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Imprecision in waggle dances of the honeybee (*Apis mellifera*) for nearby food sources: error or adaptation?

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Abstract A curious feature of the honeybee's waggle dance is the imprecision in the direction indication for nearby food sources. One hypothesis for the function of this imprecision is that it serves to spread recruits over a certain area and thus is an adaptation to the typical spatial configuration of the bees' food sources, i.e., flowers in sizable patches. We report an experiment that tests this tuned-error hypothesis. We measured the precision of direction indication in waggle dances advertising a nest site (typically a tree cavity, hence a target that is almost a point) and compared it with that of dances advertising a food source (typically a flower patch, hence a target that covers an area). The precision of dances for a nearby nest site was significantly higher than that of dances for an equidistant feeder. This was demonstrated four times with four colonies. Our evidence therefore supports the hypothesis that the level of precision in the direction indication for nearby food sources is tuned to its optimum without being at its maximum.

Key words *Apis mellifera* · Communication · Honeybee · Recruitment · Swarms · Tuned-error hypothesis · Waggle dance

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Introduction

A honeybee returning to her hive from a profitable food source performs a waggle dance, in which she codes information about the location of the source. A waggle dance consists of several waggle runs. The direction of each waggle run, relative to gravity, indicates the direction of the food source, relative to the sun. One curious feature of the dance is the conspicuous 'imprecision' of the coding of directional information for nearby food sources. Unlike dances for distant food sources, in which consecutive waggle runs are closely aligned, in dances for nearby food sources (those less than 1 km from the hive), consecutive waggle runs are produced with considerable directional scatter. Given the obvious benefits that recruitment communication provides to a colony of bees (rapid exploitation of profitable food sources), this imprecision in the recruitment behavior seems quite puzzling.

One hypothesis for how directional imprecision could be adaptive is that the honeybee's dance behavior is tuned to the typical spatial configuration of food sources (Haldane and Spurway 1954; Wilson 1962; Gould 1976). The flowers exploited by temperate-zone honeybees may usually occur rather thinly distributed over large patches. According to the 'tuned-error' hypothesis (Towne and Gould 1988), under such conditions, natural selection should favor a certain amount of imprecision in recruitment for nearby targets: a bee dancing for a nearby food source should provide relatively imprecise directional information so that the nestmates she recruits will be distributed across the flowers in her patch rather than concentrated where she is foraging. In contrast, a bee dancing for a distant food source (>1 km away) should provide precise directional information, since the natural scatter of recruits is sufficient to spread them over flowers in a patch far from the hive. Implicit in this hypothesis is the idea that a colony of bees will more efficiently exploit food sources close to the hive if its foragers do not produce waggle dances with the maximum level of precision. Towne and Gould (1988) showed that the spatial precision of recruitment is consistent with their hypothesis, for recruits are distributed over a wider angle for nearby food sources than for distant ones and as a result, the area over which recruits are spread is essentially constant for distances of 100–1000 m from the hive. Another piece of evidence supporting the tuned-error hypothesis comes from comparative studies within the genus *Apis*. Tropical honeybees exhibit less directional imprecision in their dances for nearby food sources than do honeybees native to temperate regions (Towne and Gould 1988). This supports the idea that the spatial distribution of resources is the important factor in the evolution of dance imprecision, for it is generally thought that the tropical environment typically offers flowers distributed in small clumps (such as a flowering tree), whereas the temperate environment offers flowers distributed in large clumps (such as a meadow of wildflowers). According to the tuned-error hypothesis, the dancing bee does not provide any information on the actual size of the patch she is advertising, rather, directional imprecision is tuned to the average patch size the bees encounter in their environment.

We now report an experiment that tests a prediction based on the tuned-error hypothesis, namely that the directional imprecision for nearby targets should be eliminated, or at least greatly reduced, when the target of recruitment is something that is always essentially a point in space. A nest site is just such a recruitment target (Lindauer 1955). Hence we were able to perform a further test of the tuned-error hypothesis by measuring the precision of direction indication in dances for nearby nest sites and comparing it with the precision in dances for equidistant food sources.

Methods

General plan of study

From each of four colonies of bees, we prepared first an artificial swarm and later housed the bees in an observation hive. Scout bees from each swarm located a nearby nest site and their dances were videorecorded. Foragers of the same colony were then trained to a feeder and their dances were likewise recorded. For each colony, the distance between observation hive and feeder matched the distance between swarm cluster and nest site. The videorecords of 422 dances were analyzed and the precision of direction indication was compared between the dances for the two types of recruitment targets.

Dances for a nest site, Appledore Island

Study site

To get the swarm bees interested in a nearby nest site, we worked at the Shoals Marine Laboratory of Cornell University, located on Appledore Island, Maine (42°59′ N, 70°37′ W). Because this 39-ha island is located 16 km offshore, is nearly treeless, and bears only a few buildings, it offers very few natural nest sites for honeybees. Here we could provide nestboxes near the swarms which would be highly attractive to the swarms' scout bees. Only once did the scouts discover a natural nest site beneath a pile of scrap lumber, but we destroyed this cavity and the bees quickly regained interest in our nestboxes.

Artificial swarm preparation

All observations were made with honeybee colonies from the Liddell Field Station, Cornell University. These bees are hybrids of the many honeybee races imported for beekeeping in North American, including *Apis mellifera ligustica*, *A. m. caucasica*, *A. m. carnica*, and *A. m. mellifera*. The colonies we used were all headed by queens sold as 'Italians,' so presumably they consisted primarily of *A. m. ligustica* stock. To prepare an artificial swarm, we first located a colony's queen and put her in a wooden queen cage (3.2 × 10 × 1.6 cm). Then, using a large funnel, we shook 0.75 kg of worker bees (some 6000 individuals; Fell et al. 1977) from the frames of this colony's hive into a swarm cage (15 × 25 × 25 cm) with wire screen sides. We suspended the queen cage amidst the worker bees inside the swarm cage which was then closed and kept in a cool, dark place for 2–3 days. During this time, we fed the bees liberally with sugar water. Following this treatment, the bees behaved like a natural swarm. At the end of each experiment, the queen and worker bees were returned to their original hive. We worked with just one swarm (colony) at a time.

Apparatus and videorecording techniques

To videorecord the dances for nest sites, we induced each swarm to cluster on one side of a flat, vertical board by mounting the queen cage in an opening of the board and shaking the workers out of the swarm cage at the foot of the swarm mount, whereupon they crawled upward and grouped themselves around the queen (Fig. 1). Once the bees had clustered on the mount, a wire screen (of 8-mesh hardware cloth with several passageways for bees cut into it) was mounted vertically over the swarm's surface. The distance between screen and board could be adjusted so that the outermost layer of the swarm was on the outside of the screen. Arriving scouts would land on the screen and perform their dances while walking around on it. Thus they performed their dances on a planar surface, thereby enabling us to make precise measurements of the angles of their waggle runs. Dances were recorded with a videocamera

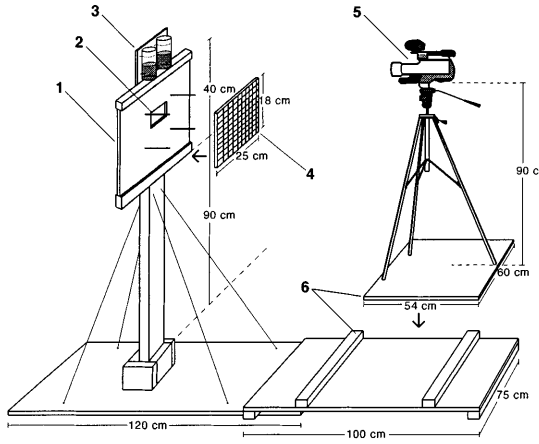

Fig. 1 Swarm mount used for videorecording the waggle dances of scout bees: *1* board on which the swarm clusters, *2* opening for queen cage, *3* feeder bottles, *4* screen on which the scout bees perform their dances, *5* videocamera, *6* tripod mounted on sliding platform for moving the camera laterally (vertical movements are made by changing the height of the tripod head)

(Panasonic WV-3240/12X with videorecorder NV-8420) positioned 1 m in front of the swarm cluster. The camera was mounted on a tripod mounted on tracks, allowing vertical and horizontal movement of the camera without the risk of creating parallax errors in the videorecordings.

Our nestboxes were cubical, 40-l wooden boxes with a 3-cm-diameter entrance hole, like those described in Seeley (1977). They were built of 1.5-cm-thick plywood. Each one was mounted inside a lean-to shelter (see Fig. 5 of Seeley 1977) to protect it from the sun, wind, and rain, and so make it as attractive as possible to the bees. In addition, we baited each nestbox with artificial Nasanov gland pheromone to make it as conspicuous as possible to the scout bees.

Experimental layout and data collection

Three colonies were taken from Ithaca, New York to Kittery, Maine. One swarm at a time was prepared on the mainland and taken out to Appledore Island. Here the swarm was placed on the swarm mount which was located on the porch of a building where the swarm was exposed to daylight but not to direct sunlight. It was liberally fed with sugar water from two feeder bottles which were part of the swarm mount (see Fig. 1). Three nestboxes were positioned on the island in distinct directions and distances from the swarm (at 200, 300, and 400 m). Observations were made from 0800 to 2100 hours. As soon as a bee began performing a dance indicating one of the nestboxes, a dot of paint was daubed on her thorax and then her appearance at the nestbox was checked to be certain that her dance indicated the nestbox. Upon her return to the swarm, her next dance was recorded. For each dancing bee, we recorded approximately 20 consecutive waggle runs of a single dance. Bees that had been recorded were marked by a second paint mark of a different color, so each bee would be recorded only once. Following the discovery of one of the nestboxes, the dancing picked up rapidly and many dances for this site could be recorded. One swarm danced for a nestbox in which we had put a 10 × 20 cm piece of honey comb; these dances were also recorded. We recorded 35–41 dances per swarm and nestbox. The time of day and weather conditions at the time of dancing were also noted. At the end of the trial, the swarm was reunited with its mother colony back on the mainland and a new artificial swarm from a different colony was prepared and taken out to the island for the next trial. This experiment was conducted in June 1995; 164 dances were analyzed.

Dances for a food source, Cranberry Lake

Study site

This part of the study was conducted at the Cranberry Lake Biological Station (44°09′ N, 74°48′ W) in the Adirondack State Park in northern New York State. This field station is located on the southern shore of Cranberry Lake and is surrounded by dense forest offering hardly any natural nectar sources. This makes it easy to train bees to an artificial food source, unlike Appledore Island where there is a rich supply of nectar sources.

Apparatus

Colonies in observation hives were prepared by housing approximately 4000 workers and their queen in a two-frame hive (see Fig. 4.2 in Seeley 1995). The hive was mounted beside a window inside a building. Two plastic tubes leading outside allowed the bees to fly freely. A wedge in the hive entrance forced all bees to enter and leave from one side of the comb. This way the dances were performed on a 'dance floor' on one side of the comb, and this enabled us to observe all the dances and to videorecord any of interest. The videorecording apparatus and techniques were identical to those used with the swarms. The bees on the dance floor were not able to view the sun or sky. Besides some diffuse daylight, the hive was illuminated by a fluorescent lamp mounted directly above the hive.

The feeder consisted of a jar-plate combination that continuously offered sucrose solution of a constant, 2.0 mol/l concentration (see Fig. 4.5 in Seeley 1995). The feeder was placed on a screen-covered dish which contained several drops of anise extract (a 27% solution of essential oil in alcohol), some of which was also added to the sucrose solution (50 µl per liter of solution).

Experimental layout and data collection

The same three colonies that had previously been used for the nest site experiment were taken to Cranberry Lake and were placed in a clearing on the northern shore of the lake. One observation-hive colony at a time was prepared and was taken across the lake (10 km) to the field station. After an adjustment period of 1–2 days, a group of five to ten foragers was trained to the feeder using standard techniques (von Frisch 1967). The feeder was positioned at a distance from the hive equal to that between nestbox and swarm on Appledore Island (for specifics, see Results). Foragers were individually labeled at the feeder with paint dots on thorax and abdomen. Additional recruits arriving at the feeder were captured in Ziploc plastic bags. As soon as a forager started performing dances with at least 20 waggle runs (usually after at least 8 trips to the feeder), she was videorecorded. Upon her next arrival at the feeder, she was captured and replaced by a recruit; this procedure prevented us from recording each bee more than once. For each dance, the time of day and the weather conditions were noted. For each colony and each feeder position, we recorded 24–37 dances. At the end of each day, all captured foragers whose dances had been recorded were killed and all captured recruits were released. At the end of each trial, the bees were returned to their mother colony on the other side of the lake and a new observation-hive colony was prepared and moved to the field station. This experiment was conducted in July 1995; 130 dances were analyzed.

Test for influence of location: dances for a nest site and for a food source, Appledore Island

To test whether the use of different locations for observing nest site and food source dances influenced dance precision, the experiment described above was repeated with one colony ('colony 4') for which we recorded both nest site and food source dances in the same location. A colony of approximately 4000 bees was installed in an observation hive and this was transported to Appledore Island. Here it was set up beside a window inside one of the laboratory buildings (Laighton House) as had been done at Cranberry Lake (i.e., without a view of the sun or sky, with fluorescent light illumination). A group of 15 foragers was trained to a feeder positioned 300 m from the hive. Data on the food source dances were collected and analyzed using the same methods as described above.

Once we had finished taking data on the food source dances, we removed the bees from the observation hive and made an artificial swarm with them using the methods described above. This swarm was then set up on the swarm mount which was positioned on the covered porch of Laighton House just outside the window inside which the observation hive had been positioned. Hence the same bees were in essentially the same location as before, but at this point they were a swarm without a home rather than a colony inside a hive. A three-sided hut (described in Seeley and Buhrman 1999) was placed around the swarm to prevent the bees from seeing the sun or blue sky, as was the case when the bees were in the observation hive. A nestbox was positioned 300 m away, exactly where the feeder had been placed. Once the bees discovered the nestbox (3 days after the swarm was set up) and began advertising it with dances, we recorded their dances using the same methods and equipment as described above. This experiment was conducted in June 1998; 12 food source and 26 nest site dances were analyzed.

Test for influence of celestial cues: dances for a food source, Cranberry Lake

To test whether viewing celestial orientation cues in blue sky influences the precision of directional indication, a colony (not one used previously) was installed in the observation hive which was set up in a small hut (see Fig. 4.4 in Seeley 1995) located beside the lake at the Cranberry Lake Biological Station. The wall nearest the lake and facing the observation hive was removed. This gave the bees on the dance floor a view of the sky from the horizon to an elevation of 40° above the horizon. A group of five to ten foragers was trained to a feeder 200 m from the hive. Their dances were videorecorded, as described above, under two different conditions: (1) the sky was cloud covered, so the bees could not view either the sun or the blue sky, and (2) the sky was cloudless, so the bees could view the blue sky but not the sun (obscured by the ceiling and walls of the hut). This experiment was conducted in September 1996; 90 dances were analyzed.

Data analysis

Measuring the precision of direction indication

Videotapes were analyzed in slow motion (Panasonic NV-8950 videoeditor). The angle of each waggle run was measured using a protractor similar to that described by von Frisch (1967). It consisted of a circular, turnable Plexiglas disk with parallel lines 2 cm apart and a peripheral scale drawn on it. This disk was mounted on a second, square Plexiglas sheet which was mounted in front of the videoscreen. At the center-top of the square plate, an index line was marked. This line corresponded with the centerline of the disk and marked 0°. To measure the angle of a waggle run, the disk was rotated until the direction of the waggle run (the direction in which the bee's head pointed while she was waggling) was aligned with the lines on the disk. The angle of the waggle run could then be read on the peripheral scale at the top of the disk where the index line pointed. The angle of each waggle run was measured five times and the average and standard deviation of the five measurements were calculated. In addition, the direction in which the bee had turned (left or right; see Fig. 2) *before* making each waggle run was noted. Measurements were taken on 14–21 consecutive waggle runs for each bee (except for the 1998 data, when we measured 10–33 waggle runs per bee). The divergence angle, defined as the angular difference between the mean direction of waggle runs following left-hand turns and that following right-hand turns (Towne and Gould 1988) was then calculated for each bee, as shown in Fig. 3. Most bees circled less than 360° between waggle runs (see the top pattern in Fig. 2), but some bees circled more than 360° between waggle runs, thereby 'overshooting' the angle of the previous waggle run (the bottom pattern in Fig. 2). We also determined for each bee the standard deviation of the angles of waggle runs following her left or right turns (see Fig. 3), and the overall range of the waggle run angles within her dance.

Measuring distance indication

The time from the beginning of one waggle run to the beginning of the next one (= dance circuit time) was measured with a stopwatch while playing the videotape at normal speed. For each dance, ten dance circuits were timed and their average value was calculated. For each swarm or observation-hive colony, at least ten of the recorded dances were measured. The distance indications of nest site and food source dances were compared.

Statistical analysis

All numerical results are given as the mean ± 1 SD. Statistical tests of the difference between two means were performed using either Student's *t*-test or the Mann-Whitney *U*-test (used when

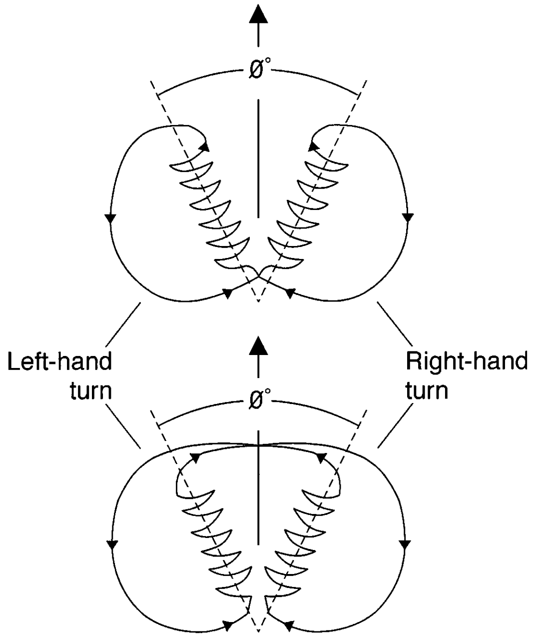

Fig. 2 Two pathways of the movements traced out by the tip of the abdomen of a bee as she performs a waggle dance for a food source or a nest site near the hive. In each pathway, the semicircular loop on the far left is a circling turn to the left, which is followed by a waggle run, then a circling turn to the right, and finally another waggle run. The directions of the two waggle runs and the resulting divergence angle (ø) are also shown. The *arrow pointing upward* denotes the direction in which the bee would orient her waggle runs if she were to indicate the target direction precisely. The figure shown at the top (where the bee circles less than 360° between waggle runs) is what is most commonly observed, but one sometimes also sees the figure shown at the bottom ('overshooting dance'), where the bee circles more than 360° between waggle runs

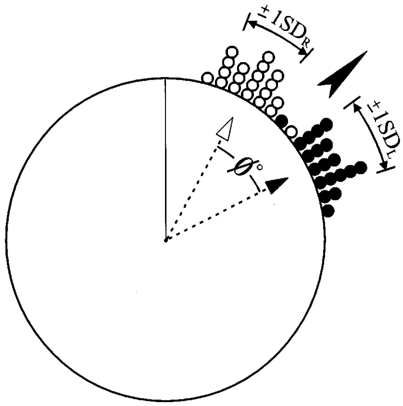

Fig. 3 Schematic drawing of a waggle dance advertising a feeder 200 m from the hive. The bimodal distribution of directions indicated in 39 consecutive waggle runs is shown. Each waggle run direction is denoted by a *circle* (bins 5°). *Open circles* denote waggle run directions following right turns, *filled circles* denote waggle run directions following left turns. The *small arrows* denote the mean direction of waggle runs following right (*open arrowheads*) or left (*filled arrowhead*) turns. SD_L and SD_R denote the standard deviations of the two distributions. The bee in this example dances with a divergence angle (ϕ°) of 34°. The *large arrowhead* denotes the direction in which the bee would orient her waggle runs if she were to precisely indicate the feeder direction

comparing the mean values of divergence angles, since the divergence angle data were not normally distributed). We also used Student's t-test of the significance of regression coefficients (Sokal and Rohlf 1981, p. 474), and the chi-squared test in a contingency table analysis of the independence of dance target (nest site vs food source) and dance type (normal vs overshooting; see Fig. 2).

Results

Comparison of precision in dances for nest sites and food sources

Nest site and food source dances performed at different locations

The distributions of divergence angles in dances for nest sites and food sources are shown in Fig. 4. The swarm prepared from colony 1 discovered the nestbox 400 m from the swarm. The dances performed by this swarm's scout bees showed a mean divergence angle of 9.7 ± 6.0° ($n = 35$). The dances performed by this colony's foragers for our feeder located 400 m from the hive showed a mean divergence angle of 16.9 ± 8.5° ($n = 24$). The swarm prepared from colony 2 discovered the nestbox at 300 m and its scouts' dances showed a mean divergence angle of 5.3 ± 4.8° ($n = 48$). When foragers from this colony were trained to a feeder located 300 m from the hive, they produced dances with a mean divergence angle of 22.8 ± 11.1° ($n = 36$). Finally, the swarm prepared from colony 3 discovered the nestbox at 200 m. These dances showed a mean divergence angle of 13.2 ± 10.9° ($n = 41$). Foragers of colony 3 danced for a 200-m feeder with a divergence angle of 28.5 ± 10.2° ($n = 37$). Hence, in all three colonies, the mean divergence angle of dances for a nestbox was significantly smaller than that of dances for the feeder at the same distance ($P < 0.001$; see Table 1).

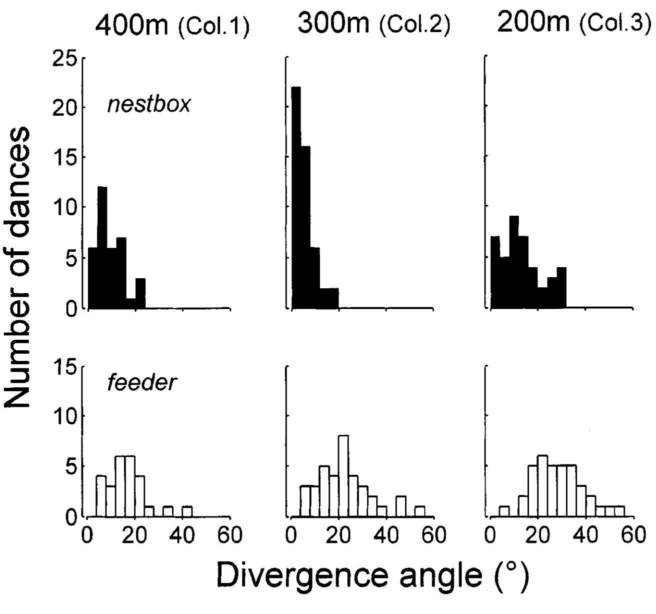

Fig. 4 Distributions of divergence angles in the dances of bees indicating either a nestbox (*filled bars*) or a feeder (*open bars*). The histogram bins are 4° wide

As shown in Fig. 3, the distribution of directions indicated in one dance is often bimodal and so the divergence angle alone provides only limited information about the actual precision in direction indication. We therefore calculated several other descriptive statistics as measures of dance precision. Both the standard deviations of the waggle run directions following left or right turns, and the range of waggle run directions, were significantly smaller in dances for a nestbox than in dances for an equidistant feeder, except for the $\mathrm{SD_L}$ comparison within colony 1 (Table 1).

Figure 5 shows the mean divergence angles of dances for a nest site or a food source in relation to the distance between swarm and nest site or between hive and food source. The mean divergence angle decreased significantly with increasing distance in the case of dances for a food source (the slope of the regression line is significantly different from 0; $b = 0.0602$, $P = 0.01$), but not in the case of dances for a nest site (the slope of the regression line is not significantly different from 0; $b = 0.0175$, $P > 0.20$).

Test for influence of location: nest site and food source dances performed at the same location

To test the possibility that some difference between our two study sites (Appledore Island and Cranberry Lake) could have caused the differences in divergence angles that we observed between dances for nestboxes and feeders, we gathered data on both nest site and food source dances using exactly the same experimental layout at one of our study sites, Appledore Island. All of these dances were performed by bees from the same colony (colony 4) and the data were gathered only a few days apart: food source dances, 8–10 June; nest site dances, 19 June 1998.

The distributions of divergence angles for the two types of dances are shown in Fig. 6 (left half) and in Table 1 (300 m, colony 4), we compare the statistics for these dances. The dances for a nestbox 300 m from the swarm showed a mean divergence angle of 6.0 ± 7.3° ($n = 26$). The food source dances for a feeder at 300 m, and performed by bees of the same colony, showed a mean divergence angle of 24.6 ± 10.2° ($n = 12$). The mean divergence angle of dances for the nestbox was significantly smaller than that of dances for the feeder in the same location ($P < 0.001$; Table 1). It should be noted that the mean divergence angle of food source dances on Appledore Island does not differ from that obtained for an equidistant food source at our other study site, Cranberry Lake. The standard deviations of the waggle run directions following left ($P < 0.05$) or right turns ($P < 0.05$), and the range of waggle run directions ($P < 0.001$) were also significantly smaller in dances for the nestbox than in dances for the feeder (Table 1).

Thus the directional precision of dances for a nestbox at 300 m was significantly higher than that of dances for an equidistant feeder (Table 1), irrespective of whether nest site and food source dances were recorded at the same location (colony 4) or at different locations (colonies 1–3).

Consideration of other parameters possibly influencing dance precision

Dance floor

Scouts of the colony 3 swarm were videorecorded when dancing for a nestbox 400 m from the hive which contained a 10 × 20 cm piece of honeycomb and the foragers of this colony were videorecorded when they danced for a feeder at 400 m. The bees visiting the nestbox fed heavily on the honey in the comb. Thus their dances were food source rather than nest site dances. As is shown in Fig. 6 (right side), the dances for this food-containing nestbox (performed on a screen) showed no significant difference ($P > 0.40$; Table 1) in mean divergence angle relative to dances for an equidistant feeder (performed on comb; food-containing nestbox: 17.5 ± 7.7°, $n = 40$; feeder: 16.2 ± 8.5°, $n = 33$). Furthermore, they did not differ from dances performed by bees of a different colony for a feeder at 400 m (see colony 1, Table 1). Thus it seems clear that dance floor substrate does not influence dance precision.

Dance orientation cues

Scout bees dancing on the surface of swarms (colonies 1–3) sometimes could see blue sky while forager bees dancing on the combs inside the observation hive could never do so. To test the possibility that different cues for orienting dances (scout bees: gravity and celestial cues; forager bees: gravity cues only) caused the difference in precision of direction indication, we trained bees to a feeder 200 m from the observation hive and recorded their dances one day when blue sky was visible (cloudless sky) and also the next day when it was not (cloud-covered sky). Comparison of their mean divergence angles revealed no significant difference: with a view of blue sky, 24.7 ± 14.6° ($n = 50$); without a view of blue sky, 21.2 ± 10.1° ($n = 40$) ($P = 0.90$). Thus it seems clear that the availability of celestial orientation cues does not influence dance precision.

Perceived distance

We compared the distance indications (dance circuit times, which reveal each dancing bee's perception of the

Table 1 Comparison of the properties of waggle dances advertising a nestbox or a feeder located at the same distance. SD_L and SD_R denote the standard deviations of the angles of waggle runs following left-hand and right-hand turns within a bee's dance (*A* Appledore Island, *C* Cranberry Lake)

	200 m Colony 3			300 m Colony 2			Colony 4			400 m Colony 1			Colony 3		
	Nestbox (A)	Feeder (C)	*P*	Nestbox (A)	Feeder (C)	*P*	Nestbox (A)	Feeder (A)	*P*	Nestbox (A)	Feeder (C)	*P*	Nestbox + food (A)	Feeder (C)	*P*
Mean divergence angle (°)	13.2	28.5	0.001	5.3	22.8	0.001	6.0	24.6	0.001	9.7	16.9	0.001	17.5	16.2	0.4
Mean SD_L (°)	6.9	9.8	0.001	5.7	8.3	0.001	9.0	12.2	0.03	7.3	7.0	0.60	7.1	9.5	0.0
Mean SD_R (°)	6.7	7.9	0.03	6.2	9.3	0.001	8.8	11.9	0.03	6.4	7.8	0.02	7.6	8.7	0.1
Range of waggle run angles (°)	32.4	54.6	0.001	24.2	49.3	0.001	27.8	53.0	0.001	33.0	39.6	0.05	41.2	43.2	0.5
Number of Overshooting dances	3	0	0.14	27	0	0.001	6	0	0.07	3	0	0.09	0	1	0.2
Dances (*n*)	41	37		48	36		26	12		35	24		40	33	
Mean ± SD dance circuit time (s)	1.74 ± 0.13 (*n* = 10)	1.92 ± 0.14 (*n* = 10)	0.01	2.09 ± 0.17 (*n* = 10)	2.02 ± 0.16 (*n* = 10)	0.14	2.29 ± 0.18 (*n* = 19)	2.28 ± 0.13 (*n* = 12)	0.60	2.15 ± 0.19 (*n* = 10)	2.27 ± 0.19 (*n* = 10)	0.08	2.46 ± 0.11 (*n* = 10)	2.35 ± 0.13 (*n* = 10)	0.20

distance to her recruitment target) for bees visiting a nestbox or an equidistant feeder. Except in the case of dances performed by bees from colony 3 for the 200-m sites, there was no significant difference between the distance indications of bees visiting a nestbox or the feeder (Table 1). This rules out the possibility that differences in the wind conditions and terrain between the Appledore Island and Cranberry Lake study site somehow caused different perceptions of distance (see Heran 1956; Esch and Burns 1996) and thus different divergence angles. And in the case of the dances by the colony 3 bees for the 200-m sites, the distance indications by the bees visiting the feeder were actually slightly longer than those by the bees visiting the nestbox. This indicates that the bees perceived the feeder as being slightly farther away than the nestbox. Nonetheless, the bees visiting the feeder produced dances with a larger mean divergence angle than did the bees visiting the nestbox.

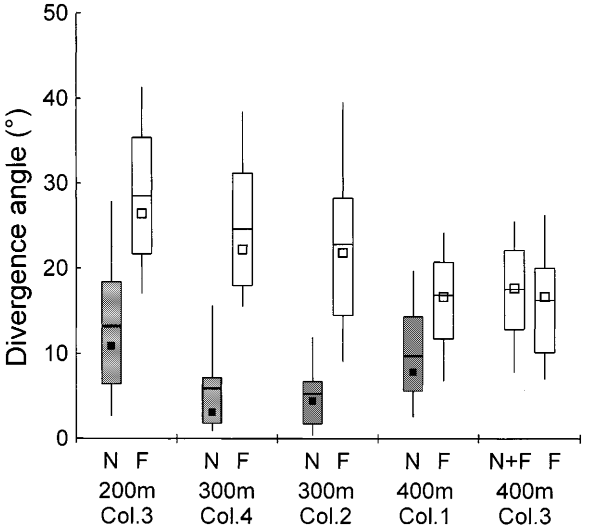

Fig. 5 Divergence angle versus distance for dances indicating either a nestbox (*N*, *shaded boxes*) or a feeder (*F*, *open boxes*). The dances performed by the colony 3 bees visiting a nestbox at 400 m (N + F) were actually dances for a food source, for the bees were able to obtain honey from a comb inside the nestbox. In each figure, the *square* denotes the median, the *horizontal bar* denotes the mean, the *box* shows the 50% of data points around the median, and the *vertical line* indicates the range of the data excluding the highest and lowest 10% of data points

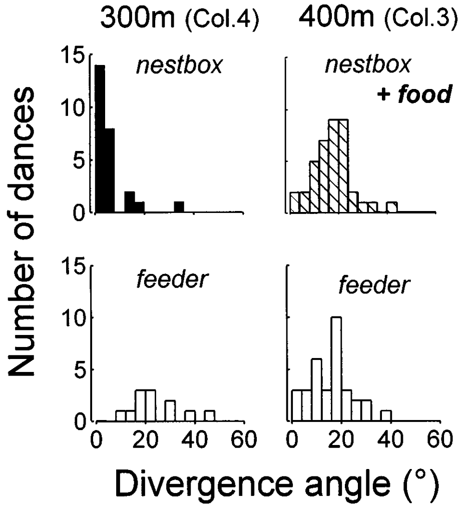

Fig. 6 Results of the test for the influence of location and dance floor substrate on dance precision: distribution of divergence angles in the dances of bees indicating either an empty nestbox (*filled bars*), a feeder (*open bars*), or a nestbox containing food (*hatched bars*). Colony 4: nest site and food source dances performed at the same location (Appledore Island). Colony 3: food source dances for a nestbox containing food (Appledore Island) and for an equidistant feeder (Cranberry Lake) performed on different dance floor substrates (nestbox + food: wire screen; feeder: beeswax comb). The histogram bins are 4° wide

Overshooting dances

Overshooting dances occurred almost exclusively in dances for a nest site (Table 1). Contingency table analyses suggest that dance target (nest site vs food source) and dance type (normal vs overshooting) are not independent variables, though this is shown convincingly only in the results for colony 2, where more than half of the nest site dances, but none of the food source dances, were of the overshooting type.

Discussion

Support for the tuned-error hypothesis

In this study, we examined the functional significance of imprecision in a communication signal, the honeybee's waggle dance. We tested the tuned-error hypothesis, which proposes that the lower precision of direction indication in dances for nearby food sources relative to distant food sources is an adaptation to the typical spatial configuration of the bees' food sources: sizable patches of flowers (Towne and Gould 1988). Our results provide strong support for this hypothesis, for we found that when the target of recruitment is a nest site (essentially a point in space) rather than a food source (usually an entire flower patch), much of the imprecision of direction indication disappears. In all four colonies studied, we found significantly higher directional precision (a smaller mean divergence angle) in dances for a nest site than in dances for an equidistant food source.

The measurements of mean divergence angle that we obtained for food source dances are consistent with data already published by von Frisch (1948) and Towne and Gould (1988), as is shown in Fig. 7. All studies show that the divergence angle decreases with increasing distance to a food source. In nest site dances, however, we found no detectable change in divergence angle with increasing distance.

The feeders used in our experiment were point targets and thus did not possess the spatial properties of natural

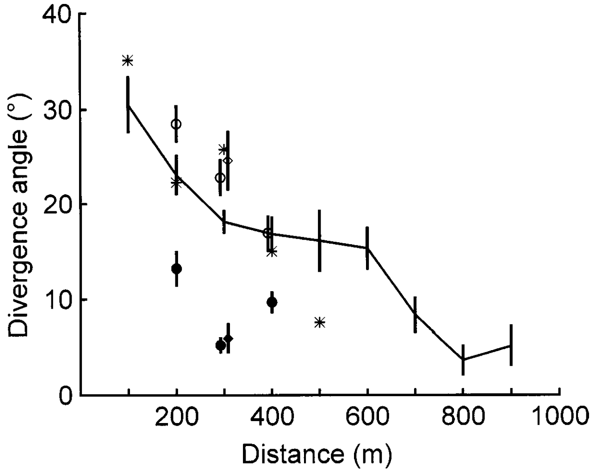

Fig. 7 Comparison of the dance divergence findings in this study and in previously published studies. *Closed* (nestbox) and *open* (feeder) *circles* denote the results of this study, *stars* denote data of von Frisch (1948) and *vertical lines connected by a line* denote those of Towne (1985)

food sources. The use of such feeders is appropriate nonetheless, since it has been demonstrated that the actual size of a food source does not influence dance divergence (Towne 1985). Individual bees do not show short-term flexibility in adjusting their divergence angles according to the particular size of the food patch visited; rather, food seems to trigger a certain amount of directional imprecision in the dance.

Our experiments were performed in two different locations. To get swarm bees interested in nearby nest sites, we performed the nest site experiments on a small island off the coast of Maine. A rich supply of blooming flowers and often poor weather makes the training of bees to a feeder extremely difficult on this island. Therefore, most of the food source experiments were performed at a different location, Cranberry Lake. There are several indications, however, that the dance precision that we measured was not influenced by the experimental settings. First, the results we obtained when we observed nest site and food source dances in the same location did not differ from the results obtained when we observed the two dance types in two different locations. Using exactly the same experimental layout on Appledore Island, we found a large difference in dance precision between nest site and food source dances. This shows clearly that there was not something about the island setting per se that caused the bees to dance with greater precision. Furthermore, dance circuit time did not differ between nest site and food source dances, even when recorded at different locations. This demonstrates that flight range conditions were comparable and that the bees perceived the two recruitment targets (nest site and feeder) as being equidistant. Thus the smaller divergence angles in dances performed on Appledore Island were not caused by an extraneous location variable.

Second, we found no difference in dance precision when we compared the dances of bees advertising a food source when they could and could not see the blue sky. Indeed, the mean divergence angle for the cloudy-sky day was actually smaller (though not significantly so) than that for the clear-sky day. This shows that the bees did not show greater precision in their dances on Appledore Island, because here the dancing bees had a view of the blue sky and so had celestial as well as gravity cues by which they could orient their dances.

Third, the possibility that the dance floor has an effect on dance precision can be ruled out by the fact that in the case of colony 3, the bees showed the same amount of imprecision when dancing on the swarm (on a wire screen) for food offered in a nestbox as they did when dancing in a hive (on beeswax comb) for food offered in a feeder.

Thus we are confident that the differences in dance precision found between nest site and food source dances resulted from the difference in recruitment target and not from the associated differences in study location, dance orientation cues or dance floor substrate.

Comparison to previous studies

When returning from a nestbox containing food, the swarm bees danced with the same low level of precision as when the hive bees danced for a feeder. Evidently, the food in the nestbox changed the behavioral context from house hunting to food collecting. Such switching of behavioral contexts in swarm bees probably also explains why Towne (1985) found no difference in the precision (mean divergence angle) of nest site and food source dances. He trained foragers to a feeder placed on top of a nestbox. After removing the feeder he recorded the foragers' dances as nest site dances, but the dancing bees may have still been responding to the nestbox as a food source rather than a nest site. The fact that we always found a low mean divergence angle in dances for the nestboxes, except the one in which we had placed food, supports this view.

The mean divergence angles that we found for dances advertising nest sites 200–400 m from the swarm are markedly lower than anything reported for dances advertising equidistant food sources in *A. mellifera* (see Fig. 7) and document a previously unknown level of precision in dances for nearby recruitment targets. Our findings contradict the idea that directional imprecision in dances for nearby food sources is merely a result of some physiological constraint associated either with producing dances with short circuit times (hence short waggle runs) or with having only short trips and thus not being able to store an exact flight angle relative to the sun's azimuth, as suggested by Towne (1985) and Edrich (1975). Obviously, the bees are able to produce dances with higher directional precision than is shown in their food source dances.

Signal production and reception

The most likely mechanism underlying the greater precision of dances for nest sites than for food sources is a discrete and adaptive switch in the bees' dance behavior when they cease functioning as forager bees and begin functioning as nest site scouts. It has already been shown that foragers and nest site scouts produce dances that differ in duration (nest site dances generally last far longer; Lindauer 1955) and that the dances of the latter, but not the former, tend to fade over time despite no change in the desirability of the recruitment target (Seeley and Buhrman 1999). Also, the idea of an adaptive switch in the bees' dance behavior is consistent with the fact that bees make other dramatic changes in their behavior as they switch from foraging to nest site scouting. For instance, a worker bee switches from seeking brightly colored, sweet-scented flowers to seeking dimly lit, musty-smelling cavities (Lindauer 1955; Seeley 1977). Alternatively, it is possible that the mechanism for the greater precision of nest site relative to food source dances involves a difference in the way bees orient to nest sites and food sources. For example, perhaps a bee visiting a food source tends to cover a large area as she flies from flower to flower whereas a bee visiting a nest site covers only the area immediately around the nest site. Such a mechanism, however, would not explain why our bees that foraged at a feeder, and so did not cover a large foraging area, produced dances with low precision.

Several puzzles remain regarding the dances that bees perform for nearby targets. First, there is the question of why the angular divergence in dances for nearby nest sites did not fall to zero (though it came close to zero in colony 2 and in colony 4). The reason for this remains unclear. Perhaps the level of precision that we measured in dances for nearby nest sites is the maximum that is adaptive for the bees, given the costs and benefits of producing highly precise dances. It may be, for example, that the divergence angle does not fall to zero in dances for extremely distant (>1 km) food sources. This remains to be determined. Unfortunately, almost nothing is known about the costs and benefits of highly precise dances or how they vary in relation to dance precision. Second, there is the puzzle of the significance (if any) of the fact that bees performing dances for nearby nest sites, but not nearby food sources, are inclined to circle back by more than 360° between waggle runs, thereby performing what we have called 'overshooting dances.' The reason for this also remains unclear.

Our study raises questions about the sending and receiving of information via waggle dances. A full understanding of the precision of communication requires assessing both the precision with which the information is sent and that with which it is received. In this study, we addressed only the sender side, the precision with which a sender codes information in a signal. Very little is known about the receiver side, i.e., the decoding process. From how many waggle runs does a dance follower acquire directional information? How precisely does she perceive the angle of each waggle run? Does she calculate an average angle of the waggle runs she follows? Are there differences in the dance-following behavior of food-collecting bees and house-hunting bees? It is clear that a dance follower typically follows a dancer through several consecutive waggle runs (Mautz 1971; Towne 1985; Bozic and Valentincic 1991; Seeley and Towne 1992). Recent observations suggest, however, that a successful dance follower extracts information only if she positions herself in a 60° arc behind the dancer (Judd 1995; Rohrseitz and Tautz 1999). In this position, a dance follower perhaps uses the orientation of her own body to determine the direction of the waggle run. This may explain why some bees follow many waggle runs whereas others follow only a few; a bee may keep following until she feels that she has achieved a good alignment directly behind the dancer. If this idea is correct, and if a dance follower extracts directional information primarily from just one waggle run, then it could explain why producing waggle runs with greater directional scatter results in the recruits arriving in a more scattered distribution, as found by Towne and Gould (1988). Clearly, further investigations of the mechanisms of dance following are needed to better understand the precision of information transfer from the sender/dancer, to the receiver/dance follower.

In conclusion, we believe that the evidence we present provides strong support for the tuned-error hypothesis of Towne and Gould (1988), that the imprecision in direction indication for nearby food sources is an adaptation to the spatial properties of flower patches, which typically cover considerable areas, not precise points in the environment. It seems reasonable, therefore, to view the angular divergence in dances for nearby food sources as another of the many striking adaptations that enable a honeybee colony to efficiently exploit the kaleidoscope of flower patches found about the hive.

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