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BEES.

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FROM OUR point of view, foraging is the bees' most important activity. While foraging, they perform their indispensable pollination service and collect the raw materials for the manufacture of honey and beeswax.

Which Bees Do the Foraging?

Both sexes of bees, except for certain members of the Apidae, forage in the field. Males take nectar or other sweet liquids for their own immediate energy needs (Fig. 1). They also consume some pollen, but this they probably take in accidentally with the nectar. In the Apidae there are nonforaging individuals in all groups except the nonsocial Euglossa and related genera. Male, worker, and queen bumble bees visit flowers, but after the first brood of workers reaches adulthood the queen spends most of her time in the nest. The female of the cuckoo bumble bee (Psithyrus) likewise does little foraging after she finds a bumble bee colony that will tolerate her. Queen stingless bees don't forage at all, but the males feed from flowers as well as in the hive. As any beekeeper knows, neither male nor queen honeybees are ever The most important activity of the honeybee is foraging and in that capacity performing the all-important service of pollination. This is the last of this series on "Bees".

Fig. 1 Male squash bees (Peponapis) sipping nectar from male squash flowers. (Note hidden nectararies, available only to long-tongued bees.)

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found on blossoms. They can't even feed themselves in the hive and must take food from the tongues of workers.

Male bees, regardless of species, never carry pollen or nectar back to the nest. Consequently, you would expect them to be less diligent than females in their foraging behavior, and therefore poorer pollinators. However, males can spare more time for foraging than females because they don't have to build nests or care for the young. As you might expect, they spend a lot of this extra time seeking females instead of visiting flowers.

Males are not always interested in the same flowers as their sisters. They don't visit such flowers as roses, poppies, and various wind-pollinated plants that produce little or no nectar. On the other hand, many of them visit a wider range of nectar-bearing plants than the females. Since neither male nor female cuckoo bees store food, they have similar foraging habits (Fig. 2). The advantage as pollinators actually goes to the male cuckoo bees. They don't have to spend as much time looking for females as the females do looking for the nests of host bees.

How Bees Forage

Although female bees gather both pollen and nectar, they don't always do it on the same field trip (Fig. 3). Sometimes the flowers are so constructed that the bees are automatically coated with pollen while they are seeking nectar. When this happens, the bee usually packs the pollen into loads, but she is likely to return with a full crop of nectar before her pollen containers are full. At least this applies to honeybees.

Solitary bees collect pollen on a higher percentage of field trips than do honeybees or bumblebees (Fig. 4). This is because they usually make a pollen cake for their young that is only slightly moistened with honey. Furthermore, they have no need to lay up extra supplies of honey for dearth periods.

Solitary bees take sips of nectar for their immediate energy needs, and even species with a restricted pollen range may use a wide variety of flowers for this purpose. After visiting such flowers they may clean the pollen from their bodies. This is a common occurrence with narrow-ranging bees, such as many *Andrena*, but even honeybees scrape themselves bald trying to get rid of cotton pollen after visiting the flowers for nectar.

Nectar “Thieves”

The partnership between bees and flowers is broken when the bees gather nectar without contacting the pollen-bearing structures. Honeybees soon learn that they can take alfalfa nectar faster by entering the flowers from the side than by going in straight and getting mixed up with the sexual column. Fortunately for the alfalfa seed grower, every nectar collector trips at least, a few flowers by accident. When bumblebees cut holes at the base of flowers with long corolla tubes (such as red clover), they are actually harmful, since other bees, including honeybees, are quick to take advantage of this “illegal” entrance for nectar “thieves” (Fig. 5).

Pollen and Nectar Loads

We have already seen the structures that bees use to carry pollen back to their nests (page 401, July issue). The three kinds of loads you are most likely to see are shown in Figure 6. The
halictid bee (related to the alkali bee) carries pollen on both her abdomen and legs. She can completely provision a cell with two or three such loads. All bees carry their nectar in an enlarged section of the fore gut known as the honey stomach. *Hylaeurus*, usually considered the most primitive of bees, carries both her pollen and nectar in the honey stomach.

**Bees and Evolution**

Botanists and entomologists concerned with evolution have always been greatly interested in the flower habits of bees. The evolution of floral structures has been shaped by the plant’s need to take advantage of pollen-carrying agents. Since bees are the most important of these agents, it is not surprising that they have played such a strong role in the evolution of flowering plants. It is equally true that flowers have played a strong role in the evolution of bees. Many of the specialized structures of bees are for the purpose of gathering nectar or pollen from particular kinds of flowers. There has been a lot of argument as to which take the lead in the evolutionary spiral, flowers or bees. Did bees develop long tongues to reach the nectar in flowers with long corollas, or did flowers develop long corollas to take advantage of long-tongued bees? The probable answer is that somehow both forms of adaptation took place more or less simultaneously and very gradually.

**Host Ranges**

Some kinds of bees limit their food gathering to a few genera or species of flowers. Others are reported to be absolutely dependent upon one species of flower, at least for pollen. For example, the common northeastern halictid *Dufourea novae-angliae* Vier. is reported to collect pollen only from pickerel weed (*Pontederia cordata*), whereas its close relative, *Dufourea monarda* Roh., is confined to the horse mints (genus *Monarda*). All degrees of host specificity can be found among bees, from the monotonous diets cited above to the almost universal tastes of the honeybee. Every family of bees has some species or genera with narrow host ranges and others with wide ranges. The fami-
ly Apidae seems to have the highest percentage with wide host ranges and the Andrenidae the highest percentage with narrow ranges. Often genera with many species (for example, *Andrena, Perdita,* and *Dufourca*) have a high percentage of species with restricted host ranges. This is probably because a bee with a tendency to limit its host range becomes isolated from others of its species as soon as it switches to a new host. Isolation is one of the prerequisites for the origin of new kinds of living things.

**Constancy of Bees**

You can't predict the selectivity of individual bees from the host range of the species to which they belong. Some of the most wide-ranging species may be highly selective as individuals. This individual behavior is spoken of as the constancy of the species. Although the honeybee appears to have the widest host range of any species of bee, individual honeybees usually visit only one kind of flower on a field trip and remain constant to it in one small zone until the flowers in that zone become scarce or non-productive. On the other hand, many of the solitary species with much narrower host ranges than the honeybee are relatively promiscuous on individual field trips. We collected an alkali bee (family Halictidae) with as many as six kinds of pollen on its legs. This represented nearly the entire host range of the species in the area where it was collected. Out of 20 loads of pollen that we examined from the nest of a bumblebee (*Bombus morrisoni*), only two were from a single source and five were from at least four sources.

Bees with a wide host range have advantages and disadvantages as pollinators. They are useful for a wide variety of crops but, if you are interested in only one crop, too many of them may forage on competing plants. Ideally, each crop should have a good supply of pollinators specially adapted to it. Since most of our economic crops have been introduced from the Old World, it would seem logical for us to explore the possibilities of introducing specially adapted pollinators.

Bees (such as the honeybee) that are host-constant as individuals have an advantage as pollinators over those that are not. It does a plant no good to receive pollen from unrelated species. Furthermore, a bee spending its time on competing plants is of no use to the crop to be pollinated.

Botanists have observed that bee-pollinated plant genera are apt to develop many closely related species in the same area. This they explain by the isolation afforded a mutant strain when individual pollinators don't visit back and forth between it and the parent type.

**Flight Range**

Flight range undoubtedly varies greatly with the kind of bees, but very little is known about flight ranges of any except the honeybee. In general, larger bees are stronger and faster fliers than smaller ones. It is logical to assume, therefore, that flight range tends to increase with body size. Honeybees fly up to 10 miles for nectar when necessary and bumblebees can probably
travel farther. Even alkali bees, which are only about two-thirds as large as honeybees, have been seen to forage as far as seven miles from their nesting site.

Honeybees have a strong tendency to spread themselves uniformly over the available forage within a mile of their colonies. Within this range, density and attractiveness of the forage are the main factors controlling density of the bee populations. Beyond it, distance from the colonies must affect the concentration of bees, but evidently not as strongly as many of us have thought. By contrast, alkali bees concentrate first on the forage nearest to their nesting site and gradually fan out as it becomes pollinated and goes to seed. You can easily see the contrasting effects of these two types of dispersal on the pattern of seed development.

**Foraging Radius**

Most biologists assume that the flight range of the insect pollinators is the important factor governing the amount of crossing that takes place between two varieties growing a certain distance apart. However, a much more important consideration is the insect's radius of operations after it starts foraging. Except for a few scouts and wanderers, individual honeybees cover only a few square rods while actually foraging and return to the same area time after time. This is an advantage for the seed grower whose crops must be kept pure. He doesn't need to worry about large isolation distances if honeybees are the principal pollinators, and he can usually tolerate a few chance crossings by scouts or wanderers. But the same limited working area is a drawback for the grower of self-sterile tree crops. He must interplant rather closely with pollinator varieties to insure that enough crossing will take place.

Many of the other kinds of bees are likely to wander around more than honeybees. Parasitic bees are homeless creatures and move their foraging areas freely. The same is true, in general, for male bees, but those of some species establish a perch from which to dart after females. Such males probably forage close to their perches. Little is known about the foraging radii of the majority of bees. Some of the Anthophora have been found to return time after time to the same small working zones. On the other hand, we have seen queen bumble bees forage across an entire apple orchard. Being young queens, they probably had not yet established their nests and this may have accounted for their wandering behavior.

**Non-floral Nectar Sources**

Although bees get most of their nectar from flowers, some species are not...
averse to taking nectar from nectaries on other parts of the plant when these are available. In cotton, for example, extra-floral nectaries are abundant and, since the nectar secreted evaporates freely, it is often more concentrated than that from the flowers (Fig. 7). Honeybees commonly lap up extra-floral nectar from cotton before seeking it in the flowers. Other cotton visitors, such as Melissodes, Emphor, and bumblebees, visit only the flowers. Even the males of these bees, although they have no interest in pollen, are faithful to the flowers. According to limited observation, extra-floral nectaries are visited principally by flies, honeybees, and (in the tropics) stingless bees.

Honeydew, secreted by sap-sucking insects, is a favorite "nectar" source for honeybees even though the honey produced from it is often unsatisfactory as bee food during the winter. As in the case of extra floral nectar, honeybees and stingless bees are the principal insects to use honeydew for making honey. However, many kinds of wasps and flies lap it up for their own nourishment. Halictids sometimes take honeydew, but this may be only for their own immediate needs.

Juices from ripe fruit are often used as a "nectar" by honeybees. They have often been accused of damaging fruit to secure the juices but, in most cases, birds or other insects, or simple cracking of the fruit, have been responsible for the skin breaks observed. In the tropics stingless bees are apparently more rightfully accused of being fruit destroyers. Halictids are the only other bees that we have seen feeding on broken fruit. It is interesting to note that the halictids observed are subsocial species. Perhaps the social habit has influenced this rather unusual tendency among bees to use non-floral sources for nectar.

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