1972

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NOTES ON THE BIOLOGY OF EMPHOROPSIS PALLIDA TIMBERLAKE

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ABSTRACT

Emphoropsis pallida Timberlake, which nests in sandy slopes along watercourses in the Colorado and Mojave deserts, is the second species in the genus to have its biology recorded. The nest architecture resembles that of E. miserabilis Cresson, which nests in coastal sand dunes, by having: (1) one-celled nests; (2) long, unlined burrows; nest entrances that remain open after nest completion; (4) barrel-shaped, vertical cells with convex caps; (5) an extremely thin cell lining in which sand granules are embedded to form the cell walls. The nests differ from those of E. miserabilis (1) in being deeper (as deep as 2 meters), (2) in having burrows plugged during and after the nesting season, and (3) in having the provisions shaped into a domelike structure not covered with a layer of nectar.

The nest architecture of E. cineraria (Smith) and E. depressa (Fowler), differs from E. pallida and E. miserabilis in having burrows branched and earthen cells urn-shaped, thick-walled, and placed singly and/or in linear series. These cells are lined with a continuous, waxlike coating, and the caps are flat or concave, similar to those found in most species of the closely related genus Anthophora.

Males of E. pallida construct irregular burrows in sand banks in which to spend the night. The females, which forage most actively shortly after dawn and before dusk, provision their cells primarily with pollen of Larrea divaricata Cav.

Two meloid beetle species were found as parasites of E. pallida: immatures and adults of Lytta magister Horn were found in burrows above the cell level and Zonitis (Neozonitis) (sp.) was found within cells.

Emphoropsis is a North American genus of large, robust, fast-flying anthophorine bees. Twenty-one species have been described (Muesebeck et al., 1951; Krombein et al., 1967), but the biology of only one, E. miserabilis (Cresson), has been studied previously (Stephen and Torchio, 1961). The present paper reports the biology of a second species, Emphoropsis pallida Timberlake.

Emphoropsis pallida is distinctive: both sexes have the abdomen covered with pale pubescence and the face marked with yellow (Figs. 1, 2). The species occupies the Colorado Desert, and its range extends west to Palm Springs, Riverside County, California; east to Buckeye, Mariposa County, Arizona; south to Palo Verde, Riverside County, and

1 Hymenoptera: Anthophoridae in cooperation with Utah State University Agricultural Experiment Station, Logan 84321. Received for publication November 24, 1971.
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California; and north to Washington County, Utah (Timberlake, 1937). It is usually found adjacent to permanent bodies of water, and adults have been collected from early March (in southern California) to late May (in Utah).

On March 25, 1967, adult *E. pallida* were discovered nesting near the shore of Lake Havasu, Lake Havasu City, Mojave County, Arizona. On March 26 and 27, 1967, observations were made of adult activities, nest architecture, life history, and parasites. The site was revisited on May 6–7, 1967 after adult activity had ceased, to obtain additional information concerning the later phases of the life history.

**DESCRIPTION OF NESTING HABITAT**

Two nesting sites were studied at Lake Havasu. One site (site A), which encompassed 0.2 hectare, was located on the southwest slope of a dune 18 meters above the lake shore. The 20°–40° slope was interrupted by a series of shallow troughs and ridges directed counter to the upward contour, and its surface was bare except for a scattering of loose gravel and an occasional annual plant (Fig. 3). The soil was composed of coarse-grained sand above a thick layer of hardpan clay 3 cm to 2 m below the surface. The sand was slightly moist from a depth of 25 cm to the hardpan. Bees were unable to penetrate the hardpan, even though they often tried. Although nests were usually scattered in loosely associated groups of 1 to 2 nests per square meter, occasional concentrations reached 6 per square meter.

The second nesting area studied (site B) was approximately 80 square meters and occupied a steeper slope (35° to 45°) immediately above the beach and 0.5 kilometers to the south of site A. It supported a scattered growth of tamarix (*Tamarix gallica* L.) and desert willow (*Chilopsis linearis* (Cav.) Sweet) from 1 to 4 meters tall (Fig. 9). The soil was composed of loose, dry sand which contained occasional layers of coarser sand mixed with fine gravel. It supported a much higher concentration of nests (as many as 30 per square meter).

**NEST ARCHITECTURE AND BIOLOGY**

**Entrances**

The entrance hole of *E. pallida* was normally oblong or broadly hemispherical, 6 mm high and 9 to 12 mm wide, and it angled into the substrate at 20° to 50° below the horizontal. A tumulus was found in front of each entrance, except those on vertical embankments. Its basic form was fan-shaped with the narrowed apex at the entrance hole. On horizontal surfaces, the tumulus was 6 mm long and 6 mm across at the widest point; on steep slopes, it was elongate. Sometimes 1 or 2 troughlike trails originating at the entrance bisected the tumulus; they were probably produced after nesting activities were well established. In some areas, several nests were close
together in horizontal rows which caused the tumuli to overlap and to form large, nearly level platforms on otherwise sloping surfaces.

**Burrows**

Although we excavated nests from horizontal, sloping, and nearly vertical surfaced areas, there was little variation in the basic architectural design. Each burrow penetrated the substrate subhorizontally for a distance of 9 to 12 mm before turning abruptly downward. This second section of burrow was straight, nearly vertical, and long, sometimes reaching 180 cm in length. The burrow then turned abruptly to a subhorizontal alignment and continued for 6.5 to 14 cm, turned again to the vertical for 5 to 15 mm, and ended at a cell (Fig. 13a).

The nest burrow gradually changed from its original hemispherical shape near the entrance to a cylindrical tube 7 to 8 mm wide. The first vertical section was 70 to 180 cm long (average of 25 nests, 130 cm), and was usually blocked by several short plugs of sand during the nesting period and by one long plug after nesting was completed. The plugs (2.5 to 6 cm long) were present in most active nests and were encountered at various depths. Sometimes 3 or 4 plugs were found in a nest, each tightly packed and indistinguishable from the surrounding soil. However, they could be dislodged by blowing a strong current of air through a rubber tube. In a few cases, the plug was composed of sand of the same color as the sand at a lower stratum. How the bee managed to construct this type of plug from above poses an interesting engineering problem.

We found one plug that was composed of orange clay particles throughout its 68-cm length, even though only the cell and terminal 18 mm of the burrow penetrated the clay layer. In another nest, the burrow plug had three color zones corresponding exactly to those of the surrounding strata. Although the nests always had plugs of various lengths, the nest entrances were never plugged, even after nesting was completed.

A short pocket was observed in most nests at the angle between the first vertical section and the second subhorizontal section, thus giving the latter the appearance of a lateral burrow (Fig. 13b). In completed nests, the pocket was tightly plugged. Some nests, however, did not have a pocket, but they also lacked a definite second subhorizontal section (Fig. 13c). This section of the burrow was, rather, directed at a 45° to 60° angle below the horizontal and terminated at the cell.

Burrows were unlined, but some were "powdered" with a thin layering of clay particles apparently collected from the hardpan stratum. These burrows were not, however, "lined" with clay particles throughout their length. Although the burrow walls were smooth, they absorbed water at the same rate as the surrounding soil.
Cells

We found that *Emphoropsis pallida* constructed one-celled nests, all of the cells were placed at an inclination of 60° to 120° below the horizontal, and they were barrel-shaped (Fig. 10). However, the size of cells varied: the outside dimensions of smaller cells were 9 mm wide at their widest point, 16 mm long (excluding the cell cap), and 8 mm wide at the cap; the corresponding dimensions of the larger cells were 11:18:9.5 mm. The fragile cell walls were composed of 1 to 3 layers of sand grains which were embedded in a waxlike coating (Figs. 6, 10, 11). This waxy lining was quite thin (0.02 to 0.04 mm.
thick) and could not be peeled away from the sand granules. The color of the lining varied between cells from nearly transparent to creamy white. The characteristic pungent odor of anthophorine cells was strong in lined cells (with or without provisions) but could not be detected in unlined cells.

In March, a few lined but unprovisioned, cells were returned to the laboratory and examined several days later. By then, each cell lining had turned brown, and its inner surface was completely covered with minute platelets shaped as small triangles with flattened apices. These platelets were most numerous at the surface of the lining, but lesser numbers were also found embedded in subsurface layers throughout the amorphous brown matrix. In addition, small, light-colored globules with reflective surfaces were found interspersed and aggregated into foamlike spheres in the brown subsurface matrix. These globules released a liquid when ruptured. The linings of those cells returned to the laboratory in May did not change color and lacked platelets and globules.

The cell cap was domeshaped and composed of five to eight layers of sand bound weakly together by a clear, liquid secretion. The concave inner surface possessed a large micropyle (2 to 3 mm wide and 1.0 to 1.5 mm deep) positioned slightly off center and surrounded by an indistinct spiral design (Fig. 4). The micropyle was conical and composed of coarse sand grains and had no lining, but the remaining inner surface of the cap was covered with a waxlike coating which was thickest toward the edge. The degree of concavity of the inner surface of the cap varied from nearly flat to strongly concave (about 110°). The outer surface of the cap was hemispherical and showed no evidence of a micropyle or spiral design.

Provisioning and development

The bright yellow provision filled the lower three-eighths to one-half of the cell, and its upper surface was shaped into an off-center, domelike structure (Fig. 14). Although it was moist and tacky, especially the upper half, its surface was not covered with a liquid layer. Each of several provisions examined contained pollen of more than one plant species, but one pollen species always predominated.

The egg was dull-white, slightly arched, 3.5 mm long, 0.5 mm wide, and the anterior tip was narrowed. It was oriented radially with the anterior tip 1 to 2 mm from the cell wall. Both tips were slightly embedded in the provision.

By early May, the bloom of Larrae divaricata had disappeared, and adult E. pallida were no longer flying. However, they had apparently been active up to a few days earlier since we excavated eggs from cells. Of the 24 cells excavated, two had eggs, 18 had half-grown larvae, and four had prepupae. This disproportionate series of life-stages suggests a long period of embryonic development fol-
allowed by rapid development of early instars, and then another long period preceding prepupal formation.

The feeding larva continually circled the outer edge of the provision, thereby shaping it into a conical structure with a grooved outer edge (Fig. 11). The provision remained pyramid-shaped until it was completely consumed.

The larva began to defecate 24–48 hours after it had consumed its provision. First, it assumed a C-shaped position with its head and anus pointed toward the cell cap (Fig. 12), and then it began to emit fecal material as a continuous, dark-brown, cylindrical mass, all the while pressing its anus against the cell wall and smearing feces
over the cell walls. Eventually, feces were deposited over the lower
two-thirds of the cell as a continuous, thin layer which could not be
peeled away from the cell lining. The larva then resumed its hori-
ztontal, C-shaped position at the bottom of the cell and slowly trans-
formed to the semiflaccid, prepupal form. No cocoon or silk strands
were found. We did not determine whether the bee passed the winter
in the prepupal or adult stage.

ADULT ACTIVITY

Sleeping quarters of males

In a 30-cm-high vertical bank along a foot path at site A, we
discovered an aggregation of burrows constructed by males and oc-
cupied by them at night. The holes were irregular in shape, from
2.5 to 10 cm deep, and many of them were joined to form a maze.
Often several males were found in a single burrow, but some were
more solitary. In the evening, the males could be seen backing out
of the burrows and pushing sand free of the entrances to accumulate
at the foot of the bank. At site B, we created a 60-cm-high
vertical bank with our nest-digging operation and observed hundreds
of new burrows in this bank the following day (Fig. 5), all apparently
made by males which were leaving them at the time of observation.
The burrows were irregular in outline and mostly from 5 to 7.5 cm
long.

Mating

Mating took place on the surface of both nesting sites throughout
the day, but activity was most intense between 7:00 and 10:00 AM.
Also, mating was especially noticeable at site B, where emergence of
females was not completed. Cruising males pounced on all females
encountered, but their behavior was more aggressive when they con-
tacted freshly emerged females. After a male grasped a female, ad-
ditional males would dart in and grasp either member of the original
pair, especially in areas where the population of males was high. The
result was a struggling mass of bees (3 to 6 cm in diameter) which
often rolled several meters down the slope, broke apart, and quickly
reformed.

When a pair was not disturbed, the male mounted the female from
behind, grasped some scutellar hairs with his mandibles, and wrapped
his front legs around her tegulae. His midlegs straddled her propodeal
constriction, and his hind legs completely encircled her posterior
abdominal segments. The male then twitched his antennae about once
a second for a short period before he extended his abdomen down-
ward and twisted it to one side preparatory to copulation. When the
female was unresponsive, courtship continued for as long as a minute,
but when she was receptive, courtship was much shorter. Coition
was completed in less than 10 seconds.
Fig. 13. Emphoropsis pallida. (a) Typical nest. (b) Nest with a short, subhorizontal blind lateral. (c) Nest without a horizontal section.

Foraging

Flight activity began shortly before sunrise and continued until sunset. However, most flight occurred between 1 hour after sunrise and 2 hours before sunset. The first load of pollen was returned to the nest 1 hour after sunrise.

Bees traveling from the nesting site to the host plants generally flew in a straight line from 3.0 to 3.5 m above ground. Returning bees usually circled the area above their nests once before landing in
front of the entrances. Two such pollen-collecting trips were timed at 29 and 31 minutes, respectively. When pollen loads from 12 females were examined, 8 were composed of *Larrea divaricata* Cav. pollen, one contained *Lupinus* pollen plus a small quantity from a composite, and 3 contained an unknown (possibly boraginaceous) pollen. Apparently, nectar was collected from many sources. Even the few plants of *Phacelia crenulata* Torr. and *Camissonia* sp. growing adjacent to the nesting site were visited frequently by both sexes for nectar during the early morning hours.

*Nest site activities*

The presence of damp sand found on top of the tumulus of many nests prior to morning flight indicated that some excavation was accomplished at night. Bees also excavated throughout the daylight hours and deposited the excavated soil in a characteristic fashion. Each bee backed out of her entrance, using oarlike motions with her front and hind legs while bracing herself against the substrate with her mid-legs. If undisturbed, she backed over 3 to 5 cm of the tumulus and created a shallow trail in the process. Sometimes she emerged head first, “viewed” her surroundings, and re-entered head first before backing out with additional soil. If her first inspection revealed the slightest movement within her range of vision, she quickly backed into her nest and remained hidden for some time.

In four instances, we observed a female with a full load of pollen actively excavating soil from her nest. Two of these nests were dissected, and in one we discovered a tight plug 0.6 m below the nest surface. Apparently, the bee had spent the night on top of this plug and had failed to remove it prior to the collection of pollen. In the second nest, a similar plug was found above an unprovisioned cell.

Although nesting bees were not aggressive, they reacted to human trespassers. At site B, both sexes rose from 0.6 to 0.9 m above the nest surface when a person approached and then flew rapidly around him in a weaving pattern. At site A where the population was much lower, a similar response was observed, but the bees did not rise more than 0.3 m above the ground.

*Parasites*

Two species of meloid beetles were found in the nests. At site A, 3 overwintering larvae (Fig. 7) and 1 adult *Lytta magister* Horn (Fig. 8) were found in the burrows well above the cells (0.6 m below the surface). Apparently, the larvae had migrated upward from the host cells before becoming dormant. At site B, an undescribed species of *Zonitis* (*Neozonitis*) (determined by W. R. Enns, Department of Entomology, University of Missouri) was found in 2 host cells. One contained an adult encased in the fourth and fifth larval skins, and the other contained a coarctate larva. These 2 cells, which seemed to be at least 1 year old, were found among a number of old cells
filled with sand. Apparently, these meloids had remained dormant in the cells for at least 2 years.

**DISCUSSION**

*Emphoropsis pallida* appears to be without close relatives in the genus. Nevertheless, its nests and cells resemble those of *E. miserabilis* (Stephen and Torchio, 1961) which also nests in sand (the coastal dunes of Oregon). Similarities of nests and cells in the two species include: (1) one-celled nests; (2) relatively long, unlined burrows; (3) open entrances in completed nests; (4) barrel-shaped cells; (5) vertical or nearly vertical cells; (6) cell lining composed of a thin layer of waxy material embedding the sand granules; and (7) convex cell caps. *Emphoropsis pallida* differed from *E. miserabilis* by having: (1) much deeper nests; (2) burrows plugged during and after nesting activities; (3) surface of provisions not covered with a layer of nectar; (4) provisions shaped into a domelike structure; and (5) provisions consumed from the outer edge.

Although the 2 species hold many nesting habits in common, it is unlikely that these characterize the genus. Rather, we feel that they reflect independent adaptations to the dry-surfaced, blow-sand nesting medium. Parallel adaptations are also found among other species in the taxon. For example, *E. cineraria* (Smith) and *E. depressa* (Fowler) nest in fine-grained soils and construct nests with branched burrows and urn-shaped, thick-walled, earthen cells (unpublished). These cells are placed singly or in linear series and are lined with a waxlike material that forms a continuous sheet which is easily separated from the cell walls. The cell caps are constructed with flat inner surfaces and concave outer surfaces.

The few *Emphoropsis* species studied exhibit an extensive range of nest types, most of which are also exhibited in the closely related genus, *Anthophora*. Present biological knowledge does not seem to provide a basis for the separation of these two genera.

**ACKNOWLEDGMENTS**

We would like to thank Gerald R. Wood, a former student at Utah State University, Logan, who assisted in field excavations and observations. Howard Potter, an Agricultural Research Technician stationed at this laboratory, took the photographs in Figures 1, 2, 4, 6, 8, 9, 10, and 11. Robbin W. Thorp, University of California, Davis, read the manuscript and offered several valuable suggestions.
LITERATURE CITED


