References and Notes

1. J. R. Ellerman and T. C. S. Morrison-Scott, *Checklist of Palaearctic and Indian Mammals, 1758–1946* (British Museum, London, 1951).
2. E. Nevo, *Mammalia* **25**, 127 (1961).
3. ———, *Science* **163**, 484 (1969).
4. I. R. Savić, thesis (Belgrad University, 1965).
5. B. Soldatović, S. Živković, I. Savić, M. Miloševic, *Arh. Biol. Nauka* **18**, 127 (1966); *Z. Saeugetierk* **32**, 238 (1967); P. Raicu, S. Bratosin, M. Hamar, *Caryologia* **21**, 127 (1968).
6. J. Wahrman, R. Goitein, E. Nevo, in *Comparative Mammalian Cytogenetics*, K. Benirschke, Ed. (Springer-Verlag, New York, 1969).
7. We thank Mrs. M. Bronstein for help in the cytological work and Mr. Y. Sivan for assistance in collecting animals.

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Honey Bee Recruitment to Food Sources: Olfaction or Language?

Abstract. *Honey bee recruits locate food sources by olfaction and not by use of distance and direction information contained in the recruitment dance. Recruitment efficiency increases as odor of the food source accumulates in the hive, from hour to hour and from day to day. Flight patterns, landing patterns, bee odor, and Nassanoff secretion apparently do not aid in recruitment of bees.*

When von Frisch generated the "dance language" hypothesis of honey bee recruitment (*Apis mellifera* L.) (*1*), it was based on the results of elegantly simple experiments and withstood the tests of repeatability and "proof" by verification (*2*). Inadequacies in this explanation have been revealed (*3*) through studying the nature of correlations between behavioral and environmental parameters. Wenner and Johnson (*4*) documented the existence and relevance of simple conditioning during recruitment, just as Lopatina (*5*) had earlier.

This demonstration led to a questioning of the assumption that the "language" was an "instinctive" act. Challenging a basic assumption (*6*), Wells and Giacchino (*7*) found that altering the sugar concentration did not alter the amount of solution ingested by foragers.

Furthermore, the language hypothesis has failed the more critical test of refutation (*8*) in that experimentation with controls not incorporated in the early experiments yielded results other than those predicted by the hypothesis (*9*). In the later experiments, recruited bees arrived at sites in the field in apparent disregard of any dance information that they could have acquired before leaving the hive.

Such data are not only incompatible with a language hypothesis but also provide a basis for the a posteriori generation of an alternative hypothesis (*10*): Potential recruits stimulated to leave the hive search the field for the odor (or odors) carried into the colony by successful foragers.

That bees locate a food source by olfaction is especially possible in view of the extremely low recruitment rate of regular foragers collecting unscented sucrose at an unscented site. On 25 July 1968, for instance, in the absence of a major nectar source for the colony, we received only five recruits from a hive of approximately 60,000 bees after ten bees had foraged at each of four stations for a total of 1374 round trips during a 3-hour period.

Although the olfaction hypothesis can explain most (if not all) of these results, no a priori experimental design has contrasted the two hypotheses. We felt that such a test was necessary and should be possible with the use of a single hive.

Despite the difficulties in designing such an experiment (*10*), some unexpected results obtained during the summer of 1967 provided the basis for just such a test. In the experimental series of 1967, ten individually marked bees routinely visited each of two clove-scented sources (0 to 0.26 ml of oil of clove per liter of 1.5 molal sucrose solution), 200 m in opposite directions from the hive. Each new recruit landing at a dish was killed in a covered jar of alcohol.

We had expected a constant number of recruits per unit time, but an increasing number of new bees arrived and were killed as the experiment progressed (Fig. 1). Since the number of new arrivals reflected the cumulative number of trips by experienced foragers, we concluded that a recruit more readily locates a site in the field as a direct consequence of odor in the hive. Furthermore, the data gathered on 1 day were not independent of the previous day's manipulations.

If odor accumulates in the hive and contributes to the relative success of a recruit searching in the field, a rationale exists for designing an experiment. Bees visiting certain scented sources in the field for 1, 2, or 3 days accumulate odor in the hive and continue to visit

Table 1. Total number of recruits received per day and the experimental procedure at the three sites. Foragers never visited the control site (No. 2), and ten bees made a relatively constant number of trips per unit time to the experimental sites (Nos. 1 and 3). On day 7 only five of the regular foragers arrived at site No. 3. On day 16 a second scent (0.13 ml of oil of peppermint per liter of 1.5 molal sucrose solution) was used at each experimental site (no peppermint scent had accumulated in the hive previous to this time). The number of times the Nassanoff gland was exposed is the average for sites 1 and 3.

Day	Procedure	Recruitment (No. at each site)			Nassanoff exposure
		No. 1	No. 2	No. 3	
1	Scent at 1 and 3	42		71	31.0
2	No scent at 1 and 3, scent at 2	15	38	3	134.5
3	Scent at 1 and 3	89		76	71.5
4	No scent at 1 and 3	20		7	182.0
5	Scent at 1 and 3	87		90	94.5
6	Scent at 1 and 3	70		55	82.0
7	No scent at 1 and 3, scent at 2	4	51	0	139.5
8	Scent at 1 and 3	111		101	136.5
9	No scent at 1, 2, or 3	0	3	17	223.0
10	Scent at 1 and 3	44		90	149.0
11	Scent at 1 and 3	159		89	160.0
12	No scent at 1 and 3, scent at 2	4	91	5	253.0
13	Scent at 1 and 3	102		61	92.0
14	No scent at 1, 2, or 3	6	2	5	161.5
15	Scent at 1 and 3	93		87	87.5
16	2nd scent at 1 and 3, 1st scent at 2	2	44	0	82.0
17	Scent at 1 and 3	71		29	55.5
18–22	[Separate experimental series, scent at 1 and (or) 3]				
23	Scent at 1 and 3	68		32	168.5
24	Scent, but no bees at 1, 2, and 3	1	0	0	0.0

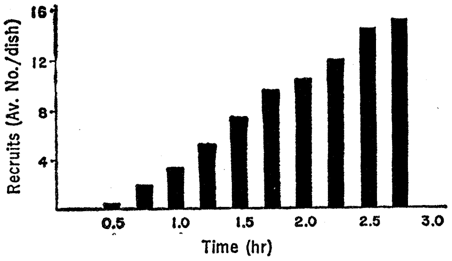

Fig. 1. Daily pattern of recruitment during 26 days in the summer of 1967. Each bar represents the mean number of new recruits killed per 15 minutes in the course of nearly 3 hours, while 20 foragers made regular round trips between the hive and feeding dishes.

the same locations on a subsequent day, even if no scent is used in the solution. The day after odor is used in the food, then, one can run an experiment by using the scented food at a third (control) site which is not visited by any foragers.

This design permits the formulation of mutually exclusive predictions from the two competing hypotheses. If the dance language hypothesis is valid, then recruits should arrive at the sites visited by the regular foragers. However, if the olfaction hypothesis is valid, one should obtain the recruits at a control station if it contains the odor brought into the hive on the previous day, even if no foragers visit such a site.

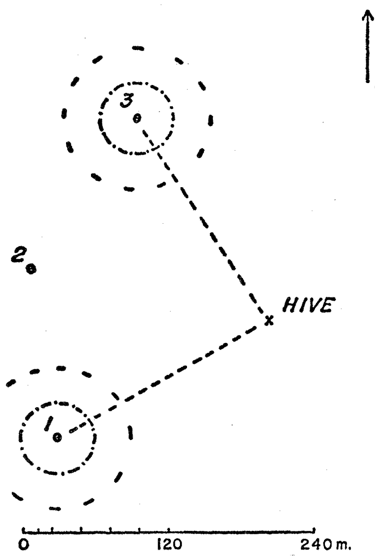

Fig. 2. Relative locations of hive, experimental sites (Nos. 1 and 3), and the control site (No. 2). All three stations were located on relatively level open grassland (dry annual grasses) with no trees between hive and stations. The broken circles around the experimental sites represent approximately one and two standard deviations, respectively, for the "dance language" information. These values were derived by studying "dance" maneuvers in the hive (*17*). The control station (No. 2), therefore, is well outside the areas where the "language" hypothesis predicts recovery of recruits. Wind direction during the series normally rotated slowly from the southeast through the south and to the southwest during the course of each experimental period. The wind never blew from the control station (No. 2) toward the hive. No measurable amount of rain fell during the summer.

The experimental design also provides the basis for a second prediction. If an olfaction hypothesis is the correct interpretation for the set of results obtained in 1967 (Fig. 1), then the number of recruits caught per unit time should not increase on days when experienced foragers collect unscented sucrose solution.

We have now run such a series of experiments. A two-story standard hive with approximately 50,000 Starline hybrid bees was moved onto the "Storke Ranch" area of the University of California, Santa Barbara, on 21 June 1968, and was used during the course of the summer. We selected two experimental sites (Nos. 1 and 3), 280 m from each other and 200 m from the hive (Fig. 2). An intermediate control site (No. 2) at the same distance from the hive was also selected. This choice of experimental and control sites precluded the possibility that new recruits could be simultaneously "misled" by wind patterns to the control site from the two experimental sites (*11*). These distances are approximately equivalent to those used by von Frisch (*1*).

The experimental series began 8 August and ran 24 consecutive days, including 5 days of a related study near the end of the series. Each day's session ran from 8:30 to 11:30 (Pacific Daylight Time). No changes were made in the format during any 1 day. Ten foragers routinely visited each experimental site, with a normal turnover of about ten bees per week. Each dish contained 1.5 molal unscented or scented sucrose solution [20 drops (0.26 ml) of oil of clove per liter of solution]. To control against odor artifacts, a clean dish with fresh solution was used each 15 minutes; each dish rested on a disk of filter paper (also replaced each 15 minutes) on a vinyl-topped feeding platform; each platform was washed at least once each day; and all scented materials were sealed in airtight plastic bags immediately after use.

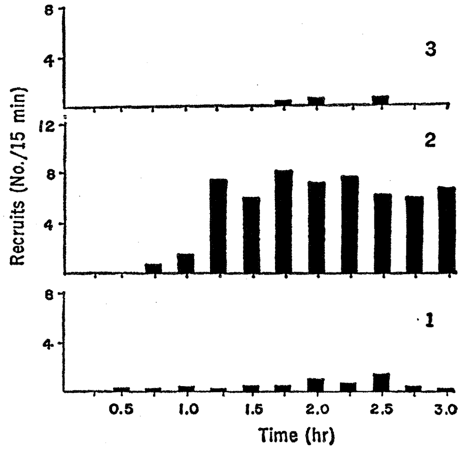

Fig. 3. The average daily recruitment at the three sites on days 2, 7, 12, and 16 of the experiment (Table 1). The control site (No. 2) had scented solution of the type used on the previous day at the experimental sites. No bees foraged at site No. 2.

The format for the first 17 days varied according to a schedule (Table 1) to provide for odor accumulation in the hive for 1 or 2 days and to permit an experimental day subsequent to a day of odor accumulation. Throughout the series we tallied (i) the number of new arrivals per unit time; (ii) the number of trips of individual foragers per 15 minutes; and (iii) the number of times the scent gland (Nassanoff gland) was exposed by each forager in each 15 minutes [some component of the scent gland secretion reportedly attracts searching bees (*12*)]. After being counted, each new recruit was placed in a covered jar of alcohol. At no time did any bees fill at station No. 2 and return to the hive.

Initially, we found that some recruits

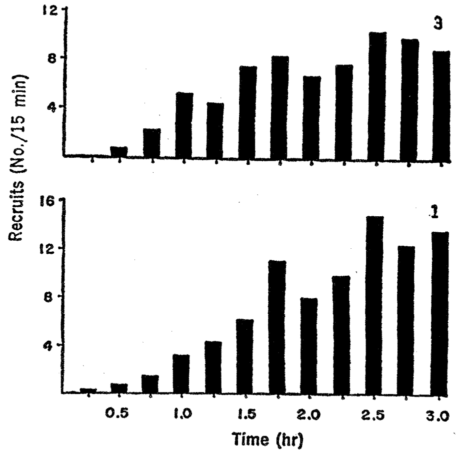

Fig. 4. The average daily recruitment at the experimental sites (Nos. 1 and 3), when no control site (No. 2) existed (that is, days 1, 3, 5, 6, 8, 10, 11, 13, 15, 17, and 23). The steady increase in the number of recruits caught per unit time (after start of experiment) matches the data obtained in the 1967 series (Fig. 1).

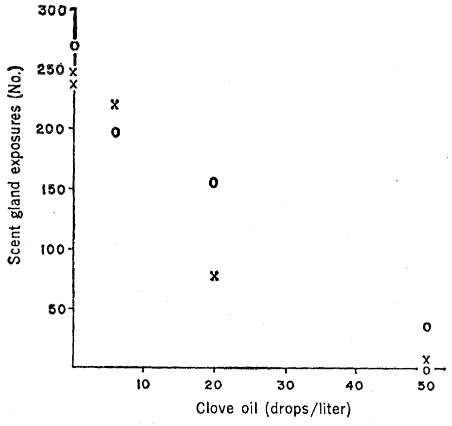

Fig. 5. Data obtained from preliminary experiments testing the effect of the amount of scent in the food on the incidence of Nassanoff gland exposure (days 18 through 22). Station No. 1 (○) had 50, 6, 0, 20, and 50 drops of oil of clove per liter of solution; and station No. 3 (X) had 0, 20, 50, 6, and 0 drops per liter, respectively, on the 5 days of odor variation.

landed only reluctantly at the control station. According to Kalmus (*13*), this is due to a lack of adequate visual and olfactory stimuli generated by the flight activity and odors of foraging bees. To prevent bees from inspecting and rejecting the middle station because of the lack of a necessary "landing factor," we lowered an insect net over the reluctant recruits as they hovered near the dish. This prevented them from arriving at the control station and proceeding upwind to one of the experimental sites (usually No. 1). However, most recruits landed at the dish, attracted in part by the visual stimulus of bee-sized pieces of cellulose sponges placed around the inside circumference of the dish. Care used in transferring bees to the alcohol bottle prevented the release of alarm odor (*14*).

Our results (Table 1) support the olfaction hypothesis and contradict the dance language hypothesis (Table 1 and Fig. 3). Recruits came to the site marked by the food odor but not necessarily to the sites presumably indicated in the hive by the dance maneuvers of returning foragers. This was true, even when the odor had not been used since the previous day. Other experiments with a different hive in another location, in which experimental and control sites were at different distances (370 and 150 m, respectively), yielded comparable results (*15*).

Our results also support the odor accumulation hypothesis. The linear increase in recruitment per unit time occurred when scent was used at the experimental sites (Fig. 4), but did not occur at the control site when foragers collected unscented sucrose at the experimental sites (Fig. 3).

Neither the odor of feeding bees nor the odor from the scent gland provided the problems anticipated (*10*). No site had odor in the food on days 4, 9, and 14; and recruitment of bees was lowest on each of these days. This indicates that searching bees had to be very close to feeding and landing bees before they could use either the odor or the visual pattern of flying or feeding bees. Apparently, the attraction afforded by foraging bees (*13*) was used only after the recruits had chemotactically oriented to the food odor (or distinctive location odor) at that site.

The degree of exposure of the scent gland varied inversely with recruitment (Table 1), and it appeared that the use of unscented sucrose solution contributed to a high rate of gland exposure. To determine whether there is a relation between amount of odor in the food and rate of gland exposure, we varied the amount of odor in the solution at the two experimental sites during a 5-day period after our 17-day sequence. The results (Fig. 5) indicate that the level of exposure of the scent gland can be adjusted by altering the amount of odor in the food. This may also explain why bees do not expose their scent glands when visiting natural food sources such as flowers (*16*).

Three concepts have been examined in the above experiments: odor accumulation in the hive, attractiveness of Nassanoff secretion, and the usefulness of the olfaction hypothesis in predicting the field distribution of recruited bees. Our results show that, although elements of the dance maneuver in the hive do correlate with the distance and direction traveled by regular foragers in the field, the presence of this information in the hive does not appear to contribute to the ecology of foraging or recruitment (*3*).

ADRIAN M. WENNER
Department of Biological Sciences,
University of California,
Santa Barbara 93106
PATRICK H. WELLS
Department of Biology, Occidental
College, Los Angeles, California 90041
DENNIS L. JOHNSON
Department of Life Sciences,
U.S. Air Force Academy,
Colorado Springs, Colorado 80840

References and Notes

1. K. von Frisch, *Osterr. Zool. Z.* **1**, 1 (1946); translation, *Bull. Anim. Behav.* **5**, 1 (1947).
2. K. von Frisch, *Tanzsprache und Orientierung der Bienen* (Springer, New York, 1965), translation, *The Dance Language and Orientation of Bees* (Harvard Univ. Press, Cambridge, Mass., 1967).
3. A. M. Wenner, P. H. Wells, F. J. Rohlf, *Physiol. Zool.* **40**, 317 (1967).
4. A. M. Wenner and D. L. Johnson, *Anim. Behav.* **14**, 149 (1966); D. L. Johnson and A. M. Wenner, *ibid.*, p. 261; D. L. Johnson, *ibid.* **15**, 487 (1967).
5. N. G. Lopatina, *Pchelovodstvo* **84**, 34 (1964).
6. K. von Frisch, *Z. Vergl. Physiol.* **21**, 1 (1934).
7. P. H. Wells and J. Giacchino, *J. Apicult. Res.* **7**, 77 (1968).
8. K. R. Popper, in *British Philosophy in the Mid-Century*, C. A. Mace, Ed. (MacMillan, New York, 1957).
9. D. L. Johnson, *Science* **155**, 844 (1967); A. M. Wenner, *ibid.*, p. 847.
10. A. M. Wenner and D. L. Johnson, *ibid.* **158**, 1076 (1967).
11. K. von Frisch, *ibid.*, p. 1072.
12. M. Renner, *Z. Vergl. Physiol.* **43**, 411 (1960); D. A. Shearer and R. Boch, *J. Insect Physiol.* **12**, 1513 (1966).
13. H. Kalmus, *Brit. J. Anim. Behav.* **2**, 63 (1954).
14. R. A. Morse and A. W. Benton, *Bee World* **45**, 141 (1964).
15. L. J. Friesen and M. Iacaboni, unpublished results.
16. C. R. Ribbands, *The Behaviour and Social Life of Honeybees* (Dover, New York, 1964).
17. E. M. Schweiger, *Z. Vergl. Physiol.* **41**, 272 (1958); A. M. Wenner, *Anim. Behav.* **10**, 79 (1962).
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Pan-Cultural Elements in Facial Displays of Emotion

Abstract. *Observers in both literate and preliterate cultures chose the predicted emotion for photographs of the face, although agreement was higher in the literate samples. These findings suggest that the pan-cultural element in facial displays of emotion is the association between facial muscular movements and discrete primary emotions, although cultures may still differ in what evokes an emotion, in rules for controlling the display of emotion, and in behavioral consequences.*

In studies in New Guinea, Borneo, the United States, Brazil, and Japan we found evidence of pan-cultural elements in facial displays of affect. Observers in these cultures recognize some of the same emotions when they are shown a standard set of facial photographs. This finding contradicts (i) the theory (*1*) that