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ORIGINAL ARTICLE

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Division of labor in a dynamic environment: response by honeybees (*Apis mellifera*) to graded changes in colony pollen stores

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Abstract A fundamental requirement of task regulation in social groups is that it must allow colony flexibility. We tested assumptions of three task regulation models for how honeybee colonies respond to graded changes in need for a specific task, pollen foraging. We gradually changed colony pollen stores and measured behavioral and genotypic changes in the foraging population. Colonies did not respond in a graded manner, but in six of seven cases showed a stepwise change in foraging activity as pollen storage levels moved beyond a set point. Changes in colony performance resulted from changes in recruitment of new foragers to pollen collection, rather than from changes in individual foraging effort. Where we were able to track genotypic variation, increases in pollen foraging were accompanied by a corresponding increase in the genotypic diversity of pollen foragers. Our data support previous findings that genotypic variation plays an important role in task regulation. However, the stepwise change in colony behavior suggests that colony foraging flexibility is best explained by an integrated model incorporating genotypic variation in task choice, but in which colony response is amplified by social interactions.

Key words Honeybee · *Apis mellifera* · Division of labor · Genetics · Pollen foraging

Introduction

Social insect colonies are known for their efficient system of task specialization, but they are also capable of extreme flexibility in task allocation as colony need or opportunity changes. Current models of behavioral organization in social insect colonies all predict that workers vary task performance based on common environmental cues (Seeley 1985; Seeley and Levien 1987; Robinson and Page 1989a; Page and Robinson 1991; Seeley et al. 1991; Tofts and Franks 1992; Franks and Tofts 1994; Bonabeau et al. 1996; Gordon 1996), but they differ in their expectations of how this is done. Because these models were developed to address different specific questions, it is difficult to compare them directly. However, they make different, and in some cases competing, assumptions about how workers receive task information and what factors constrain their response. We examine some of these assumptions in the context of honeybee (*Apis mellifera*) foraging response to graded changes in colony pollen need. We also evaluate whether these assumptions can be incorporated into an integrated model of task regulation for this behavior.

Current models of task regulation in social insects generally address one of two questions. (1) What produces variation in individual response to task stimuli? (2) How do individuals receive information about a task? Most models make the simplifying assumption that (with the exception of age polyethism) workers respond to task cues similarly; variation in task performance is directly related to variation in individual stimulus environments. However, there is strong evidence that workers vary intrinsically in their sensitivity to task stimuli (honeybees: Hellmich et al. 1985; Calderone and Page 1988, 1991; Frumhoff and Baker 1988; Robinson and Page 1988, 1989b; Oldroyd et al. 1992; Fewell and Page 1993; ants: Stuart and Page 1991; Snyder 1993; wasps: O'Donnell 1996). From this, we can generate a model in which individual differences in task performance occur as a result of genotypic variation (Robinson and Page 1989a; Bonabeau et al. 1996). In this "stimulus threshold" model, individuals within a colony vary intrinsically in their sensitivity to stimuli for a given task. As the stimulus for a task increases, the thresholds of more individuals in the colony are met, and those workers begin performing the task. Thus genetic diver-

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sity among workers produces colony flexibility in response to changes in task need.

Current stimulus threshold models also make the secondary assumption that variation in task sensitivity is a consequence of additive effects of genotype and environment (Robinson and Page 1989a; Bonabeau et al. 1996). Although each worker has an individual threshold, the distribution of thresholds in the worker population as a whole is continuous and normally distributed. However, recent genetic and phenotypic measures of honeybee pollen and nectar foraging suggest that genotypic variation in foraging tasks involves a few major loci, and that phenotypic expression of these tasks may be closer to a model of Mendelian dominance (Hunt et al. 1995; J.H. Fewell, R.E. Page, unpublished data). Consequently, variation in task thresholds may actually be bimodal or even discontinuous.

An inheritance pattern and its phenotypic expression can have a profound effect on colony task organization. A continuous model of threshold phenotypes predicts that colonies respond to graded changes in task stimuli by gradually increasing the number of workers in that task group. This response pattern is expected independently of how workers actually receive task information, because the increase in worker number is constrained by variation in individual response thresholds. In contrast, if behavioral phenotypes divide into more discontinuous groups of higher and lower thresholds, then the shape of colony response requires the additional consideration of how workers receive information about the task.

Two current models that address the question of how individuals receive task information are the "foraging for work" model (Tofts and Franks 1992; Franks and Tofts 1994) and the "information center" model (Seeley 1985; Seeley and Levien 1987; but see also Seeley et al. 1991). Although these two models differ in their specific behavioral questions, they each make useful and explicit assumptions about how individuals receive task information. The foraging-for-work model assumes that workers evaluate colony task stimuli directly from the hive environment, but essentially independently of social interactions (Franks and Tofts 1994). This model assumes that the probability of a worker performing a task is directly related to the probability of encountering task stimuli. If so, colony increases in task allocation occur in direct proportion to variation in stimulus levels for a given task.

In contrast, the information center model (and subsequent expansions; Seeley et al. 1991; Gordon 1996) expects that task recruitment is based primarily on worker communication of task need or opportunity. Information transfer about task need or availability does not require a physical information "processing center," but instead occurs as a result of social interactions between workers engaged in the task and workers available to perform it (Seeley et al. 1991). This model generates the expectation that worker interactions result in rapid information transfer, allowing the colony to respond in a coordinated and rapid manner to small changes in task stimuli (Seeley 1985; Seeley and Levien 1987; Seeley et al. 1991).

In this study we test the outlined assumptions of the stimulus threshold, foraging-for-work and information center models empirically by examining the responses of honeybee (*A. mellifera* L.) colonies to graded changes in need for pollen. In honeybees, pollen foraging is regulated homeostatically around a set point of pollen stores; colonies adjust foraging behavior as pollen storage levels move above or below that level (Fewell and Winston 1992; Camazine 1993). The dynamic interaction between colony conditions and pollen foraging provides us with an ideal context to address the question of how task flexibility at the colony level is regulated.

We predict that if colony response is driven by continuous variation, then colonies should show a graded response to changes in need for pollen. This graded increase in recruitment should be accompanied by an increase in genotypic diversity among workers in the pollen foraging group. If genetic variation is bimodal, a graded response is still expected if individual workers sample the hive environment independently (as in a foraging-for-work model). In contrast, if information transfer is based on social interactions, workers will receive information on changes in pollen need almost simultaneously, potentially producing a sharply graded or stepwise change in pollen foraging behavior as need varies beyond the colony set point.

We can additionally consider the possibility that genotypic variation is *not* important to foraging regulation. In this case, the response patterns predicted by the foraging-for-work and information center models remain the same. However, because both models assume no genetic variance for task performance, changes in colony recruitment would not be accompanied by any changes in the genetic diversity of the workers.

Methods

The study was conducted at Arizona State University, Tempe. We performed two experiments in which we examined individual and colony responses to changes in colony resource needs by manipulating the quantity of pollen within hives and by monitoring foraging behavior on pollen and nectar resource stations. To control colony access to pollen and nectar resources, we placed the hives into mesh outdoor flight cages (12 feet wide × 12 feet long × 6 feet high). Within each cage, foraging bees were provided with two resource dishes, one of freshly ground dried pollen and one containing a sponge soaked with a 40% sucrose solution scented with anise (artificial nectar). Pollen and nectar dishes were 2 m apart and 3 m from the hive. Bees were provided with fresh pollen and nectar each morning, and resources were replenished as necessary during the day.

Experiment 1

The first experiment was performed in June 1995. We placed 300 newly emerged workers from each of three genetic sources into each of two hives over a 2-day period (total 1800 workers from six sources for the two hives). Thus, the two colonies received different genotypic combinations. The workers were individually marked

with a colored, numbered, plastic tag (Opalithplattchen). Marked workers came from colonies with unrelated, naturally mated queens. The host hives each contained queens unrelated to the marked workers and approximately 7000 unmarked workers.

Two weeks after the marked workers were added to colonies, we added newly emerged unmarked workers from unrelated sources to the hives. This stimulated the marked bees to change from performing hive activities to foraging activities. At the beginning of the experimental period, we equalized amounts of honey (approximately 3700 cm^2) and uncapped brood (approximately 1800 cm^2) in the two hives. We gave each hive two full frames of packed pollen (3200 cm^2). Bees in colony 1 had full access to the pollen at the beginning of the experiment. In colony 2, the frames were completely covered with foil to block access. Every 48 h thereafter the pollen was manipulated. We reduced the accessible pollen in colony 1 by halves (3200, 1600, 800, 400, 200, 100, and 0 cm^2 of pollen). To do this, we covered exposed pollen areas with foil. We simultaneously increased access to pollen in colony 2 (0, 100, 200, 400, 800, 1600, and 3200 cm^2) by removing foil from covered pollen. The bees did not chew into the foil to gain access to additional pollen during the experiment, so that exposed pollen amounts were an accurate assessment of available stores.

To determine individual responses to changes in pollen levels, two observers simultaneously monitored foraging activities of marked bees on the two resource stations within each cage for two 40-min periods each day, one observation period beginning at 9:00 a.m. and the other beginning at 3.00 p.m. During each of these periods, we continuously recorded arrival and departure times for all marked bees. We observed the pollen and nectar resource stations simultaneously to obtain concurrent activity data and to determine if any bees were collecting from both resources on a given trip. To determine colony-level response to changes in pollen stores, we surveyed the total number of foragers (marked and unmarked) at the resource stations at the beginning and end of each 40-min observation period. Data within each manipulation were treated as repeated measures (six to eight measures per manipulation).

We determined individual foraging rates and load sizes as a measure of individual foraging effort. We calculated the average number of foraging trips made by each marked forager per 40-min observation period, for those observation periods in which the bee was sighted. These measures were averaged for each bee across the observation periods within a manipulation. We also collected unmarked bees returning to the colony from resource dishes within each treatment period, and measured the size of resource loads they were carrying. We made wet weight measures of all pollen loads, and extracted nectar crop contents to determine nectar load sizes (Fewell and Winston 1992).

Experiment 2

In August 1998, we performed a second experiment to examine the shape of the colony response in more detail. In this experiment we did not place marked workers into colonies. Instead we focused on colony allocation of workers to pollen and nectar collection. We placed three small colonies (colonies 3–5) into mesh flight cages, and manipulated pollen stores as described above. The three colonies were again equalized for amounts of honey (approximately 4200 cm^2), and uncapped brood (approximately 1300 cm^2). Colonies 3 and 4 were initially given no pollen; stores were then increased every 2 days to 100, 200, 400, and 800 cm^2. Colony 5 was initially given 1600 cm^2, and stores were decreased to 800, 400, 200, 100, and 0 cm^2.

We performed a second set of manipulations on colonies 4 and 5, where we reversed the treatments (colony 3 lost its queen after the first set of manipulations). Stores in colony 4 were decreased from 800 to 400, 200, 100, and 0 cm^2. In Colony 5, they were increased from 0 to 100, 200, 400, and 800 cm^2. At the end of this treatment set we gave colony 4 1600 cm^2 of pollen for an additional 2 days, to allow us to compare this treatment level to the equivalent one in colony 5.

Pollen foraging rates were much lower in the afternoon, probably because of high ambient temperatures. Therefore, we collected data only in the morning. We counted the number of foragers at the pollen and nectar stations seven times each morning, at half-hourly intervals from 7:30 a.m. to 10:30 a.m. Pollen and nectar stores were refreshed hourly (30 min before each observation period). The hours that foraging began and decreased varied with daily temperatures, so for each day, we dropped the first or last count that was farthest from the mean. This reduced variance, and allowed a more accurate assessment of manipulation (rather than external) effects on foraging.

Results

Experiment 1

Total pollen foraging activity

Both colonies in the first experiment showed a significant change in foraging activity, measured by counts of the number of foragers (marked and unmarked) at the pollen station. However, this was not a linear response. For both colonies, the change in pollen foraging activity was best fit by a regression model including a stepwise change from 800- to 1600-cm^2 treatments (Table 1). In each case, the step component accounted for the largest portion of the variance. The two colonies showed virtually identical responses to changing pollen levels (ANOVA, $F = 0.004$, $P = 0.95$, $n = 14$), even though

Table 1 Regression analyses of changes in pollen foraging activity with changes in pollen storage levels for colonies 1–5 (experiments 1 and 2 combined). The *arrows* after each colony number indicate the direction of changes in pollen stores. Data show the results of regression models with constant + pollen amount or constant + pollen amount + step variable. The step variable divides the data into two groups at the point where activity rates show the strongest change in pollen foraging activity. Included are the *F*-ratios and *P*-values for each of the models, and the *T*- and *P*-values for the components of the pollen treatment + step model. Degrees of freedom vary across models

	Linear model (pollen amount only) *F*-ratio (*P*-value)	Step model (pollen amount + step variable) *F*-ratio (*P*-value)	Pollen component *T* (*P*-value)	Step component *T* (*P*-value)
Colony 1 ↑	12.9 (0.004)	13.9 (0.001)	0.42 (0.69)	2.8 (0.02)
Colony 2 ↓	9.7 (0.01)	8.7 (0.006)	0.17 (0.87)	2.1 (0.06)
Colony 3 ↑	69.1 (0.000)	72.7 (0.000)	5.8 (0.000)	6.2 (0.000)
Colony 4 ↑	12.7 (0.001)	41.9 (0.000)	0.29 (0.77)	7.7 (0.000)
Colony 4 ↓	31.3 (0.000)	116.7 (0.000)	0.61 (0.54)	11.8 (0.000)
Colony 5 ↑	52.0 (0.000)	25.8 (0.000)	6.5 (0.000)	0.52 (0.61)
Colony 5 ↓	62.9 (0.000)	158.0 (0.000)	3.8 (0.000)	11.6 (0.000)

pollen levels were increased through the experiment for colony 1 and decreased for colony 2. Pollen foraging levels increased slightly from 0 to 400 cm^2 (Fig. 1), and then decreased sharply beyond 400 cm^2, stabilizing at the 1600-cm^2 treatment. The transition to low pollen foraging activity occurred in the middle of the 800-cm^2 treatment for colony 1. Foraging activity rates for the first morning after manipulation were similar to those for the 400-cm^2 treatment, but then dropped to lower levels. Colony 2 showed an immediate increase in foraging activity as stores moved from 800 to 400 cm^2.

Individually marked workers

From our 40-min surveys of individual foraging behavior, we calculated the number of marked individuals collecting pollen within each of the 2-day treatment periods. Again, the number of pollen foragers changed sharply and significantly as pollen storage levels moved between 400 and 800 cm^2 (Fig. 2). Because the response was stepwise, rather than linear, we grouped the 0–400 cm^2 treatments (low) and the 800–3200 cm^2 treatments (high) for further analysis. The number of marked foragers collecting pollen within each 2-day period decreased significantly from the low (mean = 39.9 ± 3.5) to high pollen storage treatment sets (mean = 21.7 ± 4.3), but there was no colony or interaction effect (two-way ANOVA: pollen treatment effect, $F = 10.64$, $P = 0.009$; colony effect, $F = 0.22$, $P = 0.65$; interaction, $F = 1.14$, $P = 0.31$; $n = 14$) on pollen foraging.

Changes in allocation to pollen versus nectar foraging

Colonies showed a significant change in the proportional allocation of marked workers collecting only pollen, only nectar, or both resources between the low and high storage conditions (Pearson $\chi^2 = 13.03$, $P = 0.001$; colonies pooled because of scarcity of data in some cells; Fig. 3a). This result could be generated either by changes in recruitment or by foragers switching between resources. However, when we analyzed only the subset of workers that foraged within both treatments, we saw no significant change in resource choice (Pearson $\chi^2 = 0.31$, $P = 0.86$; Fig. 3b). Therefore, the change in distribution of workers among resources was due primarily to recruitment of new foragers rather than to resource switching by workers already foraging.

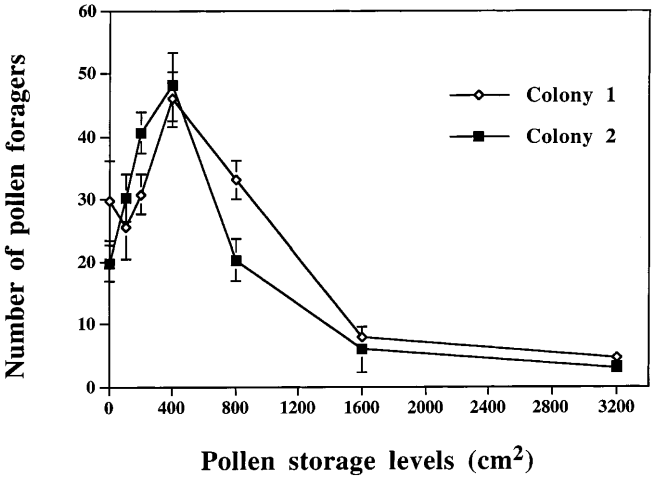

Fig. 1 Mean (±SE) number of pollen foragers found in 1-min counts at pollen stations during each treatment. Pollen storage levels for colony 1 were increased for each treatment, while pollen storage levels for colony 2 were decreased. Pollen stores were doubled or halved between treatments. Data represent six to eight measures per colony within each pollen treatment

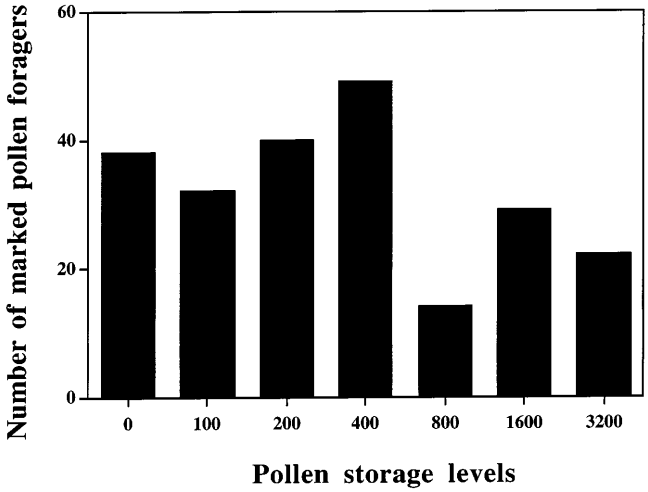

Fig. 2 The number of individually marked foragers seen collecting pollen during each treatment. Data represent the total individually marked workers collecting pollen within each 2-day treatment period. Data only for individuals seen two or more times over the experiment, and pooled for colonies 1 and 2

Individual foraging effort

Changes in colony foraging behavior can also be generated through changes in individual foraging effort. To test for this, we compared pollen foraging rates of individual workers during the high and low pollen treatment sets. Individual pollen foraging rates did not vary significantly across treatments ($mean_{low} = 2.58 \pm 0.11$, $mean_{high} = 1.98 \pm 0.10$; two-way ANOVA, pollen treatment effect: $F = 1.55$, $P = 0.16$, $n = 235$). There was a significant colony effect ($F = 46.62$, $P = 0.000$) on individual foraging rate, and a significant colony × treatment interaction ($F = 3.76$, $P = 0.001$). However, the colony and interaction effects can be best explained by a drop in mean activity rates for the 200-cm^2 treatment (mean = 1.87 ± 0.27) compared to all other treatments in colony 2.

Workers can also vary foraging effort by changing the amount they collect per trip. However, we found no significant difference between the high and low pollen treatment sets for pollen load size ($mean_{low} = 8.2 \pm 0.37$ mg, $mean_{high} = 7.7 \pm 0.41$ mg; two-way

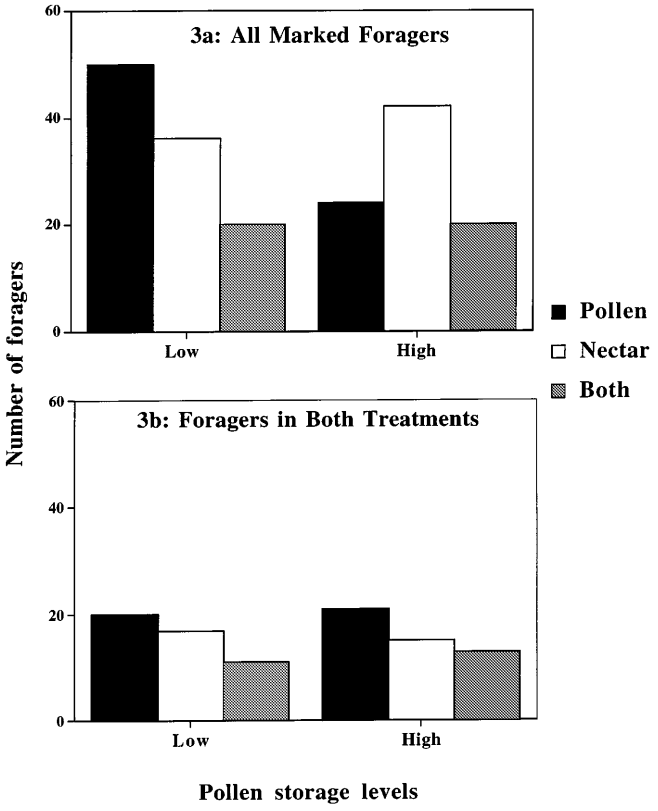

Fig. 3 The behavior of all marked workers foraging two or more times at any point through the experiment (**a**) compared to the behavior of the subset that foraged within *both* low (0–400 cm^2 of pollen stores) and high (800–3200 cm^2 pollen storage) pollen treatment sets (**b**). Shown are the number of workers collecting pollen only, nectar only, or both resources. Data are pooled for colonies 1 and 2

ANOVA: pollen treatment effect: $F = 1.82$, $P = 0.18$, $n = 163$). Additionally, we found no colony effect ($F = 0.10$, $P = 0.75$) or colony × treatment interaction ($F = 2.98$, $P = 0.09$).

Nectar foraging response

In contrast to pollen foraging, colony-level nectar foraging rates did *not* vary in response to changes in pollen stores. Each of the two hives showed a significant decrease in nectar foraging through the experimental period (colony 1: 0–3200 cm^2, slope = −8.7, $F = 25.18$, $P = 0.0003$; colony 2: 3200–0 cm^2, slope = −8.5, $F = 41.34$, $P = 0.00003$; $df = 1,12$ for each colony; Fig. 4). However, because the order of treatments was reversed for the two colonies, variation in nectar foraging rates did not correlate with changes in pollen stores (regression: slope = −0.11, $F = 0.002$, $P = 0.96$, $r^2 = 0.0003$, $n = 14$).

The number of marked bees collecting nectar also remained constant between the low (0–400 cm^2) and high (800–3200 cm^2) pollen treatment sets (two-way ANOVA: $F = 0.31$, $P = 0.59$). A mean of 32.5 (±3.3) marked bees collected nectar within each of the low pollen manipulations, compared to 35.7 (±6.0) marked bees within the high pollen manipulations. There was no change in individual foraging rates (trips per 40 min) across treatments, but rates did differ between the two colonies ($mean_{low} = 3.14 \pm 0.19$, $mean_{high} = 2.82 \pm 0.15$; two-way ANOVA, pollen treatment effect: $F = 1.22$, $P = 0.27$; colony effect: $F = 40.31$, $P = 0.00$; $n = 244$). Sampled nectar load sizes did not vary significantly between treatment sets or between colonies ($mean_{low} = 34.7 \pm 1.8$ µl, $n = 71$; $mean_{high} = 35.4 \pm 2.05$ µl, $n = 58$; two-way ANOVA, pollen treatment effect: $F = 0.018$, $P = 0.89$; colony effect: $F = 0.13$, $P = 0.67$; interaction effect: $F = 0.11$, $P = 0.74$; $n = 129$).

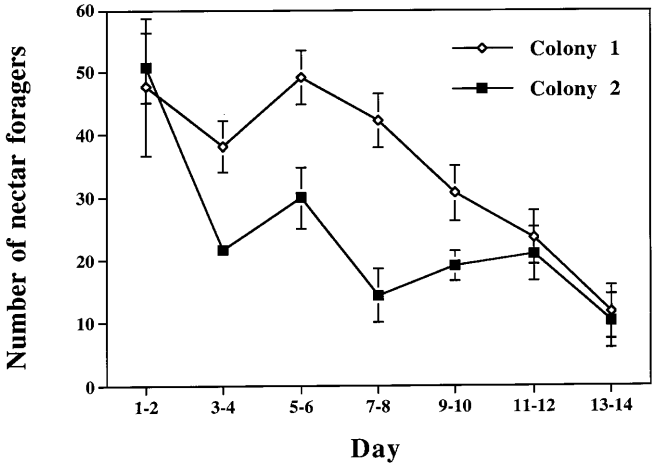

Fig. 4 Changes in nectar foraging activity through the experiment, as measured by 1-min counts of forager number at the nectar resource station. Pollen storage levels increased in colony 1 and decreased in colony 2 through the experiment. Data shown are means (±SE) calculated from six to eight repeated measures within each 2-day treatment period

Genotypic variation in resource choice

The marked bees within each colony came from different source colonies, allowing us to track genetic variation in foraging behavior. Because we used different genotypic sources for the marked workers in the two hives, we could not pool data for analysis. Colony 1 showed significant variation in the distribution of the three focal genetic groups between pollen and nectar foraging (Pearson $\chi^2 = 5.84$, $P = 0.05$, $df = 2$, $n = 117$; Fig. 5). Additionally, there was a shift in the genetic composition of the pollen foraging population between the high and low pollen storage treatments. Under conditions of high stores, the pollen foragers were overrepresented by a single genetic group, while under low pollen storage conditions, the other genetic groups had higher representation in the pollen foraging population (Pearson $\chi^2 = 9.6$, $P = 0.008$, $df = 2$, $n = 75$).

In colony 2, the marked foragers of the three introduced genetic groups did not vary significantly in foraging behavior (Pearson $\chi^2 = 0.92$, $P = 0.92$, $df = 2$,

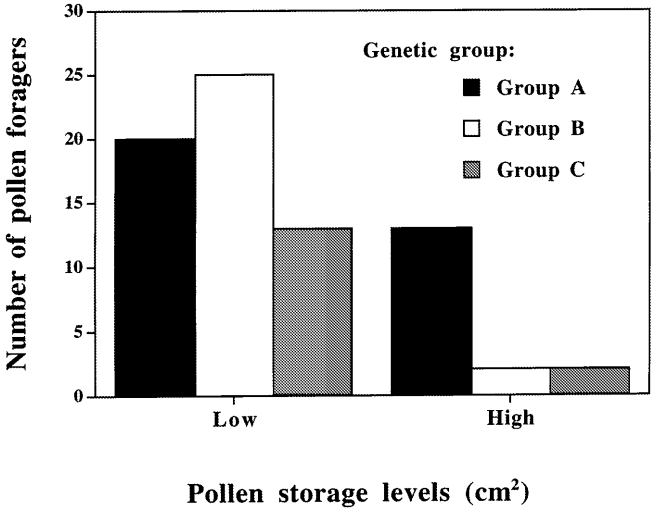

Fig. 5 Shift in representation of three genetic subgroups (*A*, *B*, and *C*) within the pollen foraging population of colony 1 under conditions of low (0–400 cm^2 of pollen stores) versus high (800–3200 cm^2) pollen storage levels. Workers that collected pollen two or more times within either treatment set were included in this analysis

n = 183). In all three groups, the majority of foragers collected nectar (n = 102), with a smaller subset collecting either pollen (n = 40) or both resources (n = 41). Because we did not have sufficient genetic differentiation in behavior we could not analyze further for changes in genotypic distributions within the pollen foraging group.

Experiment 2

Foraging response to increasing pollen stores

All three colonies were subjected to increased pollen stores. This was the first manipulation for colonies 3 and 4, and the second for colony 5. Pollen foraging response patterns were generally similar to those in experiment 1, except that the threshold at which colonies changed pollen foraging activity was lower (Fig. 6a). All three colonies maintained constant pollen foraging levels between 0 and 100 cm^2 (colony 3, T = 0.81, P = 0.4; colony 4, T = 0.35, P = 0.7; colony 5, T = 0.68, P = 0.5), and dramatically decreased foraging rates between 100 and 200 cm^2. For colonies 3 and 4, this shift was again best described by a stepwise regression model, in this case with a step change above 200 cm^2. In contrast, colony 5 showed a more linear graded response to this manipulation (Table 1).

Each of the three colonies showed a significant decrease in nectar foraging activity as pollen stores were increased from 0–800 cm^2 (Fig. 7a). However, the increase in pollen stores explained only a small part of the variance in nectar activity (colony 3: F = 14.5, $P < 0.001$, r^2 = 0.2; colony 4: F = 8.5, P = 0.005, r^2 = 0.13; colony 5: F = 6.28, P = 0.015, r^2 = 0.1).

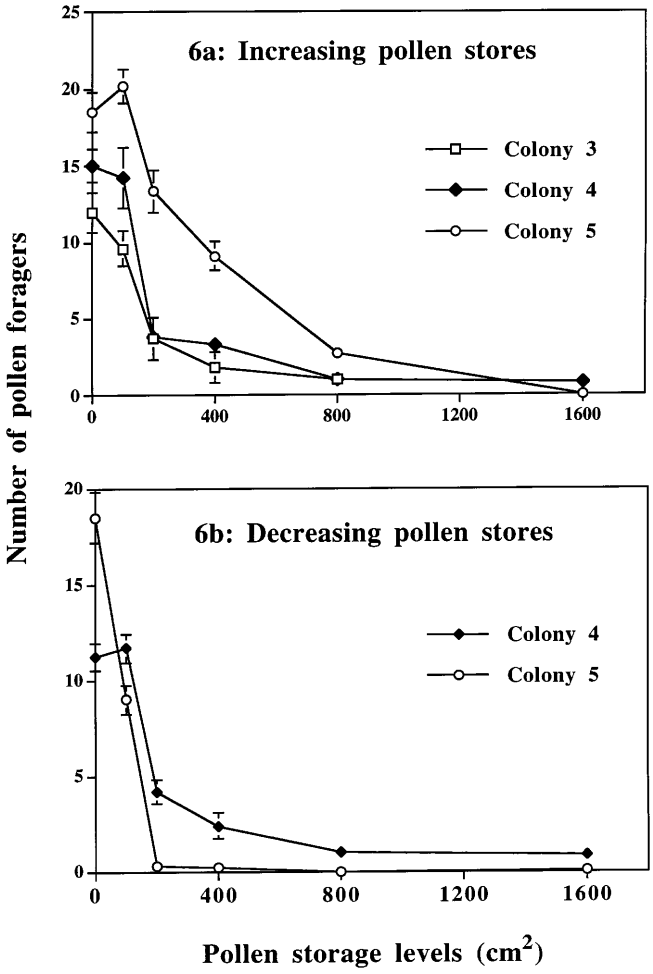

Fig. 6 Number of foragers observed in 1-min counts at pollen stations in colonies 3–5 as pollen storage levels increased between 0 and 1600 cm^2 (**a**), and in colonies 4 and 5 as pollen storage levels decreased between 1600 and 0 cm^2 (**b**). Stores were increased or decreased every 2 days. The 1600-cm^2 treatment for colony 4 was not made in sequence, but was done at the end of the experiment (after 0 cm^2). Data represent means ± SE of 12 counts made over each 2-day period

Foraging response to decreasing pollen stores

Colonies 4 and 5 were both subjected to a decrease in storage levels (colony 3 lost its queen during this manipulation, and was not analyzed). This was the first manipulation for colony 5 and the second for colony 4. Both colonies again showed a significant and stepwise increase in pollen foraging between the 200- and 100-cm^2 treatments (Table 1, Fig. 6b). Colony 4 showed a slight increase in pollen foraging between 1600 and 200 cm^2 (F = 11.23, $P < 0.001$), but a dramatic increase between 200 and 100 cm^2. Rates then remained constant between 100 and 0 cm^2 (T = 1.03, P = 0.3). Foraging rates in colony 5 remained constantly low between 1600 and 200 cm^2 (F = 1.56, P = 0.2). They then increased across the 100- and 0-cm^2 treatments (F = 35.2, $P < 0.001$). Foraging levels remained constant between

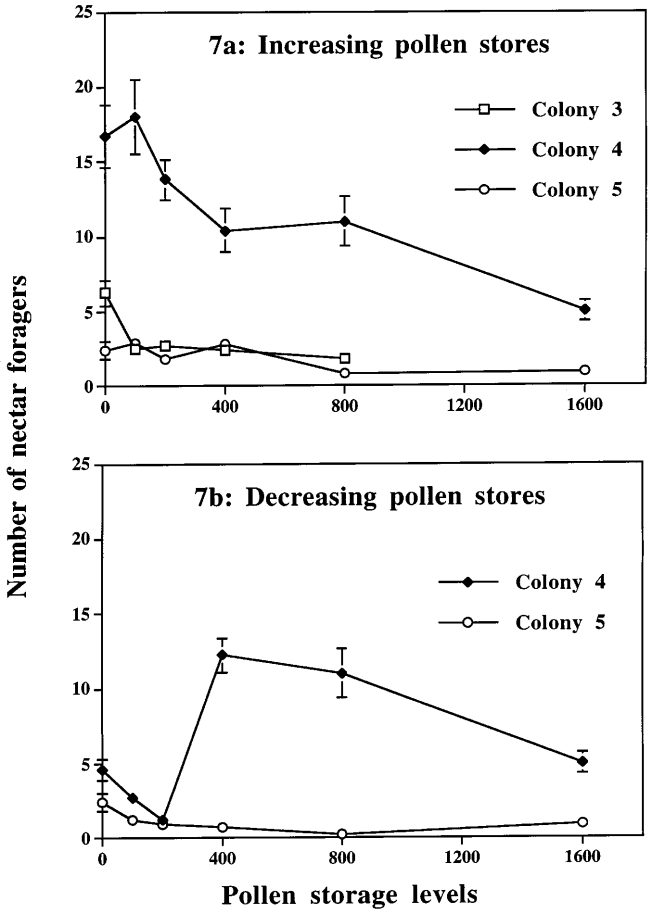

Fig. 7 Number of nectar foragers observed in 1-min counts in colonies as pollen stores were increased from 0 to 800 cm^2 (**a**) and decreased from 1600 to 0 cm^2 (**b**). Data represent means ± SE of 12 counts made over each 2-day treatment. The 1600-cm^2 treatment for colony 4 was not made in sequence, but instead was done at the end of the experiment (after 0 cm^2)

0 cm^2 of this manipulation and the 100-cm^2 treatment of the second manipulation.

There was no consistent relationship between changes in nectar foraging and decreased pollen stores (Fig. 7b). Variation in nectar foraging by colony 4 was not significantly related to the reduction in pollen stores ($F = 2.04$, $P = 0.16$, $r^2 = 0.03$). Colony 5 showed a small increase in nectar foraging as stores were decreased from 1600–0 cm^2; again, the change in pollen stores explained only a small proportion of total variation in nectar foraging ($F = 5.1$, $P < 0.05$, $r^2 = 0.2$).

Discussion

Current models of task organization in social groups can be categorized by the expectation that colony-level flexibility in task performance is based on (1) intrinsic variation in worker sensitivity to task stimuli or (2) variation among workers in their interaction with the colony environment. Our results suggest that models of task organization in honeybees require integration of these two components. Consistent with previous studies (Calderone and Page 1988; Robinson and Page 1989b; Oldroyd et al. 1992; Fewell and Page 1993), we found that genotypic variation plays an important role in task choice. However, our data suggest that the stimulus threshold model provides a better fit to observed patterns of foraging task organization when integrated with current models of social information transfer.

Genotypic effects on pollen collection

The stimulus threshold model of task organization is significant because it is the first to theoretically evaluate the role of genotypic variation in task regulation. In this model, colony behavioral response is based on intrinsic (genetically based) variation in individual thresholds for performing a given task. The model generates the testable prediction that changes in colony behavior correlate with changes in the genotypic composition of the task group. Specifically, the genotypic diversity of workers performing a task will increase as need for that task increases. Although only one of the two colonies in experiment 1 showed the initial genetic differentiation in behavior to test the prediction, this colony showed a clear change in genotypic diversity as colony task need changed. Previous studies testing this prediction have obtained similar results. Honeybee colonies with measurable genotypic variation, including feral colonies with naturally occurring genotypic diversity, consistently show a shift in the genotypic diversity of pollen foragers as need for the task varies (Fewell and Page 1993; Fewell 1999; J.H. Fewell, and D. Dubas, unpublished data). These results provide strong collective support for the basic tenet of the model, that genetic variation in worker task choice influences task flexibility.

In contrast, our results do not support the assumption of normally distributed variation in stimulus thresholds. Violation of this assumption does not invalidate the stimulus threshold model. However, the question of how genotypic variation relates to colony response is an important one. Previous studies have compared only the end points of low and high need for pollen foraging (Fewell and Winston 1992; Camazine 1993; Fewell and Page 1993). When we varied colony pollen need in a graded manner, colonies showed a dramatic stepwise change in behavior around a set point of colony pollen stores. This change occurred consistently across our two experiments, in six of seven manipulations (Figs. 1, 6). We additionally saw a stepwise shift in pollen foraging by the individually marked workers of experiment 1 (Fig. 2). The changes in allocation to pollen foraging were the primary response mechanism in our colonies. Although previous experiments have shown that individual workers can vary foraging effort in response to changes in pollen need (Fewell and Winston 1992), foragers did not vary pollen load size or foraging rates in this study.

Our results are consistent with work suggesting that phenotypic variation in pollen and nectar foraging is influenced by a few major loci with possible modifiers (Hunt et al. 1995). Further behavioral evidence suggests that the major phenotypic effects of these loci show bimodal preferences for pollen foraging. In two separate studies in which lines selected for high versus low pollen collection were crossed, the F1 hybrids showed dominance for nectar foraging, rather than an intermediate phenotype (J.H. Fewell and R.E. Page, unpublished data).

Information transfer and colony task regulation

In a related mathematical model, we simulated expected colony response to graded changes in task stimuli for colonies with a range of variation in stimulus thresholds (Fewell 1999; S.M. Bertram and J.H. Fewell, unpublished data). Colonies with normally distributed stimulus thresholds (from additive genetic and environmental effects) showed a graded response to graded changes in stimulus levels. The graded response occurred independently of how information about the task was transmitted, because the magnitude of changes in worker allocation was constrained by the distribution of thresholds in the colony.

In contrast, the responses of colonies with a bimodal distribution of task specialists and non-specialists varied depending on how individuals received information about task need. When workers assessed the stimulus environment randomly, colony response was graded, although not as linear as with the additive model. A stepwise response was generated when workers received universal information about stimulus levels (analogous to an information center model). The empirical finding of a sharply graded change in pollen foraging around a set point provides strong (although indirect) evidence that regulation of pollen intake is coordinated via some form of social information transfer, rather than by workers independently assessing the hive environment.

Additional support for a mechanism of coordinated worker response comes from the finding that changes in colony pollen collection rates occurred at similar set points across colonies. Although the colonies in each of the experiments were equalized for levels of capped and open brood as well as for nectar and empty comb, they varied in their genotypic composition. The marked bees in experiment 1 within each colony came from a total of six different unrelated source colonies, and the host colonies had unrelated queens. The three colonies in experiment 2 had unrelated queens. Thus, colony set points for pollen collection were not based on a mean or summation of intrinsic worker sensitivities. Instead the stimulus for pollen collection is likely based on cues that are evaluated similarly by workers.

Interestingly, the set points varied between the two experiments. Several factors may influence this change. The colonies in experiment 1 had higher levels of uncapped brood than those in experiment 2. Previous studies have shown a positive relationship between brood levels and pollen intake rates (Eckert et al. 1994). An additional difference between the two experiments was the time of year in which they were conducted. Experiment 1 was undertaken in June, towards the end of a seasonal increase in resource availability and brood production. Our second experiment was conducted in August, the end of the dry season in this area.

Extension of the model to other tasks

The rapid response in pollen foraging is similar to that seen when colonies respond to changes in nectar resource quality (Seeley 1985; Seeley and Levien 1987; Seeley et al. 1991). The similar response patterns were not necessarily expected. Pollen and nectar have very different functions within the colony, and are regulated independently of each other (Fewell and Winston 1992, 1996). Nectar foraging, unlike pollen foraging, is not regulated around a set point and, in contrast to pollen foraging, shows limited sensitivity to internal colony cues (Fewell and Winston 1996). Indeed, in this experiment there was no consistent relationship between pollen stores and colony- or individual-level nectar foraging behavior. The similarity in colony response for these two independently regulated tasks suggests that an integrated genotype/environment model may apply to regulation of other tasks as well.

Social transfer of information about colony pollen need

Our data generate the expectation of a mechanism for social transfer of information on pollen need, but they do not identify that mechanism. Information transfer for nectar availability and quality comes from dance activity rates of incoming foragers (Seeley and Towne 1992) and from unloading rates of nectar receiver bees within the hive (Seeley 1986; Seeley and Tovey 1994). Incoming pollen foragers also perform recruitment dances. However, they pack their own loads into cells, and so potentially sample colony pollen need independently of social interactions (Camazine 1993).

Qualitative evidence suggests that changes in pollen foraging behavior are related to the ability of colonies to match pollen intake rates to brood hunger, but it is unclear how potential pollen foragers specifically acquire this information. One possible link between brood and pollen foragers may be nurse bees, who convert pollen to brood food and who also interact with foragers through trophallaxis (Crailsheim et al. 1992; Hrassnigg and Crailsheim 1998). The process of packing pollen around the brood area (Camazine 1993) may also allow foragers to receive pheromonal information directly from the larvae.

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