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Intracolonial variance in honey bee foraging behaviour: the effects of sucrose concentration*+

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SUMMARY

The foraging response to varying sucrose concentrations of a colony of honey bees comprised of two identifiable subfamilies was determined. Bees of one subfamily never danced after foraging on a 2 mol/litre sucrose solution, while bees of the other subfamily often did so. Bees of both subfamilies responded to lowered sucrose concentration by reducing the number of foraging trips per hour, although one subfamily altered its rate of foraging more dramatically. When offered a 1 mol/litre sucrose solution at one feeding station and a 3 mol/litre solution at another after training with a 2 mol/litre solution, most bees did not switch to the more profitable feeding station. Rather, they remained faithful to their initial station, but reduced rates of foraging when sucrose concentration was reduced.

The mean duration of dances was longer for one subfamily than the other, which increased the number of bees that followed dances performed by bees of that subfamily. Under one set of experimental conditions, dances indicating a 3 mol/litre solution attracted more followers than dances for a 2 mol/litre solution. We speculate that faithfulness to a particular foraging location is adaptive, since the time needed to learn a new location has a cost. We further speculate that genetic variance for rates, duration and attractiveness of dances may be adaptive, since these differences have the effect of spreading subfamilies among locales. Thus honey bee polyandry increases fitness by increasing eclectic foraging.

Keywords: honey bees, *Apis mellifera*, dance communication, foraging, subfamilies, subfamily differences, task specialization, recruitment, genetic variance

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INTRODUCTION

When honey bee behaviour is genetically variable among the 6–17 subfamilies (reviewed by Laidlaw & Page, 1984) that make up a colony, members of different subfamilies undertake different tasks at different rates under the same stimuli. The phenomenon is known as 'task specialization' (Robinson & Page, 1988), and has been demonstrated for a wide range of honey bee behaviour (reviewed by Page & Robinson, 1991; Oldroyd *et al.*, 1992a). Similar genetic variance has also been reported in ants (Stuart & Page, 1991).

The widespread occurrence of genetic variance for behavioural characters suggests some kind of colony-level selective advantage for polyethism. Crozier and Page (1985) suggested that the selective advantage of behavioural variability within colonies may have been a factor in the evolution of polyandry in the social insects.

Behavioural differences among subfamilies appear to be regulated by the threshold that will cause an individual to initiate the behaviour (Robinson & Page, 1989). That is, the probability that an individual will initiate or cease a particular behaviour is influenced by its inherent tendency to act (genotype) and by the strength of the external stimulus (environment). The environmental component can be further divided into the individual's physical and social environment. For example, Calderone and Page (1991, 1992) demonstrated that the probability that a bee of a particular age and genotype will forage for nectar or pollen depends to some extent on the genotype of her nestmates and the environment that they provide. Thus a colony's phenotype is not an additive function of the genotypes of its constituent subfamilies (Moritz & Southwick, 1987; Moritz & Hillesheim, 1989; Robinson & Page, 1989; Oldroyd *et al.*, 1992a). Subfamily structure causes the relationship to be decidedly interactive.

One aspect of honey bee colony survival and fitness is related to their ability to efficiently allocate foraging bees to the changing array of available nectars and pollens. Seeley *et al.* (1991) suggested that allocation of foragers among available nectar resources is regulated by the combined effects of individual actions. According to their model and empirical analysis, a foraging bee assesses the relative profitability of her forage patch according to her independent assessment of such factors as distance from the colony, sugar concentration in the harvested nectar, and the needs of the colony. She modulates the duration of dances and foraging tempo according to her assessment of these criteria.

Here we investigate the role of subfamily structure on the way an experimental colony allocated its foragers among sucrose resources. We report on subfamily variance for some of the crucial variables (duration of dances, recruitment and foraging tempo) of the forager allocation model of Seeley *et al.* (1991), and discuss how subfamily variance for these variables could lead to division of labour in foraging tasks.

MATERIALS AND METHODS

Experiments were performed at the Burden Research Plantation in Baton Rouge, Louisiana, USA. We used one colony derived from a homozygous cordovan (*cd*) queen inseminated with one wild-type (+) drone (sire of subfamily 2) and one *cd* drone (sire of subfamily 1). The frequency of subfamily-1 bees in the colony was approximately 20%. Bees with the *cd* phenotype have a tan integument (Tucker, 1986). The *cd* allele is recessive, so the two subfamilies in the colony were easily identifiable. The *cd* phenotype has not been reported to affect behaviour, except perhaps that cuticle colour markers may affect subfamily recognition (Carlin & Frumhoff, 1990; Frumhoff, 1991; Visscher, 1991). The drones used for the insemination were caught at the entrance of two randomly chosen hives at the same apiary. The apiary had not been requeened for many years, therefore neither drone was from any particular line.

The colony was housed in a three-frame observation hive, and had two brood combs and 3 000–4 000 bees. We used windows in the hive to mark every bee with a small drop of rapidly-drying paint. As young bees emerged during the course of experiments, they were also marked. As these experiments were by necessity performed over several weeks, individual identification of every bee was not possible.

Experiments were performed during uniformly hot and humid conditions in August and September, 1991. Very little natural forage was available for the colony. The experimental colony was maintained with as little food as possible by removing honey-filled combs and replacing them with empty ones as the experiment progressed.

Bees were trained to feeding stations using standard techniques (von Frisch, 1967). Feeding stations consisted of a 500 ml plastic specimen jar in which 30 holes (1 mm diameter) had been drilled in a row just below the level of the lid. The jars were inverted over a blue cardboard card. Bees were trained using a 2 mol/litre sucrose solution supplemented with a few drops of peppermint essence. (A 1 mol/litre solution contains 342 g of sucrose dissolved in one litre of water.)

Each bee that arrived at a feeding station was grasped by an observer, and uniquely identified by gluing a small coloured, numbered disc on her thorax (Opalithplättchen, Chr. Graze, Endersbach, Germany). Any bee that arrived without a paint mark was assumed to be from a feral colony and was destroyed.

Experiments commenced after at least 10 bees of the least frequent subfamily were regularly seen at both feeding stations. Under two experimental arrangements, we varied the sucrose solution concentration contained in the feeders and measured the effects on foraging and recruitment behaviour. Observers at the feeding stations recorded the arrival time of every bee. Observers at the observation hive recorded the identity of every bee that performed a communication dance indicating a feeding station, the duration of those dances, and the number of bees of each subfamily that followed a dance. Follower bees were identified as those that followed the dancer for more than one revolution of the dance.

These data were collected in a slightly different way than in the studies of Oldroyd *et al.* (1991, 1992b). In the present experiment we tried to count every bee that followed at some point in the dance, if necessary calling out to the co-observer the phenotype of bees that joined the dance. In our previous studies, we did not count bees that joined the dance; only the bees following when the dance was first observed. That a bee was dancing for a feeding station and not a natural source of food was confirmed if she had been seen at the dance-specified feeding station in the previous 10 minutes. The presence of two observers at the observation hive reduced the probability that any dances were missed.

Data were analysed with ANOVA models, with all effects fixed except days which were considered random. Of particular interest were significant interactions between subfamily and sucrose concentration effects on the rates of foraging and communication dancing. That is, we focused on whether our two experimental subfamilies varied in their response to changing nectar rewards.

Experiment 1

Subfamily responses to changing rewards at two feeding stations

The experimental arrangement was similar to that of Seeley *et al.* (1991). Bees were trained to two feeding stations, one designated the Herb Garden (HG) and one the Cyprus Forest (CF), for two weeks. Both stations were 300 m from the colony. The sites were separated by dense woods, and the bee flight paths to the two sites were obvious and very different. Observations commenced on 21 August 1991, and continued the next day. The experimental design is presented in table 1. A 1 mol/litre sucrose solution was provided at one station, and a 3

TABLE 1. Plot design of the experiments.

Experiment 1.

Time	Sucrose concentrations (mol/litre)			
	HG feeding station:		CF feeding station:	
	21 Aug	22 Aug	21 Aug	22 Aug
08.00–11.00 h	2	2	2	2
11.00–14.00 h	3	1	1	3
14.00–17.00 h	1	3	3	1

Experiment 2.

Time	Sucrose concentrations (mol/litre) at the CF feeding station				
	29 Aug	11 Sept	12 Sept	14 Sept	16 Sept
09.00–10.00 h	2	2	2	2	2
10.00–11.00 h	0.5	3	4	1	2
11.00–11.30 h	2	2	2	2	2
11.30–12.30 h	3	1	2	4	0.5
12.30–13.00 h	2	2	2	2	2
13.00–14.00 h	1	4	0.5	2	3
14.00–14.30 h	2	2	2	2	2
14.30–15.30 h	4	2	3	0.5	1
15.30–16.00 h	2	2	2	2	2
16.00–17.00 h	2	0.5	1	3	4

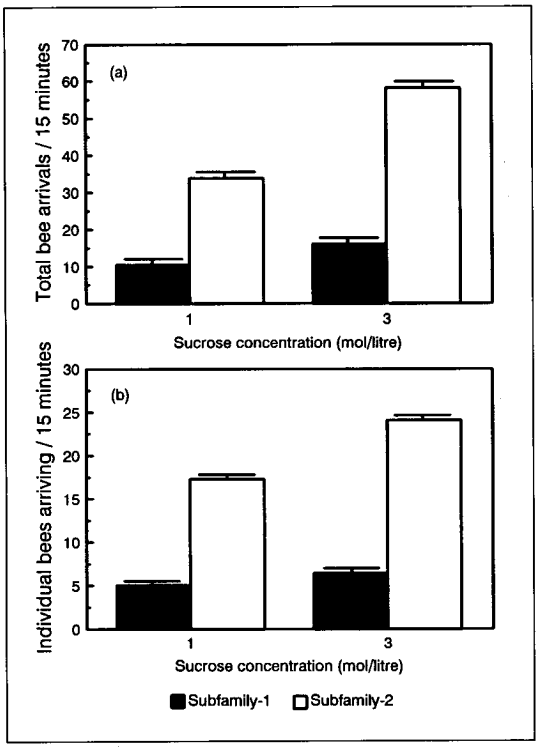

FIG. 1. Least-square mean number of bees arriving at two feeding stations. (a) Total bees arriving per 15 minutes. (b) Unique bees arriving per 15 minutes. Bars indicate the magnitude of the standard errors.

mol/litre solution at the opposite station. The response of bees of the different subfamilies in terms of foraging tempo and number and duration of dances was determined.

Experiment 2

Subfamily responses to changing rewards at one feeding station

In this experiment, conducted after experiment 1, the HG station was shut down so that bees were flying to the CF feeding station only. The concentration of sucrose solution was changed regularly, in a latin square design (Steel & Torrie, 1980) as shown in table 1. To reduce carryover effects among treatments, the feeding station was provided with 2 mol/litre sucrose solution for 30 minutes between treatments (table 1).

Ambient temperature varied from 26°C to 30°C on each day of the experiments. No rain or appreciable wind was recorded on any days of the experiments (data were not collected when the weather was unsuitable).

RESULTS

Experiment 1

The experimental colony responded to an increase in concentration of sucrose syrup by increasing both the number of individual bees which foraged on the 3 mol/litre dish and the total numbers of visits to that dish (fig. 1, table 2). However, the two subfamilies did not respond equally to changes in sucrose concentration. The interaction between the effects of

TABLE 2. ANOVA of arrival rates (total bee arrivals per 15 minutes), and bee visits (number of different bees arriving per 15 minutes), by two subfamilies offered a 1 mol/litre and 3 mol/litre sucrose solution at two different locations.

Source	d.f.	Arrival rates		Bee visits	
		Mean square	*P*	Mean square	*P*
Day (D)	1	2.44	0.3	10.04	0.0001
Concentration (C)	1	74.01	0.0001	12.03	0.0001
Location (L)	1	52.25	0.0001	34.80	0.0001
C*L	1	2.14	0.3	1.42	0.1
Time(D*C*P)	91	2.36		0.62	
Subfamily (S)	1	470.01	0.0001	224.60	0.0001
S*C	1	11.62	0.0001	1.79	0.0001
S*L	1	0.43	0.3	1.27	0.0008
S*L*C	1	0.07	0.2	0.11	0.3
Error	92	0.03		0.10	

Sources of variation are as follows: Day is one of two consecutive days in August 1991; Concentration is the effect of two concentrations of sugar syrup (1 mol/litre and 3 mol/litre); Location is the effect of feeding site; Time is the effect of time of day (i.e. the 15-minute time blocks). To stabilize variance, data were transformed with a square-root transformation.

TABLE 3. Response by foragers to a decrease in sucrose concentration from 3 mol/litre to 1 mol/litre. Entries are the numbers of foragers in each subfamily that stopped, changed or maintained their foraging activity at their feeding station.

Forager response	Day 1		Day 2	
	Subfamily 1	Subfamily 2	Subfamily 1	Subfamily 2
Stopped foraging	1	3	2	8
Continued foraging at original site	2	17	10	37
Changed sites to higher concentration	3	3	5	12

Bees arriving only for the first 15 minutes after a change have been excluded from the table.

sucrose concentration and subfamily was highly significant both for total bee visits and for the numbers of individual foragers (table 2). Therefore, the subfamilies differed in the way they responded to changing sucrose concentration, in both the number of individual bees that foraged and the total bee arrivals. Fig. 1 demonstrates that the cause of this interaction was the higher level of response to changing conditions displayed by subfamily 2 relative to subfamily 1.

Changes in resource exploitation were due more to changing effort by individuals rather than recruitment between the two feeding stations. Bees had a high degree of fidelity to their initial feeding station. Less than 20% of bees changed to the feeding station providing a higher reward when sucrose concentration was lowered (table 3); they merely reduced their rate of foraging (fig. 1) or stopped foraging altogether (table 3). There is some suggestion (table 3) that bees of subfamily 1 were more likely to change to the station providing the highest reward, although the difference is only marginally significant (χ^2 of pooled days = 5.3, $P = 0.07$, d.f. = 2).

Eighty-six different subfamily-1 and 314 different subfamily-2 bees visited at least one feeding station during the two days of the experiment. Subfamily-1 bees performed a total of of 48 dances after a total of 1 283 dish visits. Subfamily-2 bees performed a total of 342 dances after a total of 4 423 dish visits. With two exceptions, bees of neither subfamily were observed to dance for a feeding station provided with a 1 mol/litre sucrose solution. The two bees that were the exceptions danced shortly after a changeover. For the 3 mol/litre solution, 27.7 ± 4.7% ($n = 12$ hourly-observation periods over two different days) of subfamily-1 bees that visited a feeding station in any one hour danced at least once during that hour, while 37.4 ± 4.8% of subfamily-2 individuals did so. These proportions are not significantly different ($P = 0.19$). However, subfamily-2 bees were much more likely to perform repeated dances than subfamily-1 bees. Only 5.9 ± 3.5% of all subfamily-1 visits to a 3 mol/litre feeding station resulted in a communication dance ($n = 12$ hourly-observation periods, total of 48 dances) while 12.8 ± 4.7% (total of 342 dances) of subfamily-2 visits did. The difference is significant ($P = 0.003$).

The mean duration of subfamily-1 dances for 3 mol/litre sucrose was significantly longer ($P = 0.045$) than that of subfamily-2 dances for 3 mol/litre sucrose solution (table 4). Thus bees of both subfamilies followed dances performed by subfamily-1 bees at a higher rate than dances performed by subfamily-2 bees (table 4). However, there was no significant interaction between dancer and follower subfamily ($P = 0.47$), indicating no subfamily recognition.

Bees dancing for a 2 mol/litre solution attracted significantly fewer followers ($P = 0.03$) of either subfamily than bees dancing for a 3 mol/litre solution (table 4), and the duration of dances indicating a 2 mol/litre solution was significantly lower than dances indicating a 3 mol/litre solution ($P = 0.006$). Note, however, that the 2 mol/litre solution was only offered in the morning, and the 3 mol/litre in the afternoon. Thus in this case, time of day and sucrose concentration are completely confounded.

Experiment 2

The total number of bee arrivals per hour at a single feeding station was affected by the day of the experiment and the concentration of the available syrup,

but not by the time of day (table 5). The number of individual bees foraging was also affected by the day of the experiment, the concentration of syrup available at the feeder, as well as the time of day (table 5). Bees of both subfamilies responded to increasing sucrose reward by increasing the number of visits per hour (fig. 1). Rates of recruitment (as measured by the number of individual bees which arrived at the feeder per hour) also increased in response to increasing sucrose concentration (fig. 2).

The rates of arrival and recruitment increased with sucrose concentration. One exception to this trend was the 3 mol/litre solution, which produced lower rates of arrival and recruitment than expected (fig. 2). This result is probably due to day and time of day interactions.

Significant interactions were observed between subfamily and day, and between subfamily and time of day (table 5), on rates of foraging. This indicates that genotypic differences existed between the two subfamilies studied in their response to changing envi-

TABLE 4. Least square mean (± s.e.) number of bees that followed dances of various kinds, and the least square mean (± s.e.) duration (seconds) of dances.

Kind of dancer	Number of dances	Mean duration (seconds)	Subfamily of followers	
			Subfamily 1	Subfamily 2
Experiment 1.				
2 mol/litre sucrose dancers				
Subfamily 1	0	–	–	–
Subfamily 2	53	21.4 (± 4.0)	0.65 (± 0.17)	1.84 (± 0.34)
3 mol/litre sucrose dancers				
Subfamily 1	48	42.5 (± 4.8)	1.05 (± 0.19)	2.75 (± 0.36)
Subfamily 2	342	32.3 (± 1.7)	0.73 (± 0.06)	2.68 (± 0.11)
Total	390	32.9 (± 1.3)	0.77 (± 0.10)	2.69 (± 0.10)
Experiment 2.				
3 mol/litre sucrose dancer	65	54.0 (± 5.8)	1.90 (± 0.46)	3.42 (± 0.47)
4 mol/litre sucrose dancer	134	44.4 (± 5.0)	2.36 (± 0.38)	3.24 (± 0.39)
Subfamily 1 dancer	14	62.1 (± 7.3)	2.70 (± 0.57)	3.91 (± 0.59)
Subfamily 2 dancer	185	36.3 (± 2.1)	1.55 (± 0.16)	2.74 (± 0.16)

TABLE 5. ANOVA of arrival rates (total bee visits per hour), and bee visits (different bees per hour), of a two-subfamily colony foraging at a single feeding station, where sucrose concentration was continuously varied.

Source	d.f.	Arrival rates		Bee visits	
		Mean square	*P*	Mean square	*P*
Day	4	28.89	0.047	5.26	0.0003
Concentration (C)	4	53.42	0.006	1.44	0.04
Hour	4	17.23	0.160	2.48	0.007
Error (a)	12	8.66		0.41	
Subfamily	1	99.88	0.0001	14.34	0.0001
Subfamily*Day	4	9.28	0.001	1.86	0.0001
Subfamily*C	4	1.21	0.35	0.12	0.21
Subfamily*Hour	4	4.23	0.02	0.24	0.05
Error (b)	12	0.99		0.071	

To stabilize the variance, the data were transformed with a square-root transformation.

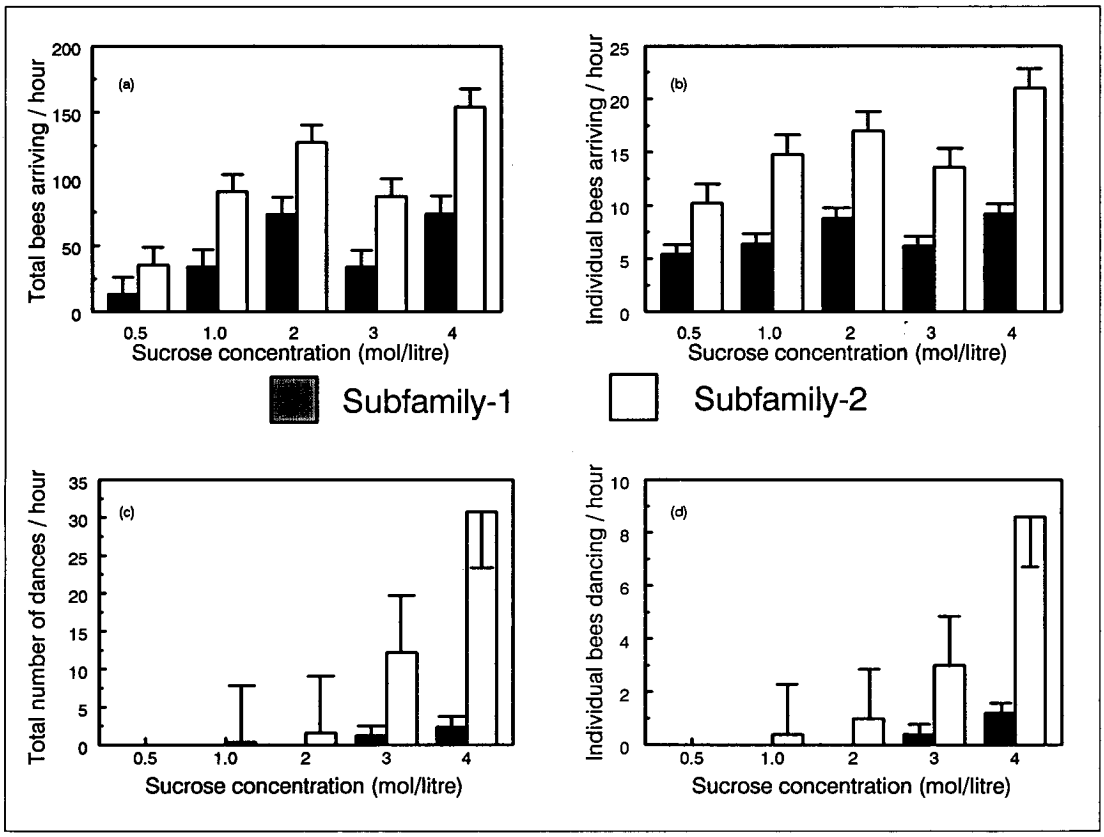

FIG. 2. Least-square means of foraging activity by a two-subfamily colony offered syrup of various sucrose concentrations. (a) Total number of bees arriving per hour. (b) Number of unique bees arriving per hour. (c) Total number of communication dances performed by bees foraging at the feeding station. (d) Number of unique bees that danced per hour. Bars indicate the magnitude of the standard errors

ronment. However, contrary to the results of experiment 1, analysis of transformed data indicated there was no significant interaction between subfamily and sucrose concentration for either rates of recruitment or total bee visits to the feeder (table 5). Despite this lack of significance, inspection of the untransformed means in figure 2 suggests that subfamily 2 showed greater response in the number of foraging bees to a changing syrup concentration. Indeed, ANOVA of these untransformed data demonstrated a significant subfamily by concentration interaction for the number of individual foragers ($P = 0.04$). Thus a weak interaction was probably present for the number of individual foragers, but obscured by the more powerful interactions with day and time of day and the smaller graduations in sucrose concentration in experiment 2.

Bees of the two subfamilies varied in the stimulus that would initiate communication dances. ANOVA revealed significant ($P = 0.002$) subfamily by concentration interactions for the probability that a bee would dance. The origin of this interaction is clear from figure 2: bees of subfamily 1 never danced for a 2 mol/litre sucrose solution, while bees of subfamily 2 often did so. These results are confirmed by those of experiment 1. During the morning training period when a 2 mol/litre sucrose solution was offered, bees of subfamily 2 were often observed to perform recruitment dances, whereas bees of subfamily 1 never did so.

As with experiment 1, subfamily-1 dances were significantly ($P = 0.0009$) longer than subfamily-2 dances, when the colony was foraging on either 3 mol/litre or 4 mol/litre solutions (table 4). Contrary to experiment 1, the number of bees that followed dances did not differ according to the concentration of sucrose solution that the dancing bee was foraging on ($P = 0.79$), but subfamily-1 dancers attracted significantly more followers than subfamily-2 dancers ($P = 0.03$) (table 4). There was no significant interaction between dancer subfamily and follower subfamily ($P = 0.95$), again indicating no subfamily recognition.

DISCUSSION

These data provide a mechanism by which bees of different subfamilies could be caused to forage at different locales, as suggested by Oldroyd *et al.* (1991, 1992b, 1992c). If we view our present data in the light of Seeley's model of collective decision-making by foraging honey bees (Seeley *et al.*, 1991), a mechanism by which such heterogeneity could come about emerges. Critical variables in Seeley's model include: rates of foraging, i.e. the frequency (tempo) of foraging trips; the probability of abandoning a feeding site in response to a falling reward; the probability of performing a recruitment dance in relation to food reward; and the duration of each recruitment dance. The experiments reported here demonstrate that responses to changing reward, rates and duration of dances can be variable among subfamilies for several of the critical variables in the model of Seeley *et al.* (1991).

This variability among subfamilies within a colony for rates of recruitment and communication dancing has the potential to generate uneven distributions of subfamilies among resources. Bees of our subfamily 2 initiated communication dances at a lower sucrose concentration than bees of subfamily 1. It is known that dances of different tempo (measured in revolutions per second) vary in their attractiveness to recruits of different subfamilies (Oldroyd *et al.*, 1992b). The data presented here suggest that under some circumstances (i.e. the conditions of experiment 1), dancers carrying sucrose loads of different concentration can attract bees of different subfamilies at different rates (table 4). Further, subfamilies can differ in the mean duration of the dances they perform. The combination of varying probability of dancing, varying probability of attending various kinds of dances, and varying duration of dances among subfamilies, could combine to distribute subfamilies in different proportions at different flower patches.

Allegiance by individuals to known forage patches (Seeley *et al.*, 1991; and this study), and differential rates of abandonment and recruitment to food resources of different kinds among subfamilies, could further enhance the processes that lead to heterogeneous distribution of bees of different subfamilies among floral patches. Forage patch fidelity is probably adaptive, since it prevents abandonment of patches which are only temporarily poor and reduces any learning cost in locating a new forage patch (Seeley, 1985).

We conclude that subfamilial variability for the components of the model of Seeley *et al.* (1991) provides a plausible mechanism for heterogeneous distribution of subfamilies in the field, and the available data suggest that such heterogeneous distributions actually exist in naturally foraging colonies (Oldroyd *et al.*, 1992b, 1992c).

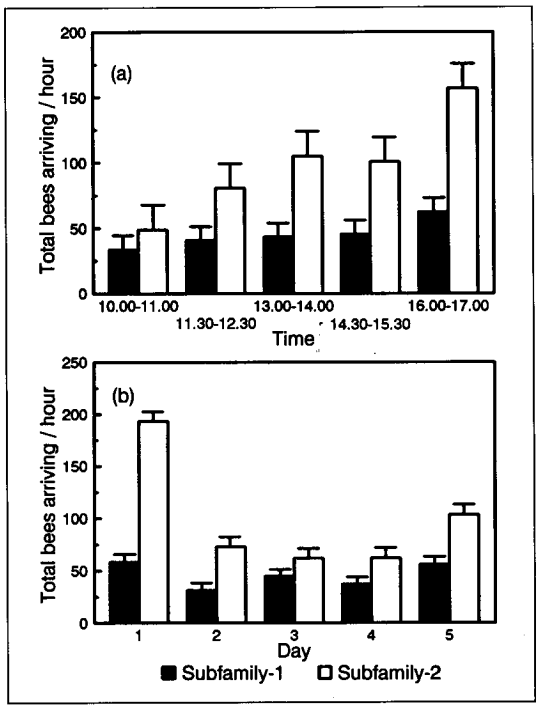

FIG. 3. Effects of date and time of day on rates of foraging. (a) Mean number of bees arriving per hour at different times of day. (b) Mean number of bees arriving on different days. Bars indicate the magnitude of the standard errors.

Age of bees affects their foraging behaviour in terms of their tendency to dance and forage for nectar or pollen (Lindauer, 1953). Age distributions among subfamilies can probably differ due to non-random sampling of sperm by the queen (Taber, 1955), and these different age profiles could probably generate differences among subfamilies in foraging behaviour. However, these differences are likely to be small in older queens such as the one used here (Laidlaw & Page, 1984; Page *et al.*, 1984). A more plausible mechanism is genetic differences among the subfamilies. We did not observe a single subfamily-1 bee perform a recruitment dance for a 2 mol/litre solution, while many subfamily-2 dances were observed. It is difficult to envisage how such a repeatable difference in behaviour could be anything but genetic in origin.

Oldroyd *et al.* (1992c) speculated how task specialization in foraging behaviour could have adaptive significance. Among several possibilities, our favoured hypothesis is that eclectic foraging increases colony nutrition by increasing the range of plant species harvested by a colony. The present experiment was limited to two subfamilies, with a genetic marker that could conceivably influence dancing behaviour, hence we cannot generalize from this

experiment that genetic variance for the traits studied is widespread in natural honey bee populations. However, there exists at least the possibility that honey bee polyandry increases fitness by increasing eclectic foraging. Of course the uncovering of genetic diversity does not indicate whether or not this diversity is adaptive. Such variance could come about through other causes, such as recent introductions of diverse genotypes into North America.

Finally, we have previously reported that bees which follow recruitment dances tend to follow dances performed by super-sisters rather than half-sisters (Oldroyd *et al.*, 1991, 1992b), but cautioned that task specialization rather than subfamily recognition was a likely cause of our observations. If bees of particular subfamilies have a genetic predisposition to particular foraging tasks, then they will be attracted to super-sister dancers of similar predisposition. Data from the present experiments show a strong tendency for bees of both subfamilies to follow dances performed by subfamily 1, giving the appearance of subfamily recognition for subfamily 1 but not for subfamily 2. Thus, overall, no subfamily recognition effect was detectable. This result is consistent with the hypothesis that such associations are due to task specialization rather than subfamily recognition.

In the present experiment, subfamily-1 bees danced longer than subfamily-2 bees, meaning they attracted more recruits of both subfamilies. No other task specialization was possible under the conditions of these experiments. Hence, overall, no positive subfamily associations could be discerned.

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