The Organization of Work in Social Insect Colonies

Task Allocation as an Ad Hoc, Dynamical Network

A social insect colony operates without any central control; no one is in charge, and no colony member directs the behavior of another. A worker cannot assess the needs of the colony. How do individual workers, using fairly simple, local information, in the aggregate produce the behavior of colonies? The dynamics of colony behavior results in task allocation [1]. Colonies perform various tasks, such as foraging, care of the young, and nest construction. As environmental conditions and colony needs change, so do the numbers of workers engaged in each task. For example, when more food is available or there are more larvae to feed, more foragers may work to collect food. Task allocation is the process that adjusts the numbers of workers engaged in each task in a way appropriate to the current situation.

I study task allocation in harvester ants (*Pogonomyrmex barbatus*) [2]. Inside the nest, ants care for the brood (the preadult forms: eggs, larvae, and pupae); process and store seeds; construct and maintain chambers; and simply stand around doing nothing. The ants that work outside the nest are a distinct group, apparently older than the interior workers. I divide the behavior I see outside the nest into four tasks: foraging, searching for and retrieving food; patrolling, assessing food supply and the presence of foragers from neighboring colonies; midden work, sorting the colony refuse pile or midden; and nest maintenance work, the construction and clearing of chambers inside the underground nest.

Tasks are interdependent; numbers engaged in one task depend on numbers engaged in another [3,4]. Ants switch tasks, though not all transitions are possible. In harvester ants, task switching funnels ants into foraging and away from tasks inside the nest [4]. An ant's decision whether to perform a task depends, first, on cues about the physical state of the environment: for example, if part of the nest is damaged, more ants do nest maintenance work to repair it. Task decisions also depend on social cues arising from interactions with other ants.

Workers from different task groups meet as they come in and out of the nest. The rate at which one ant encounters others influences its task decisions. The pattern of interactions among ants as they move around can be seen as a kind of ad hoc, dynamical network [5,6].

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When ants meet, they touch with their antennae. Antennae are the organs of chemical perception. When an ant uses its antennae to touch the antennae or body of another, it can perceive the colony-specific odor that all nestmates share. We found that in addition to the colony odor, *Pogonomyrmex barbatus* ants have an odor specific to their task, because the temperature and humidity conditions in which an ant works alter its cuticular hydrocarbon profile [7–9]. For example, a forager makes long trips outside the nest in hot, dry air, and this increases the proportion of *n*-alkanes in its hydrocarbons. An ant may assess the task of an ant it meets using these task-specific odors, so that an ant can evaluate its rate of encounter with ants of a certain task. We are investigating how patterns of interaction among workers contribute to the dynamics of task allocation in harvester ants. In laboratory studies, we found that an ant's decision whether to perform midden work depends on its recent rate of brief antennal contact with midden workers [10].

In field studies, experiments suggest other decision rules based on encounter rate. One set of experiments shows how a forager's decision whether to go out and collect food depends on its interactions with other workers. We find that the rates of interaction with at least two types of workers influence a forager's activity: interactions with patrollers and with other foragers.

Patrollers leave the nest each morning before foragers. First the nest patrollers go a few centimeters from the nest entrance and then turn back. The next set of patrollers go around the mound and then out on the trails. These trail patrollers choose the directions taken later by the foragers [11], and foragers will ignore food sources not visited earlier by patrollers [12]. It appears that the first foragers prefer the directions in which they encounter most returning patrollers, and later foragers mimic the directions of the earlier foragers. The rate of interactions with patrollers determine whether foragers leave the nest.

Removal experiments [13] show that when nest patrollers do not return, activity outside the nest ceases; there is no further patrolling and foraging never begins. When trail patrollers do not return, outside activity ceases, and foraging never begins. Thus the patrollers influence an all-or-none decision, whether to forage or not on a given day. The return of the first, nest mound patrollers seems to inform the rest of the exterior workers, including foragers, that it is feasible to leave the nest that day. Nest mound patrollers may assess humidity and temperature. After the nest mound patrollers have gone back in, trail patrollers choose foraging directions, based on encounters with the foragers with neighboring colonies and perhaps on food availability [14,15]. Once foraging has begun, a forager's decision whether to go out to forage depends in part on its rate of contact with successful returning foragers [11,13].

Experiments like these show how an ant's moment-to-moment decision about which task to perform and whether to perform it actively depends on its interactions with other workers. Interactions between workers of some task groups apparently provide negative feedback, whereas others provide positive feedback. It appears that what matters to an ant is the pattern of interactions it experiences, rather than a particular message or signal transferred at each interaction. Ants do not tell each other what to do when they meet, but the pattern of interaction each ant experiences influences the probability it will perform a task. Each ant uses a set of rules such as, "I'm a forager and if I meet a returning patroller every so often, I remain likely to go out." Evidence for such a rule is that if the forager does not meet a returning patroller, the probability it will go out diminishes.

Research on social insects is only now beginning to unravel the local rules that influence individual behavior. Social insect research is a small and young field. Most of the thousands of social insect species have never been studied at all. Honeybees have been more intensively studied than any other social insect species, because they have been agriculturally important for agriculture throughout human history. Even for honey bees many of the details of individual task decisions are not known. There is no reason to expect that the details of task allocation will be the same in all social insect species. In fact, because social insects thrive in such diverse environments, it is likely that different species have evolved very different social interactions. For example, the relation of patrolling and foraging in harvester ants allows for very slow adjustment to changes in food availability, which is appropriate in the desert where food availability changes slowly. More opportunistic ant species, which quickly take advantage of small bursts in food supply, probably operate very differently.

An important question about task allocation in harvester ants arises from intriguing results on the effects of colony age. Colonies live 15 to 20 years, founded by a single queen who produces all the workers. Colonies begin with 0 ants and grow to a size of about 10,000 ants when the colony is about 5 years old and begins to reproduce [14]; it then stays at about this size for another 10 to 15 years. The behavior of older, larger colonies, of about 10,000 ants, is more stable to perturbation and more homeostatic than that of younger, smaller ones of about 3,000 ants [3].

Because individual ants live only a year, this cannot be due to the experience of older ants. The simplest hypothesis is that individual decision rules are the same in young and old colonies, but such rules have a different outcome in a small and large system. For example, interaction rates in a small colony might be lower than those in a large one, because in a young, small colony, each ant has fewer nestmates it could meet. The dynamics of the interaction network seems to depend on its overall size.

Several types of models have been used to model task decisions in social insects (reviewed in [16]). Most of these model the behavior of workers engaged in one task, such as foraging, or in several related tasks, such as nest construction in wasps, which involves collecting both paper and water. These include self-organization models (e.g., [17]),

which have mostly been used to predict the formation and shape of foraging trails (e.g., [17]). Versions of these models have been applied to more general AI problems such as the traveling salesman problem [18]. Nest construction by wasps has also been studied theoretically and empirically [19].

There have been few attempts to model formally the allocation of workers among different tasks. One approach to modeling the allocation of workers among tasks is the "foraging-for-work" hypothesis [20] that an individual's decision whether to perform a task may depend on whether it finds itself in a location where that task is required. The threshold model of Robinson and Page [21] is an informal model of honeybee behavior based on genotypic differences among workers. It supposes that each genotype has a threshold stimulus at which it will perform a task. Empirical studies of honeybees support the threshold model with regard to some tasks but not others [22,23].

So far there have been two theoretical models of task allocation in harvester ants. The first [14] involves a parallel distributed process, such as a neural network. In this model, individual decisions are based wholly on interactions with nestmates. The second model [24] is an analytic model that uses differential equations to describe more deterministically the dynamics of task allocation. In this model, an individual's decision about which task to perform and whether to perform it actively is based on two kinds of stimuli: (1) environmental cues that determine whether the ant is "successful" at its task, e.g., whether a forager finds food and gets it back to the nest, whether a midden worker manages to carry a dead ant to the midden and dump it there, and so on, and (2) interactions with other individuals. This model is more realistic than the first in that it incorporates environmental as well as social stimuli. Following on this, we investigated how the robustness and sensitivity of the system depends on colony size and on the type of feedback between tasks [25]. Currently we are developing an agent-based simulation to model task allocation in harvester ants using empirical data to set the parameter values.

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It seems likely that in all social insects, both environmental and social cues contribute to an individual's task decisions. Picnics provide an example of an environmental cue; if ants did not respond to changes in food supply, we would not see ants at picnics. Response to environmental stimuli is a component of several previous models (e.g., [26]). Numbers of interactions, rate of interaction, transfer of material, waiting time to transfer material, or time elapsed since the last interaction are a component of several recent models of the organization of some aspect of social insect behavior (e.g., [17,27,28]). The most important outstanding questions about task allocation in social insects are probably similar to the outstanding questions about any complex biological system: How much do the attributes of the individual components (in social insects, the workers) contribute to the dynamics of the system? For example, is it reasonable as a first step to assume that all workers are alike? How do the internal dynamics of the system react to and bring about changes in the environment? The colony is not a closed system: it absorbs materials from, takes cues from, and in turn modifies its environment. Finally, how does the size of the system determine its dynamics? In social insects, this is a developmental question because colonies grow larger as they grow older. Though similar methodological questions apply to all complex systems, the answers will be in the details, and thus will certainly differ among systems.

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