1 Honeybee

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1.1 Introduction

All honeybees of the genus *Apis* are obligate social organisms that exist in colonies usually containing a single reproductive female, the queen, and many thousands of facultatively sterile females, the workers. Hundreds to a few thousand males are produced during the spring and summer months in temperate climates, but they die or are driven from the hive in the autumn. During the spring and summer, the queens of the species most commonly used commercially, *Apis mellifera*, may lay up to 2,000 eggs or more per day. If the eggs are fertilized, they develop into diploid females, while unfertilized eggs develop into haploid males. If the egg-laying rate of the queen begins to falter, the workers will feed some of the diploid larvae a special diet that causes them to develop into queens, whereas the remainder of the diploid eggs develop into smaller, less reproductively capable females whose egg laying is suppressed by queen pheromones. Workers typically live about five weeks during the summer, but have a longer life expectancy during the winter. The queen is capable of living for up to five years, but is typically killed by a replacement queen within two years. During late spring and early summer when colony numbers are at their highest in temperate climates, the workers rear replacement queens and the old queen leaves with a portion of the colony members in a swarm. In this way, colony reproduction is achieved. A similar type of colony dynamic occurs in tropical regions, but the seasonal variation is much reduced.

In temperate climates, honeybees store resources (honey and pollen) to support the colony over the winter months when resources may not be available. In both temperate and tropical regions, storage of resources also supports colony expansion and reproductive swarming. The strong resource-collecting instinct has resulted in several species of *Apis* being kept as honey producers and pollinators. At least two species are kept commercially, the Western or European Honeybee, *Apis mellifera*, and the Asian honeybee, *Apis cerana*. Another species, *Apis dorsata*, which is common in southern Asia, produces open combs in trees and on cliff faces. Though it is not managed commercially, it is often raided in wild populations. No fertile hybrids have been produced between species.

This chapter will deal with the most common and commercially important of these species, *Apis mellifera*. As a species it is native to the Old World: Europe, Africa, Eurasia, and Asia. Within *Apis mellifera* more than two dozen subspecies are recognized that correspond to the great variety of climatic zones to which the species is endemic (Sheppard and Meixner 2003). Colonies from several European subspecies were first brought to the New World in the early seventeenth century and to Australia in the early nineteenth century. Beekeeping has a very ancient and varied history, with evidence that honeybees have been kept for thousands of years. There are depictions of beekeeping from ancient Egypt and China. Remarkably many bee husbandry practices have not changed in millennia. In fact, hollow log hives as depicted in wall murals from several thousand years ago are still used in northern Africa and the Mediterranean.

Despite the extended relationship between humans and bees, the history of beekeeping is not one of domestication. Genetic improvement of honeybees is complicated by the fact that they suffer from severe inbreeding depression and cannot therefore be inbred to any great degree. Bees have even developed a vari-

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ety of behavioral characteristics that reduce the possibility of inbreeding. These behavioral traits further complicate the breeding of bees. For example, honeybees are adapted to mate during flight presumably to prevent mating with closely related males in the hive. As a result, it is not possible to get bees to mate in laboratory cages. Mating takes place in aerial "drone congregation areas" where males (drones) from the surrounding region congregate, awaiting the arrival of virgin queens. Queens will mate with about 12 to 17 drones over a period of one to several days and will not mate again for the remainder of their lives. The remote nature of mating and the large number of partners make it extremely difficult to control mating in the field. Queen breeders attempt partial control of mating by providing many drone source colonies from selected stocks but drones from the surrounding 5–10 kilometers can access the drone congregation area. Inbreeding is also prevented by specific genetic and biochemical mechanisms. Homozygosity at the sex-determining locus (*csd*) results in a phenotype known as "shot brood," in which half of the diploid larvae are killed (Beye et al. 2003). Heterozygosity at the sex-determining locus is required for female development. While males are usually haploid and therefore hemizygous at the sex-determining locus, homozygous diploids also begin to develop as males, but they apparently produce a pheromone (dubbed the "eat me" pheromone) that results in them being consumed by the worker bees within 48 hours after eclosion from the egg (Woyke 1998). As a result, the pairing of identical *csd* alleles caused by mating between a queen and closely related drones greatly reduces the overall vigor of honeybee colonies and the maximal size of a colony that can be produced. In addition, shot brood is a drain on the finite egg-laying capacity of the queen and stimulates the workers to destroy the queen whom they perceive to be failing.

The technique of artificial insemination has been developed to overcome the limitations that aerial mating to multiple drones imposes on bee breeding. It has been shown, however, that the limited volume of semen supplied to artificially inseminated queens (when using single-drone inseminations) tends to produce colonies that are weak and therefore prone to queen replacement or loss by attrition without careful management. Inbreeding, a tool typically used in genetic improvement programs, greatly exacerbates the problems associated with maintaining colonies produced by artificially inseminated queens, due to the compounding effect of shot brood and inbreeding depression on the lack of colony vigor. As a result, it is very difficult to select for certain traits by classical breeding methods. Three final limitations to breeding of bees all relate to the reproductive unit of honeybees being the colony. Many traits, particularly behavioral traits, are only apparent at the colony level and therefore must be selected at the colony level, rather than at an individual level. Thus, rapid phenotypic screening is often impossible. Furthermore, the need to maintain genotypes as colonies, limits the number of genotypes that can be screened and maintained. Finally, long-term cryogenic storage of germplasm, while theoretically possible, is not without its own inherent problems (Stort and Goncalves 1986) and as yet is not a practical option. Thus, "reference" strains must be maintained in the field as sperm has only been maintained in short-term storage for a period of up to 6 weeks (Collins 2000).

1.1.1 Taxonomic Description

The honeybee *Apis mellifera* is in the Order Hymenoptera, Suborder Apocrita, Superfamily Apoidea, Family Apidae, Subfamily Apinae, Tribe Apinini. All *Apis* species have complex societies. There are also other genera of "stingless bees" in the Apidae that are highly social. Honeybee (*Apis*) nests consist of vertical combs formed from secreted wax. Some honeybee (*Apis*) species construct their combs in the open but the two species commonly kept for honey production and pollination are cavity nesters. Honeybees are found worldwide from the tropics to subarctic temperate zones and on all continents except Antarctica. There are various subspecies of *Apis mellifera*, all of which interbreed readily, suggesting that observed differences reflect selection for adaptation to local environmental conditions. While subspecies are generally distinguished by morphometrics, color, and region of origin, behavior and size are also important characteristics. For example, the "Africanized " honeybees ranging from South to North America are derived from *A. mellifera scutellata* from sub-Saharan Africa. Even though these honeybees hybridize readily with European subspecies, they retain the small size and highly defensive stinging behavior of *A. m. scutel-*

lata. The adaptation of these bees to tropical environments has allowed them to proliferate across tropical and subtropical regions of the Americas where they are considered a major problem because of their stinging behavior.

1.1.2 Economic Importance

Honeybees are of greatest economic importance as pollinators of fruit, nut, vegetable, and pasture crops as well as many uncultivated flowering plants. Payments made to beekeepers for pollination services in the USA alone have been estimated to be approximately US$150–220 million annually (USDA 2003) with a total value of the crops that are pollinated at US$14.5 billion (Morse and Calderone 2000). Honeybees are also commercial producers of honey; according to FAO statistics (http://faostat.fao.org) the total value of global honey production was 1,345,672 metric tons in 2004 and 82,000 metric tons in the USA. Other products harvested from honeybees include beeswax, pollen, royal jelly, and propolis, often taken as nutritional supplements, used for medicinal purposes or in cosmetics and other products.

1.1.3 Breeding Objectives

One of the distinguishing characteristics of honeybees is that the most important traits for commercial beekeeping are behavioral and not physiological as with most domestic animals. Although behavioral traits are heritable, heritability tends to be much less than what is typically expected of a physiological characteristic. Assays for behavioral traits tend to be difficult, as they often depend on actions at the colony level, which result from interactions between individuals, communication, and collective "decision making."

The most positive heritable traits desirable for commercial breeding are described below.

Disease Resistance

Resistance against parasites, such as the *Varroa jacobsoni* (Kulincevic et al. 1992; deGuzman et al. 1996) and *Acarapis woodi* mites (deGuzman et al. 1998), and pathogens such as *Paenibacillus larvae* (Spivak and Reuter 2001), the causative agent of American Foulbrood (AFB), is of high importance to the beekeeping industry. Many studies suggest that a major component of colony level resistance to both pathogens and mites is the tendency to remove diseased brood from the hive, thereby significantly reducing the abundance of pathogens and pests. This activity is referred to as hygienic behavior and consists of removal of the wax caps from the brood cells and removal of infected brood (Rothenbuhler 1964; Spivak and Reuter 2001; Lapidge et al. 2002). The bees also line the interior surfaces of the hive with antibiotic-rich propolis which is collected from resins and gums secreted by plants. Significant differences in propolis collection have been observed between subspecies and propolis is a minor commercial product, but selection is most often employed to reduce propolis collection because this sticky substance makes it more difficult for the beekeeper to remove combs for inspection. Insects also contain humoral and cellular immune systems (Iwanaga and Lee 2005), but genetic variability for these traits has neither been described nor exploited in a breeding program.

Pollen Foraging

The value of honeybee-pollinated crops makes crop pollination the single most important activity of bees in terms of human economic significance. When a worker collects pollen from a flower as a protein source for the hive, this activity results in more efficient pollination than the activities of a nectar-collecting worker (Cane and Schiffhauer 2001). Bidirectional selection for the amount of pollen stored in hives showed that the trait is genetically controlled and that selection for more pollen stored in the hive increases the proportion of foragers specializing in pollen collection (Hellmich et al. 1985; Hunt et al. 1995; Page et al. 2000) Genetic markers linked to this trait are available and have been used in a breeding program (Hunt et al. 1995; Page et al. 2000). Breeding for pollen hoarding has not been carried out commercially due to a lack of commercial incentive as pollination services are contracted on a per hive basis without regard for specific genotypes. It is not known whether excessive pollen hoarding may negatively impact nectar collection and may reduce the ability of the bees to respond to resource availability or colony needs.

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