

**PROVISIONING AND PREPARATION OF THE BROOD CELL IN TWO  
CARPENTER BEES, *XYLOCOPA SULCATIPES* MAA AND *XYLOCOPA  
PUBESCENS* SPINOLA (HYMENOPTERA: ANTHOPHORIDAE)**

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**ABSTRACT**

Two Israeli carpenter bees, *Xylocopa pubescens* and *X. sulcatipes* are compared in their foraging and cell provisioning behavior. Both species make foraging flights mainly during the early morning, but *X. sulcatipes* continues to forage, also later in the day. *X. pubescens* jointly collects pollen and nectar whereas *X. sulcatipes*, whose trips are of shorter duration than those of *X. pubescens*, often conducts distinct bouts for pollen or for nectar.

Mixing nectar with pollen occurs after almost every flight in *X. pubescens*, while *X. sulcatipes* does this only after nectar collection, and therefore at irregular intervals. This causes greater variability in bee bread size, leading to size differences in the adults.

*Xylocopa pubescens* makes an average of 10 pollen and one nectar collecting trip per brood cell, whereas *X. sulcatipes* makes averages of 21 pollen and 12 nectar flights. The latter species is by far more active so that it completes and produces more brood per unit of time. This seems related to the fact that *X. sulcatipes* nests in a straight tunnel, while *X. pubescens* constructs a branched nest. In *X. pubescens*, emergence of a bee in the far end of a tunnel does not interfere with the development of younger bees, as it would in the case of *X. sulcatipes*.

In order to account for the differences between these congeners, we argue that differences in food availability and nest defense strategies have influenced the evolution of foraging patterns within *Xylocopa*.

**INTRODUCTION**

Studies on the behavior of stem and wood-nesting insects within their nests have often been based on the opening and the destruction of nests. The development of trap-nesting techniques (Krombein, 1967) and the subsequent use of transparent artificial nests enabled more direct study. Recently, the application of mobile, low intensity X-ray equipment (Gerling and Hermann, 1978) increased the number of species that could be studied directly.

Nesting biologies and behavior of two species of carpenter bees from Israel, *Xylocopa (Koptortosoma) pubescens* Spinola and *X. (Ctenoxylocopa) sulcatipes* Maa have been studied using X-ray techniques and direct behavioral observations (Ben Mordechai *et al.*, 1978; Gerling *et al.*, 1981; Gerling *et al.*, 1983; Velthuis and Gerling, 1983). The former bee generally nests in dead tree trunks forming branched nests with several short tunnels. In perennial nesting sites, these may form complex nesting aggregates. The latter bee nests in reeds, thin branches or pithy stems; its nests are unbranched and do not develop into interconnected aggregations. *X. sulcatipes* is found principally in arid environments, whereas *X. pubescens* also occurs extensively in Mediterranean climates. Both bee species may form persistent local populations where they occur sympatrically (Gerling *et al.*, 1983).

The two species show interesting differences in their foraging tactics and cell provision preparation. This paper describes these differences and discusses their possible significance.

#### MATERIALS AND METHODS

The observations were made at the Hazeva Field Study Center of the Israeli Society for the Protection of Nature, located in the Arava Valley south of the Dead Sea. Data were collected from mid-April until mid-June, 1982; data on *X. pubescens* were also obtained from mid-April until mid-May, 1981. These years had a moderate to good development of vegetation, related to the relatively wet preceding winters. We examined first generation nests of *X. pubescens* in poplar boards and nests of *X. sulcatipes* in *Arundo*. Activity outside nests was continuously observed from daybreak till sunset; times and frequencies of foraging flights were noted to the nearest 1 minute. Presence or absence of pollen loads on bees' legs were also recorded.

Within-nest behavior was observed using a Softex K2 X-ray unit (Gerling *et al.*, 1981). Such X-ray observations were made in two ways: immediately following the return into the nest, and intermittently, every 10 minutes for certain periods of time. Due to technical limitations of the X-ray source, these observations were of 3 min duration at the maximum, but were generally much shorter. Often, serial observations were made by dividing the 3 min period into several shorter parts. Photographs could be taken by moving, during the serial observations, an Agfa Curix X-ray film sheath behind the nest and exposing it for 1-2 seconds.

We assumed that flights in which bees returned to the nest without pollen on their legs were used to carry nectar. Accordingly, the terms "nectar flights" and "pollen flights" were used. As will be shown, however, a "pollen flight" may include the transportation of nectar.

#### RESULTS

##### *Daily foraging pattern:*

As reported earlier (Gerling *et al.*, 1983) both *Xylocopa pubescens* and *X. sulcatipes* forage predominantly in the early morning. *X. pubescens* starts earlier than *X. sulcatipes*, the latter being more inclined to continue foraging at low frequency

during the day (Fig. 1). *X. pubescens* carries pollen on its legs in 67% of its return flights; *X. sulcatipes* in 57%. This difference ( $P < 0.05$ ) is due to the fact that from late morning on, *X. sulcatipes* predominantly conducts nectar flights.

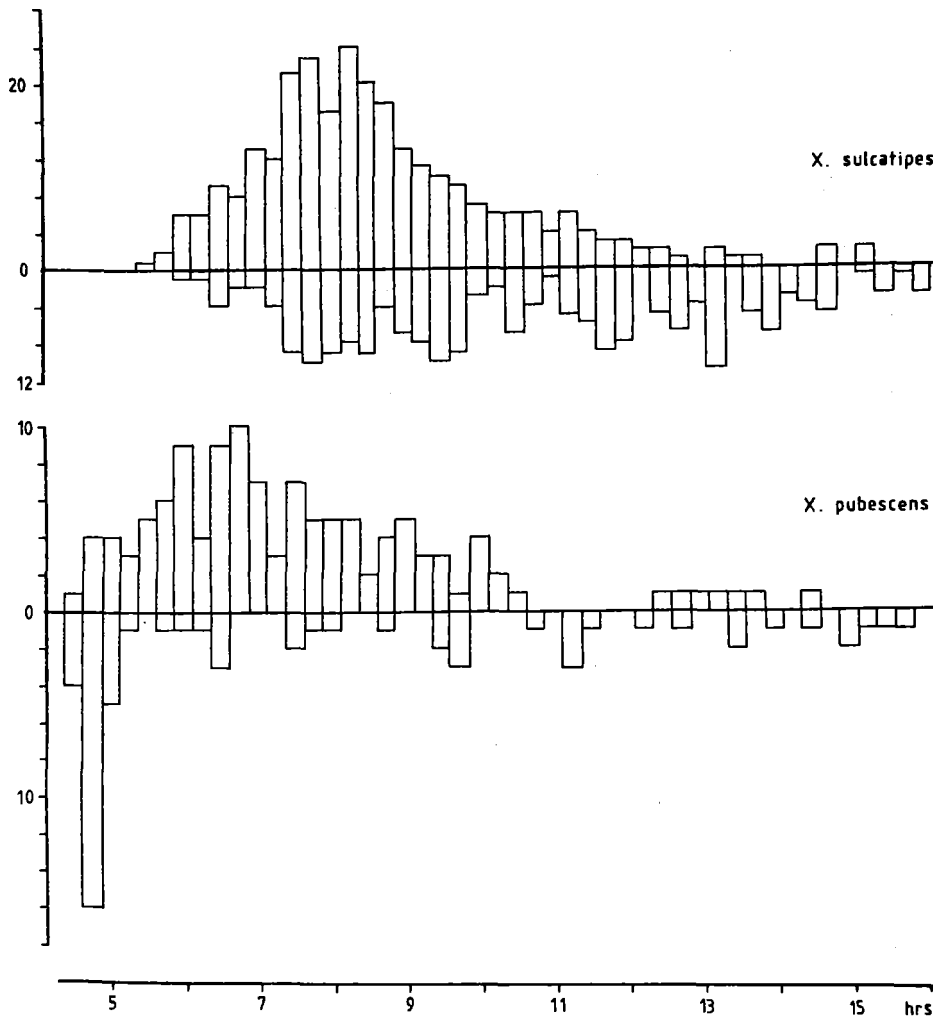


Fig. 1. Flight activity during the day of *X. sulcatipes* and *X. pubescens*. Above the axis the number of flights per 15 min on which pollen was collected, below the axis those without pollen collection, presumably nectar flights.

*Duration of foraging flights:*

The two species differ remarkably in the duration of their foraging flights (Fig. 2). *X. pubescens*' pollen flights took  $13.2 \pm .7$  min (mean  $\pm$  SD), and nectar flights  $11.9 \pm .1$  min. *X. sulcatipes*' pollen flights took  $.1 \pm .6$  min and nectar flights  $6.0 \pm .2$

min. In the latter species, the distributions are far from normal and the modes (1.5 min for pollen and 0.5 min for nectar flights) and the median values (3.5 min for both types of flights) might be more informative values.

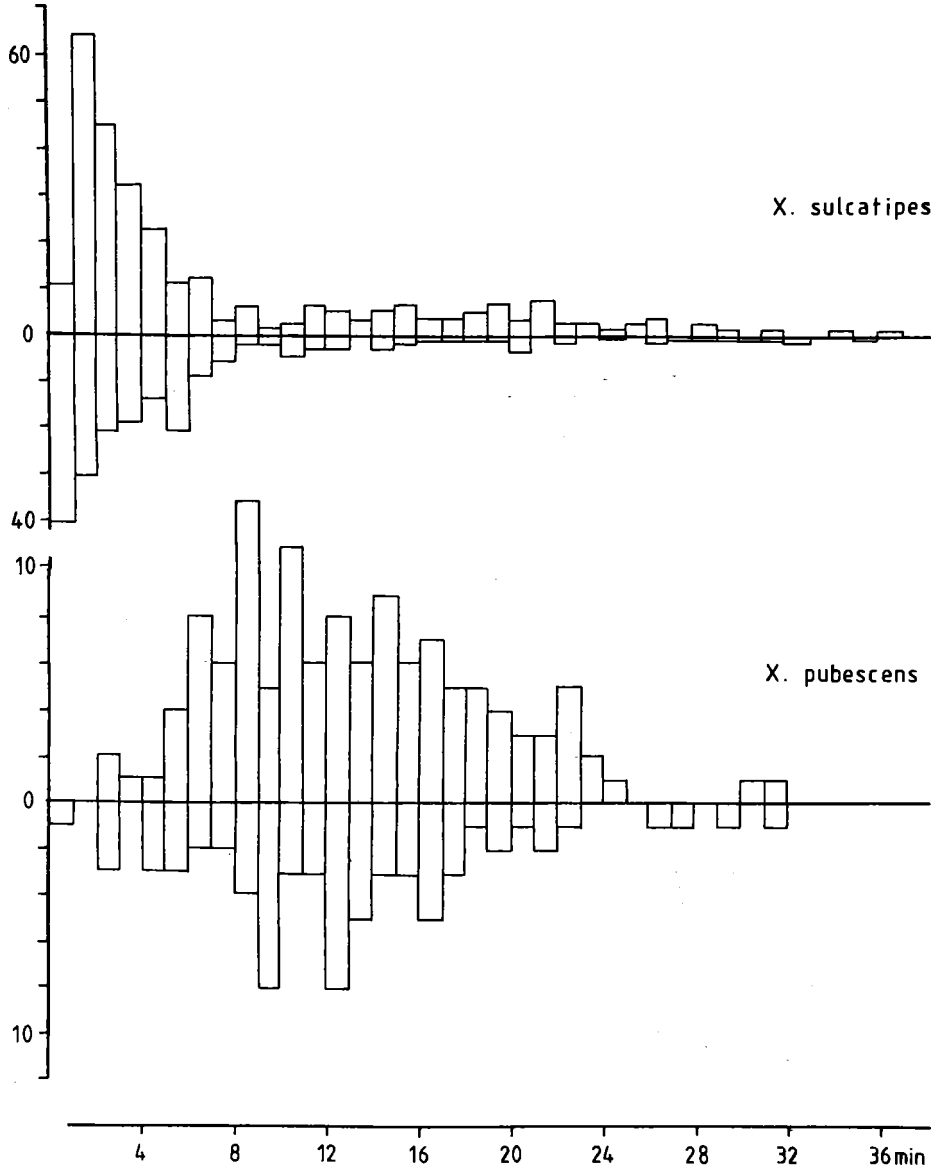


Fig. 2. The frequency distributions of flight durations. Above the axis the number of flights on which pollen was collected. Below the axis those without pollen collection is given. Duration was measured with 1 min accuracy.

### *Number of flights per day*

The complete flight activity of seven *X. pubescens* females on 97 days has been recorded. They made an average of 2.8 (0-13) pollen flights and 1.3 (0-5) nectar flights per day. Pollen was collected only on 48 days, averaging 5.6 pollen collecting trips per day. About half of the nectar flights occurred on days of low levels of flight activity. Such flights probably serve the bees' own energy supply rather than their cell provisioning.

The average number of flights of a *X. sulcatipes* females per day was 15.3 (0-53), consisting of a mean of 10.0 (0-41) pollen flights and 5.3 (0-14) nectar flights. These data pertain to 5 animals, covering a total of 35 days in the breeding season. On only 2 of these days, less than 2 flights were made, and pollen collection occurred at least once on all but 3 days. High levels of flight activity were mainly due to increased pollen collection. Pollen loads differed considerably in size, much more than is the case in *X. pubescens*.

### *Number of flights per brood cell*

Important differences also occur in the number of pollen and nectar flights made for the preparation of the bee bread. Velthuis and Gerling (1983) estimated that *X. pubescens* needs about 10 pollen flights for each cell. In our present observations, 129 pollen and 12 nectar flights were made to provision 12 brood cells. In *X. sulcatipes*, the provisioning of 14 brood cells included 292 pollen flights and 165 nectar flights, averaging 21 (13-26) pollen and 12 (3-31) nectar flights per cell. These *X. sulcatipes* cells were completed in 1 (5 cells), 2 (6 cells) or 3 (3 cells) days. Although there is a tendency that, with more flights being made for the provisioning of a single cell, the number of days needed for its completion increases, this correlation is counteracted by bees being more active when pollen loads become smaller.

In *X. pubescens*, because the number of flights per cell during which only nectar had been collected, is limited to a mean of 1, no distinct sequence in the collection can be discerned. In contrast, such a sequence is prominent in *X. sulcatipes*. The two types of provisions are not collected in a random sequence. The 350 observed pollen flights were made in 82 series, ranging from 1 to 22 consecutive flights, and the 183 nectar flights came in 95 series ranging from 1 to 8 flights. The longer series of pollen flights occur especially at the beginning, the nectar series predominantly at the end of the day's activity period, coinciding with the earlier and the later provisioning of a cell. In all 14 cells provisioning ended with a nectar flight.

### *Pollen and nectar deposition*

Gerling *et al.* (1983) described in detail the sequence associated with pollen deposition and oviposition. Our observations, which were carried out since this study, revealed numerous additional details that are reported hereunder.

In both species a pollen-laden female, upon entering her nest, goes directly to the end of the tunnel. If a pollen slant already exists there, it may be inspected and touched with mandibles and tongue. Then she turns around with the head towards the nest exit, and the abdomen above the pollen slant (Plate 1, a-c). With the mandibles, she fixes herself firmly to the bottom of the tunnel, while the abdomen is raised and curved. Although the actual mechanism of releasing the pollen from the hind tibiae is not yet clear to us, we know that it is accompanied by vigorous movements, about 8-9



at a time, of the abdominal tip in an antero-posterior direction. Such movements may be brushing movements by which pollen is thrown high up the slant. After a series of such movements, the bee releases her grip on the floor and moves a little ahead. In a relaxed posture, up and down movements of the abdomen generally occur. Sometimes the bee curves the tip of her abdomen towards the mouthparts, probably for cleaning or for transferring chemicals (Gerling *et al.*, 1983). Then again, she positions herself near, and partly above, the pollen slant, fixes the mandibles again into the tunnel floor and repeats the antero-posterior abdominal movements. This may happen several times in alternation with the relaxed posture, and is accompanied by dorso-ventral movements of the abdomen.

Release of the pollen from the hind tibiae could be through the vigorous antero-posterior abdominal movements, an interpretation presented by Gerling *et al.*, (1981, 1983). It is also possible that the middle legs rub it from the hind legs. Evidence for the latter possibility comes from photographs that show that the middle legs are not visible during pollen unloading, possibly due to their rapid movement during the exposure of 1-2 sec. The solution of this question awaits further improvement of our X-ray techniques.

The pollen slant may be wet with nectar in two ways: either by licking the surface after a return from a foraging trip, or by mixing nectar with the pollen. In the latter case, the bee, using her mandibles, pushes the upper layer of the pollen that is in front of her, downwards under her thorax. During the slower upward movement of the head, we suppose that the bee releases nectar. Once the head is in its uppermost position, the mandibles are spread, inserted into the pollen and in a relatively quick movement the new surface layer is again pulled downward. In this way the wet pollen piles up beneath the bee. Such wetting may take about 10 min.

Before having placed all the pollen under her, the bee may suddenly push the already wet material back on top of the remaining dry pollen slant. This pushing is performed with the frontal part of the head, and the deposition is completed in a rather short time. In the subsequent nectar mixing process this wet pollen paste is generally removed first before the wetting of the dryer parts of the slant is continued.

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← Plate 1

*Xylocopa sulcatipes.*

- a-c: Pollen unloading. The female, after reaching the pollen slant, turns (a) and fixes herself with her mandibles to the tunnel wall (b) before unloading (c). Only in (c) are the middle legs invisible, suggesting that they are involved in removal of pollen from the hind tibiae.
- d-k: The preparation of a brood cell. The moistened pollen mass is being removed (d, e) after which the wall is licked (f). Then the bee turns and presses the material against her abdomen with her mandibles (g, h) and shapes the frontal side of the bee bread (i) before laying the egg (j). During this process, the bee moves slowly forward. After kicking the bee bread with her abdomen (note change in form and position), a bee made the cell partition from shavings taken from her tunnel wall (k).
- l-n: Size difference in bee breads and the resulting offspring. Together with its cell the 3rd bee bread is extremely big (l), resulting in a big larva that has consumed the extra pollen (m), giving rise to a huge female pupa (n). The pupae in cells 2, 4 and 5 are considered to be males.

*X. sulcatipes* first accumulates an amount of pollen before wetting is started; then several specific nectar flights are made. In *X. pubescens* working the pollen slant occurs from a very early stage onward, almost after every foraging flight (Fig. 3). Therefore, it appears that this species collects nectar and pollen on the same flight.

An additional difference between the two species is the absence, in *X. pubescens* and the occasional presence in *X. sulcatipes*, of a ripening process of the nectar. After the return from a nectar flight, a bee may position itself in its nest with the head towards the entrance. The galeae are separated at an angle of about 60° and the tongue is extended. In between a droplet is held. This droplet is kept in motion, mainly through quick movements of the galeae, sometimes also by movements of the tongue.

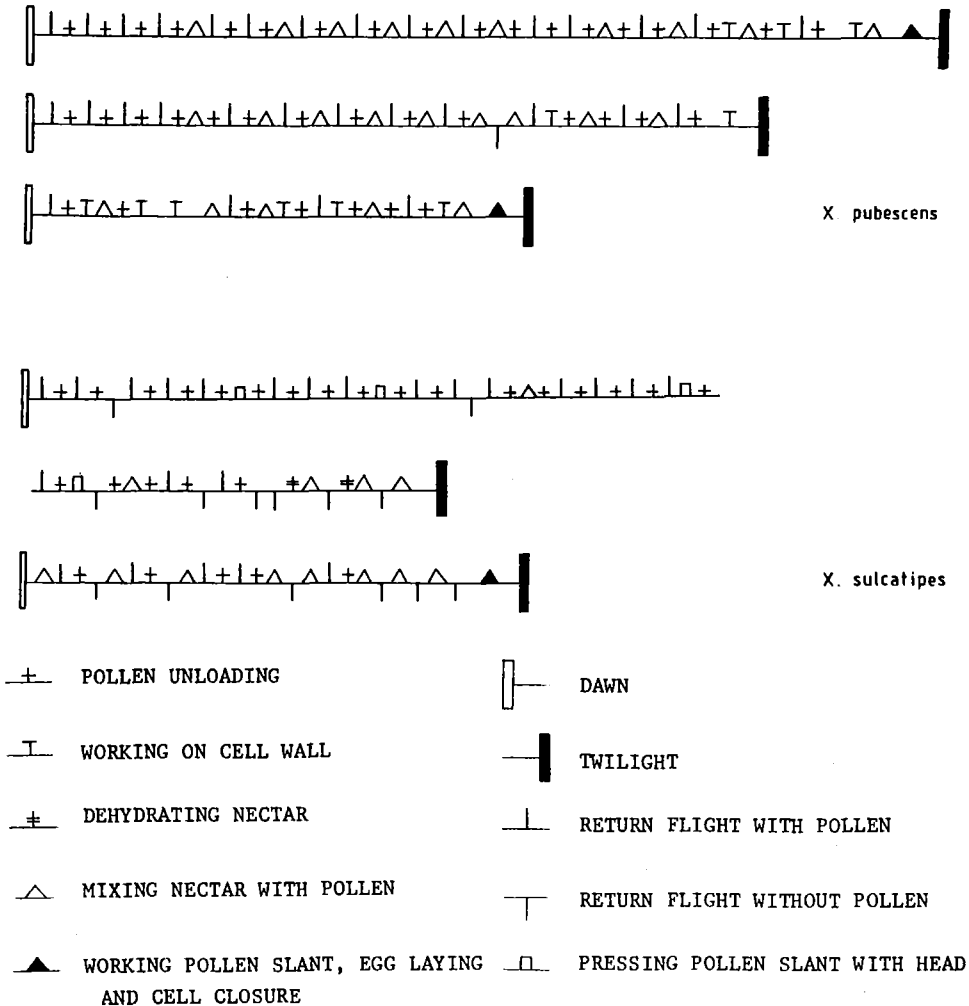


Fig. 3. Some representative examples of the activity patterns of cell provisioning and egg laying. Not in all cases observed did egg laying occur before sunset.

The movements of the galeae are at a frequency of about 240-300 per min, and may continue for 20-30 min. Then the droplet, which during the process diminishes in size, is swallowed and the bee turns towards the pollen slant. Such concentrating of the nectar mainly occurs at the end of the cell provisioning phase, when no more pollen flights occur.

#### *Preparation of the bee bread*

Initiation of the final preparation of the bee bread takes place in about the same manner as described for the addition of nectar. However, the removal of the pollen paste is done much more carefully and it is deposited at a somewhat more distant site (Plate 1, d-e). After about 10 min in *X. pubescens* and 20-25 min in *X. sulcatipes* all the food is removed from the end of the tunnel and the bee, standing in part over the pollen mass, licks the back and the side walls of the tunnel (Plate 1, f). Thus, she probably impregnates it with a waterproof secretion, visible as a thin, dark line on many of the photographs. This takes about 2 min in *X. pubescens* and about 5 min in *X. sulcatipes*. Subsequently, the bee turns, and facing the entrance while standing at the far end of the tunnel, she pushes the food mass back with her head. In the formation of the tightly packed bee bread, the curved abdomen serves as a mould against which the material is pressed, mainly by the middle legs (Plate 1, g-k). Therefore, the bee can be seen to advance slowly in the tunnel as the bee bread formation proceeds, until the more truncate anterior surface is made (Plate 1, i) probably using only the front legs. On top of the bee bread a groove, in which the egg will be laid, is formed by the ventral surface of the abdomen.

#### *Egg laying and cell closure*

During egg laying, which lasts 2-3 min, the bee moves forward slowly so that the egg does not move over the bee bread. A female of *X. sulcatipes* was once observed pushing the bee bread backward into the cell with a jerky movement of the abdomen. We often noted the bee bread to be situated more to the back after oviposition than during its formation, suggesting that such pushing is not uncommon in this species (compare Plate 1, j-k). After the bee bread has been finally placed, the bee starts scraping shavings from the tunnel wall ahead of her, sometimes at several body lengths distance. With these scrapings the cell partition is constructed. Again, the abdomen serves as a mould that is placed behind the partition and new particles are pressed with the hind legs against it. Probably the abdomen secretes a liquid with which the wood particles are glued together. The bee turns slowly around its longitudinal axis, thus forming a spiral cell partition. The construction takes 1.0-1.5 h, during which period she often works the surface of the partition with the mandibles.

Under the stereomicroscope the outside surface of a cell partition appears smooth, and the inside rather coarse. The outside is covered with a thin brownish layer, probably a waterproof secretion, applied once the partition is completed. This might have been done with the abdomen, for the bee could be seen touching continuously with the abdomen various parts of the partition. Pygidial marking could also be seen on the partition. It is noteworthy that Kronenberg and Hefetz (1984), who analysed the Dufour gland secretions of *X. sulcatipes* chemically concluded that they were not the source of the lining materials.

The completion of the cell occurs sometimes at mid-day, but often in the afternoon or early at night. In the former case, we never saw the bee starting to forage for the next cell on the same day. *X. pubescens* may start digging a new tunnel, but not *X. sulcatipes*.

#### DISCUSSION

*Xylocopa pubescens* and *X. sulcatipes* differ in their nest construction, foraging habits, and nest provisioning (Table 1). The branched nests of *X. pubescens* may be a consequence of the frequent availability of dead tree trunks occurring in the habitat of this species. In such nests the bee establishes only 2-3 cells in a row, a habit that brings about intermittent, rather than continuous nesting activity. *X. sulcatipes*, occurring in more arid habitats, is limited in its supply of wood nesting materials, and limits itself to more easily obtainable stems, culms and canes. Consequently, it nests in a straight tunnel with all cells in a row. Our previous observations showed that no appreciable differences in developmental duration of the first- vs. the last-laid eggs occur.

TABLE 1. A SUMMARY OF SOME DIFFERENCES BETWEEN  
*X. PUBESCENS* AND *X. SULCATIPES*

	<i>X. pubescens</i>	<i>X. sulcatipes</i>
Habitat	Temperate and arid	Mainly arid
Nest Structure	Branched	Linear
Brood Provisioning Trips	67% of flights with pollen	57% of flights with pollen
	Collects pollen and nectar on same trip	Separate trips for each
	Variability in trip duration	Relatively uniform duration
	Few, long trips	Many, short trips
Preparation of Provisions	No nectar ripening	Nectar ripening
	Mixes nectar and pollen frequently	Mixes nectar only after pollen collection has been finished
	Size of bee bread uniform	Size of bee bread variable

Therefore, a uniform emergence time for the sibs of this species would be advantageous, and uninterrupted nest provisioning by *X. sulcatipes* seems to serve this end.

Differences exist also in the percentage of nectar vs. pollen flights, being greatly in favor of pollen flights in *X. pubescens*. However, the latter makes mixed pollen and nectar flights, whereas *X. sulcatipes* carries them out separately (Table 1). The collecting efficiency and carrying capacities of nectar, or its modes of use by the adults, must also differ since the water content of their been breads is equal (Gerling *et al.*, 1983).

Separation of pollen and nectar flights by *X. sulcatipes* is apparently related to a specific plant-insect relationship between this bee species, and the plant *Calotropis procera* (Asclepiaceae). *C. procera* is abundant throughout the arid regions inhabited by *X. sulcatipes*, and it blooms during most of the spring and summer, when the bee is active. It serves only as a source for nectar since its pollen is confined within pollinia and thus is unavailable for utilization by the bees. However, the pollinia often adhere to the bees' legs and head during nectar collection, and are thus transported from flower to flower. Collecting nectar in *C. procera*, and therefore, also obtaining and distributing its pollinia, are limited to large bees, strong enough to separate the conant filaments with their galeae, and reach to nectar reservoirs hidden in the gynostegium. Since the *Xylocopa* bees are probably the only ones large enough to obtain nectar from *C. procera*, they are the main pollinators thereof (Wanntrop, 1974; Ramakrishna and Arekal, 1979; Eisikovitsch, pers. comm.).

The process of nectar ripening, probably linked to the food collecting strategy of *X. sulcatipes*, also occurs in other species (Nishida, 1963; Watmough, 1974; Corbet and Willmer, 1980; Camillo and Garofalo, 1982 and Gerling, 1983).

The considerable variability in sizes of bee breads of *X. sulcatipes* vs. their relative uniformity in *X. pubescens* (Plate 1, 1 vs. n) can be attributed to the different foraging strategies of these species and/or their in-nest behavior. The desert inhabiting species, may encounter difficulties in finding flowering plants, and when they find them, these may be far from each other. In order to maximize their foraging efficiency, they may return with small pollen loads, and also be less demanding about the final size of the bee bread on which the egg is deposited.

*X. pubescens*, by adding nectar to the pollen slant after almost every flight, measures the amount stored rather frequently, while *X. sulcatipes* makes such measurements much more irregularly. Assuming that the decision to prepare the bee bread depends on some quantitative comparison of the amount stored with body dimensions, *X. pubescens* probably can adjust the amount of provision more accurately than *X. sulcatipes*. Indeed, bee breads of *X. sulcatipes* appear to be more variable in size (Plate 1, 1-n), which probably leads to a greater variation in the body sizes of the adults.

For both species, the often quick return from foraging flights indicates that the bees are perfectly aware of the location of the food sources; searching for sites where food plants are located occurs apparently at other times.

*X. sulcatipes* is able to return quickly to the same food plant because it collects pollen and nectar separately and postpones mixing these components. Indeed, both pollen and nectar flights occur in series. This might be of great importance in habitat where flowering plants may be sparsely distributed and limited in number, giving rise

to competition for food. The habits of *X. pubescens* seem to be more adapted to areas where the occurrence and abundance of flowers is more certain. Thus, we believe that in the evolution of the specific foraging behavior, the competition over provision of the offsprings played a more important role in *X. sulcatipes* than in *X. pubescens*.

While *X. sulcatipes* shows much variation in the amount of pollen carried back after each flight, *X. pubescens* is characterized by much variation in the duration of its foraging trips. This species apparently continues collecting until a certain amount is gathered while *X. sulcatipes* return quickly, compensating for any less successful flights with an increase in the total number of flights. Since our data pertain to nests in their initial solitary stages, they are not influenced by a possible effect of adults in the nest on the duration of the trip (Gerling *et al.*, 1981).

At first sight, the "many short flights" strategy seems less efficient: female *X. sulcatipes* invests an estimated 221 min of foraging in preparation for a brood cell, whereas female *X. pubescens* spends only 148 min on the average in this task. However, other pressures such as the need for nest defense against robbery (Gerling *et al.*, 1983) might play a role in determining the duration of each trip, and therefore could limit the amount of pollen carried to the nest. Robbing of nest provisions is common in carpenter bees, and since a robbing female needs some time for orientation and loading of her loot, brief flights of the provisioning bee give her better chances to intercept potential robbers. We suggest that the nest defense aspect is another evolutionary force that led to the separate collection of pollen and nectar by *X. sulcatipes*.

#### ACKNOWLEDGEMENTS

We express our gratitude to the staff of the Hatzeva Field School for their hospitality and help. Dr. A. Hefetz kindly discussed the various aspects of the biology of the carpenter bees with us, including his unpublished data. Dr. D. Eisikovitsch explained the interrelations between *Xylocopa* and *Calotropis*. We are grateful to the anonymous reviewers whose comments considerably improved the manuscript.

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