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The honey bee's tremble dance stimulates additional bees to function as nectar receivers

Abstract If a forager bee returns to her hive laden with high-quality nectar but then experiences difficulty finding a receiver bee to unload her, she will begin to produce a conspicuous communication signal called the tremble dance. The context in which this signal is produced suggests that it serves to stimulate more bees to function as nectar receivers, but so far there is no direct evidence of this effect. We now report an experiment which shows that more bees do begin to function as nectar receivers when foragers produce tremble dances. When we stimulated the production of tremble dances in a colony and counted the number of bees engaged in nectar reception before and after the period of intense tremble dancing, we found a dramatic increase. In two trials, the number of nectar receivers rose from 17% of the colony's population before tremble dancing to 30–50% of the population after the dancing. We also investigated which bees become the additional nectar receivers, by looking at the age composition of the receiver bees before and after the period of intense tremble dancing. We found that none of the bees recruited to the task of nectar reception were old bees, most were middle-aged bees, and some were even young bees. It remains unclear whether these auxiliary nectar receivers were previously inactive (as a reserve supply of labor) or were previously active on other tasks. Overall, this study demonstrates that a honey bee colony is able to rapidly and strongly alter its allocation of labor to adapt to environmental changes, and

it further documents one of the communication mechanisms underlying this ability.

Key words Honey bee · Communication · Tremble dance · Division of labor · Task switching

Introduction

Every organization possessing a division of labor faces the problem of maintaining a proper allocation of its members among the various tasks performed within the organization. Ideally, for each task the labor supply is kept in balance with the labor demand, despite unpredictable fluctuations in the labor demand for certain tasks as conditions change inside and outside the organization. How this problem is solved within colonies of social insects has attracted increasing attention from biologists and engineers over the past several years (Gordon et al. 1992; Tofts 1993; Sendova-Franks and Franks 1993; Seeley 1995; Gordon 1996; Pacala et al. 1996). Social insect colonies are intriguing in this regard because they have evolved means of solving the labor allocation problem which do not involve central supervision. Instead, each social insect worker independently acquires information about the colony's labor needs and decides on its own which task it should perform. Often this results in workers switching tasks so that undersupplied tasks gain workers and oversupplied tasks lose them (reviewed by Gordon 1989, 1996; Cartar 1992; Robinson 1992). To understand fully how the labor allocation problem is solved within a social insect colony, we need to know how the workers acquire information about their colony's labor needs. In particular, we need to know what evolved signal or incidental cue serves as the indicator of the labor supply-demand ratio for each task.

In colonies of honey bees, one such indicator appears to be the tremble dance (Seeley 1992). This

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communication signal is produced by a colony's nectar foragers whenever the demand for nectar receivers – the bees which unload nectar from the foragers – exceeds their supply. This situation arises when nectar becomes plentiful in the environment, the colony mobilizes its foragers to exploit the newly abundant food, and thus the influx of nectar-laden foragers undergoes a dramatic increase. Eventually the rate of nectar collection (by foragers) can surpass the rate of nectar processing (by receivers) and when this happens the nectar foragers experience long delays in unloading their nectar (Seeley and Tovey 1994). If a forager returns from a highly profitable nectar source but then has to search more than 40 seconds to find a receiver bee, she is likely to begin to perform a tremble dance (Seeley 1992; Kirchner and Lindauer 1994). Sometimes there are dozens of bees walking slowly across the combs inside the hive, performing the conspicuous trembling movements characteristic of the tremble dance. Each bees' dance lasts typically about half an hour. Nectar foragers will continue to initiate these tremble dances after each foraging trip until they again experience ease in finding a receiver bee upon entering the hive.

The strong correlation between the need for more nectar receivers and the production of tremble dances suggests that this communication signal indicates a shortage of nectar receivers and so stimulates additional bees to function as nectar receivers. Until now, however, there has been only indirect evidence that tremble dances prompt more bees to function as nectar receivers: the production of tremble dances is followed consistently by a reduction in the search times of returning nectar foragers, which suggests that the number of nectar receivers has increased (Seeley 1989, 1992). In this paper we report an experiment which yields direct evidence that tremble dances stimulate additional bees to function as nectar receivers. Specifically, we manipulated the production of tremble dances in a colony (by controlling the colony's rate of nectar collection) and we counted the number of bees engaged in nectar reception before and after a period of intense tremble dancing. We report a dramatic increase in the number of receiver bees, consistent with the hypothesis. We also report observations that reveal which bees become the additional receiver bees.

Methods

General plan of experiment

Each trial of the experiment reported here was spread over three days. On the first, we trained approximately ten bees from a colony housed in an observation hive to a feeder providing sugar solution, the only significant source of food for the colony. Thus on the first day the colony's food collection was restricted to a low rate. On the second day, we continued to restrict the colony's food collection to a *low rate* and we monitored the production of tremble

dances by the colony's foragers, determined the number of its bees functioning as receiver bees, and took data on the age distribution of its receivers and foragers. On the third day, we allowed many more bees to visit the feeder and thus permitted the colony to collect food at a *high rate*. We also gathered the same sorts of data as the day before, to check for an increase in tremble dance production, a rise in the number of receiver bees, and changes in the age distributions of the receivers and foragers. Finally, in the evening of the third day, we measured the colony's population size.

Study site

All of the work reported here was conducted at the Cranberry Lake Biological Station (44°09'N, 74°48'W), in the Adirondack State Park, Saint Lawrence County, in northern New York State. This study site is surrounded by nearly unbroken forests and lakes, hence there are few natural food sources for bees and it is easy to train bees to forage at a feeder. The scarcity of food also makes it possible to tightly control the rate of food collection by a colony – by controlling the number of bees foraging at a feeder – even though the colony's foragers can fly freely from their hive. One indication that natural forage was indeed sparse when the present experiment was performed was the extremely low level of traffic at the hive entrance whenever the feeder was shut off: only 1 or 2 bees/min into the hive. Also, whenever we stopped providing food at the feeder, the amount of honey stored in the observation hive would steadily decline. The colony was, however, able to gather sufficient pollen to maintain brood rearing.

Apparatus

A colony of approximately 4000 Italian honey bees (*Apis mellifera ligustica*) was housed in a two-frame observation hive (see Fig. 4.2 in Seeley 1995). This hive's entrance was fitted with a wedge which forced all foragers to enter and leave the hive from one side of the comb. Because returning nectar foragers unload their nectar to receiver bees shortly after entering the hive, this wedge established a well-defined nectar unloading area on one side of the lower comb. To enable us to label the nectar receivers, we removed the glass covering this side of the lower comb and replaced it with a wooden frame covered with nylon screening ("tulle", openings approximately 3 mm in diameter). The tip of a fine paint brush could be inserted through the screen to daub paint on the thorax of any bee of interest inside the hive. The hive was housed in a small hut (see Fig. 4.3 in Seeley 1995) situated on the north end of the quadrangle of the biological station.

The feeder was designed to provide a sucrose solution with a constant concentration *ad libitum*. It consisted of a 50-ml glass jar containing sucrose solution (2.0 mol/L) inverted over a slotted plexiglass plate (see Fig. 4.5 in Seeley 1995). This plate-jar combination was placed atop a screened container of anise extract to provide the feeder with scent. Additional scent was provided by mixing 200 μ L of anise extract (a 27% solution of essential oil in alcohol) in each 1 L of sucrose solution. The feeder was positioned in a small clearing 350 m south of the hive, near the bridge over Sucker Brook. Bees were trained to the feeder using standard techniques (von Frisch 1967).

Measuring and manipulating the colony's rate of sugar solution collection

We controlled the colony's rate of food influx by controlling the number of bees allowed to forage from our feeder. To accomplish this, we labelled each bee that visited the feeder with individually identifiable paint marks and kept track of the number of different bees visiting the feeder by making rolls calls of the labelled bees at

30-min intervals. If the number of foragers began to exceed the desired level, then the excess foragers were gently captured in Ziploc plastic bags until the end of the day when they were released at the hive. We measured the colony's rate of sugar solution collection by counting, at 30-min intervals, the number of bees leaving the feeder per minute. We used these traffic rates to estimate the colony's rate of sugar solution influx by assuming that each bee brought back from the feeder 55 μ L of sugar solution, the average load volume reported in previous studies (Seeley 1986, 1994).

Measuring the production of tremble dances

Every 15 min, a scan count was made of the number of bees performing a tremble dance on the side of the observation hive that faced the observer. These scan counts of the tremble dances were synchronized with the measurements of the colony's rate of sugar solution collection, so that a measurement of the collection rate was made simultaneous with every second count of the tremble dances.

Measuring the number of receiver bees

One of us would sit beside the observation hive (equipped with a nylon screen over the lower comb) and daub paint on every bee that was seen receiving sugar solution from one of the foragers from the feeder. A helper would record the number of bees so labeled, making tallies at 15-min intervals. This process was continued for 9–12 h, during which time the rate of encounter of *unlabeled* bees receiving sugar solution gradually fell to zero, indicating that all of the receiver bees had been labeled. The cumulative number of bees labeled at this point was taken to be the total number of receiver bees in the colony.

Determining the age distributions of the foragers and receivers bees

Every 3 days, from 20 May to 19 July, 1994, fifty 0-day-old bees were labeled for individual identification and added to the colony living in the observation hive. These bees were obtained by collecting newly emerged bees from a second colony. These bees were labeled for individual identification with a colored and numbered plastic disk on the thorax (Opalithplättchen, Chr. Graze, Endersbach, Germany) combined with a dot of paint on the abdomen. Careful record was kept of which plastic disk/paint dot combinations were used for each age cohort. This procedure resulted in approximately 10% of the colony's members bearing labels which coded their ages. To determine the age distributions of foragers and receiver bees during each trial of the experiment, we simply noted which labeled bees appeared either as a forager at the feeder, or as a receiver in the hive, and then determined the age of each of these bees. Each bee was counted just once per day, even if seen several times either foraging or receiving.

In analyzing the age distributions of foragers and receivers, we created three age categories: young, middle-aged, and old. Each category represented one-third of the entire age range of the labelled bees, which ranged from 0 to 54 days old during the two trials of our experiment. Therefore we defined young bees as those 0–17 days old, middle-aged bees as those 18–35 days old, and old bees as those 36–54 days old.

Measuring the colony's population size

A grid of 5.0 cm-sided squares was drawn on a sheet of glass that could be fitted to either side of the observation hive. Then, in the evening, we counted the bees inside 20 randomly selected grid

squares on each side of the hive, calculated the average number of bees per grid square, and multiplied this by 180 (there were 180 grid squares total for the two sides of the hive).

Statistics

Measurements are given throughout this paper as the mean \pm 1SD. Statistical tests were either *t*-tests (Student's, or the test for equality of two percentages using arcsine transformations; Sokal and Rohlf 1981) or χ^2 -tests on 2×2 contingency matrices.

Results

Do tremble dances activate additional nectar receivers?

The results of the first trial of this experiment, conducted on 6–8 July 1994, are shown in Fig. 1. In this trial, 7 July was the day of low "nectar" influx. Only 10 bees were allowed to collect sucrose solution from the feeder, and the average rate at which foragers returned to the hive from the feeder was only

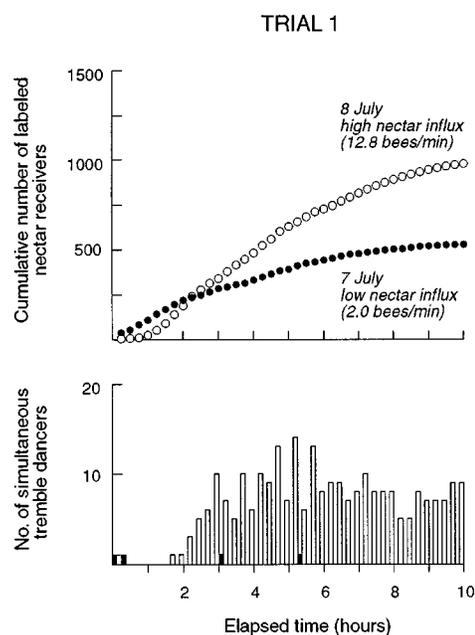


Fig. 1 Results of the first trial of the experiment testing the hypothesis that tremble dances stimulate additional bees to function as nectar receivers. A colony was established in an observation hive in a location with little natural forage and a feeder was provided that contained 2.0 mol/L sucrose solution. The number of bees foraging at the feeder was regulated to control the colony's nectar influx: 10 bees on 7 July, and 73 bees on 8 July. On both days the number of bees functioning as nectar receivers was determined by labeling each bee in the hive that was observed unloading sugar solution from one of the foragers visiting the feeder and recording the cumulative number of bees so labeled. Also, the amount of tremble dancing in the colony was measured by making a scan count of the number of tremble dancers in the observation hive every 15 min (*filled bars* 7 July counts, *open bars* 8 July counts)

2.0 bees/min (sucrose solution influx: 6.6 mL/h). Consistent with this low level of forager traffic were the very low scan counts of the number of bees performing tremble dances: 0.1 ± 0.3 bees ($n = 40$ counts). The total number of bees functioning as receivers was only about 530 bees, or about 17% of the colony whose population then numbered some 3130 bees.

The next day, 8 July, the time of high "nectar" influx, yielded a very different picture with respect to amount of tremble dancing and number of receiver bees. Throughout this day we did not capture the recruits to the feeder and as a result the number of bees foraging there rose quickly from 10 to 73, and the average rate at which foragers returned to the hive from the feeder soon reached a high level, 12.8 bees/min (sucrose solution influx: 42.2 mL/h) – more than 6 times the level of the previous day. This higher level of forager traffic resulted in many of the foragers performing tremble dances. The scan counts revealed 1–11 bees performing a tremble dance at any one time inside the hive (on average, 6.7 ± 3.7 tremble dancing bees, $n = 40$ counts). The crucial thing observed this day, however, was that the number of bees functioning as nectar receiver bees was much higher than on the previous day, with more than 970 bees, or 30% of the colony, performing this task.

A second trial of the experiment, performed on 18–20 July 1994, yielded even more dramatic results, as shown in Fig. 2. On 19 July, only 14 bees were

allowed to gather sugar solution at the feeder, the mean traffic level was 2.7 bees/min returning to the hive from the feeder (sucrose solution influx: 8.9 mL/h), and the scan counts of tremble dancers were again very low, only 0.6 ± 0.8 bees ($n = 48$ counts). Likewise, the number of receiver bees in the colony was relatively low, approximately 770 bees, representing again 17% of the colony whose population had now grown to some 4450 bees. But on 20 July, when recruits to the feeder were no longer captured, the total number of bees gathering food at the feeder soared to 267, the mean traffic level surged to 26.5 bees/min (sucrose solution influx: 87.4 mL/h), and there was a breathtaking display of tremble dancing inside the observation hive. Over the 9 h of observation, the number of bees performing tremble dances generally ranged from 10 to 30, and averaged 19.1 ± 9.0 bees ($n = 36$ counts). But most impressive of all was the huge number of bees involved in nectar reception: some 2250 bees – approximately 50% of the colony's population!

Which bees become the additional nectar receivers?

In the two trials just described, the study colony of some 4000 bees was able to muster an additional 420 bees (in trial 1) and 1480 bees (in trial 2) for nectar reception when it boosted its influx of sugar solution to a high level. Such dramatic increases in the number of bees functioning as receivers raises the intriguing mystery of where all these additional nectar receivers came from. As a first step toward solving this puzzle, we determined the age distributions of the receiver bees and forager bees both when the colony's influx of sugar solution was low and when it was high. Then, by treating these age distributions as probability distributions – which is appropriate, since an equal number of labelled bees was introduced to the colony for each age cohort – we calculated how many bees of each age class (young, middle-aged, or old) were gained or lost by the receiver bee group when this group grew.

Figure 3 shows the age distributions for both trials of the experiment. Consider first the foragers. We see that in both trials, regardless of the level of food influx, the foragers were nearly exclusively middle-aged and old bees. We also see that in both trials there was no change in the age distribution of the foragers between times of low and high food influx. Specifically, in trial 1 the mean age of the foragers was 38.1 ± 7.5 days ($n = 42$ bees) when the influx was low, and 38.5 ± 8.6 days ($n = 39$ bees) when the influx was high ($P > 0.60$), and in trial 2 the mean age of the foragers was 33.4 ± 11.1 days ($n = 53$ bees) when the influx was low, and 33.7 ± 9.6 days ($n = 44$ bees) when the influx was high ($P > 0.90$). Clearly, the age composition of the foragers was not affected by the strong rise in the colony's influx of sugar solution.

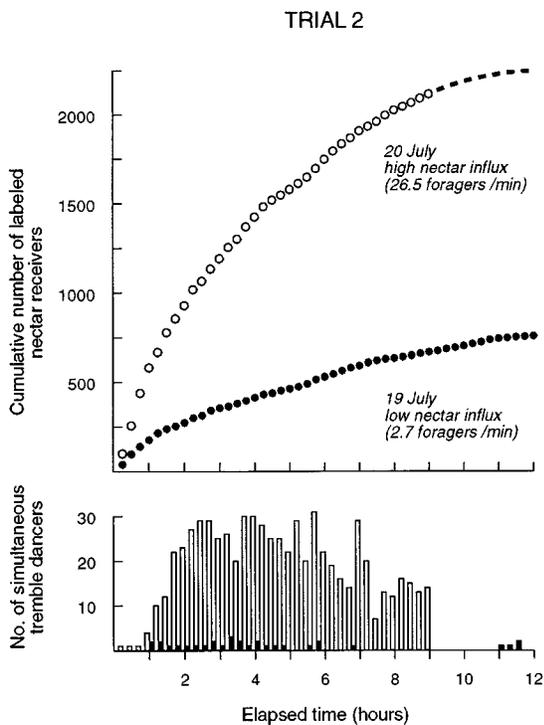


Fig. 2 Results of the second trial of the experiment, depicted as in Fig. 1. Number of bees foraging at the feeder: 14 bees on 19 July, and 267 bees on 20 July. (filled bars 19 July counts of the number of tremble dancers, open bars 20 July counts)

A different conclusion applies to the receiver bees. In both trials, a noticeable downward shift in the age distribution of the receivers occurred in association with the rise in the influx of sugar solution. In trial 1

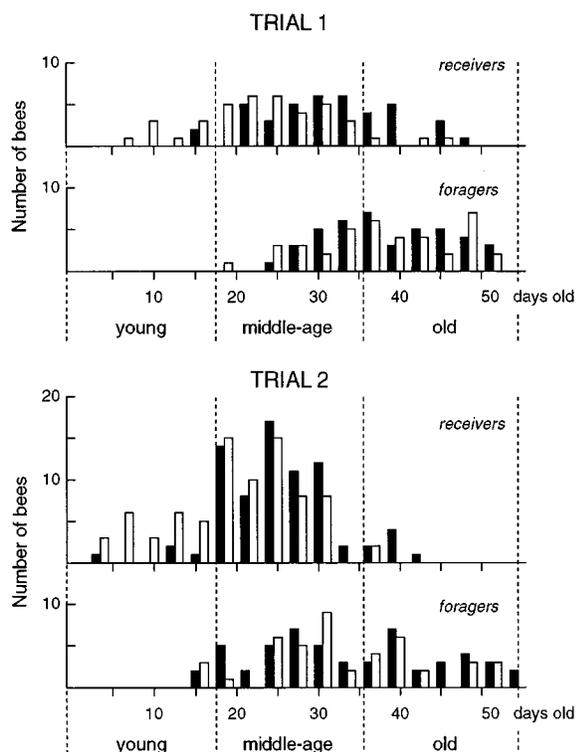


Fig. 3 Age distributions of nectar receivers and nectar foragers that were observed while conducting the two trials of the experiment represented in Figs. 1 and 2. For nearly 60 days before gathering these data, fifty 0-day-old bees were labelled and added to the study colony every 3 days, hence we could determine the ages of many of the receivers and foragers that were encountered in each trial of the experiment. *Upper diagram trial 1: filled bars* low influx of sugar solution (7 July data, $n = 40$ receivers and 42 foragers), *open bars* high influx of sugar solution (8 July data, $n = 40$ receivers and 39 foragers). *Lower diagram trial 2: filled bars* low influx of sugar solution (19 July data, $n = 75$ receivers and 53 foragers), *open bars* high influx of sugar solution (20 July data, $n = 81$ receivers and 44 foragers)

the mean age of the receivers fell from 31.0 ± 8.1 days ($n = 40$ bees) to 24.2 ± 8.7 days ($n = 40$ bees) ($P < 0.001$), and in trial 2 the mean age fell from 24.9 ± 6.9 days ($n = 75$ bees) to 19.6 ± 7.8 days ($n = 81$ days) ($P < 0.001$). In general, these declines in mean age came about because the proportion of old receiver bees fell while the proportion of young receiver bees rose.

These dynamics are expressed quantitatively in Table 1 where we see, for both trials, the percentage of young, middle-aged, and old receiver bees at times of low and high influx of sugar solution. Multiplying each percentage by the total number of receiver bees yields estimates of the number of young, middle-aged, and old receiver bees under different conditions, and with these estimates it is possible to build a precise picture of the changes in the age composition of the receiver bees as the colony underwent a transition from low to high food influx (rightmost column in Table 1). In both trials, the number of young and middle-age receiver bees increased dramatically while the number of old receiver bees actually decreased. It should be noted too that in both trials the increase in number of receiver bees was greater for the middle-aged bees than for the young bees. Thus it seems clear that none of the additional receiver bees were old bees (indeed, there was a net loss of old bees), most were middle-aged bees, while some were young bees.

Further insights into the means by which the colony was able to boost the number of receiver bees come from data gathered not at the observation hive but at the feeder. In the course of both trials of the experiment, each time a new bee (a recruit) arrived at the feeder, the person tending the feeder noted whether or not it bore a paint mark indicating that earlier in the day this bee had been labelled as a receiver bee. (On days of low influx, each recruit was captured, while on days of high influx each recruit was marked with a dot of paint on the abdomen. These measures ensured that each recruit was counted only once.) The resulting data are shown in Table 2. In both trials, it was found that when the food influx was low, a large percentage of the

Table 1 Changes in the age composition of the receiver-bee group which occurred when their colony's influx of sugar solution went from low to high

	Age range of receiver bees (days)	Low influx		High influx		Change in number of bees
		% Of group	Number of bees	% Of group	Number of bees	
Trial 1	Young, 0–17	5	63	20	190	+ 164
	Middle-aged, 18–35	63	334	73	694	+ 360
	Old, 36–54	32	170	7	66	– 104
	Total		530		950	+ 420
Trial 2	Young, 0–17	5	38	28	630	+ 592
	Middle-aged, 18–35	86	662	70	1575	+ 913
	Old, 36–54	9	70	2	45	– 25
	Total		770		2250	+ 1480

Table 2 The number of forager bees (recruits to a feeder) that earlier in the day had or had not functioned as a receiver bee, in relation to the colony's influx of sugar solution. A smaller proportion of the new foragers had previously served as a receiver bee

	Influx of sugar solution (date)	Forager had recently served as a receiver bee?		Significance of difference in proportions
		Yes	No	
Trial 1	Low-7 July	84	36	$P < 0.001$ $\chi^2 = 138.2$
	High-8 July	19	44	
Trial 2	Low-19 July	151	89	$P < 0.001$ $\chi^2 = 49.7$
	High-20 July	79	174	

recruits to the feeder had recently served as receiver bees (70% and 63% in trials 1 and 2), but when the food influx was high, this percentage was much lower (30% and 31% in trials 1 and 2). This difference in percentages is statistically significant ($P < 0.02$). To appreciate fully the meaning of this difference, one must note that a much *lower* percentage of prior receiver bees was found among the recruits on days of high food influx even though on these days a much *higher* percentage of the colony's total population was labelled as a receiver bee. This implies that on days when the food influx was high, and so the demand for additional receiver bees was strong, the existing receiver bees were less likely to switch from receiving to foraging than on days when the food influx was low and so the demand for additional receivers was weak. Thus it seems clear that the colony boosted the number of bees receiving nectar not only by raising the rate at which bees adopted this task, but also by lowering the rate at which bees abandoned this task.

Discussion

Tremble dances activate additional nectar receivers

In each trial of the experiment reported here we limited a colony's intake of sugar solution to a low level for 2 days, and then allowed the colony to raise its intake to a high level on a third day. And in both trials we observed that on the third day the colony's foragers performed numerous tremble dances and that the colony's contingent of receiver bees was much larger than on the previous day (Figs. 1 and 2). Thus it is clear that in the colony we studied the production of tremble dances was closely associated with an increase in the number of receiver bees.

This association between tremble dance production and receiver bee addition suggests strongly that tremble dances cause additional bees to function as receiver bees. The possibility remains, however, that there is some other cue or signal which is tightly correlated with the production of tremble dances and which is really the stimulus for more bees to function as nectar

receivers. This possibility seems highly unlikely to us, though, since the tremble dance possesses several properties, besides its consistent appearance when there is a need for more receiver bees, which make it well suited to function as a signal indicating the need for additional receiver bees. First, tremble dances are produced throughout the hive, not just in the unloading area (Seeley 1992). This spatial distribution seems highly appropriate for a signal that activates additional receiver bees since presumably this signal must stimulate bees located outside of the unloading area (that is, bees not already engaged in nectar reception) to move to the unloading area and begin working there. Second, tremble dances are produced in a context where a conspicuous communication signal evidently is needed. Of all the bees in a colony, it seems very likely that only those bees engaged in either nectar receiving or nectar collecting will know *automatically* when nectar collection surpasses nectar reception, hence when there is a need for more receiver bees. The nectar receivers and the nectar foragers will become informed of this need through cues sensed in the course of their work. (When a colony's nectar influx exceeds its nectar processing capacity, its nectar receivers will experience great ease in finding a nectar forager and its nectar foragers will experience great difficulty in finding a nectar receiver.) In contrast, it seems most unlikely that members of the colony not engaged in handling nectar will know when their colony needs more receiver bees through incidental cues sensed in the course of their work. Hence it makes much functional sense that the bees possess a special communication signal, the tremble dance, to announce this need. Third, tremble dances are produced by the nectar foragers, not the nectar receivers. This makes good sense in terms of colony functioning because even though both foragers and receivers probably know when to "sound the alarm" for additional receiver bees, it is the nectar foragers that are in over supply when the alarm needs to be sounded, hence it should be these bees which temporarily quit their task to sound the alarm, i.e., produce the tremble dances. Thus we see that besides the experimental evidence reported in this paper and in a previous paper (Seeley 1992), there are several lines of circumstantial evidence

which strongly support the functional interpretation of the tremble dance as a signal that indicates a need for additional receiver bees. We therefore feel it is reasonable to assume for the remainder of this paper that it was the tremble dances which stimulated the additional bees to function as nectar receivers.

We should also point out that there exists experimental evidence that tremble dances have an inhibitory effect in addition to the excitatory effect just discussed. When Kirchner (1993) and Nieh (1993) played back the vibrations produced by tremble dancers, either by loading the sound onto the combs of a hive (Kirchner) or directly onto bees (Nieh), they found that bees performing waggle dances for nectar sources tended to stop dancing and leave the hive. This tends to shut down a colony's recruitment of additional bees to nectar sources. Thus it appears that the tremble dance helps a colony restore a match between nectar collecting and nectar processing not only by stimulating a rise in the processing rate but also by inhibiting any further rise in the collecting rate.

One might wonder whether the increase in number of nectar receiver bees that we observed from one day to the next (8–9 July, and 19–20 July) was mainly a result of the activational effects of the tremble dances. After all, the colony's population was increasing throughout the experiment, so even if there had been no increase in the colony's food intake, no tremble dancing, and thus no change in the percentage of the colony's members serving as nectar receivers, presumably the *number* of nectar receivers in the colony would have increased somewhat. Fortunately, it is easy to estimate how much of the day-to-day growth in the nectar receiver group was due simply to colony growth. Between 8 July and 20 July the colony's population grew by 1320 bees, hence the colony grew by 110 bees per day, on average. If the colony's food supply had not changed, then presumably the colony would have continued to have 17% of its bees engaged in nectar reception, since this is what was observed on both days (7 July and 19 July) with a low influx of sugar solution. Moreover, in a previously published study conducted in the same location, with the same equipment, with the same size colony, and with the same low influx of sugar solution, it was likewise found that 15–20% of the colony was engaged in nectar reception (Seeley 1989). Therefore we can assume that 17% of the additional 110 bees per day, or approximately 19 bees, would have appeared as additional nectar receivers even if we had not increased the sugar solution influx and thus had not elicited tremble dancing. But 19 bees is only a small percentage (4.5%) of the 420 additional receiver bees observed in trial 1, and of course is an even smaller percentage (1.3%) of the 1480 additional receiver bees observed in trial 2. It seems clear, therefore, that in both trials most of the increase in number of nectar receivers resulted from the activational effects of tremble dances rather than simply the growth of the colony.

The additional receiver bees are young and middle-aged bees

In both trials of our experiment the colony boosted the number of receiver bees through a complex set of internal adjustments. As shown in Table 1, the greatest number of additional receiver bees came from the ranks of the colony's middle-age bees, but many also came from the ranks of the young bees. This table also shows that there was a net loss of receiver bees from the ranks of the old bees. The net effect of these dynamics was a shift in the age composition of the receiver bees, from one of 95% middle-aged *and old* bees when the nectar influx was low, to one of 93–98% middle-aged *and young* bees when the nectar influx was high. The functional basis of this shift seems clear: the colony mobilized its old bees to nectar collection as it scrambled to exploit the newly abundant food, and then the colony mobilized many young and middle-age bees to nectar reception as it struggled to process the plentiful food brought home by the mob of foragers.

The results reported in Table 2 reveal that when thinking about how a colony boosts the number of individuals engaged in a particular task, we should consider not only how a colony may *raise the recruitment* of workers to this task, but also how it may *lower the abandonment* by workers of this task. The modulation of task abandonment is shown by the fact that when the colony's food influx was high, a smaller percentage of the recruits to the feeder had previously functioned as a receiver bee than when the colony's food influx was low, even though a larger percentage of the entire colony functioned as a receiver bee on the days of high food influx. Evidently, when the colony's influx of sugar solution was high, its receiver bees were less apt to switch to foraging. (This conclusion may hold mainly for middle-aged and young receiver bees since, as we have just discussed, many of the colony's old receiver bees did indeed switch to foraging.) In hindsight, it seems obvious that to understand fully how a colony boosts its allocation of labor to a particular task we must consider both increased recruitment to this task and decreased abandonment of this task. After all, the net rate of change in any group's size is, in principle, jointly determined by the rates at which individuals join and leave the group. What this investigation makes clear is that both means of group size adjustment – tuning of recruitment and of abandonment – are not just possibilities, but actualities, as a colony of social insects adaptively adjusts its allocation of labor among tasks.

It remains unclear what the additional receiver bees were doing before they switched to functioning as receiver bees. There are two possibilities: either they were active in another task or they were inactive (or some combination of the two). Numerous studies have shown that at any moment 50% or more of the workers in a honey bee colony are simply walking around, grooming themselves, or standing still (Lindauer 1952;

Kolmes 1985; Seeley and Kolmes 1991). It seems, therefore, that a honey bee colony possesses many unemployed bees that can be activated to various tasks as needed, so it seems entirely plausible that many of the new receiver bees were previously inactive. But only further studies will tell us how much a honey bee colony copes with the need for additional receiver bees by drawing upon a reserve supply of labor.

General issues

In this study we examined the effects of the tremble dance, one of the communication processes whereby a honey bee colony is able to maintain a match between the rates of nectar collecting and nectar processing despite large day-to-day variations in nectar availability. Although this study focuses on just one species of social insect, and on just one means whereby its colonies adjust their division of labor, the findings reported here shed light on two general issues regarding the organization of work in social insect colonies.

One is the means whereby a colony achieves an adaptive allocation of labor. Recent theoretical studies (Tofts and Franks 1992; Tofts 1993) have demonstrated that if the workers in a social insect colony follow a simple algorithm called "foraging for work", then the workers will achieve an appropriate distribution of themselves among the various tasks, one in which the labor supply is matched to the labor demand for each task. According to this algorithm, each worker labors on the tasks associated with a given location until it experiences failures in finding work there, at which time it moves to a neighboring location where it works on the tasks associated with this place for as long as it succeeds in finding work there. In essence, "workers do not allocate tasks, but tasks allocate workers" (Bourke and Franks 1995). By this scheme, workers are "pushed" from one location (and its associated tasks) to another by their failures to find work in their current location. Although the theoretical studies show that this simple algorithm is sufficient for creating a proper allocation of labor, the empirical studies of the honey bee's tremble dance indicate that the mechanisms of labor allocation within a colony of social insects can be more complex than those invoked by the "foraging for work" hypothesis. In particular, this analysis of the effects of the tremble dance reveals that workers can be induced to switch tasks not only in response to the cue of failure to find work, but also in response special signals from nestmates. In other words, it is becoming clear that workers can be "pulled" as well as "pushed" to switch tasks. The use of signals to "pull" workers from one task to another seems particularly appropriate when additional workers are urgently needed in a location different from the one where they are currently working, for without such signals the needed workers might labor along in one place totally

unaware that an emergency has arisen elsewhere in the nest.

The second general issue is the capacity of a social insect colony to alter quickly its allocation of labor in response to changes in the environment. This study reveals an impressive capacity of honey bee colonies for rapid response. In particular, in the second trial of our experiment we discovered that our study colony was able to adjust itself so that within 9 h of the onset of a strong influx of sugar solution the fraction of its members functioning as receiver bees rose from below 20% to above 50%. It is important to note that this large-scale reallocation of labor is not some sociological oddity induced by bizarre experimental conditions, but instead is typical of what a colony living in nature must accomplish. This is indicated by calculating how much food our study colony collected during the day of high food influx and comparing this to what a normal colony gathers on a day of abundant food (a "nectar flow"). On the day when the colony devoted half of its members to nectar reception (20 July, see Fig. 2), it gathered 2.0 mol/L sugar solution for 9 hours at an average rate of 87.4 mL per hour, hence it gathered a total of 983 g of sucrose solution. The colony consisted of some 4000 bees, so its gathering of approximately 1.0 kg of nectar in a day was roughly comparable to a full-size colony of some 30,000 bees gathering about 7.5 kg of nectar in a day. A full-size colony can gain this much weight or more each day during a strong nectar flow, hence the high level of food influx that our study colony experienced lies within the range experienced by colonies living in nature (Visscher and Seeley 1982; Seeley 1995). Moreover, colonies in nature experience surges in food influx as great as those we imposed on our study colony, for in the real world a colony's nectar intake can skyrocket from one day to the next as the weather conditions change from cool and cloudy to warm and sunny. It seems, therefore, that the tremendous adaptability shown by our study colony falls within the response range of natural honey bee colonies. Thus it provides a striking example of the high level of adaptability that a social insect colony must possess in order to cope with the ever-changing environment.

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