Solitary Bees

Most species of bees are not social like the honeybee. They are solitary, meaning that the female builds her own nest. They play a profoundly important role in pollinating crops and wild plants

by Suzanne W. T. Batra

For most people the beehive and the intricate social organization of the honeybees that populate it are the hallmark of bee life. In reality more than 85 percent of the some 20,000 bee species are not social but solitary. Each female independently mates, makes her own nest of about 10 brood cells, stocks the cells with food for the young, lays an egg in each cell and dies before the next generation emerges. The solitary bees play immensely important roles in ecological systems, particularly in the pollination of crops and wild plants. Indeed, farmers in some parts of the world are beginning to make specific arrangements to accommodate solitary bees for the pollination of crops (such as alfalfa) that are not pollinated effectively by honeybees.

Bees apparently evolved from predaceous ancestors such as the solitary mud-dauber wasps in about the middle of the Cretaceous period (100 million years ago), when flowering plants became the dominant vegetation on the earth. Now bees live everywhere, showing the greatest abundance and diversity of species in semiarid, warm temperate climates. Many solitary bees do not resemble honeybees in general appearance but instead look more like wasps, flies or bumblebees. They range in length from 1.5 to 46 millimeters. Some species are hairless and shiny, others are densely furry. Although many of them are drab, some (such as the emerald green orchid bees) are quite beautiful. The hair or the spots and stripes may include all the colors of the rainbow.

Solitary bees are distributed among nine families: the Colletidae, or membrane bees, which are most numerous and diverse in the Southern Hemisphere; the Andrenidae, or digger bees, which are mainly in the Northern Hemisphere; the Halictidae, or sweat bees (so named because they are attracted by human sweat), of worldwide distribution; the Megachilidae, or leafcutter and mason bees, also worldwide; the Anthophoridae, or carpenter and miner bees, predominantly tropical; the Melittidae, Oxaeidae and Fideliidae, which are small families with a limited distribution and no common names, and the Apidae, or honeybees, stingless bees and orchid bees, all of which are mostly tropical, and bumblebees, which are mainly in the Northern Hemisphere and are the most able of all the bees to tolerate low temperatures.

The nests and brood cells of most solitary bees are made underground. Bare, dry, light soil exposed to the morning sun is preferred. In such habitats many nests of their relatives, the ants and the solitary wasps, may also be found. In a favorable area thousands of nests of ground-dwelling solitary bees may form dense aggregations. The females do not, however, cooperate in nest-building chores.

The largest recorded aggregation of nests occupied about 360,000 square meters extending for seven kilometers along a bank of the Barysh River in the U.S.S.R. It consisted of an estimated 12 million nests made by two species of sweat bee and a species of miner bee. In about mid-May every year I receive at my U.S. Department of Agriculture office in Beltsville, Md., many agitated telephone calls about swarms of solitary bees nesting on lawns in the Washington area. These are usually the membrane bee *Colletes thoracicus,* which is active as an adult for about six weeks. The largest aggregation of this honeybee-size insect included about 104,000 nests in a suburban backyard of 1,187 square meters.

Aggregations of nests may persist for many years. For example, a species of miner bee has occupied an adobe wall near Baltimore for at least 40 years. The aggregations are probably maintained because the young females on their first flight memorize visual landmarks in the area, just as new honeybee workers remember the location of their hive. Pheromones (chemical signals) or odors released by other females in the aggregation may also be attractive. After mating, a young bee returns to make her own nest among the other nests in an environment shown to be satisfactory by the survival of her ancestors.

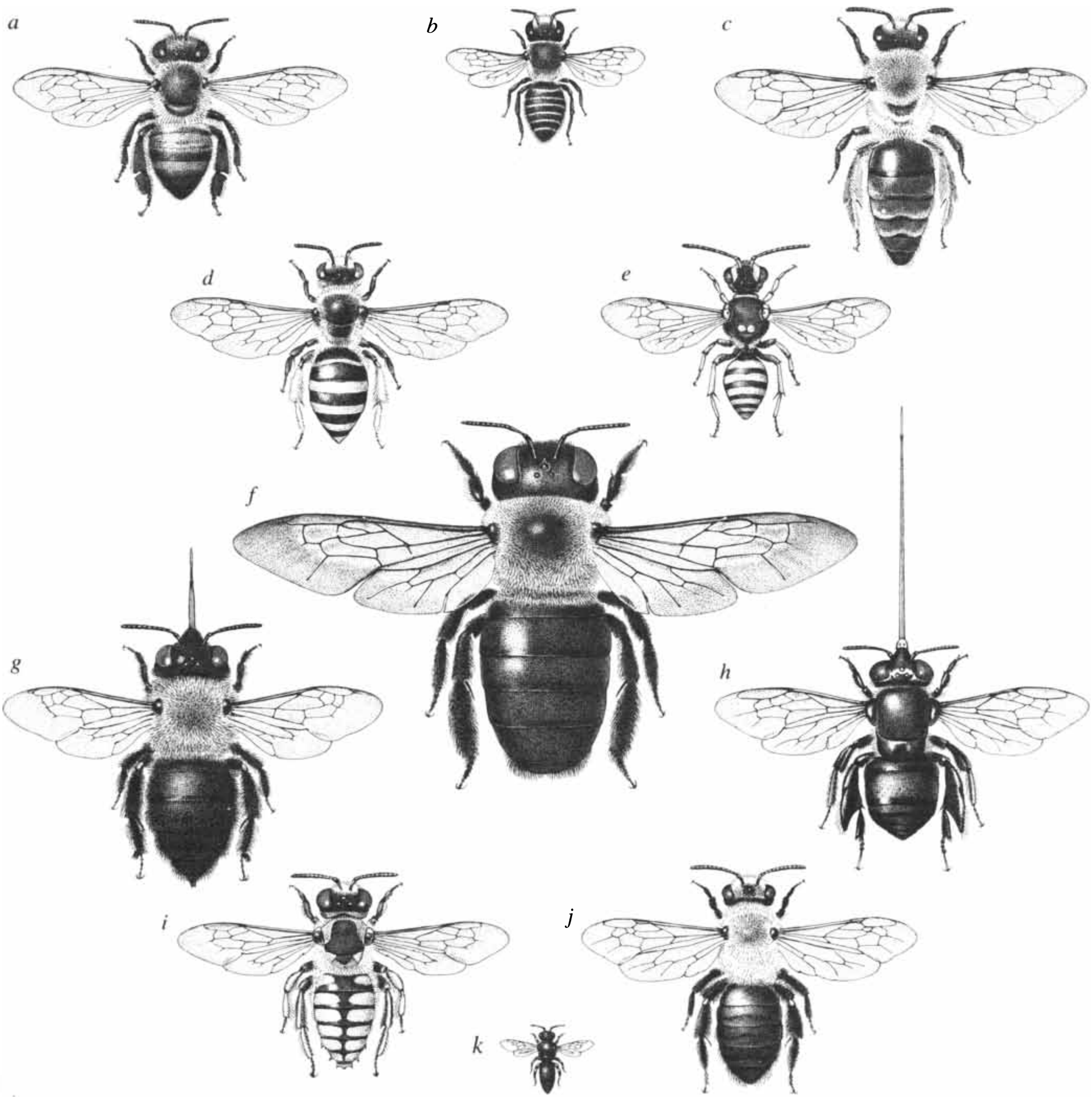
Bees that nest in the ground usually have plenty of room for nest sites. They face, however, the problem of protecting for almost a year the nutritious honey-and-pollen provision they have laid up for their brood (and the delicate, helpless, grublike brood itself) from soil moisture and a wide variety of soil organisms such as bacteria, yeasts, fungi, nematodes and mites. The large majority of ground-dwelling bees line their underground brood cells with special waterproof secretions before provisioning them. These bees possess an abdominal gland (Dufour's gland) that opens near the sting. In some species it occupies half of the abdominal cavity. The gland contains an oily liquid of a fragrant-to-musky odor. (A few species collect plant resin or cut pieces of leaf to line their brood cells. The Fideliidae and other bees that live only in deserts do not line their cells at all.)

By inducing bees to nest in narrow, glass-sided chambers filled with soil I was able to observe their subterranean nest-making behavior. After a chamber for a cell is excavated by the bee and often polished to a shiny smoothness by the pygidial plate at the end of the abdomen, dollops of Dufour's-gland secretion are deposited in it and are repeatedly smeared around by rhythmic sweeps of the bee's tongue, by special velvetlike pads on the abdomen or by hairy brushes on the legs. Most solitary bees fly about during the day collecting provisions, lay an egg in the afternoon, seal the cell, begin digging a new cell chamber in the evening and apply the Dufour's-gland secretion at night, so that the new cell is dry and ready for provisioning the next morning. Such bees work day and night with little respite.

Henry M. Fales and Abraham Hefetz of the National Heart, Lung, and Blood Institute and I analyzed the secretions of *Colletes* membrane bees. We found that the Dufour's gland contains fragrant, musky-smelling compounds (macrocyclic lactones). When they are deposited in the brood cell, they polymerize to form a flexible, transparent, waterproof membrane composed of a natural polyester (mainly 18-hydroxyoctadecanoic acid and 20-hydroxyeicosanoic acid). The membrane forms a miniature plastic bag in each cell. The bag even has a "zip lock" closure: a flap that is lifted and sealed by the female bee after she has laid an egg. The membrane is quite durable, remaining intact in soil for a year or more.

For comparison we also analyzed the Dufour's-gland secretion and brood-cell lining of *Anthophora abrupta,* a miner bee. This bee's large Dufour's gland holds a mixture of transparent, slightly fragrant oily triglycerides. When they are secreted into the brood cell, they are converted, possibly by salivary enzymes, into white, waxy diglycerides with a rancid odor. This secretion is also added to the provision for the larvae. The developing larvae eat it and even rasp away and eat the cell lining. Until the miner-bee larvae's feeding habits were discovered the honeybee was the only bee known to feed its larvae with a secretion (royal jelly, secreted orally and consisting mainly of protein).

Bees that do not live underground need not protect their young so carefully from excess moisture, and probably for this reason they have relatively small Dufour's glands. Most ma-



SOLITARY BEES are compared with the honeybee, *Apis mellifera* (*a*), in drawings that are done to a common scale. The solitary bees are the alfalfa leafcutter, *Megachile rotundata* (*b*); the membrane bee, *Colletes thoracicus* (*c*); the alkali bee, *Nomia melanderi* (*d*); a cuckoo bee, *Nomada luteoloides* (*e*), so named because it lays its eggs in the nests of other solitary bees; the carpenter bee, *Xylocopa virginica* (*f*); the miner bee, *Anthophora abrupta* (*g*); the orchid bee, *Euglossa ignita* (*h*), shown with its unusually long tongue extended; a mason bee of the genus *Anthidium* (*i*); a digger bee, *Andrena carlini* (*j*), and a silk-making membrane bee of the genus *Hylaeus* (*k*). In life *Hylaeus* is four millimeters long. The bees portrayed represent only a few of the many solitary-bee species, of which there are some 17,000.

son bees and leafcutter bees use existing aboveground holes as nests, building brood cells of mud, resin and plant fiber or of neat layers of ovals and circles precisely cut out of leaves and petals. Leafcutters may damage plants. In an extreme example the yield of two hectares of soybeans was reduced 30 percent by the removal of leaf tissue by bees nesting nearby. Some mason bees build clustered brood cells of mud or resin on branches or walls. One common species of solitary bee is notable for defacing Egyptian and Greek monuments with its numerous large, lumpy nests of dried mud.

Carpenter bees drill neat round holes with their powerful mandibles into wood, bamboo or pithy stems. In their galleries they construct series of brood cells separated by partitions of agglutinated sawdust. They sometimes do significant structural damage to the beams or eaves of buildings.

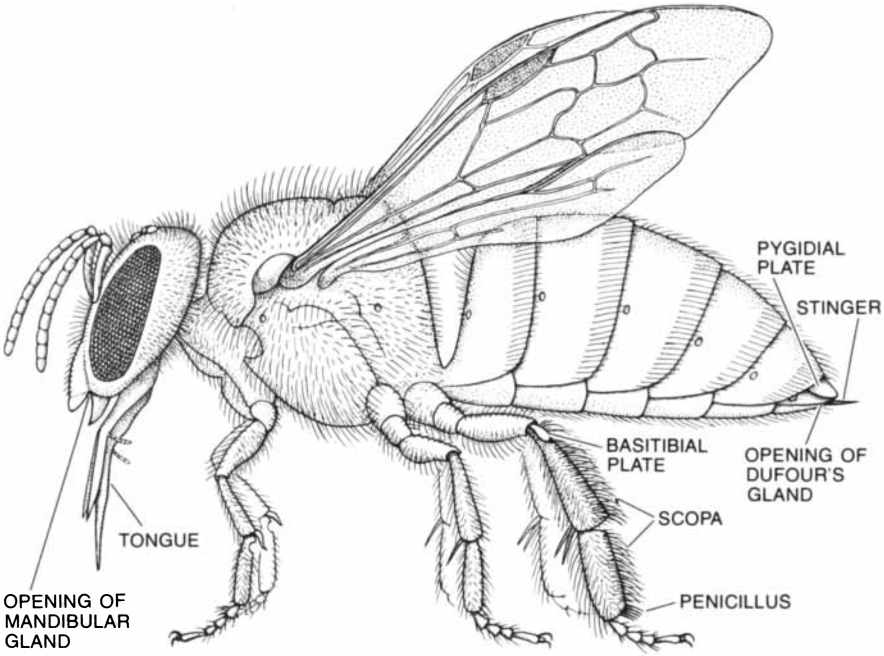
Membrane bees of the genus *Hylaeus* are wasplike in appearance and carry provisions internally as wasps do instead of on special hairs in the manner of other bees. *Hylaeus* bees are unique in making brood cells of true silk inside existing holes. The silk is secreted orally and applied by the female bee's broad tongue. Small predatory wasps belonging to the family Pemphredoninae also (uniquely among wasps) make cells out of silk. It is possible that bees have evolved, through primitive forms such as *Hylaeus,* from this group of wasps. The secretion of silk by adult insects is quite rare.

Most female solitary bees, like the honeybees and the bumblebees, can defend themselves individually by stinging, but their venom is usually mild. The nests of solitary bees, unless they are densely aggregated, seldom attract vertebrate predators to their meager provisions and brood. Therefore the bees have not developed the aggressive mass-stinging counterattack provoked when honeybee and bumblebee nests are disturbed. Solitary bees' nests, however, are particularly vulnerable to attack by other invertebrates and by microorganisms, and the bees have evolved ways to repel them.

Fungi are the primary enemies of solitary bees that nest underground. The bee must work quickly to finish the preparation of the provision and to lay an egg so that the larva can consume the food before it spoils. The brood-cell lining isolates the contents from free water in the soil. Water vapor enters many cells, however, along with the gases needed for the respiration of the larvae.

The provisions of most bees consist of a mixture of honey and pollen. The sugars of the honey are hygroscopic (they attract moisture from the air), and so they may gradually become more dilute. This may account for the fact that bee larvae may weigh more than their provision originally did. All is well with this system unless populations of yeasts and bacteria in the provision explode. These microorganisms, usually present in the nectar from flowers, are normally deposited along with the provision. Their growth is prevented, however, by the high sugar concentration; with solitary bees, as with honeybees, the excess water in the honey evaporates away as the flower nectar is converted into honey by enzymatic reactions. If yeasts grow unchecked, the bee larva gets indigestion and becomes weak or dies. The fermented provision is then overrun by filamentous fungi.

Working at Utah State University with two of my colleagues in the Department of Agriculture (George E. Bohart, an entomologist, and my husband Lekh R. Batra, a mycologist), I found that bee adults and broods are attacked by at least 124 species of fungi. The solitary alkali bee has developed an interesting method of protecting its brood from some of the 49 species of fungi that afflict it. In common with most other solitary bees the alkali bee seals each cell after provisioning it and laying an egg. It has long been assumed that such "mass provisioning" bees have no further contact with their young. When the contents of a cell become infested with a fungus, however, the mother bee opens the cell and packs soil into it. This procedure reduces the amount of air available for the growth of the fungus and so prevents the fungus from spreading to adjacent cells. Although some soil-dwelling bees may annually lose as much as half of their brood to fungi, the species that nest in drier sites such as sound wood, stems and adobe walls are usually less severely affected.



FEATURES OF THE ANATOMY of typical solitary bees include the pygidial plate, which the female uses to smooth the inside of a nest she has excavated in the ground, and Dufour's gland (within the abdomen), with which she applies a secretion that waterproofs the inside of the nest. Mandibular-gland secretions serve in communication and self-defense. The scopa, which in some species is on the abdomen, is an array of hairs for carrying pollen. A solitary bee walks on its knees (the basitibial plates) when it is excavating or provisioning its burrow.

Specialized solitary bees, known as cuckoo bees or inquilines, are common parasites of other solitary bees. Like its bird namesake, a cuckoo bee does not make its own nest but instead lays its eggs in the nests of other bees. About 15 percent of all bee species are cuckoo bees. These parasites may be quite host-specific, each attacking a single host or a group of related host species. Most families of bees include some cuckoo species, which may attack hosts belonging to their own family or to other families. The young larvae of many cuckoo bees have long mandibles that serve to crush the larva of the host bee; older cuckoo-bee larvae, feeding after the host has been eliminated, have normal small mandibles. Usually the most easily observed cuckoo bees are the slender, wasplike, rust-colored or yellow-and-black species of *Nomada* (Anthophoridae), which flit about in early spring near the ground among the woodland flowers in search of temporarily unoccupied nests of their *Andrena* hosts.

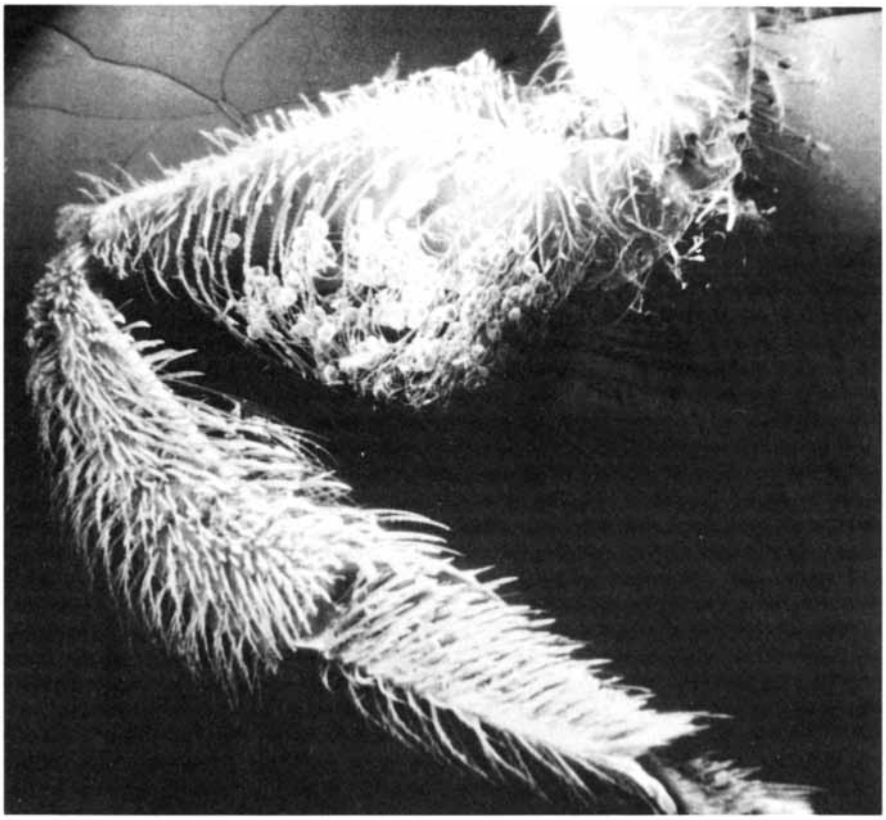
A solitary bee must spend several hours daily away from its nest foraging for nectar and pollen. During this time the helpless brood is particularly vulnerable. The brood cells of some species are tightly sealed with a thick cap of resin, secretion or clay, but the cells of many solitary bees have a permeable cap of lightly packed soil, leaves or wood dust that is readily penetrated by insect parasites and predators. The mother bee may try to protect the nest in her absence by positioning it so that the entrance is hidden, by temporarily filling the burrow with soil, by heaping soil in a small tumulus over the entrance or by building a compact turret of earth that may deter crawling insects. Nevertheless, solitary-bee broods suffer losses to a variety of predatory and parasitic wasps, ants, several kinds of flies and beetles, strepsipterons, mites and nematodes. Some of the parasites deposit their eggs or larvae on flowers, where they are accidentally picked up by the foraging bee, brought home to the nest and included in the brood-cell provision, where they lie ready to attack the bee larva.

The colorful, symmetrical and fragrant blossoms of higher plants evolved to attract pollen-dispersing animal life. Bees are the most efficient and effective of all pollinators for several reasons, including their sheer abundance, their rapid flight, their tendency to visit several flowers of the same species in succession, their need for large quantities of nectar and pollen and their specialized hairs, which can trap and hold as many as 15,000 pollen grains per bee.

An individual bee may possess several types of hair, which are grouped on the body and legs according to their function. The dense hairs on the hind legs of most solitary bees form a pollen-holding brush called the scopa. (In leafcutter and mason bees it is below the abdomen.) Honeybees and their relatives have shiny bare patches on their hind legs known as pollen baskets or corbiculae, which carry nectar-moistened lumps of pollen or nesting material. The hairs of bees are modified according to the type of pollen collected by the particular species. For holding fine, dry pollen grains a cluster of downlike, branched, plumed hairs is best. Large or sticky pollen grains call for stiffer hairs. Such hairs often have shorter branches or are formed with spiral ridges resembling a corkscrew. They may also have spatulate or hooked tips.

Combs of bristly hairs on the legs and mouthparts of bees serve for grooming and for transferrring pollen to the scopa. The Dufour's-gland secretion is applied with special straight hairs in tufts resembling a paintbrush. To collect floral perfumes or plant oils some solitary bees have velvety hairs that form sponges and flattened hairs arranged in combs.

The value of bees for the pollination of wild plants and crops is incalculable. No price can be placed on wild plants, which are pollinated primarily



POLLEN-CARRYING APPARATUS is the scopa, the group of branched hairs near the top of this electron micrograph of the hind leg of a sweat bee of the genus *Lasioglossum*. Several spherical grains of pollen are visible in the scopa. The enlargement is about 62 diameters.

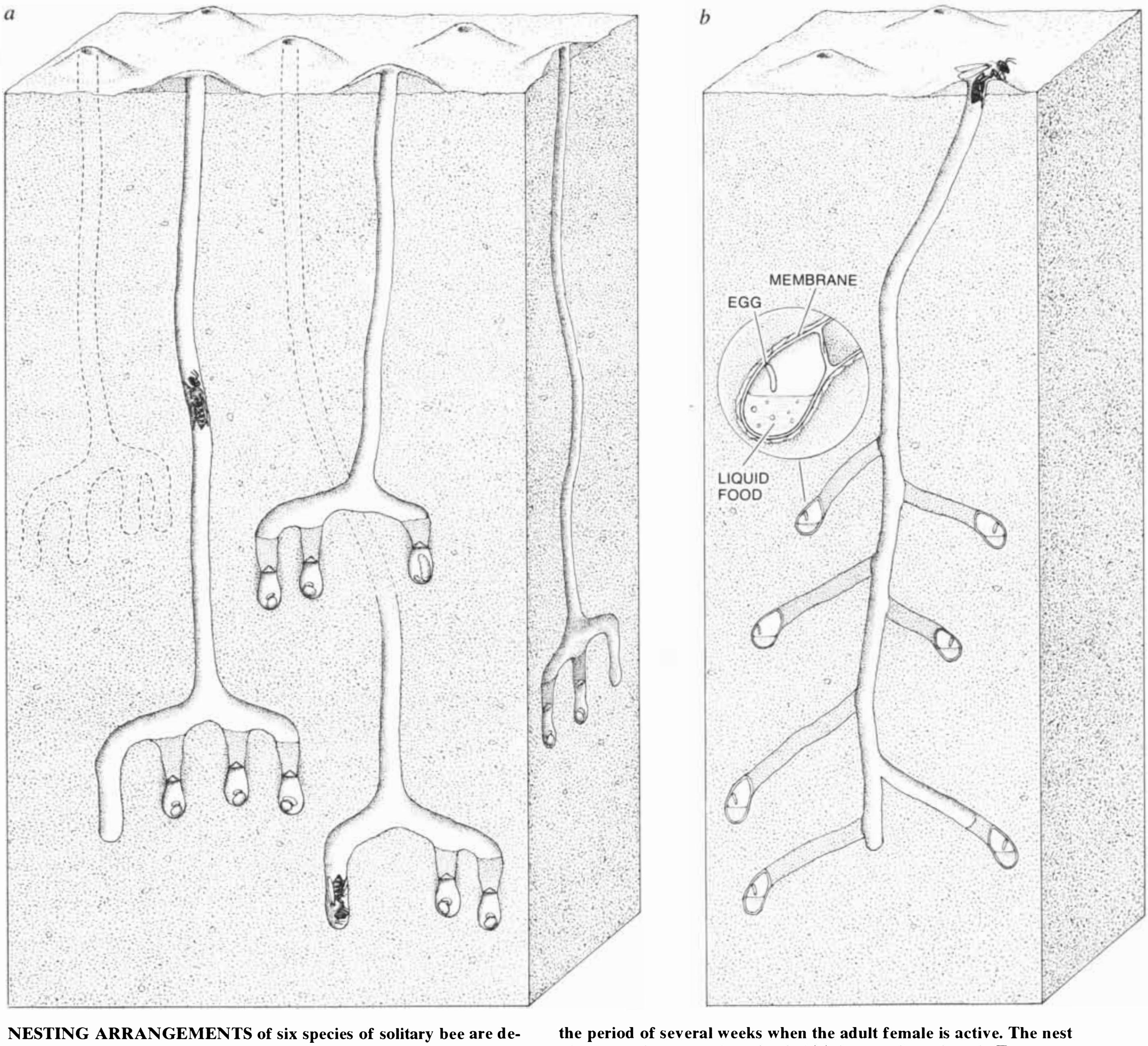
INNER SURFACE of the sweat bee's hind leg shows (*left*) the spiral-ridged hairs that serve to manipulate pollen and (*lower right*) the penicillus, used somewhat like a paintbrush for spreading a waterproof secretion in the nest. The enlargement of the hairs is 300 diameters.

by solitary bees. It has been estimated that in the U.S. the value of some 90 crops that depend on insect pollination for maximum yield is $17 billion per year. If seeds of insect-pollinated forage plants for livestock are included, about a third of the nation's food supply depends directly or indirectly on pollination by insects, mainly bees. It is reasonable to assume that solitary bees account for at least half of this crop-pollination activity in the U.S. and perhaps more in areas where beekeeping is less prevalent.

Unfortunately populations of solitary bees decline under the conditions of large-scale modern agriculture and urbanization. When large fields of single crops are planted as monocultures, where all plants flower simultaneously for a short time, solitary-bee populations may be insufficient to handle the pollination, and when the flowers finish blooming, nothing is left for the bees to eat. Cultivation and construction eliminate supplementary floral hosts and nesting areas. Irrigation may destroy nests. It also increases the damage done to the bee brood caused by fungi. The careless application of pesticides kills many bees. The sulfur dioxide in polluted air can cause bees to reduce their flying time.

These effects can be observed by comparing, say, the bee populations on flowering apples in the center of a large, well-sprayed commercial orchard with the bee populations on flowering trees in abandoned orchards or at the edge of a forest. In order to achieve adequate pollination in the absence of enough native bees, growers have to rent hives of honeybees from beekeepers at a cost of about $20 per hive. Hundreds or even thousands of hives may be needed. The value of pollination services far exceeds the value of the honey and wax obtained from honeybees.

Honeybees pollinate many types of plant, but some plants are pollinated only ineffectively. For example, the flower of alfalfa has a little spring in it that is triggered when a bee pushes her head into the flower. The stamens pop



NESTING ARRANGEMENTS of six species of solitary bee are depicted. Each nest has several individual cells, each of which the female supplies with provisions for the larva before she lays an egg. The cells are usually made at a rate of one a day (in good weather) in the period of several weeks when the adult female is active. The nest of the alkali bee, *Nomia melanderi* (*a*), is made in moist soil. The membrane bee, *Colletes thoracicus* (*b*), which also nests in soil, gets its common name from the fact that it lines the inside of each cell with a poly-

up and rap the bee on the head, dusting her with pollen. Honeybees apparently do not like being rapped on the head, and since they are fairly intelligent insects, they learn to poke their long tongue into the side of the flower, avoiding the spring. Thus they take nectar but accomplish no pollination. Because alfalfa is one of the major forage legumes, the supply of seed (a $100-million-per-year industry in the U.S.) is of critical importance.

In the northwestern U.S. and Canada two species of solitary bee—the alfalfa-leafcutter bee and the alkali bee—are intensively managed to pollinate alfalfa. These persistent insects do not seem to mind being rapped by the flowers, and they collect the pollen for provisioning their nests as it is showered on them. The alfalfa-leafcutter bee, originally European, quickly visits many flowers in succession and is a highly efficient pollinator. It nests in groups. Farmers make suitable holes in "bee boards," which they put in shedlike shelters in the alfalfa fields. The brood cells of this bee are built out of bits of alfalfa leaf.

The alkali bee is a species of sweat bee native to the U.S. It likes to nest on alkaline flats, where the subsoil stays fairly moist. Growers who accommodate this bee construct "bee beds," which consist of plastic-lined trenches in the alfalfa fields. The trenches are filled with specially prepared soil that is maintained at just the right level of moisture to attract and hold dense aggregations of alkali bees. There may be as many as 2,100 nests per square meter.

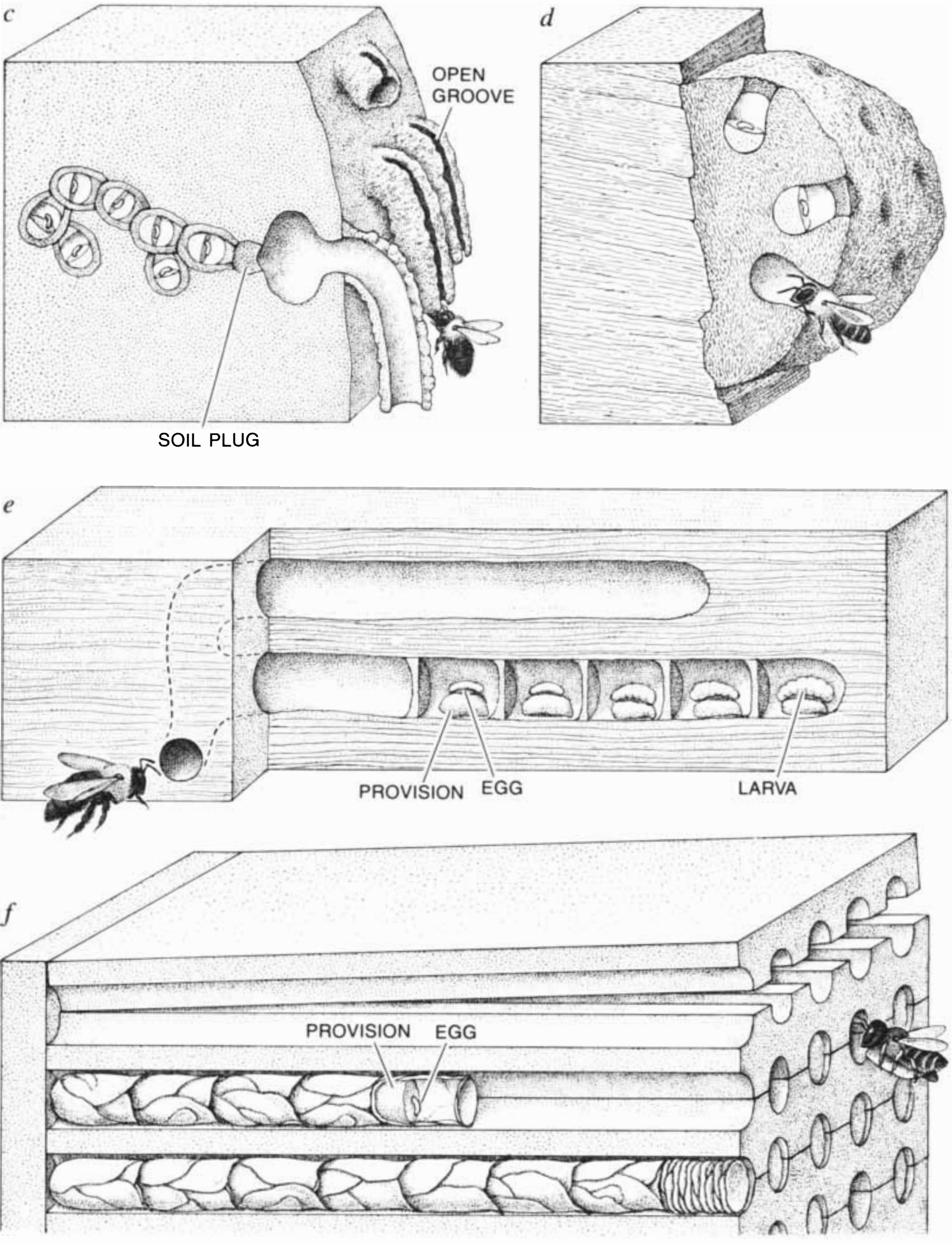
Another solitary bee utilized commercially is a mason bee, the Japanese hornfaced bee. Apple flowers are often not pollinated efficiently by honeybees, which tend to work slowly, to avoid touching the stamens and to fly away to forage on dandelions and other weeds. Some 40 years ago Japanese farmers noticed that the little hornfaced bees nesting in their thatched roofs were energetic and effective pollinators of apples. Over the years the management of this bee has been perfected, and bee shelters containing hollow reeds for nesting are seen throughout the apple-growing districts of Japan. Recently, in collaboration with Yasuo Maeta of Shimane University and other Japanese workers, I have successfully established populations of this Asian pollinator in the eastern U.S., where it is being tested for its adaptability to the climate and its acceptance of the available nesting material.

Many species of bees have life cycles and habits that depend on the availability of specific host plants. Bees that gather pollen from one species or a few closely related plants are termed oligolectic. Bees such as the honeybee, which can gather pollen from a variety of plants because of the hive's long collective period of adult activity, are termed polylectic.

Flowering plants and oligolectic bees have developed some remarkable mutualistic relations. For example, the American native gourds are most effectively pollinated by squash bees, which are several native species of miner bee. Some species of sweat bee pollinate evening primroses and fly at night, which is unusual for bees. This activity is aided by their eyes, which are enlarged for light gathering. Other specialized miner bees pollinate wild morning glories. Perhaps the most highly specialized solitary bees are those visiting flowers that yield oils, which are collected instead of nectar (for mixing with pollen in the provision for the brood); to pick up the oil these bees have hairs arrayed in comblike structures.

Orchids are among the most specialized of flowers. Some of them have evolved unique ways of exploiting the behavior patterns of solitary bees. Some orchids have false nectaries: colored spots yielding no nectar. When a bee probes a false nectary for nectar, a pollinium (pollen packet) is attached to the insect, which carries it along to pollinate the next orchid. This deception works until the bees learn that the nectaries yield nothing.

Other orchids have color patterns and aphrodisiac odors that resemble the ap-



ester membrane of its own making. The miner bee, *Anthophora abrupta* (*c*), employs a different technique in dry soil. The mason bee of the genus *Chalicodoma* (*d*) builds its nest on the surface of wood or rock; the carpenter bee, *Xylocopa virginica* (*e*), drills into wood. Some growers of alfalfa make grooved "bee boards" (*f*) for alfalfa-leafcutter nests to aid pollination.

pearance or the odor of female bees or wasps. Males are attracted. They try to copulate with the flower and in so doing pick up a pollinium, which is deposited at the next enticing orchid. Still other orchids mimic certain male miner bees. When an aggressively territorial male bee sees the orchid flower nodding in the wind, the bee strikes it in an effort to drive the "rival" away. As a result a pollinium is stuck to the bee's head.

The most complex relation is the one between certain South American orchids that yield neither nectar nor pollen and several species of orchid bee. The male bees have swollen hind legs with hair-lined slits leading to internal pockets and have velvety pads on their front feet. The males form leks, or all-male swarms, that attract females for mating. Certain males are more attractive than others because they have collected mixtures of fragrances from the orchids. They brush the flower's odor glands with their front feet and stuff fragrant particles into their hind-leg slits. While the bee is doing so it picks up a pollinium from the orchid. Since these bees can fly as far as 23 kilometers in a day, they are effective pollinators for sparsely distributed plants, such as certain of the orchids.

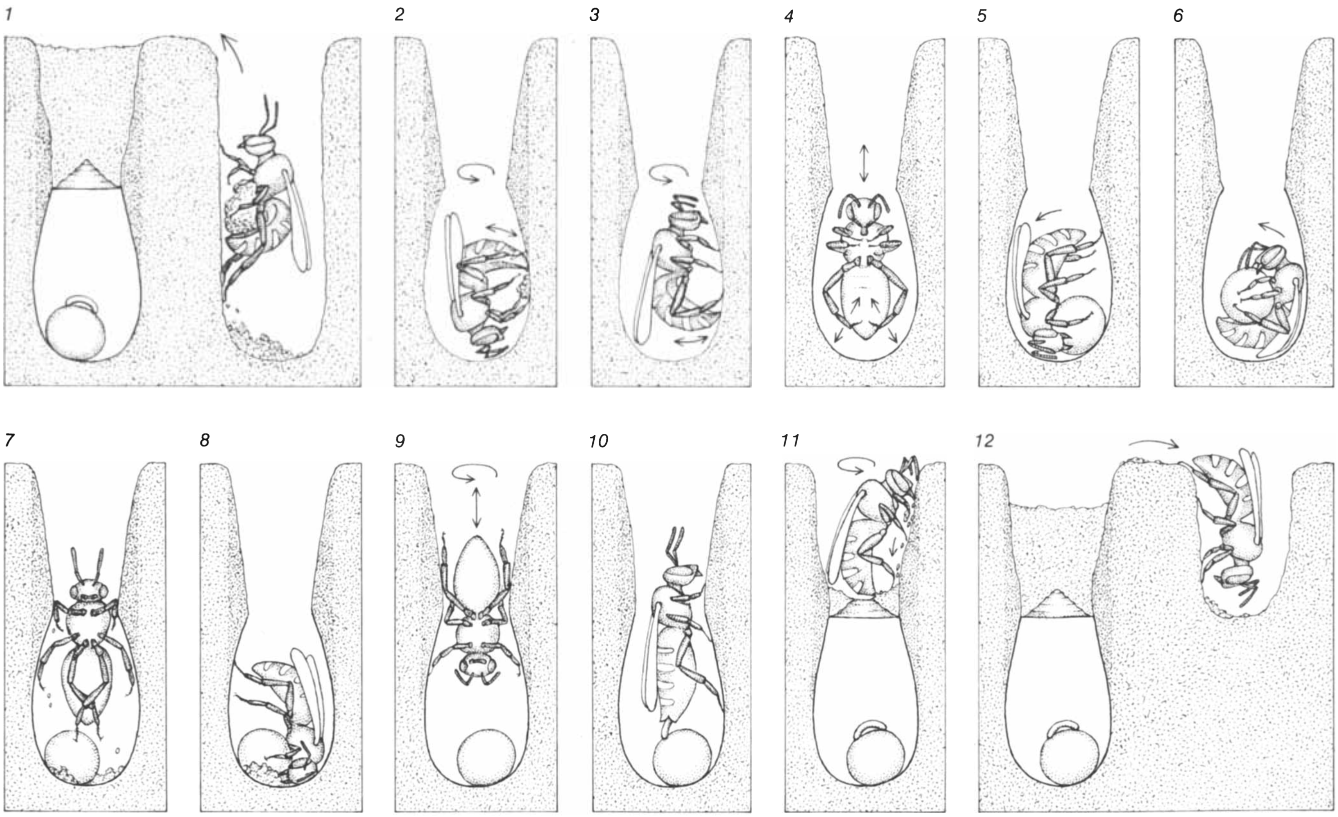
Orchid bees apparently respond to other odors. Males of one species have become a nuisance because they are attracted to houses that have been dusted with DDT for mosquito control. They collect the powder and pack it into their leg slits. The compound does not seem to harm the male bees, but whether or not it has the intended aphrodisiac effect on the females is not known.

Male solitary bees ordinarily emerge from the pupa a few days earlier than the females of their species. They feed on floral nectar and pollen and search for newly emerged virgin females. In some species the males form loose groups that jointly patrol the nesting site, nearby landmarks or flowers that are regularly visited by females. When males see a female bee or an object shaped like one, they pounce on it, but unless a sex pheromone is present they let it go immediately. If a virgin female appears, a pile of writhing males, all attempting to mate, may form rapidly on top of her. Usually the first male to grasp the female holds on to her tightly and succeeds in mating. Males of most species merely compete to reach the females first and are not noticeably aggressive toward one another. In some species of carpenter bee and mason bee the males are aggressive and battle to exclude other male bees from their small home territory.

In ancient India the territorial battles of carpenter bees were called "bee sport." It is said that the homing of such bees was exploited for the carrying of tiny messages. Much of the carpenter-bee activity noticed by homeowners today consists of males zooming after one another and even heading in the direction of passing birds and airplanes. The territorial males stage battles of bluff, zigging and zagging face to face until one of them gives up and leaves.

Some *Anthidium* mason bees are unusual among insects because the males are larger than the females. The reason is probably that the males butt and grapple with each other in their aerial battles; physical strength and weight would make it easier to retain a territory visited by females. These males attack other insects that wander into their territory. They can break the intruder's wings with their strong mandibles and puncture its body with their stout abdominal spines. Curiously, male bees that fight over territory during the day may cluster together peaceably in the evening as they sleep.

In 1802 the naturalist William Kirby



NEST-MAKING ACTIVITY of an alkali bee, *Nomia melanderi*, is followed over a period of 24 hours. At the outset (*1*) the female has finished one cell and has begun excavating another. When she reaches the appropriate depth, she packs soil along the edges (*2*). Then she smooths the inside of the cell with her pygidial plate (*3*) and applies a waterproof lining with a secretion from her Dufour's gland (*4*). Now she is ready to lay in provisions (*5, 6*), consisting of a honey-pollen mixture, which will sustain the larva. After grooming the ball of provisions (*7*) and removing debris from the cell (*8*) she does more polishing of the cell walls (*9*) and lays an egg (*10*). She caps the cell (*11*) and adds a plug of dirt that comes from the early stages of her excavation of what will be the third cell in the nest-building cycle (*12*).

wrote: "I have often thought that if gentlemen, who amuse themselves with chemical experiments, should direct their attention to insects, it might lead to the discovery of some powerful medicines. The variety of strong scents, which these little creatures emit, is wonderful.... Many Melittae have a strong scent, in some approaching to that of garlick or onion." An interesting if somewhat risky pastime is to carefully sniff captive live bees and wasps, which indeed produce a spectrum of odors that evidently serve in communication and defense. Small glands at the base of the mandibles release when the mandibles are opened various combinations of terpenes, aldehydes, ketones, esters, pyrazines and other pungent or fragrant compounds.

Some male bees apply such secretions to vegetation to delineate their territory. In other species the secretions serve as attractants for one or both sexes. For example, if a large number of bees such as species of *Colletes, Nomia* or *Anthophora* are netted at an aggregation of nests, they bite the net in an effort to escape, releasing mandibular-gland secretions as they do so. Other bees downwind are attracted toward the netful of captive bees. That it is the mandibular-gland secretions and not something else that is attracting the other bees has been demonstrated by the fact that the bees are also attracted by excised mandibular glands or by the appropriate synthetic compounds mixed in the right ratio. The small carpenter bees *Ceratina* and *Pithitis* produce pungent mandibular-gland secretions when they are annoyed. They smear them over their bodies and the intruder. These secretions are repellent to nest-invading ants.

Social behavior among the bees probably arose because the survival of the brood is enhanced if a guard bee is present while the forager is away. Another benefit is that two or more bees can share the work of nest construction and provisioning.

Such behavior could have arisen in two ways. The first is that the mother bee came to have a relatively long life span, so that she could help her daughters and be helped by them; this pattern is seen in some sweat bees and carpenter bees. The second way is that bees of the same generation came to share nests and cooperate in nest making and provisioning; this pattern is seen in a few species of sweat bees, digger bees, mason bees and orchid bees. Truly social behavior, with a division of labor in which some bees are queens, dominating the others and laying the eggs, and other bees are nonreproductive workers, is relatively rare among bees, being known only in some sweat bees and some small carpenter bees in addition to the more familiar social stingless bees, bumblebees and honeybees.