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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 luctuosum 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 aureosericeum* 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. After emergence, both females and males were released at the field. Observations on the nesting behavior were recorded for a total of 447h. The activities of females within the nests were observed with an otoscope. Voucher specimens of adult P. 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 cells, the number of prey in male and female cells, the length and width 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 \pm 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

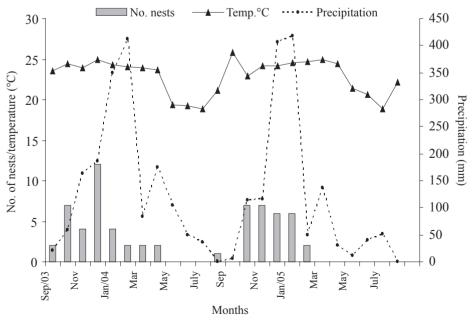


Fig 1 Number of nests of *Podium denticulatum* built monthly, from September 2003 to August 2005, on the campus of Ribeirão Preto of the Universidade de São Paulo, SP, Brazil.

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; x = 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 ± 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.

2.60; P < 0.05). Similarly to the first, subsequent cockroaches were placed venter up and heads pointing towards the inner end of the cell (Fig 3). Prey could be placed adjacent to each other, or placed so that the head of one prey rested upon the abdominal venter of the preceding prey or on top of the preceding prey.

The females either oviposited on the 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 nesting cavity was constricted by a structure similar to a ring of soil. The female continued to add mud to that structure until a 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-collecting 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 \pm 2.79 min; median = 0.97 min; n = 298). The time that the female remained in the nest between mud-colleting trips ranged from 0.08 to 5.6 min (x = 0.66 \pm 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 plug. Following the sequence described above, the female made another cell in front of the first one. After closing the last brood cell, the female initiated the collect of mud to construct the nest plug that resembles a cell partition. During the construction of the nest plug, the female repeated the behaviors exhibited when constructing the cell partition. Nine to 34 mud-collecting trips ($x = 20.8 \pm 9.4$ trips) were required to construct the nest plug (n = 10). The duration of these trips lasted from 0.17 to 23.2 min ($x = 1.94 \pm 3.20$ min; median = 0.83 min; n = 208). The time spent by the female depositing the mud load on the nest plug being constructed ranged from 0.08 to 5.25 min ($x = 0.56 \pm 0.93$ min; median = 0.22 min; n = 0.20 min; median = 0.22 min;

= 208). The empty space between the nest plug and the last brood cells was a vestibular cell.

After finishing the construction of the nest plug, the female covered it with resin of unknown origin (Fig 6), and bits of debris such as fragments of leaves, wood and pieces of other insects were glued to the resin. Of the 64 nests obtained, 59 nests had the nest plug coated with resin and other materials. The duration of resin/other materials-collecting trips ranged from 0.93 to 45.2 min ($x = 9.21 \pm 8.82$ min; median = 7.2 min; n = 45), and the time spent by the female depositing the resin/material on the plug ranged from 0.45 to 6.7 min ($x = 1.45 \pm 1.32$ min; median = 1.03 min; n = 45). The time spent by the female completing a nest was significantly correlated with the number of cells built (r = 0.41; P < 0.01; n = 60) (Table 1).

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; $x=4.2\pm1.7$ cm long; n=44) were significantly longer than male cells (range: 1.7-6.3 cm; $x=3.0\pm0.9$ 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; $x = 0.27 \pm 0.08$ cm; n = 108) at

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

Number of cell per nest	Number of nests	Time (in days)		
		Min.	Max.	$x \pm s.d.$
1	12	1	8	2.6 ± 2.1
2	28	2	5	2.8 ± 1.0
3	13	2	7	3.5 ± 1.4
4	5	3	5	3.8 ± 0.8
5	1	9		9
6	1	;	5	5

the edges than at the centre (range: 0.1-0.2 cm; $x=0.12\pm0.04$ cm; n=108). Nest plugs were always recessed 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 ($x=0.37\pm0.0$ cm; n=53) at the edges and from 0.1 cm to 0.5 cm ($x=0.18\pm0.08$ cm; 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 = 28). Intercalary cells (empty space between two brood cells) occurred in one nest only.

Cocoons were brittle, chestnut-brown, semitransparent, fusiform, and most of them were positioned with their anterior end toward the nest entrance. At the posterior end of cocoons the feces were accumulated. Female cocoons were from 1.4 cm to 2.4 cm long (x = 2.05 ± 0.45 cm; n = 32) and 0.3-0.6 cm wide (x = 0.45 ± 0.06 cm; n = 32) and they were significantly larger than the male cocoons (range: 1.3-2.1 cm long (x = 1.68 ± 0.16 cm); range: 0.3-0.4 cm wide (x = 0.37 ± 0.05 cm); n = 47) (Mann-Whitney tests, Z = 3.88 and Z = 2.88; P < 0.05, respectively).

Sequence of sexes in nests, period of development and sex **ratio.** In the nests that produced adults of both sexes (n = 43), males always emerged before females. Males were reared in cells closest to the nest entrance, and females were reared in cells further away. Deviations from this pattern occurred in one four-celled and one three-celled nest, which produced only males. In nests (n = 27) made from September to February (hot/wet season) a significant difference was found between the egg-to-adult periods for males (range: 24-38 days; x = 31.0 \pm 3.6 days; n = 33) and that of females (range: 30-42 days; x = 35.3 ± 3.8 days; n = 23) (Mann-Whitney test, Z = 3.15; P < 0.05). However, in nests (n = 2) made in March/April (late hot/wet season), with the immatures spending the dry/cold season in diapause as prepupae, no significant difference was found between the egg-to-adult periods for males (range: 166-175 days; $x = 170.4 \pm 3.6$ days; n = 5) and females (range: 173-189 days; $x = 179.3 \pm 8.5$ days; n = 3) (Mann-Whitney, Z = 1.59; P > 0.05). These figures indicate the occurrence of five/six generations per year. The sex ratio of 106 individuals produced from 64 nests was 41.5% females to 58.5% males which is not significantly different from 1:1 sex ratio (χ^2 = 3.1; P > 0.05).

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.

Discussion

Irrespectively 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.

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 & Garófalo 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. cvaneum, 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 prev 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 (Garófalo, unp. 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*.

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 weighted, 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 gorvanum* Lepeletier (Sphecidae), Camillo et al (1993) for T. lactitarse (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 sanrafaelae 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 camouflages 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 Lepeletier, and by Aguiar & Garófalo (2004) for *C. tarsata*, and P. denticulatum.

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References

Aguiar C M L, Garófalo C A (2004) Nesting biology of *Centris* (*Hemisiella*) *tarsata* Smith (Hymenoptera, Apidae, Centridini). Rev Bras Zool 21: 477-486.

Assis J M F, Camillo E (1997) Diversidade, sazonalidade e aspectos biológicos de vespas solitárias (Hymenoptera: Sphecidae: Vespidae) em ninhos armadilhas na região de Ituiutaba, MG. An Soc Entomol Brasil 26: 335-347.

Boesi R, Polidori C, Tormos J, Bevacqua S, Asís J D, Andrietti F (2005) Trap-nesting *Ancistrocerus sikhimensis* (Hymenoptera: Eumenidae) in Nepal: nest structure and associates (Hymenoptera: Chrysididae: Acarina: Saproglyphidae). Fla Entomol 88: 135-140.

Bohart R M, Menke A S (1976) Sphecid wasps of the world: a generic revision. Berkeley and Los Angeles, University of California Press, 695p.

Buys S C, Morato E F, Garófalo C A (2004) Description of the immature instar of three species of *Podium* Fabricius (Hymenoptera, Sphecidae) from Brazil. Rev Bras Zool 21: 73-77.

- Camillo E (2001) Inquilines of *Brachymenes dyscherus* nests with special reference to *Monobia schrottkyi* (Hymenoptera, Vespidae, Sphecidae). Rev Biol Trop 49: 1005-1012.
- Camillo E, Garófalo C A, Assis J M F, Serrano J C (1996) Biologia de *Podium denticulatum* Smith em ninhos armadilhas (Hymenoptera: Sphecidae: Sphecinae). An Soc Entomol Brasil 25: 439-450.
- Camillo E, Garófalo C A, Muccillo G, Serrano J C (1993) Biological observations on *Trypoxylon (Trypargilum) lactitarse* Saussure in southeastern Brazil (Hymenoptera, Sphecidae). Rev Bras Ent 37: 769-778.
- Camillo E, Garófalo C A, Serrano J C (1994) Observações sobre a biologia de *Trypoxylon (Trypargilum) rogenhoferi* Kohl (Hymenoptera: Sphecidae). An Soc Entomol Brasil 23: 299-310.
- Camillo E, Garófalo C A, Serrano J C (1997) Biologia de *Monobia angulosa* Saussure em ninhos armadilhas (Hymenoptera: Vespidae: Eumeninae). An Soc Entomol Brasil 26: 169-175.
- Coville R E, Coville P L (1980) Nesting biology and male behavior of *Trypoxylon (Trypargilum) tenoctitlan* in Costa Rica (Hymenoptera: Sphecidae). Ann Entomol Soc Am 73: 110-119.
- Cowan D P (1981) Parental investment in two solitary wasp *Ancistrocerus adiabatus* and *Euodynerus foraminatus* (Eumenidae: Hymenoptera). Behav Ecol Sociobiol 9: 95-102.
- Frankie G W, Vinson S B, Newstrom L E, Barthell J F (1988) Nest site and habitat preferences of *Centris* bees in Costa Rican dry forest. Biotropica 20: 301-310.
- Garcia M V B, Adis J (1993) On the biology of *Penepodium goryanum* (Lepeletier) in wooden trap-nests (Hymenoptera, Sphecidae). Proc Entomol Soc Wash 95: 547-553.
- Gathmann A, Greiler H J, Tscharntke T (1994) Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. Oecologia 98: 8-14.
- Gazola A L, Garófalo C A (2003) Parasitic behavior of *Leucospis cayennensis* Westwood (Hymenoptera: Leucospidae) and rates of parasitism in populations of *Centris* (*Heterocentris*) *analis* (Fabricius) (Hymenoptera: Apidae: Centridini). J Kansas Entomol Soc 76: 131-142.
- Genaro J A (1994) Inquilinos de *Sceliphron assimile*, com énfasis em *Podium fulvipes* (Hymenoptera: Vespidae, Sphecidae, Megachilidae). Carib J Sc 30: 268-270.
- Harris A C (1994) Biology of *Ancistrocerus gazella* (Hymenoptera: Vespoidea: Eumenidae) in New Zealand. New Zealand Entomol 17: 29-36.
- Hook A W (2004) Nesting behavior of *Chlorion cyaneum* (Hymenoptera: Sphecidae), a predator of cockroaches (Blattaria: Polyphagidae). J Kansas Entomol Soc 77: 558-564.
- Krombein K V (1958) Biology and taxonomy of the cuckoo wasps of coastal North Carolina. Trans Amer Entomol Soc 84: 141-168.

- Krombein K V (1964) Miscellaneous prey records of solitary wasp. V Bull Brooklin Entomol Soc 53: 118-120.
- Krombein K V (1967) Trap-nesting wasps and bees. Life-histories, nests and associates. Washington, DC, Smithsonian Press, 570p.
- Krombein K V (1970) Behavioral and life-history notes on three Floridian solitary wasps (Hymenoptera: Sphecidae). Smithsonian Contr Zool 46, 26p.
- Martins R P, Guerra S T M, Barbeitos M S (2001) Variability in egg-to-adult development time in the bee *Ptilothrix plumata* and its parasitoids. Ecol Entomol 26: 609-616.
- Matthews R W (2000) Nesting biology of the stem-nesting wasp *Psenulus interstitialis* Cameron (Hymenoptera: Crabronidae: Pemphredoninae) on Magnetic Island, Queensland. Australian J Entomol 39: 25-28.
- Morato E F (2001) Efeitos da fragmentação florestal sobre vespas e abelhas solitárias na Amazônia Central. II. Estratificação vertical. Rev Bras Zool 18: 737-747.
- Ohl M (1996) The phylogenetic relationships within the Neotropical Podiinae with special reference to *Podium* Fabricius (Hymenoptera: Apoidea: "Sphecidae"). Dtsch Ent Z 43: 189-218.
- Parker F D (1986) Nesting, associates, and mortality of *Osmia sanrafaelae*. J Kansas Entomol Soc 59: 367-377.
- Pereira M, Garófalo C A, Camillo E, Serrano J C (1999) Nesting biology of *Centris* (*Hemisiella*) *vittata* Lepeletier in southeastern Brazil (Hymenoptera, Apidae, Centridini). Apidologie 30: 327-338.
- Polidori C, Boesi R, Isola F, Andrietti F (2005) Provisioning patterns and choice of prey in the digger wasp *Cerceris arenaria* (Hymenoptera: Crabronidae): the role of prey size. Eur J Entomol 102: 801-804.
- Rau O (1937) A note on the nesting habits of the roach-hunting wasp, *Podium (Parapodium) carolina* Rohwer. Entomol News 48: 91-94.
- Vieira de Jesus B M, Garófalo C A (2000) Nesting behaviour of Centris (Heterocentris) analis (Fabricius) in southeastern Brazil (Hymenoptera, Apidae, Centridini). Apidologie 31: 503-515.
- Wearing C H, Harris A C (1999) Evaluation of the predatory wasp, *Ancistrocerus gazella*, for biological control of leafrollers in otago fruit crops: 1. Prey composition, nest structure and wasp productivity from artificial nests. Biocontrol Sci Technol 9: 315-325.
- Yanega D (1990) Philopatry and nest founding in a primitively social bee, *Halictus rubicundus*. Behav Ecol Sociobiol 27: 37-42.
- Zar J H (1984) Biostatistical analysis. Englewood Cliffs, New Jersey, Prentice-Hall, 663p.

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