HONEYBEE DEMOCRACY

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LIFE IN A HONEYBEE COLONY

. . . this being an Amazonian
or feminine kingdome.
—Charles Butler, The Feminine Monarchie, *1609*

The honeybee, *Apis mellifera*, is just one of nearly 20,000 species of bees that exist worldwide. They are a surprisingly diverse lot—some are smaller than a rice grain, while others will half fill a teacup—but they are all descended from one ancestral species of vegetarian wasp that lived approximately 100 million years ago, in the Early Cretaceous period, when huge dinosaurs were still stomping about and flowering plants were just starting to appear. Even today, many bee species are remarkably wasplike in appearance, but behaviorally the two groups are distinct. Nearly all wasps, including the familiar paper wasps and yellow jackets, are predators that kill other insects or spiders (often by stinging) to provide the egg-laying females and their growing young with proteinaceous food. Bees, however, have abandoned the carnivorous behavior of their ancestors and depend instead on collecting protein-rich pollen from flowers. This pollenivorous habit explains the decidedly fuzzy, almost teddy-bearish, look of many bees; their bodies are thickly covered with plumose hairs that efficiently catch pollen grains when a bee scrabbles through a flower.

Both bees and wasps regularly visit flowers, for both types of insects feed on sugary nectar for energy, but it is between the pollen-loving bees and the flowering plants that a strong mutual dependence has evolved over the millions of years since both groups arose. These days, the two are made for each other. Bees depend on flowers for adequate nourishment, while many flowering plants depend on bees for sexual reproduction. Bees, with their hairy bodies and fixation on flowers as protein sources, serve as flying penises for the plants, picking up pollen grains from the bursting anthers of one flower and depositing them on the sticky stigma of another. Introducing a hive of honeybees to any flowering area—garden, orchard, blooming wayside, or prairie—brings to the neighborhood, in effect, a large, dawn-to-dusk "escort" service of the flowers' little friends.

Honeybees are unusual bees in that they live in teeming societies whose massive nests of honeycomb fill the boxy hives of beekeepers or, as we shall see, suitably spacious cavities in hollow trees. In most bee species, by contrast, individuals live in solitude and build small nests in narrow tunnels excavated inside plant stems or in sandy soil. The typical life history of one of these solitary bee species starts in late spring or early summer when a mated female emerges from an overwintering burrow (the males having died off the previous fall). Over the next few weeks, this motherly bee will excavate a multichambered nest, provision each chamber with a sticky ball of pollen moistened with nectar, lay one whitish egg atop each pollen ball, seal up each chamber, and then leave her offspring to eat their way to adulthood later that summer. She will die long before her offspring emerge as adults, mate with one another, and prepare for the coming winter. Clearly, most bees are loners.

A Composite Being

When we look through the glass walls of a honeybee observation hive, or gently lift the lid from a conventional beehive and peer inside, we see the opposite of loner bees: thousands and thousands of bees living together. Virtually all are female worker bees, all of whom are daughters of the one queen bee that lives in their midst. Even though these workers are females and are fully equipped to care for offspring, they have poorly developed ovaries and they rarely lay any eggs. If we proceed to search the combs of the hive carefully, we will eventually locate the queen, who resembles the workers but is a bit bigger, with a longer abdomen and longer legs (fig. 2.1). Her greater size is impressive, but what most

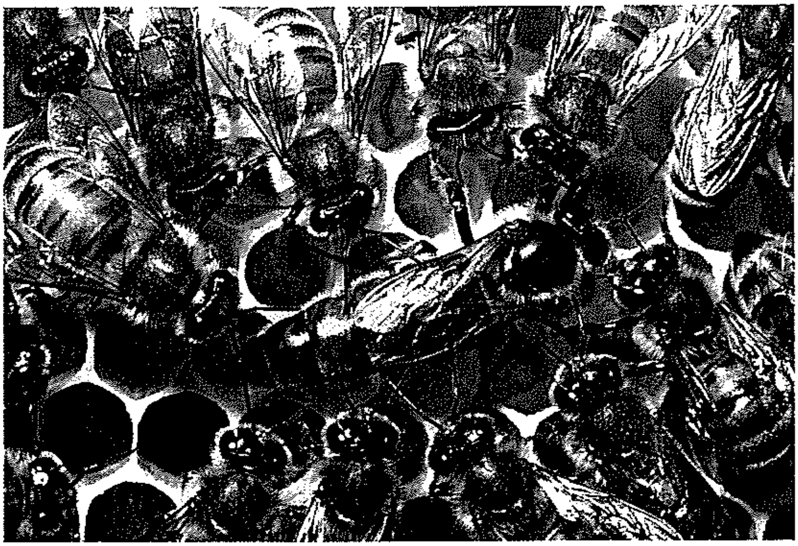

Fig. 2.1 The queen is larger than the surrounding workers, who feed and groom her.

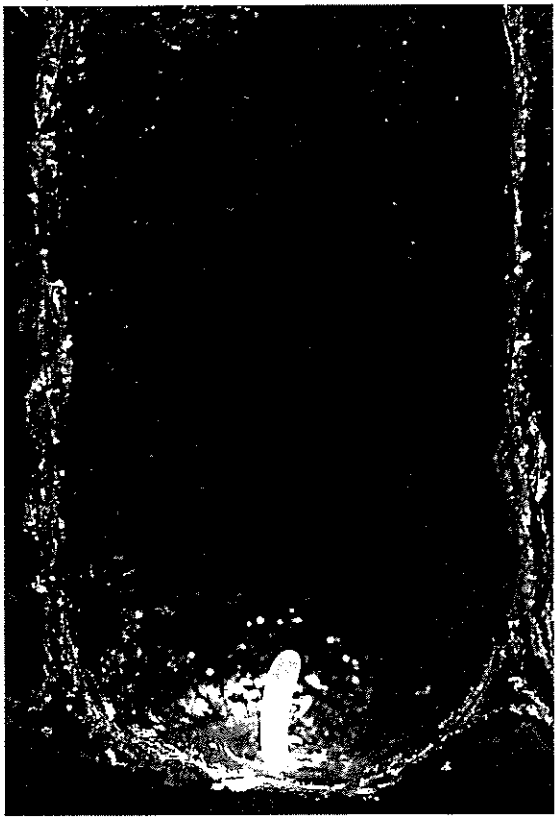

Fig. 2.2 When the queen finds a clean, empty cell, she inserts her long abdomen and lays a single egg at the base of the cell.

renders her conspicuous is how she moves slowly, indeed majestically, across the combs and how she is treated by her worker daughters. As the queen advances, the workers before her step back to clear her path, and when she pauses, the dozen or so workers beside her gingerly step forward to feed and groom her, forming a retinue of nudging bees that encircles her completely. In contrast to the workers, the queen is an amazing layer of eggs, depositing them in cells at a rate of one or more per minute, or more than 1,500 per day (with a combined weight nearly equal to her own) in late spring and early summer, when a colony's brood rearing is at its peak (fig. 2.2). Over an entire summer, a colony's queen will produce some 150,000 eggs, hence about half a million during the two or three years of her likely lifespan.

Most of the pearly white eggs the queen lays will be fertilized, but some will be unfertilized. During the first week of her life, she flew from her colony's hive and mated with 10 to 20 males from other hives in the area, and so procured a lifetime supply of approximately five million sperm. The queen stores all these sperm in suspended animation inside a spherical organ called a spermatheca, which lies in the rear of her abdomen, behind her massive ovaries. With each egg she lays, the queen decides whether to dispense a few fertilizing sperm or to hold them back, and in this way she determines the sex of her offspring: fertilized for female, unfertilized for male. Whether a fertilized egg develops into a nonbreeding worker or an egg-laying queen depends on how it is treated. If it is deposited in a standard-size cell in the combs, where after hatching into a larva it will be fed by the workers with standard-quality larval food, then it will develop into a worker. But if a fertilized egg is deposited in a large, specially built queen cell, hanging from the bottom of a comb, then the larva it gives rise to will be fed a lavish diet of nutrient-rich secretions (so-called royal jelly), and its development will be channeled to a developmental pathway that produces a queen. For the fertilized eggs of bees, food is destiny.

A queen withholds sperm from less than 5 percent of her eggs, but these unfertilized eggs are important for they give rise to her sons, the colony's drones (fig. 2.3). These are a colony's brawniest bees, endowed with huge eyes for spying young queens out on nuptial flights and massive flight muscles for chasing after the queens at speeds up to 35 kilometers an hour (about 22 miles per hour).

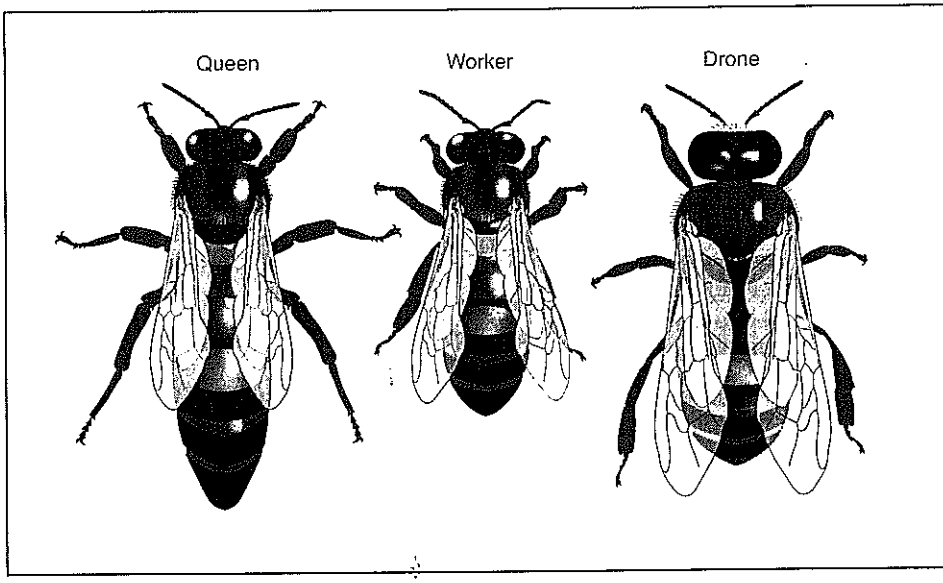

Fig. 2.3 The three types of adult honeybees.

They are also a colony's laziest bees. Unlike the workers who perform all the household tasks inside their hive—clean cells, feed larvae, build combs, ripen honey, ventilate hive, guard entrance, etc.—the drones spend their time at home simply hanging out in restful leisure, from time to time helping themselves to meals from the colony's honey reserves or begging feedings from their worker-sisters. Nevertheless, they make a fundamentally important contribution to their colony's success, for in mating with the young queens of the neighboring colonies they help their colony win in the ceaseless evolutionary competition to pass genes on to future generations. And when it comes to seeking sex, drone honeybees are no slackers. Every sunny afternoon, once a drone reaches sexual maturity at about 12 days of age, he will fly from his hive looking for action. In ways that remain mysterious, he will find his way to one of the traditional honeybee mating areas ("drone congregation areas") within a few miles of his home, and will fly about this aerial pickup spot, waiting for a young queen to appear. If one does, he will zoom after her. And if he manages to outrace his rivals and contact the queen, he will inseminate her in flight, 10 to 20 meters (30 to 60 feet) up in the sky. If he doesn't make contact, he'll fly home, rest and refuel, and come out later to try his luck again.

One way to think of a honeybee colony is, then, as a society of many thousands of individuals: the queen, workers, and drones just discussed. But to understand the distinctive biology of this species of bee, it is often helpful to think of a colony in a slightly different way, not just as thousands of separate bees but also as a single living entity that functions as a unified whole (fig. 2.4). In other words, it can help to think of a honeybee colony as a superorganism. Just as a human body functions as a single integrated unit even though it is a multitude of cells, the superorganism of a honeybee colony operates as a single coherent whole even though it is a multitude of bees. The fact that both perspectives—colony as superorganism *and* colony as society—are valid reflects the way in which evolution has repeatedly built higher-level units of biological organization: by assembling unified societies of lower-level units. For example, during the origins of multicellular organisms, natural selection favored some societies of cells whose members cooperated rather than competed. Bit by bit, this selection for close cooperation produced the thoroughly integrated societies of cells that we know today, for example, as hummingbirds and human beings. The same sort of selection for extreme cooperation also happened with some societies of animals to produce the thoroughly harmonious, smoothly running insect societies that we can call superorganisms. These include not just colonies of honeybees but also the gigantic colonies of leafcutter ants, driver ants, or fungus-growing termites.

A colony of honeybees is, then, far more than an aggregation of individuals, it is a composite being that functions as an integrated whole. Indeed, one can accurately think of a honeybee colony as a single living entity, weighing as much as 5 kilograms (10 pounds) and performing all of the basic physiological processes that support life: ingesting and digesting food, maintaining nutritional balance, circulating resources, exchanging respiratory gases, regulating water content, controlling body temperature, sensing the environment, deciding how to behave, and achieving locomotion. Consider, for example, the control of body (colony) temperature (fig. 2.5). From late winter to early fall, when the workers are rearing brood, a colony's internal temperature is kept between 34° and 36°C (93° and 96°F)—just below the core body temperature of humans—even as the

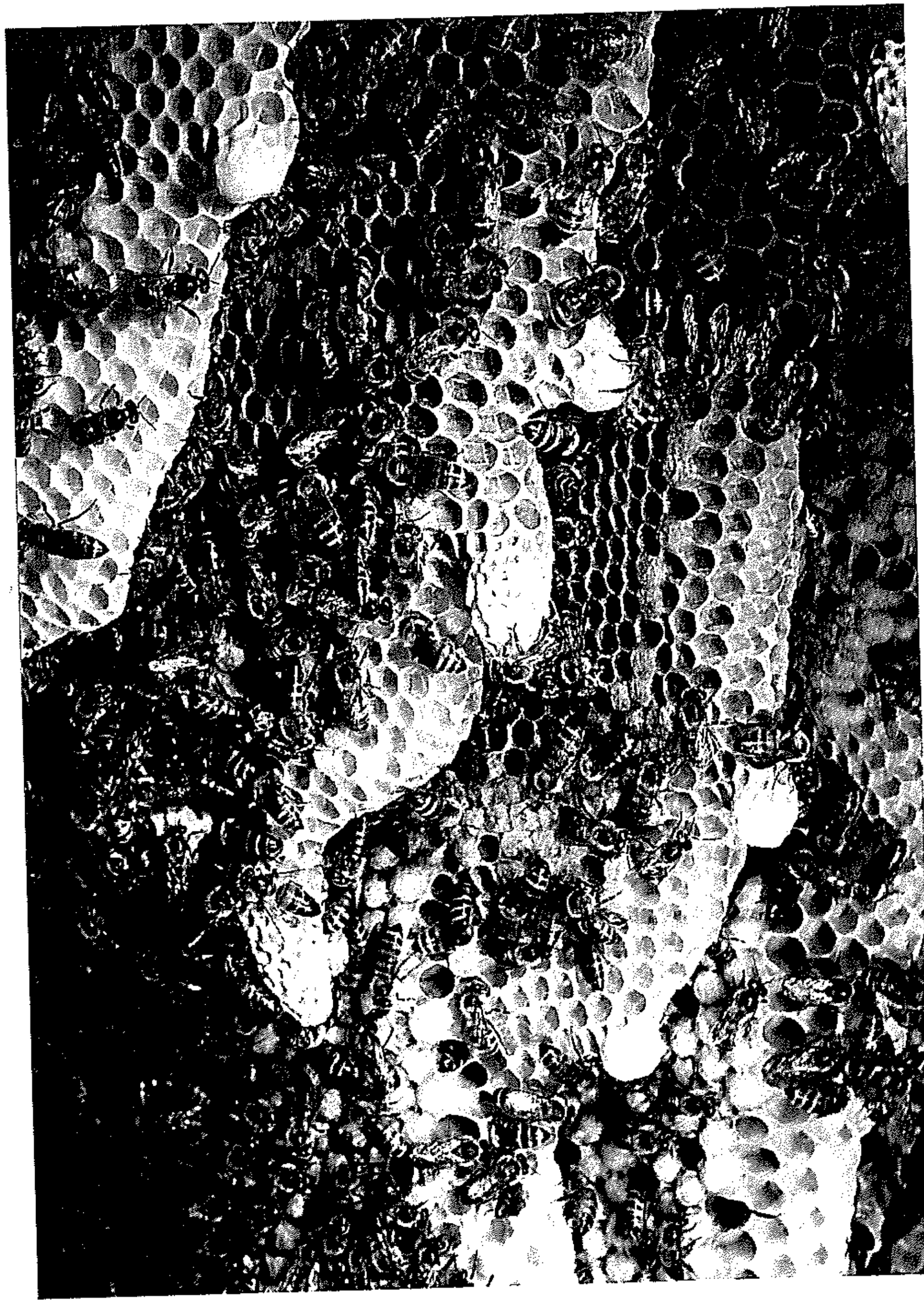

Fig. 2.4 A honeybee colony, both a society and a superorganism.

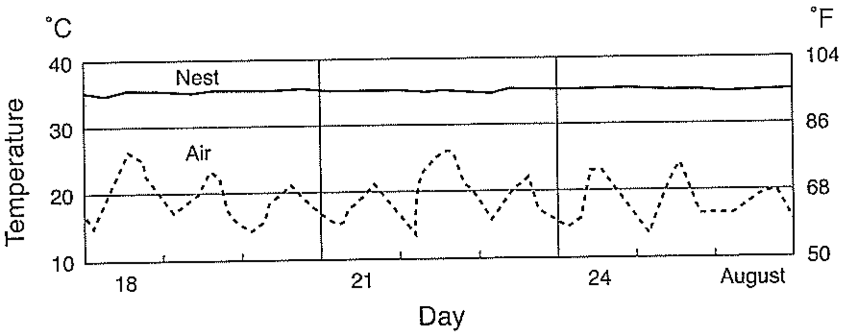

Fig. 2.5 The elevated, and stable, temperature inside a honeybee colony's nest, compared to the outside air temperature.

ambient air temperature ranges from -30° to 50°C (-20° to 120°F). The colony accomplishes this by adjusting the rate at which it sheds the heat generated by its resting metabolism and, in times of extreme cold, by boosting its metabolism to intensify its heat production. A colony's metabolism is fueled by the honey it has stored in its hive. Other indicators of the high functional integration of a honeybee colony include *colonial breathing*: limiting the buildup of the respiratory gas CO_2 inside the hive by increasing its ventilation when the CO_2 level reaches 1–2 percent; *colonial circulation*: keeping the heat-producing bees in the central, brood-nest region of the hive properly fueled with honey carried in from peripheral honey combs; and *colonial fever response*: mounting a disease-fighting elevation of the nest temperature when a colony suffers a dangerous fungal infection of the brood bees. I suggest, though, that the single best demonstration of the superorganismic nature of a honeybee colony is the ability of a honeybee swarm to function as an intelligent decision-making unit when choosing its new home.

Unique Annual Cycle

The key to understanding why honeybee swarms are meticulous in the choice of their living quarters is the unique annual cycle of the honeybee, which depends critically on colonies occupying nesting cavities that are both snug and roomy. Unlike all the other social insect species that live in cold climates, honeybees do

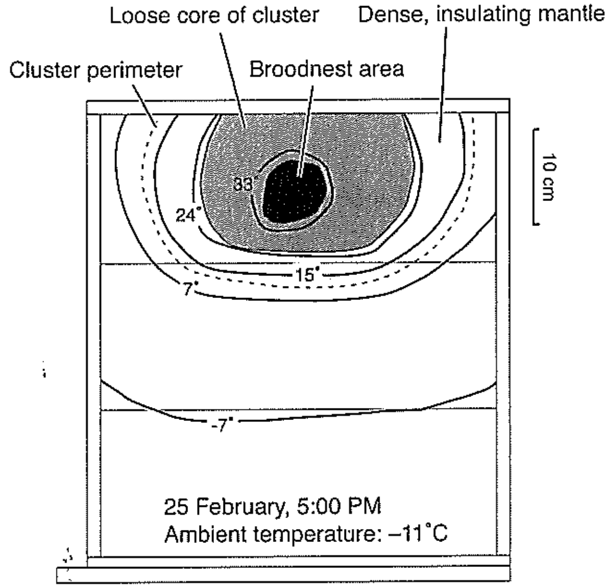

Fig. 2.6 Anatomy of a winter cluster of honeybees.

Fig. 2.7 The nest of a colony that failed to occupy a protective nest cavity.

not survive winter in dormancy, but as fully functioning colonies in self-heated nests. To achieve this means of winter survival, each colony contracts in winter into a tight, well-insulated cluster of bees about the size of a basketball. The cluster's surface temperature is maintained above 10°C (50°F), which is a few degrees above a worker bee's chill-coma threshold, and so is warm enough to keep the outermost bees alive (fig. 2.6). Heat is generated within the cluster by the bees isometrically contracting their two sets of flight muscles (one for elevating the wings and one for depressing them) thereby producing much heat but few or no wing vibrations. These flight muscles endow a bee with a surprisingly powerful means of heat production. Bees fly, of course, by flapping their wings—the most energetically demanding mode of animal locomotion—and the flight muscles of insects are among the most metabolically active of tissues. Indeed, a flying bee expends energy at a rate of about 500 watts per kilogram (250 watts per pound), whereas the maximum power output of an Olympic rowing crew is only about 20 watts per kilogram (10 watts per pound). At any moment, however, only a small portion of the clustered bees will be shivering with maximum intensity, so the total heat output by the approximately two kilograms (four pounds) of bees in a winter cluster isn't 1,000 watts, but is only about 40 watts, a rate of heat production like that of a small incandescent light bulb. In a snug cavity, sheltered from heat-robbing winds, a colony with this level of heat output will survive the winter quite nicely. The importance of inhabiting a protective cavity is demonstrated by the sad fate of the occasional colony that fails to find shelter and nests in the open (fig. 2.7); almost certainly, it will perish when winter's cold arrives.

A honeybee colony runs year-round on flower power, for what fuels a colony's heat production all winter long is the 20 or more kilograms (44+ pounds) of honey that the colony stockpiled in its honeycombs over the previous summer. If one mounts a hive of bees on scales and takes a weight reading each day for an entire year, one will see that winter is a time of steady weight losses as a colony consumes its honey stores, and that summer is a time of episodic weight gains as a colony scrambles to replenish these stores (fig. 2.8). For example, in Ithaca, New York, my colonies restock their honeycombs mainly during the 60-day period between May 15 and July 15, when there unfolds a succession of mass flowerings by plants that produce copious nectar, including black locust and basswood

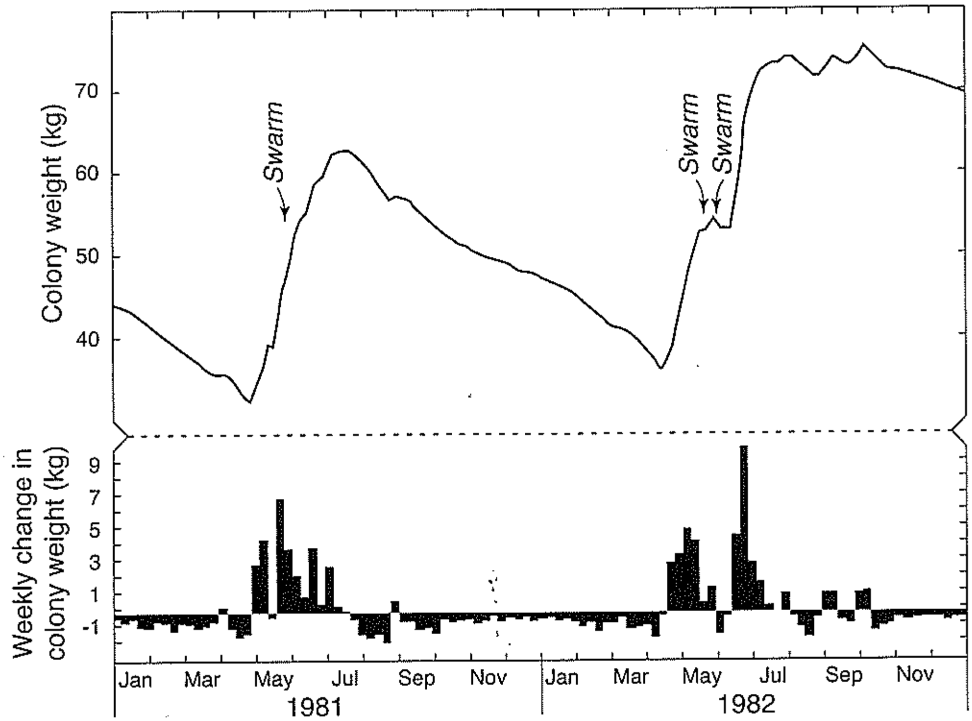

Fig. 2.8. Weekly changes in the weight of a honeybee colony (hive plus bees and stored food).

trees, sumac shrubs, and various herbaceous plants such as dandelions, raspberries, milkweeds, and clover. On a day when the air is warm, the sun is strong, and nectar is flush, the hive that I keep at home on a set of platform scales will grow heavier by several kilograms, virtually all of it fresh honey. Beekeepers call a string of such days a "honey flow."

The task of amassing within a short summer season an ample supply of winter heating fuel is one of the greatest problems faced by a honeybee colony. Honey is a dense, energy-rich food, but even so, 20 kilograms (44 pounds) of the stuff will nearly fill a 16-liter (14-quart) bucket, or more than 50 of those plastic honey bears one sees lined up beside the grape jelly at the supermarket. How much work effort and storage space is needed to create such a bulky hoard of calories? Regarding work effort, given that freshly collected nectar is (on average) a 40 percent sugar solution and fully ripened honey is roughly an 80 percent sugar solution, and given that a foraging bee typically brings home a nectar load weighing about 40 milligrams (0.001 ounces), we can calculate that the collection of enough nectar to produce 20 kilograms (44 pounds) of honey requires more than 1 million foraging trips by a colony's workers. And when one also considers the miles flown and countless blossoms visited on each foraging trip, one realizes what prodigious efforts the bees make over summer to sustain their colony through winter.

Regarding storage space, given that it takes 250 square centimeters of honeycomb to store one kilogram of honey (i.e., 18 square inches of comb per pound of honey), and given that every 250 square centimeters of honeycomb require about 0.9 liters of nest cavity space (to accommodate the honey-filled comb and the adjacent passageways for the bees), we can calculate that the storage of 20 kilograms (44 pounds) of honey requires a nesting cavity of at least some 18 liters (4 gallons). Thus we can see that when a colony chooses its future homesite, it will need to reject tree cavities smaller than these volumes. Ideally, it will find a nesting cavity somewhat roomier still, to accommodate extra honey-filled combs and still more combs for the colony's brood rearing operation, which in spring can fill more than half the cells in a colony's nest as the colony rebuilds its workforce in preparation for swarming. Beekeepers, by the way, have found a clever way to exploit the bees' drive to fill their nests with honey. By housing their colonies in hives that provide vastly more nesting space—about 160 liters (some 36 gallons)—than is needed by bees living in nature, beekeepers induce their colonies to amass astonishing amounts of honey, sometimes more than 100 kilograms (220 pounds) of honey per hive in a summer. Thus a colony of hardworking bees residing in a beekeeper's hive will often provide its landlord with dozens of combs brimming with honey.

The honeybee's annual cycle is unique in other ways besides the overwintering process. Consider how a colony starts rebuilding its workforce in the middle of winter. Shortly after the winter solstice, when the days begin to grow longer but snow still blankets the countryside, each honeybee colony raises the core temperature of its winter cluster to about 35°C (95°F), the optimum temperature for rearing new bees. With the cluster's core now serving as a cozy incubator, the queen begins to lay eggs, using cells that were emptied of their honey during

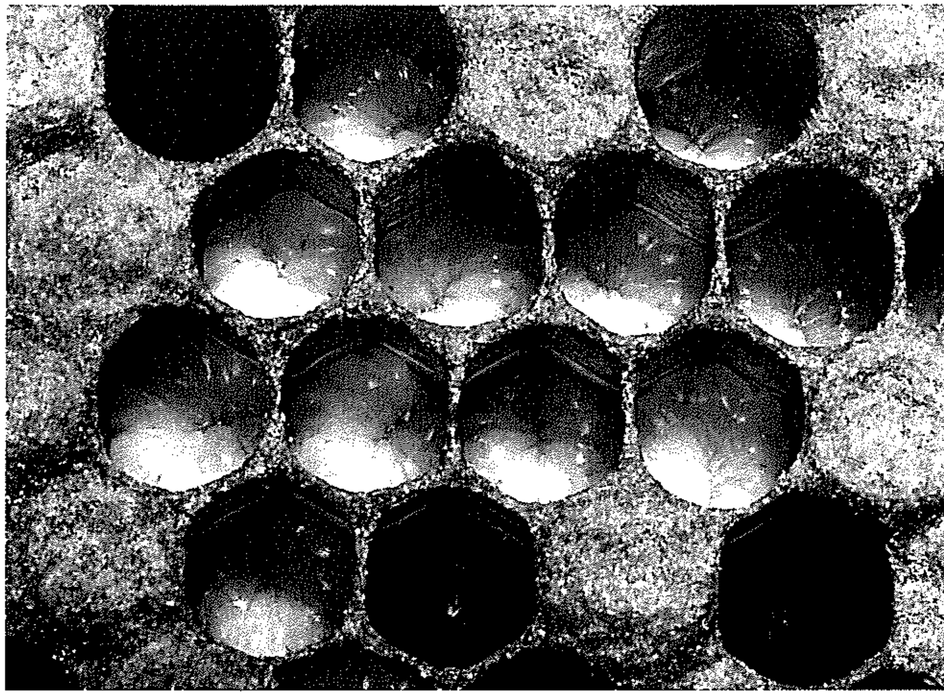

Fig. 2.9 Cells containing larvae, visible as white, C-shaped grubs.

the preceding weeks of cold. Larvae hatch from these eggs, approximately three days after they were laid, and are fed by the adult workers. At first, the workers feed the larvae a proteinaceous food secreted by glands located in their (the adult bees') heads, but after about three days they wean them to a mixture of honey and pollen. About ten days after hatching from its egg, each larva has grown to nearly fill its cell (fig. 2.9) and starts to spin the cocoon in which it will metamorphose into an adult bee. The adult workers build a wax capping over the cell to protect the immature bee during this delicate, pupal stage of development. Once metamorphosis is complete, in about another week, the fully developed worker bee chews through the capping on her cell and joins her colony's growing workforce. When a colony starts its impressive performance of rearing brood in the middle of winter, there are only a hundred or so cells containing developing bees, but by early spring, when the first flowers blossom, over one thousand cells hold developing bees, and the pace of colony growth quickens daily. Come late spring, when most other insects are just starting to become active, honeybee colonies have already grown to full size, twenty or thirty thousand individuals, and have begun to reproduce.

Colony Reproduction

Reproduction by a honeybee colony is a curiously complex affair, for each colony is a hermaphrodite, meaning that it has both male and female reproductive powers. This is decidedly different from ourselves and most other animals, where each individual is either a male or a female, but it is strikingly similar to many plants, such as apple trees. In fact, to make sense of how a honeybee colony reproduces, I find it helpful to compare how honeybee colonies and apple trees go about achieving sexual reproduction. Their basic similarity is that both types of individual—colony and tree—produce both male and female reproductive propagules. The male propagules are drone bees and pollen grains, whereas the female propagules are queen bees and egg cells. And just as the pollen grains from one apple tree fertilize the egg cells of other trees to create embryos inside seeds that will grow into new trees, the drones from one honeybee colony fertilize the queens of other colonies to create inseminated queens that will give rise to new colonies. Thus both trees and colonies rely on cross-fertilization to avoid the problems associated with inbreeding.

Colonies and trees also resemble each other in how the male and female sides of reproduction differ. For both bees and trees, the male side of reproduction is straightforward. In late spring and early summer, each colony or tree produces a great number of male propagules—thousands of drone bees per colony and millions of pollen grains per tree—that disperse over the countryside and achieve fertilizations. Any one drone bee or pollen grain has a low probability of fertilizing a queen or egg, but because a healthy individual (colony or tree) launches a huge squadron of male propagules, it has a high probability of achieving reproductive success via its small, male gene carriers.

Turning to the female side of reproduction, we find a more complex process in both colony and tree. In each, the fertilized propagule (queen bee or egg cell) is not discharged "naked," as happens with the male propagules, but instead is packaged inside a large and intricate dispersal vehicle that will give it protection and help it along. Thus, the egg cells of an apple tree are sent forth from the parent tree enclosed in apples, whereby each egg cell is surrounded by many thousands of protective cells forming the tough seed coat and delicious fruit flesh. Likewise, the queen bees of a honeybee colony are sent forth from the parent colony enclosed in swarms, whereby each queen is surrounded by some ten thousand worker bees providing a living shelter and food supply. Because each swarm or apple is many thousand times larger and more costly than each drone bee or pollen grain, it is no surprise that a colony or tree produces relatively few female units each year, usually fewer than four swarms and at most a few hundred apples. But because the costly female propagules are well protected and richly endowed, they have a high probability of successfully establishing a new colony or tree. So, despite their smaller numbers, swarms and apples match the effectiveness of drone bees and pollen grains in propagating the genes of their parents.

Swarming

In upstate New York, where I live, my colonies begin sending forth their drones in late April, and they begin casting their swarms—each one consisting of a queen accompanied by several thousand workers—a week or two later in early May. In essence, colony reproduction starts up shortly after winter shuts down. Most years, the swarming season begins after we've enjoyed a few weeks with warm days and profuse flowering by the maple trees (*Acer* spp.), pussy willow bushes (*Salix discolor*), and skunk cabbage plants (*Symplocarpus foetidus*). During this time, the colonies have collected much food, their queens have diligently laid eggs, and their worker populations have rapidly strengthened. I can predict with fair reliability when I will find my first swarm by noting when my hive of bees mounted on platform scales finally ends its six-month-long free-fall in weight and begins to bulk up again on fresh nectar and pollen (see fig. 2.8).

Swarming starts early in the summer because each new colony has much to accomplish if it is to survive the following winter. Specifically, each swarm (new colony) must locate a suitable nesting cavity, occupy it, and then build a set of beeswax combs, raise new workers, and store sufficient provisions to last through winter. Getting an early start certainly helps a colony clear these hurdles. Even so, sadly, many new colonies don't store up enough honey and so starve during their first winter. In the mid-1970s, for three years I followed the fates of several dozen feral honeybee colonies living in trees and houses around Ithaca, and I found that less than 25 percent of the "founder" colonies (ones newly started by swarms) would be alive the following spring. In contrast, almost 80 percent of the "established" colonies (ones already in residence for at least a year) would survive winter, no doubt because they hadn't had to start from scratch the previous summer. Beekeepers describe the time and energy crunch faced by swarms in a rather grim, three-line rhyme: "A swarm of bees in May is worth a load of hay, a swarm of bees in June is worth a silver spoon, a swarm in July isn't worth a fly."

Whether in May, June, or July, the first step that a colony takes to prepare for swarming is the rearing of 10 or more queens, all daughters of the mother queen. Queen rearing starts with the construction of queen cups, tiny inverted bowls made of beeswax. They are built usually along the lower edges of the combs in which the colony is producing brood and they will form the bases of the large, downward-pointing, peanut-shaped cells in which the queens will be reared (fig. 2.10). Next, the queen lays eggs in a dozen or more of the queen cups and workers feed the hatching larvae the royal jelly that ensures their development into queens. An enduring mystery about honeybees is what exactly stimulates a colony to begin rearing queens and thereby initiate the process of swarming. Beekeepers know that certain conditions inside a colony's hive (congestion of the adult bees, numerous immature bees, and expanding food reserves) and outside the hive (plentiful forage and spring time) are correlated with the start of queen rearing for swarming. Nevertheless, to this day, no one knows what specific stimuli the worker bees are sensing and integrating when they make the critical decision to start the swarming process.

The development of the new queens is remarkably rapid, requiring only 16 days from the time the egg is laid to the moment when an adult queen emerges from her cell. While these daughter queens develop, the mother queen undergoes changes that will prepare her for departure in the swarm. With each passing day, she is fed less and less by the workers. Her egg production declines, and her abdomen, no longer swollen with fully formed eggs, shrinks dramatically.

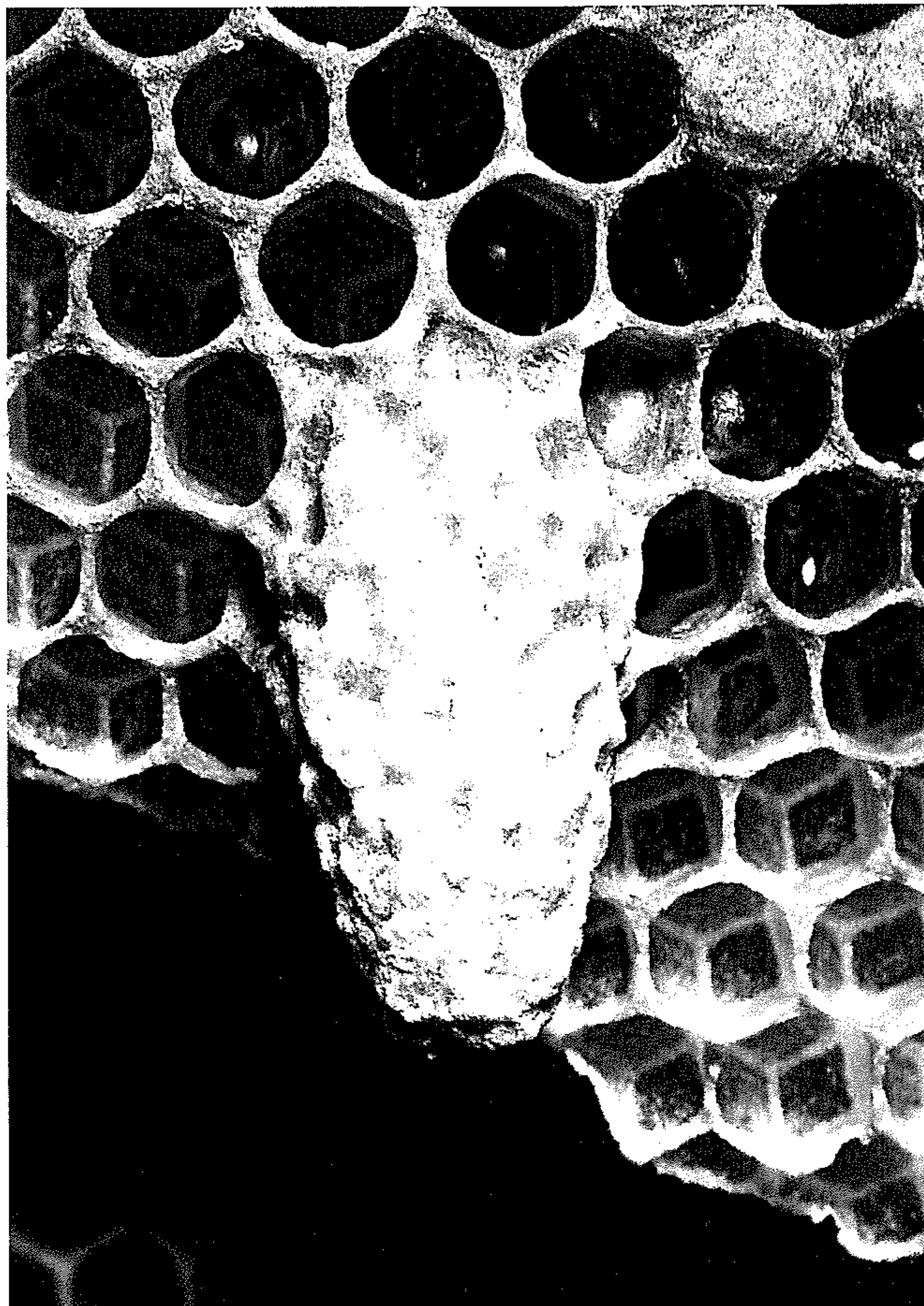

Fig. 2.10 One of the large, peanut-shaped cells in which queens are reared.

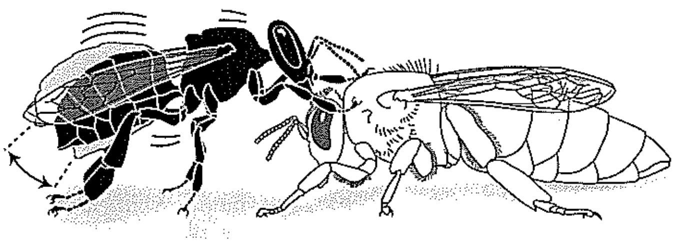

Fig. 2.11 A worker bee shaking the queen. The arrow indicates the dorso-ventral vibration of the bee's body.

Furthermore, the workers begin to show mild hostility toward their mother, shaking, pushing, and lightly biting her. Each time a worker shakes the queen, she grasps the queen with her forelegs and shakes her own body for a second or so, delivering 10 to 20 vigorous shakings of the queen (fig. 2.11). These bouts of rough handling, which eventually can become nearly continuous (occurring every 10 seconds or so), force the queen to keep walking about the nest. This increased exercise, together with the reduced feeding, results in a 25 percent reduction in the queen's body weight. In this way the mother queen, usually too large and heavy to fly, is put into flying trim.

While the daughter queens are maturing and the mother queen is slimming, the workers are also preparing for the impending mass departure of the mother queen and thousands of workers in a swarm. To ensure that they will be well supplied with energy when they leave home, the workers do just the opposite of slimming; they stuff themselves with honey, causing their abdomens to swell noticeably. A study in which the stomachs of workers from colonies preparing to swarm were painstakingly dissected and weighed found that most bees had filled their stomachs with a drop or two (35 to 55 milligrams) of honey, thereby increasing their body weights by about 50 percent. Thus when a swarm leaves on its journey to a new home, approximately one-third of its weight is a food reserve. The bloating of the workers is not their only conspicuous adjustment in anticipation of swarming. The wax glands, located on the ventral plates of four of the abdominal segments of each worker bee, become hypertrophied in preparation for the intense wax secretion needed for comb building at the new nest site. Turning over a worker bee plucked from a colony that is poised to swarm will reveal white scales of beeswax projecting from the overlapping ventral plates

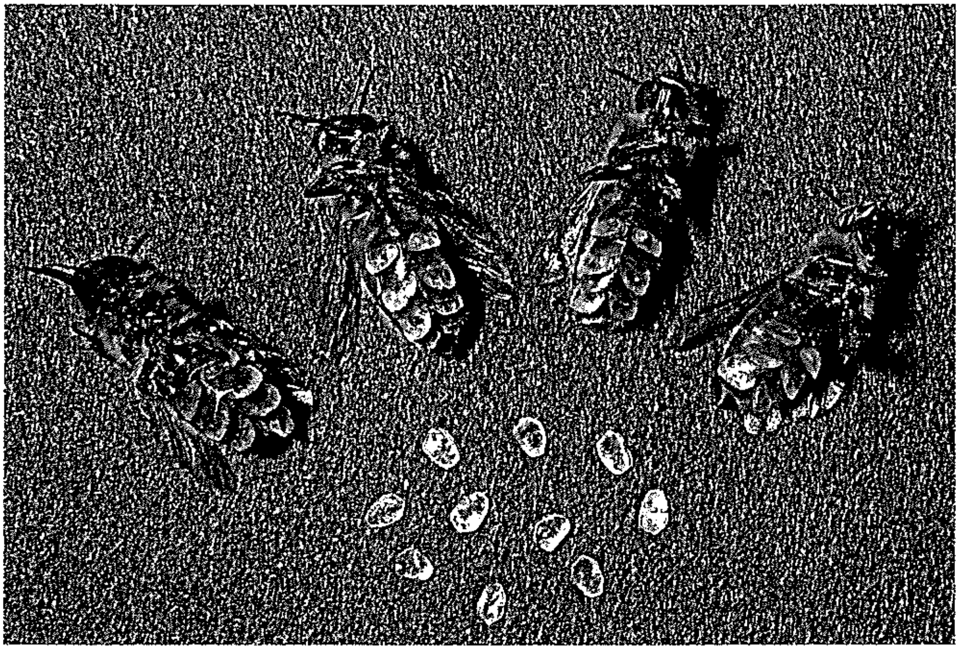

Fig. 2.12 Wax scales on the undersides of the abdomens of worker bees.

(fig. 2.12). But what is perhaps the most striking change in the workers just before swarming is their greater lethargy. Many of these laggards hang quietly on the combs, while others rest in a thick cluster outside the hive entrance, giving the alert beekeeper a helpful warning that swarming is imminent. The biologist and comic book artist Jay Hosler has nicely called this period of odd inactivity "the calm before the swarm." Several dozen bees, however, remain active and start scouring the countryside for five or more kilometers (three miles) in all directions for possible nest sites. These enterprising individuals are nest-site scouts, the central figures in this book, and in chapter 4 we will see who they are.

In the summer of 2007, I learned that the nest-site scouts play a key role in triggering the next main event in swarming: the swarm's explosive departure from the parental nest. My partner in this work was one of my graduate students, Juliana Rangel, who is a fine scientist, being smart, cheerful, and hardworking. We learned that the scout bees are especially well qualified to instigate the swarm's mass exodus because their special occupation causes them to spend time both outside and inside the nest: outside to hunt for potential dwelling places, and inside to refuel and rest. Only a bee that has information from both indoors and outdoors can get the timing right for the swarm's departure. From her time inside, a scout bee can tell when some of the developing queens have reached the pupal stage and have had their cells sealed, and from her time outside, she can tell when the weather is sunny and warm, hence favorable for a journey. When both of these requirements for swarming are fulfilled, the scouts burst into action. Starting in the cluster of bees just outside the hive entrance, the excited scouts begin scrambling among their cool, calm sisters. Every few seconds, each scout will pause by a quiet bee and briefly press her thorax against the other bee while activating her flight muscles to produce a 200- to 250-hertz (cycles per second) vibration that lasts for a second or so. This signal is called worker piping. It sounds (because of high-frequency harmonics) like the engine of a Formula One race car making an all-out acceleration, and it informs the quiescent bees that it is time to warm their flight muscles by shivering to a flight-ready temperature of 35°C (95°F) in preparation for the swarm's departure. The piping by the scout bees is intermittent and faint at first, but over the next hour or so it gradually becomes steady and loud, as more and more of the scouts blast out the message "Time to warm up!" Ultimately, the piping-hot scout bees sense that all their hive-mates are flight ready—perhaps by consistently contacting suitably warmed bees—at which point the scouts start producing a second arousal signal, the buzz-run, in which each scout bee runs about the nest in great excitement, tracing out a crooked path, buzzing her wings in bursts, and bulldozing between sluggish bees. The message now is "Time to go!"

And go they do! Now nearly all of the worker bees become excited and run about, crowding toward the entrance opening where they pour out in a torrent and take to the air, pushing the mother queen out as well, creating what beekeepers call the "prime swarm" (fig. 2.13). It contains some ten thousand bees, about two-thirds of the colony's population. These swarming bees fly round each other in a wild whirl, forming a cloud approximately 10 to 20 meters (30 to 60 feet) across, with their queen flying somewhere in their midst. They don't go far. Soon, some of the workers settle on the branch of a tree or similar object, the queen

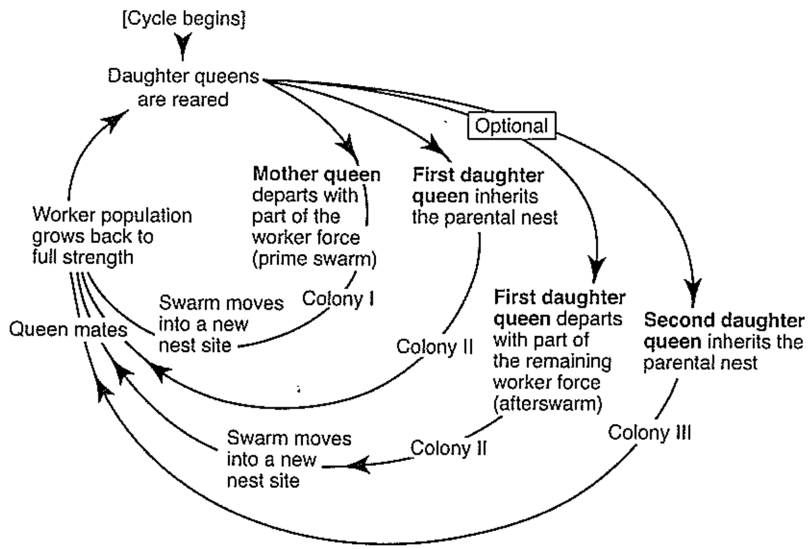

Fig. 2.13 Principal events in the life cycle of honeybee colonies.

joins them, and over the next 10 or 20 minutes the whole cloud of bees will condense into a beard-shaped cluster. The worker bees are attracted by the scent of the queen and by the strong lemony odor of the attraction pheromones that the first settlers are releasing from their scent organs (located near the tip of the abdomen) and are dispersing by fanning their wings. Over the next several hours, or several days, most of the swarm bees will hang here quietly, while the scouts will busily search the neighborhood for candidate dwelling places and choose a suitable abode. Once the scouts have completed their democratic decision making, they will induce the whole swarm to again take flight and then will guide the flying swarm to its new home.

Back in the parental nest, there remain a few thousand worker bees, a dozen or more queen cells, many thousand cells of worker brood, and much food. The stay-at-home workers are now without a queen, but not many days will pass before the first of the new queens emerges. During the waiting period, the parent colony's worker population will rebound as new workers emerge. Often, so many new workers appear that the colony's strength is restored by the time the first virgin queen emerges from her sealed queen cell. If the colony does regain its strength, then the workers will chase the first virgin queen away from the

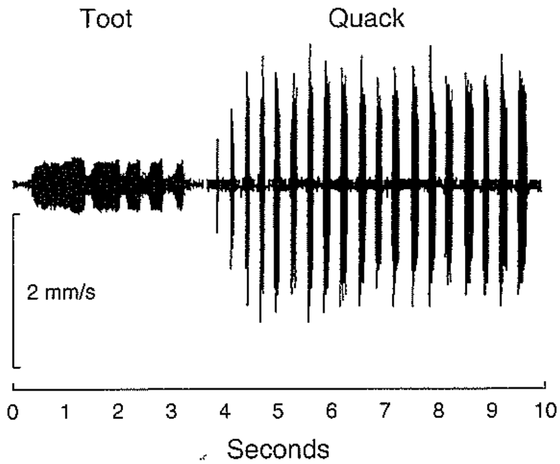

Fig. 2.14 Queen piping signals, recorded as vibrations of the comb. A virgin queen moving about on the combs produced a toot that triggered a quack by another virgin queen still confined in her cell. The units on the vertical axis—millimeters per second—are a measure of sound energy.

remaining queen cells to prevent her from destroying them. The workers will also refrain from chewing away the wax and pupal cocoon fibers on the capped ends of the queen cells to prevent the other virgin queens from getting free, and they will feed the confined queens whenever they beg for food by pushing their tongues through little slits in their cells. At the same time, the first virgin queen to emerge will announce her presence with queen piping signals, called "toots." A queen pipes the same way as a worker, by pressing her thorax against a substrate and activating her flight muscles. A queen, however, presses herself against a comb instead of against a bee, probably to give her signal a broader audience. Also, a queen's piping signals are longer than those of a worker, for they contain multiple pulses (fig. 2.14). When the first virgin queen pipes, the workers instantly cease all movement for the duration of her signal, perhaps to minimize the background noise produced by their myriad footsteps, and the virgin queens confined in their cells will pipe in response, producing lower-pitched "quacks" that are somewhat longer than the first virgin queen's "toots." These quacks almost certainly inform the first virgin queen that she has lethal rivals.

This bad news may encourage the first virgin queen to leave in a secondary swarm, what beekeepers call an "afterswarm." Doing so means that the first virgin queen relinquishes the wealth of desirable resources in the parent nest—the beeswax combs, worker brood, and honey stores—and starts down the risky path of founding a new colony. This course of action is, however, probably less dangerous for her than staying home and attempting to kill all her deadly serious competitors. Soon, the workers will start shaking the first virgin queen to prepare her for flight, and in a few days, if good weather prevails, they will push her out of the nest during the departure of a second swarm. This process is repeated with each emerging queen until the colony is weakened to the point where it cannot support further swarming. At this point, if there are still multiple virgin queens in the nest, the workers will allow them to emerge freely. The first one out usually attempts to kill those still in their cells by dashing over the combs in search of cells containing queens, chewing small holes in their sides, and stinging the occupants. If, however, two or more virgin queens emerge together, they will fight to the death, seizing each other and attempting to sting. The battling queen bees grapple and twist, each one struggling fiercely to implant her venom-laden sting in her sister's abdomen. Ultimately, one queen succeeds and the other, fatally stricken, collapses in paralysis, falls from the comb, and soon dies. The merciless sororocide continues until just one virgin queen remains alive. Several days later the victor will make her mating flights and, once fully mated, start her egg laying. Soon her daughters and sons will populate the coveted parental nest. Any virgin queen who departed in an afterswarm will likewise make mating flights once she and her workers have moved into their new home, for no queen ever mates inside a nest.