

6

X

6

NOTES ON THE BEHAVIOR OF THE CARPENTER
BEE *XYLOCOPA FIMBRIATA* IN MEXICO
(Hymenoptera: Apoidea)¹

DANIEL H. JANZEN

ABSTRACT

Nest sites and host plants of *Xylocopa fimbriata* in southeastern lowland Mexico are recorded. In addition to male behavior, female-female interactions at a nest site are described for the first time among carpenter bees. Such competitive interactions may be significant in promoting maximum utilization of natural nest sites.

One of the commonest carpenter bees in the coastal lowlands of Veracruz, Mexico, is *Xylocopa (Megaxylocopa) fimbriata* Fabricius (det. P. D. Hurd, Jr.). It is one of the largest species in the area, with black females 3 to 4 cm long and yellow males. Another large carpenter bee that is occasionally confused with *X. fimbriata* in the same area is *Xylocopa (Megaxylocopa) frontalis* (Olivier); this bee may be distinguished by its lack of large and laterally produced carinate processes in front of the lateral ocelli of the female (see Fig. 18, Hurd and Moure, 1963). During the summer of 1962 and from September, 1963, to August, 1964, I made cursory observations on the behavior of *X. fimbriata* around Campo Cotaxtla (22 km inland from the city of Veracruz on the highway to Cordoba, Veracruz, Mexico; elevation 200 m) and in the area of Temascal, Oaxaca to La Granja,

¹Contribution No. 1306 from the Department of Entomology, The University of Kansas, Lawrence. Accepted for publication December 21, 1965.

This study is a byproduct of National Science Foundation grant GB 1428 to the University of California, Berkeley (Dr. R. F. Smith) and University of California Tropical Biogeography Research Grants No. 66 and 81.



FIG. 1A. Fungus growing around entrance holes of *Xylocopa fimbriata* in wood post, Campo Cotaxtla, Veracruz, Mexico. B. Hole in cement post used as resting and preening site by a male *X. fimbriata*.

Veracruz (roughly 15 to 20 km south of Tierra Blanca, Veracruz; elevation 20 m). The nest of *X. fimbriata* has been discussed by Bodkin (1918) and Wagner (1958), but no extensive biological observations have been recorded for this species.

NESTING BEHAVIOR

At Campo Cotaxtla (1962), nests of *X. fimbriata* were common in seasoned wood fenceposts bordering open grass pastures. Entrances ranged from a few centimeters above the ground to the top of the posts (about 130 cm). During July and August (rainy season started about 17 June 1962), females were frequently observed entering nest entrances with large pollen loads and clean scopae. Active excavation of nests was in progress; wood dust was often pushed out of the entrances and was piled on the ground below. Several of the posts had been used as nest sites for more than one year. There were old but clean entrance holes that were not in use, but in many cases, a woody fungus had grown profusely around or into the entrances of some holes. This fungus started its growth in the area of excrement-contaminated wood immediately below the lower lip of the entrance hole (Fig. 1, A). The female bees chewed away the fungus as it grew into the entrances of active nests. In one case an old tunnel was reopened by a new hole cut through the fungus from the inside. The larger patches of fungus (up to 30 by 30 cm) were present but not growing during the preceding dry season (January through June); by mid-August, 1962, those entrances that started the rainy season with no fungus had, under them, small patches less than 2 cm wide.

The entrances of several nests of *X. fimbriata* were in the lower sides of 2 × 6-inch seasoned wood beams under eaves of houses. The females in these nests had an unusual reaction to disturbance. When I pounded on the wood with a hard object, on several occasions a female ejected approximately 0.2 cc of a brownish-gray fecal fluid out of the entrance with considerable force. It usually left the entrance at an angle from the beam and hit the wall of the house (1 to 2 m away) with a loud "splat". This probably is a defense mechanism, since ordinary defecation without previous disturbance involves a much smaller quantity of fluid ejected and with much less force. *X. fimbriata* commonly defecates out the entrance of the nest, and the inside of the nest appears to be free of such waste matter.

A single nest of *X. fimbriata* was found in a stable 7 km west of Campo Cotaxtla on the road to Cordoba, Veracruz. To reach the nest entrance in a seasoned 2 × 4-inch beam inside the building and against the roof, the female bee had to fly through two chicken-wire screens set about 30 cm apart and then 5 m down a dark hallway. In passing through the screens, she hovered in front of the first until directly in front of a hole, moved slowly through it while still hovering, darted

to the next screen and repeated the maneuver. Her movements were very similar to those of a female returning to her nest in a stump deep in a tangle of second growth vegetation; in this case, the female worked her way slowly down between the twigs and branches while hovering without touching them.

In a brushy pasture 8 km east of Temascal, Oaxaca, a pair of pole-walled, thatched roof houses were used extensively by *X. fimbriata* as nest sites by at least 50 females during 1963-1964. The infestation was so severe in one house that during a heavy wind storm in late May (beginning of the rainy season), the house collapsed. In the broken wood poles there were over 200 provisioned cells. Following the collapse of the nest site, many of the females shifted their efforts to the wall poles in the other house. However, many of these poles were less than 5 cm in diameter or had been split, and the females apparently did not regard them as suitable nest sites. The result was that many females tried to build nests in the few remaining large poles. Two interactions were observed between females which may be characteristic when many females try to use a restricted nest site.

On two occasions, a female entered an entrance hole made several weeks earlier by another female and began boring for her own cell series. In both cases she cut through series of provisioned cells, then left without returning. Large masses of pollen-nectar mixture were pushed out of the entrance along with the wood particles. In one pole, the bee had cut diagonally through four provisioned cells, which presumably had either eggs or first stage larvae in them, since the other four cells in the series contained eggs or first stage larvae.

The other interaction was of a direct nature. About one week after the collapse of the heavily infested house, a female *X. fimbriata* (bee A) began a burrow in a vertical pole 8 cm in diameter, at a point about 150 cm above the ground. Starting shortly before 10:00 AM on a hot day, she had bored inward and upward until out of sight (6.5 cm deep) by noon of the following day. Then a second female (bee B) began to bore 10 cm below the entrance of the first nest (that of bee A). Bee A was distinguishable from B by the former's heavily tattered wing margins. Bee B had penetrated 12 mm (so that her head and anterior half of the thorax were hidden) when the first attack occurred.

Bee A walked out of her hole, toward B, and dropped onto her back. The bees fell to the ground making a loud buzzing noise and rolled about grappling for about five seconds. They then separated and flew upwards about one meter, where they hovered facing, and then flew at each other. After bee B flew away, bee A landed at B's hole, stuck her head in for a second or two, then walked up and into her own hole. About five minutes later, B returned and began to dig in her hole again. Within a few seconds, A dropped out of her hole and hovered immediately behind B. When she approached within about

TABLE 1. Flowering periods of plants used for food by *Xylocopa fimbriata* at Temascal (P = pollen source; N = nectar source). The lines following the names of the plants show the periods when they were in bloom.

	Season:	Cool dry Dec-Feb	Warm dry Mar-May	Early wet May-Jul	Late wet Aug-Nov
<i>Solanum torvum</i> (P) (Solanaceae)		_____			_____
<i>Turbina corymbosa</i> (P,N) (Convolvulaceae)		_____			_____
<i>Tabebuia pentaphylla</i> (P,N) (Bignoniaceae)			_____		
<i>Cochlospermum vitifolia</i> (P) (Cochlospermaceae)			_____		
<i>Gliricidia sepium</i> (N) (Fabaceae)			_____		
<i>Quercus</i> spp. (P) (Fagaceae)			_____		
<i>Pterocarpus</i> sp. (N) (Fabaceae)			_____		
<i>Cassia bicapsularis</i> (P) (Caesalpinaceae)		_____			_____
<i>Bixa orellana</i> (P) (Bixaceae)		_____			_____

two cm, B backed out and flew away. Then A flew away and B returned and began to dig again. About five minutes later, A returned and landed directly on the back of B. They both fell to the ground and immediately separated; B flew away. Bec A landed on the pole, walked up and down over a 50 cm section, stuck her head into B's entrance hole, and then walked up and into her own. Bec B did not return during the next two months and no other bee continued work on the shallow hole 10 cm below A's entrance. This appears to be the first record of direct female to female competition for new nest sites among carpenter bees.

HOST PLANTS

In the Campo Cotaxtla area, *X. fimbriata* was commonly encountered while collecting pollen from the yellow-flowered fabaceous legume *Diphysa robinoides* Benth. (mid-July to mid-August) and a yellow-flowered caesalpinaceaceous legume, *Cassia* sp. (August). During July and August the females collected pollen from the white flowers of *Solanum torvum* Swartz, one of the commonest woody species of *Solanum* in heavily browsed pastures in the area. The females were observed taking nectar from *Antigonon leptopus* Hooker and Arnott (Polygonaceae) and *Cuphea ciliata* (Sw.) Koehne (Lythraceae).

In the Temascal area, observations were made of host plant visitations by female *X. fimbriata* throughout the change of seasons. Due to the difficulty of distinguishing between *X. fimbriata* and *X. frontalis* in flight, records are given only where the bee was captured and identified by close examination of the head. The plants visited are listed in Table 1; the food being obtained was determined by watching bees on the flowers. The plants utilized were visited throughout their blooming periods but quantitative records of frequency of visits were not made; it is suspected that when more than one host plant was available at a particular time, some preference was exercised. The species with the longest period of flowering, and the greatest total pollen availability, is *Solanum torvum*. This plant is a major pollen source of the other big bees in the area (*Ptiloglossa* spp., *Eulaema polychroma*, *Bombus medius*, *Xylocopa frontalis*, and other *Xylocopa* spp.). *Solanum torvum* is the only annual plant in the list.

As Table 1 shows, there is a general lack of nectar and pollen sources for large bees during the first two months of the rainy season (mid-May through mid-July). This is characteristic of most lowland Central American second-growth plant communities; the woody trees and shrubs have ceased their dry-season flowering and the herbaceous annuals are often still in the vegetative stage. The majority of the plants have at least part of their flowering season during the warm and dry part of the year; this is also the case with other woody plants whose flowers were not visited by *X. fimbriata*. However, if one were to examine the flowering schedules of the herbaceous vegetation, one would find a much reduced flower frequency during this time of year; the herbaceous plants have their major flowering period during the later part of the rainy season and a number of woody plants flower at this time as well. Finally, even though there is a gap when no flowers were seen, it is probable that some of the taller trees were visited; there appears to be no time in the year when there are no flowers available to bees.

During the cool season, *X. fimbriata* is one of the last bees to cease activity. At Temascal, the cool season (1963-1964) was December, January and February, with monthly mean daily maxima and minima of 24.1, 24.2 and 25.5°C; and 16.5, 15.7, and 17.0°C respectively. *X. fimbriata*, *X. frontalis*, *Bombus medius*, and *Ptiloglossa* spp. were generally the only bees active during cold periods. On progressively colder days, first the *B. medius* and then the two *Xylocopa* species failed to appear at flowers; it never got so cold that at least one of the *Ptiloglossa* spp. did not fly. These later bees fly one hour before to several hours after sunrise, and were twice recorded flying when air temperatures were 12°C (6:48 and 7:18 AM, visiting *Solanum torvum*).

X. fimbriata and *X. frontalis* have a place in the early morning and evening succession of bees. Using *Solanum torvum* as a morning

pollen source, first appear two species of *Ptiloglossa* (one before the other) and a *Melipona*. Then at, or just before, sunrise, *Eulaema polychroma* (often discussed as *Eulaema tropica*) appears. Within ½ to 1 hour after sunrise (actual appearance of the sun above the horizon), both *Bombus medius* (first) and the two *Xylocopa* species (second) appear. Using *Cuphea ciliata* as a nectar source throughout the day in the area of Campo Cotaxtla, *X. fimbriata* ceases its visits roughly 30 minutes before sunset (actual disappearance of the sun below the horizon). Honey bees, Megachilidae and Anthophoridae disappear shortly thereafter. Almost immediately after sunset the much smaller *Xylocopa* (*Notoxylocopa*) *tabaniformis illota* appears and is an active visitor until full darkness (Janzen, 1964).

MALE BEHAVIOR

Both in the area of Campo Cotaxtla and at Temascal, the large yellow males of *X. fimbriata* and *X. frontalis* were commonly encountered while hovering in apparent mating territories in a variety of tree or bush canopies. Since they are indistinguishable in flight, the observations in this paragraph may apply to either or both species. The hovering may start anytime but at least 1 hour after sunrise, lasts 15 minutes to 8 hours, and ceases at least 2 hours before sunset. The male selects a territory among the canopy which ranges from $2 \times 2 \times 1$ to $10 \times 5 \times 5$ meters in height, width and length. The territories may be from 2 to 25 m above the ground, but most commonly were 4 to 10 m high. It then flies through this space in rather ill-defined patterns with occasional periods of hovering lasting 1 to 55 minutes. While hovering, the male turns on a vertical axis through the middle of the thorax. They are alert, reacting to human movement at distances of less than about 3 meters by leaving. The hovering bee may be heard up to 100 m away on a quiet day. No males were observed interacting with females in any manner. However, they were frequently observed in pursuit of other large insects; whether this is attack or attempted copulation is unknown. The site chosen for the territory suggests a good site to locate females searching tree canopies for dead branch or trunk nest sites.

At Campo Cotaxtla, a male *X. fimbriata* was resting in a hole through a cement fencepost. The hole (Fig. 1; B) was 3 cm in diameter and 20 cm long, forming a horizontal tunnel. The bee was easily observed in silhouette while it was in the center of the tunnel. On 8, 9 and 10 August, it remained in the tunnel for 107, 62 and 78 minutes, between 1:00 and 3:00 PM (hot and clear weather). Almost the entire period was devoted to preening activities with the fore and hind legs. The mesothoracic legs were both used almost continuously as braces against the sides of the tunnel; the bee pivoted on the axis provided by these two braces and at times was nearly up-side down. It

occasionally buzzed its wings. This cement post was about 3 meters from a wooden fence post containing at least four active nests of *X. fimbriata*.

DISCUSSION

In respect to the female interaction at nest sites, it appears that *X. fimbriata* may have evolved a mechanism to avoid overpopulation of nest sites. To reduce boring through other bees' provisioned cell series, it appears advantageous to have the nests maximally dispersed among and within the pieces of substrate available (normally large dead branches and trunks). It also appears that any mechanism which would preserve a branch or trunk in the canopy would be favored. As the density of burrows increases, the greater is the probability that a gust of wind will blow the branch down, destroying some cells and more quickly rendering the site unfavorable for further nesting, since wood on the ground rots more quickly and the cells may be susceptible to predation by ground-nesting ants. If the observed aggression of one female toward another was not a unique event, then it could be postulated as an evolved mechanism serving to increase longevity of nest sites through forcing dispersal both to other parts of the dead wood and to other dead branches and trunks. Seasoned dead wood is an uncommon and temporary nest site under natural conditions; in the lowland tropics, the loss of dead wood from the canopy during dry season winds must be of importance to carpenter bees (and to other insects). It may be noted that the advent of man with his house structures and fence posts in lowland Veracruz has undoubtedly multiplied the available carpenter bee nest substrate many times. In view of the absence in the literature of reports of female carpenter bees destroying each other's nests, they may be able to detect the presence of other nests before breaking into them; however, the observations of *X. fimbriata* indicate that such avoidance is definitely not absolute. Such cell destruction could well serve as a selective force promoting aggression by females against other females that start boring activities near a nest being provisioned. Thus there are at least two possible factors which could favor genotypes aggressive to other carpenter bees starting nests near established nests.

It should be noted that the dispersion of nesting females which should be promoted by such aggression would favor maximum discovery rates of the suitable nest sites, increase the difficulty of parasites in finding nests, and minimize the percentage of the total population lost when an individual site is blown down.

ACKNOWLEDGMENTS

I wish to thank Dr. C. D. Michener for reviewing the manuscript.

VOL. 39, No. 4, OCTOBER, 1966

LITERATURE CITED

- Bodkin, G. E. 1918. Notes on some British Guiana Hymenoptera (exclusive of the Formicidae). Trans. Entomol. Soc. London, 1917, pp. 297-321.
- Hurd, P. D., Jr. and J. S. Moure. 1963. A classification of the large carpenter bees (Xylocopini) (Hymenoptera: Apoidea). Univ. California Pubs. Entomol. 29:1-365.
- Janzen, D. H. 1964. Notes on the behavior of four subspecies of the carpenter bee, *Xylocopa* (*Notoxylocopa*) *tabuniformis*, in Mexico. Ann. Entomol. Soc. Amer. 57:296-301.
- Wagner, H. O. 1958. Beitrag zum Verhalten einiger mexikanischer Holzbienen. Z. Tierpsychol. 14(3):303-308.
-