

7

The Success of Social Insects

CHAPTER OUTLINE

- *The power of kin selection*
 - The concept of superorganism*
 - The natural history of honeybees*
 - The honeybee's altruistic reproductive behavior has an unusual genetic basis*
 - Termites are incestuous*
- *Behavior in honeybee societies is both complex and adaptive*
 - Information is needed within the colony*
 - Foraging bees communicate their finds to their hive mates*
 - There is no central authority for assigning tasks in a bee colony*
 - The behavior of bees appears to be rational*
 - Colonies of cells and colonies of organisms use similar control principles but different mechanisms*
- *Synopsis*
- *Questions for thought and discussion*
- *Suggestions for further reading*

Why devote a chapter to insects in an account of evolution and behavior that leads to humans and other primates? There are two reasons. First, colonies of bees, ants, and termites are among the largest and most elaborate social structures on earth. Moreover, bees also provided early and important insight into the concept of kin selection.

Second, these creatures are fascinating for the complexity of their behavior. More than a few writers have sought to ennoble humanity by contrasting our free will with the unthinking behavior of social insects. This comparison is so facile, however, that it obscures an even more interesting feature of insect behavior. On looking closely we find that the roles of individual bees and ants are not so rigidly fixed as this contrast suggests. Tasks change, and the work of individuals is so well coordinated that the colony is able to adjust to shifting resources and new environmental challenges. Comparing the processes by which the behavior of social insects and humans are regulated in an adaptive manner reveals the scope and splendor of natural selection.

Photo: Ants, like bees, illustrate the power of kin selection to generate complex social structures. These leaf-cutter ants (*Atta cephalotes*) are farmers. They cut pieces of leaf, carry them to their nests, and grow a fungus on them. They then eat the fungus.

THE POWER OF KIN SELECTION

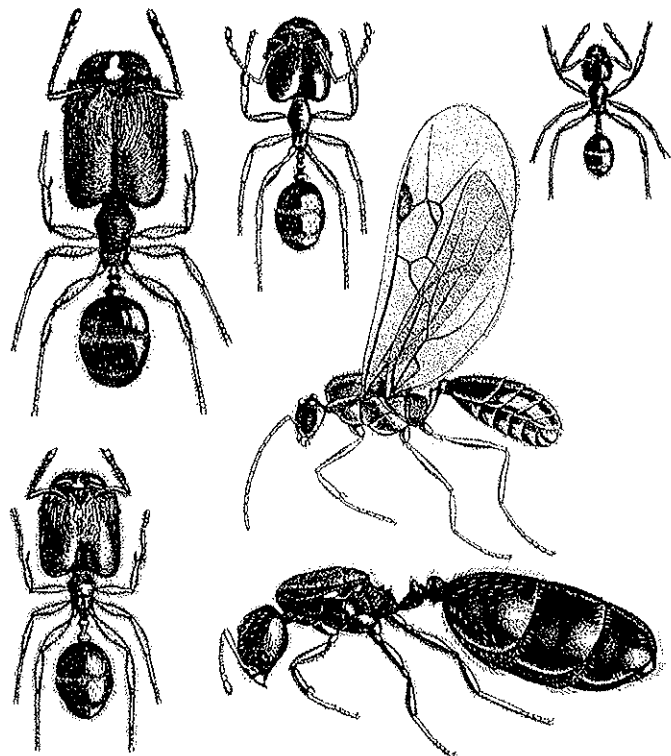
Bees, ants, wasps (order Hymenoptera), and a more distantly related group, the termites (order Isoptera), live in large colonies in which one or a few members do all of the reproducing and most of the individuals simply assist. In terms of numbers, ants and termites represent particularly successful evolutionary outcomes. In the tropics, where the diversity of species reaches a maximum, there can be 200–300 species of ant in a square mile, and as many as forty-three different kinds of ant have been collected from a single tree. Furthermore, individual colonies of ants and termites can contain millions of individuals, and in tropical rain forests these social insects make up more than three-quarters of the total insect biomass.

Colonies of bees and ants have a “queen” who lays eggs and thousands of workers that tend the eggs and larvae, build and clean the nest, and forage for food. Ants differ from bees in that the colonies are generally larger, the workers do not have wings, and the division of labor among workers is so marked that workers frequently come in two body forms or *castes*, specialized for different functions (Fig. 7.1).

THE CONCEPT OF SUPERORGANISM

A colony of bees or ants is sometimes likened to a superorganism, because the behaviors of the individual insects are so well tuned to collective need that the

FIGURE 7.1 Castes of a species of ant. The queen is at the bottom right, and a male (with wings) just above her. All of the other individuals are nonreproductives: soldiers and workers.



colony seems to function with the coordination typical of a single animal. The existence of these evolutionarily successful creatures therefore raises a number of important conceptual issues. What is the biological basis for so many individuals foregoing their own reproduction? How is information about the needs of the colony discovered? How do individual insects communicate that information? And how is the behavior of individuals coordinated so that their actions are cooperative and adaptive?

THE NATURAL HISTORY OF HONEYBEES

Although ants are equally interesting, we will use the common honeybee (*Apis mellifera*) to address these questions. Bees are exploited the world over. Honey is a source of food for humans, and in agricultural regions bees are reared commercially so that they are available in large numbers to pollinate cash crops in the spring. Most importantly, bees have been studied extensively, and understanding their way of life is a source of considerable interest.

A colony of bees consists of 20,000 or so worker bees and a queen. The workers, like the queen, are female, but only the queen is capable of laying fertilized eggs. All of the workers are daughters of the queen, and are therefore sisters. There are some males present too, called drones. They are somewhat larger than the workers (Fig. 7.2), but they make no contribution to

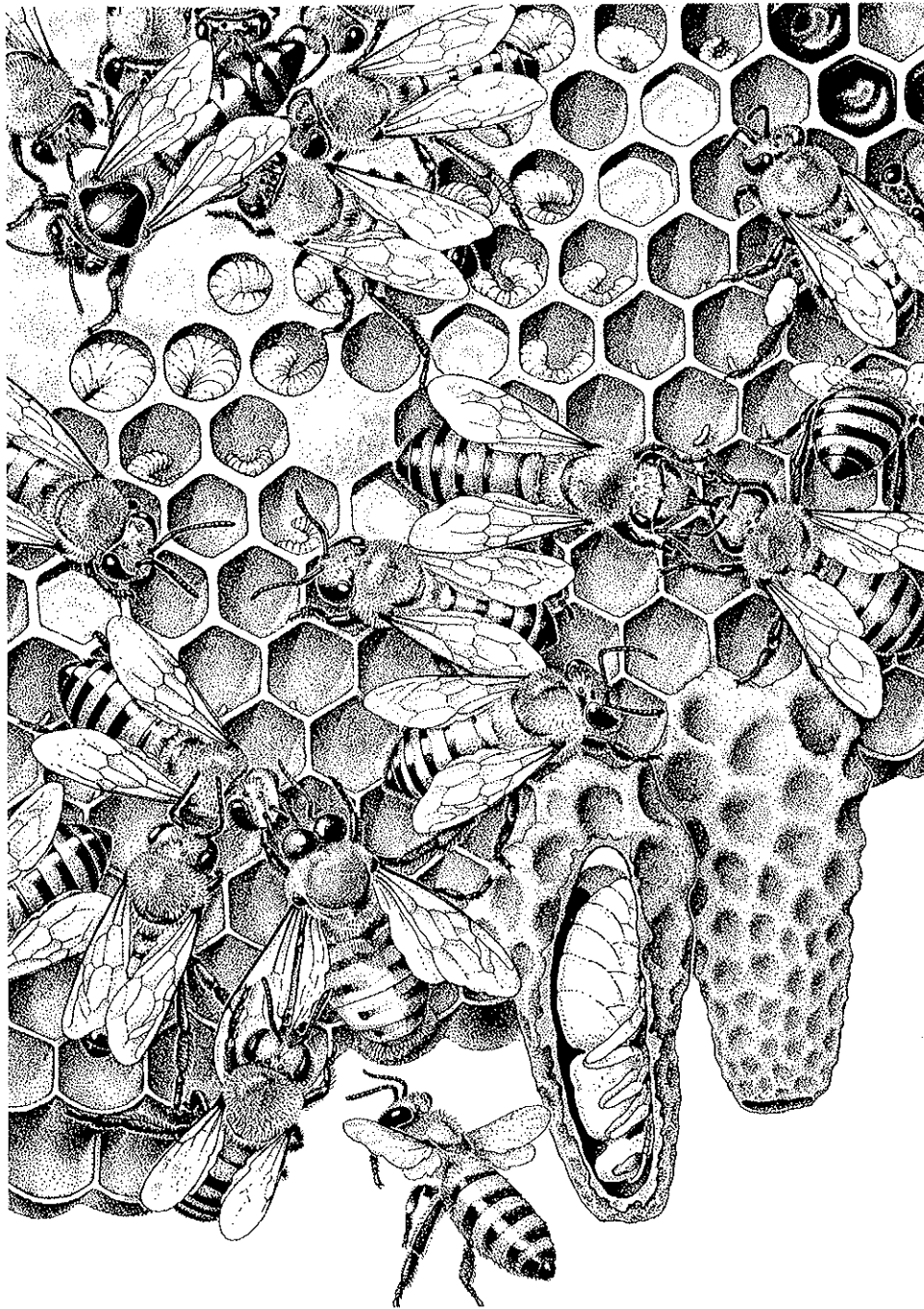


FIGURE 7.2 Portion of a comb from a colony of honeybees. The queen is in the upper left surrounded by several worker attendants. Several of the open cells on the left contain eggs or larvae in different stages of development. The open cells in the upper right contain honey. At the bottom left a drone is being dragged outside by a worker, who has seized a wing. The two large cells at the lower right contain developing queens.

the life of the hive and exist only to fertilize new queens. Their numbers are under the control of the females. When they are needed, the queen lays more drone eggs (you will see presently how she can control which eggs are to become drones and which workers), and when there are more drones present than are needed, the workers drive them from the hive.

Bees form colonies in protected places such as hollows in trees where they secrete combs of wax consisting of precise arrays of hexagonal cells (Fig. 7.2). The cells serve multiple purposes. Some are brood cells, in which the queen lays a single egg. Others are storage cells, containing either pollen that has been collected from flowers, or honey, which the bees make by con-

centrating the nectar they collect from flowers. Pollen and honey are the food of bees.

The eggs hatch after about three days, and the larvae are fed by nurse bees. About six days later the larvae pupate, still in the comb in their individual wax cells. After another twelve days the adult bees emerge. A worker bee lives for several weeks, except for those present at the end of the season, which live through the winter and continue the life of the colony when the weather warms the following spring. The queen can live for several years.

A worker bee takes on different tasks during its lifetime. The youngest bees remain in the hive and are initially engaged in cleaning the brood chamber (the region of combs used for rearing young) before becoming nurse bees. Nurse bees provide food to the larvae and attend to other tasks such as regulating the temperature in the brood chamber and accepting nectar and pollen from forager bees. Between about ten and twenty days of life the bees develop wax glands in the abdomen and secrete the waxy substance from which they make the combs. The oldest bees in the colony are foragers that leave the hive to find nectar and pollen. There is great flexibility in this sequence of different behaviors, and what an individual bee is doing is not tied in a firm way to its age. For example, if the population of foragers should decline (which can be forced experimentally by closing a hive and moving it during the middle of the day), younger bees can step forward to replace the missing foragers. Even without such drastic intervention, however, the natural needs of the colony require a dynamic shifting of labor.

There is a second mode of reproduction in which the queen and a number of the worker bees depart and form a second colony. This *swarming* happens in early summer as the number of bees in the colony outgrows the available space. Under these conditions, workers feed a few of the developing larvae a different substance, and these individuals develop into queens, with functional ovaries and an unbarbed stinging apparatus. As they near full development, the old queen leaves with about half of the workers to find a new nest site. The first of the new queens to emerge as an adult stings the other developing queens to death, then leaves for a mating flight in which she becomes inseminated by drones, generally from other hives. The sperm that she acquires on that flight are stored internally for the rest of her life and doled out as she needs them to fertilize eggs.

THE HONEYBEE'S ALTRUISTIC REPRODUCTIVE BEHAVIOR HAS AN UNUSUAL GENETIC BASIS

Why do thousands of worker bees forego their personal reproduction and cooperate for the reproductive success of one individual, the queen? Cooperation can even involve sacrifice of life: the end of the stinger of a

worker bee is barbed, and it cannot be withdrawn from the victim without pulling the poison gland out of the worker's abdomen, damage that the worker does not survive.

As a prelude to answering this question about the evolution of cooperation, consider the more familiar example of your own body. As we pointed out in Chapter 5 (Cells in an Organism Must Cooperate), your body is a colony of cells, many of which are specialized for different functions such as skin, muscle, liver, and brain. As virtually all of your cells have the genes that were present in the fertilized egg from which you developed, the cells of your body have the same genetic interests as your eggs or sperm. Success of your eggs in getting fertilized, or your sperm in fertilizing the egg of another individual, is success for the genes that are present in all your body's cells. This is the basic reason why organisms can evolve with responsibility for reproduction vested in a small subset of their cells, the germ line. The somatic cells are specialized for roles that enable the reproductive success of the germ line.

But a colony of bees or ants does not consist of genetically identical individuals. Bees and ants are sexually reproducing organisms, and during meiosis and the production of eggs and sperm, recombination produces genetic diversity (Chapters 3–4). The result is that individual, sexually reproducing organisms are genetically unique and therefore have singular reproductive interests. How, then, are we to explain the existence of colonies of bees and ants in which genetically different individuals do not reproduce but instead cooperate with others to ensure the reproduction of a third individual, the queen? The reason that a colony of bees can function as a reproductive unit is an interesting story in genetics, and understanding has undergone significant revision in the last few decades.

Charles Darwin recognized that cooperative behavior of nonreproducing social insects posed an important problem for the theory of natural selection, but knowledge of inheritance in his day was not sufficient for anyone to formulate a plausible explanation. In 1964 the evolutionary geneticist William Hamilton suggested that the explanation could be found in the way sex is determined in these insects. Females develop from fertilized eggs and are therefore diploid (with a set of chromosomes from each parent), whereas males develop from unfertilized eggs and are haploid (with only a single set of chromosomes). This is how the queen can control the production of males; when she does not fertilize an egg with the sperm she has stored, it develops into a drone. Hamilton pointed out that as a consequence of this means of sex determination, the degree of relatedness between sisters should be 0.75 (Box 7.1) rather than the 0.50 that would be expected of full sisters in humans and other monogamous animals. Thus the original explanation for the reproductive altruism of bees and ants was that sisters are more

Box 7.1

Tracing the Degree of Relatedness of Individual Bees

Recall from our discussion of kin selection in Chapter 6 that the degree of relatedness r between any two individuals is the probability that they share genes by virtue of a recent common ancestor. In bees and ants, males develop from unfertilized eggs and are haploid, and this changes the arithmetic. Refer to Figure 7.3 to follow the argument.

- (A) To determine the degree of relatedness of sisters, trace the arrows from the dark green to the light green symbol: r through their mother (the queen, Q) is $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$. That is, the probability that any gene was inherited from the mother is $\frac{1}{2}$, the probability that that gene was passed from the mother to the other daughter is also $\frac{1}{2}$, and the two probabilities are independent. Similarly, the probability that a gene came from the father is $\frac{1}{2}$, but the probability that the sister inherited that gene from her father is $\frac{1}{n}$, where n is the number of drones with which the queen mated. If n were 1, any gene received from the father by the first sister (dark green symbol) is also present in the second sister, because the drone (their common father) has only one set of genes. On the other hand, because the queen mates with a number of drones (generally about ten), the probability that two sisters share a gene through the same father is diminished by a factor of $\frac{1}{10}$. The degree of relatedness of two sisters is the sum of the probabilities through each parent: $r = (\frac{1}{2} \times \frac{1}{2}) + (\frac{1}{2} \times \frac{1}{n})$. If $n = 1$, $r = \frac{3}{4}$. If $n = 10$, $r = 0.3$.

- (B) A mother is related to her son by $r = \frac{1}{2}$; that is, the probability of any gene being passed to her haploid offspring is $\frac{1}{2}$. This is true for the unfertilized eggs of workers as well as for those of the queen.

- (C) A worker's r to her sister's son (her nephew) is calculated as for (A), but must extend for an additional generation. Examine the diagram and see that $r = (\frac{1}{2} \times \frac{1}{2} \times \frac{1}{2}) + (\frac{1}{2} \times \frac{1}{n} \times \frac{1}{2}) = 0.15$ for $n = 10$. This diagram also shows that the queen's r to her grandson is $(\frac{1}{2} \times \frac{1}{2}) = \frac{1}{4}$.

- (D) The degree of relatedness of a male to his daughter is 1; that is, because he is haploid, all of his genes are present in every one of his female offspring. He is not related to any of the queen's sons, because they develop from her unfertilized eggs. His average degree of relatedness to offspring of the queen is thus 0.5 (or would be if she were not carrying sperm from other males).

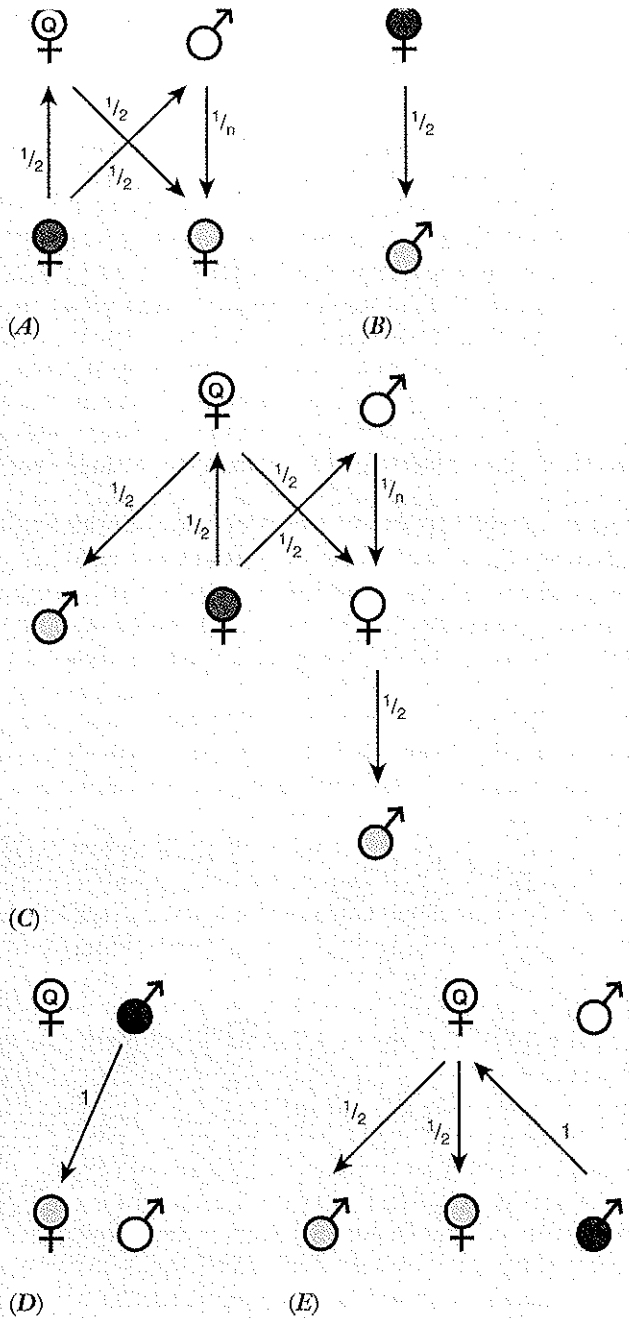


FIGURE 7.3 Tracing degrees of relatedness among bees: (A) worker females to each other; (B) workers to their sons; (C) workers to brothers and to the sons of the other workers; (D) males (drones) to their offspring; and (E) drones to their siblings. See the text for an explanation of each calculation.

- (E) The degree of relatedness of a male to his siblings is 0.5. Note again, a male has no father, but he does have a grandfather by way of his mother, the queen.

The consequences of this mode of inheritance for the colonial life of bees are described in the main text.

closely related to each other (0.75) than they are to their own offspring (0.5), so it is in their reproductive interests to cooperate with each other in rearing sisters (through the egg-laying of their mother, the queen) rather than in trying to produce their own daughters.

Why are the females the “altruists”? Drones have no genetic incentive to forego reproduction. In fact, it is to their advantage if more females than males are reproduced, because in the next generation their genes are only carried by daughters (Box 7.1).

This explanation has an elegance that led to its quick acceptance, but it has a serious problem in that all of the workers in a colony do not share the same father. During her mating flight a virgin queen accepts sperm from about ten drones. She stores those sperm and uses them to fertilize eggs more-or-less randomly throughout her reproductive life. As a consequence, the degree of relatedness of two workers in the same colony can be as high as 0.75 for sisters who share the same father, but only 0.25 for half-sisters. The average degree of relatedness r will be $(0.25 + 0.5/n)$ where n is the number of matings the queen achieved (Box 7.1, Fig. 7.3A). If $n = 10$, $r = 0.3$, which is smaller than the degree of relatedness that workers would have with their offspring if they could lay their own eggs. What, then, keeps the colony functioning as a reproductive unit?

What would be the consequences of workers reproducing? The simplest possibility for workers is to lay unfertilized eggs. A female bee—worker or queen—is related to her son by $r = 0.5$ (Fig. 7.3B). The queen, however, is related to her grandsons—any drones produced by unfertilized eggs from her worker daughters—by only 0.25 (Fig. 7.3C). Consequently, it is clearly in the queen’s interest to restrict the number of eggs laid by workers.

Although it is in the reproductive interests of an individual worker to produce sons, it is not in her interests to see her sisters do so. This is because if the queen has mated with ten drones, the average degree of relatedness of a worker to her sister’s sons is only 0.15 (Fig. 7.3C). Because a worker has so many sisters, their production of drones could readily dilute any reproductive success she might achieve by laying eggs herself. It therefore becomes a much better tactic for her to vest her reproductive success in the queen’s sons (her brothers), to all of whom she is related by $r = 0.25$ (Fig. 7.3C). Note that because drones develop from unfertilized eggs, the degree of relatedness of a worker with her brothers is independent of the number of matings the queen achieved.

Can the workers reproduce? A small number of workers (about 1%) have functional ovaries, and about 10% of the unfertilized (drone) eggs in a colony are laid by workers, but only about 0.1% of the drones in a colony have developed from eggs laid by workers.

Something is restricting the production of drones by workers, and both the workers and the queen play a role. The workers actively destroy unfertilized eggs laid by other workers (as we just saw, it is in their genetic interests to police each other), and the queen appears to mark the eggs she has deposited with a chemical signal (a *pheromone*), allowing the workers to identify which drone eggs should not be destroyed. Another queen pheromone, which is distributed around the colony by workers, prevents swarming by inhibiting the workers from rearing additional queens. Whether it also inhibits the worker’s own reproduction is not known.

The result is a balance in which the disparate, selfish interests of genetically different workers are largely quelled by other workers, to their own genetic advantage. The result is an evolutionary compromise in which the workers seek reproductive success through the rearing of brothers rather than a mixture of sons

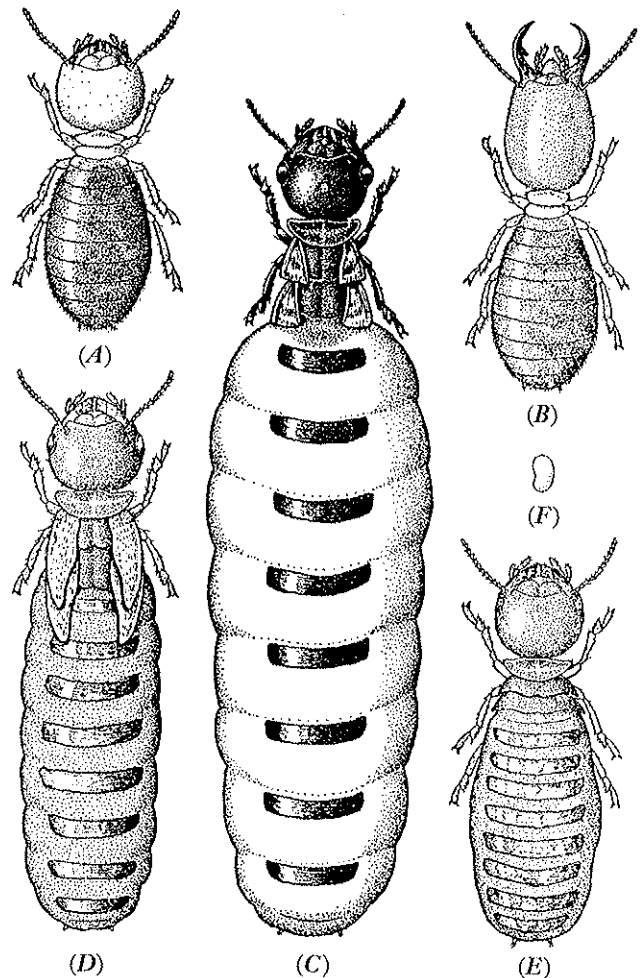


FIGURE 7.4 Castes of termites: (A) worker, (B) soldier, (C) queen, (D) and (E) secondary and tertiary queens; (F) is an egg. Compared to the nonreproductives, the queens are massive egg-laying machines. The primary queens can live for many years.

and nephews. Just as the evolution of nepotistic behavior of sexually reproducing vertebrates can be understood in terms of kin selection and degrees of relatedness of near relatives, the social structure of bee colonies, and the "altruistic behavior" of workers is based on the genetics of honeybees. Although for bees the details are more complex, kin selection is also responsible.

TERMITES ARE INCESTUOUS

Massive insect social systems organized around a few reproductives and much larger numbers of sterile individuals have evolved in a second group, the termites. This group of insects is related to roaches and is more primitive than the Hymenoptera. For example, termites grow through successive molts and do not have separate larval, pupal, and adult stages. Termite social systems are therefore probably older than those of bees and ants. As with ants, however, the nonreproductive termites can form both worker and soldier castes (Fig. 7.4). Moreover, termite colonies rival those of ants in size. The termite mounds of a fungus-growing African species house millions of individuals and can be nearly thirty feet tall (Fig. 7.5). All termites eat woody material, although only about ten percent of termite species

are economic pests. Many termites are dependent on intestinal protozoa or bacteria for digestion of cellulose (the polysaccharide of which wood is composed), and most species must remain within damp chambers of their own construction in order to keep from desiccating. Ants are a major predator of termites.

The genetic basis for termite social structure is very different from that of ants and bees. The nonreproductive castes consist of both males and females, and both are diploid. What, then, accounts for the presence of such large-scale reproductive altruism in this group of insects? The likely explanation is thought to involve inbreeding in the following way.

New colonies are periodically formed from the mating of winged males and females that have emerged from two different parent colonies. As the primary and, at first, the only reproductives, the king and queen produce all of the new colony members. Secondary reproductives are formed later, and they remain within the colony and contribute more offspring. This intensive inbreeding leads to an increase in homozygosity. Consequently, when winged individuals are produced and leave the colony, the chromosomes of each homologous pair are homozygous at many loci.

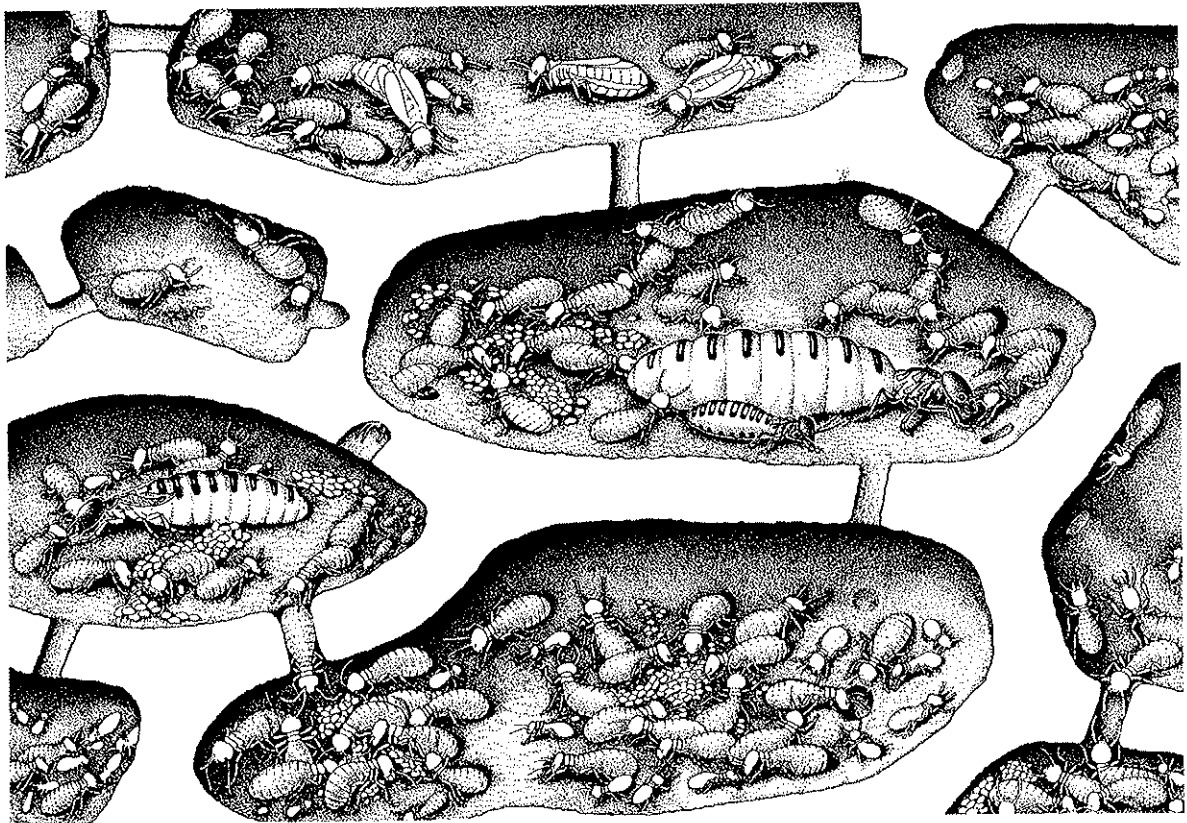


FIGURE 7.5A Internal structure of a small part of a termite colony. The primary queen is in the central compartment, and there is a secondary queen in the compartment below and to the left.

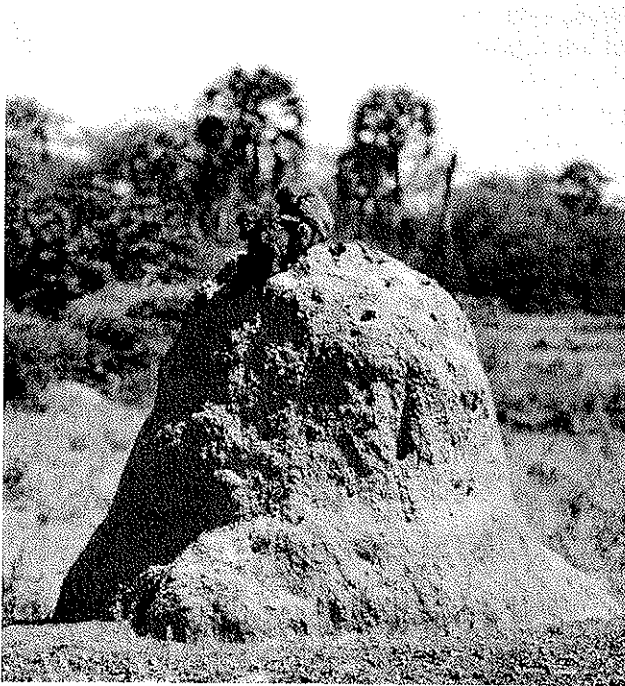


FIGURE 7.5B A large termite mound in East Africa. The animals sitting on the top are baboons.

When two individuals from different colonies mate and start a new colony, all of their offspring are genetically very much alike, just as were the offspring of the two long-inbred strains of tobacco in Figure 4.6. This is because each parent, being homozygous at many loci, produces gametes that are genetically very similar. The offspring are therefore heterozygous for the parental chromosomes, but each offspring has a very high degree of relatedness to all its siblings. Sexual reproduction by offspring leads to recombination, with the result that secondary reproductives are more related to



FIGURE 7.6 The social system of this hairless subterranean mammal is similar to that of termites, with much inbreeding and therefore high genetic relatedness among colony members. This makes it possible for reproduction to be vested in one female.

their brothers and sisters than their offspring. There is thus a genetic incentive to forego reproduction and assist the king and queen in making more siblings. When the founders of new colonies are the result of cycles of inbreeding within the old colony, however, the conditions are set for the process to repeat.

Termites thus illustrate how natural selection has found more than one way to form colonies of organisms in which reproduction is vested in one or a few individuals that are supported by numerous nonreproductives. There is in fact a mammal, the naked mole rat of east Africa, where a single female produces young and is attended by a colony of near relatives (Fig. 7.6).

BEHAVIOR IN HONEYBEE SOCIETIES IS BOTH COMPLEX AND ADAPTIVE

INFORMATION IS NEEDED WITHIN THE COLONY

The colonies of bees and ants consist of thousands of females, each of which must achieve reproductive success by working to support the colony. We have seen how genetic relatedness lies behind the extraordinary social structure, but in order for the colony to thrive, the activities of the individual worker bees must be coordinated. The problem has a superficial likeness to the running of an automobile plant. If everyone in the plant should start making fenders, the production of finished cars would soon come to a halt. Similarly, if all the bees in a colony should devote themselves to secreting wax and building comb, there would be no honey to store and nothing to feed the larvae. We saw earlier that bees perform different tasks as they grow older, but what a bee is doing at any particular time is not tied rigidly to its chronological age. The colony maintains a flexibility that enables it to respond to changes in weather and to exploit the ever-changing sources of nectar and pollen in the surrounding area.

If someone in an automobile assembly plant does not order parts in timely fashion, the plant will be forced to shut down. Similarly, bees must bring supplies into the hive—nectar, pollen, and water. Therefore, there must be an allocation of labor among the forager bees such that these items are procured as required. During a period of cool, wet weather the bees are unable to forage, and the stores of pollen in the hive may become very low. As soon as the weather permits, however, the bees replenish their supplies by devoting extra effort to collecting pollen.

Bees regulate the temperature of the hive in the region of the brood cells with remarkable precision. The temperature is held at $34.5^{\circ} \pm 1.5^{\circ} \text{C}$, and on a typical day it varies within only 1°C . In hot summer weather

when the nurse bees are unable to keep the temperature down by stirring the air with their wings, they hang drops of water and lower the temperature by evaporative cooling. But for this they need an extra supply of water, which requires water transport by a subset of the foragers.

In the automobile plant, suppliers may change their prices or be unable to deliver when required, so buyers must be ready to seek alternative sources. In the hive, the collection of nectar requires even more active shifts of effort. Patches of flowers can bloom and wither on a daily basis as the season progresses, so new sources must be discovered promptly and exploited efficiently as the blossoms open. This, too, necessitates a constant shifting of labor among the foragers.

Success leads to growth. If automobile sales are brisk and demand continuous, there may be an economic advantage to building a second plant elsewhere. In a colony of bees, rapid growth typically exhausts the available space in the hive, and there is a reproductive advantage to swarming, a process that increases the population of near relatives.

Both automobile plants and bee colonies require information in order that appropriate decisions are made. In the case of an automobile plant, a small group of individuals (top management) gathers information and hands down decisions that are intended to maximize company profits. To the degree that they are successful in furthering that goal, the decisions are intelligent. Most individuals in the company accept these decisions and do as they are instructed. Such hierarchy is a common feature of human social structures; military establishments are prime examples.

The honeybee colony works on a very different model. There is no centralized control; the queen has no imposing authority. She does little more than lay eggs. Furthermore, neither she nor any other member of the colony has all the information required for an intelligent managerial decision. The colony nevertheless responds to changes in the outside world in a reproductively adaptive fashion, *as though* the response were intelligent. How does this occur?

The answers illustrate the enormous power of natural selection. The honeybee colony is a social system in which no individual has access to more than a small fraction of the total information that is being exploited by the entire hive. Nevertheless, 20,000 individual insects behave in a coordinated fashion, achieving success for the entire colony, providing numerous examples of interlocking behavioral adaptations.

FORAGING BEES COMMUNICATE THEIR FINDS TO THEIR HIVE MATES

One of the most fascinating features of bees is the way in which foragers communicate with their sisters in the hive about sources of food and water that they have lo-

cated. When a forager has found a particularly fine source of nectar—one with a high concentration of sugar that can be easily exploited—she returns to the hive and performs a “dance” on the surface of the combs (Fig. 7.7).

The dance consists of “waggle-run” in which the bee moves forward a couple of centimeters while shaking her abdomen from side to side, then circles about and repeats the waggle-run again, remaining near the hive entrance in a restricted region referred to as the “dance floor.” The hive is dark, and the dancer also

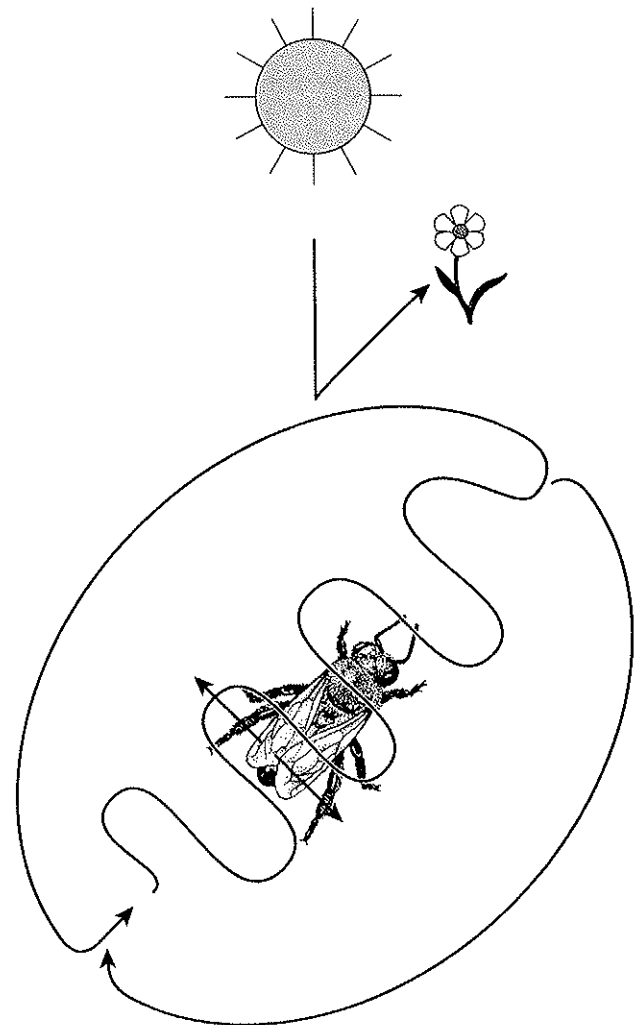


FIGURE 7.7 The waggle dance of honeybees is performed in the dark on the vertical surface of the comb by returning foragers who have discovered a particularly profitable source of nectar or pollen. The bee advances a short distance emitting a low-frequency sound and wagging her abdomen from side to side. The frequency of repetition of the waggle-run indicates distance to the food, the total number of repetitions indicates the quality of the source, and the angle between the waggle-run and the vertical indicates the angle a recruit must keep with the sun as she flies out to find the food source.

Box 7.2 Animal Communication

Communication is the exchange of information, and many animals are capable of communication. We usually communicate with each other by spoken and written language, but in suitable context a wink, a blush, or a smile can convey volumes. Although human language amplifies enormously our capacity to exchange information, it does not define communication.

This point is illustrated by Figure 7.8, which shows profiles of dogs' faces in a 3×3 matrix. Moving

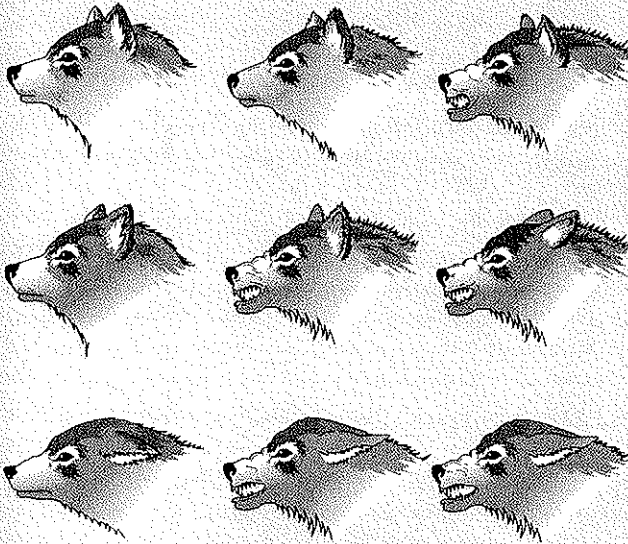


FIGURE 7.8 A familiar example of animal communication. These profiles signal increasing fear from top to bottom and increasing rage from left to right.

down the first column, these faces display increasing fear: the lips are closed, the hair lies flat, and the ears are laid back. Moving from left to the right across the top row, the faces display increasing rage; the lips are curled exposing the teeth, the hackles rise, and the ears become erect. Fear and rage are not mutually exclusive, and both can be seen in the lower right, which could be a threatened female with young pups. Anyone who knows dogs will know what these signals mean and would be reluctant to extend a hand to pat the animals that appear angry. Bared teeth and raised hackles are common among carnivorous mammals. Animal communication thus has an objective reality that can sometimes be interpreted even by other species.

We study the communication systems of animals by observing the effects the signals have on the behavior of other individuals. The dances of bees were decoded by observing their effects on the bees that surround the dancers and then by conducting experiments to verify the interpretations. For example, bees were trained to visit artificial feeding sites at various directions and distances from the hive and the orientation and tempo of their dances were carefully measured. These experiments revealed what information is communicated by the dances.

That bees communicate with each other does not mean they are consciously aware of new sources of nectar or form mental images of flowers of the sort we experience. The bees convey information to each other, but as observers we know nothing about the mental processes that are occurring in the animals' brains. We can observe the effect the information has on the behavior of the recipient, and this can tell us the nature of the information being conveyed. But what, if anything, an animal "thinks" is not revealed by watching its behavior. The only possible exceptions involve our closest living relatives, the great apes, to which we will return in Chapter 11.

emits a soft, low buzzing sound, which is important in attracting other bees and bringing them into physical contact with her.

Although she moves around on the comb while dancing, the orientation of the waggle-run with respect to the vertical remains the same, and that angle tells other workers who contact her during her dance the direction they must fly to reach the source of nectar or pollen. The angle between the waggle-run and the vertical is the angle that a recruit must maintain between her outward flight path and the sun. (Bees that are crawling on a vertical surface can sense their orientation to the vertical by the weight of the head on sensory hairs between the back of the head and the front of the thorax.)

Note that interpreting the dance requires a transposition of coordinates; the angular orientation of the dance on a vertical surface corresponds to the horizontal angle between the sun and the direction to the food source.

The frequency with which the waggle-run is repeated conveys information about the distance to the food source; the closer the flowers, the more often the waggle-run is repeated (Fig. 7.9). The dance therefore conveys specific information about both direction and distance to the food source.

A dancing bee makes other information available to her hive mates. Generally she will have picked up the odor of the flowers she has just visited, and this can be detected by chemoreceptors on the antennae of

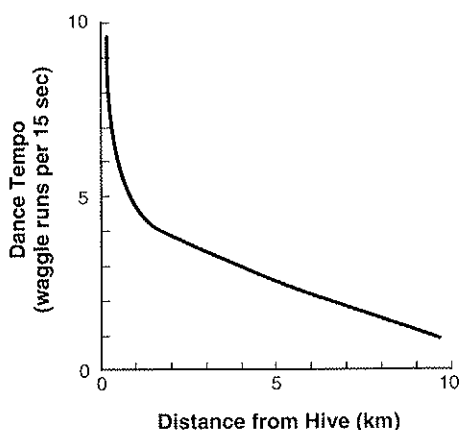


FIGURE 7.9 The relation between the frequency with which the waggle-runs are repeated and the distance to the target (nectar, pollen, water, new hive site).

other bees. This is not information coded in the dance, but it is useful to newly recruited foragers as they approach the area where the flowers are located. Once they have found the flowers the first time, they are able to locate them on subsequent trips using visual cues.

This same dance is used in other contexts besides foraging. When the colony swarms, the departing bees hang in a cluster in a bush or tree until the scouts have located a new nest site. They report their findings by dancing, but the waggle-runs are performed on the surface of the swarm, on the bodies of the other bees. The dances are followed by recruits that then visit the potential site. On their return they may also dance.

A final point about the dances: they are sometimes referred to as the “dance language” of bees. This is not only because they convey a fairly sophisticated array of information, they do it in symbolic fashion. Although bees sometimes dance on a horizontal surface, in which case the orientation of the waggle-run indicates directly the route to the food source, they usually dance on a vertical surface of a hanging comb inside the hive. Under these conditions the dance is not simply an enactment of the outward flight path, for the directional information is coded, with “up” representing the position of the sun as seen on the flight from the hive. Moreover, the interpretation of the dance by other bees depends on the context. Nevertheless, the communication system bears no real comparison with the rich syntax of human language.

THERE IS NO CENTRAL AUTHORITY FOR ASSIGNING TASKS IN A BEE COLONY

Consider first the control of queen production and swarming. Earlier we mentioned that the queen produces a chemical signal, a *pheromone*, that is distributed

about the colony by worker bees when they come in contact with her. That pheromone inhibits workers from feeding larvae the substance that causes them to develop into new queens. When the hive grows to a size at which the concentration of the queen’s signal is too low, the colony prepares to swarm. Nurse bees rear new queens, but before the new queens emerge, the old queen leaves with about half of the workers. Although it is unknown what triggers the old queen’s departure, the falling level of her pheromone has set in motion a series of behavioral responses among the worker bees that culminate in a division of the colony. The “decision” to swarm is therefore a collective response of the colony to overcrowding, initiated by a chemical signal.

A forager only dances when she has located a particularly profitable source of food. As she dances, however, her assessment of its value—the concentration of sugar in the nectar—is also conveyed to the hive. This final piece of information, like distance and direction to the food, is coded in the dance, but unlike distance and direction it *does not become available to any single bee*. The higher the quality of the food source, the *longer* she dances, and for a particularly good source she may perform a hundred waggle-runs. But an unemployed forager who has just been attracted to the dance floor does not survey all of the dances that are being performed. She follows a single dancer, probably at random and for only a few waggle-runs, before she leaves the hive and follows the dance instructions. Each new recruit therefore has no information about the relative quality of the source that she is attempting to locate. The information about quality is exploited by the hive as a whole, however, because the better the food source is, the longer the dancer performs, and the more recruits will be attracted to her waggle-runs. In similar fashion, the dances performed during swarming also contain information about the quality of the prospective nest site—size of the cavity and nature of the entrance hole.

An individual bee “knows” only about the single source of food she is visiting (or has just been induced to visit), but the population of foragers will be attracted to different sources in rough proportion to the array of individual ‘decisions’ the dancers have made about their quality. Furthermore, the system prevents the population of foragers from being drawn to a single, advantageous resource that can fail abruptly. The colony hedges its bets, so to speak, and is able to abandon declining resources quickly and shift foraging efforts to more favorable sources as they become available.

How does this happen? If a resource fails, bees will stop dancing about it, and foragers will abandon it. Conversely, if another patch of flowers should become profitable, it will elicit dancing, and new recruits will be attracted to it from the population of unemployed foragers. The shift of the population of foragers from one

source of food to another is rapid and can be completed in several hours.

How are new sources discovered? At any time about 1% of the foragers (about a hundred bees) are functioning as scouts. They do not follow the dances of other bees, but instead they explore the vicinity of the hive in a radius of several miles in order to locate new sources of food.

The collection of nectar can be influenced by the internal state of the colony as well as by the available supply in the surrounds. The time required for a returning forager to find a recipient for her load reflects the balance between nectar foragers and nectar processors; a long time signifies there are too few processors. If a forager returns from a rich source and is able to disgorge her load within about twenty seconds to a bee who is making and storing honey, she is likely to perform a waggle dance. On the other hand, if she is unable to find a recipient for her load within about fifty seconds she performs a "tremble dance" in which she walks about the hive making trembling movements, both side-to-side as well as fore-and-aft, and continually facing in different directions. The effect of these tremble dances is to increase the rate of nectar handling by bees inside the hive while decreasing the number of waggle dances. Another behavior of foragers returning from a profitable source is to move about the hive shaking other bees. This signal serves to increase the number of foragers.

When returning foragers experience difficulty in finding bees to unload their nectar, it can mean that the hive is running short of water. This can have two causes. Water is needed to prepare food for larvae as well as for evaporative cooling when the brood chamber overheats. Both of these needs are detected by bees working in the brood chamber, either assessing the water content of larval food in their mouths or with their temperature receptors. The information is conveyed to foragers by the nurse bees decreasing their receptivity for nectar. This signal diverts foragers from the collection of nectar to the collection of water from nearby streams or ponds. A small fraction of the foragers (about 1%) seem to be dedicated to collecting water.

The regulation of pollen collection is less well understood, but here too the nurse bees are involved, because they work directly with the pollen stores. They seem to be able to inhibit pollen foragers by feeding them a secretion from their hypopharyngeal glands.

Comb production is expensive; it requires several grams of carbohydrate (sugar, honey) in order to manufacture a gram of wax. The bees therefore do not invest in more comb than is needed. The amount of unfilled comb is seldom more than 20 percent of the total that the bees have made. The combined presence of few free cells and a brisk influx of nectar to the hive

trigger production of new comb. Both conditions are required to induce the bees to secrete wax.

THE BEHAVIOR OF BEES APPEARS TO BE RATIONAL

All of these behavioral strategies of the colony are rational in the sense that they are decisions that you or I would likely make if we were colony administrators. We reach rational decisions by reasoning about cause and effect, and as colony administrators we would likely apply practical, utilitarian criteria: Does redirecting workers to collect water serve the purposes of the hive? Specifically, is lowering the temperature of the brood chamber necessary to insure the survival of eggs or larvae or pupae, thus the continued prosperity of the colony? If we thought the future of the colony were at stake, we would likely decide to change the behavior of the bees in the same ways that now occur without the involvement of an administrator.

The bees' behaviors are adaptive: they foster reproductive success of the colony, and they are the products of natural selection. The bees do not use reason, but we nevertheless see their behavior as exquisitely reasonable. There is thus a similarity, which is not accidental, between the effectiveness of adaptations and the utilitarian criteria humans use in much of their everyday reasoning.

COLONIES OF CELLS AND COLONIES OF ORGANISMS USE SIMILAR CONTROL PRINCIPLES BUT DIFFERENT MECHANISMS

The mammalian body regulates its salt and water balance with receptors that monitor the concentration of salts in the blood and communicate with the kidney via a pituitary hormone. The body regulates gas exchange by monitoring CO₂ in the blood and modulating the rate of breathing. And it regulates the energy supply, in part by eating and in part by mobilizing stored reserves. In short, bodies maintain a state of internal homeostasis in which needs (demand) are adjusted to the external environment (supply). This is accomplished by processes of which we are largely unconscious, as they involve the autonomic nervous system and hormones circulating in the blood. By these means, cells, tissues, and organs with different functions are kept working in a coordinated fashion so that the organism continues to thrive.

As we have just seen, a colony of social insects faces the same general challenge. Individual animals must perform tasks in a coordinated yet ever-changing manner in order that the entire colony can exist. In each case—mammalian body or colony of ants or bees—internal and external conditions must be constantly

monitored in order to determine what corrective actions need to be taken.

Evolution has necessarily arrived at somewhat different outcomes in the two cases. Integrated control systems are possible for the intimate collection of cells that form a single mammalian body. A subset of cells—neurons and endocrine system—specialize in monitoring and control. A much more distributed system, however, is necessary for an assembly of individual organisms in a colony of social insects, a superorganism. The solution for the insects is probabilistic and also quite different from a social group of humans with a leader. No one individual has access to all of the necessary information, but the behaviors of the individual insects are such that statistically, their summed responses are adaptive for the colony as a whole.

SYNOPSIS

The insects are evolutionarily the most successful multicellular animals, in terms of both numbers of individuals or numbers of species. Social species of insects are striking for their intricate societies.

Darwin saw that colonies of bees and ants consisting of a relatively few individuals capable of reproduction supported by much larger numbers of sterile workers posed a challenge to his theory of natural selection. The dilemma: How could selection either favor individuals that do not reproduce or cause the evolution of morphological and behavioral adaptations in such sterile individuals? An explanation couched in genetic terms began to emerge only about forty years ago. It is now clear that these insect societies with their sterile castes are nature's most dramatic manifestation of the power of *kin selection*. In the bees and ants (order Hymenoptera) these social systems are based on a form of sex determination in which males develop from unfertilized eggs, and are thus haploid. In termites (order Isoptera) it is probably based on extensive inbreeding.

The social insects also display extraordinary behavior involving division of labor in the colony, communication among individuals, the capacity of individuals to learn and remember, and flexibility of the colony in meeting short-term environmental challenges. There is a constant flow of information among individuals about the needs of the colony and the availability of resources in the immediate environment. This information is used to direct foragers to new resources and to differ-

ent kinds of resources. The mechanisms, however, differ from those found in human social groups, where individuals either take orders from a central authority or share in the decisions by a process of mutual understanding and consensus. In a colony of honeybees, by contrast, no one individual has access to all the information available to the colony, and no one bee makes decisions for the group. Behavior is redirected in adaptively important ways by statistical processes. Falling concentration of a chemical signals the size of the colony; longer waggle-dances signal high-quality food sources and thus recruit more foragers; and longer unloading times experienced by returning foragers signal a surfeit of supply and redirect foraging efforts to other resources. Behavior of groups of related individuals is therefore so complex and adaptive that it appears rational to a human observer. It illustrates the power of natural selection in ways that will be useful to have in mind when we return to behavior in Chapter 11.

QUESTIONS FOR THOUGHT AND DISCUSSION

1. Why are bee colonies called "superorganisms"?
2. Suppose—perhaps in another galaxy—evolution were to produce a life form with cognitive abilities (intelligence) comparable to humans but with sex determination similar to bees or termites. What kind of social systems might emerge? How might they be similar or different from large corporate structures or feudal systems that exist (or have existed) on earth? Consider division of labor, authority, and the utilization of information.

SUGGESTIONS FOR FURTHER READING

- Seeley, T. D. (1995). *The Wisdom of the Hive*. Cambridge, MA: Harvard University Press. The details of how a colony of bees adjusts to changes in their world is revealed when all of the bees are individually marked. Natural history at its best.
- Wilson, E. O. (1972). *The Insect Societies*. Cambridge, MA: Belknap Press of Harvard University Press. One of the world's authorities on ants describes the diversity and complexity of social insects.