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# Spiders Used as Prey by the Hunting Wasp *Trypoxylon* (*Trypargilum*) *agamemnon* Richards (Hymenoptera: Crabronidae)

Maria Luisa Tunes Buschini[1,*], Talita Ribas Caldas[1], Neide Augusta Borba[1], and Antônio Domingos Brescovit[2]

[1]*Departamento de Biologia da Universidade Estadual do Centro-Oeste, Rua Presidente Zacarias 875, 85010-990, Guarapuava (PR), Brasil*

[2]*Laboratório de Artrópodes, Instituto Butantan, Av. Vital Brasil 1500, 05503-900, São Paulo, Brasil*

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**Maria Luisa Tunes Buschini, Talita Ribas Caldas, Neide Augusta Borba, and Antônio Domingos Brescovit (2010)** Spiders used as prey by the hunting wasp *Trypoxylon* (*Trypargilum*) *agamemnon* Richards (Hymenoptera: Crabronidae). *Zoological Studies* **49**(2): 169-175. The purpose of this study was to monitor the spider fauna in *Trypoxylon agamemnon* nests. The study was carried out from Dec. 2001 to Dec. 2006 in the Parque Municipal das Araucárias, in the municipality of Guarapuava, state of Paraná, southern Brazil. Nests of *T. agamemnon* were obtained using trap-nests made of wooden blocks. To investigate the similarity between spider species in *T. agamemnon*'s diet, spiders species were grouped according to their abundances, using the Bray-Curtis coefficient as a metric method and the unweighted pair group method average (UPGMA) as the clustering method. Spider species dominance was calculated, and Chi-square tests were used to test the null hypothesis that there was no significant difference among the proportions of collected juvenile, male, and female spiders. In contrast to what was recorded for other species of spider-hunting wasps, *T. agamemnon* exclusively captures spiders (of the Anyphaenidae) that forage on the vegetation. This probably maintains niche partitioning between *Trypoxylon* species that occur in the Parque Municipal das Araucárias, reducing competition for prey resources. http://zoolstud.sinica.edu.tw/Journals/49.2/169.pdf

**Key words:** Crabronidae, *Trypoxylon agamemnon*, Spider, Prey use.

*Trypoxylon* Latreille is a globally distributed genus with 630 known species (Pulwaski 2005). Having noted differences at both the morphological and biological levels, Richards (1934) divided the genus in 2 subgenera, *Trypargilum* and *Trypoxylon*. The subgenus *Trypoxylon* is distributed worldwide, while *Trypargilum* is restricted to the New World. Present estimates of the New World fauna are of 86 species of the subgenus *Trypoxylon* and 94 of *Trypargilum* (Bohart and Menke 1976, Coville 1982). The subgenus *Trypargilum* was also subdivided into 5 groups by Richards (1934): *albitarse*, *superbum*, *punctulatum*, *spinosum*, and *nitidium*. Although most species of this subgenus are solitary, species of the *albitarse* group may nest in large aggregates (Brockmann 1992, Brockmann and Grafen 1992, Molumby 1997, Camillo 1999).

All studied *Trypoxylon* (of both subgenera) build at least part of their nests with mud and provision them with paralyzed spiders (Coville 1987). They store several small spiders in each nest cell (Coville 1987, O'Neil 2001) and before closing it, lay a single egg on the last stored spider, after which, they immediately build a mud partition and begin provisioning the next brood cell (Coville 1982).

Few studies on the use of prey by the genus *Trypoxylon* have been carried out in Brazil

*To whom correspondence and reprint requests should be addressed. E-mail:isatunes@yahoo.com.br

(Camillo and Brescovit 1999a b 2000, Gonzaga and Vasconcellos-Neto 2005, Buschini and Wolff 2006, Buschini et al. 2006 2008, Araújo and Gonzaga 2007). Most of those studies reported that orb weaving spiders (Araneae, Araneidae) were used the most, even though they present many strategies to avoid predation, such as web decorations (Blackledge and Wenzel 2001).

While investigating the abundance, seasonality, and life history of *T. agamemnon* Richards in southern Brazil, Buschini and Fajardo (in press) observed that these wasps build their nests only in forested habitats where there is a predominance of *Araucaria angustifolia* (Bertol.) (Coniferae: Araucariaceae). They also observed that this wasp preys mainly on spiders belonging to the family Anyphaenidae (90.2%), with a low number of those belonging to the Araneidae (9.7%). Anyphaenids have a worldwide distribution, but are particularly common in the Neotropics. This family includes fast, active hunters, usually found on vegetation, especially tree foliage.

Considering that in the study carried out by Buschini and Fajardo (in press), the evaluation of prey collected by *T. agamemnon* was very superficial and that the results obtained by those authors differed from those reported for other species of *Trypoxylon*, the purpose of this study was to monitor the spider fauna in *T. agamemnon* nests. The main questions addressed in this paper were: what is the constancy of selected spider species in *T. agamemnon*'s diet?; and are there significant differences in the number of juvenile, female, and male spiders in *T. agamemnon*'s diet?

## MATERIALS AND METHODS

### Study area

This study was carried out in the Parque Municipal das Araucárias, in the municipality of Guarapuava, state of Paraná, southern Brazil (25°23'S; 51°27'W, at 1120 m in elevation). This area is characterized by a cool, wet season. Hoar frosts are common and severe. During the warmest months, the average temperature is < 22°C.

Collections were carried out from Dec. 2001 to Dec. 2006 and were concentrated in a very heterogeneous site, with *Araucaria* forests, swamps, and grasslands. The grasslands were physionomically characterized by areas of low grasses and no bushes. Species belonging to the Cyperaceae, Leguminosae, Verbenaceae, Compositae, and Apiaceae were dominant in this habitat. In the *Araucaria* forest, there was a predominance of *A. angustifolia* (Coniferae: Araucariaceae) and in swamps, located in the lowest regions of the park, there were mainly grasses and members of the Compositae.

### Sampling program

Nests of *T. agamemnon* were obtained using trap-nests of 0.7, 1.0, and 1.3 cm in diameter and 8.0 cm in length. For each habitat, 2 areas were studied, with 2 transects per area and 4 sampling stations per transect. Twelve trap-nests were placed at each sampling station, 4 of each opening diameter, totaling 576 traps. Each trap was placed at 1.5 m above the ground and inspected every 2 wk. 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 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.

### Statistical analyses

To investigate the similarity between spider species in *T. agamemnon*'s diet, they were grouped according to their abundances, using the Bray-Curtis coefficient, as a metric method 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 = (abundance of species ÷ total abundance) × 100. If D was > 5%, the species was termed a dominant species; if 2.5% < D < 5%, the species was termed an accessory species; and if D was < 2.5%, the species was termed an accidental species.

Chi-square tests ($\chi^2$) were used to test the null hypothesis that there was no significant difference among the proportions of collected juveniles, males, and females.

## RESULTS

### Nesting activity of *T. agamemnon* in different habitats

In total, 420 *T. agamemnon* nests were collected. Nests were found only in the *Araucaria* forest. They were built more often during the summer (between Dec. and Apr.) during high-temperature periods.

### Spider species collected by *T. agamemnon*

Twenty-one species of spiders belonging to 3 families (the Amaurobiidae, Anyphaenidae, and Araneidae) were captured by *T. agamemnon*. From an analysis of 1400 spiders, the Anyphaenidae was the most-often captured family with 1307 specimens (93%), distributed among 5 genera and 15 species. The majority of specimens ($n$ = 1087) belonging to this family were juveniles and could not be identified to genera and/or species level; when identification was possible, *Teudis* sp. 1 was the most frequently captured species with 93 specimens. *Aysha* sp. 1 was the 2nd most frequent species with 32 specimens, followed by *Sanogasta maculatipes* (Keyserling), with 30 specimens (Table 1).

The Araneidae was the 2nd most-often captured family, with 92 specimens (6.6%), distributed in 7 genera and 8 species. *Eustala* sp. 3 was the most captured species with 10 specimens. Sixty-two specimens belonging to this family were juveniles and could not be identified beyond family level.

The family Amaurobiidae, was represented by only 1 individual called *Retiro* sp. 1.

### Spider similarity

Identified spiders were divided into 3 groups according to abundance ($r$ = 0.875) (Fig. 1). The smaller group included the most abundant species (*Teudis* sp. 1, *Sanogasta* sp. 1, *S. maculatipes*,

**Table 1.** Number of juvenile (J), female (F), and male (M) spiders collected by *Trypoxylon agamemnon* in different habitats and their respective dominance indices

| Species | J | M | F | Dominance index (D) | Dominance classification |
|---|---|---|---|---|---|
| Amaurobiidae | | | | | |
| *Retiro* sp. 1 | | 1 | | 0.40 | Accidental |
| Anyphaenidae | 1087 | | 2 | | |
| *Aysha* aff *borgmeyeri* (Mello-Leitão) | | 1 | 4 | 2.00 | Accidental |
| *Aysha* gr. *brevimana* sp. 1 | | 6 | 12 | 7.23 | Dominant |
| *Aysha* gr. *brevimana* sp. 2 | | 1 | 2 | 1.21 | Accidental |
| *Aysha* gr. *brevimana* sp. 3 | | | 2 | 0.80 | Accidental |
| *Aysha guarapuava* (Brescovit) | | 1 | | 0.40 | Accidental |
| *Aysha rubromaculata* (Keyserling) | | | 3 | 1.21 | Accidental |
| *Aysha* sp. 1 | 8 | 2 | 22 | 12.85 | Dominant |
| *Josa* sp. 1 | | | 2 | 0.80 | Accidental |
| *Patrera* sp. 1 | | 1 | 6 | 2.81 | Accessory |
| *Sanogasta maculatipes* (Keyserling) | 5 | | 25 | 12.05 | Dominant |
| *Sanogasta* sp. 1 | | 3 | 19 | 8.84 | Dominant |
| *Teudis* sp. 1 | 5 | 3 | 85 | 37.35 | Dominant |
| Araneidae | 62 | | | | |
| *Acacesia villalobosi* (Glueck) | | 1 | | 0.40 | Accidental |
| *Alpaida gracia* (Levi) | | | 5 | 2.00 | Accidental |
| *Araneus corporosus* (Keyserling) | | 4 | 2 | 2.41 | Accidental |
| *Araneus omnicolor* (Keyserling) | | | 1 | 0.40 | Accidental |
| *Cyclosa caroli* (Hentz) | | | 4 | 1.60 | Accidental |
| *Micrathena* sp. 1 | | 2 | | 0.80 | Accidental |
| *Wagneriana juquia* Levi | | | 1 | 0.40 | Accidental |
| *Eustala* sp. 3 | | 5 | 5 | 4.02 | Accessory |
| Total | 1167 | 31 | 202 | | |

*Aysha* sp. 1, and *Ays*. gr. *brevimana* sp. 1), i.e., those most commonly captured by *T. agamemnon*. The 2nd group included species represented by a range of 4-10 specimens (*Eustala* sp. 3, *Araneus corporosus* (Keyserling), *Patrera* sp. 1, *Cyclosa caroli* (Hentz), *Alpaida gracia* Levi, and *Ays*. aff. *borgmeyeri* (Mello-Leitão)). The 3rd and largest group included the less-abundant species, represented by a range of 1-3 specimens (*Retiro* sp. 1, *Ays*. gr. *brevimana* sp. 2, *Ays*. gr. *brevimana* sp. 3, *Ays*. *guarapuava* Brescovit, *Josa* sp. 1, *Ara. omnicolor* (Keyserling), *Micrathena* sp. 1, *Acacesia villalobosi* Glueck, *Ays. rubromaculata* (Keyserling), and Wagneriana juquia Levi). A similar pattern emerged from the dominance indices with the groups of dominant and accidental species. Differences between the 2 analyses were observed in the group of accessory (or intermediate) species that were mixed with some accidental species in the dendrogram (Table 1).

### Numbers of juveniles, males, and females used by *T. agamemnon*

In total, 1167 juvenile spiders (83%), 202 females (15%), and 31 males (2%) were captured by *T. agamemnon*. These percentages significantly differed (juveniles × females: $\chi^2 = 56.89$, $p < 0.001$, $d.f. = 1$ ; juveniles × males: $\chi^2 = 74.81$, $p < 0.001$, $d.f. = 1$; females × males: $\chi^2 = 17.92$, $p < 0.001$, $d.f. = 1$).

## DISCUSSION

The majority of prey captured by *T. agamemnon* were spiders of the family Anyphaenidae. Although many species of *Trypoxylon* capture orb-web spiders (Camillo and Brescovit 1999a b 2000, Gonzaga and Vasconcellos-Neto 2005, Buschini and Wolff 2006, Buschini et al. 2006 2008, Araújo and Gonzaga 2007), *T. agamemnon* exclusively captured spiders that forage on the vegetation.

Many studies examined the numbers and species of spiders provisioned in wasp nests, providing an insight into which spiders might be most vulnerable to wasps. Those studies indicated that different species of wasps, hunting in the same habitat, often catch different prey (Krombein et al. 1979). This suggests that sympatric species of wasps might employ different predatory tactics,

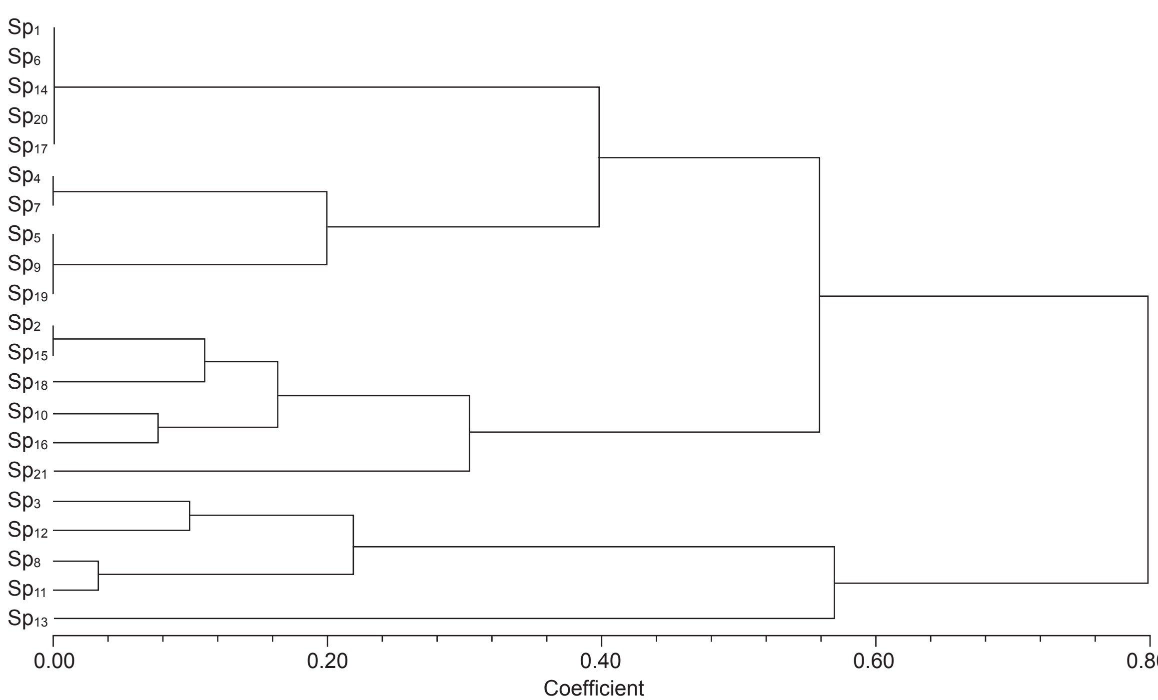


**Fig. 1.** Dissimilarity dendrogram between spiders species related to their abundances in the *Trypoxylon agamemnon* diet: $Sp_1$, *Retiro* sp. 1; $Sp_2$, *Aysha* aff. *borgmeyeri*; $Sp_3$, *Aysha* gr. *brevimana* sp. 1; $Sp_4$, *Aysha* gr. *brevimana* sp. 2; $Sp_5$, *Aysha* gr. *brevimana* sp. 3; $Sp_6$, *Aysha guarapuava*; $Sp_7$, *Aysha rubromaculata*; $Sp_8$, *Aysha* sp. 1; $Sp_9$, *Josa* sp. 1; $Sp_{10}$, *Patrera* sp. 1; $Sp_{11}$, *Sanogasta maculatipes*; $Sp_{12}$, *Sanogasta* sp. 1; $Sp_{13}$, *Teudis* sp. 1; $Sp_{14}$, *Acacesia villalobosi*; $Sp_{15}$, *Alpaida gracia*; $Sp_{16}$, *Araneus corporosus*; $Sp_{17}$, *Araneus omnicolor*; $Sp_{18}$, *Cyclosa caroli*; $Sp_{19}$, *Micrathena* sp. 1; $Sp_{20}$, *Wagneriana juquia*; $Sp_{21}$, *Eustala* sp. 3.

perhaps due to niche partitioning such as that observed for *Trypoxylon* species that occur in the Parque Municipal das Araucárias. *Trypoxylon lactitarse* Saussure, for example, occurs in *Araucaria* forests, grasslands, and swamp areas of the park. In the *Araucaria* forest, the most collected spiders were *Eustala* sp. 1, *Eustala* sp. 2, and *Alpaida* sp. 2. In the grasslands and swamp areas, despite the large number of species of *Eustala* (*Eustala* sp. 1, sp. 2, sp. 3, sp. 4, sp. 6, sp. 7, sp. 8, and sp. 10), the most collected species belonged to the genus *Araneus* Clerck (Buschini et al. 2006 2008). Thus, we noted that in *Araucaria* forests, *T. lactitarse* and *T. agamemnon* used different dietary items, and in the grassland and swamp areas, *T. lactitarse* used other species of *Eustala* and other genera not used by *T. opacum* Brèthes, another abundant wasp species that occurs only in grassland and swamp areas in this park (Buschini and Wolff 2006).

A certain plasticity in relation to wasp predation behavior was observed in the genus *Trypoxylon*, even though most collected spiders were of the family Araneidae. *Trypoxylon albonigrum* Richards, for example, is a wasp that provisions its nests with a large number of spiders belonging to at least 6 Araneidae genera, spanning a variety of sizes, web architectures, and defensive tactics (Gonzaga and Vasconcellos-Neto 2005). In one of the consumed genera, *Parawixia* F.O.P.-Cambridge, spiders remain in the center of the web and usually flee to the vegetation when disturbed, whereas members of another consumed genus, *Eustala*, remain most of the day in a cryptic position close to the vegetation. Therefore, these different spiders may potentially require different hunting skills from wasps and according to Araújo and Gonzaga (2007), impose learning tradeoffs that are related to searching for and/or handling prey.

*Trypoxylon xanthandrum* Richards differs from other *Trypoxylon* species in having more-specialized predatory behavior. According to Coville and Griswold (1983), all spiders found in nests of this wasp belonged to the family Senocuolidae and to the genus *Senoculus* Taczanowski. These spiders are well camouflaged and rest compressed against twigs during the day. Thus, *T. xanthandrum* concentrates its search close to the twigs, and air currents caused by the movement of the wings and by the antennae touching the twigs cause the spider to move and thus be captured by the wasp. Since *T. agamemnon* hunts mainly Anyphaenidae spiders, 1 hypothesis could be that these wasps present capture mechanisms similar to those of *T. xanthandrum*, considering that the Anyphaenidae has nocturnal habits (Bonaldo et al. 2008), and that the activity period of *T. agamemnon* is diurnal (Donatti and Buschini, unpubl. data), when these spiders are resting on the vegetation and are probably more susceptible to predation.

As for the proportions of juveniles and adult spiders in *T. agamemnon*'s diet, this wasp captured more juveniles than adult females and males. Collections of large percentages of juveniles were also observed for *T. texense* Saussurre (Kurczewsky 1963), *T. politum* Say (Barber and Matthews 1979), *T. orizabense* Richards (Coville 1979), *T. tenoctitlan* Richards (Coville and Coville 1980), *T. saussurei* Rohwer (Coville 1981), *T. occidentalis* Coville (Coville 1982), *T. moteverdae* Coville (Brockmann 1992), *T. subimpressum* Smith (Genaro and Alayón 1994), *T. tridentatum* Packard (Jiménez and Tejas 1994), *T. rogenhoferi* (Camillo and Brescovit 2000), *T. lactitarse* (Camillo and Brescovit 1999a, Buschni et al. 2006 2008), and *T. opacum* (Buschini and Wolff 2006). According to Camillo and Brescovit (1999a), the great preference for juveniles is probably related to the fact that in some spider species, after young individuals emerge, large numbers remain near the egg sacs (Jones 1983), and this makes them more vulnerable to predation. According to Gonzaga and Vascocellos-Neto (2005), this pattern may be a consequence of the lower ability of wasps to locate individuals moving on vegetation. Adult araneid males leave their webs to search for females, thereby reducing their exposure to predators that use webs as visual signs for approximation. Another possibility considered by Rehnberg (1987) to explain the low number of males compared to females is that adult females probably provide a richer nutritional source because of the accumulation of fat tissue involved in egg production. Therefore, Gonzaga and Vascocellos-Neto (2005) considered that the proportion of juveniles and females in the nests may depend on the phenology of the preferential prey species.

In conclusion, our observations show that in contrast to that recorded for other species of *Trypoxylon*, *T. agamemnon* exclusively captures spiders that forage on the vegetation (Anyphaenidae). A possible hypothesis could be that this wasp maintains niche partitioning between *Trypoxylon* species that occur in the Parque Municipal das Araucárias, thus avoiding competition for this resource. To test this hypothesis, more-elaborate studies on the hunting behavior of these wasps are necessary. It would also be interesting to verify the presence of functional tradeoffs in this species and if this mechanism occurs only in orb weaving species, as observed by Araújo and Gonzaga (2007) for *T. albonigrum*.

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