Honey Bee Colonies as Superorganisms: The Hive or the Honey Bee?

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I travel quite a bit, giving lectures about bees to various interested groups. One of the lectures that gets requested of me quite often is the one that I give on superorganisms. This is a topic that I have found quite interesting myself, after being introduced to it about 15 or so years ago. At that time, I was a PhD student in South Africa, studying small hive beetles. My wife was there with me, working on her MS degree. Her undergraduate was in wildlife biology. So, she pursued a MS degree in zoology while with me in South Africa. She since acquired her PhD in entomology, with honey bees no less.

South Africa is a former British colony so its citizens travel on the left side of the road. They also primarily use manual transmissions, or stick shifts, something that I can drive but that my wife cannot. Consequently, I had to drive my wife to her field stations since she refused to learn to drive a manual on the left side of the road. I cannot say this was a bad thing. My wife conducted all of her research on a five star game reserve that had all of the big five, plus some (we, in fact, almost got eaten by one of the big five – maybe I will share that story someday).

On these numerous trips, I would take books on bees and social insects with me to the field so that I could keep occupied while my wife sat beside me counting individuals of various antelope species as they crossed her research transects. These books were fascinating to me and opened my eyes to new information on honey bees. I had been a beekeeper since I was 12 so I knew quite a bit about the practical side of bees. However, I did not have knowledge of the type of information that I was reading in the books I had acquired. That period in my life was one of great intellectual exploration and discovery for me.

One of the books that changed my view of honey bees was written by Robin Moritz and Edward Southwick in 1992. Their book, *Bees as Superorganisms*, explored a topic that was foreign to me at the time but has since shaped the way that I think about bees. The book is a bit heady as it was written for scientists, but it is full of amazing information for those who are willing to wade through the science. As a side note, this book gave me such a great appreciation for Robin and the work he does that I am spending a six month sabbatical in his laboratory in Halle, Germany from September 2015 – March 2016 (I even wrote this article from Germany).

Shortly after completing my PhD and a subsequent postdoc, another book on bees as superorganisms was published by Jürgen Tautz (Tautz 2008). I read this book with equal fascination and it strengthened my subscription to the theory. I think this book is a reasonable read for most people. It also comes with the added benefit that it has, what I believe to be, the best pictures of any book in print about honey bees. I think this book provides a useful summary of the superorganism concept. Collectively, the Moritz/Southwick and Tautz books inspired me to develop a presentation, and now this article, on superorganisms.

I often start my lecture on this concept by asking the audience what they know about bees. Of course, the answers that come back to me vary, depending on the audience. Beekeepers' answers, understandably, are more complete and have greater depth. However, as you might imagine, the general public typically says the same basic things about

Figure 1. Two honey bees recovering a drop of honey. Both bees represent separate organisms. Yet, when you bring them and many like them together, a new beast, the honey bee colony, emerges. *Photograph, Mike Bentley*.

Figure 2. Multiple honey bee hives or nests, each containing a single honey bee colony. In effect, you are looking at 16 individual superorganisms, each colony behaving as a single, functioning unit, displaying many of the behaviors characteristic of other organisms. *Photograph, UF/IFAS Honey Bee Research and Extension Laboratory.*

honey bees. I list those in no particular order below.

- Honey bees make honey.
- Honey bees sting.
- Honey is bee "barf."
- Honey bees pollinate crops.
- Because honey bees pollinate crops, we get to enjoy fruits, nuts, vegetables, etc.
- Honey bees communicate by dancing.
- African "killer" bees are honey bees.
- Worker honey bees typically can sting only once and usually die as a result.
- Honey bee colonies can contain up to 60,000 *individual* bees.

I am sure this list is not complete. However, I suspect that it covers most of the limit of what non-beekeepers know about honey bees. Of course, I could go down the list and expand on these topics, or even point out some of the flaws, but I really want to focus instead on the last point made, that "honey bee colonies can contain up to 60,000 *individual* bees."

You might think I would address the 60,000 issue, after all, I have heard news reporters say that a single bee colony has millions of bees in it. To squelch this assertion, I have counted bees in numerous, maybe hundreds of colonies and never counted more than 40,000. Regardless, the number of bees in a colony is not the point that interests me most in this discussion. Instead, it is the concept of *individuality* in bees that strikes at the heart of this treatise.

It is undeniable that a honey bee colony is composed of individual bees (Figure 1) and that these bees, themselves, are organisms. According to Wikipedia, which provides a definition I happen to like, an organism is:

> "any contiguous living system, such as an animal, plant or bacterium. All known types of organisms are capable of some degree of response to stimuli, reproduction, growth and development and homeostasis."

Surely, a single honey bee meets this definition. I like, however, the two definitions of organisms that Merriam Webster's Dictionary provides because they lend themselves nicely to the idea of superorganisms.

Definition 1: an individual constituted to carry on the activities of life by means of organs separate in function but mutually dependent

Definition 2: a complex structure of interdependent and subordinate elements whose relations and properties are largely determined by their function of the whole

Of course, an individual honey bee is an organism. She is alive because of the organs that are separate in function (such as her brain or her heart) but that are mutually dependent. Take humans for example. We have a brain that does what brains do, kidneys that do what kidneys do, eyes that do what eyes do, etc. They are all separate in function, but work together, in fact are mutually dependent. Our brain could not keep us alive in the absence of kidneys and *vice versa*. To add what Wikipedia noted, individual honey bees and humans are organisms because of our ability to respond to stimuli, reproduce, grow, develop, and maintain homeostasis. Humans and bees are organisms because we do what organisms do.

However, look closely as the second definition of organism provided by Webster's Dictionary. Using that definition, one could argue convincingly that *colonies* behave much like organisms in that they are a complex structure of interdependent and subordinate elements (the bees) whose relations and properties are determined by their function as a whole (the colony). Think about it. An individual bee's behavior only makes sense in context of the colony. Though an organism itself, a single honey bee cannot live along. It needs its colony (Figure 2). The colony, though, does not need any individual honey bee.

Consider this further. The properties of a colony are more than just the sum of bee behaviors. A bee alone is just a bee. A bee with other bees is a colony, whose properties are different than those of individual bees. In fact, put a group of honey bees together and you get behaviors, attributes, characteristics, etc. that are otherwise absent in individual honey bees. To borrow an old math adage, but adding a bee twist: a honey bee colony is more than the simple sum of its parts. When honey bees come together, a new beast is produced, a beast that is different from its individual components. This is the idea of *emergent properties*, or "any unique property that "emerges" when component objects [the bees] are joined together in constraining relations to "construct" a higher-level aggregate object [the colony], a novel property that unpredictably comes from a combination of two simpler constituents" (**Dictionary.com**, with me adding the text in brackets). In short, emergent properties are those properties that a group of individuals have but that are otherwise absent in the individual members composing the group.

This discussion, then, leads directly to the idea of bee colonies as superorganisms. The word *superorganism* is an entomological term. It does not mean great or fantastic organism in the sense that super can mean either great or fantastic. It also does not mean beyond ordinary such as it does for Superman, who is a "beyond ordinary" man. Instead, the prefix *super* means *above*. [By the way, this is where "super" comes from when talking about the boxes that we add to our colonies, given that the new ones go above the old ones.] Thus, *super*organism means above the organism, or a structural order beyond that of just an organism. In entomology, the term is defined as "a collection of single creatures that together possess the functional organization implicit in the formal definition of organism." I like this definition a lot because it perfectly encapsulates the idea for honey bee colonies; but what does it mean?

Well, honey bee colonies are collections of single creatures (bees) that together (the colony) possess the functional organization implicit in the formal definition of organism (as I have defined above in a few ways). In other words, you can view the colony itself as an organism, a superorganism, because it is a level of organization beyond that of the true organisms, the bees themselves. However, in order for the concept of superorganisms to be valuable, the superorganism must do what organisms do. In other words, there must be colony level equivalents to the types of things that individual bees or other organisms do. What do other organisms do?

I do not intend to list here all of the types of activities in which organisms engage. However, I will list those that honey bee colonies also seem to do and those that are covered by Moritz and Southwick (1992) and Tautz (2008). For example, many organisms (and, I will argue, honey bee colonies) have cell or tissue specialization and rejuvenation, have glands and secretions, gather and consume food, respire, manage and excrete wastes, thermoregulate, communicate, mount immune responses, reproduce, die, etc. Thus, honey bee colonies must do the same. I hope to convince you of this by discussing the attributes of whole colonies, attributes that parallel those exhibited by other higher organisms, even those exhibited by humans. I want to note that my discussion will not be an exhaustive one. Rather, I will focus on those attributes most expressed at the colony level. Other attributes of colonies are discussed in detail by Moritz and Southwick (1992) and Tautz (2008). These authors go into considerably more detail in their books than I do here.

Cell or tissue specialization and rejuvenation

Humans have groups of similar cells that develop together to form tissues, which in turn have a specific function. For example, we have heart tissue, liver tissue, kidney tissue, etc. This is tissue specialization. [Just to chase a rabbit quickly: human (and other organism) development from single cells is one of the miracles of existence. I find it fascinating that a male human sperm and a female human egg can combine, split, and differentiate into all of the various types of cells we have in our bodies. All of our cells descend from a common, initial cell whose cell offspring divided and differentiated into the various tissues we have. Remarkable, but I digress.]

Humans and many organisms also have an astonishing ability to produce new cells to replace dead/dying cells. This is one form of tissue rejuvenation, with another being complete tissue rejuvenation like that done by lizards that regrow their tails after losing them. Regarding humans, I once heard it said that our bodies replace nearly all of their cells every few months, excluding, of course, the nerve cells. Why is this important? If honey bee colonies are to be viewed as a type of organism, a superorganism as it were, then it should possess a colony level equivalent to tissue specialization and rejuvenation, and of course it does.

For this to work, you have to imagine the individual worker bees as cells that together form the various tissues of the honey bee colony. Now, tissues cannot be assembled randomly, meaning that our hearts are not part of our brains, with little pieces of liver thrown in for proper function. Instead, similar cells must come together to form tissues that have specific functions in the beast, i.e. nerve cells unite to form the brain and central and peripheral nervous systems, etc. To that end, a "tissue" in a honey bee colony would be a group of same-age workers (cohorts) coming together to perform a specific task. Nurse bees are the nurse tissue of the colony, guard bees, the guard tissue, etc. Colonies can replace these tissues when needed. This is due to a honey bee's subscription to temporal polyethism. Do not get lost in the fancy word. It simply means timed (temporal) many (poly) behaviors (ethism) or, as beekeepers call it, age related division of labor. Bees are not born into a task in which they remain their entire lives. Instead, they progress through a series of tasks somewhat predictably as they age (see my review of this topic in my October 2015 ABJ column: Ellis 2015b). This progression through tasks can be slowed, sped up, etc. per the needs of the colony. For example, let us say that a colony is exposed to a pesticide that eliminates the foraging bee population (i.e. the older bees in the hive). The colony responds, or rejuvenates the missing tissue quickly by graduating younger bees into the foraging cohort before they otherwise would have begun foraging. Thus, the colony rejuvenated the missing tissue or function within the nest. Worker bees can move forward or backwards in their prescribed tasks based on colony need. This behavioral plasticity confers the same benefit to colonies that cell rejuvenation does to us. Thus, the colony does have tissue specialization (cohorts of bees forming important body tasks) that are able to rejuvenate themselves (replace a compromised cohort of bees) when a stressor is experienced.

Glands and secretions

Many organisms, humans and bees included, have glands located throughout their bodies. These glands may be endocrine or exocrine glands. An endocrine gland is a collection of cells that secretes chemicals (hormones) *inside* the body to produce a change in other cells *inside* the body. For example, honey bees have a gland called the corpora allata and this gland releases juvenile hormone. This hormone acts on other systems within the bee's body, causing a cascade of internal responses, including, among other things, a bee's programmed progression through its suite of age-based, behavioral tasks. Humans also have a number of endocrine glands that release hormones. The most apparent effects of these secretions occur at the onset of puberty when male and female bodies begin to take vastly different routes to sexual maturity, all as a result of hormones.

Figure 3. A worker honey bee collecting a drop of honey. This bee may consume some of the honey, but likely will pass most of it to other bees in the nest. *Photograph, Mike Bentley*.

In contrast, an exocrine gland is a collection of cells that secretes chemicals (pheromones) through ducts leading *outside* the body to produce a change in another group of organisms *outside* the body. Alarm pheromone is, perhaps, a bee's most notable pheromone, at least as far as most humans are concerned. Bees release this pheromone, produced by the alarm gland – an exocrine gland, outside of their bodies to cause a change in the behavior of other bees.

Similarly, honey bee colonies have colony-level "glands" that produce secretions that regulate all types of colony level behavior. Consider this: a pheromone to the bee is a "hormone" to the colony. The colony, being the body, has numerous bees (cells) that release pheromones to cause other bees (cells) to change their behavior. Thus, individual bee pheromones act much like hormones in the colony's body because the pheromones produce the same effect in the colony's body that hormones do in an individual bee's body. For example, brood produces a "feed me" pheromone (colony level hormone) that causes nurse bees to provide food, which, in turn, causes foraging bees to increase their foraging rate. Queens produce pheromones (colony level hormones) that cause workers to forgo laying eggs. Bees produce alarm pheromone (colony level hormone) to cause the guard cohort of bees (the defense "tissue") to elicit a colony level defensive response. There are many other examples. From the superorganism perspective, then, the individual (queens, workers, brood, etc.) or cohorts of bees are the "glands" in the colony's body, their own pheromones the colony-level hormones that cause other bees to change what they do.

Gather, consume, and digest food

All organisms must acquire and process nutrients, often from other organisms. The individual adult bee accomplishes this by eating honey for fuel (Figure 3) and bee bread for nutrients. Larval bees eat brood food or royal jelly, depending on their sex and caste, mixed with bee bread and honey. Thus, as organisms, immature and adult honey bees gather, consume, and digest food.

Imagine again, though, the honey bee colony as a beast that must acquire, consume, and process its own food. Colony level food accumulation and consumption is quite interesting. If you were able to look down on a colony from above and map the flight patterns of individual bees leaving the nest by drawing a line on the bees' flight paths, you would notice that honey bee colonies have an amoeboid-like foraging pattern. In fact, all social insects do. This foraging patterns is said to look like that of an amoeba, a single-celled organism that reaches or extends part of its cell in the direction of a food source, grabs the food, and brings it back to the center of the cell where it can be "digested". This might be hard to picture but imagine yourself to be fully inside a balloon that is just bigger than your body. Now, imagine pressing your hand against the edge of the balloon to grab something outside

Figure 4. Two honey bee adults engaged in trophallaxis. The one extending its proboscis (center of picture) is taking food from the mouth of the other bee with which it is engaged (below and to the left of the bee extending her proboscis). *Photograph, UF/IFAS Honey Bee Research and Extension Laboratory.*

the balloon to bring it to you. The balloon would push out as your hand presses against it, toward the food source.

Similarly, colonies "reach out" with groups of bees foraging on a single food source and pull in the food source to be processed and digested within the colony. In fact, colonies reach out in many directions on a given day, stretching for food that is as far as 5 miles (about 8 km) from the nest. A circle with a 5 mile radius encompasses about 79 square miles (about 201 square kilometers). This means that a single honey bee colony can forage an area of nearly 80 square miles, which is roughly the size of Baltimore, Maryland. Even more amazing is that foraging patterns change daily. They are adjusted as old resources are exhausted and new ones come into existence. Thus, the colony is reaching its foraging arms out great distances and in all directions nearly every day to take advantage of the best, richest available food sources in the surrounding environment. You can imagine, then, that a colony is a static beast (it does not move from its position), but a static beast with a long reach.

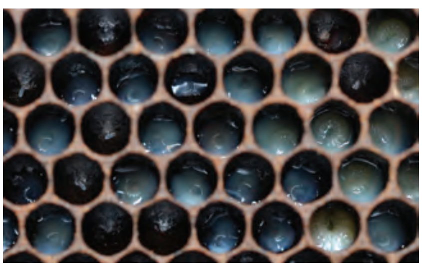

Figure 5. Young worker honey bee larvae floating in a pool of brood food. Nurse worker bees secrete brood food, a true food, from multiple sets of glands in their heads. *Photograph, Mike Bentley.*

Once in the nest, the food is group-processed, stored, and, in many ways, group-digested. Regarding the latter, bees regularly pass honey and other foodstuffs to other bees in the nest via a behavior called trophallaxis (Figure 4), which is when one bee offers food to another bee. You can think of their individual stomachs as small parts of one large colony stomach that group-digest the foodstuffs. This is the colony's communal stomach in which resources are shared and processed among many bees. I once read, though I can no longer find the source, that you can feed a few bees labeled sugar water and reintroduce them into their colony. Then, it is only a short matter of time before most of the bees in the nest contain labeled sugar water. They owe this to their communal stomach.

I have one final note about colony level food handling. Honey bees are one of the only organisms on the planet to produce a true food – a food on which one of their life stages can develop fully and that is produced by a member of the same species. Brood food and royal jelly are glandular secretions fed to larvae by nurse bees (Figure 5). The young bees need only this food to survive. These foodstuffs are not acquired by the bees from external sources, but rather are made, in fact secreted, by the bees themselves from special glands in their heads. What is another organism that produces a true food? The answer is mammals in the form of milk, a liquid that also is secreted by special glands in female members of the species.

Respiration

Respiration is the movement of oxygen from air into cells and tissues and the movement of carbon dioxide rich air in the opposite direction. It is not simply breathing, though breathing is an important part of the respiration process in many organisms, mammals included. Interestingly, individual bees *and* bee colonies respire.

For the individual bee, oxygen rich air moves into the bee's body through spiracles, or small openings that are found down the bees' sides. From there, the air moves through air sacs and into the bee's complex tracheal system.

Honey bee colonies do not have air sacs and trachea, but they still respire. In fact, they also breathe. Colonies breathe through the efforts of a cohort (colony level tissue) of bees whose job it is to regulate the movement of air into and out of the nest. These bees, the fanner bees, stand at the nest entrance and direct the movement of air into and out of the nest. A second cohort of bees (another colony level tissue) standing on the inside walls of the nest circulates air within the nest. Together, these bees direct oxygen rich air into the nest and carbon dioxide rich air out of the nest, thus allowing the colony to breathe. Some researchers have shown that a small colony takes about 3 breathes/minute during the day and less than 0.5 breathes/minute at night. This is the same breathing rate as that of a small mammal. It is notable that the colony's breathing frequency slows at night, just like ours. The next time you see bees fanning at the nest entrance, you can enjoy the fact that you are witnessing a colony breathing, as if it were an animal itself.

Oxygen rich air moved (inhaled) into the nest reaches the cells (bees) and tissues (cohorts of bees) of the beast (the colony). These cells and tissue then generate carbon dioxide rich air that is moved (exhaled) out of the nest by the colony's muscular diaphragm, the fanning bees.

Waste management

Organisms excrete wastes, many of which are produced during the digestion of food. Individual bees defecate nearly solid wastes in the form of a yellowish-orange goo. Perhaps you have seen bee feces on the front of a colony or the window of your favorite beekeeping truck. Bees have numerous organs in their bodies that assist with waste handing, most notably the Malpighian tubules (filter wastes from the hemolymph or blood) and the rectum (the rectal pads reabsorb water from the waste).

Colonies also excrete wastes. What are these wastes? They are dead bees, colony debris, bits of old wax, wax moth frass, etc. They "excrete" these wastes, or rid them from the colony, for much the same reason that any organism defecates – to remove potential sources of physical stress (i.e. toxins, contaminants, etc.) from the body (the nest).

Colony excretion, not surprisingly, is handled by a cohort (colony level tissue) of bees whose job it is to remove the debris and dead bees far away from the nest (Figure 6). I lump the hygienic bees into this category as their job is to detect sick or diseased brood and abort them by removing them from the comb and out of the nest. Collectively, these bees are the undertaker bees or colony cleaners. I want to point out that colonies void their feces far from the nest. The undertaker and cleaner bees carry their cargo, debris/dead bees/etc., out of and *away from* the nest by flying it many meters away. The way that I like to teach this is that colonies do not poop in their own water, meaning that they usually do not drop the debris right in front of the nest. Instead, they take it away from the nest to remove the potential problem completely. More often than not, colonies that have large piles of dead bees or debris in front of them are sick in some way and are otherwise unable to handle their waste. Healthy colonies usually do not have debris piles (what can be considered colony "feces") in front of their nests.

I want to note that there is a second, major way that honey bee colonies as superorganisms manage wastes within their bodies. Before I tell you how, it is important to mention that superorganism nest components and structure often are as important to the perpetuation of the beast as are the individual members of the colony. With that lead-in, I will note that beeswax is an important contributor to colony health via the management of wastes (Figure 7). For example, many of the toxins present in the environment and available to bees are lipophilic (wax loving). So, the wax absorbs these compounds, making them inaccessible to the bees in the nest. These toxins are discarded from the nest when bees remove old wax debris or when wax moths do their important job of scavenging unattended combs. This is a very important function of wax. You might think of wax, among other things, as an organ that performs a function analogous to that of the liver in mammals.

Thermoregulation

I reviewed colony thermoregulation in detail in my February 2016 ABJ column (Ellis 2016), so I will not go into much detail about how it is accomplished here. However, I will note that thermoregulation is one of the most important reasons colonies should be considered organisms themselves since the entire occurrence of thermoregulation is a true emergent property as it is not present in individual honey bees, but results when the bees live colonially.

All insects are cold blooded (well, with some arguable exceptions). They must get their warmth from the radiant heat produced by the sun or another source. The same is true with honey bees. Yet, the honey bee *colony* is different, vastly different. The temperature of a honey bee colony is maintained by its members even though the members are not warm blooded themselves. When the outside temperature is greater than the desired nest temperature of about 34.5°C (about 94ºF), bees place droplets of water throughout the nest and fan at the colony entrance to circulate air within the nest. Collectively, these behaviors cool the nest via evaporative cooling. In contrast, when it is too cold outside, the bees will cluster and shiver their flight muscles to create heat, thus heating the nest to the desired temperature. This results in a honey bee colony whose temperature is tightly controlled regardless of the outside temperature. Thus, individual honey bees are cold blooded while the honey bee colony is warm blooded. Not many organisms on the planet are able to regulate their own body temperature. Worth noting is that the core honey bee colony temperature is maintained right in the middle of the typical range of mammal temperatures. The honey bee colony superorganism is in a unique peer group.

Communication

Many organisms are able to communicate with other organisms of the same species or even of different species, the latter often only for defense purposes. They might communicate their desires by sounds, smells, vibrations, etc. Individual honey bees are no different, often using pheromones to communicate with their nestmates. On the other hand, most organisms also are able to communicate internally, meaning that their internal physiologies have developed in such a way that there is intercellular communication, or communication between cells. One part of the body may signal to another part of the body that it is time for something to happen. For individual bees, this often is done using hormones as I have discussed already. However, the bee colony employs other ways to communicate internally, including using the dance language and through the wax comb that forms the nest's skeleton.

I reviewed the honey bee dance language in detail in my February 2016 ABJ column (Ellis 2016). Thus, I will not tell you much about it here other than the dance language exists to the benefit of the colony rather than to that of the individual bee. This is another emergent property that is otherwise useless to the individual, thus supporting the superorganism concept. Why do bees dance? They dance to tell other bees information about the distance, direction, quality, and maybe even quantity of a food resource. This is almost like cell signaling where one cell (the bee) communicates information to another cell (another bee) that triggers a response in the second cell. You can think of the dance language as a type of internal resource communication system for the superorganism. The dance elicits a response in a cohort of bees (colony level tissue) whose job it is now to go get the food.

The dance language also allows me to discuss the second important function of wax: communication. [There are three main functions of wax, and I noted already that one of those was waste management. I will not discuss wax's third use as a place to house honey, pollen, and developing bee brood.] Dancing bees are able to send information through the wax combs using vibrations that are perceived and acted upon by other bees. You might call beeswax the original cell phone (yuk, yuk). Tautz (2008) talks about internal superorganism communication using wax quite a bit in his book. Regardless, now you have yet another example of how the nest structure contributes to the success of the superorganism and hopefully a greater appreciation for how communication is accomplished.

Figure 6. A worker honey bee removing a sick prepupa from the colony. This is a colony level immune response that exists to help colonies stay healthy. The adult worker will carry the sick immature many meters from the nest. *Photograph, UF/IFAS Honey Bee Research and Extension Laboratory.*

Immune Responses

To me, one of the strongest supports for the superorganism concept concerns how colonies mount immune responses. Like individual bees, bee colonies have immune

Figure 7. Beeswax comb that forms the skeleton of the honey bee nest. Beeswax is an important part of colony waste management. *Photograph, Mike Bentley.*

Figure 8. A wild honey bee colony nesting in a cliff in South Africa has closed its exposed nest using a sheet of propolis that has been pealed back to reveal the colony within. Propolis plays an important role in colony level immunity to pathogens. *Photograph, Anthony Vaudo, UF/IFAS Honey Bee Research and Extension Laboratory*.

response capabilities. To begin this discussion, you must know that the honey bee genome was sequenced and it yielded many surprises. One key finding was that individual honey bees have relatively few genes that code for immune responses, though scientists have found more such genes recently and this number may continue to grow. Initially, it was said that honey bees have fewer such genes than does the common fruit fly. If this remains true into the future, why would such a highly derived organism have such a comparatively poor immune system? The answer is simple: the colony is the unit of selection and it is in the colony that most significant immune responses occur, not in the individual bee.

Honey bee colonies combat pests and pathogens a number of ways. First, adult worker bees can detect diseased/parasitized pupae, uncap their cells, and abort the sick bee within (termed hygienic behavior). As noted, this response to unhealthy brood is performed by a cohort of bees (again, a colony level tissue) that works in this capacity to keep the nest healthy.

Another way that bees respond to pathogens to the benefit of the colony lies with their use of propolis (Figure 8). Honey bees use propolis on the walls of their nest, at their nest entrance, etc. Propolis has been shown to have antimicrobial activity and this, rather than its use as a nest weatherproofer, is the likely reason that bees use the sticky substance. Bee use of propolis, then, is another example of how the next structure contributes to the success of the superorganism, much like wax helps with waste management and internal communication.

Finally, bees also respond to pathogens by raising the temperature of their colonies, i.e. colonies get fevers (called *social fever* – not to be confused with any yet-to-be-made John Travolta movie). This is done at the colony level when the colony is infested with a given pathogen or at the level of a small cluster of bees, for example one that is grouped around an invading Asian hornet, using heat to cook the invader (only an Asian species of honey bee does this).

These are just a few of the behaviors that bees employ to fight pests and pathogens on behalf of the colony, but that otherwise do not help the individual bees performing the behavior. Arguably, the genes that code for the expression of hygienic behavior, a bee's collection, manipulation, and use of propolis, and their ability to raise the nest temperature *are* colony level immune response genes. After all, they support the colony's immune capabilities and not those of the individual bee. This is a great example of how what is lacking in the individual bee is present in the colony.

Reproduction

All organisms want to reproduce. In fact, reproduction is among the strongest drives in any organism. That bees reproduce is unquestioned. Queen bees lay eggs from which other queens, workers, or drones develop. However, it is not a colony's goal in life to reproduce successfully through the production of more and more bees. Otherwise, colonies would get stronger and stronger over time, with no perceived limit to their potential size.

However, this is not what beekeepers witness. Colonies do not keep growing indefinitely. Instead, there is what appears to be a colony level regulation in growth that limits its potential growth perpetuity. This apparent inhibitor to perpetual colony growth is called swarming, a topic I reviewed in considerable detail in my November 2015 ABJ article (Ellis, 2015a). You might have a look at it to fully appreciate the discussion that follows.

Swarming is not a colony growth inhibitor per say. Instead, colonies that are able to swarm have reached sexual maturity. Swarming, in fact, is *colony* level reproduction and it is a much stronger drive than simple *individual bee* reproduction. Colonies want to swarm more than they want to do almost anything else. This, then, is why it is so difficult to control swarming. After all, you are trying to control the very thing that colonies most want to do. How good are we anyway at limiting reproduction in any organism?

A colony issuing a swarm is a colony giving birth. The swarm is a baby bee colony, ready to go on and leave its mark in the world. Bee reproduction at the colony level is much like reproduction in an apple tree. Apples trees have two ways of contributing genetically to future apple trees. First, they have fruit that contain seeds from which other trees grow. Second, apple trees produce pollen that is dispersed to fertilize other trees' seeds. Honey bee colonies produce swarms (the fruit) that contain a queen (the seed) that produces another tree (a mature colony). Colonies also have drones (pollen) that fertilize other colonies' queens (seeds). This borders poetic and paints an accurate picture of honey bee reproduction at the colony, no the superorganism, level.

Death

What is one thing that all organisms share? They all die. Individual honey bees die. This is certain. However, colonies also die. I, personally, think it is somewhat absurd to believe that a colony will live forever or even that they do live forever. Similar to the bees that compose them, colonies are not immortal and we should not expect them to be.

Though all colonies will die, it is not so easy to address the question "when is a honey bee colony actually dead". For example, is it when all of the bees in the nest are dead? This is the easy answer and one most often given. But, it is not likely the best answer for the question. Some argue that an entity is dead when it ceases to exist genetically. Think about it. A colony is a unique entity only by virtue of its DNA, an attribute provided by the mother queen and the drones with which she mated. What happens if an old queen dies and a new one is born? The genetics of the colony change completely. It truly is no longer the colony it was before. It may occupy the same nest, but it is a new beast. Is a colony, therefore, dead when it swarms, when it goes queenless, etc.? This is worth a hearty discussion at your next bee meeting.

My view is that the old colony, the superorganism, is dead once it loses its queen for whatever reason. After all, it produces a new queen that mates with many drones, thus changing the genetic structure nearly completely. It is almost as if there are two ways for a colony to produce a new offspring – through swarming and through requeening. One infant colony leaves the nest, spending its resources wisely while trying to establish sufficiently before the impending winter (it is not a prodigal swarm), while the other colony remains behind to continue the family business. Both end up with new queens. That said, a lineage of related colonies occupying the same nest in succession is, itself, not immortal. Left alone, untended colonies (or, more appropriately, successive inhabitants of a single nest site) typically die after two or three years.

Practically speaking, of course, a colony is dead when all of the bees in the nest are dead. The colony, at this point, no longer exists. The same, though, can be said genetically. The original colony no longer exists when the queen is lost. A new colony takes its place, even if living in the same nest. Thus, our colonies are dying all the time, maybe two or more times per year, with a new phoenix arising from the ashes each time. You have to admit, bees are cool.

Figure 9. A honey bee colony is more than the simple sum of its parts, more than just the bees that compose it. It has properties that single bees do not possess, properties that emerge from the bees' complex social structure. ***Photograph, Mike Bentley.***

Conclusion

In conclusion, we are left to ask if the superorganism concept is useful. I think it not only is useful, but it also is accurate! For example, it certainly explains why bees die when they sting. The selection was for colony survival, not a given bee's survival. It explains colony level immune responses that are absent in individual bees. The selection was for the colony, not the bee. It also explains why swarming is so hard to control. After all, reproduction is the hardest drive to control in any organism. Finally, it explains the emergent properties of the colony that are otherwise absent in individual bees (Figure 9). You can argue, rightfully so, that there came a time that selection migrated away from the individual bee and began to emphasize the colony. This created a new beast, one that could exploit new opportunities and respond better to a host of stimuli. It is at this point that the superorganism was born. Think about that the next time you look at your colony. See a beast that is primed to live, feed, communicate, fight stressors, respond to stimuli, reproduce, and die.

I think Jürgen Tautz (2008) said it best when he noted:

"The bee colony superorganism is more than the simple sum of all its parts. It possesses properties that one does not find in single bees, although many of the properties of single bees determine and influence those of the entire colony, within the framework of its social physiology."

Well said indeed.

PS: Can other social organisms be superorganisms?

I wanted to finish discussing honey bee colonies as superorganisms before throwing in a final set of what I hope are thought provoking comments. This is the PS (or *post scriptum*) section of the manuscript. You might think about it as bonus material.

Given that honey bee sociality goes hand-in-hand with the idea that their colonies are superorganisms, the obvious question that arises is can groups of other social individuals be considered superorganisms? The answer likely is complicated and influenced by your thoughts of individualism versus society.

In the United States, we like to buy into the theory of individuality, that we can do anything we want and that we are independent. However, I suspect that very few of you generate your own electricity, built your own car, grow all of your own food, make your clothes, etc. This, then, means that you are dependent on others for the services they provide just as others are dependent on you for the same reason. Thus, it seems like we need others for our own existence, or at least for our current way of life. This, of course, does not prove that humans come together into superorganism-like groups, only that we rely on the efforts of others to live the lives we live.

Taking the next step, humans self-organize into groups of all types, many of which identify as almost organism-like entities. I will have to use the Christian church as an example as I am a Christian and I know quite a bit about the associated teachings. Christians identify themselves as belonging to a single body, the church body, and that they are many members working together to advance a cause. In fact, this concept is taught from pulpits and Bible studies around the world. If you step back and consider it closely, almost any similar human group (families, churches, businesses, towns, civic clubs, etc.) benefit from properties that emerge from the group that are otherwise absent in the individuals that compose it. Take a business for example. One bad employee (cancer cell) can spread its influence and cause significant problems in the overall body of employees. Recognizing that, most businesses have cohorts of employees (human resources, administration, etc.) whose job it is to recognize problem employees and work to remedy the problem before it damages the function or integrity of the body. There usually is highly developed communication within the group bodies (newsletters, meetings, email chains, memos, etc.) that allow for smooth running of the body so that it can accomplish its goals. These entities also reproduce. In theory, "successful" churches create new churches much the same way a colony swarms, with some of the church body splitting off to find a new nest and grow (though, I am afraid to say, this often is not why churches split). Businesses start spinoff companies similarly. 4-H clubs split into additional clubs as they grow. I could draw many other parallels between human groups and societies much the same way that I did for honey bee colonies as superorganisms.

I do not wish to chase the rabbit much further. I just wanted to note that social bee colonies, such as those we manage in honey bees, are not the only groups that behave as superorganisms. It is a fascinating concept and one worth spending at least a little bit of time considering. Hopefully, this will allow the philosophers in the readership to have something to discuss. For the rest of us, it remains food for thought. Until next month.

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