


Collective decision making in the red dwarf honeybee *Apis florea*: do the bees simply follow the flowers?

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Abstract Most studies on collective decision making in honeybees have been performed on the cavity-nesting Western honeybee, *Apis mellifera*. In more recent years, the open-nesting red dwarf honeybee *Apis florea* has been developed as a model organism of collective decision making in the context of nest-site selection. These studies have shown that the specifics of the species' nest-site requirements affect collective decision making. In particular, when potential nesting sites are abundant, as is the case in *A. florea*, the process of collective decision making can be simplified. Here, we ask if *A. florea* simply follows the availability of floral resources in their environment when deciding on an area to move into. We determined the locations danced for by three colonies the day before, of and after reproductive swarming. Our results suggest that colonies of *A. florea* indeed track the availability of forage in their environment and that swarms move in the general direction of forage rather than towards a specific nest site.

Keywords *Apis* · Collective decision making · Honeybees · Nest-site selection

Introduction

Nest-site selection in honeybees is a prime example of a distributed decision-making process. Swarms of agents, in this case individual bees, self-organise to a single outcome without a hierarchical command structure (Gordon 2014). Distributed decision-making systems are central to many disciplines, ranging from commodity markets to the ways schools of fish move through their environment (Couzin et al. 2005). The realisation that we can use social insects to directly link the behaviour of the individual to the behaviour of the collective has led insect colonies to become the poster child of distributed decision-making systems (Bonabeau et al. 1997). Self-organisation principles have been used to study aspects of, among others, foraging (Camazine et al. 2001; Latty et al. 2017; Seeley 1995), nest construction (Bonabeau et al. 1998; Brito et al. 2012; Deneubourg and Franks 1995; Franks and Deneubourg 1997; Karsai and Penzes 1993), comb building (Nazzi 2016) and nest-site selection (Camazine et al. 1999; Pratt 2005; Seeley 2010; Visscher 2007). These studies have shown how, despite the simplicity of both the individuals and the rules they follow, social insects are capable of choosing the best place to forage, the best nest site out of several possibilities, and of building architecturally elaborate nests.

Distributed biological decision-making processes tend to be based on similar patterns of interactions in particular feedback loops (Gordon 2014). Such similarities are expected if the processes evolved independently under similar selection pressures (Gordon 2014). At the same time, it would be naïve to think that ecological conditions do

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not affect the decision-making process. For example, the distribution of resources within an environment greatly impacts the ways by which ant species recruit nest mates towards those sources (Cabanes et al. 2015; Gordon 2014; Latty and Beekman 2013). We therefore expect ecological conditions to affect distributed decision-making in closely related species if ecological conditions differ significantly.

The 11 recognised species of *Apis* honeybees (Lo et al. 2010) differ fundamentally in their nesting biology. Both the dwarf honeybees (two species) and giant honeybees (three species) build a single comb around or under a branch of a tree or under a cliff overhang or eave of a building and have a mainly South-East Asian distribution (Oldroyd and Wongsiri 2006). The evolutionary innovation of nesting in cavities by cavity-nesting species (six species) was primarily for nest defence (Oldroyd and Wongsiri 2006), but acted as an exaptation for inhabiting more temperate regions (Ruttner 1988).

While the details differ among species, all species of honeybee go through a nest-site selection process as part of their reproductive cycle, when a queen departs from the colony with a large number of workers to establish a colony of her own. Scout bees explore the surroundings for potential nest sites and report on the location of potential sites using the waggle dance (Lindauer 1955). Via a combination of positive and negative feedback, the number of potential sites is pruned until a subset of sites remains under consideration (Seeley et al. 2012).

The bees' nest-site selection process is best studied in the cavity-nesting *A. mellifera* (Seeley 2010; Visscher 2007). Briefly, a reproductive swarm leaves its nest and clusters a few tens of metres from it. Roughly about 5% of the bees in the swarm are involved in the decision-making process (Seeley et al. 1979). The rest remain quiescent within the cluster. Once a scout has found a potential nest site, it returns to the swarm and advertises the site by means of a waggle dance. Both the duration of the dance and the number of circuits per dance is positively correlated with the scout's perception of nest-site quality. Irrespective of the quality of the site, scouts reduce the number of dance circuits after each repeat visit to the site, until they stop dancing altogether. Because scouts visiting a high quality site start with more dance circuits and the reduction in the number of dance circuits declines linearly on average, sites of high quality are advertised for longer than sites of low quality (Seeley 2003). As a result the number of scouts visiting and dancing for sites of good quality increases while the number of scouts dancing for sites of poor quality decreases (Seeley 2003) so that one site comes to dominate in visitation and dancing, a process that may take several days (Villa 2004). The decision-making process comes to an end once a quorum has been reached at one of the sites under consideration (Seeley and Visscher 2004b). Scouts that have

sensed the quorum now return to the swarm and produce an auditory signal known as piping. The piping signal informs the quiescent bees in the cluster that they should prepare themselves for flight (Seeley et al. 2003). In the final stage of the process, scouts perform 'buzz runs' by zig-zagging over the swarm while vibrating their wings every second or so (Lindauer 1955). The swarm then takes flight and flies to its chosen home guided by the scouts that know the location of the new nest (Beekman et al. 2006; Latty et al. 2009; Schultz et al. 2008).

The elaborate decision-making process of *A. mellifera* swarms is most likely the result of the difficulty of the problem with which the swarm is faced. *A. mellifera* nests in difficult-to-find cavities. The swarm therefore requires precise guidance by the scouts once the swarm is in flight (reviewed in Seeley (2010)). In contrast, swarms of the red dwarf honeybee *A. florea* are mainly concerned with staying together while in flight, as potential nest sites are abundant and colonies do not invest heavily in their new nest (Makinson et al. 2011). We have shown previously that the departure of artificial swarms of *A. florea* follows a peak in consensus vector magnitude in the dances of scouts, a phenomenon that we termed 'vectorial consensus'. Consensus vector magnitude is a combined measure of the number of dances performed on the swarm, and the degree of agreement in direction between these dances during a given time interval (Makinson et al. 2011; Schaerf et al. 2011). Our previous observations and theoretical work have led us to believe that once in an area that contains suitable nest sites, the swarm then selects the actual site, e.g. the specific twig or branch to build the nest, shaded and free from predatory ants, 'on the fly' (Diwold et al. 2011; Makinson et al. 2011; Oldroyd et al. 2008; Schaerf et al. 2011). Hence, in contrast to *A. mellifera*, *A. florea* swarms seem to depart without having decided on the exact new nesting location. Instead, the swarm's decision-making process is geared towards ensuring that the swarm travels cohesively into a particular direction. Here we ask if that direction is chosen based on the availability of floral resources. We monitor the locations indicated by *A. florea* scouts in colonies preparing to swarm by decoding the bees' dances. We asked whether colonies dispatch swarms in the direction that is most rewarding by monitoring the directional information encoded in dances the day before, on and the day after a natural swarming event.

Materials and methods

Study site and setup

We conducted our field work in and around a small longan (*Dimocarpus longan*) grove (20°2'48"N, 99°53'52"E) on

the campus of Mae Fah Luang University in Chiang Rai province, Thailand, between January and March, 2011. We collected three *A. florea* colonies from the surrounding countryside and re-located the colonies to within the lower branches of the <3 m tall longan trees. Colonies were of comparable size although we did not have the means to determine the exact colony size as we wanted to minimise disturbance (*A. florea* is very prone to absconding when disturbed; personal observations).

Once we observed queen cells being built on the lower margin of a colony, we monitored that colony daily to record any swarming events. We placed a camera so that we could continuously film the dance activity of the bees on the concave horizontal surface that forms the crown of the nest and serves as the dance floor of the colony (Oldroyd and Wongsiri 2006). Once a swarm departed, we followed it on foot for as far as possible and measured the direction of flight relative to the location of the colony. We analysed the dance data in detail from one randomly chosen swarming event from each colony. Dances were decoded without the observer knowing what day of observation the dances were performed.

Recording of dance information

We estimated the angles and durations of the waggle phases of a subset of waggle dances of three colonies from video recordings made on the day before a reproductive swarm issued, the day of swarming and the day after swarming. Following a protocol that we previously adopted for analysing dances that occurred on *A. mellifera* swarms (Schaerf et al. 2013), we decoded waggle phases from dances that started during pre-determined 30-second intervals, with the start time of each interval separated by 5 min (starting from the beginning of each day's video footage).

On a computer, we overlaid a transparent MATLAB figure that was run through a custom MATLAB programme on an external video player window (SMPlayer). During each of the 30 s intervals where dance information was to be recorded, we played back the video at slow speed. For each dance that started during each interval, the programme's user would click on a dancing bee's thorax once at the beginning and once at the end of each waggle phase of a dance (whenever possible for at least the first four circuits of each dance, if the dance was comprised of four or more circuits). We then used the (x, y) coordinates associated with each pair of clicks to deduce the angle of each waggle phase relative to vertical on screen. Writing (x_1, y_1) as the coordinates associated with the start of a waggle phase, and (x_2, y_2) as the coordinates associated with the end of a waggle phase, we estimated the angle of the waggle phase (measured clockwise relative to vertical on screen) via:

$$\theta = \text{atan2}(x_2 - x_1, y_2 - y_1)$$

where $\text{atan2}(Y, X)$ is the four quadrant inverse tangent of X and Y as implemented by MATLAB, such that $-180^\circ < \text{atan2}(Y, X) \leq 180^\circ$. We translated the resulting angles so that they were written between 0° and 360° , and then converted all angles to bearings relative to north with reference to a compass placed in the view of the video camera. We used the duration between each pair of clicks and the speed of the video playback to estimate the duration of each waggle phase, t , in seconds. We then estimated the distance, d , in metres indicated by each waggle phase using the formula:

$$d(t) = t/0.0068.$$

We determined this relationship to help visualise locations danced for by *A. florea* as in Makinson et al. (2011) and Oldroyd et al. (2008) by averaging the curves relating distance to dance circuit duration reported by Lindauer (1956), Koeniger et al. (1982) and Dyer and Seeley (1991). See the Supplementary Information for details regarding the exact calculations. Our overall approach in using a computer script to help with dance decoding was originally inspired by a similar method developed by Klein et al. (2010).

We differentiated pollen dancers from other dancing bees by the pollen loads observed on the dancing bee's corbicula (the bees' 'pollen basket' found on the hind legs of the bee). See Table 1 for total number of waggle phases and dances decoded for each colony on the 3 days.

Overview of analysis

We used scatter plots (at hourly intervals) and heat maps (using data pooled from each day of observations) to visualise the mean locations indicated by waggle dances, and the relative frequency that different regions near the colony were indicated by dances. Additionally, we determined the mean bearing, μ , polarisation, R , consensus vector, c , and 95% confidence intervals for the mean bearings of dances performed each hour starting at 9 am and concluding at 6 pm across all three days of observations for each colony. We used an r -sample uniform scores test (as described in Sect. 5.3.6 of Fisher 1993) to determine whether the distributions of dance angles observed on the day before swarming (here day 1), the day of swarming (day 2) and the day after swarming (day 3) of each colony were similar (with the results of this analysis of dance angle distributions reported in the supplementary information). We then used the latitude and longitude of the positions of each of the colonies to transfer the relative locations indicated by dances to a consistent coordinate system; within this coordinate system, we then compared the regions indicated by each of

Table 1 Number of waggle phases decoded for each colony, on each day

	Before swarming	Day of swarming	After swarming	Total
Colony 1	894 (279)	953 (307)	927 (200)	2774 (786)
Colony 2	385 (129)	439 (137)	321 (112)	1145 (378)
Colony 3	832 (209)	1352 (297)	457 (123)	2632 (629)
Total	2111 (617)	2744 (741)	1705 (435)	

The number of dances is given in parentheses

the colonies via scatter plot, examined the regions of most intense focus for all three colonies combined and compared the distributions of bearings associated with each waggle dance across the colonies. Details of all associated calculations are given in the supplementary information.

Results

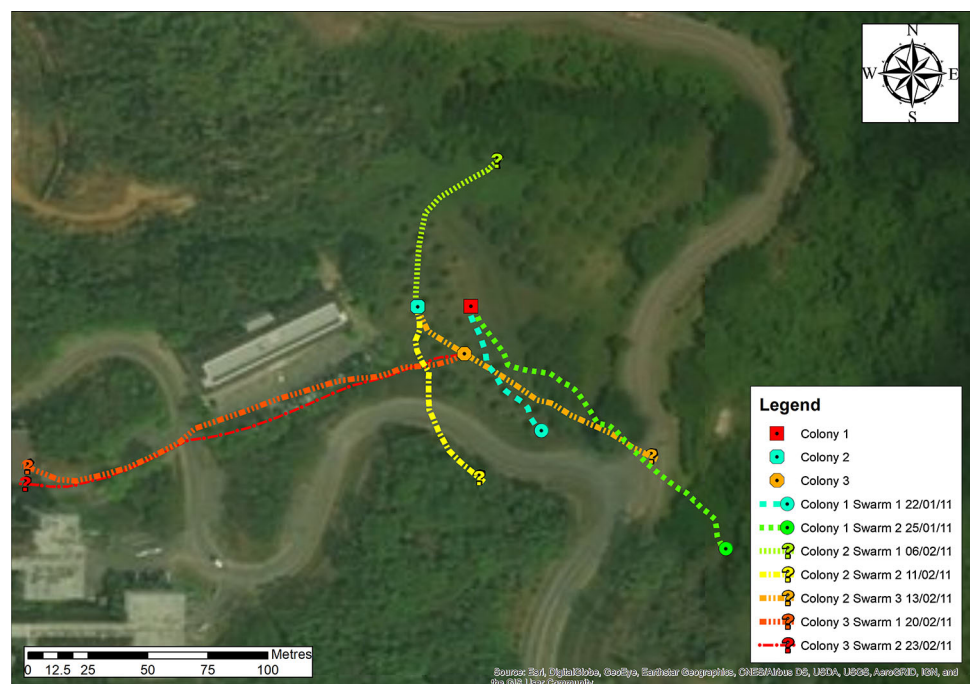
Swarming events

Each colony swarmed several times [colony 1: 2 swarms (January 22 and 25), colony 2: 3 swarms (February 6, 11 and 13) and colony 3: 2 swarms (February 20 and 23)] (Fig. 1). We managed to follow 2 swarms, both from colony 1, to their final location. The first swarm travelled across the longan grove in a south-easterly direction towards a large hill covered in secondary forest. Upon reaching the trees on the edge of the forested hill, the bees moved slowly along the edge of the forest patch above the canopy with parts of

the swarm cluster flying down into the canopy of individual trees and moving among the branches. The swarm continued in this fashion until it reached a break in the stand of trees leading to a steep slope thickly covered with a flowering liana growing over a thicket of fallen bamboo stems. The swarm flew through this gap, slowed down, spread out and lowered to about 2 m above the ground. Bees could be seen diving down into the liana before returning up to the milling swarm. After about 1 min of slowly moving through the liana thicket, the diving bees focussed on a particular location. Bee activity increased at this location until eventually the swarm clustered. Because the thicket was impenetrable, we could only observe the process from a distance of about 10 m.

The second swarm travelled slowly across the longan grove in the same direction as the colony's first swarm. We could see scout bees diving into the canopy of the longan trees as the swarm flew over the trees. The swarm halted once it reached a large longan tree on the edge of the grove. Bees were seen flying in the canopy of this tree, briefly

Fig. 1 A satellite image of the field site in which swarming events were observed. The locations of colonies 1, 2 and 3 are indicated by unique symbols. Lines indicate the approximate flight paths (as observed from the ground) of all 7 swarms that issued from colonies 1 (blue/green dashes), 2 (green/yellow/orange dashes) and 3 (dark orange/red dashed). Figure created using ArcMap 10.2



landing on branches, and excitedly bumping into branches before taking to the air again. The swarm clustered in the thickest section of the tree's foliage, out of reach and sight from the ground below.

Visualisation of locations indicated by waggle dances

While we monitored all 7 swarming events from our 3 colonies, we randomly selected one swarming event for each colony from which to extract detailed dance data. We provide heat maps (Figs. 2, 3, 4) that show the relative interest shown by dancers to locations nearby the colonies on the day before, of and after swarming. Because most dances occurred for locations relatively close to the colonies, we truncated the plots at 500 m, with the exception of colony 3, as this colony had many dances for distant sites. In addition to the heat maps, we also show the locations danced for during the hour of swarming. Superimposed on the scatter plot we give the mean vector bearing (green) and the direction the swarm flew into (red) (the complete set of scatter plots are given in the supplementary information, figures S1 to S9). Each of the colonies retained focus on similar nearby regions across all three days of observation;

these regions lay to the south east (most intense focus) and north of colony 1 at distances of approximately 100 m (Figs. 2, 5) to the south east (most intense focus) and the south-west (much less focus) of colony 2 at distances of 100–200 m (Figs. 3, 5) and to the east of colony 3 at a distance of approximately 100 m (Figs. 4, 5).

Direction of swarm flights

Swarms from colonies 1 and 2 departed in directions within the 95% confidence interval of μ determined during the hour prior to swarming (Table 2; see Supplementary Information for detailed description of the polarisation of dance angles and consensus vectors at hourly intervals). In contrast, the swarm from colony 3 travelled in a direction 252° from the swarm cluster, almost completely opposite to the mean dance bearing $\mu \approx 83.73^\circ$. However, bees of colony 3 performed dances in the approximate direction of flight from 10:00 onwards (see Figure S8 in supplementary information), often indicating locations more than 750 m away from the colony. It was not possible to estimate the 95% confidence interval for μ during the hour of swarming for colony 3, since for that set of data $R \approx 0.08$ fell below

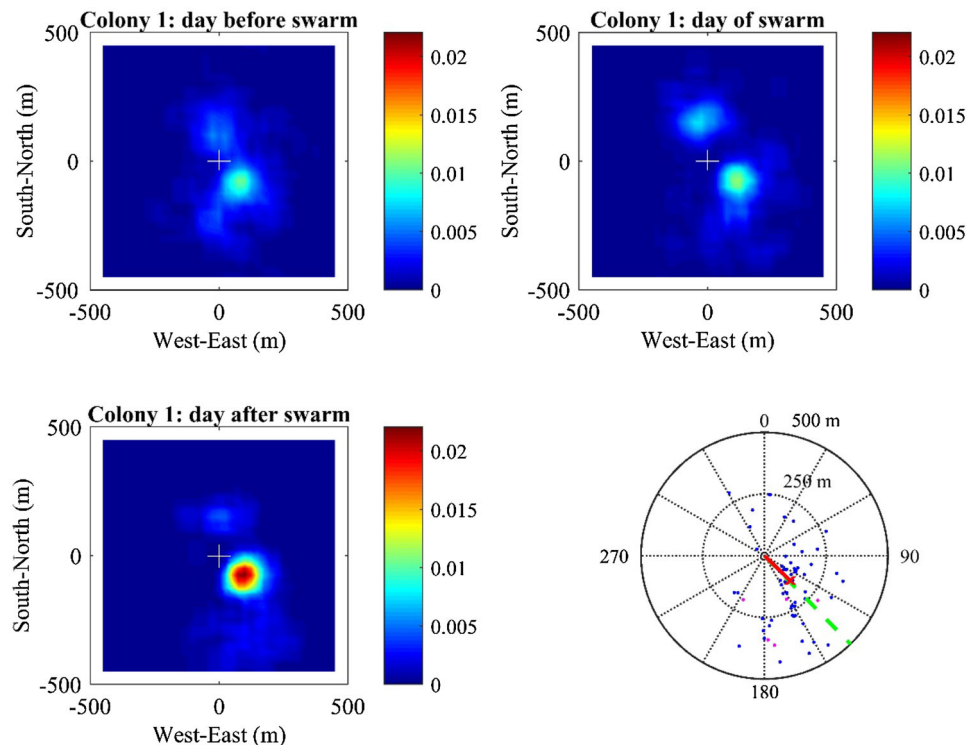


Fig. 2 Heat maps (*upper plots* and *lower left plot*) illustrating the relative frequency that different regions close to colony 1 (within 500 m in West–East and South–North directions) were indicated by all waggle dances. The colony is located at the origin in each plot, indicated by the *white cross*. The *lower right* hand plot is a scatter plot illustrating the mean locations within 500 m indicated by waggle dances during the hour from 13:00 to 14:00. *Magenta* points

correspond to locations advertised by workers carrying pollen, and *blue* points correspond to locations advertised by workers that were not carrying pollen. The swarm took flight at 13:21; the direction of flight and landing place of the swarm are plotted in *red*. The *green dashed line* in the scatter plot indicates the mean bearing indicated by dances between 13:00 and 14:00

Fig. 3 Heat maps (*upper plots and lower left plot*) illustrating the relative frequency that different regions close to colony 2 (within 500 m in West–East and South–North directions) were indicated by all waggle dances. The colony is located at the origin in each plot, indicated by the *white cross*. The *lower right hand plot* is a scatter plot illustrating the mean locations within 500 m indicated by waggle dances during the hour from 15:00 to 16:00. *Magenta* points correspond to locations advertised by workers carrying pollen, and *blue* points correspond to locations advertised by workers that were not carrying pollen. The swarm took flight at 15:33; the direction of flight of the swarm is plotted in *red*. The *green dashed line* in the scatter plot indicates the mean bearing indicated by dances between 15:00 and 16:00

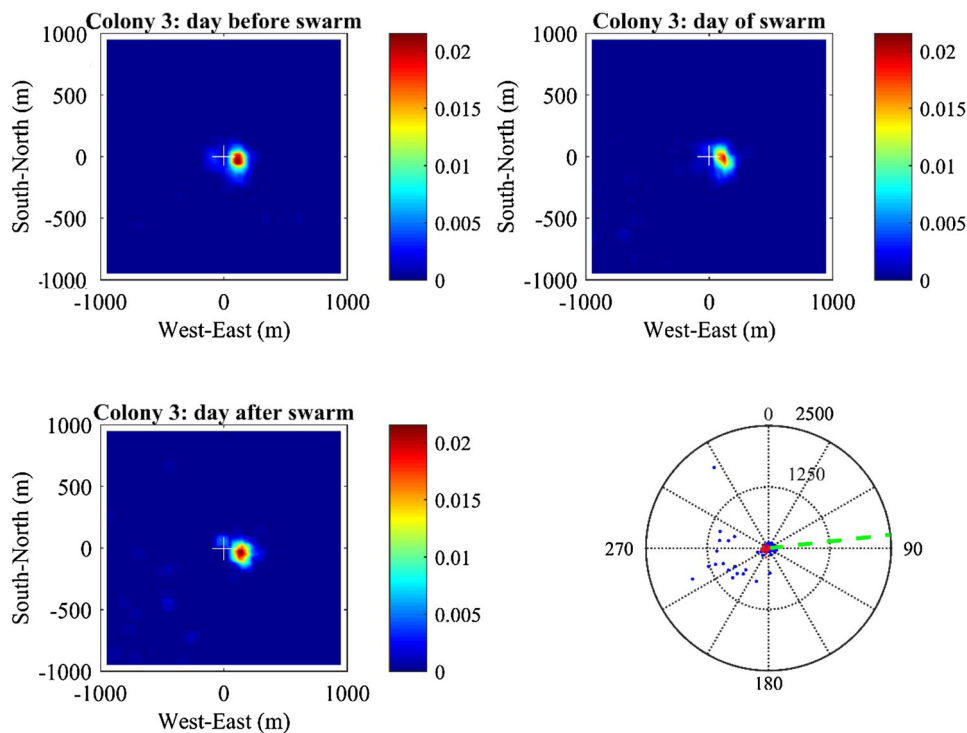
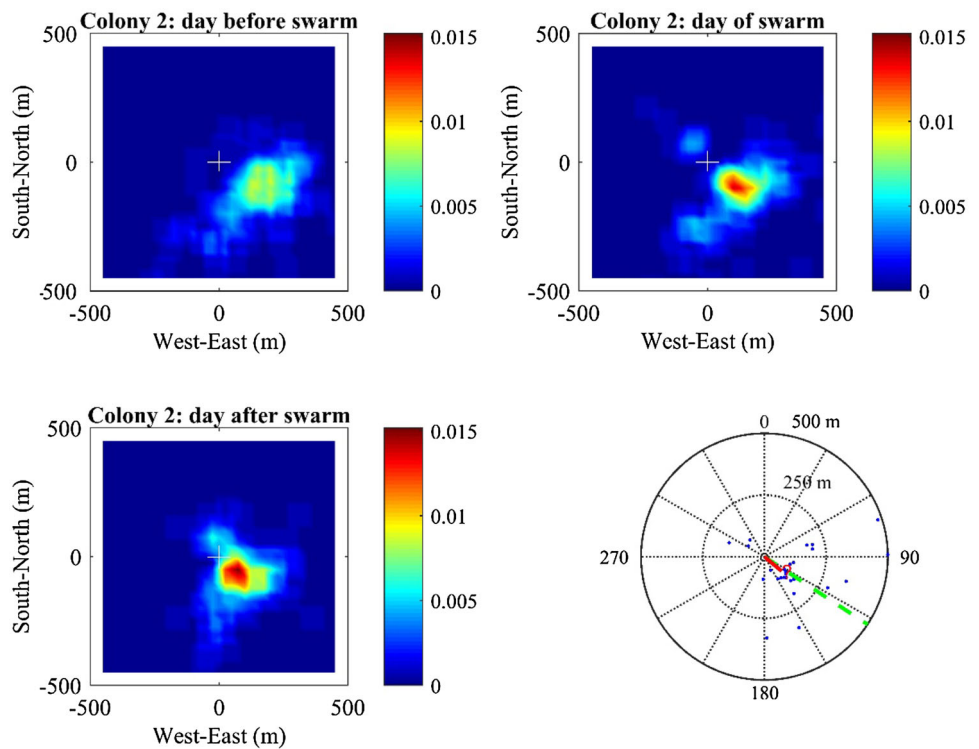


Fig. 4 Heat maps (*upper and lower left plot*) illustrating the relative frequency that different regions close to colony 3 (within 1000 m in West–East and South–North directions) were indicated by all waggle dances. The colony is located at the origin in each plot, indicated by the *white cross*. The *lower right hand plot* is a scatter plot illustrating the mean locations within 2500 m indicated by waggle dances during the

hour from 14:00 to 15:00. *Magenta* points correspond to locations advertised by workers carrying pollen, and *blue* points correspond to locations advertised by workers that were not carrying pollen. The swarm took flight at 14:55; the direction of flight of the swarm is plotted in *red*. The *green dashed line* in the scatter plot indicates the mean bearing indicated by dances between 14:00 and 15:00

Fig. 5 Location indicated by all waggle dances performed on colony 1 (yellow), colony 2 (green) and colony 3 (magenta). The locations of the colonies are indicated by the larger symbols. Figure created using ArcMap 10.2

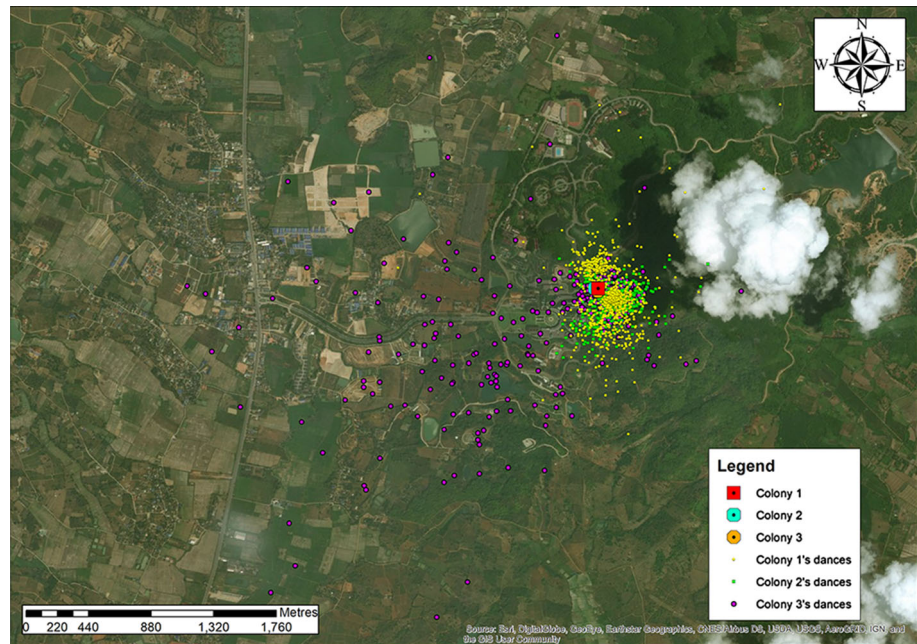


Table 2 Flight direction of swarms and mean bearing indicated by dances, μ with 95% confidence intervals for the day and hour that swarming occurred for each colony

Colony	1 (Swarm 1)	2 (Swarm 2)	3 (Swarm 2)
Time interval	13:00–14:00	15:00–16:00	14:00–15:00
Flight direction	134°	130°	252°
Mean bearing μ	135.79°	123.31°	83.73°
Lower bound for μ	122.79°	103.31°	–
Upper bound for μ	148.79°	143.31°	–

The swarm number is given within parenthesis (see Fig. 1)

the critical value of $\sqrt{\frac{\alpha}{2n}} = \sqrt{\frac{3.841}{2 \times 64}} \approx 0.17$ required to estimate the interval using our method (see Supplementary Information for more details on these quantities).

Consensus vector magnitude peaked during the hour of swarming for colony 1 (Figures S10 and S13 in the supplementary information), whereas the peak of this quantity did not occur during the equivalent hours on the days before or after colony 1's swarm took flight. Consensus vector magnitude was at a relatively high value during the hour of swarming for colony 2, but was not at the peak value observed (Figures S11 and S14 in the supplementary information). In contrast, consensus vector magnitude was at a relatively low value during the hour of swarming for colony 3 (Figures S12 and S15 in the supplementary information). The low consensus vector magnitude was due to the colony producing dances indicating almost opposite directions throughout most of the day (including the hour of swarming). A region centred approximately 100 m to the east of the colony received the most focused attention from

dancers throughout the day (see Fig. 4, and Figure S8 in the supplementary information), but there were also multiple dances indicating sites to the west and south-west of the colony at varying distances (often beyond 750 m).

Comparisons of approximate sites and regions advertised by each colony

All three colonies produced many dances for the region extending from the position of the colonies approximately 300 m to the east and from approximately 500–250 m in the south-east direction (Fig. 5). Visually, the distribution of the sites danced for across this region differed from colony to colony. The majority of dances for sites more than 500 m from the colonies were performed by scouts from colonies 1 and 3, with colony 3 in particular producing many dances spread over a relatively wide region to the west of the colonies.

The region approximately 100 m to the east and south east of the colonies was most frequently advertised by

waggle dances across all three colonies (Fig. 6) across all 3 days of observations for all three colonies (see Figs. 2, 3, 4).

The distributions of bearings to sites indicated by dances (relative to the mean colony location) differed between all pairs of colonies according to an r -sample uniform scores tests ($p \ll 0.001$, $W_3 = 54.79$, $n_1 = 786$, $n_2 = 378$, $n_3 = 629$), with colony 1 differing from colony 2 ($p \approx 0.002$, $W_2 = 12.33$), colony 1 differing from colony 3 ($p \ll 0.001$, $W_2 = 22.87$) and colony 2 differing from colony 3 ($p \ll 0.001$, $W_2 = 47.39$).

Discussion

We set out to address a simple question: do swarms of *A. florea* move to areas of abundant forage? We think the answer is yes—but not always. The swarms issued from colonies 1 and 2 seemed to track the location of abundant forage, as in both instances, swarms headed towards the area for which foragers were dancing on all three of the days we monitored the dances in detail. We are confident those areas supported productive forage plants, as bees returned from those locations carrying pollen (obviously we cannot tell the difference between a bee dancing for a potential nesting location and one carrying nectar). In addition, with the exception of the first swarm issued from colony 2, all five swarms from colonies 1 and 2 departed roughly into the same direction (Fig. 1). More than a week elapsed between the departures of colony 2's first and second swarm, and so the location of profitable forage could have changed over that period.

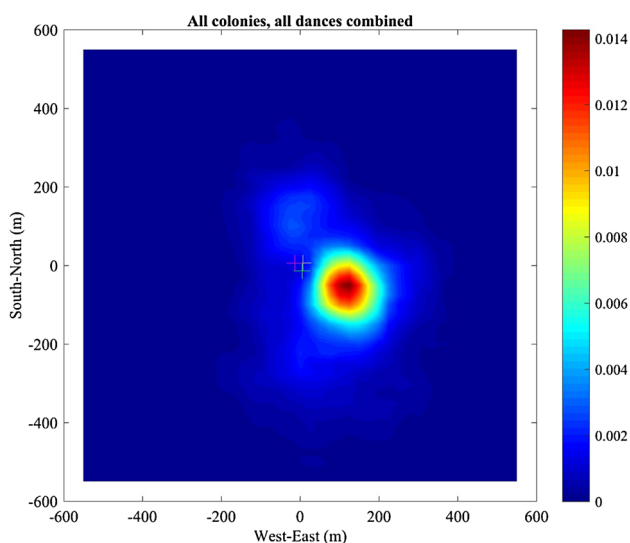


Fig. 6 Heat map illustrating the relative frequency that different regions were danced for on all three colonies

Swarms from colony 3 behaved differently. While the majority of dances were for locations similar to those danced for on the other colonies, in both instances, the swarms departed in a direction that was almost exactly opposite to the direction of the majority dances (Fig. 1). Importantly, none of the bees dancing for that direction carried pollen. Tropical *Apis* species, including tropical subspecies of *A. mellifera* (Schneider and McNally 1994), regularly migrate over long distances (Dyer and Seeley 1994; Koeniger and Koeniger 1980; Neumann et al. 2000; Oldroyd and Wongsiri 2006; Paar et al. 2000). In an earlier study on the giant honeybee *A. dorsata*, we found that despite the presence of suitable nesting locations nearby, some swarms decide to move further afield, travelling a long distance (Makinson et al. 2014). The behaviour of the two swarms from our third colony appears to follow the same pattern; instead of relocating to a nearby area of abundant forage, the swarms moved out of the local area completely. Hence, it appears that the long-distance dances performed on colony 3 were migration dances, and not nest-site selection dances. Future studies could perhaps compare the precision of such long-distance dances to the precision of dances for nearby locations, as migration dances show greater variability in precision, at least in *A. dorsata* (Dyer and Seeley 1994).

Our earlier work on nest-site selection in *A. florea* (Makinson et al. 2011; Oldroyd et al. 2008) and *A. dorsata* (Makinson et al. 2014, 2016) utilised swarms that were artificially created, a technique used routinely in *A. mellifera* (Beekman et al. 2006; Seeley 2003, 2010; Seeley and Buhrman 1999, 2001; Seeley et al. 1991; Seeley and Visscher 2003, 2004a, 2004b). Artificial swarms do not contain any comb, and hence no brood or food, as is normal for cavity-nesting species that select a nest site from a temporary cluster. For an open-nesting species, there seems no need to include a temporary cluster during the decision-making process. And indeed, our study suggests that swarms of *A. florea* move directly towards a potential new nesting location. All our swarms moved well beyond the typical distance for temporary clusters in *A. mellifera* (in which a swarm leaves the colony and settles on a nearby tree branch, typically within 10 m of the colony). Whereas, in our previous studies, all dancing bees indicated the direction of potential nest sites only, in our current study, bees danced both for forage and potential nesting sites.

Swarms are guided in flight by bees that have been involved in the decision-making process prior to swarm departure. In *A. mellifera*, scouts with knowledge of the chosen nest-site fly in the top half of the swarm, guiding the uninformed bees in the swarm by flying rapidly into the direction of travel (Beekman et al. 2006; Schultz et al. 2008). By aligning themselves with the travel direction of fast-flying bees, the uninformed majority of bees in the

swarm fly towards the intended location (Latty et al. 2009). Based on our work on artificial swarms of *A. florea*, we hypothesised that the main goal of the bees' decision-making process is to ensure a minimum level of vectorial consensus to allow the scouts to successfully guide the swarm into the intended direction of travel (Makinson et al. 2011). Once that level has been reached, all bees that were involved in the decision-making process actively guide the swarm while in flight. Theoretically such mechanism allows the swarm to fly in the general direction as advertised by the dancing bees prior to liftoff (Diwold et al. 2011), and fits with our earlier experimental work on *A. florea* and *A. dorsata* (Makinson et al. 2011, 2014). While we still saw an increase in consensus vector magnitude on colonies 1 and 2, the magnitude of the consensus may have been lower than that in artificial swarms of *A. florea* when all bees were dancing for nesting locations.

While it would be ideal to study more swarms, our results do suggest that colonies of *A. florea* track the availability of forage in their environment and swarms move in the general direction of forage rather than towards a specific nest site. Because *A. florea*'s nesting requirements are rather simple—protection against the elements and predatory ants—nesting sites are likely to be abundant in the bees' natural environment. As a result, the swarm's main challenge is to decide on the direction in which to fly, while the exact nesting location can be decided upon once that area has been reached. If the chosen nesting site does not meet expectations, *A. florea* swarms relocate until a good site has been found (Makinson et al. 2011).

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