THREE

Bee Behavior

Question 1: Can a bee hear?

Answer: Honey bees do not have ears, but they are able to sense certain frequencies, picking up the vibrations from the air or from the physical structure of the hive. Leg sensors called *subgenual* organs are fluid-filled channels that are attuned to these structural vibrations and conduct movements of the leg to sensory cells in the bee's brain. In addition to the sensors in their legs, bees have hearing organs on their antennae that are sensitive to certain frequencies.

The *flagellum* is the end segment (the third) of the bee antennae, and it is a highly sensitive detector of air particle movement, especially of low intensity stimulation in the 250 to 300 Hz range. Vibrations in this range are generated by the air flow from wing and abdominal movements produced by a dancer doing the waggle dance just millimeters away from the forager with whom she is communicating (see this chapter, question 7: What is the waggle dance?). The cues from these vibrations are transmitted to the brain by the Johnston's organ, located in the pedicel, or second section of the antennae. Only the antennae of older foragers are sensitive to these particular frequencies, and this restricts dance communication about food resources to the forager bees. Other areas of the antennae sense vibrations at frequencies used in piping behavior, a method used to communicate within the hive and to control swarming (see this chapter, question 8: What is piping behavior?).

Question 2: Is taste important to a bee?

Answer: It may seem strange at first, but bees have relatively little need to taste their food. A project completed in 2006 that examined the honey bee genome found that bees have only ten receptor genes for the sense of taste, compared to fruit flies with sixty-eight or mosquitoes that have seventy-six. Honey bee larvae spend their entire larval lives completely sequestered in a cell, eating whatever the nurse bees bring to them, and even in solitary species the larvae emerge onto a pile of food that was put in place when their mother laid their egg. So neither type of bee larvae needs to taste or select its food. Younger adult honey bees are in a similar situation when they are "hive" bees, always in the nest, eating whatever has been brought into the hive by older foragers. Venturing out of the hive to forage is the riskiest phase of life for a bee.

Bees have a mutually beneficial relationship with plants, in comparison with agricultural pests that need to be sensitive to the toxins some plants use to repel them. Fragrant flowering plants attract the forager bees and reward them with nectar for providing pollination—a simple transaction. The bees are in a hurry to return to the safety of the hive, so they will collect nectar from any flowers that are in bloom nearby and they do not have a big investment in finding the best-tasting nectar. Evolutionary ecologist James Burns reviewed a study of bumblebees and found that if they foraged for nectar hastily and indiscriminately, even if they occasionally visited flowers containing no nectar, they tended to collect more nectar than bees that spent time evaluating whether or not a flower contained nectar before they visited it.

In contrast to the behavior of bumblebees that visit multiple species of flowers, honey bees, in the course of a single foraging trip, tend to seek out flowers of the same species, a behavior known as flower constancy. Understanding why some bees are flower constant and others have more variable diet choices is the subject of a published review by an international group of scientists, Lars Chittka, James Thomson, and Nick Waser. They found that flower constancy is explained differently by scientists studying plant ecology (who ask, How does this animal behavior benefit the plant?), those interested in floral evolution (who ask, How are floral traits selected by bee behavior?), or those who study bee foraging (who ask, How do bees learn?). Psychophysicists L. Chittka and Johannes Spaethe observed the behavior of foraging bees and described the complex elements involved in their choice of floral targets, which included the role of speed, the making of productive choices, the presence of distractions and dangers, the intensity of the light, and the complexity of obtaining nectar from a particular flower. Notice that taste is not described as an important element.

Theodora Petanidou of the University of the Aegean in Greece analyzed the sugars in seventy-three plant species in the Mediterranean area and found that they contained various combinations of sucrose, glucose, and fructose, with traces of ten other minor sugars. Bees show a preference for high-sucrose nectars, while butterflies, in contrast, tend to prefer nectar with a lower sucrose content, effectively minimizing competition for the resources in the habitat. Jacobus Biesmeijer and colleagues from Leeds University in the United Kingdom did similar work in Costa Rica observing two species of stingless *Melipona* bees, both of which also showed a preference for sucrose over glucose and fructose. They reported that *M. beecheii,* a yellowish bee, preferred to forage in sunny patches which by their nature produce higher sugar concentrations, while *M. fasciata,* which has a dark brown body, foraged in shady spots but sought out nectar that was highly concentrated. These species divided the resources based on safety and potential camouflage rather than on taste.

Question 3: How do hungry bees share food?

Answer: A hungry bee approaches a sister bee and places her proboscis into the sister's mouth. This triggers a response in the sister: if she has food in her crop, she will regurgitate some of the food so that the hungry bee can ingest it from inside her mouth. This mouth-to-mouth transfer of food is known as *trophallaxis* (see color plate E). Both bees stroke each other's antennae while engaging in this behavior, and research has demonstrated that the antennae are an important part of this process because the bees are exchanging both olfactory and gustatory information. According to author and bee enthusiast Sue Hubbell, researcher John Free, while working at the Rothamsted Institute in England, found that the antennae were essential in making bees feed one another, and those bees that had lost their antennae were fed less often. In one experiment she describes, bees tried to feed freshly severed heads with intact antennae, and they even tried to feed cotton balls in which antennae-like wires had been inserted.

Recipient bees can learn the odor of a food provided by a donor bee in a single trial. Mariana Gil and Rodrigo De Marco at the University of Buenos Aires in Argentina found that honey bees' recall is better when the odor of the donated food is more concentrated. These observations support the idea that bees are exceptionally proficient at learning cues that will be useful for them when they need to locate valuable food sources in the future.

Question 4: How do bees keep themselves clean?

Answer: Bees are very hygienic animals—they don't like to be dirty or dusty. Keeping their bodies clean is a good way to keep debris out of the colony, reducing the chance that bee nurseries will develop infections and decreasing the likelihood that food supplies will be contaminated. Moreover, if a honey bee's eyes or antennae are soiled, their sensors might not function correctly, and that would be detrimental to the entire colony unit because it might put them at risk.

Honey bees have body parts specifically designed to help them stay clean, including a variety of bristles on their limbs that they use to clean body parts they can reach themselves, such as the mouth, proboscis, and antennae. The most notable cleaning structure is called the antenna cleaner, a peculiar-looking notch

Fig. 15. A specialized leg structure called the antenna cleaner allows honey bees to keep their antenna free of debris. Bees pull their antenna through these C-shaped notches on their forelegs before departing on flights. (*Drawing by John F. Cullum.*)

on the foreleg of a honey bee that is designed to slip over the antenna and remove any dust, pollen, or debris. After foraging and before flying home, honey bees will clean their eyes with their forelegs, and they will then pull their antenna through this special notch to clean up. These behaviors are stereotyped and always happen as a bee decides to head back to the hive.

When James Thomson at the University of Toronto observed certain bumblebees, *Bombus bifarius,* he found that their self-grooming as they flew between flowers sometimes significantly reduced the amount of pollen they dispersed to other flowers. Lawrence Harder at the University of Calgary reported that the amount of in-flight grooming by *Bombus* spp. depended on the pollen-dispensing mechanism of the plant; if the bee was disturbed by the accumulation of pollen on its body, the bee was more likely to self-groom. Marielle Rademaker and colleagues in the Netherlands tried to measure how much pollen was actually transferred from flower to flower by using dye to replace the pollen, and they estimated that *Bombus terrestris* removes 44 percent of the pollen grains when it visits a fresh *Echium vulgare* flower, and approximately half of the removed pollen adheres to the bee. Only a small fraction of the pollen grains on the bee were deposited on the stigma of the next flower, and a larger fraction was lost through grooming and through deposition on other parts of the flower (see sidebar: What is pollination?).

Grooming is an ordinary activity that is common among bees, but a very specialized honey bee *Apis mellifera* that seemed to be "compulsive" about social grooming was described by Darryl Moore at East Tennessee State University and colleagues. They named the bee Red 93, and she groomed other bees with her mandibles 84 percent of the time she was under observation. She never developed into a forager at the normal age of approximately twenty-one days, and even when she was thirty-one days old she was still dedicated to grooming other bees; the authors report that she is the most highly specialized bee groomer on record. Only twice among the 315 observed acts of social grooming was her grooming invited by the recipient bee. On all the other occasions, Red 93 simply approached a nest mate and directly began cleaning one or more of her body parts for a brief period, usually less than a minute. She then would immediately initiate contact with a nearby bee and commence grooming it. Uncharacteristically specialized behavior in bees has been observed by others on a few occasions, and it raises many intriguing questions about how the mechanisms that regulate behavior can go awry.

Under normal circumstances, honey bees perform a grooming invitation dance to solicit grooming from a nest mate. They stand in one spot and rapidly vibrate their body from side to side, sometimes stopping briefly to self-groom. Benjamin Land and Thomas Seeley at Cornell University determined that bees performing this dance are far more likely to be groomed by a nest mate than bees that do not solicit grooming in this way. When the researchers puffed chalk dust onto the base of the wings of bees in their experiments, they found that those bees danced more than bees that only received puffs of air, suggesting that the particles may trigger a need to be cleaned and hence the dance. In other observations of honey bees conducted by Janko Bozic and Tine Valentincic at the University of Ljubljana in Slovenia, they noted that the bees being groomed held their wings at right angles to the body, and that groomer bees tended to clean parts of the body that the receiving bee could not reach herself, usually removing dust and pollen from the base of the wings and realigning body hairs.

Bees also engage in grooming behavior to rid themselves of mites. U.S. Department of Agriculture biologists Robert Danka and Jose Villa provoked five hundred honey bees to groom themselves by placing a tracheal mite on each individual bee using an eyelash mounted on a small stick. Some of the bees were genetically mite-resistant and some were from a susceptible strain. They watched each bee for seven minutes and observed that resistant bees groomed themselves more often than susceptible bees, and they groomed themselves more on the side of the body where the mite had been placed, suggesting an awareness of the intruder. Grooming was similarly found by Frederic Ruttner and H. Hanel to be an effective defense used by some honey bees against *Varroa* mites.

Question 5: Why do bees buzz?

Answer: Sometimes buzzing is just the sound of bees at work, and sometimes bees use buzzing and other noises to guide their nest mates (see this chapter, question 8: What is piping behavior?). The sounds are not vocalizations, nor are they defensively directed against predators. The bees vibrate their bodies and their wing muscles in different ways and the vibrations resonate through the hive (see this chapter, question 6: How do bees communicate?). They cool the hive and help dehydrate the honey by beating their wings, which makes a buzzing sound. Bees buzz less in hot weather because they beat their wings more slowly to reduce the risk of overheating themselves. Queen honey bees announce a threat to the nest by making quacking noises. They are also said to toot. Quacking and tooting noises are together described as queen piping: these noises are produced by rapid contractions of the bee's thoracic muscles and occur without wing movement. The sounds are transmitted by being reflected from the beeswax substrate.

Question 6: How do bees communicate?

Answer: A honey bee's survival depends on social recognition and communication with other bees in the colony, so it is natural that bees are expert communicators, using sight, touch, movement, chemical signals, and, although they do not have ears, a sensitivity to certain vibrations that they feel with their legs and antennae. They communicate about finding food, avoiding or ejecting predators, and about conditions within the hive. There may be a surplus or a shortage of food, overcrowding, a need to start building more comb, or a queen who has stopped laying eggs—each of these situations requires a group response that has to be orchestrated.

Nobel prize–winning research by Karl von Frisch revealed that bees do different "dances" in order to tell the other bees where they have located a good nectar source. Their specific movements indicate the direction and distance of the nectar source from the hive (see this chapter, question 7: What is the waggle dance?). Sound and vibrational signals exchanged by honey bees during the performance of waggle dances have been studied extensively and recorded. The dances have been analyzed using a microphone and a laser vibrometer (an instrument that measures and analyzes vibrations without the need for physical contact with the subject), and a great deal has been learned about this direct, symbolic, movement-related form of transferring information. Kristen Pastor and Thomas Seeley studied bees that follow waggle dancers and make brief piping signals, apparently trying to beg for nectar from the dancers. They found that none of the dancers gave nectar to the bees that piped them, but the piping did seem to stimulate some of the waggle dancers to stop dancing (see this chapter, question 8: What is piping behavior?).

One of the most impressive feats of communication occurs when a queen and thousands of workers have swarmed, leaving an overcrowded colony and searching for a new nest site (see chapter 8, question 2: What is swarming?). The swarm flies out of the colony and waits as a group, perhaps all clustered on a tree branch, while hundreds of scouts fly out to search for suitable space. The scouts return and, over time, agreement is reached on which of the sites they have explored is most suitable, and the swarm takes off for its new home.

Thomas Seeley from Cornell University and Kirk Visscher from the University of California at Riverside tried to learn how this incredibly complex choice is made by closely monitoring four swarms as they engaged in this group decision-making process. They rejected the hypothesis that a consensus is somehow reached and suggested that the bees may sense a quorum when the scouts become aware that a particular site is being visited by a sufficiently large number of scout bees, perhaps as small a group as ten or fifteen bees. Using the dance, these bees somehow lead the group to approve of that site, and the decision is then communicated to the bees in the swarm by workers piping (see this chapter, question 8: What is piping behavior?). The result of this "quorum sensing" is that the swarm lifts off and moves to the new location.

Worker bees also communicate with vibration signals that are different from the waggle dance. In this multipurpose form of communication, one bee grabs another worker or the queen and rapidly vibrates her own body for a second or two while in contact with the other bee. Kristen Pastor and Thomas Seeley speculate that vibrating another bee seems to energize the recipient and causes her to alter her behavior. Prior to a swarm, workers vibrate the queen hundreds of times an hour, and she responds by reducing her food intake, slowing egg laying, and becoming more active. Then workers begin piping "at a fevered pitch," which stimulates bees to warm up their flight muscles and results in the swarm taking flight (liftoff) out of the nest. When the queen has left the nest with the swarm, the piping in the nest ceases. Andres Pierce and colleagues observed that workers rarely or never vibrated the queen inside the swarm, but piping continued in the swarm to stimulate the bees to fly again once a new nest site was selected.

In another form of communication, honey bees do a tremble dance to signal other bees not to fly off to search for more nectar because there is too much already arriving at the hive. Bees receiving tremble signals move to collect food from returning foragers instead. Corinna Thom and her colleagues were able to demonstrate that short piping signals made by workers had some relationship to the tremble dance, but this aspect of the nectar-foraging communication system is not completely clear because the behaviors were not universal among the dancers; virtually all of the piping signals were made by tremble dancers, but less than half of the dancers piped. The researchers speculated that the brief piping seemed to have some relationship to recruitment by the tremble dancers, but clearly more observations are needed.

A sense of smell is very important for bees as part of the colony's communication system so that order can be maintained in the hive through the use of pheromones or fragrant chemicals that play a role in virtually all of the hive's activities (see chapter 5, question 5: How does the queen control the hive?). When the honey bee genome was mapped, 170 odorant receptors attested to the honey bee's remarkable sense of smell, compared to fruit flies with 62 odorant receptors and mosquitoes with 79. Experiments conducted by Charles Ribbands at the Rothamsted Experimental Station in England demonstrated that honey bees can perceive greatly diluted chemical scents and can distinguish between mixtures that contain only slightly different proportions of the same two scents.

Guard bees use sensory information about the colony odor to determine if a bee trying to enter the colony is a nest mate or an intruder. Margaret Couvillon and her colleagues at the University of Hawaii transferred wax comb from a "comb donor" hive to a "comb receiver" hive, and they found that guards in the comb receiver hive became more accepting of bees from the comb donor hive. This strongly suggests that the presence of the transferred wax comb changed the odor template of the colony and that the template is used by the guards to evaluate visitors, rather than the actual scent of each individual bee. In a fascinating and confusing finding based on the colonies they studied, Madeleine Beekman and Benjamin Oldroyd, working at the University of Sydney, Australia, maintain that, contrary to prevailing lore about the effective screening ability of the guard bees, it is not difficult for a worker to enter the nest of another colony. They estimate that 10 to 50 percent of non-nest-mate workers are allowed by the guards to obtain access to a colony, a finding they verified by genetic analysis of bees in the colonies they studied.

In a unique experiment that has yet to be replicated, Songkun Su of the College of Animal Sciences in Hangzhou and colleagues from China, Australia, and Germany reported the successful creation of a mixed-species colony composed of the Asiatic bee *Apis cerana cerana* and the European bee *Apis mellifera ligustica*. Their work was not without problems, and several of their experimental colonies became unstable and many workers were killed, but they report successfully managing a colony with an *Apis cerana cerana* queen and a cohabiting mixed group of workers for more than fifty days. Despite the differences between the species, the two types of honey bees could communicate using the waggle dance. Obviously, there is a great deal more to learn about how bees communicate.

Question 7: What is the waggle dance?

Answer: The waggle dance is a form of communication that honey bees use to recruit nest mates to fly to various locations in their environment where there are good nectar sources. When a worker bee returns to the hive from a successful foraging trip, she can direct her sisters to the place where she found the food using the dance, which encodes information about its direction and its distance.

Many naturalists had observed bees waggling in their hives after foraging, but it wasn't until the research of Karl von Frisch that the meaning of the dance was decoded. He deciphered the recruiting function of the dance and experimentally determined how the bees translate their flight through the landscape into a flight plan for the bees in the hive. After years of research, we now know how the dance is organized.

The bees enter the hive and find their way to the brood areas of the comb, where they begin their dance. Recall that in European honey bees, the beeswax combs hang down in vertical sheets inside the colony. The brood area serves as the dance platform, and many unemployed forager bees wait in that area for flight instructions.

Two environmental cues, the position of the sun's azimuth (the angle of the sun against the horizon) and the force of gravity, are the bases for the information communicated in the dance. First, the bees note the direction of the sun's azimuth in relation to North, being the 0 degree position. Based on this system, the sun rises in the East at approximately 90 degrees and sets in the West at about 270 degrees. If you point toward the sun and then draw an imaginary line from the sun to the horizon, you can measure the direction of that point with a compass. The position of the sun's azimuth varies depending on the time of day, and the bees must somehow learn the rate at which the azimuth moves across the horizon. They take into account the season and latitude, both factors that influence the rate of change of the sun's position.

Inside the darkness of the hive, the bees use their memory of the sun's location and their sense of time to predict the real position of the azimuth. The bees appear to walk in circles as they dance, and they use the dance to point to their flight direction. The azimuth is represented by the direction "up" on the comb, and because the bees in flight measure the direction of their flight relative to the azimuth, they translate that direction on the comb. If they are foraging on flowers located in the same direction as the azimuth, they waggle in a line straight up. If they fly 45 degrees from the azimuth, then they produce their waggle on the comb in a similar angle. The waggle dance, then, is a systematic way for the bees to encode their three-dimensional

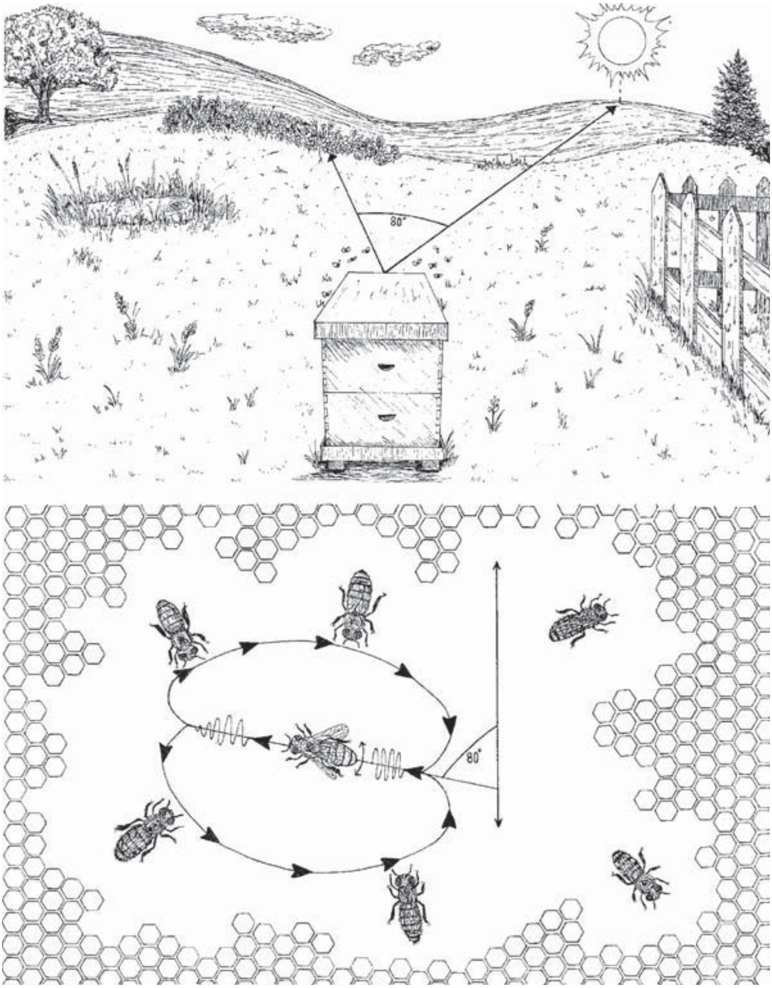

Fig. 16. Honey bees use symbolic movements to communicate the distance and the direction of profitable food sources to nest mates within the colony. The top panel shows the hive in the environment, and the bottom panel illustrates the bee dance at a moment in time. For details, see chapter 3, question 7. (*Drawing by John F. Cullum.*)

flight through the environment into a tidy, two-dimensional pattern on the comb. Figure 15 describes this directional signal in more detail.

The distance signal is encoded by the frequency of body vibration, or waggle. If the foraging site is located close to the hive, the waggle is brief; but if it is distant, the waggle is longer. The rate of the waggles is also affected by the quality of the food that the forager collected, so that if the sugar concentration is high, the dance is more vigorous and is repeated frequently; if the sugar content is low, the dance is not repeated. After a waggling run, the bees reset their signal by walking to the right, waggling again, and then walking to the left.

Dancing bees attract the attention of unemployed bees in the brood area, and these bees follow the waggle dances and make contact with the dancer's antennae as they move on the comb. The antennal contact allows the followers to detect the vibrational signals that come from the waggle. In addition, the dancer will stop between waggle runs and will feed small bits of nectar to her followers, which can then pick up floral odors from the dancer that serve as an additional recruitment signal.

Question 8: What is piping behavior?

Answer: Piping behavior describes a series of high-pitched sounds that reverberate through the colony. Karl von Frisch and others originally identified these noises as part of the language that the queen uses at particular times to assert her presence. Recent research has discovered that mature, forager-aged workers also pipe under particular circumstances, and a lot has been learned about this form of communication.

Picture the piping queen: she presses her thorax (the middle segment of her body) against the comb and vibrates her flight muscles without spreading her wings, producing short bursts of sound that are detected by other bees with sensors in their legs. The old queen (also called the mated queen) sometimes pipes before swarming, when the colony outgrows its hive and divides itself (see chapter 8, question 2: What is swarming?). After she has swarmed with a portion of the workers in search of a new nest site, one or more virgin queens normally are ready to emerge from their queen cells to supercede or replace her (see chapter 4, question 7: What is royal jelly and how does it produce a queen?). The first virgin queen to emerge produces piping sounds, and another queen that is still in her cell but is ready to emerge may respond with a deeper sound that has been characterized as quacking. The piping of the queen causes the workers in the colony to freeze in place until the piping stops, stopping their work of trying to release another queen by chewing away the wax and fibers capping her cell. This duet or dialog may continue for days at a time and may serve to suppress the emergence of an extra queen, which, if it occurred, would typically lead to a fight to the death.

Thomas Seeley and Jurgen Tautz described the piping behavior of mature workers as similar to queen piping, with the important distinction that the piping worker pipes other bees directly: the worker usually presses her body or head against the queen or a sister worker, pulls her wings tightly over her abdomen, and arches her abdomen downward. Then she vibrates her wing muscles and short, high-pitched bursts of sound are produced. An important function of this behavior is to cause the recipients to warm their flight muscles in preparation for "liftoff" prior to swarming, but workers may pipe the queen intensely for several days or weeks prior to the departure of the swarm, and the meaning of this behavior is not yet understood.

Andres Pierce and his colleagues were curious to see if piping continues once a swarm has left the nest, and they built an observation stand so that for the first time a swarm cluster hanging on a tree could be studied while the bees waited for scouts to guide them to their new location. What they found was fascinating. Workers seemed to pay little attention to the queen in the swarm until shortly before the time for liftoff approached. Then the pipers became quite excited, scrambling through the swarm cluster piping intensely and interacting with the queen at very high rates, and also piping workers at high levels, stimulating every bee to warm their flight muscles. When Seeley and Tautz experimentally removed piping bees from the outer layers of a swarm cluster and used an infrared camera to measure the temperature of the flight muscles of individual bees, they found that the bees did not warm up their flight muscles when the piping was absent. It is clear that piping behavior is a complex but very fundamental aspect of bee communication.

Question 9: Can bees tell time?

Answer: They don't wear wristwatches, but bees can certainly tell time. They are attuned to time in relation to the sun's position in the sky throughout the day. Bees can remember the time at which flowers have nectar and can use this information to guide their foraging choices. This timekeeping ability can be seen clearly in experiments conducted by Martin Lindauer in which bees were trained to feed from an artificial flower that provided sugar syrup at a particular time of day. The bees were able to learn to return to the feeder at that time, and while some scouts might look at the feeder at other times, a large majority of foragers returned when the time was right and the feeder was filled. Being time-sensitive is most likely an adaptation that enables bees to exploit food sources that are available during the hours of the day when nectar and pollen production is highest.

An awareness of the circadian clock (the day-night cycle) is involved in sensing the time as well as in navigation (see this chapter, question 12: How do bees navigate?), the division of labor, and the bees' dance language (see this chapter, question 7: What is the waggle dance?). The movements used to communicate about the location of nectar sources (the waggle dance) would be unintelligible to nest mates if a bee had a faulty sense of time.

Young adult bees, newly emerged from their pupal stage, typically engage in behaviors associated with tending the larvae in the brood combs, and the larvae are hungry around the clock with no particular sleep-wake cycle, not unlike human newborns. Like the babies, the nursing workers do not exhibit circadian rhythms, but they acquire them as they age and integrate into the light-dark cycle of the nest. The older adult workers, the foragers, have strong cycles, based on the daily clock, that are tuned to cycles of pollen and nectar production (see chapter 5, question 3: What do bees do all day?).

Guy Bloch and a team of researchers, using the honey bee genome sequence, identified a core group of "clock" genes that is responsible for circadian rhythms in honey bees. Interestingly, they found that the expression of the clock genes in the honey bee was more similar to the pattern in a mouse than in a fruit fly. The significance of this finding raises lots of new questions to be explored about the evolution of timekeeping behaviors. Why is clock gene expression in bees more similar to the expression in a mammal than in another insect? In what other ways are insects like mammals, and what does this tell us about the evolutionary conservation of molecules in various animals? Future research will undoubtedly explore questions like these.

The development of circadian rhythms in honey bee foragers is connected to the regulation of one of the clock genes, the period gene, well known for its role in circadian rhythms. Because the level of expression of this gene varies between nurses and foragers, we know that at least part of a bee's biological clock is associated with her social role in the environment of the nest. In recent research from the Hebrew University of Jerusalem by Yair Shemesh, Mira Cohen, and Guy Bloch, using a technique regularly used to study bee behavior and physiology, the researchers manipulated the social conditions in the nest by creating a colony of bees that were all the same age. In a process that is not well understood, some young bees adopt the behavior of the normally older foragers. Shemesh and coauthors found that the nurse bees could show sensitivity to activity cycles set by daylight when their social setting required it. They also found that the levels of gene expression in three other clock genes were lower or totally suppressed in nurses as compared to behaviorally cyclical foragers. This behavioral flexibility in the bees' circadian rhythms is associated with the organization of the internal clock on the molecular level.

Question 10: Do bees sleep?

Answer: The short answer is yes, indeed, bees do sleep, and they exhibit some of the same characteristics as humans when they are asleep: their muscles relax and they don't move around, their antennae become immobile in characteristic positions, they are less reactive to disturbances, and their body temperature drops. Walter Kaiser reported that, unlike mammals, bees sleep most deeply near the end of their period of sleep. A series of recent experiments and observations has been defining when and how bees sleep, and Barrett Klein has published his observations of sleep patterns in honey bees, reporting that their sleep patterns differ as they mature and as their tasks change from cell-cleaner to nurse to food-storer to forager. Younger bees sleep less often and less regularly, but the care for the brood is a round-the-clock job, so this is understandable. The circadian rhythmic sleep-wake cycle begins to be apparent in food-storers and becomes firmly established in foragers. Their active period takes place during the day, when they have access to nectar, so they sleep in a more predictable pattern, sleeping during the night for longer periods than the younger bees.

Stefan Sauer and colleagues arranged to deprive forager bees of sleep so that they could compare their sleep patterns with control bees that were allowed to maintain their normal schedule. Isolated bees were placed in a glass cylinder on a specially designed, motorized, tilting device with simulated daylight illumination. The tilting device produced a rolling movement of the cylinder, alternating with short pauses, which kept the bee awake during her normal twelve-hour sleep period. The exhausted bees compensated the following night with longer and deeper sleep, suggesting that, like in mammals, sleep is controlled by regulatory mechanisms. This conclusion is also suggested by the results of an experiment by Thomas Seeley and colleagues at Cornell University. They transplanted two colonies and trained the older bees to forage at particular times, and they found that the foragers shifted their sleep schedules so that they would be awake when resources were available.

Question 11: Do bees perceive magnetic fields?

Answer: There is some evidence that bees are sensitive to magnetic fields, but although it can be demonstrated that bees will react to changes in the local magnetic field, scientists can't explain how bees perceive it or the way they use it under normal circumstances.

Working at Princeton University, James Gould determined in 1978 that the abdomens of honey bees contain crystals of magnetite and that the bees' behavior could be altered based on artificially induced changes in the local magnetic field. Gould and colleague Joseph Kirschvink hypothesized that this substance could move within a cell and thereby convert or transfer directional information into the nervous system of the bee. Further studies conducted by learning expert M. E. Bitterman and colleagues demonstrated that the behavior of freely flying bees could be altered based on the magnetic field and that the application of magnets or magnetic wires to the bees could interfere with their behavior. There is evidence, then, that bees are sensitive to the magnetic field, or at least they are sensitive to alterations of the magnetic field; but, to date, no one has determined the degree to which this information is used. Most scientists believe that the magnetic field is used as a backup cue in the event that other, more salient cues are absent or provide ambiguous information to the bee.

Carolina Keim and others determined that there are iron-rich granules in bees' abdominal fat cells, but their research on the chemical properties and position of these granules led them to surmise that these substances are most likely *not* involved with magnetoreception, but probably are the result of the metabolism of iron from their pollen-rich diet.

Question 12: How do bees navigate?

Answer: The lives of the bees in a honey bee colony depend upon the ability of foragers to successfully fly as far as several kilometers to locate and collect nectar and pollen and then find their way back to the nest. They are considered a home-range species, defined as a navigating animal that can find its way over a relatively short distance, as compared to a migratory animal that travels quite far. Because this short-range navigational ability is so important to bees, they are "overengineered," as James Gould describes it, with an armament of several alternative methods based on various sensory cues that they use to find food. Axel Brockman and Gene Robinson of the University of Illinois at Urbana-Champaign have identified five different sensory systems that bees use to locate nectar sources and communicate their location to their nest mates, and they traced each sensory pathway to the location in the brain where it is processed (see also this chapter, question 7: What is the waggle dance?).

In simple terms, bees can see and smell the flowers when they get close enough, and if the sun is out, they can use a time-compensated sun compass, for example, keeping the sun to the left in the morning in order to fly south. They also are able to use distinctive landmarks as part of their orientation, a type of spatial memory that enables them to retain information about the location and orientation of particular details in their environment. Co-author Elizabeth Capaldi Evans and Fred Dyer studied the acquisition of visual spatial memory in honey bees and determined that bees rapidly learn the location of their hive on special orientation flights taken when they first depart from a hive in a new place. This large-scale spatial learning is similar to the learning that occurs when bees first explore new patches of food. The investigatory flights around the food were described as "turn back and look" flight by Miriam Lehrer, and were explored in more detail by Cynthia Wei and colleagues, who found that bees actively choose to spend less time on learning flights as they gain experience traveling to and from a foraging site. This finding is particularly interesting, as it indicates that bees can assess their own knowledge and can act to increase the contents of their memories. Certainly, this selective learning behavior indicates a higher level of cognitive ability than might be expected in an insect (see chapter 2, question 5: Are bees intelligent?).

Adrian Dyer and colleagues trained bees to recognize images of complex natural scenes and found that the bees were quite accurate in recognizing these landmarks and discriminating between a known scene and similar views that were introduced to confuse or distract them. Mandyam Srinivasan and colleagues in Canberra, Australia, trained bees to fly through short tunnels to collect a food reward and demonstrated with a series of experiments that their ability to monitor flight distances (their odometer) is visually driven, based on the amount of "image motion" that is experienced by their eyes as they travel along their route.

When the sun is not clearly visible, honey bees can use the pattern of polarized light in the sky as a navigational guide (see this chapter, question 13: How do bees sense and use polarized light?).

Question 13: How do bees sense and use polarized light?

Answer: The sun generates patterns of polarized light, especially in the ultraviolet range, and these patterns indicate the location of the sun when it is not directly visible on a cloudy day, or just before sunrise or just after sunset. Unlike the human eye that has receptors for only brightness and color, bees also have special receptors for ultraviolet and polarized light.

Remember that a honey bee has five eyes, three simple eyes and two compound eyes (see chapter 2, question 9: What do bees see?). Each of the compound eyes has 4,500 light sensors, called ommatidia, and there are three types of ommatidia, containing different sets of light-sensitive cells (spectral receptors), that are distributed over the retina in a pattern that is described by Motohiro Wakakuwa and colleagues as "rather random" and much more complicated than had been previously accepted. Rudiger Wehner and Stephan Strasser demonstrated that there is a group of about 150 specialized ommatidia in the uppermost dorsal area of the eye that has polarized ultraviolet receptors configured in such a way that they can translate the information from polarized light into "modulations of perceived brightness." This provides cues from which they can derive directional information in lieu of being able to see the sun. The researchers actually painted out different parts of bees' eyes and recorded their behavior, and these observations established that this group of specialized ommatidia is, indeed, the polarized light (POL) area of the eye.

The study of the homing abilities of bees has been a focal point of research because bees are excellent navigators. Foraging bees keep track of their distance and direction from the hive, and at any point on their journey they can turn and fly in a straight line, a beeline, back to the hive. Using the sun and the sun-linked patterns of polarization, the bees are attuned to their direction, and they use their ability to learn and remember the patterns in the landscape to guide their flight behavior. Some studies by Tom Collett and others by Rudiger Wehner indicate that bees' map-like spatial memories are arranged like overlapping beads on a string rather than like a typical geographic map. With their unique map and compass, these little insects can navigate up to ten miles away from their hive.

Question 14: Do bees ever get fooled by predators?

Answer: Unlike baiting a hook with a worm with the intention of trying to deceive a fish, mimicry is natural behavior of an animal trying to survive. Defensive mimicry may be more familiar, such as camouflage, where the subject tries to blend with the background, or Batesian mimicry, where a harmless species resembles a species that is toxic or harmful, duping predators into avoiding the safe prey because it appears to be harmful. In aggressive mimicry, a predator gives off signals that usually promise food or sex to their prey, and then they just sit back and wait for the prey to come to them. For example, the predator may look or smell enough like a female bee so that a male bee will be fooled into approaching.

In the Mojave Desert, a cluster of tiny, millimeter-long blister beetle larvae *Meloe franciscanus* give off a pheromone (a stimulating scent) that fools male solitary bees, *Hapropoda pallid,* into mistaking the larvae for a female bee ready to mate. When a male bee is attracted by their scent and attempts to mate with the ball of larvae, several hundred larvae attach themselves to the back of the unsuspecting bee as he struggles to get away. The larvae stay with the male, and when he actually mates with a real female bee, the larvae move onto the female; when she goes underground to lay an egg on her stockpile of nectar and pollen, they eat everything in sight, including the egg.

Some spiders are aggressive mimics that can lure bees into their webs. The golden orb weaver, also called the golden silk spider or banana spider, *Nephila clavipes,* attracts bees by spinning a golden-colored web in a brightly lit area; and while bees can associate other webs with danger, scientists speculate that the golden color of these webs mimics yellow nectar-bearing flowers and so attracts instead of warning the bees. *Argiope agentata* spiders attract bees by weaving patterns in the center of their webs that appear to mimic the nectar guides in the center of flowers. Small female crab-spiders (*Thomisus onustus*) mimic different flowers by adapting their entire body to the color of the flower and then making themselves inconspicuous on a petal until a bee comes to nectar, at which point they attack the bee.

In yet another variation of aggressive mimicry, some robber flies in the genus *Mallophora* closely resemble bumblebees, even down to hind legs that look like the pollen-carrying legs of the bees. When an unwitting bumblebee approaches the fly, it captures the bee and squeezes it tightly against its own body and then pierces a hole in the bee's body and feeds on its insides, leaving only the exoskeleton remaining. Aggressive mimicry takes many forms and is not unique to predators of bees; this mimicry subjects many insects, birds, and other animals to these types of seductive attacks.