TWO

Bee Bodies

Question 1: How does a honey bee develop from an egg to an adult?

Answer: The honey bee queen lays an egg in a small chamber or cell in an area of the colony called the brood nest. A helpless, grub-like larva emerges from each egg after a few days, and its only function is to eat. Unlike a butterfly caterpillar that must forage for food, the bee larva never strays from its cell and nurse bees (young adult worker bees that perform this task at a particular stage of their life) constantly deliver food, sometimes flooding the cell with food. It has been estimated that more than one hundred thousand visits are made to a single honey bee during its egg and larval stages, during which time the larva can increase in size one-thousand-fold (see this chapter, question 2: What do larvae eat?) Because it doesn't leave its cell, the larva's bodily wastes are stored inside its body to protect the food in the cell from fecal contamination.

All honey bees outgrow their "skin" and molt about every twenty-four hours during the first few days of larval life (see chapter 2, question 10: Do bees have bones?). Their skin is actually an external skeleton or *exoskeleton,* and when the *ecdysis* or molting occurs, the skin splits at the head and slips off the rear end of the larva's body in a process that normally takes less than thirty minutes. Underneath is a new skin that is softer and looser at first, filling up as the larva grows until it is stretched tightly

Metamorphosis

Bees undergo complete metamorphosis, which involves a significant change in both their internal and external form (morphology). The word is from the Greek word *metamorphoun,* meaning "to transform," a compound of the words *meta* (after or beyond) and *morphe* (form). The familiar transformation from a tadpole into a frog is another example of complete metamorphosis.

Complete metamorphosis in an insect involves four basic stages:

- It starts with an egg containing an embryo.
- A bee larva hatches from the egg, basically a simple grub-like eating machine that outgrows and sheds its outer skin five times. This process is called molting, and the skin is actually its skeleton, called an exoskeleton. Each time the old exoskeleton is shed, a new, looser version is revealed underneath that fills up as the larva eats. A complicated series of hormonal fluctuations accompanies each molt.
- The fully grown larva's last molt reveals the pupal stage, during which the exoskeleton totally encloses the insect and it stops eating. Within the pupa, the bodily structures reorganize, unnecessary body parts are discarded, and the insect is totally transformed.
- A fully grown adult insect emerges from the pupa.

About 12 percent of insects, including crickets and grasshoppers, go through *incomplete* metamorphosis that skips the pupal stage. The adult female lays her eggs and the eggs hatch into nymphs that look like small adults but usually don't have wings. They molt several times as they grow until they reach their adult size, by which time they have usually grown wings. In contrast to metamorphosis, a cockroach and a human are examples of a continuously developing animal that begins as a small version of its adult self and just grows larger, the only structural change being the development of its reproductive organs and, in insects, fully developed wings.

again, signaling that it is time for another molt. Each stage before the molt is called a numbered instar, and after the fourth instar has grown to its maximum size, several things happen. Prompted by hormones (internal chemical changes) and pheromones (external chemical signals), the larva stops eating and finally expels its feces, which are pushed down to the bottom of the cell. The nurse bees apply a wax cap that closes off the cell, and the larva spins a cocoon around itself using silk from a special gland in its head. Layers of silk may coat the brood cell walls, having accumulated from previous larval generations. The beeswax that makes up the combs can soften in warm weather, and the accumulated silk is thought to strengthen the cell and give extra protection to the pupae.

Soon after the cocoon is complete, the fifth molt occurs inside the cocoon and the pupa is revealed under the old exoskeleton. During the pupal stage, the larva metamorphoses into a fully grown adult bee. When the metamorphosis is complete, the bee ecloses, which means it sheds its cocoon, and then finally leaves the cell to begin its adult working life. Beekeepers sometimes describe the emergence of the adult bees from the pupal case as "hatching," a colloquial term for eclosing.

The length of each developmental stage differs slightly for each caste, although each caste spends about three days in the egg. The queen spends eight days as a larva, and after about four days in the pupal stage she ecloses. Female workers spend about eight to ten days as larvae and eight days as pupae. Drones spend about thirteen days as larvae and eight days as pupae.

Question 2: What do larvae eat?

Answer: Nursing worker bees bring the larvae a series of different foods as they develop in their cells. At each stage of growth, the larvae give off particular chemical signals (pheromones) that tell the nurse bees what to feed them, resulting in qualitative and quantitative differences in the food given to larval queens, workers, and drones. The larvae that will develop into worker bees are first fed a *brood food,* also called *worker jelly,* which is produced by the hypopharyngeal gland in the head of a nurse bee. After about six days, the nurse bees begin feeding the worker larvae a combination of nectar and *bee bread,* which is a substance made from pre-digested protein-rich pollen. After three more days, the larvae enter the pupal stage, at which time they stop eating and live off their accumulated body fat, and over the next few days they metamorphose into adult bees.

The bee larvae that will develop into queens are fed exclusively on royal jelly for their first four days of life (see chapter 4, question 7: What is royal jelly and how does it produce a queen?). Drone larvae require the most food because they grow larger than either workers or queens, and the food mixture given to older drone larvae contains the most protein-rich pollen.

Other species of bees have a different way of feeding their young. (See chapter 1, question 3: How many species of bees exist?). In solitary species there are no nest mates to care for the young. Instead, the mother prepares a nest in soil or in another small space and she places a small pellet of pollen mixed with freshly collected nectar in the nest. She lays one egg directly on this larder, and when the larva emerges it eats this food independently, without any contact with adult bees. It subsequently pupates, metamorphoses, and emerges as a fully developed adult bee.

Question 3: What do bees eat?

Answer: Bees drink nectar from flowers, either directly or regurgitated and sipped from the mouth of another bee. When nectar is in short supply, they sip honey that has been collected in the hive. Bees also require water, and Per Kryger and colleagues from the University of Aarhus in Denmark report that the task of foraging for water is carried out by approximately 1 percent of honey bees that are the same age as nectar and pollen foragers. In the desert, some bees forage for water as far as a mile (about two kilometers) from their colony, carrying it back home in a storage pouch, called a crop, located in their abdomen.

Adult bees have a tube-like *proboscis* with a tongue that sits inside it, and unlike butterflies and moths that use their proboscis like a straw to suck up watery nectar, almost all bees lap or lick up nectar that is more concentrated and sticky. This difference in the preferred consistency of the nectar is probably one of the many factors that determine which flowers will be a nectar source for each animal, allowing them to share the resources of the habitat.

A bee's tongue is encircled by rings of hairy cartilage at regular intervals, and the tip of the tongue is a small spoon-shaped lobe that is smooth on the underside and covered with branched spines along the edges and top. As the bee laps at fluids using muscles that control the tongue, a muscular sucking pump in the bee's head draws the liquid up through the proboscis. The food travels from the proboscis along a very narrow passageway through the bee's brain to the digestive system in the abdomen.

In a remarkable experiment in published in 2003, evolutionary biologist Brendan Borrell surgically removed the tongues from over seventy orchid bees (*Euglossa imperialis*), a species that has a proboscis that is longer than its body. These bees typically feed from flowers with thinner nectar than most bees prefer, and Borrell's experiments showed that these bees could efficiently drink the thin nectar (a 35 percent sugar solution) without a tongue, strongly suggesting that sucking plays a big role in their normal eating. Bees with tongues to lap the nectar in the usual bee-like manner did better with thicker solutions (around 55 percent sugar).

Question 4: How long do bees live?

Answer: As for all living things, bees' longevity is influenced by their environment as well as their genes. Under normal environmental conditions, a queen honey bee lives an average of one to two years, sometimes even longer. Unlike workers, who usually never develop a functional reproductive system, the honey bee queen remains reproductively viable throughout her

Epigenetics

Evolution has commonly been thought to occur primarily as a result of natural selection of the organism with the fittest set of genes, but natural selection does not act on genes—it acts on phenotypes. This is a critical concept. The term *phenotype* describes either the total physical appearance or constitution of an organism or a specific trait such as size, behavior, or coloring. Research has discovered that phenotypes can be influenced by environmental cues such as temperature and diet as well as by hormones, neurochemicals, and the composition and location of the DNA within the nucleus of a cell. The capacity of a phenotype to change—its plasticity—plays an important role in evolution. *Epigenetics* is the field of biology that studies changes that occur above and beyond the gene, without a mutation having occurred to modify the DNA sequence.

In the wild, the larvae of the Pipevine Swallowtail butterfly *Battus philenor* are predominantly black when they develop where the climate is cool and mostly red at temperatures greater than 86 degrees Fahrenheit (30 degrees Celsius). The red larvae are more tolerant of higher temperatures and their growth rate doesn't slow down in the extreme heat, while the black larvae don't do as well when it gets really hot. This is an example of how genetically identical organisms reared under different environmental conditions can display diversity in physical characteristics and behavior. Other butterfly phenotypes that have adapted to experimental environmental manipulation, usually involving heat-shocking or cold-shocking the larvae or pupae, are its flight patterns (*Pararge aegeria*), egg size (*Bicyclus anynana*), pupae color (Nymphalidae, Papilionidae, and Pieridae), and body size (*Hypolimnas bolina*). The shells of certain snails, *Nucella lamellose,* also show evidence of phenotypic plasticity. They grow thicker as a defense when they are exposed to the effluent discharge from the predatory native red rock crab *Cancer productus.* When they are experimentally exposed to the effluent from a relatively unfamiliar species of crab, they do not adapt defensively in response to its presence, although perhaps they would eventually adapt if that predator became a constant in their environment.

In the honey bee, anatomical, physiological, and behavioral characteristics differ among the behavioral castes, all of whom are females with the same genetic makeup. The behavior of a typical female honey bee changes from being totally occupied with nursing tasks in the hive when she is young to foraging outside of the hive in the last few weeks of her life. It has been shown that bees have some plasticity as to the age at which they begin foraging, and we know that this behavioral change is coordinated with the nectar flow and conditions within the colony—this is epigenetic regulation of aging. For example, if there is a shortage of food, more foragers are needed and somewhat younger than usual bees will begin foraging. And reversion from foraging back to brood care was reported in 1996 by Zhi-Yong (now Zachary) Huang and Gene Robinson under experimental conditions they created in colonies populated only with older, forager-aged bees.

In 2003, in order to study the differences in gene expression in the honey bee brain without having to consider age as a factor, Charles Whitfield, Amy Cziko, and Gene Robinson created colonies that were composed entirely of young bees. In the experimental colonies, some bees began foraging as much as two weeks earlier than usual, and as the colony aged, the lack of young bees caused some individuals to continue working as nurses even though they normally would have aged into becoming foragers. The researchers were able to study the brain gene expression profiles of bees of the same age in the role of young nurses, young, precocious foragers, older foragers, and older, overage nurses. These four groups were compared to nurses and foragers from typical colonies,

(continued)

for a total of six groups composed of sixty bees. The result was "a strong association between brain gene expression and behavior" demonstrating "a molecular 'signature' in the individual bee brain that is robustly associated with behavior." The researchers recognized that future experiments were needed to determine which genes are responding to environmental cues and which genes cause the behavioral changes.

Research to identify which genes are involved in responding to environmental cues and causing phenotypical differences in behavior became possible when the *Apis mellifera* gene-sequencing project was completed in 2006. Investigating the differences in genetic expression between queens and workers, Angel Barchuk, Robert Kucharski, Ryszard Maleszka, and their colleagues at the Australian National University, using data from the gene-sequencing project, found 240 genes that had different levels of expression in developing queens as compared to workers. A group from the same lab went a step further and demonstrated that the social behavior of honey bees is encoded in two groups of these genes: nine genes comprising what they labeled as the Major Royal Jelly Protein family and five genes encoding the yellow protein family. Their findings suggest that the typical royal jelly diet fed to future queen bees appears to modify the female bee larva's DNA in these groups of genes, resulting in different patterns of genetic expression in the queen than in a worker-caste female.

Subsequent results from the same lab explored DNA methylation as a key component in a network of factors controlling the reproductive division of labor among honey bees. *Methylation* is a type of chemical modification of DNA that has the effect of reducing or increasing the activity of a gene without changing its basic structure. In the latest experiment, one group of honey bee larvae were injected with a substance designed to inhibit DNA methylation, and another group of larvae were injected with a control substance. The researchers found that silencing the DNA methylation resulted in a pattern of gene expression that mimicked the pattern of larvae that were fed royal jelly, and, indeed, 72 percent of the larvae in that group developed into bees that were queen-like with fully developed ovaries. Seventy-seven percent of bees injected with the control substance became workers. The way in which these different patterns of gene expression influence the development of the bee's brains is a subject for further study.

Other researchers have described "tool kit" proteins that produce substances, called *morphogens,* that have the capacity to influence the development of cells. Morphogens are active at particular locations, and they activate DNA that tells the genes at a particular location on the wing of a butterfly, for example, to make an eyespot (part of its characteristic pattern). Research is also ongoing on the role of hormones in mediating the functioning of the genes. The ebb and flow of hormones regulate stages of development, and research is focused on the role of hormones when the organism is subjected to extreme environmental influences. An example of this occurs in humans when an adult female is extremely overweight or underweight. Under those circumstances, it is not unusual for her reproductive system to be dysfunctional and for ovulation to cease. Other factors known to affect phenotypic plasticity are the degree of looseness with which the DNA thread is wrapped around its protein spool and the variability of the location of the DNA within the nucleus of the cell.

Now that we are beginning to understand some of the subtleties of how genes function, the evolutionary relationships among phenotype, genotype, and the environment are being slowly revealed.

life. This is quite unusual since most organisms have decreased longevity the more they reproduce, and the mechanisms behind the queen's longevity are being investigated.

Drones have a very limited but important role in the colony and a very limited life. Their only function is to mate with a virgin queen. Otherwise they have no function in the colony. If the drone is successful in mating, he will normally die soon afterward (see chapter 4, question 3: How do bees mate?). If he has not successfully mated after a week or so of trying, the workers will withhold food or he will be driven out of the hive and killed because he is a drain on the group's reserves.

The hive bee caste consists of young worker bees and performs a variety of tasks inside the nest for from nine to forty days, usually ranging from eighteen to twenty-eight days. As they mature, they become members of the forager bee caste, the group that ventures outside the nest to engage in the riskier activities of guarding the nest and collecting nectar, pollen, and water. Foragers live for one or two weeks if they emerge from their pupal stage in the warm weather and if they begin foraging when nectar production is high. If they are *diutinus,* or "winter bees," having emerged in the fall and reached the foraging stage in the cold weather, they can live six months or more. During the winter the colony is cold and inactive, and the winter bees live a quiet life inside the nest, eating only small amounts of honey, taking up their roles as foragers when flowers begin to bloom in the spring.

Stig Omholt and Gro Amdam at the Agricultural University of Norway studied the role of a yolk protein called *vitellogenin* that they hypothesize plays a role as a lifespan-promoting protein. The age-based division of labor among worker bees, where the risky task of foraging is only taken on by older workers with depleted nutrient stores, seems to have evolved as a mechanism to conserve the resources of the colony. Healthy winter bees show few signs of aging during the long winter period of inactivity, although their protein stores become gradually reduced until pollen and nectar become available again in the spring. Then they start nursing and foraging and their life ends in a few weeks following the usual warm weather cycle. The researchers calculated that if winter bees were prevented from becoming active, they could live more than two years based on the gradual rate of reduction of their protein supplies during the winter.

Mapping the honey bee genome has made it possible to observe that genetic activity is quite different in young nurse bees compared to mature foragers. Although the normal aging process usually triggers this behavioral development from nurse to forager, a shortage of food can prematurely induce this transition because there is an increased need for foragers to search for food for the colony. Experimental manipulation has been able to reverse the hive bee to forager bee transition, so that a nutrient-deprived older forager can be rejuvenated into a nutrient-enriched healthier bee. With enough food and time to build up their protein reserves, the biological pathways leading to the resumption of vitellogenin synthesis were apparently activated, and old bees became capable of functioning like younger bees. Natural selection seems to have endowed honey bees with some degree of behavioral flexibility within the age-based division of labor in order to ensure optimal allocation of resources for the colony. The implications of this research are profound, suggesting that honey bees may possess the capacity for epigenetic regulation of aging (see sidebar on epigenetics), although there is obviously a long way to go before these results can be generalized.

Question 5: Are bees intelligent?

Answer: A honey bee brain has fewer than one million neurons, while a human brain has around one hundred *billion* neurons. Bees are capable of a wide range of behaviors, although they have a brain the size of a peppercorn and a nervous system that is simpler than many other animals. At one time, scientists believed that insects were not very interesting to study with regard to their intelligence, assuming that their behaviors were stereotypical and fixed—more like robots than living things. We now know that many insect behaviors are dependent on

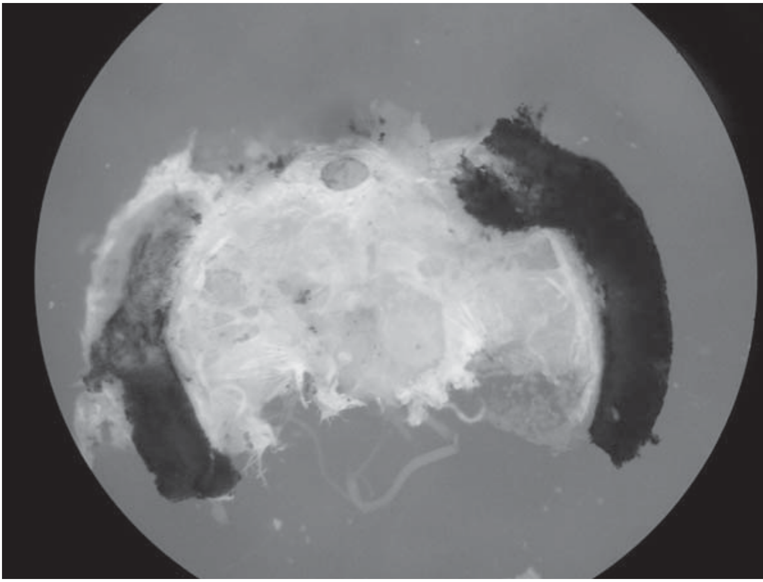

Fig. 11. A honey bee brain contains less than 1 million neurons but is responsible for many complicated behaviors. The visual pigment of the compound eyes (*far right and left*) is seen on this image of a brain dissected from the exoskeleton of the head. *(Photo by Corey J. Flynn.)*

their capacity to assess local conditions and that they can adjust their behavior depending on their perceptions, much like vertebrates. This flexibility is especially true for bees and indicates a higher level of intelligence than other insects.

Bees see color and have well-developed olfactory (smell) and gustatory (taste) systems with a fondness for sweets. Included in their behavioral repertoire is an ability to learn the location and identity of their home as well as the spatial features of the local neighborhood, to identify nest mates with an awareness of social roles, and to learn about resource availability. Honey bees use a symbolic language and employ such basic concepts as sameness and difference. One indicator of intelligence is the ability to profit from learning experience, and bees' capacity to learn complex behaviors has been amply demonstrated. Because of

Bees' Learning Abilities

Bees are fast learners, something that has been demonstrated in many experiments that explore the range of their abilities. In a typical study building on the honey bee's sensitivity to color and scent, bees were taught to associate a smell with a specific color that led to a sugar reward inside a Y-shaped maze. If the smell was lemon, the bees learned that the sugar reward lay behind a blue door where the maze branched; if the smell was mango, they learned that the yellow door hid the sugar. In 2001, a team led by neurobiologist Martin Giurfa, then working at the Free University of Berlin, designed experiments to investigate the ability of bees to make decisions based on abstract concepts. Using a similar experimental design, honey bees were trained to associate colors and patterns with food rewards in a Y-shaped maze. These scientists found that when bees were shown a blue patch at the entrance to the tube, they learned to fly down the blue arm of the maze to find the sugar. Then when the entrance patch was changed to a pattern of bars, they chose the tube with the pattern of bars identical to the one at the entrance, promptly applying the concept of sameness to a novel situation.

Another study demonstrated that bees were able to learn behavior that would seem to be counter-intuitive. Foraging honey bees and bumblebees leave a scent mark on flowers with secretions from the tarsal glands at the end of their legs, and the scent usually repels other bees because it signals that the flower was recently visited and therefore is likely to be empty of nectar. Nehal Saleh and Lars Chittka of the University of London demonstrated that, contrary to what might be seen as instinctive behavior, bees can learn to identify scent marks as an attractant rather then a repellant if the marks are consistently associated with a reward.

Trophallaxis is the process by which a forager bee transfers regurgitated nectar to a recipient in the colony. The recipi-

(continued)

ent inserts her proboscis into the donor's mouth and drinks the liquid nectar and smells its floral scent. Mariana Gil and Rodrigo DeMarco demonstrated that even after only one of these relatively brief food exchanges, the recipients learned to associate the floral scent with food, so that when they were exposed by the investigators to the scent alone, they responded by extending the proboscis in anticipation of a meal. Similar experiments conducted by Walter Farina and colleagues at the University of Buenos Aires in Argentina demonstrated that scent information is transferred to long-term memory, which has implications for programming the recipient bees to seek the nectar source associated with the scent when they mature and become foragers.

A relatively new focus of research is on a type of social learning that can occur simply as a result of observing and imitating rewarding behavior. Until recently, most scientists thought that only vertebrates that have much bigger brains were capable of this type of learning, but a number of biologists have demonstrated that bees can learn this way, too. Ellouise Leadbeater and Lars Chittka observed that bumblebees are attracted to flowers where other bees are already foraging, apparently learning through observation which flowers are currently offering good nectar rewards. In their laboratory, bees were allowed to observe through a screen as a "demonstrator" bee chose to collect nectar at a source with a randomly selected color and location. Then seven alternative sources were placed in the same area, and when the observer bees where released, they clearly preferred the nectar source that was already occupied. A similar experiment with the same results was conducted by Bradley Worden and Daniel Papaj.

When visiting some flowers, carpenter bees *Xylocopa* spp. are considered nectar thieves, biting a hole in the base of a flower and drinking the nectar through the hole instead of from inside the flower, stealing the nectar without the payback of carrying pollen. Honey bees learn to make use of these

Bees' Learning Abilities

existing perforations to rob the nectar as well, not because the nectar obtained that way is particularly sweeter or greater in volume, as measured by Selim Dedej and Keith Delaplane, but simply because it offers a shortcut—a fast food alternative. Leadbeater and Chittka observed that bumblebees also rob nectar through existing holes, and then some of them adopt this behavior and bite into the base of flowers themselves. All of these learned behaviors give bees an advantage by minimizing their exposure to the dangers of being away from the colony because they can obtain nectar as quickly as possible and return to safety.

There is a fair amount of this type of research on honey bees because they are such rewarding subjects. As we learn more about their functioning on a molecular level, researchers are beginning to understand more about the functioning of the bee brain.

their highly social lives and sophisticated behaviors, bees are thought to be among the most intelligent insects.

The neural architecture of the honey bee brain is particularly intriguing. The small brain has many highly organized and sculpted regions that are easily distinguishable under a microscope. One of these brain regions, called the mushroom bodies (MBS) (formerly known as the corpora pedunculata), has attracted the attention of behavioral biologists and neurobiologists alike because of its unique size, shape, and connectivity. Mushroom bodies appear larger in animals that are highly social, and smaller in insects that live a solitary lifestyle. Neuroscientist Susan Fahrbach at Wake Forest University described the explosion of research interest in this part of the bee brain over the last decade. The discovery by biologist Ginger Withers and others, working at the University of Illinois in Urbana-Champaign, that honey bee brains exhibit neural plasticity during the life of an adult bee has initiated both behavioral and neurobiological studies with bees. Complex forms of learning and other cognitive processes, as well as brain structures, chemistry, and neurophysiology, have been explored in great detail by Randolf Menzel and his colleagues at the Free University of Berlin. These studies aim to connect the bee brain structures to their possible functions. The mushroom bodies appear to be involved with processing information acquired through both odor and vision, essential to the life of the bee.

Question 6: Does a bee have a heart?

Answer: Yes, bees have hearts, but they are quite different than the four-chambered hearts of mammals like humans. Bees, like all insects, have an open circulatory system without veins or arteries, so there are places in its body where the body fluid (hemolymph) washes directly around the tissues and organs. A pulsating, muscular tube along its back, called the dorsal vessel, pumps the hemolymph from the abdomen to the thorax and then to the head, squeezing the hemolymph into each section of the body. Additional pulsating organs, called simple hearts, or ostia, are located at other points in the body and boost the fluid's circulation. As the muscles relax, the fluid circulates back into the dorsal vessel, moving more or less quickly depending on the insect's activity level. Unlike blood, hemolymph does not carry oxygen, so this relatively inefficient system is adequate to distribute nutrients to the cells.

Question 7: Do bees bleed?

Answer: You may have heard it said that if you pull the leg off an insect it will bleed to death because it lacks a clotting component in its blood. This does not apply to adult bees, since their "blood," actually a whitish body fluid called hemolymph, does clot to prevent large amounts of fluid loss after an injury. Justin Schmidt wrote about doing research at the Carl Hayden

Bee Research Center in Tucson that involved "bleeding" bees to sample their body fluid, and he found that the fluid samples he extracted would clot in short order.

A bee's circulatory system does not move the body fluid under great pressure (see this chapter, question 6: Does a bee have a heart?), and this minimizes the loss of fluid until clotting has a chance to close an opening caused by an injury. Hemolymph also contains cells that, like human white blood cells, defend the body against infection and gather to close openings that penetrate the exoskeleton. Honey bee larvae do not appear to have a clotting system, but since they spend their entire time in a beeswax cell, injury or predation is unlikely with the exception of *Varroa* mites, which have become a threat over the past twenty years. These are external parasites that feed on the hemolymph of the developing larvae and create open wounds, making the larvae vulnerable to pathogens. If the larvae survive, there may be effects on their defenses or behavior that we do not yet understand (see chapter 10, question 3: What parasites and insects prey on bees?).

Question 8: How do bees breathe?

Answer: Bees breathe without lungs. Air enters through openings called spiracles on the sides of the bee body, and a network of tubes called trachea weave their way around organs and through tissues, allowing air to ooze throughout the bee's body. For larvae and inactive insects, this is how they breathe, taking in oxygen and expelling carbon dioxide through this simple system. But when a bee flies, it needs more oxygen and its flight muscles move more air through its body by expanding air sacs that are part of the respiratory system and drawing air in more forcefully. Then the spiracles contract and compress the air sacs, forcing the air deeper into the body so that more oxygen reaches the cells, and then the spiracles open and carbon dioxide is expelled.

Question 9: What do bees see?

Answer: Like many insects, bees have more than two eyes—they actually have five. The two largest are compound eyes that are set on either side of the head, each containing 4,500 individual hexagonal facets (*ommatidia*), which are light sensitive units that work together to produce an integrated visual image, although what they see is different from what we see. According to Lars Chittka and Nigel Raine at the University of London, the clarity of their vision is approximately one hundred times worse than normal human vision. This is because the number of ommatidia is relatively small compared to the 1.5 million photoreceptors in the human retina or the millions of light-sensitive elements in a digital camera.

Susanne Williams and Adrian Dyer at Monash University in Australia created an optical device that simulates the way multiple lenses create an image by using 4,500 parallel-mounted black drinking straws. Using this device, they concluded that in order to see fine details, bees would have to be very close to an object. Color plate D shows how, using their device, they illustrated what a flower might look like to a honey bee. Later work from the same lab applied this imaging system to the understanding of how bees navigate and recognize complex natural landmarks with incredible accuracy.

The bee's other three eyes are simple structures, called *ocelli,* that are located on the top of its head. These are light-detecting organs that do not produce visual images. They are common in some other insects; for example, some butterflies have ocelli on their genitalia. It is thought that they help the bee sense direction and low levels of light, and they may play a role in enabling bees to follow a streaking scout bee that flies overhead to lead a swarm to its new home (see chapter 8, question 4: How does the swarm locate its new home?). Bees are also able to see fast-moving objects much better than we can, and the ocelli may play a role in this facility. Recent experiments by Gerald Kastberger at the University of Graz in Austria explored how bees with occluded ocelli react to changes in the light environment during flight. He found that the ocelli seem to help control phototactic behavior in flight course control in honey bees.

Adrian Dyer has done a series of interesting experiments to explore the limits of bee vision. After much trial and error, he trained honey bees, *Apis mellifera,* to recognize an image of a human face by associating that face with a sugar reward, and they consistently flew to the familiar face when it was placed with other images that were unfamiliar. They even flew to that face when the sugar reward was removed. But when the face was rotated 180 degrees, they were significantly less able to identify it, raising interesting questions about their visual processing.

Bees are partially colorblind. Each ommatidum or facet in the eye contains nine light-sensitive cells that are receptive to different colors. They contain six green receptor cells, according to Motohiro Wakakuwa at Yokahama City University, which are responsible for detecting motion and seeing small targets. The other color receptors vary depending on their position in the eye, and there are now understood to be three types of ommatidia. So, for example, if the bee is looking down, certain receptors are sensitive to green light, but if she is looking up, they are sensitive to ultraviolet. The brain apparently compares complex sets of signals from different sensors to identify color.

Experiments have demonstrated that honey bees can see a wide range of colors, but the spectrum visible to them is shifted into the ultraviolet range, so they can tell the difference between yellow, blue, green, and ultraviolet but cannot distinguish between red and black. They can also see a color, known as "bee's purple," that is a mixture of yellow and ultraviolet, and they can see patterns of polarized light that help them navigate (see also chapter 3, question 13: How do bees sense and use polarized light?). Rudiger Wehner and Gary Bernard demonstrated that most photoreceptors in a bee's eye are "twisted like a corkscrew," and they found that the amount of the twist corrects for the potentially false perception of colors as a result of polarized glare from reflecting surfaces on plants.

The interior of a bee colony is quite dark and yet the bees inside do all sorts of detailed work, so clearly bees can "see" in the dark; touch and scent play a large part in organizing their activities inside the colony. Because they are red/black colorblind, meaning they cannot distinguish between these two colors, observation hives and bee labs are commonly lit with red lights so that researchers can watch them while the bees carry on in what seems like normal darkness to them.

Question 10: Do bees have bones?

Answer: Instead of a bony internal skeleton, adult bees, like all insects, have a firm scaffolding, called an *exoskeleton,* that encases the outside of their body. The external covering hardens after the bee emerges from the pupa, and it protects the bee from drying out, gives the bee support, and allows for movement. All of the bee's muscles are attached to this exoskeleton, which is jointed but very solid and durable. It is also coated with a thin layer of oily wax, secreted by the bee, which has an odor that is unique to her particular hive. Guard bees use these odors to compare to sensory information from the colony to determine if a bee trying to enter the colony is a nest mate or an intruder.

Question 11: How do bees' wings work?

Answer: Bees, like most insects, have four wings, two on each side. Normally, there are two larger forewings positioned in the front of the bee's body and two smaller hind wings toward the rear. When a bee is not flying, the hind wings are folded back under the forewings and it may look as if the bee has only two wings. Other insects (flies, in particular) actually only have two wings, so the four-wing design is not essential for flight.

With rare exceptions, such as the male desert bee *Perdita portalis,* which has atrophied flight muscles and does not fly, bees are hardy fliers with large flight muscles and excellent maneuverability. Insect wings don't simply flap up and down, but rather the tips of the wings move in an oval pattern and turn over during each stroke. When the wing travels downward, the topside faces up, and then the wing rotates on an axis before the

Fig. 12. The two sets of bee wings are marked by a series of veins that vary in their dimensions by species. The forewing is longer and toward the front of the bee's body, while the hind wing is shorter and toward the abdomen. *(Drawing by Julie L. Dlugos.)*

upstroke, creating a large amount of lift. The two types of wings can be hooked together during liftoff for flight when higher power is required.

Question 12: What are the antennae used for?

Answer: A bee has two antennae, sometimes called feelers, and the name “feelers” describes what these appendages do for bees. Each antenna is a major source of environmental information, with sensors that detect odors and function as giant external noses. Other antennal sensors are mechanosensors that detect wind direction and pressure waves, including vibrations, and they help the bees stay attuned to their body position in the environment. Using a microscope to examine the honey bee antenna reveals the complexity of these sensors. See also chapter 3, question 1: Can a bee hear?

Question 13: How do bees hold onto slippery surfaces?

Answer: Like all insects, honey bees have three pairs of segmented legs. There are antennae cleaners on the forelegs (See chapter 3, question 4: How do bees keep themselves clean?) and hairy “pollen baskets” on the hind legs. At the end of each leg are small hooks, called tarsal claws, that allow the bee to hold onto some slippery surfaces. The center part of the foot, between the tarsal claws, contains a structure called the *arolium*. Accord-

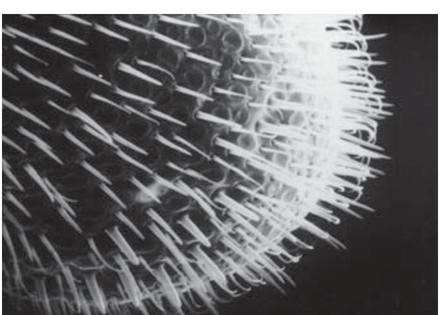

Fig. 13. A scanning electron micrograph of a worker honey bee antenna, showing the many hair-like sensors that detect odors and pressure waves. *(Image by Armand Whitehead.)*

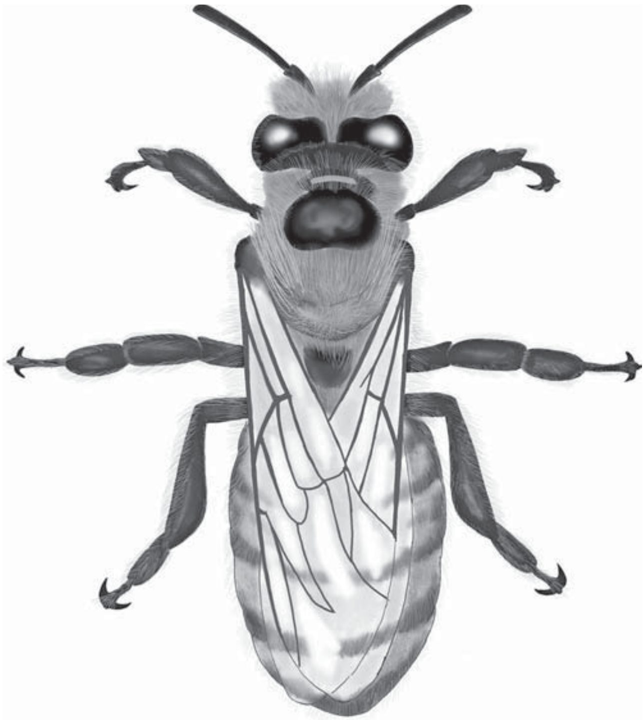

Fig. 14. The top view of a worker honey bee body. All six bee legs are attached to the middle body section, the thorax. The hair on the thorax is worn away as the bee ages due to repeated inspections of cells in the beeswax combs. *(Drawing by George C. West.)*

ing to famed honey bee anatomist H. A. Dade, this pad-like area essentially acts like a small suction cup to help the bee adhere to a slick surface (such as glass, plastic, or vegetation) when the claws cannot grip the substrate. There is also a tarsal gland that is covered with a thin, sac-like fold that forms a reservoir, and it probably fills and unfolds when the bee walks, also helping it to grip smooth or slippery surfaces.