



# Distributed problem solving in social insects

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In a social insect colony, large numbers of individuals all follow the same set of behavioral rules. Without centralized control, these individuals' interactions with each other and with their environment result in the allocation of individuals to various tasks, and in the distribution of foragers among available food sources. We review this highly parallel and distributed form of information processing, discussing its potential sophistication, its actual performance in various groups of social insects, its general strengths and liabilities, and finally, the adaptations that compensate for these liabilities.

## 1. Introduction

Colonies of social insects – ants, bees, wasps, and termites – can be viewed as highly parallel, distributed systems for solving the problems intrinsic to colony survival and reproduction. Colonies are *highly parallel* in that large numbers of individual colony members are interchangeable: the system is composed of redundant individuals behaving according to a stereotyped set of rules. Although the workers of many species exhibit a behavioral flexibility that allows them to perform more than one job in the course of their lives, all of the individuals engaged in any one job, such as foraging for food or feeding the brood, seem to follow essentially the same set of behavioral rules. Furthermore, all workers follow the same set of rules governing when they perform a given job, and when they switch to another one. In those species in which workers are morphologically and behaviorally specialized to the performance of a single task, workers of a given specialization behave in the same way, making the colony as a whole highly parallel. Colonies are *distributed* in that they function without hierarchical organization. Information is not integrated in a command center that directs the colony's activities. Instead, information remains dispersed throughout the colony, distributed across all workers and their immediate environments. Individual workers respond to local environmental cues and to interactions with each other – not to signals from central command – and this distributed process achieves the colony's coordination and execution of work.

The occurrence of parallel distributed processing is manifest in the colony's ability to respond to information that exceeds the sensory range or cognitive capacity of any given individual. This is observed in the colony's solution of three different kinds of problems.

1. Foraging [17,36,60]: In order to locate and retrieve useful resources, the colony must be responsive to a number of variable factors, including its own current needs, the

availability of specific resources, and the distribution of these resources in the environment. Determining the overall state of any of these factors exceeds the sensory range and cognitive capacity of the individual insect, and yet the colony must determine and weigh all three factors in order to forage effectively.

2. Task allocation [23,46]: In any colony, there are a number of different jobs to do, such as feeding the brood, foraging for resources, and maintaining the nest. Allocation of individuals to different jobs requires dynamic adjustment in response to the state of the environment, the needs of the colony, and the balance of labor among tasks that may be interconnected by the transfer or sharing of work. It is a problem requiring global assessment of needs and opportunities, as well as coordinated collective response, and yet task allocation is achieved by a collection of individuals with strict sensory and cognitive limitations.
3. Nest construction [59]: social insect nests exhibit architectural organization on a scale that far exceeds the sensory range of any individual. It seems that no single insect possesses a complete cognitive blueprint for the nest, or even knows the current state of a nest under construction. Yet nest building results in a stereotyped, organized structure.

Foraging and task allocation are related problems. Both require the distribution of individuals to the most profitable positions, whether these positions are geographic locations, as in the case of foraging, or jobs, as in the case of task allocation. Nest construction, on the other hand, raises a distinctive set of challenges that have been reviewed and addressed by a number of authors [20,57–59]. Although nest construction falls into the category of information processing at the scale of the colony, we will focus here on the closely related problems of foraging and task allocation. As we review the distributed solution of these problems by social insects, we will keep a general question in mind. How do these processes compare with other parallel distributed systems, such as neural networks, electric circuits, or biochemical regulatory pathways? This broad question concerns both the performance and the structure of social insect colonies as problem-solving entities. In the first section, we discuss a basic and first step in the assessment of performance: the determination of a colony's computational potential. This exercise reveals several basic structural differences between social insect colonies and other networks. In the sections that follow, we move from computational potential to algorithms used by real colonies. What rules do social insects implement in a distributed fashion to solve the problems of foraging and task allocation? How well do they work? And what aspects of a colony's organization are critical to its capacity for distributed problem solving? Investigation of these questions reveals several ways in which the colony's capacities are enhanced without requiring substantial increases in the abilities of its component parts, the individual insects.

## 2. The computationally complete ant colony

When McCulloch and Pitts [34] introduced neural networks as models for studying the central nervous system, their first analytical step was to investigate the maximum potential sophistication of information processing by such networks. They were able to show that neural networks are, in principle, computationally complete. That is, such a network can be constructed to solve any problem accessible to a finite digital computer. Lachmann and Sella [32,33] have recently applied the same methodology to information processing in social insects, addressing the following question. Is the parallel distributed organization of an ant colony capable, in principle, of processing information with the same sophistication as any computer, or is the ant colony limited in its maximum potential sophistication?

The specific aspect of colony organization investigated by Lachmann and Sella [32, 33] is task allocation, the colony's distribution of workers to different jobs in dynamic response to the shifting state of the environment and the needs of the colony. For a schematic mathematical depiction of this process, they adopt a generalization of a model originally set forth by Pacala et al. [41]. In the generalized model, each of a colony's ants can be in any one of  $M$  distinct states. Different tasks correspond to different states, but there may be more than one state corresponding to the same task. (This redundancy of states will prove important to the logical depth of the system.) The fraction of ants that are in state  $i$  at time  $t$  is denoted  $p_i(t)$ , where  $i = 1, \dots, M$ . The model assumes that the colony is sufficiently large that individual ants can be treated as infinitesimal contributions to the population of workers in any given state. An ant's state can change either in response to its environment or as a result of social interactions with other ants. Thus, the colony as a whole is constantly sensing the environment and fluidly sharing information via interactions. The rate at which the environment induces an ant in state  $i$  to switch to state  $j$  is  $A_{ij}$ , while an interaction between an ant in state  $i$  and an ant in state  $j$  causes the former to switch to state  $k$  with probability  $B_{ijk}$ . Under the assumption that the rate of interactions between ants in state  $i$  and those in state  $j$  depends linearly on the frequency of ants in each of these states, the rate at which an ant in state  $i$  encounters ants in state  $j$  is  $c_{ij} p_j$ , where  $c_{ij}$  is a constant. In a colony of ants that exhibit these transition probabilities and interaction rates, the dynamics of the fraction of ants in each state,  $i = 1, \dots, M$ , are described by the following equations:

$$\frac{dp_i}{dt} = \sum_{j=1}^M (A_{ji} p_j - A_{ij} p_i) + \sum_{j,k=1}^M (B_{jki} c_{jk} p_j p_k - B_{ijk} c_{ij} p_i p_j). \quad (1)$$

Based upon this very schematic description of colony dynamics, Lachmann and Sella build a constructive proof of computational completeness: They show that with certain sets of  $A$ 's and  $B$ 's, the essential logical devices of a Boolean network can be constructed. First, an amplifier is constructed from five ant states. States 1 and 2 are considered input states, set by the environment, while 3, 4, and 5 are output states,

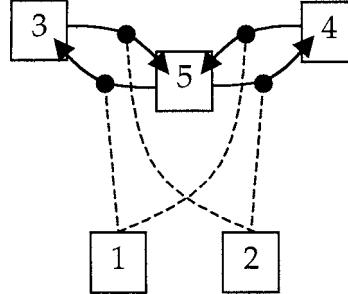


Figure 1. Transition diagram of an amplifier built of ant states. A solid arrow indicates that an ant in one state can be converted to another state. If an ant in a third state influences this rate of conversion, a dashed line connects the conversion arrow to the ant state that influences the rate.

affected by social interaction. Their frequencies are described by the following simple dynamic:

$$\begin{aligned}
 \frac{dp_1}{dt} &= \frac{dp_2}{dt} = 0, \\
 \frac{dp_3}{dt} &= -bp_3p_2 + ap_5p_1, \\
 \frac{dp_4}{dt} &= -bp_4p_1 + ap_5p_2, \\
 \frac{dp_5}{dt} &= -ap_5p_1 - ap_5p_2 + bp_3p_2 + bp_4p_1.
 \end{aligned} \tag{2}$$

Note that this is simply a specific realization of (1). It is depicted as a transition diagram in figure 1. Starting from initial conditions  $p_i(0)$ ,  $i = 1, \dots, 5$ , system (2) always converges to a steady state at which

$$\frac{p_3}{p_4} = \left( \frac{p_1}{p_2} \right)^2.$$

Thus, the initial ratio of input states is amplified. Moreover, if input is defined as  $p_1/(p_1 + p_2)$ , and output as  $p_3/(p_3 + p_4)$ , then the relationship between input and output is that of a typical sigmoidal amplifier.

The amplifier is one of two devices essential to Lachmann and Sella's constructive proof. The other is a gate that can be connected to amplifiers to yield dynamics that reflect the operation of a NOR gate, a Boolean operator that can serve as the basic building block of any Boolean network. Since a Boolean network is in principle computationally complete, the demonstration that the dynamics of ant states can operate as the essential component of such a network is sufficient to complete the proof that the colony can have the same computational capacity, in principle, as a finite digital computer. The operations of a NOR gate are summarized in figure 2. What is needed is a specific realization of (1) that maps input in the form of initial conditions to output in the form of steady

$in_1$	$in_2$	$out$
1	1	0
0	1	0
1	0	0
0	0	1

Figure 2. A NOR gate, the operator that can serve as the building block for a computationally complete Boolean network.

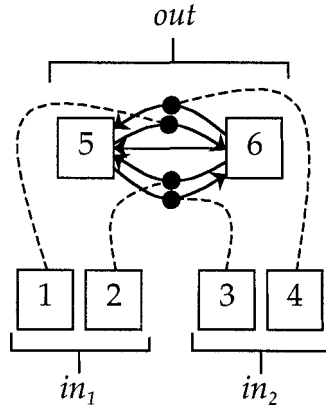


Figure 3. Transition diagram of the dynamical system of ant states that can function as a NOR gate when combined with amplifiers. The system takes input in the form of initial conditions, and produces output in the form of the steady states to which it converges. See figure 1 for an explanation of the transition diagram's notation.

states and mirrors the operations shown in figure 2. A dynamical system that meets these requirements is depicted in a transition diagram in figure 3, and written in full form here:

$$\begin{aligned}
 \frac{dp_1}{dt} &= \frac{dp_2}{dt} = \frac{dp_3}{dt} = \frac{dp_4}{dt} = 0, \\
 \frac{dp_5}{dt} &= -p_1p_5 - p_3p_5 + p_4p_6 + p_2p_6 + \frac{1}{4}p_6, \\
 \frac{dp_6}{dt} &= -p_4p_6 - p_2p_6 + p_1p_5 + p_3p_5 - \frac{1}{4}p_6.
 \end{aligned} \tag{3}$$

The ratios of state frequencies correspond to input and output: if  $p_1/p_2 > 3$ , then  $input_1 = 0$ , whereas if  $p_1/p_2 < 1/3$ ,  $input_1 = 1$ ; for ratios between  $1/3$  and  $3$ , the input is undefined.  $input_2$  and  $output$  are defined in the same way as  $input_1$ , but in terms of  $p_3/p_4$ , and  $p_5/p_6$ , respectively. Input is constrained to fulfill  $p_1 + p_2 = p_3 + p_4 = 1/3$ . When the output of the gate described by (3) is fed through three sequential amplifiers of the type described by (2), the system behaves as a complete NOR gate: Any well-defined input yields output according to the rules summarized in

figure 2. Thus, the feedbacks among ant states can produce dynamics that function in a fashion consistent with a NOR gate. Therefore, just as NOR Gates can be combined to produce a computationally complete network, dynamic modules of the type described by (2) and (3) can be similarly connected to produce a computationally complete ant colony. This completes Lachmann and Sella's proof that the system described by (1) is in principle computationally complete.

In view of earlier work in both ecology and computation, this result is not entirely surprising. Smale [52] showed that a general ecological model of  $N$  competing species – a system formally similar to (1) – can produce virtually any dynamic trajectory desired. The relationship between such complex dynamical behavior and the computational properties of a system has been investigated more recently by Moore [35]. Together, these papers presage the potential sophistication of information processing by the generalized system of task allocation described in (1). Nonetheless, the proof presented here confirms the result formally, demonstrating that there is no computational limit intrinsic in a colony's distributed method of information processing.

It is important to be clear about the meaning of this demonstration. How sophisticated a colony's information processing may be in principle is a very different question from how a colony processes information in practice. There is no reason to believe that the dynamical modules employed in the constructive proof play any role at all in a real colony. Rather, the demonstration of completeness is a basic component of what could be a much broader investigation into the computational properties of the kind of distributed information processing that operates in social insect colonies. What are the strengths and limitations of this distinctive mode of information processing? Are there categories of problems to which it is uniquely suited? The broader investigation that will answer these questions is still in its infancy. Nonetheless, we can turn to more biological research to begin to address questions about the operation and efficiency of real colonies. What kinds of problems can real colonies actually solve? And how successful are they at finding solutions?

### 3. Task allocation in real colonies

Investigation of realized, rather than potential, problem solving by colonies requires a hypothesis about the specific rules that are represented entirely generally in equation (1). The generalized dynamic of task allocation used by Lachmann and Sella was based upon the more specific model of Pacala et al. [41], in which behavioral rules were explicitly represented. Pacala et al. examined a set of rules that are biologically plausible for certain ant species, and asked whether the implementation of these rules by every individual in the colony could produce a good solution to the problem of task allocation. Based upon empirical observation of the way ants seem to use interaction rates in task decisions [24], the hypothetical rules are relatively simple. An ant that is successfully engaged in any task, such as foraging, brood-care, or tending the colony garbage pile, continues to perform that task. On the other hand, an ant that is unsuccessfully engaged in a task quits and becomes inactive at a *per-capita* rate  $q$ . (How an ant

assesses whether it is successfully or unsuccessfully engaged in its task is an important question, which we will discuss in a moment.) Ants that are unsuccessfully engaged in task  $i$ , as well as ants that are inactive, switch to performing task  $j$  ( $i \neq j$ ) when they encounter an ant who is successfully engaged in task  $j$ . The constant encounter rates of equation set (1),  $c_{ij}$ , are replaced here by a more realistic treatment, in which rates of interaction scale with colony size,  $N$ , according to the function  $I(N)/N$ . If we let  $T$  be the number of different tasks, and  $s_i$  the fraction of individuals engaged in  $i$  who are considered successful, then this simple set of rules leads to the following equation for  $n_i$ , the number of individuals engaged in task  $i$ :

$$\begin{aligned} \frac{dn_i}{dt} = & n_i(1 - s_i)q + \frac{I(N)}{N} \sum_{j=1}^T n_i s_i n_j (1 - s_j) - \frac{I(N)}{N} \sum_{j=1}^T n_j s_j n_i (1 - s_i) \\ & + \frac{I(N)}{N} n_i s_i \left( N - \sum_{j=1}^T n_j \right). \end{aligned}$$

If  $I(N) = 1$ , interactions between any given ant in task  $i$  and ants engaged in task  $j$  occur at a rate that is proportional to the fraction of individuals engaged in  $j$ . By contrast, if  $I(N) = N$ , such interactions occur at a rate that is proportional to the absolute number of individuals engaged in task  $j$ . Dividing through by  $N$  and simplifying yields a concise expression for  $p_i$ , the fraction of individuals engaged in task  $i$ :

$$\frac{dp_i}{dt} = -qp_i(1 - s_i) + p_i I(N) \left( s_i - \sum_{j=1}^T p_j s_j \right). \quad (4)$$

Note that the total number of ant states required by this set of behavioral rules is only  $2T + 1$ : an ant may be successful at one of the  $T$  tasks, unsuccessful at one of the  $T$  tasks, or inactive. Can such a simple algorithm achieve a good solution to the problem of task allocation?

First we must determine what a good solution would be. Assume that  $f_i(n_i, t)$  is the amount by which an individual performing task  $i$  at time  $t$  contributes directly to the colony's total fitness; the value of performing task  $i$  depends on  $n_i$ , the number of individuals who are already performing that task. Maximization of  $f_i$  with respect to  $n_i$  shows that the optimal  $n_i$  are determined by a version of the marginal value theorem, which arises frequently in ecology [15,42,56]:

$$\frac{\partial n_i f_i}{\partial n_i} = R, \text{ a constant.} \quad (5)$$

Task allocation is a difficult problem in part because  $f_i$  varies dynamically with the states of the environment and the colony, which affect both the difficulty and the importance of performing task  $i$ . Ideally, a colony would continuously and instantaneously adjust its allocation to maintain conformity with the marginal value theorem. Realistically, a colony is constrained by finite rates of information transmission and limited individual capacities for problem solving, both of which may restrict an individual ant's ability to

assess the profitability of its task to the colony as a whole. The quality of the solution achieved by the task-switching algorithm described in equation (4) depends on how an ant assesses whether or not it is successful. More precisely, it depends on the relationship between ants' assessments of success, which determine the  $s_i$ , and the actual value of different tasks to the colony.

Pacala et al. [41] derive several functions that could govern a colony's  $s_i$ , the fraction of ants in task  $i$  that are considered "successful" (by themselves and others) in the rules for task switching that are described by equation (4). One possibility is that  $s_i$  is a monotonically increasing function of  $f_i$ , the fitness returns due to an individual's performance of task  $i$ , and a monotonically decreasing function of  $p_i$ , the fraction of ants presently performing task  $i$ . Although this functional relationship is very simple, a critical question is whether it could actually result from the decisions of individual ants whose information is exclusively local – i.e., not integrated from the whole colony. Pacala et al. show that such a functional form will govern the  $s_i$  if the following conditions are met:

- (1) the returns due to the performance of a task change only with the supply of work – e.g., food available for gathering, or garbage available for moving;
- (2) the amount of work in a task decreases with the fraction of ants already engaged in that task;
- (3) ants in any given task are more likely to be successful (reflected in  $s_i$ ) whenever there is more work available in that task.

The third condition suggests a behavioral rule that individual ants might actually be able to follow given only local information: An ant is considered successful (by itself and other ants) whenever it is busy. Thus, provided conditions (1) and (2) are met, the first category of functions governing the colony's  $s_i$  could result from the locally informed decisions of individual ants. However, if the fitness returns of an individual's performance of task  $i$  change not only with the supply of work, but also with the colony's state of need (i.e., condition (1) is violated), then an individual could not follow this simple rule (busy = successful) for assessing its own success. An individual would instead need to respond also to a second local signal, an indicator of colony need. What this signal might be, and how it could be transmitted to each individual, is not yet understood.

In a second category of functions governing a colony's estimates of success,  $s_i$  is a monotonically increasing function of  $\partial n_i f_i / \partial n_i$ , the *marginal* rate of return from task  $i$ , and a monotonically decreasing function of  $n_i$ , the number of ants presently performing task  $i$ . In view of the optimum described by (5), this functional relationship implies that the colony's measure of success reflects the actual fitness value of tasks to the colony as a whole. How could individual ants achieve such an estimate of the value of each task? Pacala et al. identify an interesting strategy available to social insects. If an ant in task  $i$  is not only more likely to be considered successful when there is more work available in  $i$ , but is also less likely to be considered successful if task  $i$  is crowded, then the individual assessment of success can actually reflect the value of the task to the colony



as a whole. Once again, however, the situation is more complicated if the value of jobs changes not only as a result of the availability of work, but also as a function of colony needs.

If individuals follow these two, potentially local rules for assessing whether or not they are successful, how well does the task-switching algorithm described by equation (4) serve to allocate ants to different jobs? How close does the colony's allocation come to the optimum, described by equation (5)? Analysis of equation (4) shows that algorithm for task-switching results in an equilibrium distribution of ants that is exactly as good as individual assessment of success allows it to be. If ants are able to estimate the returns from a task (the first rule for assessing success), then the colony equalizes returns across all tasks. This results in an ideal free distribution, which can be different from the distribution defined by (5), but is generally not far off [5]. However, if individuals are able to estimate marginal value by assessing both returns and the density of ants in a task (the second rule for assessing success), then the colony fulfills the marginal value theorem, achieving the optimal distribution of individuals.

Although much theoretical work on social insects has focused on equilibrium distributions of workers, there is no empirical evidence to suggest that colonies spend a substantial portion of their time at equilibria rather than in the transient dynamics between them. It is, therefore, important to consider the performance of distributed problem solving when the colony has not yet reached an equilibrium (see, for example, [12,54]). To examine the responsiveness of the colony to environmental change, Pacala et al. [41] analyzed the effects of a perturbation: When the success rate associated with a specific task,  $s_j$ , is suddenly changed to a different value, how rapidly does the colony move from its prior equilibrium to the new one? The rapidity of response, not surprisingly, is directly related to colony size. The reason for this is simply that information about the success rates in different tasks is effectively transmitted by direct interaction between workers, and – for most reasonable forms of the function  $I(N)$  – the rate of these interactions is directly related to colony size. However, there is also a potential cost associated with rising interaction rates. When these rates become very high, socially transmitted information comes to predominate over individual sampling of the state of the environment or colony, and the rate of recruitment to many tasks exceeds the optimum. A potential remedy for this is regulation of contact rates as the colony grows larger and density increases. Empirical work shows that ants do in fact adjust interaction rate in response to density [24].

More recently, Pereira and Gordon [44] have investigated the transient dynamics of a model of task allocation in order to determine which aspects of the rules governing task-switching are most important to the colony's ability to track a changing environment. Pereira and Gordon [44] ask which local cues provide individuals with the information necessary for the colony as a whole to adjust rapidly to perturbations in the payoff of certain jobs. One result is that colony responsiveness is heavily dependent on workers' assessment of their own success; by comparison, individual detection of the success of other colony members has a small effect on the colony's ability to track the environment.

#### 4. Waiting time: A second layer of information

In the models of task allocation that we have discussed thus far, interactions permit the direct transmission of information between individuals. Among many social insects, however, it is not only interactions that hold useful information, but also the time periods between them. Thus, two layers of information can be superimposed: the content of interactions, and their pattern of occurrence. Honey bees provide a good example. (See [1] for an excellent review.) When a honey bee forager returns to her nest from the flower patch she has been working, she must donate her nectar to a bee who works in receiving. The receiver bee accepts the load and then temporarily disappears from the unloading area. Because receivers are in limited supply, whereas foragers return with nectar at a rate that depends on their number and rate of success, the average time that a forager must search for a receiver increases with the colony's overall foraging success [48,51]. Therefore, the time period that a forager spends in search of a receiver can provide the forager with an estimate of the availability of nectar to the hive as a whole. This information is useful in the colony's adjustment of both its foraging strategy, which we will discuss below, and its task allocation [31,49]. The forager probably weighs the time she spent searching for a receiver bee, i.e., her estimate of colony success, against the accessibility and sweetness of her own nectar source in order to determine what she will do next. If her delay is short, indicating low colony success, and her patch is productive, she performs a "waggle-dance", which signals other bees to start foraging actively. By contrast, if her delay is extremely long, indicating that receivers are in short supply, she is likely to perform a "tremble-dance", a signal that recruits more receiver bees. Thus, the colony's operative estimates of nectar supply and receiving capacity are distributed across a large number of individual waiting times, and the colony's response to this estimate is a distributed process of individual bees making decisions based on their experiences.

The social wasp, *Polybia occidentalis*, also appears to use waiting times as a distributed source of information guiding task allocation [27,29,30]. In this species, the task of nest building is partitioned into three subtasks that are interconnected by the exchange of material. One group of workers forages for water, which they bring to the nest and donate to the two other groups, woodpulp foragers and nest builders. The pulp foragers depart with the water, use it to soften wood fibers, and return with the resulting pulp. Nest builders first accept water, then accept pulp, and finally distribute the mixed material to other builders for use on the nest. There are thus a number of junctures in which the time period that an individual must wait to donate or receive material may serve as a signal indicating the balance of workers between subtasks, and a number of lines of evidence show that workers do indeed change both activity levels and jobs in order to maintain an allocation of workers that is close to optimal [28–30].

Division of a task into several subroutines, which must then exchange both material and information, incurs a number of costs. To investigate these, Anderson and Ratnieks [2,3,45] studied a simple stochastic model of a partitioned task. The model considers two groups of workers – foragers and receivers – that must meet to transfer

material; the durations of foraging trips, unloading trips by receivers, and transfers are sampled at random from normal distributions of defined mean and variance. The model's dynamics reveal two substantial costs of partitioning. The more evident one is simply the time wasted by workers while they wait to transfer or receive material. Even in the optimal worker allocation, the mean waiting time for both groups is nonzero: stochastic variation in trip time causes foragers and receivers to arrive at different moments, resulting in significant waiting time. The magnitude of this cost depends on colony size. Because the rates of arrival are greater in larger colonies, the effect of each 'mistimed meeting' is reduced, and variance in trip time incurs a lesser cost.

There is also a subtler way in which stochastic variation in trip time can take a toll on colonies. If workers use waiting times as their signal for task switching, then an individual may be cued to switch whenever its waiting time deviates significantly from the delay that is expected when the colony is in its optimum balance of workers. (This expectation is nonzero because of the mistiming problem just discussed.) However, stochastic variation in trip time causes each worker's waiting time to deviate from the optimal expectation every time it waits, regardless of the colony's current balance of task allocation. Therefore, to receive a reliable signal of imbalance in the colony's task allocation, an individual must wait for a period of time that not only exceeds the waiting time expected under optimal allocation, but exceeds it by an amount that represents a significant deviation in view of the expected variance in waiting time. In short, stochastic variation in trip time adds noise to the signals that individuals use to govern task switching.

To counteract the corruption of their cue by stochastic variation, workers could adopt at least two strategies [3,45]. First, individuals could simply average their waiting times over successive trips, reducing the standard deviation in waiting time simply by increasing sample size. However, this could be effective only if trips are short relative to the time scale over which the colony's task allocation must change to remain in balance with external conditions. In *P. occidentalis*, foraging trips take only 30 seconds to 4 minutes, so averaging may be a workable strategy [2,30]. On a shorter time scale, individuals could average their waiting times over a number of transfers each time they visit the transfer area. Although this would incur an extra cost of searching out multiple partners for sharing each foraging load, this cost may be offset by the value of more reliable information. Ratnieks and Anderson [45] observed that in their stochastic simulations, multiple transfer decreased variation in waiting times even more than would be expected by averaging effects alone [3,45]. Honeybee foragers have been observed to share single loads with multiple receivers [31]. The improvement of the informational content of the cue for task switching may be one advantage favoring multiple transfer.

Ratnieks and Anderson's work highlights a potential liability of social insects' distributed method of solving problems. Estimates of important quantities remain dispersed over a large number of individual samples, each of which is subject to stochastic variation. If these estimates are never integrated, stochastic variability is never averaged out. This introduces a potential problem of error propagation: an error in an initial estimate may not be corrected before the estimate is utilized by individuals responding to it. In

the case of multiple transfer by honey bees, it seems that a small amount of integration of cues is worth its cost in time, as it improves estimates of the state of the colony before those estimates are acted upon. The vulnerability of distributed information processing to stochastic effects will arise again in the context of foraging. In that context, as here, the problem is ameliorated by increasing the amount of integration; this slows the problem-solving process, but increases its reliability.

## 5. Foraging

The parallel structure of the problems of task allocation and foraging is reflected in their equivalent theoretical optima. The marginal value theorem, which was presented above in the context of task allocation, is also applicable to foraging. Indeed, application of equation (5) to the problem of foraging requires only a slight re-interpretation of the variables. The variable  $n_i$ , which was formerly defined as the number of individuals engaged in a particular job, will now represent the number of individuals actively exploiting food source  $i$ . Similarly, the payoff function,  $f_i(n_i, t)$ , will now represent the fitness payoff to the colony due to an individual worker foraging at food source  $i$ . This function may be a less abstract utility function in this context than it was in task allocation, as it may be possible to approximate  $f_i(n_i, t)$  with a simple surrogate for fitness payoff, such as the caloric content of a food source. In many cases, however, the utility function that determines the value of a food source to the colony may involve considerations besides energetic reward, such as the risk of predation associated with a food source [37–39], or nutritional benefits besides energy [4]. In any case, with a properly defined utility function, equation (5) determines the optimal distribution of a colony's workers among a number of accessible food sources [56].

As in task allocation, the colony's continuous conformity to the foraging optimum determined by the marginal value theorem is hindered by limitations of information flow and computational complexity. An optimal foraging decision – when to give up on the current food source and search for a new one, for example – must be based on estimates of what resources are available in the entire foraging range accessible to the organism [53]. However, unlike organisms that are physiologically integrated, social insect colonies distribute their foraging effort across many locations simultaneously. Therefore, whereas a solitary organism may be able to rapidly sample or estimate the availability of resources within its own foraging range [21,53], a colony member has no way of directly sampling the availability of resources over the entire colony's foraging range. The individual is therefore deprived of the estimates it would need to make well-informed foraging decisions that would allow the colony as a whole to forage optimally. That is the problem of information flow. The problem of computational complexity is different, but equally significant: Even if there were a way to communicate each forager's local experience to every other forager, resolving instantly the problem of information flow, every forager would have an enormous amount of information to process, and a difficult optimization problem to solve. Each food source has countless characteristics: energy, non-energetic nutritional benefits, a current population of foragers, predation risk, dis-

tance from the nest, and so on. How could an individual, supplied with a complete list of food sources and their complicated characteristics, process the information to decide where to go? Thus, foraging presents at least two challenges to the colony's parallel distributed system for information processing. How can the colony overcome the problems of information flow and computational complexity, foraging optimally in spite of the spatial dispersion and cognitive limitations of individuals?

A basic element in many species' solution of these problems is recruitment: a worker who finds a food source returns to the nest and informs its nestmates of the source's location, and sometimes also its quality [6,11,16,17,61]. In "tandem" and "group" recruitment, which are exhibited by some ants, information is transmitted directly, as the successful forager directly solicits one nestmate (tandem recruitment), or pheromonally solicits a small group of nestmates (group recruitment), to accompany her to the food source. In chemical mass recruitment, also found in ants, information is transmitted in the form of a pheromone trail that is deposited by the forager on the route from a food source to the nest. An entirely different form of recruitment is exhibited by honeybees: successful foragers directly communicate the location of a flower patch to other potential foragers.

## 6. Recruitment trails in ants

How do recruitment systems solve the problems of information flow and processing that are presented by foraging, and how closely do their solutions approximate optimality? We will first consider a simple system of chemical mass recruitment by the ant *Lasius niger* to two potential food sources. Beckers et al. [7] offer a schematic model of the system. Assume a colony has  $N$  foragers, of which  $E$  are out exploring for food,  $n_i$  are at food source  $i$ , and  $N - E - \sum n_i$  are still in the nest. Ants stay at a food source for an average period  $1/b$ . Each ant returning from food source  $i$  is assumed to solicit directly  $a_i$  nestmates to leave the nest on the trail to source  $i$ . (There is also an implicit assumption that ants return from food source  $i$  at a rate proportional to the total number of ants exploiting  $i$ ; a time delay is omitted, presumably to maintain the model's simplicity.) Of the newly solicited ants, a fraction  $f_i$  reach the food source, while  $1 - f_i$  leave the trail and wander in search of food. Wandering ants return home at rate  $p$ , and find a food source at rate  $c$ . Under these assumptions, the model for recruitment to two food sources is

$$\begin{aligned} \frac{dn_i}{dt} &= a_i \cdot n_i \cdot f_i \cdot \left( N - \sum n_i - E \right) - b \cdot n_i + c \cdot E, \quad i = 1, 2, \\ \frac{dE}{dt} &= \sum (a_i \cdot n_i \cdot (1 - f_i)) \cdot \left( N - \sum n_i - E \right) - p \cdot E - 2 \cdot c \cdot E. \end{aligned} \quad (6)$$

Two further assumptions are critical to the system's dynamics: the intensity of solicitation by a returning ant (reflected in  $a_i$ ), as well as an outgoing ant's fidelity to the trail (reflected in  $f_i$ ), increase with the quality of the food source. In biological terms,

this means that individual ants assess the quality of the food source, and accordingly modulate both their solicitation of nestmates and their deposition of pheromone. (We will discuss below what these assumptions imply about individual cognitive capacity and information flow in the colony.) With these assumptions in place, and parameter values measured directly in laboratory colonies of *Lasius niger*, equation set (6) correctly predicts a number of interesting colony-level behaviors observed in the laboratory colonies. When parameter values reflect food sources of different quality, and initial conditions show foragers exploring but not yet exploiting either food source, equation set (6) predicts that the colony will soon focus its foraging efforts on the food source of higher quality. Thus, the colony's recruitment dynamics function essentially as an amplifier: The ratio of individual assessments of two spatially disparate food sources is amplified to produce the colony's collective decision to forage on one source and ignore the other.

When parameter values correspond to food sources of identical quality, the colony does not, as one might expect, evenly divide its foragers between the two sources. Instead, the strongly amplifying character of recruitment dynamics results in a bifurcation to alternative stationary states: The colony exploits one food source and ignores the other. (Whether this surprising asymmetry in the intensity of exploitation is an adaptation that reduces the number of lost ants [13,43], the risk of predation, or the threat of competing ants [9,36], or is instead an incidental characteristic of the colony's dynamics, is not yet clear.) In certain circumstances, the recruitment dynamics described by equation set (6) result in dramatic deviation from the foraging behavior that would maximize the colony's rate of energy gain and would be considered optimal under the marginal value theorem (5). When a colony is presented first with a low-quality food source, and then with a second source of higher quality, it fails to redirect its foraging efforts to the richer source [6,7]. As equation set (6) predicts, the initial amplification of foraging effort traps the colony in its exploitation of the poorer food source.

A more recent theoretical extension of equation set (6) models the development and decay of pheromone trails to an arbitrary number of food sources [36]. The full bifurcation diagram was constructed for two distributions of resource: one with a number of equal sources; a second with a single rich source amidst a number of poorer ones. Extending the two-trail result, the model shows a concentration of ants upon a single source, not only when that source is uniquely rich, but even when multiple equivalent sources are available, or when richer sources appear too late for the colony to redirect its efforts. However, when the number of sources becomes sufficiently large relative to the number of ants, a bifurcation occurs: The colony exploits multiple equivalent sources at the same level, and manages to redirect its foraging efforts to the richest source, regardless of the order in which the sources appear. (This intriguing shift in dynamical behavior has not yet been observed empirically.) A mechanistic explanation for this bifurcation is that the dispersion of ants among numerous sources prevents the intense amplification that traps the colony in a single pheromone trail. Whether the number of food sources typically exploited by *Lasius niger* or other mass recruiting species is large enough to prevent fixation on a less profitable source has not been investigated.

Like increasing the number of food sources, reducing the total number of ants can moderate the amplification of a single trail, thereby allowing the colony to select its food source more judiciously. A recent model that adapts equation set (6) in order to investigate the effects of colony size and rates of direct interaction [10] suggests that reductions in the total number of foragers allow the colony to choose the highest quality food source. In view of these results, it seems likely that other modifications that weaken the cooperative feedback in trail formation are also likely to prevent fixation on poorer sources. This general suggestion agrees with results from recent stochastic process models [12,54], which show that although more powerful recruitment signals accelerate a colony's selection of a single food source, they also increase the likelihood of making a sub-optimal selection. In other words, collective foraging decisions that are made through the gradual integration of small contributions to pheromone trails are more likely to select the best available food source, but will take a long time to do so. Thus, as we saw in task allocation, broader integration of individual estimates prior to the activation of a collective response prevents the propagation of stochastic errors, but comes at the cost of speed.

The two source model as well as its more recent extensions [10,36], assume that foragers assess and communicate the quality of each food source: the parameter  $a_i$ , representing recruitment at the nest, and  $f_i$ , representing fidelity to the trail, increase with food source quality. What does this assumption imply about information flow in the colony and the cognitive capacity of individuals? We should emphasize that it does *not* imply that individuals receive global information about the quality of multiple food sources, or that individuals perform comparisons among separate inputs in order to select the most profitable source. To the contrary, individuals are assumed only to assess the quality of a single source and to modulate their recruitment behaviors accordingly. (Such modulation has been observed in a number of groups [11,16,26,55,61].) The processing of global information – the comparison among multiple food sources that differ in many ways – takes place at the level of the colony, through the dynamics of recruitment.

The dynamics of recruitment integrate and process not only ants' assessments of food quality, which are reflected by their behavioral modulation of recruitment, but also certain characteristics of the environment that are relevant to the colony's selection of a food source. Any characteristic of the environment that increases the average time required for a round trip from the colony to a given food source can result in a reduction of recruitment to that source, irrespective of behavioral modulation by the foragers. For example, if difficult terrain or the presence of competitors slows the return of foragers from a source, recruitment to the source is likewise slowed. Thus, important attributes of the environment are incorporated into colony information processing without requiring explicit coding of information by foragers [19].

In contrast with the ant species we have discussed, honeybees do not use trails, but instead rely on the direct transmission of fairly sophisticated signals between individuals. How does this system of information processing perform in comparison with trail-based systems, such as that described by equation set (6), as well as with the theoretical optimum, described by equation (5)?

## 7. Recruitment signals in bees

The marginal value theorem (5) gives the distribution of bees among flower patches that would maximize the hive's rate of energy acquisition. However, the rule that individual foragers use to determine when they have gathered enough nectar and should return to the nest is not in quantitative agreement with the hypothesis that individuals maximize the amount of energy they gain per unit time [40,47]. Instead, individuals seem to maximize their foraging efficiency, i.e., the amount of energy gained per unit of energy expended. The most compelling explanation for this is that a forager's performance decays not with time, but rather with energy expended on flight. As a result, if the hive can produce a limited number of foragers per season, it can maximize its return on its limiting budget if individual foragers maximize energetic efficiency, rather than energetic return per unit time. Does this mean that the hive as a whole must also maximize efficiency rather than rate of energy acquisition?

To answer this, and to see how the hive resolves the difficulties of information flow and computational complexity that were raised above, we must consider the mechanics of the process of recruitment. As was described in the context of task allocation, a forager returning from her flower patch must wait for receiver bees, and her waiting time can provide a stochastic estimate of the hive's overall foraging success. If her own flower patch is promising relative to the colony's low rate of energy intake, she will pause from foraging to perform a waggle-dance, which not only recruits inactive foragers, as was described above, but also serves to communicate the location of her flower patch [22]. On the other hand, if her colony is already foraging near its maximal capacity, she may abjure dancing and return to her patch. Finally, if her patch is of relatively low quality, she may abandon it and join the pool of potential followers on the dance floor. A model of a hive's exploitation of two sources has elucidated the dynamics of the process that allocates foragers to different patches. In brief, a better source is more heavily exploited because its foragers have both a lower rate of abandonment and a higher rate of recruitment of inactive foragers [14,50]. Interestingly, this system of direct transmission of information is not prone to the same fixation on suboptimal food sources that was described in the context of trail-based systems. Instead, honeybee recruitment redirects foragers to the most profitable nectar sources available [49,50].

What overall distribution of foragers results from this process of recruitment, and does this distribution maximize the hive's rate of energy acquisition, even though individuals seem to maximize their efficiency? This question was addressed by the concise model of Bartholdi et al. [5]. In this model,  $x$  is one flower patch in the complete set of patches,  $X$ ;  $n_x$  is the number of foragers currently working  $x$ ; and  $r_x$  is the rate at which foragers return to the hive from  $x$ . This rate is a non-decreasing function of  $n_x$ ; and  $r_x/n_x$ , the number of roundtrips a forager makes per unit time, is a non-increasing function of  $n_x$ . (Both of these assumptions about functional form are entirely reasonable biologically.) The rate at which individuals abandon  $x$ ,  $q_x$ , is a function of forager success at the patch. Finally, the duration of a forager's dance is also a function of the forager's success, and is represented by  $d_x$ .



Assume that when a worker re-enters the foraging process, the probability that it is recruited to patch  $x$  is equal to the fraction of all dancing that is for  $x$ . This fraction is simply

$$\frac{d_x r_x}{\sum_{x \in X} d_x r_x}. \quad (7)$$

If we assume that the hive has reached a steady-state distribution of foragers, then the total number of active foragers is constant, and the total rate of recruitment must equal the overall rate of abandonment, which is  $\sum_{x \in X} q_x n_x$ . Furthermore, the rate of recruitment to  $x$  must equal the rate of abandonment of  $x$ :

$$\frac{d_x r_x}{\sum_{x \in X} d_x r_x} \left( \sum_{x \in X} q_x n_x \right) = q_x n_x. \quad (8)$$

This can be rewritten as

$$n_x = r_x \left[ \left( \frac{d_x}{\sum_{x \in X} d_x r_x} \right) \left( \frac{\sum_{x \in X} q_x n_x}{q_x} \right) \right]. \quad (9)$$

The quantity in brackets is simply a measure of the colony's assessment of the quality of patch  $x$ , normalized by the colony's global assessment of the availability of resources. The equation states that the number of foragers allocated to patch  $x$  should equal the product of the rate at which foragers return from  $x$  and the colony's estimated value of  $x$ . This implies that the number of foragers in a patch is proportional to the patch's supply of resources, such that all individuals experience an equal rate of gain. This will be recognized as the ideal free distribution, already mentioned in the context of task allocation. Recall, however, that the distribution of foragers that maximizes the rate of energy gain for the colony is determined by the marginal value theorem, (5), not the ideal free distribution. Bartholdi et al. [5] offer an elegant proof that the ideal free distribution achieved by the hive provides energy at a pace that is never less than half the maximum attainable rate. Given that the optimal distribution would require instantaneous transmission of information throughout the foraging range of the colony, as well as the non-trivial computational power to determine the optimal distribution, the hive's performance represents a relatively successful heuristic. Thus, it seems that while individuals behave in a manner that maximize their efficiency, the colony distributes foragers in a manner that keeps the hive's rate of energy acquisition in the neighborhood of the maximum. We must note, however, that the theory treated here hinged upon an assumption of equilibrium. The rapidity of the hive's response to a shifting mosaic of flower patches was not considered.

## 8. The properties of signals

Why is the honeybee recruitment system able to redirect foraging effort from a poorer source to a richer one, whereas chemical mass recruitment focuses more inflexibly? The cause of this difference in dynamic behavior does not seem to lie in the

informatic content of their distinctive signals. A rough comparison between the accuracy with which fire ants follow an individual's pheromone trail, and the accuracy with which honey bees follow the instructions contained in a waggle dance, suggested that the two signals do not contain drastically different amounts of information about the location of a food source [25,62,63]. On average, both signals are expected to allow their recipients to choose the correct 1/16th of a 360° compass, and the correct quartile of the distance from the nest to the limit of the foraging range. Given that one bit is the amount of information needed to choose between two equiprobable alternatives, both signals transmit roughly 2 bits of information about distance, and roughly 4 bits of information about direction [63]. These are approximate averages, which are sensitive to the foraging distances over which the measurements are taken, but they do suggest that the signals provide roughly similar amounts of navigational information. Thus, differences between the two signals' informatic content does not seem to provide an adequate explanation for the qualitative difference in the dynamical behavior of recruitment.

The key difference seems to lie instead in other properties of the signals. The amount of pheromone on a trail, and thus the accuracy with which ants follow it, increases with the number of ants already exploiting a food source. Unlike the pheromone trail, the waggle-dance is communicated directly from one worker to another, and multiple dances cannot be compounded to improve the informatic content of the signal. As a result, the accuracy with which recruited honeybees are directed to a flower patch does not increase with the number of foragers already exploiting the patch. This difference between the signals – one can be compounded, the other cannot – is one reason trail recruitment seems to show a greater propensity to fixate on a single source.

The fidelity with which ants follow the trail seems to have two important effects on the overall dynamics of the recruitment process. A stronger trail not only increases the rate at which ants arrive at the source, but also decreases the rate at which new information is collected about the environment. As Deneubourg et al. [18] have shown, lost ants allow the colony to continue to explore, even as it exploits a given source. Thus, the positive relationship between trail fidelity and foraging intensity at a source increases the colony's fixation on a single source in at least two ways.

## 9. Conclusion

When information processing is not hierarchically organized but rather highly parallel and distributed, as is the case in social insect colonies, stochastic error may not be integrated out before information is used. Such distributed systems, therefore, may be especially vulnerable to the propagation and use of erroneous information. Furthermore, the generation of stochastic error in the acquisition or transfer of information is likely to be relatively common in social insect colonies. Relative to neural networks and biochemical regulatory systems, social insect colonies are highly dispersed in space and exposed to environmental perturbation. Information is consequently subject to a range

of disturbances, delays, and corruptions. Thus, social insect colonies would appear to be exceptionally susceptible to both the generation and the propagation of erroneous information. A number of social insect behaviors can be understood as strategies to maintain the quality and timeliness of very vulnerable information in a diffuse processing network. These strategies seem to fall into two broad categories:

- (i) the use of semi-redundant signaling methods to improve the quality of information that may be ambiguous or compromised;
- (ii) the adjustment of the rate of contact between individuals to achieve the proper flow and integration of information.

Chemical mass recruitment is vulnerable to error of two types. An individual's trail is an ephemeral and precarious link between a food source and the nest, so if mass recruitment does not quickly amplify the trail, information about the food source may be lost. On the other hand, if mass recruitment amplifies a trail that leads to a relatively poor source, the colony may be trapped in a distinctly sub-optimal foraging strategy. There is evidently a fine balance to be struck between the loss of information and responsiveness to the wrong information. However, the implementation of a second form of signaling in the early stages of recruitment may circumvent the problem. In some species, the first stages of recruitment are handled with tandem or group recruitment, while later stages utilize chemical mass recruitment [7,8,10]. This effectively places a reliable memory and filtering system prior to a powerful signal amplifier.

Bees may also employ partially redundant signaling methods to improve the quality and timeliness of information. The cue that a returning forager uses to estimate the current foraging success of the colony as a whole is a stochastic one. The time that a forager must search to find a receiver bee rises on average with the saturation of receivers, but it also has appreciable variance. As a result, the forager's estimate of her colony's state may be mistaken. Furthermore, there is a time lag between a forager's search for a receiver and her performance of a dance, so her estimate may be untimely. Either source of error may lead her to perform a waggle dance when her colony's foraging success is already high, and receivers are in very short supply. Such an error seems to be corrected, however, by the transmission of a second signal. Bees that find foragers performing a waggle dance when receivers are already in short supply will transmit a "stop signal" – an audible peep and a head butt – that causes the waggle dancer to stop dancing. Thus, the stop signal may be a correction system to maintain the timeliness and quality of signals.

In addition to their use of secondary signaling systems, social insects maintain the quality of information by regulating their rates of information exchange with other individuals. Some ant species regulate their interaction rates [24], and this seems to enable the colony to maintain information flow within the colony in proper balance with the input of information from the environment. Each honeybee forager may seek out interaction with multiple receivers in order to improve her estimate of the colony's overall foraging success. Even basic life-history attributes, such as colony size, can be understood as adaptations that improve the quality of signals. In paper wasps, large colonies

experience less stochastic variation in the waiting times that are used to cue changes of task [30]. This improvement in signal quality probably contributes to the positive relationship between per-capital productivity and colony size.

Although we are beginning to understand the most evident capacities and liabilities of the distributed systems for information processing that are exhibited by social insects, we do not yet have a general understanding of the computational properties of these systems. The proof of computational completeness of task allocation in ants is a basic first step in what could be a much broader endeavor: a rigorous investigation of the distinctive computational capacities of the diversity of strategies employed by social insects. This may elucidate what kinds of distributed systems are uniquely suited to certain categories of problems.

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