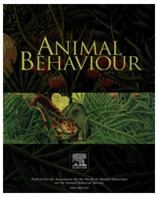
Animal Behaviour 93 (2014) 191–199

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Consensus building in giant Asian honeybee, *Apis dorsata*, swarms on the move

James C. Makinson [a,*], Timothy M. Schaerf [a], Atsalek Rattanawannee [b,1],
Benjamin P. Oldroyd [a], Madeleine Beekman [a]

[a] Behaviour and Genetics of Social Insects Lab, School of Biological Sciences & Centre for Mathematical Biology, University of Sydney, Sydney, Australia
[b] Department of Biology, Chulalongkorn University, Bangkok, Thailand

ARTICLE INFO

Article history:
Received 10 May 2013
Initial acceptance 7 June 2013
Final acceptance 3 April 2014
Published online
MS. number: 13-00394R

Keywords:
Apis
Apis dorsata
collective decision making
consensus
group movement
swarming

Many animals move in groups, but the mechanisms by which a group of animals form a consensus about where to move are not well understood. In honeybees group movement generally falls into two behavioural categories: reproductive swarming and colony migration. In both contexts the bees use the dance language to decide on a location to move to. During reproductive swarming bees choose between and dance for multiple discrete locations before departing towards one of them. In contrast, during migration bees select a single direction in which to fly, but information with respect to distance is highly variable. In this study we show that swarms of the giant Asian honeybee, *Apis dorsata*, when placed in a novel environment rapidly reach a general consensus on a single patch within the environment in a fashion similar to relocating swarms of the red dwarf honeybee, *Apis florea*. In the three swarms used in this study the patches for which bees danced prior to the swarm departing corresponded to a stand of trees. One of our swarms showed a dance pattern consistent with long-distance migration: dances during the final 15 min preceding swarm departure indicated a wide range of distances but a uniform direction. Unlike previous descriptions of migrating swarm behaviour, the direction indicated by dances on this swarm changed throughout the decision-making process. Our other two swarms landed within the canopy of the trees in the patches for which they danced in the last 15 min and then presumably searched the surrounding area for a specific location in which to construct their new comb.

When a group of animals move as a collective, the movement of the individuals within the group must be coordinated or else the group will fragment and disperse. However, individual animals do not necessarily require complex behavioural rules in order for their group to move cohesively. For example, individuals within schools of the mosquitofish, *Gambusia holbrooki*, follow three key behavioural rules that in combination result in aggregation and collective movement. First, individual fish are attracted to each other and have a weak tendency to align their body with that of their neighbour. Second, when a fish is on a collision course with another fish it will slow down to avoid collision. Third, fish only respond to their nearest-neighbours' movements (Herbert-Read et al., 2011). The emergent property of individual fish following these or similar simple rules is cohesive movement of the fish schools (Katz, Tunstrom, Ioannou, Huepe, & Couzin, 2011; Ward, Sumpter, Couzin, Hart, & Krause, 2008).

How an animal group moves through its environment is a product of the decisions of its constituent members. Small, motivated minorities within groups often influence the movement of the majority by increasing their speed of movement through the group and/or via aggressive interactions with other group members (Conradt, Krause, Couzin, & Roper, 2009). The larger the group, the smaller the proportion of motivated guides that is required to lead the group towards a destination (Couzin, Krause, Franks, & Levin, 2005). For example, desert baboons, *Papio ursinus*, collectively move to rest sites in response to observing motivated group members heading in the direction of the site (King, Sueur, Huchard, & Cowlishaw, 2011). Group movement is often self-reinforcing; individuals are more likely to conform to the group's movement pattern as more of their neighbours also conform, leading to a steady increase in group vector consensus (Couzin et al., 2005).

Honeybees (genus *Apis*) are a fantastic system to investigate how a group coordinates movement. Unlike the systems discussed above, group movement in honeybees is coordinated by only a

---

[*] Correspondence: J. C. Makinson, School of Biological Sciences, Macleay Building (A12), University of Sydney, Sydney, NSW 2006, Australia.
E-mail address: james.makinson@sydney.edu.au (J. C. Makinson).
[1] Present address: Department of Entomology, Faculty of Agriculture, Kasetsart University, 50 Ngam Wong Wan Rd., Chatuchak, Bangkok 10900, Thailand.

http://dx.doi.org/10.1016/j.anbehav.2014.04.029

subset of all group members which then guide the bees while in flight (Beekman, Fathke, & Seeley, 2006; Greggers, Schoning, Degen, & Menzel, 2013; Janson, Middendorf, & Beekman, 2005; Schultz, Passino, & Seeley, 2008). Honeybees undertake group movement during colony migration, emergency absconding and reproductive swarming. Reproductive swarming is well studied in the Western honeybee, *Apis mellifera*. During reproductive swarming the old queen and about half of the colony's workers leave the colony and form a temporary cluster in the surrounding vegetation (Fell et al., 1977). From this temporary cluster approximately 5% of the bees search the surrounding environment for new nest sites (Seeley, Morse, & Visscher, 1979). On return to the temporary cluster the scouts indicate the locations found using the waggle dance, a stylized figure of eight movement used to indicate the distance, direction and quality of the location being communicated (for more information on the biology of the waggle dance, see Dyer, 2002). Once a new nest site has been decided on, the scout bees coordinate lift-off and guide the swarm to the new site. Scouts guide the swarm by flying swiftly ('streaking') through the milling mass of slowly moving uncommitted swarm-mates in the direction of the site they have located (Beekman et al., 2006; Schultz et al., 2008). Uncommitted members of the swarm are attracted by these streaker bees, leading to the group moving in a particular direction (Latty, Duncan, & Beekman, 2009). As the goal of this group movement is to arrive at a very specific location, the guiding individuals need to have agreed on the direction of travel prior to the swarm taking off. Therefore the processes of swarm guidance and decision making during nest site selection are tightly linked in *A. mellifera* swarms. By the time an *A. mellifera* swarm lifts off the scouts have reached consensus or near consensus in their dances (Seeley, 2003; Seeley & Visscher, 2004).

Because of the tight link between the bees' decision-making process and the guidance of the group while in flight, the exact nesting requirements are likely to affect the decision-making process. Within the genus *Apis* there are currently 12 recognized species (Lo, Gloag, Anderson, & Oldroyd, 2010). These 12 species can broadly be divided into three groups: the dwarf bees, the giant bees and the cavity-nesting bees. Both the dwarf and giant bees nest in the open, building a single comb under a branch or overhang (Oldroyd & Wongsiri, 2006). So far the nest site selection processes of only two, *A. mellifera*, a cavity nester, and *Apis florea*, a dwarf bee, have been studied in detail. These studies have shown that the type of nest has implications for how the bees coordinate their movement.

Because *A. mellifera* is a cavity-nesting species, there tends to be a limited number of suitable nesting sites available to a swarm. Furthermore, because the choice of nest site is critical to the survival of the new colony there is strong selective pressure on *A. mellifera* swarms to select the best possible nest site prior to departing and founding a new colony. In contrast, the red dwarf honeybee, *A. florea*, builds a small single comb, and can build a nest on a stout twig. For *A. florea*, almost any twig will do, provided it protects the colony from the elements and predators, and so the nest site selection process is less important to colony survival than for cavity-nesting species (Makinson, Oldroyd, Schaerf, Wattanachaiyingcharoen, & Beekman, 2011; Oldroyd, Gloag, Even, Wattanachaiyingcharoen, & Beekman, 2008). Typically, *A. florea* scouts are still advertising several alternative sites via their dancing when the swarm takes to the air. This indicates that the scouts do not form a consensus on a specific nesting location prior to the swarm's departure (Makinson et al., 2011; Schaerf, Myerscough, Makinson, & Beekman, 2011). Rather, *A. florea* swarms appear to decide on the precise location of their new home on the wing, flying in a general direction until they encounter suitable landing spots which they sample along the way, and abandon if they prove unsuitable (Diwold, Schaerf, Myerscough, Middendorf, & Beekman, 2011). Therefore the main purpose of *A. florea*'s nest site selection process appears to be to determine the swarm's flight direction and not to direct the swarm to a particular location.

The common giant honeybee, *Apis dorsata*, is a migratory species (Koeniger & Koeniger, 1980) that tracks nectar resources as they become available (Itioka et al., 2001; Oldroyd & Wongsiri, 2006). *Apis dorsata* often forms large aggregations of up to 150 unrelated colonies (Oldroyd, Osborne, & Mardan, 2000). They construct large (up to 2 m wide) single comb colonies on the underside of rocky outcrops or branches of smooth-barked trees (Oldroyd & Wongsiri, 2006). Colonies are known to return to the same roosting locations every season, and seem to use the presence of old comb fragments as a cue to indicate a good nesting location (Liu, Roubik, He, & Li, 2007; Neumann et al., 2000; Paar, Oldroyd, & Kastberger, 2000). Like the nest sites of the open-nesting *A. florea*, trees and rock surfaces that are suitable for *A. dorsata* nest sites are relatively common, but, owing to *A. dorsata*'s preference to nest in aggregations, the choices deemed by the scout bees to be of higher quality are no doubt restricted.

Apis dorsata's decision-making process is interesting for two main reasons. First, *A. dorsata* selects a new nesting location both during colony migration, when colonies move over considerable distances coordinated via 'migration dances' (Dyer & Seeley, 1994; Koeniger & Koeniger, 1980; Robinson, 2012), and during reproductive swarming, when swarms settle within the vicinity of existing colonies (Woyke, Wilde, & Wilde, 2012). Second, because of the size of the colony and the fact that *A. dorsata* prefers to nest in aggregations (Oldroyd & Wongsiri, 2006), we expect their decision-making process to be more precise that the laissez faire process observed in *A. florea* (Makinson et al., 2011; Oldroyd et al., 2008), but less precise than *A. mellifera*'s elaborate process (Seeley, 2010). Here we examined whether *A. dorsata* swarms translocated to a new environment search for and move towards discrete nesting locations in a manner similar to *A. mellifera*, or whether swarms move in the general direction of forage and/or forest patches as do *A. florea* swarms. We examined this question by dissecting the process of a group's departure in three artificial swarms of *A. dorsata* presented with an unfamiliar environment.

METHODS

Study Site

We conducted our field work in Chiang Rai province, Thailand during December 2010. We collected *A. dorsata* colonies from nesting sites within and around the campus of Mae Fah Luang University (20°2′43.00″N, 99°53′42.00″E). We released artificial swarms at one of two sites: swarm 1 at Mae Fah Luang University football oval (20°3′32.26″, 99°53′43.13″E) and swarms 2–3 on the grounds of a temple Wat Pa Mark Nor (20°13′42.46″N, 100°1′5.48″E). Swarm 1 was released onto an open field next to a soccer stadium containing a small aggregation of *A. dorsata* colonies. Swarms 2 and 3 were released in a clearing within 500 m of two *A. dorsata* colony aggregations located on the sides of buildings within a stand of trees.

Artificial Swarm Production

To avoid being stung, we approached colonies at night. After we located a suitable low-hanging colony, we cut it down, using a machete attached to a 10 m bamboo pole. We captured the workers and comb as they fell using a large butterfly net also attached to a bamboo pole. We then removed the comb and transferred as many individuals as possible into a wooden box with two mesh-covered sides. We placed the box in a dark room, protected the swarm from ants with a water moat, and fed the swarm for 2 days until the bees started to produce wax scales indicating that they had achieved the engorged condition of bees in natural swarms (Combs, 1972). To estimate the number of workers in each swarm we weighed the swarm and determined the weight of a known number of workers.

We fed the swarms their own honey stores alternated with water by brushing the liquids onto the mesh sides of the box with a paint brush. When making artificial swarms of *A. mellifera* and *A. florea* it is common practice to find and cage the queen so that the swarm can be made to settle at a site convenient for observations (Camazine, Visscher, Finley, & Vetter, 1999; Makinson et al., 2011; Oldroyd et al., 2008; Seeley & Buhrman, 1999). In preliminary work we caged the queens of two *A. dorsata* swarms, but both queens died. For this reason we gave up caging the queens when making artificial swarms. We assumed that the queen was present in a swarm if the workers clustered calmly inside the cage. When bee clusters were highly agitated at all hours of the day, we assumed the swarm was queenless and did not use it further.

Swarm Release and Observation

We released swarms at nightfall onto a custom-made swarm board. We first placed a step ladder next to a table at the field site. We then placed a large 1 m × 1 m plywood board upright on the edge of the table facing the ladder and secured the board at an angle of approximately 70° by suspending it from the ladder using string (Fig. 1). The bees were released onto the table and rapidly clustered on the swarm board. We provided sugar water (2 M) to the swarm via a feeder bottle to ensure forage dances did not occur on the swarm surface.

We used a digital video camera (Sony HDR-XR100) to record the behaviour of the artificial swarm from sunrise the following day until the swarm took to the air. The moment a scout was first observed dancing we individually marked it using paint pens (POSCA, Mitsubishi Pencil Co., Japan). Once a swarm departed, we followed it on foot to their resting locations (swarms 2 and 3) or until it was lost from sight (swarm 1). We recorded the direction of travel and the resting location using a handheld GPS (GARMAN GPSmap 62).

Data Collection and Analysis

We transcribed all dances performed on the surface of swarms 1 and 3 to record the number of circuits performed per dance, as well as the spatial information encoded in each waggle circuit by timing the length of circuits with a stopwatch and measuring the angle indicated with each waggle circuit using the digital compass MB-Ruler (Markus Bader-MB-Software Solutions, Iffezheim, Germany). Similar to *A. mellifera*, *A. dorsata* scout bees use gravity to orient their waggle circuits and indicate locations of interest relative to the sun's current azimuth (Dyer, 2002).

Figure 1. The experimental set-up. An *A. dorsata* swarm is clustered on a board. All dances are recorded by the video camera. A bottle provides sugar syrup. The observer marks every dancing bee with a unique paint mark. Photo: Madeleine Beekman.

For swarm 2 we collected the same information using a MATLAB script developed for another project (Schaerf, Makinson, Myerscough, & Beekman, 2013) that places a virtual compass over an external video player window. We then played the video back at slow speed (usually at 1/2 speed); using mouse input the program's user would click on a dancing bee's thorax once at the beginning of a waggle run and once again at the end of a waggle run. The angle of each dance circuit relative to the vertical was determined using coordinates recorded at each mouse click; the duration of each circuit was determined by the duration between consecutive pairs of mouse clicks and the video playback speed. For each distinct dance the user also input dance start and end times, and the unique sequence of paint marks that identified each bee. If a bee was not marked during experimentation it was listed as 'unmarked'. If a bee recommenced dancing within 30 s of ceasing to dance we regarded this as a single bout of dancing. If the break between dance circuits was >30 s we regarded this as two separate dances. After combining appropriate dances, we used data on the azimuthal position of the sun (Gronbeck, 1998) in combination with the angles extracted from our video analysis to determine the bearing indicated by each waggle run.

We made the assumption that the duration of each waggle run made by *A. dorsata* is linearly proportional to the perceived distance to a target location (Dyer & Seeley, 1991). As a consequence the (x, y) coordinates associated with locations indicated by waggle runs are calculated via $x_w = d_w \sin \theta_w$ and $y_w = d_w \cos \theta_w$ where d_w is the duration of a waggle run (s) and θ_w is the sun-corrected bearing indicated by the waggle run. The mean (x, y) location indicated by a dance was calculated by taking the mean of the x and y coordinates of all component waggle runs of the dance. We used a dance curve that relates waggle run duration to distance (Dyer & Seeley, 1991) to convert the average length of dance waggle runs into approximate distance (m).

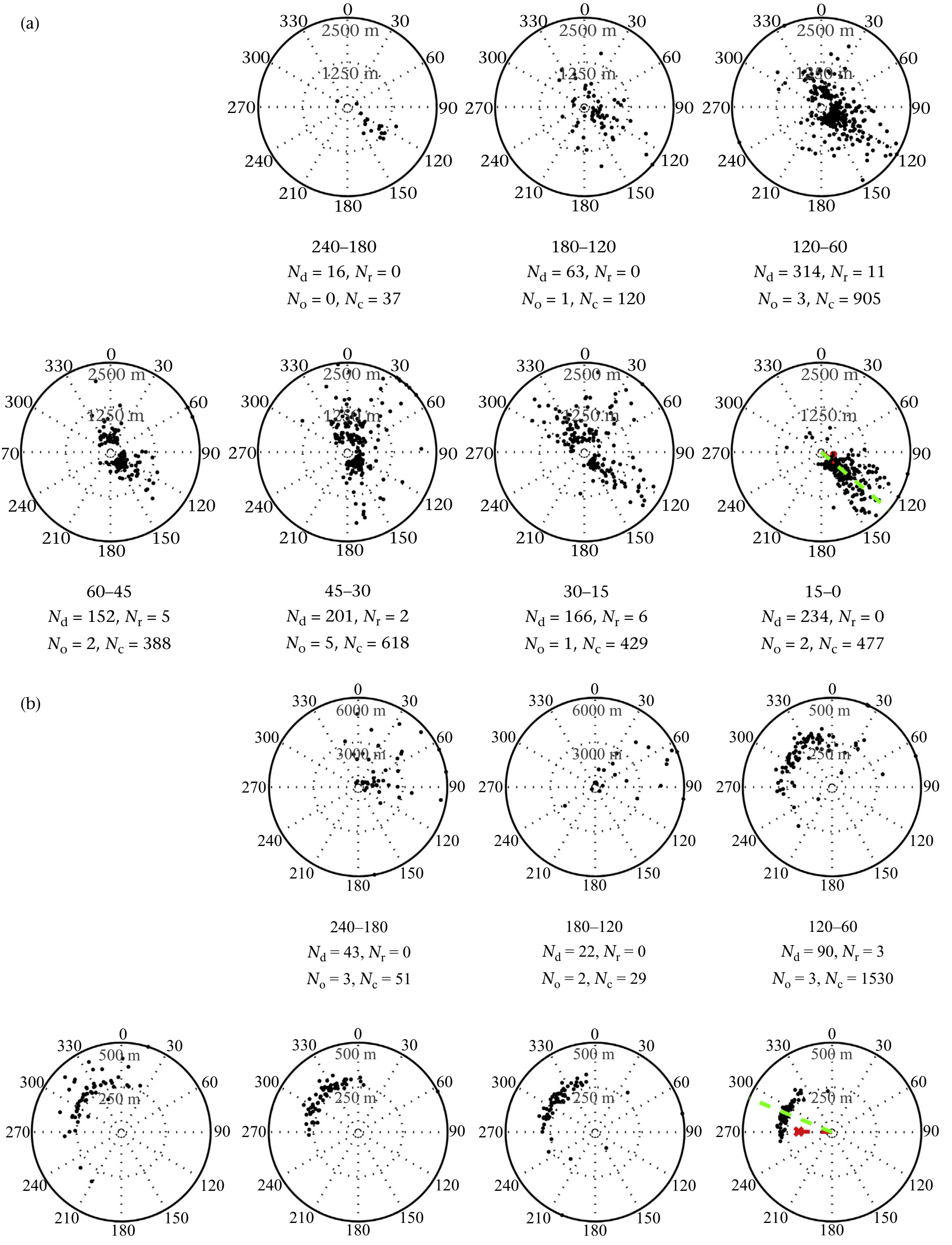
For each swarm we calculated the level of polarization of dance activity, r, at 15 min intervals. Polarization in this context is a measure of angular agreement among dances; it is identical to the measure of angular concentration associated with the calculation of mean angles using standard methods of circular statistics (Zar, 1996). Polarization is given by:

$$r = \sqrt{\left(\frac{\sum_{i=1}^{N} \sin \theta_i}{N}\right) + \left(\frac{\sum_{i=1}^{N} \cos \theta_i}{N}\right)},$$

Table 1
Swarm sizes, total number of dancing bees and time of swarm departure for swarms 1, 2 and 3

	Swarm no.		
	1	2	3
Date released	9 December 2010	11 December 2010	14 December 2010
No. of bees	8120	7780	3900
Sunrise	6:44	6:44	6:47
First dance	6:52	8:16	8:50
No. of dancers	88	47*	37
Swarm departed	10:35	12:03	10:07

* Owing to stinging attacks we were not able to mark dancing bees for a 1 h period.



(a)

240–180
$N_d = 16$, $N_r = 0$
$N_o = 0$, $N_c = 37$

180–120
$N_d = 63$, $N_r = 0$
$N_o = 1$, $N_c = 120$

120–60
$N_d = 314$, $N_r = 11$
$N_o = 3$, $N_c = 905$

60–45
$N_d = 152$, $N_r = 5$
$N_o = 2$, $N_c = 388$

45–30
$N_d = 201$, $N_r = 2$
$N_o = 5$, $N_c = 618$

30–15
$N_d = 166$, $N_r = 6$
$N_o = 1$, $N_c = 429$

15–0
$N_d = 234$, $N_r = 0$
$N_o = 2$, $N_c = 477$

(b)

240–180
$N_d = 43$, $N_r = 0$
$N_o = 3$, $N_c = 51$

180–120
$N_d = 22$, $N_r = 0$
$N_o = 2$, $N_c = 29$

120–60
$N_d = 90$, $N_r = 3$
$N_o = 3$, $N_c = 1530$

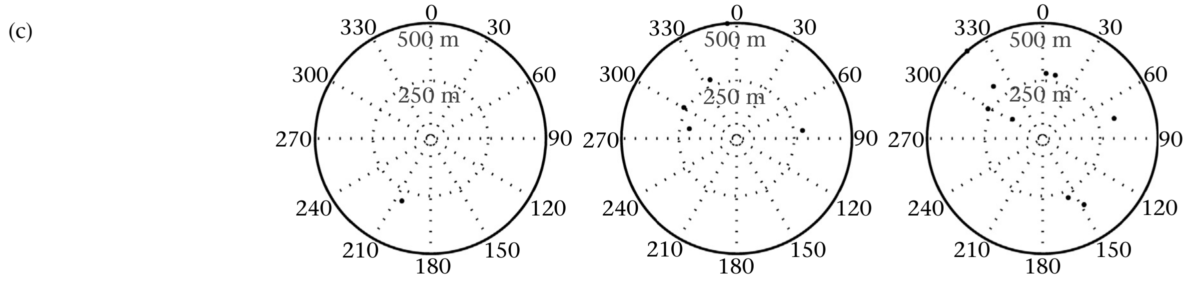
60–45
$N_d = 57$, $N_r = 1$
$N_o = 0$, $N_c = 605$

45–30
$N_d = 69$, $N_r = 3$
$N_o = 1$, $N_c = 1216$

30–15
$N_d = 68$, $N_r = 2$
$N_o = 1$, $N_c = 1377$

15–0
$N_d = 71$, $N_r = 0$
$N_o = 0$, $N_c = 922$

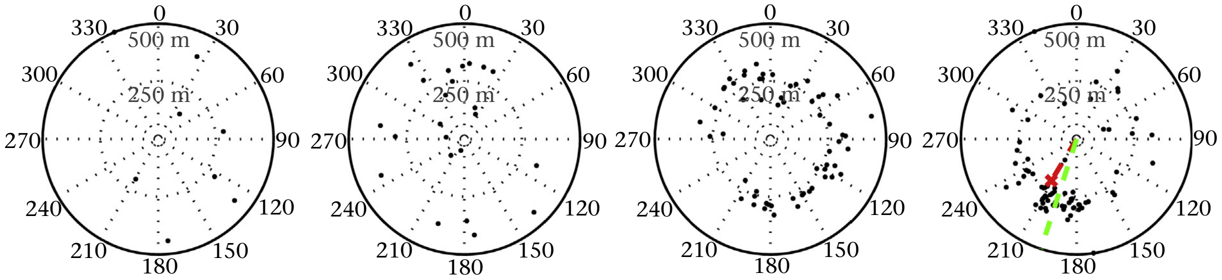
Figure 2. Radial plots representing the dance activity on (a) swarm 1, (b) swarm 2 and (c) swarm 3 leading up to the swarm taking to the air. The top row of radial plots for each swarm indicate 1 h time intervals while the four radial plots in the second row display 15 min time intervals within the last hour prior to swarming. Black circles represent the



240–180
$N_d = 1$, $N_r = 0$
$N_o = 0$, $N_c = 1$

180–120
$N_d = 6$, $N_r = 1$
$N_o = 1$, $N_c = 8$

120–60
$N_d = 11$, $N_r = 2$
$N_o = 1$, $N_c = 18$



60–45
$N_d = 8$, $N_r = 0$
$N_o = 1$, $N_c = 12$

45–30
$N_d = 28$, $N_r = 5$
$N_o = 0$, $N_c = 85$

30–15
$N_d = 73$, $N_r = 15$
$N_o = 0$, $N_c = 344$

15–0
$N_d = 82$, $N_r = 9$
$N_o = 2$, $N_c = 679$

Figure 2. (*continued*).

where θ_i is the mean bearing of the ith dance performed in a given time interval, and N is the total number of dances performed in the same time interval. A polarization value close to 1 indicates that dances are in close angular agreement whereas a polarization value close to 0 indicates there is little or no agreement in dance directions (Zar, 1996).

We determined the number of dances that occurred during each 15 min time interval preceding the departure of the swarm. We then calculated the proportion of all dances occurring in the 4 h of dance activity on the swarm that this represented. Polarization values for the dance activity within each 15 min interval were then multiplied by the proportion of active dances. This gave us a value representing the interaction between dance polarization and swarm dance activity levels. To compare the build-up of dance activity and directional polarization over time with that of other open-nesting honeybee species we calculated the same value for *A. florea* swarms using the data from Makinson et al. (2011). The average proportional polarization activity of swarms of both species over time was then compared using a one-way repeated measures ANOVA of species and 15 min time intervals. We corrected for sphericity using the Greenhouse–Geisser adjustment to degrees of freedom. Unfortunately, we did not have access to a similar data set for a cavity-nesting species so we were unable to compare open-nesting species with any of their cavity-nesting counterparts.

We calculated the mean vector bearing (MVB) indicated by the dances performed in the last 15 min time interval preceding the swarm's departure. We compared this value with the direction the swarms travelled upon departure to test whether it fell within the 95% confidence interval of the MVB (Zar, 1996).

RESULTS

Early in the morning following the placement of the swarms on the swarm board we observed hundreds of workers taking to the air and flying about in large, arcing orientation flights. On swarm 2 some of these flying workers became aggressive later in the morning and stung us (J.C.M. and M.B.) repeatedly. To minimize disruption of the swarm, we retreated to a safe distance for approximately 1 h before returning to continue marking dancing bees once flight activity had reduced. Swarms 1, 2 and 3 departed after dancing for 3 h 43 min, 3 h 47 min and 1 h 17 min, respectively (Table 1).

All three swarms performed dances for a wide variety of locations within the surrounding environment. Each swarm's dances appeared to converge on a single general direction within the final 15 min before swarm departure (Fig. 2). The dances performed on

---

estimated distance and direction of individual dances performed on the surface of the swarm cluster. The values on the vertical axes indicate the distance (m) from the swarm (note that the scales are not necessarily the same for each plot). The values in the first line below each scatterplot indicate the number of minutes prior to swarm departure. For each time interval N_d indicates the total number of dances that occurred, N_r the number of round dances (dances too short to be able to obtain directional information from them), N_o the number of dances that indicated distances outside of the maximum range of the scatterplot and N_c the total number of circuits produced by all dances. The red dotted line in the last scatterplot for each swarm represents the direction the swarm flew after take-off. In swarms 2 and 3 the red 'x' at the end of the red lines indicates the location where the swarm landed. For swarm 1 this location is unknown as this swarm flew over buildings and was lost from sight. The green dotted line indicates the mean vector bearing (MVB) indicated by the dances produced in the last 15 min time interval.

swarm 1 indicated a wide range of distances and directions. At 120–60 min prior to lift-off the swarm's dances started to cluster around two nearby forest patches, but between the 30–15 and 15–0 min time intervals the swarm rapidly switched from indicating both locations to converging on a single direction. The distance indicated by these dances ranged widely from locations matching up with the edge of the forest patch to over 2.5 km away. During the last 15 min time interval prior to swarm 1's departure 214 (91.45%) of the 234 dances performed indicated a direction within +/− 30° of the direction flown by the swarm, while only 64 (26.5%) dances were both within +/− 30° and +/− 250 m of the location at which we lost sight of the swarm (Fig. 2). In contrast the dances of swarms 2 and 3 indicated comparatively closer locations during the last time interval; swarm 2 displayed dances varying greatly in distance and direction in the first 2 h of the swarm's decision-making history, but switched to performing dances for considerably closer locations in the last 2 h. During the last 15 min time interval prior to swarm 2's departure 56 (77.78%) of the 72 dances performed indicated a direction within +/− 30° of the direction flown by the swarm. All of these dances also indicated coordinates within +/− 250 m of the location at which the swarm landed (Fig. 2). Unlike swarms 1 and 2, swarm 3 never performed dances over a distance of 900 m throughout its dance history. During the last 15 min time interval prior to swarm 3's departure 28 (57.14%) of the 49 dances performed indicated a direction within +/− 30° of the direction flown by the swarm. All of these dances also indicated coordinates within +/− 250 m of the location at which the swarm landed (Fig. 2).

Swarm 1 was released near a campus sports stadium that supported a congregation of five *A. dorsata* colonies of various sizes. The surrounding area was cleared land situated in a shallow depression between two hills covered in secondary forest. When swarm 1 departed it travelled 260 m at an angle of 123° relative to north in the direction of the closest forest patch, before we lost sight of it as it flew over a student dormitory located on the edge of the forest. Swarms 2 and 3 were released on the edge of a man-made marsh surrounding a small island covered in secondary forest. The island contained two large aggregations of *A. dorsata* colonies nesting on temple structures within the forest patch. The marsh was surrounded by a mosaic of pineapple farms and secondary forest (Fig. 3). Swarm 2 departed at an angle of 270° relative to north towards one of the colony aggregation sites before landing 190 m away on an approximately 10 cm wide smooth-barked tree branch next to the building aggregation approximately 8 m above the ground. Swarm 3 headed 118 m at an angle of 208° relative to north in the general direction of the second aggregation before clustering on the first tree with which the swarm came in contact. The swarm clustered on a branch <2 cm in width approximately 4 m above the ground. Both swarms were no longer present after 1 week, but it is uncertain whether they departed because of poor conditions as a local honey hunter had harvested honey from all visible colonies on the island resulting in most of the colonies absconding. The direction flown by swarm 1 (123°) lay outside of the +/− 3° 95% confidence interval either side of the MVB of 130° indicated by the last 15 min of dance activity. Swarm 2 flew 270° from the swarm board, also outside of the +/− 4° 95% confidence interval either side of the MVB of 292° indicated by the last 15 min of dance activity. In contrast to the other two swarms, swarm 3 flew 208° from the swarm board, within the +/− 15° confidence interval either side of the MVB of 198° (Fig. 2).

In all three swarms dances were infrequent for the first hour or so before rapidly increasing until swarm departure (Fig. 4). The level of scatter of directional information expressed in the dances on the swarm surface fluctuated greatly but in all three swarms spiked in polarity in the last 15 min before swarm departure (Fig. 4).

There was no significant difference in the build-up of dance activity and polarization over time between *A. dorsata* and *A. florea* as measured by the time interval interaction ($F_{2.356,11.781} = 0.619$, $P = 0.580$; Fig. 5). The pattern of build-up of dances was more or less identical, with both species displaying a significant linear correlation between time interval prior to swarming and polarization proportional to dance activity (Spearman correlation: *A. dorsata*: $r_S = 0.929$, $N = 16$, $P < 0.001$; *A. florea*: $r_S = 0.897$, $N = 16$, $P < 0.001$; Fig. 5).

DISCUSSION

Comparing A. dorsata *with Other* Apis *Species*

Apis dorsata, like *A. florea*, went through a rapid decision-making process, with all swarms departing for their chosen direction within the first day of the decision-making process (Table 1). A feature shared by all three *Apis* species studied so far is an increase in the number of dances as the bees approach lift-off (Camazine et al., 1999; Makinson et al., 2011). In all three species this increase is coupled with an increase in the level of directional consensus leading up to swarm departure. In *A. dorsata*, we found a positive correlation between the level of consensus (measured by dance polarization in this study) and dance activity (Fig. 4). The interplay between consensus and dance activity in *A. dorsata* is similar to that seen in *A. florea* swarms prior to swarm departure (Fig. 5). In swarm 3 the level of dance angle polarization in the last time interval was low (0.57) reflecting the significant variation in directional information prior to lift-off. Yet, the swarm successfully flew to the location indicated by the mean vector bearing in the last time interval (Fig. 2). Swarms 1 and 2 also flew towards the general direction of the locations being indicated during the last 15 min time interval prior to swarming, but unlike swarm 3 their destination did not fall within the strict 95% confidence interval either side of the mean vector bearing of their dances (Fig. 2).

The Goals of Animal Groups on the Move

The aim of our study was to investigate whether swarms of *A. dorsata* presented with a novel environment containing forested patches as well as discrete congregation areas act like *A. mellifera* swarms and search out specific nesting sites, or whether they are more like *A. florea* swarms, which only choose patches of the environment before taking to the air. We hypothesized that the bees' level of consensus formation is tightly linked to the precision with which the swarm needs to be guided once it is airborne. *Apis mellifera* swarms move to a precise location: a single point in space. In addition, the quality of the chosen site is important, as a badly chosen nest site will jeopardize the future colony's growth and survival. The nest site to which the swarm flies is hard to locate, a small hole in a tree or building, so uninformed bees cannot use visual cues to guide their flight. Thus, in *A. mellifera*, scouts need to guide the swarm carefully. To avoid scouts trying to guide the swarm to different locations, *A. mellifera* dance activity must reach near 100% consensus on a specific location prior to departure (Seeley, 2003; Seeley & Visscher, 2004).

If other honeybee species like *A. florea* also guide their swarms using streaking scout bees, we can assume that the scouts still need to reduce the level of variation in their dances prior to lift-off. Otherwise the average direction flown by streaker bees is zero and the swarm will be unable to move. In contrast to *A. mellifera*, owing to the abundance of nest sites, relocating *A. florea* swarms can afford to make the final decision about the swarm's specific resting spot while in flight. Portions of airborne swarms often land on vegetation in their path before moving on if the majority of bees

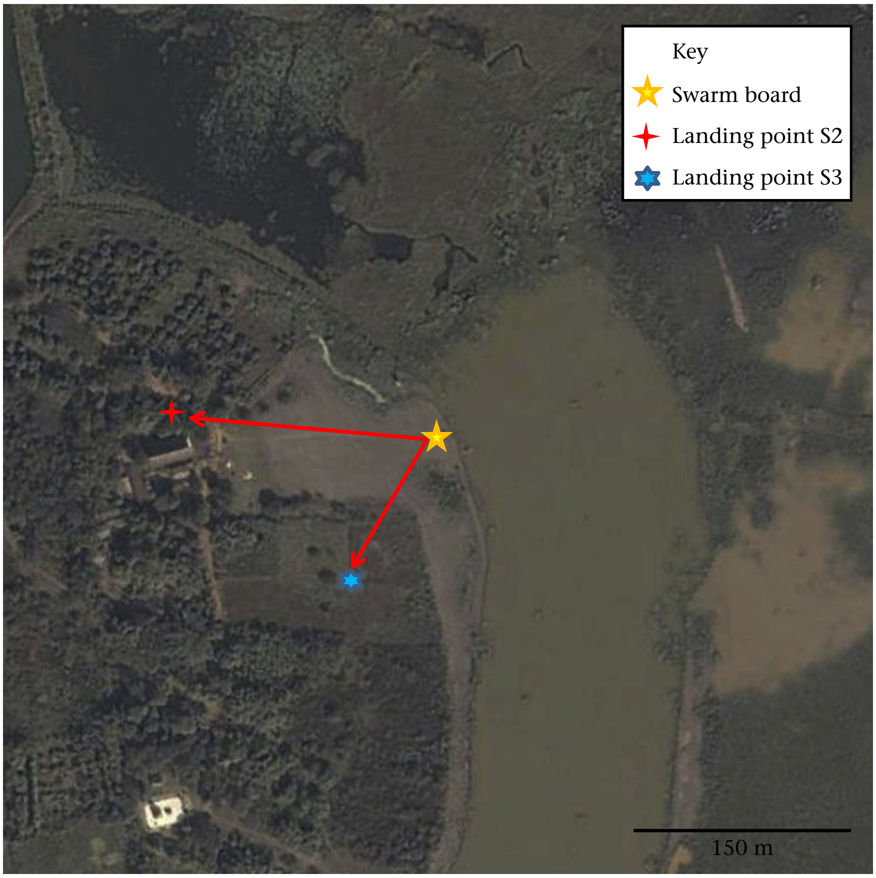


Figure 3. The directions flown and landing places of swarms 2 and 3. Both swarms landed on the branch of a tree. The branch landed on by swarm 3 (S3) was too small for the bees to construct a comb; both swarms had departed from their branches after a few days. The brown roofed structure near the landing point of swarm 2 (S2) was a temple with a large number (around 50) of colonies nesting on its awnings at the time of our experiment. The white structure at the bottom left of the image is a Buddhist stupa, which also had a large number of colonies on it. The centre point of this image is latitude 20°13′42.46″N, longitude 100°1′5.48″E. The satellite image is from 2008, while the study was conducted in 2010.

(and presumably the queen) remain airborne (Makinson et al., 2011). Because the number of scouts is small relative to the number of uninformed individuals (0.38–2.13%; Makinson et al., 2011), even if the scouts do not all agree on where to fly to, the swarm can be guided, provided there is some sort of vector consensus (Diwold et al., 2011).

Apis dorsata and *A. florea* showed similar levels of consensus prior to lift-off in this study (Fig. 5). Owing to the large directional spread of dances prior to swarm departure (Fig. 2) it is likely that the process we observed was not nest site selection, but rather coordinated group movement towards a general patch of the environment. Although the locations where we observed the swarms landing were either not suitable for nest construction (swarm 2) or not utilized as such (swarm 3), the location at which the swarms landed was clearly reflected in the waggle dances of the bees prior to swarm departure (Fig. 2). This demonstrates that we were observing goal-oriented behaviour in this last time interval, as opposed to general colony migration dances which indicate a specific direction, but vary considerably in their distance information between individual circuits of a dance (Koeniger & Koeniger, 1980; Schneider & McNally, 1994). The dances indicated by swarm 1 during the last time interval indicated a wide range of distances (between 300 and 5800 m; Fig. 2), characteristic of migration dances (Koeniger & Koeniger, 1980). Unlike the migration dances previously described in this species, the direction they indicated did not stay fixed in the hours leading up to swarming. In the last half hour in particular the swarm suddenly switched from indicating two general regions (which corresponded to forest patches in the field site) to dancing exclusively for one region (Fig. 2). This switching behaviour suggests some form of assessment of the two locations, and/or some sort of on-swarm consensus-reaching mechanism such as the ‘stop’ signal described in *A. mellifera* swarms (Seeley et al., 2012). The behaviour seen in the swarms studied therefore does not fall into the categories of specific nest site selection, as seen in *A. mellifera*, or colony migration, where bees advertise long but variable distances (Koeniger & Koeniger, 1980; Schneider & McNally, 1994). Rather, it represents an intermediate process of group relocation. Presumably, upon relocating to these forest patches, *A. dorsata* swarms will either start searching for a specific nesting location in the surrounding canopy or migrate on to a location with better forage conditions. Alternatively, *A. dorsata* swarms may behave in a fashion similar to those of *A. florea*, deciding where to land on the wing and then ‘testing’ the suitability of their roosting spot for a few days or weeks before relocating again if it proves not to be ideal (Makinson et al., 2011; Oldroyd et al., 2008).

Over the last few years, modelling studies have investigated how a minority of individuals can guide a group of uninformed group members (Buhl et al., 2006; Conradt et al., 2009; Couzin et al., 2005). Such studies have shown that provided individuals within the group have a strong tendency to stay with the group, a small number of individuals can influence the travel direction of the group. Successful group guidance is then even possible when the guiding individuals differ in their preferred direction of travel

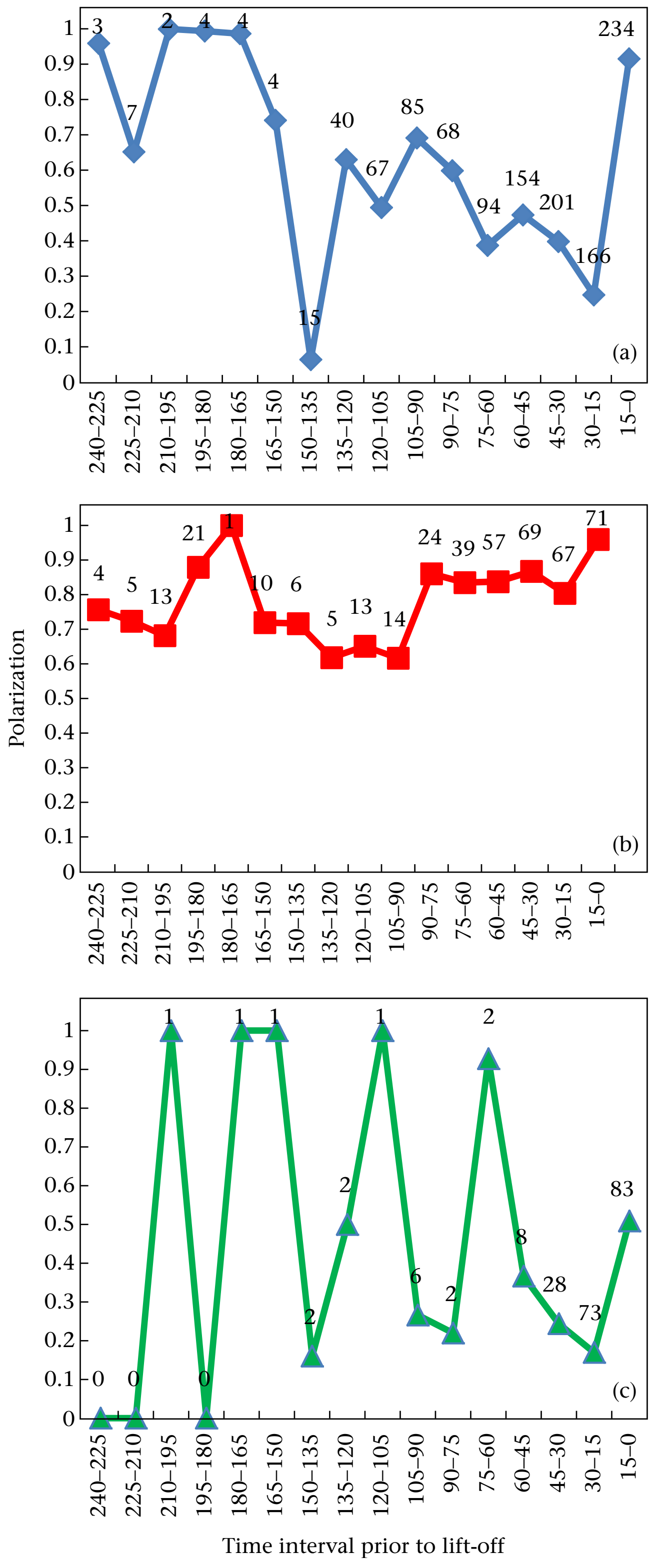


Figure 4. The level of polarization of directional information present in the dances performed on (a) swarm 1, (b) swarm 2 and (c) swarm 3 during each 15 min time interval leading up to the swarm taking to the air. Polarization values range from 0 to 1 with a value of 1 indicating perfect polarization of the directional information indicated by dances, while 0 indicates a complete lack of polarization. The numbers above each line indicate the number of dances performed on the swarm surface during each 15 min time interval.

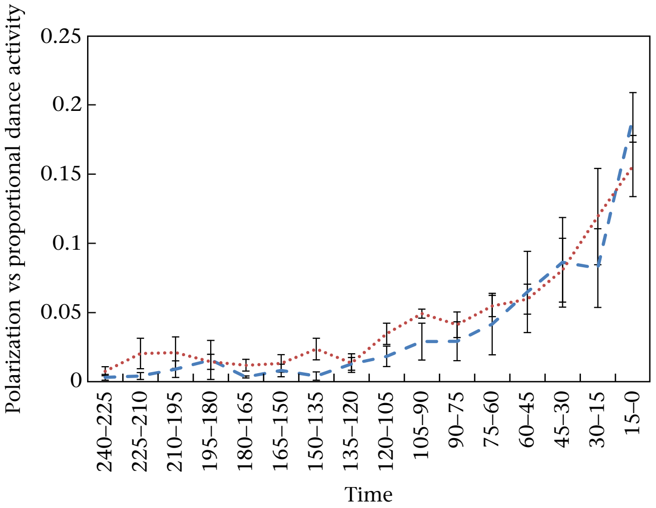


Figure 5. Polarization level times the proportion of dances at 15 min intervals leading up to swarming in both *A. florea* (dotted line) and *A. dorsata* (dashed line). Error bars indicate SE.

(Leonard et al., 2012). Mostly these studies assume that the ultimate goal is not important; in other words, groups do not necessarily have to move to a specific location as long as they move somewhere cohesively. Work on honeybees shows that this may be the case for some species, such as *A. florea* and *A. dorsata* swarms, but in other species and/or under different contexts guidance needs to be much more precise.

Acknowledgments

Funding for this project was provided by the Australia – Asia Endeavour Award programme (to JCM) and the Australian Research Council (ARC) grant no. FT120100120 for Madeleine Beekman and grant no. DP0878924 for Benjamin Oldroyd. We thank Dr Ratna Thapa for providing lab space at Mae Fah Luang University for the duration of this experiment and to Professor Siriwat Wongsiri for acting as host. We also thank the Abbot of Wat Pa Mark Nor for allowing us to perform fieldwork on the temple grounds. We thank Tom Seeley and the anonymous referees for constructive comments on the manuscript.

References

Beekman, M., Fathke, R. L., & Seeley, T. D. (2006). How does an informed minority of scouts guide a honeybee swarm as it flies to its new home? *Animal Behaviour, 71*, 161–171.

Buhl, J., Sumpter, D. J., Couzin, I. D., Hale, J. J., Despland, E., Miller, E. R., et al. (2006). From disorder to order in marching locusts. *Science, 312*, 1402–1406.

Camazine, S., Visscher, P. K., Finley, J., & Vetter, R. S. (1999). House-hunting by honey bee swarms: collective decisions and individual behaviors. *Insectes Sociaux, 46*, 348–360.

Combs, G. F. (1972). The engorgement of swarming worker honey-bees. *Journal of Apicultural Research, 11*, 121–128.

Conradt, L., Krause, J., Couzin, I. D., & Roper, T. J. (2009). "Leading according to need" in self-organizing groups. *American Naturalist, 173*, 304–312.

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature, 433*, 513–516.

Diwold, K., Schaerf, T. M., Myerscough, M. R., Middendorf, M., & Beekman, M. (2011). Deciding on the wing: in-flight decision making and search space sampling in the red dwarf honeybee *Apis florea*. *Swarm Intelligence, 5*, 121–141.

Dyer, F. C. (2002). The biology of the dance language. *Annual Review of Entomology, 47*, 917–949.

Dyer, F. C., & Seeley, T. D. (1991). Dance dialects and foraging range in 3 Asian honeybee species. *Behavioral Ecology and Sociobiology, 28*, 227–233.

Dyer, F. C., & Seeley, T. D. (1994). Colony migration in the tropical honey-bee *Apis dorsata* F (Hymenoptera, Apidae). *Insectes Sociaux, 41*, 129–140.

Fell, R. D., Ambrose, J. T., Burgett, D. M., Dejong, D., Morse, R. A., & Seeley, T. D. (1977). Seasonal cycle of swarming in honeybees. *Journal of Apicultural Research, 16*, 170–173.

Greggers, U., Schoning, C., Degen, J., & Menzel, R. (2013). Scouts behave as streakers in honeybee swarms. *Naturwissenschaften, 100*, 805–809.

Gronbeck, C. (1998). *Sustainable by design*. Seattle, Washington: SunPosition. http://www.susdesign.com/sunposition/index.php.

Herbert-Read, J. E., Perna, A., Mann, R. P., Schaerf, T. M., Sumpter, D. J., & Ward, A. J. (2011). Inferring the rules of interaction of shoaling fish. *Proceedings of the National Academy of Sciences of the United States of America, 108*, 18726–18731.

Itioka, T., Inoue, T., Kaliang, H., Kato, M., Nagamitsu, T., Momose, K., et al. (2001). Six-year population fluctuation of the giant honey bee *Apis dorsata* (Hymenoptera : Apidae) in a tropical lowland dipterocarp forest in Sarawak. *Annals of the Entomological Society of America, 94*, 545–549.

Janson, S., Middendorf, M., & Beekman, M. (2005). Honey bee swarms: how do scouts guide a swarm of uninformed bees? *Animal Behaviour, 70*, 349–358.

Katz, Y., Tunstrom, K., Ioannou, C. C., Huepe, C., & Couzin, I. D. (2011). Inferring the structure and dynamics of interactions in schooling fish. *Proceedings of the National Academy of Sciences of the United States of America, 108*, 18720–18725.

King, A. J., Sueur, C., Huchard, E., & Cowlishaw, G. (2011). A rule-of-thumb based on social affiliation explains collective movements in desert baboons. *Animal Behaviour, 82*, 1337–1345.

Koeniger, N., & Koeniger, G. (1980). Observations and experiments on migration and dance communication of *Apis dorsata* in Sri Lanka. *Journal of Apicultural Research, 19*, 21–34.

Latty, T., Duncan, M., & Beekman, M. (2009). High bee traffic disrupts transfer of directional information in flying honeybee swarms. *Animal Behaviour, 78*, 117–121.

Leonard, N. E., Shen, T., Nabet, B., Scardovi, L., Couzin, I. D., & Levin, S. A. (2012). Decision versus compromise for animal groups in motion. *Proceedings of the National Academy of Sciences of the United States of America, 109*, 227–232.

Liu, F., Roubik, D. W., He, D., & Li, J. (2007). Old comb for nesting site recognition by *Apis dorsata*? Field experiments in China. *Insectes Sociaux, 54*, 424–426.

Lo, N., Gloag, R. S., Anderson, D. L., & Oldroyd, B. P. (2010). A molecular phylogeny of the genus *Apis* suggests that the Giant honey bee of the Philippines, *A. breviligula* Maa, and the Plains honey bee of southern India, *A. indica* Fabricius, are valid species. *Systematic Entomology, 35*, 226–233.

Makinson, J. C., Oldroyd, B. P., Schaerf, T. M., Wattanachaiyingcharoen, W., & Beekman, M. (2011). Moving home: nest-site selection in the Red Dwarf honeybee (*Apis florea*). *Behavioral Ecology and Sociobiology, 65*, 945–958.

Neumann, P., Koeniger, N., Koeniger, G., Tingek, S., Kryger, P., & Moritz, R. F. A. (2000). Home-site fidelity in migratory honeybees. *Nature, 406*, 474–475.

Oldroyd, B. P., Gloag, R. S., Even, N., Wattanachaiyingcharoen, W., & Beekman, M. (2008). Nest site selection in the open-nesting honeybee *Apis florea*. *Behavioral Ecology and Sociobiology, 62*, 1643–1653.

Oldroyd, B. P., Osborne, K. E., & Mardan, M. (2000). Colony relatedness in aggregations of *Apis dorsata* Fabricius (Hymenoptera, Apidae). *Insectes Sociaux, 47*, 94–95.

Oldroyd, B. P., & Wongsiri, S. (2006). *Asian honey bees. Biology, conservation, and human interactions*. Cambridge, MA: Harvard University Press.

Paar, J., Oldroyd, B. P., & Kastberger, G. (2000). Giant honeybees return to their nest sites. *Nature, 406*, 475.

Robinson, W. S. (2012). Migrating giant honey bees (*Apis dorsata*) congregate annually at stopover site in Thailand. *PLoS One, 7*, e44976.

Schaerf, T. M., Makinson, J. C., Myerscough, M. R., & Beekman, M. (2013). Do small swarms have an advantage when house hunting? The effect of swarm size on nest-site selection by *Apis mellifera*. *Journal of the Royal Society, Interface/the Royal Society, 10*, 20130533.

Schaerf, T. M., Myerscough, M. R., Makinson, J. C., & Beekman, M. (2011). Inaccurate and unverified information in decision making: a model for the nest site selection process of *Apis florea*. *Animal Behaviour, 82*, 995–1013.

Schneider, S. S., & McNally, L. C. (1994). Waggle dance behavior associated with seasonal absconding in colonies of the African honeybee, *Apis mellifera scutellata*. *Insectes Sociaux, 41*, 115–127.

Schultz, K. M., Passino, K. M., & Seeley, T. D. (2008). The mechanism of flight guidance in honeybee swarms: subtle guides or streaker bees? *Journal of Experimental Biology, 211*, 3287–3295.

Seeley, T. D. (2003). Consensus building during nest-site selection in honey bee swarms: the expiration of dissent. *Behavioral Ecology and Sociobiology, 53*, 417–424.

Seeley, T. D. (2010). *Honeybee democracy*. Princeton, NJ: Princeton University Press.

Seeley, T. D., & Buhrman, S. C. (1999). Group decision making in swarms of honey bees. *Behavioral Ecology and Sociobiology, 45*, 19–31.

Seeley, T. D., Morse, R. A., & Visscher, P. K. (1979). The natural history of the flight of honey bee swarms. *Psyche, 86*, 103–113.

Seeley, T. D., & Visscher, P. K. (2004). Quorum sensing during nest-site selection by honeybee swarms. *Behavioral Ecology and Sociobiology, 56*, 594–601.

Seeley, T. D., Visscher, P. K., Schlegel, T., Hogan, P. M., Franks, N. R., & Marshall, J. A. (2012). Stop signals provide cross inhibition in collective decision-making by honeybee swarms. *Science, 335*, 108–111.

Ward, A. J., Sumpter, D. J., Couzin, I. D., Hart, P. J., & Krause, J. (2008). Quorum decision-making facilitates information transfer in fish shoals. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 6948–6953.

Woyke, J., Wilde, J., & Wilde, M. (2012). Swarming and migration of *Apis dorsata* and *Apis laboriosa* honey bees in India, Nepal and Bhutan. *Journal of Apicultural Science, 56*, 81–91.

Zar, J. H. (1996). *Biostatistical analysis* (3rd ed.). Upper Saddle River, NJ: Prentice Hall.