

Comparative Behavioral Biology
of Two Middle East Species
of Carpenter Bees
(*Xylocopa* Latreille)
(Hymenoptera: Apoidea)

DAN GERLING, PAUL D. HURD, JR.,
and
ABRAHAM HEFETZ

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ABSTRACT

Gerling, Dan, Paul D. Hurd, Jr., and Abraham Hefetz. Comparative Behavioral Biology of Two Middle East Species of Carpenter Bees (*Xylocopa* Latreille) (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology*, number 369, 33 pages, frontispiece, 30 figures, 7 tables, 1983.—This study is a comparative treatment of the behavior and environmental adaptations of two species of carpenter bees, *Xylocopa sulcatipes* Maa and *X. pubescens* Spinola, in Israel. *Xylocopa sulcatipes* is a cane and thin-branch nester and constructs a simple linear nest. *Xylocopa pubescens* makes ramified nests within various wooden substrates. Both species have 3–4 generations per year, from March to September. The females guard their nests against intruders, especially conspecifics. Both species may develop along a solitary pathway, with one female per nest. Additionally, *X. pubescens* may have a foraging mother cohabiting with her nonovipositing daughters, in contrast to *X. sulcatipes*, which may have more than one foraging and ovipositing female in the same nest. In both species, the incoming mother feeds her progeny by trophallaxis. Males of both species are territorial; territories of *X. sulcatipes* are conducted in locations where females may occur, whereas those of *X. pubescens* are in prominent places like flowering shrubs, tree tops, etc. The flower-visiting repertoire of *X. sulcatipes* and *X. pubescens* is extensive and overlapping; however, due to its ability to fly at earlier hours, *X. pubescens* gets to most of the flowers before *X. sulcatipes*. Both species are endothermic; the lower activity threshold for *X. sulcatipes* is 21°C and that of *X. pubescens* is 18°C. Consequently, the flight hours of the former start later than those of the latter. The duration of their outdoor activity also differs, with the former being active most of the day and the latter confining its flight hours to the early morning when the total heat load of the environment is low. The ontogenesis of the bees is described, and their few natural enemies are discussed.

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Contents

	<i>Page</i>
Introduction	1
Acknowledgments	2
Methods of Study	2
The Study Sites	2
Marking, Observation, and Recording Techniques	3
Measurement of Physical Factors	3
Nest Construction and Substrates	3
Behavior in the Nest	5
Nest Defense	6
Cell Construction, Provisioning, and Ovipositing	7
Sleeping and Nest Care	8
Interactions among Individuals	9
Behavior outside the Nest	11
Territoriality and Mating	11
Flower Visits	12
Ontogenesis	18
Diurnal and Seasonal Activity	19
Diurnal Cycles	19
Seasonal Activity	19
Natural Enemies	21
Parasites	21
Predators	21
Discussion	22
Nest Construction and Structure	22
Territoriality	23
Social Relationships	24
Literature Cited	26
Figures 5-30	28



FRONTISPIECE.—A poplar board containing two nests of *Xylocopa pubescens* in Hatzeva Field School showing the effect of robbery by ants.

Comparative Behavioral Biology of Two Middle East Species of Carpenter Bees (*Xylocopa* Latreille) (Hymenoptera: Apoidea)

Dan Gerling, Paul D. Hurd, Jr., and Abraham Hefetz

Introduction

Two species of carpenter bees, each belonging to a different subgenus, were studied in Israel. One of these species, *Xylocopa sulcatipes* Maa, belongs to the subgenus *Ctenoxylocopa*, and the other, *X. pubescens* Spinola, belongs to the subgenus *Koptortosoma*.

The subgenus *Ctenoxylocopa* was proposed by Michener (1942) for Maa's (1938) preoccupied *Ctenopoda* that was intended for the reception of two species from India, *Xylocopa basalis* F. Smith and *X. fenestrata* (Fabricius). Subsequently, Maa (1954) added the African *X. hottentotta* Smith to the subgenus. Hurd and Moure (1963) treated this subgenus in their classification and included in it five species. According to these authors, the subgenus *Ctenoxylocopa* Michener is characterized by several unique features, including the remarkably expanded pronotal lobe of the male, and is not closely related to any other known subgenus. Maa (1970) in his revision of the subgenus included only four of the previously assigned species, removing *X. hottentotta*, and described two new species, one of which was *X. sulcatipes* Maa.

The subgenus *Ctenoxylocopa* is widespread in the Old World tropics and subtropics. Its known range is between about 33°N, 20°S, 15°W, and 99°E from Imam Bara (Transcaspia) in the north to Madagascar in the south and from Gambia in the west to Burma in the east. One species, *X. fenestrata*, has also been recorded from Brazil, an occurrence that is probably accidental (Hurd and Moure, 1961:184). It should be noted that Tkalcu (1968), in his treatment of the species of *Ctenoxylocopa* occurring in Afghanistan, described a new species, *X. povolnyi*, which was overlooked by Maa (1970), and its identity and relationship to other species in the subgenus have not been established. The distributional center of this subgenus is in Northeast Africa and Southwest Asia, where four of the seven species exist and their ranges partially overlap. *Xylocopa sulcatipes* was characterized for bees that, in the past, were misidentified as *X. hottentotta* Smith. It also has been confused with *X. ustulata* F. Smith in Aden (Maa, 1970). The species has been collected in the Near East (Israel and Arabia) and Transcaspia. *Xylocopa sulcatipes* resembles *X. ustulata* and is a relative of *X. tessellata* Maa. Some of its outstanding characters that distinguish it from other members of the subgenus are a deep and wide ventral sulcus on basitarsus 3 in the male and a very weak frontal carina in the female. Up to the initiation of our studies, the

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only biological or ecological data that had been published concerning this subgenus were those of Kapil and Dhaliwal (1968a, 1969) about *X. fenestrata* Fabricius.

The extent, distribution, and affinities of the subgenus *Koptortosoma* Gribodo, to which *X. pubescens* belongs, whose type-species was designated by Sandhouse (1943:561), are listed by Hurd and Moure (1963:271) as follows:

This is the most widely distributed subgenus of *Xylocopa* and contains the largest number of species. At present there are more than 200 names applied and doubtless more names will be transferred to it from those taxa currently listed as subgenerically doubtful. It is found in all the zoogeographic realms of the Old World with the largest number of taxa, 96, being reported from the Ethiopian. In the southern hemisphere, species of the subgenus *Koptortosoma* attain the southernmost portions of Africa (several species) and Australia (a single species, *X. aruana* Ritsema). A few species are intrusive in the southern parts of the Palaearctic, but probably will not be found much farther north than latitude 30°N.

In addition to this taxonomic and geographic characterization, *Koptortosoma* has a biological one, by the fact that many of its females are the hosts for mites of the genus *Dinogamasus*, the adults of which reside in a special cuticular pouch present in the abdomen and opening onto the anterior face of the first metasomal tergum (Hurd and Moure, 1963). The immature stages of these mites are closely associated with the immature bees and may be parasitic upon them (Madel, 1975; Skaife, 1952). Likewise, the adult mites, although they do not seem to feed upon the bees, cannot survive without them.

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Methods of Study

THE STUDY SITES.—Many of the studies were conducted at the Hatzeva Field Study Center of the Israeli Society for the Protection of Nature. This place, which is located about an oasis in the Arava within the Rift Valley, has local populations of both bee species. Its location within a generally arid region allowed us to regulate some-

what its nesting substrates and to investigate its nectar and pollen sources.

The bees also nest sympatrically in the region of Ein Geddi, a very lush oasis adjacent to the Dead Sea, where an abundance of both species permitted us to follow territorial behavior, the utilization of nesting substrates, and the occupation of new nests.

In addition, many of the studies with *X. pubescens* were carried out in Tel Aviv, where the species occurs naturally. Nests occupied by this species, as well as ones of *Xylocopa sulcatipes* that were brought from its natural range, were placed on the roof of the Department of Zoology building of Tel Aviv University for close observations. Experiments were also carried out in temperature cabinets at Tel Aviv University.

MARKING, OBSERVATION, AND RECORDING TECHNIQUES.—Bees were often marked for individual observation. This was done by one or more of the following methods: gluing a small, numbered, plastic plate to the thorax (Gerling and Hermann, 1978), applying latex or oil-base paints on the thorax, painting latex-base paints on the abdominal segments, gluing small metallic fragments, like copper wires, onto the thorax, and mixing barium sulphate with Epoxy or resinous glue and applying it to the thorax. The latter two methods allowed for recognition of individual bees in X-ray observations and radiograms.

Developmental history was followed by rearing bees in the laboratory, within opened nests. Nests were also opened occasionally in the field in order to determine the stage and condition of their contents. Continuous follow-up of the ontogeny, as well as observation of in-nest behavior, was carried out by the use of X-ray radiograms and X-ray observations.

The observations were conducted with active nests that had been placed in a special, lead-shielded observation box (Figure 6). In order to cause minimal disturbance to the bees during our observations, we prepared five wooden boxes (Figure 7) that were somewhat larger than the above-mentioned observation box. Five active nests were kept permanently in these wooden

boxes, which were placed on pedestals within a covered gangway that afforded shade, a feature necessary for efficient X-ray viewing. Whenever one of the five nests was to be observed, it was placed in the observation box which, in turn, was covered by the wooden box. In this way, the bees noticed no change in the external appearance of their nesting site and entered it readily. At times, a nest within a wooden box was not suitable for observations owing to the lack of the appropriate life-history stages. Such nests were replaced with others that were allowed to remain unobserved for several days, until the bees became acclimatized and accustomed to their new setting.

Flight, territorial, and flower-visiting behavior were observed directly in the field. Tethered bees were used for some of the studies of territorial behavior, and movie films of some of the above activities were taken and analyzed for a better understanding of the behavioral patterns involved.

The physiological condition and status of the activity of nesting females were assessed after the examination of the wear of their wings and the condition of their ovaries, glands, and digestive systems.

MEASUREMENT OF PHYSICAL FACTORS.—The physical factors measured were photoperiod, incident radiation, relative humidity, and ambient temperatures. The two latter parameters were recorded by hygrothermographs that were placed in the different study stations. In addition, specific experiments called for temperatures to be taken within or near the nests and in their immediate environment, as well as in the bees' thorax and during various activities.

Nest Construction and Substrates

Xylocopa sulcatipes constructs her elongate nests in dead wood of sticks, canes, or branches. Under natural conditions, nests are made in the hollow canes of *Arundo donax* and *Phragmites australis*, the dead branches of trees, such as *Calotropis procera* and *Moringa peregrina*, and the dead flowering stalks of *Ferula* spp. Similar materials, such as old

TABLE 1.—Nesting material in which *Xylocopa sulcatipes* nests were found

Material	Location	Remarks
<i>Agave</i> sp.	Arava Valley, Eilat	cut flowering stalks
<i>Calotropis procera</i>	Arava Valley, Jericho, Ein Geddi	thin, dead branches
<i>Ferula</i> sp.	Sede Boqer Hatzeva, Ein Yahav	erect, dry stalks cut stalks
<i>Moringa peregri- na</i>	Ein Geddi	thin, dead branches
<i>Populus</i> sp.	Hatzeva	in a preformed hole within a board
Reeds <i>Arundo donax</i> <i>Phragmites australis</i>	Arava Valley, Dead Sea coast	in natural stands and in cut culms

flower-scapes of agave species and various soft, wooden, usually tubular, objects that were introduced by man, were also utilized (Table 1).

The location of the nests is variable. Nests were found in dead branches on the ground or in cut stalks or boards that were hung at various heights above ground. In most cases they are in partial shade, albeit nests thrive also in positions exposed to the extreme heat of the summer sun in the Arava Valley, such as the old agave flower-scapes that make up the covers of the bus stations in that area. Orientation of nesting materials by compass directions did not seem to play a role, nor did the angle of inclination of the substrate.

The nests of *Xylocopa sulcatipes* are unbranched, even when they are constructed in nontubular material, as they rarely are (Figure 8). The diameter of the entrance hole is about 1.2 cm and that of the excavated tunnel 1.2–1.6 cm and its length usually 12 cm or more. The bees may either cut a hole along the side of the nesting substrate, penetrate it, and then construct the nest along the grain in one or both directions, or, if a cut surface or broken cross-section exists, they will usually utilize it to gain entry into the substrate (Figures 9, 10). In flower-scapes of agave

the females will invariably dig into cut surfaces, never through the unblemished side of the scape. Pre-existing holes and old nests will often be acceptable to them as starting points for new nest construction. Old nests that have been much in use and excavated extensively are usually not reused.

The females dig with their heavily sclerotized mandibles, often passing the dorsum and apex of their abdomen along the walls, possibly varnishing the inner surfaces of the tunnel walls with glandular secretions. The resulting walls have a yellowish glazing to them that may originate from the yellow gland (Gerling et al., 1979) and/or Dufour's gland.

Xylocopa sulcatipes nests often in hollow canes in which little or no digging is necessary, or sometimes the female prefers to dig in a soft matrix like that of pithy stems (Table 1). In canes the nesting tunnel usually is extended to the next node, which apparently is difficult for the bee to penetrate. In several cases we found that two nests were established, from both stem ends, each extending to the nearest node. This is also true when the bee starts the hole on the side wall and then makes lateral tunnels, which may extend to one or both sides. Nest reuse depends upon the habits of the bees as well as on the suitability of the substrate for such an activity. The hardness of the nesting material is of importance, since the females scrape the wall in order to obtain material for the construction of partitions. At the same time, the females usually do not nest in tunnels with a diameter of over 1.6 cm.

Since *X. sulcatipes* often nests in very soft substrates that do not remain suitably firm in shape and size, the females are rarely able to reuse existing nests in materials like *Ferula*. These nesting tunnels are extended each time until they become too long, or variously unsuitable, and are consequently abandoned. Nests in canes and culms are not reused either, the probable reason being not the increased size of the nesting tunnel but the availability of material for construction of partitions. Since the walls of the culm consist of very thin and hard wood unsuitable for making

partitions, the females scrape the scant layer of downy and lignified material that lines the inside of the culm internodes and use it for cell partitions. Once that is used and disposed of, the bees are probably unable to make new partitions for the next generations and consequently abandon the nests. Nests in thin branches of *Moringa peregriana* and *Calotropis procera* do, sometimes, support several generations in the same excavated tunnel.

Xylocopa pubescens has a wider distribution and nesting range than *X. sulcatipes*. In areas of sympatry they appear to live under similar conditions, and their nests are often found side by side. The nests of *X. pubescens* are constructed in a wider selection of materials than those of *X. sulcatipes* (Ben Mordechai et al., 1978; Table 2). In the Mediterranean region, it nests in dead tree trunks that may be exposed to the winter rains or in protected locations. Nests were found in various forms of soft wood (Figures 11, 12) including wooden poles of *Eucalyptus* used for supporting the fruits in banana plantations. Canes, culms,

branches, agave stalks, and even styrofoam boxes as nesting materials were found only in the Arava and Negev areas where there is a shortage of nesting substrates.

Xylocopa pubescens constructs a sinuous, branched nest that is typified by short tunnels. The nest has an entrance hole of 1.1–1.3 cm in diameter, and a widened entryway leads into a "chamber" of 1.8–2.1 cm. The tunnels, which measure 1.4–1.8 cm in diameter, start from the chamber and usually follow the grain. Occasionally, single-cell long tunnels were also dug across the grain (Figure 13). Tunnel length is usually 5–7 cm, consisting of a few cells each. The females enlarge the nest by digging new tunnels, usually when their already developing progeny have reached the late larval or pupal stage.

The tendency to construct a branching nest with a few cells in each tunnel remains even when nesting in such substrates as agave or *Ferula* stalks. Also, nests constructed in cane (Figure 20), though necessarily unbranched, each have only 2–3 linearly arranged cells. In styrofoam boards, a very long access tunnel was dug, but the nesting tunnels were short (Ben Mordechai et al., 1978).

Progeny often remains in the tunnel complex of the mother. It is apparent that the young females build their nests by enlarging the mothers' nest, using her common chamber or one of her tunnels as a starting point. This will become the entrance to their future nest (Figure 16), while the exit hole of the mother's nest will remain the only connection with the outer world and will serve a group of internal nests.

Xylocopa pubescens was found usually to extend the existing tunnel or to excavate a new one for each nesting cycle. Occasional reuse of the same tunnel was made. In such cases the tunnel diameter was increased from one generation to the next by 0.5 or 1 mm. The two extreme cases that we found involved eight successive generations in each tunnel, with widths starting at 1.4 and 1.6 cm and ending at 1.7 and 1.8 cm, respectively.

Behavior in the Nest

As noted earlier, there may be one or more females residing in each nest, and behavior varies

TABLE 2.—Nesting materials in which *Xylocopa pubescens* nests were found

Material	Location	Remarks
<i>Agave</i> sp.	Arava Valley	cut flowering stalks
<i>Calotropis procera</i>	Dead Sea coast	thick branches and trunks
<i>Cocos nucifera</i>	Ein Geddi	dead, erect stump
<i>Eucalyptus</i> sp.	Tel Aviv area, Ein Gev	cut trunks, poles
<i>Ferula</i> sp.	Ein Yahav	cut flowering stalks
<i>Moringa peregriana</i>	Ein Geddi	thick branches and trunks
<i>Morus</i> sp.	Tel Aviv area	trunk
<i>Pinus halepensis</i>	Kfar Yehoshua	cut trunk
<i>Populus</i> sp.	Tel Aviv area, Jericho	thick branches and trunks
<i>Robina pseudacacia</i>	Tel Aviv area	thick branches and trunks
Reeds	Arava Valley, Dead Sea coast	only in precut culms
<i>Arundo donax</i> <i>Phragmites australis</i>		
Styrofoam	Ein Yahav	tool box bottom in a shed

accordingly; however, aside from the interactions among individuals, several activities were discerned: nest defense, cell construction, provisioning, ovipositing, sleeping, and nest care.

NEST DEFENSE.—Competition among conspecific females for nesting sites increases as the population grows and is reflected by more intensive guarding of nests, especially during the late spring and summer. Nest guarding is not only against conspecific females but also against other species. We often observed the potter wasp *Rynchium* sp. investigating holes of deserted nests. In several cases we found cells built by this wasp in old nests (Figure 14) or new *Ferula* stalks that were supplied as nesting sites for bees.

The most prevalent competition is among conspecific females. A female searching for a nest will hover for a long time near nest holes, possibly checking the likelihood of occupying a suitable place. The bees recognize occupied nests even if their inhabitants are out and usually avoid them; however, as the populations increase, the number of available nesting sites diminishes, and the searching bee may try to invade even active nests.

The typical defense posture is that of a female blocking the nest entrance with her head. If the nest entrance is in the side of a branch rather than in the truncate end, the bee remains at the entrance and only her antennae protrude from it (Figure 17). A female may also block the entrance with the dorsum of her abdomen. This is done either at the opening proper, or somewhat inside the nest.

At times, the guarding bee stays further within the nest, either in the middle of the tunnel or near a pollen slant. She may also perform activities such as coating the nest walls with materials that she gathers with her mouth from the tip of her abdomen. As soon as an object appears at the entrance of the nest, she rushes there and assumes a guarding posture.

Nesting history of *Xylocopa sulcatipes* may follow either a solitary or a metasocial route (see "Discussion"), and the identity of the guard will vary accordingly.

In a solitary nest, the founding mother does all

of the foraging, cell building, and ovipositing in addition to guarding. After the first progeny emerge, the young females usually share guard duties with their mother until they leave the nest. In some nests, where more than one female lives in the same nest, guarding, foraging, and egg laying are often shared. In other instances, one female does all the foraging and egg laying, while the other female inhabitants only perform guard duties.

Our specific observations of nest guarding and its consequences included a comparison of two adjacent nests of *X. sulcatipes*, one occupied by two females, a guard and a forager, and the other occupied by only a single female (Figure 17). While the forager bee would go out several times during the day (and at one time stayed out for as much as two hours), the lone female in the second nest went foraging only twice, and each time for only 10 minutes with little pollen carried back each time. Accordingly, the nest with the two founders was provided with two cells within one week, while the lone foundress was unable to finish a single bee bread in that time.

We also observed two interactions between invading and guarding bees. In one such case, a nest in which the founding female was absent foraging was invaded by a conspecific female. Later, when the forager returned to her nest laden with pollen, she was confronted by the invader, who assumed an aggressive posture at the entrance of the nest. As previously mentioned, such a posture of the guard usually suffices for the oncoming bee to give up and depart, but in this case being the true inhabitant of the nest, she persisted in her entry efforts and hung on to the entrance, and both bees buzzed loudly. This continued for about 20 minutes until the owner dislodged the invader and then managed to enter her nest. During the whole process, a series of buzzing and fighting sounds were heard, and a struggle, resulting in the eviction of the invader, was seen on the X-ray screen.

In a second case, we artificially created a similar situation. We had nests at either end of a *Ferula* stalk occupied by two females, each in a

separate nest. After bee "A" left the right-hand nest on a foraging trip, we turned the stalk 180 degrees so that the left-hand nest with bee "B" was now on the right. When bee "A" returned, she entered the right-hand hole with bee "B" in it, and a fight ensued. Since each bee was defending what appeared to her to be her own nest, the fight was fierce and included loud buzzing, biting, and fighting head to head, first in the nest and later while in the air. Finally, the invader gave up. By further searching she located her original nest and entered it. Both bees continued buzzing loudly, each in her nest, long after the fight was over.

Xylocopa pubescens encounters similar environmental pressures as *X. sulcatipes* and, therefore, also has to guard her nest (Figures 18, 19). The stance and activity of the guard are similar to those of *X. sulcatipes*; however, the relationships of the daughters to the foraging mother are better defined. The spring nest of *X. pubescens* is always established by a single female who does all the work, including defense of the nest. Once progeny have emerged, the males depart, and the daughters assume nest-guarding duties while the mother forages. After these daughters have been mated, some may establish a nest that has a common entrance with their mother's nest (Ben Mordechai et al., 1978), an arrangement that allows them to share guard duties with her.

CELL CONSTRUCTION, PROVISIONING, AND OVIPOSITING.—A female commences her nesting sequence either by digging a new tunnel or by reshaping an old one, while discarding the sawdust through the entrance. Such sawdust removal is done incrementally, suggesting that nest excavation is not a continuous process. The females dig solely with their mandibles. They have been observed excavating tunnels at all hours, regardless of the amount of light present. When disturbed, the bees usually stop digging but resume it after the disturbance is over. In order to obtain a symmetrically round tunnel, the bee changes her position during the digging process, starting usually with her ventral part down and later turning to face sideways and finally upwards.

The shavings are left to accumulate to some degree and then are pushed to the entrance using the head and the abdomen. Having finished the excavation, the bee licks the walls meticulously, covering the entire surface with a thin film that has, probably, water-repellent properties. After this treatment is completed, she begins to provision a cell with pollen and nectar.

Upon entering the nest, the pollen laden female moves directly to the site of pollen deposition. She then turns her abdomen towards the end of the cell while keeping her hind tibiae extended at about 30–40 degrees, holding the abdomen between them (Figure 23a). To unload the pollen, she keeps the hind legs still and rubs her abdomen vigorously against them in very short, abrupt movements. This activity lasted, in the instances observed by us, about one minute. During pollen unloading, the bee also rubs her forelegs against the body and middle legs to remove the pollen that adhered to the body during collection. At that time, the bee may either hold her head still or make "licking" movements with her mouthparts upon the substrate. She may add liquids such as nectar and glandular secretions to the deposited pollen. She may also regurgitate pollen that has been collected in her crop. The pollen mixture is then formed into a slant against the distal wall of the cell. Following each addition of pollen, she usually removes the entire pollen slant from its location by use of her head, mouthparts, and forelegs. It is then placed on the tunnel floor (Figure 23b,c), and she stands over the mass and works on it. Before replacing the pollen mass, she licks the distal wall from which it had been removed. She then replaces the mixture of pollen, nectar, and glandular secretions into its former place and reshapes it into a slant. Soon after finishing the manipulation of the slant, she leaves the nest on another foraging flight.

The last treatment of the pollen slant by the female is that involved in preparing the bee bread. At that time, the pollen slant is extensive, and its face is almost perpendicular to the tunnel wall. The last few trips before the bee-bread preparation are always nectar-collecting trips.

Upon returning to the nest she first moves the pollen mass under her and kneads it while regurgitating nectar. She then shapes the pollen into a cylindrical form. A few minutes later the female moves the pollen cylinder and piles it a little anterior of her (Figure 23*d*). She then licks the entire cell area repeatedly with vigorous movements for about 30 seconds. Once finished, she may proceed to shape the bee bread in one of two ways. Either she makes a depression into the pollen mass, shapes it into its final form, and moves it in toto to its final position, or she moves the ready pollen-nectar mixture, bit by bit, from the tunnel floor to its final position. There, she presses it with her legs against her abdomen while facing the nest entrance (Figure 23*e*) and gives the bee bread its shape with the distal part rounded and the proximal abrupt.

As soon as the bee-bread formation has been completed, the female stands upon it, with her head pointing towards the entrance and the abdomen along the curvature of the bee bread (Figure 23*f*). In this position, she deposits the egg while moving forward, so that the egg is laid along the curvature of the bee bread (Figure 23*g*).

The bee then proceeds to build the partition, a process that lasts about one hour. For this purpose she scrapes shavings off the side walls and the floor of the tunnel immediately near the bee bread, as well as farther on. Much of the construction work is done by the pygidial region of her abdomen (Figure 23*h*), as judged by the fact that most of the time she works with her head away from the partition. The forelegs of the bee are active in collecting shavings and putting them into piles under her body. She then pushes the shavings back using her abdomen.

When the partition is nearly finished, the female turns with her head to it, licks it, and moves her head against it. She also licks the walls around the new partition. This behavior alternates with turning the abdomen to the partition and brushing the pygidial region over it.

Bee breads were examined for their weights and caloric values. For this purpose we removed the bee breads from seven cells shortly after the

eggs had been laid on them. This insured that we were examining unconsumed, complete material. The results (Table 3) show, that in spite of their significant differences in size, both bee species studied produce bee breads that have similar weights, water content, and caloric values. Furthermore, the low standard deviation values indicate that the bee breads are rather uniform among themselves in these parameters. Special attention should be paid to the uniformity of the "per gram" caloric values that give further support to our field studies, indicating that the bees have collected the materials for the bee breads from identical plant species.

SLEEPING AND NEST CARE.—X-ray observations at night showed that although some of the bees were active, most of them were quiescent and probably sleeping in different parts of the nest. A frequently observed sleeping posture was that of a bee laying on her dorsum, face upward, on top of a pollen slant (Figure 15).

A female, whether nesting or not, spends much of her time licking the walls of the tunnels. This is done both in the area where she is about to build a new cell and along the nest tunnels in various places. At times, licking is accompanied by tapping with the tip of the abdomen. Additionally, the female sometimes folds her body, bringing her head close to the apex of the abdomen where she may obtain chemicals secreted by abdominal glands.

Observations of bees in their nests also revealed them walking around occasionally with their sting-chamber open and the sting somewhat extruded. This behavior, like the previous one, may be associated with the emission of contents of glands that open there and may serve to coat the interior of the nest with a thin, transparent film.

Nest cleaning is done principally during, and immediately after, excavation of tunnels and after progeny emergence has been completed. The young female progeny, probably together with their mother, throw out the cast pupal skins, the broken cell partitions, the meconia, and the remains of cells in which development has ceased. Defecation by adult bees is done either outside of

TABLE 3.—Evaluation of bee bread of *Xylocopa pubescens* and *X. sulcatipes* (in caloric measurements, every sample was divided into 3 portions, and the data of each were averaged; n = number of samples)

Species	Wet weight (g)	Dry weight (g)	Water (%)	Caloric value (Kcal/g dry weight)	Total caloric value (Kcal/dried bee bread)	n
<i>X. sulcatipes</i>	1.16±0.17	0.91±0.17	22.04±4.82	5.15±0.22	4.64±0.76	7
<i>X. pubescens</i>	1.09±0.17	0.87±0.17	20.16±6.17	4.77±0.18	4.16±0.85	7

the entrance hole or away from the nest and consequently needs no removal; hence, only minor cleaning activities are carried out routinely. Nest care by *X. pubescens* is similar to that by *X. sulcatipes*. Both species lick the cell walls and coat them with a thin film, and both keep the nest normally free of foreign objects.

Like those of *X. sulcatipes*, the teneral and young of *X. pubescens* clean the nest of old meconia, broken cell partitions, and other refuse. These materials and sometimes also clean wood shavings were found, at times, to be stored in the nests of *X. pubescens*, either in old nest tunnels (Figures 14, 16, 20, 21) or, in the case of cane nesters, at the end of the culm (Figure 20). Similar shavings were also seen in a nest dug in the bottom of a styrofoam box that had extremely long tunnels that probably made other methods of refuse removal difficult.

INTERACTIONS AMONG INDIVIDUALS.—More than one individual female resides within the nest of *X. sulcatipes*, either when two or more bees nest jointly or as soon as adult progeny appear. Division of labor exists in both cases, inasmuch as one bee forages and another guards the nest. The forager brings nectar, pollen, or both to the nests, and, in addition to depositing these resources in pollen slants, she feeds the remaining coinhabitants through trophallaxis. In all observed cases, trophallaxis followed "demanding behavior" performed by the prospective recipient. This behavior usually consisted of physical blocking of the passageway of the returning forager, not permitting her to reach her destination (usually for pollen or nectar deposition) before having fed the

demanding bee. Since it was the guard who first met the returning forager, it was also she who was fed first. Feeding of additional bees sometimes followed in succession.

Transfer of food during trophallaxis was accomplished while one bee stood upright and the other rested on her back and their mouthparts met. Trophallaxis occurred both after pollen and after nectar collecting trips, but we could not see if only nectar or nectar mixed with pollen were transferred. Feeding on pollen was done when the bees took it from pollen slants.

Not all incoming flights of the forager ended in trophallaxis (Table 4); when it did occur, however, except for two cases, it always took place immediately upon the arrival of the forager in the nest. In two cases, the forager managed to reach the site of pollen deposition. Once there, she was left alone to perform the normal activities associated with unloading the pollen, removing and kneading the pollen slant, and replacing it. Afterward, when the forager tried to leave the nest for another trip, the guard blocked her way until trophallaxis took place.

Trophallaxis took place at least on one occasion, not only between a forager and a guard but also between two foragers as well. In a nest of *X. sulcatipes* that was observed in Hatzeva, we found three bees: two foragers and a guard. At 0652, one forager entered the nest and fed the guard, and at 0657, only five minutes later, the second forager entered and fed both the guard and the forager that had recently entered (Table 4). Thus it appears that trophallaxis may serve in social

TABLE 4.—Forager activity and trophallaxis records, *Xylocopa sulcatipes*, 1980 (number under trophallaxis = number of bees fed in succession)

Date	Hour	Nest	♀ no.	No. bees in nest	Forager with pollen	Trophal- laxis
28 Apr	1015	M	1	6	+	-
	1030		1		+	-
	1032		2		+	-
	1038		1		+	-
	1040		3		+	+
29 Apr	0825	M	1	4	+	?
	0840		2		+	+
	0845		3		-	-
	0849		1		+	-
11 May	1111	M	1	2	+	-
	1209		1		+	+
	1248		1		+	-
12 May	1018	M	1	2	+	+
	1046		1		+	-
	1245		1		+	-
13 May	1015	M	1	2	+	-
	1045		1		+	+
	1120		1		+	+
	1208		1		+	+
15 Jul	0536	C	1	3	+	+(2)
	0552		1		+	+
	0657		2		+	+(2)
	0755		1		+	-
	0901		1		+	+
	0924		1		-	?
	0935		2		-	+
	0958		1		+	+
	16 Jul	0554	C	1	3	+
0621			1		+	+
0639			1		+	-
0710			1		+	-
0740			1		+	-
0820			1		+	?
0950			1		+	-
1050			1		+	-
12 Oct	1103	A	1	2	+	-
	1155		1		+	-
	1245		1		+	-
12 Oct	1412	S	1	4	-	+(2)
12 Oct	0925	A	1	2	+	-
	1020		1		+	-

interactions, in addition to its function in nutrition.

In some nests, individuals of *X. sulcatipes* share cell provisioning. The pollen used for bee-bread production in such nests is collected by several foragers that may collect simultaneously, always leaving a guard at the entrance of the nest. We observed such a nest during 28 and 29 April 1980. It had six resident bees, three of which were foraging (Table 4). All came back with pollen within six minutes of each other. A cell was completed and an egg laid by one of the three on 28 April within a few hours of that time. A second incident, involving three resident bees, occurred on 15 July, when two bees came in with pollen, twice in succession, once within five and once within six minutes of each other. No oviposition occurred on the date of observation (Table 4). In cases of cooperative foraging, one female, presumably the ovipositing mother (no. 1 in Table 4), will make more trips than the others.

The pollen slant was always manipulated solely by the forager. On rare occasions, the guard bee was seen licking it and, possibly, also feeding on it; however, usually she kept at a distance. This was true not only when the foraging bee was out for a short trip but also when she failed to return at night, leaving the guard in the nest alone with the pollen slant for over 14 hours.

Xylocopa pubescens (Gerling et al., 1981) shows similar behavior to *X. sulcatipes* within the nest; however, since this species has a somewhat different social structure, it also differs in the details of interaction between the individuals. There is no sharing of foraging or bee-bread preparation, and the cohabitation of females, other than progeny with the mother, is limited to short periods (Ben Mordechai et al., 1978). In this species, pollen slants that have been accumulated as provisions for future larval food were usually not touched by mature bees. Rather, sometimes special provisions were provided for this purpose, as could be attested for by the occasional disappearance of pollen stores.

The comparatively simple structure of the nest

of *X. sulcatipes* contrasts rather sharply with the complex nest structure of *X. pubescens* and results in different modes of trophallaxis in these species. *Xylocopa sulcatipes* shares food with her juvenile progeny and/or co-nesting adults. *Xylocopa pubescens*, in which a number of actively nesting females share a common nest entrance (Figure 14) as well as guard duties, has more varied associations based on trophallaxis. Thus, a foraging female may feed her own progeny (Figures 25, 26) whether guarding the nest or not. She may also feed other guards, that may be her mother, her sisters, or unrelated bees.

Behavior outside the Nest

TERRITORIALITY AND MATING.—Initial observations of territorial and mating behavior of *X. sulcatipes* were published by Velthuis and Gerling (1980). They found two distinct types of territorial behavior during March and April. One was at Ein Geddi where males aggregated en masse about flowering *Moringa peregrina* trees, and each male defended a small section of the air space around the tree by cruising back and forth. A second type was observed in the Hatzeva Field School and was typified by the cruising of individual males, each defending its own flowering plant or plants (*Calotropis procera*, *Cassia* spp., *Nerium oleander*, *Retama raetam*, and *Tamarix nilotica*).

Two other behavioral types were seen since then. These included (1) massive flight of males about the canes in which *X. sulcatipes* nested and (2) males that flew from one *X. sulcatipes* nest to the other. In Hatzeva the latter behavior was typified by a male that was passing by each of five nests (which were 10–30 meters from one another) every 1–2 minutes, occasionally circling a nest, attempting to enter it or to chase off other arriving males.

From these observations, it is apparent that males may defend territories near food sources or nesting sites, either solitarily or in groups. The use of a certain territorial strategy seems to correlate with the probability that the location will

serve as a meeting place of the sexes. In the spring time, in areas where food is not widely dispersed, the females aggregate about blooming *Moringa peregrina* plants that serve as a feeding center and a meeting place. In other areas, in which flowers are more dispersed but yet are close to the nesting sites and visited frequently by the females, each male may defend his own flowering plant. Alternatively a male may choose to observe several scattered nests, especially in the summer when feeding sites of the females are unstable and scattered about. Finally, during relatively rare occasions when *X. sulcatipes* nest gregariously in large numbers, as in cane roofs, it seems to be most profitable to guard that location rather than the food sources.

Since the territorial behavior of the bees was seen to be consistent for the same situations year after year, and since bees that arrive at new places, like Hatzeva, adopt different strategies at different seasons, we may assume that this species is flexible in its capacity to adopt the suitable territorial strategy.

After discovering the territorial behavior of males of *X. sulcatipes*, we were then able to study the communication between the sexes that led to copulation. By using tethered males and females and by dissecting females and using their mandibular glands as odor sources, it was possible to construct the following chain of communication that leads to copulation.

The territorial males chase and follow any object of their approximate size. If the object is a male, he will usually leave the territory after having been pursued; if it is a female, she may land on a flower. The territorial male will follow her to the flower and fly above her with his antennae outstretched above her abdomen. If the female is receptive at this stage, she spreads her wings and emits an odor from her mandibular glands. This odor causes the male to remain hovering above her until she leaves the flower. He will then grasp and hold her in mid-air, and they will fly together for some distance trying to copulate. Mating occurs in mid-air with the male

at about 60° to the female. Additional males often follow the mating pair (Velthuis and Gerling, 1980).

Territorial and mating behavior of *X. pubescens* are less understood. The males make their territorial flights in places that are chosen by them for this purpose, usually in the full or partial shade of a tree or shrub, at a height that varies from a few centimeters to a few meters above the ground. The places may or may not be near nesting sites. The sites suitable for territorial flights seem to have special characteristics that are recognized by other males. This was indicated by the fact that we observed marked males returning to the same site day after day and that other males compete for these sites and supersede the present males once they are gone. Moreover, the same spot harbored males year after year. Examples of locations of territorial flights are canopies of palm trees, within or under the shade of *Tamarix* trees, on top or about *Malva viscus arboreus* plants, in the thicket of a *Pistacia palaestina* tree, above a group of *Arundo* reeds, or in the shade of a *Schinus molle* tree.

The behavior associated with territorial flights is always similar. The bee flies back and forth, delimiting an area of a few meters while sounding an easily audible, monotonous hum. Defense of the territory is accomplished by the territorial male by flying towards the intruder and, if the intruder does not manage to dodge, bumping into him with the head. The intruder does not usually depart but moves aside, whereupon the same process is repeated. This behavior results in several very short charges by the defenders and evasions by the intruder, who retreats from the territory while evading the defender's attacks. Once the intruder has left the territory, a process which may last as long as half an hour, the defender returns to this territory. On several occasions we saw such interactions in which three rather than two males were involved.

Prior to defending a territory, the male touches a substrate in the future territory with this head a number of times. This behavior, which appears like a series of short bumps, was also performed

in a flight chamber; it was repeated each time prior to the territorial flight and apparently constitutes pheromonal site marking. No matings or approaches of females to the territories were observed.

Territorial flights and matings of both species of carpenter bees were usually limited to the reproductive periods of spring and summer; however, occasional flights occurred also in the fall. Moreover, a mating pair of the univoltine American species *X. virginica* (Linnaeus), which usually mates in the early spring (Gerling and Hermann, 1978), was discovered on flowers in the fall (September) by one of us (Hurd) at Lake Barcroft, Virginia, and this pair was also observed and photographed by Prof. Pe. J.S. Moure.

FLOWER VISITS.—The bees visit flowers for both pollen and nectar collection. In some flower species both are collected, whereas in others only one or the other is collected. Of the visited plants seen by us (Table 5), four species, *Calotropis procera*, *Retama raetam*, *Acacia tortilis*, and *A. raddianna* are the native plants most visited by *X. sulcatipes* and *X. pubescens* in the Arava Valley. *Calotropis procera* provides only nectar for the bees and blooms from March to September, and *R. raetam* blooms for a short period during March and April. The two species of *Acacia* provide both pollen and nectar; one blooms from April to June (*A. tortilis*), and the other in the late summer (August and September). An additional, much preferred, nectar source is *Moringa peregrina*, which is confined to a few oases (e.g., Ein Geddi and near Eilat) and blooms profusely during March and April.

Hatzevah Field School, like many of the settlements in the Arava Valley, abounds in introduced plants that thrive through irrigation by man. Among these, we found *Cassia* spp. (March–May), *Lucaena glauca* (April–May; September), *Solanum elaeagnifolium* (April–October), and *Vitex agnus-castus* (July–August) to be the most visited sources for nectar and/or pollen.

Calotropis procera, the flowers of which open continuously during the morning hours, was a much-used nectar source, so much so that bees were seen on every flowering specimen of this

TABLE 5.—Flower species visited by *Xylocopa sulcatipes* (S) and *X. pubescens* (Pu) in Israel during 1978 (N = nectar collecting, P = pollen collecting, ? = doubtful record)

Flower species	Bee species	Localities	Material collected
ACANTHACEAE			
<i>Thunbergia grandiflora</i>	Pu	wherever occurs	P? + N
AIZOACEAE			
<i>Mesembryanthemum nodiflorum</i>	S	Sede-Boqer	N
APIACEAE			
<i>Ferula tingitana</i>	S	Sede Boqer	P + N
<i>Ferula</i> sp.	S	Golan Heights, Rift Valley	P + N
ASCLEPIADACEAE			
<i>Calotropis procera</i>	S, Pu	Ein-Geddi, Arava	N
BIGNONIACEAE			
<i>Stenogium stans</i>	S	Sede-Boqer, Eilat	
CAESALPINIACEAE			
<i>Cassia</i> spp.	S, Pu	Hatzeva	P + N
<i>Cassia didymobotrija</i>	S, Pu	Hatzeva, Eilat	P
<i>Ceratonia siliqua</i>	Pu	Mt. Carmel	P
<i>Delonix regia</i> (= <i>Poinciana regia</i>)	S?, Pu	Tel Aviv, Ein-Geddi	P + N?
<i>Parkinsonia aculeata</i>	Pu	Tel Aviv, Sede-Boqer	P + N
<i>Poinciana pulcherrima</i>	Pu	Tel Aviv, Hatzeva	P + N
CAPPARACEAE			
<i>Capparis spinosa</i>	S, Pu	Ein-Geddi	N
<i>Cleome gigantea</i>	Pu	Tel Aviv	P + N
CAPRIFOLIACEAE			
<i>Lonicera etrusca</i>		Tel Aviv	P + N
<i>Lonicera japonica</i>		Tel Aviv	P + N
CARICACEAE			
<i>Carica papaya</i>	Pu	Tel Aviv, Jericho	P? + N
COMPOSITAE			
<i>Carduus argentatus</i>	S	Sede-Boqer	N
<i>Carduus getulus</i>	S	Sede-Boqer	N
<i>Carthamus</i> sp.	Pu	Ein-Geddi	P? + N
<i>Helianthus annuus</i> or <i>H. cucumerifolius</i>	Pu	Tel Aviv	P + N
CONVOLVULACEAE			
<i>Ipomoea purpurea</i>	Pu	Jericho	N
CRUCIFERAE			
<i>Brassica oleracea</i> var. <i>capitata</i>	Pu	Ramat Hasharon	P + N
<i>Erucaria uncata</i>	S, Pu	Ein-Geddi	P + N
<i>Moricandia nitens</i>	S	Sede-Boqer	N
CUCURBITACEAE			
<i>Cucumis melo</i>	Pu	Tel Aviv, Ein-Yahav	P? + N
<i>Luffa aegyptica</i>	Pu	Tel Aviv and surroundings	P + N
GERANIACEAE			
<i>Pelargonium fragrans</i>	Pu	Sede-Boqer	N
IRIDACEAE			
<i>Iris hieruchamensis</i>	Pu	Jeruham Nature Reserve	N

TABLE 5.—Continued

Flower species	Bee species	Localities	Material collected
SCROPHULARIACEAE			
<i>Antirrhinum majus</i>	Pu	Tel Aviv	N
LAURACEAE			
<i>Persea americana</i> (= <i>P. gratissima</i>) (avocado)	Pu	Tel Aviv	N
LILIACEAE			
<i>Urginea undulata</i>	S	Sede-Boqer	P + N
LOGANIACEAE			
<i>Buddleja madagascariensis</i>	Pu	Ein Yahav	N
MALVACEAE			
<i>Alcea setosa</i>	Pu	Tel Aviv	N
<i>Hibiscus</i> sp.	S, Pu	Tel Aviv	N
MIMOSACEAE			
<i>Acacia cyanophylla</i>		wherever occurs	P + N
<i>Acacia raddiana</i>	S, Pu	Negev Arava	P + N
<i>Acacia tortilis</i>	S, Pu	Negev	P + N
<i>Leucaena glauca</i>	S, Pu	Hatzeva	P + N
<i>Prosopis farcta</i>	S	Sede-Boqer	P + N
MORINGACEAE			
<i>Moringa peregrina</i>	S, Pu	Ein-Geddi	P + N
MYRTACEAE			
<i>Eucalyptus</i> sp.	S	Sede-Boqer	P + N
<i>Eugenia uniflora</i>	Pu	Tel Aviv	P + N
<i>Melaleuca armillaris</i>	Pu	Sede-Boqer	P
<i>Myrtus communis</i>	Pu	Tel Aviv	P + N
NYCTAGINACEAE			
<i>Bougainvillea glabra</i>	Pu	Tel Aviv, Hatzeva	N
PAPAVERACEAE			
<i>Eschscholzia californica</i>	Pu	Tel Aviv	P
<i>Papaver acaulis</i>	Pu	Tel Aviv	P + N
PAPILIONACEAE			
<i>Lathyrus ochrus</i>	Pu	Tel Aviv	P + N
<i>Lupinus pilosus</i>	Pu	Tel Aviv	P + N
<i>Retama raetam</i>	S, Pu	Arava	N P
<i>Tipuana tipu</i>	S, Pu	wherever occurs	P + N
PASSIFLORACEAE			
<i>Passiflora edulis</i>	Pu	Tel Aviv	P? + N
POLYGONACEAE			
<i>Antigonon leptopus</i>	Pu	Ramat Hasharon	N
SOLANACEAE			
<i>Solanum elaeagnifolium</i>	Pu	Hatzeva, Coastal Plain	P + N
<i>Nicotiana glauca</i>	Pu	Coastal Plain	N
TAMARICACEAE			
<i>Tamarix nilotica</i>	S?, Pu	Arava	P + N
VERBENACEAE			
<i>Clerodendron inerme</i>	S?, Pu	Tel Aviv, Arava	N
<i>Lantana camara</i>	Pu	Tel Aviv	N
<i>Vitex agnus-castus</i>	S, Pu	wherever occurs	P + N
ZYGOPHYLLACEAE			
<i>Zygophyllum dumosum</i>	S	Sede-Boqer	N

species during each observation day throughout the study.

Bees visiting one *C. procera* plant from sunrise until noon were registered during one day in April of 1978 and in 1981. Temperatures during these two months ranged from about 17°–30° C in 1978 and 20°–40° C in 1981. In both years there was about equal representation of *X. sulcatipes* (48.7% and 51.7%) and of *X. pubescens* (51.3% and 48.3%). The total number of flower visits per day varied, however, with 205 in 1978 and 309 in 1981. The higher number of visits during 1981 might have been associated with the higher temperatures and the accompanying greater need for liquids.

When a bee collects nectar from a *Calotropis*, it alights on the flower and inserts its proboscis into one of the five specialized nectaries (Wanntorp, 1974). She then may leave or turn to the next nectary, and so on, until she has visited all five or, on certain occasions, even six or more nectaries, thus performing over one full circle and visiting the same nectary more than once.

Our observations have shown that most visits are short, lasting an average of 2.31–6.2 seconds for *X. sulcatipes* and 4.03–8.5 seconds for *X. pubescens*. During such visits, the bees were able to visit only 1–3 nectaries. The incidence of visits to 6–7 nectaries per flower amounted to only 8%–9% of the total visits. These observations showed also that most flower visits of *X. pubescens* lasted longer by 30%–100% than those of *X. sulcatipes* for the same number of nectaries (Figure 1).

Schremmer (1972) made a thorough study of the methods of pollen collecting by *X. leucothorax* (DeGeer). He found that an important, if not the main, method of pollen collecting is the ingestion into the crop during foraging and then its regurgitation upon return to the nest. In our studies we observed numerous females of both species collecting and carrying pollen by use of the scopae on the hind legs and transporting it this way to the nest. Dissections of 14 females of *X. pubescens* actively involved in bee-bread formation during the months of March–June revealed that 13 had abundant pollen on their bodies and that eight of

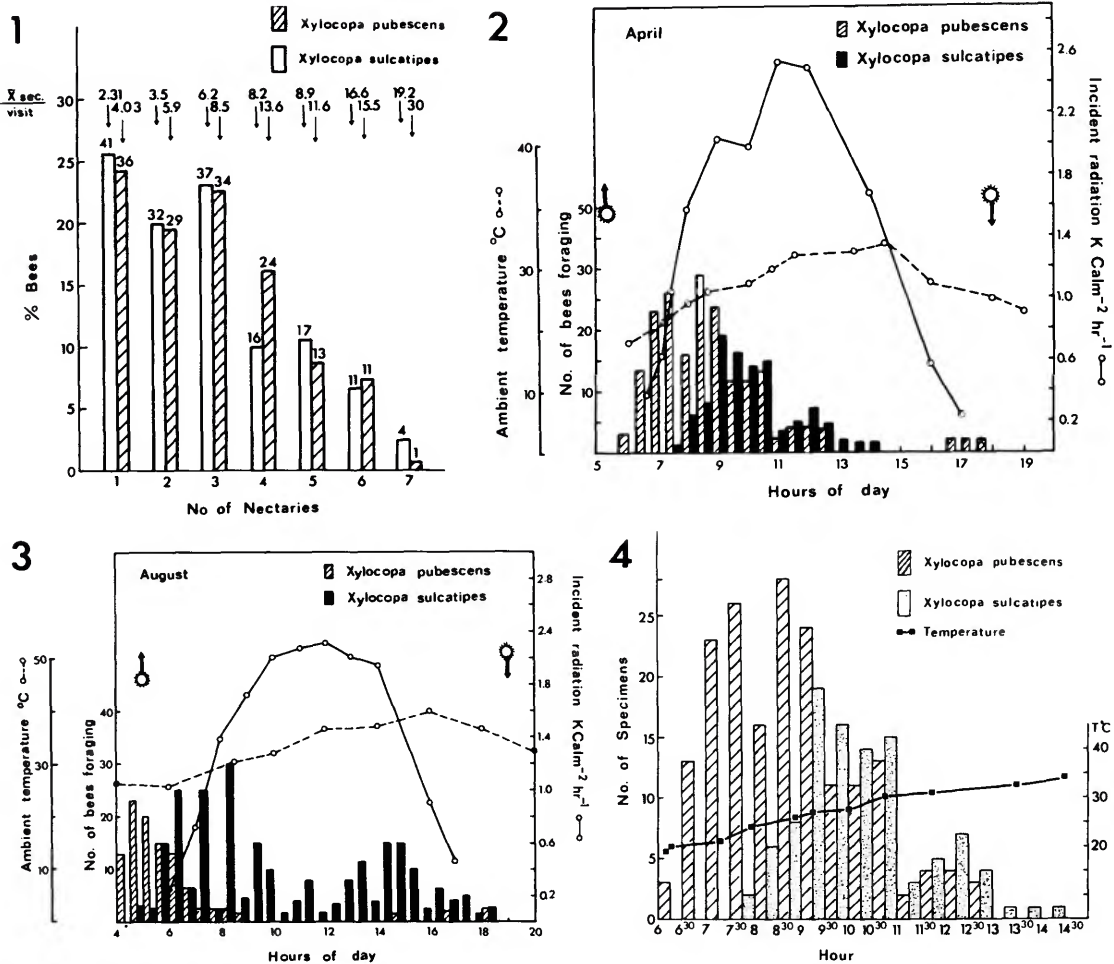
these also had pollen on the scopae. Only one had pollen in the crop and hardly any adhering to its body. No further studies were conducted to determine if the ingested pollen served for adult nutrition and production or for bee-bread formation, or both; however, we are satisfied that the presence or absence of pollen on the scopae is a reliable indication of the forager's activity at the flowers.

The method of pollen collecting varies according to the type of flower. In *Lucaena* and *Acacia*, both having composite flower heads, the bees move rapidly on the top of the flowers, "brushing off" the pollen. After visiting each flower, they hover for a few seconds in the air, transferring the pollen from all body parts to the hind legs. In *Cassia* and *Solanum elaeagnifolium*, the method of collecting involves an acoustic technique. The bee alights on the flower, inverts it, hangs onto the stamens with its forelegs, and buzzes strongly with its flight muscles. The pollen within the anthers is shaken out and covers the bee's head and thorax. The pollen grains are then removed to the hind legs by quick grooming movements.

Observations of the frequency of flower visits, both for nectar (*C. procera*) and for pollen (*L. glauca*), revealed that either the same or different bees visited the same flower over and over, all within a few minutes; however, the bees were selective in the flowers on which they alighted and could often be seen approaching a flower and then abandoning it while still in flight.

Xylocopa pubescens differs from *X. sulcatipes* in its flower relationships principally due to three characteristics: its different geographic range, its ability to become active at ambient temperatures of 18°C rather than the 21°C required by *X. sulcatipes*, and its larger size.

The range of *X. pubescens* in Israel covers, in addition to the deserts, most of the Mediterranean region, which is characterized by somewhat different flora than the Arava Valley. Among the plants that abound in the Mediterranean region, we found *X. pubescens* often visiting species of *Lonicera*, *Helianthus annuus*, *Parkinsonia aculeata*, and *Luffa aegyptica* for both pollen and nectar collec-



FIGURES 1-4.—Bee activity: 1, visits to *Calotropis procera* flowers at Hatzeva, April 1981, showing the relationships between average time spent on each flower, percentage of bees, and number of nectaries; 2, activity pattern during April, showing relationship to temperature and incident radiation; 3, same during August; 4, visit records to *Leucaena glauca*, Hatzeva, April 1979.

tion. Other plants, like *Clerodendron inerme*, *Solanum elaeagnifolium*, *Carica papaya*, and *Delonix regia*, occur and are visited in both regions.

Three of the most heavily visited plant species by *X. pubescens* are the introduced *Lonicera japonica*, *Luffa aegyptica*, and *S. elaeagnifolium*. All are sources of nectar and pollen. *Lonicera japonica* has a long tube, and nectar is robbed by *X. pubescens* through a slit that the female makes in the tube of the corolla. Pollen is also collected by flying at the

height of the anthers and combing them with all six legs. *Luffa aegyptica* is visited during all hours of the day. It is a monoecious plant with a preponderance of staminate flowers.

In Ramat Hasharon, we observed *X. pubescens* visiting *L. aegyptica* during August 1978. We chose certain individual bees and followed them from the minute they landed upon the first flower until they left the last. We found that the same flower is often visited more than once by the same female

TABLE 6.—Visits of *Xylocopa pubescens* to *Luffa* flowers on the morning of 28 Aug 1978

Bee	Total time spent on flowers (min)	No. of flowers visited	Average time per flower (sec)	Remarks
1	1	15	4.0	♀
2	1	26	2.3	♀
3	2	5	24.0	♀ old, marked
4	2	12	10.0	♀
5	2	11	11.0	♀ young
6	5	9	33.3	♂
7	5	36	8.33	♂
8	6	55	6.54	♀
9	9	45	12.0	♀ old
10	9	57	9.47	♂

and by alternative bees. No bee visited just one flower and left. Instead, the seven females and three males that we followed made between five and 57 individual consecutive flower visits, each lasting on the average 2.3–33.3 seconds (Table 6). Some of the visits were very short, lasting only one second. Only nectar was collected throughout the observation period.

The behavior of the bee within the *Luffa* flower includes arrival, a short walk or flight to the nectaries at the base of the stamens, insertion of the proboscis, obtaining nectar, and departure. The delicate corolla loses its yellow color and becomes transparent in places where it has been touched by the leg of the bee. Consequently it is easy to see which flowers have been visited and to what extent.

The recently introduced weed *Solanum elaeagnifolium* has flowers that open at daybreak, when they are visited extensively by *X. pubescens*. The bee releases the pollen from the anthers by buzzing, which creates vibrations that cause the pollen grains to fall out of the anthers and onto the bee.

The fact that *X. pubescens* always starts its activity before *X. sulcatipes* and visits *S. elaeagnifolium* at the initiation of its daily activity limits somewhat the use by *X. sulcatipes* of this plant species as a pollen source. *Lucaena glauca* flowers are vis-

ited during the typical activity hours of each bee species with a consequent, somewhat bimodal distribution of activity (Figure 4). Similarly, visits of *X. pubescens* to *Calotropis procera* are carried out more during the early morning hours; however, since flowers of this plant open continuously during the morning hours, and since this plant serves as a source of much-needed liquids, the visits to it continue after those to pollen sources like *Lucaena glauca* and *Acacia* spp. are discontinued.

An analysis of the pollen-collecting behavior of both species when visiting *L. glauca* was made during four days of continuous observation in April 1981. The days were unusually hot, with noon temperatures reaching 40°–44°C in the shade. Pollen-collecting activity started about 0435 and ceased about 0900, with *X. pubescens* being the sole visitor until around 0600 and *X. sulcatipes* being the dominant bee thereafter.

Lucaena glauca has ephemeral flowers that open, and dehisce, by dawn or shortly thereafter. Therefore, the first bees to visit the plant exploit the availability of abundant, easily collectable pollen on each flower. "Swarms" of bees cover the plant and reduce the abundant pollen supply rapidly, and by 0500, when the sun rises, a change in the behavior of the bees indicates a decrease in the availability of the pollen. The behavioral change manifests itself through a shift from a 1½–2 second "run" to a ½-second "touch" of each flower. The bees, especially during their later visits, sometimes arrived already with some pollen on their legs. Likewise, they sometimes flew to other pollen sources after having left the *L. glauca* plant. For these reasons it was not possible to draw conclusions as to the relationships between the hour of visit, pollen abundance, mode of pollen collecting, and the number of flower visits.

We counted, however, the number of visits performed by each bee and determined that after 0500, individuals of both species spent about one-half second on each flower. Accordingly, we were able to determine not only the duration of each plant visit but also the average time spent flying from one flower to another. The averages were as follows: *X. pubescens*, duration of plant visits 215.6

seconds, time spent flying from one flower to the next 6.28 seconds, $n = 18$; *X. sulcatipes*, duration of plant visits 159.1 seconds, time spent flying 4.05 seconds, $n = 29$. Statistical analysis of the results, using the Wilcoxon two-sample test (Sokal and Rohlf, 1969), showed that the average time spent flying from one flower to another was significantly ($P < 0.01$) longer for *X. pubescens*. The average number of flowers from which pollen was collected during each plant visit was about equal for each species, but this showed extreme variations (35.2, SD = 20.7 for *X. pubescens* and 38.7, SD = 26.2 for *X. sulcatipes*).

Ontogenesis

The development from egg to adult is similar for both species in question. The eggs are laid in the closed cells upon the bee breads and hatch. The small emerging larva feeds on the bee bread without changing its position. A few days later, the larva starts moving about and molts, and the second instar can be seen in various positions upon the bee bread. The next molt is followed by deposition of meconia and the exhaustion of the bee-bread supply. After this the pre-pupal stage starts. It lasts several days and terminates in pupation. All pupae are white at first and become darker as time goes on. The oldest pupa is the first to turn into an adult.

The duration of development was followed in the laboratory and in the field, mainly through the study of X-rays (Figure 30) taken 2-3 times each week. In a few cases, individuals were also reared to maturity in the laboratory at about 20°-25° C. Under these conditions, development from egg to adult took 45-49 days with the following breakdown: egg, 4-5; larva, 13-16; pre-pupa, 12-15; pupa, 12-15 days. Developmental duration of the individuals was not uniform even within the same nest, but no definite pattern relating it to the order of oviposition was found. In the summer developmental duration lasted somewhat less; however, no exact figures from the field were obtained due to technical difficulties.

The immature stages of both bee species resem-

bled those described by various workers for other species (Anzenberger, 1977; Gerling and Hermann, 1978; Rau, 1933; and others).

The progeny of *X. sulcatipes*, of which we found up to 13 in one nest, are linearly arranged (Figure 22). The time required for pollen gathering and bee-bread preparation varies greatly from one case to another, but unless circumstances are unfavorable, the bee does not need more than 1-3 days to complete preparation of a fully provisioned cell. Eight cells will therefore take some 12-20 days to prepare. Since developmental duration of all progeny is about equal, the oldest female in large nests will emerge as an adult when the youngest is a pre-pupa or very young pupa. In smaller nests the gap between youngest and oldest bees is narrower.

Upon emergence, the teneral bees break all of the partitions, and the still-unemerged pupae are allowed to lie in a disorderly fashion intermingled with meconia and broken-down cell partitions (Figure 24); however, they are unharmed. The teneral bees are located between the unemerged progeny and the nest entrance, where they are fed by their mother. Once all bees emerge, they clear the tunnel of all debris.

The *X. sulcatipes* mother remains with her progeny until all have completed the teneral stage and become independent; only thereafter does she start the construction of new cells.

Xylocopa pubescens has a very similar life history, the main difference being that it constructs short tunnels that contain usually 1-3 progeny each, which emerge within a few days of each other. The first to emerge pushes its siblings further into the next tunnel, and they occupy the niche left by its departure.

While constructing cell partitions among branching tunnels, the female of *X. pubescens* is capable of using an already existing partition as an anchoring substrate in lieu of the cell wall (Figure 28).

Xylocopa pubescens does not wait for her developing progeny to emerge and leave, before starting to provision new cells; rather, she often has,

concurrently, pupae, mature larva, with very young progeny.

Diurnal and Seasonal Activity

DIURNAL CYCLES.—Carpenter bees raise their body temperatures through muscular activity, from a certain threshold temperature to the level at which flight activity can be maintained. The threshold temperature of *X. sulcatipes* is 21°C, and the muscular temperature that has to be reached before flight activity can take place is 37°C (Hefetz et al., in prep.).

During the winter, the bees can be seen flying occasionally on warm days when they visit flowers for nectar. The frequency of such flights depends upon the frequency of warm-weather days, and we assume that the main trigger for them is hunger, since the elevation of body temperatures resulting from higher ambient temperatures causes the food supplies in the bees' crop to be consumed. During April, 21°C are reached about 0800 hours, and the bees fly from then until about 1400 hours. The main flight activity, which is carried out in order to collect pollen and nectar for progeny raising, takes place in the morning hours from 0800 to 1100 (Figure 2). From May, night temperatures in the Arava Valley usually exceed 21°C, and the first *X. sulcatipes* individuals fly at dawn. Their flight activity continues throughout the day, diminishing only slightly during the hours of the late morning and early afternoon, and declines shortly before sunset. The ability of *X. sulcatipes* to continue its activity throughout the summer day in the Arava Valley is especially remarkable when the high incident radiation at the season is considered (Figure 3), since the total heat load that the bees has to overcome consists of both temperature and incident radiation and therefore is substantial.

Xylocopa pubescens has an activity threshold at an ambient temperature of only 18°C, and the average thoracic temperature at the onset of flight is 35°C. Consequently, it can start its activity at earlier morning hours than *X. sulcatipes*. In the winter, the difference between the species is not

very evident; however, during the springtime the bees start to fly between 0600 and 0700, whereas during the summer they depart en masse 30 to 60 minutes before sunrise (Figure 3).

Contrary to *X. sulcatipes*, *X. pubescens* is strongly affected by heat load, and its activity diminishes greatly with the rise of radiation (Figures 2, 3). Therefore, the period during which they visit flowers each day is short, having a peak during 0600–1000 in the spring and during 0400–0630 in the summer. Thus, there is only partial overlap in the hours of activity of these two species in the areas of their sympatry.

SEASONAL ACTIVITY.—*Xylocopa sulcatipes* nests and develops progeny during the spring and summer and is relatively inactive during the winter, when it flies about only on warm days, mainly in the Arava Valley and the Dead Sea Basin. In contrast to the breeding season, when trips are for collecting pollen and nectar, trips made during the winter are solely for nectar collecting and enable the bee to sustain the slightly elevated metabolism during the warm days.

The physiological state of the bees during this season was assessed by several parameters: ovarian development, Dufour's gland state (full or empty), fertilization (existence of sperm in the spermatheca), the development of the yellow gland, the existence of food remains in the gut and rectum. During the months of December, January, and most of February, the bees possessed undeveloped ovaries and were mostly unfertilized, and neither the Dufour's gland nor the yellow glands showed activity.

During the spring, three critical factors coincide with the start of the breeding season: the rise of the ambient temperature above the activity threshold, the start of the blooming period of several flowers that provide nectar and pollen for sustenance and ovarian development and for the preparation of bee bread, and the mating of the virgin females.

Active nesting of *X. sulcatipes* does not start concurrently in all nests. Some nests were found already with bee bread and developing progeny during March, when others each contained 1–3

yet-unmated and inactive females. In this way, an overlapping of generations is achieved in this species.

Once active, a nest may contain one, two, or sometimes more females, all of which are fertilized and have well-developed ovaries. Consequently, we assume that the progeny in such nests were produced by several mothers. These mothers may share guard duties, but it is still unclear whether they also share other chores such as nest excavation.

From late April on, following the emergence of the progeny of the first generation, young, teneral bees may also be found in some nests. Thus, an active *X. sulcatipes* nest consists of at least one mated bee and may also contain several mated or unmated females.

The teneral bees leave the nest some 1-2 weeks following emergence and, after mating, start their own nests. The parent or parents may excavate the existing nesting substrate further and breed another generation in it or find a new substrate.

Altogether about four generations are produced during one season, ending in September or October. Thereafter the bees stop collecting pollen but still fly about actively. The cessation of nesting activity in the fall coincides with a substantial reduction of the natural pollen sources and with the shortening of the days. Temperatures very often remain high until late in November and probably cannot be correlated with the bees' activity.

Although *X. pubescens* also has about four generations per year and is active approximately during the same time as *X. sulcatipes*, it differs from the latter in a number of respects.

All spring nests, whether started by the occasional overwintering old bee or by a young bee that just mated, have only one bee in them until the progeny are at least in the pupal stage (Ben Mordechai et al., 1978). Nesting starts, more or less, contemporaneously during March in the warmer parts and April in the cooler regions.

In May when the progeny emerge, many of the nests become gregarious, inasmuch as the mother bee still retains her tunnel complex, which she

continues to enlarge and provision. During this time one or more progeny often build extension tunnels from the mother's tunnels so as to form complex ramifying nests that have only one entrance (Ben Mordechai et al, 1978). Therefore, the nest of *X. pubescens* changes with the season from a single nest into a nest-complex that becomes more elaborate as the season advances.

With the increase of population, many bees that are not accommodated within their mother's nesting board try to invade various occupied nests, usually without success because the latter are well guarded. Therefore, they usually establish new nests.

We added eight new nesting boards (the "B" series) to already occupied "A" series boards in Hatzeva in July of 1978. Each board measured some 20-30 × 10-15 cm and was about 3-5 cm thick. They were made of very old and soft poplar, and each had one or two holes drilled in its narrow side (the side that measured 15×5 cm). The holes were a few centimeters deep and 1.0 cm in diameter. The boards were placed on top of fully occupied nests of *X. pubescens* within old flowering stalks of agave; nesting started shortly thereafter, and progeny were seen during the same month. In a total population sample that we made on the 26th of November, we found that all the boards had nests in them and that the overwintering sex ratio was about 0.8 (Table 7). A similar sex ratio (41 females and 34 males) occurred in a log (Figure 12) found in Jericho on 29 January 1981.

Of the 51 female bees found in the "B" boards, only five were old (had worn wings) (Table 7). All the rest appeared too young to have ever had progeny. They were found in a total of 36 holes within 11 boards all of which were either extensions of the drilled holes that we provided originally or newly dug ones. The bees averaged about three per hole, but 16 cases were found in which one bee only was found, and holes with as many as 13 bees were also found. Knowledge of the ontogeny of these indicates that they do not develop alone and that there are several individuals that reach maturity about the same time.

TABLE 7.—Nest occupancy record of *Xylocopa pubescens* in 14 nesting boards, Hatzeva, 26 Nov 1978 ("B" boards installed 10 Jul 1978)

Sex	In all nesting boards				In "B" boards only	
	Inhabitants	Holes	Bees	Old bees	Bees	Old bees
Males	65	6 ^a	9 ^b	0	41	0
Females	81	16 ^a	22 ^b	6	51	5
Totals	146	42 ^c	31 ^b	6	92	5
Sex ratio (♂/♀)	0.8					

^a Number of holes containing bees of indicated sex only.

^b Total number of bees per respective (a) holes.

^c Includes 20 holes containing both ♂ and ♀ bees.

Contrarily, there are no records of 13 more or less simultaneous emergences from the same nest. Therefore we may postulate that the bees move from one next hole to another and even from one board to another in the fall. This process is associated with a breakdown of the guarding activity after progeny production ceases.

Natural Enemies

PARASITES.—A single parasite species, *Coelopen-cyrtus* sp. (Encyrtidae), was found. These are polyembryonic, internal parasites of mature larvae, with hundreds of individuals emerging from each larva. They run about in large numbers on top of the nesting boards, where matings were also seen. The empty skins of host larvae remain in the tunnel (Figure 29) and can be seen in X-ray radiograms. These parasites were observed running on top of nests during all of the nesting season. Largest numbers were found in the fall when their populations apparently reach peaks. Overwintering apparently takes place in or near dead hosts, as well as in refuge places like old nests, as found by us during the end of January 1981. All cases of parasitization found by us involved *X. pubescens*; however, the parasites were seen also on the outside of the nests of *X. sulcatipes*. Although we made only few collections of parasites, primarily in the Arava Valley, the occasional occurrence of parasitization in the Tel Aviv

area seems to indicate that the parasites are sympatric with *X. pubescens* throughout its range.

PREDATORS.—Insects: A *Sphodromantis viridis* Forskal (Mantidae) female caught and ate a male *X. sulcatipes* on a hedge of *Clerodendron inerne* in Ein Geddi in July 1978. *Vespa orientalis* L. (Vespidae) was seen chasing males and females of *X. pubescens* at Ein Geddi. One possible success of catching a male was reported.

Ants: Occasionally, ants of various species were found to invade *Xylocopa* nests that were left by us on the ground. These occurrences were considered artifacts, since the nests have been removed from their natural locations. During April 1981, however, we were able to witness the robbery of in situ nests of *X. pubescens* in the Hatzeva Field School (Frontispiece).

Two nests that were located in the same poplar board were invaded by *Monomorium gracillimum* Smith. The invasion took place through small holes that the ants dug in the tunnel walls, rather than through the nest entrance. The ants then removed, bit by bit, the contents of five cells, each of which contained a pupa. The removal occurred through a hole dug in each partition without breaking it, with a resulting X-ray picture of complete, but empty cells. The mother bee, which was at the nest entrance during this time, apparently sensed that a calamity had befallen her progeny and removed the contents of two cells with their partitions; however, no confrontation

between the ants and the bee was observed. The time required by the ants for penetrating, dismembering, and removing the five pupae lasted not more than 24 hours, since that was the interval between our observations preceding the robbery and the one in which the robbery was noticed and stopped.

An additional case of robbery was seen in a nest of *X. sulcatipes* in a *Ferula* stalk near Sede-Boqer on 2 June 1981. Ants (*M. venustum* Emery) entered through notches in the stalk that resulted from mechanical damage and consumed both the bee bread and the young bee larvae. Here, again, the mother was present near the nest entrance throughout the robbery act.

Termites: *Ferula* stalks in the high desert around Sede-Boqer are favorite sites for both termites and nests of *X. sulcatipes*. Once termites penetrate a bee's nest, they devour some of its walls and fill it with refuse, wherein the dead bee larvae or pupa was found imbedded (Figure 27). The bees are apparently aware of the danger that their progeny face as a result of termite activity. Consequently, they discontinue tunnel digging once they meet even the slightest evidence of termite damage in their path of nest construction.

Birds: *Merops apiaster* (L.) was seen catching *Xylocopa* spp. in Ein Geddi and Hatzeva, *Pycnonotus xanthopygus* (Ehrenberg) was seen with a carpenter bee in its beak, and *Lanius* sp. (probably *excubitor aucheri* Bonaparte) as well as fly catchers were suspected of catching carpenter bees. Woodpeckers, *Dendrocopos syriacus* (Hemperich and Ehrenberg), were common predators of *X. pubescens* in the Mediterranean regions of the country, wherever trees existed that supported a population of the woodpecker. The technique used by the woodpeckers was for them to watch the bees' activity and, after learning that the wood had bees within it, to tear open the tunnels and extricate the bees. A crow, *Corvus corone sardonius* (Kleinschmidt), that was kept as a pet in Hatzeva, nearly annihilated a large colony of carpenter bees belonging to both species by tearing their nests open with its beak and feeding upon the bees. This activity was during the winter of 1978/

1979, when the bees were inactive due to the cold weather. The bird located the bees in the wood by knocking upon the wood and waiting for the bees to emit a buzzing sound.

Discussion

NEST CONSTRUCTION AND STRUCTURE.—Hurd and Moure (1963) have assembled information on nidification and have discussed by subgenera the known nesting substrates for the world fauna of these bees. The nesting materials used by some carpenter bees, such as *X. flavorufa* DeGeer and *X. caffra* (L.) (Watmough, 1974) and of *X. pubescens*, may range from hollow canes, flowering stalks, and tree trunks to structural timber. Other species, like *X. iris* Christ (Malyshev, 1947) and *X. nogueirai* Hurd and Moure (1960), limit themselves to special substrates, the former to thin pithy stems and the latter to bamboo culms. *Xylocopa sulcatipes* belongs to the latter group and thus differs in most of its nest site selections from *X. pubescens*. Some overlap occurs because of the very general nesting site selection by *X. pubescens* and because "predilection for a particular nesting substrate, though restrictive, does not preclude pioneering individuals and subsequently local populations from selecting nesting substrates new in character to the species as a whole" (Hurd, 1958:336).

Sakagami and Laroca (1971) studied five of the former and two of the latter types of nesters and concluded that the latter group is probably derived from the former since they make their entrance holes on the "side walls of the stalks and culms, against the grain, never on the cut surface as practiced by most stem and branch nesting bees." Our two species do not seem to fit with this theory since both prefer to dig their entrance holes, especially when nesting in dead flowering stalks of agave and *Ferula*, in cut surfaces rather than in the side walls. Therefore, a decision about their relative primitiveness cannot be reached by using the criteria of Sakagami and Laroca.

Janzen (1966), after having seen an established bee preventing a conspecific female from digging

a nest near her burrow, and after noting that the nest containing timber was not fully utilized, theorized that it might have been advantageous for the bees not to have very large nesting colonies in the same substrate. Limited aggregations of nests would, according to him, attract fewer parasites and be less apt to cause the collapse of the logs in which they nested. The findings of Sakagami and Laroca (1971) regarding 30 different nests belonging to five bee species and those of Gerling and Hermann (1978) with *X. virginica* L. seemed to support Janzen's hypothesis; however, the timber-nesting *X. pubescens* does not conform with this pattern, since it utilizes the nesting substrate until it is completely excavated and nothing but very thin partitions remain of it (Figures 11, 12). A similar degree of excavation has been noted for *X. varipuncta* Patton in North America (Hurd, 1958) and *X. sonorina* Smith in Hawaii (Gerling, in press). The bees' activity in both cases caused pronounced weakening and sometimes the collapse of the wood.

The strategy employed by *X. pubescens* in order to reach extensive utilization of the nesting substrate involves digging behavior, the sequence of cell building and provisioning, and the social structure of this species. The female of *X. pubescens* digs short laterals that may ramify in different directions and constructs only few (usually 1–3) cells at a time. Since the females of this species, like those of many others, are able to sense, possibly through vibrations, when the wood between close tunnels is about to be perforated, they are probably able to avoid such happenings. The resulting short tunnels ramify in different directions so that most of the available wood is utilized. In contrast to *X. sulcatipes* and *X. virginica* (Gerling and Hermann, 1978) that dig the whole tunnel length for the present generation before starting to construct cells, *X. pubescens* builds a few cells at a time, and later when these young are about $\frac{1}{2}$ or $\frac{3}{4}$ grown, she digs a few more. In this way continuous excavation of the wood takes place, utilizing the wood more fully. Finally, in contrast to *X. fimbriata* Fabricius (Janzen, 1966), *X. pubescens* allows her progeny to nest not only near her

nest but also within it (Ben Mordechai et al., 1978). Since this process of joint sib-nesting continues often for many years, it results in very extensive utilization of the available nesting material.

The significance of the wood utilization habit of *X. pubescens* may be in the high efficiency at which each suitable wooden log may be exploited, enabling the bees to thrive in the semi-arid and arid realms of its distribution, where wood, especially thick logs, is scarce. Other advantages, some of which are shared with less gregarious *Xylocopa* species, include labor sharing, especially that of nest guarding, and the forced continuous interaction between the individuals that brings about the sharing of food and possibly also that of information.

TERRITORIALITY.—The three main types of male territories were already recognized by Jacobson (1927): (1) near the nest entrance, (2) about flowers that serve as food sources, and (3) in "prominent places." Since then, numerous descriptions of territorial behavior and some explanations of the possible strategies involved have been published. These were reviewed by Alcock et al. (1978), Anzenberger (1977), Velthuis and Camargo (1975), and Velthuis and Gerling (1980). The latter two works, as well as Wheeler et al. (1976), showed the importance of pheromonal activity in the system, while Anzenberger (1977) suggested acoustic communication between the males and the females of *X. nigrita* (Fabricius) in Africa.

The large volume of information about the choice of territorial locations for *Xylocopa* males can be classified into two categories; location in which females may be present due to their normal activities such as nesting or feeding sites, and special mating locations. The latter constitutes much of the category mentioned in the literature as "prominent places" and was recently discussed by Alcock (1980), who named it "male dominated polygamy." All the rest of the territorial locations belong to the former category. *Xylocopa sulcatipes* and *X. pubescens* each serve as an example of one category. *Xylocopa pubescens* males have their ter-

ritories only in "prominent places," whereas *X. sulcatipes* males are in places where females occur.

It seems that the behavioral adaptations necessary for a bee species to increase its repertoire of territorial sites within a category are more easily attained than the adaptations to change from one category to another. Consequently, *X. pubescens* adheres to the "prominent places" however varied they may be (tree canopies, the shade of trees, about shrubs near the ground, etc.). *Xylocopa sulcatipes*, on the other hand, adopts various strategies all within its category. These seem to correlate with changes in the ecological conditions that influence the probabilities of finding females. A similar phenomenon was observed for *X. virginica* (Gerling, unpubl. obs.; Orlove, unpubl.) where the males, who usually patrolled only nest sites, were found also near flowers.

Most females overwinter as virgins and mate mainly in springtime; however, territorial flights and a single mating (of *X. virginica*) were observed during the usually "non mating" fall season. Since virgin females of all species fly about contemporaneously with their males from the time of emergence on, but no mating occurs except as designated above, it must be assumed that territoriality and mating are governed by periods of female receptivity. Therefore, the above-mentioned information indicates that even though most females become receptive only in springtime, some do so in the fall, and that this intraspecific variation is not particular to one species or subgenus of carpenter bees.

SOCIAL RELATIONSHIPS.—A critical review of the interactions between and among individuals of the four species studied so far by means of X-rays, *X. pubescens* (Gerling et al., 1981), *X. sonorina* (Gerling, in press), *X. sulcatipes*, and *X. virginica* (Gerling and Hermann, 1978), reveals some features that appear to be common to the genus *Xylocopa*. These features, in whole or in part, were also pointed out by previous workers who studied varying aspects of the social life of *Xylocopa* species (Rau, 1933; Hurd, 1958; Hurd and Moure, 1960; Iwata, 1964, 1971; Bonelli, 1974, 1976; Sakagami

and Laroca, 1974; Watmough, 1974; and Anzenberger, 1977).

All species seem to be able to develop and raise progeny as solitary bees, since they may dig, build, and maintain their nests alone. The mothers may or may not remain in the nest until after their progeny have matured and care for them during their juvenile development. The female progeny in turn guard the nest while their mother is foraging; however, this association is of temporary nature.

In addition, carpenter bees may exhibit more highly evolved social relationships, as shown for the four abovementioned species in Figure 5. Using Michener's (1974) classification to describe the labor-sharing behavior, this behavior would be classified as parasocial and mostly communal, where several females nest in and provision individual tunnels or nests but share guard duties. *Xylocopa sulcatipes*, however, is more socially advanced in that in addition to communal nests, this species also has quasi-social colonies with two or more females sharing the labor of constructing and provisioning cells. We also found nests in which some bees had developed, and others underdeveloped, ovaries. Possibly these colonies were semisocial, but a more detailed study of their behavior will be required to ascertain this point.

Michener's classification defines not only the labor-sharing properties but also the familial relations of the participating bees. Parasocial relationships pertain to "a colony in which adult females belong to a single generation" (1974:373). In this respect *Xylocopa* species often don't fit into the parasocial framework, because they may have some cooperation between females of more than one generation (our findings; Bonelli, 1976; Gerling and Hermann, 1978). Bonelli (1976:30) referred to these relationships by commenting that "under other aspects they may show typically eusocial characteristics." It seems to us that the *Xylocopa* species under consideration are not eusocial, and the fact that more than one generation of adults participates in some nesting activity

should not preclude it from being classified at the parasocial level. As an alternative, we propose the term "metasocial" to be applied to otherwise parasocial bees who may have more than one generation cooperating in some way within the nest.

The present X-ray observations of the activity of *Xylocopa* species within the nests as well as the

meticulous studies conducted by Bonelli (1974, 1976) show that the bees cohabit in a nest, and they interact often, in various ways. They are fed by the forager, share guard duties, and pay special attention to the larval provisioning. The full meaning of these activities and their significance in the relationships between and/or among the individuals in the nest are yet to be determined.

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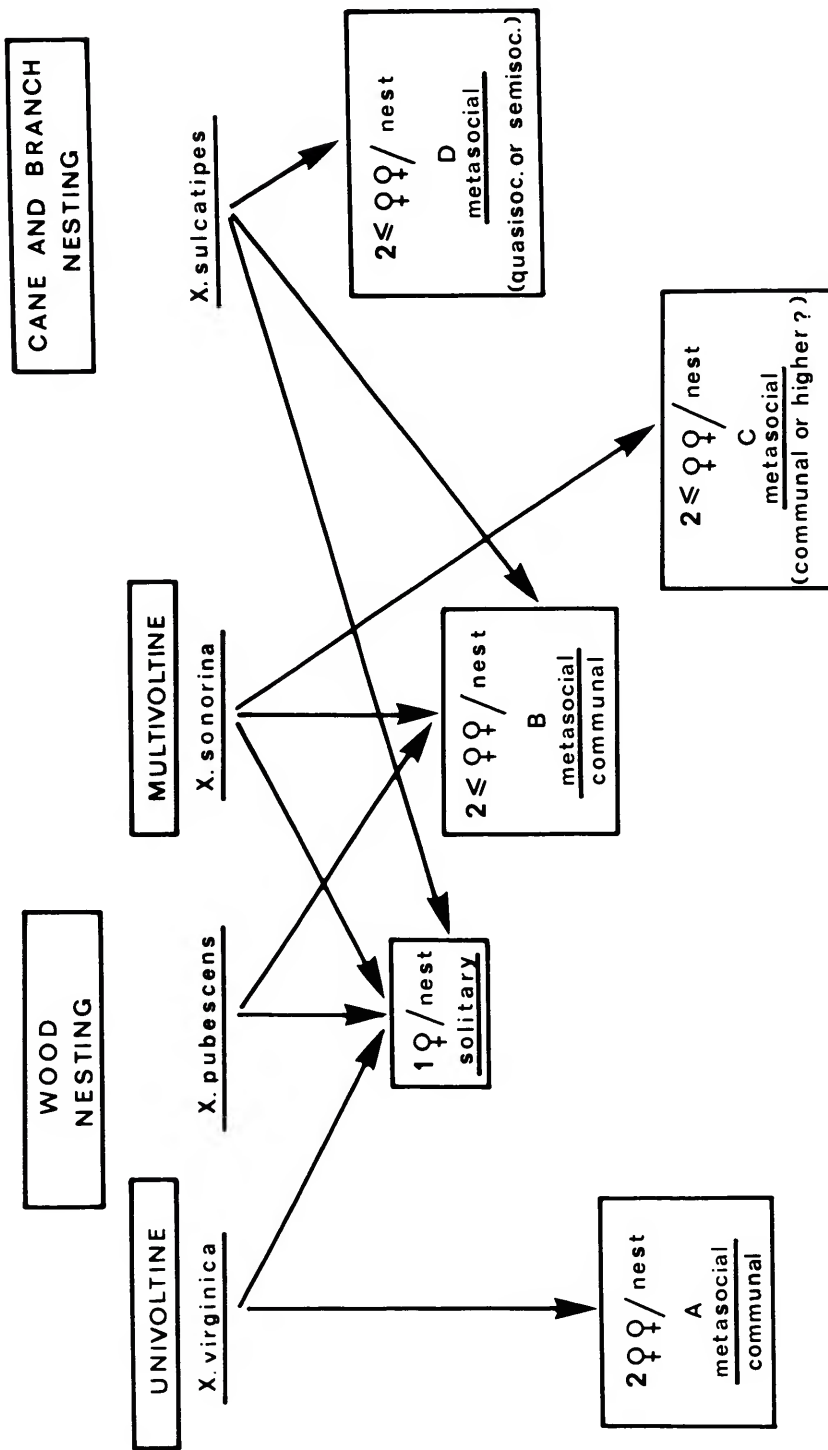
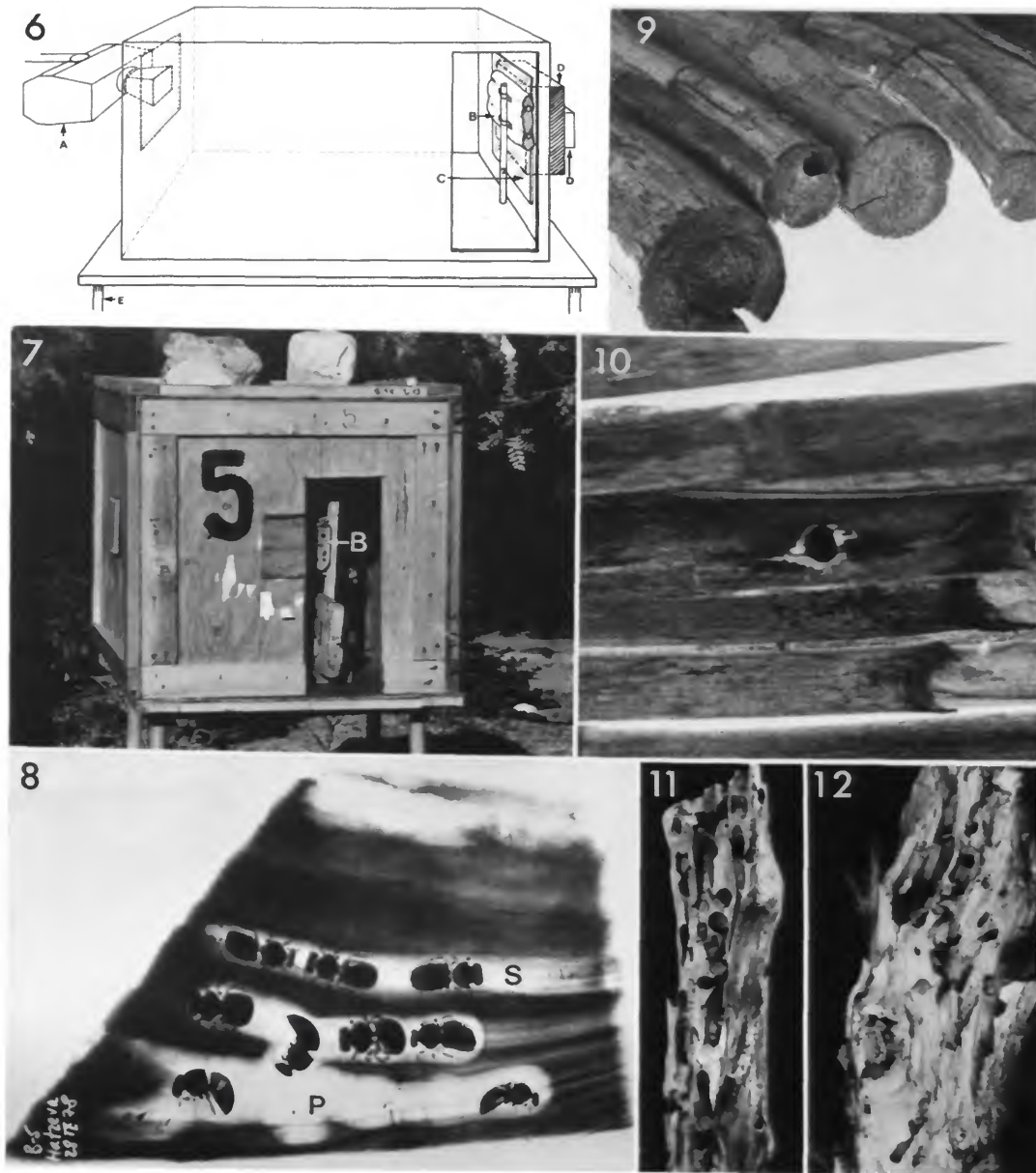
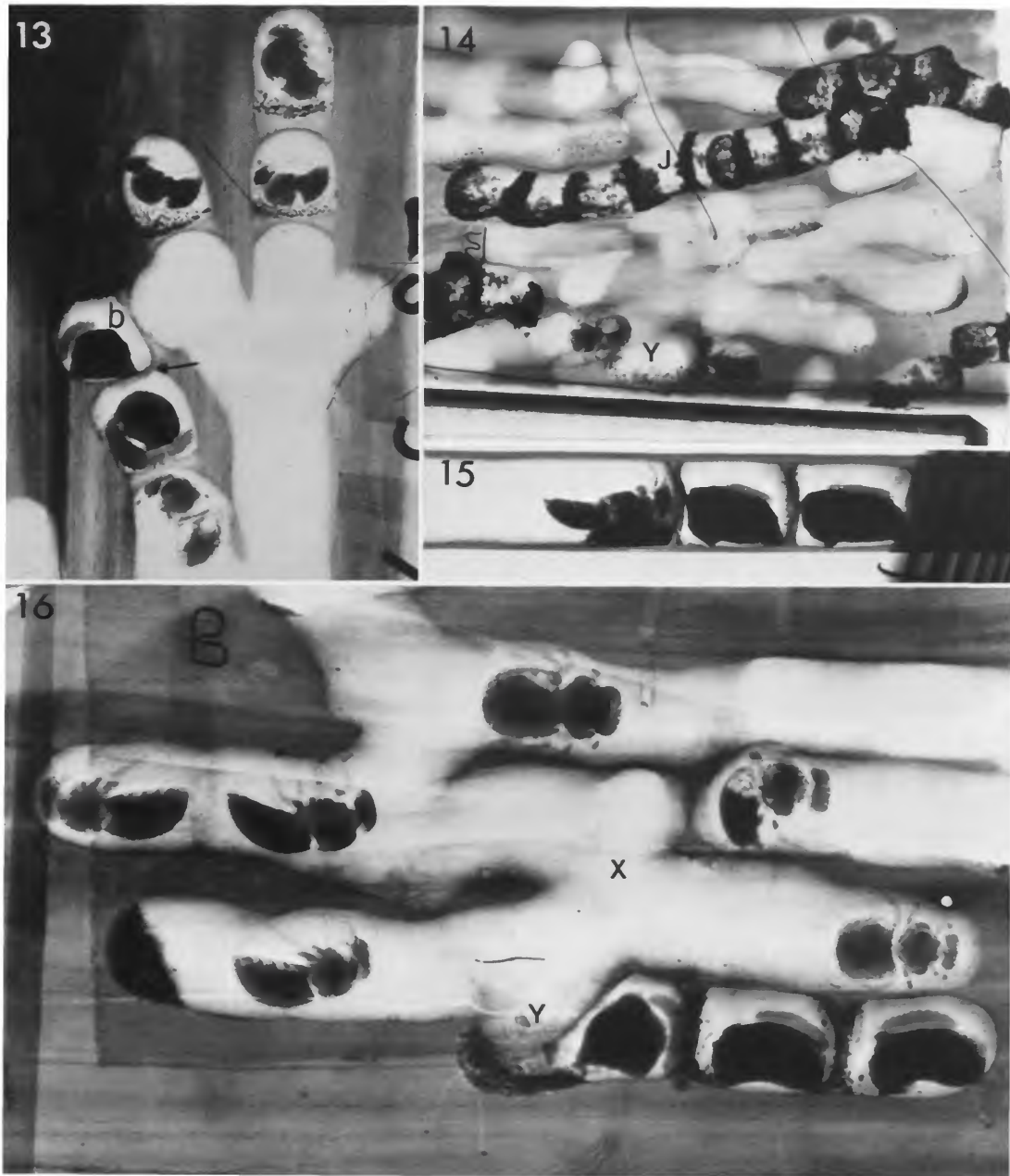


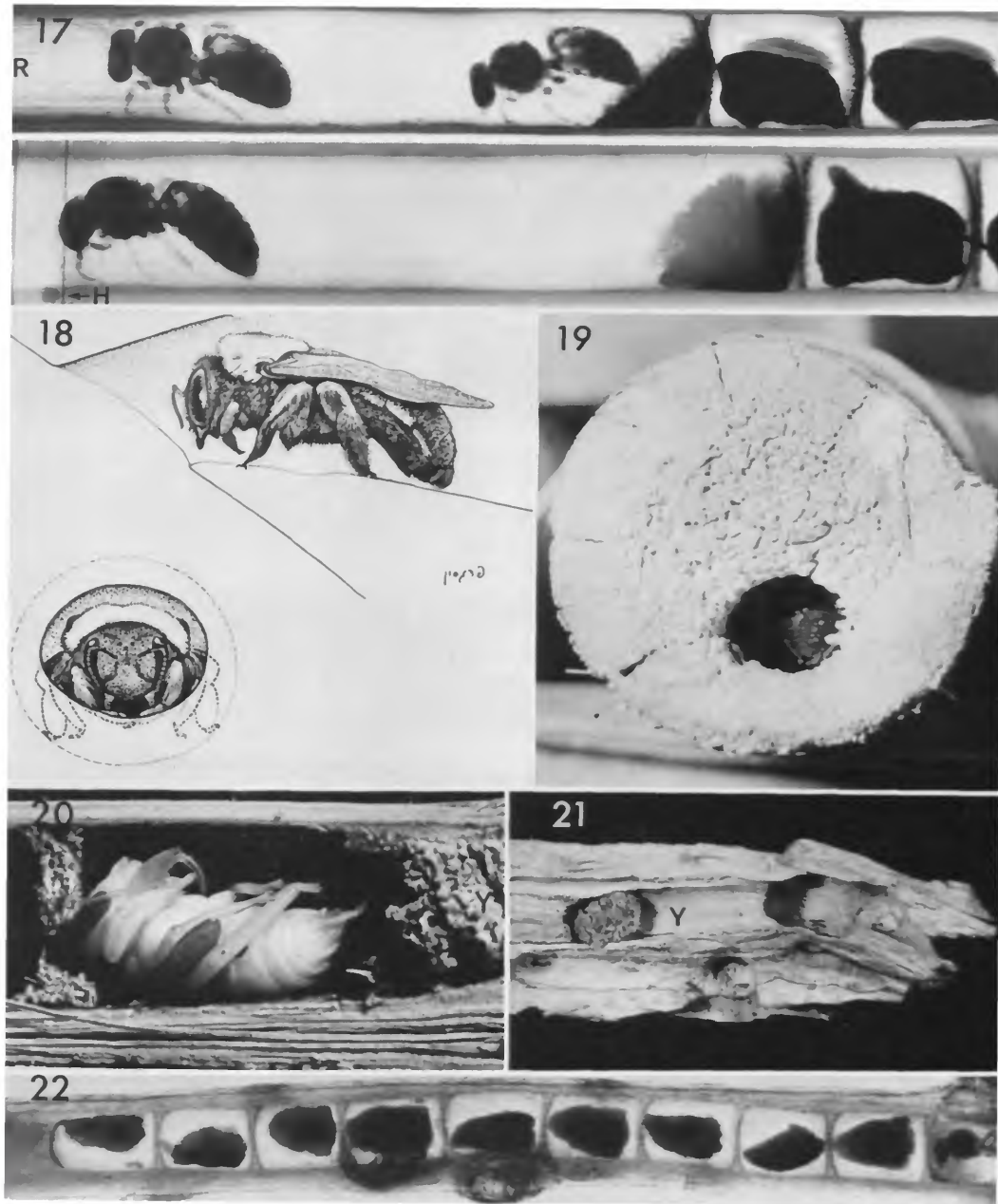
FIGURE 5.—Diagrammatic representation of the social relations exhibited by 4 species of carpenter bees for which X-ray data are available: A, 1 one-year-old guard, 1 two-year-old mother; B, 1 mother of previous generation co-nesting with young, each in its own tunnel, sharing exit; C, some or all are of same generation, may be labor sharing; D, all nesters share pollen collection.



FIGURES 6-12.—Equipment and nests: 6, lead-shielded box with X-ray and nests in situ (A = X-ray, B = nest, C = lead-glass plate, D = observation port, E = stand); 7, cover box in which nests were kept when no observations were conducted (B = nest); 8, X-ray showing one side of a board being used by *Xylocopa pubescens* (P) and other by *X. sulcatipes* (S); 9, nest entrance of *X. sulcatipes* in *Agave* species; 10, same in *Arundo donax*; 11, nests of *X. pubescens* in *Eucalyptus* species; 12, same in *Populus euphratica* (contained 41 ♀ and 34 ♂ when collected January 1981).



FIGURES 13-16.—Nests and bee activity: 13, nest of *Xylocopa pubescens* showing cell (b) dug across the grain; 14, nest of same showing nests of *Rhynchiium* species (j) built in old tunnels (y = refuse dump); 15, female of *X. sulcatipes* sleeping on top of pollen slant; 16, nest of *X. pubescens* made up of mother's nest from which daughter's nest branches off (x = entrance to daughter's nest, y = refuse dump).



FIGURES 17-22.—Nests and bee activity: 17, nest defense of *Xylocopa sulcatipes* showing 1 bee guarding nest with cross-cut entrance (R) and another with hole (H) in middle of culm; 18, 19, nest defense of *X. pubescens*; 20, refuse dump in opened nest of *X. pubescens* constructed in cane; 21, same constructed in poplar (Y = refuse dump); 22, X-ray, nest of *X. sulcatipes* in branch of *Moringa peregrina* showing 9 closed cells.

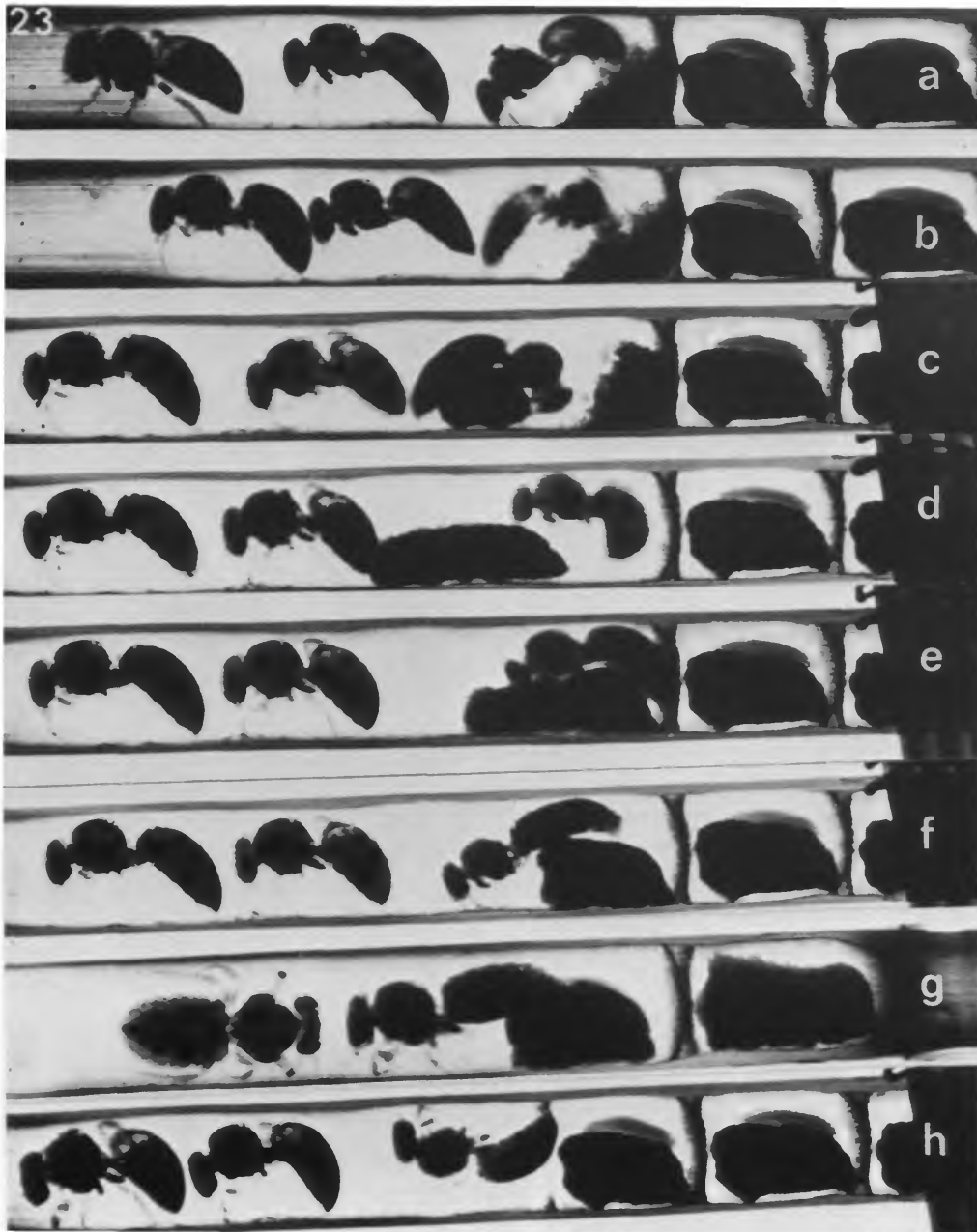
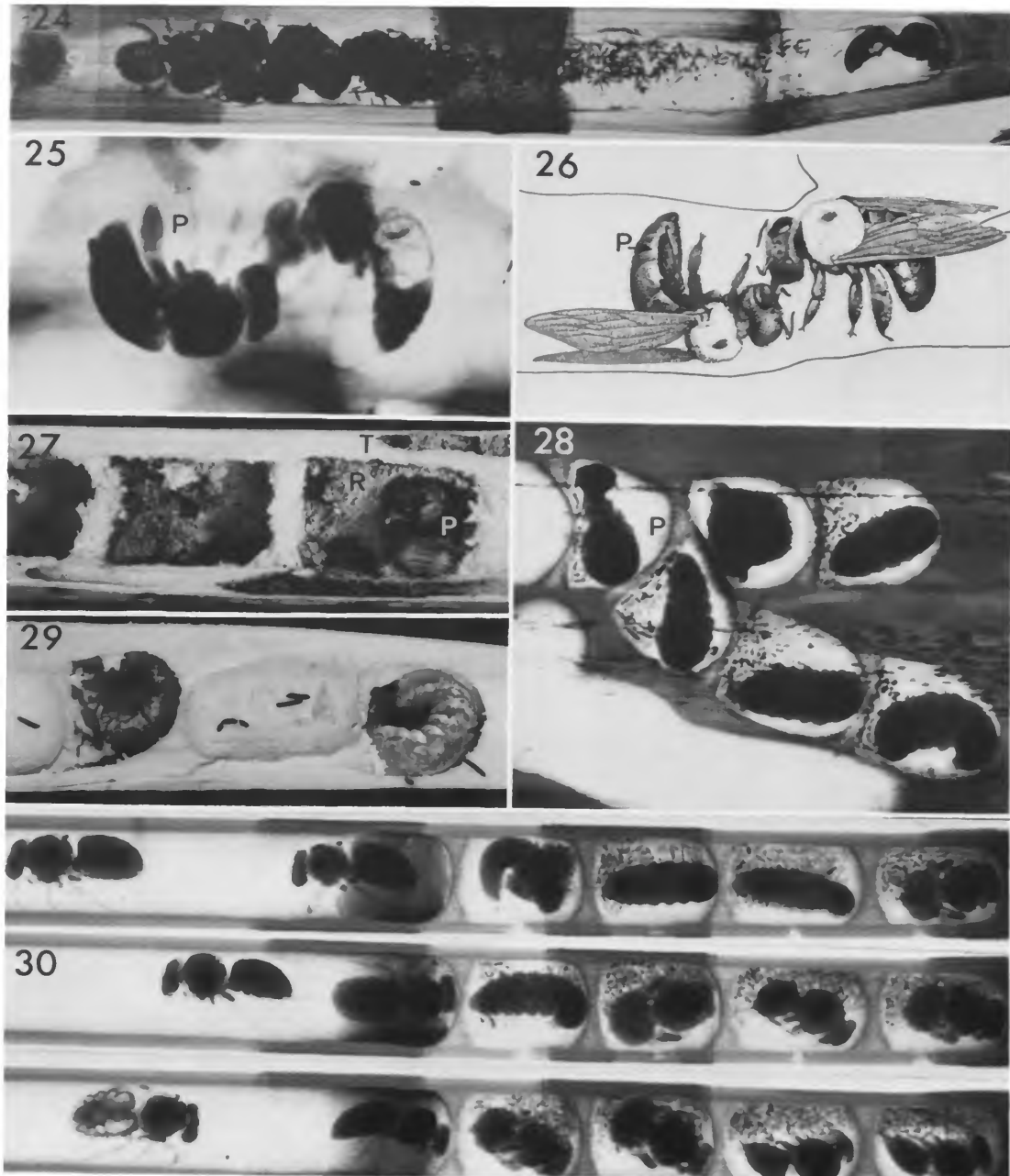


FIGURE 23.—Reconstructed sequence of cell provisioning and oviposition by *Xylocopa sulcatipes*: a, deposition of pollen; b, c, manipulating pollen slant and moving material to tunnel floor; d, piling pollen in front of female; e, shaping bee-bread; f, female in ovipositing posture; g, oviposition; h, initiation of partition making.



FIGURES 24–30.—Nests and bee activity: 24, nest of *Xylocopa sulcatipes* showing recently emerged progeny intermingled with cast skins and meconia; 25, X-ray, trophallaxis in *X. pubescens* (P = pollen on hind leg on incoming bee); 26, drawing of same; 27, portion of *X. sulcatipes* nest invaded by termites, showing termites' tunnel and refuse, and remnants of pupal case of bee; 28, nest of *X. pubescens* showing cell partitions used as a foundation for a second partition (P = partition); 29, empty skins of *X. pubescens* larvae parasitized by *Coelopencyrtus* species; 30, X-rays of an *X. sulcatipes* nest taken during August 1976, showing 2 active females and progeny at advanced stages of development.

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