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Honey Bee Recruitment: The Dance-Language Controversy

Unambiguous experiments show that honey bees
use an abstract language for communication.

James L. Gould

More than 2000 years ago, Aristotle pondered the phenomenon of honey bee recruitment. He observed that, although a source of food placed near a hive might remain undiscovered for hours or even days, once a single bee had located the food, many new bees soon appeared (1). Aristotle supposed that the bee which found the food and learned its location—the “forager”—led the new bees—“recruits”—to it. It was later shown that if the forager were to be captured on its way back to the food, some recruits still were able to locate the source (2).

By 1920, von Frisch had discovered how to train bees to forage at artificial feeding stations, a technical breakthrough which opened the door to the experimental analysis of honey bee behavior. When von Frisch set out an array of plates near the hive containing various scents, he found that recruits approached only those which contained the odor of the food upon which the forager had been feeding. In an elegant series of experiments, von Frisch demonstrated that odors carried back on the waxy hairs of the forager provide recruits with the information necessary to locate the food (3). Recruits obtain this information by following “dances” which the forager may perform upon its return to the hive.

In the 1940's, however, while working with food sources at greater distances, von Frisch found that recruits arrived only in the vicinity of the forager's station, and not at the scent plates containing the same food odor set out at very different distances and directions (4). At first he supposed that recruits were attracted by the sight, unique hive odor, or the assembly pheromone of the foragers (or all three). This latter odor, produced by a specialized scent gland in the abdomen, had long been known to attract bees. Because recruits continued to arrive preferentially at or near the forager station even at distances

of 300 meters, and when the wind carried odors away from the hive, von Frisch concluded that recruits must be provided with other cues, either in the hive or in the field. As a control, he sealed the pheromone-producing scent gland of each of his foragers with shellac, but still most recruits arrived at or near the forager station.

When he observed the behavior of foragers in the hive, von Frisch discovered that the tempo of the dances decreased as the food was moved farther and farther away from the hive, while the orientation of the “waggle run” phase of the dance (relative to gravity in the absence of light on the vertical combs) corresponded to the direction of the food source with respect to the sun. When the food source was moved very close to the hive, on the other hand, a “round” dance was observed, containing neither distance nor direction correlations (4).

The dance-language hypothesis which grew out of these observations proposes that recruit bees use the symbolic information in the dances as a guide to the approximate location of the food, and then use the odor information—that on the body of the dancing forager as well as odors left by foragers in the field—and visual information to locate the source exactly.

Objections to the Hypothesis

In 1967, Wenner and Johnson challenged the evidence supporting the dance-language hypothesis, and proposed that recruitment is accomplished solely on the basis of odor information. They repeated von Frisch's experiments with certain modifications, but found that when forager odor was provided at all scent plates, the preference for the vicinity of the actual forager station disappeared (5). They challenged many of the more unguardedly en-

thusiastic statements about recruitment [for example, that recruits fly “rapidly and with certainty” to the food (6, p. 57)] as being without experimental foundation.

In response to the challenge, von Frisch reiterated his opinion that the olfaction hypothesis was unlikely and cited two of his own experiments as further evidence (7). In one series of “detour” experiments (6, pp. 173–182), recruits had successfully located a food source on the other side of an obstacle (in one case a 12-story building) which foragers had been trained to fly around. Because some recruits were observed flying over the center of the obstacle, von Frisch concluded that they must have “known” where to go.

In another experiment (6, pp. 153–156) foragers had been trained to a station in one direction, while scent plates were set out at various distances in four directions. The hive was laid flat in the morning so that the dances were performed on a horizontal surface. Under these circumstances the dances were disoriented (although the distance correlation was preserved). Recruits in the morning displayed no preference for either the correct distance or the correct direction. The hive was restored to its normal position in the afternoon, and the dances became oriented. After a time, recruits began to arrive preferentially at scent plates near the forager station. As is discussed below, neither approach is immune to criticism (8).

Experiments to Control for Forager Odor

The work of Wenner and his colleagues stimulated new research designed to investigate recruit behavior more closely (9). Gould *et al.* (10, 11) and Lindauer (12) devised similar techniques to control for forager odors. They trained groups of foragers in two different directions, then fed one group a concentrated sugar solution and the other a dilute solution. Both solutions contained the same odor. In the hive, only foragers collecting the more concentrated food danced. Since the food odors and bee odors were the same at both stations, only the dance information might be thought to distinguish them. If recruits used the symbolic information, they would be expected to show a preference for the station with the more concentrated sucrose. In fact, they did just that (13).

Esch and Bastian (14), Gould *et al.* (11), and Mautz (15) sought to follow the behavior of individual recruits. Each found that

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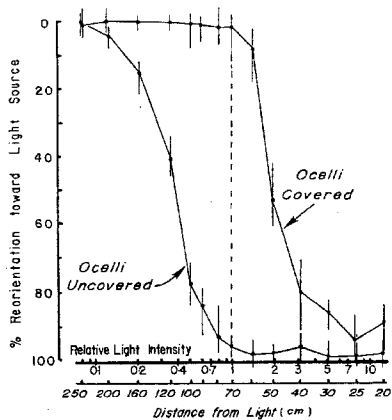


Fig. 1. Dance reorientation to light. The dance orientations of foragers were unaffected by a distant light source. When the source was moved closer, thereby increasing its apparent brightness (illumination), the dance directions shifted until they were oriented completely with respect to the light rather than to gravity. Further increases in brightness were without effect. Bees whose ocelli had been covered also reoriented their dances, but only when the light was much brighter. At an intermediate level (dashed line), the dances of normal bees were completely reoriented, while those of the ocelli-painted foragers were unaffected. Virtually all bees in each group were reoriented to the same degree (the bars indicate the scatter about the average). About 20 dances were measured for each point.

recruits locate the food neither quickly nor reliably. Instead, recruits typically observe a single dance for about six cycles, fly out for about 6 minutes, return and attend another dance, fly out again, and so on. In the end, only about half of the recruits located the single food sources (situated 120 to 400 m away—in theory only 19 to 57 seconds flying time away).

Locale Odor

About the same time, Wenner and his colleagues began to gather evidence that odors specific to the location of the food (as well as the odors of the food itself) are important (16). Hence, if recruits know the "olfactory landscape," site-specific odors would provide information about the location of the food. Needless to say, distinguishing between recruits that are supposed to be using site-odor information rather than dance-language information would be difficult. The predictions of the two theories are virtually identical. Of course, they are not mutually exclusive—recruits could, in theory at least, use both sorts of information.

Excepting the experiments reported here, the locale-odor hypothesis can effectively account for all the results achieved to date without recourse to the dance-lan-

guage theory. Even the clever experiment discussed above, in which the hive was first placed on its side and then returned to its normal orientation, can be disposed of in this way (17). Indeed, in similar experiments by New and New and by Wells and Wenner, recruits found the food source whether the dances were correctly oriented or not (18). Presumably bees could have been using site odor in these cases.

Evolutionary Argument

It has been argued that the dance correlations *must* be useful, or they would not exist; that is, evolution would not have selected for a nonfunctional behavior (12, 19). This argument depends on our belief that all behavior that seems somehow "special" is functional to the animal and is open to direct selection. It further supposes that we can correctly guess the function the behavior serves. This same proposition was put forward in a preevolutionary context by Leibniz, and effectively and entertainingly countered by Voltaire in *Candide*. In the present circumstances it seems reasonable to remain cautious, lest we glibly explain away phenomena and inhibit research. There can be no doubt that evolutionary considerations can suggest ingenious theories, but those theories must be tested if ethology is to remain an experimental science.

In the case of the dance language, the evolutionary argument appears particularly persuasive. But if every special behavior must have a "purpose," what can be the purpose of the oriented "dances" of flies? What is the function of the distance correlations of the lateral movements of moths, or of the buzzing runs of stingless bees? What is the adaptive value of the transformation of angles flown or walked with respect to the sun into angles with respect to gravity, as is observed in ants, bees, beetles, spiders, and so on? In each case there is no evidence that the function is communication (20). If there is a "purpose," we must not yet know it; and that same unknown function could presumably explain the dance correlations as well. If there is *no* adaptive value to these behaviors, then the dance correlations need have none either. In the search for certainty, evolutionary arguments unaccompanied by critical experiments leave much to be desired.

Misdirection Experiments

The results not only of Wenner and his colleagues, but those of experimenters stimulated by the controversy, suggest

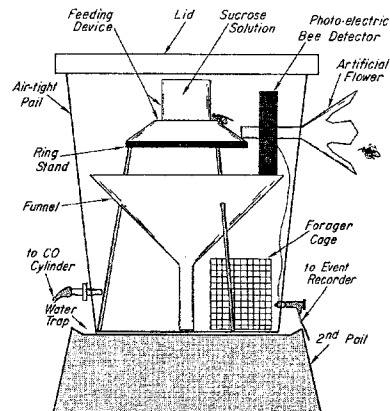


Fig. 2. A recruit station. The station was constructed from an airtight plastic pail. A decoy bee was placed in the artificial flower to induce landing. The "flower," fashioned from a plastic funnel, was painted to appear dark in the center and light on the edge under ultraviolet light. A wire cage of anesthetized foragers located in the station served as a source of bee odors. When a recruit entered a station, it interrupted a beam of red light, causing a photoelectric circuit to signal an event recorder, thereby registering the arrival. As the bee continued in, it came upon a feeding device offering a sucrose solution with the experimental scent. The station was filled with carbon monoxide so that while the recruit fed, it became anesthetized and tumbled off the inclined feeding device into a funnel. The stations stood on the water-filled bottoms of larger pails. The water helped to prevent ants from entering the stations. The pails were about 40 centimeters tall.

that, at the very least, odors may affect the speed and accuracy of recruits. An unambiguous experiment might be one in which the symbolic information in the dance would indicate a specific location well away from the place actually being visited by the dancer. One way in which to accomplish this might be to construct a model bee whose dance parameters would be under the control of the experimenter. Progress on this front has been substantial, but this important technique has yet to be perfected (10, 21). Another way would be to cause the dancer to "lie"—to orient its dances to one parameter while recruits would be orienting their "interpretations" to another.

Under some circumstances, honey bees seem to interpret a bright light as the sun, and will orient their dances to it rather than to gravity (6, pp. 135–137, 196–203). (Under certain natural conditions such as swarming, dancing bees regularly substitute sun orientation for gravity orientation.) Since both dancers and dance attenders are reoriented, no misdirection of recruits occurs (6, pp. 203–204). When the ocelli, the three simple eyes located between the compound eyes, are covered, bees become six times less sensitive to

light. They require higher light levels to fly or display phototaxis, but are still capable of foraging and dancing (22). When a light is made bright enough to reorient the dances of normal bees, the dances of ocelli-covered foragers are unaffected (Fig. 1). Only when the light is made still brighter do these treated bees begin to reorient their dances from gravity to light.

Using a light intensity just bright enough to reorient the dances (and dance interpretations) of normal bees, but not sufficient to affect the ocelli-covered bees, it should be possible, assuming that recruits use the dance correlations, to "misdirect" untreated recruits. For example, if the food were in the direction of the sun, forager dances would normally be pointed up on the comb. A bright light 90° to the left of vertical, on the other hand, would cause normal dances to be directed 90° to the left, toward the artificial sun. Ocelli-covered foragers, however, would not be reoriented, and would continue to perform dances pointing up. If the dance information is used, untreated recruits attending these dances would be expected to interpret the dance directions as being 90° to the right of the artificial sun, and hence 90° to the right of the sun in the field. If, on the other hand, recruits rely solely on odor cues, they would be expected to ignore the dance direction and proceed to the forager station on the basis of odor cues.

Experimental Procedures

Two groups of 10 to 15 foragers were trained in each experiment on orange-scented 0.5M sucrose with the use of the Gary and Witherell improvement (23) of von Frisch's technique (6, pp. 17-20). The first group served as a control to measure the degree of reorientation of the dances to light. The ocelli of the foragers in the second group were covered with flat-black enamel paint. Dances of foragers in this second group were monitored, and any that showed some degree of reorientation to the light were eliminated. The light was left on and in the vertical ("up") position for 30 minutes before the experiment began, to adapt the bees to its presence. (Since, in the absence of light, bees orient with respect to vertical, placing a bright light in that same direction does not affect the dances.)

The light was a 650-watt quartz movie light with reflector. To prevent the hive from overheating, an infrared-absorbing filter mounted in an asbestos mask was placed just in front of the light for shielding. The Plexiglas covering the hive acted as a sharp ultraviolet filter for wavelengths shorter than 340 nanometers. The light was directed onto the only dance area eas-

ily accessible to returning foragers. Since the light was a finite distance away, dancers on opposite edges of this area saw the light at slightly different angles. The distribution of 100 dances was plotted, and from that the mean parallax error was calculated to be 1.14°.

Another minor source of error arose from the phenomenon known as "residual misdirection." Foragers returning from

the field regularly make slight errors in transposing the flight angle into a dance angle (6, pp. 204-217). Oddly enough, this effect disappears when the earth's magnetic field is canceled in the vicinity of the hive (24). In the 400-m direction experiments reported here, the angle of the light was corrected periodically to allow for this effect. (The metal shed in which the hive was located provides substantial shielding from the earth's magnetic field.) Later measurements from video tapes of the dancing revealed that the mean uncorrected error from this source was about 0.8°. The mean total error from both parallax and residual misdirection was of the order of 1.4°.

The observation hive was one frame (comb) thick and three frames high. It contained approximately 8000 Italian bees. The colony was not allowed to accumulate stores of food—a procedure which served to facilitate training and to enhance the tendency to dance.

When the experiments began, the solution at the control station was changed to anise-scented 1M sucrose (25). Hence the foragers at this station began to dance occasionally. The solution at the ocelli-treated forager station was switched to 2M sucrose containing the experimental scent. These bees began dancing vigorously. The light was moved to the appropriate position, and six recruit stations nearly identical to the forager station were opened.

The recruit stations were conceptually similar to ones designed by Renner (26). They were constructed from airtight plastic pails (Fig. 2). Entering recruits passed through a beam of red light shining on an array of photodiodes. (Bees do not react to red light.) The resulting signal was amplified and transmitted to an event recorder. Thus, the arrival time and location of each arriving bee was automatically registered for later analysis.

In order to attract recruits, it was necessary to bait the stations with food containing the experimental scent, and with a cage of six anesthetized, ocelli-treated foragers to provide bee odors. To provide visual landing encouragement, the station was equipped with a "flower" fashioned from a plastic funnel which was cut and painted to present the appropriate pattern when viewed under ultraviolet light (6, pp. 481-491; 27) and onto which was glued the body of a sun-dried, alcohol-extracted bee. To prevent recruits from returning to the hive where they might dance and indicate the locations of the stations, each recruit station was filled with carbon monoxide. Entering recruits generally fed for about 30 seconds before becoming completely anesthetized, tumbling off the inclined feeding platform into the funnel below.

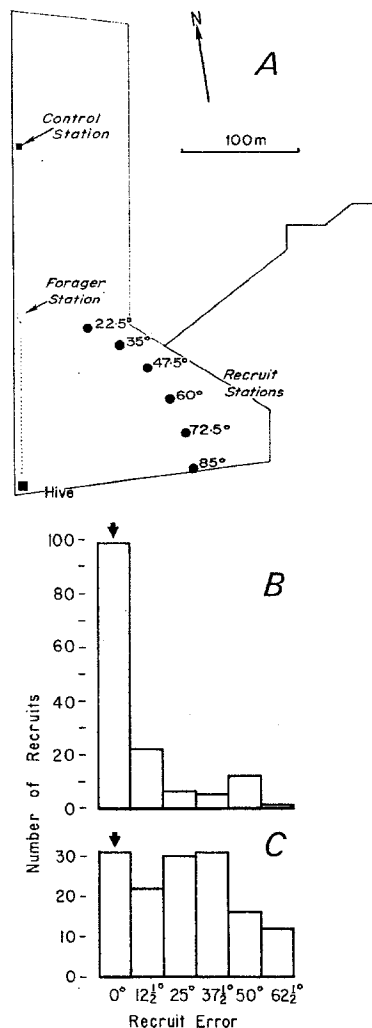


Fig. 3. Direction experiments at 150 meters. The array (A) consisted of recruit stations set out at 12½° intervals as shown. Ocelli-treated foragers were trained to the forager station, while untreated foragers were trained to the control station. The results of two misdirection experiments (Table 1, experiments A and B) have been combined to summarize the recruit distribution (B). The left bar—indicated by the arrow—represents the station specified by the dancing, while the bars to its right represent the averages for single stations at various distances. When the experiment was repeated using Wener's training technique, quite a different distribution was obtained (C). The data for two experiments (Table 1, experiments C and D) are summarized.

Table 1. Direction experiments at 150 meters. Asterisks indicate the station signaled by the dancing. Experiments A and B are summarized in Fig. 3B. Experiment A was performed on 28 June 1974. The experimental scent was peppermint. The wind was from 001° at 4.2 miles per hour. The sky was cloudy, the barometric pressure was 771.6 mm-Hg, the relative humidity was 63 percent, and the temperature was 21°C. Experiment B was performed on 16 July with geranium scent. The wind was from 032° at 2.9 miles per hour. The sky was clear, the pressure was 770.8 mm-Hg, the humidity was 66 percent, and the temperature was 22°C. Experiments C and D (Wenner controls) are summarized in Fig. 3C. Experiment C was performed on 10 August with rose scent. The wind was from 191° at 0.9 mile per hour. The sky was clear, the pressure was 752.7 mm-Hg, the humidity was 61 percent, and the temperature was 22°C. Experiment D was performed on 11 August with rosemary scent. The wind was from 358° at 3.4 miles per hour. The sky was clear, the pressure was 772.7 mm-Hg, the humidity was 67 percent, and the temperature was 23°C.

Experiment	Period (min)	Forager visits	Forager dances	Recruit arrivals						
				FS	22½°	35°	47½°	60°	72½°	85°
A	30	92	70	4	1	0	1	0	5	19*
	30	98	99	7	7	31*	7	0	3	12
	30	90	83	3	0	11	6	28*	3	1
B	30	60	27	3	0	0	0	1	10*	3
	30	59	49	8	3	10*	4	0	1	0
C	30	52	29	19	5	6	9	14	8	13*
	30	52	36	22	18*	14	16	22	10	7
D	30	60	39	22	11*	8	14	15	7	6
	30	52	36	22	12	18	32	27	12	18*

The order of arrival of recruits at each station was preserved in the order of anesthetized bees in the neck of the funnel. This made it possible to edit the event recorder data accurately on the rare occasions when a fly or small bumble bee was found in the station. At the end of each experiment, the number of anesthetized recruits in each station was compared with the number of "events" registered by the recorder for that station. The numbers always corresponded.

Recruits arriving at the ocelli-treated forager station were captured manually by a technique which precluded the release of alarm odor (11). The dancing in the hive was recorded on video tape for later analy-

sis. Wind speed and direction were recorded continuously with a calibrated Taylor "Windscope" interfaced to two Rustrak recorders. Wet- and dry-bulb temperatures were continuously recorded in the corner of the video field by a Heath two-channel digital thermometer. A Heath digital clock recorded the time in the same manner. Sky conditions and barometric pressure were recorded manually at 10-minute intervals.

At the end of each experiment the forager food was removed and the light was returned to the "up" position. After about 10 minutes, the recruit stations were closed.

The experiments were performed on a relatively flat, mowed field at the Rockefel-

er University Center for Field Research, Millbrook, New York. The field (Fig. 3A) was bordered on most sides by forest, but beyond the boundary line marked to the northeast, it fell away into an unmowed, grassy valley. Experiments were generally performed in the early morning while the heavy dew typical of this region remained on the ground. Good results could be obtained while the vegetation remained wet, presumably because competition from natural food sources was minimal. The hive was located in a small metal shed in the southwest corner of the field.

Is Direction Communicated?

Control foragers were trained to the control station 300 m north of the hive. Ocelli-painted foragers were trained to the forager station 150 m north of the hive. Six recruit stations were set out 150 m from the hive at 12½° intervals as indicated in Fig. 3A. In the first experiment, the light shining on the hive was moved every 30 minutes, first to 85° left of vertical, then to 35° left, and finally to 60° left. In each case, recruits favored the recruit station in the direction indicated by the dance in preference to recruit stations located in other directions (as well as to the forager station itself) (Table 1, experiment A). The same results were obtained when the experiment was repeated (Table 1, experiment B). In this case, the light was again moved every 30 minutes, first to 72½° left, then to 35° left (Fig. 3B).

When recruits were presented with odor information for one location—the forager station—and abstract dance information for another—a particular station in the recruit array—they flew to the station specified by the dance correlations. Hence, recruits must be able to use the symbolic direction information in the dance. Analogous results were obtained using distance arrays (28).

Recruit Accuracy

In the 150-m direction experiments, the mean recruit error was 11.9° (31 m). In order to judge the accuracy of recruits at greater distances, the recruit stations were set out 400 m from the hive at 3° intervals (Fig. 4A). The ocelli-treated forager station and control station were established along a line to the northeast at 500 and 400 m, respectively. In the first experiment the light was moved to 42° to the right of vertical for 40 minutes, and then to 33° to the right for another 40 minutes (Table 2, experiment A). In the second experiment the procedure was reversed, with the light first

Table 2. Direction experiments at 390 to 400 meters. Asterisks indicate the station signaled by the dancing. In experiments C and D the daggers indicate the direction of the forager station. Experiments A and B are summarized in Fig. 4B. Experiment A was performed on 31 July 1974. The experimental scent was rose. The wind was from 171° at 2.9 miles per hour. The sky was clear, the barometric pressure was 765.3 mm-Hg, the relative humidity was 71 percent, and the temperature was 28°C. Experiment B was performed on 1 August with rosemary scent. The wind was from 167° at 2.3 miles per hour. The sky was clear, the pressure was 766.5 mm-Hg, the humidity was 67 percent, and the temperature was 25°C. The results of experiments C and D are shown in Fig. 4, C and D. Experiment C was performed on 2 August with sassafras scent. The wind was from 037° at 0.6 mile per hour. The sky was hazy, the pressure was 768.3 mm-Hg, the humidity was 69 percent, and the temperature was 27°C. Experiment D was performed on 4 August with ilang-ilang scent. The wind was from 006° at 1.1 miles per hour. The sky was partly cloudy, the pressure was 766.6 mm-Hg, the humidity was 76 percent, and the temperature was 29°C. Abbreviation: FS, forager station.

Experiment	Period (min)	Forager visits	Forager dances	Recruit arrivals						
				FS	45°	42°	39°	36°	33°	30°
A	40	89	69	12	16	19*	8	5	6	3
	40	83	66	9	4	4	5	11	16*	12
B	40	104	76	5	5	2	4	8	12*	13
	40	111	87	1	16	16*	10	2	4	1
C	30	75	45	33*†	8	15	31*†	10	10	6
	30	76	47	55*†	11	18	46*†	19	10	8
D	50	95	80	82†	30*	24	12	15	34	68†

at 33° right for 40 minutes, and then at 42° right for the same period (Table 2, experiment B). In all cases, recruits favored the end of the array indicated by the dancing (Fig. 4B).

In the 400-m direction experiments, the mean recruit error was 4.2° (29 m). The smaller angular error for 400 m is consistent with von Frisch's results, as well as with the observation that the scatter of direction indications between cycles of individual dances is smaller at 400 m. Why the dance scatter should be so large at short distances, but small at large distances is another question (29).

Wenner's Techniques

When Wenner and his colleagues perform their experiments, they obtain quite different results. A number of factors might be responsible for this disparity. Von Frisch suggested (7) that Wenner's training technique might be the cause. Wenner trains his bees on a concentrated sucrose solution containing the scent which will later be used during the experiment (30). Virtually all other experimenters use a dilute solution with either no scent, or a scent other than the one to be used later. With Wenner's technique the foragers dance throughout training, and recruits are constantly being captured at the forager station. When techniques with less concentrated solutions are used, however, little or no dancing and recruitment occur. With Wenner's technique, the hive accumulates stores of solution containing the experimental scent for hours or even days before the experiment begins. The other technique does not result in any accumulation of experimental odor.

To test the effects of Wenner's techniques, the 150-m direction experiments were repeated after foragers were trained on a 2*M* sugar solution containing the experimental scent. In the first experiment the light was first placed 85° to the left of vertical for 30 minutes, then moved to 22½° left for the same period (Table 1, experiment C). In the second experiment, the procedure was reversed (Table 1, experiment D).

In both cases recruits showed virtually no preference for the direction indicated by the dances (Fig. 3C); the mean error was 29° (77 m). This result might be due, as von Frisch suggests (7), to recruits becoming lost while the forager station is being moved rapidly away from the hive during training; or, as Free implies (31) and von Frisch had shown earlier (6, pp. 23, 33-34, 257-264), the results might be due to recruitment to a prevailing food odor in the hive. In any case, a small change in experi-

mental technique seems sufficient to switch recruitment from a largely dance-directed form to a largely odor-directed one. Apparently honey bees are sufficiently complex to find food by more than one strategy.

Von Frisch's Techniques

From analyzing dance films, von Frisch and Jander (32) were able to calculate that a recruit would have to receive and use without error the information from five to six dance cycles in order to account for the accuracy inferred from von Frisch's famous step and fan experiments (6, pp. 84-96, 156-163). As von Frisch points out, "bees are not computers that work without making mistakes" (6, p. 108). Since recruits typically follow individual dances

for about six cycles, von Frisch concluded that they must follow two or more different dances and average the information. Since recruits follow only one dance before flying out in most cases (14, 15), Lindauer proposed that bees must be able to average dances separated by many minutes (12). Another possibility, of course, is that the step and fan data do not represent precise measures of recruit accuracy.

Von Frisch did not capture recruits that approached his scent plates. Hence, a recruit could be counted any number of times (until, that is, it landed at the forager station and was killed). In order to examine the possible effects of von Frisch's techniques, my recruit stations were modified to prevent recruits from feeding on the scented food, and to allow them to escape through the top of the station. Hence, recruits could be counted more than once. The stations contained no cage of anesthetized foragers to provide bee odors. As always, recruits arriving at the ocelli-treated forager station were captured.

The recruit stations were again set out at the north end of the field, 390 m from the hive at 3° intervals (Fig. 4A). This time, however, the forager station was placed near the array as it had been in von Frisch's work. In the first experiment the forager station was placed 20 m beyond the 39° station, while the control station was placed 50 m farther out, along the same line. The experiment lasted for 60 minutes, and during this time the light was in the "up" position. Under these circumstances, no misdirection of recruits would be expected. Just as von Frisch found in his fan experiments, recruits favored the station indicated by the dancing—that is, the station immediately in front of the forager station (Fig. 4C). The mean error was not as large as in the 400-m direction experi-

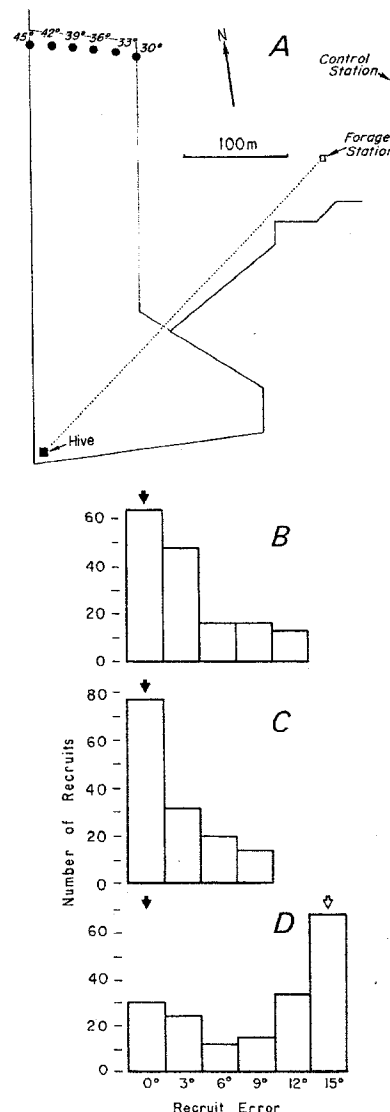


Fig. 4. Thirty-nine direction experiments at 390 to 400 meters. The array (A) consisted of recruit stations set out at 3° intervals as shown. In the misdirection experiments, the ocelli-treated forager station and control station were set out as illustrated. The data from two experiments (Table 2, experiments A and B) were combined to summarize the recruit distribution (B). The left bar—indicated by the arrow—represents the station specified by the dancing, while the bars to its right represent the averages for single stations at various distances away. In the two von Frisch controls, the forager station was moved near the array, and the control station was placed 50 m beyond it. In the first control (Table 2, experiment C), the forager station was 20 m behind the 39° station. The recruits displayed a stronger preference than before for the "correct" direction (C). In the second control, the forager station was placed 20 m behind the 30° station, but the dances indicated the 45° station. Recruits preferred both the indicated station (solid arrow in D) and the one near the forager station (open arrow).

ments: 3.3° instead of 4.2° (22 m versus 29 m).

In order to examine more closely the effect of having the forager station near the array, I performed a second experiment. In this case the forager station was placed 20 m beyond the 33° station—the most easterly in the array. The control station was placed 50 m beyond the forager station. The light was moved to 15° right of vertical in order to direct recruits to the station at the other end of the array—the 45° station in Fig. 4A. The experiment lasted 50 minutes. Recruits favored *both* ends of the array—not only the station indicated by the dancing, but also the one near the forager station (Fig. 4D and Table 2, experiment D).

Taken together, these experiments suggest that von Frisch's techniques can affect the observed distribution of recruits, exaggerating the apparent accuracy. If recruits are not as accurate as the step and fan experiments suggest, then von Frisch's conclusion that recruits must average separate dances may not be correct. If recruits were to attend more than one dance, averaging the information for a more precise estimate of distance and direction, then these recruits would average the directions of separate dances; and, since the second dance is attended only after an unsuccessful flight, recruits should take quite some time to locate the food. Both predictions were tested experimentally.

Dance Integration?

Lindauer proposed that recruits might average—"integrate" in his terminology—two or more dances to separate targets. This hypothesis gives rise to testable expectations. If one station at the end of a direction array were being signaled, recruits would receive information for only that one direction regardless of how many dances they attended. If two olfactorally identical stations at opposite ends of the array were being signaled by similar numbers of dances, and recruits attended only one dance each, then the distribution of recruits in the array would be composed of two *separate* single-station distributions—one the mirror image of the other—summed across the array. If, however, recruits arrived after attending two dances each, averaging the information from both, quite a different distribution would be expected. The chance of following two dances to one particular station would be 0.25, while the chance of attending one dance to each station would be 0.50. The overall recruit distribution in this case would be the sum of three distributions—one about each end station, and a third,

with twice as many bees, about the center of the array.

This intriguing prediction was tested with the use of the array pictured in Fig. 5A. The five recruit stations were set out at 7½° intervals. Two stations of ocelli-treated foragers were established to the north. The light was placed 58° to the left of vertical, thereby directing recruits to the 58° station. The distribution of recruit arrivals in this part of the experiment was

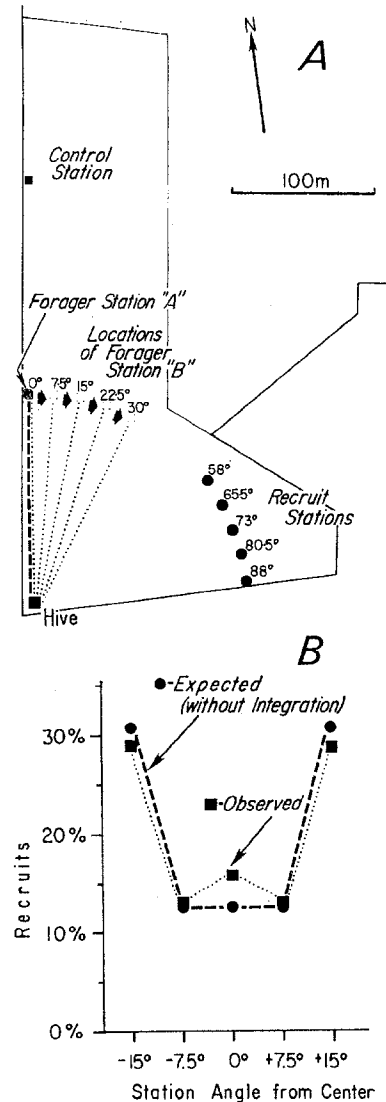


Fig. 5. Integration experiments. The array (A) consisted of recruit stations set out at 7½° intervals as shown. Two ocelli-treated forager stations were set out. One forager station (A) was always to the north, while the other (B) was moved to the various positions indicated. The data, when the dancing by both groups of foragers indicated the same end of the array, was used to predict the distribution if no integration of separate dances was taking place. This model and the results when both ends of the array were being signaled simultaneously are compared (B).

taken as a measure of recruit accuracy (Table 3). After 20 minutes in the first experiment and 30 minutes in the second, one of the two ocelli-treated forager stations was moved 7½° to the right every 10 minutes until it reached a point 30° to the right of the other ocelli-treated forager station. At this stage, dances in the hive indicated both the 58° and 88° stations. This part of the experiment lasted 40 minutes. Recruits favored both ends of the array (Table 3).

If any integration of the two dance directions was taking place, more recruits would be expected at the center stations than would be predicted on the basis of normal recruit error alone. By taking the data when only one end station was being indicated (and, hence, no integration could be occurring), and adding it to its "mirror image," a model was generated for recruit distribution when both end stations are being indicated simultaneously, but *no* integration is taking place. By comparing the actual results with the model, the prediction was tested (Fig. 5). Under these conditions, little averaging of separate dances appears to have taken place.

Recruit Search Times

How can it be that in these experiments recruits did not integrate separate dances, while in the experiments of Esch and Bastian (14), Gould *et al.* (11), and Mautz (15), recruits were often observed to attend several different dances before being captured at the forager station? The critical difference between their experiments and mine cited above lies in the fact that they used single isolated food sources, whereas my experiments and von Frisch's step and fan experiments used wide arrays. With an array, perhaps even a recruit with relatively inaccurate information is likely to arrive near *some* station, whereas the same recruit searching far from the single forager station offered in other experiments (14, 15) might not find it and return to the hive to attend another dance. If this is true, recruits in array experiments should take considerably less time to find a station than the 15 minutes required by recruits in the single-station experiments (14, 15).

To test this prediction, I examined the change in recruit arrival rates. When the light was moved, recruits were instantaneously presented with dances indicating a new target. The time course over which recruit arrivals at the newly indicated station increased and arrivals at the formerly indicated station decreased provides a measure of recruit search dynamics. The combined data for six experiments are presented in Fig. 6 (33). The simple model shown in the inset fits the data fairly well. This

model supposes that a constant number of recruits were dispatched from the hive during each minute of dancing, but that individual recruits took varying amounts of time to reach the station. The average time of 6 minutes indicated by the data agrees well with the results of Mautz (15) and Esch and Bastian (14) for the duration of successful flights. Again, recruits presented with an array rather than a single station seem to arrive with neither the need nor the opportunity of averaging multiple dances (34).

As was mentioned above, von Frisch discovered that his recruits in the step and fan experiments performed too well to have attended only a single dance. Either von Frisch's recruits attended additional dances, or the accuracy which he measured was an artifact of his experimental technique. The second alternative is far more likely since, as demonstrated above, recruits in array experiments attend only *one* dance, and von Frisch's techniques *do* artificially enhance recruit accuracy.

Do Recruits Make Mistakes?

Since the data from the experiments reported here represent recruit accuracy after attending only a single dance and with the forager station well away from the array, and since the scatter of forager dances may be measured directly from video recordings, it is possible to estimate how much error is introduced into the system by recruits using the dance information. The data from the 150-m direction experiments have been used for the following calculations since the dance scatter is larger, and therefore easier to measure, at shorter distances.

The mean scatter, averaged over six dance cycles (as we suppose recruits to be doing) was about 8.1 percent. The mean total recruit scatter was about 11.9 percent. Since recruit errors may cancel dance errors, it is appropriate to use the sum-of-the-squares method to calculate the mean total recruit error. With this technique, recruit error over and above the error in the dance was 8.8 percent. Thus, von Frisch's intuitive prediction that recruits must also contribute errors seems to be confirmed. In his step and fan experiments, the presence of the forager station in the array combined with the nature of his recruit stations probably served to "focus" the recruit distribution.

On the basis of these data, the general form of recruit distributions may be represented as

$$\frac{1}{2\pi} \exp[-\frac{1}{2}(x^2 + y^2)]$$

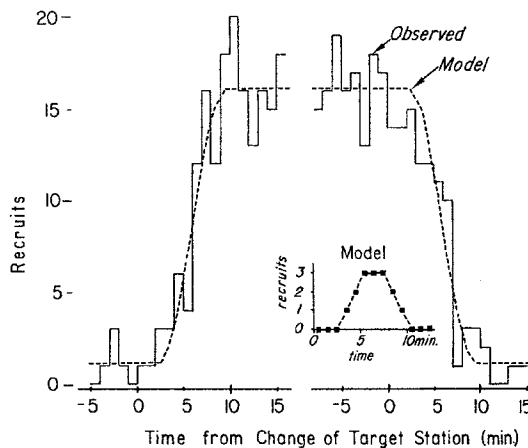


Fig. 6. Recruit search times. The number of recruits arriving at various times before and after a new station was signaled (at 0 minute) is shown at left. Before the station was indicated, a background level of recruitment can be observed. Recruitment reaches a maximum after about 10 minutes of dancing. The situation when the station is no longer signaled is illustrated at right. (The dancing to the station stops at 0 minute.) Recruitment continues for a time, then falls off to a background level. The inset depicts a simple model of recruit search-time scatter for bees sent out during each minute of dancing. The model matches the data fairly well.

where x and y are the distances from the target. The y -axis may be taken to be along the line from the hive to the target, so that $y = 1$ for 1 standard deviation (S.D.) of recruit distance scatter (or approximately $1/2\sqrt{2}$ of the S.D. of the scatter of six-cycle averages of the distance correlations in the dance). The x -axis may be taken as the horizontal line orthogonal to the y -axis, where $x = 1$ for 1 S.D. in direction scatter of arriving recruits (or approximately $1/2\sqrt{2}$ of the S.D. of direction scatter averaged over six cycles of the dance; minor corrections must be made since the target is only a finite distance away from the hive). Distance and direction scatter in the dance vary independently, giving rise to the prediction that recruits should in general be distributed about the target in an ellipse, whose major axis should be along the x -axis near the hive, along the y -axis at intermediate distances, and along the x -axis again at still greater distances. Although my data tend to support this prediction, the wind must be taken into account in any attempt to describe recruitment more pre-

cisely. The odors for which recruits are searching are presumably moved about and distributed in the field depending on wind direction and speed (35). Two-dimensional arrays might be useful in this regard, but for a complete description of recruit behavior the path taken by individual recruits as they get from the hive to the food must be directly determined.

Conclusions

Depending upon conditions, honey bee recruits use either the dance language *and* odor information, or odors alone. Wenner's conclusion that "one cannot have it both ways" (36)—that bees can have only one strategy for recruitment which they must use under all circumstances—is clearly incorrect. On the other hand, recruitment to odors alone might be the usual system in honey bee colonies not under stress. (Even in these experiments, a substantial number of recruits arrived at the forager station, presumably without having used

Table 3. Integration experiments. Each asterisk indicates a station signaled by one group of foragers. Figure 5B summarizes the data. Experiment A was performed on 8 August 1974 with jasmine as the experimental scent. The wind was from 003° at 2.8 miles per hour. The sky was partly cloudy, the barometric pressure was 769.5 mm-Hg, the relative humidity was 76 percent, and the temperature was 24°C. Experiment B was performed on 9 August with lavender scent. The wind was from 004° at 4.6 miles per hour. The sky was partly cloudy, the pressure was 768.5 mm-Hg, the humidity was 80 percent, and the temperature was 23°C.

Experiment	Period (min)	Forager visits		Recruit arrivals				
		A	B	58°	65½°	73°	80½°	88°
A	20	13	18	19**	10	6	1	2
	10	8	10	8*	6*	3	2	0
	10	7	12	5*	5	3*	2	2
	10	10	10	6*	1	4	4*	1
	40	44	41	21*	13	12	9	25*
B	30	17	16	18**	4	2	1	0
	10	11	9	8*	3*	2	1	1
	10	14	15	6*	5	3*	0	0
	10	9	15	3*	1	4	4*	1
	40	38	37	21*	9	12	10	21*

the dance information.) For example, when a single, abundant, and (presumably) extensive crop is available, the odor of that source in the hive might grow strong enough to eliminate dance-language recruitment. However, even in the early stages (just after the food is first located), the dance language would be necessary to alert foragers to the new source.

By their very different training techniques, von Frisch and Wenner may have been sampling two stages of the same process: exploitation of an abundant food source. Von Frisch's experiments could be seen as examining the early phase, while Wenner's would be exploring a later phase.

The inherently "spectacular" nature of the dance language may have helped to emphasize it out of proportion to its actual place in the ecology and dynamics of foraging. Alternatively, single, abundant, extensive food sources may be more typical of current agricultural practices than of the tropical forests in which the honey bee and its language evolved. In that case, the ability to direct recruits to a distant, isolated patch of food quickly—either before it was found by another colony or another species, or before the potentially brief blooming period ended—might have been a real advantage. Only further work can establish whether the dance-language communication is common or rare under normal circumstances. Even a rare phenomenon may still be real, however, and the dance language is a real and very significant phenomenon indeed.

Some of the resistance to the idea that honey bees possess a symbolic language seems to have arisen from a conviction that "lower" animals, and insects in particular, are too small and phylogenetically remote to be capable of "complex" behavior. There is perhaps a feeling of incongruity in that the honey bee language is symbolic and abstract, and, in terms of information capacity at least, second only to human language (37). Despite expectations, however, animals continue to be more complex than had been thought, or than experimenters may have been prepared to discover (38). Especially in ethology, it is difficult to avoid the unprofitable extremes of blinding skepticism and crippling romanticism.

References and Notes

1. Aristotle, *History of Animals*, book IX, chapter 40.
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5. A. M. Wenner, *Science* 155, 847 (1967); D. L. Johnson, *ibid.*, p. 844.
6. K. von Frisch, *The Dance Language and Orientation of Bees* (Harvard Univ. Press, Cambridge, Mass., 1967).
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8. Although considered conclusive by some, the study by R. Boch [*Z. Vgl. Physiol.* 40, 289 (1957)] is not cited by von Frisch. This experiment sought to take advantage of "dialects" in the distance correlations. Two races of bees with different distance dialects were mixed in a hive. When foragers of one race danced, recruits of the other race would have been expected to misinterpret the information and fly either too far or not far enough, depending on which race had the quicker dance tempo at that distance. Two scent plates were set out—one between the hive and the forager station, and the other one beyond. In all, 644 recruits arrived at the station predicted on the basis of differences in racial dialects while 667 arrived at the other station. When compared to the distribution of recruits of the foragers' own race, however, a slight tendency in the expected direction may be computed.
9. Another little-known study, again considered conclusive by some, is pointedly ignored by von Frisch and colleagues—perhaps with good reason. L. S. Gonçalves [*J. Apic. Res.* 8, 113 (1969)] sought to take advantage of A. R. Bisetzky's discovery [*Z. Vgl. Physiol.* 40, 264 (1957)] that foragers trained to walk to a food source perform dances whose tempos are appropriate for far greater distances. If the dance language were used, recruits would be expected to fly to scent plates beyond the forager station, but in the same direction. Gonçalves arranged a circle of scent plates around a hive, and forced his foragers to walk through a short tube to their station. Although most recruits flew to the forager station, the remaining bees showed some preference for the scent plates in the "correct" direction. Both Bisetzky and Gonçalves used the Italian race of honey bee. Bisetzky showed that, for distances up to 2.5 m, these foragers perform exclusively round dances—the dance form without any direction information. Although in his first seven experiments Gonçalves used walking distances of only 1 and 2 m, his recruits did as well at finding the "correct" station as the recruits in the two experiments with a distance of 3 m—a condition yielding, according to Bisetzky, about 80 to 90 percent waggle dances. Indeed, only in these latter experiments were the dance angles recorded. Since recruits seem to have done as well with or without the dance information, this experiment is unconvincing. The preference for the direction of the forager station was probably due to the fact that the wind always blew in that direction.
10. J. L. Gould, thesis, Rockefeller University (1975).
11. ———, M. Henerey, M. C. MacLeod, *Science* 169, 544 (1970).
12. M. Lindauer, *Am. Nat.* 105, 89 (1971).
13. Since foragers tend to expose their scent glands at rich food sources, both experimenters sealed these glands shut. Gould *et al.* sealed the glands of both groups of foragers, while Lindauer sealed the glands of only the dancing group. Since the odor of shellac is a potent odor cue for recruits (6, pp. 22-23) and was to be found on the bodies of the dancing bees, and only at the station with the more concentrated sucrose, Lindauer's stations may not have been olfactorily identical. (The same criticism may be applied to many of von Frisch's experiments.)
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17. For example, one could suppose that there had been no site odor in the morning, but by the afternoon the distinctive odors had appeared to guide the recruits. Trampled vegetation around the experimental stations or afternoon-blooming flowers could, in the terms of this explanation, have accounted for the results. Alternatively, one could suppose that scent gland odors explain the data. The exposure of the gland is related to the quality of the food with respect to natural sources. If natural competition was high in the morning, but low in the afternoon, scent gland odor would be present to guide recruits only in the afternoon. Since recruits seem not to have been caught, it could also be supposed that experience played a role. After first following the food odor upwind (north) in the morning without finding any food, recruits might be supposed to have searched elsewhere, downwind (south) for example, in the afternoon.
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22. M. Lindauer and B. Schrickler, *Biol. Zentralbl.* 82, 721 (1963); B. Schrickler, *Z. Vgl. Physiol.* 49, 420 (1965).
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24. M. Lindauer and H. Martin, *Z. Vgl. Physiol.* 60, 219 (1968).
25. In all cases, 25 μ l of scent was used per liter of solution. The scents were the gift of International Flavors and Fragrances, Inc.
26. M. Renner, *Z. Vgl. Physiol.* 42, 449 (1959).
27. J. B. Free, *Behaviour* 37, 269 (1970).
28. For results of one such experiment, see J. L. Gould, *Nature (Lond.)* 252, 300 (1974). For additional distance experiments, see J. L. Gould, *J. Comp. Physiol.*, in press.
29. One possibility might be that the reduced angular scatter compensates for increasing distance; and that, taken with the nearly constant distance scatter, could serve to generate the same recruit distribution about a target regardless of its distance from the hive. (A formula for calculating the distribution is offered later.) If food sources exist in "patches," it could be to a colony's advantage to spread out its searching recruits to exploit the patches more efficiently. The area around the hive for which round dances are performed might be thought of as the first such "patch." Italian bees have both a smaller round dance zone and recruit scatter than Carniolan bees. If this difference has (or had) an adaptive value, one might suppose that the two races evolved in habitats with different patch sizes or colony spacings, or that some compensating difference in search strategy in the field may exist. Such speculations might be best tested by looking for racial differences in any of the three species of honey bees that inhabit the tropical forests of Asia, India, and the Philippines.
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31. J. B. Free, *Nature (Lond.)* 222, 778 (1969).
32. K. von Frisch and R. Jander, *Z. Vgl. Physiol.* 40, 239 (1957).
33. Two minor adjustments were necessary to make the data from all six experiments comparable. Since the stations in the 400-m direction arrays were 36 seconds flying time further from the hive than the stations in the 150-m array, the times for the 400-m bees were shortened by that amount. Data were also used from two 90- to 210-m distance-array experiments. In these cases the forager station, rather than the light, was moved in order to signal a new station (28). Hence, the new station (that is, the new distance) was not signaled instantaneously, but only after the foragers then and subsequently feeding returned to dance. This period—30 to 60 seconds—was measured from the video recordings, and the corresponding corrections were made to recruit arrival times.
34. Since food sources such as flowers may commonly exist as extended patches rather than as discrete point sources, array experiments may represent a particularly "natural" way to measure recruitment.
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36. A. M. Wenner, *The Bee Language Controversy* (Educational Products Improvement Corp., Boulder, Colo., 1971), p. 59.
37. The repertoire size of the dance language—that is, the number of unique messages it can communicate—may be calculated and compared with that of other species. Each dance may be considered as a sentence specifying a food source's distance, direction, type, quality, and odor. For a graded system, the number of "bits" in a signal is given by $[\log (R/S.D.)/\log 2] - 2.047$ [J. B. S. Haldane and H. Spurway, *Insectes Soc.* 1, 247 (1954)], where R is the range of signal values (0° to 360° in direction, for example) and $S.D.$ is 1 standard deviation of recruit scatter. A "bit" is taken to be the amount of information necessary to distinguish between two equally probable alternatives. The $S.D.$ for direction scatter in recruit arrivals varies with distance, but a conservative average is 4° . By the formula, this corresponds to 9.3 bits of information. The range of distance indications is 0 to 12 km (6, p. 73). An average value for the $S.D.$ of distance accuracy is 60 m (extrapolating the relationship between dance and recruit scatters as measured in my distance experiments). This corre-

sponds to 5.6 bits of information. The goal may be either nectar, pollen, propolis, or nesting cavities (water being taken as merely dilute nectar)—2 bits of information. The quality of the goal is given by the unquantified "vigor" of the dance. This factor may be conservatively estimated as adding 2 bits of information. The dance also contains information about the odor of the food. Von Frisch (3) showed that bees could distinguish all 46 floral odors he had available. On another occasion, recruits successfully located the correct plants from among 700 other flowering species (6, p. 48). As a conservative estimate, the number of different odors will be taken to be 100—that is, 6.5 bits. From these estimates, the lower limit to the repertoire size of the dance is 25.4 bits, or 4×10^7 dis-

crete "sentences." This is far higher than the value which can be calculated for any other known non-human system. The closest competition comes from the recent attempts to teach chimpanzees to use human language [for example, R. A. Gardner and B. T. Gardner, *Science* 165, 664 (1969); D. M. Rumbaugh, T. V. Gill, E. C. von Glaserfeld, *ibid.* 182, 731 (1973)]. If Washoe, for example, could use all of her 130-odd signs to form four-word sentences in the pattern noun-verb-modifier-noun, and if her repertoire of mostly nouns were actually to consist of 70 nouns, 30 verbs, and 30 modifiers, then 3.25×10^6 sentences would be theoretically possible. (Of course, only a fraction of these would make any sense; Lana's considerable aptitude in learning experiments may allow less crude esti-

mates in the future.) The minimum equivalent figure for the repertoire size of a 10,000-word human vocabulary is more than 10^{22} seven-word sentences, or 74 bits.

38. A phenomenon admirably reviewed by D. R. Griffin [in *Animal Communication*, T. A. Sebeok, Ed. (Indiana Univ. Press, Bloomington, ed. 2, 1975)].
39. I thank N. E. Gary for technical advice, M. Brines for technical assistance, R. O'Connell for obtaining the scents, M. Rosetto for designing the electronics, J. Crane for lending the video tape equipment, and P. Marler, C. G. Gould, F. Nottebohm, and especially D. R. Griffin for their criticisms and encouragement. Supported in part by the Mary Flagler Cary Charitable Trust, Millbrook, New York.

The American Birth Rate: Evidences of a Coming Rise

The proportion of young women who have not yet had any children is rising rapidly in this country.

June Sklar and Beth Berkov

With only one minor exception (in 1969 and 1970), the American birth rate dropped steadily after its peak in 1957. By 1973, the latest year for which nationwide data are available, the general fertility rate hit the lowest point ever recorded for it—69.2 live births per 1000 women aged 15 to 44 (1). The question naturally emerges, How long will the decline or the low rate already reached continue?

A tentative answer to this question is suggested by an examination of recent data from the state of California. As a result of a cooperative research project between the University of California, Berkeley, and the California Department of Health, more recent birth information is available for that state than for the country generally, permitting study of current fertility trends by legitimacy status, race, age, and parity of mother (2). Because it was one of the first states to liberalize abortion laws and to show high rates of legal abortion, we can also include in our investigation the impact of abortion. Our analysis is based on final birth figures through 1973 and estimates for 1974 derived from counts of all birth

records in that year except for a small number of late filings. We examine also recent birth information from four other states where, as in California, the potential for complete fertility control has been enhanced through the widespread availability and use of legal abortion (3). Selected data for the United States as a whole are presented for comparative purposes.

This examination suggests that the decline in the nation's birth rate is coming to a halt and that an upturn is in the making. To begin with, the proportion of childless young women is now very high, and there is evidence that they do not desire to remain childless permanently. To reach their reproductive goals, they will have to begin their families soon. Evidence that young women may be starting to make up for lost time is provided in the latest data for California. There, despite somewhat adverse economic conditions, birth rates rose in 1974. Further, in California and the United States as a whole, contrary to the original expectations of some observers, liberalized abortion has had only a small effect on legitimate fertility and has not stopped the upward trend in illegitimate births. To understand why the country may now be entering a period of rising fertility requires an examination of the reasons why fertility fell in the first place.

The Fall in Fertility

As is well known, the fall in the general fertility rate after 1957 was not expected to continue into the late 1960's and early 1970's, because during that period the large cohorts of women born during the baby boom of the 1940's and 1950's would be in or coming into the age bracket 15 to 24, in which more than half of all births occur. The proportion of all women in the childbearing ages who were in this age group rose substantially after 1960 (Table 1). Yet, except for the slight rise in 1969 and 1970 (which is discussed later), the general fertility rate continued falling rapidly in the late 1960's and early 1970's in both California and the nation generally (Fig. 1).

In part, the drop came from a declining marriage rate among the young. During the years that the number of women aged 15 to 24 was increasing, the proportion who were marrying at those ages was declining (Table 2). In California the percentage of single (never-married) women in the age bracket 20 to 24 rose from 24.5 in 1960 to 37.9 in 1973; in the United States as a whole it rose from 28.4 to 38.3. At the same time there was a steady rise in the proportions of women whose marriages had been disrupted (Table 2). In California the percentage of divorced, widowed, and separated women aged 25 to 44 increased from 9.7 in 1960 to 13.8 in 1973. As a result of both these influences, the percentage of women of childbearing age in California who were currently married and living with their husbands fell from 71.1 to 58.9 between 1960 and 1973.

To determine how much of the decline in the general fertility rate could be attributed to changes in the proportion of women married and living with their husbands, we applied the 1973 age-specific legitimate and illegitimate birth rates to the population of married and unmarried women that would have existed in California in 1973 if the percent unmarried in each age group had remained at the 1960 level. This

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