



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



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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.

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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

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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 than 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

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