Table 1. Median latency (in seconds) for dogs to approach cohabitant and noncohabitant rabbits. Separate analyses of variance upon the scores obtained in a logarithmic transformation of the prime data indicate that the three groups of dogs differed in their latency in approaching both the familiar ($F = 6.61$, df $= 2/27$, $P < .01$) and unfamiliar ($F = 6.21$, df $= 2/27$, $P < .01$) test animals.

Condition	Test animal	
	Cohabitant	Noncohabitant
Interaction	4.0	9.0
Noninteraction	8.0	52.5
Isolation	128.0	193.0

did not approach the test animal within 5 minutes, the test was terminated. Again, the groups differed markedly in their approach behavior. Median latencies are presented in Table 1. Animals in the interaction condition had the shortest latencies, while animals in the isolation condition had the longest latencies, with the latter dogs frequently failing to contact the test rabbit in the entire 5-minute period (*5*). Apparently the essential phenomenon is trans-situational, and not restricted to a given test arrangement or limited to the particular rabbit with which the pup had cohabited.

These data are consistent in showing that interspecific rearing conditions have a pervasive influence on the young dog's response to another species to which it has been exposed. One of the more remarkable features of these results was the rapidity of formation of the interspecific attachment. Subsequent experiments confirmed that the phenomenon was not an artifact of the test procedures adopted nor of the response index employed. Independent removal-replacement results were obtained from a new group of 31 dogs maintained in an interaction condition similar to that of the first experiment, but tested only after 88 hours of cohabitation (*6*). These results, which were free of the influence of repeated testing, were not significantly different from those obtained after 96 hours of interaction-cohabitation in the first experiment. Nor were the effects restricted to the vocalization-disruption measure. After 4 days in the interaction condition, a significant shift was obtained in the preference of the experimental dogs for the rabbits. These data strongly suggest that significant changes in social preference occur over relatively short periods. A recently completed study by Fleener (*7*) indicates that human infants share this capacity for the rapid establishment of social preferences.

Observations of the animals in the first week of cohabitation yielded data which were consistent with the quantitative results. After an initial period of mutual avoidance, a considerable portion of the young dog's time was spent in grooming, lying upon, and gnawing at the extremities of his cohabitant. Such behavior continued throughout the duration of the experiment. As the dogs grew older and more capable of inflicting physical damage through grooming and "play" activities, the outcomes became increasingly more noxious to the rabbit cohabitant. By the 8th week of cohabitation, six of the ten rabbits in the interaction condition were severely injured and the pairings were discontinued. Contrary to the earlier reports of Kuo (*8*), continued cohabitation is not necessarily associated with the development and maintenance of peaceful relationships between species.

Preliminary information was obtained on the post-experimental sexual adaptation of dogs that had cohabitated with rabbits. A follow-up study of the subgroup of six female beagles used in the two experiments indicated that alien cohabitation does not necessarily inhibit the development of species-appropriate reproductive activities. Of the six animals observed in maturity, four were successfully mated and produced litters in their first heat. Parallel data on male dogs unfortunately were not obtained.

Our results clearly indicate that the young dog's experience prior to the 3rd week of life does not preclude the rapid establishment of a "new" social bond with respect to a member of another species. Moreover, early exposure to an animal of another species does not insure against the subsequent development of antagonistic patterns of interaction with that species.

The present findings thus are consistent with recent reports which emphasize the role of contemporary events, both endogenous and exogenous, in the control of the social behavior (*9*). Specifically, studies of the post-emergence behavior of dogs reared in complete isolation have demonstrated that the intensity of the treatment effects can be greatly modified by varying the conditions of emergence (*10*). Similarly, our previous work indicates that the primary effects of interspecific rearing in sheep can be reversed (*11*). While some long-term effects of early experience on social and sexual behavior patterns cannot be gainsaid (*12*), our data indicate that a critical examination of the conditions required for the persistence of such effects is in order.

ROBERT B. CAIRNS
Department of Psychology,
Indiana University, Bloomington
JACK WERBOFF
Jackson Laboratory, Hamilton
Station, Bar Harbor, Maine 04609

References and Notes

1. V. H. Denenberg, G. A. Hudgens, M. X. Zarrow, *Science* **143**, 380 (1964); L. Hersher, J. B. Richmond, A. U. Moore, *Behaviour* **20**, 311 (1963); Z. Y. Kuo, *J. Comp. Physiol. Psychol.* **11**, 1 (1930); G. J. Romanes, *Nature* **12**, 553 (1875).
2. R. B. Cairns, *Psychol. Rev.* **73**, 409 (1966).
3. O. Elliot and J. P. Scott, *J. Genet. Psychol.* **99**, 3 (1961).
4. See also C. L. Pratt and G. P. Sackett, *Science* **155**, 1133 (1967); R. B. Cairns, *J. Comp. Physiol. Psychol.* **62**, 298 (1966).
5. It should also be noted that dogs maintained in isolation tended to approach rabbits which had previously cohabited with other dogs more rapidly than they approached rabbits that had not so cohabited (first and second columns, Table 1). This trend, of borderline significance ($.10 > P > .05$), suggests that the cohabitation experience modified the behavior of the rabbits as well as of the pups.
6. R. B. Cairns and J. Werboff, in preparation.
7. D. E. Fleener, thesis, Indiana University (1967).
8. Z. Y. Kuo, *J. Genet. Psychol.* **97**, 211 (1960). In this report Kuo indicated that attempts were made to inhibit fighting among dogs assigned to the experimental groups.
9. J. P. Scott, *Ann. Rev. Psychol.* **18**, 65 (1967).
10. J. L. Fuller and L. D. Clark, *J. Comp. Physiol. Psychol.* **61**, 251, 258 (1966).
11. R. B. Cairns, *ibid.* **62**, 298 (1966); R. B. Cairns and D. L. Johnson, *Psychon. Sci.* **2**, 337 (1965).
12. Including those effects related to the development of social preferences [see, for example, D. G. Freedman, J. A. King, O. Elliot, *Science* **133**, 1016 (1961)] and the sexual behaviors of dogs reared in isolation [see, for example, F. A. Beach in *Social Behavior and Organization among Vertebrates*, W. Etkin, Ed. (Univ. of Chicago Press, Chicago, 1964), p. 117].
13. E. B. Page, *J. Amer. Statist. Ass.* **58**, 216 (1963).
14. These experiments were conducted at the Jackson Laboratory while R.B.C. was on leave from Indiana University (PHS special fellowship 1-F3-NH-30, 205-10) and were supported in part by PHS research grants HD-01082 and GRS FR-05545-03-05 from NIH.

21 August 1967

Honeybees: Do They Use Direction and Distance Information Provided by Their Dancers?

My experiments on the language of the bees (*1*) received new impetus when I discovered that successful forager bees upon their return to the hive inform their hive mates of the location of the feeding place by wagging dances (*2, 3*). The direction of the goal in relation to the sun's position and to the polarized light of the sky is indicated by means of the straight part in the wagging run. The distance to the feeding place is announced by the speed of the dance movement (*2*, *3*).

Recently Johnson (*4*) and Wenner (*5*) have expressed a different view. They agree that the dancers in the hive indicate the distance as well as the direction of the goal, but they believe that the hive mates do not make any use of the indication of distance (*5*) and that the information about direction is not used (*4*) to the accuracy stated in my publications. They propose that the newcomers in their search for the goal are guided by local scents at the feeding site.

I thought the same when I first observed the straight flight of the newcomers toward a distant feeding place. I found that a forager, upon its return to a rich feeding place, will evert its scent organ; this scent is attractive to other bees and is far more intense to their sense of smell and hence is perceived for a greater distance than any other relevant odor (*6*, pp. 517–520 and Table 44, p. 520). Thus the recruits might follow the odor of the abdominal scent organ. However, I have not been able to confirm this hypothesis. Sealing of the openings of the scent organs, while not impairing the collecting and dancing activities of the treated bees, prevents them from everting their glands so that no odor is given off; nevertheless, recruits alarmed by these dancers still find the feeding place with surprising speed and precision (*3*, pp. 30–32; *6*, pp. 53, 128, 228).

A comprehensive survey of our methods and results has been published (*6*). I shall relate a few of the experiments, the results of which show that, for the discovery of a good feeding place by recruits, the distance and direction given by the dancers are essential.

1) Whenever a feeding place is close to the hive, foragers upon their return perform round dances. These contain no information about the distance or direction of the food source (*6*, p. 85). However alerted recruits, closely following the dances learn the odor of the visited blossoms because it clings to the body of the dancers. In most of our experiments, such an odor was the scent of some volatile oil added to the feeding place. Consequently, the newcomers start swarming out in all directions in the neighborhood of their hive in search of this scent, visiting in about equal numbers all the scented foodless plates set up around the hive. If the feeding place is now moved stepwise to greater distances from the hive, an indication of distance and direction from about 25 m becomes recognizable in the dance. This becomes clearer the greater the distance is, and it is quite pronounced at 100 m. By then the round dance has turned into a wagging dance. Accordingly, from a distance of 25 m and up, the recruits begin to search preferably in the direction of the feeding place, while at a distance of about 100 m there are hardly any newcomers searching in the wrong direction or at the wrong distance (*6*, pp. 150–152). The whole arrangement has not changed except for the increase in distance, which certainly would make it not easier but more difficult for the newcomers to be attracted by the scent organ of the foragers or by any other local odors. The distances stated refer to carniolan bees (*Apis mellifera carnica*). Other races begin indicating direction at even smaller distances (*6*, pp. 294–295, Fig. 251).

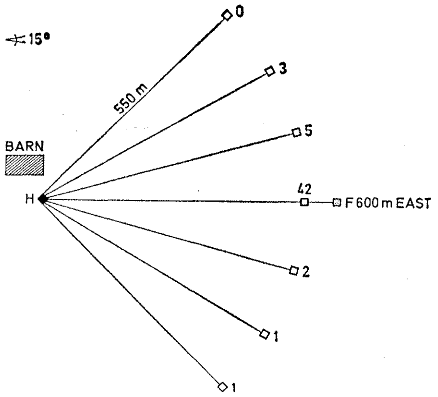

Fig. 1. Fan experiment, 30 August 1955, in a plain, open field. *H*, beehive; *F*, feeding place 600 m to the east. White squares represent scent plates 550 m from the hive; added are the numbers of visits by recruits during the first 50 minutes counted from the beginning of the experiment. Weak winds from east-northeast.

2) Inside their dark hive, bees dancing on a vertical comb transpose the solar angle into the gravitational angle; in this way, even without seeing the sky, they inform their companions about the direction they must take in relation to the sun when flying out. After the observation hive is tilted horizontally, the dancing bee simply retains the angle which she kept in relation to the sun during her flight to the feeding place; thus the wagging run points directly to the goal. When the sun and the blue sky are screened off, her dances at once become disoriented and indicate neither a certain distance nor direction (*6*, p. 133). Even these disoriented dances arouse her companions, which now behave as if alarmed by round dances, searching in all directions in the vicinity of the hive (*6*, p. 152, Fig. 132). If the hive is tilted up again into its previous vertical position—all other external and internal factors remaining the same—in a few minutes the disoriented swarming of the recruits turns into an oriented search for the goal (*6*, pp. 154–157, Figs. 134 and 135).

3) In our detour experiments, a mountain ridge or a high building lay between bee hive and feeding place. When we established these feeding places the numbered bees were guided around these obstacles along a hairpin curve; they remained faithful to this route during their foraging flights. Dancing inside the hive they had a remarkable ability to integrate the actually flown detour by indicating the direction of the "beeline." Observers at the top of the obstacle noticed that recruits sent out by these foragers indeed followed the beeline, overcoming the obstacle by flying over its top to reach the feeding place on the other side. There had been no chance for them to perceive any scent marks of the feeding site from this side of the obstacle nor could they have followed a trail of scent left in the air by foragers who had actually followed quite a different route. Hence there had been nothing to guide them but the information obtained inside their hive (*6*, pp. 177–186, Figs. 164 and 167). Many more of our observations cannot be reconciled with the opinions of Johnson and Wenner. However, the three mentioned above should suffice to clear up the situation.

If one compares Johnson's and Wenner's experimental procedures with ours it can be explained why their results differ from ours. To find out how accurately the recruits follow the direction information, we carried out fan experiments. After setting up an observation hive in a plain, open field, we establish a feeding place at a distance of, for example, 600 m from the hive; this is visited by numbered foragers. As long as this group of bees is gradually moved away from the hive to the 600-m mark the sugar solution offered as food is kept so weak that the bees hardly, if at all, dance upon return and hence arouse no recruits. This procedure requires constant and accurate observation of the bees at the feeding place, as well as inside the hive. Both Wenner and Johnson refer to Wenner's training method (*7*). When gradually bringing the bees to the goal, he offers a strong sucrose solution from the very beginning. Consequently newcomers are continuously aroused; many of them, judging from our own experience, may loose contact with the group while it is moved along. During the next days of testing when food is offered, these bees can be rearoused by feeding, and they go searching all over the surroundings, so providing a serious source of error to the experiments.

At the start of our experiment, seven scent plates without food are set up in the form of a fan, at a distance of 550 m at an angular separation of 15° (Fig. 1). Only now, strongly concentrated sugar solution provided with the same scent as at the scent plates is offered at the feeding place. And only now the foragers begin to dance vividly within the hive; the recruits, following the dances, go searching for the scent they perceived at the dancers' bodies. The number of bees appearing at the various scent plates reveals the direction in which the recruits are searching. In assessing the results we have, in contrast to Johnson and Wenner, not taken into account the number of visitors appearing at the actual, more distant feeding place (600 m) since conditions here are different owing to the presence of foragers using their scent organs. Moreover, the additional attractiveness of the bee scent may vary greatly for it depends on the degree to which the scent organ is used during the experiment and on wind conditions.

Up to now we have carried out twelve fan experiments (*6*, pp. 85–96). They show clearly that newcomers in fact do search in the direction of the goal. Johnson carried out some experiments of a similar kind, stating that with this experimental setup he, too, has obtained results expected according to the "dance language," for 78 percent of his recruits arrived in the correct direction of the feeding place. However, this figure is not comparable to results of our experiments since he has summed up the numbers of visits counted at two different places in the direction of training; above all one of them was the feeding place, naturally favored by the coming and going foragers and the attractive odor of their scent organs. In the two other directions there was only one scented plate, without foraging bees (Fig. 2; *M*+*A* against *N* and *S*, or *N*+*B* against *M* and *S*). If, as we ourselves have done, one does not take into account the number of visits at the feeding place, in Johnson's experiments not more than 56 percent of the recruits came to the scent plate in the direction of training.

Johnson states that our experiments lack an essential control since the scent plates are not uniform. First, he says, the newcomers could have been attracted in this direction by the feeding foragers. To rule this out I had in control experiments eliminated the strongest attractant, the odor of the scent organ. Besides, as long as there is only one feeding station, it is easy to check the influence of local scent factors by taking the wind conditions into consideration. Second, he states that the recruits might have aimed at the place in the middle of the fan, this being the geometric center of all feeding places; however, he does not say why they did so. He does not note that in our first experiments on direction information the feeding place was established, not in the center of the fan, but on its outer margin, or even farther outward. The newcomers arrived in this case in this direction and not at the center (*3*, pp. 27–29). When the feeding place, which at the beginning was close to the center of the fan, was transferred 15° to the outside, under otherwise identical conditions the stream of newcomers turned correspondingly (*6*, p. 157) to this new direction.

The control experiments carried out by Johnson differed from ours. To create more uniform conditions at all the different stations he set up a second colony of bees with lighter color at the side of the first. While he fed the dark bees at their usual feeding place (*A* in Fig. 1), he offered food to the light bees at all four places simultaneously. In another series of experiments, he removed the second colony and kept feeding groups of dark bees at all four places. If he moved the feeding place, at 270 m, from *A* to *B*, most of the recruits still appeared in a central direction in both series of experiments, a fact which he ascribes to an effect of the geometric center. However, a simpler explanation takes into account the strong wind from the south, prevailing during his experiments. This wind must have carried along scent from those bees foraging at the central station toward the recruits flying in the direction of *B*; many of these may have been led astray by it to the central station. In our fan experiments we have observed examples of such deviations even with volatile oils

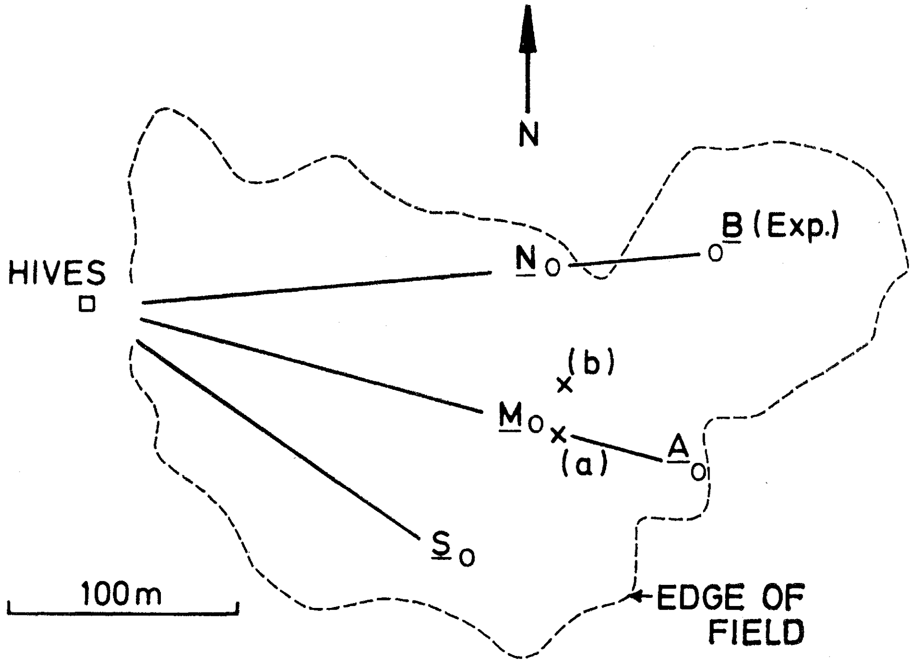

Fig. 2. Map of the experimental area. The experimental (dark-colored bees) and control hives (light-colored bees) were adjacent to one another at the edge of a football practice field (outined by the broken line). The experimental site in the first series of experiments was *A*; in the second series *B*. The three sites, north (*N*), midde (*M*), and south (*S*) served as controls and had dishes of sugar solution to which recruits could come. Points *a* and *b* indicate the geometric center of each set of four feeding sites for each experimental series. [After Johnson (*4*, Fig. 1)]

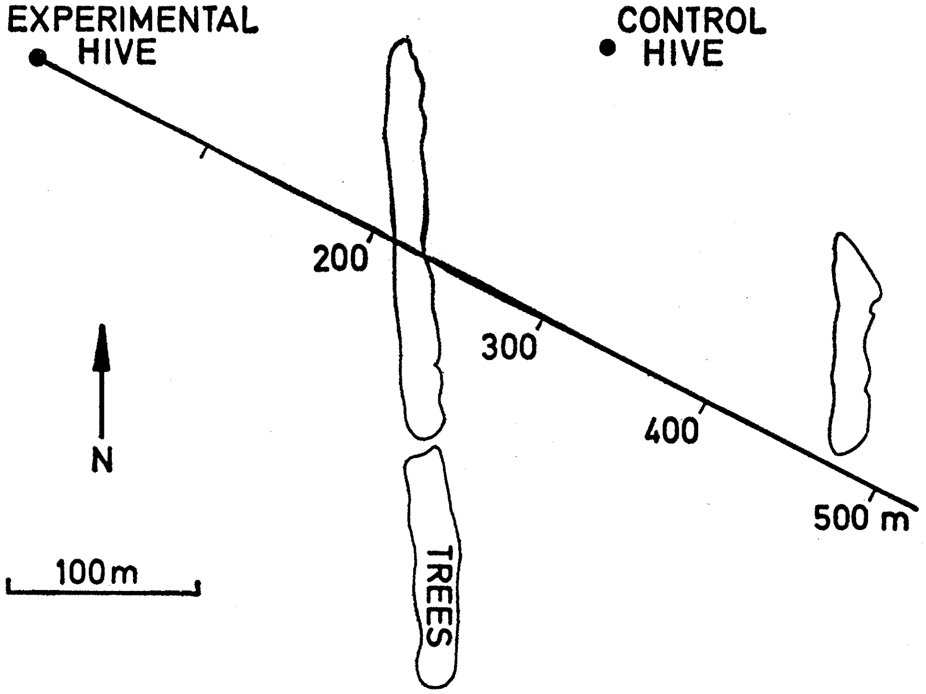

Fig. 3. Map of the experimental area, showing placement of experimental hive (dark-colored bees) and control hive (light-colored bees) in relation to the four training sites. Bees from the experimental hive were trained to forage at either the 400- or 500-m site, depending upon the particular experiment. Trained bees from the control hive foraged at none, three, or four of the sites in different experiments. [After Wenner (*5*, Fig. 1)]

with less intense odors (*6*, pp. 156–163, Fig. 136).

While Johnson's tests included visits of newcomers in only three different directions, we usually checked a much wider field, setting up a fan, as a rule consisting of at least seven scent plates. Moreover, while he established his feeding places at distances not exceeding 200 m and 270 m, respectively, from the hive, in our control experiments the distances between hive and feeding place amounted to 600 m (Fig. 1) and even to 1250 m. With such great distances, it is not likely that the direction of the newcomers' flights could have been influenced by local scent marks of the feeding place. We are well informed about the capability of their organs of smell (*6*, pp. 517–22). While those scent plates lying in the direction of the goal received a great number of visits from recruits, the rest were but poorly visited in our experiments. Both facts are equally remarkable, showing that no stray recruits were roaming about, as seems to have been the case in Johnson's experiments.

While bees were fed at a feeding place 400 m from Wenner's experimental hive, (*5*) three more places were being provided with the same food and scent, but were not yet frequented by any foragers (Fig. 3). Out of a total of 123 recruits counted arriving at the various stations, the percentages were as follows: 74 at the feeding place itself (400 m), 10 at 200 m, 14 at 300 m, 2 at 500 m. While he maintains that these figures do not differ fundamentally from those to be expected according to the distance communication in the dance "language" hypothesis, they do not really contribute anything to the solution of this question. The visits to the feeding place at 400 m may have been due just as well to distance information as to the attractiveness of the scent organ of the foragers there (and only there). For this reason we carried out our experiments in a different way (Fig. 4).

Here the distance between hive and feeding place was 300 m. Only those recruits visiting the seven scent plates without any food have been evaluated. The number of visitors given at each site in the figure show clearly that the recruits had followed the distance indication. If in this experiment there had been an attractive effect of the scent organ at the adjacent scent plates 50 m to both sides of the feeding station, we should have expected a greater number of recruits arriving at 350 than at 250 m, since a soft wind (north-northwest to northwest) had been blowing.

Wenner's controls consisted of a second colony of bees of lighter color set up 150 m to the north of the line of flight (Fig. 3); 25 and 26 of these bees were fed at the 200- and 300-m sites, respectively, while 13 dark bees together with 13 light-colored ones were frequenting the 400-m site. Now it appears as if the newcomers of the dark race hardly followed the distance information given by their foragers since 18 percent of their recruits paid visits to the light bee's feeding place at 200 m, and 48 percent visited the 300-m site; only 33 percent visited the one at 400 m, that is, the original feeding site of their own colony. However, we could have predicted such a result. Those recruits who had been given the 400-m information were bound to fly over the nearer feeding places at 200 and 300 m located in the same line, and were therefore likely to be attracted to them by the sight of the foraging bees as well as the odor of their scent organs and the scent used for training, particularly with strong southerly winds prevailing there at the time of the experiment (9 knots, or about 4.6 m/sec). When-

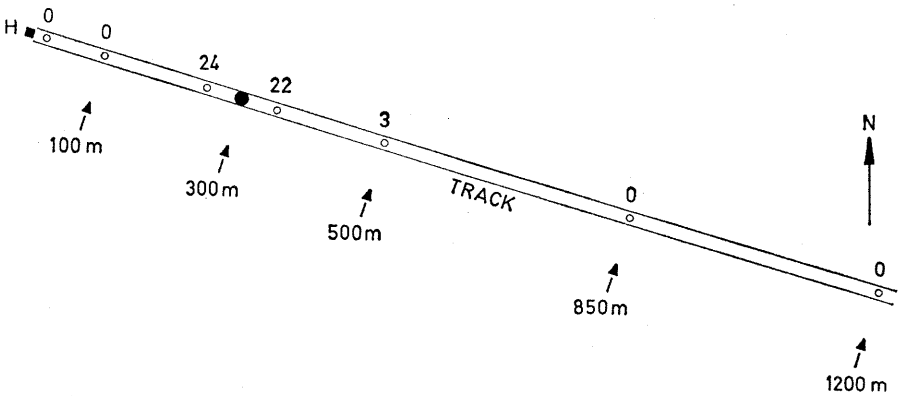

Fig. 4. Step experiment of 3 September 1962. *H*, beehive. Feeding-site (black dot) at 300 m from the hive. Scent plates (white rings) with numbers of visits by recruits during the time of the experiment (2.5 hours).

ever the wind is that strong, bees will keep close to the ground, and attraction by the odor of the scent organ or the training scents at the closer sites will be favored (*6*, pp. 95–96 and Table 12). In one of our experiments a wind with force similar to that in Wenner's experiments caused the bees to fly close to the ground and to pay more visits than usual to the scent plates (in our case only scented and no foragers visiting) situated nearer to the hive. For this reason, we selected calm weather whenever possible. Results can be spoiled by wind conditions in step as well as in fan experiments.

We still have to discuss the behavior of recruits belonging to the control hive set up sideways. After groups of its lighter bees were fed at the 200-, 300-, and 400-m sites, the light-colored recruits appeared, similar to the results with dark bees, in the following proportion: 12 percent at 200 m, 62 percent at 300 m, and 26 percent at 400 m. As an explanation, Wenner also refers to an assumed geometric center, without going into details about this relation. After a glance at Fig. 3, we may suspect other causes to have been at work. The fact that the site at 200 m was screened by trees offers a possible explanation for the scarce visitation by bees from the control hive. Because of its direction, the wind (220 degrees), blowing the odor of the scent plates as well as of the foragers' scent organs across the path of recruits flying to the 400-m site, might well have misled these bees to the 300-m site. Wenner's third experiment, being only a variation of the second, does not add any fundamentally new aspect.

Wenner's experiments, just as Johnson's, extended only over a small distance (500 m). In our own step experiments the distance from hive to feeding place has often been much greater: 750 m, 1050 m, 2000 m, and 4400 m (*6*, pp. 89–95, Figs. 84–89). Again I must state that local scent marks cannot possibly be held responsible for the arrival of recruits at the proper place over such great distances.

Some of my colleagues, having read the two papers published in this journal, spontaneously declared their readiness to repeat the crucial experiments in collaboration with Johnson and Wenner and neutral observers. I sincerely hope that this can be done.

KARL V. FRISCH
D 8000 München 90 (Germany)
Über der Klause 10

References and Notes

1. K. v. Frisch, *Zool. Jahrb. Physiol.* **40**, 1 (1923).
2. ———, *Experientia* **2**, 397 (1946); *The Dancing Bees* (Methuen, London, 1966).
3. ———, *Österreichische Zool. Z.* **1**, 1 (1946).
4. D. L. Johnson, *Science* **155**, 844 (1967).
5. A. M. Wenner, *ibid.*, p. 847.
6. K. v. Frisch, *Tanzsprache und Orientierung der Bienen* (Springer-Verlag, New York, 1965). English translation in press at Harvard Univ. Press, Cambridge, Mass.
7. A. M. Wenner, *Bee World* **42**, 8 (1961).

8. I thank Prof. Dr. M. Lindauer, Dr. H. Markl, and Dr. W. Rathmayer for reading the manuscript.

26 June 1967

Our experimental analysis of the dance-language hypothesis during the past 3 years has led us to a new and tentative interpretation of all available evidence. A statement of this interpretation has not yet appeared in print (*1*, *2*). A sketch of it is as follows:

We find that the hive, its surrounding environment, and its past history are part of a dynamic system and must be studied as such. In discussing recruitment of bees to a source in the field, for example, one must first distinguish between those recruits that have previously fed at the same site visited by a successful forager and those that have not been there before (preferably, those that have not even been in the same area before). The importance of this distinction is not clear in the literature (*2*, *3*).

Bees experienced at visiting a given source can rely upon their memory of the location and can be recruited by means of a conditioned response to either food odor or location odor brought back into the hive by hive mates (*3–5*). The time spent searching for a source, no matter how long, is negligible compared to the time spent exploiting such a source. Thus, we conclude that the experienced bees, which require no language for re-recruitment (*3*), are basically responsible for providing the food for their colony.

Those bees that have never been to a source before apparently experience a great deal of difficulty in finding it—their ability to use a variety of odors and wind patterns enables them to do so. Even then, only a small percentage of those that leave the hive succeed in finding a point source (*3*). Most of those that do succeed in finding the source appear to have spent enough time after leaving the hive to have searched a considerable area before finding the site, even up to 10 minutes for a site at a distance having a direct flight time of 30 seconds (*6*). Our work to date indicates that naive recruits function in the following manner:

1) Recruits stimulated to leave the hive associate a number of location odors, first sensed on the recruiters, with a potential source of food. These include odor of the food, both from the bee which stimulated the recruit to leave and from other bees successful at the same source; and other odors in the locality visited by successful foragers (which may adhere to them) including those of other flowers, those of various associated plants, and any inorganic odors.

2) Recruits leave the hive and drop 200 m, 300 m, or more downwind from the hive before commencing their search, depending on wind speed and on individual differences among bees. In strong winds they drop further downwind. This maneuver permits them to: negate the influence of their own hive odor and find those potential sources which are closest to the hive—those which are downwind as well as those which are in other directions.

3) Recruits search for the proper combination of odors. In addition to those odors which they have previously associated with the food source, they search for the odor of other bees which are feeding on crops, particularly the crop most impressed on them while in the hive. This search pattern is complicated by: (i) attractance of hive-specific odors of feeding bees from the same hive, (ii) repellency of hive-specific odors of feeding bees from other hives, and (iii) Nasanoff gland attractance. Covering this gland with the strong odor of shellac may even increase the discrepancy between odor of the experimental site and odor of control sites (*3*). The use of shellac on experienced bees does not eliminate this factor, since newly arriving recruit bees often expose their Nasanoff gland before landing.

Apparently, the disagreement in interpretation which has arisen stems largely from the question of adequate control in experimental design. After wrestling with the problem of "proof" over the past few years, we have had to agree with various statements (*7*) that one cannot obtain absolute verification for any hypothesis, no matter how many times experiments are repeated (also, apparently, any attempt to establish the "truth" of a hypothesis introduces an unwelcome bias). Progress apparently depends, rather, upon the sharpening of experimental design and the use of ever better controls, when such controls are found to be necessary. In this context, a hypothesis is best considered as an interim statement until a better hypothesis can be formulated. In that sense the contribution of von Frisch (*8*) was a dramatic step forward in its incorporation of controls, in the use of logic, and in the reserved interpretation of results.

We would like to emphasize, therefore, that we consider that our results (*9*) do not disprove of the dance-language hypothesis (since this is never possible), but indicate that a more simple interpretation exists for previous experimental results.

The third experiment of Wenner (Fig. 3 of von Frisch's letter) provides an excellent example for weighing the relative efficacy of the two interpretations provided in these letters. This experimental design is particularly valuable in that each hive serves as a control against the other.

Individually marked bees from the experimental hive foraged only at the 500-m site, while individually marked bees of a different color from the control hive foraged at all four sites. Under these conditions foragers visiting the 500-m site from the experimental hive could provide only a 500-m distance information in their hive by means of their waggle dances. Bees foraging at all four site from the control hive, on the other hand, could collectively furnish distance and direction information about all four sites in their hive. Yet, when the experiment was run, the distribution of recruits at the four stations from the experimental hive was identical to the distribution of recruits that had come from the control hive.

When sets of results not predicted by a particular hypothesis arise, one has to choose a course of action. Either he can keep the hypothesis intact and rationalize that in this case the bees have been "misled," or he can trust the data furnished by the bees and proceed accordingly. Whereas von Frisch (and many others, apparently) has chosen the former course, we have chosen to explore the alternative. It is for this reason that we pay such close attention to the similarity between the distribution of bees from the experimental hive at the four stations (6, 43, 42, and 9 percent) and a potential multinomial distribution about the geometric center of all sites (12, 38, 38, and 12 percent). To us, the data are more suggestive of a probablistic search pattern than of a goal-directed flight.

We conclude that while the classic dance-language hypothesis has been a reasonable interpretation for results obtained in the past, it is not necessarily an exclusive interpretation. Our results indicate, instead, the validity of the more simple interpretation outlined above and forms the basis for a fruitful line of research. Some questions which must now be studied include (i) What is the disposition of recruits unsuccessful at finding a source in the field? (ii) How long does an unsuccessful recruit search before returning to the hive? (iii) Why are recruits more successful at finding one site than at finding another apparently identical site? (iv) What are the relative contributions to the attractiveness of a site of location odor, food odor, and bee odor? (v) What are the effects of the duration of an experiment upon recruitment?

Although these are difficult problems, we believe that progress toward an understanding of bee behavior will be more rapid if experimental design is not restricted by the assumption that bees have a "language." The assumption of the language notion would, in fact, prohibit the study of some questions.

The history of biology is replete with predicaments similar to that indicated in this exchange. We hope that our results and interpretation will be welcomed as a stimulus to further and more critical experimentation and that others will repeat both our experiments and the classic experiments and ponder the question of controls. On the basis of our work, the following seem necessary: (i) Control and experimental sites must be in areas with nearly identical locality odors (*5*). (ii) An equal number of bees must be feeding at each control site and at the experimental site. (iii) The experimental site must not be near the center of a cluster of sites, since this is also the center of the odor field. (iv) Bees arriving at the experimental site must be tallied and considered, since they have obviously been recruited. When this is done, recruit performance in the field is considerably better than the accuracy of dance information (see *10*). (v) All recruits must be caught and killed at control as well as at experimental stations (see *10*). (vi) Ideally, recruits should never before have been in the locality of the experimental site. (vii) The duration of the experiment must be short enough to eliminate the possibility that recruits can repeatedly leave the hive and learn where not to go. For those who cannot repeat the experiments we urge a study of the experimental design of the various studies alluded to above as a basis for a decision on whether the controls specified by us are necessary (*11*).

ADRIAN M. WENNER
Department of Biological Sciences, University of California, Santa Barbara
DENNIS L. JOHNSON
Department of Chemistry and Physiology, U.S. Air Force Academy, Colorado Springs, Colorado

References

1. D. L. Johnson, thesis, University of California, Santa Barbara (1967).
2. A. M. Wenner, in *Animal Communication—Techniques of Study and Results of Research*, T. A. Sebeok, Ed. (Indiana Univ. Press, Bloomington, in press).
3. D. L. Johnson and A. M. Wenner, *Anim. Behav.* **14**, 261 (1966).
4. A. M. Wenner and D. L. Johnson, *ibid.*, p. 149.
5. D. L. Johnson, *ibid.*, in press.
6. A. M. Wenner, unpublished data.
7. C. Bernard, *An Introduction to the Study of Experimental Medicine* (Dover Press, New York, 1957); W. S. Beck, *Modern Science and the Nature of Life* (Doubleday Anchor, New York, 1961); K. R. Popper, in *British Philosophy in the Mid-Century: A Cambridge Symposium*, C. A. Mace, Ed. (Macmillan, New York, 1957), pp. 155–91; T. S. Kuhn, *The Structure of Scientific Revolutions* (Univ. of Chicago Press, Chicago, 1962).
8. K. v. Frisch, *Österreichishe Zool. Z.* **1**, 1 (1946).
9. D. L. Johnson, *Science* **155**, 844 (1967); A. M. Wenner, *ibid.*, p. 847.
10. A. M. Wenner, *Anim. Behav.* **10**, 79 (1962).
11. We thank D. Davenport, L. Friesen, and P. Wells for reading the manuscript.

28 August 1967