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Source: *American Scientist*, Vol. 77, No. 6 (November-December 1989), pp. 546-553

Published by: [Sigma Xi, The Scientific Research Society](#)

Stable URL: <http://www.jstor.org/stable/27856005>

Accessed: 01/11/2013 16:53

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The Honey Bee Colony as a Superorganism

Thomas D. Seeley

In an essay titled "The Architecture of Complexity," the economist Herbert A. Simon (1962) presented a parable about two watchmakers. Although both craftsmen built fine watches and both received frequent calls from customers placing orders, one, Hora, grew richer while the other, Tempus, became poorer and eventually lost his shop. This difference was traced to different methods used in assembling the watches, which in both cases consisted of 1,000 parts. Tempus's procedure was such that if he had a watch partially assembled and then had to put it down—to take an order, for example—it fell apart and had to be reassembled from scratch. Hora's watches were no less complex than those of Tempus but were designed so that he could put together stable subassemblies of about ten parts each. Ten of the subassemblies would, in turn, form a larger and also stable subassembly, and ten of the latter subassemblies constituted a complete watch. Thus each time Hora answered his phone he sacrificed only a small part of his labors and consequently was far more successful than Tempus at finishing watches.

The lesson of this story is that complex systems most likely arise through a sequence of stable subassemblies, with each higher-level unit being a nested hierarchy of lower-level units. This is certainly the path followed in the evolution of life (Margulis 1981; Bonner 1988). The biological hierarchy of functionally organized units consists of macromolecules within prokaryotic cells, prokaryotic cells within eukaryotic cells, eukaryotic cells within organisms, and, in certain species, organisms within thoroughly unified societies which have been called superorganisms (Wheeler 1928; Wilson 1971). To explain why natural selection has favored the formation of ever larger units of life, Richard Dawkins (1982) pointed out that all functional units above the level of the genes can be viewed as "vehicles" built by the genes to enhance their survival and reproduction, and that larger

and more complex vehicles have evidently proved superior to smaller and simpler vehicles in certain ecological settings. By virtue of its greater size and mobility and other traits, a multicellular organism is sometimes a better gene-survival machine than is a single eukaryotic cell (Bonner 1974). Likewise, the genes inside organisms sometimes fare better when they reside in an integrated society of organisms rather than in a single organism, because of the superior defensive, feeding, and homeostatic abilities of functionally organized groups (Alexander 1974; Wilson 1975).

What is especially puzzling about the evolution of life is how each of the transitions to a higher level of biological organization was achieved. Individual units, each honed by natural selection to be a successful, free-living entity, must have begun somehow to interact cooperatively, eventually evolving into a larger, tightly integrated unit composed of mutually interdependent

parts. The details of how this happened in the origin of prokaryotic cells or the advent of multicellular organisms are particularly obscure because in both instances the evolution of separate parts into integrated wholes has progressed so far that the original components have become altered beyond recognition. Furthermore, the integration of cells and organisms is so far advanced that it is difficult to see how the original cells or multicellular organisms were built.

The situation is quite different for the transition from organism to superorganism. This transition began relatively recently and indeed can possibly be viewed as the current frontier in the evolution of biological organization. Whereas the origin of prokaryotic cells occurred 3,500 million years ago, the advent of eukaryotic cells took place 1,300 million years ago, and multicellular organisms arose 700 million years ago (Margulis 1981), superorganism-grade insect societies began to appear only about 100 million years ago and presumably are still taking shape (Burnham 1978). Therefore, it is perhaps not surprising that even in the most advanced insect societies, such as army ants, fungus-growing termites, or honey bees, the differentiation and integration of a society's members have not reached the point at which each member's original nature has been erased. A colony of honey bees, for example, functions as an integrated whole and its members cannot survive on their own, yet individual honey bees are physically independent and

*Natural selection has
made the colony a vehicle
for the survival of genes*

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Figure 1. Signals are stimuli that convey information and have been molded by natural selection to do so; cues are stimuli that contain information but have not been shaped by natural selection specifically to convey information. Information can also pass between the members of a colony indirectly, through any component of their shared environment. Shown at the left are bees following another bee performing waggle dances, which are elaborate signals that indicate with precision the distance and direction of rich patches of flowers. In the top photograph, a food-storer bee (*left*) is unloading nectar from a forager. The delay a forager experiences before she can pass off her nectar is a cue that indicates the colony's nutritional status. In the photograph above, bees are fanning their wings in order to expel warm, moist air from their hive. The effect of this fanning—a cooler, drier atmosphere inside the hive—conveys information to other bees about the colony's need for ventilation. (Photos courtesy of P. K. Visscher, *left and top*, and S. Camazine, *above*.)

closely resemble in physiology and morphology the solitary bees from which they evolved (Fig. 1). In a colony of honey bees two levels of biological organization—organism and superorganism—coexist with equal prominence. The dual nature of such societies provides us with a special window on the evolution of biological organization, through which we can see how natural selection has taken thousands of organisms that were built for solitary life and merged them into a superorganism.

Is it a superorganism?

The term “superorganism” was coined by William Morton Wheeler (1928) to denote insect societies that possess features of organization analogous to the physiological processes of individual organisms. These include advanced social insects like army ants, leaf-cutter ants, fungus-growing termites, stingless bees, and honey bees. Although sociologists dealing with insects have used the superorganism concept more as a heuristic device than as a category of societal complexity (Lüscher 1962; Southwick 1983), recent insights into the logic of natural selection support the use of this term in a manner close to Wheeler’s original intent (Hull 1980; Dawkins 1982; Wilson and Sober 1989). It seems correct to classify a group of *organisms* as a superorganism when the organisms form a cooperative unit to propagate their genes, just as we classify a group of *cells* as an organism when the cells form a cooperative unit to propagate their genes. By this definition, most groups of organisms are not perfect superorganisms because there is usually intense intragroup conflict when members compete for reproductive success (Trivers 1985). Indeed, in many species of social insects the female members of a colony (queens and workers) fight over who will lay eggs (West-Eberhard 1981; Bourke 1988). In the most advanced species of social insects, however, there appears to be little if any conflict within colonies, so that these colonies do represent superorganisms.

How complete is the cooperation in a honey bee colony, and thus to what extent is a colony of honey bees truly a superorganism? The best way to answer these questions is to determine the degree of congruence in the genetic interests of a colony’s members. Consider the typical situation of a colony comprising one queen and some 20,000 workers, all daughters of the queen. At first glance, it might seem that there will be tremendous divergence of genetic interests within the colony. As a result of sexual reproduction, the queen’s genotype does not match that of her workers; furthermore, although the workers are all offspring of the queen, because of segregation and recombination of the queen’s genes during meiosis and because the queen has mated with ten or more males (Page 1986), the workers possess substantially different genotypes.

A closer look, however, reveals several features of the biology of honey bees that indicate a close alignment of genetic interests among the members of a colony, despite these genetic differences (Ratnieks 1988). Although worker bees possess ovaries and will lay eggs to produce sons if they lose their queen (Page and Erickson 1988), in the presence of the queen, workers engage in essentially no direct, personal reproduction. Workers

cannot mate, so their only possible avenue of direct reproduction is through haploid sons from unfertilized eggs. A recent study in which the extent of worker reproduction in colonies with queens was measured using genetic markers to distinguish drones from queen-laid and worker-laid eggs, reported that only one in one thousand drones in a colony is the offspring of workers (Visscher, in press). This means that as long as the queen is present there is a reproductive bottleneck in which every individual’s gene propagation occurs virtually exclusively through a common pathway—the reproductive offspring (queens and drones) of the mother queen. This situation promotes strong cooperation among the queen and all workers; ultimately each worker focuses her efforts on the welfare and reproductive success of one individual, the queen.

This reproductive bottleneck does not, however, indicate that a perfect alignment of the genetic interests of a colony’s members has evolved. The workers in colonies with queens may still disagree over which eggs should be reared into queens when it is time to produce new queens. This potential conflict of interest traces to the multiple mating of honey bee queens, which produces a set of patriline within each colony. Because workers share three times as many genes with full-sister queens (same patriline) as with half-sister queens (different patriline), they are expected to prefer that queens produced in a colony be their full sisters. Over the last few years several investigators have searched for intra-colony competition during queen rearing, and a growing body of evidence indicates that some patrilines within a colony do achieve a small bias in their favor (Noonan 1986; Visscher 1986; Page et al. 1989). However, all studies that have reported preferential rearing of more closely related queens involved somewhat artificial test conditions, such as transfers of larval queens between colonies or use of colonies containing only two or three instead of the normal number (ten or more) of patrilines. It may be that even the slight bias in queen rearing observed in these studies is greater than what occurs under natural conditions (Hogendoorn and Velthuis 1988).

Given the bottleneck for gene propagation and the strong indication that workers have nearly equal genetic stakes in a colony’s production of reproductives (due to meiosis in the queen, together with little patriline bias in queen rearing), we can conclude that the genetic interests of the workers in a colony led by a queen are nearly, though not perfectly, congruent. Furthermore, we know that the mother queen and the workers have evolved similar interests in matters such as who lays the eggs that produce the colony’s drones, the ratio of the colony’s investment in queens and drones, and the timing of replacement of the queen (Seeley 1985; Ratnieks 1988). Thus it appears that there is minimal conflict within honey bee colonies as long as the mother queen is present. Therefore, we may conclude that honey bee colonies containing queens are nearly true superorganisms.

This conclusion, based on analyses of the genetic interests of a colony’s members, is reinforced by the picture of pervasive cooperation which has emerged from analyses of colony functioning. In choosing a nest site, building a nest, collecting food, regulating the nest

temperature, and deterring predators, a honey bee colony containing a queen resembles a smoothly running machine in which each part always contributes to the efficient operation of the whole (Seeley 1985; Winston 1987). As we will see, in a normal honey bee colony, food, information, and aid appear to pass freely among the members in ways that apparently promote the economic success of the whole colony.

It should be very revealing, and at most only slightly misleading, to view a honey bee colony as an integrated biological machine that promotes the success of the colony's genes. Given this perspective, the outstanding biological question becomes: How did evolution take a large number of organisms built for solitary life and forge them into a single vehicle of gene survival? The answer to this question has two parts. One concerns the ultimate forces of natural selection, which caused the evolution of unified colonies; the other involves the proximate mechanisms by which colonies function as integrated wholes. This article focuses on the second half of the answer. The key to understanding this aspect of the puzzle involves understanding the flow of information within colonies. Coordination in any complex system depends upon each part having access to appropriate information at the right time and place (Wiener 1961). Coherence implies communication.

Architecture of information flow

Coordination of the activities in a honey bee colony arises without any centralized decision making. There is no evidence of an information and control hierarchy, with some individuals taking in information about the colony, deciding what needs to be done, and issuing commands to other individuals who then perform necessary tasks. As the biblical King Solomon observed, there is "neither guide, overseer, nor ruler." In particular, it is clear that the queen does not supervise the activities of her workers. She does emit a chemical signal, the queen-substance pheromone, which plays a role in regulating the colony's production of additional queens (Free 1987), but this signal cannot provide comprehensive supervision of the activities of the tens of thousands of workers in a colony.

A colony's coherence depends instead upon the ability of its members to circulate throughout the hive, gather information about the colony's needs, and adjust the supply of their labor to the demands they sense. This idea was suggested in the early 1950s by Martin Lindauer (1952), who painstakingly followed individual workers within colonies living in glass-walled observation hives. He learned that the bees devote about 30% of their time to walking about the nest, and that this patrolling is punctuated by bouts of activity in a wide variety of tasks (Fig. 2). A typical 30-minute segment from Lindauer's records reveals the following behavior for a seven-day-old bee: patrolling, shaping comb, patrolling, feeding young brood, cleaning cells, patrolling, shaping comb, eating pollen, resting, patrolling, shaping comb. The task performed at any given moment presumably depends upon the specific labor need sensed by the bee.

Why are honey bee colonies organized in this way? Decentralized control is possibly superior to centralized control for bees. Systems with decentralized control

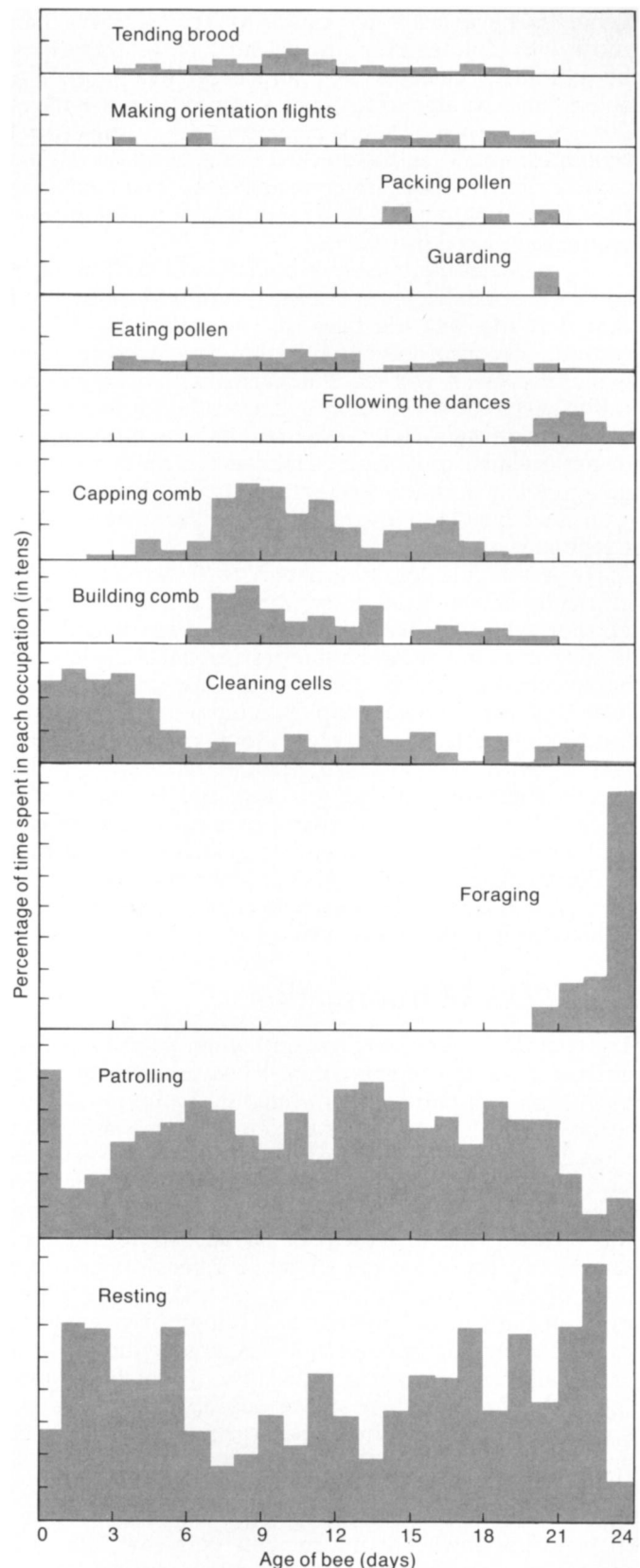


Figure 2. In the course of her life, a worker honey bee performs a variety of tasks. As the distribution above indicates, she can perform several different tasks on any given day and at any given age. She thereby behaves flexibly, responding to different needs encountered in the hive. The large amount of time spent patrolling is evidently related to the gathering of information—through cues, signals, and the shared environment—about the colony's labor needs. (After Lindauer 1952.)

generally have faster responses to local stresses than those with centralized control (Miller 1978), and this may be extremely valuable to colonies of honey bees. A colony may be able to respond to a predator's attack at the nest entrance or to a temperature rise in the central broodnest much more quickly if the workers at the trouble sites can perform corrective actions immediately than if information has to be sent to a supervisor, who would then issue instructions.

A perhaps more likely explanation of decentralized control is not that it is superior to centralized control, but that it is the best the bees can do given the limited communication processes that have developed through evolution. As we will see, the mechanisms of communication in colonies of social insects are rather rudimentary, at least relative to what exists in human organizations or in multicellular organisms. Colonies of army ants, fungus-growing termites, honey bees, and other superorganisms have yet to invent anything like a mail system, telephone, or computer network. Such technologies make it possible for information to flow rapidly and efficiently between the different parts of a human organization with centralized control. One piece of evidence in support of this second hypothesis is that at the level of organization just below the superorganism, the multicellular organism, where a sophisticated intercellular communication system has evolved, there exists centralized control, with the brain taking in information about the whole organism and issuing commands to cells of the body. Whatever the underlying reason, the fact of decentralized control in honey bee colonies tells us that understanding how colonial coordination arises follows from understanding how each worker acquires information about her colony's needs.

Pathways of information

To what do worker bees respond when patrolling? The answer to this question is complex because evolution has been highly opportunistic in building pathways for information in honey bee colonies. It has shaped the workers so that they are sensitive to virtually all variables and stimuli that contain useful information: the temperature of the nest interior, the degree of crowding at a food source, the moistness of larvae, the recruitment dances of nestmates, the shape of a beeswax cell, the odor of dead bees. Furthermore, given the close alignment of the genetic interests of a colony's workers, we can expect that natural selection has molded the workers to be skilled at generating signals for information transfer. Within colonies there are various tappings, tuggings, shakings, buzzings, strokings, waggings, crossing of antennae, and puffings and streakings of chemicals, all of which seem to be communication signals. The result is that within a honey bee colony there exists an astonishingly intricate web of information pathways, the full magnitude of which is still only dimly perceived.

Information can flow between colony members in two ways: directly, through signals and cues, as we will discuss below, or indirectly, through some component of the shared environment. An example of the latter process is the transfer of information through the process of comb building. The construction of a particular cell in a beeswax comb may involve several bees, yet these bees

never need to come together and exchange information directly. The building activities can be completely and efficiently coordinated by information embodied in the structure of the partially completed cell. Thus one bee might begin a cell wall by depositing a small ridge of beeswax; a second bee might finish sculpting the wall, guided by the shape of the wax ridge left by the first bee. Another example of information flow through the shared environment is thermoregulation of the nest. A colony maintains the central broodnest at 34 to 36°C in the face of ambient temperatures that may range from -20 to 40°C. The coordinated heating and cooling of a nest occurs automatically: each bee responds to the temperature of her immediate environment by appropriately heating it (by making intense isometric contractions of her flight muscles) or cooling it (by fanning her wings to draw cooler air into the area) (Heinrich 1985). In effect, the temperature of the air and comb inside a hive provides a communication network regarding the colony's heating and cooling needs.

Several authors have expressed the concept of information flow through the shared environment in social insect colonies. These include Pierre-Paul Grassé (1959), who coined the term "stigmergy" to explain coordination in nest construction by termites, and Charles D. Michener (1974), who pointed out that "indirect social interactions," such as transfers of information through the food stored in the nest, are an important integration mechanism in colonies of social bees. Future studies of information flow in social insect colonies may reveal that more information is transmitted indirectly than directly. The use of the shared environment as a communication pathway has certain attractions, including easy asynchronous transfer of information between individuals and virtually automatic transfer of information between any two individuals sharing some portion of the nest environment. It also has the important feature whereby information can pass from a group to an individual whenever an individual responds to the environmental effects of a group. Because the process of integration of a group is largely a matter of information flow from group to individual, it may be that information flow through the shared environment has been natural selection's principal technique of integration in building superorganisms.

Signals and cues

There are two types of direct communication channels: signals and cues (Lloyd 1983). Signals are stimuli that convey information and have been shaped by natural selection to do so, whereas cues are stimuli that contain information but have not been shaped by natural selection specifically to convey information. Cues carry information only incidentally. The distinction between signals and cues deserves emphasis because studies of information flow in social insect colonies have tended to overlook cues and have focused instead on conspicuous visual, tactile, acoustical, and chemical signals (reviewed by Wilson 1971; Hölldobler 1977). The emphasis on signals reflects the fact that information transfer via signals is relatively easily detected by humans because in the mutualistic setting of a social insect colony natural selection will have shaped signals to be powerful and unam-

biguous carriers of information (Markl 1985). In contrast, information transfer via cuing will usually be subtle; cues are simply by-products of behaviors performed for reasons other than communication.

The famous dance language, through which a bee can inform her nestmates of the direction and distance of a rich food source, is a classic example of a signal (von Frisch 1967). Given the richness of the information and the high precision of encoding the information in the dances, there is no doubt that the dance language has been intensively molded by natural selection for the efficient transfer of information.

One example of a cue involves the regulation of a colony's choosiness among nectar sources in relation to its nutritional status. When a colony is well nourished, its foragers exploit only highly profitable patches of flowers, but if the colony is near starvation, the foragers exploit both highly profitable and less profitable flower patches. This raises the question of how foragers stay informed about their colony's nutritional status. My research (Seeley 1989) has recently confirmed a hypothesis originally proposed by Lindauer (1948) that the delay a returning forager experiences before she can unload her nectar to a food-storer bee suggests to the forager the colony's nutritional status. (The food storers are bees who are slightly younger than the foragers and who specialize in receiving the fresh nectar, concentrating it into honey, and storing it in the honeycombs.) If a forager can find a food-storer bee within approximately 15 seconds of entering the hive, then she knows that there is little nectar coming into the hive and little honey stored in the hive—her colony is approaching starvation. But if a forager has to wait more than about 15 seconds (and as much as 100 seconds or more), then she knows that either there is much nectar currently being gathered or there is much honey already stored in the hive—either way, her colony is well nourished.

The link between waiting time and the colony's nutritional status is shown schematically in Figure 3. Nectar collection involves two cycles, a forage cycle and a storage cycle, which intersect at the point of nectar transfer from foragers to food storers. This sort of system, in which there is a stream of individuals in one group arriving at a location to be serviced by individuals in a second group, is quite common. It occurs at toll booths along highways, at the service windows of banks, and at the checkout counters of supermarkets. A critical variable of all such systems is the utilization factor, U , which is the ratio of the rate of arrival of individuals needing servicing and the rate at which the servers can provide service. The mathematical theory of queues (Morse 1958) reveals that the average length of the waiting line, Q , that an arriving individual will face is a simple function of the utilization factor: $Q = U/(1-U)$. Thus in the case of honey bees, if U is low—say less than

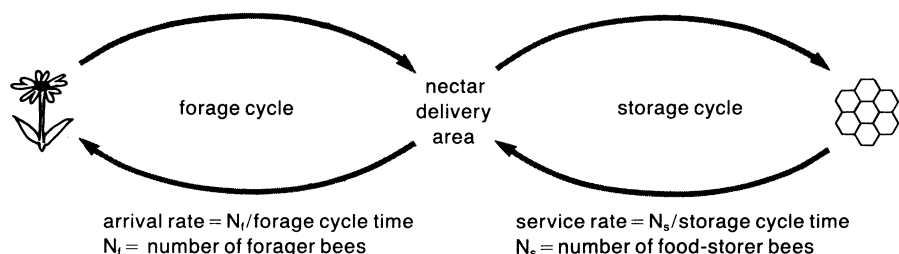
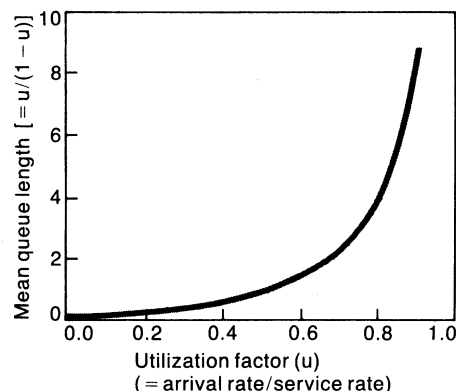


Figure 3. The process of collecting nectar in honey bee colonies is shown schematically as two separate but intersecting forage and storage cycles. In the forage cycle, foragers collect nectar from flowers, bring it back to the hive, and then return to the flowers to gather more nectar. The storage cycle takes place entirely within the hive as food-storer bees in the delivery area (just inside the entrance) unload the fresh nectar from foragers, transport it deep inside the hive to the honey comb for storage, and then crawl back to the delivery area. The amount of time a nectar forager has to wait to begin unloading to a food-storer bee is a cue that indicates the nutritional status of the colony.



0.5—then the average queue size does not exceed one, and nectar unloading proceeds with little delay. If U reaches 0.8, the wait becomes appreciable, with an average waiting line of four individuals. Any further rise in the utilization factor entails a disproportionately sharp increase in the length of the waiting line.

Consider the case of a colony near starvation. Little nectar is being gathered, so the arrival rate of foragers is low and there is abundant empty storage comb, enabling the food storers to complete each storage cycle quickly (usually in less than ten minutes). The effect of these conditions is a low utilization factor, and a negligible waiting time for returning foragers. Now consider a well-nourished colony whose hive is brimming with honey. In this situation there is little empty storage comb, which can cause the food storers to take 40 minutes or more to complete a storage cycle, so the service rate is low. The utilization factor is therefore high and the waiting time to begin unloading is long. Experiments have demonstrated that the foragers do indeed respond to the waiting time in determining their colony's nutritional status (Seeley 1989). The critical test involved removing most of the food-storer bees from a colony with little honey in its hive, thereby reducing the service rate and so increasing the waiting time to begin unloading. The colony's foragers were then observed to cease recruiting nestmates to a feeder with a concentrated sucrose solution. These bees behaved as if their hive were packed with honey, although the combs were nearly empty!

Coordinated group action

Let us now consider an example that illustrates how natural selection has linked multiple pathways of information flow to achieve an impressive feat of coordination at the colony level. As flower patches bloom and wither across the countryside, a hive of bees continuously adjusts the distribution of its foragers among the patches

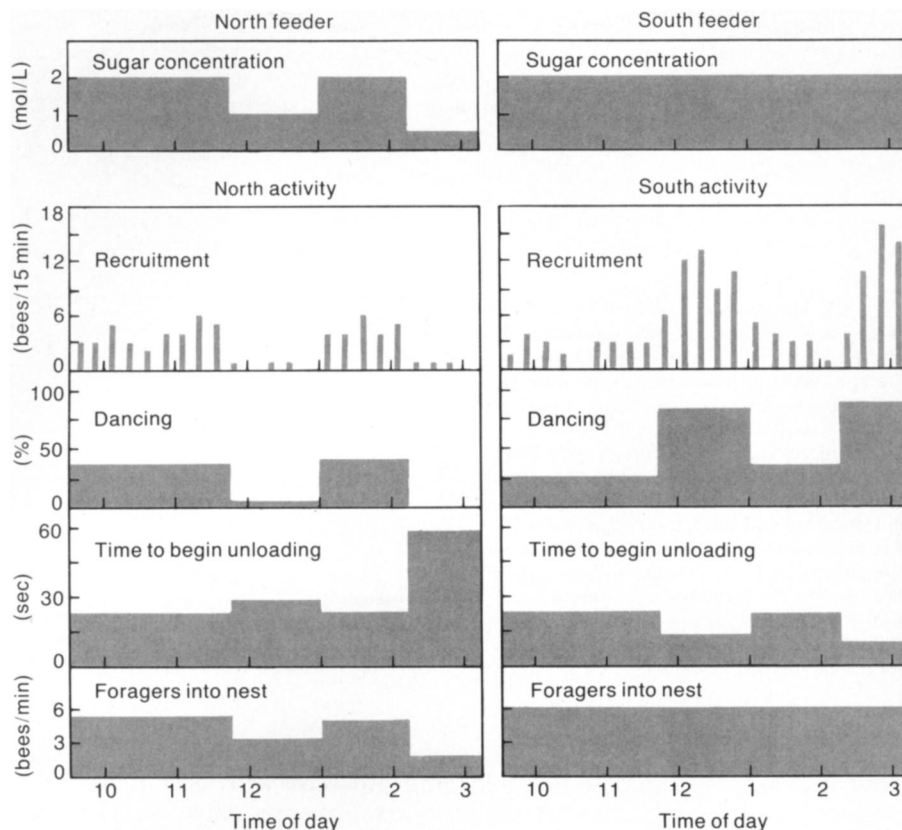


Figure 4. In a six-hour experiment, the quality of one food source (north feeder) was decreased, increased, and decreased again while the quality of a second source remained fixed. When the food source in the north deteriorated, the bees promptly increased recruitment of foragers to the food source in the south. This can be explained by the following scenario: When the north food source declined, the bees foraging there lowered their foraging rate, which depressed the total arrival rate of foragers at the hive. This caused the foragers from the south food source to experience a shorter wait when unloading nectar. This in turn stimulated these foragers to increase their production of recruitment signals, thereby producing a rise in the number of recruits at the south feeder. (After Seeley 1986.)

to track the changes in foraging opportunities (Visser and Seeley 1982). This process is depicted in Figure 4, which shows how a colony foraging from two experimental food sources deftly altered its behavior following changes in the profitability of one of the sources.

From mid-morning to shortly before noon, the two feeders, north and south of the hive, offered equal sucrose solutions, and the colony exploited each at the same moderate level. Loaded foragers returned to the hive from each feeder at a rate of six bees per minute, and approximately four recruits joined the work force for each feeder every 15 minutes. (All recruits were captured, so each feeder's work force actually remained stable.) Then the sucrose solution of the north feeder was diluted from a two- to a one-molar concentration. The colony responded within 15 minutes, shifting to a strongly asymmetrical pattern in which the rate of forager visits to the feeder with the dilute solution fell by nearly 50%, whereas the rate of visits to the other feeder held steady. The rate of recruitment of additional workers to the feeder with the dilute solution dwindled to zero, while the rate of recruitment to the other feeder rose threefold.

The most intriguing aspect of this reallocation of foraging effort is that it involved behavioral changes by bees foraging at *both* food sources. Foragers at both

sources were distinctively labeled, and each feeder was monitored for bees from the other feeder; no cross visits were observed. Information about the waning food source must have passed from one group of foragers to the other; only with this information could the foragers at the steady food source have known to boost their dancing.

The multistage pathway of this information transfer can be traced using a flow diagram. Following the dilution of the north food source, the north foragers virtually ceased dancing, which shut off recruitment to the north, and they halved their foraging tempo. These adjustments reduced the arrival rate of foragers from the north, thereby diminishing the colony's total rate of arrivals at the hive. This lowered the colony's utilization factor and nearly halved the period during which south foragers had to wait to begin unloading—13 seconds instead of 22 seconds. (The waiting time for the north foragers rose somewhat—to 28 seconds instead of 22 seconds—because these bees no longer tried to make contact with food storers immediately upon entering the hive.) The drop in waiting time for south foragers stimulated them to recruit foragers more vigorously; the percentage of the south foragers dancing upon returning to the hive soared from 30 to 90% (Fig. 4). In sum, the colony responded to a

decline in one part of its food-source array with adjustments in the foraging effort throughout the array, and this coordination involved information passing between four groups of bees (north foragers, food storers, south foragers, recruits) via a combination of signals and cues.

Building integration

This article began by noting what is perhaps the single most important question raised by colonies of honey bees and other advanced social insects: How did evolution take a large number of organisms built for solitary life and forge them into a unified, group-level vehicle of gene survival? With respect to the mechanisms of integration, the solution to this puzzle lies in how information flows among the members of a colony, enabling them to coordinate joint efforts in nest construction, thermoregulation, social foraging, and other colony-level adaptations. The message that is emerging from studies of integrative phenomena in honey bee colonies is that much of the intricate orchestration of a colony's members is achieved through surprisingly rudimentary information transfer. Traditionally, studies of communication in the social insects have emphasized sophisticated and conspicuous communication processes that involve signals honed by natural selection, such as the dance

language behavior. There is no question that these processes are important. Nevertheless, I predict that the relatively subtle communication mechanisms of cues and the shared environment will prove even more important than the more obvious signals. If so, then the impressive feats of internal coordination shown by superorganisms will often prove to be built of rather humble devices. This should not surprise us, for as Colin Pittendrigh (1958) so nicely put it, adaptive organization is "a patchwork of makeshifts pieced together, as it were, from what was available when opportunity knocked, and accepted in the hindsight, not the foresight, of natural selection."

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"There was a steak restaurant here, and this is the menu."