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# Caste and change in social insects

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Most models of the organization of social insect colonies start with a collection of individuals, each of which is assigned to a particular task. The notion of caste is fundamental to current thinking about social insects. The term was originally used to distinguish classes of insects within a colony, the members of which show strong differences of morphology and reproductive status, such as queens, workers, and males. In the mid-1960s, 'caste' came to refer to a finer subdivision: classes of workers that do particular tasks (Wilson 1963). Species with 'physical castes', such as some polymorphic ant species, contain workers of various different sizes, and those of a particular size class do a particular task. In species with 'temporal castes', such as honeybees, and many ant species, task is age-dependent; a class of adult workers of a particular age tends to do a particular task. The use of the word 'caste', which also refers to stable distinctions between groups in human societies, reinforces the notion of a task as determining a fixed attribute of particular, individual insects.

About 20 years ago, results on task specificity of individual workers began to suggest a working hypothesis for the study of the evolution of colony organization (Wilson 1968): The behaviour of a colony is a result of the numerical distribution of workers into a set of essential tasks. For example, a colony with more individuals of the caste that forages will forage more; a colony with more individuals devoted to the task of brood care will raise more brood, or raise them faster. Based on this view, Wilson (1968) introduced the notion of a caste distribution, that is, the proportion of colony members belonging to each caste, as a species character that may evolve towards the most adaptive one. For example, if natural selection favours colonies that forage more, a species may evolve colonies that contain a larger proportion of individuals of the foraging caste.

This line of argument underlies the work of Oster and Wilson (1978), to date the most comprehensive and influential attempt to model the organization and evolution of social insect colonies. In their words (p. 21):

The guiding proposition of our inquiry is that variations in caste structure and division of labor reflect differing adaptations on the part of individual species of social insects. Thus, caste is not just central to social organization; it should provide the key to the ecology of social insects, insofar as those insects differ from their solitary counterparts. We regard many of the principal processes of colony life ... as



subordinate to the evolution of caste. We postulate them to be the enabling devices by which labor is allocated and by which the colony as a whole precisely adjusts its relationship to the nest environs.

Here, I argue that this approach to the study of colony organization is now being revised in the light of recent empirical results. I will concentrate on the literature on ant behaviour, with some reference to honeybee behaviour. First I outline the evidence that colony behaviour does not depend on caste distributions, and then discuss the evolutionary implications of this conclusion. (I use 'colony behaviour' to refer to a sequence of transient behavioural states. These could be specified in various ways. For example, one could list the activities of each colony member, or use some measure, such as numbers or proportions of workers, of the intensity of colony effort devoted to certain activities). What matters in natural selection is what a colony does, for example, how much it forages or how many reproductives it produces in particular conditions. I will argue that what a colony does, its behavioural phenotype, cannot be predicted reliably by specifying the habitual task of each of its workers and counting the numbers of workers in each task category, or caste. There are three reasons why colony behaviour is not a simple function of caste distributions: (1) individuals switch tasks; (2) the intensity of colony effort devoted to various tasks changes; and (3) different colonies vary in the dynamics that link colony behaviour and environmental conditions.

## 1. COLONY BEHAVIOUR DOES NOT DEPEND SIMPLY ON CASTE DISTRIBUTIONS

### 1.1 Individuals switch tasks

There is a substantial literature to show that individuals tend to do particular tasks. A relatively new line of research examines the relation between individual task and colony environment. It is becoming increasingly clear that when colony conditions change, individuals switch tasks. Both task specificity and switching have been reviewed in Calabi (1987), who lists 26 studies showing task switching among age classes and 27 showing task-switching among size classes. Here I cite a few examples. Task-switching has been shown to occur in several kinds of situations.

1. *Disturbances* that obstruct colony activities, temperatures that endanger the brood, and newly available food sources (Meudec and Lenoir 1982; Miranda and Vinson 1981; Gordon, in press), can all cause individuals to change tasks to meet new exigencies of the colony environment.

2. *Changes in numbers of workers.* When workers engaged in one task are removed from the colony, workers previously committed to other tasks will fill in for the missing workers (Wilson 1984). Carlin and Holldöbler (1983)

added pupae of different species of the carpenter ant *Camponotus* to existing colonies, and found that differences in the species composition of a colony caused workers to change tasks.

3. *Changes in the age structure of the colony.* In species in which age cohorts do particular tasks, removals of older age cohorts accelerate the usual sequence of age polyethism for younger workers (in ants, McDonald and Topoff 1985; in bees, Winston and Punnett 1982; Winston and Fergusson 1985).

The question of task-switching arises in any attempt to specify the relation between the set of available individuals and the set of necessary tasks. There might be a simple one-to-one relation: there are  $x$  tasks,  $x$  individuals, and each individual always does one, unique task. There might be a random relation: any individual is equally likely to do any task. There might be  $x$  groups of individuals, and  $x$  tasks, each group consisting of individuals that always do a particular task. This is the relation implied by the simplest view of the caste concept. In fact, most evidence points to a fourth relation. There are distinct groups of individuals, which are sometimes classifiable by size or age. At any time, each group contains individuals that usually do a particular task. However, when environmental conditions and colony composition change, new groups form. That is, when conditions change, individuals switch from one task group to another.

It may seem intuitively obvious that an organization that utilizes a division of labour based on permanently specialized individuals is inherently more efficient. But is it? Is an organization consisting of specialized individuals necessarily more efficient than one in which each individual is capable of a variety of tasks? This question suggests an analogy with human industry, from which the phrase 'division of labour' is borrowed. When Adam Smith introduced the idea of division of labour in 1776 in his book *The wealth of nations*, he suggested three reasons why it constitutes an efficient way to organize manufacture: (1) Workers will learn to do their jobs better if they repeat the same job over and over. (2) Workers have an opportunity to slack off when they change from one job to another. 'The habit of sauntering and of indolent careless application, which is . . . necessarily acquired by every country workman who is obliged to change his work and his tools every half hour . . . renders him almost always slothful and lazy, and incapable of any vigorous application even on the most pressing occasions.' (3) When a man has only one task to do, he is likely to occupy his mind with thinking up a machine that can do it better.

Since Adam Smith's time, there has been considerable controversy about whether division of labour in a factory increases its productivity (Rose 1988). Advocates of assembly line methods disagree with those, such as the manufacturers of Saab automobiles, who believe that people work more efficiently when they have a variety of jobs to do.

However, none of Adam Smith's three advantages of individual specializa-



tion seem to apply directly to social insects. Insects are not likely to invent machines, and there is no evidence that individual specialization in animals promotes the evolution of tool use. Workers do show considerable variation in activity level, but there is no evidence that spells of worker inactivity are especially likely to occur if workers change from one task to another, rather than performing bouts of a single task, more or less interrupted by bouts of inactivity. Division of labour does not seem to reduce 'indolent careless application'. Most discussion of the division of labour in social insects seems to centre around the first of Adam Smith's reasons for it. It is not generally clear whether workers learn to do their tasks better by repeating them (although see Heinrich 1979), and experimental studies have revealed little capacity for learning an artificial task in social insects (e.g. for ants, Weiss and Schneirla 1976; Bernstein and Bernstein 1969).

However, workers may be physiologically adapted to particular tasks, and because all social insect workers are fully mature adults, one may expect such adaptations to be permanent. This is why there has been considerable attention to the ways that a worker's size may contribute to the efficiency with which it performs a particular task (Wilson 1968). But most ant species are monomorphic, that is, have only one size of worker; only 44 out of 263 genera contain polymorphic species (Oster and Wilson 1978). Task-switching goes on even in polymorphic species (Wilson 1984). Proliferating examples of task-switching suggest that the 'ergonomics of caste', that is, the fit between an individual's body size and its task, may not be the primary selective force shaping the evolution of social insect behaviour.

Oster and Wilson's models include predictions about the evolutionary consequences of behavioural flexibility. In their formulation, there is a range of tasks that an individual can perform successfully, and the magnitude of this range may vary. Thus tasks are assigned to individuals, and the repertoire of each individual may be more or less broad. Their prediction is that in species in which individuals are more flexible, that is, can perform a wider range of tasks, fewer distinct castes are needed. Their concept of behavioural flexibility maintains the primacy of caste, and considers its elasticity: within a behavioural caste, how much can a specialized individual change its task?

Oster and Wilson (1978) argue that the behavioural repertoires of social insects have decreased in the course of evolution; that is, in more advanced hymenopterans, such as ants, each individual is capable of a smaller number of different activities than in more primitive species such as solitary wasps. They suggest that one reason for this may be the increased efficiency of specialization. But the original assertion, that individual specialization has increased in colonial species in the course of evolution, is open to question. The assertion is based on estimates of the sizes of behavioural repertoires. Recently, it has been pointed out that these estimates, and comparisons among species of such repertoires, are problematic at best (e.g. Jaisson *et al.*

1988). To estimate the behavioural repertoire of a species, an observer must classify all acts into different types. The number of types is the magnitude of the reportory, and different observers tend to make very different classifications.

Oster and Wilson's models may seem to demonstrate that the social organization of colonies must depend on individual specialization because this is the most efficient type of organization. This is not the case. The models provide a theoretical framework within which to test the hypothesis about the efficiency of individual specialization. An unexpected result of such investigations is that individual specialization is not as pervasive as previously believed. Individuals change tasks. Arguments for the efficiency of individual specialization in social insects were proposed to explain the apparent pervasiveness of specialization. Put very simply, the argument is 'If individual specialization is more efficient, more specialized individuals will evolve'. If this assertion is true, any absence of permanent individual specialization is evidence against its efficiency.

Oster and Wilson (1978) do argue that parallel operations are more efficient than operations carried out in series. They explain this very clearly, using an example (pp. 13–14):

Suppose that several persons were trying to stack a specified number of bottles one on top of the other in the middle of a room. If one person tried it from the floor up, and then another started fresh, and so on, the group result would equal the average individual result. Now suppose that two or more persons work together. If their competence is low, they will tend to cancel out one another's actions. The chance of making the right combination of correct movements will be even lower than the chance of doing one thing correctly by itself, and fewer bottles will be stacked. However, as individual competence increases, the group will reach a point at which they are able to put together the right combination of moves and balance a significantly higher number of bottles. This improvement will be greater still if they divide the labor. For example, one can hold and readjust the bottles already stacked, a second can put more bottles on top, while a third can fetch still more bottles to add to the attempt.

The first part of the example describes an operation carried out in series; each person attempts to complete a series of tasks. A group of individuals can also work in parallel, each contributing to the stacking operation by doing one of the tasks involved. If individuals are competent enough, a parallel operation will be more efficient than a series one.

But the increased efficiency of parallel operations is not necessarily due to individual specialization. In the paragraph quoted above, 'divide the labor' does not imply consistent individual specialization, and this ambiguity may have misled some readers. If a particular individual holds the bottles one time and fetches more bottles the next, the advantages of working in parallel will not be diminished (Jeanne 1986*a,b*). Individual specialization is only an advantage if one individual is especially good at holding bottles, and another



at fetching them, and so on. Oster and Wilson's examples of the advantages of individual specialization in social insects are based on polymorphic species. In cases where morphological differences make particular tasks easier for certain individuals, the advantages of individual specialization are clear. But as we have seen, such cases are relatively rare.

In other parts of Oster and Wilson's book, the advantages of consistent individual specialization are confounded with advantages due to replication, or the presence of multiple workers able to do a particular task. Comparisons are frequently made between the efficiency of a solitary wasp, that does a range of tasks herself, and that of a colony of specialized individuals. But there are several differences between these two organizations. One difference is that a group of workers can be in more places, and do more things, per unit time, than a single worker can. This leads to economies of scale: the benefits in productivity of an increased worker force outweigh the average costs of supporting it. In the discussion following the paragraph quoted above, Oster and Wilson (1978) point out that the reliability of a system is increased by redundancy. As they put it (p. 15) 'if a designer is given two sets of "parts", it is better to build a single system with redundant components than to build two separate systems'. If one worker does not accomplish a task, another worker might. Economies of scale, and enhanced reliability due to replication, do not depend on permanent individual specialization. They are advantages that arise from the presence of more workers. These advantages remain even if individual workers do not specialize on a particular task.

Individual specialization, to the extent that it exists in any species, may contribute to the efficiency of that species' social organization. But, as Oster and Wilson point out, the evolution of behaviour may be strongly affected by other factors. Until we have investigated the evolutionary consequences of other aspects of colony organization, there are no grounds for assuming that natural selection acts primarily to promote individual specialization. It may be, for example, that the efficiency of specialized individuals is less important than the colony-level efficiency of switching rules. A colony's ability to re-allocate workers as colony needs change may be more important than the efficiency of individuals at particular tasks. An individual would perform one task one day, another the next. In this case, the notion of caste, which posits a fixed relation between individual and task, is difficult to apply.

The problem of individual specialization raises methodological questions as well as theoretical ones. If individuals change tasks frequently, it may not be appropriate to describe or model the system in terms of what individuals do. This would involve specifying both individuals and conditions: Ant 1 does task  $x$  in condition  $A$ , task  $y$  in condition  $B$ , task  $z$  in condition  $C$ . Ant 2 does task  $y$  in condition  $A$ , task  $z$  in condition  $B$ , and so on. From the perspective of evolutionary ecology, as Oster and Wilson (1978) emphasize, the behavioural phenotype of the colony is its important characteristic. What matters is how colonies vary in the extent to which task  $x$ ,  $y$ , and  $z$  are done.

If individuals frequently change tasks, it may be sufficient to specify the relationship between numbers of ants and various conditions, without regard to individual identity.

Individual task fidelity and the variability of environmental conditions may be linked. In many species, colonies contain large numbers of reserve workers. Presumably these reserves contribute to the flexibility of colony behaviour by providing individuals that can be channelled into tasks when they are needed. The dynamics of task switching are the rules that relate individuals and tasks in various environmental conditions. These rules govern both the recruitment of reserves to do particular tasks, and individual decisions to change tasks in particular circumstances. Selection may act as strongly on the dynamics governing individual decisions to change tasks in particular circumstances, as it does on the relation between an individual's body size and its usual or baseline task.

For example, the dynamics of task switching in harvester ant colonies reflect the species' ecological situation in a community in which a diverse guild of granivorous species are all competing for food (Davidson 1980). A series of perturbation experiments with marked individuals shows a clear trend in the direction of task-switching (Gordon, in press). In undisturbed colonies, various exterior tasks are each performed by a distinct group of workers. But when a new source of seeds suddenly becomes available, workers switch tasks. In this situation, workers previously committed to any other task, or to the reserves available for any other task, will switch tasks to forage. In contrast, no other group of workers will change tasks to do nest maintenance work. Foraging acts as a sink; nest maintenance is a source. It appears that the high priority of foraging may have shaped this species' rules for changes of task. To understand the dynamics that determine how and when individuals change task, it will be essential to compare such dynamics in a variety of ecological communities.

## 1.2 The intensities of colony activities change

Within a colony, individual workers show considerable variation in the extent to which they are active (Plowright and Plowright 1988; Lindauer 1961; Herbers 1983). Some individuals tend to be consistently more active than others; others show extremely variable activity levels. This means that even taking the tasks of particular individuals to be fixed, the numbers of workers that actually engage in them are not necessarily constant. More foragers does not necessarily imply more foraging.

The numbers that actually engage in a task may change according to changes in colony requirements for the products of that task (e.g. Kolmes 1985; Moore *et al.* 1987; Sorensen *et al.* 1985). For example, the work of Seeley (1986) and Schmid-Hempel and Schmid-Hempel (1987) shows that the activity level of individual honeybee foragers on a given day depends on



the amount of nectar obtained in the colony that day. The amount of nectar obtained is determined not just by numbers of foragers but by the dynamics relating foraging behaviour and nectar stores.

The numbers that actually engage in one task may also vary according to changes in the behaviour of workers engaged in other tasks. For example, I found that in harvester ants, nest maintenance work and foraging are done by two distinct groups of workers, and foragers do not switch tasks to do nest maintenance work (Gordon, in press). But when experimental perturbations cause larger numbers of workers to do nest maintenance work, the foragers become less active. Several exterior activities, including patrolling, are interdependent in this way (Gordon 1986, 1987).

Perturbations that change the numbers engaged in one task, cause changes in the numbers engaged in other tasks. When two or more of these perturbations are done simultaneously, the results are non-additive. The response to combined perturbations is different from the sum of responses to single ones. This means that workers engaged in one task do not have a simple, all-or-nothing response to changes in other activities. Instead, the response is modulated according to the ways that all other activities are affected.

Calabi (1987) makes a strong case that the notion of 'caste' is obsolete, on the grounds that there is so much evidence that individuals switch tasks. She goes on to present a model of colony organization in which task-switching functions to keep the colony's labour profile constant. In other words, she assumes that colonies maintain stable numerical distributions of active workers into various tasks, and that individuals switch tasks to keep these distributions at constant levels. The results described above show that this assumption is unrealistic. Colonies alter their labour profiles significantly in complex but rule-governed ways. Task-switching does not function merely to maintain constant labour profiles. It also contributes to changes in numbers of workers engaged in different tasks.

The result that colonies change their allocations of efforts to various tasks, depending on environmental conditions, has important implications for future research. One is that activities cannot be understood independently of each other. For example, models of foraging in ants (e.g. Taylor 1978) predict how forager behaviour and morphology will evolve in response to conditions affecting the efficiency of foragers. However, forager behaviour changes significantly in response to events affecting workers engaged in other tasks. This means that selective pressures on foraging success are as likely to act on the dynamics of interactions between foragers and other worker groups, as they are on the characteristics of foraging itself.

Several time-scales, from the hourly to the ontogenetic, are relevant to the dynamics of colony behaviour. Individuals adjust their behaviour based on moment-to-moment (Meudec and Lenoir 1982) and hour-to-hour (Seeley 1986; Gordon 1987) changes of colony environment. The dynamics of colony

behaviour also change as a colony matures. In younger colonies, individuals appear to be more flexible with respect to task (Lenoir 1979; Gordon, in press). I found that in 2-year-old harvester ant colonies, interactions among worker groups are different from those in 5-year-old colonies. That is, events affecting workers engaged in one task elicit changes in the numbers engaged in other tasks, and such changes are qualitatively different in older and younger colonies. For example, when older colonies are exposed to several simultaneous disturbances, their behaviour emphasizes foraging. That is, as things get worse for an older colony, it devotes more effort to foraging. This is not the case in younger colonies. Also, different groups of older colonies show similar responses to the same experiments. But the responses of different groups of younger colonies to similar experiments are much less consistent than those of older colonies. As ants live only for a year, behavioural differences in 2- and 5-year-old colonies cannot be due to the accumulated experience of 5-year-old ants. Instead, the organization of the colony must change as it matures. The dynamics of interactions among worker groups, which determine the allocation of colony effort, depend on colony age.

Caste distributions alone, or ontogenetic changes in a colony's caste distributions, are insufficient to predict these results. Specifying the task that individuals usually do, even if they do not switch tasks, does not specify how much of the task will be done in particular conditions. That is, caste distributions do not predict allocation of effort. To predict colony behaviour, we also need to know how the allocation of effort varies as the environment changes.

### 1.3 Variation among colonies

No one expects all colonies of a species to behave in exactly the same way. But in the past 20 years of research on social insects, two trends seem to reinforce each other: the use of caste distributions to explain colony behaviour, and concern with variation in behaviour among individuals within a colony, rather than with variation among colonies.

The literature on task-specificity in ants provides an example. To determine how likely individuals are to continue with particular tasks, it is necessary to mark individuals engaged in particular tasks, and to observe what tasks they do subsequently. I surveyed the literature of the past 10 years for reports of such experiments. Table 1 shows some features of the experimental design of such studies. I exclude references to work that does not examine behaviour independently of physical caste, that is, which assumes but does not document a correlation between behaviour and worker size. Most of the studies are based on data from a very small number of colonies. Data for different colonies are frequently pooled, making it





Table 1  
 Variation among colonies in investigations of task fidelity. F=field, L=laboratory  
 X=discussed, -=not discussed

Lab. or field	No. of colonies observed	Data given for colonies		Variation		Reference
		Pooled	Separately	Among colonies	Within colonies	
F	3	?		-	-	Calabi <i>et al.</i> (1983)
L	1	1		-	-	Carlin (1981)
F	4	4		-	-	Fowler and Roberts (1980)
L	5		5	-	-	Gordon (1984)
F	44		44	X	-	Gordon (in press)
F	21	19		X	X	Herbers (1979)
L	3	3		X	-	Herbers (1983)
F	1	1		-	-	Herbers (1977)
L	1	1		-	-	Hölldobler and Wilson (1986)
L	5	5		-	-	Lenoir and Ataya (1983)
L	2	2		-	-	Meudec and Lenoir (1982)
L	3	?		-	-	Mirenda and Vinson (1981)
F	4	4	2	-	X	Porter and Jorgensen (1981)
F	3	3	2	X	X	Rosengren (1977)
L	1	1		-	-	Traniello (1978)
L	1	1		-	-	Wilson (1976)
L	1	1		-	-	Wilson (1978)
L	1	1		-	-	Wilson (1980)
L	1 per species	1?		-	X	Wilson (1984)
L	1	1		-	-	Wilson and Hölldobler (1985)
L	3	3		-	-	Wilson and Hölldobler (1986)

impossible to discern variation among colonies. Fifteen out of 21 studies are done in laboratory conditions.

The way least likely to reveal task-switching is to look at small numbers of colonies in the laboratory. Small numbers of colonies would tend to vary less in colony requirements than larger numbers because a small sample can capture less of the natural range of variation than a large one. Laboratory

conditions tend to be more stable than field conditions, so changes in colony environment that lead to task switching would be less likely to occur in the laboratory.

A methodology that ignores variation has wide-ranging consequences for theories of social organization in insect colonies. Consider an example from a different field. A developing embryo passes through critical periods during which particular stimuli can drastically alter the course of differentiation. An investigator who observes but one embryo, in conditions under which these stimuli do not occur, would never guess at the existence of these dynamics. An investigator who observes a large number of embryos may happen to observe one that undergoes alteration, and decide to examine the causes of the alteration. Finally, an investigator who undertakes a series of experiments in which embryos are exposed to crucial stimuli at different stages of development, will be most likely to understand the dynamics of differentiation.

Observations of few colonies, in very stable conditions, over short time periods, are likely to lead to uniform results, which can be deceptive in two ways. First, they can give the impression that what is true of one colony is true for all colonies of that species. In other words, they can suggest that certain, stable attributes are characteristic of the species in general. Secondly, such observations can mask the presence of a dynamic process. Variation brought about by different conditions leads to an investigation of dynamics, the rules relating different states of colony behaviour to different conditions. Apparent uniformity leads to the assumption that there are no such dynamics, that only one state of the system is typical.

Johnston and Wilson (1985) expressed some surprise on finding significant variation among the caste distributions of four *Pheidole* colonies, and pointed out that inter-colony variation has received insufficient attention. To study the evolution even of caste distributions, it is clearly essential to know how they vary. Herbers (1983) goes further to point out, as I do here, that variation within colonies over time may be the consequence of interesting dynamics that have yet to be investigated.

For colony organization to evolve by natural selection, there must be variation in behaviour among colonies. The variation should be investigated. It is reasonable to consider, first, variation in those aspects of colony behaviour that affect reproductive success. As Oster and Wilson (1978) suggest, the amount of food a colony acquires, the extent to which it protects its nest and claims new territory, the numbers of new workers it produces to carry out its work—all can be expected to affect colony survivorship and reproductive success. The results discussed above show that these aspects of colony behaviour all depend on the dynamics that determine how foragers, patrollers, nurses, etc., react to each other and to changes in the colony's environment. Such dynamics are characteristic of species, but will vary among colonies of a species, as will environmental conditions. The evolution



of colony behaviour involves the evolution of these dynamics. To understand the dynamics of colony organization, and how these dynamics evolve, students of social insect behaviour will have to adopt the experimental techniques of population biology. As well as looking at large numbers of individuals within colonies, we will have to look at large numbers of colonies, and how their behaviour changes with time.

## 2. THE EVOLUTION OF THE DYNAMICS OF SOCIAL INSECT BEHAVIOUR

Current theory of the evolution of social insect behaviour comes from two sources, kinship theory (Hamilton 1972), and the theory of the division of labour based on physical and temporal castes. Asymmetries in the relatedness of queens, males, and workers help to explain why a sterile worker class is perpetuated by natural selection. Kinship theory has also led to predictions about the sex ratios of colony reproductives (Trivers and Hare 1976). But kinship theory has not generated explanations of the complexities of the day-to-day behaviour of social insect colonies. On the other hand, optimization theory on the division of labour among worker subcastes *has* led to predictions about colony behaviour (Oster and Wilson 1978). However, the model is based on an assumption that colony behaviour is a function of caste distributions. This assumption is unrealistic.

Caste distributions are only a first step in predicting colony behaviour. In addition, the following factors must be considered:

1. For each task, baseline numbers of workers available to do it; caste distributions.
2. Switching rules: although individuals are committed to some baseline task, they may also switch tasks according to certain dynamic rules. These rules can be catalogued according to baseline task. For each group of workers, what tasks will they switch to, and under what conditions?
3. Intensity rules: at any moment, each of the colony's tasks has a certain group of workers committed to it. (This group may or may not contain workers that have switched over from some other task.) The intensity with which a given task is done, in terms of numbers of individuals carrying out the task and the amount of effort these individuals devote to it, depends on the dynamics of group-level interactions. That is, the intensity of effort devoted to a given task depends both on factors affecting how much of *that* task is done, and on factors affecting how much of *other* tasks are done. For each task, what causes the numbers engaged in it to increase and decrease? How do the numbers and effort devoted to a given task depend on the numbers and effort engaged in other tasks?

4. Developmental rules: switching and intensity rules change during the life history of the colony. How do the dynamics of (2) and (3) depend on colony age and colony size?

5. Variation among colonies in (1)–(4); in caste distributions, and in switching, intensity, and developmental rules.

The transition away from a research programme based on caste requires conceptual changes that are familiar in biology. The 'one gene–one protein' dogma of Beadle and Tatum was welcomed because it furnished a simple starting point for molecular biology. Jacob and Monod's discovery of the lac operon paved the way for new research which eventually showed that the dogma had to be abandoned. One cannot simply assign particular functions to particular genes; instead there are complex dynamics which regulate which genes are transcribed, when, and how much; and how the gene products function in the organism. In the same sense, though 'one worker–one task' provided a fruitful starting point for social insect research, it is now clear that more complex processes regulate what a worker does, when, how much, and what the colony-level consequences of a worker's behaviour will be.

We need new ways of understanding the organization of social insect colonies. In recent theoretical articles, Wilson and Holldobler (1988) and Seeley (1987) have emphasized two important aspects of colony organization. The first is that colonies function without hierarchically organized control systems. A version of this can be found in the Old Testament (Prov. 6:6) 'Look to the ant . . . who having no chief, overseer or ruler, provides her bread in the summer and gathers her food in the harvest'. The organization of social insect colonies is fundamentally different from that of hierarchically organized human groups, such as armies, corporations, orchestras, or governments. The behaviour of social insect workers is not directed by other insects in positions of authority.

A second point, discussed above, is that many of a colony's tasks are carried out in parallel, not in series. This is an efficient way to organize any system of interactive units, including social insect colonies, brains, and computers. There is an obvious analogy between brains and social insect colonies. Both are composed of relatively simple units, workers or neurons, that interact to do relatively complicated things: in colonies, maintain a nest, obtain food, and reproduce; in brains, think, learn, and remember. A long-standing debate in neurobiology centres around the question of whether particular functions are associated with particular neurons. Hebb (1949) and Lashley (1950) suggested that mechanisms for learning must be based on connections among neurons, and that particular neurons could play a variety of roles in the resulting interactions. At the time this seemed a radical suggestion, but it is now widely accepted (Dreyfus and Dreyfus 1988).



In neurobiology and artificial intelligence research, current interest in parallel processes extends to models that go a step further than the ideas outlined by Seeley and Wilson and Holldobler, to parallel *distributed* processes (Rummelhart and McClellan 1987). A system's functions are distributed when tasks are not assigned to specialized units, but are carried out by different units at different times. A parallel distributed processes (PDP) model of a social insect colony would attempt to describe the rules that structure the interactions of interchangeable workers, such as the rules governing changes of individual task and changes of colony activity. PDP models provide one way to take into account a third aspect of colony organization: colonies can behave predictably and adaptively without permanent individual specialization. Such models may be useful in formulating new theories of the evolution of social organizations not based on caste.

A PDP model of the dynamics of harvester ant behaviour (in preparation with B. Goodwin and L. Trainor) has several interesting properties. The predictions of the model can be formulated in terms of an energy landscape. The landscape sits in a space whose axes correspond to the numbers of ants engaged in various tasks. Any point or location in the landscape corresponds to a particular behavioural state of the colony, specified as the numbers of ants active in various tasks, and the numbers of ants inside the nest available to do each task. The height of any point in the landscape corresponds to an 'energy' value, a metaphor used to specify how likely it is for the colony to reach that state. An arbitrary convention, based on the idea of gravity, determines that colonies are more likely to be found in behavioural states of lower height or energy. In other words, colony behaviour tends to roll into the valleys of the landscape. Workers are assigned to different tasks, and can be either active or inactive participants in that task. Changes in the numbers of workers engaged in each task can come about in one of two ways: (1) individuals can switch tasks, and (2) the numbers engaged in various tasks can vary as individuals move back and forth between the active and inactive members of a particular task group. Such changes are determined by summing many simple interactions between pairs of ants, such as interactions between two active patrollers, or between an active patroller and an inactive forager, etc. The sign of the interaction determines its outcome. For example, a negative interaction between active workers of the same task group causes them to become inactive when they meet. If all permitted interactions are equal and negative, a system of simple negative feedback is set up. This can be adjusted to produce the stable distributions of individuals into task groups first suggested by early formulations of caste models.

The strength or magnitude of such interactions can also be varied. The relative magnitude of the interactions between different pairs of worker groups determines the bumpiness of the energy landscape. Smaller ratios produce a smoother landscape. A smoother landscape is more stable because the heights or energies of neighbouring regions of the landscape are similar.

This means that the probability of being in a particular behavioural state is close to the probability of being in a slightly different, neighbouring state. Suppose the interaction between foragers and patrollers is similar in magnitude to the interaction between nest maintenance workers and foragers. In this case, the dynamics of colony behaviour will be relatively stable. If interactions between the first two groups have little effect, while interactions between the second two produce large changes in the colony's behavioral state, colony behaviour will be much less stable. By varying the interaction strengths, it is possible to simulate the behavioural dynamics observed in harvester ant colonies. These results suggest that it may be useful to envisage the organization of behavioural flexibility in an ant colony as a parallel distributed process. Such models have provided interesting new questions about the flexibility that enables brains to learn and remember, and are now generating empirical hypotheses about the organization of social insect colonies.

New kinds of empirical research are needed to complement the formulation of new models of colony organization. Beginning a study of a social insect species, it is no longer sufficient to ask, how many tasks does this species do, and which individuals do each task? A study of flexibility may begin with these questions but must proceed towards some new ones. In a range of environmental conditions, how does this species' behaviour change? At least two kinds of change can be investigated. First, there are changes in task fidelity, the relation between individuals and tasks; that is, changes in which individuals do which tasks. Secondly, there are changes in the numbers of workers allocated to various tasks. Natural selection will act on variation within species in behavioural phenotype; thus variation in extent and type of flexibility, a crucial aspect of behavioural phenotype, must be measured. Understanding the relationship between variation in flexibility, and variation in survivorship, will open the way for ecological and evolutionary predictions. The ontogeny of these rules can be followed by testing how colonies of varying ages respond to alterations of their environments. In many species, mortality varies with colony age. This strongly suggests that ontogenic variation in a colony's reaction to its environment is a crucial life history characteristic.

There are a multitude of empirical questions to be addressed, analogous to those originally raised about caste distributions. We will need to know a great deal about the dynamics of colony behaviour: how species differ, how colonies of a species vary, how such dynamics change during a colony's life history, how they affect colony survivorship, and the extent of their heritability. The work reviewed above shows that considerable progress has been made towards addressing these questions. It is no longer possible to fit most empirical results into a theoretical framework that accounts for colony behaviour in terms of caste distributions. The theory of adaptive caste distributions inspired 20 years of productive work in social insect behaviour. The results call for new theoretical and empirical directions.



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