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Nesting Behavior of *Philanthus albopilosus* with Comparisons Between Two Widely Separated Populations[1]

HOWARD E. EVANS

Department of Zoology and Entomology, Colorado State University, Fort Collins 80523

ABSTRACT

Nesting behavior of *Philanthus albopilosus* Cresson was studied near Albany, N.Y., and Roggen, Colo. In both localities the mounds of soil at nest entrances were partially leveled. In New York, 2 of 5 newly completed nests had one accessory burrow each, while in Colorado 26 of 33 such nests had accessory burrows numbering 1 to 6 per nest. Nests consisted of a nearly horizontal section (vestibule) followed by a nearly vertical section (gallery) penetrating the soil deeply. Cells, up to 4 per nest, were constructed at the ends of long side burrows and were provisioned with from 6 to 10 paralyzed bees or wasps per cell. Comparison of the 2 widely separated nesting aggregations revealed only one important difference: mean length of the gallery was 18.7 cm in New York (n=7) as compared to 45 cm in Colorado (n=8).

Philanthus, the genus of the so-called "bee wolves," occurs throughout the northern hemisphere as well as in Africa. There are about 25 North American species, several of which have been studied recently by Evans (1964, 1970), Evans and Lin (1959), and Alcock (1974, 1975). Although *P. albopilosus* Cresson is widely distributed east of the Rockies, the only account of its biology is a brief note by Evans and Lin concerning the partial excavation of a single nest.

The lack of studies of this species is probably a consequence of its local distribution, as it nests only in broad expanses of bare, fine-grained sand. When other species of *Philanthus* occur in this habitat (e.g., *P. psyche* Dunning) their nests are typically confined to the periphery, where there is sparse vegetation. The nests of *P. albopilosus*, on the other hand, tend to occupy more central areas where there is no vegetation at all and where high surface temperatures and a certain amount of blowing sand are common features. Only a few other insects occupy this habitat during the day, notably the sand wasps *Bembix pruinosa* Fox and species of *Microbembex*.

Aggregations of *P. albopilosus* were studied at the eastern and western extremities of the range. The first aggregation was studied July 7–Aug. 13, 1970, in a large, slightly sloping, artificial excavation just west of the city of Albany, N.Y. The second was studied July 8–Sept. 10, 1974, just north of the town of Roggen, Weld Co., Colo. At this site several nests were found in a broad, natural blowout, several more in a sloping bank resulting from an artificial cut into a partially anchored sandy ridge. Several nests were also found in a blowout among dunes just south of the Arkansas River near Hasty, Bent Co., Colo., on June 27, 1974. Only one nest was excavated here, and the data are combined below with those from Roggen, since all details were very similar. Voucher specimens of wasps and prey have been deposited at Colorado State University along with associated field notes.

This species evidently has 2 generations per year both in New York and in Colorado. In New York, I found several active nests July 7–11, but after a careful search, I failed to find any on July 23, although on Aug. 7–13 numerous females were active. Comparable dates in Colorado were June 27–July 8, with a midsummer hiatus until August and early September.

MALE BEHAVIOR

Males were abundant in both study sites, and numerous interactions between males and between males and females were observed. Males typically perch on the sand or less frequently on a pebble or stick, assuming an "alert" posture, with the antennae extended rigidly forward, the head slightly elevated, and the abdomen curved upward slightly posteriorly. The front of the head is densely clothed with silvery pubescence which glitters in the sun and may represent a signal of importance in the spacing of the males. Distance between perching males is rarely less than 1.5 m except very temporarily. When males perch more closely than this, or a male flies close to another male, the result is a brief encounter during which the wasps butt one another repeatedly while rising in a spiral to a height of 0.5–1.0 m. Males often also fly toward other passing insects, without actually butting them, and sometimes fly up and land elsewhere in the absence of any obvious stimulus.

Although I did not mark any males or perches, I obtained the impression both in New York and in Colorado that the wasps moved readily from one point to another and that in fact there were no "favorite" perches, occupied by the same or different males over a period of time. Rather, males maintained a certain distance between them by a more or less random series of moves from one part of the sand surface to another. Use of a "marking pheromone" as described for some species of *Philanthus* by Alcock (1975) seems most unlikely in this species.

On several occasions males were seen to fly after and attempt to mate with females carrying prey. Two or three males would sometimes form an ascending spiral, butting one another frequently, in the close presence of a female. No complete matings were observed. No differences in male behavior were noted between New York and Colorado populations.

[1] Hymenoptera: Sphecidae. Received for publication Feb. 25, 1975.

NESTING BEHAVIOR

In both study areas, nests of the females were widely spaced, commonly 1.0–1.5 m apart, and in no case closer than 0.8 m. The largest number of nests was found toward the bottom of the sloping bank near Roggen, Colo., where 26 nests active at the same time occupied a 3×30-m area. All nests in sloping sand here and elsewhere were dug into the slope, whereas nests in flat sand were dug in various directions.

Females typically begin a nest in the morning (0900–1100) and dig intermittently throughout the day. When they discontinue digging and fly off, as they do periodically, they invariably close the entrance of the hole. Digging wasps appear just outside the entrance from time to time and scrape the sand into a mound (Fig. 1). Since they do not emerge more than ca. 1 cm from the entrance, but tend to turn from side to side slightly while clearing the entrance, the resulting mound is close to the entrance and somewhat circular in outline. Mounds in New York measured from 11 to 16 cm wide ($\bar{x} = 13.2$), from 9 to 12 cm long ($\bar{x} = 10.8$) ($n = 4$). In Colorado, mounds measured 12 to 15 cm wide ($\bar{x} = 13.5$), 15 to 28 cm long ($\bar{x} = 19.0$) ($n = 7$). In both areas the maximum depth of mounds approximated 1 cm. The appreciably greater length of mounds in Colorado doubtless reflected the much greater depth of the nests there (see below).

Following completion of the nest, the female backs somewhat further from the entrance (3–6 cm) and, by a series of zigzag movements facing the entrance, levels off that portion of the mound close to the entrance. This behavior requires several minutes and results in the mound assuming a somewhat crescentic shape. The flattened area close to the entrance typically contains a somewhat star-shaped pattern of lines, formed when the female makes the initial and later closures by scraping sand over the entrance from all sides. The initial closure is especially prolonged, and at this time soil is often excavated from the ends of the radiating lines, resulting in one or more quarries or "accessory burrows" (Evans 1966). Of 5 newly completed nests studied in New York, 2 had 1 accessory burrow each, the burrows measuring ca. 1.5 cm deep in each case. Of 33 newly completed nests studied at Roggen, Colo., 26 had 1 or more accessory burrows, these varying from 0.5 to 7 cm in depth (the majority 0.5–2.0 cm; any less than 0.5 cm were not counted as accessory burrows). Of the 26 nests, 14 had 1 accessory burrow, 6 had 2 burrows, 2 had 3, 2 had 4, and 2 had 6 (Fig. 2). These burrows were constructed immediately after completion of the nest, at the time of initial closure, and were not renewed later. Nests more than a few hours old rarely had any evidence of accessory burrows, as these tended to be filled by wind action or in the course of subsequent closures.

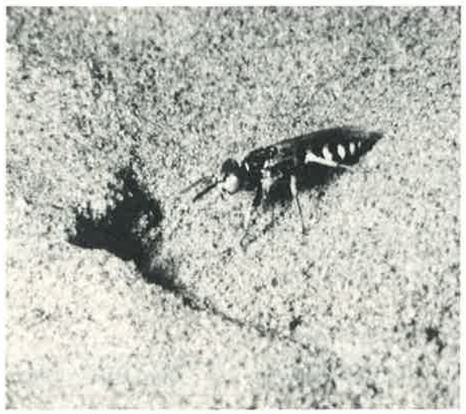

FIG. 1. — Female *Philanthus albopilosus* clearing the entrance of her burrow (Roggen, Colo.).

FIG. 2. — Appearance of a newly completed nest of *Philanthus albopilosus* at Roggen, Colo., showing 6 shallow, open accessory burrows. The right end of the straw is directly over the closed entrance of the true burrow. Note that the portion of the mound away from the entrance has not been leveled.

In no cases were wasps actually seen closing these burrows, although a closure of the true burrow was maintained at all times except when the wasp was bringing in prey. Similar accessory burrows have been reported in several other species of *Philanthus* (Tsuneki 1943, Evans 1964).

NEST STRUCTURE

The nest of *P. albopilosus* is of unique structure, consisting of a nearly horizontal section (vestibule) which runs close beneath the surface and leads to a more or less vertical section (gallery) which penetrates the soil deeply. The vestibule passes only 2 to

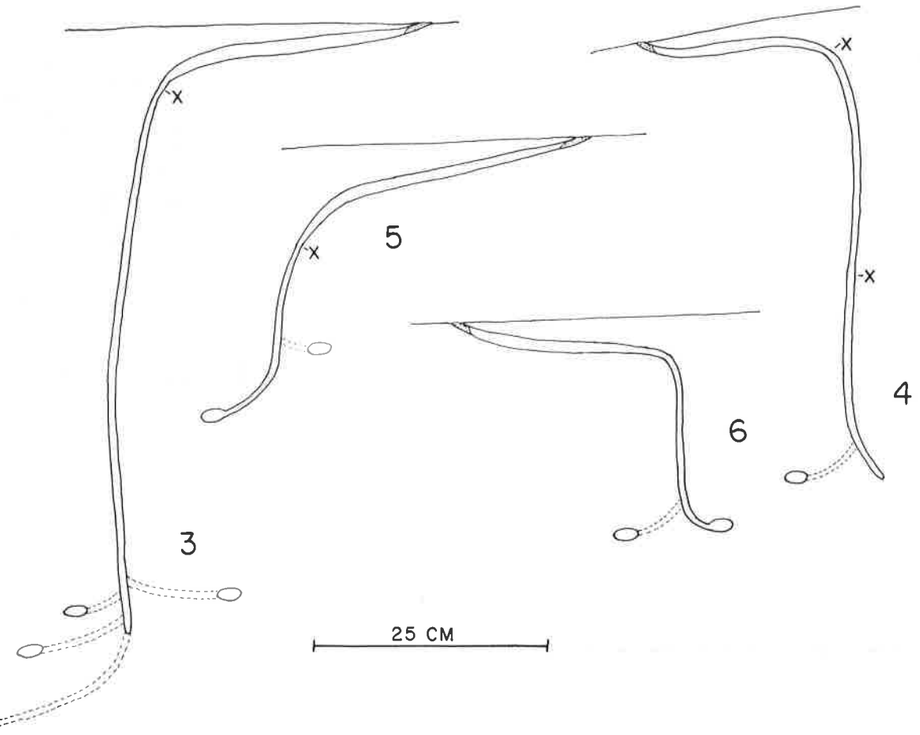

FIG. 3–6.—Profiles of 4 active nests of *Philanthus albopilosus*. Fig. 3, nest no. 2437, near Roggen, Colo. Fig. 4, nest no. 2438, near Roggen, Colo. Fig. 5, nest no. H81, near Albany, N.Y. Fig. 6, nest no. 70B, near Albany, N.Y. Side burrows which could not be traced are indicated by dashed lines. In each case the position of prey stored in the burrow is indicated by an "X".

5 cm beneath the surface and is commonly of greater diameter than the gallery, often 5 to 12 mm as compared to ca. 4 mm for the gallery. Whether this results from cave-ins from the ceiling which are removed by the wasp, or from actual excavation, is not clear. Presumably nests are dug only in situations where there is a sufficient slight crust to maintain a ceiling for a burrow so close to the surface. Although on flat soil the vestibule does dip down slightly (up to about a 10° angle with the surface), when the burrow is dug into a sloping bank the vestibule may actually slant upward slightly (Fig. 4). This section is of appreciable length, about the same in the New York and Colorado localities; in constrast, the cells averaged about 2.5 times as deep in Colorado, with no overlap in the range of variation (Table 1; Fig. 3–6).

Although I have spoken of the gallery as being nearly vertical, in some nests it curves down rather gradually before becoming essentially vertical (Fig. 5). Cells are constructed from rather long (5–20 cm) side burrows from near the end of the gallery. Since these side burrows are closed as soon as the cell is provisioned, they can rarely be traced. Indeed, the cells of any one nest tend to be spaced so widely that it is difficult to locate all of them. The maximum found in any one nest was 4, but it seems likely that more are sometimes made. Cells measure 12–15 mm long by 7–8 mm high.

Table 1.—Nest dimensions of *P. albopilosus*.

Locality	No. nests	Length (cm): vestibule	Length (cm): gallery	Depth (cm) of cells
New York	7	16–31 ($\bar{x}$=24.6)	11–22 ($\bar{x}$=18.7)	13–25 ($\bar{x}$=19.2)
Colorado	8	18–32 ($\bar{x}$=23.1)	23–57 ($\bar{x}$=45.0)	31–62 ($\bar{x}$=52.0)

Table 2.—Prey records for *P. albopilosus*.

Species	No. specimens New York	Colorado
EUMENIDAE		
Ancistrocerus catskill Saussure	1 ♂	
SPHECIDAE		
Aphilanthops frigidus Smith	1 ♂	
Mimumesa fuscipes Packard	1 ♀	
Oxybelus bipunctatus Olivier	1 ♀	
Oxybelus quadrinotatus Say	5 ♂	
COLLETIDAE		
Colletes hyalinus Provancher		21 ♂
Colletes simulans armatus Patton	1 ♂	
Colletes ? willistoni Robertson		1 ♀, 3 ♂
ANDRENIDAE		
Andrena robertsonii Dalla Torre	1 ♀	
HALICTIDAE		
Agapostemon angelicus Cockerell		27 ♂
Dialictus imitatus Smith	1 ♀	
Dialictus lineatulus Crawford	1 ♂	
Dialictus pilosus Smith	2 ♀, 6 ♂	
Halictus confusus Smith	2 ♀, 2 ♂	
Halictus ligatus Say	1 ♀	21 ♂
Halictus rubicundus Christ	17 ♂	
Lasioglossum leucozonium Schrank	9 ♂	
TOTALS	9 ♀, 43 ♂	1 ♀, 72 ♂

It may be noted that *Bembix pruinosa,* which commonly nests in the same situations as *P. albopilosus,* also makes a long "preliminary burrow" close beneath the surface before penetrating the soil deeply (Evans 1957). However, this is filled-in when the gallery is dug, and a new entrance is made at some distance from the original entrance. This is not the case in *P. albopilosus,* which continues to use the original entrance.

PROVISIONING

Females prey upon a variety of small bees and (at least in New York) occasional small wasps (Table 2). They approach the nest swiftly, flying only 3–6 cm above the sand, holding the paralyzed prey with their middle legs. At the entrance, the closure is removed with several strokes of the fore legs and the wasp enters, sliding the prey backward slightly and holding it with the hind legs, in the usual manner of philanthine wasps. Miltogrammine flies were not abundant at either study site, and I saw no evidence of the evasive flights characteristic of many *Philanthus* species (e.g., Alcock 1974).

Provisioning occurs at a slow pace, one female (New York) bringing in 2 bees over a 45-min period. Prey is not taken directly to a cell, but is left near the far end of the vestibule, near the point where the gallery angles down sharply (in 2 nests I found bees in the gallery itself, in one case at considerable depth, Fig. 4). Approximately enough bees are stored here to provision one cell; when enough have accumulated, the female discontinues provisioning and spends a long period inside the nest, removing the prey to a cell much deeper in the soil. Data on the number of prey stored and their distance from the entrance and from the surface are shown in Table 3.

Within the cell, the bees are piled mostly venter-up, with the egg being laid longitudinally on the topmost prey as usual in the genus. The number of prey per cell varied from 7 to 10 in New York ($\bar{x} = 8.3$, $n = 6$), and from 6 to 8 in Colorado ($\bar{x} = 6.7$, $n = 6$), doubtless a reflection of the fact that New York wasps used a number of quite small prey, such as species of *Oxybelus*.

Of 73 prey taken from nests in Colorado, only 1 was a female (Table 2). Capture of prey was not observed, but it seems very probable that it occurs on flowers, as is common in *Philanthus*. It is interesting to note that 73 prey records from Colorado involved only 4 species, while 52 from New York involved 14 species. Probably this does not reflect a richer fauna of Hymenoptera at the New York site, but simply that a few species of bees of suitable size were exceedingly abundant at the Colorado localities.

DURATION OF NESTS

It is known that some species of *Philanthus* maintain a single multicellular nest for their lives, while others make a series of nests, each with only a few cells (Evans 1970). Clearly *albopilosus* belongs to the second group. As mentioned above, no more than 4 cells were found in any one nest. On Aug. 8, 1970, in New York, I marked 5 nests in the process of being dug. On Aug. 11, 2 of these were no longer active, and on the 13th all appeared to have received a final closure. Of 26 nests marked near Roggen, Colo., on Sept. 6, 1974, only a very few were still being provisioned on the 10th.

NATURAL ENEMIES

Near Albany, N.Y., a female was seen to enter a hole ca. 15 cm from her nest, apparently by accident. This hole was occupied by a tiger beetle larva (*Cicindela* sp.) which promptly seized the wasp and began to feed upon it. At this same locality, 1 of 11 cells excavated contained maggots. These formed their puparia a few days later (Aug. 15) and gave rise to adult flies, *Phrosinella fulvicornis* Coquillett (Sarcophagidae: Miltogramminae), the following spring (April 15). No attacks by flies or other natural enemies were observed at the Colorado sites.

Table 3.—Storage of prey in vestibule, *P. albopilosus*.

Nest no.	Locality	No. prey	Distance from entrance (cm)	Distance from surface (cm)
H81	New York	1	35	8
2377	Colorado	1	28	10
2431	Colorado	7	21	3
2433	Colorado	6	22	5
2436	Colorado	3	27	5
2437	Colorado	6	32	5
2438	Colorado	6	18	5

DISCUSSION

Most of the distinctive behavioral features of this species were consistent in populations near the eastern and western extremities of the range. These include the unique nest structure, with a long vestibule close beneath the surface followed by a gallery penetrating the soil deeply; preparation of one or more accessory burrows in most new nests; leveling of only that part of the mound nearest the entrance; construction of widely spaced cells deep in the soil; spacing and aggressive behavior between males. Some apparent differences between New York and Colorado wasps are doubtless a reflection of small sample size, e.g., occasional use of wasps as prey in New York, greater incidence of accessory burrows in Colorado. An important difference in the 2 populations occurred in only one feature: nest depth, also reflected in mound size. Whether the much deeper nests in Colorado resulted from a response to higher temperatures and decreased soil moisture, or whether the shutting off of digging behavior is genetically controlled, was not determined in these studies. It may be worth noting that *Microbembex monodonta* (Say) nested beside *P. albopilosus* in New York and *M. hirsuta* Parker in Colorado. The nests of these 2 species did not differ appreciably in depth. *Bembix pruinosa* nested in both localities, but in Colorado nests averaged only slightly deeper than in New York (35 as compared to 27 cm).

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