Field Guide to Beekeeping

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Colony Level Thermoregulation and the Honey Bee Dance Language

In recent months, I have spent significant time writing about various aspects of the biology of honey bees. The articles included the members of a honey bee colony (June 2015), the components of a honey bee nest (July 2015), the external (August 2015) and internal (September 2015) anatomy of the honey bee, the tasks of a worker honey bee (October 2015), swarming behavior in honey bees (November 2015), mating biology of the honey bee (December 2015), and the honey bee sting (January 2016). In my March 2016 article, I will discuss honey bees as superorganisms. I will bring this series on bee biology to a close by synthesizing all of the articles I have written on this topic into a single article on honey bee biology (April 2016). I think understanding bee biology, or at least the basics of bee biology, makes people better beekeepers. Knowing what the bees are trying to do and when they are trying to do it allows you to adjust your management style such that your beekeeping goals and the goals of a honey bee colony overlap. In May 2016, I will go back to discussing beekeeping management topics.

If you look closely at the topics I am including in my series on honey bee biology, you will notice that there are two major items that I failed to discuss. These items, or behaviors, are colony level thermoregulation and the honey bee dance language. These are the topics that I am going to discuss in this article.

Of course, you might guess that these topics have little in common, other than the fact that bees are engaged in the behaviors and both behaviors ensure the survival of the colony. However, I thought it best to include them both in the same article, if for nothing more than to introduce you to the intricacies of two amazing group behaviors performed by honey bees. I include at the end of this document a list of references that I used when compiling the information I am presenting to you herein. In particular, I relied heavily on Seeley's (1985, 1995) and Winston's (1987) books on honey bee ecology/biology/behavior. However, I include a few other references that I believe you will find helpful if you wish to explore either topic in greater detail.

Overview of colony thermoregulation

The ability to thermoregulate is one of the greatest attributes of the honey bee colony. When it is cold outside, honey bees can keep their colonies warm. When it is hot outside, honey bees can cool the nest. These simple truths cannot be overstated because they are what make honey bees, particularly the cavity-nesting honey bees, able to live in a range of environments and promote nest homeostasis. This feat is especially pronounced in the honey bee species we keep, *Apis mellifera*.

Depending on whose side you take, there are nine or so honey bee species on the planet. Four of those species (*A. florea*, *A. andreniformis*, *A. dorsata*, and *A. laboriosa*) are open nesting honey bees, meaning that they live on single combs that they suspend from tree limbs, cliff overhangs, etc. These honey bee species are, somewhat, at the mercy of the environment as their nests are exposed and vulnerable to the whims of Mother Nature. Consequently, these species are distributed mainly in the tropics of Asia, particularly Southeast Asia, where the genus as a whole calls home. There, it is warm much of the year so cooling the nest is not such a high priority.

The other five honey bee species (*A. mellifera*, *A. cerana*, *A. nigrocincta*, *A. koschevnikovi*, and *A. nuluensis*) all preferentially nest in cavities, though some members of these species will build exposed nests. This movement toward cavity nesting allowed these species to inhabit different climates than those to which their open-nesting cousins are confined. In particular, *A. mellifera*, the western honey bee – the bee we keep, has fine-tuned its cavity nesting behaviors, so much so that it can be found in near-desert environments all the way to the coldest temperate ones. This happens because it can thermoregulate its nest.

A single honey bee is a cold blooded insect; but the honey bee colony is warm blooded creature. It can make its temperature different from that of the surrounding environment, and this makes it one of the most unique of all the insects. I like the way that Jones and Oldroyd (2007) put it:

> *…part of the ecological success of social insects (all termites, ants, and some wasps and bees) is that they have at least some ability to regulate temperatures within their nests. This allows them to be physiologically active when other insects might be too cold."*

Bees are so good, in fact, at thermoregulating colonies that they can keep the colony within a 33 - 36°C (91.4 - 96.8°F) temperature range when the ambient temperature falls within a range of -40 to 40°C (-40 to 104°F). They are fine tuned to detect small temperature fluctuations, doing this with the temperature receptors on the five distal (end) segments of their antennae. They can, in fact, detect a temperature difference of 0.25°C (0.45°F). Thus, they can tell when the colony is getting dangerously hot or perilously cold.

How bees warm colonies

The western honey bee's normal distribution is from northern Europe, through the Middle East, and down to the southern tip of Africa. As you might imagine, the environments represented within these latitudes are among the most extreme on earth. Honey bees nesting in these areas, especially in Europe, have developed effective ways of warming the nest when the nest is too cold. They warm the nest for a couple of primary reasons. First, brood (their developing young) develops best around 34.5°C (about 94°F), with an acceptable range being between 32 - 35°C (89.6 - 95°F). The brood rearing temperature varies by less than 1°C daily. Any deviation from this temperature, even a degree or two, can have dire consequences on the developing brood or the adult that results. In fact, few bees emerge below 28°C (82.4°F) or above 37°C (98.6°F). At these extremes, the emerging bees usually have malformed wings and mouthparts, abnormal behaviors, and short lives. Second, optimum brood rearing conditions allow brood to develop faster, thus helping foster rapid colony growth in spring, colony recovery after swarming, and colony recovery after being attacked by pests or predators. Third, keeping the nest warm allows bees to be ready to fly when necessary. Like for all other insects, cold-blooded bees must reach a certain temperature before they are able to fly. Otherwise, cold colonies would be hard to defend and cool temperatures would prohibit the bees from foraging for food. Fourth, the ability to warm colonies has allowed honey bees to maintain populous colonies through winters, thus allowing them to inhabit colder climates. This is very important because where the warming trait is absent, as in *A.m. scutellata* (the "African" honey bee), the bees cannot survive temperate winters. Finally, the ability to raise the nest temperature allows colonies to get fevers, much like humans do, in an attempt to overcome pathogen infections. Thus, the nest must be heated.

Honey bees heat the nest these two primary ways: via passive thermoregulation and active thermoregulation. Passive thermoregulation is accomplished, in part, by the overall structure and architecture of the nest in which they reside. For example, bees select nest sites that allow them to optimize the internal nest temperature. These cavities often facilitate internal air movement, have small entrances (<60 cm^2 or 9 in^2) toward the bottom of the cavity, have insulated walls (the walls of a tree cavity, for example), are elevated at least 3 m (about 10 feet) from the ground, etc. Bees will seal drafty cracks or unwanted, small, holes with propolis. The nest cavities also must be a minimum volume (usually around 15 liters or 4 gallons, but preferentially about 40 liters or 10.6 gallons) so that there is sufficient space to store adequate, insulating honey around the nest core (Figure 1). Honey bees usually keep their brood in the center of the nest and surround it with a thin layer of pollen and a much thicker layer of honey, all stored in sheets of wax comb. Pollen, honey and wax act as insulators for the developing bees. Finally, queens often lay eggs on the side of the nest that is warmest. I often see the brood area shift in winter to the sunny side of the nest, likely to help keep it warm. All of these qualities help the bees thermoregulate the nest passively.

Bees also warm the nest actively. This means that they engage in behaviors that allow them to modify the nest temperature physically. They use two main behaviors to do this: directly incubating brood and clustering. Warm bees are able to incubate brood cells directly by pressing their warm thoraces onto individual capped brood cells in a crouching posture. They also heat brood by entering empty cells adjacent to cells containing brood so that their warm thoraces can radiate heat in all directions. This way, a worker is able to warm up to six brood cells at one time.

The second way that bees warm the nest is by initiating and maintaining a colony cluster. A cluster of bees, sometimes called a winter cluster, is one in which the bees are grouping tightly together to conserve the heat that the bees in the center of the cluster are able to generate. Bees begin to cluster when ambient temperatures are around 18°C (64°F) and typically not 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. When incubating brood, bees try to keep the cluster around 34.5°C (about 94°F). In the absence of brood, the core of the cluster will decrease to about 18°C (64°F) while the outer edges of the cluster, the mantle, will reach about 10°C (50°F). The core cluster temperature can fluctuate significantly (as much as 20°C or 36°F). In short, bees will keep the core cluster temperature as cool as they can handle it to minimize the amount of fuel (honey) it takes to generate the heat. Bees chilled below 18°C (64°F) cannot generate the action potential needed to fly. Below 10°C (50°F), bees become immobile and enter a chill coma. This can kill them within 48 hours unless they are warmed.

In a cluster, the bees are trying to group together as much as possible to regulate to a target temperature. Thus, clusters are loose during warm temperatures and quite compact during cool temperatures. Bee clusters reach maximum contraction at around -10°C (14°F). From 18°C (64°F) to -10°C (14°F), the cluster shrinks 5-fold in size. The contraction of the cluster conserves heat by diminishing the surface area over which heat can be lost and by reducing the airflow through the cluster. At -10°C (14°F), the bees shift from clustering tighter to creating more heat.

The anatomy of a bee cluster is quite interesting. The center of a cluster, the core, is composed of bees that are the heat generators and these bees are > 2 days old. Bees in the core are able to generate heat by contracting and releasing the flight muscles in their thoraces while having their wings disengaged. The resulting response is that the bees are actively moving their flight muscles without moving their wings. This shivering generates heat that alone is not very much, but when grouped with the efforts of other heat generators produces the same amount of heat as a 40 watt bulb. The center of the cluster is somewhat open, with bees having room to crawl, feed on honey stores, fan wings, tend brood, etc.

The heater bees in the cluster core are surrounded by several layers of densely packed bees who are oriented with their heads pointing toward the center of the cluster. These bees compose the cluster's mantle. They occupy the space between combs and will even enter empty cells in the nest to ensure a more solid, contiguous cluster. The mantle of bees forms an insulation blanket that limits the escape of heat generated by the core bees. The temperatures of the thoraces and the abdomens of the bees composing the mantle are the same, suggesting that these bees are not generating heat but rather simply helping to keep heat generated by

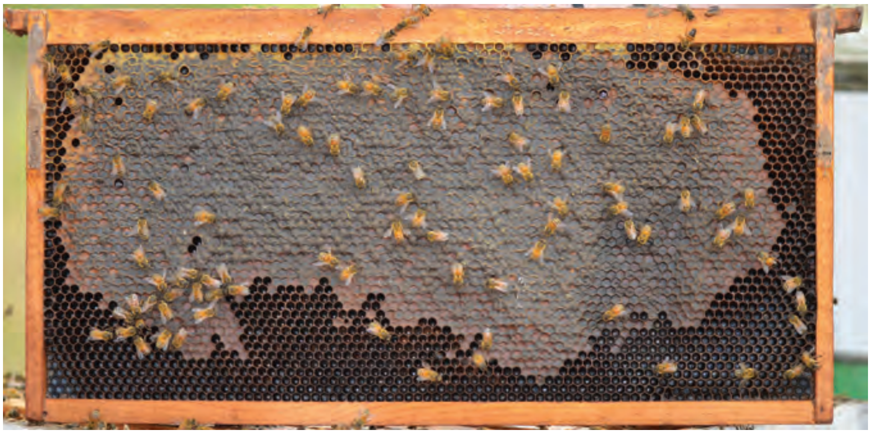

Figure 1. A frame of honey. Honey is a good colony insulator. It usually is stored around and above the brood. ***Photograph: Mike Bentley.***

the core bees in the cluster. Interestingly, this constriction of the mantle reduces the surface area over which heat can be lost significantly. The surface area of a single bee is about 2 cm^2 (0.3 in^2). In a cluster with 15,000 bees, it is about 0.07 cm^2 (0.01 in^2), thus reducing the surface area nearly 30-fold. Mantle bees are in danger of over-chilling and thus must move (sometimes being pulled by their warm sisters because they, otherwise, are immobile) into the center of the cluster to get warm. They usually will stay in the cluster for around 12 hours before rejoining the workers in the mantle.

Bees need fuel to generate heat and honey serves as that fuel. This, incidentally, is one of the main reasons that honey bees, especially temperate race honey bees, collect nectar and convert it into stored honey. They need to consume honey to power their flight muscles to produce heat. It costs the colony about 1 kg (2.2 lbs) of honey per week to warm the nest. About 50 kg (110 lbs) of nectar is needed to produce 20 kg (44 lbs) of honey that is needed to fuel colony heat production through winter. Notably, clusters must "break" on warmer days to feed. This truth has surprised many beekeepers who have had colonies starve to death even though the nest was full of honey. This happens when it is too cold for the cluster to break and the bees exhaust the food immediately available to them. Typically speaking, clusters slowly migrate up in the nest cavity, which is why it is important to have honey above a winter cluster and why many beekeepers take their queen excluders off during winter – i.e. to avoid trapping the queen in a lower hive body while the cluster leaves her behind as they migrate to the stored honey above.

It seems important to note that bees do not attempt to warm the nest, despite my and others use of the phrase "heat the nest." Instead, they are only interested in heating the cluster, i.e. the collective group of bees and any brood it may contain. As far as is known, they do not attempt to heat the entire cavity in which they live, but rather only themselves.

How bees cool colonies

Colonies are in danger of overheating in warmer locations and during warm times of the year. Not surprisingly, honey bees have a way of dealing with this as well. Bees want to keep the nest below a certain temperature for a few reasons. First, brood will die or will develop poorly at temperature extremes above 36°C (96.8°F). Because bee activity generates heat, 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. Second, beeswax combs will soften and collapse under their own weight when nest temperatures are above 40°C (104°F). Third, adult bees can survive only a few hours at temperatures between 45 - 50°C (113 - 122°F). They seem to have a lower tolerance to high heat than they do to cool temperatures. Despite this, bees seem to be really good at keeping the nest temperature down to their desired target temperature. For example, a bee colony put on a 60°C (140°F) lava field was able to keep the core temperature between 35 – 36°C (95 - 96.8°F). Thus, bees have efficient mechanisms in place to deal with high temperatures. These include worker dispersal throughout a colony, ventilating the nest by fanning, cooling the nest by evaporating water, and partially evacuating the nest when it is in danger of overheating.

Figure 2. Ventilating bees. These bees stand at the nest entrance, face the entrance, tilt the tip of their abdomen slightly down, and fan their wings. This fanning helps move warm air out of the colony, thus cooling the nest. *Photograph: Mike Bentley.*

Perhaps the first thing bees do when the nest is warming too much is disperse throughout the nest. The brood nest, the part of the hive whose temperature needs to be regulated most closely, is a very active place. This activity is administered by the worker bees who need to be warm in order to work. When colonies begin to get warm, many of the worker bees will migrate within the nest, away from the brood area. This helps diffuse the heat.

Next, bees will begin to ventilate the nest when the core temperature is around 36°C (96.8°F). Ventilating bees will line up on the inner walls of the nest, all mostly facing the same direction. Other ventilating bees will move outside the nest and stand near the nest entrance, facing the nest (this is often the first outside task that a bee will perform – Figure 2). All of these bees will fan their wings. Fanning bees use a different pattern of wing beats than do flying bees. These beats are designed to move air horizontally rather than generate the lift they need to fly. The fanning activity of bees within the nest circulates air within the nest. The fanning activity of bees at the nest entrance, facing the nest, pulls warm air from the nest and creates cool air currents in the nest. Bees must be fanning at the nest entrance to accomplish this. Otherwise, nest entrances usually are too small to facilitate air movement from them.

If fanning the nest fails to reduce the nest temperature to the target, the bees will begin to cool the nest via water evaporation. At high temperatures, some forager bees switch to water collection (Figure 3). They will return to the nest and offload the water to receiver bees. The receiver bees will place the water in small puddles on combs, on capped brood cells, as a thin layer on the rim of open cells, or as hanging droplets on the roofs of open cells in the nest. The ventilating bees then circulate air over the combs, evaporating the water, and cooling the nest.

Water collection by bees is under a fairly tight regulation. Bees normally collect water from spring to fall to dilute honey, make brood food, etc. There are almost al-

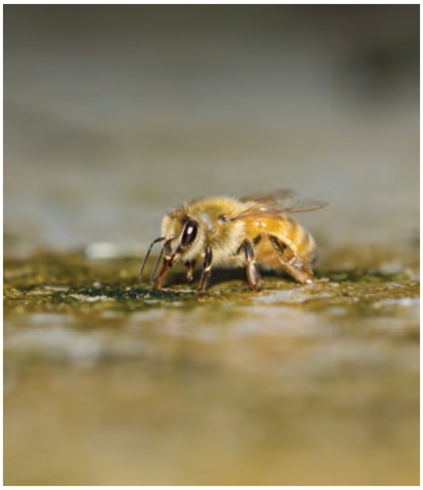

Figure 3. A forager bee collecting water. Water foragers will return to the hive and offload their cargo to a receiver bee. The droplets of water are placed on combs in the brood area and help cool the colony as they are evaporated. *Photograph: Mike Bentley.*

Figure 4. Bees bearding on the front of a honey bee colony. These bees have left the nest on a warm summer evening so that the nest can cool. This site alarms many new beekeepers, but it is a normal part of bee biology. *Photograph: Mike Bentley.*

ways bees foraging for water, even if only a few bees. So, the colony needs to know to increase water collection somehow and this is regulated by an event that happens upon the return of the water forager from the field. As noted, returning water foragers need to offload their cargo to a receiver bee. The time it takes water foragers to find receiver bees dictates the urgency with which a colony will forage for water. If returning water foragers find a receiver bee quickly, they will continue to hunt for water and perform water foraging recruitment dances, thus recruiting more workers to the job. If it takes a while to unload the water, their propensity to collect more water and dance to recruit more water foragers will decrease. Thus, colonies upregulate water collection, in part, by having more receiver bees ready to offload water from the water foragers as this signals to the foragers that the colony needs more water. Since water evaporation is so important for cooling the nest, colonies often have a greater difficulty keeping nests cool on hot *nights*, when they cannot forage for water, than during the day, when they can.

Two final behaviors contribute to nest cooling. Some workers will "tongue-lash" which is where they position themselves over brood cells, extend/contract their proboscis over and over, and press a drop of water from their mouths into a thin film that evaporates quickly. As a last cooling resort, some worker bees will leave the nest and cluster outside the colony (Figure 4). This is commonly seen on warm summer evenings and is one of the causes of bee-bearding (a bee behavior where they cluster outside, around the entrance of the nest, looking like a beard on the hive). Evacuating the nest reduces the amount of heat produced in the nest and facilitates nest ventilation.

Final thoughts on colony level thermoregulation

It seems remarkable that bees are able to use passive and active behaviors to heat and cool the nest. Many social insects thermoregulate their nests passively. Ants and termites excavate tunnels in such a way to encourage airflow through the nest. Some develop mounds that are designed to receive solar radiation when cool or release warm air when hot. However, no other social insect has the ability to regulate their nest temperature so thoroughly. Perhaps what makes it so remarkable is that they physically use themselves to do it. Developing strategies for keeping a stable brood nest temperature despite the ambient environment has allowed western honey bees to colonize much of the world. They are truly a successful organism.

THE HONEY BEE DANCE LANGUAGE

Honey bee use of dances to communicate information about available food resources is one of the group behaviors about which most people who otherwise know little about bees have heard, and for good reason. The behavior is a remarkable example of fairly complex animal communication outside of that used by many vertebrates. It would be novel, in fact, if a "higher" organism such as a monkey or dolphin used it. That a bee, an insect, can have such a derived behavior makes it all-the-more amazing.

I do not wish to digress too far into the history of the investigations that resulted in the collective knowledge that we have concerning the dance language. I think, for the time being, that it is important to know that most of the discoveries made regarding the dance language, certainly the initial and most profound ones, were made by a German bee scientist, Dr. Karl van Frisch. Von Frisch and his colleagues worked to decipher various aspects of the honey bee dance language over many decades in the mid 1900's. His work on this led to his receipt of the Nobel Prize, making him the only bee scientist to date to win this prestigious honor. Perhaps most remarkable, von Frisch used the simplest of tools to study the bees: observation hives, feeding stations, sugar water, and paint. Of course, it helped that he also employed the most complex of tools, the human mind, over time to understand what the bees were saying. He produced a seminal book on the topic (von Frisch 1967) that explains his work and discoveries in greater detail. Since von Frisch's time, others have added to the great wealth of knowledge on which I relied to generate the following description of the honey bee dance language.

Why do bees dance?

I will begin this section with a quote from Dr. Mark Winston who published *The Biology of the Honey Bee* in 1987. In it, he stated:

> "As social insects, bees are able to integrate their activities so that the sum of colony functions is much greater than what individuals could achieve independently. For this integration to occur in a meaningful way, individuals must be able to communicate, particularly to inform nestmates about available resources outside the nest."

Thus, bees dance to share information, but what information?

To answer this question, it is important to know who the dancers usually are[1]. At any given time, about a quarter of all of the bees in the nest are foragers. Forager bees returning from the field with their cargo of nectar, pollen, water, or propolis (Figure 5) are the bee dancers of lore. They spent significant time in the field collecting these valuable resources. When the bounty was particularly good and the source is still ripe for the harvest, the forager bees will dance to communicate to other would-be foragers the direction, distance, and quality of the forage source. Usually, only bees returning from highly profitable sources will dance. Thus, the dances are skewed toward communicating information on profitable sources and not poor ones.

The dance language is most beneficial when food resources are hard to find or have different qualities (see Price and Grüter 2015). They also come with some small liability. The recruited bees, those watching the dances, do not always find the site. When this happens, they have to return to the nest

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[1] I say "ususally" given that bees also use dances to communicate information about new nest sites to their nestmates, though this happens for a short period of time only during swarm season. In this case the dancers are scout bees who are advocating a given nest site.

to receive more information. Dances also are temporally and energetically expensive (i.e. they cost the bees in time and energy). Finally, the information communicated in a dance is easy to lose in a dynamic landscape (in a landscape that is always changing). In this case, information can fade, become outdated, and ultimately be unreliable (Price and Grüter 2015). Despite these liabilities, the dance language, in its entirety, communicates information about food resources and other bees are able to attend the dances and return to the food sources with reasonable consistency.

Dance basics

If a worker bee lives long enough, she will join the colony's foraging work force. Foraging forces are composed of two types of bees, both of which can switch to becoming the other type at any given time. The first type of forager is a scout bee that is somewhat resource naïve. She is not going to look for a specific resource of a specific food at a specific location. Instead, she is leaving the colony in search of any site that will provide what the colony needs (nectar or pollen usually, but also water or propolis depending on the bee). The scout bees have not watched any dance to know where they are going. Instead, they are going on a fact-finding mission and desire to bring back fresh news on potential foraging sites (Figure 6). Scout bees may be new foragers or old bees that have quit visiting a depleted patch. Only about 10% of a colony's foragers are scout bees.

The other type of forager is one ready to be recruited to a new forage site that has proven worthy of additional attention from the bees. Like others before me, I will call these "recruits" in this article. Recruits will sit in the nest and wait to attend dances performed by their forager sisters. Once recruited, they will visit a site until it has been depleted and then reenter the recruitment force. To borrow nomenclature from Seeley (1985, 1995), recruits can be "employed" or "unemployed." Employed recruits were once in the recruitment pile, but have become foragers as a result of watching other dancers. Unemployed recruits are those waiting to be asked to join the forage force. Employed recruits reenter the unemployed recruit demographic when they cease foraging at a particular site.

Both scout and employed recruit bees dance to attract unemployed recruits to sites that they are visiting. The only difference is that scout bees are conveying new information about a newly discovered site while the employed bees, that, themselves, were once recruited to a forage site, are updating information made about previous findings. Both types of bees are conveying useful information. The scout is telling the colony where the next big thing is while the employed recruit tells about the quality of an existing site and communicates the site's decline over time. Only unemployed foragers, the true recruits, receive information through dances. They are the ones whose attention the dancing foragers are trying to get.

Figure 5. Foraging honey bees returning to their hive laden with the bounty from their hard work. *Photograph: Mike Bentley.*

The information about the resource has to be communicated by employed forager bees to unemployed ones reliably. Bees employ a few variations of the dance to communicate forage availability close to or far from the nest, with most dances occurring within 24 cm (about 9.5 in) of the nest entrance where most unemployed recruits are found. Bees perform a round dance when forage resources are close to the nest (<15 m or about 49 feet) and a waggle dance for resources >100 m (328 feet) from the nest. Obviously, one, then, is left to wonder how bees communicate information about resources between 15 - 100 m (49 – 328 feet) from the nest. The answer is that at distances greater than 15 m (49 feet), the dance pattern begins to morph from that of the circle to that of the waggle relatively linearly as the distance increases up to about 100 m (328 feet). Ap-

Figure 6. A honey bee collecting pollen from a flower will return to the nest and tell her sisters where her goods were collected. *Photograph: Mike Bentley.*

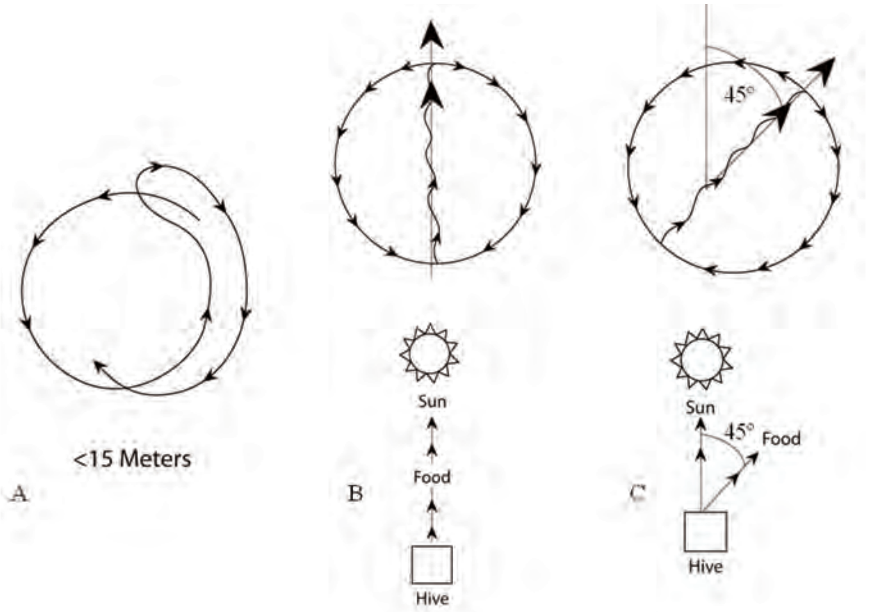

Figure 7. The dance language of the honey bee. A – The round dance communicates the food resources are <15 m (49 feet) from the nest. The waggle dance communicate food sources >100 m (328 feet) from the nest. B - When the returning forager bee dances a straight run point up on the face of the comb, the food source is in the direction of the sun's azimuth. C – When the returning forager bee dances 45º to the right of up on the face of the comb, the food source is 45º to the right of the sun's azimuth. Drawing by Kay Weigel, University of Florida. Published in Ellis, J.D., Atkinson, E.B., Graham, J.G. 2014. Honey bee biology. In: W. Ritter (ed) Bee Health and Veterinarians. OIE World Organization for Animal Health, Paris, France. pp. 15-28.

propriately, the dance variations communicating forage resources within this range are collectively called transition dances. Some argue that there are no true round dances and transition dances, that everything is just a variation of the waggle dance. I suppose this is just a matter of semantics and I do not have the experience to argue either way. Regardless, new data suggest that distance and direction is coded into all recruitment dances, regardless of distance to the food source.

There seems to be some discrepancy over the number of dances that an unemployed recruit will watch before beginning to forage. Some suggest that a recruit will attend multiple dances for the same site and average the information together to make a more informed decision about the site. Others note that dance-following bees do not conduct an extensive survey of all of the information available on the dance floor. In fact, they may not even watch an entire single dance before leaving for the site. At the end of the day, it appears that "unemployed foragers do not follow multiple dances and do not respond selectively to those advertising the best food source" (Seeley, 1995). Thus, each bee appears to sample one dance, chosen at random, before leaving the hive in search for the site/resource. As you might imagine, this means that many bees will fail to find the best food source. However, spread out over a few thousand foragers, the colony seems to be good at exploiting the available resources in the surrounding landscape.

The round dance

Many scientists believe that this dance mainly communicates information about the resource and not so much about the direction and exact distance. The term "round dance" may be a bit of a misnomer as the distinction between round and waggle dances seems increasingly artificial. In fact, they may be interpreted as waggle dances with short-distance signals encoded in the dance. Regardless, dancing foragers use round dances to tell recruits that food is close to the nest (<15 m or about 49 feet).

Foragers about to perform a round dance enter the nest after a trip and exchange nectar with other workers located just inside the nest. She moves to a dance floor and begins to perform the dance, with potential recruits following her dance. As the name implies, the round dance has a round shape (Figure 7), with the dancer making small circles, reversing and going the opposite direction every 1-2 revolutions. As many as 20 of these reversals can occur during the dance, with the total dance lasting from a few seconds to a few minutes. While dancing, the forager emits sounds and exchanges foodstuffs collected on the trip with the watching recruits.

The recruits, believing themselves to have received the information they need to find the resource, leave the hive and fly all around the nest, which is one of the reasons investigators feel that it does not communicate direction. They usually find the resource within 5 or so minutes. How do they do this if the dance is not loaded with information? They acquire odor cues from the resource while exchanging food with the dancer and learn of the overall quality of the foodstuff via the vigor with which the dancing bee dances. In fact, the dancers can share information on the profitability of the food reward given that a higher sugar concentration elicits more vigorous (measured in abdominal vibrations) and longer-lasting dances. Pollen foragers using the round dance recruit for pollen foragers much the same way. The pollen odors are transmitted during the interactions between the dancing bees and their recruits. Thus, recruits "watching" the round dance (as if it could be watched in a dark nest) have a pretty good idea of the type and quality of the resource they are hunting.

The waggle dance

The waggle dance goes by a lot of different names, including transition dance, figure 8 dance, wagging dance and even wagtail dance. In this dance, the returning forager dances a figure 8 pattern on the comb, with the middle of the 8 being referred to as the straight run and the two loops being called circuits. During the straight run, the bee will shake her body violently, wagging it from side to side, with most of the movement occurring in the abdominal section. She moves her body from side to side about 13-15 times per second during the straight run. At the end of the straight run, the bee turns one direction (to the right or to the left) to start a loop, through which she returns to the starting point of the next straight run (Figure 7). After completing the second straight run, she typically turns to start a new loop, usually opposite the direction she took the preceding loop (hence, the figure 8 pattern). She will omit bursts of sound while dancing, a sound that is produced by the buzzing of her flight muscles and wings. The dancing bee will stop throughout the dance and exchange food with unemployed recruit bees, usually around six or so bees, watching the dance. These bees may emit squeaking sounds, which some have called the "begging signal," a behavior that likely causes the dancing bee to stop and offer food.

Waggle dances are used to communicate distance, direction and quality of the resources (including nectar, pollen, water, and maybe even propolis) at distances greater than 100 m (328 feet). This is quite a bit of information that the dancing bee needs to communicate and that the recruits need to receive, process, and to which they need to respond. The dancing bee codes information into the various components of the dance.

1) *Distance* - Bees from feral colonies routinely forage 6 km (3.7 miles) and up to 10 km (6.2 miles) from the nest. In nature, bees rarely forage within 500 m (about 1,641 feet) of the nest, though it is common for bees to forage this close to the nest in managed apiary settings. Thus, bees have to communicate the distance of a food resource for a wide range of possible distances. The

distance of a resource from the nest is communicated by (a) the length of the straight run in comb cell diameters (i.e. the number of cells over which the straight run occurs) or in the overall length (for example, in mm or inches) of the straight run (longer runs = greater distance); (b) the duration of the body wags or buzzing sounds emitted during the straight run (longer wags or buzzing = greater distance); (c) the dance tempo (number of dance circuits or loops; lower tempo = greater distance), and (d) the time spent in the straight run (longer times = greater distance). These are all highly correlated and seem to provide redundant information about distance. Some have suggested that the bees, which surely cannot measure true distance as they do not possess an odometer and cannot use a GPS or ruler, measure instead the amount of energy it took them to reach the resource (the energy hypothesis) while more recent data suggest that it is not the amount of energy, but rather the "optic flow" (movement-induced streaming of visual texture across the visual field – Dyer 2002) a bee experiences while flying that bees are communicating. Regardless, distance communication is not perfect as not all recruits find the resource on the first trip. This could be due to the fact that dance tempo varies between dancing bees dancing for the same resource, with older bees having a lower tempo leading to young recruits attending the dance overestimating the distance. They usually get within 2-10% of the distance to the resource and then use odors they acquired during the dance to hone in on the correct resource.

The role odor plays in a bee's successful identification of a resource cannot be understated. Interpreting the dance gets bees close to the site. The odors get them the rest of the way. The original findings on how bees use odor during the resource finding process led to one of the most significant debates on a biological topic in the 20th century. In short, some scientists concluded that von Frisch's experiments were faulty and that bees cannot receive much useful information from a dance. Instead, the scientists argued, odors are the most important factor bees use to find a resource. This produced the "dance language controversy" that is summarized nicely in Dyer (2002) and Munz (2005). The truth is that dances and the odors accompanying them both are important in a recruit's ability to find a resource successfully. At the end of the day, clearly relevant information is communicated in the actual dance. After all, a trained human observer can be taught to read a dance and successfully find/identity the communicated resource.

2) *Direction* - The direction of the food source from the colony is encoded in the most intriguing of ways. Keep in mind, bees are performing their dances on a vertically oriented comb. So, they cannot simply point to the food source by dancing towards it. Instead, they communicate direction by representing the sun's position, more correctly – the sun's azimuth (draw a line from the sun down to the horizon: where that line meets the horizon is "up" on the comb), in the sky on the vertically oriented comb. In a bit more technical way of explaining it: the solar angle is transposed into the gravitational angle on the comb. What does this mean? While dancing, the position of the sun's azimuth is always indicated as "up" on the comb. The direction of the dancing bee's straight run relative to the position of "up" on the comb is the direction of the food source relative to the sun's azimuth outside the hive, within 1° angular deviation. Imagine, then, that a bee's straight run is pointing straight up (Figure 7). That means the resource lies directly toward the sun's azimuth. If she dances straight down, the food source is away from the sun's azimuth. A bee dancing a straight run 45° to the right of up on the comb is telling the recruits that the resource is 45° to the right of the sun's azimuth from the colony. Recruited workers are able to use organs at the base of their necks to detect the gravitational angle of the dance and translate that into the colony angle to the azimuth of the sun when they exit the colony to begin their flight.

There are pros and cons with using the sun for orientation. One major problem is that the sun appears to move across the sky and sometimes clouds hide it. Of course, the sun is not moving; the earth is rotating, but the end effect is the same: the sun appears to move across the sky. Amazingly, dancing bees are able to adjust for this movement while dancing. Furthermore, recruits seem to be able to adjust for this movement while watching a dance and when flying to/from the resource. When it is cloudy, bees can use polarized light to "see" the sun's position in the sky. There are times when the sun is so obscured that polarized light cannot be seen by the bees. When this happens, it appears that the bees use landmarks to orient and can even learn the normal position of the sun relative to the landmarks so that they can retrieve this information from memory and correct the dance angle. Again: amazing. With all of that said, using the sun to navigate does come with certain advantages. The sun is reliable (it always comes back), conspicuous, and does not deviate its course (Dyer, 2002).

Direction communication in the dance is not perfect. The physical dance and physical interpretation of the dance seem to have the same margin of error (around 9 - 12° from the resource). Furthermore, environmental factors, such as crosswinds (for which bees can adjust) can alter a dance and a bee's interpretation of it. Less than 50% of recruits find the resource on the first flight and they may need to make 2 – 5 flights, on average, before finding it.

3) *Quality* - The quality of a resource is communicated primarily through the wagging, the total number of dance circuits, and the intensity of the buzzing vibrations. The greater the intensity each of these is done, the better the resource. The odor of the dancing bee and quality of the food they share while dancing also communicates information about resource quality.

The transition dance

Also known as the sickle dance, the transition dance is simply the morphing of the round dance into the waggle dance. It can take any shape in between, from that of almost the circle dance to that of almost the waggle dance. Similarly, information is coded into this highly variable dance somewhere between how it is done in a round dance and a waggle dance.

Other notes of interest about the dances

1) The dancing foragers have to process a lot of information before performing a dance. They have to know how far they have flown, what direction, the quality of the source, etc. and adjust for head-/tail-/cross-winds and the seeming movement of the sun. They have to process this information in a way that they can code it into a dance. I think you will agree that how they do this is quite fascinating. They are even able to seem to learn a direct route even "if they have flown a circuitous searching path to get there, a process called path integration" (Dyer, 2002). This simply means that a bee may zig-zag back and forth out to the site, but they can determine the straight line from that and code it into the dance. To make things more interesting, different bees, different colonies, and different races of honey bees may have their own dance "dialects" that other bees "viewing" the dance perceive differently than those who "speak" the same language. Thus, a northern bee watching a southern dancer may go the wrong direction (my attempt at humor).

2) The recruit bees attending the dance receive information being communicated to them multiple ways. But first, there is one obvious way that they do not receive information: sight. Bee dances take place in dark nests so recruits are not simply watching the dance. Instead they follow the dancing bees and appear to mimic the dance moves, perhaps learning valuable information by reproducing the angles. Second, they use their antennae to perceive vibrations produced by the dancers and for odor reception. They can receive airborne sounds using their antenna as well and may even be able to receive vibratory information from the dancing bees through the comb on which they both stand.

3) A fourth dance is used in the foraging/recruitment process and it is called the shaking signal, jerking dance, vibration dance, shaking dance, or dorso-ventral abdominal vibrations (DVAV). In this behavior, a bee vibrates her entire body dorso-ventrally (i.e. shaking her abdomen up and down) while grasping another bee with her front legs. They do this to about 1 – 20 bees per minute, up to 200 bees. The shaken bees sit motionless until the shaking bee is done. It seems that the shakers are foragers who are trying to "wake up" other bees and get them to become recruits on the dance floors. This is their way of saying "I have found something great and you need to follow me, learn about it, and go get it." As the quality of the resource declines, the foragers decrease or cease shaking their sisters to activate them.

Figure 8. These two bees are receiver bees. They have offloaded nectar from returning foragers and now are depositing it into wax cells. *Photograph: Mike Bentley.*

4) A final dance, the tremble dance, is also an important regulator of colony foraging behavior. Foragers returning from the field want to offload their contents to receiver bees (Figure 8) so that they can return to the field to collect more resources. However, there are times when they return to the nest and are unable to find bees to relieve them of their resources. When it takes longer than about 50 seconds to find a receiver bee, the foragers will walk slowly around the nest, making trembling motions forward/backward, right/left, etc. while rotating their bodies to face different directions. About 3 – 4 times per minute, the bee performing the tremble dance will lunge forward and head butt another bee, using her flight muscles to generate a high pitched sound. This behavior seems to cause the buzzed bees to become receiver bees, thus allowing the foraging efforts of the colony to ramp up given that receiver bees are ready to offload the heavily laden foragers. In general, bees returning from a good nectar source will perform tremble dances if it takes longer than 50 second to offload their nectar and waggle dances if it takes them less than 20 seconds (telling them that there is an ample supply of receiver bees ready to handle an influx of quality resources). Seeley (1995) says:

> "Waggle dances and tremble dances play complementary roles in keeping a colony's rates of nectar collecting and nectar processing well matched, for the former enables a colony to boost its collecting rate while the latter enables it to boost its processing rate."

At the end of the day, both the shaking signal and tremble dances seem to help a colony respond to current foraging needs. The tremble dance stimulates young bees (often nurse bees) to switch to food storing when additional receiver bees are needed and the shaking signal may stimulate the receivers to switch to foraging when additional foragers are needed.

Conclusion

In conclusion, I hope that my review of colony level thermoregulation and the dance language of honey bees has brought you a greater appreciation for the bees that we keep. I look forward to sharing with you how all of these behaviors integrate to form a fully functioning colony in the next two articles in my series on honey bee biology

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