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# Task Partitioning in Insect Societies. II. Use of Queueing Delay Information in Recruitment

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**ABSTRACT:** The collection and handling of colony resources such as food, water, and nest-construction material is often divided into subtasks in which the material is passed from one worker to another. This is known as task partitioning. If tasks are partitioned with direct transfer of material between foragers and receivers, queueing delays can occur as individuals search or wait for a transfer partner. Changes in environmental conditions and relative number of foragers and receivers affect these delays as well as colony ergonomic efficiency. These delays are used in recruitment in both honeybees and *Polybia* wasps. This study investigates the distribution of queueing delays and the information content and quality of those delays using a stochastic-simulation model. Information quality increases with colony size. When the relative proportions of foragers and receivers are suboptimal, the group in excess has better information. Individuals can increase information quality of delays by two mechanisms: averaging over consecutive trips and averaging over multiple transfers within a trip where direct transfer occurs. We suggest that multiple transfer occurs in the honeybee in order to improve information quality.

**Keywords:** social insects, task partitioning, ergonomics, queueing delays, information, honeybee.

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Efficient organization of work in insect societies requires frequent adjustments to the numbers of workers undertaking different tasks (Oster and Wilson 1978; Robinson 1992; Seeley 1995; Gordon 1989, 1996). One factor that makes adjustment necessary is change in external condi-

tions. As the profitabilities of food patches change, colonies should diminish foraging at the less profitable patches and recruit to the more profitable patches (Cosens and Tous-saint 1985; Pasteels et al. 1987; Seeley et al. 1991). Similarly, species that store food, such as the honeybee and seed harvester ants (Seeley 1995; Hölldobler and Wilson 1990), may adjust the total foraging effort in response to changes in the availability or cost of collecting food.

To function to the advantage of the colony, and thereby to enhance the inclusive fitness of individual workers, recruitment to food patches must be combined with an information source that causes adjustments that enhance colony efficiency (Seeley 1995). Honeybee nectar foragers use the delay experienced in locating a receiver to modulate recruitment dances (Lindauer 1961; Kirchner and Lindauer 1994; Seeley 1995, 1997). Foragers experiencing a short delay are more likely to perform waggle dances, thereby recruiting unemployed foragers, while those experiencing a long delay are more likely to perform tremble dances, thereby recruiting additional receivers (Seeley 1992, 1995, 1997). Intermediate delays typically result in neither dance being performed (Seeley 1992, 1995, 1997). Delays are also used by *Polybia occidentalis* wasps in harmonizing the work effort of the wood pulp and water foragers, who collect the nest-building materials, and the builders, who utilize those materials (Jeanne 1986b).

Tasks involving the collection and utilization of forage are frequently divided into subtasks in which material is passed from one worker to another. This is called task partitioning (Jeanne 1986a, 1991; reviewed in Ratnieks and Anderson 1999). When the collection and use of forage are partitioned, the queueing delays experienced by individuals will provide information about whether the number of receivers and foragers is optimal (Anderson and Ratnieks 1999a, 1999b). That is, the delays indicate whether the amount of forage being processed is close to the maximum for a given number of workers. Whichever group is in excess will experience longer average queues (Anderson and Ratnieks 1999b). Thus, a long delay "tells" a honeybee forager that a large amount of nectar is currently being collected because the delay is caused by over-

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working the receivers (Seeley 1992, 1995, 1997). However, the transfer delays experienced by individuals vary, even under constant external and internal conditions (Kirchner and Lindauer 1994; Seeley 1995). One factor causing this variation is the duration of any “searching” delay necessary for detecting a transfer partner when both are present in the transfer area (Seeley 1992, 1995; Seeley and Tovey 1994). A second factor, the focus of this study, is variation in the queueing delay itself. Queueing delays are an inescapable consequence of task partitioning with direct transfer and are caused by stochastic fluctuations in the rate of arrival of foragers and receivers in the transfer area. Although the delays diminish with increasing colony size (Jeanne 1986*b*; Anderson and Ratnieks 1999*b*), they occur even if the numbers of foragers and receivers are such that both groups satisfy the work capacity of the other.

This study focuses on the ability of individual workers to assess whether or not the relative proportions of foragers and receivers are in balance by using the information they acquire from their own queueing delays. Whereas our companion study (Anderson and Ratnieks 1999*b*) focuses on the mean queueing delays experienced by all workers and the effect this has on the ergonomic efficiency of the colony as a whole, this study focuses on the variation in the queueing delays experienced by individuals and the effect this has on the information available to individuals for determining colony status and recruiting appropriately. We examine the queueing delays experienced by individuals when the ratio of forager to receiver work capacity is optimal, close to optimal, and far from optimal, for a range of colony sizes. We then explore the ability of individuals to assess colony status from these queueing delays. Because these delays are used by honeybees to regulate the colony’s foraging and nectar processing capacity through recruitment (Kirchner and Lindauer 1994; Seeley 1992, 1995, 1997), minimizing error rates will be of selective importance.

We then examine two potential mechanisms for improving the quality of queueing-delay information by combining the information from several queueing delays. First, we examine averaging delays over multiple trips; and, second, we examine averaging over multiple transfers within one trip. Transfer of nectar to multiple receivers per foraging trip occurs in the honeybee (Kirchner and Lindauer 1994; Seeley 1992, 1995), and no convincing explanation is known for its significance. Our study examines the hypothesis that multiple transfer is adaptive in improving information quality.

We take information quality to refer to the variability (standard deviation) of queueing delays. Although “information quality” could have been defined in many other ways, standard deviation is most appropriate here. The bees are trying to gauge colony status by relying solely on

individual queueing delays as an indicator. Smaller standard deviations lead to a better reflection of the true mean, just as a sample mean more closely approximates the true mean.

### Simulation Model

The results were obtained by using the simulation model (with the same parameters and notation) in Anderson and Ratnieks (1999*b*). The only modification was to relax the assumption that a forager transfers her complete nectar load to a single receiver before the next foraging trip and that a receiver receives just one nectar load before leaving the transfer area. This modification was made in order to simulate multiple transfer.

When multiple transfer occurs, we assume that a forager splits her load of nectar into  $S_f$  subloads. In the transfer area, each forager pairs with a receiver and donates  $1/S_f$  of the load. She then pairs with another receiver, possibly after incurring a queueing delay, and donates another subload. This is repeated until the forager has paired with  $S_f$  receivers. Similarly, receivers receive  $S_r$  subloads before leaving the transfer area. Transfer durations are assumed to be proportional to the size of the subload. That is, transfer durations come from the distribution  $t(\cdot)/S_f$ , where both mean and variance of  $t(\cdot)$  are scaled by  $S_f$ . Thus, the mean transfer duration is  $\mu_r = \text{expected value of } t(\cdot)/S_f$ .

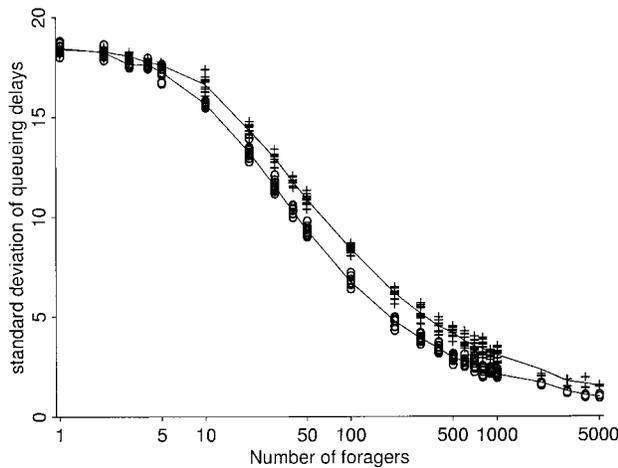
In addition to the parameters used in Anderson and Ratnieks (1999*b*), two more, concerned with the numbers of transfers per trip for foragers and receivers ( $S_f$  and  $S_r$ ), have been added. However, in the simulation part of this article, we only consider the case in which  $S_f = S_r$ , and thus we refer to  $S_f$  and  $S_r$  by a single parameter,  $S_w$ . This parameter set is used throughout with any changes indicated.

### Results

#### *Standard Deviation of Queueing Delays*

Figure 1 shows the effect of colony size on the standard deviation of queueing delays. Delays are equal for both foragers and receivers, by symmetry and because the simulation was run at optimal conditions, meaning that the work capacity of the foragers and receiver groups are equal,  $p = p^* = 0.5$  and  $\mu_f = \mu_r$ . There is a roughly exponential decrease in standard deviation with increasing colony size. Thus, in addition to experiencing greater mean queueing delays (Anderson and Ratnieks 1999*b*), individuals in smaller colonies also experience more variable queueing delays. This shows that when queueing delays are used as an information source, workers in larger colonies have better-quality information.

Figure 1 also shows the effect of the two queueing dis-



**Figure 1:** Effect of colony size (number of foragers plus receivers) on the standard deviation of queueing delays for two queueing disciplines, first come first served (*circle*) and serve in random order (*plus*). Because this is a symmetric case at optimal conditions ( $p = p^* = 0.5$  and  $\mu_f = \mu_r$ ), the results are the same for both foragers and receivers. Each datum is the mean of at least 6,000 queueing delays derived from 500 foragers or 500 receivers. Thus, each worker contributes an average of 12 queueing delays to the mean. For each colony size, there are 10 replicates (except for colonies of 2,000 or more foragers, where there are only two due to computational time constraints).

ciplines, first come first served (FCFS) and serve in random order (SIRO; Anderson and Ratnieks 1999b). According to queueing theory, no difference is expected in the mean queueing delay because the queue is subject to the same “service time” and because individuals are anonymous. However, it is expected that the variance of FCFS will be lower than that of SIRO (Flatto 1997) because FCFS is a more predictable and orderly regime. With SIRO, a forager could experience a short delay, even if several other foragers were queueing. Similarly, she could experience an unusually long delay. FCFS tends to reduce these “lucky” and “unlucky” effects. SIRO is more realistic than FCFS for insect societies.

In addition, figure 1 shows that at both low and high colony sizes there is little difference between the two queueing disciplines. In small colonies, queues are short because there are few individuals available to queue, and thus queueing discipline has little effect. In large colonies, although queues are longer on average, the mean queueing delay is shorter (fig. 2 in Anderson and Ratnieks 1999b), resulting in a smaller absolute difference in standard deviation, which increases with colony size to a maximum of approximately  $N_f = 100$  and then decreases. There is a broad intermediate range in which FCFS results in less variable queueing delays; this range is biologically relevant

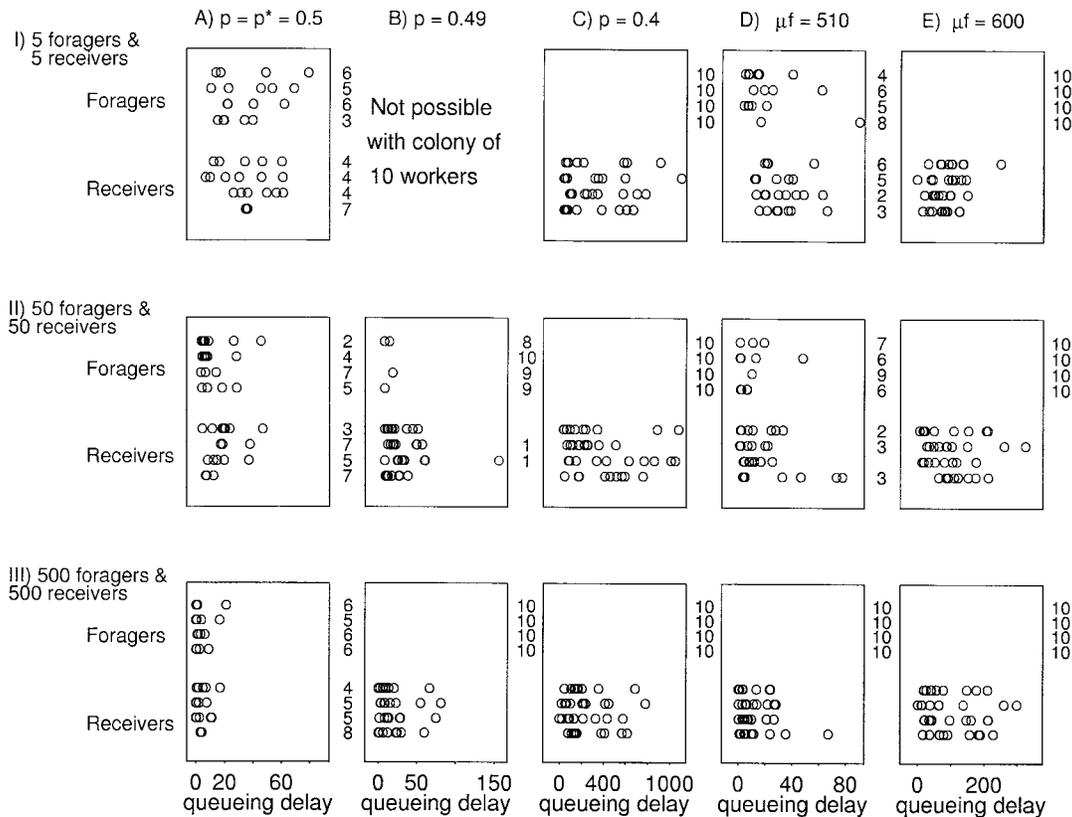
because it corresponds to the colony sizes of most insect societies.

#### *Distribution of Queueing Delays*

Because many changes in division of labor and task allocation are accomplished at the individual level through recruitment and task switching (Robinson 1992; Seeley 1995; Gordon 1996; Bonabeau et al. 1997), it is important to study the queueing experiences of individuals and their ability to assess colony status. Figure 2 shows 10 consecutive queueing delays for four typical foragers and receivers. These results are shown for three colony sizes at optimal conditions ( $p = p^* = 0.5$ ,  $\mu_f = \mu_r = 500$ ), near-optimal conditions, and far-from-optimal conditions. Suboptimal conditions are simulated either by decreasing the relative proportion of foragers from 50% (optimal, fig. 2A) to 49% (near optimal, fig. 2B) to 40% (far from optimal, fig. 2C), as would occur when some foragers die during their hazardous foraging career (Winston and Fergusson 1985; Visscher and Dukas 1997), or by increasing the mean duration of foraging trips from 500 time units (optimal, fig. 2A) to 510 (near optimal, fig. 2D) to 600 (far from optimal, fig. 2E), as would occur if food took longer to collect. The near-optimal conditions both correspond to a 2% reduction in the total work effort of the foragers, and the far-from-optimal conditions to a 20% reduction. These two situations are not identical, however. Increasing the duration of foraging trips does not directly affect the receivers, whereas reducing the proportion of foragers to 49% also increases the proportion of receivers to 51%.

Figure 2A shows that queueing delays are highly variable, despite optimal proportions of foragers and receivers, with the variation decreasing with colony size. The delays experienced by foragers and receivers are similar because of symmetry. Figures 2B and 2D show that even a 2% reduction in the total work effort of the foragers has a significant effect on the distribution of queueing delays. In particular, most of the foragers now have zero delays, and most receivers have nonzero delays. Nevertheless, the distributions of queueing delays are broadly comparable to the optimal situation, with most queues of both foragers and receivers being short,  $<50$  time units. Figures 2C and 3E show that the far-from-optimal situation gives a very different distribution of delays. Many of the queueing delays of the receivers are long,  $>50$  time units, and receivers rarely have zero delay. Foragers always have zero delay. The means and standard deviations of the data in figure 2 are shown in table 1.

These results indicate that individual foragers will find it difficult to distinguish between the near-optimal and optimal situations, whereas the far-from-optimal situation



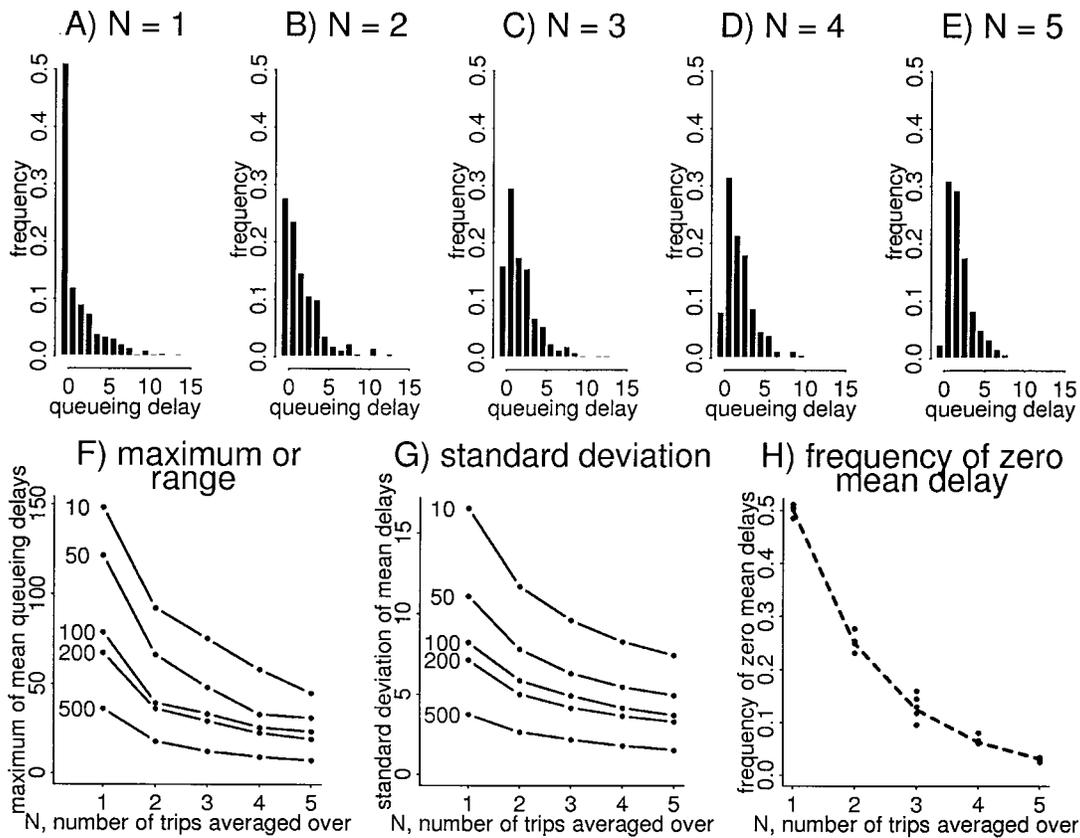
**Figure 2:** Distribution of 10 consecutive queueing delays for four foragers and four receivers in colonies of 10, 100, and 1,000 foragers and receivers for a variety of conditions: A, optimal,  $p = p^* = 0.5$ ,  $\mu_f = \mu_r = 500$ ; B, near optimal,  $p = 0.49$ ; C, far from optimal,  $p = 0.4$ ; D, near optimal,  $\mu_f = 510$ ; and E, far from optimal,  $\mu_f = 600$ . Numbers to the right of the figures represent the number of the 10 trips to the transfer area in which the worker had a zero delay. Means and standard deviation of these data are summarized in table 1. The results shown are from a single simulation for each column and each colony size.

can quite easily be distinguished from the optimum. In particular, a single long queueing delay is a good indication that a worker belongs to the group that is in excess. Similarly, consistently short or zero delays are an indication that a worker belongs to the group that is in shortage. The two states, excess and shortage, cannot be determined with equal ease: although a single long delay is a reliable indicator of being in the group in excess, a single short or zero delay is not a reliable indicator of being in the group in shortage.

From the perspective of natural selection, which should act to cause greater work efficiency (Oster and Wilson 1978), a 2% discrepancy in the optimal proportion of foragers would be of much lower importance than a 20% discrepancy (see fig. 6 in Anderson and Ratnieks 1999b). Indeed, given constantly changing external (e.g., change in food availability) and internal conditions (e.g., death of foragers), both the actual and the optimal proportions of foragers will be changing constantly. Thus, our conclusion

that a 2% discrepancy can only be distinguished with difficulty from the constantly shifting optimal situation is probably of little selective importance. Because a 20% discrepancy will likely be selectively significant, it is interesting that our results show that this deviation can be recognized relatively easily.

Different-sized colonies exhibit the same general response to suboptimal conditions (fig. 2I–2III). However, as colony size increases, the means of the delays show a consistent decrease, and the ranges narrow. The exceptions are figure 2C and figure 2E, both far-from-optimal situations, in which all three colony sizes exhibit roughly the same distribution of queueing delays. In short, the behavior becomes more like the deterministic case as colony size increases. That is, nonzero delays are experienced by the group in excess and small delays (or zero in the deterministic case when at  $p^*$ ) are experienced by the group in shortage (Anderson and Ratnieks 1999b). In summary, queueing delays provide a reliable indicator of colony



**Figure 3:** Effects of averaging queueing delays over consecutive trips. *A–E* show the distributions of mean queueing delays for a typical worker from a colony of 500 foragers and 500 receivers averaged in groups of 1 to 5 consecutive trips to the transfer area. Sample sizes for *A–E* are  $3,263/N$ . *F* and *G* show the effects of averaging on the maximum (which, as the minimum is always 0, is also the range) and standard deviation of mean queueing delays for a range of colony sizes. The numbers shown next to the curves in *F* and *G* are the number of foragers (=number of receivers) in the colony. The data points on *H* show the proportion of those mean delays that were 0, that is, where all trips to the transfer area had zero delay. This is plotted for the same series of colony sizes as *F* and *G*, but there is no colony size effect. The dashed line in *H* is the expected proportion of zeros given by the relationship,  $\text{proportion} = 0.5^N$ . Sample sizes in *F* and *G* range from  $3,263/N$ , for colonies of 500 foragers to  $174,706/N$  for colonies of 10 foragers.

status, especially as colony size increases and when conditions are suboptimal, but the information has predictable deficiencies.

#### *Effects of Averaging over Consecutive Trips*

Figure 3*A–E* shows the effects of averaging queueing delays over one to five consecutive trips for a typical worker at optimal conditions. Figure 3*A* shows that, as expected, the worker experiences zero delay in half the trips. It also shows that these delays, when they occur, are distributed roughly exponentially. When the number of trips averaged over increases, the mean value remains constant, but the variation decreases.

The standard deviation of the mean delays decreases rapidly (fig. 3*G*) in inverse proportion to the square root

of the sample size, as would be expected from the properties of the sample mean of independent and identically distributed variables. That is, standard deviation is halved when  $N$  increases from 1 to 4. As a consequence of this, the range of mean delays (fig. 3*F*), which is also the maximum (given that the minimum is always zero), also decreases in the same manner. As smaller colonies have larger standard deviations at  $N = 1$ , they gain the most in terms of absolute decrease in the standard deviation of mean queueing delays.

The results show that individuals in smaller colonies have a greater increase in information quality of queueing delays by averaging over several trips than individuals in larger colonies. However, as larger colonies start with smaller standard deviations, their workers still have better-quality information than workers in smaller colonies.

**Table 1:** Mean queueing delays with standard deviation (in parentheses) for the combined data for foragers and receivers in figure 2

| Colony size<br>and worker<br>type | Optimal<br>$p = p^*$ | Near optimal  |               | Far from optimal |               |
|-----------------------------------|----------------------|---------------|---------------|------------------|---------------|
|                                   |                      | $p = .49$     | $\mu_f = 510$ | $p = .4$         | $\mu_f = 600$ |
| 10:                               |                      |               |               |                  |               |
| Foragers                          | 15.07 (21.4)         | ...           | 8.16 (17.96)  | 0 (0)            | 0 (0)         |
| Receivers                         | 16.03 (20.3)         | ...           | 17.75 (19.06) | 281.3 (292.6)    | 86.04 (45.59) |
| 100:                              |                      |               |               |                  |               |
| Foragers                          | 5.36 (9.58)          | .49 (2.11)    | 2.80 (8.27)   | 0 (0)            | 0 (0)         |
| Receivers                         | 7.54 (11.54)         | 21.07 (27.35) | 12.59 (18.27) | 341.5 (316.7)    | 97.87 (73.58) |
| 1,000:                            |                      |               |               |                  |               |
| Foragers                          | 1.81 (4.49)          | 0 (0)         | 0 (0)         | 0 (0)            | 0 (0)         |
| Receivers                         | 1.95 (3.85)          | 18.5 (20.64)  | 11.4 (13.07)  | 234 (198.5)      | 95.1 (81.49)  |

Figure 3H shows the probability of experiencing a zero mean queueing delay. That is, all  $N$  delays experienced are zero as the number of trips averaged over increases. As shown in figure 3A, the probability of experiencing a zero delay is 0.5. If consecutive delays are independent, it is expected that for consecutive trips the probability of a zero mean delay is  $0.5^N$  (fig. 3H). The data fit this expected relationship across all colony sizes, demonstrating that consecutive delays are independent, a factor that would alter the informational content of the delays if it were not the case. In figure 6 of Anderson and Ratnieks (1999b), it was shown that zero delays carry little information, indicating to an individual only that the colony is near the optimum or is a member of the group in shortage, but not indicating how far the colony is from the optimum. Positive delays, however, can indicate how far the colony is from the optimum (fig. 6 of Anderson and Ratnieks 1999b). Thus, this averaging technique greatly increases the probability of obtaining a nonzero mean delay, which can indicate how far the colony is from the optimum (Anderson and Ratnieks 1999b). (Similar results were obtained at near-optimal and far-from-optimal conditions, as this averaging mechanism does not affect the dynamics of the system, which is not true for averaging over multiple transfers [below].)

#### Effects of Averaging over Multiple Transfers

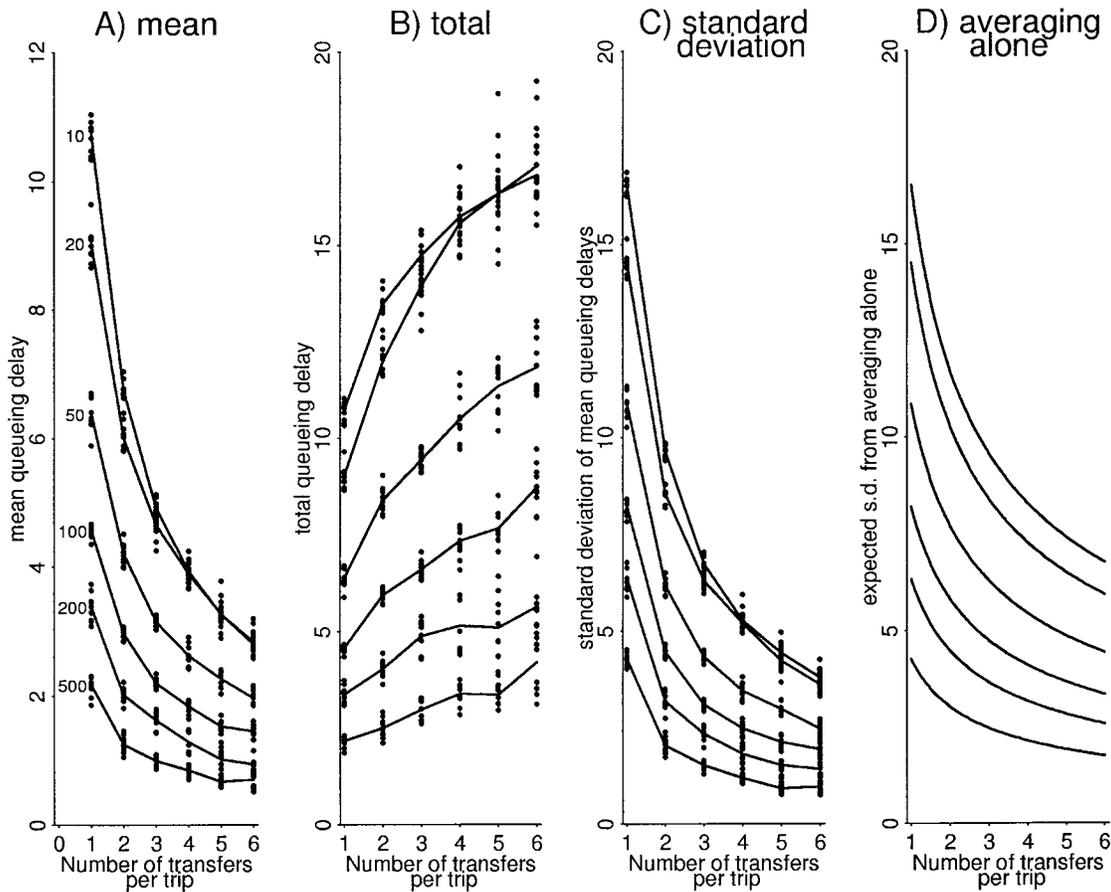
*Optimal Conditions.* Figure 4 shows the effects of averaging over multiple transfers. Figure 4A shows the decrease in mean queueing delay as the number of transfers per trip is increased. This decrease occurs because multiple transfer increases the arrival rate of foragers and receivers at the transfer area.

Figure 4B shows that there is always a time cost because the total queueing delay (mean delay  $\times$  number of transfers) per foraging or receiving trip is always an increasing

function of number of transfers per trip. However, the gradient of this relationship is relatively shallow. For example, in a colony of 500 foragers and 500 receivers, the total queueing delay increases by 2.09 time units when the number of transfers increases from 1 to 6. This cost is especially low for large colonies because the total queueing delay is still only a small amount of time in relation to the duration of a foraging trip (Anderson and Ratnieks 1999b). However, our model has not considered the additional search delays that may occur.

Figure 4C shows the informational benefit of multiple transfers in terms of decreased standard deviation of queueing delays. Standard deviation decreases with increasing number of transfers. Once again, small colonies gain the most in absolute decrease in standard deviation. Figure 4D shows the expected relationship, in which the decrease is in inverse proportion to the square root of the number of transfers, given the initial standard deviation of single transfers. The actual decreases seen in figure 4C are greater than those expected from averaging effects alone (fig. 4D). This is because multiple transfer affects the system favorably, in terms of information content, in comparison to averaging over independent delays, one delay per trip.

*Near-Optimal and Far-from-Optimal Conditions.* Figure 5 shows the effect of colony size and number of transfers on means, totals, and standard deviations of the queueing delays, with an increasing number of transfers per trip for near-optimal, 2% ( $\mu_f = 510$ ), and far-from-optimal, 20% ( $\mu_f = 600$ ), conditions. As in the previous section, multiple transfer greatly increases the information quality of queueing delays through reduced standard deviations. However, the situation is now asymmetric. Because foragers spend longer on their task, on average, than receivers, the receivers are in excess and have to queue more often than foragers and experience longer and more variable



**Figure 4:** Effects of averaging over multiple transfers. Foragers make one to six transfers at the end of each trip. Each transfer may involve a queueing delay. Receivers also make the same number of transfers. By symmetry, the results are identical for both foragers and receivers. The numbers within *A* refer to the number of foragers (=number of receivers). *A* shows the mean queueing delay against number of transfers per trip for a variety of colony sizes; *B* shows the total queueing delay per trip, that is, the mean  $\times$  the number of transfers; *C* shows the standard deviation of the mean queueing delays; *B* and *C* show the ergonomic cost and the information benefit of multiple transfer, respectively; and *D* shows the expected effect from averaging alone. Note that curves are lower in *C* than in *D*. There are 10 replicates for each value of the number of transfers ( $S_i$ ) and sample sizes are  $8,330/S_i$  for colonies of 10–200 foragers, and  $16,663/S_i$  for the largest colony.

queueing delays. Averaging decreases the standard deviation more in absolute terms for receivers, who are in excess, than for foragers, who are in shortage.

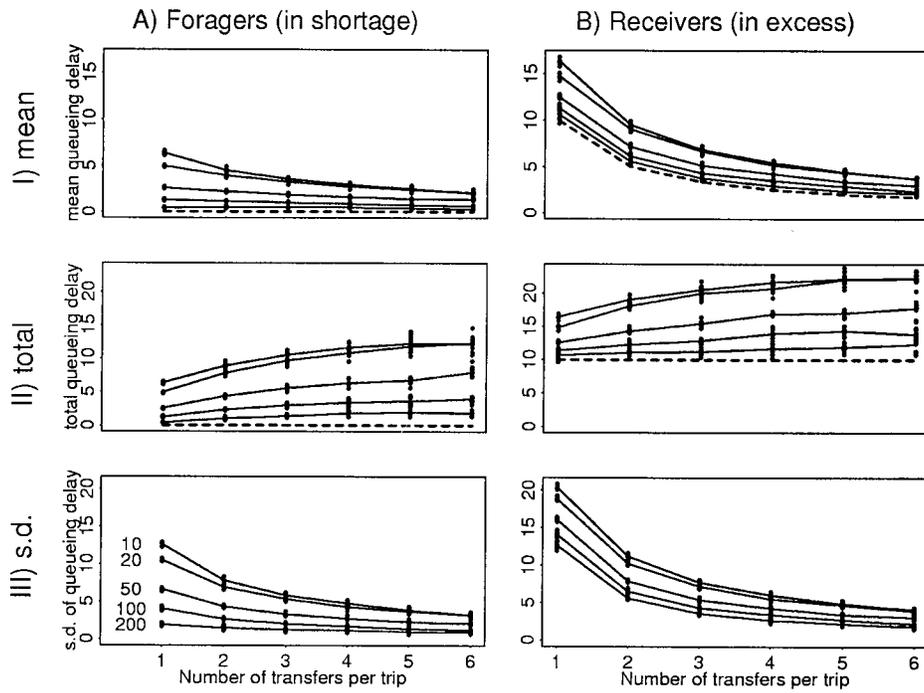
At far-from-optimal conditions, mean foraging duration 600 (fig. 5), the results are even more dramatic: the cost of multiple transfers, in terms of total queueing delay, is minimal; and there is a great absolute reduction in the standard deviation of the excess group. Thus, multiple transfer has both increased benefits and reduced costs the further conditions are from optimal. The colony size ordering has been reversed for standard deviation for receivers; larger colonies now have the greater variation in delays and gain the most informational quality benefit.

## Discussion

The results confirm that queueing delays can provide information relevant to the recruitment of additional foragers or receivers in response to suboptimal proportions of foragers and receivers. However, our results also show that the information arising from queueing delays is imperfect in quality and is affected by many factors, including the type of queueing discipline followed, colony size, the degree to which the ratio of foragers to receivers is suboptimal, and, if suboptimal, whether or not a worker belongs to the group in excess or that in shortage.

In small colonies, the queueing delays experienced by

### Near-optimal



### Far-from-optimal

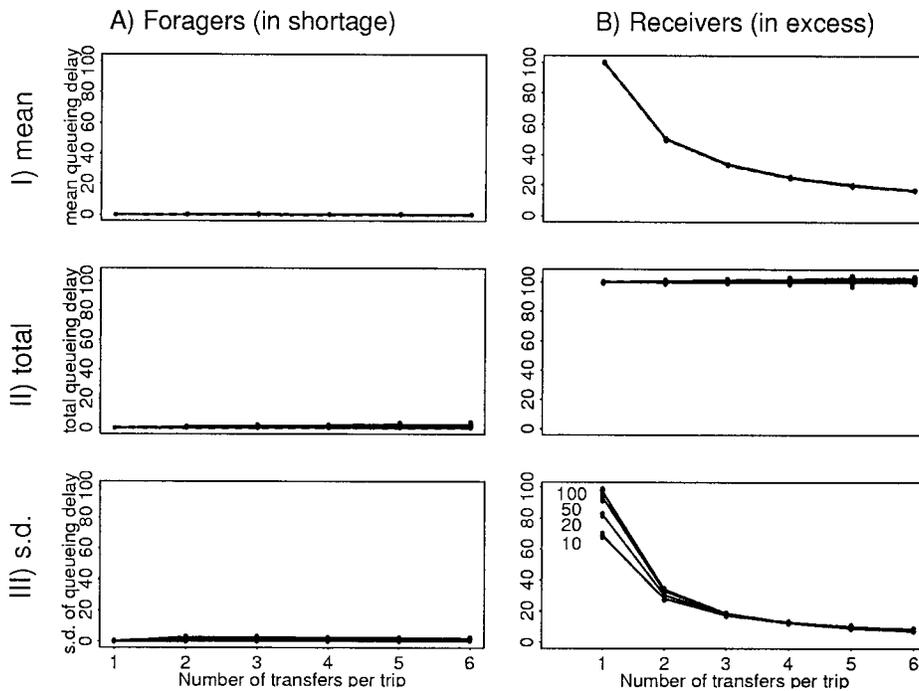


Figure 5: Effects of multiple transfer at near-optimal and far-from-optimal conditions. In both cases, mean receiving duration was 500 but with a mean foraging duration of 510 for the near-optimal case and 600 for the far-from-optimal case. The dashed lines in *I* and *II* show the expected delays for the deterministic case (appendix). Sample sizes are the same as those for figure 4.

individuals are more variable than those in large colonies. Thus, task partitioning with direct transfer not only causes a greater ergonomic cost to small colonies than larger colonies (Anderson and Ratnieks 1999b) but also results in queueing delays that are less reliable as a source of information for recruitment decisions. Relative to large colonies, small colonies are disadvantaged both ergonomically and informationally when task partitioning with direct transfer occurs.

Zero duration queueing delays are a major cause of informational uncertainty. In a colony with an optimal ratio of foragers to receivers, workers experience no queueing delay on approximately one half their trips to the transfer area and exponentially distributed delays on the other (fig. 3A). Because the duration of a single delay can range from zero to a relatively large value (fig. 2A), single delays at (or near) optimal conditions are not precise indicators of a colony's ergonomic status. When conditions deviate from optimal, the group of workers in shortage experiences a greater proportion of zero delays (fig. 2C, 2E). Zero delays give little information because a zero delay indicates either that the ratio of foragers to receivers is close to optimal or that the worker belongs to the group in shortage. For the group in excess, the situation is somewhat different. Although individual workers can experience zero delays when conditions are near optimal, they mostly experience nonzero delays in which the average magnitude of delay is correlated with the degree of deviation from optimal conditions (fig. 6 of Anderson and Ratnieks 1999b). However, workers in the excess group will still be subject to variable queueing delays and can experience both informationally nonuseful short delays and informationally useful long delays. The proportion of zero delays declines as conditions deviate further from the optimal ratio of foragers to receivers.

Our results show two biologically feasible mechanisms that significantly improve the information quality of delays. The first mechanism is averaging over consecutive trips. Because a single delay, unless long, provides little information about whether a worker belongs to the group in excess or shortage, basing a decision on a number of delays increases the quality of information. As shown in figure 3, the range and standard deviation of queueing delays experienced by individual workers decreases rapidly when the number of trips averaged over increases. In addition, the proportion of workers experiencing at least one nonzero delay (which was shown to be a good indicator of the degree of the amount of deviation from optimal conditions) increases as  $1 - 0.5^N$ , where  $N$  is the number of delays averaged.

One situation in which averaging over multiple trips would not be advantageous is when foraging and receiving trips are long relative to the time scale over which colony

or environmental conditions change, particularly if information is retained overnight (Kearse et al. 1996). For example, if nectar availability changes relatively rapidly with respect to foraging-trip length, delays from previous trips provide out-of-date information and cannot be used to predict current conditions. Seeley (1995) showed that in the honeybee, colony nectar influx can fluctuate greatly between consecutive days. In addition, honeybee foraging trips are relatively long, lasting from around 20 min to several hours (Ribbands 1953; Anderson 1998). Thus, in the honeybee, the duration of foraging trips may sometimes be close to the duration over which nectar conditions can change. In the wasp *Polybia occidentalis*, the situation is different. Foraging trips for building materials are very short, around 40 s for water and 3–4 min for pulp (Jeanne 1986b), and resource availability, such as fallen trees or puddles, is almost certainly less variable. Thus, averaging over trips may be a more practical strategy for *Polybia* than for the honeybee.

A second mechanism that is effective in improving the information quality of delays is multiple transfer. Simply put, multiple transfer generates more transfer delays and, therefore, more information. More important, this information gain occurs more rapidly than with averaging over delays, that is, within a single trip, which for many species is important given the rapidity of changes in forage availability (Ratnieks and Anderson 1999b). Our results (figs. 4, 5) indicate that multiple transfer increases information quality more than expected by averaging alone and at a surprisingly low ergonomic cost, in terms of increased total queueing delay. Furthermore, multiple transfer is even more effective at suboptimal conditions (fig. 5), which is precisely the situation in which information is most needed for recruitment to redress the balance between foraging and receiving capacities. Kirchner and Lindauer (1994) report that returning honeybee nectar foragers made an average of 2.3 (range 1–5; W. F. Kirchner, personal communication) trophallactic contacts to receivers per foraging trip. Seeley (1989, table 1) reports means of  $1.1 \pm 0.3$  to  $2 \pm 0.5$  bouts of nectar transfer per return to hive. As far as we are aware, there is no convincing explanation of the purpose of multiple transfer. Seeley (1995) and Winston (1987) both state that receivers ripen honey by evaporating water from the nectar through manipulations in their mouthparts and by adding enzymes to the nectar (Simpson 1960; Simpson et al. 1968). It may be that ripening is more efficient with smaller loads, given that evaporation is more rapid the higher the surface to volume ratio. However, there is no good evidence to support the ripening hypothesis. We suggest that a major purpose of multiple transfer is improving information acquisition. Suitable experimental studies to test this hypothesis against alternative hypotheses would be worth-

while. Published data on multiple transfer are not suitable for testing the information hypothesis. Although the number of transfers per individual forager varies from 1 to 5 (Kirchner and Lindauer 1994), data on the transfer delays of individuals with different numbers of transfers per trip are not given.

One difference between our simulation and the natural situation is that in our simulation all foragers and receivers made the same number of transfers, whereas, in the honeybee, foragers make variable numbers of transfers per trip (Seeley 1992; Kirchner and Lindauer 1994). We did not investigate the effect of variation in the number of transfers per individual because of the need to keep our simulation tractable. However, we think that it is unlikely that inter-individual variation in the number of transfers will affect the main result—that information quality is enhanced at a relatively low ergonomic cost. This is because the processes that cause these results, “recycling” of transfer partners and a larger sample size of queueing delays, will still occur when variation in the number of transfers per trip occurs. From the perspective of testing the information hypothesis, variation in the number of transfers among individuals within colonies will actually be helpful because the variation needed for testing occurs within each colony.

From a historical perspective, the relationship between task partitioning, ergonomics, and information is likely to be as follows. Initially, task partitioning in foraging evolves in the absence of informational benefits. The benefits of task partitioning, which must outweigh any ergonomic cost of queueing delays, include better use of individual abilities and more favorable work organization (Anderson and Ratnieks 1999*b*; Jeanne 1986*a*, 1991). When task partitioning has evolved, any information generated in the process can then potentially be used. Multiple transfer can relatively easily evolve from single transfer, assuming that multiple transfer is beneficial, because no modifications of the transfer system are needed to permit foragers or receivers to transfer multiple times. The critical point is that informational benefits, and in particular the greater informational benefits of multiple transfer, are unlikely to have been important at the origin of task partitioning.

Queueing discipline has an important effect on the variability of queueing delays. Figure 1 shows that FCFS always produces less variable delays than SIRO, as expected from analytical studies (Flatto 1997). Figure 1 also shows that as colony size increases beyond approximately 100, the difference in standard deviation for the two disciplines

decreases. If FCFS occurred in colonies, it would greatly reduce the incidence of zero or very short queueing delays in the excess group and, as a result, would enhance the quality of the information available in the delays. Despite the potential advantages, FCFS is not likely to occur in insect societies because it requires an additional form of organization, an ordered queue, which is not needed in SIRO. The organization could be in the form of a specialized queueing behavior or, more likely, a nest structure that physically imposes an ordered queue. For example, if foragers entered the nest through a long and narrow entrance tunnel, the tunnel could function as a queue template. From a historical perspective, the informational advantage of FCFS would not be relevant to the origin of task partitioning because, as discussed above, it is probable that task partitioning is initially selected for or against based on ergonomic, not informational, factors. Because SIRO and FCFS are ergonomically equivalent (Anderson and Ratnieks 1999*b*), FCFS would not initially be favored over SIRO.

In conclusion, this study provides novel insights into the information present in the queueing delays that arise from task partitioning via the direct transfer of forage. The most important findings are that this information has predictable shortcomings when used for recruitment decision making and that these shortcomings can be ameliorated by strategies such as averaging several delays, multiple transfer, and feedback on recruitment (e.g., by dancing) being principally generated by the worker group in excess. The hypothesized importance of averaging over and multiple transfer are amenable to experimental testing, with the clear prediction that the recruitment behavior depends not only on the previous queueing delay experienced but also on the recent history of delays. The most surprising finding is that multiple transfer causes only modest increases in the total queueing delay, particularly when the relative numbers of foragers and receivers are suboptimal

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## APPENDIX

## Analytical Results for Multiple Transfer

It is assumed that if  $S_f > 1$  then transfer duration is proportional to  $1/S_f$  and that it is solely foragers who determine transfer durations. That is, the mean transfer duration is

$$\frac{\text{expected value of } t(\cdot)}{S_f}.$$

Optimal Proportion of Foragers,  $p^*$  (Deterministic Case)

As in appendix C of Anderson and Ratnieks (1999b) at  $p^*$ ,

$$\frac{\text{number of foragers}}{\text{mean duration of a foraging cycle}} = \frac{\text{number of receivers}}{\text{mean duration of a receiving cycle}}. \quad (\text{A1})$$

However, now

$$\text{mean duration of a foraging cycle} = \mu_f + \mu_t \quad (\text{A2})$$

and

$$\text{mean duration of a receiving cycle} = \mu_r + \frac{S_r \mu_t}{S_f}. \quad (\text{A3})$$

So, in the deterministic case for any  $\mu_f$ ,  $\mu_r$ ,  $\mu_t$ ,  $S_f$ , and  $S_r$ , substituting (A2) and (A3) into (A1) gives

$$\frac{p^*(N_f + N_r)}{\mu_f + \mu_t} = \frac{(1 - p^*)(N_f + N_r)}{\mu_r + (S_r \mu_t / S_f)}, \quad (\text{A4})$$

which can be arranged to give

$$p^* = \frac{S_f(\mu_f + \mu_t)}{S_f(\mu_f + \mu_r) + \mu_t(S_r + S_f)}. \quad (\text{A5})$$

Thus,

$$\frac{\text{optimal proportion of foragers} = \text{mean foraging cycle duration}}{\text{mean foraging cycle duration} + \text{mean receiving cycle duration}}. \quad (\text{A6})$$

## Mean Queueing Delay (Deterministic Case)

Applying the same logic as in appendix C (pt. 3) of Anderson and Ratnieks (1999b) but with multiple transfers,

$$\begin{aligned} & \text{no. of foragers} \times (\text{proportion of foraging cycle spent transferring}) = \\ & \text{no. of receivers} \times (\text{proportion of receiving cycle spent transferring}), \end{aligned} \quad (\text{A7})$$

that is,

$$N_f \left( \frac{\mu_t}{\mu_f + \mu_t} \right) = N_r \left( \frac{S_r \mu_t / S_f}{\mu_r + S_r (\mu_t / S_f) + S_r \mu_{q,r}} \right), \quad (\text{A8})$$

which gives

$$\mu_{q,r} = \max \left\{ 0, \frac{N_r}{N_f} \left( \frac{\mu_f}{S_f} + \frac{\mu_t}{S_f} \right) - \left( \frac{\mu_r}{S_r} + \frac{\mu_t}{S_f} \right) \right\}. \quad (\text{A9})$$

In other words,

$$\begin{aligned} \mu_{q,r} = \max \left\{ 0, \right. & \text{(ratio of receivers to foragers)} \\ & \times \frac{\text{mean foraging cycle duration}}{S_f} \\ & \left. - \frac{\text{mean receiving cycle duration}}{S_r} \right\}. \end{aligned} \quad (\text{A10})$$

Note that this is the mean queueing delay for a single subload. The mean queueing delay for a full nectar load, that is,  $S_f$  subloads, is simply  $\mu_{q,r} \times S_r$ .

Similar logic can be applied to obtain the foragers' mean queueing delay. That is,

$$\mu_{q,f} = \max \left\{ 0, \frac{N_f}{N_r} \left( \frac{\mu_r}{S_r} + \frac{\mu_t}{S_f} \right) - \left( \frac{\mu_f}{S_f} + \frac{\mu_t}{S_f} \right) \right\} \quad (\text{A11})$$

and

$$\begin{aligned} \mu_{q,f} = \max \left\{ 0, \right. & \text{(ratio of foragers to receivers)} \\ & \times \frac{\text{mean receiving cycle duration}}{S_r} \\ & \left. - \frac{\text{mean foraging cycle duration}}{S_f} \right\}. \end{aligned} \quad (\text{A12})$$

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