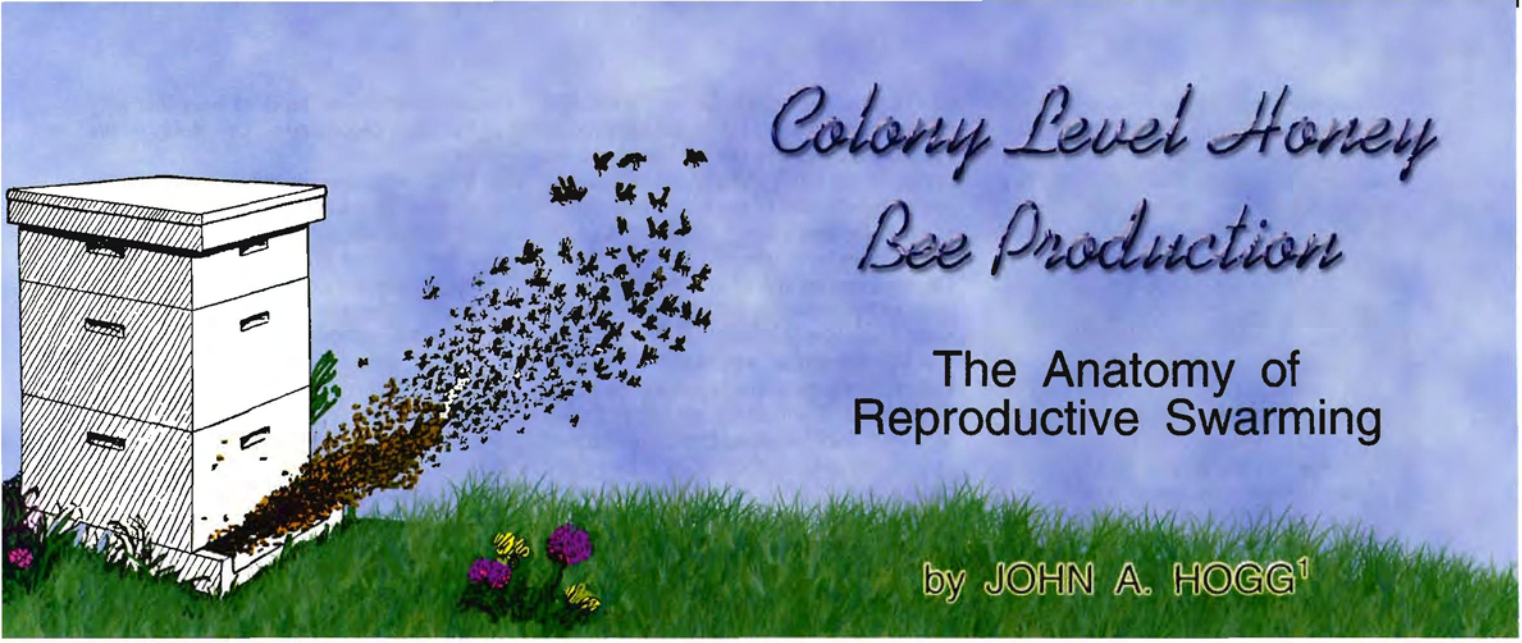

Colony Level Honey Bee Production

The Anatomy of Reproductive Swarming

by JOHN A. HOGG[1]

It is inevitable that a rapidly expanding population of bees in a fixed cavity nest (feral or unmanaged) will become space bound (congested). Almost without exception such bees will swarm at least once in a season.

The timing of the swarming season may vary significantly due to environmental factors and differences in the genetic traits of the bees.

The *cause of swarming*, Phase I, is well understood to be "physical" due to congestion in the brood nest, which triggers natural mechanisms for reproductive colonization automatically, modulated by environmental factors.

The events which follow in Phase II, the *implementation of swarming*, are "behavioral" and not well understood; these behaviors, aside from queen rearing and the issue of the swarm itself which are conspicuous, are known only through the recorded observations of distinguished behavioral scientists.

The foregoing distinction between the cause of swarming as *physical* and the implementation of swarming as *behavioral* is important to shaping a clear vision of the anatomy of swarming.

It is the belief of this scientist beekeeper that we already have all of the critical information and anecdotal evidence needed to visualize a useful and reliable gross anatomy of swarming from cause to consummation; and that this will not change as further information on which pheromones do what emerges.

This analysis links the currently accepted view of the *cause of swarming*, Phase I, congestion in the brood nest by surplus workers, with the new concept that the *implementation of the swarm*, thereafter in Phase II, is orchestrated by a temporal caste of swarm control bees.

To my knowledge, there is as yet no scientific data that could suggest swarm control bees physiologically. However, we will see that the concept of a temporal division of labor in female reproductive behavior for the purpose of swarming has been proposed by E. O. Wilson[2] to explain the observed implementation of the swarm by worker bees. This concept, to my knowledge, does not appear to have found its way into contemporary books or scientific journals about honey bees.

Basic research on swarming during the mid-1900's and beyond has established the currently accepted view that the initial *cause of swarming* (Phase I) is interference with the distribution of queen pheromones secondary to congestion in the brood zone.

Quoting Mark Winston (*Swarming*, Bee Culture Aug. 2000)

> *".....the behaviors of swarming remain as complex as they ever were. I think the cause of swarming is more on the simple side of things. That is, as colonies grow in population and become congested, the distribution of queen pheromone is restricted and the amount of pheromone per bee diminishes, leading to the release of workers from the queen's inhibitory influence and the rearing of new queens."*

It is congestion centrally in the brood nest that restricts the outward distribution of pheromones to the periphery and beyond.

Winston also notes the complex behaviors that follow the release of workers from the queen's influence. These behaviors are attributed to swarm control bees in this article.

> *"Swarming has always been a subject of intense speculation and research by beekeepers and scientists alike. It is, after all, one of the most complex behaviors in the world of social organisms, with upward of 30,000 individual workers coordinating the precise choreography involved in rearing queen cells, exiting the hive, clustering, scouting and eventually moving to a new nest site.*
>
> *The key to understanding swarming is in the rearing of new queens, for this is the first and most critical step that eventually results in colony reproduction. Reproductive swarming cannot occur without new queens developing in cells....."*

Which worker bees are responsible for coordinating all of these functions, including queen rearing, and why?

PREMISE

It may be that the missing factor in explaining Phase II of the anatomy of swarming is a temporal caste of swarm control bees assigned to orchestrate queen management and all subsequent preparations for swarming, including the consummation of the swarm itself.

This fundamental factor may account for the mystery of *swarm fever*, which in turn explains how the complexities of reproductive colonization are coordinated naturally in Phase II from the start of actual queen rearing to consummation of the swarm.

E. O. Wilson[2], in a discussion of the evolution of polyethism in social bees and wasps (*Social Insects* 1971, chapter 9, page 182) recognizes a division of female reproduction labor assigned to the worker caste.

> *The queen of Apis mellifera "controls" the worker caste only in a very narrow sense. Her attractive scents make her a rallying point for colonies, and during colony fission swarming can be consummated only if she is present. The queen also suppresses the rearing of new queens and the development of worker ovaries by means of a pheromone.*

Otherwise the workers are very much in charge of colony reproduction. They build the royal cells, create new queens, and initiate and guide the swarms. They even prepare the virgin queens for the nuptial flights by reducing their food supply and encouraging them on their way by aggressive shaking movements (M Delia Allen, 1965). For several days before a swarm emerges from the hive, the workers give the queen less food than usual and frequently behave aggressively toward her; the queen loses weight and consequently is able to fly the longer distances required in colony fission. Workers initiate the swarm by the buzzing run, and they often actively pursue the queen and force her to leave the hive (von Frisch, 1967a). In short, female reproductive behavior itself has undergone a division of labor in which new supporting roles have been secondarily assigned to the worker caste.

As yet unaware of the foregoing, the author suggested in a publication entitled *Comb Honey and The Swarm Syndrome in Perspective*, (ABJ, Dec. 97, pg.877) that "It is helpful to view swarm fever as a manifestation of a temporary assignment of female worker bees, a feminine oligarchy, to the reproduction role of colonization."

This was influenced at that time by the perception of a general endorsement of the notion that swarming is instinctive, driven by worker bees with "swarm fever". The Russian, G.F. Taranov, one of the early pioneers in swarm research in the mid-1950's, published a paper entitled *The Occurrence and Development of the Swarming Instinct in Colonies* (1947).

Recently I learned that the great naturalist Francois Huber, a blind pioneer of bee research in Switzerland working through Francois Burnens, is said to have held the notion in the late 1700's that swarming is driven by a "spirit of the hive which infuses all at the same time". Their work, published under the title of "New Observations on Bees" in 1793, was translated and published in 1926 by Dadant and Sons, Hamilton IL.

Also influential was the well known Killion/Kruse system of swarm control[3], in the process of which the queen is clipped to avoid loss of bees in an attempted swarm; the bees and queen of a two-story colony are crowded into a single story at the start of a honeyflow, timed intentionally to enhance swarm fever and swarm cell construction. After a few days the queen is killed and *all swarm cells are removed except one* - knowing that the bees by instinct will not swarm when they have no backup gyne (virgin or cell) left to requeen the parent hive. If a second cell is left, they will swarm.

ANATOMY OF THE SWARM

PHASE I: THE CAUSE OF SWARMING, Amended to link with Phase II.

All reproductive swarming is caused by congestion in the brood zone with adult bees, which induces the development of swarm control bees by interfering with the distribution of inhibiting queen pheromones.

In this discussion the role of environmental factors such as weather and nectar abundance are considered only as enabling, stimulating or moderating - the template of colony growth and timetable. Also, there are numerous genetically innate differences in habit and behavior between strains or races of bees that may influence (accelerate or delay) the timetable.

Most swarming occurs in the early season when brood rearing is dominant. The explosive production of young bees on the threshold of the honey flow quickly outpaces the capacity of the brood zone proper to accommodate and employ them.

In managed colonies there will be no swarms if the adult workers that are forced to crowd the brood zone are given employment or cluster space. This is usually done by generous and timely addition of supers of extracting comb. Instead, in practice, many beekeepers simply use temporary tactics early in the season to delay congestion until ready to add supers. (Examples: reversing brood chambers, the simplest; interspersing brood and honey frames; or simply rotating lesser used or accessible peripheral frames inward.) They then add supers of comb or foundation for surplus when nectar intake exceeds consumption (the honeyflow).

Without adequate employment elsewhere, inactive young bees are observed to be clustered in layers in and around the brood area - more inside than at the periphery, according to Winston.

Crowding reduces both contact and antennal distribution of queen pheromones; the queen's movements as well as the circulation of messenger bees and of the bees themselves are restricted. Apparently the young bees at the periphery of brood and the edges of damaged comb are the most deprived of inhibiting queen as well as brood pheromones. Swarm cell cups and swarm cells are always found at such peripheral locations.

Comb building stops abruptly when swarm cells are built.

The fact of the location of swarm cells in the margins is considered to be evidence for linking congestion, the accepted cause of swarming, with the recruitment of swarm control bees there. Not all queen cells at the edge are swarm cells, but all swarm cells are found at the edge of brood.

There are several circumstances that induce congestion by adult bees, other than young bees, which may occur at any time of the season in the brood zone. These are:

1. *Neglect*: Foraging is shut down when nectar storage space becomes full or in the absence of timely supering; the colony becomes honeybound; honey storage encroaches on brood rearing space. Food processors become idle and engorged with honey as temporary storage cells and hang in clusters. The field bees stop foraging and crowd the brood zone.

2. *Periods of bad weather* confine and crowd the foragers in the hive. Intermittent bad weather is associated with swarming. According to Cale (*The Hive and the Honey Bee*) feeding a light sugar solution to keep the bees busy until the return of good weather will prevent swarming. This

simple remedy, simulating a honeyflow, suggests that queen pheromone distribution has been restored. Presumably this renewed in-hive worker travel is associated with renewed queen pheromone distribution by antennal and body contact.

3. When there is a *sudden heavy honeyflow* in the absence of immediately useable storage space, the food gathering and storage bees crowd into the brood zone to process and store nectar there on a temporary basis. Fresh nectar literally drips from the brood frames. Droplets of nectar are hung even in cells containing young brood. Brood nest congestion is acute, identical to that which occurs at the peak of brood rearing, except for the caste of bees.

Congestion early in the spring by a surplus of new young bees, the most common cause of swarming, can easily be avoided or delayed by reversing the brood chambers of over-wintered colonies at least once before the swarming season, as noted before.

NOTE: There are several other more invasive procedures for rearranging a colony so the bees can make full use of it all; or to provide new space for brood by exchange of frames of brood for frames of foundation.

This gives the bees access to immediately useable space - either brood rearing or food storage during the transition from dominantly brood rearing to dominantly hoarding. After the honeyflow starts, swarm control is largely maintained by timely supering.

The generally accepted view of congestion in the brood nest, discussed earlier, explains how queen pheromone distribution to the periphery of brood is reduced.

By this scenario, the bees at its periphery of brood would in general terms be expected to experience significantly reduced exposure to all queen pheromones, including queen substance and queen tracking pheromones. Also, there would be little exposure to brood pheromones by contact, at the periphery, but the bees would be aware of the aroma of brood. Queen substance, when combined with tracking substances, suppresses queen cell construction, but not queen substance alone. (Lenski and Slabezki[5], reviewed by Winston[4], pgs. 38, 86 and 141. Brood pheromones that suppress ovary development do not suppress queen cell construction, at least supersedure cells.

The special case of queen loss swarms: If one were to design an experiment to show that reduced queen pheromones leads to swarming, it would be difficult to match the simplicity of just removing the queen. Queen loss swarming has been recognized and studied by several investigators. (See review by Winston[4], pgs. 123, 124). They show that hives which have lost their queen will swarm up to 100% of the time.

Queen loss swarming is proof only that the complete absence of queen pheromones leads to swarming in a broodright colony, but does not provide evidence for how much the level must be reduced to induce swarming.

It is well known that bees, which have lost their queen just when they are preparing to swarm, stop foraging and comb building. Do they then become swarm control bees?

The queen's worker castes are known and classified by observing the work of age-marked workers. The presence of a swarm control caste of bees is known only by observations of unmarked workers while preparing to swarm and also at the time of swarming.

The bees that orchestrate swarm activities must come from the ranks of the idled queen worker castes.

PHASE II - IMPLEMENTATION OF THE SWARM BY SWARM CONTROL BEES.

As now envisioned the construction of queen cells at the periphery of brood signals the beginning of a division of colony level female reproductive labor for implementing the swarm. Every task of queen rearing in reproductive swarming and the orchestration of the swarm from here to the finish is visualized to be instinctively coordinated naturally by the swarm control bees.

The location of swarm cells reveals where bees are recruited as control bees, and the congestion scenario (Phase I) explains how they are recruited there automatically. It seems that their numbers would escalate rapidly, especially if the release from the inhibiting influence of pheromones is direct, not mediated by physiologic change.

It is well known that swarm cells containing larvae or pupae are often torn down by the queen and her workers (Allen 1956 and 1965, Gary and Morse 1962, Otis 1980 and Winston 1990). Of particular interest is that they sometimes do this in a hive preparing to swarm, while other cells are being constructed (Winston[4] pg. 183).

This mystery has the appearance of a contest between the control caste of workers, which build cells, and the queen and her workers, which tear them down.

Presumably each caste does its thing independently at different locations. It is not difficult to imagine that even in a congested hive preparing to swarm as described under Phase I (The Cause of Swarming), the queen still visits the periphery of brood where swarm cells at all stages are being built, but less frequently than before congestion developed. When a swarm cell is encountered, it is torn down.

The coexistence of these two opposing activities does not contradict the aforequoted statement of E. O. Wilson that "The workers are very much in charge of reproduction colonization." Rather, it demonstrates that the queen never loses her instinct to destroy rivals during the swarming process, but she has slowed down and her control of cell building by pheromonal

inhibition has been interrupted.

Cell building for reproductive swarming usually outpaces their destruction, and the bees swarm; the exceptions being when the state of congestion is relieved, either circumstantially or managed. We know that swarming cannot be prevented by manually destroying swarm cells.

The queen's worker castes are never completely recruited into the swarm control caste because new young baby bees are being born continuously into the brood zone to join the queen.

Presumably, the swarm control caste of worker bees are endowed innately with full knowledge of how to orchestrate all swarm related events, just as the worker castes 1,2, and 3 "know how" to perform each task in the age-related division of labor, which varies considerably according to need, unless all of those skills are the result of many obscure stimuli. See H.R. Hepburn in his book entitled *Honey Bees and Wax*, chapter 10, for a review of the work of Darchen, attempting to explain how bees build honeycomb as the result of many obscure cues.

DISCUSSION

The fact of a swarm control caste of bees appears to be sound, yet unequivocal proof would help dispel reasonable doubt about the implementation and coordination of all of the events in Phase II of swarming by swarm control bees.

There is already sufficient evidence to accept the reality of swarm control bees and to use it in shaping the anatomy of the swarm. The evidence for a swarm control caste of bees, unless a physiological marker is discovered, will likely always be based on their behavior; just as the queen's worker castes are still recognized by their behavior.

1. QUEEN CELL CUPS: Queen cell cups are said by some to be the first sign of swarming. Yet, every hive, whether it swarms or not, will build many cell cups throughout the season. (Butler[7] pg. 70 and Winston[4] pg. 182.)

Yes, cell cups are the first act of swarming, but not the first sign. Still they need to be explained.

The first queen cell cups usually appear two to four weeks before the actual swarm, whereas the swarm issues 8 - 10 days following the appearance of eggs in cups.

To explain the presence of unused cups, please be reminded of the several circumstances after the honeyflows begin which induce swarm control bees secondary to congestion (discussed in Phase I). The cell cups were probably built by swarm control bees, which existed temporarily during short-lived episodes of congestion, then reverted to worker castes when re-exposed to pheromones, having left their signature. Thus the cups, all identical, are always available on a contingency basis (although easily renewable) for immediate use when needed in either supersedure or swarming.

2. SUPERSEDURE CELLS: Supersedure cells can be distinguished from swarm cells when they are located centrally in brood. They are few in number and all of the same age. They are built by the failing queen's worker castes in response to reduced pheromone.

Supersedures are variously reported to take place in about 20 to 50% of hives in a given season, usually undetected unless the queen has been marked.

Queen supersedure is never the cause of swarming. But supersedure may occur concurrently with the swarm whenever the queen's failure was caused by being overtaxed while generating the bees for that swarm. Significantly, it is the virgin queen that is then selected to accompany the swarm. The failed queen is retained in the parent to be superseded in turn.

Again we see a demonstration of the wisdom of swarm control bees.

Apparently, just as the survival instinct of the bees in control won't allow a swarm to leave the hive without a replacement queen in the parent, they won't allow a failing queen to issue with the swarm.

Supersedures may occur at any time of the season following an extended egg-laying marathon causing queen failures, which makes spring supersedure the most common. Aging queens are the most susceptible.

3. SWARM CELLS: Swarm cells are always found at the edge of brood. They are more numerous than supersedure cells and are generally of all ages. Swarm cells, as now proposed, are built by a temporary caste of swarm control bees.

The queen's pheromone production in a hive preparing to swarm is not reduced. Reduced pheromone anywhere has to be due to flawed distribution.

The location of swarm cells at the periphery of brood pinpoints the periphery of brood as the location within the occupied nest where queen pheromone distribution is diminshed - consistent with contemporary theory of the cause of swarming.

Bees can and do move eggs or larvae. (Winston[4] pg. 82. Presumably swarm control bees could move eggs or larvae promptly into cups at the periphery of brood as needed if the queen's movements are severely restricted. The author has experienced the transfer of eggs into cups across an excluder. (ABJ, December 97).

Apparently some of the swarm control caste of workers prevail after the prime swarm leaves. This also is based on recorded testimonials of their behavior by behavioral scientists. They describe the incredible sagacity of workers in the micromanagement of virgin queens to accompany afterswarms. Thomas D. Seeley[6] 1995 reviewed this role in his book HONEY BEE ECOLOGY, page 64.

> *Although the internal events in a colony following the mother queen's departure have only rarely been observed closely (Huber 1792, Allen 1956, Simpson and Cherry 1969), the available observations suggest that workers are capable of closely regulating the further fissioning of their colony. Most importantly, the workers evidently can control the interactions between rival virgin queens. Their control techniques include postponing a virgin queen's emergence from her cell by not removing the tough wax and cocoon fibers on the tip of her cell, chivying already emerged queens away from unopened queen cells, keeping two emerged queens apart by pinning them in place, and forcing queens to leave the nest in afterswams. Overall, it appears that the virgin queens have relatively little control over whether they will leave in an afterswarm, or inherit the parental nest.*

Apparently not all control bees accompany the prime swarm or they are continuously recruited. The author has observed virgins imprisoned in their cells on several occasions following a swarm.

ADDENDUM

The fact of swarm control bees is of practical significance; beekeepers can exploit the known behavior and habit of swarm control bees on a rational basis to devise swarm intervention and/or prevention procedures according to the rule of natural law.

The Killion plan[3] for comb honey production, which forces the bees to prepare for swarming, relies on the knowledge that the (swarm control) bees will not consummate the swarm if all possibilities for a replacement queen are removed, no matter how much they are crowded.

A radically new two-queen plan for comb honey, *The Juniper Hill Plan for Comb Honey Production (J. A. Hogg, ABJ Feb. 05),* was designed for use with the Halfcomb cassette. The plan induces the bees to raise new queens naturally in-hive without inducing swarm control bees so that the bees will not swarm, no matter how much they are crowded while also producing comb honey during the "queen rearing" stage. Swarming in the two-queen stage is unlikely especially with judicious supering and the advancing seasonal decline in brood rearing.

The Juniper Hill Plan was the result of years of study, experimentation and experience with the special problem of swarm-free comb honey production. This was the motivation for an in-depth study of swarm control methods, theory and relevant research that led to this analysis of the complete anatomy of swarming.

The plethora of anecdotal testimony chronicling the existence of a swarm control caste of bees provides convincing reasons for further research. It is possible that the swarming imperative in the honey bee, evolved by natural selection, is a demon-

stration of nature over nurture.

Why the bees of all castes (1 to 5) have the know-how and skills to perform each task is a mystery! If the honey bee genotype of all strains and races wasn't molded by natural selection to endow each bee with the skills and know-how to perform all the tasks in the division of labor when called upon by signals and cues, then, how is it that they learn or acquire them?

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