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Behavioral Discretization and the Number of Castes in an Ant Species

Edward O. Wilson

Museum of Comparative Zoology Laboratories, Harvard University,
Cambridge, Massachusetts, USA

Summary. 1. Two extreme possibilities in the evolution of temporal castes can be envisaged. First, workers can undergo changes in responsiveness to various kinds of stimuli in a strongly discordant manner as they grow older, so that each task is addressed by a distinctly different frequency distribution of workers belonging to different age groups. Because these age-frequency distributions change almost gradually from one task to another in covering many such tasks, the resulting temporal caste system is referred to as continuous. At the opposite extreme, the aging worker can undergo changes in responsiveness to different stimuli in a highly concordant manner, so that all of the tasks are attended by one or relatively few frequency distributions of workers belonging to different age groups. The resulting temporal caste system is referred to as discrete, and the evolutionary process leading to it is called behavioral discretization (Fig. 1).

2. The temporal system of the minor worker caste of *Pheidole dentata* proves to be much closer to the discrete state, although it is not extreme in form (Figs. 3, 4). On the basis of ethograms constructed of stressed and unstressed colonies in which the approximate ages of the minor workers were known, it is possible to recognize five discrete female castes: the queen, a single temporal subcaste of the major worker, and three temporal subcastes of the minor worker. These are the elements which can now be employed in ergonomic analyses of the species' caste system.

Introduction

A basic but hitherto unsolved problem of insect sociobiology is the exact number of castes found in each colony of a given species. The exact analysis of ergonomics depends on the specification of this parameter. Until the present time an imaginary number has been set for the purposes of model building and the analysis pursued as a largely theoretical exercise (Wilson, 1968; Oster, 1976).

The problem can be partly solved where physical castes exist and are discrete enough simply to be counted. Even when variation is continuous it is often possible to equate castes with the distinct modes of multimodal size-frequency distributions. But this solution takes us only half the way. Most eusocial insects, and virtually all those characterized by advanced traits in communication, queen-worker differentiation, and other important social qualities, also display temporal polyethism: the worker changes roles, usually progressing from nurse to forager, as it grows older (reviews by Wilson, 1971; Michener, 1974; Schmidt 1974). The temporal shift is ordinarily complex. Earlier I showed that for the purposes of optimization studies it is useful to define age groups as equivalent to physical castes (Wilson, 1968). The castes can then be conveniently defined as discrete age-size groups. The present report examines the intriguing question of whether in the course of evolution eusocial species themselves have discretized age-size groups or whether they have opted for more complex continuous systems. Data are then presented to show that in at least one ant species (*P. dentata*) discretization has occurred, and fits what appear to be peculiar spatial arrangements in the colony.

Results

1. The Alternatives Open to Evolving Ant Species

Figure 1 presents the two extreme alternatives open to an ant species in the process of evolving temporal castes. The ageing period depicted is that which occurs from the moment of the adult worker's eclosion from the pupal skin to the moment of its death by senescence. The worker's entire life span is arbitrarily divided into six periods (the number was chosen to conform with the six periods used in the experimental work to be reported later). The worker is envisaged as undergoing physiological change with age such that its responsiveness to each of various contingencies is altered out of phase with reference to the alteration of the other contingencies. Suppose that T_1 is the responsiveness to a misplaced egg: the curve indicates that when the worker is very young (age I) it is likely both to be in the vicinity of the egg and to react by picking the egg up and putting it on an egg pile. Its location and/or behavioral responsiveness change as it ages in such a way that its probability of response to the contingency drops off rapidly after ages I or II.

Let us now consider the possibilities. In the upper half of Figure 1, labeled Model 1, the response curves to four contingencies (T_1 through T_4) are all out of phase. The curve of response to T_1 (misplaced egg) is different from the curve of response to T_2 (say, a hungry larva), and so on. As a result, the ensemble of age groups, represented on the right-hand side by the frequency distribution of workers in different age groups that attend to task T_1, is different from that attending to T_2, and so on. As the number of contingencies is increased, and their response curves are all made discordant, there will be one age-group ensemble for each task. *Let us now define an age-group ensemble as a caste, a temporal caste to be exact, and state that in Model 1 there is a caste for each task.* However, the distinction of age-group ensembles will soon be blurred as more tasks are added. The overlap in the age-group frequency

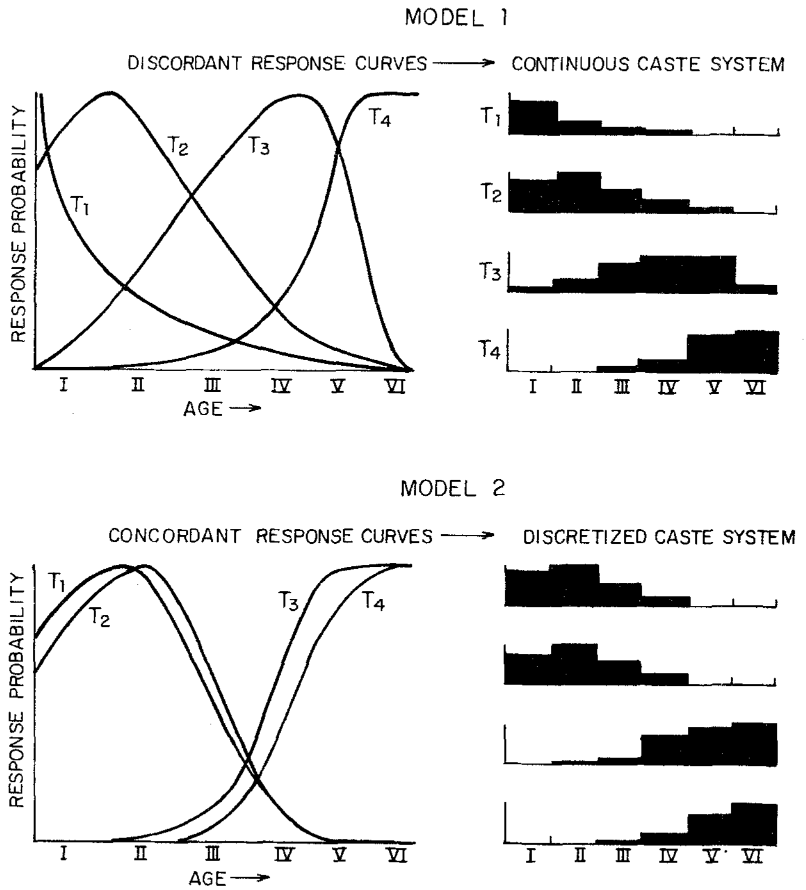

Fig. 1. The two extreme alternatives open to an ant species in the evolution of temporal castes. The age of adult workers is arbitrarily divided into six periods. In the first model (*upper*) the responsiveness of the worker to each of four contingencies (T_1 through T_4) changes markedly out of phase with reference to its responsiveness to the other contingencies. As a consequence each of the four contingencies are met by a distinct ensemble of age groups (temporal castes) which are represented on the right by the frequency distributions of workers in different age groups attending to the contingency. If the number of contingencies were increased substantially, the overlap of the age-group ensembles would increase to a corresponding degree and the resulting system would approach a continuous transition. In the second model (*lower*) the response curves are clustered into groups that are approximately in phase, resulting in more than one contingency being attended to by the same age-group ensemble (caste). If the number of contingencies were increased substantially, the number of age-group ensembles would remain small

curves is so extensive that after ten or so contingencies are added, the system becomes effectively continuous. For this reason I suggest that such an arrangement be called a *continuous caste system*.

The approach to continuity in Model 1 is marked by complexity and subtlety. The evolving ant species can easily adjust the programming of individual worker responsiveness to attain discordance, which in turn yields one caste specialized for each task. Thus only a relatively elementary alteration in physiology is needed to produce a complex caste system.

Next consider the alternative option, depicted in the lower half of Figure 1. Here various of the response curves are concordant, or at least approximately so. As a result the same statistical ensemble of workers attends to more than one task. As the number of tasks increases, the number of castes does not keep pace; conceivably it could remain low, say corresponding to as few as 2 or 3 distinct ensembles. Thus the species has chosen to operate with a *discrete caste system*—comprised of a relatively few, easily recognized age-group ensembles. The evolutionary process leading to such a system can be called "behavioral discretization." It is attained through physiological alterations as potentially simple as those that yield continuous cyste systems.

2. *An Analysis of Temporal Castes*

Which evolutionary route have ant species actually followed? We know that the behavior and physiology of workers change profoundly with age, and that this shift is a widespread if not universal pattern in the 12,000 or more living ant species. In general, workers begin their adult lives nursing immature forms and gradually progress to the status of full-time foragers. Many aspects of the change have been documented in detail in the genera *Formica* (Otto, 1958; Dobzrańska, 1959) and *Myrmica* (Ehrhardt, 1931; Weir, 1958; Cammaerts-Tricot, 1974, 1975), but the data are still not complete enough or of such a character as to distinguish the presence or absence of discretization in temporal castes.

In order to make this distinction I selected an ant species, *P. dentata,* which has proved especially favorable for laboratory studies of caste (see Wilson, 1975, 1976a). The analysis consisted of three sequential stages, which are (1) construction of ethograms, (2) age determination, and (3) measurement of temporal division of labor.

a) Behavioral Repertories. The study began with the cataloging of behaviors of the workers caste of *P. dentata.* Over a period of a week, a total of 14 h was devoted to the accumulation of 1,406 records of separate acts by a single colony. Although the acts were recorded at random within a given region of the nest or nest vicinity under surveillance, the region itself was not chosen randomly; instead, the brood area was consistently favored. The result, then, is not a precise frequency diagram but rather a list of the great majority of activities in which these ants engage.

The repertories are presented in Table 1. Recognition is made of the fact that the workers of *P. dentata* are divided into two very different subcastes unconnected by intermediate forms: the minor workers, which have the ordinary body proportions of myrmicine worker ants and which conduct most of the foraging, nest construction, nursing of immature stages, and other quotidian tasks; and the major workers, which have massive heads filled mostly with the adductor muscles of the mandibles and which are anatomically and behavio-

Table 1. Relative frequencies of behavioral acts by the two physical castes of the ant *P. dentata* in an undisturbed colony. N, total number of behavioral acts recorded in each column

Behavioral act	Frequency of behavioral acts minor workers (N=1,222)	 major workers (N=204)
Self-grooming	0.18003	0.56373
Allogroom adult		
Minor worker	0.04992	0
Major worker	0.00573	0
Alate or mother queen	0.01146	0
Brood care		
Carry or roll egg	0.01391	0
Lick egg	0.00245	0
Carry or roll larva	0.12357	0
Lick larva	0.09984	0.02941
Assist larval ecdysis	0.00409	0
Feed larva solid food	0.00573	0
Carry or roll pupa	0.03601	0
Lick pupa	0.01882	0
Assist eclosion of adult	0.00818	0
Regurgitate		
With larva	0.02128	0
With minor worker	0.03764	0.22059
With major worker	0.00573	0
With alate or mother queen	0.00327	0
Forage	0.12111	0.02941
Feed outside nest	0.04337	0.01471
Carry food particles inside nest	0.05237	0
Feed inside nest	0.05810	0.01471
Lick meconium	0.00573	0
Carry dead nestmate	0.01882	0.04902
Carry or drag live nestmate	0.00246	0
Eat dead nestmate	0.06383	0.07843
Handle nest material	0.00655	0
Totals	1.0	1.0

rally specialized for colony defense. The major workers also store more liquid food in their crops on a per-gram basis with respect to their body weight and can therefore also be regarded as a storage subcaste. The repertories reveal strong behavioral differences between the two subcastes, as well as an overall behavioral impoverishment of the major workers. Both are qualities found generally in such completely dimorphic ant species. The minor workers were observed in the performance of 26 kinds of behavioral acts. This number is arbitrary to an extent, in the sense that some of the categories could be combined or

Table 2. Relative frequencies of responses by the two physical castes of the ant *P. dentata* to stress. The responding individuals of both castes were recorded up to the moment that 200 minor workers had been counted

Stress imposed on colony	Number of minor workers responding	Number of major workers responding
Assault: a white card was placed on top of the nest, which was then tapped and shaken; the ants swarming over the card were then counted	200	1
Assault: ten fire ants (*Solenopsis geminata*) were placed 20 cm from the nest, and the *Pheidole* emerging from the nest to fight were counted	200	47
Burial: soil and leaf litter were dumped over the nest entrances, and the ants engaged in digging the colony out were counted	200	0
Exposure: a large quantity of larvae and other immature stages were dumped from the nest onto the floor of the foraging arena; the ants that retrieved them were counted	200	8

subdivided to make a lower or higher number. Through the employment of the Fagen-Goldman method based on the fitting of the frequency data to a lognormal Poisson distribution (Fagen and Goldman, 1976), the true number of behavioral acts in the minor worker repertory was estimated to be 27, with a 95% confidence interval of [26, 28]. These numbers are comparable to those based on repertories of the worker caste of monomorphic *Leptothorax* species and of the minor worker subcaste of *Zacryptocerus varians* (see Wilson, 1976b). The major workers of *P. dentata* were observed performing 8 kinds of behavioral acts; the true number was estimated to be 9, with a confidence interval of [8, 10]. Unlike the minor workers, the major workers do not appear to undergo significant age-related changes within this limited repertory.

In order to assess division of labor further between the two subcastes, a colony was subjected to four kinds of major stress encountered in nature. The results, given in Table 2, again demonstrate strong differences between the two forms. Major workers apparently never participate in excavation, even when the colony has been buried. They respond strongly to invasion by fire ants, which are among the chief enemies of *P. dentata* in nature (but much less strongly to other kinds of ants; see Wilson, 1976a). Surprisingly, major workers hardly respond at all to a mechanical disturbance of the surface of the nest, the kind of stimulus that would be associated with the approach of a vertebrate. However, many of the minor workers swarm out excitedly and attack any alien object they encounter. When the brood is suddenly exposed, which would occur if the nest were broken apart, a few major workers join in the retrieval effort. However, they are proportionately less represented than the minor workers, and they quit sooner, even when brood pieces still lie about exposed.

b) Age Determination. The second step in the study was to devise a way of estimating the age of individual minor workers. Advantage was taken of the fact that the integument of individuals is clear yellow when the ants first eclose, and gradually darkens to a deep blackish-brown as the ant grows older. With practice I was able to separate workers into six color classes, which were then labeled I (lightest and youngest) through VI (darkest and apparently oldest).

In order to estimate the true ages of workers in these six stages, 21 minor worker pupae were segregated in artificial nests with groups of stage-VI workers. The latter workers were chosen to be the companions because their already dark color made them easy to distinguish from the young workers under observation. Following their eclosion the young workers were then classified each day according to color. During the period of the observation the temperature varied from 21° C to 35° C and averaged about 28° C. A description of each color phase and its average duration (to the nearest day) are given in the following list. With the exception of one worker that remained in stage V for 10 days (instead of the average of 6), the 21 workers changed through all color phases within three days of each other.

Stage I. Body uniformly clear yellow. Newly eclosed; duration of stage: 0 to 2 days after eclosion.

Stage II. Body mostly clear yellow but gaster ("abdomen") a slightly contrasting light yellowish-brown. Duration of stage: 2 to 7 days after eclosion.

Stage III. Thorax clear yellow, head and gaster a slightly contrasting light yellowish-brown. Duration of stage: 7 to 9 days after eclosion.

Stage IV. Thorax clear yellow to light brownish-yellow, head and gaster a contrasting medium to dark brown; occasionally the head is also light yellowish-brown. Duration of stage: 9 to 10 days after eclosion.

Stage V. Head and gaster dark brown, thorax a slightly contrasting medium brown. Duration of stage: 10 to 16 days after eclosion.

Stage VI. Body nearly uniformly dark brown, with at least extensive patches of dark brown covering most of the pronotum and mesonotum of the thorax. Duration of stage: 16 days after eclosion to death.

As soon as the behavioral studies had been completed, the entire adult population of the main observation colony was censused. The physical castes present were 6 queens (5 alate, virgin individuals born in the nest, plus a single dealate, mother queen), 1,093 minor workers, 82 major workers. The proportions of age groups among the minor workers are given in Figure 2. It will be

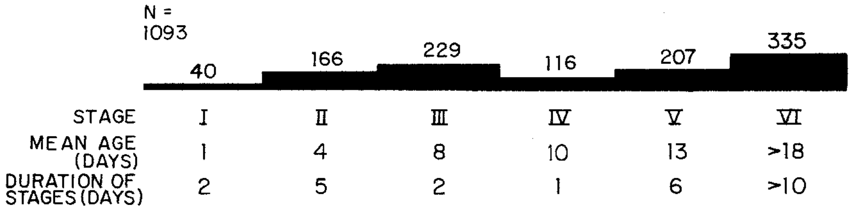

Fig. 2. The mean age, duration, and representation in the main observation colony of the six color stages of the *P. dentata* minor worker

noted that these proportions do not correspond closely to the relative durations of the age periods, as would be expected in a continuously growing colony with a steady rate of oviposition by the queen. In fact, brood development is not uniform; eggs appear to be laid in surges, and occasional peak periods of eclosion have been noted. The present study, as suggested by the data in Figure 2, was conducted when the number of young adult workers (Stages II-III) was relatively high.

c) Measurement of Temporal Division of Labor. In the third and final stage of analysis, information gained from the ethograms and aging studies were employed in a further study of the division of labor by the various age groups of minor workers. Additional ethograms were now compiled, taking into account the ages of the individuals. The results, based on 2,331 behavioral acts recorded during a five-day period, are presented in Figure 3. In two categories, "defend nest" and "excavate nest", stresses identical to those described in Table 2 were applied. Otherwise, the colony was observed in an undisturbed condition. The colony used in the study was in a mature, vigorous state, having recently produced a crop of winged virgin queens. Two conditions of a fleeting nature happened to exist during the study: the brood contained few larvae of intermediate size and, as just noted in the discussion of the adult census data of Figure 2, there was a relatively large number of younger workers. However, some "unusual" circumstance or other will always prevail in particular colonies, since oviposition and brood rearing are not uniform through time. The conditions that were encountered did not appear of such a nature as to influence the results in any important way.

Frequency data were taken for all 26 categories of behavior (reduced to 25 by lumping "regurgitation with the queen" and "allogroom the queen" into one category called "attend mother queen") plus two other categories, "guard nest entrance" and "guard food site" which are based on the location of workers rather than behavior as such. Still one other, "retrieve prey" was not in the original ethogram because of its rarity, but was added for this stage of the analysis. Thus a total of 28 categories was considered. *The data indicate discretization of the minor workers into three temporal castes; the relatively small size of this set conforms to Model 2 of Figure 1.* Fifteen of the 28 categories are represented in Figure 3. The remaining 13 categories can be characterized as follows:

1. Five (self-grooming, allogrooming minor and major workers, regurgitating with minor and major workers) are engaged in by all the minor workers, without apparent age bias. They do not contribute in any evident way to temporal division of labor, although if the direction of flow during regurgitation could have been ascertained, it is possible that an age-dependent pattern would have been detected.
2. Three categories (feed larva solid food, carry dead nestmate, eat dead nestmate) conform to pattern B, while three (feed outside nest, feed inside nest, carry food particles inside nest) conform to pattern C.
3. Two categories (assist larval ecdysis, lick meconium) were observed on too few instances to permit an assessment.

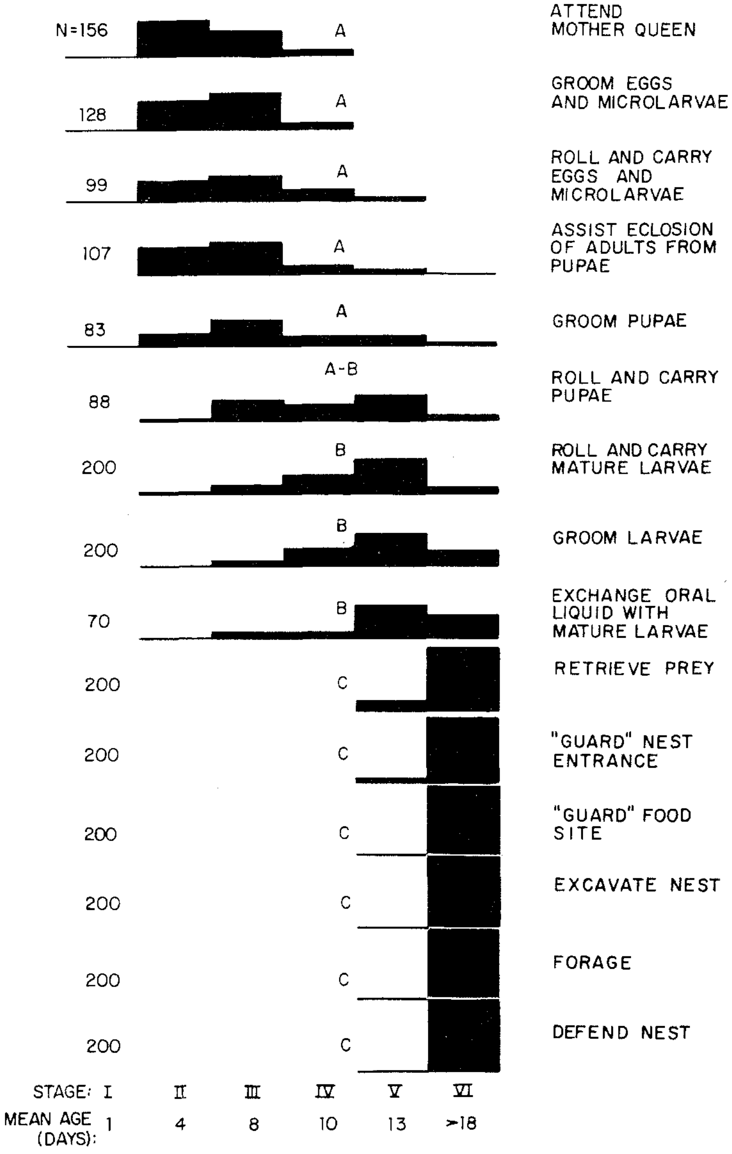

Fig. 3. The proportions of workers of the six age groups attending to all of the principal tasks are given in a series of histograms. The number of observed performances of each task, totaled through all of the age groups, are given on the left. The age groups (I-VI) and the average age of workers in each are given at the bottom. The histograms are classified into three groups (*A*, *B*, *C*), which are then identified as the temporal castes

In summary, 20 of the 28 behavioral categories are divided among three discrete age-group ensembles. Of the remaining 8 categories, 5 are conducted by workers with no evident age bias and can be eliminated from the analysis; 2 others are based on insufficient data and cannot be assessed. This leaves

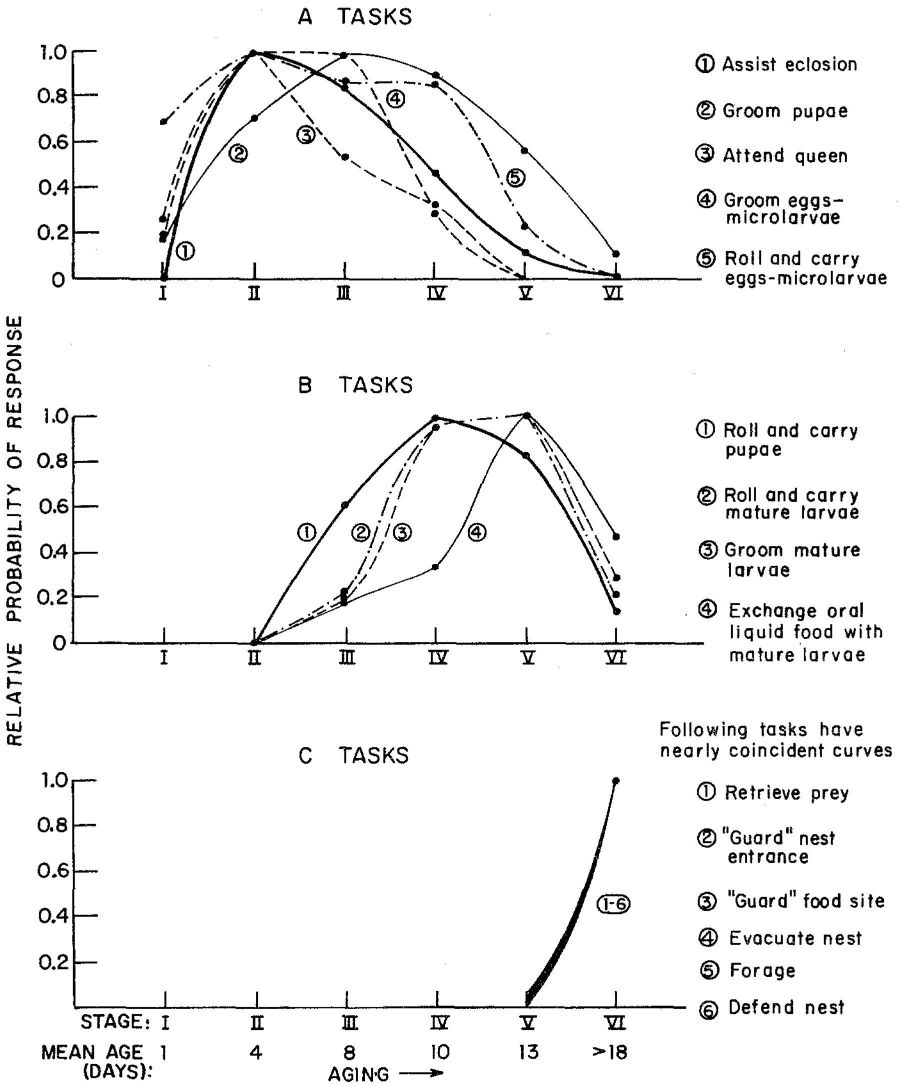

Fig. 4. The estimated curves of relative probability of response, to 15 contingencies, by minor workers of different ages

only one category which is known to be attended to by a fully intermediate ensemble, in this case (roll and carry pupae) intermediate between ensembles *A* and *B*. One might argue for recognizing a fourth caste for the last category, instead of calling it intermediate. However, this seems excessive in view of the fact that there is only one category; also individual workers performing the tasks were seen frequently to switch to the *A* or *B* tasks.

As suggested in the original model (Model 2 in Fig. 1), such discretization can be achieved by concordant response curves. Although these curves could not be drawn from data taken in the present study, their general form can be deduced from the age-group frequency data of Figure 3. The "relative probability of response" is defined as the probability that a worker in a given age group will attend to a particular contingency relative to the probability that a worker in some other designated age group will attend to a similar contingency. The age group designated for comparison is arbitrarily selected to be the most responsive one; as a result the "relative probability of response" can range from zero to one. The measure is derived in two steps as follows:

$$\begin{array}{c}\textit{Probability of response}\text{ by a}\\ \text{member of a given age group}\end{array} = \frac{\begin{array}{c}\text{Proportion of workers attending to the task}\\ \text{that belong to the age group}\end{array}}{\begin{array}{c}\text{Proportion of workers in}\\ \text{the total colony population}\\ \text{that belong to the age group}\end{array}}$$

$$\begin{array}{c}\textit{Relative probability of response}\\ \text{by a member of the age group}\end{array} = \frac{\begin{array}{c}\text{Probability of response by a member}\\ \text{of the age group}\end{array}}{\begin{array}{c}\text{Probability of response by a member of the}\\ \text{age group with the highest such probability}\end{array}}$$

In Figure 4 the curves of the relative probabilities of response are given with reference to the 15 behavioral categories for which frequency data were given previously (in Fig. 3).

Discussion

Why have the minor workers of *P. dentata* been discretized into just three temporal castes? The question can now be more precisely phrased: why have certain tasks been so closely coupled with each other in the response patterns of aging workers? For example, the age group of workers that assist the eclosion of others from pupal skins is nearly or exactly the same age group that attends the mother queen but it is strongly different from the age group that attends mature larvae. The age group that searches for food is nearly or exactly the same that excavates the nest but wholly distinct from the workers that nurse the first instar larvae. Furthermore, direct observations showed that the same individual workers shift from one task to another within the purview of their age group. If specialization within a temporal caste occurs, for example if one *A*-caste worker devotes itself mostly to the queen and another to the eggs, such specialization is at best very weak.

I would like to suggest that the observed discretization of temporal castes is an adaptation that increases *spatial efficiency*. It is obviously more efficient for a particular ant grooming a larva to regurgitate to it as well, or for the worker standing "guard" at the nest entrance to join in excavation when the entrance is buried. The other juxtapositions make equal sense when the spatial arrangement of the colony as a whole is considered. The queen, eggs, first instar larvae (microlarvae), and pupae are typically clustered together and apart from the older larvae, although the positions are constantly being shifted and pupae in particular are often segregated for varying periods of time well away from other immature stages. Thus the *A*-ensemble of workers can efficiently care for all of these groups, moving from egg to pupa to queen with a minimum of travel. The mean free path of a patrolling worker, to put the matter another way, is minimized by such versatility; it utilizes the least amount of energy in travelling from one contingency to another. It makes equal sense for *A* workers to assist the eclosion of adults from the pupae, since the latter developmental stage is already under their care.

It can be shown that in a purely abstract system, species of social insects should proliferate specialists until there is one caste for each distinguishable task (Wilson, 1968). In other words the twenty or so age ensembles should be evenly spread out to minimize overlap. The present study has revealed, on the other hand, that the advantages of spatial efficiency as a countervailing force has helped restrict the actual number of castes to less than 20% of the maximum conceivable.

A second constraint may exist: the small size of the worker's brain and the shortness of its life (especially true in *P. dentata*) could limit its ability to discriminate among stimuli. Thus if there were a single common attractant pheromone on the surface of pupae, eggs, and newly eclosed adults, the *A*-ensemble of workers could groom all three as virtually a single response to one stimulus. In the end we may discover that a great deal of complex social activity has been generated by the evolution of a relatively small number of pheromones made adequately efficient by the process of the discretization of temporal castes.

Trivers (personal communication) has suggested still another possible constraint on caste proliferation. As shown by Trivers and Hare (1976) it is to the advantage of the worker caste to control the sex ratio of the newly developed reproductive castes. For example, in species such as *P. dentata,* where workers are physiologically unable to produce offspring of their own, the inclusive fitness of the workers will be maximized when the ratio of investment is 3:1 in favor of new queens as opposed to new males. Workers having the most frequent contacts with brood are given the most opportunities to control the ratio of investment. Thus, temporal castes might evolve in such a way that foragers still come directly back to the brood and participate in their care; or, in a still more precise manner, workers nursing larvae might find it advantageous to monitor the eggs and pupae, and vice versa. The result would be less discretization of temporal castes. However, it turns out that in *P. dentata* older workers surrender much of their control over the brood. The foragers (mostly *C* individuals, 16 days and older) participate to a greatly diminished degree in larval care and contribute almost nothing to the care of eggs and larvae. Younger workers specializing on larvae (the *B* individuals) pay less attention to pupae and far less attention to eggs. The youngest workers seldom leave the eggs and queen to care for the larvae. In short, the evolutionary process of discretization does not appear to have been significantly diminished in intensity, nor the details of division of labor altered, in ways that facilitate control of the ratio of investment. The same statement is even more true with respect to the major worker ("soldier") subcaste, which has virtually nothing to do with the immature stages from eclosion to death.

The number of castes in *P. dentata* appears to be five: the queen, a single temporal subcaste of the major worker, and three temporal subcastes of the minor worker. For purposes of ergonomic analysis each of these can be treated as a full caste. Purists may wish to add the males as a sixth caste, but for reasons given elsewhere (Wilson, 1971) this extension creates more problems than it solves. It might also be argued that each and every age-group ensemble attending a task which is distinguishable from other ensembles at any level—say, statistically different at the 95% confidence level—deserves recognition as a caste. In this way, for example, workers grooming pupae can be distinguished (just barely) from workers grooming eggs and microlarvae. The counter-argument, on which the present analysis has been brought to a conclusion, is that major differences among ensembles are what matter in the economy of the colony, and that clusters of such ensembles are the features of interest, even if some variation can be demonstrated among the ensembles within each cluster. In this study visual assessment of clustering was deemed sufficient. More complex, ambiguous sets of data may demand formal clustering analysis of the kind used in numerical taxonomy.

It will be of paramount interest in the future to learn whether other species of social insects with temporal division of labor have undergone discretization. If they have, ergonomic analysis should prove easier than originally anticipated. Are the number of discretized castes small, as in *P. dentata*? And does the pattern of division of labor among them reflect the particular ecological adaptations of each species? Both of these questions seem tractable at the present time.

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Edward O. Wilson
Department of Biology
Harvard University
MCZ Laboratories
Oxford Street
Cambridge, Mass. 02138, USA