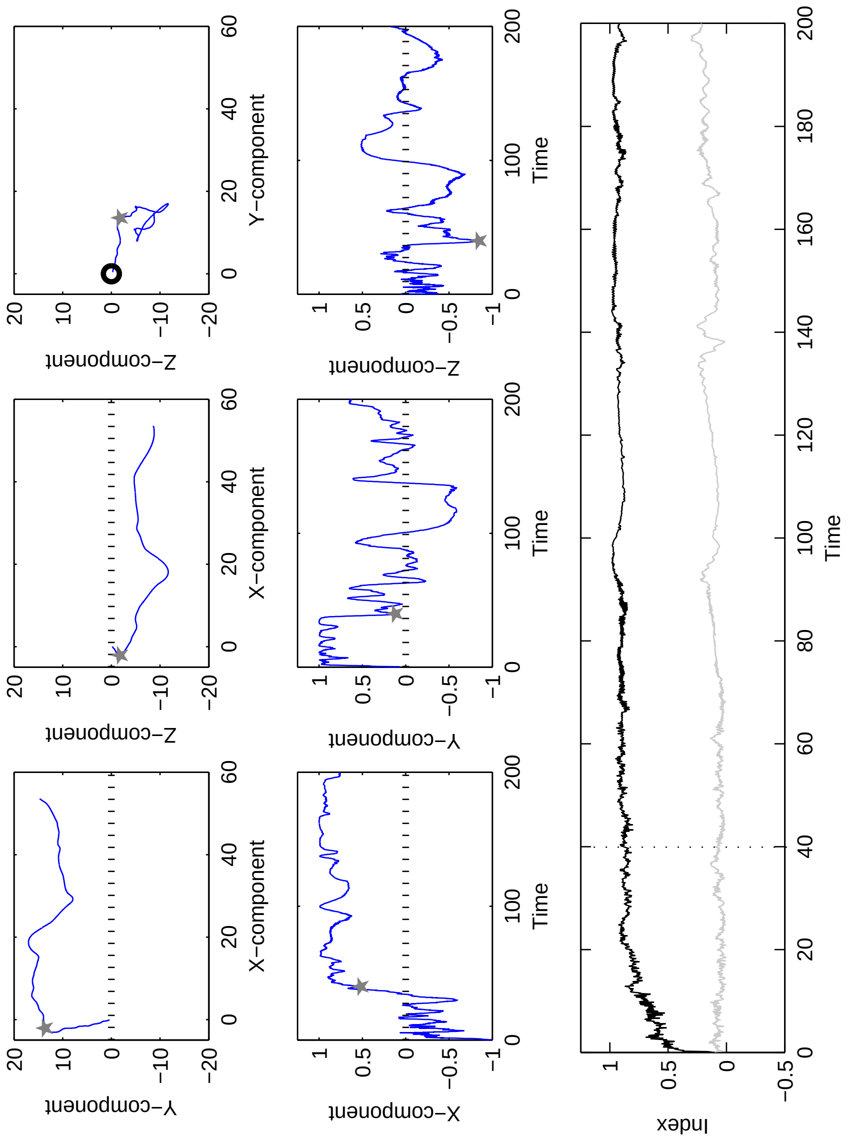

Figure 4.9. Results of simulations where knowledgeable individuals are introduced to the model after a delay (40 timesteps, as indicated by the star marker). The knowledgeable individuals are distributed according to configuration 1. The first row shows the centre of group, the second row the components of the spherical mean and the third shows polarisations (black) and momenta (gray).

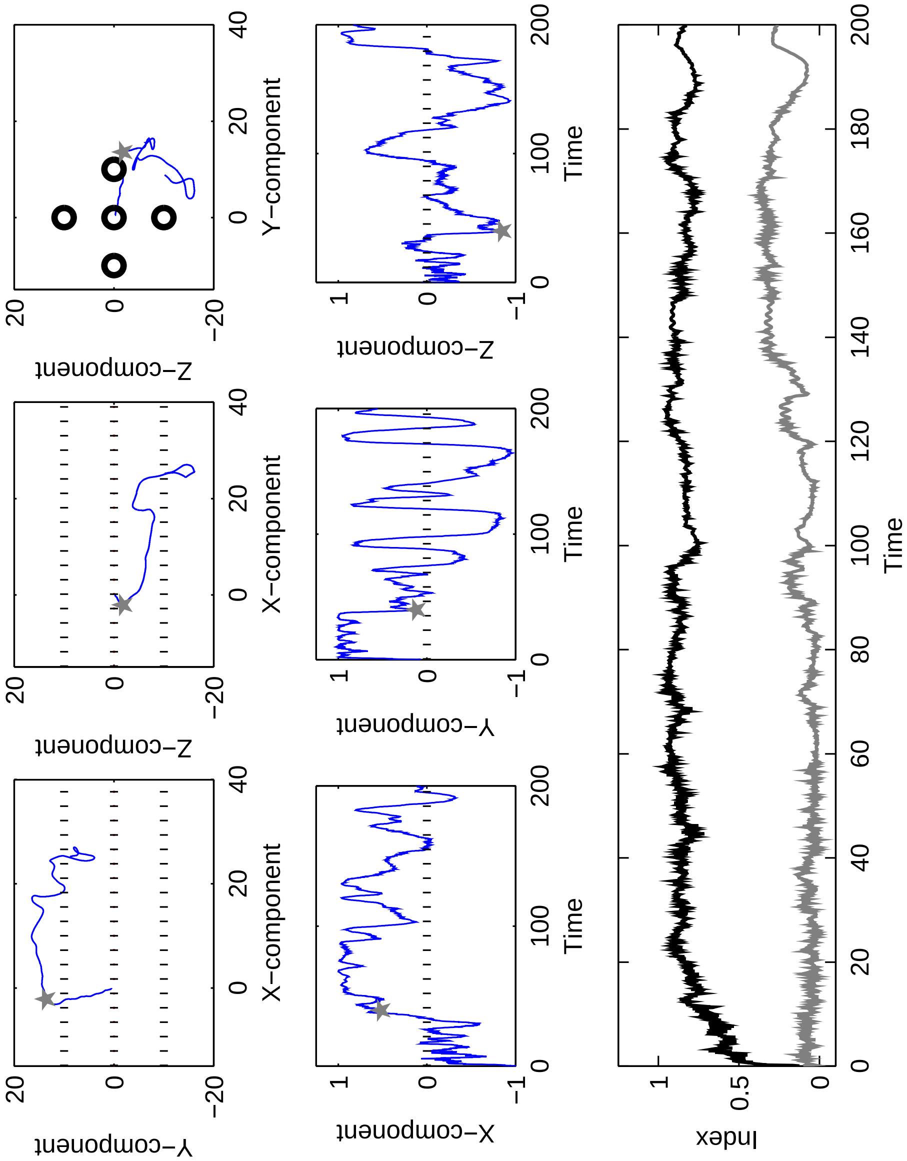

FIGURE 4.10. Results of simulations where knowledgeable individuals are introduced to the model after a delay (40 timesteps, as indicated by the star marker). The knowledgeable individuals are distributed according to configuration 2. The first row shows the centre of group, the second row the components of the spherical mean and the third shows polarisations (black) and angular momenta (gray).

of the groups since the knowledgeable individuals are introduced to these groups? Does the group directions at the end of the simulations match up with the direction of the goal? Is there a change in group polarisations to an aligned configuration, during the simulation?

We can test (using Lemma 7) to see if the average direction of the group of uninformed individuals (whose informed individuals are distributed with configuration 1) coincides with the direction of the goal (along the x-axis). We use the directions of the group of uninformed individuals at the conclusion of the simulation, and calculate the test statistic to be 3.49 (corresponding to a p-value of 0.17). These directions are consistent with the null hypothesis that the average direction of the ignorant components coincides with the direction of the goal, for configuration 1. However, the test statistic for the group using configuration 2 is 389.65, with a corresponding small p-value (see Table 4.1). We reject the null hypothesis of alignment with the goal direction. It seems that once the group has formed an aligned configuration, the knowledgeable individuals in configuration 2 are not able to influence group members sufficiently to cause them to align with the goal. Configuration 1 may be more successful as knowledgeable individuals are able to influence group members in three dimensions. When the knowledgeable individuals are distributed on the edge of the group, their influence is reduced, because they come in contact with fewer individuals. For the remainder of this section, we shall concentrate on configuration 1.

We use the samples of directions of ignorant members prior to introduction of the knowledgeable members. We compare these with the samples of directions of the ignorant members at the conclusion of each simulation, when they have had the opportunity to be under the influence of knowledgeable individuals for a considerable period of simulation time. The estimate of spherical correlation ($\hat{\rho}_3$) is 0.0997, meaning the two samples can effectively be regarded as independent for the hypothesis test. The approximating distribution of the test statistic $2T$ (from Lemma 8) follows a χ_2^2 distribution ($q = 3$, $m = 2$). We calculate the test statistic to be 374.69 and the p-value to be approximately 0. We conclude that there has been a significant change in average group direction (with configuration 1) once the informed individuals have been introduced to the group. We reject the null hypothesis that the direction of the ignorant group coincides with that of the goal.

Finally, we assess that we have a coherent group by testing the polarisations of the group initially and at the end of the simulation. To decide whether the group of uninformed individuals have formed an organised aligned group, we use Lemma 9. The two samples consist of the initial (random) and the final positions of the ignorant individuals in the simulation. The correlation between these two groups is estimated to be -0.0003. The null hypothesis is equality of polarisations. Using (2.39), we calculate the test statistic for the initial and final directions to be 10.74. The test statistic is significant (p-value is approximately 0). The polarisation of ignorant individuals in the final positions is significantly larger than those of the same individuals in the initial positions. In fact, the polarisation of the ignorant group is initially 0.06 and changes after the conclusion of the simulation to be 0.83. This reflects that the group has had a transition during the simulation from a group with random orientations (relative to one another), to one whose orientations are highly polarised.

We have shown that the ignorant group in the simulation with configuration 1 has had a significant change once the knowledgeable individuals are introduced to the group, to align with the goal direction in the polarised group. This provides strong evidence that the informed members with this configuration have been able to influence the ignorant members, during the simulation.

4.3.1.3. *Randomisation tests for analysing the results of models.* In Section 2.3, we formulated a randomisation test using the angle between the direction of the goal and the mean group direction. This idea was a prototype, which was used in an initial analysis. We include the randomisation test assessment for interest's sake.

Recall from Section 2.3, the null hypothesis is that the sample of spherical means of the orientations of the ignorant individuals is random. Effectively, the alternative is that the ignorant individuals general direction of travel coincides with the flight paths of the knowledgeable individuals. Define the angle between the spherical mean of the sample and the x-axis, as ψ. We define the test statistic, T (2.13), as:

$$T = \frac{\psi}{p_{group}},$$

where p_{group} is the polarisation of the sample of mean orientations. Permutations of the data are generated from the polar coordinates θ_i and ϕ_i $(i = 1, ..., 1000)$ of the sample of means. From these randomised samples, 1000 test statistics are calculated to generate the empirical reference distribution. The observed value of T is compared with this distribution, to decide if T is a typical value from the reference distribution.

We calculate the observed tests statistics (T) and compare them with the randomised test statistics (obtained from 1000 permutations of the data, whose histograms are shown in Figure 4.11). The observed test statistics are 0.01255, 0.05352, 0.03748 and 0.13978 for these simulations. These test statistics are for the models with configuration 1 and 2, and for the models with delayed informed individuals (configuration 1 and 2), respectively. In each case, comparison of the observed test statistic with the appropriate histogram in Figure 4.11 leads to the conclusion that the observed test statistics are not typical values from the randomisation distributions. In all four cases, the test statistics

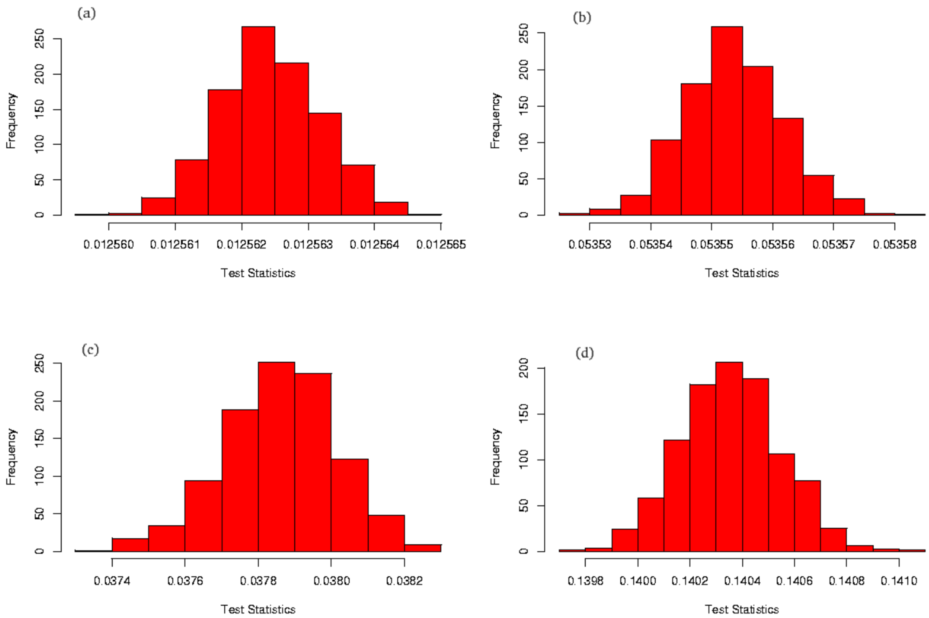

FIGURE 4.11. Histograms of randomised test statistics. Corresponding to (a) = Figure 4.5, configuration 1 (observed T = 0.01255), (b) = Figure 4.5, configuration 2 (observed T = 0.05352), (c) = Figure 4.10 (observed T = 0.03748) and (d) = Figure 4.9 (observed T = 0.13978).

lie to the left of the histograms, in Figure 4.11. The corresponding p-values are low, giving strong evidence against the null hypothesis (of a random arrangement) and leading us to conclude that the current arrangements have not arisen purely due to chance alone. Again, it seems likely that the ignorant members directions are aligned with the direction of the goal. This is a confirmation of the findings in the previous two sections.

4.3.2. Miscellaneous issues related to the directed motion model. In this section, we discuss variations of the model used in previous sections. We consider the relative speed of the informed individuals and show it must be at least as large as that of the ignorant members for successful navigation. We discuss the impact of different configurations of the knowledgeable individuals distributed throughout the group. Finally, we examine the effects of stochastic components on the directed motion model.

4.3.2.1. *Analysis of the speeds of the knowledgeable individuals.* How fast (relative to the ignorant group) do the knowledgeable individuals have to move, before the ignorant members pay attention to them? We answer this question by simulating the directed motion model for varying ratios of the knowledgeable individual speeds to those of the ignorant members. We discuss how the accuracy of guidance is related to the proportion of knowledgeable individuals. We use the model discussed in Section 4.3.1.1, with knowledgeable individuals that move through the centre of the group (configuration 1).

The movement of the centre of the groups are shown in Figure 4.12, for various speed ratios. Paths become increasingly orientated with the direction of the goal once the ratio is 80% or more so, in the x-y and x-z planes. This is reflected in the histograms of the *NGDR*'s in Figure 4.13. With increasing speed ratios, the individuals within the model tend to have more linear trajectories. Certainly, for ratios of 70%-80% and larger, the histograms are biased towards values of 1, indicating less path curvature.

We can use Lemma 7, the directional hypothesis test of group alignment with the direction of the goal. Figure 4.14 shows test statistics for these simulations, for different speed ratios. We compare these test statistics with the critical value of a χ^2_2 distribution (5.9915 at the 5% significance level) to decide if the null hypothesis of alignment is credible. We reject this hypothesis for test statistics larger than the critical χ^2_2 value. These test statistics indicate that as the speeds ratio approaches 1, the group direction of travel can be considered as aligned with the goal direction.

Finally, we examine the angle between the x-axis and the ignorant group direction (ψ, refer to Section 2.3). We calculate this angle for

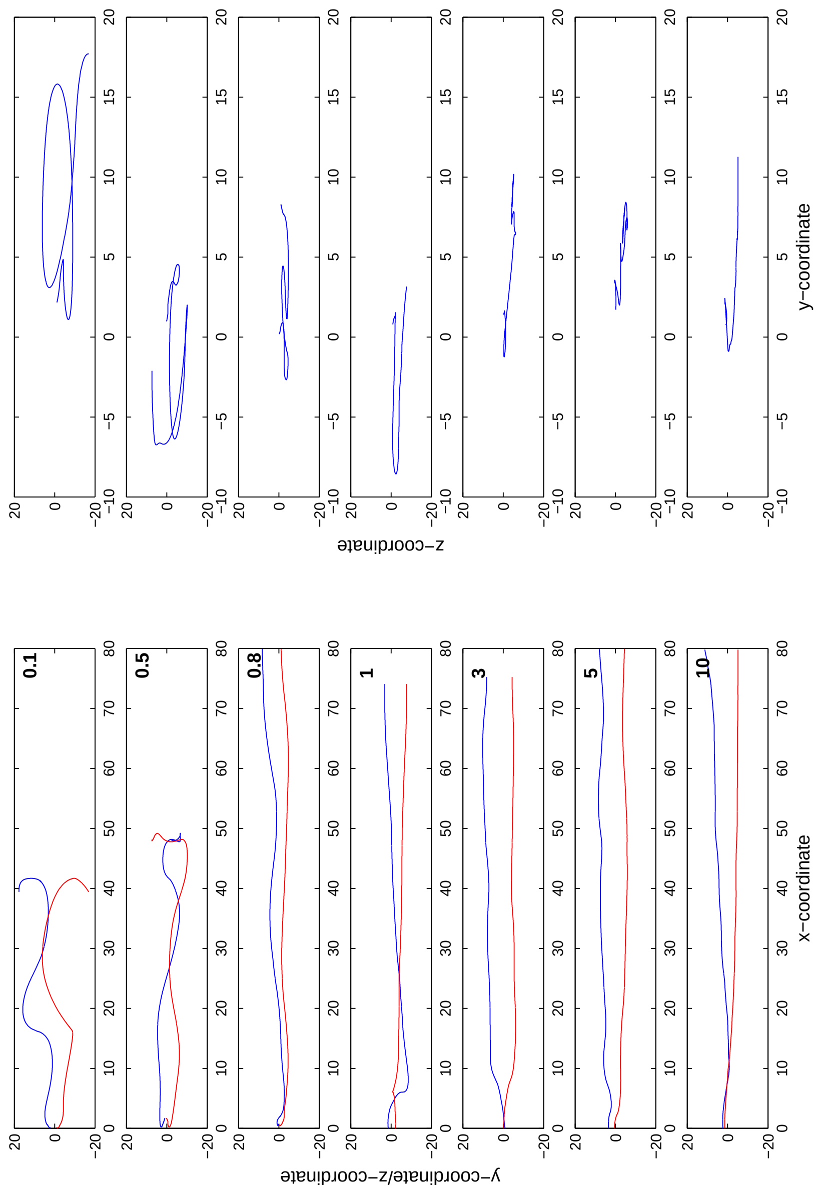

FIGURE 4.12. Movement of the centre of the group, for selected simulations with differing knowledgeable individual relative speeds. The lefthand column shows the actions in the x-y and x-z planes (blue and red, respectively). The righthand column shows the actions in the y-z plane. The relative speed of knowledgeable individuals is noted by the number in the top right corner of the panes in the left column.

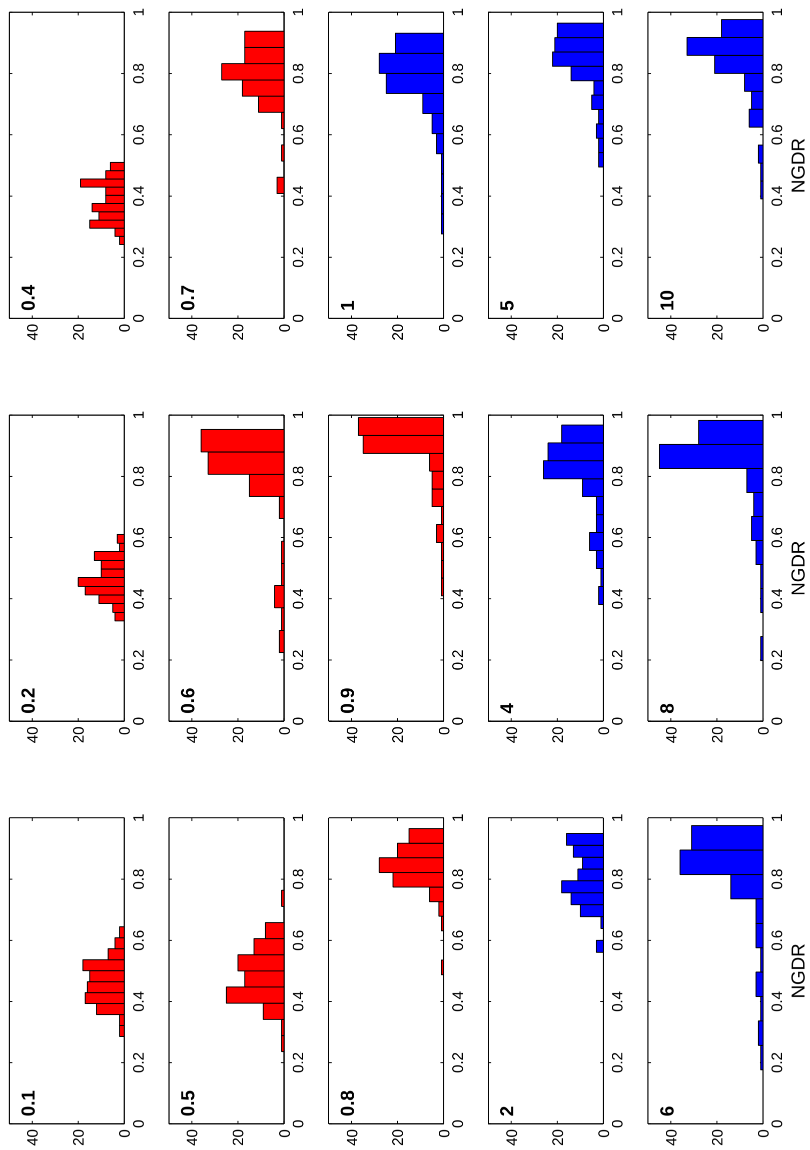

FIGURE 4.13. Histograms of *NGDR*'s, for select simulations with differing knowledgeable individual relative speeds (to naive members). The relative speed of knowledgeable individuals is noted by the number in the top left corner of the panes.

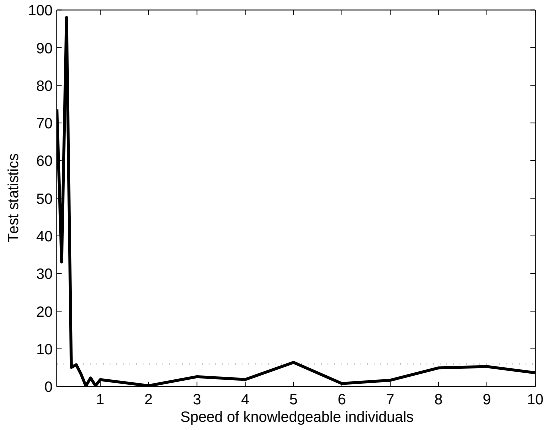

Figure 4.14. Test statistics from the test (Lemma 7) of alignment with a particular direction (the x-axis) for differing knowledgeable individual relative speeds. The dashed line indicates the critical value of 5.99 ($\Pr(\chi_2^2 \geq 5.9915) = 0.05$).

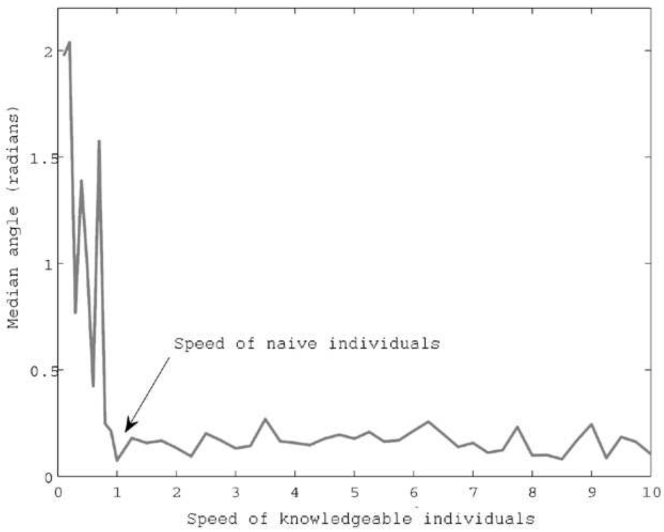

Figure 4.15. Speed of scout components (relative to ignorant members) compared to the median angle between the worker groups (spherical) mean direction of travel and the knowledgeable individuals' flight paths. A distinct change is noted once the knowledgeable individuals speed matches that of the ignorant members.

the last 100 timesteps of the simulation and use the median of these angles in Figure 4.15. This is done to examine the change in directions in time. An abrupt change is seen once the speed ratio approaches 1. The change is from a large median angle, to a low one. This means that as the ratio increases, most individuals are aligning with the goal direction. This low level is also maintained for ratios larger than 1.

We conclude that the knowledgeable individuals can influence the ignorant members, provided their speed is at least as large as that of the ignorant members. If the knowledgeable individuals are slower than the ignorant members, the group of ignorant members ignore the knowledgeable individuals. Presumably, the group of naive members travel faster than the knowledgeable individuals and leave them behind.

Couzin et al. (2005) do not consider the impact of different speed ratios between the two types of individuals. Janson et al. (2005) considers the issue of effective speeds of knowledgeable individuals. The authors only consider speeds of knowledgeable individuals moving as fast as the ignorant group members, 2.5 times faster and 5 times faster. This is a small set of speeds to trial, we have examined a greater range. In their model, Janson et al. (2005) observe the ignorant group splitting into separate groups, when the higher speeds are used. These groups tend to reform later in the simulation. We do not observe this effect in our model, however the mechanisms of knowledgeable individuals' movements in their model are more complicated than ours. Janson et al. (2005) conclude that if their knowledgeable individuals travel considerably faster than their group members, the two groups become disconnected and the quality of guidance decreases.

4.3.2.2. *Analysis of the relative numbers of the knowledgeable individuals.* Experimental evidence suggests that a remarkably small percentage of knowledgeable individuals are required to guide naive groups to the goal. Observations of honeybees indicate that only 5% of the swarming bees are scouts and this ratio is adequate to accurately guide the swarm to the new location (Seeley et al. 1979). How reliable is this ratio?

To examine this, we alter the ratios of the knowledgeable individuals to the ignorant members in the directed motion model. We use the directed motion model discussed in Section 4.3.1.1, with the knowledgeable individuals travel paths concentrated through the centre (configuration 1). These individuals are with the group from the start of the simulation. Other model parameters are the same as those in Section 4.3. We consider the consequences of these alterations on the outcomes of the simulations.

Figure 4.16 shows the resulting motions of the centre of the group for each simulations. All simulations show a distinct drift along the x-axis. However, simulations with 2% and 3% knowledgeable individuals show less tendency to drift along the x-axis and their movements in the y-z plane tend to be more erratic, than those simulations with 4% or more knowledgeable individuals.

The net to gross displacement ratios of ignorant members are shown in Figure 4.17, which sheds light on the linearity of paths individuals take during the simulation. Recall the closer the *NGDR* is to 1, the more linear the path. The simulations with 2% and 3% knowledgeable individuals show a broad spectrum of *NGDR*'s; some individuals have linear paths, other less so. Once the ratios are increased from 4% to 8%, the histograms of the *NGDR*'s show some bias towards the upper scale of values. This change is quite distinct for ratios of 9% or more. Consequently, for ratios above 3%, ignorant individuals tend to take more linear trajectories. The *NGDR* does not allow us to infer direction of the group. However, coupled with the information in Figure 4.16, we can conclude that for ratios greater than 3%, the ignorant members are taking more direct paths in the general direction of the goal.

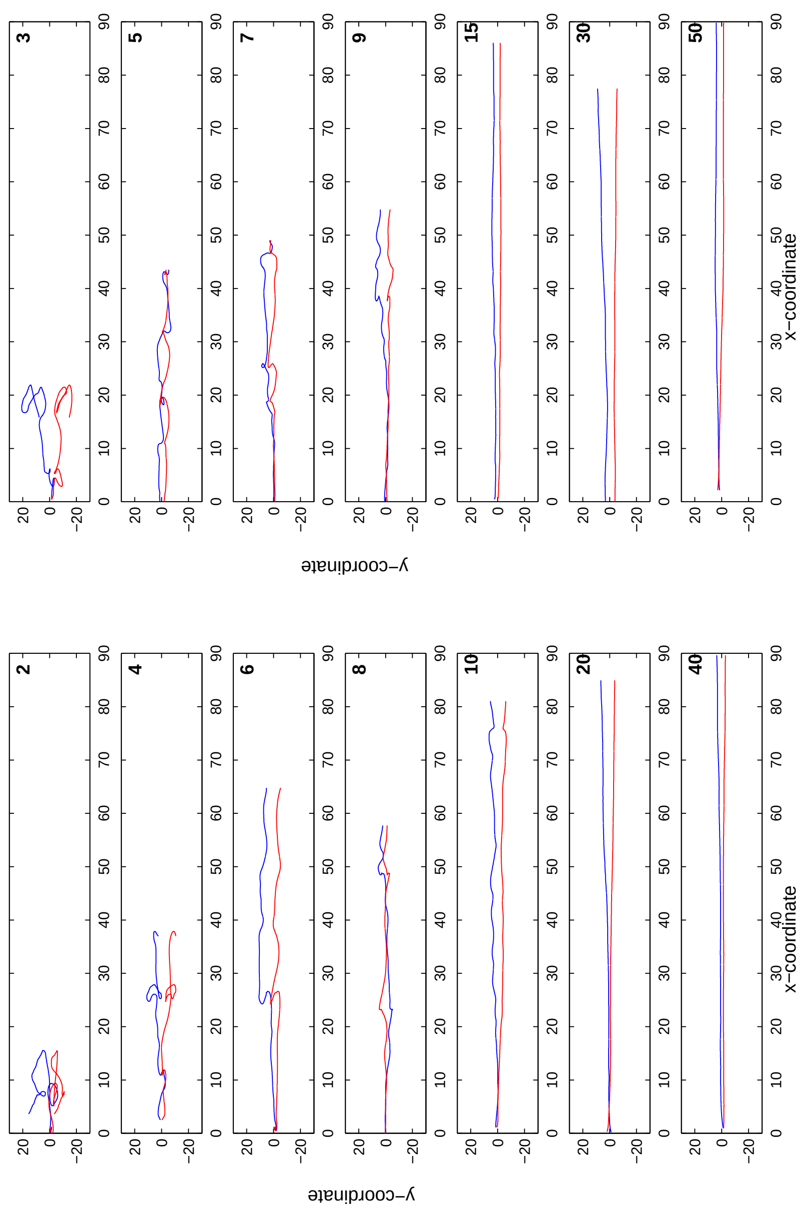

Figure 4.16. Movement of the centre of the group, for selected simulations with different numbers of knowledgeable individuals. The panes show the actions in the x-y and x-z planes (blue and red, respectively). The number of knowledgeable individuals is noted by the number in the top right corner of the panes. The x-axis of the figures shows the x-coordinates, while the y-axis shows the y- and z-coordinates, as appropriate.

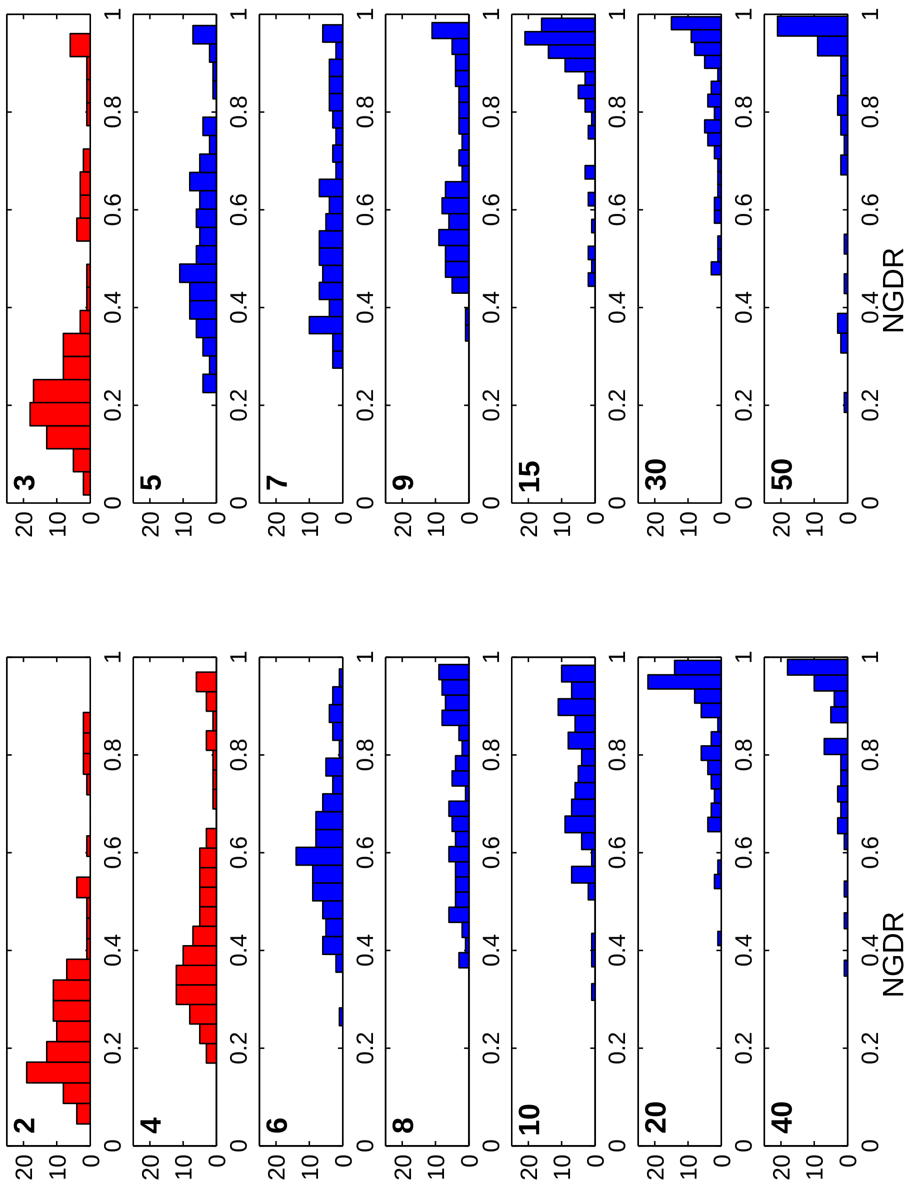

FIGURE 4.17. Histograms of *NGDR*'s of ignorant members, for selected simulations with different numbers of knowledgeable individuals. The relative percentage of knowledgeable individuals is noted by the number in the top left corner of the panes.

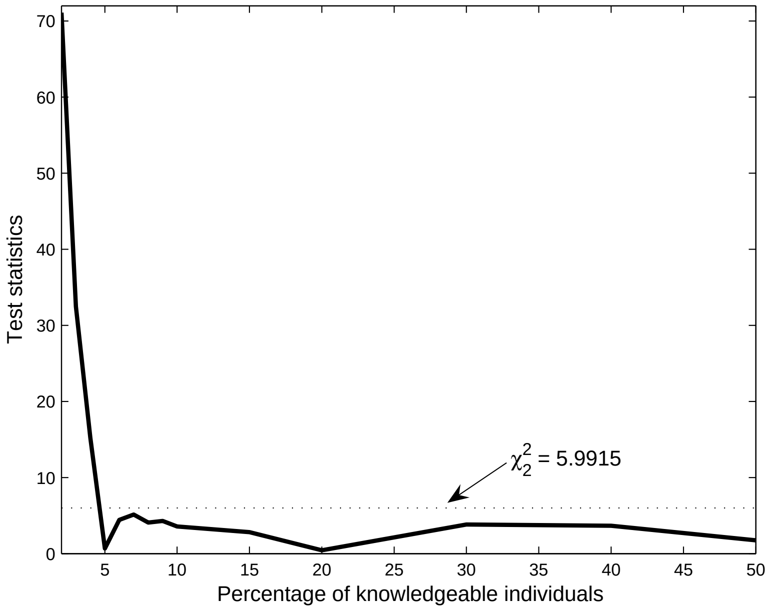

FIGURE 4.18. Test statistics from the directional hypothesis test of particular common direction (Lemma 7), for selected simulations with different numbers of knowledgeable individuals. The hypothesised direction is the x-axis. The dashed line indicates the critical value of 5.9915 ($\Pr(\chi^2_2 \geq 5.9915) = 0.05$).

We can use Lemma 7 to assess which simulations may have group directions aligned with the direction of the goal. Figure 4.18 shows the test statistics from these tests, for different ratios of knowledgeable individuals. We can compare these statistics to the critical value of a χ^2_2 distribution (5.9915, at the 5% significance level) to decide whether the null hypothesis is credible. If the test statistic is larger than the critical value, we reject the null hypothesis. This is an alternative (and equivalent) approach to using a p-value. We can see that the test statistics decrease rapidly initially, for increasing ratios. For ratios of 5% and above, the test statistics are below the critical value. For these ratios, the hypothesis tests indicate that the groups may be considered as aligning with the direction of the goal (the x-axis).

Both Couzin et al. (2005) and Janson et al. (2005) consider effective proportions of knowledgeable individuals in their models. Couzin et al. (2005) came to the same conclusions as we do in this section, that 5% is an adequate proportion for successful guidance. Couzin et al. (2005) compare results for different group sizes and conclude that as the group size increases, the effective proportion of informed individuals may decrease asymptotically to approximately 5%. The authors postulate that biological aggregations have evolved to reach this limit. Janson et al. (2005) examine ratios of 1%, 2.5% and 5%, again a narrow range to consider. They suggest that a proportion of 1% is still effective, this is in contradiction to our results. We observe that proportions below 4% are ineffective in inducing guidance. However, Janson et al. (2005) mention that an increasing proportion dramatically improves the quality of guidance.

We find no evidence to the contrary that a ratio of 5% knowledgeable individuals is adequate for accurate guidance. Results indicate that 4% may be regarded as also sufficient, however 5% seems to quite acceptable as a heuristic (and is compatible with experimental work).

4.3.2.3. *Analysis of effective configurations of the knowledgeable individuals.* What configuration of knowledgeable individuals is most effective in guiding the mass of ignorant individuals to the goal? We run the simulation with five possible configurations of the informed entities (configurations shown in Figure 4.2). The first configuration constrains the informed individuals to travel through the centre of the group (configuration 1). The second configuration allows the informed individuals to be distributed around the perimeter of the ignorant group (configuration 2). We have already used these configurations in Section 4.3. The third is a compromise between the first two, where the informed units are distributed within the group (configuration 3). Beekman et al. (2006) suggest that the scout bees fly in the top portion of the swarm of workers, sandwiching the swarm between themselves and the ground. We therefore allow the informed individuals to fly in parallel formation on one side of the ignorant members (configuration 4). We include a reflective boundary in configuration 4 to simulate the effect of the ground (configuration 5). Lastly, once we have examined these first five scenarios, we shall find it useful to distribute knowledgeable individuals both on the periphery and throughout the group (configuration 6). These configurations are for the initial distributions of the knowledgeable individuals; however we know from Figures 4.5, 4.9 and 4.10 that the group tend to stay with the knowledgeable individuals throughout the simulation.

We firstly allow our uninformed individuals to form an organised group, travelling in an arbitrary direction. After some time in the simulation has elapsed, we introduce a small number of informed individuals to the group (Section 4.2). The informed individuals move with paths of travel aligned with the x-axis and were dispersed in certain formations amongst the group (Figure 4.4).

We examine the uninformed groups' final directions of travel using Lemma 8 (testing differences between several group mean directions), to see whether there is in fact a difference between the five configurations. The approximating distribution of the test statistic $2T$ follows a χ^2_8 distribution ($q = 3$, $m = 5$). The result of the hypothesis tests indicates there is some significant difference between the resulting directions of the five simulations (p-value is small, test statistic is 5963.26). At least one of the five groups of ignorant individuals has a different average direction compared to the others.

We test each of the first five configurations using Lemma 7 (testing that a directional sample has a particular average direction), to assess if the resulting directions can be regarded as aligning with the x-axis (the results are summarised in Table 4.1). Results from two configurations stand out as having samples of directions that can be regarded as coinciding with the direction of the goal. Those configurations are configuration 1 (p-value is 0.38, test statistic is 1.95) and configuration 3 (see previously discussed work in Section 4.3.1.2; p-value is 0.17, test statistic is 3.49). From the results of the hypothesis tests, configuration 2 does not appear to be an effective one for facilitating guidance.

We can divide the configurations into two classifications. One classification where the knowledgeable individuals impact is felt in all directions (configurations 1 and 3) and the second, where the knowledgeable individuals are based on the perimeter of the group (configurations 2, 4 and 5). It appears that the former category is more successful for guiding the group, as the knowledgeable individuals have more impact due to their positioning. We examine the former classification in more detail. We can test in a pairwise sense (using Lemma 8) that the average directions of the results of configurations 1 and 3 are coincidental; the directional sample indicates that the hypothesis of equal directions is possible, subject to fluctuations in the data (a moderate p-value of 0.06, test statistic is 5.80).

Armed with the information that configurations where the knowledgeable individual's influence are effective once the said individuals are distributed within the group, and are ineffective when these individuals are based on the perimeter of the group, we examine an intermediate configuration. We distribute some of the knowledgeable individuals throughout the group, the others on the perimeter (configuration 6, Figure 4.4). The informed individuals move through a portion of the group along a plane. Using Lemma 7 (see Table 4.1), the directions of the naive individuals in this scenario suggest that the group direction can be tentatively regarded as being the goal direction (border-line p-value of 0.05, test statistic is 5.91).

We conclude that configurations 1, 3 and 6 (where knowledgeable individuals are able to influence naive individuals on all sides) are effective for guiding the ignorant mass. Results from these three configurations indicate that the three configurations have coincident average directions (moderate p-value is 0.06, test statistic is 8.94). These predictions can be tested in a very real sense. If scout bees can be marked by paint or with electronic equipment and their trajectories recorded during flight, we can examine the trajectories to see if the scouts fly through swarm, rather than on the outside.

The configurations with knowledgeable individuals flying on one side of the group (configuration 4 and 5) are not effective for inducing the ignorant group to follow. In configuration 4, the ignorant individuals are able to escape the influence of the informed members. During the simulation of configuration 5, the ignorant mass consistently elude the knowledgeable members by eventually flying around the informed fixed flight paths and follow their own course. We observed during the simulation that the informed individuals are able to influence the group in the short- and medium-term. Applications of Lemma 7 to the directions of the group during this time period bear this out. For example, for the directions of the group members at the half-way point of the simulation, the test statistic from Lemma 7 has the value of 5.72 and a moderate p-value of 0.06. At this point, the directional data suggests the group direction may be aligned with the x-axis. As time progresses, the group moves beyond the reach of the knowledgeable members. This does not suggest that the proposition that the scout bees move through the top portion of the swarm (Beekman et al. 2006) is incorrect in the long-run; to properly investigate this idea the simulation needs to allow the knowledgeable members to have the flexibility to adjust their flight paths with movements of the group.

4.3.2.4. *Effects of stochastic components in the directed motion model.* We consider the impact of introducing a stochastic component to the directed motion model, which has been discussed in Sections 3.2.2 and 3.3.2. This stochastic component affects only the naive group members in the simulation. Recall, the key parameter in the Fisher distribution controlling the level of stochasticity is the concentration parameter κ. As mentioned in Section 3.2.2, small values of the concentration parameter κ lead to a nearly Uniform spherical distribution and large values of κ cause the Fisher distribution to collapse to a point distribution. Hence, we expect with lower values of κ, there will be a corresponding reduction in the ability of the knowledgeable individuals to influence the group.

We simulate the directed motion model for various concentration parameters ($N = 100$; $N_{informed} = 5$; $\Delta r_o = 17.5$, $\Delta r_a = 2$, $T = 200$, $\Delta r_r = 1$, $\delta = 330°$, $\gamma = 400°$/unit time). We show the polarisations of the naive group of individuals in Figure 4.19. For all values of κ, there is a consistently low associated polarisation. Using the hypothesis test of the alignment of the group with the x-axis (Lemma 7), we show the corresponding p-values and values of κ. None of these p-values indicate that the naive groups' general direction can be regarded as coinciding with the goal direction, for all the values of κ. We know from work in Section 3.3.2 on the collective motion model, that large values of κ result in self-organised groups. Yet, in the stochastic version of the directed motion model, organised groups don't occur. It seems that the combined effects of randomness and the 'pointing' individuals are non-linear and inhibit the naive individuals' ability to follow the informed individuals.

We provide a more extensive analysis for $\kappa = 100$. Figures 4.20, 4.21, 4.22 and 4.23 show the results of a simulation of the directed motion model, where the concentration parameter κ is set to 100. The

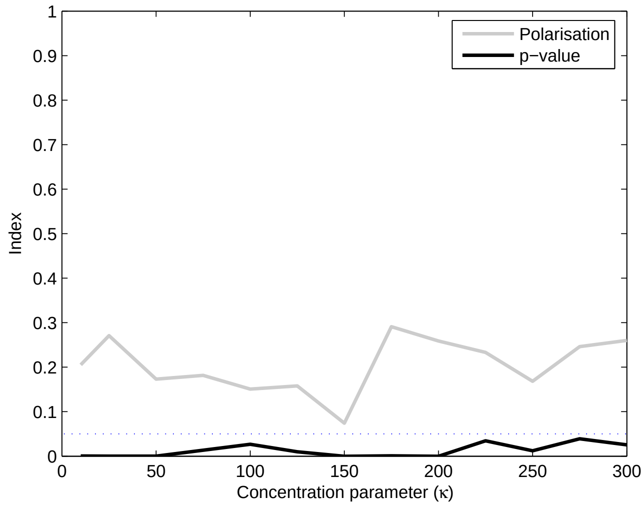

FIGURE 4.19. Polarisations and p-values (Lemma 7) for various values of the concentration parameter (κ) in the directed motion model. The dashed line indicates the 5% significance level.

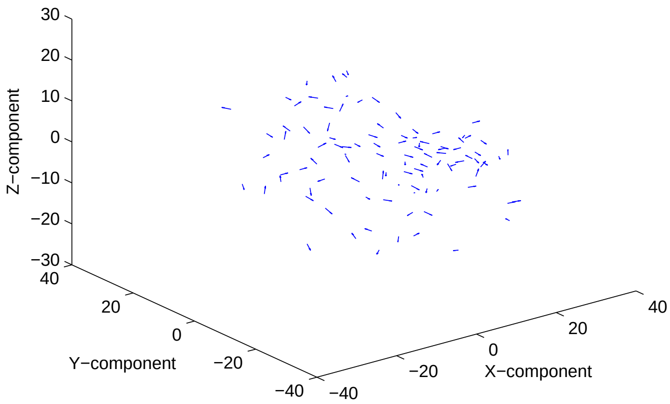

FIGURE 4.20. Simulation of the stochastic version of directed motion model. The concentration parameter (κ) is set to 100. Model parameters of the model are the same as those used in Figure 3.10.

individuals in the simulation have not organised themselves, their positions resemble swarm behaviour (Figure 4.20). Figure 4.21 shows the actions of the centre of the group and the average group direction during the simulation. The centre of the group has a slight tendency to drift along the x-axis, but at a reduced rate in comparison to the simulations (Sections 4.3.1.1 and 4.3.1.2). The deterministic spherical means fluctuate greatly in time. While the x-component of the spherical mean tends to stay in the positive realm, the y- and z-components oscillate over the entire spectrum of values. Polarisations in Figure 4.22 show little evidence of self-organising into an aligned group. A histogram of net to gross displacement ratios (Figure 4.23) shows the majority of *NGDR*'s are distributed towards the lower end of the spectrum, the individuals have not been travelling in linear paths.

We conclude that stochastic components in the directed motion model are not conducive to successful directed motion. The ignorant members have too many competing effects upon themselves, between the influence of the knowledgeable individuals and the stochastic effects.

4.4. Summary

Having gained a greater understanding about the collective motion model in Chapter 3, we were able to adapt that model for this chapter. We have allowed a prescribed number of knowledgeable individuals (these individuals move in a straight line and don't obey the alignment, attraction and repulsion rules, otherwise they are indistinguishable from the other group members) to travel through the collective motion model, 'pointing' in the direction of the goal. We simulate this directed motion model and use the descriptive statistics and hypothesis tests from Chapter 2 to analyse the results.

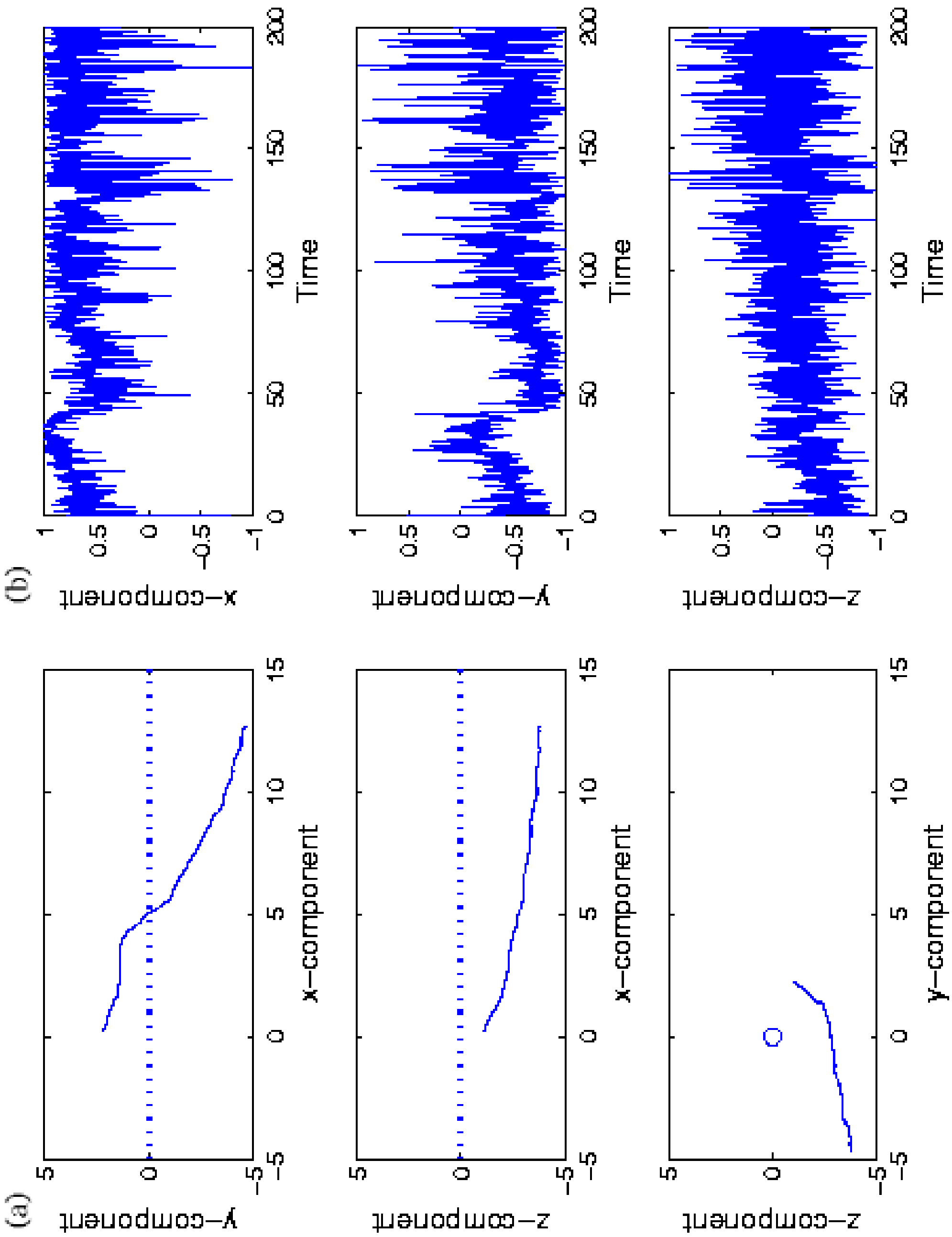

Figure 4.21. Simulation of the stochastic version of directed motion model. The concentration parameter (κ) is set to 100. Column (a) shows the movement of the group centre, column (b) shows the spherical mean.

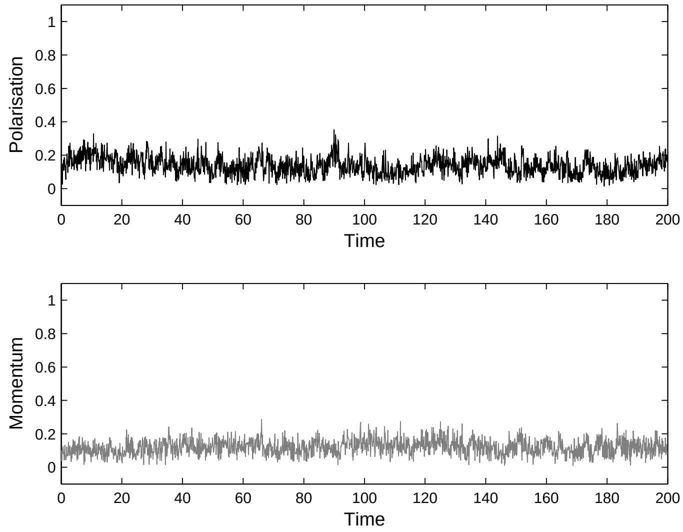

Figure 4.22. Polarisations and angular momenta resulting from the model in Figure 4.21.

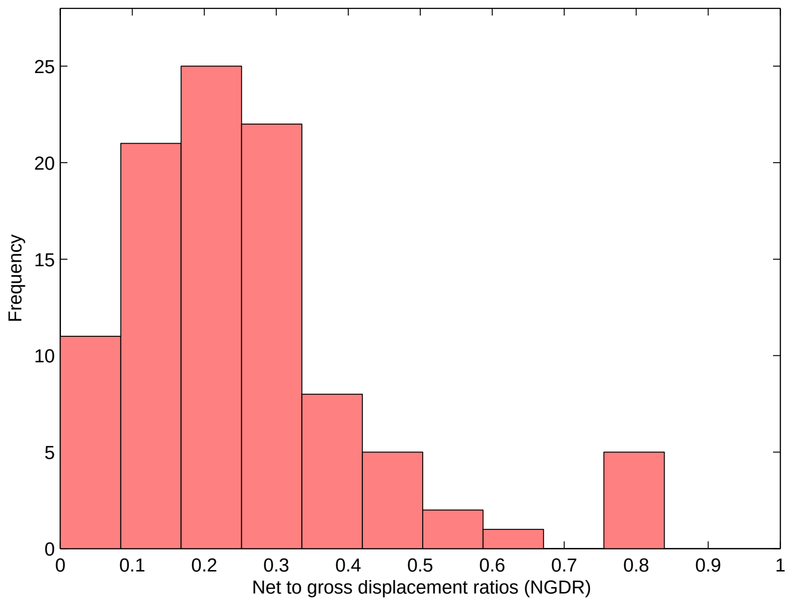

Figure 4.23. Net to gross displacement ratios resulting from the model in Figure 4.21.

We illustrate the advantages in the statistical techniques outlined in this thesis, over existing methods employed in literature. Neither Couzin et al. (2005) or Janson et al. (2005) take into account the variability within their directional samples. We show that with a decreasing variability within the sample (resulting in a more aligned group), analysis using 'normalised' angular deviation (Couzin et al. 2005) falsely accepts the hypothesis that the sample of directions are aligned in a particular mean direction. Our methods correctly reject this possibility. The chances of accepting the null hypothesis when the null is incorrect is called a *Type 2 error* in statistical literature. Because our methods take the group alignment into account and detect a true difference between the hypothesised and true means, our tests are more powerful (in a statistical sense) than previous methods.

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. We allow the informed group members to be distributed around the perimeter of the group and concentrated through the centre. By using the tools from Chapter 2 and the actions of the ignorant group over time, we show that the mechanism of 'pointing' knowledgeable individuals is plausible for successful guidance of the ignorant group in most of these scenarios. When the knowledgeable individuals are distributed on the periphery of the group, they are less successful in their guidance. Individuals flying through the naive group leads to more efficient guidance. This work backs up experimental observations (Beekman et al. 2006) that the main trigger causing honeybees to organise in practice is a visual one (chemical and vibrational cues being less important for successful guidance). Individuals, whether they are in a honeybee swarm or cyber space, 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 the knowledgeable individuals being identical in all other respects to the other group members. These results are in agreement with Janson et al. (2005).

We have shown that this mechanism is successful, even with a relatively small percentage of knowledgeable individuals present to guide the group and provided that the knowledgeable individuals move with a speed as least as great as those of the ignorant group members. We predict that a ratio of 4% or 5% informed individuals is adequate for successful guidance, this is in agreement with Couzin et al. (2005). However, this contradicts Janson et al. (2005), who predict that ratios of 1% or 2.5% are adequate, as we see no evidence to suggest this is the case. Janson et al. (2005) show that the informed individuals must travel at a speed at least as large as the group for successful guidance. We consider a larger ranges of speeds than their article does and our results suggest that informed individuals travelling at 80% or 90% of the speed of the group may also be adequate for guidance. Overall, a ratio of 5% informed individuals travelling at least as fast as the group seems to be a reasonable heuristic rule for successful guidance of the naive group.

The success of the guidance depends on the distribution of the knowledgeable individuals throughout the group. The particular distributions that are successful tend to be ones where the knowledgeable individuals have more impact on the group members, by benefit of interactions on all sides with the naive individuals. Errors in decision making have a large impact on ignorant individual's abilities to react to the knowledgeable members, even small stochastic effects cause the organised state of the group to be disrupted.

It could be possible to improve on this directed motion model by 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 have the ability to travel with the ignorant group. Allowing the individuals to have a more complex mechanism to move to the rear of the group (once they have moved past the group front) is another possibility. This largely depends on the objective of the researcher. Recall the statistician George Box's quote "All models are wrong; some models are useful" (Box & Draper 1987). The principle of Occam's razor suggests we adopt the simplest plausible model to explain the situation, this model will be 'wrong' in the sense of Box. However, so will a more complicated model. The point of the directed motion model is to show that guidance by 'pointing' knowledgeable individuals is a plausible theory and the model presented in this thesis has been useful in doing so. We can never model this situation in its entirety. We have stripped the elements of the situation down to those we feel are essential to the situation and shown that these elements produce significant behavioural changes to the group. It is true the model in this thesis is an oversimplification of the situation, yet a more complicated model giving more flexibility to knowledgeable individuals will still be 'wrong'. Researchers will need to question whether the expected gains of a more complicated model are worth the effort.

A worthwhile improvement to the model may be to examine successful distributions of knowledgeable individuals throughout the group. A mechanism could be put into place to allow the knowledgeable individuals to maintain a similar position in the group, throughout the duration of the simulation. In this chapter, we have examined examples of leadership by example, the naive individuals may or may not follow the knowledgeable individuals' rigid paths. By allowing the knowledgeable individuals to adjust their movements in relation to movements of the naive group, this becomes a example of leadership by sheparding. It could then be possible to more rigorously test the idea of Beekman et al. (2006), that the scout bees fly in the top portion of the swarm of workers.