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HONEY BEE PESTS,
PREDATORS, AND DISEASES

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CHAPTER 16

Abnormalities and Noninfectious Diseases

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Introduction

Honey bees of all three castes manifest a variety of unusual conditions due to agencies other than pathogens or pests. These conditions include death, malformation, and genetic and physiological misfunction, and can be caused by unfavorable environment, inadequate nutrition, social dysfunction, gene mutation or recombination, and chromosomal rearrangements.

The assignment of a cause to any biological event, however, must always be tempered with the recognition that an organism's genotype acts jointly with its environment to produce the phenotype we see. The classification of biological events into "genetic" or "environmental" is an artifact of human thought, which seems to fit reality best when we know the least.

Furthermore, assignment of causes should be considered provisional until all factors impinging upon the phenotype, including biochemical and biophysical ones, are understood (Martignoni 1964, O'Brien 1967).

Our knowledge of noninfectious diseases and abnormalities in bees is poor. Most such syndromes are known only superficially, often as by-products of studies with other goals. Even though gynandromorphism is the most widely studied abnormality, the literature is still replete with fundamental questions.

Abnormalities in honey bees ought not to be viewed as mere curiosities, but as valuable research tools to help us understand normal, as well as abnormal development and behavior. For example, in addition to genetic research, mutant markers have been used to study a variety of nongenetic events including the mating range of honey bees (Peer and Farrar 1956), the distribution of foragers (Levin 1960), and the survival of honey bee sperm in liquid nitrogen (Harbo 1977).

The distribution of most of the anomalies presented below can be reasonably expected to be as wide as the distribution of honey bees themselves. The control of most of these conditions is the replacement of stock. Exceptions will be mentioned where appropriate.

The following provides an account of departures from normal development and form, arranged generally in the sequence of the bee's life continuum from egg through adult.

Sterile Eggs

Infrequently, a newly mated queen begins and continues apparently normal egg laying, but most of the eggs do not hatch (Hitchcock 1956; Fyg 1959). The eggs eventually shrivel if they are not removed by worker bees of the colony. Sometimes, the queen may lay a second egg in a cell already containing a shriveled egg. Nurse bees may deposit brood food in a few of the cells containing unhatched eggs. Sterile eggs laid in drone comb survive no better than those laid in worker comb. Embryonic development takes place for a variable stage of development (Hitchcock 1956), from first cleavage to near completion of the larva (Fyg 1972).

However, a few eggs of such progenies do hatch and develop into apparently normal workers and drones (Hitchcock 1956), and one queen has been reared from such larvae (Laidlaw and Tucker, unpublished). The proportion of survivors in these progenies is quite low. Hitchcock (1956) estimated about 0.1 per cent. However, this is probably an overestimate, because it did not take into account the possible sequences of eggs that died and were replaced during the two weeks preceding his observation. Thus a better estimate might be about 0.03 per cent.

The per colony incidence of sterility is usually quite low. It may not occur at all among thousands of daughters of some queen mothers, and only a few per thousand daughters of others. But in one instance it occurred in 35 of a lot of 200 queens shipped by a queen breeder (Hitchcock 1956). Probably more cases occur than are reported, since this condition is most likely seen by queen producers who may consider reporting it detrimental to their reputations.

The cause of egg inviability in bees is not known, but it probably includes genetic influence. The evidence for this probability is the clustering of occurrences within individual queen progenies (Hitchcock 1956) or in queen progenies of related mother queens (Roberts, cited by Hitchcock 1956; Tucker, unpublished). It seems to me that several of the cases of egg sterility cited by Hitchcock (1956) are different from the one case involving five queens that he saw, and were probably due to other causes.

The most likely hypothesis for egg sterility in which survivors are very infrequent is that the mothers of the progenies are triploid, at least in their germ tract. If this were so, most of the eggs would be aneuploid and inviable, and the rare survivors would be euploid or nearly so. Von Borstel and Rekemyer (1959) observed similar sterility in progenies of known triploid female braconids (*Bracon hebetor* Say).

For egg sterility with a higher proportion of survivors, the mother of the progeny could be heterozygous for an inversion or translocation. This condition is well known in other insects (von Borstel and Rekemyer 1959). The egg sterility reported by Isaacson (cited by Hitchcock 1956), with up to 5 per cent surviving worker bees, might fit this type.

Some of the reports on sterile eggs (cited by Hitchcock 1956) involved queens who produced normal eggs, then later produced sterile eggs. The explanation of this condition, if not supersedure by an abnormal daughter queen, is probably other than those above.

Scattered Brood

Departures from the compact and solid brood pattern necessary for most efficient brood production are frequently encountered in honey bees. Such a condition is referred to as scattered brood or spotty brood. The amount of brood lost can vary greatly between different colonies from less than 10 per cent to 50 per cent or more, yet be due to the same causes.

Scattered brood affects colony buildup and strength. Where moderate to severe brood loss is common, colonies do not become exceptionally strong (Woyke 1976a). The effect of low but constant brood loss is yet to be measured precisely, but probably such colonies are slow to build up to a large population. Slow buildup is a liability where time is limited before the main honey flow, but may be an asset where only fall flows exist.

Scattered brood is an elusive phenotype. It is a consequence of nonpathogenic, as well as pathogenic conditions. More than one of these conditions can coexist. Therefore, a quick assignment than the United States. Even in the United States few attempts have been made to assess the economic significance of this important pest of the beekeeping industry. Paddock (1918) assumed the number of hives of comb destroyed in Texas by *Galleria* to be approximately 5 per cent annually (14,000 units), and Oertel (1969) estimated annual losses in Louisiana to be approximately 31,000 dollars. In the United States *Galleria mellonella* (L.) presently causes extensive losses in the areas that produce the most queens and package bees (Gulf Coast states, Georgia, and California), where the climate is warm. Based on a survey of 114 southern commercial and semicommercial beekeepers who operated over 180,000 Langstroth colonies and over 250,000 queen-mating nuclei, *Galleria*-caused losses in the United States were estimated to be about three million dollars or more during 1973 and about four million in 1976 (Williams 1976). Losses in the three main beekeeping states in the south averaged nearly $1.00 per colony in California, $1.50 per colony in Texas, and $3.00 per colony in Florida.

Annual losses from American foulbrood in the United States, including operational costs for state apiary inspection programs, probably reach five million dollars or more. Wax moth losses may approach those caused by American foulbrood nationally and equal or exceed them in the states covered by the survey.

Morphology

Newly hatched *Galleria* larvae have a creamy-white body color that becomes gray to dark gray on the dorsal and lateral surfaces in older larvae; strains of larvae that are white-bodied at maturity have been bred commercially in the United States. *Galleria mellonella* (L.) larvae are the largest of the comb-infesting Lepidoptera, reaching as much as 28 millimeters in length and 240 milligrams in weight (Hase 1926).

Greater wax moth cocoons are usually bare and white, but some are almost completely covered with dark fecal pellets and frass; they usually are 12 to 20 millimeters long and about five to seven millimeters in diameter. Often the last-instar larvae migrate from the feeding site and spin cocoons on hive bodies or the inner cover. Large sheets of several thousand cocoons or more are a distressingly familiar sight to beekeepers in warm climates, including those in the southeastern United States. As many as 10,000 cocoons may be found in a two-story, 10-frame Langstroth hive, but normally only about 250 normal-sized larvae are able to develop on proportion would be an 8 per cent loss for unrelated matings (Woyke 1976a). Matings between relatives, as two successive generations from the same queen mother, could give an average loss of 13 per cent, and the percentage would be higher for individual colonies.

The severity of this problem has been documented for the closed and somewhat inbred bee population on Kangaroo Island, South Australia (Woyke 1976a). Scattered brood was found in many colonies, which did not become very populous. A sample of 34 colonies showed an average brood loss of 24 per cent (range 2 to 47 per cent), and an estimate of only six of the 12 sex alleles present.

Genetic Lethality

Another cause of scattered brood is semilethality or subviability found in all stages of brood development, but showing signs and symptoms other than those of known pathologies (Borchert 1966). If one had not seen the dead worker larvae, prepupae, and pupae before they were removed by adult bees of the colony, the condition could not be distinguished from a scattered infection with a known disease organism or loss of brood as diploid drones. However, this condition can be found in haploid drone brood as well (Mackensen 1958), where no effect is expected from the sex alleles, except for rare parthenogenetic diploids.

Losses due to genetic subviability vary from one progeny to another, from quite low to as high as 18 per cent for both workers and drones (Mackensen 1958). Since this condition has been observed only incidentally to genetic studies, comprehensive data are lacking. In my opinion, genetic subviability can explain scattered drone brood, and must also be a candidate explanation for scattered worker brood.

The superficial appearance of the dead brood is known only for sealed brood, although death at all stages is possible. My own observations were made on sealed drone brood during the last 9 to 14 days before eclosion. During this time, drones may die as larvae, prepupae, pupae, or imagoes that fail to chew open their cell cappings. Often, more dead prepupae than other stages are found. Dead larvae and prepupae appear grey or black and are saclike, with watery contents. Fyg (1959) described a noninfectious phenocopy of sacbrood that may be part of this syndrome.

To explain genetic subviability, Mackensen (1958) suggested two separate semilethal genes, one linked to the brick locus, the other to the snow locus. An alternative hypothesis I prefer is that six or more polygenes for subviability act jointly to produce one lethal event; and that under minimal developmental stress the presence of more subviable genes are required for death, but fewer subviable genes are required for death under greater developmental stresses (as with certain wing mutants, see Laidlaw, el-Banby, and Tucker 1965). The possibility that an unknown infection is one of the stresses in genetic subviability should not be ignored.

Queen's Egg-laying Behavior

Scattered worker brood is often mentioned as a direct sequel to scattered egg laying by a queen. But as far as I know, this connection has not yet been documented by careful study.

Drone brood in worker comb is often scattered. This scattering may be in part a consequence of irregular egg laying behavior. Harbo (1976) found irregular placement of eggs in worker comb to be more frequent by unmated queens and queens inseminated with dead sperm (33 to 94 per cent) than by queens inseminated with live sperm (0 to 7 per cent). Of the irregularly placed eggs, some were sideways on the cell bases, and others were attached to the sides of the cells. Harbo (1976) did not follow further development, but perhaps scattered brood could ensue if some of the irregularly placed eggs were removed or eaten by worker bees.

Drone Brood in Worker Cells

There is usually some mortality of drone brood in worker combs, even though the drone brood from the same queen or laying workers is reasonably viable in drone comb. In worker cells, well-fed drone brood develops well up to sealing, some larvae die soon after sealing. If the dead larvae are removed by the bees, a scattered brood pattern results; otherwise, the brood looks diseased.

The superficial appearance of the nondiseased dead larvae does not resemble common brood diseases. They appear gray or black and saclike with watery contents.

The cause of death of drone larvae in worker comb is not known, but may be due to confinement within cells that are too small.

Cannibalism

Another possible cause of scattered brood is cannibalism by worker bees. This is a major cause of spotty brood for the plains variety of *Apis cerana* (Woyke 1976b), and may be an occasional cause for *Apis mellifera* (Woyke 1977). Cannibalism seems to be a response to the lack of pollen (Newton and Michl 1974). In *Apis cerana* solid brood patterns exist only during good pollen flows (Woyke 1976b).

Cleaned-up Disease

Scattered brood could be the consequence of a scattered brood disease, after the diseased brood has been removed from the comb (Morse 1976); however, usually there is some other evidence of disease.

Pupal Anomalies

Fyg (1959) described two pupal anomalies that die as pupae. One of these was called "white-headed bees" (not to be confused with white-eyed bees) in which the pupa's entire head and appendages remained white after the rest of the cuticle had darkened. Fyg (1959) believed the white heads were due to a lack of oxygen caused by a blockage of the prothoracic spiracles. In the other pupal anomaly, called "Muttenz anomaly," the abdomen appears greatly shortened by becoming telescoped anteriorly, the head enlarged, and the digestive system displaced anteriorly. Laidlaw and Eckert (1962) mention "humpbacked" queen pupae that have enlarged thoraces and compressed heads.

Chilled Brood

Brood will die if it becomes too cold. Chilling may occur during the spring buildup when the amount of brood is greater than the adult worker bees can cover and keep warm when tightly clustered during a frosty night. It can also happen during cold weather following any sudden reduction of the adult worker bee population of a colony, as consequences of such events as insecticide poisoning, or the partial or complete desertion of a newly-made division of a larger colony.

Chilled brood can occur during the colder months in temperate climates, including the subtropics. It may also be possible at very high altitudes in the tropics. A certain length of time at temperatures below 14° Celsius must be necessary; however, as far as I know, the time has not been determined. Brood can survive for a considerable length of time at temperatures below 35° Celsius, and this ability varies with different ages of brood (Jay 1963).

Chilled brood is found at the lateral and lower peripheries of the cluster. All the brood in an outer comb may be dead, and a crescent of dead brood may be found below healthy brood in a comb in the cluster's center.

The appearance of chilled brood is variable (Borchert 1966). In color, it is often yellowish-white, tinged with black on segmental margins, brownish, or black. The texture is dry-crumbly, greasy, or watery, but never ropy. The odor is usually weak, but sometimes disagreeable and sour. Sometimes the cappings of dead sealed brood cells are perforated.

Diagnoses based on microscopic observations of smears of dead, chilled larvae are variable (Borchert 1966). Usually no microorganisms are seen. Occasionally some bacteria are found, which Borchert (1966) believes invade the larvae after death.

Overheated Brood

Death of brood from overheating is likely if a colony's ability to cool itself in hot weather is impaired. Such conditions could occur if many of the hive bees as well as foragers were killed by pesticides (Atkins 1975). Brood dead of this cause was reported by Root (1966) for colonies confined on hot days. Such death of brood in incubators is well known. The minimum lethal temperature for brood has been reported to be 37° Celsius (Himmer 1928).

Other Brood Mortality

Brood may die from other environmental hazards. Starvation is possible if there are too few hive bees to feed the starving larvae. Normally in a colony short of food, larvae are removed (eaten) by nurse bees. Pesticide poisoning is possible if the pesticide had not killed the foragers or the nurse bees, but under such conditions the brood also may be dead of starvation, chilling, or overheating. Some brood can be killed by jarring the combs (Tucker, unpublished), probably during the prepupal and pupal stages, when it is vulnerable (Jay 1963).

Abnormal Adult Bees

Departures from the usual appearance of bees occur occasionally. These abnormal bees can be consequences of cytological accidents, mutant genes, or unfavorable environment during development.

Visible Mutations

About 30 mutant phenotypes have been found in honey bees (Rothenbuhler, Kulincević, and Kerr 1968; Laidlaw, unpublished).

Of these, there are about 20 for eye color, three for eye structure, five for wings, and one each for body color and body hair. Recessive genes are readily discovered in drones, whose haploid chromosomes can contain only one allele per locus. Most of these mutants occurred spontaneously, and many of them were first found by commercial beekeepers.

The eye color mutants can have a variety of eye colors with each color variant typical of a particular mutant. The colors range from almost white through various shades of yellow, red, and brown. The eye colors are due to incomplete formation of eye pigments, and Dustmann (1969, 1973) has assigned most of the mutants to specific reactions in the biosynthetic pathways of these pigments. Drones of only the darkest eye color, garnet, fly well enough to mate naturally. The genes for all known eye color mutants are inherited as Mendelian recessives.

Of the eye structure mutants, eyeless has neither ommatidia nor testes, reduced facet has a variable reduction in ommatidia, and cyclops has only one eye over the top of the head (Laidlaw and Tucker 1965, see also Fyg 1959). Usually eyeless and reduced facet occur only in drones, cyclops in both workers and drones. Reduced facet appears almost exclusively along with brick or garnet eye colors. The gene for eyeless is inherited from one heterozygous queen to the next as a Mendelian recessive. The causes of reduced facet and cyclops are probably genetic, because these phenotypes cluster within individual progenies, but their inheritance is obscure.

The wing mutants include four phenotypes with modified structure and one phenotype with modified comportment (Laidlaw, el-Banby, and Tucker 1965, Rothenbuhler, Gowen, and Park 1953, Witherell 1973). The phenotypes of short and diminutive are short and narrow wings; that of truncate is wings that are quite short and squared at the tip; and that of wrinkled is a wrinkled area in the distal portion of the forewing. The phenotypes of wrinkled and short include anomalous wing venation. The wings of the droopy phenotype droop to the sides. Of these wing mutant phenotypes, only diminutive and wrinkled can fly. The gene for each of these is inherited as a single Mendelian trait; droopy is dominant and probably lethal in drones, the others are recessive.

The body color mutant, cordovan, dilutes the color of normally black portions of the cuticle to a cordovan brown color (Mackensen 1951). The gene for cordovan is inherited as a single Mendelian recessive. Other genes for body color are sometimes classed as mutants when used as genetic markers in bee populations where their frequency is low, such as a gene for black body color in golden bees (Laidlaw and el-Banby 1962). Also, it may be possible that the cordovan gene is fixed in homozygous condition in isolated bee populations in desert oases in the Old World.

With the phenotype of the body hair mutant, hairless, body hair is produced normally but sloughs off after eclosion, to give the adult bee a hairless appearance (Mackensen 1958). The gene for hairless is inherited as a Mendelian recessive.

A variable amount of subviability accompanies several mutant gene phenotypes. Most strongly affected are truncate wing, short wing, and eyeless. To a lesser extent, other mutant genes and even wild types are subviable, as mentioned above. Subviability for the same gene varies between progenies and at different times within progenies (Laidlaw, el-Banby, and Tucker 1965), which may indicate variable stresses during development imposed by variable genetic load and environment.

Gynandromorphs

Gynandromorphic bees are sex mosaics whose bodies are partly male and partly female in structure (Rothenbuhler 1958, Fyg 1959). Sometimes, especially in older references, they have been called hermaphrodites, but this is a misnomer because a hermaphrodite produces both sperm and eggs, but gynandromorphs do not.

The distribution of male and female tissues in various parts of the gynandromorph's body can take several patterns. Divison of female and male tissue may be by body region, such as a worker head with a drone thorax and abdomen, or bilaterally, or even patches of male and female tissues. The most likely arrangement of tissues is male anteriorly and female posteriorly, and tissues near one another are most likely to be the same sex (Drescher 1975, Milne 1976). Most often the female parts are diploid worker and the male parts haploid drone.

The female and male tissues of gynandromorphs can have several different origins, detectable in genetically marked stock. However, the most frequently found so far have been those with biparental female tissues and paternal male tissues; thus they are zygogenetic-androgenetic, or Z-A (Rothenbuhler, Gowen, and Park 1952, Drescher and Rothenbuhler 1963). In these, the female tissues arise from the usual zygote and the male tissues arise from one or more accessory sperm, which in nongynandromorphic bees take no part in development. Another far less frequent origin is biparental (zygotic) female tissues, and maternal male tissues (Mackensen 1951, Drescher and Rothenbuhler 1963, Woyke 1962b). In this type it is not certain whether fertilization takes place after cleavage, or the combination results from a single fertilization of a binucleate egg. Gynandromorphs are known also from unmated queens, and seem to originate from unusual binucleate eggs in which haploid cleavage precedes union of descendants of the two egg nuclei to give rise to female tissue (Tucker 1958). In these, all tissues are maternal, and the male tissues are mosaics of two haploid products of meiosis.

The tendency to produce Z-A gynandromorphs is inherited (Rothenbuhler 1955). The frequency of gynandromorphs was increased in a gynandromorph-producing stock by selection and inbreeding, but was lost in four generations of outcrossing to drones of non-gynandromorph-producing stock. The reciprocal crosses took three generations to establish a low level of gynandromorph production into a non-gynandromorph-producing stock. Thus, the inherited factors are at least partly chromosomal, whether there is also cytoplasmic inheritance is not clear.

Gynandromorphs are rare in unselected stocks. If they appear at all, there are usually only a few in a given progeny. But occasionally Z-A gynandromorphs appear in greater numbers (Rothenbuhler, Polhemus, Gowen, and Park 1949), and with subsequent selection and inbreeding can be increased to as high as 40 per cent of the progeny from fertilized eggs (Rothenbuhler 1958).

The frequency of Z-A gynandromorphs can be conditioned by environmental factors. Within gynandromorph-producing stocks, gynandromorphs were most frequent during periods of accelerating oviposition (Rothenbuhler, cited by Drescher and Rothenbuhler 1963). Furthermore, gynandromorphs were induced by chilling very young eggs (20 to 30 minutes old) of some non-gynandromorph-producing stocks, but not others (Drescher and Rothenbuhler 1963). Also heat treatment of eggs has been reported to induce gynandromorphs (Hachinohe, cited by Drescher and Rothenbuhler 1963).

How Z-A gynandromorph-producing eggs differ from normal eggs is not known. Drescher and Rothenbuhler (1963) suggest the possibility that some chemical that inhibits further development of accessory sperm nuclei in normal eggs is somehow inactivated in gynandromorph-producing eggs. But whatever the system is, it is affected by the queen's genes (and not the zygote's genes), and the environment.

Gynandromorphs other than the Z-A type have been too infrequent to be adequately studied.

Other Mosaics

Several other mosaics have been found in genetically marked stocks. Clearly related to Z-A gynandromorphs in origin are mosaic drones, whose zygogenetic component is diploid drone, rather than female, along with androgenetic haploid drone tissue (Rothenbuhler 1957, Drescher and Rothenbuhler 1964). For several years these mosaic drones were the only evidence of the existence of diploid drone tissue, until Woyke (1962a) demonstrated the viability of diploid drones. Laidlaw and Tucker (1964) found gynandromorphs with paternate (androgenetic) female tissue, indicating development from union between accessory sperm. Two other types of mosaics seem to originate from binucleate eggs: mosaic drones similar to the mosaic drone tissue of gynogenetic gynandromorphs from unfertilized eggs (Tucker 1958, Woyke 1962b), and mosaic females presumably from doubly fertilized binucleate eggs (Taber 1955, Woyke 1962b). Woyke (1962b) found a three-way mosaic worker of parthenogenetic female and two different biparental origins, so all four haploid products of meiosis, two of them fertilized, could have been involved.

Parthenogenetic Females

Although parthenogenetic females are apparently normal bees, they originate in an unusual way; they result from unfertilized eggs that usually produce drones. Bees of a colony usually rear parthenogenetic females as workers, but it is possible to rear queens from parthenogenetic female larvae (Mackensen 1943).

Parthenogenetic females have been found in various stocks, usually at low frequency (Mackensen 1943, Tucker 1958, Woyke 1962b). Their incidence is higher in the Cape bee of South Africa (Jack 1916). They can be found in progenies of either laying workers or unmated queens.

Parthenogenetic females possibly develop from binucleate eggs, following unusual meiosis (Tucker 1958). According to this hypothesis, the two haploid egg nuclei unite to form a diploid cleavage nucleus from which the female develops. With each of the two haploid nuclei originating from each of the two secondary oocytes separated by meiosis I, retained heterozygosity would vary inversely with the distance of the gene from each chromosome's centromere. This explanation is consistent with the patterns of segregation observed among parthenogenetic workers from heterozygous unmated queens (Tucker 1958).

The frequency of parthenogenetic females is highest during accelerating oviposition either during initial laying or following an interruption in laying (Tucker 1958).

The tendency to produce parthenogenetic females can be increased by selection (Tryasko 1969).

Dwarf Bees

Very small but apparently well formed worker bees are found from time to time. I have seen them among normal sized workers reared by old bees. Fyg (1959) reports them from colonies with nosema disease. Dwarf workers probably develop from larvae that are poorly fed during late larval life, since it is possible to produce them by starving older worker larvae (Jay 1963).

Dwarf drones develop from drone brood in worker cells. Whether they are partially starved by nurse bees or stop eating as cramped larvae has not been studied, as far as I know. However, dwarf drones can be produced by starving older larvae (Jay 1963).

Dwarf queens can also result from underfeeding (Jay 1963, Fyg 1959).

Crippled Bees

Crippled bees are found occasionally in colonies known to be of normal stock. Most often the wings are crippled so that the bees cannot fly. The wings may be missing, or present and not expanded, or partially expanded and crumpled. All three castes can have crippled wings, but those most often seen are drones. Queens with crumpled wings usually emerge from queen cells reared near the periphery of the cluster during cool weather. Crippling of this sort is probably due to subnormal temperatures during the pupal stage (Jay 1963, Fyg 1959).

Crippling of the antennae, mouthparts, and legs of workers and drones due to abnormal pupation was described by Fyg (1959). Such cripples can be produced in the laboratory with normal stock, but also occur spontaneously in some colonies (Schneider and Bruger, cited by Fyg 1959). This anomaly seems to be inherited, as it persisted for three related generations.

Internal Anomalies of Queen Bees

In the course of surveying maladies of queen bees, Fyg and others (Fyg 1964) described several abnormal conditions of the queen's internal structure: ovaries that did not develop; one or both of the lateral oviducts missing (mentioned also by Laidlaw and Eckert 1962); two spermathecae instead of the usual one; and accessory ovarioles not included in the ovaries, but located elsewhere in the abdomen.

Within the considerable information on the histology of sick queens (Fyg 1964, Vecchi 1976) conditions may be described whose fundamental functional lesion is not influenced by an infection. However, with a few exceptions, most of these maladies still require experiments to elucidate their etiology.

Catalepsy in Queen Bees

Queens rarely faint, but they have been observed to do so by beekeepers who have handled large numbers of queens. This condition has been called catalepsy (Brunnich 1922), epilepsis (Laidlaw and Eckert 1962), fainting (Miles 1922), or shock (Latham 1922). When it happens, it occurs just after a queen is picked off the comb by her wings. According to Latham (1922) the queen hooks her abdomen by the last sternite with a hind leg, pulls the tip of the abdomen forward, then stiffens momentarily, next becomes motionless for a few minutes, and then gradually revives, and returns to normal activity. Not every queen who hooks her abdomen is so affected, but Latham believed it most likely in large queens with enlarged abdomens that are laying heavily. In Miles's (1922) experience, catalepsy happened only to young queens; moreover, most of the cases described by Brunnich (1922) were also young queens. In some cases, the queen does not revive, but dies (Miles 1922). Catalepsy is apparently due to a temporary nervous disorder.

Overheated Bees

A condition called overheating can develop in worker bees when they are confined during hot weather without access to water. Even before the bees are irreversibly damaged, they may be stressed sufficiently to affect their subsequent performance (Weaver 1969). Before the bees die of overheating, those I have seen crawl rapidly and flutter their wings, which assume a cloudy appearance. If released in this state, overheated bees disperse by crawling in a disorderly manner, and regain no vestige of organized activity. Bees dead of overheating are often wet (Grimsley and Sadler 1936), perhaps from regurgitating fluids in vain attempts to cool themselves, as bees do under hot conditions (Esch

1976). The temperature within an overheated cluster probably exceeds 38° Celsius and may be as high as 50° Celsius, as can be inferred from data on upper lethal temperatures (Free and Spencer-Booth 1962, Lensky 1964).

Overheating bees is a hazard to be expected during hot weather when starting queen cells in a swarm box (Newswander 1977) and when shipping package bees (Grimsley and Sadler 1936). The hazard is obviated if the bees can be kept cool; Weaver (1969) suggests 18° Celsius as optimal for package bees.

Laying Workers

Although not normally productive in queenright colonies, worker bees can lay unfertilized eggs when their ovaries are functionally developed. Ovary development in workers is suppressed by the queen's pheromones, but released when this influence is removed (Butler 1957).

Therefore, laying workers develop most frequently under queenless conditions, but the rate at which they occur varies with different stock. The Cape bees of South Africa develop laying workers with only a few days of queenlessness, whereas other bees take much longer (Ruttner, Koeniger, and Veith 1976). In my experience, laying workers develop after about two weeks of queenlessness and broodlessness. However, in some stocks workers begin laying before all the brood emerges, and in other stocks sometimes no workers will lay.

Occasionally (how commonly or rarely remains to be seen), worker bees will lay at least a few eggs in queenright colonies. Partial ovarian development is common in queenright bees of a swarm or colonies with poor queens (Koptev 1957) and complete development must occur in at least a few workers of some stocks. Laying workers are probably responsible for the few cells of drone brood sometimes found above a queen excluder when the queen is confined below. In some colonies when supersedure of a poor queen is prevented, workers can produce considerable drone brood along with the queen's drone brood. If a queen is successfully introduced into a laying worker colony, the workers may continue to lay at a gradually diminishing rate along with the queen before they stop completely. For each of these possible instances of coexistence of laying workers and a queen, I have seen evidence; the progeny of the workers and the queen were distinguishable by body color or by mutant eye-color genes. Moreover, my observations are consistent with the experimental results of Jay and Nelson (1973).

Laying workers are usually revealed by the presence of eggs and brood in a queenless colony, and by the brood's appearance. The pattern of egg laying is usually diagnostic; there are many eggs in a cell, and some of the eggs are attached to the walls rather than to the base of the cell. Some of the eggs develop into larvae, but many eggs and young larvae must be eaten to leave only one larva per cell. The brood is virtually all drone brood, which is usually but not always scattered. Atypically, the egg laying pattern of some laying workers is so queenlike that much time is lost in a futile search for a queen.

The usual fate of laying worker colonies when left alone is that the adult workers eventually die, and the colony dwindles. Three to four weeks following the onset of laying by workers, there are considerable numbers of small drones, sometimes more drones than remaining worker bees. In times of dearth, laying worker colonies may be robbed of their honey and the remaining bees starved. However, laying worker colonies of the Cape bee (Anderson 1963) dwindle more slowly, because parthenogenetic workers are frequent enough to replace the adult population to some extent.

It is puzzling why laying worker colonies miss the opportunity to raise a new queen. Contrary to popular belief, one or a few female larvae are available in many laying worker colonies. Despite the fact that parthenogenetic females are infrequent in terms of numbers of larvae, they may not be rare. Tucker (1958) found six of eight laying worker colonies producing one or more worker bees. Either the nurse bees do not recognize the sex of the unusual female larvae, or they are not inclined to build queen cells. In light of the recent finding that laying workers produce queen substance (Ruttner, Koeniger, and Veith 1976), I think it likely that the production of queen cells could be inhibited in laying worker colonies. Even in laying worker colonies of the Cape bee, where parthenogenetic females are common, queen rearing is less frequent than one might expect (Anderson 1963).

How to return a laying worker colony to a productive queenright condition is usually the practical beekeeper's concern. Laying worker colonies usually will not accept a laying queen. Chances of acceptance are improved if their brood is removed and replaced with emerging worker brood. Örösi-Pál (1929) reported that queen acceptance is returned to a satisfactory level if all the combs are removed, and the bees of the laying worker colony confined without food for two days. During this time the ovaries of the worker bees will return to a nonfunctional condition. A widely recommended means of getting rid of laying workers in a queenless colony is to shake the bees off the combs at some distance from the hive. The laying workers are said not to return to the hive.