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Why do honey-bee (*Apis mellifera*) foragers transfer nectar to several receivers? Information improvement through multiple sampling in a biological system

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Abstract The task of nectar foraging in honey-bees is partitioned between foragers and receivers. Foragers typically transfer a nectar load in the nest as sub-loads to several receivers rather than as a single transfer. Foragers experience delays in finding receivers and use these delays to balance the number of foragers and receivers. A short delay results in the forager-recruiting waggle dance whereas a long delay results in the receiver-recruiting tremble dance. Several nectar transfers increase the cost of this system by introducing additional delays in finding extra receivers. We tested four hypotheses to explain the occurrence of multiple transfer. We found no evidence that multiple transfer is due to different crop capacities of foragers and receivers or that it results from extensive trophallactic interactions with nest-mates. Receiver bees frequently evaporate nectar in their mouthparts to hasten the production of honey. The suggestion has been made that multiple transfer is driven by receivers who take partial loads from foragers to enhance nectar evaporation. An alternative suggestion is that foragers drive multiple transfer to gain better information on the balance of foragers and receivers. Multiple sampling of the delay in finding a receiver reduces the standard deviation of the delay mean and so provides foragers with better information than is provided by a single delay. The enhanced-evaporation hypothesis predicts that receivers break foragers' first transfer whereas the information improvement hypothesis predicts foragers break their first transfers. Furthermore, only the information improvement hypothesis predicts a high level of multiple receptions. Data on transfer break-off and receiver behaviour strongly support the information improvement hypothesis and reject the enhanced-evaporation hypothesis. We suggest that multiple transfer is an adaptive sampling mechanism,

which improves foragers' information on colony work allocation, and that multiple sampling is a common feature of social insect societies.

Keywords Honey-bee · Nectar transfer · Receiver · Foraging · Information improvement

Introduction

Adaptive organisation and integration depend upon information and communication (Detrain et al. 1999). Nowhere is this more pertinent than in the organisation of the activities of the many individuals that comprise an insect society (Seeley 1995). Foraging is one vital area of colony life that uses information to co-ordinate individual activities. Efficient organisation of foraging normally involves two complementary processes. One is directing foragers to profitable food patches, via mechanisms such as tandem running, pheromone trails or the waggle dance of honey-bees (Wilson 1971; Hölldobler and Wilson 1990; Seeley 1995). The second is adjusting the total foraging effort to the colony's ability to use, process or store food (Seeley 1995; Anderson and Ratnieks 1999). In the honey-bee, for example, nectar collected by foragers is transferred to receiver bees, who then store it in cells. Efficient nectar collection, therefore, requires both the direction of unemployed foragers to good food patches and a balance between the work capacities of nectar foragers and receivers.

Waggle dances made by honey-bee foragers function in both processes. The dance directs foragers to profitable food patches and, because the bees recruited were previously unemployed foragers (Seeley 1995), it also functions in balancing the work capacities of foragers and receivers (Anderson and Ratnieks 1999). Clearly, the waggle dance, and more generally whether or not a forager should dance, is at the heart of efficient foraging organisation in the honey-bee (Seeley 1995). As a result, there should be strong selection making the ability of individual foragers to dance or not appropriate to the

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conditions both inside and outside the nest. Foragers transfer nectar to receivers, a partitioning which causes delays, both in finding a transfer partner and during the transfer itself. The delays experienced by foragers in finding a receiver provide the forager with information on colony work organisation, specifically the relative work capacities of foragers and receivers. A forager bases her decision whether to waggle dance on the delay she experiences in finding a receiver. A short delay indicates that the work capacity of foragers exceeds that of receivers and a waggle dance is usually performed, recruiting further foragers to the flower patch (Seeley 1995). A long delay, indicating that nectar collection exceeds the work capacity of receivers, usually causes the forager to perform another type of dance, the tremble dance, which recruits more receivers (Seeley 1992; Kirchner and Lindauer 1994). Delays in finding a transfer partner are, therefore, of key importance in regulating colony work organisation.

Transfer delays impose an unavoidable ergonomic cost (Ratnieks and Anderson 1999). Surprisingly, therefore, foragers normally transfer nectar to several receivers, with reported means of 1.9–2.7 transfer partners per foraging trip (range 1–5) (Kirchner and Lindauer 1994). Given that transfers cause unavoidable delays, and that these delays reduce the time a bee can work, why does multiple transfer occur? One hypothesis for the benefit of multiple transfer focuses on receivers. Before receivers deposit nectar into cells they often use movements of their mouthparts to expose portions of their nectar load to the air, thereby evaporating water and speeding up the production of honey (Park 1925; Maurizio 1975). Ratnieks and Anderson (1999) suggest that because smaller volumes of nectar have a higher surface area to volume ratio, the ripening process may be more efficient with smaller loads. They also suggest that foragers are responsible for multiple transfer to gain better information on the relative work capacities of foragers and receivers. Multiple transfer provides foragers with several measurements of the delay in finding a receiver. This reduces the error associated with single measurements of delay and so provides improved information by increasing sample size. Here, we test four hypotheses concerning multiple transfer.

Alternate hypotheses for multiple transfer and their predictions

(1) *Crop size*

If receiver bees have smaller crops, multiple transfer could be a consequence of receivers being unable to physically handle as much nectar as older foragers.

- Prediction: bees of receiver age, circa 10–16 days, should have smaller crops than bees of foraging age, circa 20 days (Seeley 1995).

(2) *Transfers to other types of receiving bee*

Foragers give nectar to dance followers as well as to receivers (Seeley 1995). Trophallactic interactions may also occur between foragers (von Frisch 1967; Farina 1996). Therefore, what appears to be multiple transfer to receivers could in fact be a single transfer to a receiver plus additional transfers to dance followers.

- Prediction: a high proportion of transfers from nectar foragers are to other foragers.

(3) *Enhanced evaporation*

Receivers cause multiple transfer by not filling their crops.

- Prediction: this hypothesis predicts that receivers drive multiple transfer and so should be the partner breaking off transfer. Foragers' first transfers should be broken off mainly by receivers and receivers should neither receive multiple nectar loads nor fill their crops.

(4) *Information improvement*

By making several transfers, foragers gain a more accurate estimate of the labour allocation in the nectar collection and storage system (Ratnieks and Anderson 1999).

- Prediction: this predicts that multiple transfer is forager driven. Foragers' first transfers should be broken off mainly by foragers and receivers should receive multiple nectar loads.

Hypotheses 3 and 4 do not predict that all foragers' first transfers will be broken by receivers or foragers, respectively. A receiver who is full, or nearly full, when receiving nectar would break a foragers' first transfer, irrespective of whether or not the information hypothesis is correct. Thus, some foragers' first transfers will be broken by receivers simply because the receiver has a full crop. Enhanced evaporation predicts that receivers should usually break foragers' first transfers. If the enhanced-evaporation hypothesis is correct, foragers will be less like to break off their first transfer because this hypothesis requires that receivers typically accept less nectar than is offered by a newly returned forager. Under this hypothesis, a forager is only expected to break a transfer when she has less nectar in her crop than the receiver wants. The enhanced-evaporation hypothesis also predicts that receivers will not multiply receive. If receivers break off transfers to keep their crops less than full, they are not expected to receive additional nectar from foragers except when a forager only has a small quantity of nectar to give. The information improvement hypothesis predicts that receivers continue receiving nectar until they are full (or perhaps above a certain threshold capacity) and, therefore, multiple

Table 1 The enhanced-evaporation and information improvement hypotheses make opposing predictions about which transfer partner breaks foragers' first transfers and the existence of multiple receiving

	Who breaks foragers' first transfer?	Do receivers multiply receive?	Do receivers have a full crop?
Hypothesis 3: enhanced evaporation	Mainly receivers, some foragers	No (rarely)	No
Hypothesis 4: information improvement	Mainly foragers, some receivers	Yes (usually)	Yes

receiving is expected. Table 1 shows the contrasting predictions of the enhanced-evaporation and the information improvement hypotheses

Methods

Testing the predictions

Crop size

To determine whether crop size varies with age, a frame of cells containing pupae was removed from a queenright honey-bee (*Apis mellifera*) colony of mixed European race and put in an incubator (34°C). Newly emerged bees were paint marked on the thorax, with a different colour used for each of three consecutive 24-h emergence periods. After marking, the bees were returned to their natal hive.

To span the age of both receivers and foragers, bees 5, 10 and 20 days old were studied ($n=20$ for each group). Bees were recaptured, chilled for 5 min (5°C) and placed into a cylindrical holder (a modified drinking straw) with only the head protruding. After regaining consciousness, bees were fed a 2 M sucrose solution from a capillary tube. When a bee refused to accept more, she was left for 10 min and again offered solution. This was repeated until every bee had refused on two successive presentations. The bees were then killed by chilling (-3°C) and dissected. The crop, plus its contents, was then weighed to 0.1 mg.

Transfers to other types of receiving bee

Observations were conducted during July, August, and September 1999 using two queenright, two-frame observation hives (Seeley 1995) of mixed European race bees. Wooden entrance wedges were used to concentrate nectar transfer and dancing to one side of the hive (Seeley 1995). A plastic tube 40 cm long connected the hive to the outside. Colony 1 had approximately 10,000 workers, colony 2, 5,000 workers. Both colonies were free to forage naturally.

Receiving bees were identified by following a forager from when she entered the hive until her first transfer of nectar. Her transfer partner was a receiver. Receiving bees were sub-divided into those that were "true" receiver bees, that is those who store nectar, and those that received nectar for other reasons, such as dance followers. A "true" receiver often receives nectar from additional foragers (this study) but at the end of her receiving cycle she either goes to a storage cell to unload or to an uncrowded area of the nest where she manipulates the nectar with her mouthparts (see Park 1925 for a description). Transfers to dance followers are typically brief and the receiving bee usually stays in the dance arena for a short period before disappearing into the entrance tube.

Enhanced evaporation versus information improvement

To test the predictions made by hypotheses 3 and 4 (Table 1), the behaviour of incoming foragers was recorded on video using a Canon 3CCD digital camcorder with a 5.5–88 mm ×16 zoom lens. Returning foragers were followed from when they came into view in the entrance tube until either after their second transfer of nectar to a receiving bee or 10 min without a second transfer (but after a

first transfer) had elapsed. This gave a record of the first transfer of nectar from a forager to a receiving bee and showed whether a forager made a second transfer. Knowing whether a forager made a second transfer was important in showing that a forager did not break the first transfer simply because she was empty. It also confirmed that multiple transfer occurred in this study. We did not measure the total number of transfers per forager, since such data were not needed to distinguish between the two hypotheses. Receivers were identified by following incoming foragers until their first transfer. The first transfer partner was the receiver. The behaviour of the receiver was recorded on video until the bee either began to evaporate nectar using her tongue or deposited the nectar into a cell. If dance followers or pollen foragers were the recipients of nectar from the forager, these were not followed further. In this way we recorded the final transfer of receiver bees and could determine which partner broke transfer. Furthermore, this gave quantitative data on the occurrence of multiple receiving.

The video record of forager-receiver transfers was examined in slow motion to determine which of the two parties was responsible for terminating the transfer. The transfer begins with the forager opening her mandibles and forcing a drop of nectar out over the upper surface of the proximal portion of her tongue. The receiver approaches the forager and extends her tongue to full length, taking the nectar from the forager's tongue (Park 1925). If it is the receiver who breaks off the transfer, she retracts her tongue and moves away from the forager. However, when the forager terminates the transfer, she moves away from the receiver, who continues to protrude her tongue.

To determine how full receivers' crops were, a modified two-frame observation hive was used. The glass front was replaced with a wooden frame fronted by 0.2-mm transparent polythene. A series of vertical cuts into the sheet allowed receiver bees to be removed. Finding nectar transfer partnerships and identifying the bee with its proboscis extended identified receiver bees. The receiver was then followed until she had finished receiving and begun walking to the top of the hive. She was removed through one of the cuts in the polythene sheet, dissected and the crop was removed and weighed. The concentration of the crop contents was measured using a Bellingham and Stanley Field Refractometer. This was repeated for 20 receivers. Since a receiver could return to the transfer area to take on further nectar, the estimate of crop content provided by this method is likely to be an underestimate.

Results

Crop size

There were no significant differences among the mean crop weights of 5, 10 and 20-day-old bees (Fig. 1; one-way ANOVA, $F=0.55$, $df=2,57$, $P=0.582$; overall mean=0.049 g, SE=0.00157 g, $n=20$ for each age group).

Transfers to other types of receiving bee

Figure 2 shows the behaviour of 230 receiving bees in hive 1 and 114 in hive 2. Both hives showed the same

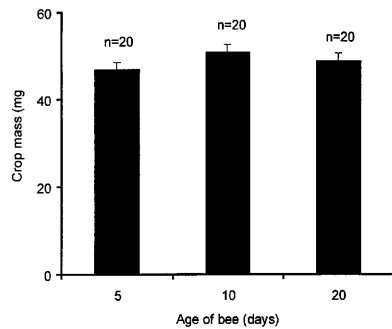


Fig. 1 Crop weight of bees satiated with 2 M sucrose solution (error bars 1 SD)

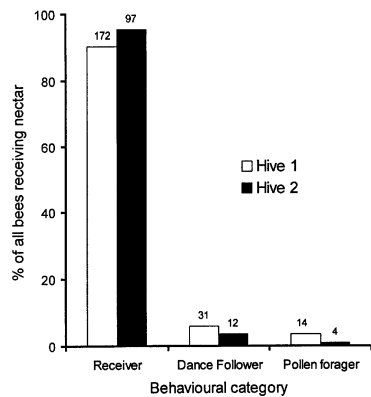


Fig. 2 Activities of bees receiving nectar from foragers. Across both hives only 8.0% of bees receiving nectar were dance followers or pollen foragers. Numbers above the bars are the numbers of bees observed

general pattern. The non-receiver categories of receiving bees (dance followers and pollen foragers) accounted for only 8.0% of transfers summed across both hives. In the course of following foragers into the hive, five foragers from hive 1 and none from hive 2 (1.5% of all foragers) were seen to deposit their nectar load without transferring to a receiver, that is without the occurrence of task partitioning (difference between hives not significant, Yates-corrected $\chi^2=1.18$, $P>0.05$).

Enhanced evaporation versus information improvement

There were no significant differences between the two hives as to which partner broke off transfer for either foragers' first transfers or receivers' last transfers (Fig. 3; foragers' first transfers, $\chi^2=0.889$, $df=1$, $P=0.889$; receivers' last transfers, $\chi^2=0.476$, $df=1$, $P=0.476$). Data were therefore combined across hives. Ninety-one of 133 (68%) foragers' first transfers but only 12 out of 40 (30%) of receivers' final transfers were terminated by the forager. This difference was highly significant ($\chi^2=18.843$, $df=1$, $P<<0.001$). Eighty-four percent of foragers (112 of 133) were observed to transfer nectar

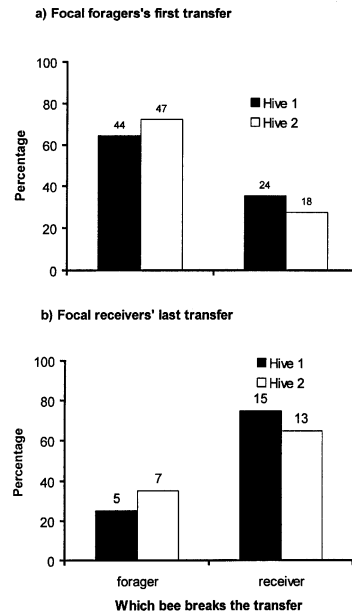


Fig. 3 Break off in transfer on foragers' first transfer (a) and receivers' last transfer (b). There are no significant differences between the two hives, and in total 68% of foragers first transfers were broken off by the forager and 70% of receivers' first transfers were broken off by the receiver. Numbers above the bars are the numbers of bees observed

more than once. We did not count the actual number of transfers, but the occurrence of multiple transfer is comparable to previous studies (e.g. Kirchner and Lindauer 1994) and was occurring in this study. Receivers received a mean of at least 1.6 nectar loads from foragers ($n=20$, range 1–4), showing that multiple receiving took place.

There was no significant difference between the mean crop capacity of receivers and the mean crop capacity of 10-day-old bees determined above (receiver mean=0.0414 g, $SD=0.0093$ g, $n=20$; 10-day-old mean=0.0412 g, $SD=0.0104$ g, $n=20$; $t=1.85$, $df=37$, $P>0.05$; mean concentration of receivers' nectar=44.04%, $SD=7.59\%$; concentration of 10-day-old bees' nectar=36%).

Discussion

Hypothesis 1: crop size

Crop content was not found to vary with age. Hypothesis 1, variable crop size, can, therefore, be rejected.

Hypothesis 2: transfers to other types of receiving bee

Hypothesis 2, that multiple transfer is in fact a single transfer to a receiver and transfers to dance followers and pollen foragers, is also rejected. Although nectar is transferred to bees other than true receivers, transfers to dance followers and pollen foragers together accounted for only 8.0% of all transfers. The transfers to pollen

foragers are presumably to provide them with energy for foraging, and are rare (2.7% of transfers). Transfers to dance followers or pollen foragers would need to be far more frequent than 8% for such transfers to non-receivers to account for the observed levels of multiple transfer (mean 1.9–2.7, range 1–5; Kirchner and Lindauer 1994; this study).

Hypotheses 3 and 4: enhanced evaporation versus information improvement

Foragers break off 68% of their first transfers to receivers. Because 84% of these foragers then went on to make at least one further transfer to a receiver within 10 min, transfer was not terminated because the forager had emptied her crop. In addition, receivers receive nectar from a number of foragers (a mean of at least 1.6, range 1–4, $n=20$) and fill their crops to a level comparable to that of bees fed to satiation. These data support the information improvement but not the enhanced-evaporation hypothesis.

It is important to reiterate that neither the enhanced-evaporation nor the information improvement hypothesis predicts that either foragers or receivers will break 100% of nectar transfers. For example, if foragers all have the same load and unload two half-loads to receivers, then half the full foragers will be unloading to half-full receivers. In this simple example, we would expect half of these transfers to be broken by the forager and half by the receiver, as the foragers become empty at approximately the same point that the receiver becomes full. Therefore, 25% of foragers' first transfers are broken by the "wrong" partner whichever hypothesis is correct. Further analysis of this question is premature before data are available on factors such as how full returning foragers are, how full receivers get and the crop capacity thresholds governing when transfers are broken. However, even this simple example shows that our data conform more closely to predictions when such additional factors are considered. Importantly, the information improvement hypothesis would have been falsified either if receivers had broken a high proportion of foragers' first transfers or if there had been a low incidence of multiple receiving, or both.

Receivers' last transfers provide further support for the information hypothesis. The proportion of foragers and receivers breaking this transfer is opposite to foragers' first transfers. The most parsimonious explanation for this pattern is that foragers drive multiple transfer by not filling receivers on their first transfer. Receivers, however, continue receiving nectar until they are full. A nearly full receiver topping up, therefore, does break transfer. Our data on receiver crop capacity support this argument.

Can foragers adjust their behaviour to gain better information on colony work allocation? A facultative system of multiple transfer would be advantageous, enabling foragers to reduce transfer costs if informational benefits are not required. Farina (1996) has found evidence for facultative changes in nectar transfer behaviour.

He simulated a nectar flow and as the availability of nectar in an automatic feeder rose, so the number of transfers per returning forager rose (from 1 to >2). He suggests that this is an alternate channel for communication regarding a nectar source. Transfers from foragers to nest-mates could "stimulate, by performing a higher frequency of nectar-sharing, a great number of experienced hive-mates to resume their visit to a known, previously exhausted nectar source." However, 92% of the transfers we observed were to receiver bees, which are known to be younger than foragers and are unlikely to be experienced hive-mates (Seeley 1995). Instead, we suggest that an increase in multiple transfer is a facultative and rapid reaction to a recent increase in nectar availability. Returning foragers need to ensure that the colony has a forager:receiver ratio that is suitable to efficiently exploit the profitable nectar source. An increase in the number of nectar transfers made by a forager can provide her with better information on the colony's work allocation status.

Task partitioning did not occur for 1.5% of nectar loads. In these cases, foragers did not appear to seek out a receiver but instead proceeded directly to a cell to deposit nectar. This is a novel result. In his study of nectar storage and ripening, Park states that he "failed to observe it [foragers depositing nectar into cells without transfer] in the many hundreds of cases which [were] observed." Further, Park cites only one anecdotal report of non-transfer prior to 1925 [A.C. Milner, reported by Latham (1907) in Park (1925)]. Although older literature frequently ignores the transfer of nectar from foragers to receivers (Park 1925), modern literature does not report, or fails to observe, the low incidence of non-transfer (e.g. Seeley 1995). Other studies of task partitioning have also revealed occasional non-transfer. The leaf-cutting ant, *Atta cephalotes*, partitions the transport of waste material from its fungal chambers to garbage chambers. Workers from the fungus chambers deposit particles outside the garbage chamber in caches from where it is taken to the garbage chamber by workers living there. This is almost certainly an adaptation for nest hygiene. But a minority (3%) of particles are taken directly into the garbage chamber without transfer (A.G. Hart and F.L.W. Ratnieks, unpublished data). In *Atta*, occasional breakdowns may be costly because workers entering the chamber become exposed to pathogens harmful to both ants and their symbiotic fungus (A.N.M. Bot, C.R. Currie, A.G. Hart, J.J. Boomsma, unpublished data). However, breakdowns in the honey-bee are unlikely to impose a disease cost. Perhaps non-transferring honey-bee foragers are workers in a transition phase from receiver to forager, or workers which for some reason have low thresholds for performing both behaviours.

Our findings, combined with modelling studies (Ratnieks and Anderson 1999), predict that foragers use a measure of average searching delay (i.e. time to find a transfer partner) as a basis for the decision whether to tremble dance, waggle dance or make no dance. The current data on the cause of tremble dancing is problematic. Kirchner and Lindauer (1994) supported the hypothesis

that a long total delay to find a receiver, consistent with the information improvement hypothesis, is the proximate cause of tremble dancing. However, their method relies on artificial conditions and a visual similarity between plots of total delay and the probability of tremble dancing. They compared the total transfer delays of foragers, called search times, with the probability of tremble dancing under experimental conditions (salt added to nectar, scent added, crowded feeder and isolated workers). The visual similarity between total delay time and the probability of tremble dancing appears to be largely an artefact of the abnormally long total delays, caused by high levels of multiple transfer (tenfold that of natural colonies), and a high probability of tremble dancing for the salt-added condition. Seeley (1992) found evidence of a relationship between initial search delay and the probability of performing each dance under more natural conditions. This relationship is not inconsistent with the information improvement hypothesis because a long initial delay may be a predictor of whether a forager will perform a tremble dance. A single delay is still an estimate of the true mean (likely to be highly variable), but this estimate can be improved with a larger sample. Seeley's study, however, did not account for multiple delays and so ignored this crucial element of the nectar transfer system. We suggest that a long average delay is likely to be the proximate cause of tremble dancing.

The benefits of information improvement must offset the costs of multiple delays. Kirchner and Lindauer's (1994) results on the searching and delivery times of foragers suggest that multiple transfer adds between 6.9 s [when few ($n=25$) foragers are present with mean transfers=2.3] to 11.4 s (when 200 foragers are present with mean transfers=1.9) to the time taken to singly transfer nectar. Single-transfer duration varies from 45.4 to 64.5 s. Therefore, multiple transfer should add between 15–17.5% to the total time required to transfer the same volume of nectar. This time increase is small compared to the time spent foraging. Published values of foraging trip duration range from 725 s (Seeley 1995, p. 95), to 2,418 s or more (Ribbands 1953). Assuming that foraging trips last 725 s and using 11.4 s as the transfer cost, then multiple transfer increases the foraging cycle from 789.5 s to 800.9 s, an increase of only 1.4%. This decreases as foraging trip duration increases. Computer modelling of the transfer process also suggests that the added time delay of multiple transfer is small (Ratnieks and Anderson 1999). Thus the ergonomic costs of introducing additional nectar transfer delays seem to be small compared to the benefits of improved information, which can be used to improve colony work allocation.

Our study presents two novel findings. First, we show that the system of nectar transfer from foragers to receivers in the honey-bee is, like other systems of task partitioning, subject to occasional exceptions. Second, we provide strong support for the information improvement hypothesis. Our work paves the way for further studies to provide direct evidence that forager bees who carry out more transfers have better information about colony work organisation

than those who carry out fewer transfers. For example, we predict that as the number of transfers made by a forager increases, she will make fewer errors in performing the appropriate recruitment dance, waggle or tremble, to match colony needs. Honey-bees have long been known to use their dances for communication (von Frisch 1967). Our study adds to this by suggesting that they use the principles of the central limit theorem in deciding when to dance. Sampling seems to occur elsewhere in social insects (Franks 1999). Harvester ants (*Pogonomyrmex barbatus*) base their decision on whether to join the colony's midden workforce on sampling other ants in the colony. If a focal ant encounters high numbers of garbage workers, she is more likely to switch tasks to the garbage heap. What is important in this system of task allocation is that the decision is based not on a single encounter but on multiple encounters (Gordon and Mendiabadi 1999). It seems likely that in other systems of task partitioning, individuals would be able to collate information such as the delay to find a transfer partner over a number of transfers and so improve their information. For example, in *Polybia occidentalis* nest building, pulp foragers can collect enough pulp for several builders and so multiple transfer of pulp occurs (Jeanne 1986). Whilst this occurs for reasons of work efficiency, this does not preclude the use of the information acquired on the relative work capacities of pulp collectors and builders. Further research may show that sampling is an important strategy used by social insects to gain better information about the work situation in their colony.

Multiple nectar transfer in the honey-bee is an overt, and thus easily studied, process by which a forager may gain additional information. Sampling may be less clearly seen in many other contexts. For example, a worker patrolling the nest may be collecting data on work allocation without performing explicit behaviours. Information is used in sophisticated ways by many social insects. Gathering that information is likely to involve equally sophisticated mechanisms.

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