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Introduction

LIKE OURSELVES, nearly all animals communicate. Primates have sophisticated vocal and facial signals, and birds are famous for their visual and acoustic displays. Electric fish generate voltage signals to court and to attack, while water striders delicately manipulate the surface of ponds, rippling out their messages of dominance and mating availability. On the shore, ants can lay odor trails made of specialized molecules that recruit nestmates to food and nest sites. The range and cleverness of these strategies are a source of wonderment and controversy. Against this broad backdrop, I want to tell the story of how one kind of animal, bees, communicate and share information, essentially telling their companions where to go, what to do, and how to respond.

To understand why bees communicate as they do, we must first consider the societies in which they live. Some bees are social insects, and as such, they form highly organized colonies where cooperation is the norm. Generations overlap, individuals divide labor, and workers care for their siblings. In such intricately structured communities, communication is not just useful, it is essential. Among the many remarkable forms of communication in bees, one in particular captured my attention early on: the waggle dance. In this dance, a forager bee performs a repeating figure-eight pattern, waggling her body in the central run of each loop. The angle of her waggle run points in the direction of a food source, and its duration tells her nestmates how far to fly. It is, in effect, a symbolic map, a form of referential communication, in which the signal stands in for something else. A bee is not simply leading others to food; she is encoding distance and direction in movement, just as a person might say, "Go north for a kilometer." In this book, we will explore why systems such as the waggle dance evolved, how they work, and what they can teach us, not only about bees, but about animal communication more broadly.

Much of this story revolves around evolutionary pressures: predators, competition, cooperation, and the challenges of navigating a complex world. Over the past century, scientists have made major discoveries about how bees communicate, and their findings reach far beyond the nest. Because bees evolved to share information in such sophisticated ways, they offer an unusually clear lens through which to examine how communication systems arise and adapt. While it would be accurate to title this book *The Languages of Bees*, reflecting the diverse communication systems found across species, my goal is to highlight the shared evolutionary pressures that have shaped these systems. I therefore invite the reader to focus on the common principles that underlie these communication systems.

Before we go further, I should pause to talk about what is meant by language. Scientists typically speak of animal communication, but for particularly complex forms of animal communication, they sometimes use the term "animal language," a debated term because some prefer to reserve "language" for humans. I distinguish between animal language and human language, which I acknowledge is incredibly complex and more sophisticated than any animal communication system we have yet decoded. Still, I think there is a danger in placing human language on too high a pedestal. Every time science uncovers a new parallel between animal and human communication, definitions of language tend to shift, redefining language just far enough to keep it uniquely human. What does this moving target teach us? A new generation of researchers is increasingly asking this question, and they are showing that nonhuman animals can combine signals to create new meanings and change meaning by altering signal order.[1] These newly discovered features suggest that the roots of language may run far deeper in the animal world than we once believed.

The Multitude Is Great

Why focus on bees? With more than 20,000 known species in the clade Anthophila (the scientific group that includes all bees), bees are among the most diverse and intriguing animals on Earth. Their lifestyles range from solitary foragers to tropical species that form large colonies with complex social behavior. A valuable guide to this diversity is a foundational work in modern bee biology, *The Bees of the World,* by American scientist Charles Michener.[2] Among this wide array of lifestyles, social species exhibit the most intricate communication systems. Colonies must coordinate food collection, defense, and labor, creating evolutionary pressure for elaborate signaling systems, especially around foraging. These systems are not only fascinating in their own right; they also serve as powerful models for understanding how communication evolves. The variation in bee social structure, from solitary to highly social or eusocial (the most cooperative form of insect society), offers a rich comparative framework for exploring the origins and functions of communication. Overlapping generations, shared care of the developing young (brood), and reproductive division of labor define social bees, with queens laying eggs and daughters performing most of the work of building, foraging, and defending the colony. Males, in contrast, typically contribute little to daily colony life beyond mating, if they succeed. Thus the social world of bees, wasps, and ants is largely shaped by female workers. Eusociality is especially prominent in two families: Halictidae and Apidae. Within the Apidae, the subfamily Apinae (which includes honey bees, stingless bees, bumble bees, and orchid bees*) is

* Although "bumble bee" and "honey bee" are sometimes written as single words, I follow the convention of writing them as two words, consistent with "stingless bee" and "orchid bee," to reflect their shared taxonomic status. Throughout this book, I distinguish between groups and individual species. When I mean a group, I say so explicitly; when I mean a single species, I specify it as in "the stingless bee *Melipona panamica*." When a common name uniquely identifies a species, I pair it with the scientific name in parentheses, as in "the western yellowjacket (*Vespula pensylvanica*)." At times, I use the genus name as shorthand when the context makes the species clear. If I am referring to an entire genus, I state this explicitly, for example: "All species in the genus *Apis* can waggle dance." I write genus and species names in full at first mention or at the start of a sentence (*Apis mellifera*), and thereafter abbreviate the genus (*A. mellifera*), unless doing

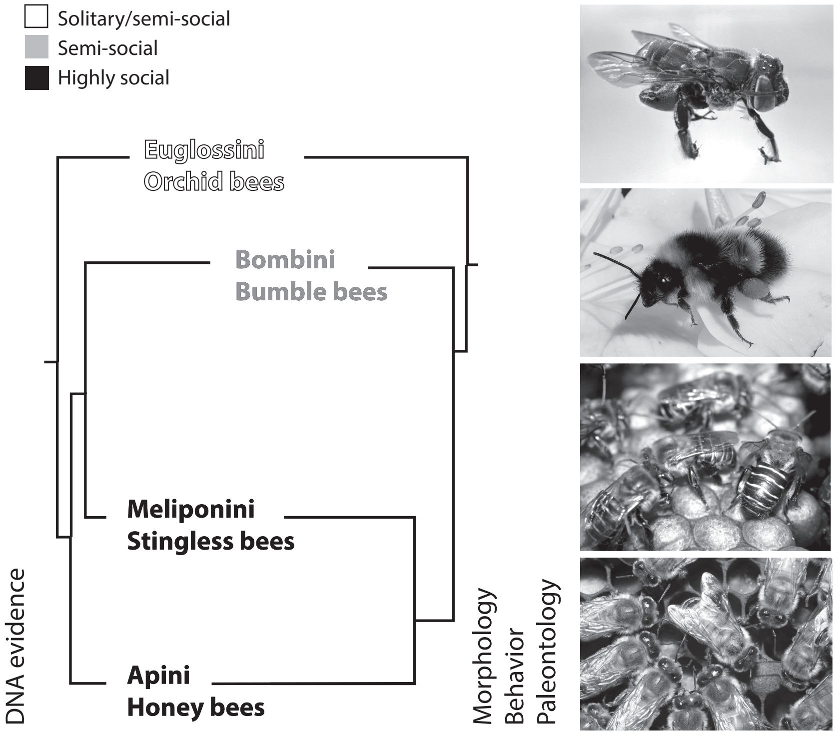

FIGURE 1.1. This diagram shows the evolutionary relationships among the four major groups (tribes) of bees featured in this book: orchid bees, bumble bees, stingless bees, and honey bees. (Phylogeny redrawn from Engel et al. [2020], p. 4.)

the primary focus of this book because more is known about communication in these groups (figure 1.1).[3]

Each of these groups illustrates different degrees of sociality and role specialization (often called castes). Honey bees and stingless bees are highly eusocial, forming perennial (multi-year) colonies with queens

so could cause ambiguity or if I think using the full name would be a helpful reminder. If you ever wonder about a species name, please consult the index, which lists the full scientific names and points you to the pages where each species is prominently discussed. Finally, species names can and do change. Such changes are less likely for bumble bees and honey bees, but they have occurred, and can continue to occur, in stingless bees, where even genus names sometimes change. Here, I use the names found in the papers I cite, which provides a consistent baseline.

that are specialized for reproduction. Bumble bees, by contrast, form annual (one-year) colonies and are sometimes called "primitively social," with more flexible caste roles that change over the course of a colony's life. Orchid bees, native to Central and South America, are mostly solitary, but a few species form small, temporary colonies, offering a window into the early stages of social evolution.

Bees' global diversity and life cycles also reflect these distinctions. The approximately nine honey bee species (Apini) are native to Eurasia and Africa. Stingless bees (Meliponini), common in tropical regions, are remarkable for their lack of functional stings and behavioral diversity across more than 500 species. Bumble bees (Bombini), widespread in temperate zones, number over 250 species and follow a seasonal cycle in which queens emerge from hibernation to found new colonies. Orchid bees (Euglossini), with their beautiful metallic colors and famous perfume-gathering behaviors, include over 200 species. Though most are solitary, their rare social variants could provide important clues about how bee communication evolved.

Signals vs. Cues

To appreciate how communication systems function and evolve, it is important to distinguish between two key concepts: signals and cues. This distinction, which recurs throughout the book, helps to clarify what it means to communicate. Signals are traits that natural selection has shaped specifically to convey information. For example, the contrasting yellow and brown warning coloration of a honey bee, or the volatile alarm pheromones (scents) released from its sting gland to mobilize nestmates, are signals.[4] In contrast, while cues provide information, they have not evolved primarily for that purpose. When bees walk across a flower, they may leave behind waxy footprints. Other bees can use the scent of these footprints to judge if the flower was visited, but unless those footprints evolved specifically to transmit such information, they are cues.

Whether something is a cue or a signal depends upon the sender (the animal producing it), the receiver (the animal detecting it), and the context. For instance, ticks can use human body odors to find a host, but humans have not evolved body odors to enable parasitism by ticks. In this context, the human body odor is a cue. However, parasites, predators, or even competitors can take advantage of odors that have evolved as signals, a theme we discuss in detail in chapter 7. In some cases, particularly when there is uncertainty about what is a signal vs. a cue, researchers prefer to speak about "information transfer." So why all the fuss about discriminating between signals and cues? It helps to ask whether the information is a signal, what it is for, and who it is meant for. Signals, by definition, have evolved to provide information. Trying to discern the evolutionary pressures that shaped specific signals helps us understand how animal communication has evolved and why signals have their specific form.

Origin Story

The questions in this book have shaped the course of my career. As an undergraduate, I had only a vague idea of what I wanted to do, but I was fascinated by a course, Animal Behavior, that I took as an elective. It was captivating to learn about animal communication, particularly the honey bee waggle dance. As a result, I found a summer opportunity to work with two professors, Evan Balaban and Donald Griffin, on honey bee acoustic communication. Griffin's book *Animal Minds* inspired me in many ways, but his special love of sound communication had a particular significance for my work. We set up an observation colony inside a rented trailer at the Concord Field Station in Bedford, Massachusetts, about 22 kilometers from Harvard University. The field station was above deep concrete bunkers that housed surface-to-air Nike missiles in the 1950s. Today, these cool bunkers house a more innocuous cargo, including whale bones from Harvard's Museum of Comparative Zoology, and the field station is used to study a wide assortment of creatures.

Don was fascinated by many different animals, including beavers, and regrettably broke his foot when it got stuck in a beaver lodge while he was inserting a microphone to eavesdrop on the beavers. That summer, the beaver family had its privacy, and I was left to my own devices with a honey bee observation colony whose front glass had a large cutout through which I could listen to bee sounds with a microphone while filming their behaviors. We had planned to study the sounds produced by waggle dancing bees, and Tom Seeley (whose research at Cornell University focused on honey bee communication and foraging) had kindly invited me to his summer field site at Cranberry Lake Biological Station in the Adirondack region of New York State. There, I learned the basics of observing honey bee behaviors and dancing.

However, I was immediately distracted by something I found even more interesting than dancing: piping sounds directed at the dancer from her followers, bees that were obtaining information about where to forage for food. A follower would usually do this by butting her head up against the body of a waggle dancer while producing a fairly loud "beep" that was often audible even without a microphone.[†]

In older scientific literature, stop signals have also been called a "brief piping signal" or a "nectar forager pipe" and were described as a food-begging signal. I asked my advisor about this because I almost never saw a bee receive any food after giving this "begging signal." Dancers would stop briefly when the signal was being delivered but then appeared to just pick up where they left off. We looked through what Karl von Frisch (who discovered the honey bee dance language) had written, were perplexed, and a research project was born. I would no longer study sounds produced by the waggle dancer, but rather these mysterious stop signals. Who produced them? Who received them? And what was their function? That hot, humid summer, I answered some of these questions. The joy of it inspired me to pursue the academic study of animal behavior, focused on bee signaling.

The stop signalers I was tracking maddeningly often walked out of view beyond the cutout in the glass pane covering the combs. The observation hive itself looked like a tall, thick, double-paned window holding three combs stacked vertically between the panes of glass (see plate

[†] Take a look at the stop signal video that is linked via the book's QR code on page ii. It is helpful to visualize and hear this signal.

12). The glass let us watch both sides of the combs, but it also muffled the sounds the bees made. I removed the protective glass from one side so I could follow bees producing stop signals as they walked over the three combs. Without the insulating glass, however, the bee brood began to cool, and the bees responded by clustering tightly over the exposed combs to keep the brood warm. The bees I was tracking frequently slipped beneath these newly formed layers and disappeared from view. To reduce this problem, I installed a heat lamp to warm the combs, which thinned the cluster and allowed me to continue tracking and recording the stop signals. This allowed me to follow individual bees, each of which could produce hundreds of stop signals within an hour. The heat lamp, combined with the summer heat inside the metal trailer, made the work so uncomfortable that I wore thin, loose pants. Bees typically flew from the open frames and out the window, but sometimes they fell on the floor and crawled back up to the hive. Regrettably, some of them crawled inside my pants and stung me. I learned two lessons. First, tuck your pants legs into your socks when working with an open bee colony. Second, riding a bicycle several kilometers to the nearest bus stop to get to Harvard University Health Services is not a good idea when a bicycle seat is poorly designed to accommodate certain injuries. The doctor was astonished.

After I recovered, I was still (perhaps surprisingly) enthusiastic about the project, and continued my observations. Because I was working alone, I could not both videotape the bees in the nest and control the number of bees at the feeder. Thus, the feeder rapidly attracted too many bees and quickly ran out of food. This seeming failure was fortuitous. When the feeder became overcrowded, I recorded the greatest number of stop signals and found that they inhibited waggle dancing. This made sense, since waggle dancers should not continue recruiting for an overexploited and depleted food source. But there was a problem. Bees typically do not encounter this kind of concentrated, incredibly rich resource in nature, leaving open the question of why they evolved stop signals. I was able to publish my initial observations, but it took about 20 years for me to find the real answer. This is part of the story that I want to tell.

For me, the main thing about this experience was that I had finally found an approach to biology that I could grasp and study in a direct, physical way. I could see, hear, touch, and, regrettably, be stung by the bees. I was also hooked on chasing the waggle dance, trying to understand why it and other complex animal signals had evolved. The two decades after my work at Concord were largely spent pursuing this question in Panama and Brazil, following up on Martin Lindauer's research. Lindauer was a prominent German scientist who studied under Karl von Frisch and conducted seminal work on stingless bees, a closely related and highly social sister group to honey bees. Lindauer and his colleagues showed that several stingless species can also communicate food location to nestmates, and were intrigued by the question of how and why the waggle dance evolved. Could the stingless bees shed light on these questions? The search for answers took me to Yunnan Province in China and then to Thailand. In both places, I was grateful to see the giant and dwarf honey bee species living in a complex world of competition and predators and competing in an arms race, not only of weapons, but also of signals.

Those experiences, chasing bees through forests and fields, following questions from Panama to Brazil, and eventually to Asia, not only shaped my research but also the motivation for this book. I want to share the story of how I came to study bee communication and what I, along with many others, have learned about it. Beneath this account, however, lies a deeper theme: that failure, though usually unwelcome, is a frequent companion in science and can open the way to unexpected discovery. I hesitated for years to write this book, aware of how many questions remain unanswered. I tried to weave together threads, some my own and some inherited from others, but the fabric remains incomplete. I hope its open spaces invite others to continue the work.

In the chapters that follow, I explore how social bees use communication to coordinate their lives, from foraging and recruitment to alarm signaling, defense, and even interspecies deception. I begin by examining the sensory foundations of bee communication, then trace how recruitment systems like the waggle dance may have evolved and diversified across species. Later chapters focus on how bees respond to threats, engage in warfare, spy on rivals, and respond to habitat changes, revealing how communication serves not only cooperation but also competition and survival in a changing world. Throughout, I draw on fieldwork and laboratory studies to uncover the evolutionary forces that shape how bees share information in a complex and often dangerous world. Overall, I hope this book conveys the joy of biology and of following the bees to everyone, and encourages others to keep exploring the mysteries of bee communication.

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Page numbers in *italics* indicate figures; *plate #s* are also in italics.