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Review Article

Waggle Dances and Azimuthal Windows

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Because the waggle dances of honeybees contain celestial components, modifications of the dances occur with changing celestial moves relative to a honeybee nest. Since the direction of a particular resource is static, the dances must alter to compensate for the sun's passage. The position of the sun is seasonal between the Tropics of Cancer and Capricorn so that turns at the end of waggle runs will vary with season and latitude. The bees are confronted with a new difficulty when the sun closely approaches its zenith because only slight errors in the bees' estimation of the relative positions of the sun and zenith generate very large errors. So, the sun compass loses its usefulness when at its zenith. We review experiments and observations on both foraging and absconding in relation to the azimuth. The honeybees' solution for the paradox of the azimuth includes an azimuthal lull, preferences, and time windows.

1. Foraging and the Azimuth

Navigation in honeybees is a reference system in which vector information is derived from path integration encountered en route to a specific goal [1]. The cavity nesting bees and giant honeybees perform waggle dances only in the vertical mode so that the direction and distance of a target resource are in relation to the position of the sun as a vector relative to gravity. However, the dwarf honeybees, *A. andreniformis* and *A. florea*, perform their waggle dances on a horizontal plane at the top of their nests. They dance directly relative to the sun [2, 3] so that less complex calculations are required. Whatever level of behavioural sophistication the waggle dances may represent, direct measurements now show that the system is not without the noise of statistical scatter and indeed is ameliorated by olfactory and visual cues [4]. The worker bees recruited only by the information from dances are not able to find a highly localized and unscented food sources on their own. To pinpoint those food sources, the experienced foragers provide additional cues to new recruits by circling the food source and scenting it. Similarly, the new recruits which are exposed to dances without a precise indication of the position of the sun can overcome a navigation gap by following the buzzing flight or marked scent of experienced foragers around food source [5].

In any event, because the intricate displays of the waggle dances contain celestial components, it can be expected that modifications of the dances will occur with changing celestial moves relative to a honeybee nest somewhere on earth. Indeed, long ago von Frisch [6, 7] demonstrated that a forager which has located a desirable resource returns to its nest and communicates its distance and direction in the waggle dance. The angle between the direction of the dance and the vertical is equal to the angle between the azimuth (compass direction) of the resource and the azimuth of the sun [6, 7]. Since the direction of a particular resource remains the same, the dances must gradually alter to compensate for the sun's passage if the dances are to work at all.

If the path of the sun lies to the south, the alteration of the direction component of the dance should be anticlockwise, but clockwise to the north. The position of the sun is seasonal, north alternating with south within the Tropics of Cancer so that the axis of the waggle phase will vary with

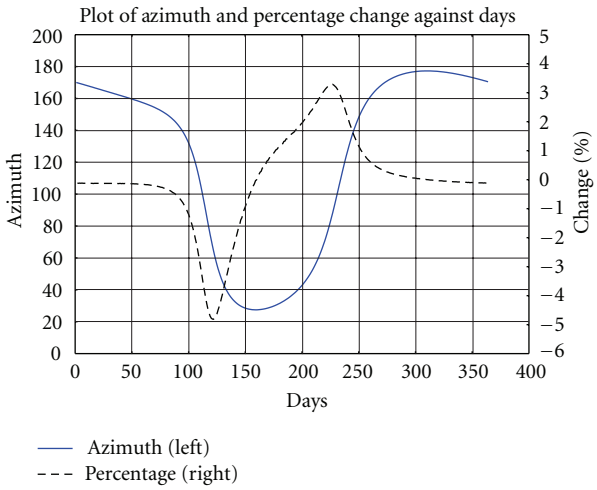

Figure 1: Plot of azimuth and percentage change against days of the year for Chom Bueng, Thailand (13.37N, 99.35E, altitude 86 m). Sharp peaks in the percentage change represent winter and summer solstice. The percentage change is simply the rate of increase or decrease of the azimuth from one day to the next, then multiplied by 100.

both season and latitude [2]. Anticlockwise turns switch over to clockwise as the daily path of the sun moves from south to north of the observer [8, 9]. When the sun closely approaches its zenith at noon the bees are confronted with a new difficulty because only slight errors in the bee's estimation of the relative positions of the sun and zenith generate a very large error estimation of the sun's azimuth.

2. The Azimuth Paradox

The azimuthal position of the sun provides navigation guidance to the honeybees. The particularly precise compass cue is provided by the pattern of polarized light, that is, the pattern of the electric (E−) vectors of light in the sky [10].

In the waggle dance of honeybees, the direction of the target source is indicated by performing a dance on the vertical and so is equal to the angle between the azimuth of a food source and the azimuth of the sun [9]. The dance for the same food source will alter progressively during the day to compensate for the movement of the sun across the sky. As the sun approaches near to the zenith at noonday, the bees would encounter problems in accurately reading its azimuth. In the first of such studies, Lindauer [2] observed in very nearly equatorial Ceylon (= Sri Lanka), that honeybees exhibited disoriented waggle dances when the sun was within ±3° of its zenith and that this was associated with a decline in foraging numbers. Further, von Frisch [11] confirmed that the sun compass loses its usefulness to bees at the zenith of the sun. Lindauer [12] noted that honeybees between the tropics of Cancer and Capricorn experience sun compass failures twice a year at the solstices. This is because when the sun moves through its zenith twice a year, it is impossible to deduce any direction based on the sun's position. Although outgoing bees might memorize landmarks, how could successful foragers communicate the direction during their waggle dances if they fail to integrate precisely the azimuthal position of the sun?

Indeed, Lindauer [12] concluded from his observations that when the sun passes within 2.5° of the zenith in Sri Lanka that the dances are in fact disorientated. Moreover, the sun's azimuth at these times is altering rapidly and at a varying rate [8, 9]. This suggested to D. A. T. New and J. K. New [9] "that bees might solve the problem of communication at small zenith distances of the sun by dancing to sun positions memorized from a few days previously." They tested this idea when the sun was close to the zenith, at three different islands in the Caribbean within the tropics, respectively, at 5°N, 10°N, and 18°N, by further observations of the dances. What they observed was that when the dance angles were plotted against time, there were smooth and symmetrical curves around noon, but of smaller maximum slope than for the changing azimuth. Turns at the end of the waggle phase were often the obverse of the expected. Their final interpretation was the proposal of two possible mechanisms of control: (1) a mechanism using all information about the real azimuth limiting the possible dance angles which become increasingly wide the nearer the sun is to the zenith; (2) an ancillary mechanism based on memory such that angles are proportional to time [9].

This ancillary mechanism arises from Lindauer's observations [12] that dances performed at any time during night indicated approximately the angle between the daytime resource and the azimuth of the sun at the particular time of night. This led to the hypothesis that the bees extrapolate the complete 24 h circle of azimuth change from the part that they are able to see. The problem here is that Lindauer [12] and D. A. T. New and J. K. New [9] invoked Zeitgedächtnis (= finely tuned internal clocks of honeybees [13–15]) to compensate for azimuth change. Zeitgedächtnis enables bees to continuously modify and adjust their behaviour with respect to memory and time [2, 16, 17]; but these clocks can be modulated by external factors [1, 15] of which the sun is particularly important [11]. In reality, time and memory would be extremely hard put to calculate the actual changes in the azimuth on sequential days throughout the year (Figure 1) so that it is inescapable that honeybees require clear readings of the sun for successful communication.

3. Resolving the Paradox

Avoiding times when there would be confusion in taking the sun's angle from the zenith is probably the common cause of noonday lulls in honeybee foraging [18, 19] and is even more acute in cases of swarming or absconding. Koeniger et al. [20] demonstrated that the sun is important in the orientation of dances in *A. florea* because if a "surrogate" sun (a hand-held mirror) is reflected on the bees as a reference point for dancing, changing the angle of the mirror affects the angle at which the bees dance. This shows that the bees can use the surrogate sun in their orientation dances; therefore, if the sun is placed by a mirror at the zenith, it might be possible to increase the bees dancing at noontime. The experiment with the mirror showed that even though changes in solar attitude does not influence the orientation, nonetheless, the accuracy

Table 1: Numbers of directional and nondirectional components in the waggle dances observed over three time periods—10:00 to 11:00 h, 12:00 to 13:00 h, and 13:00 to 14:00 h ($n = 5$ colonies).

	Waggle dances				
Time	Directional	Nondirectional	χ^2-value	*df*	*P*-value
10:00-11:00	87	13	54.8	1	<0.0001
12:00-13:00	51	49	0.04	1	0.8415
13:00-14:00	89	11	60.8	1	<0.0001
Heterogeneity *G*			49.7	2	<0.0001

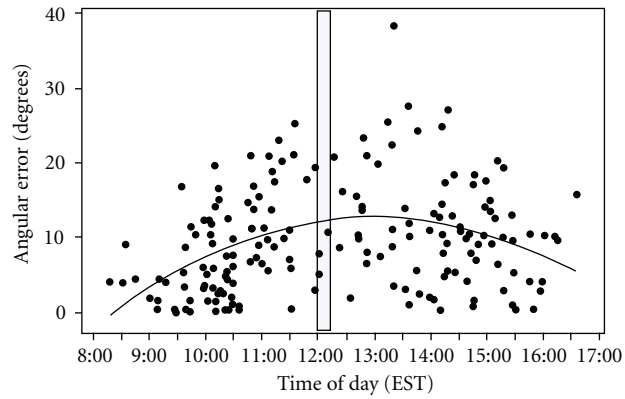

Figure 2: Inaccuracy in the dances of honey bees over the course of a day. The shaded area indicates the time during which the sun is at its highest altitude for the dates that dances were recorded [25].

of the compass reading decreases with the increasing solar elevation [21]. This might effect in the noonday lull of dancers because of errors in compass reading. Interestingly, in comparisons of the precision of dances by *A. florea* for food sources and nest sites, Beekman et al. [22] showed that workers of *A. florea* dance with the same imprecision irrespective of context. Combining the above observations of Koeniger et al. [20], Beekman et al. [22], and Duangphakdee et al. [23], Duangphakdee et al. [24] performed experiments that demonstrate the importance of the position of the sun for individual waggle dancers of *A. florea* foragers at different times of day.

Gardner [25] found changes in accuracy in the dances of honeybees over the course of a day, particularly at noon (Figure 2), and subsequent studies have confirmed this finding. Foragers of five colonies of *A. florea* were observed between July 2009 and March 2010 at Chom Bueng, Thailand (13.37N, 99.35E, altitude 86 m). Waggle dancing was bimodally distributed with a pronounced lull at noontime, 12:00-13:00 h (Figure 3(a)). The angular accuracy of the deviation of all waggle phases from the mean vector (expected waggle phase) of the waggle dances over time was significantly reduced during the noon hour compared with other times (Heterogeneity *G*-test: $\chi^2_2 = 49.7$, $P < 0.0001$; Table 1). Typically in a waggle dance, the dancer runs straight ahead and returns in a semicircle to the starting point then runs again through the previous straight line direction and returns in a semicircle in the opposite direction [26]. The straight part of the run represents the "direction component" of the target, and the axis angle of this waggle phase relative to the vertical represents the angle of the goal in relation to the sun's azimuth. Most of the dances observed between 10:00-11:00 h and between 13:00-14:00 h clearly had a direction component in the waggle phase, while between 12:00 h and 13:00 h about half of the dances had no direction component (Table 1). Moreover, angular accuracy between 10:00-11:00 h and between 13:00-14:00 h was significantly lower than that between 12:00-13:00 h.

The number of foragers dancing significantly declined at noontime compared to the morning or afternoon. Most of the waggle dances performed at noontime consisted of great errors in the accuracy of angle measurement, or a direction component was absent from the waggle dance. Similarly, in *A. mellifera,* waggle dances became disoriented when the sun was within $\pm 3^\circ$ of the zenith [2, 8, 9]. There are several possibilities as to why the red dwarf honeybees may have difficulty in dancing accurately and so avoid noontime. The changing azimuth is a major factor in this case. The closer the sun approaches the zenith, the more rapidly the azimuth changes at noon, particularly in the tropics. This makes it very difficult for the bees to accurately determine the azimuth because very slight errors in perception of the relative positions of the sun and zenith will lead to a very large error in estimating the azimuth of the sun.

The error of reading the sun's azimuth also affects other activities of honeybee colonies. Consequently, between 12:00-13:00 h, the waggle dances become disoriented and less accurate and the bees take off for new nesting sites significantly less frequently at noontime [23]. This is also associated with the fact that the bees largely avoid dancing at noontime both for foraging (Figure 3(a)) and finding new nest sites (Figure 3(b)). Beekman et al. [22] showed that *A. florea* workers dance with the same imprecision irrespective of whether at a colony level seeking new nest sites or at an individual level as in foraging. To this we add that the level of imprecision in the dance language is exacerbated by the movement of the sun about high noon.

4. Absconding and the Azimuth

The movements of honeybee colonies away from the maternal nest come about in two ways: reproductive swarming and absconding/migration. Reproductive swarming is defined as the movement of at least one queen and part of a honeybee colony from the maternal nest to an entirely new site for colony reproduction. On the other hand, migration in its broadest sense is the seasonally predictable movement of many whole colonies of the same population from one region to another while absconding usually refers to abandonment of one or a few colonies away from the maternal nest site to another place, usually caused by local environmental perturbations [19, 27]. Indeed, seasonal migration and absconding are characteristic of *Apis florea*, throughout Asia, and these traits are linked to a combination of resource depletion and adverse microclimatic conditions [28–32].

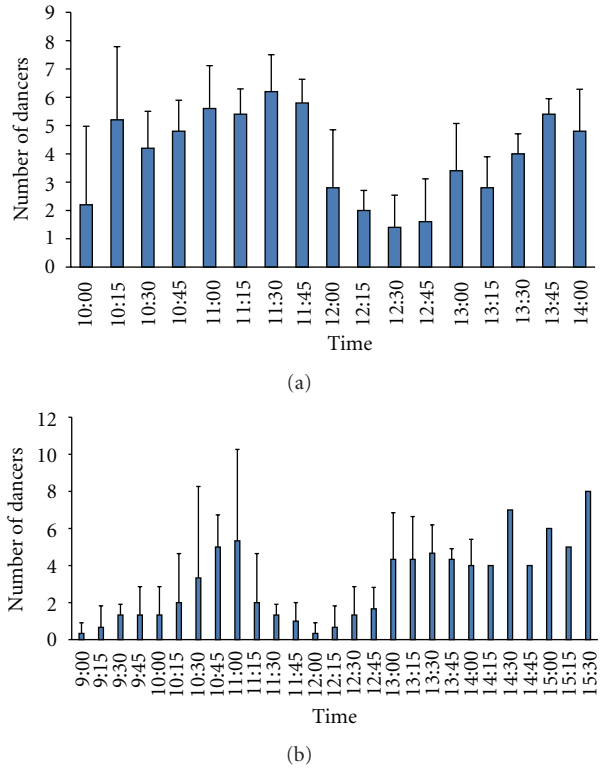

Figure 3: (a) The mean frequency distributions of the numbers of dancing bees for (a) food sources at Chom Bueng, Thailand (13.37N, 99.35E, altitude 86 m). (b) The mean frequency distributions of the numbers of dancing bees for new nest sites [23].

For a honeybee colony to successfully swarm or abscond requires, as in foraging, navigational skills. However in this section we are discussing the integrated behaviour of whole colonies and not just individual foragers. Given the daily rotation of the earth, honeybees have quite a range of solar angles available on each day that they choose to abscond. However, as seen with foraging, the noon hour in the tropics presents honeybee colonies with difficulties leading to a reduction in effective dances which results from inaccurately determining the sun's position, and, as for foraging, slight errors in the perception of the relative position of the sun result in very large orientation errors [8, 9]. Similarly, Gardner [25] reported that the angular accuracy of waggle dances was correlated with the altitude of the sun even at 42°N. Because this becomes especially crucial when a colony decides to find a new nest site, Duangphakdee et al. [24] hypothesized that colonies of *A. florea* defer from absconding during that time of the day when perception errors might result in large orientation errors. Oldroyd et al. [33] suggested that dances of *Apis florea* for nest sites may only indicate a general direction, so that precise information in dances may be unnecessary because scout bees may release Nasonov pheromones to attract flying nestmates to join the cluster. However, accurate information communicated by the dances plays a role in the swarm movement by firstly advertising the target nesting site to the scout recruits, and the accuracy of dancing becomes important because imprecise information will not lead bees to check the right site and will later influence the "voting mechanism" of the whole colony. Secondly, during swarm movements, scout bees release Nasanov pheromone for the guidance for other bees to move to a specified nesting site.

5. Azimuthal Lull

The observations of Duangphakdee et al. [23] were made on 37 separate absconding events by colonies of *A. florea*, between 2007/05/22 and 2009/02/18 at Chom Bueng, Thailand (13.37N, 99.35E, altitude 86 m). The brood comb extending below the crown was cut away and removed to induce absconding. Time was local clock time, *not* solar time. Once the absconding time data was entered into a spreadsheet, the altitude angles at which the bees absconded were calculated as was the sun's zenith [34] for that particular day. Video recordings of each colony were made on the day of absconding from morning until the colony absconded. To assess any possible effects of daily temperature fluctuations on the temporal frequency of dancing, they also obtained hourly ambient temperature values for those days on which the colonies actually absconded.

Duangphakdee et al. [23] found that the frequency distribution of absconding with respect to local clock time was bimodal with a pronounced lull between 12:00 h and 13:00 h. Nearly 90% of absconding occurred between 09:00 h and 12:00 h (32.3%) and between 13:00 h and 16:00 h (57.1%) (Figure 4(a)). The altitude angle (sometimes referred to as the "solar elevation angle") describes how high the sun appears in the sky. The altitude angle is measured between an imaginary line between the observer and the sun and the horizontal plane the observer is standing on, in this case, the apiary colonies at Chom Bueng. The mean (±SD) altitude angle corresponding to the times of absconding between 11:50 h was 56.2 ± 6.3° and between the absconding times between 13:05 h and 14:45 h was 66.1 ± 9.7°. No absconding took place below an altitude angle of 38.7°, nor above an altitude angle of 81.4°. The distribution of the altitude angles averaged 60.0 ± 10.3°. The altitude angles when the sun was at its zenith were determined for each day (Figure 4(b)). The mean angle was 71.7 ± 11.4°, with a range from 55.0° (in November) to 88.3° (in May). The records of absconding time in 35 cases taken from other species (*A. dorsata*, *A. cerana*, *A. Mellifera*, and *A. andreniformis*) also show that only 8.5% absconded at noon (Figure 4(c)).

From Figures 4(a) and 4(c), it can be seen that the bees merely abscond in the early morning and late afternoon, and this can be explained by the bees needing time for navigation to a food source/nest site and it requires about two hours to reach a quorum. For example, if the bees had started dancing between 18:00 and 19:00 h the bees would only have an available time window for absconding from about 21:00 h by which time darkness has fallen.

The mean frequency distribution of the numbers of foragers dancing in three colonies is shown in Figure 3(a) from which it is clear that dancing was bimodally distributed with a pronounced trough between 12:00 h and 13:00 h. Until the time of actual absconding, foragers were advertising

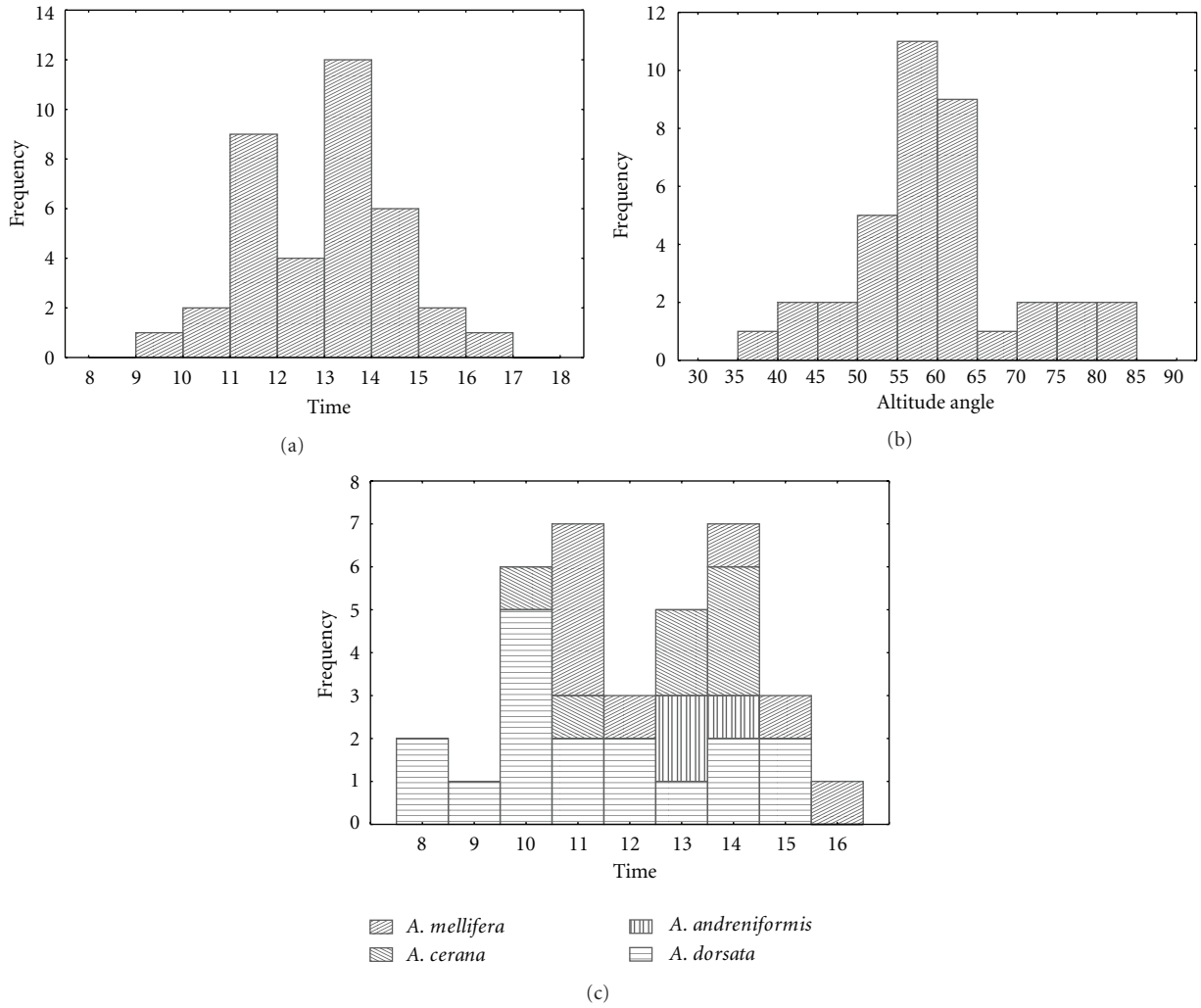

Figure 4: (a) Frequency distribution for local clock time of absconding by the red dwarf honeybee at Chom Bueng, Thailand (13.37N, 99.35E) during 2007–2009 ($n = 37$) [23]. (b) Frequency distribution for absconding by the red dwarf honeybee at Chom Bueng, Thailand (13.37N, 99.35E) with respect to altitude angle of the sun (in degrees) during 2007–2009 ($n = 37$) [23]. (c) Frequency distribution for local clock time of absconding by *A. dorsata* ($n = 3$ [35], $n = 14$ [36]), *A. cerana* ($n = 1$ [37], $n = 4$ Duangphakdee, O. personal observation, $n = 2$ Wongvilas, S. pers. comm.), *A. mellifera* ($n = 6$ [38], $n = 2$ [39]), and *A. andreniformis* ($n = 3$ Wongvilas, S. pers. comm.).

different directions for a new nest site. Turning to angular accuracy of the waggle dance over time, during the morning period 10:00-11:00 h, of 60 observed dances, 51 clearly had a direction component in the waggle dance and 9 did not. Between 12:00 h and 13:00 h, only 17 of 60 dances had a direction component while 43 were nondirectional. Of those dances with a direction component performed between 10:00 h and 11:00 h, the deviation in angle accuracy was 0.24°; however between 12:00 h and 13:00 h, the deviation in angle accuracy was 10.11° [23].

The possibility that both the noonday lull and actual absconding time might be related to particular temperature profiles was considered. However, the temperature data from 07:00 h to 17:00 h during February 2009 at Chom Bueng, Thailand, which is shown in Table 2, indicates that the noonday lull is not associated with the highest temperatures of the day for any of the 7 days shown. Moreover, another indication that the noonday lull is not related to the temperature is given by the fact that absconding was clearly not inhibited by high temperatures because in 7 out of 8 absconding events occurred at temperatures greater than the corresponding noonday lull [23].

6. Azimuthal Preferences

The results on the frequency distributions of absconding by the red dwarf honeybee with respect to both time (Figure 4(a)) and altitude angle of the sun (Figure 4(b)) make it evident that these bees largely avoid flying off between 12:00 h and 13:00 h on the one hand and that their preferred departure angle of the sun is between 55° and 65°, on the other. However, there is no linear correspondence or relationship between time and sun angle (Figure 1). The preferred altitude angles at which the bees absconded were

Table 2: Hourly temperatures at Chom Bueng, Thailand on absconding days for 8 colonies of *Apis florea* and absconding times and ambient temperatures (T) at absconding events.

Date	Colonies	Absconding		Time of day								
		Time	T (°C)	9:00	10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00
2/8/2009	1	11:00	33.45	25.79	30.64	32.51	34.69	36.97	38.82	40.07	38.99	36.6
2/9/2009	2	13:40	37.20	26.01	31.41	33.13	35.32	37.6	39.09	40.19	40.16	37.27
2/12/2009	3	14:36	43.14	21.79	33.32	35.4	37.75	39.9	41.93	43.22	41.39	38.49
2/13/2009	4	13:52	41.26	24.25	32.42	34.86	37.29	39.39	40.85	41.47	42.64	39.26
2/16/2009	5	13:22	42.80	29.4	33.27	34.77	37.63	40.05	42.06	43.64	43.16	39.08
	6	13:46	42.25									
2/17/2009	7	12:25	43.24	27.33	34.06	35.9	38.37	40.91	43.34	44.53	44.59	40.91
2/18/2009	8	12:45	39.14	25.43	33.63	34.82	36.39	38.74	41.07	42.73	43.59	38.7
Average (°C)				25.71	32.68	34.48	36.78	39.08	41.02	42.26	42.07	38.66
SD				2.38	1.25	1.22	1.36	1.40	1.63	1.73	1.99	1.40

on average about ±6° on either side of the sun's zenith for that particular day, despite the fact that the visual acuity of honeybees is about 1° [40]. The mean frequency distribution of the numbers of foragers dancing in three colonies declined in the noontime lull, and likewise, the angular accuracy of the direction component declined precipitously. To understand the rationale of the nest site selection process of honeybees, it extends through group decision making processes at the end of which only one site becomes dominant in further scouting and dancing [38, 39]. A reduction of dancing and the presentation of nonconstructive dances (or disoriented dances) would have greatly disturbed the decision making process.

There are no other similar datasets for swarming, migrating, or absconding in honeybees, but there are three relevant reports with respect to foraging. First there is the report of Lindauer [2] that waggle dances became disoriented when the sun was within ±3° of the zenith. There are other reports by New et al. [8] and D. A. T. New and J. K. New [9] which noted similar difficulties for waggle dancers between ±3° and 4° at tropical latitudes similar to those of Chom Bueng. New et al. [8] and D. A. T. New and J. K. New [9] also observed that when over a few days the sun's position switched from north to south, the bees began to confuse observed sun angle with both clockwise and anticlockwise dances.

There are several possibilities to consider as to why the red dwarf honeybee may avoid the noonday period. Temperature can be excluded because the noonday lull was not associated with the highest daily temperatures (Table 2) and the bees were absconding at higher temperatures than those of the noonday lull. Alternatively, Dyer and Dickinson [41] suggested that celestial compass orientation requires the use of a time-compensated measure of the sun's azimuth, based on an innate template that can be adjusted by learning. Be that as it may, learning takes time that absconding bees lack. The time element becomes critical because the closer the sun passes to the zenith, the more rapidly the azimuth changes at noon particularly in the tropics. Before a colony will swarm or abscond, it goes through a process of reaching a consensus on where to ultimately go [38].

7. Azimuthal Windows

In *Apis mellifera*, a new nest site will be selected through the bee's decision making process. A priori, scouts will go out and find a prospective home site. Different scouts will return to the nest/swarm and communicate the location of her finding by means of waggle dances. Initially, the scouts perform dances for a number of different sites, but eventually they all dance for just one site by "reaching consensus," shortly before whole colony takes off [38, 39]. It is generally assumed that the chosen site is the best of the sites that they have discovered. The nest site selection process of *Apis florea* has been reported to be quite similar to that of *Apis mellifera* [3, 33]. One difference is that nondirectional dances occur significantly more in *Apis florea*. Nevertheless, like *Apis mellifera*, all waggle dances also eventually converge on one site shortly before becoming airborne.

In the case of the red dwarf honeybee, video recordings of absconding dances indicate that consensus takes about 2 h to achieve (Duangphakdee, unpublished observations). No days at Chom Bueng have less than 12 h sunlight, and no days have ambient temperature too low for honeybee flight, yet the red dwarf honeybees only use a time window almost exactly one half of that available to abscond. The hour from 12:00 h to 13:00 h is a definite lull period for *A. florea* (noontime laziness of von Frisch [11]). Given the difficulties of taking an accurate reading of the sun at angles ±6° of the sun's zenith (resulting in a 1 h loss around noon) and the 2 h required to reach consensus, the bees are simply left with two time windows, morning and afternoon, in which to abscond and, indeed some 90% of the red dwarf honeybee colonies do so.

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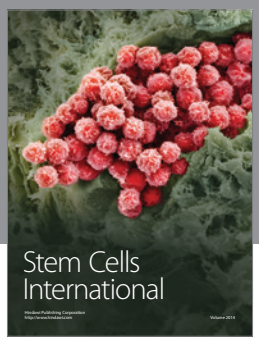

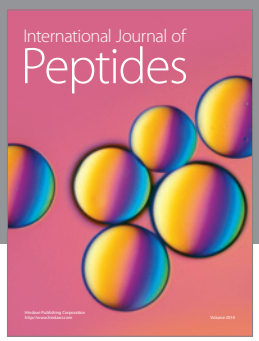

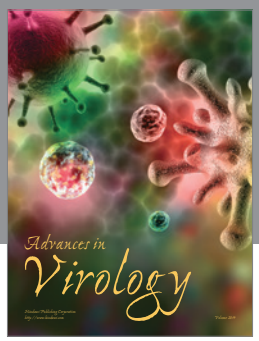

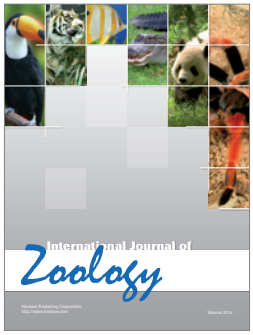

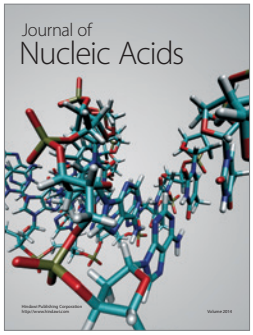

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