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Genotypic variability in age polyethism and task specialization in the honey bee, *Apis mellifera* (Hymenoptera: Apidae)

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Summary. The currently accepted model for division of labor in honey bees, *Apis mellifera,* explains variation in the frequency at which workers perform specific tasks as the result of differences in age and environment. Although well documented, the model is incomplete because it fails to take genotypic variability among workers into account. We show that workers from two genetically distinct strains of honey bees differed in the age at which they began foraging and in the relative frequency at which they foraged for pollen. Workers from the two strains also exhibited significant spatial heterogeneity within the nest, suggesting that they differed in the frequency at which they performed within-nest tasks as well. A heuristic model of division of labor that incorporates genotypic effects is presented.

Introduction

Division of labor is a cornerstone of insect societies. It is generally believed that division of labor results in increased efficiency of task performance because individuals specialize on fewer tasks (Oster and Wilson 1978). Colonies of highly social insects are characterized by a primary division of labor between reproductive and worker castes and a secondary division of labor among workers (worker polyethism). Within the worker caste, specialization has been achieved primarily through the evolution of morphological and age castes.

Division of labor in the honey bee, *Apis mellifera,* has been extensively studied (Rösch 1925, 1927, 1930; Lindauer 1953a, b; Seeley 1982; and reviewed by Free 1965; Seeley 1985). Our current interpretation of this body of research is that workers progress through a series of overlapping age castes. Workers in a given age caste perform a specific set of tasks more frequently than other sets of tasks. One of the clearest demonstrations of this mechanism is seen in the difference between young bees that undertake work in the nest and older bees that forage.

This model of division of labor has been widely accepted (cf Kolmes 1986), but it may be deficient because it does not account for genetic variability with respect to the rate of age-caste ontogeny or to the probability of performing specific tasks within an age caste. Ribbands (1952) concluded that division of labor is not genetically influenced. Summarizing the existing research at the time, Oster and Wilson (1978) state that workers start development genetically fixed only to sex and are otherwise totipotent with respect to caste. More recent research suggests that this is not the case.

Genotypic variability in worker honey-bee behavior has been reported. Genetic differences between bees of South American (Africanized) and North American (European) origin in the ontogeny of age polyethism are suggested by the work of Winston and Katz (1982). Dominance behavior, as reflected in the frequency of receiving versus giving food during trophallaxis, was shown to be heritable in *A. m. capensis* (Moritz and Hillesheim 1985). Hellmich et al. (1986) found that Africanized workers produced 15 times as many drones as European workers in mixed colonies following removal of the queen. Collins et al. (1982) found racial differences among Africanized and European workers in several components of defensive behavior.

Selection experiments with honey bees have revealed genetic variability in the frequency of performance of specific tasks. Workers from a strain susceptible to American Foulbrood (AFB, a lethal bacterial infection of honey bee brood) did not

uncap or remove diseased brood, but workers from a resistant strain performed both tasks (Rothenbuhler 1964). Hellmich et al. (1985) selected different strains of honey bees that hoarded high versus low amounts of pollen, thereby demonstrating a significant genetic component to variation in that colony phenotype. These strains provide a valuable tool with which to investigate the significance of genotypic variability among workers on specific behavioral components of division of labor. We studied workers from these strains, and in this paper we present evidence for genotypic effects on three behavioral traits related to worker polyethism: 1) the age at which bees first begin foraging, 2) the distribution of foragers among foraging age-caste tasks, and 3) the distribution of workers within the nest with respect to locations at which different tasks are performed.

Methods

Stocks and rearing conditions

Worker honey bees were obtained from the 1985 generation of high and low pollen-hoarding strains descended from stocks originally selected by Hellmich et al. (1985) and maintained at The Ohio State University since 1979. Each strain has three sublines within which individuals are bred according to the mating system depicted in Fig. 1.

Generally, six queens per subline were evaluated each generaton. Selection was based on colony performance. Queens from colonies with the greatest amount of hoarded pollen (high sublines) or the least amount of hoarded pollen (low sublines) were chosen to be parents of the next generation. In each generation each queen was instrumentally inseminated with the semen from a single drone (one drone per queen) (for details see Hellmich 1983).

Virgin queens from high and low sublines were mated in 1984 to unrelated drones from colonies exhibiting high and low pollen-hoarding phenotypes, respectively, to maintain satisfactory brood viability and to introduce additional genes. Subsequent generations were evaluated for quantities of hoarded pollen to insure that these strains continued to exhibit significant differences in pollen-hoarding behavior. In 1985, the average amount of pollen hoarded by all colonies from the high strain was 574.1 $cm^2 \pm 32.59$ S.E. ($n=20$) (S. E.'s are used throughout this paper) and 91.9 $cm^2 \pm 10.48$ ($n=17$) for all colonies from the low strain (F-test, $P<0.01$).

Variation in the rearing environments of workers from the two strains was controlled. A colony from each strain was provided with an empty comb that had previously been used for brood rearing. After 48 h, the combs with eggs were transferred to a single nursery colony that was unrelated to either strain. Thus, all brood from both colonies were raised by workers at the same time in the same environment. After pupation, combs were transferred to a single incubator (50% RH and 32–35° C) until adult emergence.

Three-hundred fifty newly-emerged workers, 0–12 h old, were collected from a brood comb of a single queen of each strain. Each worker was individually marked on the thorax and then placed in a wire mesh holding cage. Immediately after tagging all workers, 175 from each strain were placed into each

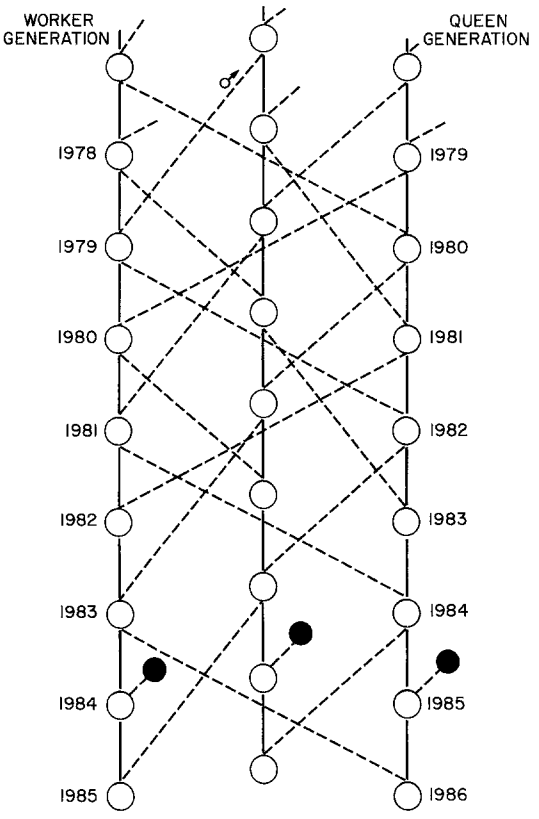

Fig. 1. Mating system used for the selection and maintainance of high and low pollen-hoarding strains. This is the pedigree for one strain (high or low). *Each vertical column* represents a maternal subline. *Dotted lines* represent male gametes. *Solid circles* indicate unrelated queens used in an outcross

of 2 colonies. Each colony had a naturally-mated queen and contained about 10000 adult workers that were unrelated to the test bees. Each colony contained approximately 2.5 combs of brood in all developmental stages, and stores of pollen and honey. Colonies were transferred to four-frame observation hives (Gary and Lorenzen 1976) on the morning following introductions and placed in an observation-hive shelter (Rothenbuhler et al. 1968). One colony faced south and the other west (hereafter referred to as the south and west colonies). Observations began the following day when the workers were in their third day of adult life.

Observations of pollen foraging activity

Foraging activity was monitored in both colonies. Colony entrances were provided with glass-covered ramps that permitted observations of arriving and departing bees. A small quantity of vegetable oil was applied to the lower surface of the glass to prevent the workers from walking upside down on the glass surface insuring that the tags of bees on the ramp were always visible (N.E. Gary, unpublished). Observations were made at each entrance for 1.5 h periods on 24 consecutive days beginning around noon each day. The following information was recorded whenever a marked bee was observed: 1) the identity of the individual worker, 2) whether the bee was arriving or departing, 3) the time of day, and 4) the presence or absence of any pollen in the corbiculae (arriving only).

Incoming workers were initially scored as either carrying pollen or not carrying pollen based on the presence or absence of any pollen in the corbiculae. Workers that carried pollen were classified as pollen foragers. Workers that did not carry pollen were subdivided into two groups: those on an orientation flight (difference between the times of departure and return was less than 5 min) and undetermined foragers (round-trip time was greater than or equal to 5 min). A round-trip time of at least 5 min has been widely supported as a valid criterion by which to differentiate foraging flights from orientation flights (Sekiguchi and Sakagami 1966; Winston and Katz 1982; Robinson 1985). Bees observed returning without pollen during the first 5 min of an observation period and workers leaving but not seen returning to the hive during the last 5 min of an observation period were not included in any category. Bees leaving more than 5 min before the end of the period and not seen to return during that period were classified as foragers but were not included in any comparisons between pollen foragers and undetermined foragers.

The distributions of foragers between pollen foraging and undetermined foraging tasks for each strain were compared using 2×2 contingency table analyses. The chi-square statistic is used throughout this paper unless otherwise indicated. Data from daily observation periods were combined into six larger periods as follows: days 7, 8, 9, 10, 11 and 12; days 13, 14 and 15; days 16, 17 and 18; days 19, 20 and 21; days 22, 23 and 24; and days 25, 26 and 27. This was done in order that all cells in the contingency tables would have a minimum expected value of five or more. The *G*-test adjusted for small sample size (see Sokal and Rohlf 1981) was used when the minimum expected cell frequencies were less than 5 even after combining. Data from each of the combined periods in each colony were analyzed separately. Colony effects on each strain were evaluated by comparing the foraging trip distributions for a given strain from one colony with the distributions for the same strain from the other colony.

Differential mortality combined with age polyethism within the foraging-age caste, or with task-specific mortality, could produce spurious results. Survivorship of workers of the two strains within each colony was investigated in each of the six combined periods. The number of workers surviving during a period and the number dying during that period for each strain were analyzed using 2×2 contingency tables (*G*-test). The number of workers alive at the beginning and end of each period were obtained from census data (see below).

Age at first foraging flight

Data for the number of workers foraging for the first time on each of the 24 days were used to construct cumulative relative frequency distributions for each strain within each colony. Comparisons between strains within each colony and between workers of the same strain in different colonies were made using the Kolmogorov-Smirnov Test (*K-S* Test; see Sokal and Rohlf 1981). This non-parametric test was used because the distributions did not meet the assumption of normality required for an analysis of variance.

Location within the nest

The genotype of a worker may affect its location within the nest because of the spatial organization of tasks (Seeley 1982). If workers of different genotypes perform within-nest tasks at different frequencies, then a spatial heterogeneity of genotypes may be observed.

Observations were made of tagged workers inside the nest on days 7, 9, 10, 11, 12, 15, 17, 18, 20, 21, 23, 24, 26 and 27 by visually scanning both sides of each frame of each observation hive from top left to bottom right (one scan/side/day). Each side of both observation hives was overlaid with a transparent Plexiglas® grid containing 128, 58 mm × 58 mm squares that facilitated scanning. The identity of every observed tagged bee and the contents of the cells upon which that individual was seen (or the location within the nest where that individual was seen) were recorded.

Observations were grouped into the following 5 categories: 1) FOOD: bees were on cells that contained pollen, nectar or honey; 2) OPEN BROOD: bees were on cells that contained eggs or larvae; 3) CAPPED BROOD: bees were on cells that contained capped brood only; 4) FLOOR: bees were located in the area below and adjacent to the bottom comb; and 5) OTHER: bees were located on wooden frames and empty cells.

Data from daily observations were combined into three periods: days 7, 8, 9, 10, 11 and 12; days 15, 17 and 18; and days 20, 21, 23 and 24. Data from each period in each colony were analyzed separately using 2×5 contingency tables. Combining was done in order that all cells in the contingency tables would have an expected value of 5 or more. Survivorship of workers from each strain within each colony was investigated in each of the three combined periods using the previously described method.

Population census

Estimates were made of the number of marked bees present in colonies on days when data were available from both the foraging and location observations. A bee was considered present on any given day if it was seen on that day or on a subsequent day. The number of bees present in a colony on days for which both types of data were not available were estimated by linear interpolation. These data were used to assess differential mortality between strains within combined observations periods.

Results

Workers belonging to different selected strains show differences in the way they partition their labor among tasks. These differences demonstrate the presence of genotypic variability for components of division of labor within honey bee populations.

Observations of pollen foraging activity

Pollen foraging behavior is dependent upon both the genotype of the bee and the environment in which that behavior is expressed. In the west colony, workers from the high pollen-hoarding strain returned with pollen loads a greater proportion of the time than did workers from the low-hoarding strain in each of the 6 combined periods (Fig. 2A; $P < 0.01$ in each period). The proportion of pollen-foraging trips among all foraging trips was 0.65 for the high strain compared to 0.04 for the low strain. In the south colony, significant differences between strains in the proportion of pollen-foraging trips occurred in the last 4 combined periods (Fig. 2B; $P < 0.01$ in periods 3, 4, 5 and

6). The overall proportion of pollen foraging trips was 0.65 for the high strain compared to 0.18 for the low strain. These differences are not an artifact resulting from differential mortality combined with age polyethism within the foraging-age caste or with task specific mortality. Differential mortality was found only in period 4 in the south colony (Table 1).

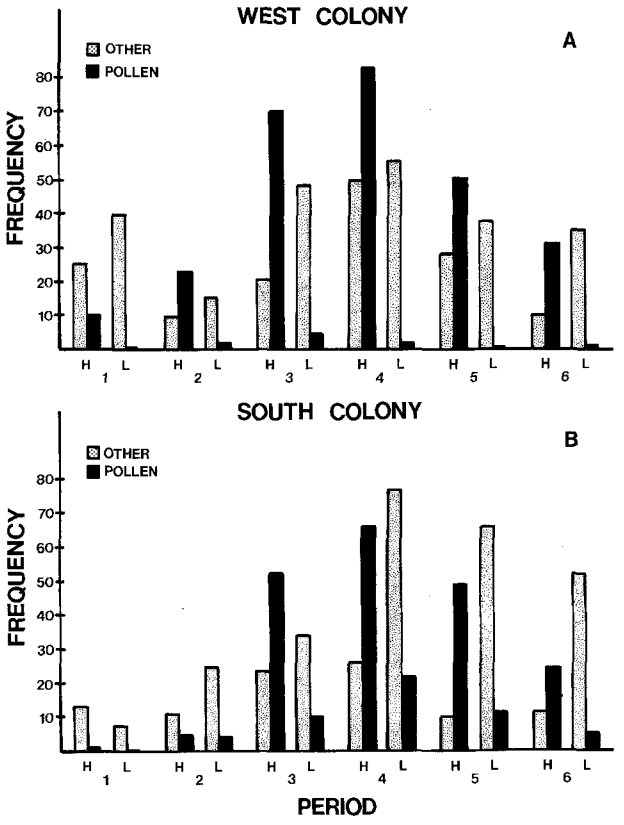

Fig. 2A, B. Frequency of POLLEN foragers and undetermined (OTHER) foragers for each strain (*H* high strain, *L* low strain) in the west colony (**A**) and the south colony (**B**) during each of the 6 combined periods. Individual workers are counted each time they were seen in each period. Significant differences ($P < 0.01$) were found in each of the 6 periods in the west colony and in periods 3, 4, 5 and 6 in the south colony

Data shown in Fig. 2A, B were used to evaluate colony effects on each strain. For the high pollen-hoarding strain, there were significant colony effects on the proportion of pollen-foraging trips in period 2 ($P < 0.01$) and period 4 ($P < 0.05$). For the low-hoarding strain, colony effects were significant in period 2 ($P < 0.05$) and periods 4 and 5 ($P < 0.01$).

Two additional analyses were performed to establish the specific behavioral mechanism responsible for the observed differences in foraging activity. The proportions in the preceding analyses were based on all foraging trips recorded during each observation period. This may include more than one observation per period on some individuals. Consequently, they provide a measure of pollen-foraging activity as a proportion of total foraging activity and are independent of a specific behavioral mechanism. One explanation for the observed differences in the proportion of pollen foragers between these two strains is a higher level of foraging activity on the part of a few individuals. The influence of increased activity levels was reduced by repeating the above analyses but counting each individual only once in each daily observation period. For these analyses, the foraging category assigned to an individual was based on the first time that individual was seen during an observation period.

Strain differences do not appear to be the result of increased activity on the part of a few individuals. Analyses of the data sets in which each individual was counted only once during any daily ob-

Table 1. Tests for differential mortality between High and Low strains in the West and South colonies in each of the 6 combined periods (analysis of observations on pollen foraging activity)

Period	Days	West colony					South colony				
		High strain		Low strain			High strain		Low strain		
		S	D	S	D	G	S	D	S	D	G
1	7–12	132	18	112	26	2.60 ns	122	13	141	15	0 ns
2	13–15	124	5[a]	102	7[a]	0.50 ns	115	5[a]	137	3[a]	0.93 ns
3	16–18	108	11	87	10[a]	0.02 ns	103	80	129	6[a]	1.13 ns
4	19–21	77	22	64	15	0.28 ns	64	27	109	16	9.31*
5	22–24	43	20[a]	42	16	0.32 ns	35	19	69	25	1.19 ns
6	25–27	30	9[a]	27	10	0.22 ns	20	10	38	21[a]	0.03 ns

*$P < 0.01$; ns = not significant; S = number of workers surviving during a period; D = number of workers dying during a period; G = G-statistic, see Sokal and Rohlf (1981)

[a] Value by linear interpolation rounded to closest integer

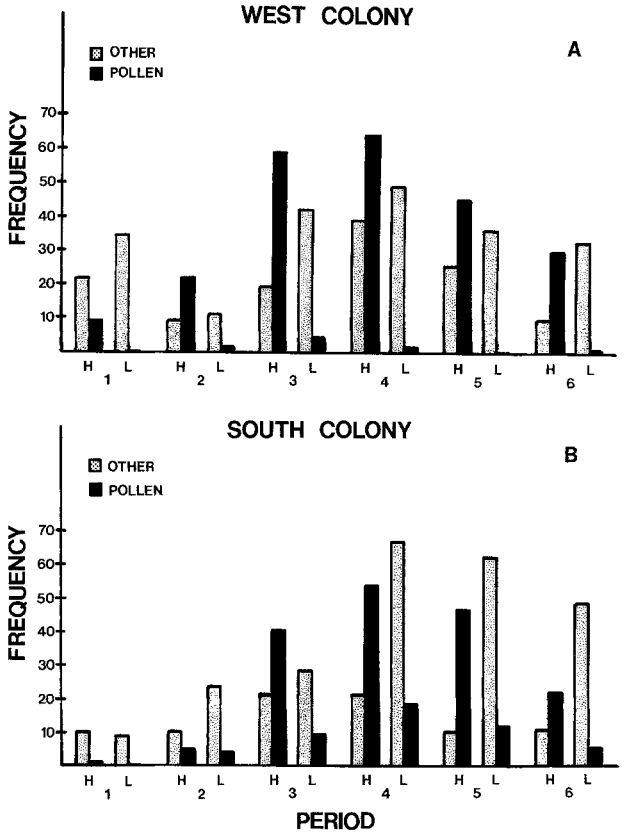

Fig. 3A, B. Frequencies of POLLEN foragers and undetermined (OTHER) foragers for each strain (*H* high strain, *L* low strain) in the west colony (**A**) and the south colony (**B**) during each of the 6 combined periods. Individual workers are counted only the first time they were seen on each day. Significant differences ($P<0.01$) were found in each of the 6 periods in the west colony and in periods 3, 4, 5 and 6 in the south colony

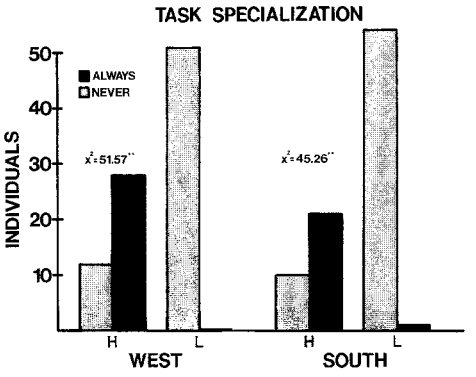

Fig. 4. Frequencies of workers from both strains (*H* high strain, *L* low strain) in the west and south colonies observed either returning with pollen every time they were seen (ALWAYS) or never observed to return with pollen (NEVER). Significant differences were found in each colony (west colony: $X^2=51.57$, $P<0.01$; south colony: $X^2=45.26$, $P<0.01$)

servation period, yield nearly identical results to those found for the original data sets (Fig. 3A, B).

An alternative mechanism explains the observed differences as a result of variation in the degree of task specialization at the individual level. This was investigated using the most stringent classification available: the number of individuals seen to carry pollen on all trips on which they were observed compared to the number of individuals never seen to carry pollen on any of the trips on which they were observed (only those individuals seen more than one time were considered). Data from each colony were analyzed separately using 2×2 contingency tables. Colony effects were evaluated as previously described.

Seventy percent (west colony) and 68% (south colony) of workers from the high strain satisfying the above criterion specialized in pollen foraging compared with 0% (west colony) and 2% (south colony) of workers from the low strain (Fig. 4; $P<0.01$ in each colony). Colony effects were not significant for either strain ($P>0.05$).

Age at first foraging flight

Groups of workers made the transition from within-nest tasks to outside tasks at different ages in one colony but not in the other. In the south colony, workers from the high strain took their first foraging trip at an average age of 16.8 ± 0.32 days ($n=100$); workers from the low strain at an average age of 18.1 ± 0.40 days ($n=122$) (*K-S* Test: $d_{max}=0.25$, $P<0.01$; Fig. 5B). In the west colony, average ages were 15.9 ± 0.40 days ($n=131$) for workers from the high strain and 15.8 ± 0.49 days ($n=110$) for workers from the low strain (*K-S* Test: $d_{max}=0.09$, $P>0.05$; Fig. 5A).

Environmental effects were also observed. Both strains foraged earlier in the west colony than did their super sisters (see Laidlaw 1974 for the use of the term super sister) in the south colony (*K-S* Test: $d_{max}=0.21$, $P<0.05$ for the low pollen-hoarding groups; $d_{max}=0.28$, $P<0.01$ for the high pollen-hoarding groups).

Location within the nest

Workers belonging to high and low pollen-hoarding strains exhibit significant spatial heterogeneity with respect to the 5 location categories previously described. This suggests that workers from these strains differ in the frequencies with which they perform within-nest tasks. In the south colony, there were significant genotypic effects in each of the combined periods (Fig. 6; $P<0.05$ in period 1, and $P<0.01$ in periods 2 and 3). In the west colony, genotypic differences were significant in one

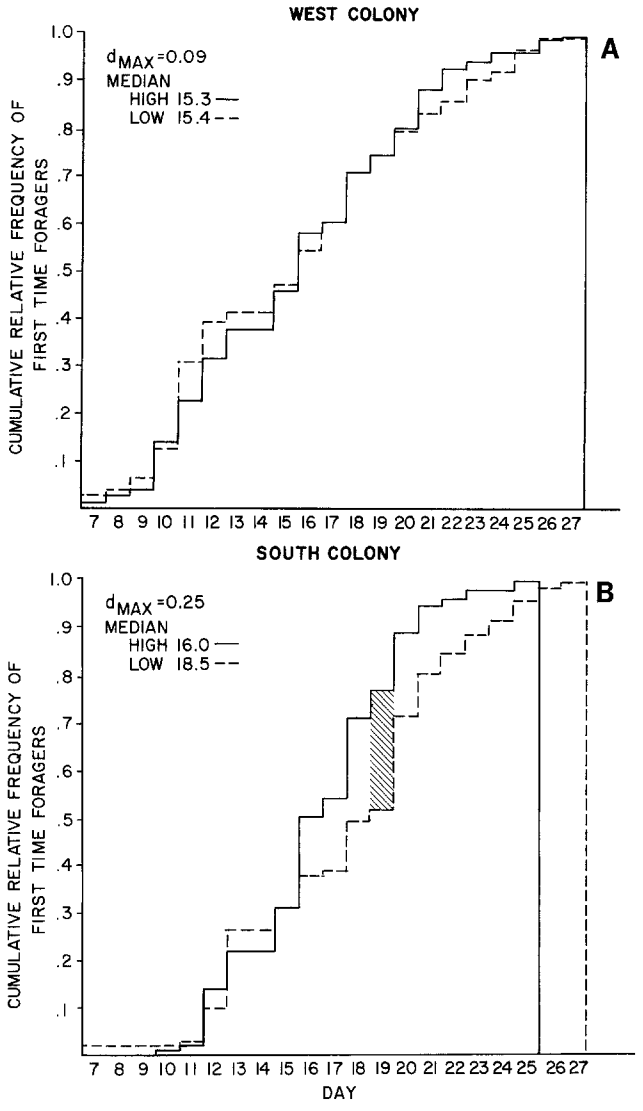

Fig. 5A, B. Cumulative relative frequency distributions of workers observed foraging for the first time on each day in the west colony (**A**) and the south colony (**B**). The height of a curve on any day indicates the proportion of those workers that would eventually become foragers that had already begun to forage by the end of that day. Distributions were compared using the Kolmogorov-Smirnov Test. In the south colony the d_{max} value was significant ($P<0.01$)

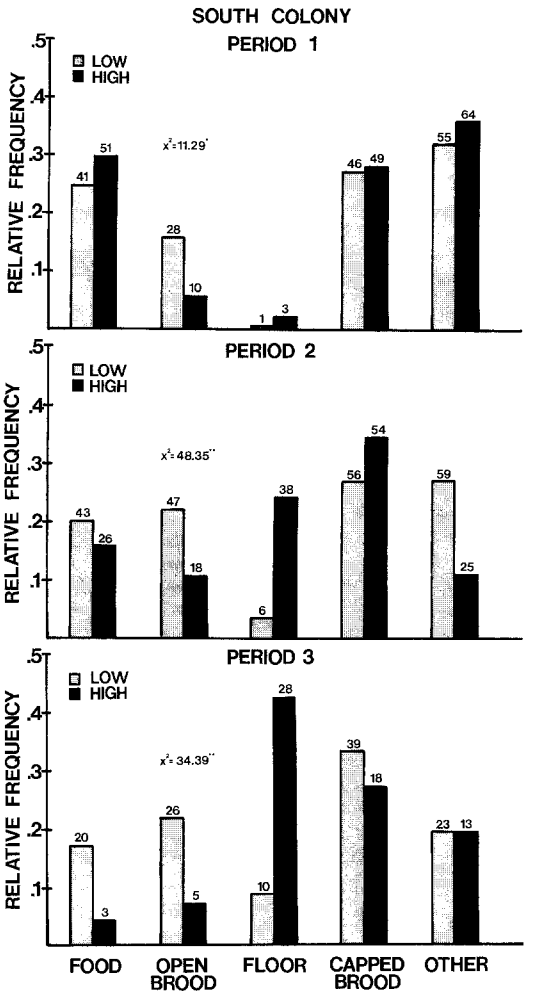

Fig. 6. Relative frequencies of workers from the high and low pollen-hoarding strains at each of 5 task performance locations in the south colony in each of the 3 combined periods. See text for complete description of these locations. Significant differences were found in each period (*$P<0.05$, **$P<0.01$; $df=4$ for each test). Numbers on each bar are the actual number of individuals counted

of three periods (Fig. 7; $P<0.05$ in period 1). These differences are not a simple consequence of differential mortality combined with age polyethism or with task specific mortality. Differential mortality was not detected in any of the combined periods.

In the south colony, a greater relative frequency of workers from the low strain were observed on open brood (eggs and larvae) compared to workers from the high strain. This difference is evident in each of the 3 periods. This suggests that workers from the low strain spend a greater proportion of their time engaged in brood care tasks compared to workers from the high strain. Similar conclusions can be drawn for each of the other location categories where the two strains showed distributional differences.

The data in Figs. 6 and 7 suggest that the distributions of workers with respect to the location categories change over time and do so in a way unique to each strain. A preliminary investigation of this question was conducted. Specific comparisons were made between pairs of location categories for each strain over the 3 periods in each colony (2×3 contingency table analyses using the G-test; data from Figs. 6 and 7). To minimize the problem of

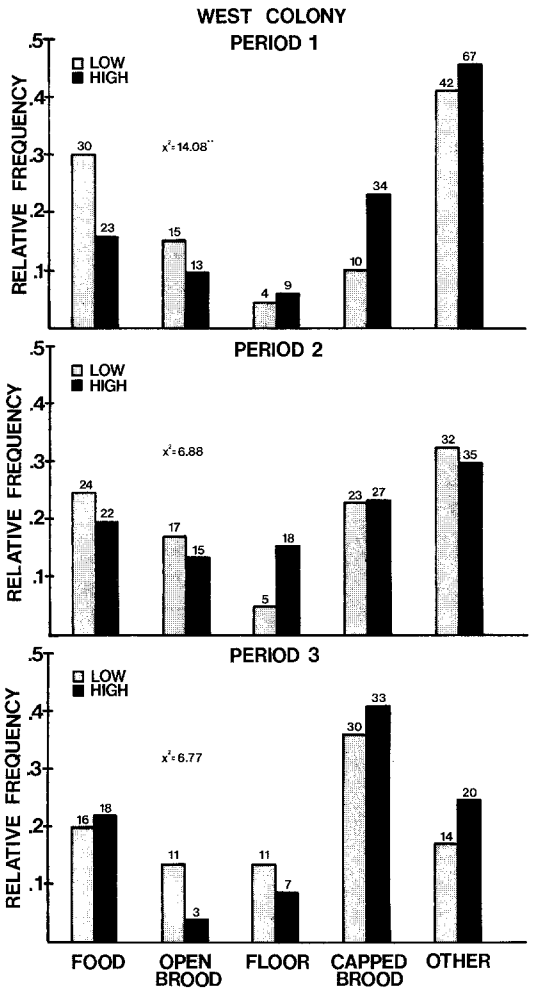

Fig. 7. Relative frequencies of workers from the high and low pollen-hoarding strains at each of 5 task performance locations in the west colony in each of the 3 combined periods. See text for a complete description of these locations. Significant differences were found in period 1 (**$P<0.01$; $df=4$ in each test). Numbers on each bar are the actual number of individuals counted

an inflated error rate resulting from a large number of multiple comparisons, only three predetermined comparisons of biological interest were made: 1) FOOD versus BROOD (OPEN BROOD+ CAPPED BROOD); 2) FLOOR versus the total of all remaining observations; and 3) OTHER versus the total of all remaining observations.

In the south colony, significant temporal effects on the distribution of workers between FOOD and BROOD locations were found in the high-hoarding strain ($P<0.01$) but not the low-hoarding strain ($P>0.05$). Workers from the high strain were observed in approximately equal numbers on brood and food locations in period 1. In periods 2 and 3, a large shift to brood locations is evident. Workers from the low strain did not exhibit this temporal shift. A fairly constant bias towards brood locations is evident in each of the 3 periods. Significant temporal effects ($P<0.01$) on the distribution of workers between empty cells and wooden hive parts (OTHER) versus all other locations were found in the high strain. A similar but non-significant trend was observed in the low strain ($P>0.05$). The distribution of workers between FLOOR versus all other locations changed with time in both strains ($P<0.05$).

In the west colony, significant temporal effects ($P<0.05$) on the distribution of workers between FOOD and BROOD locations were found in the low strain but not the high strain. Temporal effects ($P<0.05$) on the distribution of workers between FLOOR versus all other locations were found for both the low strain and the high strain. The distribution of workers between OTHER versus all other locations changed with time in both strains ($P<0.01$).

Discussion

Colony level selection for high versus low pollen-hoarding has produced workers of two strains that exhibit significant differences in several behavioral components of division of labor. These include the probability of performing a specific task within the foraging age caste (i.e. pollen foraging), the degree of task specialization, and possibly the rate of age-caste ontogeny. The finding that strains differed in the age at which workers began foraging in one colony (environment) but not in the other suggests a significant interaction between genotype and environment.

Spatial heterogeneity between strains within the nest suggests that a worker's genotype may affect the probability of performing a specific task within the nest. Heterogeneity could result from either differences between strains in the rate at which they make transitions between age castes or from differences in the frequency with which tasks were performed at different locations, independent of differences in rates of change, or both. These differences are probably not a simple consequence of differences in age polyethism rates because differences were found in the west colony where there was no evidence of differential age-caste ontogeny. An examination of temporal effects on spatial distributions suggests that the differences among the workers from the two strains change with time.

Two points need to be made regarding the foraging data. First, foragers returning with pollen

may also carry nectar (Parker 1926). Further research may provide greater resolution of the actual task categories. Second, colonies from the low strain (headed by multiply inseminated queens) store similar or greater amounts of nectar than colonies from the high strain (Hellmich 1983); therefore, the differences in foraging behavior between these strains cannot be attributed to differential foraging ability.

We propose a heuristic model for division of labor in honey bees. Workers pass through a series of age castes (Seeley 1982). The probability of performing a particular task within a specific age caste is determined by the genotype of the worker, the immediate environment, and probably her previous experience. Genotype may affect the probability of task performance at any given age in three ways. First, there may be genotypic effects on the rate of age-caste ontogeny that determine the duration of a particular age caste.

Second, genotypically mediated differences in threshold-response levels for specific stimuli may result in differences in the distribution of probabilities within an age caste independent of changes in the rate of age-caste ontogeny. This can occur in two ways: a) threshold-response levels within each age caste may be genetically influenced independently of levels at other ages, or b) threshold-response levels in more than on age caste may be the result of pleiotropy (genetic covariance among tasks).

Third, genotypic effects on task performance within an age caste may affect the probability of task performance in subsequent age castes. If experiences at one age alter threshold response levels for stimuli important to task performance at a later age, then workers with genotypes coding for different probabilities of task performance during an early age caste will have different experiences in the nest and may subsequently exhibit a canalization of their behavioral ontogeny. The variation in foraging behavior of high and low pollen-hoarding strains may be the result of genotypic effects specific to that age caste, the result of genetic covariance, the result of genotypic effects expressed during an earlier age caste, or all three. Spatial heterogeneity may be explained the same way.

Complex interactions among age, genotype and environment are suggested by Momot and Rothenbuhler (1971). They tested colonies of young and old, AFB susceptible and resistant workers under environmental conditions of plentiful nectar and dearth. Young, resistant workers invariably engaged in uncapping and removal behavior, but older, resistant workers did so only under conditions of plentiful nectar. Neither young nor old susceptible workers exhibited either behavior under either plentiful nectar or dearth conditions. Similarly, our demonstration that a worker's genotype had a significant effect on the age at which it made its first foraging flight in one colony but not in another suggests the importance of interactions between genotype and environment.

Hellmich et al. (1985) applied artificial selection to a population of honey bee colonies exhibiting considerable natural variation in pollen-hoarding behavior. The rapid and progressive selection of high and low pollen-hoarding strains suggests that there is a large amount of additive genetic variability present for this trait in the population. Large amounts of genetic variability in a population may suggest that the given trait is not a very important component of fitness, otherwise selection would have reduced it. However, spatial and temporal heterogeneity within local environments could result in the lack of an optimal genotype and maintain variability for the trait (Pianka 1974). Alternatively, the structure of the original population from which queens were drawn to establish the high and low strains (a composite of colonies drawn from several geographical areas) suggests that the observed variation may be the result of local adaptation of individual colonies to diverse environments. Another mechanism for maintaining the observed variation is behavioral dominance which could protect some portion of the variation from selection (Owen 1986).

Genotypic variability could be important to individual colony survival and reproduction through its effect on division of labor. Honey bee queens mate with up to 17 different males (reviewed in Page 1986) resulting in up to 17 different patrilines of workers at any given time. Each patriline may possess unique genotypic characteristics resulting in different probabilities of performing specific tasks, rates of age-caste ontogeny or both. Our results indicate a *potential* for genotypic variability among workers within a colony to contribute to the overall pattern of worker polyethism but do not reveal its significance in that context. Whether there is any distinct advantage to a genetically-structured division of labor within a honey bee colony remains to be investigated.

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