

Colony state and regulation of pollen foraging in the honey bee, *Apis mellifera* L.

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Summary. To place social insect foraging behavior within an evolutionary context, it is necessary to establish relationships between individual foraging decisions and parameters influencing colony fitness. To address this problem, we examined interactions between individual foraging behavior and pollen storage levels in the honey bee, *Apis mellifera* L. Colonies responded to low pollen storage conditions by increasing pollen intake rates 54% relative to high pollen storage conditions, demonstrating a direct relationship between pollen storage levels and foraging effort. Approximately 80% of the difference in pollen intake rates was accounted for by variation in individual foraging effort, via changes in foraging activity and individual pollen load size. An additional 20% resulted from changes in the proportion of the foraging population collecting pollen. Under both high and low pollen storage treatments, colonies returned pollen storage levels to pre-experimental levels within 16 days, suggesting that honey bees regulate pollen storage levels around a homeostatic set point. We also found a direct relationship between pollen storage levels and colony brood production, demonstrating the potential for cumulative changes in individual foraging decisions to affect colony fitness.

Introduction

Social insect foraging systems present a unique test of evolutionary models of foraging behavior, because workers that forage generally do not reproduce. To place individual social insect foraging decisions in an evolutionary context, it is not enough to demonstrate that they increase individual short-term gain; we also must establish that those decisions positively affect colony fitness. Despite the generation of a number of models pre-

dicting individual foraging strategies in social insects (Heinrich 1979; Waddington 1980; Pyke 1984; Schmid-Hempel 1984, 1987; Schmid-Hempel et al. 1985), the relationships between individual foraging behavior and most aspects of colony state are still not known (Houston et al. 1988; Tschinkel 1991). We address this problem by examining interactions between colony pollen storage conditions and foraging strategy in the honey bee, *Apis mellifera* L.

A number of studies have examined variation in foraging behavior by individual social insects as a response to resource variation (Lindauer 1952; Nuñez 1970; Davidson 1978; Waddington 1980; Pyke 1981; Schmid-Hempel 1984; Seeley 1986; Breed et al. 1987; Fewell and Harrison 1991). However, few studies have examined whether individual foraging decisions are sensitive to changes in colony parameters (Seeley 1986, 1989; Eckert 1990; Wolf and Schmid-Hempel 1990; Fewell et al. 1991). There also is no direct evidence that foraging strategy changes at the individual level affect colony fitness. In this study, we examine the relationships between foraging strategy, pollen storage levels and brood production. Examination of these relationships allows us to determine some of the principle mechanisms underlying colonial regulation of food intake and storage in honey bees.

Foraging models traditionally have focused on currency measures based on energetic return (Stephens and Krebs 1986; Cheverton et al. 1985). However, social insect foragers must obtain a range of nutrients, one of the most important of which is protein (Winston 1987). Although the nitrogen contained in protein is known to be a critical, often limiting nutrient (Haydak 1935), surprisingly little is known of how animals assess or regulate collection of this resource (Sorenson et al. 1985). Honey bees provide one of the few systems in which we can examine protein foraging independently of energy intake, because individuals forage for protein and energy separately by collecting either pollen or nectar.

Pollen storage levels may have a more directly mea-

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surable effect on colony fitness than honey because they are related to immediate colonial growth rates via brood production (Allen and Jeffree 1956; Fukuda 1960; Todd and Reed 1970; Al-Tikrity et al. 1972). In honey bees, population growth is the best predictor of a colony's ability to survive overwinter and to reproduce by swarming (Michener 1964; Winston 1979, 1980; Winston et al. 1981; Seeley and Visscher 1985; Lee and Winston 1985, 1987). Thus, foraging decisions which increase pollen intake rates are predicted to positively affect fitness if they result in increased brood production.

Methods

This study was conducted in May 1989, in Abbotsford, British Columbia. A total of six colonies were used in the study. Each colony contained approximately 35,000 adults and was housed in a hive containing two Langstroth deep bodies. Colonies were surveyed before the experiment to determine amounts of pollen, honey, open brood (eggs and larvae), and capped brood (pupae). Each frame in a hive contains 1600 cm² of comb space. To survey colonies, we placed a plexiglass plate divided into 32 squares of 25 cm² each over both frame sides, and counted the number of squares containing each resource. Pre-experimental levels of pollen averaged 2240 cm² per colony (SE = 136).

To examine the relationships between colony pollen storage levels and foraging behavior, we performed two sets of manipulations in which we either removed or supplemented the amount of pollen in the colony. In the first manipulation, half of the colonies received high pollen levels (\bar{x} = 4455 cm²; Table 1) and the other half received low pollen levels (\bar{x} = 240 cm²; Table 1). All hives were equalized for amounts of capped and uncapped brood and honey (Table 1). We also equalized the amount of empty comb by removing a frame of comb from colonies given low pollen storage levels. In the second manipulation we reversed the treatments; colonies that had previously been given high pollen storage levels received low pollen amounts, and colonies that were pollen-deprived in the first manipulation received high pollen storage levels. Foraging observations were made for 16 days after each manipulation. We surveyed colony contents on days 8 and 16 after manipulations, to determine changes in levels of pollen, honey and brood within hives. Because colony 2 lost its queen at the beginning of manipulation 2, subsequent data for this colony were not used in analyses.

To determine colony and individual-level responses to changes in pollen levels, we monitored foraging rates at colony entrances every second day, by counting the number of pollen and non-pollen foragers returning to the hive in a 5-min period. Foraging surveys were made in the morning, and colonies were surveyed in random order. We made seven foraging rate surveys for each colony within each manipulation period. Foraging rate data were averaged to provide one measure of foraging activity for each colony, within each manipulation. We analyzed the data using a two-way ANOVA with repeated measures, to examine the effects of pollen storage levels on foraging and also to determine possible interactions between pollen treatments and manipulation date.

We collected sets of ten pollen foragers from the entrances of each colony at approximately 4-day intervals. Collected bees were placed into individual containers and frozen on dry ice. In the laboratory, we removed pollen loads and measured wet weights of individual bees and pollen loads. We then dried and reweighed individual pollen pellets, and analyzed them for percent nitrogen, using an elemental analyzer.

To examine the effect of pollen storage levels on individual foraging activity, we individually marked 50 pollen foragers from each of four colonies (two from each treatment group), during each manipulation. Bees were marked with small dabs of Testor's

Table 1. Pre- and post-manipulation levels of pollen, honey and brood in colonies

	High pollen stores	Low pollen stores	Pre-experimental
Pollen	4455 (±53)	240 (±48)	2240 (±136)
Honey	9694 (±448)	10515 (±222)	10960 (±992)
Open brood	3693 (±397)	3720 (±804)	3120 (±664)
Capped brood	5031 (±301)	5806 (±366)	5568 (±648)

Amounts are measured as total cm² of comb space within the colony allocated to each resource. Data are given as means (±SE)

enamel of different colors, placed on the thorax and abdomen. On the day following marking, we observed colonies for 4 h, between approximately 1100–1500 hours. During this time we recorded the times that individual bees left or returned to the colony, and whether returning bees had pollen loads. At the start of each hour we recorded ambient temperatures, and made 2-min surveys of foraging activity at colony entrances. We observed both high and low treatment colonies on any given day, to control for weather and temperature effects on foraging activity. Although all of the marked bees were known to have collected pollen at some time, data were analyzed only for those bees that collected pollen at least once during an observation period. We calculated foraging trip times only for trips in which bees returned with pollen loads. Data on foraging trip times and time in the hive between trips were averaged for bees that made multiple trips.

We also measured gross colonial intake rates of pollen by placing pollen traps on hives. Pollen traps remove pollen loads from incoming foragers when collection screens are inserted. Pollen collecting screens were inserted into each trap for 1 h on the third and eighth days after each manipulation. The amount of pollen collected during these times was less than 12% of total daily intake, and so was unlikely to affect experimental conditions

Results

Colony foraging activity

We found no significant difference between high and low pollen storage treatments in the total number of foragers returning to the hive in 5 min (F = 0.03, P > 0.8; Fig. 1). However, the proportion of foragers returning with pollen loads increased significantly from 27.9% per 5 min (SE = 1.8) under high pollen storage conditions to 35.1% (SE = 2.2) under low pollen storage conditions, resulting in a significant difference in the proportion of foraging trips in which pollen was collected (two-way ANOVA; F = 15.4, P < 0.005, n = 11; data arc-sin transformed before analysis). There was no significant effect of manipulation date on either the total number of foragers returning per 5 min (F = 1.202, P > 0.3), or on the proportion of returning foragers carrying pollen (F = 0.227, P > 0.6). Likewise, there was no interaction between manipulation date and pollen treatment effects (F_{total} = 0.006, P > 0.9; F_{pollen} = 0.241, P > 0.6).

Individual foraging response

We measured foraging times and rates for individually marked bees to determine the effects of colony pollen

levels on individual activity. Foragers spent significantly less time on pollen foraging trips when pollen storage levels were low than when storage levels were high (ANOVA, $F=5.22$, $P<0.05$; Table 2). Foragers also spent significantly less time in the hive between trips under low pollen storage conditions than when pollen stores were high (ANOVA, $F=6.59$; $P<0.02$; Table 2). Trip

frequencies for pollen foragers were significantly higher for bees foraging when colonies had low pollen storage levels than for foragers from high treatment colonies (ANOVA, $F=4.82$, $P<0.05$; Table 2).

Pollen load size and nitrogen content

Fresh weights of individual pollen loads were significantly larger for foragers from colonies with low pollen stores than for foragers from colonies with high pollen stores ($F=13.47$, $P<0.001$; Table 2). There was no significant change in pollen load size between the first and second manipulation ($F=2.2$, $P>0.1$), and no significant interaction between manipulation date and pollen treatment effects ($F=0.6$, $P>0.4$).

The percent nitrogen present in pollen loads differed significantly between the two treatment groups. Pollen loads returning to colonies with high pollen storage levels were significantly higher in percent nitrogen than loads returning to colonies with low pollen stores (two-way ANOVA, data arc-sin transformed, $F=13.63$, $P<0.001$; Table 2). We also found an effect of manipulation date on pollen nitrogen content. Pollen collected in the first manipulation was significantly lower in percent nitrogen than pollen collected in manipulation 2 ($F=16.9$, $P<0.001$). There was also a significant interaction between manipulation date and pollen storage level treatment effects ($F=10.6$, $P<0.001$).

We multiplied pollen dry weights by proportional nitrogen content to determine total nitrogen amounts for each pollen load. Despite the difference in proportional nitrogen content, total nitrogen per pollen load did not differ significantly between the two treatment groups ($F=2.6$, $P>0.1$; Table 2). Total nitrogen content per pollen load was not significantly affected by manipulation date ($F=2.9$, $P>0.08$), and there was no significant interaction between pollen treatment and manipulation date ($F=1.46$, $P>0.2$). We also found no significant correlation between percent nitrogen content and dry weight of pollen loads (Pearson product moment correlation coefficient = -0.115 , $P>0.1$, $n=183$).

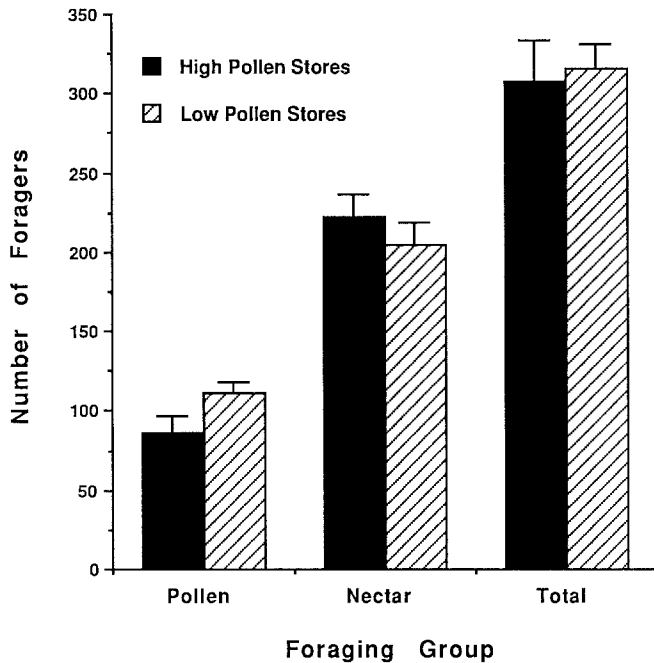


Fig. 1. Differences in colony foraging activity rates under high (solid bars) and low (shaded bars) pollen storage conditions. Activity rates were measured as the number of foragers returning within a 5-min period. Nectar foraging rates were measured by the number of returning foragers without pollen loads. A total of 6 colonies in the high treatment group and 5 colonies in the low treatment group were measured. Data were analyzed by two-way ANOVA with repeated measures to determine possible interactions between treatment effects and manipulation date. Pollen foraging rates differed significantly for the two groups ($F=5.4$, $P<0.05$), but total foraging activity and the number of non-pollen foragers returning per 5 min did not differ significantly between treatment groups

Table 2. Effects of pollen storage levels on individual pollen load attributes and foraging activities of individually marked pollen foragers

	High pollen stores			Low pollen stores		
	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>
Individual foraging rate (# trips/h)	0.65	0.275	71	0.78	0.042	60
Trip length (min)	49.9	3.28	22	38.0	4.02	19
Time in hive (min)	30.0	4.29	32	15.6	2.23	25
Pollen load size (mg)	14.0	0.59	144	16.7	0.71	114
Pollen nitrogen content (%)	4.20	0.051	98	3.85	0.098	78
Total nitrogen (mg/pollen load)	0.44	0.022	98	0.49	0.023	83

Data were collected for a total of five colonies in the low treatment group and six colonies in the high treatment group. All data were analyzed by two-way ANOVA. All measures were significantly different for the two treatment groups ($P<0.05$), except total nitrogen content (statistical analyses are given in the text)

Colony pollen intake rates

We calculated estimated colony intake rates by multiplying the mean individual pollen load size by the number of individuals returning with pollen loads per unit time. From these calculations we estimate pollen intake rates to be 22.3 g/h for colonies with low pollen storage levels, and 14.5 g/h for colonies with high pollen stores. To confirm these estimates, we made colony-level measures of pollen intake by placing pollen traps on hives. Pollen traps did not remove all pollen loads from foragers, resulting in lower intake measures than estimated. The mean amount of pollen collected in traps was 15.4 g/h (SE=3.68) for colonies with low pollen storage levels, and 9.1 g/h (SE=1.82) for colonies with high pollen storage levels.

Changes in colony contents

We examined changes in pollen, honey and brood within each treatment group by comparing censuses of colony contents at days 1 and 16. Comparisons were made between treatment groups by comparing the censuses for high and low treatment groups made on day 16. Data were analyzed by two-way ANOVA, to determine possible effects of manipulation date on results. We found no significant effect of manipulation date on any of the statistical comparisons of colony contents ($P=0.10$ or greater in all cases). We also found no significant interaction between manipulation date and treatment effects in any of the statistical comparisons ($P=0.50$ or greater in all cases).

Pollen storage levels changed significantly in both high and low treatment colonies through the 16 days after each manipulation. In colonies that were given low pollen storage levels, the amount of stored pollen increased (Fig. 2). Conversely, pollen storage levels decreased in the high pollen treatment colonies, so that, at the 16 day census, pollen storage levels were not significantly different for the two treatment groups ($F=2.06$, $P>0.2$, $n=11$; Fig. 1). At this time, colonial pollen storage levels had returned to levels not significantly different from pre-experimental conditions (paired t -test, $t=1.86$, $P>0.09$).

Honey storage levels did not change between the initial manipulations and the 16 day census for either the low pollen ($F=1.5$, $P>0.2$, $n=10$) or the high pollen treatment groups ($F=0.14$, $P>0.7$, $n=12$; Fig. 2). However, there was a significant response to pollen storage treatments in the amount of brood produced by colonies (Fig. 2). In colonies given low pollen storage levels there was no change in open brood ($F=1.6$, $P>0.2$, $n=10$) over the experimental period. Although amounts of capped brood decreased slightly, the difference between days 1 and 16 was not significant ($F=4.7$, $P>0.06$, $n=10$). Both initial total brood amounts (capped and open), and total brood amounts at day 16 averaged 9500 cm² (SE_{initial}=0.771; SE_{day 16}=0.50; Fig. 2).

In contrast, brood production increased significantly when colonies were given high pollen storage levels. Amounts of open brood increased from an initial mean

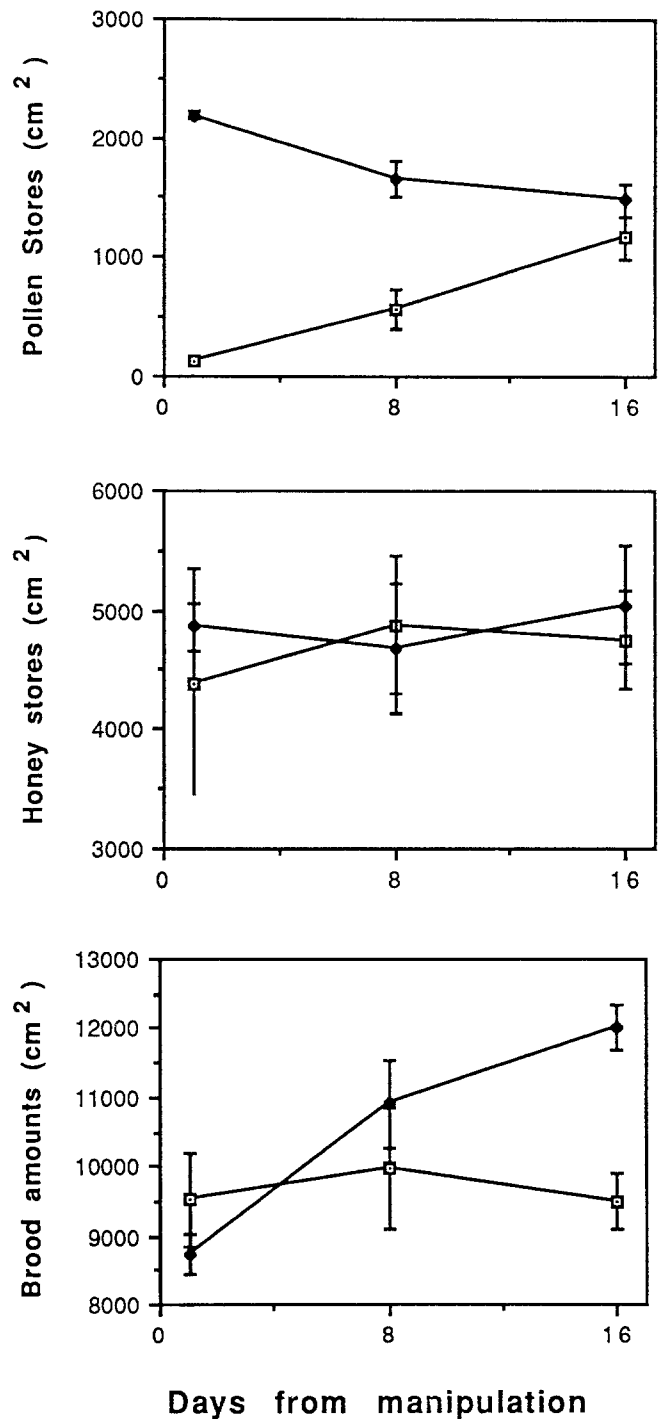


Fig. 2. Changes in pollen stores, honey stores and total brood amounts of colonies given high (solid symbols) versus low (open symbols) initial pollen storage levels. Amounts of each commodity were measured at days 1 (initial), 8 and 16 after each manipulation. Data were collected for a total of 6 colonies under high storage conditions and 5 colonies under low storage conditions. Statistical analyses are given in the text

of 3680 cm² to a mean of 6240 cm² at day 16 ($F=20.4$, $P<0.001$, $n=12$). Amounts of closed brood also increased from an initial mean of 5040 cm² to 5760 cm², but this difference was not significant ($F=3.52$, $P>0.08$, $n=12$). Because of the combined increases in open and closed brood levels, total brood production in high pollen treatment colonies increased by 38%. As a result,

total brood amounts at day 16 were significantly higher in colonies under high pollen storage conditions than under conditions of low pollen storage levels ($F=21.3$, $P<0.002$, $n=11$).

Discussion

We found dramatic changes in both colony-level and individual foraging behavior in response to changes in pollen levels. Individual foragers adjusted both foraging effort and the type of pollen resource collected in response to colony pollen storage levels. Colonies also adjusted pollen foraging effort by increasing the number of foragers collecting pollen when pollen storage levels were reduced. Both population-level foraging changes and the cumulative changes in individual response affected colony pollen storage levels. Because we also found a direct relationship between pollen storage levels and colony brood production, our results demonstrate the potential for cumulative changes in individual foraging decisions to affect colony fitness.

Changes in foraging population

Colonies increased pollen foraging rates by 38% when deprived of pollen stores, in comparison to when they were provided with supplemental pollen. Pollen foraging activity levels have previously been shown to decrease in response to the addition of pollen to colonies (Free 1967; Danka et al. 1987; Camazine 1990), and to be stimulated by pollen removal (Free 1967; Camazine 1990) and by substitution of honey for pollen stores (Free 1967; Barker 1971). Colony pollen intake rates also vary in response to changes in brood levels (Free 1967; Jaycox 1970; Eckert 1990), suggesting that this is a relatively flexible component of colony foraging strategy.

In contrast, we found no significant changes in total foraging rates throughout the experiment, suggesting that colonies respond to changes in food storage levels by covarying nectar and pollen foraging rates. A similar pattern of response has been reported when colonial brood levels are manipulated (Eckert 1990; Higo et al. 1992), suggesting that, under these conditions, honey bee colonies are flexible in terms of the proportion of nectar and pollen foraging trips, but not in total foraging levels.

Contribution of individual response to colony pollen intake

We estimate that colony pollen intake rates (g/h) increased approximately 54% between the high and low pollen treatments. The difference between treatment groups in pollen trap intake rates was even higher, approximately 70%. However, these data are somewhat biased, because pollen traps are more likely to remove larger than smaller loads. Increased intake rates by low treatment colonies were due to increases in pollen forag-

ing rates and in the amount of pollen collected per trip. An estimated 80% of the difference in pollen intake between treatments was accounted for by increased individual foraging effort (changes in foraging intensity and load size), rather than to an increase in the total pollen foraging population. Clearly, variation in individual foraging response can contribute significantly to colony foraging resiliency.

Colonies can alter pollen foraging rates via changes in the number of individuals collecting pollen versus nectar, by changes in the foraging activity levels of individuals already collecting pollen, or by both. In our experiments, pollen foraging rates increased by 29% under low pollen storage conditions (Fig. 1). The increased activity rates of individual pollen foragers accounted for approximately 70% of this variation. An additional 30% was due to changes in the actual number of foragers collecting pollen.

Foragers from low pollen storage colonies increased foraging effort by collecting 19% larger loads per trip. Eckert (1990) and Higo et al. (1992) also found that foragers varied pollen load size as a component of foraging strategy. Individuals also increased relative foraging intensity by spending less time in the hive between trips under low pollen storage conditions. Interestingly, despite the differences in pollen load size, foragers in the low treatment group had foraging trips of shorter duration. These data demonstrate that time spent foraging, examined apart from other variables, is not necessarily a good measure of foraging effort.

Pollen choice in relation to colony need

Although floral choice by honey bees is influenced by a range of factors (reviewed by Menzel 1985; Seeley 1985; Winston 1987; Kolmes 1990), individual nectar choice decisions fit well with economic models based on energetic reward (Schmid-Hempel et al. 1985; Seeley 1986; Schmid-Hempel 1987). In contrast, there is still debate over how well pollen choice criteria match nutritional value (Jay 1986; Winston 1987). Although pollen choice is influenced by non-nutritional phagostimulants (LePage and Boch 1968; Schmidt 1985), there is some evidence that bees are also capable of assessing some measure of protein content. Levin and Bohart (1955) found that, of six pollen types offered at feeding stations, preference rankings of five matched rankings according to crude protein content. The sixth pollen type, alfalfa, had high protein content, but was not collected. However, this pollen was at least 4 years old.

Our data also indicate that foragers assessed pollen in ways that correlated with nitrogen content. However, foragers varied selection criteria as colony requirements changed. We suggest that when pollen storage levels are low in relation to need, individuals collect from plants providing copious pollen amounts. When colonies have high pollen storage levels, foragers select pollen in a way that correlates with higher nitrogen content. Pollen selection also may vary with brood requirements. Buchmann (unpublished data) found that the nitrogen content of

pollen coming into colonies increased during periods of increased brood rearing.

The decrease in proportional nitrogen content for pollen loads in the low pollen treatment group was matched by increased load sizes, so that total nitrogen collected per trip did not change as treatments changed. Total nitrogen intake was increased in colonies with low pollen storage levels by increased pollen foraging activity. However, we cannot determine how well that increase matched requirements for brood development, because we have no data on relative assimilation into developing brood. Therefore, the physiological significance of changes in nitrogen content of individual pollen loads is unclear.

Effects of foraging strategy on colony state

Changes in individual foraging strategy can be examined in an evolutionary context only if they have measurable effects on fitness. In social insects, fitness effects of individual foraging behavior can be determined if foraging decisions are shown to affect colony parameters related to fitness. An important component of this study is examination of the relationship between observed changes in foraging strategy and changes in pollen storage levels and brood production.

The pollen storage levels of all colonies changed in response to changes in individual foraging effort, demonstrating a direct relationship between individual foraging strategy and colony pollen stores. However, the relationship between pollen foraging and brood production is more complex. In our study, brood production was directly affected by pollen storage levels, but was not immediately affected by pollen intake rates themselves. Colonies under high pollen storage conditions increased brood production, but decreased relative foraging effort, while colonies under low pollen storage conditions directed increased pollen intake rates to restoring pollen storage levels, rather than to increased brood production. Our results show that, although cumulative changes in individual foraging behavior affect colony condition, fitness effects are mediated by mechanisms regulating food storage and brood production.

In our experiments, pollen storage levels in all colonies returned to pre-experimental levels within a 16 day period, suggesting strongly that colonies regulate pollen storage levels around a homeostatic set point. Evidence of this and other studies suggests that pollen storage levels are closely regulated around brood production (Filmer 1932; Cale 1968; Allen and Jeffree 1956; Al-Tikrity et al. 1972; Hellmich and Rothenbuhler 1986; Eckert 1990). Both brood production and pollen requirements vary within the life-cycle of a honey bee colony (Fukuda 1960; Winston 1987). If pollen collection shunts worker effort away from other activities, such as nectar collection (Calderone and Page 1988; Robinson and Page 1989; Wolf and Schmid-Hempel 1990), then homeostatic regulation of pollen storage levels around brood production would allow a colony to be resilient to changes in pollen need, while minimizing costs to other colony requirements.

Pollen intake regulation and colony size

Clearly the colonies in our study are capable of increasing rates of pollen collection and brood production above initial levels. Why not maximize immediate growth rates? Studies by Schmid-Hempel and Wolf (1988) and Neukirch (1982) show a correlation between individual foraging effort and mortality, resulting in a potential trade-off between high rates of short-term colony growth and total worker productivity (Houston et al. 1988). Therefore, large colonies, such as those in this study (approx 35,000 adults) may increase long-term efficiency by maintaining more moderate levels of productivity. However, Houston et al. (1988) suggest that strategies for colony growth should vary with colony life cycle, so that smaller colonies increase foraging effort and immediate growth rates relative to full sized ones. Fewell et al. (1991) and Eckert (1990) found that foraging strategies in large and small colonies varied in ways predicted by the model of Houston et al. (1988). An important question remaining from our study is whether smaller colonies also maintain intermediate pollen storage levels, or whether they match brood production with pollen intake to maximize growth rates.

Pollen as a foraging currency

Nectar foraging by honey bees has been one of the principle systems in which questions of the currencies governing individual decisions have been addressed (Cheverton et al. 1985; Schmid-Hempel et al. 1985; Schmid-Hempel 1987; Stephens and Krebs 1986). However, models of nectar foraging in social insects have been problematic because of the difficulty of establishing relationships between individual behavior and fitness (Houston et al. 1988; Wolf and Schmid-Hempel 1990). Despite its importance as a food commodity, pollen has traditionally been overlooked in foraging models addressing fitness questions. Our findings that (1) pollen foraging activity is tightly regulated, and (2) pollen stores have a measurable relationship with fitness variables, suggest that models of the evolution of foraging in social insects can be greatly enhanced by consideration of non-caloric foraging rewards such as nitrogen.

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