You do not have to be around honey bee colonies very long before you encounter one of their most complicated group behaviors—the swarm. Beekeepers usually do not like to see a colony swarm after all, it means that their colony split in half usually right before or during the major nectar flow of the year. Bees, on the other hand, want to swarm more than nearly anything else they do. This sets the stage for a complicated tug-of-war between colonies that want to reproduce and beekeepers who want to stop this reproduction at all costs. Herein, I discuss the marvel of the honey bee swarm. A lot of what I discuss comes from Dr. Tom Seeley’s (Professor, Cornell University) book Honeybee Democracy or from his lectures on the topic available online at https://www.youtube.com/watch?v=JnnjY823e-w and https://www.youtube.com/watch?v=dVfC0P_a43o. The book and videos are worth reviewing, especially if this is a topic that is of interest to you.

What is a swarm?
To answer the question succinctly, and to set the stage for the discussion that follows, a swarm is honey bee reproduction at the colony level. This, of course, demands additional information because one must understand what “at the colony level” means. After all, most people believe that honey bee reproduction occurs when a queen lays an egg. Of course, this is true in the simplest sense. A bee making more bees is reproduction. However, honey bees are social insects and social insects have a peculiar reproductive strategy that one can see at the colony level. Colony level reproduction is best understood within the paradigm of the superorganism concept. Those who study social insects (ants, termites, some bees and wasps) do not look at a colony of social insects only as a collection of individuals. Instead, they look at the colony as the individual. In short, the honey bee colony can be viewed as a type of organism, a superorganism. The prefix super means above, thus suggesting a level of organization above that of the simple organism. The honey bee colony has become a unit of selection, or the most basic biological entity (cell, gene, organism, etc.) on which pressure is exerted, ultimately resulting in a change in that entity. While it is true that individual honey bees reproduce, given we know that queens lay eggs, colonies also reproduce because colonies produce more colonies. In fact, one can argue reasonably well that it is colony reproduction about which bees most care.

Think about it: if bees wanted simply to make more bees, then they would grow their colonies indefinitely, with there being no end in sight to the potential strength and size of a given colony. Yet, they do not do this. Consequently, there must be more to honey bee reproduction than just producing more bees—and there is. Honey bees want more than anything, to make more colonies. This is important for beekeepers to know and understand. Reproduction is among the strongest drives in any organism. An organism that can reproduce goes to great lengths to make it happen. This is why bee colonies want to swarm so badly, often to the chagrin of their keepers, and why swarming is so hard for beekeepers to stop. Swarming is how honey bees survive.

Given that swarming is colony level reproduction, watching a colony swarm is watching a colony give birth. This is a very poetic way to think about swarming. I often think about a mammal giving birth when I see bees rushing out of a colony, heading to the air, with the resulting cluster of bees very much like a baby bee hive. However, Dr. Seeley notes that bee colonies reproduce much more like an apple tree than they do like a mammal. Apple trees reproduce (spread their genes) two primary ways—(1) by dropping fertilized seeds in fruit to the ground to grow new trees and (2) by spreading pollen that goes out to fertilize the seeds of other apple trees. An apple tree that has produced a seed has invested as much of itself (its DNA) in the seed as it does in the pollen that fertilizes another tree’s seed. Thus, the daughter tree growing from a seed produced by a parent tree (parent tree A) is as related to parent tree A as much as is a daughter tree growing from a seed from a second parent tree (parent tree B) that was fertilized by parent tree A’s pollen.

How, then, is honey bee colony reproduction like that of an apple tree? First, the swarm is analogous to the apple that falls away from the parent tree (the parent colony). That swarm harbors the fertilized seed (the queen) that contains the genetic material necessary to grow a new colony. The swarm, when planted in the right place, grows into a new colony of its own, one that is ready to produce its own fruit and pollen. What is the bee equivalent to pollen? Why, the drones that fly daily from the nest in search of other colonies’ seed (queens) to pollinate are. Thus, colonies drop fruit (swarms) and disperse pollen.
Stimuli leading a colony to swarm

Given that swarming is colony level reproduction and reproducing is one of the strongest drives in a honey bee colony, why do all colonies not swarm all the time? After all, the more one reproduces, the more one gets his or her genes into the environment. The answer is simple. Colonies prefer to swarm when the offspring colony (the swarm) is most likely to survive, as determined by the bees responsible for processing the stimuli available to them. Consequently, I next will discuss a number of stimuli that lead a colony to swarm, many of which are correlated. For example, nectar availability and lengthening days are stimuli leading a colony to swarm. Of course, nectar becomes available as more plants bloom. More plants bloom when temperatures are warmer. Temperatures typically get warmer as days lengthen. So, some of my discussion on stimuli leading to swarming becomes a chicken/egg argument. Regardless, it is worth knowing the important stimuli leading a colony to swarm because swarm control is simply the art of reducing the stimuli, or at least those we can control through normal bee management practices.

**Stimulus 1: Resource availability** — It is not always advantageous for a colony to swarm. Thinking about it practically, the new colony, being a swarm, is leaving the warm, protected confines of its original nest and heading out into the wild to try to survive in an environment replete with danger. In fact, the bees are leaving without much food (only that which they store in their crops before leaving the nest), no brood, no stored honey, no stored bee bread, no propolis, no constructed comb, no nest protection, etc. The new hive has to find a new nest site, move into it, construct comb, rear brood, store pollen and store enough honey to survive the coming winter. Consequently, there are optimum and less optimum times to swarm.

Bees want to swarm during a time of year when resources to grow a colony are most available. The resources of particular interest are pollen and nectar. Bees need pollen to feed and rear new brood. Bees need nectar to fuel their activity and ensure their winter survival. This last point cannot be overemphasized. Bees need nectar to function and survive, but swarming bees leave their parent colony with only a little nectar. Accordingly, bees typically swarm immediately before or during major nectar flows, and I mean THE major nectar flows. This is why colonies begin to swarm a few weeks in advance of the spring nectar flow, and continue to swarm in high frequency through the first half of the major nectar flow. They are trying to swarm at a time when the resources needed for life are available in large quantities. From a practical perspective: bees want to swarm most when you least want them to swarm.

Not surprisingly, the timing of a swarm is correlated with that colony’s likelihood of surviving the coming winter, especially in temperate or colder climates. The later a colony swarms during a major nectar flow, the less likely it is to survive winter, the converse being true as well.

Herein lies the fundamental management dilemma of beekeepers. Bees want to swarm, and they want to do it before or during the major nectar flow. Beekeepers, on the other hand, want to keep their colonies as strong as possible to maximize the amount of honey the colonies will produce. Beekeepers find themselves working against nature, i.e. working to stop the most fundamental drive in an organism at a time when the organism most wants to do it. This is why swarm control is important for honey producers and why it is not always successful. I mean, really, how good are we at stopping anything from reproducing? I realize I have made quite a few generalizations about the timing of swarming. Of course, a colony can swarm at any time of the year, especially in warmer climates. They can swarm late in the major nectar flow. They even can swarm more than once during times of low resource availability. These, though, are the exceptions to the rule. Most colonies begin swarm preparations/attempt to swarm in the weeks leading up to and during the year’s major nectar flow(s). Typically, a colony’s desire to swarm wanes shortly thereafter.

**Stimulus 2: Weather** — Colonies begin to swarm as days get longer and warmer (early to mid-spring). Longer, warmer days seem to convince bees that winter is behind and abundant resources are on the way. Conversely, shortening, cooling days indicate to bees that winter is approaching and that it is not advantageous to swarm.

**Stimulus 3: The production of drones** — Drones, or male honey bees, are needed in order to mate with all of the virgin queens that are produced during the swarm season. Drones typically are the first reproductive that a colony will produce when coming out of winter. Colonies try to swarm once they perceive a critical mass of drones available in their colony, in their colonies, and perhaps in the environment.

**Stimulus 4: Congestion** — Congestion, more specifically adult bee congestion, plays a role in colony swarm tendencies. While it is true that strong colonies are prone to swarming, it seems that the number of bees per unit nest area is a more important factor, not just that there are a lot of bees. Congested nests are full of bees and offer no extra space to expand. This congestion is a result of increased food resources and an actively laying queen.

**Stimulus 5: Lack of open cells in which the queen can lay** — This is similar in many ways to congestion, but it is the brood version. Essentially, the queen is laying so prolifically (a resource dependent behavior) and the colony growing so rapidly that the queen has very few open brood cells in which she can lay eggs. There simply is nowhere else to put brood. At this point, the queen will begin to lay eggs in queen cups, thus leading a colony to initiate the swarming process.

**Stimulus 6: A dilution in queen pheromones** — Not surprisingly, this is also related to adult bee congestion in the nest. Attendant worker bees constantly lick the queen, acquire her pheromones and pass those pheromones to other bees that, in turn, pass them to other bees, etc. This lets all of the bees in the nest know that she is alive, present, functioning, etc. This same volume of pheromones dilutes when passed among bees in a very congested nest. The more bees that are in the nest, the more dilute the pheromone becomes.

**Stimulus 7: Queen age** — Colonies headed by older queens are more likely to swarm than those headed by younger ones.

**Stimulus 8: The production of new queens** — All of the aforementioned stimuli lead colonies to invest in the production of new queens. The queen cups in which the queen lays are pulled or drawn out into queen cells as the larvae develop inside. Colonies preparing to swarm will raise a lot of queens, perhaps dozens, that race to replace the mother queen soon to leave the colony. It is the presence of ripe, or capped, queen cells that seem to serve as a final stimulus for swarm happening. I often wonder that it is hard to get a colony to think about anything other than swarming once it has produced ripe queen cells during swarm season.

How swarms occur

Now that you know what swarms are, why they happen, and the stimuli leading to them, it is time to learn, in part, how they happen. Swarm preparation begins in the hive some weeks leading up to the swarm event. Worker bees in the nest begin to develop queen cups (Figure 1), which are simply the starter cells that become queen cells. Queen cups are about 1/4-1/3 the length of a queen cell and are open on one end. The colony’s queen will lay eggs in the queen cups and the worker bees will nurse the female larvae emerging from the eggs as queens. They do this by feeding the female larvae lots of royal jelly, more in fact than the developing larvae can eat. The royal jelly fed developing queens is exclusively a glandular secretion and it does not contain bee bread (processed pollen) or honey as does the food fed to developing workers. Incidentally, it has been shown recently that the addition of bee bread and honey to brood food is partly responsible for reduced ovary development in the resulting worker bees. Thus, queens are not just queens because of what they do eat (royal jelly) but also because of what they do not eat (honey or bee bread), given that the latter would inhibit ovary development.

All queens develop in queen cells. Typically speaking, beekeepers recognize two types of queen cells: (1) swarm cells and (2) supersedeure cells. The latter are made during times of emergency, when the queen is lost, maimed, killed, or not productive. Resultantly, supersedeure cells usually are produced on the face of a comb because the...
workers had to go to existing female larvae and direct them from becoming workers to becoming queens. In contrast, swarm cells are produced during a series of purposeful events. The colony wants to swarm (swarming is a planned event) and the queen purposefully lays an egg in a queen cup. Consequently, swarm cells usually, though not always, are constructed on the perimeter of the brood comb (Figure 2).

It is the old queen in the nest who swarms, not usually the new queen(s). Ordinarily, queens that are laying actively are too heavy to fly. They must lose weight to be able to leave the nest with a swarm. There are three main things that happen to get queens down to their flying weight. First they reduce their egg output. Second, worker bees begin withholding food from the queen. Finally, some workers will contact and buzz the queen, causing the queen to run to the nest. What we find, then, is that diet and exercise help a queen lose weight. This way, a queen can lose up to 1/3 of her weight, making her able to leave the colony with the swarm. Near the end of swarm preparation, when capped/ripe queen cells are present in the nest (Figure 3), some worker bees in the nest begin to engage on food to ready themselves for flight. They also begin to stop their daily regimen of tasks (i.e. they stop working). Worker bees are the ones that decide when it is time to swarm, not the queen. When ready, about 30-70% of the workers in the colony begin to rush out of the nest, with the queen rushing with them. This usually happens during warm, rain-free periods of the day.

The issuing of a swarm is a sight to behold. Thousands of bees begin pouring out of the nest entrance, with little on their mind other than swarming. Colonies are quite docile while this is happening. I often have sat, veil-free, at the entrance of a colony as swarming bees exiting the colony rushed past my face to take flight. It is quite a sensation. I have never seen a queen leave the hive first. In fact, according to my casual observations, the queen usually leaves when 1/3 to 1/2 of the workers who are leaving the hive have left and taken to the air. Thousands of bees circle near the colony entrance in the air once the swarm has issued. They are all working their way to a common location at which to land, usually no more than a few yards to a few dozen yards from the nest. The bees group together at this temporary landing place, forming a bivouac or cluster (Figure 4). This cluster site is not the permanent home of the new colony, but rather a temporary base of operation from which the homeless bees begin to search for a new nest cavity.

This part of swarm biology is quite interesting as a number of questions regarding the necessity of swarm clusters arrive. For example, why do bees need to form a cluster during the swarm process? Why can they not simply choose their new nest site while still in their original nest and then fly straight to the nest site when they swarm? The answers to these questions are not fully known. However, we do know that swarms leave the nest before the new queens emerge from their cells, thus reducing any potential negative interactions between the mother and her daughter queens. This seems particularly important because the swarm clustering stage can last a few days while the bees search for an adequate home. They cannot afford to do this from the original nest since the new queen emergence clock is ticking.

At this point, it is important to make a quick, temporary return to the parent colony, the one from which the swarm issued, before moving forward with a discussion of the swarm. This colony is now queenless, though it contains sometimes dozens of queens developing in swarm cells. These queens are engaged in a race to emerge first. The first to emerge usually becomes the reigning matriarch of the colony, but she has some unfinished business to which she must attend if she hopes to become the established reproductive in the hive. After emerging, this queen finds the cells in which her queen sisters are developing, bites holes in the cells, and stings her competition to death (Figure 5). If more than one queen emerges at roughly the same time, the queens will engage in a mortal combat until one, or rarely both, is killed. The surviving queen will mature over the next few weeks, going on her mating flight(s), and then become the sole

Figure 1. A queen cup. The comb on which the queen cup has been built is leaning back to the left. In its proper orientation, the opening of the queen cup would be pointing down. Photograph by Mike Bentley.

Figure 2. Swarm cells (the longer cells pointing down) and queen cups (the smaller cells pointing down) being developed at the top of a frame. The queen cups contain no eggs while the two longer swarm cells contain developing queen larvae feeding on royal jelly. These cells will remain open until the larvae are finished eating and the adult worker bees cap them. Photograph by Mark Dykes, University of Florida (now with Texas A&M University).
reproductive female in the nest. Occasionally, the colony can be of sufficient population that the first virgin queen to emerge will not just be looking for any old nest site available in the surrounding environment. What is the best nest site for bees? Many bee scientists have tackled parts of this question and have arrived at the following, very general consensus. The bees we keep like to nest in cavities (like those in hollow trees, chimneys, walls, etc.) that are about 10 gallons (40 L) in volume, about 15 feet in the air, and having a modest nest entrance of about 3 inches. These nest characteristics appear optimum for accommodating a typical hive and the honey it needs to store as fuel to generate enough heat to survive winter (40 or more pounds). Living trees that have sturdy walls and contain a cavity are ideal (Figure 6). Occasionally, the bees may choose to nest in a site that is less than ideal (Figure 7), though it usually is the best of the available options.

Scout bees leave the surface of the swarm cluster to search for potential nest sites. When a scout bee finds such a site, she spends about 45 mins going in and out of the cavity, making numerous internal visits. The bee is trying to gather information about the potential nest site. She walks the internal surfaces of the nest site while visiting it, likely in an attempt to gauge its size. The scout bee even may become covered in debris from the potential nest site and appear “dirty” after her visit. Dr. Seeley regularly recounts a story where a former colleague of his noted that scout bees he was observing smelled like ashes and soot, only to discover that they had visited a chimney while searching for a home.

Once the scout bee is satisfied that she knows enough about the site to communicate information effectively, she flies back to the swarm cluster and begins to dance. The dancing scout bee is able to communicate the direction, distance, and quality of the nest site through the dance. The direction of the would-be nesting site is communicated by the dancing scout bee much the same way that the direction of a food source is. She dances on the vertical surface of the swarm using a variation of the figure 8 or waggle dance (I discussed it in my October 2015 American Bee Journal article). Think about the shape of the number 8. It has two loops, and a straight run in the middle between the two loops. The bee will run a loop (the top of the 8) and return to the straight run (the middle of the 8). During the straight run, the bee waggles her abdomen and emits various vibrations for about 2 seconds. Then she runs another loop (the bottom of the 8) and returns to the straight run, now repeating the process a number of times. The direction of the straight run relative to “up” on the surface of the swarm cluster is the direction of the potential nest site from the swarm, relative to the sun (or, more correctly, the sun’s azimuth). For example, imagine the number 8 turned completely on its side, with the bee running up in the straight run. This would indicate that the potential nest site is in the direction of the sun from the swarm cluster. If the straight run of the 8 was tilted 90 degrees to the right of “up” on the surface of the swarm, then the potential nest site would be 90 degrees to the right of the sun from the swarm cluster.

Of course, there are many scout bees leaving the swarm cluster in search of a potential nest site and all of them come back and communicate their findings to the bees in the cluster, bees who will not visit any site before making a decision regarding what location ultimately to occupy. Interestingly, the bees collectively nearly always seem to choose the best available nest site in the area, despite the fact that many scout bees originally had advocated for the lesser quality nest sites they had visited. How do the bees collectively do this? They vote of course.

Bees vote for a given nest site by visiting the site. This happens in a series of steps. First, different scout bees advertise multiple potential nest sites in an area. A single scout alternates between dancing for her site and revisiting the site between dances. Unlike humans, scout bees seem to present an honest assessment of the site they are visiting, with no bias toward the site just because they found and are proposing it. They only
strongly advocate the very best sites. Thus, this scout bee can be persuaded to lose interest in her site and visit/advocate for a new site over time.

There are many uncommitted scouts (we would call the “swing voters”) watching the dances at the swarm cluster. They are coerced into visiting the potential nest sites while watching the various dancing scout bees. Dancing scouts do more dance circuits (loops and straight runs of the waggle dance) for good sites and fewer ones for less desirable sites. A bee going to good potential nest locations averages around 90 dance circuits while those visiting lower quality sites perform an average of 30 or so dance circuits. Scout bees completing more dance circuits, then, attract more non-committed scout bees to go and visit the better potential nest sites. The scout bees dancing for the lower quality sites seem to know that their sites are less than ideal, stop dancing, and reenter the pool of uncommitted scout bees. Sometimes, they are persuaded to stop dancing for a lesser quality site by bees visiting the better sites. The latter bees will head-butt and buzz the scouts dancing for a poorer site. The head-butt/buzz is an inhibitory signal to tell the bee to quit dancing. The average scout bee quits dancing for a poorer site when hit 10 or so times by the head-butter bees.

This entire event may appear like the scout bees are debating on the surface of the swarm, each advocating its site as the best available. However, it is much less like a debate (where one scout bee would say “my site is better than your site”) than simply an honest portrayal of the potential nests’ qualities (where the scout bee would say “here is what I know about the site I visited”). This discussion on the surface of the cluster can last a few hours to many days, sometimes three or more. During this time, hundreds of scout bees can be involved in the discussion of a couple of dozen potential nest sites. This discussion of potential nest sites on the surface of the cluster leads bees to ignore certain sites and visit others. Over time, there is a shift in visit totals from the less desirable sites to the more desirable, and even the best, one. A site appears to win the election by achieving a quorum. At the end, all of the site visits and dances performed by scouts begin to shift to only one location, the best one, before the swarm cluster migrates to the chosen site.

It only takes the swarm about 60 seconds to diffuse from its holding pattern, the cluster, and begin to fly to its new home once the best site is identified. How this happens is quite interesting. Only the scout bees that were looking and dancing for a nest site are warm enough to fly (bees must warm their flight muscles before they are able to fly). These bees will trigger the warming up of the other bees by pushing their thoraces onto cool bees and emitting a vibration that can be heard as a piping noise. This lasts 0.5 – 1 second. Essentially, the piping scout bees are telling the other bees to “warm up, it is time to leave.” At some point, the scout bees are not piping and the other bees have stopped cooling. The piping is then presumed to have ceased. At that point, the scout bees are thought to have entered the holding pattern because they have not yet been oriented to the best nest site. The bees that are not piping are then assumed to be those that were unsuccessful in finding a good nest site. They are then presumed to have been forced to reorient to the best site or be replaced by scouts that are already oriented to the best site.

Figure 5. Swarm cells at the bottom of a frame. A virgin queen emerged correctly from the cell on the left (the tip of the cell is open) and killed her sisters while they were developing in the cells (the queen cells were opened from their sides). These cells suggest that the swarm has happened already and that the colony will not swarm again. How can this be known? The placement of the queen cells on the perimeter of the brood comb suggests that they are swarm cells rather than supersedeure cells. The fact that one is opened from the tip suggests a virgin queen has emerged and replaced the swarming mother queen. Swarm cells opened from the side suggest that the virgin queen is not going to swarm with a secondary swarm given that no replacement queens for her remain alive. Photograph by Keith Delaplane, University of Georgia.

Figure 6. An opening leading to a potential nest site in a tree. Photograph University of Florida.
bees begin encountering more and more warm bees, this signaling that everyone is ready to leave. Finally, the scout bee will run around the swarm cluster with their wings spread and while buzzing. This Dr. Seeley describes as a “ritualized version of a takeoff movement.” Ultimately this behavior of the scouts causes the clustering bees to release from the cluster and fly into the air.

The resulting cloud of swarming bees is a site to behold. The cloud usually is about 30 feet long, 20 feet wide, and about 10 or so feet high. The bees moving at the bottom of the cloud fly only slightly over human head level, flying at a maximum of about 6 miles per hour. Not surprisingly, the swarm accelerates after disbanding the cluster, reaches a cruising altitude and speed, and seems to put on the breaks right before they arrive at the chosen nest site. From takeoff to landing, swarm migration to the new nest site takes only about 15 mins, of course depending on how far away the new nest site is.

As you might imagine though, the story is not that simple. Only a fraction of the bees in the swarm cloud have visited the nest site to which the entire cloud of bees is now moving. Thus, the site-naïve bees have to be shown where to go by the scout bees who have visited the nest site. This is accomplished via the flight patterns of the scout bees. Bees at the top of the swarm cloud fly at a high rate of speed and streak down the cloud in the direction of the nest site. They then fall back into the cloud, rise to the top at the back of the cloud, and streak forward again in the direction of the nest site. These streaker bees essentially are pointing the swarming bees in the direction of the new nest site. The other bees in the cloud, often flying somewhat erratic patterns, are able to receive information on the direction of the nest site visually by being in the depths of the cloud and looking at the streaking bees. Bees in the cloud latch visually onto a streaker bee and repeat its flight pattern. This way, the cloud moves in unison toward the new nest site.

The arrival of the swarm at the new nest site means the swarm has completed its journey and now is ready to build a new home. The scout bees land at the site, stand at the nest entrance (Figure 8), and release a pheromone from the Nasonov gland. This pheromone is a homing pheromone, calling the other bees into the new nest. The landing swarm of bees seems to flow into the nest entrance much like water flows through a funnel into a container. The swarm process is complete. The swarming bees have a new home and the parent colony has reproduced itself successfully.

Conclusion

Swarm behavior is a remarkable adaptation of honey bees for the perpetuation of the species. The biology of a swarm is a scientific marvel. Many of the behaviors exhibited by bees during a swarm manifest only during the swarm; yet, all honey bees in a colony possess the ability to engage in these behaviors when it is time to swarm. The diversity in behaviors shown by the scout bees alone is enough to cause one to appreciate the intrinsic beauty of a honey bee.

Despite a colony’s natural propensity, in fact – its innate desire, to swarm, beekeepers managing colonies for honey production find it necessary to control swarming in order to maximize honey production. Herein lies the biggest dilemma in beekeeping. Beekeepers work hard to control one of the most dynamic and beautiful reproductive displays in the animal kingdom. Nevertheless, all experienced beekeepers know that swarming is impossible to control all of the time. Organisms always seem to find a way to reproduce.