

NOTES ON THE NESTING BEHAVIOR OF  
*PHILANTHUS LEPIDUS* CRESSON  
(HYMENOPTERA, SPHECIDAE)\*

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Several years ago Evans and Lin (1959) discussed the nesting behavior of four species of *Philanthus* which occur commonly in the northeastern United States. The four species were found to have many ethological similarities as well as several interesting differences. The larger species tend to take larger bees as prey, and certain of the species nest earlier in the season than others or seem to prefer more sloping earth in which to nest. The fact that there is much overlapping with respect to these slight ecological differences suggests that competition for prey and nesting sites has been of minor importance in the evolution of these species; this may in part be a consequence of the fact that populations of all four species appear to be kept well below their maxima by parasites. In point of fact, all of the major behavior differences between these four species appear "to represent mechanisms which have evolved as a response to parasite pressure": for example, differences in closure, in mound-leveling, and in burrow profile.

I am now able to add a fifth species to this picture without necessitating any change in these conclusions. *Philanthus lepidus* is a locally common species which occurs in much the same situations as the four studied earlier and preys upon much the same kinds of bees: in fact one common green "sweat bee", *Augochlorella striata*, has been found in the nests of all five species, and several others have been found to be used by three or four of them. The distinctive features of *P. lepidus*, as in the case of the other four species, appear to be associated with parasitism. In particular, this species prepares one or more "false burrows", which remain open at all times, although the true burrow is closed. False burrows have to my knowledge not been reported for other philanthine wasps, but they occur in certain species of at least two other subfamilies, as discussed further in the final section of this paper. It cannot be proved that these false burrows do, in fact, divert parasites in any important way, but there is now considerable circumstantial evidence that this is their function.

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\*Manuscript received by the editor October 29, 1964.



*Ecology.* — I first encountered *Philanthus lepidus* in an area of extensive small sand dunes and blow-outs near Granby Center, Oswego Co., N. Y., on August 31, 1960. Here I found some thirty nests, mostly in two well separated aggregations about ten meters apart. Within each colony the nest entrances were separated at times by no more than 10 cm. Many of the nests were in depressions amongst ferns, and the soil was so full of roots as to make it very difficult to dig out the nests successfully. I spent only a few hours with these nests, as I was gathering data on *Bembix pruinosus* and on a species of *Tachytes* which nested in more open sand in the same locality. I noted no other philanthine wasps in the area on that date.

For the past several summers *P. lepidus* has nested in considerable numbers in a large, eroded sand bank near my home in Lexington, Massachusetts. Each year the species appears at the end of August and remains active well into September. In 1962, when most of my studies were made, I noted much activity on September 7, which was a cool day (73°F maximum), and on September 23 a few females were noted digging sluggishly at an air temperature of 60°F, after several nights of frost. On this date virtually all other solitary wasps had disappeared. Even *P. solivagus*, another species characteristic of the late summer, emerges and disappears one to two weeks before *lepidus*. However, the nesting cycle of the two species overlaps for two or three weeks at Lexington, and the nests of the two species are sometimes intermingled. However, in this particular sand bank *solivagus* occurs mostly near the top, in a moderately steep slope, while most nests of *lepidus* are near the bottom, in weakly sloping, firm sand eroded from above. In this very same place, *P. politus* is common in early summer, but I saw none nesting after mid-August. *P. gibbosus* also occurs in this sand bank, nesting in small numbers both in the *solivagus* and *lepidus* areas, but mainly in mid-summer.

Both males and females of *P. lepidus* visit the flowers of *Solidago* in considerable numbers. The males are otherwise rarely seen, though they do appear from time to time around the nests of the females, landing on the sand with their antennae extended rigidly and now and then pursuing females. I have taken males as late as September 14 at Lexington.

*Nesting behavior.* — From three to six hours are required to complete the burrow. Then sand is allowed to plug the entrance, and from time to time the wasp comes out and clears it away,



sweeping it into a broad mound in front of the opening. Mounds of completed nests measure from 8 to 13 cm in length by 6 to 8 cm in width and 0.5 to 1.5 cm in depth. No true leveling movements occur at any time, but mounds may weather away after several days, particularly if there has been a heavy rain or strong wind.

Following completion of the burrow, but before making a cell or bringing in prey, the wasp digs a short, blind burrow on one side of the entranceway, sometimes one on each side. Whether these are dug before or after the initial closure of the true burrow was not determined. Thereafter these "false burrows" are never closed, but the true burrow is closed from the outside when the female is hunting, from the inside when she is inside the nest for more than brief periods. I obtained the impression that the wasps keep these false burrows "in repair", although they do not use them in any way. One female was seen to bring a bee into the true burrow, then emerge and enter a false burrow for a moment and come out and fly off.

I found no fresh nests without at least one false burrow. At Granby Center, N. Y., I took notes on four nests, three of which had one false burrow and one of which had two. These false burrows began 1-4 cm from the opening of the true burrow and started out at roughly a right angle to it, but often curved toward or away from the true burrow. They varied in length from 6.5 to 9 cm, and for the most part were at only a 15 to 30° angle with the horizontal (like the beginning portion of the true burrows) (Fig. 1).

In Lexington, Mass., I observed many nests with false burrows, but took measurements on only seven. Of the seven, four had one and three had two false burrows beside the entrance of the true burrow and forming a 45 to 90° angle with it; these varied in length from 1 to 3 cm (notably less deep than those at Granby Center). In addition, four of these nests had additional, very shallow false burrows (0.5-1.0 cm deep), not beside the nest entrance but farther back on the mount. One nest had a total of five false burrows, one of them with a double entrance (Fig. 3). Such nests presented a confusing picture of holes going in various directions, with the true nest entrance well concealed and discoverable only when the female arrived with prey.

*Nest structure.* — Diameter of both the true and false burrows is about 5 mm. As already mentioned, the top section of the true burrow is at only a 15 to 30° angle with the horizontal; after some 8 to 15 cm the burrow bends down sharply, attaining an angle of from



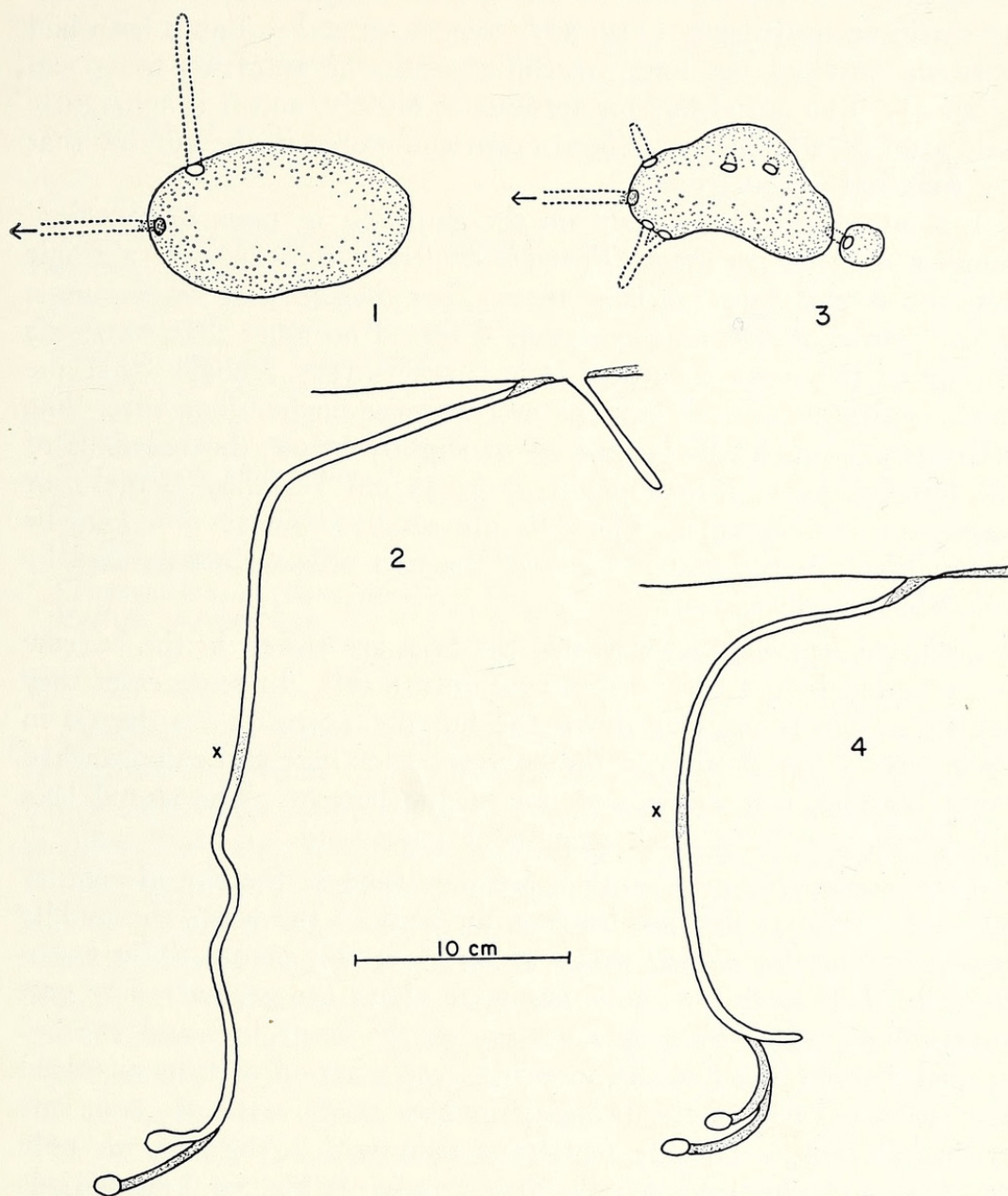


Fig. 1. Mound of nest no. 1674, Granby Center, N. Y., showing true burrow (left) and false burrow (top). Fig. 2. Same nest in profile; one bee was found in the burrow at *x*, several others in each cell. Fig. 3. Mound of nest no. 1848-3, Lexington, Mass., showing five false burrows, one with a double entrance. Fig. 4. Nest no. 1846, Lexington, Mass., in profile; eight bees were found in the burrow at *x*, several others in each cell; the false burrow was destroyed accidentally and hence is not shown here.



70 to 90° with the horizontal. In the one nest successfully excavated at Granby Center, the burrow was 48 cm long and reached a point 37 cm in vertical depth (Fig. 2). Two nests at Lexington both had burrows only 24 cm long, reaching depths of from 17 to 19 cm (Fig. 4). The initial burrow terminates blindly, and it is apparently only after several bees have been taken and stored in the burrow that the first cell is constructed.

I obtained no precise data on the duration of nests or the final number of cells per nest. Females evidently remain with a single nest for several days (at least three), but they prepare several nests in the course of the nesting season. I found no more than two cells in any of the nests excavated, but it seems very probable that the final number of cells in any one nest averages higher than this. The cells were found to be located at or slightly below the terminus of the burrow, at a vertical depth of 33-35 cm (Granby Center) or 24-26 cm (Lexington). The cells are small, about 10 mm long by 8 mm high; in the nests excavated the two cells were separated by only about 2 cm of soil.

As usual in philanthine wasps, the bees are stored in the burrow for a period before being introduced into a cell. In some cases they are stored about halfway down the burrow (9 to 17 cm deep), in some cases at the bottom of the burrow. One nest at Lexington had seven bees halfway down and one at the bottom. The stored bees are surrounded by a small amount of loose sand.

*Provisioning the nest.* — Bees are paralyzed at the site of capture and are carried to the nest beneath the body of the wasp, the middle legs providing the major grasp as usual in this genus. The wasps fly in to their nests low, only 10-15 cm above the ground. The nest entrance is opened by a few scrapes of the front legs and the bee carried directly in. Females watched over a period of time appeared to provision very slowly, bringing in bees at the rate of about one every half hour. Usually females remain within the nest for only 20-30 seconds, but occasionally they remain within for long periods of time, presumably digging a cell and introducing the bees into the cell. From 9 to 11 bees are provided per cell. The egg is laid longitudinally on the venter of one of the topmost bees in the usual manner of members of this genus (Evans and Lin, 1959, Fig. 9).

In both areas of study, *P. lepidus* preyed upon a considerable variety of small bees, all but one of the 69 specimens taken belonging to the family Halictidae. Individual nests always contained a mixture of species (from 3 to 7). Male and female bees were used in roughly equal numbers. Many of these same species of bees appear on the



lists of prey taken by *P. solivagus*, *politus*, *gibbosus*, and *bilunatus* (Evans and Lin, 1959). The complete list follows (determinations made by myself, using the keys in Mitchell, 1960, in connection with specimens determined by Mitchell):

Species of prey	Number taken	
	Granby Center, N. Y.	Lexington, Mass.
ANDRENIDAE		
<i>Pseudopanurgus andrenoides</i> (Smith)	1 ♀	
HALICTIDAE		
<i>Augochlora pura</i> (Say)		2 ♂ ♂
<i>Augochlorella striata</i> (Provancher)	1 ♀, 3 ♂ ♂	1 ♀, 1 ♂
<i>Dialictus apertus</i> (Sandhouse)		1 ♂
<i>D. cressonii</i> (Robertson)		1 ♀, 6 ♂ ♂
<i>D. inconspicuus</i> (Smith)		16 ♀ ♀, 1 ♂
<i>D. laevissimus</i> (Smith)	10 ♂ ♂	3 ♂ ♂
<i>D. tegularis</i> (Robertson)		7 ♀ ♀
<i>D. versans</i> (Lovell)		1 ♀
<i>D. spp.</i>	1 ♀, 2 ♂ ♂	5 ♂ ♂
<i>Evyllaenus divergenoides</i> Mitchell		3 ♂ ♂
<i>E. macouzensis</i> (Robertson)		2 ♂ ♂
<i>Halictus ligatus</i> Say		1 ♀
TOTAL	3 ♀ ♀, 15 ♂ ♂	27 ♀ ♀, 24 ♂ ♂

*Parasites.* — Parasitic flies were much in evidence in both localities. In both areas several of the flies were captured as they pursued females laden with prey; all were determined by C. W. Sabrosky as members of the *Senotainia trilineata* complex (Sarcophagidae: Miltogramminae). Members of this complex are known to attack a wide variety of ground-nesting wasps. None of the six cells excavated contained maggots, and no maggots were noted on any of the bees found in storage in the burrows.

Provisioning females being pursued by *Senotainia* undertake a characteristic flight, hovering near the nest or flying slowly forward 3-6 cm high, sometimes to a distance of several meters from the nest. The fly usually follows just behind the wasp and slightly below. If unable to rid herself of the fly, the wasp may fly rapidly and deviously and may leave the area altogether, to return a few moments later, usually without the fly. Presumably the flies larviposit successfully on the prey at times, as described in the case of *P. solivagus* and these same flies by Ristich (1956), but I observed no cases of successful larviposition and, as already mentioned, found no maggots in the few nests excavated.

In Lexington, the mutillid *Dasymutilla nigripes* was very common. On several occasions females were seen entering the open false burrows, digging a bit, and then leaving. None were seen entering



the true nest entrances. Shappirio (1948) observed this same species of mutillid entering nests of *P. gibbosus* at Washington, D. C. It seems very probable that this species is a parasite of several species of *Philanthus*, although no one has actually reared it from cells of these wasps.

*Discussion.* — False burrows are a characteristic feature of the nests of several nyssonine digger wasps (e.g., Tsuneki, 1943, Evans, 1957) and of at least one sphecine wasp (Tsuneki, 1963). There are now many observations of mutillid wasps and miltogrammine flies being attracted to these burrows, and bombyliid flies have been observed ovipositing in false burrows of certain species. There is no evidence whatever that these burrows play a role in orientation, resting, or storage of prey. Tsuneki and I are in agreement that their function must be to divert parasites, and in a paper in preparation I shall attempt to trace their evolution, in the Nyssoninae, from quarries used for soil for closure to ritualized false burrows serving a very different function. The occurrence of false burrows in the Philanthinae has not, to my knowledge, been recorded previously. They were found to occur in all nests in both areas of study, but they may not occur in all individuals throughout the range of this species (geographic variation in this feature was found to occur in *Bembix pruinosa* by Evans, 1957, and has since been found in certain other species). It is important that this behavior be recorded in all species in which it occurs, and in various localities.

In the case of *P. lepidus*, the false burrows would seem to afford no protection against *Senotainia*, which appeared to be the major enemies in both areas of study. Presumably the selection pressure was provided at a time and place when hole-searching miltogrammines, bombyliids, chrysidids, and mutillids were of major importance.

Otherwise the behavior of *P. lepidus* does not differ in any major way from that of *gibbosus* and *bilunatus*, which make similar nests, maintain an outer closure, and do not level the mound at the nest entrance. *P. lepidus* nests later in the season than those species, emerging slightly later even than *solivagus*. The latter is a larger species which preys mostly on larger bees, sometimes on wasps; in the area of study *solivagus* nested in a slightly different situation, although there was some intermingling of nests. That the five species of *Philanthus* common in the northeastern states have been only partially successful in "dividing up the sand + bee niche" probably means, as suggested earlier, that the populations of all five are kept fairly low by parasite pressure. All five have developed certain behavioral mechanisms apparently serving to reduce the incidence



of parasitism, and in each case the mechanism is different, at least in part. In a given area, the species whose behavior patterns are most successful in combating the parasites most prevalent in that location may well inherit the bulk of the sand + bee niche.

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<https://doi.org/10.1155/1964/29519>.

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