

## ORIGINAL RESEARCH ARTICLE

### Azimuth-dependent waggle dances; flight and foraging activities of the red dwarf honeybee, *Apis florea* Fabricius (1787)

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Waggle dances are a fundamental form of communication in honeybees. The patterns of a waggle dance contain both distance and directional information. Nevertheless, the dance varies depending on the context in which it is performed; absconding, swarming, or foraging. This study is an extension of the study by Duangphakdee, Radloff, Pirk, and Hepburn (2009), who investigated whether the sun's azimuth (altitude angle of the sun) affected *Apis florea* F. absconding waggle dances and what effect this had on colony decision-making and behavior. In this study, we add flight and foraging activities to the absconding data from Duangphakdee, Radloff, Pirk, and Hepburn (2009) and tested what effects, if any, the altitude angle had on other behavior and activities both at colony and individual levels. We report the number of waggle dances performed per unit time by *A. florea* foragers from 07:00 to 17:00 h. The mean frequency distribution of the number of foragers dancing showed a clear-cut trough between 12:00 and 13:00 h. The angular deviation in the run portion of the waggle dances increased significantly by 7° between 12:00 and 13:00 h relative to dance angles recorded prior to or post the noon period. We suggest that the imprecision of forager waggle dances, for an hour around noon, is caused by the honeybees' difficulty in determining the location of the sun's azimuth, as was shown by Duangphakdee, Radloff, Pirk, and Hepburn (2009) in *A. florea* scout dances over the noon period. Colony-based decision-making relies heavily upon the precision of waggle dances, especially when a major event such as absconding or swarming occurs; based on accurate dance information, the colony prepares to move its stores and synchronize its relocation as a cohesive unit to the new nest site. However, decision-making by foragers on an individual level was not negatively affected by the inaccuracy of the waggle dances performed during the noon period, nor did it affect the number of foragers in the field.

#### La danza oscilante dependiente de acimut; actividades de vuelo y de alimentación de la abeja melífera enana roja, *Apis florea* Fabricius (1787)

Las danzas oscilantes son una forma fundamental de comunicación en las abejas melíferas. Los patrones de la danza de la abeja contienen tanto la distancia como la información direccional. Sin embargo la danza varía en función del contexto en el que se lleva a cabo; bien sea una fuga, una enjambrazón o para pecoreo. Este estudio es una extensión del estudio de Duangphakdee, Radloff, Pirk, and Hepburn (2009), que investigaron si el acimut del sol (ángulo de altitud del sol) afectada la danza oscilante para la fuga de *Apis florea* F. y el efecto que esto tuvo en la toma de decisiones de la colonia y el comportamiento. En este estudio añadimos las actividades de vuelo y pecoreo a los datos fuga de Puangpakdee et al. (2009) y probamos qué efectos, si los hay, tenía el ángulo de altitud sobre otros comportamientos y actividades tanto al nivel colonia como individual. Se presenta el número de danzas oscilantes realizadas por unidad de tiempo por pecoreadoras de *A. florea* de 07: 00–17: 00 h. La distribución de frecuencia media del número de pecoreadoras danzando mostró un claro corte entre las 12:00 h y la 13:00 h. La desviación angular en la parte de ejecución de las danzas oscilantes aumentó significativamente 7° entre 12: 00–13: 00 h en relación a los ángulos grabados antes o alrededor del período del mediodía. Sugerimos que la imprecisión de las danzas oscilantes de pecoreo, durante una hora alrededor del mediodía, es causada por la dificultad de las abejas de la miel en la determinación de la ubicación de acimut del sol, como se demostró por Duangphakdee, Radloff, Pirk, and Hepburn (2009) en las danzas de exploración de *A. florea* en el período del mediodía. La toma de decisiones basada en la colonia depende en gran medida de la precisión de las danzas oscilantes, sobre todo cuando se produce un evento importante, como una fuga o la enjambrazón; basado en una información precisa de danza, la colonia se prepara para mover sus reservas y sincronizar su reubicación como una unidad cohesiva para el nuevo sitio para anidar. Sin embargo, la decisión realizada por pecoreadoras al nivel individual no se vio afectada negativamente por la inexactitud de las danzas oscilantes realizadas durante el período del mediodía, ni afectó al número de pecoreadoras en el campo.

**Keywords:** honeybee; *Apis florea*; waggle dance; altitude angle; azimuth; foraging

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## Introduction

### Honeybee communication through dance language

Abscending and swarming events are ubiquitous among colonies of African and Asian honeybee species (Hepburn, 2011; Hepburn & Radloff, 1998). One of the most important decisions to be made by a honeybee colony to ensure its survival and reproductive success is locating a new nest site, in particular, during absconding events. Nest site selection is usually prompted by some initial stimulation (diminishing resources, habitat changes, microclimatic changes, disturbances to, or growth of the colony), after which scout bees will be tasked to find suitable new nest sites (Duangphakdee, Hepburn, & Tautz, 2011). Honeybee scouts and foragers communicate information to the rest of the colony through dance language, as described in the work by von Frisch (1923, 1949, 1967), to ensure continued growth and succession of the colony.

In von Frisch's studies on the European subspecies of the Western honeybee *Apis mellifera* L. both distance and direction information is encoded in the waggle dance. Along the straight section of the dance, known as the run, the dancer will buzz its wings and its abdomen will vibrate. This is known as the 'waggle.' The angle of the axis of this waggle relative to the vertical represents the angle of the goal to the sun's azimuth; this component of the dance encodes the directional information. The duration of the waggle is positively correlated to the distance component; the longer the waggle, the further away the goal is (von Frisch, 1967).

Although the waggle dance plays an extremely important role in finding resources, it is only one aspect of the many signals, including visual and olfactory cues, which honeybees use to detect a goal (Tautz, 2008). A number of behavioral adaptations are made at both a colony and an individual level in exploiting abundant floral resources over the vast area around the nest have been extensively studied (Dyer & Seeley, 1991; Seeley, 1985; Seeley & Levien, 1987; Tautz, 2008; von Frisch, 1967).

### Dance area and plane

Although some of the Asian honeybee species differ to *A. mellifera* in the location of their dance area, and sometimes the plane on which they perform, this is largely limited by the structure of their nest (Tautz, 1996). The Asian cavity-nesting honeybees *Apis cerana* F. dance on the vertical plane of their combs near the entrance. The structure of the giant honeybee *Apis dorsata* F. nest does not provide any flat, horizontal area on the comb on which to dance, and the bees are forced to dance on a vertical plane atop the curtain of bees at the mouth area of the comb (Dyer & Seeley, 1991; Morse & Laigo, 1969). As with *A. mellifera*, both *A. cerana* and *A. dorsata* do not point directly to the goal, but use the sun's azimuth (also known as the altitude angle or 'solar

elevation angle') which describes the position and height of the sun in the sky to locate the objective (Lindauer, 1956, 1957a, 1957b). Therefore, *A. cerana*, *A. dorsata*, and *A. mellifera* compensate by modifying their waggle dances with the changing position of the sun (Duangphakdee et al., 2011).

The dwarf honeybees, *Apis andreniformis* Smith and *Apis florea* F., dance on the horizontal plane along the relatively flat surface of the crown of the comb. The dancer indicates directly toward the goal without having to refer to gravity, as hived or cavity-nesting species do. Whatever obstructions and disruptions are put in the path of *A. florea* waggle dancers, they will normally continue to dance on a horizontal plane. Scout bees returning with information as to the location of a nest site before absconding tend to dance on the dense side of the crown, whereas foraging dancers perform along the top of the crown nearest in distance to where the resource is indicated (Koeniger, Koeniger, Punchedhewa, Fabritius, & Fabritius, 1982; Duangphakdee personal observation). *Apis florea* do not adapt their dances according to the changing azimuth, and always orientate directly toward their objective (Dyer, 1985).

### Role of the sun's azimuth on orientation and flight

Although the dance the scout bees perform upon their return to the colony has been described as waggle dance (Lindauer, 1955), it has been reported that some honeybee species do not complete the full cycle of the waggle dance and just perform round dances; Koeniger and Koeniger (1980) on *A. dorsata*, Sasaki (1991) on *A. cerana*, and Oldroyd, Gloag, Even, Wattanachaiyingcharoen, and Beekman (2008) on *A. florea* and *A. andreniformis*. These dances are encoded with information on the direction of possible new nest sites (Dyer & Seeley, 1991, 1994; Koeniger & Koeniger, 1980; Oldroyd & Wongsiri, 2006). Nevertheless, honeybees include references to conspicuous structural objects and landmarks for flight orientation in their dances (von Frisch, 1949, 1967; Tautz, 2008). The sun's position is encoded in *A. mellifera* waggle dances as a mobile reference point which assists newly recruited foragers to navigate the goal (von Frisch, 1967). Bees are also able to find their goal in overcast conditions by estimating the position of the sun by perceiving the plane of vibration of the polarized sky (von Frisch, 1967; Tautz, 2008). It has been shown in *A. mellifera* colonies that the slightest error caused by individuals misinterpreting the relative position of the sun near its zenith resulted in large orientation errors in waggle dances and real-time lapses (Gardner, 2007; Gardner, Seeley, & Calderone, 2007; New & New, 1962). Therefore, recruited scouts and foragers need to be able to read the angle of the waggle run relative to gravity and translate this directional information to locate the goal using the sun as a compass. Duangphakdee, Radloff, Pirk, and Hepburn (2009) showed the changing position of the sun, relative

to the date and time of day greatly affected *A. florea* absconding waggle dances.

As the sun's azimuth moves, *A. cerana*, *A. dorsata*, and *A. mellifera* dancers compensate to incorporate these changes, whereas *A. florea* do not alter their dances and always indicate directly toward the goal (Duangphakdee et al., 2011). Dyer (1985) suggests that *A. florea* differ to other *Apis* species in that they seem to have a more refined information processing system (Duangphakdee et al., 2011). The sun and a clear, cloudless sky provide actual references for *A. florea* waggle dancers, and have been reported to incorporate symbolic landmark information in their dances (Dyer, 1985). Koeniger et al. (1982) showed the importance of the sun to the orientation of *A. florea* dances; when the sun was blocked off from a colony, dances became disorientated. Using a hand-held mirror as a "surrogate" sun, the light was reflected on the bees, which they then used as a point of reference. The authors also showed that the bees changed the angle at which they danced whenever the angle of the mirror was adjusted (Koeniger et al., 1982).

#### ***Apis florea* absconding and foraging dances**

In the study by Duangphakdee et al. (2009), the results showed a bimodal frequency distribution in relation to the noontime lull throughout the year for absconding events. They showed *A. florea* colonies avoided absconding between 12:00 and 13:00 h; their preferred altitude angle of the sun for departure was between 55° and 65° and there was no linear correspondence or relationship between time and sun angle. The authors also showed that the mean frequency distribution of dances declined over the noontime lull and the angular accuracy of the direction component declined precipitously. Duangphakdee et al. (2009) also reported that temperatures over the noonday lull were not associated to the highest temperatures over the day, and absconding in *A. florea* was not inhibited by high temperatures as seven of the eight absconding events occurred at higher temperatures than those reached over the corresponding noonday lull.

Lindauer (1956) reported that forager waggle dances became disorientated when the sun was within  $\pm 3^\circ$  of its zenith. New and New (1962) reported similar findings for waggle dances at tropical latitudes similar to that of Chom Beung, of  $\pm 3^\circ$  to  $4^\circ$  (Duangphakdee et al., 2009). Indeed, noon lulls in *Apis* foraging have been well documented by Lindauer (1961), Hepburn and Magnuson (1988), Crane (1990), Hepburn and Radloff (1998), and Gardner (2007). Beekman, Gloag, Even, Watanachaiyingchareon, and Oldroyd (2008) suggest that in some honeybee species but not others, greater precision is probably required in accurately reporting the angle of the sun for nest site selection purposes than for foraging. The object sought in foraging is patch

directed, while in swarming or absconding, the object is site specific (Ribbands, 1953; Seeley & Morse, 1978).

Successful absconding, however, ultimately requires the integration and synchronization of thousands of honeybees so the entire colony can move as a cohesive unit, promptly and accurately to the new nest site. An average-sized *A. florea* colony contains between 5000 and 7000 individuals; a large colony can have up to as many as 10,000 bees. During the decision-making process of nest site selection, scout bees may have difficulty in accurately determining the sun's azimuth at noon, resulting in defective navigational directions. The precision and accuracy of the scouts waggle dance in reporting the angle of the sun is probably crucial for the colony to abscond successfully. Dancing activities in *A. florea* colonies decrease over the noon hour; colonies usually relocate to their new nest sites within the morning or afternoon window period, either before or after noon (Duangphakdee et al., 2009).

The imprecision of *A. mellifera* waggle dances are well studied (Lindauer, 1956; New & New, 1962). In this study, we wanted to assess whether *A. florea* waggle dances, performed in a different area of the nest and along a horizontal plane, would differ considerably in accuracy to those performed by *A. mellifera*. Prior studies by Koeniger et al. (1982) and Beekman et al. (2008) showed the importance the sun's azimuth plays in *A. florea* dance communication, and Duangphakdee et al. (2009) showed a decrease in the number of absconding dances over the noon period. We also wanted to test whether the sun's position in the sky, at different times of the day, and the lull over the noon period would have any effect on *A. florea* flight and foraging activities. Unlike absconding, which is based on group decision-making, foraging choices are made by individuals acting alone and not in concert. Therefore, the degree of precision is more important for the survival of the colony than in the later where it only affects an individual forager. Moreover, we also wanted to determine whether scout waggle dances, advertising new nest site selection, would differ to forager waggle dances which indicate resources for the colony.

#### **Materials and methods**

Eight *A. florea* colonies were set up in an apiary at the Ratchaburi Campus, King Mongkut's University of Technology Thonburi, Chom Bueng, Thailand (13.37 N, 99.35E, altitude 86 m). Before the commencement of the experiments, an area measuring 1 km in radius around the apiary was searched for feral *A. florea* colonies. Throughout the study periods, feral colonies were removed and relocated to ensure that all foragers originated from the experimental colonies. During the time these experiments were conducted, the surrounding vegetation comprised a number of small trees and dense shrubs. The main foraging plants, within the 1 km radius

of the apiary, were identified substantiating that the dances recorded indicated food sources already known to the foragers.

Two large plantings of cultivated bee flora, the chain-of-love/coral vine, *Antigonon leptopus* Hook. and Arn. (Polygonaceae: Antigonon) (95 m<sup>2</sup>), and yellow cosmos, *Cosmos sulphureus* Cavanilles (Asteraceae: Cosmos) (250 m<sup>2</sup>), were within flying distance of the apiary. These plants are regularly grown as nectar (*A. leptopus*) and nectar and pollen (*C. sulphureus*) honeybee resources at the Ratchaburi Campus of King Mongkut's University of Technology Thonburi, Chom Bueng.

The colonies were left to settle for more than a month. Observations on five of the colonies were made between July 2009 and March 2010 and on the remaining three colonies from December 2013 to March 2014.

## Measurements

### Dance performances

Twenty *A. florea* foragers from each of the eight colonies were individually marked and video recordings made of their waggle dances on the nests from 07:00 to 17:00 h. These video recordings were replayed at 0.5 normal speed; the angles indicated in the waggle dances were measured using a protractor superimposed on a computer screen and recorded at hourly intervals from 10:00 to 14:00 h. The number of dancers performing was counted over 1 min, at 15 min intervals.

It was necessary to clearly distinguish between waggle dances encoded with a direction component and those without this component. In *A. florea*, the direction component is evident in the straight line or "run" of the dance. This straight line points in the exact direction the forager wants to indicate (the angle deviation of each cycle of the dance is less than 90°). In dances without a direction component, the bees alter the direction of the straight line component between different circuits apparently at random (the angle deviation of each cycle of the dance is more than 90°).

### Foraging activities

Observations of flight activities, the number of forager bees leaving from and returning to the colonies were recorded from 06:00 to 17:00 h. Observations of honeybee foraging activity were recorded from the areas planted to *A. leptopus* and *C. sulphureus*. 5 1 m<sup>2</sup> quadrates of each plant species were sampled and the number of foragers counted for 1 min, at 15 min intervals, from 07:00 to 17:00 h. Quadrates were randomly selected for each observation interval. The azimuth data were calculated using the online software "Sun angle" (Gronbeck, 2005). The time was local clock time based on Coordinated Universal Time (UTC + 7 h) and not solar time.

## Statistical analyses

Analyses for heterogeneity using Chi-square tests (Greenacre, 1988; Sokal & Rohlf, 1995) were performed to check whether there were differences in the numbers of directional (straight run, angle deviation <90°) and non-directional (direction of straight run randomly altered, angle deviation >90°) components of the dances. *Apis florea* honeybees from the experimental colonies ( $n = 8$ ) were observed over four time periods: 10:00–11:00 h; 11:00–12:00 h; 12:00–13:00 h, and 13:00–14:00 h. Statistical methods for circular distributions were used to calculate the mean angles indicated by the waggle dances over the four time periods (Zar, 2010). The angular accuracy of the dances was determined by the mean angular deviation of the waggle run angles, defined as  $s = (180^\circ/\sqrt{2})(1 - r)$ , where  $r$  is the measure of the concentration of angles (Zar, 2010). All tests were performed using Statistica 12 software (StatSoft, 2014).

## Results

### Dance performances

There was a bimodal pattern in the distribution of waggle dances for absconding and foraging, with a pronounced lull at noon (12:00–13:00 h) (Figure 1). Out of 152 waggle dances observed between 10:00 and 11:00 h, 132 had an evident direction component, and 20 did not. Of 166 dances observed between the time period 11:00–12:00 h, 136 dances clearly had a direction component, and 30 did not. Between 12:00 and 13:00 h, only 76 of 156 dances had a direction component, while 80 were non-directional. Of the 152 dances between 13:00 and 14:00 h, 134 had a direction component, and 18 did not (Table 1). The distribution of the directional and non-directional components in the waggle dances observed over the four time periods differed significantly (Heterogeneity  $G$ -test:  $\chi^2_3 = 64.8$ ,  $p < 0.0001$ ). Individual Chi-squared statistical analyses were conducted for each of the time periods, the prediction being that an equal number of directional and non-directional dances would occur within each period. The accuracy of the angle component of the waggle dances of foraging over the noon hour was significantly different to the other three time periods (Figure 2). The mean angular deviations of angle accuracy were: 10:00–11:00 h ( $0.46^\circ \pm 0.57^\circ$ ); 11:00–12:00 h ( $2.14^\circ \pm 6.11^\circ$ ), and 13:00–14:00 h ( $1.15^\circ \pm 3.78^\circ$ ), all significantly lower, and therefore more precise, than the noon period 12:00–13:00 h ( $9.21^\circ \pm 11.04^\circ$ ) ( $F_{3,474} = 41.4$ ,  $p < 0.0001$ ). There was no significant difference in mean angular deviation between absconding and foraging colonies during 13:00–14:00 ( $t = 0.08$ , 128  $df$ ,  $p = 0.9341$ ). However, the accuracy observed over noon time periods for absconding and foraging colonies was significantly different ( $t = 2.51$ , 72  $df$ ,  $p = 0.0144$ , Table 2).

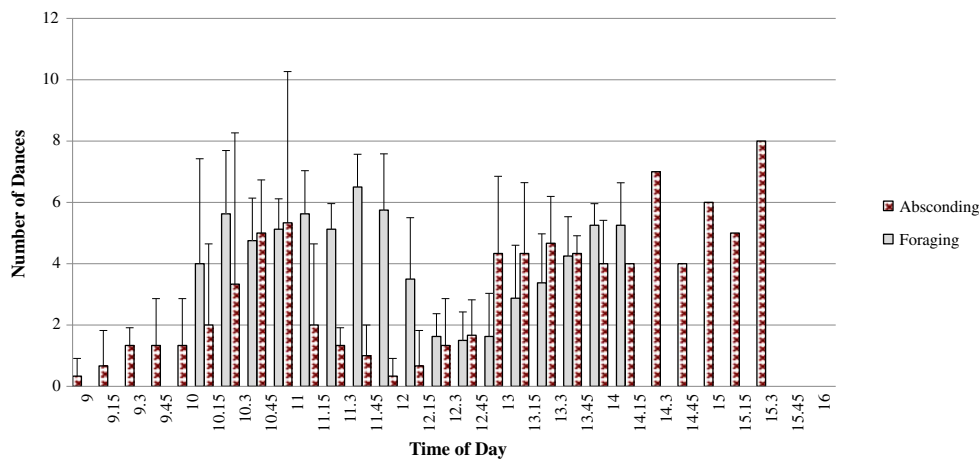


Figure 1. The mean frequency distributions of the number of *Apis florea* waggle dances indicating new nest sites and forage resources. Abscending data collected from colonies ( $n = 3$ ) (from Duangphakdee et al., 2009). Foraging data collected at colonies ( $n = 8$ ).

Table 1. The number of directional and non-directional components in the waggle dances of foraging, mean dance angles, and angular deviations observed over four time periods ( $n = 8$  colonies).

Time	Waggle dances		<sup>2</sup>	df	p-value	Mean Angle	Angular Dev.
	Directional	Non-directional					
10:00–11:00 h	132	20	82.5	1	<0.0001	63.0°	0.46°
11:00–12:00 h	136	30	67.7	1	<0.0001	76.6°	2.14°
12:00–13:00 h	76	80	0.102	1	0.7488	69.4°	9.21°
13:00–14:00 h	134	18	88.5	1	<0.0001	63.1°	1.15°
Heterogeneity G			64.8	3	<0.0001		

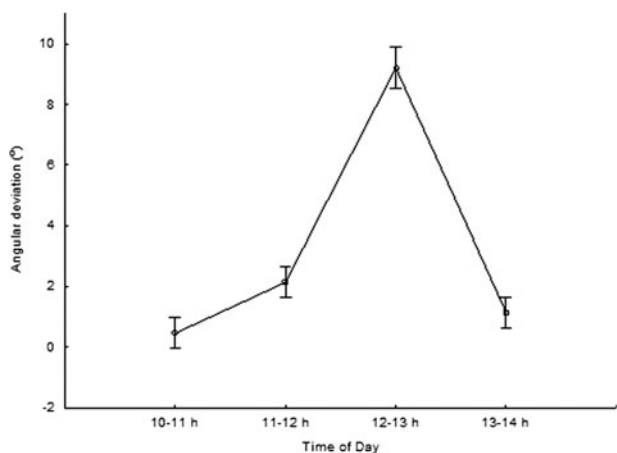


Figure 2. The precision of *Apis florea* honeybee dances in experimental colonies ( $n = 8$ ) indicating food resources over the course of a day; a significant and precipitous increase in deviation of the angle occurred over the noon period.

### Foraging activities

The *A. florea* colonies became active around 06:15 h, with foragers returning approximately an hour later (Figure 3). Flight activity peaked between 08:30 and 10:00 h after which the bees continued foraging but at a lower

rate;  $40.13 \pm 38.48$  individuals per 15 min observation interval period. Although there was a slight decrease in the number of honeybees returning to the colonies during noon, this was not significantly different.

The bees started foraging at the *A. leptopus* site at 07:45 h; the number of foragers gradually increased and reached a peak between 12:15 and 16:00 h (Figure 4). The mean number of bees foraging was  $12.1 \pm 10.9/m^2$  quadrat with a range of 0–39 individuals. At the *C. sulphureus* site, bee activity began later at 08:30 h (Figure 5). The frequency distribution pattern on this plant was that of multiple peaks, the highest of which was between 10:00 and 11:30 h. The mean number of bees foraging was  $2.76 \pm 3.56$  per  $m^2$  quadrat with a range of 0–15 individuals. Far fewer foragers visited the *C. sulphureus* site. *Apis florea* foraging activities on these two species of honeybee flora show no correlation to a noon lull ( $p = 0.65$ ).

### Discussion

The total number of *A. florea* foragers dancing significantly declined at noon compared to the morning and afternoon periods. Most of the waggle dances performed at noon contained erroneous information with

Table 2. The mean dance angles and angular deviations (accuracy) observed over two time periods for absconding ( $n = 3$ ) and foraging ( $n = 5$ ) colonies.

	No. waggle dances	Time	Mean angle	Angular deviation
Absconding	24	12:00–13:00 h	107.4°	2.44° ± 2.44°
	41	13:00–14:00 h	109.8°	0.76° ± 1.66°
Foraging	0	12:00–13:00 h	78.6°	6.94° ± 8.59°
	89	13:00–14:00 h	67.3°	0.74° ± 1.29°

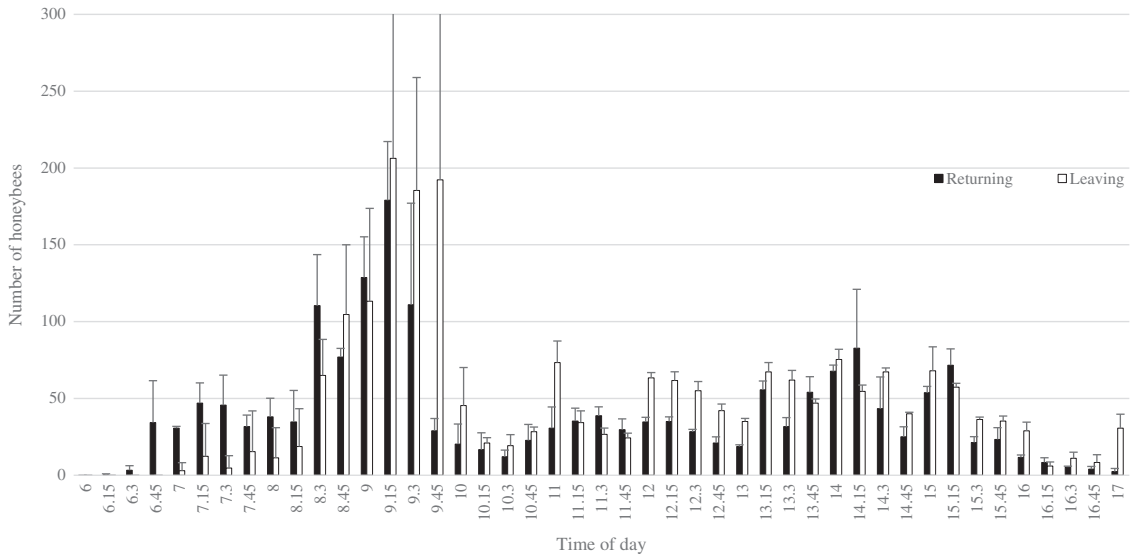


Figure 3. The mean frequency distributions of flight activities; the numbers of *Apis florea* foragers leaving and returning to the nest ( $n = 5$ ).

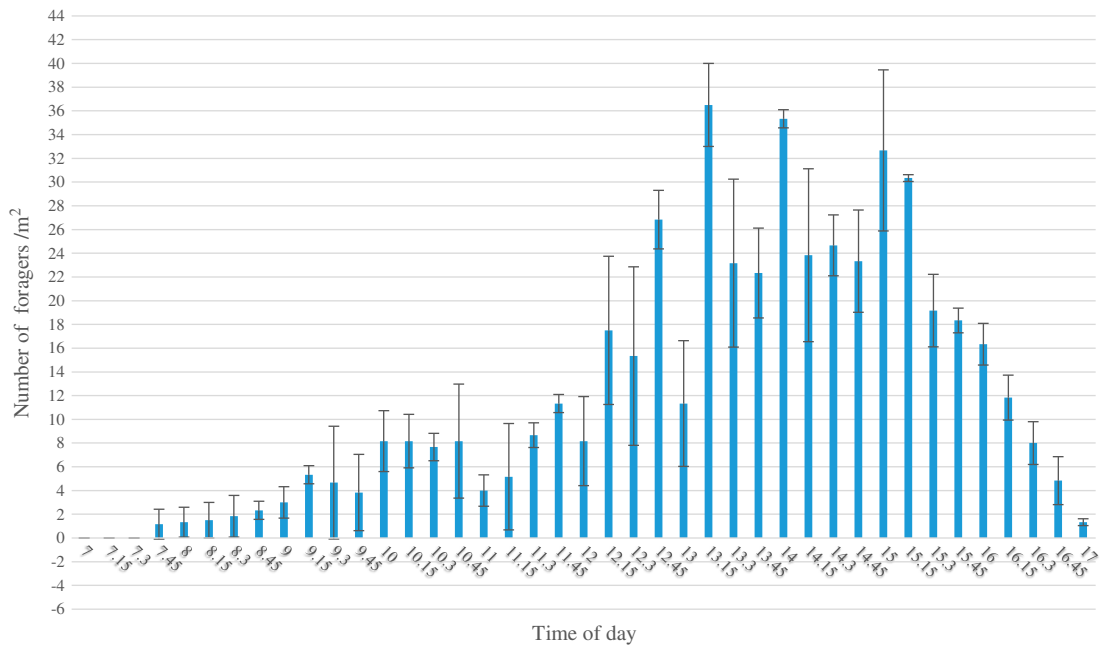


Figure 4. The mean frequency distributions of the numbers of *Apis florea* foragers visiting *Antigonon leptopus* flowers.

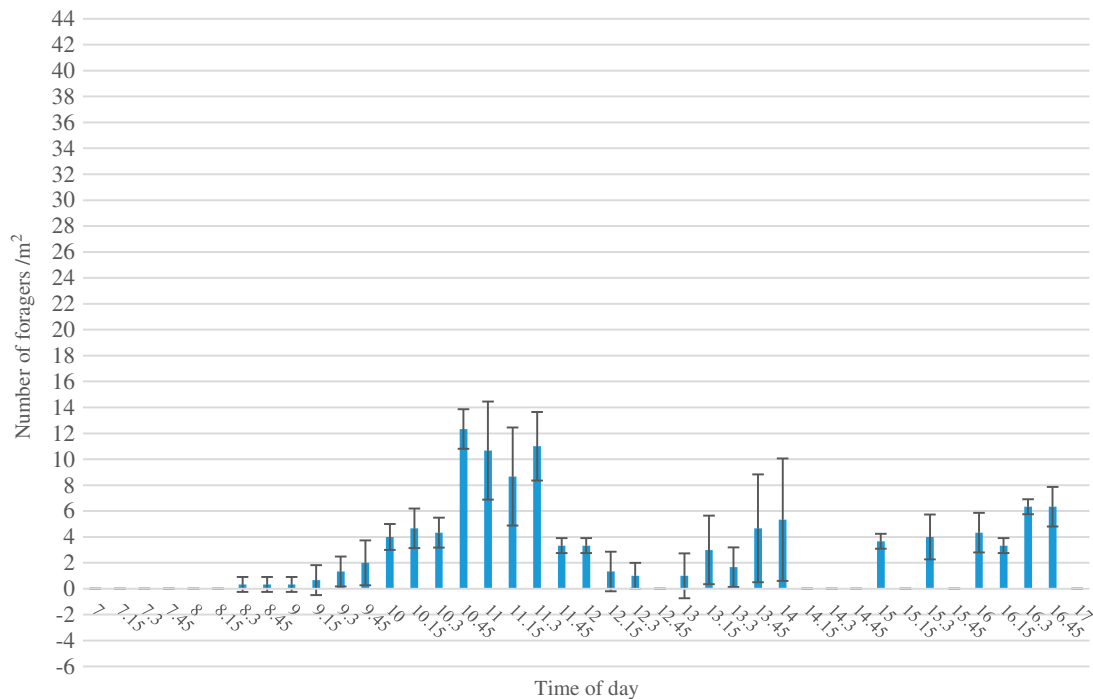


Figure 5. The mean frequency distributions of the numbers of *Apis florea* foragers visiting *Cosmos sulphureus* flowers.

regards to the accuracy of angle measurement, or the direction component was totally absent from the waggle dance. The changing azimuth offers a parsimonious explanation as to why *A. florea* has difficulty in dancing accurately and so avoid flights at noon. The closer the sun approaches its zenith, the more rapidly the azimuth changes at noon, particularly in the tropics, thus making it difficult to accurately determine the azimuth, as even the slightest error in the bees perception of the relative position of the sun will result in intensifying the error.

Even though *A. florea* can learn to use physical landmarks in the vicinity of the nest (Dyer, 1985), the sun remains important for their orientation (Koeniger et al., 1982). The error of reading the sun's azimuth affects other activities of honeybee colonies which require extremely precise information on which decisions are based. The time at which an absconding colony takes off for a new nest site is significantly less frequent at noon (Duangphakdee et al., 2009). *Apis florea* also largely avoid performing waggle dances at noon, both for foraging and finding new nest sites as the dances become disoriented and less accurate. Beekman et al. (2008) showed that *A. florea* workers dance with the same imprecision irrespective of whether it is at a colony level, as for seeking new nest sites, or at an individual level as in foraging. However, we show that at a colony level when dancing for new nest sites, the imprecision is significantly lower compared to foraging during noon, suggesting a trade-off between imprecision and task. The previous work only compared dances performed between 8:00 and 11:00 h, which might explain why they

did not find any differences in the precision of the dances. Moreover, to this, we add that the level of imprecision in the dance language is exacerbated by the movement of the sun about high noon. Our findings suggest that although the overall flight activities decreased, this was not specific to the noon period. The honeybees were largely active during the morning (08:30–09:45 h), after which the number of bees leaving and returning to the colonies declined.

The results from these experiments show that the flow patterns of flight activities at the colonies reflect a combination of multiple factors, not only the sun's azimuth. Foraging activities at the floral resources were not associated to the azimuth during noon, suggesting that the imprecision has less of an impact and/or can be compensated for by information regarding landmarks. The foraging patterns in this study varied according to types of resources and showed no correlation to noon lulls; this has also been shown in studies by Oldroyd, Rinderer, and Wongsiri (1992), Thapa and Wongsiri (1997), and Wongsiri, Thapa, and Kongpitak (1998).

The process of nest site selection, and consequently absconding, is clearly dependent on the precision of information, timing, and the collective behavior of thousands of individual bees. To prevent possible mistakes being made which could ultimately lead to the demise of the colony, honeybee refrain from communicating and moving over the noon period; preferentially relocating to new nest sites either during the morning or afternoon window periods before or after noon (Duangphakdee et al., 2009). However, the behavioral decisions

made by honeybee foragers collecting nectar or pollen resources are simply those of individuals as they act alone and not in concert. Although waggle dances indicating food sources decreased during noon, this did not affect the overall foraging activity at the honeybee floral resources. This shows a trade-off between the level of precision required in locating a new nest site, and that required for foraging flights around noon. In the latter case, foragers could compensate using landmarks and/or the negative effects of not finding the food source is restricted to the individual, whereas imprecision during absconding affects the whole swarm.

### Disclosure statement

No potential conflict of interest was reported by the authors.

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