

**Biology of *Trypoxylon (Trypargilum) superbum*  
(Hymenoptera: Sphecidae), a Spider-hunting Wasp with  
Extended Guarding of the Brood by Males**

ROLLIN E. COVILLE AND CHARLES GRISWOLD<sup>1</sup>  
Division of Entomology and Parasitology, 201 Wellman Hall,  
University of California, Berkeley, California 94720

**ABSTRACT:** *Trypoxylon (Trypargilum) superbum fulvipes* (Cameron), a sphecid spider-hunting wasp, was studied at the Organization for Tropical Studies' field station at La Selva, Costa Rica. The wasps nested in trap-nests with 9.5 ( $N = 4$ ) and 6.4 ( $N = 22$ ) mm  $\times$  15.5 cm tubes. Nests consisted of a linear series of brood cells ( $\bar{x} = 9.5$  in 9.5 mm diameter nests, and  $\bar{x} = 8.3$  in 6.4 mm diameter nests) separated by thin mud partitions. Unlike nests of other *Trypargilum*, there were no thick final closure plugs and no vestibular cells. Male and female cells were generally segregated with male cells placed at the inner end of nesting tubes and female cells close to the entrance. The sex ratio based upon reared specimens was male-biased, especially in 6.4 mm diameter nests (9♂♂:2♀♀). Upon completing the last brood cell, females departed, but the males continued guarding nests until all larvae had made cocoons. Nest structure, cocoon morphology, and male behavior are discussed regarding their possible role as an adaptation against ant predation. Brood cells were provisioned primarily with spiders of the family Salticidae, but also small numbers of Ctenidae, Oxyopidae, and Araneidae. Natural enemies of *T. superbum* include *Brachymeria* sp. (Hymenoptera; Chalcididae) and *Phalacrotophora punctiapex* Borgmeier (Diptera; Phoridae).

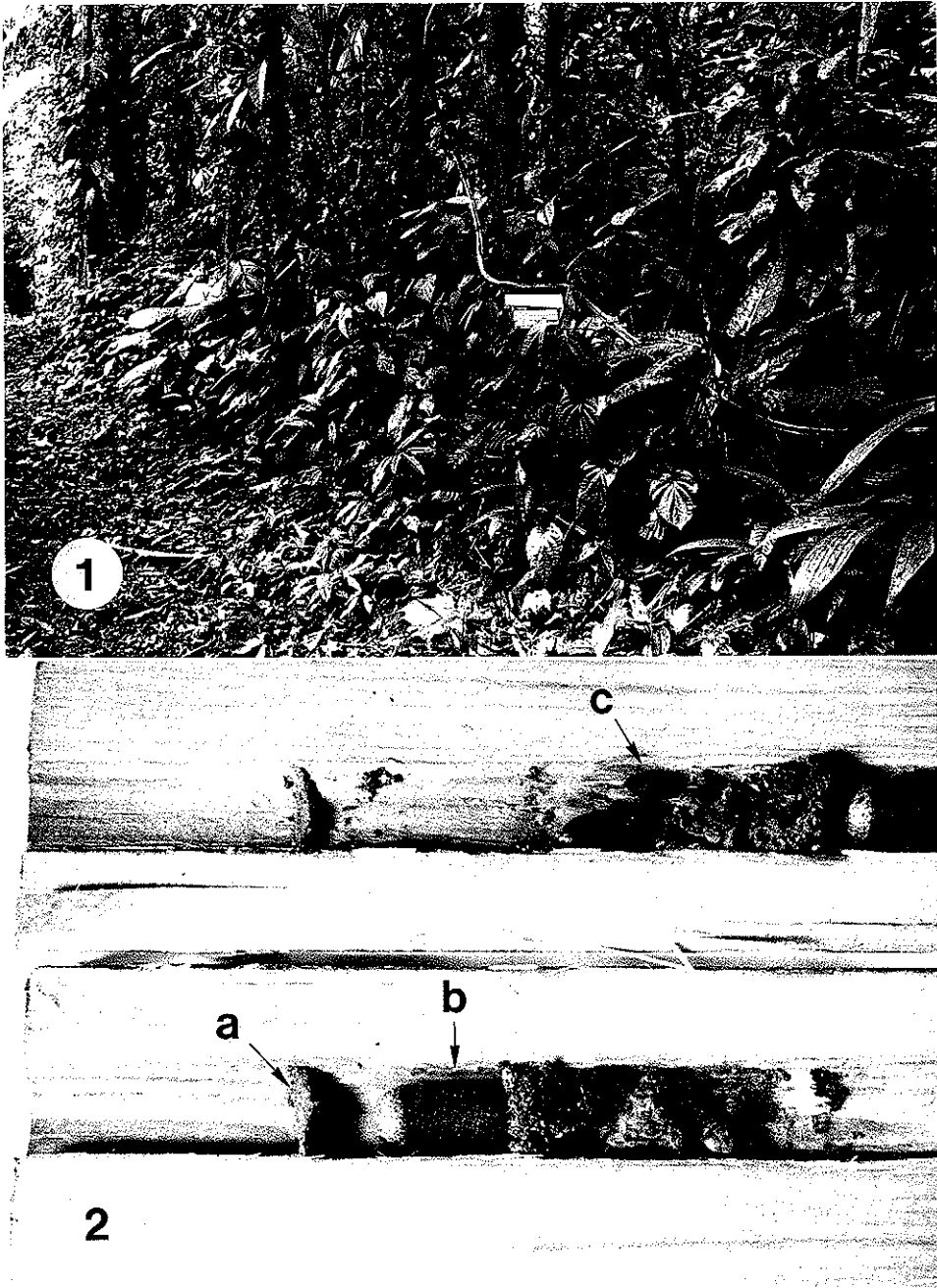
The solitary spider-hunting wasp, *Trypoxylon (Trypargilum) superbum* Smith, is a widespread polytypic species in the Neotropics (Coville, 1982; Richards, 1934). Richards (1934) recognized three subspecies (varieties) because of differences in color pattern: *fulvipes* (Cameron) based on 2♂♂, 3♀♀ from Panama; *superbum* Smith based on 5♀♀ from the Amazon Basin in Brazil; and *superciliosum* Richards based on 1♂ from Corioco, Bolivia. Coville (1982) reported another color pattern in 1♀ from the state of Veracruz, Mexico. Richards (1934) placed *T. superbum* in the *superbum* species group, comprised of distinctive Neotropical species that possess a transverse carina on the frons below the median ocellus. Of the 3 species groups of *Trypoxylon* subgenus *Trypargilum* (*albitarse*, *nitidum* and *superbum* groups), the *superbum* group is the least known taxonomically and biologically. This paper reports the first observations on nests, spider prey, cocoons, and enemies of *T. superbum fulvipes*.

#### Study Sites

A trap-nest survey was conducted in 1980 and 1981 in the Atlantic lowlands of Costa Rica at the Organization for Tropical Studies research station at La Selva, near Puerto Viejo de Sarapiquí, Heredia Prov. (see Coville and Griswold, 1983). Nests of *T. superbum* were obtained in several habitats described below.

**SUCCESSIONAL STRIPS:** Trap-nest bundles were placed along the edge of newly cut strips bordering an abandoned cacao plantation in 1980; the cut strips bordered lowland tropical rainforest in 1981 (see Fig. 1 in Coville and Griswold, 1983).

<sup>1</sup> Present address: Dept. of Arachnology, Natal Museum, Pietermaritzburg, 3201 Natal, South Africa.  
Accepted for publication 18 July 1983.



Figs. 1, 2. 1. Trap-nest bundle, that produced a nest of *Trypoxylon superbum*, on the Holdridge Trail at La Selva. 2. Outer end of a nest of *T. superbum* in an opened trap-nest showing (a) the thin, recessed outer cell partition that separates the last brood cell from the outside, (b) a cocoon of *T. superbum*, and (c) one of several puparia of *Phalacrotophora* whose maggots destroyed the second cell from the entrance (on right side of photo).

Table 1. Summary of trap-nest study at La Selva during 1980 and 1981 at locations frequented by *Trypoxylon superbum*.

Location	No. of trap-nest bundles	Bundle configuration <sup>a</sup>	Date bundles set out	Date study ended	No. of bundles with <i>T. superbum</i> nests	No. of <i>T. superbum</i> nests
Successional strips	5	1	9-II-80	5-IV-80	0	0
	10	1	30-VII-80	13-IX-80	1	2
	10	2	4-IX-81	22-X-81	2	2
Arboretum	13-15	1	12/13-IV-80	13-IX-80	5	9
	20	2	3-IX-81	24-X-81	4	4
	4	3	9-IX-81	24-X-81	0	0
Holdridge Trail	10	2	5-IX-81	22-X-81	1	1
Rafael's House	5	3	5-IX-81	22-X-81	2	3
West River Road	15	3	7-IX-81	22-X-81	3	5

<sup>a</sup> In configuration 1, bundles contained one 9.5, two 6.4, two 4.8, and two 3.2 mm diameter trap-nests. In configuration 2, bundles contained two each of 11.0, 9.5, 8.0, 6.4, 4.8, and 3.2 mm diameter trap-nests. In configuration 3, bundles had one each of 11.0, 9.5, 8.0, 6.4, 4.8, and 3.2 mm diameter trap-nests.

**ARBORETUM:** Trap-nest bundles were placed throughout a 3.5 ha arboretum surrounded by undisturbed lowland tropical rainforest and an abandoned cacao plantation (see Fig. 2 in Coville and Griswold, 1983).

**HOLDRIDGE TRAIL:** Trap-nest bundles were placed within 10 m to either side of a foot trail with 13-15 year old second growth on one side and lowland tropical rainforest on the other (Fig. 1).

**RAFAEL'S HOUSE:** Trap-nest bundles were placed in trees within and along the edge of the yard of a residence of the late Rafael Chavarria. The rectangular yard was bordered by the Rio Puerto Viejo, an abandoned pasture, an abandoned cacao plantation, and lowland tropical rainforest.

**WEST RIVER ROAD:** Trap-nest bundles were set out within 20 m to either side of the foot trail through an abandoned cacao plantation and a small section of lowland tropical rain-forest.

### Methods

Trap-nests were 2 × 2 × 16.5 cm blocks of straight-grain pine or fir, each with an 11.0, 9.5, 8.0, 6.4, or 4.8 mm × 15.5 cm hole drilled in it, and also 1 × 1 × 10-12 cm blocks, each with a 3.2 mm × 8.5 cm hole drilled in it. Trap-nests with different hole sizes were wired together and suspended from branches and trunks of trees generally 1-2 m above the ground, except 4 bundles in the arboretum suspended by fishline from branches 5-15 m above ground level. Bundles of trap-nests were checked 1-3 times per week. Configuration and distribution of bundles among the study sites are summarized in Table 1. More detail on trap-nesting and rearing techniques used in the study is provided by Coville and Griswold (1983). Voucher specimens of the wasps, prey, and enemies are in the collection of the Essig Museum of Entomology, Department of Entomological Sciences, University of California, Berkeley, CA.

### Results

Our rearing of wasps from trap-nests revealed that in addition to *T. superbum* an undescribed species in the *superbum* group also occurs at La Selva. The undescribed species is similar to *T. superbum* in all aspects of its biology. Several nests from which no adults were reared could not be assigned to either species. Therefore, this paper is based only upon nests from which adults of *T. superbum* were collected, or reared.

During the day, males of *T. superbum* guarded nests by stationing themselves face outward at the nest entrances. Each male apparently guarded his nest for up to a week or more after the female had left. When nests of other *Trypargilum* species are opened within 2 days after the wasps have left, cells closest to the entrance contain spider prey and wasp eggs or early 1st instar larvae (pers. obs.). We suspected that males of *T. superbum* were remaining at nests longer than males of other species, when several nests opened within 2 days of the males' departure were discovered to have cocoons in cells nearest the nest entrance.

Subsequently, we closely monitored 4 nests. After the same mud wall behind the male had been observed on 2 inspections separated by 2–4 days, the nests were collected and opened. Three nests had fully formed cocoons in the last cell and 1 had a well-developed feeding larva, indicating that females in all 4 nests had finished provisioning them several days before. Females of *T. superbum* usually constructed one nest in a bundle of trap-nests.

*Trypoxylon superbum* occupied 26 trap-nests in 18 bundles; 25 were from bundles placed 1–2 m above the ground and 1 was from a bundle placed 5 m above the ground. Table 1 presents the distribution of these nests and bundles among the study sites. Of the 26 nests 17 were completed, 7 were collected while they were still under construction, 1 was abandoned by wasps after ants had invaded the nest, and 1 had been abandoned for unknown reasons.

**NEST STRUCTURE:** Table 2 shows the trap-nest size preferences of *T. superbum*. In 1981, when equal numbers of all trap-nest sizes were used, *T. superbum* strongly preferred 6.4 mm diameter tubes (13) but also used 9.5 mm tubes (2). Intermediate 8.0 mm diameter tubes were ignored. Of the total 26 trap-nests occupied by *T. superbum* during the 1980–1981 study, 22 were in 6.4 mm tubes and 4 were in 9.5 mm tubes.

Wasps initiated nests by either depositing a small bit of mud at the inner end of the trap-nest tube or in 4 cases by constructing a mud wall or partition between 2.1 and 25.0 mm from the tube's inner end. A linear series of 7 to 10 brood cells were then constructed ( $\bar{x}$  = 8.3 in fifteen 6.4 mm-diameter tubes;  $\bar{x}$  = 9.5 in two 9.5 mm-diameter tubes). Wasps provisioned the cells with paralyzed spiders, oviposited, and then sealed the cell with a mud partition. The partition's inner surface forming the outer wall of the brood cell had a rough, bumpy, convex surface. The outer partition surface forming the inner wall of the next cell was smooth and concave. The cell partitions were fragile and crumbled when lightly probed or handled. One exceptional uncompleted nest had an empty 4.6 mm cell preceding the first brood cell and an empty 5.0–5.6 mm cell (intercalary cell) between each 2 of the 4 brood cells. In all but one completed nest the anterior partition of the last brood cell functioned as the closure plug (Fig. 2). In the exceptional nest a 6.8 mm-long empty cell (vestibular cell) was in front of the last brood cell; as in other nests, the closure plug was similar to a cell partition. Closure

Table 2. Trap-nest sizes used by *Trypoxylon superbum* at La Selva.

Year	Trap-nest diameter in mm					
	11.0	9.5	8.0	6.4	4.8	3.2
1980	x*	2	x	9	0	0
1981	0	2	0	13	0	0

\* Trap-nests with tube diameters of 11.0 and 8.0 mm were not used in 1980.

plugs were always recessed by 14.6–45.7 mm from the nest entrances. Table 3 summarizes the nest measurements.

ARRANGEMENT OF MALE AND FEMALE CELLS AND SEX RATIOS: In 6.4 mm nests the first 3 brood cells produced only males; females were produced in increasing proportion in cells closer to the entrance (Table 4). Because adults emerged in only two 9.5 mm nests, the pattern of male and female cell placement was not as clear. Nevertheless, female cells are probably placed closer to the inner end of the tube than in 6.4 mm nests, since 1 female did emerge from the second brood cell in one of the 9.5 mm nests. Male and female cells were usually segregated with 3–8 male cells at the inner end and 1–4 female cells close to the entrance. Male and female cells were mixed in only 2 of the 18 nests used to compile Table 4 and in 1 of the 9.5 mm nests.

In 1980 all nests produced 34♂♂ and 7♀♀; in 1981 they produced 43♂♂ and 16♀♀. Nests in 6.4 mm diameter tubes produced 72♂♂ and 16♀♀; nests in 9.5 mm tubes produced 9♂♂ and 7♀♀.

The sex ratio is strongly skewed toward males, especially in 6.4 mm nests, but probably not quite as much as the rearing data suggest. As mentioned above, female cells were generally situated closer to the nest entrance than male cells. Cells closest to the entrance were the best source of samples of spider prey. As a result the contents of the outer cells were preserved more frequently than the

Table 3. Dimensions of nests of *Trypoxylon superbum* in trap-nests. Measurements are in mm.

		Trap-nest diameter in mm	
		9.5	6.4
♀ cell length	range	11.1–15.9	14.0–20.3
	mean ( <i>N</i> )	13.3 (6)	16.8 (14) <sup>a</sup>
♂ cell length	range	11.3–12.7	11.1–19.5
	mean ( <i>N</i> )	12.1 (3)	14.2 (49)
Vestibular cell length	range	—	6.8
	mean ( <i>N</i> )	—	6.8 (1)
Cell partition thickness	range	0.7	0.4–0.9
	mean ( <i>N</i> )	0.7 (1)	0.7 (12)
Closure plug thickness	range	0.5	0.4–0.6
	mean ( <i>N</i> )	0.5 (1)	0.5 (8)
Distance from closure plug to entrance	range	32.0	14.6–45.7
	mean ( <i>N</i> )	32.0 (1)	23.1 (12)

<sup>a</sup> In 6.4 mm diameter tubes female cells were significantly longer than male cells ( $t = 4.67$ , d.f. = 61,  $P < 0.05$ ).

Table 4. Number of males and females of *T. superbum* reared and mortality in each cell position in 18 nests that began within 5 mm of the inner end of trap-nests 6.4 mm in diameter.

	Cell positions, numbered from the inner end of the nests										Totals
	1	2	3	4	5	6	7	8	9	10	
No. of cells	18	18	17	16	16	15	15	13	6	2	136
No. of males	17	16	10	8	9	5	2	1	1	0	69
No. of females	0	0	0	2	2	2	3	3	3	1	16
Losses <sup>a</sup>	1	2	7	6	5	8	10	9	2	1	51
Percentage losses	6	11	41	38	31	53	67	69	33	50	—
Estimated total no. of male cells <sup>b</sup>	18	18	17	13	13	11	6	3	1	0	100
Estimated total no. of female cells	0	0	0	3	3	4	9	10	5	2	36

<sup>a</sup> Losses include mortality from natural enemies, mold, preservation of cells, and undetermined mortality such as failure of eggs to hatch.

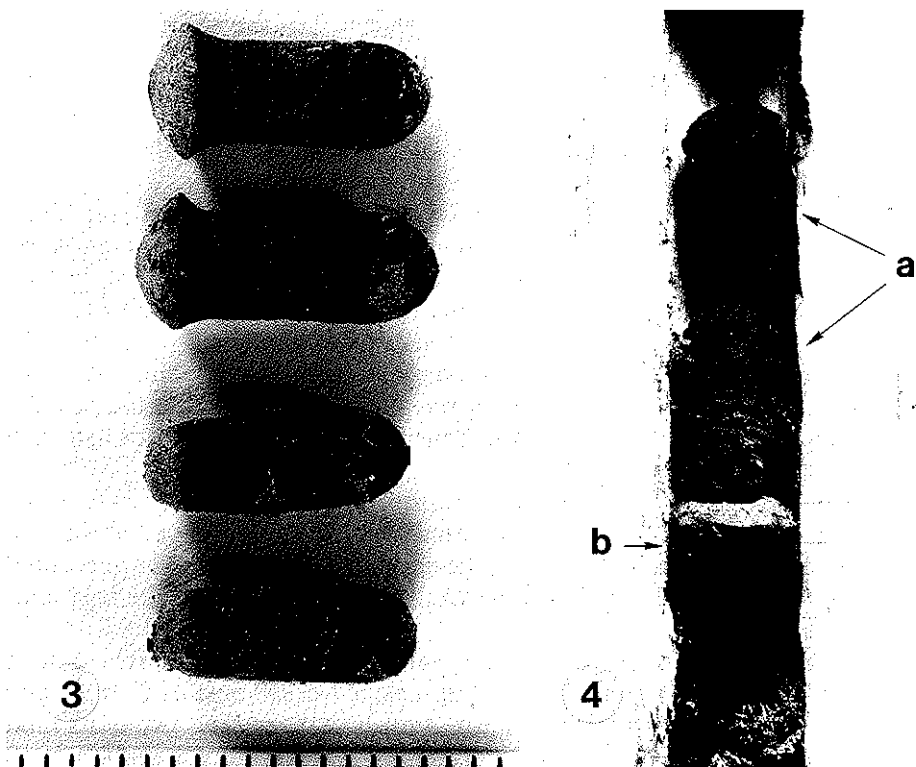
<sup>b</sup> This is an estimate of the number of males and females that would have been produced if no mortality occurred.

innermost cells. This produced a stronger male bias in the sex ratio, based upon offspring produced. Table 4 illustrates this effect upon 6.4 mm diameter nests. In these nests 69♂♂ and 16♀♀ were reared; males represented 81.2% of the offspring, and females 18.8%. If no mortality among the cells had occurred we estimated that 100♂♂ and 36♀♀ would have been reared with males representing 73.5% of the offspring and females 26.5%. There is a 7.7% difference between the proportion of males and females reared and the proportion estimated with the assumption of no larval mortality.

**LIFE HISTORY:** Little information was obtained on the length of the immature stages, because all larvae had completed feeding by the time most nests were collected. In other cases the spider provisions were preserved. Each cell was provisioned with 6 to 22 ( $N = 13$ ) paralyzed spiders. The pearl-white, sausage-shaped egg (about 2 mm long) was variably attached to a spider abdomen near the front of the provisions. Under cool laboratory conditions in 1981 (see Coville and Griswold, 1983) 3 wasps took approximately 63 to 72 days to develop from egg to adult.

**COCOONS:** Outside measurements of cocoons of *T. superbum* are in Table 5. Our subjective judgement was that the cocoons were the hardest of any *Trypargilum* species we have examined from North and Central America. Their color was dull, dark gray-brown with a coarsely granular, light gray anterior end. Their shape was variable. Thirteen of 14 measured female cocoons from 6.4 mm trap-nests were cylindrical with the posterior end rounded and the anterior end flaring outward (Fig. 3). In nests the expanded anterior ends of the cocoons blocked the tubes. All other male and female cocoons from 6.4 and 9.5 mm tubes were rounded at both ends but tapered slightly toward the anterior (Fig. 3). In cells containing cocoons only a few fragments usually remained of the inner cell partitions. The wasp larvae probably incorporate most of the mud from the partitions into their cocoons.

**MORTALITY AND NATURAL ENEMIES:** Twelve nests were opened after larvae and



Figs. 3, 4. 3. Two female (top) and two male (bottom) cocoons of *T. superbum* from a 6.4 mm diameter trap-nest. Note the outward flaring anterior ends (right) of the female cocoons. Scale at bottom is in mm increments. 4. Nest supersedure in which a pompilid wasp, *Auplopus* sp., made two of its mud brood pots (a) on top of a female cocoon of *T. superbum* (b) in a 6.4 mm diameter nest.

parasites had completed feeding. Adult wasps emerged from 52 of 91 provisioned cells in the nests; maggots of the phorid fly, *Phalacrotophora punctiapex* Borgmeier destroyed 11 cells (Fig. 2); a chalcid wasp, *Brachymeria* sp., emerged from a cocoon of *T. superbum* in 1 cell; moldy provisions were in 3 cells; and no emergence from cocoons was recorded in 24 cells. These last cocoons contained 23 dead, fully formed adults and 1 dead prepupa of *T. superbum*. There were in-

Table 5. Cocoon dimensions of *Trypoxylon superbum*. Measurements are in mm.

Nest diameter	Sex	Length		Width	
		Range	Mean (N)	Range	Mean (N)
6.4 mm	♂	8.5-11.6	10.7 (46)	3.1-4.4	3.8 (46)
	♀	11.4-12.7	12.0 (14) <sup>a</sup>	4.0-4.7	4.2 (14) <sup>a</sup>
9.5 mm	♂	10.6-11.3	11.0 (2)	4.1	4.1 (1)
	♀	11.3-12.8	12.2 (6)	4.1-4.9	4.6 (6)

<sup>a</sup> In 6.4 mm diameter nests female cocoons were significantly longer ( $t = 7.08$ , d.f. = 58,  $P < 0.05$ ) and wider ( $t = 5.68$ , d.f. = 58,  $P < 0.05$ ) than male cocoons.

sufficient data to determine if mortality was correlated to the position of cells in the nest.

Ants also invaded completed nests of *T. superbum* in the laboratory and in the field. Two recently completed nests of *T. superbum* in which the males had been removed were partially looted by ants in the laboratory. The vulnerability of unguarded nests is clearly apparent. However, in one of the nests ants had destroyed the 2 outermost cells and then invaded a cell containing a completed cocoon of *T. superbum*. The cocoon was undamaged. In another observation, an 8-celled nest was found to have had the 4 outer cells (5th–8th) destroyed by *Phalacrotophora* maggots. The maggots had moved further into the nest and formed their puparia in the 3rd and 4th cells, which contained cocoons of *T. superbum*. Ants (determined by type of damage and debris left behind) had later invaded the nest and destroyed the *Phalacrotophora* puparia. Again, the cocoons of *T. superbum* were undamaged, although their supporting silk threads had been severed.

Only one active nest of *T. superbum* was successfully attacked by ants in the field. On the day of attack the male and female wasps were observed at the nest in the morning. Many ants were raiding the nest in the afternoon. The ants could have overwhelmed the wasps, but, more likely, the wasps had left the nest temporarily unguarded.

NEST SUPERSEDURE: Two or more species of wasps and bees constructed nests in the same tube in 2 trap-nests. In one trap-nest a 7-celled nest of *T. superbum* was at the inner end, but a pompilid wasp, *Auplopus* sp., stacked two of its mud brood pots on top of the last cocoon of *T. superbum* (Fig. 4). We could not tell if the last cell's outer partition was destroyed by the pompilid or something else. In the other trap-nest a leaf cutter bee had placed 1 leaf cell at the inner end, then *T. superbum* constructed an 8-celled nest and finally in the last 28 mm of the tube the sphecid wasp, *Podium rufipes* Fabricius, built a 1-celled nest. Before the nest was opened a megachilid bee had emerged from the cell at the inner end of the tube, but it was unable to get by the first cocoon of *T. superbum* and thus died. The cocoon was still intact.

SPIDER PREY: *Trypoxylon superbum* specializes on salticid spiders, which made up 97% of 265 prey taken from 12 nests. The prey included a surprising diversity of salticids. Among the prey were 55 distinguishable species of Salticidae, including the ant mimics *Simonella*, *Myrmarachne*, and *Uluella*. Identifications of spider prey are listed below.

SALTICIDAE (257): 2 imm., 2♂♂, 7♀♀ *Cobanus* sp.; 15 imm., 9♂♂ *Thiodina* sp.; 14 imm., 10♂♂, 14♀♀ *Hypaeus*—2 spp.; 1♂ *Noegus* sp.; 2 imm., 6♂♂, 3♀♀ *Atelurius* sp.; 2 imm. *Chira* sp.; 2 imm., 1♂, 2♀♀ *Metacyrba* sp.; 2♂♂, 1♀ *Pensacola* sp.; 1♀ *Hentzia* sp.; 2 imm., 8♂♂, 5♀♀ *Chapoda*—3 spp.; 2 imm., 4♂♂, 3♀♀ *Eustiromastix* sp.; 2♀♀ *Lyssomanes*—2 spp.; 3 imm. *Freya* sp.; 2 imm., 3♂♂ *Phiale*—4 spp.; 8 imm., 16♂♂, 10♀♀ *Corythalia*—7 spp.; 2 imm., 10♂♂, 5♀♀ *Sidusa*—3 spp.; 1♀ Euphrydinae sp.; 1 imm., 1♂, 1♀ *Ashtabula* sp.; 3 imm. *Phidippus* sp.; 1 imm. *Dryphias* sp.; 1 imm., 3♂♂ *Eris*—2 spp.; 2 imm., 2♂♂ *Avitus*—2 spp.; 7 imm., 11♂♂, 15♀♀ *Metaphidippus*—6 spp.; 9 imm., 7♀♀ Dendryphantinae—4 spp.; 1♂ *Balmaceda* sp.; 1♀ *Marpissa* sp.; 1♀ *Simonella* sp.; 2 imm. *Myrmarachne* sp.; 1 imm. *Uluella* sp.; 4 imm., 1♀ undetermined Salticidae.

OXYOPIDAE (5): 4 imm., 1♀ *Hemataliwa*.



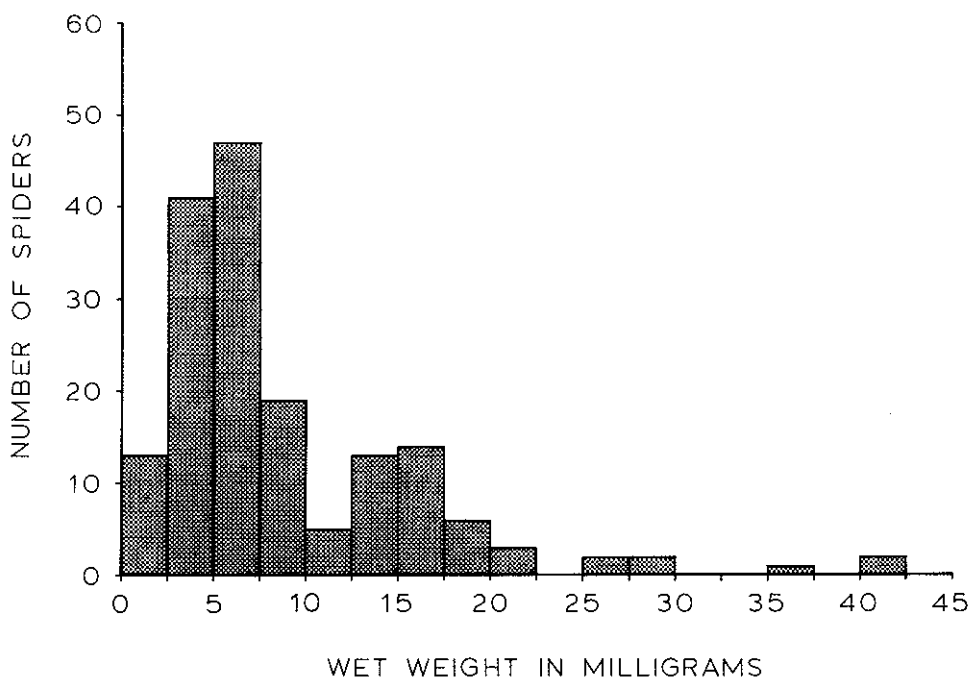


Fig. 5. Frequency distribution showing the size classes of 168 newly provisioned spider prey of *T. superbum*. Note that the smaller size classes (on the left) contain most of the prey.

CTENIDAE (1): 1 imm. undetermined sp.

ARANEIDAE (2): 1 imm. *Eustala* sp., 1 imm. *Araneus* sp.

Figure 5 shows the distribution of size classes of 168 newly provisioned spiders. *Trypoxylon superbum* takes spiders that weigh between 1.4 and 43.2 mg ( $\bar{x} = 9.0$  mg), but the distribution is skewed toward the smaller size classes. Most spiders weighed between 2.5 and 10.0 mg.

Our observations of spiders at La Selva indicated that prey of *T. superbum* included primarily (1) wandering rather than snarebuilding spiders and (2) diurnal rather than nocturnal spiders. Among the wandering spiders that stalk, pursue, or ambush their victims were Salticidae, Oxyopidae, and Ctenidae. These three families accounted for 263 of the 265 prey of *T. superbum*. Snarebuilding spiders that use webs to ensnare their victims were the Araneidae. Salticids and oxyopids, which accounted for 262 of the 265 prey of *T. superbum*, were diurnal, often moving about on foliage, especially the upper surface of leaves. Nocturnal spiders included Ctenidae and Araneidae. Although generally nocturnal predators, juvenile ctenids such as the one in the prey often rested exposed on the upper surface of leaves during the day. The araneids had variable diurnal behavior, but most *Eustala* and *Araneus* of the type in the prey either hid in a retreat or maintained a cryptic posture outside of webs, unless disturbed.

#### Discussion

In most species of *Trypargilum* that nest in existing holes, the male and female wasp leave the nest immediately after it has been completed (Coville and Coville,

1980; Paetzel, 1973; pers. obs.). The last brood cell in their nests is usually separated from the outside by 1 or more empty vestibular cells and a thick mud closure plug that form a protective barrier between the brood cells and natural enemies on the outside. The last provisioned cell in nests lacking a vestibular cell would probably suffer high mortality from natural enemies that can oviposit through the closure plug (Coville, 1982; Coville and Coville, 1980). For that reason selection has probably favored wasps that leave the last cell empty.

Adult behavior and nest structure of *T. superbum*, however, differ from the pattern in other species of *Trypargilum*. In *T. superbum* the male continues defending nests for up to a week or more after the female has finished the last cell and has departed. The last brood cell of the completed nest is usually separated from the outside only by the thin outer cell partition; there is no thick mud closure plug and usually no vestibular cell. The outermost cell partition is recessed by 14 mm or more, leaving sufficient space for the male to remain within the tube. Our observations at La Selva support a hypothesis that the divergent behavior and nest characteristics of *T. superbum* are elements of another adaptation to protect progeny from natural enemies, especially several kinds of ants, that dig into completed nests.

At La Selva we observed ants attack recently completed nests of several *Trypargilum* species. Many attacks took place immediately after the wasps had departed, before the newly deposited mud closure plugs had dried. In successful attacks, the ants opened one small hole in the closure plug and cell partitions. Upon reaching the brood cells, the ants dismembered and carried off the spider prey and wasp eggs or larvae in several cells. Nests damaged by ants were encountered often enough to indicate that ants probably cause significant mortality of wasp eggs and larvae. In 1981 wires supporting many bundles of trap-nests were coated with "Stickum" to exclude ants.

In *T. superbum* effective defense of brood cells against most ants is probably provided in the following manner. While remaining in the nest for many days after the female has left, the male guard prevents entry of foraging ants. His prolonged nest defense allows the wasp larvae in the brood cells to complete their development. By the time the male guard has left, all the larvae have finished their cocoons. Cocoons of *T. superbum*, the strongest cocoons of any *Trypargilum* that nests in existing holes, provide the larva with the protection against many natural enemies that the thick mud closure plug and cell partitions provide in other species. As noted in the results, each larval *T. superbum* eats all but a few fragments of its inner cell partition. The soil is presumably incorporated into the cocoon and probably contributes to the cocoon's strength. With no effective cell partitions remaining in the nests, the only barriers preventing intruders from moving freely from one cell to another are the cocoons and their matrix of fine, fragile silk threads, anchoring cocoons to the cell walls. Most female cocoons in trap-nests of 6.4 mm diameter had their anterior ends flared outward to occlude the tube; thus female cocoons functioned as tough plugs, preventing intruders from penetrating further into nests. It is noteworthy that female cocoons, when present, were usually in cells close to the nest entrance. Cocoons of several *Trypargilum* in the *punctulatum* and *fugax* species complexes resemble those of female *T. superbum* in shape of the anterior ends (see Coville, 1981, 1982; Coville and Coville, 1980; Coville and Griswold, 1983; and Krombein, 1967) and in

frequent placement close to the nest entrance. These cocoons probably also function as plugs or barriers in nests.

Although we did not experimentally determine that cocoons of *T. superbum* were resistant to ants, observations reported in the results suggested that this is the case. In nests that were invaded by ants, wasp larvae within cocoons survived; but feeding larvae, spider prey and puparia of *Phalacrotophora* were destroyed.

Male-biased sex ratios and tendency of females to build only one nest in a bundle of trap-nests are consistent with the observed nesting habits of *T. superbum*. Although offered trap-nests with tube diameters of 11.0 to 3.2 mm in 1981, *T. superbum* showed an extreme preference for those with 6.4 mm diameters, while ignoring the next larger (8.0 mm) and next smaller (4.8 mm) diameters (Table 2). Therefore, the strongly male-biased sex ratio (9♂♂:2♀♀) in progeny produced from 6.4 mm diameter nests probably indicates a male-biased sex ratio in the natural population. Extra males would enable the female to leave her mate on guard at the original nest while she paired with a new male in order to promptly initiate another nest. (We do not know if a male must be present before the female will provision her nest, but this is the case with some species—see Coville and Coville, 1980.) On the other hand, if the female, as with other *Trypargilum* at La Selva, began her new nest next to the original one, the male guard may be inclined to follow her to the new nest, or at least be distracted from his guarding of the old nest. This could be a reason why females usually made one nest in a bundle of trap-nests and then presumably went elsewhere to build the next nest.

*Trypoxylon superbum* specializes on Salticidae (97% of the prey) to a greater degree than any other *Trypargilum*, including species in the *spinosum* complex (see Coville, 1982, for a review of *Trypargilum* prey preferences). With the exception of 2 immature araneid spiders all the prey species are often found on the upper surface of foliage during the day. In addition, the salticids and oxyopids (257 and 5, respectively, of the 265 prey of *T. superbum*) were diurnally active. Our observations suggest that *T. superbum* locates prey by flying over foliage in search of exposed, probably moving arthropods. The wasps probably discriminate spiders from other arthropods at close range. The ability of *T. superbum* to distinguish salticids was impressive to us because the salticid prey included some of the most convincing ant mimics found at La Selva (e.g., *Simonella*, *Myrmarachne*, and *Uluella*). How *T. superbum* distinguishes the ant mimics from their models is unknown, since the mimics resemble their models in behavior as well as in body form and color.

In summary, *T. superbum* possesses several biological characteristics that separate it from other species in the subgenus *Trypargilum*. First, each male remains as a guard in the female's nest for several days after she has left. Second, the last brood cell is separated from the outside only by its thin outer cell partition, which is recessed 14 or more mm from the nest entrance. Third, cocoons of *T. superbum* are the hardest of any *Trypargilum* that nest in existing holes. The anterior end of most female cocoons flare outward as in species of the *punctulatum* and *fugax* complexes. Other cocoons taper slightly toward the anterior end which is rounded. Fourth, *T. superbum* preys heavily on jumping spiders, and when hunting the wasps probably search foliage for moving spiders. The first 3 characteristics could be interrelated elements of an adaptation for defending progeny against ants. Males prevent entry of ants and other predators into nests until the larvae have completed

feeding on spider provisions and formed their cocoons. The hardened cocoons are probably impervious to ants, so once the cocoon is formed the larvae are safe from ant predation. The nesting behavior of *T. superbum* deserves study in greater detail, but unfortunately the wasps are uncommon at La Selva.

#### Acknowledgments

We gratefully acknowledge Drs. David and Deborah Clark and the Organization for Tropical Studies for their assistance and logistic support. Thanks go to J. A. Chemsak for comments on an early draft of the manuscript. The following individuals kindly identified natural enemies of *Trypoxylon*: J. Johnson and E. E. Grissell (Chalcididae), W. W. Wirth (Phoridae), and A. S. Menke (Sphecidae-*Podium*). This research was supported by a grant from the National Geographic Society (R. E. Coville, principal investigator).

#### Literature Cited

- Coville, R. E. 1981. Biological observations on three *Trypoxylon* wasps in the subgenus *Trypargilum* from Costa Rica: *T. nitidum schulthessi*, *T. saussurei*, and *T. lactitarse* (Hymenoptera: Sphecidae). Pan-Pacific Entomol. 57:332-340.
- . 1982. Wasps of the genus *Trypoxylon* subgenus *Trypargilum* in North America (Hymenoptera: Sphecidae). Univ. Calif. Publ. Entomol. 97:1-147.
- Coville, R. E., and P. L. Coville. 1980. Nesting biology and male behavior of *Trypoxylon* (*Trypargilum*) *tenocitlan* in Costa Rica (Hymenoptera: Sphecidae). Ann. Entomol. Soc. Am. 73:110-119.
- Coville, R. E., and C. Griswold. 1983. Nesting biology of *Trypoxylon xanthandrum* in Costa Rica with observations on its spider prey (Hymenoptera: Sphecidae; Araneae: Senoculidae). J. Kans. Entomol. Soc. 56:205-216.
- Krombein, K. V. 1967. Trap-nesting wasps and bees: life histories, nests, and associates. Smithsonian Inst. Press, Washington, D.C. 570 pp.
- Paetzel, M. M. 1973. Behavior of the male *Trypoxylon rubrocinctum* (Hymenoptera: Sphecidae). Pan-Pacific Entomol. 49:26-30.
- Richards, O. W. 1934. The American species of the genus *Trypoxylon* (Hymenopt., Sphecoidea). Trans. R. Entomol. Soc. Lond. 82:173-362.