A Model Of Spatial Sorting In Animal Groups, With An Application To Honeybee Swarm Movement

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Abstract

A self-organising model of group formation (in three dimensional space) based on simple rules of avoidance, attraction and alignment is used to examine the spatial dynamics of animal groups. We discuss the different types of behaviour resulting from this model due to changes in these rules. In particular, the phenomenon of honeybee swarms migrating to a new nesting site is examined. The vast majority of the migrating swarm is uninformed as to the particular location of their new home. A small number of bees (in the swarm) have prior knowledge of the new location and guide the rest of the swarm to the new site. The model investigates a hypothesis of how this guidance procedure occurs. We conclude from the results of the model that one possible way for this process to occur is for the knowledgeable bees to guide the other members of the swarm with spatial cues.

Key words: Self-organisation, spherical probability distribution, swarming behaviour, randomisation tests, Apis mellifera.

1 Introduction

Physical aggregation occurs in a diverse range of animals, from small and uncomplicated entities such as bacteria, to the larger ones like whales. Aggregation occurs in large and small groups. African army ant colonies (*Dorylus (Anomma) nigricans*) raid in swarms composed of millions of workers. Killer whales (*Orcinus orca*) tend to hunt in pods of smaller numbers (transient pods typically contain less than ten individuals). Other animals that congregate in

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this fashion include honeybees (*Apis mellifera*) and schools of migrating fishes (such as herring (*Clupea harengus*)). Further discussion can be found in Parrish *et al.* (2002) and Camazine *et al.* (2001).

Animals form groups for numerous reasons. A large group offers protection from predators because the larger numbers lower the chances of being caught. In addition, groups can perform organised evasive manoeuvres to outwit a predator. These evasive actions include groups splitting up (exploding) into individuals or forming tightly-knit ball shaped clusters, both designed to confuse predators. Highly coherent, aligned arrangements of individuals offer obvious aerodynamic or hydrodynamic advantages, resulting in energy savings. Other advantages of groups include socialising and more efficient foraging.

Practically speaking, in many species it is difficult to obtain empirical data on group behaviour. Models, either mathematical or computational, can provide useful insights into aggregative behaviour. Mathematical models of social aggregations have used a variety of approaches. Models can be categorised into either Eulerian or Lagrangian approaches. A Lagrangian approach considers the position and velocity of each individual within the group. An Eulerian approach models the density of a population over space at a particular time. Classically, Eulerian models have been favoured, as they lead to well-studied partial differential equations (Okubo, 1980). Grünbaum & Okubo (1994) discuss both possibilities in detail. In this article we will adopt a Lagrangian modelling approach.

Self-organisation is a process in which 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). With a full knowledge of the individuals of the group and of the interactions between individuals, the pattern obtained from the process of self organisation could not be deduced - implying that there is something more complicated than simple additive interactions (Anderson, 2002) and that nonlinear effects may be important.

The process of self organisation can be implemented in animal groups by either direct or indirect social interactions and communications between individual group members. We develop a model for the movement of animal groups based on direct social interactions between individual group members. We use this general model to explore the effects of individual behaviour on group behaviour and then apply the general model to a specific problem in honeybee groups.

1.1 Introduction: honeybees

A typical honey bee (*Apis mellifera*) colony consists of approximately 25,000 adult worker bees, 1000 or more male drones and a single queen. Honeybee colonies reproduce by splitting into two. One group stays with the original home, whilst the other moves off to a new location. Typically in spring a swarm of honey bees leaves the hive and settles in a cluster, whilst 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 via the waggle dance. After some time, one dance 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 by various signals (Seeley & Buhrman (1999), Myerscough (2003), Donahoe *et al.* (2003)).

In a swarm of approximately 10,000 bees, approximately 5% are scouts and these are responsible for guiding the swarm toward the new home. The rest of the bees are uninformed as to the whereabouts of the new home.

One possible way for scouts to guide the swarm to their new home is to fly continuously through the swarm, with flight paths aligned toward the direction of the new home. This follows the observation that some bees have been seen to fly rapidly through the swarm, "pointing" in the direction of the new home (Lindauer (1971), Janson *et al.* (2004)). Having developed a model for honeybee swarming, we use this model to investigate this idea of scouts guiding the rest of the uninformed swarm.

2 Model formulation

Couzin *et al.* (2002) devised a self-organising model of group formation in three-dimensional space, with the intention of explaining interactions in aggregative behaviour. We use their model as a base and expand upon it, in order to apply it to honeybee swarms and attempt to explain how scout bees may guide the rest of the uninformed swarm to the colonies' new home.

The model of Couzin *et al.* (2002) simulates the behaviour of individuals as the result of local repulsions, alignments and attractive tendencies, based on the position and orientation of individuals relative to one another.

Within the model, there are N individuals ($i = 1, \ldots, N$), each with a unique position vector $\vec{c}_i(t)$ and unit direction vector $\vec{v}_i(t)$ at time t. Time is partitioned into discrete time steps of an equal interval width of τ (defined in the simulation to be 0.1 time units). Each individual assesses other individuals within a local neighbourhood, in order to determine a desired direction vector ($\vec{d_i}(t+\tau)$) to travel.

An individual attempts to maintain a minimum distance from its immediate neighbours, who are within a zone of repulsion (modelled as a sphere with radius r_r). If an individual has n_r neighbours in the zone of repulsion at time t, then the direction vector generated by interactions with these other individuals in the zone of repulsion is defined as:

$$\vec{d}_{r,i}(t+\tau) = -\frac{\sum_{j\neq i}^{n_r} \vec{r}_{i,j}(t)}{|\sum_{j\neq i}^{n_r} \vec{r}_{i,j}(t)|}, \quad \text{where } \vec{r}_{i,j}(t) = \frac{(\vec{c}_j(t) - \vec{c}_i(t))}{|\vec{c}_j(t) - \vec{c}_i(t)|} \ . \tag{1}$$

Here $\vec{r}_{i,j}(t)$ is the unit vector in the direction of neighbour j ($j = 1, \ldots, N$, $j \neq i$). Individuals respond to neighbours in the zone of repulsion with the highest priority, so if neighbours are present in an individual's zone of repulsion ($n_r > 0$), then $\vec{d_i}(t+\tau) = \vec{d}_{r,i}(t+\tau)$. The individual's response is equally weighted for each neighbour in the zone of repulsion.

If there are no neighbours within the zone of repulsion, individual i then responds to neighbours within the zone of orientation and zone of attraction. Both of these zones are spherical (with radii r_o and r_a, respectively), except for a blind volume defined behind individual i such that neighbours cannot be detected. This volume is a cone with interior angle of $(360-\delta)^\circ$, where δ (degrees) is defined as the field of perception. There are n_o detectable neighbours present in the zone of orientation, such that $r_r \leq |\vec{c}_j(t) - \vec{c}_i(t)| < r_o$. Similarly, there are n_a detectable neighbours in the zone of attraction for whom the condition $r_o \leq |\vec{c}_j(t) - \vec{c}_i(t)| \leq r_a$ is satisfied. The desired direction vector arising from the zone of orientation is defined as:

$$\vec{d}_{o,i}(t+\tau) = \frac{\sum_{j\neq i}^{n_o} \vec{v}_j(t)}{|\sum_{j\neq i}^{n_r} \vec{v}_j(t)|} \tag{2}$$

and the desired direction vector in the zone of attraction is:

$$\vec{d}_{a,i}(t+\tau) = \frac{\sum_{j\neq i}^{n_a} \vec{r}_{i,j}(t)}{|\sum_{j\neq i}^{n_a} \vec{r}_{i,j}(t)|} \ . \tag{3}$$

If neighbours are found only in the zone of orientation, then $\vec{d_i}(t+\tau) = \vec{d}_{o,i}(t+\tau)$. If the neighbours are only in the zone of attraction, $\vec{d_i}(t+\tau) = \vec{d}_{a,i}(t+\tau)$. If neighbours are present in both zones, the desired direction vector becomes the average of $\vec{d}_{a,i}(t)$ and $\vec{d}_{o,i}(t)$. In the situation where the social forces cancel out and give a zero vector as a result or no individuals are detected in any of the zones around individual i, then the individual proceeds on its original course ($\vec{d}_i(t+\tau) = \vec{v}_i(t)$).

Once this assessment has been carried out for each individual in the group, the group members orientate towards their individual desired direction vectors ($\vec{d}_i(t+\tau)$) by the turning rate γ. Provided the angle between the vectors $\vec{v}_i(t)$ and $\vec{d}_i(t+\tau)$ is less than the maximum turning angle $\gamma\tau$, then $\vec{v}_i(t+\tau) = \vec{d}_i(t+\tau)$. If not, the individual rotates by $\gamma\tau$ towards the desired direction vector. This is the approach of Couzin *et al.* (2002). We now modify the model for our own purposes.

To introduce speed into the model, we update the array of position coordinates with the new positions of the individuals (we assume that speeds of the system components are constant). Suppose at time t, individual i with position $\vec{c}_i(t)$, travels with speed s_i in the direction $\vec{v}_i(t+\tau)$. Between time t and $t+\tau$, individual i travels a distance $\Delta_i = \tau s_i$. The individual travels in the direction $\vec{v}_i(t+\tau) \times \Delta_i$. The updated position at time $t+\tau$ is:

$$\vec{c}_i(t+\tau) = \vec{c}_i(t) + \vec{v}_i(t+\tau) \times \Delta_i \ . \tag{4}$$

2.1 Simulating the scout guidance hypothesis

Let the number of scouts in the model be N_{scouts} and the number of workers is $N_{workers} = N - N_{scouts}$. The scouts fly with a given speed from random starting positions within the swarm, towards the goal (the new home). For convenience, this direction is assumed to coincide with the positive x-axis direction. To update the scouts position at each time step τ, we can use (4).

We need to introduce a condition to allow the scouts to fly back through the swarm when they fly past the swarm front. We assume that the swarm is approximately spherical in shape. We define the centre of the group as the mean of the individual position vectors:

$$\vec{c}_{group}(t) = \frac{1}{N_{workers}} \sum_{i=1}^{N_{workers}} \vec{c}_i(t) \ . \tag{5}$$

Let the origin of our coordinate system coincide with the centre of the group. We assume scouts fly in the x-direction, hence the location of the front of the swarm becomes the maximum of the x-coordinates of the workers. Let $\vec{c}_{scout,x}(t)$ denote the x-coordinate of the scout in question at time t and $\vec{c}_{group,x}(t)$ be the x-coordinate of the centre of the group of workers. If the distance between the scouts' position and the centre of the group is larger than the distance between the centre of the group and the maximum x-coordinate (provided $\vec{c}_{scout,x}(t) - \vec{c}_{group,x}(t) > 0$), then the scout is assumed to have flown beyond the limits of the swarm. If so, the scout is then moved to a corresponding position at the rear of the swarm and flies through the swarm again, in the direction of the goal.

2.2 Random errors in decision making

Decision making in animal groups is subject to error. To simulate this, the individual worker's desired direction vector calculated previously is modified by an angle drawn at random from a spherical probability distribution.

Spherical probability distributions are characterised by their probability density, which is defined as the probability per unit area on the surface of a unit sphere.

We commence by defining a coordinate system. We define the point $P = (\lambda, \mu, \nu)$ in terms of three dimensional Cartesian co-ordinates and let O be the origin. The point P can also be determined by its polar coordinates in the following fashion. Let longitude be measured in the anticlockwise sense from the x-axis and be denoted by ϕ. The distance from O (or the length of OP) is denoted by r. The value of r is 1 (a unit sphere). Instead of latitude (the angular distance from the equator), we use the colatitude (the complement to $90°$), denoted θ. The relationships follow $\lambda = \cos(\phi)\sin(\theta)$, $\mu = \sin(\phi)\sin(\theta)$, $\nu = \cos(\theta)$. Let colatitude and longitude be independently distributed random variables, such that $\theta \in [0, \pi]$ and $\phi \in [0, 2\pi)$.

We perturb the desired direction vector by an angle drawn at random from the Fisher distribution. This distribution closely approximates the spherically wrapped Gaussian distribution (Roberts & Ursell, 1960). We define the probability density function of the Fisher distribution, $F((\alpha, \beta), \kappa)$, on a unit sphere as:

$$f(\theta, \phi) = C_F \sin\theta e^{\kappa(\sin\theta \sin\alpha \cos(\phi-\beta) + \cos\theta \cos\alpha)} \tag{6}$$

$$\text{such that } C_F = \frac{\kappa}{2\pi(e^{\kappa} - e^{-\kappa})},$$

where (α,β) is the mean direction (in polar coordinates) and κ is the concentration parameter, such that $\kappa \geq 0$ (Fisher *et al.*, 1987). The angle ϕ is uniformly distributed on the interval $[0, 2\pi)$. The parameter κ controls the spread of the distribution. The larger the value of κ, the more the probability density function is concentrated towards the direction of (α,β). Fisher *et al.* (1987) give an algorithm for generating a random sample from a Fisher distribution. We simulate error by modifying each individuals' desired direction vector by rotating it by a random angle from a Fisher probability distribution.

2.3 Descriptive statistics

To analyse the collective behaviour of the model, a variety of descriptive statistics are employed. The group polarisation ($p_{group}(t)$) measures the degree of alignment amongst individuals within the group. Angular momentum ($m_{group}(t)$) is a measure of the degree of rotation of the group around the group centre. The group centre ($\vec{c}_{group}(t)$) is calculated as the mean of the individual position vectors (5). These statistics are defined by Couzin *et al.* (2002) in the following way:

$$p_{group}(t) = \frac{1}{N_{workers}} \left| \sum_{i=1}^{N_{workers}} \vec{v}_i(t) \right| \tag{7}$$

$$m_{group}(t) = \frac{1}{N_{workers}} \left| \sum_{i=1}^{N_{workers}} \vec{r}_{i,c}(t) \times \vec{v}_i(t) \right| \tag{8}$$

$$\text{where } \vec{r}_{i,c}(t) = \frac{\vec{c}_i(t) - \vec{c}_{group}(t)}{|\vec{c}_i(t) - \vec{c}_{group}|} \ .$$

These statistics are useful in characterising the different types of collective behaviour emerging from the model. Couzin *et al.* (2002) identifies four distinct types of behaviour of particular interest. A swarm is an unorganised group of individuals with low polarisation and momentum. A torus arrangement can occur when individuals rotate indefinitely around an empty core; polarisation is low, but group momentum is large. A dynamic parallel group is a loosely aligned group of individuals, with a large polarisation and low group momentum. Lastly, a highly parallel group is an extremely aligned arrangement where individual members are travelling in the same direction, the group has a very large polarisation and small momentum.

In addition, we also require a measure of average direction of the group. Let the direction cosines $(\lambda_i, \mu_i, \nu_i)$ be N observation vectors ($i = 1, \ldots, N$). Define

$$R_\lambda = \sum_{i=1}^{N} \lambda_i \ , \quad R_\mu = \sum_{i=1}^{N} \mu_i \ , \quad R_\nu = \sum_{i=1}^{N} \nu_i \ . \tag{9}$$

The spherical mean is:

$$\left(\bar{\lambda}, \bar{\mu}, \bar{\nu}\right) = \frac{1}{R} \left(R_\lambda, R_\mu, R_\nu\right) \tag{10}$$

where $R^2 = R_\lambda^2 + R_\mu^2 + R_\nu^2$. If the observations are clustered around a particular direction, the value that R takes must be close to N. Conversely, if the observations are dispersed (such as in the uniform case), the value of R will be small. R is a measure of concentration about the mean direction and we may define the spherical variance as:

$$S = 1 - \frac{R}{N} \tag{11}$$

where $0 \leq S \leq 1$ (Mardia, 1971).

2.4 Randomisation tests

When a model of interest is investigated using a classical hypothesis test, we can regard it as alternative to a null hypothesis of randomness. That is, the model under investigation suggests that there will be a tendency for a certain type of pattern to appear in the data and the null hypothesis says that if this pattern is present, then it is due to a random effect of observations in a random order.

Randomisation testing is a way of determining whether the null hypothesis is reasonable in this type of situation. A test statistic is selected to measure the extent to which the data shows the pattern in question. The observed test statistic value is compared with the distribution of the test statistics obtained by randomly reordering the data. If the null hypothesis is true then all possible orders of the data are equally likely to have occurred. The observed data order is one of the equally likely orderings and the test statistic from the observed data should appear as a typical value from the randomisation distribution of test statistics obtained by randomly reordering the data. If this is not the case, the test statistic for the observed data is "significant". The null hypothesis is discredited and the alternative hypothesis is considered the more reasonable (Manly, 1997).

In the context of the self-organising model, randomisation tests have an advantage over standard statistical methods: with the former, it is relatively simple to take into account the peculiarities of the situation using non-standard test statistics. This advantage will be applied in Section 3.2.

3 Results and discussion

3.1 General model

To analyse the collective behaviour of the model, we examine the result of altering the width of the zones of attraction and orientation, and how they affect the behaviour of the group. We refer to the types of group behaviour discussed in Section 2.3. Figures 1 and 2 show the effects of altering the width of the zones of attraction and orientation on group polarisation and momentum. Define the width of the zone of attraction as $\Delta r_a = r_a - r_o$ and the width of the zone of orientation as $\Delta r_o = r_o - r_r$. Fragmentary or explosion-like behaviour (indicated by the region marked (a) in Figures 1 and 2) results in low momentum and polarisations: this occurs when Δr_a and Δr_o are both relatively small. The repulsive forces dominate the behaviour of individuals, forcing them apart from one another. The effectiveness of this behaviour has been demonstrated in aquatic animals. The aim of this behaviour is to present a predator with multiple moving targets, making it difficult to single out solitary vulnerable prey (Wittenberger, 1981). Individuals can form a single cluster when Δr_a is relatively large, whilst Δr_o is of a medium size (region (c)). The strong attractive forces dominate and keep the individuals together as a whole. Several unorganised clusters of individuals are formed when Δr_a and Δr_o are small, but not small enough to cause fragmentary behaviour (region (g)). Swarm behaviour (indicated by region (b)) occurs when Δr_a is a medium to large size and Δr_o is small. The individuals do not have the opportunity to align themselves and their respective attractive and repulsive tendencies balance out to create unorganised behaviour. This formation is used by terrestrial, aquatic and airbourne animals alike, for predator evasion. The motivation for this behaviour is that individuals can gain protection from predators by heading toward the center of the group and thereby shielding themselves using other individuals. An example of this behaviour occurs in starling flocks, where individual starlings employ this tactic when under attack from falcons (Wittenberger, 1981).

Dynamic parallel behaviour is typical when both Δr_a and Δr_o are medium sized (region (d)). If the attraction zone decreases, several groups of aligned individuals are created. An optimal hydrodynamic arrangement is not necessarily effective for predator evasion. Predation has the effect of causing fish to organise themselves in a less hydrodynamically efficient arrangement (a dynamic parallel group) that is more likely to reduce predator risk (Krause & Ruxton, 2002). As the size of Δr_o increases, the group of individuals form a more cohesive arrangement as a highly parallel group (region (e)). Migratory fish have a tendency to travel in this fashion (seabass, *Centropristis striata* and tuna species) to take advantage of energy savings (Krause & Ruxton, 2002). As the size of Δr_a decreases, there is a disincentive for individuals to stay together, should they become separated from the main group (region (f)).

3.2 Scout model

Now the combinations of parameters which give rise to aligned groups are known, we use these to generate parallel behaviour and use this to test the scout guidance hypothesis.

We need to choose how to distribute the scouts amongst the swarm. One arrangement is to allow the scouts to fly along the same flight path (one after another). This may be interpreted as the scouts following one another closely, pointing in the direction of the goal and moving with a velocity larger than that of the workers. Figure 3 illustrates an example of this situation. There are 5 scouts present in the model, flying one behind the other and these scouts are available to influence the group from the outset of the simulation. The graphs of the centre of the group's travel path (through the time period of the simulation) show that the group's general direction of travel is consistent with the scouts' flight path. The graphs of the y-x and z-x components of the centre of the group travel path show a distinct drift along the x-axis. The z-y plane shows some oscillation in the plane. This oscillation is negligible in comparison with the movement in the z-x and y-x planes. The mean direction components over time show a tendency for the group average direction to align with the direction of the scouts' path (along the x-axis). The x-component quickly tends towards the value of 1, whilst the z- and y-components oscillate around the zero value. Further evidence is provided when the polarisation and spherical variance over the time period are examined. Both graphs suggest a highly polarised cohesive group (with low rotational movement) moving throughout the simulation. Given that the groups' travel path is generally in the x-direction towards the goal and the group is highly ordered, it leads to the conclusion that the individual workers have been influenced by the scouts (rather than heading off in an arbitrary direction).

An arrangement of scouts distributed around the perimeter of the group is also useful to enable scouts to influence workers, by enabling any stragglers from the workers to be redirected by the scouts. Figure 4 shows the results of a simulation with this arrangement. An examination of the x-, y-, z- components of the mean direction and the centre of the groups' travel show a tendency for the group to move in the positive x-direction. The centre of groups' travel path oscillates between the scouts' positions in the y-z plane. The arrangement of scouts' distributed around the outside of the group of workers has effectively contained the workers. The graphs of polarisation, spherical variance and momentum suggest an organised, cohesive group structure is maintained throughout the simulation.

Previously, scouts have been present to influence the group from the beginning of the simulation. In Figures 5 and 6, the workers are allowed to form an organised group, free from any influence of scouts. Once this group has been formed, scouts are introduced to see if the workers alter their behaviour to align with the scouts flight paths. The flight paths of the scouts in these two simulations have the same configurations of the previous ones (Figures 3 and 4, respectively). In both simulations, the workers' direction of travel has changed from an arbitrary direction, to be aligned with the flight path of the scouts. The addition of scouts to a cohesive group of workers travelling in an arbitrary direction will cause the group to change their behaviour. These two simulations provide evidence that scouts are able to guide an uninformed group by flying through the group, in a straight line in the direction of the goal. Janson *et al.* (2004) also address the problem of scout guidance. They use more complicated rules which, among other things, allow the scouts to get an errant swarm back on track to the nest site. They do not consider the general case of animal movement and their use of conventional statistical techniques may lead to paradoxical results. We have recognised that our data consists of directions. The methods we present here, using spherical probability theory, better reflects the physical situation being modelled.

The concept of a randomisation test (discussed in Section 2.4) is applied to the results of the simulations incorporating the scout guidance hypothesis. We aim to evaluate how our data has evolved in time and gain some indication as to whether or not the scouts have been able to influence the group during the time period of the simulations. The null hypothesis is that the sample of spherical means of the orientations of the workers is random. Effectively, the alternative is that the workers general direction of travel coincides with the flight paths of the scouts.

Once we have the sample of mean orientations, the spherical mean of this sample is calculated. Define the angle between the spherical mean of the sample and the x-axis, as δ. The angle δ can be calculated using the scalar product of vectors (where $\delta \in [0, \pi]$). The observed angle δ_{obs} is calculated directly from the sample. We define the test statistic, T, as:

$$T = \frac{\delta}{p_{group}} \ , \tag{12}$$

where p_{group} is the polarisation of the sample of mean orientations. A cohesive group ($p_{group} \to 1$) heading towards the direction of the x-axis ($\delta \to 0$) will lead to low values of the test statistic. As the group becomes more disorganised, the value of the test statistic will increase.

Permutations of the data are generated from the polar coordinates θ_i and ϕ_i ($i = 1, ..., 1000$) of the sample. These polar coordinates are randomised 999 times (θ_i and ϕ_i separately, as they have different ranges). From these randomised samples, 999 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. A p-value can be calculated, the probability that a test statistic at least as extreme as that already observed will occur (assuming that the null hypothesis is correct). Small p-values lead to the conclusion that the pattern in the data is unlikely to have arisen by chance alone. In this case, we have a one-sided test, as values of δ close to zero support the alternative alignment hypothesis.

Figure 7 shows histograms of randomised test statistics for the simulations in Figures 3, 4, 5 and 6. The observed test statistics are 0.01255, 0.05352, 0.03748 and 0.13978 for these simulations, respectively. In each case, comparison with the appropriate histogram in Figure 7 leads to the conclusion that the observed test statistics are not typical values from the randomisation distributions. The p-values in each case are low, giving strong evidence against the null hypothesis and leading us to conclude that the current arrangements have not arisen due to chance alone.

Statistics	*Prior*	*Concentrated Scouts*	*Dispersed Scouts*
1st Quartile	1.6230	0.3383	0.9811
Median	1.7840	0.5210	1.1790
3rd Quartile	1.9510	0.6281	1.4190
Mean	1.7720	0.4819	1.1600
std. dev.	0.3365	0.2160	0.3656
N	399	1600	1600

Table 1
Summary statistics for angles of the mean orientation, before and after introduction of scouts (concentrated and dispersed flight paths).

Table 3.2 and Figure 8 represent the values of the angles of the mean orientations (relative to the x-axis) for the data prior to the scouts being introduced to the swarm, and after (calculated at each timestep of the simulation). The data appear in Figures 5 and 6. A comparison of the two distributions of the angles, reveals that the scouts have had a significant impact on the orientations of the groups of workers. The boxplots of angles (post introduction of scouts) show a shift towards the lower end of the scale of angles, in comparison to the distribution of angles before the scouts are present. The distribution of angles of workers who have had the opportunity to be influenced by scouts flying in an arrangement dispersed around the group also shows a less dramatic, but still noticeable, shift towards the lower values of angles. Specifically, the upper and lower quartiles are distinct from the unguided group's distribution of angles. There are only 72 angles (4.5 %) in the sample from the time period before the scouts were introduced that have angles greater than the first quartile of the distribution of angles of the unguided workers. There is evidence that the scouts have had some influence over the swarm.

How fast (relative to the workers) do the scouts have to fly before the workers pay attention to them? To answer the question, we set the speeds of all workers to 1 distance unit/time unit and simulate the scout guidance model for varying scout speeds. The results are shown in Figure 9, where the median of the mean angle between the directions of the workers at each timestep of the simulation (the median of δ) and the x-axis is plotted. An abrupt change in the angles are seen once the speed of the scouts coincides with that of the workers. We conclude that the scouts can influence the workers, provided their speed is at least as large as that of the workers. If the scouts are slower than the workers, the group of workers ignore the scouts. Presumably, the group of workers leave the scouts behind.

3.3 Errors in decision making

We consider the impact of allowing individuals to make errors in their decisions by introducing random angles. As mentioned in Section 2.2, small values of the concentration parameter κ lead to a Uniform spherical model and large values of κ will cause the Fisher distribution to collapse to a point distribution and tend to the deterministic model. Figure 10 where κ is set to 1000, shows what appears to be typical unorganised swarm-like behaviour. The plots of the components of the mean direction of the group show large oscillations and the graphs of the group centres show less of a tendency to move in a similar direction to the scouts (compared with the deterministic models).

How is the influence of the scouts altered by introducing errors in individuals decision making? We simulated the model for various values of κ ($\kappa = 0.5, 1, 10, 100, 1000, 10,000$ and $100,000$). The mean components were smoothed by a moving average filter (with a window of size 10) to reveal general trends. The randomisation test was applied to the smoothed data. Simulations with values of $\kappa = 0.5$ and 1 yielded p-values of 0.198 and 0.136, respectively. All other simulations gave extremely small p-values. Hence, the group of workers were influenced by the scouts (to some extent) for values of κ being 10 and larger.

4 Conclusion

The purpose of this investigation was to construct a model for group interactions and use this to consider how scout honeybees with knowledge of the location of the new home guide a swarm of uninformed workers towards the new site. A three-dimensional model based on simple rules of avoidance, attraction and alignment was formulated and implemented to investigate a hypothesis of guidance; namely that scouts fly continuously through the swarm "pointing" in the direction of the goal or new home.

The behaviour of the general model in relation to the relative sizes of the zones of orientation and attraction has been discussed and we considered the different types of group behaviour arising due to the relationships between the sizes of these zones. Simulations of the scout bee guidance hypothesis have been presented, showing that the group of uninformed workers have a tendency to drift towards the direction of the goal as indicated by the scouts. Notably, if scouts are introduced to an already organised parallel group of workers, the scouts are able to exert enough influence to guide the workers from an arbitrary path to the goal. A statistical test has been formulated to determine whether the scouts have had some influence over the swarm.

The results of these models show that it is plausible that the scouts can guide the uninformed swarm by using spatial cues in this way. This may not be the only way in that scouts guide workers, but it is a reasonable suggestion as a mechanism for guiding a swarm.

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5 Figures

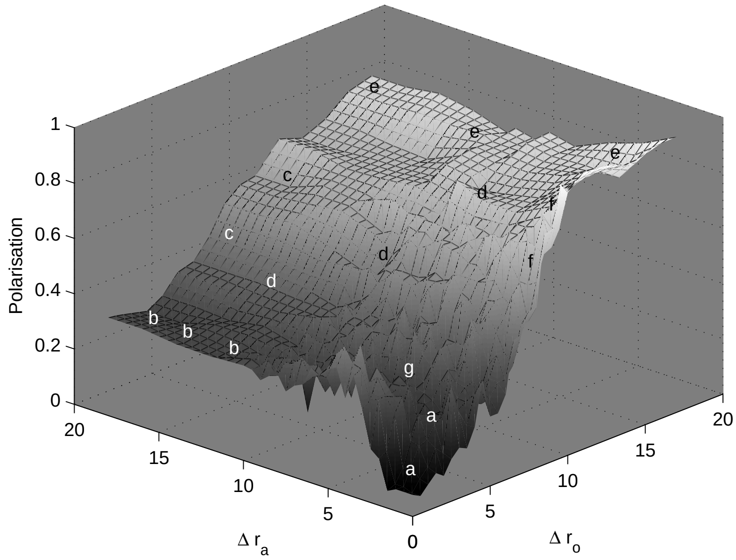

Fig. 1. Effects on group polarisation (p_{group}) from altering the width of the zones of attraction and orientation. Region (a) corresponds to fragmentary behaviour, (b) to swarm behaviour, (c) to a single distinct cluster, (d) to dynamic parallel behaviour, (e) to highly parallel behaviour, (f) to seperate independent groups of highly aligned members and (g) to several unorganised clusters of individuals forming. Values of parameters used are: $N = 100$; $r_r = 1$; $T = 200$; $\tau = 0.1$; $\gamma = 400°$; $\delta = 330°$.

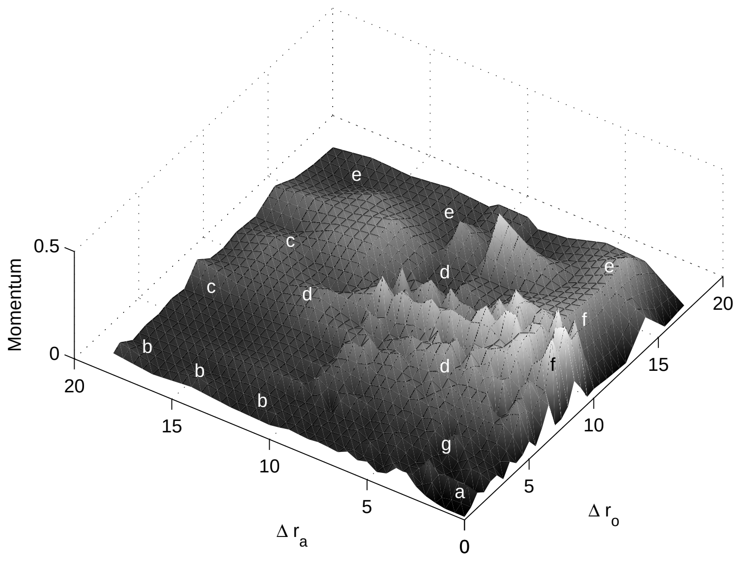

Fig. 2. Effects on group momenta (m_{group}) from altering the width of the zones of attraction and orientation. Regions correspond to those in Figure 1.

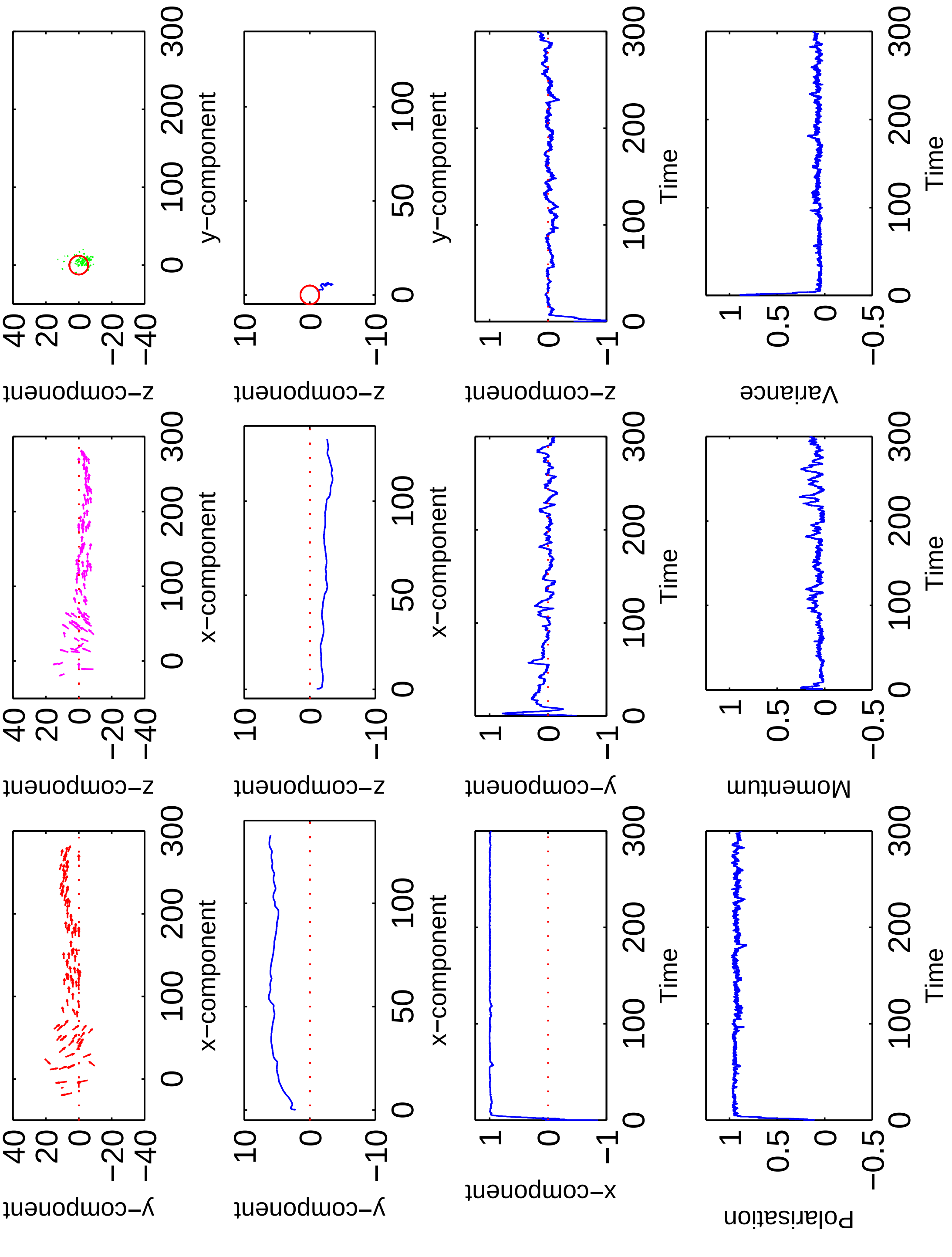

Fig. 3. Simulation of the scout components guiding the worker components of the group to the goal. The scouts' flight paths are coincident with one another, through the centre of the initial positions of the group (indicated by the dashed lines or circles). $N = 100$; $r_r = 1$; $r_o = 15$; $r_a = 16$; $T = 200$; $\tau = 0.1$; $\gamma = 400°$; $\delta = 330°$.

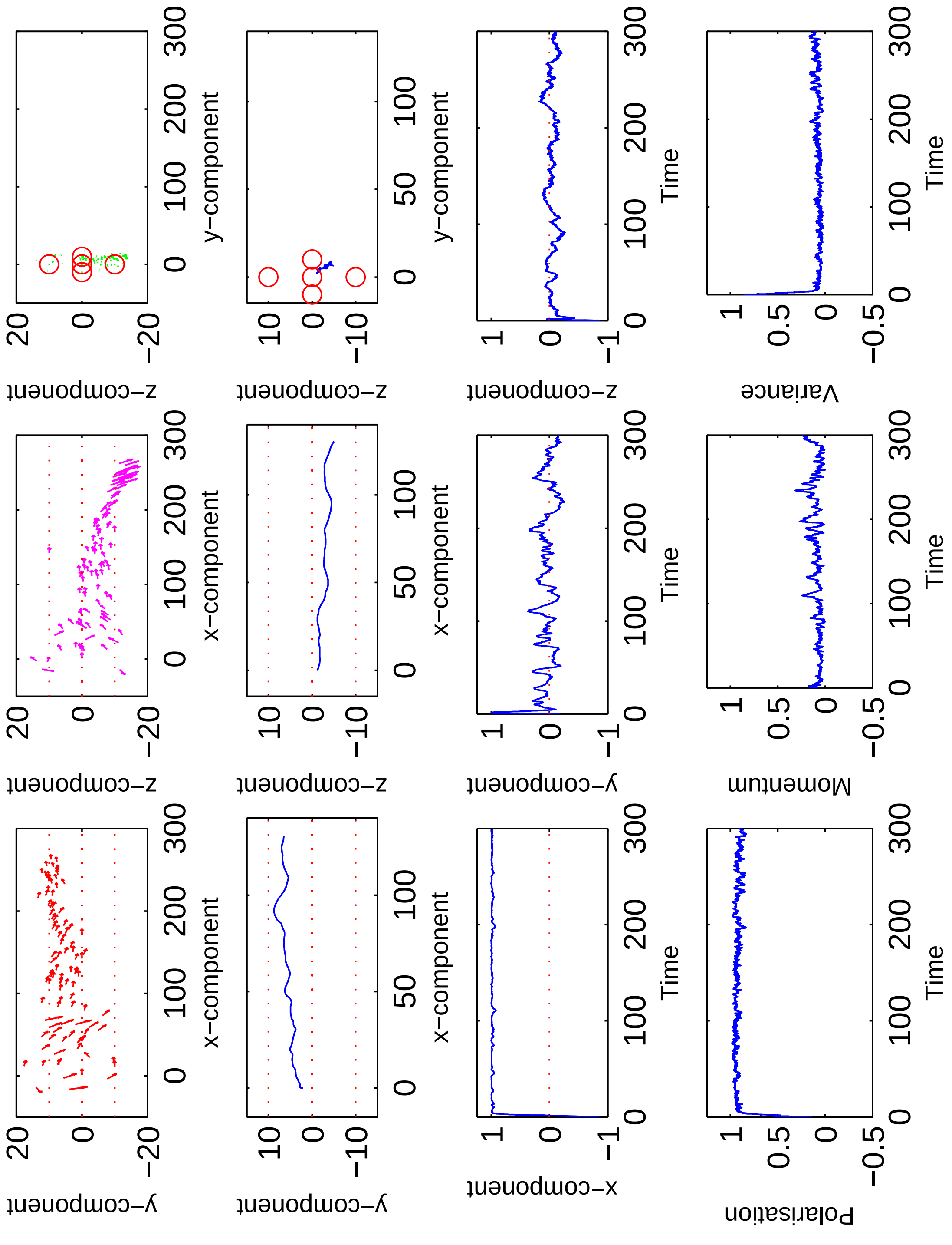

Fig. 4. Simulation of the scout components guiding the worker components of the group to the goal, where the scouts' flight paths are distributed around the outside of the workers initial positions. Parameters of the model are the same as those used in Figure 4.

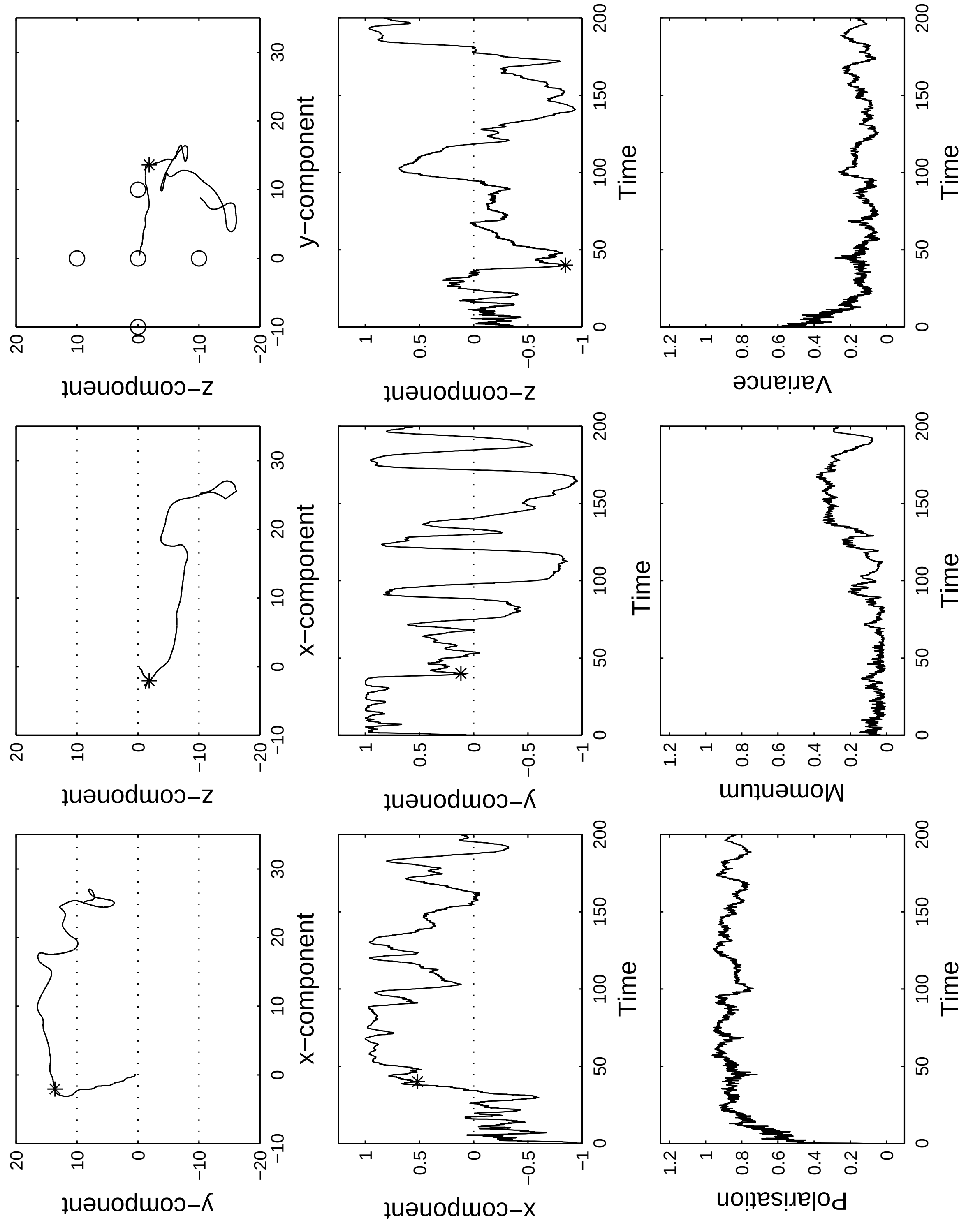

Fig. 5. Simulation of the scout components guiding the worker components of the group to the goal, where the scouts' flight paths are distributed around the outside of the workers initial positions. Initially, the workers are allowed to organise themselves without scouts present to influence them. The scouts are introduced in the model after T = 40 (marked by the asterisk). Parameters of the model are the same as those used in Figure 3.

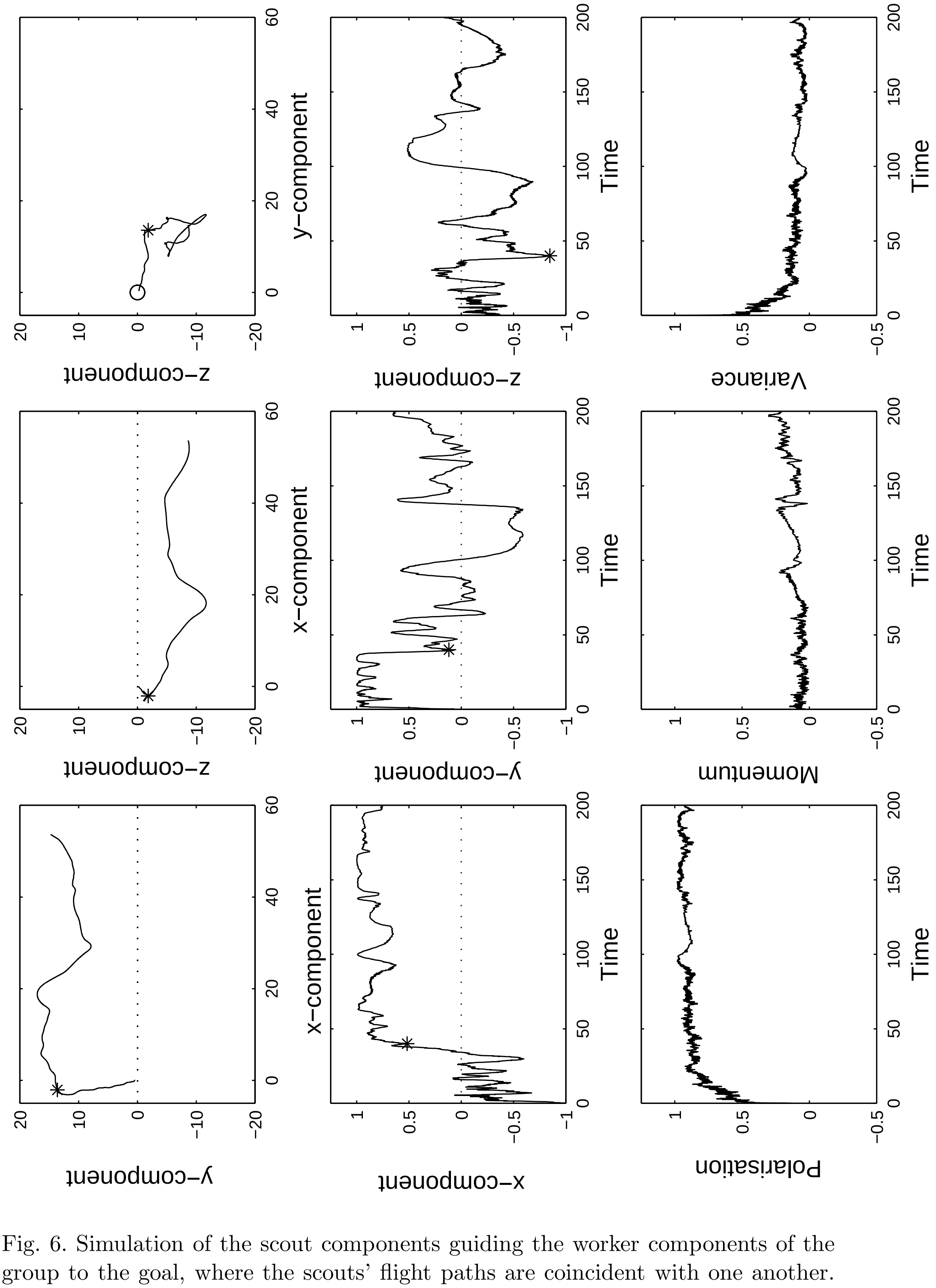

Fig. 6. Simulation of the scout components guiding the worker components of the group to the goal, where the scouts' flight paths are coincident with one another. The scouts are introduced in the model after T = 40. Parameters of the model are the same as those used in Figure 5.

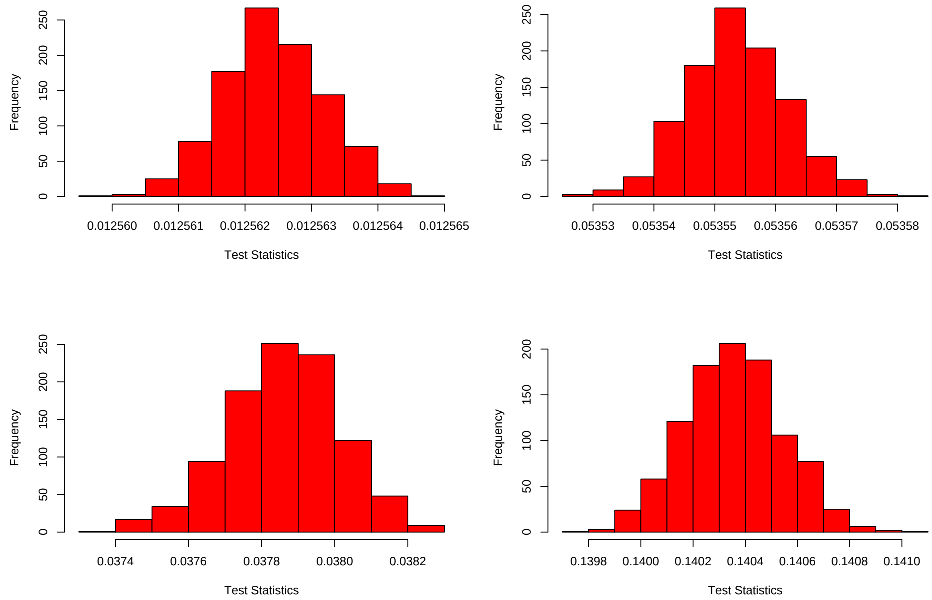

Fig. 7. Histograms of randomised test statistics. Corresponding to (a) = Figure 3 (observed T = 0.01255), (b) = Figure 4 (observed T = 0.05352), (c) = Figure 5 (observed T = 0.03748) and (d) = Figure 6 (observed T = 0.13978).

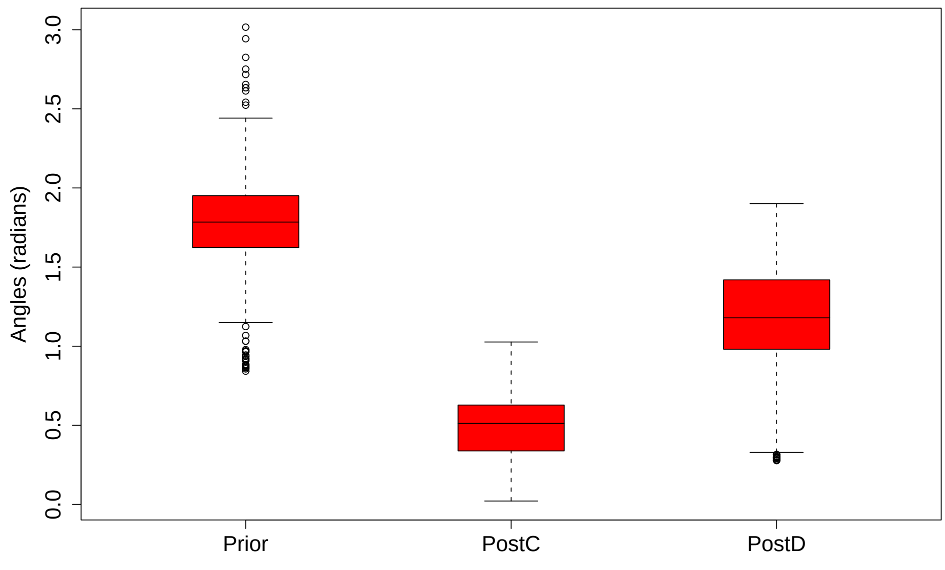

Fig. 8. Boxplots of distribution of angles of workers (between mean direction of group and x-axis) for the swarm that is initially unguided (Prior), then guided by scouts flying on one another's flight path (PostC) and scouts in a dispersed arrangement (PostD).

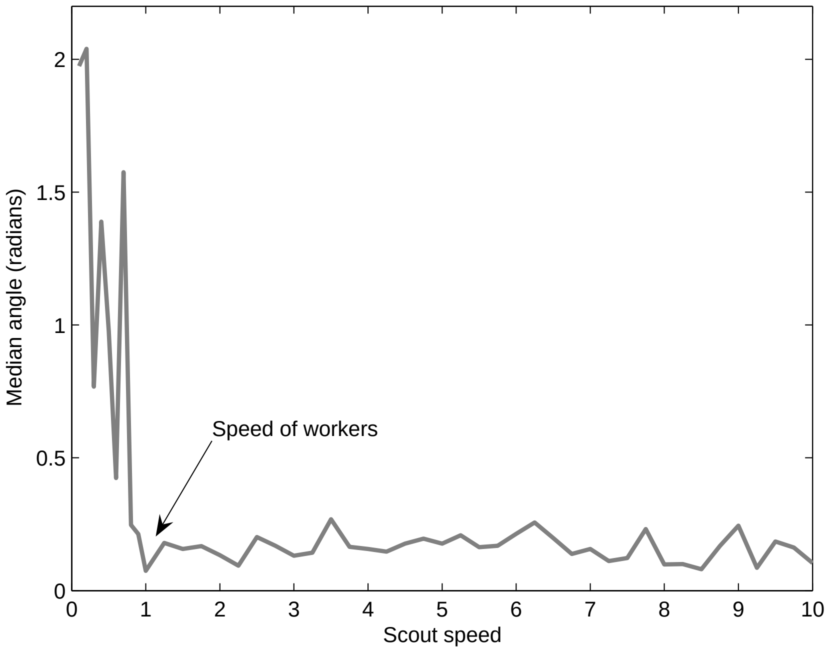

Fig. 9. Speed of scout components (relative to workers) compared to the median angle between the worker groups (spherical) mean direction of travel and the scouts' flight paths. A distinct change is noted once the scouts speed matches that of the workers.

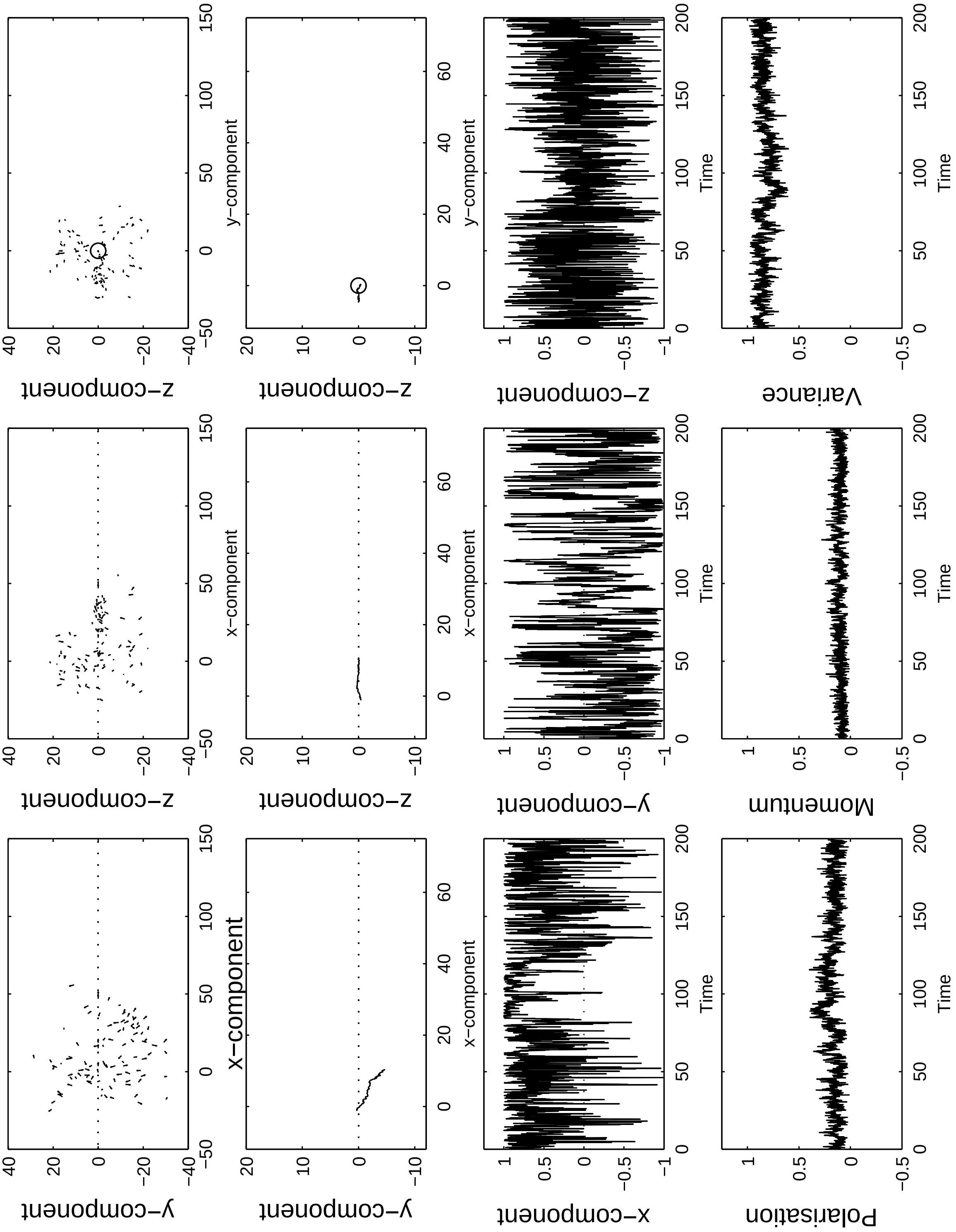

Fig. 10. Simulation of the scout components guiding the worker components of the group to the goal, where the scouts' flight paths are coincident with one another. Errors in the workers' decisions are introduced into the model. Parameters of the model are the same as those used in Figure 3, with the addition of a stochastic component $\kappa = 1000$.

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