

Prey selection in the trap-nesting wasp *Trypoxylon (Trypargilum) opacum* Brèthes (Hymenoptera; Crabronidae)

Buschini, MLT.^{a*}, Borba, NA.^{a*} and Brescovit, AD.^{b*}

^aDepartamento de Biologia, Universidade Estadual do Centro-Oeste – UNICENTRO, Rua Presidente Zacarias, 875, CEP 85010-990, Guarapuava, PR, Brazil

^bLaboratório de Artrópodes Peçonhentos, Instituto Butantan, Av. Brasil, 1500, CEP 05503-900, São Paulo, SP, Brazil

*e-mail: isatunes@yahoo.com.br, neideaugusta@yahoo.com.br, address@terra.com.br

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(With 5 figures)

Abstract

The purpose of our research was to document and discuss the temporal patterns of prey use shown by the trap-nesting wasp *Trypoxylon opacum* in two different habitats in Southern Brazil. It was carried out from December 2001 to December 2004. Twenty nine species belonging to five families of spiders were captured by *T. opacum*. Araneidae was the most captured family and has been strongly represented by the genus *Eustala*. Through Bray-Curtis's coefficient and the unweighted pair group method average (UPGMA), the spiders can be divided into three groups: the smaller group includes the most abundant species (*Alpaida* sp2, *Bertrana rufostriata*, *Eustala* sp1, *Eustala* sp2, *Eustala* sp3 and *Eustala* sp4), the second group includes species with intermediate abundance (*Alpaida*, *Alpaida gracia* and *Mangora* sp2), and the third and largest group includes the less abundant species, (*Acacesia villalobosi*, *Alpaida argenata*, *Alpaida* sp1, *Araneus blumenau*, *Araneus sicki*, *Crysmeta boraceia*, *Crysmeta* sp3, *Eustala* sp8, *Eustala* sp11, *Larinia t-notata*, *Mangora* sp1, *Ocrepeira aff gnomo*, *Sanogasta* sp., *Sanogasta* sp2, *Sanogasta* sp3, Salticidae sp2, *Theridion* sp1, *Theridion* sp2, *Wagneriana eupalaestris*, *Wagneriana iguape*). Of 1,053 identified spiders, 362 were captured in the grassland areas and 691 in the swamp, since *T. opacum* built nests only in these two habitats. The diversity, richness and evenness of spiders in *T. opacum* nests were higher in grassland than in the swamp.

Keywords: Crabronidae, *Trypoxylon opacum*, spider, prey use.

Seleção de presas por vespa que nidifica em ninhos-armadilha *Trypoxylon (Trypargilum) opacum* Brèthes (Hymenoptera; Crabronidae)

Resumo

O objetivo desta pesquisa foi documentar e discutir o padrão temporal de uso de presas por *Trypoxylon opacum* em dois ambientes diferentes no Sul do Brasil. Ela foi realizada de dezembro de 2001 a dezembro de 2004. Vinte e nove espécies de aranhas pertencentes a cinco famílias foram capturadas por *Trypoxylon opacum*. Araneidae foi a família mais capturada e foi fortemente representada pelo gênero *Eustala*. Pelo coeficiente de Bray-Curtis e pela análise de agrupamento, (UPGMA) as aranhas foram divididas em três grupos: o menor deles, incluindo as aranhas mais abundantes na dieta de *T. opacum* (*Alpaida* sp2, *Bertrana rufostriata*, *Eustala* sp1, *Eustala* sp2, *Eustala* sp3 and *Eustala* sp4); o segundo com as espécies cujas abundâncias foram intermediárias (*Alpaida*, *Alpaida gracia* and *Mangora* sp2); e o terceiro e maior grupo com as espécies pouco abundantes (*Acacesia villalobosi*, *Alpaida argenata*, *Alpaida* sp1, *Araneus blumenau*, *Araneus sicki*, *Crysmeta boraceia*, *Crysmeta* sp3, *Eustala* sp8, *Eustala* sp11, *Larinia t-notata*, *Mangora* sp1, *Ocrepeira aff gnomo*, *Sanogasta* sp., *Sanogasta* sp2, *Sanogasta* sp3, Salticidae sp2, *Theridion* sp1, *Theridion* sp2, *Wagneriana eupalaestris*, *Wagneriana iguape*). Das 1.053 aranhas identificadas, 362 foram capturadas em área de campos naturais e 691 em área de várzea, visto que *T. opacum* fundou ninhos apenas nestes ambientes. A diversidade, a riqueza e a equitabilidade de aranhas nos ninhos de *T. opacum* foram maiores nas áreas de campos do que aquelas de várzeas.

Palavras-chave: Crabronidae, *Trypoxylon opacum*, aranhas, uso de presas.

1. Introduction

Most wasps belong to the families Pompilidae, Sphecidae, Crabronidae, use terrestrial arthropods as food supply for their offspring. Most of them paralyse their prey, drag it to a burrow, and lay one egg on the prey item. When the wasp larva hatches, it feeds on the paralysed host (Coville, 1987). Their efficiency as hunters is enhanced by their ability to walk on plants covered by wax bloom (Eigenbrode et al., 2000) and by their ability to learn (Jones et al., 2002).

Predatory wasps may exert selective pressures on their prey, and studies of the hunting mechanisms and ecosystem impacts of predation by solitary wasps may provide insight into the evolutionary mechanisms, defining the niches of generalist and specialist predators (Evans, 1963).

Solitary nesting sphecids, a group including both Crabronidae and Sphecidae wasps, show a high degree of prey specialisation ranging from one single species to many species of one single insect family or order (O'Neill, 2001). Moreover, individuals within a population might vary their resource use because they inhabit different microhabitats (Coville, 1987).

In *Trypoxylon* and in other genera in the family Crabronidae and in the related family Sphecidae, females hunt spiders to provide food for their larvae (Coville, 1987). These wasps capture a wide range of spider taxa, including orb-weaving spiders (Araneidae, Tetragnathidae, Nephilidae), araneoid sheet web weavers (Theridiidae), and even several taxa that usually do not use webs to capture prey (Lycosidae, Oxyopidae, Clubionidae) (Camillo and Brescovit, 1999a, 1999b; Blackledge et al., 2003; Buschini and Wolff, 2006; Buschini et al., 2006). They have great flexibility in selecting the spider's size, since they can supply the nutrients required for larval development by depositing several small specimens in each cell (Gonzaga and Vasconcellos-Neto, 2005).

A number of biological traits of prey can be relevant during hunting, in particular, anti-predator mechanisms. Within the large range of defensive mechanisms that have evolved in spiders in response to predation (Cloudsley-Thompson, 1995), the three-dimensional webs of the Orbiculariae are probably among the most effective against capture by hunting-wasps (Blackledge et al., 2003). Moreover, one of the main factors inducing a particular prey capture is the availability of suitable prey in the locality. Studies have demonstrated that prey capture might be related to either the availability of prey or the prey-predator size relationship, or to the hunting behaviour, in particular, the preferred hunting habitat (O'Brien, 1982; Weaving, 1988; Polidori et al., 2005).

Few studies concerning the temporal patterns of prey selection shown by *Trypoxylon* species have been undertaken in Brazil (Camillo and Brescovit, 1999a, 1999b; Camillo and Brescovit, 2000). Buschini et al. (2008) investigated the patterns of prey selection of *Trypoxylon lactitarse* Saussure in the Parque Municipal das Araucárias. According to these authors fifty three species of spiders

belonging to seven families were captured by *T. lactitarse* and Araneidae was the most captured family. *Trypoxylon opacum* also occurs in this Park and like *T. lactitarse* it is one of the most abundant species (Buschini and Woiski, 2008), although it is a poorly known species of solitary wasp. The only investigation on this species was carried out by Buschini and Wolff (2006) who reported on several aspects of its biology. In the light of this, the purpose of our research was to verify if the prey spectrum of *Trypoxylon opacum* varies across nesting seasons and between two different habitats.

2. Methods

2.1. Study areas

This study was carried out in the Parque Municipal das Araucárias, in the municipality of Guarapuava, State of Paraná, Southern Brazil (25° 23' S and 51° 27' W, 1,120 m of altitude). This area is characterised by a wet, cool season. Hoar frosts are common and severe. During the warmest months the average temperature is less than 22 °C.

Collections were carried out from December 2001 to December 2004 and were concentrated in a very heterogeneous site, with araucaria forests, swamps and grasslands. The grasslands are characterised, physiologically, by areas of low grasses and no bushes. Species belonging to Cyperaceae, Leguminosae, Verbenaceae, Compositae and Apiaceae are the main ones found in this habitat. In Araucaria forest, there is a predominance of *Araucaria angustifolia* (Bertolini) (Coniferae; Araucariaceae) and in swamps, which are located in the lowest regions of the park, there are mainly grasses and Compositae.

2.2. Sampling program

Nests of *T. opacum* were obtained using trap-nests made out of 25 × 20 × 120 mm wooden blocks (*Araucaria angustifolia*), drilled longitudinally to a depth of 80 mm with 7.0, 10.0, and 13.0 mm aperture diameters. Before being drilled, they 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, totaling 576 trap-nests which were constantly kept in the field. They were placed at 1.5 m above the ground and inspected every two weeks. In each inspection, all completed wasps nests were removed and immediately replaced with empty traps of the same diameter. The nests were then brought to the laboratory in order to investigate their contents. If live eggs and/or larvae were present, the nest was closed to allow the completion of the life-cycle and the emergence of the adults. All spiders from cells with dead eggs or larvae were removed and identified. Spider abundance was calculated according to sex, development stage, family, genus and species.

2.3. Statistical analyses

Three indices were used to investigate the diversity of spider species in the diet of *T. opacum* in each of the habitats where they founded their nests: species richness (Margalef's index), Shannon-Wiener diversity and species evenness (Pielou's J index) (Ludwig and Reynolds, 1988).

To investigate the similarity between spider species abundances in *T. opacum*'s diet they were grouped according to their abundances, using the Bray-Curtis coefficient, as

a metric and the unweighted pair group method average (UPGMA) as the clustering method (Ludwig and Reynolds, 1988). The cophenetic coefficient of correlation was calculated in order to assess the appropriateness of the dendrograms. Similarity matrices were compared using the Mantel test (Mantel, 1967).

Spider species dominance was calculated according to Palma (1975):

$$D = (\text{Abundance of species} \div \text{Total abundance}) \times 100 \quad (1)$$

if $D > 5\%$, the species is termed a dominant species; if $2.5\% < D < 5\%$, the species is termed an accessory species; if $D < 2.5\%$, the species is termed an incidental species.

Chi-square tests were used to test the null hypothesis related to the proportion of collected juveniles, males and females according to the BioStat 5.0 programme (Ayres et al., 2003).

3. Results

3.1. Nesting activity of *Trypoxylon opacum* in different habitats

A total of 312 *T. opacum* nests were collected. Nests were more frequently found in the grassland than in the swamp areas. *Trypoxylon opacum* did not build nests in araucaria forest. They were built mainly during the summer (between December and March), during high temperature periods (Figures 1 and 2).

3.2. Species of spiders collected by *Trypoxylon opacum*

Twenty nine species of spiders belonging to 4 families were captured by *T. opacum*. Araneidae was the most captured family with 1,042 individuals (99%), distributed among 9 genera (69%) and 21 species (72%). Although the majority of the individuals ($n = 850$) belonging to this family were juveniles and could not be identified, of species identified *Eustala* sp2 was the most frequently captured species with 34 individuals (Table 1). This species was

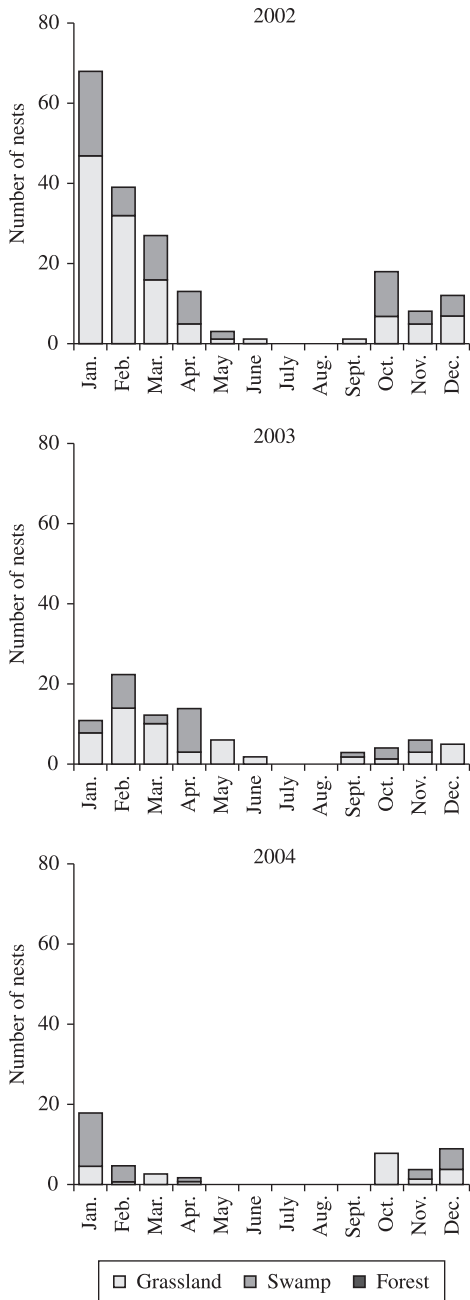


Figure 1. Seasonal variation in the number of nests of *T. opacum* obtained monthly, in different habitats, from December 2001 to December 2004.

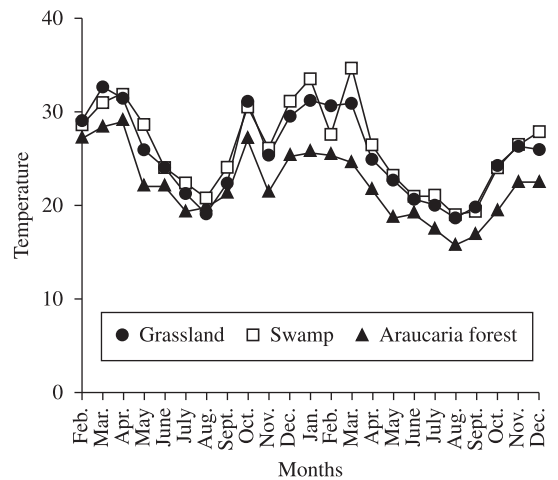


Figure 2. Air temperature (°C) in different habitats from February 2002 to December 2003 (Buschini et al., 2006).

captured throughout 6 months, most frequently during January, February and April. *Bertrana rufostriata*, the second most frequent species with 30 individuals, was captured throughout 4 months, most frequently in April. *Eustala* sp1 also with 30 individuals captured, was most frequent in January, March and April (Figure 3).

Tetragnathidae was the second most captured family, with 4 individuals, distributed in 1 genus and 2 species. *Crysmeta boraceia* was the most captured species with 3 individuals collected during the months of January and April.

Anyphaenidae, represented by 3 individuals, belonging to the same genus and 3 species, Theridiidae also with 3 individuals to the same genus and Salticidae with a single individual, were the other families captured by *T. opacum*.

3.3. Species of spiders in the grassland and swamp areas

Of 1,053 spiders, 362 were captured in grassland areas and 691 in swamp. Of identified species *Alpaida* sp2, *Alpaida gracia*, *Eustala* sp1, *Eustala* sp2, *Eustala* sp3, *Eustala* sp4 and *Crysmeta boraceia* were common to the two habitats.

Table 1. Number of juvenile (J), female (F) and male (M) spiders collected by *T. opacum* in different habitats.

Species	Grassland			Swamp		
	J	M	F	J	M	F
ANYPHAENIDAE Bertkau, 1878						
<i>Sanogasta</i> sp Mello-Leitão, 1941		1				
<i>Sanogasta</i> sp2			1			
<i>Sanogasta</i> sp3		1				
ARANEIDAE Simon, 1895	850					
<i>Acacesia villalobosi</i> Glueck, 1994			2			
<i>Alpaida</i> O. P.-Cambridge, 1889				10		
<i>Alpaida argenata</i>		1				
<i>Alpaida gracia</i> Levi, 1988			2			3
<i>Alpaida</i> sp1 Cambridge, 1889			1			
<i>Alpaida</i> sp2			1			15
<i>Araneus blumenau</i> Levi, 1991		2				
<i>Araneus sicki</i> Levi, 1991			2			
<i>Bertrana rufostriata</i> Simon, 1893						30
<i>Eustala</i> sp1 Simon, 1895		10	8	2	2	8
<i>Eustala</i> sp2	12	6	3	3	5	5
<i>Eustala</i> sp3		9	10		1	
<i>Eustala</i> sp4		2		21		
<i>Eustala</i> sp8						1
<i>Eustala</i> sp11					1	1
<i>Larinia t-notata</i> (Tullgren, 1905)			1			1
<i>Mangora</i> sp1 O. P.-Cambridge, 1889		1				
<i>Mangora</i> sp2		2	5			
<i>Ocrepeira</i> aff <i>gnomo</i> (Mello-Leitão, 1943)			1			
<i>Wagneriana eupalaestris</i> Levi, 1991			1			
<i>Wagneriana iguape</i> Levi, 1991		1				
SALTICIDAE Blackwall, 1841						
sp2	1					
TETRAGNATHIDAE Menge, 1866						
<i>Crysmeta boraceia</i> Levi, 1986			2		1	
<i>Crysmeta</i> sp3 Simon, 1894						1
THERIDIIDAE Sundevall, 1833	1					
<i>Theridion</i> sp1 Walckenaer, 1805						1
<i>Theridion</i> sp2						1
Total	864	36	40	36	10	67

Sanogasta sp., *Sanogasta* sp2, *Sanogasta* sp3, *Acacesia villalobosi*, *Alpaida* sp1, *Araneus blumenau*, *Araneus sicki*, *Larinia t-notata*, *Mangora* sp1, *Mangora* sp2, *Ocrepeira* aff *gnomo*, *Wagneriana eupalaestris*, *Wagneriana iguape* and one individual of the family Salticidae were captured only in grassland areas, while *Alpaida*, *Bertrana rufostriata*,

Eustala sp₈, *Eustala* sp11, *Crysmeta* sp3, *Theridion* sp1 e *Theridion* sp2 occurred only in swamp. *Eustala* sp4 was the most captured species in swamp (n = 21), while *Eustala* sp1 was the most collected species in the grassland areas (n = 21).

3.4. Spider diversity and similarity

The diversity of spider species used by *T. opacum* was higher in grassland ($H' = 1.003$) than in swamp area ($H' = 0.909$). Although the grasslands presented higher spider species richness ($D_{Mg} = 10.773$) than the swamp area ($D_{Mg} = 6.819$), the evenness was higher in swamp area ($J' = 0.773$) than in the grasslands ($J' = 0.747$).

Figure 4 shows that, not taking into account the different habitats, identified spiders can be divided into 3 groups according to abundance ($r = 0.962$). The smaller group includes the most abundant species (*Alpaida* sp2, *Bertrana rufostriata*, *Eustala* sp1, *Eustala* sp2, *Eustala* sp3 and *Eustala* sp4), i.e., those most commonly captured by *T. opacum*. The second group includes species represented by a range of 7 to 10 individuals (*Alpaida*, *Alpaida gracia* and *Mangora* sp2). The third and largest group includes the less abundant species, represented by a range of 1 to 3 individuals (*Sanogasta* sp, *Sanogasta* sp2, *Sanogasta* sp3, *Theridion* sp2, *Crysmeta* sp3, Salticidae

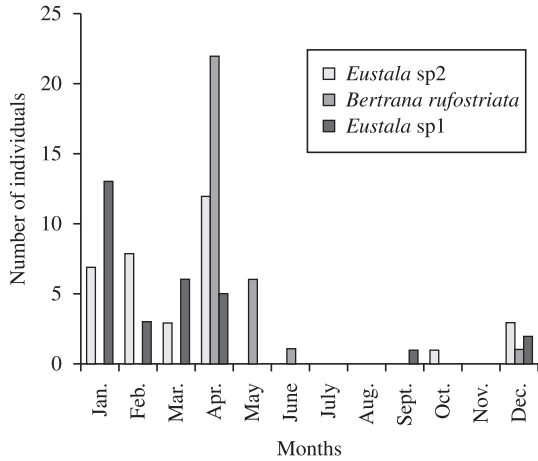


Figure 3. Monthly number of prey species most frequently collected by *T. opacum*.

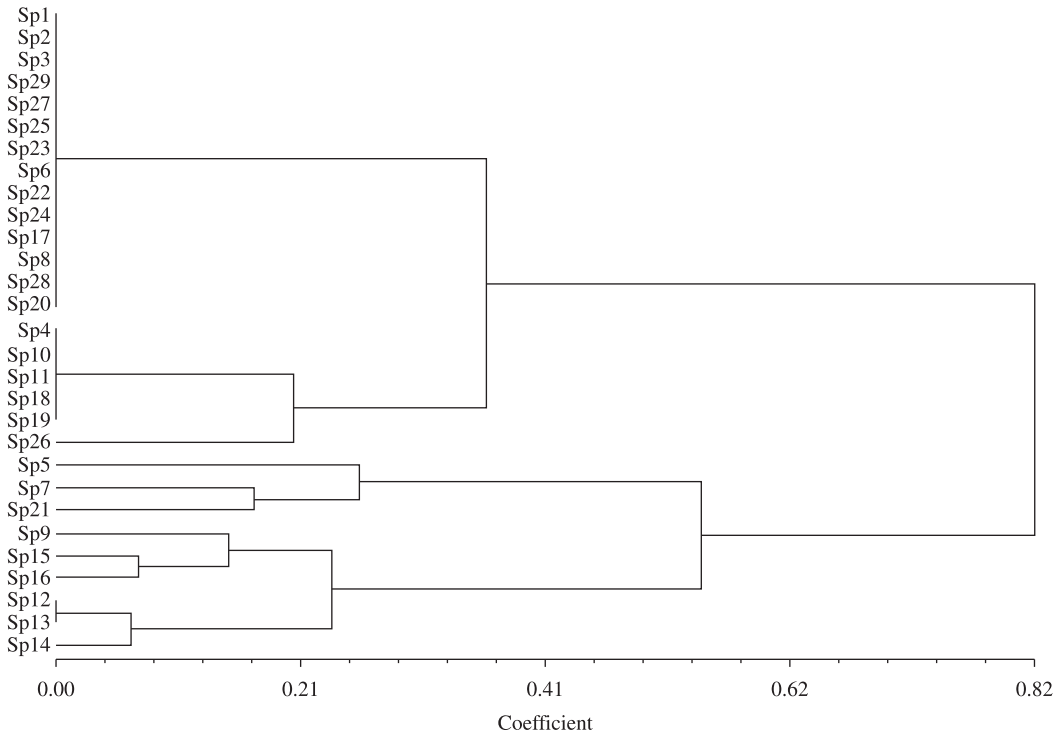


Figure 4. Dissimilarity dendrogram between spiders species related to their abundances on *T. opacum* diet: Sp1 = *Sanogasta* sp.; Sp2 = *Sanogasta* sp2; Sp3 = *Sanogasta* sp3; Sp4 = *Acacesia villalobosi*; Sp5 = *Alpaida*; Sp6 = *Alpaida argenata*; Sp7 = *Alpaida gracia*; Sp8 = *Alpaida* sp1; Sp9 = *Alpaida* sp2; Sp10 = *Araneus blumenau*; Sp11 = *Araneus sicki*; Sp12 = *Bertrana rufostriata*; Sp13 = *Eustala* sp1; Sp14 = *Eustala* sp2; Sp15 = *Eustala* sp3; Sp16 = *Eustala* sp4; Sp17 = *Eustala* sp₈; Sp18 = *Eustala* sp11; Sp19 = *Larinia t-notata*; Sp20 = *Mangora* sp1; Sp21 = *Mangora* sp2; Sp22 = *Ocrepeira* aff *gnomo*; Sp23 = *Wagneriana eupalaestris*; Sp24 = *Wagneriana iguape*; Sp25 = Salticidae sp2; Sp26 = *Crysmeta boraceia*; Sp27 = *Crysmeta* sp3; Sp28 = *Theridion* sp1; Sp29 = *Theridion* sp2.

sp2, *Wagneriana eupalaestris*, *Ocrepeira* aff *gnomo*, *Eustala* sp8, *Alpaida argenata*, *Wagneriana iguape*, *Alpaida* sp1, *Theridion* sp1, *Mangora* sp1, *Araneus sicki*, *Acacesia villalobosi*, *Araneus blumenau*, *Eustala* sp11, *Larinia t-notata* and *Crysmeta boraceia*). A similar pattern emerged from the dominance indices, with the groups of dominant, accessory and accidental species (Table 2).

3.5. Number of juveniles, males and females used by *Trypoxylon opacum*

A total of 900 juvenile spiders (86%), 107 females (10%) and 46 males (4%) were captured by *T. opacum*. These proportions are significantly different between them (Table 3).

Juveniles were present throughout the 10 month sampling period, but were most frequent in January (18%), April (23%) and May (15%). Females were captured during 8 months, being most frequent in January (14%), February (23%) and April (39%). Males were captured during 7 months and were most frequent in January (30%), February (17%) and April (26%) (Figure 5).

4. Discussion

Prey of *T. opacum* were almost exclusively araneid spiders. Similar data has been obtained for other species of *Trypoxylon* (Camillo and Brescovit, 1999a, 1999b; 2000; Coville, 1981, 1987; Rehnberg, 1987; Garcia and Adis, 1995; Buschini and Wolff, 2006; Araújo and Gonzaga, 2007; Buschini et al., 2008).

Buschini et al. (2008) studied the prey selection pattern of *T. lactitarse* also in the Parque Municipal das Aruacárias. These authors observed a pattern similar to that of *T. opacum*, with Araneidae and the genus *Eustala* being the most captured, even though *T. lactitarse* captured twenty four species more than *T. opacum*. It is interesting that, in addition to nidifying in both field and swamp areas during the same period as *T. opacum*, *T. lactitarse* also nidifies in forest areas, where *Alpaida* and *Acacesia* were also frequently captured. The genus *Bertrana* was the second most used by *T. opacum*, but not by *T. lactitarse*, that used more spiders of the genus *Araneus* in field and swamp areas.

Another abundant species in this park is *Trypoxylon agameannon* Richards. This species nidifies solely in forest areas (Buschini and Farjardo, in press) and captures almost exclusively wandering spiders of the family Anyphaenidae and genus *Teudis*. Although Araneidae is the second most frequent family in the diet of this wasp, the genus *Eustala* wasn't very used.

Camillo and Brescovit (1999a) studied spiders captured by *T. lactitarse* in three different regions of Southeastern Brazil. Spiders belonging to the family Araneidae (96.6%) were also most frequently captured. They used the Shannon-Wiener index to investigate the amplitude of the reproductive niche of this wasp in the different localities. The values obtained in the three areas were: $H' = 2.24$, $H' = 2.72$ e $H' = 1.76$. Although in the

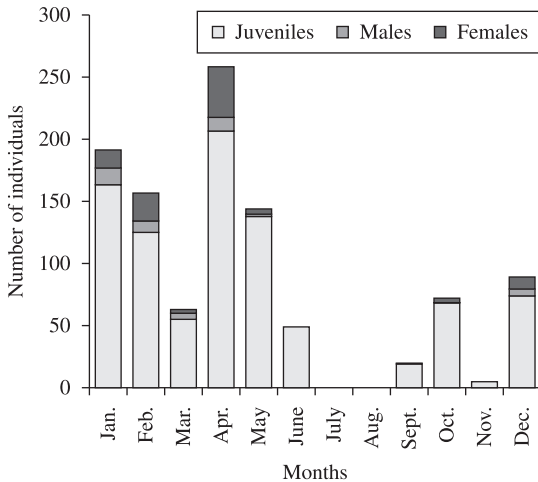
present study the Shannon-Wiener index was used to evaluate the diversity of spiders in the diet of *T. opacum* in different habitats, the results can be compared to those of Camillo and Brescovit (1999), since they were obtained in a similar manner. For *T. opacum* the value obtained for the field was $H' = 1.00$ and for the swamp $H' = 0.91$. This indicates a lower amplitude than that obtained by these authors for *T. lactitarse*. Considering the results obtained by Buschini et. al. (2008), using the same index for *T. lactitarse*, the values obtained in araucária forest, field and swamp areas were $H' = 1.00$, $H' = 0.97$ and $H' = 1.16$, respectively. These values were similar to those obtained for

Table 2. List of spider species and their respective dominance indices.

Family/species	Dominance index (D)	Dominance classification
ANYPHAENIDAE		
<i>Sanogasta</i> sp1	0.5	accidental
<i>Sanogasta</i> sp2	0.5	accidental
<i>Sanogasta</i> sp3	0.5	accidental
ARANEIDAE		
<i>Acacesia villalobosi</i>	1.0	accidental
<i>Alpaida</i>	5.0	accessory
<i>Alpaida argenata</i>	0.5	accidental
<i>Alpaida gracia</i>	2.5	accessory
<i>Alpaida</i> sp1	0.5	accidental
<i>Alpaida</i> sp2	7.9	dominant
<i>Araneus blumenau</i>	1.0	accidental
<i>Araneus sicki</i>	1.0	accidental
<i>Bertrana rufostriata</i>	14.9	dominant
<i>Eustala</i> sp1	14.9	dominant
<i>Eustala</i> sp2	16.8	dominant
<i>Eustala</i> sp3	9.9	dominant
<i>Eustala</i> sp4	11.4	dominant
<i>Eustala</i> sp ₈	0.5	accidental
<i>Eustala</i> sp11	1.0	accidental
<i>Larinia t-notata</i>	1.0	accidental
<i>Mangora</i> sp1	0.5	accidental
<i>Mangora</i> sp2	3.5	accessory
<i>Ocrepeira</i> aff <i>gnomo</i>	0.5	accidental
<i>Wagneriana eupalaestris</i>	0.5	accidental
<i>Wagneriana iguape</i>	0.5	accidental
SALTICIDAE		
sp2	0.5	accidental
TETRAGNATHIDAE		
<i>Crysmeta boraceia</i>	1.5	accidental
<i>Crysmeta</i> sp3	0.5	accidental
THERIDIIDAE		
<i>Theridion</i> sp1	0.5	accidental
<i>Theridion</i> sp2	0.5	accidental

Table 3. Qui-square test between the proportions of juveniles, females and males used by *T. opacum* in its diet.

Comparisons	Qui-square values	Probabilities
Juveniles × Females	55.44	p < 0.001
Juveniles × Males	62.80	p < 0.001
Females × Males	7.36	p < 0.001

**Figure 5.** Monthly number of juveniles, males and females of the spiders prey hunted by *T. opacum*.

T. opacum in the same habitat in this park, but were lower than those obtained for this same species in southeastern Brazil. Camillo and Brescovit (1999a) do not discuss these results but comment that Genaro et al. (1989) obtained, for *Trypoxylon subimpressum* Smith in Cuba, values that were similar to those obtained in their study.

Trypoxylon rogenhoferi Kohl also showed a preference towards spiders of the family Araneidae (Camillo and Brescovit, 2000). This species captured 55 species of spiders, with *Alpaida* being the most collected genus. The amplitude of the reproductive niche for this species in the three studied regions was $H' = 1.25$, $H' = 1.30$ and $H' = 1.29$ and, according to these authors, were not significantly different. When compared to those obtained for *T. lactitarse* in these same regions (Camillo and Brescovit 1999a) those of *T. rogenhoferi* were lower. According to Camillo and Brescovit (2000), these results indicate that these species do not compete in any significant manner for food in the three studied habitats.

A comparison between the spiders captured by *Trypoxylon albonigrum* Richards and by *T. lactitarse* and those found in the environment was carried out by Gonzaga and Vasconcellos-Neto (2005). Again, the genus *Eustala* was observed most frequently. Since the species composition and their abundance in the nests of these wasps were markedly different from the results obtained by visually searching the study area, the authors considered that they

are extremely selective, and prey on relatively rare species while ignoring other abundant ones.

Coville (1986), while studying spider prey of *Trypoxylon tridentatum* Pakard from Arizona and California, observed that Araneidae and Theridiidae were the most frequent families. According to the author, the relative proportions of the two families varied from one locality to another, but in general araneids were more abundant. According to Coville (1987) this might result from females hunting in different areas, exploring aggregations of spiders or becoming conditioned to certain types of spiders or hunting behaviour. In the nests of *Trypoxylon tenocitlan* Richards, individual differences were observed, but a variation was observed between the nests (Coville, 1987). For Araújo and Gonzaga (2007) an individual variation in the use of resources, as is the case of *T. albonigrum*, is possibly a result of learning trade-offs associated with prey searching and/or handling times. This wasp preys on spiders showing a wide range of defensive tactics that, in turn, might require different skills from the wasp to locate and subdue their prey. Thus, the individual would enhance its foraging efficiency and despite its individualism, the population as a whole becomes generalist.

Another result obtained in our study and that has also been observed for other *Trypoxylon* species (Rehnberg, 1987; Genaro and Alayón, 1994; Camillo and Brescovit, 1999a, 1999b; Gonzaga and Vasconcellos-Neto, 2005; Buschini et al., 2008) was the low number of adult spiders in *T. opacum* nests. A total of 900 juvenile spiders, 107 females and 46 males were captured by *T. opacum*, the number of juveniles being significantly higher than that of males and females. For some authors this pattern might be a consequence of the lower ability of the wasps to locate individuals moving on vegetation. Adult araneid males leave their webs to search for females, thereby reducing their exposure to predators that might use the web as a visual sign for approximation (Gonzaga and Vasconcellos-Neto, 2005; Polidori et al., 2007). In contrast to our study, Gonzaga and Vasconcellos-Neto (2005) observed, in some periods, that the number of captured females was higher than juveniles. For Rehnberg (1987), females could be preferred for their higher content in lipids compared to juveniles and adult males. It is possible that the high number of juveniles in *T. opacum*'s diet is related to the facility of transportation of smaller stages and also with the lower risks they present to the wasps, since adults spiders can catch wasps (Brockmann and Graffen, 1992).

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References

- ARAÚJO, AS. and GONZAGA, MO., 2007. Individual specialization in the hunting wasp *Trypoxylon (Trypargilum) albonigrum* (Hymenoptera, Crabronidae). *Behavioral Ecology and Sociobiology*, vol. 61, no. 12, p. 1855-1863.

- AYRES, M., AYRES Jr., M., AYRES, DL. and SANTOS, AS., 2003. *BioStat 3.0: aplicações estatísticas nas áreas das ciências biológicas e médicas*. Brasília, DF: Sociedade Civil Mamiaráu, CNPq.
- BLACKLEDGE, TA., CODDINGTON, JA. and GILLESPIE, RG., 2003. Are three-dimensional spider webs defensive adaptations? *Ecology Letters*, vol. 6, no. 1, p. 13-18.
- BROCKMANN, HJ. and GRAFEN, A., 1992. Sex ratios and life-history patterns of solitary wasp, *Trypoxylon (Trypargilum) politum* (Hymenoptera: Sphecidae). *Behavioral Ecology and Sociobiology*, vol. 30, no. 1, p. 7-27.
- BUSCHINI, MLT., BORBA, NA. and BRESCOVIT, AD., 2008. Patterns of prey selection of *Trypoxylon (Trypargilum) lactitarse* Saussure (Hymenoptera: Crabronidae) in southern Brazil. *Brazilian Journal of Biology*, vol. 68, no. 3, p. 519-528.
- BUSCHINI, MLT. and WOISKI, TD., 2008. Alpha-beta diversity in trap-nesting wasps (Hymenoptera: Aculeata) in southern Brazil. *Acta Zoologica (Stockholm)*, vol. 89, no. 4, p. 351-358.
- BUSCHINI, MLT. and WOLFF, LL., 2006. Notes on the biology of *Trypoxylon (Trypargilum) opacum* Brèthes (Hymenoptera, Crabronidae) in southern Brazil. *Brazilian Journal of Biology*, vol. 66, no. 3, p. 907-917.
- BUSCHINI, MLT., NIESING, F. and WOLFF, LL., 2006. Nesting biology of *Trypoxylon (Trypargilum) lactitarse* Saussure (Hymenoptera, Crabronidae) in trap-nests in southern Brazil. *Brazilian Journal of Biology*, vol. 66, no. 3, p. 919-929.
- CAMILLO, E. and BRESCOVIT, AD., 1999a. Spiders (Araneae) captured by *Trypoxylon (Trypargilum) lactitarse* (Hymenoptera: Sphecidae) in southeastern Brazil. *Revista de Biología Tropical*, vol. 47, no. 1-2, p. 151-162.
- CAMILLO, E. and BRESCOVIT, AD., 1999b. Aspectos biológicos de *Trypoxylon (Trypargilum) lactitarse* Saussure e *Trypoxylon (Trypargilum) rogenhoferi* Kohl (Hymenoptera: Sphecidae) em ninhos armadilhas, com especial referência a suas presas. *Anais da Sociedade Entomológica do Brasil*, vol. 28, no. 2, p. 251-261.
- CAMILLO, E. and BRESCOVIT, AD., 2000. Spider prey (Araneae) of *Trypoxylon (Trypargilum) rogenhoferi* (Hymenoptera: Sphecidae) in southeastern Brazil. *Revista de Biología Tropical*, vol. 48, no. 2-3, p. 647-656.
- CLOUDSLEY-THOMPSON, JL., 1995. A review of the anti-predator devices of spiders. *Bulletin of the British Arachnological Society*, vol. 10, no. 3, p. 81-96.
- COVILLE, RE., 1981. Biological observations on three *Trypoxylon* wasps in the subgenus *Trypargilum* from Costa Rica: *T. nitidiuschultessi*, *T. saussurei* and *T. lactitarse* (Hymenoptera: Sphecidae). *Pan-Pacific Entomologist*, vol. 57, no. 2, p. 332-340.
- COVILLE, RE., 1986. Spider prey of *Trypoxylon tridentatum* (Hymenoptera: Sphecidae) from Arizona and California. *Pan-Pacific Entomologist*, vol. 62, no. 2, p. 119-120.
- COVILLE, RE., 1987. Spider-hunting sphecid wasps. In NENTWIG, W. (Ed). *Ecophysiology of spiders*. New York: Springer. p. 309-318.
- EIGENBRODE, SD., RAYOR, L., CHOW, J. and LATTY, P., 2000. Effects of wax bloom variation in *Brassica oleracea* on foraging by a vespid wasp. *Entomologia Experimentalis et Applicata*, vol. 97, no. 2, p. 161-166.
- EVANS, HE., 1963. Predatory wasps. *Scientific American*, vol. 208, no. 4, p. 144-154.
- GARCIA, MVB. and ADIS, J., 1995. Comportamento de nidificação de *Trypoxylon (Trypargilum) rogenhoferi* Kohl (Hymenoptera, Sphecidae) em uma floresta inundável de várzea na Amazônia Central. *Amazoniana*, vol. 13, no. 3-4, p. 259-282.
- GENARO, JA. and ALAYÓN, G., 1994. Las presas (Araneae) de *Trypoxylon (Trypargilum) subimpresum* (Hymenoptera: Sphecidae) em Cuba. *Revista de Biología Tropical*, vol. 42, no. 1-2, p. 353-356.
- GENARO, JA., SANCHEZ, C.S. and ALAYÓN, G., 1989. Notas sobre la conducta de nidificación de *Trypoxylon (Trypargilum) subimpresum* (Hymenoptera: Sphecidae). *Caribbean Journal of Science*, vol. 25, no. 1, p. 228-229.
- GONZAGA, MO. and VASCONCELLOS-NETO, J., 2005. Orb-web spiders (Araneae: Araneomorphae: Orbiculariae) captured by hunting-wasps (Hymenoptera: Sphecidae) in an area of Atlantic Forest in southeastern Brazil. *Journal of Natural History*, vol. 39, no. 31, p. 2913-2933.
- JONES, MT., CASTELLANOS, I. and WEISS, MR., 2002. Do leaf shelters always protect caterpillars from invertebrate predators? *Ecological Entomology*, vol. 27, no. 6, p. 753-757.
- LUDWIG, JA. and REYNOLDS, JF., 1988. *Statistical ecology: a primer on methods and computing*. New York: John Wiley and Sons.
- MANTEL, N., 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research*, vol. 27, no. 1, p. 133-153.
- O'NEILL, KM., 2001. *Solitary wasps. Behavior and natural history*. London: Comstock Publishing Associates.
- O'BRIEN, MF., 1982. *Trypargilum tridentatum* (Packard) in trap nests in Oregon (Hymenoptera: Sphecidae: Trypoxylinae). *Pan-Pacific Entomologist*, vol. 58, no. 2, p. 288-290.
- PALMA, S., 1975. Contribución al estudio de los sifonoforos encontrados frente a la costa de Valparaiso. Aspectos ecológicos. In *II Simpósio Latino americano sobre Oceanografía Biológica*. Venezuela: Univ. D'Oriente. P. 119-133.
- POLIDORI, C., BOESI, R., ISOLA, F. and ANDRIETTI, F., 2005. Provisioning patterns and choice of prey in the digger wasp *Cerceris arenaria* (Hymenoptera: Crabronidae): the role of prey size. *European Journal of Entomology*, vol. 102, no. 4, p. 801-804.
- REHNBERG, BG., 1987. Selection of spider prey by *Trypoxylon politum* (Say) (Hymenoptera: Sphecidae). *Canadian Entomologist*, vol. 119, no. 2, p. 189-194.
- WEAVING, AJS., 1988. Prey selection in several sympatric species of *Ammophila* W. Kirby (Hymenoptera: Sphecidae) in southern Africa. *Annals of the Cape Provincial Museums (Natural History)*, vol. 16, no. 1, p. 327-349.