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Establishing the Dance Floor: Frame Manipulation Experiments

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Establishing the Dance Floor: Frame Manipulation Experiments

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By

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ABSTRACT

Past studies of honey bee populations, in both natural and laboratory settings have allowed researchers to elucidate the dance language of honey bees within the hive. While the intent and meaning of the waggle dance is thoroughly understood, the area within the hive on which the bees dance is poorly understood. Several factors that may contribute to waggle dancing were studied: substrate, scent and hive entrance proximity. Two separate honey bee colonies were placed in three-frame observation hives. After establishing the dance floor, new experimental conditions were introduced by changing the position of the frames and watching for three days per experimental manipulation. Every experimental manipulation but one was followed by an adjustment period, which lasted at least a couple of days. Dancers eventually resumed dancing close to the hive entrance, though a possible predisposition towards brood and/or capped brood substrates was noted on two occasions. Some bees appeared to follow the old dance floor, but this apparent tendency quickly dissipated. Proximity to hive entrance appears to be the determining factor, and any influence of substrate and scent is secondary.

INTRODUCTION

Apis mellifera, the European honey bee, plays essential roles ecologically, agriculturally and economically worldwide. This well-studied social insect is a key pollinator that forages for pollen and nectar amid patches of flowering plants. Upon returning to the hive, foragers may engage in the waggle dance to advertise a profitable food source. While numerous studies have focused on honey bee chemistry, neurobiology, physiology and genetics (Guo et al., 2013; Toma et al., 2000; Zhu et al., 2014), few have followed the development of the dance floor, the area within the hive where the majority of waggle dances occur.

A first step to better understanding the dance floor will require detailed quantitative and qualitative descriptions. These parameters have been provided in part by several past studies. Seeley and Towne found that 94% of dances occurred within 24 cm of the hive entrance (Seeley and Towne 1992). They also noted that most waggle dances were above the level of the hive entrance. However, the hive entrance typically is found at the bottom of the hive cavity,

eliminating any alternative to dancing above it. The factors used by bees to determine the location of the dance floor within the colony are unknown. Experiments performed by our research group are designed to test several possibilities: there is an innate (i.e. not resulting from the environment) tendency to dance near the hive entrance, an innate tendency to locate the dance floor near the bottom of the hive, and interactions between entrance placement and forager experience.

More recent research has shown that dancing honey bees exude greater quantities of the alkanes, tricosane and pentacosane, as well as the alkenes, Z-(9)-tricosene and Z-(9)-pentacosene (Thom et al. 2007). Emitted from the abdomen, these chemical compounds possibly may act to maintain the dance floor or improve recruitment of foragers. In the study, artificial injections of a solution with three of the compounds increased the number of bees exiting the hive, so the latter hypothesis seems more likely. A newer study by Gilley (2014) suggests that these hydrocarbons may improve recruitment by intensifying waggle dancing in the hive. However, whether the compounds directly correlate to the establishment of a dance floor is currently unknown.

Substrate (the comb: capped honey, nectar, pollen, brood, etc.) may be another factor in a bee choosing where to dance, or in the success level of recruitment. In one study, for example, three times as many foragers were recruited by honey bees waggle dancing on empty combs, compared to bees dancing on capped brood combs (Tautz 1996). The relevance of this finding to dance floor location, however, is unclear. A preference for dancing on empty comb has not been demonstrated.

Tautz and Lindauer (1997) tried to test some of these factors. Using a two-frame observation hive and a queenright colony of 2500 honey bees (*Apis mellifera carnica*), the researchers placed a hive entrance straddling the two frames, coming in from the side parallel to the glass. Over three days, the two frames were exchanged with each other seven times during daylight hours. An initial ten-minute observation period wherein all dances were recorded was followed by a ten-minute period during which the frames where exchanged. During the frame swap, the bees were shaken off the frames, and then all waggle dances were observed for thirty minutes. Waggle dancers consistently followed the old dance floor immediately after a frame swap, but reset the dance floor the next day. The researchers suggested a chemical marker played a role in bringing dancers and dance followers together to specific comb sites.

The frame manipulation experiments in the present study hold many similarities to Tautz and Lindauer (1997); however, there are some significant differences. Tautz and Lindauer conducted their frame swaps during the daylight hours; the frame swaps in this study were conducted at night. They shook bees off the frame, while we moved the frames with minimal disturbance to the bees. They used thirty-minute observation periods to assess the response of the dance floor, while we had four thirty-minute observation periods per day and at least three days of observation after each experimental manipulation. Consequently, our experiments tested for more long-term effects within a day and across days. Finally, Tautz and Lindauer did not keep track of substrate changes across days, and thus could not account for substrate as a potential factor, while we noted the substrate layout each day.

The focus of this study was to determine how honey bees decide where to dance. We had three main hypotheses: (1) waggle dancers will follow the old dance floor (Tautz and Lindauer 1997), (2) dancers will be more attracted to particular substrate type(s), and (3) proximity to the hive entrance will ultimately trump other factors (Seeley and Towne 1992). To test our hypotheses, we conducted frame manipulation experiments in three-frame observation hives. Our findings show that although waggle dancers do indeed follow the old dance floor, this preference dissipates quickly with time. The results support the roles of substrate and hive entrance in establishing a dance floor.

MATERIALS AND METHODS

The hive

Two experiments were carried out with queenright *Apis mellifera ligustica* colonies in three-frame observation hives with the entrance fixed halfway up the right side of the hive so that bees could only enter through one side of the comb. This setup also ensured that the bees had a choice of going up, down or dancing on the frame on which they entered the hive. All three phases of the 2014 experiment had the same queen, colony and hive. Manipulations occurred at night and involved the exchange of two adjacent frames within the hive, except in Phase 2 of the 2014 experiment, in which a frame from outside the hive was inserted into the top frame

position, after the top frame was removed from the hive. The frames were exchanged along with the bees on them.

General observations

The dance floor was mapped via scan-sampling techniques carried out repeatedly over a thirty-minute observation period. Observations were conducted at 11:00, 12:00, 13:00 and 14:00 hours in the dark to prevent bees sensitizing to white light. Red light was used to note and manually record the location of waggle dances. Substrate was recorded after the last waggle dance scan of the day using white light from headlamps. The hive's entrance-side glass was partitioned into five by five centimeter squares to keep track of waggle dances and two and a half by two and a half centimeter squares for substrate. After each manipulation, at least three days of adjustment was allowed, longer in cases where the dance floor still appeared to be in flux. Adobe Illustrator and Microsoft Excel software were used to compile and analyze maps of the dance floor and substrate.

2012 Frame Swap

The first three days of experimental observations were conducted as a control. On the evening of Day 3, the middle and bottom frames of the three-frame hive were exchanged. Dancers were then watched for three more days, and waggle dance and substrate maps were made.

2014 Frame Manipulation Experiment: Phase 1

The dance floor was mapped for three days prior to any experimental manipulations. The middle and bottom frames were swapped at night on Day 3. After three more days of observations, the middle and bottom frames were exchanged in the evening on Day 6. Three more days of waggle dance scans and substrate scans concluded Phase 1.

2014 Frame Manipulation Experiment: Phase 2

The dance floor was mapped for three consecutive days to start Phase 2. At night on Day 3, a frame from outside the hive was inserted into the top frame position, while the top frame was

removed from the hive. The inserted frame contained a capped brood center, along with capped honey and pollen. The new arrangement was kept in place for four days of observations.

2014 Frame Manipulation Experiment: Phase 3

At night on Day 7 of Phase 2, the top and middle frames were swapped and the resultant dance floor was monitored for three days. The middle and bottom frames were exchanged on Day 3 at night, and three days of observations followed. Due to an unexpected shift in dancing, three more days of observation were added. At night on Day 9, the middle and bottom frames were swapped, and the dance floor was monitored for an additional six days to allow time for the dance floor to resolve.

RESULTS

2012 Frame Swap

Our first frame manipulation experiment was a frame swap conducted in 2012 to assess how the bees would react when frame positioning was changed such that a new frame lay adjacent to the hive entrance. During the first three days observations were made to determine the location and shape of the dance floor. The dance floor was highly similar through Days 1-3 (Figure 1), with the bees dancing entirely on the middle frame. Dances were spread mostly over capped brood (orange) in somewhat of an oval formation. Dance numbers were higher towards the hive entrance.

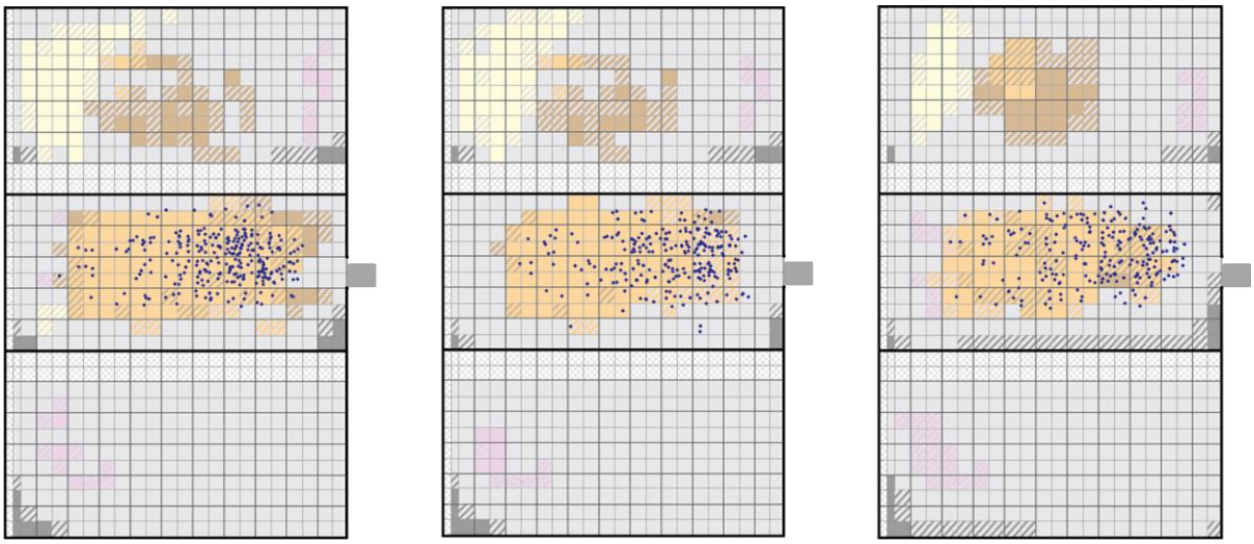

Fig. 1. The first three days of observations for Days 1-3 (left – Day 1; middle – Day 2; right – Day 3) of the 2012 frame swap experiment. The blue circles represent individual dances, while the colored squares represent particular substrates; gray rectangles demarcate hive entrance. Each small square represents a 2.5 by 2.5 cm section of frame.

Substrate throughout all experiments was recorded and substrate maps were created by allocating unique color codes to substrate types (see Figure 2).

Fig. 2. Substrate type by color. Striped cells indicate that at least one third of a 2.5 by 2.5 cm quadrat was occupied by a second kind of substrate.

On the evening of Day 3, the middle and bottom frames were swapped. The dance floor split into three distinct segments, which failed to resolve over the next three days of observations (Figure 3). Dancers on the top frame kept to a small zone in the center, often on or near brood substrate (brown). On the middle frame, dancing occurred predominantly on the right half of the frame, close to the hive entrance. The proportion of dancers on this frame increased substantially from

Day 4 to Days 5 and 6. Initially all dancing on the central frame was at or above the level of the entrance, though by Day 6 roughly a fifth of dances seen on the frame were below the hive entrance (see Figure 3). Dances on the bottom frame were noted mainly on the right side towards the entrance. Most of the dancing here was on capped brood and brood (orange and brown respectively). On both bottom and top frames a moderate decrease in proportionate dancing was observed from Day 4 to Day 6.

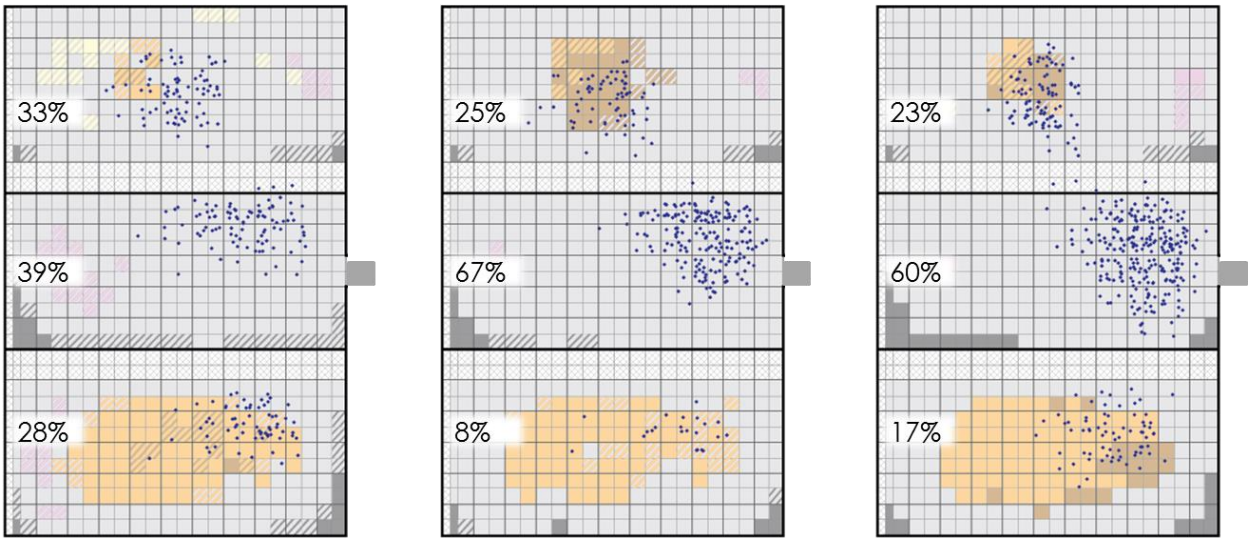

Fig. 3. Days 4-6 (after frame exchange) with dances overlaid over substrate. From left to right – Day 4, Day 5 and Day 6 of 2012. Percentages of each day's dances that occurred are denoted by frame.

2014 Frame Manipulation Experiment: Phase 1

In 2014, we conducted a large three-phase experiment to study the effects of frame manipulations. Phase 1 was a nine-day frame exchange with a similar intent to the 2012 frame swap: to see if some factor in a new frame placement (substrate, scent, etc.) would alter dance behavior. During Days 1-3 foragers danced almost exclusively on the middle frame. The dance floor resembled that of the first three days of the 2012 experiment (see Figures 1 and 4), though here the oval-like spread was nearly at the center of the frame for Days 2 and 3. Most of the dances occurred on capped brood or brood substrate (see Figure 4).

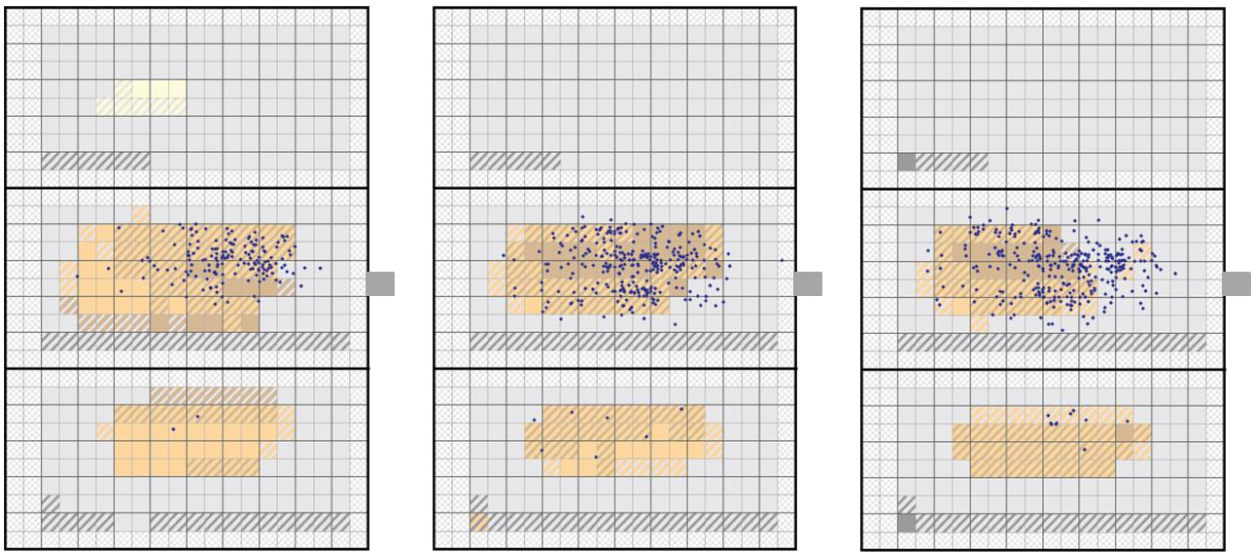

Fig. 4. Days 1-3 of Phase 1 experimental observations.

At night on Day 3, the middle and bottom frames were exchanged. Over the next three days the dance floor was observed. More dances were seen on the bottom frame on the day immediately after the switch (see Figure 5). The two dance floors observed on Day 4 were both towards the top centers of their respective frames. The shape of the dance floor on the middle frame was roughly oval, and there was slightly more dancing. On Day 5 substantially less dances took place on the bottom frame (11% as opposed to 34% the previous day) and those that did were somewhat scattered towards the top of the frame. The dance spread on the middle frames was a loosely slanted oblong in nature on Days 5 and 6, with the majority of dances on the right side of the frame close to the hive entrance (see Figure 5). Only five dances were noted on the bottom frame on Day 6, indicating a clear downward trend in dance numbers on this frame over the three days. Only a few dances occurred on brood or capped brood, mostly because these substrates were almost completely absent.

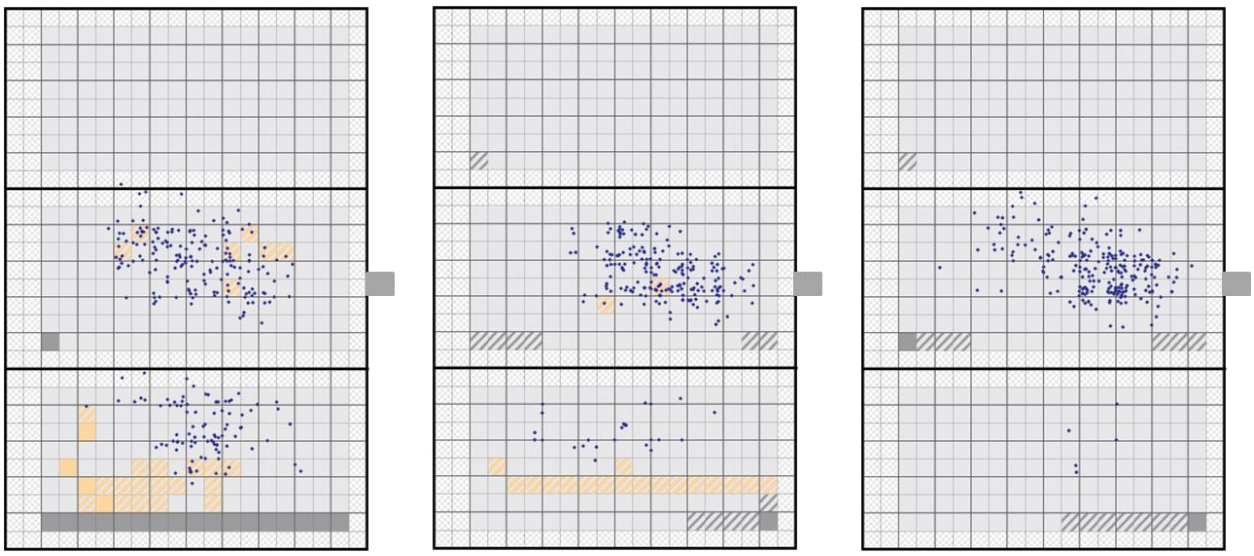

Fig. 5. Waggle dance map overlaid on substrate map for Days 4 (left), 5 (middle) and 6 (right).

The bottom and middle frames were switched once again on Day 6 at night. Observations continued for three more days to conclude Phase 1. The general initial reaction and progression of the dance floor closely resembled Days 4-6 (see Figures 5 and 6). There were two discrete dance floors on Day 7, while a handful of dances were also note on the top frame. The middle frame's dance floor was oval-shaped and contained the majority of the day's dances. The dance floor on the bottom frame clustered near the top of the frame to the right, its center roughly the same horizontal distance from the rightmost edge of the hive as the dance spread of the middle frame. Less dances were noted on the bottom frame on Day 8 (15% compared to 36% for the preceding day), though those that were occupied a very similar location on the frame. Dancing on the middle frame took on a nearly circular shape centered to the right side of the frame near the entrance. On Day 9, dance distribution on the bottom frame was comparable to Day 8. On the middle frame the dance floor expanded to take on an oval shape, with its fairly dense center near the hive entrance, but shifted slightly to the left of Day 8's center. The number of dances was greater for Day 9 than for the preceding day. For these three days as well as the previous three days of the experiment, the substrate remained almost completely empty (gray). This suggests that substrate had no real effect on this part of the experiment (See Figures 5 and 6).

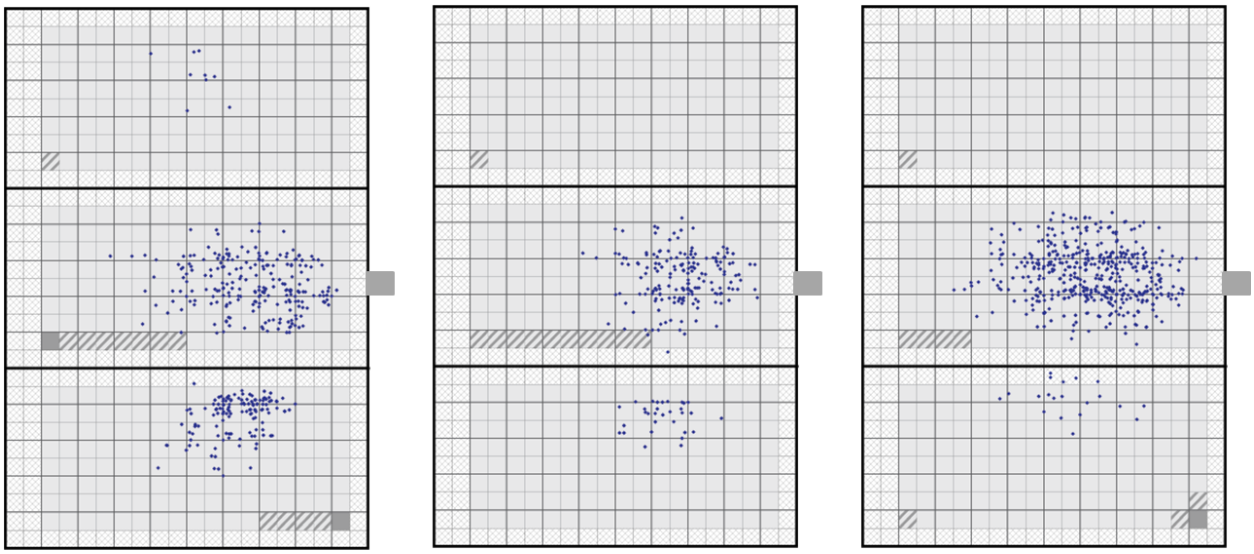

Fig. 6. Waggle dance and substrate maps for Days 7-9 (left to right respectively).

Figure 7 shows the adjustment of the dance floor after the frame swap on Day 6. The proportion of waggle dances on each frame is shown by day and by time of day. On Day 7, about 80% of the first observation period's dances were seen on the bottom frame. This number decreased significantly as the day progressed so that by the last set of observations, roughly 6% of the dance floor occupied the bottom frame with the rest on the middle frame. To a lesser degree, a similar pattern occurred on Day 8 (see Figure 7). The middle frame is closer to hive entrance, so the overall migration of dances within a day was toward the hive entrance. All of this suggests that the dance floor underwent an adjustment period with the most adjusted time being latest in the day and the most adjusted dance floor being the last day of a set of observations.

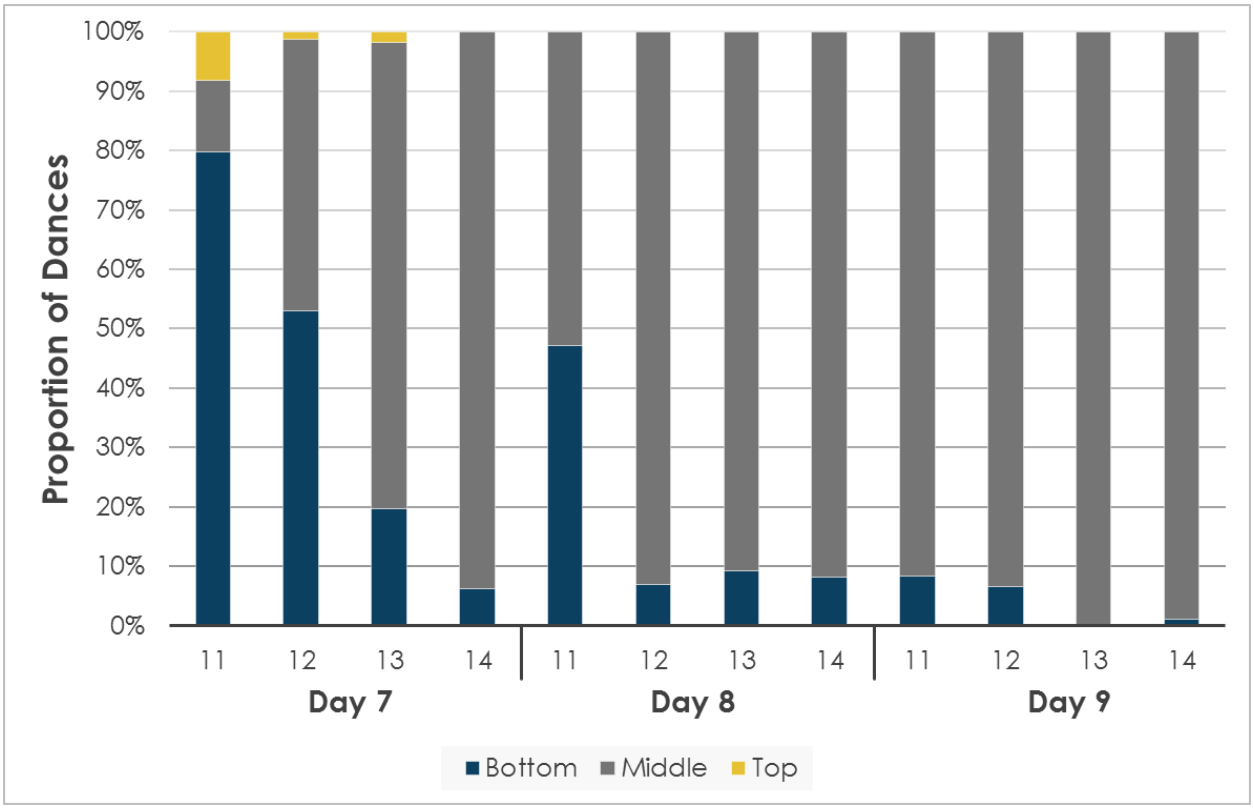

Fig. 7. Adjustment of the dance floor. Dance percentages by frame across days and across observation periods within a day. The numbers on the x-axis reflect the hour; hence 11 = 11:00 hours, 12 = 12:00 hours and so on. Blue = bottom frame; gray = middle frame; gold = top frame.

2014 Frame Manipulation Experiment: Phase 2

Phase 2 of 2014 took a slightly different approach than the 2012 frame swap and Phase 1 of 2014 did to the same question. The seven days of Phase 2 were devoted to seeing how the dance floor changed in response to an outside frame being placed in the hive. Days 1-3 were used to establish a baseline dance floor before the frame manipulation took place. Sparse dancing on Day 1 (see Figure 8) occurred entirely on the middle frame, on the right side of the frame. More dance activity was seen the following day, forming an oval-like spread. The dance floor on Day 2 was slightly to the right side of the frame and its center was located above the hive entrance. On Day 3, the middle frame showed a similar distribution of dances, but a scattered minority of the dancing took place on the top frame, with a comparable shape.

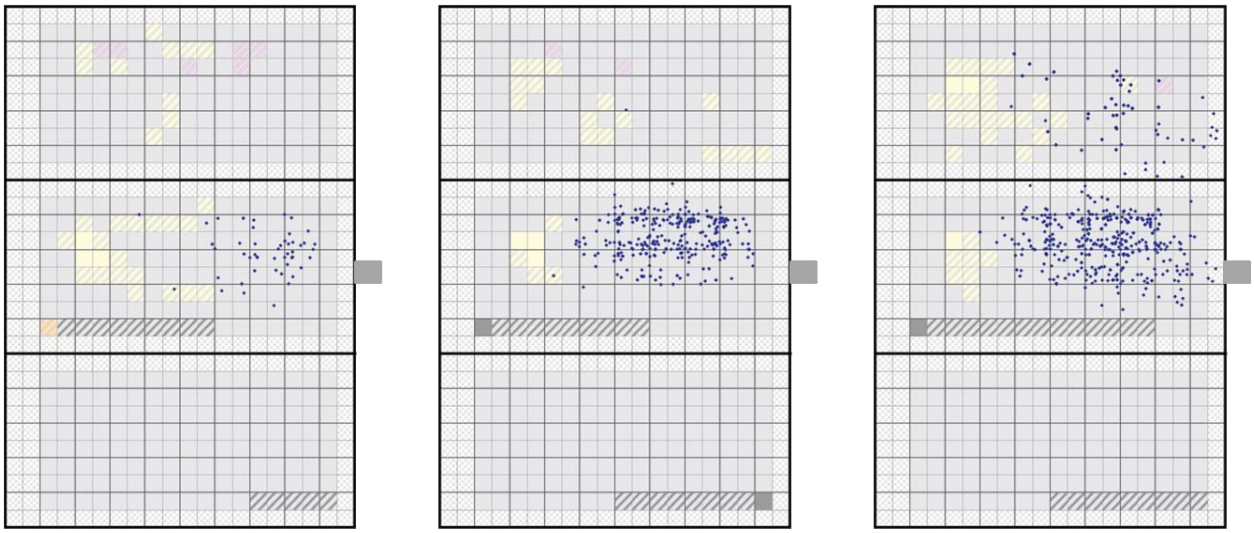

Fig. 8. Observations Days 1-3 (left to right) of Phase 2.

On the night of Day 3, the top frame was removed from the hive and a frame from outside the hive was inserted as a replacement. The new frame had capped brood (orange), pollen (purple) and capped honey (green). Day 4's dance floor was somewhat oval-like and above the level of the hive entrance (Figure 9). Low dance numbers were essentially all on the middle frame, positioned towards the right side of the hive and near the entrance. Day 5 had a dance floor that was somewhat like Day 4. On Day 6, dancing on the middle frame was highly similar to Day 5, but a smattering of dances were noted on the top frame as well. The next day saw a return to a dance floor that was nearly identical to Day 5 (see Figure 9).

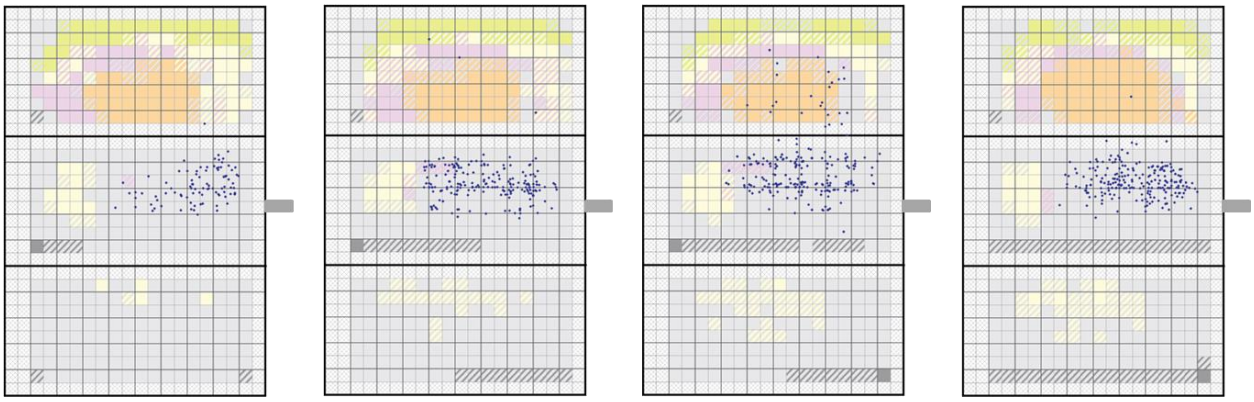

Fig. 9. Dance and substrate maps for Days 4-7 (4 on the left; 7 on the right) of Phase 2.

2014 Frame Manipulation Experiment: Phase 3

On the evening of Day 7 of Phase 2, the top and middle frames were exchanged, beginning Phase 3 of the 2014 frame manipulation experiment. Phase 3 was conducted with very similar aims to Phase 1. Days 1-3 show observations of the dance floor after the frame swap that occurred prior to Day 1. On Day 1 the dance distribution was almost completely on the middle frame. The shape of the dance floor was roughly oval; most of the dances were clustered towards the right side of the hive, nearly evenly grouped above and below the entrance. The dance floor's shape was comparable on Day 2, but heavy clustering was seen on several quadrats to the right side of the oval. Dancing on Day 3 was generally similar but more circular in shape, and the center of the dance floor was slightly closer to the hive entrance.

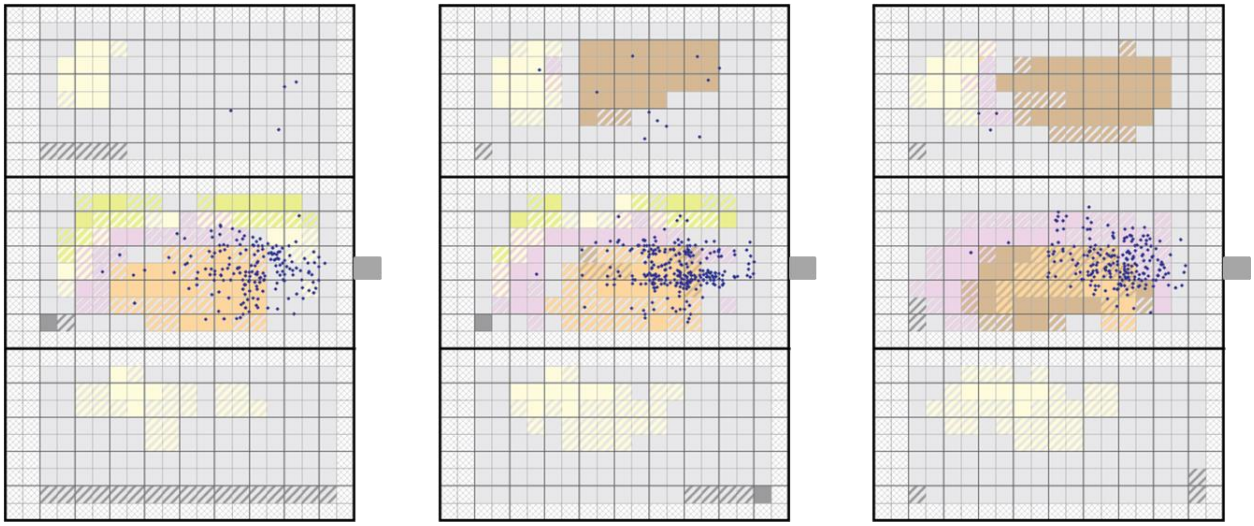

Fig. 10. Waggle dance maps overlaid onto substrate maps for Days 1-3 (left to right respectively) of Phase 3.

At night on Day 3, the middle and bottom frames were exchanged. Rather than dancing on the bottom frame (i.e. following the old dance floor), a second dance floor formed on the top frame on (or near) brood substrate (brown). The majority of dances on Day 4 took place on the top frame. The shape of the top dance floor was circle-like, while the middle frame's dance floor small and approximately trapezoidal (see Figure 11). Both dance floors were centered to the right. The dominant dance floor was roughly halfway between the top and bottom of its frame; the dance floor on the middle frame was elevated above the hive entrance. Most of the dances up top were spread over brood (brown). On Day 5 only a quarter of the dances occurred on the top frame, a roughly threefold decrease from the previous day. The top frame's dance floor was

arched somewhat around the brood (see Figure 11). Dancing on the middle frame was similar to Day 4, except the number of dances increased. Dancing on the top frame increased from Day 5 to Day 6. The dance floor on the top frame was characterized by a roughly oblong shape with a similar but lower center compared to Day 4. Most of the dances on the frame were observed on brood, which had a wider distribution on Day 6 than it did on Day 5. The dance floor on the middle frame was nearly identical to that of the previous day.

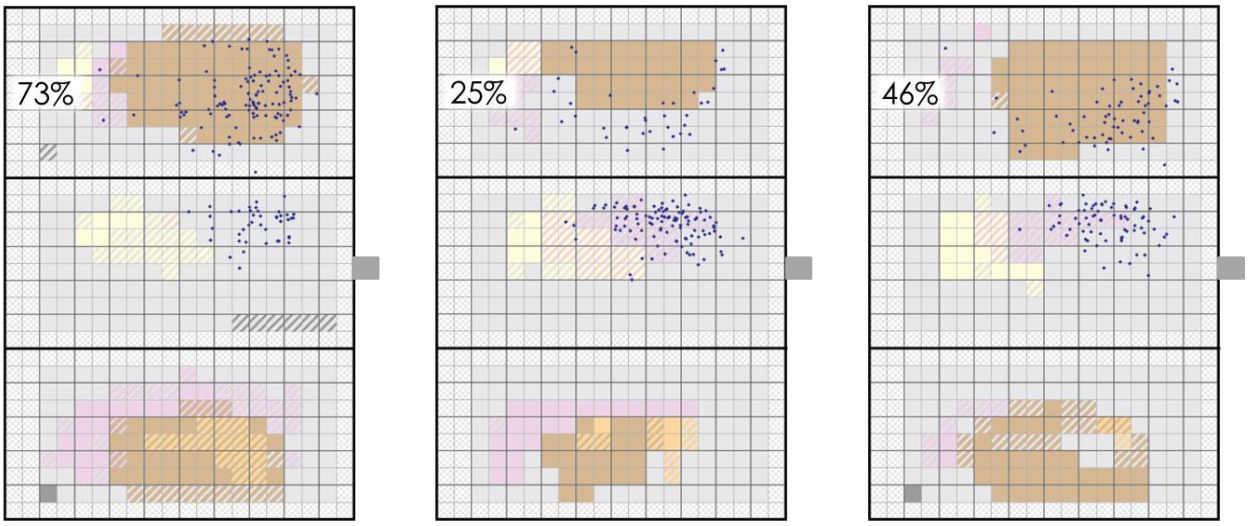

Fig. 11. Waggle dance maps overlaid onto substrate maps for Days 4-6 (left to right respectively). Percentage of dances on top frame is given by day as well.

Because the two dance floors remained through three days, an additional three days of observations were used to determine whether the bees would continue to dance up top. Almost two-thirds of the dances were on the top frame (see Figure 12). On Day 7 dancing on the top frame was spread completely over brood (brown) and formed an approximately circular distribution to the right side of the frame. Dancing on the middle frame formed a much smaller circle and was entirely above the level of the hive entrance, also to the right side of the hive. The proportion of dances on the top frame grew on Day 8. The middle frame's dance floor was comparable to Day 7. The dances on the top frame formed a more widespread oval over the brood. On Day 9 the percentage of dances on the top frame reached its maximum. Dancing on the top frame appeared to curve around the capped brood (orange) and form an arc on the brood (brown). On the middle frame, the small number of dances noted were in almost the same area as the previous two days.

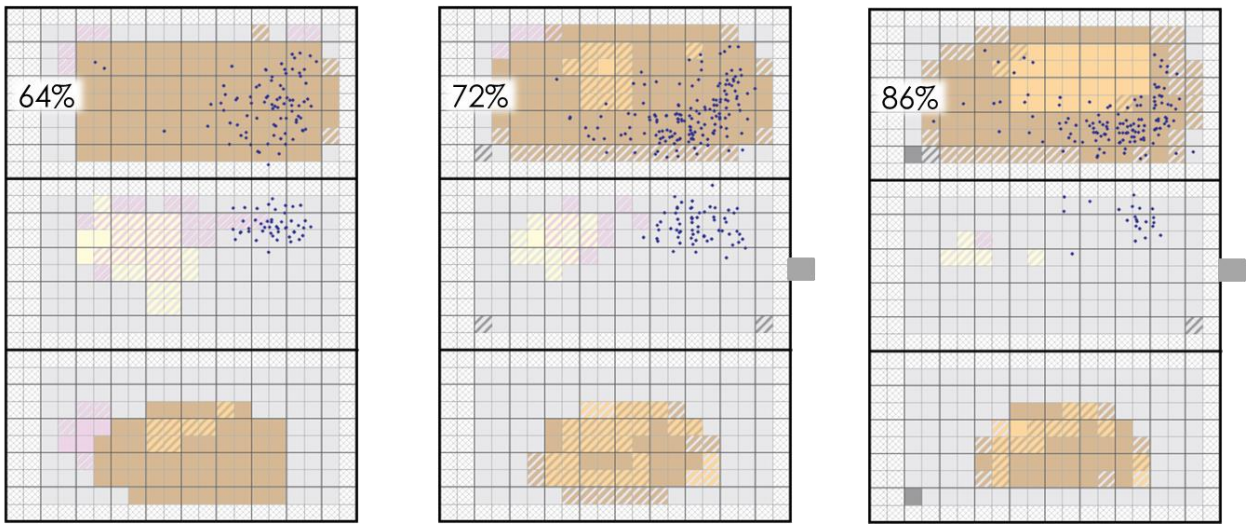

Fig. 12. Waggle dance maps overlaid onto substrate maps for Days 7-9 (left to right respectively). Percentage of dances on top frame is given by day as well.

At night on Day 9, the bottom and middle frames were swapped, and the dance floor was observed for six days. Two discrete dance floors remained on Day 10 (see Figure 13). The top frame's dance floor was somewhat circular and located towards the lower right end of the frame, with the dances split between brood and capped brood substrates. On the middle frame the distribution of dances is slightly to up and to the right of the frame's center. Dance floors on Days 11, 12 and 13 were fairly similar, with dance floors on the middle frame being distinct but with a somewhat indistinct shape except for Day 13, which had an oval dance formation. The proportion of dances on the middle frame increased consistently during this time. By Day 14 dancing on the top frame was considerably lower than on Day 10, though in the same general location and shape (Figure 13). The dance distribution of the middle frame shifted slightly upward compared to the previous day. On Day 15 only a few dances were seen on the top frame. The shape of the middle frame's dance floor was similar to Day 13, but heavily weighted to the right end of the dance floor.

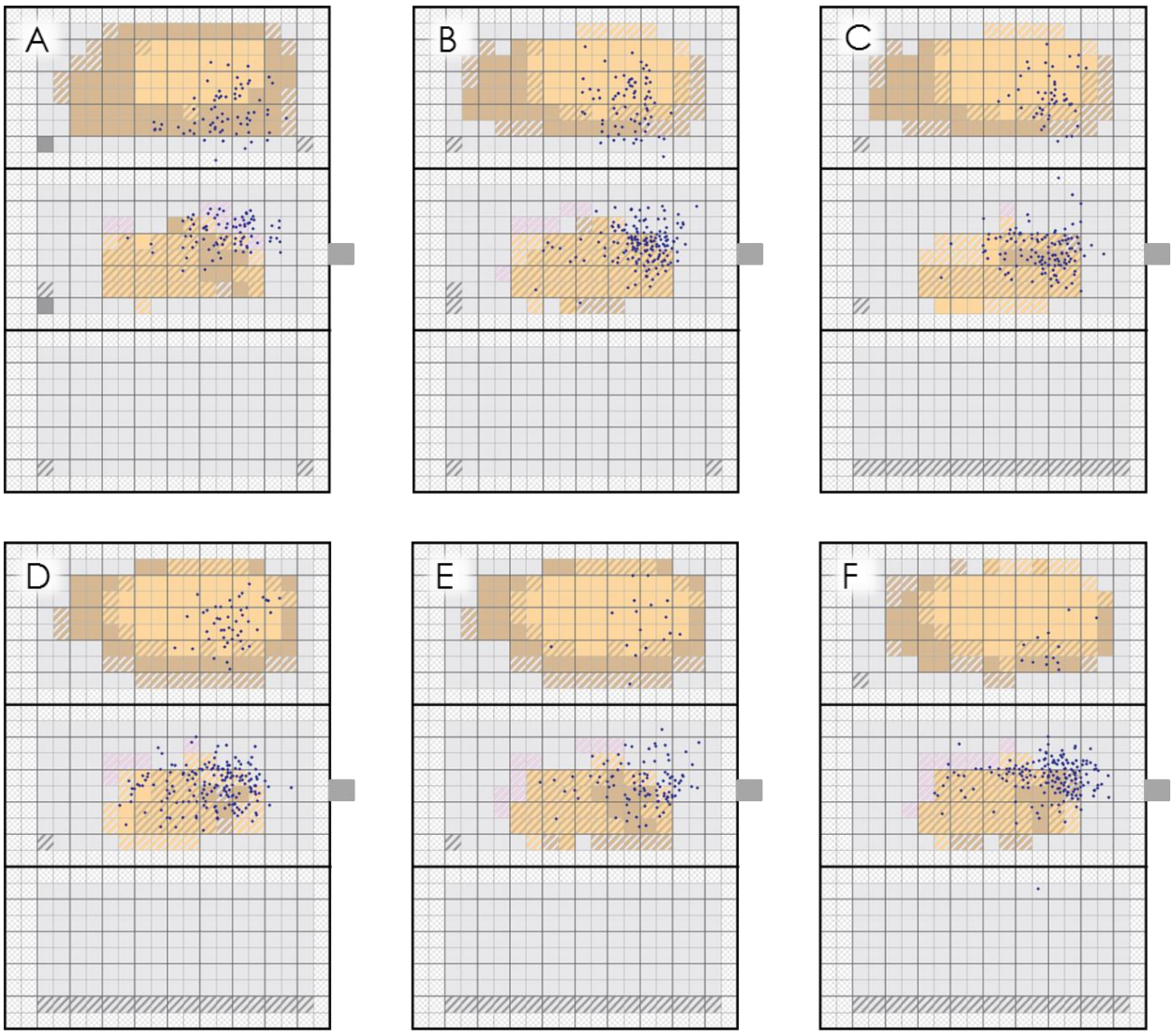

Fig. 13. Waggle dances and substrate for Days 10-15 (A = Day 10; B = Day 11; C = Day 12; D = Day 13; E = Day 14; F = Day 15).

All dancing occurred on the top and middle frames from Days 10 to 15. In a consistent, almost stepwise fashion, Figure 14 shows the movement of dancers from the top frame to the middle frame. Approximately fifty-five percent of dances were observed on the middle frame on Day 10. This proportion enlarged to just under seventy percent the following and day. By Day 15, over 90% of dances occurred on the middle frame.

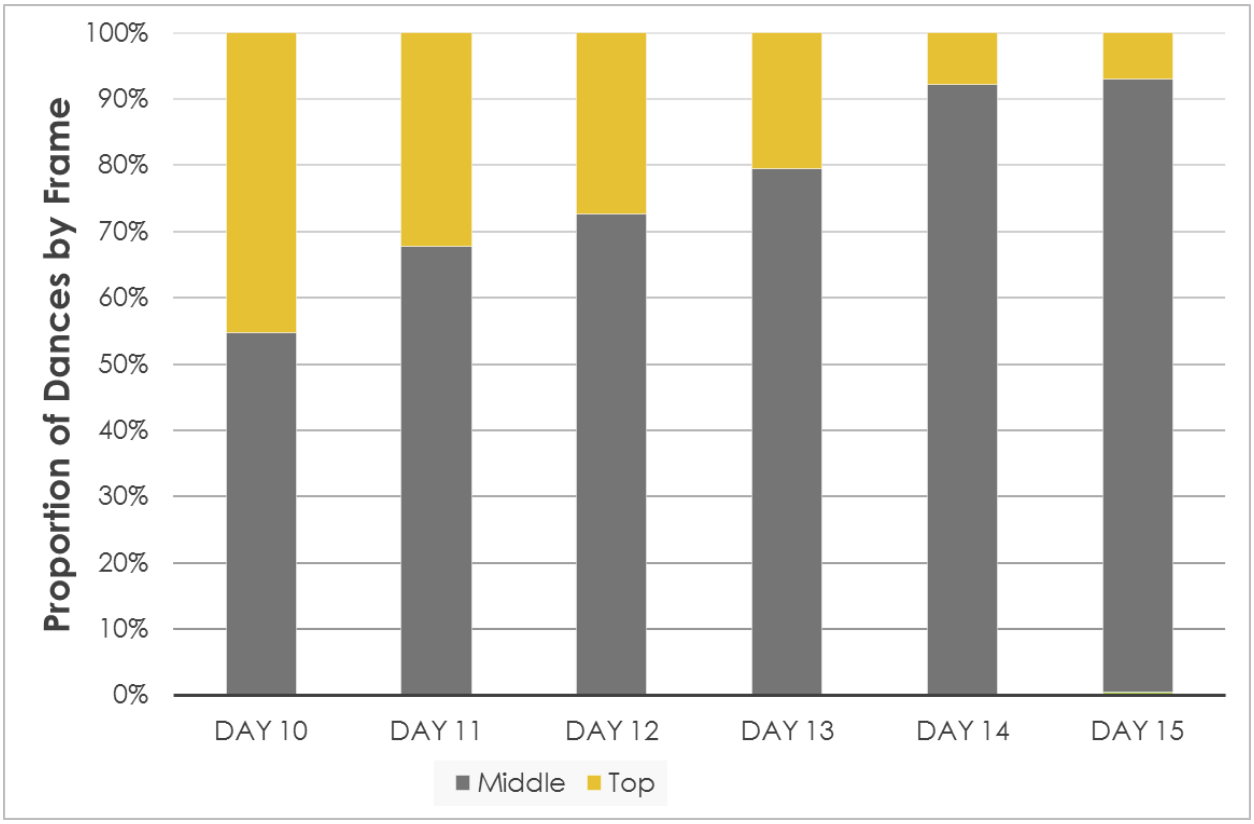

Fig. 14. The adjustment of the dance floor over Days 10-15. Percentages of dances by day and by frame. Gray = middle frame; gold = top frame.

DISCUSSION

Throughout both experiments, dancing on the middle frame close to the hive entrance was normative prior to manipulations. After an experimental manipulation, a different dance floor was generally observed the following day. This can be seen in Figures 3, 5, 6, 11 and 13. In the 2012 experiment, bees dancing on all three frames after the experimental manipulation failed to resolve into a single dance floor over three days' time (see Figures 1 and 3). On the other hand, Phase 2 of 2014 showed no real response to the insertion of a new frame (Figures 8 and 9).

In all other cases, an adjustment period followed the exchange of frames. Days 4-9 of Phase 3 (Figures 11 and 12) show an interesting upward shift of dancers from the middle frame to the top frame, along with a corresponding increase of brood (brown) being laid on the frame. During this portion of the experiment, recruitment of foragers actually shifted away from the hive entrance for six days. When the middle and bottom frames were exchanged, dancing

gradually shifted back to the middle frame once more (Figures 13 and 14). Based on the composition of substrate through this time period, this behavior appears attributable to an attraction to the substrate – in this case, brood and a smattering of capped brood. In 2012, Days 4-6 may reflect on a preference for brood substrate as well. Most of the dances occurring in top and bottom frame positions center around brood and capped brood localities (Figure 3; brood is brown; capped brood is orange). Despite this apparent preference for brood combs, the frame insertion on the night of Day 3 in Phase 2 of 2014 failed to influence the dance floor. Dancers continued to occupy the middle frame near the hive entrance (Figures 8 and 9).

More commonly, however, a frame exchange was followed by the movement of a minority of dancers toward a different frame. This finding is clearly illustrated by Days 4-6 and 7-9 of Phase 1 of 2014. In both instances the majority of dancers continue to occupy the middle frame while some dancers head for the bottom frame (Figures 5 and 6). It is noteworthy that the substrate here is empty comb (gray). The downward shift in the dance floor was temporary, as demonstrated by the progression of the dance floor on the days afterward. This adjustment takes place across multiple days (Figures 5 and 6) as well as during an individual day (Figure 7). Interestingly, the change from Day 7's first observation period to its last observation period was greater than the change from Day 7's first waggle dance scan to Day 8's first scan (Figure 7).

In Phase 1 of 2014 we see some bees follow the old dance floor (Figures 5 and 6), a tendency which dissipates rapidly with time. Dancers in Phases 2 and 3 of 2014, on the other hand, displayed no preference for the substrate on which they danced the previous day (Figures 9 and 11). The experimental evidence does not support the hypothesis that dancers follow the old dance floor (i.e., Tautz and Lindauer 1997), at least not in the presence of other factors (substrate, hive entrance proximity, etc.). Phase 1 mostly lacks these other factors, so it may be that the honey bees are attracted to the old dance floor. Whether such an attraction would take place as a result of a chemical marker left on the dance floor (suggested by Tautz and Lindauer) or through a potential dance scent (Thom et al.; Gilley) is unclear.

The bulk of experimental data lend support to the hypothesis that proximity to hive entrance is a determining factor in the establishment of the dance floor. With the exception of Days 4-9 of Phase 3 and possibly the 2012 frame swap experiment, the dance floor eventually ended up on the middle frame, close to the hive entrance (Figures 5, 6, 9 and 13; note also that the dance floor always started predominantly [>90%] on the middle frame). Figure 14, for

example, is especially telling, with the proportion of dances occurring on the middle frame consistently growing from 55% on Day 10 to roughly 93% by Day 15 of Phase 3. Although the confluence of multiple factors may have prevented hive entrance proximity from taking over in 2012 and Days 4-9 of Phase 3, the overall picture forming places closeness to hive entrance as the central factor in establishing the dance floor (remember Seeley and Towne), with substrate possibly acting as a secondary factor.

What does all of this mean in terms of dancing behavior? The apparent preference for dancing locations close to the hive entrance could reflect on a number of things. It might simply be expediency (saving energy and time) or a result of forager distributions within the hive. Food-receiver bees, which receive and store nectar and/or pollen from returning foragers, may influence the proximity of the dance floor to the entrance, or dancing in other areas of the hive might be impeded by worker bee behavior within the hive. It is even possible that dancing close to the hive entrance is an innate tendency (an instinct). In all likelihood, this behavior comes from an interplay of the factors listed above.

Likewise, substrate's influence on dance floor location is confounded by several possibilities. It may not be the substrate but what the bees are doing on the substrate that makes it an attractive dance site. Potentially, substrate could influence the distribution and density of honey bees within the hive and thereby influence the dance floor. Regardless, more controlled and detailed studies would be necessary to assess the behavioral origins of the outcomes noted in this study.

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