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The Sociogenesis of Insect Colonies

Edward O. Wilson

Summary. Studies on the social insects (ants, bees, wasps, and termites) have focused increasingly on sociogenesis, the process by which colony members undergo changes in caste, behavior, and physical location incident to colonial development. Caste is determined in individuals largely by environmental cues that trigger a sequence of progressive physiological restrictions. Individual determination, which is socially mediated, yields an age-size frequency distribution of the worker population that enhances survival and reproduction of the colony as a whole, typically at the expense of individuals. This "adaptive demography" varies in a predictable manner according to the species and size of the colony. The demography is richly augmented by behavioral pacemaking on the part of certain castes and programmed changes in the physical position of colony members according to age and size. Much of what has been observed in these three colony-level traits (adaptive demography, pacemaking, and positional effects) can be interpreted as the product of ritualization of dominance and other forms of selfish behavior that is still found in the more primitive insect societies. Some of the processes can also be usefully compared with morphogenesis at the levels of cells and tissues.

Together with flight and metamorphosis, colonial life was one of the landmark events in the evolution of the insects and evidently served as a source of their ecological success. Preliminary studies indicate that approximately one-third of the entire animal biomass of the Amazonian terra firme rain forest may be composed of ants and termites, with each hectare of soil containing in excess of 8 million ants and 1 million termites (*1*, *2*). On the Ivory Coast savanna the density of ants is 20 million per hectare, with one species, *Camponotus acvapimensis*, alone accounting for 2 million (*3*). Such African habitats are often visited by driver ants (*Dorylus* spp.), single colonies of which occasionally contain more than 20 million workers (*4*). And the driver ant case is far from the ultimate. A "supercolony" of the ant *Formica yessensis* on the Ishikari Coast of Hokkaido was reported to be composed of 306 million workers and 1,080,000 queens living in 45,000 interconnected nests across a territory of 2.7 square kilometers (*5*).

The environmental impact of these insects is correspondingly great. In most terrestrial habitats ants are among the leading predators of insects and other small invertebrates (*3*, *6*, *7*), and leafcutter ants (*Atta* spp.) are species for species the principal herbivores and most destructive insect pests of Central and South America (*8*). *Pogonomyrmex* and other harvester ants compete effectively with mammals for seeds in deserts of the southwestern United States (*9*). Other ants move approximately the same amount of soil as earthworms in the woodlands of New England, and they surpass them in tropical forests. Both are exceeded in turn by termites, which also break down a large part of the vegetable litter and diffuse the products through the humus (*10*, *11*).

The Reasons for Success

In general, the most abundant social insects are the evolutionarily more advanced groups of ants and termites, in other words, those with the highest percentage of derived traits in anatomy and physiology as well as the more populous and complexly organized societies (*6*, *12*, *13*). What is the real origin of this competitive advantage in the environment as a whole? At the risk of oversimplification, it can be said that entomologists have come to recognize three qualities as being most important. First, coordinated groups conduct parallel as opposed to serial operations and hence make fewer mistakes, especially when labor is divided among specialists. If different cadres of workers in an ant colony simultaneously forage for food, feed the queen, and remove her eggs to a safe place, they are more likely as a whole to complete the operation than if they perform the steps in repeated sequences in the manner of solitary insects (*13*). Second, groups can concentrate more energy and force at critical points than can single competitors, using sheer numbers to construct nests in otherwise daunting terrain, as well as to defend the young, and to retrieve food more effectively. Finally, there is caste: in ways that vary among species, the food supply is stabilized by the use of larvae and special adult forms to store reserves in the form of fat bodies and nutrient liquids held in the crop, while defense, nest construction, foraging, and other tasks are mostly accomplished by specialists (*14*).

The aim of much of contemporary research on social insects is to identify more fully the mechanisms by which colony members differentiate into castes and divide labor—and to understand why certain combinations of mechanisms have produced more successful products than others. The larger hope is that more general and exact principles of biological organization will be revealed by the meshing of comparable information from developmental biology and sociobiology. The definitive process at the level of the organism is morphogenesis, the set of procedures by which individual cells or cell populations undergo changes in shape or position incident to organismic development (*15*). The definitive

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Edward O. Wilson is Frank B. Baird, Jr., Professor of Science and Curator in Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. This article is based on the lecture of the 1984 Tyler Prize for Environmental Achievement, delivered at the University of Southern California on 24 May 1984.

process at the level of the colony is sociogenesis, the procedures by which individuals undergo changes in caste, behavior, and physical location incident to colonial development. The question of interest for general biology is the nature of the similarities between morphogenesis and sociogenesis.

The study of social insects is by necessity both a reductionistic and holistic enterprise. The behavior of the colony can be understood only if the programs and positional effects of the individual members are teased apart, ultimately at the physiological level. But this information makes full sense only when the patterns of colonial behavior of each species are examined as potential idiosyncratic adaptations to the natural environment in which the species lives. At both levels social insects offer great advantages over ordinary organisms for the study of biological organization. Although no higher organism can be readily dissected into its constituent parts for study and then reassembled, this is not the case for the insect colony. The colony can be fragmented into any conceivable combination of sets of its members, manipulated experimentally, and reconstituted at the end of the day, unharmed and ready for replicate treatment at a later time. The technique is used for analysis of optimization in social organization as follows: the colony is modified by changing caste ratios, as though it were a mutant. The performance of this "pseudomutant" is then compared with that of the natural colony and other modified versions. The same colony can be turned repetitively into pseudomutants in random sequences on different days, eliminating the variance that would otherwise be due to between-colony differences (*16*). At a still higher level of explanation, that of the ecosystem, the large numbers of species of various kinds of social insects (more than 1000 each in the ant genera *Camponotus* and *Pheidole* alone) give a panoramic view of the evolution of colonial patterns and make correlative analysis of adaptation more feasible.

Principles of Sociogenesis

In all species of social insects thus far studied, caste differences among colony members have proved to be principally or exclusively phenotypic rather than genetic. The environmental factors in each instance belong to one or more of the following six categories: larval nutrition (which is especially important in ants); inhibition caused by pheromones or other stimuli from particular castes (the key factor in many kinds of termites); egg size and hence quantity of nutrients available to the embryo; winter chilling; temperature during development; and age of the queen (*6, 17, 18*). Phenotypic caste determination is similar to restriction during cell differentiation. That is, the growing individual reaches one or more decision points at which it loses some of its potential, and this diminution continues progressively until it reaches the final decision point, where it is determined to the caste it will occupy as an adult. For example, in the ant genus *Pheidole* the restriction to either the queen line or worker line occurs in the egg; then larvae in the worker line become committed to development as either minor or major workers in the fourth and final instar. The cues affecting these two decisions, which include nutrition, winter chilling of queens, and inhibitory pheromones, are mediated to the developing tissue by juvenile hormone (*19, 20*).

The differentiation of the colony members into physical castes is supplemented in the great majority of social species by a regular progression on the part of most workers through different work roles during aging. In this way the individual belongs not only to one physical caste but to a sequence of temporal castes as it passes through its life-span. By far the most common sequence is for the worker to join in the care of the queen or immature stages shortly after it emerges into the adult stage, then to participate in nest building, and, finally, to forage outside the nest for food. Temporal castes are a derived trait in evolution, having become most clearly demarcated in species with the largest societies. They are typically weak or absent in anatomically primitive species with small colony populations (*6, 21*).

Although individual workers are flexible with respect to caste at the start of their personal development in the egg stage, the colony as a whole is rigidly limited to a single array of castes. Each species also has a particular size-frequency distribution of adult workers (*13, 22, 23*). Workers in the ant genus *Pheidole*, for example, are divided into two subcastes, the minors and the majors, by size and body proportions. Among ten species selected for their taxonomic diversity, the majors were found to range from 3 percent in *Pheidole distorta* to 25 percent in *Pheidole minutula* (*23*). A lesser amount of variation exists among colonies belonging to the same species, and recent work suggests indirectly that some of the variation is genetic. Seven colonies of *Pheidole dentata* raised under uniform laboratory conditions through three brood cycles maintained relatively constant major worker percentages, and these levels varied significantly among the colonies, from approximately 5 to 15 percent (*24*).

The size-frequency distribution can also persist through relatively long periods of geological time. A fragment of a colony of the extinct weaver ant *Oecophylla leakeyi* preserved intact from the African Miocene (the only fossil insect society collected to date) proved to have the same distinctive pattern as the two living species of the genus, *Oecophylla longinoda* and *Oecophylla smaragdina.* In particular, the frequency curve was sharply bimodal, with the major workers somewhat more numerous than the minors and with a small number of medias connecting the two moieties. The allometry, or disproportionate variation in body parts, is also similar between the extinct and living species (*25*).

These several lines of evidence have led to the hypothesis of adaptive demography (*13, 26*), which can be summarized as follows. The vast majority of insect, vertebrate, and other animal populations evolve primarily through selection at the level of the individual organism. As a consequence, survivorship curves and natality schedules are directly adaptive, whereas the age-frequency distribution of the population as a whole emerges as an epiphenomenon. In the advanced social insects, in contrast, selection occurs primarily at the level of the colony, with workers mostly or entirely eliminated from reproduction and colonies competing against one another as compact units. Colonies whose members possess the most effective age-frequency distribution are more likely to survive and to reproduce, regardless of the fate of individual colony members. It is generally believed that the workers will increase the replication of genes identical to their own by promoting the physical well-being of the colony, even if they sacrifice themselves to achieve this end. Hence the age-frequency distribution of the colony members is directly subject to natural selection. Survivorship and natality schedules are indirectly subject to natural selection, in the sense of being shaped according to the effect they have on the age-frequency distribution of the colony as a whole.

The adaptive demography hypothesis has begun to be tested by both correlative analysis and experimentation. For example, linear programming models predict that as a caste specializes, its members should decrease in proportion within the colony membership (*26*). This relation does hold among the species of *Pheidole* so far studied: the repertory size of the major caste is correlated significantly across species with the percentage of the majors in the worker force. Put another way, as the majors perform fewer tasks and devote more time proportionately to roles for which they are anatomically specialized, they become scarcer in the colony population (*23*).

And yet the major workers of *Pheidole* retain a remarkable flexibility. When the minor-major ratio was experimentally reduced to below 1:1 in three widely different species of the genus, the majors increased the number of kinds of acts they performed by as much as 4.5 times and their rate of activity 15 to 30 times. The change occurred within 1 hour of the ratio change and was reversed in comparably short time when the original ratio was restored. Thus the major workers were found to respond in a manner reminiscent of the genome of a somatic cell. Under normal circumstances most of their brain programs are silent: the active repertory is limited in a fashion appropriate to the tasks for which the majors are anatomically specialized. But when an emergency arises a much larger program is quickly summoned, the majors supply about 75 percent of the activity of the missing minors, and as a result the colony continues to feed and grow (*23*).

A second line of evidence of adaptive demography has been provided by studies of the leafcutter ant *Atta cephalotes*. New colonies of *Atta*, like those of most kinds of ants, are founded by single queens after the nuptial flights. These individuals dig a shaft into the ground, then eject a wad of symbiotic fungus from their mouths onto the ground and fertilize the hyphae with droplets of feces. During the next 6 weeks they rear the first brood of workers with reserves from their own bodies while bringing the small garden to flourishing condition. The queens have only enough ovarian yolk and other storage materials to rear one small group to maturity. In order for the colony to survive thereafter, the workers must range in size from a head width of 0.8 mm, which is small enough to culture the fungus, through 1.6 mm, which is just large enough to cut fresh leaves for the fungal substrate. It turns out that the first brood of workers possess a nearly uniform frequency distribution from 0.8 through 1.6 mm, which comes close to maximizing the number of individuals and at the same time achieves the minimum size range required to grow the fungus on which the colony depends (*27*).

As the leafcutter population expands afterward, the size-frequency distribution of the workers changes in dramatic fashion. The range is increased at both ends and the curve becomes strongly skewed toward the media and major worker classes (Fig. 1). An interesting question then arises: suppose that by some misadventure most of the population of a leafcutter colony were destroyed, reducing it to near the colony-founding state. Would the size-frequency distribution of new workers produced by the colony be characteristic of the beginning stage, or would it remain at the older stage? In other words, which is the more important in the ontogeny of the caste system, the size of the colony or its age? If age were more important, causing much of the available energy to be invested in workers larger than the minimum required to harvest leaves, the colony would be imperiled because of a

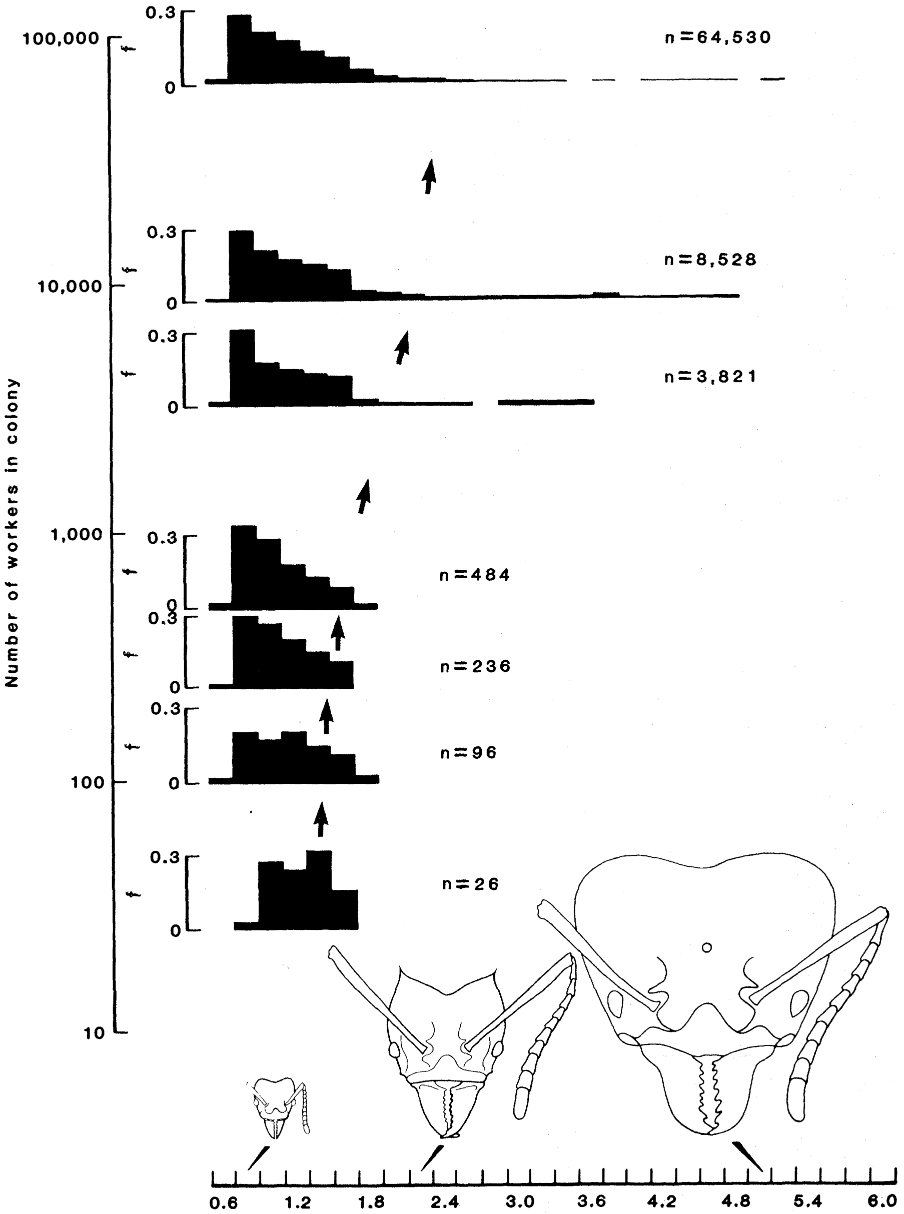

Fig. 1. The ontogeny of the caste system of the leafcutter ant *Atta cephalotes*, illustrated by seven representative colonies collected in the field or reared in the laboratory. The worker caste is differentiated into subcastes by continuous size variation associated with disproportionate growth in various body parts. The number of workers in each colony (*n*) is based on complete censuses; *f* is the frequency of individuals according to size class. The heads of three sizes of workers are shown in order to illustrate the disproportionate growth. Modified from Wilson (*27*).

shortage of the small gardener classes. The creation of just one new major worker, possessing a body weight 300 times that of a gardener worker, would bankrupt the already impoverished colony. In order to provide an answer, I selected four colonies 3 to 4 years old and with about 10,000 workers and reduced the population of each to 236, giving them an artificially imposed juvenile size-frequency distribution. The worker pupae produced at the end of the first brood cycle possessed a size-frequency distribution like that of small, young colonies rather than larger, older ones. Thus colony size is more important than age, and "rejuvenated" colonies are prevented from extinguishing themselves through an incorrect investment of their resources (*27*).

Such programmed resiliency implies the existence of control mechanisms operating at the level of the colony during population growth. An increasing fraction of the research on social insects is now being directed at the discovery of such mechanisms. This work has begun to reveal a fascinating pattern of feedback loops, pacemakers, and positional effects.

An example of negative feedback is provided by the events leading to the fission of honeybee colonies. The queen secretes a "queen substance," *trans*-9-keto-2-decenoic acid, which under most circumstances inhibits the construction of royal cells by the workers and hence the rearing of new queens (*28*). However, in large, freely growing colonies this pheromone must be supplemented by a second substance, the footprint pheromone, which is secreted in relatively large amounts from glands in the fifth tarsal segment of the queen. When bee colonies become overcrowded, the queen is unable to walk along the bottom edges of the comb, where the royal cells are ordinarily built. As a result the inhibition fails in that zone, the cells are built, and the colony reproduces. With the population density now reduced to below threshold density, the queen is able to resume her inhibitory control (*29*).

Most such controls are negative and hence contribute to physiological stability and smooth growth cycles within the colony. What appear to be properties of positive feedback and explosive chain reactions nevertheless do occur during nest evacuation in a few species. When attacking fire ant workers press closely on nests of the ant *Pheidole dentata*, the defending minor workers start laying odor trails back into the brood area. This causes excited movement through the nest and further bouts of recruitment. At the height of this expanding activity the workers and queen suddenly scatter from the nest and seek individual cover. When the fire ants are then experimentally removed, the *Pheidole* adults return to the nest and reoccupy it (*30*).

The coordination of activity is still imperfectly understood. Although the typical insect society is not quite the "feminine monarchie" envisioned by early entomologists (*31*), it is also much more than a republic of specialists. According to the species, certain immature stages and castes function as pacemakers and coordinators of colony activity. Ant larvae are specially effective in initiating foraging and nest construction by the adult workers. In army ants (*Eciton*), the hatching of larvae triggers the monthly nomadic cycle during which the entire colony marches to a new location daily (*32*). But in the great majority of other species thus far studied it is the queen that provides the maximum regulation. In more primitive societies, such as those of bumblebees (*Bombus*) and paper wasps (*Polistes*), she physically dominates her daughters and other females occupying the nests, prevents them from laying eggs, and by these actions forces most into foraging and other nonreproductive tasks. Such influence can transcend simple displacement. For instance, the presence of the queen of *Polistes fuscatus*, probably a typical species at this evolutionary level, increases and synchronizes overall worker activity (*33*). In carpenter ants (*Camponotus*), the mother queen is the principal source of the nest odor (*34*). When she is removed, the workers, now in a more chaotic state, fall back on odor cues emanating from their own bodies (*35*).

Workers of social insects move to different positions with reference to the queen and brood according to their ages. This pattern is usually centrifugal: soon after the worker emerges from the pupa into the adult stage, it attends the queen and immature stages, then drifts toward the outer chambers to assist in nest construction, and finally devotes itself primarily to foraging outside the nest. The progression is accompanied by physiological change. The details vary greatly among species, and even among members of the same colony, but in general the ovaries reach maximum development early in adult life, along with fat bodies and exocrine glands devoted to nutritive exchange (*6, 17, 36–38*). Afterward these tissues regress more than enough to counterbalance the growth of exocrine glands associated with nest construction and foraging, so that the worker declines overall in weight. Mortality due to accidental causes increases sharply among workers when they commence foraging. But this attrition has far less effect on the size-and-age structure of the worker population than if individuals commenced foraging early in life, because the natural life-span is curtailed in any case past the onset of foraging by physiological senescence. In the best documented case, the honeybee worker born in early summer typically begins foraging at 2 to 3 weeks of adult life and dies from senescence by 10 weeks into this period (*39*).

The workers of advanced insect societies are not unlike cells that emigrate to new positions, transform into new types, and aggregate to form tissues and organs. With relatively small adjustments in response thresholds according to size and age, intricate new patterns are created at the level of the colony. In the fungus-growing termite *Macrotermes subhyalinus*, for example, 90 percent of the foragers are large major workers past 30 days of age. Younger major and minor workers accept the grass collected by these foragers, consume it, and pass the partly digested material out into the fungus comb. Workers of various castes older than 30 days eat the fungus comb and produce the final feces (*40*). In the leafcutting ant *Atta sexdens* most of the fresh vegetation is gathered by workers of intermediate size (which, incidentally, achieve the highest net energetic yield of all the size groups). The material is then converted into new fungus substrate within the nest by an assembly-line operation that penetrates ever more deeply into the combs: successively smaller workers cut the leaves into tiny fragments, chew them into pulp, stick the processed lumps onto the growing combs, and transfer strands of fungi onto this newly prepared substrate. Finally, the smallest workers of all care for the proliferating fungus, virtually strand by strand (*16, 41*).

Such patterns are in fact much more intricate than a description of sequences alone indicates. In the ant *Pheidole dentata* and the honeybee *Apis mellifera* the tasks are broken into sets that are linked not by the similarity of the behaviors performed but by the proximity of the objects to which they are directed, thus reducing the travel time and energy expenditure of the individual workers (Figs. 2 and 3). The similarities between the two patterns can only be due to convergent evolution, since ants and bees arose during Mesozoic times from widely different stocks of aculeate wasps (*42*).

The Imperfection of Insect Societies

Although insects as a whole originated at least 350 million years ago, higher social insects did not appear until the Jurassic Period, roughly 200 million years ago, and they began an extensive evolutionary radiation only in the late Cretaceous and early Tertiary Periods, about 100 million years later (*42*). Even then, advanced social organization originated in as few as 13 stocks, 12 within the aculeate Hymenoptera (ants, bees, and wasps) and one in the cockroach-like orthopteroids that produced the termites (*6*).

Two possible explanations for this evolutionary conservatism have emerged from more detailed studies of individual colony members. The first is that the small size of the insect brain and the heavy reliance of social forms on chemical signaling place inherent limits on the amount of information flow through the colonies. This circumstance leads to frequent near-chaotic states and the dependence on colony decision-making by *force majeure*, a statistical preponderance of certain actions over others that lead to a dynamic equilibrium rather than clean binary choices (*6, 13, 43, 44*). Thus when released from threshold concentrations of the queen inhibitory pheromones, some honeybee workers build royal cells while a smaller number of workers set out to dismantle them. The final result is an equilibrial number of cells sufficient for the rearing of new queens (*44*).

On the other hand, a few mechanisms are coming to light that sharpen the precision of mass response and bring it closer to binary action. Markl and Hölldobler (*45*) reported the existence of "modulatory communication" in ants, a form of signaling in one channel that alters the threshold of response in another. For example, when harvester ants of the genus *Novomessor* encounter large food objects they make sounds by scraping together specialized surfaces on the thin postpetiole and adjacent abdominal segment. This stridulation does not cause an overt behavioral change in nestmates but raises the probability that they will release short-range recruitment chemicals. The overall result is a speeding and tightening of the coordination process.

The second force inhibiting social evolution, at least in the case of hymenopterans, is the substantial conflict among individuals for reproductive privileges. Dominance rank orders, once thought to be confined to simply organized societies of halictine bees, bumblebees, and polis-

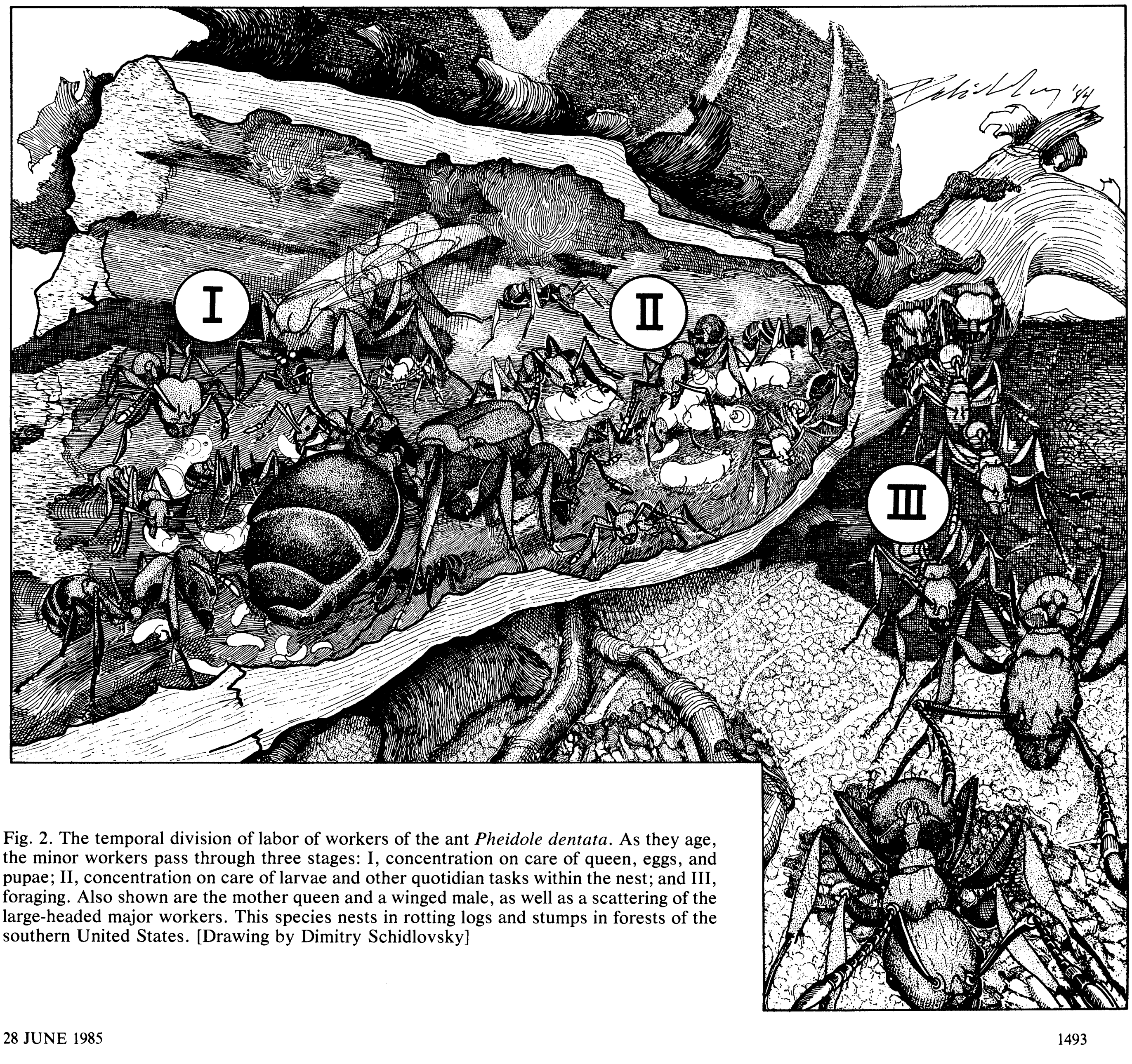

Fig. 2. The temporal division of labor of workers of the ant *Pheidole dentata*. As they age, the minor workers pass through three stages: I, concentration on care of queen, eggs, and pupae; II, concentration on care of larvae and other quotidian tasks within the nest; and III, foraging. Also shown are the mother queen and a winged male, as well as a scattering of the large-headed major workers. This species nests in rotting logs and stumps in forests of the southern United States. [Drawing by Dimitry Schidlovsky]

tine wasps, as well as associations of queens of a few kinds of ants [*Nothomyrmecia, Myrmecocystus*, and *Eurhopalothrix* (*46*)] have also been discovered in the workers of some species of ants as well (*47*). West-Eberhard has argued that competition among workers is more pervasive among advanced societies than has been recognized and that selection at the level of the individual has consequently played a key role in the division of labor (*36, 48*). She explains the centrifugal pattern of temporal castes (Figs. 2 and 3) as the product of such selection. The individual worker, by staying close to the brood chambers while still young and while her personal reproductive value is highest, maximizes her potential to contribute personal offspring. But as death approaches and fertility declines because of senescence, the optimum strategy for contributing genes to the next generation is to enhance colony welfare through more dangerous occupations such as defense and foraging, thus producing more brothers and sisters as opposed to personal offspring. By this criterion, Porter and Jorgensen (*37*) were correct to call foraging harvester ants the "disposable" caste. Hölldobler (*49*) has recently described what may be the ultimate case: aging workers of the Australian tree ant (*Oecophylla smaragdina*) occupy special "barracks nests" around the periphery of the main nest area. They stand idle most of the time and are among the first defenders to enter combat during territorial battles with other tree ant colonies.

Individual selection appears likely to have inhibited the refinement of social behavior, especially in the earliest stages of the evolution. Indeed, there is evidence that species of the bee genus *Exoneurella*, trading production of siblings for the production of offspring, have returned from primitive sociality back to a more nearly solitary state (*50*). Yet there does appear to be a point of no return in the rise of sociality. When colonies become very complex, organized by an intricate caste system and highly coordinated group movements, the advantages of queenlike behavior on the part of workers is diminished and may even disappear. In a few advanced ant genera, such as *Pheidole* and *Solenopsis*, the workers no longer even possess ovaries (*51*).

The pattern emerging from comparative studies suggests that as reproductive competition has declined during the elaboration of sociogenesis, dominance interactions have been ritualized to serve as part of the communicative signals dividing labor. In the more complex societies of bees and wasps, overt aggression is replaced by queen pheromones, but the inhibition of the ovaries of the subordinates and their induction into worker roles remain essentially the same (*6, 14*). Also, traces of aggressive and subordinate interactions persist in ritual form. The workers of stingless bees either hurriedly withdraw from the area when the

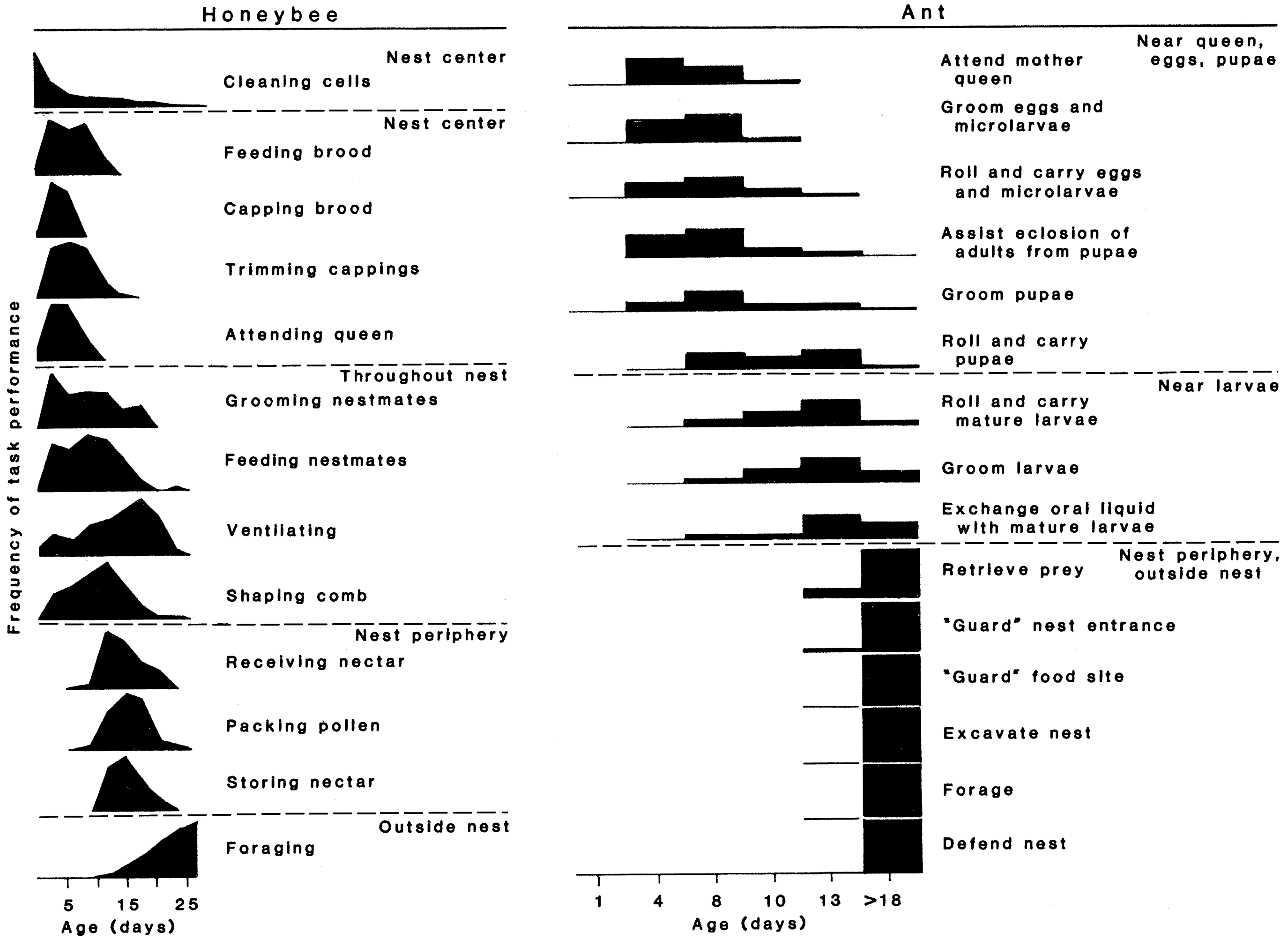

Fig. 3. The temporal division of labor, based on changes of behavior in the adult workers with aging, is shown in the ant *Pheidole dentata* and honeybee *Apis mellifera*: the insects shift from one linked set of tasks to another as they move their activities outward from the nest center (see Fig. 2). The similarities between the two species are convergent and believed to be adaptive. The sum of the frequencies in each histogram is 1.0. Adapted from Wilson (*54*) and Seeley (*55*).

queen approaches, thus clearing a path for her, or else they mock-attack, then bow to her head, and finally swing to her side to become part of the retinue (*52*). Ritualized dominance interactions may also be important between sterile workers. Major workers of the ant *Pheidole pubiventris* turn away from minor workers when they encounter them around the brood, thus yielding most of the care of the immature forms to these smaller nestmates. This aversion neatly divides colony labor into several principal categories (*23*).

Although seldom acknowledged in the literature, regulatory mechanisms are often found lacking even when they are intuitively anticipated by the investigator. For example, the major workers of *Pheidole dentata* are specialized for response against fire ants and other members of the genus *Solenopsis*, but when colonies are stressed continually with these enemies the major-minor ratio remains the same.

In other words, there is no increase in the defense expenditure in the face of a major threat (*24*). Leafcutter workers with head widths from 1.8 through 2.2 mm are responsible for most of the foraging, but when members of this important caste are removed experimentally, the colonies fail to compensate for the loss by increasing representation of the size class in later broods. The result is a reduction in energetic efficiency through two brood cycles (*53*).

On the whole, insect societies display impressive degrees of complexity and integrity on the basis of what appear to be relatively few sociogenetic processes. The mechanisms that do exist, together with their strengths, precision, and phylogenetic distribution, constitute a subject in an early and exciting period of investigation. Of comparable importance are the expected mechanisms that do not exist, so that investigators are likely to pay closer attention to them than has been the case in the past. As the full pattern becomes clearer, it may be possible to compare sociogenesis with morphogenesis in a way that leads to a more satisfying general account of biological organization.

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