The extraordinary honey bee mating strategy and a simple field dissection of the spermatheca

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A. Mating behavior

The queen, mother of all individuals in a hive, determines the inherited characteristics of the colony. Her success, productivity and lifespan are dependent upon the number and genetic diversity of drones with whom she mates.

The mating habits of honeybees are extraordinary, though may appear risky and inefficient. Queens and drones mate in flight, flying significant distances from their colonies. This makes them vulnerable to predation and presents the risk of loosing the queen. For the drone, mating is fatal, and his only function. If successful, he will mate only once and leaves a portion of his endophallus in the queen as the mating sign.

The queen proceeds to seek the service of many drones and discards most of the semen collected. Remarkably, she stores some sperm from each drone. Their mating habits favor out-crossing and this enables the queen to maintain a genetically diverse social unit, enhancing colony fitness.

Egg-laying begins a few days after the last successful mating, and mating will not occur again. To assure her longevity, the queen must store enough sperm to maintain a strong colony. During peak production she will produce 1500 to 2000 eggs a day, releasing several sperm to fertilize each worker egg.

Mating occurs in specific aerial sites, called drone congregate areas, DCAs. These locations remain surprisingly constant, season after season and year after year, despite the short seasonal lifespan of drones. DCAs have distinct aerial boundaries and are defined by physical characteristics in open areas, protected from the wind. They tend to be away from high tree lines and hills, and are not found in flat, featureless areas (Taylor, 2002).

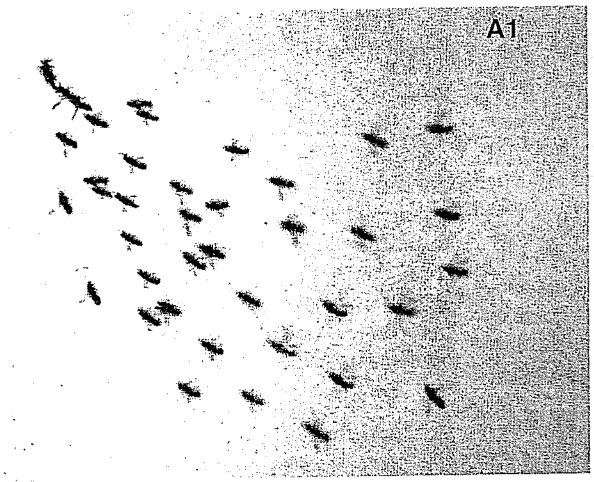
Drone congregating areas are generally 10 to 40 meters (about 30 - 130 feet) above ground and as high as 60 meters (about 200 ft), (Gary, 1963, Loper et al. 1992). They vary in size, from 30 to over 200 meters (about 130 to 690 feet) in diameter, dependent upon the terrain and bee populations (Koeniger and Ruttner, 1989). These also vary in shape though tend to be circular at the bottom and become elliptical, leaning to the wind with increasing heights. Several DCAs can merge together (Taylor, 2002).

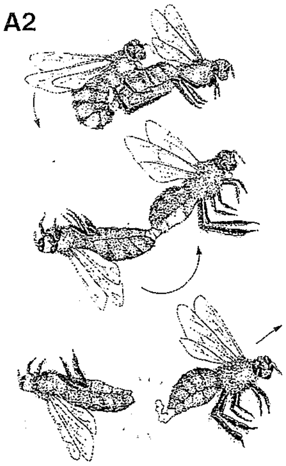
Flying from their colonies, the average distance between apiaries and mating sites is about 2 km (over a mile), and as far as 5 km (3 miles), (Koeniger, 1986). Under extreme experimental conditions, a few successful matings were reported when queen and drone source colonies were placed 16 km (about 10 miles) apart (Peer, 1957).

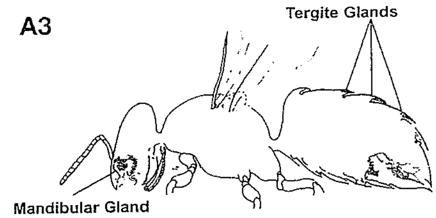
The virgin queen initially takes brief orientation flights, about 4 days after emergence. Over the next several days she will fly to several DCAs, taking several flights and mating several times on each flight. During this small window of time, she will mate with as many as 17 drones (Adams et al., 1977).

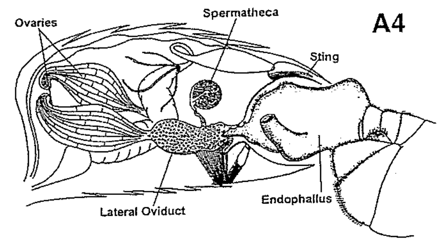
Drones, which are slower to develop and mature, fly to DCAs when they are about 12 days old and have mature sperm (Witherell, 1971). As their only purpose is to mate, they continue flying to various DCAs for the duration of their lives, as weather permits. This enables queens to mate with many drones from different apiaries in a short period of time.

Drones from the queen's apiary are the least likely to mate with her. Initially, she flies low leaving her colony, avoiding nearby DCAs. The differential flight patterns and the genet-









Mating Behavior

A1: A comet of drones chasing a queen in a drone congregating area. The queen, top right, is tethered. (Photo by N.Gary)

A2 Mating sequence of the queen & drone. Top: Pairing of the drone (left) and Queen (right) in flight. Middle: After eversion, the drone is paralyzed and falls backwards. Bottom: Drone parts remain in the queen as mating sign, marking her with an orange color and mucus reflecting ultra violet. (Modified from; Winston, M. 1987. Biology Of The Honey Bee)

A3 Pheromone produced by the queen's mandibular and tergite glands are strong sex attractants. (Modified from; Winston, M. 1987. Biology Of The Honey Bee)

A4 The Mating. The drone (right) delivers semen directly into the lateral oviduct of the queen (left). Semen migrates to the spermatheca, the sperm storage organ. (Modified from Koeniger, 1986)

ic diversity of drones within DCAs favors out-crossing, mating with unrelated drones (Taylor and Rowell, 1988).

The number and genetic mix of drones in DCAs is impressive. Drones from many different locations and directions fly to these specific sites. DCAs normally consist of 10,000 drones, though this can vary greatly. An estimated 25,000 drones from 200 colonies were reported in one DCA (Page and Medcalf 1982). Another study in Germany reported similar findings, drones from 240 different colonies visited a DCA (Koeniger, 1986).

Drone congregating areas have interconnecting pathways or flyways. Drones follow these flyways, visiting several DCAs in an afternoon. They enter in one direction and leave in another. The older, experienced drones fly the farthest, progressively learning new pathways. DCAs appear to be points where flyways merge, defined by the end of physical features or a depression in the horizon. Here drones appear to reorient and take other flyways. (Loper et al. 1991., 1992., Taylor, 2002).

Among the mating frenzy of DCAs, the clumsy buzz of flying drones creates a swarm-like sound. When mating occurs, the popping of the drone eversion can actually be heard. I have seen queens crash to the ground with the weight of several competing drones. A rock tossed in to the air or a passing insect will result in the instant formation of a drone comet chasing this. Yet beyond these specific sites, drones are not attracted and their buzz disappears. Apparently, queens flying outside these areas are ignored.

Groups of drones from numerous colonies are continuously forming comets and dissociating in DCAs. Virgin queens, flying into these sites, are instantly chased by these comets. In flight, the drone grasps the queen and everts his endophallus into her sting chamber, injecting semen into the oviducts Mating is instant and explosive, and as a consequence the drone is paralyzed and falls backwards. Part of his endophallus remains inside the queen as a mating sign (Koeniger, 1988).

Drones are attracted to queens by visual and olfactory cues. Pheromones produced by the queen's mandibular and tergite glands interact to produce strong sex attractants. The size of these glands increases at mating age. Queen pheromone production is age dependent, those of a virgin are different from a laying queen.

Queen mandibular gland pheromones, QMP, is produced in the head of the queen and distributed over her body surface. Drones are attracted and can detect this from as far as 60 meters (about 200 feet) with special sensory cells on their antennae (Koeniger, 1986).

The tergite gland pheromones are produced in dermal glands on the dorsal abdomen of the queen. As an aphrodisiac, this is detected at close range and stimulates copulation. Drones also produce pheromones. These appear to attracts virgin queens and flying drones to DCAs and may also help to form drone comets (Free, 1987).

After pairing, part of the drone's endophallus left as a mating sign provides a visual cue and increases the attractiveness of the queen to other drones. This marks her with a sticky orange substance and mucus which reflects ultra violet. The mating sign also holds the queen's sting chamber open and provides protection from the sting, encouraging additional matings (Koeniger, 1990). Mucus deposited by the drone during mating may also help to facilitate retention of sperm, as the queen's oviducts are heavily distended with the large volume of semen collected.

Koeniger (1990) suggests the mating sign is a form of cooperation between males to encourage further matings. A well-mated queen is more likely to pass on each drones genetic contribution. This is another amazing oddity of honey bee mating behavior, as in the animal world most males attempt to eliminate the competition, rather than encourage it.

As the queen mates several times in rapid succession, the mating sign of the previous drone is removed by specialized hairs on the endophallus of the next successful drone (Koeniger, 1990). Upon return to her colony, the queen's last mating sign is removed with the help of workers (Koeniger and Ruttner, 1989).

Multiple mating of the queen has major consequences on colony makeup and performance. What appears as risky behavior is actually beneficial to colony production and survival.

B. The colony as a superorganism

The honey bee colony, often referred to as a super-organism, is a populous, genetically diverse and highly cooperative society. Every individual bee is dependant upon the colony for its survival. Multiple mating of the queen creates an intricate social structure of relationships within the colony. Complex behavior patterns are remarkably flexible in response to changing needs and environmental influences. The dynamic range of tasks performed benefit productivity and survival in an impressive range of habitats.

Sperm storage and usage

The process of mating, sperm storage and usage provide the means to maintain this superorganism. The queen and the sperm she stores, determine the inherited characteristics of the colony, and fundamentally, its economic value.

The queen normally stores 5 to 6 million sperm in her spermatheca, the sperm storage organ. Mating with 10 to 20 drones, she may collect up to 200 million sperm in her oviducts. Most of the semen, about 90%, is discarded and expelled as a dry discharge. However, each drone produces about 10 million sperm, more than a single queen can store (Koeniger & Ruttner, 1989).

This mating strategy may initially appear wasteful, though it is actually highly efficient in terms of obtaining semen from many different drones. Of the fraction of semen that does migrate to the spermatheca, sperm from each drone contributes. Considering all the sperm produced by a single drone is identical, this process ensures high genetic variability among worker progeny in a colony.

Colonies headed by well mated queens are generally more successful. In a review of mating studies, Tarpy and Neilson (2002) reported 80% of queens mated with more than 5 drones and 54% with more than 10 drones. Population densities and time of year influence the number of times a queen mates. An increase in the number of available drones increases the mating frequency.

How the sperm is used and distributed in the spermatheca is a frequently asked question. Is this layered or mixed? Are the genotypes of workers representing the different drones produced in batches or uniformly mixed? Early investigations suggested the sperm was clumped or layered (Taber, 1955). Further research shows this is actually mixed, with some fluctuation in sperm usage (Page and Metcalf 1982, Laidlaw, & Page, 1984)).

More recently, Haberl & Tautz (1998) confirmed that sperm in the spermatheca is mixed and used randomly, and the rate of clumping is less than 6 %. However, they report the transfer and storage of sperm from different drones is not equal. The proportion of subfamilies in a colony ranges from 4% to 27%, with only moderate change over time. The conclusion is that a queen randomly uses sperm from all her mates, all the time, though some subfamilies are larger than others.

The superorganism

Genetic variability within a hive, the result of multiple mating, benefits colony fitness. Complex and dynamic behavior patterns are shaped by the interaction of several components. Genetic makeup determines the inherited potential and the environment influences expression. Each individual bee's social interaction and earned experience also affect behavior.

Specific tasks are often accomplished by groups of bees, each individual bee performs a step in a series of behaviors. Considering this and the diversity of tasks, the decision as to when and what behavior an individual performs is amazingly organized and lacking in conflict.

Age is a factor in determining division of labor. Groups of worker bees have a tendency to perform activities based upon their age. This is referred to as temporal polyethism. During the two few weeks of life bees generally tend to inside housekeeping, brood rearing and queen care activities. At three to four weeks, workers change to outside duties, such as foraging and guarding.

The ability to perform certain tasks is also dependent upon physiological conditions. Nurse bees have well developed hypopharyngeal and mandibular glands necessary for feeding larvae, and comb builders have well developed glands for wax production. The development of these glands peaks at 5 to 15 days of age, though can range widely (Winston, 1987). While age dependent, gland development is also affected by environmental influences such as nutrition, availability of resources and seasonal change.

The range in age of bees performing certain tasks is dynamic, flexible and overlapping. This enables colonies to be highly adaptable in response to colony needs and environmental fluctuations. For example, under extreme conditions brood food and wax glands can be reabsorbed or regenerated. A loss of field foragers, due to predation or moving colonies mid-day, will result in a shift of young house bees to foraging. Of the multitude of tasks displayed, there is great interaction and plasticity, creating a highly flexible colony population.

Division of labor is also determined by genetics. Various subfamilies, also called genotypes or patrilines, have a genetically based preference for certain tasks. This is referred to as task polymorphism, and has been shown for many activities including; grooming, scouting, foraging, guarding, undertaking, dance communication, and resistance to diseases and pests (Calderone & Page, 1988, Frummhoff & Baker, 1988, Robinson and Page,1989). Genetic variability between members of the same subfamily also occurs, as observed in the care of queen larvae (Page et al.,1989). Genetic specialists increase the efficiency of particular traits.

Studies of foraging behavior demonstrate how many factors collectively interact to organize division of labor. Genotype can affect development. In colonies selected for pollen collection, Pankiw & Page (2001) found high-pollen foragers begin foraging at an earlier age. High-pollen foragers were also reported to collect low-quality nectar, while the low-pollen foragers preferred higher sucrose concentrations and were more efficient nectar collectors.

The outside physical environment and the internal colony conditions affect behavior. Pollen foraging is stimulated by brood pheromones of developing larvae and a lack of adequate pollen stores. Nectar foraging is stimulated by high sugar concentrations. This initiates a chain of activity to increase foraging efficiency. The result is an increase in the number of foraging trips, the collection of larger nectar loads and a higher rate of recruitment and longer duration of dance communications (Seeley, 1995).

Among foragers, a genetic basis to preferred foraging distances and dialects of dance language have been demonstrated. Karl Von Frish (1967) observed this in the progeny of a queen mated with a racial mix of drones. Carniolan foragers used a round dance and Italians used a sickle dance to indicate a feeding station 10 meters (about 30 feet) from the hive. Carniolan foragers tend to fly longer distances than Italian foragers. Further studies by Oldroyd et al (2001) confirm this and suggest variations of the dance language, performed by different genotypes within a colony, may increase foraging efficiency.

While some bees are genetic specialists, others are generalists, each responding to the various and different levels of stimuli in different ways. An individual bee performs multiple tasks at any age and has a unique threshold of sensitivity to different stimuli. Simple localized cues form complex behavior patterns that can rapidly shift colony behavior. The diversity and flexibility of activities performed enable bees to be highly adaptable in response to changing conditions. Genetics and environment interact to shape behavior and development.

At a more basic level, the interaction of genes affects behavior. Most traits are quantitative; controlled by many genes, each having an effect. Groups of genes can influence a single trait with varying degrees of dominance. Specific behaviors can be dominated, masked or modified. This can result in higher or lower levels of expression, or a trait can be expressed differently, or not at all. The behavior displayed can be different from an individual's genetically determined tendency.

One genotype may dominate another, masking the true genetic makeup of a colony. For example, a particular subfamily displaying highly defensive behavior when disturbed, can mask the docile temperament of the majority of bees in a colony. This is observed when a European queen mates with a few African drones, among a majority of Europeans. The African genotype tends to respond faster and release more alarm pheromone, stimulating other nestmates to respond.

The other extreme occurs. Common traits that are recessive or exist in low frequency are often not expressed by a colony, such as hygienic behavior or SMR, suppressed mite reproduction. However, the presence of rare genes is crucial to ward off threats, such as diseases, parasites and stressful situations. Selection pressure enhances the frequency and expression of particular genes when these are essential to survival.

Too many, or the lack of a particular specialist genotype in a colony can be a disadvantage (Motitz and Fuchs, 1998). Extreme selection for a specific trait minimizes the diversity of behaviors responsible for productivity and survival. Also, other traits are often and unexpectedly affected. For example, the original Brown line selected for hygienic behavior in the mid 1960's by Walter Rothenbuhler was notoriously defensive.

The impressive array of traits and flexibility in behavior patterns of honey bees are due to their genetic variability. This enables colonies to exploit and survive in wide ecological ranges, endure extreme climatic conditions and resist pests and diseases. Their adaptability, productivity and survivability tend to be greater in out-crossed stocks (Cornuet,1986, Sherman et al.,1988, Fuchs & Schade , 1994, Palmer & Oldroyd, 2000, Tarpy & Page, 2002).

Multiple mating, a mechanism to avoid inbreeding

Multiple mating of the queen, referred to as polyandry, serves another essential function. It is a mechanism to avoid inbreeding. This is critical because bees are self-incompatible. The mating of closely related individuals results in inbreeding depression. This is characterized by spotty brood pattern, reduced vigor, slow growth, reduced survivability and increased susceptibility to pests and diseases.

Sensitivity to inbreeding is a function of the process of sex determination. Honey bees have a haplo-diploid reproductive system. Drones develop from unfertilized eggs and have one set of chromosomes, referred to as haploid. Females, queens and workers, develop from fertilized eggs and have two sets of chromosomes, referred to as diploid. Of the many genes on the chromosome, one determines sex.

Genes have multiple forms, called alleles. Normal females have two different alleles for the sex gene and therefore are heterozygous. These are derived from one set of chromosomes from the egg and a second set from the sperm. The problem arises when two identical sex alleles align, referred to as homozygous. This is a lethal condition resulting in a diploid drone. Workers recognize and remove the homozygous larvae soon after egg hatch. The empty cells create a spotty brood pattern.

There are an estimated 6 to 19 sex alleles in honey bee populations (Adams et.al. 1977). Multiple mating and the number and frequency of sex alleles in the gene pool increases the probability of out-crossing. This assures a high rate of brood viability.

Multiple mating and the haplo-diploid reproductive system also effect the degree of relatedness between sister groups within a colony. Half-sisters, workers fathered by different drones, have only 25% of their genes in common. Super-sisters, workers with the same father, have 75% of their genes in common. Full sisters, workers fathered by brother drones, which is rare, have 50% of their genes in common.

There is kin recognition among these different subfamilies, which also influences interactions and behavior. For example, reproductive favoritism within subfamilies occurs. Workers more closely related to the queen tend to swarm with her, and workers rearing a queen will choose a larva that is more closely related to itself (Breed, 1985).

The out-crossing mating habits of honey bees serve a purposeful strategy. It is the genetic diversity and social complexity that enable colonies to display an impressive range of behaviors and adapt and thrive in many different environments. However, for the beekeeper, this can complicate the process of selective breeding, if not given adequate consideration.

C. The spermatheca

The queen and her colony's survival is dependant upon her ability to maintain a large population. During peak season she will lay more than her own body weight in eggs, producing an impressive 1500 to 2000 eggs a day. Her paired ovaries contain about 360 ovarioles, where the eggs are produced (Snodgrass, 1956). She must store enough sperm to fertilize and support a high rate of egg production. Incredibly, the queen stores and keeps sperm alive for the duration of her life.

The role of the spermatheca

The spermatheca, the sperm storage organ, is common in the female reproductive organs of insects and many other invertebrates. The honey bee queen's spermatheca is a spherical, fluid filled organ, over a millimeter in diameter. The cell wall consists of a single layer of epithelial cells covered by a net of trachea.

The sperm in the spermatheca is maintained in a state of quiescence with very low metabolism. Special physiological conditions maintain its fertilizing ability. The cell wall of the spermatheca allows the active transport of oxygen and nutrients. Oxygen is supplied by the tracheal net, and nutrients are supplied by the spermathecal gland. (Fye,1983., Koeniger, 1986).

After mating, the sperm takes about two days to migrate from the oviducts to the spermatheca. Conditions during this period are important to facilitate sperm migration. This is influenced by the care of worker attendants, colony nutrition and population size (Woyke, 1983). These are all factors that beekeeper can enhance through colony management.

Upon return from her mating flight, the queen receives great attention from the workers. They chase her as she runs over the combs, antennate, lick and feed her, and help remove her mating sign. Sperm migration is enhanced by this attention and the queen's activity. She begins egg laying within a few days after the last mating.

Colony conditions and seasonal changes influence egg production. Proper nutrition is essential for egg development. A healthy and substantial population of bees is necessary to provide the warmth of brood nest temperature, and care for the queen and her developing brood. The queen will adjust her egg laying rate to the resources available, colony demands and seasonal fluctuations.

As queens age, they release less sperm to fertilize each egg (Harbo, 1979). Older queens produce less worker brood and more drone brood. The aging process may be marked by deposits of a carbohydrate protein complex that forms as a mass on the spermatheca. Fyg (1983) suggests this can degenerate the cell wall of the spermatheca and may have a negative effect on sperm. Deposits can begin forming when queens are about 2 years old

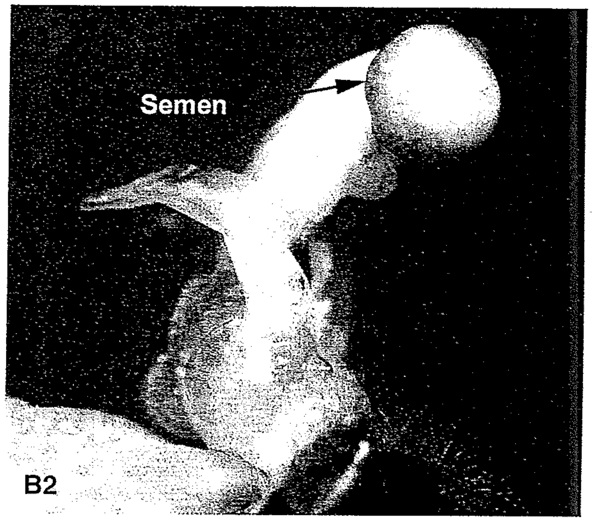
The importance of reproductive status

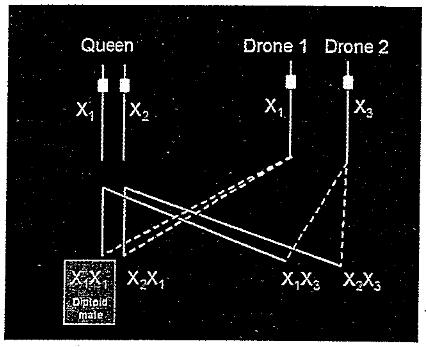
To maintain highly productive colonies with economically valued traits, beekeepers need to know the origin, age and reproductive status of queens in their apiaries. Uncontrolled supersede of queens often results in a loss of production and desirable colony characteristics.

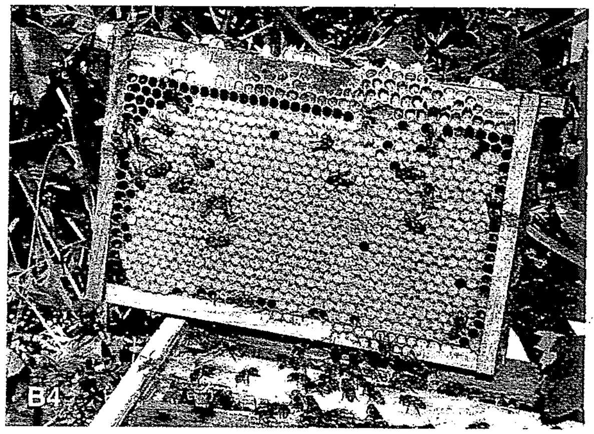
The uncertainty of a queen's performance potential can be confirmed by a simple field dissection of the spermatheca. Verifying interpretations of colony observations will help to more readily recognize problems and to accurately make evaluations and decisions.

I routinely check the spermatheca of old queens when re-queening colonies or any queens that do not appear to be at peak performance. This reveals how well queens have mated and indicates how long you can expect them to perform under your conditions and management practices.

Colony assessments and the status of virgin or failing queens can be easily confirmed. A young queen, suspected to be un-mated or poorly mated, or queens with abnormal laying patterns, as indicated by several eggs in a cell or eggs placed on the side walls of cells, can be checked. Hive conditions must be considered, as these signs can also indicate laying workers or inadequate comb space. Recognition of queen condition is increasingly important as miticide treatments are known to cause fertility problems in both queens and drones.







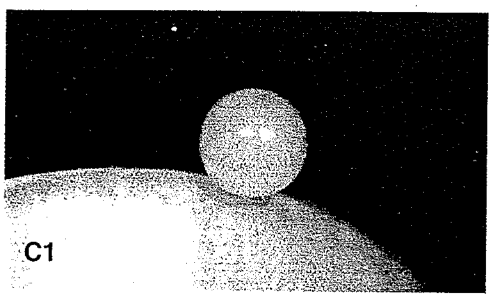
The colony as a superorganism

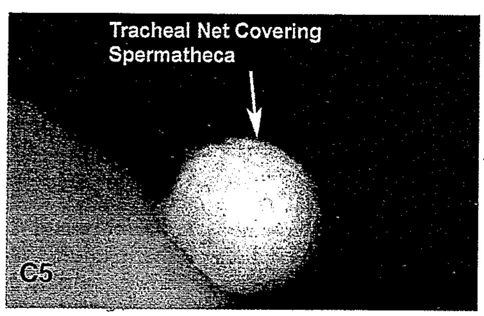
B1 Each drone produces about 10 million identical sperm. Drones are haploid, developing from unfertilized eggs and have only one set of chromosomes.

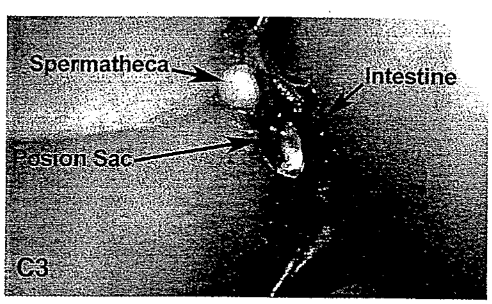
B2 The endophallus of a drone with exposed semen. Mating with numerous drones, the queen stores only a small fraction of the semen collected, 5 to 6 million sperm from a mix of each drone she mated.

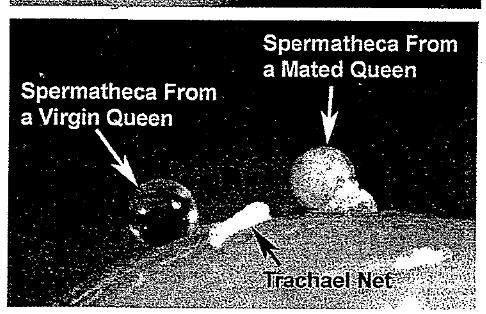
B3 Sex is determined by a single gene (X), with different alleles, (X1, X2, X 3 , etc.). Females have two different sex alleles, drones have only one. The Queen, represented as (X1, X2) has mated with two drones X1, , and X 3 . The resulting worker progeny consists of four genotypes (X1X1) , (X2,X1), (X1X 3) ,(X2,X 3). The eggs with two identical alleles (X1X1) have a lethal condition and the larvae are removed causing a spotty pattern in 25% of the brood. (Redrawn from Page & Laidlaw 1997)

B4 A solid brood pattern results from the mating of a queen to a genetically diverse source of drones carrying a variety of sex alleles.









The Spermatheca

C1 The cloudy appearance of this spermatheca indicates the queen was poorly mated or has used most of her stored sperm. She is or soon will become a drone layer.

C2 The spermatheca of mated queen is the same color as fresh drone semen. Notice the light and darkish swirl pattern of densely packed sperm.

C3 In the pulled abdomen, the clear poison sac, spherical spermatheca and intestine are exposed.

C4 The spermatheca, covered with tracheal net, can be teased out of the body cavity with a fingernail

C5 Comparison of spermathecas from a virgin and a mated queen. The tracheal net coverings have been removed.

C6 The rough, whitish texture of the spermatheca is due to the tracheal net covering. This is removed by gently rolling the spermatheca between your fingers.

For queen producers, field dissection of the spermatheca is a valuable tool to determine if the supply of drones is adequately mature and sufficient in number for the size of the mating yard established. Recognizing the importance of drone flooding and the benefits of out-crossing are essential. For mating, Taylor & Rowell (1988) recommend locating drone source colonies 1 to 2 km (about a half to 1 mile) from queen mating yards.

When weather conditions are questionable, the spermatheca test will reveal if queens have successfully and sufficiently mated. This information helps to determine quality control, enabling more accurate culling of production queens in mating yards.

The spermatheca test also provides valuable feedback when learning to use the technique of instrumental insemination. During the classes I teach, this procedure is used to provide quick feedback as to how successful inseminations are progressing. After insemination, queens are banked for a day or two and checked to see if sperm has migrated to the spermatheca.

It is best to wait two days after the queen has been inseminated before testing, as the sperm requires this time to migrate from the oviducts to the spermatheca. After 24 hours migration is incomplete and the oviducts are often still distended with sperm, though a milky cloudiness of the spermatheca is evidence that some sperm has successfully migrated.

Field dissection of the spermatheca

Examination of the queen's spermatheca is accomplished by a simple field dissection. The only tools required are your fingers. However, a pair of fine forceps can also be used. To perform this test the queen must be sacrificed. Have replacement queens on hand, as this should be a routine management practice.

The first step is to humanly sacrifice the queen, pinch her head and thorax. With your fingernails or forceps, grasp the queen's last abdominal segment, dorsally and ventrally (top and bottom). Pull the terminal segment apart from the rest of the queen's body.

At this stage, you will see the intestine and a large, shapeless, clear poison sac. Among this is a remarkably sturdy, spherical shaped structure, about 1 mm in diameter. This is the spermatheca. It is made up of a transparent, chitinous membrane.

Initially the spermatheca will appear whitish and rough in texture. This appearance is due to a covering net of trachea. From this, tease the spermatheca out of the body cavity with your thumbnail.

To remove the tracheal net covering, gently roll the spermatheca between your fingers. The tracheal net will collapse in a small separated white mass, exposing the spermatheca.

Reading the spermatheca

The reproductive status of a queen is revealed in the color shade and density of her spermatheca. Experience observing various samples will enable you to recognize these differences. A virgin and a mated queen are readily distinguishable. You can also recognize whether a young queen is well mated or poorly mated and if an older queen's sperm supply has been depleted.

The color or lack of color of the spermatheca is due to the quantity of sperm it contains. The transparent membrane of the spermatheca is apparent in the virgin queen, this is crystal clear.

The spermatheca of a well mated queen is the color of drone semen. This is a creamy, coffee au lait color with a pattern of light and darkish marbled swirls. The sperm tends to clump in bundles and is densely packed, creating the swirl patterns. A comparison of the spermatheca from a virgin and a well mated queen are pictured.

A cloudy or milky whitish appearance of the spermatheca indicates an inadequate supply of sperm. The queen was poorly mated or has depleted most of her sperm supply. Varying color shades of the spermatheca reveal different densities of stored sperm.

As a general rule, the queen's sperm supply is insufficient if the spermatheca does not show the marbled contrasting color shades. She is or will soon become a drone layer or partial drone layer. Observing the spermatheca of queens in various life stages will enable you to recognize their reproductive status.

Assessing queens

Assessing queens is an essential part of beekeeping. Beekeepers who follow good management practices and evaluate colonies individually can learn to make generalized predictions and decisions based upon the sacrifice of an occasional queen. Problems, resulting in economic loss, can be foreseen and prevented.

This simple field dissection of the spermatheca eliminates guessing and can be preformed anywhere, without special equipment. Becoming familiar and recognizing the varying degrees of spermatheca coloration and density is something every beekeeper can do.

You can diagnose and confirm the status of queens. Recognizing; when a queen is failing, when her egg-laying capacity has declined, why she is unresponsive to the needs of the colony, and if she has superseded, is important. Identifying the unknown status of a suspected virgin or rogue queen eliminates guessing.

Good management requires the routine replacement of failing, superseded or lost queens. Poor queens never improve. Supersedure queens are often inferior and in the process of natural mating the selected traits valued are genetically diluted. Tolerance of this costs beekeepers time, labor and production loss.

Judicious use of the spermatheca test enables beekeepers to become more perceptive of queen performance levels, and to readily predict and remedy problem situations. This is a good management tool to help maintain uniformly, strong apiaries with desirable characteristics.

Conclusion

Beekeeping has changed tremendously with the introduction of parasitic mites. We have run the chemical treadmill to find that mites and American foulbrood disease are now resistant to routine chemical treatments. Inadvertently, in this process we have maintained susceptible bees and selected for more virulent strains of mites and disease.

We are entering a new era of beekeeping focused on stock improvement. The challenge is to select and breed bees that are both productive and naturally resistant to pests and diseases. To accomplish this a basic understanding of how biology affects honey bee breeding is essential.

Geneticist Rob Page described bee breeding as a balloon. Pressure applied at one point causes unexpected things to pop out in other places. The complexity and dynamics of honey bee behavior presents a unique set of obstacles. We are just beginning to discover the nuances of how this all works.

Major advances in agriculture are due to the accomplishments of selective breeding in livestock and crop production. The beekeeping industry has not shared the same level of success. Many of these programs rely on inbreeding to fix traits and establish uniform stocks. Honey bees are sensitive to inbreeding because of their haplo-diploid reproductive system, presenting a major constraint.

The diversity and flexibility in expression of traits are what make the honey bee "superorganism" successful. Productive stocks must be selected for several characteristics simultaneously. Economically valued traits are behavioral and polygenic (controlled by many genes) and strongly influenced by their interaction with the environment. This makes the evaluation process more difficult.

Another complicating factor is the lack of ability to control mating. It is impossible to maintain selected stock when queens randomly mate with many drones of unknown genetic origin. Isolated mating, drone saturation of mating areas, and/or instrumental insemination must be employed. Bee breeding programs are also labor intensive, require a dedicated effort and a long term commitment.

Our knowledge of honey bee genetics and inheritance is basic, and we are in the infancy stages of bee breeding. Research has been focused on studying single specific traits. Specialty stocks, such as the SMR, are being developed and can be used to seed traits of mite resistance into commercial apiaries. This is a first step. However, there is not much information available to beekeepers as to the mechanics of how to develop and manage practical bee breeding programs.

The Page-Laidlaw Closed Population Bee Breeding Program probably offers the most practical and effective means of commercial stock improvement (Page & Laidlaw, 1982). Their book, Queen Rearing & Bee Breeding, covers basic techniques. A practical working model of this system is the New World Carniolan Program. The selection process used for this is described on the web site http://iris.biosci.ohio-state.edu/honeybee/breeding.

The increased interest among beekeepers to establish bee breeding programs, and the development of new technologies and methodologies for stock improvement by the scientific community, offers an exciting future. The intention of this article is to provide some basic background and insight into the factors that affect practical bee breeding. The availability of a variety of high quality stocks will provide the best and most enduring solution to our current apicultural problems, and is essential to the future health of our industry.

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