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# Nesting Biology of *Podium angustifrons* Kohl (Hymenoptera, Sphecidae) in an Araucaria Forest Fragment

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(With 4 figures)

## Abstract

*Podium angustifrons* Kohl 1902 is a species of solitary wasp which nests in pre-existing cavities, with neotropical distribution in Argentina, Bolivia, Brazil, Colombia, Guyana and French Guyana. The aim of this study was to investigate the nesting biology of *P. angustifrons,* discussing aspects of their life history. To capture its nests, wooden trap-nests were installed in the Parque Municipal das Araucárias, Guarapuava (PR), Brazil, from January 2003 to April 2009. A total of 29 nests were collected, all during the warmer months. These showed no vestibular and intercalary cells, and their closures were made up of chewed plants and mud mixed with organic materials and resin-coated surfaces, sometimes showing a layer of lichens. The cells were provisioned with various wild species of cockroaches (*Chorisoneura* sp, *Riata* sp and *Helgaia* sp) in the nymph stage and/or adults. The sex ratio was 4.6 females per male, significantly higher that the expected 1:1. Most pre-pupae entered diapause in winter with development time ranging from 187 to 283 days for females and 180 to 283 days for males. Deaths occurred in 41.66% of cells provisioned, 33.33% were attributed to faulty development and 8.33% to Chrysididae.

*Keywords:* araucaria forest, solitary wasp, trap-nests.

## Biologia de nidificação de *Podium angustifrons* Kohl (Hymenoptera, Sphecidae) em um fragmento de floresta com araucárias

## Resumo

*Podium angustifrons* Kohl 1902 é uma espécie de vespa solitária que nidifica em cavidades pré-existentes, com distribuição na Argentina, Bolívia, Brasil, Colômbia, Guiania e Guiana Francesa. O objetivo deste estudo foi investigar a biologia de nidificação desta espécie*,* discutindo aspectos de sua história de vida. Para captura seus ninhos, foram instaladas ninhos-armadilha de madeira no Parque Municipal das Araucárias, Guarapuava (PR), Brasil, de Janeiro 2003 até Abril de 2009. Foram coletados 29 ninhos, durante todos os meses quentes. Os ninhos não apresentaram células vestibulares e intercalares, seus fechamentos são constituídos por material vegetal mascado, seguido de barro misturado a materiais orgânicos, revestidos por resina, podendo ter uma camada de liquens. As células foram aprovisionadas com diferentes espécies de baratas silvestres (*Chorisoneura* sp, *Riata* sp e *Helgaia* sp) em estágio de ninfa e/ou adulto. A maioria das pré-pupas entrou em diapausa no inverno com tempo de desenvolvimento de 187 a 283 dias para as fêmeas e 180 a 283 dias para machos. Ocorreu mortalidade em 41,66% das células aprovisionadas, sendo 33,33% causado por falha de desenvolvimento e 8,33% por cleptoparasitas da família Chrysididae.

*Palavras-chave:* araucaria forest, solitary wasp, trap-nests.

## 1. Introduction

The family Sphecidae have approximately 19 genera and 724 species (Pulawski, 2012) of predatory wasps of some insect orders. These wasps are cosmopolitan, however, in some continents such as Africa, Australia and South America they have endemic genera (Bohart and Menke, 1976).

The genus *Podium* belongs to the tribe Podiini and the subfamily Sceliphrinae, which has the habit of nesting in a variety of substrate (Camillo, 2001) and also in pre-existing cavities (Krombein, 1967; Morato, 2001). Like some species of Apoid wasps, females of *Podium* inspect several sites before selecting one for nest building. The nest structures such as cell partitions are made of mud and nest plug of mud, resin and organic debris (Ribeiro and Garófalo, 2010). *Podium denticulatum* Smith 1856, only nest in trap-nests that do not have cracks and are in good condition (Krombein, 1970; Ribeiro, 2006).

Another important aspect of this genus that makes the offspring less susceptible to predation and increases their survival rate is the mass supply, with the female providing all necessary resources essential for the development of the larval stage. Thus, the larvae can survive in confined spaces as the cell supply and the defecation takes place only shortly before pupation, thus preventing contact of food with feces (Santoni, 2008).

Although information is available about the life history of *Podium,* its geographic distribution, nesting habits, materials used for nest building and natural enemies, several aspects of the nesting biology of many species must be described and understood. The species most studied with respect to the points mentioned above are *Podium rufipes* Fabricius 1804 and *P. denticulatum* (Krombein, 1967, 1970; Camillo et al., 1996; Vargas and Beitía, 1996; Assis and Camillo, 1997; Morato, 2001; Buys et al., 2004; Ribeiro, 2006).

*Podium angustifrons* Kohl 1902 (Figure 1), is a species with wide geographical distribution, with records of their existence in Argentina, Bolivia, Brazil, Colombia, Guyana and French Guyana (Amarante, 2002). In southern Brazil this species was found nesting in fragments of Araucária forest (Buschini and Woiski, 2008), an ecosystem that is part of the Atlantic Forest which is currently the second largest Brazilian biome, and one that has seen increased exploitation and fragmentation. As a result, the species in these ecosystems have been subjected to intense changes and have become more prone to local extinction (Mantovani, 2003). It is therefore necessary and urgent to conduct basic studies on biological, ecological and behavioural aspects of particular groups such as *Podium* that use various resources to build their nests, and play an important role in population control of wild cockroaches (Morato, 2001). The purpose of this study was precisely to investigate the nesting biology of *Podium angustifrons,* discussing aspects of their life history such as seasonality, nesting environments, architecture of the nests, prey collected, development time, sex and mortality rates and natural enemies.

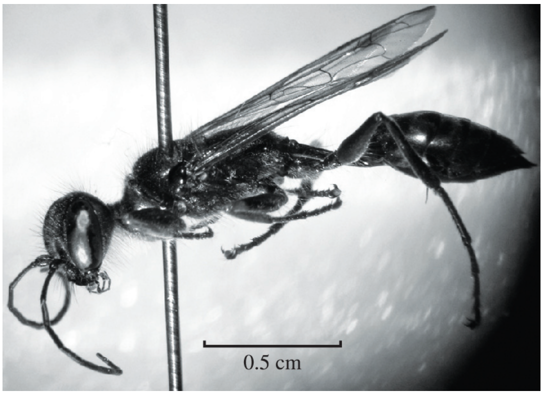

**Figure 1.** Female *P. angustifrons.*

## 2. Methods

### 2.1. Study area

This study was carried out from January 2003 to April 2009 in the Parque Municipal das Araucárias, located in the municipality of Guarapuava (PR), Brazil (25°21’06”S, 51°28’08”W). The park comprises an area of approximately 104 ha. The vegetation is composed of Mixed Ombrophilous Forest (42.75%), gallery forest (10.09%), fields (6.8%), swamps (7.13%) and altered areas (33.23%). This area is characterised by a wet, cool season, and during the warmest months the average temperature is less than 22 °C. Hoar frosts are common and severe in this region.

### 2.2. Sampling program

Nests of *Podium angustifrons* were obtained using trap-nests made out of 25 X 20 X 120 mm wooden boxes, which were drilled longitudinally to a depth of 80 mm with 7.0, 10.0, and 13.0 mm aperture diameters. Before being drilled, the wooden blocks were sawed in half longitudinally and then held together with adhesive tape to allow the examination of the cavities when opened.

For each habitat, two areas were studied, with 2 transects per area and 4 sampling stations per transect. Twelve trap-nests were placed at each sampling station, four of each opening diameter, totalling 576 traps. Each trap was placed 1.5 m above the ground.

From 2005, after it was recorded that *P. angustifrons* did not nest in open areas, trap-nests were kept only in the Araucaria forest, and six blocks were also installed 8 m high in the trunk of Araucaria randomly distributed in the forest. A pulley system was used to raise and lower the blocks. A total of 192 trap-nests were installed and maintained in this environment. These were inspected every two weeks. After each inspection, all completed *P. angustifrons* nests were removed and immediately replaced by empty traps of the same diameter. The nests were then brought to the laboratory to investigate their contents. If eggs and/or larvae were present, the nest was closed to allow the completion of the life-cycle and the emergence of the adults. Newly emerged adults were carefully removed and weighed.

### 2.3. Data analysis

The sex ratio was calculated by the ratio between number of females and males, and the chi-square test was used to check the extent by which the observed sex ratio deviated from the expected frequency (1 female:1 male).

Mann-Whitney’s U test was used to test the null hypothesis relating to nest architecture, premature development time and adult body size and mass.

## 3. Results

### 3.1. Seasonality and nesting environment

Although over the seven years of study several trap-nests were kept in the field, *P. angustifrons* built nests in only 29 of them, all in the Araucaria forest and 1.5 m high. Nesting took place only among the hottest months of the year (from November to April). The nesting activity in trap-nests was more frequent in 2005 and 2007 but was less intense in 2006 and absent in 2008 (Figure 2).

### *3.2. Nest architecture*

*Podium angustifrons* nested only in trap-nests of 0.5 cm and 0.7 cm in diameter. Most of the nest closures were made of layers of chewed plant material, very similar to moss, with spongy consistency and were beige or green in color with small fragments of mud (Figure 3). This was followed by a layer of mud mixed with insect exoskeleton and/or pieces of leaves, coated externally by a delicate layer of glossy resin. Some nest closures (n=5) had an additional outer layer composed of whole lichen. The partitions between the cells were similar to nest closures; made up of chewed plant material externally, and a thinner layer of mud internally, but without the resin coating. The bottom and sides of this wasp´s nests were not coated by mud.

The average nest length ranged from 6.2 to 7.8 cm in trap-nests of 0.5 cm diameter and from 6.3 to 8.4 cm in those with 0.7 cm diameter, without significant difference between their medians (Mann-Whitney: U= 1.6307, P= 0.1029) (Table 1).

The number of provisioned cells ranged from 1 to 3 in trap-nests with 0.5 cm diameter and from 1 to 2 cells in those with 0.7 cm diameter, also without significant difference between their medians (Mann-Whitney: U= 0.6400, P= 0.5222). Intercalar and vestibular cells were not observed in any of the nests (Table 1).

The median length of provisioned cells of the nests with 0.5 cm diameter was not significantly different from that of nests 0.7 cm in diameter (Mann-Whitney: U= 2.0081, P= 0.0446). The median of the cell partition thickness was also not significantly different, being 0.8 cm and 0.6 cm for 0.5 cm and 0.7 cm in diameter, respectively (Mann-Whitney: U= 1.1339, P= 0.2568). The same was observed between the median thicknesses of the closures of these nests (Mann-Whitney: U= 1.3339, P= 0,1822) (Table 1).

Female and male cell volumes ranged from 0,4 cm$^3$ to 1.2 cm$^3$ and from 0.6 cm$^3$ to 1.4 cm$^3$, respectively, without significant difference between their medians (Mann-Whitney: U= 0.6124, P= 0.5403) (Table 2).

### *3.3. Collected prey*

The nests were provisioned with wild species of cockroaches in the nymph stage and / or adults. The number of cockroaches in each cell ranged from 7 to14 (s=2.95; n=5), with 141.1mg (s=18.24; n=5) being the average weight of these cockroaches. Of the 31 cockroaches analysed, three species were identified, with *Chorisoneura* sp being

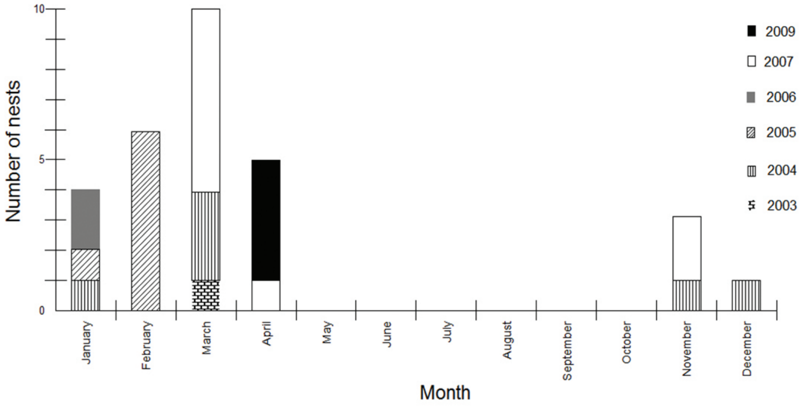

**Figure 2.** Seasonal variation in the number of nests of *P. angustifrons* obtained from 2003 to 2009.

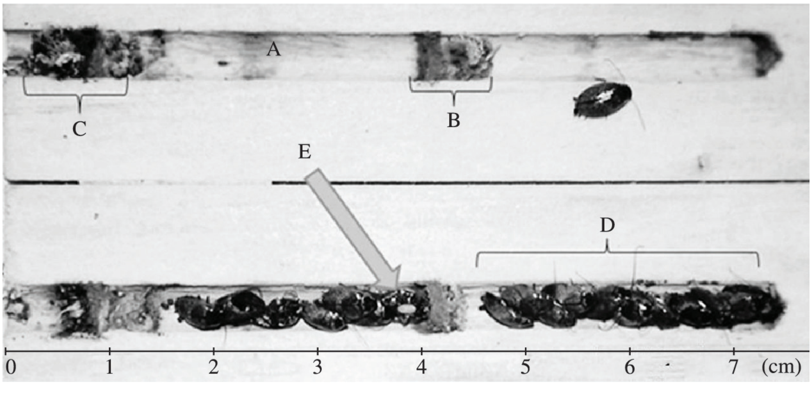

**Figure 3.** Nest of *P. angustifrons* established in 0.5 cm trap-nests with: (*a*) linear cells, (*b*) cells partitions, (*c*) nests plug, (*d*) disposition of cockroaches in cells, (*e*) egg on cockroaches thorax.

**Table 1.** Struture of nests of *P. angustifrons* in trap-nests of different diameters.

| Diameter | Total of nest length | Number of provisioned cells | Thickness of cell partition | Thickness of closure plug |
|---|---|---|---|---|
| 0.5 cm | 7.4 ± 0.50<br>N= 21<br>Median=7.58 | 1.8 ± 0.50<br>N= 25<br>Median=2.0 | 0.9 ± 0.34<br>N=7<br>Median=0.84 | 1.3 ± 1.21<br>N=8<br>Median=0.97 |
| 0.7 cm | 7.6 ± 1.10<br>N=3<br>Median=7.95 | 1.6 ± 0.55<br>N=4<br>Median=2.0 | 0.8 ± 0.55<br>N= 3<br>Median=0.56 | 1.6 ± 0.77<br>N= 4<br>Median=1.41 |

Values are means ± SD, with sample sizes indicated.

**Table 2.** Development time (days), cocoon length, thorax width and weight of females and males.

| | Male | Female |
|---|---|---|
| Weight | 28.1 mg ± 5.34<br>n= 5<br>Median = 28.20 | 43.8 mg ± 7.01<br>n= 18<br>Median = 45.25 |
| Cell volume | 0.8 $cm^3$ ± 0.37<br>n=5<br>Median = 0.62 | 0.8 $cm^3$ ± 0.24<br>n= 15<br>Median=0.74 |
| Cocoon length | 1.4 cm ±0.18<br>n=5<br>Median=1.35 | 1.7 cm ± 0.16<br>n= 19<br>Median=1.75 |
| Thorax width | 0.3 cm ± 0.02<br>n=3<br>Median= 0.27 | 0.3 cm ± 0.03<br>n= 6<br>Median= 0.28 |
| Direct development (without diapause) | 31 | 34 ± 3<br>n=5<br>Median= 34 |
| Delayed development (with diapause) | 208.8± 49.58<br>n=4<br>Median= 186.0 | 233.2 ± 33.62<br>n=18<br>Median= 193.0 |

Values are means ± SD, with sample sizes indicated.

the most abundant (14 individuals), followed by *Riatia* sp (2) and *Helgaia* sp (2). Thirteen cockroaches were not identified because they were in the nymphal stage and hence could not be identified.

### *3.4. Cocoon structure*

The cocoons of both males and females are thin and delicate, brown and shiny with only a translucent layer. Their anterior extremities are more tapered than the posterior and face the bottom of the nests (Figure 4).

The median length of the male cocoons was significantly lower than that of the cocoons of the females, being 1.4 cm and 1.8 cm, respectively (Mann-Whitney: U= 2.5945 P= 0.0095) (Table 2).

### *3.5. Development time, sex ratio and adult size*

The larvae that originated males and females took an average 2 (s=0 n=1) to 2.3 days (s=0.58 n=3) to hatch, respectively. The development time of larvae from hatching until the formation of the cocoon was 6.8 days ± 0.84 (n=5) for females and 7.0 days ± 0.41 (n=3) for males. In all the cells observed the cocoons were formed in just one day.

Most pre-pupae entered in diapause during the winter varying the development time of females from 187 to 283 days and from 180 to 283 days for males, without significant difference between their medians (Mann-Whitney: U=15.748 P= 0.1153). The average development time of females that did not enter in diapause ranged from 31 to 37, while it was 31 days for the only male that emerged.

Sex ratio was strongly female-biased as 23 females and 5 males emerged (4.6 females: 1 male, significantly different from 1 : 1 ($c^2$ = 11.57; d.f. = 1; P< 0.001).

Females had a mean weight of 43.8 mg and the males of 28.0 (Table 2), with a significant difference between their medians (Mann-Whitney: U=3.0187 P= 0.0025).

The width of the thorax of females ranged from 0.2 cm to 0.3 cm (0.3 cm ± 0.03; n= 6) and for the males it ranged from 0.2 to 0.3 cm (0.3 cm ± 0.02; n=3).

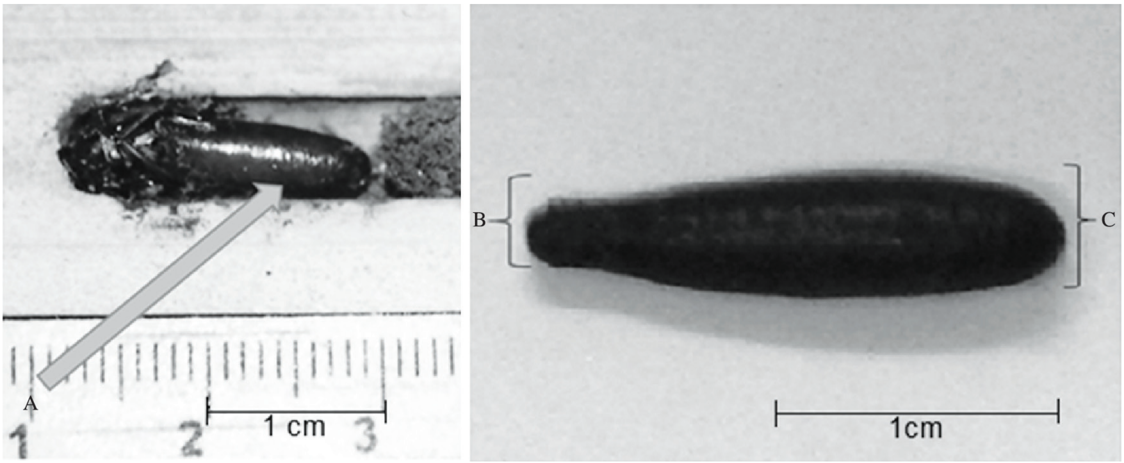

**Figure 4.** *P.angustifrons* cocoon (*a*) with the anterior end more tapering (*b*) than the posterior end (*c*) and facing towards the bottom of the nest.

### *3.6. Mortality and natural enemies*

Of the 43 provisioned cells, 20 (46.5%) resulted in the death of enclosed individuals. In eight cases, (18.6%) deaths were possibly related to developmental failure in larval stage, while in another eight (18.6%), adults died inside the nest as they emerged as they could not possibly go through the mud partitions. Chrysididae (Hymenoptera) accounted for 9.3 of the cases (4 cells).

## 4. Discussion

The study found that *P. angustifrons* existed exclusively in the Araucaria forest areas at the Parque Municipal das Araucárias. As this species uses cockroaches to feed their offspring, one of the possible factors explaining the existance of this wasp in this environment could be the increased availability of prey as forests areas have a lot of wet litter and a significant amount of organic matter. In addition, the insolation rate in the forest is lower than in the open areas because of the dense Araucaria forest canopy. Buschini and Wolff (2006) noted that in this environment humidity was significantly higher and the temperature significantly lower than in the swamp and the grassland. According to Wilson et al. (2007) these two factors together generate the ideal conditions for the population growth of wild cockroaches.

The preference for forested areas with more vegetation cover has also been observed in *P. rufipes* and *Podium* sp in Panama (Vargas and Beitía, 1996), in *P. rufipes* and *P. sexdentatum* Taschenberg 1869 in Central Amazon (Morato and Campos, 2000; Morato, 2001), in *Podium* sp in Western Amazon (Storck–Tonon and Morato, 2005) and in *Podium* sp. in Minas Gerais, southeastern Brazil (Loyola and Martins, 2006). However, *P. denticulatum* has been collected in São Paulo state, southeastern Brazil, mainly in altered areas with low vegetation (Camillo et al., 1996; Assis and Camillo, 1997; Ribeiro, 2006).

The height of the nests built by *P. angustifrons* is only 1.5 m, which differs from results found by Morato (2001) in studies on the biology of *P. rufipes* and of *P. sexdentatum,* which nested at heights of 8-15 m in the Amazon forest. Schal and Bell (1986) cited by Morato (2001) showed in a study of vertical stratification in communities of cockroaches in a tropical forest in Costa Rica, that most individuals of all species of cockroaches collected were found approximately at a height of 0.5 m. If prey availability is an important factor in determining the height of nesting, this could explain *P. angustifrons'* preference for cavities 1.5 m high.

The nesting activity of these wasps also varies between the seasons. In Guarapuava, *P. angustifrons* starts its nesting activities in November, i.e. in the hotter months of the year, and enters into diapause during the winter. The same occurred with *P. denticulatum* (Camillo et al., 1996; Ribeiro, 2006) and *Podium* sp. (Loyola and Martins, 2006), however these species began nesting in September. This variation among species of *Podium* can be related to climatic differences between southern and southeastern regions of Brazil. The city of Guarapuava-PR, southern Brazil, does not have a dry season and its summer and winter seasons are characterised by mild and low temperatures, respectively. In contrast, southeastern Brazil has a hot and humid summer and a cold and dry winter (Ribeiro, 2006). According to Chapman (1998) changes in metabolism that induce diapause in insects are initiated by signals from the environment like adverse weather conditions and resource shortages (Ribeiro, 2006).

As for the nest architecture, *P. angustifrons* showed similarities with information recorded for *P. rufipes* by Krombein (1970), though females of this species built only one cell per nest. The nests of *Podium luctuosum* Smith 1856 and *P. denticulatum* showed a greater number of cells and sometimes vestibular cells (Krombein, 1967; Ribeiro, 2006). Unlike the nests of *P. rufipes* and *P.denticulatum* reported by Krombein (1967) and by Camillo et al. (1996), the nests of *P. angustifrons* showed no empty spaces and mud in their backgrounds, nor layers of mud on their side. Krombein (1967) suggested that these coatings in the back of the nests are built by the female to avoid contact with possible roughness or fibres present.

Some structures in the nests of *P. angustifrons* are common to those of other species of the same tribe as *Penepodium goryanum* Lepeletier 1845 (Garcia and Adis, 1993) and *P. rufipes* (Krombein, 1970). Generally females of these species build cell partitions with mud, the inner part being concave and the outer, convex. The nest´s closing is thicker than cell partitions and is coated with resin. This substance appears to play an important role in protecting the nest because it has hydrophobic potential besides being bactericidal and a repellent against insects (Ghisalberti, 1979). For Krombein (1967) the deposit of materials such as kindling, leaves, exoskeleton of insects and lichens over the nest's closing could be part of its defense strategy as it acts as a camouflage against predators and parasitoids.

Generally these wasps showed a preference of cavities with smaller diameters. For some authors, the preference for nests of certain diameters may be related to factors such as the size of the female's body, interspecific interactions, the size of the prey collected, offspring size and resource availability (Krombein, 1967; Garcia and Adis, 1995; Camillo et al., 1996; Vargas and Beitía, 1996; Assis and Camillo, 1997). Assis and Camillo (1997) showed using trap-nests that smaller wasps used with higher frequency the nests of smaller diameters, while the reverse occurred with larger wasps. Consistent with this information, Camillo et al. (1996) and Ribeiro (2006) demonstrated that *P. denticulatum's* preference for larger nests is related to the size of prey collected since the diameter of the head of the female was much smaller than the diameter of the nest. According to Vargas and Beitía (1996) a factor that may discourage solitary wasps from using trap-nests with diameters larger than their requirements may be the need for larger amounts of materials to supplement the cell partitions. Since they need to spend more time to collect and transport these materials, their prey is likely to be exposed to parasitoids and cleptoparasites. In addition, large diameter closures tend to be more fragile and vulnerable to attacks by natural enemies. Another factor that may determine the preference for certain sizes of cavities could be the interspecific competition for nesting sites (Krombein, 1967). For Begon et al. (2006) the nests species' overlap in time and/or in space in an environment can promote competition. Moreover, the specialisation of certain resources is an adaptive alternative to reduce the effect of competition.

There is variation among species of *Podium* in relation to prey used in the supply of their nests. In Guarapuava, the cockroaches collected by *P. angustifrons* were *Chorisoneura* sp, *Riatia* sp. and *Helgaia* sp., while in other regions *P. rufipes* collected *Latiblattella rehni* Hebard 1917*, Chorisoneura texensis* Saussure and Zehntner 1893*, Eurycotis floridana* (Walker)*, Parcoblatta pennsylvanica* (De Gerr 1773)*, Cariblata lutea* (Saussure and Zehntner, 1893) and *Cariblata minima* Hebard 1916 (Krombein, 1967), *P. denticulatum* collected *Cahita borero* Rehn 1937 and *Pseudomops neglecta* Shelford 1906 (Camillo et al., 1996; Ribeiro and Garófalo, 2010) and *P. fulvipes Euthlastoblatta* spp., *Cariblata* sp., *Latiblattella rehni* Herbard, 1917, *Epilampra* sp. and *Plectoptera* sp. (Genaro, 1994). However, *P. luctuosum* was more specialist and provisioned its nests only with *Parcoblatta uhleriana* (Saussure, 1862) (Krombein, 1967).

In this study, the number of females was significantly higher than that of males. As this was quite unexpected, the data needs to be investigated in more detail. It should be mentioned that studies concerning sex allocation of *P. angustifrons* in this region have already begun. We cannot disregard the possibility of nests of cells that produced males were built in holes with diameters below those sampled in this study. It was observed that in most cases, the nests were formed by cells that gave rise to females which would also explain the discrepancy in the sex ratio.

Although the cell volumes of females and males and the median width of their thorax were not significantly different, females were significantly heavier than males and their cocoons bigger. In general, males and females of Sphecidae are dimorphic in relation to body size, with males being smaller (Peruquetti and Del Lama, 2003). If the body size of males and females is influenced by the amount of food received in the larval stage, then the female offspring would benefit most from receiving a greater quantity of food. This is justified since males do not require a large amount of food as their role is restricted to mating and they do not need to capture, transport or supply the prey, activities that are carried out by females (Molumby, 1997).

As for the natural enemies, Chrysididae was the only cleptoparasitic which caused death in cells of *P. angustifrons.* The rate of parasitism in the nests of *P. angustifrons* was low compared to that of *P. denticulatum* (Ribeiro, 2006). Besides Chrysididae, *P. denticulatum* was also parasitized by *Melittobia* sp. (Eulophidae), Tachinidae, *Anthrax* sp. (Bombyliidae), Perilampidae and Phoridae in southeastern Brazil (Camillo et al., 1996; Ribeiro, 2006). In southern parts of the United States the nests of *P. rufipes* were parasitised by *Melittobia* sp. (Eulophidae) and *Neochrysis panamensis* (Cameron) (Chrysididae) (Krombein, 1970). As mentioned earlier, the architecture, as well as materials used in the nest-building by *Podium* may have an influence on the rate of parasitism. Unlike the nests of *P. denticulatum* those of *P. angustifrons* have closures with additional coats of plants and lichens, and layers of mud and exoskeleton were relatively thicker (Camillo et al., 1996; Ribeiro, 2006). It is possible that the thicker layers of mud and exoskeleton hinder the invasion by parasitoids and cleptoparasites (Vargas and Beitía, 1996) and additional plant layers camouflage the nest against natural enemies (Krombein, 1967).

Considering the results presented here we can conclude that *P. angustifrons* is a relatively rare species in Guarapuava, southern Brazil, with the habit of nesting in Araucaria forest. Given the variety of materials used in construction of their nests and considering that it uses more than one prey species as food for its offspring, it is clear that the degree of interaction of this wasp with other species in these forests is remarkable. Like any other Brazilian ecosystem, the Araucaria forests have seen rapid exploitation and fragmentation, and as a result there is only about 3% of its original coverage in the state of Paraná today. Since forest fragmentation results in the reduction and isolation of populations of animals and plants, forest dynamics are eventually affected. Therefore parallel to the studies on the species that compose an ecosystem, those on their natural history and the way these species interact with each other thus promoting the resilience of the ecosystem, are necessary and urgent because only through this information can we come up with more accurate measures of conservation towards greater sustainability.

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