Hive Control & Decision Making

Super Families, Super Sisters, and Luck Determine What Happens

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One of the most fascinating aspects of recent honey bee biological research has been the attempts to integrate the impact of the multiple drone mating with the concept of colony control and the decision making processes within the colony. Because the worker bees in a colony have one mother and many fathers, the sister workers of the hive are not identical. Instead they form various sub-families of sister workers who share a particular drone father. These are called super-sisters, and the entire colony of these different super-sisters make up the super-family that we call the bee colony.

It has been shown that individual worker bees belonging to the same sub-family are able to recognize each other and distinguish their super-sisters from their half-sisters. This has lead some researchers to test to see if there may be some effort by these super-sisters to promote their special interests and increase the reproductive fitness of their particular subfamily. However, any potential nepotism must be mediated by the evolutionary drive to insure the success of the hive, especially during hive reproduction.

One review of research reports the specialization of super-sisters (also called patrilines), in a wide range of bee behaviors: pollen gathering; nectar gathering; guarding; undertaking; nectar foraging; nest site scouting; queen rearing; oophagy (egg cannibalization), oviposition and larval care in queenless colonies; grooming behavior; plant choice for pollen collection; and foraging distance[1]. The authors then used microsatellite DNA analysis (a system that uses short "snippets" of DNA to identify genetic information) to show that there were 16 sub-families in one colony of honey bees, and that two subgroups were represented in significantly higher levels in two tasks: water collection and scenting. This suggests a genetic component to task choice.

Five queen cells of different stages of maturity in a Russian stock colony, June 2006, Durham, CT. The worker bees are paying greatest attention to the second cell on the left, where the developing queen has been producing pheromones and the worker bees have removed the wax from the pupal casing. A very narrow slit is evident at the foot of the worker bee at the tip of the cell. This is the cut the queen has made with her mandibles to free herself from the cell-prison.

One subfamily of bees with the same father (as determined by genetic testing) may provide specialized services within the colony. This reflects another advantage of the queen mating to multiple drones and the resulting drone diversity. No one subfamily is apparently able to control a particular hive behavior, but certainly influences the hive's welfare through decentralized decision making.

Because there is no central control of the bee social structure, no governmental center, decisions must be based on group decisions utilizing the different sub-families. We observe colonies make decisions about foraging, nest maintenance, comb building, and reproduction. Perhaps the strongest example of the group decision-making process at work as there is in the process of producing a new queen, which we will discuss next. We will follow that with a discussion on how colonies make decisions about the comb building process.

Queen Rearing as Influenced by Colony Decision-Making

Queen replacement occurs in the hive during the whole colony's instinctive reproductive division, the process we call swarming. Queen replacement also takes place when the queen fails to produce the normal amount of worker brood, in what we call the supersedure process, or when the queen is accidentally killed or lost, using the emergency response. Researchers[2] have reviewed the literature and divided the queen replacement process into three discrete behaviors: queen production (selection and feeding), queen emergence, and surplus queen elimination. There are also individual differences as seen

[1] Per Kryger, Ute Kryger & Robin F. A. Moritz. 2000. Genotypical Variability for the Tasks of Water Collecting and Scenting in a Honey Bee Colony. Ethology 106 (2000) 769-779

[2] Tarpy, D.R., and D.C.Gilley. 2004. Group decision making during queen production in colonies of highly eusocial bees. Apidologie 35 (2004) 207-216

This close-up view of the cell tips show where the wax has been removed from the tip of the cell, except along the line of the slit cut by the queen inside the hive. In the time it took these photos (under three minutes), the queen was able to cut the cell open and emerge. This is a strong indication that the worker bees were keeping her confined in the cell, feeding her through the slit. Note that the other queen cells have heavier wax along the line where the queen slit would be made by the queen inside. These cells contained younger queen pupae, indicating that the queen laid the eggs for these cells at different times.

The virgin queen emerges from the cell moments later. She was one of a number of virgin queens that all emerged during this hive inspection. The humans disturbing the bees apparently interfered with the worker bees ability to keep the queen confined.

in individual queens, as shown in piping behavior, when an audible 'piping' sound made by one queen serves to delay the emergence of other mature queens from their queen cells. The queen doing the "piping" has been shown to have a much higher likelihood of becoming the new queen of the hive.

Queen Rearing Decisions

Honey bees rear surprisingly few queens during the replacement process, perhaps finishing as few as three to six, but usually starting between 12-24 individuals – starting many and finishing few. This is in sharp contrast with the 5,000 to 20,000 drones produced by the average colony during one season. Swarming behavior is observed only when conditions favor the collection of pollen and nectar needed to support high brood rearing and queen cell production. New queens are started in the queen cups that are prepared for the queen to lay into; they are on a queen track even before the egg is laid, unlike supersedure and emergency queens. Sometimes the workers place royal jelly in queen cups before the queen lays into them. In fact, a queen larva receives continuous and abundant royal jelly by large numbers of nurse bee visits, and are provided an even greater amount of the rich food about 24 hours before the queen larva pupates, just prior to the time the cell is sealed with wax by the worker bees.

The total time for queen cell construction, egg laying, larval hatching and feeding is 15 to 16 days, depending upon genetic and environmental differences. This gives the different subfamilies within the hive time to decide which larvae will continue toward final queen production. If a frame of newly hatched larvae is placed into a recently de-queened and artificially broodless colony, a large number of cells will be started as emergency queen cells, perhaps as many as 200 on one frame. But as larval feeding progresses the number of queen cells dwindles. Part of this may be due to less than ideal conditions for cell development, for queen cells are very sensitive to chilling and overheating and may be rejected if they are on the perimeter of the comb where the temperature is less than optimal. Worker bees may decide to destroy a queen cell at any point during its development. This is often seen in queen rearing operations, where a careful count of the number of cells the day after the cells are sealed is larger than the number of ripe cells containing mature queens ready to emerge. Some of this cell count reduction may be a form of hygienic behavior removing diseased individuals, and some may be due to the decision making process of the bees.

There is adequate evidence to show differential treatment of certain eggs, larvae and pupae destined to become queens over those that fail to become queens. During the incubation period, worker bees vibrate certain cells. The workers "shake" queen cells for one to two seconds at approx. 16 Hz. Some cells are shaken three times as much as others, although this does not predict outcome. Instead, queen cells that are started earlier are found to be shaken more, and have higher emergence success.

In emergency queen cell production, the age of the brood used for cell production determines the fate of the queen cell; fully developed queen cells will be destroyed if they contain the wrong age brood. Thus the queen is able to monitor the developing queen and eliminate those queens that will not become vigorous queens.

Efforts to prove that super-sisters, with a level of relatedness of G=0.75, favor queens from their subfamily over half-sister queens, with a degree of relatedness of G=0.50, have failed to show that there is a clear and statistical significant bias. But if workers do not select super-sisters for queens, they may employ group decisions to improve the quality of the queen produced in the hive.

Emergence of new queens

Worker bees routinely keep fully developed queens imprisoned in their queen cells for prolonged periods of time. I witnessed a dramatic example of this when I inspected a Russian colony during peak swarm season (all colonies in the apiary had swarm cells after a very rainy buildup period, not just the Russian colonies). As the

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colony owner and I opened the hive we observed many queen cells. I suggested we harvest a few cells and use them to make up increase colonies, so we carefully cut a few cells off the comb and placed them on top of the neighboring hive. As we inspected the remaining frames in the colony we noticed virgin queens running about on the combs, and soon I was rapidly stuffing queens into empty cages I carried in my beesuit pocket. Then we noticed that the queens from the cells we placed on the hive cover were emerging. The simple act of opening the hive had apparently disrupted the process the worker bees use to confine queens within their cells, and, thus prevent them from emerging.

After our momentary excitement died down I looked at the queen cells and saw that some queens had cut open the cells to emerge, but the workers had imprisoned them by adding additional wax to the slit at the tip of the cell where the queen had cut open the pupal silk and wax. It was through this narrow slit where the worker bees feed the queen inside the cell-prison. While Francis Huber first recorded this process in 1792, it remains a dramatic and exciting experience to observe. Our timing was unique in that we observed a large number of queen cells, over a dozen, of mixed ages and some with confined queens.

Why do bees keep perfectly good queens entombed in the cells? There is some evidence that the worker bees are using their collective consensus building to control the fate of these queens. The imprisoned cells that are shaken by worker bees are more likely to be the first to emerge. The workers control the timing of queen emergence by adding or reducing wax deposits on the incision at the tip of the cell (they must keep just ahead of the queen, for our hive visit must have disrupted the bees ability to control emergence). Finally, there is some evidence that bees will selectively confine half-sister queens over super-sister queens, one of the best examples yet of potential genetic control of the final queen.

Two other queens have emerged during the hive inspection. The chewing and control of the emergence process is under the control of the worker bees; the queens' instincts are to get out of the cells!

Queen elimination

Once a queen emerges from a cell, the worker bees continue to control her fate. They can favor one queen so she emerges first, allowing her to systematically sting her sisters still confined in their queen cells. Or the workers may kill the queen by arranging two queens to "duel" on the comb until one queen is dead (this is the simplistic example of queen elimination we have seen in nature films). The workers often have control over the success of the fight, keeping one queen in a "ball" of bees so she is less able to defend herself; indeed, a queen is more likely to win if related to the worker bees.

New queens usually do not leave with the primary swarm (the colony's original queen does this), but will depart with an afterswarm – this is most often the explanation for the workers keeping queens confined in their cells. Many swarms contain multiple virgin queens. This may reflect the large number of confined virgins, as well as a selective advantage of getting a new queen to the new nest successfully. Once the hive is in the new location, dead virgin queens may be found at the entrance of the hive, so the queen to queen duel happened in the new nest site.

Just how any preferential treatment of one queen over another is decided is unknown, and requires further study.

Selection Pressure

Control of the selection, release and destruction of queens is one of the most critical duties the worker bees have, if not the MOST important in terms of colony survival and selective advantage. While a colony could employ a policy of "any queen will do" the selection pressure on a colony appears to produce a significant number of queen candidates that are evaluated at several points in the production cycle and culled to eliminate those queens that are poorly produced, developmentally defective, wrong-aged, or of unacceptable genetics. The ability of a colony to survive within an environment undoubtedly places strong selective pressure on queens that must perform within this environment, and the only means for elimination is through the worker bees.

Worker and Drone Comb Construction as Influenced by Colony Decision-Making

During the active foraging season honey bee colonies are forced to decide between the need for food for the colony OR the need to build open comb for storage of incoming pollen and nectar. Either the colony builds comb for food storage (a process they cannot reverse once the comb is built), or they may utilize food coming into the hive and, because of the lack of empty comb, run the risk of losing abundant food when it becomes available. Recently Stephen Pratt[3] reviewed colony control aspects of worker and drone comb construction. He reported that in nature a new colony builds 1 m^2 of comb in one year, or a little more than 10 ft^2. A colony metabolizes about one-eighth of the honey it collects during the year to

[3] S.C. Pratt, 2004. Collective control of the timing and type of comb construction by honey bees (*Apis mellifera*). Apidologie 35 (2004) 193-205

secrete wax for comb construction. Bees must respond to hive and environmental conditions in such a manner as to optimize comb construction while preventing over- or under-production of wax comb at the cost of lost resources.

Lacking a central government, the worker bees must have some feed-back mechanism to reach a consensus of *when* it is beneficial to build comb, and in the case of worker and drone comb production knowing which *type* of comb to produce. Pratt has determined that to build comb colonies must fill two needs: "adequate nectar collection in the field, and the filling of their comb above a threshold level." The combination of *comb fullness* and *nectar intake* must align to stimulate worker bees in the hive to secrete wax and initiate comb construction.

The concept of comb fullness may remind the reader of G.M. Doolittle's recommendation to keep three full frames of honey in the colony all of the time (See Connor, *Increase Essentials*, 2006), suggesting that a certain level of fullness of the comb is required for bees to build new comb and initiate other expansive behaviors. Without a certain level of comb fullness, the colony will not build comb. Once the amount of filled comb and the incoming level of food reached the critical threshold, both comb construction and food storage will proceed.

We see this in the buildup period of the Spring when the bees are actively gathering pollen and nectar, but are not engaged in new wax building. Even if supers filled with foundation are added to the hive, the bees often delayed building new wax in these frames. During this time, if you look at the brood nest of the colony, you will find that the bees are busy filling the brood rearing areas of the hive with food reserves – pollen and nectar essential for new bee production and colony growth. The bees may be stimulated to draw out a brood comb if a frame is removed and a frame of foundation is added to the center of the brood nest. But sometimes this frame serves to divide the brood nest, as the bees are not yet ready to draw wax and build this comb.

Seasonal patterns of nectar availability show that surplus nectar is gathered only on certain days, just 14-35% of the days in the nectar season. When bees are not gathering nectar it is because the flow has curtailed, perhaps because one plant has stopped blooming and the bees are awaiting for the next plant to flower. The comb production of a hive reflects this pattern, and since there are generally several major periods of nectar availability during the season, there are corresponding periods of active comb building. When the supply of incoming nectar stops, the bees stop comb building as well; the bees have adapted their comb building to suit several periods of rich food availability during the season.

The individual bee plays an important role in this process, since returning foragers must find house bees to unload their nectar. The house bees are also involved in wax secretion, so there is a feedback mechanism at work that allows the bees to monitor incoming food and wax secretion. Then, when the supply of nectar falls, the stimulus is absent and the house bees stop producing wax.

The actual wax-building process is highly dynamic, as one bee adds wax to a cell, another bee moves to the same area and reworks the same area of comb. This process continues until the comb is built, filled and capped.

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This allows all the bees to know the size of the cell being produced, and ensures uniform cell construction.

Drone or worker comb?

In general, small colonies of bees are unlikely to produce drone comb – unless the queen's status supports the production of drones. Queenless colonies are more likely to produce drone and large-celled worker comb, but if queen pheromone is provided, the bees produce only worker cells. In hopelessly queenless colonies, the production of drone comb for drone production is the only genetic legacy the colony is able to pass on to the pool of reproductive bees.

In normal colonies, there is an average 17% drone comb. Since the bees do not produce this level of drone brood, this comb is used for both male bee production as well as for food storage. When colonies do not have drone comb present in their hive, they will instinctively build drone comb to balance the ratio of the two comb sizes. When there is a large amount of drone comb present, the bees automatically adjust and build more worker comb.

How do the bees know how to do this? Since the bees make direct contact with the combs, they must somehow measure the number and ratio of drone cells and worker cells. Since house bees have their heads into cells routinely, they may measure cell size in the same manner that the queen does, and this may provide them with the stimulus to produce the necessary cell size. Thus a large amount of drone comb, and even drone brood, may have a strong inhibitory effect on production of more drone comb. The bees are doing nothing more than measuring the hive environment, and adjusting it to some inherited, genetically regulated standard.

Finally, there must be some sort of comb building peer pressure – preventing one worker bee from building one drone cell in the middle of a comb of worker cells. The individual bees are undoubtedly influenced by the collaborative method of same-cell size construction on the comb, and this keeps the comb construction uniform and highly efficient. When damaged comb is placed in a hive the bees will sometimes build drone comb in the area where worker comb once existed. It is not the nature of the damaged comb that determines the type of cell that will be built there, but the integrated dynamic of the comb building bees, their evaluation of the colony's comb needs, and the ratio of comb that already exists within the hive that makes their comb building decision. BC

When not day-dreaming about selecting a patriline of bees to perform human chores (cleaning, cooking, bill paying), Larry Connor is sometimes found fussing at his website: www.wicwas.com. He is the worker bee who answers all messages to ebeebooks@aol.com. Thanks to Jim Clinton for assistance with these photos.