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Regulation of pollen foraging in honeybee colonies: effects of young brood, stored pollen, and empty space

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Abstract Pollen storage in a colony of *Apis mellifera* is actively regulated by increasing and decreasing pollen foraging according to the "colony's needs." It has been shown that nectar foragers indirectly gather information about the nectar supply of the colony from nestmates without estimating the amount of honey actually stored in the combs. Very little is known about how the actual colony need is perceived with respect to pollen foraging. Two factors influence the need for pollen: the quantity of pollen stored in cells and the amount of brood. To elucidate the mechanisms of perception, we changed the environment within normal-sized colonies by adding pollen or young brood and measured the pollen-foraging activity, while foragers had either direct access to them or not. Our results show that the amount of stored pollen, young brood, and empty space directly provide important stimuli that affect foraging behavior. Different mechanisms for forager perception of the change in the environment are discussed.

Key words Honeybees · *Apis mellifera* · Pollen foraging

Introduction

Honeybees forage for two kinds of food: pollen and nectar. Pollen is the sole protein source for honeybees. Adult bees eat pollen to fulfill their individual needs and to produce brood food. Nectar is the carbohydrate source for larvae as well as adult bees. One-fourth of the adult bees in a colony are active at a given time as foragers (Seeley 1985), and somehow foragers individually "decide" to collect one or both food types. In general, nectar stores in the colony are quite large (up to 25 kg), whereas the amount of stored pollen is fairly small, about 1 kg at any given time (Jeffrey and Allen 1957). Most pollen is collected on an "as needed" basis and a relatively small amount is kept on reserve compared to the total amount of pollen that a hive uses over the year (about 75 kg; Dadant & Sons 1975).

Therefore, honeybees regulate actively the quantity of pollen stored in the nest. When pollen was added to a colony, pollen-foraging activity decreased until the excess pollen had been depleted by the nurse bees and the quantity of stored pollen returned to near its previous level (Barker 1971; Free and Williams 1971; Moeller 1972; Fewell and Winston 1992). Conversely, when stored pollen was removed from colonies, there was a concomitant increase in the number of pollen foragers and the sizes of the loads of pollen collected until the preexisting quantities were restored (Lindauer 1952; van Laere and Martens 1971; Fewell and Winston 1992; Eckert et al. 1994). These results suggest a mechanism of negative feedback inhibition associated with quantities of stored pollen.

Quantities of brood also affect pollen-foraging activity. Several studies have demonstrated that pollen foraging behavior increases in colonies that have increasing amounts of brood (Filmer 1932; Free 1967; Cale 1968; Todd and Reed 1970; Al-Tikrity et al. 1972; Calderone 1993). Increasing quantities of brood result in more pollen foragers and larger collected loads. Thus, pollen-foraging activity of honeybee colonies appears to be regulated by two factors, the amount of brood which acts as a positive stimulus, and the quantity of stored pollen which acts as an inhibitory stimulus. The mechanisms underlying these effects are unknown. Camazine (1993; see also Seeley 1995) suggested that the two factors are integrated into a single inhibitory signal. Nurse bees are consumers of pollen and deplete the pollen reserves. They convert the proteins in the pollen into glandular secretions that are fed to the larvae. When there are plentiful pollen reserves but few young larvae to feed, nurse bees have an excess of glandular proteins

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that are available for feeding to foragers. According to Camazine's hypothesis, these glandular proteins then inhibit pollen-foraging behavior. When pollen reserves are low relative to the number of larvae, there is little excess protein available to feed foragers and, therefore, no inhibition. We refer to this as the "indirect-inhibitor" hypothesis because neither the brood nor the pollen directly provide cues that affect foraging behavior. An alternative is the "direct-multifactor" hypothesis, which maintains that the quantities of stored pollen and quantities of young larvae themselves provide inhibitory and activating stimuli. This hypothesis is derived directly from empirical results demonstrating the effects of adding or removing brood and stored pollen from colonies (see citations above). The mechanisms are unknown but could involve direct assessment of quantities of brood and stored pollen by foragers.

Returning pollen foragers locate combs containing young larvae (Dreller and Tarpy, in press), inspect cells presumably as they search for cells that are not full of pollen, then back into the cells and remove the pollen from their hind legs. Seeley (1995; based on unpublished data from Camazine) reported that the mean number of cells that a forager inspects before depositing her pollen load is significantly smaller when the pollen reserve is small than when it is large, indicating that pollen foragers might assess storage space. The presence of empty space near the brood may serve as a stimulus for pollen foraging or, conversely, the absence of empty comb space may inhibit pollen-foraging behavior. However, the stimuli could be volatile compounds that accumulate in the hive and are perceived even at a distance.

We conducted experiments designed to compare these two hypotheses. First, we tested the indirect-inhibitor hypothesis by separating foragers from nurse bees. We used methodology similar to Camazine (1993), but compared the behavior of 20 normal-sized colonies instead of two observation hive colonies. The indirect-inhibitor hypothesis predicts that foragers that are separated from nurse bees should be released from inhibition and be more likely to forage for pollen relative to those that are able to maintain trophallactic interactions. We then tested the effects of extra pollen on foragers in the absence of most of the nurse bees of the colony. The indirect-inhibition hypothesis predicts that contact with pollen in the absence of nurse bees should have no effect on pollen-foraging behavior while the direct-multifactor hypothesis predicts that contact between foragers and extra pollen should reduce pollen foraging. Further, we tested the effects of extra brood when foragers were or were not able to directly contact the brood. According to the indirect-inhibitor hypothesis, foragers should react to the need for pollen because they perceive it through trophallactic interactions with nurse bees, even if they are separated from the brood nest. And finally, we tested the effect of empty space, which has been shown to affect nectar-foraging activity (Rinderer and Baxter 1978). According to the indirect-inhibition hypothesis, empty space should not affect pollen foraging, while according to the direct-multifactor hypothesis, empty space might serve as a cue to stimulate pollen collection.

Methods

All experiments were conducted in the Arboretum of the University of California, Davis, in summer 1995. Twenty colonies derived from naturally mated queens (*Apis mellifera ligustica*) were obtained from a commercial beekeeper. The queens were reared from two queen mothers. The colonies were established in the same manner, equalized several times by adding additional frames (of honey, empty comb, or foundation) and/or switching their location. All equalizing among the 20 colonies was performed in advance of the experimental period. Each colony had a total of nine frames in Langstroth equipment during the experiments. Foraging activity was measured by counting returning pollen and non-pollen foragers. Before the experiments started, entrances were reduced to 7.5 cm with fine mesh screen (3.25 mm). An additional coarse mesh screen (12.7 mm) was placed over the entrance of each hive to slow down returning foragers. These screens facilitate counts. All experiments except experiment 4 were performed in the same week in July. The least intrusive experiments were performed first and the most intrusive experiments last to prevent one experiment affecting the next (July 10: experiment 2; July 11: experiment 1; July 13: experiment 3A, July 14: experiment 3B). Experiment 4 was performed in May, when the amount of brood and, therefore, pollen need was very high.

Pollen-foraging activity was measured in the morning to early afternoon, between 8:00 a.m. and 1:00 p.m., by counting the returning pollen and non-pollen foragers while they were walking in. The number of non-pollen foragers served as an estimate for nectar-foraging activity. A count lasted 4 min, and the order in which the colonies were measured was changed randomly. Each colony was measured three times per experiment and the observers doing the counts rotated among colonies. The mean total number of pollen foragers and non-pollen foragers during the entire observation period served as an estimate for the colony's foraging activity and was compared between the ten control and ten test hives using Student's *t*-test.

Separating nurse bees from foragers

According to Camazine (1993), nurse bees are prime candidates for providing indirect signals to the foragers concerning the pollen need. To separate these two worker groups, we made use of the fact that foragers tend to cluster close to the entrance at night, while nurse bees stay in the brood nest (see also Crailsheim et al. 1996). After H.H. Laidlaw (personal communication), foragers and nurse bees can be efficiently separated in a normal-sized colony by putting a screen between the upper hive body with brood and the lower one with empty frames. In a pilot study, we marked 428 presumed nurse bees located on brood combs and 450 foragers returning to the hive (Table 1). In the evening, foragers were expected to cluster in the lower hive body. A screen was placed between the upper and the lower hive body at dark. Early the next morning, we counted the marked bees above and below the screen and found 260 bees

Table 1 Pilot study to determine the distribution of foragers and nurse bees in a hive which was divided by a screen into two compartments

	Marked	Observed in the upper hive body	Observed in the lower hive body
Nurse bees	428	260 (60.7%)	8 (1.9%)
Forager bees	450	25 (5.6%)	58 (12.9%)

originally marked in the brood nest in the upper compartment and only 8 in the lower one. Out of 450 forager bees which were marked at the hive entrance, 58 were observed to be in the lower hive body and 25 in the upper one ($\chi^2 = 185.743$, $P < 0.0001$). This demonstrates a high efficiency for separating the nurse bees from the foragers that are restricted below a screen.

Experiment 1: testing the influence of interaction between nurse bees and foragers on foraging behavior

In this experiment, foragers and nurses were separated by a single or a double screen, as done by Camazine (1993). The colonies were two-story hives with nine frames in the upper section and three empty frames in the lower one. The amounts of pollen, honey, sealed and unsealed brood were equivalent in all 20 colonies. Either a double screen or a single screen was placed between the two hive bodies of a colony at 9:00 p.m. on the evening before foraging activity was measured. Each colony was randomly assigned to one of the two treatments. A single screen prevented foraging bees from entering the brood nest, but allowed feeding and antennal contact with the nurse bees. In colonies with a double screen, no interactions between nurse bees and foragers were possible.

Experiment 2: adding pollen as a direct stimulus

The afternoon prior to this experiment, a Langstroth hive body with two empty combs was placed under the original hive body of nine frames in all colonies. In the evening, a full frame of pollen was added to the lower hive body of ten colonies (test: pollen added) and an empty frame covered with aluminum foil was added to the remaining ten colonies (control: no pollen). This way, the number of frames and additional empty space was kept constant for both groups. At the same time, a single screen (mesh width 3.2 mm) was put between the upper and the lower part of the hive separating the nurse bees from the foragers. The screen prevented the nurse bees (above) from eating the added pollen, but allowed them to interact trophallactically with the foragers (below). Since the conditions for pollen need above the screen were the same for all colonies, there was no difference in the *indirect* stimulation of the pollen foragers, but only in the *direct* stimulation as a result of the added pollen. Pollen-foraging activity was measured the following morning.

Experiment 3: adding young brood as a direct or indirect stimulus

An additional hive body with two empty frames was placed below each hive body. A frame with mainly unsealed brood was exchanged with a frame of sealed brood between pairs of colonies, creating ten colonies with a high brood stimulus (high BS: more unsealed brood) and ten colonies with a low brood stimulus (low BS: more sealed brood). The pairs of colonies were chosen randomly. Counts of pollen and nectar foragers were performed the next morning.

In the evening following the forager counts, a single screen was added to all colonies between the upper and lower hive body to keep the foragers from the brood nest. We could not add brood to the lower compartment as we did with pollen because it may lead to behavioral reversion in forager bees. It has been shown that in the absence of nurse bees, foragers take care of the brood (Page et al. 1992; Robinson 1992; Robinson et al. 1992). Since a single screen was used to separate both compartments, it was still possible for nurse bees to transmit potential information to foragers about the pollen need as proposed by Camazine (1993). If the foragers receive the information *indirectly*, via the nurse bees, differences in foraging activity should still exist between the high BS and the low BS group and resemble the results of the first part of the experiment. If the foragers gather information about the need of pollen by walking over the brood nest, there should be no differences between high BS and low BS, since the screen prevents them from doing so.

Colony evaluations were made blindly at the end of the experiment (Table 2) and revealed that the two groups differed significantly in the amount of unsealed brood ($P < 0.0001$) and in the amount of sealed brood ($P < 0.0001$). They were equal in the number of bees ($P = 0.8$), the total amount of brood ($P = 0.27$), the amount of honey ($P = 0.72$), and the amount of pollen ($P = 0.35$) present in the colonies. Therefore, the only potential stimulus influencing the foraging behavior differently in both colony types was the proportion of unsealed brood.

Table 2 Measurements of the internal colony conditions in the test and control group during experiment 3. Colonies were evaluated with respect to the amount of unsealed and sealed brood, the number of adult bees present in the colonies, total brood, honey area, and pollen area. Measurements are given in comb area covered (mean ± SD) for all parameters, except pollen area, which is given in cm^2. Ten high brood stimulus (*High BS*) and ten low brood stimulus (*Low BS*) colonies were evaluated. The colonies differed only in the amount of unsealed and sealed brood

	High BS test ($n = 10$)	Low BS control ($n = 10$)	P (t-test)
Unsealed brood	2.1 ± 0.4	0.7 ± 0.3	< 0.0001
Sealed brood	1.8 ± 0.4	3.7 ± 0.9	< 0.0001
Total brood area	3.9 ± 0.8	4.3 ± 0.7	0.27
Amount of bees	8.2 ± 0.7	8.1 ± 0.7	0.80
Honey area	3.2 ± 1.0	3.1 ± 0.6	0.72
Pollen area	90.3 ± 61.8	131.4 ± 128.5	0.35

Experiment 4: adding empty space

To test whether foragers perceive that empty cells are available, we added an additional frame to the colonies. Under natural conditions, empty cells would always be correlated with an indirect stimulus, i.e., when nurse bees do not have any pollen to feed to the foragers. However, by adding an additional frame next to the brood nest, the *direct* influence of empty space can be changed without affecting the indirect stimulation provided by nurse bees, unless the empty space interferes with the ability of nurse bees to access the stored pollen. This is unlikely in this case because the empty combs were added at the edge of the brood nest in a position where it did not disrupt the distribution of stored pollen in the colony or access to pollen reserves by nurse bees.

Pollen-foraging activity was measured in 20 colonies on the first day as a control. In the evening, an empty frame was added to each colony. In 10 test hives, the frame was placed next to the unsealed brood nest (comb inside); in the control group, it was placed far away from the brood at the outer end of the hive body (comb outside). Foraging activity was compared between the first day and the next morning by Student's t-test.

Results

Experiment 1: interactions between nurse bees and foragers through a screen do not affect foraging behavior

To test for inhibitory signals transmitted from nurse bees to foragers as has been suggested by Camazine's (1993) experiments, we separated the foragers from brood nest and nurse bees by either a double or a single screen. The double screen prevented any interaction between nestmates in both compartments, whereas the single screen allowed trophallactic interactions. The conditions with respect to empty space, pollen supply, and brood in the upper and lower compartments of the hive were the same in both groups. If inhibitory information is transmitted by the nurse bees, there should be an increase in pollen foraging in colonies with a double screen, where interactions were impossible. If the *direct* assessment of the colony's need by foragers themselves is more important for foraging regulation, the foraging activity should be the same.

There was no difference between hives with a double screen and hives with a single screen (Fig. 1) for the number of pollen foragers (double screen: 40.1 ± 21.1, single screen: 47.5 ± 15.6; $t = 0.89$ $P = 0.39$), the number of nectar foragers (double screen: 341.7 ± 73.4, single screen: 405.9 ± 102.7; $t = 1.609$, $P = 0.13$), or the total number of foragers (double screen: 451.8± 201.7, single screen: 453.4 ± 110.2; $t = 0.022$, $P = 0.98$).

Experiment 2: additional pollen stores can be directly perceived by pollen foragers

To test direct effects of excess pollen on foragers, we separated the foragers in the lower hive body from the rest of the colony in the upper hive body by a single screen, added pollen to the compartment with foragers and measured the foraging activity the following morning.

The total number of pollen foragers (mean ± SD) was significantly lower in colonies which were provided with supplementary pollen (test colonies: 42.3 ± 25.9, $n = 10$; control colonies: 73.1 ± 36.4, $n = 10$; $P < 0.05$), whereas the number of nectar foragers was higher (test: 314.1 ± 79.4, $n = 10$; control: 242.1 ± 88.3, $n = 10$; $P < 0.05$) (Fig. 2). The total number of foragers was not different between the two treatments.

Experiment 3: unsealed brood is perceived by foragers who have access to the brood nest, but not through a screen

In this experiment, the total amount of brood and pollen was held constant, but the amount of unsealed brood was significantly higher in the test colonies and the amount of sealed brood was higher in the controls. Consequently, the pollen need was experimentally increased in test colonies (Table 2). In the first part of the experiment, the pollen foragers had access to both the brood and the nurse bees and, therefore, direct and indirect stimulus perception was possible. Colonies with a

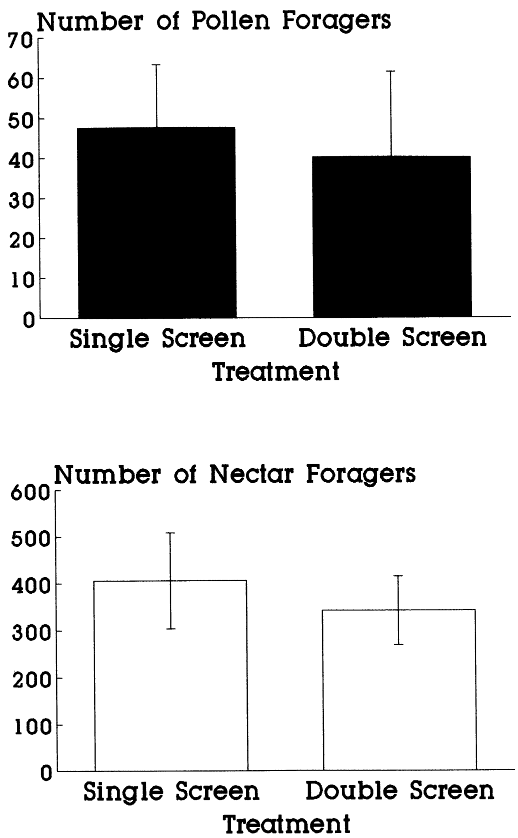

Fig. 1 The number (mean ± SD) of pollen and nectar foragers, when interactions between foragers and nurse bees were prevented by using a double screen to separate them or when interaction was enhanced through a single screen

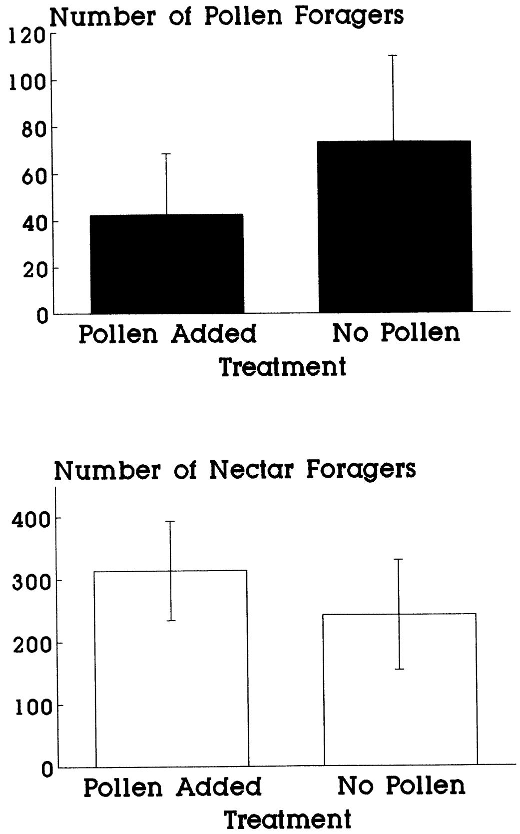

Fig. 2 Total number (mean ± SD) of pollen foragers and nectar foragers in colonies which have been provided with an additional pollen comb (*Pollen Added*) compared to colonies which were provided with an empty comb covered with aluminum foil (*No Pollen*). In both groups, only foragers had access to the added comb

high brood stimulus (high BS) had a significantly higher number of pollen foragers (Fig. 3a, left; 274.8 ± 87.1, $n = 10$) compared to colonies with a low brood stimulus (low BS: 190.6 ± 31.1, $n = 10$; $t = -2.835$, $P < 0.05$), whereas the number of nectar foragers was not different (high BS: 450.1 ± 77.7, low BS: 420 ± 95.2; $t = -1.571$, $P = 0.15$). Overall foraging activity was also higher in the colonies of high brood stimulus (high BS: 724.9 ± 111.4, and low BS: 610.6 ± 103.5; $t = -4.385$, $P < 0.01$).

In the second part of the experiment, foragers were separated from the brood nest by a single screen. Therefore they could only *indirectly* receive information about the pollen need from nestmates in the upper brood nest via trophallactic and antennal interactions. In this situation, the number of pollen foragers was not different (Fig. 3a, right) between high BS colonies (166.4 ± 36.3, $n = 10$) and low BS colonies (142.9 ± 62.4, $n = 10$; $t = -1.029$, $P = 0.32$). The same is true for the number of nectar foragers (Fig. 3b, right: high BS: 403.7 ± 85, low BS: 420.8 ± 101.1; $t = 0.409$, $P = 0.69$) and the total number of foragers (high BS: 570.1 ± 96.9, low BS: 564 ± 146.6; $t = -0.11$, $P = 0.91$).

A repeated-measures ANOVA revealed that the introduction of the screen changed the pollen-foraging behavior of the colonies drastically ($P < 0.001$). Nectar foraging was not affected ($P = 0.44$), indicating that the separation from the brood nest had a strong effect only on pollen-foraging behavior.

Experiment 4: additional empty space increases pollen-foraging activity

Adding an empty frame to the colony does not affect the brood-to-pollen ratio, or any indirect signals by nestmates about the pollen need. However, foragers might directly detect empty cells when they unload the pollen. Comparing the foraging rates between the day before and after manipulation revealed that there was a significant increase in the total number of pollen foragers from day 1 to day 2 ($P < 0.01$) when the comb was inside the brood nest (Table 3). There was no increase in pollen-foraging activity when the empty comb was placed outside the brood nest ($P = 0.35$). The number of nectar foragers also increased significantly only in colonies with the comb next to the brood ($P < 0.05$).

Discussion

Honeybee colonies regulate their nectar- and pollen-foraging activities based on the current amounts of stored pollen and young brood (Filmer 1932; Lindauer 1952; Free 1967; Cale 1968; Todd and Reed 1970; Barker 1971; Free and Williams 1971; van Laere and Martens 1971; Al-Tikrity et al. 1972; Fewell and Winston 1992; Moeller 1972; Calderone 1993; Eckert et al. 1994). Our results suggest that pollen foragers *directly* perceive the availability of filled or empty pollen cells and quantities of young brood, and react to them by adjusting their foraging efforts accordingly.

Camazine (1993) separated pollen foragers from the nurse bees by placing them on a comb located at the bottom of two observation hives. The bottom comb was separated from the rest of the nest with either a double or a single screen. The single screen allowed the exchange of food between bees, the double screen blocked trophallaxis. Camazine (1993) observed a decrease in pollen foraging when there was just a single screen compared to the double-screen treatment. He interpreted these results to suggest that nurse bees were feeding a protein inhibitor to the pollen foragers and thereby regulating pollen-foraging activity.

Our study, however, failed to demonstrate the same effect. We found no difference between our single- and double-screen treatments (Fig. 1). It is likely that we had some nurse bees below our screens with our foragers (Table 1), but there was an equal expectation for both of our treatments. Crailsheim et al. (1996) also demonstrated that most nurse bees remain in the brood nest. Trophallaxis was not restricted in the single-screen treatment, so we still would expect a greater inhibition in the single-screen treatment relative to the double-screen treatments if pollen foraging is regulated by protein inhibitors produced and distributed by the nurse bees.

The addition of a pollen frame decreased pollen foraging when foragers were allowed direct access to the comb in the absence of normal contact with nurse bees (Fig. 2). Trophallaxis through the screen should have been equal in colonies of both treatment groups; however, we cannot rule out the possibility that a small number of nurse bees located below the screen with the foragers (<2% by our estimates in Table 1) consumed the pollen in the absence of brood and fed protein to the pollen foragers. This large effect of a small group of individuals would complicate the models for pollen-foraging regulation because it would imply a more complex mechanism for distribution of protein inhibitor. Also, based on data of Crailsheim et al. (1996), it is unlikely that this occurred. They showed that trophallactic exchanges of nurse bees and other adult bees (including non-foraging adult bees) are rare – an average of about once per hour.

Unsealed brood acts as a positive factor increasing the pollen-foraging activity, but only if foragers have direct access to the brood nest in our experiment (Fig. 3). The indirect-inhibitor hypothesis predicts that more brood above the screen should still result in more pollen-foraging activity because more protein will be fed to the brood by the nurses and less inhibitor will be available to be fed to the foragers below the single screen. One could argue that we saw no effect through the screen because our high-brood colonies also had more stored pollen resulting in a balance between supply and demand. However, estimation of colony conditions following the

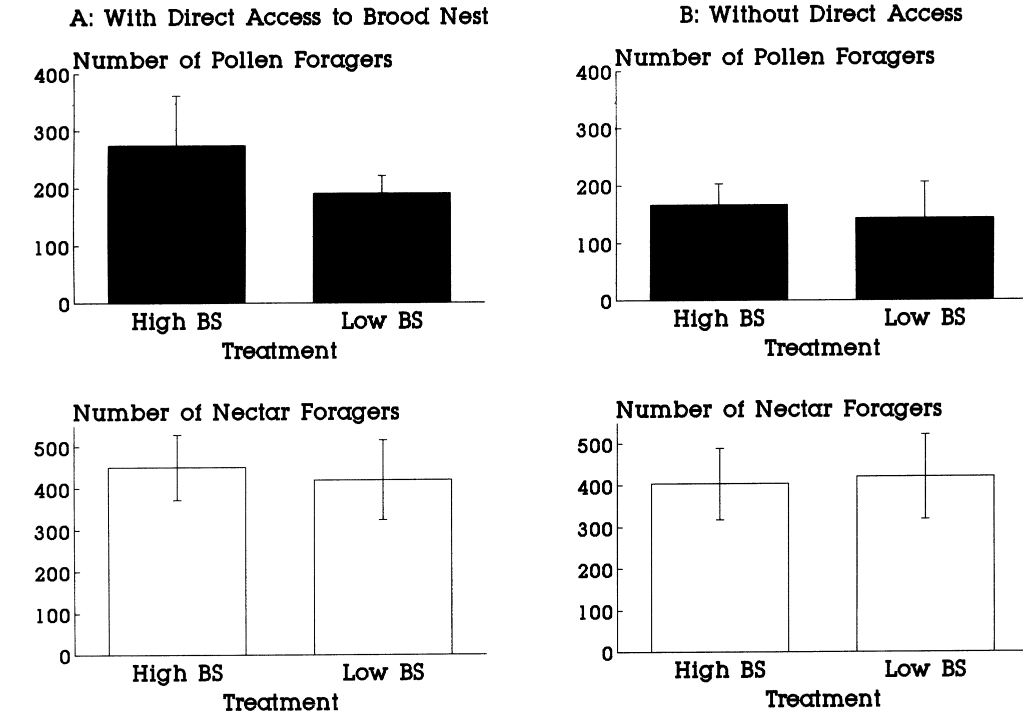

Fig. 3 Total number (mean ± SD) of pollen and nectar foragers in colonies with a high brood stimulus (*High BS*), i.e., more unsealed brood, or a low brood stimulus (*Low BS*), i.e., more sealed brood

addition of the screens demonstrated that our high-brood-treatment colonies had less stored pollen than the low-brood colonies, resulting in an even greater brood-to-pollen ratio in the high-brood treatment. According to the indirect-inhibitor hypothesis, this should have led to even more pollen foraging, which was not the case.

Empty space also increased pollen-foraging activity when it was located at the edge of the brood nest where foragers normally unload their pollen. It is unlikely that the change in foraging behavior resulted from a signal provided by nurse bees which integrates the information about pollen supply and amount of brood. This brood-to-pollen ratio was not changed by an additional frame in our experiment (Table 3). Our result rather supports the hypothesis that pollen foragers directly assess pollen storage areas and are stimulated by empty space. It appears that foragers perceive the empty cells directly while crossing the brood area. This assumption is supported by the observation that an empty frame at the edge of the nest did not increase the pollen-foraging activity.

In social insects, worker-worker interactions have been postulated to play important roles in the integration of colony division of labor (Huang and Robinson 1992). Different treatment of nestmates during trophallaxis influences the nectar-foraging behavior (Seeley 1989, 1995; Seeley and Tovey 1994). Without assessing the honey area, nectar foragers can collect information about the nectar supply in the colony at the entrance just by measuring the time they need to unload. Pollen foraging seems to be regulated by another mechanism. How many factors are involved in the regulation of pollen foraging? Our results suggest at least three: young larvae, stored pollen, and empty space. These may not necessarily be independent, but our results suggest that their effects are direct, rather than integrated into a single indirect signal. Young brood and empty space stimulate more pollen foraging while stored pollen inhibits it. Stored pollen and empty space may be negatively correlated under normal conditions because as more pollen is stored, less empty space is available.

Table 3 The effect of empty space on pollen- and nectar-foraging activity. The empty frame was added either next to the open brood (*Comb inside*) or at the outer end of the hive body (*Comb outside*). Foraging activity was measured before (day 1) and after (day 2) the introduction of the empty frame

	Pollen foragers		Nectar foragers	
	Day 1	Day 2	Day 1	Day 2
Comb inside ($n = 10$)	223 ± 69	278 ± 80 $P < 0.01$	263 ± 64	333 ± 81 $P < 0.05$
Comb outside ($n = 10$)	250 ± 75	274 ± 79 $P = 0.35$	287 ± 74	328 ± 67 $P = 0.14$

However, in our experiments, we controlled for empty space when we added combs of pollen below the separating screens. Areas for brood and stored pollen are also negatively correlated.

Nectar-foraging activity estimated by the number of non-pollen foragers was also measured in our experiments. While additional pollen (with the same amount of brood) seems to stimulate nectar foraging at the cost of pollen foraging, an increase in the amount of unsealed brood increases both nectar and pollen foraging. In Camazine's (1993) experiments, additional pollen did not lead to a switch from pollen to nectar foraging. Pollen foragers instead quit foraging. However, it is difficult to compare those results with our study, because in his study, brood was also present in the compartment with foragers, which is known to cause behavioral reversal (Robinson et al. 1992). However, if one assumes that the brood-to-pollen ratio is somehow integrated in a signal provided by nurse bees, the reaction to a change in each factor should be the same. Pollen foragers would not know whether a change in the level of inhibitor provided by nurse bees is due to a decreased brood area or an increase in pollen stores. Our results show that pollen and nectar foraging are, to some extent, influenced independently. Pollen foraging can be increased at the same time as nectar foraging; on the other hand, if enough pollen is available, pollen foragers are likely to switch to nectar.

The effects of brood have recently been demonstrated to be direct, independent, and stimulating for pollen foraging (Pankiw et al. 1998). Hexane rinses of young larvae resulted in dramatic and immediate increases in the number of pollen foragers when placed into the brood nest of colonies. The numbers of pollen foragers can be directly and quantitatively modulated by varying the amount of brood pheromone presented to the colony. In contrast, although much evidence exists for inhibitory effects of pollen, the actual mechanisms of inhibition remain to be demonstrated.

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