RESEARCH ARTICLE

Moving without a purpose: an experimental study of swarm guidance in the Western honey bee, *Apis mellifera*

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ABSTRACT

During reproductive swarming, honey bee scouts perform two very important functions. Firstly, they find new nesting locations and return to the swarm cluster to communicate their discoveries. Secondly, once the swarm is ready to depart, informed scout bees act as guides, leading the swarm to its final destination. We have previously hypothesised that the two processes, selecting a new nest site and swarm guidance, are tightly linked in honey bees. When swarms can be *laissez faire* about where they nest, reaching directional consensus prior to lift off seems unnecessary. If, in contrast, it is essential that the swarm reaches a precise location, either directional consensus must be near unanimous prior to swarm departure or only a select subgroup of the scouts guide the swarm. Here, we tested experimentally whether directional consensus is necessary for the successful guidance of swarms of the Western honey bee *Apis mellifera* by forcing swarms into the air prior to the completion of the decision-making process. Our results show that swarms were unable to guide themselves prior to the swarm reaching the pre-flight buzzing phase of the decision-making process, even when directional consensus was high. We therefore suggest that not all scouts involved in the decision-making process attempt to guide the swarm.

KEY WORDS: Consensus, Behavioural cues, Swarming, *Apis mellifera*, Collective decision making

INTRODUCTION

Despite the absence of centralised control in their societies, the social insects (bees, ants, wasps and termites) are capable of impressive collective behaviour. Even though the individual insects only have limited cognitive abilities, as a collective they build nests many times their own size (Bonabeau et al., 1998; Camazine, 1991; Deneubourg and Franks, 1995; Franks and Deneubourg, 1997; Karsai and Pénzes, 1993), focus their foraging efforts on the best food sources (Biesmeijer and Ermers, 1999; Bonser et al., 1998; Pasteels et al., 1987; Seeley, 1985) and coordinate group defence against predators and intruders (Camazine, 1985). The collective behaviour of insect colonies is achieved through feedback mechanisms arising from the activities of individual insects, each following a basic set of rules (Bonabeau et al., 1997; Camazine et al., 2001). One of the best-studied examples of collective behaviour is the process of nest site selection during reproductive swarming in honey bees (*Apis* spp.). During this complex task the bees not only have to choose the best available nest site from a set of alternatives

but also then have to move as a cohesive group towards the chosen site (Seeley, 2010). Presumably, only bees involved in the decision-making process will attempt to guide the swarm in flight, thus linking the two processes.

When a colony of the Western honey bee *Apis mellifera* Linnaeus is ready to reproduce, the old queen, along with a subset of the colony's workers, leaves the colony and forms a temporary cluster in close proximity to the old nest (Seeley and Morse, 1978). From this immobile temporary cluster, ~5% of the bees (older, forager age scout bees) take flight and search the surrounding environment for a new nesting cavity (Seeley et al., 1979). Once a scout bee has found a suitable nesting site, she returns to the swarm cluster and starts communicating her finding to nest-mates using the waggle dance [see Dyer for details on the biology of the waggle dance signal (Dyer, 2002)]. After completing a bout of dancing, the scout bee will return to the nest site that she is dancing for in order to re-evaluate it. On her next return to the swarm she will continue dancing for the nest site, but will slowly lose motivation with each subsequent return until eventually she ceases her activities altogether (Seeley and Buhrman, 1999). The number of dance circuits produced in a scout bee's dance for a given nesting location is correlated with the perceived quality of the nest site, with higher quality nest sites receiving dances of higher circuit number (Seeley and Visscher, 2008). The net effect of this difference in initial circuit number and constant reduction in enthusiasm over time is that higher quality sites persist longer and have the potential to recruit more followers than lower quality sites (Britton et al., 2002; Janson et al., 2005; Perdriau and Myerscough, 2007; Seeley, 2003).

During the process of dancing for and re-evaluating a potential nest site, scout bees also monitor the number of other scout bees present at the nesting location. If the number of other scout bees at the new nesting site has reached a quorum threshold level (Seeley and Visscher, 2003; Seeley and Visscher, 2004) then on her next return to the swarm cluster the scout bee will start producing an auditory signal known as the piping signal (Seeley and Visscher, 2003). As the levels of piping signal increase within the swarm, the inactive swarm bees start to warm up their flight muscles to the 35°C required to sustain flight (Seeley et al., 2003; Seeley and Tautz, 2001) so that the swarm can take to the air.

Although the piping signal is only produced by scout bees that have perceived a quorum at a given nest site (Visscher and Seeley, 2007), it is not necessarily related to a directional consensus in dances (e.g. all bees dancing for the same site) performed on the swarm cluster itself. The bees use several mechanisms to increase directional consensus levels prior to swarm departure in addition to dance cessation. Scout bees produce an auditory signal known as the stop signal throughout the decision-making process. The stop signal is used to actively silence the dances of other scout bees, and is greatly upregulated once worker piping has commenced, resulting in a reduction of flight and dance activity (Seeley et al., 2012). Reducing flight activity presumably is important to ensure that scout

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bees remain on the swarm surface during the final phase of the decision-making process in order to act as guides for the swarm. With the swarm's scouts returned to the swarm cluster, and the rest of the swarm's bees warmed up in preparation for flight, all the swarm needs is an activation signal to coordinate the departure of the swarm. This signal is produced by excited scout bees that have been producing the piping signal, and have sensed that the inactive bees on the swarm cluster have warmed their flight muscles sufficiently for flight. These then proceed to burrow and run through the swarm cluster producing the buzz-run signal, which physically dislodges the swarm and forces it into the air (Rittschof and Seeley, 2008). Once in the air, scout bees act as swarm guides, streaking through the swarm cluster in the direction needed to travel in order to lead the group to its new home (Beekman et al., 2006; Greggers et al., 2013; Janson et al., 2005; Latty et al., 2009; Schultz et al., 2008).

Reaching directional consensus would appear to be an important aspect of the decision-making process in *A. mellifera*, as swarms need to travel to a specific point in the environment (a cavity in which to construct their new colony). Therefore, any directional conflict during swarm guidance could result in the swarm not being able to reach its destination. Two previous studies describe observing split decisions prior to lift off, resulting in swarms that were unable to guide themselves after taking to the air. One swarm monitored by Seeley and Visscher took to the air after a quorum had been reached at two separate sites at the same time (Seeley and Visscher, 2003). The swarm split in the air and, unable to guide itself, resettled on the swarm board and continued dancing until a consensus was reached and it took to the air again, this time successfully travelling to its new nest site. Similarly, two swarms observed by Lindauer took to the air while the swarms still lacked consensus (Lindauer, 1955). When these swarms took to the air they split in half and the swarm halves headed in opposing directions. It therefore seems that swarms of *A. mellifera* are only capable of coordinated flight once consensus or near-consensus has been reached at the time of lift-off.

In this study, we further investigated, in an experimental setting, whether swarms of *A. mellifera* are capable of successfully flying to a new nest site in the absence of directional consensus prior to swarm departure. To test this, we forced swarms into the air while scouts were still advertising multiple nest sites and monitored the movement patterns of these swarms.

RESULTS

We tested 11 different swarms: eight experimental swarms, two control swarms and one natural swarm that was allowed to go through the complete nest site selection process uninterrupted. Of these, none of the eight experimental swarms managed to guide themselves to a nest box (Table 1). Only three experimental swarms (swarms 1, 2 and 6; Table 1) moved away from the swarm board after being forced into the air, but these three swarms only travelled distances of 5–10 m from the swarm board before clustering on the nearest clump of grass (the field site did not contain any trees or shrubs). The other experimental swarms re-clustered on the swarm board after all bees had been airborne. Both swarms in the procedural control, and the natural swarm successfully guided themselves to one of the four nest boxes provided.

In each of the 11 swarms the number of bees dancing for the four nest sites provided increased over time (Fig. 1). Dance activity fluctuated over time for all 11 swarms (Fig. 2), with all three successfully moving swarms displaying 100% consensus in dance activity during the last recorded time interval. Interestingly, in

procedural control swarm 1 (Fig. 2I) the consensus direction prior to lift off was not the same as the direction flown (Table 1), but this could possibly be explained by our misinterpretation of light-dependent 'misdirection'. Unfortunately, while interpreting the nest boxes being danced for in the field we failed to take into account that dancing *A. mellifera* bees orientate their dances relative to the sun's current azimuth rather than directly vertical when they can see the open sky [termed light-dependent 'misdirection' in von Frisch (von Frisch, 1967)]. Even though the bees were shaded, we cannot exclude the possibility that they could determine the position of the sun from viewing the sky. Because of this error it could be that we misinterpreted the direction being indicated by dancers for some directions early in the morning and late in the afternoon when the sun's azimuth diverged greatest from vertical. The two procedural controls that did reach a nest box were significantly different from the eight experimental swarms with respect to their ability to coordinate movement to their new home (two-tailed Fisher's exact test: $N=10$, $P=0.022$).

Of the swarms that did successfully travel to a nest box, procedural control swarm 1 travelled slowly in the direction of the swamp hive box despite having danced solely for the gate hive box in the previous six time intervals (Fig. 1I and Fig. 2I). Procedural control swarm 2 spent ~5 min after lift-off hovering in the air in a wide-spread mass before slowly moving in the direction of the gate hive box. The swarm had only started dancing strongly for the gate box in the 5 min time interval prior to being forced to the air, and had previously been dancing vigorously for the swamp hive box (Fig. 1J and Fig. 2J). The natural swarm (Fig. 1K and Fig. 2K) travelled in a slow but steady pace towards the swamp hive box after taking to the air as expected based on the dance activity prior to lift-off.

DISCUSSION

Not one of the eight experimental swarms was able to successfully coordinate swarm movement (Table 1). This is despite the fact that swarm 5 was very actively dancing for a single location during the time interval in which it was forced into the air (Fig. 2E), and swarms 3, 7 and 8 had a large number of marked scouts for more or less one location (Fig. 1C,G,H). We did observe scout bees producing long flight arcs from the main swarm cluster in the general direction of nest boxes in experimental swarms 4 and 8, while three swarms (swarms 1, 2 and 5) managed to fly some distance before re-clustering in nearby grass clumps, suggesting that some attempt to guide the swarm was present in some but not all swarms. Differences in the swarms' behaviour are perhaps linked to differences in directional consensus. However, our data do not allow a statistical comparison of directional consensus among our swarms mainly because it is impossible to choose the correct time period to perform the analysis. For example, in many of our experimental swarms, the last time point prior to lift off showed directional consensus. Yet, our swarms did not move to the nest box advertised. We can therefore only compare our swarms' ability to reach a nest box or not.

One could argue that our experimental swarms simply could not fly as the bees were not sufficiently primed for flight because of a lack of buzz-running [buzz-running causes bees not involved in decision making to warm up their flight muscles (Seeley et al., 2003; Seeley and Tautz, 2001)]. Whereas such a signal seems necessary in temperate climates or when ambient temperature is relatively low, we do not think our experimental swarms were too cold to fly. Bees incapable of flying simply drop to the ground, and the bees we scraped off did not. In addition, ambient temperature was high (often well over 30°C) when we performed our experiments.

Table 1. Summary of the important features of the decision-making process for swarms from the experiment, the procedural control, and a swarm allowed to go through an uninterrupted process of swarming

	Experiment								Procedural control		Uninterrupted swarm
	1	2	3	4	5	6	7	8	1	2	
Date	17/01/2012	23/02/2012	8/11/2012	9/11/2012	11/11/2012	15/11/2012	30/11/2012	1/12/2012	19/11/2012	24/11/2012	22/11/2012
Time swarm released	09:08 h	07:00 h	10:00 h	10:00 h	10:00 h	07:10 h	10:10 h	10:10 h	07:00 h	10:00 h	10:00 h
Time forced into air/departed	12:15 h	13:30 h	14:10 h	14:30 h	14:30 h	13:30 h	14:30 h	14:00 h	16:00 h	13:36 h	12:59 h
Time taken to force into air	15 min	30 min	10 min	10 min	10 min	<5 min	10 min	<5 min	<5 min	<5 min	N/A
No. marked dancing bees											
All time	32	80	65	75	84	180	57	97	113	71	82
Last hour	10	18	24	21	24	61	27	30	37	53	57
Last 30 min	5	13	16	8	16	26	20	15	22	35	30
Last 15 min	1	11	9	4	12	10	12	10	18	26	18
No. dancers recruited to most popular nest box											
All time	11	31	60	33	30	81	32	61	53	34	58
Last hour	4	12	21	12	19	29	13	27	21	23	51
Last 30 min	3	9	14	5	15	13	9	13	21	20	27
Last 15 min	1	9	7	2	11	4	6	9	18	20	17
Most popular nest box											
All time	Forest	Forest	Gate	Glasshouse	Forest	Glasshouse	Swamp	Forest	Swamp	Swamp	Swamp
Last hour	Swamp	Forest	Gate	Glasshouse	Forest	Glasshouse	Swamp	Forest	Gate	Gate	Swamp
Last 30 min	Forest	Forest	Gate	Gate	Forest	Gate	Gate	Forest	Gate	Gate	Swamp
Last 15 min	Forest	Forest	Gate	Glasshouse/gate	Forest	Glasshouse	Gate	Forest	Gate	Gate	Swamp
Nest box swarm flew to	10 m, gate direction	5 m, glasshouse direction	–	–	5 m, swamp/gate direction	–	–	–	Swamp	Gate	Swamp
Temp. during lift-off (°C)	25	29	25	21	19	24	30	35	18	26	19

Bees in the experiment underwent forced lift-off; bees in the procedural control underwent forced lift-off after the piping crescendo had been heard on the swarm surface. For the swarm allowed to go through an uninterrupted process of swarming, the decision-making process was not artificially disrupted.

Because we could not control for light-dependent 'misdirection', the most popular nest box rows should be considered an approximation, as misidentification of the direction of dances may have occurred.
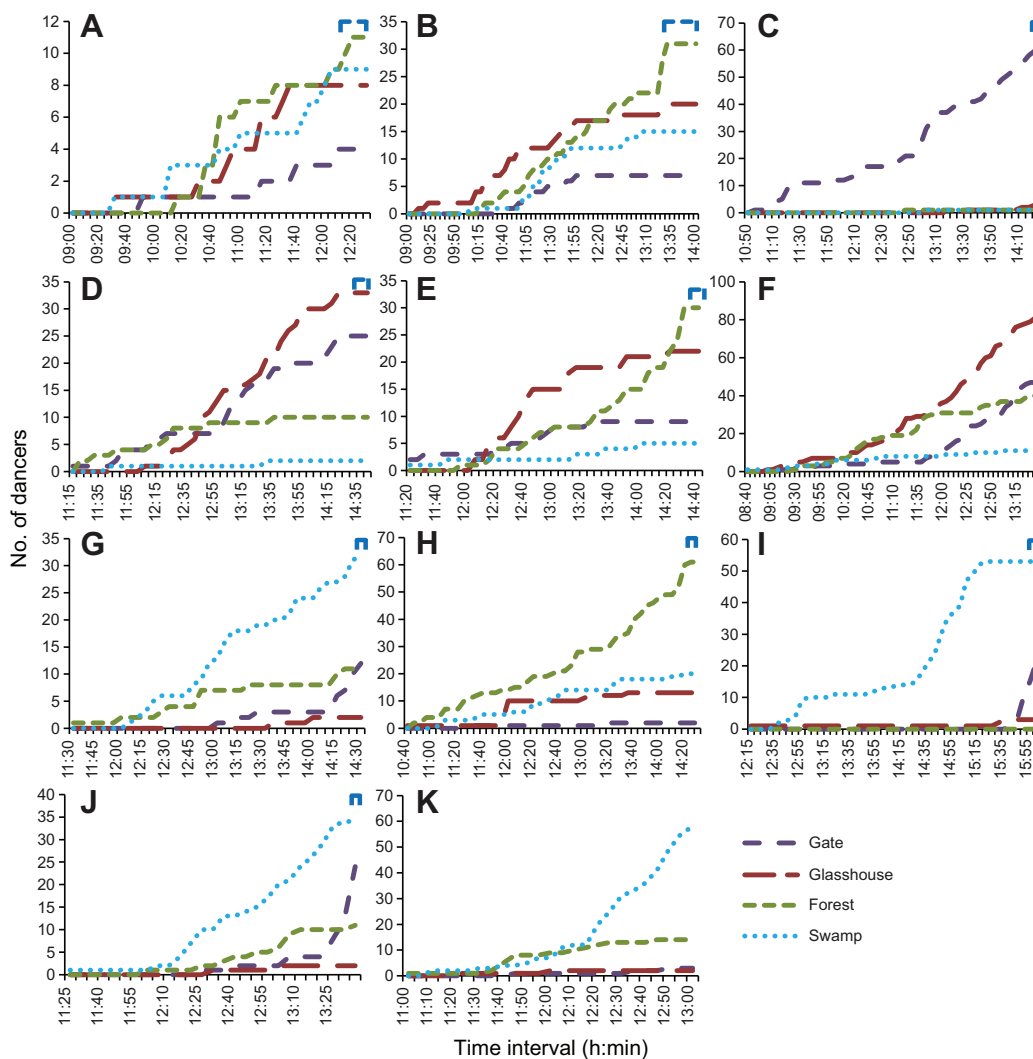
Fig. 1. Cumulative increase in marked dancers for the four different hive boxes over time for each swarm studied. (A–H) Experimental swarms 1–8 (forced lift-off); (I,J) procedural control swarms 1 and 2; (K) swarm going through an uninterrupted process of swarming. The dashed blue horizontal lines in the top right-hand corner of panels A–J indicate the period of time spent attempting to physically force the swarm into the air by scraping bees off the swarm board. Because we did not control for possible light-dependent 'misdirection', the number of marked dances for different nest boxes should be considered an approximation, as misidentification of the direction of dances may have occurred. Note that the scales are not the same in the different panels.

In contrast to the experimental swarms, the procedural control swarms were able to coordinate movement to a hive box, showing that the major disruption caused by us physically scraping bees off the swarm board does not explain the swarms' inability to fly towards a nest site. Interestingly, both swarms flew in unexpected directions based on the complete lack of dance activity for the direction flown in within the last six time intervals (procedural control swarm 1, Fig. 2I) or the build-up of dancers for a different location (procedural control swarm 2, Fig. 1J). These findings, if not due solely to our misinterpretation of light-dependent misdirection, are interesting as they illustrate how the currently active scout bees (procedural control swarm 1) or the significantly larger group of scouts (procedural control swarm 2) are not necessarily the ones that will guide the swarm once it takes to the air.

Who guides the swarm in *A. mellifera*? We can think of two mutually exclusive hypotheses regarding the identity of swarm guides. Either all bees involved in the decision-making process, or more precisely all bees still dancing prior to lift off, attempt to guide the swarm. Alternatively, only those bees that have experienced the quorum at the nest site they were visiting at the time of lift off will guide the swarm. We can now use our experimental results to decide which of the two hypotheses is the most likely. If all scouts that were still actively involved in the decision-making process at the time of lift off (e.g. those still dancing at the time of lift off) attempted to guide the swarm, we would have expected most, if not all, of our

experimental swarms to either have split in two in mid-air as did the swarms in Lindauer's (Lindauer, 1955) and Seeley and Visscher's (Seeley and Visscher, 2003) studies, provided the angular divergence between the two sites still being danced for was high enough, or to have travelled in the average direction advertised by the dancing bees. Most of our swarms were advertising two nest boxes that were separated by 90 deg; hence, if all scouts still dancing for nest sites at the time of lift off had guided the swarm, we predict that most of our experimental swarms would have travelled in a direction halfway between the two nest boxes (assuming the nest boxes received a similar number of dances). This was clearly not the case. We therefore think that only those bees that have experienced the quorum at their site will attempt to guide the swarm. This would explain not only why none of our experimental swarms flew any distance of significance but also why one of our procedural controls actually flew to a nest box other than the one it was advertising at the time of lift off. Because we did not record what site bees that performed the piping signal were dancing for, we cannot say if only bees dancing for the swamp box were producing the piping signal indicating that site, and that site only, had reached the quorum. However, we cannot fully rule out the possibility that the discrepancy between the direction indicated and the direction flown in procedural control swarm 1 (Fig. 2I) was due to misreading of (some of) the dances.

The behaviour of the two swarms observed by Lindauer (Lindauer, 1955) in which the decision was split prior to lift off is
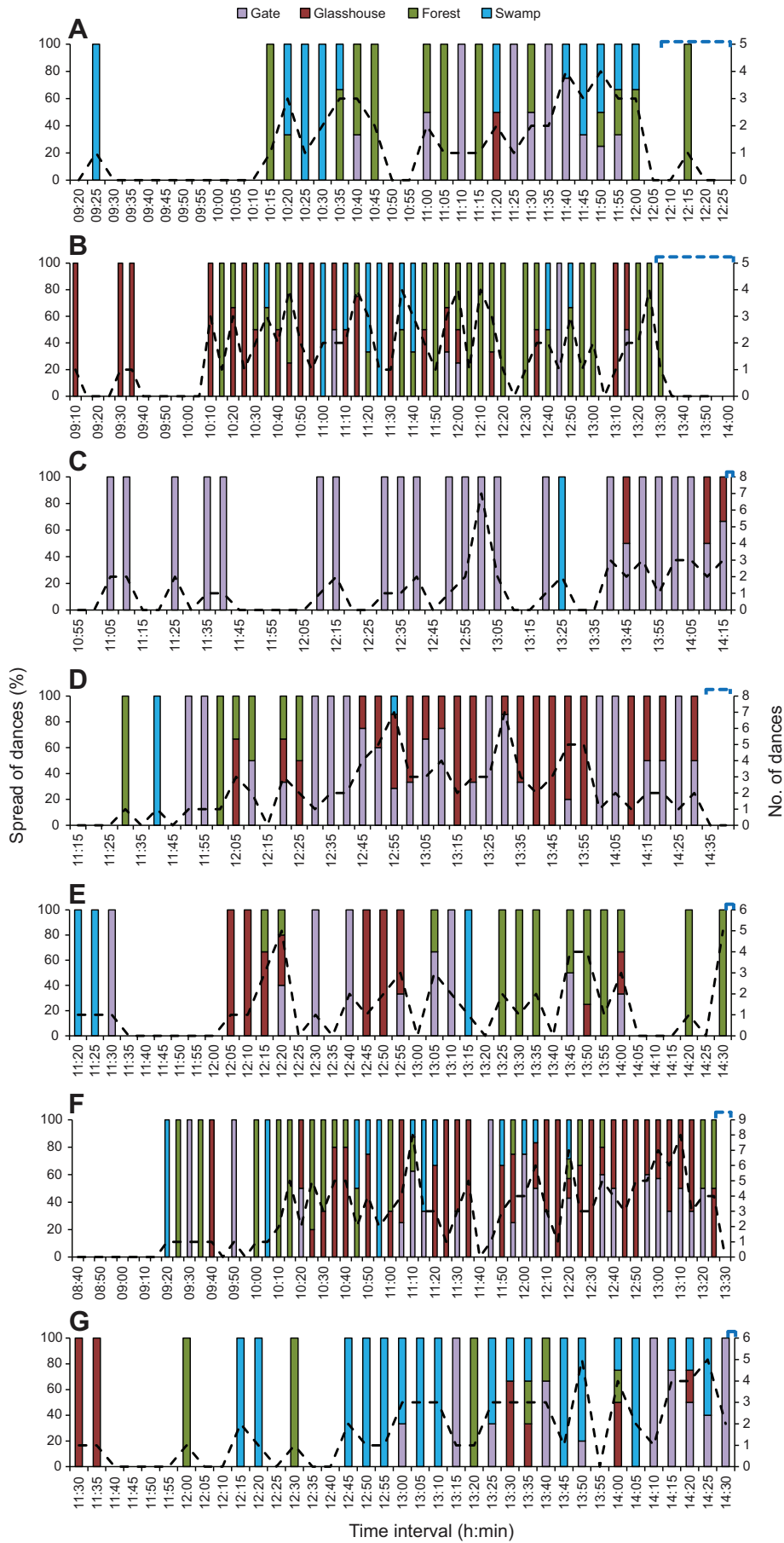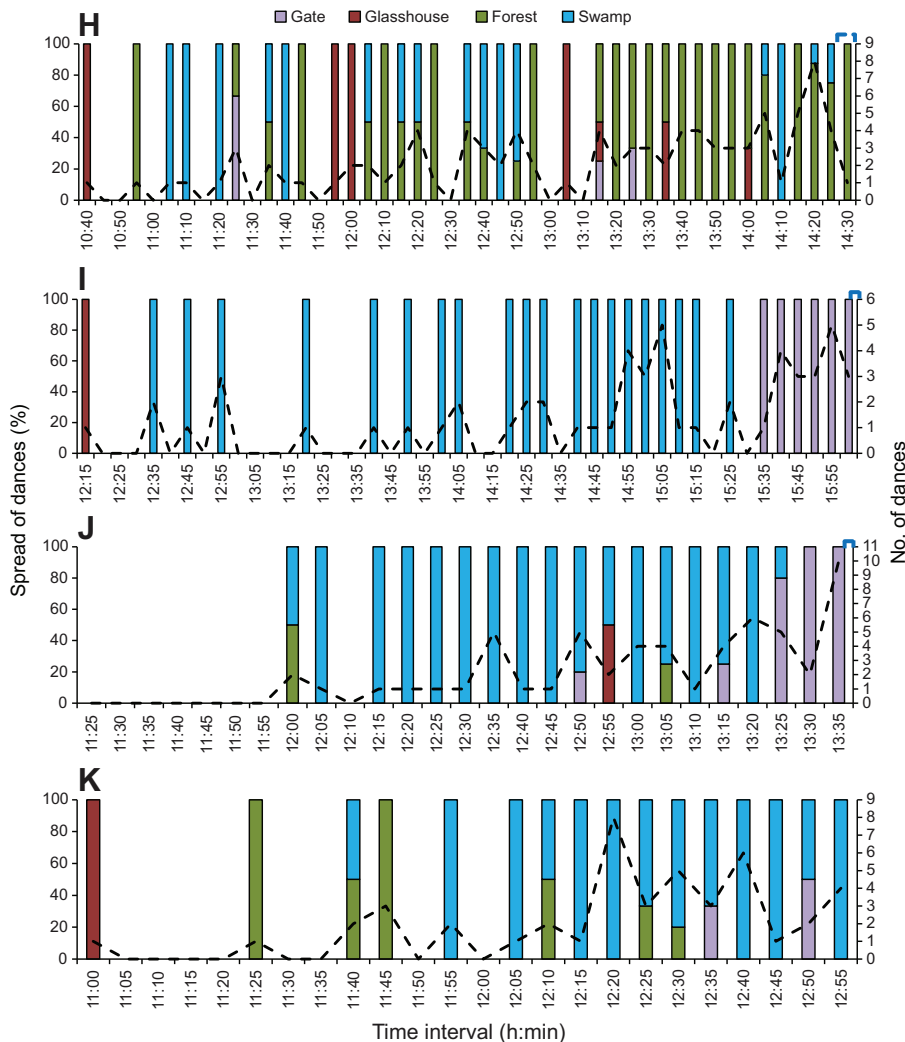
Fig. 2. See next page for legend.

Fig. 2. Locations indicated by dancing scout bees monitored over a 30 s time period every 5 min from the time of the first recorded dance until the completion of the replicate. Each column represents the proportional dance activity for the different locations during each 30 s interval (left-hand *y*-axis). Columns are divided into different colours to indicate the four different hive boxes presented to the swarms. The dashed black line connecting the different columns indicates the number of scout bees dancing during each interval (right-hand *y*-axis; note that the scales are not the same in the different panels). (A–H) Swarms 1–8 of the experiment (forced lift-off); (I,J) procedural control swarms 1 and 2; (K) swarm going through an uninterrupted process of swarming. The dashed blue horizontal lines in the top right-hand corner for panels A–J indicate the period of time spent attempting to physically force the swarm into the air by scraping bees off the swarm board. Again, we may have misinterpreted some of the dances because of possible light-dependent 'misdirection'. Therefore, the historical trends in proportional dance for different nest boxes should be considered an approximation. Note that this should not affect the reported proportion of dance activity for the different sites at each time interval.

consistent with our hypothesis if during both events observed by Lindauer the scout bees for the two competing sites had perceived a quorum at their nest sites. The split swarm described by Seeley and Visscher (Seeley and Visscher, 2003) had reached a quorum at two nest sites, suggesting that this swarm's inability to coordinate movement was due to two camps of bees attempting to guide the swarm in different directions. Obviously, our hypothesis requires experimental testing, but at this point in time we think it is the most parsimonious explanation of our results as well as the published results of Lindauer and Seeley and Visscher.

What can the bees tell us about the guidance of moving animal groups in general? One of the potential risks of multiple subgroups of motivated individuals attempting to guide the same group in different directions is that the group may move in an average path, which results in both subgroups' goals being missed. This is not a problem in animal groups such as fish shoals that are not orientating towards a specific end point goal, but rather move in a general direction while the main aim of individuals is to stay with the group. Modelling studies have shown that such groups are able to compromise and head in a direction that is a middle ground between the two subgroups' locations (Leonard et al., 2012). Moving in the average direction also seems to be the tactic used by red dwarf honey bee (*Apis florea*) swarms, which often take to the air while still dancing for multiple locations (Oldroyd et al., 2008; Diwold et al., 2011; Makinson et al., 2011; Schaerf et al., 2011), and the giant

honey bee *Apis dorsata* (Makinson, 2013). Both *A. florea* and *A. dorsata* build nests in the open and are rather tolerant with respect to where exactly they nest. As a result, it appears that open-nesting honeybee species move more like fish shoals in that staying together is more important than the actual end point of the journey.

In contrast, in swarms of cavity-nesting bees such as *A. mellifera* it is essential that the group moves in a precise direction to be able to find the nest site the scout bees selected prior to lift off. Thus, to ensure that the swarm ends up where it should, *A. mellifera* scouts employ a number of behavioural tactics during the decision-making process on the temporary cluster such as waggle dance decay (Seeley and Buhrman, 1999) and stop signalling (Seeley et al., 2012). Our results suggest that in addition to waggle dance decay and stop signalling, in *A. mellifera* swarms only scout bees that have perceived a quorum at a given nest site will act as swarm guides. Under most circumstances this results in only one group of motivated individuals attempting to guide the swarm by the time that it takes to the air and ensures the arrival of the group at a predetermined location.

MATERIALS AND METHODS
Study site
The experiment was conducted within a grass-covered grazing paddock in the grounds of the University of Western Sydney (UWS) Hawkesbury campus (33°36′45.69″S, 150°44′0.93″E) during the summer months of January–February and November–December of 2012.
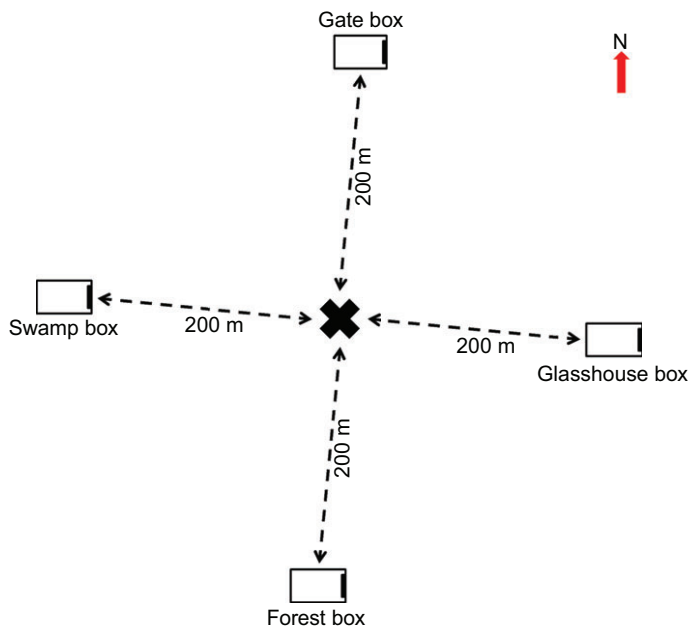
Fig. 3. Sketch of the experimental set-up. Bait hive boxes were positioned 200 m from the swarm cluster (denoted by the black cross). Hive box entrances were positioned to face east.

Swarm preparation and experimental setup

We created swarms from colonies headed by newly mated queens to ensure that the queens were in a suitable condition for flying (a swarm whose queen cannot fly will not travel to the chosen nest site). To create artificial swarms, we first captured a colony's queen and placed her in a queen cage. The queen cage was then suspended with string into a small wooden box with two mesh-covered sides. We shook ~500 g (around three frames worth of bees) into the wooden box and sealed it. Caged swarms were then placed in a darkened room and fed 1:1 sugar/water solution for 3 days until the workers started to produce wax scales. Wax scale production is characteristic of the physiological state worker bees are in prior to natural swarming (Combs, 1972).

On the morning of the day of each experiment, swarms were released onto a vertical swarm board similar to that described previously (Seeley and Buhrman, 1999). To protect the bees from the sun, we positioned an umbrella so that the swarm was shaded. About 30 min after releasing the swarm, we released the swarm's queen from her queen cage. Four empty 8-frame Langstroth-style hive boxes (39 l in volume) were positioned 200 m away from the swarm board and equidistant from their two nearest neighbours (Fig. 3). Each box was elevated 1 m off the ground and positioned so that its hive entrance was facing east. To make the hive boxes more attractive for swarms, we used previously occupied swarm boxes containing small remnant comb fragments and placed Nasonov swarm lures (C. B. Palmer and Co.) inside each box.

Data collection and forced lift-off

We marked dancing scout bees as they first appeared on the swarm surface using Posca paint pens (Mitsubishi Pen Co., Japan). We monitored the number of dancing scout bees every 5 min for a 30 s period and noted the direction of the nest site danced for by each bee by the direction in which the bee was dancing. Scout bees that appeared to be dancing for locations other than the four nest boxes provided were removed from the swarm.

When a total of at least 30 scouts were dancing and at least two nest boxes were advertised on the swarm, we forced swarms off the swarm board by slowly physically scraping bees off the board with a pen, starting with the lower half of the swarm until the whole swarm took to the air. We gradually scraped bees off the swarm board to mimic the increase of airborne bees as a swarm takes to the air due to the activity of buzz-running bees.

Initially we wanted to more precisely control the level of directional consensus prior to forcing the bees into the air to investigate at what level swarms were still able to fly successfully. However, this proved to be extremely difficult, and we therefore used the rough guide described above, although in later swarms we decided to wait until more bees were dancing than the 30 used in our first swarm to ensure sufficient bees were involved in the decision-making process. As a procedural control, we allowed two swarms to go through the decision-making process until piping had reached a crescendo similar to that heard by swarms in the last 30 min or so before departure. These two swarms were then forced into the air by scraping bees off the swarm board before they themselves had initiated lift-off. A further swarm was allowed to go through the entire decision-making and swarm lift-off processes as a control to demonstrate normal decision making.

Our aim was to study the effect of lack of directional consensus on the swarms' ability to fly to one of the nest boxes advertised in the dances. We therefore simply recorded the direction in which the swarms flew, how far they flew and which nest box, if any, they ended up in.

Data analysis

We used a two-tailed Fisher's exact test to test whether the difference in successful swarm guidance between experimental swarms and procedural controls was statistically significant.

Author contributions

J.C.M. and M.B. designed the experiment. J.C.M. conducted the experiment and performed the data analysis. J.C.M. and M.B. wrote the manuscript.

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