This article was downloaded by: [University of Bath]

On: 13 February 2014, At: 15:38

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK

Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

Orb-web spiders (Araneae: Araneomorphae; Orbiculariae) captured by hunting-wasps (Hymenoptera: Sphecidae) in an area of Atlantic Forest in south-eastern Brazil

Marcelo O. Gonzaga^a & João Vasconcellos-Neto^a

^a Departamento de Zoologia, UNICAMP, Campinas, SP, Brazil

Published online: 19 Aug 2006.

To cite this article: Marcelo O. Gonzaga & João Vasconcellos-Neto (2005) Orb-web spiders (Araneae: Araneomorphae; Orbiculariae) captured by hunting-wasps (Hymenoptera: Sphecidae) in an area of Atlantic Forest in south-eastern Brazil, *Journal of Natural History*, 39:31, 2913-2933, DOI: [10.1080/00222930500183520](https://doi.org/10.1080/00222930500183520)

To link to this article: <http://dx.doi.org/10.1080/00222930500183520>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms &

Orb-web spiders (Araneae: Araneomorphae; Orbiculariae) captured by hunting-wasps (Hymenoptera: Sphecidae) in an area of Atlantic Forest in south-eastern Brazil

MARCELO O. GONZAGA & JOÃO VASCONCELLOS-NETO

Departamento de Zoologia, UNICAMP, Campinas, SP, Brazil

(Accepted 19 May 2005)

Abstract

Members of two hunting-wasp families, Pompilidae and Sphecidae, are among the major predators of orb-web spiders. In this study, we collected paralysed spiders from natural nests and trap-nests provisioned by sphecids in an area of Brazilian Atlantic Forest, and compared these data with the composition of species collected by visual searching during one year. Prey preferences were analysed based on the relative abundance of spider species, their size and web characteristics. We also compiled a list of orb-weavers captured by four sphecid genera reported in 40 other studies. A large number of prey was obtained from natural nests of *Trypoxylon* (*Trypargilum*) *albonigrum* in Parque Estadual Intervales, especially species of *Eustala*, *Parawixia*, and *Araneus* (Araneidae). Other prey, stored in trap-nests by *T. lactitarse* and unidentified hunting-wasp species, included *Nephila* (Tetragnathidae), *Parawixia*, *Ocrepeira*, *Mecynogea*, *Acacesia* (Araneidae), and other spider species that were less abundant. All the species that were heavily preyed upon had a relatively lower abundance in our samples of prey availability. The range of body sizes of spiders captured by *Trypoxylon* in our study area include the size of some abundant orb-weavers always absent in their nests. These results indicate that factors other than abundance in the field and the spider's size influence prey selection or susceptibility to attack.

Keywords: Orb-web spiders, predation, Sphecidae, trap-nests, *Trypoxylon*

Introduction

All members of the wasp family Pompilidae and six genera of Sphecidae (*Trypoxylon*, *Chalybion*, *Sceliphron*, *Pison*, *Miscophus*, and *Pisonopsis*) use exclusively spiders to provide food for their larvae (Bohart and Mencke 1976; Wasbauer 1995; Blackledge et al. 2003). Some parasitoid pompilids attack spiders within host refuges (usually cavities dug in the soil or shelters made of plant parts and silk). In these cases, the spiders are not removed and transported to a nest, but remain paralysed by the wasp's venom in their own lairs. Other species attack wandering spiders, laying an egg on their bodies after inflicting only

Correspondence: Marcelo O. Gonzaga, Departamento de Zoologia, IB, UNICAMP, Caixa Postal 6109, 13083-970, Campinas, SP, Brazil. Email: mogonzaga@yahoo.com.br

Published 15 September 2005.

ISSN 0022-2933 print/ISSN 1464-5262 online © 2005 Taylor & Francis

DOI: 10.1080/00222930500183520

temporary paralysis. When the effect of the venom wears off, the spider is able to continue its normal activities until seriously injured by the larva attached to its body (Kaston 1959; O'Neill 2001). Most of these wasp species, however, capture a single spider and deposit this prey in a nest constructed of mud and attached to the surface of sheltered substrates, or in a nest created by the modification of a natural cavity or the excavation of a new one (O'Neill 2001). All of these three nesting habits are also found in sphecids (Coville 1987; Hanson and Menke 1995), and wasps of both families are responsible for a significant impact on their prey populations (see McQueen 1978; Conley 1985; Laing 1988; Polis et al. 1998).

The main difference between sphecid and pompilid prey storage behaviours is the number of spiders stored for each larva. Sphecids store several small (relative to their own size) spiders in each cell of their nests, while pompilids supply their brood cells with a single large spider (Coville 1987; O'Neill 2001). The foraging efficiency of both strategies is constrained by the energy costs of transportation and by the time required to find appropriate prey items. Pompilids must choose their prey size very carefully because the size and fecundity of their offspring will be correlated with the amount of nutrients contained in each specimen captured (Endo and Endo 1994; Rayor 1996). Sphecids, however, have greater 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. However, if the captured spiders are too small, the wasps will have to make more trips to the foraging area and hence spend more energy and expose their nests to parasites for a longer time.

In addition to the spider's size and availability in the habitats exploited by the wasps, anti-predator mechanisms can also be important in determining which species are located and captured. Within the large range of defensive mechanisms that have evolved in spiders in response to predation (see 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). By surrounding themselves with web threads, the spiders can prevent the approximation of wasps and perceive an imminent attack (Uetz and Hieber 1994). Blackledge et al. (2003) compiled all the records of spiders captured by sphecids published over the last century and compared this data set with the records of potential prey available in habitats from 26 faunal surveys. These authors concluded that the relative abundance of araneoid sheet web weavers found in wasp nests was much lower than expected based on their abundance in the field. In most studies, orb-weavers were captured at a higher frequency than spider species that build webs with a three-dimensional architecture. This finding suggested that, despite their efficiency in retaining flying insects and their need for less silk, two-dimensional orb-webs are associated with a higher risk of predation by wasps. Modifications of this web design to one that includes additional protection could account for the great diversity and abundance of araneoid sheet-weavers (Blackledge et al. 2003).

A number of web characteristics and variations in the behaviour and morphology of orb-web spiders suggest that the susceptibility to predation varies among species. The resting position (Herberstein and Heiling 2001) and escape behaviour (Blackledge and Pickett 2000) of spiders, the addition of web decorations (stabilimenta) (Blackledge and Wenzel 2001), the spider's size (Camillo and Brescovit 1999a), body shape (Freeman and Johnston 1978) and thickness of the integument (Elgar and Jebb 1999), the presence and types of refuges (Eberhard 1970), and the establishment of aggregations (Uetz and Hieber 1994; Henschel 1998; Alves-Costa and Gonzaga 2001) are factors that may influence the success of wasps in locating and capturing orb-web spiders.

In this study, we evaluated the species composition of orb-web spiders captured by wasps in an area of Atlantic Forest, and assessed the size and relative abundance of these species in the field, as well as their web characteristics. We also compiled a list of orb-web spiders captured by sphecids based on 40 other studies in four sphecid genera (*Trypoxylon*, *Pison*, *Chalybion*, and *Sceliphron*).

Methods

Study site

This study was done in Parque Estadual Intervales (24°16'S, 48°25'W), a state park that is part of a large protected forest continuum (120,000 ha), located in the State of São Paulo, in south-eastern Brazil. This area is composed of old secondary growth and primary evergreen forest. The climate is characterized by a relatively dry cold season from May to October and a wet warm season from November to April.

Spiders in wasp nests

Spiders captured by wasps were obtained by placing 301 trap-nests in the field and by sampling natural nests of *Trypoxylon* (*Trypargilum*) *albonigrum* Richards, 1934 (Sphecidae). Mud nests of *T. albonigrum* were found in the walls of two houses located close to the trails selected for the fixation of trap-nests (Figure 1). Although some females had constructed nests composed of more than one pipe tube, we collected only spiders provisioned in the last tube. This procedure was used because in old tubes prey items were generally in poor condition because of consumption by the larvae.

The trap-nests consisted of bamboo stems with one extremity closed by the nodal septum. The stems varied in internal diameter between 6.1 and 17.5 mm and all of them were about 150 mm long. Groups of seven trap-nests were placed in plastic involucre and fixed on wooden poles (Figure 2). Forty-three of these units were distributed along secondary trails and river margins. The distance between each unit along a trail was about 10 m.

Traps were inspected once a month for 1 year, from December 2001 to November 2002. Mud nests of *T. albonigrum* were collected at the same time as the inspections. The inspections were done using an otoscope to determine nest occupation. Occupied trap-nests were removed and replaced by unoccupied nests of approximately the same internal diameter. The spiders present in the nests were identified and measured to assess prey size preference and the biomass investment for each larva in dry and wet seasons. Some very damaged specimens (and the cells where they were found) were excluded from the analysis.

Voucher specimens of the sphecids were deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil. The spiders were deposited in the Instituto Butantan, São Paulo, Brazil.

Estimates of spider weight

Since some spiders were frequently found partially consumed by the wasp larvae, we calculated the weight of spiders and the biomass investment per provisioned cell based on spider's body size. Specific models of length–weight relationships are available for many insect orders (Beaver and Baldwin 1975; Sample et al. 1993; Schoener 1980). However,

Figure 1. (A) *Trypoxylon albonigrum* nests. (B) Female arriving at the nest site after collecting mud. The male keeps guarding the nest entrance while she is hunting or collecting mud. (C) Spiders stored in a cell. Scale bars: 1 cm.

the corresponding equations for spiders are based on very small samples and frequently do not specify how many and which species or higher taxonomic groups were analysed (see Hóðar 1996; Rogers et al. 1977). Therefore, to obtain a better estimate of weight, we

Figure 2. Bamboo stems used as trap-nests: (A) longitudinal section of a trap-nest; (B) a group of seven trap-nests in the field.

calculated the length–weight relationship using only orb-web spiders captured by wasps during this study.

The total body length (distance between the anterior margin of the carapace and the distal point of the abdomen) was measured, as was the dry weight of five adult females of six orb-weaver genera (one species per genus). The species used for this analysis were *Parawixia audax*, *Araneus venatrix*, *Wagneriana janeiro*, *Alpaida venilae*, *Eustala* sp., and *Mangora* sp. (Araneidae). Body length was measured to the nearest 0.01 mm using a dissecting microscope with an ocular micrometer, and weight was determined to the nearest 0.1 mg after drying the specimens for 12 h in an oven at 100°C. The data were log-transformed to reduce heteroscedasticity and allow the conversion of a power equation ($W=aL^b$) into a linear regression ($\log W=\log a+b\log L$) (Schoener 1980; Zar 1999). The biomass investment in each cell was calculated by multiplying the number of spiders by their estimated weight, determined from the length–weight regression equation.

Prey availability

The relative abundance of potential prey for the wasps was established by sampling the first 100 orb-web spiders located by visual searching. This procedure was repeated every month for 1 year, at the same time that the trap-nests were inspected and the mud nests of *T. albonigrum* were sampled. Spiders were collected between 8:00 and 16:00 h along trails, river margins and within forest, at distances of up to 300 m from the nesting sites. All adult and juvenile spiders with webs placed up to 2 m above the ground were collected, preserved in 70% ethanol, and transported to the laboratory where they were measured (as described above) in order to compare the size distribution of available prey with the size of the spiders found in the wasp nests.

Some web characteristics supposedly associated with the avoidance of predation were recorded for each species collected, and included the presence of silk and detritus stabilimenta, refuges composed of silk and/or curled leaves, and barriers of silk threads. In addition, the position of each spider (at the hub of the web or at web periphery, close to vegetation) was recorded.

Prey lists from other studies

We compiled 40 studies, published from 1928 to 2002, that reported lists of orb-web spiders captured by sphecids wasps. Since we were interested in prey preferences, studies involving very small samples (number of spiders collected < 10) were not considered. Those included all of the studies on the genus *Miscophus*, which capture mainly spiders with other kinds of webs (Blackledge et al. 2003), and *Pisonopsis*. For the latter genus, there has been only one study on prey selection in which, of 41 spiders collected, only one was an orb-weaver (Evans 1969).

Results

Spiders captured by wasps

Trap-nests. Twenty-one trap-nests were provisioned by hunting-wasps in Parque Estadual Intervales, but in 12 of them the larvae had already consumed all of the spiders when we opened the traps. In the remaining nine, we collected 125 spiders belonging to four families

(Mimetidae, Tetragnathidae, Araneidae, and Salticidae). All mimetids (20 individuals) were deposited in a single nest (collected in January 2002) that consisted of six mud cells shaped as vessels. The other eight trap-nests containing spiders were divided into cells by mud plugs. All of the 51 immature individuals of *Nephila clavipes* (Tetragnathidae) were collected in two nests, also in January. These nests also contained specimens of the araneids *Acacesia villalobosi*, *Araneus workmani*, *Mecynogea biggiba*, *Ocrepeira jacara*, *Parawixia audax*, *Eustala* sp. 1, and *Eustala* sp. 8. The only specimen of Salticidae encountered was collected in March, in a nest composed of three cells, two of which were partially destroyed and without any prey. We were unable to capture the female wasps or raise the larvae until they reached the adult stage in order to identify the species that constructed these nests. The remaining nests (another one from March and four from November), were provisioned by *Trypoxylon* (*Trypargilum*) *lactitarse* Saussure, 1867 and contained only species of Araneidae, especially *Parawixia audax* (41.6% of the total number of spiders captured by this wasp species) and *Eustala* spp. (30.5%) (Table I).

Table I. Number of specimens collected from December 2001 to November 2002 in Parque Estadual Intervales.

Species	Visual search	Trap-nests		Natural nests
		Unidentified wasp species	<i>T. lactitarse</i>	<i>T. albonigrum</i>
Araneidae				
<i>Acacesia</i> sp. 1	0	0	3	0
<i>Acacesia villabosi</i>	1	1	0	0
<i>Alpaida veniliae</i>	21	0	4	0
<i>Alpaida truncata</i>	1	0	0	0
<i>Araneus bogotensis</i>	5	0	1	1
<i>Araneus corporosus</i>	6	0	0	1
<i>Araneus uniformis</i>	0	0	0	47
<i>Araneus venatrix</i>	38	0	0	0
<i>Araneus vincibilis</i>	2	0	0	0
<i>Araneus workmani</i>	7	8	1	1
<i>Araneus</i> sp. 1	0	0	0	1
<i>Argiope argentata</i>	24	0	0	0
<i>Bertrana rufostriata</i>	0	0	1	0
<i>Cyclosa bifurcata</i>	2	0	0	0
<i>Cyclosa fililineata</i>	392	0	0	0
<i>Cyclosa morretes</i>	92	0	0	0
<i>Eustala</i> sp. 1	0	1	1	5
<i>Eustala</i> sp. 2	0	0	0	6
<i>Eustala</i> sp. 3	0	0	1	167
<i>Eustala</i> sp. 4	12	0	6	124
<i>Eustala</i> sp. 5	6	0	0	0
<i>Eustala</i> sp. 6	0	0	0	16
<i>Eustala</i> sp. 7	0	0	0	8
<i>Eustala</i> sp. 8	9	0	2	96
<i>Eustala</i> sp. 9	0	0	0	7
<i>Eustala</i> sp. 10	0	0	0	4
<i>Eustala</i> sp. 11	0	0	0	1
<i>Eustala</i> sp. 12	0	0	0	2
<i>Eustala</i> sp. 13	0	0	0	6
<i>Eustala</i> sp. 14	0	0	1	5
<i>Eustala</i> sp. 15	0	0	0	3
<i>Eustala</i> sp. 16	0	0	0	3

Table I. (Continued.)

Species	Visual search	Trap-nests		Natural nests
		Unidentified wasp		<i>T. albonigrum</i>
		species	<i>T. lactitarse</i>	
<i>Eustala</i> sp. 17	3	0	0	0
<i>Eustala</i> sp. 18	0	0	0	2
<i>Eustala</i> sp. 19	0	0	0	2
<i>Gasteracanthacancriformes</i>	14	0	0	0
<i>Hypognatha</i> sp.	5	0	0	0
<i>Mangora</i> sp. 1	14	0	0	0
<i>Mangora</i> sp. 2	17	0	0	0
<i>Mangora</i> sp. 3	18	0	0	0
<i>Mangora</i> sp. 4	1	0	0	0
<i>Mangora</i> sp. 5	0	0	0	21
<i>Mecynogea biggiba</i>	4	5	0	0
<i>Metepeira</i> sp. 1	3	0	0	0
<i>Micrathena crassispina</i>	9	0	0	0
<i>Micrathena digitata</i>	1	0	0	0
<i>Micrathena fissispina</i>	15	0	0	0
<i>Micrathena guanabara</i>	4	0	0	0
<i>Micrathena jundiai</i>	6	0	0	0
<i>Micrathena plana</i>	12	0	0	0
<i>Micrathena spitzzi</i>	10	0	0	0
<i>Micrathena triangularis</i>	2	0	0	0
<i>Ocrepeira jacara</i>	0	1	0	0
<i>Paravixia audax</i>	8	1	15	133
<i>Paravixia velutina</i>	2	0	0	0
<i>Pozonia bacillifera</i>	0	0	0	39
<i>Verrucosa arenata</i>	108	0	0	0
<i>Wagneriana eupalaestris</i>	1	0	0	0
<i>Wagneriana gavensis</i>	0	0	0	1
Uloboridae				
<i>Philoponella</i> sp. 1	8	0	0	0
<i>Philoponella</i> sp. 2	25	0	0	0
<i>Miagrammopes</i> sp. 1	2	0	0	0
<i>Miagrammopes</i> sp. 2	1	0	0	0
<i>Zosis</i> sp. 1	2	0	0	0
Theridiosomatidae				
<i>Naatlo</i> sp. 1	9	0	0	0
Theridiosomatidae—sp. 1	5	0	0	0
Tetragnathidae				
<i>Crysometa</i> sp. 1	1	0	0	0
<i>Leucauge</i> sp. 1	43	0	0	0
<i>Leucauge</i> sp. 2	4	0	0	0
<i>Leucauge</i> sp. 3	52	0	0	0
<i>Leucauge</i> sp. 4	8	0	0	0
<i>Leucauge</i> sp. 5	92	0	0	0
<i>Nephila clavipes</i>	69	51	0	0
<i>Tetragnatha</i> sp. 1	1	0	0	0
Salticidae				
Salticidae—sp. 1	0	1	0	0
Mimetidae				
<i>Gelanor</i> sp. 1	0	12	0	0
<i>Gelanor</i> sp. 2	0	8	0	0
Total	1197	89	36	702

Trypoxylon lactitarse captured prey with a body length varying from 3 to 10.4 mm (mean $\pm$ SD = 6.1 ± 2.0 mm, $n=34$ spiders). We did not calculate the biomass provisioned for each larva in *T. lactitarse* nests because many cells contained at least one spider that was almost entirely consumed. In addition, we collected only five nests of this species so that the results would be inconclusive. The orb-web spiders found in trap-nests provisioned by the unidentified wasp species varied from 4.2 to 11.7 mm in body length (mean $\pm$ SD = 6.6 ± 1.7 mm, $n=52$ spiders).

Trypoxylon albonigrum mud nests. We collected the contents of 69 individual nests of *T. albonigrum*. The mean number of nests in contiguous positions was 2.4 ± 1.4 (varying from 1 to 6, $n=40$) and the mean number of cells provisioned by each female was 8.7 ± 6.7 (varying from 2 to 30, $n=40$ nests or nest aggregations). Although these numbers represent only nests with the entrance already closed, we cannot be sure whether each female had completed the egg-laying process, and new nests could still be added to small aggregations or contiguous to individual nests.

A total of 702 orb-web spiders were present in the natural nests, most of them (91.3%) belonging to three genera: *Eustala* (65.1%), *Parawixia* (18.9%), and *Araneus* (7.3%). These genera represented more than 70% of all spiders collected by *T. albonigrum* in every month of this study (Figure 3), but they were rarely collected in prey availability surveys: *Eustala* (2.5%), *Parawixia* (0.8%), and *Araneus* (4.8%) (Table I). Furthermore, the most abundant species of *Araneus* captured by *T. albonigrum*, *A. uniformis*, was absent in our samples.

The body length of prey in *T. albonigrum* nests varied from 1.5 to 11.8 mm (mean $\pm$ SD = 6.5 ± 1.8 mm, $n=700$ spiders). This wide range included the body size of the most abundant spider species captured in prey availability surveys: *Cyclosa* (Araneidae), *Leucauge* (Tetragnathidae), and *Verrucosa* (Araneidae). However, their small juveniles

Figure 3. Relative abundance of the three most common spider genera in *Trypoxylon albonigrum* nests.

(which represented most individuals in our samples) were in size categories rarely exploited by *T. albonigrum* (Figure 4).

The overall proportion of adult female spiders in *T. albonigrum* nests (42.3%) was similar to that of juveniles (44%). Adult males corresponded to only 1% of the prey items and 12.7% were subadult males. Most mature females were found at the end of the wet season, from February to May (Figure 5).

Estimates of spider weight

The regression between body length and dry weight was significant and had a high r^2 value (Figure 6) that allowed the latter variable to be estimated based on the former. There was no significant difference between the biomass stored for each larva (Mann–Whitney $U=470$, $P=0.421$, $n_1=38$, $n_2=28$) or the number of spiders deposited per cell (Mann–Whitney $U=487$, $P=0.332$, $n_1=39$, $n_2=29$) in *T. albonigrum* nests in dry and wet seasons.

Web characteristics

Eustala webs are occasionally found during the daytime, but are generally destroyed or consumed in the morning, and rebuilt in the evening. These spiders rested in a cryptic position on stems of vegetation or leaves (Figure 7), and this made their location by visual

Figure 4. Comparison between size distribution of spiders collected in *Trypoxylon albonigrum* nests with spiders belonging to the three most abundant genera in prey availability surveys.

Figure 5. Proportion of adult spider males, adult females, juveniles and subadult males in *Trypoxylon albonigrum* nests, during the year. The numbers at the top indicate the numbers of spiders collected in each month and, in parentheses, the numbers of nests.

inspection very difficult when webs were not present. All of the five species of *Araneus* were found resting at the margin of their webs, in retreats made of web threads and curled-up leaves. Some specimens of *A. venatrix* were seen leaving these shelters and capturing insects during the day. Both of the *Cyclosa* species build detritus stabilimenta, and rest between two segments of these linear structures or, less often, at the extremity of the column. *Parawixia audax* and *P. velutina* were generally found at the hub of the webs, but occasionally in rolled-up leaves outside the spiral zone. *Leucauge* spp. also remained exposed in their horizontal webs, but ran to the bridge threads after perceiving a threat.

Prey lists from other studies

Although most sphecids capture a wide variety of orb-web spider genera, a maximum of three genera accounted for more than 50% of the orb-weavers captured in each population of all species of *Chalybion*, *Pison*, *Sceliphron*, and *Trypoxylon* included in the 41 studies analysed (Table II). In some species, such as *T. monteverde* (see Coville 1982) or *T. palliditarse* (see Bruch 1932), all of the spiders collected belonged to a single genus. In many others, only one or two genera represented more than 80% of all orb-weavers deposited in the nests (see Muma and Jeffers 1945; Cross et al. 1975; Matthews 1983). *Eustala*, *Araneus*, and *Neoscona* appeared as the most abundant prey in many lists. Others, such as *Cyclosa* and *Verrucosa*, were absent or present in low abundance in prey lists for most wasps species, but were heavily captured by at least one of them.

Figure 6. Regression between body length and dry weight of six spider genera captured by *Trypoxylon albonigrum* and/or *T. lactitarse* ($r^2=0.951$, $P<0.001$, $n=30$). 1, *Araneus*; 2, *Alpaida*; 3, *Wagneriana*; 4, *Mangora*; 5, *Parawixia*; 6, *Eustala*.

Figure 7. *Eustala* sp. 8 resting on vegetation. The spider remains holding a thread connected with the web hub. Scale bar: 1 cm.

Table II. Main prey of four sphecid genera.

Wasp species	Spider genera (% of total orb-weavers)																									n (most abundant genera)	% of total orb-weavers	% of total spiders		
	<i>Eustala</i>	<i>Araneus</i>	<i>Neoscona</i>	<i>Argiope</i>	<i>Alpaida</i>	<i>Paravixia</i>	<i>Acanthepeira</i>	<i>Paraneus</i>	<i>Micrathena</i>	<i>Gasteracantha</i>	<i>Larinia</i>	<i>Eriophora</i>	<i>Dolichognatha</i>	<i>Gasteracantha</i>	<i>Singa</i>	<i>Metepeira</i>	<i>Metaeygia</i>	<i>Mangora</i>	<i>Uloborus</i>	<i>Plesiometa</i>	<i>Tetragnatha</i>	<i>Araniella</i>	<i>Verrucosa</i>	<i>Cyclosa</i>	<i>Acacesia</i>				<i>Pachygmatha</i>	
<i>Chalybion</i>																														
<i>C. californicum</i> ²⁶	37.5						22.8																					88	60.3	42.0
<i>C. coeruelum</i> ³³		45.8	24.1																									174	69.9	18.8
<i>C. fuscipenne</i> ¹⁹		9.9						70.0																				162	79.9	50.0
<i>C. zimmermanni</i> ⁴⁰		50.0		45.8																								23	95.8	57.5
<i>Pison</i>																														
<i>P. morosum</i> ³⁰		100.0																										12	100.0	46.2
<i>Sceliphron</i>																														
<i>S. caementarium</i> ³	42.4			36.0																								359	78.4	62.3
<i>S. caementarium</i> ³⁴		42.1	49.2																									978	91.3	48.4
<i>S. caementarium</i> ²¹	61.4																							31.8			82	93.2	91.1	
<i>S. caementarium</i> ²⁶	55.7	23.5																									175	79.2	23.5	
<i>S. caementarium</i> ³⁹			60.6	8.6																							2115	69.2	61.0	
<i>S. fistularium</i> ⁶					100.0																						57	100.0	100.0	
<i>S. fistularium</i> ⁶								85.9																			122	85.9	85.9	
<i>S. jamaincense</i> ²⁸	20.2										17.3	16.3															56	53.8	7.8	
<i>S. laetum</i> ²⁰			41.1	24.0					24.0																		230	89.1	88.2	
<i>Sceliphron</i> sp. ¹⁸			18.7																17.3					20.4			241	56.4	25.4	
<i>Sceliphron</i> sp. ²⁴								92.3																			385	92.3	92.3	
<i>S. spirifex</i> ¹⁹		45.7					17.4																				29	63.1	15.1	
<i>Trypoxylon</i>																														
<i>T. albonigrum</i> ⁴¹	65.1					18.9																					590	84.0	84.0	
<i>T. antropovi</i> ⁵						25.0					63.9																32	88.9	88.9	
<i>T. attenuatum</i> ¹		46.4																							33.3		67	79.8	29.0	
<i>T. clavatum</i> ³⁴				53.3																							387	92.6	88.2	

Table II. (Continued.)

Wasp species	Spider genera (% of total orb-weavers)																								n (most abundant genera)	% of total orb-weavers	% of total spiders		
	<i>Eustala</i>	<i>Araneus</i>	<i>Neoscona</i>	<i>Argiope</i>	<i>Alpaida</i>	<i>Paravixia</i>	<i>Acanthepeira</i>	<i>Paraneus</i>	<i>Micrathena</i>	<i>Gasteracantha</i>	<i>Larinia</i>	<i>Eriophora</i>	<i>Dolichognatha</i>	<i>Gasteracantha</i>	<i>Singa</i>	<i>Metepeira</i>	<i>Metazygia</i>	<i>Mangora</i>	<i>Uloborus</i>	<i>Plesiometa</i>	<i>Tetragnatha</i>	<i>Araniella</i>	<i>Verrucosa</i>	<i>Cyclosa</i>				<i>Acacesia</i>	<i>Pachygnatha</i>
<i>T. clavatum</i> ³⁶	100.0																										10	100.0	10.8
<i>T. collinum</i> ²⁹			100.0																								18	100.0	100.0
<i>T. figulus</i> ¹⁷														77.9													162	77.9	77.9
<i>T. lactitarse</i> ⁹	18.4				23.7	14.9																					65	57.0	53.7
<i>T. lactitarse</i> ⁷	35.1																							21.1			104	56.2	54.7
<i>T. lactitarse</i> ⁷	64.3					19.2																					548	83.5	81.9
<i>T. lactitarse</i> ⁷	27.4					17.3																			16.2		218	60.9	57.0
<i>T. latro</i> ³²												95.5															127	95.5	95.5
<i>T. monteverde</i> ¹²	100.0																										31	100.0	100.0
<i>T. occidentalis</i> ¹²		50.0														47.1											33	97.1	97.1
<i>T. orizabense</i> ¹¹		26.9 ^a														26.9 ^a											58	53.7	50.9
<i>T. palliditarse</i> ⁴		100.0																									39	100.0	100.0
<i>T. politum</i> ²			98.0																								49	98.0	98.0
<i>T. politum</i> ³⁴	24.9		67.7																								387	92.6	23.7
<i>T. politum</i> ³⁷			86.2																								25	86.2	86.2
<i>T. politum</i> ³¹	16.7		83.3																								36	100.0	100.0
<i>T. politum</i> ³⁸		28.9	62.2																								722	91.1	91.1
<i>T. politum</i> ³⁹	24.6		64.9																								830	89.5	88.1
<i>T. rogenhoferi</i> ⁸					76.5																						692	76.5	76.0
<i>T. rogenhoferi</i> ¹⁰					97.8																						178	97.8	97.3
<i>T. rogenhoferi</i> ⁸					93.3																						461	93.3	92.9
<i>T. rubrocinctum</i> ³³																		56.3									27	56.3	20.5
<i>Trypoxylon</i> sp. ¹⁸	24.4		31.9																								240	56.3	25.3
<i>T. spinosum</i> ³¹			22.2																55.6								7	77.8	14.0
<i>T. spinosum</i> ²⁵																			69.2								9	69.2	12.7

Table II. (Continued.)

Wasp species	Spider genera (% of total orb-weavers)																		n (most abundant genera)	% of total orb-weavers	% of total spiders								
	<i>Eustala</i>	<i>Araneus</i>	<i>Neoscona</i>	<i>Argiope</i>	<i>Alpaida</i>	<i>Paravixia</i>	<i>Acanthepeira</i>	<i>Paraneus</i>	<i>Micrathena</i>	<i>Gasteracantha</i>	<i>Larinia</i>	<i>Eriophora</i>	<i>Dolichognatha</i>	<i>Gasteracantha</i>	<i>Singa</i>	<i>Metepeira</i>	<i>Metazygia</i>	<i>Mangora</i>				<i>Uloborus</i>	<i>Plesiometa</i>	<i>Tetragnatha</i>	<i>Araniella</i>	<i>Verrucosa</i>	<i>Cyclosa</i>	<i>Acacesia</i>	<i>Pachygnatha</i>
<i>T. striatum</i> ³³	45.1		39.4																								60	84.5	81.0
<i>T. striatum</i> ¹⁶	58.5	32.3																									59	90.8	90.8
<i>T. subimpressum</i> ²²			21.3																								153	56.2	40.6
<i>T. subimpressum</i> ²³	42.1															42.1				34.9							16	84.2	37.2
<i>T. tenoctitlan</i> ¹⁴																42.7	53.8										382	96.5	46.7
<i>T. texense</i> ³¹	41.7																				44.4						31	86.1	44.3
<i>T. tridentatum</i> ²⁷	32.2															29.9											322	62.1	40.9
<i>T. tridentatum</i> ¹³	85.2			9.1																							351	94.3	68.2
<i>T. tridentatum</i> ¹³		10.0								90.0																	10	100.0	58.8
<i>T. tridentatum</i> ¹³		47.4								36.8																	16	84.2	23.8
<i>T. tridentatum</i> ³⁵																100.0											182	100.0	100.0
<i>T. tridentatum</i> ¹³	28.5																				51.5						104	80	29.8
<i>T. vagulum</i> ¹⁵	30.2																					17.1	17.1				335	64.4	61.0

In all 41 studies analysed including lists of orb-weavers captured by sphecids, more than 50% of prey items were represented by a maximum of three genera. These genera of preferential prey are presented here for each wasp species or population. References: 1, Asis et al. (1994); 2, Barber and Matthews (1979); 3, Branson (1966); 4, Bruch (1932); 5, Camillo (1999); 6, Camillo (2002); 7, Camillo and Brescovit (1999a); 8, Camillo and Brescovit (1999b); 9, Camillo et al. (1993); 10, Camillo et al. (1994); 11, Coville (1979); 12, Coville (1982); 13, Coville (1986); 14, Coville and Coville (1980); 15, Coville et al. (2000); 16, Cross et al. (1975); 17, Danks (1970); 18, Dorris (1970); 19, Edmunds (1990); 20, Elgar and Jebb (1999); 21, Genaro (1996); 22, Genaro and Alayon (1994); 23, Genaro et al. (1989); 24, Gonzales-Bustamante (1994); 25, Hook (1984); 26, Horner and Klein (1979); 27, Jiménez and Tejas (1994); 28, Jiménez et al. (1992); 29, Krombein (1970); 30, Laing (1988); 31, Lin (1969); 32, Matthews (1983); 33, Medler (1967); 34, Muma and Jeffers (1945); 35, O'Brien (1982); 36, Rau (1928); 37, Rau (1944); 38, Rehnberg (1987); 39, Volkova et al. (1999); 40, Ward (1970); 41, present study. ^aPooled data for *Araneus* and *Metepeira*.

Discussion

The species composition and abundance of spiders collected by wasps were markedly different from the results obtained by visually searching the study area. These findings suggest that wasps are extremely selective, and prey on relatively rare species while ignoring other abundant ones. However, the estimate of prey availability for the wasps involve some problems that require careful analysis. First, the foraging habits of most wasp species are unknown, and some may capture their prey in places usually not inspected by researchers. Roble (1985), for example, showed that the pompilid *Anoplius depressipes* is able to capture the spider *Dolomedes triton* (Pisauridae) under water. In addition, prey availability surveys generally do not include the higher strata of vegetation and the relative abundance of the spider species in these layers may be different from that in the lower bushes and herbaceous stratum, which are usually inspected (Silva 1996; Sørensen 2003).

Even considering only the usually sampled sites, we cannot be sure about the size of the hunting area used by the wasps. In addition, the distribution of spiders may vary in space according to the density of the vegetation, microclimatic conditions, and prey availability (Enders 1972; Ward and Lubin 1993). However, this latter problem is minimized by the fact that hunting-wasp species must reduce the distance between the nesting area and foraging sites to a minimum, in order to limit the time and energy expended in provisioning the nest, to reduce the risk of having the prey stolen by another wasp or other insects, and to avoid parasitism by flies. The distance between nesting sites and the hunting area is usually unknown for wasps, but observations on the sphecids genera *Tachytes* (Kurczewski and Spofford 1986), *Podalonia* (O'Brien and Kurczewski 1982), and *Aphilanthops* (O'Neill 1994), for example, suggest that it is restricted to a few metres. We collected spiders in the area around the trap-nests and around the two houses where we found the natural nests of *T. abonigrum*. The discrepancy between the list of prey collected by wasps and those we collected may be partly explained by differences between sampling sites.

A further problem is that any sampling method may be more effective for some spider species or species groups than for others (Sørensen et al. 2002; Scharff et al. 2003). Sweeping the lower herb layer with a net or beating branches to catch the falling spiders, for example, may include specimens that are actually unavailable because they were resting inside their refuges. The spiders may be safe in these refuges because sphecids are generally unable to pursue spiders into confined spaces (Coville 1987—but see Blackledge and Pickett (2000) for an example of an alternative strategy used by wasps to capture spiders in retreats). Furthermore, by staying in refuges, spiders are less conspicuous to their predators. On the other hand, visual searching probably underestimates the abundance of species that construct webs only at night, but can be located and captured by wasps while resting relatively unprotected on vegetation during the day. This is the case of *Eustala*, the main prey item in *T. abonigrum* nests and also in nests of many other sphecids (see Table II). Since these spiders consume their webs in the morning, the main visual sign that usually attracts our attention to the spiders is no longer available. Sphecids, however, can use many techniques to locate spiders, including alighting on bumps and spots, tapping surfaces with the antennae, and examining webs and attracting spiders by pulling and vibrating web threads (Coville 1987; Laing 1988). Using a visual searching method we were able to locate webs and conspicuous spiders, but the relative abundance of cryptic spiders that can be touched by wasps during tactile inspections was probably underestimated.

Finally, insect vision is very distinct from human vision in several aspects. For example, colour differentiation in insects is made fundamentally by contrast, while humans

distinguish colours through differences in brightness (Backhaus 1991; Lunau et al. 1996). The resolution of the human eye is also much better and allows the identification of a spider web from a distance substantially higher than that of any insect. In addition, objects that reflect white plus ultraviolet light are perceived by insects as having the same colour as a background composed of leaves or soil (Blackledge 1998). Humans perceive these objects as white because of the ability to see red light wavelengths, to which very few insects are sensitive (Briscoe and Chittka 2001). Hence, some spider species that construct very conspicuous webs and/or have bright colours as perceived by human eyes, may be located by wasps at a lower frequency. This may be the case for the *Cyclosa* species collected in abundance during prey availability surveys in our study area. The researchers frequently used the presence of stabilimenta to locate otherwise inconspicuous *Cyclosa* webs. However, the shape and colour pattern of the detritus column (the most common type of stabilimentum for *C. morretes* and *C. fililineata*) may be overlooked by predators searching for spiders (see Gonzaga and Vasconcellos-Neto 2005).

All of these limitations affect our ability to evaluate prey availability for wasps. Nevertheless, a comparison of the samples made by humans and wasps can provide a useful indication of the types of potential prey that are being avoided or not located by these predators. This is an important consideration when assessing the effectiveness of different types of anti-predator strategies in spiders. Some spider species or individuals in specific stages of maturation can be avoided by wasps simply because they are too small to feed the larvae or too heavy to be transported. The relationship between wasp and spider sizes can be an important variable in influencing the success of predatory attacks, and a positive correlation between the size of females and that of their prey has been described for many species of solitary wasps (Gwynne and Dodson 1983; O'Neill 1985). Our results indicate that *T. albonigrum* and *T. lactitarse* use a wide range of prey sizes. The most abundant genera of orb-web spiders collected in our prey availability surveys in Parque Estadual Intervalas (*Cyclosa*, *Leucauge*, and *Verrucosa*) had body sizes included in this range. Adult females of *Cyclosa fililineata*, *C. morretes*, *Leucauge* spp., and some subadult and adult *Verrucosa* are in the same size range of most prey captured by *T. albonigrum*. Nevertheless, these potential prey were always absent in the mud nests of this wasp and in the trap-nests provisioned by the other wasp species. This finding indicates that the foraging behaviour of wasps is not determined solely by the selection for spider prey of specific sizes.

Two of the most abundant spider genera (*Eustala* and *Araneus*) collected by *T. albonigrum* and *T. lactitarse* in Parque Estadual Intervalas usually remain outside their webs during the day. *Araneus* was often found hidden in retreats. The other highly frequent species, belonging to the genus *Parawixia*, remained exposed at the hub of their webs or, more often, hidden close to vegetation. On the other hand, the two *Cyclosa* species and *Verrucosa arenata*, absent in the wasp nests, remained exposed in their orb-webs during the day. Both of these genera construct stabilimenta (the latter composed only of silk). Hence, retreats composed of leaves and silk are not completely effective in protecting these spiders against sphecids, although silk and detritus stabilimenta may reduce the risk of predation. This conclusion is supported by empirical data on the araneid genus *Argiope*. Blackledge and Wenzel (2001) showed that wasps (*Chalybion caerulum*) were 36% more likely to capture individuals of *Argiope trifasciata* that had not included stabilimenta in their webs, and argued that the linear silk stabilimenta built by this species could distract wasps during an attack.

Web characteristics may also be an indication of the search and attack methods used by wasps. The presence of *A. workmani* in the nests of *T. albonigrum* and in the nests of the

unidentified wasp species, for example, indicated that these wasps were probably capable of locating spiders searching for their webs (since spiders remain hidden during the day) and of removing them from their retreats. The capture techniques of some other species include attracting spiders, vibrating their webs in order to simulate an intercepted prey (aggressive mimicry), and hitting the web to capture the resident spider when it jumps (Laing 1988; Blackledge and Picket 2000). These strategies may be effective in capturing *Araneus* species.

There are few descriptions of the types of webs constructed by most spider species listed as preferential prey for hunting-wasps. However, the webs of some spider species in genera heavily preyed upon by many wasp species are well described. *Neoscona arabesca*, for example, rests in the centre of its vertical web during the night and stays in a retreat (usually a curled-up leaf) during the day (Berman and Levi 1971). This species is very abundant at many locations in the USA and Canada (Berman and Levi 1971) and was found in nests of *Trypoxylon* and *Sceliphron* species (e.g. Medler 1967; Dorris 1970; Volkova et al. 1999—see Table II). Many species of *Eustala* rest on shrubs or dead twigs during the day and make their webs in the evening (Levi 1977). This is the case of *E. anastera* (see Levi 1977 for web description), a prey of *T. politum* (Muma and Jeffers 1945), *T. striatum* (Medler 1967), and *S. caementarium* (Branson 1966). The high proportion of these genera in the nests of many wasp species indicates that the protection provided by their defensive devices is not completely effective against these predators. Some important information necessary to assess this issue, however, is not included in most previous studies. Data on the relative abundance of spider species or genera that construct retreats, stabilimenta, or that remain close to vegetation in cryptic positions during the day, associated with their frequency in wasp nests, are frequently lacking. In addition, it is important to reduce the great geographical bias in these studies, including the large and comparatively almost unknown diversity of the Neotropical species, for example.

Finally, another usually neglected aspect of prey selection is the sex ratio and the stage of maturation of the spiders collected. The low number of adult and subadult male spiders in the natural nests of *T. albonigrum* and in our trap-nests has also been observed for other *Trypoxylon* species (e.g. Rehnberg 1987; Genaro and Alayón 1994). 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 may use the web as a visual sign for approximation. Another possibility is that males are avoided because they are of poor nutritional value. Rehnberg (1987) measured the lipid content of cells provisioned by *Trypoxylon politum* and found that those with adult females were richer in lipids than those with juveniles, and subadult and adult males. In addition, males of many araneids are much smaller than females (Hormiga et al. 2000). The proportion of juveniles and females in the nests may depend on the phenology of the preferential prey species. Adult females probably provide a richer nutritional source because of the accumulation of fat tissue involved in egg production. However, the ability of wasps to discriminate between the stages of maturation is unknown.

Acknowledgements

We are especially grateful to Adalberto J. Santos for his assistance during the identification of the spiders, and Sérgio Túlio P. Amarante for identifying *Trypoxylon* (*Trypargilum*) *albonigrum* and *Trypoxylon* (*Trypargilum*) *lactitarse*. We also thank Glauco Machado, Paulo S. Oliveira, Hilton F. Japyassú, and Andrea L. T. Souza for comments on the manuscript,

and Fundação Florestal do Estado de São Paulo and IBAMA for allowing our studies in Parque Estadual Intervales. This study was financially supported by FAPESP (Proc. 99/06089-4 to M.O.G.) and CNPq (Proc. 300539/94-0 to J.V.N.), and is part of BIOTA/FAPESP—The Biodiversity Virtual Institute Programme (www.biotasp.org.br, Proc. 99/05446-8).

References

- Alves-Costa CP, Gonzaga MO. 2001. Prey capture and spatial distribution of *Philoponella vittata* (Araneae: Uloboridae) in host webs. *Ethology, Ecology and Evolution* 13:239–246.
- Asís JD, Tormos J, Gayubo SF. 1994. Biological observations on *Trypoxylon attenuatum* and description of its mature larva and its natural enemy *Trichrysis cyanea* (Hymenoptera: Sphecidae, Chrysididae). *Journal of the Kansas Entomological Society* 67:199–207.
- Backhaus W. 1991. Color opponent coding in the visual system of the honeybee. *Vision Research* 31:1381–1397.
- Barber MC, Matthews RW. 1979. Utilization of trap nests by the pipe-organ mud-dauber, *Trypargilum politum* (Hymenoptera, Sphecidae). *Annals of the Entomological Society of America* 72:260–262.
- Beaver DL, Baldwin PH. 1975. Ecological overlap and problem of competition and sympatry in the western and Hammond's flycatchers. *Condor* 77:1–13.
- Berman JD, Levi HW. 1971. The orb weaver genus *Neoscona* in North America (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 141:465–500.
- Blackledge TA. 1998. Signal conflict in spider webs driven by predators and prey. *Proceedings of the Royal Society of London B* 265:1991–1996.
- Blackledge TA, Coddington JA, Gillespie RG. 2003. Are three-dimensional spider webs defensive adaptations? *Ecology Letters* 6:13–18.
- Blackledge TA, Pickett KM. 2000. Predatory interactions between mud-dauber wasps (Hymenoptera, Sphecidae) and *Argiope* (Araneae, Araneidae) in captivity. *Journal of Arachnology* 28:211–216.
- Blackledge TA, Wenzel JW. 2001. Silk mediated defense by an orb web spider against predatory mud-dauber wasps. *Behaviour* 138:155–171.
- Bohart RM, Mencke AS. 1976. *Sphecids of the world*. Berkeley: University of California Press. 695 p.
- Branson BA. 1966. Spiders of the University of Oklahoma Biological Station, Marshall County, Oklahoma, with observations on species used by muddaubers as larval food, and a review of the species known from Oklahoma. *Southwestern Naturalist* 11:338–371.
- Briscoe AD, Chittka L. 2001. The evolution of color vision in insects. *Annual Review of Entomology* 46:471–510.
- Bruch C. 1932. Apuntes sobre costumbres de *Trypoxylon palliditarse* Sauss (Hymenoptera). *Anales de la Sociedad Científica Argentina* 114:49–61.
- Camillo E. 1999. Bionomics of *Trypoxylon (Trypargilum) antropovi* and *Trypoxylon (Trypargilum) aestivale* (Hymenoptera, Sphecidae). *Iheringia Serie Zoologia* 87:29–36.
- Camillo E. 2002. The natural history of the mud-dauber wasp *Sceliphron fistularium* (Hymenoptera: Sphecidae) in southeastern Brazil. *Revista de Biologia Tropical* 50:127–134.
- Camillo E, Brescovit AD. 1999a. Spiders (Araneae) captured by *Trypoxylon (Trypargilum) lactitarse* (Hymenoptera: Sphecidae) in southeastern Brazil. *Revista de Biologia Tropical* 47:151–162.
- Camillo E, 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* 28:251–262.
- Camillo E, Garofalo CA, Muccillo G, Serrano JC. 1993. Biological observations on *Trypoxylon (Trypargilum) lactitarse* Saussure in southeastern Brazil (Hymenoptera, Sphecidae). *Revista Brasileira de Entomologia* 37:769–778.
- Camillo E, Garofalo CA, Serrano JC. 1994. Biological observation of *Trypoxylon (Trypargilum) rogenhoferi* Kohl (Hymenoptera: Sphecidae). *Anais da Sociedade Entomológica do Brasil* 23:299–310.
- Cloudsley-Thompson JL. 1995. A review of the anti-predator devices of spiders. *Bulletin of the British Arachnological Society* 10:81–96.
- Conley MR. 1985. Predation versus resource limitation in survival of adult burrowing wolf spiders (Araneae: Lycosidae). *Oecologia* 67:71–75.
- Coville RE. 1979. Biological observations on *Trypoxylon (Trypargilum) orizabense* Richards in Arizona (Hymenoptera: Sphecidae). *Journal of the Kansas Entomological Society* 52:613–620.

- Coville RE. 1982. Wasps of the genus *Trypoxylon* subgenus *Trypargilum* in North America. University of California Publications on Entomology 97:1–147.
- Coville RE. 1986. Spider prey of *Trypoxylon tridentatum* (Hymenoptera: Sphecidae) from Arizona and California. Pan-Pacific Entomologist 62:119–120.
- Coville RE. 1987. Spider-hunting sphecid wasps. In: Nentwig W, editor. Ecophysiology of spiders. Berlin: Springer-Verlag. p 309–318.
- Coville RE, Coville PL. 1980. Nesting biology and male-behavior of *Trypoxylon tenocitlan* (*Trypargilum*) in Costa Rica (Hymenoptera, Sphecidae). Annals of the Entomological Society of America 73:110–119.
- Coville RE, Griswold C, Coville PL. 2000. Observations on the nesting biology and behavior of *Trypoxylon* (*Trypargilum*) *vagulum* (Hymenoptera: Sphecidae) in Costa Rica. Pan-Pacific Entomologist 76:28–48.
- Cross EA, Stith MG, Bauman TR. 1975. Bionomics of organ-pipe mud-dauber, *Trypoxylon politum* (Hymenoptera, Sphecoidea). Annals of the Entomological Society of America 68:901–916.
- Danks HV. 1970. Biology of some stem-nesting aculeate Hymenoptera. Transactions of the Royal Entomological Society of London 122:323–395.
- Dorris PR. 1970. Spiders collected from mud-dauber nests in Mississippi. Journal of the Kansas Entomological Society 43:10–11.
- Eberhard WG. 1970. The predatory behavior of two wasps, *Agonoideus humilis* and *Sceliphron caementarium*, on the orb weaving spider, *Araneus cornutus*. Psyche 77:243–251.
- Edmunds J. 1990. Wasp predation on orb web spiders (Araneidae) in Ghana. Acta Zoologica Fennica 190:117–122.
- Elgar MA, Jebb M. 1999. Nest provisioning in the mud-dauber wasp *Sceliphron laetum* (F. Smith): body mass and taxa specific prey selection. Behaviour 136:147–159.
- Enders F. 1972. Selection of habitat by the spider *Argiope aurantia* (Araneidae). American Midland Naturalist 90:47–55.
- Endo T, Endo A. 1994. Prey selection by a spider wasp, *Batozonellus lacerticida* (Hymenoptera: Pompilidae): effects of seasonal variation in prey species, size and density. Ecological Research 9:225–235.
- Evans HE. 1969. Notes on the nesting behavior of *Pisonopsis clypeata* and *Belomicrus forbesii* (Hymenoptera, Sphecidae). Journal of the Kansas Entomological Society 42:117–125.
- Freeman BE, Johnston B. 1978. The biology in Jamaica of the adults of the Sphecid wasp, *Sceliphron assimile* Dahlbom. Ecological Entomology 3:39–52.
- Genaro JA. 1996. Sobre la nidificación de *Sceliphron caementarium* y primer registro de *Trypoxylon texense* para Puerto Rico (Hymenoptera: Sphecidae). Caribbean Journal of Science 32:243–244.
- Genaro JA, Alayón G. 1994. Las presas (Araneae) de *Trypoxylon* (*Trypargilum*) *subimpressum* (Hymenoptera: Sphecidae) en Cuba. Revista de Biología Tropical 42:353–356.
- Genaro JA, Sanchez CS, Garcia GA. 1989. Notas sobre la conducta de nidificación de *Trypoxylon* (*Trypargilum*) *subimpressum* Smith (Hymenoptera: Sphecidae). Caribbean Journal of Sciences 25:228–229.
- Gonzaga MO, Vasconcellos-Neto J. 2005. Testing the functions of detritus stabilimenta in webs of *Cyclosa fillineata* and *Cyclosa morretes* (Araneae: Araneidae): do they attract prey or reduce the risk of predation? Ethology 111:479–491.
- Gonzales-Bustamante L. 1994. *Micrathena* spp. (Araneida: Araneidae), presa preferida por *Sceliphron* sp. (Hymenoptera: Sphecidae) en Pilcopata (Cusco). Revista Peruana de Entomología 36:22.
- Gwynne DT, Dodson GN. 1983. Nonrandom provisioning by the digger wasp, *Palmodes laeiventris* (Hymenoptera: Sphecidae). Annals of the Entomological Society of America 76:434–436.
- Hanson P, Menke AS. 1995. The sphecid wasps (Sphecidae). In: Hanson PE, Gauld ID, editors. The Hymenoptera of Costa Rica. Oxford: Oxford University Press. p 621–649.
- Henschel JR. 1998. Predation on social and solitary individuals of the spider *Stegodyphus dumicola* (Araneae, Eresidae). Journal of Arachnology 26:61–69.
- Herberstein ME, Heiling AM. 2001. Positioning at the hub: does it matter on which side of the web orb-web spiders sit? Journal of Zoology 255:157–163.
- Hódar JA. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. Acta Oecologica 17:421–433.
- Hook AW. 1984. Notes on the nesting and mating behavior of *Trypoxylon* (*Trypargilum*) *spinosum* (Hymenoptera, Sphecidae). Journal of the Kansas Entomological Society 57:534–535.
- Hormiga G, Scharff N, Coddington JA. 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). Systematic Biology 49:435–462.
- Horner NV, Klein JH. 1979. Spider prey of two mud dauber wasp species in Comanche County, Oklahoma (Hymenoptera, Sphecidae). Environmental Entomology 8:30–31.

- Jiménez ML, Servin R, Tejas A, Aguilar R. 1992. La composición de presas de la avispa lodera *Sceliphron jamaicense* Lucae en la region del Cabo, México. *Southwestern Entomologist* 17:169–180.
- Jiménez ML, Tejas A. 1994. Las arañas presa de la avispa lodera *Trypoxylon (Trypargilum) tridentatum tridentatum* en Baja California Sur, Mexico. *Southwestern Entomologist* 19:173–180.
- Kaston BJ. 1959. Notes on pompilid wasps that do not dig burrows to bury their spider prey. *Bulletin of the Brooklyn Entomological Society* 54:103–113.
- Krombein KV. 1970. Behavioral and life-history notes on three Floridian solitary wasps (Hymenoptera: Sphecidae). *Smithsonian Contributions to Zoology* 46:1–26.
- Kurczewski FE, Spofford MG. 1986. Observations on the nesting behaviors of *Tachytes parvus* Fox and *T. obductus* Fox (Hymenoptera: Sphecidae). *Proceedings of the Entomological Society of Washington* 88:13–24.
- Laing DJ. 1988. The prey and predation behaviour of the wasp *Pison morosum* (Hymenoptera: Sphecidae). *New Zealand Entomologist* 11:37–42.
- Levi HW. 1977. The American orb-weaver genera *Cyclosa*, *Metazygia* and *Eustala* North of Mexico (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 148:61–127.
- Lin CS. 1969. Biology of *Trypargilum spinosum*, with notes on *T. texense* and *T. politum* at Lake Texoma (Hymenoptera: Sphecidae: Trypoxyloninae). *Wasmann Journal of Biology* 27:125–133.
- Lunau K, Wacht S, Chittka L. 1996. Colour choices of naïve bumble bees and their implications for colour perception. *Journal of Comparative Physiology A* 178:477–489.
- Matthews RW. 1983. Biology of a new *Trypoxylon* that utilizes nests of *Microstigmus* in Costa Rica (Hymenoptera, Sphecidae). *Pan-Pacific Entomologist* 59:152–162.
- McQueen DJ. 1978. Field studies of growth, reproduction, and mortality in the burrowing wolf spider *Geolycosa domifex* (Hancock). *Canadian Journal of Zoology* 56:2037–2049.
- Medler JT. 1967. Biology of *Trypoxylon* in trap nests in Wisconsin (Hymenoptera: Sphecidae). *American Midland Naturalist* 78:344–358.
- Muma MH, Jeffers WF. 1945. Studies of the spider prey of several mud-dauber wasps. *Annals of the Entomological Society of America* 38:245–255.
- O'Brien MF. 1982. *Trypargilum tridentatum* (Packard) in trap nests in Oregon (Hymenoptera: Sphecidae: Trypoxylinae). *Pan-Pacific Entomologist* 58:288–290.
- O'Brien MF, Kurczewski FE. 1982. Ethology and overwintering of *Podalonia luctuosa* (Hymenoptera: Sphecidae). *Great Lakes Entomologist* 15:261–275.
- O'Neill KM. 1985. Egg size, prey size, and sexual size dimorphism in digger wasps (Hymenoptera: Sphecidae). *Canadian Journal of Zoology* 63:2187–2193.
- O'Neill KM. 1994. The male mating strategy of the ant *Formica subpolita* Mayr (Hymenoptera: Formicidae): swarming, mating, and predation risk. *Psyche* 101:93–108.
- O'Neill KM. 2001. Solitary wasps: behavior and natural history. Ithaca (NY): Cornell University Press. p 406.
- Polis GA, Hurd SD, Jackson CT, Sanchez-Pinero F. 1998. Multifactor population limitation: variable spatial and temporal control of spiders on Gulf of California Island. *Ecology* 79:490–502.
- Rau P. 1928. Field studies in the behavior of the non-social wasps. *Transactions of the Academy of Sciences, St Louis* 25:325–489.
- Rau P. 1944. The prey and hunting habits of the wasp, *Trypoxylon politum* Say. *Entomological News* 55:9–10.
- Rayor LS. 1996. Attack strategies of predatory wasps (Hymenoptera: Pompilidae; Sphecidae) on colonial orb web-building spiders (Araneidae: *Metopeira incrassata*). *Journal of the Kansas Entomological Society* 69:67–75.
- Rehnberg BG. 1987. Selection of spider prey by *Trypoxylon politum* (Say) (Hymenoptera: Sphecidae). *Canadian Entomologist* 119:189–194.
- Roble SM. 1985. Submergent capture of *Dolomedes triton* (Araneae, Pisauridae) by *Anoplius depressipes* (Hymenoptera, Pompilidae). *Journal of Arachnology* 13:392.
- Rogers LE, Buschom RL, Watson CR. 1977. Length–weight relationships of scrub-steppe invertebrates. *Annals of the Entomological Society of America* 70:51–53.
- Sample BE, Cooper RJ, Greer RD, Whitmore RC. 1993. Estimation of insect biomass by length and width. *American Midland Naturalist* 129:234–240.
- Scharff N, Coddington JA, Griswold CE, Hormiga G, Bjørn PP. 2003. When to quit? Estimating spider species richness in a northern European deciduous forest. *Journal of Arachnology* 31:246–273.
- Schoener TW. 1980. Length–weight regressions in tropical and temperate forest-understory insects. *Annals of the Entomological Society of America* 73:106–109.
- Silva D. 1996. Species composition and community structure of Peruvian rainforest spiders: a case study from a seasonally inundated forest along the Samiria river. *Revue Suisse de Zoologie* Volume Hors Série, 597–610.

- Sørensen LL. 2003. Stratification of the spider fauna in a Tanzanian forest. In: Basset Y, Novotny V, Miller SE, Kitching RL, editors. Arthropods of tropical forests—spatio temporal dynamics and resource use in the canopy. Cambridge: Cambridge University Press. p 92–103.
- Sørensen LL, Coddington JA, Scharff N. 2002. Inventoring and estimating subcanopy spider diversity using semiquantitative sampling methods in an Afromontane forest. *Environmental Entomology* 31:319–330.
- Uetz GW, Hieber CS. 1994. Group size and predation risk in colonial web-building spiders: analysis of attack abatement mechanisms. *Behavioral Ecology* 5:326–333.
- Volkova T, Matthews RW, Barber MC. 1999. Spider prey of two mud dauber wasps (Hymenoptera: Sphecidae) nesting in Georgia's Okefenokee swamp. *Journal of Entomological Sciences* 34:322–327.
- Ward GL. 1970. Growth of *Chalybion zimmermanni* Dahlbom in captivity (Hymenoptera: Sphecidae). *Proceedings of the Indian Academy of Sciences, Animal Sciences* 79:231–233.
- Ward D, Lubin Y. 1993. Habitat selection and the life history of a desert spider *Stegodyphus lineatus* (Eresidae). *Journal of Animal Ecology* 62:353–363.
- Wasbauer MS. 1995. Pompilidae. In: Hanson PE, Gauld ID, editors. *The Hymenoptera of Costa Rica*. Oxford: Oxford University Press. p 522–539.
- Zar JH. 1999. *Biostatistical analysis*. Upper Saddle River (NJ): Prentice Hall. 663 p.