

BACKGROUND

Honey bee dancing, perhaps the most intriguing aspect of their biology, is also one of the most fascinating behaviors in animal life. Performed by a worker bee that has returned to the honey comb with pollen or nectar, the dances, in essence, constitute a language that "tells" other workers where the food is. By signaling both distance and direction with particular movements, the worker bee uses the dance language to recruit and direct other workers in gathering pollen and nectar.

The late Karl von Frisch, a professor of zoology at the University of Munich in Germany, is credited with interpreting the meaning of honey bee dance movements. He and his students carried out decades of research in which they carefully described the different components of each dance. Their experiments typically used glass-walled observation hives and paint-marked bee foragers. First, they trained the foragers to find food at sources placed at known distances from the colony. When the bees returned from gathering food from those sources, von Frisch and his students carefully measured both the duration and angle of the dances the foragers performed to recruit other bees to help gather food. Their findings led them to the concept of a dance language. Von Frisch's work eventually earned him the Nobel Prize for Medicine in 1973.

The concept of a honey bee dance language, however, has had its skeptics.

Several scientists, among them Adrian M. Wenner, professor emeritus of natural history at the University of California at Santa Barbara, have a different idea. They believe the dance exists, but they are not certain it communicates the location of a food source. These critics have argued that floral odors on a forager's body are the primary cues that enable the recruit-bees to locate new food sources. Many experiments have directly tested this alternate hypothesis and demonstrated the importance of floral odors in food location. In fact, von Frisch held this same opinion before he changed his mind and developed the theory of the dance language.

The biological reality probably lies 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 on the flower patch using odor cues. Indeed, researchers have built a robotic honey bee that is able to perform the dance language and recruit foragers to specific locations. But the robot is unable to properly recruit foragers to a food source unless it carries an odor cue on its surface. Nevertheless, it is clear that honey bees use the distance and directional information communicated by the dance language.

COMPONENTS OF THE DANCE LANGUAGE

When an experienced forager returns to the colony with a load of nectar or pollen that is sufficiently nutritious to warrant a return to the source, she performs a dance on the surface of the honey comb to tell other foragers where the food is. The dancer "spells out" two items of information distance and direction—to the target food patch. Recruits then leave the hive to find the nectar or pollen.

Distance and direction are presented in separate components of the dance.

DISTANCE

When a food source is very close to the hive (less than 50 meters), a forager performs a round dance (Figure 1). 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 on the comb to repeat it. 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," in this example), but not direction.

Food sources that are at intermediate distances, between 50 and 150 meters from the hive, are described by the sickle dance. This dance is crescent-shaped and represents a transitional dance between the round dance and a waggle dance.

The waggle dance (Figure 2), or wag-tail dance, is performed by bees foraging at food sources that are more than 150 meters from the hive. This dance, unlike the round dance, communicates both distance and direction. 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 from side to side. This vibration of the body produces a tail-wagging motion. At the same time, the bee emits a buzzing sound, produced by wingbeats at a low audio frequency of 250 to 300 hertz or cycles per second. The



Figure 1. Round dance Figure 2. Waggle dance on Frisch, 1976

buzzing occurs in pulsebeats of about 20 milliseconds, delivered at a rate of about 30 per second.

While several variables of the waggle dance relate to distance (such as dance "tempo" or the 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 3). For example, a forager that performs a waggle run that lasts 2.5 seconds is recruiting for a food source located about 2,625 meters away.

DIRECTION

Although the representation of distance in the waggle dance is relatively straightforward, the method of communicating direction is more complicated. The orientation of the dancing bee during the straight portion of her waggle dance indicates the location of the food source relative to

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 the hive. In other words, the dancing bee transposes the solar angle into the gravitational angle. Figure 4 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 traveling directly upward on the honey comb. Conversely, if the food source is located directly away from the sun, the straight run will be performed vertically downward. If the food source is 60 degrees to the left of the sun, the waggle run will be 60 degrees to the left of vertical.





Figure 4. Waggle-run direction

Because directional information is given relative to the sun's position and not to a compass direction, a forager's dance for a particular resource will change during a day. This is because the sun's position moves during the day. For example, a food source located due east will cause foragers to dance approximately straight up in the morning (because the sun rises in the east), but in the late afternoon, the foragers will dance approximately straight down (because the sun sets in the west). Thus, the location of the sun is a key variable in interpreting the directional information in the dance.

The sun's position also is governed by geographic location and 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 move from southeast to southwest, whereas below the Tropic of Capricorn, the sun will move from northeast to northwest. Within the tropics, the sun may be located to the south or to the north, depending on the time of year.

Thus, to translate the directional 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 3. The relationship of distance to waggle-run duration.

MORE INFORMATION

Visit the Web site for the Apiculture program at North Carolina State University to try out an interactive movie that enables the user to change, in real time, a forager's dance, depending on the numerous variables that are important for the bee's communication of distance and direction to recruits. The Web site is: http://entomology. ncsu.edu/apiculture/Dance_tutorial.html

CONCLUSION

The honey bee dance language serves as a model of animal communication in classroom situations at all levels. It is one of the more intriguing behaviors in the animal kingdom and solidifies honey bees as one of the most interesting systems in biology.

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Prepared by David R. Tarpy Assistant Professor and Extension Apiculturist



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