Field Guide to Beekeeping

An Overview of Honey Bee Biology

by JAMIE ELLIS
Gahan Endowed Associate Professor
of Entomology
Honey Bee Research and Extension Lab
Dept of Entomology and Nematology
University of Florida

jdellis@ufl.edu
www.ufhoneybee.com

Follow my lab on
Twitter and Instagram:
@ufhoneybeelab

This article marks the end of my short series on honey bee biology. Since my June 2015 article, I have spent considerable time discussing the members of a honey bee colony, their external and internal anatomy, their individual and group behaviors, and even their qualities as a superorganism. I am going to wrap up this series by bringing it all together into this single article on honey bee biology.

Of course, honey bees and their colonies are complicated organisms. A lot is known about honey bees, this due to man's longstanding relationship with the bee and the bee's general economic importance. These facts have caused the honey bee to be one of the most studied insects on the planet. Consequently, a short series on various aspects on honey bee biology culminating into this penultimate piece in which I provide a general overview cannot, no matter how hard I try, do justice to the beasts that are the honey bee and its colony. The more I researched to develop these articles, the most I grew to appreciate how amazing honey bees really are. Regardless of the difficulty associated with bringing all of this together into a single treatise, I feel it is important for every beekeeper to have a general understanding of honey bee *and* colony biology. After all, the best beekeepers know what they are trying to accomplish *and* what the bees are trying to accomplish. They then work to harmonize the two. No discussion of bee behavior, colony nest architecture, superorganism theory, etc. would be complete without an effort to try to highlight the common thread through all of this. I hope you find this approach useful.

By now, you should have a sense of the difference between the individual honey bee and its colony. I spent quite a bit of time discussing this in my March 2016 article on honey bee colonies as superorganisms (Ellis 2016b). To summarize that article: while the behaviors of the individual bees steer the colony ship, it nevertheless is the colony that is moving forward, regardless of the individual efforts of its crew. Everything an individual bee, from worker to queen to drone, does advances the cause of the colony. The individual's behavior and resulting biology, while amazing and noteworthy, manifests most perfectly in the attributes of the honey bee colony. Consequently, it will be somewhat difficult to separate the biology of individual honey bees from that of a colony and you might find me switching between the two during this article without announcement.

Figure 1. A honey bee swarm. Swarms are baby honey bee colonies.

To understand honey bee biology, you must know what a colony's goals are. Put simply, a colony's goals are the same as nearly every organism's goals. Honey bee colonies want to survive and reproduce. Everything a bee colony does results from wanting to accomplish those two goals. I cannot stress this point enough. The first major desire of a honey bee colony is to survive winter, and to survive it uncompromised, i.e. they want to be healthy and strong on the other side of winter. The second major desire of a honey bee colony is to reproduce, which they accomplish by swarming. Absolutely everything about honey bee colony biology is centered around those two goals.

Of course, there are many possible ways to discuss honey bee biology. However, I find it most helpful to think about the colony's progression through a typical year, just to give the effort a linear feel. The only problem with this is that one has to deal with the philosophical question of when a colony's year starts. Most approach their discussion of this topic in winter because it, outwardly, appears to be the time of year when colonies are dormant. However, I find it most helpful to start a discussion of honey bee and colony biology when a new honey bee colony springs into existence. I call this week 0. As noted in my article on superorganisms (Ellis 2016b), that is when a honey bee colony produces a child, when the colony swarms.

One final note: I have decided to subsection this article by week, grouping like colony experiences and behaviors in the week grouping when the experiences are realized or the behaviors are performed. This should make more sense as you progress through the article. I thought this might be a useful way to discuss the overall biology of a colony. In short, I am discussing a colony as it ages. It is important to know that the week range will vary based on your colony's proximity to the equator. For example, a summer in Florida (or, at least, summer-like weather) is a lot longer than that in England. So, the week range I present is a bit generic and corresponds with the "weather season" (time of year having a given weather pattern, rather than the actual time period defined by dates). For example, "summer" where I live is when temperatures are consistently over 80ºF (about 27ºC), nectar and pollen resources are somewhat low and of poor quality, and we get quite a bit of rain. This occurs from May through September, despite meteorologists telling us that summer starts in late June. Thus, my colonies engage in summer-type behaviors and display summer-like biologies for a much longer time than would colonies, say, in a Canadian summer.

Week 0 (early spring): Congratulations, it's a swarm!

Reproductively mature honey bee colonies are those that can produce swarms (Figure 1). It is not the honey bee colony's goal to make more bees and a colony that keeps growing indefinitely. Rather, colonies want to make more colonies. This is superorganism reproduction. A colony issuing a swarm is a colony giving birth. A colony that has swarmed has fulfilled its primary purpose. It has ensured the continuance of its genetic lineage by producing an offspring.

What a dynamic offspring indeed: swarms, like our own children, contain within them all the tools necessary to duplicate or even exceed their parents' success. That is one of the amazing things about being a parent. You can see in your own children their near limitless potential and you hope to give them the resources and training necessary (and, of course, unconditional love) for them to be even greater than you were. Honey bee colonies cannot love their children, but they do frontload them every way possible to help ensure their success. A colony in labor gives up its own queen and over half of its adult population to form the child that must make a name for itself in a complicated and dangerous world.

The swarm leaves the parent colony with a queen, some drones, thousands of workers, and enough honey to power their flight to and initial activities at the new nest site (see Ellis 2015b for more information on swarm biology). Besides that, the bees pack light when leaving the nest. They have no wax combs, no stored pollen, no emerging adult bees, no brood, and limited time. The latter point is worth emphasizing because the new colony must discover a nest site, move into it, build the wax infrastructure needed to support their colony, begin raising brood, forage for and store pollen, and (here is the kicker) store enough honey to survive the winter that is only four to nine months away, depending on the location's latitude and local climate. Considering all of this, it would seem that the odds are stacked against the new colony; yet, bees in swarms are industrious and, as noted already, are frontloaded with the tools they need to thrive in the world into which they were born.

The timing of a swarm is critical to its likelihood of surviving the impending winter. Colonies typically swarm immediately before or at the beginning of the year's major spring nectar flow, a period of about five to six weeks when the most nectariferous flowering plants are in bloom. This happens in most areas in early-to-mid-spring. Where I live in Florida, for example, colonies begin to swarm in late March given that our area's major nectar flow is April and May. Colonies have to time their decision to swarm just right. If they swarm too early (i.e. too far before the main nectar flow), there may not be enough resources available for the new colony to use to develop its nest. If they swarm too late (i.e. too far into the main nectar flow), there may not be enough nectar flow left to provide the colony the resources it needs to build its home and store enough honey to survive winter.

Even if the timing of a swarm is right, the new colony can still fail for any number of reasons. For example, the quality and quantity of nectar provided during the nectar flow is unpredictable. Additionally, weather impacts a new colony's chances of survival. A colony can swarm at what is normally the right time but it could be a dry spring, a wet spring, a cold spring, etc. Furthermore, the swarm could be too small, with too few bees to form the critical mass needed to survive. Likewise, a colony could issue a second or third swarm headed by a virgin queen. This swarm will need to establish and the virgin queen mate before it is too late. Finally, the new swarm could be harboring dangerous bee pests or be sick with a myriad of pathogens that are set to doom it before it ever gets off the ground. All of these would cause added stress to the new colony, giving the colony something it must address immediately after it is born. It is perhaps for these reasons that colonies founded by swarms often exhibit explosive growth. It is as if they are trying to outrun any potential stressors that otherwise would lessen their likelihood of surviving winter. Assuming, though, that the conditions are right and the cards are stacked in the new colony's favor, the swarm will move into its new nest site and begin to make itself a home.

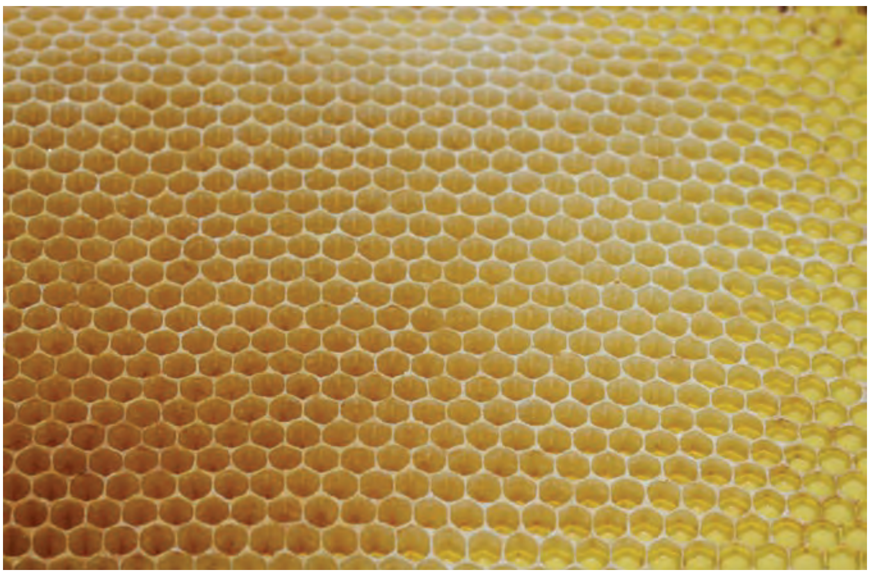

Figure 2. Comb construction. Worker bees secrete wax from special glands underneath their abdomens. They use their mandibles to fashion the wax into the comb they use for multiple purposes. *Photograph by Mike Bentley.*

Weeks 1 – 8 (mid-to-late spring): Colony growth and development

Immediately after inhabiting a new nest site, the bees composing the young colony get to work. However, their typical cycle of age-related tasks (temporal polyethism) is a bit askew the first few weeks a new swam inhabits a nest. As noted in my October 2015 ABJ article (Ellis 2015c), worker honey bees progress through a series of fairly predictable, though somewhat fluid, tasks as they age. Young bees engage in nest-based tasks while old bees engage in tasks undertaken outside the nest. New swarms leave all of the emerging bees behind in its parent's nest. Consequently, there is a period of time, about 3-4 weeks, between the time when a swarm occupies a new nest and the time when a new round of adult bees emerges from the yet-to-be-constructed wax combs. By the time the first round of adult bees emerges, other adult bees as old as four weeks or older, those that left the parent colony with the swarm, are still engaged in young bee tasks. One of the beauties of a new colony founded by a swarm is that despite the lack of age-appropriate bees, all the tasks seem to be addressed when the colony needs a given task performed. The bees composing the new colony have to get right to work to ensure the survival of the colony. And get to work quickly they do…

First, a cohort of the bees in the colony begins constructing the wax comb (Figure 2) that is intrinsically important to the colony's survival. Wax provides the skeletal infrastructure of the colony beast and it serves five very important functions in the nest. First, the bees raise the queen's offspring in the wax comb. Consquently, the combs support the brood area or colony's nursery. Second, bees use the wax cells composing the comb as storage areas for beebread, nectar, and honey. Third, wax plays an important role in bee communication. Bees communicate using the comb by sending vibrations through it, vibrations that other bees can detect with their tarsi (feet). Fourth, wax also plays an important role in colony toxin and pathogen management. Regarding the former, wax traps lipophilic (wax loving) toxins in its lipid structure, keeping them away from the bees. For the latter, old combs are replaced by the bees as they are destroyed by wax moths and time, thus ridding the nest of any accumulating pathogens. Fifth and finally, wax supports the thermoregulatory efforts of the bees who take advantage of its shape and properties while heating and cooling the nest.

Another cohort of bees begins foraging for the resources necessary to fuel and grow the developing colony. These bees get to quick work scouring the area around the colony for (1) water for thermoregulatory purposes, (2) resins to use as propolis, (3) pollen to consume and (4) nectar to convert to honey for fuel. I have seen bees begin foraging for foodstuffs within 30 minutes of occupying a new nest site. The new colony's first foragers may be among the most important they will ever have, given that the colony's fate rests on the wings of that small group of bees who will gather the resources needed to grow the colony quickly.

Once a small section of comb is developed, the queen will begin to lay eggs in it. This is the first brood that will develop in the new nest and it represents the future of the new bee colony (Figure 3). A colony will produce only the amount of brood that the incoming resources permit. Consequently, it is imperative that the incoming resources be of sufficient quantity and quality to support the necessary rapid growth of the new colony.

Why is it necessary that the colony grows rapidly? It is because abundant resources are available at that time and those resources are what are needed to provide the fuel necessary for colony winter survival, mainly in the form of nectar which is converted to honey for winter storage. Given that colonies typically swarm just before or during the major nectar flow, most of what they could need to collect to fuel their rapid growth and collect for winter storage is only available for a few remaining weeks. I suspect most major spring nectar flows last about five to six weeks. Thus, a colony swarming during the first week of the major nectar flow has five weeks left to take advantage of the available nectar. A colony swarming at the end of the nectar flow has less time and, consequently, is considerably less likely to survive the coming winter.

By mid-spring, around weeks 4-6, the new honey bee colony has constructed a lot of comb, is emerging its first cycle of adult bees, has stored a lot of honey and pollen, and is growing rapidly. A peak inside a colony of this age will reveal lots of new, white comb, open cells with ripening nectar, large and full brood patterns, and bee bread (Figure 4) stored everywhere.

Bees are quite meticulous during the comb production and resource storage process. They have a very set way that they want to construct their inner nest, starting where they place the brood. Typically speaking, the queen lays eggs toward the bottom of the available wax comb. Her egg laying pattern is circular on any given comb, with the pattern being the largest in the center combs and the smallest on the peripheral combs. If you could remove all of the nest contents except the brood, you would notice that the area of the nest occupied by the brood resembles something similar to a large, slightly squashed basketball. The bees, then, will jacket the upper half of the brood area with a 1-2 inch (2.5 – 5 cm) thick layer of bee bread or stored and processed pollen. They put the bee bread near the brood since the brood has the greatest demand for the stored pollen. Finally, bees store honey above the pollen jacket and upwards into the upper part of the nest cavity. To help you visualize this, think of a basketball placed into an empty tree cavity, resting toward the bottom of the cavity. Then, take a bowl that is slightly larger than the upper half of the basketball and place it upside down on the basketball such that it jackets the entire upper half of the first ball. Finally, take a large, tall top hat without a rim and place it on the bowl. The first ball would be the area occupied by the brood. The bowl would be the pollen layer. The top hat would symbolize the area occupied by the stored honey (Figure 5). Rapid colony growth and appropriate nest occupation is a sign that everything is going well.

Despite this, things can derail quickly. Imagine, for example, that without warning, the nectar flow ceases or is otherwise poor. The growing colony, then, can outpace its resources, leading to significant stress and an inability to fuel its activities. It also may be too wet (rain prohibits swarming) or too dry (drought affects nectar supply) for bees to store enough honey. As long as bee colonies do not grow too large too quickly, they should be able to take advantage of the meager resources available throughout summer and fall. I cannot emphasize enough, though, that colony success during the rest of the year hinges on its ability to grow steadily and stably in spring and to take advantage of all available good weather to forage for the nectar they must convert to the honey they need to survive winter.

Typically, weeks 7 and 8 represent a shift in colonies from nectar foraging to nectar

(l) Figure 3. A comb containing young brood. You can see eggs and young larvae developing in the cells. New colonies are full of developing immature bees. (r) Figure 4. Pollen stored as bee bread. Bees keep bee bread near the brood chamber since they mix it into the food they feed their developing larvae. ***Photographs by Jamie Ellis.***

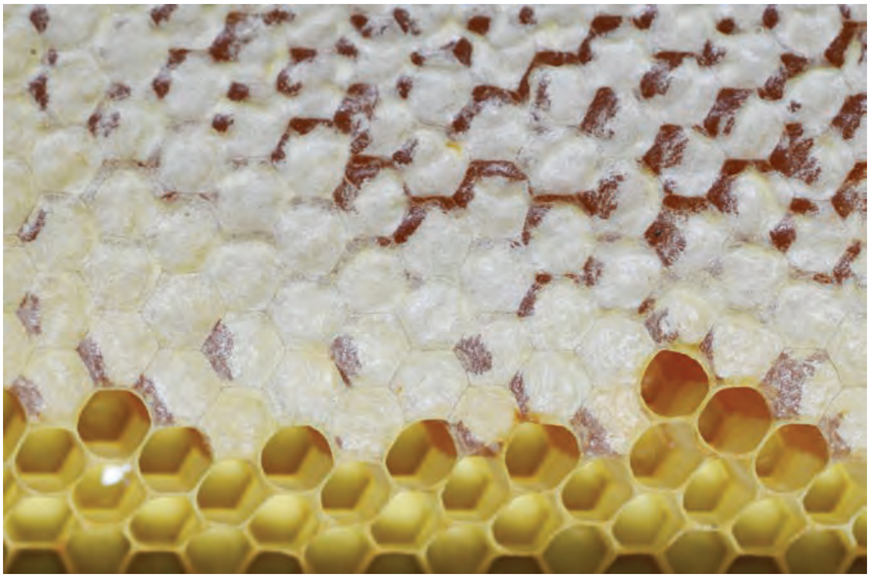

Figure 5. Stored honey. Bees store honey to survive dearths. Stored honey is *capped with white wax, thus preserving it for later use. Photograph by Mike Bentley.*

ripening and storage. This, usually, is when the nectar flow begins to wane. Consequently, the bees use the available incoming nectar to process the nectar they have into the honey that will serve as their fuel for much of the rest of the year. Bees need to store, in fact, about 20 kg (44 lbs) of honey to fuel their production of heat through winter. To do this, they have to collect about 50 kg (110 lbs) of nectar to produce the 20 kg (44 lbs) of honey that is needed to fuel colony heat production through winter. Of course, the typical honey bee colony must have honey on hand to power its activities until winter, especially since nectar flows can be sparse during the summer and fall months. My guess, then, is that bees need to collect considerably more nectar, maybe two-to-three times more, than that needed during winter just to survive *to* winter. Hopefully, you can appreciate how important the main nectar flow is to bees, especially given that subsequent summer and fall nectar flows are not guaranteed.

Toward the end of the main nectar flow, many of the adult bees that composed the original swarm have died and have been replaced with adult bees born at the new nest site. These bees now represent the correct ages and typical demographics of a colony, unlike the swarm that founded it which was composed of mainly older bees. Furthermore, the original queen often is lost during these first few weeks, being replaced with a new queen produced by the growing colony. The colony is now a new beast, with new bees, new brood, new comb and often a new queen.

A final comment about colony biology during weeks 1 to 8: all honey bee colonies usually are infested/infected with at least one pest or pathogen, or at least all honey bee colonies I have ever seen. Even new swarms carry *Varroa*, viruses, bacteria, fungi, etc. with them to their new nest sites. In early spring, pest and pathogen pressures in the parent colony, the one producing the swarm, are usually low. Thus, the new colony (the one started as a swarm) has some pests and pathogens accompanying it, even if only at low levels. For the most part, the swarming bees leave behind many of the brood pathogens. That said, even if they are not affected as adult bees, they can continue to carry the organisms with them to the new colony to infect the next generation of brood. All that aside, new colonies tend to grow so rapidly during the major spring nectar flow that they outpace the levels of pests and pathogens growing in number with them. Thus, the new colony appears very healthy as it expands, with its growth masking the sleeping pests and pathogens that tend to rear their ugly heads later.

Weeks 8 – 20 (early-to-mid summer)

In most of the temperate world, honey bee colonies leave the bounty of spring behind around about eight weeks after swarming. Now they enter summer, when the temperatures are high, water availability is variable, and pest/pathogen pressures are beginning to grow. Colonies experience new stressors and exhibit different behaviors after the major nectar flow ceases. At this point, the colony is usually as strong as it will be all year. It has the largest number of adult bees that it will have and it is producing lots of brood (Figure 6). By now, the nest should be full of honey. You might think of the colony as "fat and happy." However, this is a dangerous time of the year for the young colony and much of the summer is spent simply surviving.

In early summer, many colonies around the world benefit from minor nectar flows and lessening, but available, pollen flows. The major nectar flow that persisted in spring can come to an abrupt stop and this can be more problematic for colonies that were functioning productively, but now are without the resources needed to keep up the high pace. Colonies at this time are strong, but with little to do. An entire work force of foraging bees now may be without a useful job, thus crowding the colony with a cohort of bees looking for something to occupy its time.

As nectar and pollen availability wanes in early summer, queens will begin to curtail their egg laying, even if slightly. This usually happens slowly so the colony's steady decline in population may be otherwise unnoticed. In fact, colonies can be very strong in early-to-mid summer, even without a

Figure 6. Capped brood under the watchful eyes of healthy adult bees. Maturing colonies in spring and summer contain lots of capped brood. *Photograph by Jamie Ellis.*

substantial amount of incoming resources to support the full nest. This can be a problem, in fact. Strong colonies with few resources tend to tap into the reserves. Bees store honey to survive dearths, with the longest being the one presented by winter. Occasional dearths in summer can be problematic, but bees usually are able to overcome these owing to the intermittent availability of resources. Prolonged summer dearths can doom a colony, especially if the bees exhaust the resources they stored in spring to survive the upcoming winter.

By midsummer (week 12 or so), colonies usually have a new need – water. Bees need water, among other things, to cool the nest. Given that the ambient temperatures are now high, the brood nests are in danger of overheating (see Ellis 2016a). In fact, brood dies/develops poorly at temperatures above 36°C (96.8°F). Furthermore, bee activity generates heat. Thus, ambient temperatures above 30°C (86°F) put the colony at great risk from itself given that the temperature can rise quickly on a hot day. Because of all of this, bees forage for water quite a bit during summer. You can find these bees at ponds, rivers, lakes, streams, swimming pools, leaky outside taps, etc.

Bees in midsummer also display another behavior that is indicative of high ambient temperatures. They begin to beard on the front of their colonies during the warm summer evenings. Certainly, this is a behavior aimed at helping colonies keep from overheating the brood by removing heat generating bees from the nest. These beards appear as large clusters of bees hanging from the entrance of the nest (Figure 7).

If the colony is lucky, it may benefit from a moderate or even significant nectar flow. There are many places around the temperate world where summer nectar flows can be quite good. For example, sourwood trees, from which bees produce one of the world's most famous honeys, bloom in the middle of summer, as do other trees or shrubs. I would guess, though, that most of the bee colonies in temperate areas have meager access to quality resources during the summer months. For my own bees, as an example, the major nectar flow ceases in early March and my bees have very little that they can collect during the hot summer. This is most evident in July (right in the middle of weeks 8 – 20) when my bees begin to collect low quality pollen from bahiagrass. This is my signal that there simply is nothing of quality available to the bees, thus their propensity to collect whatever they find.

Bees spend quite a bit of summer keeping the colony cool or foraging for any available nectar/pollen. Toward late summer (closer to week 20), colonies have another growing problem. Throughout summer, the adult bee and brood population in the nest has been on a steady decline. In contrast, their pest and pathogen populations have been rising steadily. It usually is mid-to-late summer when the "balance of power" between adult honey bees and their pests/pathogens makes an unfavorable change.

Figure 7. Colonies with bee beards. Many bees in these colonies left the colonies during warm temperatures in an effort to avoid overheating the nest. *Photograph by Mike Bentley.*

Resource-stressed colonies investing in keeping colonies cool can be prime targets for pests looking to gain the upper hand. Most notably, *Varroa* and small hive beetle populations begin to reach critical levels. This is true especially for *Varroa* (Figure 8), the most threatening of all of the colony's biological stressors. Bees do not ignore the threat posed by *Varroa* in summer. In fact, most colonies have cohorts of bees within the nest that can detect *Varroa* developing in capped brood cells, remove the cell capping, and abort the developing bee/*Varroa* contained within. This behavior is called hygienic behavior and it can help keep *Varroa* populations low, though it cannot stop *Varroa* altogether.

Varroa populations get damagingly high in late summer, so-much-so that managed colonies often have to be saved by beekeepers willing to treat them or work with them in some way to otherwise reduce the *Varroa* loads. Though variable, it appears that the average colony starts to suffer when *Varroa* populations reach the 3-5 mites/100 adult bees (3-5% infestation rate) threshold. When colonies are left alone, this level usually is reached in mid-to-late summer. Also problematic, *Varroa* usually are accompanied by viral pathogens that they seem very able to transmit. There is growing evidence, for example, that Deformed Wing Virus (DWV) is a significant colony stressor, perhaps even a killer of colonies, and *Varroa* are the major transmitter of this deadly disease. *Varroa* and DWV problems manifest most in colonies as colonies naturally decline in strength in summer. This, then, means the number of *Varroa* per adult bee and the resident viral titers reach levels that bees simply cannot withstand. The end result is a dead colony.

Colonies in areas where small hive beetles (Figure 9) are present can be overrun by the beetles in the latter stretches of summer. This is when beetle populations are greatest and when colonies are already combatting the notable adversaries *Varroa* and DWV. Small hive beetles, for the most part, are secondary colony stressors and tend to overrun colonies that are already taxed by other problems. Thus, strong, healthy colonies are better able to combat this menace than are weak or compromised colonies.

By now, you can see that summer is very difficult for the bee colony. Typically speaking, resource availability is lacking, considerable time is spent on keeping the colony cool, and disease and pest pressures are growing. Late summer is a critical period for most colonies, especially those in cooler temperate regions. This is because this is when colonies begin investing in the production of "winter" bees, or the bees that will carry the colonies through winter. For the most part, adult bees produced during spring and summer have a five-to-six week life expectancy. If this were true of all the bees produced during the year, colonies would run out of bees about six weeks after the queen ceases egg laying in late fall. Of course, this does not happen. Instead, the bees produced in late summer are those that will carry the colony through winter, hence their name "winter bees." These bees can live up to six months. Most notably, they have greater fat reserves and a few other physiological differences that permit the longer lifespans. It also helps that these bees do not have to forage as much as their spring and summer sisters. Literally, foraging is what kills the bees produced earlier in the year.

Given that bees produced in late summer are so vital for the overall success of the colony, colonies stressed in any way during the production of these bees can produce lower quality winter bees. As you might imagine, this hurts the colony's chances of survival during winter if the bees they produce are not up to the task of getting the colony through winter.

(l) Figure 8. A Varroa mite. This is one of the main killers of honey bee colonies around the globe. ***Photograph by University of Florida Staff.*** **(r) Figure 9. A small hive beetle peaking its head out of the end of an open cell.** ***Photograph by Mike Bentley.***

In the best case scenario, colonies in summer have reasonable access to a few, moderate quality nectar and pollen flows, mild temperatures, adequate quality water, low pest and pathogen pressures, and good food stores. If these criteria are met, the colony has a good chance at surviving winter. Otherwise, the colony's chances of survival are significantly lower.

Weeks 20 – 32 (fall)

Bee colonies entering fall are in full winter preparation mode. The warm-to-hot days of summer are behind them and shorter/cooler days lie ahead. Fall is an important time for bee colonies. The colonies have to make final preparations to enter winter when resources will no longer be available. Any little problem for colonies in fall can doom their chances of surviving winter.

Many colonies come out of summer stressed. They spent a lot of their energy keeping the nest cool. They were without the abundant, flowing resources available in spring, and they usually are heavily laden with pests and pathogens, unless they were managed by beekeepers who have been taking steps to keep these pressures low. Thus, fall is the "do-or-die" time for colonies.

Despite these setbacks, weeks 20 – 32 of the now-mature colony's life can be productive. Many, maybe most, temperate areas have an assortment of flora that bloom and are available to bees. In fact, fall nectar and pollen flows can be quite significant, so-much-so that the colonies are able to top off their reserves and finalize their storage of honey for the impending winter.

In preparation for winter, the typical queen begins to reduce her egg output from early fall to nearly eliminating it altogether by late fall. Thus, the vast majority of colonies spend weeks 20 – 32 (fall) transitioning from life as an active colony to that as a more dormant one, where winter survival is the only goal. In warmer temperate regions, such as the southern U.S. and southern Europe, queens never stop laying and brood can be maintained in colonies straight through winter. This may be viewed as advantageous by the beekeeper, but it can be somewhat taxing to a colony. The maintenance of brood through winter means that the colony must consume resources that were stored for heating in order to maintain the brood. Thus, most beekeepers hope to see their queens curtail their egg-laying habits in late fall.

Given that colony growth ceased in early summer and populations fall rapidly through fall, disease and pest pressures can derail a colony's chances of surviving the coming winter. *Varroa* and associated problems pose great risks to bees at this time. While some colonies left unattended may survive the *Varroa* onslaught, most will not make it without some sort of beekeeper intervention. Of course, in the most natural sense (i.e. without human interference), colonies left unmanaged by beekeepers stand the greatest chance of becoming tolerant of *Varroa*. But make no mistake, this will come at great cost to the susceptible colonies that will cease to exist in the face of *Varroa*. It is somewhat discouraging to talk about colony biology in light of the pressures exerted by *Varroa*. *Varroa* are not natural pests of the honey bees we keep (*Apis mellifera*). Instead, their native host is *Apis cerana*, the Asian honey bee. Thus, it seems strange to talk about honey bee biology and how it is affected by a non-native parasite. In the absence of *Varroa*, colonies would march through summer and winter with the biggest threat to their survival likely being resource dearths. However, *Varroa* are a reality for our bees and they affect bee biology significantly. Many, perhaps most, colonies would not have a fall/winter biology without some level of *Varroa*-control intervention on the part of beekeepers.

Assuming that the colony and beekeeper have worked harmoniously to limit *Varroa* and associated pathogen impacts during fall, the next biggest stressor will be resource availability. Colonies try to be conservative with their use of stored resources through summer and early fall. However, there are locations where there simply is nothing else available to the colony looking to overwinter. A colony facing this dire situation will consume its stored resources, thus facing a grim outlook for surviving winter. Colonies can, in fact, starve in fall.

The good news is that when left alone, bees usually can store enough in spring and the modest fall nectar flows to survive winter. By late fall, the colony should have all the honey it needs, a queen that has stopped or significantly slowed her egg output, low or no pest/pathogen pressures, and a nest full of "winter bees." The next step colonies take toward winter survival is the eviction of the drones that live within it. Drones are resource sinks in fall. They do no work. There are no available virgin queens with which to mate. In fact, drones otherwise sit around and consume honey. Put together, they tax colony resources and give nothing back this time of year. Worker bees take this so seriously that they evict the drones remaining in the nest at this time and will not let them back into the colony. During late fall, you often can see drones on the outside entrance of the nest, with worker bees limiting their ingress back into the nest. Outside the nest, the drones are left to die to whatever executioner claims them first, be it predation, starvation, or cold.

In late fall, colony behavior begins to change significantly. Usually, the weather in most temperate areas in mid-to-late fall begins to cool substantially, first at night and then during the day. When the temperature drops below 18ºC (64ºF), bees begin to cluster in an effort to keep the colony warm (Ellis 2016a). They do not usually cluster at higher temperatures, presumably because coalescing into a tight cluster can disrupt other colony functions. Clusters are almost "all or nothing" events as many of the other normal colony activities cease when a colony is clustering.

Given that temperatures get cooler and cooler as fall progresses, the bees cluster more and more into late fall. In most temperate areas, bee colonies are in a near-constant state of clustering in late fall. Colony production of heat relies on bee consumption of honey. Bees on the outer shell of the cluster are unable to move. Thus, they cannot break free from the cluster to go and eat more honey. Clustering bees, then, have to cluster as close to stored honey (Figure 10) as possible so that they can access it when their individual personal reserves dwindle. In fact, a colony can "starve" to death during winter, even when the nest is full of honey. This happens during prolonged cold spells during which the bees are unable to break cluster and move closer to the stored honey. In fall, though, cold days and nights are interspersed with warm days during which bees can forage and continue their normal activities. By late fall, when the temperatures are nearly always cold, the colony is ready to enter its visibly most dormant state of the year.

Figure 10. A frame of stored honey. Bees typically fill the perimeter combs with stored honey as winter approaches. The honey is a good insulator against the cold, but also serves as a source of fuel for the bees trying to heat the colony. *Photograph by Mike Bentley.*

Weeks 32 – 44 (early-to-mid winter)

Around week 32 post swarming, the typical colony in the typical temperate climate enters winter (Figure 11). As we would say it in the south, this is "fish or cut bait" time for the colonies. There is little other preparation a colony can make for winter survival. The pests and pathogens have weeded out the sick colonies. The summer and fall of poor resource availability have taken down the colonies that did not store enough resources during the primary nectar flow. The wintering colonies, then, either have what they need to survive winter or they will die.

In most temperate areas, there are no significant resources available to colonies outside what the colonies stored for themselves earlier in the year. Hopefully, by this time, the bees have stored the 20 kg (44 lbs) of honey they need as fuel to heat the nest. Also important is that there are intermittent days of warm weather during which they can break cluster and reach the food.

Clustering bees that move toward the nearest honey reserves tend to migrate up in the nest over the course of the winter. The reason for this is obvious. The bees store honey in the area of the nest that is above the brood. Given that most clusters start in the brood area during late fall, there is nowhere for the cluster to go but up as the winter progresses. There can be one problem related to clustering during winter. Bees produce moisture when metabolizing honey. This moisture can rise in the nest, collect on the ceiling of the nest, and rain back down onto the clustering bees. This is less than ideal as it can cause bees to become chilled. For managed colonies, many beekeepers ensure that there is an upper ventilation hole in the nest to allow moisture to escape.

Fortunately, most pest and pathogen populations also decrease substantially during winter. The typical colony only has two main winter pests/pathogens to fear. They include the two *Nosema* species (*N. apis* and, most notably, *N. ceranae*) and tracheal mites. The *Nosema* species are single cell microsporidia (fungi) that infect bee guts. These spores compete against the bees for nutrition and they also rupture cells in the lining of the gut. Tracheal mites, as the name implies, inhabit the trachea of the bees. Both *Nosema* spp. and tracheal mite populations can grow in the tightly clustering bees and cause the colonies to present symptoms of infection/infestation in late winter. In general, tracheal mites are considered a minor problem while *Nosema* spp. ranges from a moderate to a significant problem. Most beekeepers ignore tracheal mites, but worry a lot about *Nosema*.

Unfortunately, tracheal mites and *Nosema* can produce similar symptoms in a sick colony in late winter so it can be hard to know with certainty which is causing the problem in the colony. A sick colony may have disorganized clusters of bees. It may die in early spring. You may see bees crawling on the ground around the colony entrance. You also may see bees exhibiting K-wing which is a symptom where the front and hind wings of a bee become unhinged and open to the shape of a letter K. Assuming, though, that the bees have both of these issues under control, starvation, then, poses the greatest threat to any overwintering colony. Colonies ill prepared for winter, especially the long, cold winters of extreme temperate climates, never make it to the warmer spring days.

Figure 11. A cold winter. Bee colonies should enter winter with all that they need to survive. By this point, there is little a beekeeper can do to help the bees. *Photograph by Amanda Ellis.*

Weeks 44 – 52 (late winter – early spring)

Colonies in late winter have their smallest populations of the year. They may be clustered tightly, but there are signs of life in the center of the cluster. In late winter, especially as temperatures begin to rise a bit and late winter trees/shrubs begin to bloom, the center of the cluster is raised to about 34.5ºC (94ºF) in an effort to accommodate brood rearing. Queens in the center of the loosening cluster will begin to lay eggs, thus creating the demand for pollen. Usually, most colonies have enough stored honey to power their early activity. It is the pollen that they lack for successful colony growth.

Arguably, the most (or second-most, depending on who you ask) important bloom of the year starts to happen in late winter/early spring. These blooming trees and shrubs provide those first tastes of nectar and pollen that the colony needs to raise copious amounts of brood. To me, this is the most exciting time of the year for the honey bee colony. It reminds me a lot of a bear coming out of hibernation. It has used most of its winter resources. Its legs are a bit wobbly, but it is primed and ready to embrace the coming year.

Bee colony growth can be explosive, especially as spring approaches and those first nectar and pollen laden plants release their bounty. These can be some of the most resource rich blooms available to bees all year, but the beekeeper largely will not notice them because the bees consume the nectar and pollen "in real time," meaning that they are using these resources to produce new bees as quickly as it is coming into the nest.

Colonies coming out of winter have one goal in mind. They want to mature to the point of reproduction and everything they collect is used toward that goal. Bee colonies cannot reproduce (swarm) until the conditions are right. Three conditions must be met to allow colony reproduction to happen. First, the colony must be of sufficient size to allow it to reproduce. Second, drones must be produced. Drone honey bees were not needed during fall and winter. But now, they are very important for a simple reason: colonies that swarm produce new queens to remain behind in the parent colony. New queens must mate, meaning that drones must be available in the area. Thus, colonies heading full steam into early spring begin to invest heavily in the production of drones. Once you start seeing drones in a colony, swarm season will follow soon. Third, and finally, virgin queens must be produced before a colony can be ready to swarm. This is the last "swarm" condition that must be met and it happens toward the end of early spring. This, of course, is true because colonies most want to begin to swarm just a few weeks prior to or during the beginning of the major nectar flow. Once a colony begins to produce virgin queens, it has officially entered swarm mode and there is no turning back.

By the end of early spring, around week 52, most healthy honey bee colonies go into labor. The colonies have grown to a critical size. Pollen and nectar resource availability is growing. Ripe queen cells are in the nest. Finally, the old mother queen has lost weight, largely thanks to the diet and exercise regimen her worker offspring initiated for her. These sexually mature colonies contain within them a baby bee colony that is ready to emerge for its own week 0.

I have four children of my own and there is very little that is more beautiful than the birth of one's child. I can say the same for the birth of a colony. Go into an apiary on a warm day in the latter parts of early spring. The bees are flying, the colonies are strong, and some are in labor. A colony in labor is a sight to behold. Worker bees in the nest begin to rush out of the nest entrance with a fervor that is unmatched by other bee behavior. When about 1/3 of the swarming bees have left the nest, the old queen, now down to her flying weight, rushes out of the nest and takes to the air. The smells, sights, and sounds emitted by a colony in labor are miraculous. The swarming bees make a cluster and start their week 0. You now know what follows.

Week 53 and beyond…

For the parent colony, the one issuing the swarm, life is just as complicated, opportunistic, and dangerous as it is for the swarm. I want to conclude this article, then, by following the parent colony to its moment of stability, when the new queen is born, mated, and laying.

Colonies left behind after the swarm (what I call the "parent colony" even though the old queen left with the swarm) are queenless, at least they do not contain a mature adult queen. These colonies, in fact, *do* contain queens, lots of them. The queens, though, are immature and developing in the numerous queen cells scattered about the brood area of the nest. See Ellis 2015a for more details.

The first new queen to emerge from her queen cell seeks out her developing queen sisters, bites holes in their cell walls, inserts her stinger into the cells, and stings her competition to death. There are times when multiple queens emerge simultaneously. These queens either fight to the death or one or more early emerging queens may lead secondary (2nd) or tertiary (3rd) swarms from the parent colony. At the end of it all, the colony usually is left with only one virgin queen who goes on her mating flight when she is somewhere between six to ten days old. The average queen will mate with a dozen or more drones on one (most often) or two mating flights. Once mated, she will return to the colony to lead it through its second year's major spring nectar flow. By mid-to-late spring, the size and condition of the parent colony is not all that different from that of the colony it birthed as a swarm.

Older colonies can have bigger problems with pests, pathogens, and toxins than do the swarms they issue. This, simply, is because they continue to inhabit a nest that has seen the accumulation of these stressors. While the swarming bees can escape these issues and inhabit/create a new nest in which pest/pathogen loads are low, the parent colony continues to inhabit the nest where these issues have accumulated over time. Thus, a new dynamic is in place for colonies entering week 53 and beyond. Regardless, honey bee colonies are dynamic by nature and seem to be able to combat these stressors, within reason.

The life cycle of this very mature colony can, in theory, continue indefinitely. However, it usually does not. I believe it is errant to think that a colony can live forever. The colony is a beast and all beasts eventually die. Left completely alone, and assuming no behavioral tolerance to *Varroa* has developed, the typical colony will die two-to-three years after it was birthed as a swarm. Even if the colony is somewhat *Varroa* tolerant, it is faulty to think that it is immortal. After all, each new year produces its own obstacles, from poor nectar flows to bad weather during queen mating flights. There is a lot that can go wrong in the life of a colony. So, all colonies eventually die. I, of course, realize that we can keep our colonies alive in managed settings much longer. However, that requires significant intervention on our part and the remedies we offer often are missing in the natural world. I also know that I may be challenged on this point by those of you (me included) who have seen a feral nest site occupied for many years, perhaps a decade or longer. In this setting, however, one usually is seeing a nest site that is continuously occupied, *not* the same colony occupying the nest site. Regardless, I want to note that death is a natural part of life, the grand finale, and that honey bee colonies experience it the same way that you and I will.

Conclusion

As you might imagine, the biology of a honey bee colony is more complex than I was able to communicate in the pages of this article. The bee colony truly is a beautiful beast, with amazing intricacies. Each colony almost has its own personality, born out of the unique set of genetic and environmental factors creating it. However, there are some transcendent biological properties that nearly every colony has and those are the properties to which I tried to introduce you in this article. I hope you find the biology of a honey bee colony as fascinating as do I. If anything, I hope this has given you a greater appreciation for the bees you keep, or that keep you. Happy Beekeeping.

References

Ellis, J.D. 2015a. Mating biology of honey bees. *American Bee Journal*, 155(12): 1293-1299.

Ellis, J.D. 2015b. Swarms. *American Bee Journal*, 155(11): 1187-1192.

Ellis, J.D. 2015c. The tasks of a worker honey bee. *American Bee Journal*, 155(10): 1077-1081.

Ellis, J.D. 2016a. Colony level thermoregulation and the honey bee dance language. *American Bee Journal*, 156(2): 147-154.

Ellis, J.D. 2016b. Honey bee colonies as superorganisms: the hive *or* the honey bee. *American Bee Journal*, 156(3): 273-279..