Arizona-Sonora Desert Museum

Bees

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Photo by Glenn Seplak

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Current Edition: **November, 2021**

Previous Edition(s): 2010, 2013

Bees

Goals & Objectives

- To illustrate the vital ecological role that bees play within the Sonoran Desert region, especially their role as pollinators
- To develop a basic understanding among our visitors of pollination and its human significance
- To familiarize visitors with morphological and behavioral characteristics that make pollination biology a fascinating subject
- To show the great diversity in bee speciation and lifestyles in the Sonoran Desert region
- To show examples of social and nesting behaviors different from honey bees

Classification

Kingdom: Animalia
Phylum: Arthropoda
Class: Insects
Order: Hymenoptera
Families: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae
Sonoran Desert Bioregion Genera: *Agapostemon, Ancyloscelis, Andrena, Anthidium, Anthidiellum, Anthophora, Anthophorula, Apis, Ashmeadiella, Augochlorella, Bombus, Calliopsis, Conanthalictus, Caupolicana, Ceratina, Centris, Coelioxys, Colletes, Diadasia, Dufourea, Epeolus, Eucera, Exomalopsis, Halictus, Hylaeus, Lasioglossum, Megachile, Melecta, Melissodes, Melipona, Neolarra, Nomada, Nomia, Osmia, Panurginus, Peponapis, Perdita, Protoxaea, Pseudopanurgus, Sphecodes, Stelis, Svastra, Tetraloniella, Trigona, Triepeolus, Xenoglossa, Xeromelecta, Xylocopa*

Spanish names: *abeja* (bee), *jicote, abejorro* (bumblebee, carpenter bee)

Introduction

Welcome to the "Bee Capital of the United States." There are over 20,000 bee species in the world with more to be described. There are about 4,000 species of bees in the United States and there may be as many as 1,300 species of bees in Arizona. The Sonoran Desert Region has one of the richest bee faunas in the world with an estimated 700-800 species.

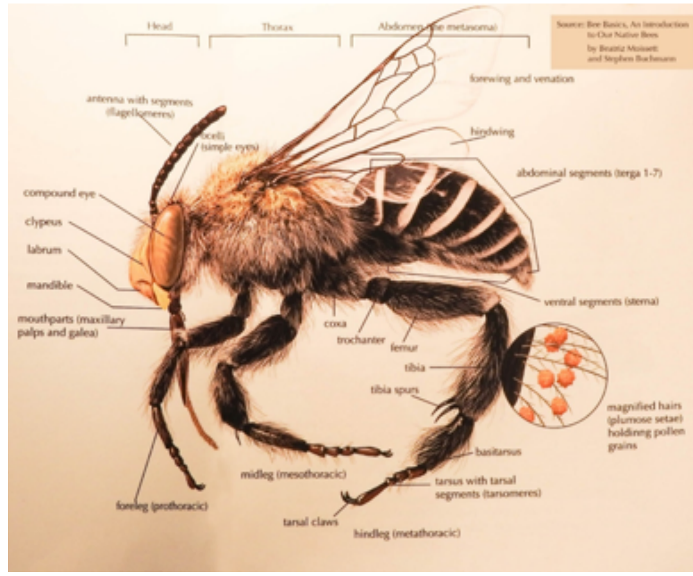
Taxonomy

Bees comprise a highly diverse group of hymenopterous insects that are closely related to four families of parasitic and predatory wasps known as hunting wasps, Heterogynaidae, Ampulicidae, Sphecidae and Crabronidae. Until recently it was thought that bees were a sister group to all four of these hunting wasp families. Now, there is strong evidence that bees are actually highly derived descendants of wasps in one of the families, the family Crabronidae (subfamily Pemphredoninae) that hunt pollen-collecting thrips (fringe-winged insects). See Danforth, et al. (2019) for an in-depth discussion of this relationship. Bees, together with ants and wasps form a natural group referred to by taxonomists as the aculeate, or "stinging" Hymenoptera; the stinger is called an aculeus. Only females sting, since the aculeus evolved from the ovipositor or egg-laying tube.

Most bees have solitary lifestyles in which females act alone to construct and provision nests, but there are also social forms, such as the familiar black and yellow bumblebees (aka bumblebees, bumble-bees, or humble-bees). Most of our native solitary bees nest in holes in the ground dug by a single female or in preexisting holes such as the abandoned tunnels left by wood-boring beetles. In contrast to wasps that are carnivorous, bees are herbivorous and feed on pollen, nectar, and oils offered as floral rewards by flowering plants. Solitary bees reach their highest diversity in arid regions of the world, such as the Sonoran and Chihuahuan Deserts of western North America.

Sonoran Desert bees range in size from one of the smallest bees in the United States, *Perdita minima,* which is less than .08 inches (2 mm) to carpenter bees (the genus *Xylocopa),* gentle giants that may have body lengths of one inch or a little more (25 mm) and weigh over a gram. The following photo of *Perdita minima* superimposed on the head of a large carpenter bee is included in the kit materials.

Morphology



Like all insects, bees have three body parts: a head, thorax and abdomen. The head features a pair of compound eyes, three simple eyes, two antennae (12 segments in females and 13 segments in males) and mouthparts. The thorax has two pairs of membranous wings and three pairs of legs. In flight, the wings are connected by small hooks located on the leading edge of the hind wing. The abdomen is divided into segments, six segments in females and seven segments in males.

Superficially, bees (especially the parasitic cuckoo bees) resemble some wasps, except that bees are usually hairier, more robust, have stout legs with few spines and they possess specialized structures for carrying pollen back to their nests. Unlike wasps, bees have hairs that are branched somewhere on their body. Bees also resemble some flies. However, bees have long slender antennae, four wings and pollen-collecting hairs on the legs or abdomen. These bee-like flies have short antenna, one pair of wings and no pollen collecting hairs. There is a graphic in the kit that explains the differences between bees, wasps, and flies.

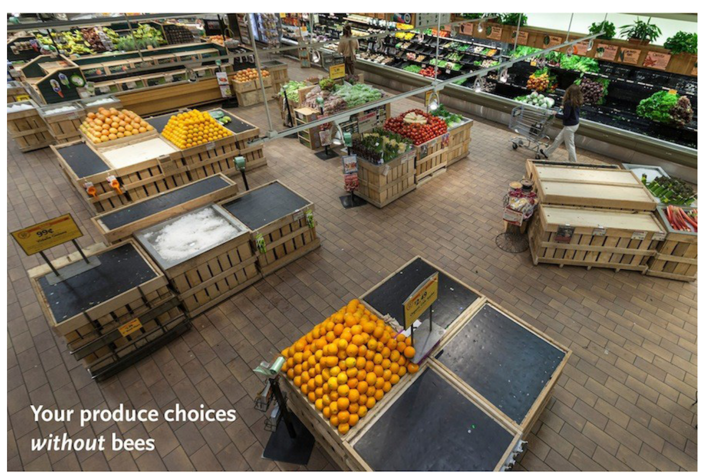
Ecology

Bees live in almost all terrestrial habitats within our region. Except for the cleptoparasitic "cuckoo bees," female bees make their living by foraging in search of protein-rich pollen and sugary nectar from flowering plants. By moving pollen around from flower to flower and plant to plant, bees perform vital and often unappreciated roles as the most important group of pollinating animals on earth. Of the approximately 640 flowering plant taxa growing in the Tucson Mountains near the Desert Museum, approximately 80% of these species have flowers adapted for and pollinated by bees. Similarly, 80% of crops benefit from insect pollination and about 35% of global food production requires animals, primarily bees, to move pollen between flowers. The following photo shows produce in a grocery store with and without bees. This photo is included in the kit materials.

Not only are we dependent upon bees for about a third of our food, but for other products as well. Cotton cloth is a product that eventually results from bee pollination, and so are many beverages, medicines and nutraceuticals made from other fruits and seeds. Without the pollination services bees provide, many plants would not produce seed-laden fruits from which the next generation of plants would grow. Without bees, there would be few or no fleshy berries or fruits to sustain birds, mammals and other wildlife.

Flowers attract bees by both color and scent. Brightly colored petals provide a sharp contrast to the background, making them visible and attractive to foraging bees. The spectrum of colors visible to bees is at the blue end so they are sensitive to ultraviolet light. Bees are particularly attracted to blue, green, yellow and orange. Bees are red-blind. However, because some red flowers reflect ultraviolet light they may also attract bees. Scent is another way flowers attract bees. Flowers have special glands, usually on the petals that produce and secrete attractive scents.

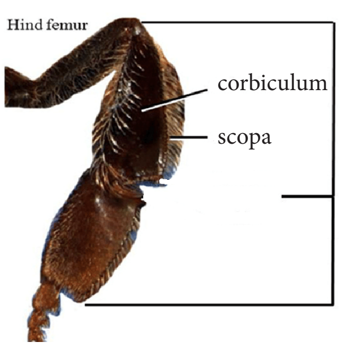
The male, pollen-producing parts of the flower, the anthers, are situated around the female part, the central stigma. When a bee arrives with pollen from a flower of the same species, and moves around collecting more pollen, she will transfer pollen grains to the stigma. A pollen grain will germinate and form a microscopic pollen tube that extends down the stigma into one of the ovaries where one of the sperm nuclei combines with an egg nucleus, completing fertilization.



The role of bees as pollinators is unquestioned. Yet bees are not out to "help" flowers. In their daily quests, bees harvest foodstuffs from flowers for themselves and their larvae. Pollen is a rich food source of amino acids, proteins, fatty acids, vitamins, minerals and carbohydrates. Bees have numerous hairs on the body and when the bees fly, the hairs become electrostatically charged. When a bee visits a flower, the anthers release pollen that adheres to the charged body hairs. Pollen scattered among the body hairs is not of much use to the bee. Consequently, bees use their first two pairs of legs to transfer the pollen on their body to special structures where it is concentrated before going back to the nest. Most solitary bees carry compacted pollen in the **scopa,** a patch of modified hairs on the hind leg. Bees in the family Megachilidae have scopa on the underside of the abdomen and some bees have scopa on the sides of the thorax. Honey bees, bumblebees, and stingless bees have a pollen basket called a **corbiculum** on their hind legs. This structure is formed from the concave surface of the tibia, which is fringed in stiff hairs. It is adapted for transporting pollen moistened with nectar.


Honey bee showing corbiculum without pollen (the corbiculum is on the longer segment of each hind leg that has a shiny concave surface fringed with stiff hairs), (Photo by Glenn Seplak)

Hind leg of a corbiculate bee



https://www.researchgate.net/figure/Hind-leg-of-a-corbiclate-bee-showing-the-corbicula_fig1_320532101


Honey bee with corbiculum loaded with pollen (Photo by Glenn Seplak)


Solitary bee with pollen in the scopa on the hind leg (Photo by Glenn Seplak)


Megachilid with pollen on the underside of the abdomen (Photo by Glenn Seplak)

The anthers of some plants are tubular and have apical pores, e.g., legumes in the genus *Senna* and plants in the genus *Solanum*. These plants do not readily release pollen and require **buzz pollination**. Bumblebees, carpenter bees and several species of solitary bees will grasp the pollen containing flowers and turn themselves into living tuning forks by rapid fire contractions of their flight muscles. The vibrations release the pollen from the anthers in an explosive cloud, some of which is deposited on the bees, and subsequently transferred to other plants. The audible buzzing sound made by bumblebees when they are buzz-pollinating is different from that when the bees are in flight. The fundamental frequency of each buzz is typically around middle C and ranges from 200-400Hz. About 8% of the world's 250,000 species of flowering plants have anthers with apical pores and require buzz pollination. Crop plants that are buzz pollinated include tomatoes, blueberries, cranberries, chili peppers, and eggplants. There is a tuning fork in the kit that you may use to demonstrate buzz pollination. **A word of caution:** The tuning fork in the kit is in the key of A not C. A visitor with perfect pitch may point this out to you.

Most flowers provide nectar as a reward. Nectar is a liquid solution of sugars, mostly sucrose, fructose and glucose that is produced in glands called nectaries, which are usually located at the base of the petals. Nectar provides the energy boost that bees need to fly and carry out their other activities, and is mixed with pollen as food for bee larvae. In *Bees of the World* (O'Toole and Raw, 1999), the authors describe bees as being very energy efficient and provide the following comparison: *"a female worker honey bee has a fuel consumption of 700km/cc—or in more familiar car-owner terms, 2 million mpg!"*

Some desert bees *(Centris)* have specialized scrapers on their legs for harvesting oils from glands on the undersides of flowers in the ratany and malpighia families. These energy-rich oils are mixed with pollen or with pollen and nectar as larval food and are also used to help construct brood cells. Danforth et al. (2019) describe female bees as *"flying tool kits with combs, mops, sponges, rakes and brushes"* on their legs for handling pollen and floral oils.

In addition to the important role bees play as pollinators of flowering plants, they play other important environmental roles. The tunneling activity of ground nesting bees aerates the soil and allows water from infrequent rains to quickly penetrate and reach plant roots. The bees' nitrogen-rich feces fertilize the soil. The bees themselves are an important part of the food chain and provide food for many animals.

Predators and Parasites of Bees—Some predators, such as assassin bugs, crab spiders, ants, robber flies, beewolves (a wasp) and birds prey on foraging bees. Others such as woodpeckers, lizards, armadillos, mice, skunks, weasels, badgers and voles will attack and consume bee larvae and adults in their nests. There are a number of parasitoids that attack and kill bee larvae or adults. Parasitoids are a type of parasite that gradually consumes its host, ultimately killing it. Bee parasitoids include big-headed flies, bee flies, satellite flies, mutillid wasps ("velvet ants"), jewel wasps, blister beetles and wedge-winged beetles. Some brood-parasitic wasps and flies kill the host bee egg or larva and then consume the pollen/nectar provisions but not the host egg or larva. There are also flies that don't attack the host bee egg or larvae but feed on the pollen/nectar provisions. And finally, there are the rather bizarre twisted-winged insects that are endoparasites of a wide variety of hosts including bees, ants and wasps. See Danforth et al. (2019) and Wilson and Carril (2016) for more information on the various predators and parasites of bees.

Life History

Solitary Bees—The majority of the earth's bees are solitary (>75%). Each female selects a site for her nest, constructs and provisions brood cells with pollen and nectar, and lays a single egg within each cell. This behavior is called “mass provisioning,” since the mother bee collects and prepares at one time all the food each developing larva will need to complete its life cycle from larval stages to pupa and finally, through complete metamorphosis into a newly emerged adult. After laying an egg in each cell, the solitary female has no further contact with her progeny. Solitary bees essentially live alone. However, some solitary bees nest communally, with several female bees sharing the same nest entrance. Inside the nest tunnel, each communal-nesting female bee has her own nest cells that she prepares for her eggs.

Solitary bees typically have but one generation per year, with adults usually emerging with the spring or summer flower blooms. Solitary bees have both broad and narrow host-plant preferences. Adult males and females mate soon after emergence from their natal cells. Females construct and provision the nests with pollen and nectar and then lay eggs. The adults are short-lived, usually just a few weeks to a month. The period of adult activity coincides with flower availability, which for plant specialists may be very narrow. The egg stage is the shortest stage in a bee’s life, with eggs hatching typically within hours of being laid. The grub-like larvae go through five stages. The first stage larvae don’t feed on the pollen and nectar provided by their mother. Molting of the first stage larva occurs in the chorion of the egg and both the first larval skin and chorion are shed at the same time. Larval stages two through five are the stages that actively feed. In most solitary bees larval development is rapid and feeding is usually completed in one to three weeks. The last larval stage is called the prepupa. The prepupa may undergo a long diapause that may last almost a year and would include the cooler months of fall and winter. The prepupae of some bees will spin a silky, water-resistant cocoon around themselves that provides protection against desiccation and from attack by predators and parasites. Hormones trigger the change from prepupa to pupa, the last stage of an immature bee. Bee pupae look very similar to the adult except that the wings are greatly reduced and the fuzzy hair of an adult bee has not appeared. The pupal stage is relatively short, usually one to two weeks, and soon the fully developed adults appear and chew and dig their way out of the nest. Some solitary bees may have more than one generation per year and in some bees it is the adults that overwinter, not the prepupae.

The vast majority (70%) of solitary bees dig tunnels in the ground for their brood cells. There is a lot of variability in the structure of a ground-nesting bee nest; however, a typical nest has a vertical tunnel with lateral tunnels ending in brood cells. Most ground-nesting bees make multi-celled nests but some species make nests with a single cell. Nests may be on flat ground or in a vertical clay or sand bank. The brood cells of ground-nesting bees can be just a few inches deep or six or more feet down in sandy soils. Most ground-nesting species smooth the brood cell wall and line it with waxy or cellophane-like secretions produced by glands within their abdomens. This lining waterproofs the cells, maintains humidity, and keeps organisms like fungi from destroying food and developing larvae. In some bees the tunnels are also lined with these materials. The Bee Kit has a Riker mount showing a typical ground-nesting bee nest.

Some of our Sonoran Desert solitary bees routinely nest with other females in very large aggregated nest sites. However, each female constructs her own nest tunnel and brood cells. The largest aggregations are found in ground-nesting bees such as our common cactus bee *(Diadasia rinconis),* which pollinates prickly pear, cholla, and saguaro cacti. Aggregations of this bee during the spring cactus bloom may number in the hundreds or thousands of individual nests over an area the size of two or three tennis courts.

Many ground-nesting bees, particularly species that nest in large aggregations, construct freestanding turrets at the nest entrance as shown in the previous photo. The entrance to nests located on banks may be concealed by a down-slanted chimney made of mud. Several possible functions have been attributed to the turrets, including 1) the prevention of soil and sand from falling into the entrance, 2) providing a barrier to flooding, and 3) creating an obstacle to parasites. Some turrets are impregnated with glandular secretions that may aid in nest recognition in species that nest in large aggregations. The down-slanted turrets of nests constructed on vertical banks may aid in thermoregulation as these nests were found to be warmer than nests without these turrets. This enabled female bees in nests with turrets to begin foraging 15-30 minutes earlier than bees in nests without turrets.

Other native solitary bees don't bother excavating their own nest tunnels. Instead, they actively search out preexisting holes such as the abandoned exit holes and tunnels of wood-boring beetles (usually buprestids and cerambycids) in dead limbs or standing dead trees. Preexisting nest sites might also include, pock marks in rocks, tiny holes in bricks, cracks in wood, or even snail shells. Some solitary bees construct free-standing, above-ground nests, while other bees build nests on exposed surfaces such as a vertical wall. Once a suitable nest site is found, females use a variety of different materials to construct brood cells, such as cut pieces of leaves, fluffy plant down, plant resins, pebbles or mud.

The greatest diversity of solitary bees occurs in arid environments. Several reasons for this have been proposed. One possible reason is because most solitary bees are ground nesting and do better in well-drained, sandy soils that don't allow fungi to invade and overcome their brood cells. Danforth et al. 2019 (Reference 6) believe that a more important reason is because solitary, univoltine (one generation/year), host plant specialists may be ideally suited for desert environments where flowering occurs over a very short period of time. Solitary bees can time their emergence to correspond with the peak flowering of their host plant and can delay emergence to avoid mortality when conditions are not suitable, such as in drought years. This gives solitary bees an advantage in desert environments where rainfall is rare and unpredictable.

Social Bees—Danforth et al. (2019), describe three features of female social bees that distinguish them from solitary bees:

1) "Social taxa exhibit reproductive division of labor, meaning some females reproduce (usually described as "queens"), and others build and defend the nest and gather pollen and nectar for the developing offspring (usually described as "workers").
2) Social taxa exhibit cooperative brood care (or alloparental care), meaning females help rear offspring that are not their own.
3) Sociality typically involves overlap of generations such that females are long-lived, and mothers and daughters occupy the same nest for an extended period of time."

These authors divide social bees into two principal groups:

Cooperatively Breeding Bees—The wood-nesting carpenter bees exhibit a form of sociality called "cooperative breeding." Mothers and daughters remain in the nest for an extended period of time and there is a reproductive division of labor. The mother does most of the reproduction and the daughters serve as non-reproductive guards or foragers. This differs from true eusociality, because the association between mothers and daughters is temporary. The mothers will eventually die while their reproductively active daughters remain in the nest.

Eusocial Bees—Eusocial taxa exhibit a reproductive division of labor, cooperative brood care, and overlap of generations. Unlike cooperatively breeding societies, the reproductive division of labor and caste status of an individual remains constant over their lifetime. The only advanced eusocial bee in our immediate area is the honey bee. Honey bee queens do not resemble the workers and can't survive without them. New colonies are established by swarming, with the queen and large numbers of workers leaving the nest together. In addition, honey bees have advanced communication and their colonies are huge with several thousand members working together. Farther south in Sonora, Mexico (near Alamos), advanced social bees live in colonies with many thousands of individuals—the so-called "stingless bees." In contrast, bumblebees and some bees in the family Halictidae are considered to be primitively eusocial. The queens of these bees differ from workers only in body size and are capable of surviving on their own. In fact, they build the founding nest by themselves. They do not have advanced communication and their colonies are much smaller.

Social bees always have more than one generation per year and usually have broad host plant preferences compared to solitary bees. The highly advanced social bees in the tribes Apini and Meliponinae have their highest diversity in the humid tropics, while as noted above, the greatest diversity of solitary bees occurs in arid regions. The advanced eusocial bees that flourish in the tropics require floral resources that are available long enough for them to rear multiple worker broods.

There are some species of bees in the family Halictidae that are socially polymorphic, i.e., some populations are solitary and some are eusocial. Populations typically vary depending on latitude or altitude. Populations at higher latitudes or altitudes tend to be solitary while populations at lower latitudes or altitudes are eusocial.

Cleptoparasitic Bees—Approximately 13% of the world's bees have developed the parasitic habit, and almost all are found in three families, Apidae, Halictidae, and Megachilidae. Parasitic bees are called cuckoo bees because of the similarity to the female European cuckoo bird, which lays her eggs in the nest of another bird species that then raises only young cuckoos. Cuckoo bees are technically referred to as cleptoparasites or brood parasites. In this document the terms cleptoparasite, brood parasite and cuckoo bee are used interchangeably. *Clepto* means "thief" in Greek; therefore, a cleptoparasitic bee lives off another bee by stealing its food. Female cleptoparasitic bees may be recognized from other bees because they have a wasp-like appearance, fewer body hairs, and lack structures to transport pollen. They are also more heavily armored with spines, ridges and crests to protect themselves from attacks by host females.

Female cleptoparasites enter the nest of a pollen and nectar-collecting host bee and deposit one or more eggs in a fully or partially completed nest cell. The eggs may be laid next to or on the pollen/nectar provisions, but egg placement is variable. Sometimes the eggs are hidden in or on the nest wall away from the provision mass. The eggs or larvae of the host bee are killed by either the adult brood parasite or her larvae. Then, the brood-parasitic larvae feed on the provisions (pollen/nectar mass) of the host bee. Danforth et al. (2019) describe three ways that brood parasitic female bees in the families Apidae and Megachilidae attack the nest of a host bee:

- Females enter the nest of a host bee, open a closed, fully provisioned nest cell, kill the host bee's eggs or larvae with their mandible or sting, and then deposit an egg and seal the cell.

- Females lay an egg through a small opening in a closed cell and the host female closes the cell. Since the female parasitic bee doesn't kill the host egg or larva, one or more stages of the female parasite's larvae do the job. The first instar parasitic larvae of some species have modified mandibles that are used to kill the host bee's eggs and larvae.

- Females lay their eggs in open, partially provisioned cells of the host bees. The eggs are laid directly into the cell wall or on or within the pollen/nectar mass. The parasitic larvae use sickle-shaped mandibles or projections on the labrum for killing the host eggs and larvae. The largest number of brood-parasitic bees fall into this category.

There are some bees that are social parasites. These bees enter the nest only of social bees and kill or replace the host female as the primary egg layer.

Family Andrenidae

Andrenidae is a large family of nearly 3,000 described species, with greatest diversity in arid western North America, South America, and the Palearctic. All andrenids are solitary, but some nest in large aggregations, usually where vegetation is sparse, while others are communal and share the same nest entrance. Andrenids are "short-tongued" bees and can be identified by the two grooves below the antenna called subantennal sutures. There is one on each side of the antennal socket. Bees in this family are often called mining bees because they nest in the ground. Some nest in shallow tunnels just an inch or two below the surface, while others dig a long, branching tunnel in the soil, the entrance to which has a small mound of excavated earth called **tumulus.** Andrenid females either line their nest or cover their pollen balls with a waterproofing substance that protects the developing larvae from soil moisture and bacteria. Andrenids are important pollinators, visiting many different plants.

Four genera of Andrenids are represented in the kit *Andrena, Perdita, Calliopsis,* and *Pseudopanurgus.* Eighty percent of Andrenidae are in two genera, *Andrena,* with over 1500 species in the world and *Perdita* with over 650 species described, all in North America.

Andrena has about 550 species in the United States. *Andrena* are among the first bees to become active early in the year and might be considered a harbinger of spring. They are particularly cold hardy and can fly when their body temperature reaches 50-60 degrees F. This makes them very good pollinators of plants that bloom early in the season, before honey bees become active. Most *Andrena* are host-plant specific and the preferred plants are in a number of different families. *Andrena* are important pollinators of blueberries, cranberries, and apples.

Perdita are minute bees that are often brightly colored. Included in this genus is one of the smallest bees in the world, *Perdita minima,* which measures about .08 inch long, and is active in the Sonoran Desert during July and August. Other species are scarcely larger. Most species are floral specialists and their activity period coincides with the flowering of their particular plant. One small species, *P. hurdi,* pollinates the flowers of some species of Devil's Claw (Proboscidea), but it does so in an odd manner. The pollen ripens before the flower opens. Female *P. hurdi* cut a hole in the buds and enter to steal the pollen to provision their nests. They also visit open flowers to get nectar; however, this bee is too small to contact the stigma in the roof of the large floral tube. But, male bees are sometimes waiting for a potential mate to show up. While the pair grapples to copulate, the female may touch the stigma and leave some pollen stuck to it. These tiny bees nest in the ground in tunnels, usually only an inch or two below the surface. Most *Perdita* nest alone, but a few species are communal and share the same nest entrance.

Calliopsis are small to medium-sized bees that often

Bee Families and Genera Represented in the Kit

The large Riker mount in the kit displays some of the bees that occur in our region. They are divided into two principal groups: the solitary bees and bees that are social. There is one cleptoparasitic bee in the display. Information about the bee genera in the display are discussed below by Family. This information relies extensively on Danforth et al. (2019) and Wilson and Carril (2016).

BEES

Solitary bees that nest in the ground:

Genus	*Family*
1. *Agapostemon*	Halictidae
2. *Augochlorella*	Halictidae
3. *Lasioglossum*	Halictidae
4. *Nomia*	Halictidae
5. *Halictus*	Halictidae
6. *Exomalopsis*	Apidae
7. *Anthophorula*	Apidae
8 & 9. *Melissodes*	Apidae
10 & 11. *Diadasia*	Apidae
12. *Calliopsis*	Andrenidae
13. *Pseudopanurgus*	Andrenidae
14 & 15. *Perdita*	Andrenidae
16 & 17. *Melissodes*	Apidae
18. *Caupolicana*	Colletidae
19 - 26. *Centris*	Apidae
27 & 28. *Eucera*	Apidae

Bees that nest in preexisting holes

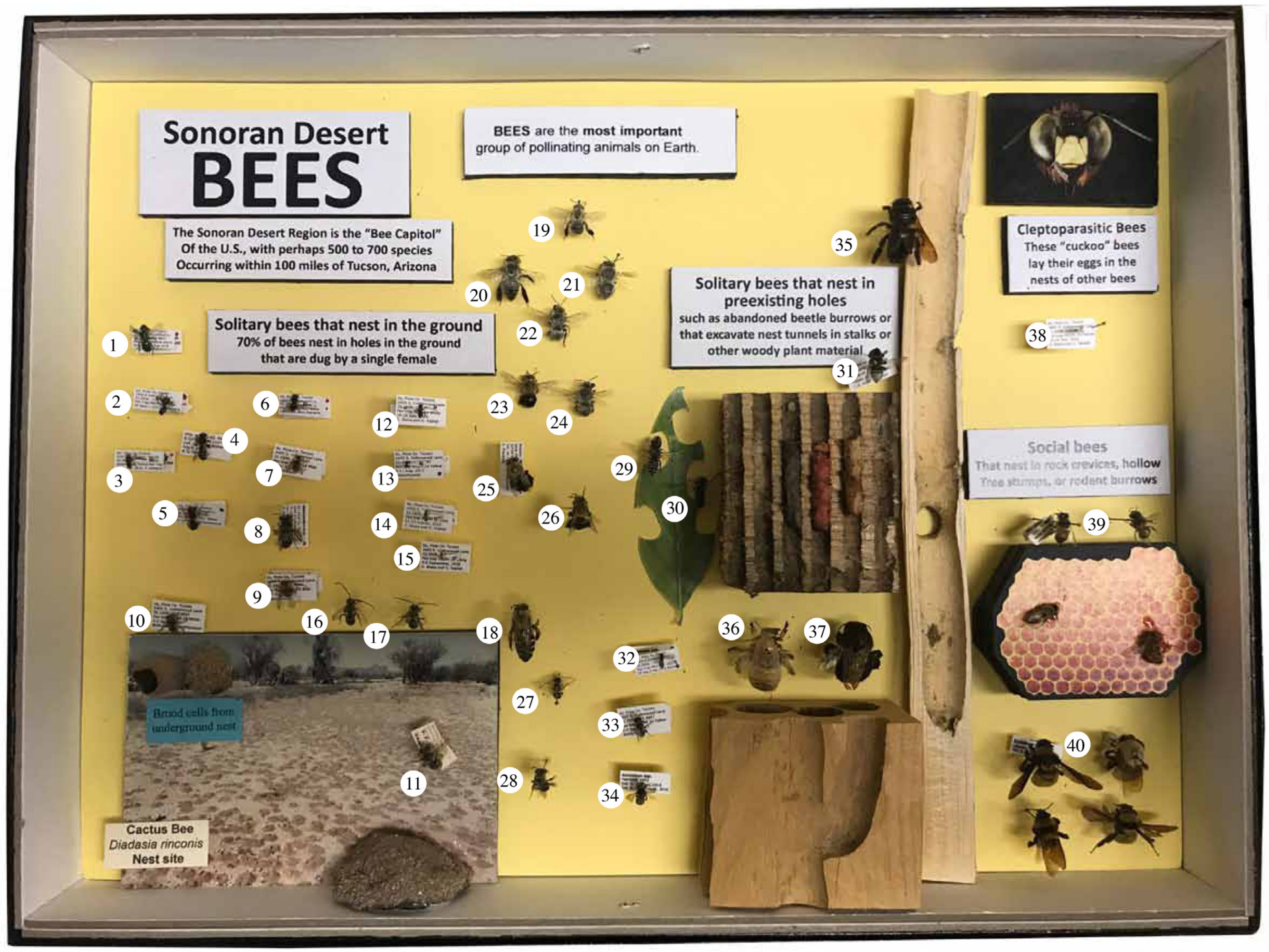
29 - 31. *Megachile*	Megachilidae
32. *Ceratina*	Apidae
33. *Ashmeadiella*	Megachilidae
34. *Anthidium*	Megachilidae
35. *Xylocopa californica arizonensis* (Carpenter Bee)	Apidae
36 & 37. *Xylocopa varipuncta* (Valley Carpenter Bee 36. male, 37. female)	Apidae

Cleptoparasitic Bees

38. *Neolarra*	Apidae

Social Bees

39. *Apis mellifera* (Honey Bee)	Apidae
40. *Bombus* (Bumble Bees)	Apidae



have yellow bands on the abdomen and yellow areas on the face. This genus is only represented in the Western Hemisphere with almost 90 species. There are about 70 species north of Mexico, mostly in the United States. *Calliopsis* are for the most part floral specialists. Like all bees in the family Andrenidae, *Calliopsis* nest in the ground and are all solitary. They sometimes nest in dense aggregations. Female *Calliopsis* line their nest cells with a waterproofing substance and also cover their pollen and nectar loaves with the substance.

Pseudopanurgus is represented by 12 species in the United States. These small, mostly black bees are specialists on flowers in the sunflower family. All are solitary but some nest in dense aggregations. As with other bees in the family Andrenidae, *Pseudopanurgus* line their nest cells with a waterproofing substance.

Family Apidae

The family Apidae is the largest family of bees with nearly 6,000 species. Most species are relatively large, hairy and fast-flying. Apids have a diversity of lifestyles, 57% are solitary, 17% are social and 27% are brood parasites. Many species have well-developed scopa (pollen collecting hairs) on the hind legs that look like saddlebags. Bees in this family may be separated from bees in other families by the morphology of the mouthparts and by wing venation. Historically, bees in the family Apidae and Megachilidae were known as "long tongued" bees and bees in the families Andenidae, Colletidae, Halictidae, and Melittidae were called "short tongued" bees. The distinction between the two groups is not based on tongue length per se but on the morphology of the mouthparts, particularly the pair of labial palpi. In "long tongued" bees the first two segments of the labial palpi are long, slender, flattened and blade-like and the third and fourth segments are very short. In the "short tongued" bees all four segments are morphologically similar.

The family Apidae includes ground-nesting solitary bees, the social carpenter bees, bumblebees, stingless bees, and honey bees, and a number of genera that are brood parasites.

Solitary Apidae

The solitary bees in the family Apidae are mostly ground-nesting, fast-flying bees that are active from April to September. They are sometimes called "flower-loving bees" because they visit such a wide variety of flowering plants. They are important pollinators of legumes, creosote, nightshades, cacti, and other plants. Several genera of ground-nesting solitary bees are included in the kit display: *Anthophorula, Centris, Diadasia, Eucera, Exomalopsis* and *Melissodes.*

Bees in the genus *Anthophorula* are small, hairy bees. Because of the dense scopal hairs on their hind legs, these bees have been described as "wearing cargo pants with full pockets" (Wilson and Carril, 2016). Most bees in the genus *Anthophorula* are generalists and visit a wide variety of flowers. A few species are specialists. *Anthophorula* are solitary bees but are known to nest communally, with several females, and in a few species hundreds of females using the same nest entrance. There are 40 species in the U.S., mostly distributed in the southwest. Related bees in the genus *Exomalopsis* include species that are both generalists and specialists and that have pollen preferences similar to *Anthophorula.* There are 10 species of *Exomalopsis* in the U.S., found primarily in the southwestern deserts.

Centris are large, robust, fast-flying bees that are active during the hottest part of the day. Twenty-three species occur north of the Mexican border. Most *Centris* are floral generalists and *Centris pallida* is an important pollinator of palo verdes. Most *Centris* are ground-nesting and some nest in large aggregations. Some *Centris* species collect oils from specialized flowers in the ratany and malpighia families. These bees have specialized hairs on the front and mid legs that collect the oil, which, with the help of a hind tibial spur that has projections like the teeth of a comb, is then transferred to the pollen-collecting hairs (scopa) on their hind legs. The oil may be used in nest construction or mixed with pollen and used as a larval food. *Centris pallida* males have a very interesting mating behavior. The males, which are larger than the females, dig short holes in the ground to intercept emerging virgin females from their underground nest site. The males will carry the females off to a perch to mate. Often the male must fight off competing males for the right to mate. See Alcock (1990) for a more detailed account of the mating behavior of this species.

Cactus bees in the genus *Diadasia* are medium to large, hairy, blond or tawny brown bees. There are 25 species in the United States and Canada. In our area they are particularly active between April and June, which is the time to pollinate various species of cacti. They are also important pollinators of mallows. *Diadasia* are ground-nesting and often make their nest on hard soil surfaces, such as on dirt roads and trails. To construct a nest in the hard-packed soil, the female rubs her head on the hard soil, chews the soil with her mandibles until it is loose, and then softens the loose soil with saliva. She then digs a vertical tunnel about 12 inches deep, and constructs four to twelve brood cells near the end of the main tunnel. *Diadasia* build turrets around the nest entrance. As mentioned previously, female cactus bees may nest together in groups of hundreds or thousands of individual nests.

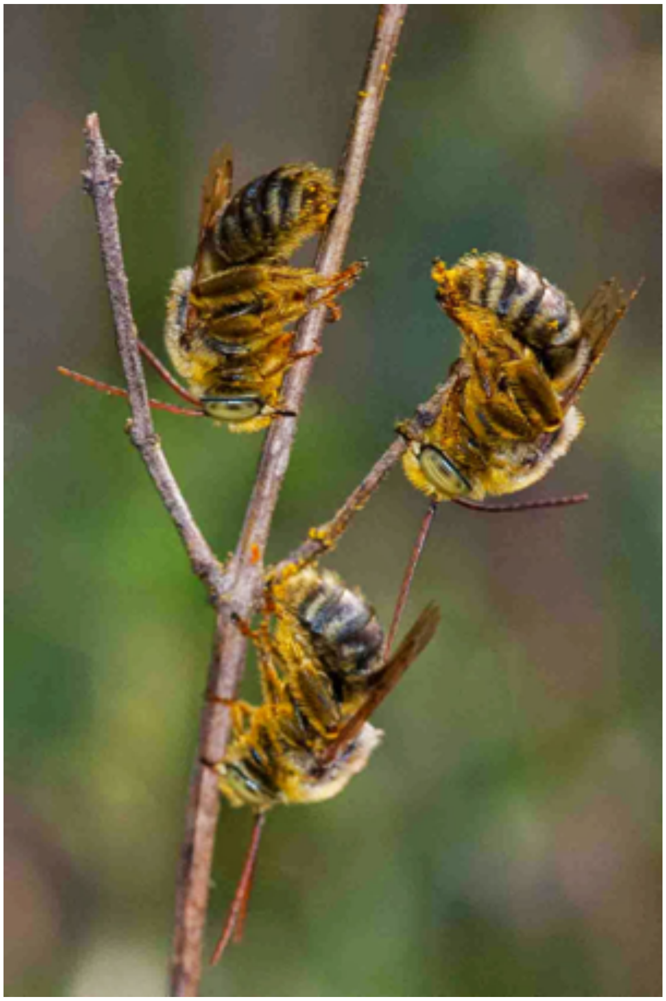
Eucera are large, hairy, fast flying bees in the tribe Eucerini. The Eucerini are called long-horned bees, because of the very long antennae of the males. The following photo of a long-horned bee is in the kit.

There are about 55 species in the U.S., mostly in the west. *Eucera* are among the first bees to emerge in the spring and are only rarely seen by August. Some species are floral generalists while others are specialists. The specialists seem to prefer flowers in the pea family and are seldom seen on plants in the sunflower family. *Eucera* prefer to nest in sandy or clay soils in flat areas or in shallow embankments. The nest entrances have a mound of soil piled around them. Males may hover in swarms over a nest tunnel waiting for virgin females to emerge. Once a female is mated, she gives off a different scent and the males leave her alone. Some species of *Eucera* may nest communally.

Melissodes are very similar in appearance to Eucera, and are also long-horned bees in the tribe Eucerini. There are almost 100 species in the U.S. A few species are generalists, but most species, unlike *Eucera,* are specialists on flowers in the sunflower family. Some *Melissodes* nest in aggregations, and communal behavior has been observed, with several females using the same nest entrance. Female *Melissodes* sleep in their nests at night. Males are known to sleep in groups of up to 20 bees on flowers and plant stems. When sleeping on plant stems, they grasp the stem tightly with their mandibles and essentially hang, sometimes upside down, in place throughout the night. The following two photos of sleeping bees are included in the kit materials.

Male Long-horned Bee (Photo by Steven Mlodinow)

Sleeping *Melissodes* bee. Photo by Alfredo D. Colón Archilla



Sleeping long-horned bees. Photo by Sheryl Smith-Rodgers

The males may also sleep in cracks or crevices near their nesting sites. The same males have been observed to return to the same sleeping site each night.

The squash bees in the genus *Xenoglossa* (not represented in the kit) are among the chief pollinators of squash and gourds, including the native coyote and buffalo gourds (Cucurbita) and the cultivated varieties such as zucchini. These bees are more effective pollinators of plants in this family than most other bees. They seem to be holding their own under competition from introduced honey bees (which collect the pollen, but are inefficient pollinators of these flowers), probably because squash bees are active earlier in the morning.

Social Apidae

Social bees in the family Apidae include the cooperatively breeding carpenter bees and the eusocial bumblebees, stingless bees, and honey bees. The large carpenter bees, bumblebees and honey bees are included in the kit display.

Carpenter bees are named for their habit of excavating nests in dead wood or plant stems. There are two North American Genera, *Ceratina* and *Xylocopa*, both of which are represented in the kit display. The small carpenter bees in the genus *Ceratina* (less than 8mm in length) are shiny, almost hairless, black or bluish green. There are 22 species north of Mexico. Almost all *Ceratina* are generalists and visit many plant species to obtain pollen and nectar. Females excavate pith from burnt or broken plant stems and twigs and nest in the resulting tunnels. They won't nest in intact twigs or stems because they are unable to chew through the hard, woody material. The cell partitions are made of compacted pith and most reports suggest that the nest tunnels are unlined. However, the female of one species has been found to line her nest with a hydrophobic, wax-like material. *Ceratina* show evidence of social behavior as a female will watch over their eggs until the adults emerge and are fully developed. She may even open up previously closed cells to check on her eggs. Some species have been found to be parthenogenic, which is unique among bees. In these species female offspring can be produced without mating.

There are two species of large carpenter bees that are commonly seen at the Arizona-Sonora Desert Museum, *Xylocopa californica arizonensis* and *Xylocopa sonorina*. *X. c. arizonensis* prefers softer wood for nesting, and in xeric habitats prefers the flower stalks of plants such as *Agave* spp., *Yucca elata* (soaptree yucca), and *Dasylirion wheeleri* (desert spoon or sotol). *X. sonorina* has a preference for larger diameter nesting materials such as in trees or structural wood.

The large carpenter bees are floral generalists and seek pollen and nectar from a variety of different plants. There are several photos of carpenter bees in the kit.

Large Carpenter Bee (Photo by Howard Byrne)

In desert environments they have been found to be important pollinators of bat-pollinated plants and can assume that role when not many bats are around. One of the interesting things about the large carpenter bees is that they are nectar robbers. They obtain nectar without pollinating a plant. Because of their large body size, they are unable to get nectar from long-throated, tubular flowers such as Yellow Trumpet Bush, *Tacoma stans.* Instead, they get to the nectar by cutting a slit with their mandible at the base of the flower. They never contact the pollen releasing anther or stigma of the flower. The following photo, which is in the kit, shows a nectar-robbing carpenter bee.

Photo by Ron Hemberger

Carpenter bees are one of the pollinators of Ocotillo. One may wonder how a nectar-robbing carpenter bee can be a pollinator of this plant. While they obtain nectar by making a slit at the base of the flower, they collect pollen on their rear ends that contact the reproductive structures of the flower that, unlike *Tacoma stans,* extend out from the flower opening. They are able to transfer pollen to other flowers in this way.

Often, one can often observe insects, such as other bees, ants, butterflies, and even a hummingbird obtaining nectar from a slit made by a carpenter bee. The following photo, which is in the kit, shows a Marine Blue Butterfly taking advantage of the carpenter bee's activity.

Photo by Buzz Hoffmann

As mentioned previously, at least some wood-nesting carpenter bees exhibit a form of sociality called "cooperative breeding." Mothers and daughters remain in the nest for an extended period of time and there is a reproductive division of labor. In 2012, a large female carpenter bee *(Xylocopa sonorina)* was observed flying around a wooden bench in the Desert Garden at ASDM. Upon further observation, the mother was seen, apparently, feeding one of her daughters at the nest entrance. This photo is in the kit.

A Mother *X. sonorina* feeding her daughter in the nest. Photo by Buzz Hoffmann

We know the bee in the nest is a female, because otherwise in this species, the bee would look like the male bee in the following image, which is in the kit. The male and female of the other large carpenter bee in our area, *X. c. arizonensis,* are both black

Male *X. sonorina* (photo is in the kit) Photo by Peter J. Bryant

The term for this mouth-to-mouth exchange of food is trophallaxis. Trophallaxis in carpenter bees may occur between mothers and teneral male and female adults (adults that have emerged from the pupa but are not fully mature and are not ready to leave the nest). Trophallaxis also occurs between mature females that remain in the nest.

There are a series of 5 photos in the kit showing the carpenter bee life cycle beginning with a photo of the adult. This is the second photo in the series that shows the interior of a nest in a sotol stalk with developing larvae and the nest after the new adults have left.

The fertilized eggs at the bottom of the nest develop into females, while the unfertilized ones above develop into males, and reach adulthood more quickly. This explains how the eldest females at the bottom of the nest can eventually get out because the males have already vacated the nest before the females have finished adult development.

See also Appendix 1 for additional natural history information on the two large carpenter bee species seen at ASDM. Appendix 2 contains frequently asked questions about carpenter bees.

Bumblebees are medium-sized to large, hairy bees in the genus *Bombus* and may be recognized by their black and yellow coloration (photo is in the kit).

Photo by Glenn Seplak

There are fewer than 50 species in North America. Bumblebees are among the few native North American bees that are eusocial with colonies having both a queen and workers. The Bee Kit display has four bumblebee specimens.

Bumblebees are active between March and October and are among the first bees to appear in the spring and the last ones to be seen in the fall. They have adaptations that enable them to be active during colder weather. Bumblebees are generalists and forage on a wide variety of plants including squash and gourds, sunflowers, and legumes. Some species have very long tongues so that they are able to collect pollen from plants with long flower tubes, such as beardtongues and foxgloves. They are also pollinators of important crop plants that require buzz pollination such as tomatoes, peppers, eggplants, potatoes, and blueberries.

Bumblebee colonies are annual in nature, established by an already inseminated queen who emerges from her winter retreat in spring and finds a suitable rodent burrow or other underground cavity in which to nest. The queen uses wax from glands in her abdomen to produce a single cell in which she may lay up to 12 eggs. She also makes a wax pot where she stores pollen and nectar. Although the first eggs are laid in a single cell, after the larvae emerge, the queen surrounds each larva with its own wax cell. In some cases, the queen's first daughters are so small they can't fly and only work in the nest. With warmer weather new wax pots and brood cells are constructed, producing larger workers that do the work of the colony. This permits the queen to carry out the main task of egg-laying. As the season progresses, the size of the colony increases because new workers are raised faster than the older workers die. The size of the colony will depend on the species and climate. The colony size of our most common desert bumblebee, *Bombus sonorus* is in the range of 300-500 bees. Early season workers lay few eggs, and these are eaten by the queen. Late in the season a mature colony contains many workers, and the number of eggs laid by the workers has increased. Some of these eggs will not be eaten by the female. Since the workers do not mate, the offspring from unfertilized eggs will be all males. Only the fertilized queen is capable of laying diploid eggs that may become workers and new queens. What determines whether a larva from a fertilized diploid egg will become a worker or queen may depend on the amount and nutritional value of the food they are given. The males and queens mate, the males die, and the inseminated queens spend the fall and winter "hibernating" below ground until the next spring. Only young mated females (new queens) overwinter; the rest of the colony, including the old queen dies. Unlike the honey bee worker, a bumblebee can sting many times. Because there is reproductive competition between queens and workers, bumblebees are considered to be primitively eusocial.

Bumblebee populations are in decline in Europe, Asia and North America. Causes for the decline may include habitat loss, land-use changes that reduce food plants, pesticides, and climate change.

Stingless bees in the Sonoran Desert Region are found in Sonora Mexico near Alamos. The common name of this group of bees is a little misleading. These bees do have stingers, but they are much reduced and not functional. Stingless bees protect the colony by biting and some species can release formic acid that can cause painful blisters. The queens of stingless bees are **physogastric,** with abdomens swollen full of eggs. They are not able to fly once they begin laying eggs, and never leave the colony again. Thus, these highly social bees live in colonies of thousands of individuals and represent a still greater caste differentiation between queens and workers. Stingless bees store as much as several quarts (liters) of honey in waxen storage pots that look like clusters of grapes. Indigenous peoples who find these nests within hollow trees sometimes transport the hives back to their villages, where they tend the bees and routinely harvest their honey and beeswax. Stingless bees are not currently represented in the kit display.

Honey Bees *(Apis mellifera),* shown in the following photo, are one of the best known insects and one of the best understood of all animal species (photo is in the kit).

Photo by Glenn Seplak

The common honey bee occurs naturally in Africa, the Middle East, and Europe and has been introduced to many other parts of the world where beekeepers maintain artificial nests called hives. The common honey bee was introduced to North America from Europe by the Jamestown colonists almost 400 years ago. This bee, now known as the European honey bee, is recognized by its golden brown color and characteristic shape. European honey bees are crucial pollinators, often the only managed pollinators for the more than 100 major crop plants grown in the United States. Few people other than some ecologists and conservation biologists realize the possible downside of honey bees, e.g., competition with native bees for floral resources and nesting sites, competition with other pollinating animals and spreading weedy plants by pollinating them. See Appendix 3 for more information on the natural history of honey bees.

Honey Bee FAQ:

When interpreting the Bee Kit, one may discover that visitors are familiar with honey bees and perhaps the large and sometimes colorful bumblebees and carpenter bees. However, they know practically nothing about the native, mostly solitary bees that occur in our area. For this reason most of the questions docents will receive when interpreting the kit relate to honey bees. Here are five of those questions, with answers provided.

1. What is killing all the honey bees?

A spring 2007 survey found that a fourth of United States beekeepers reported suffering substantial losses in their honey bee colonies the previous fall and winter. The worker bees just seemed to leave the colony and disappear as no dead bees were in sight. The workers left behind a queen and a few nurse bees to take care of the immatures. This malady became known as **Colony Collapse Disorder** (CCD). During the six years following the 2007 survey, more than 10 million colonies were lost, often to CCD. In 2017, honey bee operations with more than five colonies lost nearly 78,000 hives with CCD symptoms, while operations with fewer than five colonies lost 6,000 hives with CCD symptoms. Between October 2018 and April 2019, 40% of honey bee colonies died, the highest winter loss in 13 years. Despite the losses of bee colonies to CCD, the total number of honey bee colonies has grown or remained stable since CCD was first identified.

Honeybees are evolutionarily prone to diseases and have a weak immune system. Sudden honey bee die offs similar to CCD have been known as far back as 1869. Despite numerous studies, the cause or causes of CCD have been difficult to pin down. Among the possible causes of CCD that are being studied include:

- *Varroa* mites and the diseases they transmit

- Pathogens such as Israeli acute paralysis virus and the fungal parasites *Nosema ceranae* or *N. apis*
- Exposure to pesticides, such as the neonicotinoids that are applied to crops or pesticides used for in-hive insect or mite control
- Stress caused by management practices such as transportation to many locations across the country for pollination services
- Habitat changes where bees forage
- Inadequate forage/poor nutrition
- Immune-suppressing stress on bees caused by one or more of the factors identified above

The current scientific consensus is that there is no single factor causing CCD and there very well may be a combination of factors involved.

2. Are the honey bees we see on the Museum grounds "killer bees"?

The bees at ASDM are **Africanized,** a term we prefer rather than "killer bees." Africanized bees are found throughout Arizona except for higher elevations in the northern part of the state. In 1956, queen bees of an African honey bee race *(Apis mellifera scutellata)* were imported into Brazil to breed a more productive honeybee that was better adapted to a Neotropical climate. Africanized queens inadvertently escaped the following year and now have spread over a large part of South and Central America and the southern part of the United States, including Arizona. Africanized bees arrived in Arizona by 1993 and quickly established colonies in rock outcrops, tree hollows, and saguaro boots. The spread of Africanized honey bees from South to North America is one of history's most notable examples of biological invasion. The negative effects of advancing Africanized bee populations are especially dramatic on people, native plants, and animals. Some organizations and natural parks in Arizona have made attempts to remove feral bee colonies in rock outcroppings because they are not part of our native fauna.

Several traits have contributed to the success of Africanized bees: 1) their colonies grow faster than those of European honey bees, 2) they can establish nests in a wider variety of situations, 3) they exhibit more nest usurpation behavior, 4) they will move their entire colony readily (abscond) if food is scarce, 5) Africanized drones have mating advantages, and 6) genetic characteristics in hybrids favor loss of European honey bee traits.

Africanized and European honey bees are similar in that they:

- Look the same
- Sting in defense of themselves or their colony
- Can only sting once
- Have the same type of venom
- Pollinate flowers
- Produce honey and wax

When interpreting the Bee Kit, one can display the Riker mount shown in the photo below. It is practically impossible to distinguish between the European and Africanized honey bees based on appearance alone. Africanized honey bees are about 10-15 percent smaller than other subspecies and races of *Apis mellifera.*

be found in trees, in the sides of buildings, in drain pipes, in water meter valves, in old abandoned appliances, in piles of junk, and even in holes in the ground.

Africanized honey bees are very protective of their colony. Compared with the European honey bee, Africanized honey bees will defend a larger area around their colony, are more easily disturbed, and will respond in greater numbers once an intruder has been detected. Africanized bees may continue to follow a perceived enemy for up to ¼ mile. Once an Africanized bee colony is disturbed it takes an average of about 28 minutes for the bees to settle down, while European bees settle down within an average of about 3 minutes (Rahimian et al., 2019). The only clear danger to humans is encountering a colony and provoking it. Stimuli that alert and engage the defensive guard bees are ground vibrations, rapid movements, dark clothing, and the carbon dioxide in exhaled breath. Often a guard bee will bounce off your head without stinging. This is a warning that more bees and stings may follow. Do not swat at the bees; walk calmly out of the area. If you are attacked by numerous bees and being stung, pull your shirt or blouse over your head to protect your eyes. Hold your breath if you can and get out of the area. Do not jump into a swimming pool or lake to avoid them. Get indoors as quickly as possible; an automobile is a safe place to escape them. Don't worry about a few bees getting in with you, as they will soon disperse and fly toward a lighted window.

The toxic effects of bee venom may result in serious medical complications such as anaphylaxis, an acute allergic reaction to the venom that may include breathing difficulties, loss of consciousness, or even death. Rahimian et al. (2019) reported information obtained from the Arizona Poison and Drug Information Center on bee stings during the period January 2017 and June 2019. There were a total of 312 victims of bee stings. Of these victims, 251 received only one sting, 42 individuals had up to 10 stings, four victims had 11 to 49 stings, and 13 individuals had >50 stings (so-called massive stinging). Three persons were admitted to ICU and moderate to severe clinical effects were observed in 32 individuals; 30 of them experienced anaphylaxis. Of these 30, 16 were stung only once, and one of these victims died. Other toxic but non-lethal effects occurred in 13 victims. To be safe, people should stay away from areas where they have seen groups of bees. If a colony is apt to be provoked, stay clear of it and contact a beekeeper or pest control company. On the other hand, remember that bees on flowers are working to gather pollen and nectar (foraging). Foraging bees are away from their colony and are not as likely to sting unless they are trapped or harmed in some way. Visitors do not need to be excessively alarmed about bees visiting flowers. See appendix 4 for more information on Africanized bees.

3. Do All Bees Sting or is it just honey bees?

Male bees don't sting. It is the female bees that can sting. The stinger is a modified egg laying tube (ovipositor). Female stingless bees have stingers, but they are nonfunctional. Out of the more than 20,000 bees in the world, about 500 are stingless bees (Meliponines). Stingless bees protect the colony by biting and some can release formic acid that may cause painful blisters. Female solitary bees can sting but rarely do as they are on a mission to collect food for their young and want to have no interaction with humans. One would most likely have to squeeze a solitary bee to cause it to sting. One exception might be the sweat bees that are attracted to the sweat on your arm. If one were disturbed by swatting, squeezing, or brushing off, it might be enticed to sting in self-defense. Unless one is allergic to the venom, the sting of a sweat bee would be inconsequential.

4. Do all bees die after they sting you?

Only honey bees die after stinging. The honey bee stinger is barbed. Consequently, when a person is stung, the stinger becomes lodged in the skin. As the bee pulls away, some of their muscles, a portion of their abdomen and their venom sac (with stinger) rips off and stays lodged in the skin. The bee dies shortly thereafter. Muscles associated with the venom sac can continue to pump venom into your body even when it becomes separated from the bee. The best way to remove the stinger is to just scrape a fingernail over it. Native solitary and social bees don't die after stinging, and can sting more than once.

5. Do bees other than honey bees produce honey?

Yes, the stingless bees referred to earlier produce honey, some species enough to farm. The native solitary bees do not produce honey.

Cleptoparasitic Apidae

The name "cuckoo bee" is technically best applied to the apid subfamily Nomadinae, which has about 1200 species in the world. Almost half of these occur in North America. Cleptoparasitic bees in the genus *Nomada* are the ones most likely to be seen. However, cuckoo bees are also found in other apid subfamilies, e.g., in the subfamily Apinae (some bumblebees), and in the families Halictidae, Megachilidae, and rarely in the family Colletidae. At present, the genus *Nomada* is not represented in the Bee Kit display. The kit display does include *Neolarra,* a tiny cuckoo bee also in the subfamily Nomadinae. This bee is about the size of the head of a pin, some only a little more than 1mm in length. They are even smaller than *Perdita minima,* the bee referred to above as one of the smallest bees in the world. The name *Neolarra* means "new Larra." *Larra* is a genus of wasp that this bee resembles. *Neolarra* steals the nest provisions of equally small bees in the genus *Perdita,* Family Andrenidae. There are 14 described species of *Neolarra,* distributed mostly in the southwest.

Family Colletidae

Colletidae is a diverse family of bees with about 2,600 described species. All are solitary except for five that are brood parasites. The bees in this family are often referred to as cellophane bees because many species secrete a cellophane-like substance to line their nest cells. Colletids are "short tongued" bees and may be identified by wing venation and by their tongue (especially the glossa), which is very short and split and rounded at the end. The structure of the tongue is now believed to be associated with the application of the cellophane-like material lining the brood cells. Some Colletids nest in the ground while others prefer pre-made holes, such as beetle burrows and the hollow stems of dead plants. Some species are floral generalists while others are specialists. The only Colletid in the kit display is *Caupolicana,* a beautiful bee with orange hairs and white stripes on the abdomen.

Photo by Bob Barber

These bees prefer flowers in the pea and mint families but are also found on creosote. *Caupolicana* nest in the ground in a tunnel as deep as 3 feet, with upward projecting side tunnels that then drop sharply down again. These bees waterproof their nests with the cellophane-like material.

Bees in one genus, *Hylaeus,* are almost hairless and look like wasps. These bees don't have pollen-collecting hairs but instead consume the pollen and nectar, which is stored in their crop and then regurgitated when they return to the nest. *Hylaeus* nest in pre-made holes.

Family Halictidae

Halictidae is the second largest bee family with about 4,400 described species. The bees in this family have a diversity of lifestyles 71% are solitary, 21% are social, and 8% are brood parasites. Halictids can be identified by wing venation (curved basal vein in the forewing) and by their "short tongues." The bees in this family are generally small to medium sized, usually black or brown in color but some have brilliant metallic green, blue, or copper bodies. Bees in this family are called sweat bees because some species are attracted to human perspiration, which they lap up, probably for the salts and small amounts of proteins it contains. Halictids usually nest in the ground, often in clay banks. In terms of floral preferences, some halictids are generalists, while others are specialists. Bees in this family are generally active from February to October and are important pollinators for chilies, tomatoes, and many crops with small flowers.

Five genera of Halictidae are represented in the kit display, *Agopostemon, Augochlorella, Dufourea, Halictus* and *Lasioglossum)*. Some of our most beautiful bees, are in the genera *Agapostemon* and *Augochlorella* (the photo of Augochlorella is in the kit).

Augochlorella spp. (Photo by Glenn Seplak)

Augochlorella are ground nesting, primitively eusocial bees, and are attracted to a wide variety of plants. There are only two species found west of the Great Plains. The life cycle of these social bees begins when a fertilized female overwinters and emerges in the spring to construct a nest, provision it with pollen and nectar, and lay mostly female eggs. When her daughters become adults, they take over the work of collecting pollen and nectar and the foundress female remains in the nest and continues to lay eggs—she is the queen. There may be three generations of eggs laid each year. Fertilized females from the last brood overwinter and become the foundresses for the next year.

Agapostemon are solitary, mostly ground nesting bees, and have a variety of floral preferences. *Agapostemon* are particularly common in the southwest with about a dozen species. They are frequently seen on plants in the sunflower family. *Agapostemon* usually build nests that are widely scattered, except for aggregations of nests made by some communal species that have females sharing the same nest entrance. One species builds her nest under the bark of a rotted log.

Females in the genus *Dufourea* are considered to be floral specialists and restrict themselves to specific families or genera of plants for collecting pollen. Bees in this genus are believed to have a solitary lifestyle. As with other halictids, they nest in the ground and line their brood cells with aliphatic esters. Other members of the family Halictidae line their brood cells with a mixture of lactones, which have a shiny, varnish-like finish that impregnates the soil.

Halictus are nondescript, ground nesting, medium-sized bees, usually black or brown in color. There are 10 species in the United States and all are floral generalists. Most species are eusocial and produce several generations per year. Eusocial species are interesting because all females can lay eggs and can become a queen if a queen dies. They can also leave the nest and establish a new colony. Also interesting, is whether a female establishes a eusocial or solitary nest seems to depend on environmental conditions. Under poor environmental conditions, such as unpredictable rainfall, nests tend to be social. Under favorable weather conditions with an abundance of resources, nests are solitary.

Bees in the genus *Lasioglossum* are among the most abundant bees in North America, with about 400 species north of Mexico. These small bees (2-8mm) are found in every continent and *Lasioglossum* is the largest bee genus in the world with close to 1,800 species. *Lasioglossum* includes solitary, eusocial, and a few are parasitic species. Almost all species nest in the ground, but a few use preexisting holes, such as holes made by beetles in rotting wood. Most species are floral generalists, but there are exceptions. *Lasioglossum* are active for much of the year, beginning in early spring through the fall.

Halictids in the genus *Nomia* are called alkali bees because they prefer to nest in clay or alkali soils. They are such important pollinators that, where alfalfa is grown for seed, artificial nests have been constructed to attract more bees. Females are gregarious but excavate nests in the ground with many cells. Full-grown larvae overwinter in brood cells and pupate in early spring. Adults fly in July and August.

Family Megachilidae

Megachilidae is a large and diverse family with over 4,000 species in the world and over 600 species in the United States and Canada. Most species are solitary (85%) and the remainder are brood parasites. The name Megachilidae means "big lipped" and refers to their large mouthparts. Megachilids are "long tongued" bees and have the following characteristics that distinguish them from bees in other families: 1) two submarginal cells in the forewing with the second cell longer than the first, 2) scopa on the underside of the abdomen in females that are not cleptoparasites, and 3) a labrum that is longer than it is broad. Some species have hooked hairs on their faces for collecting pollen from tube-shaped flowers that are too narrow to collect pollen with their legs or abdomen. Many species do not make their own nest tunnels but will use almost any preexisting tunnel as a nest site such as beetle burrows in dead wood, between shingles, in steel pipes, in abandoned bee nests in the ground, even in pine cones and old snail shells. Megachilids use a variety of materials from the environment in constructing their nest cells, including snips of plant leaves or flower petals, the hairy fuzz on some plant leaves, pebbles, mud, and plant resins. Some species do not use preexisting tunnels, but rather use mud and other materials to construct their own free-standing nests. Many species are floral specialists. Genera included in the kit display are *Megachile, Osmia, Ashmeadiella,* and *Anthidium.*

Leafcutter Bees (Genus *Megachile*)

Leafcutter bees are small to large-sized and are active throughout the spring and summer. They are called leafcutters because female bees cut circular or oval leaf or flower petal fragments and use them to line nest cells often constructed in tunnels made by beetles in dead wood or rotting wood.

Leafcutter bee activity (photo is in the kit)

A leafcutter bee can snip off a leaf fragment in seconds, using its sharp mandibles. They will also nest between rocks, under dried cow patties, in man-made structures and a few species make their nest in the soil. Most leafcutters are floral generalists and important pollinators of many species of cacti, as well as sunflowers and legumes. They also pollinate alfalfa and other crops, and are considered highly beneficial.

Some *Megachile* species use plant resins along with other materials to construct their nests primarily in insect holes in dead wood. These other materials might include bits of bark, wood chips, palo verde leaves, bits of tiny stems and even insect parts. These bees are very common in the Sonoran Desert around Tucson. The world's largest bee species is the female Wallace's giant bee, *Megachile pluto,* with a body length of up to 1.5 inches (39 mm) and a wingspan of 2.4 inches (63 mm). This rare species is found on a few of the Moluccan Islands at the eastern end of the Malay Archipelago. The females excavate a tunnel in termite nests and use tree resin and wood chips to line the main burrow and nest cells.

Wallace's Giant Bee

Mason Bees (Genus *Osmia* and *Ashmeadiella)*

Bees in the genus *Osmia* are called mason bees, because many species use mud in the construction of their nest cells. The nests of some species are made entirely of mud, while in other species just the cell partitions and the end plug that closes the entire nest are made of mud. Some species mix in plant fragments, pebbles, or chewed up plant material with the mud. *Osmia* may construct nest cells in existing cavities such as old beetle tunnels, hollow plant stems, cracks in rocks, holes in the ground dug by other bees, and even in snail shells or on exposed surfaces of rocks or twigs. A few species line each nest cell with snips of leaves or flower petals. Adults are seen in April through June and there is one generation per year. Many species of *Osmia* are floral generalists and other species are important pollinators of orchard crops such as apples, cherries, plums, and almonds. *Osmia lignaria,* the blue orchard bee, is an important commercial pollinator.

Ashmeadiella, which is included in the kit display, is a bee that is in the same Tribe as *Osmia*. The floral preferences of *Ashmeadiella,* include *Penstemon,* mesquite, *Salvia,* and cacti. Bees in this genus nest in abandoned beetle burrows, plant stems, under rocks, and in shallow holes in the ground. One species was discovered nesting in a snail shell. *Ashmeadiella* use mud and chewed up plant leaves to construct their brood cells.

Carder Bees (Genus *Anthidium)*

Anthidium are beautifully colored black and yellow bees that use fluffy plant down rather than leaves to line their nests.

Photo by Margarethe Brummermann

The term "carder" refers to teasing out or "carding" cotton fibers using a comb-like tool. The carding tool of female carder bees is the sharp comb-like teeth on each mandible. The floral preferences of *Anthidium* are not well known, but a few species have been found to be generalists, while others are specific to a single family or genus of plants. *Anthidium* nest in preexisting holes either in wood, in thick plant stems, in the ground, or in man-made walls. They use the plant fuzz to not only line their nest cells but to separate one cell from another. Glandular secretions from plants may be added to the plant fuzz to help reduce wasp parasitism. At the nest entrance the plant fuzz is often mixed, pebbles, bits of wood, chewed up plant material. One scientist discovered lizard feces mixed with the plant down. In most bees, eggs that become male bees have a shorter development time and are laid near the front of the nest. *Anthidium* is an exception as the eggs that will become males are laid in the back of the nest. This may be because the males are bigger than the females and take longer to develop.

There are several genera (not represented in the kit display) in the Tribe Anthidiini that are called resin bees. These bees construct freestanding nests made of plant resins or plant resins combined with other materials such as pebbles, plant hairs, pith, small sticks and bark. The nests may be attached on a variety of exposed surfaces, such as the undersides of leaves, on rocks, trees, plant stems and walls. This nest that was discovered on the wall near the Interpretive Animal Building at ASDM is believed to have been built by a resin bee in the Tribe Anthidini (photo is in the kit).

Photo by Buzz Hoffmann

To encourage the nesting of native bees that use preexisting holes for nest sites, one may construct or purchase a bee condo, such as the one included in the bee kit.

See the following link for information on constructing a suitable bee condo:
https://www.pollinator.org/pollinator.org/assets/generalFiles/Build-a-Bee-Condo-2019.pdf

Family Melittidae

Melittidae is a small family with only about 200 species. They are all solitary, exclusively ground-nesting bees, and mostly floral specialists. Melittids have a "short tongue" that is pointed and not forked and a middle coxa that is longer compared with other bees. These bees can be very difficult to identify even to family.

Hesperapis are the most commonly seen melittids in North America. Twenty-five species occur in the United States and all are pollen specialists. *Hesperapis* occur primarily in the arid deserts and grasslands of the western United States. All species are ground-nesters and many prefer sandy soils. Unlike most ground nesting bees, *Hesperapis* females don't line their nest with a waterproof coating. However, there is some evidence that larvae might apply a waterproof coating before they pupate. Many species of *Hesperapis* in the deserts have two generations per year. A representative of this family is not included in the kit display.

Threats to Native Bees

Globally, pollinators are in peril from a number of sources including habitat loss, invasive species, pesticides, pollution and climate change. The National Research Council of the National Academies published a report in 2007 on the status of North American Pollinators. The report found evidence of long-term population declines of several wild bee species, most notably bumblebees. The report also found that for most pollinator species there is a paucity of long-term population data that make status assessments very difficult. The Center for Biological Diversity issued a 2017 report reviewing the status of 4,337 North American and Hawaiian native bees. Data were sufficient to assess approximately 33% (1437) of those bees. More than half of the bees whose status could be assessed are declining (749) and nearly one in four is imperiled and at increasing risk of extinction. Unfortunately, baseline data to establish trends with the remaining 67% of bees was not available. The declines are not limited to North America. A 2016 report from the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services found that 9.2% of European native bees are threatened with extinction and 37% are in decline.

The Xerces Society for Invertebrate Conservation is dedicated to the conservation of invertebrates and their habitats (https://xerces.org). One of the Society's key program areas is pollinator conservation. The Society monitors at-risk invertebrates including bees. Another major pollinator conservation effort is being led by Pollinator Partnership a nonprofit organization dedicated to the protection and promotion of pollinators and their ecosystems (https://pollinator.org/).

The US National Native Bee Monitoring Research Coordination Network (RCN) is a new USDA-funded effort to coordinate and support efforts to monitor native bee populations in the US, with the broader goal of conserving our nation's native bee fauna. From 2020-2023, native bee biologists from across the US will work together to develop a national plan for native bee monitoring. The plan will include components such as monitoring protocols and the designation of priority areas for monitoring. The RCN will also develop new educational and training opportunities in areas that are fundamental to native bee monitoring. The website of this effort is at the following link: https://www.usnativebees.com/

ASDM Bee Research

The native bees of the Sonoran Desert Region are very different from the familiar non-native honey bee, and they are extremely important members of our Sonoran Desert ecosystems. Yet, we know relatively little about them. To address this lack of knowledge, ASDM, under the direction of Conservation Research Scientist Dr. Kim Franklin, initiated a study to learn more about our native bee fauna. Specifically, this study is intended to obtain important baseline information on the diversity, abundance, distribution and **phenology** (seasonal activity) of our native bees. Only with such baseline data can we assess the impact of climate change on native bee populations as well as the impact on such populations of habitat loss, pesticides, and pathogens, factors known to be affecting honey bees.

The initial study site was an urban community farm, Las Milpitas de Cottonwood, located along the Santa Cruz River in Tucson. The study has been expanded and ASDM is now collaborating with the University of Arizona, Pima Community College, and several local high schools to identify bees to species through DNA barcoding, a technique that uses the sequence diversity, in short, standard DNA regions for species-level identification. The resulting data will be made public through the University of Arizona Insect Collection for anyone to use to ask a wide range of questions about the incredible bee fauna of our desert.

This collective effort is called the **Tucson Bee Collaborative.** The Tucson Bee Collaborative is a partnership effort to increase awareness of Tucson's exceptional bee diversity, and to empower future scientists by engaging them in research activities.

Researchers, students, teachers, artists, photographers, and citizen scientists are working together to understand and monitor the health of native bees of the Sonoran Desert Region. Our partnerships cultivate awareness, understanding, and appreciation of biodiversity — one bee at a time.

DOCUMENTING BIODIVERSITY
We are enhancing the University of Arizona's Insect Collection by growing it to include at least one specimen of every bee species known from our region. Every species will be documented with high-resolution images and will be DNA barcoded; this information will be available online for researchers, students, and the general public.

ENABLING RESEARCH
We are providing tools for researchers and conservationists working in the Sonoran Desert Region to identify bee species in research and monitoring programs by providing molecular-genetic identification tools and high resolution photographs.

EMPOWERING YOUNG SCIENTISTS
We are engaging future scientists at Pima Community College and local high schools in the collection of bees and the generation of genetic identification tools through course-based research experiences for undergraduates and high school students.

PROMOTING AWARENESS
We are inspiring wonder and appreciation of Sonoran Desert native bees by engaging with interested students, teachers, artists, and art programs. We are connecting with the community through presentations and exhibits at the Arizona Insect Festival, Arizona-Sonora Desert Museum, UA Insect Collection, and other venues.

For more information on this collaborative effort, see the following link:
https://www.tucsonbeecollaborative.com/

Bee Friendly Landscaping Practices

- **Plant some native plants!** The relationships between bees and flowers have evolved over millions of years. Therefore, our Sonoran Desert bees are generally better able to utilize Sonoran Desert plants than plants from other parts of the world. Here in the Sonoran Desert we have no shortage of attractive trees, shrubs, cacti, and succulents with which to landscape your yard.

- **Plant flowers in clumps.** Most bees will visit only one, or at most, a few types of flowers on each foraging trip. They learn how to deal with a certain type of flower, and then tend to stick with it, which allows them to be efficient foragers. Therefore, most bees will benefit from a fair-sized patch of a single flower species. Planting a flowering tree (eg. palo verde tree, mesquite tree) native to the region provides the same benefit.

- **Plant a diversity of flowers to attract a diversity of bees.** Since most bees are specialists to some degree, a greater diversity of plants will benefit a greater diversity of bees. Some websites may suggest that there is some minimum number of plant species required to create a pollinator garden, but in truth, even a single patch of flowers will almost certainly benefit some bees.

- **Provide nesting habitat!** This is one of the simplest things that anyone can do to help bees. Since most of our wild bees nest in the soil, they need some bare ground into which they can tunnel to build a nest. This means leaving a portion of your yard free of gravel and mulch, and preferably an area of the yard that receives a lot of sun. These narrow tunnels will be difficult to spot, their diameter no bigger than an eraser on the end of a pencil, but they have benefit beyond bees, increasing soil moisture and aeration.

Ground-nesting bee exiting her nest. Note the small diameter of the nest entrance by comparison to the pinky finger.
Photos by Anna Howell

• **Provide a source of mud, which is an important material for nest construction for some bees.** Water is not necessary for most Sonoran Desert bees, but providing water (e.g. a bird bath or small fountain) can attract a variety of pollinators, including birds and butterflies, as well as other beneficial insects. Water also tends to attract large numbers of honey bees.

• **Avoid pesticides.** Fortunately, native plants rarely suffer much from insect damage. On the other hand, vegetable gardens can attract some hungry insects eager for a meal. First, take a step back and assess the size of your problem. A dozen or so hungry caterpillars might be removed just as easily by hand as with the use of pesticides. Aphids and other soft bodied bugs are easily treated with soapy water. If you do decide to use pesticides, never apply pesticides when plants are blooming. When shopping for plants at the big box stores, check labels. Many plants are treated with neonicotinoids, a class of insecticide that is absorbed and distributed throughout all of the plant tissues, including nectar and pollen. Both Home Depot and Lowes have committed to phasing out neonicotinoids over the next few years, but in the meantime, purchase neonicotinoid-free plants.

• Plant sunflowers (plants in the genus Helianthus). Some exciting new research suggests that the nectar and pollen of flowers within the genus Helianthus may help bees reduce their parasite loads. And why not plant some sunflowers, they add beauty to any garden!

As our city continues to grow, what will sustain a thriving bee fauna is not just a few spectacular gardens, but rather a network of small patches of pollinator habitat scattered throughout our city. Your yard or pollinator garden doesn't need to be perfect to be of value to bees. I am reminded of the popular saying that it takes a village to raise a child. This is as true for bees as it is for children!

Volunteers planting a pollinator garden at Las Milpitas
Photo by Kim Franklin

Interpret the Bees!

Because of the ecological importance of bees and because pollinators, including bees, are threatened, docents are encouraged to look for opportunities to interpret bees, not only while doing the Bee Kit, but while roving on the grounds and conducting grounds tours. The opportunities to interpret bees on the Museum grounds are almost unlimited. Some of the possibilities include:

- Carpenter bees flying on the grounds
- Carpenter bees making a slit at the base of flowers; other insects (other bees, ants, and butterflies) using the slit to gain access to nectar
- Sotol or agave stalks with holes made by carpenter bees or carpenter bees flying around the stalks
- Carpenter bees excavating nest tunnels in the beams near the Arthropod Architecture Kit location
- Leaves with segments cut out by the leafcutter bee, e.g., mountain grape in the Mountain Woodland habitat
- Numbers of small bees (megachilids) buzzing about the Agave and other ramadas during the spring and summer. They likely have nest sites in the mesquite and agave components of the ramadas and can be seen entering holes made by wood-boring beetles.
- Bees of many species foraging for nectar and pollen on flowers—palo verdes, mesquite, desert willow, cacti, agaves, desert spoon, Mexican Crucillo, etc.
- Sweat bees landing on your arm to feed on perspiration
- Colored bee pan traps located around the grounds that attract a visitor's attention offer an excellent opportunity to interpret native bees and discuss the Museum's research.

When discussing bees with museum visitors, docents can point out actions individuals can take to protect and conserve native bees including the following:

- Protect habitat by landscaping with native Sonoran Desert plants, particularly plants that bloom for long periods of time.
- Use few or no insecticides on your property.
- Don't discard dead tree limbs or even dead trees as they will attract wood-boring beetles, whose holes will provide nest sites for leafcutter and mason bees.
- Build a "bee condominium" attractive to leafcutter and mason bees and place it in a location protected from sun and rain, e.g., under the eaves of the house.
- Provide some bare ground on your property for ground nesting bees.

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Appendix 1

Carpenter Bees at the Arizona-Sonora Desert Museum

By

Buzz L. Hoffmann, Docent

There are two species of large carpenter bees that are commonly seen at the Arizona-Sonora Desert Museum, *Xylocopa californica arizonensis* and *Xylocopa sonorina* (Hymenoptera: Apidae). *X. c. arizonensis* males and females are both shiny black. Male *X. c. arizonensis* can be distinguished from females because males are smaller, have silvery white shoulder patches and bluish grey eyes. The eyes of females are jet black.

X. c. arizonensis prefers softer wood for nesting, and in xeric habitats prefers the flower stalks of plants such as *Agave* spp., *Yucca elata* (soaptree yucca), and *Dasylirion wheeleri* (desert spoon or sotol). The nests are typically single, non-branched tunnels. However, there may be multiple branches if the nest substrate is thick enough. Because the nest substrate selected by *X. c. arizonensis* is short-lived and lasts only 1-2 years, the nests usually contain only a single female and her progeny.

Docents know the importance of nurse plants such as *Parkinsonia microphylla* (foothill palo verde), *Olneya tesota* (desert ironwood), and *Ambrosia deltoidea* (triangle leaf bursage) in protecting young seedlings from extreme heat and cold, damaging radiation, and from herbivores. However, nurse plants also benefit carpenter bees. Research by Minckley (1987), found that in his study area near Tucson, *X. c. arizonensis* females prefer nesting sites in flower stalks shaded by perennial nurse plants, particularly foothill palo verdes.

X. sonorina is sexually dimorphic; the females of this species are black (not as shiny as *X. c. arizonensis)* and the males are yellow or tawny.

X. sonorina has a preference for larger diameter nesting materials, and makes nests with more branches that are shorter in length than those made by *X. c. arizonensis.* Nests last several years, permitting multiple generations at the same location and allowing colonies to build up their numbers and attain a higher level of social organization. Nesting substrates may include mesquite *(Prosopis* spp.), chinaberry *(Melia* spp.—non-native), cottonwood *(Populus fremontii),* or structural wood. The carpenter bees that nest in the beams above the Arthropod Architecture station are *X. sonorina.*

When interpreting the Arthropod Architecture kit, carpenter bees can often be seen "robbing nectar" from nearby yellow trumpet bush flowers by making a small slit at the base of a flower. This behavior also benefits other insects such as ants and butterflies that have access to the nectar through the slits made by the carpenter bee. The image below shows Ceraunus Blue butterflies feeding on nectar made available by the carpenter bees.

Carpenter Bee Life History.[1] Overwintering male and female carpenter bees become active in late February or early March. In *X. sonorina,* the overwintering period ends when the ambient temperature exceeds 68° F (20° C) for 4 days. Mating activity begins about 2 weeks later. The males of both species establish mating territories, but the territorial behavior of the two species is different. A Male *X. c. arizonensis* hovers or patrols near flowering plants or at nest sites and attempts to mate with any females that enter his territory. In contrast, a male

X. sonorina hovers about a shrub on a ridgetop or a prominent tree in dry washes where he will emit a chemical (pheromone) to attract females (Alcock, 1990). The territorial behavior in *X. sonorina* is called "lek territoriality" because the males are not involved in the care of the young and their territories are located in non-flowering trees and bushes away from nests. In contrast to *X. c. arizonensis, X. sonorina* females, not the males, make the mate choice. Mating activity in *X. sonorina* lasts between five and eight weeks in the spring. In *X. c. arizonensis,* mating activity is most intense during this period but continues through the season at a much lower level.

Nest Construction. After mating, the females use their strong mandibles to construct new nest galleries. The mandibles are operated by muscles that fill the entire head. Nest tunnel construction is described by Gerling et al. (1983), and is paraphrased as follows: The female makes a cylindrically round tunnel by changing her position as she digs. She usually starts with her ventral side down, then turns to face the side and finally upwards. The shavings accumulate to some extent and then she pushes them out with her head and abdomen. When she finishes the excavation she licks the entire surface of the tunnel walls with a thin film that may have water repellent properties. Hurd (1955) reported on a study showing that in the boring process, female *Xylocopa tabiniformis orpifex,* a California species, turns slowly in the burrow, requiring thirty minutes per cycle. There was no uniformity or regularity in the rate or direction of turning. Nest construction by *X. c. arizonensis* begins by about mid-March and by *X. sonorina* about mid-April. It takes a female *X. c. arizonensis* two or three days to dig thru the outer layer of an old flower stalk. Once she reaches the pithy material in the center of the stalk, nest excavation proceeds at a much faster rate. A female X. c. arizonensis digs only during the day and returns to the natal nest at night. It takes about two weeks for females of this species to construct the nest gallery. Specific information on the time for *X. sonorina* females to excavate a nest tunnel is not available. However, because *X. sonorina* typically chooses harder wood, nest construction may take longer than two weeks. Female *X. t. orpifex,* which often make their nest in structural timbers, take about six days to lengthen the nest by one inch (Hurd 1955).

Nest Provisioning, Egg Laying, and Cell Closure. After a female carpenter bee constructs the nest tunnel, she provisions the nest with a mixture of two substances. The first substance is pollen she removes from her hind legs. The second is regurgitated nectar. This mixture is formed into a moist, yellow ball and a single egg is laid on each food mass, called **bee bread.**[2] The cell is then partitioned off using shavings she scrapes with her mandibles off the side wall and floor of the tunnel. The shavings are mixed together with salivary and /or Dufours gland secretions to form a concave, spiral-shaped partition or plug. The partitions are about .04–.06 in. (1–2 mm) thick and have a flat, rough and spiral-shaped pattern inside the cell and a smooth concave surface outside the cell (Silveira 2002). This type of cell closure is characteristic of bees but not wasps. The construction of cell partitions is described in Gerling et al. (1983) and is paraphrased as follows: The female constructs the partition using primarily the end of her abdomen. She uses her forelegs to collect the shavings and put them in piles under her body, and then pushes them back with her abdomen. When the partition is nearly finished, she turns her head, licks it and the walls around the partition and then pushes her head against the partition. She alternates this behavior with brushing the end of her abdomen over the partition. The carpenter bees studied by Gerling took about an hour to construct the partition. It may take other species of carpenter bees longer to construct it. Two carpenter bees endemic to Australia , *Xylocopa (Lestis) aeratus* and *X. (L.) bombylans* took 3-6 hours to construct the partition (Steen and Schwarz 2000).

Typically, one cell is provisioned each day, but there may be some skipped days. In one study involving *X. c. arizonensis,* early season nests consisted of 4–14 cells, probably made by a single female. *X. sonorina* nest galleries usually have 15–20 cells, but may have as many as 24 cells. *X. sonorina* nests are not single tunnels as is usually the case with *X. c. arizonensis,* but are nests that have more branches that are shorter in length. Carpenter bee eggs that will become females are laid in the back of the nest tunnel while eggs that will become males are laid in front. Males have a shorter development time than females. Consequently, if male eggs were laid first at the back end of the nest tunnel, the age difference between resulting males and females would be greater, increasing the likelihood that older males could potentially injure younger females that were not fully hardened.

Growth and Development. It takes about 3–5 days for carpenter bee eggs to hatch into larvae. Carpenter bee development in the nest is further described in Gerling et al. (1983) and is paraphrased as follows: After hatching, each larva begins to feed on the store of food in its cell. The larva molts twice and by the time the bee-bread supply is exhausted, the prepupal stage starts. This stage lasts several days and ends in pupation. Finally, the adults emerge. Under laboratory conditions at about 68–77°F (20–25° C), the development time from egg to adult was about 45-49 days. The development time would be somewhat less at higher temperatures. The newly emerged adults are called teneral adults, because they are not fully hardened and they don't leave the nest. The teneral adults destroy all the cell partitions, leaving the still-unemerged pupae in a disorderly fashion but unharmed. The teneral adults are located between the unemerged progeny and the nest entrance, where the teneral adults are fed by their mother.[3] Once all bees emerge as adults, they clear the tunnel of debris. The development time reported in Gerling, is consistent with the 45–55 day development time found by Minckley (1987), in his studies on *X. c. arizonensis* and *X. sonorina.*

Adult Emergence and Survival. First generation *X. c. arizonensis* adults emerge from the natal cells in early June and begin flying 10–20 days later. In this species, there may be a second generation during the monsoon. It is not clear whether individual females are having a second brood or whether females that did not mate earlier in the season are responsible for the second generation. Mating activity in *X. c. arizonensis* continues to October at a much reduced level. Males and usually unmated females overwinter in the old nest. There is some evidence suggesting that if the nest substrate remains intact, the first (or second generation) males and females may remain in their natal nest until they overwinter. *X. sonorina* adult metamorphosis is completed in June. The new adults will usually remain in the nest, especially the males, and will be fed regurgitated nectar by mothers and sisters (Alcock, 1990). These individuals will not mate during the year they become adults and will overwinter in the old nest as prereproductive adults. *X. sonorina* has only one generation per year.

Female carpenter bees live much longer than other solitary bees. *X. c. arizonensis* females may live up to two years. In *X. sonorina*, there can be females in the nest that are 2 or sometimes 3 years old. Female carpenter bees usually live long enough to see their offspring and may have social interactions with them (O'Toole and Raw, 2004). The males are not as long-lived and usually die after the mating season.

One of the major mortality factors for carpenter bees is woodpeckers that attack the nest when the larvae are large and tasty. The following images compare the almost-cylindrical entrance hole made by the female carpenter bee with the hole excavated by the Gila Woodpecker that is looking for carpenter bee larvae to eat. The remains of a cell partition are visible at the bottom of the hole made by the woodpecker.

Footnotes:

1 Except where other references are noted, the natural history information presented on the two large carpenter bee species in the Tucson area was obtained from Minckley (1987), and from personal communications with Stephen Buchmann and Robert Minckley (References cited below). One of the other references cited in several places is by Gerling et al. (1983), who conducted research on two Middle East species of carpenter bees, *Xylocopa sulcatipes* and *Xylocopa pubescens.* These authors used X-ray analysis to study the behavior of the bees in the nest. Another reference cited, Hurd (1955), reported on nest behavior of a California species, *Xylocopa tabiniformis orpifex.* It is believed that the behavior shown by the two Middle East species and the California species is similar to other species in the genus Xylocopa, including the two species we see at the museum.

2 Carpenter bee eggs are the largest of any insect. *X. sonorina* eggs may be 0.6 on (15 mm) long (University of California, Davis, 2009).

3 Carpenter bees are unique among bees that exhibit social behavior because it is the female reproductives that do the work, i.e., nest construction, foraging and provisioning the nest, guarding the nest, and feeding their offspring. This is in contrast to honey bees, tropical stingless bees, and sweat bees whose non-reproductive females (workers) perform these nest functions.

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Appendix 2

Carpenter Bees: Frequently Asked Questions

How many species of large carpenter bees are commonly seen at ASDM?

Two, *Xylocopa californica arizonensis* and *Xylocopa sonorina.*

What nest substrates do the two ASDM carpenter bees prefer?

X. c. arizonensis prefers softer wood for nesting such the flower stalks of plants such as *Agave* spp., soaptree yucca, and sotol. *X. sonorina* has a preference for larger diameter nesting materials that may include mesquite, chinaberry, cottonwood, or structural wood. The carpenter bees that nest in the beams above the Arthropod Architecture station are *X. sonorina.*

How can I tell male carpenter bees from female carpenter bees?

X. c. arizonensis males and females are both shiny black. Male *X. c. arizonensis* are smaller than females, have silvery white shoulder patches and bluish grey eyes. The eyes of females are jet black. *X. sonorina* is sexually dimorphic; the females of this species are black (not as shiny as *X. c. arizonensis)* and the males are yellow or tawny.

How long does it take for a carpenter bee to drill the nest gallery?

It takes about two weeks for female *X. c. arizonensis* to construct the nest gallery. Specific information on the time for *X. sonorina* females to excavate a nest tunnel is not available. However, because *X. sonorina* typically chooses harder wood, nest construction may take longer than two weeks. A female *Xylocopa tabiniformis orpifex*, a California species that often makes its nest in structural timbers, takes about six days to lengthen the nest tunnel by one inch.

How long does it take for the carpenter bee to lay all of the eggs?

Typically, one cell is provisioned and an egg laid each day, but there may be some skipped days. The time required to lay all of the eggs will depend on the number of cells constructed by a female. In one study involving *X. c. arizonensis,* early season nests consisted of 4–14 cells, probably made by a single female. *X. sonorina* nest galleries usually have 15–20 cells, but may have as many as 24 cells. More than one female may be involved in nest building.

X. c. arizonensis usually makes single, non-branched tunnels while *X. sonorina* nests have multiple branches that are shorter in length.

How are cell partitions made?

The female scrapes shavings off the side wall and floor of the tunnel with her mandibles. She uses her forelegs to collect the shavings and put them in piles under her body. She then constructs a concave, spiral-shaped partition using primarily the end of her abdomen. The shavings are mixed together with salivary and/or Dufours gland secretions and then pushed back with the end of her abdomen. When the partition is nearly finished, she turns her head, licks it and the walls around the partition and then pushes her head against the partition. She alternates this behavior with brushing the end of her abdomen over the partition.

How long does it take to make a cell partition?

No data are available for the two ASDM species. The females of two Middle East species took about an hour to construct the partition and females of two species endemic to Australia took 3–6 hours to construct the cell partition.

How long does it take for all of the eggs to hatch and the adults to emerge?

It takes about 3–5 days for carpenter bee eggs to hatch into larvae. The development time from egg to adult is about 45-55 days, depending on temperature conditions. The newly emerged adults are called teneral adults. These adults are not fully hardened and cannot fly. The teneral adults destroy the cell partitions and move to near the nest entrance where they are fed by their mother and in some cases sisters.

What is a typical carpenter bee seasonal life cycle?

Overwintering males and females emerge in the spring. After mating the females construct and provision a nest gallery and lay an egg on each food mass (pollen and nectar). After about 6–8 weeks, adult carpenter bees emerge from the pupa. New *X. sonorina* adults will usually remain in the nest, especially the males, and will be fed regurgitated nectar by their mothers and sisters. These individuals will not mate during the year they become adults and will overwinter in the old nest as prereproductive adults. *X. sonorina* has only one generation per year. First generation *X. c. arizonensis* adults emerge from the natal cells in early June and may begin flying 10–20 days later. There is some evidence suggesting that if the nest substrate remains intact, the first (or second generation) males and females may remain in their natal nest until they overwinter. In *X. c. arizonensis* there may be very limited mating activity into the fall. Males and usually unmated females overwinter in the old nest. *X. c. arizonensis* may have a second generation the first year.

How long do carpenter bees live?

Female carpenter bees live much longer than other solitary bees. *X. c. arizonensis* females may live up to two years. In *X. sonorina,* there can be females in the nest that are 2 or sometimes 3 years old. Female carpenter bees usually live long enough to see their offspring and may have social interactions with them. The males are not as long-lived and usually die after the mating season.

Can a carpenter bee sting?

Female carpenter bees do have a stinger but are not aggressive to humans and have been reported to sting only when handled or provoked. The males do not have a stinger.

What is a carpenter bee doing when its head is facing the base of a tubular flower?

The carpenter bee is a making a slit in the base of the flower and is removing nectar without pollinating the plant. This phenomenon is referred to as "nectar robbing." This behavior also benefits other insects such as ants and butterflies that have access to the nectar through the slits made by the carpenter bee.

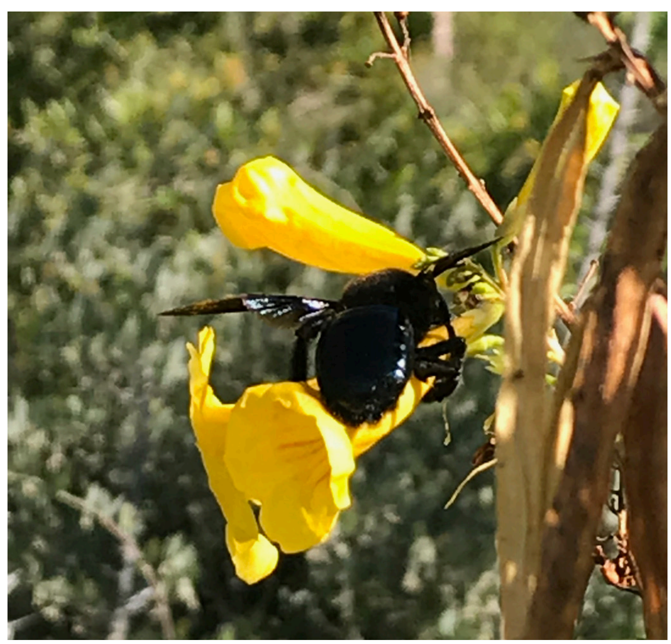


Photo by Philip Brown

Appendix 3

The Life of the Honey Bee

Excerpts from: *The Life of the Honey Bee, Its Biology and Behavior with an Introduction to Managing the Honey-Bee Colony.* by C. L. Farrar. This paper originally appeared as three articles in the American Bee Journal; December 1967, pages 461-462, 464; January 1968, pages 21-23; February 1968, pages 60-64.

Worker Honey Bees

The worker bees are sexually underdeveloped females smaller than the queen but capable of laying small numbers of eggs under some conditions. Worker bees that lay eggs are called laying workers. Their eggs, usually placed in worker cells, develop into undersized but functional drones.

Worker-bee larvae hatch from the eggs in 3 days, are fed royal jelly for 2 1/2 days, and then their diet is changed to include pollen and honey for 2 1/2 days. They are sealed in their cells for 12 days, during which time they spin a cocoon and transform from the larvae to the pupae, emerging as adult bees 20 days after the eggs were laid.

The difference in the cell and food environment causes the worker bees to require 5 days longer than the queen to develop, yet their life expectancy is only 5 weeks during the summer and a few months during the winter. Any worker larva under 24 to 48 hours old can be developed into a queen under the proper colony conditions that insures the nurse bees will construct a queen cell and feed royal jelly lavishly to the developing larva. The rearing of queens for the market is a highly specialized field of beekeeping.

The worker bees differ markedly from the queen in many respects other than function, length of life, and behavior. Structurally they have a longer tongue for gathering nectar, modified mandibles (jaws) especially designed for comb building, special glands for secreting royal jelly, enzymes for the conversion of nectar into honey, and glands that function in communication, highly specialized leg structures for gathering and carrying pollen, four pairs of wax glands on the underside of their abdomen for the secretion of wax, and a straight barbed sting for the defense of the colony. The queen's sting is curved and smooth and is used only to destroy rival queens.

The worker bees exhibit a well-defined division of labor based primarily upon their physiological age but modified to some degree by the needs of the colony. The physiological age of bees is similar to their actual age during the active season when the colony is raising brood and storing food. During dearth periods, especially in winter, a 60-day old bee may be younger physiologically than a 20-day old bee in summer.

In a general way, bees under 3 days old clean and polish the cells for the queen to lay in and for food storage; those 3 to 7 days old feed the older larvae; those 7 to 14 days old secrete royal jelly for feeding the queen, younger worker larvae, and queen larvae of any age, and they secrete wax for comb building; those 14 to 21 days old forage primarily for pollen; and those over 21 days old forage for nectar. All the bees in the colony probably contribute to the process of changing nectar into honey and in the air conditioning of the colony to maintain a suitable temperature and humidity. Other labor activities include gathering water and propolis, and defense of the colony.

There is considerable overlapping of the age groups engaged in the various duties. When the age groups are not in normal balance, bees of any age can do the work necessary, but not so efficiently. Bees under 3 days old and the field bees can feed the queen and raise brood or they can secrete wax and build comb even though their glands are not fully developed or they have degenerated from lack of use. Similarly, very young bees can forage for pollen and perhaps nectar when there are no field bees of normal age to do this work.

Worker bees inherit many skills man employs that they manifest purely on a behavioral basis whereas man has had to develop these through intellectual inquiry, learning, and experience. They are skilled architects and craftsmen, qualified dieticians and nurses, proficient house keepers, experts in heating and air conditioning, and fully qualified to police and defend their colony.

Their architectural skill and craftsmanship is exemplified by the beauty of the honey comb, its structural strength, economy of material, and the rapidity with which they construct the uniform hexagonal cells. The building of comb is accomplished by first "plastering" the wax into approximate position in the form of round cells, and then thinning down the wax walls to a uniform thickness to produce the hexagonal cells for strength and economy of wax. As dietitians they prepare one kind of food for the queen larvae and another for the worker and drone larvae. Each larva receives approximately 10,000 visits from the nurse bees during development. The hive is maintained immaculately clean at all times, and the guard bees with their stingers for armor protect the hives against all intruders.

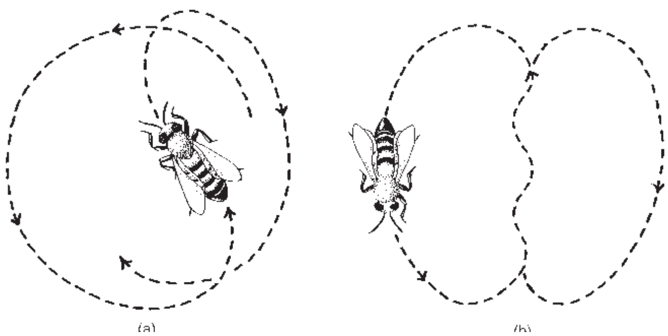
Honey bees, like other insects, are coldblooded and have a body temperature close to that of their environment. However, the honey bee colony functioning as a single organism can maintain uniform hive temperatures under northern winter conditions identical with those in summer or in the tropics. Only recently has man accomplished this by developing elaborate heating and air-conditioning equipment. By clustering together, they generate and conserve heat, or they lower the temperature by evaporating moisture and establishing air currents through the colony to maintain a uniform temperature of 93° F. within the cluster, even though the outside temperature is at -50° F. or 120° F. Under low temperatures, the cluster temperature ranges from 45° F. on the surface to as high as 93° F. within when brood is being reared.

The most conspicuous characteristic dominant in honey bees is their great industry. Honey bees do not procrastinate by doing tomorrow what they can do now. They may fly 50,000 miles and visit 5,000,000 blossoms to gather enough nectar to produce one pound of honey, which is stored not for themselves but for the survival of the colony. The bees that gather this food do not live long enough to enjoy it. One bee, of course, cannot fly such a distance, yet the bees of a colony may store 5, 10, or even 20 pounds of honey in a day. They must gather 200 to 300 pounds of nectar and 50 pounds of pollen (10 gallons) to meet the colony's needs each year. The beekeeper also expects to harvest a surplus of 100 or more pounds of honey for his efforts. The bees have to be industrious to gather so much food, rear so many young, build comb, air condition the hive, and perform all the other duties peculiar to the colony.

How Honey Bees Communicate

A society as efficiently organized as the honey-bee colony certainly would be expected to have a means of communication. The language of bees doesn't involve an alphabet or words and it was little understood until recent years. Professor Karl von Frisch, after some 40 years of observation and research, was able to interpret the language of bees. His experiments clearly showed that the bees have an accurate language based upon characteristic dances, odor, and taste perception. When a foraging bee locates a source of pollen or nectar, she can communicate this information to other bees in the colony accurately as to direction, distance from the hive, and the kind of plants supplying it.

The language dance performed within a colony is oriented on the combs in relation to the sun. The angle between the sun, food source, and hive determines the direction of the dance orientation. A dance straight up on the combs vertical axis means towards the sun; to the right, so many degrees to the right of the sun; and to the left, so many degrees to the left of the sun. A rapid dance means a short distance; a slower dance means increased distance. The bees do not actually have to see the sun to be capable of transmitting or interpreting this food source information since they can perceive and interpret direction from the polarized light they receive from the sky. The plant producing the food is identified by the odor association of the food gathered by the dancing bee.



Assume that a scout bee finds food in an apple orchard one mile to the east in the direction of the sun at 8:00 o'clock in the morning, the dancing forager will move over several cells straight up the vertical axis of the comb, vibrating its abdomen from left to right at a frequency appropriate to the distance. She then turns first right then left to reverse herself and repeats the straight-line run of the wagtail dance, pausing occasionally to give food to surrounding bees. She usually repeats the dance a number of times in one location and then moves on to another and performs the identical dance again. The bees of a certain age respond to food gathering leave the hive in search of food from the same source in the direction and distance indicated by a dancing bee. These bee recruits will not stop to visit plums, pears, dandelions, or some other kind of blossom after receiving the odor association of food from apple blossoms. If food is available from this same orchard at noontime, the dancing foragers will make the straight-line run of their wagtail dance 90° to the left of the vertical axis of the comb. If food is still available in the evening, the dance will orient along the vertical axis but in a downward direction.

Scout bees forage for food sources before the main force of food-gathering bees venture forth to the harvest. The recruited bees also dance when they return to the colony as long as food is available. Thus, the number of foragers increases at a rapid rate, the increase being limited by the food available. When the supply from a given plant species is limited, other scouts from the same colony may find plants of a different species and location producing pollen or nester. Thus, there may be more than one informative dance performed in the hive at one time. Honey bees once oriented to a plant species rarely visit others as long as the first source continues to supply food.

Dances similar to those giving direction for food are performed by scout bees who locate a domicile to be occupied by a swarm that has issued from a colony. There are many other dances performed by bees that obviously extend the area of communication beyond food gathering and locating a domicile.

Bees Do Sting

Many people know only that bees make honey and sting. Practically all bees, hornets, and wasps are stinging insects. Only the females have stingers and only the worker honey bee has a barbed stinger. These barbed stingers are left in you when you are stung. A sting from a bumblebee, hornet or wasp is often more severe than that from a honey bee. If you are attacked by these insects, they are likely to sting several times in rapid succession as their sting is not barbed.

If stung by a honey bee, scrape the stinger free from the wound as quickly as possible. This will reduce the amount of venom injected and the consequent irritation. Because the poison sac of the honey bee stinger is attached to it, any attempt to grasp the stinger to pull it out will only squeeze more poison into the wound.

Beekeepers usually receive enough bee stings to become immune to the swelling within a short time, but the initial pain which lasts 10 to 15 seconds is just as intense following the last sting as the first one. Local swelling following a sting is normal. The various treatments you may have heard about have only psychological value because you do "something."

Stings are rarely serious, though the swelling that follows is uncomfortable for 1 to 3 days if no immunity has been developed. Those rare individuals who experience difficulty in breathing or have some other abnormal reaction following a sting should see a doctor immediately.

If you learn how interesting a study of bees can be before you get stung and your reaction to stings is normal, that is only local swelling with the accompanying itching, you are not likely to let a few stings deter you from the bees. Honey bees will not attack unless they are disturbed by yourself or someone else. Honey bees, like people, differ in temperament. While some strains of honey bees are vicious and some are cross, the great majority can be handled without difficulty. When the bees of a colony are unusually prone to sting, the colony should be re-queened with a more gentle strain.

Avoid Accidents Because of Bees

An accident is unlikely to occur when the element of fear is not present. If a bee stings because it is sat on or gets under a person's clothing, the victim is just as apt to think he or she was stuck by a pin as stung. Bees that happen to get into moving vehicles can cause severe accidents if the drivers or occupants panic because of fear of being stung. It is well to remember that none of the "stinging bees" will attack the occupants under such circumstances, so the driver should pull off the road, stop, and let the bee out.

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Appendix 4

Africanized Bees in North America

by **Michael R. Kunzmann**
National Biological Service
Stephen L. Buchmann
John F. Edwards
Steven C. Thoenes
Eric H. Erickson
U. S. Department of Agriculture

The honeybee genus *Apis* likely has the greatest breadth of pollen diet of any insect and, because of its human-caused cosmopolitan distribution, the species directly affects the reproductive biology of about 25°/a of the world's flowering plants (Schmalzel 1980; Buchmann et al, 1992). This situation has profound consequences for agribusiness, native plants and animals, and ecosystems. In 1956, bee geneticist Warwick E. Kerr imported queen bees of an African race (Apis mellifera scutellata) into Brazil to breed a more productive honeybee that was better adapted to the Neotropical climate and vegetation (Kerr 1967). The following year, 26 of Kerr's Africanized honeybee queens were inadvertently released into the surrounding forest (Winston 1987). Since then, the Africanized hybrids have been expanding their range northward, with an average rate of between 330 and 500 km (200 and 300 mi) each year (Fig. 1).

The first U.S. Africanized honeybee colony was reported in October 1990, at Hidalgo, Texas, along the international boundary. By fall 1993, Africanized honeybees (AHBs) had extended their territory north and west into numerous counties of Arizona, New Mexico, and Texas (Fig. 2). Since the first U.S. AHB swarm was detected, the rate of spread has accelerated to over 600 km (375 mi) per year in the southwestern United States (Guzman-Novoa and Page, 1994).

European honeybees (EHBs) were introduced into North America as early as the 16th century by Spanish conquistadors and missionaries (Brand 1966). Today, one of the three most common subspecies or races of the EHB, the Italian honeybee (A.m. ligustica), is nearly pandemic throughout North America because of its popularity with professional and hobbyist beekeepers. As a consequence, these non-native bees have become naturalized and have been a part of the North American arthropod biota for about 3,500 bee generations, or at least the past 200 years (Buchmann et al.1992). European honeybees are commonly seen visiting agricultural food crops, cultivated flowers, and roadside wildflowers to gather nectar and pollen. They are even common in areas far from human population centers. These bees are also the preferred, "managed" pollinator for over 100 U. S. agricultural crops (e.g., fruits, vegetables, and some nuts), most of which depend on or benefit from insect pollination. The value of these pollination services by EHBs is estimated at $5-$10 billion annually in the United States (Southwick and Southwick 1992).

Africanized and European honeybees represent divergent subspecies within the *mellifera* species of the genus *Apis.* Both have nearly the same biochemistry, morphology, genetics, diet, and reproductive and other behaviors. Their diet includes pollen and spores from most seed plants. Both EHBs and AHBs are social bees living in perennial colonies. They are active on most days collecting nectar, water, pollen, and plant resins for their subsistence. These honeybees "hoard" excess honey as energy-rich carbohydrate reserves in hexagonal wax combs. Energy from honey consumption partially supports brood-rearing and, most importantly, supplies the energy necessary for foraging flights by thousands of adult worker bees.

Africanized and European honeybees exhibit different foraging strategies (largely tropical versus temperate attributes). Africanized honeybee colonies in Africa, and now in much of the Neotropics, are attuned to finding and exploiting isolated mass-flowering tropical trees, and also use pollen and nectar from the nocturnal flowers of bat-pollinated flowering plants. Some tropical *Apis* species even migrate to follow nectar and pollen flows across the floral landscape. Consequently, these trees depend on increased colony mobility (reproductive swarming and abandoning the hive) as behavioral responses to seasonal floral richness or dearths. EHBs are better at hoarding vast amounts of honey and surviving long, cold winters.

Although preliminary evidence for behavioral differences between the two races have been documented in the Neotropics (French Guiana, Venezuela, Panama; see reviews by Taylor 1977; Seeley 1985; Roubik 1989), the behavioral ecology of AHBs and their interactions with EHBs and thousands of species of native U.S. bees remain largely unknown. Africanized honeybees have slightly shorter developmental times than do European bees, enabling them to produce more bees per unit time compared with EHBs. Africanized bees will also accept smaller cavities to nest in than European bees. This behavior increases potential competition for nesting sites with birds and other animals and also increases the potential for greater numbers of honeybee colonies in an area. Africanized honeybees commonly abandon their hives, often 15%-30% annually or even much greater in some localities. Absconding colonies may travel as far as 170 km (about 100 mi) before selecting a new nesting site (USDA 1994). Thus they have been able to rapidly colonize new areas in the Neotropics.

The most often-discussed characteristic separating the two races is the AHBs' propensity to vigorously defend their colony and nest site. Although all honeybees respond to threats to their colonies, AHBs respond more quickly and in much greater numbers than do EHBs. In comparison to EHBs, greater numbers of AHBs will pursue intruders for much greater distances to defend their colonies. Recent research reported that 3 to 4 times as many AHBs responded and left 8 to 10 times more stings in a black leather measuring target in stinging experiments (USDA 1994).

Biochemical comparisons of AHB and EHB venoms indicate they are nearly identical. Nineteen stings per 1 kg (2.21b) of human victim body weight is the predicted median lethal dose (Schumacher et al. 1992). Massive stinging incidents by AHBs are more likely to result in toxic envenomation. Reported 1993 stinging incidents in Mexico have involved more than 60 human fatalities (one death per 1.4 million). From 1988 to 1992, the Mexican national African Bee Program eliminated 117,000 AHB swarms in densely populated urban areas (Guzman-Novoa and Page 1994). To date, the worst U.S. stinging incident occurred in July 1992, when a 44year-old man mowing his lawn experienced a massive bee attack resulting in 800–1,000 stings (McKenna 1992) [Note: Approximately 600–700 stingers were removed from the patient and the patient's jeans were covered with stingers that didn't result in envenomation.]

Ecological Implications

Competition among nectar-and pollen feeding invertebrate and vertebrate pollinators, resource partitioning, insect and plant community interactions, and ecosystem processes are affected by introduced EHBS and AHBs, with important short-and long-term ecological and perhaps evolutionary consequences. The influence of exotic honeybees on individual species or communities of native tropical (or temperate) plants or animals can only have one of three outcomes: the native species will suffer, benefit, or remain more or less unaffected.

The key to understanding these seemingly obvious outcomes is, however, based on obtaining sufficient information to delineate the very complex short- and long-term competitive dynamics between introduced bees, native bees and pollinators, and native plants in diverse, interacting, natural communities.

One observational and manipulative competition study between honeybees, bumblebees, solitary bees, and ants was at mid elevations in the Santa Catalina Mountains in the Sonoran Desert near Tucson, Arizona (Schaffer at al. 1983). Dramatic shifts in abundance of ants and bumblebees were detected when honeybees were present (introduced) or sealed inside their hives. The researchers suggested that direct competition between introduced honeybees and native hymenopteran floral visitors was caused by honeybees numerically dominating the site. Initial evidence seems to indicate that honeybees seek out and preempt the most profitable habitats and partially exclude native bees indirectly by rapidly reducing the standing crop of plant nectar and pollen (Agave in this study).

Both species of non-native bees forage vast expanses of territory containing native and non-native floral resources. Estimates of the amount of terrain foraged annually by an average-sized honeybee colony in New York hardwood forests (Visscher and Seeley 1982) are 80-100 km2 (30-40 mi2). Forage area estimates for AHB colonies living in lowland Panamanian rain forests (Roubik 1989) are 200-300 km2 (75-115 mi2), although 90% of these foraging flights are completed within 5 km (3 mi) of the nest (Visscher and Seeley 1982). Even given this restrictive caveat, the amount of "bee pasture" grazed by these aerial herbivores is immense.

In studying honeybee colonies foraging in temperate forests in New York State, Visscher and Seeley (1982) found that these cold-hardy EHB colonies amassed 15-30 kg (33-66 lb) of pollen and 60-80 kg (132-176 lb) of nectar honey each year. To collect this amount of food, a colony must dispatch tens of thousands of foragers on many millions of foraging bouts with the bees flying 20-30 million km (12-19 million mi) overall. Similar studies of AHBs in Panama (Roubik 1989) determined that AHBs placed more emphasis on pollen collection. The Sonoran Desert of northern Mexico and southern Arizona is perhaps one of the richest areas in the world in floral resources because of the relative high plant diversity and the many fair-weather days for worker bee foraging.

Many important nectar-and pollen-producing plants visited by AHBs bloom at night and are pollinated by bats. Africanized honeybees find and exploit these rich flowers at first light, and we predict that saguaros and other columnar cacti will be heavily used as food plants for AHBs in Arizona. Early Arizona data for AHB colonies illustrate that most AHB colonies have been found in the subtropical climate zones in Sonoran desertscrub.

Determining which plants are used primarily for nectar versus pollen, or both, depends on direct observations of bees on flowers or indirectly by identifying pollen grains in stored nest samples of honey. In Panama, Roubik (1989) found that AHB colonies harvested pollen from at least 245 flowering plant species in a forest containing about 800–1,000 species. European honeybees collected pollen or nectar from about 185 plant species from a secondary forest and agricultural area in Mexico (Villanueva 1984). These studies suggest that honeybees are using about 25% of the local flora, but intensively use far fewer species at any given time (Roubik 1989). In Arizona EHBs will often harvest pollen from more than 60 species annually, but of these, only 10-15 are harvested heavily and consistently from year to year (Buchmann et al., 1992). Because of their pollen herbivory and reproductive contact with so many plants, there can be serious long-term ecological and evolutionary consequences of these interactions that we simply do not yet understand.

Ecological Monitoring

Although we have made a case for potential serious, competitive displacement of food resources by honeybees to the exclusion of some native bees and pollinators, there is a little-appreciated yet unique ecological application for using EHB colonies (A. mellifera) as short-and long-term local and regional monitoring devices of vegetation diversity, plant productivity, flowering phenology, precipitation, climate, and general ecosystem health. No expensive equipment is required since the bees do all the "fieldwork." In addition, floral changes in landscapes can be determined from the rich "fossilized" source of pollen dietary information in old, dark brood combs or in 75 to 100-year-old "debris middens" in the Sonoran Desert (Buchmann et al., 1992). Long-term records (some spanning decades) for certain beekeeping locations are invaluable aids to beekeepers, ecologists, and resource managers for ecological evaluation and monitoring.

To validate any AHB range-expansion prediction or to measure potential effects on native pollinators or ecosystem components, we must monitor the bees and evaluate habitats on national and local scales. Information must be collected, integrated, and shared by researchers, individuals, and agencies. Public-and private-sector partnerships have been developed to exchange AHB information and develop monitoring protocols.

Researchers use geographic information systems (GIS) and global positioning systems (GPS) technologies to track the locations of known AHB and EHB colonies; delineate honeybee habitat parameters such as preferred vegetation community, climatic zone, elevation, and distance to water; investigate potential ecological consequences to native bees and other nectar-dependent species: monitor and detect habitat productivity changes; and develop computer models to illustrate and predict preferred AHB habitats and potential ecological consequences (Fig. 3).

The Future

Knowing how far north AHBs will spread is critical in predicting their ecological effects. There is general agreement that they have a climatic limit, but precise limits of their U. S. range expansion is disputed. Some researchers suggest that all will disperse almost as far north as Canada; others propose that they will go no farther than the U.S. southwestern and southeastern corners. In all likelihood, AHBs will become established as a dominant ecosystem forager in the southern third of the United States, where EHB overwintering behaviors less critical for survival. If conditions are favorable, however, the AHBs may expand into marginally productive or colder habitats in higher latitudes or elevations.

While the ecological range limits and economic consequences of non-native AHB migration into the United States are not precisely known, researchers agree that honeybees are economically important, and that sufficient biological information exists to develop adequate inventory and monitoring programs. Added benefits to honeybee monitoring programs are also important because bee colonies can also serve as excellent indicators of flowering plant productivity, ecosystem stability, and relative ecological health.

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