

INTRODUCTION

Everybody likes bumble bees. As colorful and familiar visitors to flowers, these insects have long been appreciated by artists, naturalists, and farmers. The eighteenth-century German pioneer of pollination biology, Christian Konrad Sprengel, made observations of their behavior at flowers, and Charles Darwin went on to describe their importance as pollinators at a time when this ecological function had not been widely recognized. In North America, naturalists have been describing their diversity for more than two centuries, but a great deal remains to be done. This guide is aimed at making that easier.

The value of bumble bees as pollinators of wild and cultivated plants is increasingly appreciated. Each year more than a million commercially produced bumble bee colonies are sold around the world. Most of these colonies are used in greenhouses, where their pollination service is worth more than \$10 billion annually. The total value of crop pollination by wild bumble bees is far higher than this. Unfortunately, there is convincing evidence that many species of bumble bees in Asia, North America, South America, and Europe are in decline, in part because of accidental introductions of bee diseases by the bumble bee pollination industry. Several of the species described in this guide were commonly encountered through their ranges just 15 years ago, but they are now exceedingly rare. Others have not been seen for years, and one may now be extinct.

North American bumble bees have been the subject of numerous regional guides, but the only comprehensive revision was by Henry J. Franklin in 1913. In recognizing 59 species north of Mexico, Franklin gave full species status to some taxa now considered parts of a species (e.g., “*B. californicus*,” a color pattern of *B. fervidus*), but did not describe four taxa now generally agreed to be distinct species with ranges in North America (*B. caliginosus*, *B. distinguendus*, *B. franklini*, and *B. vandykei*). H. E. Milliron started a monograph on the bumble bees of the Western Hemisphere in multiple volumes between 1970 and 1973. He recognized only 34 species north of Mexico, but never completed sections on the subgenera *Pyrobombus* or *Psithyrus*. Milliron described a number of the species in this book as subspecies (e.g., he interpreted *B. terricola* as being composed of two subspecies, *B. terricola terricola* and *B. terricola occidentalis*, whereas we recognize these as two separate species). Apparently missing from Milliron’s work is *B. franklini*, which he regarded as a variety of *B. occidentalis*, and completely missing is *B. distinguendus*, a species well known in the Old World, but only recently discovered in Alaska. Among the larger regional publications since Franklin are those on the bumble bees of the eastern United States (Plath 1934, Mitchell 1962), western United States (Stephen 1957), California (Thorp, Horning, and Dunning 1983), and eastern Canada (Laverty and Harder 1988). Despite our familiarity with bumble bees and the imperative to address their conservation, in North America there remains a need for a comprehensive modern review of the status of bumble bees and an effective identification manual for those interested in them. Franklin openly expressed uncertainty about his separation of some pairs of closely related North American bumble bee taxa as species, and these issues are still debated in the literature. One reason for our uncertainty about bumble bees is that the color patterns of their hair, which include the most obvious characteristics one might use for identification, can be strikingly variable within species and strongly convergent between them. For example, *B. bifarius* (the so-called Two Form Bumble Bee) occurs throughout western North America in distinctly different red and black color patterns, and at any one site it may bear closer resemblance to other bumble bee species present than to *B. bifarius* color patterns from other parts of its range. To exacerbate the problem, bumble bees

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The color patterns of *Bombus bifarius* workers vary around its range.

have relatively few distinctive physical characteristics useful for distinguishing one species from another; the bee systematist Charles Michener has called them “morphologically monotonous.” Thankfully, recent molecular analyses have illuminated this debate. This guide presents some new views of species based on molecular phylogenies (family trees) of bumble bees that we hope will improve understanding of these insects.

In addition to describing the distribution and diversity of North American bumble bees, this book is primarily about how to identify them to species. As in some previous guides, we describe hair color patterns in a diagram for each caste (queen or worker), dividing the body into differently colored parts to produce a simplified representation. But for many bumble bee specimens, identification is not possible by use of these color patterns alone. We therefore emphasize the importance of other morphological characteristics, for example the shape of the face and of the male genitalia. Identification of this group of insects is more difficult than is commonly assumed, and experience has shown that there is no substitute—even for experts—for these more subtle characters. That said, we have attempted to make the process of identifying bumble bees as straightforward as we can, stripping away technical language where possible and presenting a system that specialists and beginners alike should be able to use.

— BUMBLE BEE DISTRIBUTION AND DIVERSITY

Bumble bees belong to the insect order Hymenoptera, which includes the bees, ants, wasps, and sawflies. Like other similar insect groups such as Diptera (flies), Coleoptera (beetles), and Lepidoptera (butterflies and moths), the Hymenoptera go through a complete metamorphosis between the larval and adult stages of development. Within this group, bees are essentially hairy wasps, from which they diverged more than 100 million years ago. Bees differ from most living wasp lineages in that plant pollen, rather than animal tissue, provides the protein necessary for larval development, and it is thought that bee diversification tracked the adaptive radiation of flowering plants in the late Cretaceous period. Bees differ from wasps in a number of ways, not only in that they have branched body hairs and other adaptations for harvesting and carrying pollen, but also in having an array of tongue morphologies that facilitate feeding from nectar at flowers of different depths.

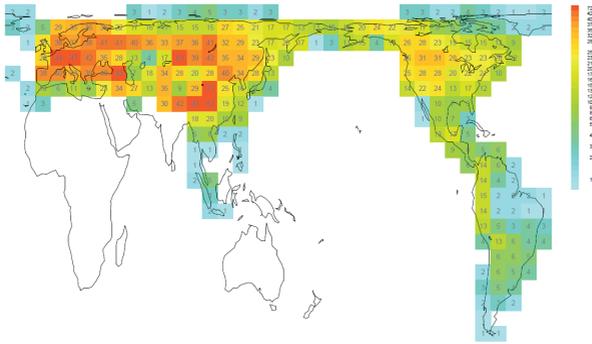


Plant pollen is the primary protein source for virtually all bees, including bumble bees. LR

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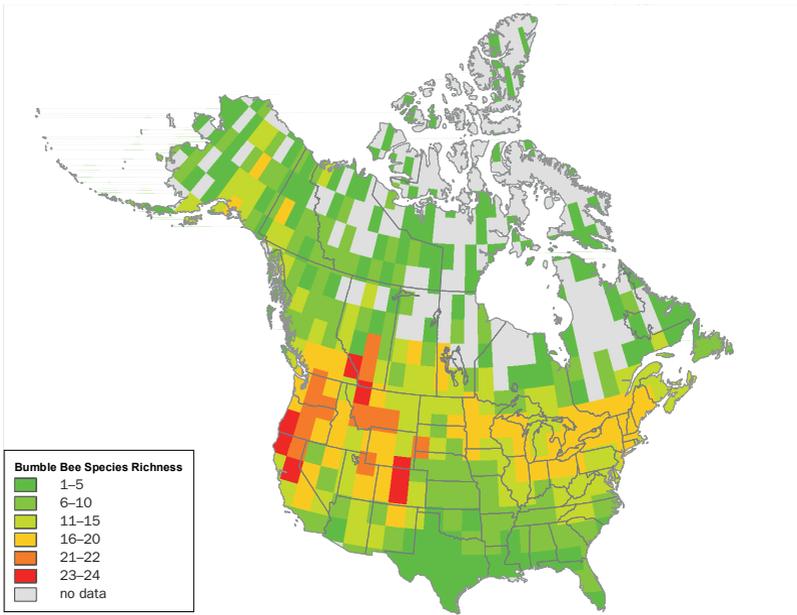
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There are nearly 20,000 species of bees worldwide, of which just 250 belong to the genus *Bombus*, or bumble bees. While bees in general are most diverse in areas with a warm dry “Mediterranean” climate (e.g., coastal California, South Africa, Chile, and the land around the Mediterranean Sea), bumble bee diversity is greatest in cool temperate and montane situations. They are found throughout the Northern Hemisphere, from Arctic tundra to deserts and subtropical forests, with the greatest diversity in the mountains around the Tibetan plateau. Bumble bees are native in the Southern Hemisphere only in South America, although a few species have been introduced, along with clover, in New Zealand and Tasmania. Forty-six species of bumble bees are found across North America



LEFT: Bumble bees are most diverse in temperate and montane regions.

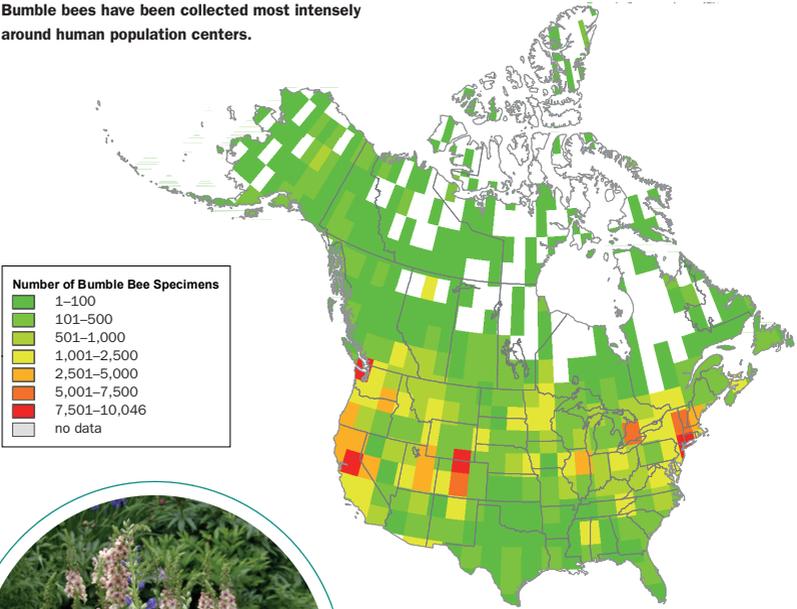
BELOW: North American bumble bee diversity is highest in western coastal and montane regions, though not all areas have been well surveyed.



north of Mexico; although not all areas of the continent have been surveyed equally thoroughly, undoubtedly the greatest diversity occurs in and around the western mountain ranges.

Within their area of occurrence, bumble bees may be found almost anywhere there are suitable flowers. They occupy a wide variety of habitats, reaching peaks of local abundance and diversity

Bumble bees have been collected most intensely around human population centers.



Farms (BELOW) and gardens (INSET) are habitat for bees, especially when pesticide use is minimized and hedgerows are retained or planted.



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where a continuous supply of pollen and nectar is available throughout the growing season. Bumble bees occur in mountain meadows, prairies, desert uplands, savannas, agricultural landscapes, gardens, and wetlands, and some species, such as *B. impatiens*, are common even in urban habitats. Forests, especially coniferous forests, usually support relatively fewer bumble bees, but may be attractive to them when spring flowers are in bloom.

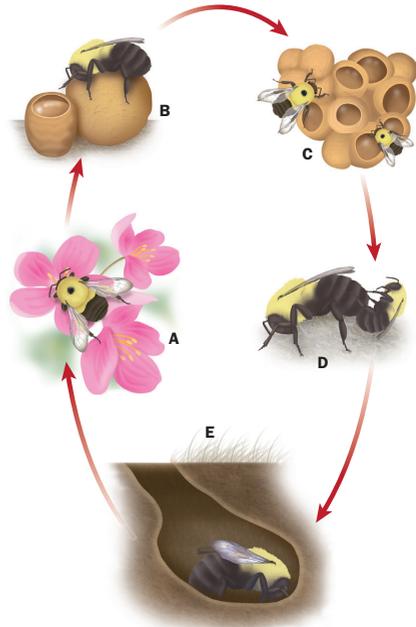
COLONY CYCLE

Bumble bees are social insects. This means that related individuals cooperate to forage for food, rear offspring, and defend their nests. Queens, workers, and males perform different functions within the colony, and there is also specialization within the worker caste. There is evidence of communication between and within groups. As social insects, bumble bees are similar to their close relatives the honey bees, but with an important exception: honey bee colonies can persist with the same queen for years, depending on stored resources during the winter months spent inside the nest, whereas bumble bee colonies die at the end of each growing season, with new ones founded each year. (There is at least one exception to this rule from the American tropics, where climate does not curtail the bees' access to resources as it does in the temperate latitudes.)

The bumble bee life cycle can be thought of as starting in spring (A), when mated, overwintered queens emerge from hibernation to begin the business of founding a colony. At this time, the large, brightly colored bees are a familiar sight as they gather nectar and pollen from the few flowering



ABOVE: Bumble bees are found in a variety of habitats, including urban centers. LR RIGHT: Bumble bee life cycle (A–E). See text for details of each stage. AS





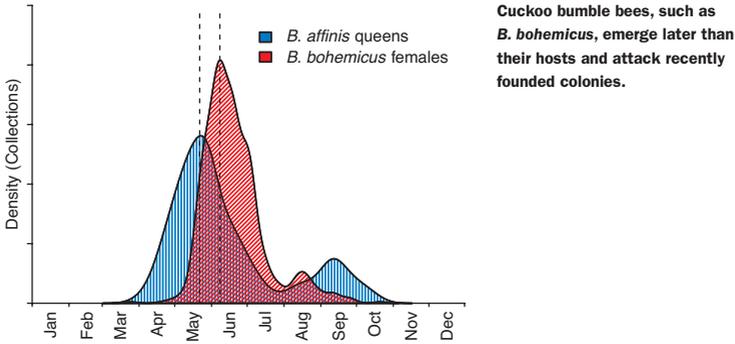
A *B. griseocollis* queen in her nest (exposed) before the first batch of workers emerge. LR

plants in an otherwise quiet landscape, including willows, rhododendrons, and ephemeral spring wildflowers. Bumble bees are not warm blooded, but they can maintain a relatively consistent body temperature regardless of the ambient temperature, generating heat by shivering their thoracic flight muscles, so they can be active in the cool, wet weather of early spring. The queen searches for a suitable nest site, flying low over the ground and repeatedly landing to investigate holes in the ground. Bumble bees do not dig their own nest cavities, relying instead on abandoned rodent dens, open grass tussocks, hollow logs, and aboveground manmade structures. Many species choose different nesting substrates, and some have more specific habitat requirements (e.g., those that nest only aboveground in open herbaceous habitats).

When the queen has located a nest site (B), she constructs a wax honeypot for nectar storage. She lays her first clutch of eggs on a mass of pollen moistened with nectar in a small wax cup known as a brood clump. After hatching, the young larvae feed on this pollen, and the queen alternates between incubating the larvae and foraging for more food. This is a vulnerable time in the life of a colony, as vagaries of weather and food—not to mention aggressive interactions with other bumble bee queens in search of nest sites—may determine the fate of the queen and her eggs. Bumble bee species employ two distinct behaviors to provide larvae with pollen. The “pocket-making” species place lumps of pollen into wax pockets attached to the base of the brood clump, and larvae feed together from this supply. The “pollen storers” feed their larvae directly, and larvae leave the brood clump as they grow. Each of these behaviors is associated with one of the two principal evolutionary lineages of bumble bees. Larvae feed for about two weeks before spinning a silk cocoon and pupating for another two weeks. The adult bees that emerge from these pupae are females who will not, in most cases, produce their own offspring, living instead as workers in their mother’s colony (C). The queen now stays at home laying eggs, and workers forage for resources, tend new clutches of eggs and larvae, regulate the nest temperature, and defend the nest.

It is in the early stages of development that the colony may be attacked by cuckoo bumble bees. These members of the subgenus *Psithyrus* were long thought to be a group separate from the “true” bumble bees, but we now understand them to be part of the same evolutionary lineage as the rest of the genus. Cuckoo bumble bees do not forage for pollen or found their own colonies; instead, they enter the nests of other species, sometimes kill the queen, and overcome the workers through a combination of aggression and pheromones. The workers then rear the

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offspring of this usurper, which will be exclusively males and females (no workers). Timing of the attack is critical—to succeed, a social parasite must invade a host nest large enough to raise as many of its offspring as possible, but not so large that the workers will kill it. Cuckoo bumble bees possess a range of adaptations related to their life history, but they lack some of the morphology associated with other bumble bees, such as the pollen-carrying corbiculae of the hind tibiae in females. Cuckoo species often attack a broad range of host species, but some specialize in attacking the members of just one species or subgenus (e.g., *B. variabilis* has been documented as a parasite only in the nests of *B. pensylvanicus*). This social parasitism can be quite common, but cuckoo bumble bee populations must be smaller than those of their hosts, and population trends are constrained by those of their hosts. Many species are now of conservation concern.

Bumble bee colonies grow quickly as successive broods of workers are produced and more floral resources become available. At some point in summer, the colony switches over to the production of males and new queens. This switch is thought to be related to the age of the queen and the size of the colony, though it is not well understood. As with other Hymenoptera, sex determination in bumble bees is controlled by a system known as *haplodiploidy*, in which fertilized eggs (which are diploid, with different genetic material from both parents) develop into female adults and unfertilized eggs (haploid, containing only DNA from their mothers) into males. The queen thus produces males simply by laying eggs not fertilized by the sperm she has stored in her body since mating the previous fall. Unfortunately, in populations with low genetic diversity, fertilized eggs may also develop into males that develop and behave as normal, but are sterile. This reduces a colony's output of reproductive females while introducing males to the population that may mate with but cannot fertilize queens. How fertilized eggs become queens instead of workers is not fully understood, but it is probably associated with larval diet and possibly exposure to queen pheromones.

Adult males do not forage for the colony (with rare exceptions), leaving the nest after emergence to feed at flowers and search for mates (D). In some species, males patrol for queens and advertise their presence with pheromones. In other species, the males occupy pheromone-scented perches while waiting for queens to fly past. The latter (e.g., *B. griseocollis*) tend to have greatly enlarged eyes, a trait that can be useful in identification. Newly emerged queens leave the colony to feed during the day, often returning at night. They eat a great deal of pollen and nectar,



LEFT: Adults tending the brood cells of a *B. impatiens* colony. LR
BELOW: *B. huntii* mating pair. NS



building fat reserves that will carry them through a winter of hibernation (E). Bumble bee queens usually mate once with only one male. They then search for a suitable overwintering site and enter a period of torpor. Relatively little is known about where bumble bee queens spend the winter, but they have been reported to use burrows of other animals and to excavate holes in loose dirt or in debris such as that of compost piles. The new queen having reproduced, the colony declines, with males, workers, and the old queen dying before winter.

— INTERACTIONS WITH PLANTS

Bumble bees have specific habitat requirements for nesting and overwintering, and a third aspect of habitat, forage, is even more important. Relative to many other bees, bumble bees have a long period of summer activity, and with only modest resources stored in the nest, pollen and nectar must be available continuously. These animals collect resources from a patchy environment and return to one central point—the nest—to consume them. The distance bees are capable of traveling on a foraging trip is a critical aspect of their foraging ecology, as are the energetics of flight for a resource-laden bee. Bumble bee species vary in their ability to travel the landscape, and the farthest they have been demonstrated to fly from the nest is about 10 km. Whether or not they often fly this far, to be successful foragers they must return with more resources than they left with, the cost of the flight included. For this reason, most resource acquisition is likely to take place considerably closer to the nest.

Because bees eat pollen, their evolutionary history is entwined with that of flowering plants, and they are well known as pollinators. Bumble bees possess a number of traits that make them effective pollinators of both wild and cultivated plants. They are classic generalist foragers, capable of working a wide variety of plants for their resources. Although neither they nor any other bees deliberately pollinate flowers, pollen sticks easily to their copious hair and is transferred

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effectively between flowers. An individual worker often visits just one species of plant at a time, minimizing pollen transfer to other, unreceptive plants. Bumble bees can learn complex foraging tasks such as working the flowers of closed gentians and pea family plants. Unlike most other bees (including honey bees), they often “buzz” flowers by vibrating their flight muscles. This shaking helps them extract pollen from the anthers and greatly facilitates pollination for certain plants. In fact, many plants are adapted to dispense pollen when vibrated, and some even require this. Plants that benefit from “buzz” pollination include those in the nightshade (*Solanaceae*), rose (*Rosaceae*), heath (*Ericaceae*), and melastome (*Melastomataceae*) families. Numerous crop plants (e.g., blueberry, cranberry, tomato, and kiwi) have improved yields when buzzed by pollen-collecting bumble bees, which is why commercial bumble bee colonies, rather than honey bee hives, are maintained in many greenhouses where crops are grown.

It is common for multiple species of bumble bees to be present in an area, placing them in potential competition with each other for resources. Foraging niches are usually partitioned to some extent by variation in tongue length, and bee species can often be divided roughly into artificial groups by tongue length. Species with long tongues (including, for example, *B. fervidus* and *B. pensylvanicus*) can reach nectar in tubular flowers with long corollas, while those with short tongues (e.g., *B. morrisoni* and *B. terricola*) cannot, and are most efficient at harvesting nectar from smaller flowers. Some short-tongued species circumvent this limitation by biting holes in the base of long flower corollas, allowing them direct access to nectaries. This “nectar robbing” behavior is especially common in species of the subgenus *Bombus s. str.*, in which females’ mouthparts seem to have adaptations for cutting. Nectar robbing opens a shortcut to harvesting nectar resources, and many other bees will subsequently switch from typical “legitimate” foraging behaviors to secondary nectar robbing. This can have negative consequences for plant reproduction, and plants have a range of floral traits that prevent bees from nectar robbing. Interestingly, however, research has demonstrated that in many cases the reproductive consequence of nectar robbing for plants is neutral or even positive.

A number of excellent publications detail the life history and biology of bumble bees. A list of resources is provided on page 203.



Nectar robbing holes left in flowers of Squirrel Corn (*Dicentra canadensis*) by queen bumble bees. LR