

If I can with confidence say That still for another day, Or even another year, I will be there for you, my dear, It will be because, though small As measured against the All, I have been so instinctively thorough About my crevice and burrow. —Robert Frost, A Drumlin Woodchuck, 1936



Like Robert Frost's woodchuck, a honeybee colony is "instinctively thorough" about its dwelling place, for only certain tree cavities provide good protection from predators and sufficient refuge from harsh physical conditions, especially strong winds and deep cold. No fewer than six distinct properties of a potential homesite—including cavity volume, entrance height, entrance size, and presence of combs from an earlier colony—are assessed to produce an overall judgment of a site's quality. The care with which honeybees choose their homes has been known for only about 30 years, which might seem surprising given that humans have been culturing these bees since ancient times. The reason that humans have only recently learned about the bees' real estate preferences is that the essence of beekeeping is the tending of colonies living in hives fashioned by a beekeeper and sited where the beekeeper wants them. The earliest solid evidence of beekeeping comes from Egypt, around 2400 BC, and consists of a stone bas-relief in

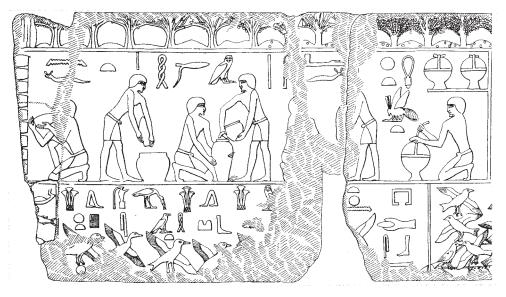


Fig. 3.1 Earliest known drawing of beekeeping and honey preparation, from the sun temple of Niuserre, Abu Ghurab, Egypt, built around 2400 BC. Harvesting honey from a tall stack of cylindrical hives on the left, handling honey in the middle, and packing honey on the right.

a temple that depicts peasants removing honeycombs from a stack of cylindrical clay hives and also packing the honey in pots (fig. 3.1). Thus for some 4,400 years the people living in closest association with honeybees have focused on devising housing arrangements for bees that serve human purposes and have largely ignored what the bees' themselves seek in a home. For example, manmade hives are usually much more spacious than natural nest cavities, so bees living in an apiary will store more honey and swarm less often than will bees living in nature. Likewise, a beekeeper's hives are located at ground level, which is convenient for humans but dangerous for bees. Honeybee colonies living low to the ground are easily found and attacked by destructive predators, such as bears.

Nests of Wild Colonies

In 1975, when I began to study the democratic house-hunting process of honeybees for my PhD thesis project, I decided that a logical first step was to try

to identify what makes a dream homesite for a honeybee colony. This would tell me what a swarm is seeking as it locates multiple candidate sites and works to select the best one. I suspected that to identify the perfect dwelling place for a honeybee colony would be a challenge, because the bees might evaluate several attributes of each candidate site, and they might weigh each attribute differently when judging the overall goodness of a site. Nevertheless, I figured that if I could identify what attributes are important to the bees and if I could determine what preference they have for each attribute, then I would be close to achieving my goal.

I also figured that to determine the bees' real-estate preferences, I should start by finding trees housing wild colonies of honeybees, sawing them down, and splitting open the tree sections housing the bees' nests so that I could scrutinize their natural living quarters (fig. 3.2). Each colony living in nature occupies a site chosen by scout bees, so it seemed reasonable to expect that consistencies in the nest sites of these wild colonies would yield clues about the bees' nest-site preferences. And there could be little doubt that these preferences lie at the heart of the bees' whole house-hunting process, for it is these preferences that guide swarms to take up residence in suitable nesting cavities.

Back in 1955, Lindauer had reported experiments, conducted in the open countryside east of Munich, in which he presented one swarm at a time with a pair of nest boxes that differed in some property, and then he observed which one attracted the greatest interest from the swarm's scout bees. These experiments yielded only preliminary findings, because Lindauer could perform just a few trials for each test of a particular nest-site property. Nevertheless, they suggested to him that his bees had chosen among his nest boxes based on differences in protection from the wind, cavity size, presence of ants, and sun exposure. Lindauer was impressed by the bees' apparent attention to multiple properties of a possible residence when assessing its desirability, wondered what the ideal bee dwelling might be, and suggested that to solve this mystery "it would be best to ask the bees themselves about this matter." I would start to do so by examining their nests.

The prospect of carefully describing the nests of wild honeybee colonies living in the woods attracted me for emotional as well as rational reasons. While an undergraduate student, I had majored in chemistry and done several small research projects in organic chemistry, biochemistry, and biophysics. Of course,

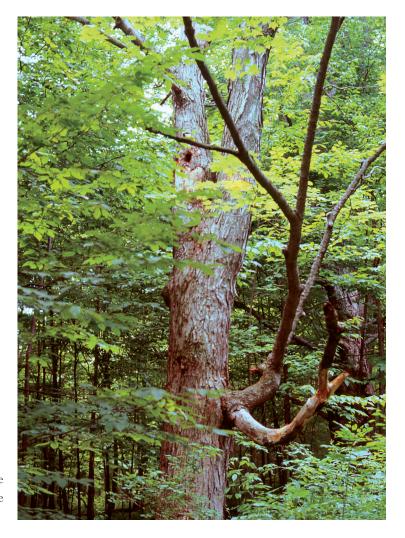


Fig. 3.2 Bee tree, with a knothole that serves as the nest entrance visible high up in the left fork.

these investigations were all conducted indoors in clean, brightly illuminated, and nearly lifeless laboratories. But now, as a beginning graduate student in biology and novice investigator of animal behavior, I was keen to work outdoors using what has been called the von Frisch–Lindauer approach to animal behavior research. In their autobiographical book, *Journey to the Ants*, Bert Hölldobler and Edward O. Wilson explain that von Frisch and Lindauer had a philosophy of research based on:

a thorough, loving interest in—a feel for—the organism, especially as it fits into the natural environment. Learn the species of your choice every way you can, this whole-organismic approach stipulates. Try to understand, or at the very least try to imagine, how its behavior and physiology adapt it to the real world. Then select a piece of behavior that can be separated and analyzed as though it were a bit of anatomy. Having identified a phenomenon to call your own, press the investigation in the most promising direction.

My thesis advisor, Bert Hölldobler, had presented this way of studying behavior in his ethology course at Harvard and, more importantly, had demonstrated its power by his own spectacularly beautiful studies of ant social behavior. So, by the end of my first year in graduate school, I was raring to go. I wanted to gain a feel for honeybees living in nature, to further analyze the house-hunting piece of their behavior, and to see if I could press the investigation on from where Martin Lindauer had left it some 20 years before.

I knew that I would abscond from Harvard the moment I had finished taking my final exams for the spring semester, and I had my mind set on returning to the Dyce Laboratory for Honey Bee Studies, at Cornell, where I had worked for the previous four summers when an undergraduate student. The director of the lab, Professor Roger A. Morse, was truly a generous man. He welcomed me back, assigned me a desk, and provided several essential tools for the project—a powerful chain saw, steel wedges and maul, and one of the lab's green pickup trucks. Most importantly, "Doc" Morse arranged for me to team up with a member of the Entomology Department's technical staff, Herb Nelson, who had worked as a logger in the Maine woods when a teenager and could teach me how to cut down big trees without getting killed.

Herb and I started with some of the bee trees I had discovered back in high school while exploring the woods around my family's home. These were augmented with ones that I located through a want ad I placed in the local newspaper, the *Ithaca Journal*. The ad read, "**BEE TREES** wanted. Will pay \$15 or 15 lb of honey for a tree housing a live colony of honeybees. 607-254-5443." I feared I'd get no calls, but within a week I had secured the rights to 18 accessible bee trees in the woods around Ithaca. Two owners took payment in money; all the rest wanted honey.

The procedure for collecting these nests was simple but somewhat dangerous. Shortly before sunrise, when all bees were still at home, I would hike to a bee tree with a can of calcium cyanide powder (Cyanogas), an old spoon, and some rags. If the nest entrance was high in a tree that I couldn't climb, I'd also bring an aluminum extension ladder. My aim was to spoon cyanide powder into the nest entrance and then quickly plug it with the rags. The cyanide powder would react with moisture in the air producing cyanide gas that would kill the bees but, if all went according to plan, not me. (Once I did drop the can of Cyanogas from the ladder, spilling much of its contents, but I managed to hold my breath long enough to climb down, get the lid back on the can, and dash out of the expanding cloud of deadly gas.) By first killing the bees, we could later fell the tree and collect the nest without being ferociously attacked. This protocol also enabled me to census the bee population of each wild colony when I dissected its nest.

Having killed the bees, I'd return to Dyce Lab to pick up Herb and load the truck with the tools we'd need for the day: chain saw, wedges and maul, rope, ramp boards, tape measure, magnetic compass, 35 mm camera, and notebook. Our goal was to cut down the bee tree I had just visited, saw out the trunk section housing the nest, wrestle it onto the truck, and haul it back to the lab. I recall being impressed by Herb's confidence in driving the truck deep into the woods to get near each bee tree ("We'll have plenty of traction for getting back out, once we get that big log loaded on.") and by his careful inspection of each tree's lean and crown before starting his cutting ("You gotta know which way the tree wants to fall."). Herb's lumberjack skills weren't rusty, and each tree arced down neatly into the woods opening he had chosen. Once we had a tree lying on the ground, we proceeded to cut out the section containing the nest. We did this by making a series of crosscuts, starting far above and far below the nest entrance, and then working our way closer and closer to the entrance until the chain saw started spitting dark-brown punk wood or yellow-brown beeswax, indicating we had breached the nest cavity. We then rolled the nest-containing log—sometimes a massive, 2-meter-long (6-foot) and nearly 1-meter-thick (3-foot) section of the tree's bole—up into the truck, got it back to the lab, and split it open (fig. 3.3). Finally, we would lug the opened nest indoors where I could dissect it carefully under good light while measuring important features of the nest cavity and its



Fig. 3.3 Natural honeybee nest in the bee tree shown in figure 3.2. The tree section housing the nest has been split open, revealing the combs containing honey (above) and brood (below). The entrance hole is on the left side, about two-thirds of the way up the cavity.

contents. To measure the volume of the cavity, I filled it with liter after liter of sand after removing the combs. As I picked through the broken combs and dead bees, sooner or later coming across the lifeless queen, I felt sad to have killed a whole colony, but also excited, knowing that I was the first human to describe in detail the natural homes of honeybees.

Over the summer of 1975, we collected and I dissected 21 bee tree nests, enough to give us a broad picture of the nests of wild colonies living in the woods. I also located another 18 nests in trees that were left standing and so yielded information only about their entrance openings. Since the nest entrance is the "front door" of a colony's home it is probably especially important to the bees, so I gave it extra attention. We found that the bees occupied many kinds of trees, including oaks (*Quercus* spp.), walnuts (*Juglans* spp.), elms (*Ulmus* spp.), pines (*Pinus* spp.), hickories (*Carya* spp.), ashes (*Fraxinus* spp.), and maples (*Acer* spp.). This suggested that the bees don't have a strong preference for certain tree species.

Not surprisingly, the tree cavities occupied by the bees were generally tall and cylindrical, consistent with the shape of tree trunks. But what was surprising was the discovery that most of these wild colonies were occupying tree cavities much smaller than the hives provided by beekeepers. The average nest cavity was only about 20 centimeters (8 inches) in diameter and 150 centimeters (60 inches) tall; hence, it had a volume of only about 45 liters (41 quarts) (fig. 3.4). A tree cavity of this size provides only one-quarter to one-half of the living space provided by a beekeeper's hive. Were the bees telling me that they prefer relatively small and snug nest sites, ones in which it might be easier to keep warm in winter? Some of the colonies even occupied tree cavities with only 20 to 30 liters of nesting space, though none was found in a space smaller than 12 liters. Was this lower limit of about 12 liters a sign that bees carefully avoid excessively cramped quarters, ones lacking sufficient room for storing the honey needed to survive winter? Certainly the bees living in these tree cavities were making good use of their living space, for each colony had nearly filled its nest cavity with multiple combs. Because each comb formed a wall-to-wall curtain spanning the (generally) narrow tree cavity, I was impressed by the way the bees had built small passageways in the combs where they were attached to the cavity's wall, so they could crawl easily from one comb to the next. And it was clear that these bees had organized their use of their combs in the way familiar to all beekeepers, storing honey in the upper region of the nest and rearing brood below. The nests collected in August, by the way, revealed that most colonies had been making good progress in stockpiling their winter heating fuel. The nests that I dissected contained, on average, 14 kilograms (30 pounds) of golden honey. Regrettably, it was all laced with cyanide.

The entrance openings of the bees' nests also showed consistencies that suggested possible nest-site preferences by the bees. Most nest entrances consisted of a single knothole or crack with a total area of just 10 to 30 square centimeters (2 to 5 square inches) (fig. 3. 5). And typically they were located near the floor of the tall tree cavity, on the south side of the tree, and close to ground level.

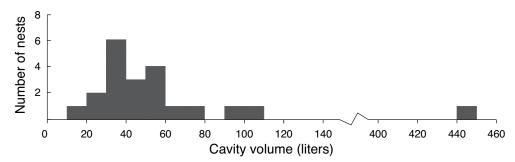


Fig. 3.4 Distribution of nest-cavity volumes for 21 nests in hollow trees.

The trends toward small size, floor level, and southern orientation all made good sense to me, for they would make the nest cavity inaccessible to most predators, relatively free of drafts, and perhaps warmed by the sun—all things that would be good for a colony. But the preponderance of nest entrances just a few feet from the ground puzzled me greatly. I figured that a low nest entrance must render a colony vulnerable to detection by predators, such as bears, whose attacks can be fatal. And I knew that in medieval times, in the forests of northern Europe (Germany, Poland, and Russia), one of the ancestral homes of the honeybees imported to North America, raids by bears on honeybee nests in trees were such a great trouble for the forest beekeepers who owned these nests that they invented horrific devices to kill honey-loving bears. One was a hinged platform mounted outside a bee nest. When a bear climbed onto it to attack the bees, it would collapse, causing the bear to tumble onto a grid of deadly sharp stakes below.

So at first I was perplexed by the rarity of nests high in trees. But as will be explained shortly, we now know that bees actually have a strong preference for nesting cavities with entrances located high above the ground. I also now know that my initial report of most nests being near ground level was an error generated by an unintentional bias in the way I had sampled the population of natural nests. Because the nests I studied were ones that had been noticed inadvertently by a person walking past a bee tree, and because people are much more likely to notice bees trafficking from a ground-level nest entrance than a tree-top one, I unwittingly studied nests whose entrances were far lower than is typical. I am confident on this point because several years later, when I became a bee hunter



Fig. 3.5 Knothole entrance of the nest in the bee tree shown in figure 3.2, showing some of the bees inside. This entrance opening is approximately 5 centimeters (2 inches) wide and 8 centimeters (3 inches) tall.

and mastered the ancient craft of lining bees (locating bee trees by baiting foragers from flowers and observing their flights back to their nests), I found that every hunt ended with me straining to spy the bees zipping in and out of a nest entrance high in a tree, like the one shown in figure 3.2. To date, I have located 27 bee trees by bee lining and can report that the average height of their nest entrances is 6.5 meters (21 feet). Needless to say, I'm now alert to the hidden danger of unintentional sampling bias.

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