Apidologie 33 (2002) 367–373
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DOI: 10.1051/apido:2002026

Original article

How a honey bee colony mustered additional labor for the task of pollen foraging

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(Received 21 January 2001; revised 26 January 2002; accepted 5 February 2002)

Abstract – This study examined how a honey bee colony supplied additional labor for a foraging task, pollen collection, when the demand for this task was increased. When we experimentally raised a colony's pollen need from one day to the next, we found that the colony boosted the labor devoted to pollen collecting (measured in terms of the number of pollen collection trips per day, P) by a factor of 24.8. The number of pollen foragers (N) was increased (by recruiting and task switching) by a factor of 12.4, while the number of collecting trips per pollen forager per day (T) was increased by a factor of 2.0 (note that P = N × T). The increase in number of pollen foragers was produced mostly (73%) by the recruiting of non-foragers to the task and to a smaller extent (27%) by the switching of non-pollen foragers to the task.

foraging / pollen collection / recruitment / task switching / work tempo

1. INTRODUCTION

In colonies of social insects, the workers adjust their contributions to their colony's labor pool in response to changes both inside and outside the nest (reviewed by Oster and Wilson, 1978; Seeley, 1995; Gordon, 1996). This adaptive plasticity in worker behavior is exemplified by the task of pollen foraging in honey bee *(Apis mellifera* L.*)* colonies: workers will adjust their pollen collection behavior, and thus the amount of pollen that is gathered, in relation to their colony's need for pollen (Fewell and Winston, 1992; Camazine, 1993; Fewell and Bertram, 1999). In nature, large fluctuations in a colony's pollen need are common; although a colony's consumption of pollen changes little from day to day, its collection of pollen can vary markedly as the weather changes (Seeley, 1995). For example, a colony may be blocked from pollen foraging for several days by rainy weather, during which time it may deplete its pollen stores and become starved for pollen. Hence it is highly adaptive that workers can change their behavior, thereby enabling their colony to adjust the labor devoted to pollen foraging. In this study we saw how additional labor for pollen foraging was roused when a colony's need for pollen was raised.

In principle, a social insect colony has three ways to boost the amount of labor devoted to a particular foraging task: (1) *recruit non-foragers* to the task, (2) *switch foragers* not engaged in the task to the task, and (3) *activate foragers* engaged in the task to work harder (Anderson and Ratnieks, 1999). Numerous studies have demonstrated one or another of these processes

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(e.g., recruitment: Wilson, 1962; von Frisch, 1967; task switching: Gordon, 1989; Kühnholz and Seeley, 1997; raising work tempo: Waddington, 1990; Fewell and Winston, 1992). So far, however, no study has shown explicitly how all three processes can function together, or even if all three processes are employed simultaneously, when a colony must devote additional labor to a task. In this study, we documented the operation and relative importance of these three processes in one instance of labor reallocation in a honey bee colony. We did so by experimentally manipulating a colony's need for pollen and seeing how the colony boosted its pollen collection efforts.

2. MATERIALS AND METHODS

We monitored the foraging activities of a large cohort of individually identifiable bees on two sequential days with virtually identical weather conditions. On the first day, the study colony's need for pollen was set at a low level while on the second day its need was set at a high level. On both days, every time a labeled bee entered or exited the hive we recorded the bee's identity, time of arrival or departure, and presence or absence of a pollen load. This observation protocol enabled us to determine how individuals responded to the induced change in their colony's need for pollen.

2.1. Study colony

In June 1998, a virgin queen was artificially inseminated with the homogeneously mixed semen of ten unrelated drones and installed in a small (nucleus) colony. The colony was left undisturbed for two months to give it time to become populated with the workers of the new queen. Then, to create a cohort of individually identifiable bees in this colony, we collected 1 500 newly eclosed workers from the colony over a 3-day period (27–29 August 1998) and labeled them for individual identification with Opalithplättchen bee tags and abdominal paint marks using standard techniques (see Seeley, 1995). An additional 900 newly eclosed workers from the colony were marked with just abdominal paint marks; these bees helped us determine when our individually labeled bees had matured into foragers. All the labeled bees were returned to their parent colony shortly after labeling and were left undisturbed for a little more than two weeks (by which time many had begun foraging) at which point certain manipulations of the colony were performed.

2.2. Colony manipulations

On 9 September 1998, the colony was moved from an apiary in Ithaca, NY to an isolated location in Newfield, NY (42°19'N, 76°34'W) where it was surrounded by fields of goldenrod (*Solidago* spp.) in bloom. This setting provided a high availability of pollen. Also, the colony was transfered to a hive consisting of two 5-frame nucleus boxes, joined top to bottom. This hive was equipped with two glass-covered entrance tunnels (20.3 cm wide × 25.4 cm long × 2.0 cm high) on opposite ends of the hive. To slow the passage of the bees through the tunnels, we installed wooden obstacles projecting diagonally inward from the sides of each tunnel. Also, to minimize the number of bees passing upside-down through the tunnels, we coated the ends of the glass ceiling of each tunnel with vegetable oil. These entrance tunnels made it possible for two observers to monitor the labeled bees as they entered or exited the hive. When we installed the colony in our special hive, its bees covered 8 of the 10 frames and so we estimated its population at some 16 000 bees.

The colony's pollen need was set at different levels on the two days of data collection: low on day 1 and high on day 2. To create these two levels, we performed the following manipulations in the evening before each day of data collection. *Low pollen need:* colony was given 3 combs filled with pollen, 5 combs partially filled with honey, and 2 combs completely filled with honey. There were few cells of brood in the hive, at most 10 per comb. *High pollen need:* colony was given 3 combs filled with larvae, 5 combs partially filled with honey, and 2 combs completely filled with honey. There were few cells with pollen in the hive, at most 10 per comb.

To increase the proportion of individually labeled bees among the pollen foragers, we removed from the study colony approximately 300 pollen foragers (but none of the individually labeled ones) on the day before the first day of data collection.

2.3. Data collection

Once the paint-marked bees began to forage for pollen, we began to gather detailed data on the individually labeled bees. We collected data for 2 days: 13–14 September, hence when the bees were 15–18 days old. On each day, data were gathered from when foraging began (about 10.00 h, following a cool night) to when it ended (about 16.00 h, when the air began to turn cool). For each individually labeled bee seen entering or exiting the hive, we

Table I. Transitions in the pollen foraging behavior of 206 foragers when their colony's pollen need went from low on day 1 to high on day 2.

Day 1: low pollen need		Day 2: high pollen need	
Pollen foraging	Number of bees	Pollen foraging	Number of bees
Never	182	Never	103
		Always	17
		Sometimes	62
Always	2	Never	0
		Always	2
		Sometimes	0
Sometimes	22	Never	5
		Always	9
		Sometimes	8

recorded the time of arrival or departure and the presence or absence of a pollen load. Data were recorded on audiotape.

2.4. Behavioral categories

As a first step in analyzing our data, we assembled for each of the two days a list of all bees that we saw entering and exiting the hive. Next, in order to exclude bees that simply were making orientation flights (Winston, 1987), we excluded from further consideration any bee on each list that made fewer than 2 trips that day. Then, working with the bees remaining on each list, we sorted the bees among three behavioral categories based on each bee's fidelity to pollen collection. Specifically, each bee observed on either day 1 or day 2 was categorized as never [N], always [A], or sometimes [S] bearing loads of pollen when she returned to the hive that day. Using this scheme, we created 9 categories (N-N, N-A, etc.) for the bees seen on both days (see Tab. I).

Finally, we placed each of the bees seen collecting pollen on day 2 into one of three categories: recruit, switcher, and continuer. *Recruits* to the task of pollen foraging were defined as those bees that were not seen on day 1 but were seen returning with pollen at least once on day 2. *Switchers* to the task of pollen foraging were defined as those bees that were seen on both days and that had records of N-A or N-S for the two days (see Tab. I). *Continuers* with the task of pollen foraging were those bees that were seen on both days and had records of A-A, A-S, S-A, and S-S (see Tab. I).

3. RESULTS

3.1. Weather conditions and pollen collection efforts

The weather conditions were essentially identical on the two days of data collection. Both were sunny and warm. The temperature mean and the temperature range for the period of data collection were the same for both days: mean, 20 °C; range, 15–26 °C. Nonetheless, our counts of the number of pollen foraging trips performed by the individually identifiable bees differed greatly between the two days of data collection: 74 trips on day 1 (low pollen need) vs. 1839 trips on day 2 (high pollen need). This difference was most likely a result of our manipulation of the colony's pollen need.

3.2. Recruits to pollen foraging

Among the individually identifiable bees, there were 200 that were recruited to the task of pollen foraging, that is, they were not seen leaving the hive on day 1 but were seen returning with pollen at least once on day 2. Of these, 60 always gathered pollen and 140 sometimes did so.

Table II. Summary of how the colony boosted the labor for pollen collection. Note that P = N × T.

Variable	Day 1: low pollen need	Day 2: high pollen need	Increase
No. of pollen collecting trips (P)	74	1839	24.8×
No. of pollen foragers (N)	24	298 – 200 recruits – 79 switchers – 19 continuers	12.4×
No. of collecting trips/pollen forager (T)	3.08	6.17	2.0×

3.3. Switchers to and continuers of pollen foraging

There were 206 of the individually identifiable bees that were candidates for being a switcher to or a continuer of the task of pollen foraging, that is, they satisfied our criterion of making at least two trips from the hive on both days 1 and 2. As shown in Table I, of the 182 bees that never gathered pollen on day 1, 79 switched to the task of pollen foraging on day 2. Of these 79 bees, 17 always brought home pollen and 62 sometimes did so. Also, of the 24 bees that gathered pollen on day 1, 19 did and 5 did not continue to do so on day 2. And of the 19 continuers, 11 always brought home pollen and 8 sometimes did so. The overall number of switchers to and continuers of pollen foraging on day 2 was 98 bees.

3.4. Increased per capita rate of pollen foraging

The total number of pollen collecting trips on a given day (P) is the product of the number of pollen foragers that day (N) and the number of pollen collecting trips per pollen forager that day (T), where P = N × T. Given that P rose from 74 trips on day 1 to 1839 trips on day 2, and that N rose from 24 to 298 bees, we can deduce that T rose from 3.08 to 6.17 trips per bee.

3.5. Overview

We summarize our findings in Table II. The total number of pollen collecting trips performed by the individually identifiable bees increased by a factor of 24.8, from 74 to 1839 trips. This overall increase was generated by a 12.4-fold increase in the number of pollen foragers and a 2.0-fold increase in the number collecting trips per pollen forager. The 12.4-fold increase in number of pollen foragers was produced partly (27%, reflecting a net addition of 74 bees) by non-pollen foragers switching to the task of pollen foraging and by most of the pollen foragers on day 1 continuing with this task. However, the 12.4-fold increase in number of pollen foragers was produced primarily (73%, reflecting an addition of 200 bees) by non-foragers being recruited to the task of pollen foraging.

4. DISCUSSION

This study has examined the three possible ways of supplying additional labor for a particular foraging task in a colony of social insects: recruiting non-foragers to the task, task switching by foragers not engaged in the task, and activating foragers engaged in the task to labor more mightily.

4.1. Recruiting non-foragers

We found that most of the additional labor for pollen foraging in our study colony was supplied by recruiting non-foragers to the task of pollen collection. This result is consistent with what Fewell and Bertram (1999) report in a study in which they manipulated the pollen needs of colonies (by manipulating pollen stores) and monitored how the colonies adjusted their labor allocation between the tasks of pollen and nectar foraging. They found that at times of high pollen need, relative to times of low need, their colonies had more bees engaged in pollen foraging, and that the addition of pollen foragers at times of high pollen need came about primarily by recruitment of non-foragers, not by task switching of foragers.

It should be noted that the strong recruitment of non-foragers to the task of pollen collection that we observed may not have been due entirely to our manipulation of the colony's pollen need. Even if we had not manipulated the colony's pollen need, it is possible that additional members of the labeled cohort would have become pollen foragers due simply to their becoming older. At this point we cannot say for sure how much of the recruitment was due to the change in the colony's pollen need vs. the change in the labeled cohort's age. However, the fact that there was a sudden surge in the recruitment of labeled bees to pollen foraging on day 2 (from 24 recruits at most on day 1, to 200 recruits for sure on day 2) suggests that most of the recruitment was due to the change in the colony's pollen need.

It may be adaptive for a colony to rely primarily on the recruitment of non-foragers to a particular foraging task as the means of adjusting it's allocation of labor among foraging tasks, especially when the colony is not heavily engaged in foraging. After all, recruiting non-foragers to a particular foraging task will minimize disruption of the other aspects of a colony's foraging activity. In support of this idea is the finding that a social insect colony is indeed able to supply additional labor to one foraging task without disrupting the labor devoted to a second foraging task. This is what Kühnholz and Seeley (1997) observed when they monitored two sectors of a honey bee colony's foraging operation – nectar collection and water collection – while manipulating the colony's need for water. When they elevated a colony's water need by heating the colony's nest, they found that the colony roused additional labor for water collection without reducing the labor devoted to nectar collection. It should be noted, however, that this colony was located in a nectar-poor environment and therefore was not heavily engaged in nectar collection. If it had been, it might have needed to reduce the labor devoted to nectar collection to cope with the need for increased water collection. Kühnholz and Seeley (1997) reported vigorous waggle dancing by water collectors at times of high water need, so it is possible that their colony coped with the higher demand for water collectors mainly by recruiting non-foragers to the task, just as our colony coped with the higher demand for pollen collectors mainly by recruiting non-foragers to this task.

4.2. Task switching by foragers

We detected some switching from one foraging task to another, but it was not nearly so important a source of extra pollen foragers as recruitment of non-foragers. Of the 206 bees that we observed foraging on both days 1 and 2, only 84 switched their foraging task. Given that the colony's pollen need was much higher on day 2 than on day 1, it is not surprising that most of the switchers (79 bees) switched from non-pollen foraging on day 1 to pollen foraging on day 2. Only a few (5 bees) switched in the opposite direction.

As mentioned above, the functional significance of the fact that non-foragers were the source of many (200) additional pollen foragers on day 2, whereas foragers were the source of relatively few (a net total of just 74), may be that rousing non-foragers to a foraging task may be less costly than switching foragers to this task. This would seem to be the case in our study if we assume that the non-foragers that were called forth to collect pollen were mostly bees that were unemployed on day 1, hence were a low-cost source of pollen foragers. We know that the foragers that switched to pollen foraging were all bees that were gainfully employed in nectar or water collection on day 1, hence probably were a high-cost source of pollen foragers. Looking at the matter in terms of relative costs, it begins to look a bit surprising that we found such a large fraction (74 out of 274, or 27%) of the newcomers to the task of pollen foraging on day 2 were bees that had been engaged in another foraging task on day 1. Clearly, an important topic for a future study is determining what non-foragers that get recruited to a foraging task were doing shortly before they were recruited. Were they truly unemployed or were they just poorly employed in in-hive tasks for which there was little demand? Also, we need to know more about what foragers that switch foraging tasks were experiencing shortly before they switched. Were they experiencing little success in their current task or were they successfully working on one task but then encountered stimuli indicating strong demand for labor in a different task?

4.3. Activating foragers

We found that there was a higher work tempo of the bees engaged in pollen foraging on day 2 relative to those engaged in this task on day 1, and that this made a relatively small but important contribution to our colony's greater effort in pollen collection on day 2. On average, the number of collecting trips per pollen forager on day 2 was twice what it was on day 1. It should be noted that by measuring the per capita work tempo just in terms of collecting trips per bee per day, we may have underestimated the role of increased work tempo in boosting a colony's pollen collection effort. It is possible that each pollen forager not only made more trips on day 2 than on day 1, but also gathered larger pollen loads on day 2 than on day 1. However, because we did not see a noticeable increase in pollen load size, we feel it is likely that the amount by which we underestimated the role of increased work tempo is small.

Fewell and Winston (1992) have also reported a higher work tempo (number of foraging trips per unit time) of pollen foragers from colonies with high pollen need compared to those from colonies with low pollen need. However, when Fewell and Bertram (1999) treated colonies with different levels of pollen stores and looked for a correlated difference in rate of foraging trips per pollen forager, they found no significant difference. This suggests that one sees a difference in the work tempo of pollen foragers only if one makes a comparison between colonies with extremely high and extremely low pollen needs, as was done in the present study and in the study of Fewell and Winston (1992), but not that of Fewell and Bertram (1999). If this is so, then it seems that the adjustment of pollen collecting effort in honey bee colonies is mainly a matter of tuning the number of pollen foragers, not the effort per pollen forager.

The heart of this study is a fine-grained description of how a colony of honey bees responded to an increased need for labor in one foraging task: pollen collection. Obviously, the limited nature of our results (just one colony was observed making just one response) precludes broad generalizations about how colonies of honey bees make adjustments in the allocation of their labor among foraging tasks. Nevertheless, our results show that the adaptive tuning of a honey bee colony's pollen collection efforts can involve simultaneous changes in both *the number* of pollen foragers and *the effort* per pollen forager. And our results show that increasing the number of pollen foragers can involve both *recruiting* of non-foragers and the *switching* of foragers to the task. Hence this study makes clear the complexity of the mechanisms by which a honey bee colony can adjust its allocation of labor among foraging tasks.

ACKNOWLEDGEMENTS

This research was conducted by the senior author to fulfill the requirements for a Senior Honors Thesis from the Department of Neurobiology and Behavior, Cornell University. She gives deep thanks to Bernard Brennan, Eric Daza, Shaun Geer, Sandra Marshall, Rebecca Riba, and Mace Vaughn for their help in completing the many 100's of person-hours of data collection, transcription, and analysis that this "little" study required.

Résumé – Comment une colonie d'abeilles domestiques mobilise un surplus de travail dans la tâche de récolte du pollen. Dans les colonies d'insectes sociaux, lorsque la demande de travail pour une tâche particulière augmente, la fourniture de travail pour cette tâche augmente aussi généralement ; il en résulte que la demande et la fourniture de travail se maintiennent en équilibre. Cette étude examine les moyens par lesquels une colonie d'abeilles domestiques (*Apis mellifera* L.) fournit un surplus de travail pour une tâche de butinage, la récolte de pollen, lorsque la demande pour cette tâche augmente. En augmentant expérimentalement les besoins en pollen d'une colonie d'un jour à l'autre, on a trouvé que la colonie renforçait le travail consacré à la récolte de pollen de 24,8 fois (74 voyages au jour 1 et 1839 voyages au jour 2). On a trouvé trois mécanismes différents : *le recrutement* de non-butineuses, *le changement de tâches* par des butineuses qui ne récoltaient pas de pollen, et *la stimulation* des butineuses de pollen à récolter plus. Le nombre de butineuses de pollen a augmenté par recrutement et changement de tâche, de 12,4 fois, alors que le taux de travail par butineuse de pollen augmentait de 2,0 fois. L'augmentation du nombre de butineuses de pollen était dû principalement (73 %) au recrutement de non-butineuses et, dans une moindre mesure (27 %) au changement de tâche par des butineuses qui ne récoltaient pas de pollen. La mise en œuvre de trois processus pour renforcer le travail fourni (recrutement, changement de tâche et stimulation) montre la complexité des mécanismes qui peuvent être impliqués pour maintenir une répartition adéquate du travail au sein d'une colonie d'insectes sociaux.

butinage / récolte de pollen / recrutement / rythme de travail / changement de tâche

Zusammenfassung – Wie ein Volk der Honigbienen zusätzliche Arbeit für Pollensammeln aufbringt. In Völkern der sozialen Insekten erhöht sich mit der Notwendigkeit zusätzlicher Arbeit für eine bestimmte Aufgabe meistens auch das Arbeitsangebot für diese Aufgabe. Dadurch stehen Angebot und Nachfrage für diese Arbeit im Gleichgewicht. Hier wird untersucht, auf welchem Wege ein Bienenvolk zusätzliche Arbeit für einen vermehrten Polleneintrag zur Verfügung stellt, wenn der Bedarf für diese Aufgaben steigt. Wenn wir im Versuch den Bedarf an Pollen von einem Tag zum anderen erhöhten, verstärkte das Volk die Tätigkeit, die das Sammeln von Pollen betraf, um einen Faktor von 24,8 (von 74 Flügen zum Pollensammeln an Tag 1 auf 1839 Flüge an Tag 2). Drei verschiedene Mechanismen wurden beobachtet: *Rekrutierung* von Nicht-Sammlern, *Aufgabenwechsel* von Sammlerinnen, die zuvor keinen Pollen eingetragen haben, und *Aktivierung* der Pollensammlerinnen mehr zu sammeln. Die Anzahl der Pollensammlerinnen wurde (durch Rekrutierung und Aufgabenwechsel) um einen Faktor von 12,4 erhöht, während die Sammelrate pro Pollensammlerin um den Faktor 2,0 zunahm. Die Zunahme der Pollensammlerinnen wurde vor allem durch Rekrutierung (73 %) von nicht sammelnden Bienen erreicht, und zum geringeren Anteil durch Umstellung von anderen Trachtflügen (27 %) auf Pollensammeln. Die Zusammenwirkung von 3 Prozessen (Rekrutierung, Aufgabenwechsel und Aktivierung) zur Erhöhung der Sammeltätigkeit zeigt die Komplexität der Mechanismen, die im Erhalt der erforderlichen Einteilung der Arbeiten innerhalb eines Volkes von sozialen Insekten beteiligt sein können.

Trachtflüge / Pollensammeln / Rekrutierung / Aufgabenwechsel / Arbeitstempo

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