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 Anthophoridace. 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 de Philanthus sanbornii
en la Estación Biológica "Archbold", Lake Placid, FL. Las hembras se
quedaban en las entradas con las cabezas hacia afuera, investigaban los
nidos con especímenes, luchaban cerca de las entradas, removían arena de sus
madrigueras, capturaban abejas mellíferas 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, Mega-
chilidae y Anthophoridae. Tres nidos largos y profundos contenían camarás
de abastecimiento terminales y desde 3 hasta 8 celdas de crianza. Se guardaba
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 ovipositalo en la abeja en la posición
típica 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),
Chemsak (1969), 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 ex-
pances 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 back-
wards 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 zones 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 (x = 29.2; N = 18) minutes between consecutive returns to the nest. Such wasps reappeared head first in their entrances from 3 to 17 (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 (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 mini-
imum 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 18.7 cm
wide (range = 11-26 x 8-17 cm; N = 7). The non-circular entrances, aver-
aging 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, hori-
zontally 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 bur-
rows 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 26 (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 (\( \bar{x} = 7.0; 
N = 18 \)) 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. mel-
li*fera. 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 provisionizing bees in the cells were devoid or nearly de-
void of pollen. Yet 2 *A. mellifera* workers collected from provisioning fe-
males 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 (l) and moldy contents (x). Scale beside side view refers to both views.
shown in Fig. 8, 9 in Evans and Lin (1969). 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. crbroniformis* 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, IIalictidae, 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. crbroniformis* (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 conspecific's 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. crbroniformis* and *P. albopilosus* Cresson irregularly or partly level the tumulus (Evans 1970, 1973) 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 furthest from the burrow in one nest were built first and cells closer to the burrow

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.

ACKNOWLEDGMENTS

We thank the late Richard Archbold and his staff, particularly James Lane, for providing the excellent facilities of the Archbold Biological Station, Lake Placid, FL, where our study was made. We are indebted to Howard E. Evans, Colorado State University, for critically reading the manuscript, and George C. Eickwort, Cornell University, for determining the solitary bees used as prey and for providing information about their possible capture sites.

REFERENCES CITED


