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# Moving home: nest-site selection in the Red Dwarf honeybee (*Apis florea*)

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**Abstract** The Red Dwarf honeybee (*Apis florea*) is one of two basal species in the genus *Apis*. *A. florea* differs from the well-studied Western Hive bee (*Apis mellifera*) in that it nests in the open rather than in cavities. This fundamental difference in nesting biology is likely to have implications for nest-site selection, the process by which a reproductive swarm selects a new site to live in. In *A. mellifera*, workers show a series of characteristic behaviors that allow the swarm to select the best nest site possible. Here, we describe the behavior of individual *A. florea* workers during the process of nest-site selection and show that it differs from that seen in *A. mellifera*. We analyzed a total of 1,459 waggle dances performed by 197 scouts in five separate swarms. Our results suggest that two fundamental aspects of the behavior of *A. mellifera* scouts—the process of dance decay and the process of repeated nest site evaluation—do not occur in *A. florea*. We also found that the piping signal used by *A. mellifera* scouts to signal that a quorum has been reached at the chosen site, is performed by both dancing and non-dancing bees in *A. florea*. Thus, the piping signal appears to serve a different purpose in *A. florea*. Our results illustrate how differences in nesting biology affect the behavior of individual bees during the nest-site selection process.

**Keywords** *Apis florea* · Nest-site selection · Group decision-making · Swarming

## Introduction

Social insects regularly need to search for new sites to live in. Reasons for doing so include reproduction, damage or destruction of the old nest, or changes in the availability of resources within the surrounding habitat. The selection of a new nest site is one of the most important decisions an insect colony has to make, as its reproductive success depends on the quality of the site chosen. For example, the site must be large enough to allow colony growth while still affording the colony protection from predation and bad weather (Seeley and Buhrman 1999; Franks et al. 2003). As colonies often invest considerable resources in nest construction by producing structures such as combs or protective resin barriers (Seeley and Morse 1976; Hepburn 1986; Roubik 2006), moving nest is costly, especially if the new site proves to be unsuitable. Some species invest heavily in their new nest site even before they have moved in. For example, stingless bees move to a new home gradually (Michener 1974), with scouts searching for a new nest while still returning to the mother colony. Workers and a queen gradually translocate to the selected nest site, moving resources over extended periods. Thus, there is considerable incentive for colonies to make the best decision possible.

For an insect colony to choose the best possible nest site within a given environment, it would require complete information on the quality of all available nest sites.

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However, as most decision-making processes, nest-site selection is time-constrained. If, for example, the old nest has been destroyed, a decision on where to move to needs to be made fast. Because the collection, processing, and evaluation of information requires time, a decision must be reached without exhaustively exploring all available alternatives. This tension between speed and accuracy has been termed the speed–accuracy trade-off paradigm (Osman et al. 2000). Nest-site selection by colonies of insects is an excellent model system to study the interplay between speed and accuracy within decentralized decision-making systems (Franks et al. 2003; Passino and Seeley 2006). This process has been especially well-studied in the cavity-nesting Western Hive bee (*Apis mellifera*) and is probably one of the best understood examples of group decision-making in the animal kingdom (Seeley and Visscher 2004).

During periods of high food availability, colonies of *A. mellifera* become overcrowded and go through a process of fission (known as reproductive swarming) whereby a large proportion of workers and the mother queen leave the nest and form a temporary cluster tens of meters away, while a young queen will inherit the old nest (Winston 1987). The resulting swarm then needs to search for a new home, such as a cavity in a tree, a hollow space in a building, or an abandoned bee hive. About 5% of the workers, the nest-site scouts, fly from the clustered swarm and start searching the surrounding environment for potential nest sites (Seeley et al. 1979). Upon finding a potential site, individual scouts assess the quality of the cavity found for characteristics such as volume, height, aspect of the entrance and entrance size (Seeley and Morse 1978; Schmidt 2001). After returning to the swarm, the scout that has previously visited a potential nest site performs a series of waggle dances if she has rated the site of sufficient quality to be considered. The dance encodes information on the distance, direction and quality of a potential food source or nest site. The waggle dance is a stylized figure-eight movement which has two components: the waggle run, wherein the bee strides forward waggling her body side to side while emitting a buzzing sound, followed by the return phase in which the bee loops around alternatively left or right, to return to the spot she commenced her waggle run and to start a new waggle circuit (von Frisch 1967). In *A. mellifera*, directional information is encoded by the angle of the waggle run relative to a vertical line of zero degrees, which corresponds to the angle the target location is from the sun's current position in the sky (the azimuth), while the duration of the run is correlated with the distance to the site (Dyer 2002). Dance followers use the information encoded in the dance to locate the advertised site, which they then independently evaluate for quality.

In *A. mellifera*, the number of dance circuits in the first dance performed by a returning scout is positively correlated with the scout's perception of the site's quality (Seeley 2003). After completing her dance, the scout leaves the swarm to re-evaluate the nest site before returning again and dancing another time for the same site. Each time an individual scout dances for the same nest site after having re-evaluated that site, she reduces the number of dance circuits by a fixed number of waggle runs (approximately 17 dance circuits in *A. mellifera*; see Seeley and Visscher 2008), regardless of the site's quality (Seeley 2003). This means that high quality sites are advertised for longer than poor quality sites because the initial number of circuits is higher. Thus, over time, more individuals are recruited to high quality sites compared with sites of lower quality and individual bees dancing for low quality sites cease dancing sooner than bees dancing for those of higher quality. However, even when dancing for a site of high quality, a scout will cease dancing, thereby avoiding deadlock. Dance decay is therefore a form of dance attrition whereby individuals and the sites they are dancing for disappear over time.

While inspecting a potential nest site, a scout estimates the number of other scouts that are also evaluating the site. If this number exceeds a threshold, a “quorum”, the scout returns to the swarm and signals that the quorum has been reached by producing the “piping signal”, a mechanical signal produced by wing vibration (Seeley and Visscher 2003). This piping signal informs other swarm members to prepare for flight by warming up their thoracic muscles to the 35°C required for liftoff (Seeley et al. 2003), as a decision on the new site has been made (Visscher and Seeley 2007). Finally, when the swarm is prepared to travel to its new nest site, scouts from the chosen site run excitedly through the swarm producing a signal known as the “buzz run”, breaking up the swarm's structure and activating inactive bees thus triggering the swarm to take off (Rittschof and Seeley 2008). Although the process of swarm guidance is not completely understood, it is thought that the scouts guide the swarm by flying rapidly through the swarm in the direction of the nest site (Janson et al. 2005; Beekman et al. 2006; Schultz et al. 2008; Latty et al. 2009).

For a cavity-nesting species like *A. mellifera*, it seems likely that the number of high quality nest sites is limited due to a lack of sufficiently old trees that contain hollows large enough to house a honey bee colony. Moreover, as the entrance to these cavities represent rather small points in space, they may be hard to locate. But not all honey bee species live in cavities. Open nesting species like *Apis florea* build a small nest comprised of a single comb suspended from a twig of a shrub or tree in the open (Oldroyd and Wongsiri 2006). Thus, in most habitats, there is an abundance of shaded twigs that would be equally suitable for building a nest. This would remain true even if factors such as proximity to food, water, or other nests of *A. florea* caused certain areas of the general environment to be favored as nesting sites over other areas. In *A. mellifera*, the relative quality of potential nest sites is critical to the house-hunting process. Hence, this complex nest-site selection process ensures that near-consensus is reached on which site to move to prior to the swarm lifting off. Given that there will usually be a large number of equally good twigs within flying distance of *A. florea* swarms, how is a decision on a new nest site reached by scouts assuming that there is no compelling reason to choose one twig over another?

A previous study on nest-site selection in *A. florea* showed that, in contrast to *A. mellifera*, *A. florea* does not seem to select a particular twig or branch prior to the swarm flying off as evident by the wide divergence in dances prior to liftoff (Oldroyd et al. 2008). Instead, *A. florea* swarms fly in the general direction indicated by the average direction of the dances performed in the last half hour or so before lifting off. Swarms of *A. florea* also appear to make rapid decisions as every swarm observed took only a few hours to move to a new home (Oldroyd et al. 2008). Thus, whereas *A. mellifera* swarms take longer to reach a consensus on a specific location, accurately choosing the highest quality nest site out of those found by the scout bees, *A. florea*'s decisions are fast, but inaccurate, as they fail to reach a consensus upon a specific location before swarm departure. Moreover, Oldroyd et al. (2008) managed to follow two of their *A. florea* swarms as they moved to their new nest site and both stayed at the chosen nest-site location only for about a week, after which time they departed leaving behind a comb (Oldroyd et al. 2008). Hence, it appears that *A. florea* swarms make a quick decision about a general area in which to nest, test a specific location for a few days, and leave again if this location turns out not to be ideal.

Here, we examine the behavior of individual *A. florea* workers during the nest-site selection process and compare our observations to phenomena that are typically seen in *A. mellifera* swarms. We were particularly interested to investigate if ubiquitous individual behaviors seen in *A. mellifera* workers during the decision-making process are present in *A. florea*. To this end, we determined if dance decay occurs as this would indicate that scouts reassess potential nest sites they are dancing for. Re-assessment of sites can only take place if scouts regularly take off; hence, we also determined if scouts were seen to leave the swarm after bouts of dancing. We further studied the behavior of dance followers and established when the piping signal was detected.

## Methods

### Study site

All experiments were performed on the grounds of Naresuan University, Phitsanulok, Thailand (16°44’29.68” N, 100°11’47.63” E), using wild *A. florea* colonies captured in and around the university campus. Experiments were performed during the period from the twenty-sixth of April to the tenth of June 2008.

### Creating artificial swarms

In order to study individual behavior during the nest-site selection process, we created five artificial swarms (1–5) using the technique described in Oldroyd et al. (2008). We first located and captured the queen from a colony and placed her in a wire cage, measuring 3.5×3×1 cm. This queen cage was then suspended in a screened box with the dimensions 20×22×18 cm. The colony's workers were then placed in the box. To estimate the number of bees in the swarms, we weighed the empty and full box as well as the queen cage in which the swarms were kept prior to feeding the bees (the weight of an individual *A. florea* worker is approximately 30 mg; see Burgett and Titayavan 2004). During a natural swarming process, the workers engorge on honey prior to leaving the old colony and start producing wax scales (Combs 1972). We therefore fed our artificial swarms a 1:1 sucrose/water solution *ad libitum* for 2 or 3 days until workers started producing wax scales.

In two swarms (4 and 5), we marked each bee individually. *A. florea* are too small to use the standard queen marking tags normally used in experiments with *A. mellifera* (Seeley and Buhrman 1999), so we used the method described in Beekman et al. (2006) to immobilize the bees and then painted each individual with a unique combination of colors on the thorax and abdomen. After bees were marked, they were placed in a box as described above and fed 1:1 sucrose/water solution *ad libitum* until the workers started to produce wax scales.

### Observations

To observe the nest-site selection process, we suspended an approximately 1-m long and 1.5-cm-diameter stick horizontally from a shady tree, 1 m above the ground. Both ends of the stick were covered in grease to prevent ants from climbing onto it. On the evening of the second or third day of feeding the swarm, the queen was fixed in her cage to the stick using twine and the workers were shaken out of their box. The workers quickly settled around the queen cage and formed a cluster. The queen cage was opened to release the queen the following day just before dawn (5:30 AM) when observations commenced. When a swarm did not leave within 1 day, we returned again the next day prior to dawn to start our observations. In swarms 1, 2, and 3, all dancers were individually marked with a paint dot on the thorax as they danced for the first time on the swarm. As soon as we noticed that a bee had returned with nectar (successful foragers transfer nectar to other bees using trophallaxis), we fed the bees 1:1 sucrose/water solution by painting sugar-solution onto the stick close to the bees continuously until satiated. This was done to ensure that bees did not start dancing for food sites instead of nest sites. Feeding was only needed for swarms 2 and 4, which took more than 1 day to reach a decision about were to move to.

A video camera (Sony Handycam HDV) was positioned 0.5 m above the suspended swarm and continuous recordings were made of all activity on the swarm's surface during daylight hours until the swarm departed. A compass was placed in the field of view of the video camera every time tapes were changed or the camera's position was altered. We regularly spoke the current time and the identity of individual bees observed on the swarm's surface into the audio track of the recordings. When a swarm took off, we followed it on foot until it landed and settled (swarm 2), or was lost from sight (1, 3, and 5), and the distance and direction traveled was recorded using a Global Positioning System device. Swarm 4 attempted to liftoff after 3 days but failed, at which point we ceased recording its nest-site selection process. We infrequently monitored this swarm without filming its behavior until it left for an unknown location on day 6. Only the data collected on the third day when the scouts reached a decision were analyzed.

## Video analysis

Video recordings were downloaded onto a personal computer for analysis using Windows Media Player (Version 11). For each swarm, we recorded the identity of all marked bees that took off or landed on the swarm, the identity of each dancing bee, the number of dances performed by each bee and the number of dance circuits per dance. For the individually marked swarms (4 and 5), we also recorded the identity of dance followers, defined here as any bee that followed a single dance circuit within a 30° radius behind the dancer (Judd 1995) and the number of dance circuits they followed. We also listened for the piping signal (Visscher and Seeley 2007) throughout the decision-making process by directing a small plastic tube held to the ear towards individual bees that we suspected of producing the signal.

In *A. florea*, spatial information is communicated through the waggle dance, which, in this species, involves the dancer performing the dance on a horizontal surface and using celestial cues to point her body in the direction of the advertised site (Dyer 1985; Oldroyd and Wongsiri 2006). As in *A. mellifera*, the dance is separated into a waggle run and a return phase. During the waggle run, the bee aligns her body in the direction of the site being advertised while shaking her abdomen side to side with her wings outstretched and slowly walking forward. During the return phase, the bee returns to the location where she had commenced her previous waggle run (Dyer 2002).

To determine the location danced for by our scouts, we aligned a circular protractor similar to that described by von Frisch (1967) along the axis of a dancing bee during freeze-frame playback and recorded the deviation of the bee's body from straight up the computer screen during its waggle phase to the nearest degree. Using the image of a compass placed in the video's field of view, we converted these readings into the compass direction that the worker had faced during her waggle phases. We also measured the duration of the waggle phase of each dance to the nearest 1/10 s.

Three calibration curves that relate duration of the dance circuit to distance to feeder have been determined empirically for *A. florea* (Lindauer 1956; Koeniger et al. 1982; Dyer and Seeley 1991). These three calibration curves include the duration of the return phase of the dance: the time it takes the dancing bee to return to its original position before performing the next waggle phase. However, in *A. florea*, the duration of the return phase is highly variable between each waggle phase of the same dance. We therefore did not include the return phase in our measurement but added a fixed return phase of 1.5 s (Gardner et al. 2007) to all our dances to obtain a relative measure of the distance of the advertised sites.

The published curves relating distance to dance circuit duration (Lindauer 1956; Koeniger et al. 1982; Dyer and Seeley 1991) are quite variable. This is not surprising because distance perception by flying bees is heavily influenced by the visual environment (Srinivasen et al. 2000). Because we were interested in visualizing the relative location of the sites advertised on the swarms rather than their absolute position, we used an average of the three published curves to estimate the distances that the dances were indicating. The equation relating circuit duration to distance we used was: circuit duration$=1.5+0.0068$(distance) (Oldroyd et al. 2008).

## Data analysis

We followed the method of Seeley (2003) with a few modifications to suit the biology of our species, to create dance decay curves for *A. florea*. For each of the 197 dancing bees, we counted the combined number of dance circuits performed in the dances of each bee for each period of time prior to the bee taking off from the swarm. We then recorded the instances where bees left the swarm, returned and continued dancing for the same site upon their return, until they returned to the swarm without dancing, or started dancing for a new location. A new location was arbitrarily defined as an average direction that differed more than 90° from the previous dance performed by that bee. These bouts of dancing were defined as a "dance series" and were grouped together depending on the number of returns to the swarm that were performed before the series ceased. We then omitted dance series that were still in progress during the last hour before the swarm took off or during the last hour before nightfall (in swarm 2). This was done to allow for the possibility that these bees may have been forced to cease dancing due to the departure of the swarm or the arrival of nightfall rather than due to dance decay.

The data collected for dances, dance-following, and takeoff and landing of individually marked bees was used to produce individual activity histories for all dancers in swarms 4 and 5. All dances performed by the bees were included, irrespective of the number of waggle runs performed per dance. These activity histories were used to make general observations about the behavior of the scout bees, such as the number of dances performed and/or followed, as well as the number of times the scout bees left the swarm.

To visualize the location of sites danced for by individual bees, we created radial plots of the direction and the distance danced for every hour for each swarm. We then performed a Rayleigh's test on each of these radial plots to determine if the dances were significantly non-random in direction (Zar 1996). In all radial plots, only dances that comprised at least three waggle circuits were included.

### Quantifying on-swarm agreement

We calculated a swarm's consensus vector to visualize if the dancing bees reached some form of consensus prior to liftoff. A swarm's consensus vector for a given time interval, *T*, $t_0 \le t \le t_1$, was determined as follows. First, all the waggle runs performed during the time interval *T* were extracted from the swarm's complete data set (we only included dances of at least three waggle runs). The average bearing of the dances performed by an individual during *T* was calculated by constructing a unit vector for each of that bee's waggle runs, adding all the unit vectors together head to tail and determining the bearing of the resultant vector. More formally, the average bearing, $\theta_i$, danced by bee *i* during the time interval *T* is given by:

$$\theta_i = \tan^{-1}\left(\frac{x_i}{y_i}\right)$$

where

$$x_i = \sum_{j=1}^{n_i} x_j,$$

$$y_i = \sum_{j=1}^{n_i} y_j \ .$$

$x_j = \sin\phi_j$, $y_j = \cos\phi_j$, $n_i$ is the number of waggle runs performed by bee *i* during the interval *T*, and $\varphi_j$ is the bearing of the *j*th waggle run for bee *i*.

Once all the average bearings, $\theta_i$, had been calculated, we then constructed unit vectors in the direction of these average bearings. The *x* and *y* components of the unit vectors are given by:

$$\bar{x}_i = \sin\ \theta_i$$

$$\bar{y}_i = \cos\ \theta_i$$

A resultant consensus vector, **v**, was then calculated by adding all the individual unit vectors. The magnitude and bearing of **v** are given by:

$$|\mathbf{v}| = \sqrt{{x_r}^2 + {y_r}^2}$$

and

$$\theta_r = \tan^{-1}\left(\frac{x_r}{y_r}\right)$$

where

$$x_r = \sum_i \bar{x}_i$$

and

$$y_r = \sum_i \bar{y}_i \ .$$

The bearing of the consensus vector, **v**, corresponds to the average angle indicated by dancers during a time interval *T* and the magnitude of **v** is a measure of how much agreement existed among the dancers on the average dance direction.

## Results

### Final swarm sizes

We individually marked 1,885 workers in swarm 4 and 3,032 workers in swarm 5. Approximately 250 bees of swarm 4 and 350 bees of swarm 5 were found dead when the swarms were released. Hereafter, the swarm sizes have been corrected for the number of bees that died during the procedure. We marked a total of 34, 102, and 22 dancing bees in swarms 1, 2, and 3, respectively. Based on the weight of the swarm and the average weight of an *A. florea* worker, swarm 2 comprised 4,790 bees and swarm 3 comprised 5,780 bees. Swarm 1 was not weighed, so we do not have exact information on the number of bees. However, it appeared to be roughly the same size as swarm 5. In total, 1,459 waggle dances by 197 bees were analyzed.

### Dance behavior and recruitment success

The number of dancing bees in each swarm represented a very small percentage of the total number of bees in the swarm (0.38–2.13%, Table 1). Examination of the dance histories of the 39 scouts observed in swarms 4 and 5 (Fig. 1) showed that the vast majority (31 bees or 79.5%) of bees followed at least one circuit of a dance prior to dancing themselves. Twenty-three (59%) of the dancing bees followed at least one circuit of a dance indicating a location within 30° of the location they commenced dancing for before they started to dance. However, only 13 (33%) of these 23 bees danced within 30° of the last dance they observed prior to dancing themselves, 12 of which did so within 15 min of either following a dance or returning to the swarm. Of the 13 bees that danced within 30° of the last dance they observed prior to dancing themselves, nine took off from the swarm prior to dancing, and four commenced dancing without leaving the swarm. Hence, these 13 bees appeared to have been recruited by following a dance. The remaining ten bees that followed a dance within 30° of their own dance direction followed dances indicating other directions between following a dance and then dancing in the same direction. Therefore, it is unclear if these bees had been recruited by the dance that they had followed earlier. Sixteen out of the 39 bees studied (41%) danced for sites that they had never previously observed dances for, and therefore can be considered to have been independent scouts. Eight of these (20.5%) commenced dancing without ever having followed a dance by another bee. Therefore, somewhere between 33–59% of dancing bees were recruited while 41–67% of bees independently scouted for a site.

In swarms 4 and 5, the number of bees that followed one or more dance circuits was 10.6% and 21.2% of all the swarm bees, respectively (Table 2). Of these dance-informed bees, 27.8% and 44.9%, respectively, also took off from the swarm during the decision-making process. Recruitment success (defined as the percentage of dance followers that commenced dancing in the indicated direction after following a dancing bee) was extremely low (1.2% of dance followers in swarm 4 and 1.9–3.7% in swarm 5, Table 2). However, it is possible that some bees were recruited to a direction by the dance that they followed, but did not themselves dance upon returning to the swarm. Therefore, our measure of recruitment success should be regarded as the lower bound.

Of the 197 bees from the five swarms, 31 (15.7%) changed the direction they danced for (defined arbitrarily as an average direction that differed more than 90° from the previous dance performed by that bee) during the decision-making process. There was large variation of the number of bees per swarm which changed direction during the decision-making process with one (2.94%), 26 (25.49%), three (13.64%), 0 (0%), and one (3.13%) bees in swarms 1–5, respectively, changing direction. The 31 bees that did change the direction they danced for changed direction a total of 52 times. Nineteen (35.8%) of these events occurred after a bee left and returned to the swarm, while 12 (22.6%) did so after following one or more dances indicating a direction within 30° of the new direction they danced for. A further 11 (20.8%) of those bees that changed the direction they danced for both followed a dance within 30° of the direction they changed to and took off from the swarm. Eleven (20.8%) instances occurred where a bee changed the direction indicated by the dance without either taking off from the swarm or observing similar dances. It is possible that we failed to observe these bees leaving the swarm or being recruited by following a dance.

**Table 1** The number of dancers, percentage of bees dancing, percentage of bees dancing in the last hour prior to takeoff, and number of hours taken for the swarms to takeoff

| | Swarm | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| Number of dancing bees | 34 | 102 | 22 | 7 | 32 |
| Swarm size (number of bees) | – | 4,800 | 5,800 | 1,600 | 2,700 |
| Percentage of bees dancing | | 2.13 | 0.38 | 0.43[a] | 1.19 |
| Percentage of bees dancing in last hour | | 0.50 | 0.24 | 0.31 | 0.75 |
| Hours of swarm activity prior to takeoff (hours/minutes) | 4:43 | 18:31 | 3:00 | Unknown | 8:50 |

Swarm activity is defined here as the period of time from the first dance activity of the day until the swarms either took off or ceased activity for the day

[a] On day 3 only

### Dance decay

We did not find evidence of dance decay, i.e., a linear decrease in the number of dance circuits performed after each consecutive dance period as is observed in *A. mellifera* in *A. florea* (Fig. 2). The relationship between the number of waggle runs and returns to the swarm prior to ceasing dancing was not significant (linear regression; $F_{1,4}=0.08$, $P=0.78$, Fig. 3). Moreover, out of the 197 scout bees seen dancing in all swarms, the majority (61%) were not seen taking off from the swarm to re-evaluate the nest site in between bouts of dancing (Fig. 4). Despite this, individual bees did cease dancing at some stage during the nest-site selection process.

### Dance directionality

As in a previous study on nest-site selection in *A. florea* (Oldroyd et al. 2008), dances were highly variable, both

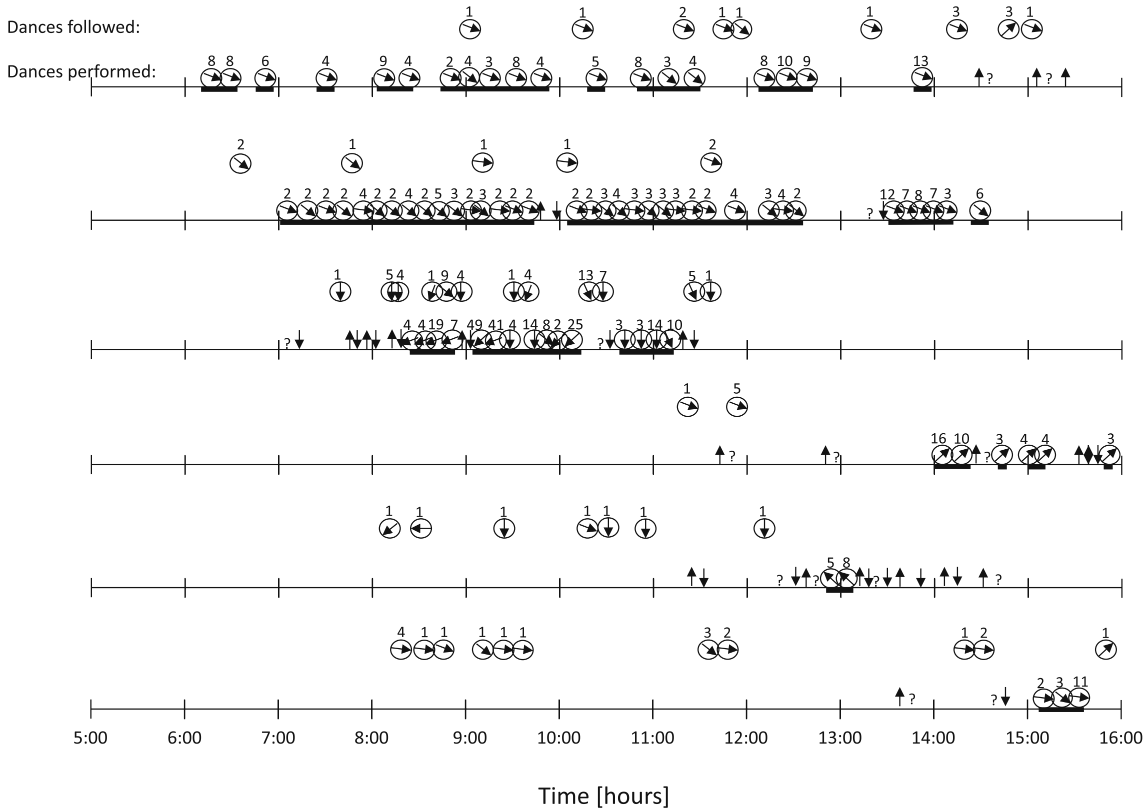

**Fig. 1** Individual dance histories of a subset of six bees that danced on swarms 4 and 5. The *horizontal black bars* denote the time spent dancing. The *arrows in circles* directly *above the black line* represent the average angle indicated by a single dance performed by the bee, while the *arrows in circles* above those indicate the direction indicated in dances followed by the bee. The numbers next to either symbol show the number of waggle runs performed or followed. *Upward arrows* denote the bee's departure from the swarm; *downward arrows* denote her return. *Arrows with question marks* represent a time when either only taking off from or landing on the swarm was observed. Time is given at the *bottom*

with respect to distance and direction. Oldroyd et al. did not mark their dancing bees; hence, they were unable to discern if the observed variance arose from many individual bees dancing for different locations or to intra-individual variation. We therefore determined how variable consecutive dances are performed by the same bee (using the actual angles of the waggle runs). Our results show that individual bees showed large variation in the directions indicated by dances within all five swarms. As an example, we have plotted the dance behavior of a single bee from swarm 5 as she danced over a period of 4 h (Fig. 5). The dance behavior of this bee is representative of dance behavior observed in all dancing bees.

To determine if the dances were significantly non-random in direction, we pooled the dances performed by all bees within 1-h intervals and performed Rayleigh's tests (Zar 1996). At all hours in all five swarms, scouts danced in a non-random direction ($p<0.05$) with the exception of swarm 2 on day 1 from 9–10 AM and 12–1 PM and on day 2 from 6–7 AM. Three of the hourly intervals had insufficient dances ($n<5$) to perform a Rayleigh's test (swarm 5, 12–1 PM; swarm 4, 12–1 PM and 1–2 PM; Table 3) and have therefore been excluded.

In swarms 1, 2, 3, and 5 (that managed to successfully take off from their temporary cluster), the last hour of the decision-making process was characterized by a surge in the number of bees actively dancing on the swarm (Table 3). Evidently, previously uninvolved bees were involved in the decision-making process as the process reached its climax. Interestingly, in only two out of the four swarms that successfully took off (swarms 2 and 3) was the direction flown by the swarm within the 95% confidence interval of the mean vector bearing of dances in the last hour prior to liftoff (Table 3).

## Detection of the piping signal

Once a scout had finished a waggle dance, it would often disappear beneath the cluster, pushing excitedly through the cluster while making an intermittent high-pitched piping noise. This could happen at any time during the decision-making process. Non-dancing bees were also observed producing the piping signal in two of the five swarms.

**Table 2** Observations of dancing bees and recruitment of dance followers on *A. florea* swarms 4 and 5

| Characteristic | Swarm number | |
|---|---|---|
| | 4 | 5 |
| Total number of bees in swarm | 1,600 | 2,700 |
| Total number of bees following a dance (% of total) | 169 (10.6%) | 572 (21.2%) |
| Total number of bees flying from or to the swarm (% of total) | 85 (5.3%) | 626 (23.2%) |
| Total number of bees that both followed a dance and left the swarm (% of total dance followers) | 47 (27.8%) | 257 (44.9%) |
| Total number of dancing bees (% of total) | 7 (0.4%) | 32 (1.2%) |
| Total number of bees recruited by the last dance followed (by any dance previously followed) | 2 (2) | 11 (21) |
| Proportion of dance followers recruited (by any dance previously followed) | 1.2 (1.2)% | 1.9 (3.7)% |
| Proportion of dance followers that left swarm | 28.6% | 44.9% |
| Proportion of flying bees that danced | 4.3% | 5.1% |

*Following a dance* is defined as a bee that followed one or more dance circuits within a 30° arc behind the dancer

*Recruitment* is defined as a bee that followed a dance and subsequently performed a dance within 30° of the followed dance

## Vectorial consensus

The data in Table 3 show that, in combination with the surge in the number of dancers observed during the hour prior to takeoff, the angle of many of the dances performed closely match that of the mean vector bearing of all dances (values of $R$ close to 1 correspond to tighter clustering of the individual dances about the mean). To further explore this apparent correlation between the peak number of dancers and approximate agreement on a direction of dance, we calculated the vectorial consensus of our five swarms at hourly intervals (Fig. 6). The data show that, as the swarm progressed through its decision-making process, vectorial consensus increased until the swarm reached an agreement on the general direction in which to fly (Fig. 6). Swarm 2 appears to be an exception. When the data are plotted hourly, the peak vectorial consensus magnitude for swarm 2 occurred in the third last hour of day 1 rather than in the final hour of day 2 before takeoff. However, when we constructed vectorial consensus plots for 15-min intervals, the peak magnitude for day 1 was 6.3, but the peak magnitude observed during day 2 was 11.6 occurring in the final 15 min before takeoff (data not shown). In fact, when the data were plotted in 15-min intervals, the increase in vectorial consensus towards the end of the decision-making process became even more pronounced (data not shown due to the large number of graphs).

It is important to realize that vectorial consensus is not sufficient for the swarm to liftoff as otherwise even when two bees would be dancing in the same direction, the

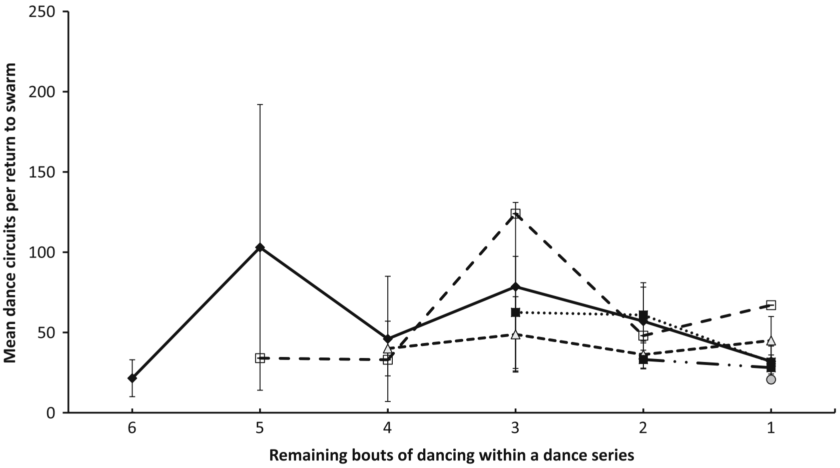

**Fig. 2** Mean number of dance circuits performed by bees on each successive return to their swarm during a dance series (defined as a series of waggle dancing events separated by the dancing bee leaving the swarm before returning and dancing for the same location again). Each *line* represents dance series of different size, *Diamonds*: six bouts of dance activity before ceasing dance activity ($n$=2); *Squares*: five bouts ($n$=1); *triangles*: four bouts ($n$=5); *circles*: three bouts ($n$=8); *crosses*: two bouts ($n$=42); and *circles*: one ($n$=154). *Bars* indicate standard error

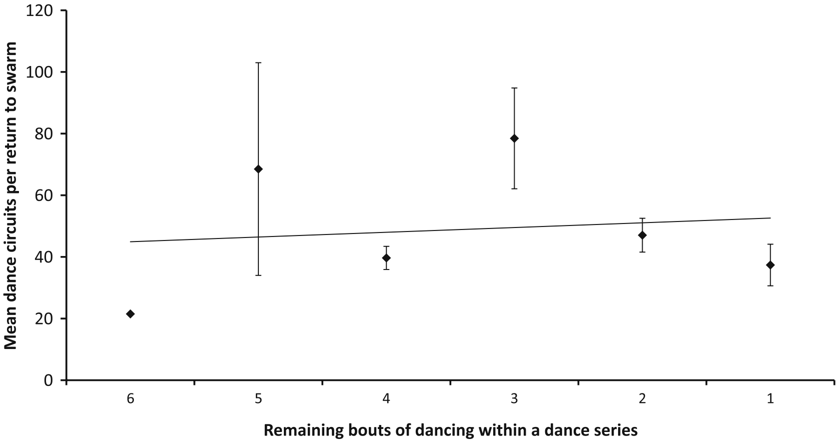

**Fig. 3** Summary plot showing the change in number of waggle runs per period of dancing for a particular location over consecutive returns to the swarm. Each *data point* represents the mean of the mean values depicted here in Fig. 3 for each bout number and each *error bar* value represents ±1 SE of these mean values. The regression line is not significantly different from zero: $F_{1,\,4}=0.08$, $P=0.78$

swarm would depart. Our non-normalized measure of vectorial consensus shows the combined effects of having both a sufficient number of dancers and enough directional consensus.

### Liftoff

Approximately half an hour prior to liftoff, the bees on the surface of the swarms became progressively more excited, with bees conducting a behavior similar to the buzz run performed in *A. mellifera* (Rittschof and Seeley 2008) while running over the surface of the swarm. Eventually, this frenzy of activity reached a crescendo and bees started taking to the air en masse. Individual bees were initially observed repeatedly taking off and landing in quick succession, but by the end of liftoff bees started streaming off the cluster.

Once in the air, the swarms hovered in place for approximately 1 min before they headed off. Of the four swarms that took off during the period of study, two swarms (swarms 1 and 5) disappeared over a building after a distance of only 30 and 20 m, respectively. We were able to follow swarm 2 to the location where it landed, and we followed swarm 3 for 100 m until it disappeared flying over a tall (>10 m) tree.

Swarm 2 traveled across a field for 120 m before reaching a line of trees. The swarm then slowly made its way along the line of trees, hovering around canopy height. Bees were observed on three different occasions to start to land on a patch of foliage or branches, before taking to the air again and continuing to move on. Eventually, the bees commenced landing within the canopy of a tree, forming small clusters on leaves until they coalesced into a cluster around a thin branch. We could not find the cluster the next morning, indicating that the swarm had moved on.

## Discussion

### General observations

We set out to describe the behavior of individual *A. florea* workers during the nest-site selection process and compare this to that seen in *A. mellifera.* We were particularly interested to investigate if dance decay occurs in *A. florea* as this would indicate that scouts reassess the potential nest sites they are dancing for. We further studied the behavior of dance followers and established whether the piping signal was detected.

Our results demonstrate that the decision-making behavior of *A. florea* during nest-site selection is fundamentally different to that of *A. mellifera*. The behaviors associated with nest-site selection appear to reflect the nesting biology of this species. Because of the abundance of potential nest

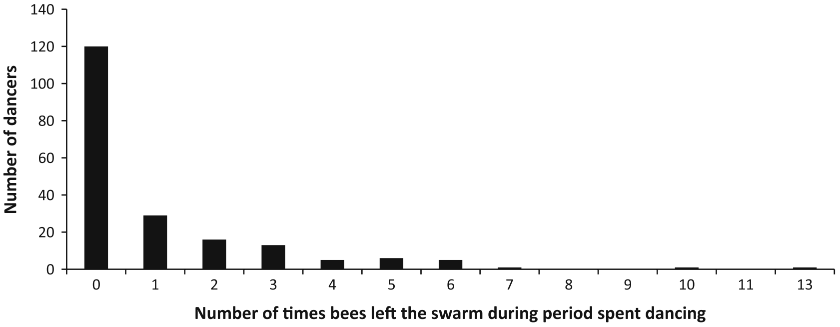

**Fig. 4** Number of times a dancing bee left the swarm in between periods of dancing during the nest-site selection process. Dancers with a score of 0 (61%) were never seen to leave the swarm in between bouts of dancing

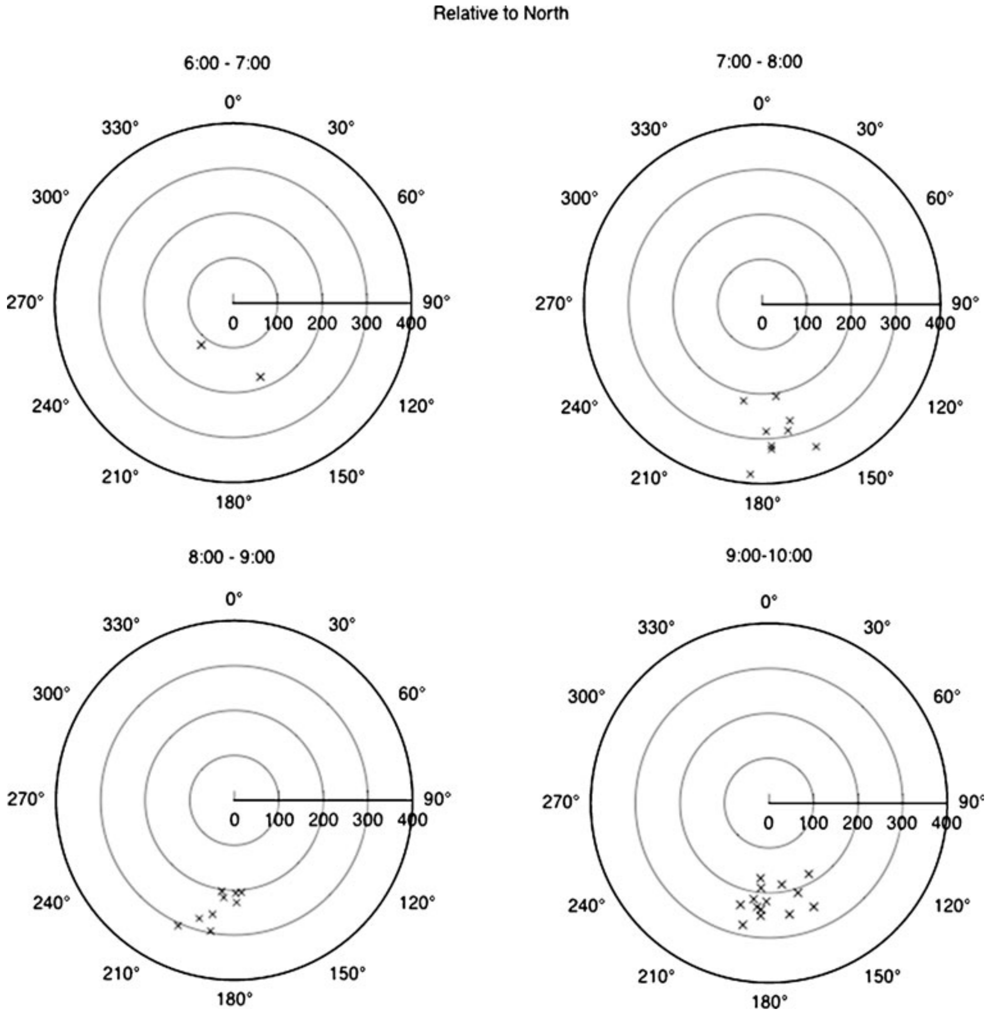

**Fig. 5** Distance and direction as encoded in the dance of one scout bee of swarm 5 over the history of the nest-site selection process. *Plots* represent 1-h periods of the decision-making process. Each *symbol* represents the average direction and distance from three or more dance circuits. It is clear from the plots that the dances are not precise with respect to distance and, to a lesser extent, direction

sites available to *A. florea*, individual behavior of scout bees is simpler than that of *A. mellifera* scouts engaged in nest-site selection. Whereas in *A. mellifera* scouts carefully judge the quality of nest sites they visit by frequently revisiting and re-evaluating the site (Seeley and Buhrman 1999), we did not find a clear pattern of flight activity during the nest-site selection process, with 61% of bees never taking off from the swarm during the period they spent dancing. Even though it is likely that we did not exhaustively observe all instances of takeoff and landings by scouts thus making it more difficult to clearly identify dance bouts, the fact that more than half of all bees seen dancing were never seen to leave the swarm after dancing, strongly suggests that regular inspection and re-evaluation of a potential nest site does not occur in *A. florea*. This is in strong contrast to *A. mellifera* where dance decay is intimately associated with the quality of the advertised site and scouts revisit their site after each bout of dancing. The absence of dance decay in *A. florea* suggests that site quality is not reflected in the bees' dance behavior. However, scouts could still perform more dance circuits when they perceive their site to be of high quality. This, combined with dance attrition, would still allow more bees to be attracted to sites of higher quality. In order to conclusively determine if quality-dependence is present in *A. florea*, one first needs to elucidate what site characteristics *A. florea* is looking for and then observe the dances by scouts dancing for sites that differ in their quality.

The absence of both dance decay and re-assessment of potential nest sites combined with the imprecision of the recruitment dance seems to suggest that nest sites appear to be selected *in situ* as the swarm is in the air, as we observed with swarm 2 that attempted multiple times to land on different patches of vegetation before finally settling. Swarm 2 left the place where it first settled the following day. This is not surprising because the tree the swarm settled on supported weaver ant (*Oecophylla smaragdina*) colonies. *O. smaragdina* is a major predator of *A. florea* (Oldroyd and Wongsiri 2006).

It appears that the main challenge an *A. florea* swarm faces is to reach consensus on the general direction of travel in order to reach a patch of trees. Indeed, we found that

**Table 3** Details of dances performed per hour for each swarm

| Swarm | Hour | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | No. dancers | 3 | 12 | 16 | 28 | | | | | | | Direction swarm flew | 299 |
| | *R* value | 1.00 | 0.85 | 0.67 | 0.84 | | | | | | | MVB last hour | 256 |
| | MVB (degrees) | 206° | 215° | 234° | 255° | | | | | | | 95% confidence interval | 14 |
| 2 (day 1) | No. dancers | 1 | 3 | 6 | 8 | 15 | 16 | 23 | 27 | 25 | 24 | | |
| | *R* value | 1.00 | 1.00 | 0.87 | 0.80 | 0.59 | 0.15 | 0.35 | 0.58 | 0.44 | 0.33 | | |
| | MVB (degrees) | 285° | 270° | 287° | 287° | 312° | 326° | 305° | 337° | 348° | 357° | | |
| 2 (day 2) | No. dancers | 8 | 8 | 8 | 8 | 13 | 13 | 19 | 6 | 20 | | Direction swarm flew | 226 |
| | *R* value | 0.37 | 0.46 | 0.49 | 0.38 | 0.79 | 0.75 | 0.52 | 0.05 | 0.71 | | MVB last hour | 208 |
| | MVB (degrees) | 320° | 289° | 317° | 335° | 10° | 320° | 281° | 191° | 209° | | 95% confidence interval | 25 |
| 3 | No. dancers | 1 | 2 | 11 | 14 | | | | | | | Direction swarm flew | 311 |
| | *R* value | 1.00 | 0.15 | 0.82 | 0.79 | | | | | | | MVB last hour | 310 |
| | MVB (degrees) | 338° | 277° | 285° | 310° | | | | | | | 95% confidence interval | 26 |
| 4 | No. dancers | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 5 | | | |
| | *R* value | 1.00 | 1.00 | 0.99 | 0.98 | 1.00 | 1.00 | 1.00 | 1.00 | 0.66 | | | |
| | MVB (degrees) | 325° | 318° | 324° | 319° | 317° | 316° | 322° | 321° | 222° | | | |
| 5 | No. dancers | 2 | 4 | 3 | 4 | 2 | 3 | 2 | 7 | 20 | | Direction swarm flew | 345 |
| | *R* value | 0.99 | 1.00 | 1.00 | 0.88 | 1.00 | 0.45 | 0.60 | 0.94 | 0.76 | | MVB last hour | 214 |
| | MVB (degrees) | 195° | 194° | 194° | 175° | 184° | 208° | 247° | 213° | 214° | | 95% confidence interval | 23 |

Swarms 1, 3, and 5 took off on day 1 while swarm 2 took off in 2 days and swarm 4 took 6 days (see text). The hours of activity were calculated backwards from the time that liftoff occurred, resulting in the first 1 hour value for each swarm containing less than 1 h worth of dance activity. If the direction that a swarm flew was within ± of the 95% confidence interval, then there is no significant difference between the direction flown and the MVB in the last hour

*MVB* the mean vector bearing of all dances (e.g., the average direction weighted by the number of bees dancing in each direction), *R* the degree of clustering around the MVB where $R=0$ indicates a random distribution and $R=1$ indicates identical orientation of dances

prior to liftoff, the vectorial consensus in the dances performed by all bees was highest. This suggests that the bees do have a mechanism that allows the build-up of a consensus about the general direction of travel. Interestingly, we found that recruitment success was extremely low (as low as 1.2% of dance followers in swarm 4 and 1.9–3.7% in swarm 5). Although a large percentage of dance-following bees took off from the swarm during the decision-making process, only a small proportion (4.3% and 5.1% in swarms 4 and 5, respectively) of these bees started dancing upon return to the swarm. We did find that 15.7% of the scouts changed the direction danced for after having followed waggle dances or after taking to the air and returning again. The percentage of bees that changed direction during the decision-making process ranged from 25.5% of dancers in swarm 2 to none in swarm 4. Perhaps, the tendency of dancing bees to change dance direction during the decision-making process plays an important role in determining the direction that the swarm will ultimately travel. *A. mellifera* nest-site scouts are also known to occasionally switch dance direction (Camazine et al. 1999; Seeley and Buhrman 1999), but, because such switching is rare in *A. mellifera* (Seeley and Buhrman 1999), it is unlikely to contribute significantly to the decision-making process. This assumption is supported by a study in which bees that were seen to assess multiple nest sites were removed from the decision-making process. Removal of these bees had no significant effect on the time taken by control and manipulated swarms to reach a decision (Visscher and Camazine 1999).

### How do *A. florea* swarms reach consensus and coordinate liftoff?

One possible mechanism by which *A. florea* reaches consensus about the general direction in which the swarm should fly is through individual scouts switching directions danced for or ceasing dancing altogether after following dances for sites other than their own. This is a plausible mechanism as dancers follow other dances even during periods when they themselves are active dancers. Hence, it is entirely possible that scouts are discouraged from dancing for their nest site by observing dances for a different site. Similarly, observing other bees dancing for a similar direction could encourage bees to continue dancing for that site and thus lead to the formation of a general directional consensus.

In *A. mellifera* swarms, the piping signal is thought to be produced solely by scout bees that have encountered the quorum at the chosen nest site (Visscher and Seeley 2007).

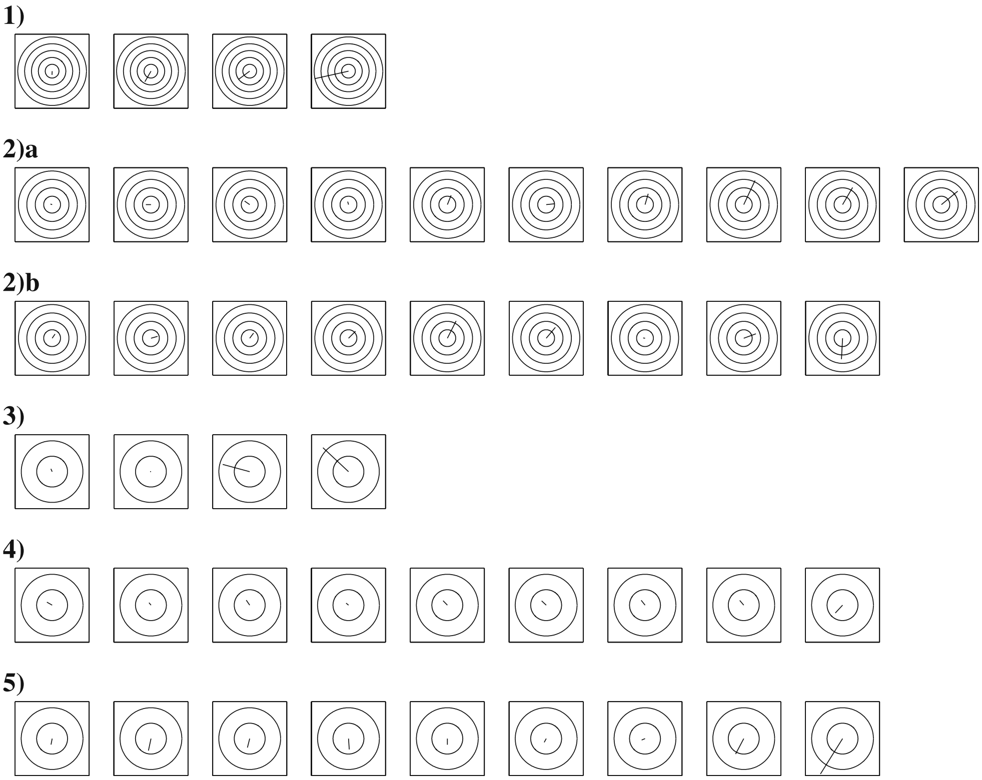

**Fig. 6** Vectorial consensus for each of the five swarms studied. Each *graph* represents the level of vectorial consensus in the dance direction indicated by the scout bees in each hour of the nest-site selection process. *Rows 2)a* and *2)b* indicate the first and second days, respectively, for the nest-site selection process in swarm 2. The *length* of the *lines* in each graph indicated the level of vectorial consensus within the dances in each hour. Each *concentric ring* represents a 5-unit increase in the level of vectorial consensus

Piping therefore acts a priming signal for swarm takeoff (Seeley and Tautz 2001; Seeley et al. 2003). Although further investigation is required to determine exactly what the relative contribution is of dancing and non-dancing bees, we can unequivocally say that the piping signal is produced by non-dancing as well as dancing bees. Moreover, the piping signal was not restricted to the end of the decision-making process. It thus seems that, in *A. florea*, the piping signal is not related to a quorum being reached at a nest site. Moreover, the variability of dances performed by individual bees makes it unlikely that dance recruits are guided towards a specific location and hence that a quorum could be reached at a potential nest site. Although recruits could, potentially, evaluate the general area indicated in a dance, it is unlikely they can judge the number of other bees also evaluating the same area.

In the absence of a quorum at a particular nest site, how do *A. florea* swarms coordinate liftoff? A possible mechanism for quorum measurement in this species could involve bees which have followed a number of dances in a similar direction commencing the piping signal and therefore activating the swarm to take off. Alternatively, dancing bees could start piping after dancing for any particular site and once the number of piping bees reaches a threshold, regardless of the directions indicated by dances, the swarm takes off. Our results show that both the number of dancing bees and the vectorial consensus of dance direction increased within the last hours of the decision-making process. This suggests that, in order to take off, swarms require a suitable clustering of directional information, combined with a threshold number of dancing bees.

Throughout the decision-making process, but particularly during the last 5 minutes or so before liftoff, scout bees were seen performing buzz runs (Rittschof and Seeley 2008), often taking off from and landing back on the swarm in quick succession. This behavior would often be accompanied by the piping signal. It is possible that taking off and landing in quick succession by many bees stimulates more bees to do the same, until the entire swarm takes flight. If the number of bees taking off and landing is small, this may not result in sufficient positive feedback and the swarm does not take off. Swarm 4, which was our smallest swarm (containing a total of 1,635 bees), provides support for this hypothesis. This swarm's initial takeoff was unsuccessful. As there were only five bees involved in the decision-making process during the last hour of swarm activity (as opposed to 28, 20, 14, and 19 in the four colonies that successfully took off), there may have been insufficient dancing bees to precipitate successful departure in swarm 4.

## Swarm guidance

Given that *A. florea* swarms liftoff when only a general directional consensus has been reached, how are swarms guided? In *A. mellifera*, swarms are guided by bees flying rapidly through the swarm "pointing" to the direction of travel

(Beekman et al. 2006; Schultz et al. 2008; Latty et al. 2009). Most likely, only those bees that have experienced the quorum at the new nest site are involved in guiding the swarm. As our results strongly suggest that quorum sensing is not used in *A. florea* nest-site selection, it is probable that all bees that dance prior to liftoff attempt to guide the swarm in their preferred direction. Modeling studies have shown that such guidance (where only a subset of individuals have a preferred direction while the majority of group members do not have a preference for a particular direction of travel) can indeed lead to groups traveling into the average direction as preferred by all knowledgeable individuals (Couzin et al. 2005). *A. florea* swarms are most likely guided by the scouts who are active prior to liftoff, which represented a tiny percentage of total bees in the swarm. Large groups are still able to travel in a particular direction, even when leading individuals give conflicting directional information as the group merely moves in the direction that the majority of the leading individuals are headed (Dyer et al. 2008). The larger a group is, the smaller the percentage of knowledgeable individuals required to accurately guide the other group members.

## Conclusion

*A. mellifera* appears to have evolved its more complex decision-making process for nest-site selection from the more basal behavior observed in *A. florea*. Traits such as dance decay and re-assessment of potential nest sites appear to be derived traits in *Apis* and most likely follow the increased complexity of the decision-making process required in cavity-nesting species. Whereas cavity-nesting species are faced with a small number of sites that differ greatly in quality, the main concern for *A. florea* swarms is to stay together as a coherent group during flight rather than pre-selecting the best possible site prior to liftoff. The main purpose of the decision-making process in *A. florea* seems to be to ensure the majority of the dancers indicate the same direction for travel prior to liftoff. Once the swarm reaches a suitable area, such as a clump of trees, the swarm coalesces on a suitable branch randomly. The quality of the site (e.g., freedom from predatory ants and sufficient shade throughout the day) is then assessed *in situ*. If the site proves unsuitable, or if no food is located, the colony simply moves again.

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