

Genetic variance in honey bees for preferred foraging distance

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Abstract. In a colony of honey bees (*Apis mellifera* L.) containing two identifiable subfamilies, one subfamily preferentially attended a feeding station close to their hive, rather than a more distant station. Bees working at their 'preferred' distance executed communication dances at a higher frequency than bees working at their non-preferred distance. Recruited bees preferentially attended dances that described a feeding site at their subfamily-preferred distance. Analysis of dances performed by these bees for natural sources of food confirmed that these subfamilies had the foraging distance preferences suggested by the feeding station experiment. Different distributions of subfamily dances were found in all three colonies examined. These results suggest that specialism in foraging tasks may improve colony foraging efficiency and may help maintain polyandry in the species.

Part of the ecological success of honey bees, *Apis mellifera*, relates to the ability of colonies to recruit large numbers of foragers to profitable patches of flowers, and to reduce rates of foraging when flowers are less profitable (von Frisch 1967; Seeley 1985; Seeley et al. 1991; Visscher & Seeley 1982). Successful foragers can stimulate nestmates to seek specific sources of food using odour cues and a body movement known as the wag-tail dance (von Frisch 1967). Information about the distance and direction of the food source is encoded in the dance, and this information is discernable by human observers (von Frisch 1967). A colony works several patches of flowers during the course of a day (Visscher & Seeley 1982), in a fashion that presumably reduces competition, both within and among colonies while maximizing food intake.

Seeley et al. (1991) suggested that division of labour of a colony's foraging bees among the available nectar sources is primarily determined by the cumulative consequence of individual actions. Rates of foraging and communication dancing by individual bees increase when an individual independently judges its forage patch to be profitable, but decline when the individual assesses profitability to be low. By this process, the number of foragers tends to increase at profitable patches and decline at less profitable ones.

Despite this well-developed recruitment system, individual honey bee foragers exhibit extreme specialism in foraging tasks (Free 1963; Wells & Wells 1983). An individual foraging bee has minimal short-term variance in the forage patch or flower species she harvests. Such fidelity maximizes returns to the forager and colony by allowing the bee to become proficient in travelling to a floral patch and in handling a specific flower morphology (Seeley 1985, page 103).

A honey bee queen mates with several haploid drones to produce six to 17 subfamilies of supersisters (reviewed by Page & Laidlaw 1988). A consequence of haplo-diploidy and multiple mating is that bees in different subfamilies have different levels of relatedness. If the parents are not inbred, bees in a particular subfamily have an average coefficient of relatedness of 0.75, while bees of different subfamilies are related by only 0.25 (Page & Laidlaw 1988). Genetic variance for behavioural characters among subfamilies within colonies can manifest as 'task specialization', with members of some subfamilies performing certain tasks at higher frequency than members of other subfamilies (Frumhoff & Baker 1988; Robinson & Page 1988). One of several hypotheses to explain the evolution of polyandry in eusocial insects is the proposal that task specialism may increase colony fitness (Crozier

& Page 1985; Page et al. 1989a; Oldroyd et al. 1992a), since polyandry increases the opportunities for task specialism.

We speculated that individual foraging specialism might have a genetic basis, and would therefore be detectable as subfamily specialism. Genetically determined preferences for pollen or nectar foraging have been demonstrated previously (Calderone et al. 1989; Robinson & Page 1989; Oldroyd et al. 1991). Oldroyd et al. (1991) reported that in four different two-subfamily colonies, members of different subfamilies were found to be distributed at different relative frequencies among two feeding sites and on the roof of a screen cage. Based on that information, we suggested that genetic specialism for foraging distance may also exist in honey bees. In the present paper we describe experiments designed to test that hypothesis.

It has been suggested that honey bees have the ability to recognize super-sisters, and even to act nepotistically towards them (e.g. Evers & Seeley 1986; Noonan 1986; Page et al. 1989b). Oldroyd et al. (1991) demonstrated that bees preferentially follow dances performed by members of their own subfamily compared with dances performed by half-sisters. The mechanism of this bias was not clarified in that study. Bees might be attracted to dances performed by super-sisters because of subfamily recognition, or because super-sisters tend to give information that is attractive to super-sisters. In the present study we further investigate these competing hypotheses.

MATERIALS AND METHODS

The three colonies (A, B, C) produced for these experiments were headed by sister queens homozygous for the *cordovan* (*cd*) mutant. This recessive mutant affects cuticle colour, but has not been reported to affect behaviour. Each queen was inseminated with one hemizygous *cd* drone, and one wildtype (+) drone, producing colonies with two identifiable subfamilies (see Frumhoff & Schneider 1987 for details). In each colony, bees with the *cd* phenotype were designated subfamily-1 and bees with the + phenotype were designated subfamily-2. The *cd* mutant is at high frequency in the population of bees we used, and drones were taken from colonies in an apiary that had not been requeened for many years. Thus, the drones used were not associated with any particular line, and

may be regarded as a random sample of drones in the Baton Rouge area.

Colony A served as the focus for these experiments. During early spring we placed the colony in a three-comb observation hive during a floral dearth. The colony was well populated; we estimate that it had about 5000 bees. Using windows in the hive, we placed a small correction-fluid mark on every bee. Bees were trained to feed at a petri dish containing approximately 2 M sucrose solution supplemented with 10% honey 600 m from the colony. Training took 14 days. After the bees were established at the 600-m station for several days, a second feeding station containing identical food was established 15 m from the colony. Bees could not be trained to both feeders simultaneously because we found that the closer feeder interfered with training for the further distance. When training was completed, 27 bees of each subfamily were marked at both feeders with coloured paints as described by von Frisch (1967), so that each bee was individually identifiable.

Bees worked both feeding stations for 3 days before observations commenced. This should have eliminated any founder effects on subfamily relative frequency by allowing bees to shift allegiance to their preferred feeding station. Observations took place on 7, 11 and 13 March 1991 from 1300–1630 hours. We recorded the arrival of individually identifiable bees at both feeding stations. The total number of subfamily-1 and subfamily-2 bees present at each station were counted and recorded every 10th minute. Any unmarked, (feral) bees that arrived at either station were killed. We also recorded the subfamily of 500 foragers returning to the colony at the beginning and end of each daily observation period.

An observer at the observation hive recorded dances by identified bees. He assessed whether the dance was a wag-tail dance, indicating the 600-m dish, or a round dance for the 15-m dish. That a dancer was dancing for a feeding station and not another source of food was confirmed if she had been seen at the dance-specified feeding place in the previous 10 min.

After the feeding station experiment and during light honey flow, we recorded (1) the subfamily of 844 dancers that did not carry pollen, (2) the number of bees that followed each of these dances for more than one dance revolution, (3) the subfamily of each follower, and (4) computed the number of seconds per dance revolution during the

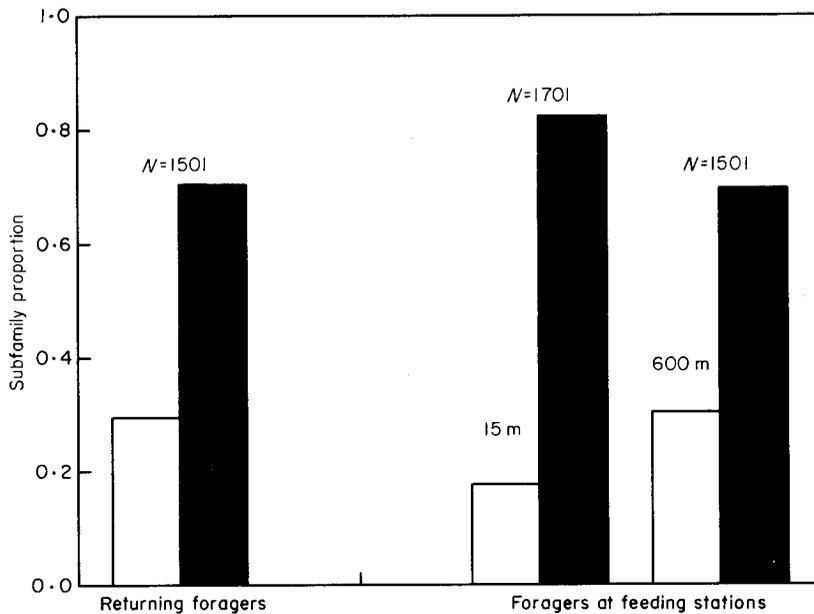


Figure 1. Subfamily proportions at the colony entrance and at 15- and 600-m feeding stations in colony A. □: Subfamily-1; ■: subfamily-2.

period of observation. Data were collected over a 3-week period, and the minimum dance duration recorded was 15 s. These observations were designed to test the hypothesis that the two subfamilies would preferentially work at different feeding sites. If this were so, then a different distribution of dance frequencies among the subfamilies would be expected.

This experiment was repeated on two additional colonies (B and C), except that data on follower bees were not recorded. To ensure that subfamilies within all three colonies did not differ in their dance tempo for the same dance-specified distance, we trained bees to visit a 300-m feeding station using standard techniques (von Frisch 1967), except we used concentrated syrup during training. Dance tempo was determined for individually marked bees of each subfamily at this distance.

For both natural dances and dances by individually marked bees, we used a nested analysis of variance (ANOVA) to test hypotheses concerning dance participants according to the model

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + e_{l(ij)} + \delta_k + (\alpha\delta)_{ik} + (\beta\delta)_{jk} + (\alpha\beta\delta)_{l(ij)k} + \varepsilon_{ijkl}$$

where: Y_{ijkl} = the number of bees of the k th subfamily that followed a dancer of the i th subfamily

dancing for the j th distance in the l th dance. Significant interaction terms from this analysis indicate genetic differences among the two subfamilies for their tendency to follow different kinds of dances. A significant $(\beta\delta)_{jk}$ mean square from this analysis indicates that bees of different subfamilies followed dances for different distances at different frequencies. A significant $(\alpha\delta)_{ik}$ mean square indicates that bees of different subfamilies followed dancing bees of different subfamilies at different frequencies. The model is additive, meaning that the effects of dance-specified distance, subfamily and interactions on numbers of follower bees are fitted simultaneously. Therefore each interaction mean square is independent of the other, and distance specialism cannot give the appearance of subfamily recognition.

RESULTS

For colony A, subfamily proportions differed at the colony entrance, and at the 15- and 600-m feeding stations (G -test of heterogeneity, $P < 0.0001$; Fig. 1). The difference in feeding place ratio was consistent over days ($G_{\text{heterogeneity}} = 5.3$, $df = 3$, $P > 0.25$). Although the total number of bees of both sub-

Table I. Rates of dancing and feeding-station fidelity by colony A

	Feeding station			
	15-m subfamily		600-m subfamily	
	1	2	1	2
7 March 1991				
Total bees observed*	18	27	25	24
Bees recruited†	0	0	0	0
Bees dancing‡	1	6	3	1
Total number of dances	1	8	3	1
% Bees dancing	5.5	22.2	12.0	4.2
Likelihood ratio $\chi^2 = 3.31$ $P = 0.07$ §				
11 March 1991				
Total bees observed	25	29	20	20
Bees recruited	4	5	4	0
Bees dancing	4	16	5	3
Total number of dances	5	47	5	7
% Bees dancing	16.0	55.2	25.0	15.0
Likelihood ratio $\chi^2 = 6.04$ $P = 0.01$				
13 March 1991				
Total bees observed	15	20	11	15
Bees recruited	4	3	4	0
Bees dancing	0	6	3	5
Total number of dances	0	15	3	17
% Bees dancing	0.0	30.0	27.3	33.0
Likelihood ratio $\chi^2 = 4.13$ $P = 0.04$				

*Number of different identifiable bees seen on that day, including bees recruited from the other feeding station.

†Number of bees recruited from the opposite feeding station.

‡Number of bees that danced at least once.

§Probability of independence between subfamily, distance and rates of dancing. Data were analysed using a maximum likelihood, log-linear categorical analysis. Variance was partitioned into the following sources: (1) subfamily, (2) distance, (3) whether the observed bee danced, (4) all possible two-way interactions among the sources of variance and the three-way interaction. The reported χ^2 ($df = 1$) is that associated with the three-way interaction.

families was higher at the 15-m station, the proportion of subfamily-1 bees was higher at the 600-m station than at the 15-m station (Fig. 1).

Subfamily-1 bees marked at the 15-m station performed a total of six dances, while the same number of bees marked at the 600-m feeder performed 11 dances (Table I). Therefore bees of this subfamily were more likely to perform dances for the 600-m station. The reverse was true for subfamily-2. Marked bees of this subfamily at the 15-m feeder performed a total of 70 dances, but only 13 dances at the 600-m station. Thus subfamily-2 bees were much more likely to dance for the nearby location than the distant location (Table I).

Subfamily-1 bees followed dances indicating the 600-m station more often than dances indicating the 15-m station, while subfamily-2 bees followed both kinds of dance in approximately equal numbers (Fig. 2). The mean square for the interaction between follower subfamily and dance distance, $(\beta\delta)_{ik}$ was significant ($P = 0.02$), indicating that dancers for the two distances varied in their attractiveness to recruits of the different subfamilies, independent of the subfamily of the dancer. However, the mean square for the follower subfamily by dancer subfamily interaction, $(\alpha\delta)_{ik}$, was also marginally significant ($P = 0.063$), indicating that recruits of one or both subfamilies may

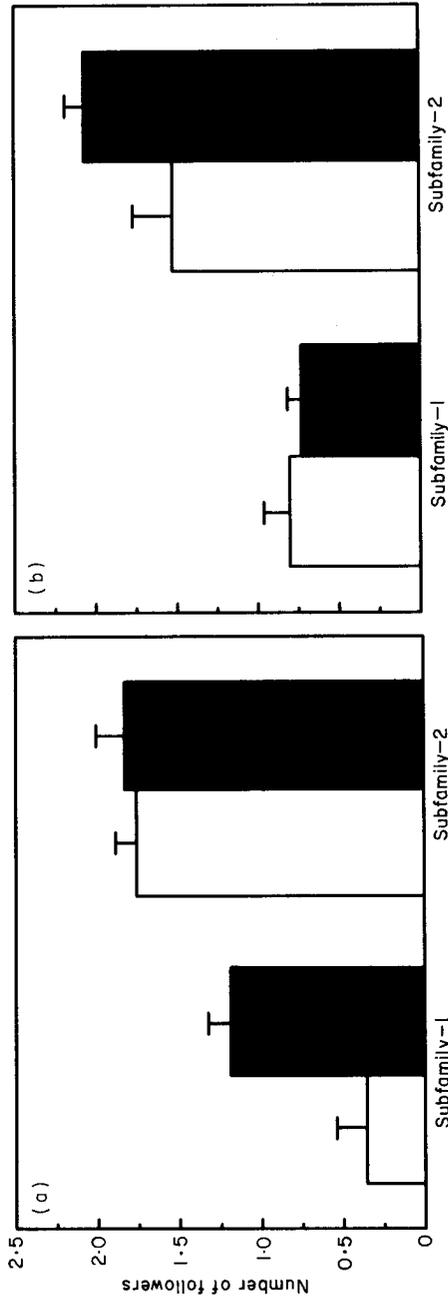


Figure 2. Least-square-mean (\pm SE) number of followers of the two subfamilies in colony A that followed dances of various kinds. (a) Bees that followed dances indicating the 15-m feeding station (\square ; $N = 78$ dances) and the 600-m station (\blacksquare ; $N = 58$). (b) Bees that followed dances performed by subfamily-1 (\square ; $N = 23$) and subfamily-2 (\blacksquare ; $N = 113$). The total number of dances is higher than that in Table I as several additional dances were recorded when one or the other feeding station was unattended by an observer.

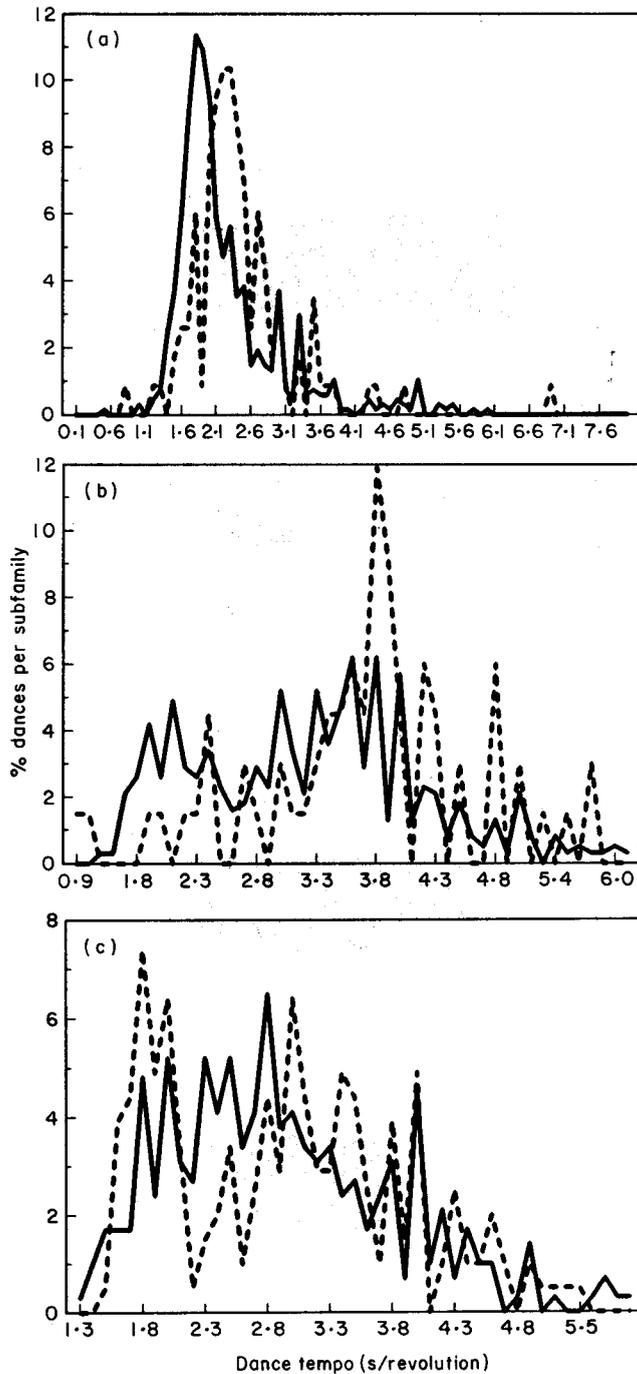


Figure 3. Dance tempo of dances for natural sources of nectar. The figure shows the percentage of dances per subfamily (excluding round and transition dances) observed for each dance frequency for subfamily-1 (---) and subfamily-2 (—). (a) Colony A, data collected in April 1991. The distributions were significantly different (Kolmogorov–Smirnov test $P < 0.01$, subfamily-1: $N = 119$ dances; subfamily-2: $N = 725$ dances). (b) Colony B, data collected September–October 1991. The distributions were significantly different ($P < 0.01$; subfamily-1: $N = 67$, subfamily-2: $N = 385$). (c) Colony C, data collected October–November 1991. The distributions were significantly different ($P = 0.01$; subfamily-1: $N = 158$; subfamily-2: $N = 266$).

Table II. Dance tempos (s/revolution) of bees of different subfamilies dancing for a 300-m feeding station

	Colony A	Colony B	Colony C
Mean subfamily-1 (N*)	2.1 (6)	2.0 (12)	2.4 (11)
Mean subfamily-2 (N)	2.0 (34)	2.0 (12)	2.3 (8)
Range subfamily-1	1.9-2.4	1.8-2.3	2.2-2.8
Range subfamily-2	1.6-2.6	1.7-2.3	2.1-2.5
Total dances	84	33	26
F-test, nested ANOVA†	$P=0.25$	$P=0.76$	$P=0.23$

Data for colony C were collected in cool windy weather.

*Number of different bees that danced.

†Probability that the observed differences among subfamilies were due to chance.

have preferentially followed dancers of a particular subfamily, independent of the dance-specified distance. Bees of both subfamilies preferentially followed dancing super-sisters, with subfamily-2 displaying the strongest preference (Fig. 2).

Figure 3 indicates substantial differences between subfamilies in their dance-specified distances to natural feeding sites in all three colonies examined. Although both subfamilies showed the same peaks of dance activity at many dance frequencies, the overall distribution of dances differed significantly among subfamilies within every colony examined (Fig. 3). This suggests that in all three colonies, subfamilies were distributed differently in the field. In colonies A and B, subfamily-1 showed a tendency to forage further away from the hive than subfamily-2. In colony C, the distribution of subfamily-1 appeared to be bimodal, but appreciably different from that of subfamily-2. These differences are not due to a subfamilial difference in the algebraic relationship between feeding-site distance and dance tempo. Subfamilies in all colonies showed the same peaks of activity at particular dance tempos. Furthermore, analysis of dance tempos for bees foraging at a 300-m feeding station showed no subfamilial differences in all colonies (Table II).

In Colony A, the subfamily-2 recruits to dances for natural sources showed distance preferences, although no such preferences were evident for subfamily-1 (Fig. 4). Independent of dancer subfamily, subfamily-2 bees attended dances indicating nearby sources of food, and twice the rate of

dances indicating the most distant sources of food. Thus subfamily-2 recruits to dances showed the same preference for shorter distances as they did in the feeder study, while subfamily-1 bees showed no discernable preference for dances indicating long or short distances. The interaction between dance-specified distance and follower subfamily was highly significant ($P=0.0029$). Again, however, even after the effects of dance-specified distance were accounted for by the model, bees of both subfamilies attended more dances by members of their own subfamily than the other subfamily ($P=0.0097$; Fig. 4).

DISCUSSION

The results from the feeding station demonstrated variance in allocation of foragers of different subfamilies to different locations. Bees of subfamily-2 were found in a higher proportion at the 15-m feeder than at the 600-m feeder, suggesting a preference by bees of this subfamily for nearby sources of food. Bees of subfamily-1 were found at a higher proportion at the 600-m feeder, suggesting that bees of this subfamily were less affected by distance.

These distance preferences are reflected in dancing data from both the feeder and natural forage study for colony A. In the feeder study, bees of subfamily-1 were extremely unlikely to dance for the 15-m feeder, but had a higher rate of dancing for the 600-m feeder. The reverse was true for subfamily-2: the rate of dancing was much lower for the 600-m feeder than for the 15-m feeder. We may speculate that had a feeding station been established even further away from the colony, rates of dancing might have further declined for subfamily-2, while remaining constant for subfamily-1.

In the study of dances for natural forage by colony A, the distribution of dances performed by subfamily-1 bees indicated sources of food further from the colony than those performed by bees of subfamily-2. Furthermore, the bees of different subfamilies were differentially attracted to dances indicating different distances. The attractiveness of dances rapidly declined with distance for bees of subfamily-2, but less rapidly for bees of subfamily-1.

Thus, a short distance preference by subfamily-2, and a longer distance preference by subfamily-1 was reflected in forager distribution among feeding stations, the probability of dancing and the

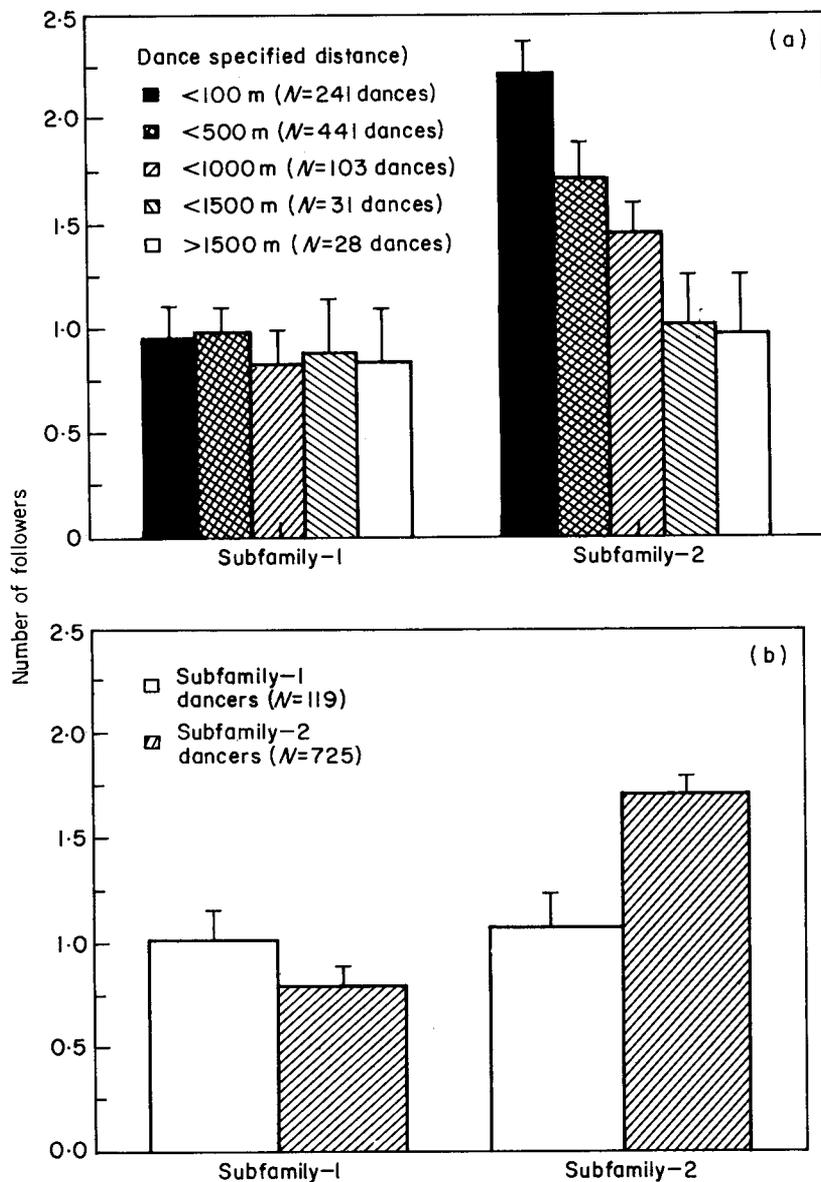


Figure 4. Least-square-mean (\pm SE) number of bees of each subfamily in colony A that followed dances for natural sources of nectar. (a) The effect of dance-specified distance on the number of followers of each subfamily. The dance specified distance was estimated from Fig. 63 in von Frisch (1967). (b) The effect of dancer subfamily on the number of followers of each subfamily.

attractiveness of dances to recruits. These differences were never inconsistent, but not always apparent. For example subfamily-1 showed no distance preferences when following dances for natural foraging sources, but showed a strong preference for 600-m dances over 15-m dances in the feeder study.

Perhaps factors other than dance-specified distance play a role in the attractiveness of dances.

The model of Seeley et al. (1991) predicts that different thresholds for dancing would have the effect of distributing subfamilies at different locales in the field. Observations on the dancing behaviour

of three colonies foraging on natural sources of nectar revealed different distributions of dance tempos among subfamilies, indicating that subfamilies in our experimental colonies were distributed differently in the field. If these results can be extrapolated to natural colonies with many subfamilies, then genetic variance for foraging distance could increase the foraging efficiency of colonies by increasing the probability that a colony would discover new sources of food and reduce the possibility that certain floral patches would be over-exploited.

In summary, our data suggest that subfamily differences can occur in honey bee colonies for: (1) relative attractiveness of food sources located at different distances from the hive; (2) tendency to dance for food sources located at different distances from the hive; and (3) tendency to attend dances indicating food sources at different distances from the hive. Each of these lines of evidence supports the hypothesis that genetic variance among subfamilies for foraging distance exists in honey bees. A falsifiable prediction of this hypothesis is that honey bees foraging on natural resources would be heterogeneously distributed according to subfamily. Our observations of three colonies foraging for natural sources confirmed that such heterogeneity does exist. Furthermore, Oldroyd et al. (1992b) demonstrated that bees of different subfamilies tend to forage on different species of plants for pollen. For these reasons we conclude that genetic variance for foraging preference was present among the subfamilies studied. We speculate that genetic variance in the threshold of stimulus that will cause participation in a communication dance is the mechanism by which these differences in foraging preference are determined.

Why does this genetic variance exist? A plausible explanation is a selective advantage of a genetically diverse foraging population (Page et al. 1989a). Crozier & Page (1985) suggested that polyandry maximizes the opportunity for genetic diversity among workers in social hymenoptera. Under this hypothesis, species like honey bees which are found over a broad ecological range are expected to be polyandrous and to display polyethism for foraging. Our data demonstrate that such polyethism does exist, thereby supporting their hypothesis. An alternative explanation is that introductions of different ecotypes of bees into the New World may have generated genetic variance for the characters studied that would not normally be present in natu-

ral populations. Bees used in this study were bred from colonies that had not been requeened for many years, and were therefore not associated with any particular 'line', reducing the possibility that recent selection or immigration caused the effects we observed. In any case, demonstration of behavioural genetic variance even in completely natural populations of social insects (as has been recently reported in ants by Stuart & Page 1991) can only be supportive of explanations for the evolution of polyandry; never prove them.

We were unable to determine whether the unequal proportions of bees foraging at the feeders were due to foraging rate or recruitment rate. Crowding at the feeding stations made it impossible to record exact arrival and departure times of individually marked bees.

Differential sperm usage by a queen may produce different age profiles between subfamilies. Young bees are more likely to attend communication dances and to forage for nectar rather than pollen (Lindauer 1953). Thus different age profiles might result in different subfamily-related distributions of bees in the field, and influence the probability of bees attending or performing dances. However, non-genetic models are inadequate to explain the tendency of subfamily-2 bees of colony A to be found at consistently higher frequency in dances specifying nearby sources of nectar in both experimental and field situations. Furthermore, subfamily proportions did not change during the course of these experiments (data not presented) and older queens, such as we used, have higher stability of subfamily relative frequency than younger queens (Laidlaw & Page 1984; Page et al. 1984).

We previously reported (Oldroyd et al. 1991) that honey bees preferentially follow dances performed by super-sisters, but cautioned that task specialization could cause bees with genetic predisposition to particular floral sources to attend dances specifying those sources, thus giving the appearance of subfamily recognition when none in fact exists. In the analyses presented in Figs 2 and 4, the effects of task specialization are controlled. Nectar and pollen specialism is not a factor, since only bees without pollen on their corbiculae are reported. The effects of distance are partially removed by the statistical model. The tendency of bees to preferentially follow dances executed by super-sisters remains evident, suggesting either that there may be further elements to foraging

specialism which remain to be identified, or that subfamily recognition is an element of honey bee sociality.

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