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Stingless-Bee Communication

Searching for a proto-dance language reveals possible stages in the evolution of methods by which experienced foragers lead others to food

James C. Nieh

At the close of World War I in the spring of 1919, an Austrian scientist, Karl von Frisch, sat in a former Jesuit cloister feeding honeybees. He had just designed a glass-walled observation hive, and, as he wrote in *The Dance Language and Orientation of Bees*, he was delighted to observe one of his returning foragers performing "a round dance in which the … bees sitting nearby showed lively interest. They tripped along after the dancer, and then left the hive to hasten to the feeding station." Scientists as early as Aristotle had alluded to this recruitment behavior, in which one bee finds a source of food and then advertises its location to nestmates. Nevertheless, von Frisch was the first systematically to study it and crack its code.

The discovery of the honeybee's so-called waggle dance served as the core of von Frisch's achievements. In this dance, a returning forager makes a short, straight run, during which it performs a waggling motion, and then circles off to the right or left to make another straight run. This dance involves multiple sensory cues that communicate the distance and direction of a food source. It also provided the first

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animal example of sophisticated representational communication: the ability to encode and transmit spatial information. Although Adrian Wenner of the University of California at Santa Barbara later challenged many of these claims, subsequent research showed that honeybee recruits are able to perceive and use information provided in the waggle dance to find a food source at the correct distance and direction.

Finding this dance in just one species of bee intrigued von Frisch, and he wondered how such a complex system had evolved. Therefore, von Frisch urged his student Martin Lindauer, later of the Universität Würzburg, to study other honeybee species and the stingless bees. In 1985 Lindauer quoted von Frisch as saying, "we cannot believe that the bee dance of the European bees has come from heaven as it is and since the Indian honeybees and the stingless bees there live in a more primitive social organization, we should expect some phylogenetically primitive stages of the bee dance." Lindauer discovered that the dwarf honeybee, *Apis florea*, performs waggle dances on the horizontal surface of its comb, directly orienting toward the sun. Nevertheless, this was the most primitive variant, and it could not explain how the waggle dance evolved.

Lindauer's work on the stingless bees proved more fruitful and is the starting point of my story. The stingless bees are a large monophyletic group of more than 450 species spread through 30 to 50 genera. Although their greatest diversity is in the Neotropics, they are also found in Africa, Asia and Australia. Consequently, they probably evolved prior to the breakup of Gondwanaland. Stingless bees attracted von Frisch's attention because they were

thought to be the most closely related sister group to honeybees. Although this relationship is now uncertain, stingless bees and honeybees share much in common because they are the only highly social bees.

Lindauer and Warwick Kerr of the Universidade de São Paulo discovered a wide variety of communication systems among stingless bees, ranging from random search strategies, which do not communicate food's location, to systems employing scent trails and undirected excitatory "dance" motions inside the nest. In 1965, Harald Esch of the University of Notre Dame discovered that recruiting foragers in stingless bees of the genus *Melipona* produce longer sound pulses inside the nest for food sources that are more distant from it. A similar correlation between sound pulses and distance was known in honeybees, so von Frisch's hope of finding a proto-dance language seemed closer to fulfillment.

Unfortunately, the stingless-bee discoveries failed to ignite further research and laid dormant for decades, despite raising intriguing new questions. Results from recent work, however, should renew interest in stingless bees. As I shall show, one species of stingless bee uses a wide range of communication techniques, from simply watching where other bees go to encoding information in sounds. A careful examination of this behavior suggests how food-recruitment communication might have evolved.

Direction, Distance and Height
In 1991, my doctoral advisor at Cornell University, Tom Seeley, suggested that I take up this story and carefully analyze the communication system of a stingless bee. I chose the *Melipona* because

of Esch's previous work, and I went to Panama to collaborate with David Roubik of the Smithsonian Tropical Research Institute. Confident that I would be able to record recruitment sounds, I came during the Panamanian dry season armed with a videocamera and microphones to record behavior in Roubik's observation colonies. For my experiments, I selected *Melipona panamica* because it is one of the most common species of *Melipona* and is relatively unaggressive.

Although I spent a long, hot month working in Panama, little came from my efforts. I could barely train bees to my artificial feeder, observed scarcely any recruitment behavior even for natural food sources and discovered that intriguing sounds or movements were generally concealed inside a waxy funnel built by the bees from the nest entrance to the food-storage pots. Any attempts to remove this funnel disrupted foraging. Foragers were also extremely sensitive to light and air currents. Consequently, I could not easily follow recruiting foragers with a moving microphone as I had done before with honeybees. The colony needed to be sealed and placed under special lighting. A month of frustration convinced me that I could not take a shortcut ap-

Figure 1. Stingless bees (*above*) are a large category of insects encompassing more than 450 species spread through 30 to 50 genera. Like honey bees, stingless bees are highly social, and many species are able to communicate the locations of food sources. Foragers of *Melipona panamica*, the subject of the author's study (*left*), lead others to sources of food through various forms of communication, including sounds, smells and visual cues. By testing food-source locations that vary in height, distance or direction, and then studying the resulting behavior by bees, the author reveals that these bees use a variety of signals to communicate where other bees in the nest can find food. In addition, his work suggests how food-recruitment communication might have evolved. (Except where noted, all photographs by the author.)

proach. I needed to choose a time when I could train bees to artificial feeders and to resolve several technical issues in order to observe recruitment behavior inside a nest.

On my next trip, I came at the end of the rainy season, when the fewest natural food sources are available. In addition, I had designed a new observation nest that consisted of a chamber for the central brood comb, a smaller chamber for honey- and pollen-storage pots and an unloading platform—a flattened, triangular chamber that mimicked the natural nest's waxy in-

ternal funnel. I covered all the chambers with glass and illuminated the nest with a fiber-optic lamp to localize the lighting and reduce the effect of lamp heat. To my surprise, the new observation nest worked well. Bees unloaded food and danced normally on the unloading platform. Microphones inserted along the sides of the unloading platform allowed me to record recruitment sounds.

My first goal was to determine if *Melipona panamica* foragers could actually communicate food location. To test for direction, David Roubik and I
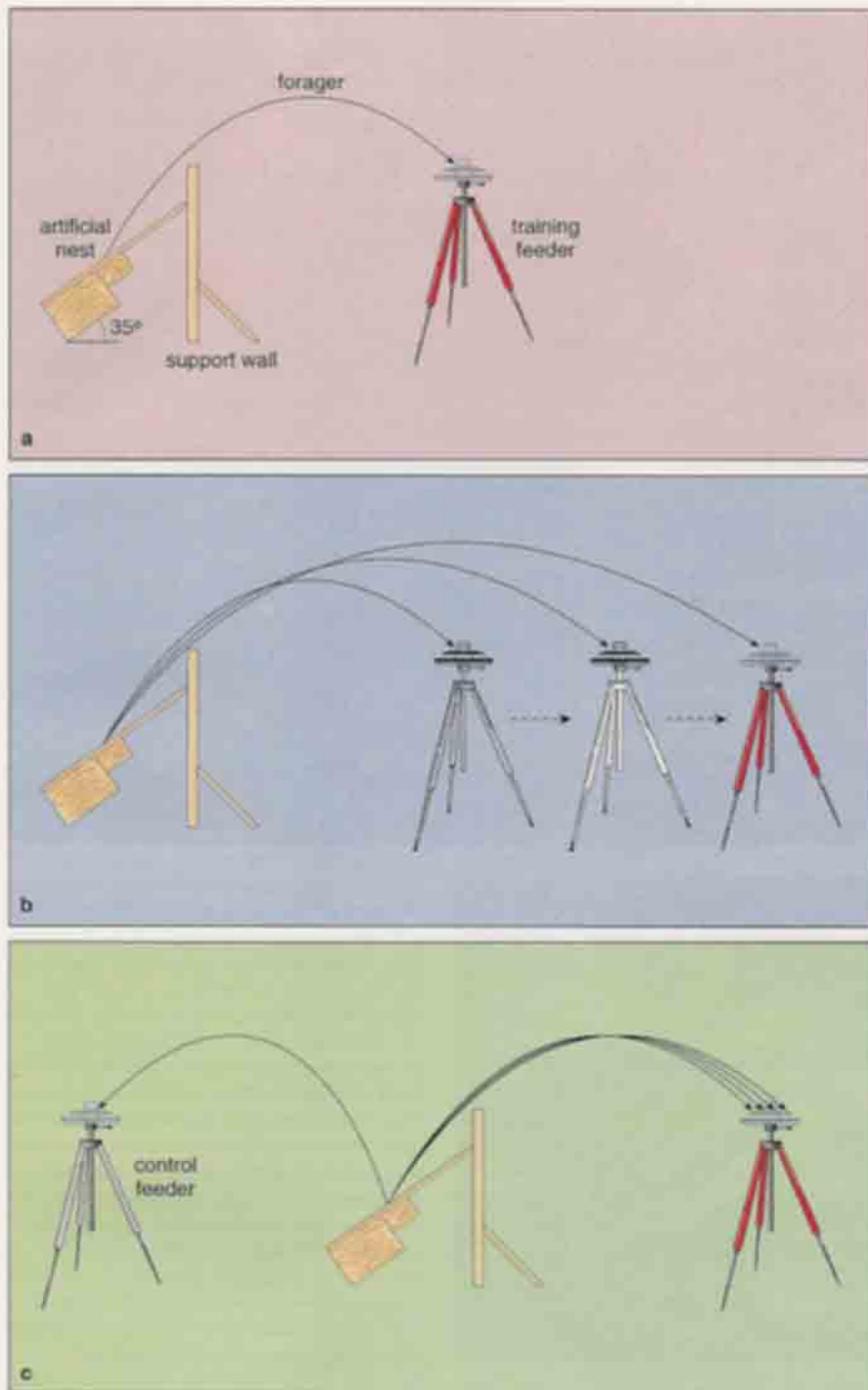
Figure 2. Foragers communicate the direction to a food source to other bees. The author revealed this by training bees from an artificial nest to visit a nearby training feeder (red), which contained sugar water (a). Foragers visited the feeder and then returned to the nest to recruit other bees. Next, the author slowly increased the distance between the training feeder and the nest (b). Once the bees had been trained to the desired distance, the investigators placed a control feeder (gray) at the same distance but in the opposite direction (c). Nearly all inexperienced foragers visited the training feeder, indicating that experienced foragers had communicated its direction.

placed two sucrose-solution feeders equal distances from the nest but in opposite directions. We trained bees to a feeder by placing it close to the nest, waiting for bees to feed and then moving it in small steps toward a goal loca-tion. All bees landing on this feeder were marked with unique tags or paint dabs. Once this training feeder reached its final site, we set up a control feeder with the same scented-sucrose solution but located in the opposite direction. Assistants immediately captured all bees coming to this control feeder, so that none could return to the nest and communicate its location.

If experienced foragers cannot com-municate direction, then newcomers, which can be identified as unmarked bees, should search randomly for a feeder and arrive in equal numbers at both. On the other hand, if experienced foragers can communicate direction, then significantly more newcomers should arrive at the training feeder. In order to control for potential site bias, we also switched or changed the loca-tion of the training feeder in half of the trials. Through these experiments, we discovered that these bees can communicate a food source's direction. Related experiments showed that M. panamica can also communicate a food source's distance and height. The com-munication of height was a welcome surprise because von Frisch and Lin-dauer reported that the European honeybee cannot communicate food-source height.

How Do They Do It?
At this stage, simple mechanisms could account for all of our data. For example, a recruiter might leave a scent trail between the hive and a feed-er, so that newcomers could follow it. Newcomers might also simply follow an experienced forager to the food. A recruiter might even mark a feeder with a pheromone. We needed to test these possibilities.

Roubik and I tested the scent-trail idea by training bees across a water gap, where a scent trail would "disap-pear" by diffusing immediately into the water. By placing a feeder in a ca-noe, we trained bees to the opposite shore. As is typical in field research, we encountered unexpected prob-lems. For one thing, other animals ate our carefully trained foragers! After fi-nally building a toad- and basilisk lizard–proof enclosure, we managed to train 20 foragers over the water gap. Af-ter that, we observed that significantly more newcomers still arrived at the training feeder than at the control feed-er. Recruits apparently did not need a scent trail to find the right feeder.

Recruits also did not appear to fol-low experienced foragers directly to a food source, because recruits and for-agers rarely arrived at a feeder together.

To see whether experienced foragers marked a feeder with a pheromone, I

Figure 3. Artificial nest *(left)* allowed the author not only to observe stingless-bee behavior and record the sounds the bees produce but also to capture and tag *(above)* experienced foragers and control which bees left the nest.

trained bees to a feeder 100 meters from the nest and allowed them to feed for several hours. After recruitment had begun, I placed a suction tube over the nest entrance and began capturing all exiting bees. Meanwhile, my assistant captured all remaining bees at the feeder, sealed them in plastic bags and placed an identical but unvisited control feeder 1 meter to the right or the left of the training feeder. Next, I released potential newcomers one by one from the nest. Significantly more newcomers chose the training feeder, even when it was moved to a new location that experienced foragers had never visited. So the experienced foragers had apparently deposited some odor cue on the food source to guide newcomers. Subsequent experiments showed that the scent beacon has a maximum effective radius of 6 to 12 meters from a food source. The source of the scent beacon, however, remains a mystery.

Throughout my previous experiments, I had heard intriguing sounds through the glass cover of the observation hive and saw recruiting foragers running and spinning inside of the nest. Now, I wondered whether these bees could communicate direction, distance or height inside the nest.

To test each of these parameters, I designed experiments that forced newcomers to search for food based only on information received inside the nest. In each experiment, David Roubik and I allowed bees to forage freely for one hour, and then released bees that had never visited a feeder but that had been exposed to returning for-

agers. In the direction experiment, equal numbers of newcomers arrived at both the control and the training feeder. So recruits apparently do not receive directional information inside the nest. Nevertheless, significantly more newcomers did find the training feeder in the height and distance experiments. Consequently, these experiments suggested that foragers communicate direction outside the nest and height and distance inside it.

Trilling and Twisting

After three years of groundwork, I was prepared to revisit the intriguing behaviors of recruiting foragers inside the nest. An experienced forager returning from a rich food source enters the nest and often begins producing loud pulsed sounds while unloading her food to other bees. As she unloads, other bees cluster around her and often hold their antennae over her vibrating wings. Unloading typically lasts for 20 seconds. Just as she stops unloading, one sometimes hears a short series of pulses, like a slow trill, followed by a dance. The dance phase typically lasts 10 seconds and consists of a recruiter making rapid clockwise and counterclockwise turning motions—about one complete turn per second—while continuing to produce pulsed sounds.

There is no correlation between the degree of turning, rate of turning or order of turning and the direction to the food source. Other bees attend to the dancer during the turns and continue to cluster around her, but they do not follow her every turn in the manner of

honeybee followers. Nevertheless, the followers shift their body positions to face the dancer's general location. Occasionally, they beg a food sample from her. Between turns, a particularly excited forager will sometimes run around the nest, contacting other bees and giving them brief food samples. The followers usually do not keep up with her during these excursions.

Analyzing videotapes of recruiters trained to known feeder locations revealed no correlations between dance movements and the direction to a food source. In addition, recruiter sounds did not correlate with a food source's direction. This was not surprising, because previous experiments suggested that these bees communicate direction outside the nest. However, David Roubik and I did find unloading sounds that corresponded to the height of a food source and dance sounds that corresponded to the distance to a food source.

Foragers recruiting for a feeder 40 meters up in the canopy, for example, produced shorter unloading sound pulses than foragers recruiting for a feeder at the base of the same canopy. This difference was particularly clear for the longest unloading pulse per performance. However, David Roubik and I repeated these measurements with the same colony and feeder locations in 1995 and 1996 and were surprised to observe a change in the unloading pulses. Although the higher feeder consistently elicited shorter unloading pulses, the absolute magnitude of these pulses was not fixed. The durations of 1995 unloading pulses were
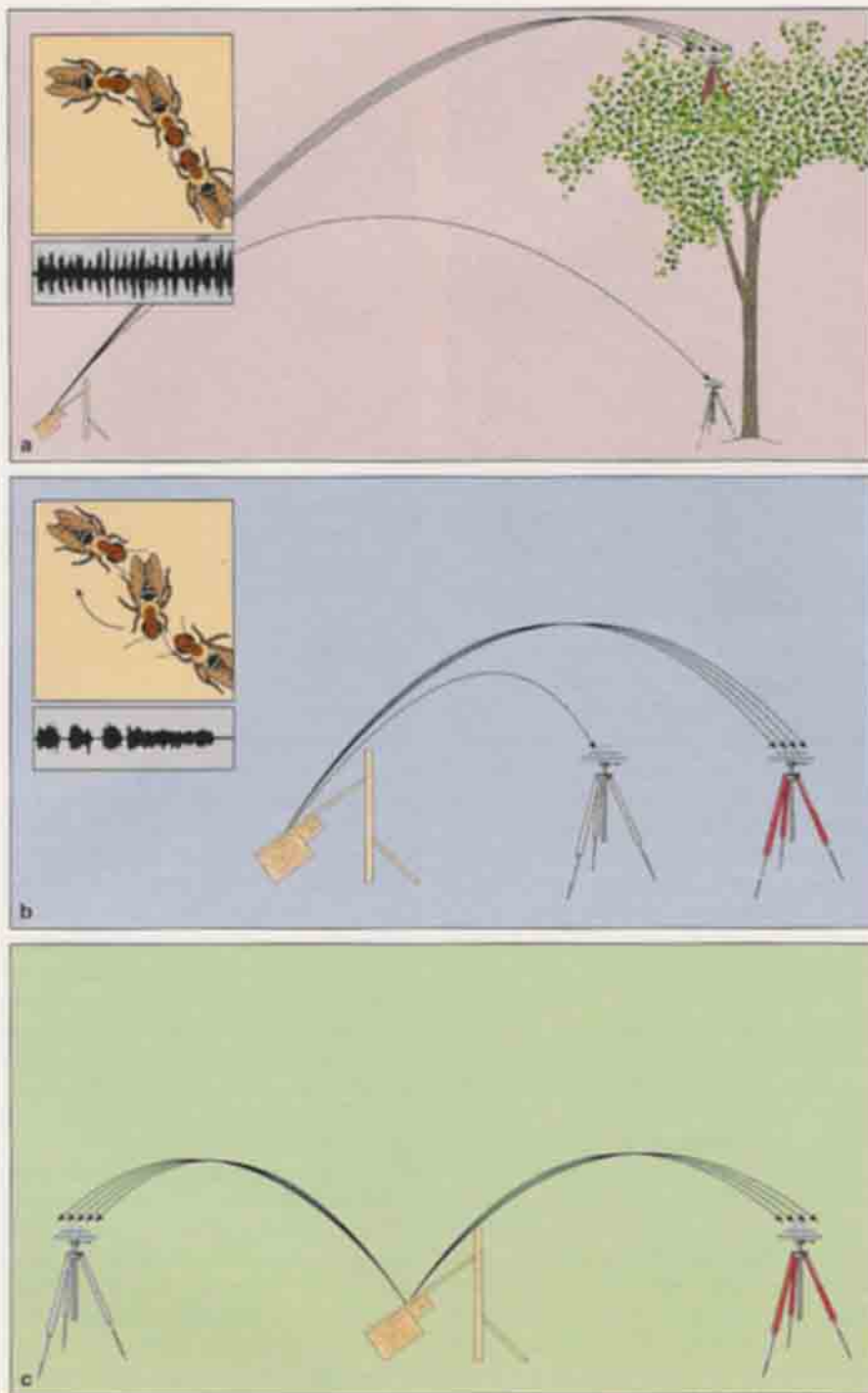
Figure 4. Information about the location of a food source is communicated inside and outside a nest. This can be shown by training bees to a feeder, letting experienced foragers interact with inexperienced bees (ones that have not visited the feeder) inside the nest, and then letting only the inexperienced bees leave the nest and attempt to find a new feeder placed at the same final training location. (The original feeder was removed to eliminate forager-deposited scent marks.) Under these conditions, more of the inexperienced bees find the training feeder (red) high in the forest canopy than find the control feeder (gray) at the base of the canopy (a). Thus height information is communicated inside the nest, potentially by sounds during the dance phase (inset panel), which involves clockwise and then counterclockwise rotations. If a control feeder is placed between the nest and the training feeder, most of the new bees go to the latter (b). Thus foragers convey distance information inside the nest (inset panel), potentially through sounds made during food unloading. When the author put the control feeder in the opposite direction from the training feeder, however, about equal numbers of new bees arrived at both feeders, indicating that directional information is conveyed outside the nest.

generally longer than the durations of 1996 unloading pulses. Thus a 1996 forager transported back in time to 1995 would mistakenly assume that both feeders were located high in the canopy if she relied solely on unloading pulse durations. Conversely, a 1995 forager transported to 1996 would mistakenly assume that both feeders were located on the forest floor.

Thus the mechanism of height communication presents an intriguing problem. Part of the variation in unloading-pulse durations might come from a poor understanding of what constitutes a good recruitment performance. Recruiters varied in the "strength" of their performances and the number of followers that they attracted. During the seemingly weakest performances, recruiters produced very brief, sporadic sound pulses and did not perform dance turns. Because no one knows precisely what constitutes a strong versus a weak recruitment performance, we collected data on all recruitment performances and thereby averaged the weak and the strong ones. Future studies will focus on teasing out those parameters of the recruitment performance that are most relevant to recruits.

The mechanism of distance communication is clearer. As bees begin making the swift clockwise and counterclockwise turns of the dance phase, they continue to produce pulsed sounds. The duration of these sounds correlates closely with the distance to the food source, with longer pulses indicating greater distances. The longest dance pulse per performance provides the best indication of distance. In fact, in our experiments, distance explained 96 percent of the variance in the average duration of the longest dance pulse. As with the unloading pulses, dance-pulse duration varied considerably for a given food location. However, the variance in dance-pulse duration increased linearly with increasing distance to a food source. In other words, the mechanism was accurate to a fixed percentage of the total distance. If the error was 10 percent, for example, then it would be ±10 meters for a food source 100 meters away and ±100 meters for a feeder 1 kilometer away. Recent studies indicate that this type of error also applies to honeybee distance estimation, but other mechanisms appear to compensate for it so that the absolute error does not in-

crease as the distance to the food source increases.

Because the recruiter apparently communicates both height and distance with sound durations, the recruits must have some way of knowing when she is communicating height and when she is communicating distance. One key might be the relatively motionless state of the recruiter during the unloading phase versus her swift spinning motions during the dance phase. The sounds generated by a bee's vibrating wings are highly directional, so a stationary listener should detect a relatively stable sound field from an unloading bee and a rapidly changing one from a spinning bee. Perhaps this is why follower bees gradually shift their positions to remain close to the dancer but do not closely pursue her as she spins.

The communication of direction remains a mystery. Perhaps recruits gain the directional vector from following the foragers outside the nest for a brief distance. Esch described an intriguing behavior in Brazilian *Melipona* species where recruiters in front of the nest appear to fly in a zigzag pattern pointing in the direction of a food source.

The Evolution of Communication

The initial hope for discovering "missing links" in the form of species with simpler forms of the honeybee-dance language has not been directly fulfilled. The stingless bees might be the closest sister group to the honeybees, but the stingless-bee communication systems probably evolved independently into the wonderful forms and diversity that we see today. Nonetheless, the recruitment communication system of *Melipona panamica* provides fascinating insights into the evolution of sophisticated representational communication systems in highly social bees.

For one thing, both honeybees and *Melipona panamica* foragers use a series of multiply redundant communication channels, what Bert Hölldobler of the Universität Würzburg called "multimodal signals." For example, both honeybees and *Melipona panamica* mark their food sources with scents, and these marks assist orientation near the food source. Long-distance orientation, on the other hand, is guided by cues given at the nest: direction and distance with the honeybee waggle dance and height and distance with the sounds of *Melipona panamica*'s recruit-

Figure 5. Sounds made during the unloading of food communicate the height of a food source. For example, bees trained to a feeder at the top of the canopy made short unloading pulses, whereas bees trained to a feeder at the bottom of the forest canopy made much longer unloading pulses.
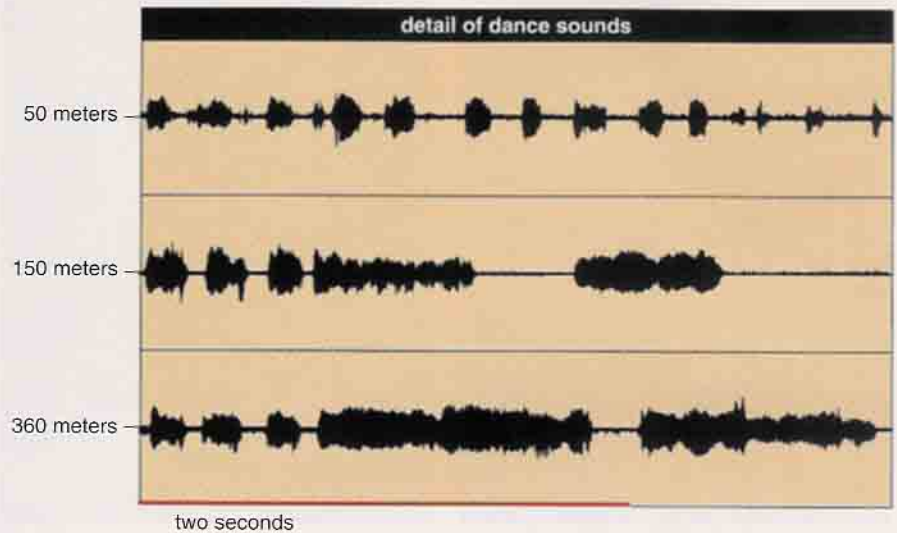

Figure 6. Sounds made during dancing appear to communicate a food source's distance from the nest. The length of sound pulses goes up with increasing distance between the nest and the feeder, as shown here for distances of 50, 150 and 360 meters.

ment performance. Moreover, honeybee and *Melipona panamica* foragers return with the scent of a food source adhering to the their bodies, provide direct food samples and give acoustic cues during their recruitment performances. In other words, both provide olfactory, gustatory, acoustic and perhaps even tactile cues. In some honeybee species, vision might also help followers orient toward dancers. Vision might play a stronger role in *Melipona panamica*, which communicates direction outside the nest, possibly by recruits following the recruiter for a short distance. These findings show that these bees exploit many sensory modalities for the vital task of communicating food-source location. Moreover, multi-modality probably characterizes the recruitment systems of all highly social bees.

Still, one wonders how and why this system has evolved. The manner in which *Melipona panamica* divides up the communication task is revealing. Directly following a forager to the food source is presumably the simplest and most primitive state of a directional communication system. The disadvantages of direct following remain unclear, but they might include problems with tracking a lead forager for long distances, especially in the dim light and dense growth of the forest understory. One backup system found in many stingless bee species is a scent trail, a series of pheromone marks deposited along the substrate. Lindauer and Kerr reported that recruits losing track of an experienced forager would drop close to ground and begin searching for this trail. Yet a scent trail can also guide foragers from other colonies
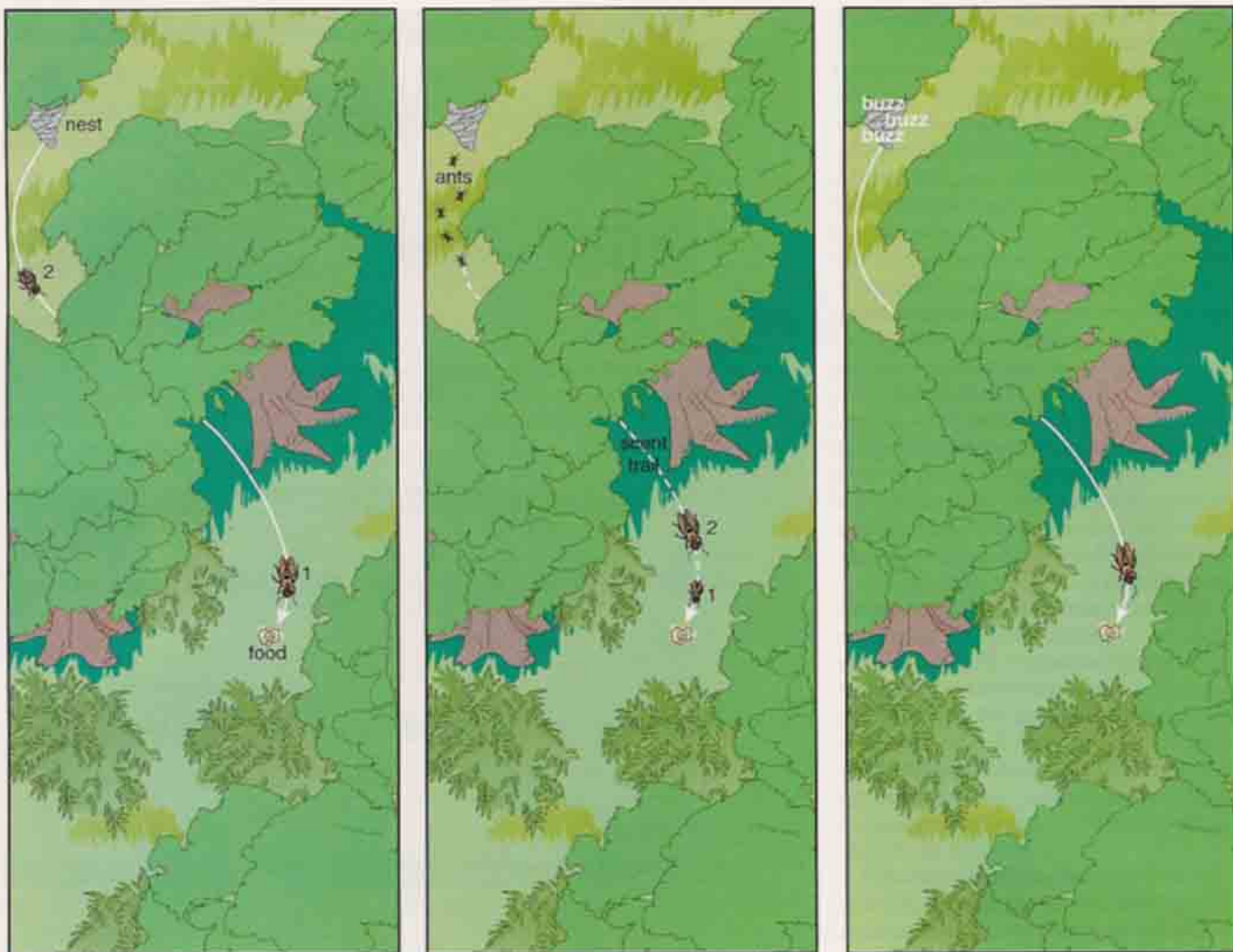
Figure 7. Food-source communication probably evolved in response to pressures from the local habitat and competitors. In the simplest scenario, an experienced bee *(1)* might lead an inexperienced one *(2)* to a food source. Nevertheless, an obstacle (such as dense foliage) between a nest and food might cause the inexperienced bee to lose track of the leader *(left)*. To solve that problem, bees could lay down a scent trail from a nest to food *(middle)*; some species appear to do this. A scent trail, however, could lead other colonies from the same or other species of bees to the same food source. To solve both the obstacle and competiton problems, bees could communicate a food-source location through information provided inside and near the nest *(right)*, just as *Melipona panamica* does.

and even different species to a food source. Stingless bees face intense inter- and intra-specific competition for limited food sources, and some species apparently specialize on taking over food sources discovered by others. This potential espionage might have driven the evolution of concealed communication at the nest. Once the transfer of spatial information is restricted to the nest, the transfer must become representational. As a result, espionage might have selected for complex representational communication in stingless bees. The potential role of espionage remains speculative for now but is one focus of my current research.

One hypothesis of waggle-dance evolution suggests that living on an open comb was a primitive state in honeybees, and that the waggle dance

ritualized outbound and inbound flights because it was oriented horizontally with the waggle run facing the direction of the food source. The buzzing sounds produced by foragers during the waggle run were thought to have evolved from the sounds produced when foragers warm up their flight muscles prior to take-off. Although the status of open nesting as a primitive state is now uncertain, all honeybees, including cavity nesters, retain the "primitive" ability to orient to a sun cue if the comb is tilted until it becomes a horizontal surface. The simplicity of the hypothesis that the waggle run represents ritualized flight is attractive, despite its speculative nature.

In *Melipona panamica*, the communication of direction outside the nest might, therefore, reflect evolutionary

history, but this remains pure conjecture until comparative data on other *Melipona* species are gathered. Some recent evidence suggests that a few Brazilian *Melipona* species possess a more primitive variant of *Melipona panamica*'s communication system, because a few of these Brazilian species communicate direction well but communicate distance poorly.

We remain at an early stage of understanding *Melipona panamica*'s communication system, and several important questions remain. The most interesting questions concern the basic configuration of the recruitment system. Apart from evolutionary history, what is the advantage of communicating direction outside the nest and height and distance inside the nest? In other words, what are the benefits of a

complex symbolic communication system? With *Melipona panamica* alone we cannot resolve the question of which traits are actually primitive. However, this genus contains more than 50 species, and the stingless bees in general contain between 450 to 800 species, which exhibit a broad range of communication complexity. This phylogenetic and behavioral diversity provides the necessary raw material to trace out the evolution of advanced representational recruitment systems. The comparative approach should also enable us to understand how species with simple communication systems can coexist with more sophisticated ones.

As von Frisch observed, "we cannot believe that the bee dance of the European bees has come from heaven," and indeed this representational communication system has now been joined by the communication system of *Melipona panamica*. Nevertheless, two examples out of hundreds of highly social bee species beg the larger question: Why is advanced representational communi-

cation so rare? Perhaps we have not yet studied sufficient species, but I believe that the answer to this question might be one of the most important outcomes of the search for a proto-dance language. We could do well by thinking deeply about the precise costs and advantages of such representational communication systems.

Acknowledgements

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