CHAPTER 4

THE HONEY BEE COLONY:
LIFE HISTORY

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The honey bee, *Apis mellifera*, is one of the most familiar and best-studied animals on earth. Humans and honey bees have had a close association for thousands of years. We have developed a complex symbiotic relationship with bees that is based on sophisticated methods of beekeeping and colony management. These methods make it possible for us to maintain bees for commercial purposes and scientific investigations. Our ability to control honey bees for our own purposes is truly phenomenal: we maintain them in artificial nests and glass-walled observation hives, we manage them to control swarming, increase honey production and prevent diseases, we artificially inseminate queens to control breeding and develop special genetic lines, we ship queens and colonies through the mail, and in the U. S. we transport up to a million colonies each year for commercial migratory beekeeping practices.

Because of our remarkable ability to manipulate honey bees, it is tempting to view them as domesticated animals. But in reality, they are feral organisms that can readily move between the natural environment and our bee yards and research settings. Honey bees are remarkably adapted creatures. They have evolved a complex life history that allows them to survive in both temperate and tropical habitats throughout their natural range in Europe and Africa, as well as many regions of North and South America where they have been introduced by humans. Despite our long history of beekeeping, we have altered the biology of honey bees very little. Rather, our success at managing them is based on our ability to mimic and manipulate different aspects of their life history, including their nesting biology, brood rearing, queen production, communication, nutrition, disease control and swarming. Thus, knowledge of honey bee natural history is essential, not only for understanding honey bee biology, but also for developing better management practices.

The purpose of my review is to discuss the life history of honey bees by examining their nesting habits, the biology and behavior of the different castes, and the seasonal cycles of growth, reproduction and movement. In addition to summarizing the current knowledge on these topics, I will also address how the different life history traits contribute to the strategies used by colonies to survive in their natural habitats. Much of this chapter will focus on European races of honeybees, which are adapted to temperate climates. The greatest challenge facing these bees is winter survival, and I will discuss how their life history traits help them cope with prolonged periods of cold in which there is little or no available forage. I will also discuss how knowledge of European honey

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bee life history has contributed to the development of our beekeeping practices.

In the last section of my review, I will examine the life history of tropical honey bee races, particularly those of the African continent. Although there are over 25 geographic races (subspecies) of *A. mellifera* adapted to a wide variety of habitats and climates, most research has concentrated on the 4-5 European races most commonly used in beekeeping in Europe and North America. In comparison, we know much less about the races of tropical and subtropical Africa, even though the African continent contains at least 10 distinct races of honey bees and accounts for two-thirds of the natural distribution area of *Apis mellifera*. Honey bee evolution occurred primarily in the tropics and the only truly tropical races of *A. mellifera* occur in Africa (Ruttner 1977; Seeley 1985). Comparisons of the life histories and survival strategies of European and African races are therefore necessary to fully understand the adaptability and evolution of the honey bee social system. In addition, interest in tropical honey bees has increased dramatically during the past 50 years, following the introduction of the African race, *Apis mellifera scutellata*, into Brazil and its rapid spread throughout much of South, Central and North America. It is only by understanding the natural history of this African race that we can comprehend its phenomenal success in the New World and develop procedures to manage and incorporate it into our beekeeping practices.

**NEST ARCHITECTURE AND NESTING BIOLOGY**

*The Nest Cavity:* The survival of a temperate-climate colony depends upon its ability to build and maintain a nest of wax combs in a suitable cavity. Although colonies will sometimes build exposed combs in the open (Fig. 1), the vast majority of nests occur within enclosed cavities in trees, the ground, and man-made structures. The nest cavity is critical to colony success. It provides protection and helps maintain the constant internal nest conditions that are necessary for proper colony function. Workers often

**Fig. 1.** An exposed nest of honey bee combs. The nest consists of a series of parallel wax combs separated from one another by 3/8", referred to as “bee space.”
coat the inside walls of the cavity with propolis, which weatherproofs the nest and has antimicrobial and antifungal properties that contribute to colony health (Wilson-Rich et al. 2009; Simone-Finstrom & Spivak 2010).

Honey bees show distinct preferences for cavity characteristics when selecting nest sites. In experimental trials that offer side-by-side choices, swarms prefer cavities with a volume of 30-40 L which have small, bottom-located, southward-facing entrances (Schmidt & Thones 1987 a,b; Seeley & Morse 1978). Colonies also prefer elevated nest sites, and will select cavities 3-5 m off the ground over those 1 m in elevation. Previously occupied cavities are preferred over those that have never been occupied, especially if they contain old combs (Visscher et al. 1985). Studies of feral colonies have revealed tremendous variability in nest cavity characteristics, which probably reflects the availability of nest sites in different study areas (Seeley & Morse 1976; Avitabile et al. 1978; Gambino et al. 1990; Oldroyd et al. 1994; Baum et al. 2005). Nevertheless, several attributes frequently reported for natural nests are consistent with the preferences exhibited by bees during experimental manipulations. For example, most natural nest cavities have a volume of 20-80 L, with an average volume of 40 L (Seeley & Morse 1976). Feral colonies often occupy cavities located 2 m or more above ground, with small (10-100 cm²), bottom-located entrances that frequently face in a southerly direction (Seeley & Morse 1976; Avitabile et al. 1978; Gambino et al. 1990; Oldroyd et al. 1994; Baum et al. 2005).

The preferences that honey bees exhibit for nest cavities convey strong survival advantages. Elevated cavities in trees provide protection from predators and are well insulated against cold, especially when cracks and crevices are sealed with propolis. Cavities with a volume of 30-40 L provide a space in which nest temperature can be maintained during the winter months, while simultaneously housing a sufficient amount of comb to store the huge honey reserves necessary for winter survival. Bottom-located entrances minimize convective heat loss, and in temperate climates southward-facing entrances receive more direct sunlight, which may help to heat colonies during the winter (Seeley 1985; McNally & Schneider 1996). A preference for previously occupied sites is also advantageous, because it results in the selection of sites that have been successful in the past, and the presence of old combs and propolis may reduce the costs of nest construction.

**The Combs:** The wax combs of a honey bee nest provide the substrate for virtually all colony activities, including brood rearing, food storage, queen production, and the many different social interactions that occur among nest mates. A feral European colony typically contains 4-8 combs that are attached to the tops and sides of the nest cavity. The combs hang parallel to one another and are separated by 3/8 of an inch, referred to as “bee space” (Fig. 1). This space enables bees to move easily between combs and cluster to maintain the internal nest temperatures needed for proper brood development and winter survival.

Honey bee combs are truly “organic,” in that they are created entirely by workers from wax scales secreted by their own bodies and shaped into hexagonal cells using their mandibles and legs. Two types of hexagonal cells are constructed: smaller cells, which are used for brood rearing and food storage, and larger cells (drone cells), which are used for raising drones (Fig. 2). Drone cells can also be used for food storage. A third type of cell, the queen cell, is usually built along the lower edges of combs and is used to raise virgin queens (Fig. 2). Queen cells lack the hexagonal pattern of worker and drones cells and instead have an elongated conical shape. Queen cells are constructed only during periods of queen production and the number built can range from 2-3 to several dozen. Unlike worker and drone cells, which are permanent parts of the combs that can be reused re-

![Fig. 2. The different types of cells that make up honey bee comb. The majority of comb consists of worker cells. Drone cells tend to be located at the margins of the comb. Queen cells are often constructed along the lower comb edges, and their presence indicates that a colony is preparing to swarm or replace a lost or failing queen. (photo courtesy of Randy Oliver)](image)
peatedly for years, queen cells are torn down by
workers after the virgin queens emerge.

Comb construction is expensive in terms of energy
and resources. It takes 6.25 kg of honey to produce 1
kg of comb. Most comb is built during a colony’s first
year and a fully developed nest contains about 1.2 kg
of comb. A colony consumes 60 kg of honey each
year. Thus, during the first year when a colony is
becoming established, it must devote at least 7.5 kg
(12.5%) of its total honey consumption to comb con-
struction, while simultaneously accumulating sufficient
food reserves to survive its first winter (Seeley
1995). Combs are a non-reclaimable resource. Bees
do not eat wax and after comb is built workers cannot
recycle the resources and direct them to other needs.
Yet, colonies must construct comb for proper growth
and development. It is therefore not surprising that
workers tightly regulate comb construction and care-
fully adjust building activity to changes in colony
conditions and the external foraging environment.
But, how do workers know when, how much, and

which type of comb to build?

Comb is constructed only when necessary and
colonies do not build all of their combs at once. When
a swarm settles in an empty cavity, it has an initial
burst of comb construction to initiate brood rearing
and food storage. It then adds to these combs in a se-
ries of pulses throughout the spring and summer, such
that by the end of its first season it has largely con-
structed its full complement of combs (Pratt 2004).
Colonies start comb construction when there is a high
level of nectar intake, but little or no empty comb
available for food storage. This ensures that new con-
struction is initiated only when the existing space has
been filled and additional space is needed to take ad-

cantage of a nectar flow. However, while both nectar
intake and comb fullness are required to start con-
struction, continued nectar intake alone is sufficient
to maintain building activity (Pratt 2004). This allows
colonies to build comb and store nectar throughout a
strong flow, even if construction outstrips intake such
that there is a temporary increase in empty space. In
this way colonies are less likely to miss opportunities
to amass the honey reserves necessary for winter sur-
avival.

Workers also carefully regulate the type of cells
constructed. When newly settled in a nest cavity, a
swarm constructs only worker cells. This allows for
the rapid initiation of brood rearing and food storage
to develop the population size and food stores needed
for winter. In a mature nest, workers cells usually
make up 75-85% of the combs. Drone cells are con-

structed only when colonies become larger and more
established, and tend to be built along the edges of
combs (Fig. 2). The absolute amount of drone comb
is highly variable among different nests and changes
as a colony ages and grows. Nevertheless, the per-
centage of total comb area devoted to drone comb is
remarkably consistent among colonies. It averages
around 17% and rarely exceeds 25% of total comb
space (Seeley & Morse 1976). The amount of drone
comb built depends on how much already exists, and
the presence of drone comb and drone brood slow or
inhibit further drone cell construction. In this manner,
colonies can maintain a relatively constant proportion
of drone comb as they grow in size (Pratt 2004; Boes
2010).

Colonies show a distinct pattern of comb use (Fig.
3). Brood is concentrated in a spherical area in the
central regions of the combs, pollen tends to be stored
in a relatively narrow band of cells above and to the
sides of the brood area, and honey is stored in the
upper and peripheral regions of the combs (Fig. 3).
This spatial arrangement of the nest helps to organize
colony labor. The aggregation of brood in the center
concentrates nursing activity and facilitates the clus-
tering of workers necessary to warm the developing
bees. Food processing and storage occur in the more
peripheral parts of the nest. How does this impressive
nest organization come about? There is no central
control in a honey bee colony and no one individual
has global knowledge of the nest. Rather, each indi-

cidual bee operates on only local information using

Fig. 3. The typical arrangement of the con-
tents of honey bee combs. The brood area is
located in the central region of the nest.
Pollen is stored in a band of cells above the
brood. Honey is stored at the sides and top
of the combs. (photo courtesy of Susan
Cobey)
simple “rules of thumb” for what to do. Queens have a tendency to lay eggs in cells next to those that already contain brood, which results in a clustering of larva (Seeley 1995). Workers can store food anywhere in the nest, but have a tendency to place pollen in cells near brood and nectar in cells at the top of the nest (Johnson & Baker 2007). Food stores are shifted and rearranged as the brood area grows, ultimately resulting in the pattern of organization characteristic of a mature nest. Thus, the complex organization of colony contents emerges from a decentralized system based on simple innate guidelines, and does not require that individuals possess a “master plan” for the entire nest (Camazine 1991).

The extent to which European colonies devote comb space to food storage and brood rearing is tightly linked to their survival strategy in temperate climates. Of the 23,500 cm² of comb that make up a mature nest, 55% is used for honey and pollen storage, 25% for brood rearing, and 20% is empty (Seeley & Morse 1976). The large amount of comb space devoted to food storage underscores the need to accumulate vast honey reserves for winter survival. Although temperate climate colonies emphasize food storage over brood rearing, the approximately 6000 cm² devoted to the brood area enables colonies to maintain a worker population of 18,000-20,000 bees. This, in turn, promotes the growth of the large foraging force needed to gather food reserves and helps to ensure that a sufficient number of workers will survive through the winter to maintain nest temperature and initiate brood rearing the following year.

**Colony Density and Nest Aggregations:** The density and distribution of wild colonies in natural habitats have been studied in many regions of the world, including the U.S. (Taber 1971; Wenner 1989; Visscher & Seeley 1982; Baum et al. 2005; 2008), Central and South America (Borcher & Roubik 1987; Otis 1991; Ratnieks et al. 1991), Russia (Galton 1971), Australia (Oldroyd et al. 1994; 1995; 1997) and Botswana, Africa (Schneider & Blyther 1988; McNally & Schneider 1996). Colony densities range from less than 1 to more than 100 nests per km². Densities vary with colony survival and the availability of nest cavities in different regions. The manner in which colonies are distributed throughout the environment is also highly variable, and probably reflects the distribution of available nest sites. Nevertheless, when cavities are abundant, honey bee nests are often aggregated. Colonies can occur in clusters separated from one another by only 100-200 m, and sometimes several nests can occur in the same tree separated by only vertical distance (Oldroyd et al. 1995; 1997; McNally & Schneider 1996).

The reasons for this spatial clumping of nests are unclear. Clusters of colonies could form if swarms have short dispersal distances and settle near the parental nest. However, this seems unlikely. Although some swarms may prefer nearby cavities (Seeley & Morse 1978; Schmidt 1995), many travel 2-5 km from the natal nest (Schneider 1995). Short dispersal distances should result in clusters of related colonies that settle near the parental hive. However, genetic analysis has revealed that relatedness among clustered colonies can be low (Oldroyd et al. 1995). Scout bees searching for nest cavities are attracted to Nasonov pheromone and prefer previously occupied cavities, which they may locate partly by odor (Seeley & Morse 1978; Schmidt 1994). Thus, clusters of colonies may form because swarms are attracted to the odors of existing colonies and select nearby nest cavities, provided any are available.

Regardless of the reasons for clumping, colonies may benefit from clustering by improving mating efficiency. To mate successfully, a virgin queen must leave the nest, locate a drone congregation area, mate with unrelated drones (because inbreeding reduces brood survival), and then navigate back home. The farther a queen has to fly and the longer she must remain in the open, the greater her risk of predation and not finding her way back to the nest. Aggregations of unrelated colonies could therefore promote mating success by reducing both inbreeding and the duration of mating flights, provided that drones congregate near the nest clusters (Oldroyd et al. 1995; McNally & Schneider 1996).

**Nest Architecture and Beekeeping:** Many aspects of our bee management practices are based on our knowledge of honey bee nesting habits. A standard Langstroth hive body has a bottom entrance and a volume of about 45L, similar to the 40 L of natural nest cavities. The discovery of bee space was essential for developing moveable frames, because it allows us to space combs inside a hive to prevent workers from building cross connections of wax which interfere with easy removal. An understanding of cell construction has made possible the development of wax foundation, which ensures that combs are built with the proper orientation inside the
wooden frames. The use of queen excluders and honey supers allows for the easy harvesting of honey because they take advantage of the natural tendency of workers to store nectar above the brood area. The natural tendency of colonies to cluster may facilitate our ability to maintain dense aggregations of hives in our bee yards. Thus, much of our beekeeping is designed around the natural nesting biology of honey bees. Continued studies of feral nests and the natural distributions of colonies should promote improved management methods.

THE BIOLOGY AND BEHAVIOR OF HONEY BEE CASTES

Gender and Development: A honey bee colony contains three castes: the sterile female workers, the fertile female queen, and the drones (males) (Fig. 4). Gender in honey bees is determined by haplodiploidy, in which fertilized (diploid) eggs develop into females and unfertilized (haploid) eggs develop into males. The haplodiploid method of sex determination is based on a single gene, the complementary sex determining (csd) gene (Heimpie & de Boer 2008; Gempe et al.

![Diagram showing the determination of gender and caste in honey bees.](image)

Fig. 4. The determination of gender and caste in honey bees.)
A fertilized, diploid egg contains two csd alleles, one inherited from the queen mother and the other from the drone father. If a fertilized egg is heterozygous for the csd gene (has two different csd alleles), then it will develop into a female (Fig. 4). If an egg is unfertilized, then it is hemizygous for the csd gene (has only a single allele received from the queen mother) and it will develop into a male (Fig. 4). Thus, gender depends solely upon whether an individual has two different alleles or only a single allele for this one particular gene. This is why worker-laid eggs develop into drones. Although some workers can activate their ovaries and produce eggs, they can never mate. As a result, they can lay only unfertilized, haploid eggs that contain a single allele for the csd gene, and these eggs invariably develop into drones.

The csd gene can result in some developmental abnormalities. For example, it is possible for both a queen’s egg and a drone’s sperm to carry the same csd allele. The resulting fertilized egg will be homozygous for the csd gene (have two copies of the same csd allele) and will hatch into a diploid male larva (Fig. 4). Such “diploid drones” are eaten by workers shortly after hatching. If experimentally removed from a colony and reared in the laboratory, a diploid male larva will grow into an adult drone, but it is sterile. Diploid drones contribute nothing to colony reproduction and are a drain on colony resources. Thus, by cannibalizing diploid male larvae, workers ensure that colonies raise only fertile, haploid drones and don’t waste time and energy producing infertile, diploid males. Another developmental oddity that involves gender occurs in the Cape honey bee, *Apis mellifera capensis*. Whereas workers of other honey bee races can lay only unfertilized haploid eggs that give rise to drones, Cape honey bee workers can lay unfertilized eggs that develop into females (Neumann & Moritz 2002).

A fertilized egg that is heterozygous for the csd gene has the potential to develop into either a fertile queen or a sterile worker (Fig. 4). What a female larva ultimately becomes depends on the type and amount of food it receives during its larval development. Workers feed larvae glandular secretions called “brood food,” which consist of protein-rich substances produced by the hypopharyngeal glands and mandibular glands. If a larva receives large amounts of royal jelly (mandibular gland secretions plus sugars) throughout its developmental period, it will become a queen. If that same larva instead receives smaller amounts of food that consist primarily of hypopharyngeal gland secretions, plus pollen and honey during the latter part of its development, it will become a worker. A female larva has the potential to become either a queen or worker during the first three days of its development. By the fourth day, its developmental pathway has been set.

The influence of nutrition on the caste determination of workers and queens has been known for almost two centuries (Huber 1821). However, we have only recently begun to understand the details of this system. During the first three days of development, when a larva has the potential to become either a worker or a queen, a wide variety of gene programs become active. If receiving primarily hypopharyngeal gland secretions, a larva maintains these initial gene expression profiles and develops into a worker. In contrast, if receiving large amounts of royal jelly, many of the initially expressed genes are down-regulated and a distinct set of caste-related genes is turned on, resulting in the development of a queen. Several of the genes that are overexpressed in queen-destined larvae code for metabolic enzymes that contribute to the greater growth rate of queens, and may influence cellular responses to hormones (Evans & Wheeler 1999; 2000). In particular, queen larvae have much higher levels of expression of several genes associated with the insulin signaling pathway (Wheeler et al. 2006), which is a genetic mechanism that plays a central role in integrating nutrition, metabolism and growth in a wide variety of animals. This ancient genetic system, which is inherently responsive to nutrition in many different species, may have been co-opted during honey bee evolution and incorporated into a nutrition-based mechanism of caste determination. Caste differentiation is also associated with differences in juvenile hormone (JH) levels during the first 2-3 days of development. The level of JH in a developing larva depends upon the type and amount of food it receives, and queen larvae have higher levels than worker larvae. The activity of the insulin signaling genes and levels of JH follow similar time courses during queen development. Although the precise relationship between these systems is not fully understood, the available data suggest there is a nutrition-mediated link between genetic and hormonal pathways that determines caste (Wheeler et al. 2006). Recently, it was demonstrated that royal jelly contains a specific compound, royalactin, which induces the differentiation of honey bee larvae into queens (Kamakura 2011).

Regardless of a honey bee’s caste, all individuals pass through the same four stages of development: egg, larva, pupa and adult (Fig. 5). Three days after an egg is laid in a cell, it hatches into a maggot-like
Fig. 5. The developmental stages of honey bees.

larva that feeds on the brood food supplied by workers and grows in size by undergoing a series of molts. During the last larval stage, workers cap the cell with wax and the larva spins a cocoon. The final larval stage undergoes a metamorphosis and molts into a pupa. The pupa undergoes a final molt, during which the bee completes its metamorphosis into an adult. The adult then chews through the wax capping and emerges from its cell. The total developmental time from egg to adult averages 16 days for queens, 21 days for workers and 24 days for drones. Development of the adult bee continues for the next few days after emergence, during which the exoskeleton hardens, and additional feeding is required for glandular and fat body development.

Life span differs dramatically among the different castes. Workers typically live only 4-6 weeks during the spring and summer, but can live for 4-5 months during the winter. The brief lifespan of spring and summer workers is a consequence of the energetic demands and predation risks associated with foraging outside the nest. Drones usually live for 3-5 weeks, although their lifespan is highly variable because a drone dies when it ejaculates. Thus, the longer-lived drones are those that have been unsuccessful at mating with virgin queens. Drones typically survive for only a single summer, because workers force them out of the nest in the fall. In contrast to workers and drones, queens typically live for 1-3 years, and life spans in excess of 8 years have been reported (Winston 1992a). The dramatic differences in the lifespan of queens and workers is a remarkable biological phenomenon, because the same fertilized egg has the potential to develop into a worker that rarely lives more than 35 days or a queen that can live 10-80 times longer! The vastly different lifespan of workers and queens provides an excellent opportunity for studying the genetic mechanisms that control the aging process, and in fact, honey bees have become a model organism for understanding aging in all animals, including humans (Rueppell 2008).

The Behavior of the Queen: The queen is usually the sole egg layer in a colony and the only female that can mate and lay fertilized eggs. A queen lays up to 1000-1500 eggs each day during the spring and summer months, depending upon the availability of comb space. Before a queen lays an egg, she inspects a cell by inserting her head and forelegs. This inspection process enables her to assess if she will lay in a worker or drone cell, and the angle of her abdomen during oviposition may also contribute to this determination (Winston 1992a). If laying in a worker cell, the queen releases sperm from her spermatheca as the eggs travels down the oviduct, resulting in a fertilized diploid egg that develops into a worker. If laying in a drone cell, the queen withholds sperm as the egg moves down the oviduct, resulting in an unfertilized haploid egg that becomes a male. The queen also fertilizes eggs that she lays in queen cells. Colony survival and strength are dependent upon the continued laying of the queen. If the queen leaves with a swarm, dies or begins to fail, workers initiate the queen replacement process by constructing queen cells and rearing virgin queens.

Queens are highly polyandrous, meaning that they mate with multiple different males. Indeed, the honey bee queen is one of the most polyandrous animals on earth. During the first week of a queen’s life, she takes a series of mating flights and copulates with an average of 12 different drones (Tarpy & Nielson 2000). She then stores a portion of the sperm in her spermatheca and uses it to fertilize all the eggs she lays throughout her lifetime without ever mating again. Polyandry is relatively rare in the animal kingdom, because a female usually receives enough sperm from one male to fertilize all of her eggs.
eggs, and mating with additional males incurs energetic costs and increases the risk of attracting predators and contracting diseases. Why then have honey bee queens evolved such extreme promiscuity?

By mating with multiple males, queens increase the genetic diversity of their offspring. This increased diversity may have two main advantages. First, it decreases the likelihood that a queen will produce diploid drones (Tarpy & Page 2002). There are a large number of csd alleles in the honey bee population. Consequently, most of the drones that mate with a queen will carry an allele different from her own. Most of the queen’s fertilized eggs will therefore be heterozygous for the csd gene and give rise to viable female workers rather than sterile diploid drones. Second, increased genetic diversity among workers promotes colony fitness and survival. Experiments in which queens have been instrumentally inseminated with equal volumes of semen from one versus multiple (10-15) drones have shown that genetically diverse colonies have less disease, are better able to maintain nest temperature, have greater recruitment and foraging activity, gather food over larger areas of the environment, have larger worker populations, build more comb, store more food, and are more likely to survive the winter (Matilla & Seeley 2007; 2010; Mattila et al. 2007; Oldroyd & Fewell 2007; Tarpy & Seeley 2006; Seeley & Tarpy 2007). Workers may prefer queens that have mated with a greater number of drones. Compared to queens inseminated with a single drone, multiple-inseminated queens show different patterns of gene expression in their brains, produce different pheromone profiles, and receive more attention from workers (Richard et al. 2007). Although the function of this preference is unclear, it could contribute to colony success by promoting queens that will produce a genetically diverse workforce.

Other than laying eggs, the queen does no physical labor in the colony. Nevertheless, she is the single most important individual for influencing colony organization, and she exerts her influence by producing pheromones (Fig. 6). The main pheromone signal produced by queens is called queen mandibular pheromone, or QMP. It is actually a blend of five different pheromones produced by the mandibular glands. Four additional pheromones, three of which are produced in glands other than the mandibular glands, work synergistically with QMP (Pankiw 2004; Slessor et al. 2005). The entire 9+ pheromone blend is called “queen retinue pheromone” (QRP), because it causes young workers to form a court around the queen, and antennate, lick and groom her (Slessor et al. 2005; Le Conte & Hefetz 2008)(Fig. 6). QRP and the retinue response it elicits are essential to the proper health and vitality of the queen. Furthermore, the queen uses QRP to signal her presence and influence colony reproduction and worker physiology (Slessor et al. 2005; Strauss et al. 2008). Workers remove QRP when interacting with the queen and then distribute it throughout the colony (Seeley 1979; Naumann et al. 1991). A major influence of this continuous distribution of QRP is that it inhibits workers from rearing new queens. This is why when a colony becomes very crowded (a condition that often initiates swarming preparations), workers begin to build around the queen, and antennate, lick and groom her (Slessor et al. 2005; Le Conte & Hefetz 2008)(Fig. 6). QRP and the retinue response it elicits are essential to the proper health and vitality of the queen. Furthermore, the queen uses QRP to signal her presence and influence colony reproduction and worker physiology (Slessor et al. 2005; Strauss et al. 2008). Workers remove QRP when interacting with the queen and then distribute it throughout the colony (Seeley 1979; Naumann et al. 1991). A major influence of this continuous distribution of QRP is that it inhibits workers from rearing new queens. This is why when a colony becomes very crowded (a condition that often initiates swarming preparations), workers begin to build

Fig. 6. The honey bee queen and her attendants. The queen produces QRP (queen retinue pheromone) which contains QMP and at least 4 additional pheromones. QRP elicits retinue behavior from younger workers, who touch, lick and groom the queen. In the process they acquire QMP and the other queen pheromones, which are then distributed throughout the colony. QRP and QMP influence many aspects of worker activity, including foraging, comb building, the age-based division of labor, worker ovary activation and queen cell construction.
queen cells. In crowded conditions, queen attendants cannot spread QRP quickly and effectively throughout the colony and workers lose the inhibition for queen rearing. Absence of QRP, which indicates the loss of the queen, results in the onset of queen rearing in only a few hours. Additionally, the distribution of QMP inhibits the development of worker ovaries. Pheromones produced by the brood also suppress worker ovarian development (Le Conte & Hefetz 2008). In this manner, when a colony has a healthy laying queen and large areas of developing larvae, few or no workers activate their ovaries and attempt to lay their own eggs. However, if a colony loses its queen and remains queenless until there are no developing larvae, then the long-term absence of QMP and brood pheromone result in some workers developing active ovaries and laying unfertilized eggs that develop into drones (Slessor et al. 2005; Strauss et al. 2008).

In addition to their effects on queen rearing and worker ovarian development, QRP and QMP influence many other aspects of colony life (reviewed in Slessor et al. 2005; Le Conte & Hefetz 2008). Recent work has revealed that exposure to QMP alters gene expression patterns in the brains of worker bees, which may affect many aspects of their behavior and development (Grozinger et al. 2003). For example, queen pheromone influences comb construction and food collection. Colonies with a queen have greater comb building and foraging activity compared to those that are queenless. QMP affects the production of hormones in workers that regulate the age-based division of labor (Le Conte & Hefetz 2008). QMP also influences worker learning (Vergoz et al. 2007). Certain compounds in QMP are involved in swarm settling, and still others are components of the queen’s sex pheromone, which attract drones to her during mating flights.

Queens also produce an egg-marking signal, which may be associated with the Dufour’s gland (Oldroyd et al. 2002; Le Conte & Hefetz 2008). Both queens and laying workers produce compounds that may be applied to eggs during oviposition. However, the egg-marking signal of the queen contains several compounds that laying workers lack, resulting in a distinctive queen signal applied to each egg she lays. Worker use this signal to distinguish between queen-laid and worker-laid eggs, and “police” worker oviposition by eating virtually all eggs produced by workers (Fig. 7). Additionally, workers will physically attack other workers that possess developed ovaries, which further inhibits laying activity (Schneider & McNally 1991). In combination, worker policing and aggression result in the queen producing 99.99% of all drones raised in a colony (Visscher 1989). Because worker laying results in reproductive competition that disrupts normal colony function, the queen’s egg-marking signal helps to ensure the cohesion and cooperation that are necessary for colony survival (Ratnieks et al. 2006).

The Behavior of Workers: Sterile workers perform all of the labor in a colony, including cell cleaning, brood rearing, queen care, comb construction, nest maintenance, food processing, nest hygiene, foraging and colony defense. However, not every worker performs all of these activities. Rather, honey bees have an elaborate division of labor, in which tasks are divided among different worker groups, resulting in highly efficient colony organization. But, how does an individual worker decide which tasks to perform and how long to perform them? At any given moment in time, a worker inside the nest is exposed to stimuli emanating from the brood, food stores, the queen, returning foragers, and the combs, yet she ignores much of this information and pays attention to only a portion of the stimuli that are associated with a few particular tasks. How individual workers formulate task decisions is one of the most studied aspects of
honey bee biology, and this research has greatly advanced our understanding of the flexibility and adaptability of the honey bee social system.

At least three main factors influence an individual worker’s task decisions: her age, genetics, and interactions with the nest and nest mates. Honey bees have an age-influenced division of labor in which a worker progresses through a series of tasks as she gets older. In general, a worker performs tasks inside the nest when she is young and then switches to foraging outside the nest when she is older (Fig. 8). Although there is tremendous variation in the ages at which workers perform specific tasks (Fig. 8), bees show the following general progression of behavior. During the first few days after emergence, workers primarily engage in cell cleaning and brood capping. When 2-11 days old, they act as “nurse bees” and concentrate on brood care and attending the queen. At 12-20 days of age, workers are “middle aged” and engage in food storage and processing, nest maintenance, comb construction, and toward the end of this period they function as guards. Finally, when around 19-21 days old, workers make the transition to foraging and begin spending increasing amounts of time gathering pollen, nectar, water and propolis from the external environment (Winston 1987).

These behavioral transitions are associated with complex suites of genetic and physiological changes. Nurse bees and foragers show distinct patterns of gene expression in their brains, and many of the genes that are up-regulated in nurses are down-regulated in foragers, and vice versa (Whitfield et al. 2004). The different patterns of gene expression may influence a worker’s response thresholds, such that younger bees are more responsive to the stimuli that trigger brood care, whereas older bees are sensitive to foraging stimuli. The different patterns of gene expression are also associated with differences in glandular development. Younger bees have active hypopharyngeal and mandibular glands for the production of brood food. As they reach middle age, these glands regress and their wax glands and alarmpheromone glands become fully active, coincident with the transition to comb construction and guarding. All of these glands regress with the transition to foraging (Winston 1987; 1992a). The age-influenced division of labor is regulated by juvenile hormone (JH). JH levels are low when a worker first emerges and increase steadily with age, reaching a high and relatively constant level at the transition to foraging. Changing JH levels are associated with changes in gene expression and glandular development, and thus may drive a worker’s progression through the series of tasks that are performed during its lifetime. The importance of JH in determining worker behavior can be shown experimentally by treating young workers with extra JH or a JH “mimic.” Such bees become “precocious foragers,” and begin food collection when only 8-10 days old. Precocious foragers show patterns of gene expression and glandular regression similar to those found in older, normal-aged foragers, even though they are chronologically the age of nurse bees (Whitfield et al. 2004).

JH results in an extremely flexible division of labor that allows a colony to respond quickly and adaptively to changes in social and environmental conditions. For example, both the queen and older foragers produce a pheromone, ethyl oleate, which slows the rate of JH biosynthesis in young workers, resulting in a normal increase in JH levels and the typical age-based progression through tasks (Le Conte & Hefetz 2008). Older workers produce ethyl oleate in their crops and pass it to younger bees during trophallaxis (mouth-to-mouth exchange of liquid food). If young workers are experimentally prevented from contacting older bees, or if there is a sudden loss of large numbers of foragers in the field such that interactions with older bees are reduced, then the JH levels of some young workers increase rapidly, resulting in the development of precocious foragers (Leoncini et al. 2004). In this manner, colonies can quickly replace a diminished foraging force and continue harvesting the resources necessary for colony growth and winter survival.

Changing JH levels can also cause older bees to revert to brood care. Such a situation often happens during swarming. By the time a swarm selects a new nest cavity, builds comb and has large amounts of developing larvae, many of the workers are past the age typically associated with nursing behavior. In response to the increased needs for brood care, the JH levels of some older, foraging-age workers decline. As a result, their hypopharyngeal glands redevelop and they become over-aged nurses. The reversion to brood care is also associated with changing patterns of gene expression in the brain. Over-aged nurses develop gene expression patterns similar to young nurses, even though previously their gene expression patterns were characteristic of older foragers (Whitfield et al. 2004).

In addition to age, a worker’s task decisions are also influenced by its genetics. Because honey bee queens are polyandrous and mate with an average of
Fig. 9. Some of the worker interactions and communication signals that influence task decisions. A: *Patrolling and cell inspection*, which expose workers to comb contents and convey information about colony conditions; B: *Trophallaxis*, which exchanges food and pheromones and provides information about colony energy status and food needs; C: *Brood pheromone*, which is produced by developing larvae and triggers nursing behavior, stimulates pollen foraging, and works with QMP to inhibit worker ovarian development and slow the rate of JH increase; D: *Alarm pheromone*, which is released during stinging and recruits other workers to defend the colony; E: *Nasonov pheromone*, which is released from a gland at the tip of the abdomen and causes worker aggregate; F: *Worker piping*: which consist of a pulsed sound that causes bees to warm their flight muscles for flight; G: *Vibration signal*, which enhances information acquisition in workers of all ages by increasing patrolling, cell inspections and trophallaxis, which, in turn, increases the performance of many different tasks; H: *Waggle dance*, which conveys information about the location of profitable food sites and stimulate foraging behavior in older bees; I: *Tremble dance*, which stimulates younger bees to become food receivers and causes foragers to stop performing waggle dances.
12 different drones, colonies contain workers of multiple patrilines that all share the same mother but have different fathers. Genetic differences among the drones that sire the different patrilines result in differences among workers in their tendencies to engage in particular tasks and the age at which they begin performing them. Differences in behavior between patrilines have been demonstrated for brood care, queen rearing, nest maintenance, guarding, communication behavior, foraging distances, and the tendency to collect pollen vs. nectar (Robinson & Huang 1998; Arnold et al. 2002; Chapman et al. 2007; Oldroyd & Thompson 2007). There is also pronounced behavioral variability among workers within the same patriline, which may arise from individual experience and genetic differences inherited from the queen (Duong & Schneider 2008). Inter- and intra-patriline variability in task performance allow for fine-grained, smoother adjustments in labor allocations and a more resilient system of division of labor, which contributes to increased colony success (Oldroyd & Fewell 2007; Oldroyd & Thompson 2007; Matilla & Seeley 2007; Duong & Schneider 2008).

While age and genetics provide a general framework for a worker’s tendency to perform particular tasks, its immediate task decisions are often determined by its interactions with the nest and nest mates. Workers spend much of their time “patrolling,” in which they meander over large areas of the nest and frequently inspect cells (Johnson 2008). Patrolling and cell inspection expose workers to information about colony food stores and brood-rearing activity that influence task decisions (Fewell & Winston 1992; 1996; Dreher & Tarpy 2000; Pankiw 2004)(Fig. 9). Workers also frequently engage in trophallaxis with one another (Fig. 9). Trophallaxis distributes food and pheromones among nest mates, and is an important means of acquiring information about colony food needs that affects foraging and brood care decisions (Weidenmüller and Tautz 2002; Grüter et al., 2006; De Marco and Farina 2001; 2003; De Marco 2006).

Honey bee workers and larvae produce a wide variety of pheromone signals that influence task performance. Brood pheromone is a chemical communication signal produced by the salivary glands of larvae (Fig. 9). It contains 10 components that stimulate a variety of tasks, including brood care and cell capping in younger workers, and pollen foraging in older bees (Pankiw 2004; Le Conte & Hefetz 2008). Brood pheromone also works in conjunction with QMP to inhibit worker ovarian development and slow the rate of JH increase in young workers, so that workers remain nurse bees longer. Alarm pheromone is produced in the sting gland of workers (Fig. 9). It is released when a worker stings and recruits other bees to defend the colony, which can quickly mount a group attack that drives away predators. Workers also produce Nasonov pheromone, which is released from a gland at the tip of the abdomen. Nasonov pheromone is an attractant that is released at the hive entrance to help workers find the nest and during swarming to facilitate the formation of the swarm cluster (Schmidt 1994).

Workers also produce several tactile communication signals that influence task decisions. The grooming dance consists of a worker moving its body jerkily and vigorously from side-to-side. It recruits other bees to groom the dancer, which can contribute to colony hygiene and also help to remove parasites. The waggle dance is used to communicate the distance and direction to profitable resources (Fig. 9). It is performed by successful foragers, who also produce sound signals in conjunction with the figure-8 pattern of the dance. The waggle dance is used to recruit workers to pollen and nectar sites and potential new nest cavities (Seeley 1995). Foragers are sensitive to minor changes in the quality of food sites and increase or decrease their waggle dancing accordingly, which helps adjust recruitment to changes in food-site profitability (Dyer 2002). During a given day, foragers may perform waggle dances for 12-15 food sites scattered over areas of up to 100 km² (Visscher & Seeley 1982; Schneider 1989). In this manner, colonies can monitor food availability over vast areas while focusing recruitment on the most profitable sites (Seeley 1995; Dyer 2002).

Another tactile signal that influences worker behavior is the vibration signal (sometimes called the shaking signal), which consists of a worker rapidly vibrating her body dorso-ventrally for 1-2 s while grasping a recipient with her legs (Fig. 9). The vibration signal is one of the most commonly occurring communication signals in honey bees and is associated with many aspects of colony life, including foraging, brood care, food processing, queen rearing, queen mating activity, and swarming (Schneider & Lewis 2004). The signal is usually produced by successful foragers who roam throughout large areas of the nest while performing vibration signals on hundreds of different workers. Workers of all ages can receive vibration signals, and signaling activity is preferentially directed toward less active bees (Lewis et al. 2002; Hyland et al. 2007). The signal causes a
non-specific increase in activity that enhances two main aspects of worker behavior. First, it increases the rate at which workers acquire information about colony needs by causing greater patrolling, cell inspection activity and trophallaxis (Cao et al. 2007; 2009). Second, it stimulates the increased performance of a wide variety of tasks, depending upon recipient age. Younger workers respond to the signal with increased brood care, food processing and nest maintenance, whereas older workers are more likely to contact the waggle dances and odor cues that stimulate foraging (Schneider & Lewis 2004; Hyland et al. 2007). Because the vibration signal is performed by foragers and exerts a general effect that increases information acquisition and task performance, it can help to adjust many aspects of colony activity simultaneously to the rate at which food enters the hive (Schneider & Lewis 2004).

A final tactile signal that influences worker behavior is the tremble dance, which consists of a worker holding her front pair of legs in the air, while moving her body side-to-side and up-and-down in a trembling or shivering movement that lasts approximately one second. She then turns her body in a different direction and continues her trembling movement, sometimes for up to an hour while meandering over the combs (Fig. 9). The tremble dance is performed by foragers that return to the nest with nectar and experience a long delay in unloading the nectar to receiver bees (Seeley 1995). When a nectar forager returns to the hive, she does not regurgitate her nectar into a cell herself. Rather, she transfers it to a receiver bee (usually a middle-age worker) through trophallaxis. The receiver bee then seeks out an empty cell to deposit the nectar. The speed with which a forager is unloaded by a receiver bee is related to the amount of stored honey in a colony. If a forager gets unloaded quickly, this means that receiver bees can rapidly find empty cells to regurgitate the nectar and run back to the dance floor to unload other incoming foragers. This in turn indicates that the colony has a shortage of nectar and needs food. In contrast, if a returning forager has to wait to get unloaded, this means that the receiver bees are busy looking for empty cells to deposit their current crop of nectar and aren’t available to unload additional foragers. This in turn indicates that the colony has large stores of honey and is developing a backlog for handling incoming nectar. If a forager is unloaded quickly (within 20 second of entering the hive), she is stimulated to perform waggle dances. In this manner, workers are recruited to visit the nectar site at a time when the colony needs food. In contrast, if a returning foraging has to wait more than 50 seconds to get unloaded, she will perform a tremble dance. The tremble dance has two effects: it causes younger workers to become receiver bees and it causes foragers to stop performing waggle dances and leave the dance floor. Tremble dancers also produce a sound called the “stop signal” which may further inhibit other foragers from waggle dancing. In this manner, new receiver bees are recruited to handle the backlog of incoming nectar and there is less recruitment to nectar sites at a time when the colony is struggling to handle the additional food. The relationship between unloading time, the waggle dance and the tremble dance helps to ensure that food intake and recruitment activity are carefully balanced with colony food needs (Seeley 1995).

In combination, the age-related division of labor, differences in genetic tendencies to perform tasks, and the complex system of pheromone and tactile communication signals result in a flexible, highly dynamic system of cooperative labor that enables colonies to adjust the number of workers performing different tasks to colony needs. This in turn results in a resilient social system that can respond quickly and efficiently to changes in both internal nest conditions and the external foraging environment. (The behavior of workers is examined in more detail in Chapter 8.)

**The Behavior of Drones:** The only function of drones is to mate with virgin queens away from the nest. Drones perform no labor in the colony and, as a result, there is a tendency to view them as inconsequential. Indeed, beekeepers often try to minimize or prevent drone production so colonies can focus on brood rearing and honey storage. However, drones are essential for reproduction and play an integral role in the natural history of honey bee colonies. Without drones, the female-based society of honey bees that is so admired by beekeepers and researchers would not exist.

The most common behavior of drones is sitting motionless inside the nest, often clustered together in groups. Young drones tend to congregate in the brood area of the nest where it is warmer, but then move to the periphery of the combs as they age. Worker interactions with drones consist primarily of trophallaxis and grooming. Trophallactic interactions are most common when drones are younger. The proteins received through these feedings are necessary for drones to develop their flight muscles and reach sexual maturity, which occurs around 12 days of age. As a drone ages, it is fed less by workers and obtains
more of its food by feeding directly from honey cells. In addition to trophallaxis and grooming, workers may also use communication signals to influence drone development and behavior. In particular, workers will perform vibration signals on drones. Drones of all ages can receive the signal, although sexually immature drones are vibrated at higher rates than sexually mature males (Boucher & Schneider 2009; Stout et al. 2011). Drones respond to the vibration signal by increasing the rates at which they move through the nest and the amount of time spent receiving trophallaxis and grooming from workers (Boucher & Schneider 2009). Because trophallaxis provides the proteins necessary for development, workers may use the signal to fine-tune the care drones receive, thereby contributing to greater colony reproductive output. Indeed, workers may direct vibration signals towards slightly less developed drones, which may help them acquire the care needed to address developmental deficiencies (Slone et al. 2011). Vibration signals performed on drones are relatively uncommon and the precise function is not well understood. Nevertheless, the signal may provide a valuable tool for investigating colony-level decisions for drone production.

Drones fly from the hive under two conditions. Sexually immature drones take orientation flights, which occur during the afternoon hours, last for 1-6 min, and help drones learn the location of their nest. After reaching sexual maturity, drones take 1-4 mating flights each afternoon, weather permitting. A mating flight lasts 20-30 min and usually occurs between 3-5 PM. Between mating flights, drones return to the nest for a few minutes, during which time they run excitedly on the combs, feed from honey cells, and may receive trophallaxis from workers. Workers have little influence on when drone flight occurs. Rather, drone flight activity is controlled by a circadian rhythm. As the day progresses, drones begin congregating near the nest entrance and then initiate flight based on their own internal time sense (Winston 1987; Boucher & Schneider 2009). The circadian control of drone flight activity was demonstrated by Koeniger et al. (1994), who cross-fostered drones of *A. cerana* in *A. koschevnikovi* colonies and drones of *A. koschevnikovi* in *A. cerana* colonies. The drones flew at their species-specific time and not the time characteristic of their host colony.

During a mating flight, drones fly to a drone congregation area (DCA) where they congregate in the air as a large swarm. The factors that cause drones to congregate at a particular site are unclear, but may involve visual landmarks such as stands of vegetation or geographical features. DCAs can be stable over time and used by drones for many years. Virgin queens fly through a DCA with their sting chamber open, emitting a pheromone (a component of QMP) that attracts drones. Drones form a cone-shaped cluster behind the queen (a “drone comet”), and copulate with her one at a time. When a drone everts his penis into the queen’s reproductive tract, it paralyzes him and he is dragged behind the flying queen (Fig. 10).
When he ejaculates, his penis often separates from his body, which ultimately kills him. As a result, a drone can mate only once. The penis left behind in the queen’s mating chamber, along with mucus secretions deposited by the drone, is known as the “mating sign” (Fig. 10).

A colony can produce several thousand drones each year, only a few of which will successfully mate with virgin queens. Drones that are still alive in the fall are evicted from the colony by workers, whereupon they die from starvation, exposure, or predation. This reduces the number of individuals that must be supported by the winter honey reserves and increases the chance that a sufficient number of workers will survive to initiate brood rearing in late winter (Boes 2010).

**Honey Bee Castes and Beekeeping:** Knowledge of the development and behavior of honey bee castes has had a huge impact on beekeeping and bee management. An understanding of mating biology and behavior was essential for developing instrumental insemination of queens, breeding programs, and the creation of special genetic lines selected for traits such as pollen collection and disease resistance. An understanding of brood care and the nutritional requirements of the different castes has contributed to the development of queen-rearing programs and a wide variety of dietary supplements for stimulating colony growth. Knowledge of the genetic basis of foraging preferences and honey bee communication has enhanced our ability to use colonies in fields and orchards in a manner that maximizes pollination efficiency. Some of the most exciting and promising advances in bee management have developed from our growing understanding of the structure and function of honey bee pheromones and how these signals are spread throughout the nest. This area of research has resulted in the development of synthetic pheromones, such as QMP, brood pheromone, and Nasonov pheromone, which are commercially available and used to enhance foraging activity, promote colony development, and attract swarms. Now that the honey bee genome has been sequenced, our understanding of the genetic regulation of honey bee behavior is growing rapidly, which should yield a wide array of advances in beekeeping.

**THE ANNUAL COLONY CYCLE**

*The Colony in Winter:* For temperate-climate colonies, the annual colony cycle of growth and reproduction begins in the winter. At this time the surviving workers and the queen are clustered inside the nest living on the honey reserves accumulated during the previous spring and summer. Workers maintain a temperature inside the cluster of about 20 °C by contracting their flight muscles without moving the wings (Winston 1992a). The energy for heat production is supplied by the stored honey. However, colonies with large honey reserves can freeze to death if it becomes too cold for workers to move to the honey in the periphery of the combs.

There is little or no brood rearing during the coldest part of the winter and colonies reach their lowest population size as the winter progresses. However, in late winter the queen begins to lay and brood rearing commences. This requires that workers elevate the temperature to 34-35 °C inside the cluster around the brood. The energy and nutrients for winter brood rearing are supplied by the honey and pollen reserves accumulated during the previous summer, as well as by workers using the reserves stored in their fat bodies. It is unclear what triggers winter brood rearing, but it occurs even if colonies are buried under snow. Early initiation of brood rearing is critical to colony survival. Once it begins, colonies increase in size rapidly, such that when spring arrives there is a large work force to harvest the available pollen and nectar. This abundance of spring resources fuels continued, rapid colony growth, culminating in reproductive swarming.

**Swarming:** One of the most spectacular and mysterious aspects of honey bee behavior is swarming, the method of colony reproduction. During swarming, a large proportion of the workers and the old queen leave the natal nest in the “prime swarm,” which forms a cluster in nearby vegetation. Scout bees then fly from the cluster to search for new nest cavities and, after one has been selected, the entire swarm becomes airborne and moves *en masse* to the chosen site. Meanwhile, back in the old nest the remaining workers finish raising virgin queens, who may leave in smaller “afterswarms” or, more typically, battle among themselves to the death until there is a sole survivor. The surviving virgin queen then takes mating flights and becomes the new laying queen of the old nest. It is truly amazing to witness the explosive exodus of a swarm from the nest, the liftoff of a swarm cluster, and the “heat-seeking missile” relentlessness of battling virgin queens. Humans have been captivated by swarming for centuries, and swarm prevention remains one of the most important
management problems facing beekeepers worldwide. As a result, a huge amount of research has been devoted to swarming behavior. Yet, swarming remains poorly understood and we still do not fully comprehend what triggers swarming or how colonies make the complex social decisions that govern nest-site selection, swarm movement, and queen replacement.

The timing and size of swarms are critical for success. In temperate climates, most swarming occurs from late April-June. Spring swarming is essential, because only early swarms will have sufficient time to establish a nest and amass the food reserves necessary for winter survival. Swarms experience high mortality rates: never more than 24% survive until the following season and it is usually only the early swarms that make it through their first winter (Seeley and Visscher 1985; Winston 1992a). In contrast, established colonies that survive their first winter have an average lifespan of almost six years. Thus, one of the major hurdles in the honey bee colony lifecycle is the rapid establishment of a nest for first-winter survival; once established, survival increases dramatically, resulting in a long-lived social group. Many aspects of swarming behavior may reflect adaptations to cope with the high risks of swarm failure. For example, storing honey and pollen for winter brood rearing results in early population growth and spring swarming. Prime swarms and first afterswarms are typically large (16,000 and 11,500 workers, respectively) and larger swarms are better able to accumulate food reserves and survive. Swarm size declines with each subsequent afterswarm, and colonies pro-

![Fig. 11. During swarming, multiple virgin queens are raised in specially constructed queen cells. Workers interact with the developing queens by feeding and grooming them, incubating the cells, and performing vibration signals on sealed cells, all of which contribute to successful development. (photo courtesy of Randy Oliver)](image-url)
duce only as many after swarms as the brood and adult populations can support (Winston 1992a). Swarms usually contain large numbers of young bees, and workers engorge with honey and often begin producing wax scales before swarm departure. This allows for the rapid onset of comb construction and brood rearing upon arrival in the new nest cavity. The ability of some older workers to reduce their JH levels and revert to nursing behavior further helps to ensure brood rearing and rapid colony growth.

Swarming begins with the raising of new queens in specially constructed queen cells (Fig. 11). Despite many years of research, we still do not fully understand the factors that control the onset of queen rearing and swarm preparations. However, it is clear that swarming occurs only when several colony characteristics reach critical levels simultaneously. The initiation of queen rearing and swarm preparations involve a complex interaction between colony size, brood nest congestion, worker age structure, and a reduced transmission of QRP, which normally inhibits queen production by workers. As a colony becomes crowded, queen attendants are less able to distribute QRP, which removes the inhibition and allows for queen cell construction (see Chapter 10).

Workers may initiate as few as 2-4 and as many as several dozen queen cells during the queen-rearing process (Engels et al. 1993; Pettis et al. 1995; Schneider & DeGrandi-Hoffman 2002). Workers exhibit an array of behavioral interactions with queen cells that may influence successful development (Fig. 11). Queens may be initiated from larvae as old as 3 days, but those that are initiated from eggs or young larvae are more likely to develop to emergence than are those initiated from older larvae (Hatch et al. 1999). Workers continuously interact with developing queen larvae to groom and feed them, and there is a positive association between the rate of interaction and developmental success (Schneider & DeGrandi-Hoffman 2002). Workers also cluster on queen cells to incubate them, and incubation temperature strongly influences the likelihood that a queen will develop to emergence (DeGrandi-Hoffman et al. 1993; Schneider & DeGrandi-Hoffman 2002). Furthermore, workers will perform vibration signals on queen cells after they are sealed, and cells that are vibrated at higher rates are more likely to complete their development (Schneider & DeGrandi-Hoffman 2002). Workers may also use the vibration signal to influence the timing of virgin queen emergence (Schneider et al. 2001). Little is known about the factors that influence which larvae are selected by workers for queen rear-

![Fig. 12. Vibration signals performed per min on a laying queen in a colony during the 28 days preceding swarming. Signaling activity begins on the queen several weeks before swarm departure and often shows a peak in the final days before swarming. (figure provided by author)](image-url)
ing, or why workers feed, incubate and vibrate developing queens at different rates. Workers sometimes show a slight preference for rearing the queens they are more closely related to (Breed et al. 1994; Visscher 1998). However, most evidence suggests that workers focus their efforts on raising queens of higher quality, rather than queens with higher relatedness (Schneider & DeGrandi-Hoffman 2002; Tarpy & Gilley 2004). Indeed, workers often destroy about 50% of all queen cells before development is completed (Hatch et al. 1999; Schneider & DeGrandi-Hoffman 2002), which may act to “weed out” lower quality individuals and promote the rearing high-quality, rival queens. However, the factors that influence worker choices during queen rearing are poorly understood and more research is needed in this area to develop better queen-production programs and increase the acceptance and retention of introduced queens.

In addition to raising new queens, a colony must also prepare the laying queen to leave the nest with the swarm. An actively laying queen is too heavy for flight and must lose weight and reduce egg production before she can become airborne. Also, a laying queen normally pays little or no attention to the external environment, but her sensitivity to outside stimuli must increase if she is to be attracted out of the nest with the swarm. These changes in queen condition are essential, because if the laying queen fails to leave the old nest or travel to the new nest site, the swarming attempt will be interrupted or may fail entirely. Workers use at least three mechanisms to prepare laying queens for swarming. First, they reduce the rate at which they feed the queen through trophalaxis, which contributes to weight loss and may also reduce egg production. Workers never completely stop feeding the queen, nor does she completely stop laying eggs. This ensures that a continuous supply of eggs and young larvae will be available in the old nest for queen rearing, and facilitates the rapid initiation of brood rearing once the old queen arrives at the new nest. Second, workers perform vibration signals on the queen. Laying queens are vibrated throughout the 2-4 week period preceding swarming, and workers often begin performing the signal on queens several days, or even weeks, before queen cells are initiated (Fig. 12). Indeed, vibration signals performed on the laying queen are often the first indication that a colony has begun swarming preparations. Queens are vibrated at increasing, but variable, rates throughout the swarm-preparation period, and there is usually an increase in vibration activity during the final 1-2 days before swarm departure (Schneider 1991; Pierce et al. 2007). Laying queens respond to the vibration signal with increased rates of movement (Schneider 1991). This increased activity, in combination with reduced feeding from workers, results in a noticeable slimming of the queen that may help prepare her for flight. Vibrated queens also exhibit altered responses to a variety of stimuli, which may further help prepare them to leave the old nest (Schneider 1991; Pierce et al. 2007). Third, workers perform “piping” (Fig. 9) on the laying queen during the last few days of swarm preparations and there is always a dramatic increase in piping on the queen immediately before swarm departure (Pierce et al. 2007). Piping causes bees to warm their

Fig. 13. Monitoring a swarm on an observation stand. Such studies have revealed that house hunting and swarm movement involve at least 4 communication signals: the waggle dance, which is used to select a new nest cavity; worker piping, which causes bees to warn their flight muscles in preparation for flight; the buzz run, which is the final trigger for swarm liftoff, and the vibration signal, which enhances responsiveness to the other signals and helps coordinate a rapid, efficient liftoff and movement to the new nest site. (photo provided by author)
flight muscles in preparation for flight (Fig. 9). In combination, trophallaxis and the vibration signal may be used to gradually prepare the queen physiologically and behaviorally to leave the nest, whereas piping may be the signal to initiate flight. Workers also perform piping on one another during the final hour before swarm departure and produce “buzz runs” (a rapid running through the nest while buzzing the wings), which may be the final signal that triggers mass departure from the hive (Ritttschof & Seeley 2008; Rangel & Seeley 2008). Thus, workers possess a suite of communication signals to help coordinate the behavior of queens and workers during swarming.

Upon leaving the nest, the swarm quickly forms a beard-like cluster in nearby vegetation and then almost immediately begins “house hunting” to locate a new nest cavity. The house-hunting process involves a complex interaction of at least four different communication signals: the waggle dance, worker piping, the vibration signal, and the buzz run (Fig. 13). Scout bees that find a potential nest cavity return to the swarm and perform waggle dances on the surface of the cluster to communicate the distance and direction to the site (Fig. 9). Initially, many different sites are communicated, but eventually all waggle dance activity becomes focused on a single site, which represents the new nest cavity to which the swarm will move. How do bees achieve this remarkable consensus in nest site choice? Each scout bee performs waggle dances for her site for a certain amount of time, then leaves the swarm to re-visit the site, and then returns to dance again. On each consecutive return to the swarm, a scout dances for less time until eventually she stops completely. However, within a given bout of dancing, the vigor and duration of a scout’s dances vary with site quality. Better quality sites elicit more dancing for longer periods of time before the scout leaves the swarm, which recruits greater numbers of other bees to visit the site and perform their own dances. In contrast, poorer sites elicit less dancing and fewer bees are recruited to visit them and dance in return. The end result is that dancing and recruitment for lower quality sites dwindles, then ceases, and all dance activity becomes focused on the single site that is the best among those that have been discovered (Seeley 2003; Seeley et al. 2006; Visscher 2007).

After a particular nest cavity has been selected, the swarm begins preparing for liftoff and mass movement to the chosen site. Bees that have visited and danced for the chosen site begin to perform piping (Fig. 9). Piping activity builds steadily during the final 30-60 min before takeoff, reaching a peak at the moment of liftoff (Seeley & Tuutz 2001; Donahoe et al. 2003). In this manner, the workers that have the most complete knowledge of a new nest site inform the rest of the swarm to warm their flight muscles in preparation for takeoff (Visscher & Seeley 2007). Nest-site dancers and other workers also begin to perform piping on the queen, to ensure that she leaves with the swarm for the chosen site (Pierce et al. 2007). During liftoff preparations, there is also often a dramatic increase in vibration signal activity (Fig. 9). Vibrators begin to weave repeatedly into and out of the swarm cluster producing long series of signals on many different workers. Vibrated bees respond by increasing their rate of movement, which may enhance the likelihood that they will contact and respond to the other signals that orchestrate liftoff (Lewis & Schneider 2000). Vibration and piping activity build steadily and reach a crescendo, at which time the entire swarm is in motion and has a “roiling” appearance. Buzz-runs are then performed on the cluster, which is the final signal that triggers the mass liftoff of the entire swarm (Ritttschof & Seeley 2008). The importance of the vibration signal in the liftoff process was demonstrated by removing vibrators from swarms. Compared to swarms from which randomly selected, non-vibrating bees were removed, those from which vibrators were removed took 4-7 times longer to achieve liftoff, even though both swarm types had similar levels of waggle dancing.

Fig. 14. Virgin queens fighting. Queen fighting behavior is influenced by the production of “piping” (a loud, pulsed sound that may advertise fighting ability), and “spraying” (the ejection of gut fluid). Additionally, workers feed, harass and perform vibration signals on queens, and these interactions may be the primary factors for determining which virgin queen will ultimately inherit the nest. (photo courtesy of Ken Lorenzen)
and piping (Donahoe et al. 2003). Liftoff eventually occurred without vibration activity, but the signal was necessary for the process to happen quickly and efficiently. Taken together, these studies reveal that house hunting is a colony-level effort organized through a complex cascade of communication signals that result in the rapid relocation of thousands of bees and their queen to the best available nest cavity. Once inside the new cavity, the swarm quickly initiates comb construction and brood rearing, and exhibits increased levels of waggle dancing and vibration signal activity, which enhances the rapid colony growth and accumulation of food stores necessary for winter survival (Hyland et al. 2007).

While the swarm is engaged in house hunting, the remainder of the original colony finishes the rearing of virgin queens in the old nest. After the queens emerge, some may leave with afterswarms. However, given the survival risks experienced by swarms, virgin queens will usually experience greater benefits by inheriting the old nest with its fully constructed combs, large worker population, and food stores. As a result, virgin queens typically attempt to kill their rival sister queens and become the new laying queen of the old nest. Emerged virgin queens will attack sealed queen cells, chew a hole in the cell wall, and then sting their unemerged rivals to death. Emerged queens will also battle each other and attempt to sting one another to death (Fig. 14). The end result is a sole survivor who becomes the new laying queen of the colony. Thus, the outcome of queen replacement depends, in part, on fighting ability and virgin queens exhibit a variety of behaviors that influence fighting success. Virgin queens produce two types of piping sounds, which consist of long series of very loud, pulsed notes. The first type of queen piping, “tooting,” is produced by emerged queens. The function of tooting is unclear, but it may be a battle cry that advertizes a queen’s willingness and ability to fight. Virgin queens that produce tooting at higher rates kill more of their rivals and are more likely to become the new queen of the colony (Schneider et al. 2001). Tooting may also inhibit the emergence of queens still in their cells, which could give the caller more opportunities to eliminate her rivals before they can fight back. The second type of piping, “quacking,” is produced by queens still in their cells. Unemerged queens may quack in response to the tooting of an emerged queen; however, the function of quacking is unknown. Virgin queens also exhibit a behavior called “spraying,” in which they eject a fluid from their hindgut during fights (Tarpy & Fletcher 2003).

The function of spraying is unclear. However, the ejected fluid is highly attractive to workers who cluster tightly in sprayed areas, which may form a barrier of bodies that prevents the spraying queen from being attacked by her rival.

Despite the well-developed fighting ability of virgin queens, it is ultimately the workers who determine the final outcome of the queen-replacement process. Workers can interact with virgin queens, sometimes at extremely high rates, and these interactions influence a virgin queen’s emergence and fighting success, and determine her ultimate fate. Workers can prevent emergence by resealing the cell cap as a queen attempts to exit her cell, and perhaps by performing vibration signals on sealed queen cells (Schneider et al. 2001; Tarpy & Gilley 2004). The timing of a queen’s emergence can have a profound effect on her success. Queens that emerge early may have more opportunities to kill their unemerged rivals and inherit the nest (Schneider et al. 2001; Schneider & DeGrandi-Hoffman 2008). Workers may actually protect queens that are prevented from emerging, to ensure that a sufficient number survive to complete the requeening process (Schneider et al. 2001). Workers also chase, harass, and perform vibration signals on emerged queens, which may prevent or interrupt aggressive interactions and determine the victor in queen battles (Schneider et al. 2001; Schneider & DeGrandi-Hoffman 2003; 2008).

The degree to which workers interact with virgin queens depends upon whether afterswarms are produced. If afterswarms are not produced after the prime swarm leaves the nest, then the laying queen must be replaced as quickly as possible to minimize the interruption to brood rearing. Under these conditions, workers interact little with queens and allow early emerging queens to quickly kill their unemerged rivals. The end result is that the queen elimination process is completed in 24-48 hours and the first-emerging virgin queen almost always becomes the new queen of the colony. In contrast, if afterswarms are produced, several virgin queens must survive: one to leave with each afterswarm and one to inherit the old nest. In these circumstances workers interact with queens and queen cells at much higher rates and the queen elimination process takes 3-5 days to complete. When afterswarms are produced, a queen’s fate is not dependent upon her emergence order, but rather on her interactions with workers. In particular, queens that receive vibration signals at higher rates are more likely to survive and become laying queens (Schneider et al. 2001; Schneider &
The Honey Bee Colony: Life History

DeGrandi-Hoffman 2008). However, we know almost nothing about the characteristics of virgin queens that influence worker interactions and a queen’s ultimate fate.

**The Colony in Summer:** After a swarm has settled into a nest cavity, and after the old nest has a new laying queen, the remainder of the season is devoted to building up the worker populations and food reserves necessary for winter. A colony uses 15-30 kg of pollen and 60-80 kg of honey a year (Winston 1987). Harvesting these food stores requires a remarkable effort, involving over a million pollen foraging trips and four million nectar foraging trips. Furthermore, in temperate climates the harvesting of resources must be accomplished within a few months, and sometimes during only a few weeks during spring and summer (Seeley 1985). Foragers search for floral resources over huge areas of the environment, although most food collection occurs within 1-2 km of the nest (Visscher & Seeley 1982; Schneider 1989). The harvesting of food is facilitated by a highly efficient recruitment system based on the waggle dance (Fig. 9), which is used to communicate the location and quality of food sites and continuously redistribute recruits among available flower patches as profitability waxes and wanes over time. The end result is that a colony can monitored food availability over a vast area of up to 80-100 km², visit 15 or more flower patches each day, yet focus foraging effort on the most profitable and closest patches available (Visscher & Seeley 1982; Schneider 1989). The use of the vibration signal, the tremble dance, and pheromones (Fig. 9) further help to organize colony foraging and increase the chance that sufficient reserves will be collected for winter survival. Nevertheless, the amassing of honey reserves is one of the greatest challenges facing temperate climate honey bees, and many feral colonies starve to death during the winter (Seeley & Visscher 1985; Winston 1992a).

As autumn approaches, colonies reduce brood rearing and foraging and evict drones in preparation for winter. As the days shorten and the weather becomes colder, the workers form the winter cluster and consume the food reserves accumulated during spring and summer. If they survive, they then initiate the late-winter brood rearing that starts the next annual cycle.

**The Annual Colony Cycle and Beekeeping:** Many aspects of modern beekeeping are based on an understanding of the honey bee annual cycle of growth and reproduction. Knowledge of annual patterns of growth and food storage form the basis of many of our procedures for enhancing brood production through food supplements, determining the timing of honey harvest, and manipulating colonies to control swarming. An understanding of queen rearing and the queen replacement process forms the basis of commercial queen production programs and our ability to requeen our colonies each year. Our knowledge of the house-hunting process of honey bee swarms and the selection of nest cavities has contributed to the development of traps and pheromone lures that enable us to catch swarms for commercial and hobby beekeeping, as well as capture and remove unwanted swarms that threaten human welfare. Continued study of the honey bee annual cycle, particularly of swarming and queen replacement, will continue to yield results that improve our ability to manage and control this remarkable insect.

**Tropical Honey Bees**

The tropical races of *Apis mellifera* are adapted to the tropical and subtropical environments of the African continent. Unlike European honey bees, African races do not experience a prolonged winter and are less dependent upon large honey reserves for survival. However, they experience greater nest predation, which selects for greater swarming and reproduction rates (Schneider & Blyther 1988; Winston 1992b; McNally & Schneider 1996). As a result, although both European and African honey bees belong to the same species and have the same social structure, they exhibit pronounced differences in colony life histories and survival strategies. Comparisons of African and European bees therefore provide a powerful method for understanding the adaptability and evolution of honey bee social behavior. In the final section of this chapter, I summarize the life history differences of African vs. European bees and discuss how these differences reflect different colony survival strategies. I close with a discussion of the history and consequences of the African bee in the New World. I will focus on the African honey bee race, *A. m. scutellata*, which is the best studied of the African honey bees and the race that was introduced into South America in the 1950s and subsequently colonized much of the western hemisphere.

**Life Histories of African vs. European Bees**

Table 1 summarizes the major differences in the nesting biology and behavior of African and Euro-

Table 1. Comparisons of the different life history traits of feral African and European honey bee colonies. Data compiled from Seeley & Morse (1976); Winston et al. (1981); Visscher & Seeley (1982); Schneider & Blyther (1988) Ratnieks et al. (1991); Winston (1992b); McNally & Schneider (1996); Schneider & Hall (1997); DeGrandi-Hoffman et al. (1998).

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>African Honey Bees</th>
<th>European Honey Bees</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Nest Characteristics</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cavity types</td>
<td>Equal use of tree and ground cavities; exposed-comb nests common</td>
<td>Most often hollow trees, less often ground cavities; exposed-comb nests rare</td>
</tr>
<tr>
<td>Cavity entrance</td>
<td>Top-located; south-facing</td>
<td>Bottom-located; south-facing</td>
</tr>
<tr>
<td>Median cavity volume</td>
<td>17 L</td>
<td>45 L</td>
</tr>
<tr>
<td>Total comb area</td>
<td>4000-8000 cm²</td>
<td>23,400 cm²</td>
</tr>
<tr>
<td>-- % brood comb</td>
<td>50-80%</td>
<td>25%</td>
</tr>
<tr>
<td>-- % food comb</td>
<td>16-25%</td>
<td>55%</td>
</tr>
<tr>
<td>Colony Predation Rate</td>
<td>High (up to 48%/year)</td>
<td>Low</td>
</tr>
<tr>
<td>Foraging Characteristics</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Emphasize collection of:</td>
<td>pollen</td>
<td>nectar</td>
</tr>
<tr>
<td>Average (and median) foraging distance</td>
<td>1175m (430m)</td>
<td>2260m (1650m)</td>
</tr>
<tr>
<td>Colony foraging area</td>
<td>67 km²</td>
<td>113 km²</td>
</tr>
<tr>
<td>Colony Growth &amp; Movement</td>
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<td></td>
</tr>
<tr>
<td>Colony population size</td>
<td>6000-8000 workers</td>
<td>18,000-20,000 workers</td>
</tr>
<tr>
<td>Worker development time</td>
<td>18.5 days</td>
<td>21 days</td>
</tr>
<tr>
<td>Queen development time</td>
<td>14-15 days</td>
<td>15-16 days</td>
</tr>
<tr>
<td>Worker lifespan</td>
<td>12-18 days</td>
<td>20-35 days</td>
</tr>
<tr>
<td>Swarms/year</td>
<td>6-12</td>
<td>1-3</td>
</tr>
<tr>
<td>% colonies undergoing seasonal absconding</td>
<td>30-100%</td>
<td>0%</td>
</tr>
<tr>
<td>Colony Defensive Behavior</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reaction time</td>
<td>1-5 sec</td>
<td>&gt; 10 sec</td>
</tr>
<tr>
<td>Alarm pheromone production</td>
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<td>lower</td>
</tr>
<tr>
<td>Stings/min</td>
<td>80</td>
<td>10</td>
</tr>
</tbody>
</table>
pean honey bees. Compared to feral European colonies, feral African colonies tend to occur at greater densities, occupy smaller nest cavities that have bottom-located, south-facing entrances, and are more likely to build exposed-comb nests. Feral African colonies also maintain smaller worker populations, build a smaller amount of comb, store little food and devote the vast majority of comb space to brood rearing. African colonies harvest food from smaller areas of the environment, may have shorter average foraging distances to food sites, and emphasize pollen over nectar collection.

These differences reflect the different survival strategies the honey bee races have evolved in their different environments. As adaptations for winter survival, European colonies occupy large well-insulated cavities that prevent heat loss, build a large amount of comb to foster the large worker populations and food stores necessary for overwintering, and emphasize nectar collection to build up large honey reserves. In contrast, African honey bees do not experience a prolonged winter and can often forage year-round (Schneider & McNally 1992b), which lessens the need to amass large honey reserves and allows colonies to build smaller amounts of comb and occupy smaller cavities. The greater predation rates experienced by African colonies selects for high reproduction through swarming, which requires a greater emphasis on brood rearing and colony growth, which in turn necessitates a greater emphasis on pollen collection to provide the nutrients for increased brood production. African workers develop faster than European workers, which also enhances rapid colony growth and higher swarming rates (Table 1). More frequent swarming keeps colonies smaller, which further contributes to the occupation of smaller cavities and the construction of less comb. The use of nest cavities with top-located, south-facing entrances may help prevent overheating in tropical environments, because top-located entrances facilitate convective heat loss and in the southern hemisphere south-facing entrances receive less direct sunlight. Thus, relatively subtle differences in nest cavity preferences, comb use patterns, foraging behavior and worker development have enabled the basic social system of Apis mellifera to become modified for different survival strategies adapted to dramatically different environments.

African and European colonies also differ in their annual colony cycles, especially with respect to swarming and absconding (nest abandonment). Whereas European colonies must swarm during the spring to facilitate colony establishment and winter survival, the prolonged foraging season and continued brood production of African colonies allows for more extensive swarming. Whereas European colonies typically produce only 1-3 swarms per year, African colonies can produce 6-12 swarms in the

Fig. 15. The migration dance of the African honey bee, Apis mellifera scutellata. The dance differs from the waggle dances used in foraging in that the waggle runs are of very long durations (60 s or longer), they lack the "figure 8" pattern of typical dancing, and workers who follow the dances do not leave the hive to investigate the indicated site. The migration dance may help to gradually prepare the entire colony for long-distance movement and determine the route of travel. (figure provided by author)
same amount of time and may have several swarming seasons during the year (Table 1).

European and African bees differ dramatically in their tendency to engage in absconding, which involves an entire colony abandoning a nest and relocating to a new area. Both swarming and absconding involve the formation and movement of swarm clusters. However, absconding is not a reproductive process and does not involve colony fission or the rearing of new queens. Whereas European colonies rarely abscond, African honey bees are notorious for their tendency to abandon a nest. African bees exhibit two types of absconding, disturbance-induced absconding and seasonal absconding. Disturbance-induced absconding can occur at any time of the year in response to a sudden deterioration in nest-site quality caused by predator attacks, ant invasions, and overheating. Seasonal absconding occurs during specific times of the year in response to deteriorating foraging conditions (Winston 1992b; Schneider & McNally 1992a). During the absconding season, up to 100% of colonies may abandon an area. There is often a mass movement of colonies back into the same area 5-6 months later (McNally & Schneider 1992). Seasonal absconding may therefore be a type of migratory movement that allows colonies to follow the shifting patterns of floral abundance that occur because of the seasonal rainfall patterns of the African continent. While European colonies may exhibit disturbance-induced absconding, they never undergo seasonal absconding. It would be impossible for European colonies to migrate the distances necessary to escape winter conditions. Rather, they have been selected to “stay put” and develop stockpiles of food to survive the prolonged resource dearth of winter.

Seasonal absconding in African colonies involves 2-4 weeks of preparations, during which brood rearing stops, developing larvae are cannibalized, foraging virtually ceases, all food reserves are consumed, and pupating brood may be uncapped and eaten (Schneider & McNally 1992a). The end result is that the colony leaves behind only empty comb and takes all available resources with it in the stomachs of the workers. Preparations for seasonal absconding also involve a unique type of waggle-dance behavior called the “migration dance” or “relocation dance” (Fig. 15), which is performed more or less continuously throughout the preparation period (Schneider & McNally 1994; Lewis & Schneider 2008). Migration dances are also performed on the surface of swarms that form at temporary stopping points along the migratory route.

Migration dances differ from normal waggle dances in four ways. First, they lack the “figure 8” pattern of waggle dances. After completing a waggle-run, the dancer does not circle back to her starting point but rather walks forward on the comb to a new location before repeating her waggle, resulting in the dances being performed throughout the nest (Fig. 15). Second, migration dances communicate extreme distances (up 25-35 km) that are well beyond the normal foraging range of a colony. Third, the dances can occur when there is little or no flight from the nest, suggesting that they do not stimulate immediate recruitment. Fourth, the distances communicated by the consecutive dances performed by the same bee can vary by 5-10 km, suggesting that the dances do not communicate the location of specific sites. However, migration dances communicate a consistent direction, which is the direction that the absconding swarm travels when it becomes airborne. Taken together, these observations suggest that migration dances help to gradually prepare a colony for seasonal absconding by establishing a general route of travel, but do not communicate a specific destination. This function may reflect the nature of the migratory process. Colonies can travel 100 km or more in search of better foraging conditions (Winston 1992b; Schneider & McNally 1994). Along the way, they may form temporary swarm clusters to assess forage availability, and then continue traveling in the same direction if conditions are unsuitable. If a colony cannot assess the quality of distant areas in advance, it may be impossible to pre-select a final destination. Instead, an absconding swarm may be better served by maintaining a constant direction of travel and periodically sampling the quality of the foraging environment until suitable conditions are found.

African honey bees are best known for their greater defensiveness and increased tendency to sting. Massive stinging responses by African bees have resulted in over a thousand human deaths in the New World, which have earned them the moniker “killer bees” and resulted in considerable public concern as this insect has advanced northward (Winston 1992b). Compared to European honey bees, A. m. scutellata and its descendants in the New World produce more alarm pheromone and mount greater stinging responses to a given level of disturbance (Table 1). The heightened defensiveness of African bees has a genetic basis and may be a dominant characteristic, because first-generation colonies arising from European queens mated with African drones often show the
The same level of defensiveness as “pure” African bees (Winston 1992b; DeGrandi-Hoffman et al. 1998b; Breed et al. 2004). It is likely that the heightened stinging behavior of African bees evolved in response to the greater predation rates experienced in the native African environment. However, African colonies are not invariably defensive. Schneider and McNally (1992c) reported virtually no defensive behavior for 65% of the 104 naturally occurring A. m. scutellata colonies they dissected in Botswana and, indeed, many of the colonies absconded during the dissection process with few or no attempts to sting. A colony’s level of defensiveness is influenced by a wide range of factors, including worker population size, stage of development, level of food reserves and weather (Winston 1992b; Schneider & McNally 1992c). Nevertheless, African colonies must always be treated with caution and the potential for massive stinging responses makes it difficult to maintain them near humans and livestock.

The African Bee in the Americas
One of the greatest challenges ever to face bee-

Fig. 16. Introductions of Apis mellifera scutellata into Brazil began in 1956. Within 50 years this tropically adapted race of bee colonized 17 countries over two continents. Throughout its range in the New World, the African bee shows a remarkable ability to displace resident European honey bee colonies.
keeping in the New World was the introduction and spread of the highly invasive African honey bee, *Apis mellifera scutellata*. Within 50 years of its introduction into Brazil in 1956, the African honey bee (also called the Africanized bee or the African-derived bee) colonized 17 countries on two continents (Fig. 16). Throughout its range it has established enormous feral populations that have replaced the European honey bee, which has dramatically and permanently altered beekeeping. The public’s awareness and perception of honey bees has also been affected. The ability of a single race of bees to colonize most of the western hemisphere in 50 years is one of the most rapid and dramatic biological invasions in history (Schneider et al. 2004a; 2006a). We are still trying to unravel how the African bee has been so successful so quickly. In the final sections of this chapter, I give a synopsis of the history of the African bee in the Americas, the mechanisms that have enabled it to displace European bees, and the possible impact it may have on beekeeping and agriculture in the U. S.

**The History of the African Bee Invasion**

Prior to the 1950s, several Latin American countries had large populations of managed European colonies and well-developed beekeeping industries. However, European bees are not adapted to tropical conditions. As a result, they never established large feral populations in the Neotropics and were maintained in managed apiaries only with considerable human effort. Thus, in the 1950s, Brazil initiated a program to import the tropically adapted *A. m. scutellata*. The plan was to hold the introduced colonies in captivity and subject them to controlled breeding to reduce the behavioral traits that were undesirable for beekeeping. Unfortunately, the bees escaped and quickly became established in the wild, where they thrived and began to multiply and spread rapidly (Schneider et al. 2004a; 2006a)

![Fig. 17. An African honey bee usurpation swarm actively invading a European honey bee colony. The arrow is pointing to a ball of African bees that are surrounding and protecting the queen. (photo courtesy of Gloria DeGrandi-Hoffman)](image-url)
African and European honey bees will readily interbreed and produce viable offspring. Because the initial tiny African population interbred with the much larger population of managed European bees, it was assumed that during their northward expansion the undesirable African traits would become diluted (and possibly eventually eliminated) by European genetics. In fact, the opposite happened. In almost all areas where the African bee has become established, European bees and European genetic material have largely disappeared within 10-20 years, despite interbreeding between the two populations (Schneider et al. 2004a). Even in areas with extremely large European populations, the African bee quickly becomes dominant. For example, when the African bee arrived in the Yucatan region of Mexico in 1985-1986, the area supported one of highest densities of managed European colonies in the world. Thus, at initial contact, the African population was vastly outnumbered by the European population. However, within only 12 years, the European honey bee genome had been largely replaced by the African genome (Clarke et al. 2002). Indeed, in most Africanized areas in the Americas the frequency of European genes rarely exceeds 35% in the feral honey bee population, and European characteristics can be maintained in commercial populations only with continuous management. Because of interbreeding with European bees, the African bee in the New World is no longer genetically identical to its ancestors on the African continent, which is why it is referred to as the “Africanized” honey bee, the New World African bee, or the African-derived honey bee. Nevertheless, throughout its range in the Americas, the bee has largely retained its African genetic make up and is predominantly African in its nesting biology, foraging behavior, diet selection, swarming activity, and absconding behavior (Schneider et al. 2004a; 2006b). This is one of the greatest and most enduring mysteries of the African bee invasion: its ability to displace established European populations and largely preserve its African genetic make up, despite 50 years of interbreeding and gene exchange with European bees.

Factors Contributing to the Displacement of European Bees

The preservation of the African genome in the Americas arises from a complex interaction of at least six factors involving swarming, mating behavior, reproductive biology, queen behavior, social parasitism, and development processes.

Colony growth and swarming rates: Because of their greater emphasis on brood rearing and pollen foraging, African colonies grow faster and swarm more frequently than European colonies (Table 1). In the Neotropics, African colonies can increase 16-fold per year, which is 3-5 times greater than the rate of increase for European colonies (Winston 1992b). Consequently, African populations increase quickly and dominate their habitat.

Mating advantage for African drones: When African bees colonize an area, queens mate with more African than European drones. Because African colonies are more abundant than European colonies in invaded areas, African drones occur in higher numbers at mating congregations. The timing of mating flights may result in European queens having a high probability of mating with African drones, whereas African queens are unlikely to mate with European drones. Furthermore, even if a queen mates with equal numbers of African and European drones, she may preferentially use African sperm to fertilize her eggs (DeGrandi-Hoffman et al. 2003). In combination, these factors increase the expression of African characteristics and the loss of European behavioral and genetic traits.

African-patrilin advantages during queen replacement: Because queens in invaded regions mate with African and European drones, their colonies contain both African and European patrilines. When these “mixed” colonies raise new queens, they produce virgin queens (VQs) of African and European paternity. African-patrilin VQs may have a competitive advantage during queen replacement. Compared to European-patrilin queens, African-patrilin VQs develop faster and emerge sooner, which may give them more opportunities to kill rival queens confined in queen cells (DeGrandi-Hoffman et al. 1998a). Emerged African-patrilin VQs may be superior fighters compared to their emerged European-patrilin sister queens. African-patrilin VQs kill more of their rivals and produce more bouts of “piping”, a sound signal associated with fighting success (Schneider et al. 2001; Schneider & DeGrandi-Hoffman 1993). Also, African-patrilin VQs receive more vibration signals from workers, which may further promote survival (Schneider & DeGrandi-Hoffman 2003). The end result is that an African-patrilin VQ is more likely to survive the queen elimination process and become the new laying queen of her colony. Because she will then mate mostly with African drones, there will be a rapid loss of European characteristics through both maternal and paternal inheritance.
Nest usurpation: Nest usurpation is a type of social parasitism in which a small African swarm invades a European colony and replaces the resident European queen, resulting in the instantaneous loss of a European matriline (Fig. 17). The importance of nest usurpation in the spread of the African bee is unclear, but it may account for the loss of up to 20% of European colonies in some areas (Schneider et al. 2004b). Weakened and queenless colonies are especially susceptible to usurpation, although thriving European colonies can also be taken over (Schneider et al. 2004b). However, we know almost nothing about how African usurpation swarms locate susceptible colonies, bypass host colony defenses, and replace the European queen with an African queen.

Fitness of African-European hybrid bees: Although African and European bees will interbreed, the resulting hybrid offspring may have reduced viability. Compared to African queens and workers, hybrid queens and workers have lower metabolic rates (Harrison & Hall 1993; Harrison et al. 2005). This could hinder flight performance and interfere with foraging and swarming. Also, hybrid workers may show slight developmental abnormalities compared to “pure” African and European workers, which could potentially compromise their survival (Schneider et al. 2003). Reduced fitness could account for the repeated observation that hybrid colonies in invaded areas tend to die out over time unless managed by humans.

Dominance of African genes: Several studies have suggested that some African genetic traits are dominant over European traits. Hybrid workers, therefore, behave like African bees, even though they carry European genetic material. The dominance of African genes has been suggested for some aspects of foraging behavior, queen behavior, resistance to parasitic mites, and defensive behavior (reviewed in Schneider et al. 2004a).

In combination, the factors described above inevitably lead to a loss of European traits when African bees invade a new area. Although the relative importance of each particular factor may vary from one region to the next, the cumulative effects have resulted in the displacement of European populations and the retention of African behavioral and

![Spread of Africanized honey bees by year, by county](image-url)

Fig. 18. The current distribution of the Africanized honey bee (AHB) in the U.S. (Courtesy USDA Agricultural Research Service)
genetic characteristics throughout much of the Americas.

The African Bee in the United States

The African bee arrived in Texas in 1990, and in the intervening 21 years has spread throughout much of the southern U. S. and California (Fig. 18). Initially, the spread of the bee was largely confined to the southwest. However, the African bee has recently been reported in Arkansas, Louisiana, Oklahoma, Georgia and Florida, suggesting that it will eventually become established throughout the southeast. At present, we cannot predict the ultimate range of the bee in North America. It is generally assumed that the northward expansion will be halted by colder climates, but the African bee has repeatedly surprised us with its ability to adapt to novel environments. The arrival of the African bee in the U. S. coincided with the decimation of European colonies by the parasitic mite, Varroa destructor. Up to 90% of feral European colonies in the U. S. have been killed by mites, which has eliminated competition for forage and nest sites and diminished the chances for interbreeding between African and European bees. This ecological vacuum has undoubtedly helped the African bee become established in the U. S. and may allow it to expand further than initially predicted (DeGrandi-Hoffman et al. 2006). The rate of spread in the U. S. is slower than the rate experienced by Latin America. However, the African bee is displacing European bees in most areas of the U. S. that it has colonized (Schneider et al. 2004a; Pinto et al. 2004), suggesting that it may eventually dominate habitats at least throughout the southern tier of the country, and perhaps in other regions as well.

So far, the economic impacts of the African bee in the U. S. have been less severe than predicted. Nevertheless, it is likely that the bee will affect pollination services. In the U. S., pollination by European honey bees accounts for almost $15 billion in agricultural productivity each year. U. S. agriculture is increasingly reliant on “migratory beekeeping,” in which more than a million colonies are transported around the country each year for pollination purposes. However, U. S. beekeeping is currently facing a major crisis, with almost 50% of managed colonies eliminated by parasitic mites and a mysterious new ailment termed Colony Collapse Disorder. Many beekeepers replace lost colonies by purchasing packages of bees and queens, most of which are produced in the southern states. Also, the colonies used for migratory beekeeping are overwintered in the southern states. Thus, U. S. agriculture is becoming increasingly dependent upon the ability to maintain and freely transport European colonies to and from the south. Yet, many southern states are now colonized by the African bee (Fig. 18). Because African and European bees will freely interbreed, it may become increasingly difficult to maintain the quality of European colonies necessary for U. S. pollination needs. Also, if European colonies are usurped by African swarms when overwintered in invaded areas, then African colonies may be inadvertently transported into new areas through migratory beekeeping. It is too soon to know how U. S. beekeeping and agriculture will be affected by the interaction of the African bee, parasitic mites, Colony Collapse Disorder, commercial queen production, and migratory beekeeping. However, the fallout from this convergence of events could potentially have dramatic consequences for the U. S. beekeeping industry. The African bee is now a permanent part of the beekeeping landscape and the most practical solution may be to manage it and incorporate it into U. S. beekeeping and agriculture practices. And, this could have benefits in the long run. Under some conditions, the African bee is a highly efficient pollinator and might be more resistant to Varroa mites than the European bees (Schneider et al. 2004a; DeGrandi-Hoffman et al. 2006).

In conclusion, studies of honey bee life history and survival strategies have contributed to virtually every aspect of our beekeeping practices and have been essential for understanding and coping with the invasion of the African bee in the New World. Although we know a tremendous amount about honey bee ecology, biology and evolution, much remains to be learned. Continued investigations of honey bee life history will undoubtedly enhance our ability to maintain healthy, productive colonies, as well as increase our fascination with this remarkable insect that is so intertwined with our lives.

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