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NESTING BEHAVIOR OF *PHILANTHUS SANBORNII* IN FLORIDA (HYMENOPTERA: SPHECIDAE)

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ABSTRACT

The activities of an aggregation of *Philanthus sanbornii* were studied at the Archbold Biological Station, Lake Placid, FL. Females sat head outward in the entrances, investigated conspecific nests, grappled near entrances, removed sand from their burrows, captured honey bees in front of hives, and flew with prey to their nests. *Apis mellifera* (Apidae) workers and *Colletes brimleyi* (Colletidae) males comprised 20 and 24 of 49 prey, respectively, with the remainder being a *C. brimleyi* female, Halictidae, Megachilidae and Anthophoridae. Three long, deep unfinished nests contained terminal storage chambers and from 3 to 8 rearing cells. From 4 to 9 bees, usually of 2 or 3 families, were stored in a cell. The bees were totally or nearly devoid of pollen and some had presumably been cleaned

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by the wasps in the storage chambers or burrows. The wasp's egg was laid on a bee in the cell in the typical *Philanthus* position.

RESUMEN

Se estudiaron las actividades de un agregado do *Philanthus sanbornii* en la Estación Biologica "Archbold", Lake Placid, FL. Las hembras se quedaban en las entradas con las cabezas hacía afuera, investigaban los nidos conespecíficos, luchaban cerca de las entradas, removían arena de sus madrigueras, capturaban abejas meliferas en frente de sus colmenas, y volaban con sus presas a sus nidos. De 49 presas, 20 eran obreros de *Apis mellifera* (Apidae) y 24 eran machos de *Colletes brimleyi* (Colletidae). El resto incluían una hembra de *C. brimleyi*, y especies de Halictidae, Megachilidae y Anthophoridae. Tres nidos largos y profundos contenían camaras de abastecimiento terminales y desde 3 hasta 8 celdas de crianza. Se guardaban en una celda desde 4 hasta 9 abejas, usualmente de 2 o 3 familias. Las abejas eran totalmente o casi desprovistas de polen y algunas presumiblemente habían sido limpiadas por las avispas en las madrigueras o en las celdas. El huevo de la avispa fue ovipositado en la abeja en la posicion tipica de *Philanthus*.

Species of *Philanthus* have served as subjects for studies of comparative and experimental behavior for nearly a century. The Peckhams (1898, 1905) and the Raus (1918) devoted sections of their books on solitary wasps to this genus. Some of N. Tinbergen's (1932, 1935) pioneering studies in animal orientation focused on the "beewolf," *Philanthus triangulum* (F.). More recently, significant papers on the nesting behaviors of some of the species have been published by Alcock (1974, 1975), Armitage (1965), Evans (1964, 1966, 1970, 1973, 1975), Evans and Lin (1959), Powell and Chemsak (1959), Gwynne (1981), and Simon Thomas and Simon Thomas (1972).

Philanthus sanbornii Cresson received little attention in these studies. Evans and Lin (1959) reported briefly on this species (as *P. eurynome* Fox) nesting in Florida and preying upon *Apis mellifera* L. workers. Evans (1955) noted honey bees and halictids as prey of *P. sanbornii* in Kansas. The purpose of our paper is to describe in detail some components of the nesting behavior of this species in order to expand the biological knowledge of species in this genus.

Our studies were made at the Archbold Biological Station, Lake Placid, FL, during 16-29 April 1973. About 35 nests of *P. sanbornii* occupied the main east-west firetrail of the Station. Individual nests were situated in the slopes of loose sand on the periphery of a red clay car path running through the center and the flat, loose, wind-blown sand of the lateral expanses of the firetrail.

Females spent much time removing sand from their burrows, sitting head outward in the entrances, and investigating conspecific nests. One male was collected in front of an entrance but males never entered female nests.

Fighting between females of *P. sanbornii* occurred inside and in front of entrances. A female entering another's burrow was often driven backwards out of the nest, after which a period of grappling on the sand near the entrance took place. Skirmishes between conspecific females sometimes

occurred when a female, backing out of her nest removing sand, was pounced upon by another female. The resident would shake off the intruder, turn to face her, and then the pair would grapple with the mandibles and forelegs. The resident would drive away the intruder and continue to remove sand from the burrow.

Prey capture by females of *P. sanbornii* in front of honey bee hives was observed 3 times. Wasps flew back and forth in front of the several-tiered hives which were located about 40 meters from the *Philanthus* aggregation. Periodically, females flew at worker honey bees as they left their hives. Prey capture involved the wasp pouncing upon the smaller bee in flight followed by the pair falling to the ground. The wasp then stung the bee in the underside of the thorax, released it on the sand, cleaned and groomed herself, and repositioned the prey prior to transport to the nest. We did not observe any wasps taking fluids from the bees at this time. Not all honey bees were captured as they left their hives since we collected provisioning females carrying workers of *Apis mellifera* that still had much pollen on the corbiculae of the hindlegs.

In addition to worker honey bees, which comprised 40% of the prey, we recovered a variety of solitary bees from the nests and provisioning females of *P. sanbornii* as follows: COLLETIDAE: *Colletes brimleyi* Mitchell, 1 ♀, 24 ♂; HALICTIDAE: *Augochloropsis metallica* (Fabricius), 1 ♀; MEGACHILIDAE: *Megachile mendica* Cresson, 1 ♀; and, ANTHOPHORIDAE: *Epeolus zonatus* Smith, 1 ♀, 1 ♂.

Prey transport involved the wasp holding the bee ventral side upward and head forward in flight with the middle legs. Entry into the open nest was rapid; however, many females circled the entrance several times at some distance before entering. Occasionally, the wasp made a false entry by turning away from the entrance at the last second and flying off. One female was prevented from entering her nest by a conspecific female which had entered the burrow several seconds earlier, but other wasps turned away without such intrusion. In the former case, the provisioning female released the prey in front of the entrance and grappled with the other female for nearly one minute before driving her away.

Provisioning females of *P. sanbornii* spent from 11 to 77 ($\bar{x}$ = 29.2; N = 18) minutes between consecutive returns to the nest. Such wasps reappeared head first in their entrances from 3 to 17 ($\bar{x}$ = 6.5) minutes after taking their prey inside, and remained stationed with the head in the entrance for an additional 0.5 to 8 ($\bar{x}$ = 3.9) minutes before leaving. The longest periods of time spent inside nests occurred during the morning hours at low temperatures and during periods of human interference. The wasps performed 3-75 sec orientation flights above the entrances after exiting. These flights varied from simple aerial twists to extensive, rather symmetrical arcs and circles. The most extensive orientation flight followed a period of sand removal from the burrow. Two wasps each did not orient following an exit.

Females brought prey to their nests between 1057 and 1653 h (EST) on bright, sunny and slightly overcast days. One wasp abandoned her prey on the sand during a brief period of rainfall. Four females with prey and one wasp without prey returned to their nests between 1620 and 1657 h, entered, and closed themselves inside by plugging the entrances with sand.

The construction of additional cells and the periodic removal of sand

from the nests were observed commonly between 0835 and 1545 h with morning and late afternoon peaks in activity. Females brought sand up their burrows by backing out and raking it backward with the forelegs. Some leveling of the tumulus in front of the entrance took place at this time, despite the fact that females made no temporary closure. The minimum and maximum times expended for sand removal and tumulus leveling were 25 and 85 minutes ($\bar{x}$ = 56; N = 6) per cell.

Tumuli in front of active entrances averaged 19.0 cm long and 13.7 cm wide (range = 11-26 x 8-17 cm; N = 7). The non-circular entrances, averaging 10.2 (9-15) mm high and 16.7 (12-25) mm wide, were situated off-center in depressions 5-8 ($\bar{x}$= 6.4) cm long, 3-12 ($\bar{x}$ = 6.6) cm wide, and 2-5 ($\bar{x}$ = 3.6) cm deep (N = 7). The depressions were the result of the female's digging and leveling activities.

The burrows, 8 mm in diameter, entered the sand at angles of 25-60° to the surface for 8-14 cm and then plunged almost vertically with an occasional undulation for 55-80 cm before coursing, more or less, horizontally for an additional 40-58 cm (Fig. 1). Burrows ranged from 132 to 152 ($\bar{x}$ = 144, N = 3) cm in total length from entrance to storage cell. In 2 nests we found enlarged, ovoidal storage chambers at the ends of the burrows at depths of 74 and 77 cm beneath the sand surface. The rearing cells were unearthed at depths of from 77 to 85 ($\bar{x}$ = 81.7; N = 15) cm beneath the surface. The number of cells in 3 unfinished nests ranged from 3 to 8. The cells themselves averaged 28 (26-31) mm long and 15 (12-20) mm high. In 2 nests the deeper cells contained larvae and the shallower cells eggs, indicating that the latter were made and provisioned last (Fig. 1).

We found as many as 9 bees, including both cleptoparasitic and nesting species, in a storage cell. The rearing cells contained from 4 to 9 ($\bar{x}$ = 7.0; N = 15) bees, usually of 2 or 3 families. Cells containing fewer bees held more *Apis mellifera*, whereas cells with 8 or 9 prey contained no *A. mellifera*. The individual weights of 36 bees ranged from 19.4 (*Colletes brimleyi*) to 94.0 mg (*Apis mellifera*). One female wasp weighed 134 mg. The total weight of the bees in a single cell ranged from 241 to 465 ($\bar{x}$ = 314; N = 4) mg.

The bees were placed in the cells in a mostly head inward and ventral side upward position. The corbiculae of the worker honey bees and the bodies of the other provisioning bees in the cells were devoid or nearly devoid of pollen. Yet 2 *A. mellifera* workers collected from provisioning females at the nest entrance had a considerable amount of pollen on the corbiculae; and, one female of *Colletes brimleyi* collected from a wasp prior to nest entry had much pollen on the body. We believe the wasp cleans the bees and then seals off the pollen at the end of a deep, short side passage. We unearthed a solid ball of pollen several cm from the end of the storage chamber; the surrounding sand was loose and moist but we could not find evidence of a tunnel connected to the main burrow.

The egg-bearing bee was invariably positioned head inward and ventral side upward, either at the bottom of the cell near the middle (N = 2) or at the end (1). In 2 cells the egg-bearing bee (*Colletes brimleyi*) was the smallest prey, weighing 33.0 and 33.6 mg. The eggs attached to these bees measured 4.3 x 1.1 and 4.8 x 1.3 mm in length and diameter. They were affixed behind the forecoxae and extended longitudinally backward either down the midline or slightly to one side between the bases of the legs, as

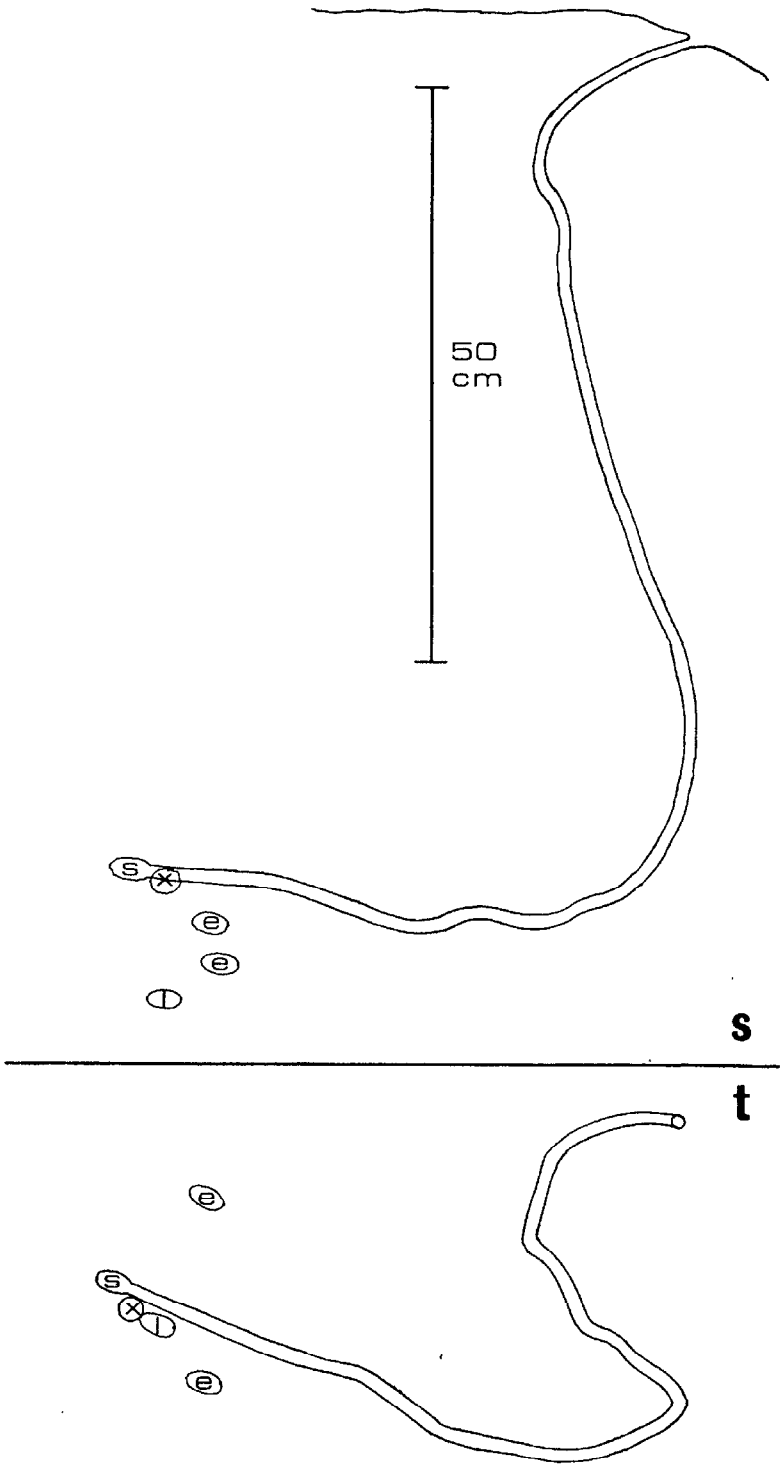

Fig. 1. Side (S) and top (T) views of nest of *Philanthus sanbornii*, showing burrow, storage chamber (s) and rearing cells containing eggs (e), larva (1) and moldy contents (x). Scale beside side view refers to both views.

shown in Fig. 8, 9 in Evans and Lin (1959). The eggs were hyaline at the ends and rather straight.

Discussion

Philanthus sanbornii Cresson is one of 3 Nearctic species known to prey upon worker honey bees, the others being *P. crabroniformis* Smith (Bohart 1954, reported as *P. flavifrons* Cresson) and *P. bicinctus* Mickel (Gwynne 1981). In the last 2 species honey bees comprised unusual prey, but in *P. sanbornii* they were common provender. Evans (1955) observed several females of *P. sanbornii* provisioning nests with worker honey bees and, less commonly, other bees in Kansas. Evans and Lin (1959) reported workers of *Apis mellifera* being used exclusively in nests of *P. sanbornii* in Florida. Working at the same locality we found 40% worker honey bees in nests of *P. sanbornii* in addition to a high proportion of *Colletes brimleyi* (Colletidae) males, and, rarely, *C. brimleyi* females, Halictidae, Megachilidae or Anthophoridae. Such euryphagous provisioning behavior with concentration on one or a few groups of bees characterizes the majority of species of *Philanthus*.

In *P. sanbornii* the species, sex, and behavior of the prey and amount of pollen adhering to the body of the bee indicate that prey capture may have taken place as the bees collected pollen, as they rested on the ground, or as males patrolled female nesting sites (G.C. Eickwort pers. comm.). Tinbergen (1935), Armitage (1965) and Evans (1966) reported the capture of bees on flowers by *P. triangulum, P. bicinctus* and *P. pulcher* Dalla Torre, respectively, and many other species of *Philanthus* are believed to hunt and capture their prey on flowers. We observed the capture of worker honey bees by *P. sanbornii* in front of their hives as they exited to go in search of food. The capture of honey bees near their hives, even on the alighting board, was noted for *P. triangulum* by Simon Thomas and Simon Thomas (1980), who associated such captures with the relative lack of flowers near the wasps' nests.

Frequent bouts of grappling between conspecific females of *P. sanbornii* were seen in the entrances and on the tumuli in front of the entrances. Attempted takeover of conspecific nests has been reported in *P. crabroniformis* (Alcock 1974) and *P. bicinctus* (Gwynne 1981), and temporary communal nesting has been documented in *P. gibbosus* (F.) (Evans 1973). Whether there is a relationship between attempted nest takeover and temporary communal nesting or parasitizing a conspecifics' efforts in species of *Philanthus* has not been ascertained.

Females of *P. sanbornii* partly level the tumulus in front of the entrance but do not close the opening with sand when they go in search of prey. There is no clear-cut correlation between mound-leveling and whether or not a temporary closure is made in species of *Philanthus*. For example, *P. crabroniformis* and *P. albopilosus* Cresson irregularly or partly level the tumulus (Evans 1970, 1975) and *P. lepidus* Cresson and *P. zebratus* Cresson do not level the mound (Evans 1964, 1966), but all 4 species make a thorough temporary closure.

Two nests of *P. sanbornii* had the first cells built deeper and later cells shallower, as indicated by the stages of the wasps in the cells (Fig. 1). This arrangement agrees with that of *P. zebratus* in which 2 cells farthest from the burrow in one nest were built first and cells closer to the burrow

later (Evans 1966). Other species of Nearctic *Philanthus* construct cells nearest the entrance first and those farthest from the entrance last (Alcock 1974, 1975, Evans 1966, 1970, 1973, Gwynne 1981, Rau and Rau 1918).

No mention has been made in the Nearctic literature of species of *Philanthus* removing pollen from the bodies of the bees, i.e., cleaning the prey; yet all of the worker honey bees in the storage chambers and cells of *P. sanbornii* had the corbiculae of the hind legs devoid of pollen, and the other nesting bees in the cells were especially clean.

P. sanbornii is similar to some other species of *Philanthus* in its nesting aggregation, manner or burrow construction and orientation flight, length of time spent inside the nest, method of prey transport and provisioning flight, degree of prey paralysis, placement of prey in storage and rearing cells, position of egg on prey and low rate or lack of parasitism. The nests of *P. sanbornii* are longer and deeper than those of other Nearctic *Philanthus* which correlates with it being a large species; likewise the prey of this species, especially *Apis mellifera*, are large. In addition, the numerous aggressive encounters between conspecific females, lack of false burrows and temporary closure, partial tumulus leveling and cleaning pollen off the prey should further serve to separate *P. sanbornii* ethologically from other Nearctic *Philanthus*. Future avenues of research on the behavior of this species should focus on individual recognition of conspecifics, foraging behavior of hunting wasps, and the functions of continual nest visitation, aggressive encounters between females and removal of pollen from the prey.

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