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INTRODUCTION

We have never known what we were doing
because we have never known what we were undoing.
We cannot know what we are doing until we know
what nature would be doing if we were doing nothing.
—*Wendell Berry, "Preserving Wildness," 1987*

This book is about how colonies of the honey bee (*Apis mellifera*) live in the wild. Its purpose is to provide a synthesis of what is known about how honey bee colonies function when they are not being managed by beekeepers for human purposes and instead are living on their own and in ways that favor their survival, their reproduction, and thus their success in contributing to the next generation of colonies. Our goal is to understand the natural lives of honey bees—how they build and warm their nests, rear their young, collect their food, thwart their enemies, achieve their reproduction, and stay in tune with the seasons. Besides looking at *how* honey bee colonies live in nature, we will examine *why* they live as they do when they manage their affairs themselves. In other words, we will also explore how natural selection has shaped the biology of this important species during its long journey through the labyrinth of evolution. Doing so will reveal how *Apis mellifera* achieved a native range that includes Europe, western Asia, and most of Africa, and so became a world-class species even before beekeepers introduced it to the Americas, Australia, and eastern Asia.

Knowing how the honey bee lives in its natural world is important for a broad range of scientific studies. This is because *Apis mellifera* has become one of the model systems for investigating basic questions in biology, especially those related to behavior. Whether one is studying these bees to solve some mystery in animal cognition, behavioral genetics, or social behavior, it is critically important to become familiar with their natural biology before designing one's experimental investigations. For example, when sleep researchers used honey bees to explore the functions of sleep, they benefited greatly from knowing that it is only the elderly bees within a colony, the foragers, that get most of their sleep at night and in comparatively long bouts. If these researchers had not known which bees are a colony's soundest sleepers come nightfall, then they might have failed to design truly meaningful sleep-deprivation experiments. A good experiment with honey bees, as with all organisms, taps into their natural way of life.

Knowing how honey bee colonies function when they live in the wild is also important for improving the craft of beekeeping. Once we understand the natural lives of honey bees, we can see more clearly how we create stressful living conditions for these bees when we manage them intensively for honey production and crop pollination. We can then start to devise beekeeping practices that are better—for both the bees and ourselves. The importance of using nature as a guide for developing sustainable methods of agriculture was expressed beautifully by the author, environmentalist, and farmer Wendell Berry, when he wrote: "We cannot know what we are doing until we know what nature would be doing if we were doing nothing."

The current state of beekeeping shows us all too clearly how problems in the lives of animals under our management can arise when we fail to consider how they would be living if we were not forcing them to live in artificial ways that serve mainly our own interests. Many beekeepers—especially those in North America who practice industrial-scale beekeeping with tens of thousands of colonies of *Apis mellifera*, the species that is the focus of this book—are experiencing colony mortality rates of 40 percent or more each year. To be sure, this is not due entirely to the colony management practices of beekeepers. Changes in the crop production practices of farmers, especially the use of systemic insecticides that are absorbed by plants and contaminate their nectar and pollen, and the switch in many places to growing corn and soybeans instead of clover and alfalfa, also play roles in this sad story. But the heavy-handed manipulations of the lives of the honey bee colonies housed in beekeepers' hives certainly do contribute to the sky-high rates of colony mortality. We will see that when beekeepers force colonies to live crowded together in apiaries—where the bees' homes are less than 1 meter (ca. 3 feet) apart, rather than the hundreds of meters (at least 1,000 feet) apart in nature—beekeepers boost the efficiency of their work but they also foster the spread of the bees' diseases. Likewise, when beekeepers supersize their colonies by housing them in huge hives that are nearly as tall as themselves, rather than in smaller hives the size of the bees' natural nesting cavities, they boost the honey production of their colonies, but they also turn them into stupendous hosts for the pathogens and parasites of *Apis mellifera*, such as the deadly ectoparasitic mite *Varroa destructor*.

Given the harmful effects on the bees that arise from the standard practices of beekeeping, it is not surprising that many beekeepers are now exploring alternative approaches to this craft. These folks are keen to use nature as a model, and this requires a solid understanding of how honey bees live on their own in nature. To help readers who want to adjust their beekeeping practices to make them more bee-friendly, I have included a final chapter on what I like to call "Darwinian beekeeping," which is an approach to beekeeping that aims to give bees the opportunity to live the way they do in the wild.

FOCUS ON WILD COLONIES IN THE NORTHEASTERN UNITED STATES

This book does not attempt to provide a comprehensive account of how *Apis mellifera* lives in nature across its vast geographic range, which now includes Europe, some of Asia, all of Africa except the great desert regions,

FIG. 1.1. *Left:* Bee-tree home of a wild colony of honey bees living in the Arnot Forest, of Cornell University, in the United States. Red arrow indicates the small knothole entrance of this colony's nest. *Right:* Nest entrance of a wild colony of honey bees living in Munich, Germany.

most of North and South America, and parts of Australia and New Zealand. Instead, it focuses on how colonies of our most important pollinator are living in the wild in the deciduous forests of the northeastern United States, a place where they have thrived as an introduced species for nearly 400 years. This is also the place where, for more than 40 years, my collaborators and I have studied the behavior, social life, and ecology of honey bees living in the wild (Fig. 1.1). Although our studies are based on honey bees living outside their native range, I believe that what we have learned about how honey bees live in the woods in the northeastern corner of the United States can help us understand how these bees originally lived in nature in Europe, especially in its northern and western regions.

Until the mid-1800s, all the honey bees living in the northeastern United States were descendants of the colonies of honey bees that were brought to North America from northern Europe starting in the early 1600s. Insect taxonomists recognize some 30 subspecies (geographic variants) of *Apis mellifera*, and they refer to the honey bees native to northern Europe as members of the subspecies *Apis mellifera mellifera* Linnaeus. This subspecies of *Apis mellifera*—also called the dark European honey bee—has the distinction of being the first kind of honey bee to be described taxonomically. This was done 360 years ago, in 1758, when Carl Linnaeus, a professor of botany and zoology at Uppsala University in Sweden, published his work *Systema Naturae*, in which he presented the system of taxonomic classification that biologists have used ever since.

The dark European honey bee is so named because its body color ranges from dark brown to jet black and historically it lived throughout northern Europe, from the British Isles in the west to the Ural Mountains in the east, and from the Pyrenees and Alps in the south to the coasts of the Baltic Sea in the north (Fig. 1.2). We know from archaeological studies, which have found traces of beeswax in fragments of pottery vessels dating from 7,200 to 7,500 years before present, that this bee was living in Germany and Austria some 8,000 years ago. We also know from genetic studies of the bees themselves that as the climate of northern Europe underwent postglacial warming, starting about 10,000 years ago, this bee expanded its

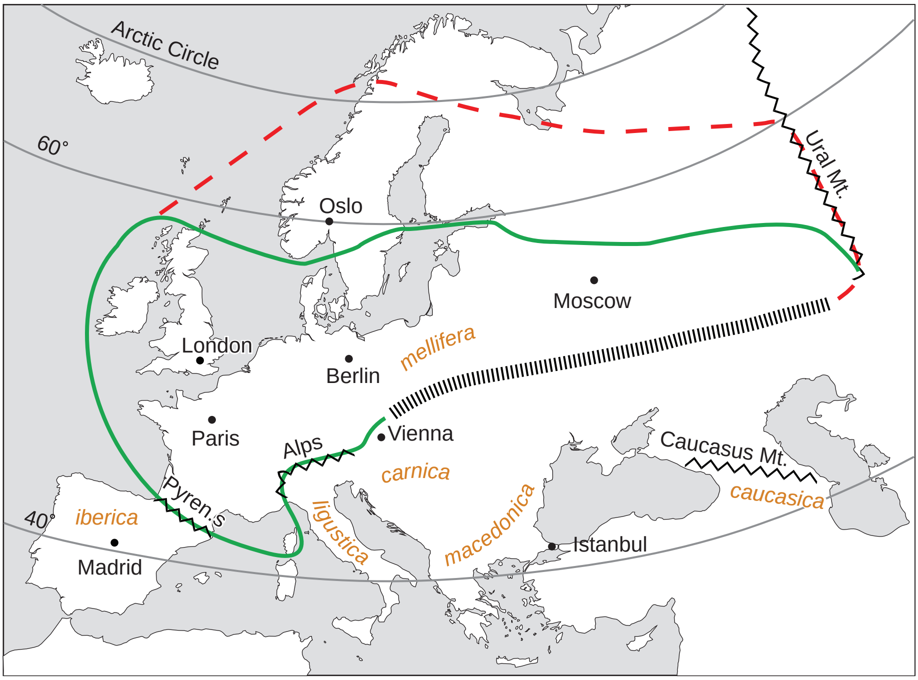

Fig. 1.2. Distribution map of the dark European honey bee, *Apis mellifera mellifera*. Green line: original distribution limits to the west, north, and east. Vertically hatched line: transition zone to the honey bee races of southern and eastern Europe (*A. m. ligustica*, *carnica*, *macedonica*, and *caucasica*). Red dashed line: northern limit of beekeeping.

range north and east from Ice Age refugia—pockets of woodlands in the mountains of southern France and Spain—as it tracked the expansion of forests populated with thermophilic trees such as willow, hazel, oak, and beech. Evidently, *Apis mellifera mellifera* flourished as it spread and eventually extended its range farther north within Europe than any other subspecies, drawing on the adaptations for winter survival that it had evolved during the glacial period. It is estimated that within the eastern, heavily forested two-thirds of its range (from eastern Germany to the Urals) there once lived millions of colonies of the dark European honey bee. And there is no doubt that tree beekeeping—cutting cavities in trees to create nest sites and then harvesting honey without killing the colonies living in the artificial hollows—provided most of the beeswax and honey traded in Europe in the Middle Ages. A vestige of this centuries-old tradition of tree beekeeping is found in the South Ural region of the republic of Bashkortostan, part of the Russian Federation. Colonies of pure *A. m. mellifera* still inhabit the forests of this region, and Bashkir tree-hive beekeepers still harvest basswood (*Tilia cordata*) honey from colonies residing in man-made nest cavities high in the trees.

The dark European honey bee is superbly adapted to living in forested regions with relatively cool summers and long, cold winters. It is not surprising, therefore, that when bees of this subspecies were brought to Massachusetts, Delaware, and Virginia in North America by English and Swedish immigrants starting in the early 1600s, they escaped (swarmed) from the beekeepers' hives and soon became an important part of the local fauna. Already in 1720, a Mr. Paul Dudley published, in *Philosophical Transactions*, a journal of the Royal Society of London, a letter titled "An account of a method lately found out in New-England for discovering where the bees hive in the woods, in order to get their honey." Analysis of letters, diaries, and accounts of travels in North America written in the 1600s and 1700s has revealed that these honey bees spread speedily across the heavily forested eastern half of North America below the Great Lakes (Fig. 1.3). Also, the journals of the Lewis and Clark Expedition document the dark European honey bee's rapid colonization of North America east of the Mississippi River. For example, on Sunday, 25 March 1804, shortly after the expedition party had left St. Louis and was camped along the Kansas River, William Clark wrote in his journal: "River rose 14 Inch last night, the men find numbers of Bee Trees, & take great quantities of honey."

These days, the honey bees living wild in the forests of the northeastern United States are no longer a genetically pure population of *Apis mellifera mellifera*. This is because, in 1859, following the advent of steamship service between Europe and the United States, American beekeepers began importing queen bees of several other subspecies of *Apis mellifera*, ones that are native to southern Europe or northern Africa. These imports continued for more than 60 years, during which time many thousands of mated

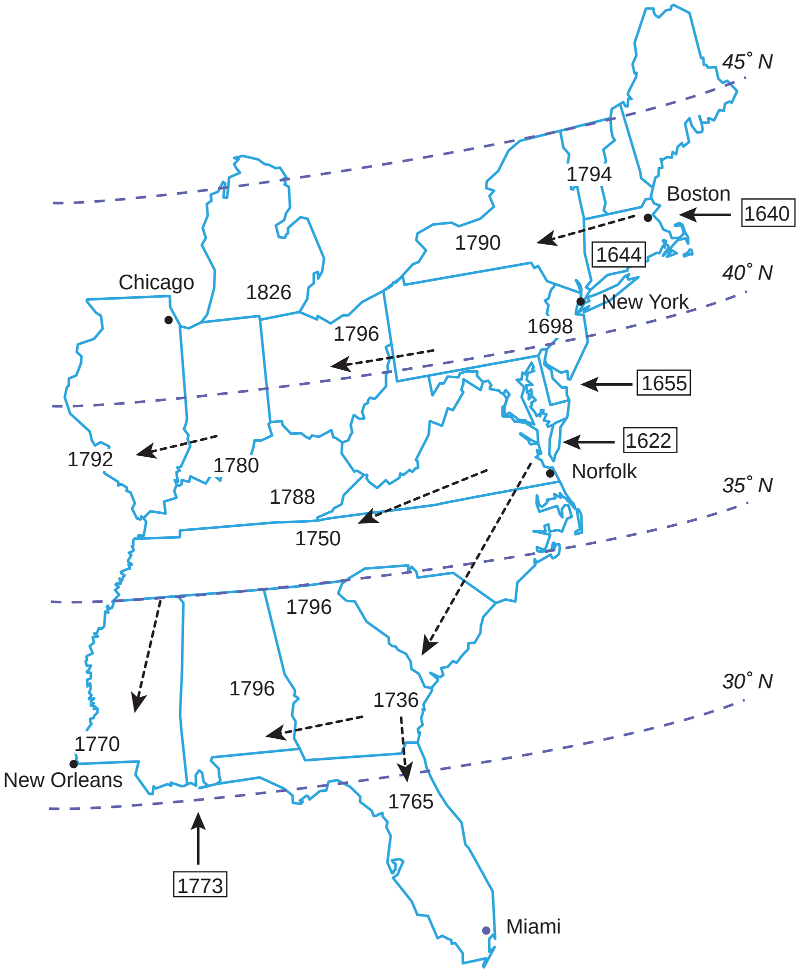

Fig. 1.3. The dispersal of the dark European honey bee across eastern North America following introductions (indicated by solid arrows) in Virginia, Massachusetts, Connecticut, and Maryland in the 1600s, and in Alabama in 1773. Dashed arrows indicate the bee's subsequent spread.

queen bees were shipped to North America, but they abruptly ceased in 1922. This was the year the U.S. Congress passed the Honey Bee Act, which prohibited further imports to protect honey bees in the United States from the Isle of Wight disease, an unspecific but supposedly highly infectious and lethal disease named for the location of its first reputed outbreak, in southern England. As we shall see, the genetic composition of the wild honey bees living in the northeastern United States is now a blend of the genes of *A. m. mellifera* and several other subspecies of *Apis mellifera*. Of those introduced in the late 1800s and early 1900s, the three most important all came from south-central Europe: *A. m. ligustica* (from Italy), *A. m. carnica* (from Slovenia), and *A. m. caucasica* (from the Caucasus Mountains). Several other subspecies were introduced from the Middle East and Africa—*A. m. lamarckii* (from Egypt), *A. m. cypria* (from Cyprus), *A. m. syriaca* (from Syria and the eastern Mediterranean region), and *A. m. intermissa* (from northern Africa)—but they did not prove popular, and it seems that they are not well represented genetically anywhere in the United States.

More recently, in 1987, a subspecies of *Apis mellifera* that is native to eastern and southern Africa, *A. m. scutellata*, entered the southern United States by way of Florida, perhaps when a beekeeper, seeking bees that would thrive in subtropical Florida, smuggled in some queens of this tropically adapted subspecies. Since then, colonies of *A. m. scutellata* have indeed thrived in Florida and have greatly influenced the genetics of the honey bees living in the southeastern United States but not of the honey bees living in the northeastern United States, probably because colonies of *A. m. scutellata* cannot survive northern winters. Bees of the African subspecies *A. m. scutellata* entered the United States a second time and in a second place in 1990, when swarms flew across the U.S.–Mexico border into Texas. Here again they mixed with the European honey bees already in residence. Since then, populations of colonies that are hybrids of African and European honey bees (so-called Africanized honey bees) have developed in the humid, subtropical parts of southern Texas and in the southernmost parts of New Mexico, Arizona, and California. As of 2013, the gene pool of the Africanized bees in southern Texas still had a small genetic contribution (ca. 10%, for both mitochondrial and nuclear genes) from European honey bees.

The complex history of countless introductions to North America of honey bees from various regions of Europe, the Middle East, and Africa raises an important question: What is the mix of subspecies of *Apis mellifera* in the wild colonies living in the northeastern United States, the main subjects of this book? Fortunately, we now have a clear answer to this question for the colonies living in the vast woodlands of southern New York State. In 1977 and then again in 2011, I collected worker bees from 32 wild colonies living in this heavily forested region. The 32 sets of bees from 1977 were stored as pinned (voucher) specimens in the Cornell University Insect Collection, and the 32 sets of bees from 2011 were stored in vials filled with ethanol, which preserves DNA quite nicely. In 2012, specimens from both groups of bees were shipped to one of my former students, Professor Alexander S. Mikheyev, who heads the Ecology and Evolution Unit at the Okinawa Institute of Science and Technology in Japan. There the DNA was extracted from one bee from each of the 64 colonies that I had sampled and an analysis based on whole-genome sequencing was performed to determine the subspecies composition of both the 1977 ("old") and the 2011 ("modern") populations of bees (Fig. 1.4).

This genetic detective work found that the bees in both the old and modern samples are primarily descendants of two of the subspecies of *Apis mellifera* that were imported from southern Europe, specifically from Italy and from Slovenia: *A. m. ligustica* and *A. m. carnica*, respectively. This finding was not surprising, because these are the two subspecies that have proven the most popular among beekeepers in North America since the 1800s. Colonies of these two subspecies tend to be good-natured (not prone to stinging) and good producers of honey. What was surprising, however, was the discovery that the bees in both the old and modern samples also possessed many genes from the dark honey bees imported from north of the Alps (*A. m. mellifera*) starting in the 1600s and from the gray mountain honey bees (*A. m. caucasica*) imported from the Caucasus Mountains starting in the late 1800s (see Fig. 1.4). This genetic sleuthing also revealed that the bees in the modern (2011) sample, but not those in the old (1977) sample, have a small percentage (less than 1%) of genes from two African subspecies: *A. m. scutellata*, native to Africa south of the Sahara, and *A. m. yemenetica*, native to the hot arid zones of Arabia (e.g., Saudi Arabia, Yemen,

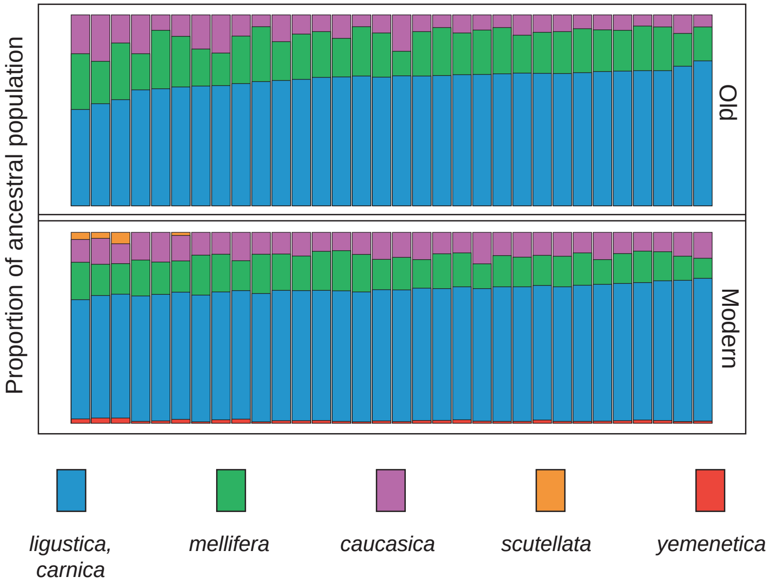

FIG. 1.4. Ancestries of the honey bees (*Apis mellifera*) living in the forests south of Ithaca, New York. Both the old (1970s) and the modern (2010s) populations are largely descendants of bees from southern and southeastern Europe: the subspecies *A. m. ligustica*, *carnica*, and *caucasica*, which have been popular with beekeepers in North America since the 1880s. Both old and modern populations also have clear ancestry from the dark European honey bees (*A. m. mellifera*) of northern Europe that were introduced to North America starting in the 1600s. The modern population also shows a small ancestry of bees from Africa (*A. m. scutellata*) and the Arabian peninsula (*A. m. yemenitica*).

and Oman) and eastern Africa (e.g., Sudan, Somalia, and Chad). This slight introgression of African genes into the modern population of wild colonies living in the forests near Ithaca, New York, is probably a result of Africanized honey bees—hybrids of African and European races of *Apis mellifera*—becoming established in parts of the southern United States in the late 1980s and early 1990s. These southern regions—which include the states of Florida, Georgia, Alabama, and Texas—have warm climates favorable to Africanized honey bees, and they are where much of the commercial queen production in the United States takes place. Evidently, for the last

25 or so years, queen producers in the southern states have been shipping queens carrying some genes of African descent to beekeepers in the northern states. Migratory beekeepers who keep their colonies in Florida over winter and then truck them north in spring to pollinate apples, cranberries, and other crops, have probably also contributed to the northward trickle of genes of the Africanized honey bees.

This new, high-tech look at the genes of the honey bees living in the woodlands south of Ithaca has revealed two important things. First, it has shown us that the arrivals of African honey bees in Florida and Texas in the 1980s and 1990s have affected only very slightly the genetic composition of the wild colonies living in the forests near Ithaca. In other words, the genetic makeup of these wild colonies still reflects mainly the nearly 400-year history of imports of honey bees from Europe. Second, it shows that the genes in this population of wild colonies have come predominantly from honey bees native to *southern* Europe, even though the introductions of honey bees from *northern* Europe started some 200 years earlier. Presumably, this reflects the greater popularity among beekeepers of bees from Italy and Slovenia (*A. m. ligustica* and *A. m. carnica*), in southern Europe, relative to the dark European honey bees (*A. m. mellifera*) from various places in northern Europe. Most beekeepers prefer bees that are calm and produce much honey, and the lighter-colored bees of southern Europe, compared to the darker-colored bees of northern Europe, tend to be less likely to run around when a hive is opened and more likely to build up large populations of worker bees and amass large stores of honey.

Given that most of the genes in the wild colonies living near Ithaca are from honey bees adapted to the relatively mild climates of southern Europe, and given that Ithaca winters are long, snowy (Fig. 1.5), and often bitterly cold (lowest temperatures about −23°C/−10°F), we need to ask: Are the wild honey bees living near the Ithaca area well adapted for life in this northern region of North America? We will see in the coming chapters that the answer to this question is a solid yes; multiple studies have found that the wild colonies of honey bees living in this region are impressively skilled at living here. These studies have looked at how the colonies' nest-

FIG. 1.5. Winter look of an apiary located in Ellis Hollow, near Ithaca, New York.

site preferences, seasonal patterns of brood rearing and swarming, foraging skills, overwintering abilities, and defenses against pathogens and parasites are all highly adaptive for life in this northeastern corner of the United States. Perhaps the most compelling indication that these wild colonies are well adapted to their current environment is that they possess a powerful set of behavioral defenses against the aptly named ectoparasitic mite *Varroa destructor*. In chapter 10, we will see how the population of wild colonies living near Ithaca was decimated when this mite—whose original host is an Asian honey bee species, *Apis cerana*—reached the Ithaca area in the mid-1990s but then recovered through strong selection for multiple defensive behaviors in worker bees that kill these mites. Indeed, we now know that the density of wild colonies of honey bees in the 2010s (ca. 20 years post-*Varroa* arrival) matches what it was in the 1970s (ca. 20 years pre-*Varroa* arrival).

We should not be surprised that the wild colonies of honey bees living in the forests around Ithaca are well adapted to survive and reproduce in these northern woodlands, where the winters are far longer and colder than the winters in many of the bees' ancestral homelands in Europe. After all, these colonies have been exposed to strong natural selection to adapt to the climate throughout their nearly 400-year history of living in the northeastern United States, and there are countless studies by biologists that demonstrate that evolution by natural selection can produce a population of plants or animals with a robust solution to a new problem in just a few years. Besides the rapid evolution of *Varroa* resistance in the wild colonies of honey bees living in the forests around Ithaca, there is the example of the Africanized honey bees (*Apis mellifera scutellata*) in Puerto Rico evolving docility in only 10 or so years. Evidently, this rapid evolutionary change, which occurred between 1994 and 2006, was driven by natural selection favoring genes for reduced aggression in honey bees living where there are no major predators. Another striking example of an insect's rapid behavioral adaptation to a changed circumstance is the adaptive disappearance between the late 1990s and 2003 of the calling song of male field crickets (*Teleogryllus oceanicus*) on the Hawaiian island of Kauai. This behavioral change followed the accidental introduction of parasitic flies that locate host crickets by orienting to the crickets' chirps. Male crickets with mutations for wing structures that silenced their singing were strongly favored by natural selection. Quick evolution led to quiet crickets!

ROAD MAP TO WHAT FOLLOWS

This book aims to provide you with a clear view of the natural lives of honey bee colonies, especially those living in cold climate regions of the world. To enjoy this view, you will need to work your way through some new scientific terrain, make dozens of stops along the way, and look carefully in a different direction at each stopping place. You will soon see that this book is partly a synthesis of the work of many research biologists and partly a travelogue of my personal quest to better understand this special piece of nature. Here is a road map to what follows.

Chapter 2 describes when, where, and how I became intrigued with the puzzle of how colonies of the "domestic" honey bee, *Apis mellifera*, live in the wild. This chapter introduces you to the landscape and forests south of the small city of Ithaca, in central New York State, which is where many of the investigations described in this book were conducted. It also describes how, in the late 1970s, I began studying the population of wild colonies living in one of these forests, the Arnot Forest. It further describes how, in the early 2000s, I was amazed to find wild colonies still living in this forest even though the deadly ectoparasitic mite *Varroa destructor* had spread to the Ithaca area sometime in the early 1990s. This chapter goes on to review what we know about the abundance (and persistence) of wild colonies of *Apis mellifera* in other places. By the end of chapter 2, you will see clearly the two main puzzles that are solved, step-by-step, in the rest of the book: 1) How are the wild colonies of honey bees living in the woods around Ithaca able to survive without being treated with miticides? And, more broadly, 2) How do the lives of wild and managed colonies of honey bees differ, and what can we learn from these differences to be better stewards of our most important pollinator?

Chapters 3 and 4 take a step back from the present-day biology of *Apis mellifera* to explore why, until recently, we have known so little about the natural lives of honey bees. We will see that honey bee colonies probably began living in man-made structures (hives) as soon as humans made the shift from being mobile hunters and gatherers to living as sedentary herders and farmers, some 10,000 years ago. It is likely that as soon as we humans stopped being destructive honey hunters, we began to become manipulative beekeepers. We will also see how, over thousands of years, we gradually refined our artificial housing of managed honey bee colonies to make it easier and easier for us to reach into their homes and steal their golden honey. Thus, step-by-step, we grew increasingly disconnected from how honey bees live in the wild. Meanwhile, the bees never yielded their nature to us and instead continued to follow a way of life set millions of years ago. It was not until about 70 years ago that we perfected the means—

artificial insemination of queen bees—to control this insect's mating and breed it for our purposes. Fortunately, even today, precious few queens are artificially inseminated. Most still mate with whatever drones they encounter.

Chapters 5 through 10 review what has been learned, mostly over the last 40 years, about the natural history of honey bees living in temperate regions of the world. Here we will examine the interwoven topics of nest architecture, annual cycle, colony reproduction, food collection, temperature control, and colony defense. Throughout these chapters, we will see how the marvelous inner workings of a honey bee colony have been shaped by natural selection for life in the wild, not in domestic settings, so honey bees are still perfectly able to survive and reproduce without a beekeeper's supervision. More specifically, we will see how the bees build and use their beeswax combs, time their swarming and drone rearing, operate a factory-like organization of food and water collection, maintain thermal homeostasis in their nests, and sustain an arsenal of colony defenses. These are all parts of a honey bee colony's complex suite of adaptations for passing on its genes to the next generation of colonies.

Finally, chapter 11 presents the take-home lessons from what we have learned about how *Apis mellifera* lives in its natural world. The chapter first summarizes the findings reported in the previous chapters in the form of a 21-point comparison between the lives of colonies living in the wild and those of colonies managed for apicultural purposes. It then offers 14 practical suggestions of ways beekeepers can help their bees live closer to their natural lifestyle and so enjoy less stress and better health.

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