



RESEARCH ARTICLE - WASPS

Polistes canadensis (Linnaeus, 1758) (Vespidae: Polistinae) in the Western Amazon: a Potential Biological Control Agent

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Abstract

Wasps of the genus *Polistes* (Vespidae: Polistinae) are eusocial, considered valuable biological control agents. The objective of this work was to determine the resources collected by *Polistes canadensis* wasps, evaluate their performance and importance as a natural enemy and possible agent of biological control in the Brazilian Amazon. Between October 8th and November 20th, 2014, 20 evaluations were performed, totalizing 101 hours of observations of the foraging activity of an aggregation out in stage of development post-emergence with approximately 50 adult individuals distributed in 15 colonies. Additionally, observations of the predatory activity of *Polistes canadensis* on *Plutella xylostella* on a small organic plantation of kale (*Brassica oleracea* L. var. *acephala* DC), were also made. During the evaluations 1742 returns were recorded, 11.72% of them with prey, 3.10% with plant fiber, 16.76% with nectar, 45.17% with water and 23.25% without any visible load. All the preys identified were classified as Lepidoptera, belonging to ten morphospecies. Only one morphospecies was identified as *Spodoptera frugiperda*, which was the most commonly resource used by the wasps in 37 % in immature feeding. Only returns with nectar had statistically significant difference between the evaluated schedules. *Polistes canadensis* wasps did not prey *Plutella xylostella* caterpillars. The wasp aggregation studied was able to prey an average of 10.2 caterpillars per day, which demonstrates the potential of this species for the biological control of pests in the Amazon region.

Introduction

Wasps are Hymenoptera that present different behaviour, ranging from solitary species to social groups with female caste variations (Prezoto et al., 2007). The wasps reveal an opportunistic characteristic: they return to places with a great supply of resources or food, in search of the optimization of the foraging and reduction of the search effort (Raveret-Richter, 2000). In general, wasps perform several ecological functions; a relevant point among these ecological functions is their role as natural enemies, since predatory wasps contribute to the regulation of insect populations and consequently to the reduction of insecticide use, with natural biological control being a significant contribution in

this process (Gallo et al., 2002). They use a large source of resources present in the environment: water (used to cool the colony); plant fibers (construction and maintenance of the colony); nectar and pollen (a rich source of energy) and prey (used to feed the immature).

Polistes (Vespidae: Polistinae) is one of the most common genus among social wasps (Carpenter, 1996). It is a cosmopolitan genus, with 222 valid species distributed in all biogeographical zones, except in Antarctica, most of which occur in the tropics (Carpenter, 1996; Pickett et al., 2006). Some authors pointed out the importance of *Polistes* in the regulation of insect-plague populations of crops of economic importance and for the facility of manipulation and translocation of their colonies to artificial shelters (Figueiredo



et al., 2006; Elisei et al., 2010; Prezoto, 1999; Prezoto et al., 1994; Giannotti et al., 1995; Prezoto & Machado, 1999a, 1999b; Andrade & Prezoto, 2001).

The species *Polistes canadensis* (Linnaeus, 1758), is a social wasp found in the New World, with a wide distribution, occurring from the southern United States to southern Brazil and Argentina (Carpenter, 1996). The nests are established by independent foundation, where only one or a few queens begin to construct the nest, oviposit and feed the immature forms (Wenzel, 1998). They are able to obtain resources at 650 meters from the colony, but with radius of action of 125 meters, foraging in an area of approximately 49,000 m² (Santos et al., 1994). This species is relatively non-aggressive, which allows translocate their nests easily (Marques et al., 1992; Marques, 1996). The pattern of foundations and dropouts of colonies of *P. canadensis canadensis* occurring all year round, presents an asynchronous pattern between nesting and environmental variables (Masques et al., 1992; Torres et al., 2009b).

The social wasp *P. canadensis* presents several characteristics which qualifies it as important natural enemies of pest insects. Studying aspects related to their foraging activity and the resources collected by them, may contribute to ecological and agricultural benefits. Therefore, the objective with this work was to determine the resources collected by *P. canadensis* and to evaluate their performance and importance as a natural enemy and possible agent of biological control.

Material and methods

The experiment was carried out at the experimental field of Embrapa Western Amazon called Caldeirão (Fig 1), located

at coordinates 03° 14'22 "and 03°15'47" south latitude and at 60° 13'02 "and 60° 13'50" west longitude, in the municipality of Iranduba, Amazonas, during the period from October 8 to November 20, 2014. Were evaluated an aggregation of *P. canadensis* colonies with approximately 50 adult individuals distributed in 15 colonies (Fig 2 A). Besides, observations on an organic small plantation of kale (*Brassica oleracea* L. var. *acephala* DC), were also realized.

Resources collected by Polistes canadensis

In total, 101 hours of observations of foraging activity of the aggregation were carried out in stage of development the colony post-emergence (Jeanne, 1972). The method used in the evaluations was adapted from Prezoto et al. (1994), where the identification of the material collected by the wasps was carried out by observing the behaviour presented by them when they returned to the nest: nectar collection, when there were trophallaxis, adult-adult or adult-larvae (Fig 2B); water collection (Fig 2C), when the liquid was deposited directly on the cell walls; the returns with wood pulp used in cells construction (Fig 2D) and returns with prey used in feeding of the immatures (Fig 2E, F and G) were identified by the observation of the resources in the mouthparts besides the slow flight.

The evaluation of foraging activities occurred in 16 non-consecutive days. On each day, the foraging activity was observed and registered every 30 minutes, with intervals of the same time, during the hours of highest foraging activity of the colonies, between 10 am and 15:30 pm. The wasps that returned to the colony with some material between the jaws were intercepted with the use of entomological

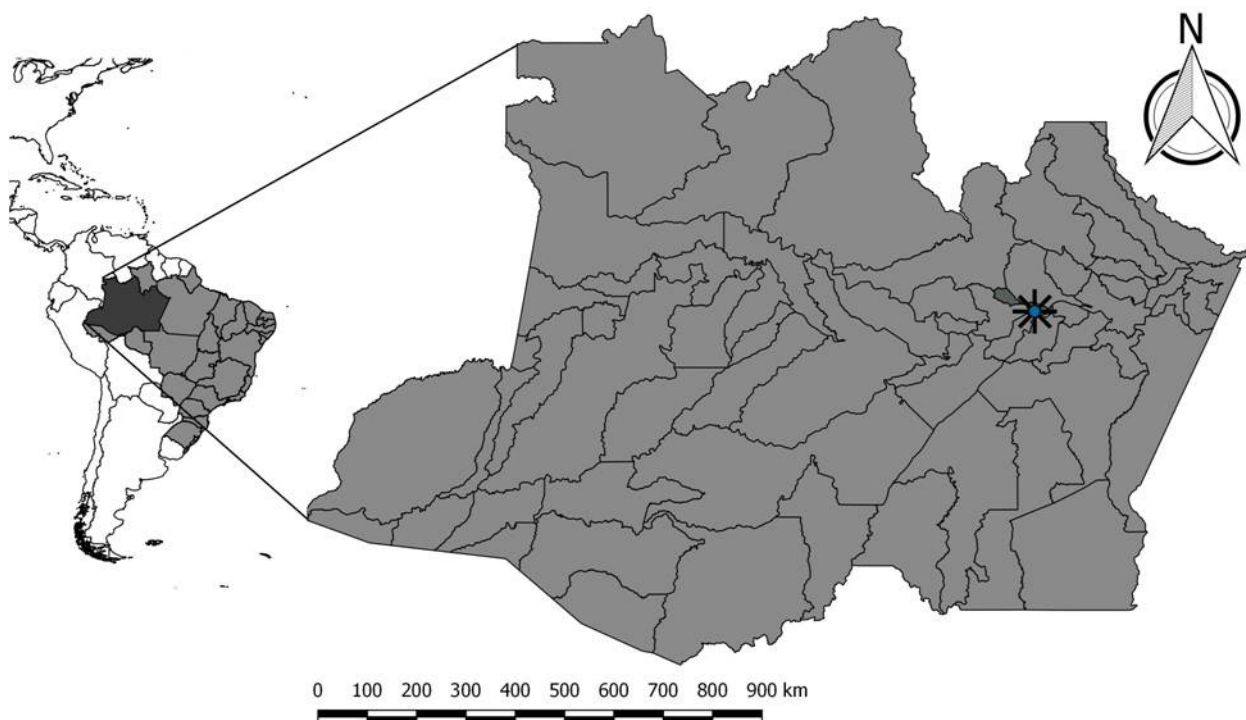


Fig 1. Location of the Experimental Field of Caldeirão of EMBRAPA Western Amazon, Iranduba, Amazonas, Brazil.

net and the material that they carried was collected. The preys carried by the wasps were collected and fixed in 70% alcohol, inside microtubes. In the Entomology Laboratory of Embrapa Western Amazonia the samples were screened using a stereomicroscope equipped with a camera and categorized in morphospecies, based on corporeal structures such as cephalic capsule, pseudopodia and seta, according to Elisei et al. (2010). Some data on atmosphere conditions such as mean temperature, relative air humidity, precipitation and wind speed were obtained at the weather station of the same experimental field.

Based in an empirical knowledge that *P. canadensis* could be a regulated agent of *Plutella xylostella* (Linnaeus, 1758), during the intervals between evaluations of foraging activity (every 30 minutes), some observations of this expected predatory activity were performed. Two small kale plantation measuring 6m long and 1m wide were observed, each plantation had 20 plants in 2.8 liter pots, spaced 50 x 50cm, distant approximately 12m from the wasps colonies evaluated. The plantations were covered with voile cloth to ensure the fixation and spread of *P. xylostella* insects that were later released. The observations were made very close to the plants allowing the record of the predatory action of the wasps and their foraging behaviour.

Data analysis

Variance analysis (ANOVA) and a Tukey's post-test (5% significance) were done in order to compare the data collected by the wasps in every 30 minutes per hour observed. The analyses were performed with R Core team software (2017).

Results and discussion

Polistes canadensis foraging wasps presented homogeneously return activity with resources practically at all times evaluated, with no peaks of returns (Table 1). In total, 1742 returns of foraging wasps to the colonies were recorded during this study. Of these returns, 45.17 % were returns with water, 11.72 % with prey, 3.10 % with vegetal fiber, 16.76 % with nectar and 23.25 %, returns were considered frustrated based on behavior during the arrival at the colony. Following, these returns will be better evaluated individually.

Resources collected by *Polistes canadensis*

Water: Most of the recorded returns during the evaluations were identified as water 45.17 % (N = 787).

Table 1. Average and standard error of returns with water, prey, plant fiber, nectar and frustrated returns of the foragers of *Polistes canadensis*. Values followed by the same letter in the column do not differ from each other, by the Tukey test at 5% significance.

Assessments	Water	Prey	Fiber	Nectar	Frustrated
10:00-10:30 h	7.37±5.61 A	1.62±1.58 A	0.5±0.83 A	3.81±2.26 A	3.93±2.95 A
11:00-11:30 h	7.06±4.40 A	2.25±1.61 A	0.37±0.5 A	2.62±1.96 A	4.12±2.44 A
12:00-12:30 h	8.12±6.11 A	1.75±1.73 A	0.62±0.80 A	3.12±1.66 AB	3.62±2.5 A
13:00-13:30 h	5.87±5.09 A	1.81±1.47 A	0.25±0.44 A	1.81±2.00 AC	3.18±3.35 A
14:00-14:30 h	7.5±6.11 A	1.68±1.13 A	0.37±0.61 A	2.25±1.65 A	4.31±2.62 A
15:00-15:30 h	6.43±5.98 A	2.18±1.60 A	0.5±0.81 A	1.18±1.37 CD	2.93±2.37 A

This resource was provided to the immature or divided between the wasps and placed inside the cells, mainly with immature ones, being also deposited in the back part of the colonies. The water is used to cool the colony and is collected by the foragers in large quantity, mainly in hours with higher temperature (Akre, 1982; Greene, 1991). The effort employed by *P. canadensis* in the collection was higher than compared to other species of *Polistes*: *P. simillimus*, *P. versicolor*, *P. lanio*, in studies conducted on days with temperature between 22 and 35°C (eg: Prezoto & Machado 1999a; Prezoto et al., 1994; Elisei et al., 2010; Giannotti et al., 1995). The large amount of water collected shows that the availability of this resource nearby the colonies is fundamental for the maintenance of the nest microclimate and colony equilibrium.

Preys: 11.72 % (N = 204) of worker wasps returns were recorded as returns with preys. The behavior presented by the wasps as soon as they arrived at the colony was to remain still while chewing the prey. After a few moments, the macerate

was divided with other wasps, which later fed the larvae. This same behavior was recorded and described by Torres et al. (2009a) for this same species of wasp. An average of 10.2 returns with prey per day was recorded, a similar value to this one was found by Prezoto et al. (2006) for *P. versicolor* and Prezoto et al. (1994) for *P. simillimus*, with averages of 11 and 16.9 returns with preys per day. These results demonstrate the potential of *P. canadensis* as a biological control agent, when compared to the previously mentioned species, as a controlling agent of herbivores of agricultural importance (Elisei et al., 2010; Prezoto & Machado, 1999b).

Preys captured by *P. canadensis*: was possible to characterize 49 % (N = 100) of the prey captured by the size, color and body structures, for 51 % (N = 104) of the preys specimens, the identification was not possible due to the high level of maceration of the samples. All samples with possible identification were classified as immature of Lepidoptera order, being categorized as belonging to 10 different morphospecies

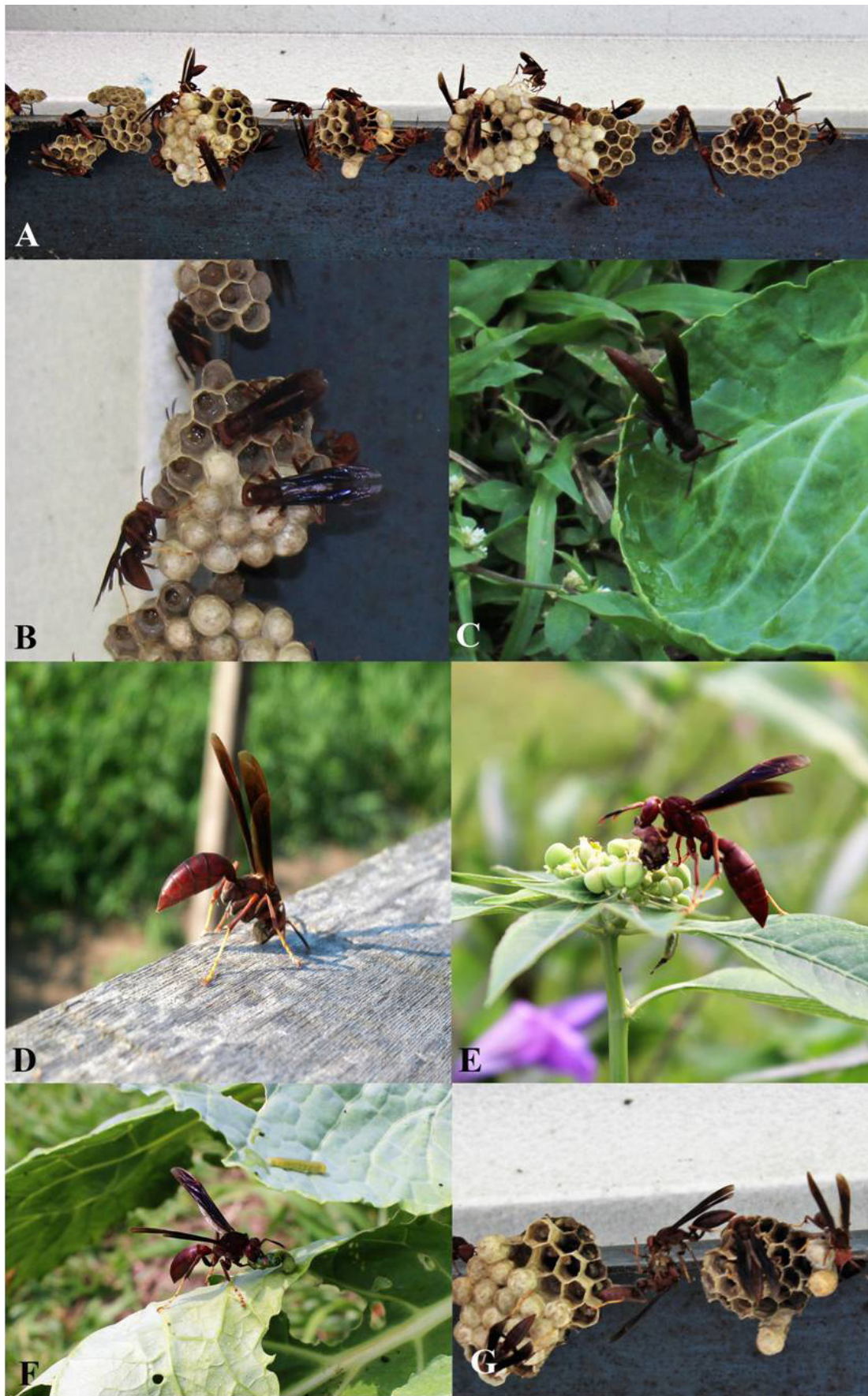


Fig 2. A – Evaluated colonies of *Polistes canadensis*.; B- Nectar collection, when there were trophallaxis adult-larvae.; C- Water collection.; D- Gathering of vegetable fiber in the vicinity of the colonies.; E and F returns with prey used in feeding of the immatures.; G- Prey being shared.

(Fig 3). Only one morphospecies was identified, as *Spodoptera frugiperda* (Smith, 1797) (morphospecies 1), which was the most commonly resource used by the wasps in 37 % in immature feeding. Caterpillars (Lepidoptera) are the major food source to the immature of *P. canadensis* and other species of this genus (Prezoto et al., 1994; Giannotti et al., 1995; Andrade & Prezoto, 2001; Torres et al., 2009a). In other studies showing the efficiency of *Polistes* spp. As a predator, wasps were also related to the predation of large caterpillars, such as *S. frugiperda* predated by *P. simillimus* (Prezoto & Machado, 1999a) and *Chlosyne lacinia saundersii* Doubleday & Hewitson, 1849 predated by *P. versicolor* (Prezoto et al., 2006). Considering the agricultural importance of the fall armyworm *S. frugiperda* and the resistance presented by the insect to both insecticides (Omoto & Diez-Rodriguez, 2001) and transgenic crops (Farias et al., 2014), a biological control agent stands out as a great option in the management this pest. From the results obtained with this study, it can be estimated that an aggregation of a colony containing 50 individuals is able to prey on an average of 10.2 caterpillars per day, which demonstrates the potential of *P. canadensis* as a biological control agent, including the possibility of agent control of the armyworm *S. frugiperda*.

Plant fiber: 3.10 % (N = 54) of the foraging wasps returns were characterized as returns with fibers of vegetal material. Approximately 60 % (N = 34) of the foragers returning to the colony with fibers, divided this resource with other wasps, which later deposited it in the cells, mainly with immature ones. The objective of this activity and behavior is probably due to the need to increase the height of the cells, as a function of immature development, as proposed for this species by Torres et al. (2009a) and for other species of the genus, such as *P. lanio* (Giannotti et al., 1995) and *P. versicolor* (Zara & Balestieri, 2000).

Trophallaxis: 16.76 % (N = 292) of the returns were considered as returns with nectar to the colony followed by trophallaxis. The foraging wasps performed the behavior considered as trophallaxis when they returned to the colony, apparently with no visible recourse between mouthparts, but always followed, soon after, by trophallaxis with the immature or with the adult present at the colony. Elisei et al. (2010) quantified this behavior associated with the nectar collection for *P. versicolor* in 51.6 % (934) and Andrade & Prezoto (2001) in 54.2 % for *P. ferreri* in the post-emergence period. Yet Prezoto et al. (1994) quantified a lower percentage to *P. simillimus* (28.5 %). And Torres et al. (2009a), studying the division of labor of 15 colonies of *P. canadensis* under natural conditions in Mundo Novo, Mato Grosso do Sul, showed that 35% of returns of wasps were with nectar. The percentage of returns with nectar followed by trophallaxis in this study was lower than the others mentioned previously, however, the differences of species, biome and experimental conditions prevent further generalizations or conclusions in this respect.

Frustrated returns: Practically $\frac{1}{4}$ of the returns (23.25 %, N = 405) were considered frustrated, in other words, without

any behavior or apparent material or prey at the return, performing an efficient foraging index of 76.75 %. Similar value was found by Prezoto et al. (1994) and Elisei et al. (2010) for *P. simillimus* and *P. versicolor*, with 72.93 % and 80.13 % returns with resources.

Foraging activity

The average of returns with prey at the different times did not present significant differences (Table 1). Foraging wasps collected prey at all times evaluated. Despite the post-emergence development stage of the 15 colonies assessed,

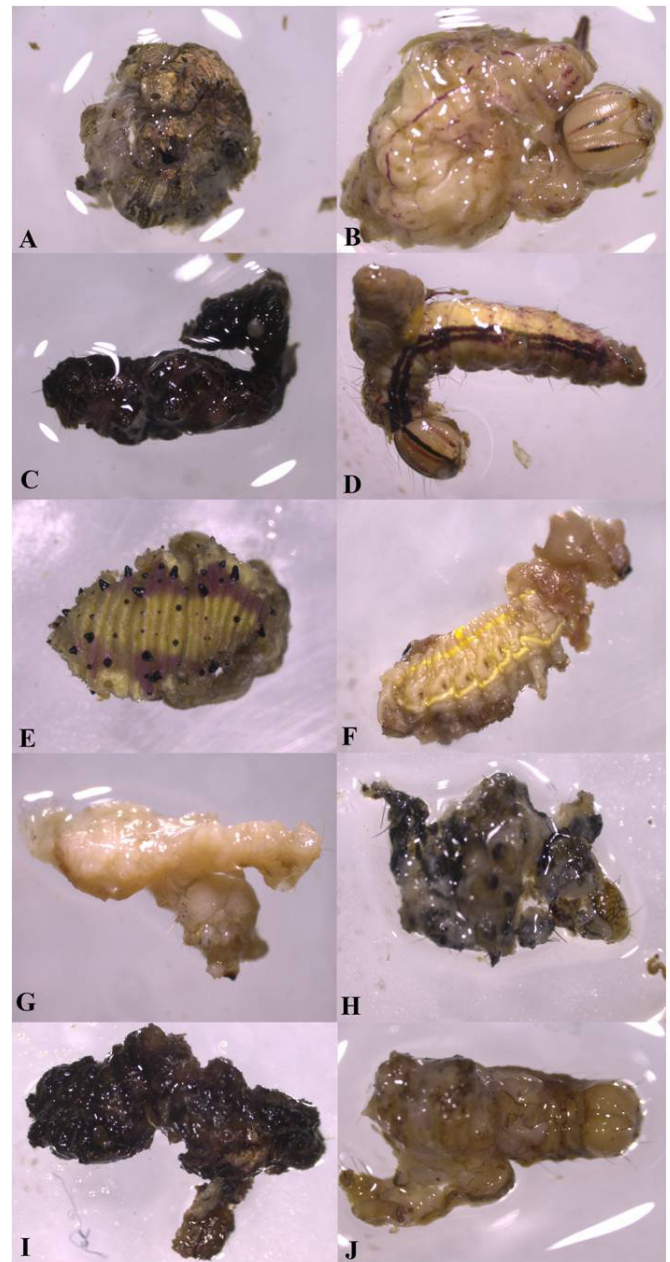


Fig 3. Caterpillar morphospecies collected through flight interception of *P. canadensis* returning to the colony: A- *Spodoptera frugiperda* (N = 37) (Morphospecies 1); B- Morphospecies 2 (N = 7); C- Morphospecies 3 (N = 3); D- Morphospecies 4 (N = 6); E- Morphospecies 5 (N = 3); F- Morphospecies 6 (N = 15); G- Morphospecies 7 (N = 2); H- Morphospecies 8 (N = 18); I- Morphospecies 9 (N = 4); J- Morphospecies 10 (N = 5).

plant fiber was the least used resource, approximately 3.1 %, with no difference between the 30-minute evaluations (Table 1). Return with nectar was the only resource with statistically significant difference between the evaluated schedules ($p = 0.001$). Although there was a tendency to decrease the amount of nectar returns, a significant difference was observed only in the half hour evaluations performed from 12:00 to 12:30, 13:00 to 13:30 and 15:00 to 15:30 (Table 1). The production and availability of floral resources, such as nectar, may be directly related to the number of floral visitors/pollinators visited during the day (Waddington, 1983). Therefore, the decrease in the amount of nectar returns may be related to the availability of this resource in the environment. Water was the most used resource, also with no significant difference. According to Torres et al. (2009a), *P. canadensis* collects more water at temperatures above 22°C. During our evaluations of the foraging activity, the temperature was higher than that, ranging from 23.85 to 35.29°C, with an average of 26.59°C and a standard deviation of 2.90°C, therefore, requiring a large amount of water returns to maintain the thermal comfort of the colonies. There was also no significant difference in frustrated returns, showing that the resources used by *P. canadensis* are available throughout all the period studied.

Predatory activity of P. canadensis on P. xylostella

During the evaluations of the foraging activity of *P. canadensis* in the small plantation of kale, the predation of *P. xylostella* caterpillar wasn't observed. However, other social wasps of the genus *Polybia*, which were collected and identified as *P. bistriata*, *P. rejecta* and *P. sericea*, preyed *P. xylostella* in small amounts. *P. canadensis* wasps were frequently observed above the kale plants seeking drops of water and predating another larger caterpillar species identified as Pieridae family, which used kale as host. Most of the *P. canadensis* wasps observed in kale presented the behavior of removing the cephalic capsule from the caterpillar. In addition, cephalic capsules of caterpillars were also found on kale leaves, possibly predated by this species or other social wasps.

Conclusion

In several regions of the Amazon, the advance of agriculture is undeniable and crescent, thought this activity presents great gaps in the knowledge of sustainable agricultural practices adapted to the local reality, especially in the phytosanitary area. For this reason, the biological control with predatory wasps is an excellent strategy for the Amazon, in order to regulated the pest insect population, reducing the use of insecticides and consequently reducing the environmental impacts.

The species *P. canadensis* is widely distributed in the new world, showed intense foraging activity and generalist habit of predation for the selection of caterpillars in the Amazon

region studied, predating caterpillars of several species and preferring larger caterpillars. Due to the high index of captured prey and the intense foraging activity, this species should be considered as a potential species for the biological control of agricultural pests in crops in the Amazon region.

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References

- Akre, D. (1982). Social wasps. In H.R. Hermann (Ed.). Social insects (pp. 1-105). New York: Academic Press.
- Andrade, F.R. & Prezoto, F. (2001). Horários de atividade forrageadora e material coletado por *Polistes ferreri* Saussure, 1853 (Hymenoptera, Vespidae), nas diferentes fases de seu ciclo biológico. *Revista Brasileira de Zoociências*, 3: 117-128.
- Carpenter, J.M. (1996). Distributional checklist of species of the genus *Polistes* (Hymenoptera: Vespidae; Polistinae, Polistini). *American Museum Novitates*, 3188: 1-39.
- Elisei, T., Vaz, J., Junior, C.R., Junior, A.J.F., & Prezoto, F. (2010). Uso da vespa social *Polistes versicolor* no controle de desfolhadores de eucalipto. *Pesquisa Agropecuária Brasileira*, 45: 958-964. doi: 10.1590/S0100-204X2010000900004
- Farias, J.R., Andow, D.A., Horikoshi, R.J., Sorgatto, R.J., Fresia, P., Santos, A.C. & Omoto, C. (2014). Field-evolved resistance to Cry1F maize by *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Brazil. *Crop Protection*, 64: 150-158. doi: 10.1016/j.cropro.2014.06.019
- Figueiredo, M.D.L.C., Mantins-Dias, A.M.P. & Cruz, I. (2006). Relação entre a lagarta-do-cartucho e seus agentes de controle biológico natural na produção de milho. *Pesquisa Agropecuária Brasileira*, 41: 1693-1698. doi: 10.1590/S0100-204X2006001200002
- Gallo, D., Nakano, O., Silveira Neto, S., Carvalho, R.P.L., Baptista, G., Berti Filho, E., Parra, J.R.P. (2002). *Entomologia agrícola*. Piracicaba: FEALQ, 282 p.
- Giannotti, E., Prezoto, F. & Machado, V.L.L. (1995). Foraging activity of *Polistes lanio lanio* (Fabr.) (Hymenoptera, Vespidae). *Anais da Sociedade Entomológica do Brasil*, 24: 455-463.
- Greene, A. (1991) *Dolichovespula* and *Vespula*. In K.G. Ross & R.W. Matthews (Eds.) *The social biology of wasps* (pp. 263-304). Ithaca: Cornell University.
- Jeanne, R.L. (1972). Social biology of the neotropical wasp *Mischocyttarus drewseni*. *Bulletin of the Museum of Comparative Zoology of Harvard*, 144: 63-150. doi: 10.5962/bhl.part.14948

- Marques, O.M. (1996). Vespas sociais (Hymenoptera, Vespidae): características e importância em agroecossistemas. *Insecta*, 5: 18-39.
- Marques, O. M. Carvalho, C. A. L. Costa, J. A. (1992). Fenologia de *Polistes canadensis canadensis* (L., 1758) (Hym., Vespidae) em Cruz das Almas, Bahia. *Insecta*, 1: 1-8.
- Omoto, C. & Diez-Rodríguez, G.I. (2001). Herança da resistência de *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) a lambda-cialotrina. *Neotropical Entomology*, 30: 311-316. doi: 10.1590/S1519-566X2001000200016
- Pickett, K.M., Carpenter, J.M. & Wheeler, W.C. (2006). Systematics of *Polistes* (Hymenoptera: Vespidae), with a phylogenetic consideration of Hamilton's haplodiploidy hypothesis. *Annales Zoologici Fennici*, 43: 390-406.
- Prezoto, F. (1999). A importância das vespas como agentes no controle biológico de pragas. *Revista Biotecnologia, Ciência e Desenvolvimento*, 9: 24-26.
- Prezoto, F. Giannotti, E. & Machado, V.L.L. (1994). Atividade forrageadora e material coletado pela vespa social *Polistes simillimus* Zikán, 1951 (Hym., Vespidae). *Insecta*, 3: 11-19.
- Prezoto, F., Giannotti, E. & Nascimento, F. S. (2007). Entre mandíbulas e ferrões: O estudo do comportamento de vespas. In: Del-Claro, K., Prezoto, F., & Sabino, J. *As distintas faces do comportamento animal* (pp. 43- 45). Campo Grande: UNIDERP.
- Prezoto, F. & Machado, V.L.L. (1999a). Ação de *Polistes (Aphanilopterus) simillimus* Zikán (Hymenoptera: Vespidae) na produtividade de lavoura de milho infestada com *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae). *Revista Brasileira de Zoociências*, 1: 19-30.
- Prezoto, F.; Machado, V.L.L. (1999b). Transferência de colônias de vespas (*Polistes simillimus* Zikán, 1951) (Hymenoptera, Vespidae) para abrigos artificiais e sua manutenção em uma cultura de *Zeamays* L. *Revista Brasileira de Entomologia*, 43: 239-241.
- Prezoto, F., Santos, H.H., Machado, V.L. & Zanuncio, J.C. (2006). Prey captured and used in *Polistes versicolor* (Olivier) (Hymenoptera: Vespidae) nourishment. *Neotropical Entomology*, 35: 707-709. doi: 10.1590/S1519-566X2006000500021
- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Raveret- Richter, M. (2000). Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annual Review of Entomology*, 45: 121-150. doi: 10.1146/annurev.ento.45.1.121
- Santos, G. M. M., Marques O. M. & Carvalho C.A.L. (1994). Raio de ação de *Polistes canadensis canadensis* (L., 1758) (Hymenoptera, Vespidae). *Insecta*, 3: 20-24.
- Torres, V.D.O., Antonialli-Junior, W.F. & Giannotti, E. (2009). Divisão de trabalho em colônias da vespa social neotropical *Polistes canadensis canadensis* Linnaeus (Hymenoptera, Vespidae). *Revista Brasileira de Entomologia*, 53: 593-599. doi: 10.1590/S0085-56262009000400008
- Torres, V.D.O, Santos V.M, Bortoluzzi, T.G. & Antonialli-Junior, W. F. (2009). Aspectos bionômicos da vespa social Neotropical *Polistes canadensis canadensis* (Linnaeus) (Hymenoptera, Vespidae). *Revista Brasileira de Entomologia*, 53: 134-138.
- Waddington K.D. (1983). Floral visitation sequences by bees: models and experiments. In Jones C. E., Little R. J. (eds.) *Handbook of experimental pollination biology* (pp. 461–473). New York: Scientific and Academic Editions.
- Wenzel, J.W. (1998). A generic key to the nests of hornets, yellow jackets, and paper wasps worldwide (Vespidae: Vespinae, Polistinae) *American Museum Novitates*, 3224:1-39.
- Zara, F. J., & Balestieri, J. B. P. (2000). Behavioural catalogue of *Polistes versicolor* Olivier (Vespidae: Polistinae) post-emergent colonies. *Naturalia*, 25: 301-319.

