The Nesting Behavior of Philanthus multimaculatus Cameron (Hymenoptera, Sphecidae)

ABSTRACT: *Information is presented on the nesting behavior of* Philanthus multimaculatus *Cameron including dimensions and design of the burrows, prey species taken, the manner in which prey-laden females approached the nest entrance and their response to parasitic satellite flies. Their distinctive approach flight supports the hypothesis that selection exerted by satellite flies has favored divergence in approach patterns among digger wasps which nest in mixed-species aggregations.*

INTRODUCTION

This paper describes the nesting behavior of *Philanthus multimaculatus* Cameron with special reference to the antiparasite adaptations of the females. (A report on male territorial behavior in this species is in preparation.) The study complements previous work on other North American *Philanthus* by the Peckhams (1905), the Raus (1918), Reinhard (1924, 1929), Powell and Chemsak (1959), Armitage (1965), Evans (1964, 1966, 1970; Evans and Lin, 1959), Cazier and Mortenson (1965) and Alcock (1974). I observed the wasps on an open ridge composed of sand, earth and clay located just E of Portal, Arizona, about 1 km N on the road to San Simon. The general area and its flora have been described by Linsley and Cazier (1972). Twelve nests, all under or near vegetation, were discovered at the site. Several were dug into the side of a vertical rodent burrow near its entrance; others were under overhanging branches of a squaw bush (*Condalya spatulata*) or near the base of clumps of a dried weed, peppergrass (*Lepidium montanum*). The results of observations of females at these nests from 18-26 July 1973 are presented below.

RESULTS

Activity at the nest.—The first activity of the day consisted of working within the burrow (presumably lengthening the main tunnel and adding cells) and removing the soil which accumulated inside the nest. Individual wasps were first seen at the entrance of their nest between 0815 and 1005 hr (10 records); females flew from their burrows after an average of 45 min of nest digging (seven records; range, 15-126 min). Nest provisioning began in midmorning (earliest record, 1010 hr) and continued through the afternoon (latest record, 1630 hr). In the late afternoon females entered their burrows and remained there throughout the night.

Burrow design.—Figure 1 shows the outline of a typical nest which initially descends gradually, then becomes steeper before leveling out 25-30 cm below the surface. The total length of the main shaft could reach 62 cm. Invariably, the burrow made one and usually several sharp, nearly right-angle turns during its descent ($\overline{X}$=3.8 turns; range 1-6; N=6 burrows). Judging from one case, the wasp first digs a shaft of about 35 cm long and then begins to collect bees which are stored at the end of the burrow. When she has gathered enough to fill a cell (11 in one fully provisioned cell with a small larva), she then must lengthen the burrow and build side branches leading to a cell (or cells). These side branches were short (roughly 5 cm) and the cells (N=5) were constructed at depths of 25-35 cm.

Prey taken.—This species apparently takes small (5 mm) halictids exclusively (Table 1). Interestingly, all the *Sphecodes* were captured by the same female.

Hunting females frequented a strip of Russian thistle (*Salsola kali*) at the edge of the road, perhaps 50 m from the nesting site. The weed attracted numerous bees and wasps, among them the prey of *P. multimaculatus.* The females, which also stopped to take nectar at intervals during foraging, flew slowly around and through the plants 2-15 cm above the ground. They oriented to and approached almost any moving insect, including flies and Lycaenid butterflies and were observed striking many nonprey species including ants and other Hymenoptera as large or larger than themselves. For example, one individual darted at and struck a moderate-sized *Ammophila* three times its own size. Females approached within 5 cm of small halictids at Russian thistle flowers and, after a brief hover, rushed straight forward striking and grasping the bee (two misses and five captures were seen). Upon falling to the ground, the wasp manipulated its prey, stung it, and then flew to its burrow while holding the prey head forward, venter up, with its middle legs. I did not see a female of this species strike a conspecific while hunting, unlike the case of *P. crabroniformis* (Alcock, 1974). On 26 July, when I concentrated specifically on this, I observed a foraging female come within 5 cm of another on nine occasions. Three times one wasp oriented to the other; on six encounters, the two individuals ignored each other.

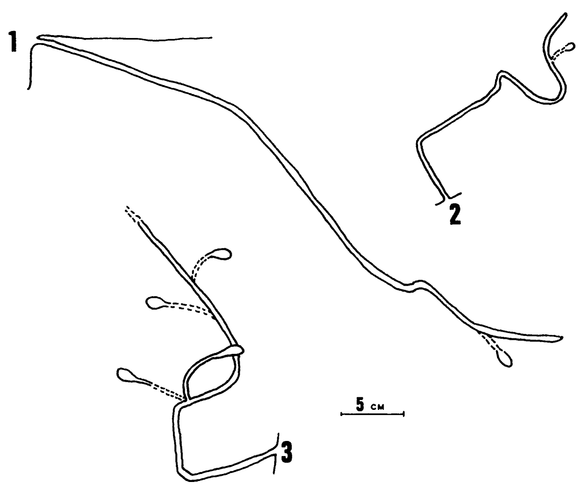

Fig. 1.—Diagram of the nest of *P. multimaculatus.* (1) A view from the side of one nest. (2) A view from above the same nest (not drawn to scale). (3) A view from above a second nest showing sharp right angle turns in the main burrow

TABLE 1.—The prey of *Philanthus multimaculatus* at Portal, Arizona

Halictidae	♀♀	♂♂
Halictus tripartitus Cockerell	5	..
Dialictus pruinosiforme (Crawford)	8	..
D. perparvum (Ellis)	9	..
D. clematisellum (Ellis)	1	..
D. sp. 1	1	1
Sphecodes spp.	3	..
S. sp. 1	..	1
S. sp. 2	..	1

Wasps provisioned their nests fairly rapidly. The intervals between provisioning trips averaged a little more than 12 min (21 intervals; range 4-30 min).

The approach to the nest.—An interesting feature of *Philanthus* behavior is the final approach to the nest, which in most species is highly distinctive. *P. multimaculatus* flew rapidly toward the burrow on a horizontal path some 50-100 cm above the ground. This flight was usually terminated by a dive downward with the wasp suddenly alighting and freezing (the "freeze-stop") for as much as 30 sec on a perch 15-50 cm high in a bush or weed (16 observations). Once a female landed on a small pebble on the ground, and three times a wasp made her first stop at a height greater than 50 cm. In all these cases the female was no more than 1 m from its burrow entrance. On an additional six occasions a female was believed not to have alighted at all but to have continued directly from the downward dive to the nest entrance. Those wasps that did "freeze-stop" eventually left their perch and flew somewhat more slowly down to within a few cm of the ground before proceeding forward to the nest. Six times a prey-laden female made another abrupt stop, usually within 10 cm of the entrance, before entering. The burrow was sometimes, but not always, left unclosed. If open, the returning female could enter her nest very quickly.

A combination of factors (the rapid flight to the vicinity of the nest, the "freeze-stop" often followed by a vertical descent through foliage to a partly concealed entrance, and often a quick dash into an open burrow with no removal of an external closure) gave the approach of provisioning females a stealthy and secretive appearance to a human observer, and made location of nests difficult.

The response to miltogrammine flies.—Satellite flies (probably *Senotainia trilineata* Wulp), which follow prey-laden digger wasps and attempt to larviposit on the prey as the wasp enters her burrow, were common at the site. On 21 July when special attention was devoted to this matter, females were pursued by a parasite on nine of 17 provisioning trips, and on three occasions (18%) the fly appeared to make contact with the prey as the wasp reached her burrow entrance. *P. multimaculatus* usually responded to the presence of a pursuer. The wasps employed a variety of strategies (frequently more than one on the same provisioning trip) apparently designed to rid themselves of parasites:

(a) No response—one record; (b) slow flight a few cm above the ground directed away from the nest entrance with one or more "freeze-stops" on foliage before returning to the nest—six records; (c) initially a slow flight a few cm above the ground but with noticeable changes in flight speed; instead of using "freeze-stops" the female usually darts around a weed or bush before returning to the nest—six records; (d) moderately rapid and erratic flight taking the wasp well away from the nest; the female does not return for a minute or more—three records; (e) wasp flies upwards and into the wind reaching a height of 2-6 m before turning and flying very rapidly downwind; wasp returns to the nest after an absence of about 1 min —2 records.

The adaptive significance of responses (c), (d) and (e) seems obvious enough; the wasp acts in ways that make it difficult for a pursuer to remain in visual contact with it. Response (b) is another matter because the slow, low-flying female does not attempt to elude a trailing parasite. This behavior is essentially identical to the primary approach pattern of *P. crabroniformis*

(Evans, 1970; Fig. 2). Unlike *P. multimaculatus,* this species makes no special effort to slip into its nest unnoticed, perhaps because it nests in relatively open areas with sparse vegetation. Evans (1970) and I (1974) have seen parasites, waiting on the ground behind a "frozen" *P. crabroniformis,* leave to pursue another wasp that happened to fly by at this time. Thus, response (b) may take advantage of the possibility that a satellite fly will be distracted by other members of a nesting aggregation.

DISCUSSION

The behavior of female *P. multimaculatus* is similar in almost every respect to that of other members of the genus (Evans and Lin, 1959; Evans, 1970). Perhaps the single most distinctive aspect of the wasp's behavior is its approach to the nest with prey (Fig. 2). It is probable that for all species of *Philanthus* the manner in which prey-laden females return to the nest helps thwart attempts of satellite flies to detect and follow them (Evans, 1970; Alcock, 1974). For example, the rapid and secretive initial approach of *P. multimaculatus* may reduce the chance that a female will be spotted by her enemies. However, the question arises, why should there be such diversity in the approach patterns of *Philanthus.* Elsewhere (Alcock, 1974), I have speculated that if several species are provisioning at the same time in the same general area, then divergence in approach flights might enhance the antiparasite effectiveness of the behavior. It should be difficult for a satellite fly to scan all the areas utilized by different species returning to their nests in a mixed species aggregation. By coming to the nesting area in many different ways the wasps may force their parasites to inspect a limited approach zone used by only one or a few of the nesting species present or to attempt to examine all possible avenues of entry. Either way individuals are likely to benefit from reduced parasite pressure. If this argument is correst, then selection should favor divergence in the approach patterns of digger wasps. Certainly this seems to be the case for the species of *Philanthus* (Fig. 2) which frequently nest in aggregations containing two or more members of their genus (Alcock, 1974; Cazier and Mortenson, 1965; Evans, 1970).

One would not predict similar divergence in the strategies designed to free a pursued wasp from a trailing parasite. Once a female has been detected and followed, there can be little advantage in possessing a species-specific escape pattern. Instead, one might expect behavioral convergence with different species evolving the same few best techniques to elude satellite flies. Although there is little evidence on this issue, five species (*P. multimaculatus, P. crabroniformis, P. zebratus, P. lepidus* and *P. gibbosus*) which have been studied in some detail share one basic response to being followed (the low flight away from the nest entrance with erratic changes of speed and direction). In addition, the first three of these fly rather slowly upward and then dive rapidly downward in an attempt to leave a pursuer behind. However, more information on escape strategies is required before reasonably firm conclusions can be drawn on the degree of convergence or divergence among species with respect to this behavior. At the moment, comparative data suggest that selection may have acted in opposite ways on the evolution of approach patterns and escape flights in the genus *Philanthus.*

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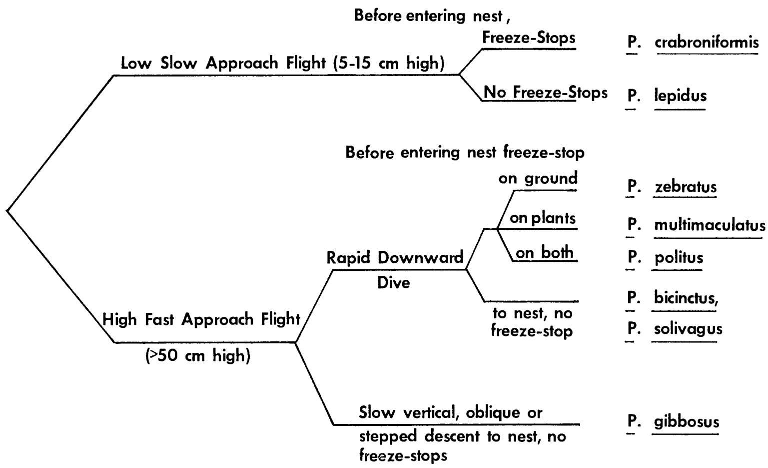

Fig. 2.—A chart of the diversity in approach flights exhibited by various species of *Philanthus*. Data from Evans (1970, 1964), this paper, Evans and Lin (1959), Powell and Chemsak (1959), Armitage (1965), Cazier and Mortenson (1965), Reinhard (1924) and personal observations

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