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Do honeybees use the directional information in round dances to find nearby food sources?

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Throughout his writings about how honeybees communicate with dances, Karl von Frisch described two types of recruitment dance: the round dance, which supposedly indicates the presence of a food source somewhere near the hive, and the waggle dance, which indicates the distance and direction of a food source more than 100 m from the hive. The view that round dances and waggle dances are distinct recruitment signals has been revised in light of the finding that distance and direction information are encoded (albeit imprecisely) in round dances. It has remained unclear, however, whether dance followers can use the location information in round dances. In the present study, we looked at recruitment to nearby food sources and found that dance followers can use the directional information in the dances advertising these food sources. Directional bias in recruitment was found for food sources as close as 5 m from the hive. Controls for effects of assembly pheromone and bee presence at the advertised food sources indicate that these factors play a minimal role, relative to dance information, in producing the directional recruitment. Our results provide further support for the view that round dances are best viewed as waggle dances indicating nearby food sources, not as a separate type of dance.

Few forms of animal communication have been as thoroughly studied as the dance language of the honeybee, *Apis mellifera*. This behaviour was first investigated in the 1920s by Karl von Frisch, who went on to discover in the 1940s that bees perform dances to indicate the locations of rich food sources to nestmates (von Frisch 1946, 1948). Throughout his career, he described the dance language in terms of two separate types of dance: the waggle dance and the round dance. According to von Frisch, a waggle dance indicates the distance and direction of a food source further than 100 m from the hive, whereas a round dance indicates only the presence of a food source somewhere near the hive (von Frisch 1967, 1974). To produce the waggle dance, a bee walks in a straight line at a certain angle on the vertical surface of a comb while waggling her body vigorously, then turns to circle back to her starting point, again walks through a straight length, then makes another turn in the opposite direction and so on in regular alternation. The vigorous waggling of the body gives emphasis to the straight part of the waggle dance and it is often called the 'waggle phase' (Tautz et al. 1996). The round dance is similar to the waggle dance, but differs in that waggle phases are extremely short and at first glance appear to be randomly oriented (Fig. 1).

Why did Karl von Frisch view waggle dances and round dances as two separate types of dance? The answer is rooted in his earliest studies of the bees. While performing these studies, he saw that foragers that brought in pollen (usually from flowers far from the hive) produced waggle dances whereas foragers that brought in sugar-water (from feeders near to the hive) produced round dances. Based on these observations, he concluded that the bees have two separate dances for advertising their two separate foods: pollen and nectar (von Frisch 1923). Evidently, his initial belief that waggle and round dances are distinct signals for different foods strongly shaped his later thinking, for even after he discovered that waggle dances and round dances represent food sources that differ in distance from the hive rather than type of forage (von Frisch 1946, 1948), he continued to write about 'the type of dance' (von Frisch 1948, page 10), that is, round dance or waggle dance. He even devoted separate chapters to them in his masterwork (von Frisch 1967). Curiously, von Frisch did describe a gradual transition from round dances to waggle dances when a feeder's distance from the hive is increased from 10 to 100 m (von Frisch 1967, page 61), but he never emphasized the basic similarity in form of round dances and waggle dances.

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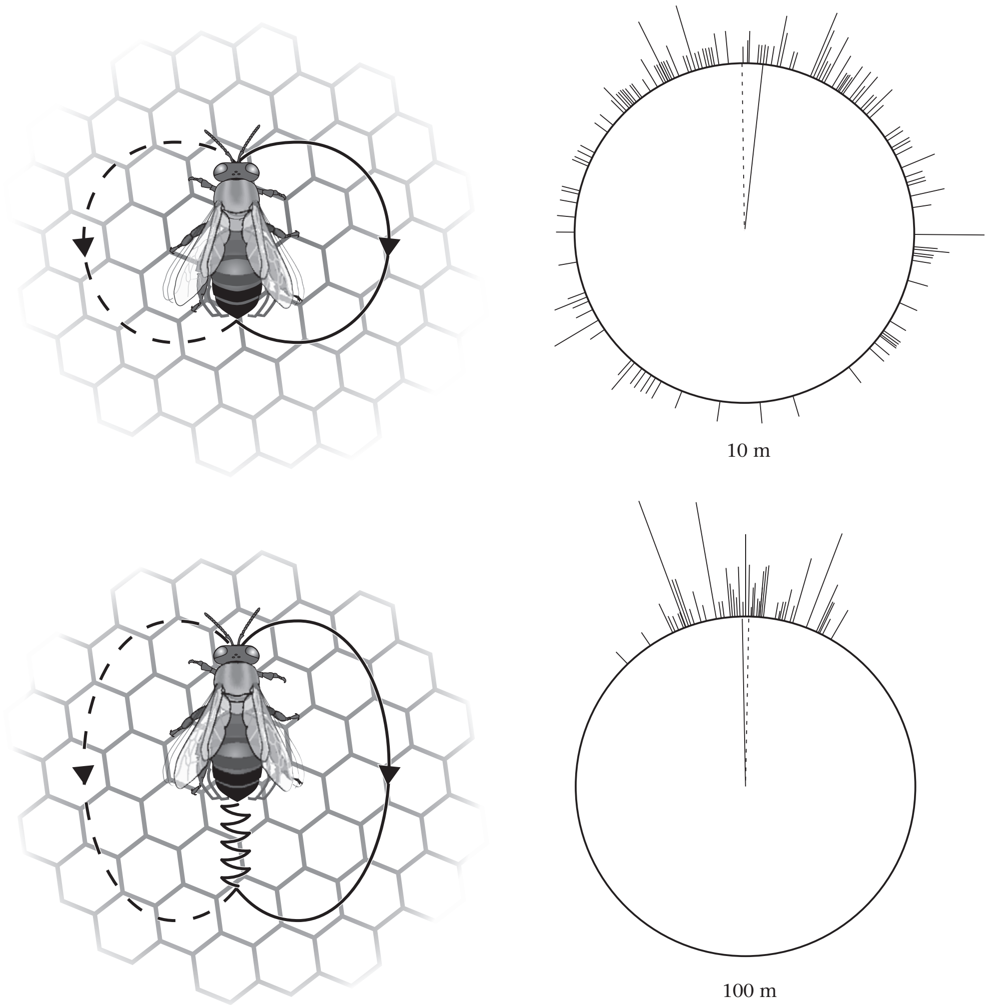

Figure 1. Forms of honeybee dancing that Karl von Frisch described as two separate recruitment dances. Top left: the round dance, wherein the dancing bee performs rapid circular manoeuvres, each one starting with a brief waggling of the body, then a turn to the left or right, and finally a circle back to the starting point. Bottom left: the waggle dance, wherein the dancing bee performs elongate manoeuvres, each one starting with a conspicuous and prolonged period of body waggling, then a turn to the left or right, and finally a walk back to the starting point. The circular distributions on the right show the directional scatter of waggle runs in round dances advertising a feeder 10 m from the hive (top, $N = 144$ waggle runs from 12 dances) and in waggle dances advertising a feeder 100 m (bottom, $N = 70$ waggle runs from 7 dances) from the hive (after Jensen et al. 1997). Dashed line: direction to food; solid line: the circular mean vector.

Over the past 25 years, several groups of researchers (Kirchner et al. 1988; Jensen et al. 1997; Gardner et al. 2008) have closely examined round dances and have reported that these dances, like waggle dances, actually do encode distance and direction information. This work showed that the round dance is better viewed as a form of the waggle dance appropriate to nearby food sources rather than as a separate dance. It remained unclear, however, whether or not bees that follow round dances can use the rather noisily encoded directional information contained in these dances. Karl von Frisch repeatedly asserted that bees that recruited to nearby food sources by following round dances show no directional recruitment and so ‘swarm out in all directions and examine the surroundings of the hive’ (von Frisch 1967, page 46), but he provided surprisingly little evidence in support of this assertion (von Frisch 1923, pp. 105–109). To clarify this matter, we tested whether bees that have been recruited to a nearby food source (by following round dances) show a directional bias. The bees did show a directional pattern of recruitment, so we tested whether the bees achieved this by using the information encoded in the dances or instead by responding to the assembly pheromone or the presence of bees at the nearby food source.

METHODS

Basic Test for Directional Recruitment

We used two colonies of honeybees (*A. mellifera*). They were housed, one at a time, in a two-frame observation hive (see Figure 4.2 in Seeley 1995). We worked from 27 June to 8 July 2011 at the Cranberry Lake Biological Station (CLBS) located in the Adirondack State Park in northern New York, U.S.A. (44°09′N, 74°48′W). We chose the CLBS as our study site for its lack of natural forage, which enabled us to easily train foragers to feeders filled with sucrose solutions (see Figure 4.6 in Seeley 1995). We conducted all trials in a 60 × 140 m lawn area, with the observation hive positioned in the centre (see Figure 5.27 in Seeley 1995). We marked sites for the feeders at 5, 10, 20, 30, 40 and 50 m from the hive and in opposite directions (north and south) from the hive. The observation hive was mounted in a small hut (see Figure 4.4 in Seeley 1995). Working with one colony at a time (the colony not in use was stored 6.5 km from the CLBS), we trained 5–10 bees to collect a sucrose solution from one of the two feeders. To train bees to a feeder, we placed a 4 × 4 cm square of beeswax comb filled with sugar solution at the observation hive's entrance and, as soon as bees were feeding from the comb, we put the comb atop a feeder that was also placed just outside the hive's entrance. Eventually, the bees switched from the comb to the feeder. At this point, we gradually moved the feeder to the location desired for the start of the trial: a spot 5 m north or south of the hive.

Once we had 5–10 bees foraging from the feeder 5 m from the hive, we labelled each bee while she was at the feeder by gently putting shellac-based paint marks on the thorax. We next adjusted the concentration of the sucrose solution (1.0 M to 2.5 M), as needed to elicit dancing. The sucrose solution was scented with anise (60 μl of anise extract per litre of solution; McCormick and Co., Hunt Valley, MD, U.S.A.). We also pinned a 1 × 2 cm piece of filter paper to the feeder and applied 5 μl of anise extract every 10 min to the filter paper, to help recruits locate the feeder by orienting to its scent. Once the labelled bees were travelling consistently between the hive and the first feeder, a second feeder identical to the first was set up at the same distance from the hive but in the opposite direction (north or south). The only difference between the two feeders was that one had foragers visiting it while the other did not. A person was stationed at each feeder to collect data. We then began our data collection, which consisted of capturing and counting all the recruits (recognized as unlabelled bees) immediately upon arrival at each feeder. Each recruit was captured by placing a clear plastic bag over her shortly after she landed at the feeder; the bee flew up into the bag without releasing alarm pheromone. The labelled bees were allowed to continue foraging and dancing in the hive to advertise the feeder that they were visiting. The captured recruits were sacrificed at the end of the day, by freezing, so each recruit was counted only once.

Once enough recruits were caught with the two feeders 5 m from the hive, we moved both feeders simultaneously to locations 10 m from the hive. The labelled bees were given 10 min to adjust to the new location of their feeder, during which time all recruits were caught but not counted as data. At the end of the 10 min transition period, we resumed collecting data on recruitment to the two feeders. This procedure was repeated over the day with the two feeders located farther and farther (at 20, 30, 40 and 50 m) from the hive. In further trials, we repeated the experiment but with the labelled bees visiting and advertising the feeder in the opposite direction, to control for any inherent biases for one direction (north or south), and with a second colony of bees.

We predicted that if dance followers cannot obtain directional information from the dances performed by the labelled bees, then at each distance we should find no significant difference in the number of recruits arriving at the visited (advertised) feeder versus the unvisited feeder. However, if dance followers do obtain directional information from the dances, then we should observe a significantly greater number of recruits arriving at the advertised feeder.

Control for Effect of Assembly Pheromone

A forager imbibing sugar solution from a feeder sometimes releases assembly pheromone (Free 1987) by exposing the membrane connecting the last two tergites of the abdomen, which bears the secretion from the Nasonov gland (von Frisch 1923, 1967; Goodman 2003). Indeed, when we watched the labelled bees visit our feeders, we noticed that some individuals released assembly pheromone when approaching, landing and feeding at the feeder. This created the possibility that the directional recruitment that we found in the basic test (see Results) was due to recruits responding to the assembly pheromone rather than to the information encoded in the dances. To control for possible effects of the assembly pheromone, we sealed together the last two tergites of the labelled bees with three to five coats of nail polish. The labelled foragers were repeatedly inspected in the hive and at the feeder to confirm that their seals were still intact. Data were then collected as described above for the basic test.

Control for Effect of Bee Presence

The presence of bees at a feeder can attract recruits searching for the feeder (Tautz & Sandeman 2003). To control for possible effects of bee presence, we trained a group of 5–10 labelled bees to each feeder. All of these bees had their last two tergites sealed together with nail polish to prevent release of assembly pheromone. The concentrations of the sucrose solutions in the two feeders were adjusted so that all the labelled bees continued to visit their feeders, but only the bees visiting one of the feeders (the advertised feeder) were sufficiently stimulated by a high sucrose concentration to perform dances. Trials were conducted in the same way as in the previous trials, with recruits caught at each feeder, but with the addition of a third person continually monitoring the labelled bees in the observation hive to confirm that only those visiting the feeder with the more concentrated sugar solution (the advertised feeder) performed dances. If the bees from the advertised feeder did not dance sufficiently strongly, or if any bee from the control feeder began dancing, then we immediately adjusted the concentrations of the sugar solutions in the feeders and waited 10 min for the bees to adjust to the new conditions before resuming data collection.

Statistical Analysis

To test for a significant directional bias in recruitment for each distance of the feeders from the hive, we calculated the binomial probability of obtaining by chance alone the observed distribution of recruits. Our null hypothesis was that the recruits could not obtain directional information from the dances performed by the labelled bees, hence each recruit had a probability of 0.5 of arriving at each feeder. The probabilities of the observed distributions were calculated using the website http://faculty.vassar.edu/lowry/binomialX.html. We used one-tailed tests because we predicted a priori that directional biases, if any, would be in favour of the feeder advertised by the dancing bees. To test for significant differences between treatments in the mean percentage of recruits to the advertised feeder at each distance, we used one-tailed *t* tests after making arcsine transformations of the percentages to give them a normal distribution.

RESULTS

Basic Test for Directional Recruitment

We found a significant ($P < 0.05$; see Table 1, Fig. 2a) directional bias in recruitment in favour of the advertised feeder already at 5 m in all trials and for both colonies. This pattern of a significant directional bias in favour of the advertised feeder increased in strength as the distance to the feeders increased, with approximately 80% of the recruits arriving at the advertised feeder at 10 m, and typically more than 90% arriving there at 20–50 m.

Control for Effect of Assembly Pheromone

When we repeated the test, but this time prevented the release of assembly pheromone by sealing the abdomens of the foragers, we found that the percentage of recruits captured at the advertised feeder at 5 m was lower than in the basic treatment (Fig. 2b). At the 5 m distance, approximately 50% of the recruits arrived at the

Table 1
Results of statistical tests for directional recruitment in honeybees

	Distance (m)					
	5	10	20	30	40	50
Basic test						
Colony 1	14, 3	15, 4	22, 1	32, 3	26, 0	29, 0
27 Jun 2011	$P=0.0064$	$P<0.0096$	$P<0.0001$	$P<0.0001$	$P<0.0001$	$P<0.0001$
North						
Colony 1	25, 14	28, 8	28, 4	20, 0	16, 1	21, 0
28 Jun 2011	$P=0.0541$	$P=0.0006$	$P<0.0001$	$P<0.0001$	$P=0.0001$	$P<0.0001$
South	17, 6	24, 8	24, 1	23, 0	20, 0	29, 1
Colony 2	$P=0.0173$	$P=0.0035$	$P<0.0001$	$P<0.0001$	$P<0.0001$	$P<0.0001$
4 Jul 2011						
North						
Pheromone control						
Colony 1	17, 18	21, 11	15, 3	25, 6	28, 1	24, 0
30 Jun 2011	$P=0.6321$	$P=0.0551$	$P=0.0037$	$P=0.0004$	$P<0.0001$	$P<0.0001$
North						
Combined control						
Colony 1	16, 19	16, 9	15, 3	15, 1	14, 0	14, 0
2 Jul 2011	$P=0.7502$	$P=0.1148$	$P=0.0038$	$P=0.0003$	$P<0.0001$	$P<0.0001$
North						
Colony 2	11, 8	26, 9	21, 9	17, 0	13, 0	11, 0
7 Jul 2011	$P=0.3238$	$P=0.0030$	$P=0.0214$	$P<0.0001$	$P=0.0001$	$P=0.0005$
South						

For each trial in each treatment, we show the numbers of recruits that arrived at the two feeders (advertised, unadvertised) and the one-tailed binomial probability of the observed distribution of recruits to the two feeders.

advertised feeder, as expected if recruitment to a food source at 5 m is nondirectional. Nearly significant directional recruitment was found at 10 m ($P < 0.06$; see Table 1), and highly significant directional recruitment was found at 20 m and beyond ($P < 0.004$). Over 80% of recruits were captured at the advertised feeder at 20 m and 30 m and nearly 100% of recruits were captured at the advertised feeder at 40 and 50 m. Complications due to weather prevented us from obtaining data from Colony 2 for this control.

Control for Effect of Assembly Pheromone and Bee Presence

The directional recruitment observed for food sources at 10 m and beyond, even after controlling for effects of assembly pheromone, could have arisen in part from the presence of bees at the advertised but not at the unadvertised feeder. To test for effects of bee presence, we performed a third set of trials in which we controlled for the effects of both assembly pheromone and bee presence at the advertised feeder. We obtained results similar to those obtained when we controlled for the assembly pheromone alone (Fig. 2c). Approximately 50% of the recruits arrived at the advertised feeder at 5 m, indicating no directional recruitment. Colony 2, but not Colony 1, showed significant directional recruitment at 10 m, and both colonies showed significant directional recruitment at 20 m and beyond. For both colonies, more than 90% of recruits arrived at the advertised feeder when the feeders were at 30 m, and 100% of recruits arrived there when the feeders were at 40 m and 50 m.

Comparison of Treatments

When we averaged the results across trials within a treatment and then compared the mean values for the three treatments, we found similar levels of directional recruitment in all three treatments except when the bees were tested with the feeders at 5 m (Fig. 2d). When the feeders were 5 m from the hive, we found a strong and significant difference in the level of directional recruitment between the basic test (available information: dance + pheromone + bees) and the assembly pheromone control (available information: dance + bees), and between the basic test (available information: dance + pheromone + bees) and the combined control (available information: dance only) (see Table 2). However, we found no difference in the level of directional recruitment between the assembly pheromone control and the combined control (in both controls, there was no sign of directional recruitment) at the 5 m distance. When the feeders were 10 m or more from the hive, we observed clear directional recruitment in all of the treatments, although when the feeders were at 10 and 20 m, there were still some significant differences in the level of directional recruitment between the basic test treatment and the control treatments.

DISCUSSION

Karl von Frisch repeatedly stated that when honeybees follow ‘the round dance they swarm out in all directions and examine the surroundings of the hive… they do not know *where* to look’ (von Frisch 1967, page 46; see also von Frisch 1923, page 108). We were somewhat surprised, therefore, to find in our basic test that bees that followed round dances advertising a feeder 5–50 m from the hive arrived mainly at the advertised feeder rather than equally at this feeder and at an identical feeder in the opposite direction (Fig. 2a). This result was not completely unexpected because several previous studies (Kirchner et al. 1988; Jensen et al. 1997; Gardner et al. 2008) had shown that dances for food sources as close as 10 m from the hive contain directional information. But, we could not be sure at first that the recruits had arrived primarily at the advertised feeder by responding to the location information in the round dances that were being performed in the hive. The recruits might have instead been responding to the odour of assembly pheromone at the advertised feeder or to the sight of bees at the advertised feeder, or both.

To clarify how the bees produced their pattern of directional recruitment to nearby food sources, we performed further trials in which we controlled for any effects of assembly pheromone (Fig. 2b) and for any combined effects of assembly pheromone and bee presence (Fig. 2c). Our results indicate that the directional recruitment that we found at 5 m in the basic test was mainly, if not entirely, a result of attraction to assembly pheromone. Preventing pheromone release by the bees foraging at the advertised feeder eliminated the directional bias in favour of the advertised feeder

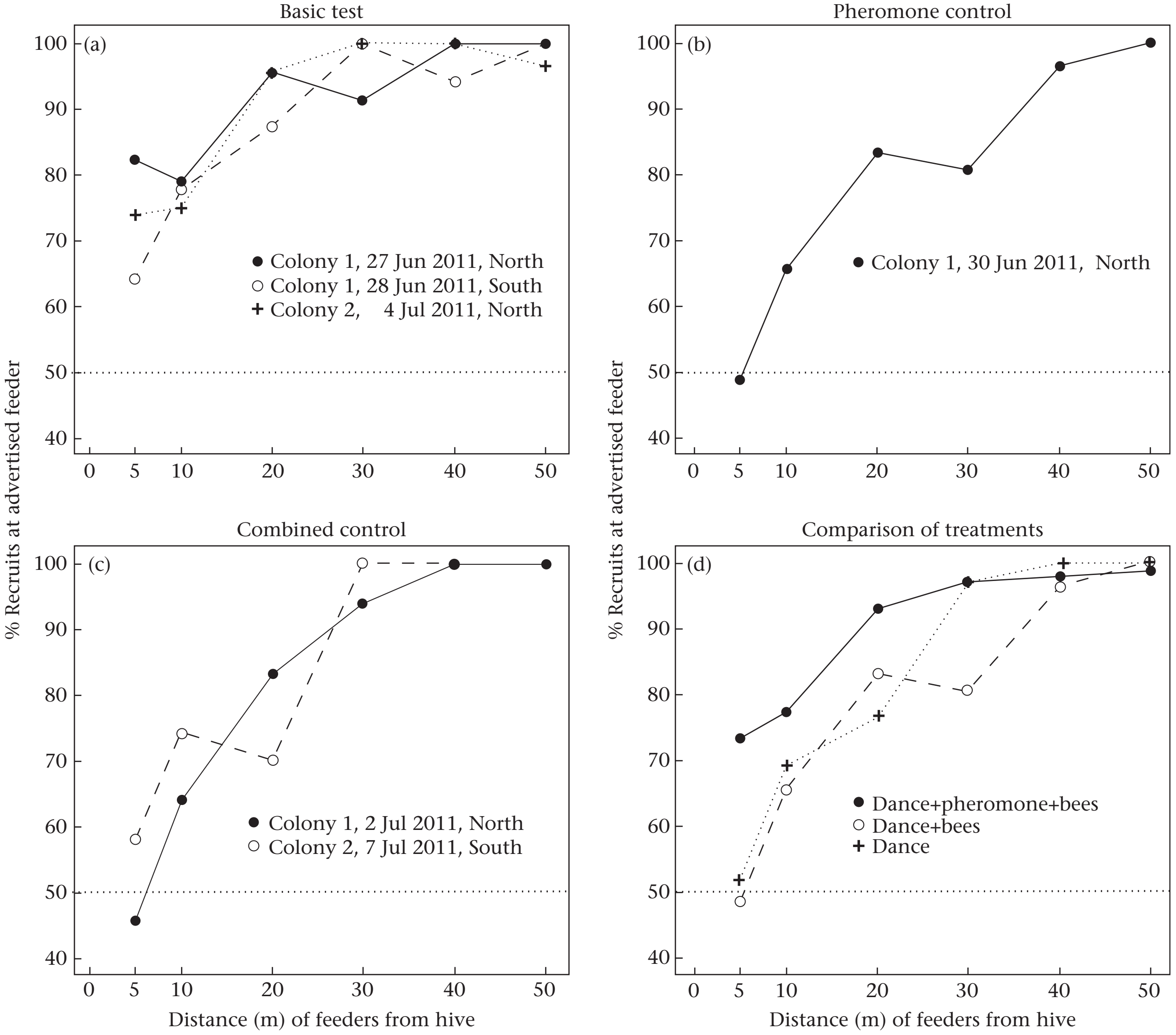

Figure 2. Percentages of honeybee recruits that arrived at the advertised feeder, rather than the unadvertised feeder, for various distances of the feeders from the hive. (a) Basic test: no controls for effects of assembly pheromone or bee presence at the advertised feeder. The direction of the advertised feeder was switched between trials to control for any bias among the bees for one direction over the other. (b) Pheromone control: the last two tergites of each bee visiting the advertised feeder were sealed shut, to control for effects of assembly pheromone on directional recruitment. (c) Combined control: bees were trained to both feeders and the last two tergites of each bee were sealed shut, to control for effects of assembly pheromone and bee presence on directional recruitment. (d) Comparison of the three treatments: treatment names denote the possible sources of information used by recruits to find the advertised feeder.

Table 2
Results of one-tailed *t* tests for equality of the percentage of honeybee recruits to the advertised feeder for various pairs of treatments at each distance

Distance (m)	Treatment groups compared	*t*	*df*	*P*
5	Basic test vs Pheromone control	2.07	2	<0.10
	Basic test vs Combined control	2.50	3	<0.05
	Pheromone control vs Combined control	0.31	1	>0.70
10	Basic test vs Pheromone control	4.61	2	<0.025
	Basic test vs Combined control	2.01	3	<0.10
	Pheromone control vs Combined control	0.41	1	>0.70
20	Basic test vs Pheromone control	1.56	2	<0.20
	Basic test vs Combined control	2.71	3	<0.05
	Pheromone control vs Combined control	0.58	1	<0.45
30	Basic test vs Pheromone control	1.78	2	<0.10
	Basic test vs Combined control	0.17	3	<0.45
	Pheromone control vs Combined control	1.49	1	<0.20

No significant differences between treatment groups were found for the 40 m and 50 m trials.

when the feeders were at 5 m. Preventing pheromone release did not eliminate the directional recruitment when the feeders were 10 and 20 m from the hive, but it seems to have reduced it slightly. Once the feeders were 30 m or more from the hive, however, we found no evidence of an effect of assembly pheromone in producing the observed directional recruitment. We also found no evidence that the presence of bees at the advertised feeder contributed to the directional recruitment in the basic test, because the combined control for assembly pheromone and bee presence did not further reduce the directionality of recruitment relative to the control for assembly pheromone alone (Fig. 2d). Tautz & Sandeman (2003) found an effect of bee presence at a feeder on recruitment to the feeder, but they worked with unscented feeders; evidently the strong scent that we provided at our feeders eliminated the effects of the visual cue of bees at our feeders. We conclude that the directional recruitment that we found in our basic test when the feeder was 10 m or more from the hive was produced mainly by the recruits using the location information in the round dances advertising the feeder.

Given the strong directional recruitment that we found in our basic test, even at distances as close as 5 m to the hive, it is curious that Karl von Frisch stated categorically that followers of round dances show no sign of obtaining directional information from these dances. A careful review of the evidence on which von Frisch based his statement on this matter reveals that his tests with food sources near the hive (von Frisch 1923, pp. 105–109) actually suggest that there is directional recruitment to nearby food sources. In his first test, conducted on 5 August 1920, he trained two foragers to a feeder at 15 m and he set out four feeders at approximately the same distance but in various directions from the hive. Of the 12 recruits that he captured at these four feeders, most (9) arrived at two feeders that were in the general direction of the advertised feeder. He performed a second test similar to the first (date not given), with 10 foragers trained to one feeder (presumably at 15 m) and with 12 other feeders in various locations (not specified) around the hive. In this test, he captured 47 recruits at the advertised feeder and only 22 recruits total for the other 12 feeders. His third test consisted of a brief, 30 min experiment on 20 August 1920 in which he trained 11 foragers to one feeder 15 m west of the hive and he set up 14 other feeders in various directions and at various distances (10–75 m) from the hive. Over the half hour of this test, he captured four recruits at the eight feeders west of the hive (the advertised feeder and seven other feeders), and he captured two recruits at the seven feeders east of the hive. He explained the results of his three tests, especially his second (which had a good sample size) as the result of a high level of bee traffic to and from the feeder being visited by the trained foragers. But it is also possible, and our results indicate, that the hints of directional recruitment that he found were a result of the recruits acquiring directional information from the dances performed by the trained foragers. All things considered, we feel that Karl von Frisch (1967, page 46) was premature when he drew the conclusion that dances for nearby food sources cause recruits to 'swarm out in all directions'. Based on our more careful testing for directional recruitment to food sources near the hive, we draw the conclusion that dance followers obtain directional information from dances advertising food sources as close as 10 m from the hive and that they swarm out in the indicated direction.

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