CONTENTS

EPICHARIS ZONATA

South American Benthic Bee

Waterproof brood cells

SCIENTIFIC NAME	*Epicharis zonata*
FAMILY	Apidae
LIFESTYLE	Solitary
NESTING HABITAT	Underground tunnels

Epicharis zonata **is a neotropic bee found from Mexico to southern Brazil. The genus *Epicharis*, along with *Centris*, form an ancient lineage of floral oil-collecting bees and are likely the sister group of modern pollen-collecting bees. All of these bees build their nests in soil, on inclines or flat ground.**

They feed their larvae pollen and floral oils, collecting this oil with combs on their front legs. The oils are used as brood cell lining and as larval food, essentially replacing floral nectar for these tropical bee species. Floral oils are the consistency of olive oil and are much more energetically dense than the simple carbohydrates of nectar. The South American Benthic Bee is a floral specialist and collects oil only on flowers from plants in the family Malpighiaceae.

The nest architecture of the South American Benthic Bee (after Roubik & Michener, 1980)

1. The lateral burrows are soil filled. 2. A sand-filled cell at the top with pollen packed in the bottom. 3. A sand-filled cell with larval frass at the bottom.

In the mid-1970s David Roubik and Charles Michener studied a nesting population of South American Benthic Bees 7 ½ miles (12 km) south of Kourou, French Guiana in South America. This site was dominated by small trees and shrubs. Females were seen foraging and nest building but males were not observed on flowers in the area. This site was characterized by a large number of nests, each built by a single female. They consisted of a vertical tunnel with branching burrows that ended in single brood cells.

Each cell was positioned vertically and lined with floral oils. The wall was made of three layers, with the innermost made of floral oil. There was a thicker middle layer, perhaps made of resin, and an outer layer with silt. Pollen provisions were placed at the bottom of the cell and a single egg, or developing larvae, was in each cell. At the top of each tapered cell was a resin plug and all tunnels were filled in after cell closure. The larvae itself did not construct a cocoon. In the mid-1970s annual rainfall in this region of French Guiana could reach up to 16 ½ feet (5 m). During the dry season the soil was wet enough that the bees could construct nests, but the area was inundated with water during the wet season. It is thought that these waterproof cells, at 14 inches (35 cm) deep, are adaptations to this wet environment.

→ The South American Benthic Bee builds special nests that protect developing larvae from seasonal flooding.

EUCERA (PEPONAPIS) PRUINOSA

Eastern Cucurbit Bee

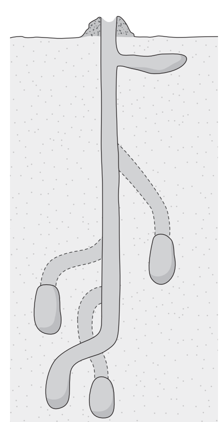
Underground tunnel nests

SCIENTIFIC NAME	*Eucera (Peponapis) pruinosa*
FAMILY	Apidae
LIFESTYLE	Solitary
NESTING HABITAT	Underground tunnels

The Eastern Cucurbit Bee, also known as the Pruinose Squash Bee, is a commonly seen medium-sized bee in North America that originated in central Mexico. It is a pollen specialist on *Cucurbita*, particularly on pumpkins, squash, and gourds. Eastern Cucurbit Bees nest in the ground near their preferred host plants in open fields and often in aggregations. Since they have a propensity to nest where they emerge; they can persist for decades if not disturbed.

These fast-flying bees are black and orange with white banding on the abdomen. Males have a somewhat more black abdomen and a yellow triangular spot in the front of the head. Females are most often active in the early morning, whereas males are found a bit later in the morning and in the evening.

To create the nest, females construct a vertical tunnel up to 8 inches (20 cm) in the ground and horizontal side branches containing brood cells at the terminus. Each cell is provisioned with pollen and nectar, then a single egg is laid, and the horizontal tunnel is collapsed. Female eggs are laid in the lowest, and first-prepared cells, with males near the surface. Just below the entrance is a small chamber where the female will rest overnight. Adult bees emerge when *Cucurbita* plants bloom in the following year, with the males emerging a few days before females. Both males and females collect nectar in pumpkin and squash flowers, where mating occurs. Eastern Cucurbit Bees have greatly expanded their geographic range from their original habitats in central Mexico following the human cultivation of *Curcurbita* crops. Domestication by Meso-American societies of these crops began some 10,000 years ago, and they then spread through continental North America in pre-Columbian times. The bees followed and are now distributed as far as southern Canada.



The underground nest of the Eastern Cucurbit Bee
Individual females construct the underground nest with a central tunnel and chambers to each side where they provision the developing larvae with pollen and nectar.

→ A female Eastern Cucurbit Bee collecting pollen from a squash flower.

BOMBUS IMPATIENS

Common Eastern Bumble Bee

Renovating underground rodent burrows

SCIENTIFIC NAME	*Bombus impatiens*
FAMILY	Apidae
LIFESTYLE	Eusocial
NESTING HABITAT	Underground cavities

In North America, the typical black-and-yellow bees of summer, Eastern Bumble Bees, are a vital part of agriculture, providing pollination services to crops including blueberry, raspberry, cucumber, pumpkin, and squash.

They are also raised commercially, on an industrial scale, for pollination in greenhouses, particularly of tomatoes and cucumbers. Whole colonies are raised in boxes just larger than a shoe box and can be shipped in regular mail. Unlike honey bees, which will fly to the top of a greenhouse and ignore flowers, bumble bees are efficient pollinators in this environment.

Queens, males, and workers tend to look the same but the queens are slightly larger. Queens mate in the fall and hibernate over winter in an underground chamber (see page 29). When spring arrives the queen emerges to find an old rodent burrow about 2 feet (61 cm) underground to build their nest. The queen builds pots for nectar and pollen provision and then lays an egg. Once the first clutch of worker daughters emerge, the queen will spend the rest of her life in the nest, eating food collected by the workers and laying eggs. The workers will raise subsequent daughters, reaching over 400 bees, until the end of the year when male and female reproductive are produced. The mated females will then start the cycle over again. The old queen, workers, and males all die at the end of the year.

In summer, Eastern Bumble Bee foragers will leave their burrows in the early morning and establish a "trapline" where they sample flowers. This is an efficient means of provision collection and it allows the bees to exploit their most preferred host plants. Once established they will forage on these plants until they deplete their resources and then switch to another species. It turns out that although they visit many flower types across a day or season, these bumble bees are cryptic specialists. Detailed experiments have shown they can detect and prefer a specific pollen type that contains a 5:1 protein-to-lipid ratio—certain plant species, and their most preferred plant, have just this ratio. This suggests other species of bee may have similar preferences.

→ A Common Eastern Bumble Bee probing flowers with its antennae while nectaring. Note the pollen on specially adapted hairs.

APIS DORSATA

Giant Honey Bee

Shimmering bee curtains

SCIENTIFIC NAME	*Apis dorsata*
FAMILY	Apidae
LIFESTYLE	Eusocial
NESTING HABITAT	Open nesting

The Giant Honey Bee of the Asian tropics has been called "the most ferocious stinging insect on Earth." This is because of its large body size (¾ inch, or up to 2 cm) accompanied by its large stinger and aggressive colonies.

These bees are distinguished by large vertical wax combs, often 3 feet (over 1 m) in length, suspending from branches or other substrates (see pages 33–35). Colonies tend to aggregate in "bee trees" where nearly every large branch is occupied.

The comb is organized into regions. The top nearest the branch is where honey is stored and brood is located below. The worker and any drone brood are reared together. The whole comb is covered by a curtain of bees that protects it from rain and insulates the brood. The bees in the quiescent zone, where the honey is produced, cover most of the comb and their heads face upward. The so-called mouth zone is in the bottom corner and is the area where foraging bees will land and take off. Returning forager bees also waggle dance in this zone to indicate the quality and location of resources on this vertical surface. Giant Honey Bees also seem to use the waggle dance to inform migration behavior.

Because the nest is so exposed there are many predators that must be deterred, from the Greater Death's Head Hawk-moth (*Acherontia Lachesis*) to the Crested Honey Buzzard (*Pernis ptilorhynchus*). The bees do this by "shimmering"; as a predator approaches, the bees will wave their stinger-laden abdomens in a wave motion, similar to those done by fans at a sports game. This sudden flickering is enough to deter some of their most common enemies such as wasps.

The life cycle of the colony is similar to other tropical honey bee species. During periods of abundant flowering, the colonies grow and reproduce by a process of colony fission called swarming. When flowers are not available, such as in dry or rainy periods, these bees can migrate to new locations. Giant Honey Bee queens mate with 13 or more males. Drones are only produced at certain periods and will fly to congregation sites to encounter females. Upon mating they die, their evolutionary job complete. Newly emerged workers are house bees, forming the curtain or tending brood. As with other honey bees, older workers forage.

Humans have had a long history honey hunting Giant Honey Bees in southern Asia, and their close relatives, the Himalayan Giant Honey Bee (*Apis laboriosa*) in the Himalayas. In parts of southern Asian there is passive management of bee tree colonies. Here, a beekeeper will climb a tree at night when the bees are more quiescent, or in a period of inactivity, and heavily smoke the bees. Then a small portion near the top of the comb will be cut out, leaving the brood comb intact. This process allows the bees to rebuild, and honey harvesting to continue throughout the year.

→ Giant Honey Bees are the largest of the honey bees, with workers, such as the bee shown here, reaching ¾ inch (2 cm) in length.

TETRAGONULA CARBONARIA

Sugarbag Bee

Spiral nests

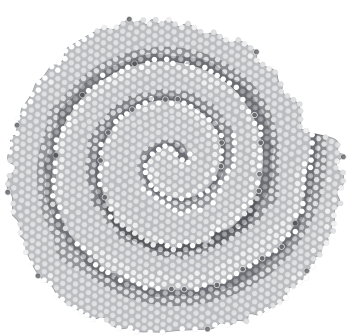
SCIENTIFIC NAME	*Tetragonula carbonaria*
FAMILY	Apidae
LIFESTYLE	Eusocial
NESTING HABITAT	Above-ground cavities

Sugarbag Bees, found in northeastern Australian forests and woodland, form an elaborate collection of structures made of a combination of plant resins and beeswax, secreted from special glands of worker bees, called cerumen. These nests are often located high in a cavity in the trunk of a tree.

Each nest has a large aggregation of brood cells in a characteristic spiral comb covered by a protective dome—the involucrum. The queen lays eggs at the newly constructed spiral top so that the older developing brood is lower down, with the pupae near the bottom. A single egg will be laid in a comb cell that is provisioned with honey and pollen and then sealed. In addition, stores of honey and pollen are made outside the brood area in separate large pots. Wax entrance tubes may extend beyond the side of the nest, and entrance tunnels are guarded to prevent intruders.

Stingless bees, such as the Sugarbag Bee, and honey bees likely share a common ancestor and possess similar traits, including caste distinction, sterile workers, cooperative brood care, comb building, and production of honey. However, unlike honey bees, outside the colony, Sugarbag Bees will attack with a "fight swarm." This is a large aggregation of bees that will mob the intruder, regardless of size, and hopefully deter disturbing the nest. When young, the bees are house bees that take care of brood, build the nest, and other in-house activities. As these bees age they transition to foragers.

Unlike honey bees, which can communicate the location of the best floral resources, Sugarbag Bees collect nectar, pollen, and resin using an opportunistic strategy, but also by marking food sources with a pheromone for nestmates. Sugarbag Bee colonies have only one reproductive female, the queen. Studies have shown that she is the sole mother of the males, although other species of stingless bees can have queen-like workers that produce males as well.



The typical structure of a spiral brood combof a Sugarbag Bee nest

At the top are eggs, just below are developing larvae, and pupae are at the very bottom of the spiral. The brood comb is at the center of the nest and is surrounded by storage cells of pollen and honey.

→ The stingless Sugarbag Bee from northeastern Australia, collecting pollen.

EUGLOSSA HYACINTHINA

Communal Blue Orchid Bee

Resin nests

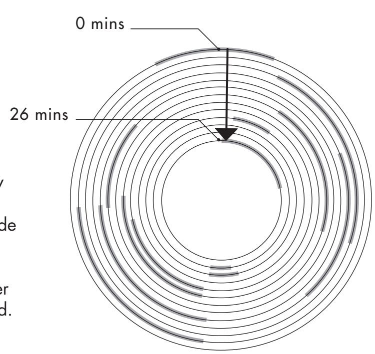
SCIENTIFIC NAME	*Euglossa hyacinthina*
FAMILY	Apidae
LIFESTYLE	Quasisocial
NESTING HABITAT	Above-ground nests

These long-tongued bees of tropical Central America have jewel-like blue metallic bodies and translucent wings. Males and females of this species are very similar with a slight difference in the thorax. Bees in the tribe Euglossini, to which this species belongs, have no worker or queen bees. They also do not form large colonies.

Mated females build complex nests on the stems of plants in mixed tropical habitats. Completed nests are about 2½ inches (6 cm) long and 1½ inches (4 cm) in width and shaped like a top, with a narrow point at the bottom presumably to shed water—the plant stem runs through the center of the nest. A single female constructs the nest by making successive trips to collect resin. The resin is deposited in sequential layers and shaped into arches that eventually form the spheroid shape. Once completed, the nest will have a single entrance covered by a small resin roof.

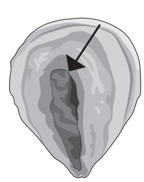
Nests are inhabited either by a single female or by a group of females. Unlike in other bee species, the females living in the latter arrangement are all similarly reproductive and do not show a division of labor. Having two nesting strategies is unusual and seems likely to be advantageous under different environmental conditions. Solitary nesting females have a higher number of offspring but their nests are left unattended for longer periods and become prey to predators. Co-nesting females have fewer offspring but provide their brood with more protection.

Orchid bees get their name from the fact that males of the species are pollinators of large orchids in the American tropics. Male bees collect aromatic fragrances from the orchids and use these to attract females during territorial mating displays. Males will collect the fragrance in hind leg pouches in the early morning and then fly to a relatively open territory area to encounter females. The fragrance is thought to evaporate and act as a pheromone-like attractant for females. Orchids visited by these males have evolved fantastic structures to attract the bees and to place pollinia in exactly the right position to ensure pollination of another plant of the same species.



Building a nest

Detailed observations by Wcislo et al., 2012, show how Communal Blue Orchid Bees make a nest by moving from side to side, from the exterior to the interior. Each arc represents a 1- to 2-minute work session over a 26-minute construction period.



→ A female Communal Blue Orchid Bee on her resin nest.

FINDING FOOD IN A COMPLEX WORLD

Choosing from the floral buffet

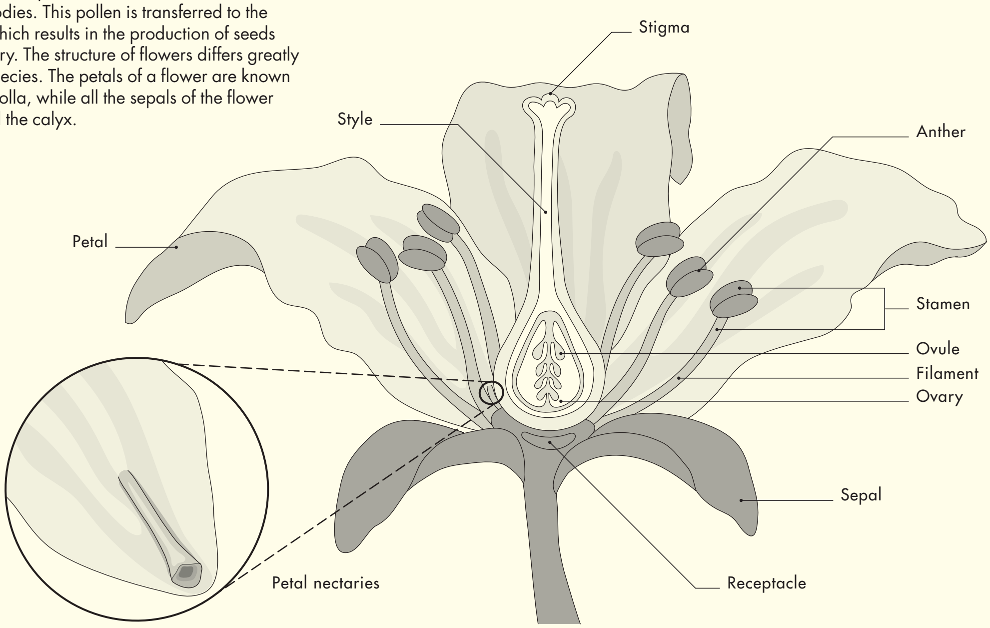
Flowers vary tremendously in their shapes, colors, scents, and the types and amount of the food rewards they provide. How do bees choose which flowers to visit? Do they visit all flowers available, or specialize in a few?

Most bee species obtain all their nutritional resources from the nectar and pollen provided by flowering plants. Nectar serves as bees' primary source of carbohydrates, while pollen is their primary source of protein and fats. Nectar can also contain amino acids, while pollen provides essential sterols, vitamins, and minerals. The quantity and the nutritional composition of nectar and pollen vary significantly across plant species, and this can shape the foraging preferences of bees. Not all bee species use nectar and pollen, however: we will discuss the special cases of oil-collecting and meat-eating bees later in this chapter.

Feeding and pollination

When bees visit flowers to collect nectar, pollen, or oils, pollen from the anthers attaches to their bodies. This pollen is transferred to the stigma, which results in the production of seeds in the ovary. The structure of flowers differs greatly among species. The petals of a flower are known as the corolla, while all the sepals of the flower are called the calyx.

COMMON FLOWER PARTS



SPECIALIST OR GENERALIST?

Ecologists who watch bees on flowers have long recognized that some species visit one plant family or genera, while others go to a great variety. This has led to distinguishing bees in a pollinator community as specialists or as generalists.

Most bees are nectar generalists, visiting a wide range of plants for nectar rewards. Flowers may sometimes limit the bees that visit by making floral nectaries inaccessible to bees of a certain size or shape. However, some bees do have preferences for certain nectar concentration, sugar types, or volume. Long-tongued bees have been reported to like sucrose-rich nectars, and short-tongued bees tend to prefer nectars with more glucose and fructose. Sucrose is a disaccharide while glucose and fructose are monosaccharides.

↑ Pollen grains comes in many different shapes and colors, and vary between plant species. Scientists can look at bee-collected pollen under the microscope to determine which plant species that bee was foraging on.

In terms of pollen foraging, bee species are classified as polylectic (collecting pollen from a variety of flowering plant species, genera, and families), oligolectic (collecting pollen from a few related plant species), or monolectic (collecting pollen from only one species). For example, *Andrena florea* (see page 80) collects pollen from *Bryonia* plant species (vines in the bryony gourd family); Eastern Cucurbit Bees (*Eucera [Peponapis] pruinosa;* see page 42) collect pollen only from *Cucurbita* plant species, which include squashes and gourds; while *Macrotera (Perdita) texana* collects pollen from *Opuntia* species, commonly known as prickly pear.

↑ Buff-tailed Bumble Bee (*Bombus terrestris*) foraging on Common Heather (*Calluna vulgaris*). Compounds in the nectar of this plant help the bee fight off infections of a gut parasite.

↗ Some mason bee species, such as the Spined Mason Bee (*Osmia* [*Hoplosmia*] *spinusola*) shown here, specialize on Asteraceae pollen. Other *Osmia* bees and *Osmia* parasites cannot survive on Asteraceae pollen. By using this pollen, the Spined Mason Bee may avoid competition or parasitization.

Interestingly, recent studies of *Bombus impatiens* bumble bees (see page 44) suggest that these polylectic bees may be selectively foraging for pollen that matches a particular protein-to-lipid ratio. Thus, although the bees may be foraging across a number of plant species, they may be acting as cryptic nutritional specialists.

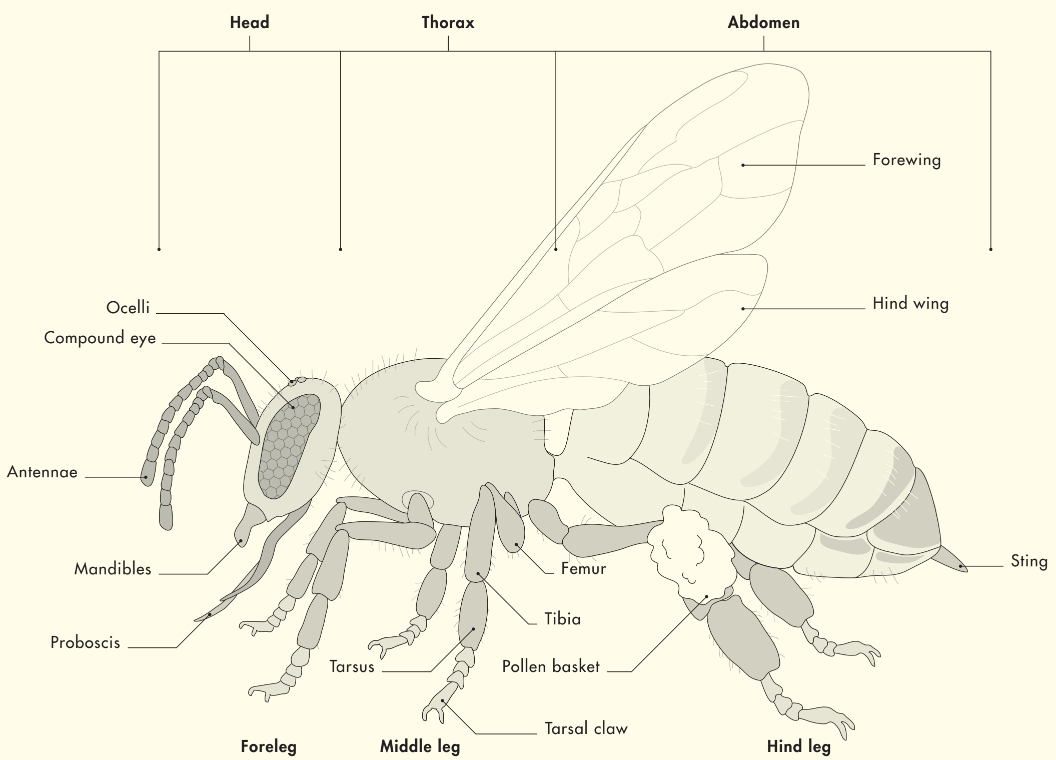
Alternatively, studies of the Asteraceae specialist, *Osmia californica* (a species of mason bee), found that its larvae can survive on pollen from other plant species, but larvae from a polylectic *Osmia* species (*Osmia lignaria*), or from wasps that parasitize *Osmia* nests, cannot develop well on Asteraceae pollen. Thus, these *O. californica* bees may be specializing not to obtain a particular nutritional content, but rather to avoid paratisization or competition with other bee species.

Pollen and nectar also contain plant compounds that can be toxic or beneficial to bees. For example, Common Heather (*Calluna vulgaris*) nectar contains the compound callunene, which reduces infections of a gut parasite (*Crithidia bombi*) in the Buff-tailed Bumble Bee (*Bombus terrestris*; see page 264), by causing the parasite to lose the structure (the flagellum) that anchors it to the bee's intestinal cells. In other cases, bees will mix pollen from different plant species in order to dilute toxins in the diets of their larvae.

Tools for collecting food

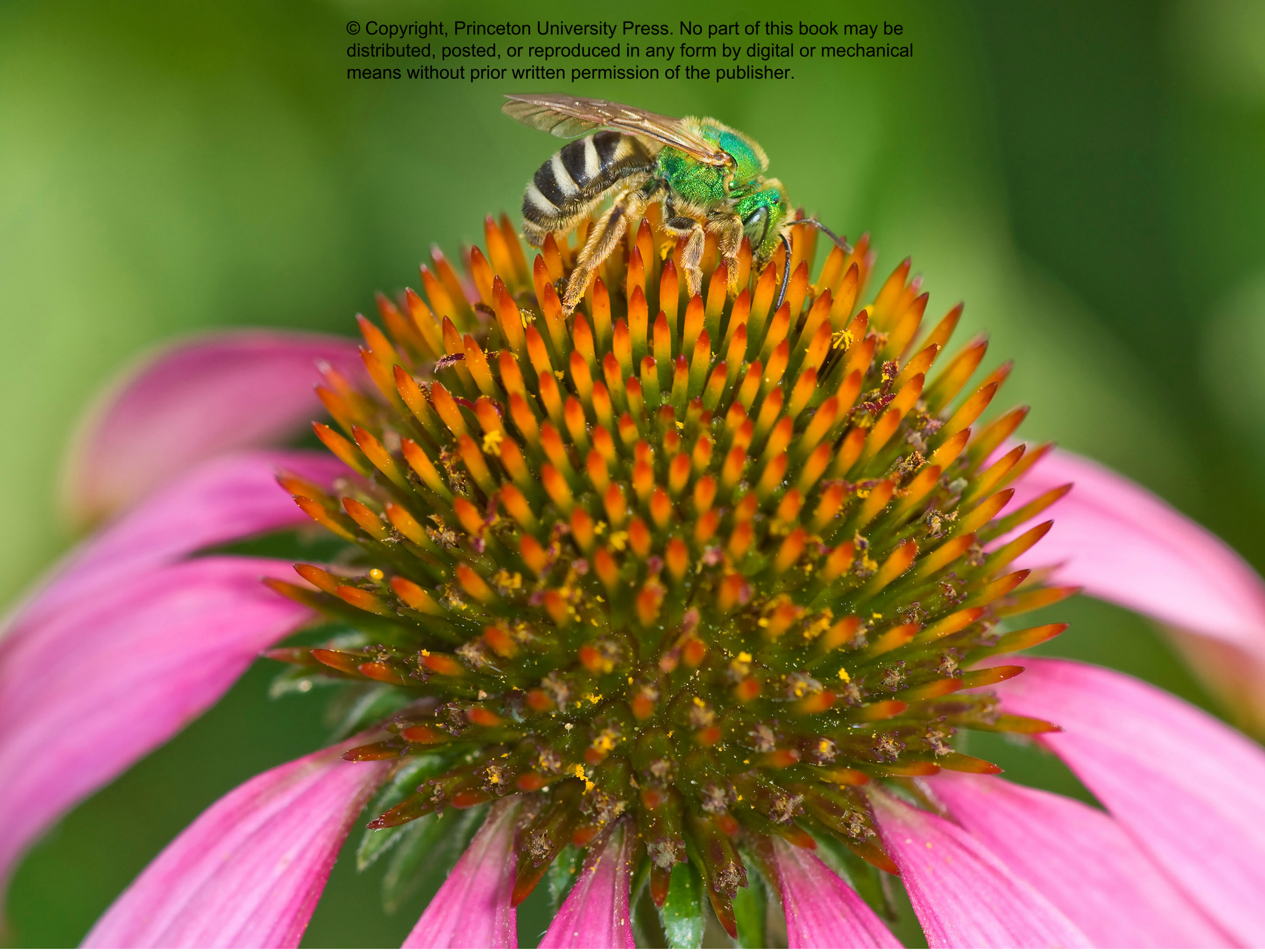
Bees have many physical structures to help them access the nectar or pollen from different plants, and efficiently collect and carry their food back to their nest. These structures include the proboscis, which allows them to collect nectar, and specialized hairs that allow them to collect and transport pollen or floral oils. Different bee species have hairs on different parts of their body, which allow them to efficiently collect pollen or oils from their preferred plant species.

ANATOMY OF A BEE



A typical corbiculate bee

Bees have many structures that allow them to detect and collect floral resources. Corbiculate bees (including honey bees, bumble bees, stingless bees, and orchid bees) have special pollen baskets on their hind legs.



↑ The open shape of the coneflower (*Echinacea*) means it is accessible to many different kinds of bees.

SHAPE IS KEY

For visiting bees, the shape and size of flowers and the position of their reproductive parts is all important. There is something of a lock-and-key relationship in the shape of flowers. The length and diameter of the corolla (made of petals) and calyx (made up of sepals) can determine which bee can access the floral rewards. For example, if a flower has a deep and narrow corolla, only a bee with a long tongue can reach the nectar at the bottom of the corolla. The internal arrangement of the male and female reproductive parts relative to the nectar and pollen rewards bees of the right size and shape in exactly the right place to receive pollen or pollinate the female stigma. The degree to which the shape of flowers accommodates many species, a few, or just one, is the subject of a great deal of research.

COLLECTING NECTAR

Most bees extract nectar from flower nectaries using their proboscis. Nectaries can be found in different parts of the flower. Petals can be folded, cupped, or curled to form nectar reservoirs in the base of an open flower. Many bee flowers have petal nectaries. Sepals, which in many flowers are green at the base of the colored petals, can be similarly modified to hold nectar. Stamens, which bear the male pollen and the male reproductive structures, can also have secretory nectaries. Often these are found at the base of the filament in the form of a tail or nectar spur. Gynoecial nectaries are associated with the ovary bearing carpel tissue that is found in the center of most flowers. Petal and sepal nectaries tend to be shallow and thus accessible to short-tongued bees, while staminal and gynoecial nectaries are deeper and more easily accessed by long-tongued bees.

The mouthparts of a bee are intricate and involve many movable structures that fold and unfold as needed. The proboscis (essentially the

→ A Green-eyed Flower Bee (*Anthophora bimaculata*) taking nectar and pollen from a Common Fleabane (*Pulicaria dysenterica*) flower. The pollen is clearly visible on its scopa.

↓ While the shape of a flower can make it more accessible for certain types of pollinators, bees can find ways to get nectar and pollen from a variety of different flower shapes. Here, a Western Honey Bee (*Apis mellifera*) is entering a flower with a deep corolla to reach the pollen and nectar inside.

tongue of the bee, see page 58) is a hardened, straw-like tube made up of intricately fitted labial palps at the posterior and galeae at the anterior. This tube can be folded back when not in use, making it easier for the bee to fly. Inside this tube is the hair-covered glossa, which automatically fills with hemolymph (analogous to blood) when a bee is presented with nectar (or when sugar is sensed)—not dissimilar to a child's party blower. The glossa expands out of the harder casing, acting as a dipstick. The watery nectar becomes trapped in the hairs and is pulled into the food canal inside the proboscis. Muscle attachments allow the bee to manipulate the exact positioning of the glossa to maximize nectar extraction even deeper within flowers.

In this way, sugar-rich nectar can be consumed directly. Foraging honey bees (*Apis* spp.) and some other bee species draw the nectar into a honey crop to transport back to the hive. The honey crop is located in the abdomen, just before the bee's digestive tract, and can take up half the abdomen when filled with nectar. The bee can consume the nectar or regurgitate it back at the nest into a wax cell to be chemically processed and dried by her sisters for long-term storage as honey.

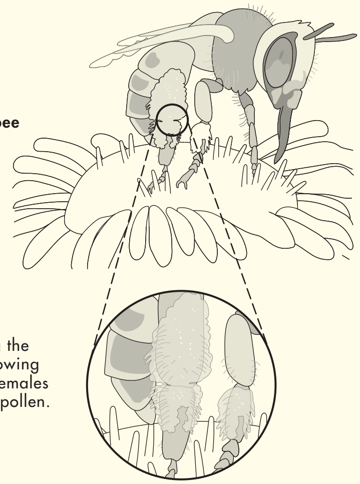
COLLECTING POLLEN

Bees have several physical adaptations to help them collect and transport pollen. Compared to wasps, bees generally have more hairs, to which the pollen attaches while they are interacting with the flower. Bees will groom and pack the pollen collected on their bodies onto specialized hairs called scopa. Different bee species carry the pollen on different parts of the body. For example, Alfalfa Leafcutting Bees (*Megachile rotundata;* page 84) collect pollen on scopa on the bottom surface of their abdomens, while sweat bees (*Agapostemon* spp.) collect pollen on scopa on the bottom surface of their legs. Corbiculate bees—which include honey bees, bumble bees, stingless bees, and orchid bees—have evolved special pollen baskets on their hind legs, which allow them to pack and transport large amounts of pollen. Cellophane bees (*Hylaeus* spp.) eat pollen and nectar and store it in their stomach, before regurgitating it to create the food provisions for their larvae.

POLLEN COLLECTION ADAPTATIONS

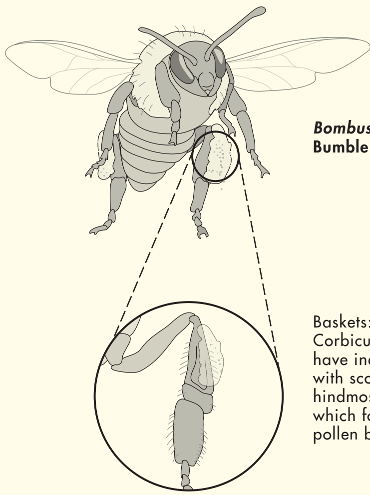
Female bees must collect large quantities of pollen from flowers and carry it back to their nests to feed their larvae. Different bee taxa have developed different strategies—and anatomical features—to carry pollen. In most bees, specialized hairs called scopa are used to keep the pollen attached to the body.

Anthophora
Burrowing bee



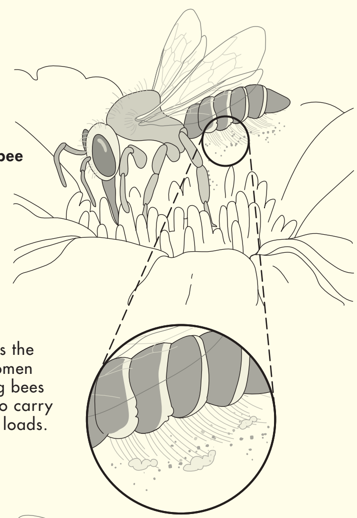
Hairy legs:
Scopa along the legs of burrowing bees allow females to transport pollen.

Bombus
Bumble bee



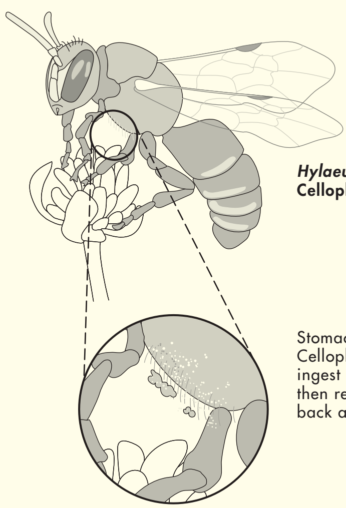
Baskets:
Corbiculate bees have indentations with scopa on their hindmost legs, which form pollen baskets.

Megachile
Leafcutting bee



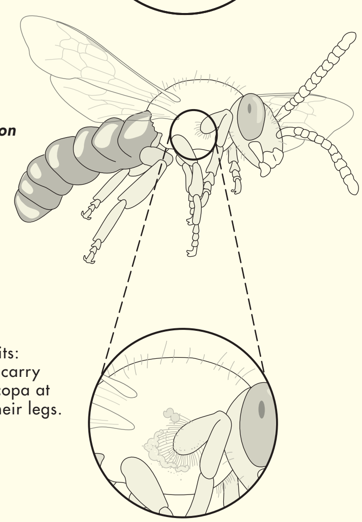
Hairy belly:
Scopa across the ventral abdomen of leafcutting bees allow them to carry large pollen loads.

Hylaeus
Cellophane bee



Stomach:
Cellophane bees ingest pollen and then regurgitate it back at the nest.

Agapostemon
Sweat bee



Hairy armpits:
Sweat bees carry pollen on scopa at the top of their legs.

COLLECTING OIL

Some plants produce oils as rewards. These oils are mixed with pollen to feed to offspring, or are used to line the bees' nest. To collect floral oils, bees also use hairs on their legs or abdomen. These hairs can be dipped into or rubbed against pools or layers of oil found on the flowers, to collect the oil by capillary action or by mopping. The position of the hairs on the body and the morphology of the flowers and its oil-containing sections coevolve so that specific bee species can collect oil from and pollinate specific plants. For example when the oil bee *Rediviva peringueyi* (page 82) visits *Pterygodium*, *Corycium*, and *Disperis* orchids, each orchid genera deposits its pollinaria at a different location on the bee's body, ensuring it is transferred to the female parts of the same orchid species. Similarly, when *Centris (Paracentris) brethesi* bees visit *Monttea aphylla* flowers to collect oil, they insert their forelegs into the corolla tube to soak up the oil. As the head inserts in the flower, the anthers deposit pollen on the underside of the head and between the forelegs. This area is difficult to groom, ensuring the pollen is transferred to the next flower.

↓ Female Dark-legged Yellow Loosestrife Bees (*Macropis nuda*) have specialized hairs on their hind legs to collect both pollen and oil from their preferred host plants, Loosestrifes (*Lysimachia* spp.).

Finding flowers

Flowers, the true gems of the biological world, have evolved marvelous design innovations to help bees and other pollinators find and remember nectar and pollen food resources in complex landscapes.

CONSTANT COMPANIONS

The uniqueness of flower types assures that, once identified as a good resource by a bee, a plant species will be the only one visited within a given time period, a behavior called "floral constancy." Therefore, pollen will only be transferred between plants of the same species. While wind-pollinated plants produce copious amounts of pollen that blanket the landscape in the hope of finding a plant of the same species, flowering plants have harnessed the behavior of bees, and other pollinators, for precision pollination.

For pollination biologists, the floral structure (see page 54) is a clue to which animal may pollinate the flower. Floral form is influenced by a number of factors. The anatomy of the animal, or groups of animals that are the most efficient pollinators, such as body size and

↗ To make sure the right pollinator finds and forages from them, flowers come in many shapes and sizes, with different colors and scents, and different types of nutritional rewards. Bee-pollinated flowers include *Agastache foeniculum* (A), *Echium vulgare* (B), and *Digitalis purpurea* (C). Fly-pollinated flowers include *Angelica sylvestris* (D). Butterfly-pollinated flowers include *Lantana camara* (E). Bird-pollinated flowers include *Campsis radicans* (F). Bat-pollinated flowers include *Mucuna holtonii* (G).

HOW DO BEES SMELL FLOWERS?

Bees and other insects can detect chemical odors through sensory neurons found in their antennae, mouthparts, and legs. Generally, the sensory neurons in the antennae detect odors that are volatile—they disperse easily in the air—while the mouthparts and legs detect chemicals through direct contact. Thus the antennae can "smell" while the mouthparts and legs can "taste." In the antennae of bees, the sensory neurons are underneath circular plate sensilla that indent the surface; small holes in these allow the odor molecules to pass through and bind with these neurons. Thus, the chemical signal is changed into the electrical signal language of the brain.

Given the wide diversity of scents in the world, how do bees detect them all? Bees, like other animals, including humans, use a "combinatorial code"; they have a number of different receptors (60 have been found in honey bees), and each receptor can detect multiple odor molecules. A single odor activates a set of different receptors and receptor neurons, and different odors activate various combinations of receptors. Thus, bees are able to detect and learn single odors or blends of odors because they activate a distinct combination of receptors compared to other odors.

The olfactory systems of different bee species may be "tuned" to be more sensitive to odors produced by their preferred plant species. For example, studies of *Andrena vaga*, a specialist on willow (*Salix*) plants, found that this bee had a much greater neuronal response in its olfactory system to a *Salix*-specific odor, 4-oxoisophorone, than the generalist Western Honey Bee (*Apis mellifera*) did.

→ Willow (*Salix*) flowers are a favorite of the Grey-backed Mining Bee (*Andrena vaga*).

tongue length, influence the size of the flower and the depth of the nectary. Bees tend to favor medium-sized flowers with relatively long corolla tubes. Floral scents and colors help pollinators locate and remember flowers in a complex environment. They also learn how to handle specific flower types to be efficient in gathering rewards.

Bees generally prefer blue to purple flowers with sweet floral scents and medium nectar concentrations. Since bees have a limited ability to see in the red range they tend to avoid these flowers, many of which are instead pollinated by birds. Bees in most parts of the world are active from the morning to midday and their flowers bloom at this time. But it is important to remember that environmental context, competitors, and floral availability will influence which flowers bees visit. Although bee species have innate preferences, they are also excellent at learning so are able to exploit resources of plants that they have not coevolved with.

SCENT

Bees live in a chemical world. Sensory neurons on their antennae and mouthparts can detect tens of thousands of chemical compounds. Flowers produce particular bouquets of scents to attract their most efficient pollinators, often from a distance. They can also emit repellent compounds to dissuade non-pollinating visitors. To further increase efficiency, floral scents are emitted when their pollinators are most active. Flowers that attract bees have scents that are often described as sweet, fresh, and pleasant. In contrast, flowering plants that attract flies as their pollinators usually have floral scents that smell quite putrid, like rotting meat, offering a scent to which the flies are already more sensitive and responsive.

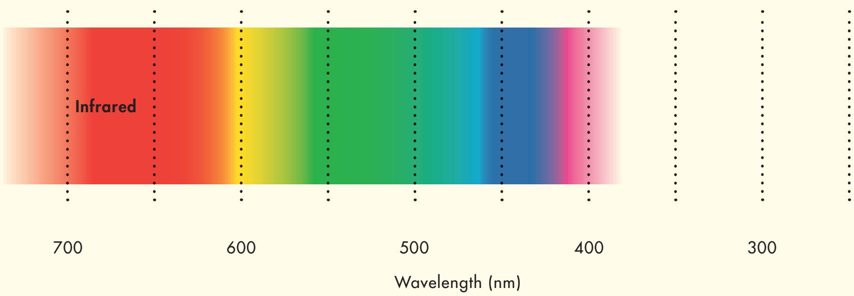
CAN YOU SEE WHAT I SEE?

Unlike humans, bees can see into the ultraviolet range, though with a limited ability to see red (most red flowers have evolved to attract birds, butterflies, and other pollinator species). It is clear that many bees have an innate preference for particular colors. For instance, honey bees and bumble bees will innately prefer a particular blue-purple, found in flowers such as Meadow Sage (*Salvia pratensis*), Viper's Bugloss (*Echium vulgare*), and Hound's Tongue (*Cynoglossum officinale*).

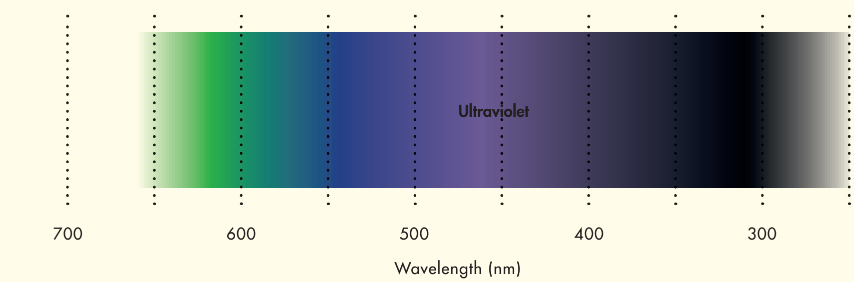
Human vision

Bee vision

HUMAN VISION



BEE VISION



↖↖ Western Honey Bee (*Apis mellifera*) foraging on Meadow Sage (*Salvia pratensis*) flowers.

↖ A sunflower viewed under natural light and ultraviolet light, showing the difference between human and bee vision.

↗ Bumble bees innately prefer blue-purple flowers, such as this thistle.

Ultraviolet vision

Bees see a different range of the color spectrum than humans do. Their vision is shifted to the ultraviolet wavelengths. Many flowers have ultraviolet patterns that are invisible to the human eye, but which help the bees find the nectaries in the flower.

In studies conducted in Germany, plant species with flowers of this color seem to produce a higher-quality nectar reward than co-flowering plant species with different-colored flowers, suggesting an adaptive relationship. But bees have a great potential to learn, allowing for ecological flexibility in which flowers they visit.

These color preferences can vary in individual bees and among bee populations. This can allow for individuals from the same species to take advantage of different resources in the same landscape, or allow for populations to evolve to become adapted to locally available resources. For example, among bumble bee species—populations of the same species and different nestmates within a colony—there can be variations in the degree to which they prefer blue-purple versus red flowers. This variation has been associated with differences in foraging efficiency, where colonies with greater blue-purple preference perform better in landscapes where there are more rewarding blue-purple flowers. Interestingly, the Giant Patagonian Bumble Bee (*Bombus dahlbomii*; see page 266) may have evolved to perceive red.

Cognitive ecology of bee foraging

Bees require complex cognitive skills to efficiently collect floral resources. First, bees need to be able to effectively explore the landscape to locate rewarding flowers. They then need to learn and remember where a rewarding flower is, when the flower is providing nectar and pollen (since flowers can open at different times of day), and how to access its nectaries or anthers. When a flower's resources have been depleted or a plant stops blooming, the bee needs to learn to stop visiting these flowers.

FORAGING STRATEGIES

Bee species use a variety of strategies for searching the surrounding landscape for flowering resources. Some bee species, such as bumble bees, honey bees, and orchid (*Euglossine*) bees, use "traplining," where they follow the same route every day to visit the same set of flowering plants, as a human trapper would examine their traps along a same route every time. This behavior allows the bees to obtain floral resources more efficiently, since they find the shortest route, learn and remember how to handle the flowers to obtain these resources, and can visit the most resource-rich plants first. Moreover, many flowering plants release their pollen over several days. If one of the flowering plants on the trapline ceases to flower, the bee will continue to visit the plant for several days (a hallmark of traplining behavior). Studies with bumble bees have suggested that traplining is particularly effective if floral resources are limited or hard to find.

Social bee species have developed a number of behaviors to recruit nestmates to flowering plants. Some stingless bee species, such as *Trigona recursa*, lay a scent trail by marking the flowering plant and plants found along the route to the flowering plant from the nest with pheromones. The stingless bee *Melipona panamica* (see page 86) recruits nestmates to food resources using the scent of the floral resource, sound signals within the nest, and directional (zig-zag) flights outside the nest.

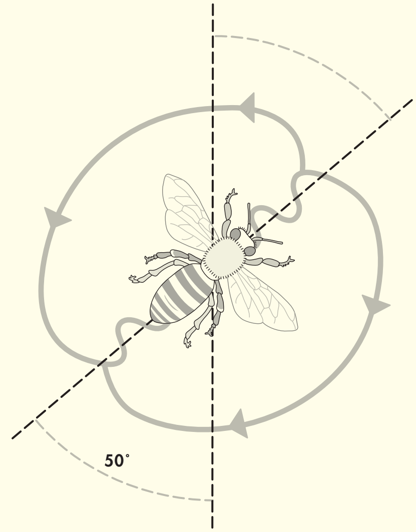
↑ A sleeping habit shared with many other solitary bee species that don't have a hive to return to at night, this orchid bee (*Euglossa* spp.) passes the night suspended in the air by biting into a leaf in Utría National Natural Park, Colombia.

← Euglossine bees approaching orchid flowers (*Gongora leucochila*) located on their traplining route in Gamboa, Panama.

DANCE LANGUAGE OF HONEY BEES

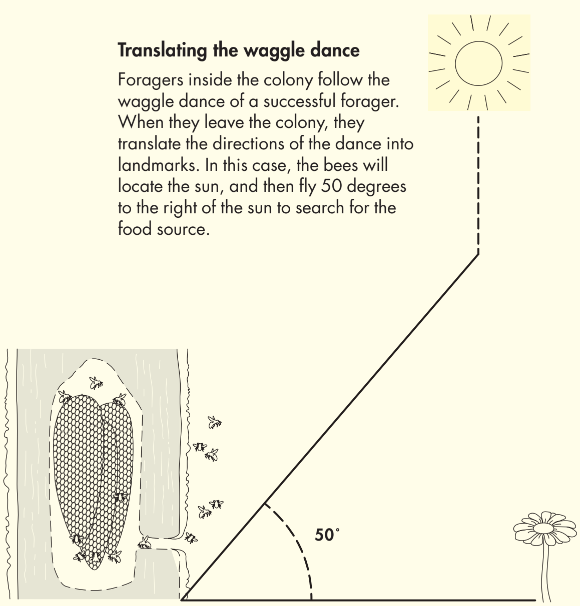
Honey bees use a symbolic language to communicate information. A foraging honey bee that finds a highly rewarding food resource can recruit her sister foragers to it through this dance language. The behavioral biologist Karl von Frisch received the Nobel Prize in 1973 for elucidating the basic components of this dance language; subsequent research has continuously revealed new insights into how this language is generated and interpreted by honey bees.

When the successful forager returns to the colony, she will perform a dance on the honeycomb. The nearby bees will orient toward the dancing forager, touching her with their antennae and following her through the dance. If the foraging resource is nearby (less than 160 feet/50 m) the bee will perform a "round dance," where she dances in a circle and changes direction between the dance "runs." If the foraging resource is further away, the bee will perform a "waggle dance" in the shape of a sideways figure eight.



Waggle dance

Western Honey Bees (*Apis mellifera*) will dance in a figure-eight pattern on the surface of the honeycomb. The central "straight" run of the dance is angled to the vertical axis according to where the food source is relative to the sun. Here, the bee is dancing 50 degrees to the right of the sun.



Translating the waggle dance

Foragers inside the colony follow the waggle dance of a successful forager. When they leave the colony, they translate the directions of the dance into landmarks. In this case, the bees will locate the sun, and then fly 50 degrees to the right of the sun to search for the food source.

In the middle part of the figure eight, the bee will waggle her abdomen vigorously from side to side.

The waggle dance provides information on the direction, distance, and quality of the food resource. The direction of the middle part of the dance indicates the direction of the food source from the colony entrance, relative to the sun. The duration of this waggle run—how many milliseconds it takes the bees to complete it—provides information about the distance to the food resources. The quality of the food resource is provided by the time it takes for the bee to return to the middle part of the dance from the side loops of the figure eight, and how often she waggles her abdomen during the middle part of the run.

→ Western Honey Bee (*A. mellifera*) performs the waggle dance on a honeycomb to communicate the location of flowering plants with nectar and pollen to other colony members.

(continued...)

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