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RESEARCH ARTICLE - WASPS

Niche overlap and daily activity pattern of social wasps (Vespidae: Polistinae) in kale crops

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Abstract

Kale (*Brassica oleraceae* var. *acephala*) is of great importance in human nutrition and local agricultural economies, but its growth is impaired by the attack of several insect pests. Social wasps prey on these pests, but few studies report the importance of this predation or the potential use of wasps as biological control for agricultural pests. This study aimed to survey the species of social wasps that forage in kale (*B. oleraceae* var. *acephala*), recording the influence of temperature and time of day on the foraging behavior of these wasps. The research was conducted at the Federal Institute of Education, Science and Technology of Minas Gerais - Bambuí Campus, from July to December 2015, when twelve collections of social wasps that foraged on a common area of kale cultivation were made, noting the temperature and time of collection for each wasp. *Polybia ignobilis*, *Protonectarina sylveirae* and *Protopolybia sedula* were the most common wasp species foraging in fields of kale. Interspecific interactions between wasp species did not affect their coexistence within kale fields, with peak foraging occurring between 1000 and 1100 hours. Social wasps are important predators of herbivorous insects in the agricultural environment and the coexistence of a great diversity of these predators can help control pest insects that occur in the crop. Moreover, knowing factors that influence foraging behaviors of common wasp species that occur in this crop is important for effective use of these insects in the biological control of pests.

Introduction

Insects from the Vespidae family, order Hymenoptera, popularly known by wasps, include species with solitary or eusocial habits. Social wasps comprise three subfamilies (Stenogastrinae, Polistinae and Vespinae) (Carpenter & Marques, 2001). Wasps from the subfamily Polistinae are the only social species that occur in Brazil and belong to three tribes, Polistini, Mischocyttarini and Epiponini, representing 21 genera and 343 species (Hermes et al., 2017).

Social wasps forage to find water for nests and cooling, for plant fibers for nest materials, and for carbohydrates, such as pollen and nectar, for adult and larval nutrition (Raveret-Richter, 2000; Lima & Prezoto, 2003; Clemente et al., 2017). In addition, they forage for animal protein, especially insects from the orders Diptera, Hemiptera, Hymenoptera, and Lepidoptera, which comprise about 90-95% of captured prey (Prezoto et al., 2005; Bichara-Filho et al., 2009). These prey are torn, macerated and fed to larvae, being the main source of protein for social wasps in their early stages of development (Rabb & Lawson, 1957; Jeanne et al., 1995; Gomes et al., 2007). Nutrients, carbohydrates and proteins, can be stored inside the cells for later consumption, constituting a reserve for unfavorable periods (Barbosa et al., 2017; Michelutti et al., 2017).

Foraging activity is one of the most important and complex behaviors exhibited by social wasps (Lima & Prezoto, 2003) and it depends on the insects' ability to interact with the environment, as well as the availability of essential resources to support the colony (Gomes et al., 2007). These wasps, like other generalists, forage predominantly on the most abundant resource, without preference or selective behavior (Raveret-Ritcher, 2000; Santos et al., 2007). However, these wasps may return to hunt in locations of previous successful predation activity and feed several times on the same prey species, with individuals acting as facultative specialists (Raveret-Richter, 2000; Bichara-Filho et al., 2009). In general, higher temperatures, higher light intensity, lower humidity and lower wind speed are favor foraging conditions (Lima & Prezoto, 2003; Ribeiro-Junior et al., 2006).

Kale (*Brassica oleraceae* var. *acephala*) belongs to the Brassica family, which has the most oleaceous species, totaling 14 vegetables (Filgueira, 2008), and is of great importance to human nutrition, as they exhibit good adaptation to a variety of climates (Filgueira, 2008). Several species of insect pests attack kale, such as the whitefly, *Bemisia tabaci* (Genn.) (Hemiptera: Aleyrodidae), and the aphids *Brevicoryne brassicae* (L.) and *Myzus persicae* Sulzer (Hemiptera: Aphididae) (Galo et al., 2002). These insects weaken plants by sucking sap and introducing toxins into their vascular system, causing leaf tissue deformations and gall formation, as well as contributing to the appearance of sooty mold on the foliage through honeydew excretion (Galo et al., 2002; Van Emden, 2013).

Several Lepidoptera also attack kale crops, such as the black cutworm *Agrotis ipsilon* (Hufnagel) (Noctuidae), the cabbage looper *Trichoplusia ni* (Hübner) (Noctuidae), the cabbage caterpillar *Ascia monuste orseis* (Godart) (Pieridae) and the diamondback moth *Plutella xylostella*(L.) (Plutellidae) (Gallo et al., 2002). *A. monuste orseis* and *P. xylostella* constitutes key-pests of this crop in the Neotropical region, mainly in Brazil (Maranhão et al., 1998; Barros & Zucoloto, 1999). These species larvae feed on the leaves (Gallo et al., 2002), resulting in losses of up to 100% of crop production (Vendramim & Martins, 1982; Chen et al., 1996).

The control of kale pests is mainly carried out by the application of insecticides (Gallo et al., 2002; Andrei, 2013). These synthetic chemicals can lead to a number of problems, such as residues in food, the death of natural enemies, poisoning of the applicators, and the emergence of resistant pest populations. Therefore, the use of biological control agents could be an effective, cheap and safe alternative to the use of these toxic products.

Social wasps have been recorded preying on kale pests (Picanço et al., 2010), however few studies report the importance of this predation or potential for the use of wasps in the biological control of agricultural pests (Rabb & Lawson, 1957; Morimoto, 1961; Prezoto & Machado, 1999a,b; Freitas et al., 2015).

This research aimed to survey the species of social wasps that forage in kale (*B. oleraceae* var. *acephala*) crops, recording the influence of temperature and time of day on the foraging activity of these wasps and the temporal niche overlap of this community. With these data, we can identify which species have the greatest potential to be used in biological control programs for kale pests.

Material and Methods

This research was carried out at the Federal Institute of Education, Science and Technology of Minas Gerais - Bambuí Campus, from July to December 2015. The *campus* has a total area of 328 ha, being a human dominated but diverse landscape with a predominance of agricultural areas and buildings. A total of 175 ha are used for agricultural crops (corn, beans, sugarcane, orange, banana, coffee and vegetables) and pastures, and 34 ha are occupied by buildings, most of them are close to the cultivars. The *campus* has a high diversity of social wasps, with 29 species and 8 genera (Jacques et al., 2015).

Twelve collections were carried out in a 5 x 10 m area of kale (*B. oleracea* var. *acephala*) (Adapted from Picanço et al., 2010) between the period from 09h00 to 15h00, in which the social wasps that were foraging on the crop were collected with an entomological net, placed in a bottle containing ethyl ether and preserved in 70% ethanol (adapted from Souza et al., 2013). The time and temperature of the day at the time of collection of each wasp were recorded throughout the experiment to be correlated with the foraging activity. Collection data were used to analyze the daily patterns of activity, diversity, dominance and temporal niche overlap of social wasp species.

The collected individuals were identified with entomological keys (Richards, 1978; Carpenter, 2004), and the diversity of species calculated via Shannon-Wiener diversity (H') and Berger-Parker dominance (Dpb) indices, using the program Past, v. 2.17c (Hammer et al., 2005).

Temporal niche overlap for each possible pair of wasp species was determined using the Schoener index (Schoener, 1986). The Kolmogorov-Smirnov test for two samples was used to evaluate the interspecific differences between activity patterns for each pair of species (Siegel, 1956). Temporal niche overlap was calculated only for species of social wasps represented in the samples by more than eight specimens to minimize the effect of low abundance on the essay.

The results of the regression analysis were performed for the foraging frequency of the wasps, taking into account the variables "air temperature" and "time of day" with $p < 0.05$ (Picanço et al., 2010). For all species, it was considered the linear regression model or the model with quadratic effects. The selection of the best model was performed based on the determination coefficient. The assumptions of the model were verified through graphical analysis and through the Shapiro-Wilk, Durbin-Watson and White tests to verify error normality, residual autocorrelation and variance heterogeneity, respectively. All analyzes were conducted in the 3.3.1 version of R software (R Core Team, 2017). For the Durbin-Watson test, the *lmtest* package was used (Zeileis & Hothorn, 2002).

Results and Discussion

Three hundred and fifty-eight specimens belonging to six genera and 16 species of social wasps were collected in kale crops with a Shannon-Weiner diversity of H' = 1.84 (Table 1). The species diversity was similar to visitation in cherry trees (*Eugenia uniflora* Linnaeus) (Souza et al., 2013) and higher than other studies which analyzed only one species of plant (De Souza et al., 2010; Santos & Presley, 2010; De Souza et al., 2011; Barbosa et al., 2014).

Social wasps flew over the crop and explored the kale plants, especially those with damaged leaves. This foraging behavior may be related to the presence of *A. monuste orseis*, *B. brassicae* and *B. tabaci* in kale plants. These pests belong to the orders of insects that are most captured by the social wasps (Prezoto et al., 2005; Bichara-Filho et al., 2009; Freitas et al., 2015). The presence of leaves damaged by herbivores in herbaceous plants attracted *Polybia occidentalis* (Olivier), *Polybia diguetana* Buysson and *Polybia fastidiosuscula* Saussure (Saraiva et al., 2017). Tobacco plants previously damaged by *Manduca sexta* (L.) (Lepidoptera: Sphingidae) and *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae) attracted more foraging individuals from *Mischocyttarus flavitarsis* (de Saussure) than non-damaged plants (Cornelius, 1993).

Assumptions of error normality, autocorrelation and variance heterogeneity were met in all adjusted models, considering the graphical analysis and the appropriate usage of the tests (results not shown).

The foraging behavior of the social wasps was related to the timeof day (p = 0.025) with the maximum number of wasps collected between 1000 and 1100 hours (Fig 1). Results similar to those found in cashew trees (*Anacardium occidentale* L.) (Anacardiaceae), with greater foraging between 0900 and 1200 hrs (Santos & Presley, 2010). The air temperature directly affects foraging behavior of social wasps (Santos et al., 2009; De Castro et al., 2011), with foraging occurring mainly during warmer times of day (Picanço et al., 2010; Barbosa et al., 2014), however air temperature was not an effective predictor of wasp activity (p = 0.2184). Other factors not analyzed, such as the amount of light, wind speed and humidity, also affect foraging behavior (Santos et al., 2009; De Castro et al., 2011).

There was high dominance (Dbp = 0.41), with *Polybia ignobilis* (Haliday) (N= 147), *Protonectarina sylveirae* (Saussure) (N= 80) and *Protopolybia sedula* (Saussure) (N= 41) representing 75% of the total sampled individuals. The other most frequently collected species were *Polybia paulista* (R. von Ihering) (N= 22), *P. occidentalis* (N= 15), *Polistes satan* (Bequaert) (N= 12), *Brachygastra lecheguana* (N= 11), *Polistes versicolor* (Olivier) (N= 9), *Mischocyttarus drewseni* (Saussure) (N= 8) and *Polybia sericea* (Olivier) (N= 4). *Mischocyttarus latior* (Fox), *Polistes simillimus* (Zikán) and *Polybia jurinei* (Saussure) (N= 2) and *Mischocyttarus labiatus* (Fabricius), *Polistes ferreri* (Saussure) and *Polybia fastidiosuscula* (Saussure) (N= 1) were uncommon and considered of accidental occurrences.

Table 1. Number of individuals, species richness (S'), Shannon-Wiener diversity (H') and Berger-Parker dominance (Dpb) of the collected social wasps, per hour, in twelve collections made in kale (*Brassica oleracea* var. *acephala*) at the Federal Institute of Education, Science and Technology of Minas Gerais (IFMG), Bambuí *Campus*, Minas Gerais.

Species	09:00	10:00	11:00	12:00	13:00	14:00	15:00	Total
1 *Brachygastra lecheguana* (Latreille, 1824)	3	4	1	2	1	-	-	11
2 *Mischocyttarus drewseni* (Saussure, 1857)	1	1	-	2	2	1	1	8
3 *Mischocyttarus labiatus* (Fabricius, 1804)	-	-	1	-	-	-	-	1
4 *Mischocyttarus latior* (Fox, 1898)	-	-	-	1	-	1	-	2
5 *Polistes ferreri* (Saussure, 1853)	-	-	-	1	-	-	-	1
6 *Polistes simillimus* (Zikán,1951)	-	1	1	-	-	-	-	2
7 *Polistes versicolor* (Olivier, 1971)	-	-	3	1	1	3	1	9
8 *Polistes satan* (Bequaert, 1940)	1	1	2	4	3	1	-	12
9 *Polybia fastidiosuscula* (Saussure, 1854)	-	1	-	-	-	-	-	1
10 *Polybia ignobilis* (Haliday, 1836)	28	29	22	23	21	19	5	147
11 *Polybia jurinei* (Saussure, 1854)	-	-	1	-	1	-	-	2
12 *Polybia occidentalis* (Olivier, 1971)	-	5	1	2	6	1	-	15
13 *Polybia paulista* (R. Von. Ihering, 1896)	2	7	4	3	4	2	-	22
14 *Polybia sericea* (Olivier, 1971)	-	2	2	-	-	-	-	4
15 *Protonectarina sylveirae* (Saussure, 1854)	16	17	13	13	11	8	2	80
16 *Protopolybia sedula* (Saussure, 1854)	8	4	4	4	7	11	3	41
Number of individuals	59	72	55	56	57	47	12	358
Species richness (S')	7	11	12	11	10	9	5	16
Shannon-Wiener index (H')	1,35	1,78	1,85	1,81	1,88	1,58	1,59	1,84
Berger-Parker dominance (Dpb)	0,48	0,40	0,40	0,41	0,36	0,41	0,38	0,41

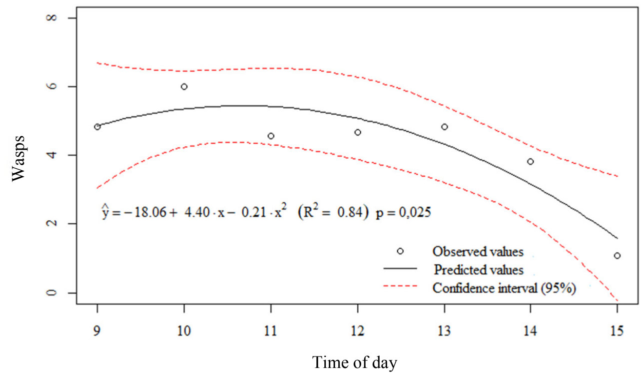

Fig 1. Effect of time of day on average number of social wasps foraging in kale (*Brassica oleraceae* var. *acephala*) from July to November 2016, in Bambuí, MG.

Polybia ignobilis is the main predator of *A. monuste orseis* (Picanço et al., 2010), and the predation of this wasp on the cabbage caterpillarswas recorded (Fig 2). Thus, the presence of this pest may have stimulated the greater presence of *P. ignobilis* in the crop. Social wasp workers forage alone and opportunistically (Jeanne et al., 1995; Michelutti et al., 2017), being able to return to hunt in locations of previously successful hunts and feeding several times of the same species of prey (Raveret -Richter, 2000; Bichara-Filho et al., 2009). To optimize this form of foraging, signals can be exchanged among workers to facilitate the acquisition of resources for the colony (Taylor et al., 2011). This behavior was reported in colonies of *P. occidentalis* (Hrncir et al., 2007; Schueller et al., 2010).

Species of the genus *Polybia* (Lepeletier) are also dominant in cashew, mango (*Mangifera indica* L.) and cherry trees (Santos & Presley, 2010; Souza et al., 2013; Barbosa et al., 2014). Wasps of this genus form large colonies, founded by a swarm composed of dozens of queens and hundreds of workers, which makes their local abundance greater than that of species whose colonies can be founded by one or a few wasps (Barbosa et al., 2014).

Fig 2. Social wasp *Polybia ignobilis* (Hymenoptera: Vespidae) preying on *Ascia monuste orseis* (Lepidoptera: Pieridae) on a kale plant (*Brassica oleracea* var. *acephala*).

The highest number of *P. ignobilis* was found at 0930 h, using a quadratic model for time of day (Fig 3A), different from that observed in the same crop in Viçosa/MG, where the highest foraging occurred at 1330 h (Picanço et al., 2010). Through a linear model for the air temperature it was observed that the amount of *P. ignobilis* individuals tended to decrease with increasing temperature (Fig 3B). In Viçosa/MG the result was similar, with the number of individuals increasing up to 29ºC, and decreasing after this temperature (Picanço et al., 2010). Time of day was a better predictor than temperature and accounted for 87% of the variation in mean *P. ignobilis* abundance (Fig 3). Higher temperatures occur after the period of greatest foraging for predation, 0930 h, thus we find a smaller number of individuals after this time of day. In the period of higher temperatures, the wasps are concentrated in the collection of water to cool the colony (Akre, 1982; Montefusco et al., 2017).

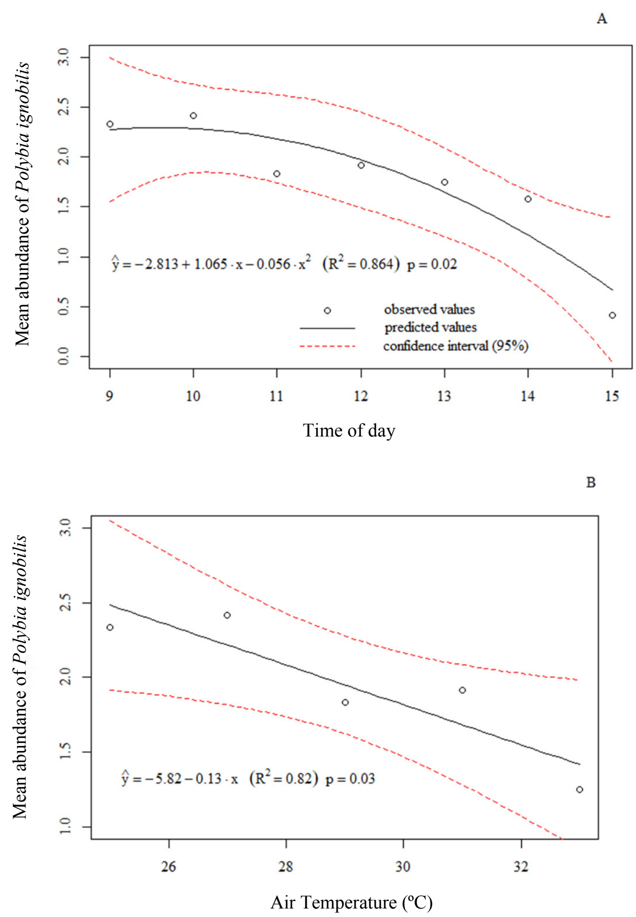

Fig 3. Average number of wasps of *Polybia ignobilis* (Hymenoptera: Vespidae) foraging in kale plants (*Brassica oleracea* var. *acephala*) as a function of: A -timeof day and; B - air temperature, from July to November 2016 in Bambuí, MG.

The quadratic model for time of day explained 96% of the variation in mean *P. sylveirae* captures, with peak abundance observed early in the day (0900 hr) (Fig 4). This time is different from the time found for all species, which was between 1000 and 1100hrs. Temperature did not affect *P. sylveirae* abundance. The presence of *A. monuste orseis* may attract *P. sylveirae*, as this is a common prey species of *P. sylveirae* (Bueno & Souza, 1993). In addition, this species preys on Hemiptera such as *Aleurothrixus floccous* (Maskell) (Hemiptera: Aleyrodidae) (Souza & Zanuncio, 2012), probably being attracted by the presence of *B. brassicae* and *B. tabaci*.

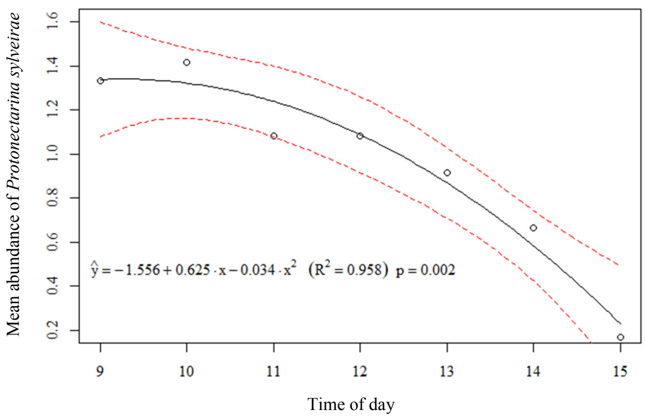

Fig 4. Effect of time of day onaverage number of wasps of *Protonectarina sylveirae* (Hymenoptera: Vespidae) species foraging in kale plants (*Brassica oleracea* var. *acephala*) from July to November 2016 in Bambuí, MG.

None of the statistic models fit the data considering the time of day for *P. sedula*. In contrast, observations of colonies of this species indicate that peak foraging activity occurs between 1030 and 1430 (Detoni et al., 2015). For the air temperature, the quadratic regression model was selected, in which the minimum number of wasps was obtained around 29º C (Fig 5). The climatic variables possibly have a low effect over the foraging rhythm of this wasp (Detoni et al., 2015). The presence of an envelope that protects *P. sedula* nests can generate a certain level of homogenization of the internal environment in terms of temperature and humidity, increasing the importance of internal colony stimuli when it comes to foraging outflows (Detoni et al., 2015). Moreover, this research recorded the foraging behavior only in kale, and this species may be foraging in another plant species. This species preys on *A. floccous* (Souza & Zanuncio, 2012) and probably is also attracted by the presence of *B. brassicae* and *B. tabaci*.

The temporal niche overlap between pairs of species of social wasps varied between 0.31- 0.96 (Schoener index) (Table 2), being smaller between *B. lecheguana* and *P. versicolor* and higher between *P. ignobilis* and *P. sylveirae*. In general, the activity overlap was relatively high, being greater than 50% in 31 of the 36 pairs, and there was no significant difference based on Kolmogorov-Smirnov 2-sample tests. This high value of temporal niche overlap was also found in *A. occidentale* and *E. uniflora* (Santos & Presley, 2010; Souza et al., 2013), suggesting a trend of coexistence among species of this group. The agricultural features of the campus, with the presence of many crops, and consequently many herbivores, may have led to a decrease in interspecific competition allowing greater coexistence of wasps in the crop. The division of resources by guild members and the resulting competitive structure can only be seen if they are maintained over time by competition for limiting resources (Pianka, 1980). Moreover, the generalist tendencies of social wasps allows them to have low dependence on particular food resources (Santos et al., 2007). This dietary flexibility likely facilitates coexistence by reducing interspecific competition.

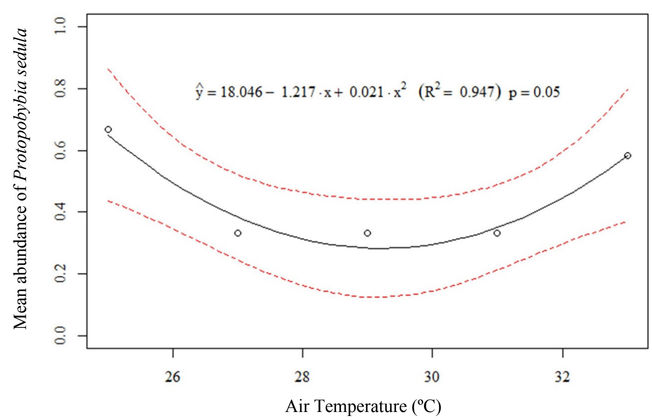

Fig 5. Effect of air temperature on average number of wasps of *Protopobybia sedula* (Hymenoptera: Vespidae) species foraging in kale plants (*Brassica oleraceae* var. *acephala*) from July to November 2016 in Bambuí, MG.

Table 2. Temporal niche overlap (Schoener index) among pairs of species of social wasp (species with more than eight individuals) collected in kale (*Brassica oleracea* var. *acephala*) crops at the Federal Institute of Education, Science and Technology of Minas Gerais (IFMG), Bambuí *Campus*, Minas Gerais. Significance (P≤0.05) for the Kolmogorov-Smirnov test for two samples used to evaluate differences between the patterns of temporal activity among pairs of species of social wasps is indicated above the diagonal.

	Br. le.	*Mi. dr.*	*Po. ve.*	*Po. sa.*	*Po. ig.*	*Po. oc.*	*Po. pa.*	*Pr. sy.*	*Pr. se.*
Brachygastra lecheguana	-	NS	NS	NS	NS	NS	NS	NS	NS
Mischocyttarus drewseni	0,61	-	NS	NS	NS	NS	NS	NS	NS
Polistes versicolor	0,31	0,46	-	NS	NS	NS	NS	NS	NS
Polistes satan	0,62	0,75	0,47	-	NS	NS	NS	NS	NS
Polybia ignobilis	0,77	0,71	0,54	0,70	-	NS	NS	NS	NS
Polybia occidentalis	0,72	0,58	0,36	0,60	0,61	-	NS	NS	NS
Polybia paulista	0,82	0,63	0,49	0,73	0,81	0,77	-	NS	NS
Protonectarina sylveirae	0,79	0,68	0,51	0,71	0,96	0,62	0,83	-	NS
Protopolybia sedula	0,64	0,69	0,65	0,62	0,79	0,50	0,65	0,75	-

We recorded 4 species, *M. labiatus*, *P. ferreri*, *P. fastidiosuscula* and *P. sylveirae* that had not been collected previously at the IFMG – Bambuí *Campus* according to a diversity survey of social wasps previously performed by Jacques et al. (2015).

Wasp species exhibited similar temporal activity patterns in a small patch of kale, suggesting that interspecific interactions among these species did not affect their ability to coexistence as predators on pest species. Social wasps are important predators of herbivorous insects in the agricultural environment and the coexistence of a great diversity of these can lead to a greater control of the pest insects that occur on the crop. Furthermore, knowing the period and the factors that influence the foraging of the main species that occur in the crop is important for the effective use of these insects in the biological control of pests.

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