ECOLOGY, BEHAVIOR AND BIONOMICS

Nesting Behavior of *Podium denticulatum* Smith (Hymenoptera: Sphecidae)

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ABSTRACT - The nesting behavior of *Podium denticulatum* Smith was studied on the campus of Ribeirão Preto of the Universidade de São Paulo, SP, Brazil, from September 2003 to August 2005. The wasps established their nests in bamboo canes ranging from 11.4 cm to 26.2 cm in length and from 0.7 cm to 1.8 cm in internal diameter. *Podium denticulatum* nested almost exclusively in the hot and wet season (September-April), producing at least five generations per year. The cell provisioning was made with adult and nymphal cockroaches (Blattellidae) which were arranged venter-up and with the head inward toward the inner end of the cell. The construction of a temporary closure occurred in cells that took more than one day to be provisioned. The cells provisioned with a greater number of prey were more likely to produce females than males. The nests included 1-6 brood cells separated by mud partitions and arranged in a linear series. The innermost cells of the nests produced females, and the outermost cells produced males. Nests were parasitized by Eulophidae (*Melittobia* sp.), Chrysididae and Tachinidae.

KEY WORDS: Trap-nest, solitary wasp, phenology, natural enemy

*Podium* is a primarily tropical genus that includes 21 species, 20 of which are distributed in three species-groups: the *rufipes* and the *agile* groups, both with four species each, and the *fumigatum* group, with 12 species (Bohart & Menke 1976, Ohl 1996). Knowledge concerning the nesting biology of *Podium* is very limited. The available information shows that the nests can occur in a variety of substrate such as abandoned nests of other wasp species (Rau 1937, Genaro 1994, Camillo 2001), cavities in dead trees (Krombein 1964) and trap-nests (Krombein 1967, 1970, Camillo et al 1996, Assis & Camillo 1997, Morato 2001). The nest structures such as cell partitions and nest plug are made of mud and mud, resin and organic debris, respectively. The nests can be unicellular (*Podium rufipes* Fabricius) or multicellular (*Podium lactuconum* Smith and *Podium denticulatum* Smith) and the cells are provisioned with paralyzed adults and nymphs of cockroaches (Rau 1937, Krombein 1958, 1967, 1970, Genaro 1994, Camillo et al 1996).

*Podium denticulatum* belongs to the *fumigatum* group. It is a solitary wasp that has a broad geographic range from Mexico to Brazil (Bohart & Menke 1996). Aspects of the nesting biology of *P. denticulatum* such as nesting periods, nest architecture, prey utilized to provision the cells, sex ratio, and natural enemies were reported by Camillo et al (1996). Recently, Buys et al (2004) described the immature instars of *P. denticulatum*, *Podium fumigatum* Perty and *Podium aureosericum* Kohl. In this paper the first information on the nesting behavior *P. denticulatum* is presented. Besides that information, new data concerning nest architecture, sex ratio, number of generations per year and natural enemies are reported.

Materials and Methods

Study area. The study was conducted on the campus of Ribeirão Preto (between 21°05´- 21°15´ S and 47°50´- 47°55´ W) of the Universidade de São Paulo, state of São Paulo, Brazil, from September 2003 to August 2005. The local climate has two well defined seasons, a cool and dry season extending from May to August, with the mean monthly temperature ranging from 18.9°C to 22.1°C and precipitation from 0 to 104.7 mm, and a hot and wet season extending from September to April, with the mean monthly temperature ranging from 22.9°C to 25.8°C and precipitation from 5.3 mm to 417.3 mm.

Methods. In accordance with Camillo et al (1996), trap-nests used in this study consisted of hollow bamboo canes of various diameters and lengths, which were cut so that the nodal septum closed one end of the cane. A total of 380 canes were placed horizontally in bundles of 8-12 units along eight shelves in two shelters built near the laboratory. The shelves were 1.1, 1.3, 1.4 and 1.6 m from the ground. During the study period the traps were inspected with an otoscope, and information was recorded from those with active and completed nests. Ten days
after being completed, 20 nests were taken to the laboratory and each of them was introduced into a transparent plastic tube, 4.0-5.0 cm longer than the trap, with one end closed with a cork. After that, they were put again on the shelves and left undisturbed until the adults emerged. As one adult emerged into the plastic tube, the cork was removed, the individual was collected, sexed and released thereafter. Ten to 15 days after the last emergence the nest was opened to analyze its structures and to take measurements. Other nests (n = 44) were opened in the laboratory 25 days after being completed. Besides analyzing their structures and taking measurements, the cocoons found in the nests were removed from the cells and their length and maximum width were taken. After that, the cocoons were put in individual vials labeled with the nest number and cell number, kept at room temperature (21-29°C) and observed daily until the adults emerged. As one adult emerged into the plastic tube, the cork was removed, the individual was collected, sexed and released thereafter. Ten to 15 days after the last emergence the nest was opened to analyze its structures and to take measurements. After emergence, both females and males were released at the field. Observations on the nesting behavior were recorded for a total of 447h. Voucher specimens of adult *Podium denticulatum* are deposited in the collection of the Department of Biology, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto – USP.

**Statistical analyses.** Statistical tests follow Zar (1984) and were performed by using the statistical package SigmaStat for Windows (1994 - Jandel Corporation, San Rafael, California). Pearson correlation analyses were performed to verify the intensity of association between climate variables and nesting frequency, number of cells constructed per nest and the length of bamboo cane utilized, the space of the bamboo cane occupied by nest, and the time spent by female to complete the nest. The Mann-Whitney test was used to compare the length of male and female cocoons, and the thickness at the edge and at the centre of the nest plug. Chi-square test was used to compare the proportions of sexes. Throughout the text all means (x) are given ± SD.

**Results**

**Phenology of nesting.** Of the 64 nests obtained, 35 were established in the first year (September 2003-August 2004) and 29 in the second one (September 2004-August 2005). In both years, *P. denticulatum* nested during the hot and wet season (September-April) with only one nest being constructed at the end of the dry and cold season (August 2004). However, the monthly frequencies of nesting differed between the years. In the first year, the maximum of constructed nests occurred in December while in the second year, the highest frequencies of constructed nests occurred in October and November 2004 (Fig 1). Significant correlations were found between nesting frequency and temperature, in the first year (r = 0.685; P = 0.014; n = 12), and precipitation, in the second year (r = 0.652; P = 0.021; n = 12), and no correlation with precipitation (r = 0.234; P = 0.464; n = 12) in the first year, and temperature (r = 0.298; P = 0.347; n = 12) in the second one.

**Nest selection.** *Podium denticulatum* females began their activities at the nesting area at about 8:30-9:00h and they remained active until 16:00-16:30h. When searching for a nesting place, the female usually inspected several trap-nests before selecting one for a nest. During the inspections, the female walked to the end of the trap, remained there for some seconds, and backed up a few centimeters and returned to the end again. While walking, the female moved her antennae up

![Fig 1 Number of nests of *Podium denticulatum* built monthly, from September 2003 to August 2005, on the campus of Ribeirão Preto of the Universidade de São Paulo, SP, Brazil.](image-url)
and down touching the internal walls of the cavity. If during the
inspection some materials such as bits of cob-webs or plant or
clay fragments adhered to the body of the female, after leaving
the trap she stopped at its entrance and cleaned her body using
the fore, mid or hind legs to remove the material. After selecting
a suitable trap, the female stays at its entrance for some seconds
and after that leaves the trap to collect prey.

**Provisioning behavior and oviposition.** When returning to her
nest with a cockroach, the female usually landed on the shelf
in the vicinity of her nest, or on the bundle of bamboo canes
containing her nest (Fig 2). The female then walked quickly
to the nest with the prey. The female carried the prey utilizing
her mandibles and forelegs. The prey was held dorsum-up and
the female grasped the base of the antennae with her mandibles
and the prothorax with her forelegs. The trips to collect a prey
lasted from 4.1 to 155.1 min ($x = 40.1 \pm 23.9$ min; $n = 102$).
After entering the nest, the female walked to the end of the
nest and placed the prey venter-up and with its head towards
the inner end of the cell. The time spent by female entering the
nest with the prey and leaving the nest to collect another one
ranged from 0.1 to 1.03 min ($x = 0.35 \pm 0.18$ min; $n = 102$).
The nest entrance usually remained open while the wasp was
provisioning.

The provisioning of one cell could be either completed
within one day or the female interrupted prey collecting and
started to collect mud for a temporary cell partition. Once
the construction of that structure had finished, the female
left the nesting area and passed the night taking shelter in
an unknown place. When returning to her nest in the next
morning, the female opened a hole in the temporary cell
partition just large enough for her to pass carrying a prey.
After that, she completed the provisioning of the cell bringing
in other prey. The number of prey per cell ($n = 39$) ranged
from two to 10, with three (30.8%), four (17.9%) and six
(17.9%) prey items being the most frequent numbers. The
number of cockroaches necessary to provision a female cell
ranged from three to 10 ($x = 5.2 \pm 2.23$ prey; $n = 12$), and
this was significantly greater than for male cells (range: 2-6
prey; $x = 3.4 \pm 1.5$ prey; $n = 19$) (Mann-Whitney test, $Z =$

Figs 2-6 *Podium denticulatum* - some aspects of behavior and nest. 2. Female transporting a paralyzed cockroach to her nest.
3. Arrangement of prey inside cell; note the cockroaches lying on their dorsum. 4. Egg placed between fore coxae of a cockroach.
5. Female carrying a pellet of mud held beneath mandibles to her nest. 6. Bundle of bamboo canes containing a completed nest; note the nest plug coated with resin.
The females oviposited on the preceding prey before or after entering the nest. In three cases, when oviposition occurred before entering the nest, the female oviposited on the first prey collected. On these occasions when the female returned to her nest, she landed on the bundle of bamboo canes, assumed an upright position, curved her abdomen upward and deposited an egg between the fore coxae of the prey (Fig 4). After that, she entered the nest and placed the prey inside the cell.

Cell closing. After provisioning was completed, the female initiated new collections of mud to close the hole made on the temporary cell partition or to construct the definitive cell partition. The mud was collected from a wet soil site or from a soil site moistened by the female with water previously collected. The female worked the soil with her mandibles to make a pellet of mud that she carried to the nest using her mandibles and fore coxae. After landing near her nest (Fig 5), the female entered quickly in it. In the place where the cell partition would be made, the female pressed the mud with the fore legs and mandibles against the walls of the nest while rotating her entire body around the circumference of the nest. As additional loads of mud were deposited, the diameter of the nest cavity was constricted by a structure similar to a ring of solid wall of soil formed a partition across the nest cavity. After depositing the last mud load, the female began to turn clockwise and/or counterclockwise several times, and used her head and fore legs to smooth the outer surface of the cell partition. During these activities the female emitted a set of buzzing sounds that can be heard to a small distance from the nest.

Nine to 24 mud-carrying trips were required to construct one cell partition (n = 18), and their duration was highly variable, ranging from 0.15 to 20.4 min (x = 1.97 ± 2.79 min; median = 0.97 min; n = 298). The time that the female remained in the nest between mud-carrying trips ranged from 0.08 to 5.6 min (x = 0.66 ± 1.04 min; median = 0.27 min; n = 298). The time required for cell provisioning, oviposition, and cell closing ranged from one to five days (n = 112), but 75.9% and 20.5% of the cells were completed in one and two days, respectively.

Nest architecture. The bamboo canes utilized by the wasps ranged from 11.4 cm to 26.2 cm in length and 0.7 cm to 1.8 cm in internal diameter (n = 64). However, 79.7% of nests were made in bamboo canes with 14.1 cm to 22.0 cm in length, and 57.8% of used canes were 1.0 cm to 1.2 cm in internal diameter. Space occupied by the nest within the trap ranged from 3.5 cm to 21.2 cm, and it was significantly correlated with the number of cells built (r = 0.64; P < 0.05; n = 64). In three nests, the females initiated the nesting activities constructing a mud wall between 3.5 cm and 9.0 cm from the trap’s inner end. This wall corresponded to the inner end of the first cell of the nest. Two other nests were established in traps containing old nests of Trypoxylon (Hymenoptera: Crabronidae) which occupied 8.5 cm and 2.0 cm of the length of the cane.

Cells were constructed in a linear series, and the number of brood cell per nest ranged from one (n = 2) to six (n = 4), with two (n = 20) and four (n = 19) being the most frequent number of cells. The number of cells was not significantly correlated with the length of bamboo canes (r = 0.04; P > 0.05; n = 64). Cell lengths ranged from 1.7 cm to 10.0 cm (n = 174). Female cells (range: 2.0-10.0 cm; x = 4.2 ± 1.7 cm long; n = 44) were significantly longer than male cells (range: 1.7-6.3 cm; x = 3.0 ± 0.9 cm; n = 62) (Mann-Whitney test, Z = 4.23; P < 0.05).

The cell partitions were rough and convex on the inner side and smooth and concave on the outer side. They were thicker (range: 0.1-0.7 cm; x = 0.27 ± 0.08 cm; n = 108) at

Table 1 Time (in days) spent by Podium denticulatum females to complete a nest, according to number of cells constructed.

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<th>Number of cell per nest</th>
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the edges than at the centre (range: 0.1-0.2 cm; \( x = 0.12 \pm 0.04 \); \( n = 108 \)). Nest plugs were always reessed from the trap entrance and were similar in shape to cell partitions but were always thicker. The thickness of the nest plug ranged from 0.2 cm to 0.7 cm (\( x = 0.37 \pm 0.01 \); \( n = 53 \)) at the edges and from 0.1 cm to 0.5 cm (\( x = 0.18 \pm 0.08 \); \( n = 53 \)) at the centre. Both the edges and the centres of the nest plugs were significantly thicker than those of cell partitions (Mann-Whitney tests, \( Z = 6.19 \) and \( Z = 4.60; P < 0.05 \), respectively).

Of the 64 nests obtained, 28 nests (43.7%) had one vestibular cell. In nests without vestibular cells (36 nests; 56.3%) the cell partitions closing the last brood cells corresponded to the closure plugs. The mean length of the vestibular cells was 5.34 ± 3.14 cm (range: 1.5-12.8 cm; \( n = 56 \)) (Camillo et al. 1993). Trypoxylon rogenhoferi Kohl (Camillo et al. 1994) and Monobia angulosa Saussure (Camillo et al. 1997), other wasp species that occur at the same region. Such pattern reflects certainly a greater availability of resources during that season since the biotic resources used by wasps (insects or spiders) are also positively influenced by temperature and precipitation of the hot and wet season.

The behavior shown by females of *P. denticulatum* when searching for a nest site was similar to that reported for some other wasp (Coville & Coville 1980) and bee (Vieira de Jesus & Garofalo 2000) species nesting in pre-existing cavities. As reported by Polidori et al. (2005) for Cerceris arenaria L. (Crabronidae), after beginning the provisioning activities the females of *P. denticulatum* spent most of their time away from their nests. According to Bohart & Menke (1976), that occurs in almost all species of solitary wasps that do not close their nests while foraging, as observed in *P. denticulatum*.

The use of mandibles and forelegs to transport the prey, as observed in *P. denticulatum*, was also described by Krombein (1970) for *P. rufipes* and Hook (2004) for *Chlorion cyaneum* (Dahlbom) (Sphecidae), and similarly to *C. cyaneum*, during transportation females of *P. denticulatum* hold the prey dorsum-up. The placement of all prey venter-up and with the head inward toward the inner end of the cell, as observed in *P. denticulatum*, was similar to the reported by Krombein (1967) for a nest of *P. rufipes*. However, in two other nests described later (Krombein 1970), only the prey bearing the wasp egg was placed venter-up while subsequent cockroaches were placed venter-down. According to that author, the difference could be due to the nests belonging to different populations or the arrangement of prey storage being an individual idiosyncrasy. Additional observations are needed to verify if different populations of *P. denticulatum* show different arrangement of prey in nests.

In two nests of *P. rufipes* described by Krombein (1970), the wasps oviposited on the first prey brought to the nests, as observed in three nests of *P. denticulatum* whose females oviposited before entering the nests. It is probable that in other nests here studied, females have also oviposited on the first prey placed in the nests although detailed observations on this were not made. From observations made on other occasions (Garofalo, unpub. data), it is possible to suggest that the occurrence of oviposition before or after female enters the nest depends on the diameter of the cavity utilized for nesting. Thus, the smaller the diameter of the cavity, the higher is the probability of the oviposition to take place before female enters the nest. The position of the egg on the prey was similar for both species, *P. rufipes* and *P. denticulatum*.

**Discussion**

Irrespective of being correlated with temperature or precipitation, the nesting activities of *P. denticulatum* occurred almost exclusively in the hot and wet season, like the pattern described by Camillo et al. (1996). This phenological pattern resembles those reported for *Trypoxylon lactitarse* Saussure (Camillo et al. 1993), *Trypoxylon rogenhoferi* Kohl (Camillo et al. 1994) and *Monobia angulosa* Saussure (Camillo et al. 1997), other wasp species that occur at the same region. Such pattern reflects certainly a greater availability of resources during that season since the biotic resources used by wasps (insects or spiders) are also positively influenced by temperature and precipitation of the hot and wet season.

**Immature mortality and nest associates.** Adult wasps emerged from 91 (52.3%) of 174 cells constructed in 64 nests; among the remaining cells, 36 (20.7%) contained dead immatures from unknown causes, 18 (10.3%) contained both dead adult females and males, and 29 (16.7%) had been parasitized. The immatures died either in the egg stage or first instar larva (29 cells), or the pupal stage (7 cells). Among the parasites, *Melittobia* sp. (Hymenoptera: Eulophidae) was reared from 16 cells and individuals of Chrysididae (Hymenoptera) and Tachinidae (Diptera) emerged from 10 and three cells, respectively.
Variation in the number of prey items per cell within a species can result from differences in allocation of resources to male and female offspring and from variation in the availability of prey of different sizes. According to Camillo et al (1996), in *P. denticulatum*, males are significantly smaller than females with very little overlap in their respective size ranges. Since body size is associated with the amount of food a larva consumes (Krombein 1967, Cowan 1981, Harris 1994), smaller amounts of food are likely deposited in the cells from which males are produced. Although the cockroaches stored in the cells of *P. denticulatum* have not been weighed, a smaller number of them required to provision the male cells suggests that they receive smaller amounts of food. This smaller amount of food could be the responsible factor for the shorter egg-to-adult period in males. This would explain the sequence of sexes in nests because rearing males in the cells closest to nest entrance would facilitate their earlier emergence. The rearing of females from the inner cells and male from the outer cells, as observed in nests of *P. denticulatum*, is a characteristic exhibited by many solitary wasp and bee species (Krombein 1967, Camillo et al 1997, Pereira et al 1999, Wearing & Harris 1999, Matthews 2000, Vieira de Jesus & Garófalo 2000) also nesting in trap-nests.

As reported for some *Chalybion* and *Sceliphron* species (Bohart & Menke 1976), and observed in this study, the construction of a temporary closure occurred in cells that took more than one day to be provisioned. As the wasps do not spend the night inside the nests, the construction of such structure must be related with nest defense against natural enemies.

The total mortality of *P. denticulatum* was relatively high and unlike data observed in other studies with twig-nesting species (Coville & Coville 1980, Boesi et al 2005), the natural enemies were not the primary cause of immature mortality. Similar results have been reported by Garcia & Adis (1993) for *Penepodium goryanum* Lepeltier (Sphecidae), Camillo et al (1993) for *T. lactiisarce* (Crabronidae), Gathmann et al (1994) for several bee and wasp species, and by Camillo et al (1996) also for *P. denticulatum*. As suggested by Parker (1986) for *Osmia sanraefaels* Parker (Megachilidae), by Frankie et al (1988) for some *Centris* species, Vieira de Jesus & Garófalo (2000), Gazola & Garófalo (2003) for *Centris analis* (Fabricius), and Aguiar & Garófalo (2004) for *Centris tarsata* Smith, high environmental temperatures may be a factor causing death of immature stages. Since the maximum monthly temperatures during the nesting period of *P. denticulatum* were relatively high, ranging from 31.5°C (April/2004) to 37.8°C (September/2003) and from 32.3°C (January/2005) to 36.9°C (September/2004), for the period from August/2004 to February/2005, it is probable that this climatic factor has contributed for the observed mortality.

In general, the architecture of the nests studied here was similar to that recorded by Camillo et al (1996). Also, as related by Camillo et al (1996), and observed in this study, most of the nests of *P. denticulatum* had the plug covered externally with resin. The covering of the nest plug with such material has also been reported by Krombein (1970) for *P. rufipes*, and Garcia & Adis (1993) for *P. goryanum*. This coating with resin probably provides greater protection to the nest, as suggested for several *Centris* species (Apidae) (Aguiar & Garófalo 2004, and references therein), since the plug becomes harder after being covered and may reduce the possibility of nest invasion by natural enemies. Besides this protection, the presence of organic debris glued to the resin camouflage the nest entrance.

The number of generations per year observed in this study was higher than that suggested by Camillo et al (1996). On the other hand, irrespectively of the number of generations, the occurrence of prepupal diapause in nests established in late hot/wet season, here documented, was also reported by those authors. Considering that diapause acts as a mechanism of protection from the unfavorable season reducing the risk of extinction (Martins et al 2001), prepupal diapause observed in some nests of *P. denticulatum* would be a survival strategy to face adverse conditions, the dry/cool season. According to Camillo et al (1996), however, prepupal diapause is not the only survival strategy showed by *P. denticulatum* during the adverse period. The simultaneous occurrence of nests with and without immatures in diapause, as documented by those authors, shows that some adults must pass the adverse season taking shelter in unknown places. Although adult diapause is considered a rare event in wasp and bee tropical species (Yanega 1990), strong evidences of its occurrence were reported by Pereira et al (1999) for *Centris vittata* Lepeltier, and by Aguiar & Garófalo (2004) for *C. tarsata*, and *P. denticulatum*.

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**References**


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