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Research article

Nectar distribution and its relation to food quality in honeybee *(Apis mellifera)* colonies

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Abstract. In honeybees (*Apis mellifera*), the process of nectar collection is considered a straightforward example of task partitioning with two subtasks or two intersecting cycles of activity: (1) foraging and (2) storing of nectar, linked via its transfer between foragers and food processors. Many observations suggest, however, that nectar collection and processing in honeybees is a complex process, involving workers of other sub-castes and depending on variables such as resource profitability or the amount of stored honey. It has been observed that food processor bees often distribute food to other hive bees after receiving it from incoming foragers, instead of storing it immediately in honey cells. While there is little information about the sub-caste affiliation and the behaviour of these second-order receivers, this stage may be important for the rapid distribution of nutrients and related information. To investigate the identity of these second-order receivers, we quantified behaviours following nectar transfer and compared these behaviours with the behaviour of average worker hive-bees. Furthermore, we tested whether food quality (sugar concentration) affects the behaviour of the second-order receivers. Of all identified second-order receivers, 59.3 % performed nurse duties, 18.5 % performed food-processor duties and 22.2 % performed forager duties. After food intake, these bees were more active, had more trophallaxes (especially offering contacts) compared to average workers and they were found mainly in the brood area, independent of food quality. Our results show that the liquid food can be distributed rapidly among many bees of the three main worker sub-castes, without being stored in honey cells first. Furthermore, the results suggest that the rapid distribution of food partly depends on the high activity of second-order receivers.

Keywords: Apis mellifera, nectar collection, trophallaxis, task partitioning.

Introduction

Task partitioning, the division of a piece of work among two or more colony mates, is likely to enhance the performance of the individual and the colony (Ratnieks and Anderson, 1999a). Nectar collection in honeybees have been described as a straightforward process of two intersecting cycles of activity, a forage cycle and a storage cycle (Seeley, 1989; Ratnieks and Anderson, 1999a). Successful foragers transfer the gathered liquid to hive mates, the food processors (also called receivers or food storers), through trophallaxis (mouth-to-mouth contacts), which then initiate the processing of the fresh nectar to honey and store the food in honey cells (Park, 1925).

Observational and experimental evidence suggests, however, that nectar collection and processing is a more complex process, i.e. the nectar flows into various directions before or even without being stored in honey cells. First, observations on the behaviour of food processors show that bees often feed other bees (second-order receivers) on their way to the honey cells, sometimes large nectar samples (von Frisch, 1923; Rösch, 1925; Seeley, 1989; Pírez and Farina, 2004). Aspects of this feeding behaviour of the processor bees have been shown to depend on variables such as food source profitability (Pírez and Farina, 2004) and the nutritional state of the colony (Seeley, 1989). The proportion of food processors donating food to second-order receivers is

between about 50 % (Pírez and Farina, 2004) and 95 % (Seeley, 1989). Secondly, it has been shown that small quantities of food collected by foragers can become widely distributed among the members of different worker castes of a colony within a few hours (Nixon and Ribbands, 1952; see also DeGrandi-Hoffman and Hagler, 2000), which suggests that the view of a primarily unidirectional nectar flow from foragers to food processors to honey cells misses important aspects of nectar collection.

Information about nectar flow, about the behaviour and the caste of bees that receive food from food processors is not only important from a nutritional perspective, but also from an informational one. The major disadvantage of task partitioning with direct transfer of material is the time costs caused by queuing, searching and transfer delays. However, these delays may in fact offer opportunities for information acquisition about environmental conditions and colony work allocation as shown by empirical (Lindauer, 1948; Seeley, 1995; Hart and Ratnieks, 2001) and theoretical studies (Ratnieks and Anderson, 1999b). Furthermore, information cues and signals present in the transferred nectar such as the sucrose concentration (Pankiw et al., 2004), food scents (von Frisch, 1967; Farina et al., 2005, 2007; Gil and De Marco, 2005, 2006; Grüter et al., 2006) or pheromones (Wilson, 1971; Naumann et al., 1991; Crailsheim, 1998) may spread rapidly within the entire colony if nectar flow is multidirectional, involving many bees performing different tasks. Finally, aspects of trophallactic behaviour such as the transfer rate during single trophallaxes or chains of trophallaxes (Farina and Núñez, 1991; Farina and Wainselboim, 2001a; Goyret and Farina, 2005; Tezze and Farina, 1999) and the frequency of trophallaxes (Farina, 1996; De Marco and Farina, 2001) correlate with food source characteristics and may convey information about food source profitability. The ability to respond to these different information cues which are available as a consequence of nectar transfer from bee to bee might allow for a more accurate colony response to the current environmental conditions (Seeley, 1995; Dall et al., 2005).

For a better understanding of nectar flow within the honeybee hive, information about the caste affiliation and behaviours related to food processing after food reception of second-order receivers is needed. Therefore, we did an experiment in order to find out what kind of tasks the second-order receivers mainly perform after nectar reception. Furthermore, we quantified various behaviours of second-order receivers after they received liquid food and compared their behaviour with the behaviour of average worker bees of unknown age and caste. We were interested in behaviours relevant for nectar and information flow like trophallactic and locomotion activity. As forager and food processor behaviours are affected by food source profitability (Núñez, 1966, 1970; von Frisch, 1967; Seeley, 1986; Farina, 1996; De Marco and Farina, 2001; Farina and Wainselboim, 2001a; Pírez and Farina, 2004), we also tested whether the sucrose concentration of the liquid food affects the behaviour of second-order receivers.

Material and methods

Study site and animals

The experiment was conducted at the ethological field station near Bern, Switzerland. We used two two-frame observation hives (Schneider measure, brood comb 30 × 30 cm, Fig. 1) containing a colony of about 2'500 Buckfast honeybees (a cross between *Apis mellifera ligustica and A. m. mellifera*) each. Colonies had a queen, brood and honey reserves. A group of bees was trained to collect unscented sucrose solution that was of 15 % w/w sucrose concentration at an *ad libitum*-feeder located 85 m from the hive. Bees were marked individually and a number of about 5 to 15 foragers was maintained throughout the experiment.

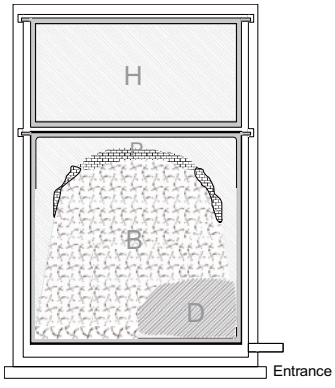

Figure 1. The observation hive with two frames of unequal size. The indicated areas are the honey area (H), the brood area (B), the delivery area (D) and the pollen area (P).

Experimental procedure

4 to 6 numbered foragers collected unscented sucrose solution that was either of 56 % w/w sucrose concentration (high quality food; H treatment) or 13 % w/w sucrose concentration (low quality food; L treatment) for about 60 minutes once or twice a day between 10:00 and 17:00 hours. Newly arriving bees were captured to maintain a constant number of foragers in both treatments. Bees that received solution from the numbered bees for at least 5 sec were considered food processor bees (first-order receiver). These first-order receivers were observed until they transferred solution to another bee (second-order receiver) for at least 1.5 sec. It has been shown that shorter trophallactic contacts often do not guarantee successful food transfer (Farina and Wainselboim, 2001b). Since we were also interested in the flow of information in the colonies, our threshold accounted for that fact that learning of food odours can happen during contacts as short as 1.2 seconds (Gil and De Marco, 2005). These second-order receivers were then filmed with a digital camera for a maximum of 20 min (561 ± 49.3 s, $N = 49$, mean ± SE). Often it was not possible to observe the bee for the 20 min because other bees covered them or they were simply lost. For the behavioural analysis we analysed the behaviour of the filmed bees (only bees that had been filmed for at least 3 min were used). Furthermore, we filmed worker bees randomly chosen throughout the hive to compare their behaviour with the behaviour of the second-order receiver bees. Therefore we divided the entire area on one side of the observation hive into 35 (5×7) equally sized rectangles. The rectangles were numbered and a sequence of random numbers was generated to randomly choose rectangles and therefore randomise the position of the chosen bee. The bee that was closest to the right upper

corner of a rectangle was chosen and filmed (579.2 ± 10.6 s, N = 35, mean ± SE). Bee densities were similar in the different hive areas (2'500 bees approach the carrying capacity of our hives).

Behavioural observations

To identify a second-order receiver as forager, food processor or nurse bee, we looked for behaviours that are typical for bees working in a particular caste. A bee was considered a

(i) forager if the bee was *foraging*, *dancing* or *following dances* (Rösch, 1925; Lindauer, 1952; von Frisch, 1967; Seeley, 1995)
(ii) food processor if the bee *unloaded food* (>5 sec) from a returning forager (Rösch, 1925; Lindauer, 1952; von Frisch, 1967; Seeley, 1995). These unloading contacts had to occur after bees received food from first-order receivers.
(iii) nurse bee if the bee was observed *entering* (>4 sec) *brood* or *pollen cells* (Rösch, 1925; Lindauer, 1952; von Frisch, 1967) or *fanning* on brood comb (Winston, 1987).

Even though in particular cases one can not be sure, that a bee performing one of these behaviours belongs to the corresponding group, an analysis based on these criteria's provides a good general representation of the distribution of bees among the three main worker castes.

To compare the behaviour of bees that received high quality food, low quality food and average workers, we analysed the following behaviours or states:

(a) States (% of total duration): walking, standing, entering a honey cell, entering a brood cell, entering a pollen cell, dancing.
(b) Frequency of behaviours (per 10 min): trophallactic contacts, offering contacts, begging contacts, honey cell inspections, brood cell inspections, pollen cell inspections.
(c) Duration of behaviours (in seconds): offering contacts, begging contacts.
(d) Position (% of total duration): delivery area, brood area, honey area, position of the 1st and the 2nd trophallaxes (Fig. 1).

To get a general estimation of the activity of second-order receivers and average bees, we calculated an activity index, which is the time walking divided by the total time the bee was walking and standing. All filmed observations were recorded with the OBSERVER 3.0 program (Noldus, Wageningen, the Netherlands).

Estimation of trophallactic activity

To get a general estimation of the trophallactic activity of hive bees under the two reward conditions, we filmed six 8 x 10 cm rectangles for 1 min with a digital camera. Of these six rectangles, three were filmed on each side of the hives, one in the lower part of the hive (delivery area and brood area), one in the middle part of the hive (brood area) and one in the upper part of the hive (honey area). The filming of all 6 rectangles for 1 minute constituted one sampling period. The area filmed during one sampling period represents 16 % of the total comb area. The recordings were later watched once at normal speed by one observer and all trophallactic contacts were counted.

Statistical analysis

For most analyses, we used general linear models (GLM) in SPSS 12.0. We mostly used both treatment and colony (hive 1 and 2) as explanatory variables to test for effects on the dependent variable. The treatments were (1) H treatment, (2) L treatment and (3) average worker. Cases were only H and L treatments were compared are indicated. We pooled the data of average workers observed under both reward conditions because we found no significant differences between the two groups of workers (not shown). When we tested data sets several times, we corrected for multiple testing and adjusted the significance level using the sequential Bonferroni method (Sokal and Rohlf, 1995). Values of $p < 0.05$ after correction are indicated with one asterisk, results no longer significant are indicated with two asterisks. To test for differences in the position data and the cell inspection data between the 3 bee groups, we used non-parametric statistics because the assumptions for parametric statistics were not met. Descriptive statistics are given as mean ± SE (standard error) or median [quartiles]. All tests were two tailed.

Results

We observed 54 second-order receivers and found caste specific behaviours in 27 bees (13 of 30 in the L treatment; 14 of 24 in the H treatment). 16 (59.3 %) of the identified bees performed nurse duties (mean time in brood or pollen cell: 204 ± 57.8 sec, N = 16; mean time fanning: 83 sec, N = 2), 5 (18.5 %) performed food processor duties (duration of unloading contacts: 18.4 ± 3.8 sec), 6 (22.2 %) performed forager duties (3 bees followed between 2 and 5 dances; 2 bees danced; 3 bees left the hive at least once during recording (2 were numbered foragers). These proportions were almost identical in the H and the L treatment (Fig. 2).

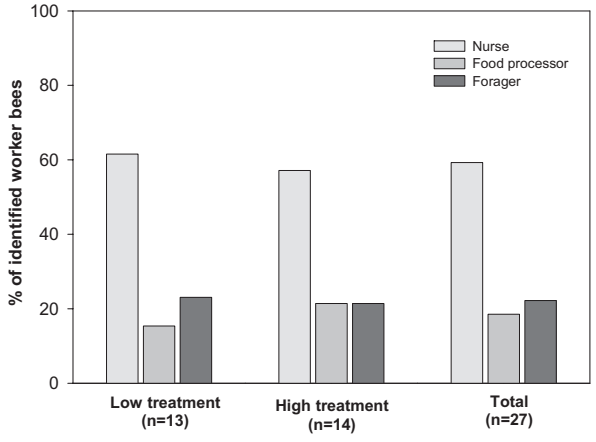

Figure 2. The percentage of second-order receivers identified as nurse bees, food processors or foragers of all identified bees, L treatment bees and the H treatment bees.

Behavioural observations

We found a significant positive relation between the duration of the 1st (23.3 ± 1.04 sec, N = 53) and the 2nd (11.8 ± 1.37 sec, N = 58) trophallactic contact but no effect of treatment (L and H) or colony (GLM: 1st troph. x 2nd troph.: $F_{1,53} = 5.25$, $p = 0.026$; treatment x 2nd troph.: $F_{1,53} = 0.58$, $p = 0.45$; colony x 2nd troph.: $F_{1,53} = 0.51$, $p = 0.481$) was found. All 1st trophallaxes took place in the delivery area, but only 40 % (H treatment) to 37.9 % (L treatment) of the 2nd trophallaxes took place in this area. A substantial proportion of 2nd trophallaxes, between 55 % (H treatment) and 48.3 % (L treatment), took place in the brood area. Between 5 % (H

treatment) and 13.8% (L treatment) took place in the honey area (Fig. 3).

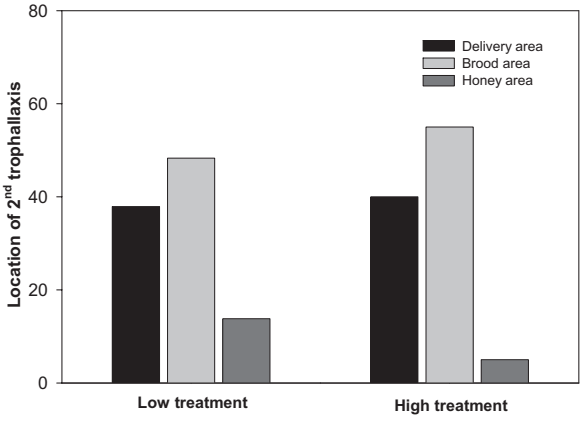

Figure 3. The area in which the trophallaxis between first-order receivers (food processor bees) and second-order receivers took place (2nd trophallactic food transfer).

When we compared the activity of bees of the H treatment, the L treatment and the average workers, we found that both H treatment bees and L treatment bees were more active than the average worker, while there was no difference between H treatment bees and L treatment bees (GLM: treatment x activity: $F_{2,82}=8.57$, $p<0.001$*; colony x activity: $F_{1,82}=1.4$, $p=0.24$; Fig. 4. Post hoc Tukey-Kramer comparison between groups: H vs. average worker: $p=0.001$; L vs. average worker: $p=0.006$; H vs. L: $p=0.6$). When we tested for the effect of treatment and colony on the number of trophallactic contacts/10 min, we again found that H and L treatment bees had significantly more trophallactic contacts than average workers, while there was no difference between the H and L treatment groups and the two colonies (GLM: treatment x troph./10 min: $F_{2,84}=18.4$, $p<0.001$*; colony x troph./10 min: $F_{1,84}=1.1$, $p=0.3$. Post hoc Tukey-Kramer comparisons between treatments: H vs. average worker: $p<0.001$; L vs. average worker: $p<0.001$; H vs. L: $p=0.87$). We then tested whether this difference in the number of trophallactic contacts between groups was due to differences in the number of offering contacts or begging contacts or both. When we compared the number of offering contacts between groups we found that H and L treatment bees had more offering contacts than average workers and a significant positive relation with the number of begging contacts (bees having more offering contacts also had more begging contacts), but no effect of colony (GLM: treatment x troph. offering/10 min: $F_{2,84}=14.9$, $p<0.001$*; troph. begging/10 min x troph. offering/10 min: F1,84 = 6.74, p = 0.011*; colony x troph. offering/10 min: $F_{1,84}=1.07$, $p=0.3$; Fig. 5. Tukey-Kramer comparisons: H vs. average worker: $p<0.001$; L vs. average worker: $p<0.001$; H vs. L: $p=0.72$). The number of begging contacts, on the other side, did not differ neither between bee groups nor between colonies (GLM: treatment x troph. Begging/10 min: $F_{2,84}=2.89$, $p=0.061$; colony x troph. begging/10 min: $F_{1,84}=0.32$, $p=0.57$; Fig. 5). In both the H treatment and the L treatment bees had more offering contacts than begging contacts (GLM: H treatment: type of troph. x number of troph.: $F_{1,40}=7.5$, $p=0.01$*; colony x number of troph.: $F_{1,40}=3$, $p=0.091$; L treatment: type of troph. x number of troph.: $F_{1,52}=7.15$, $p=0.01$*; colony x number of troph.: $F_{1,52}=0.54$, $p=0.46$; Fig. 5).

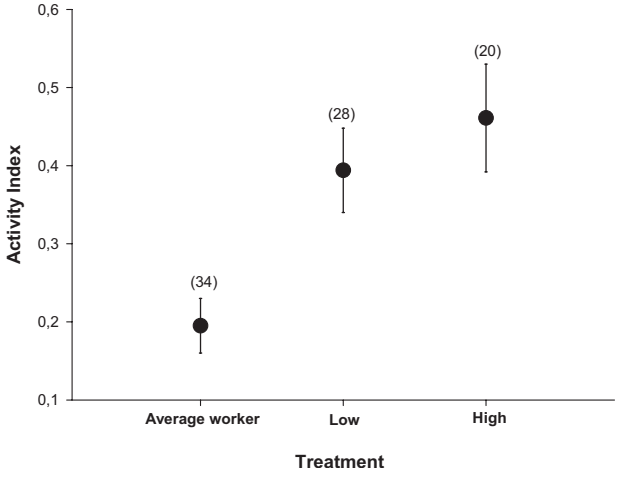

Figure 4. The activity index (mean ± SE) of bees from the L treatment, the H treatment and average bees. Numbers above bars represent the number of bees.

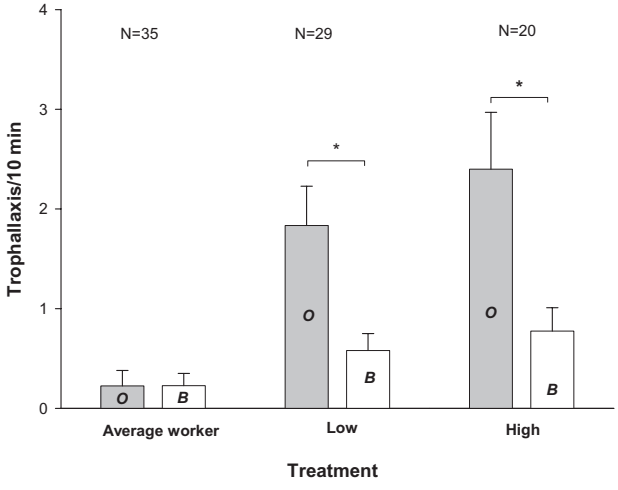

Figure 5. The number of offering contacts (G; grey) and begging contacts (R; white) per 10 minutes (mean ± SE) of bees from the H treatment, the L treatment and average bees.

We also tested whether the mean duration of trophallactic contacts differed between the H and L treatment bees. We found no differences between both groups in the mean duration of offering contacts and begging contacts that the second-order receivers had during the filming (GLM: offering contacts: treatment x duration offering troph.: $F_{1,36}=0.4$, $p=0.53$; H treatment: 4.4 ± 1.02 sec, L

treatment: 3.5 ± 0.51 sec; colony x duration offering troph.: $F_{1,36} = 0.88$, $p = 0.354$; begging contacts: treatment x duration begging troph.: $F_{1,21} = 1.48$, $p = 0.24$; H treatment: 12.2 ± 5.97 sec, L treatment: 4.6 ± 1.95 sec; colony x duration begging troph.: $F_{1,21} = 0.002$, $p = 0.97$).

Only 2 of 84 filmed bees inspected pollen cells during the observation period. Brood cell inspections (35 of 84 bees) and honey cell inspections were more frequent (21 of 84 bees). We found significant differences between the 3 bee groups in both brood cell inspection frequencies (Kruskal-Wallis ANOVA: $\chi^2 = 7.64$, $df = 2$, $p = 0.022$) and honey cell inspection frequencies (Kruskal-Wallis ANOVA: $\chi^2 = 9.84$, $df = 2$, $p = 0.007$). Post-hoc Dunn tests showed that average workers inspected fewer brood cells than H treatment bees, but more honey cells than L treatment bees (Table 1).

Table 1. Dunn's test for multiple comparisons of frequencies. Frequencies of brood and honey cell inspections and percentages of observation time in delivery area, brood area and pollen area between bees of the L group, H group and average workers.

Comparisons	*N*	*mean rank difference*	*critical value*	*p*
Brood cell inspections				
L vs. H	20/29	3.45	14.87	n.s.
L vs. average worker	29/35	11.85	12.85	n.s.
H vs. average worker	20/35	15.14	14.34	$p < 0.05$
Honey cell inspections				
L vs. H	20/29	6.37	12.61	n.s.
L vs. average worker	29/35	14.53	10.90	$p < 0.05$
H vs. average worker	20/35	8.16	12.17	n.s.
Delivery area				
L vs. H	20/29	4.22	16.59	n.s.
L vs. average worker	29/35	25.69	15.99	$p < 0.05$
H vs. average worker	20/35	21.57	14.33	$p < 0.05$
Brood area				
L vs. H	20/29	1.71	16.59	n.s.
L vs. average worker	29/35	19.8	15.99	$p < 0.05$
H vs. average worker	20/35	18.09	14.33	$p < 0.05$
Honey area				
L vs. H	20/29	3.46	16.59	n.s.
L vs. average worker	29/35	26.7	15.99	$p < 0.05$
H vs. average worker	20/35	3.2	14.33	$p < 0.05$

Comparison between identified and unidentified bees

The distribution of bees among the three worker castes found in identified bees is probably not representative for all second-order receivers. To find evidence for behavioural differences between identified and unidentified bees, we compared activity (GLM: group x activity: $F_{1,48} = 1.873$, $p = 0.178$; treatment x activity: $F_{1,48} = 0.177$, $p = 0.68$; colony x activity: $F_{1,48} = 4.87$, $p = 0.033$**), the total number of trophallaxes per 10 min (GLM: group x troph/10 min: $F_{1,49} = 0.71$, $p = 0.41$; treatment x troph/10 min: $F_{1,49} = 0.431$, $p = 0.52$; colony x troph/10 min: $F_{1,49} = 2.73$, $p = 0.105$) and the time spent in the brood area (GLM: group x brood: $F_{1,49} = 1.41$, $p = 0.24$; treatment x brood: $F_{1,49} = 2.25$, $p = 0.14$; colony x brood: $F_{1,49} = 15.5$, $p < 0.001$*; the colony effect is caused by a smaller brood area in hive 2) between these two groups of bees and found no differences.

Position of bees

Behavioural differences between the different bee groups may also concern the position of the second-order receiver during the observations. Therefore we compared the percentage of the observation time bees spent in the three most important hive areas, the delivery area, the brood area and the honey area (Table 1). We found that bees of the H and the L group spent significantly more time in the delivery area than average workers (Kruskal-Wallis ANOVA, $\chi^2 = 24.4$, $N = 84$, $p < 0.001$; H group: 20.17 % [0, 59.5], L group: 3.86 % [0, 61.6], average worker: 0 % [0, 0]; Table 1). They also spent more time in the brood area compared to average workers (Kruskal-Wallis ANOVA, $\chi^2 = 13.11$, $N = 84$, $p = 0.001$*; H group: 56.24 % [25.4, 81.9], L group: 90.74 % [5.4, 99.48], average worker: 0 % [0, 63.27]; Table 1). But H and L treatment bees spent less time in the honey area than average bees (Kruskal-Wallis ANOVA, $\chi^2 = 25.3$, $N = 84$, $p < 0.001$; H group: 0 % [0, 9.18], L group: 0 % [0, 1.99], average worker: 49.22 % [2.2, 99.1]; Table 1). Table 1 shows the results of the pair-wise Dunn tests for multiple-comparisons.

General trophallactic activity

We recorded 11 sampling periods (6×1 min per sampling period), 4 under high quality food conditions and 7 under low quality food conditions. There were no effects of food condition and colony on the total number of trophallaxes observed during a sampling period (GLM: treatment x troph.: $F_{1,11} = 0.074$, $p = 0.792$; colony x troph.: $F_{1,11} = 0.0$, $p = 0.99$; in total 10.1 ± 0.99 trophallaxis per sampling period, range: 6–16). Using these values to estimate the average number of trophallaxes/bee in 10 min provides a value of about 0.25 trophallaxes per average worker in our colonies. Average workers recorded individually with

video had 0.5 ± 0.15 trophallaxes in 10 minutes. One reason for the difference may be that the sampling of many bees at the same time (scan sampling) made it more difficult to see all short contacts than when filming one single bee for a longer period.

Discussion

On the way from the delivery area to the honey cells, food processors feed various bees which indicates that nectar is distributed rapidly amongst hive bees (von Frisch, 1923; Rösch, 1925; Seeley, 1989). However, it was not yet known what kind of bees receive food from food processors. In our study, we identified bees performing foraging duties (22.2 %), food-processing duties (18.5 %) and mainly nurse duties (59.3 %) as second-order receivers. This shows, that hive bees of the three major worker castes receive food samples within a few minutes after the nectar has been carried to the hive. These results help to explain how small quantities of food collected by foragers can become widely distributed among the members of different worker castes of a colony within a few hours (Nixon and Ribbands, 1952). Second-order receivers of unknown sub-caste showed similar trophallactic behaviours and locomotion activity as the identified bees. The conclusion that nurse bees are the main recipients of food from food processors is also supported by the findings that most trophallaxes between food processors and second-order receivers took place in the brood area and that second-order receivers subsequently spent most of their time in the brood area. It also accords with observations showing a general tendency for food to pass from older bees to younger bees within colonies (Free, 1957; Crailsheim, 1998). The young nurse bees, normally 3–11 days old, are responsible for preparing nutrients from pollen and distribute the nutritionally valuable proteins produced by their hypopharyngeal glands, nectar and honey mainly to larvae but also to other hive bees (Winston, 1987; Crailsheim, 1998). 22.2 % of the identified second-order receivers performed foraging duties. This shows that foragers can obtain information cues about the current foraging opportunities (such as floral scents) not only from foragers, but also via food processors.

The second-order receivers were much more active than the average worker bees during the observation period. The low activity of our average workers accords with the high rate of inactivity found in other studies (Rösch, 1925; Lindauer, 1952; Seeley, 1995) and may be more pronounced in our study, because the study has been performed at the end of the flowering season. The increased activity of the second-order receivers was found to correlate with a high trophallactic activity. While the average number of trophallaxes/10 min was between 0.25–0.5 in average bees, second-order receivers had almost 4. This difference between second-order receivers and average worker bees was mainly due to a high number of trophallactic-offering contacts (Fig. 5). In other words, the liquid food received from the food processors is rapidly distributed to other hive workers. Seeley (1989) found that active food processors (first-order receivers) had between 4.3 and 10.5 offering contacts per 10 minutes, depending on the nutritional state of the colony (calculated from his Table 3). These result and our own suggest that the rapid distribution of food within a colony may be the result of a very high trophallactic-offering activity of a relatively small proportion of bees in a colony. However, since we filmed on average only about 10 min per bee, it is not possible to say for what time period second-order receivers show this increased behavioural activity.

Results further show, that the 1st trophallaxes (between foragers and food processors) are about twice as long as 2nd trophallaxes (between food processors and second-order receivers), while 2nd trophallaxes are about twice as long as 3rd trophallaxes (offering contacts of second-order receivers). Bees retain food for themselves or for additional offerings. This coincides with results obtained in a laboratory study (Goyret and Farina, 2005), which found a similar reduction in transfer time from the 1st to the 2nd trophallaxis and a reduction in the transfer rate of about 35–40 %. The transfer rates of the 1st and the 2nd trophallaxis correlated positively. As there is a positive relation between transfer rate and food source profitability (Farina and Núñez, 1991; Tezze and Farina, 1999), bees momentarily not involved in foraging potentially obtain quantitative information about the profitability of the exploited food sources from hive-bees. This may affect the decision to start or resume foraging activities or it may cause adjustments of in-hive activities related to nectar processing.

It has often been shown, that the food source profitability, either expressed in terms of nectar flow rate or sucrose concentration, affects in-hive behaviours such as dancing (Lindauer, 1948; von Frisch, 1967; Seeley, 1995) or trophallactic behaviour of foragers (Farina, 1996; De Marco and Farina, 2001) and of food processors (Pírez and Farina, 2004). The changes in forager and food processor behaviours according to food source profitability can be seen as part of a colony level response to the current environmental conditions (Seeley, 1995). In our study, we found no significant effect of sucrose concentration on the second-order receiver behaviours that were analysed. Our *ad libitum*-feeders did not allow the adjustment of the nectar flow rate. The nectar flow rate has been shown to affect food processor behaviour previously (Pírez and Farina, 2004). It is possible that our bees evaluated the low sucrose concentration food as a high quality food source. We observed that a substantial number of foragers showed recruitment dances even when foraging at the food source with 13 % sucrose concentration. This indicates low thresholds for dancing, caused by a lack of alternative food sources at this late stage of the flower season (Seeley, 1995). In summary, food source profitability has an effect on the nectar flow

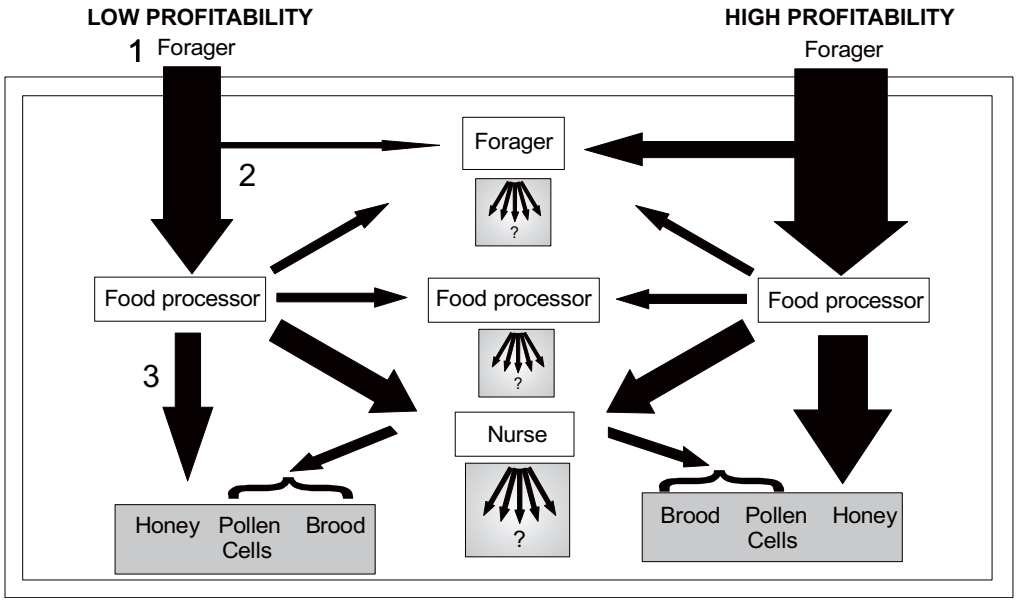

Figure 6. The schematic flow of nectar of a single forager load in a honeybee colony in late summer, coming either from a food source of high or low profitability (either in terms of nectar flow or sugar concentration). The width of the arrows reflects roughly the estimated amount of nectar flowing along its route. 1) From Núñez, 1966; 2) Farina, 1996, De Marco and Farina, 2001; 3) from Pírez and Farina, 2004.

pathways, but probably not at all stages. Fig. 6 graphically shows the flow of nectar inside the honeybee colony in late summer and its relation to food source profitability. (1) The width of the arrows coming from the returning foragers reflects the positive dependence of the crop load on food source profitability (Núñez, 1966, 1970). (2) Foragers exploiting high profitability food sources perform more offering trophallaxes upon arrival at the hive and interact with other foragers more frequently (Farina, 1996; De Marco and Farina, 2001). (3) Subsequently, food processors receiving food from foragers exploiting high profitability food sources are more likely to go directly to the storing area and less likely to engage in offering contacts only compared to food processors under low reward conditions (Pírez and Farina, 2004). With the exception of the time spent in the brood area (where we found a difference between the two colonies due to a smaller brood area in H2), we found no effect of colony with respect to the main results.

Food collection by honeybee colonies is a rather complex process, which involves bees of different subcastes and, as a consequence of the numerous interactions, creates a food network. It is important to mention that aspects of food sharing potentially depend on many more factors such as nutritional state of a colony, amount of brood, nectar influx, season and colony size (Free, 1959; Istomina-Tsvetkova, 1960; Howard and Tschinkel, 1980; Seeley, 1989). The relative amount of nectar that is transported either to honey cells or is fed directly to other bees, for example, may be very variable, depending on these factors.

Food sharing seems much more extensive than would be required merely to prevent individuals from starving when food is available (Ribbands, 1953). Hence, it has been suggested that the majority of trophallactic contacts serve communicational purposes rather than being food transfer attempts (Korst and Velthuis, 1982). The numerous social interactions have a potential benefit in the spread of information through the colony (Ribbands, 1953; Crailsheim, 1998; Grüter et al., 2006). Information cues and signals present in the processed and shared nectar, such as food scents, sucrose concentration or pheromones can affect the behaviour of potentially all hive bees (Wilson, 1971; Pankiw et al., 2004; Grüter et al., 2006). In our study, 49.5 % of all trophallaxes of second-order receivers and 44 % of all trophallaxes in average workers were shorter than 1.5 seconds. These contacts are normally too short for effective food transfer (Farina and Wainselboim, 2001b). But even when trophallactic interactions are too short to guarantee food transfer, they may have important informational implications. These contacts (i.e. search time for a receiver bee) cause time delays which in turn offer opportunities for information acquisition about environmental conditions and colony work allocation (Lindauer, 1948; Seeley, 1995). Natural selection may favour a high trophallactic activity and extensive circulation of liquid food, if this leads to better informed hive individuals which in turn allow for a more adequate colony level response to present internal and external conditions.

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