Collective decision-making in honey bees during nest-site selection

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Statement of Authorship

The research described in this thesis is the original work of the author, except where specifically acknowledged.

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Cover photo: An aggregation of *A. dorsata* colonies nesting in a 'bee tree' located in Chiang Rai province, Thailand.

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Preface

"But if the swarm be not gathered by man, its history will not end here. It will remain suspended on the branch until the return of the workers, who, acting as scouts, winged quartermasters, as it were, have at the very first moment of swarming sallied forth in all directions in search of a lodging. They return one by one, and render account of their mission; and as it is manifestly impossible to fathom the thought of the bees, we can only interpret in human fashion the spectacle that they present. We may regard it as probable, therefore, that most careful attention is given to reports of various scouts. One of them, it may be, dwells on the advantage of some hollow tree it has seen; another is in favour of a crevice in a ruinous wall, of a cavity in a grotto, or an abandoned burrow. The assembly often will pause and deliberate until the following morning. Then at last the choice is made, and approved by all. At a given moment the entire mass stirs, disunited, sets in motion, and then, in one sustained and impetuous flight that this time knows no obstacle, it steers its straight course, over hedges and cornfields, over haystack and lake, over river and village, to its determined and always distant goal. It is rarely indeed that this second stage can be followed by man. The swarm returns to nature, and we lose track of its destiny."

- Maurice Maeterlinck, The Life of the Bee (English edition, 1908).

The Life of the Bee by Maurice Maeterlinck heralds the beginning of over 100 years of modern scientific enquiry into the biology and behaviour of honey bees. Researchers such as Karl von Frisch, Martin Lindauer and all those who have followed since have advanced our understanding of the fascinating and complex systems of communication and collective behaviour exhibited by honey bees. But humanity's fascination with the honey bee is an ancient one indeed, long predating the advent of the written word. The oldest testament to this long held interest is depicted in a 15,000 year old cave painting from the municipality of Bicorp in Spain of a human figure robbing honey combs from a bee colony.

The ancients were not solely concerned about exploiting bees for their sweet produce; humans have always been intrigued by the behaviour of these tiny animals. Plinius Secundus

talks at long length and with impressive insight about the workings of bees and the colonies they inhabit, and hints as to the sources of his knowledge;

"Nobody must be surprised that love for bees inspired Aristomachus of Soli to devote himself to nothing else for 58 years, and Philiscus of Thasos to keep bees in desert places, winning the name of the Wild Man."

- Natural history (book 11, 1st century CE)

Unfortunately the works of Aristomachus and Philiscus are long lost, but their mention serves as a reminder of humanities perpetual captivation with understanding the natural world, even if our observations are not always entirely accurate;

'They are known [honey bees]*, by observation, to be born from the corpses of oxen. In order to obtain bees, the flesh of dead calves are beaten; from its putrefying blood worms emerge, which later become bees.'*

- Bodley, Bestiary 764 CE.

I gain inspiration from reading the accounts of the countless others before me who have strived to understand the natural world. I hope that my findings continue to ring true well into the future, and can serve as inspiration for others.

This thesis is dedicated to the memory of my grandfather, Thomas Crabbe Massey Makinson.

22nd October, 1922 – 5th October, 2011

Chapter 1

General Introduction

Eusocial insects are characterised by overlapping generations, cooperative brood care and division of labour (Wilson, 1971). To say that eusociality is a highly successful strategy is something of an understatement; while social insects make up only 2% of described insect species, they contribute to more than half of global insect biomass (Hölldobler and Wilson, 1990). Eusocial insect species include examples from bees, wasps (Order Hymenoptera), thrips (Thysanoptera), beetles (Coleoptera), all ants (Hymenoptera) and termites (Isoptera) (Costa, 2006)(Figure 1). The ability of social insects to coordinate behavioural responses through division of labour and various communications systems allows them to consistently outperform their solitary relatives. In many instances social species dominate the landscape they inhabit, forcing their solitary rivals to exploit resources on the fringes of whatever habitat they co-occupy (Wilson and Hölldobler, 2005).

The superorganism and colony reproduction

Insect colonies are often referred to as 'superorganisms' (Johnson and Linksvayer, 2010; Moritz and Fuchs, 1998; Moritz and Southwick, 1992; Page, 2013; Seeley, 1989; Tautz, 2008) since the colony itself can be considered as a single unit for the purpose of reproduction while the individuals that comprise the colony cannot survive by themselves for extended periods (Hölldobler and Wilson, 2008). Individual workers have comparable roles as the cells in a multicellular organism, undertaking tasks related to food acquisition, digestion, thermoregulation, waste removal, control of parasites and diseases, learning about the resources available in the environment, and collectively forming memory of those resources. The reproductive role is mostly restricted to one or a few individuals (queens and males), analogous to the gonads of a multicellular organism. As the workers in social insects cannot mate, they rely on the queen or queens for reproduction. The queen in turn depends on her workers for food collection, nest maintenance and defence. When it is time to reproduce, depending on the species, either a single queen will found a colony by herself

a)

b)

c)

d)

e)

Figure 1: Some examples of social insects; a) Weaver ants (*Oecophylla smaragdina*) killing a blue banded bee (*Amegilla sp.*). b) Termites (Infraorder *Isoptera*) repairing a damaged mound. c) A foraging bumblebee (*Bombus terrestris*). d) A stingless bee (Tribe *Meliponini*) hesitating to leave the colony entrance funnel. e) A giant Asian hornet (*Vespa mandarina*) devouring the brood of a paper wasp colony (*Polistes sp.*). All photos taken by James C Makinson.

(solitary colony founding), or one or more queens along with a subset of the colony's workers leave the old colony to establish a new one (swarming or fission) (Peeters and Ito, 2001). Both modes of reproduction have advantages and disadvantages. The solitary founding strategy allows a colony to produce large numbers of reproductive individuals relatively cheaply, but the rate of successful founding events is low. Alternatively, swarming or fission involves a much greater level of resource investment per reproductive event, but typically leads to an increased survival of the incipient colony due to the assistance of workers that leave with the queen(s). Moreover, the new colony will be able to grow faster compared with incipient colonies established by solitary individuals. The rapid establishment of offspring colonies is particularly important in species that depend on the exploitation of ephemeral resources. However, swarming or fission also poses a problem; while a solitary female decides where to build her nest herself, in species that swarm or fission, the collective has to somehow make that decision. How are the actions of often many thousands of individual workers co-ordinated so that the group is able to choose where to nest?

Enter the honey bee

It seems only natural that the honey bee, and specifically the Western hive bee (*Apis mellifera*), with its eons of shared history with humanity, is the first species in which the dynamics of collective decision-making during swarming was studied and described. Following the discovery of the dance language and the deciphering of its meaning by von Frisch (1942), scientists were provided with a window directly into the workings of a honey bee colony's psych. The waggle dance, a figure 8 movement, communicates the distance and direction of a resource to nest mates via a highly stylised re-enactment of the dancer's

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flight to the resource (see Dyer (2002) for a review). The ability to decode the bees' dance language allows researchers to tap into the flow of information through a honeybee colony allowing us to start to discover how honey bees use social information to assess and share knowledge of the surrounding world, and to collectively build a picture of that world in the colony's 'mind'.

A student of von Frisch, Martin Lindauer, later discovered that the bees also use the dance when communicating potential nest sites during reproductive swarming (Lindauer, 1955). During reproductive swarming, the swarm containing a queen and a few thousand workers clusters a few tens of metres from the old colony. Scout bees then begin searching the environment for suitable nest sites for the colony's new home. Lindauer was the first person to study the behaviour of honey bee swarms, observing the behaviour of honey bees communicating their discovery of nesting cavities within the ruins of post WW2 Berlin (Lindauer, 1955). What he found was truly extraordinary. Upon leaving the swarm cluster scout bees searched the surrounding habitat for potential nesting sites. On return to the swarm cluster these scouts would communicate their findings to their swarm-mates using the waggle dance. Initially the scouts danced for multiple locations, but by the final hour or so prior to swarm departure the number of locations typically reduced to one, and upon taking to the air the swarm almost invariably headed in the chosen direction. Sometimes the bees did not settle for a single location prior to lift off. In 2 out of the 19 swarms that Lindauer studied he found that the bees reached a split decision, and these undecided swarms would separate mid-air, with each fragment heading in a different direction. Lindauer (1955) theorised that scout bees individually compare all the nest sites danced for on the swarm surface. Lindauer's idea had exciting implications about the cognitive ability of insects and was latched onto with enthusiasm (Gould and Gould, 1986; Griffin, 1992).

Since the time of Lindauer, much more detail has been added to the story of reproductive swarming in *A. mellifera*. We now know that scout bees prefer dry, approximately 40L volume nesting cavities, preferably located >1m off the ground and with a small entrance hole towards the bottom of the cavity facing the direction of the morning sun (Seeley and Morse, 1978). Only about 5% of all the bees in the swarm are involved in the decision-making process while the rest remain quiescent within the cluster (Seeley et al., 1979). Both the duration of nest-site dances and the number of circuits produced by a scout upon her

first return to the swarm is positively correlated with the bee's perception of nest-site quality (Seeley and Buhrman, 2001). With each return to the potential nesting site, the number of dance circuits performed by an individual declines linearly, but bees that have rated their site as being of high quality start with more dance circuits per dance than those that have visited a poor quality site (Seeley, 2003). As a result, sites of high quality are advertised for longer than sites of low quality. The outcome of this process is an increase in the number of bees visiting and dancing for sites of good quality, and a decreasing number of bees dancing for sites of poor quality (Seeley, 2003). Eventually, through a process which may take several days in *A. mellifera,* one site comes to dominate in visitation and dancing (Villa, 2004). When one site under consideration is being visited by a sufficient number of bees, the bees at the new nest site sense that a quorum has been reached (Seeley and Visscher, 2004b). Once the quorum has been achieved, bees that have sensed the quorum return to the swarm and signal the end of the decision-making process by producing an auditory signal known as piping. This signal informs the quiescent bees in the cluster that they should prepare themselves for flight (Seeley et al., 2003). At the same time, scouts also produce another auditory signal known as the 'stop' signal. Scout bees preferentially produce this signal to scouts dancing for other locations, and modelling has demonstrated that this active silencing of opposing dancers reduces the likelihood that swarms reach a split decision by the end of the decision-making process (Seeley et al., 2012). The final signals for flight are 'buzz running' in which a scout runs in zigzags over the swarm vibrating its wings every second or so (Lindauer, 1955). In response to this signal the swarm cluster breaks up and the swarm takes flight, flying to its chosen home, presumably guided by the same scout bees that moments earlier were dancing for the same location (Beekman et al., 2006; Latty et al., 2009; Schultz et al., 2008).

Reproductive swarming is not the only context under which *A. mellifera* colonies must co-ordinate group motion. Colonies are sometimes forced to abscond due to the physical destruction of their nesting site (disturbance-induced absconding) or the seasonal deterioration of forage conditions in the surrounding environment (seasonal absconding or migration). Migration is only seen in tropical races of the Western honey bee, and is preceded weeks beforehand by a marked reduction in foraging rate, as well as the cessation of brood production. By the time a migrating colony takes to the air, it has consumed all its

stores and leaves behind and an empty brood comb (Schneider and McNally, 1992). The dance behaviour leading up to the departure of migrating colonies differs considerably from that of reproductive swarms. A separate class of dances, migration dances, start being produced 2-4 weeks prior to the colony departing. Migration dances indicate distances 10s of kilometres away (significantly further afield than the colony's typical forage dances (Schneider, 1990)) and are regularly produced during periods of little or no flight activity (Schneider and McNally, 1994). In contrast to waggle dances, migration dances do not form the figure 8 pattern of waggle dances, as dancers do not loop back to their starting point after each circuit but instead continue moving forwards on the dance surface (Schneider and McNally, 1994). In addition to this migration dance circuits are extremely variable in length, with individual circuits within a single bout of dancing differing greatly from one another. Therefore, migration dances appear to indicate the general route of travel to be undertaken by a departing colony, rather than a specific location (Dyer, 2002).

The Asian honey bee; A. mellifera's less popular sister

Given the vast number of publications on *A. mellifera*, one could be forgiven for assuming that there is only one extant honey bee species in the world. But *A. mellifera* is one of 11 currently recognised honey bee species (Cao et al., 2012). Furthermore, the genus *Apis* can be divided into 3 broad categories based on nesting biology. The cavity nesters (such as *A. mellifera*), the migratory giant open nesters (such as *A. dorsata*) and the migratory dwarf open nesters (*A. florea* and *A. andreniformis*) (Figure 2). The differences in nesting biology (cavity versus a tree branch) have the potential to strongly influence the decision-making process in these species. Dwarf open-nesting species for example can nest practically anywhere provided there is sufficient shade and absence of predators, in particular the weaver ant *Oecophylla smaragdina* (Duangphakdee et al., 2005). The dwarf bees can build their small single comb colonies on almost any twig or horizontal surface the bees come across (Kushwah et al., 1998). *A. florea* colonies migrate seasonally to follow the ephemeral supply of floral resources within the environment, and thus are regularly on the move (Oldroyd and Wongsiri, 2006; Pandey, 1974; Sheikh and Chetry, 2000). For a cavity nesting species like *A. mellifera* there are only a limited number of potential nest sites that can be

Figure 2: a) Asian hive bees (*Apis cerana*) as seen from the inside of a traditional wooden hive. b) Western hive bee (*Apis mellifera*) colonies in Jardin du Luxembourg, Paris. c) Giant Asian honey bees (*Apis dorsata*) nest on the awnings of a temple in Chiang Rai province, Thailand. e) A small red dwarf honey bee (*Apis florea*) nesting amongst bramble. f) A colony of black dwarf honey bees (*Apis andreniformis*) displaying its characteristic 'tail'. All photos taken by James C Makinson.

located by a swarm and it is essential the colony moves cohesively to the chosen cavity. In contrast, for an open nesting species like *A. florea*, there is an abundance of shaded twigs that are 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 favoured as nesting sites. Given that there must be millions of equally good twigs within flying distance of most *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?

Based on the different nesting requirements of cavity and open-nesting bees, one can predict that the decision-making process of *A. florea*, and by extension other dwarf honey bee species, does not place as strict an emphasis on consensus formation as in the cavity nesting *A. mellifera*. Indeed a previous study on *A. florea* demonstrated that swarms in this species continue dancing for multiple directions right up to the end of the decision-making process (Oldroyd et al., 2008). Given this lack of nest-site specificity, which, if any, of the decision-making behaviours described in *A. mellifera* are present in this species?

A fundamental difference between *A. florea* and *A. mellifera* is the number of potential nest sites a swarm can choose from. This number is likely to be much larger for *A. florea* than for *A. mellifera*. *A. florea* have a greater choice of sites of high quality while the number of high quality sites is more limited for *A. mellifera.* The giant open nesting species such as the giant Asian honey bee (*Apis dorsata*) have nest site requirements that are intermediate between the cavity nesting *A. mellifera* and the open nesting *A. florea*. As with *A. florea*, *A. dorsata* colonies are migratory, following the flow of nectar through the environment, but due to the size of their combs (in excess of 1m wide) and their preference to nest in large

congregations (personal obs.; Wongsiri et al., 1996; Oldroyd et al., 2000; Oldroyd and Wongsiri, 2006) it is likely *A. dorsata* swarms are more restricted in their choice of potential nest sites than is *A. florea*. Thus, *A. dorsata* may exhibit a decision-making process more similar to the cavity nesting *A. mellifera* than to open-nesting *A. florea*. *A. dorsata* is not an easy species to work with; it prefers to build its single comb colony up in very tall trees or buildings and is often extremely defensive (Oldroyd and Wongsiri, 2006). It is therefore not surprising that to this date there have been no experimental studies on nest-site selection in *A. dorsata*.

Despite the dearth of information about the nest-site selection process in the various Asian *Apis* species we do know something about their migratory behaviour. The migration dance is produced on colonies prior to seasonal absconding (migration) in the Asian honey bee (*Apis cerana*) (Sasaki et al., 1990) and *A. dorsata* (Dyer and Seeley, 1994). It has also been observed in absconding colonies of the dwarf bees *A. florea* (Duangphakdee et al., 2012) and *Apis andreniformis* (Robinson, 2011), as well as in bivouacked swarms of *A. dorsata* before the swarms continue along their seasonal migration route (Dyer and Seeley, 1994; Robinson, 2012). Given the ubiquitous nature of the migration dance within the genus, as well as the simpler nesting requirements of the more basal open nesting species such as *A. florea* and *A. dorsata*, it is possible that these species do not display a distinct nest-site selection process at all. Rather, it is the spatially specific requirements of cavity nesting that have driven the evolution of the nest-site selection process from the more basal group movement co-ordinating behaviour seen in absconding bees.

Thesis outline

This thesis has two broad aims; 1) to study collective decision-making in honey bee species that differ in their nest site requirements; 2) to identify which bees act as scouts during the flight of the swarm. To address these aims I studied the decision-making process of both *A. florea* and *A. dorsata* and the flight of swarms of *A. mellifera*.

In Chapter 2 I address the process of collective decision-making in the red dwarf honey bee (*Apis florea*) by creating *A. florea* swarms in which all bees were individually marked. This

allowed me to analyse the interactions of individual scouts as the swarms reached a decision upon where to move to.

In Chapters 3 and 4 I describe the process of consensus formation in giant Asian honey bee swarms released into a novel habitat. In Chapter 3 I discuss specifically the process whereby directional consensus is reached on the swarm cluster and compare this consensus level with the *A. florea* swarms described in Chapter 2. In Chapter 4 I describe the behaviour exhibited by *A. dorsata* scouts as the swarm makes its decision and discuss how these behaviours appear to facilitate the departure of the swarms.

In Chapter 5 I manipulate the decision-making process of Western hive bee (*Apis mellifera*) swarms in order to determine which bees decide to act as guides as the swarm takes to the air and travels towards its destination. I also investigated how much consensus *A. mellifera* swarms require before a swarm is able to fly to its chosen destination.

In Chapter 6 I discuss the implications of my findings and suggest areas of further research.

Chapter 2

Moving home: nest-site selection in the red dwarf honeybee (*Apis florea*)

James C. Makinson, Benjamin P. Oldroyd, Timothy M. Schaerf, Wandee Wattanachaiyingcharoen, Madeleine Beekman

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 behaviours that allow the swarm to select the best nest site possible. Here, we describe the behaviour of individual *A. florea* workers during the process of nest-site selection and show that it differs from that seen in *A. mellifera*. We analysed a total of 1,459 waggle dances performed by 197 scouts in five separate swarms. Our results suggest that two fundamental aspects of the behaviour 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 behaviour 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 (Franks et al., 2003; Seeley and Buhrman, 1999). As colonies often invest considerable resources in nest construction by producing structures such as combs or protective resin barriers (Hepburn, 1986; Roubik, 2006; Seeley and Morse, 1976), 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. 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, 2004a).

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 (Schmidt, 2001; Seeley and Morse, 1978). 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.*

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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 lift-off (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 (Beekman et al., 2006; Janson et al., 2005; Latty et al., 2009; Schultz et al., 2008).

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 favoured 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 lift-off (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. 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 behaviour 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 behaviours 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 behaviour 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 behaviour 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 colours 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.

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Observations

To observe the nest-site selection process, we suspended an approximately 1m long and 1.5cm diameter stick horizontally from a shady tree, 1m 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 travelled was recorded using a Global Positioning System device. Swarm 4 attempted to lift-off after 3 days but failed, at which point we ceased recording its nest-site selection process. We infrequently monitored this swarm without filming its behaviour 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 analysed.

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* (Dyer and Seeley, 1991; Koeniger et al., 1982; Lindauer, 1956). 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 (Dyer and Seeley, 1991; Koeniger et al., 1982; Lindauer, 1956) are quite variable. This is not surprising because distance perception by flying bees is heavily influenced by the visual environment (Srinivasan 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 take-off 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 behaviour 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 lift-off. A swarm's consensus vector for a given time interval, *T*, $t_0 \leq t \leq t_i$, 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, θ_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

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

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

$x_j = \sin\phi_j$, $y_j = \cos\phi_j$, n_i is the number of waggle runs performed by bee i during the interval T, and φ_j is the bearing of the jth waggle run for bee i. Once all the average bearings, θ_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:

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

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 analysed.

Dance behaviour 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,

Table 1: The number of dancers, percentage of bees dancing, percentage of bees dancing in the last hour prior to take-off, and number of hours taken for the swarms to take-off

	Swarm				
	1	**2**	**3**	**4**	**5**
Number of dancing bees	34	102	22	7	32
Swarm size	-	4,800	5,800	1,600	2,700
Percentage bees that dance		2.13	0.38	0.43*	1.19
Percentage bees dancing in last hour		0.50	0.24	0.31	0.75
Hours of swarm activity prior to take-off (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
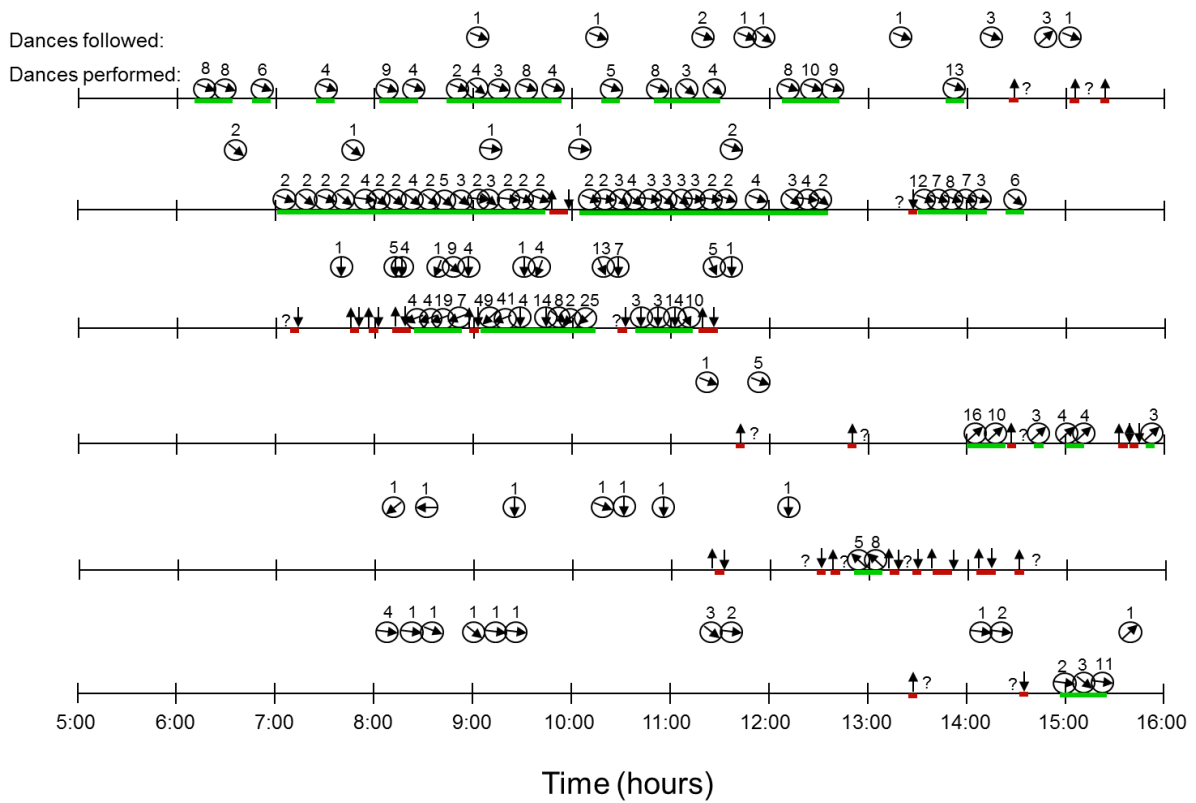
Figure 1: Individual dance histories of a subset of six bees that danced on swarms 4 and 5. The *horizontal black bars* denote the time spent dancing. The *arrows in circles directly above the black line* represent the average angle indicated by a single dance performed by the bee, while the *arrows 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*.

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.

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.

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
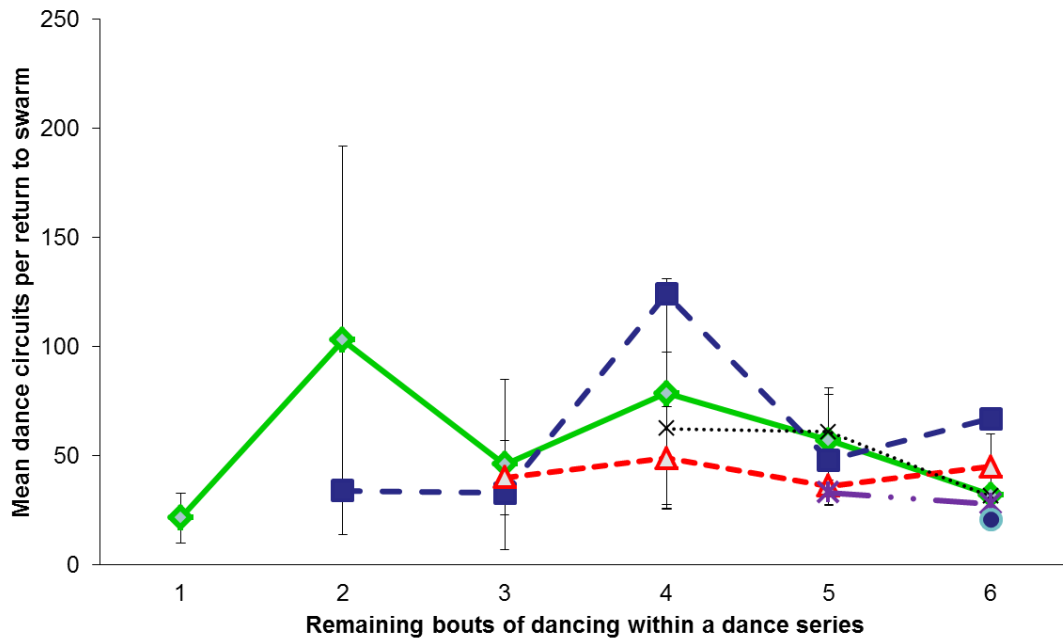
Figure 2: Mean number of dance circuits performed by bees on each successive return to their swarm during a dance series (defined as a series of waggle dancing events separated by the dancing bee leaving the swarm before returning and dancing for the same location again). Each *line* represents dance 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.

Figure 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: $F_{1, 4} = 0.08$, $P = 0.78$.

dancing (Fig. 4). Despite this, individual bees did cease dancing at some stage during the nest-site selection process.

Dance directionality

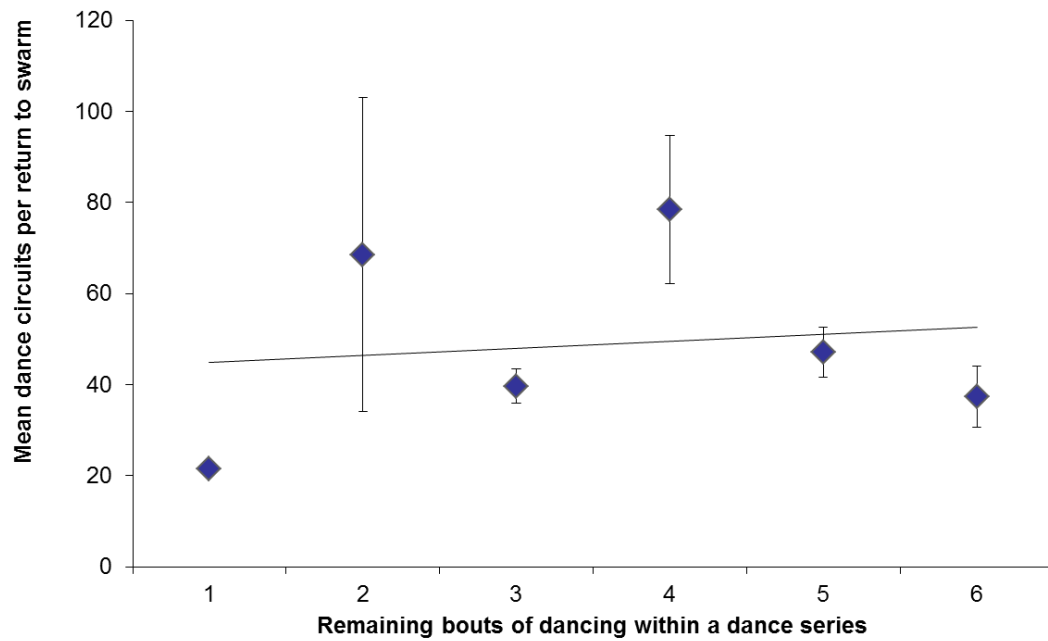As in a previous study on nest-site selection in *A. florea* (Oldroyd et al., 2008), dances were highly variable, both with respect to distance and direction. Oldroyd et al. did not mark their dancing bees; hence, they were unable to discern if the observed variance arose from many individual bees dancing 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 behaviour of a single bee from swarm 5 as she danced over a period of 4 h (Fig. 5). The dance behaviour of this bee is representative of dance behaviour 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 lift-off (Table 3).
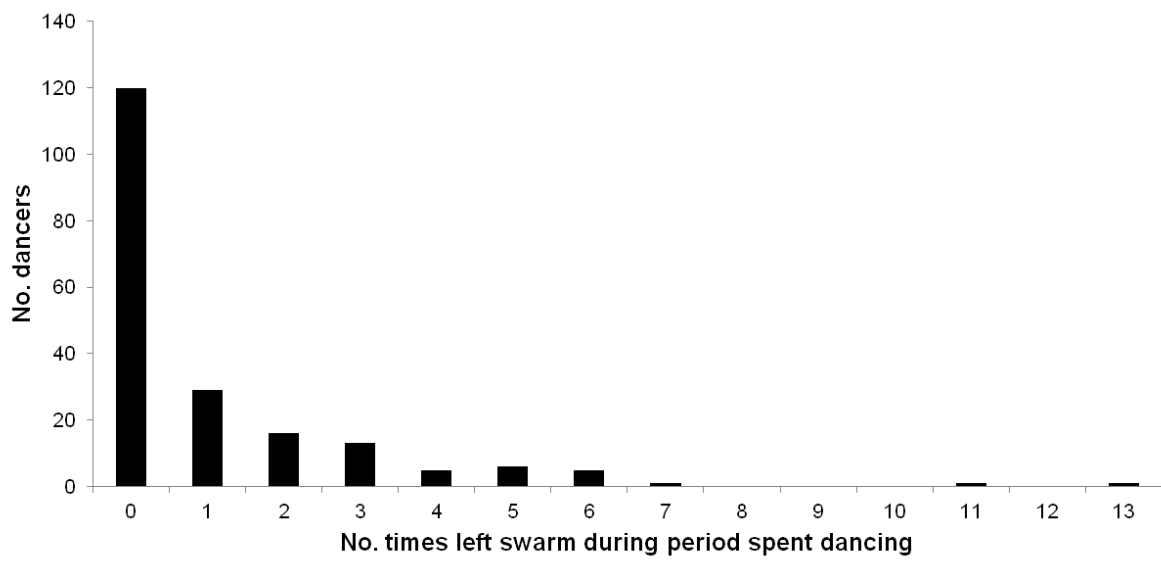
Figure 4: Number of times a dancing bee left the swarm in between periods of dancing during the nest-site selection process. Dancers with a score of 0 (61%) were never seen to leave the swarm in between bouts of dancing
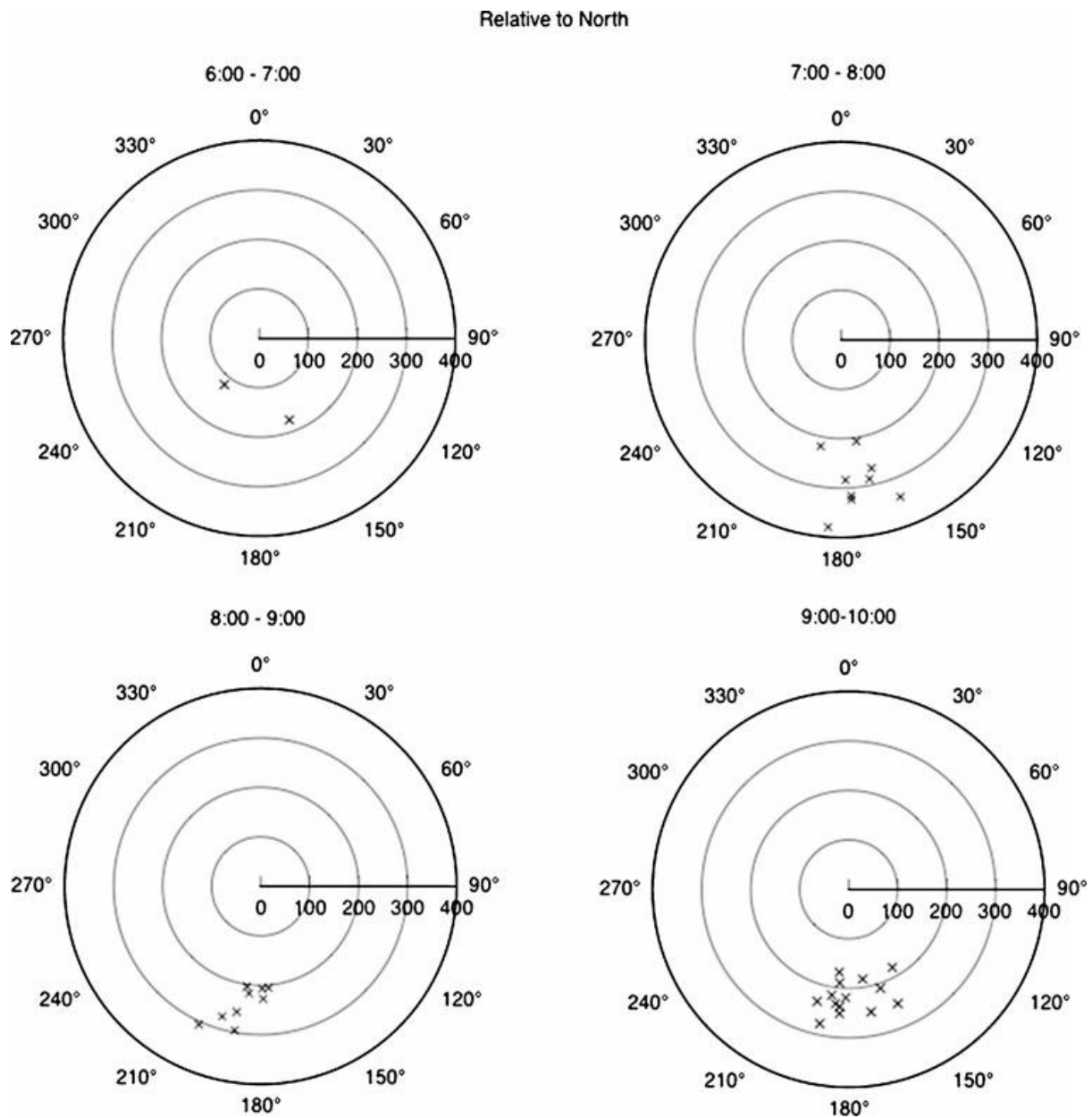
Figure 5: Distance and direction as encoded in the dance of one scout bee of swarm 5 over the history of the nest-site selection process. Plots represent 1-h periods of the decision-making process. Each symbol represents the average direction and distance from three or more dance circuits. It is clear from the plots that the dances are not precise with respect to distance and, to a lesser extent, direction

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

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.

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 take-off, 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 take-off. 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 take-off (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 lift-off as otherwise even when two bees would be dancing in the same direction, the 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.
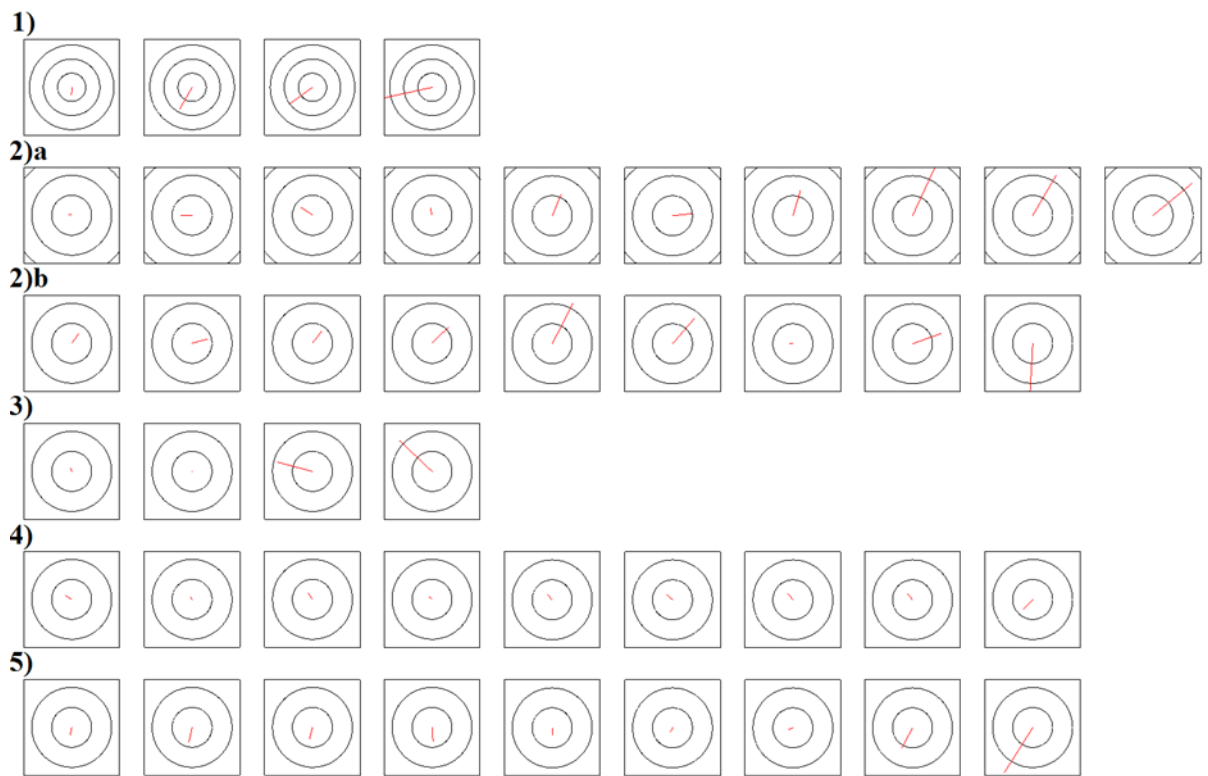
Figure 6: Vectorial consensus for each of the five swarms studied. Each *graph* represents the level of vectorial consensus in the dance direction indicated by the scout bees in each hour of the nest-site selection process. Rows *2)a* and *2)b* indicate the first and second days, respectively, for the 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

Lift-off

Approximately half an hour prior to lift-off, the bees on the surface of the swarms became progressively more excited, with bees conducting a behaviour 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 lift-off 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 travelled 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 behaviour 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 behaviour of dance followers and established whether the piping signal was detected.

Our results demonstrate that the decision-making behaviour of *A. florea* during nest-site selection is fundamentally different to that of *A. mellifera*. The behaviours associated with nest-site selection appear to reflect the nesting biology of this species. Because of the abundance of potential nest sites available to *A. florea*, individual behaviour 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 take-off 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 behaviour. 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 prior to

lift-off, 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 (Seeley and Buhrman, 1999; Visscher and Camazine, 1999), but, because such switching is are 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 lift-off?

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). Piping therefore acts a priming signal for swarm take-off (Seeley and Tautz, 2001; Seeley and Visscher, 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 lift-off? 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 lift-off, 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 behaviour 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

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swarm's initial take-off 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 lift-off 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; Latty et al., 2009; Schultz et al., 2008). 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 lift-off attempt to guide the swarm in their preferred direction. Modelling 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 travelling 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 lift-off, 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 behaviour 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 preselecting the best possible site prior to lift-off. 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 lift-off. 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.

Chapter 3

Consensus building in giant Asian honey bee (*Apis dorsata*) swarms on the move

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Abstract

Many animals move in groups, but the mechanisms by which a group of animals forms consensus about where to move to are not well understood. Honey bee (*Apis spp*) swarms provide an excellent model system in which to study decision-making processes about group movement. The 11 currently-recognised honey bee species are classified into 3 groups based on their nesting biology; the cavity nesters such as the well-studied European honey bee (*A. mellifera*), dwarf open nesters such as the red dwarf honey bee (*A. florea*), and the giant open nesters exemplified by the common giant honey bee *A. dorsata*. The differing nest site requirements of these bees are predicted to have profound effects on their extent of consensus formation prior to swarm departure. Species like *A. mellifera* with fastidious nest site requirements require a precise and quality-dependant nest-site selection process, whereas the diminutive *A. florea* can nest almost anywhere, has an imprecise nest site selection process. *A. dorsata* migrates in response to changes in local floral conditions, and produces large (>1m) single-comb colonies often in aggregations of 10s to 100s of colonies. Due to the size of the colonies and the species' gregarious nature, the availability of suitable nest sites is often restricted. In this study we determine whether the levels of consensus formation used in *A. dorsata* swarms relocating to nearby trees is similar to the quality dependant process seen in *A. mellifera*, or the very simple, quality independent process

seen in *A. florea*. We show that prior to departure, *A. dorsata* swarms rapidly reach a general consensus on a patch of trees in a fashion similar to *A. florea*. The swarms land within the canopy of the trees and then presumably search the surrounding area for a specific location in which to construct their new comb.

Keywords: *Apis*, *Apis dorsata*, group movement, collective decision-making, swarming, consensus.

Introduction

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 et al., 2011; Ward et al., 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 et al., 2009). The larger the group, the smaller the proportion of motivated guides that is required to lead the group towards a destination (Couzin et al., 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 et al., 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 vectorial consensus (Couzin et al., 2005).

Honey bees (genus *Apis*) undertake group movement during colony migration, emergency absconding and reproductive swarming. Reproductive swarming is well studied in the Western honey bee (*Apis mellifera*). During reproductive swarming the old queen together with 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 et al., 1979). On return to the temporary cluster the scouts indicate the locations found using the waggle dance, a stylised figure 8 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 et al., 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 and Visscher, 2004b).

Because *A. mellifera* is a cavity nesting species, there tends to be a limited number of suitable nesting sites available to a swarm. Further, 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 honey bee (*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 compared with cavity-nesting species (Chapter 2; Oldroyd et al., 2008). Typically, *A. florea* scouts are still advertising several alternate sites via their dancing when the swarm

takes to the air. This indicates that the scouts do not form consensus on a specific nesting location prior to the swarm's departure (Chapter 2; Schaerf et al., 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 et al., 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 honey bee *A. dorsata* is a migratory species (Koeniger and Koeniger, 1980) that tracks nectar resources as they become available (Itioka et al., 2001; Oldroyd and Wongsiri, 2006). *A. dorsata* often forms large aggregations of up to 150 unrelated colonies (Oldroyd et al., 2000). They construct large (up to 2m wide) single comb colonies on the underside of rocky outcrops, or branches of smooth-barked trees (Oldroyd and 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 et al., 2007; Neumann et al., 2000; Paar et al., 2000). Like the open-nesting *A. florea*, trees and rock surfaces that are suitable for *A. dorsata* nest sites are relatively common. But, due 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.

Here we examine whether *A. dorsata* swarms translocated to a new environment search for and move towards discreet 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 examine this question by dissecting the process of group's departure in 3 artificial swarms of *A. dorsata* presented with an unfamiliar environment.

Methods

Study site

We conducted our field work in Chiang Rai province, Thailand from the period of December 2010 to March 2011. 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). Both swarms were released in close proximity to a natural aggregation of *A. dorsata* colonies on a man-made structure.

Artificial swarm production

To avoid mass stinging 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 practise to find and cage the queen so that the swarm can be made to settle at a site convenient for observations (Chapter 2; Camazine et al., 1999; Seeley and Buhrman, 1999; Oldroyd et al., 2008). 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 1m x 1m 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 & 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 (Bader, 2011). Similar to Western hive bees (*A. mellifera*), *A. dorsata* scout bees use gravity to orientate their waggle circuits and indicate locations of interest relative to the sun's current azimuth (Dyer, 2002).

For swarm 2 we collected the same information using a MATLAB script developed for another project (Schaerf et al., 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

 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.

mouse input the programme'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 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 sec of ceasing to dance we regarded this as a single bout of dancing. If the break between dance circuits was > 30 sec 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 produced by *A. dorsata* is linearly proportional to the perceived distance to a target location (Dyer and 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 (in seconds) 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 and Seeley, 1991) to convert the average length of dances waggle runs into approximate distance indicated in metres.

For each swarm we calculated the level of polarisation of dance activity, *r*, at 15 minute intervals. Polarisation in this context is a measure of angular agreement amongst 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). Polarisation is given by:

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

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 polarisation value close to 1 indicates that dances are in close angular agreement whereas a polarisation 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-minute time interval preceding the departure of the swarm. We then calculated the proportion of all dances occurring in the 4 hours of on swarm dance activity this represented. Polarisation value for the dance activity within each 15 minute interval was then multiplied by the proportion of active dances. This gave us a value representing the interaction between dance polarisation and swarm dance activity levels. In order to compare the build-up of dance activity and directional polarisation over time with other open-nesting honey bee species we calculated the same value for *A. florea* swarms using the data from Chapter 2. The average proportional polarisation 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 minute time interval preceding the swarm's departure. We compared this value with the direction the swarms travelled in 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 (JCM and MB) repeatedly. In order to minimize disruption of the swarm, we retreated to a safe distance for approximately 1 hour before returning to continue marking

dancing bees once flight activity had reduced. Swarms 1, 2 and 3 departed after spending 3:43, 3:47 and 1:17 hours respectively of dancing (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 minutes before swarm departure (Fig. 2). The dances performed on swarm 1 indicated a wide range of distances and directions. At 120-60 minutes prior to lift-off the swarm's dances started to cluster around two nearby forest patches, but between the 30-15 and 15-0 minute 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 2.5km away. During the last 15 minute time interval prior to swarm 1's departure 241 (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 +/- 250m 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, with swarm 2 displayed dances varying greatly in distance and direction in the first 2 hours of the swarm's decision-making history, but switched to performing dances for considerably closer locations in the last 2 hours. During the last 15 minute 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 +/- 250m of the location the swarm landed (Fig. 2). Unlike swarms 1 and 2, swarm 3 never performed dances over a distance of 900 metres throughout its dance history. During the last 15 minute 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 +/- 250m of the location the swarm landed (Fig. 2).

Swarm 1 was released near a campus sports stadium. The stadium supported a congregation of 5 *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 metres 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

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	9/12/2010	11/12/2010	14/12/2010
No. Bees	8120	7780	3900
Sunrise	6:44	6:44	6:47
First dance	6:52	8:16	8:50
No. dancers	88	47*	37
Swarm departed	10:35	12:03	10:07

* Due to stinging attacks we were not able to mark
dancing bees for a 1 hour period

Swarm 1
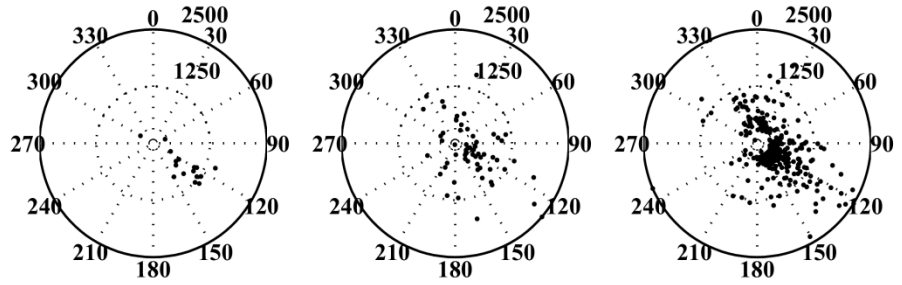
240-180
$N_d = 16$, $N_r = 0$
$N_o = 0$, $N_c = 37$

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

Swarm 2

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

51

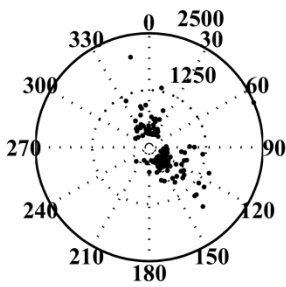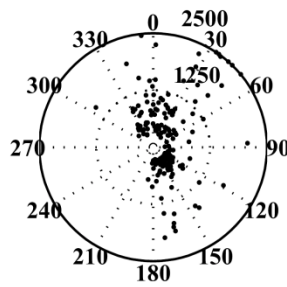**Swarm 3**

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

180-120
$N_d = 6, N_r = 1$
$N_o = 1, N_c = 8$
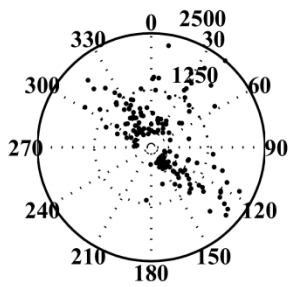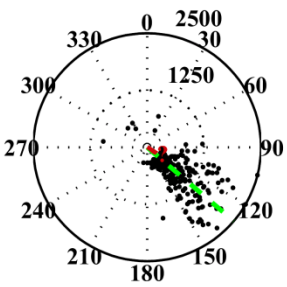
120-60
$N_d = 11, N_r = 2$
$N_o = 1, N_c = 18$

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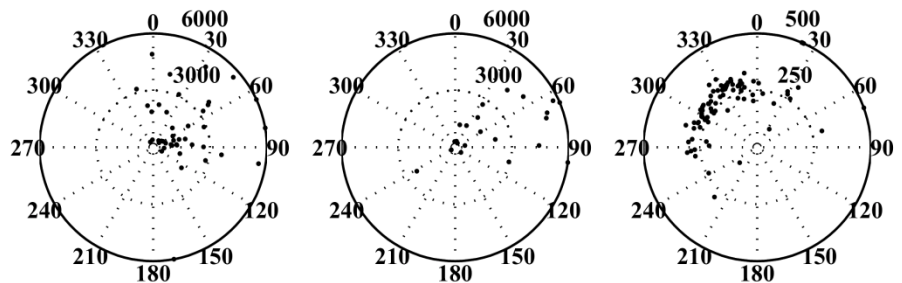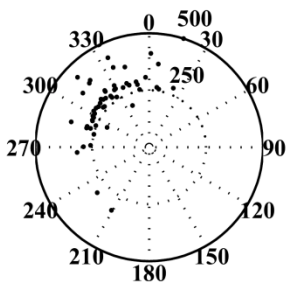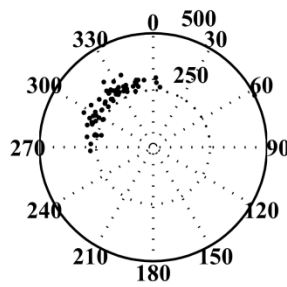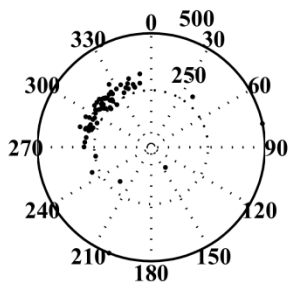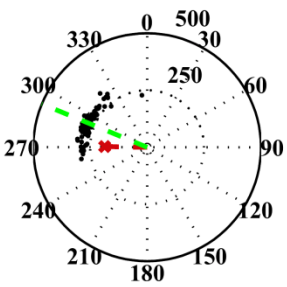$N_d = 73, N_r = 15$
$N_o = 0, N_c = 344$

15-0
$N_d = 82, N_r = 9$
$N_o = 2, N_c = 679$
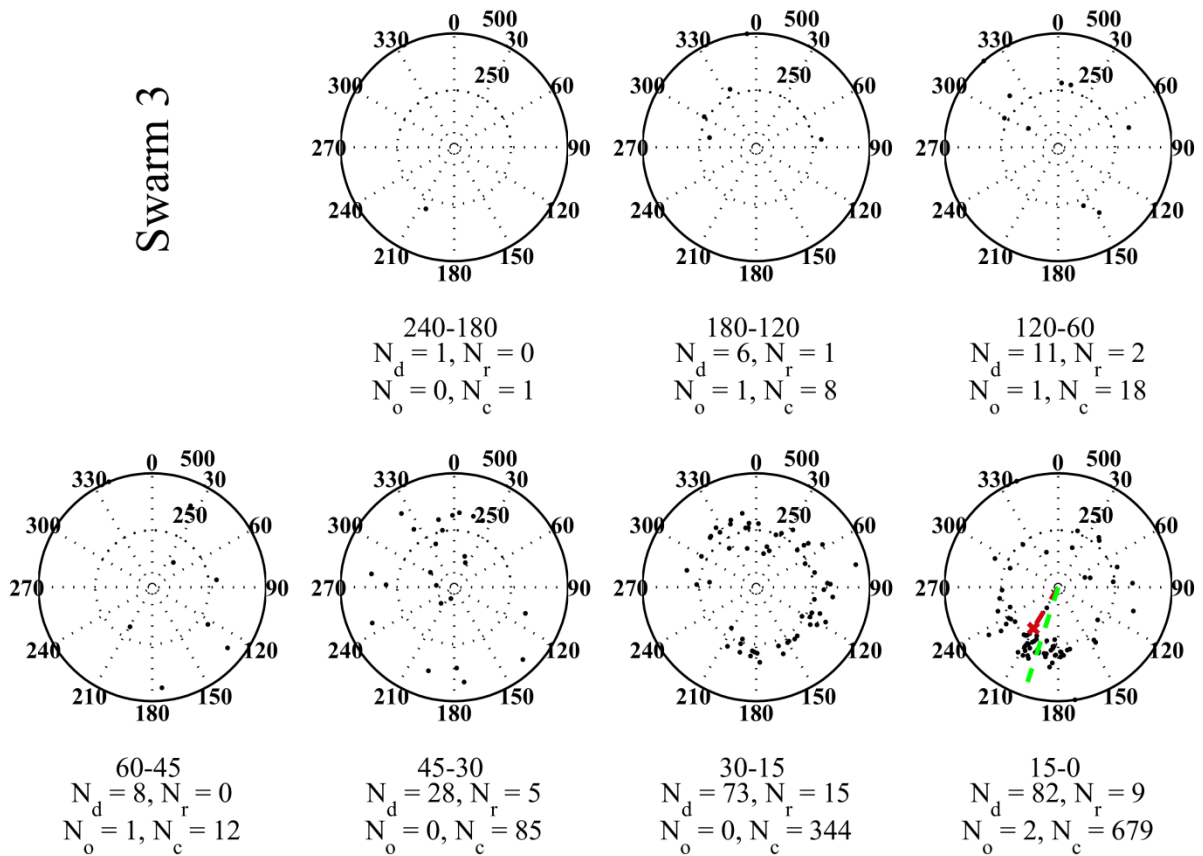
Figure 2: Radial plots representing the dance activity on swarms 1-3 leading up to the taking to the air. The top row of radial plots for each swarm indicate 1 hour time intervals while the 4 radial plots in the second row display 15 minute time intervals within the last hour prior to swarming. Black circles represent the estimated distance and direction of individual dances performed on the surface of the swarm cluster. The values on the vertical axes indicate the distance in metres from the swarm (note that the scales are not necessarily the same for each plot). The values in the first line below each scatter plot 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), N_o the number of dances which indicated distances outside of the maximum range of the scatter plot and N_c indicates the total number of circuits produced by all dances. The red dotted line in the last scatter plot 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 minute time interval.

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 metres away on an approximately 10cm wide smooth-barked tree branch next to the building aggregation approximately 8 m above the ground. Swarm 3 headed 118 metres at an angle of 208° relative to north in the general direction of the second aggregation before clustering on the first tree the swarm came in contact with. 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 if they departed due to 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 minutes 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 minutes 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 3 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 polarisation over time between *A. dorsata* and *A. florea* as measured by time interval interaction $F_{(2.356, 11.781)}$ = 0.619, p = 0.580 (Fig. 5). The pattern of build-up of dances is more or less identical, with both species displaying a significant linear correlation between time interval prior to swarming and polarisation proportional to dance activity (*Apis* dorsata: Spearman's rho = 0.929, p < 0.001, n = 16. *Apis* florea: Spearman's rho = 0.897, p < 0.001, n = 16 (Fig. 5).
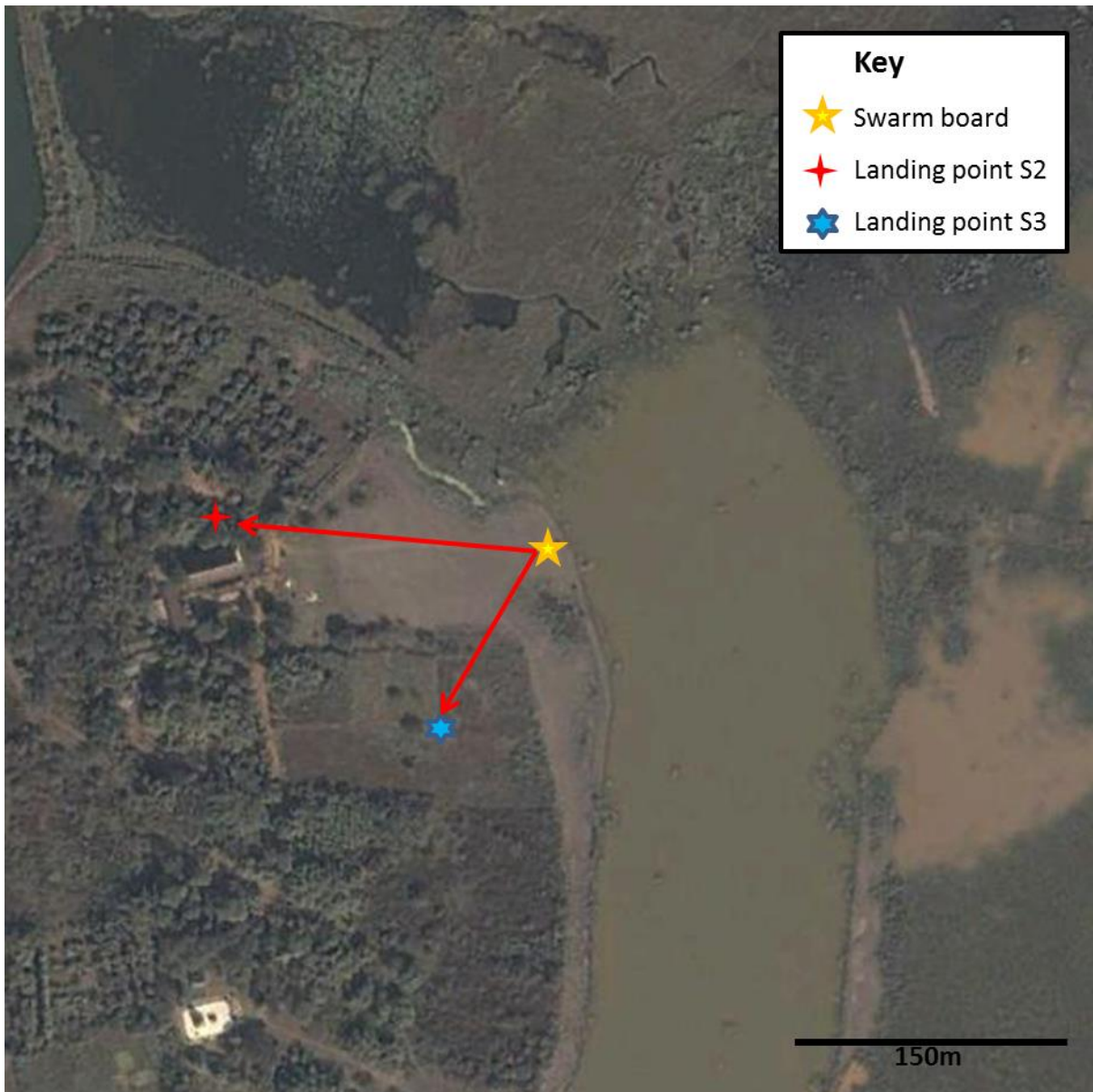
Figure 3: Indicates the directions flown and landing places of swarms 2 and 3. Both swarms landed on the branch of a tree. The branch landed on by swarm 3 was too small for the bees to construct a comb; both swarms had departed from their branches after a few days. The brown roofed structure near the landing point of 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.
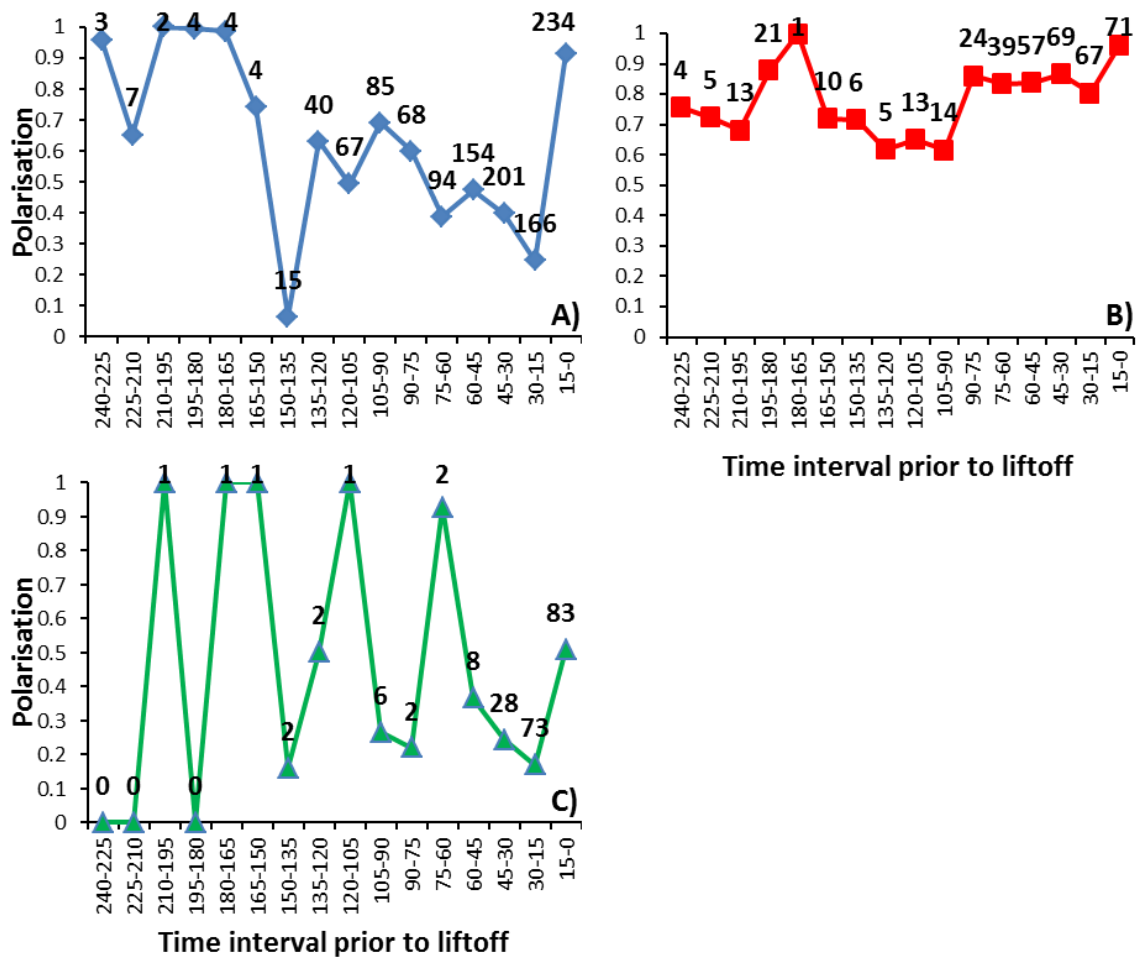
Fig. 4: The level of polarisation of directional information present in the dances performed on swarms 1-3 (A-C) during each 15min time interval leading up to the swarm taking to the air. Polarisation values range from 0-1 with a value of 1 indicating perfect polarisation of the dirrectional information indicated by dances, while 0 indicates a complete lack of polarisation. The numbers above each line indicate the number of dances performed on the swarm surface during each 15min time interval.
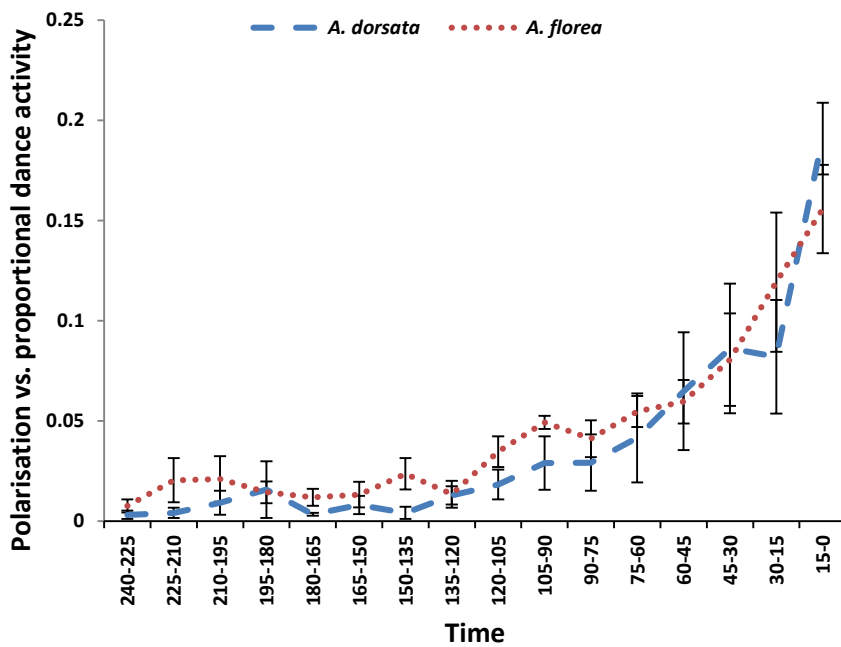
Fig. 5: The y axis represents the polarisation level times the proportion of dances at 15 minute intervals leading up to swarming in both *A. florea* (dotted line) and *A. dorsata* (dashed line). Errors bars indicated SE.

Discussion

Comparing A. dorsata to other Apis species

Apis dorsata, like *A. florea*, goes 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 get closer towards lift-off (Chapter 2; Camazine et al., 1999). 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 polarisation 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). It is interesting to note that in swarm 3 the level of dance angle polarisation 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 minute 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 discreet congregation areas act like *A. mellifera* swarms and search out specific nesting sites, or more like *A. florea* swarms, which only choose patches of the environment before taking to the air. We hypothesised 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. *A. 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 bees' growth and survival. The nest site the swarm flies to 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 and Visscher, 2004b).

If other honey bee 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*, due to the abundance of nest sites, relocating *A. florea* swarms can afford to make the final decision about the swarm's specific resting spot in the air. Portions of airborne swarms often land on vegetation in their path before moving on if the majority of bees (and presumably the queen) remain airborne (Chapter 2). Because the number of scouts is small relative to the number of uninformed individuals (0.38-2.13%) (Chapter 2), even if the scouts do not all agree on where to fly to, the swarm can be guided, provided there is some sort of vectorial consensus (Diwold et al., 2011).

A. dorsata and *A. florea* show similar levels of consensus prior to lift off in this study (Fig. 5). Due 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 utilised as such (swarm 3), the location the swarms landed is clearly reflected in the waggle dances of the bees prior to swarm departure (Fig. 2). This demonstrates that we were observing goal orientated 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 and Koeniger, 1980; Schneider and McNally, 1994). The dances indicated by swarm 1 during the last time interval indicated a wide range of distances (between 300 and 5800 metres) (Fig. 2), characteristic of migration dances (Koeniger and Koeniger, 1980). Unlike the migration dances previously described in this species, the direction they indicate does not stay fixed in the hours leading up to swarming. In the last half hour in particular the swarm suddenly switches from indicating two general regions (which correspond 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 and Koeniger, 1980; Schneider and 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 (Chapter 2; 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 (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 honey bees 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.

Chapter 4

Decision-making in giant Asian honey bee (*Apis* dorsata) swarms on the move: keep moving or settle down?

James C Makinson, Timothy M Schaerf, Atsalek Rattanawannee, Benjamin P Oldroyd, Madeleine Beekman

Abstract

Swarms of migratory honey bee species such as the giant Asian honey bee (*Apis dorsata*) are faced with two options upon entering a new environment. They can either continue to move in order to locate a better foraging environment, or settle somewhere nearby to construct a new nest. We monitored the behaviour of scout bees on three artificially-created *A. dorsata* swarms to determine the mechanisms that scout bees may use to collectively decide on whether to remain within the current locality or move on to a new area. A small number of dances occurred before orientation flights commenced in all three swarms, but these dances comprised low numbers of circuits. Flight activity then increased and peaked about one hour after dancing commenced, coinciding with an increased frequency of dancing. Scouts repeatedly left the swarm surface during the decision-making process. Differences in the number of circuits per dance for different locales suggests that *A. dorsata* makes some sort of assessment of site quality, with higher numbers of circuits per dance indicating sites of higher quality. Similarly to the red dwarf honey bee, *A. florea*, but in contrast to *A. mellifera*, *A. dorsata* scouts do not reduce the duration of their dance after repeated returns from scouting flights. Many scouts that dance for a non-preferred location switch preference during the decision-making process after following dances for the consensus direction in which the swarm eventually departed. We therefore conclude that the concensus-building process of *A. dorsata* swarms relies on the interaction of scout

bees on the swarm rather than the process of dance attenuation as occurs in the consensus building process of *A. mellifera* swarms.

Keywords: Collective decision-making, migration, swarming, individual behaviour.

Introduction

Many animals move in groups. Some groups such as shoals of fish or flocks of starlings are thought to move as a group to reduce the risk of predation (Hamilton, 1971). Individuals within such groups behave so that the group retains cohesion without regard to the direction of travel. The behavioural rules followed by individuals within such herding species can be as simple as keeping a fixed distance to the nearest neighbour while aligning with the direction of travel of other individuals in the vicinity (Hildenbrandt et al., 2010). Other animal groups move to a specific location cohesively. In such species it is necessary that a decision regarding the direction of travel is made prior to the group's departure. Without such consensus the group may not reach its target location or will break up. Honey bee (*Apis spp.*) swarms are an example of such groups. Swarms need to know where they are going prior to lift-off or they may split (Lindauer, 1955).

Honey bee swarms form in different contexts. Tropical species in particular typically migrate to new environments when under threat from a predator or when forage is depleted (Hepburn and Radloff, 2011). Under this *migratory* impulse, the colony leaves its old nest site and moves to a new locale. In contrast, during *reproductive swarming*, the old queen departs the nest site with a sub-set of the workers, leaving the old nest and all its resources to a daughter queen. Notwithstanding these significant differences, both reproductive and migratory swarming involve similar processes in which the bees comprising the swarm co-ordinate their behaviour as a collective, even though the two kinds of swarms differ in their overall goal. Reproductive swarms will generally search the surrounding environment for a new nesting location, while migratory swarms must co-ordinate the movement of the swarm over a long distance towards more favourable foraging conditions.

The process of nest-site selection during reproductive swarming is well studied in the Western honey bee (*Apis mellifera*). When an *A. mellifera* colony is ready to reproduce a

subset of the colony's workers, headed by the queen, leave the colony and form a temporary cluster nearby the old nest (Fell et al., 1977). From this cluster scout bees search the environment for large (approx. 40L), dry cavities, preferably >3m off the ground with entrance holes facing the morning sun (Seeley and Morse, 1976; Seeley and Morse, 1978). Once a scout has found a potential nest site, she assesses its quality using the above criteria (Seeley and Buhrman, 2001). If the scout judges the site to be worth reporting, she returns to the swarm surface and communicates the site's location to other bees via the famous waggle dance (von Frisch, 1956). The number of waggle circuits in the initial waggle dance for a given site is correlated with the perceived quality of the site (Seeley and Visscher, 2008). After dancing, the scout may return to the site to re-evaluate it. Through a process known as waggle dance decay (Seeley, 2003), the number of dance circuits declines each time the scout re-visits a site, and eventually she stops dancing altogether (Seeley, 2003). As a result, dances for higher quality sites persist longer during the decision-making process and have the potential to recruit more scouts (Seeley, 2003). An emergent property of this process is that the best site attracts the most dances and the most recruits (Passino and Seeley, 2006; Seeley and Visscher, 2008).

Each time an *A. mellifera* scout returns to the nest site she is evaluating, she assesses the number of other scout bees that are present at the site. Once this number exceeds a quorum threshold, the scouts start producing an auditory signal known as piping on their return to the swarm (Seeley and Tautz, 2001; Seeley and Visscher, 2003). The piping signal informs inactive bees in the swarm that a quorum has been reached at a nest site and that a decision about where to build the new nest has been made. In addition, throughout the decision-making process, returning scouts produce an inhibitory stop signal that is directed towards scouts that are dancing for sites other than the site the focal bee is dancing for (Seeley et al., 2012). Once the piping signal commences, the frequency of stop signals increases greatly, leading to a cessation of dancing and scouting for non-favoured sites. The result of the scouts' deliberations is that a single location is selected prior to the swarm taking to the air.

When a swarm does not need to move to a specific location, the decision-making process can be less elaborate. Some *Apis* species do not live in cavities, but build their single comb in the open, on a tree branch or under eves of buildings (Oldroyd and Wongsiri, 2006). The red

dwarf honey bee (*Apis florea*) is such a species. *A. florea* builds single-comb nests around linear structures, typically 1-4 cm diameter branches of shrubs or trees (Oldroyd and Wongsiri, 2006). In contrast to *A. mellifera*, *A. florea* scouts rarely take to the air during the nest-site selection process, suggesting they do not re-evaluate sites. Thus, *A. florea* scouts cannot determine if a quorum has been reached at a particular site to determine that the decision-making process has been completed (Chapter 2). As a result, although *A. florea* scouts produce a piping signal that signals 'time to go!', this signal is not linked to quorum formation at a particular favoured nest site (Chapter 2). *A. florea* swarms typically take to the air while several potential nest sites are still being advertised, flying into the average direction advertised by dancing bees at the time of lift-off (Chapter 2; Oldroyd et al., 2008). Because nest sites suitable for *A. florea* are abundant in the environment, the main purpose of the decision-making process seems to be to ensure a coordinated lift-off and to narrow down the direction of travel so that the swarm remains cohesive in flight.

In contrast to reproductive swarming, migrating colonies abandon their nest and move in one or more steps towards more suitable nesting conditions often forming temporary and unplanned bivouacs along the way, (Dyer and Seeley, 1994; Koeniger and Koeniger, 1980; Robinson, 2012). In the hours prior to the departure of a migrating colony or bivouacked swarm, flight activity drops off markedly, while scouts start producing a specific form of waggle dance known as the migration dance (Dyer and Seeley, 1994; Koeniger and Koeniger, 1980; Sasaki et al., 1990; Schneider and McNally, 1994). The migration dance is not a typical figure-8 movement, as bees do not loop back to their starting point with each new waggle circuit, but instead wander forward on the swarm surface between each waggle circuit. Migration dances typically indicate distances that are highly variable, but are consistent in their directional information (Sasaki et al. 1990; Dyer and Seeley 1994; Schneider and McNally 1994). It is therefore suspected that the migration dance acts as a simple preparation signal, allowing the swarm to prepare for coordinated movement towards a general direction (Dyer, 2002; Schneider and McNally, 1994), similarly to the behaviour seen in reproductive swarms of *A. florea*.

The giant Asian honey bee (*Apis dorsata*) is a species of migratory, open nesting honey bee found throughout Southeast Asia, and the Indian subcontinent (Oldroyd and Wongsiri, 2006). *A. dorsata* colonies typically migrate from season to season most likely to follow the

seasonal flow of nectar (Ahmad, 1989; Deodikar et al., 1977; Dyer and Seeley, 1994; Itioka et al., 2001; Kahono et al., 1999; Koeniger and Koeniger, 1980; Paar et al., 2004; Sattigi and Kulkarni, 2001; Singh et al., 2007; Venkatesh and Reddy, 1989; Woyke et al., 2012). *A. dorsata* prefers to nest in aggregations, often in excess of 100 colonies (Wongsiri et al., 1996). Individual colonies often return to the same nest site in subsequent seasons (Neumann et al., 2000; Paar et al., 2000), despite the fact that they are thought to travel distances of up to 100-200 km per season (Koeniger and Koeniger, 1980).

In a recent study we demonstrated that prior to taking to the air, artificially created swarms of *A. dorsata* reach a level of pre-flight consensus similar to that seen in *A. florea* swarms (Chapter 3, Fig. 5). In the swarms observed scouts focussed their dance activity on an arc that encompassed 1/6 of all possible directions (i.e. 60 degrees) and then travelled in the consensus direction indicated by the dances at the time of lift-off. Yet, one of our swarms produced migration dances for distances in excess of 6000m, suggesting this swarm decided to migrate instead of selecting a nest site location nearby. These observations suggest that *A. dorsata* swarms weigh up the relative merits of staying within the local environment, versus migrating over a longer distance. In this study we analyse the individual behaviour of scouts on the swarms studied in Chapter 3 to identify the behavioural rules used by scouts to reach a pre-flight consensus and to choose between migrating and staying within the local environment.

Methods

Study site and artificial swarm production

We conducted the field work for this study in Chiang Rai province, Thailand, from December 2010 to March 2011. To create artificial swarms we located colonies around the campus of Mae Fah Luang University, caged the adult workers, and fed them *ad libitum* for two days (see Chapter 3). Three swarms were released at one of two field sites. Both sites were environments surrounded by patches of secondary forest, and contained *A. dorsata* colony congregations nearby. See Chapter 3 for more information on the field sites and how we created artificial swarms.

Releasing swarms and recording swarm activity

We released swarms onto a custom-made swarm board at night the day prior to the experiment (see Chapter 3). Video footage of swarm activity was recorded using a Sony HandyCam (Sony HDR-XR100) while audio recordings were made using an electret microphone pointed towards the swarm cluster and connected to a (Sony ICD-PX720) pocket audio recorder.

Measuring waggle dance, flight and piping activity

To identify individual scouts involved in the decision-making process, we marked dancing bees with a combination of colours and positions so that all dancers were individually identifiable. We extracted the distance and direction information encoded in each dance from the video footage using a digital stop-watch and a custom MATLAB script that records the x,y co-ordinates and time elapsed between individual mouse clicks. By clicking on the bee's thorax at the beginning and end of each circuit, the script calculated the direction and length of all circuits performed by dancing bees on the swarm surface. We determined the approximate distance indicated by waggle circuits produced by the scouts based on the dance-distance relationship reported by Dyer and Seeley (1991) for this species.

To measure flight activity we recorded when bees took off from and landed on the swarm for 30 second time periods at 5 minute intervals. We also measured the number of auditory piping signals produced at 30 second time periods at 5 minute intervals.

For analysis we divided the data into 15 min time intervals relative to the time of swarm lift-off. We then took the average of 3 time intervals for both flight and piping activity in order to get an estimate of the average flight and piping frequency per 15 minute time interval. We similarly determined the distance and number of circuits produced by all dances per 15 minute time interval.

Monitoring individual activity histories

We collated individual activity histories for 49 scouts from all three swarms. Because swarm 1 was quite large the camera was positioned too far away to be able to reliably identify all of the active scouts, so we selected 5 clearly-marked scouts and followed their behaviour throughout the decision-making process. For swarm 2 we were forced to stop marking bees on the swarm after receiving a number of stings. We retreated from the colony for an hour in order to let the aggressive airborne bees settle and to minimise the disturbance of the swarm's dance behaviour. We followed the individual dance history of the first 10 dancing scout bees only. On swarm 3, we successfully collated the individual activity histories of 34 of the 37 dancing scouts. To create plots of the dance activity of individual scouts, we recorded the number of circuits and directional information of all the dances performed by that bee. We noted when focal scouts followed the dances of other bees on the swarm surface and how many circuits they observed.

In order to assess whether 'dance decay' (Seeley and Buhrman, 1999) occurs in *A. dorsata*, we required a sample of activity records from dancing scouts that ceased dancing prior to swarm departure. For this purpose we selected 4 bees from swarm 1, 10 from swarm 2 and 10 from swarm 3 that either did not dance in the last 30 min before the swarm departed, or changed the direction for which they danced (defined arbitrarily as a change in average dance circuit direction of $> 60^{\circ}$ between two consecutive dances). Similar to the method used by Seeley and Visscher (2008), for the purpose of dance decay we defined the number of circuits in a bout of dancing as all circuits produced by a scout bee between returning to the swarm cluster and taking to the air again. A series of dance bouts was considered to have ended if the dancing scout did not dance for more than 30 minutes, returned to the swarm and did not dance before taking to the air again, or changed the direction for which it danced (defined above as an angular change of $> 60^{\circ}$ between two consecutive dances).

Statistical analysis

We used a Mann-Whitney U test to compare the median number of circuits performed per dance on the three swarms before and after the swarms went through a peak in flight

activity. Using the same test we compared the number of circuits produced for 'chosen' and 'non-chosen' directions. We also compared the number of circuits of bees that changed direction of their dance with those that never changed the direction they danced for. We further used Spearman's correlation to test whether piping activity increased over time, and if the number of circuits produced by individual bees per bout of dancing decreased over time (i.e. dance decay). Lastly, we used Fisher's exact tests to compare the frequency of different behaviours exhibited by scout bee between bouts of dancing that either changed the direction they were dancing for between dancing events or did not change between dancing events. We also used Fisher's exact tests to compare the behaviour of scouts that initially started dancing for directions within 60° of the direction flown by the swarm versus scout bees which initially started dancing for directions outside of 60° of direction flown by the swarm. All statistical analysis were performed using IBM SPSS Statistics 22. All statistical analysis were performed using IBM SPSS Statistics 22.

Results

Dance characteristics

Chapter 3 describes the details of sites danced for and direction flown by the three swarms examined here. In the 15 minutes prior to departure of the three swarms the majority of scouts performed dances that indicated an approximately 60° arc (see Fig. 2 in Chapter 3). Dances that contained the highest number of circuits corresponded to sites at the distance actually flown or estimated to be flown (swarm 1, which flew out of view) (Fig. 1a-c). Similarly in all three swarms, dances that indicated the direction eventually flown had the highest number of circuits (Fig. 1d-f).

Flight activity and associated changes in dance activity

The extent of flight activity was variable among the three swarms, but all swarms underwent one or more peaks in flight activity at some stage during their decision-making process (Fig 2a-c). Dances performed on swarms 2 and 3 after the last of these pre-departure peaks in flight activity (swarm 2; 120-135 min before lift-off, and swarm 3; 90-
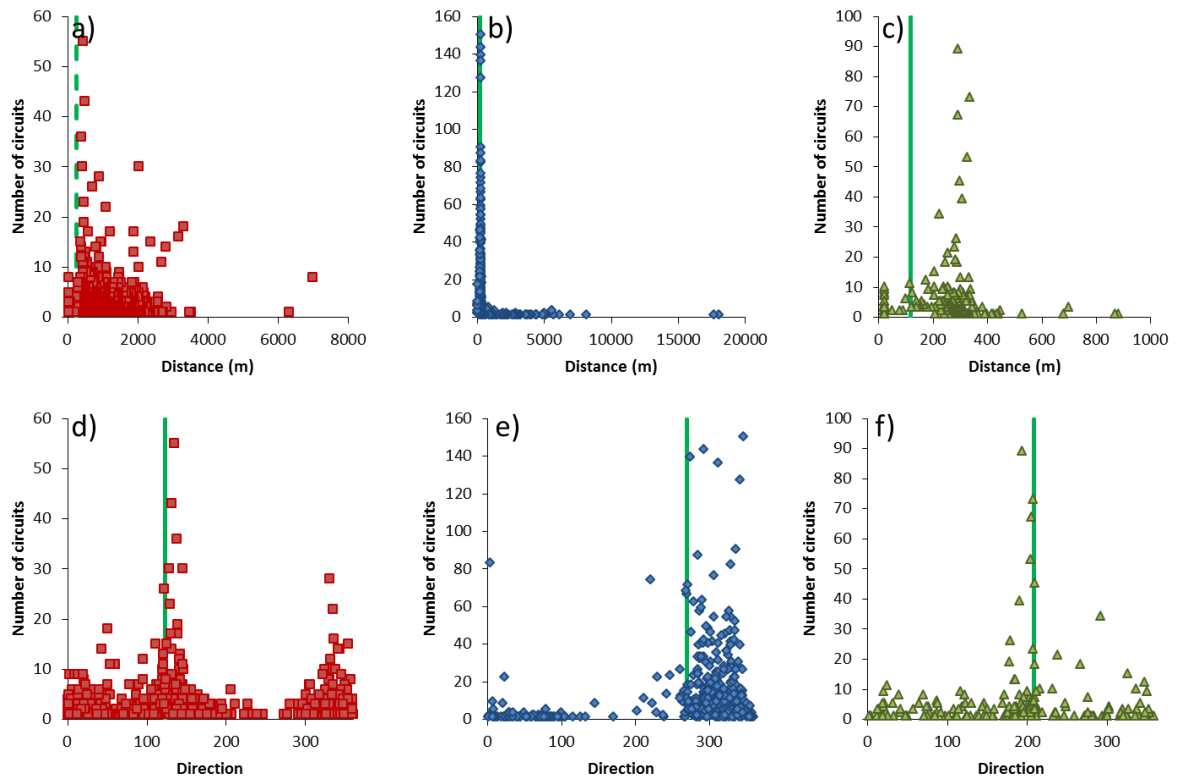
Figure 1: Direction and distance information of dances performed on the surface of three *Apis dorsata* swarms. Plots a), b) and c) depict the number of circuits produced per dance for locations of different distances from swarms 1-3 respectively. The vertical green line indicates the distance the swarm flew before being lost from view (Swarm 1) or landed (Swarms 2 and 3). Plots d), e) and f) depict the number of circuits produced per dance for locations of different directions on swarms 1-3 (d-f). The green vertical line indicates the actual direction flown by the swarm.
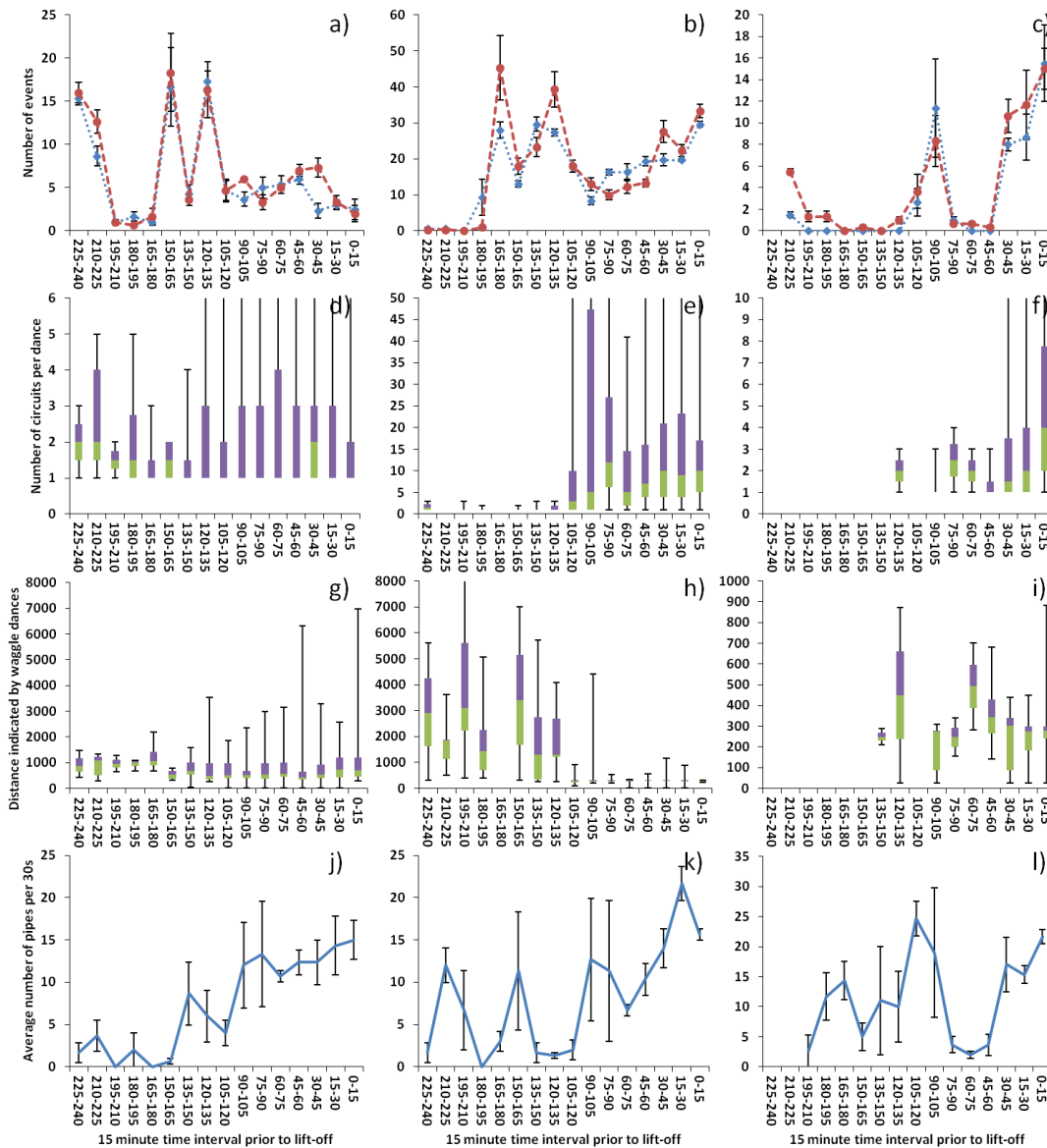
Figure 2: Fight activity on three *A. dorsata* swarms. a-c represent the average frequency of flight activity on swarms 1-3 in each 15-minute time interval leading up to the departure of the swarm (measured in three 30 second time intervals 5 minutes apart). Flight activity is measured as the average number of scouts that took to the air (the blue dotted line with rectangular points) or landed (the red dotted line with circular points) measured in three 30 second time intervals 5 minutes apart. Error bars are standard errors of the mean. Figs. 2 d-f are boxplots representing the number of circuits produced by scouts on swarms 1-3 in each 15 minute time interval leading up to the departure of the swarm. The 75th percentile is represented by the purple columns, while the 25th percentile is represented by the green columns. Many of the whiskers are not plotted in their entirety as they indicate values vastly higher than those found in other time intervals. The whisker values omitted are as follows; a) '120-135'= 17, '105-120'= 26, '90-105'= 15, '75-90'= 15, '60-75'= 55, '45-60'= 30, '30-45'= 43, '15-30'= 36, '0-15'= 19, b) '105-120'= 82, '90-105'= 150, '75-90'= 143, '45-

60'= 54, '30-45'= 127, '15-30'= 139, '0-15'= 66, c) '30-45'= 11, '15-30'= 89, '0-15'= 73. Figures 2g-i are boxplots representing the distance indicated by scout bees on swarms 1-3 in each 15 minute time interval leading up to the departure of the swarm. The whisker value of 18,111 metres at time interval '195-210' was not plotted in its entirety to make the other values in the figure more readable. Figures 2j-l represent the average number of piping signals produced on swarms 1-3 in each 15 minute time interval leading up to the departure of the swarm. Piping activity is measured as the average number of piping signals performed on the swarm within a 30 second time interval. Error bars are SE.

105min before lift-off) comprised significantly more circuits per dance than dances prior to the mass flight event (Mann-Whitney U test, Swarm 2; U = 1675.5, $p < 0.001$, swarm 3; U = 636, $p = 0.001$) (Fig 2b-c and e-f). The median dance number did not change after the pre-swarming peak in swarm 1 (U = 38929.5, $p = 0.211$) (Fig. 2a & 2d). Flight activity increased steadily in the final time intervals prior to lift-off in swarms 2 and 3, but not in swarm 1 (Fig.2a-c).

In all swarms, dances with higher circuit number (indicative of the site danced for being of higher quality (Seeley and Buhrman, 2001)) started to appear as swarms got closer to departure (swarm 1: 135 minutes prior to lift off; swarm 2: 120 minutes; swarm 3: 45 minutes; (Fig 2d-f). On swarm 1 dances indicated increasing distances 135 minutes before lift-off, but the median distance was consistently less than 1000m throughout the decision-making process (Fig. 2g). In contrast, scouts dancing on swarm 2 initially indicated sites very distant, before switching to dances for much closer locations 120 minutes before swarm departure (Fig 2h). Swarm 3 consistently indicated locations < 1000m distant throughout their decision-making process (Fig 2i).

Piping activity

The frequency of piping (piping events per 30 second time interval) was variable in all three swarms but invariably increased in the period leading up to the departure of the swarm (2j-l). There was a significant positive correlation between the number of dancing scouts per 5 minute period and piping events across all three swarms (Spearman's $\tau = 0.334$, n = 162, p <

.001). The piping signal was variable in length and pitch throughout the decision-making process.

Scout dancing histories

In our experimental set up, scouts performed waggle dances on the vertical swarm surface. With every dance circuit a scout advanced slightly across the swarm surface. For this reason, bouts of dancing were often interrupted as the dancer reached the periphery of the swarm. At this point the dancer moved back across the swarm surface and continued the dance. After performing a series of waggle circuits, the scout often took to the air and travelled away from the swarm cluster (Fig. 3). On her subsequent return to the swarm the scout often continued dancing for the location she was indicating prior to departure. On our swarms, there was no significant correlation between the mean number of circuits per dance, and the dancing bout (Fig. 4, *r* = 0.071, *p* = 0.879 n = 7 bouts of dancing); thus we found no evidence for 'dance decay' observed by Seeley (2008) in *A. mellifera* in *A. dorsata*. Importantly, our data suggest that dances reflect differences in site quality: scouts dancing for the 'chosen' location produce more circuits on average than scouts dancing for 'non-chosen' locations (Fig. 5, U = 811.5, p = 0.033).

As scouts wandered across the swarm surface between bouts of dancing or flight activity they often encountered other dancing bees and would sometimes follow one or more circuits of these dances (Figs. 6 & 7). Seventeen of the 49 bees we tracked individually changed the direction of their dances (defined as a change in dance direction >60°) (Table 1). A scout that followed a dance indicating a different location to her own preferred location was significantly more likely to change her dance direction on her subsequent dance than a scout that followed a dance indicating her own preferred location (Table 1, Fisher's exact test *p* = 0.002, n= 31). Scouts that followed a dance and then took off from the swarm can be divided into two classes: those that had followed a dance for the same location, and those that had followed a dance for a different location (Table 1). Scouts that took off after following dances indicating the location for which they were dancing were less likely to change dance direction than scouts that had followed a dance for an alternative location (Table 1, Fisher's exact test, *p* = 0.041, n = 21). Scouts that changed the direction of their dance in a subsequent dance had performed significantly fewer dance circuits in the
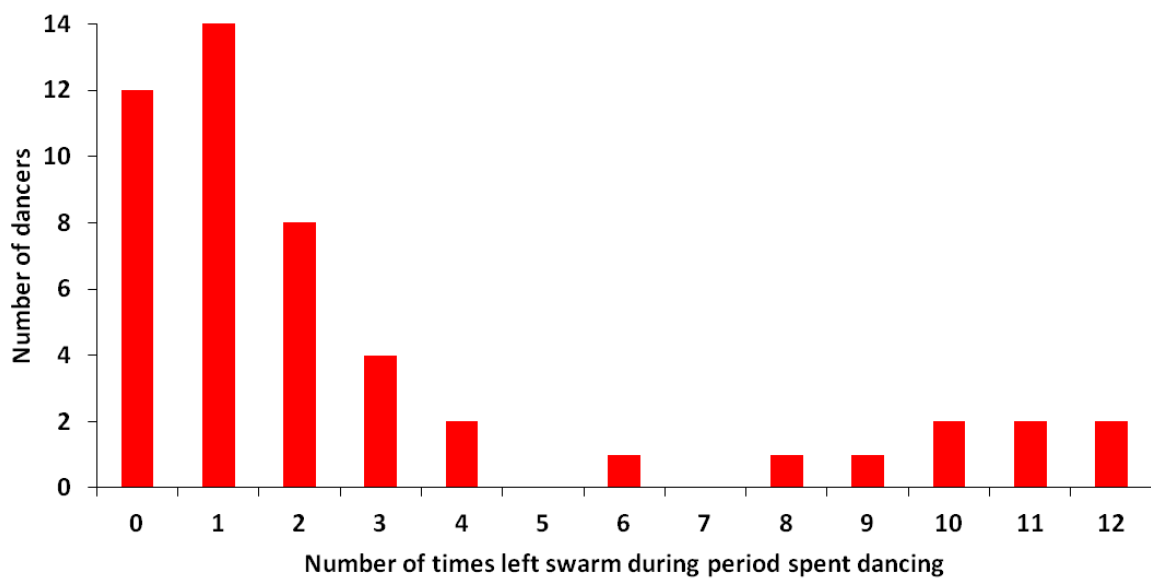
Figure 3: The number of times dancing scouts left the swarm surface for periods greater than 30 seconds after their initial dance. 75.5% of scout bees across all three swarms left the swarm cluster more than once (n = 49).
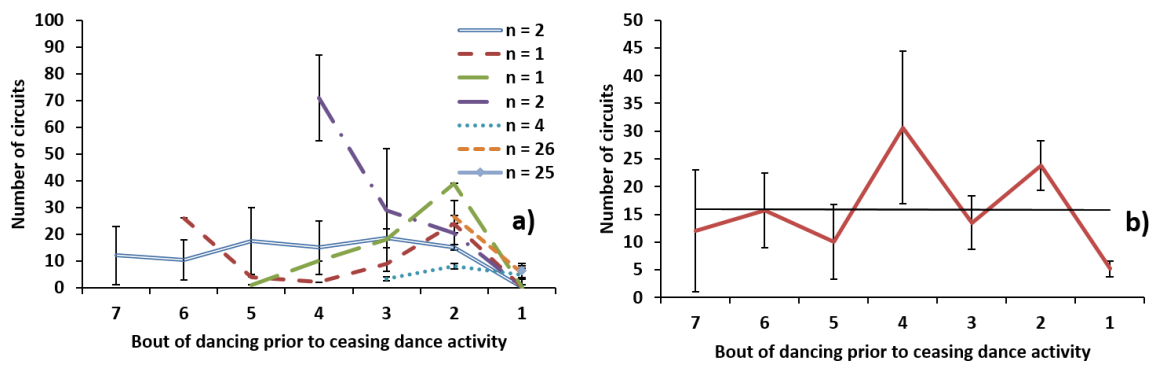
Figure 4: The average number of circuits produced by scouts with each return to the swarm surface before they ceased dancing or change direction danced for. a) Separates the dancing bee's dance series based on the number of bouts of dancing prior to ceasing dance activity. b) Mean number of circuits for each bout of dancing prior to dance cessation. There were two instances of a scout producing 7 bouts, one instance of 6 bouts, one of 5 bouts, two of 4 bouts, four of 3 bouts, 26 of 2 bouts and 25 of 1 bout were observed. The total number of dance series (N) is 62, taken from 25 scouts across the three swarms.
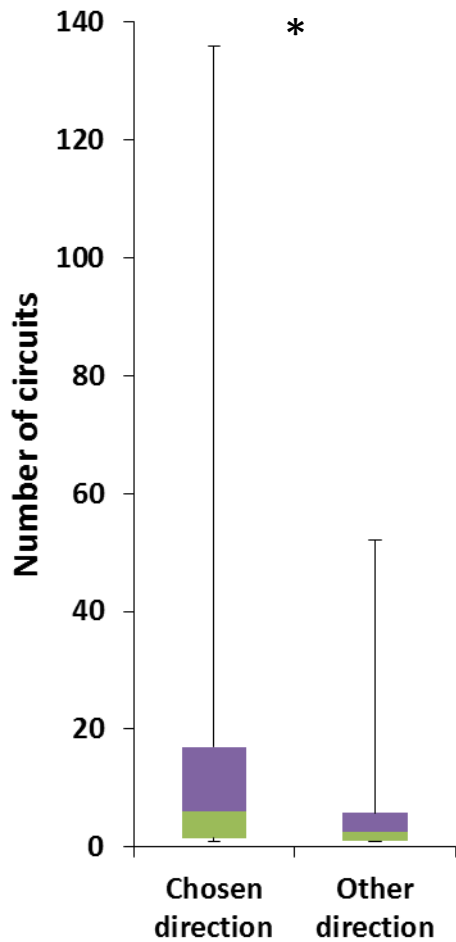
Figure 5: Boxplots indicating the number of circuits in the first dance by bees dancing for the 'chosen' direction (within 60° of the direction flown) (n = 35), and the 'non-chosen' direction (>60° of the direction the swarm flew) (n=36) across all 3 swarms. The 75th percentile is represented by the purple columns, while the 25th percentile is represented by the green columns. Whiskers indicate the minimum and maximum number of circuits. The two categories of dances were significantly different (see text).
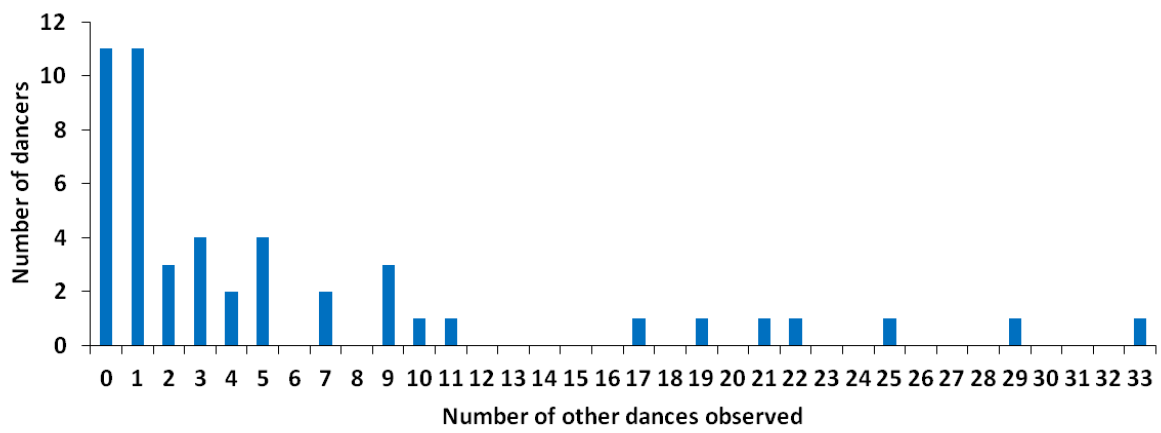
Figure 6: The number of other dances followed (defined as following one or more dance circuits of another dance) by scouts after their first dance. 77.6% of scouts across all three swarms observed one or more dances by another scout on the swarm cluster (n = 49).
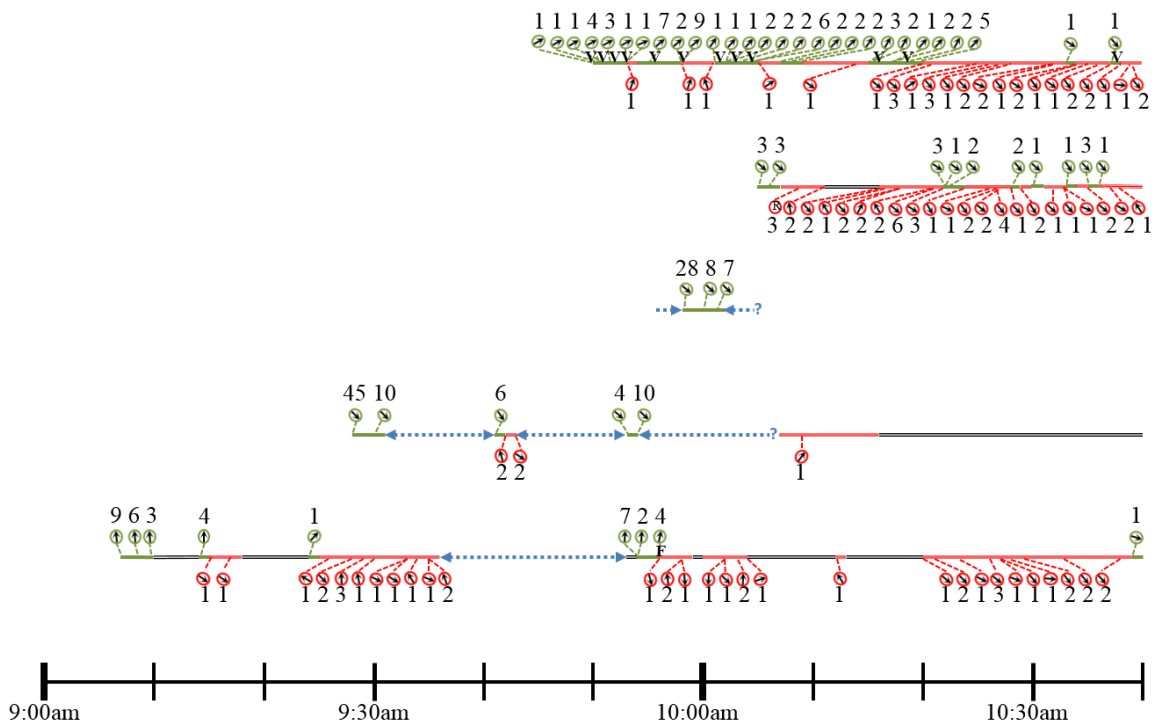
Figure 7: Individual dance histories of 5 randomly selected dancing scouts from swarm 1. Each horizontal line represents the observed activity of a scout bee over time. An unbroken green line represents time the scout bee spent performing waggle dances. Dotted blue lines represent periods of time spent in the air while the three red parallel lines represent time periods when the scout was actively following dances performed by other bees. The 2 parallel black lines represent periods of time where the scout was known to be on the swarm cluster but was either sitting inactive or hidden within the swarm cluster. V symbols denote time periods the scouts spent vibrating other workers (Donahoe et al., 2003; Lewis and Schneider, 2000; Visscher et al., 1999) while F symbols represent feeding (worker trophalaxis) events. Arrows enclosed in circles symbolise waggle dances. The arrows encapsulated in green positioned above the scout's activity line indicate dances performed by the scout, with the number above the circle denoting the number of circuits produced while arrows encapsulated in red represent dances followed, with the number below the circle denoting the number of circuits followed by the scout bee. Both the top and bottom bee can be seen to change the direction they are dancing for after having observed other dances for a similar direction.

Table 1: The frequency of different behaviours exhibited by individual *A. dorsata* scouts between dancing events. Dancing events are separated into two groups: those which changed the direction danced by >60° from their previous dance, and those which continued dancing for a location within 60° of their previously observed dance. *P* values are Fisher's exact tests of the null hypothesis that the specified event caused a change in dance orientation relative to the individuals that did not experience the event. For each test the total number of dance events is 150.

Event	Dance orientation		*P*
	Changed direction	**Did not change**	
None observed	13 (36.1%)	40 (35.1%)	0.53
Left the swarm cluster	5 (13.9%)	31 (27.2%)	0.076
Followed dance/s for a similar direction to last dance performed	1 (2.8%)	18 (15.8%)	0.03
Followed dance/s for a different direction to last dance performed	7 (19.4%)	5 (4.4%)	0.008
Followed dances for both different and similar directions to last dance performed	4 (11.1%)	1 (0.9%)	0.012
Followed dance/s for a similar direction to last dance performed and left the swarm cluster	1 (2.8%)	17 (14.9%)	0.039
Followed dance/s for a different direction to last dance performed and left the swarm cluster	2 (5.6%)	1 (0.9%)	0.14
Followed dances for both different and similar directions to last dance performed and left the swarm cluster	3 (8.3%)	1 (0.9%)	0.043
Sum	36	114	

preceding dance relative to scouts that did not change the direction of their dance (Fig. 8, U = 2973, z = 4.105, p < 0.001).

We also found interesting differences in the behaviour of scouts whose first dance was for a location within 60° of the direction flown relative to those that danced for a different location (Table 2). Scouts dancing for the 'chosen' direction were more likely to have commenced dancing in the 15 minutes prior to swarm take off compared with those that danced for other locations (Table 2, Fisher's exact test, *p* = 0.02, n = 150). Those that initially danced for locations outside the chosen direction were more likely than scouts that initially commenced dancing for the 'chosen' direction to switch their allegiance in the last 15 minute time interval (Table 2, Fisher's exact test, *p* = 0.002, n = 150).

Discussion

Migration vs. Nest-site Selection

All three swarms initially performed dances for a variety of locations before converging on a single general direction in the last 15 minutes prior to lift off (Chapter 3). Whereas swarms 2 and 3 converged on locations nearby, the dances produced by swarm 1 differed substantially in distance but not direction. Based on the distance indicated in the bees' dances we concluded that the scouts of swarm 1 decided to migrate to a more distant location rather than settling for a nesting location nearby (Chapter 3). Even though we only observed one migrating swarm and two relocating swarms, can we identify differences in the bees' behaviour that reflect the different behaviour of our three swarms?

The most striking difference between the behaviour of swarm 1 and the other two swarms is that scouts from swarm 1 did not change the median number of dance circuits per dance throughout their decision-making process (Fig. 2d). In contrast, both swarm 2 and swarm 3 increased the median number of circuits per dance as time went on (Fig. 2e-f), suggesting that the number of dance circuits is positively correlated with the perceived quality of the site danced for. Another major difference between swarm 1 and our other 2 swarms was the high levels of variation in the distance information conveyed in the dances on swarm 1, in particular towards the end of the decision-making process. Such high variation, coupled
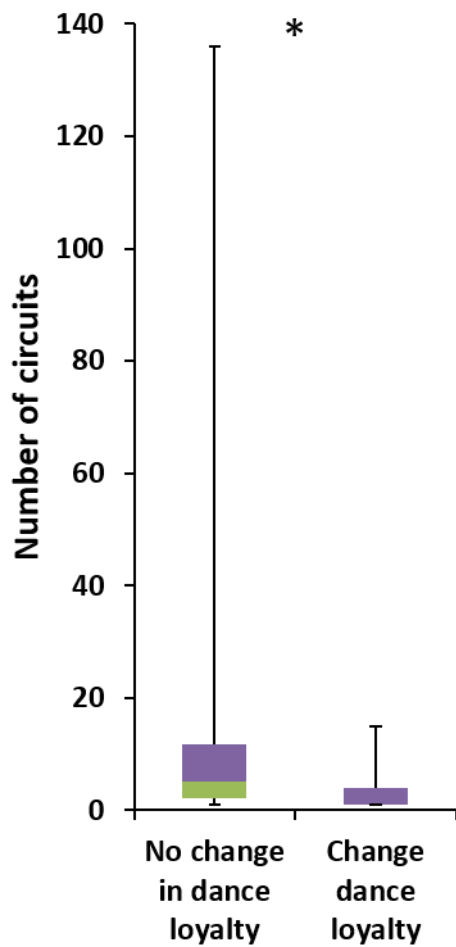
Figure 8: Boxplots indicating the number of circuits produced in the last dance performed by bees across all 3 swarms which did not change their allegiance for a particular direction (defined as a difference of 60° or greater from the previous dance performed) (n = 35), and those that subsequently changed their allegiance to a particular direction (n = 36). The 75th percentile is represented by the purple columns, while the 25th percentile is represented by the green columns. Whiskers indicate the minimum and maximum number of circuits. The two categories of dances were significantly different (see text).

Table 2: Behaviour of *A. dorsata* scouts that initially started dancing for directions within 60° of the direction flown by the swarm versus scout bees which initially started dancing for directions outside of the direction flown by the swarm. *P* values are Fisher's exact tests of the effect of a scout's first observed dance on its dance behaviour, n = 49. The number of scouts starting in the last time interval and the number of scouts which changed allegiance is significantly different between the two categories of bees.

Dance behaviour	Orientation of Initial dance with respect to direction flown by swarm		*P*
	Within 60°	**Outside 60°**	
Started dancing in last 15 minute time interval	10 (45.5%)	4 (14.8%)	0.02
Changed allegiance by the last 15 minute time interval	0 (0%)	9 (33.3%)	0.002
Ceased dancing before last time interval	6 (27.3%)	8 (29.6%)	0.556
Changed allegiance and ceased dancing	1 (4.5%)	4 (14.8%)	0.245
Continued dancing until last time 15 minutes without changing allegiance	5 (22.7%)	2 (7.4%)	0.133
sum	22	27	

with a reduction in flight activity, as observed in swarm 1, and an increase in directional consistency in dance activity are all characteristics of *A. dorsata* swarms preparing to migrate (Dyer and Seeley, 1994; Koeniger and Koeniger, 1980). Thus, the behaviour of swarm 1 is consistent with our previous conclusion that this swarm decided that the surrounding environment was unsuitable for the construction of a new nest (Chapter 3).

Comparisons with other Apis *species*

In contrast to *A. mellifera* (Seeley and Buhrman, 1999) and similar to *A. florea* (Chapter 2), *A. dorsata* scouts do not appear to utilize a process of dance decay to reach colony-level consensus about the best available site (Fig. 4). While both the lack of dance decay and the selection of a general direction of travel prior to lift off make *A. dorsata* swarms similar to *A. florea* swarms, the decision-making process of *A. dorsata* is characterised by behavioural features that are similar to those of *A. mellifera*. As in *A. mellifera*, *A. dorsata* scouts regularly take to the air between bouts of dancing and the majority of scouts restricted their dancing to a single location (an approximately 60° wide patch of the environment; Fig. 2 in Chapter 3) towards the end of the decision-making process. Moreover, we found a clear difference in the number of circuits per initial dance performed by a scout between dances for the location ultimately chosen and dances for sites that were not chosen (Fig. 5). This suggests that *A. dorsata* scouts make some sort of quality assessment of the sites they dance for. Site-quality assessment is also essential to *A. mellifera*'s decision-making process (Seeley and Visscher, 2008), but is unlikely to be important to *A. florea* (Chapter 2).

Swarm guidance and consensus formation

Seventeen of the 49 *A. dorsata* scouts (34.7%) whose behaviour we monitored switched their location allegiance during the swarm's decision-making process (Table 1). These switching scouts were more likely to be individuals that danced less enthusiastically for their initial location (Fig. 8), and appeared to switch their loyalty after following dances for other locations, and without necessarily taking to the air. This suggests that these switchers were mimicking the dances they had followed without visiting the advertised site personally. Site

allegiance switching without flight has also been observed in *A. florea*, with 31 out of 197 (15.7%) scouts across five swarms changing the direction they danced for a total of 52 times (defined as a difference of 90° or greater between dances) during the site selection process (Chapter 2). For *A. florea*, the majority of directional changes occurred after taking to the air from the swarm surface (35.8% of switching events) while the next most common occurrence was for bees to change direction after following a dance and without taking to the air (22.6% of change events). Similar switching has been described in *A. mellifera*, where 18 ± 10% of scout bees assess multiple nest sites (based on observing the scout bees at multiple nest sites: Visscher and Camazine (1999) and 11-22% (based on observing dancing scout bees, but not nest sites: Seeley and Buhrman (1999)) of scouts change the direction of the site they danced for. Interestingly, removing such 'unfaithful' bees from the swarm does not slow or speed-up *A. mellifera*'s decision-making process (Visscher and Camazine, 1999). Switching is therefore assumed to be of no importance in *A. mellifera* decision-making (Visscher and Camazine, 1999). However, *A. mellifera* swarms take much longer to reach a decision than do swarms of *A. dorsata* (13.2 ± 1.7 hours (Visscher (1999), c.a. 20 hours (Villa, 2004)) in *A. mellifera* versus 2.9 ± 1.4 hours in *A. dorsata* (Chapter 3). In addition, unlike *A. mellifera*, allegiance switching appears to be more important for consensus formation than dance decay in *A. dorsata*. It could well be that the switching of scouts' loyalty plays a role in the rapid decision-making process of *A. dorsata*. However, even in *A. mellifera* an effect of switching cannot be excluded when the swarm needs to decide between sites that differ in quality. Studies that dismissed the significance of loyalty switching in the decision-making process provided the experimental swarms with identical nest sites (Visscher and Camazine, 1999). Thus it may be premature to dismiss switching behaviour as unimportant for consensus formation in *A. mellifera* when choosing between sites that differ in quality.

Both experimental and theoretical studies have suggested that the internal process of reducing enthusiasm for a given nest site over time through dance decay is an important aspect in the formation of directional consensus prior to lift-off in reproductive swarms of *A. mellifera* (Britton et al., 2002; Janson et al., 2007; Myerscough, 2003; Seeley, 2003; Seeley and Buhrman, 1999). *A. mellifera* scouts reduce the number of circuits performed in each dance by an average of 17.2 until they cease dancing altogether (Seeley and Visscher, 2008). This internal process, coupled with the longer persistence and higher recruitment potential

of high quality nest sites and the direct silencing of opposing sites through stop signalling, allows *A. mellifera* swarms to reach consensus. Our data show that, as in *A. florea* (Chapter 2), dance decay does not occur in *A. dorsata* (Fig. 3). Therefore dance decay does not contribute to consensus formation in *A. dorsata* swarms. Instead the large increase in recruited bees in the last time intervals before swarm lift-off, coupled with switching of dance allegiance by individual bees, seems to be fundamental to the build-up of directional consensus in *A. dorsata* swarms (Table 1). This is particularly apparent in swarm 1 (see Fig. 2, Chapter 3), where the swarm suddenly switched from dancing for two patches in the environment at around 30 minutes prior to lift-off, to indicating a single patch in the last 15 minutes before swarm lift off. It seems impossible for such a sudden switch in dance consensus to occur without scouts taking into account the 'opinions' of other bees involved in decision making.

Signalling swarm departure

A. mellifera scouts change their behaviour once they have perceived a quorum at the nest site. Instead of continuing to dance on the swarm they prepare the swarm for lift-off via the piping signal (Seeley and Visscher, 2004b). Similarly to *A. florea* (Chapter 2), we observed a piping signal on *A. dorsata* swarms, and, as in *A. mellifera*, the strength of the signal produced increased over time with increasing dance activity (Fig. 2i-l). As we are unable to follow the scouts we are unable to say that the piping signal is linked to scouts having perceived a quorum at a potential nesting site. We did observe buzz runners (rapidly moving bees that produce a buzzing sound while moving (Rittschof and Seeley, 2008)) and the stop signal (recently described in *A. mellifera* as a signal used to suppress dance activity (Seeley et al., 2012)) on our *A. dorsata* swarms, although we did not quantify their occurrence. The activity of buzz runners encourages the swarm to take to the air, while the stop signal prevents scouts from dancing, especially after the swarm has reached a decision. Both mechanisms are critical in preparing *A. mellifera* swarms for departure, and likely play a similar role in *A. dorsata*.

Conclusion

Honey bee colonies regularly need to decide whether to remain within a given environment or to move on because forage conditions are poor. It is important to make the correct decision as remaining in a sub-optimal environment is likely to have a strong impact on the colony's survival and reproductive success, whereas migration ends with an uncertain future and the certain loss of a comb and nest site. Our results demonstrate how *A. dorsata* swarms go through the assessment process. On return to the swarm cluster, successful scouts communicate locations of different quality. If they find a location of sufficient quality within the immediate environment (as we saw in swarms 2 and 3), then the bees form a consensus on this location and depart. If the swarm does not find the immediate environment suitable (as in swarm 1), the scouts pick a promising direction, but not a specific location, and the swarm departs towards it. Our study is the first to directly compare the individual behaviour of scout bees going through the decision to either migrate or relocate within the environment. We demonstrate that in both contexts scouts deliberate between multiple locations before the swarm takes to the air. Therefore the process of co-ordinating the migration of a swarm is akin to the process of nest site selection, with the obvious difference that the scouts are unlikely to have visited the location the colony ultimately migrates to.

Chapter 5

Moving without a purpose: directional conflict and swarm guidance in the Western honey bee (*Apis mellifera* Linnaeus)

James C. Makinson, Madeleine Beekman

Abstract

During reproductive swarming honey bee scouts perform two very important functions. Firstly, they find new nesting locations and return to the swarm cluster to communicate their discoveries. Secondly, once the swarm is ready to depart informed scout bees act as guides, leading the swarm to its final destination. We have previously hypothesised that the two processes, selecting a new nest site and swarm guidance, are tightly linked in honey bees. When swarms can be *laissez faire* about where they nest, reaching directional consensus prior to lift off seems unnecessary. If, on the other hand, it is essential that the swarm reaches a precise location, directional consensus is most likely crucial before the swarm heads off. Here we test experimentally if directional consensus is necessary for the successful guidance of swarms of the Western honey bee *Apis mellifera* by forcing swarms to the air prior to the completion of the decision-making process. Our results show that swarms were unable to guide themselves prior to the swarm reaching the pre-flight buzzing phase of the decision-making process.

Keywords: Consensus, swarming, *Apis mellifera*, collective decision-making

Introduction

Despite the absence of centralised control in their societies, the social insects (bees, ants, wasps and termites) are capable of impressive collective behaviour. Even though the individual insects only have limited cognitive abilities, as a collective they build nests many times their own size (Bonabeau et al., 1998; Camazine, 1991; Deneubourg and Franks, 1995; Franks and Deneubourg, 1997; Karsai and Penzes, 1993), focus their foraging efforts on the best food sources (Biesmeijer and Ermers, 1999; Bonser et al., 1998; Pasteels et al., 1987; Seeley, 1985) and coordinate group defence against predators and intruders (Camazine, 1985). The collective behaviour of insect colonies is achieved through feedback mechanisms arising from the activities of individual insects, each following a basic set of rules (Bonabeau et al., 1997; Camazine et al., 2001). One of the best-studied examples of collective behaviour is the process of nest site selection during reproductive swarming in honey bees (*Apis* spp). During this complex task the bees not only have to choose the best available nest site from a set of alternatives, they then also have to move as a cohesive group towards the chosen site (Seeley, 2010). Presumably only bees involved in the decision-making process will attempt to guide the swarm in flight, thus linking the two processes.

When a colony of the Western honey bee *A. mellifera* is ready to reproduce, the old queen along with a subset of the colony's workers, leaves the colony and forms a temporary cluster in close proximity to the old nest (Seeley and Morse, 1978). From this immobile temporary cluster approximately 5% of the bees (older, forager age scout bees) take flight and search the surrounding environment for a new nesting cavity (Seeley et al., 1979). Once a scout bee has found a suitable nesting site, she returns to the swarm cluster and starts communicating her finding to nest-mates using the waggle dance (see Dyer (2002) for details on the biology of the waggle dance signal). After completing a bout of dancing, the scout bee will return to the nest site that she is dancing for in order to re-evaluate it. On her next return to the swarm she will continue dancing for the nest site, but will slowly loose motivation with each subsequent return until eventually she ceases her activities altogether (Seeley and Buhrman, 1999). The number of dance circuits produced in a scout bee's dance for a given nesting location is correlated with the perceived quality of the nest site, with higher quality nest sites receiving dances of higher circuit number (Seeley and Visscher,

2008). The net effect of this difference in initial circuit number and constant reduction in enthusiasm over time is that higher quality sites persist longer and have the potential to recruit more followers than lower quality sites (Britton et al., 2002; Janson et al., 2005; Perdriau and Myerscough, 2007; Seeley, 2003).

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

Although the piping signal is only produced by scout bees which have perceived a quorum at a given nest site (Visscher and Seeley, 2007), it is not necessarily related to a directional consensus in dances performed on the swarm cluster itself. The bees use several mechanisms to increase directional consensus levels prior to swarm departure in addition to dance cessation. Scout bees produce an auditory signal known as the stop signal throughout the decision-making process. The stop signal is used to actively silence the dances of other scout bees, and is greatly up-regulated once worker piping has commenced, resulting in a reduction of flight and dance activity (Seeley et al., 2012). Reducing flight activity presumably is important to ensure that scout bees remain on the swarm surface during the final phase of the decision-making process in order to act as guides for the swarm. With the swarm's scouts returned to the swarm cluster, and the rest of the swarm's bees warmed up in preparation for flight, all the swarm needs is an activation signal to coordinate the departure of the swarm. This signal is produced by excited scout bees that have visited the nest site at which the quorum has been reached, who run through the swarm cluster producing the buzz-run signal, which physically dislodges the swarm and forces it to the air (Rittschof and Seeley, 2008). Once in the air scout bees act as swarm guides, streaking through the swarm cluster in the direction needed to travel in order to lead the group to its new home (Beekman et al., 2006; Greggers et al., 2013; Janson et al., 2005; Latty et al., 2009; Schultz et al., 2008).

Reaching directional consensus would appear to be an important aspect of the decision-making process in *A. mellifera*, as swarms need to travel to a specific point in the environment (a cavity in which to construct their new colony). Therefore any directional conflict during swarm guidance could result in the swarm not being able to reach its destination. Two previous studies describe observing split decisions prior to lift off, resulting in swarms which were unable to guide themselves after taking to the air. One swarm monitored by Seeley and Visscher (2003) took to the air after a quorum had been reached at 2 separate sites at the same time. The swarm split in the air, and unable to guide itself resettled on the swarm board and continued dancing until a consensus was reached and it took to the air again, this time successfully travelling to the it's new nest site. Two swarms observed by Lindauer (1955) also took to the air while the swarms still lacked consensus. In response to a lack of consensus, when these swarms took to the air they split in half and the swarm halves headed in opposing directions. It therefore seems that swarms of *A. mellifera* are only capable of coordinated flight once consensus or near consensus had been reached at the time of lift-off.

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

Methods

Study site

The experiment was conducted within a grass covered grazing paddock on the grounds of the University of Western Sydney (UWS) Hawkesbury campus (33°36'45.69"S, 150°44'0.93"E) during the summer months of January-February and November-December of 2012.

Swarm preparation and experimental setup

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

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

Data collection and forced lift-off

We marked dancing scout bees as they first appeared on the swarm surface using Posca paint pens (Mitsubishi Pen Co., Japan). We monitored the number of dancing scout bees every 5 minutes for a 30 second period and noted the direction of the nest site danced for by each bee.

When a total of at least 30 scouts were dancing and at least two nest boxes were advertised on the swarm, we forced swarms off the swarm board by physically scraping bees off the board with a pen starting with the lower half of the swarm until the whole swarm took to
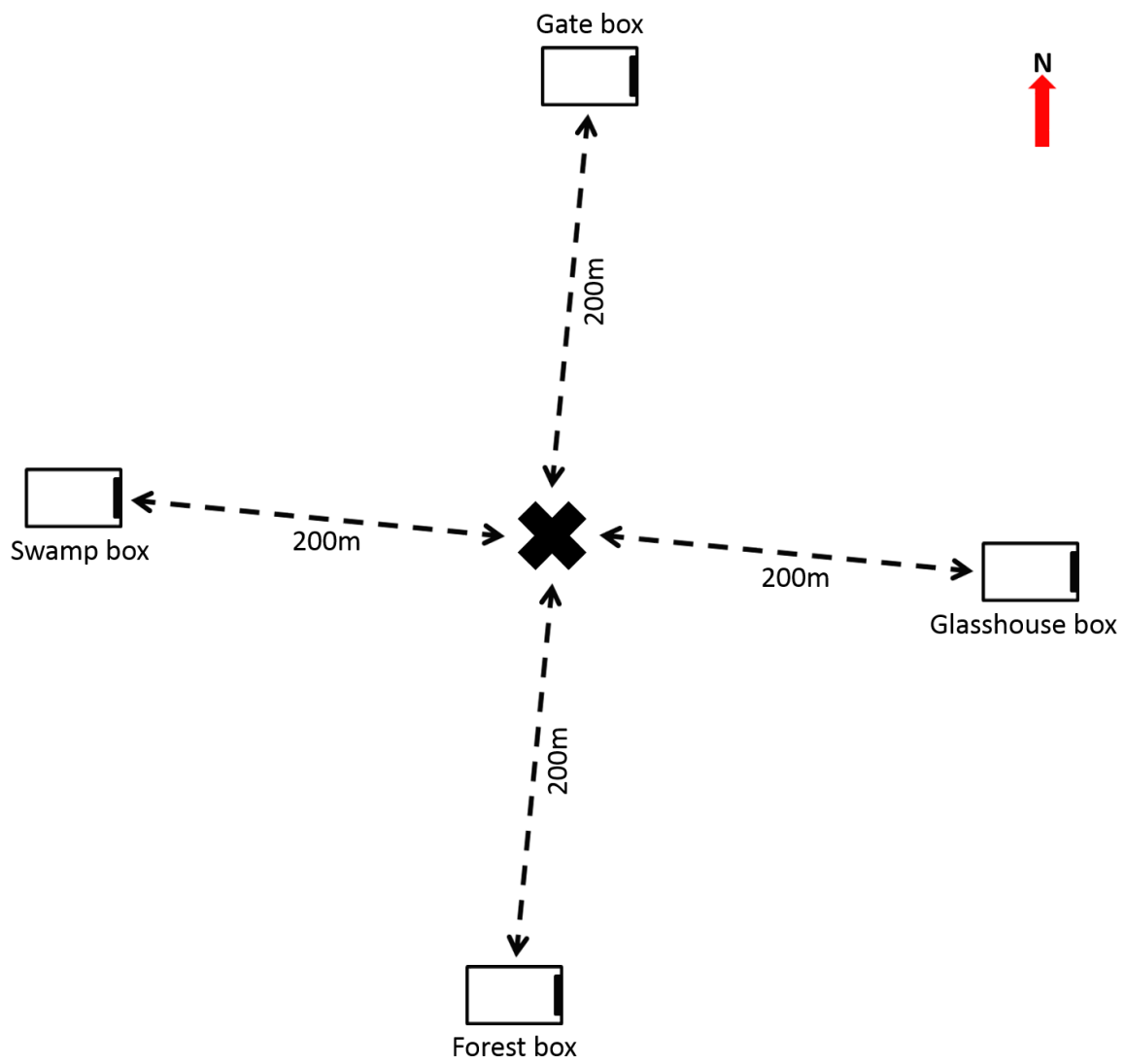
Figure 1: Sketch of the experimental set-up. Bait hive boxes were positioned 200m from the swarm cluster (denoted with a black x). Hive box entrances were positioned to face east.

the air. We gradually scraped bees of the swarm board to mimic the increase of airborne bees as a swarm takes to the air due to the activity of buzz running bees.

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

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

Data analysis

A two-tailed Fisher's exact test was used to test whether the difference in successful swarm guidance rate between experimental swarms and procedural controls was significantly different.

Results

None of the eight experimental swarms managed to guide themselves to a nest box (Table 1). Only three experimental swarms (swarms 1, 2 and 6, Table 1) moved away from the swarm board after being forced into the air, but these three swarms only travelled distances 5-10 metres from the swarm-board before clustering on the nearest clump of grass (the

Table 1: A summary of the important features of the decision-making process for swarms from the experiment (forced lift-off), the procedural control (forced lift-off after piping crescendo heard on the swarm surface) and a natural swarm (decision-making process not artificially disrupted).

	Experiment								Procedural control		Natural swarm
	1	2	3	4	5	6	7	8	1	2	1
Date	17/01/2012	23/02/2012	8/11/2012	9/11/2012	11/11/2012	15/11/2012	30/11/2012	1/12/2012	19/11/2012	24/11/2012	22/11/2012
Time swarm released	9:08 AM	7:00 AM	10:00 AM	10:00 AM	10:00 AM	7:10 AM	10:10 AM	10:10 AM	7:00 AM	10:00 AM	10:00 AM
Time swarm forced to air	12:15 PM	1:30 PM	2:10 PM	2:30 PM	2:30 PM	1:30 PM	2:30 PM	2:00 PM	4:00 PM	1:36 PM	12:59 PM
Time taken to force to air	15mins	30mins	10mins	10mins	10mins	<5mins	10mins	<5mins	<5mins	<5mins	N/A
Marked dancing bees											
- All time	32	80	65	75	84	180	57	97	113	71	82
- last hour	10	18	24	21	24	61	27	30	37	53	57
- last 30 mins	5	13	16	8	16	26	20	15	22	35	30
- last 15 mins	1	11	9	4	12	10	12	10	18	26	18
Number of dancers recruited to most popular nest box											
- All time	11	31	60	33	30	81	32	61	53	34	58
- last hour	4	12	21	12	19	29	13	27	21	23	51
- last 30 mins	3	9	14	5	15	13	9	13	21	20	27
- last 15 mins	1	9	7	2	11	4	6	9	18	20	17
Most popular nest box											
- All time	Forest	Forest	Gate	Glasshouse	Forest	Glasshouse	Swamp	Forest	Swamp	Swamp	Swamp
- last hour	Swamp	Forest	Gate	Glasshouse	Forest	Glasshouse	Swamp	Forest	Gate	Gate	Swamp
- last 30 mins	Forest	Forest	Gate	Gate	Forest	Gate	Gate	Forest	Gate	Gate	Swamp
- last 15 mins	Forest	Forest	Gate	Glasshouse/ Gate	Forest	Glasshouse	Gate	Forest	Gate	Gate	Swamp
Nest box swarm flew to	10m - gate direction	5m - glasshouse direction	-	-	5m – swamp/ gate direction	-	-	-	Swamp	Gate	Swamp
Temp (°C) during lift-off	25	29	25	21	19	24	30	35	18	26	19

field site did not contain any trees or shrubs). The other experimental swarms re-clustered on the swarm board after all bees had been airborne. Both swarms in the procedural control, and the natural swarm successfully guided themselves to one of the four nest boxes provided.

In each of the 11 swarms the number of bees dancing for the four nest sites provided increased over time (Fig. 2). Dance activity fluctuated over time for all 11 swarms (Fig. 3), with all 3 successfully moving swarms displaying 100% consensus in dance activity during the last recorded time interval. Interestingly in procedural control swarm 1 (Fig. 3i) the consensus direction prior to lift off was not the same as the direction flown (Table 1), but this could possibly be explained by our misinterpretation of light-dependant "misdirection". Unfortunately, while interpreting the nest boxes being danced for in the field we failed to take into account that dancing *A. mellifera* bees orientate their dances relative to the sun's current Azimuth rather than directly vertical when they can see the open sky (Termed light-dependant "misdirection" in von Frisch (1967), pages 196-204). Even though the bees were shaded, we cannot exclude that they could determine the position of the sun from viewing the sky. Due to this error it is likely that we misinterpreted the direction being indicated by dancers for some directions early in the morning and late in the afternoon when the sun's Azimuth diverged greatest from vertical. The two procedural controls that did reach a nest box were significantly different from the eight experimental swarms with respect to their ability to co-ordinate movement to their new home (two-tailed Fisher's exact test: N = 10, P = 0.022).

Of the swarms that did successfully travel to a nest box, procedural control swarm 1 travelled slowly in the direction of the swamp hive box despite having dancing solely for the gate hive box in the previous 6 time intervals (Figs. 2i & 3i). Procedural control swarm 2 spent approximately 5 minutes after lift-off hovering in the air in a wide-spread mass before slowly moving in the direction of the gate hive box. The swarm had only started dancing strongly for the gate box in the 5 minute time interval prior to being forced to the air, and had previously been dancing vigorously for the swamp hive box (Figs. 2j&3j). The natural
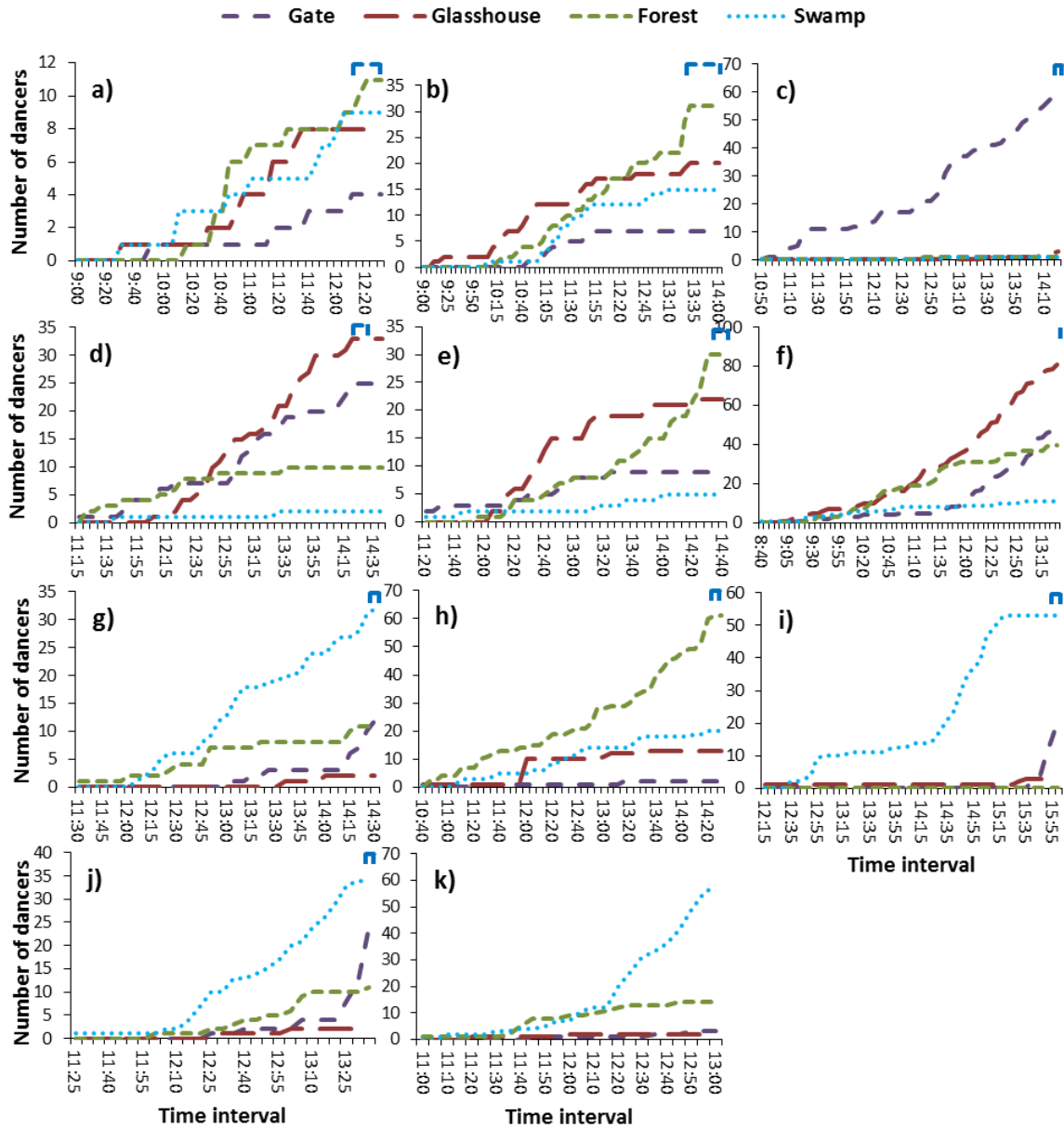
Figure 2: Cumulative increase in marked dancers for the 4 different hive boxes over time on each swarm studied. Figs. 2a-h represent the experimental swarms 1-8 (forced lift-off). Figs. 2i-j represent procedural control swarms 1 and 2 and Fig. 2k represents a swarm going through an uninterrupted process of swarming. The blue horizontal lines in Figs. 2a-j indicate the period of time spent attempting to physically force the swarm to the air by scraping bees off the swarm board. Note that the scales are not the same.

95
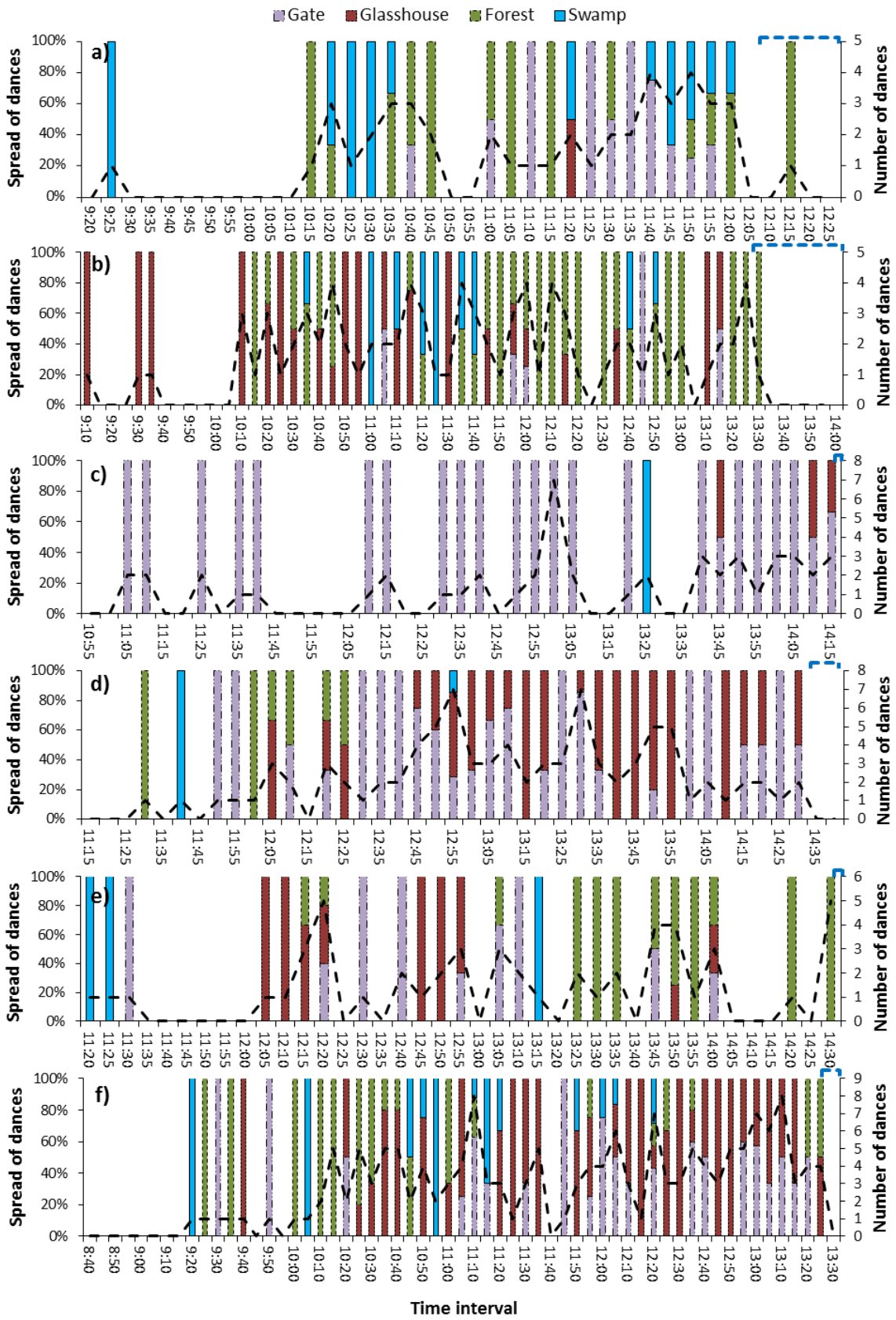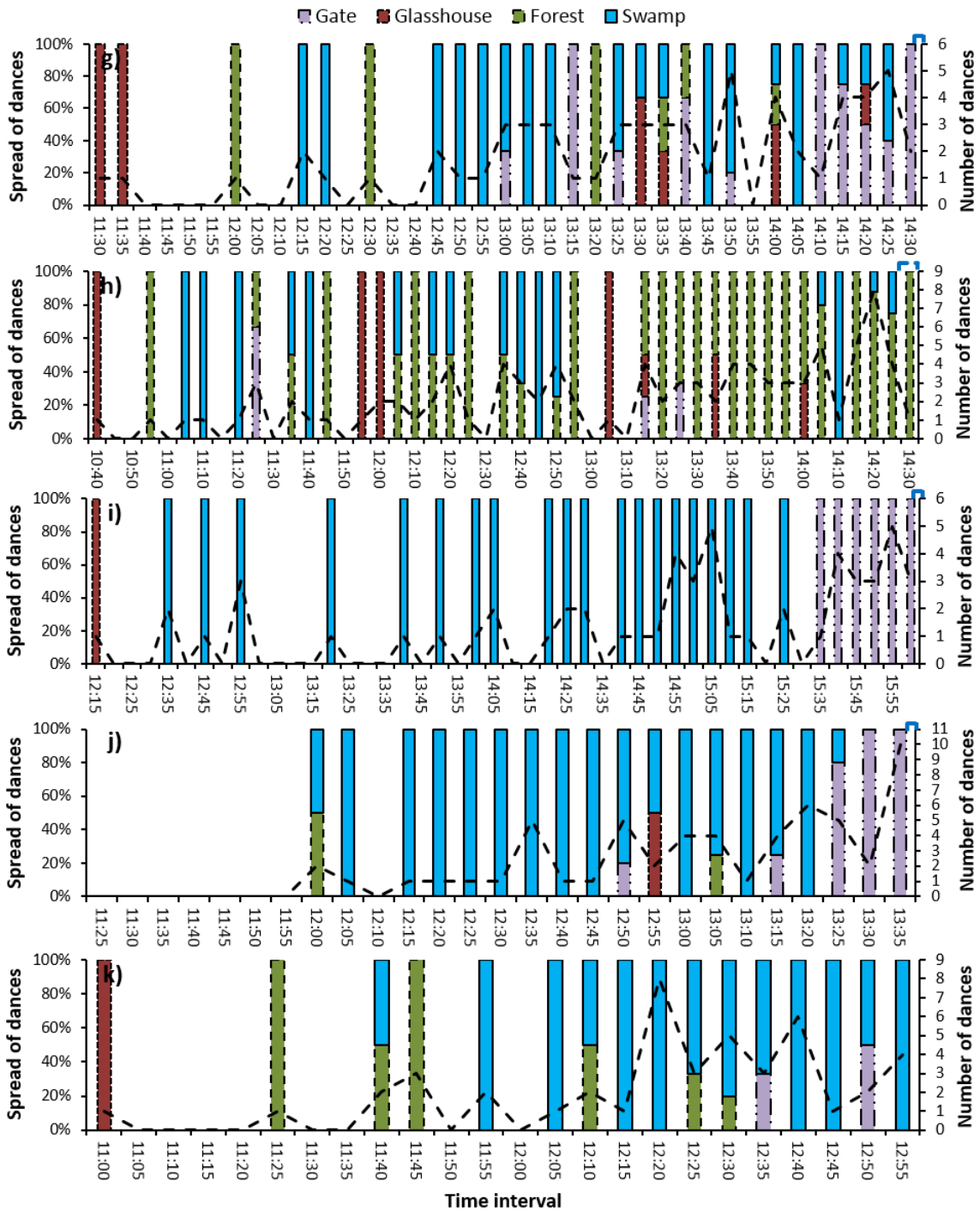
Fig. 3: Locations indicated by dancing scout bees monitored over a 30 second time period every 5 minutes from the time of the first recorded dance until the completion of the replicate. Each column represents the proportional dance activity for different locations during each 30 second interval (left-hand side y-axis). Columns are divided into different patterns to indicate the 4 different hive boxes presented to the swarms. The dashed black line connecting the different columns indicates the number of scout bees dancing during each interval (right-hand side y-axis; note that the scales are not the same). Figures 3a-h represent swarms 1-8 of the experiment (forced lift-off). Figs. 3i-j

represent procedural control swarms 1 and 2 while figure 3k represents a swarm going through an uninterrupted process of swarming. The blue horizontal lines in Figures 3a-j indicate the period of time spent attempting to physically force the swarm to the air by scraping bees off the swarm board.

swarm (Figs. 2k&3k) travelled in a slow but steady pace towards the swamp hive box after taking to the air as expected based on the dance activity prior to lift-off.

Discussion

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

In contrast to the experimental swarms, the procedural control swarms were able to coordinate movement to a hive box showing that the major disruption caused by us physically scraping bees off the swarm board does not explain the swarms' inability to fly towards a nest site. Interestingly both swarms flew in unexpected directions based on the complete lack of dance activity for the direction flown in within the last 6 time intervals (procedural control swarm 1, Fig. 3i) or the build-up of dancers for a different location (procedural control swarm 2, Fig. 2j). These findings are interesting as they illustrate how

the currently active scout bees (procedural control swarm 1) or the significantly larger group of scouts (procedural control swarm 2) are not necessarily the ones which will guide the swarm once it takes to the air. Alternatively, these discrepancies in direction indicated and direction flown could be due to our misinterpretation of light dependant "misdirection" in the field. Even though we attempted to prevent the bees from seeing the sky, we cannot guarantee that the bees were indeed incapable of using the actual location of the sun instead of gravity.

Who guides the swarm in *A. mellifera*? We can think of two mutually exclusive hypotheses regarding the identity of swarm guides. Either all bees involved in the decision-making process, or more precisely all bees still dancing prior to lift off, attempt to guide the swarm. Alternatively, only those bees that have experienced the quorum at the nest site they were visiting at the time of lift off will guide the swarm. We can now use our experimental result to decide which of the two hypotheses is the most likely. If all scouts that were still actively involved in the decision-making process at the time of lift off (e.g. those still dancing at the time of lift off) would attempt to guide the swarm, we would have expected most, if not all, of our experimental swarms to have travelled in the average direction advertised by the dancing bees. Most of our swarms were advertising two nest boxes that were separated by 90°; hence if all scouts still dancing for nest sites at the time of lift off would have guided the swarm, most of our experimental swarms would have travelled in a direction halfway between two nest boxes. This was clearly not the case. We therefore think that only those bees that have experienced the quorum at their site will attempt to guide the swarm. This would not only explain why none of our experimental swarms flew any distance of significance, but also why one of our procedural control actually flew to a nest box other than the one it was advertising at the time of lift off. Because we did not record what site bees that performed the piping signal were dancing for, we cannot say if only bees dancing for the swamp box were producing the piping signal indicating that site, and that site only, had reached the quorum.

The behaviour of the two swarms observed by Lindauer (1955) in which the decision was split prior to lift off is consistent with our hypothesis if during both events observed by Lindauer the scout bees for both competing sites had perceived a quorum at their nest sites. The split swarm described by Seeley and Visscher (2003) had reached a quorum at two nest

sites, suggesting that this swarm's ability to coordinate movement was due to two camps of bees attempting to guide the swarm in different directions. Obviously our hypothesis requires experimental testing, but at this point in time we think it is the most parsimonious explanation of our results as well as the published results of Lindauer and Seeley and Visscher.

What can the bees tell us about guidance of moving animal groups in general? One of the potential risks of multiple subgroups of motivated individuals attempting to guide the same group in different directions is that the group may move in an average path which results in both subgroups' goals being missed. This is not a problem in animal groups such as fish shoals which are not orientating towards a specific endpoint goal, but rather move in a general direction while the main aim of individuals is to stay with the group. Modelling studies have shown that in such groups, groups are able to compromise and head in a direction which is a middle ground between the two subgroups' locations (Leonard et al., 2012). Moving in the average direction also seems to be the tactic used by red dwarf honey bee (*Apis florea* Fabricius) swarms which often take to the air while still dancing for multiple locations (Chapter 2; Oldroyd et al., 2008; Diwold et al., 2011; Makinson et al., 2011: Schaerf et al., 2011) and the giant honey bee *Apis dorsata* (Fabricius) (Chapter 3). Both *A. florea* and *A. dorsata* build nests in the open and are rather lenient with respect to where exactly they nest. As a result, it appears that open-nesting honeybee species move more like fish shoals in that staying together is more important than the actual end point of the journey.

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

Chapter 6

General discussion

The literature on collective decision-making by swarming honey bees is dominated by studies of the cavity nesting Western hive bee (*Apis mellifera*). My thesis has addressed this imbalance by presenting the first studies of scout behaviour and interactions during swarming in the Asian bee species *Apis florea* and *Apis dorsata*. Expanding our knowledge of the decision-making process in *Apis* species other than *A. mellifera* provides insight into the evolution of decision-making strategies and its relationship to each species' natural history. My studies have also increased our understanding about the individual bees that become guides during the flight of *A. mellifera* swarms.

Nest-site specificity vs. behavioural complexity

By contrasting the decision-making behaviour of swarms of a species that is non- nest -site limited (*Apis florea)* with that of swarms of species that are more constrained (*Apis dorsata)* or strongly nest -site limited (*Apis mellifera)* my studies have demonstrated that within the genus *Apis* increasing nest-site specificity is correlated with increasing behavioural complexity with respect to the behaviour exhibited by scouts during swarming.

In Chapter 2 I described the process of nest-site selection during reproductive swarming in the open nesting red dwarf honey bee, *Apis florea*. Scout bees in this species differ markedly in behaviour from *A. mellifera*. I found no evidence of 'dance decay' (Seeley, 2003) that is thought to be central to the decision making process of *A. mellifera* (Chapter 2, Figs. 2&3). I further showed that bees that dance on the surface of *A. florea* swarms often do so without leaving the swarm (Chapter 2, Fig. 4). These results suggest that unlike cavity-nesting *A. mellifera*, *A. florea* scouts do not choose a specific nesting location prior to taking to the air, nor do they possess a mechanism for quorum detection away from the swarm cluster. Therefore the decision-making process of *A. florea* appears to be geared towards ensuring coordinated lift off and the selection of a general direction of travel. Where the bees ultimately end up is determined more democratically, as while in flight the swarm

investigates several trees and shrubs within the chosen area before settling down. This initial selection is often reversed when it turns out that the site is not ideal, for example when the tree also harbours nests of the ant *Oecophylla smaragdina*; the swarm then moves on (pers obs).

In Chapter 3 & 4 I illustrated how *A. dorsata* swarms display similar behaviour to that seen in *A. florea* with respect to the selection of a target direction prior to the swarm taking off. As in *A. florea,* the change in polarisation of the dances was coupled with an increase in dance activity (Chapter 3, Fig. 5). The *A. dorsata* swarms studied consistently narrowed the majority of their dance activity to an approximately 60° arc of the surrounding environment in the last 15 minutes prior to swarm departure (Chapter 3, Fig. 2). In swarms 2 and 3, dances in the final 15 minutes were also precise in their communication of distance, while in swarm 1, distance information was highly variable (Chapter 3, Fig. 2). The dance pattern of individual scouts on swarm 1 with respect to the communication of distance is consistent with prior descriptions of scouts on absconding *A. dorsata* swarms (Koeniger and Koeniger, 1980). I therefore concluded that this swarm decided to leave the area and migrate to a distant location.

Upon examining the individual behaviour of scouts on the *A. dorsata* swarms studied, I found that much like in *A. florea*, the scouts did not go through a clear process of waggle dance decay (Chapter 4, Fig. 4). But, unlike *A. florea*, *A. dorsata* scouts regularly take to the air throughout the decision-making process (Chapter 4, Fig. 3). Moreover, scouts differed in the number of circuits performed per dance, with dances for the direction ultimately chosen comprising more circuits than dances for alternative directions (Chapter 4, Fig. 5). This phenomenon indicated that *A. dorsata* scouts evaluate specific sites rather than a general area. It therefore, appears that *A. dorsata* swarms exhibit behaviour that is intermediate between the simple, quality-independent decision-making process of *A. florea* and the quality-dependant decision-making process of *A. mellifera*.

Directional consensus, quorum signals and swarm guidance

In Chapter 5, I tried to tease apart the roles of quorum signalling and consensus in the

guidance of *A. mellifera* swarms. It is well established that in *A. mellifera* the piping signal follows quorum formation at a nest site currently under evaluation by the swarm (Visscher and Seeley, 2007). We also know that knowledgeable scouts act as swarm guides once the swarm takes to the air (Beekman et al., 2006; Janson et al., 2005; Latty et al., 2009; Schultz et al., 2008). But we do not know if all the scouts that are involved in the decision-making process guide the swarm, or only a subset, for example those that were present at the nest site when the quorum was reached. If one hypothesises that it is only the scouts that perceived the quorum that act as swarm guides, then we should expect that swarms can only be guided successfully once a quorum has been reached. If, on the other hand, all scouts involved in the decision-making process attempt to guide the swarm (or more likely those still actively dancing for sites at the time of lift off) we would expect that swarms without directional consensus would be unable to reach a nesting location. Evidence presented in Chapter 5 supports the hypothesis that a quorum is necessary for successful swarm guidance. None of the swarms that I forced to the air prior to the swarm having gone through the complete decision-making process were able to fly to one of the nest boxes I offered. Yet both control swarms that I forced into the air during the final stages of the decision-making process were able to fly to one of the nest boxes, although not necessarily to the box that was receiving the most dance attention prior to lift off. One control swarm flew in the direction of a site that it had previously been dancing for, but not at the time of lift off. The other control swarm successfully flew in the direction of the location that it had only recently been dancing for (Chapter 5, Table 1). The behaviour of the control swarms can be explained by assuming that the scouts had reached a consensus at the site the swarms ultimately flew to, and that therefore only those bees that have perceived the quorum guide the swarm in *A. mellifera*. This hypothesis remains to be tested experimentally.

Future directions

Temporary clusters in dwarf open nesting bees; are they necessary?

In order to reproduce, a cavity nesting *A. mellifera* colony must first issue a swarm that clusters in the vegetation close to the natal colony (Seeley et al., 1979). It is then the task of

the bees on this temporary cluster to choose the best available nest site from the surrounding environment in order to establish a new colony. Swarming in *A. mellifera* is therefore a two-step process. Given that the open nesting *A. florea* has simple nesting requirements, combined with the observation that swarms appear to select suitable nesting locations *en route*, a temporary bivouac seems unnecessary. It makes more sense for an *A. florea* swarm to set off in a general direction in which forage can be found. Once the swarm arrives in the general area chosen, it lands, and if the location turns out to be convivial with respect to shade, ants and other predators, the cluster will remain and build a comb. In a sense, all *A. florea* colonies are temporary clusters, as colonies migrate to follow the available forage leaving their old abandoned combs in their wake (Oldroyd and Wongsiri, 2006; Pandey, 1974; Pirk et al., 2011; Sheikh and Chetry, 2000). I predict that a natural *A. florea* reproductive swarm selects an area replete with forage prior to departure. By studying natural swarming events, one could then compare the forage dances in the days prior to swarming with the dances conducted by the bees just before a swarm departs the mother colony. My prediction is that the distance and direction flown by the departing swarm will match up with the forage dances that were performed on the colony in the days prior to swarm departure. In support of this prediction, Akratanakul (1977) observed a reproductive swarm that clustered just a few meters from the natal nest, and eventually built a comb.

One can speculate on an evolutionary transition with respect to the bivouac. The ancestral condition, as seen in *A. florea*, is that a colony divides so that there is the original nest and a swarm. If the swarm finds itself in a convivial location, that is the end of the matter and the swarm will build a comb. If not, the foragers will now act as scouts and seek out an environment with more forage to which the swarm will travel to next. The cavity-nesting species go through this same process, but the bivouac has become an integral part of the process of reproductive swarming. There seems no compelling reason why a cavity-nesting species needs the bivouac; the swarm could select a site before leaving the old colony. It seems to me that the bivouac of cavity-nesting species is an evolutionary relic of the simpler nest-site selection process as seen in *A. florea*.

Patch vs. nest-site evaluation; what are A. dorsata scouts up to?

My study of *A. dorsata* swarms (Chapter 3 & 4) is the first to examine the interactions of individual scouts during swarming. Previous studies of *A. dorsata* swarms have described the waggle dance information and flight activity on swarm clusters in the context of swarm migration (Dyer and Seeley, 1994; Koeniger and Koeniger, 1980; Robinson, 2012), but have not provided evidence of nest-site evaluation, or observed swarms that appeared to decide to establish a colony in the surrounding environment. My results demonstrate that on the swarms I observed, scouts were selecting a location within the environment prior to departure (Chapter 3, Fig. 2), and made some sort of quality evaluation (as evidenced by the number of dance circuits produced for different locations (Chapter 4, Fig. 5)) while repeatedly departing from the swarm cluster (Chapter 4, Fig. 3). It remains unclear what exactly the scout bees I monitored where dancing for. It is possible the scouts were locating patches of suitably sized trees in the environment, and that much like *A. florea*, *A. dorsata* swarms then select a suitable nesting surface upon arriving at the chosen location. Alternatively, the nest-site evaluation process could be more specific as seen in *A. mellifera*, with scouts selecting a specific nesting location and then recruiting other scouts to independently evaluate it before the departure of the swarm. Given the differences in the number of dance circuits performed by *A. dorsata* scouts I discussed above, I strongly suspect that contrary to *A. florea*, but similarly to *A. mellifera*, *A. dorsata* scouts evaluate the quality of the site they dance for.

While in the field I observed a number of instances of the build-up of scout bees evaluating old comb fragments among colony aggregations of *A. dorsata* (Fig. 1). The build-up of scouts on these comb fragments presages the arrival of a new swarm. I also observed the workers of nearby colonies crawling up to these comb fragments and attempting to dislodge the arriving scout bees. These observations indicate that *A. dorsata* scout numbers build up at a given nesting location during reproductive swarming, and that scouts can come into conflict with bees from other colonies at these presumably high-quality nesting locations, in a similar fashion to house hunting *A. mellifera* scouts (Rangel et al., 2010).

When designing my *A. dorsata* swarming experiment I decided to release my swarms

Figure 1: Giant honey bee (*Apis dorsata*) scouts evaluating part of a temple façade covered in small wax dots. The temple pictured was home to a population of over 20 *A. dorsata* colonies at the time of the picture being taken. Photo by James C Makinson.

adjacent to colony aggregation sites in the hope of observing the build-up of scouts at comb fragments within the colony aggregations. I found it too difficult to divide my attention between the swarms where I needed to mark the dancers and the locations I hoped to see their scouts evaluating. The compelling need was to watch the swarms, and so I was unable to monitor the aggregations. On departure from the swarm board none of my swarms flew directly to a nesting location within the colony aggregation, but rather they landed in the canopy of nearby trees (swarms 2 & 3), or migrated to an unknown location further away (swarm 1). Nevertheless, on analysing the dance activity of the swarms, I saw that they did in fact go through a decision-making process, and that scouts appeared to be dancing for the patches of trees that they flew towards in all three swarms. As I was unable to monitor the branches the swarm landed on prior to the arrival of the swarms, I was unable to determine whether scout activity had increased prior to the swarm's arrival. It remains an open question as to whether *A. dorsata* swarms select the exact location to move to (as do cavity-nesting bees) and go through the process of quorum sensing. However my observations of scouts thoroughly investigating a nest site prior to the arrival of a swarm (Fig. 2) strongly suggest that *A. dorsata* scouts investigate a specific nest location and may undergo quorum sensing at that location prior to swarm lift off.

Future studies of swarming in *A. dorsata* should attempt to answer if scouts indeed select the nest site prior to swarm departure by either continuing to observe colonies once they have arrived at their new destination to determine if they then go through a second decision-making step. Due to the defensive nature of *A. dorsata* and their preference for lofty nest sites this is easier said than done!

Losing interest vs. changing your mind

While studying the interactions of scout bees in *A. florea* (Chapter 2) and *A. dorsata* (Chapter 4) I found that neither species goes through a process of waggle dance decay (*A. florea*; Chapter 2, Figs. 2 & 3: *A. dorsata*; Chapter 4, Figs. 3a & 3b). In addition, a proportion of scouts change their allegiance during the decision-making process. In *A. florea* this equated to 31 (15.7%) of the scouts monitored changing direction a total of 52 times

(Chapter 2). Interestingly, eleven (20.8%) of the allegiance-switching events seen *A. florea* appeared to occur immediately after a scout followed the dance of another scout (Fig. 2). Referring to this behaviour as mimicking, my colleagues and I showed in a modelling study that mimicry of unverified dance information received on the swarm surface greatly improves the ability of *A. florea* swarms to rapidly make a decision (Schaerf et al., 2011). I observed similar allegiance switching in *A. dorsata*, in which an even larger proportion (34.7%) of observed scouts switched dance direction a total of 36 times across all three swarms (Chapter 4, Table 1). Scouts dancing for locations which ultimately lost out by the end of the decision-making process were much more likely to change their dancing allegiance, with 33.3% of scouts that initially danced for non-chosen nest-sites ultimately switching to dance for the chosen location by the end of the decision-making process (Chapter 4, Table 2). While some scouts did cease dancing and thereby fell out of the decision-making process, they did so at an equal rate for the chosen nest site and other locations. I therefore concluded that switching of nest-site allegiance is an important part of the decision-making process observed in *A. dorsata* as it appears to be in *A. florea*.

How does the phenomenon of switching compare to *A. mellifera*? Switching of nest-site allegiance has been described several times in *A. mellifera*, with rates of switching varying from 6.7-9.2% (Camazine et al., 1999) to 11-22% (Seeley and Buhrman, 1999). However Visscher and Camazine (1999), who removed scouts that had been observed at multiple nest boxes, showed that the removal of switching scouts had no effect on the speed of the decision-making process. Thus the importance of switching has been largely ignored in the nest-site selection process of *A. mellifera*. I feel that the role of switching in the decision making process needs further consideration. First, Visscher and Camazine (1999) did not provide their swarms nest boxes of variable quality. While it has been shown that removing switchers does not slow down the decision-making process, it is possible that switching allegiance may improve the ability of swarms to select higher quality sites. Second, although Visscher and Camazine (1999) removed scouts which they observed at both nest boxes offered, they did not control for scouts that switched direction through following dances on the swarm. As mimicking scouts may not visit the locations they have switched their allegiance to, Visscher and Camazine (1999) failed to remove scouts that switched their

Figure 2: Swarm 4 from Chapter 2. A dancing *A. florea* scout (marked light blue thorax, red abdomen) is followed by a number of other scouts. Will her dance convince her sisters to switch their allegiances? If so, will they independently evaluate the location indicated, or simply mimic her dance? Photo by James C Makinson.

dance allegiance after having observed dances on the swarm without visiting the actual nest sites.

A potential way to investigate the role of allegiance switching in the nest site selection process of *A. mellifera* is to present swarms with multiple nest sites of varying quality as in Seeley and Buhrman (2001), marking dancing scouts for the various locations on the swarm and identifying how many and when dancing scouts switch their allegiance. The experiment could then be repeated, this time with the removal of switching scouts on the swarm surface, therefore ensuring that bees that switch the site danced for based on mimicking dances, and those that directly compare sites, are removed. I predict that the number of switching scout bees will be much higher when nest sites vary significantly in their quality, and that the removal of these bees will slow down the decision-making process, impairing the ability of the swarm to rapidly select the best available nesting option.

Auditory signals in honey bees; what makes a scout pipe?

Quorum sensing is an integral aspect of the decision-making process of *A. mellifera*. Once a scout has perceived a quorum of other scout bees at the site she is evaluating she returns to the swarm cluster and starts producing the piping signal (Visscher and Seeley, 2007). Upon perceiving this signal, the inactive bees in the swarm cluster respond by warming up their thoraxes to the 35° necessary to sustain flight (Seeley et al., 2003). Piping was detected but not quantified in the *A. florea* swarms studied in Chapter 2 (Fig. 3). As it seems unlikely that *A. florea* scouts evaluate specific locations at which they have the opportunity to interact with other scouts, it also seems unlikely that the piping signal has the same meaning in *A. florea* as it does in *A. mellifera*. Moreover, there may be no need to warm up flight muscles in tropical species, as ambient temperatures are often high enough to sustain flight without the bees actively increasing their thoracic temperature (Dyer and Seeley, 1987). Furthermore the cues that scout bees use to determine when to pipe are currently unknown. Scout bees could potentially determine when to start piping based on cues obtained on the swarm surface such as observing other scouts dancing for their preferred site. Alternatively scouts may rely on internal stimuli such as their own intrinsic motivation

Figure 3: Swarm 5 from Chapter 2. *A. florea* scout bees appear to pipe in the absence the formation of an external quorum. What cues are scouts using in order to commence piping? Photo by James C Makinson.

or perception of the suitability of a nesting area to determine when to produce the piping signal.

I also observed piping in my *A. dorsata* swarms (Chapter 4, Figs. 2j-l). I found that the number of piping signals per 30s time interval increased over time in concert with the number of actively-dancing scouts, In addition, there seemed to be a high degree of variability in the sounds being produced by the bees, suggesting that perhaps I was hearing a number of different signals. Although I occasionally saw scouts producing the stop signal to dancers, I did not hear any obvious stop signals (Schlegel et al., 2012) on my audio recordings.

Future studies into the significance of the piping signals in open-nesting honey bee species such as *A. florea* and *A. dorsata* are needed to determine under what context the various signals are produced. Tracking individual scout bees throughout the decision-making process while specifically monitoring when individuals commence piping would allow us to tease apart the range of different signals and the cues used to determine when to produce them.

Migration dances; who produces them and what do the bees who perform them know of their future route?

On first inspection, our understanding of the process of migration in *Apis* species seems to be more than adequate. We know that colonies migrate due to changing forage conditions (Fig. 4) (Hepburn and Radloff, 2011; Oldroyd and Wongsiri, 2006; Schneider and McNally, 1992) and that migration is preceded weeks beforehand by a reduction in foraging rate, the consumption of colony stores and the cessation of brood production (Schneider and McNally, 1992). The dance behaviour leading up to the departure of migrating colonies has also been described, with non-figure 8 migration dances indicating the general direction the swarm will travel (Duangphakdee et al., 2012; Dyer, 2002; Dyer and Seeley, 1994; Koeniger and Koeniger, 1980; Robinson, 2012).

Figure 4: Five out of the six colonies in this *A. dorsata* nest aggregation have migrated, leaving behind combs empty of both stores and brood. How do scout bees decide to become migration dancers? What, if any, first-hand knowledge do they have of the quality of sites in the general location indicated by their dances? Photo by James C Makinson.

What remains to be determined is the identity of these migration dancing bees. Are they experienced scouts who have been prompted into migration dance activity after experiencing a reduction of available forage in the field and/or reduction of colony stores?

Do the migration dancers indicate patches in the environment which they have directly experienced in the past, or do they simply dance for a predetermined direction that they have no first-hand experience of? If migration dancing scouts indicate locations which they have some prior knowledge of, can these dancers also switch directional allegiance in a fashion similar to that described in the three swarms in Chapter 4? With the advent of modern tracking programs and marking techniques (e.g fiducial markers and RFID tags) it is now possible to track individuals within the colony for the entire duration of their life span, allowing in depth information on the social interactions of individual bees, as well as time spent away from the colony or assessing stores. It is my hope to turn these technologies towards the question of migration dancing in the near future.

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