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ORIGINAL ARTICLE

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# Pollen phenolics and regulation of pollen foraging in honeybee colony

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**Abstract** Honeybee colonies can regulate their collection of pollen in response to pollen stores within the hive. The question as to how colonies or individual foragers detect changes in pollen quantity or quality is intriguing. Although forager bees seem unable to directly assess pollen protein content, other nonnutritional factors (particularly changes in pollen odor) may act as cues for assessing pollen stores. Pollen is enriched with nonnutritional phenolic compounds, which are responsible for the strong pollen odor to which honeybees are sensitive and which are also plant-defensive compounds against herbivores. Here we examine the bees' foraging activity for pollen of different floral species in relation to their phenolic contents. We show that honeybee foragers of *Apis cerana* prefer species with low phenolic content, thus suggesting that they can detect and estimate the amount of phenolics in pollen. Furthermore, feeding colonies with sugar syrup seems to increase their acceptance of pollen with high phenolic contents. When such feeding was stopped, a decrease in the collection of pollen with high phenolic content was observed, which was accompanied by an increase in the collection of pollen with low phenolic content. This shift resulted in a reduction of the overall phenolic intake rate a few days after colony manipulation. These results suggest that pollen-foraging activities of a honeybee colony are regulated by quantitative changes in phenolic contents of pollen. Honeybees could, therefore, use nonnutritional factors, such as pollen phenolics, to assess colony requirements and to change foraging dynamics accordingly.

**Keywords** Honeybee · *Apis cerana* · Behavior · Phenolics · Pollen foraging

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## Introduction

Pollen is an extremely important protein source collected by honeybee foragers (Winston 1987). Honeybees are especially sensitive to sudden fluctuations in environmental pollen supply (Fewell and Winston 1992; Fewell and Batram 1999), and they tightly regulate their rates of pollen collection in response to changes in pollen stores within the colony (Barker 1971; Free and Williams 1971; Moeller 1972; Fewell and Winston 1992; Camazine 1993; Dreller et al. 1999; Fewell and Batram 1999). A decrease in the level of stored pollen increases the pollen-foraging activities of the colony. However, not all pollens are equally collected. Honeybees clearly prefer to collect some pollen types over others, both in a natural context (Roubik and Villanueva 2004) and in controlled-choice experiments (Boch 1982; Boelter and Wilson 1984). They also change their pollen choice in response to pollen stores (Fewell and Winston 1992).

The questions as to how individual workers detect changes in pollen quantity or quality and how such changes determine their foraging responses remain unanswered (Calderone and Johnson 2002). "Direct assessment" hypothesis suggests that pollen foragers assess pollen availability directly through physical contact with pollen stores, empty cells, or larvae (Dreller et al. 1999; Vaughan and Calderone 2002). Due to limited comb space, pollen storage would compete with brood rearing and nectar storage (Dreller et al. 1999) such that an interplay should exist between these activities. However, other studies do not necessarily favor this hypothesis. Pollen foragers can differentiate between empty cells and cells with pollen

(Camazine 1991) and prefer to store pollen in cells that already contain it (Calderone and Johnson 2002) instead of competing for empty cells with nectar-storing or brood-rearing hive mates.

Alternative "indirect assessment" hypothesis posits that honeybee workers assess pollen availability by means of variables that differ from the direct amount of stored pollen (Camazine 1993). For instance, food exchanges among nest mates could provide information about a colony's current needs (Hrassnigg and Crailsheim 1998). Camazine (1993) suggested that stored pollen indirectly affects the behavior of pollen foragers through a single inhibitory signal providing negative feedback on pollen-foraging activities. Brood food is the most likely inhibitor (Camazine 1993) of these activities: if pollen is in surplus, nurse bees secrete a surplus of proteins that is fed to foragers and inhibits pollen foraging (Camazine 1993). Colonies supplemented with pollen decrease their pollen collection activity and increase the amount of radiolabeled amino acids being transferred to pollen foragers (Camazine et al. 1998). A shift in floral preference of foragers might also be related to the nutritional quality of pollen (Roubik and Villanueva 2004). Fewell and Winston (1992) suggested that honeybees frequently choose high-protein pollen when pollen stores within the colony are high, and they accept low-protein pollen when stores are low. However, experimental evidence indicates that individual foragers do not possess the ability to assess pollen protein content (Pernal and Currie 2001). Other nonnutritional factors (particularly changes in pollen odor) may act as cues for assessing pollen stores and quality (Pernal and Currie 2001).

Besides proteins, pollen also contains phenolic compounds (Stanley and Linskens 1974), which are plant-defensive compounds against herbivores (Haslam 1988; Schoonhoven et al. 1998). Honeybees are sensitive to phenolics, both in a natural context (Gronquist et al. 2001) and in controlled-choice experiments (Liu et al. 2004). Pollen phenolics emit odors that may attract pollinating bees (Gronquist et al. 2001) and, at the same time, can produce a defensive astringent taste against herbivores (Haslam 1988; Schoonhoven et al. 1998). Indeed, evolution of some plant traits may be constrained by opposing selection from herbivores and pollinators (Adler 2000). It could be argued, for instance, that phenolics increase pollinator attraction if decreased herbivory improves floral displays or rewards. Contradictory evidence with respect to the effect of phenolics in nectar exists. While Haglar and Buchman (1993) reported the deterrence of bee foragers by phenolics, Liu et al. (2004) found the opposite effect. Phenolics present in pollen might exert considerable influence on pollen foraging in honeybees.

In the present work, we compared changes in pollen-foraging activities of colonies fed or not fed sugar syrup. Feeding sugar syrup to bee colonies is widely practiced in many beekeeping countries to stimulate pollen collection because it is argued that sugar provides the energy necessary for foraging activities (e.g., Faegri and van der Pijl 1979). However, whether or not such feeding changes the foragers' floral choice remains unknown. Here we studied whether the types and proportions of pollen species collected by honeybee colonies differ in response to such manipulation. Specifically, we evaluated the phenolic contents of pollen loads to determine whether pollen foraging is regulated by pollen phenolics.

## Materials and methods

### Experimental design

Experiments were conducted in March 2005 in the experimental farm of the Institute of Sericulture and Apiculture, Yunnan Academy of Agricultural Sciences (Mengzi County, Yunnan Province, PR China; 23°24–23°27°N, 103°17–103°26°E, 1,260 m elevation). At the time during which the experiments were performed, few flowers were open and produced minute amounts of nectar. Two three-frame colonies of Chinese honeybees (*Apis cerana*) were used in these experiments. At the beginning of the experimental period, the colonies were matched to ensure equal levels of adult bees and were both deprived of brood and food frames, which were replaced by empty frames. Despite the fact that colony sample size was reduced, treatment performed in this work included within-colony control as well as between-colony control. This was achieved by comparing an experimental colony and a control colony throughout the experiment and by swapping treatments between the first and the second experimental phases (see below). This ensured therefore that changes observed were not due to intrinsic factors of a given colony, but did indeed result from our experimental manipulations.

Colony 1 (treatment) was provided fresh syrup (25% sucrose, wt/wt) in beakers inside the hives. These were replenished throughout the first phase of the experiment in order to provide a constant input of sugar. Colony 2 (control) was not fed during the entire first phase of the experiment. We intercepted at least ten returning foragers once every 30 min during the period of normal foraging activity (between 0930 and 1630 hours, local time). We froze them and removed the pollen loads from one of two legs. The pollen species and phenolic contents of pollen samples at 1-day intervals were compared between the treatment and the control colonies. When differences in pollen species sampled by the two colonies were detected, we swapped the treatment and the control colonies during the period between the end of a break and the start of the second experimental phase. Swapping treatments between colonies allowed the determination of whether differential collection of pollen was due to intrinsic differences between colonies or due to the syrup-feeding treatment employed.

### Identification of pollen species

Chinese worker bees tend to collect unifloral pollen in a single foraging bout (Liu et al. 1998). The color of single-species (unifloral) pollen loads provides a preliminary

indication of species composition (Kirk 1994). Light microscopy (ECLIPSE, E2000; Nikon) was used to identify pollen species from collected pollen loads. Routine identification of pollen was performed by means of microscopic examination of pollen grains in aqueous suspension, which were mounted on glass slides with coverslips. Identification was achieved by comparing observations to a reference set of honey plants (ZITT and HIP 1987) or to field observations. The proportion of each species collected by each colony was calculated.

### Measurement of pollen-foraging rate

At the same time during which we sampled pollen loads, we counted the number of returning pollen foragers within 30-min duration at the entrance of hives. The pollen-foraging rate of the colony was expressed as the number of foragers per 30 min. The data were also pooled at 1-day intervals and were averaged on each day for the two colonies.

### Determination of phenolic content

The phenolic content of each pollen species was determined from pollen samples during the experimental period. Determination of the phenolic content of unifloral pollen loads followed the procedure of Liu et al. (2005). Briefly, 1 g of fresh pollen loads (M) was added to 20 ml of boiling distilled water (100°C) for 30 min. After cooling, the infusion was filtered and then diluted with distilled water up to a volume of 50 ml ($V_1$). An amount of 0.5 ml of diluted phenolic–aqueous solution ($V_2$) was mixed with 1% $AlCl_3$ up to a volume of 10 ml and then was shaken. In contrast with the 1% $AlCl_3$ aqueous solution, absorbance of the diluted phenolics–aqueous solution at 420 nm (A) was measured by using a spectrophotometer (721-2000; Shanghai). The phenolic content of pollen loads was calculated according to $320AV_1/1000V_2M$.

### Analysis of phenolic intake

Phenolic intake rates per colony were expressed as the mean phenolic content of pollen loads within each 30-min observation.

### Statistical analysis

During the entire experimental period, bad weather greatly affected the foraging activity of worker bees. There were times when we could not obtain more than ten pollen loads in the morning and in the afternoon. The data that were pooled in the morning (between 0930 and 1000 hours) and in the afternoon (between 1600 and 1630 hours) were not included for a more accurate assessment. The proportions of pollen species sampled by colony were transformed using arcsine transformation; pollen-foraging rates were transformed using square root transformation (see Pernal and Currie 2001). The phenolic intake rate of a colony was square-root-transformed prior to analysis (see Pernal and Currie 2001). Data were analyzed by means of ANOVA to test for significant differences between our treatments. SPSS 12.0 for Windows was used for statistical analyses.

## Results

### Pollen species

Due to bad weather (rain and snow), the first experiments were performed on 7–11 March. During this period, we collected 572 and 488 sets of corbiculate loads from colony 1 (fed syrup) and colony 2 (not fed), respectively. Seven pollen species were identified in pollen loads. The five most abundant floral species were *Bidens bipinnata*, *Punica granatum*, *Ligustrum lucidum*, *Melilotus suaveolens*, and *Taraxacum mongolicum* (Table 1). We also identified pollen from *Raphanus sativus*, but it was too scarce to be included in the analyses. A seventh unidentified abundant species was found recurrently and was henceforth called US (for unidentified species). Figure 1 shows that the proportions of pollen of the five most abundant species and the US collected by each colony varied significantly ($F_{5,102}$=26.302, $P$<0.001 for colony 1; $F_{5,102}$=94.441, $P$<0.001 for colony 2). This result thus indicates that each colony had pollen preferences.

We compared the distributions of pollen collected by the two colonies. No significant differences between colonies were found for *B. bipinnata* ($F_{1,23}$=0.424, $P$=0.529), *P. granatum* ($F_{1,23}$=1.302, $P$=0.28), *L. lucidum* ($F_{1,23}$=0.272, $P$=0.614), and US ($F_{1,23}$=1.853, $P$=0.203) (Fig. 1). *B. bipinnata* represented more than 50% of all pollen loads, while the other species were less represented. The two colonies collected mostly *B. bipinnata* and much less *P. granatum* and *L. lucidum*. Significant differences between colonies were nevertheless found for the pollen of *M. suaveolens* and *T. mongolicum* (Fig. 1). These differences were opposite in direction: colony 1 collected less *M. suaveolens* ($F_{1,23}$=12.487, $P$=0.005) and more *T. mongoli-*

**Table 1** Occurrence, weight, phenolic content and proportion of pollen species sampled by forager bees

| Pollen species | Occurrence time | Dry weight of single pollen load (mg) | Phenolic content of single pollen load (mg/g) |
|---|---|---|---|
| *Punica granatum* | 9:30–10:30 | 3.09 | 11.2 |
| *Ligustrum lucidum* | 9:30–11:30 | 4.25 | 4 |
| *Melilotus suaveolens* | 10:30–12:30 | 5.46 | 3 |
| *Taraxacum mongolicum* | 10:30–13:30 | 3.63 | 5.568 |
| *Bidens bipinnata* | 9:30–16:30 | 6.12 | 0.864 |
| Unidentified species | 15:30–16:30 | 4.27 | 2.39 |

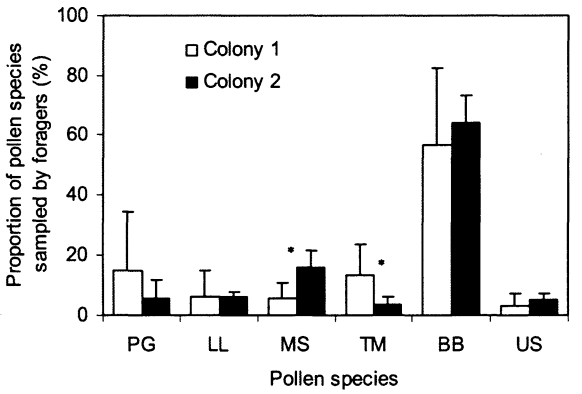


**Fig. 1** Mean proportion of pollen loads of dominant floral species collected by the two colonies (*white bars*, colony 1; *black bars*, colony 2). Pollen species comprise >90% of the total number of pollen grains per load. *PG Punica granatum*, *LL Ligustrum lucidum*, *MS Melilotus suaveolens*, *TM Taraxacum mongolicum*, *BBBidens bipinnata*, *US* unidentified species. Plotted data are nontransformed means and standard errors. *Asterisks* indicate significant differences at the $P$=0.05 level

*cum*, while the opposite was true for colony 2 ($F_{1,23}$=4.962, $P$=0.05).

We attempted to relate these differences to phenolic contents. We thus evaluated the phenolic contents of the pollen loads collected by foragers (Table 1). The pollen loads of *B. bipinnata* contained the least phenolics (0.864 mg/g), while those of *P. granatum* contained the most phenolics (11.2 mg/g). The pollen loads of *T. mongolicum* and *L. lucidum* also contained relatively high phenolics (5.568 and 4 mg/g, respectively). The pollen of *M. suaveolens* contained 3 mg/g. Thus, the two colonies preferred the pollen species with the lowest phenolic contents (*B.bipinnata*). Species with high to moderate phenolic contents were significantly less chosen (see Fig. 1). Colony 1, which collected more *T. mongolicum* than colony 2, thus had, in principle, a higher intake of phenolics (see Table 1).

Figure 2 shows that pollen-foraging rates were not significantly different between colonies ($F_{1,35}$=0.86, $P$=0.36). Furthermore, no significant differences were found between the three recording periods (on the second and fourth days of the first experimental phase and on the second day of the second experimental phase, after swapping treatments) ($F_{2,34}$=0.386, $P$=0.683). Thus, despite having different feeding regimes, global foraging activities were similar in both colonies.

However, because the proportion and the phenolic content of each pollen species collected by the two colonies were different, the phenolic intake rate of colony 1 was significantly higher than that of colony 2 at the beginning of the first experimental phase (Fig. 3; on the second day of the first experimental phase: 0.5277±0.2714 vs 0.3341± 0.1323 mg/30 min, mean±SE in both cases; $F_{1,23}$=14.779, $P$=0.001). This indicates that forager bees of colony 1 were less reluctant to collect pollen with higher phenolic contents than were those of colony 2. Such a difference in sensitivity to phenolics may reflect a higher resistance to these compounds in colony 1 than in colony 2. Interestingly, this difference was no longer present on the fourth day of the first experimental phase. This suggests that colony 1 reduced its phenolic intake, probably because of accumulation of phenolics within the hive.

To determine whether differences in sensitivity to phenolics were due to intrinsic differences between colonies or resulted from our feeding manipulations (feeding syrup or not), we swapped treatments in the second experimental phase (colony 1 received no syrup while colony 2 was provided sufficient syrup). After swapping treatments, the phenolic intake rates of colonies 1 and 2 were reverted with respect to those recorded at the beginning of the first experimental phase ($F_{2,15}$=18.850, $P$<0.001 for colony 1; $F_{2,15}$=14.717, $P$<0.001 for colony 2). Now it was colony 2, the colony now fed sugar syrup, that had a higher intake rate of phenolics (0.2115±0.0391 mg/30 min for colony 1 vs 0.3071±0.0657 mg/30 min for colony 2, mean±

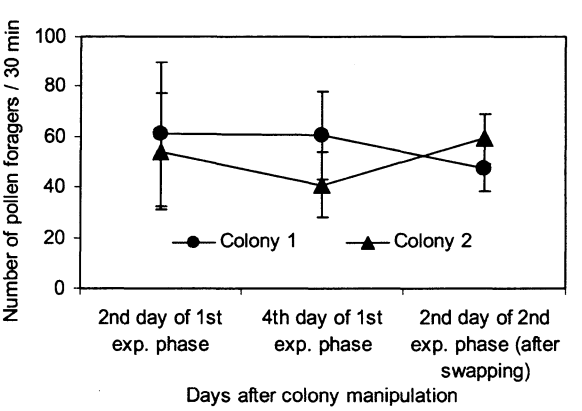


**Fig. 2** Means of pollen-foraging rates (mean number of pollen foragers per 30 min) of colony 1 (*circles*) and colony 2 (*triangles*) along the three recording periods of the whole experiment. The first two data points correspond to the first experimental phase (second and fourth days); the third and last data point corresponds to the second experimental phase during which time feeding treatments of colonies were swapped. Plotted data are nontransformed means and standard errors

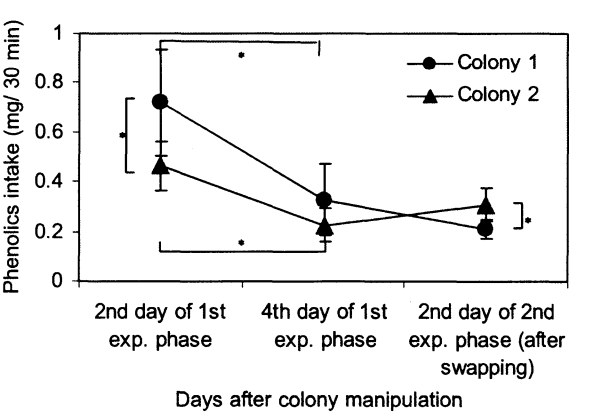


**Fig. 3** Mean phenolic intake rates (mg/30 min) of colony 1 (*circles*) and colony 2 (*triangles*) along the three recording periods of the whole experiment. The first two data points correspond to the first experimental phase (second and fourth days); the third and last data point corresponds to the second experimental phase during which time feeding treatments of colonies were swapped. Plotted data are nontransformed means and standard errors. *Asterisks* indicate significant differences at the $P$=0.05 level

SE in both cases; $F_{1,23}$=9.384, $P$=0.012; see Fig. 3). Thus, the colony fed sugar syrup (now colony 2) was now more resistant to phenolics than the one that was not fed (now colony 1). This indicates that mean phenolic intake was dependent on sugar provisions of the colony, which may have determined changes in pollen preferences.

To verify that there was a change in pollen preferences resulting from phenolic intake and feeding treatments, we focused on the distribution of pollen collected by colony 1 in the second and fourth days of the first experimental phase and in the second day of the second experimental phase, after swapping feeding treatments. During the first experimental phase, colony 1 significantly decreased its collection of *P. granatum* and *T. mongolicum*, which had high phenolic contents [multiple comparisons, least significant difference (LSD)=7.8333, $P$=0.015 for *P. granatum*; LSD=8.8333, $P$=0.039 for *T. mongolicum*], and simultaneously increased its collection of *B. bipinnata*, which has a low phenolic content (LSD=36.3500, $P$=0.018) (Fig. 4). As mentioned above, the fact that bees already increased the collection of *B. bipinnata* pollen at the end of the first experimental phase may be due to the accumulation of phenolics within the hive, which led bees to collect pollen with less phenolics. In the second experimental phase, after swapping feeding treatments, colony 1 practically stopped the collection of *P. granatum* pollen with high phenolic content (LSD=24.700, $P$=0.027) and focused almost exclusively on the pollen of *B. bipinnata*, which had the lowest phenolic content (LSD=38.800, $P$=0.013) (Fig. 4). No changes were found for the other pollen species ($F_{2,15}$=1.592, $P$=0.236 for *L. lucidum*; $F_{2,15}$=0.389, $P$=0.684 for *M. suaveolens*; $F_{2,15}$=0.471, $P$=0.634 for US) (Fig. 4).

A similar analysis performed on colony 2 showed that there were also significant differences in the distribution of pollen collected along the experimental phases. Like colony 1, colony 2 significantly decreased its collection of *P. granatum* (LSD=12.2667, $P$=0.045) and *T. mongolicum* (LSD=7.4500, $P$=0.007), which had the highest phenolic contents, in the first experimental phase (Fig. 5). This shows that both colonies decreased their collection of pollen with high phenolic contents, probably because of the accumulation of phenolics in the hive. The main difference between colonies in the beginning (on the second day) of the first experimental phase was that colony 1 collected more pollen with higher phenolic contents than did colony 2. Colony 2 did not show temporal variations in its sampling of *L. lucidum* ($F_{2,15}$=0.548, $P$=0.589) and *M. suaveolens* ($F_{2,15}$=0.545, $P$=0.591) (Fig. 5).

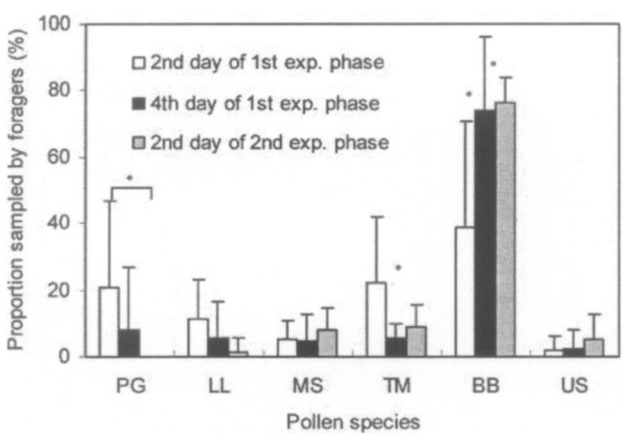


**Fig. 4** Temporal changes in the proportion of pollen species sampled by colony 1 along the three recording periods of the whole experiment (second and fourth days of the first experimental phase, *white bars* and *black bars*, respectively; second day of the second experimental phase, *hatched bars*). *PG Punica granatum*, *LL Ligustrum lucidum*, *MS Melilotus suaveolens*, *TM Taraxacum mongolicum*, *BBBidens bipinnata*, *US* unidentified species. Plotted data are nontransformed means and standard errors. *Asterisks* indicate significant differences at the $P$=0.05 level

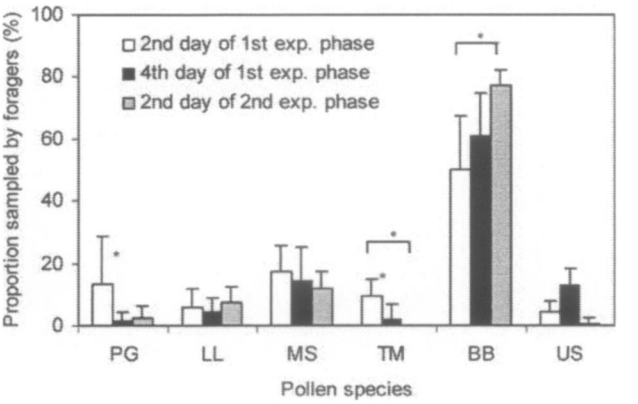


**Fig. 5** Temporal changes in the proportion of pollen species sampled by colony 2 along the three recording periods of the whole experiment (second and fourth days of the first experimental phase, *white bars* and *black bars*, respectively; second day of the second experimental phase, *hatched bars*). *PG Punica granatum*, *LL Ligustrum lucidum*, *MS Melilotus suaveolens*, *TM Taraxacum mongolicum*, *BBBidens bipinnata*, *US* unidentified species. Plotted data are nontransformed means and standard errors. *Asterisks* indicate significant differences at the $P$=0.05 level

## Discussion

Here we showed that honeybee foragers preferred pollen species with low phenolic content over those with high phenolic content, thus suggesting that they can detect phenolic content in pollen and choose pollen types accordingly. We also showed that feeding sugar syrup to a colony seems to affect pollen choice such that higher phenolic contents are more tolerated. This tolerance is nevertheless transient because accumulation of phenolics within the hive results in a decrease in the collection of pollen with high phenolic content. Furthermore, depriving a colony of syrup after a feeding period results in dynamic changes in phenolic intake rates: after such a treatment, a colony decreases the collection of pollen species with high phenolic contents and simultaneously increases the collection of pollen with low phenolic contents in order to even more reduce the overall phenolic intake rate within a few days posttreatment. These results suggest that the pollen species and their proportions, as sampled by honeybee foragers, are regulated by quantitative changes of pollen phenolic contents within the colony. This, in turn, supports

the hypothesis that honeybees can use nonnutritional factors (such as phenolic contents) to assess colony requirements and to change foraging dynamics.

The data from this study show that individual bees and/or colonies clearly prefer some pollen types. Similar observations have been reported by other studies (Boch 1982; Boelter and Wilson 1984). Previous experiments, which focused on foraging choices based on nutritional criteria, suggested that foragers cannot perceive protein contents of pollen as a basis for such preferences (Shaw 1990; Pernal and Currie 2001). We report here that phenolic content, instead of protein content, could underlie specific pollen preferences of honeybee foragers. The proportion of pollen species sampled by forager bees is possibly linked to floral availability. However, our results point out that the variation in the proportions of sampled pollen results from increasing deterrence associated with the accumulation of pollen phenolics within the colony. In this sense, a reduction in foraging for pollen with high phenolic contents and a concomitant increase of foraging for pollen with low phenolic contents would help reduce the overall pollen phenolics within honeybee colonies.

Differences in pollen types collected by foragers and in phenolic intake rates are dependent on syrup supply to a colony. The breakdown of pollen phenolics by honeybees may account for these differences. Honeybees increase the intake of sugar to control nest homeostasis for the deactivation of phenolics in nectar (Liu et al. 2005). Indeed, phenolic content in nectar is reduced after the nectar is incubated in the nest (Liu et al. 2005). One could assume that the breakdown of pollen phenolics occurs via similar mechanisms because pollen foragers deposit pollen in the middle cells of a honeybee comb (Camazine 1991), which undergoes incubation to reach a desired nest homeostasis (Winston 1987). Thus, the higher tolerance for phenolics found in the colony fed syrup would be due to the possibility of achieving a better nest homeostasis (and thus of deactivating phenolics) through sugar intake. We suggest that the sugar intake of a colony be related to pollen phenolics hoarded in hives.

Previous studies also found an increase in pollen foraging when syrup was fed to honeybee colonies (see Faegri and van der Pijl 1979). These studies differ somewhat from our work in the explanation of this phenomenon. It has been argued that sugar syrup provides pollen foragers with the energy necessary for foraging bouts (Heinrich 1975; see also Faegri and van der Pijl 1979). Other authors who examined the composition of forager populations suggested that pollen foraging increases due to an increase in the number of pollen foragers boosted by feeding of syrup (Fewell and Winston 1992; Eckert et al. 1994). Although our results cannot exclude these different hypotheses, we suggest additionally that feeding of syrup facilitates the breakdown of accumulated phenolics, thus decreasing potential deterrence to pollen foraging.

The ability of a honeybee colony to increase the proportion of pollen foragers is an adaptive mechanism for satisfying the protein demands of the colony. Our results suggest a novel mechanism of regulation of pollen foraging, which would be mediated by pollen phenolics. Low phenolics in food can stimulate foraging activity (Liu et al. 2004). However, the accumulation of phenolics within the hive could be aversive (Haslam 1988; Schoonhoven et al. 1998) and could inhibit pollen foragers from collecting more pollen. Thus, the "on or off" responses of honeybees to colony requirements (Pernal and Currie 2001) may result, in the case of pollen collection, from a homeostatic regulation around a set point of pollen stores, above or below which colonies would respond by adjusting their foraging behavior (Fewell and Winston 1992; Camazine 1993). Such a set point could be defined by the overall phenolic levels within the colony.

In conclusion, our research has examined honeybee pollen foraging in relation to pollen phenolics—an aspect that was, until now, unexplored. We have demonstrated that foragers can detect phenolic contents in pollen and that they choose pollen species accordingly. A honeybee colony can respond to phenolics present in the pollen stores by regulating the types and proportions of pollen samples. Our data furthermore show that pollen foraging at a colony level is dependent on the provision of sugar syrup. Colonies fed no syrup or fed scarce syrup tend to specialize in pollen with low phenolic contents or to decrease the sampling of pollen with high phenolic contents. Honeybees' responses to changes in the quantity and quality of stored pollen in the colony may be thus linked to changes in pollen phenolics.

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