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Genotypic variation in foraging responses to environmental stimuli by honey bees, *Apis mellifera*

J. H. Fewell and R. E. Page Jr.[a]

Department of Zoology, Arizona State University, Tempe (Arizona 85287-1501, USA) and [a]*Department of Entomology, University of California, Davis (California 95616, USA)*
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Abstract. We experimentally tested a model predicting that colony-level genotypic diversity contributes to colony-level foraging flexibility in honey bees. We established a colony into which we placed individually marked workers from three genetically distinct groups. The colony was placed in an enclosure that contained feeding stations with pollen and sugar syrup. Foraging resources, stores of pollen and the quantity of brood within the colony were varied temporally. Individual foragers switched between resource types in response to changes in relative resource quality and colony need, demonstrating flexibility in resource choice at the individual level. However, genetic groups within the colony varied in their tendency to collect pollen versus nectar, and in lability of response to changes in foraging stimuli. Our data suggest that within-colony genotypic diversity contributes to a resilient foraging response to environmental variation.
Key words. Honey bee; nectar foraging; pollen foraging; genotypic diversity; division of labor.

Colonies of social insects change their organizational structure in response to changes in the environment, a characteristic believed to be responsible for their tremendous ecological success[1]. A well documented example of this characteristic is the ability of honey bee colonies (*Apis mellifera*) to change the allocation of foragers to pollen or nectar foraging in response to variation in colony conditions and the abundance of resources[2–6]. Honey bee colonies are composed of diverse worker genotypes, in part as a consequence of polyandry (multiple mating by the queen)[7]. Honey bee queens have been reported to mate with 7–17 males during mating flights (reviewed in ref. 7). This level of polyandry can generate relatedness values among workers that are much lower than those predicted to be necessary for the evolution of eusociality through kin selection. An important question therefore is what, if any, functional significance can be attributed to the genotypic diversity produced through polyandry. In a recent model, Robinson and Page[8] proposed that the genotypic diversity resulting from polyandry functions to integrate behavioral variation into a dynamic system of task regulation. In this study, we test whether within-colony genotypic diversity of honey bees contributes to flexibility in the allocation of workers to two foraging tasks: pollen and nectar collection.

Foraging by honey bee colonies is quite responsive to environmental variation. Foragers receive and integrate information about the foraging environment, as the quality and availability of resources change[3,4,9,10]. They also change foraging behavior in response to changes in colony conditions, as colony requirements for specific resources vary[11–13]. Changes in the foraging environment clearly influence individual effort for workers performing a specific task[2,6,13,14]. However, little is known about the mechanisms by which colonies change allocation of foragers between pollen and nectar collection in response to changes in foraging stimuli.

Several recent studies have demonstrated genetically based individual specialization on specific foraging tasks, including nectar and pollen collection[15–20]. Genetic differences in foraging task specialization persist regardless of rearing environments[16]. Genetically-based task specialization can potentially place constraints on individual behavioral flexibility and on colony-level division of labor by limiting the ability of foragers to change tasks in response to changing environments. If so, then the genotypic diversity gained through polyandry should confer an advantage by providing the colony with a worker population that is behaviorally more diverse and flexible.

Robinson and Page[8] propose a stimulus threshold model for task regulation, in which individual workers are predicted to have genetically based thresholds for performing given tasks, such as pollen or nectar foraging. When the environmental stimuli for collecting pollen or nectar exceed the stimulus threshold for a given individual, she performs that behavior. Genotypic variation within a colony results in variation among workers in the tendency to collect pollen or nectar. Colonies that are more genotypically diverse are expected to have wider or more graded responses to environmental change than those that are genotypically less variable. The stimulus threshold model makes the prediction that the genotypic diversity of workers collecting a resource will increase in response to increases in colony need for

a specific resource, as the stimulus for collecting that resource reaches a wider range of worker thresholds. The model also makes two important testable assumptions: 1) that the foraging decisions of an individual worker are constrained in part by its genotype, and 2) that workers are capable of switching between tasks in response to changes in the stimulus environment. In this study, we examine the relationship between genetically based resource preferences and the abilities of individuals to switch between resources. We also test whether the extent of individual flexibility in resource choice is itself genetically based. These questions provide insight into the genetic basis for variation in foraging behavior, and into the potential pathways for colony-level evolutionary responses to natural selection on foraging.

Materials and methods

This study was conducted in early June, 1990, at the University of California, Davis, USA. Identifying and controlling foraging stimulus conditions is a problem with testing models of how foragers respond to changing environments. We examined individual responses to changes in external resources by controlling the quality of nectar and pollen available to foragers, and to changes in colony conditions by varying amounts of brood and stored pollen. To control access to pollen and nectar resources, we placed a nucleus hive containing 4 frames into a mesh flight cage that was approximately 6 m long, 3 m wide, and 2 m high. We placed into the hive a total of 450 newly emerged worker progeny, 150 from each of 3 presumably unrelated queens. Each of the workers was individually marked with a colored, numbered, plastic tag. All of these workers were marked and added to the colony within a two-day period, so that they were of similar age.

Workers were assigned to one of three genetic groups, A, B, or C, depending on their queen mother. Two of the worker-source queens (A and B) were instrumentally inseminated with sperm from different single males. The queen and drone parents for workers in group A were unrelated, and came from two unrelated commercial colonies chosen because they contained large quantities of stored pollen. The queen and drone parents of group B workers were taken from two unrelated commercial colonies with low pollen stores. Pollen hoarding has previously been demonstrated to be highly heritable, and related to the foraging preferences of individual workers[15, 17, 18, 21]. We expected, therefore, that workers of groups A and B would represent extreme genotypes, and, consequently, extreme behavioral phenotypes. The third queen (C) was naturally mated; this group was expected to provide a broader distribution of worker genotypes. Because of their different parental sources, individuals within each genetic group could be expected generally to be more genotypically similar to each other than to individuals in the other groups.

At the same time that marked workers were added, the colony was also provided with an additional 950 newly emerged bees from another unrelated colony, and a laying, naturally-mated queen that was also unrelated to all of the initially introduced workers. The additional workers were provided to bring the population size to that of a small functional colony, but were not focal animals for our observations. An unrelated source was used because we were unable to collect sufficient additional workers in equal numbers from our focal groups. The addition of unrelated workers increased the total number of genetic groups in the colony; however, it did not create potential bias from over-representation of one of the 3 focal groups.

We provided the colony with approximately 1600 cm^2 (one frame) of honey, 400 cm^2 of pollen, and 800 cm^2 of unsealed brood. When the individually marked bees were 14 days old, we added 1500 newly emerged workers from unrelated sources. This manipulation stimulated the individually marked bees to move from performing hive activities to foraging, because the young bees displaced the older bees from the brood nest[22].

Foragers were provided with separate dishes of sugar solution and dried sieved pollen, positioned 2 m apart, and 5 m from the hive entrance. Resource dishes were made available starting on day 7 after colonies were established. The experiment began on day 14. By this time, foragers were collecting freely from both the nectar and pollen dishes. During the experiments, resource dishes were placed in the flight cage 30 min before each observation period, and were left until all of the resource was consumed (approximately 1.5 h). We did not provide additional resources between observation periods. The two feeding stations were monitored simultaneously for two 30 min observation periods each day, during which we recorded all individually marked bees observed at each station.

Experiment 1. In the first experiment, we determined the effect of pollen and nectar quality on resource choice by offering foragers nectar and pollen of either high or low concentrations. High concentration nectar contained 50% sucrose; low concentration nectar contained 15% sucrose. The high concentration pollen was pure ground pollen that had been collected in mid-March from hives located in almond orchards near the university. Pollen was dried and kept frozen until use. Low concentration pollen consisted of 25% pollen and 75% brewers yeast. Although brewers yeast is used by bees as a protein source, it was less acceptable to foragers than pollen. Some proportion of the foraging population collected each resource under both concentrations, indicating that all concentrations presented were acceptable to at least some members of the colony. We initially provided resource dishes with high concentration nectar and pollen. During the experiment,

foragers were offered combinations of: 1) high concentration pollen, high concentration nectar (HP/HN), 2) low concentration pollen, high concentration nectar (LP/HN), and 3) high concentration pollen, low concentration nectar (HP/LN). On days 14–21 we offered either the HP/HN, or the LP/HN treatment. These two combinations were re-selected arbitrarily each day; bees experienced each combination for a total of 8 observation periods. On days 22 and 23 (4 observation periods), we provided high concentration pollen with low concentration nectar (HP/LN). We then compared individual resource choices among the 3 treatments.

Experiment 2. On day 24, we manipulated relative amounts of pollen, honey and brood within the colony to examine the effect of changes in internal colony conditions on foraging behavior. Colony-level pollen foraging effort is positively correlated with brood levels, and negatively correleted with pollen storage levels[6, 11, 12]. We created a low colony-level stimulus for pollen foraging by replacing the combs within the hive with combs containing 790 cm^2 of pollen, approximately 400 cm^2 of honey, and no brood. After 5 d, we removed the pollen from the colony and replaced it with 400 cm^2 of uncapped brood, and 1600 cm^2 of honey, providing a high pollen foraging stimulus. During each of the manipulation periods we provided 40% nectar solution and pure ground pollen at the feeding stations.

Data analysis. Data were analyzed by 2- and 3-way G-tests for heterogeneity[23]. This statistic tested for interactions among genetic group, treatment (manipulation of resources or colony stores), and individual resource choice. In experiment 1, we examined interactions among forager group (based on the queen-source for the worker), relative resource quality (HP/HN, LP/HN, HP/LN), and the resource collected (pollen only, nectar only, or both resources). In experiment 2, we examined interactions among forager group, internal hive conditions (high versus low pollen stores), and the resource collected (pollen only, nectar only, or both resources). Data were pooled among those observational periods in which the same treatment conditions occurred. Individuals were included in the 'both' category if they were observed switching between pollen and nectar resources during successive observation periods within a treatment, or if they were observed collecting both resources within a single observation period.

Results

Experiment 1. To determine population-level changes in foraging behavior, we compared the number of foragers within each foraging task group under different resource treatments. We analyzed data only for individual workers that made at least two trips during any one of the 3 treatments. The restriction of analyses to workers making multiple trips allowed us to consider bees collecting both resources within a resource treatment as a behavioral category separate from that of individuals that collected only pollen or only nectar.

We analyzed observational data for a total of 145 marked foragers that foraged multiple times during the HP/HN treatments, 101 during the LP/HN treatments, and 75 bees during the HP/LN treatments. There was no significant 3-way interaction among genetic group, resource quality, and individual resource choice, allowing us to examine two-factor interactions independently[23]. The three genetic groups varied significantly in their foraging preferences. (G-test, $G = 33.95$, $p < 0.01$, 4 df; fig. 1). The C group (rather than A, as expected) showed the strongest preference for collecting pollen. Apparently, our choice of parents for group A did not represent genotypically extreme groups.

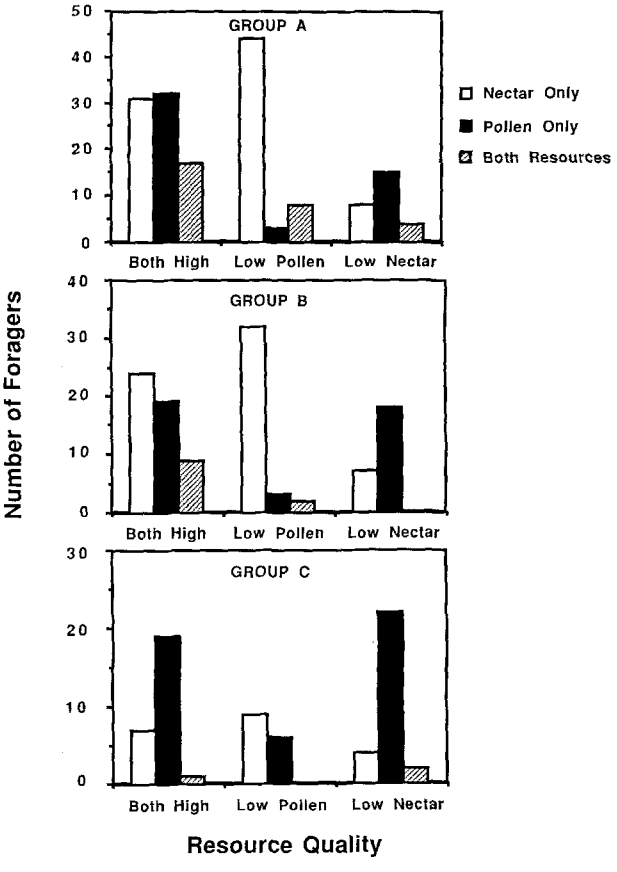

Figure 1. The number of foragers within each of 3 genetic groups that collected only pollen, only nectar, or both pollen and nectar during treatments of varying resource quality. The 3 resource treatments were: 1) high quality pollen and nectar (HP/HN), 2) low quality pollen, high quality nectar (LP/HN), and 3) low quality nectar, high quality pollen (HP/LN). High quality pollen consisted of pure ground pollen collected using pollen traps on managed colonies. Low quality pollen consisted of 25% pure pollen mixed with 75% brewers yeast. High quality nectar contained 50% sucrose; low quality nectar contained 15% sucrose. Pollen and nectar stations were located 2 m apart. Data were collected at the pollen and nectar stations for a total of 8 observation periods for the HP/HN and LP/HN treatments, and for 4 observation periods for the HP/LN treatments.

Workers also varied resource choice in response to changes in resource quality ($G = 70.33$, $p < 0.01$, 4 df). When the 3 groups were analyzed separately, workers of groups A and B responded to decreases in pollen concentration by decreasing their relative tendency to collect pollen (group A: $G = 29.22$, $p < 0.01$, 4 df; group B: $G = 37.88$, $p < 0.01$, 4 df; fig 1). In contrast, group C showed no significant change in resource choice in response to changes in relative resource quality; this group maintained high levels of pollen foraging independently of quality ($G = 9.21$, NS, 4 df). However, this group experienced a strong drop in total foraging activity when pollen quality was reduced (a 43% decrease), which could have biased statistical analyses.

Changes in the relative number of workers collecting nectar, pollen or both resources were due to a combination of changes in individual foraging activity rates and task switching by individual bees. To analyze data on individual resource choice and activity changes independently, we compared changes in individual behavior between the HP/HN and LP/HN treatments. The number of observation periods was the same for these 2 treatments, allowing analysis of treatment effects on activity levels. A total of 147 bees were observed twice within at least one of these treatments; 66 from group A, 53 from group B, and 28 from group C. Of those workers, 69% (102) foraged under both treatment conditions. Group C workers showed the greatest change in foraging activity; 43% of workers in group C foraged under only one of the 2 treatment conditions, compared to 24% of workers from group A and 32% of workers from group B.

To answer the question of how changes in individual resource choice affected foraging behavior, we examined data for individuals that foraged at least twice in each of the 2 treatments ($n = 81$). The 3 groups varied little in their levels of individual resource switching. Of those workers foraging in both high and low pollen quality treatments, 28, 22 and 23% of groups A, B and C respectively changed resource preferences between treatments. We performed a statistical analysis on bees foraging under conditions of high versus low pollen quality, to address the question of whether this level of switching by individuals affected resource collection at the population-level. To provide sample sizes adequate for the analysis, we collapsed the data on resource choice into 2 categories: individuals that collected pollen (pollen only and both categories), and individuals that did not collect pollen (nectar only category). There was a significant shift in the distributions of pollen and non-pollen foragers as pollen quality decreased (G-test, $G = 10.0$, $df = 1$, $p < 0.01$, $n = 81$). Under conditions of high pollen quality, 46% of foragers collected pollen; under conditions of low pollen quality the proportion of foragers collecting pollen decreased to 22%. Data for this analysis were pooled among genetic groups, however, all 3 groups showed the same trend; individuals switched from pollen to nectar foraging when pollen quality decreased.

Experiment 2. In the second experiment, we examined responses to changes in pollen and brood storage levels. We analyzed data only for those bees that made 2 or more trips within each of the 2 treatment periods (a total of 4 or more trips), allowing us to make comparisons of individual resource choice between treatments without considering changes in activity levels. In these analyses, changes in the number of individuals performing different foraging tasks between treatments were due entirely to task switching by individual bees. Data were analyzed for a total of 95 bees. As in experiment 1, there was no significant 3-way interaction among genetic group, colony condition, and individual resource choice. We found significant genotypic differences in resource preference ($G = 18.84$; $p < 0.01$, 4 df; fig. 2), with group C again showing a higher preference

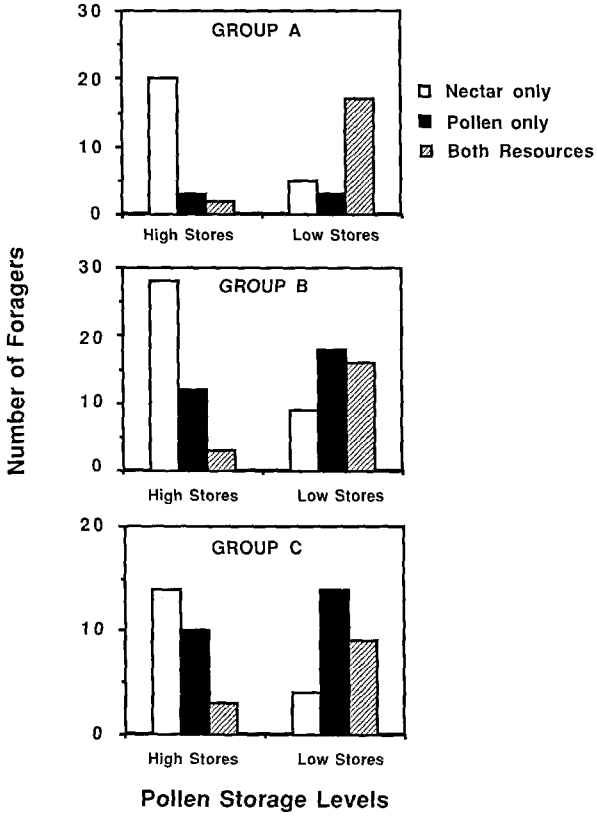

Figure 2. The number of foragers from each of 3 genetic groups collecting 1) pollen only, 2) nectar only, or 3) both pollen and nectar, under conditions of low and high pollen storage levels. In the high pollen storage treatment we added pollen to the colony, and removed brood; this treatment provides a low hive stimulus for pollen foraging. For low pollen storage conditions, we removed pollen and added brood, creating an increased stimulus for pollen collection. Each treatment lasted 5 days. Bees foraged at separate feeding stations containing either a 40% sucrose solution or pure ground pollen. Data were collected at pollen and nectar feeding stations for a total of 8 observation periods within each treatment.

for pollen than the other 2 genotypic groups. There was also a significant interaction between colony conditions and resource choice; the relative numer of individuals collecting pollen only or both resources increased under conditions of higher colony need for pollen (G-test, $G = 49.36$, $p < 0.001$, 2 df).

The 3 groups varied in their qualitative responses to changes in the hive environment. To test this, we classified foragers collecting both resources into a category of 'generalist' foragers, and pooled the pollen only and the nectar only foragers into a single category of 'specialists'. The relative numbers of individuals that were generalists or specialists (all 3 groups combined) changed significantly between colony treatments ($G = 7.2$, $p < 0.05$, 2 df). However, the association between colony conditions and resource choice (specialists versus generalists) varied among the genetic groups (3-way G-test, genetic group × colony treatment × resource choice interaction, $G = 7.2$, $p < 0.05$, 2 df). Although the distribution of specialists and generalists was similar for the three groups under conditions of high pollen stores (fig. 2), it varied significantly under conditions of low pollen stores ($G = 7.9$, $p < 0.02$, 2 df).

Discussion

Our results provide evidence for an effect of genotypic diversity on honey bee task flexibility. As predicted by the stimulus threshold model[8], the genotypic diversity of the foraging population changed in response to variation in foraging stimuli. Genotypic groups with a high threshold for collecting a particular resource increased in representation as the stimulus for that resource increased. We also found genetically based variation in the magnitude and type of individual foraging responses to changing stimulus environments.

These effects were apparent even though our colony may have had relatively high genotypic diversity within the foraging population. Higher levels of diversity could be expected to make it more difficult to observe small changes in the genotypic distributions of foragers with changing stimuli. However, we concentrated on the behavior of individual foragers from specific genotypically diverse 'marker' populations. By drawing focal animals from more diverse genotypic origins, we were possibly able to increase the resolution of the relationships between genotype and behavioral response.

Resource switching in response to changes in foraging stimuli. Optimal foraging models make the assumption that, given universal knowledge, individual foragers make foraging choices that maximize some measure of gain[24,25]. Therefore, the question of how constraints on behavioral flexibility affect foraging decisions is important to foraging theory. The potential behavioral constraints imposed by genotype are a particular concern in social insects because foragers of different genotypes within a colony tend to specialize on different foraging tasks[15–21,26]. We found that, within the constraints imposed by genetically based thresholds, individual foragers were capable of flexibility in resource collection. Workers of all 3 genetic groups showed some level of response to changes in internal (colony) and external (resource) stimulus conditions, resulting in colony-level shifts in resource collection. Further, flexibility in individual resource choices contributed significantly to colony regulation of resource intake, suggesting that it is an important component of colony foraging behavior. Our results qualitatively fit the prediction of the stimulus threshold model that genotypic diversity contributes to flexible task regulation by creating a wide distribution of worker thresholds of response[8]. As predicted, when stimulus conditions for pollen foraging changed from low to high, the composition of the pollen foraging population shifted to include a larger number of individuals from genetic groups with higher pollen foraging thresholds (figs 1 and 2). For example, under conditions of high colony need for pollen, approximately 80% of the foragers from each of the genetic groups collected pollen (fig. 3).

Additional genotypic effects on foraging. Activity patterns provided another mechanism by which genotypic variation affected colony response to a dynamic environment. In the first experiment, a subset of foragers responded to stimulus changes not by switching resources but by changing foraging activity levels. Foraging activity changes were most dramatic in group C,

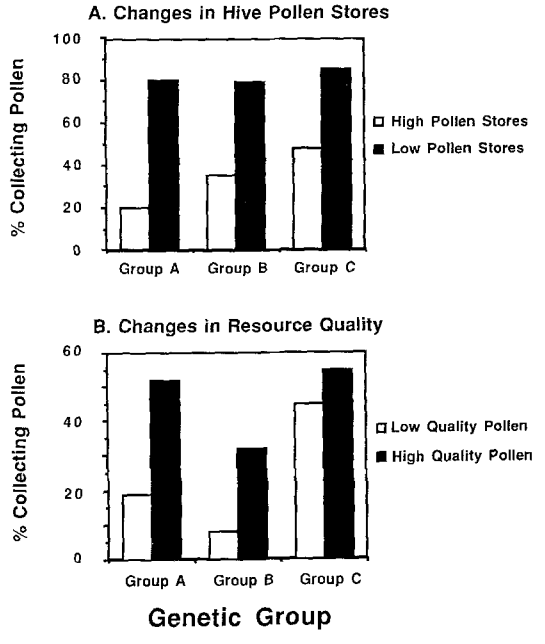

Figure 3. The proportion of foragers within each of the 3 genetic groups that are collecting pollen under conditions of *A* high and low pollen storage levels within the colony, and *B* low (25% pollen) versus high pollen (pure pollen) resource quality (nectar was constant at 50% sucrose). The pollen foraging category included workers that collected either pollen only or both pollen and nectar.

which also had the highest preference for pollen. Because we did not have equivalent data on how nectar quality affects foraging response, it is difficult to determine whether this variation in activity response among groups was linked to variation in preference.

The composition of the foraging population can also be strongly affected by genotypic variation in the ontogeny of foraging[15]. In experiment 1, the foraging population was dominated by workers of group A. By the second experiment, group B was the most strongly represented in the foraging population. A younger age of first foraging was associated with nectar foraging in our experiments. However, Calderone and Page[15] found genotypic variation in the age of first foraging associated with pollen foraging. It is likely, therefore, that the age of first foraging is another independent and genetically based component of foraging organization, and one that is potentially important in regulation of foraging response.

Genotypic variation in the tendency to specialize on a resource. We found significant variation among the genetic groups in the tendency to specialize on foraging tasks, with individuals of group A showing a much greater tendency than those of group C to collect both resources. We were able to differentiate between individuals specializing on one resource and individuals collecting both, because we provided separate resource dishes. Previous studies at flowers were unable to distinguish a clear generalist category because individuals collecting both nectar and pollen at a single flower may choose the flower for one resource, but collect the other resource opportunistically[15–18]. In our experiments, bees had to fly between resource dishes to collect both pollen and nectar, demonstrating that this is an active decision for the forager, not simply opportunistic exploitation of an available resource.

The existence of generalist bees suggests that pollen and nectar foraging can be performed independently by individual workers. From selection studies on pollen hoarding levels, it is clear that pollen and nectar foraging covary genetically to some degree[15,16]. However, how closely the behaviors are linked behaviorally is less well known. Despite evidence that individual nectar and pollen collection covary genetically, the two resources seem to be regulated independently at the colony level[5]. The ability of some workers to collect both resources is important, because it provides a behavioral mechanism at the individual level by which regulation of nectar and pollen collection can be uncoupled. Generalist bees may also represent a transitional state in which the stimulus environment just matches an individual's behavioral threshold. If the type of transition between foraging tasks is itself genetically linked, this would also provide a genetic mechanism for variation in task flexibility.

Assessment of the foraging environment. Our data suggest that foragers assess resources and colony need for those resources in different ways. As an example, individuals of group A increased the breadth of resources collected in response to within-colony changes, but not to changes in resource quality. Most models pool all stimuli as a single value[8], or evaluate stimuli separately without attempting to integrate them[3,4,6]. Our data indicate that foragers are capable of evaluating external foraging stimuli and stimuli within the nest somewhat independently, and that the evaluation criteria of different stimulus sources may differ among genotypes.

Polyandry and task regulation in socal insects. The variation in task performance among the genetic groups examined in this study demonstrates that regulation of division of labor in social insect colonies is affected by genotypic diversity within the colony. Multiple mating systems and systems of colony co-founding are common in social insects. These systems are problematic to models of social evolution through kin selection, because they lower the relatedness among workers in the colony. The research of Oldroyd et al[27] suggests that increases in the number of subfamily groups may contribute to colony fitness via changes in foraging success and in brood rearing. Our study examined the behavior of focal groups only. However, our results suggest a functional role for the genetic diversity produced by polyandry in colony task regulation, by providing behavioral flexibility at the colony level under dynamic environmental conditions.

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