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## Changes in food source profitability affect the trophallactic and dance behavior of forager honeybees (*Apis mellifera* L.)

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**Abstract** Since nectar constitutes a highly variable resource, forager honeybees (*Apis mellifera*) always adjust their social foraging activities according to the current profitability of the nectar sources they exploit. If trophallaxis, food exchange among individuals of the same colony, serves to improve the coordination among nectar foragers, as occurs with the dance behavior, a high correlation might be expected between the foragers' trophallactic behavior and the profitability of the food sources they exploited. The aim of this work was to analyze whether a forager bee changes her trophallactic behavior with the varying profitability of a food source. In addition, since food source profitability affects dance behavior, we also analyzed the degree of coupling between the trophallactic and dance behavior of returning honeybees. Results show that trophallaxis by forager bees inside the hive changed rapidly with fluctuations in food source profitability. After an increase in profitability, returning foragers (1) increased the number of trophallactic offering contacts, (2) decreased the average duration of offering contacts, (3) shifted the temporal distribution of offering contacts from being mainly near the beginning of the time in the hive to being more evenly distributed throughout the entire visit, (4) begged for food less frequently, and (5) shifted their begging toward the very end of the visit. Regarding their dance behavior, foragers danced earlier in their visits to the hive and performed more waggle runs when the profitability of the food source was increased. Furthermore, the trophallactic and dance behaviors were affected not only by the absolute profitability of the food source but also by changes in profitability. Taken together, these results indicate that,

in addition to dance behavior, short trophallactic interactions of returning foragers (which include both offering and begging contacts) may help foragers to communicate information about rapidly fluctuating resource opportunities.

**Keywords** *Apis mellifera* · Honeybee · Communication · Foraging

### Introduction

Social food collection allows honeybee colonies to exploit continuously changing resources efficiently (von Frisch 1967; Seeley 1995). The coordination of foraging tasks among foragers arises from the honeybee's capacity to exchange information within the nest about the location and other characteristics of food sources. In particular, forager bees display recruiting behaviors that cause nest-mates to congregate at some point in space where work is required. Among their recruiting behaviors, the bees' dance communication is one of the most extensively studied mechanisms of communication among the social insects (von Frisch 1967; Wilson 1971; Seeley 1995).

Previous studies of the dance communication have shown that the information shared within the hive consists almost exclusively of information about highly profitable food sources (Seeley and Visscher 1988; Seeley and Towne 1992; Seeley 1995). Nevertheless, flowers sometimes produce nectar at low and highly variable rates (Núñez 1977; Vogel 1983), which suggests that bees might benefit from communicating with nest-mates about changes in the quality and abundance of nectar even in the absence of dancing and recruitment. However, how non-dancing foragers collecting nectar at sources of low or intermediate profitability might transfer information on the recently visited sources to their nest-mates is not known.

Thus, it is necessary to analyze behaviors other than the forager dancing displays which might allow the rapid

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exchange of information about resource opportunities. These behaviors could involve the capability of bees to learn odors and to orient their searching flights according to odor cues (Wilson 1971). Since foragers transfer the nectar they collect to nest-mates via trophallaxis (mouth-to-mouth exchange of food), the possibility arises that floral scents might indeed play a role during recruitment. von Frisch (1923), for example, reported that the exchange of scented food stimulates unemployed foragers to resume their nectar-foraging activity even without dancing. Furthermore, he reported that during dancing displays, foragers distributed small quantities of nectar to nest-mates. Thus, receivers that already had some successful foraging experiences could have been alerted by the familiar odors (von Frisch 1967). Moreover, Ribbands (1955), who also showed that foragers are stimulated by odors alone to fly out and search for food, stated that "food sharing serves as a means of communication between the members of the colony, playing the key role in the system of communication which enables the new forager to learn about suitable crops."

On the other hand, a returning forager can also perform trophallactic begging contacts within the hive by touching the prementum of a nest-mate with its protruded proboscis. These interactions allow the foragers to receive food or just taste it and were long considered acts of refuelling (von Frisch 1967). Since fuel requirements differ according to the distance to be flown (Beutler 1950; Istomina-Tsvetkova 1960; von Frisch 1967), no change in forager begging behavior would be expected when the distance of the exploited food source remains constant. Nevertheless, Núñez (1970) found that when the distance to the food source remained constant, the amount of begging by foragers changed after changes in reward. He therefore suggested that begging contacts could allow foragers to exchange information within the hive in order to regulate their subsequent foraging behavior. Consistent with this, he reported that non-dancing foragers returning from nectar sources of low profitability began to display dance behavior only after performing begging contacts with their nest-mates.

If trophallaxis serves to improve coordination among foragers, a correlation might reasonably be expected between the forager's trophallactic behavior and the profitability of the exploited food sources. Accordingly, Farina (1996) reported that the frequency of a forager's begging contacts decreases and the frequency of its offering contacts increases as the flow rate of sugar solution presented at a feeding place increases. Thus, the number of trophallactic interactions varies according to the flow rate at a feeder. However, profitability also depends on the sucrose concentration of the solution. Thus, one purpose of the work reported here was to analyze whether a forager bee changes her trophallactic behavior (offering and begging interactions) when she exploits a food source of variable sucrose concentration. In addition, if trophallaxis allows the foragers to share information about resource opportunities, variations in food source

profitability (sucrose concentration) should rapidly alter the forager's trophallactic behavior. Therefore, the second purpose of our work was to evaluate whether forager trophallactic behavior represents variations in profitability with accurate temporal resolution.

Foragers mainly offer nectar samples between dancing events (Ribbands 1955; von Frisch 1967), which suggests that food sharing and dance behavior might be coupled. However, if food sharing plays a key role in the system of communication, as was proposed by Ribbands (1955), the forager's trophallactic offering contacts could be autonomously modulated according to food source profitability. Thus, assessing the degree of coupling between food sharing and dance behavior would be useful. To address this issue, we also analyzed the distribution of both offering contacts and dancing events over time throughout the foragers' stay inside the hive.

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## Methods

Experiments were performed in the experimental field of the Department of Biological Sciences of the University of Buenos Aires (34°32' S, 58°26' W) during 1996, at the end of the summer and beginning of the autumn season, i.e., when natural nectar sources are reduced. A colony of nearly 2000 *Apis mellifera* (hybrid of *A. mellifera ligustica*) bees in a one-frame observation hive with honey and brood was used (see von Frisch 1967).

### Overview

Individual forager bees were trained to collect scented sucrose solution (80 µl mint essence per liter) at an artificial food source located 160 m from the nest. At the feeding place, we presented a single artificial flower connected to a set of feeders offering different sucrose concentrations (0.6, 1.2, 1.8, and 2.4 M). In this way, we were able to change the sucrose concentration delivered at the feeding place over a series of visits by a forager in order to evaluate the forager's responses to variations in food source profitability. The feeders (henceforth rate-feeders) allowed control of the solution flow rate and are described in detail elsewhere (Núñez 1966, 1970). Essentially, the feeder's design enables the researcher to control indirectly the forager's intake rate by offering a solution flow rate that is beneath the maximal intake rate of a bee (ca 60 µl/min for 50% w/w sucrose solutions; see Núñez 1966). Under these conditions, the final nectar load depends on the offered flow rate, and foragers show a broader behavioral repertoire than observed under ad libitum conditions (Núñez 1966; Varjú and Núñez 1991; Farina 1996; Grosclaude and Núñez 1998). We presented the same solution flow rate (5 µl/min) for all of the sucrose concentrations used in this study.

### Experimental series

Three different reward series were used. Throughout each, we recorded the behavior of a trained bee that individually collected sucrose solution for twenty successive round trips to the feeder. We used two different changing reward series. For these series, an initial sucrose concentration of either 1.2 or 0.6 M was offered at the rate-feeder during the first four successive foraging trips. Then, while the trained bee was absent after its fourth visit, the sucrose concentration was increased to 1.8 M. Thereafter, the concentration was changed every four visits until the bee completed a total of 20 visits. One of these series (henceforth called the small-difference series) presented a sequence of 1.2–1.8–1.2–2.4–1.2 M. The other series (henceforth called the large-difference series) pre-

sented a sequence of 0.6–1.8–0.6–2.4–0.6 M. In addition, we presented a series (henceforth called the constant series) in which the rate-feeder offered an unchanging concentration of 1.8 M. The constant series allowed us to evaluate possible effects of time of day on the recorded behavioral parameters.

### Procedure

Each experimental day started when a single trained bee was allowed to collect sucrose solution at the rate-feeder. To establish steady-state foraging conditions at the start of each series, the trained bee collected the initial concentration of the series for approximately 2 h. Thus transient rewards that could affect the bee's motivational state at the start of the experiments were avoided (Mc Farland 1971). The experiments were performed from 0900–1500 hours. Only one bee was recorded each day, and all recruited bees were captured. Seventeen bees were recorded altogether, 6 in the small-difference series, 6 in the large-difference series, and 5 in the constant series.

### Measurements

An observer at the rate-feeder maintained direct contact with an observer at the hive through walkie-talkies. Since the rate-feeder was only turned on while the trained bees were at the feeding place, foragers never found any accumulated sugar solution upon their arrival.

We recorded several behavioral variables on videotape during each visit to the observation hive by each forager: (1) hive time (in seconds), defined as the time the forager spent inside the hive between two consecutive foraging trips; (2) number of trophallactic offering contacts, defined as the number times the forager opened her mandibles while one or more recipient bees contacted her prementum with their protruded proboscis; (3) duration of each offering contact (in seconds); (4) number of trophallactic begging contacts, defined as the number of times the forager touched the prementum of a nest-mate with her protruded proboscis; (5) number of waggle runs performed.

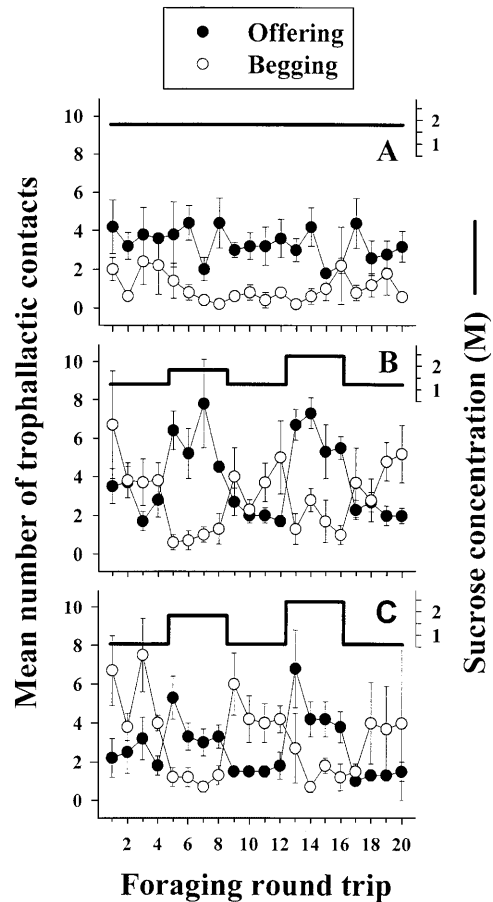
### Statistical analysis

Data were analyzed by means of repeated-measures ANOVA (Sokal and Rohlf 1981).

## Results

### Trophallactic and dancing events as a function of the different reward series

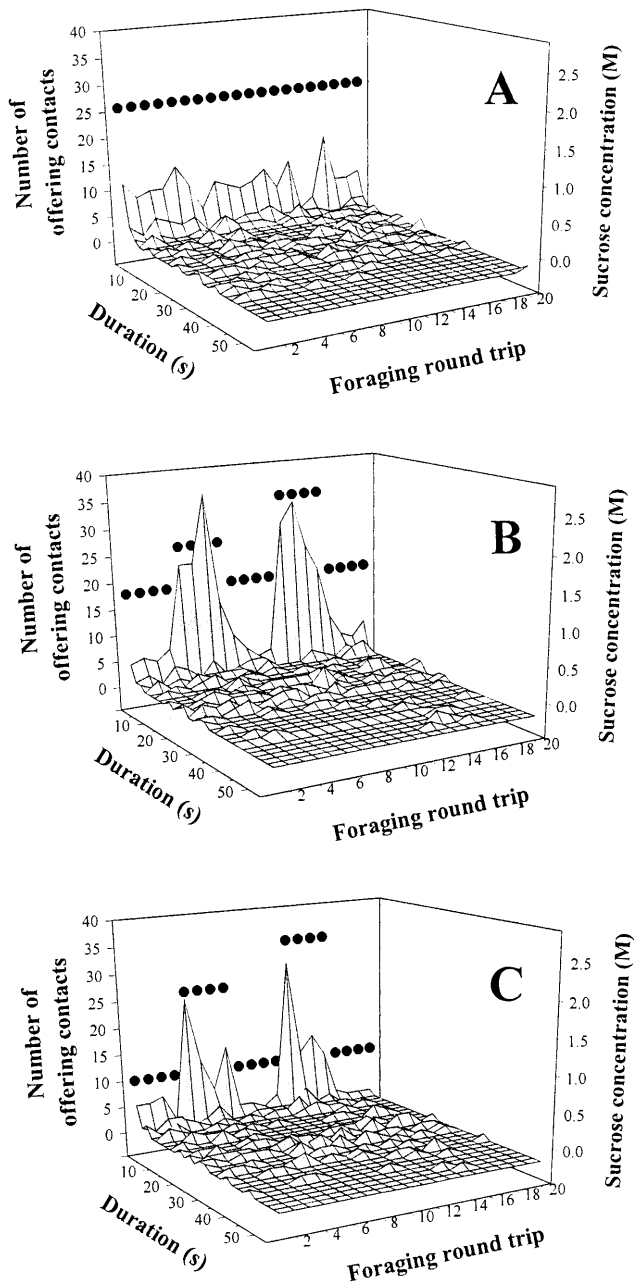
In the constant series, we observed no significant changes in the number of the foragers' trophallactic offering contacts throughout the series (Fig. 1A, filled circles,  $P=0.72$ ). In both the small- and large-difference series, offering contacts increased when the sucrose concentration was increased (Fig. 1B, filled circles, small-difference series:  $P=0.0001$ , large-difference series:  $P=0.001$ ; Fig. 2B). In the large-difference series, the highest number of offering contacts was recorded immediately after the first encounter with an increased concentration at the rate-feeder (Fig. 1C, filled circles). Moreover, although offering contacts increased as the sucrose concentration increased throughout both changing reward series, different numbers of these interactions were recorded for



**Fig. 1** Mean ( $\pm$ SE) number of trophallactic offering contacts (filled circles) and begging contacts (open circles) performed by foragers during successive foraging trips. Twenty successive foraging trips were recorded per assay. The rate-feeder delivered a constant flow rate of 5  $\mu$ l/min. Results from the corresponding repeated-measures ANOVA were; constant series – offering contacts,  $F_{19,76}=0.75$ ,  $P=0.72$ ,  $n=5$ ; begging contacts,  $F_{19,76}=1.06$ ,  $P=0.41$ ,  $n=5$  (A); small-difference series – offering contacts,  $F_{19,76}=5.34$ ,  $P<0.0001$ ,  $n=6$ ; begging contacts,  $F_{19,76}=1.82$ ,  $P=0.036$ ,  $n=6$  (B); large-difference series – offering contacts,  $F_{18,18}=4.5$ ,  $P=0.001$ ,  $n=6$ ; begging contacts,  $F_{18,18}=2.82$ ,  $P=0.017$ ,  $n=6$

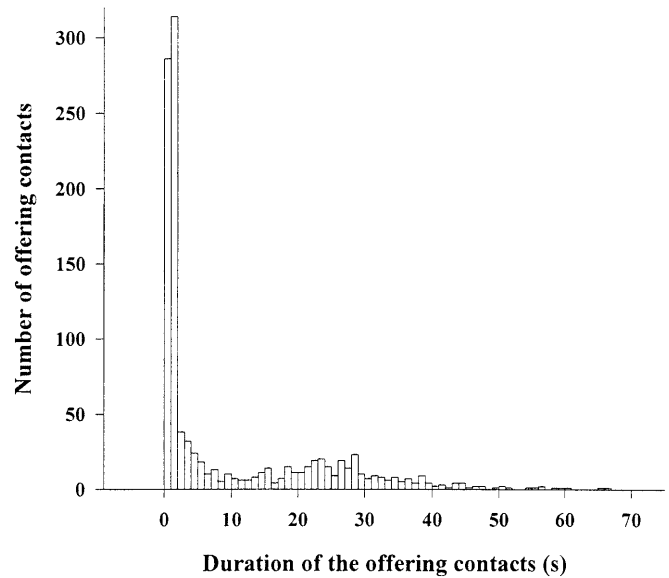
the same concentrations of 1.8 or 2.4 M in the two series (compare Fig. 1B and C, filled circles).

Since foragers can behave as food beggars as well as food donors, we recorded the begging behavior of the same foragers that had offered food. Throughout the constant series, the number of begging contacts did not change (Fig. 1A, open circles,  $P=0.41$ ). In the changing-reward series, by contrast, foragers performed more begging contacts when they returned from the foraging trips of lower profitability (0.6 and 1.2 M in comparison with 1.8 and 2.4 M). These foragers performed few begging contacts when they returned from the most highly profitable trips. Thus, changes in the forager's begging behavior were clearly correlated with the offered sucrose concentration (small-difference series, Fig. 1B, open circles,  $P=0.036$ ; large-difference series, Fig. 1C, open circles,  $P=0.017$ ).



**Fig. 2A–C** The total number of trophallactic offering contacts performed by all of the recorded foragers during successive foraging trips presented for each series. Offering contacts were categorized according to their duration using 2-s intervals. **A** Constant series ( $n=5$ ). **B** Small-difference series ( $n=6$ ). **C** Large-difference series ( $n=6$ )

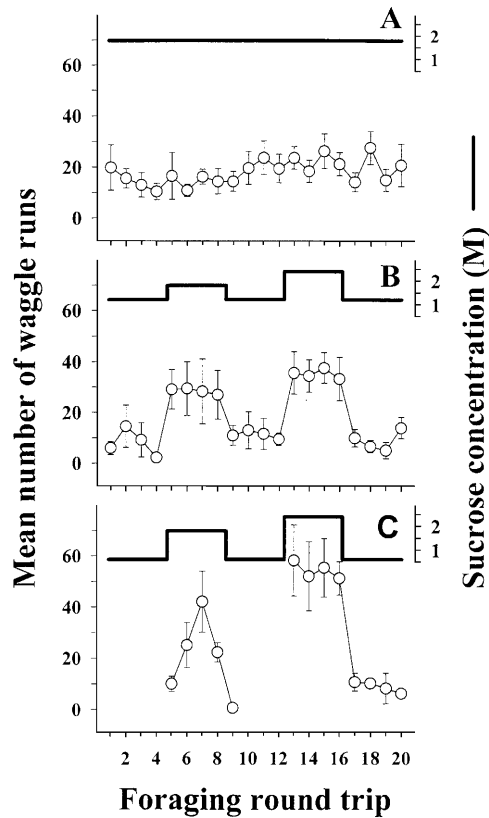
The time foragers invested in each trophallactic offering contact was also analyzed. Fig. 2 shows both changes in food source profitability and the number of offering contacts of different duration performed by all bees for each series. Foragers increased the number of offering contacts of short duration after the profitability of the food source increased (Fig. 2B, C). Additionally, for each series, we pooled the data from the successive foraging round trips to analyze the distribution of these con-



**Fig. 3** Frequency distribution of the trophallactic offering contacts categorized according to their durations. The distribution was adjusted to an inverse polynomial function (see Results for details). The data are from 17 foragers individually recorded during the three reward series

tacts independently of the sucrose concentration presented at the rate-feeder. Each distribution fit an inverse polynomial function (constant series:  $r=0.97$ ,  $P=0.0001$ ,  $n=333$ ; small-difference series:  $r=0.95$ ,  $P=0.001$ ,  $n=448$ ; large-difference series:  $r=0.93$ ,  $P<0.0001$ ,  $n=312$ ). The corresponding equation for each experimental series was  $N=n_0+(a/d)+(b/d^2)+(c/d^3)$ , where  $N$  is the number of offering contacts, and  $d$  represents the contact duration, while  $a$ ,  $b$ , and  $c$  are constants. Given the similarity between the distributions from the different series, we pooled all of the observations to create the total distribution shown in Fig. 3 ( $r=0.96$ ,  $P=0.0001$ ,  $n=1,093$ ). Significant values were found for each of the coefficients of the final equation:  $N=16.1+(-452.1/d)+(3,057.2/d^2)+(-2,332.1/d^3)$ . Thus, the results show that trophallactic offering contacts lasting less than 2 s constitute more than half (54%) of the offering interactions performed by the returning foragers. Given these results, we analyzed separately the occurrence of offering contacts lasting more than 2 s (henceforth long offering contacts) according to the profitability of the food source. We found no changes in the number of these long contacts throughout any of the series (constant series:  $F_{19,76}=0.79$ ,  $P=0.747$ ,  $n=5$ , small-difference series:  $F_{(19,76)}=0.90$ ,  $P=0.589$ ,  $n=6$ , and large-difference series:  $F_{18,80}=1.07$ ,  $P=0.116$ ,  $n=6$ ). Thus, foragers performed a mean ( $\pm$ SE) of  $1.5\pm 0.05$  long offering contacts per foraging round trip.

All of the trained foragers performed dances throughout all of their foraging cycles during both the constant series and the small-difference series. There was no significant difference in the number of waggle runs performed per visit to the hive throughout the constant series (Fig. 4A,  $P=0.98$ ). In the small-difference series, by



**Fig. 4** Mean ( $\pm$ SE) number of waggle runs performed by foragers during successive foraging trips. Values were calculated only from data of bees that had performed dances (see Results for details). Twenty successive foraging trips were recorded per assay. The rate-feeder delivered a constant flow rate of 5  $\mu$ l/min. Results from the corresponding repeated-measures ANOVA were: constant series,  $F_{19,57}=0.43$ ,  $P=0.98$ ,  $n=5$  (A); small-difference series,  $F_{19,76}=2.67$ ,  $P=0.001$ ,  $n=6$  (B); large-difference series, statistical analysis was not performed due to the lack of data in some foraging trips (C)

contrast, foragers increased the number of waggle runs each time the offered sucrose concentration was increased (Fig. 4B,  $P=0.001$ ). In the large-difference series, on the other hand, it was the probability of dancing that changed most dramatically with food source profitability. In this case, all the foragers started to perform waggle runs only after the concentration presented at the rate-feeder was tripled from 0.6 to 1.8 M, and they stopped dancing when the concentration was decreased to 0.6 M. Foragers performed the highest number of waggle runs when the offered sucrose concentration was highest (2.4 M, from the 13th to the 16th foraging trips). When the concentration was decreased from 2.4 to 0.6 M for the final four foraging trips, some foragers still performed waggle runs, although four of the six bees quit before the end of the series (Fig. 4C).

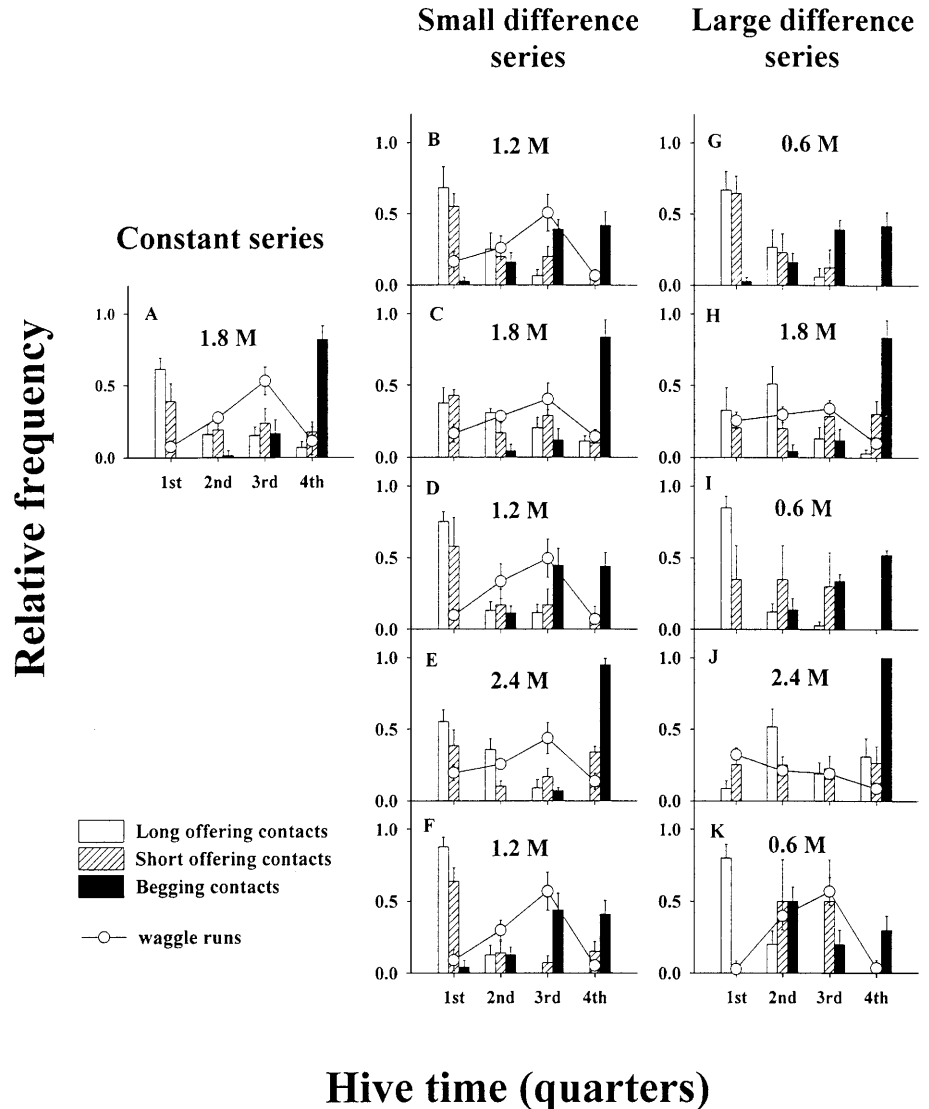
Temporal distribution of the trophallactic and dancing events during the forager's time in the hive

The above results showed that after finding an increased sucrose concentration, foragers increased or started to perform dancing events (Fig. 4B, C), simultaneously increasing the number of short trophallactic offering contacts (Fig. 2B, C). However, the number of short offering contacts recorded during the large-difference series was not tightly correlated with the number of waggle runs, since while short offering contacts increased immediately after the sucrose concentration was increased from 0.6 to 1.8 M, the number of waggle runs increased only gradually (Fig. 1C, filled circles, and Fig. 4C). To further focus on this issue, we analyzed the occurrence of both short offering contacts and dancing events during the forager's time in the hive. If short offering contacts and waggle runs are temporally coupled, the distribution of the two behavioral events should match throughout the bee's time in the hive.

However, since foragers transfer their nectar loads to receiver bees, foragers have to search or wait for a food receiver once they enter the nest (Ratnieks and Anderson 1999). Thus, returning foragers may find differences in the availability of receivers able to accept their nectar (Lindauer 1961; Seeley 1995). Hence, with a decreased availability of receivers, a forager could perform more offering contacts before finding a receiver who can unload her. These interactions could be interpreted as failures to unload and, therefore, should necessarily occur before the long offering contacts. To evaluate this hypothesis, we compared the temporal distributions of short and long offering contacts during the forager's time in the hive. Additionally, we extended this temporal analysis to the begging contacts, in order to evaluate whether food source profitability also affects the temporal distribution of these interactions.

We considered four behavioral categories for this analysis: short offering contacts (lasting less than 2 s), long offering contacts (lasting more than 2 s), begging contacts, and waggle runs. The duration of visits to the hive changed across successive foraging trips during two of the series: the constant and large-difference series (constant series:  $F_{18,18}=4.02$ ,  $P=0.005$ ; small-difference series:  $F_{19,95}=1.03$ ,  $P=0.434$ ; large-difference series:  $F_{19,57}=2.42$ ,  $P=0.003$ ). Thus, to compare information from different bees and different foraging trips, the time spent in the hive on each visit was divided into four periods of equal duration (quarters). An event was included in a given quarter based on the time that had elapsed from the arrival of the bee until the occurrence of the event, and dividing this time lapse by the total time spent by the forager in the hive. Therefore, all relative frequency values represent the number of events that were performed during a given quarter over the total number of events performed during the entire visit. Additionally, relative frequencies were calculated separately for each of the sucrose concentrations that were offered at the feeding place, to evaluate possible effects of changes in

**Fig. 5A–K** Distribution of trophallactic and dancing events throughout the time foragers were in the hive. We considered four behavioral categories of events: long offering contacts (lasting more than 2 s, *open bars*); short offering contacts (lasting less than 2 s, *hatched bars*); begging contacts (filled bars), and waggle runs (*open circles*). Hive time was divided into quarters of equal duration, and relative frequencies (mean±SE) of events were calculated for each quarter (see Results for details). Additionally, relative frequencies were calculated separately for each sucrose concentration offered at the feeding place. Thus, for the changing reward series, foraging trips were grouped according to the sequence of sucrose concentrations presented at the rate-feeder. **A** Constant series (mean values of 20 visits). **B–F** Small-difference series (mean values of the four visits exposed to the same concentration). **G–K** Large-difference series (mean values of the four visits exposed to the same concentration)



food source profitability on the temporal distribution of events.

Figure 5 shows that long offering contacts (open bars) were mainly performed shortly after returning to the hive (Fig. 5A, B, D, F, G, I, K). However, after an increase in sucrose concentration, these contacts were delayed (Fig. 5C, E, H, J, open bars). Short offering contacts (hatched bars) were more regularly distributed than long ones, especially after a large increase in sucrose concentration (Fig. 5E, H, J). Begging contacts (filled bars) occurred mainly during the last quarter of the time in the hive when the sucrose concentration was high (1.8 or 2.4 M; Fig. 5A, C, E, H, J) and mainly in the second and third quarters when the sucrose concentration was low (0.6 or 1.2 M; Fig. 5B, D, F, G, I, K). Waggle runs were displayed mainly during the third quarter of the hive time (Fig. 5A–F, K, open circles). However, large variations in profitability affected not only the probability of displaying dance maneuvers (Fig. 4) but also the temporal distribution of dancing. In particular, after a large in-

crease in sucrose concentration, foragers displayed proportionally more waggle runs during the first quarter of the hive time (Fig. 5H, J).

## Discussion

### Offering contacts

We observed long offering contacts lasting up to 66 seconds. The frequency distribution of these events showed a large proportion of contacts of intermediate duration, between 20–30 s (Fig. 3). Undoubtedly, returning donor foragers unload their crops through these longer trophallactic contacts. Only small numbers of these long offering contacts were observed per visit (foragers always performed one or two during each visit), and this number did not change with food source profitability.

On the other hand, foragers rapidly increased their number of short offering contacts each time they found

an increased food source profitability (Fig. 1, filled circles; Fig. 2 B, C). These short offering contacts (less than 2 s) represented more than 54% of the total offering interactions performed by the foragers (Fig. 3). Through these interactions, only small amounts of sugar solution are likely to be transferred, but taste and odor will almost certainly be transmitted. However, although the odor carried in the collected nectar has been previously associated with the recruitment of hive-mates to a target site (von Frisch 1923, 1967; Ribbands 1955), nectar samples were mainly described in these studies as occasional events occurring in close association with the forager's dance behavior. Nevertheless, our results indicate that short offering contacts, which increased in number with increased food source profitability, were not temporally coupled with dance behavior, since their temporal distribution during the foragers' time in the hive was clearly different from that of waggle runs (Fig. 5, hatched bars and open circles).

Since the availability of receiver bees affects the ease with which returning foragers can unload (Lindauer 1961; Seeley 1995), short trophallactic offering contacts could be interpreted as failures to unload. Thus, a rapid increase in the number of short offering contacts may be explained by a rapid decrease in the availability of receivers, which in turn depends on the colony's nectar intake rate and the overall foraging activity (Seeley 1995). However, we performed the experiments during the autumn when nectar availability is low, and a relatively high and constant availability of receivers would be expected because of the colony's low intake rate. Thus, short offering contacts would not be expected to change with food source profitability. Nevertheless, our results show a high correlation between these variables. In addition, by assuming that short offering contacts represent failures to unload, one would expect these interactions to be performed before the long offering contacts during the forager's time in the hive. However, we found that short offering contacts were distributed throughout the entire visit, while long offering contacts occurred mainly near the beginning (Fig. 5, hatched and open bars). Thus, the temporal analysis of short offering contacts does not support the idea that these contacts represent failures to unload.

Short offering contacts might also be interpreted as an attempt to complete unfinished nectar unloading. Under this hypothesis, however, it is difficult to explain why we found little variation in the number of these interactions while the foragers exploited sources of constant profitability in the constant series (Fig. 1A, filled circles; Fig. 2A) but a strong temporal correlation between short offering contacts and food source profitability in the changing-reward series (Fig. 1B, C, filled circles).

Interestingly, the number of short offering contacts seems to be related not only to the current profitability but also to previous foraging experience. During the changing-reward series, foragers that exploited the 1.8 M solution varied the number of short offering contacts depending on whether they had previously collected 0.6 or

1.2 M food. Similar results were observed when foragers exploited the 2.4 M solution (Fig. 1B, C, filled circles). Moreover, in the large-difference series, the highest number of offering contacts was recorded immediately after the first increase in concentration at the feeder (Fig. 1C, filled circles). This would seem to be a consequence of the large increase in concentration (0.6–1.8 M), since this effect was not observed in the small-difference series in which the corresponding increase in concentration was smaller (1.2–1.8 M).

### Begging contacts

Previous results (Núñez 1970; Farina 1996) have shown that increases in the availability of nectar, expressed in terms of the flow rate, decrease the number of begging contacts. The present results show that begging behavior is also related to food source profitability expressed in terms of sucrose concentration. We observed that after an increase in sucrose concentration, returning foragers begged less frequently and shifted their begging contacts toward the end of the visit (Fig. 1, open circles; Fig. 5, filled bars). Thus, as we expected from previous studies (Núñez 1970; Farina 1996), there was a negative relationship between the occurrence of begging contacts and food source profitability. However, what is interesting from the present results is that the forager's trophallactic begging behavior may also represent sudden *changes* in food source profitability with high temporal resolution (Fig. 1, open circles).

Throughout the present experiments, the feeding place was always at the same distance from the hive, ruling out any possible effect of the distance to the food source. Yet the hypothesis of refuelling (von Frisch 1967) could conceivably explain variations in the number of begging contacts if the quality or availability of fuel supplied by the hive bees changed throughout the series of foraging trips. However, this would not explain the high temporal correlation we found between the number of begging contacts and food source profitability (Fig. 1B, C, empty circles).

The number of hive bees offering nectar of a given odor may be related to the profitability of the source producing that nectar, since there is usually a direct relationship between the number of bees exploiting a nectar source and its profitability (von Frisch 1967; Seeley 1995). Thus, since the odor of the nectar collected can be transferred through short offering contacts (von Frisch 1967), odor cues of highly profitable nectar sources could be communicated to begging foragers through the increased number of short offering contacts initiated by the bees exploiting the highly profitable sources. Therefore, a forager's begging contacts could serve as a means by which a forager assesses the abundance and diversity of the nectar sources currently being exploited by the colony, especially when the profitability of the forager's own source is marginal (because that is when her begging increases). In this way, foragers could use their

trophallactic begging contacts to adjust their subsequent foraging behavior according to both the profitability of their own food sources and the stimulation available within the hive, which in turn depends on the nectar currently being handled by the colony. Adjustments of foraging behavior could include visiting the same source again, staying inside the hive, or even visiting another source. Foragers could even initiate dancing displays when the nectar collected at other sources is scarce (Núñez 1970). According to this view, foragers would preferentially beg for food from other active foragers (as opposed to non-foraging bees), although presently no direct evidence exists to support this hypothesis.

### Dance behavior

As we expected, forager dance behavior was correlated with food source profitability. Foragers were more likely to start dancing and to perform more waggle runs when they found an increased sucrose concentration at the feeder (Fig. 4). Moreover, under the rewarding conditions we presented at the feeding place (which included a regulated flow rate of sugar solution), the number of waggle runs was clearly affected by recent past foraging experiences. For example, foragers collecting 2.4 M sucrose performed markedly more waggle runs when they had previously collected a 0.6 M solution (Fig. 4C) compared to a 1.2 M solution (Fig. 4B). Moreover, after collecting the highly concentrated sucrose solution (2.4 M), some of the foragers continued to perform waggle runs even after the concentration was switched to the lowest level (0.6 M), which had not previously elicited dancing (Fig. 4C). Similar effects of past foraging experiences on forager dance behavior have been reported previously (Raveret-Richter and Waddington 1993).

Dancing was mainly displayed during the third quarter of the hive time (Fig. 5, open circles), except after a large increase in profitability, which caused dancing to become more frequent during the first quarter of the hive time (Fig. 5H, J, empty circles) and the forager's food unloading to be correspondingly delayed (Fig. 5H, J, open bars). Thus, variations in food source profitability also affected the temporal distribution of dancing.

### Effects of recent past foraging experience on recruitment

The current results indicate that sudden changes in food source profitability may lead to differences in the number as well as the temporal distribution of both short trophallactic offering contacts and waggle runs (Fig. 1, filled circles; Figs. 2, 4, and 5). Moreover, within the range of profitability we offered, foragers showed behavioral outputs depending on the magnitude of the stimulus variation. Thus, these behaviors were quantitatively modified according to both the current level of food source profitability and recent past foraging experience. Accordingly, we would expect that after a large increase

in food source profitability, both the current profitability as well as the magnitude of the recent increase will affect the arrival of new recruits at the feeding place. This has indeed been observed (P. Fernández and W.M. Farina, unpublished data).

### Trophallactic interactions as a behavioral mechanism for the exchange of information about resource opportunities

Both von Frisch (1923, 1967) and Ribbands (1954, 1955) mentioned that trained foragers fly out immediately to known feeding places when presented with conditioned scents within the hive. Moreover, Ribbands (1955) proposed that elaborate methods of communication such as the honeybee dance must have evolved in simple stages and that the recognition of the food delivered by foragers may have been a primitive method of information exchange. Our present results show that, in addition to modulating their dance behavior according to resource quality, returning foragers also rapidly change the number of both their short offering contacts as well as their begging contacts according to food source profitability. Thus, among honeybees, trophallactic interactions may represent both a primitive mechanism of information exchange about fluctuating resource opportunities as well as a separate and well-regulated mechanism that works alongside the dance communication in modern bees to allow colonies to exploit efficiently ever-changing sets of resources.

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