Behavior of *Philanthus pulchellus* (Hymenoptera: Sphecidae) with a Description of Its Mature Larva

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ABSTRACT In a population of *Philanthus pulchellus* Spinola in eastern Spain, the males establish themselves in territories which they scent mark with pheromones to attract females. Females dig multicelled nests, do not level the tumulus during excavation, and temporarily close nests during provisioning. They show low specificity in the capture of prey, which is represented by bees and wasps (including conspecific males and females). The mature larva is described and compared with others in the genus.

KEY WORDS *Philanthus pulchellus*, territoriality, nesting behavior, larval morphology

THE GENUS *Philanthus*, commonly known as beewolves, includes ≈140 species of wasps. It is particularly well represented in the Holarctic and Ethiopian regions but is unknown from Australia. All species studied establish their nests in the ground, often within aggregations that persist from year to year; females capture Hymenoptera (usually bees and wasps) to feed their larvae.

Some European authors have studied the biology of *Philanthus triangulum* (F.) in detail (Grandi 1931, Rathmayer 1962, Simon Thomas 1966, Simon Thomas and Poorter 1972, Simon Thomas and Simon Thomas 1972, Simon Thomas and Veenendaal 1978). However, concerning the remaining Palearctic species (≈30), only isolated data exist. Ferton (1905, 1910), Grandi (1928), and Krombein (1972) provided data on nest structure and prey of *Philanthus venustus* (Rossi). Berland (1925) and Tsuneki (1943) contributed data on the prey and nests of *Philanthus coronatus* (Thunberg). This situation contrasts with the numerous studies carried out on Nearctic species (Evans and O'Neill 1988).

Philanthus pulchellus Spinola is found in Southwest Europe. Its biology is practically unknown—only Gayubo (1982) mentions the capture of a female transporting a *Halictus* sp. as prey. In this article, we report on the nesting behavior of this species, present some data on the behavior of the males, and describe its mature larva.

Materials and Methods

Observations of nesting behavior were carried out at a nesting aggregation 4 km south of Sagunto (Valencia Province, Spain). We remained at the nesting site from 17 June to 10 July 1994, normally from 0930 until 1900 hours. Forty active nests were situated in an area (2 by 9 m) of compact sandy soil that contained many stones but no vegetation. The site was surrounded by *Arundo donax* L., *Phragmites communis* Trin, and *Thymelaea hirsuta* L. Twenty-three nests were located in flat ground and the remaining 17 in an area with a slope of 10–40°. The data were augmented with additional observations carried out in Rabanera del Campo (August 1991) (Soria Province), Sagunto (June 1992), Moncofar (September 1988), Segorbe (August 1987), and Soneja (July 1987) (Castellón Province), for a total of 195 h of observation.

The behavior of males was studied in a zone 300 m to the north of Rabanera del Campo in a flat, sandy area with the scattered small plants *Bromus diandrus* Roth, *Artemisia campestris* L., *Scirpus holoschoenus* L., and *Thymus mastichina* L. The observations were carried out from 8 to 15 July 1994 for a total of 64 h of observation.

We captured 49 females and 19 males and measured them to the nearest 0.05 mm (maximum head width) with a digital caliper. Before release, we marked them with 1–3 dots of colored enamel paint on the dorsum of the thorax with Pentel Paint Pen 0.5 (Pentel, Japan) markers. The correlation between the fresh weight and the head width of 13 females of *P. pulchellus* was significant (Pearson correlation, $r = 0.86$, df = 11, $P < 0.001$). It has also been demonstrated that head width correlates strongly with dry mass in other species of the genus (O'Neill 1983a, 1985; O'Neill and Evans 1983).

While observing marked males on territories, we recorded the number and duration of "scent marks" (in accordance with Evans and O'Neill [1988]) during 10-min intervals throughout the day. To analyze the possible correlation between female size (head width) and prey weight, 58 prey

Table 1. Scent marks observed throughout the day

Time of day, hours	Observation length, min	Avg no. scent marks
1000–1100	20	0.80
1100–1200	80	2.93
1200–1300	100	0.76
1300–1400	50	0.04
1400–1500	30	0.00
1500–1600	20	0.00
Total	300	—

from 19 marked females were weighed fresh to the nearest 0.5 mg on a COBOS A-150-SX (Cobos, Spain) electronic balance. Taxonomic and prey size niche breadths were determined using Simpson's expression for the calculation of diversity (Magurran 1988). To compare our results with those of O'Neill and Evans (1982), we used prey genus in the calculation of taxonomic niche breadth and the product of prey thorax width and body length in the calculation of prey size niche breadth. We measured prey to the nearest 0.1 mm. All indications of time refer to GMT + 2.

Results

Male Behavior. Males appeared several days before the females (middle of June in Sagunto and beginning of July in Rabanera). They spent the night in small sleeping burrows (2.5–5 cm long, 1.5–2.5 cm diameter). During the day, these galleries remained open and some were occupied on successive nights.

In Rabanera, we observed 5 territories (1–1.4 m diameter) in a strip of flat land (8 by 1.5 m) sparsely covered with a few clumps of *B. diandrus* and *A. campestris*. Only 1 nest was observed here, but 9 m to the north of the territories, 11 grouped nests were located, separated by an average distance of 27.6 cm (range ± SD, 8–106 ± 34.4). Prevailing wind direction was south to north; the territories were located upwind of the principal area of nesting.

By studying the occupation of the 5 territories for 5 consecutive days, we observed that the males arrived between 1035 and 1200 hours and departed between 1121 and 1851 hours. Maximal occupation occurred at ≈1130 hours (64% of the territories occupied on average). By 1400 hours, males were present in only 40% of territories, declining to 16% at 1600 hours. Territories were occupied only when they were fully insolated.

Perches were on grasses (*B. diandrus*) 20–45 cm high or on patches of bare soil. Grasses in the territories were scent marked like that of other species of *Philanthus* (for instance, Alcock 1975, Gwynne 1978, Evans and O'Neill 1988). Scent marking was always preceded by a "weaving flight" similar to that described by O'Neill (1979).

Males began to scent mark shortly after arrival on the territories. They carried out bouts of variable duration (7–262 s) with 1–13 scent marks in each bout (mean ± SD, 3.1 ± 2.5; n = 63) and often marked adjacent stems. Studying 3 males in periods of 10 minutes, we observed that there were more scent marks at the beginning of the occupation, decreasing rapidly after the territory had been occupied for a certain time. In the interval from 1100 to 1200 hours, the average number of scent marks produced per minute was 2.9; after 1400 hours, although territories remained occupied, no scent marking was observed (Table 1).

Table 2. Provisioning flights by 18 females of *P. pulchellus*

Time of day, hours	Observation length, h	No. provisioning flights	Avg no. prey/h
0900–1000	1.0	2	2.00
1000–1100	6.0	42	7.00
1100–1200	8.5	67	7.88
1200–1300	8.5	70	8.24
1300–1400	7.5	45	6.00
1400–1500	4.0	30	7.50
1500–1600	3.0	11	3.67
1600–1700	3.5	9	2.57
1700–1800	3.5	3	0.86
1800–1900	1.5	1	0.66
Totals	47.0	280	—

Some territories were occupied more frequently than others—one for >90% of the time, during which at least 1 of the territories contained a territorial male; on the other hand, another was occupied only sporadically (<10% of the time). The territories most frequently occupied were those closest to the nesting area and downwind of the rest of the territories; the territory least occupied was the farthest away. The period during which males remained on the territories was variable. One marked male established himself for 4 consecutive days in 1 territory, occupying it for 199–367 min per day (291.3 ± 71.6) at intervals of 3–220 min (105.9 ± 71.1, n = 11), and being absent from 1 to 3 times a day in periods of 3–94 min (39.7 ± 30.0, n = 7), probably to feed. The period the remaining males spent in the territories was shorter—18–168 min per day (69.4 ± 63.7, n = 5).

Occupied territories were defended against other conspecific males. Casual observations showed that the interactions were most frequent at the beginning of the occupation of the territory and diminished throughout the course of the day.

In addition to the territorial males, other males, designated as "floaters" by O'Neill (1983a, b), were in the study area. These floaters interacted with the territorial males but did not scent mark. We could obtain only the head width of 7 territorial males and 9 floaters; the territorial males (mean, 2.5 mm; range, 2.3–2.7 ± 0.1; n = 7) were significantly larger than the floaters (mean 2.2 mm; range, 2.0–2.4 ± 0.1; n = 9)(Mann–Whitney U test, U = 1.5; $P < 0.01$; n = 9, 7).

Table 3. Prey of *P. pulchellus* taken from females or extracted from nests (73 species: 22 wasps, 51 bees)

Taxon	No. and sex
PARASITICA	
BRACONIDAE	
Isomicus intermedius Szepligeti	1♀
CHALCIDIDAE	
Brachymeria sp.	1 Undet.
GASTERUPTIONIDAE	
Gasteruption diversipes Abeille	2♀♀
Total	3♀♀, 1 Undet.
ACULEATA	
ANDRENIDAE	
Andrena hystrix Schmiedeknecht	1♀
Andrena sp.	3♂♂, 12♀♀
Panurgus calcaratus Scopoli	2♂♂
Total	5♂♂, 13♀♀
ANTHOPHORIDAE	
Ceratina cucurbitina Rossi	1♀
Ceratina dentiventris Gerstaecker	1♀
Eucera elongatula Vachal	1♂
Nomada sp.	3♂♂
Total	4♂♂, 2♀♀
COLLETIDAE	
Colletes abeillei Pérez	1♂
Colletes dimidiatus Brullé	1♂
Colletes sp.	1♂
Hylaeus absolutus Gribodo	1♂, 1♀
Hylaeus angustatus Schenck	1♀
Hylaeus annularis Kirby	5♀♀
Hylaeus bisinuatus Forster	1♂, 1♀
Hylaeus brevicornis Nylander	4♀♀
Hylaeus conformis Forster	1♀
Hylaeus euryscapus Forster	2♂♂, 1♀
Hylaeus imparilis Forster	1♀
Hylaeus pictus Smith	4♂♂, 3♀♀
Hylaeus sp.	2♂♂, 3♀♀
Total	13♂♂, 21♀♀
HALICTIDAE	
Halictus pollinosus Sichel	9♂♂, 10♀♀
Halictus smaragdulus Vachal	2♀♀
Halictus subauratus Rossi	3♀♀
Halictus sp.	1♂, 11♀♀
Lasioglossum albocinctum Lucas	1♂
Lasioglossum callizonium Pérez	5♂♂
Lasioglossum glabriusculum Morawitz	2♂♂
Lasioglossum lucidulum Schenck	1♀
Lasioglossum malachurum Kirby	4♂♂, 3♀♀
Lasioglossum minutissimum	2 Unsex.
Lasioglossum nitidiusculum Kirby	6♀♀
Lasioglossum sphecodimorphum Vachal	1♂
Lasioglossum truncaticolle Morawitz	4♂♂
Lasioglossum zonulum Smith	1♂
Lasioglossum sp.	10♂♂, 2♀♀
Nomioides facilis (Smith)	2♀♀
Nomioides minutissimus (Rossi)	2♀♀
Sphecodes marginatus Hagens	1♀
Sphecodes rufiventris Panzer	1♀
Sphecodes sp.	4♂♂
Total	42♂♂, 44♀♀, 2 Unsex.
MEGACHILIDAE	
Anthidiellum strigatum Panzer	1♂
Heriades crenulatus Nylander	1♂, 1♀
Hoplitis leucomelana Kirby	1♂
Hoplitis sp.	1♂
Megachile argentata F.	1♀
Metallinella brevicornis F.	1♀

Table 3. Continued

Taxon	No. and sex
Osmia argyropyga Pérez	1♀
Osmia emarginata Lepeletier	1♀
Osmia ferruginea Latreille	1♀
Total	4♂♂, 6♀♀
CHRYSIDIDAE	
Hedychridium jucundum Mocsary	1♀
EUMENIDAE	
Ancistrocerus gazella (Panzer)	1♂
FORMICIDAE	1 Undet.
MUTILLIDAE	1 Undet.
SPHECIDAE	
Cerceris sabulosa (Panzer)	3♂♂
Diodontus insidiosus Spooner	1♂, 2♀♀
Ectemnius confinis (Walker)	4♂♂
Lindenius ibericus (Kohl)	7♂♂
Lindenius mesopleuralis (Morawitz)	1♀
Pemphredon lethifera (Shuckard)	1♀
Philanthus pulchellus	6♂♂, 1♀
Oxybelus latro Olivier	1♂
Oxybelus quattuordecimnotatus Jurine	3♂♂
Oxybelus subspinosus Klug	1♂
Oxybelus variegatus Wesmael	1♂
Tachysphex panzeri (Vander Linden)	1♂
Tachysphex tarsinus Lepeletier	2♂♂
Total	30♂♂, 5♀♀
TIPHIIDAE	
Meria sp.	1♂
Poecilotiphia sp.	1♂
Total	2♂♂

Female Behavior. Females established their nests in flat soil (Moncofar, Rabanera, Sagunto, Segorbe) in areas without vegetation, although at times the entrance was located close to the bases of plants. Nests were also observed on gradients of 12–40° (Sagunto) or in embankments (Soneja).

Nests of this species tended to be somewhat clumped, in some cases with the entrances only 4 cm apart. In the main study area (Sagunto), the mean nearest-neighbor distance for the nests situated at the center of the aggregation was 16.4 cm (range, 4–49 ± 10.9; $n = 25$). We also observed some nests separated from others by 70–140 cm.

Mounds at nest entrances were conspicuous, measuring 4.5–9 cm long (6.8 ± 1.7, $n = 9$), 2.5–5.5 cm wide (4.4 ± 0.9, $n = 9$), and up to 1.5 cm deep in the center. The mound was not leveled, but sometimes showed 1 or several grooves across it from the nest entrance. Those grooves were formed by the female when she scraped soil from the burrow during nest excavation. When females nested in vertical banks (Soneja), the soil from the burrow fell down the slope.

We never found accessory burrows near the entrances. In all cases studied, the females made temporary closures while away from the nest. They also closed them from within while provisioning brood cells or resting in the nest.

The nests were of the proclinate diffuse type (in the sense of Evans and O'Neill 1988). The oblique burrow penetrated the soil at an angle of 20–30° and, beyond 10–16 cm, it assumed an angle of 35–45°. After having reached a depth of 12–30 cm, it tended to level off or descend very slightly, although some undulations sometimes occurred. The length of the oblique burrow varied between 23 and 58 cm (37.6 ± 9.5, $n = 14$), and the 1st cell was located at a depth of 14.5–37 cm (21.2 ± 7.8, $n = 16$). There were 2–4 cells in 5 unfinished nests.

Females spent the night in the nests and left early in the morning. Provisioning occurred irregularly, and the intervals between successive provision flights varied from 5 to 136 min (39.7 ± 29.3, $n = 115$). One female captured 5 prey in 55 min.

When prey were introduced, the nest remained open. The stay in the nest varied from 0.5 to 6.5 min (2.3 ± 1.4, $n = 61$). On other occasions, the female introduced the prey into the nest and closed it from within, remaining inside for long periods.

Females provisioned their nests from 0937 and 1811 hours but primarily between 1000 and 1500 hours. During this period, the number of prey captured per hour was more or less constant (Table

2). The number of prey captured in 1 d by a single female varied between 1 and 9 (3.2 ± 2.0, $n = 57$).

The transport of the prey was of the mesopedal type. In all cases, the wasp approached the nest at a low altitude (<50 cm above the ground). She opened the nest with her forelegs and entered without releasing the prey. The prey were stored at the end of the oblique burrow before being transferred to the cell. There were 4–9 prey per cell (6.5 ± 1.5, $n = 15$) (Table 3).

Parasites were not detected in any of the 27 cells examined. On 3 occasions, the female removed prey from her nest, although parasite eggs or larvae were not detected. Females of *Chrysura dichroa* Dahlbohm, *Hedychridium jucundum* Mocsary, and *H. reticulatum* Abeille (Hymenoptera: Chrysididae) and *Bisigilla chiesii* (Spinola) and *Myrmilla calva* (Villers) (Hymenoptera: Mutillidae) were observed in the nesting area, exploring the tumuli and the entrances of the nests and in some cases digging in the temporary closures.

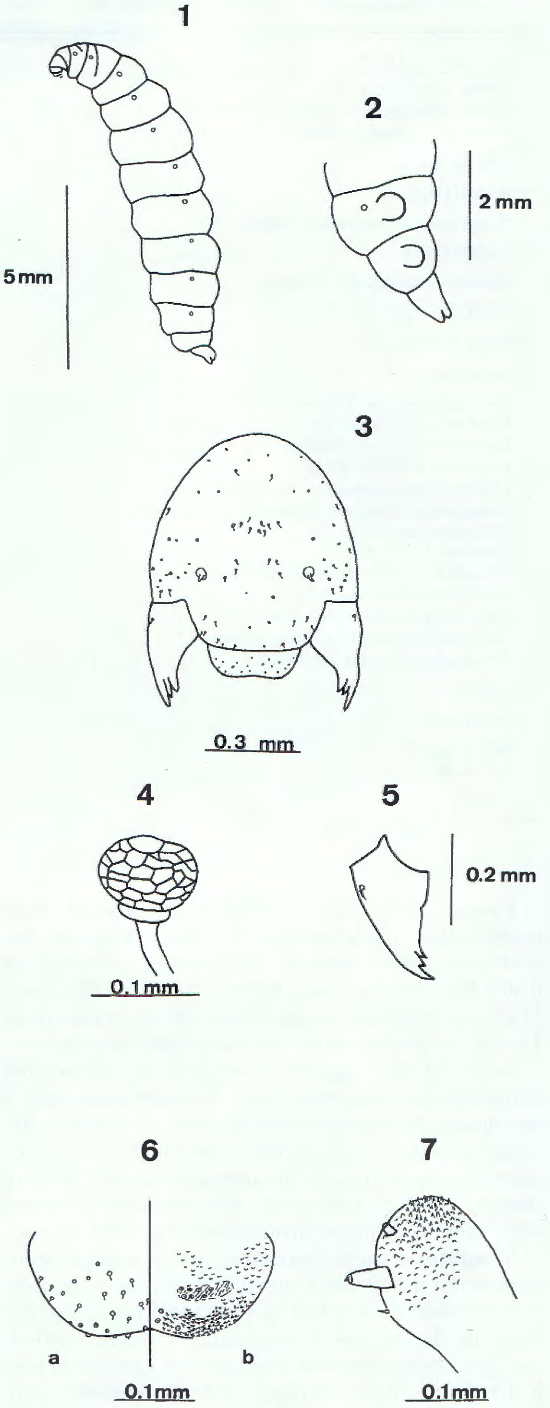
Description of Mature Larva. The description is based on specimen 920302, extracted from a nest established in Rabanera.

General Appearance. Body (Fig. 1) fusiform (9.72 mm long, 2.33 mm wide). Pleural lobes scarcely developed. Anus (Figs. 1 and 2) terminal, at end of a small, tubular projection (10th abdominal segment). Supraanal and infraanal lobes unequal, former slightly larger. Tegument entirely covered with fine, numerous spinules (8–19 μm long) and some isolated setae (1–30 μm). Prothoracic spiracles (Fig. 4) slightly larger (53–57 μm diameter; mean, 55 μm) than others (45–49 μm diameter; mean, 48.5 μm).

Head. (Fig. 3). Subcircular (653 μm high, 643 μm wide) with abundant setae (7–14 μm long). Antennal orbits subcircular (60 μm long, 40 μm wide) with well-developed antennae (14 μm long, 12 μm diameter). Labrum (Fig. 5) (125 μm high, 299 μm wide) with setae (10 μm long) and some sensilla (6 μm diameter) along the anterior margin. Epipharynx (Fig. 5) spinulose, mainly on its margin, spinules most highly developed anteriorly (5 μm long). Pigmented area on each side of medial line with 7 sensilla (5 μm diameter), these areas not interconnected. Three sensilla on each side of medial line anteriorly.

Mouthparts. Mandibles (Fig. 6) (322 μm long, 167 μm wide) tridentate, with 1 basal seta (12 μm long). Maxillae (Fig. 7) with spinulose lacinial area, remainder papillose. Maxillary palpi (55 μm long, 29 μm diameter) far surpassing galeae (14 μm long, 10 μm diameter). Labium papillose on oral face, with isolated setae on lower part. Spinnerets (24 μm long, 11 μm diameter) slightly larger than labial palpi (21 μm long, 14 μm diameter).

Currently the larval morphology of the following 6 species of the genus is known: *Philanthus bicinctus* (Mickel) (Evans 1964); *P. bilunatus* Cresson; *P. gibbosus* (F.); *P. politus* Say; *P. solivagus* Say (Evans 1957); and *P. triangulum* (F.) (Grandi



Figs. 1–7. Mature larva of *P. pulchellus*. (1) Body (lateral view). (2) Last 3 segments of abdomen. (3) Head. (4) Spiracle. (5) Mandible. (6) Labrum (a), epipharynx (b). (7) Maxilla.

Table 4. Type and sex of prey of *P. pulchellus* in populations of 2 provinces in Spain

Locality	No. prey	No. species	% wasps	% wasp species	% bees	% bee species	Ratio ♂:♀
Sagunto	165	62	20.0	29.0	80.0	71.0	1.3:1
Rabanera	36	19	33.3	26.3	66.7	73.7	1:2.6
Totals	201	73	22.4	30.1	77.6	69.9	1.1:1

1931). All are very similar in the appearance of the tegument, mandibles, and maxillae, but some differences exist. The presence of setae scattered over the tegument separates *P. pulchellus* from the all other species, and the epipharynx, not very spinulose and with 3 sensilla on the lower part, is a character shared with *P. politus.* In all species except *P. gibbosus,* the spinnerets are slightly larger than the labial palpi.

Discussion

Male Behavior. Males are territorial as in other *Philanthus* spp., but only the larger ones were able to establish themselves in territories, which they marked with pheromones to attract the females. The smaller males, unable to occupy such territories, acted as floaters; their territories are not established in the nesting area but nearby, as in other species which nest in small, diffuse aggregations (*P. barbiger* Mickel, *P. crabroniformis* F. Smith, and *P. serrulatae* Dunning [Evans and O'Neill 1988]).

In *Philanthus pulcher* Dalla Torre and perhaps in *P. tarsatus* Smith, the number of scent marks remains constant throughout the daily period of occupation of the territory (Evans and O'Neill 1988). However, typically this number declines over the daily period of territory defense, as in *P. pulchellus*, *P. barbatus* Smith (Evans 1982), *P. basilaris* Cresson (O'Neill 1983b), *P. bicinctus* (Gwynne 1978), and *P. multimaculatus* Cameron (Alcock 1975). During the period of maximal activity, the average number of scent marks observed was 2.93. This value is intermediate between those found by Evans and O'Neill (1988) in other *Philanthus* spp.of the same size as *P. pulchellus*.

Female Behavior. Like many Nearctic species of *Philanthus*, which prey on a great variety of wasps (Evans and O'Neill 1988), *P. pulchellus* also captures wasps and even some Parasitica (Table 4).

Philanthus pulchellus is a generalist predator. Of a total of 201 prey, 34 genera were represented. In the population at Sagunto, the taxonomic niche breadth of prey was 8.10 and that in Rabanera was 6.82. Both values surpass those for most populations of the *Philanthus* analyzed to date (O'Neill and Evans 1982, Evans and O'Neill 1988). The breadth of the niche for the size of the prey was 3.42 in Sagunto. This value appears intermediate among those found to date for 4 species of the genus (from 2.48 for *P. barbiger* to 6.23 for *P. basilaris* [O'Neill and Evans 1982]).

The correlation between the weight of 13 females of *P. pulchellus* and the average weight of the prey captured was significant (Spearman rank correlation, $r_s = 0.6061$, $P < 0.05$, $n = 13$), as was the correlation between the head size of the females and the weight of the prey (variables for which more pairs of values were available) ($r_s = 0.5857$, $P < 0.02$, $n = 19$). Positive correlations have also been found between the weight or size of the females and the weight of the prey in other species of the family (Byers 1978, Gwynne and Dodson 1983, Alexander 1985, O'Neill 1985, Kurczewski 1991). However, Stubblefield et al. (1993), in a thorough study carried out on *Philanthus sanbornii* Cresson, show that the females of this species catch almost every kind of bee or wasp found at flowers, and they state that much of the variation in prey specifity among Nearctic *Philanthus* spp. might reflect only size restrictions or sampling error. In our study, the correlation between the size of the females and the weight of the largest prey caught is significant (Spearman rank correlation, $r_s = 0.5239$, $P < 0.05$, $n = 19$). However, on calculating the weight of the smallest prey caught by each female, the correlation found is not significant ($r_s = 0.2683$, $0.5 > P > 0.2$, $n = 19$). These results might be explained considering that, although the large females can subdue larger prey, they do not renounce catching small ones.

It is noteworthy that *P. pulchellus* females captured several conspecific males and 1 female. Rathmayer (1962, 1978) indicated that *P. triangulum* is immune to the effect of its own venom; however, O'Neill and Evans (1981) cited the capture of conspecific males of *P. basilaris,* postulating that perhaps the immunity indicated by Rathmayer (1962, 1978) was restricted to the females. The capture of both males and a female by *P. pulchellus* suggests that such immunity does not exist in this species. The female captured as prey was much smaller (head width, 2.1 mm) than average (2.5 ± 0.24). Three males were captured by 1 female in 1 d and 2 by another female, also on the same day.

Evans and O'Neill (1988) identified several behavioral traits typical of the ancestral beewolf; none of the Nearctic species studied exhibited all these attributes. Nevertheless, all these 6 characteristics, as follows, are present in *P. pulchellus*: (1) an unlevelled tumulus; (2) temporary closure; (3) absence of accessory burrows; (4) proclinate diffuse nests; (5) relaxed specificity in the capture of prey, represented by bees and wasps; and (6) territorial males that scent mark. Therefore, *P. pulchellus* demonstrates behavior similar to that considered ancestral for the genus.

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