BALLROOM BIOLOGY: RECENT INSIGHTS INTO HONEY BEE WAGGLE DANCE COMMUNICATIONS

EDITED BY: Roger Schürch, Margaret J. Couvillon and
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BALLROOM BIOLOGY: RECENT INSIGHTS INTO HONEY BEE WAGGLE DANCE COMMUNICATIONS

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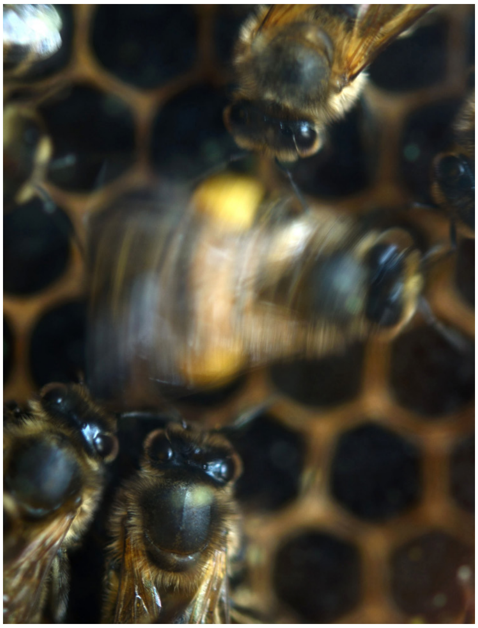

A successful honey bee forager communicates with the waggle dance the distance and direction from the hive to the resource, which for this dancer is pollen.
Image by: Roger Schürch

The honey bee waggle dance communication is a complex, unique, at times controversial, and ultimately fascinating behavior. In an elaborate figure-of-eight movement, a returning forager conveys the distance and direction from the hive to resources, usually the nectar and pollen that is their food, and it remains one of the most sophisticated, known forms of non-human communication. Not surprisingly, since its discovery more than 60 years ago by Karl von Frisch, the dance has been subject to investigations that span from basic biology through human culture and neurophysiology to landscape ecology. Here we collate recent advances in our understanding of the dance.

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EDITORIAL
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Editorial: Ballroom Biology: Recent Insights into Honey Bee Waggle Dance Communications

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Keywords: waggle dance, honey bee, recruitment, foragers, social insects, animal communication

The Editorial on the Research Topic

Ballroom Biology: Recent Insights into Honey Bee Waggle Dance Communications

In his 1950 book *Bees: Their Vison, Chemical Senses, and Language*, Karl von Frisch recounts his decades of research into how honey bees perceive the world, concluding "The bee's life is like a magic well: the more you draw from it, the more it fills with water." (von Frisch, 1950). Sixty-five years on, science continues to draw from that magical well, and we have learned a tremendous amount about honey bee foraging, nest site selection and recruitment. We now understand a great deal about how the decisions made by individual bees, which usually have limited information, translate into colony-level decisions in an unpredictable environment. When studying honey bee behavior, it is impossible to ignore the role the unique waggle dance plays in the life of the bee. Honey bees use the dance to communicate the location of resources. The discovery and subsequent decoding of the waggle dance would earn Karl von Frisch a Nobel Prize in 1973.

The waggle dance is the inspiration behind the nine contributions, spanning from original experimental research to emerging methods, which we present here in this special *Frontiers* issue.

AVAILABLE INFORMATION FOR HONEY BEES

We begin with an exploration of the information available to honey bee foragers. Rivera et al. used the duration of trophallaxis as a proxy for that individual's experience of resource quality, where a decrease in trophallaxis duration from a marked forager may suggest a decrease in forage quality. They also used forager wait time as a proxy for social information, where increased wait time for the marked returning nectar forager indicates that the colony no longer requires that resource so acutely. However, the authors did not find an effect of either on an individual bee's decision to stop foraging, reflecting that honey bee decision-making in a natural environment remains poorly understood. We do know that honey bees forage at long distances (von Frisch, 1967; Seeley, 1995). Ratnieks and Shackleton conclude that these distances, which may be up to 10–14 kilometers (Waddington et al., 1994; Beekman and Ratnieks, 2000; Couvillon et al., 2014), are exceptional, given the bee's body size. Ratnieks and Shackleton hypothesize it is the dance language that makes long distance foraging possible. The question of exactly how much information is conveyed by the waggle dance is examined directly in the contribution by Schürch and Ratnieks. By reanalyzing the information content in both vector components (direction and distance) of the dance, they demonstrate that 2.9 and 4.5 bits of information are conveyed respectively, showing that a little bit of information can go a long way if it is the right information (Schürch and Ratnieks). l'Anson Price and Grüter then review what is currently known about the circumstances that have led to

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the evolution of dance communication. They conclude that the dance information is most useful in an environment where resources are clustered, difficult to find, and of variable quality and when the environment itself is relatively stable for periods of time. Lastly, Avarguès-Weber et al. take a slightly different focus by looking not at the details conveyed from specialized signals such as the dance, but at the indirect, environmental information that bees may obtain. In doing so, they draw from work on both bees and fruit flies and discuss the evidence for observational learning and the neural circuits that may underpin it.

WITHIN THE DANCE: INTRA-DANCE VARIATION AND BEE STOP SIGNALS

Two contributions deal with specific aspects of the dance itself. Firstly, Beekman et al. examine intra-dance variation among *Apis* species by analyzing the dance precision of *A. florea, A. dorsata,* and *A. mellifera* in the contexts of both foraging and swarming. They find that all three species improve the precision of the dance with increasing distance to the source but that dance precision levels off. Their data supports the idea that intra-dance variation reflects an unavoidable constraint in the bees' ability to communicate more precisely. Kietzman and Visscher examine the bee's stop signal, which counters the waggle dance by providing negative feedback toward an advertised location. The combination of both positive feedback from the waggle dance and negative feedback from the stop signal, allows the colony to more rapidly respond to changes in the foraging environment.

DANCING INTO THE FUTURE

Lastly, two contributions look ahead toward potential research avenues that pertain to the bees' communication system. Couvillon and Ratnieks argue that the waggle dance, specifically the ability of researchers to decode the dances to determine where honey bees are foraging, may be applied as a future tool for ecology to inform on a range of ecological, conservation, and land management issues. The authors concede, however, that decoding dances by hand, which is the current methodology to extract the spatial information from the dance, is time-consuming, an issue that may be helped by the contribution of Wario et al., where they present in their methods article the full specifications of the recording setup and the software for automatic recognition of individually tagged bees and the decoding of dances. With the development of this technology, it may be possible to track all individuals of a honey bee colony and to detect and to decode the communication dances automatically.

CONCLUSION

The diverse nature of the contributions in this special issue illustrates how, 93 years after von Frisch's first description of the honey bee's waggle dance (von Frisch, 1923), there still remains much to be learned. We hope that this eBook will continue to motivate scientists to draw from the well that is the bees' lives and further elucidate how such a tiny brain in a small insect can generate such amazingly complex behaviors as the waggle dance communication.

AUTHOR CONTRIBUTIONS

RS and MC came up with the topic idea, and MB contributed to its description and to the overall organization of the special topic. All editors contributed to the overseeing of reviews for this special issue and wrote the cover editorial.

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Quitting time: When do honey bee foragers decide to stop foraging on natural resources?

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Honey bee foragers may use both personal and social information when making decisions about when to visit resources. In particular, foragers may stop foraging at resources when their own experience indicates declining resource quality, or when social information, namely the delay to being able to unload nectar to receiver bees, indicates that the colony has little need for the particular resource being collected. Here we test the relative importance of these two factors in a natural setting, where colonies are using many dynamically changing resources. We recorded detailed foraging histories of individually marked bees, and identified when they appeared to abandon any resources (such as flower patches) that they had previously been collecting from consistently. As in previous studies, we recorded duration of trophallaxis events (unloading nectar to receiver bees) as a proxy for resource quality and the delays before returning foragers started trophallaxis as a proxy for social need for the resource. If these proxy measures accurately reflect changes in resource quality and social need, they should predict whether bees continue foraging or not. However, neither factor predicted when individuals stopped foraging on a particular resource, nor did they explain changes in colony-level foraging activity. This may indicate that other, as yet unstudied processes also affect individual decisions to abandon particular resources.

Keywords: social insects, foraging, honey bees, *Apis mellifera*, decision making, collective behavior

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Introduction

Animals are often faced with the challenge of foraging on resources whose quality and availability change over space and time. In order to maximize foraging success, animals have evolved mechanisms to judge which resources are worth exploiting (Belovsky, 1978; Pyke, 1978; Pleasants, 1989; Van Nest and Moore, 2012). Many animals forage on resources to which they may make multiple trips (such as bees, nectar foraging ants, and birds); in these cases, foragers need to choose when to return to the same resource and when to abandon it to search for a new one. This is known as the "exploitation vs. exploration" trade-off (Krebs et al., 1978; McNamara and Houston, 1985). In social animals, both the information available to make this decision, and the consequences of foraging success, may be shared among individuals. Social insects have been particularly well studied in this respect.

Honey bees (*Apis mellifera*) provide a great model for social foraging due to their ability to rapidly adapt their foraging efforts to changing resource availability, studied particularly in the context of nectar foraging (Seeley, 1986). This is accomplished through the collective actions and decisions of individual foragers, with the benefits and costs of these decisions affecting the colony as a whole. Individual bees integrate several sources of information, including personal and social, when making decisions about foraging (Biesmeijer and Seeley, 2005). Honey bee foragers use information gained in their own experience, such as memory of time and place, sugar concentration and amount of nectar previously collected, to decide whether to continue or resume foraging on particular resources (Wainselboim et al., 2002; Grüter and Farina, 2009a; Van Nest and Moore, 2012; Al Toufailia et al., 2013). They also make use of various sources of social information, such as information about resource location and quality transmitted via the waggle dance (von Frisch, 1967; Grüter and Farina, 2009b), and information about resource quality and type from nectar samples unloaded in the hive (Grüter and Farina, 2009a). Other communication signals and interactions can also affect foraging decisions, such as the tremble dance (food storer activation) and the stop signal (forager inactivation) (Seeley, 1989; Nieh, 1993; Balbuena et al., 2011; Seeley et al., 2012).

But what kind of information do foragers use to decide when to stop visiting a particular resource? The colony's dynamic ability to allocate foragers to the best resources available can only be maintained if foragers frequently re-evaluate their short-term commitment to resources (Seeley et al., 1991; Detrain and Deneubourg, 2008). While foragers may revisit and check on resources over long periods of time (days or weeks), we are particularly interested in how foragers decide on which resources to continue foraging (Beekman, 2005; Al Toufailia et al., 2013). How do foragers make the decision to stop foraging on a particular resource? Two main processes have been identified. First, an individual personally experiencing a decline in the quality of the resource is more likely to abandon it, and to stop foraging entirely or look for other resources (Seeley et al., 1991; Townsend-Mehler et al., 2010). Second, if the colony's need for foragers in general, or the need for the particular forage brought in by that forager (e.g., if other foragers are bringing higher-quality nectar), has decreased, individuals may also abandon the resource they are currently exploiting (Lindauer, 1952; Seeley, 1989). Foragers get this information from interactions with nestmates, particularly receiver bees (Lindauer, 1952; Seeley, 1989; Biesmeijer and de Vries, 2001).

In honey bees, foragers can assess resource quality directly when foraging, using several criteria, including concentration and volume of the nectar itself, but also the flight distance to the resource from the hive and the likelihood of predation at the resource (von Frisch, 1967; Tan et al., 2013). These measures are integrated by bees and affect both when bees share information about this resource by dancing and the bees' decision to continue foraging on it (Seeley, 1994; De Marco and Farina, 2001). Nectar can be highly temporally and spatially variable, affected by abiotic factors (rainfall, sunlight, nutrients) and biotic factors (pollinator visitation and nectar replacement rates) (Real and Rathcke, 1991; Boose, 1997; Edge et al., 2011). Even over the course of a day nectar volume can change quite rapidly, by several microliters in an hour (Raihan and Kawakubo, 2014).

A honey bee forager can also gain valuable social information about the quality of her resource relative to others exploited by her colony, and the need for this resource, from her nest mates. Foragers, after gathering liquid food such as flower nectar or honeydew, return to the hive to pass this food to another bee, called a "receiver bee," who will carry it deeper into the hive, process it, and either deposit it in a honey store or pass it on to nurse bees (Seeley, 1995). The time it takes from entering a hive to securing a receiver bee we call "wait time," and is thought to reflect colony foraging needs in one of two ways (Seeley and Tovey, 1994). Receiver bees have access to multiple foragers, and may thus experience multiple sources of nectar; in response they may be reluctant to accept a lower-quality or novel resource compared to what they have recently experienced (Seeley, 1989; Seeley and Tovey, 1994; Gil and Farina, 2002; Wainselboim and Farina, 2003; Goyret and Farina, 2005). Thus a forager who experiences a longer wait time may be informed that her resource is of poorer quality relative to what is being brought into the hive by others. Difficulty of finding a receiver may also indicate the general state of hive-level foraging to the forager: increased wait time could be a result of a redistribution of workers away from unloading to more pressing colony tasks, or a result of a sudden increase in foragers bringing nectar that overwhelms the capacity of the existing receiver bees to process that nectar (Lindauer, 1952; Seeley and Tovey, 1994). In both of these cases, it may be adaptive for a forager experiencing long wait times to stop foraging on its particular resource. Indeed, in an empirical test using artificial feeders and removal of receiver bees, lower densities of receiver bees resulted in longer wait times, decreased the probability that a forager would perform waggle dances, and increased the probability that a forager would stop foraging on its current resource (Seeley, 1989).

While independently shown to affect foragers' decisions to abandon resources, personal and social information's relative contributions to forager decisions, as well as their importance under natural foraging conditions with many small, temporally and spatially rapidly varying resources, have not been investigated. Does personal or social information more often determine a bee's decision to quit foraging at a resource, and are the bees' decisions fully explained by these two factors, or are other processes also important? For example, bees might simply stop foraging on any particular resource with a fixed probability, which could help the colony maintain flexibility, since it prevents large numbers of foragers from being "locked in" to foraging on particular resources (Detrain and Deneubourg, 2008; Lanan et al., 2012). Does this occur, and how relevant is it compared to quitting in response to the two known factors?

We thus quantify the influences of decreased trophallaxis duration and increased wait time on the decision to abandon resources under natural foraging conditions. Using detailed foraging histories based on in-hive observations of returning foragers, we test (1) the effect of personal information, in the form of a decline in resource quality, on the decision to stop foraging. To do this we compare the average trophallaxis duration (a proxy for nectar load and thus a potential correlate of resource quality) after the last trip before a forager abandons a resource with its previous average trophallaxis duration over recent trips that are likely to be to the same resource. We also test (2) the effect of social information, in the form of wait time to unload nectar, by measuring this directly in the hive, and comparing wait time on the last trip with that on recent trips.

Methods

Set Up and Marking

Each experiment was performed with two colonies of about 2000 domestic Italian honeybees (*Apis mellifera ligustica*) each, with roughly 500 bees individually marked in each colony. They were housed in a glass sided, two frame observation hive with the exit, a clear plastic tube, connected to the hive near the bottom corner. Foragers were marked at the USDA Carl Hayden Bee Center over a period of 1 week prior to the start of the experiment. Foragers were captured by selectively collecting individuals that had left the hive. Individuals were uniquely marked with a colored/numbered tag and paint. After being sealed into their hives for ∼24 h, the colony was transported to a new location and left sealed overnight before the beginning of the experiment the next morning.

Dates and Location

The two experiments took place in two locations in southern Arizona. Experiments 1a and 1b were located at Appleton–Whittell Research Ranch, an Audubon Society preserve near Elgin, Arizona and took place on June 20 and 27, 2010. Experiments 2a and 2b were performed at the Santa Rita Experimental Range Headquarters in Florida Canyon on Aug 9 and 16, 2010. (These dates and locations correspond to experiments 3 and 4 in Donaldson-Matasci and Dornhaus, 2012).

Recording

Hives were opened at dawn and remained open until dusk. During that time all marked bees were recorded coming in and out of the hive. From video recordings taken, we observed all returning marked bees and recorded all instances of trophallaxis within 5 min of entering the hive. Wait time (amount of time from entering the hive until the beginning of the first trophallaxis, an indication of colony foraging needs) and trophallaxis duration (the sum of all trophallaxis event durations in a single hive visit, a proxy for the profitability of the exploited resource) were determined for each returning bee (Wainselboim and Farina, 2003). Trophallaxis duration has been used as a metric for non-invasively determining resource quality (Seeley and Visscher, 1988). We only analyzed foraging histories from foragers who were performing repeated, consistent, successful foraging trips, which we termed to be "employed" (see below); we did this to maximize the likelihood that foragers were indeed repeatedly visiting the same resource. To see if a relationship existed between the decision to quit foraging and declines in trophallaxis duration and/or increases in wait time, we compared these measures on a forager's last trip to the average measure on previous trips of that forager (during its "employment").

Individual Foraging Histories

Foraging histories were constructed using the following operational definitions, based on the framework in Biesmeijer and de Vries (2001).We consider a forager to be "employed" while it consistently keeps foraging at the same resource (e.g., a patches of flowers that a bee would return to repeatedly). We operationally defined this as a forager who performs three or more consecutive successful foraging trips (where trophallaxis is performed in the hive after each trip), with less than 2 min variability in duration, and less than 10 min spent in the hive between trips. This was a consistent pattern that emerged from our foraging data, in other words most bees that performed several consecutive successful trips conformed to this pattern. Through the lens of these foraging histories we are able to determine when an individual stops foraging at a particular resource (see **Figure 1**). We found 29 individual bees out of the 227 individuals observed (184 of which showed at least one successful trophallaxis event) over the 4 experiment days and the 2 colonies that showed such consistent foraging patterns. This was perhaps due to many foragers only performing a few short bouts of trophallaxis over the entire day.

Colony Level Foraging Activity

To measure the influence of average trophallaxis duration and wait time on colony-level foraging activity, we divided each experiment into 15-min time bins. For each bin we recorded the number of marked foragers who left the hive (employed or unemployed), average length of all trophallaxis events, and the average wait time. Due to the likely presence of autocorrelation in these data series, simply testing for correlations among these factors could lead to erroneous results. Instead, we use a cross-correlation test, which measures the correlations between the two time series as a function of time lag (Venables and Ripley, 2002). If wait time were a major factor affecting foraging activity, we would see a negative correlation (as wait time increases, number of foragers leaving decreases) with a positive time lag (the decrease in the number of foragers would occur after the increase in wait time). If, on the other hand, colony-level foraging activity affected wait time (e.g., because with fewer foragers, bees

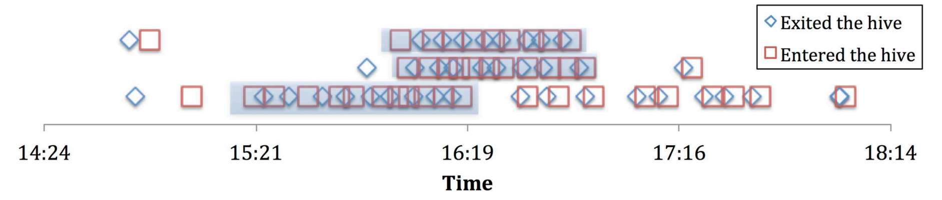

FIGURE 1 | Sample employment histories for 3 employed foragers from experiment 2a. Highlighted portion is the "employment" phase.

can unload faster), we would see a positive correlation with a negative lag (decreases in the number of foragers would precede decreases in wait time). Similarly, if changes in trophallaxis duration affected foraging activity, we would see a positive correlation (as resources decline in quality, fewer bees leave the hive) with a positive time lag (a decline in the resource precedes a decline in foragers). We considered only time lags within biologically relevant time scale (less than an hour). To account for multiple testing, i.e., consideration of multiple time lags, we applied a Bonferroni correction (significance level $\alpha = 0.05/11$, where 11 is the number of potential time lags considered in each experiment). All analyses were performed using the R statistical package (R Core Team, 2013).

Results

Individual Level Foraging

Contrary to expectations, we did not find a statically significant effect of either decreased trophallaxis duration or of increasing wait times on individual bees' decision to stop foraging. That is, foragers did not experience a longer-than-average wait time just before quitting any more often than expected by chance (Binomial test $p = 0.326$, $n = 29$, see **Table 1**). Their trophallaxis durations were also not shorter than average any more often than expected by chance (Binomial test $p = 0.845$, $n = 29$, see **Table 1**). Looking at it in a different way, the trophallaxis duration experienced by foragers on their last trip before quitting was not significantly shorter than that experienced on previous trips (Wilcoxon signed-rank test $p = 0.56$, $W = 370.5$, $n = 29$). Neither was wait time on a forager's last trip significantly longer than on previous trips (Wilcoxon signed-rank test $p = 0.98$, $W = 336$, $n = 29$) (**Figure 2**). These analyses were performed on "employed" foragers, which showed trophallaxis durations on average seven times longer than non-employed categorized foragers (T-test $p = 0.0498$, $n = 4$, colony averages for employed and non-employed successful foragers).

TABLE 1 | The number of "employed" foragers in each experiment, and whether they experienced a longer wait time/shorter trophallaxis duration on the last trip of their employed period compared to the average for previous trips.

		On last trip experienced			
Colony	Number of employed foragers	Longer wait time	Binomial test *P*-value	Shorter trophallaxis duration	Binomial test *P*-value
1a	7	4	0.571	4	0.571
1b	11	7	0.636	3	1.000
2a	7	2	0.286	3	0.726
2b	4	3	0.625	3	0.625
Total	29	16	0.517	13	0.845

P-values are reported for a test of whether foragers experience a longer-than-average wait time (or shorter-than-average trophallaxis duration) on their last trip more often than expected by chance (exact binomial test).

Colony Level Foraging

The level of colony foraging activity varied considerably throughout the day, as did trophallaxis and wait times (**Figure 3**). Experiments 1a and 1b (in June) showed strong foraging peaks in the morning, while experiments 2a and 2b (in August) showed more consistent activity across the day, with more foraging in the afternoon.

We found no evidence that changes in trophallaxis duration across all successful foragers affects colony-level foraging activity (**Figure 4**—Trophallaxis duration). If changes in trophallaxis duration affected foraging activity, we would expect to see a positive correlation (as resources decline in quality, fewer bees leave to forage) with a positive time lag (a decline in the resource is followed by a decline in foraging activity). However, the only significant correlations we observed were positive correlations with negative time lags, suggesting that decreases in foraging activity preceded decreases in trophallaxis duration (experiments 1b and 2b). In the other experiments, no significant correlations were observed.

We also found no evidence that the wait time experienced by foragers influences the colony's foraging effort (**Figure 4**—Trophallaxis duration). If wait time were a major factor affecting foraging activity, we would expect to see a negative correlation (as wait time increases, number of foragers leaving decreases)

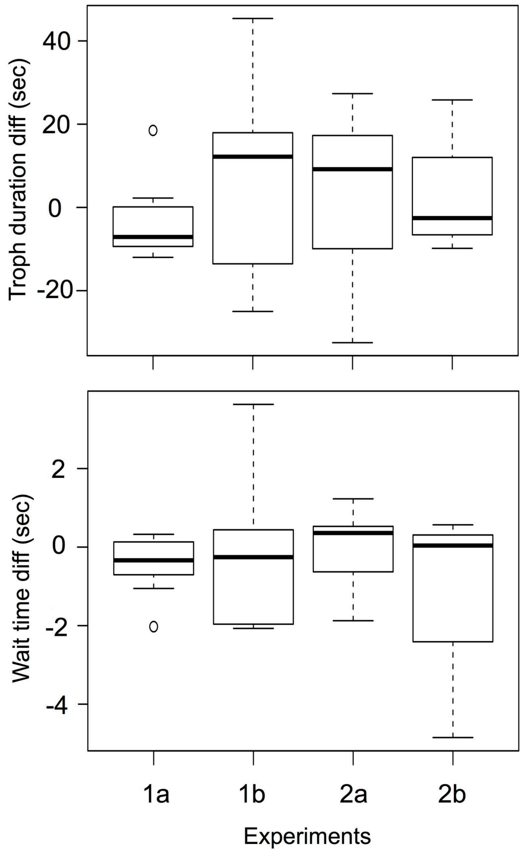

FIGURE 2 | Difference between the last and average trophallaxis duration/wait time during a forager's employment period.

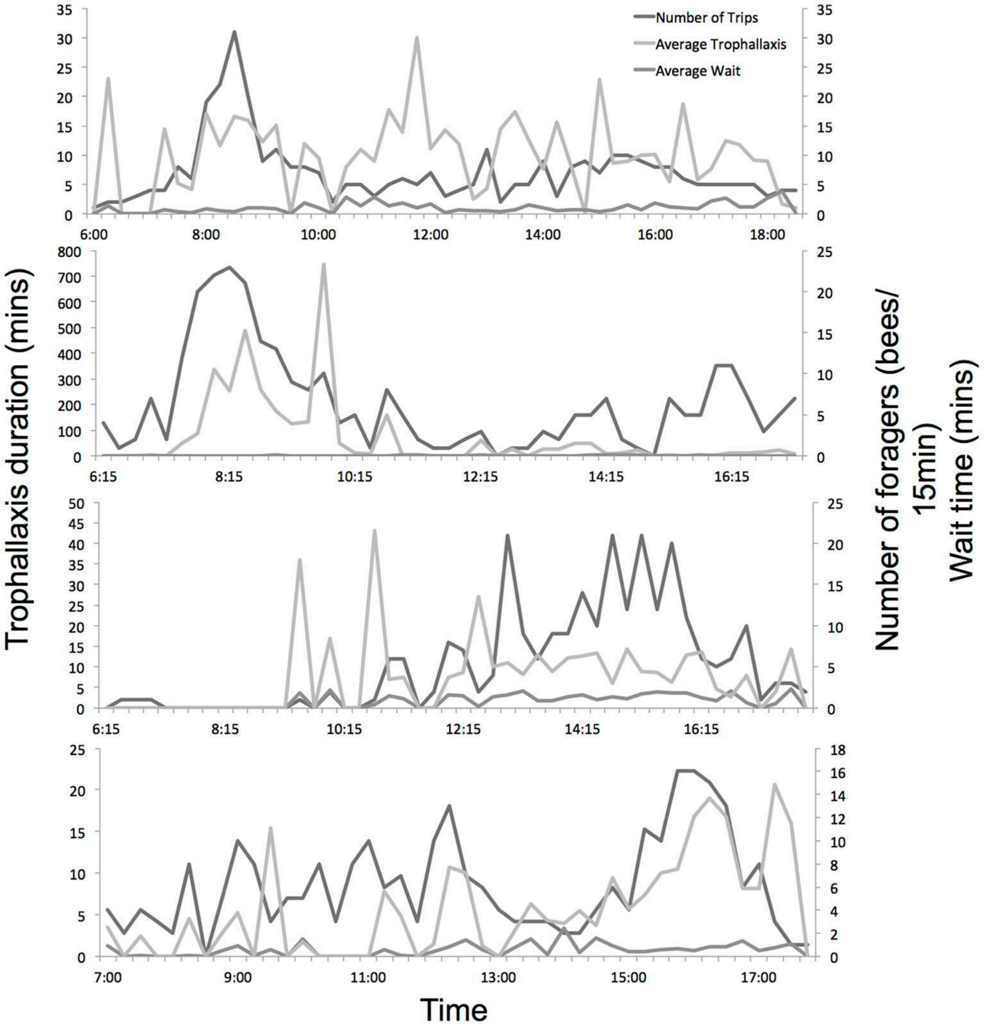

FIGURE 3 | Daily foraging activity, average trophallaxis duration and wait time of all marked foragers across the 4 experiments. Hives were opened and recorded from dawn until dusk.

with a positive time lag (the decrease in the number of foragers would occur after the increase in wait time). No significant negative correlation between wait time and foraging effort was observed in any experiment. In experiment 2a, significant positive correlations were observed with both positive and negative time lags. A positive correlation with a negative time lag might indicate that high levels of foraging activity tend to increase wait times (because receiver bees are busier), but the occurrence of correlations at positive time lags as well makes it difficult to infer the direction of causation. In the other experiments, there were no significant correlations observed.

Discussion

Our study aimed to quantify and compare the effects of (1) personal experience of a decline in resource quality and (2) social information about a decrease in the colony's need for a particular resource, in a natural setting. Both of these factors had independently been shown to affect honey bees' short term decisions to stop foraging on artificial food sources (Seeley, 1986; Seeley and Tovey, 1994). We also looked for evidence of these effects at the colony level, by testing whether a honey bee colony's overall foraging activity decreases in response to either factor. In our experiment, neither factor appeared to have a noticeable effect: we saw no relationship between changes in trophallaxis duration (our proxy for resource quality) or wait time to unload (a proxy for colony need) and the decision to quit foraging at either the individual or colony levels.

A crucial assumption made here is that trophallaxis duration and wait time are valid proxies for resource quality and colony foraging need respectively. These two measures have been tested several times with conflicting results. For trophallaxis duration, Farina and Núñez (1991) and Farina and Wainselboim (2001) found no relationship between resource quality and trophallaxis duration, but Wainselboim and Farina (2003) and Seeley et al.

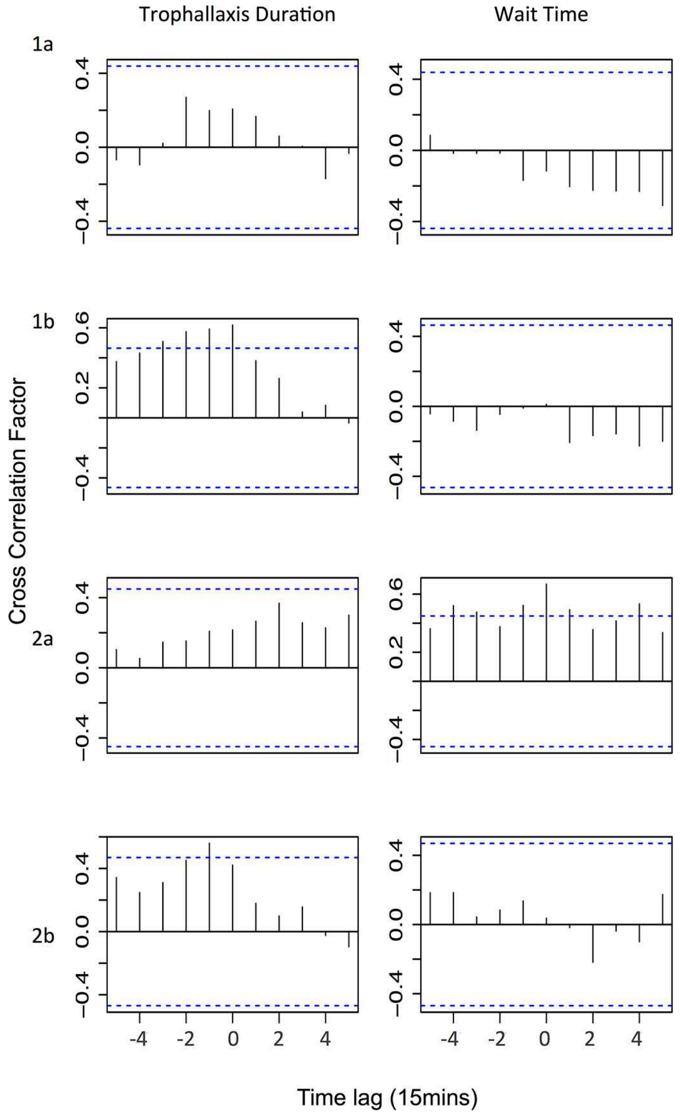

FIGURE 4 | Cross correlation test results showing correlations between either trophallaxis duration or wait time and the number of foragers leaving. Horizontal lines signify critical values corrected for multiple testing (Bonferroni correction: $\alpha = 0.0045$); a correlation at any time lag above that line is considered statically significant. Time lag is for foragers leaving relative to trophallaxis duration/wait time (i.e., positive time lag indicates that changes in the factor precede changes in foraging activity by the specified time lag).

(1991) did. Perhaps these differences are reflections in the variation in methods, particularly in terms of feeders used (capillary tubes vs. multi-well feeders) or where the trophallaxis duration measurements were made (in separate observation chambers or within the hive). In general, no artificial feeder mimics resource delivery of natural resources: flowers deliver tiny and extremely variable nectar amounts, but secrete nectar so slowly that they effectively have no "flow rate" where a bee can wait to fill up, and bees generally visit up to several hundred flowers on each trip (Castellanos et al., 2001). By utilizing trophallaxis duration we are able to make direct comparisons against previous studies (Seeley, 1986) using the same metric, but with natural resources. Thus, while there is perhaps not a consensus on how trophallaxis time relates to resource quality, it is a non-invasive measure previously shown to predict foraging decisions.

Wait time has universally been seen as a source of social information about the need for the particular food brought by a foraging honey bee (Seeley, 1989; Seeley and Tovey, 1994; Gil and Farina, 2002; Wainselboim and Farina, 2003; Goyret and Farina, 2005). What information precisely is contained in this cue, i.e., what social processes affect wait time, has been interpreted somewhat differently in different studies. It may be that the forager mainly receives information about the nutritional status of her colony (Seeley, 1989; Seeley and Tovey, 1994); others conclude that wait time is a reflection on the quality of the foragers resource relative to other resources exploited by the hive (Lindauer, 1961).

While our colony-level analysis included only marked bees (∼500, 25% of the colony), they represented a majority of the foragers, thus providing a good measure of colony foraging effort. Nevertheless, for the individual-level analysis we only recorded 29 bees foraging consistently ("employed" according to our operational definition). This sample size is similar to previous studies of this nature (Seeley and Tovey, 1994: 39 foragers; De Marco and Farina, 2001: 17 foragers), however, a larger study, with more foragers recorded as well as including more different days of foraging, would likely have made any effects of both resource quality and colony need for the resource more apparent. We do not conclude from our results that neither factor ever plays a role; after all, the possible effects of both had been demonstrated previously (Seeley, 1986; Seeley and Tovey, 1994). Despite this, however, our results do show that neither factor explains most of the variation in forager decisions.

One reason that we may not have seen an effect of either change in resource quality or wait time on the decision to stop foraging is that the magnitude of both of these effects is small under natural conditions. While several previous manipulative studies have demonstrated these effects, this study is the first that uses natural resources and no manipulation of worker allocation (Seeley, 1986; Seeley and Tovey, 1994; Wainselboim and Farina, 2003; Balbuena et al., 2011). Unlike the artificial feeders used in previous experiments, natural resource quality may change quite dramatically or subtly (Real and Rathcke, 1991; Boose, 1997; Edge et al., 2011). Furthermore, the potentially wide variety of resources being exploited may buffer large changes in the overall quantity and quality of nectar being brought into the hive (Donaldson-Matasci and Dornhaus, 2014). Barring any large-scale simultaneous resource landscape changes, the colony may experience relatively subtle and slow changes in resource intake. Continual adjustments in the ratio of receiver bees to foragers may allow the colony to track those changes without ever experiencing long wait times (Seeley, 1986). Thus colonies under natural conditions may rarely experience the dramatic increase in wait time induced by artificially removing receiver bees from the hive. Wait times could be primarily a byproduct of other colony level functions (such as shifts in worker allocation) rather than a result of resource dynamics. For example the density of bees in the entrance area (often called the dance floor) may be a good indicator to foragers on such shifts, and have been shown to vary throughout the day (Seeley, 1995). Such effects would increase the noise in the wait time cue, and may make its effect on foraging decisions less clear. By comparing these measures over the average time to the last, we hope to capture the greatest amount of change (i.e., the greatest decline in trophallaxis duration). However, it could be with the noise or subtly that natural conditions bring, that foragers use a series of poor indicators to make foraging decisions.

Another possible explanation for the observed lack of effect in our experiment is that both factors are important in nature, but which factor is most influential could change depending on the observed time frame. Our small sample size precluded analyzing the effects separately over different time periods, which might have kept us from finding a significant effect. In the morning, when resources are of higher quality, foraging bees might be willing to wait longer to unload to capitalize on the high quality nectar, in which case these foragers should be relativity insensitive to wait time and highly sensitive to changes in resource quality. Later in the day when there is a higher demand for workers elsewhere in the hive (for example cooling or water collecting) no matter the quality of the resource, the wait time to unload nectar could take precedence in their decision making (Johnson, 2003). At this later time we might then see the sensitivity to wait time increase relative to their response to changing nectar quality. As **Figure 3** illustrates, resource quality and unload time were dynamic across the day, which could have been due to the effects of changing resources or additional factors affecting colony organization. However, because we had relatively few employed foragers working consistently across the day, we did not have enough statistical power to test for changes in the importance of each factor over the course of the day. Additionally these factors could impact the decision much differently over a longer time period. While our study looked only at foraging dynamics within a relatively short time frame, previously studies have shown that bees will be more persistent on a previously strong rewarding resource even if it declines in quality (Al Toufailia et al., 2013).

In addition to variation within a single environment, differences in foraging conditions between environments could have shaped the foraging patterns we saw (Sherman and Visscher, 2002). Whether personal or social information is most important in an individual's decision to stop foraging at a particular resource may change depending on the foraging environments. For example previous work has shown that the benefit a colony receives from communication via the waggle dance depends on the resource environment (Donaldson-Matasci and Dornhaus, 2012). This could be true for the benefits of using a particular type of personal or social information (like waiting times) as well. For example, in environments with short lived, rich resources, using personal information about resource quality may allow a forager to secure a highly profitable resource before it disappears, regardless of possibly out-of-date social information. If resources are long-lived, the colony-level foraging effort should perhaps be more driven by colony need than resource availability. In that case, following wait time to learn about colony needs may ensure that the colony's nectar collection and processing rates are well balanced and efficient. Generally each of these sources of information have been shown to vary in their accuracy, with personal information being more accurate about a single exploited resource, but naïve about the resource landscape (Franks et al., 2003). Social information is thought to operate on a slower timescale than personal, potentially leading inaccuracy about specific resource due to transmission errors and the potential for it to be outdated (Rendell et al., 2010). However, social information allows for comparison among resources without requiring direct comparison by individuals. Thus what may favor the use of either social or personal information may be driven by the need for short term accuracy on about a specific resource (personal) or longer term information across resources (social) in a particular context. Further more different types of social and personal information exist and may be affected by environmental conditions separately. For example the waggle dance may be more suitable for ephemeral resources due to its fast response time, while floral odors shared among foragers may lend to steady resource patches.

In addition to being context dependent, what information a foraging honey bee uses to quit foraging on a particular resource could vary among individuals and among colonies. It has been shown that nectar response thresholds (the concentration of sucrose at which individuals respond) vary among individuals and colonies (Pankiw and Page, 2000). Individual variation in nectar response thresholds could provide a mechanism for the variation we see in the decision to abandon a resource, with high threshold individuals being more likely to abandon a resource when it declines in quality and low threshold individuals being more persistent. Similarly, inter-individual variation in sensitivity to wait time could obscure the colony-level correlation between increased wait time and quitting foraging. Future studies with larger numbers of marked individuals foraging over the course of several days could show whether individuals are consistent across their foraging careers in their sensitivity to declines in resource quality and/or wait time.

We have focused on two sources of information that foraging honey bees might use in making the decision to abandon a resource: personal information about resource quality, and social information about colony needs. However, it is likely that there is a stochastic element to their decision-making as well. Some have argued that individuals living in groups can afford to be less precise: individual variance in decision-making may be compensated by the reliability of the system as a whole (Oster and Wilson, 1978). Furthermore, some randomness in individual behavior can actually be good, in the context of collective behavior, because it may allow the group to respond more flexibly to changing environmental conditions (Deneubourg et al., 1983, 1986; Seeley et al., 1991; Detrain and Deneubourg, 2008; Townsend-Mehler and Dyer, 2011). For example, individuals may sometimes persist in foraging at even rather poor nectar sources ("inspectors"), just in case the resource increases in quality (Biesmeijer and de Vries, 2001; Biesmeijer and Seeley, 2005; Granovskiy et al., 2012). Likewise it could be advantageous for some individuals to abandon even a strong nectar source, in order to keep the colony from overcommitting to any single resource while potentially missing out on even stronger ones. Given the potential for rapid resource dynamics, a colony being "locked into" one or a few resources may miss newly emerging ones (Detrain and Deneubourg, 2008; Lanan et al., 2012).

If there is a strong element of randomness in a forager's decision to abandon a resource, it may be difficult to detect the subtler effects of personal or social information under natural foraging conditions. Our results may reflect a complex interplay of factors influencing honey bee decision making in natural environments, but the potential importance of stochasticity in these systems should not be overlooked.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Does the waggle dance help honey bees to forage at greater distances than expected for their body size?

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A honey bee colony has been likened to an oil company. Some members of the company or colony prospect for valuable liquid resources. When these are discovered other group members can be recruited to exploit the resource. The recruitment of nestmates to a specific location where there is a patch of flowers should change the economics of scouting, that is, the search for new resource patches. In particular, communication is predicted to make scouting at longer distances worthwhile because a profitable resource patch, once discovered, will enhance the foraging not only of the discoverer but also of nestmates that can be directed to the patch. By virtue of having large colonies and dance communication, honey bees are predicted to be able to profitably scout, and hence forage, at greater distances from the nest than either solitary bees or social bees without communication. We test this hypothesis by first examining existing data on foraging distance to evaluate whether honey bees do indeed forage at greater distances than other bees given their body size. Second, we present a simple cost-benefit analysis of scouting which indicates that communication causes longer range scouting to be more profitable. Overall, our analyses are supportive, but not conclusive, that honey bees forage further than would be expected given their size and that the waggle dance is a cause of the honey bee's exceptional foraging range.

Keywords: waggle dance, foraging distance, honey bee, central-place forager, foraging ecology

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Introduction

Honey bee workers, *Apis mellifera*, have a great foraging range. This is known from a variety of types of evidence, including training bees to syrup feeders, observing workers of rare body color on flowers at known distances from their hives, honey production in relation to distance to key forage sources, and the decoding of waggle dances (von Frisch, 1967; Visscher and Seeley, 1982; Beekman and Ratnieks, 2000; Ratnieks, 2007). Overall, it appears that the maximum foraging distance is in the region of 14 km (Beekman and Ratnieks, 2000). However, these long distances are not typical. Mean honey bee foraging distances range from a fraction of a kilometer to several kilometers (Visscher and Seeley, 1982; Beekman and Ratnieks, 2000; Couvillon et al., 2014a). Honey bees are economically sensitive foragers and prefer more rewarding food sources, such as those with higher sugar concentration (Seeley, 1995). Foraging further from the hive will incur greater costs (e.g., time, energy, risk) and distant food sources are likely used when high quality food patches are scarce or unavailable locally (Beekman and Ratnieks, 2000; Couvillon et al., 2014a).

Before a bee can forage on a patch of flowers, that patch must first be discovered. In the honey bee there is division of labor between scout and non-scout foragers (Seeley, 1995).

The location of a rewarding flower patch discovered by a scout bee, or being worked by any forager bee, can be communicated to nestmate workers via the waggle dance (von Frisch, 1967). Honey bee foraging has been likened to an oil company in which some members of the company or colony prospect for valuable liquid resources (Ratnieks, 2002). When these are discovered other group members can be recruited to exploit the resource. In solitary bees or social bees that do not communicate the locations of food sources to nestmates, such as bumble bees, each foraging bee must scout for its own flower patches. Bumble bee foragers invest time in "minoring," visiting a range of flower species, rather than just a single "major" species (Heinrich, 1976, 1979). This is a form of individual scouting and monitoring of foraging opportunities.

The ecological benefits of the waggle dance have been shown to vary with season and habitat. Through experimentally denying honey bees the ability to communicate the directional information in the dance, Sherman and Visscher (2002) showed that dance communication increased foraging success only at certain times of the year. Dance communication has also been shown to increase food collection in some habitats, namely those with clustered resources, higher flower species richness and number of flowers per patch, but not other habitats (Dornhaus and Chittka, 2004; Donaldson-Matasci and Dornhaus, 2012). Models have been slightly less conservative in predicting the benefits of dance communication. Dornhaus et al. (2006) and Schürch and Grüter (2014) both found that dance communication should be beneficial under a wide range of resource densities, but especially when resources were sparsely distributed. Beekman and Lew (2008) meanwhile, found that dancing was beneficial when resources were hard to find independently, i.e., they were small and distant, and dancing became detrimental when resources were both large and nearby. While the precise circumstances under which dance communication improves colony foraging, and the extent of these benefits, may be difficult to determine, what seems clear is that benefits depend on the distribution and abundance of floral resources in the environment.

The ability of honey bees, and also of other social insects including many ants (Wilson, 1971; Czaczkes et al., 2015) to direct nestmates to resource patches should change the economics of scouting, which is the search for new resource patches. In particular, Ratnieks (2002) proposed that communication should make scouting at longer distances from the nest more worthwhile. This is because a profitable resource patch, once discovered, will enhance the foraging not only of the discoverer but also of any nestmates that can be directed to it. This will benefit the colony as a whole, and will also increase the inclusive fitness of the worker who made the communication signal and those that received and acted on that signal. In other words, communication should change the optimal scouting strategy because it changes the cost to benefit ratio of scouting. By virtue of having both an effective means of communicating resource locations via the waggle dance and large colonies with many potential recruits, honey bees are predicted to be able to profitably scout, and hence forage, at greater distances from the nest than expected given their body size.

Here we develop the logic behind this hypothesis by formalizing it as a simple benefit-cost model, in which scouting at greater distance is more costly but can detect more high-quality resource patches because a larger area is surveyed. In support of the hypothesis, we show that there are foraging conditions under which a communicating bee will benefit more from far scouting while a non-communicating bee will benefit more from near scouting. In addition, we examine published data on the foraging range of different bee species to evaluate whether honey bees, *Apis* spp., have longer foraging ranges than other bees without the waggle dance. Unfortunately, the available data do not allow a conclusive test to be successfully made. In particular, it seems that *A. mellifera* may be the only bee species in which the existing data are sufficient to determine maximum foraging distance as opposed to actual foraging distances, which, from our knowledge of honey bee foraging distances, will often underestimate the maximum. Nevertheless, the data are compatible, and even suggestive, of greater foraging range in honey bees than expected from their body size.

Comparative Analysis of Bee Foraging Distances

Bee foraging distances have been determined using a wide variety of methods. In homing experiments, bees are captured and then released at various distances from the nest and the proportion of returning individuals is recorded (Janzen, 1971). In feeder-training experiments, foragers are trained to artificial syrup feeders near the nest, which are then incrementally moved to greater distances from the nest until foragers cease to visit (van Nieuwstadt and Iraheta, 1996). Tracking individuals with harmonic radar involves fitting bees with transponders and tracking them in real-time using radar (Osborne et al., 1999). Mark-recapture methods involve marking bees at the nest and locating them again in the field or vice-versa (Dramstad, 1996). In dance decoding, which is only possible with bees in the genus *Apis*, dances made by foragers when back at the nest are decoded to give the direction and distance vector to the food source from the nest (Visscher and Seeley, 1982; Dyer and Seeley, 1991; Beekman and Ratnieks, 2000; Couvillon et al., 2014b).

Each method has advantages and disadvantages for determining maximum foraging distance. For example, training honey bees to syrup feeders at long distances is difficult, especially when natural forage is abundant (Lindauer, 1948; FR personal experience). Beutler (1951) was able to train bees to 3 km while Lindauer (1948) did so to 12 km, but only under exceptional environmental circumstances: warm, sunny, and settled weather after autumn frosts had killed most flowers (von Frisch, 1967). Lindauer was also an exceptionally patient and talented experimenter (Seeley et al., 2002). Harmonic radar has the advantage of allowing insects to be tracked in real-time, but cannot detect insects behind obstacles such as hedges or buildings (Osborne et al., 1999). In practice, its range is limited to approximately 600 m, which means that it is not well-suited to determining maximum distances if they are greater than this.

Waggle dance decoding can be used to determine the foraging distances of thousands of bees, and can give a picture of how foraging distance changes seasonally (e.g., Couvillon et al., 2014a). If carried out in seasons of nectar dearth, some dances that are close to the maximum will be included, given that the maximum in the honey bee is also known from other methods and concurs with that found from dance decoding (Ratnieks, 2007). However, dance decoding may slightly underestimate the maximum as the bees trained to syrup feeders by Lindauer foraged to 12 km but did not dance beyond 11 km (von Frisch, 1967; Ratnieks, 2007). Decoding the distance information of a dance becomes increasingly imprecise the greater the distance indicated (Schürch et al., 2013), meaning that overestimation can also occur. Perhaps the biggest disadvantage of the waggle dance is that it is only made by the genus *Apis*, including *A. mellifera* and approximately eight additional species (Oldroyd and Wongsri, 2006), several of which have been studied using dance decoding (Dyer and Seeley, 1991).

Bees are capable of flying great distances. For example, a female of the large euglossine bee *Euplusia surinamensis* was recorded returning from 23 km in a homing experiment (Janzen, 1971) which suggests but does not prove great foraging range. Most individual bees however, typically forage much closer to the nest than the recorded maximum for their species (Zurbuchen et al., 2010; Couvillon et al., 2014a,b). This suggests that long distance foraging is only a profitable strategy under certain ecological conditions.

There is a well-established positive relationship between body size and foraging distance in birds and mammals (Haskell et al., 2002). For bees, a meta-analysis of 96 records for 62 species by Greenleaf et al. (2007) showed that larger bees also foraged at greater maximum distances. Separate analyses were made for distances obtained through homing and feeder-training experiments, and the latter included data from four honey bee species: *A. cerana, A. dorsata, A. florea,* and *A. mellifera* (**Figure 1**). However, the authors did not analyze waggle dance data as this was not available from other species. Most data points fell close to the regression line, but two for *A. mellifera* have large positive residuals (i.e., a greater foraging range that expected given body size). Since *A. mellifera* is better studied than the other bees analyzed, it is likely that this resulted in more extreme distances being recorded and hence the positive residuals. Indeed, two other data points for *A. mellifera* lie on the regression line. A suggestion from these data, but not a clear conclusion, is that *A. mellifera* is able to forage at greater distances than predicted by its body size.

What about the other honey bee species? All have waggle dances and so, if the communication hypothesis is correct, should also have greater than expected foraging distances. However, their data points fall close to the regression line. The feeder-training data for *A. cerana*, *A. dorsata,* and *A. florea* originated from Dyer and Seeley (1991), who studied colonies in a tropical rainforest in Thailand at the time of year when natural forage was at its peak. This will likely underestimate maximum foraging range for two reasons. First, we know from studies in both temperate and tropical ecosystems that honey bees travel furthest when resources in the landscape are most scarce (Schneider and McNally, 1993; Couvillon et al., 2014b,c). Second, training bees to feeders is difficult, especially when natural forage is abundant (Lindauer, 1948; FR personal experience).

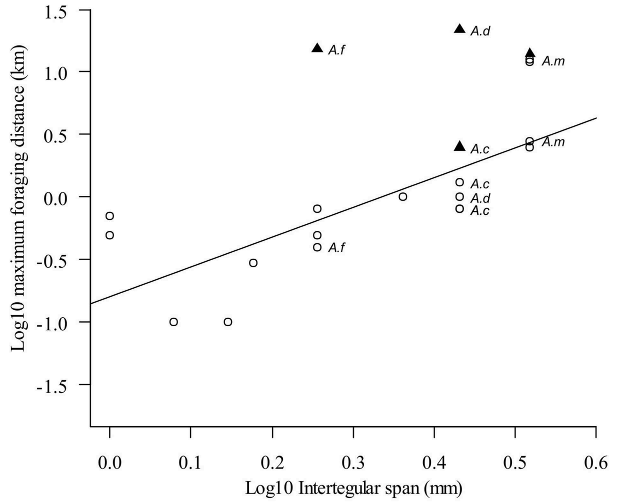

FIGURE 1 | Larger bees are capable of foraging at greater distances, but dance data indicates that honey bees forage further than predicted from their body size. White circles indicate maximum ranges from feeder training experiments analyzed in Greenleaf et al. (2007). Black triangles indicate maximum ranges from dances to natural foraging sites from Dyer and Seeley (1991) for *A. cerana*, *A. dorsata,* and *A. florea* and Beekman and Ratnieks (2000) for *A. mellifera*. Dance data indicate that all members of the genus *Apis* forage further than predicted by their body size. Reproduction of Figure 1b from Greenleaf et al. (2007) with permission.

Dyer and Seeley (1991) also recorded waggle dances to natural forage locations during their study. These dances indicated that some bees were foraging further than their feeder-trained bees. They were able to train *A. dorsata* to feeders at a maximum distance of 1 km, and bees danced for feeders only up to 900 m away. However, some dances for natural forage indicated distances of 21 km. In **Figure 1**, we plotted the foraging distances indicated by the foragers' dances alongside the data from Greenleaf et al. (2007). All four honey bee species now appear as positive residuals. For example, a bee the size of *A. mellifera* would be predicted to have a maximum foraging range of approximately 2.5 km, but the dance data indicates an actual foraging range of 14 km (from Beekman and Ratnieks, 2000). With the exception of *A. cerana*, all forage at least 10 km further than predicted by the regression line in Greenleaf et al. (2007). This suggests that all four honey bee species are able to forage further than predicted by their body size.

While there is compelling evidence for impressive maximum foraging distance in honey bees, *Apis*, we need to be wary about drawing a firm conclusion that honey bees forage at greater distances than expected from their body size. We have compared data gathered using two different methods, feeder-training and dance-decoding, which may not give comparable results for maximum foraging distance unless extensive data are available, as for *A. mellifera*. Greenleaf et al. (2007) also compared their predicted values from feeder-training data against observed measures gathered using alternate techniques such as mark-recapture and molecular methods. They found that their model using feeder-training data underestimated foraging distance vs. most other techniques.

All the non-*Apis* species shown in **Figure 1** are stingless bees (Apidae: Meliponinae), which also live in eusocial colonies but do not perform the waggle dance. However, stingless bees do have mechanisms for recruiting nestmates to specific locations (Lindauer and Kerr, 1958; Nieh and Roubik, 1995; Jarau et al., 2000; Nieh, 2004). These mechanisms, while less well-understood and perhaps less sophisticated than the waggle dance, could enhance the ability of these species to forage profitably at longer distances.

One of the methods used by stingless bees, trail pheromone marking (Lindauer and Kerr, 1958; Nieh et al., 2004), is unlikely to work at long distance as it would be energetically expensive and difficult to implement due to the volatile nature of pheromones. However, sound pulses, which are made by some *Melipona* (Nieh and Roubik, 1998), may function similarly to the waggle dance (Nieh et al., 2003). Unfortunately, compared with the wealth of studies measuring foraging distance in honey bees, the literature is less comprehensive for stingless bees. In one study, *M. mandacaia* foragers were trained to feeders up to 2.1 km away (Kuhn-Neto et al., 2009). This is almost the exact distance predicted by its body size, but the distance was based on visits to feeders, not natural forage.

Cost-benefit Analysis of Scouting Distance

Our argument is shown in **Figure 2**, which shows the benefit minus the cost for the maximum scouting distance for bees in a colony. Scouting at greater distances from the nest should have benefits as the chance to locate a high quality food patch is increased, although additional costs are incurred through increased time, energy expenditure and mortality risk. The benefit for the communicating bee is multiplied however, as scouts can recruit nestmates to the flower patches discovered. More importantly, the distance at which the benefit minus the cost is maximized is greater in the communicating bee than the non-communicating bee as is the maximum distance at which foraging remains profitable. This is because longer distance scouting will result in the discovery of more high quality patches to which recruits can be directed.

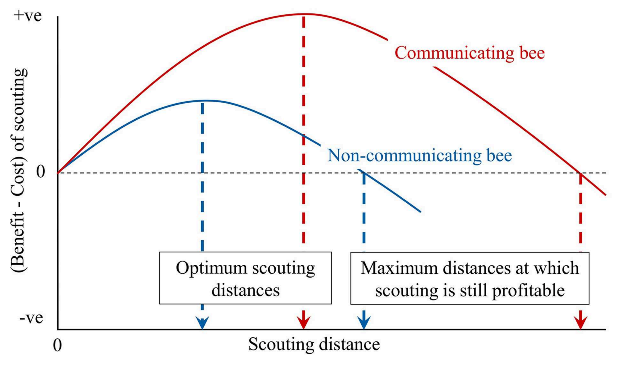

FIGURE 2 | Benefit minus cost for scouting distance for scout bees in a colony. In a communicating bee, such as a honey bee, the benefit is increased as scouts can recruit nestmates to high quality flower patches. More importantly, the distance at which benefit minus cost is maximized is greater in a communicating bee because longer distance scouting results in the discovery of more high quality patches to which recruits can be directed. In a non-communicating species, all bees are scouts as they have to find their own foraging patch. In the honey bee approximately 10% of the foragers are scouts.

Figure 3 shows scenarios that make this argument clearer. Here, two maximum scouting distances are considered, in which the "far" maximum is arbitrarily set at twice the "near" maximum. There are two types of flower patches in the environment, "high" and "low" quality. In **Figure 3B**, the rarer high quality resources (solid flowers) are quite common and so will be easy to find. In this situation near scouting will discover enough high quality patches to allow all or most of the colony's foragers to be directed to high quality patches. However, in **Figure 3A** the high quality patches are scarce. In this situation far scouting will enable more high quality patches to be discovered so that a greater proportion of the colony's foragers can be directed to high quality patches.

The two environmental scenarios shown in **Figure 3** reflect differences in foraging availability that may occur at a single location in different seasons, with different overall flower abundance (Couvillon et al., 2014a,b). In some seasons longer range foraging may be more important than in others. Indeed, in some seasons waggle dance communication does not enhance overall colony foraging performance, but seems to be most valuable in seasons when resources are scarce (Sherman and Visscher, 2002).

Discussion

Overall, our cost-benefit analysis shows how communication could increase the maximum distance at which bees should scout for flower patches and our comparative analysis provides empirical support for this. However, in carrying out this research we have been struck by the difficulty in making more than modest progress in either area. In particular, the data needed to go further seem not to be available, whether this is to build a detailed cost-benefit model of optimal scouting (and hence foraging) distances or to make a fair analysis of maximum foraging distance as a function of body size and communication ability.

Honey bee colonies simultaneously exploit multiple resources in the landscape (Seeley, 1995; Beekman et al., 2004). Locating nectar sources in the landscape is probably not that hard. However, locating high quality patches is likely far more difficult especially in habitats or during times of year when total available forage is low (**Figure 3A**). Between them, scouts will locate and advertise many resource patches. Scouts are more likely to dance for high quality patches (Seeley, 1995), and nestmates are more likely to be recruited by dances to the more profitable resources (Seeley et al., 1991). Recruits can thus bring back greater rewards on average than scouts (Seeley and Visscher, 1988). A colony whose workers scout at greater distances will discover more flower patches, including more high quality patches, than a colony in which scouting is at lesser distances. The colony can therefore, exploit the best resources in the landscape while ignoring the poor ones (Beekman and Lew, 2008). This will especially be the case in species with large colonies, as scouting at shorter distances will result in the same resource being discovered multiple times and so will not provide additional opportunities to other workers in the colony via communication.

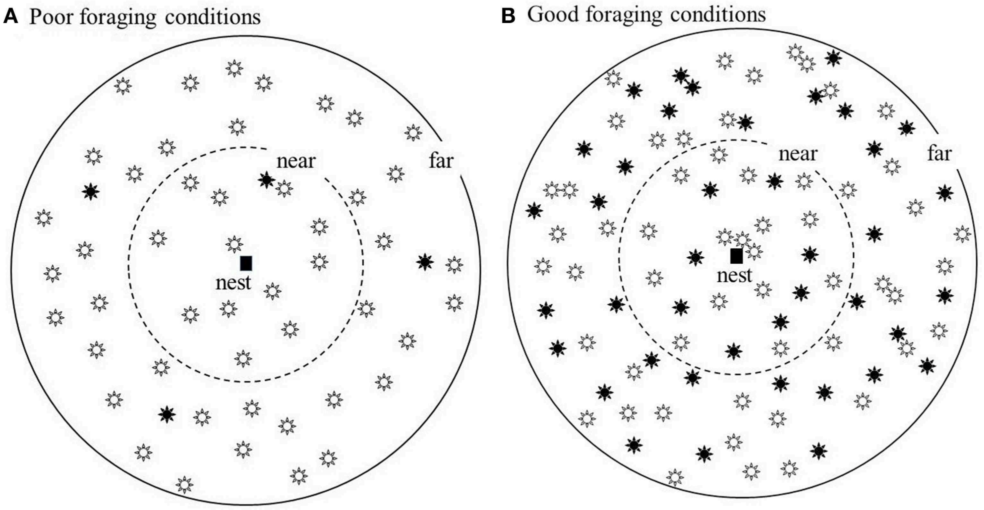

FIGURE 3 | Showing conditions where high quality resource patches, filled flowers, are scarce (A) or common (B); low quality resource patches are shown as open flowers. In **(B)**, high quality patches are sufficiently common that enough to satisfy the colony can be found within the "near" scouting distance. In **(A)** but not **(B)** scouting to the "far" distance is needed to find enough to satisfy the colony's foragers.

Our cost-benefit analysis follows the advice of the late Maynard Smith (1998, 2002), of our Department, who was of the opinion that "any theory to explain the complicated activities of organisms must always be simple." The cost-benefit analysis provides a scenario where communication will favor longer distance scouting and supports the previous conjecture to this effect (Ratnieks, 2002). This conclusion is based on what would appear to be sound assumption, namely that scouting at longer distance increases the chance of locating high quality resources.

This conclusion will not satisfy biologists who would like to be told the distances honey bees would scout at, were they unable to communicate via the waggle dance vs. able to do this. However, to make a more complete cost-benefit analysis of this would require data that would be hard to obtain. Among other things, we would need to know the sizes and distributions of resource patches and the costs of locating them. Indeed, there are many additional parameters involved, including the probability that a recruit will find the advertized resource patch as a function of distance to the nest (e.g., Schürch and Grüter, 2014). Our model also treats foragers in a binary fashion as either scouts or recruits. The situation in nature is more complex with foragers existing in several more dynamic states (Biesmeijer and de Vries, 2001; Biesmeijer and Seeley, 2005; Beekman et al., 2007).

The large numbers of workers in honey bee colonies probably has an influence on the benefits of the waggle dance to colony foraging. All things being equal, larger colonies will make long distance foraging more profitable, as there are a greater number of potential recruits. There is some evidence for this, as Beekman et al. (2004) found that while both small and large colonies of honey bees foraged further in the summer than spring, large colonies traveled further in the summer than did small ones. Large and small colonies exploited a similar number of patches, so rather than a large colony exploiting more patches, the data suggest that they may only exploit the best ones but must travel further to do so.

In the comparative analysis the main problem is that maximum foraging distances are imperfectly known. Indeed, it may well be the case that they are only well-known in *A. mellifera*. In this species several lines of evidence all give foraging maximum foraging distances of >10 km. In other *Apis* species, the maximum distances determined by training foragers to syrup feeders are markedly less than in *A. mellifera*. This almost certainly reflects the fact that *A. mellifera* is well-studied and more researchers have trained it to feeders than other *Apis* species. Furthermore, the *A. mellifera* distances were determined under environmental conditions that were suitable for determining the maximum distance, and by a highly skilled researcher. In our lab, we have trained honey bees to syrup feeders numerous times and have never been able to get them to visit feeders at great distances. In August, which is a month when foraging conditions are relatively poor (Couvillon et al., 2014c), the maximum was 1.28 km (Schürch et al., 2013), one tenth of what Lindauer achieved but close to what Dyer and Seeley (1991) achieved with *A. dorsata*.

On balance, we must accept the fact that the data for a full comparative analysis of bee foraging ranges in relation to the waggle dance are lacking. Ideally we would have actual maximum foraging ranges to natural food sources for several *Apis* species, non-*Apis* social bees known to communicate food locations (e.g., several stingless bees), social bees which do not communicate food locations (e.g., bumble bees), and solitary bees. There would be problems however, with collecting this data. As detailed here and in Greenleaf et al. (2007), there is no perfect method applicable to all bee species. If such a method did exist, the effort in collecting the data would still be huge. Additionally, if such a data set did exist it would have phylogenetic constraints, as there are no non-*Apis* species which make waggle dances (although similar mechanisms exist in stingless bees), and no *Apis* species which do not.

Another option is an experimental approach. Honey bee colonies can be manipulated so that they cannot communicate the direction element of the dance (e.g., Sherman and Visscher, 2002; Donaldson-Matasci and Dornhaus, 2012). This involves removing gravity and other factors (such as a directional light source) which might be used as a directional cue. This causes the now disorientated bees to dance in random directions. Under these conditions, the colony would forage at the locations found by bees scouting individually, without the quality filtering provided by the waggle dance in which only the best patches are advertised (Grüter et al., 2010). We predict that when waggle dance information is used to find flower patches, the average foraging distance will be greater in seasons of forage dearth due to the increased use of higher quality but more distant patches.

Despite the gaps which exist in the data, we can be sure that honey bees do forage at very great distances. The data are also suggestive that this is more than expected from their body size when compared to other bees. Our model indicates that the waggle dance should permit longer distance foraging under environmental conditions that can readily exist. However, our progress is modest and we cannot be conclusive in stating that the waggle dance is what makes long range foraging possible. Since von Frisch's early work, research on the waggle dance has continued to give insights into the behavior and ecology of the honey bee. The dance is now being studied with applications to environmental management, such as using honey bees as indicators of forage quality in the landscape (Couvillon et al., 2014b). Our analysis adds a small piece to this picture. However, we remain hopeful that the hypothesis will be more thoroughly tested when additional data allow a more complete comparative analysis and perhaps, also, through experiments that manipulate dance communication. Not only is the waggle dance an extraordinary behavior in itself, but it allows the honey bee to accomplish extraordinary things.

Acknowledgments

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The spatial information content of the honey bee waggle dance

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In 1954, Haldane and Spurway published a paper in which they discussed the information content of the honey bee waggle dance with regard to the ideas of Norbert Wiener, who had recently developed a formal theory of information. We return to this concept by reanalyzing the information content in both vector components (direction, distance) of the waggle dance using recent empirical data from a study that investigated the accuracy of the dance. Our results show that the direction component conveys 2.9 bits and the distance component 4.5 bits of information, which agrees to some extent with Haldane and Spurway's estimates that were based on data gathered by von Frisch. Of course, these are small amounts of information compared to what can be conveyed, given enough time, by human language, or compared to what is routinely transferred via the internet. Nevertheless, small amounts of information can be very valuable if it is the right information. The receivers of this information, the nestmate bees, know how to react adaptively so that the value of the information is not negated by its low information content.

Keywords: honey bee, waggle dance, information theory, spatial information, *Apis mellifera*

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1. Introduction

In 1954, Haldane and Spurway (1954) published a paper in the scientific journal *Insectes Sociaux* with the title "A statistical analysis of communication in *Apis mellifera* and a comparison with communication in other animals." Haldane and Spurway (1954), using the data set of Karl von Frisch, looked at the waggle dance communication using an information theory approach, at least in terms of the direction communicated by a dancing bee (von Frisch, 1946, 1967). Of course, von Frisch's primary target was to understand the dance language, not to obtain a precise calibration to study where the bees had foraged: he chose to work only with good dancers (Chittka and Dornhaus, 1999), which seems to underestimate systematically the error present in the dances (Schürch and Couvillon, 2013; Schürch et al., 2013) and therefore bias the data.

Many years have now passed since the original paper, and we have a better understanding of what—and how well—the bees indicate with their dance (Couvillon, 2012; Couvillon et al., 2012; Schürch et al., 2013). Therefore, we were interested to revisit the ideas and theories put forward by Haldane and Spurway (1954) by analyzing them with our own calibration data from Schürch et al. (2013).

Here we first present the components of information theory that are necessary to understand the information content of events with continuous outcomes, such as foraging distance and direction. We then apply the theory thus presented to the data from our previous calibration experiment (Schürch et al., 2013). Our estimates should give a more accurate depiction of the information content of the dance and therefore will have implications for research on the evolution of the waggle dance communication.

2. Information and Communication

When a bee performs a waggle dance, she transfers information to her unoccupied nestmates about the location of a resource, for example food or a new nest site she has visited (von Frisch, 1946, 1967). In information theory, information is defined as a reduction in uncertainty (Shannon, 1948). Hence, from an information theory viewpoint, a dancing bee will reduce in her dance followers the uncertainty of where she, the dancer, has been collecting her food, or where she has found a suitable nest site. Information theory affords us a way of quantifying the initial uncertainty and the uncertainty remaining after a dance has occurred, which therefore allows for a quantification of the information.

The uncertainty in information theory is usually termed entropy and commonly represented by the symbol H (Shannon, 1948; Norwich, 1994). If we first consider a random event with x discrete outcomes and the probability of the *ith* possible outcome has probability p_i, H is defined as

$$H = -\sum_{i=1}^{x} p_i \log(p_i). \tag{1}$$

For example, in the case of waggle dance communication, the outcomes could represent honey bee foraging distances in hundreds of meters, that is we look at the probabilities that a returned forager has foraged at 0–100 ($i = 1$), 100–200 ($i = 2$), 200–300 ($i = 3$), … meters, and p_i is the probability that a forager has foraged in the ith interval. In words, the uncertainty H is the sum of the weighted logarithms of the probabilities of the outcomes (Norwich, 1994). Choosing the base of the logarithm in the calculation of H is arbitrary. In computer science, the choice falls on base 2 because it reflects the on/off state of electronic switches, and the unit of H is the familiar bit. Following Norwich (1994) we use base e and natural units here, but we then convert our calculations to bits:

$$\text{bits} = \frac{\text{natural units}}{\ln 2}. \tag{2}$$

If information is the reduction in entropy, then, when H is reduced completely because we observe one of the discrete x outcomes, then information, $\mathcal{I}$, is given by $\mathcal{I} = H$.

In our example of honey bee foraging distances measured in hundreds of meters, we would exactly know whether a bee has foraged between 200 and 300 m, or 300 and 400 m. Of course, interference may prevent the dance followers from exactly determining the duration of a dance's waggle run that reflects the foraging distance, or dancing bees may be constrained in how accurately they can dance (Tanner and Visscher, 2010; Couvillon et al., 2012; Preece and Beekman, 2014). For a dance follower, or for human observers, some residual uncertainty may remain, and hence the number of possible intervals at which a bee could have foraged after we have observed her dance is greater than 1, and $\mathcal{I} < H$ (**Figure 1**).

Norwich (1994) gives an example related to language transmission over a noisy channel, for example a radio. We are asked to consider 10 possible numerals that are equally probable to be transmitted, so that entropy equals log 10. The spoken words for "five" and "nine" can be confused. So, even after one has heard the spoken numeral, there may be some uncertainty about whether "five" or "nine" was uttered at the sender's end. If after the transmission the probabilities of confusing "five" with "nine" and vice versa are equal, the entropy has been reduced from log 10 to log 2, but not to $\log 1 = 0$. The information in this case is given by the uncertainty before hearing the word minus the uncertainty remaining after hearing the word, that is

$$\mathcal{I} = H_{\text{before}} - H_{\text{after}} = \log 10 - \log 2 = 2.3 \text{ bit}. \tag{3}$$

From the definition of entropy, it also follows that the information, $\mathcal{I}$, depends on the set of values of the *a priori* probabilities, p_i. If we observe the dances of marked bees that have been trained to feeders at known distances, we cannot gain information about foraging distance by observing waggle run durations. The received information is not an absolute quantity (Norwich, 1994).

Regarding the waggle dance communication, we are now only left with one thing to consider. The foraging distance, as well as the directional component, are not communicated discretely but on a continuous scale. Let us suppose that the probability density function $p(x)$ represents the probability of a bee having foraged at distance x. Let x be measured in meters, and Δx is the constant length between discrete partitions of the continuous foraging distance. Then $p(x)\Delta x = p(500)(1)$ is a reasonable approximation to the probability that the foraging distance of a returned forager selected at random from the population will be found to have foraged between 500 and 500 + 1 m. We can also choose a convenient upper limit for our considerations; 14 km is maximum foraging distance in bees reported in the literature and seems a reasonable choice (Eckert, 1933). We could fragment the probability density function into a number of narrow rectangles with $\Delta x = 1$ m and calculate the entropy H:

$$H = -\sum_{i=1}^{14,000} p(\mathbf{x} = x_i) \log p(\mathbf{x} = x_i) \tag{4}$$

Note that if we would change our unit of measurement of bee foraging distances to cm, the uncertainty expressed by the entropy H would increase. If, on the other hand, we would take coarser measurements, say if we measured foraging distance in km, H would decrease. Similarly, we would see a change in the information conveyed by waggle dances. If we changed our unit of measurement to cm, we could receive a higher quantity of information, and with smaller and smaller units of measurement ($\Delta x \to 0$), we could in the end obtain an infinite quantity of information (Norwich, 1994). This is a question of resolution.

Of course, we do not gain an unlimited amount of information from a dance, because Δx is not getting smaller without boundaries. The accuracy with which the foraging distance of a bee can be estimated from observing a dance is limited (Schürch et al., 2013), and this seems to be true also for nestmates, not only

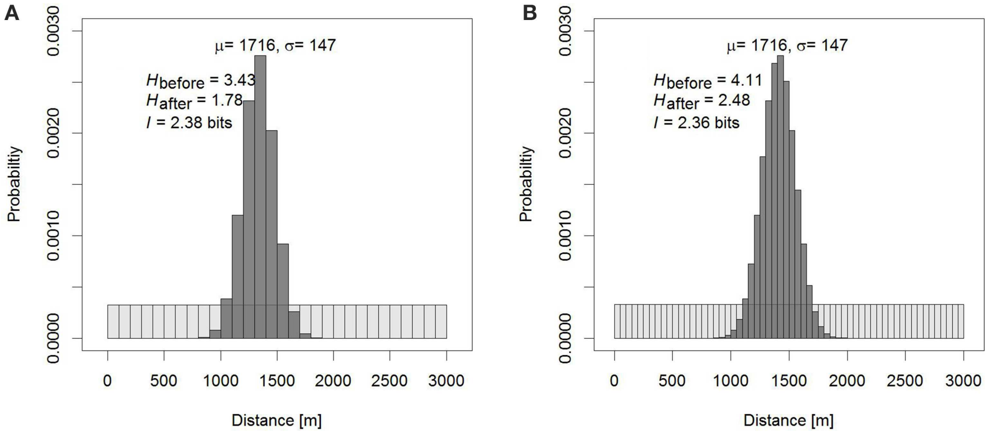

FIGURE 1 | Information of the dance as the reduction in uncertainty in the dance. (A) If we know that a bee has foraged between 0 and 3 km, but not where, our prior knowledge attributes equal probabilities to the possibilities that the bee has visited any of 30 × 100 m bins (light gray bins). Knowing how the dance translates into distance, after observing the dance our uncertainty is reduced to a narrower area around the estimated distance μ, which is dependent on the standard deviation σ (dark gray bins). The difference between our prior uncertainty and the uncertainty that remains after observing the dance is the information communicated by the dance. The uncertainties, the entropies H, depend on the size of the bins, but the information $\mathcal{I}$ does not. In **(B)**, smaller bins have been chosen, and the entropies increase compared to **(A)**, but the information does not change other than that the measurement of $\mathcal{I}$ is more accurate.

human observers (Seeley and Visscher, 1988; Towne and Gould, 1988; Tautz and Sandeman, 2003). It is unlikely that the accuracy of the measurement is as small as 1 m. Therefore, there is little point to measuring H with $\Delta x = 1$ m other than convenience, and therefore, we do not obtain an infinite quantity of information from a measurement of foraging distances through the waggle dance.

Luckily for us, while the differential entropy H_{after} tends toward infinity, for our practical considerations, it does not play a role. Since the terms that tend toward infinity in both H_{before} and H_{after} are the same, they cancel each other out when the difference is formed. As our prior expectations of where a bee has been, that is H_{before} is also increasing as our measuring intervals decrease, $\mathcal{I} = H_{\text{before}} - H_{\text{after}}$ approaches a constant as measuring intervals get smaller and smaller. For the purpose of measuring the information content empirically, it should therefore suffice to use discrete approximations for estimating H_{before} and H_{after}.

Using the information theory outlined above, we chose to pursue the procedure outlined below. When observing foragers that have returned, but before having observed their dances, we assume a flat prior knowledge: in terms of the direction the forager has flown, we give equal probability to any possible angle on the interval $[0, 2\pi)$. Similarly, we assume that the probability that a bee has flown any distance in the potential foraging range from $[0, 14 \text{ km})$ is equal to any other distance. That is, for both vector components, we assume uniform random distributions for our p_i before we observe the dance. How wide should our intervals for the p_i be? Should we measure distance in meters, or tens or hundreds of meters? In reality, the measurement would be a continuous one. If we were interested in the uncertainty before or after observing a dance exclusively, we would run into problems if we choose infinitesimally fine resolutions ($\Delta x \to 0$) for our measurements. As outlined above, for continuous random variables, entropy tends to infinity. As we also have seen, the information $\mathcal{I} = H_{\text{before}} - H_{\text{after}}$ will quickly approach our desired value, as we choose finer and finer resolutions. We therefore think it sufficient to consider a discrete approximation of our random variables, for distance, for example on the meter scale because that is convenient. To measure the information contained in both vector components, we use a numerical approach.

In our calibration experiment, we used normal errors to model the waggle run duration–distance calibration, and for the angles, we used the von Mises distribution. We will need to be able to calculate the probability densities for both vector components to calculate the entropy after observing a dance (H_{after}) using the respective probability distribution. To calculate H_{after} for the distance, we calculate the probabilities p_i at each discrete step i using the built-in function `dnorm` in R (R Core Team, 2013) using our empirical estimates of how accurately we could measure distance (Schürch et al., 2013; Couvillon et al., 2014a,b). To calculate H_{after} for the direction component of the vector, we used the `dvonmises` function from the circular package (Agostinelli and Lund, 2013) in R for all discrete steps i. Once we have p_i, we can then calculate the information easily, which we will do here for distance and direction separately. The programs to estimate the respective information contents can be found in the electronic Supplementary Material.

3. Distance

As the information gained when observing the waggle dance depends on the prior information available, much in our calculations depends on the choice of the functions for these prior expectations. If we observe a bee that we know is a returning forager, for example because she is trophallaxing, what is our knowledge? In a previous paper on the waggle run duration–distance calibration, we have argued that we only really know that the bee has not been further than 14 km (Eckert, 1933; Schürch et al., 2013), and we attributed equal probabilities to all distances between 0 and 14 km as our prior knowledge. We follow this argument here as well. However, we would like to caution the reader that we will probably get an estimate of the maximum information that can be transferred by the dance. An experienced forager (or human dance decoder) who has followed many dances on a given day already could "gain" less knowledge, because, for example, she already knows that average foraging distances are much shorter than the 14 km maximum foraging range.

Calculating H_{before} is straight-forward. If we measure foraging distance in meters, the probability p_i that a bee has visited any given ith distance is 1/14,000 for each of the is, and the entropy is

$$H_{\text{before}} = -\sum_{i=1}^{14,000} \frac{1}{14,000} \log \frac{1}{14,000} = 9.55. \tag{5}$$

For the H_{after} we have to discretize the continuous normal distribution and calculate the probability density at each step i

$$\begin{aligned} H_{\text{after}} &= -\sum_{i=1}^{14,000} \frac{1}{14,000} \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(i-\mu)^2}{2\sigma^2}} \\ &\quad \log \frac{1}{14,000} \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(i-\mu)^2}{2\sigma^2}} \end{aligned} \tag{6}$$

where μ is the mean and σ is the standard deviation of the normal distribution. Both these parameters can be estimated from observed dances using our calibration curve (Schürch et al., 2013; Couvillon et al., 2014a,b). Briefly, to get the probability distributions of foraging distances in Couvillon et al. (2014b) and Couvillon et al. (2014a) we used a linear calibration model using Gibbs sampling (described in Schürch et al., 2013, R and jags scripts for the calibration are available as Supplementary Material). From the posterior samples of this model ($N = 1000$ per dance) we then calculated the mean and the standard deviation for a given dance. **Table 1** lists these parameters from 10 dances of Couvillon et al. (2014a) selected at random. Note that for the calculation of the H_{after}, we have used 100 dances selected at random to calculate a mean $\mu = 1716.011$ m and a mean $\sigma = 147.246$ m. We then use a computer program (see Supplementary Material) to calculate H_{after} and consequently $\mathcal{I}$. If we do that, we get

$$H_{\text{after}} = 6.41 \tag{7}$$

and hence

$$\mathcal{I} = H_{\text{before}} - H_{\text{after}} = 9.55 - 6.41 = 3.14 \text{ natural units} \tag{8}$$

or 4.53 bits.

4. Direction

As for distance, we calculate the information of the directional component. Calculating H_{before} is once again straight-forward.

TABLE 1 | Ten randomly selected dances from Couvillon et al. (2014a).

Mean	SD
1896.5	152.6
2222.1	156.6
2263.7	162.5
1133.7	129.0
544.6	128.5
3204.2	176.2
923.3	133.4
657.2	136.3
1279.7	145.5
676.8	131.6

The number of steps i will depend on how we divide the circle. For example, if we divide the circle into 16 slices, our step size will be $\pi/8$. Through trial and error, we found that a step size of $\pi/512$ is sufficient for an accurate measurement of the information content. H_{before} is then simply

$$H_{\text{before}} = -\sum_{i=1}^{1024} \frac{1}{1024} \log \frac{1}{1024} = \log 1024 = 6.93 \tag{9}$$

For the calculation of H_{after} we employ the same method as in the distance situation, replacing the normal probability density function with the probability density function of the von Mises distribution:

$$H_{\text{after}} = -\sum_{i=1}^{1024} \frac{1}{1024} \cdot \frac{e^{\kappa \cos(i-\mu)}}{2\pi I_0(\kappa)} \log \frac{1}{1024} \cdot \frac{e^{\kappa \cos(i-\mu)}}{2\pi I_0(\kappa)} \tag{10}$$

where μ is the mean direction, κ is the concentration parameter and I_0 is the modified Bessel function of order 0. We used the circular package in R to calculate these probability densities (see Supplementary Material). We find that for $\mu = 0$ and $\kappa = 24.9$ (Schürch et al., 2013), the entropy is

$$H_{\text{after}} = 4.92, \tag{11}$$

and the information in the directional component is

$$\mathcal{I} = H_{\text{before}} - H_{\text{after}} = 6.93 - 4.92 = 2.01 \text{ natural units} \tag{12}$$

or 2.90 bits.

5. The Total Information in the Dance

The benefit of our recent approach to map the dance as a cloud of probabilities instead of a single point (Schürch et al., 2013; Couvillon et al., 2014a; Garbuzov et al., 2014) will now also allow us for the first time to calculate the combined spatial information directly (see **Figure 2**). We can overlay a finite landscape with a grid, and based on the simulated dances used in Couvillon et al. (2014a), we can calculate the probability that each of the squares in the grid has been visited. If each dance is represented by many simulations, the probability that a grid square had been visited by that dance was calculated as the number of simulated dances falling on that square divided by the total number of simulated dances.

We can again use a uniform prior expectation that each square has been visited, that is, our prior expectation of the probability that any square has been visited are assumed to be equal for all squares. We can calculate both H_{before} and H_{after}, and then the information is the reduction of the uncertainty. The electronic Supplementary Material provides an R script calculating the information on an ever finer grid. Our numerical computations demonstrate that for our prior assumption of uniform probability within a 14 km radius, and as we choose finer and finer grid squares, the information content of the dance approaches a value around 7.3 bits (**Figure 3**).

Note that for the calculation of information on the grid, we are now also limited by the number of simulated dances predicted from the calibration curve, and the smallest grid size we have chosen here is approximately 110 m. If we choose smaller grid sizes for 1000 simulations per dance, the probability landscape becomes discontinuous. More specifically, some of the grid squares will have no simulated dances on them, even though the probability that the general area had been visited was high. In that situation our discrete calculations do not reflect the true uncertainty anymore.

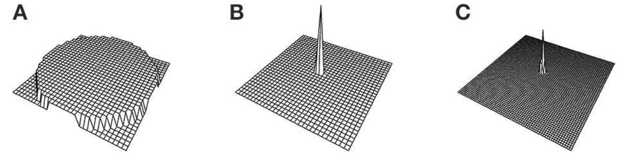

FIGURE 2 | If we lay a grid over a finite landscape, we can calculate for each grid square the probability that a dance has pointed to it. In **(A)** we see depicted the prior probability assuming equal probability for each square within a 14 km radius. In **(B,C)** we depict the probabilities after a dance has been observed for 1750 and 875 m grid square length, respectively. This corresponds to the 3rd and 4th iteration in **Figure 3**.

6. Discussion

Here we have shown, using previously published waggle dance calibration and waggle dance data, how to calculate the information content of the waggle dance. We also present an update on how much information is conveyed in waggle dances. In our first approach, where we discretized the distance and angular outcomes, we were able to calculate that the information about foraging distance conveyed by the dancing bees amounts to 4.53 bits, and that the angular information is 2.90 bits, for a summed information content of 7.43 bits. In a second approach, we have used simulated locations based on 10 waggle dances ($N = 1000$ per dance from Couvillon et al., 2014a) to show that the combined information content of the dance is about 7.3 bits, agreeing well with the single dance components measurement of information.

More than half a century has passed since the last attempt to calculate the information in the dance (Haldane and Spurway, 1954). Haldane and Spurway's seminal paper used data from von Frisch (1946). Since von Frisch and his pupils were more interested in the principles of the dance language instead of quantifying the information, they sought to eliminate variation in their experiments as much as possible (Chittka and Dornhaus, 1999), which creates difficulties for the calculation of information, as such calculations depend on this variation (Shannon, 1948; Norwich, 1994). Furthermore, Haldane and Spurway did not calculate the information for the distance component (Haldane and Spurway, 1954), which we have now done. We thought it therefore prudent to calculate the information conveyed by dancing bees by using our recent calibration and waggle dance data (Schürch et al., 2013; Couvillon et al., 2014a).

Our measurement for the angular information differs slightly from Haldane and Spurways (2.9 vs. 2.0 Haldane and Spurway, 1954), which could potentially be explained by a few reasons. First, as we have pointed out before, Haldane and Spurway used

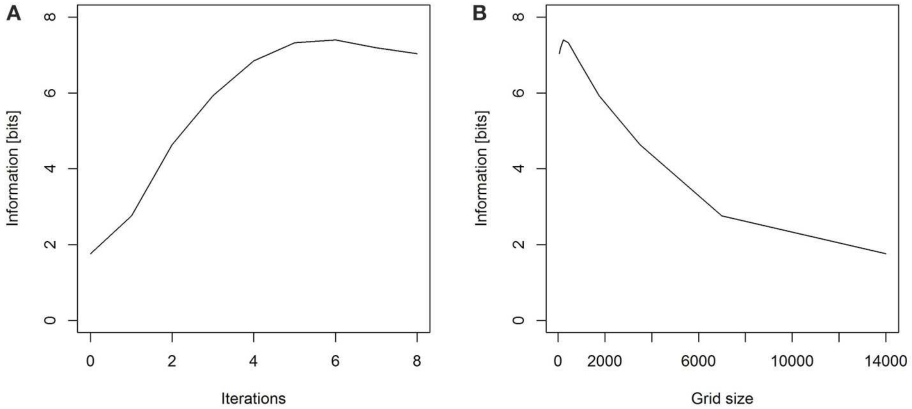

FIGURE 3 | (A) As the number of iterations increases and hence **(B)** the size of the squares in the grid decreases, the information gained by observing a dance approaches a value of around 7.3 bits.

data that were not collected in a manner that would make it suitable for the calculation of information. Secondly, the data they used were from a different bee sub-species. If there are dialects among bee species (Boch, 1956; Su et al., 2008), then the information contained in the dance might also differ from species to species (but see Dyer and Seeley, 1991).

We cannot compare our calculated information for distance with other values in the literature. Additionally, as this calculation depends on the prior distribution, comparing values will also only make sense if these prior assumptions are the same. For example, our decision to assume a uniform prior distribution is somewhat arbitrary, even if the interval over 0–14 km is based on the literature (Eckert, 1933), which probably gives a physiological upper limit for foraging distance. In our environment, in vicinity of the Laboratory of Apiculture and Social Insects in Sussex, bees seem not forage at distances greater than 7 km (Couvillon et al., 2014a,b). If we were to use only half the distance for our prior uniform distribution, the estimate of information changes accordingly (3.56 bits for a 7 km uniform prior). Of course, the same is true when using our second approach, where we calculated the information from a grid. We therefore urge the reader to focus not only on the specific values presented in this or any other paper. Clearly, more calibration data covering the whole diversity of honey bee races and species in a range of environments will be necessary to get a clearer understanding on how much information is in the dance.

Despite the limitations outlined above, our calculations are a first step, and important questions arise from the calculations. For example, how much information in a dance is useful to a colony? Is one bit of spatial information helpful, that is, fly north or south? How useful are two bits that could communicate four directions unambiguously (north, east, south, west)? And how much better are the 2.9 bits, that is sectors of the circle of about 50°, that bees communicate? Much will probably depend on the environment (Sherman and Visscher, 2002; Donaldson-Matasci and Dornhaus, 2012; Okada et al., 2012), or the benefits of the spatial information may also depend on colony size (Donaldson-Matasci et al., 2013). For example, if a hive were situated in the middle of a large-scale farming landscape with mass flowering crops, a dance with relatively little information might be informative, whereas in a more fragmented landscape with small flower patches, more information will be necessary to allow a dance follower to find an advertised resource. Future honey bee foraging models should incorporate variability in the dance's information to investigate the relationship between spatial information content and adaptiveness of the dance.

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Author Contributions

FLWR contributed to the concept and the writing of the manuscript. RS contributed to the concept, the numerical calculations, and the writing of the manuscript.

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Supplementary Material

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Why, when and where did honey bee dance communication evolve?

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Honey bees (*Apis* sp.) are the only known bee genus that uses nest-based communication to provide nest-mates with information about the location of resources, the so-called "dance language." Successful foragers perform waggle dances for high quality food sources and, when swarming, suitable nest-sites. However, since many species of social insects do not communicate the location of resources to their nest-mates, the question of why the "dance language" evolved in honey bees is of ongoing interest. We review recent theoretical and empirical research into the ecological circumstances that make dance communication beneficial in present day environments. This research suggests that the "dance language" is most beneficial when food sources differ greatly in quality and are hard to find. The dances of extant honey bee species differ in important ways, and phylogenetic studies suggest an increase in dance complexity over time: species with the least complex dance were the first to appear and species with the most complex dance are the most derived. We review the fossil record of honey bees and speculate about the time and context (foraging vs. swarming) in which spatially referential dance communication might have evolved. We conclude that there are few certainties about when the "dance language" first appeared; dance communication could be older than 40 million years and, thus, predate the genus *Apis*, or it could be as recent as 20 million years when extant honey bee species diverged during the early Miocene. The most parsimonious scenario assumes it evolved in a sub-tropical to temperate climate with patchy vegetation, somewhere in Eurasia.

Keywords: honey bee, waggle dance evolution, dance language, evolution of communication, honey bee foraging, honey bee evolution, social insect communication

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INTRODUCTION

In 1973, the Austrian scientist Karl von Frisch was awarded the Nobel Prize for his research on the honey bee waggle dance (Von Frisch, 1967). He recognized how this unique form of communication allowed bees to share information on the location of food sources with nest-mates. Von Frisch described the dance as "the most astounding example of non-primate communication that we know" (Von Frisch, 1967). However, there are still considerable gaps in our understanding of the ecological significance and evolutionary history of the honey bee "dance language" (Grüter and Farina, 2009). The dance, performed by a honey bee upon returning to the colony having successfully located a food source, offers information on the presence, odor, quality, direction, and distance of said food source, enabling nest-mates to exploit it (Von Frisch, 1967; Farina et al., 2005; Riley et al., 2005; Grüter and Farina, 2009). The direction information is conveyed through the orientation of the waggle run, whereas the distance information is expressed through the duration of the waggle run (for details see Von Frisch, 1967; Riley et al., 2005; Preece and Beekman, 2014). This direction and distance communication (also called "dance language") is unique to honey bees and will be the focus of this review. We aim to bring together research on how the honey bee and this complex form of communication evolved. We will do this by looking at theoretical and empirical studies on living honey bee species, and also phylogenetic and fossil studies on extinct and extant species. In bringing these studies together we hope to offer scenarios about where, when and why the dance language evolved.

ECOLOGICAL CONTEXT: WHEN IS DANCE COMMUNICATION BENEFICIAL?

An important feature of dance communication is that bees dance more for better resources (Von Frisch, 1967). A resource is graded depending on its energetic value with reference to the colonies current needs (Seeley, 1986, 1989). As a consequence, recruits of waggle dances can discover high quality food sources without having to sample other options in the area first-hand. There are, however, costs when using social information that do not exist when using other foraging strategies (memory or searching for new food sources) (Giraldeau et al., 2002; Grüter and Leadbeater, 2014). Recruited individuals often fail to find the advertised food source and must return to the colony to receive more information (Seeley and Visscher, 1988; Couvillon et al., 2014; Grüter and Leadbeater, 2014). Such failures are both temporally and energetically expensive. Furthermore, in rapidly changing environments social information can quickly become outdated and therefore unreliable (Giraldeau et al., 2002; Grüter and Leadbeater, 2014). Hence, there might be conditions when using spatial information within a waggle dance is not the most effective strategy. There are many examples of social insect species that do not communicate spatial information to nest mates, making the use of such communication in honey bees all the more interesting (Dornhaus and Chittka, 1999; Nieh, 2004).

The results of empirical and theoretical studies using *Apis mellifera* as a model system suggest that the benefits of spatial dance information depend critically on the spatiotemporal distribution of food sources (Sherman and Visscher, 2002; Dornhaus and Chittka, 2004; Beekman and Lew, 2008; Bailis et al., 2010; Donaldson-Matasci and Dornhaus, 2012; Schürch and Grüter, 2014). In particular, studies using horizontally oriented dance floors in the dark have provided interesting indications about the habitats in which the waggle dance is beneficial. By orienting the dance floor so the bees have no reference to gravity, the dance is disrupted and the spatial information (distance and direction, but not presence and olfactory information) is lost (Von Frisch, 1967). Consequently, bees still perform and follow dances but no useful spatial information is passed on. In a pioneering study, Sherman and Visscher (2002) looked at the effect of spatial information in the dance on foraging success during different periods of the year in California. They found that the spatial information improved foraging success in the winter, but not in the summer or autumn months. During winter, resources are sparser than in summer and using spatial information could be more beneficial during this period since the chances of discovering resources by independent scouting are lower. Similarly, a study carried out by Dornhaus and Chittka (2004) found spatial information to be beneficial to colony foraging success in a tropical habitat but not in two temperate habitats (Dornhaus and Chittka, 2004). Again the spatiotemporal distribution of resources was considered to be the reason for the result as tropical habitats are characterized by clustered and shorter-lived food sources when compared to temperate habitats. Donaldson-Matasci and Dornhaus (2012) assessed the benefits of spatial information in five habitats and found a positive effect in just one, a habitat characterized by many flower species. High species richness might increase the variability of floral rewards in the environment and spatial dance information could allow the colony to concentrate foraging on the most rewarding resources (Donaldson-Matasci and Dornhaus, 2014). Taken together, these empirical studies suggest that the benefits of the "dance language" are highly dependent on patterns of resource availability.

It is important to mention that the failure to detect foraging benefits of spatial information in certain habitats could be caused by methodological problems. First, sample sizes were small in these studies (2–6 colonies per location). Second, it has been argued that experimental designs were prone to being confounded by memory effects (Schürch and Grüter, 2014). Colonies were switched between normal and disrupted dance conditions every 2–3 days (Dornhaus and Chittka, 2004; Donaldson-Matasci and Dornhaus, 2012) or a variable number of days (Sherman and Visscher, 2002). Given that bees can return to the same resource location for many days (Ribbands, 1949; Moore and Doherty, 2009; Grüter and Ratnieks, 2011; Al Toufailia et al., 2013), it is not possible to determine whether the food sources exploited during one treatment were discovered during the same or a previous treatment period. In other words, a bee exploiting a food source during disoriented conditions might have been recruited to this food source days earlier by following an oriented dance. Schürch and Grüter (2014) used an agent based model to investigate this effect of memory by simulating various experimental designs (Schürch and Grüter, 2014). Their simulations suggest that the use of individual memory could have masked the benefits of spatial information in many environments.

Despite the aforementioned caveats, theoretical modeling studies strongly support the hypothesis that the benefit of spatial information depends on the spatiotemporal distribution of resources. Dornhaus et al. (2006) found that dancing should be most beneficial in environments where patches are few and of variable quality (Dornhaus et al., 2006), whereas Beekman and Lew found that dancing should be advantageous if patch sizes are small and therefore difficult to find (Beekman and Lew, 2008). Schürch and Grüter (2014) similarly found dance recruitment to a resource to be most beneficial when food sites are at low densities, but their simulations also revealed a more unexpected finding. It is usually thought that dancing is most beneficial when resource patches are ephemeral (Sherman and Visscher, 2002;

Grüter and Ratnieks, 2011), but Schürch and Grüter's results suggested spatial information helps most when food sources are stable for longer periods of time because successful recruitment events lead to long-term benefits through individual memory (Schürch and Grüter, 2014).

Given these empirical and theoretical findings it has been suggested that the "dance language" evolved in a tropical habitat in response to the clustered spatial distribution of food patches and the great diversity of food sources (Sherman and Visscher, 2002; Dornhaus and Chittka, 2004; Dornhaus et al., 2006). However, it is important to note that details of dance communication, e.g., the precision of dancing or the ability of dance followers to extract information and locate advertised food sources, would most likely have been different when it first evolved. These aspects affect the costs and benefits of dancing and, therefore, the colony-level performance gains for dancing ancestors might have been different.

EVOLUTIONARY CONTEXT: WHERE AND WHEN DID THE "DANCE LANGUAGE" EVOLVE?

Extant Species of *Apis*

The greatest diversity of extant *Apis* species is found in tropical Asia. There is debate as to the true number of *Apis* species: at the conservative end there are 6 or 7 (Alexander, 1991; Engel and Schultz, 1997) recognized extant species of *Apis,* while others have argued that there are 10 or 11 species (Arias and Sheppard, 2005; Lo et al., 2010). All extant species dance to communicate the location of food resources and nest sites (Dyer, 2002; Oldroyd and Wongsiri, 2006; Beekman et al., 2015). There is a general consensus between morphological, molecular and behavior studies as to the evolution of the honey bees (Engel and Schultz, 1997). The dwarf honey bees (extant species *A. florea* and *A. andreniformis*) were the first to diverge from an *Apis* ancestor (Kotthoff et al., 2013). Dwarf honey bees are open-nesting species that construct a single wax comb on a tree branch (Alexander, 1991; Wongsiri et al., 1996; Michener, 2000; Arias and Sheppard, 2005). The next species to diverge were the open-nesting giant honey bees (extant species *A. dorsata* and *A. laboriosa*). Giant honey bees construct a single wax comb under tree branches, rocks and also human buildings. The most derived species are the cavity nesting honey bees (extant species *A. mellifera, A. cerana, A. nigrocincta,* and *A. koschevnikovi*).

All extant species dance to communicate the location of food resources and nest sites (Dyer, 2002; Oldroyd and Wongsiri, 2006; Beekman et al., 2015). Pioneering research by Martin Lindauer on three of these species led to his proposal that there is a progression in dance complexity that corresponds to phylogenetic development of the dance (Lindauer, 1956). *A. florea* (dwarf honey bee) uses celestial cues when orienting its dance and is unable to use gravity as a reference (Lindauer, 1956). This honey bee indicates food source location by dancing on a horizontal or sloped (Dyer, 2002) surface in the direction of the food source (**Figure 1A**) (Koeniger et al., 1982). *Apis dorsata*, (giant honey bee) dances on the vertical comb surface and therefore cannot point in the direction of the food source (Dyer, 1985), but instead translates the direction to the food source in relation to the position of the sun into a waggle run angle relative to gravity (**Figure 1B**) (Dyer, 2002, Figure 1.2). Interestingly, *A. dorsata* can use gravity without direct sight of the sun (Dyer, 1985), for example when foraging nocturnally (using the suns position despite it being beyond the horizon) or under a blanket of other bees (Dyer, 1985; Oldroyd and Wongsiri, 2006). *Apis dorsata* also produce auditory signals when dancing, which might assist followers in finding and following dances performed in the dark (Michelsen et al., 1986; Kirchner and Dreller, 1993). Finally, the most derived form of the waggle dance is carried out by cavity dwelling *A. cerana, A. mellifera, A. nuluensis, and A. nigrocinta.* Cavity dwelling species are able to use celestial cues on a horizontal dance floor when swarming or on experimentally manipulated combs (only studied in *A. cerana* and *A. mellifera*), but most of the time they orientate their dances

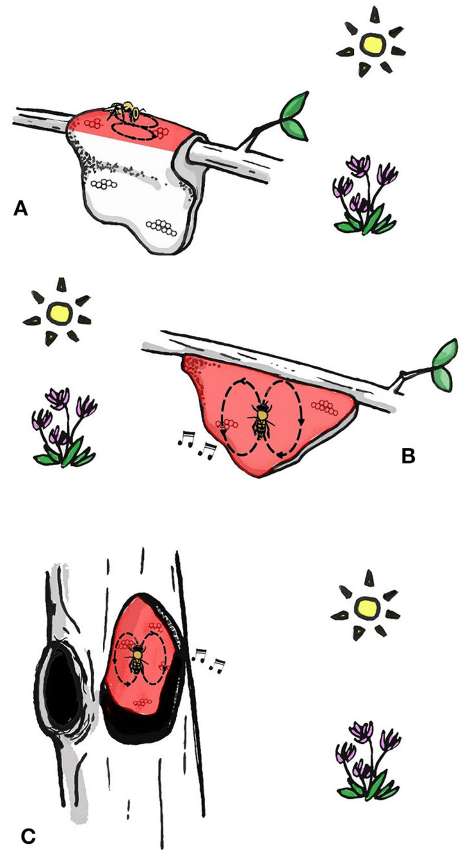

FIGURE 1 | The increasing sophistication of the dance language with phylogenetic development of the dance. (A) Dwarf honey bees perform dances on horizontal surface in the direction of the food source. **(B)** Giant honey bees perform dances on vertical surface and orient dances with gravity and celestial cues. *Apis dorsata* also has auditory cues when dancing. **(C)** Cavity-nesting honey bees perform dances in darkness on a vertical surface. Dances are oriented with gravity and celestial cues. All species produce auditory cue when dancing. Bees in **(B,C)** are both dancing directly upwards, indicating that the food source is in the direction of the sun. Areas of the comb on which bees dance are colored red.

with reference to gravity in the dark nest (**Figure 1C**). These species also produce auditory signals when dancing (Michelsen et al., 1986). The ability to orientate dances in complete darkness might have enabled bees to nest in cavities, because prior to this they could not communicate in the dark. However, it is possible that cavity-nesting evolved before the ability to orient dances in darkness using gravity (Oldroyd and Wongsiri, 2006). The dances of *A. mellifera* and *A. cerana* are so similar that each species will follow and decode dances of the other (Tan et al., 2008).

A study carried out by Raffiudin and Crozier supports several aspects of Lindauer's hypothesis of an evolutionary sequence from open nesting with less complex dances to cavity nesting with more complex dances (Raffiudin and Crozier, 2007). Based on DNA sequences of several honey bee species they found that the common ancestor of extant honey bees probably nested in the open and likely to have produced silent dances on a single vertical comb (Engel and Schultz, 1997). Raffiudin and Crozier (2007) suggest that the common ancestor of *Apis* danced vertically, not horizontally like the dwarf honey bees (but see Engel and Schultz, 1997). The common ancestor of the giant and cavity-nesting honey bees was inferred to have had a sound-producing vertical dance (Oldroyd and Wongsiri, 2006) suggesting that sound production when dancing evolved once. Interestingly, the giant honey bee *A. laboriosa* does not seem to produce sounds and it remains unknown whether this acoustical addition was lost in *A. laboriosa* or if it were gained independently in giant and cavity-nesting honey bees (Kirchner et al., 1996).

Extinct Ancestors

Bees evolved from apoid wasps (Apoidea) approximately 140–110 million years ago (Danforth et al., 2013). The oldest known eusocial bee fossil is *Cretotrigona prisca*. It was found in Cretaceous New Jersey amber and is estimated to be 65–70 million years old (Michener and Grimaldi, 1988; Engel, 2000). This fossil is remarkable because of its similarities with workers of present day stingless bees (Meliponini), which are a derived group of highly eusocial bees. The fossil indicates that sociality most likely existed in bees during this period and this is a key prerequisite for the evolution of dance communication. The weak fossil record of bees older than 50 million years means that it is difficult to put an accurate date on the origin of the genus *Apis*. Many fossilized Hymenoptera have been found in Baltic amber (40–50 million years old) (Ruttner, 1988). During this period global temperature started to decrease (Zachos et al., 2001) and Europe became more temperate. Such changes would have affected resource distribution and therefore may have affected the costs and benefits of foraging communication.

It was long believed that *Apis* evolved and diversified in tropical Asia (e.g., Ruttner, 1988), but *Apis* fossils discovered in France and Germany in recent years, in combination with the current distribution of honey bee species, suggest that the center of origin was in Europe, most likely around the time of the major climatic shift of the Eocene-Oligocene transition (c. 30 million years ago, see **Figure 2**) (Engel, 2006; Kotthoff et al., 2013). These fossils show a remarkable morphological diversity in European Apini during the late Oligocene and early Miocene (Kotthoff et al., 2011). If the dance did originate at the same time as *Apis* then it might have evolved in Europe, rather than in Asia. Fossils from Japan and the US suggest that different species of honey bee were present in many areas of the world during the Miocene (Nel et al., 1999; Engel, 2006; Engel et al., 2009; Kotthoff et al., 2011, 2013), but a global cooling starting in Mid-Miocene (c. 15 million years ago) probably brought the demise of ancient honey bees in Europe, some parts of Asia and Northern America (Ruttner, 1988; Engel et al., 2009).

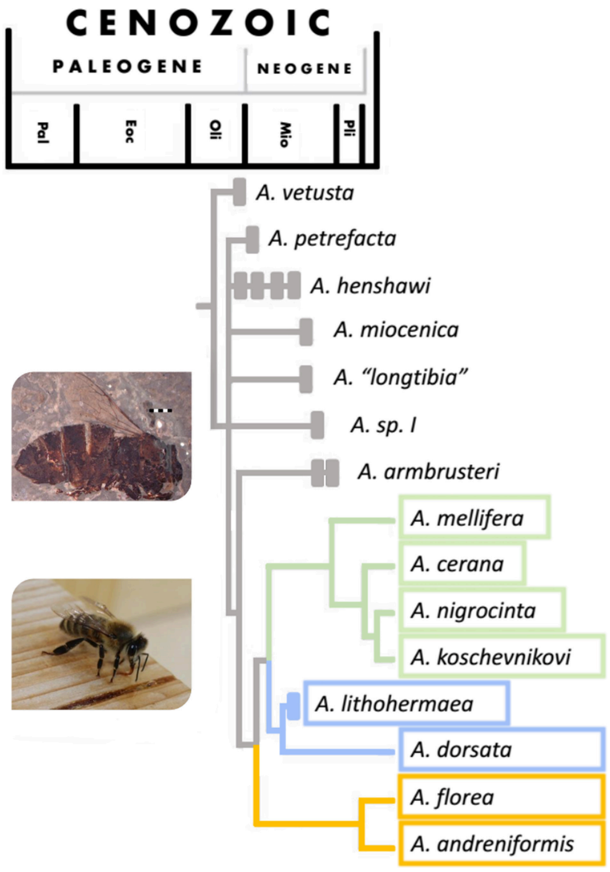

FIGURE 2 | Phylogeny of the *Apis* genus with timeline (figure adapted from Engel, 2006). For a more recent phylogeny see Raffiudin and Crozier (2007). Solid bars show periods from which major fossils have been found. Species whose timeline finishes with a solid bar are extinct. Colors relate to nesting/dancing behavior of the groups: green—cavity nesting, vertical dancing species, blue—open nesting, vertical dancing species and orange—open nesting, horizontal dancing species. Images show a fossilized honey bee found in Randeck Maar (*Apis armbrusteri* Zeuner) (Scale bar = 2 mm. Photo from Kotthoff et al., 2011) and an *Apis mellifera* worker.

We can see evidence of advanced eusociality in *Apis* fossils (worker-like morphology), though it is highly likely that it evolved well before the first *Apis* appeared [both *Cretotrigona prisca* (65–70 million years old) and *Electrapis* (33.9–56 million years old) are considered highly eusocial (Engel, 1998; Grimaldi and Engel, 2005)]. Fossilized *A. armbrusteri* (see **Figure 2**), a honeybee that lived around 25–20 million years ago in Europe resemble the workers of *A. mellifera* and one particular *A.*

armbrusteri fossil contains 17 closely packed individuals; possibly a fragment of a swarm (Seeley, 1985).

When and in What Context Did Waggle Dance Communication Evolve?

Some authors have proposed that the honey bee dance originally evolved to allow bees to select a nest site and that the dance was only later co-opted for foraging (Oldroyd and Wongsiri, 2006; Beekman et al., 2008; Beekman and Lew, 2008). Indeed, dance communication plays a fundamental role during swarming and nest-site selection (Seeley, 2010): when colonies look for a new nest site they send out scouts to evaluate and propose different options to their sisters with their dances. This leads to the build-up of more scouts at good nest sites until a quorum is reached at a particularly good site. Then the swarm lifts off and flies to this new nest location (Seeley, 2010). Thus, it is hard to see how honey bee swarming would work without dance communication. Of course if swarming functioned in a different way in ancestral honey bees then the "dance language" may not have been required. As we have seen earlier, the "dance language" does not seem to be equally important in foraging. There are other species of social insects that communicate the location of nest sites, but not of food sources. Many swarm-founding wasps, for example, use pheromone trails to recruit nest-mates to new nest-sites, but not to food sources (Jeanne, 1980). On the other hand, early *Apis* were probably open-nesting species and therefore nest sites (branches on a tree) would have been relatively easy find in the vicinity of the mother nest. Food sites, however, were subject to competition and the dance would enable a colony to locate and exploit them even if they were at a substantial distance from the nest (Ratnieks and Shackleton, 2015). The dance may then have been co-opted for nest site location as bees diversified and became more specialized. A third possibility is that it evolved simultaneously in both contexts. If high quality nest sites and high quality food sources both represent rewards for bees and are processed in similar ways in the bee brain, then dance communication might have been used in both contexts as soon as it appeared. Work on the neurological basis of reward learning in bees has shown that there are particular neurons within the bee brain that encode and process reward information (Hammer, 1997). It would be interesting to know if the same neurons are involved when evaluating new nest sites.

Dance communication probably evolved in a highly eusocial species. However, because the phylogenetic relationships among the corbiculate bees are still not resolved (reviewed in Almeida and Porto, 2014) it remains unclear when honey bee ancestors evolved higher eusociality. If it evolved twice, once in the Meliponini and once in the Apini (Cameron, 1993; Koulianos et al., 1999; Cameron and Mardulyn, 2001; Cardinal and Danforth, 2011), then higher eusociality evolved after the two groups separated c. 80 million years ago (Cardinal and Danforth, 2011). If, however, Apini and Meliponini are sister groups with a common highly eusocial ancestor (Roig-Alsina et al., 1993; Engel, 2001; Noll, 2002; Cardinal and Packer, 2007), then higher eusociality in *Apis* ancestors is probably older than 80 million years. Thus, there is a possibility that spatially referential dance-like communication evolved as early as c. 70–80 million years ago. However, this seems very unlikely and the "dance language" is probably much younger. Extant honey bees diverged in the early Miocene (ca. 20 million years ago) (Engel, 2006; Cardinal and Danforth, 2011). Because all extant species use the "dance language" we can be confident that their common ancestor also used a dance communication (Oldroyd and Wongsiri, 2006; Raffiudin and Crozier, 2007). This provides a lower boundary of c. 20 million years before present for the evolution of the "dance language." Genetic analyses suggest the split between the cavity nesting *A. mellifera* and *A. cerana* may have occurred 8 million years ago (Han et al., 2012), which would imply that the dances in dark cavities are at least 8 million years old.

Seeley (1985) suggested that a period of honey bee diversification around the Eocene/Oligocene boundary was followed by a period of 30 million years of relative stasis in their morphological evolution. He argued that if social behavior and worker morphology evolved in tandem, the social organization and communication system (including the waggle dance) we see today in honey bees would be at least 30 million years old (Seeley, 1985). On the other hand, fossils discovered in recent years show a great amount of morphological diversity in European Apini during the Miocene (23–5.3 million years ago) (Kotthoff et al., 2011, 2013). In our opinion, it is currently not possible to exclude a much earlier or a later origin of the "dance language."

CONCLUSIONS

A combination of theoretical and empirical studies has increased our understanding of why present day honey bees dance to indicate the location of valuable resources. These studies suggest that the spatial information acquired from a dance is most valuable in environments with resources that are spatially clustered, difficult to find, temporally stable, and variable in quality. Phylogenetic studies offer support for the theory of progressing dance complexity with phylogenetic development. The fossil record of *Apis* has become more informative in recent years and this information suggests that the genus originated in Europe rather than in Asia. This raises the possibility that the "dance language" evolved in Europe as well. We cannot exclude that the "dance language" pre-dates the earliest *Apis*, but it is likely to be younger and could have evolved as recently as 20 million years ago when the extant honey bee species diverged during the early Miocene.

Future empirical work should further explore the costs and benefits of dance communication. The work of Seeley (1983) and Seeley and Visscher (1988) suggests that dance following in *A. mellifera* living in temperate habitats is more costly in terms of time than independent food search, but leads to better food sources. However, what about costs and benefits in other habitats and in other species? Furthermore, if the waggle dance is of less benefit to the colony in temperate climates, do bees in temperate areas use the language more selectively?

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Information transfer beyond the waggle dance: observational learning in bees and flies

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Social information transfer is part of the success of animal societies and has been documented in a variety of taxa, from slime molds to humans. In invertebrates, the historical research focus has been on the specialized signals shaped by selection to convey information, such as the honeybee waggle dance. However, growing evidence shows that invertebrates also commonly glean critical information about their environment by observing others. For instance, a bumblebee's choice between novel flower species is influenced by the observation of the foraging choices of more experienced conspecifics. Recent studies suggest that these seemingly complex learning abilities can be explained in terms of simple associative learning, whereby individuals learn to associate social cues (conditioned stimuli) to reward cues (unconditioned stimuli). Here, we review the behavioral evidence of observational learning both in bees and *Drosophila*. We discuss the validity of associative accounts of observational learning and the potential neural circuits mediating visual social learning in these model species to define future research avenues for studying the neurobiology of social cognition in miniature brains.

Keywords: bumblebees, *Drosophila,* social cognition, social learning, visual cognition

Introduction

The waggle dance of the honey bee constitutes one of the most sophisticated systems known for information transfer about profitable food sources (Von Frisch, 1967). A successful forager performs a stereotyped behavior within the hive, originally described as a "dance," which conveys information about the direction and distance from the hive of an exploited food source (Riley et al., 2005; Grüter and Farina, 2009; Seeley, 2010). This dance "language" is a case of true communication (Markl, 1985) whereby the sender explicitly transfers information to the receivers in order to modify their behavior. Yet, many animals use social information to learn about their environment simply by attending the behavior of others (Danchin et al., 2004; Galef and Laland, 2005). This type of social learning differs from true communication in that the demonstrator does not explicitly attempt to modify the receiver's behavior. In this review we will focus on social learning based on visual observation of a demonstrator's behavior (Zentall, 2012).

Invertebrates provide paradigmatic examples of observational learning. For instance, *Octopus* observers that are allowed to watch conditioned *Octopus* demonstrators choosing one of two different colored objects presented simultaneously, consistently select the same object as the demonstrators did (Fiorito and Scotto, 1992). Other fascinating cases are found among insects. These animals exhibit developed learning capacities and accessible miniature nervous systems, thereby constituting ideal organisms for dissecting the neural and molecular bases of learning (Giurfa, 2013). Model species, such as the honey bee *Apis mellifera* (Menzel, 1999; Giurfa, 2007; Galizia et al., 2012), and the fruit fly *Drosophila melanogaster* (Heisenberg, 2003; Davis, 2005; Guven-Ozkan and Davis, 2014) have been extremely useful for pioneer studies on the mechanisms of learning and memory.

Here we focus on social bees (Hymenoptera) and *Drosophila*, in which observational learning has been documented. Our goal, beyond various excellent reviews on the topic of social learning in insects (e.g., Leadbeater and Chittka, 2007b; Dukas, 2008; Grüter and Leadbeater, 2014; Leadbeater, 2015) is to provide a mechanistic view of these complex behaviors. It has recently been suggested that social learning can emerge from simple associations between a relevant stimulus (unconditioned stimulus, US), such as a food reward or a predator threat, and a conspecific's presence or behavior (conditioned stimulus, CS), which is not different from individual learning of non-social cues (Leadbeater and Chittka, 2007b; Avarguès-Weber et al., 2011; Heyes, 2011; Giurfa, 2012). Using this idea, we discuss the nature of learning associations and the neural circuits potentially involved in insect observational learning.

Observational Learning in Bees

Behavioral Evidences

During their foraging activities, bees need to exploit multiple floral resources whose reward levels change rapidly and unpredictably (Heinrich, 1979, 2004; Goulson, 2010; Lihoreau et al., 2012b). A forager's choice of plant species is guided by unlearned preferences and learned information about current reward levels gained through individual sampling (Raine et al., 2006). As many pollinators often work concurrently in a meadow, information acquired individually can be complemented by social information (Grüter and Leadbeater, 2014), but also by information gained inside the nest through communication and food exchange (Biesmeijer and Seeley, 2005; Arenas et al., 2008). It has long been known that during foraging, bees are attracted to visibly occupied flowers [e.g., bumblebees (Brian, 1957); stingless bees (Slaa et al., 2003); honey bees (Von Frisch, 1967), suggesting that they learn to exploit food resources by copying the choices of other bees (Romanes, 1884)]. Recent studies with bumblebees have shown that individuals can indeed glean information from watching other foragers, and change accordingly their floral choices (Leadbeater and Chittka, 2005, 2007a; Worden and Papaj, 2005; Kawaguchi et al., 2007; Baude et al., 2011; Avarguès-Weber and Chittka, 2014a,b), their choice of location (Leadbeater and Chittka, 2005, 2009; Kawaguchi et al., 2006; Baude et al., 2008; Dawson and Chittka, 2012; Plowright et al., 2013) and their handling strategies (Leadbeater and Chittka, 2008; Goulson et al., 2013; Mirwan and Kevan, 2013).

In particular, when bees observe the floral choices of conspecific demonstrators from behind a transparent screen (**Figure 1A**), they land more often on the flower type chosen by demonstrators in tests where the demonstrators are absent, than compared to non-observing controls (conspecifics separated from demonstrators by an opaque screen) (Worden and Papaj, 2005). Similar results are obtained with artificial demonstrators (inanimate model bees made of resin), thus indicating that visual cues associated with the presence of conspecifics are sufficient to promote social acquisition of flower preferences (Worden and Papaj, 2005; Dawson et al., 2013; Avarguès-Weber and Chittka, 2014b).

An Associative Account

The fact that bees acquire flower preferences by observing foragers through a screen (Worden and Papaj, 2005; Dawson et al., 2013; Avarguès-Weber and Chittka, 2014b) is incompatible with a simple associative hypothesis in which foragers associate profitable flowers (US) with the presence of the conspecifics (CS). In this case, the demonstrators are no longer present when the observer makes its choice, which implies that the positive value of conspecifics has been transferred to the associated flowers themselves. An explanation based on associative learning is still possible but in the form of a phenomenon termed second-order conditioning (Pavlov, 1927). Under second-order conditioning, bees learn a positive association between a conspecific (CS1) and a food reward (US), due to past-shared foraging experience on the same resources. When observing a conspecific feeding from an unknown flower, the close association between the CS1 (conspecifics) and the flower induces the bee to consider flower cues themselves as indicative of reward (CS2). Such a mechanism would lead to a socially acquired preference for all flowers sharing the same characteristics and not only for the occupied flowers (Leadbeater and Chittka, 2007b; Dawson et al., 2013).

If observational learning for new flower preferences is the consequence of a second-order conditioning, then impeding or modifying the first association should alter flower preference. In bumblebees, this hypothesis is supported by the fact that naive bees with no previous social foraging experience tend to ignore the choices of conspecifics in their foraging decision (Dawson et al., 2013; Avarguès-Weber and Chittka, 2014a), suggesting that there is a decisive role of prior associations between social cues and a reward. Additionally, the preference for socially demonstrated flowers can be reversed into avoidance if the tested bees are allowed to form an association between the conspecifics and a bitter aversive solution beforehand (Dawson et al., 2013).

The associative learning hypothesis also predicts that non-social cues should promote social-like learning behavior given that they have been previously associated with rewarding flowers. However, bumblebees follow different flower choice strategies when social cues (model bees) or non-social cues (wooden white blocks) are used as indicators of reward (Avarguès-Weber and Chittka, 2014a). If they have learned that the white blocks are present on a rewarded flower color, they will choose afterwards a different color, only if it displays the presence of the blocks. Unoccupied flowers presenting that same color will not be chosen. This behavior can be explained in simple associative terms as the blocks were previously associated with reward. The situation is different if bees have learned to forage on a flower color on which bees were present. In this case, they will choose afterwards a novel

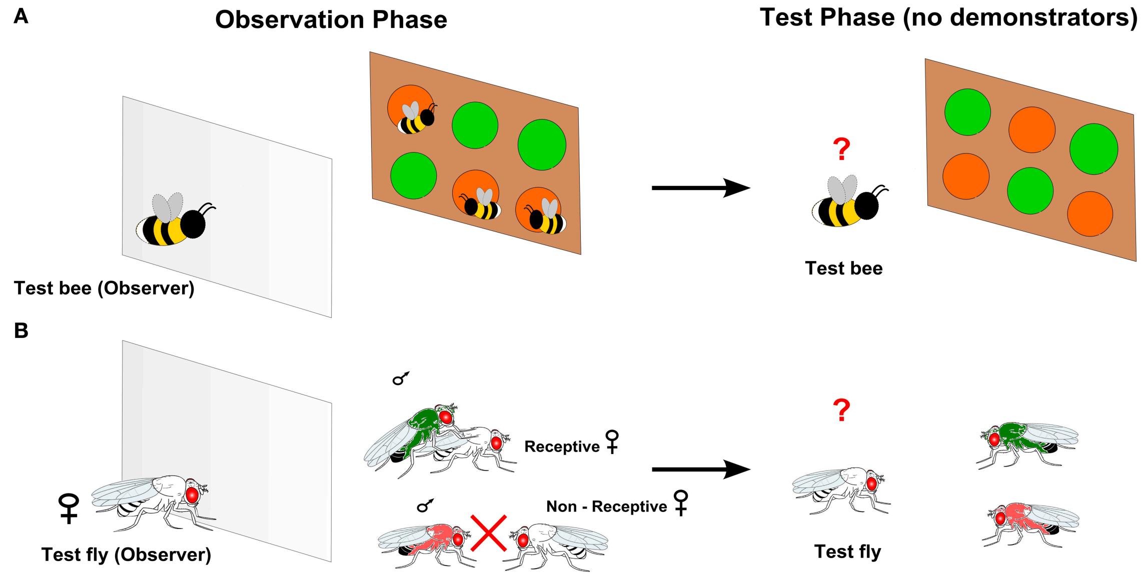

FIGURE 1 | Experimental set-ups used to study observational learning in insects. (A) An observer bumblebee can observe a vertical array of two unfamiliar flower types (e.g., green or orange) through a transparent screen. Demonstrators (e.g., living bees, dead bees or model bees) are associated to one flower type (e.g., green). Observational learning is successful if the observer bee preferentially visits flowers of the same type as the demonstrators did, when subsequently tested alone (Worden and Papaj, 2005; Avarguès-Weber and Chittka, 2014b). **(B)** An observer *Drosophila* (virgin female) can observe interactions between two pairs of demonstrator males (dusted with color pigments) and females through a screen. The observer is first presented a colored male (e.g., green) mating with a sexually receptive female. The pair of demonstrators is then replaced by a male of a different color (e.g., pink) and a non-sexually receptive female. Observational learning is successful if the observer preferentially copulates with the male of the same color as the demonstrator did, when subsequently given the choice between new males of each color (Mery et al., 2009).

color if dummy bees are present on it but, in addition, they will extend their choice to unoccupied flowers with that same color. Thus, in the latter case, the bees' choice is not restricted to the flowers occupied by a model bee but includes all flowers presenting the same characteristics (Avarguès-Weber and Chittka, 2014a). The difference between these two scenarios may reside in the fact that foragers gather experience in the field in which conspecifics, contrary to wooden blocks, are not only predictive of reward but also mobile. This mobility may allow transferring the choice form the occupied flower to the unoccupied flower as long as both share the same color. This strategy may be advantageous: in many typical flower species, it might not be adaptive for a pollinator to visit a flower that is currently being drained by another visitor. Instead, it would be more useful to steer toward unvisited flowers of the same plant species where the visitation activities of others indicate that the flower type is profitable. Therefore, specific mechanisms might have evolved to promote efficient social information use in flower foraging, suggesting that social and asocial learning are dissociated.

It is, however, also possible that there is no special role of conspecifics in the flower generalization pattern observed, specifically when demonstrators indicate rewarding flowers. Bees that never got the chance to see live conspecifics within or outside the nest and were only familiarized with model static bees pinned on flowers show a pattern of choices similar to that of bees familiarized and tested with non-social cues (Avarguès-Weber and Chittka, 2014a). By contrast, bees exposed to live bees experienced that the socially indicated flower species will sometimes be occupied by demonstrators and sometimes not, occasionally in rapid succession, and the situation might change while the observer is on the flower. Thus, observers will get exposure to mobile demonstrators physically dissociated from the flowers, and this in turn may favor future generalization to unoccupied but socially indicated flowers. The possibility that non-social moving objects could generate a social-like flower choice pattern remains to be tested. Alternatively, social learning specificity may require a familiarization phase with live conspecifics to learn to associate the conspecific's chemical signature acquired within the nest (Krasnec and Breed, 2012), and with the species visual characteristics.

Relying on the choices of others is not always an adaptive strategy (Giraldeau et al., 2002; Laland, 2004; Rieucau and Giraldeau, 2011; Grüter and Leadbeater, 2014). In the most extreme case of a population always favoring social learning over individual sampling, an ecological dead end would be quickly reached with some resources being overexploited while others are left unexplored. From the colony perspective, keeping enough individual information acquisition is essential for social learning behavior to remain beneficial (Giraldeau et al., 2002; Rieucau and Giraldeau, 2011; Grüter and Leadbeater, 2014). Bumblebees present restrictions in the use of social over individual learning that are consistent with the theory. Indeed, the response to social cues is flexible, depending on the context of the observation (Leadbeater and Chittka, 2005; Kawaguchi et al., 2007; Baude et al., 2011). In a field study, *B. diversus* foragers were given a choice between two inflorescences attached to a stick ("interview bouquet"), one of which was occupied by a conspecific (freshly killed bee pinned on flowers). While bees preferred occupied inflorescences when they were presented two unfamiliar flower species, they avoided conspecifics when confronted with flower species found in their daily environment (Kawaguchi et al., 2007). Presumably, this conditional use of social information enables bees to maximize their foraging efficiency when searching for novel food items while minimizing the costs of competition when they know resource locations (Laland, 2004; Dall et al., 2005). Competition level is also reduced by another flexible usage of social information as *B. terrestris* foragers do not follow the preferences of demonstrators when the conspecifics density on the flowers patch is too high (Baude et al., 2011; Plowright et al., 2013).

All these results suggest that observational social learning in bumblebees is the consequence of simple associative processes and specific enhanced attention toward conspecifics as cue providers (stimulus enhancement) and/or places where these conspecifics can be seen (local enhancement) (Zentall, 2006; Leadbeater, 2015). An intricate interplay between evolutionary adaptation to attend to conspecific cues, individual experience with such cues and their contingencies with salient aspects of the environment is probably at hand to generate the observed complexity of observational social learning.

Observational Learning in *Drosophila*

Behavioral Evidence

Although considerable knowledge on insect observational learning comes from research on bumblebees, visual social learning has also been described in a non-social species, the fruit fly *D. melanogaster*. In this species, females learn the quality of potential mating partners by observing their success with other females (Mery et al., 2009) (**Figure 1B**). This capacity was shown in experiments in which two artificial male phenotypes were produced by dusting flies with green or pink pigments (Mery et al., 2009). An observer (virgin) female was placed in a glass tube where she could see demonstrator males and females through a colorless screen. In the first observation phase, the demonstrator male (e.g., green) successfully mated with the demonstrator female. In the second phase, a male of another color (e.g., pink) was paired with a non-receptive female, thus leading to unsuccessful copulation attempts by the male. When the observer female was later presented with two males (green and pink) simultaneously, she preferentially mated with the male of the color that was associated with a successful copulation (e.g., green) (**Figure 1B**). This effect disappeared when the observers could not directly observe the demonstrator flies (Mery et al., 2009). This example shows that observational learning is not restricted to social insects. Rather, it seems to be a general capacity issued from the insects' faculty to learn associations in their environment. Observational learning in *Drosophila* could also be interpreted as a special case of associative visual learning. It is possible that the vision of a female copulating with a male acts as a biologically relevant reinforcement to be associated with the male color (CS). Under this hypothesis, observer flies should learn to associate a male color phenotype with a successful mating signal. Later, when confronted with males of different phenotypes, observers would preferentially choose the learned color based on a simple associative memory. Visual associative learning has been extensively documented in *Drosophila* in an individual context (Heisenberg et al., 2001; Foucaud et al., 2010; Schnaitmann et al., 2010; Ofstad et al., 2011; Vogt et al., 2014) so that transferring this capacity to a mating, observational context is plausible.

Genetic and Molecular Basis

The discovery of mate choice copying in a main model organism holds considerable promises to unravel the genetic and molecular substrates of observational learning in insects, an approach that is currently not possible in bees. While such analysis has not been conducted yet, recent studies have begun to identify the neural substrates of *Drosophila* visual learning that may also be involved in observational learning in particular if the associative learning hypothesis is verified.

Different forms of visual learning are mediated by the central complex (CX). This neuropil is located between the protocerebral brain hemispheres and comprises four interconnected regions: the fan-shaped body, the ellipsoid body, the protocerebral bridge and the paired noduli (**Figure 2**). It receives information from visual processing neuropils (lamina, lobula, medulla) connected to each compound eye, and whose learning-dependent plasticity has not been explored until now. The implication of the CX in visual recognition was first demonstrated using a flight simulator, in which a fly whose head is attached to a torque meter controls the position of visual patterns on the walls of a circular arena with its flight direction (Heisenberg et al., 2001). Using this approach, flies can be trained to learn to avoid visual cues (such as colors and geometric forms, CS) due to their association with an aversive stimulus (a heat beam, US). The sequence of CS and US stimuli can either be controlled by the fly itself (operant training) or by the experimenter (Pavlovian training) (Brembs and Heisenberg, 2000). Memory mutants lacking the Rutabaga (Rut) protein—a type 1 Ca2+/Calmodulin-dependent adenylyl cyclase that produces cAMP—display impaired operant and Pavlovian visual learning, indicating that Rut plays a decisive role in the US/CS association, probably as a coincidence detector of the visual CS and the heat US (Liu et al., 2006). By using the UAS/GAL4 system to differentially express Rut in specific subsets of cerebral neurons, it has been shown that the discrimination of visual patterns of different elevations or orientations requires two different groups of neurons extending branches in the fan-shaped body, respectively the F5 and F1 neurons (Liu et al., 2006). Another subset of large field neurons located in the ellipsoid body (the ring neurons R2 and R4m) are also involved in recognition of several pattern features through excitatory and inhibitory visual subfields (Pan et al., 2009; Seelig and Jayaraman, 2013) (**Figure 2**). Taken together, these results demonstrate the implication of the CX in visual learning and memory through dynamic interactions between the ellipsoid-body and the fan-shaped body.

Recent studies also point toward a contribution of the mushroom bodies (MBs) in visual memories. The MBs are central brain structures involved in olfactory learning and

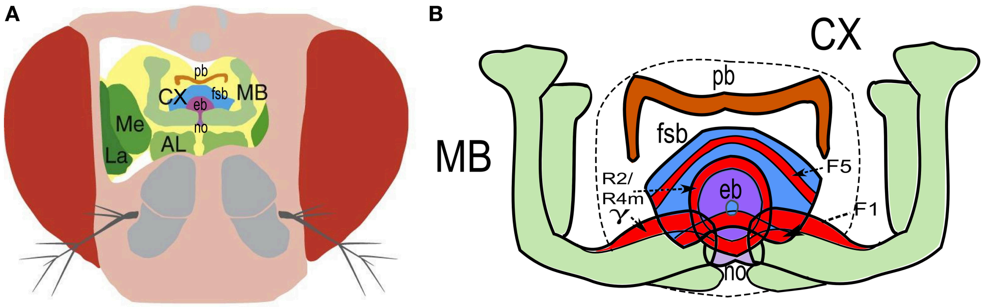

FIGURE 2 | Neurobiological structures involved in visual learning in the *Drosophila* brain. (A) A schematic diagram of the head of *D. melanogaster* revealing several major neuropiles: the lamina (La) and medulla (Me) involved in visual processing, the antennal lobes (AL) involved in olfactory processing and the mushroom bodies (MB) and the central complex (CX) involved, among other functions, in visual learning. Subdivisions of the central complex: the protocerebral bridge (pb; orange), the fan-shaped body (fsb; blue), the ellipsoid body (eb; magenta) and the noduli (no; purple). Adapted from Niven (2010) with permission. **(B)** Enlargement of the central part of the brain showing the neuropiles and their substructures involved in visual learning (highlighted in red), as the F1 and F5 neurons extending branches in the fan-shaped body, the R2 and R4m ring neurons located in the ellipsoid body, and the MBs gamma-neurons.

memory (Davis, 2005), courtship (McBride et al., 1999), locomotion (Martin et al., 1998), and sleep (Joiner et al., 2006; Pitman et al., 2006), among others. Despite the absence of obvious anatomical connections between the optic lobes to the MBs (Barth and Heisenberg, 1997; Otsuna and Ito, 2006; Mu et al., 2012), the volume of the MB calyces (dendrites) changes with light regime, suggesting that MBs are involved in visual information processing (Barth and Heisenberg, 1997). Indeed, it has been shown that MBs are required in visual context generalization (Liu et al., 1999) and could stabilize visual memories against context changes (Brembs and Wiener, 2006). Interestingly, the MBs (γ neurons) seem also necessary for the memorization of simple associations between color stimuli and a sugar reward or with an electric shock (Vogt et al., 2014). Presumably, the implication of the CX or the MBs might be dependent of the locomotion state (flying vs. walking) as flies were trained in a flight simulator in one case (Liu et al., 2006; Pan et al., 2009) vs. a walking plate in the other (Vogt et al., 2014). Locomotor activity is known to affect the activity of octopamine neurons and the behavioral response to CO_2 (Suver et al., 2012; Wasserman et al., 2013), and thus possibly modifies neural pathways involved in visual information memorization (Kottler and Van Swinderen, 2014; Vogt et al., 2014). Additionally, walking activity has no direct effect on the activity of ring neurons of the CX while flying activity significantly decreases their responses to visual stimuli (Seelig and Jayaraman, 2013).

Importantly, the MBs and their associate dopaminergic signaling are also involved in visual attention in the form of visual tracking of a moving bar (Xi et al., 2008; Van Swinderen et al., 2009). They may consequently mediate the specific attentional state elicited by social visual cues during an observational learning task.

Conclusion

Placing social learning within the conceptual framework of associative learning is an appealing approach for explaining seemingly complex behavior in insects with pinhead-sized brains. However, bumblebee studies are beginning to suggest that observational learning by insects does not only reflect visual associative learning but also involves attentional processing of social cues as information providers.

In parallel, the neurogenetic approaches well mastered in *Drosophila* hold considerable promises in revealing the neural basis of such complex behavior. Future investigations may target the CX and MBs as the potential neuronal structures involved, given their implication in visual learning and attention.

The popularity of bees and fruit flies as models for visual cognition research associated with the abundance of genomic information available make them ideal study systems to explore the genetic, molecular, neuronal, and behavioral basis of visual social learning, a major challenge on the way of understanding the evolutionary relationships between animal brains, cognitive capacities and their social environment (Lihoreau et al., 2012a).

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Honeybee linguistics—a comparative analysis of the waggle dance among species of *Apis*

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All honeybees use the waggle dance to recruit nestmates. Studies on the dance precision of *Apis mellifera* have shown that the dance is often imprecise. Two hypotheses have been put forward aimed at explaining this imprecision. The first argues that imprecision in the context of foraging is adaptive as it ensures that the dance advertises the same patch size irrespective of distance. The second argues that the bees are constrained in their ability to be more precise, especially when the source is nearby. Recent studies have found support for the latter hypothesis but not for the "tuned-error" hypothesis, as the adaptive hypothesis became known. Here we investigate intra-dance variation among *Apis* species. We analyse the dance precision of *A. florea*, *A. dorsata*, and *A. mellifera* in the context of foraging and swarming. *A. mellifera* performs forage dances in the dark, using gravity as point of reference, and in the light when dancing for nest sites, using the sun as point of reference. Both *A. dorsata* and *A. florea* are open-nesting species; they do not use a different point of reference depending on context. *A. florea* differs from both *A. mellifera* and *A. dorsata* in that it dances on a horizontal surface and does not use gravity but instead "points" directly toward the goal when indicating direction. Previous work on *A. mellifera* has suggested that differences in dance orientation and point of reference can affect dance precision. We find that all three species improve dance precision with increasing waggle phase duration, irrespective of differences in dance orientation, and point of reference. When dancing for sources nearby, dances are highly variable. When the distance increases, dance precision converges. The exception is dances performed by *A. mellifera* on swarms. Here, dance precision decreases as the distance increases. We also show that the size of the patch advertised increases with increasing distance, contrary to what is predicted under the tuned-error hypothesis.

Keywords: *Apis dorsata, Apis florea, Apis mellifera,* dance precision, tuned-error hypothesis, communication

INTRODUCTION

In September 1999 NASA's US$125 million Mars Climate Orbiter probe was lost due to miscommunication between engineers. Unlike NASA, engineers at the company that helped build the probe, Lockheed Martin, used English instead of metric units of measurement. Inability to communicate the correct measurement resulted in the probe being 100 km too close to Mars when it tried to enter the planet's orbit. The probe never entered Mars' orbit and may now well be orbiting the sun instead[1]. Clearly precise communication matters. Non-human animal communication should not be an exception. Yet, the animal probably most studied in terms of non-human animal communication, the honeybee, is notoriously messy when communicating the location of forage and nest sites (Towne and Gould, 1988; Beekman et al., 2005; Schürch and Couvillon, 2013). Why would this be?

The honeybee's dance language is essential during nest-site selection when scout bees explore the surroundings for potential nest sites and communicate their location upon their return to the swarm (the basic process in *Apis mellifera* is reviewed in Seeley, 2010, for *A. florea* see Makinson et al., 2011 and Oldroyd et al., 2008 and for *A. dorsata* Makinson et al., 2014). Although not strictly essential in the context of foraging (Sherman and Visscher, 2002; Dornhaus and Chittka, 2004; Beekman and Lew, 2008; Granovskiy et al., 2012), the dance does allow the bees to rapidly exploit newly discovered food sources (Seeley and Visscher, 1988; Beekman and Lew, 2008), utilize resources that are patchily distributed (Sherman and Visscher, 2002; Dornhaus and Chittka, 2004; Dornhaus et al., 2006; Donaldson-Matasci and Dornhaus, 2012), difficult to find (Beekman and Lew, 2008) or very far (Beekman and Ratnieks, 2000). Moreover, a recent modeling study showed that the dance most likely provides long-term benefits to the colony (Schürch and Grüter, 2014). Yet the precision of the location information conveyed in the dance is rather low,

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[1] http://edition.cnn.com/TECH/space/9909/30/mars.metric.02/index.html?_s=PM:TECH

particularly for locations that are nearby (Haldane and Spurway, 1954; Von Frisch, 1967; Towne and Gould, 1988).

The angular component of the bees' dance [the part of the dance that conveys directional information (Von Frisch, 1967)] contains an inherent error. This error, or the degree of angular deviation, decreases with increasing distance to the resource advertised (Towne and Gould, 1988; Beekman et al., 2005; Gardner, 2007; Gardner et al., 2007). Initially the argument was made that the bees adaptively "tune" their error so that the dance always advertises a patch of similar size irrespective of distance (Haldane and Spurway, 1954; Towne and Gould, 1988). More recently, however, it has become clear the bees dance as best they can (Preece and Beekman, 2014) but that the precision of the dance is influenced by the substrate the bees dance on (Tanner and Visscher, 2006), context (forage or nest sites) (Tanner and Visscher, 2006), point of reference used (gravity or visual) (Tanner and Visscher, 2010), and angle of the waggle phase relative to vertical (Couvillon et al., 2012a).

Ever since Karl von Frisch described the bee's dance (Von Frisch, 1923, 1967), the honeybee's unique communication mechanism has been studied widely (a Web of Science search using *honeybee AND dance* yields 712 references). Almost all studies, however, are on only one of the 11 recognized species of *Apis* (Lo et al., 2010): the Western honeybee *A. mellifera*. Yet all species of *Apis* use the dance to communicate both forage locations and nest sites (Dyer, 2002; Oldroyd and Wongsiri, 2006). In this study we compare the variation in the angular component of the bees' dance of *A. mellifera* and the red dwarf honeybee *A. florea* dancing for nest sites and forage, and the giant Asian honeybee *A. dorsata* when dancing for nest sites. *A. mellifera* is a cavity-nesting species and uses gravity as point of reference when dancing for forage in the dark hive. Dances take place on the wax comb. When dancing for nest sites, however, scout bees dance on top of other bees and can use the sun as their point of reference. Thus, in *A. mellifera* both the substrate and point of reference depend on context. *A. florea* and *A. dorsata* are open-nesting species and all their dances are performed on the curtain of bees surrounding the single comb. Like *A. mellifera*, *A. dorsata* uses gravity as point of reference, even though the bees are able to see the position of the sun (Dyer, 2002) and in both species dancing takes place on the vertical surface of the colony or swarm. *Apis florea*, on the other hand, communicates directional information by "pointing" toward the direction in which the source can be found while dancing on the horizontal part of the colony (Dyer, 1985). So far the only other *Apis* species on which some data have been collected on dance precision is *A. florea* in the context of nest site selection (Beekman et al., 2005; Makinson et al., 2011). These studies seemed to suggest that the nest site dances of *A. florea* are less precise than the nest site dances of *A. mellifera* which could potentially be explained by their different nest site requirements (Diwold et al., 2011; Schaerf et al., 2011). Here we look at dance precision amongst species of *Apis* in more detail. We were particularly interested to determine if the relationship between waggle phase duration and angular deviation differs among the different species and contexts, and to what extent the size of the patch advertised remains constant across distance.

MATERIALS AND METHODS

This work as a meta-analysis brings together data from several studies of bee dances. The first data were collected in 2008 and the last in 2014. Thus, the way vector information was extracted from the dances differs among studies. Below we outline the origin of the dances and give a brief explanation about how information was extracted.

APIS MELLIFERA SWARM DANCES

We decoded dances from three artificial swarms of *A. mellifera* as they selected a new nest site. The swarms were located at the University of Sydney's Crommelin Field Station, Pearl Beach, New South Wales, Australia (33.55° S, 151.30° E). We collected dance data from 28 September 2009 to 20 January 2010 (see Schaerf et al., 2013 for more details). From video data we analyzed a subset of dances that occurred on the vertical surface of each swarm during 1 day of their decision-making process. We only decoded waggle phases (the phase of the dance that contains location information) that occurred during 30-s intervals, with the start time of each interval separated by 5 min (starting from the beginning of our video footage). We determined the angles of the waggle phases with the aid of a MATLAB programme that we developed (inspired by a similar approach by Klein et al., 2010). A transparent MATLAB figure was overlaid on an external video player window (SMPlayer) and video was played back at slow speed (usually 1/4 speed). The programme's user would click on a dancing bee's thorax once at the beginning and once at the end of each waggle phase. We then used the (x, y) coordinates associated with each pair of clicks to deduce the angle of each waggle phase (relative to vertical on the screen). We used the duration between each pair of clicks and the speed of the video playback to deduce the duration of each waggle phase (indicating the distance to the source advertised in the dance). We collected data from 775 dances comprised of 5424 waggle phases (as each dance typically contains more than one waggle phase).

We supplemented the above data with data collected from a single artificial swarm, placed in the same location in October 2013. To extract dance data, we used a new MATLAB script. Unlike the programme used to extract information from dances from the 2009–2010 fieldwork, we were now able to play the video back frame by frame within MATLAB. By clicking on the thorax of the dancing bee in a given video frame, the script recorded the bee's relative (x, y) coordinates (in pixels, with y inverted to take into account the fact that pixel coordinates increase moving from the top of the screen to the bottom of the screen). We set up the programme so that a left click would indicate the waggle phase, and a right click the return phase (the phase of the dance in between waggle phases, when the bee positions herself to perform the next waggle phase). A mouse click also advanced the video to the next frame, until the user instructed the programme to stop, thus recording the bee's complete trajectory during a portion of her dance (a bee's body and wings appear blurry during the waggle phase in still images, due to her rapid vibrations, so it is usually straightforward to separate waggle and return phases visually). We developed two additional scripts to help manually correct any obvious errors or ambiguities in identifying components of a dance as part of a waggle or return phase. With the aid of the left/right mouse-click data, we identified the first and last video frames of each waggle phase, and the corresponding coordinates of the bee in these frames, (x_f, y_f) and (x_l, y_l). The bearing of the waggle phase relative to vertical was then approximated via:

$$\theta = \mathrm{atan2}(x_l - x_f, y_l - y_f).$$

(A similar formula was used to determine bearings based on coordinates in our previous MATLAB programme.) We determined the number of frames associated with each waggle phase from first and last frame indices; the duration of each waggle phase was then approximated by dividing the number of frames by the video frame rate (25 frames per second). We collected data from 87 dances comprised of 390 waggle phases.

APIS MELLIFERA DANCES FOR FORAGE

We collected dance information from three colonies housed in observation hives at the University of Sussex, Falmer, Brighton, UK (50.51° N, 0.05° W) from August through to October 2009 (see Couvillon et al., 2012b for more details). We simultaneously video recorded dance activity on one side of a frame in each colony. To decode the dances, we placed an acetate sheet over a computer screen and manually marked the center of a dancing bee's thorax during two separate frames of the waggle phase (usually during the middle portion of the waggle phase). We then determined the angle between the straight line that passed through the two points and a vertical plumb line that was in the camera's field of view. To determine the duration of the waggle phase we identified the number of frames that made up each waggle phase to an accuracy of 0.08 s. We collected data from 273 dances comprised of 3752 waggle phases.

We supplemented the above forage dance data with data collected from *A. mellifera* workers dancing for sources of pollen (either natural pollen, or mixtures offered at a feeder as part of a separate experiment) in two observation hives. One hive was housed at the University of Sydney's Crommelin Field Station (see above), and the other was housed at the main campus of the University of Sydney, New South Wales, Australia (33.89° S, 151.19° E). Video recording and observations took place from November 2013 to January 2014. Subsequent extraction of waggle phase angles and durations was performed using the new MATLAB script developed to decode dances from the supplementary *A. mellifera* nest site selection experiment from October 2013 (described above). We decoded 69 dances comprised of 409 waggle runs from the pollen foraging experiments.

APIS DORSATA SWARM DANCES

We decoded dances from three artificial swarms of *A. dorsata* as they relocated after having been placed in a novel environment. One swarm was placed at Mae Fah Luang University football oval, Thailand (20.06° N, 99.90° E) and two on the grounds of Wat Pa Mark Nor temple, Thailand (20.23° N, 100.02° E) in December 2010 (see Makinson et al., 2014 for details). We decoded all dance circuits from all dances for each of the swarms from video recordings. For two of the swarms, we determined the angles of the waggle phases (relative to vertical on the screen) by superimposing a digital compass over a video window during freeze frame playback. We recorded waggle durations using a stopwatch. For the third swarm we used our original MATLAB script as described above (and in Schaerf et al., 2013), but with video usually played back at 1/2 speed. We collected data from 1776 dances comprised of 9905 waggle phases.

APIS FLOREA SWARM DANCES

We decoded dances from five artificial swarms of *A. florea* as they selected a new nest site. The swarms were placed on the grounds of Naresuan University, Phitsanulok, Thailand (16.74° N, 100.20° E) and we collected data from April to June 2008 (see Makinson et al., 2011 for details). We filmed all dance activity on top of the swarms where *A. florea* bees perform their dances. To determine the angle of a waggle phase, we stopped the video during playback during a waggle phase and measured the angle between the axis aligned with the dancer's body and vertically up on a computer screen with a circular protractor. We then converted the measured angle to a bearing relative to north with the aid of a compass placed in the video's field of view. We recorded waggle durations using a stopwatch. We collected data from 2166 dances comprised of 15,480 waggle phases.

APIS FLOREA DANCES ON COLONIES

We filmed dances from three colonies of *A. florea* over a period of 9 days during swarming season in Northern Thailand (January to March, 2011). These colonies were translocated from their original locations in the countryside surrounding Mae Fah Luang University, Chiang Rai to a small longan (*Dimocarpus longan*) grove (20.05°N, 99.90°E) on Mae Fah Luang University campus. The colonies were fed *A. mellifera* honey on a regular basis to supplement their forage intake and ensure they did not abscond. The colonies were monitored continuously, as the main aim was to observe natural swarming events (Makinson et al., in revision). We decoded a subset of dances, and circuits therein, for each colony starting 1 day before a swarming event (as *A. florea* colonies typically produce multiple swarms), the day of swarming, and the day after. As with the *A. mellifera* data set from Schaerf et al. (2013) we decoded waggle phases that occurred during 30 s intervals, with the start time of each interval separated by 5 min (commencing at the start of each day's footage). To determine the angles of waggle phases (relative to vertical on screen) we used the MATLAB script developed in Schaerf et al. (2013). We then converted angles to bearings relative to north with reference to a compass placed in view of the video camera. Similarly, waggle durations were determined using the same MATLAB script, with video played back at slow speed. We collected data from 1778 dances comprised of 6514 waggle phases. The dances collected from the colonies comprised a combination of nest-site dances and dances for forage. Although we could determine which bees had collected pollen and were thus clearly dancing for forage, we could not distinguish between bees dancing for nectar and nest sites.

COLLATION OF DATA

We first reduced data from the seven studies into a standard format that reported the number of waggle phases decoded in each dance, the mean duration of waggle phases during each dance, *t*, the mean angle of the waggle phases (relative to vertical for *A. mellifera* and *A. dorsata*, and relative to north for *A. florea*), θ_r, and the angular deviation of waggle phases within a dance, α. Mean angle and angular deviation were determined using standard methods of circular statistics (Zar, 1996). To determine the mean angle of the waggle phases within a dance, we first made the intermediate calculations:

$$X = \sum_{i=1}^{n} \sin\theta_i,\ \ Y = \sum_{i=1}^{n} \cos\theta_i,$$

where θ_i was the bearing of the ith (out of n) waggle phase. The mean waggle angle relative to the vertical (or north for *A. florea* dances) in degrees was then calculated via:

$$\theta_r = \left(\frac{180^\circ}{\pi}\right) \operatorname{atan2}(X,\ Y)$$

Angular deviation (also in degrees) was defined as:

$$\alpha = \left(\frac{180^\circ}{\pi}\right) \sqrt{2\,(1 - r)},$$

where r was given by:

$$r = \frac{\sqrt{X^2 + Y^2}}{n}.$$

We then filtered our data to exclude dances with only one circuit recorded since the angular deviation associated with such dances would automatically be 0. We also excluded dances with a mean waggle duration of less than 0.5 s [such dances are too short to obtain reliable location information (Sen Sarma et al., 2004) and are often referred to as "round dances" (Von Frisch, 1967)]. We pooled the remaining data into five groups separated by species and the context in which dances were performed: nest-site dances by artificial swarms of *A. mellifera* (598 dances); forage dances (for either nectar or pollen) collected from *A. mellifera* housed in observation hives (299 dances); dances performed on artificial swarms of *A. dorsata* (700 dances); dances performed on artificial swarms of *A. florea* (1734 dances); and dances by *A. florea* colonies for a mixture of nest sites and forage (1436 dances).

ANALYSIS

We used our analysis to address the following questions for each of the five data sets: (1) Does dance precision (quantified via angular deviation, α) increase as mean waggle phase duration increases? (2) If dance precision increases, is the rate of change as a function of mean waggle phase duration the same for all groups? (3) Is there evidence that dances indicate regions of equal area independent of distance? (4) Is there a waggle phase duration after which dance precision remains the same?

To address (1) we first performed linear regression analysis on each group of data treating angular deviation as a function of mean waggle phase duration. The choice of linear regression, rather than some other form of regression or correlation analysis, was necessary to allow us to make a sensible comparison across groups for question (2).

To examine (2), we then performed an analysis of covariance (ANCOVA) to compare the slopes of the regression lines (following the method outlined in Zar, 1996) and a subsequent multiple comparison test (Tukey test) to explicitly determine which lines shared the same slope. All statistical tests were performed using custom code that we developed in MATLAB. Values of the cumulative distribution function for the q-distribution (required for calculation of p-values within the Tukey test) were determined using the function *cdfTukey.m* available from MATLAB Central (http://au.mathworks.com/matlabcentral).

When we looked closer at the data within each of our five groups, it became clear that there was inequity between the groups in the way data were distributed as a function of mean waggle phase duration. **Figure 1** illustrates the distribution of data points for each group, with data separated into bins of width of 0.25 s, with a minimum mean waggle phase duration of 0.5 s (our threshold for inclusion in this study), and a maximum of 18.5 s (the greatest mean waggle phase duration in our data was 18.40 s, from an *A. dorsata* nest-site dance). We were concerned that such inequity in the distribution of data could have an effect on our analysis, particularly the ANCOVA. We therefore repeated our analyses using random subsets of each group's data to account for a potential effect of unequal data.

To construct random subsets of data, we first divided our data into bins based on mean waggle phase duration with a width of 0.25 s and the same minimum and maximum values as in **Figure 1**. We determined the number of elements in each bin for each group, and then determined the minimum number of elements for each bin/time-division across all groups (denoted $n_{i,\ \min}$ for the ith bin). We then randomly selected $n_{i,\ \min}$ elements from each bin i for each group, and then recombined these randomly selected data points in a form suitable for our regression and ANCOVA tests (ordered vectors of paired values of angular deviation and mean waggle phase duration). In practical terms all the random subsets were truncated at a mean waggle phase duration of 6.75 s, as the last bin that contained more than zero elements for all groups extended from 6.5 to 6.75 s.

We performed linear regression analysis of angular deviation vs. mean waggle phase duration for each random subset of each group's data. We then performed an ANCOVA to compare the slopes of these regression lines, excluding any lines that had slopes that did not significantly differ from zero, and followed up the ANCOVA with a Tukey test (as we did with the complete sets of data for each group).

We performed 10,000 iterations of the process of randomly selecting data from each group's pool as described above, linear regression analysis, ANCOVA, and multiple comparison tests. We recorded the outcomes of all multiple comparison/Tukey tests that were performed (conditional on the outcomes of the ANCOVA) in a cell array that indicated which pairs of regression lines shared a common slope. We then identified all the unique forms that the cell array assumed across our 10,000 randomizations, and tallied the number of occurrences of each of these unique forms. Finally we identified all the forms of the cell array (and hence associations between regression slopes) that

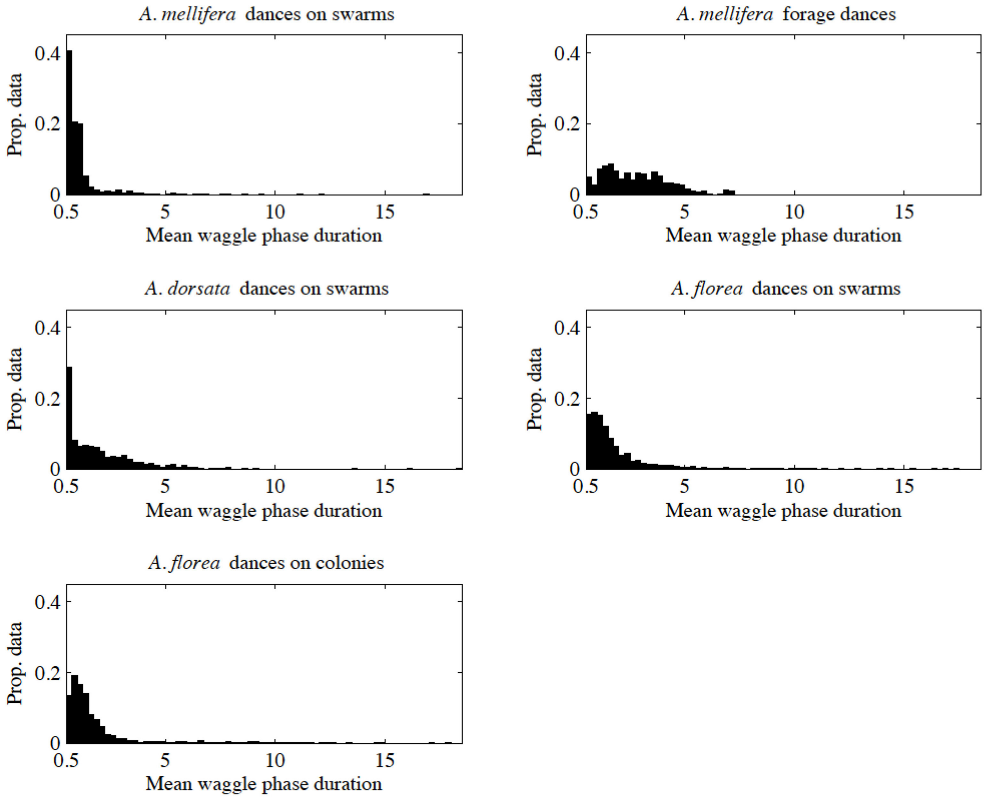

FIGURE 1 | Distribution of data against mean waggle phase duration for our five data sets. We separated data into bins of width 0.25 s.

occurred at least 500 times (effectively all outcomes that occurred with sample probability greater than or equal to 0.05). To determine the effect of transforming our data on both the linear regression analysis and analysis of covariance, we repeated our analyses (including random selection of data) using the natural logarithm of mean waggle phase duration as well as the natural logarithms of both the mean waggle phase duration and angular deviation.

To answer (3) we first obtained a radius-like measure of a region that could be indicated by a dance. We assumed that distance, d, to an object indicated by a dance is linearly proportional to the mean duration of the waggle phases in that dance, such that $d = \beta t$, consistent with the findings of Schürch et al. (2013). However, we did not make use of any existing dance calibration curves to determine β, as the details of the conversion are affected by a bee's perception of the complexity of her environment (Esch et al., 2001) and no on-site calibration was performed for any of the observations used in this study. We further assumed that a target that a bee was dancing for was centered along the straight line with bearing θ_r (the mean bearing of a dance, now assumed corrected for the Sun's current azimuth for *A. mellifera* and *A. dorsata*) from the dancer's location, at a distance d, and that the edges of the region lay on straight lines at angles of $\theta_r \pm \alpha$ (also from the location of the dancing bee). The radius of such a region is:

$$R = d \tan \alpha = \beta t \tan \alpha.$$

We then performed linear regression analysis on the radius-like measure, R, vs. mean waggle phase duration, t. For convenience we set $\beta = 1$ in our calculations. Some details of the regression analysis, such as the slope and intercept of the regression line, are dependent on β. However, the components of the regression analysis critical for this study (the correlation coefficient, observed value of the test statistic and consequently the p-value that suggests if the slope of the regression differs from zero) are independent of β. (β is effectively a scaling factor for the dependent variable R; Pearson's correlation coefficient and the observed value of F are invariant under linear transformations (such as scaling by a constant) to data in both the x and y directions.)

To address question (4), we again divided our data into bins based on mean waggle phase duration (using the same divisions of data described above). We then removed data contained in the first i bins (starting from the lowest mean waggle phase duration, with $i = 0, \ldots, 72$) from each group and performed linear regression analysis on the remaining data for angular deviation vs. mean waggle phase duration. For each group and particular comparison we identified the least value of i (and corresponding time interval) where the slope of the regression line was no longer significantly different to zero. At this stage the precision of the dance no longer changed (improved or declined) across the remaining data.

RESULTS

Contrary to all other dances, the angular deviation of dances for nest sites performed by scouts on *A. mellifera* swarms increased with increasing waggle phase duration, and hence distance to the advertised site (**Figure 2**, **Tables 1**, **2**). The rate of change in angular deviation with waggle phase duration was not the same across our data sets (**Figure 2**, **Tables 3**, **4**). Angular deviation decreased most rapidly with increasing waggle phase duration in dances by *A. mellifera* foragers and this change was statistically equivalent to the change in dance precision of *A. dorsata* swarm dances (**Figure 2**, **Tables 3**, **4**). *A. dorsata* and *A. florea* swarm dances showed the same decrease in angular deviation as dances recorded from *A. florea* colonies (**Figure 2**, **Tables 3**, **4**).

All 10,000 ANCOVA tests with random sampling of data indicated that at least one of the linear regression slopes differed from the others. In **Tables 5–8** we list all outcomes of subsequent multiple-comparison tests (Tukey tests) that occurred with a frequency of at least 0.05 (that is, at least 500 times). If an entry in row *i*, column *j* of a table contains an integer value, then the slopes of the regression lines for the randomly selected data from groups *i* and *j* were equivalent. Groups with common slopes may also be identified as groups that share a common integer value in either their row or column of the table. If linear regression was non-significant for a given group's data, then that group was excluded from the ANCOVA (and the multiple comparison test that followed). What all significant outcomes have in common is that *A. mellifera* nest-site dances are always statistically significantly different from all other dances (**Tables 6–8**). This remained true after transformation of our data (results not shown).

With the exception of *A. mellifera* nest-site dances, dance precision (measured via a decrease in angular deviation) increased with increasing distance to the advertised source (measured as waggle phase duration). Does this mean that independent of distance, the bees always advertise the same patch size? Clearly not (**Figure 3**). Using our complete data sets, the estimated radius of the region advertised (*R*) is an increasing function of mean waggle phase duration (**Table 9**). This suggests that despite the decrease in angular deviation, at some stage the bees are unable to reduce the angular deviation any further. The waggle phase duration beyond which angular deviation ceases to change differs among the different data sets. When we excluded dances with mean waggle phase durations up to 1.50 (*A. mellifera* swarm dances), 3.25 (*A. mellifera* forage dances), 1.00 (*A. dorsata* swarm dances), 2.50 (*A. florea* swarm dances), or 0.75 (*A. florea* dances on colonies) s, the change in angular deviation associated with a change in mean waggle phase duration is no longer present.

DISCUSSION

Overall, the dances of the three species of honeybee studied here are very similar with respect to the change of angular deviation with waggle phase duration, with the exception of nest-site dances by *A. mellifera*. Using our complete data set, the rate of decrease in angular deviation with increasing waggle phase duration was highest for forage dances by *A. mellifera* and swarm dances by *A. dorsata*. When we corrected for inequality of sample sizes,

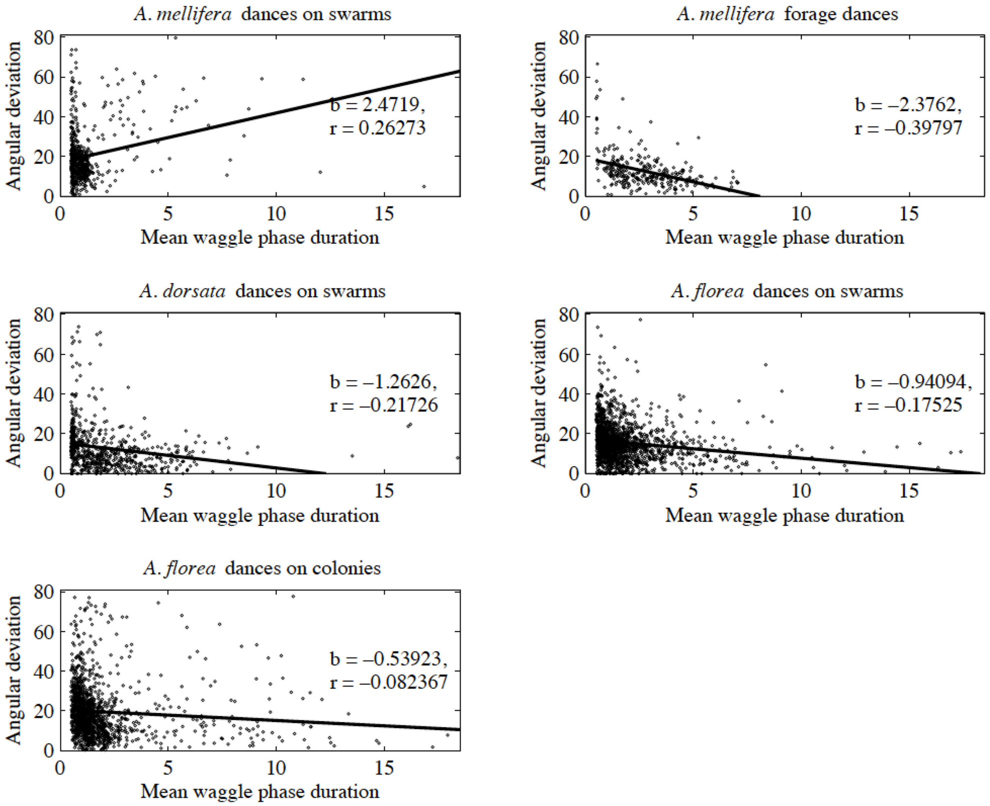

FIGURE 2 | Angular deviation plotted against mean waggle phase duration. Each dot represents the mean of all waggle phases within **one** dance performed by a bee. The solid line is the line of best fit determined by ordinary least squares regression (see **Table 1** for details of the linear regression analyses).

Table 1 | Linear regression statistics, angular deviation α (degrees) vs. mean waggle phase duration t (s) for our five data sets.

Source	*df*	*SS*	*MS*	*F*	*p*-value
***APIS MELLIFERA* SWARM DANCES**					
Regression	1	7560.6	7560.6	44.19	6.7×10^{-11}
Residual	596	1.0197×10^{5}	171.1		
Total	597	1.0953×10^{5}			
***APIS MELLIFERA* FORAGE DANCES**					
Regression	1	3697.5	3697.5	55.89	8.7×10^{-13}
Residual	297	1.9648×10^{4}	66.2		
Total	298	2.335×10^{4}			
***APIS DORSATA* SWARM DANCES**					
Regression	1	4031.4	4031.4	34.58	6.3×10^{-9}
Residual	698	8.1379×10^{4}	116.6		
Total	699	8.541×10^{4}			
***APIS FLOREA* SWARM DANCES**					
Regression	1	4658.0	4658.0	54.88	2.0×10^{-13}
Residual	1732	1.4700×10^{5}	84.9		
Total	1733	1.5166×10^{5}			
***APIS FLOREA* DANCES ON COLONIES (FORAGE AND NEST SITES)**					
Regression	1	1696.9	1696.9	9.80	1.8×10^{-3}
Residual	1434	2.4843×10^{5}	173.2		
Total	1435	2.5013×10^{5}			

Table 2 | Results of our ANCOVA analysis comparing the slopes of the linear regressions detailed in Table 1.

Source	*df*	*SS*	*MS*	*F*	*p*-value
Common minus pooled regression	4	1.5471×10^{4}	3867.8	30.7455	0 (<0.001)
Pooled regression	4757	5.9843×10^{5}	125.7997		
Common regression	4761	6.1390×10^{5}	128.9436		

Table 3 | Summary of the results of the Tukey pairwise comparison tests.

Samples ranked by slope	*A. mellifera* forage	*A. dorsata* swarm	*A. florea* swarm	*A. florea* colonies	*A. mellifera* swarm
Slope, *b*	$-2.38^{\wedge}$	$-1.26^{*\wedge}$	-0.94^{*}	-0.54^{*}	2.47

Data sets that share a symbol have statistically equivalent slopes (e.g., show the same relationship between angular deviation and mean waggle phase duration). See ***Table 4*** *for details of the statistics.*

Table 4 | Statistics associated with pairwise comparisons using the Tukey test.

Comparison (B vs. A)	Difference in slopes (b_B-b_A)	*SE*	*q*	*p*-value
A. mellifera swarm vs. *A. mellifera* forage	4.85	0.3988	12.16	2.0×10^{-4}
A. mellifera swarm vs. *A. dorsata* swarm	3.73	0.2920	12.79	2.0×10^{-4}
A. mellifera swarm vs. *A. florea* swarm	3.41	0.2310	14.77	2.0×10^{-4}
A. mellifera swarm vs. *A. florea* colonies	3.01	0.2908	10.36	2.0×10^{-4}
A. florea colonies vs. *A. mellifera* forage	1.84	0.3626	5.07	3.3×10^{-3}
A. florea colonies vs. *A. dorsata* swarm	0.72	0.2094	3.46	0.10
A. florea colonies vs. *A. florea* swarm	No explicit comparison required—slopes inferred to be equivalent since slopes of *A. florea* colonies and *A. dorsata* nest site dances lines are equivalent			
A. florea swarm vs. *A. mellifera* forage	1.43	0.2656	5.40	1.4×10^{-4}
A. florea swarm vs. *A. dorsata* swarm	No explicit comparison required—slopes inferred to be equivalent since slopes of *A. florea* colonies and *A. dorsata* nest site dances lines are equivalent			
A. dorsata swarm vs. *A. mellifera* forage	1.11	0.3124	3.56	0.086

depending on the outcome of random sampling, the only consistent result was that dances by *A. mellifera* for nest sites differed significantly from all other dances. Excluding the nest-site dances by *A. mellifera* scouts for the time being, our results thus indicate that substrate and point of reference do not significantly affect the precision of the bees' dance.

Why would the angular deviation increase when *A. mellifera* scouts advertise potential nest sites? After all, the bees are perfectly capable of reducing the angular deviation when dancing for forage when waggle phase duration increases. The original tuned-error hypothesis argued that spreading recruits out over a larger area when foraging could be advantageous (note that such spread could still be advantageous even if the bees do not deliberately adjust dance precision but instead are constrained when waggle phase duration is short). Weidenmüller and Seeley (1999) correctly pointed out that there is no such advantage when advertising a potential nest site, which comprises a single point in space for a cavity-nesting bee. Thus, if anything, cavity-nesting bees should increase the precision of their dance when dancing for nest sites if they are capable of doing so (tuned-error), or at least dance with the same precision (constraint). Towne (1985, cited in Tanner and Visscher, 2006) and Tanner and Visscher (2006) found no difference in angular deviation in dances for nest sites and nectar. In contrast Weidenmüller and Seeley (1999) did find that nest-site dances were more precise, but their results were later shown to be due to dance substrate and not dance context (Tanner and Visscher, 2006). We think our results too can be explained by dance substrate. Of the three species we studied here, *A. mellifera* is the only species that dances on a different substrate depending on context. It thus appears that the bees have more difficulty reducing the angular deviation of their dance when dancing on top of other bees, particularly when dances are longer. The longer the dance, the more likely a dancing bee may be bumped into by other bees resulting in a deviation from a straight line. Because open-nesting species always dance on top of other bees, they seem more capable of aligning themselves with their point of reference, particularly when waggle phase duration increases. Alternatively, the change in dance precision could be due to *A. mellifera* nest-site scouts using a different point of reference when dancing on a

Table 5 | Most frequent outcome of randomization analysis (4226 occurrences out of 10,000 randomizations).

	***A. mellifera* swarm**	***A. mellifera* forage**	***A. dorsata* swarm**	***A. florea* swarm**	***A. florea* colonies**
A. mellifera swarm					Non-significant regression
A. mellifera forage			1	1	Non-significant regression
A. dorsata swarm		1		1	Non-significant regression
A. florea swarm		1	1		Non-significant regression
A. florea colonies	Non-significant regression	Non-significant regression	Non-significant regression	Non-significant regression	

All pairs of data sets that are identified by the same integer have equivalent slope. The slopes of regression lines for angular deviation vs. mean waggle phase duration were the same for A. mellifera forage dances, A. dorsata swarm dances, and A. florea swarm dances.

Table 6 | Second most frequent outcome of randomization analysis (2397 occurrences out of 10,000 randomizations).

	***A. mellifera* swarm**	***A. mellifera* forage**	***A. dorsata* swarm**	***A. florea* swarm**	***A. florea* colonies**
A. mellifera swarm				Non-significant regression	Non-significant regression
A. mellifera forage			1	Non-significant regression	Non-significant regression
A. dorsata swarm		1		Non-significant regression	Non-significant regression
A. florea swarm	Non-significant regression	Non-significant regression	Non-significant regression		Non-significant regression
A. florea colonies	Non-significant regression	Non-significant regression	Non-significant regression	Non-significant regression	

The slopes of linear regressions for A. mellifera forage dances and A. dorsata swarm dances were equivalent.

Table 7 | Third most frequent outcome of randomization analysis (891 occurrences out of 10,000 randomizations).

	***A. mellifera* swarm**	***A. mellifera* forage**	***A. dorsata* swarm**	***A. florea* swarm**	***A. florea* colonies**
A. mellifera swarm					Non-significant regression
A. mellifera forage			2		Non-significant regression
A. dorsata swarm		2		1	Non-significant regression
A. florea swarm			1		Non-significant regression
A. florea colonies	Non-significant regression	Non-significant regression	Non-significant regression	Non-significant regression	

Here, the slopes of regression lines for A. mellifera forage dances were equivalent to those for A. dorsata swarm dances, and additionally regression lines for A. dorsata swarm dances had the same slope as A. florea swarm dances.

swarm (sky vs. gravity, or a combination of both). However, that would contradict other studies that found that a view of the sky reduces angular deviation in the dance (Rossel and Wehner, 1982; Tanner and Visscher, 2010).

We did not find that bees advertise a constant patch size. Although, with the exception of *A. mellifera* nest-site dances, angular deviation was reduced with increasing waggle phase duration, this reduction is insufficient to keep the size of the patch the same. Moreover, at some waggle phase duration the bees can no longer reduce angular deviation; thus the more distant the advertised source, the larger the advertised patch becomes. This effect is exacerbated in the context of nest-site selection in *A. mellifera*, as here angular deviation does not decrease with waggle phase duration. To give an indication of patch size advertised, let us assume that a waggle phase duration of 1 s corresponds with a source that is 1000 m from the bees [taken from (Von Frisch, 1967); this is a very rough approximation because we now know that the terrain through which the bee flies affects her perception of distance (Esch and Burns, 1996; Esch et al., 2001; Menzel et al., 2010) and the dance duration-distance relationship is most likely different for different species (Lindauer, 1957)]. The average radius of the area advertised by *A. mellifera* nest site scouts in our pool of data would then be 690 m (538 m in the context of foraging).

Table 8 | Fourth most frequent outcome of randomization analysis (575 occurrences out of 10,000 randomizations).

	***A. mellifera* swarm**	***A. mellifera* forage**	***A. dorsata* swarm**	***A. florea* swarm**	***A. florea* colonies**
A. mellifera swarm					
A. mellifera forage			1	1	1
A. dorsata swarm		1		1	1
A. florea swarm		1	1		1
A. florea colonies		1	1	1	

Here, regression lines for A. mellifera forage dances, A.dorsata swarm dances, A. florea swarm dances and dances that occurred on the top of natural colonies of A. florea all had equivalent slopes.

The size of the patches the bees advertise begs the question how dance followers ever find the site the bee is dancing for. In the context of foraging, dance followers use the average of the waggle phases they have followed to determine the direction to fly into (Tanner and Visscher, 2008). Moreover, bees will follow more waggle phases the more distant the site advertised (Toufailia et al., 2013). Following more waggle phases and using the mean direction indicated in those waggle phases decreases the effect of angular deviation and thus increases the accuracy of the information obtained from the dance. Thus, the location indicated by the average direction indicated by a dance is probably closer to the target than the area we estimated via angular deviation.

Again in the context of foraging, we know that bees use a myriad of other cues to locate food sources, such as visual cues (Von Frisch, 1914), plant odor (Von Frisch, 1967; Kirchner and Grasser, 1998; Reinhard et al., 2004; Beekman, 2005; Farina et al., 2005, 2007; Menzel et al., 2006; Arenas and Farina, 2012), scent marking (Giurfa and Nunez, 1992; Stout and Goulson, 2001), and memory (Gil and Farina, 2002; Menzel et al., 2006; Granovskiy et al., 2012). In fact, Grüter and Farina (2009) have argued that the dance language serves more as a "back-up" system for when information obtained from personal experience and the environment is insufficient. It is easy to see how foraging bees can make use of a large number of information sources. After all, there is no need for all

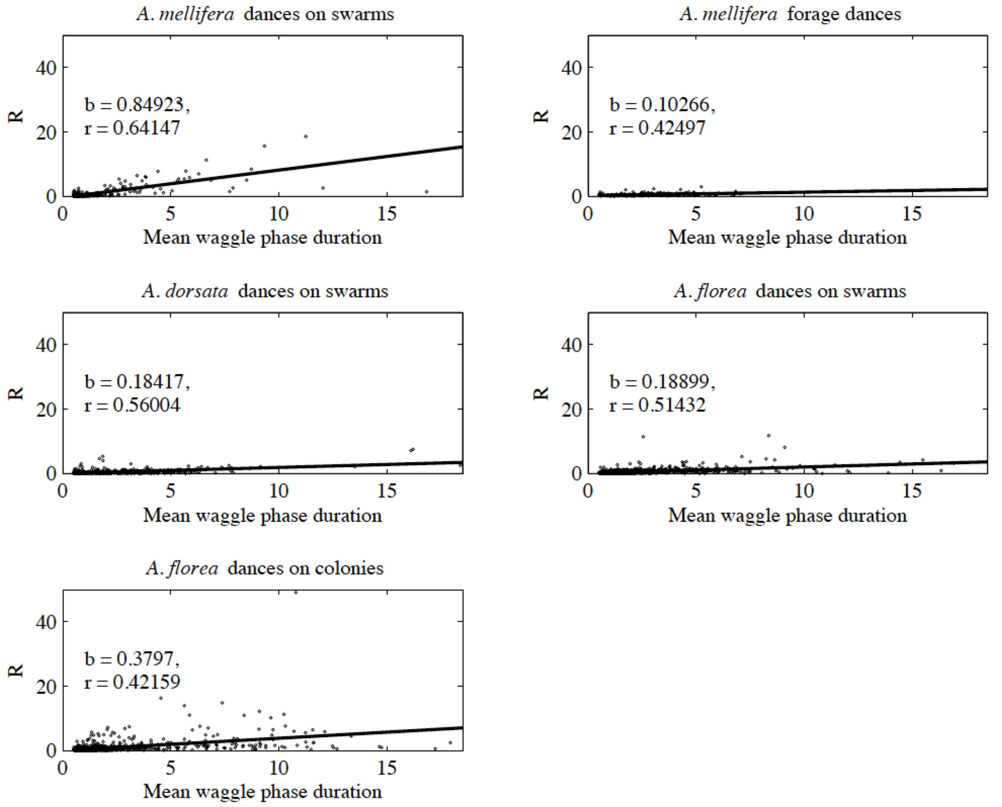

FIGURE 3 | Estimated radius (*R*) of the patch advertised within a dance against mean waggle phase duration. The solid line is the line of best fit (see **Table 9** for details of the linear regression analyses).

Table 9 | Linear regression statistics, estimated radius of region advertised by dance, R, vs. mean waggle phase duration t (s) (full data set).

Source	*df*	*SS*	*MS*	*F*	*p*-value
***APIS MELLIFERA* SWARM DANCES**					
Regression	1	892.36	892.36	416.71	0 ($<$0.001)
Residual	596	1.2763×10^3	2.14		
Total	597	2.1687×10^3			
***APIS MELLIFERA* FORAGE DANCES**					
Regression	1	6.90	6.90	65.46	1×10^{-14}
Residual	297	31.31	0.1054		
Total	298	38.21			
***APIS DORSATA* SWARM DANCES**					
Regression	1	85.77	85.77	318.96	0 ($<$0.001)
Residual	698	187.69	0.27		
Total	699	273.46			
***APIS FLOREA* SWARM DANCES**					
Regression	1	187.90	187.90	622.93	0 ($<$0.001)
Residual	1732	522.44	0.3016		
Total	1733	710.34			
***APIS FLOREA* DANCES ON COLONIES (FORAGE AND NEST SITES)**					
Regression	1	841.39	841.39	309.97	0 ($<$0.001)
Residual	1434	3892.5	2.71		
Total	1435	4733.9			

bees from the same colony to forage at the same source. In fact, the opposite is the case, as foragers from the same colony should not compete with each other and the colony as a whole most likely benefits from the collection of nectar and pollen from a diverse range of flowers.

When selecting a nest site, it is essential the bees all arrive at the same site. Studies on nest-site selection in *A. florea* have suggested that due to *A. florea*'s nest-site requirements (basically a shaded twig on a tree) and the abundance of potential nest sites, *A. florea* swarms only decide on the general direction they need to fly in to (Diwold et al., 2011; Makinson et al., 2011; Schaerf et al., 2011). Hence, the angular deviation in the dance will not necessarily negatively affect the ability of *A. florea* swarms to move cohesively to a new site (Diwold et al., 2011). *A. dorsata* most likely uses visual cues to locate potential nest sites, as these bees prefer to nest in aggregations, mostly in trees that stand out in the environment or on conspicious buildings such as water towers or spires of temples (Oldroyd and Wongsiri, 2006). Thus, here too we suspect that the precision of the bees' dance is sufficient to allow *A. dorsata* to select a new nest site (Makinson, 2014).

Although we can envision that the honeybee's dance is sufficiently precise to understand how open-nesting species coordinate their nest-site selection, the same cannot be said for cavity-nesting species. We do know that *A. mellifera* scout bees mark the entrance to the nest site they have found with Nasanov pheromone, and that the presence of the pheromone assists the swarm locating the entrance to the cavity (Beekman et al., 2006). Most likely Nasanov pheromone also attracts scouts that are searching in the vicinity of the cavity marked by a previous visitor, but whether it could attract a bee from a distance of 690 m seems dubious. It would therefore be interesting to learn more about the cues nest-site scouts of cavity-nesting bees use when searching for potential nest sites.

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The anti-waggle dance: use of the stop signal as negative feedback

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Numerous activities within honey bee (*Apis mellifera* L.) colonies rely on feedback loops for organization at the group level. Classic examples of these self-organizing behaviors occur during foraging and swarm nest site selection. The waggle dance provides positive feedback, promoting foraging at a specific location or increased scouting at a potential nest site. Rather less well known than the waggle dance is the stop signal, a short vibration often delivered while butting against a dancing bee. It is currently best understood as a counter to the waggle dance, offering negative feedback toward the advertised foraging location or nest site. When the stop signal is received by a waggle dancer she is more likely to terminate her dance early and retire from the dance floor. Bees that experienced danger or overcrowding at a food source are more likely to perform the stop signal upon their return to the colony, resulting in an inhibition of foraging at that location. During a swarm's nest site selection process, scout bees that visited a different site than the one being advertised are more likely to stop-signal the waggle dancer than are scouts that had visited the same site. Over time, the scout bees build recruitment to a single site until a quorum is reached and the swarm can move to it. The balance between the positive feedback from the waggle dance and the negative feedback from the stop signal allows for a more sensitive adjustment of response from the colony as a unit. Many of the processes associated with the feedback loops organizing a honey bee colony's activities are in striking parallel to other systems, such as intercellular interactions involved in motor neuron function.

Keywords: honey bee, behavior, decision-making, vibration, sound, negative feedback, recruitment

INTRODUCTION

Honey bees (*Apis mellifera* L.) employ numerous chemical, tactile, and vibratory communication signals to coordinate their activities. Here, we will focus on a few of the vibratory ones including the well-known waggle dance, which signals the distance and direction of a resource such as a food source or a potential nest site to nestmates (von Frisch, 1967). We will also discuss the tremble dance, which is performed by foragers who have experienced delay in unloading, and recruits more bees to assist in unloading food from incoming foragers (Seeley, 1992). An additional signal, and the focus of this article, is the stop signal. Sometimes referred to as the "brief piping signal," (e.g., Seeley and Tautz, 2001; Thom et al., 2003) in addition to "peeps" (Esch et al., 1965), "squeaking" (von Frisch, 1967), and "short squeaks" (Kirchner, 1993a), the stop signal is an acoustic signal produced by a bee briefly vibrating her wing muscles (with little wing movement), often while butting her head against another bee (a video of honey bees performing the stop signal can be found in the online Supplementary Material).

Here we review what is known about the stop signal and its uses. The focus will be on exploring the balance among communication signals used by individuals and the resulting adjustment of response by the colony as a unit.

EARLY WORK ON THE STOP SIGNAL

The first recorded observations of the stop signal did not find clear uses and meanings for it. Esch (1964) observed bees attending waggle dances and noted that they occasionally emitted squeaking sounds, after which they sometimes received food samples from the dancer. Wenner (1962) reported that disturbed bees emit short bursts of sound, similar to the stop signal. von Frisch (1967) also observed it in use by bees interacting with waggle dancers, and agreed with an interpretation by Esch (1964) that it was a begging call for food.

The sounds made by these bees were later identified as vibrations of the comb made by pressing the thorax briefly to it and pulsing the wings (Michelsen et al., 1986), or by a bee butting her head into a dancer and pulsing the wing muscles (Nieh, 1993). Michelsen et al. (1986) described these sounds as typically lasting approximately 100 ms at approximately 380 Hz. The results of Schlegel et al. (2012) averaged 407 Hz for 147 ms. Honey bees also make a similar-sounding acoustic signal known as worker piping, but this can be differentiated from the stop signal by its much longer duration, approximately 602 ms, and a higher and upward sweeping frequency, (451–478 Hz, Schlegel et al., 2012).

The term "stop signal" seems an appropriate name for the signal, since von Frisch (1967) reported that the dancer and surrounding bees are "paralyzed" by the sound. Similarly, Michelsen et al. (1986) found that artificial signals made by vibrating the comb caused bees in the area immediately surrounding the point of vibration to briefly freeze their movements. When Nieh (1993) observed bees on the dance floor and recorded the behavior of individuals before and after sending or receiving the stop signal he found that the sender very seldom receives food (once out of 576 stop signals delivered to waggle dancers), discrediting the idea that the stop signal is a begging call. The most common occurrence after a waggle dancer received the stop signal was to leave the dance floor (Nieh, 1993). Similarly, in a later study Pastor and Seeley (2005) investigated the behavior of waggle dancers and dance followers. They found that dancers that received the stop signal were more likely to stop dancing and they never observed an instance of food exchange between a stop signal sender and receiver. A summary of the roles of the stop signal can be found in **Table 1**.

WHICH BEES PRODUCE THE STOP SIGNAL?

In an effort to determine which bees within a colony produce the stop signal and which receive it, Nieh (1993) trained foragers from an observation hive to visit an artificial feeding station filled with sugar water and made observations on the bees populating the dance floor. Recently-returned foragers were observed with a video camera and microphone. The study focused on classifying the stop signal senders and receivers, and found that tremble dancers are the most likely individuals to perform the stop signal, although they can occasionally be performed by waggle dancers and dance followers (Nieh, 1993). Waggle dancers and tremble dancers were the most common stop signal receivers, although food exchangers, dance followers, and "other" bees not dancing or observing dances were also targeted (Nieh, 1993).

Pastor and Seeley (2005) revisited the question of which bees send and receive the stop signal after noting that the bees in Nieh's (1993) study may not have been behaving normally due to the large influx of food they were receiving from the feeding station. When they observed a colony that was foraging on naturally-available food resources with no access to a feeder, most of the waggle dance followers that used the stop signal had not previously been tremble dancing (Pastor and Seeley, 2005). Additionally, though Nieh (1993) found that dance followers occasionally use the stop signal on waggle dancers, in Pastor and Seeley's (2005) results the majority of stop signalers were dance followers.

When waggle dancers receive a stop signal they are more likely to leave the dance floor (Nieh, 1993; Pastor and Seeley, 2005) and their average dance length is shorter (Kirchner, 1993b). These factors, combined, likely result in an inhibition of recruitment to that food source and an overall decrease in foraging.

It is possible that this effect was also observed by Wenner (1962), as he described waggle dancers being interrupted in their dances by other bees or abruptly halting their dances, sometimes even in the middle of a waggle run, for unknown reasons. He also mentioned the short sounds made by disturbed bees, which may have been stop signals. Unfortunately, insufficient information was given to determine if these short sounds were stop signals.

WHAT ELICITS THE STOP SIGNAL?

Aside from its effect of halting waggle dances, the stop signal can also be seen in use by bees not located on the dance floor and received by bees that are not waggle dancers. Thom et al. (2003) observed colonies both when they had access to a sugar water feeding station and when they were foraging under natural conditions.

Stop signaling increased when a feeding station was available (Thom et al., 2003). Most of the stop signaling activity was by tremble dancers, although non-waggle dancing nectar foragers also performed the stop signal (Thom et al., 2003). Tremble dancers that used the stop signal ended up staying in the hive for longer than those that did not use the stop signal (Thom et al., 2003). Foragers that performed the stop signal tended to spend less of their time within the colony on the dance floor, and often continued performing the stop signal outside of the dance floor (Thom et al., 2003). Tremble dancers that performed the stop signal tremble-danced for longer than non-stop signalers and traveled deeper into the hive (Thom et al., 2003). Also, bees that used the stop signal sometimes inspected cells by entering them up to the thorax, which was a behavior not exhibited by non-stop-signaling bees (Thom et al., 2003).

It can be inferred that by inhibiting the waggle dance, the stop signal strengthens the nectar-receiver-recruiting effect of the tremble dance (**Figure 1**), but this does not account for the bees observed using the stop signal outside of the dance floor.

Table 1 | A summary of the roles of the stop signal in honey bee colonies.

Role	Evidence	References
Stop other bees' movements	Bees surrounding a stop signaler briefly freeze movements	von Frisch, 1967; Michelsen et al., 1986
Inhibit waggle dancing	Waggle dancers receiving the stop signal leave the dance floor	Kirchner, 1993b; Nieh, 1993; Pastor and Seeley, 2005
Modulate the tremble dance	More stop signaling by tremble dancers when a feeding station is present	Thom et al., 2003
Decrease recruitment to a food source	More stop signaling when a feeding station is crowded; more stop signaling when there is danger or competition at a feeding station	Lau and Nieh, 2010; Nieh, 2010
Provide cross-inhibition during a swarm's nest site selection process	Waggle dances are shorter when stop signaling occurs; stop signalers target dancers advertising nest sites not visited by the stop signaler	Seeley et al., 2012

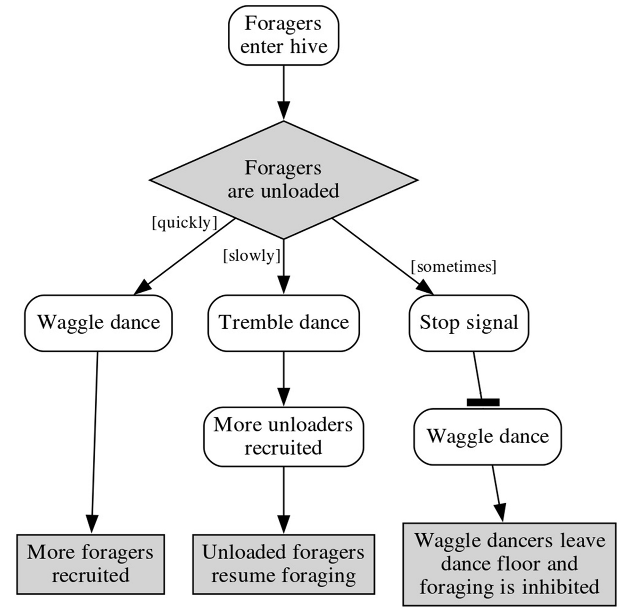

FIGURE 1 | Feedback loops in a foraging colony, showing the effect of the stop signal on waggle dances and forager recruitment.

Thom et al. (2003) suggested that the off-dance-floor stop signaling could be an effort to modulate the recruitment of more nectar receivers by lowering potential nectar receivers' response thresholds to the tremble dance.

An interesting finding of this study (Thom et al., 2003) was that many of the tremble dancers that also performed the stop signal began signaling as soon as they entered the colony, i.e., before having an opportunity to be met by a nectar receiver and be influenced by the time-delay cue described by Seeley (1992). Thom et al. (2003) suggested they may have been acting based on their experiences from prior foraging trips or by cues sensed outside of the hive. One source of such cues may have been scramble competition at the feeding station (Thom et al., 2003). This conclusion seems possible, especially since it has been shown that rich food resources such as feeding stations lead to a spike in tremble dancing and stop signaling within the colony (e.g., Nieh, 1993; Pastor and Seeley, 2005). Thom et al. (2003) might have been able to determine the effect of the feeding station on the timing of tremble dancing if they had compared the behavior of the tremble dancers in their colony foraging under natural conditions to that in their colonies that had access to the feeding station. However, they scanned the natural conditions colony for communication signals but did not closely examine the behaviors exhibited by the individual signalers, thus, an effective comparison cannot be made using their results.

PROXIMATE STIMULI THAT ELICIT THE STOP SIGNAL

Lau and Nieh (2010) hypothesized that a food source that is declining in quality, for example running out of food or becoming overcrowded, may provoke the use of the stop signal by foragers. Supporting this, they found that as a feeding station grew more crowded, the rate of stop signaling within the colony increased. The foragers that had to wait to access the feeder were not more likely to perform the stop signal themselves, but they were more likely to receive stop signals from other bees that had visited the feeder and also from individuals that had not been observed there. This may be because some bees were not able to access the feeder at all due to overcrowding and returned to the colony without feeding. Thus, feeder crowding probably increases the number of foragers within the nest, thereby increasing the number of opportunities for them to use the stop signal (Lau and Nieh, 2010). Lau and Nieh (2010) conjectured that it is likely that the stop signal is present in the colony at low levels at all times, but does not have a colony-wide effect until some threshold level is reached. Additionally, using the stop signal may enable bees to rapidly adjust foraging efforts in response to shifts in their environment's nectar flow.

The stop signal is also used when foragers experience some form of danger or competition at a food source (Nieh, 2010). Under natural conditions this would likely be a response to being attacked by other bees or a predator while foraging. Nieh (2010) observed fights between conspecifics at a feeding station, and he simulated a predator attack by pinching bees visiting a feeder on the metathoracic femur with forceps. Both the bees that had experienced intraspecific competition and those that were attacked by forceps were more likely to perform the stop signal toward other foragers waggle-dancing for the same food source than they were toward dancers for other locations. Bees that had not had the negative experiences were much less likely to use the stop signal at all (Nieh, 2010).

The intraspecific competition that the bees experienced at the feeding station was probably somewhat artificial. When bees forage on natural food sources such as flowers, these are usually spread across a patchy landscape, individually offer small amounts of food, and are seldom simultaneously visited by more than one bee. In contrast, a feeding station is a very rich food source found only at a single location. Nieh (2010) acknowledged this and suggested that competition at the feeding station may be more similar to the competition experienced when bees rob food from other colonies (though Johnson and Hubbell, 1974, and others, have reported competitive interactions at floral sources.). In a paper modeling a hive-robbing event, Johnson and Nieh (2010) showed the stop signal in use to rapidly shut down robbing by countering the waggle dance. Aside from this model, however, an actual assessment of the signaling that occurs during an actual robbing or dense-flower situation and comparing it to the signaling used while foraging at a feeding station is an area of research that has not yet been explored.

STOP SIGNALS AS CROSS-INHIBITION

Another observed use of the stop signal is during the swarm nest site selection process. When honey bees swarm (reviewed in Visscher, 2007), thousands of workers and the original queen leave the hive and settle in a cluster a short distance away. From there, scout bees depart and search for potential new nest sites that the colony could inhabit. When a scout locates a favorable site, she returns to the swarm and advertises its location using the waggle dance. Over time, multiple sites maybe be advertised by many different dancers, with each group competing to recruit additional scouts to their site. Support for the different sites will wax and wane until a threshold number of scouts, or quorum, is reached at one of the sites, after which recruitment declines, and the swarm can be mobilized to move to its new home. This deadlock avoidance is of key importance to the nest site selection process because unlike during foraging, a decision for a single site must be reached.

The stop signal is used to provide cross inhibition in the form of negative feedback during this decision making process (Seeley et al., 2012). This study made video recordings of waggle dancers on the surfaces of swarms and recorded stop signals performed on the dancers by following bees on video with audio from a microphone held close to dancing bees. The dancers stopped dancing soon after receiving stop signals, and their dances were shorter than those of dancers not receiving stop signals When swarms simultaneously scouted two identical nesting boxes, dancers for either box received more stop signals from bees that had visited and been marked at the other site (contra-signalers) than bees that had visited the same site (ipsi-signalers). After a decision was reached about which nest box to occupy (inferred from the initiation of worker piping, which prepares the swarm for takeoff), the stop signalers no longer selectively targeted dancers advertising the opposing site and dancers received contra- and ipsi- signals equally. Seeley et al. (2012) inferred that negative feedback from the stop signal was provided cross inhibition between the two potential nest sites while the swarm was still making a decision, and that after a decision had been reached it contributed to shutting down waggle dancing. This contributes to having nearly all the swarm's bees at the swarm cluster when it takes off for cross-country flight, which will be guided by the scouts that know the way to the chosen site.

NEGATIVE FEEDBACK IN OTHER SOCIAL INSECT SYSTEMS

It is of interest to note that negative feedback is present in other social insect systems. Trail pheromones, which are also used by termites, stingless bees, and social wasps, are used to recruit other individuals to food sources and nest sites (Czaczkes et al., 2015). These can encode complex information as a result of having varying chemical blends, concentrations, and operating synergistically with other factors (Czaczkes et al., 2015). Positive feedback from trail pheromones can cause groups of ants to focus inflexibly on a single food source due to the strong, non-linear response of recruits to the trail, even when other potentially better options exist (e.g., reviewed in Camazine et al., 2001). This effect can be countered by negative feedback from overcrowding at a food source, which results in an equal distribution of foragers across multiple food sources or the quick reallocation of the majority of foragers to a superior food source (Grüter et al., 2012). Negative feedback can also come from encounters with other foragers on a trail, where greater crowding leads to less trail pheromone deposition (Czaczkes et al., 2013), or from repellant trail pheromones used as "no entry" signals marking unrewarding paths (Robinson et al., 2005).

DISCUSSION

Decision-making by groups of animals has received increasing recent attention in part because of recognition of its significance to other systems, in particular complex nervous systems and human engineered systems. Mechanisms of coordination discovered in social insect colonies have provided models for human-engineered systems in computing and robotics, because in both kinds of systems there is a need for reliable, robust decision-making based on simple interactions among components (e.g., Bonabeau and Meyer, 2001; Tsuda et al., 2006) Also, recent discoveries in decision-making mechanisms of vertebrate brains and swarms of honey bees have revealed striking parallels in their mechanisms (Passino et al., 2008; Marshall et al., 2009).

In all such systems, individual units are able to use a relatively small repertoire of behaviors or actions to achieve a complex task as a whole. Each unit, be it an insect, a robot, or a neuron, accumulates evidence until some threshold is reached and a decision can be made. The stop signal reviewed here provides negative feedback that can help modulate achieving that threshold and tune the behavior of honey bee colonies during foraging and swarming. The findings reviewed here suggest that the stop signal has diverse uses and effects. It is quite likely that not all of these have yet been described.

For example, the question of stop signaling during swarming is still not well understood. The results of Seeley et al. (2012) support the idea that cross-inhibition during the decision-making phase by contra-signalers provides negative feedback from scouts that had visited a different nest site. This, however, does not explain the lower-level occurrence of the ipsi-signaling that was also present. In a follow-up study using two nest boxes of differing volumes, much of the stop signaling observed was ipsi-signaling rather than contra-signaling, and some of stop signalers had not visited either nest site (Visscher, Schlegel, and Kietzman, unpublished data). These are puzzling results that beg the immediate questions of what might have been motivating the bees to signal and what the signals' effects were on the decision-making process. There is clearly more to learn about the uses and effects of the stop signal during swarming.

Another not-yet-explored avenue is the idea that tremble dancers that use the stop signal outside of the dance floor may be modulating the recruitment of more nectar receivers by lowering potential nectar receivers' response thresholds to the tremble dance (Thom et al., 2003). This could be tested by assessing whether or not non-dancers that received the stop signal were more likely to become nectar receivers after being contacted by a tremble dancer than individuals that did not. If so it would be a novel use of the stop signal within the context of a foraging colony.

A variety of conditions external to the colony have been explored to determine their effects on the communication signals used by bees, but few have considered the factors within the hive that may influence the bees' communication. We now know that a lack of nectar receivers stimulates tremble dancing, which results in the recruitment of more nectar receivers (Seeley, 1992). We also know that stop signaling inhibits foraging and is also associated with tremble dancing (e.g., Thom et al., 2003). A useful line of research would be to determine what factors, if any, within the hive might help drive bees' decisions to tremble dance or stop signal. For example, decreasing the food storage space available to the bees might be expected to result in an increase in tremble dancing, as the nectar receivers would be unable to store the food brought in by foragers. There would likely also be in an increase in stop signaling as the colony's nectar-handling capacity would be exceeded and foraging would need to be shut down.

While there are unanswered questions about the use of the stop signal, most of what has been discovered fits a picture of the stop signal as a negative-feedback component in recruitment, a sort of anti-waggle dance. The use of such a signal allows the bees to tune their recruitment more accurately and quickly in response to changing conditions, and in a variety of contexts.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fevo.2015.00014/abstract

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Environmental consultancy: dancing bee bioindicators to evaluate landscape "health"

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Here we explore how waggle dance decoding may be applied as a tool for ecology by evaluating the benefits and limitations of the methodology compared to other existing ways to evaluate the honey bees' use of the landscape. The honey bee foragers sample and "report" back on large areas (c. 100 km^2). Because honey bees perform dances only for the most profitable resources, these data provide spatial information about the availability of good quality forage for any given time. We argue that dance decoding may inform on a range of ecological, conservation, and land management issues. In this way, one species and methodology gives us a novel measure of a landscape's profitability, or "health," that may be widely relevant, not just for honey bees, but for other flower-visiting insects as well.

Keywords: waggle dance, *Apis mellifera*, dance decoding, bee foraging, environmental monitoring

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Introduction

Wilhem Nylander, a Finnish-born botanist, liked to stroll around Paris, finding perhaps that the more verdant parts of the city reminded him of his Helsinki origins. It was during one of these walks, through the Jardin du Luxembourg, that the idea of bioindication was born (Skye, 1979). For years, Nylander had studied lichens, which occur worldwide from the humid tropics to the arctic and can even colonize bare rock. However, they are very sensitive to air pollution. Nylander noticed that there were more lichen species growing in the Luxembourg Gardens than in other parts of Paris. He hypothesized that lichens were susceptible to atmospheric pollutants and therefore failed to thrive in much of Paris, which was very polluted at that time (Nylander, 1866).

Today, lichens are still routinely used as an assessment of air quality (Pinho et al., 2004). In the years since Nylander, strides have been made to clean up the air, and the lichens have responded by returning to Paris (Skye, 1979). Pollution, however, is not the only challenge humans have introduced to the earth. In the last century, man-made landscape changes, such as agricultural intensification, have had a large, negative impact on biodiversity. For example, insect pollinators that depend on the presence of flowers and flower-rich habitats have been recently challenged by the conversion of those areas to intensively farmed land (Matson et al., 1997; Tilman et al., 2001; Robinson and Sutherland, 2002; Carvell et al., 2006; Winfree et al., 2011; Wright and Wimberly, 2013). The link between landscape changes and pollinator declines has generated intense interest from both government and private sectors (Berenbaum et al., 2007; Kluser et al., 2011), such as a recent announcement by the United States government that they are giving $8 million to increase available forage for Midwestern honey bees (USDA, 2014). However, it is difficult to know not only when and where supplementary forage would be most beneficial, but also to know if such policies, once in place, are having the intended effect.

The answer may lie with the honey bee, an organism that itself would benefit from a healthy landscape. Honey bees, with their unique waggle dance communication, may be an untapped, biologically relevant resource to provide cost-effective bioindication by surveying, monitoring, and reporting on a landscape's "health," specifically in regards to floral abundance.

What Information Is Available From Waggle Dance Decoding?

Honey bees, *Apis* species, possess a remarkable and unique behavior. A successful forager communicates to her nestmates the vector (distance and direction) from the hive to the nectar or pollen (von Frisch, 1946, 1967; Grüter and Farina, 2009; Couvillon, 2012) by making waggle dances. The vector information, which the bee repeats many times within a single dance and which is encoded in the waggle phase portion of the dance, can be decoded by researchers (Visscher and Seeley, 1982; Beekman and Ratnieks, 2000; Steffan-Dewenter and Kuhn, 2003; Couvillon et al., 2012b; Schürch et al., 2013). By decoding many dances, a map of where the colony as a whole (or indeed several colonies) is foraging can be made. Importantly, honey bee foragers only dance for profitable resources, which means that, on average, observed dances are for the "best" forage that is available at any given time (von Frisch, 1967; Seeley, 1994) after the forager has weighed the benefit of the forage against the costs, including the distance she must fly (von Frisch, 1967; Seeley, 1994; Couvillon et al., 2014b,c). The dance allows the honey bee colony to exploit either particularly good resources or resources when availability is low, and it therefore contributes to the fitness of the colony (Seeley, 1995; Sherman and Visscher, 2002; Dornhaus et al., 2006; Donaldson-Matasci and Dornhaus, 2012; Schürch and Grüter, 2014).

Dancing foragers also give direct and indirect information about the forage quality, which could include quantity and the molarity of the nectar. Directly, the number of repeated circuits within a single dance per return to the hive indicates the forager's assessment of quality: when resource quality increases, the forager makes more waggle runs per dance, and this results in the recruitment of more nestmates to the advertised location (von Frisch, 1967; Seeley, 1995; Seeley et al., 2000). Indirectly, a particularly good location may be indicated by multiple dances by the same or different bees, as more and more bees become recruited to the location that they indicate themselves in subsequent dances. When such multiple dances are plotted, "hotspots" of good quality forage become visible (Beekman and Ratnieks, 2000; Steffan-Dewenter and Kuhn, 2003; Couvillon et al., 2014b).

Lastly, it is also possible to know if a particular dance is for a pollen or a non-pollen, usually nectar, source because the pollen is visible in the corbiculae (Couvillon et al., 2014a). Although it is quite difficult to obtain the pollen from a dancing bee for identification, it is possible for pollen traps to be placed over the entrance to collect pollen from all returning foragers (e.g., colony-level information about pollen collection). These data on plant type composition, particularly a high representation of a single plant type (Garbuzov and Ratnieks, 2014), can then be correlated to the forage location information obtained by dance decoding (**Table 1**). Knowing the breadth of the plant community composition gives indication of the landscape's biodiversity.

What Information Is Not Available from Waggle Dance Decoding?

Firstly, it is not possible to know the route, including obstacle avoidance, that a forager took from the hive to the resource (von Frisch, 1967). Route information can be partially reconstructed if dance decoding is combined with harmonic radar (**Table 1**), where a radar signal is received by a transponder on an insect and re-emitted such that the flight path of a honey bee is tracked (Riley et al., 2003, 2005; Menzel et al., 2005). However, the antenna for harmonic radar can only be applied after a dancing *A. mellifera* forager exits the hive, when it would actually be better to obtain the path information from the flight that precedes the dance. Additionally, harmonic radar is limited by a range of approximately 900 m, or the first hedge, for signal reception (Riley and Smith, 2002; Chapman et al., 2011). This would not cover the long-distance foraging of many kilometers that honey bees are capable of performing (von Frisch, 1967; Visscher and Seeley, 1982; Beekman and Ratnieks, 2000; Couvillon et al., 2014c).

It is equally challenging to know exactly what flowers were visited by a dancing bee. As previously mentioned, pollen samples can be obtained from the pollen traps at the entrance, which gives colony-level information on the plants that have been visited, but individual dances cannot then be linked to the samples. It is potentially possible to collect a pollen forager mid-dance (Hart and Ratnieks, 2001), once she has danced long enough for the data to be extracted (Couvillon et al., 2012b), but this would involve using a cover (e.g., polyurethane and not glass) that can be easily cut through, which may be intractable for large scale analyses. The pollen then could be identified, either by shape (Synge, 1947; McLellan, 1976; Cresswell, 2011; Garbuzov and Ratnieks, 2014), or by DNA markers, such as barcoding (**Table 1**, Bruni et al., 2015).

Lastly, because the honey bee is not a very precise dancer, decoding dances does not give exact location information. An individual honey bee often forages in a small area of approximately 10 × 10 m (Ribbands, 1953); however, the waggle dance made by her at different times or made by other bees working the same patch will display considerable scatter in both vector components of distance and direction (e.g., inter-dance variation, Schweiger, 1958; von Frisch and Lindauer, 1961). The variation found within a dance between successive, repeated circuit (intra-dance variation) (Beekman et al., 2005; De Marco et al., 2008; Tanner and Visscher, 2010a,b; Couvillon et al., 2012b; Schürch and Couvillon, 2013; Schürch et al., 2013; Preece and Beekman, 2014) also makes the signal challenging to understand. Certainly it is simply a limitation in dance accuracy that we cannot pinpoint a foraging location to, for example, a hedge.

One way to combat the issue of dance imprecision when we want to know where a bee foraged is to incorporate the variability

TABLE 1 | Comparison of methodologies to investigate honey bee foraging.

Method	Description	Obtained data	Benefits of data	Data limitations	Cost	References
Dance decoding	Eavesdropping on waggle dances of returning foragers and using the vector from hive to resource to determine where bees forage	Approximate location of where honey bees collected nectar and pollen	Can determine where and when food is available, use of particular areas or land-types. Dances can be from video, so no time/number limitation	Cannot know route information, exact floral type, precise location	Cheap equipment, easy for training, but takes time	Visscher and Seeley, 1982; Waddington et al., 1994; Seeley, 1995; Beekman and Ratnieks, 2000; Steffan-Dewenter and Kuhn, 2003; Beekman et al., 2004; Donaldson-Matasci and Dornhaus, 2012; Couvillon et al., 2014a,b,c; Garbuzov et al., 2014, 2015
RFID Tags	Automatic identification and data capture of tags that are glued to individual bees and then read by a reader	Timing of foragers' departure and return to hive and arrival and departure from a fixed site, such as a feeder (e.g., homing rate, speed, and displacement)	Can assess unlimited numbers and record many events, little disturbance to colony, data collection automatic	Cannot obtain natural foraging data, as a tag reader must be set up at a single, fixed location	Reader costs £320–£1300; each tag costs £0.90.	Desneux et al., 2007; Decourtye et al., 2011; Pahl et al., 2011; Schneider et al., 2012
DNA Barcoding (pollen or honey)	Using a short genetic marker in DNA to identify it as belonging to a particular species	Plants that are visited by foraging honey bees	Can know particular plants that are visited from a certain forager (pollen) or hive (honey)	Differing resolution between species, no spatial information	£1.30–3.20 per sample	Valentini et al., 2010; Wilson et al., 2010; Bruni et al., 2015; Soares et al., 2015
Harmonic radar	Foragers fitted with a tag that echoes back the signal from centrally-located receiver	Flight route taken by departing foragers	Can construct short distance flight paths	Range limited to ~900m, antennae cumbersome; only possible to track 1–2 individuals at a time	£10–30 per tag and £1500 to rent receiver for a field season	Riley and Smith, 2002; Riley et al., 2003; Menzel et al., 2005; Riley et al., 2005; Chapman et al., 2011
Observe directly in the field	Transects are walked through target areas	Counts of insects and flowers that are present in a particular area or landtype	Can make calculations of abundance and interactions between species and correlate with area, landtype	Correlative, cannot know source of unmarked insects	Equipment cheap, but man-power is costly	Steffan-Dewenter and Tscharntke, 2000; Kremen et al., 2002, 2004; Greenleaf and Kremen, 2006; Garibaldi et al., 2013
Pollen analysis under microscope	Obtain pollen from entrance and determine plant type using microscope	Type and relative contribution of plant types currently being visited by honey bee colony	Can see dynamics of pollen collection and plant exploitation	Only colony-level information (e.g., not individual forager)	Relatively cheap, but requires training and microscope	Synge, 1947; McLellan, 1976; Cresswell, 2005; Leonhardt and Blüthgen, 2012; Garbuzov and Ratnieks, 2014; Garbuzov et al., 2015

from within the dance into the mapping of the dance itself. In Schürch et al. (2013), a Bayesian approach combined with simulations allowed for the production of a spatial probability distribution for a forage location. Instead of plotting a dance as a point, which over-represents our certainty about a location, dances were plotted as a heat map (Schürch et al., 2013; Couvillon et al., 2014c). Additionally, when multiple dances, either from different bees going to the same location or the same bee dancing multiple times, are rasterized together, a more accurate estimation of a "hot spot" can be achieved (Couvillon et al., 2014b; Garbuzov et al., 2015).

It should be noted that for many specific investigations, we do not need to know a precise location to obtain biologically-relevant information about honey bee foraging ecology. For example, because distance is such a relevant cost in a bees' decision to recruit and because honey bees have evolved exceptional sensitivity to relative energetic reward, communicated distance is a proxy for forage availability: the further a dancer indicates in her recruitment, the relatively less available forage is nearby (Couvillon et al., 2014c). Because dance duration translates into flight distance, examining the average dance duration per month provides important information about in what months forage is relatively less or more available (Beekman and Ratnieks, 2000; Couvillon et al., 2014c) or how relative distances (durations) vary between urban and rural and suburban settings (Waddington et al., 1994; Garbuzov et al., 2014) or across differently structured landscapes (Steffan-Dewenter and Kuhn, 2003).

Why Is the Honey Bee a Useful Bioindicator of Landscape Floral Profitability?

Even given the above limitations, honey bees possess great potential for monitoring the landscape for floral resources. One reason is because the foraging range of the honey bee is so great, probably greater than other bees. Honey bees routinely forage at a distance of a few kilometers and have been known to fly 10–12 km to collect food when it is less available closer to the hive (von Frisch, 1967; Waddington et al., 1994; Beekman and Ratnieks, 2000; Steffan-Dewenter and Kuhn, 2003). In Couvillon et al. (2014b), by statistically correcting for distance, authors were able to assess honey bee foraging preferences across 94 km^2, which represents the "surveying power" of three glass-walled observation hives from one location (Couvillon et al., 2014b). A second reason why the honey bee is an ideal bioindicator is because they are generalists in their foraging preferences (Biesmeijer and Slaa, 2006). The flower species visited by honey bees for nectar and pollen will also be visited by other pollinators, which makes information about honey bee foraging preferences broadly relevant to a range of flower-visiting insects. As a proof of concept to the general nature of honey bee foraging, the bees indicated that the highest visited area in the 94 km^2 was a National Nature Reserve that is an area well known as being good for butterflies (Ellis et al., 2012; Couvillon et al., 2014b).

Thirdly, the honey bees possess the waggle dance, which is the only known recruitment behavior that also communicates a distance and direction, information available to eavesdropping researchers. A honey bee forager, in her decision to perform a waggle dance, integrates all relevant costs of flight distance, potential competition with other flower-visiting insects, and nectar and pollen availability, and if her assessment comes out in the positive, she performs a dance. Imagine how difficult it would be to obtain those data directly on the availability of good forage across a landscape-wide area. An ecologist would need to walk transects to count competing flower-visiting insects and flowers and determine forage availability. If an ecologist walks a straight-line transect at 1 m/s and can see a meter to the left and to the right, s/he will cover about 200 m^2 in 5 min. Even at this speedy clip and if s/he worked 24 h/day, it would take that ecologist 1632 days to cover 94 km^2 one time. Therefore, it is safe to say that the data obtained from decoding waggle dances is not available by surveying.

What Are the Potential Subject Areas That Would Benefit from Waggle Dance Decoding Data?

In addition to the applied application of landscape evaluation, data obtained from waggle dance decoding could be relevant in a variety of yet-unexplored contexts (Härtel and Steffan-Dewenter, 2014). Honey bees are important pollinators for many crops (Aizen and Harder, 2009), contributing £27 billion annually to the world economy from this ecological service. Combining waggle dance information with the colony-level pollen collection will help farmers better manage *pollination services*: pollen analysis would allow growers to determine if a target crop was visited or not, and dance information would allow growers to determine which field areas were visited (Kremen et al., 2002; Duan et al., 2008). These data would then work together to help manage the process (e.g., to fine-tune the bloom time such that bees are not attracted elsewhere). Additionally, dance information can also give other information, such as the time taken for a colony's foraging to recover following relocation (Riddell Pearce et al., 2013), which also helps for optimal management of pollination services.

In recent decades, there has been increasingly intense interest in mitigating the harmful effects of anthropogenic landscape changes through government incentives to encourage more wildlife-friendly farming. These stewardship schemes are required for all EU-member states and carry an impressive price-tag of €41 billion in the past 20 years. And yet there are little data evaluating the efficacy of such schemes, probably because it is hard to survey at the landscape scale. However, by monitoring the dances of honey bees foraging naturally in the landscape, Couvillon et al. (2014b) determined that some management stewardship schemes, such as the ones that encouraged set-asides or field margins in High Level Stewardship, may be more beneficial to honey bees than others, such as Organic Entry Level Stewardship that require the regular mowing of grass, including wildflowers (Couvillon et al., 2014b). The study provided biologically relevant data that may directly impact *land management* and existing efforts at *nature conservation* for honey bees and other flower-visiting insects and adds to a growing body of work linking pollinator health to landscape composition/"health" (Kremen et al., 2004; Klein et al., 2007; Brittain et al., 2013).

Because the honey bees are collecting their food in the landscape, they are potentially exposed to man-made toxins and may therefore provide useful information in *environmental risk assessment*. For example, in 2013 the European Union imposed a moratorium on the use of neonicotinoid insecticides as seed treatments for bee-attractive crops, such as oilseed rape (canola). However, one potentially missing element in the assessment of pesticide exposure is a better understanding of just how much foraging bees carry out on the treated crops. Recently it was demonstrated that in a typical European landscape that contains the mass-flowering crop of oilseed rape, which is a potential source of neonicotinoids, honey bees visit the nearby fields between 0 and 23% of the foraging time, depending on distance from hive and time of year (Garbuzov et al., 2015). By decoding waggle dances, researchers will better understand the dynamics of exposure (Garbuzov et al., 2015).

The waggle dance is one of the few Nobel Prize winning discoveries that can be seen with the naked eye in real time. The finding was exciting and, at times, controversial (Gould, 1976; Munz, 2005; Couvillon, 2012). "Language," as von Frisch diplomatically called the behavior, was thought to be in the exclusive domain of humans. In the waggle dance, not only a non-human but an invertebrate is able to communicate symbolically, using the sun and gravity as a reference, where she has collected good forage. Decoding waggle dances therefore is also a wonderful *gateway to biology*, providing an observable, interesting behavior to get the public engaged in science. Dance decoding also may be easily demonstrated in the classroom and to the larger, non-scientific community. In fact, the interest and amazement that the public express about the waggle dance and dance decoding may also represent a powerful opportunity for *citizen science*. It is possible to instruct anyone, even someone without a science background, into the fundamentals of waggle dance decoding, such that video recordings of dancing bees, uploaded to videos, can be decoded by community volunteers. There is great interest at the moment in helping bees, and tapping into the lay community may represent a powerful workforce that in turn are afforded an opportunity to help the honey bee in a very real way by contributing to our understanding of how and where they collect their food.

Lastly, although this article has mostly underscored the applied uses of the honey bee waggle dance, it is worth noting that studies involving decoded waggle dances also generate significant gains for basic biology, specifically *behavioral ecology*, *foraging ecology,* and *neuroscience*. Karl von Frisch, the Austrian-born ethologist who shared the 1973 Nobel Prize for discovering the waggle dance communication, famously remarked that the honey bee "is like a magic well," in that the discoveries never end. Certainly this applies to the waggle dance. In recent years, for example, we have witnessed many exciting discoveries about the nature of the honey bee waggle dance. These discoveries include the honey bee dance stop signal, which is made by foragers when they encounter a nestmate dancing for a location that is dangerous (Nieh, 2010), a discovery that helps our understanding of positive and negative feedback loops in self-organizing systems; the flexible use of dance information vs. memory by honey bees (Grüter et al., 2008; Grüter and Ratnieks, 2011); the effect of gravity on the angular intra-dance (im)precision (Couvillon et al., 2012a), which demonstrates how a biological entity manages to communicate in the presence of noise; the increased benefit of the dance for larger-sized colonies (Donaldson-Matasci et al., 2013), which aids in our understanding of how to optimize collective exploitation; and the ability of flying bees to obtain and to signal compass information purely from polarized light (Evangelista et al., 2014), which provides important insight into the capabilities of invertebrate visual navigation. The list is in no way exhaustive and only serves to demonstrate that there are still exciting and unknown features to be uncovered about this amazing behavior.

Conclusion: Is It Worth It?

Dance decoding is a relatively easy task. No specialist scientific training is needed and a person can be instructed on how to do it within a few hours. However, the method is time-consuming, especially if one wishes to decode hundreds or thousands of dances. After training, a decoder can decode a dance in under 5 min, but this estimate does not include the time spent watching a video to find a bee that is dancing. In all, it may take a trained worker several hours to locate and decode 20 dances from 1 h of video of the dance floor area of an observation hive. Therefore, it is worth considering a discussion on whether or not dance decoding is worth it? Perhaps decoding large numbers of dances, which would take the contributions of many people over many months, would not be worthwhile for basic biology alone. However, the applied benefits that may be gained that can be used to help honey bees and other insect pollinators could outweigh the costs.

Inherent in the discussion of "Is dance decoding worth it" is a comparison between dance decoding with other methods that may be used to assess where and when honey bees are collecting nectar and pollen (**Table 1**). Across all the methods, dance decoding is the only way to obtain, at the level of the individual, location information about where nectar and pollen has been collected, and it remains the superior method to use when investigating honey bee use of the landscape for forage (e.g., to assess *WHERE* bees are foraging; **Table 1**). Tagging foragers with RFID tags or harmonic radar can provide data on the timing of departure and return from a fixed site (e.g., the hive) or a short-distance flight path; however, neither can be applied realistically to field foraging conditions to determine where bees are collecting nectar and pollen. Tagging foragers generates information on *HOW* bees are foraging (**Table 1**). Likewise, methods that analyze the forage itself, such as DNA barcoding or pollen analysis, while providing important information about *WHAT* the bees are visiting, are limited in that neither provides location information, and both are challenging to perform at the level of the individual (**Table 1**). Lastly, field observations remain correlative, as it would be difficult to mark insects to identify their colony of origin.

Because each method carries its own unique benefits and costs, interesting results can be obtained if methods are combined. For example, because RFID tags require a tag reader, they can be used in conjunction with feeder experiments, where tagged foragers are trained to collect sugar water from a set feeder location. These bees, which may carry an additional identifying paint mark, may then analyzed for their dance behavior. In this instance, the actual vector information in the dance is less interesting, as it will communicate the feeder; however, the other interesting questions that require individual-level information regarding dancing and recruitment behavior may be investigated. Secondly, dance decoding can be effectively combined with forage analysis (barcoding or pollen microscopy) in circumstances where the bee may be foraging upon a particular target crop that is growing in known locations to generate powerful individual and colony level information about food collection and pollination services (Garbuzov et al., 2015).

Currently, there is no reliable method to automate the process, despite decades' worth of effort and even with recent advances in machine vision and automated video analysis for other organisms (Mersch et al., 2013). The goal has always been to create a system that can detect and decode waggle runs reliably. Although some advancement has taken place in the latter (Kimura et al., 2011; Landgraf et al., 2011), the process of detecting dances remains problematic. The dancing bee is just one moving part of a larger, very busy, and also moving background of her nestmates, and attempts to detect dances automatically leads to a large number of false positives [e.g., 199 true dances detected and 25 false positives (Rau, 2014)]. Also, no one has a real sense of the number of false negatives (waggle dances that fail to be detected). However, recently the field appears to be right on the cusp of observing significant advances in this area (see Landgraf et al. in this special issue).

In conclusion, it is our opinion that, given the time cost of dance decoding by hand, if the data obtained by the methodology were relevant only from a basic honey bee behavioral ecology perspective, it would not be worth to undertake large-scale projects. However, given that these data are unique and not possible to obtain any other way, and given that it may provide biologically-relevant information that could be used to help honey bees and other pollinators and to use resources wisely, we say yes. In dance decoding, we let the honey bees do the hard work to survey huge areas of land. Our job is only to listen to the bees.

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Automatic methods for long-term tracking and the detection and decoding of communication dances in honeybees

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The honeybee waggle dance communication system is an intriguing example of abstract animal communication and has been investigated thoroughly throughout the last seven decades. Typically, observables such as waggle durations or body angles are extracted manually either directly from the observation hive or from video recordings to quantify properties of the dance and related behaviors. In recent years, biology has profited from automation, improving measurement precision, removing human bias, and accelerating data collection. We have developed technologies to track all individuals of a honeybee colony and to detect and decode communication dances automatically. In strong contrast to conventional approaches that focus on a small subset of the hive life, whether this regards time, space, or animal identity, our more inclusive system will help the understanding of the dance comprehensively in its spatial, temporal, and social context. In this contribution, we present full specifications of the recording setup and the software for automatic recognition of individually tagged bees and the decoding of dances. We discuss potential research directions that may benefit from the proposed automation. Lastly, to exemplify the power of the methodology, we show experimental data and respective analyses from a continuous, experimental recording of 9 weeks duration.

Keywords: waggle dance, honeybee, animal behavior, animal tracking, computer vision

Introduction

A honeybee colony is a striking example of a complex, dynamical system (Seeley, 1995; Bonabeau et al., 1997). It is capable of adapting to a variety of conditions in an ever-changing environment. Intriguingly, the colony's behavior is the product of myriads of interactions of many thousand individuals, who each measure, evaluate and act on mostly local cues. Besides the mechanisms that regulate individual behavior, the flow (and hence processing) of information in the network of individuals is a crucial factor for the emergence of unanimous colony behavior (Hölldobler and Wilson, 2009). The most prominent example of honeybee social interaction, the waggle dance, has been investigated intensely throughout the last seven decades (Von Frisch, 1965; Seeley, 1995; Grüter and Farina, 2009), still leaving some important questions unanswered.

Foragers or swarm scouts, who have found a profitable resource or new nest site return to the hive and perform symbolic body movements on the comb surface or directly on the swarm.

Intriguingly, properties of the dance correlate with properties of the resource in the field. It was Karl von Frisch who postulated that bees showing high interest in the dance can decode the information content and exhibit a high probability of finding the advertised site (Von Frisch, 1965; Seeley, 1995; Riley et al., 2005). The waggle dance consists of two portions, a waggle run in which the dancer shakes her body laterally while moving forward on the comb surface; and a return run in which the dancer circles back to initiate a new waggle run from her previous approximate starting location (Von Frisch, 1965; Landgraf et al., 2011). Return runs are alternatingly performed clockwise and counterclockwise, consecutive waggle runs exhibit an angular difference inversely proportional to the target distance (Von Frisch, 1965; Weidenmüller and Seeley, 1999; Tanner and Visscher, 2010; Landgraf et al., 2011). Distance from the hive to the food or nest site is encoded in the duration of the dancer's waggle oscillation; direction from the hive to the resource is encoded in the body angle in the waggle phase relative to the vertical (Von Frisch, 1965). The quality of the resource is reflected in the absolute number of waggle run repetitions and inversely proportional to the return run duration: profitable resources are advertised with longer dancer exhibiting a higher waggle production rate (Seeley et al., 2000). Interested bees (dance followers) track the movements, decode relevant information and search for the resource in the field (Seeley, 1995; Biesmeijer and Seeley, 2005; Riley et al., 2005; Menzel et al., 2011; Al Toufailia et al., 2013a). Successful finders may themselves return to the hive and dance, resulting in a cascade of recruitment. The positive feedback nature of the waggle dance can be regulated by a negative feedback mechanism, the stop signal. Foragers, nest scouts or follower bees knock their head against the dancer's body in conjunction with a short burst of thorax vibrations. Waggle dancers are more likely to stop dancing after receiving the stop signal, as has been observed in the context of swarming (Seeley et al., 2012) and foraging (Nieh, 1993, 2010; Kirchner, 1994; Pastor and Seeley, 2005). The waggle dance/stop signal system therefore is a wonderful example of how multi-individual interactions, such as between dancers and dance followers, may result in a collective behavior, such as the adaptive, colony-level exploitation of dynamic resource availability (Seeley et al., 1991; Seeley, 2010).

However, even this well-investigated communication system offers ample room for further research. If, for example, two individuals meet as dancer and follower, it is still unknown which factors determine this event. How does one bee *become* a dance follower? Surely, some general requirements, like the respective motivational state, must be met for the follower. But that specific animal might not follow other dances prior to the focal one. Does random dance-attending (Bozic and Valentincic, 1991) increase her likelihood to follow *any* dance? Or can we identify preferences for certain dance locations on the comb, dance properties or even dancer identities? How do dancer and follower *find* each other? Do dancers seek followers, or vice versa? Does the follower's history of in-hive interactions determine future decisions to follow specific dances, and if so, how far back in time can specific experiences influence this decision?

In decades since the waggle dance was first discovered (Von Frisch, 1965), most analysis on the waggle dance has moved from a real-time collection of dance data (Visscher, 1982; Waddington et al., 1994; Steffan-Dewenter and Kuhn, 2003) to one that occurs after the fact from video, using a manual (e.g., Beekman and Ratnieks, 2000), semi-automatic (e.g., De Marco et al., 2008) or automatic technique (e.g., Landgraf et al., 2011) for the extraction of focal properties. This allows the analysis of many individuals simultaneously by replaying the video as often as necessary and improves the spatial and temporal data resolution. However, like most video analysis, it is limited by either technical parameters (disk space, temporal, and spatial recording resolution) or available personnel for analyzing the video to extract the data: oftentimes the analysis takes a multiple of the video's real-time duration.

The dancer and the message she is communicating has been thoroughly investigated (Von Frisch, 1965; Seeley, 1995, 2010). However, the dance is not self-contained. It is likely embedded in a network of, potentially still unknown, interactions. Previous experience plays an important role in attracting a follower to certain dances (Grüter et al., 2008; Grüter and Ratnieks, 2011; Al Toufailia et al., 2013b) or, after following the dance, in her propensity to attempt finding the location of the advertised site. This experience might include in-hive interactions as well. Since these memories can build up over many days, we need to observe the individuals over a broad timespan of up to a few weeks. Rather than starting the recording when a waggle dance occurs, we need to track any given follower *back in time*. Optimally, we would like to record her entire life.

However, this is only possible with appropriate automation for a hierarchy of tasks such as image acquisition and storage, animal identification and tracking, and the recognition of focal behaviors. Overall, this constitutes a considerable technical challenge. Especially the automatic recognition of interaction types seems infeasible, since some behaviors involve subtle body movements, which are hard to detect for machine vision systems. However, some interaction types, such as the waggle dance, the dance-following behavior and the exchange of food exhibit properties that seem sufficiently discriminable so that their characteristics can be formulated in a respective detection algorithm. Such automation would provide datasets of unprecedented magnitude in the duration of data collection, the number of traced individuals, and the bandwidth of detectable behaviors. This would allow for profound and comprehensive analyses of the interplay of individual and colony behavior.

Computer programs are increasingly used to help annotating or measuring parameters of animal behavior in video data (Noldus et al., 2001; Pérez-Escudero et al., 2014). A few automatic procedures have been proposed to track unmarked bees (Landgraf and Rojas, 2007; Kimura et al., 2011, 2014), but none are applicable for long-term tracking because of the high degree of ambiguity in the appearance of unmarked bees, frequent occlusions and the property of foragers to leave the hive. To our knowledge, tracking and identification software for uniquely marked bees has not been proposed yet. Only one marker-based system was developed in Lausanne (Mersch et al., 2013) for the use with a few hundred ants which were kept in an open arena. The ID tags used in these experiments were rectangular and planar. It is unknown whether this system can be used with bees. In the liveliness of a hive, tags supposedly have to tightly adapt to the round thorax to ensure their sustained hold over weeks.

The automatic detection of honeybee dances has been proposed earlier (Kimura et al., 2011). However, the analysis is reportedly 360 times slower than real-time and cannot reveal the identity of the dancer. To our knowledge, no system is available for the continuous long-term tracking of uniquely identifiable bees and the automatic recognition of the waggle dance, the dance-following behavior and trophallaxis.

In this contribution, we propose such a system, in the following called the *BeesBook* system. It comprises the automatic recording and storage of high-resolution images, an on-line waggle dance detection software, computer vision software for recognizing and identifying uniquely marked bees and post-processing software for various tasks such as the recognition of follower bees and trophallaxis. The system is conceived as a budget-priced framework for the incremental development of software and hardware components. This way, the BeesBook system can be used to detect other focal behaviors in dance-unrelated research. The paper is organized in two parts: A thorough technical description of the system and the experimental validation, including the quantification of performance measures for the system's components. We will conclude with a discussion of the system's current and future capabilities, and provide examples of further applications in and beyond the waggle dance communication.

Beesbook: Tracking All Bees in the Hive

Hive and Recording Setup

A modified one-frame honeybee observation hive with a custom glass replacement mechanism is used. Bees frequently smear small portions of honey, wax, and propolis on the glass, which impairs the image quality. The custom hive allows replacing the glass once it is necessary without having to open it. The hive stands in an aluminum scaffold that holds infrared LED cluster lamps and six cameras in total (shown in **Figure 1**). The entire skeleton is enveloped with IR reflector foil that has small embossments for light dispersion. The foil reflects 80% of infrared light and helps creating a homogeneous ambient lighting which reduces reflections on the glass pane or the tags.

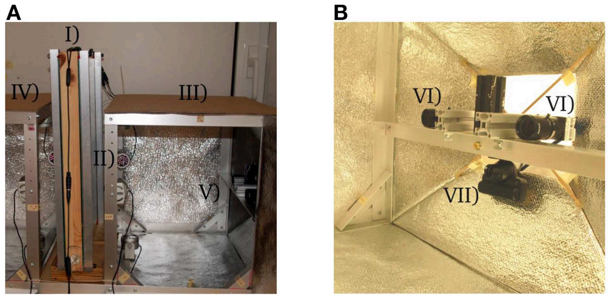

FIGURE 1 | (A) Experimental setup: (I) observation hive, (II) infra-red lamps, (III) right side of observation cage, (IV) left side of observation cage, (V) right side camera array. **(B)** Detailed view of a camera array: (VI) high resolution cameras, (VII) PS3Eye webcam.

Individual Block-code Tags ("Circulatrix")

To optimally exploit the space on a bee's thorax and to create a smooth surface that endures heavy duty activities, we have designed a circular, curved tag (**Figure 2**). The tag adapts to the thorax and displays a ring divided in 12 segments, each of which holds one bit of information. The center of the tag is divided into two semicircular segments, which are used to determine the tag's orientation and to align the decoder properly. A fully functioning, queen-right observation hive can be populated by approximately 2000 worker bees. Twelve bits of information are sufficient to encode the identity of a maximum of 4096 animals. In case fewer animals are used, a coding scheme that allows for error detection or correction can be employed. If for example a single bit is spare, it could be used as a parity bit. If three or more bits are spare, Huffman coding (Huffman, 1952) can be employed. The tags are printed on backlit polyester film by a commercial print shop and manually punched out. This procedure bends the tags for optimal fit to the bees' thorax.

Bee Marking Procedure

Bees are marked prior to the start of the video recording with the help of coworkers over a period of several hours. We use two hives: one standard observation hive containing the unmarked colony and one modified observation hive to which the individuals are transferred once they have been marked. We extract approximately 50 bees from the original hive at a time into a tubular container with a vacuum cleaner and distribute single bees to marking personnel. First, hair is removed from the thorax, then shellac is dispersed onto it, and finally the tag is attached with the white semi-circle rotated toward the anterior. Tagged bees are then put in a small container. Once all bees of that batch have been tagged, the bees are poured to the hive entrance hole (which now connects to the new hive). This procedure is repeated with all remaining, untagged bees from the original hive. The queen is handled differently. After tagging, she is introduced to the hive through a separate entrance. The tags have been tested previously. Almost all bees survive the tagging procedure and behave normally with the tags. Only a small fraction (<7%) of the tags wears off before the animals reach their natural life expectancy (6–7 weeks). By the time of writing this article, after more than 8 months, the queen's tag was still properly attached.

Cameras and Camera Modifications

Four high-resolution cameras (PointGrey Flea3) are employed to observe the surface of the comb, two per side. They feature a 1/2.5″ CMOS color sensor with a resolution of 12 megapixels (4000 × 3000 pixels) and are connected to the central recording computer via USB3. We use inexpensive 12 mm lenses (RICOH FL-CC1214A-2M). Two additional cameras (PS3Eye webcams) are connected to a second personal computer. Each of these cameras observes the full comb side at 320 × 240 pixels resolution. The PS3Eye cameras are low cost (10 $) and deliver

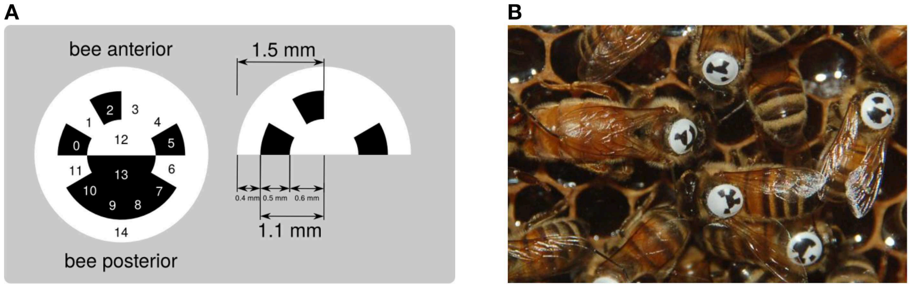

FIGURE 2 | (A) The circular matrix design exhibits 15 regions used to represent a unique binary code (cells 0–11), to encode the tag's orientation (cells 12 and 13) and produce a clear contrast with the bee thorax (ring 14). **(B)** Tagged bees inside the hive.

uncompressed images at 120 fps using a modified third party driver ("CL Eye"). Both camera types are shipped with an infrared block filter glass. We replaced the one of the Flea3 with a cold light mirror with the same refraction index (bk Interferenzoptik bk-HT-45-B). This modification renders the Flea3 an inexpensive alternative to similar IR-sensitive cameras. To optimize the performance of the PS3Eye, not only the IR block filter was removed, but also the original lens was replaced with an 8 mm IR corrected Megapixel lens (Lensagon BM8018), in order to fit the new lens to the camera a customized 3D printed lens mount was produced.

Software

The implemented functionalities of the BeesBook system are divided into three software suites that reflect the experimental chronology: (I) data acquisition with online dance detection, (II) offline image processing on a supercomputer, and (III) data post processing.

Data Acquisition and Data Hierarchy

One personal computer (PC_1) is used for image acquisition and transfer. Another computer (PC_2) is running the online dance detection algorithm. The acquisition computer queries 3.5 frames per second from each high-res camera and stores each image using JPEG compression (95% quality). A second program on PC_1 bundles images to packages of 512 MB size (256 images per archive) and transfers them to the Zuse Institute Berlin (ZIB), where the HLRN (North German Supercomputing Alliance) provides sufficient storage space. A subset of the data, currently 6 stripes of 10 min duration (distributed over the day), is stored on a local storage device (QNAP NAS). PC_2 analyzes the images of the PS3Eye webcams in real-time and stores frame coordinates and 20×20 pixel image regions for each detected waggle run. These data are mirrored onto the NAS completely. The detection method is described in Section Automatic Waggle Dance Detection and Decoding. Possible errors of any of the above programs are exported to a log file and signaled to the administrator via email. In case a program crashes or freezes (which renders them unable to report errors themselves), so-called watchdog programs are used for the automatic recognition of critical events and the termination of unresponsive processes. These events are rare but might lead to substantial data loss.

We organize all data in a hierarchy of data levels. The raw image recordings represent the lowest, most fundamental level. The computer vision software searches and decodes circulatrix tags in these image recordings (see Section Image Analysis) and creates the next level of data, the bee detections. This data, in turn, serves as input for the tracking software that identifies corresponding detections in time (see Section Tracking and Temporal ID Filter). The trajectory level is then analyzed primarily by behavior recognition algorithms which create the upmost data level representing the focal behaviors. Except the raw image level, all other data levels are efficiently organized in a spatial database (see Section Database Design).

Image Analysis

We have developed computer vision algorithms to locate and to decode the circulatrix tags in high-res images. The image processing software, from here on called "pipeline," is organized in five layers, each of which processes the results of the previous one.

(1) **Preprocessor:** The first layer processes the original camera frame. Throughout the experiment, lighting conditions were optimized. To normalize the brightness in the darker recordings shot in the beginning of the experiment, histogram equalization is applied. Some areas on the comb exhibit empty cells whose sharp edges would impair the performance of later stages. We have designed a spatial frequency filter to attenuate comb cell edges. Full honey cells are very bright in the image and also lead to false positives in the next stage. A special image heuristic recognizes patches of honey cells which are then ignored downstream.

(2) **Tag localization:** This layer detects image regions that contain strong edges and therefore likely exhibit circulatrix tags. Those are identified by detecting a multitude of strong edges in close proximity. This definition applies to other objects in the image as well but reduces the amount of pixels that enter downstream stages drastically. Initially, the first derivative of the image is computed using a Sobel filter. The result is binarized (only pixels on strong edges are retained), eroded and dilated (Serra, 1986) to remove noise and to join adjacent patches. Large binary patches are reported as regions of interest to the next layer.

(3) **Ellipse fitting:** This layer detects elliptic contours in the regions of interest. We use a probabilistic Hough transform (Xie and Ji, 2002) to find likely ellipse configurations defined by a high amount of edge pixels agreeing with an ellipse equation for a range of plausible parameter values (we exclude heavily rotated tags since those are likely to be decoded incorrectly).

(4) **Grid fitting:** For each ellipse that has been detected, this layer fits a three-dimensional model ("Grid") of the circulatrix tag to the underlying image. When rotated in space, the contour of the circular tag becomes an ellipse in the camera image. There are two possible 3D rotations of a circular contour that project to a given ellipse in the image. We identify the two sets of rotation parameters from the ellipse parameters and apply a gradient ascent from the two starting configurations. The quality of the fit is expressed by a scoring function that evaluates a) the homogeneity of the pixel brightness in each cell (Fisher, 1936) and b) the match of the outer Grid contour to the image edges. The three best Grid configurations are reported to the decoder layer.

(5) **Decoding:** Each ring segment of the grid represents either a "0" (black) or a "1" (white). The sequence of zeros and ones constitutes the unique identifier of the bee. Local contrast enhancement is applied to account for light intensity gradients on the circulatrix tag. The decoder computes a statistic of the brightness of all underlying pixels for each ring segment to classify the cells to either of the two classes and reports the number as the final result.

Each layer of the image processing pipeline extracts more information from an initial detection (see **Figure 3**). For every pipeline layer a confidence value is calculated. Only if the confidence value of the current layer exceeds a certain reliability threshold, its result is reported to the following stage. In layer 3, for example, this confidence value correspond to the number of edge pixels that accord with an ellipse equation. The ellipses detected in layer 3 are assumed to identify a tag and are therefore reported as the most basic part of any detection. In layer 4, if more than one grid can be matched to the image with a sufficient confidence value, the respective grid configuration (center coordinate, scale and three rotation angles) is added to a list and the best three configurations are reported to the next layer. Similarly, the last layer reports up to three IDs for every grid configuration, yielding up to 9 different output configurations.

The pipeline has various parameters such as thresholds for the edge detection or the number of iterations of the morphological operations (48 parameters in total). Manually determining the optimal combination of parameters can be very time consuming and might result in a suboptimal performance. We use a global optimization library (Martinez-Cantin, 2014) to automatically select the best set of parameters.

Highly parallelized image analysis on supercomputer

A prototypical data acquisition over 60 days would produce a total of four cameras 3.5/s·60 s/min·60 min/h·24 h/d·60 d = 72.576.000 images. The image processing on the supercomputer reduces the raw image data (~170 Terabytes), corresponding to the lowest data level, to a few hundred Gigabytes of second-level data. If the analysis of a single image would take 1 s, the complete analysis would take almost 3 years. To speed up this process, we use computing and storage resources granted by the North German Supercomputing Alliance (HLRN). The image data are stored on the supercomputer's file system, which circumvents additional data transfers. The HLRN houses a Cray XC30 supercomputer, which features 1872 compute nodes with 24 CPU cores each (this yields a total of 44928 processors). The system has 117 TiB of RAM and 4.2 Petabyte of hard disk space, organized as RAID 6. The image analysis is partitioned into jobs that each run on a single image at a time. The degree of parallelism can vary from a few hundred to a few thousand jobs as determined by the Cray's scheduler (a program that automatically selects jobs from a list of ready jobs). Some of the supercomputer's components are still in development and might prevent an arbitrary job from finishing its analysis. Since it is impossible to check manually if 72 million result files have been written to disk, we have implemented a recovery system that automatically detects and recovers from failures in the job submission and execution phase. The results of the decoding process are stored in a.csv file for each image.

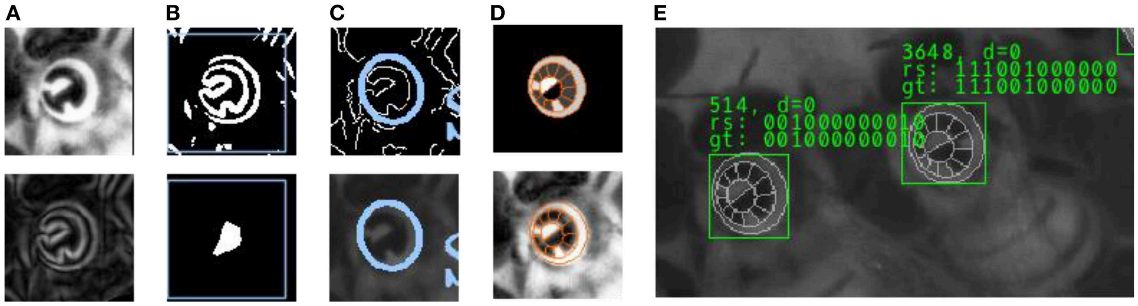

FIGURE 3 | Intermediate processing stages for tag detection and decoding. (A) Histogram equalization and Sobel edge detection. **(B)** Edge binarization and morphological operations in the Localizer layer. Only regions of interest (marked with a blue rectangle) are processed in the next layer. **(C)** Ellipse fit using probabilistic Hough transform. **(D)** 3D Grid model and fit to underlying image. **(E)** Result: The sequence of 0's and 1's is determined in the Decoder layer, based on the fit of the tag model. For a subset of the image data we have created a reference "ground truth" that is used to validate the output of the pipeline.

Post-processing

The image analysis is a data reduction step which creates the basic data level for all further analyses. The tracking algorithm (Section Tracking and Temporal ID Filter) creates the trajectory data level which links detections over time. Both data levels are used for detecting focal behaviors (dance, dance-following and trophallaxis detection, see Section Identification of Dancers, Followers, and Trophallaxis).

Database design

Due to performance reasons, all post-processing steps are designed to query data from a specialized database. The detection datasets produced by the pipeline are uploaded to a PostgreSQL database which holds all available information as described in Post-processing. The detections are organized in the form of a table with each row representing a detection. We have recorded 65 million images, each of them containing up to several hundreds of tags. Therefore, several billions of detections have to be stored. We have implemented interface functions into the database to accelerate interaction with the data. If, for example, we would like to know all neighboring bees of a focal bee, this query is optimized on the database level. The data has to be processed before uploaded to the database. To this time, the data processing and upload process takes approximately 90% of the recording period's duration but runs in parallel to the image processing. The analyses described in the following query data from the database, process it on local PCs and enrich particular entries in the database with additional information, such as corrected IDs, associations to trajectories or behavior labels.

Tracking and temporal ID filter

Keeping track of individuals through consecutive frames is a crucial procedure because it creates motion paths that may be required for behavior analyses. Under optimal circumstances, tracking an individual and generating its path is as simple as connecting consecutive detections of the same ID. However, the decoder layer might extract erroneous IDs for a variety of reasons (see discussion). In this case, merely connecting successive appearances of the same ID would yield erroneous tracks. To address this problem we have developed tracking software which links consecutive detections through time by selecting the best match among a number of candidate detections. The tracking process pursues two goals: the generation of reliable motion paths of single individuals and the correction of misread IDs.

Our solution to this problem is a probabilistic approach. For an arbitrary track T, containing consecutive detections up to time t, we maintain a probability distribution P_t reflecting all previous ID measurements. All detections in frame $t + 1$ within a certain range are evaluated following a criterion that comprises:

- the Euclidian distance of the track's last detection to a candidate detection
- a distance measure of P_t and the putative next detection's ID
- a convergence criterion for P_t
- an image processing error estimate representing the likelihood of misread bits in the ID

The information contained in the new candidate detection is integrated into the probability distribution P_t via a Markov process: $P_{t+1} = P_t * p$, where p is a probability distribution estimated from the detection at time $t + 1$. The probability of misreading a bit is influenced by neighboring bits. For example, due to image blur, it might be more likely to read a single white bit as a black one when it is enclosed by two black bits. We have estimated the probability of all possible errors for all combinations of three consecutive bits (using manually tracked ground truth). After integrating the a-priori information p, P_t represents the current likelihood for each bit to have a certain value. A convergence value can be computed over P_t to express our confidence in the current ID estimate. In timestep $t + 1$, we assign each detection to the most likely path T_j using a greedy selection scheme (the decision to assign a detection to a path is immutable even if future information renders it suboptimal). If no match for a single detection can be found with sufficient confidence, a new path with a new probability distribution is initialized.

The tracking must handle two problematic scenarios. (1) Newly appearing detections and (2) detections that disappear.

In the former case, no history of detections can be used to determine the most probable ID. The probability distribution has not yet converged (see **Figure 4** Top). If a track cannot be elongated enough, it stays anonymous.

The greedy assignment of all detections to a path can only be guaranteed to be correct when no detections are missing. In this case the tracker might erroneously assign a detection in the vicinity of the actual tag. This is problematic for quickly moving bees since the motion blur increases the likelihood of a missing detection (see discussion). If we were not able to find a likely match, we add placeholder detections to the path. After exceeding the certain number of consecutive placeholder detections the path sequence is finalized (no further detections can be added).

Identification of dancers, followers, and trophallaxis

Due to motion blur and the low sampling frequency, the IDs of waggle dancing bees are hard to determine from the high-res image data. Therefore, we use an automatic waggle dance detection algorithm that runs in parallel with the image acquisition, detecting the location of the dancer in real-time (see Section Automatic Waggle Dance Detection and Decoding for details). However, due to low sensor resolution, it is not possible to extract the bee's ID in those recordings. Another post-processing step is performed to find the ID of the respective waggle dancers in the previously described high-resolution dataset. Apart from waggling, a dancer exhibits other features that, in combination with the dance detection data, we can use to identify her with high accuracy. First, dancers alternatingly perform waggle and return runs. Only the former is likely to be missing in the dataset. This "on-off" pattern is reflected in the trajectories. We look for those patterns and quantify their periodicity and regularity (all return and waggle runs should have similar length, respectively). Second, the start and end positions of the waggle run often exhibit readable tags. The dance detection results in a location on the comb, the dance angle and a duration which - together with an average forward motion

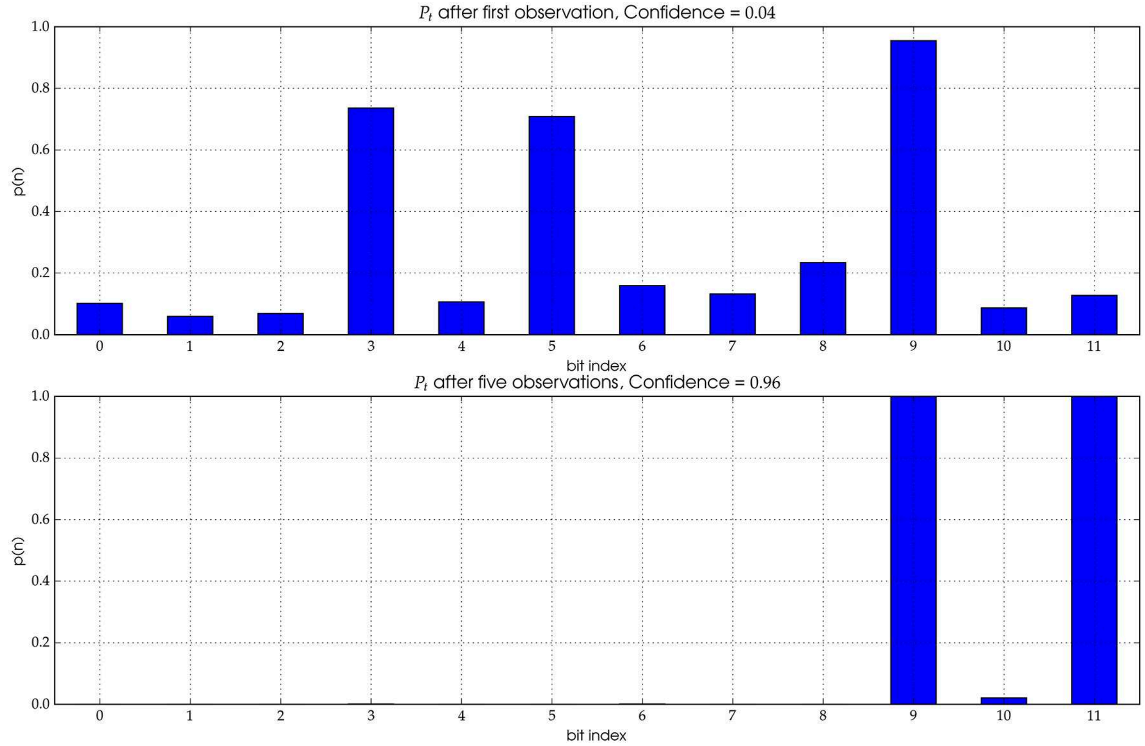

FIGURE 4 | The distribution P_t represents the likelihood for each individual bit to be of value "1." Top: A single observation yields a distribution with significant uncertainty (see text for details). The correct ID for the underlying image is (000000000101). However, the most likely ID according to the initial distribution is (000101000100), i.e., the first observation exhibits three wrong bits. **Bottom:** After five observations the distribution has mostly converged and the true ID can be extracted with high confidence.

in the waggle phase - define an axis that dancers align to. If detections close to start and end point of a waggle run agree in orientation and ID they are collected to the candidate set. A third feature we test for is the turn of the animal of almost 360° in the return runs. For a single waggle run, there might be a few detections that exhibit those features sufficiently. Over many waggle runs the ID of the dancer can be determined with high accuracy. Followers are easier to find. The criterion animals have to satisfy is (1) proximity to the dancer and (2) the body oriented toward the dance position. Animals that engage in trophallaxis can be recognized as well. Therefore, four consecutive, non-moving detections in head-to-head configuration are sought and reported.

Automatic Waggle Dance Detection and Decoding

The waggle motion creates motion blur in the high-resolution recordings but can be detected in high-speed video. The dancer swings her body laterally at a frequency of around 13 Hz. A pixel in the image corresponds to a small area on the comb surface. If this point measurement over time intersects with a waggle dancing bee we obtain samples that reflect her surface texture and motion dynamics combined. Since bees contrast with the background, we observe brightness changes with spectral components of either the waggle frequency or harmonics. At the core, our automatic waggle dance detector evaluates how well, for a given pixel coordinate, the temporal variation of its brightness matches this "waggle frequency." The camera observes the full comb with an image resolution of 320 × 240 pixels. This corresponds to a resolution of ~1 mm/pixel, or approximately 60 pixels/bee (**Figure 5**). For each of the $320 \times 240 = 76800$ pixel locations the most recent 32 values of their temporal evolution are stored in a ring buffer. When a new frame arrives, the oldest pixel value is overwritten. We then calculate a statistical measure of how well the pixel brightness evolution matches the waggle frequency by correlating the input signal with a number of cosine and sine signals with different target frequencies. Neighboring locations exhibiting that property are then clustered in a second step. If the detection is sustained over time, the image location and the respective sub-images (an image sequence of 20 × 20 pixels size) are stored to disk. It is possible to extract waggle duration and waggle orientation as well. The former is identified by the duration of consecutive detections; the orientation is defined by the first principal component (Hotelling, 1933) of the image locations of all consecutive detections. The software can be used either in conjunction with the high-resolution tracking system or as a stand-alone tool to anonymously detect and decode dances. Image coordinates as reported by the software can automatically be rectified with the help of a user defined area whose dimensions are known. We describe the evaluation

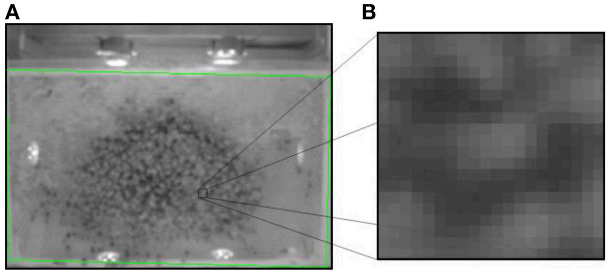

FIGURE 5 | A screenshot of the waggle detection camera stream. **(A)** The green rectangle demarcates the comb borders. Note the low image resolution. Waggle dance detections are reported with their image and comb frame coordinates and a **(B)** sub-image of 20 × 20 pixels size (shown right).

procedure for this system in Section Dataset 2: Dance Detection and Decoding and report the respective results in Section Dance Detection and Decoding.

Experimental Validation and Results

Datasets

Two separate honeybee colonies were used to experimentally validate the function of the described system and system components. Therefore, two datasets were recorded.

Dataset 1: Tag Detection and Decoding

We have continuously recorded all animals of a small colony (<2000 marked individuals) from July 24th until September 25th 2014 (63 full days). Most bees were marked 1 day prior to the start of the recording. During the first week, young bees were tagged and introduced to the experimental hive on the day they emerged from a separate, incubated brood comb kept under standard conditions at 34.5°C (Crailsheim et al., 2013). High-resolution images were transferred to the remote storage location. One of the four cameras failed 1 day prior to the experiments. Unfortunately, it took the manufacturer 3 weeks to replace the camera. Thus, one quarter of the comb could not be observed and around six million images are missing from the expected number of 72 million. In the beginning of the experiment we optimized parameters such as illumination, camera position and camera viewing angles. No data was recorded in the maintenance periods (∼4 million images). This yielded 65 million recorded images in total. Approximately 6% of the total data was mirrored locally. Over the entire period the dance detection software observed both sides of the comb and saved detections to disk. These data were mirrored as well. Results of an analysis of dataset 1 are reported in Section Tag Detection and Decoding. The validation of this dataset spans different data levels. The image analysis recognizes and decodes the circulatrix tags and stores separate detections per timestep. To validate this software component we manually fitted a three-dimensional model of a tag in a number of image recordings we randomly picked from dataset 1. This "ground truth" serves as a reference (for location, orientation and identity). Each software layer (see Section Image Analysis) is validated separately by calculating two common performance measures, recall and precision. Those reflect the proportion of the reference data that were correctly identified, and the proportion of the reported detections that are correct, respectively. The tracking software, i.e., the component that connects corresponding detections through time, is validated on a different ground truth reference. Fifty animals were traced manually with custom software by selecting the correct detection (as produced by the pipeline) with the mouse pointer. The validation analysis investigates the correctness of the path and the ID obtained from consecutive measurements over time.

Dataset 2: Dance Detection and Decoding

A second observation hive (two frames, located at 52.457075, 13.296055) was used to detect and decode dances in an unmarked colony. The recording period spanned 57 days (July 04th to September 1st 2014). We employed two cameras to observe the lower comb from both sides. Bees were trained over 2 days to a feeder that was moved in an arc around the hive. The feeder was first moved north (115 m) and then moved east along a street perpendicular to the initial flight route until a distance of 180 m was reached. The feeder was then moved along a small road decreasing distance to the hive down to 80 m (E-SE direction). From there the feeder was moved to its final destination (52.455563, 13.298462) 235 m, 135° east from north, as seen from the hive.

We created a reference dataset to validate the dance detection and decoding software by randomly selecting waggle detections from the results set after the recording period. The detections were visualized in a graphical user interface and a human observer classified the sequence of images to either correctly contain a dance or not. By dragging a line over the image the bee's orientation was manually approximated. Since we selected test data *post-hoc* from the results only waggle detections were reviewed. Thus, it was not possible to gauge how many dances were missed (false negative rate) or to manually define the correct dance duration (the software might have detected the waggle too late and stored only a fraction of the complete image sequence). We therefore ran the software on a set of video recordings containing waggle dances to the same feeder recorded in 2008. We reduced the image resolution to match the recording resolution of the PS3Eye. The frame rate was 100 Hz in both sources. Tracking data was available for this dataset (Landgraf et al., 2011) which was used to measure false negative rate and to evaluate dance duration and detection position accuracy.

The automatically extracted dance parameters in the training period were translated to field locations. To this end, dance duration and orientation were averaged over consecutive detections. Thus, the average waggle run was projected to the field with respect to the azimuth at the time of the first waggle run. Dances with less than four waggle detections or waggle durations smaller than 200 ms were discarded (see discussion). The obtained field locations were mapped using Matlab and cartographical material provided by OpenStreetMap.

Results

Tag Detection and Decoding

Runtime and performance

We have invested a significant amount of time in the optimization of the tag decoding software with respect to the runtime. Still, on a single processor, the image analysis takes approximately 500 times longer than real-time (86 years for the dataset at hand). The image analysis run on the supercomputer takes only 10% of the original recording time (average numbers of processors used: 1000).

We have evaluated the results of the tag detection and decoding software with respect to manually defined ground truth. All layers yield high rates in recall (how much of the ground truth could correctly be identified) and precision (how much of the software output is actually covered by ground truth data).

	Recall (%)	**Precision (%)**
Localizer	90.60	84.13
Ellipse fitter	88.03	97.17
Grid fitter	88.03	89.32
Decoder		65.98/94.07 (0/< 3 hamming distance)

Up to 88% of the tags can be recognized. Only 65% of the detections can be decoded correctly for a given image recording. However, 94% of the decoded IDs have less than three misidentified bits. It is important to note that those detections are still valuable as the true ID can be retrieved via probabilistic filtering (see Section Tracking and Temporal ID Filter). As an additional way to measure the decoder's accuracy, we checked the number of misread bits on the decoded IDs. This metric known as Hamming distance (Hamming, 1950) has an average value of 0.74.

Tracking and dancer identification

We manually tracked 50 bees over a time period of 240 frames by mouse-clicking the detection that corresponds to the focal bee. The performance of the tracking algorithm was then evaluated by comparing its output to the ground truth paths.

There are two functionalities of the tracking algorithm that were validated. The core component of the tracking is the probabilistic filter we employ to integrate consecutive measurements to robustly obtain the true ID of the animal (see Section Tracking and Temporal ID Filter). The filter has to be robust against two types of errors. First, incorrect ID decodings coming from the pipeline and second, incorrect detection assignments in the tracking process. The former error has been quantified and is used in the filter (see **Figure 4**). The latter introduces incorrect positions and IDs to the path. Since this might not be completely avoidable, this error should not affect the outcome of the ID filter process. To investigate how robust our filter algorithm is, we introduced incorrect IDs to paths of a manually tracked animal. The paths were unfiltered, i.e., they exhibited IDs that were pairwise similar but not equal (see Section on decoder accuracy Runtime and Performance). With 10% incorrect IDs along the path, the algorithm was able to recover the correct ID after approximately 50 observations. Even when one third of the IDs are erroneous the correct ID can be obtained in most cases after approximately 100 observations (see **Figure 6** for details).

To assess the quality of the paths generated by the algorithm we compared how many detections along the ground truth path were correctly assigned to the same path. In the tracking algorithm a minimum value for the similarity of new ID and time-filtered ID along the current path has to be set. This threshold might be chosen such that only very similar detections are added. This would produce piecewise trajectories, each with high precision. By relaxing the threshold the resulting trajectories are longer but the probability that incorrect detections have been added is increased. Using a manually chosen threshold, we found that most bees (>90%) can be tracked with high precision (>99% of correctly assigned detections, see **Figure 7**). Note that results may vary significantly in quality depending on the activity of the focal animal (see Discussion).

Dance Detection and Decoding

Detection performance

For validation, 1000 random samples were drawn from 220127 waggle run detections. Seventy-nine percent of the manually reviewed detections were dances (false positive rate is 21%). The same software produced significantly better results on high-speed videos of dances. Almost all dances could be detected (recall 96.4%) with low numbers of false detections (precision: 89.5%). This difference was likely caused by the inferior optics of the webcams.

The positional error is in both planar dimensions almost zero (mean: 0.02 mm with std: 1.7 mm).

Decoder performance

The proposed method overestimates dance duration by an average of 98 ms (std: 139 ms). The angular error of single waggle run detections is in average 1.7° and has a standard deviation of 22°. By averaging over a minimum of four waggle runs the error standard deviation decreases significantly (SD: 12°). Note that short dances due to the nature of the method are reported with higher angular error and influence the overall error. Discarding short waggle runs (<200 ms), the angular error's standard deviation is 5°.

Dance maps

To exemplify the use cases of the waggle dance detection we have mapped all dances of foragers in a second observation hive. **Figure 8** shows the endpoints of a vector obtained from averaging the duration and angle of a minimum of four consecutive waggle runs and projecting them to the field using the sun's Azimuth. On the test day, we detected 471 dances with an average of 6.75 waggle runs per dance. The average dance angle matches the expected angle derived from the feeder location almost exactly (134 and 136°, respectively). Still, dances to other directions were detected. There is notable spread around the hive, which in close range is more likely to arise from incorrect detections, since the method of extracting the dance angle is error prone in short waggle runs. It is not unlikely,

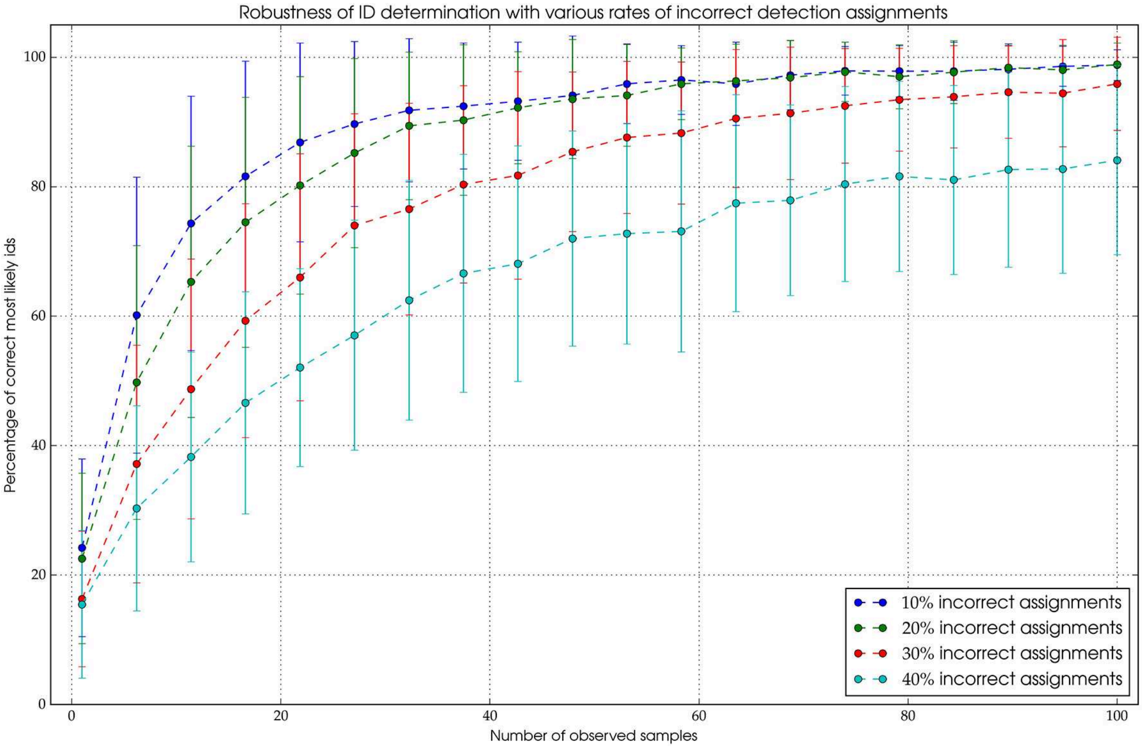

FIGURE 6 | The mechanism is highly robust against erroneous assignments. Even when 30% of the assigned detections are originating from different bees, it's possible to extract the correct ID with a high probability after a sufficient amount of observations.

however, that bees have foraged not exclusively on the artificial feeder. The spread around the feeder location is notable and matches the angular standard deviation of previously reported dances to the same location (SD: 28°, see Landgraf et al., 2011).

Discussion

We described an automatic observation system with its respective hardware and software components for the automatic detection, identification and tracking of marked honeybees. The system can automatically detect and decode honeybee communication dances and related behaviors such as dance-following and trophallaxis. The BeesBook system is unique in its spatial and temporal resolution and its capacity to reflect the complex interplay of a few thousand individuals within the hive over large time windows.

We see potential use of our automation in many aspects of waggle dance research. Basic biological investigations have in the past been limited in scope because it was impossible to reliably track enough individual workers for long enough to create a holistic understanding of worker-worker interactions or to build up a forager profile. For example, it would be fascinating to have knowledge of foraging locations that a dancer previously communicated and to consider this information if the dancer then becomes a follower. Given that foragers relate private information (e.g., memory of a resource) to social information (Grüter et al., 2008, 2013) the BeesBook system can help to investigate this relationship. Another useful application of the proposed system would be applied investigations. A dance indicates a positive assessment and represents an integrated signal that the forage or nestsite is valuable (Seeley, 1994, 2010; Seeley and Buhrman, 2001; Couvillon et al., 2014a). Decoding and plotting many dances from an area can indicate locations of high or low interest and may even help land managers evaluate the landscape for bee sustainability and nature conservation (Couvillon et al., 2014b). Additionally, because the honey bees are “sampling” from the environment, their dances could also help with environmental risk assessment, as the products of the forage could concurrently be tested for chemicals. Being able to decode large numbers of dances could help pollination services, as beekeepers would possess very quickly an idea of when the bees are visiting a target crop.

Besides dance communication, the BeesBook system can facilitate various scientific investigations in wider contexts, such as network analysis, self-organization and the emergence of specific colony behavior. Tracking large numbers of individuals over long periods of time might reveal detailed characteristics of the network dynamics of disease spread (Naug, 2008) and collective anti-pathogen defenses (Theis et al., 2015). The distribution of pesticides in the hive or the effect of various environmental stress factors on the colony behavior and the intriguing field of division of labor (Robinson, 1992) could

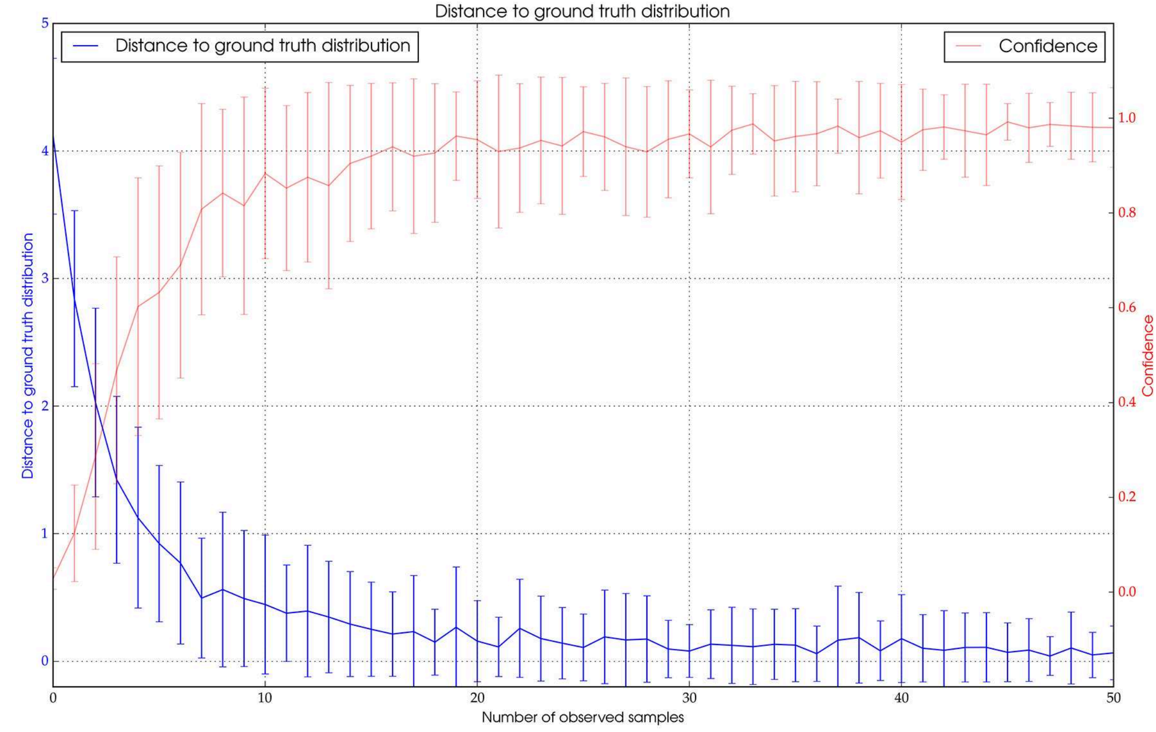

FIGURE 7 | Blue: The distance of P_t to the expected ground truth distribution over the number of observations. **Red:** The confidence value of P_t.

be observed in unprecedented detail. Network studies (Croft et al., 2008) might be applied to honeybees as well as research investigating the effect of individual differences (Réale et al., 2007) on the group behavior.

We believe the BeesBook datasets have great potential to foster a pervasive understanding of societies in general. We support interdisciplinary research and plan to grant public access to our data so that the members of the scientific community can analyze it in the context of their respective areas of interest.

Automation might enable many high impact applications, but also entails significant challenges, costs and peculiarities associated with the acquisition, storage, analysis and interpretation of "big" data. The efforts described in this paper comprise the recording and analysis of only one rather small colony. Although memory and computational costs decline exponentially and the aforementioned requirements will become affordable soon, one still might have to carefully balance reasons for using such a system.

The size of the various datasets, common network bandwidths and/or relatively low local storage capacities render the manual review of recordings and tracks a very time consuming task. Thus, most of the results obtained by either the computer vision or the post-processing software can only be trusted on the statistical level, as determined under average conditions.

While it is impractical to grant access to our raw data (due to data volume), it is much more feasible to share the post-processed data levels. This, however, would require high confidence in the correctness of the data, since there would be no way of validating the data without the image recordings. It's noteworthy that accurately validating the performance of the individual system components itself is a significant challenge. As demonstrated, the performance of the system depends on multiple factors. For example, there are days a colony may be calm, with only a small proportion of quickly moving bees. The system would be able to detect and decode most bees with high accuracy. Under certain circumstances, however, the same colony can exhibit an increased activity level with almost all bees moving very fast. The quality of the decodings will be affected significantly; the dance detection system might produce more false alarms. Other factors such as colony size play a role as well (yielding more or less occlusions). The colony state must therefore be registered and a mapping to an expected system quality level needs to be devised in order to be able to interpret and judge the data correctly.

The data levels generated by the BeesBook system are still incomplete in the proportion of correctly tracked and identified bees, but they constitute the most detailed and extensive dataset available. In order to improve accuracy and reliability, we currently enhance some of its components.

In the forthcoming season we will sustain the proportion of marked bees during the whole season by replacing capped brood combs with empty combs periodically every 3 weeks. The brood will then be incubated and newly emerging bees will be tagged and re-introduced to the hive.

The hardware components will be significantly improved. In the upcoming season we use a bigger room, what makes possible

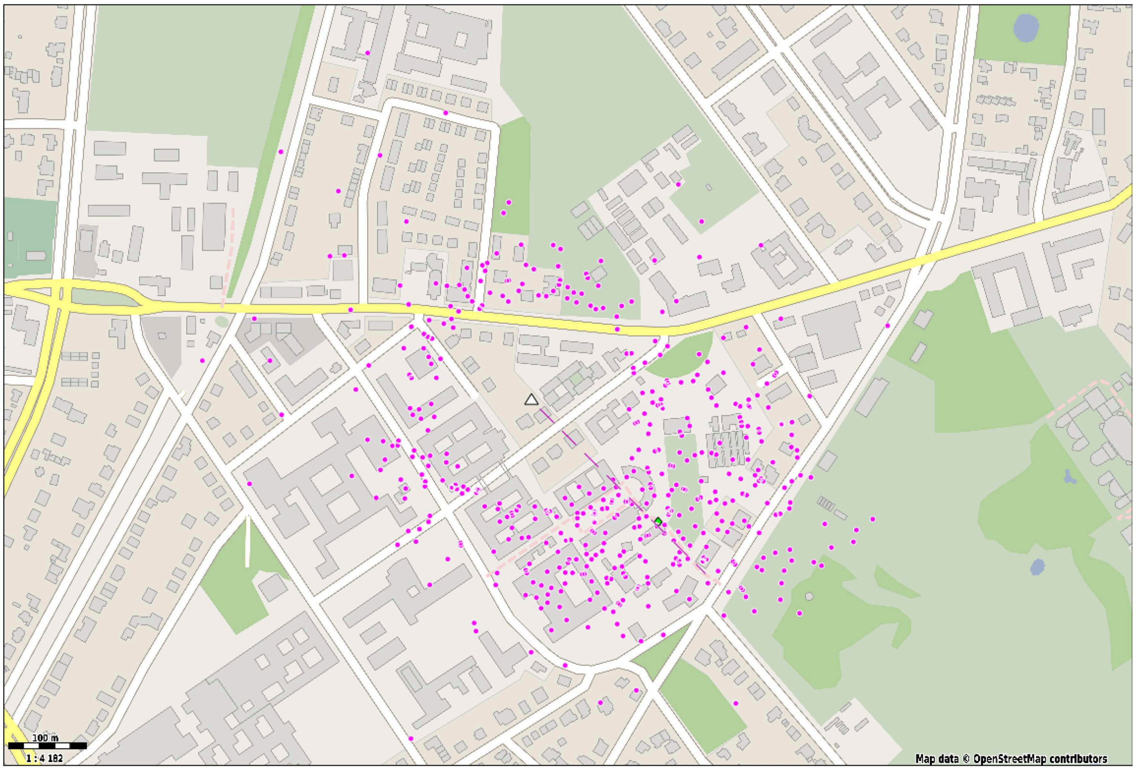

FIGURE 8 | Dance detections (waggle duration and direction) were averaged over at least four waggle runs and translated to a field location with respect to the sun's Azimuth. A linear mapping was used to convert waggle duration to metric distance Each dot represents a waggle dance with at least four waggle runs. The hive is depicted with a white triangle. The dashed line represents the average dance direction.

using better optics (lenses with larger focal length and a lower degree of peripheral blur). We have built a bigger scaffold with the capacity for more light sources. Hence, we will use lower exposure durations to minimize motion blur, which was the prominent cause for missing or erroneous detections.

We have identified two software components whose improvement will have a positive impact on the overall system performance. We currently test a replacement for the localizer layer based on deep convolutional networks (Krizhevsky et al., 2012) that reduces the number of false positives significantly. This enables the tracking the create trajectories with less gaps, which in turn renders the ID filter more successful.

The tracking software currently uses a greedy selection scheme. For every timestep detections are added to the path, irrespective of future information that might render this decision suboptimal. In the future we plan using a non-greedy selection scheme: In each time step up to three detections (possible continuations of the path) will be collected. All three are then traced in future frames and, in the worst case, they too are elongated with three potential candidates each (yielding nine possible tracks). In each time step, a fourth hypothesis will be incorporated, representing the possibility that the tag could not be detected. This creates a detection graph that might contain cycles (a detection in time t has at least two possible paths ending in the same location at time $t + n$, with $n > 1$). These cyclic graphs are finally pruned by deleting less probable paths (with regard to its accumulated Pt). The tracking is computationally expensive. The more layers in time the graph is allowed to have, the more numerous the possibilities and the longer the computation but also the more precise the ID assignment and the tracking will become.

While the BeesBook components already produce valuable data, convenience functions to access, integrate, compare and test the data are still in development. To exemplify the power of the data integration we have tracked a randomly selected dancer and have manually combined the available data as depicted in **Figure 9**. A video that shows raw image recordings zoomed in on the focal animal can be found in the Supplementary Information (Video 1).

In the upcoming months we will finish the image analysis and complete the data analysis with respect to social structures in the dance context by the end of the year. In the summer months we will record a new dataset which will be analyzed over the winter months. We hope, by that time, we will be able to grant public access to the most complete honeybee colony motion and behavior dataset, the *virtual hive*.

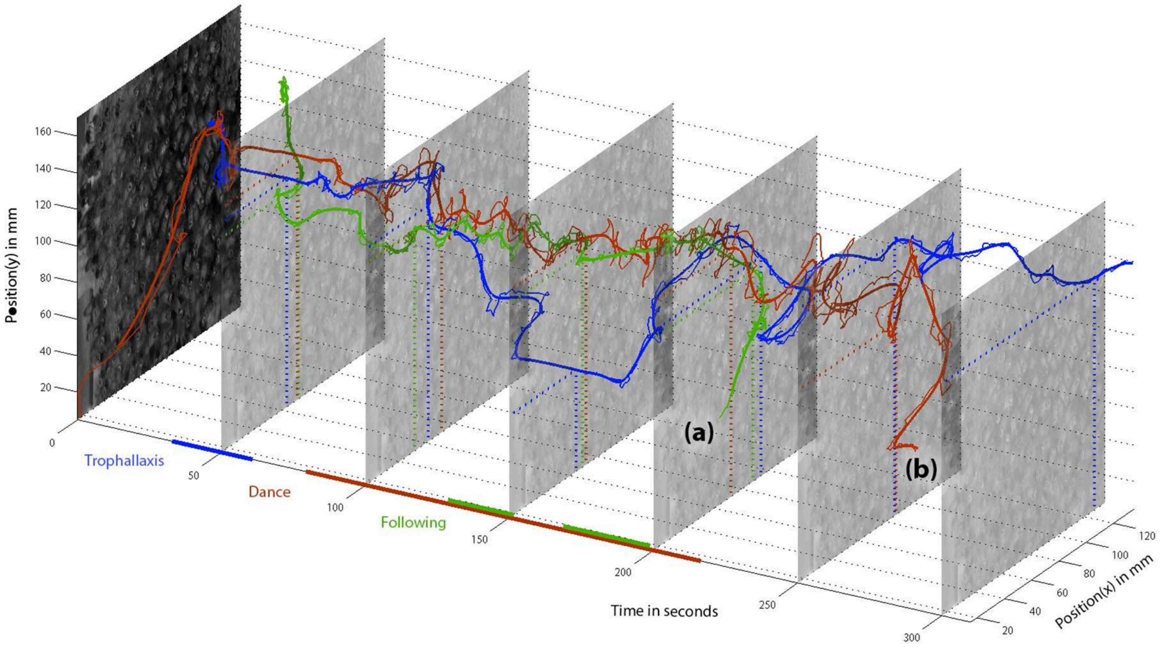

FIGURE 9 | Positions of dancer "3007" (red), follower "2641" (green), and food receiver "3464" (blue) over time. Detected behaviors are depicted as colored lines along the time axis. The dancer was initially detected at the comb periphery, directly moves to her future dance location and engages in trophallaxis, recognizable by the blue and red parallels around $t = 50$ s. The food receiver stays in close contact with the dancer only shortly and leaves the dance floor. She finds another food receiver at $t = 150$ (again, the straight blue line segment reflects her motionlessness). The bee "2641" meets the dancer around the time of the first trophallaxis and stays in her vicinity for about a minute until she starts following. The follower leaves the dance comb (a) before the dancer does (b). Afterwards, both bees were not detected in the hive for more than 5 min. Therefore, we assume both bees left the hive.

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Supplementary Material

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fevo.2015.00103

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