The organization of work in social insect colonies

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In social insect colonies, workers perform a variety of tasks, such as foraging, brood care and nest construction. As the needs of the colony change, and as resources become available, colonies adjust the numbers of workers engaged in each task. Task allocation is the process that results in specific workers being engaged in specific tasks, in numbers appropriate to the current situation.

TASK allocation operates without any central or hierarchical control to direct individuals into particular tasks. The queen does not issue commands, and workers do not direct the behaviour of other workers. We can compare the diverse tasks performed by a colony to the many proteins generated by gene transcription, to the various cell types of a developing embryo, or to the firing patterns of neurons in the brain. What all of these have in common is that, without any central control, individual units (genes, cells, neurons or workers) respond to simple, local information, in ways that allow the whole system (cells, brains, organisms or colonies) to function: the appropriate number of units performs each activity at the appropriate time.

How does task allocation work? What determines, at any moment, which individuals are actively engaged in each task, and how does a colony adjust its effort to the demands of a changing environment? Diverse approaches to these questions include the investigation of the internal states of workers, the sensory physiology of workers' perception of the environment, the development of colony organization as the colony grows older, and the evolutionary pressures on the effectiveness of task allocation. Answers to these questions generally fall along a gradient between two kinds of factors that determine what task an individual worker performs, and when she performs it: internal factors, based on some attribute of the individual, and often considered to be fixed; and external factors, based on some environmental stimulus, and considered to be transient. There are now sufficient data to show that both internal and external factors influence task allocation.

Internal factors

Throughout the 1970s and mid 1980s, research emphasized the internal factors within an individual that determine its task. The idea of a social insect colony as a factory with assembly-line workers, each performing a single task over and over, had widespread appeal. Such a view was consistent with contemporary thinking about analogous systems; examples were the 'one gene, one protein' view of gene action, and the idea that each neuron performs a single function. In social insects, a worker of a given behavioural 'caste' was thought to be intrinsically suited to a particular task, and to perform this task more or less exclusively.

One internal factor associated with task is body size. In some species of ants, colonies include adult workers of two or more sizes. Workers of a particular size might specialize in the task for which their size makes them most suited[1]; smaller workers might forage, larger workers might define the nest, and so on. Empirical studies support this for a few species[2], but polymorphic species, which have more than one size of worker, occur in only a minority of ant genera (44 out of 263); bees and wasps have only one size of worker. Thus polymorphism cannot account for task allocation in most social insects. Other studies show that, regardless of body size, it is rare for individuals to specialize on a particular task throughout their lives. Although most researchers have moved beyond the idea of division of labour among innate, specialized castes, this idea provided a starting point for the study of task allocation.

A second internal factor associated with task is worker age. It has long been known that honeybee workers move from one task to another as they grow older[3]. This phenomenon, known as age polyethism, also occurs in some ant species[4–6]. Young honeybees work inside the nest and older ones forage; juvenile hormone levels influence this transition[7]. In the study of task allocation in honeybees, it was clear from the outset that an individual could not be assigned to a single task on the basis of a static trait such as body size. Instead, much research has examined the internal causes of the predictable progression of tasks performed by a worker as she ages.

Third, genetic factors influence an individual's tendency to perform a task. Honeybee queens mate many times, and selection experiments indicate that worker offspring of different fathers differ in their propensity to engage in certain tasks (though the fathers, as drones, do not perform those tasks)[8]. In one ant species, genotypes differ in this propensity[9]; in others, such individual differences depend both on an ant's early experience and on intrinsic, possibly genetic, variation[10–12]. Genetic factors influence age polyethism; honeybees from different patrilines vary in the rate at which they proceed from one task to the next as they grow older[13–15].

External factors

Since the mid 1980s, there has been growing interest in how external factors affect task allocation. Task allocation has been shown to be dynamic and labile, in that the number of workers engaged in any given task may continually change.

From day to day, or even hour to hour, an individual worker may perform a variety of tasks[16–18], changing its task as circumstances require[19–21]. (Note that task switching here refers to a more rapid shift in task than those, on the scale of weeks or months, that lead to age polyethism.) An individual may also adjust its activity level, responding to environmental stimuli either by actively engaging in a task or by remaining inactive inside the nest. For example, a honeybee forager's decision whether to collect nectar or remain in the nest depends on how much nectar is already stored in the nest[22,23]. Such adjustment of activity level in response to environmental stimuli is apparently widespread in social insects[24–26].

In general, it appears that tasks are interdependent. The number of workers that join in a task at any instant depends on the numbers currently engaged in other tasks. The numbers engaged in various tasks are always changing, owing to individual shifts in task and, on a longer timescale, the birth and death of

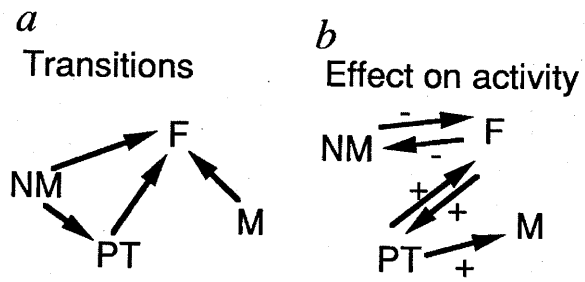

FIG. 1 Interactions among task groups in harvester ants[20,24,30]. *a*, How individual workers switch tasks when more ants are needed to perform the targeted activity. Arrows show the direction that workers switch tasks. All are one-way only. *b*, How numbers actively engaged in one task affect numbers actively engaged in another. An increase in numbers engaged in the task where the arrow begins has the indicated effect on numbers engaged in the targeted task. F, foraging (searching for and retrieving food); NM, nest maintenance (carrying out soil accumulated at nest entrance during construction of tunnels and chambers); PT, patrolling (scouting for new food sources and responding to disturbances near nest); and M, midden work (sorting the refuse pile).

workers. The mutual relation of numbers engaged in different tasks has been demonstrated dramatically in experiments in which a specific group of workers is removed, for example workers of a certain size[27], age cohort[28] or task[29–31]. In response to the removal, the remaining workers shift to perform the tasks previously done by the removed ones. Changes in colony composition also affect age polyethism in honeybees, with individuals proceeding faster from one task to the next if the number of older workers is experimentally decreased[32,33]; removal of an age cohort also affects age polyethism in some ant species[34].

A second demonstration that the activities of different task groups are interdependent comes from perturbation experiments that manipulate worker activity[20,24,30]. Experiments in the field with colonies of seed-eating ants provide examples of task switching and of changes in activity level (Fig. 1). When extra food becomes available, workers previously engaged in other tasks will switch tasks to forage. When extra clean-up work requires more nest- maintenance workers to be recruited from the reserves inside the nest, the current foragers, a distinct group of workers, are more likely to remain inside the nest. This decision not to forage seems puzzling, but conditions that require extra nest maintenance, such as summer floods that sweep debris onto the nest mounds, may not be ideal for foraging.

Thus individuals constantly alter their task status in two ways: they switch from one task to another, or move between a resting state and the active execution of some task. It is clear that both intrinsic and extrinsic factors contribute to task allocation. Individuals vary in predisposition to participate in certain tasks, and the tendency to perform a particular task changes as the individual grows older. Moreover, these age-dependent predilections are strongly influenced by at least two types of external cues: actions of other individuals, and events in the colony's environment.

There are many analogies with biological systems of other kinds. Genes alter their activity in response to changes in the activity level of other genes; cells in a developing embryo change type in response to the proximity of other cells; and neurons change function in response to signals from other neurons. How can we best understand the regulation of such systems? The next two sections review, first, theoretical models of task allocation, and second, empirical studies of the factors affecting individual task decisions.

Models of task allocation

The growth of theory in social insect research has been inspired by the artificial-intelligence community, who enthusiastically took up the analogy between ant colonies and computational systems spelled out by Hofstadter[35]. Many agent-based simulations and their computer-game offspring now have their elements named after social insects. These models have encouraged the development of new ones, based on empirical observation of various aspects of social-insect behaviour[36]. Here I will outline briefly some models of task allocation, that is, models of processes that could lead to the appropriate numbers of workers engaged in specific tasks.

Recent theoretical work shows how task allocation can operate in the absence of intrinsic differences between individuals. In this work, all individuals are considered to be identical; that is, any individual can perform any task, and an individual's task and activity level are determined by forces external to the individual. The point of these models is to find out how much of the behaviour we observe could arise from interactions between individuals and responses to external stimuli. The models offer an alternative to the view that colony organization arises from the intrinsic properties of individuals.

In some models[37–39], task allocation arises solely from interactions among individuals. In one such model, a neural network[37], the 'neurons' or units are ants, and an individual's task and activity level depend on the weighted sum of its interactions with others. The results show that even in a system requiring individuals to respond only to simple interactions, the number engaged in one task depends on the number engaged in another.

'Self-organization' models[40] are another example of models based on interactions between individuals. If individuals tend to follow others with whom they interact (for example, by sensing a pheromone deposited by the other individuals), random movement can coalesce into spatial patterns such as foraging trails. These models have been applied mostly to describe the formation of foraging trails by ants[41,42], with recent application to other tasks[29].

The 'foraging-for-work' model[43–45] differs from neural network and self-organization models in that environmental stimuli are more important than interactions among individuals. An individual's decision whether to engage in a task depends on whether it finds itself in a location where execution of that task is required. Extrinsic factors do not fully determine an individual's task because unspecified factors, possibly intrinsic differences among individuals, may determine each ant's location[46].

Some models refer both to environmental stimuli and to interactions among individuals[23,47,48]. One such model[47] is general in the sense that it describes the allocation of workers either to different tasks, or to different aspects of one task (for example, foragers to different resources). The model predicts a colony's ability to track and respond effectively to a changing environment by showing how quickly the colony can allocate the optimal distribution of workers to tasks or resources. The results show how a colony's response to its environment depends on the number of workers, the rate of information transfer among them, and whether task performance generates negative feedback for further execution of the same task (Fig. 2).

I know of no formal models of the dynamics of task allocation based primarily on intrinsic factors. However, the discovery of genotypic differences in the behaviour of honeybee patrilines has led to the following informal model[49] (and another is described below[33]). Suppose each genotype has a threshold stimulus at which the bee will engage in a task. At low levels of stimulus, the task will be accomplished by the individuals with a low threshold; at high levels of stimulus, individuals of other genotypes, that normally perform other tasks, will switch to respond to the high stimulus. So far, empirical studies support the threshold model with regard to some tasks but not others[50,51].

What determines an individual's task?

Individuals decide which task to perform, and whether to engage in it actively in a given situation. Social insects communicate mostly through chemical and tactile cues. What determines an individual's task and activity level?

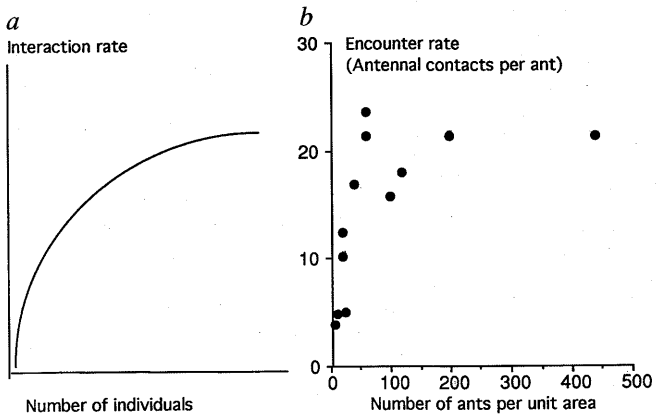

FIG. 2 Theoretical and observed relation of interaction rate and density. *a*, Theoretical prediction of optimal rate of information transfer[47]. In the model, an individual's task is determined by the environmental stimuli it encounters (for example, foragers' encounters with food), and by the rate at which it interacts with successful individuals engaged in the same and other tasks. Regulating interaction rate at high density prevents excessive numbers of individuals from performing a task. *b*, Observed relation of interaction rate and density[57]. Interaction rate was measured as the number of antennal contacts per ant, over a range of densities (number of ants per unit area), in the ant *Lasius fuliginosus*. Ants regulate interaction rate at high densities.

The results summarized above show that individuals respond to changes in the number of individuals engaged in some other task. Because no insect is capable of counting, or understanding the whole pattern of colony behaviour, no individual can communicate a global assessment to the others such as "Hey, you! There are now more than 35 ants over there doing urgent nest maintenance so stop foraging!" Because individuals move around, and many pheromones are highly volatile, the relevant cues are unlikely to be based on the quantity of pheromone accumulated over a long time in one place. Instead, each individual probably responds to local, transient cues that reflect the global situation.

In some cases, individuals respond to cues based on the ways that others have modified the environment through their work. The construction of the paper nest by colonies of *Polybia* wasps provides examples of this[25,48,52–54] (Fig. 3). A forager's decision whether to collect more building material (wood pulp) depends on how long she had to wait before a builder accepted her last pulp load; this in turn depends on how much pulp is currently available to nest builders.

Individuals may also respond to the rate of interaction with others engaged in like or unlike tasks. Workers would have to recognize the task of other workers they meet, perhaps by chemical cues associated with particular tasks (for example, foragers might carry the odour of food)[55]. Interaction rate, or the interval between successive encounters, depends on the total number of individuals present per unit area. Thus each individual need only keep track of the interval between its encounters with others to monitor changes in the density of the whole group.

Several lines of evidence support the hypothesis that encounter rate can influence the task decisions of individuals. Task allocation depends on colony size in ants, because the effect of one task group's activity on that of another task group varies with colony size[24,56]. Interaction rate also depends on colony size, as the more individuals there are per unit area, the more encounters each one will experience. Ants can regulate encounter rate; one ant can perceive another at a distance and will avoid excessive encounters at high ant densities[57]. Theoretical work shows that this allows a large colony to match its efforts to environmental changes[47] more effectively (Fig. 2). The role of interaction rate in task allocation remains an intriguing area of investigation.

We know that intrinsic factors influence what task an individual does, because task is sometimes correlated with age, genotype or both. We also know that extrinsic factors affect task performance, because colonies respond in a multitude of ways to changes in the environment and in the current distribution of workers among different tasks. However, we know very little about the interaction of the two, that is, how an alteration of internal state affects an individual's response to external stimuli[58], or how environmental stimuli can trigger an individual's internal state to change. For example, young honeybees will move more quickly into foraging tasks, typically performed by older bees with high levels of juvenile hormone, if old bees disappear from the colony. It seems that interaction between old and young bees inhibits biosynthesis of juvenile hormone in younger bees, and, when older bees are removed, biosynthesis of juvenile hormone is increased[33]. Thus an extrinsic factor (colony composition) somehow influences a physiological factor (the level of juvenile hormone) and this relation is mediated by interactions among workers. The relations of internal to external factors that influence an individual's task decisions still require further study.

The evolution of task allocation

A colony's survival and reproduction depend on how well it can match its efforts to the challenges of a variable environment. The evolution of task allocation could be seen as a process that generated a set of dynamical rules that determine how much a task will be performed in each ecological situation.

Questions about how task allocation systems have evolved are inseparable from questions about how such systems work. If an individual's task depends entirely on some fixed and innate attributes of the individual, the evolution of task allocation could be seen as a process that led to individual differences that cause certain individuals to perform the right task at the right time. Early work on the evolution of task allocation was based on the idea of division of labour among specialized individuals. Natural selection would shape the distribution of specialized individuals in a colony to provide the requisite number of individuals to perform each task[1]. Thus, for example, if a colony's reproductive success is increased by abundant food, natural selection might favour a high proportion of workers that specialize in foraging.

Individuals switch tasks, however, so the evolution of task allocation systems cannot be merely the production of distinct types of individuals, each suited to a particular task. Instead, there may have been natural selection for individuals to switch from one task to another in the most ecologically appropriate way. For example, when a new food source suddenly becomes available to a harvester ant colony, which competes with other seed-eating species for food[59], ants previously engaged in other tasks will

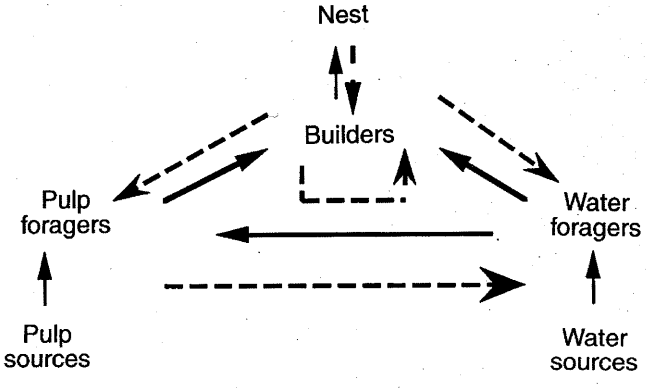

FIG. 3 Flow of information and materials among task groups during nest construction by the wasp *Polybia occidentalis* (modified from ref. 25). Solid lines represent direction of flow of nesting materials, water and wood pulp; broken lines represent direction of information transfer through interaction of workers.

switch to foraging (Fig. 1) allowing colonies to take advantage of sudden increases in food availability. There may have been selection for a propensity in any outside worker to switch to foraging when a new food source appears, rather than selection for higher numbers of specialized foragers.

Individuals decide whether or not to perform a task actively, and this influences the extent to which a task is accomplished. Selection might be expected to shape the processes that determine when individuals are active. For example, harvester ant foragers reduce their activity from one hour to the next when the colony's rate of food intake declines[60], which prevents foragers from spending energy to forage when food availability is low. Genotypic variation among honeybee patrilines suggests that natural selection could act on task allocation through queens' mating decisions. If the progeny of different honeybee fathers differ in propensity to accomplish a task, the distribution of patrilines in a colony would influence its ability to respond to its environment[61].

The study of the evolution of task allocation is still in its infancy. With some important exceptions[62–66], most effort is devoted to understanding how task allocation operates in particular species, and until we know more about what kinds of task allocation systems have evolved, we will not be able to say much about how they evolve. Although there has been considerable theoretical work on the evolution of the partitioning of reproduction among individuals—who lays the eggs, and which sex is produced—this does not address the question of how workers are allocated to day-to-day colony tasks.

The evolutionary ecology of task allocation could be investigated empirically. We could examine how variation among colonies in task allocation is related to variation among colonies in reproductive success. Such studies could provide new insight into the evolution of other systems of interacting or cooperating units that function without central control.

Conclusion

The behavioural ecology of social insects has only recently begun to generate a variety of approaches and attract interest from many different disciplines. So far only a tiny fraction of social insect species have been studied. Social insects obtain food, build nests, and defend their colonies in an astounding variety of ways. We will probably discover the same diversity in the ways that these tasks are regulated. The data show that some combination of the internal and external factors outlined above contribute to individual decisions about task performance, and eventually we may abandon the dichotomy between internal and external causes. Current theoretical work far outreaches the data, but the models show that task allocation could operate even in a colony of identical individuals, if regulation is mediated by local cues that reflect the numbers of workers performing a task and the extent to which the task is accomplished. □

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