



RESEARCH ARTICLE - WASPS

Social Wasps on *Eugenia uniflora* Linnaeus (Myrtaceae) Plants in an Urban Area

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Abstract

Social wasps (Hymenoptera: Vespidae) of the subfamily Polistinae can be effectively incorporated into IPM systems for urban forestry. This study, conducted in Viçosa, Minas Gerais State, Brazil, in May 2011, identified species of this group foraging on *Eugenia uniflora* Linnaeus (Myrtaceae) plants. The study area was monitored once a week and data collected included daily activity pattern, diversity, dominance and overlap of temporal niches by social wasps. Data analysis revealed that *E. uniflora* plants were visited by 217 individuals of 16 species of the subfamily Polistinae. Foraging behavior of social wasps bore no relationship with sampling time, but overlap of temporal niche was high. Wasps were not observed damaging healthy fruits, but were probably searching for Lonchaeidae and Tephritidae larvae. This study highlights the need for conservation of predator diversity in order to provide a partial alternative to the environmentally degrading chemical pesticides currently used in urban forestry for pest control.

Introduction

Social wasps (Hymenoptera: Vespidae) belong to the subfamilies Polistinae, Stenogastrinae and Vespinae (Schmitz & Moritz, 1998). Among these families, only Polistinae can be found in the Neotropical region, with approximately 319 species occurring in Brazil (Carpenter & Marques, 2001). Social wasps are an important part of food webs, preying on insects of the orders Coleoptera, Diptera, Hemiptera, Hymenoptera and Lepidoptera (Prezoto et al., 2005) in terrestrial ecosystems (Richter, 2000; Torezan-Silingardi, 2011).

Studies of social wasps have focused on their habitat preferences (Da Cruz et al., 2006; De Souza et al., 2010b), nest density (Diniz & Kitayama, 1994), seasonal number of colonies, nesting habits (Strassmann et al., 1997; Diniz & Kitayama, 1998; Santos et al., 2009a), insecticide selectivity (Galvan et al., 2002; Bacci et al., 2009), and floral visitation (Da Silva-Pereira & Santos, 2006). However, diversity of these insects in urban areas has not been well studied.

Floristic diversity and vegetation structure can deter-

mine composition of social wasp communities (Santos et al., 2007) by affecting foraging activity during their search for water, vegetable fiber, carbohydrates, and proteins (Richter, 2000; Elisei et al., 2010). Social wasps, like other generalist organisms, forage predominantly on the most abundant resource, without preference and/or selective behavior (Santos et al., 2007), but they can focus their resource collection activities on a small group of plants (Aguar & Santos, 2007). Their generalist condition allows them to have low dependence on specific or constant food resources (Real, 1981).

Brazilian Myrtaceae includes trees and shrubs with potential for fruit production and use in urban forestry (Donadio & Moro, 2004). *Eugenia uniflora* Linnaeus (Myrtaceae) is a semi-deciduous tree native to the south and southeast regions of Brazil used in urban forestry (Alves et al., 2008). Its popularity is mainly due to the pleasant and refreshing taste of its fruits, which resemble cherries. However, the occurrence of insect pests such as *Eugeniomyia dispar* Maia, Mendonça & Romanowski (Diptera: Cecidomyiidae) and *Anastrepha fraterculus* (Wiedemann) (Diptera: Tephritidae) (Bierhals et

al., 2012) has been discouraging the use of *E. uniflora* for landscaping and urban forestry in Brazil.

Social wasps are important natural enemies of insect pests (Prezoto et al., 2005; De Souza et al., 2010a; Picanço et al., 2010, 2011) and their diversity is similar or even higher in urban areas than in natural environments (Jacques et al., 2012). In this study we identified the social wasp species foraging on *E. uniflora* (Myrtaceae) plants in order to evaluate the potential of this group to provide biological control in an integrated pest management program.

Material and Methods

Diversity of social wasps (Vespidae: Polistinae) on *E. uniflora* plants was evaluated at the Universidade Federal de Viçosa (UFV) in an urban area of Viçosa, Minas Gerais State, Brazil, in May 2011. Two people monitored four heavily fruiting *E. uniflora* plants used in the urban forestry of the university once a week between 9:00 h and 15:00 h over a period of four weeks, and living specimens of social wasps foraging on these plants were collected with an insect net and preserved in a vial with 92.8% ethanol. Collected specimens were taken to the Laboratory of Biological Control of Insects at UFV, mounted and identified. Collection data were used to analyze daily activity pattern, diversity, dominance and temporal niche overlap of social wasp species.

The diversity of social wasps was calculated with the Shannon index (Shannon, 1948) using the formula $H' = -\sum p_k \ln p_k$. The evenness of visits by each wasp species to *E. uniflora* plants was calculated with the formula $J' = H'/H'_{\max}$ (Pielou, 1969). The dominance index was calculated with Berger Parker (May, 1975) with the formula $d = N_{\max}/N_T$.

The temporal niche overlap per pair of wasp species was determined by using the Schoener index (Schoener, 1986) with the formula $NO_{ih} = 1 - 1/2 \sum_k |p_{ik} - p_{jk}|$. Species with very small numbers of individuals ($n < 10$) were excluded from the analysis. A Kolmogorov-Smirnov test for two samples was used to evaluate interspecific differences between activity patterns per pair of social wasp species (Siegel, 1956).

Results and Discussion

Plants of *E. uniflora* were visited by 217 individuals of 16 species of social wasps of the subfamily Polistinae (Table 1). Species diversity was similar to that of the Atlantic Forest (Santos et al., 2007), but it was lower than that of Cerrado (De Souza & Prezoto, 2006; Elpino-Campos et al., 2007) and Amazon Forest (Silveira et al., 2008; Silva & Silveira, 2009) areas. The similarity between the fauna of these insects and the species commonly found in the urban area sampled and the Atlantic Forest region is important. Viçosa is included in this biome, which shows that social wasps have a high capacity to adapt to urban environments. Besides occurring in different ecosystems, differences in collection methods and sample

sizes may have contributed to differences in diversity between this study and those from other regions. On the other hand, surveys considering only one plant species showed similar or lower diversity than that of the present study (De Souza et al., 2010a; Santos & Presley, 2010; De Souza et al., 2011), suggesting that social wasp diversity may be determined more by variation in tolerance levels between species than by habitat complexity (Bomfim & Antonialli Junior, 2012).

Table 1. Number of species and individuals of social wasps (Hymenoptera: Vespidae: Polistinae) collected on *Eugenia uniflora* (Myrtaceae) fruits in Viçosa, Minas Gerais State, Brazil

	Number of individuals				Total
	04 May	18 May	25 May	30 May	
<i>Agelaia multipicta</i>	4	14	20	10	48
<i>Agelaia vicina</i>	2	0	0	0	2
<i>Brachygastra lecheguana</i>	0	0	1	6	7
<i>Mischocyttarus atramentarius</i>	1	0	0	0	1
<i>Mischocyttarus cassununga</i>	7	6	8	8	29
<i>Mischocyttarus drewseni</i>	0	0	1	0	1
<i>Polistes actaeon</i>	0	1	3	0	4
<i>Polistes simillimus</i>	1	1	6	3	11
<i>Polistes versicolor</i>	9	5	4	3	21
<i>Polybia bifasciata</i>	1	0	1	0	2
<i>Polybia fastidiosuscula</i>	7	9	8	7	31
<i>Polybia ignobilis</i>	1	0	0	0	1
<i>Polybia jurinei</i>	1	0	0	0	1
<i>Polybia platycephala</i>	5	5	23	18	51
<i>Polybia sericea</i>	0	2	2	1	5
<i>Protopolybia exigua</i>	0	1	1	0	2
Total	39	44	78	56	217

Species of the dipteran families Lonchaeidae and Tephritidae, and *Trigona spinipes* (Fabricius) (Hymenoptera: Apidae) foraged on *E. uniflora* fruits. *Apis mellifera* Linnaeus (Hymenoptera: Apidae) and *T. spinipes* visited flowers of this plant, but social wasps were not observed in these structures. These last insects can collect nectar to feed their larvae and adults (Da Silva et al., 2011), but this survey was conducted during the dry season, when nectar production could have been insufficient to attract them. Social wasps have no specialized structures for transporting pollen (corbicula) as do *A. mellifera* and *T. spinipes*, which were visiting *E. uniflora* flowers to collect pollen.

All social wasp species exploited mainly green fruits

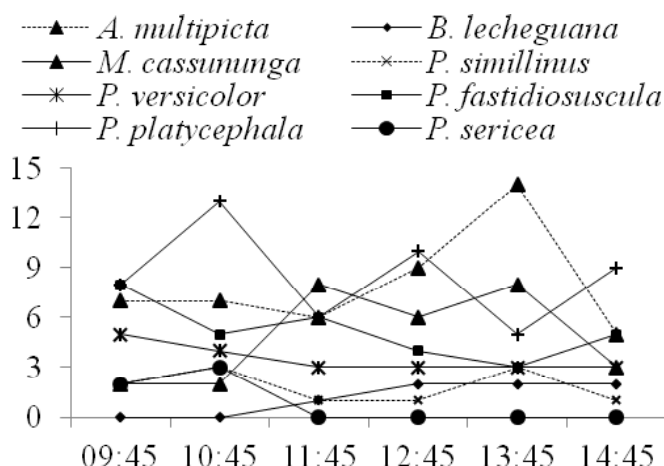
Table 2. Dominance (Berger-Parker) of social wasp species (Hymenoptera: Vespidae: Polistinae) collected on *Eugenia uniflora* (Myrtaceae) fruits as function of time of the day and total period. Viçosa, Minas Gerais State, Brazil.

	09:45	10:45	11:45	12:45	13:45	14:45	Total
<i>Agelaia multipicta</i>	0.194	0.180	0.177	0.243	0.333	0.172	0.221
<i>Agelaia vicina</i>	-	-	0.059	-	-	-	0.009
<i>Brachygastra lecheguana</i>	-	-	0.029	0.054	0.048	0.069	0.032
<i>Mischocyttarus atramentarius</i>	-	-	-	-	0.024	-	0.005
<i>Mischocyttarus cassununga</i>	0.056	0.051	0.235	0.162	0.191	0.103	0.134
<i>Mischocyttarus drewseni</i>	-	-	-	-	0.024	-	0.005
<i>Polistes actaeon</i>	0.028	0.026	-	-	0.024	0.035	0.018
<i>Polistes simillinus</i>	0.056	0.077	0.029	0.027	0.071	0.035	0.051
<i>Polistes versicolor</i>	0.139	0.103	0.088	0.081	0.071	0.103	0.097
<i>Polybia bifasciata</i>	-	0.026	0.029	-	-	-	0.009
<i>Polybia fastidiosuscula</i>	0.222	0.128	0.177	0.108	0.071	0.172	0.143
<i>Polybia ignobilis</i>	0.028	-	-	-	-	-	0.005
<i>Polybia jurinei</i>	-	-	-	0.027	-	-	0.005
<i>Polybia platycephala</i>	0.222	0.333	0.177	0.270	0.119	0.310	0.235
<i>Polybia sericea</i>	0.056	0.077	-	-	-	-	0.023
<i>Protopolybia exigua</i>	-	-	-	0.027	0.024	-	0.009
Number of individuals	36	39	34	37	42	29	217
Shannon-Winner index (H')	0.843	0.828	0.847	0.820	0.869	0.806	0.911
Pielou Evenness index (J')	0.884	0.868	0.888	0.859	0.835	0.892	0.757

with damaged areas and pre-existing holes caused by *T. spinipes*, and by oviposition behavior of fruit flies, as observed in *Anacardium occidentale* Linnaeus (Anacardiaceae) plantations (Santos & Presley, 2010), and on *Myrciaria* sp. (Myrtaceae) plants (De Souza et al., 2010a). *Brachygastra lecheguana* (Latreille), *Polistes simillinus* Zikán, *Polistes versicolor* (Olivier), *Polybia ignobilis* (Haliday), *Polybia platycephala* Richards, and *Polybia sericea* (Olivier) prey on larval forms of coleopteran, dipteran, and lepidopteran pests of agricultural and forest crops (Prezoto et al., 2005; Prezoto et al., 2006; Bichara et al., 2009; Elisei et al., 2010). Foraging behavior of social wasp species may be related to the presence of larvae of fruit flies in *E. uniflora*.

Polybia platycephala (n = 51, d= 0.235) and *Agelaia multipicta* (Haliday) (n= 48, d= 0.221) were the social wasp species with the higher values of frequency and for the dominance index, followed by *Polybia fastidiosuscula* Saussure (n= 31, d= 0.143), *Mischocyttarus cassununga* (Von Ihering) (n= 29, d= 0.134), *P. versicolor* (n= 21, d= 0.097), *P. simillinus* (n= 11, d= 0.051), *B. lecheguana* (n= 7, d= 0.032), *P. sericea* (n= 5, d= 0.023), and *Polistes actaeon* Haliday (n= 4, d= 0.018) (Tables 1 and 2). *Polybia bifasciata* Saussure, *Protopolybia exigua* Saussure, and *Agelaia vicina* (Saussure) (n= 2, d= 0.009), and *Mischocyttarus atramentarius* Zikán, *Mischocyttarus drewseni* (Saussure), *P. ignobilis* and *Polybia jurinei* (Saussure) (n= 1, d= 0.005) were less frequent (Tables 1 and 2) and of accidental occurrence. The active collection

of social wasps is an efficient process and can include most species in a survey (De Souza & Prezoto, 2006; De Souza et al., 2011; Jacques et al., 2012), but some of them, such as *A. vicina* and *P. bifasciata*, may only be collected in baited traps (De Souza & Prezoto, 2006; Jacques et al., 2012), which may explain their low frequencies in this study.

**Fig 1.** Temporal foraging activity of social wasps (Hymenoptera: Vespidae: Polistinae) on *Eugenia uniflora* (Myrtaceae) fruits. Viçosa, Minas Gerais State, Brazil.

The foraging behavior of social wasps showed no relationship with sampling time (Fig 1), differing from that in *A. occidentale* plantations, where species of this group foraged more frequently between 09:00 h and 12:00 h, and from

14:00 h to 16:00 h (Santos & Presley, 2010), or the higher foraging activity of the social wasp *Parachartergus fraternus* (Gribodo) on sunny days, between 12:00 h and 14:00 h (Santos et al., 2009b). Climatic factors, such as light, temperature and wind speed, directly affect the foraging behavior of social wasps (Kasper et al., 2008; Santos et al., 2009b; De Castro et al., 2011), so changes in these factors during the collection periods may have affected the results. Diversity and evenness values for social wasp species were also similar during all collecting periods (Table 2).

The temporal niche overlap between pairs of species of social wasps was high, 0.65-0.91 (Schoener index) (Table 3), with the highest value for *P. fastidiosuscula* and *P. versicolor* (NO_{ih} index= 0.9109). Only five of the 15 comparisons

between pairs of species differed statistically, that is, with low value of temporal niche overlap (Table 3). These results are similar to those of social wasps sharing the same food resource (Santos & Presley, 2010), again suggesting a tendency of co-existence between species of this group.

Social wasps are important predators of insect herbivores and preserving their diversity can contribute significantly to reduced application of chemical pesticides in urban forestry. Social wasps can be easily found in anthropized environments (Zanette et al., 2005; Alvarenga et al., 2010; Jacques et al., 2012), but small changes like adding floral resources to gardens or even the creation of public squares will enhance their presence and efficiency.

Table 3. Interspecific pairwise comparison of activity patterns of social wasps (species with more than 10 individuals) collected on *Eugenia uniflora* (Myrtaceae) fruits in Viçosa, Minas Gerais State, Brazil. Values above the diagonal correspond to statistical significance by the Kolmogorov-Smirnov test for two samples (significant values in bold, $P < 0.05$). Values below the diagonal correspond to temporal niche overlap between pairs of species of social wasps (Schoener index).

	<i>A. m.</i>	<i>M. c.</i>	<i>P. s.</i>	<i>P. v.</i>	<i>P. f.</i>	<i>P. p.</i>
<i>Agelaia multipicta</i>	-	0.8096	0.0122	0.0361	0.2090	0.6974
<i>Mischocyttarus cassununga</i>	0.8297	-	0.2090	0.2090	0.9996	0.2090
<i>Polistes simillinus</i>	0.8371	0.6834	-	0.2090	0.0361	0.0361
<i>Polistes versicolor</i>	0.8065	0.6700	0.7879	-	0.2090	0.0361
<i>Polybia fastidiosuscula</i>	0.7466	0.6607	0.7126	0.9109	-	0.2090
<i>Polybia platycephala</i>	0.7990	0.6531	0.7825	0.8487	0.8229	-

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References

Aguiar, C.M.L. & Santos, G.M.M. (2007). Compartilhamento de recursos florais por vespas sociais (Hymenoptera: Vespidae) e abelhas (Hymenoptera: Apoidea) em uma área de Catinga. *Neotrop. Entomol.*, 36: 836-842. doi: 10.1590/S1519-566X2007000600003

Alvarenga, R.B., Castro, M.M., Santos-Prezoto, H.H. & Prezoto, F. (2010). Nesting of social wasps (Hymenoptera, Vespidae) in urban gardens in southeastern Brazil. *Sociobiology*, 55: 445-452.

Alves, E.S., Tresmondi, F. & Longui, E.L. (2008). Leaf anatomy of *Eugenia uniflora* L. (Myrtaceae) in urban and rural

environments, São Paulo State, Brazil. *Acta Bot. Bras.*, 22: 241-248.

Alves-Silva, E., Barônio, G.J., Torezan-Silingardi, H.M. & Del-Claro, K. (2012). Foraging behavior of *Brachygastra lecheguana* (Hymenoptera: Vespidae) on *Banisteriopsis malifolia* (Malpighiaceae): Extrafloral nectar consumption and herbivore predation in a tending ant system. *Entomol. Sci.*, 16: 162-169. doi: 10.1111/ens.12004

Bacci, L., Picanço, M.C., Barros, E.C., Rosado, J.F., Silva, G.A., Silva, V.F. & Silva, N.R. (2009). Physiological selectivity of insecticides to wasps (Hymenoptera: Vespidae) preying on the diamondback moth. *Sociobiology*, 53: 151-167.

Bichara, C.C., Santos, G.M.D., Resende, J.J., Da Cruz, J.D., Gobbi, N. & Machado, V.L.L. (2009). Foraging behavior of the swarm-founding wasp, *Polybia (Trichothorax) sericea* (Hymenoptera, Vespidae): prey capture and load capacity. *Sociobiology*, 53: 61-69.

Bierhals, A.N., Nava, D.E., Costa, V.A., Maia, V.C. & Diez-Rodriguez, G.I. (2012). *Eugeniomyia dispar* in surinam cherry: associated parasitoids, population dynamics and distribution of plant galls. *Rev. Bras. Frut.*, 34: 109-115.

Bomfim, M.G.C.P. & Antonialli Junior, W.F. (2012). Community structure of social wasps (Hymenoptera: Vespidae)

- in riparian forest in Batayporã, Mato Grosso do Sul, Brazil. *Sociobiology*, 59: 755-765.
- Carpenter, J.M. & Marques, O.M. (2001). Contribuição ao estudo dos vespídeos do Brasil (Insecta, Hymenoptera, Vespidae) [CD - ROM]. Série publicações digitais, 2. Cruz das Almas, Bahia, Brasil: Universidade Federal da Bahia, Escola de Agronomia, Departamento de Fitotecnia/Mestrado em Ciências Agrárias.
- Da Cruz, J.D., Giannotti, E., Santos, G.M.M., Bichara-Filho, C.C. & Rocha, A.A. (2006). Nest site selection and flying capacity of neotropical wasp *Angiopolybia pallens* (Hymenoptera: Vespidae) in the Atlantic Rain Forest, Bahia State, Brazil. *Sociobiology*, 47: 739-749.
- Da Rocha, A.A., Giannotti, E. & Bichara, C.C. (2009). Resources taken to the nest by *Protopolybia exigua* (Hymenoptera, Vespidae) in different phases of the colony cycle, in a region of the medio Sao Francisco River, Bahia, Brazil. *Sociobiology*, 54: 439-456.
- Da Silva, E.R., Togni, O.C., Locher, G.A. & Giannotti, E. (2011). Distribution of resources collected among individuals from colonies of *Mischocyttarus drewseni* (Hymenoptera, Vespidae). *Sociobiology*, 58: 135-147.
- Da Silva-Pereira, V. & Santos, G.M.M. (2006). Diversity in bee (Hymenoptera: Apoidea) and social wasp (Hymenoptera: Vespidae, Polistinae) community in "Campos Rupestres", Bahia, Brasil. *Neotrop. Entomol.*, 35, 165-174. doi: 10.1590/S1519-566X2006000200003
- De Castro, M.M., Guimarães, D.L. & Prezoto, F. (2011). Influence of environmental factors on the foraging activity of *Mischocyttarus cassununga* (Hymenoptera, Vespidae). *Sociobiology*, 58: 133-141.
- De Souza, M.M. & Prezoto, F. (2006). Diversity of social wasps (Hymenoptera, Vespidae) in Semideciduous Forest and Cerrado (Savanna) regions in Brazil. *Sociobiology*, 47: 135-147.
- De Souza, A.R., Venâncio, D.F.A. & Prezoto, F. (2010a). Social wasps (Hymenoptera: Vespidae: Polistinae) damaging fruits of *Myrciaria* sp. (Myrtaceae). *Sociobiology*, 55: 297-299.
- De Souza, M.M., Louzada, J., Serrão, J.E. & Zanuncio, J.C. (2010b). Social wasps (Hymenoptera: Vespidae) as indicators of conservation degree of riparian forests in Southeast Brazil. *Sociobiology*, 56: 387-396.
- De Souza, A.R., Venâncio, D.F.A., Zanuncio, J.C. & Prezoto, F. (2011). Sampling methods for assessing social wasp species diversity in a eucalyptus plantation. *J. Econ. Entomol.*, 104: 1120-1123.
- Diniz, I.R. & Kitayama, K. (1994). Colony densities and preferences for nest habitat of some social wasps in Mato Grosso State, Brazil (Hymenoptera, Vespidae). *J. Hymenopt. Res.*, 3: 133-143.
- Diniz, I.R. & Kitayama, K. (1998). Seasonality of vespid species (Hymenoptera, Vespidae) in Central Brazilian Cerrado. *Rev. Biol. Trop.*, 46: 15-22.
- Donadio, L.C. & Moro, F.V. (2004). Potential of Brazilian *Eugenia* (Myrtaceae) - as ornamental and as a fruit crop. *Acta Hort.*, 632: 65-68.
- Elisei, T., Vaz e Nunes, J., Ribeiro-Junior, C., Fernandes-Junior, A.J. & Prezoto, P. (2010). Uso da vespa social *Polistes versicolor* no controle de desfolhadores de eucalipto. *Pesq. Agropec. Bras.*, 45: 958-964. doi: 10.1590/S0100-204X2010000900004
- Elpino-Campos, A., Del-Claro, K. & Prezoto, F. (2007). Diversity of social wasps (Hymenoptera: Vespidae) in *Cerrado* fragments of Uberlândia, Minas Gerais State, Brazil. *Neotrop. Entomol.*, 36: 685-692. doi: 10.1590/S1519-566X2007000500008
- Galvan, T.L., Picanço, M.C., Bacci, L., Pereira, E.J.G. & Crespo, A.L.B. (2002). Selectivity of eight insecticides to predators of citrus caterpillars. *Pesq. Agropec. Bras.*, 37: 117-122.
- Jacques, G.C., Castro, A.A., Souza, G.K., Silva-Filho, R., De Souza, M.M. & Zanuncio, J.C. (2012). Diversity of social wasps on the *campus* of the "Universidade Federal de Viçosa" in Viçosa, Minas Gerais State, Brazil. *Sociobiology*, 59: 1053-1062.
- Kasper, M.L., Reeson, A.F., Mackay, D.A. & Austin, A.D. (2008). Environmental factors influencing daily foraging activity of *Vespula germanica* (Hymenoptera, Vespidae) in Mediterranean Austrália. *Insectes Soc.*, 55: 288-295.
- Loomans, A.J.M., Murai, T. & Greene, I.D. (1997). Interactions with hymenopterous parasitoids and parasitic nematodes. In T. Lewis (Ed.), *Thrips as Crop Pests* (pp. 355-397). Wallingford, UK: CAB International.
- May, R.M. (1975). Patterns of species abundance and diversity. In M.L. Cody & J.M. Diamond (Eds.), *Ecology and Evolution of communities* (pp. 81-120). Harvard University, Massachusetts: Belknap Press.
- Picanço, M.C., De Oliveira, I.R., Rosado, J.F., Da Silva, F.M., Gontijo, P.D. & Da Silva, R.S. (2010). Natural biological control of *Ascia monuste* by the social wasp *Polybia ignobilis* (Hymenoptera: Vespidae). *Sociobiology*, 56: 67-76.
- Picanço, M.C., Bacci, L., Queiroz, R.B., Silva, G.A., Miranda, M.M.M., Leite, G.L.D. & Suinaga, F.A. (2011). Social wasp predators of *Tuta absoluta*. *Sociobiology*, 58: 621-633.
- Pickett, K.M. & Carpenter, J.M. (2010). Simultaneous analysis and the origin of eusociality in the Vespidae (Insecta: Hymenoptera). *Arthropod Syst. Phyl.*, 68: 3-33.

- Pielou, E.C. (1969). An introduction to mathematical ecology. New York: Wiley-Interscience.
- Prezoto, F., Lima, M.A.P. & Machado, V.L.L. (2005). Survey of preys captured and used by *Polybia platycephala* (Richards) (Hymenoptera: Vespidae: Epiponini). *Neotrop. Entomol.*, 34: 849-851. doi: 10.1590/S1519-566X2005000500019
- Prezoto, F., Santos-Prezoto, H.H., Machado, V.L.L. & Zanuncio, J.C. (2006). Prey captured and used in *Polistes versicolor* (Olivier) (Hymenoptera: Vespidae) nourishment. *Neotrop. Entomol.*, 35: 707-709. doi: 10.1590/S1519-566X2006000500021
- Real, L.A. (1981). Uncertainty and pollinator-plant interactions: the foraging behavior of bees and wasps on artificial flowers. *Ecology*, 62: 20-26.
- Richter, M.R. (2000). Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annu. Rev. Entomol.*, 45: 121-150.
- Santos, G.M.M., Silva, S.O.C., Bichara-Filho, C.C. & Gobbi, N. (1998). Influencia del tamaño del cuerpo en el forrajeo de avispas sociales (Hymenoptera, Polistinae) visitantes de *Syagrus coronata* (Martius) (Arecacea). *Rev. Gayana Zool.*, 62: 167-170.
- Santos, G.M.M., Aguiar, C.M.L. & Gobbi, N. (2006). Characterization of the social wasp guild (Hymenoptera, Vespidae) visiting flowers in the Caatinga (Itatim, Bahia, Brazil). *Sociobiology*, 47: 1-12.
- Santos, G.M.M., Cruz, J.D., Bichara-Filho, C.S.C., Marques, O.M. & Aguiar, C.M.L. (2007). Utilização de frutos de cactos (Cactaceae) como recurso alimentar por vespas sociais (Hymenoptera, Vespidae, Polistinae) em uma área de caatinga (Ipirá, Bahia, Brasil). *Rev. Bras. Zool.*, 24: 1052-1056. doi: 10.1590/S0101-81752007000400023
- Santos, G.M.M., Bispo, P.C. & Aguiar, C.M.L. (2009a). Fluctuations in richness and abundance of social wasps during the dry and wet seasons in three phyto-physiognomies at the tropical dry forest of Brazil. *Environ. Entomol.*, 38: 1613-1617. doi: 10.1603/022.038.0613
- Santos, G.M.M. & Presley, S.J. (2010). Niche overlap and temporal activity patterns of social wasps (Hymenoptera: Vespidae) in a Brazilian cashew orchard. *Sociobiology*, 56: 121-131.
- Santos, G.P., Zanuncio, J.C., Pires, E.M., Prezoto, F., Pereira, J.M.M. & Serrão, J.E. (2009b). Foraging of *Parachartergus fraternus* (Hymenoptera: Vespidae: Epiponini) on cloudy and sunny days. *Sociobiology*, 53: 431-441.
- Schoener, T.W. (1986). Resource partitioning. In J. Kikkawa & D.J. Anderson (Eds.), *Community Ecology - Pattern and Process* (pp. 91-126). Melbourne: Blackwell Scientific Publications.
- Schmitz, J. & Moritz, R.F.A. (1998). Molecular phylogeny of Vespidae (Hymenoptera) and the evolution of sociality in wasps. *Mol. Phylogenet. Evol.*, 9, 183-191.
- Shannon, C.E. (1948). The mathematical theory of communication. In C.E. Shannon & W. Weaver (Eds.), *The mathematical theory of communication* (pp. 3-91). Urbana: University Illinois Press.
- Siegel, S. (1956). *Nonparametric statistics for behavioral sciences*. New York: McGraw-Hill Book Company.
- Silva S.S. & Silveira, O.T. (2009). *Vespas sociais* (Hymenoptera, Vespidae, Polistinae) de floresta pluvial Amazônica de terra firme em Caxiuanã, Melgaço, Pará. *Iheringia, Sér. Zool.*, 99: 317-323. doi: 10.1590/S0073-47212009000300015
- Silveira, O.T., Costa Neto, S.V. & Silveira, O.F.M. (2008). Social wasps of two wetland ecosystems in Brazilian Amazonia (Hymenoptera, Vespidae, Polistinae). *Acta Amaz.*, 38, 333-344. doi: 10.1590/S0044-59672008000200018
- Strassmann, J.E., Solis, C.R., Hughes, C.R., Goodnight, K.F. & Queller, D.C. (1997). Colony life history and demography of a swarm-founding social wasp. *Behav. Ecol. Sociobiol.*, 40, 71-77.
- Torezan-Silingardi, H.M. (2011). Predatory behavior of *Pachodynerus brevithorax* (Hymenoptera: Vespidae, Eumeninae) on endophytic herbivore beetles in the Brazilian Tropical Savanna. *Sociobiology*, 57: 181-189.
- Zanette, L.R.S., Martins, R.P. & Ribeiro, S.P. (2005). Effects of urbanization on Neotropical wasp and bee assemblages in a Brazilian metropolis. *Landscape Urban Plan.*, 71: 105-121. doi: 10.1016/j.landurbplan.2004.02.003

