The Honey Bee Dance Language

There can be no argument that the most famous aspect of honey bee biology is their method of recruitment, commonly known as the honey bee dance language. It has served as a model example of animal communication in biology courses at all levels, and is one of the most fascinating behaviors that can be observed in nature.

The dance language is used by an individual worker to communicate at least two items of information to one or more other workers: the distance and direction to a location (usually a food source, such as a patch of flowers). It is most often used when an experienced forager returns to her colony with a load of food, either nectar or pollen. If the quality of the food is sufficiently high, she will often perform a “dance” on the surface of the wax comb to recruit new foragers to the resource. The dance language is also used to recruit scout bees to a new nest site during the process of reproductive fission, or swarming. Recruits follow the dancing bee to obtain the information it contains, and then exit the hive to the location of interest. The distance and direction information contained in the dance are representations of the source's location (see Components of the Dance Language), and thus is the only known abstract “language” in nature other than human language.

The dance language is inextricably associated with Dr. Karl von Frisch, who is widely accredited with interpreting its meaning. He and his students carefully described the different components of the language through decades of research. Their experiments typically used glass-walled observation hives, training marked foragers to food sources placed at known distances from a colony, and carefully measuring the angle and duration of the dances when the foragers returned. His work eventually earned him the Nobel Prize (in Medicine) in 1973.

The concept of a honey bee language, however, has not been free of skepticism.

Several scientists, such as Dr. Adrian Wenner, have argued that simply because the dance exists does not necessarily mean that it communicates information about the location of a food source. Those critics have argued that floral odors on a forager's body are the major cues that recruits use to locate novel food sources. Many experiments have directly tested this alternative hypothesis and demonstrated the importance of floral odors in food location. In fact, von Frisch held this same opinion before he changed his mind in favor of the abstract dance language.

The biological reality, however, is somewhere between these two extremes. The most commonly accepted view is that recruits go to the area depicted in the dance, but then “home in” to the flower patch using odor cues. Indeed, researchers have built a robotic honey bee that is able to perform the dance language and recruit novice foragers to specific locations. The robot, however, is unable to properly recruit foragers to a food source unless there is some odor cue on its surface. Nevertheless, it is clear that honey bees use the distance and direction information communicated by the dance language, which represents one of the most intriguing examples of animal communication.

Figure 1. Honey bee.

Components of the Dance Language

At its core, there are two things communicated in a dance: distance and direction. These two pieces of information are translated into separate components of the dance.

Distance

When a food source is very close to the hive (i.e., less than 50 meters away), a forager performs a round dance (Figure 2). She does so by running around in narrow circles, suddenly reversing direction to her original course. She may repeat the dance several times at the same location or move to another location to repeat the dance. After the round dance has ended, she often distributes food to the bees following her. A round dance, therefore, communicates distance ("close to the hive"), but no direction.

Food sources that are at intermediate distances, between 50 and 150 meters away from the hive, are recruited to with the sickle dance. The form of this dance is crescent-shaped, a transitional dance between a round dance and a figure-eight waggle dance (Figure 2).

A waggle dance, or wag-tail dance, is performed by bees foraging at food sources that are over 150 meters away from the hive. This dance, unlike the round and sickle dances, communicates both distance and direction to potential recruits. A bee that performs a waggle dance runs straight ahead for a short distance, returns in a semicircle to the starting point, runs again through the straight course, then makes a semicircle in the opposite direction to complete a full, figure-eight circuit. While running the straight-line course of the dance, the bee's body, especially the abdomen, wags vigorously sideways (Figure 3). This vibration of the body gives a tail-wagging motion. At the same time, the bee emits a train of buzzing sound, produced by wingbeats, at a low frequency of 250-300 Hertz (cycles per second) with a pulse duration of about 20 milliseconds and a repetition of frequency of about 30 seconds.

While several variables of the waggle dance are correlated with distance information (e.g., dance "tempo", duration of buzzing sounds), the duration of the straight run portion of the dance, measured in seconds, is the simplest and most reliable indicator of distance. As the distance to the food source increases, the duration of the waggling portion of the dance (the "waggle run") also increases. The relationship is roughly linear (Figure 4). For example, a forager that performs a waggle run that lasts 2.5 seconds is recruiting for a food source located approximately 2625 meters away.

Direction

While the representation of distance in the waggle dance is relatively straight-forward, the method of communicating direction is more complicated and abstract. The orientation of the dancing bee during the straight portion of her waggle dance indicates the location of the food source relative to the sun. The angle that the bee adopts, relative to vertical, represents the angle to the flowers relative to the direction of the sun outside of the hive. In other words, the dancing bee transposes the solar angle into the gravitational angle. The figure below gives three examples. A forager recruiting to a food source in the same direction as the sun will perform a dance with the waggle run portion directly up on the comb.

Conversely, if the food source were located directly away from the sun, the straight run would be directed vertically down. If the food source were 60 degrees to the left of the sun, the waggle run would be 60 degrees to the left of vertical.

Because the direction information is relative to the sun's position, not the compass direction, a forager's dance for a particular resource will change over time. This is because the sun's position moves over the course of a day. For example, a food source located due east will have foragers dance approximately straight up in the morning (because the sun rises in the east), but will have foragers dance approximately straight down in the late afternoon (because the sun sets in the west). Thus the time of day (or, more importantly, the location of the sun) is an important variable to interpret the direction information in the dance.

The sun's position is also a function of one's geographic location and the time of year. The sun will always move from east to west over the course of the day. However, above the Tropic of Cancer, the sun will always be in the south, whereas below the Tropic of Capricorn, the sun will always be in the north. Within the tropics, the sun can pass to the south or to the north, depending on the time of year.

In summary, in order to translate the direction information contained in the honey bee dance, one must know the angle of the waggle run (with respect to gravity) and the compass direction of the sun (which depends on location, date, and time of day).

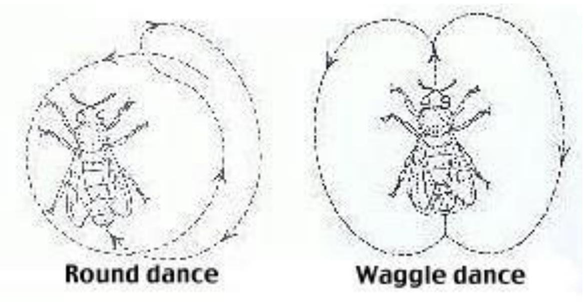

Figure 2. Round and waggle dance.

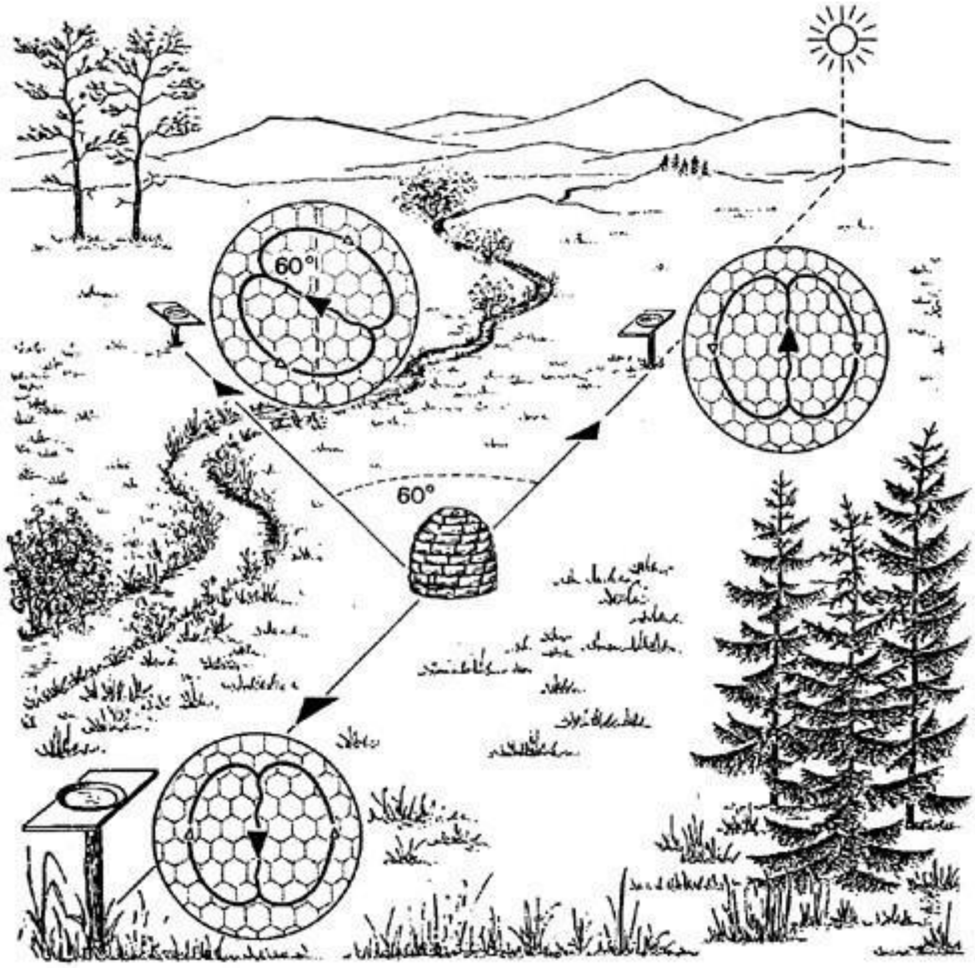

Figure 3. Waggle diagram.

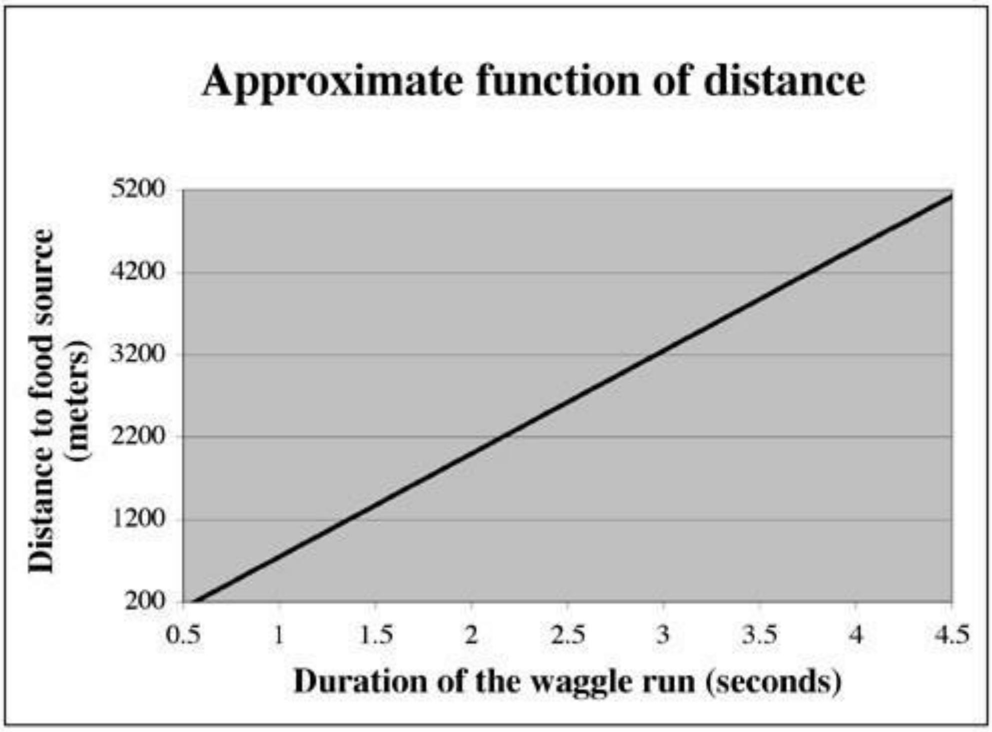

Figure 4. Correlation between distance and duration.

Types of honey bee pheromones

Alarm pheromone

Two main alarm pheromones have been identified in honeybee workers. One is released by the Koschevnikov gland, near the sting shaft, and consists of more than 40 chemical compounds, including isopentyl acetate (IPA), butyl acetate, 1-hexanol, *n*-butanol, 1-octanol, hexyl acetate, octyl acetate, *n*-pentyl acetate and 2-nonanol. These chemical compounds have low molecular weights, are highly volatile, and appear to be the least specific of all pheromones. Alarm pheromones are released when a bee stings another animal, and attract other bees to the location and causes the other bees to behave defensively, i.e. sting or charge. The alarm pheromone emitted when a bee stings another animal smells like bananas. Smoke can mask the bees' alarm pheromone.

The other alarm pheromone is released by the mandibular glands and consists of 2-heptanone, which is also a highly volatile substance. This compound has a repellent effect and it was proposed that it is used to deter potential enemies and robber bees. The amounts of 2-heptanone increase with the age of bees and becomes higher in the case of foragers. It was therefore suggested that 2-heptanone is used by foragers to scent-mark recently visited and depleted foraging locations, which indeed are avoided by foraging bees. However, this has recently been proven false. In a new discovery, it was determined that bees actually use 2-heptanone as an anesthetic and to paralyze intruders. After the intruders are paralyzed, the bees remove them from the hive.

Brood recognition pheromone

Another pheromone is responsible for preventing worker bees from bearing offspring in a colony that still has developing young. Both larvae and pupae emit a "brood recognition" pheromone. This inhibits ovarian development in worker bees and helps nurse bees distinguish worker larvae from drone larvae and pupae. This pheromone is a ten-component blend of fatty-acid esters, which also modulates adult caste ratios and foraging ontogeny dependent on its concentration. The components of brood pheromone have been shown to vary with the age of the developing bee. An artificial brood pheromone was invented by Yves Le Conte, Leam Sreng, Jérome Trouiller, and Serge Henri Poitou and patented in 1996.

Drone pheromone

Drone Mandibular Pheromone attracts other flying drones to suitable sites for mating with virgin queens.

Dufour's gland pheromone

The Dufour's gland (named after the French naturalist Léon Jean Marie Dufour) opens into the dorsal vaginal wall. Dufour’s gland and its secretion have been somewhat of a mystery. The gland secretes its alkaline products into the vaginal cavity, and it has been assumed to be deposited on the eggs as they are laid. Indeed, Dufour’s secretions allow worker bees to distinguish between eggs laid by the queen, which are attractive, and those laid by workers. The complex of as many as 24 chemicals differs between workers in "queenright" colonies and workers of queenless colonies. In the latter, the workers’ Dufour secretions are similar to those of a healthy queen. The secretions of workers in queenright colonies are long-chain alkanes with odd numbers of carbon atoms, but those of egg-laying queens and egg-laying workers of queenless colonies also include long chain esters.

Egg marking pheromone

This pheromone, similar to that described above, helps nurse bees distinguish between eggs laid by the queen bee and eggs laid by a laying worker.

Footprint pheromone

This pheromone is left by bees when they walk and is useful in enhancing Nasonov pheromones in searching for nectar.

In the queen, it is an oily secretion of the queen's tarsal glands that is deposited on the comb as she walks across it. This inhibits queen cell construction (thereby inhibiting swarming), and its production diminishes as the queen ages.

Forager pheromone

Ethyl oleate is released by older forager bees to slow the maturing of nurse bees. This primer pheromone acts as a distributed regulator to keep the ratio of nurse bees to forager bees in the balance that is most beneficial to the hive.

Nasonov pheromone

Nasonov pheromone is emitted by the worker bees and used for orientation and recruitment. Nasonov pheromone includes a number of terpenoids including geraniol, nerolic acid, citral and geranic acid.

Other pheromones

Other pheromones produced by most honey bees include rectal gland pheromone, tarsal pheromone, wax gland and comb pheromone, and tergite gland pheromone.

Types of queen honey bee pheromones

Queen mandibular pheromone

Queen mandibular pheromone (QMP), emitted by the queen, is one of the most important sets of pheromones in the bee hive. It affects social behavior, maintenance of the hive, swarming, mating behavior, and inhibition of ovary development in worker bees. The effects can be short and/or long term. Some of the chemicals found in QMP are carboxylic acids and aromatic compounds. The following compounds have been shown to be important in retinue attraction of workers to their queen and other effects.

- 9-Oxodec-2-enoic acid (9-ODA) – inhibits queen rearing as well as ovarian development in worker bees; strong sexual attractant for drones when on a nuptial flight; critical to worker recognition of the presence of a queen in the hive
- 9-Hydroxy-2-enoic acid (9-HDA) promotes stability of a swarm, or a "calming" influence
- Methylparaben (HOB)
- 4-Hydroxy-3-methoxy phenylethanol (HVA)

Work on synthetic pheromones was done by Keith N. Slessor, Lori-ann Kaminski, Gaylord G. S. King, John H. Borden, and Mark L. Winston; their work was patented in 1991. Synthetic queen mandibular pheromone (QMP) is a mixture of five components: 9-ODA, (−)-9-HDA, (+)-9-HDA, HOB and HVA in a ratio of 118:50:22:10:1.

Queen retinue pheromone

The following compounds have also been identified, of which only coniferyl alcohol is found in the mandibular glands. The combination of the 5 QMP compounds and the 4 compounds below is called the queen retinue pheromone (QRP). These nine compounds are important for the retinue attraction of worker bees around their queen.

- Methyl oleate
- Coniferyl alcohol
- Cetyl alcohol

- α-Linolenic acid

The queen also contains an abundance of various methyl and ethyl fatty acid esters, very similar to the brood recognition pheromone described above. They are likely to have pheromonal functions like those found for the brood recognition pheromone.

Bees use chemical cues to interact with each other and to manage colony organization. Alarm pheromone is used to recruit bees to defend the colony, while Nasanov pheromone is used for aggregation (during swarming or if bees are displaced from the colony). The forager bees produce a pheromone which slows the behavioral maturation of young bees so that they remain in the nursing state longer – this allows the colony to adjust the worker force to have the optimal number of nurses and foragers. The virgin queen releases a pheromone which is used to signal to drones during mating. After mating, the chemical composition of this pheromone changes, and it will inhibit the rearing of new queens, slow behavioral maturation of workers, and inhibit the development of ovaries in workers (so they remain sterile). Queen pheromone also attracts workers from a short distance, and causes them to lick and antennate the queen in a "retinue response". The workers in the retinue thus pick up the pheromone and spread it throughout the colony. The developing larvae produce brood pheromone, which stimulates feeding of the larvae, capping of the cells prior to pupation, and also slows the behavioral maturation of workers and inhibits worker ovary development. Exposure to both brood and queen pheromone will stimulate foraging behavior in forager bees.