Sociobiology 70(3): e9211 (September, 2023) DOI: 10.13102/sociobiology.v70i3.9211

Sociobiology
An international journal on social insects

SHORT NOTE

Hey, hold on, we are good guys! Colony defensive behavior and notes on nesting of *Parachartergus fulgidipennis* (de Saussure, 1854) (Vespidae: Polistinae: Epiponini)

Marcos Aragão[1], Bruno C. Barbosa[2], Rodolpho S. T. Menezes[3], Alexandre Somavilla[2], Marcio Luiz de Oliveira[1,2]

1 - Programa de Pós-Gradução em Ciências Biológicas (Entomologia), Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil
2 - Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil
3 - Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, lhéus, Bahia, Brazil

Article History

Edited by
Evandro Nascimento Silva, UEFS, Brazil
Received 23 February 2023
Initial acceptance 31 May 2023
Final acceptance 07 July 2023
Publication date 22 August 2023

Keywords
Aggressiveness; Hymenoptera; Marimbondos; Social wasps; Swarm-founding.

Corresponding author
Marcos Aragão
Programa de Pós-Gradução em Ciências Biológicas (Entomologia), Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA)
Av. André Araújo, 2.936, Petrópolis,
CEP: 69067-375, Manaus, Brasil.
E-Mail: marcosaragaowasp@gmail.com

Abstract

Parachartergus wasps are known for having very aggressive behavior, especially the large black species with white wings tip, which have painful stings. They exhibit a unique and interesting characteristic, the capacity to venom spraying during the colony defense or self-defense. However, for the Amazonian species *Parachartergus fulgidipennis* (de Saussure, 1854), little is known about its behavior and nesting. In this way, we tracked and described the nesting site, the number of combs, cells, immatures, and adults and performed an *ad libitum* method to record behavioral activities. The nest was vertically attached to a concrete column, 1.2 m above the ground, measuring 25.0 x 6.0 cm. It contained four combs with approximately 74 cells, 31 eggs, seven larvae, 30 pupae, and 42 adults. With a flat thin grayish envelope with weak corrugations, the nest is very similar to the substrate's color, which turns cryptic. The colony defense behavior exhibited by this species is unaggressive and very docile, suggesting that it is not similar to those observed for other *Parachartergus* species.

Introduction

Parachartergus R. Von Inhering, 1904 is a Neotropical genus of swarm-founding social wasps that diversified during the Miocene (Menezes et al., 2020; Noll et al., 2020). It currently comprises 17 species (Willink, 1959; Richards, 1978; Carpenter, 1999; Cooper, 2000), occurring from Mexico to Argentina (Willink, 1959; Richards, 1978; Carpenter & Marques, 2001). According to Cooper (2000), *Parachartergus* can be divided into three groups of species: apicalis, colobopterus, and fulgidipennis. This hypothesis is partially supported by works employing genomic scale data (Menezes et al., 2020) as well as morphological, behavior, and DNA (Sanger sequence) analyses (Noll et al., 2020). However, it is important to note that not all species have been included in these investigations. Despite the diversity in the nest form variation with species constructing flask-shaped nests, without camouflage or aposematic, with regular corrugations attached to branches or leaves, on the other hand, some species construct cryptic flat nests, with tiny corrugations on the envelope or cover with collected lichen, beneath the leaves or on tree trunk (Richards & Richards, 1951; Richards, 1978; Wenzel, 1998; Hunt & Carpenter, 2004). However, the nests of *Parachartergus* species are structurally similar, being *stelocyttarous calyptodomous* (de Saussure, 1853-1858; Hunt & Carpenter, 2004).

Parachartergus is known for its highly aggressive behavior under disturbance, particularly the large black species of the group apicalis, which comprehend painfully stings, and among the Epiponini, they exhibit a unique and interesting characteristic: the capacity to venom spraying during the colony defense or self-defense (Richards & Richards, 1951; Richards, 1978; Strassmann, 1990; Hunt

Open access journal: http://periodicos.uefs.br/index.php/sociobiology
ISSN: 0361-6525

& Carpenter, 2004). This behavior is possible due to two features: (1) an unobstructed venom canal through the sting; and (2) forceful ejection during stinging. Furthermore, an abdominal press work with specialized muscles on the venom reservoir contributes to this phenomenon (Maschwitz & Kloft, 1971; Hermann et al., 1993; Mateus, 2001). Another function of this behavior was documented by Mateus (2011) for *Parachartergus fraternus* (Gribodo, 1892), where the wasps used venom spraying to mark the new nest site to colony emigration. On the contrary, species of the group colobopterus and group fulgidipennis have been observed to exhibit less degree of aggressive defensive behavior or even docility under disturbance, with or without venom spraying (Jeanne & Keeping, 1995; Souza et al., 2020).

Despite a consensus that this behavior is unique to the genus, whether all species exhibit this type of defense under disturbance remains unknown. To date, this capacity for venom spraying has been documented in five species: *Parachartergus aztecus* Willink, 1959 (Hermann et al., 1993); *Parachartergus colobopterus* (Lichtenstein, 1796) (Strassmann, 1990; Jeanne & Keeping, 1995); *P. fraternus* (Richards & Richards, 1951; Richards, 1978; Jeanne & Keeping, 1995; Mateus, 2011); *Parachartergus richardsi* Willink, 1959, and *Parachartergus pseudapicalis* Willink, 1959 (pers. obs. M.A.).

Within *Parachartergus,* a poorly known species is *Parachartergus fulgidipennis* (de Saussure, 1854), a small reddish testaceous or blackish species that measures approximately 8.0 mm. Their forewings are blackish with a yellow fascia at the pterostigma (Richards, 1978; Cooper, 2000). The colonies of this species are mainly found attached to leaves or on tree trunks in horizontal or vertical positions, and they are inconspicuous and difficult to find in the field (Richards, 1978; Wenzel, 1998; Hunt & Carpenter, 2004). The species is distributed along the Amazon basin (Richards, 1978; Somavilla et al., 2021).

The present study aimed to investigate aspects of the natural history of the swarm-founding social wasp *P. fulgidipennis* to address the knowledge gap regarding its defense behavior and nest material reuse within the genus.

Material and methods

The study was performed on April 2022 in Sítio Santa Maria, Iranduba, Amazonas state, Brazil (03º 06'S; 60º 19'W) (Figure 1). Firstly, some specimens were collected for identification using the keys proposed by Richards (1978) and Cooper (2000). The vouchers and the nest were deposited in the Invertebrates Collection at Instituto Nacional de Pesquisas da Amazônia (INPA).

Here, we designed an experiment to describe the defensive behavior of social wasps precisely. Our methodology included a description of the nesting site, the number of combs, cells, adults, and immatures. Additionally, we documented the colony through photographs, and behavioral activities were recorded using the *ad libitum* method (Altmann, 1974; Del-Claro, 2010). Behavioral acts exhibited by wasps during disturbances were noted. A single colony was subjected to periodic stimulations, totaling 24 hours of fieldwork, following proposed protocols (cf. Strassmann, 1990; Jeanne & Keeping, 1995) with few adaptations: (1) producing noise with an adapted shaker or claps at a distance of approximately 10-15 cm from the nest (Figure 2A); (2) beating on the substrate

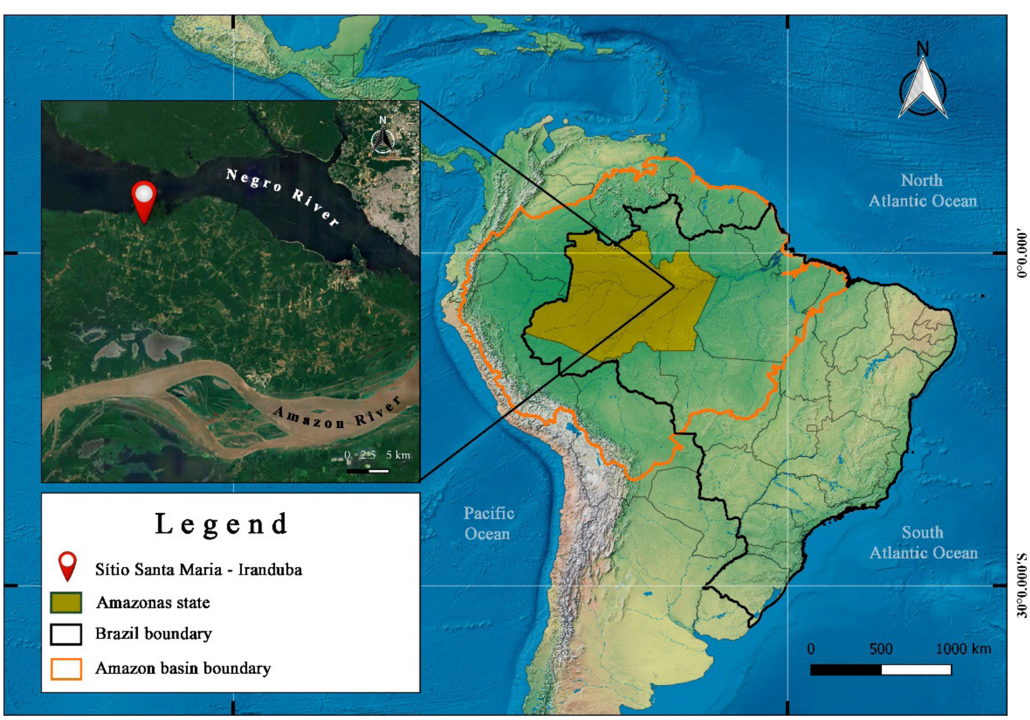

Fig 1. Study area: locality map of Sítio Santa Maria, Iranduba, Amazonas, Brazil.

around the nest with a steel bar (Figure 2B); (3) inserting a stick into the nest entrance (Figure 2C); (4) scraping a stick on the surface of the nest envelope (Figure 2D); and (5) blowing air at the nest entrance. To capture any droplets during venom spraying by the wasps, we placed a mirror near the nest during these stimuli as an adapted technique (Jeanne & Keeping, 1995) (Figure 2F).

Each stimulus was produced for one minute, with five minutes intervals between them. This trial was repeated for two hours over two days from 09:00 am to 5:00 pm. On the third day, before removing the envelope, we collected specimens using a plastic bag; then, we disturbed them with a stick and recorded the behavior displayed by the wasps that remained (Figure 2E). At the end of the experiment, the envelope and three out of four combs were collected, following the adapted technique for transferring nests as proposed by Prato et al. (2022) and kept in the laboratory facility (De Souza et al., 2021). A beekeeping protective clothing was dressed to maintain the researcher's security during the experiment. The photos were taken using a Nikon D3200 DSLR camera equipped with a 50 mm f/1.8 lens and a macro extension tube. To generate a locality map, the geographic coordinates were imported into a free and open-source geographic information system, QUANTUM-GIS v2.18.18. Las Palmas, combined with Google Satellite plugin QuickMapServices (https://www.google.at/permissions/geoguidelines/attr-guide.html).

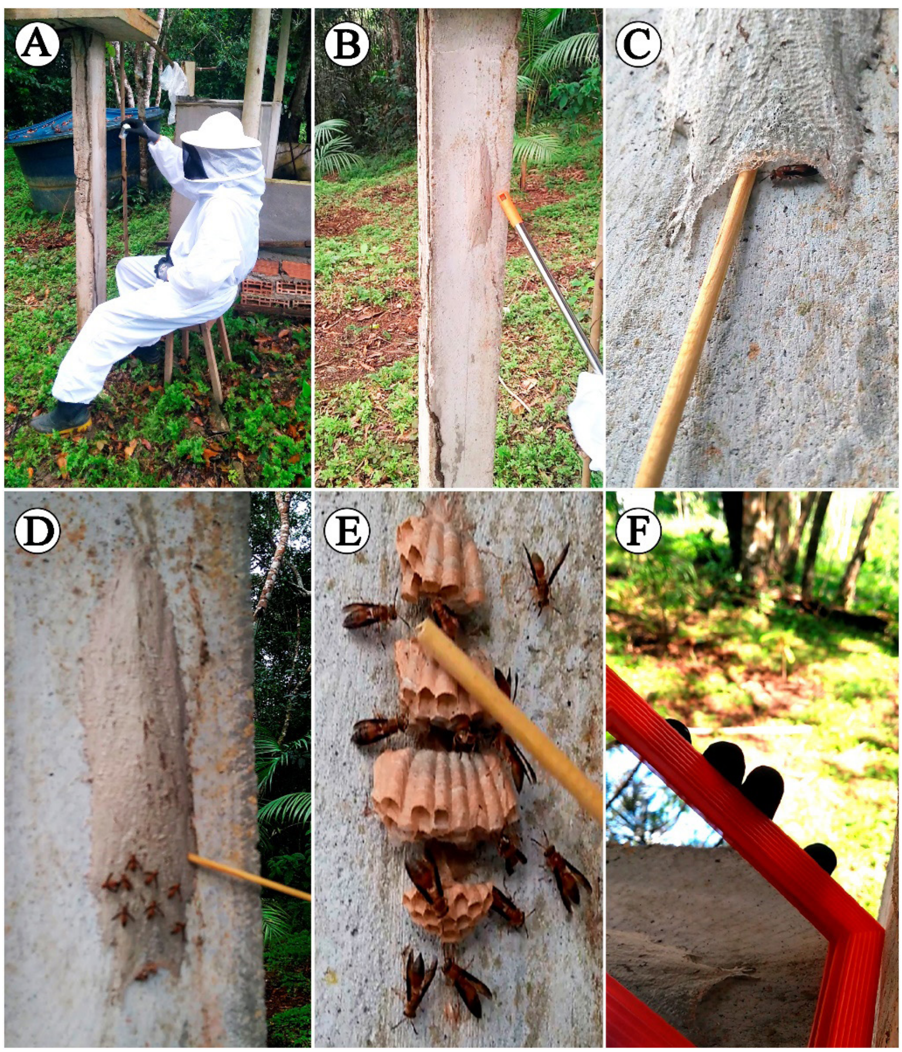

Fig 2. Some stimuli present in this work: (A) producing noise with adapted shaker; (B) beating on the substrate around the nest; (C) inserting a stick into the nest entrance; (D) scraping a stick on the envelope surface; (E) scraping a stick on the combs; and (F) a mirror close to the nest in case of spraying venom.

Results and discussion

Nest structure and habits

Differing from those arboreal nests beneath leaves reported by Ducke (1910) and Orlando Tobias Silveira (pers. comm.), the present study documented a vertically fixed nest on a concrete column, positioned 1.2 m above the ground, measuring about 25.0 x 6.0 cm (Figure 3A). The nest contained four combs (the arrangement measuring 7.0 cm) with approximately 74 cells, 31 eggs, seven larvae, 30 pupae, and 42 adults (26 females collected). The nest showed a flat thin grayish envelope with weak corrugations; it is very similar to the substrate's color, which turns cryptic (Figures 3A and 3B). The nest entrance is downward flatted narrow (Figure 3C). Curiously, the colony was built nearby a trace of an abandoned gallery of the termite *Nasutitermes peruanus* (Holmgren, 1910) (Termitidae: Nasutitermitinae), which on the envelope contain some pieces of material that seem to be from there. We do not know if this part of the gallery was active when the wasps started to build the nest (Figure 3B).

Colony defense behavior

The stimuli experiment yielded the following observations: **(1) shaker or claps**: no visible response or sound such as wing buzz was produced by the wasps in any trial; also, the wasps did not even appear at the nest entrance (Quiet!); **(2) beating around the nest**: as the shaker, we did not record any response; **(3) inserting a stick into the nest entrance**: our observations led us to conclude that wasps showed no response to aggressiveness. However, we occasionally observed workers trying to touch the stick, a behavior toward seeking information (Figure 2C). Curiously, even with these stimuli, some foragers arrived at the same time of the disturbance and proceeded to enter the nest as usual; **(4) scraping a stick on the nest envelope**: in response to all stimuli, the wasps went out of the nest. Some individuals went away immediately, while others moved to the outer surface of the envelope and showed the warning behavior (alarm recruitment), characterized by the opening of their wings ("V" shape), contraction of the abdomen, and active patrolling (Figure 2D). Then, they went away without any attack or trace of venom spraying. They began to return after one or two minutes, landing nearby the nest entrance and entering directly into the nest; **(5) blowing air at the nest entrance**: this disturbance is the most vigorous display exhibited by this species. A loud noise produced by buzz wings was recorded whenever this stimulus occurred. Then, a group of wasps flew out of the nest speedily, did not move to the envelope, or did not attempt to sting or trace on the mirror or scent of venom spraying. We suggest that this behavior is probably due to increased temperature and carbon dioxide (CO_2) inside the nest with exhaled air, indicating a potential threat. After that, the wasps began to return to the nest after one or two minutes. A distinct response to this stimulus was documented by Strassman (1990) in the case of *P. colobopterus*. In this species, the workers exhibit a behavior in which they exit the nest and ascend over the envelope while vibrating their gasters against it, producing an arrhythmic rustling sound.

It is worth mentioning that on the final day of the experiment, as we were removing the nest envelope, almost the entire colony went away, with only a few individuals, no more than five, trying to sting but quickly returning to the combs. We disturbed the wasps several times with a stick, but they did not manifest any aggressive behavior; instead, they just took short flights or ran away (Figure 2E). Then, as we

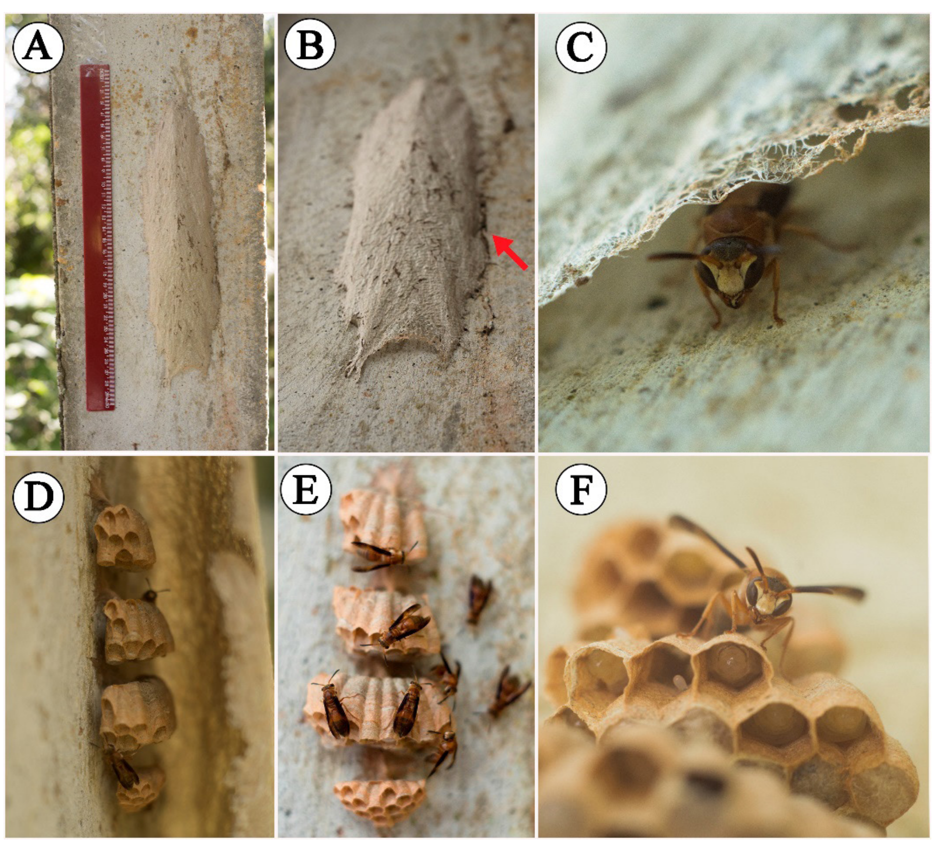

Fig 3. (A) Size of the nest in frontal view; (B) view from the bottom showing the nest entrance, and the red arrow pointing abandoned termite's gallery; (C) close up of the nest entrance; (D) lateral view of the combs arrangement; (E) frontal view of the combs arrangement without envelope; (F) an individual exhibiting a defensive behavior on a comb with eggs, larvae and pupae.

exposed the combs, we noticed an intriguing behavior among the wasps: a dominant individual began to interact with other nestmates, which performed a subordinate behavior, including trophallaxis and/or grappling on the back of the others (Figure 4A and 4B).

This behavior can be described as the dominant individual staying over the subordinate, paralyzing it while scratching the head, especially in the clypeus and the thorax. Some wasps did not allow this behavior avoiding the dominant individual and running away through the combs. Furthermore, some wasps started to remove the larvae in different stages of development from the cells and went away (Figure 4C and 4D), while the others monitored the pupae. Just once, we recorded a pupa being removed from the cell.

Fig 4. (A) Food sharing by nestmates "the kiss"; (B) submissive posture of subordinate female; (C) an individual pulling a larva from the cell; (D) an individual with a larva ready to leave the nest.

Thus, we suggest that the behavior displayed by the colony of *P. fulgidipennis* here analyzed is unaggressive or docile and present the following strategies as defense behavior: **(1)** a preference for constructing cryptic nests, trying to mix up the envelope with the background avoiding predators; **(2)** maintaining silence in the face of some threats; **(3)** temporarily leaving the nest and remaining nearby until the disturbance is over. This behavior, absconding, was observed when some social wasps were repeatedly struck by birds (McCann et al., 2013). However, rather than forming clusters and leaving the nest (Sonnentag & Jeanne, 2009), the wasps in our experiment displayed a distinct behavior of returning promptly. This behavioral act can be explained due to the stressful stimuli we induce, which are known to increase the levels of the Octopamine hormone, which is responsible for modulating behaviors such as the "fight or flight" response (Roeder, 2005); **(4)** finally, according to our observations, the behavioral act that wasps remove the larvae and pupae from the cells may be indicative of some survival strategy that needs further studies. Here, with this intriguing behavior such as a "Birkenhead drill", we presume they tried to prioritize the most vulnerable as immatures. We do not know if these stimuli in the colony provoked a social hierarchy conflict among females. Colonies that suffer disturbance, such as transfers or stimuli that increase stress hormone levels, can trigger larviphagy (wasps) or hygienic behaviors (bees) (Roeder, 2005; Prezoto et al., 2018). Larviphagy behaviors usually occur during resource shortages, where it is replaced by foraging activity (Giannotti, 2012). However, larviphagy was not observed during this study. The wasps removed the immature and flew away into the dense forest.

An unaggressive or docile defense strategy was observed in other *Parachartergus* species. Strassmann (1990) suggests that the lack of aggressive behavior in *P. colobopterus* can be explained by the nest camouflage or the rarity of some vertebrate predators. Moreover, Jeanne and Keeping (1995) indicated that the defense behavior of *P. colobopterus* against vertebrates relies on the wasps landing on the nest envelope and spraying a mist of venom through the air rather than attacking with stings or spraying venom like its congeners. Other species, such as *Parachartergus pacificus* Cooper, 2000, *Parachartergus smithii* (de Saussure, 1854), and *Parachartergus wagneri* (du Buysson, 1904), also display an unaggressive or docile behavior as classified on disturbance, and the venom spraying was not mentioned (Cooper, 2000; Souza et al., 2020). On the other hand, *P. pseudapicalis* builds large and aposematic nests due to colony investment in offspring (colonies have a high number of pupae) and displays a higher defense intensity by nestmates with stings and venom spraying (Brito et al., 2018).

The present study did not record the behavior of venom spraying by *P. fulgidipennis*. Jeanne and Keeping (1995) reported that the contact of droplets of venom spraying in the eyes by *P. fraternus* and *P. aztecus* caused swelling, redness, and scratchiness. Venom spraying by *P. pseudapicalis, P. richardsi,* and *P. fraternus* can cause significant irritation and tear to the eyes (for at least 10 hours), throat irritation (accompanied by coughing), and runny nose (pers. obs. MA and RSTM). Therefore, it is advisable to use additional Personal Protective Equipment (PPE), such as safety goggles and a face mask, when collecting nests of this genus to minimize the risk of venom contact.

Regarding the collected combs, over ten days, 15 out of 16 pupae emerged in the laboratory (all females). As a result, we deposited 41 specimens at the end of the experiment. The largest comb, which had the greater number of pupae, remained in the field with 14 pupae and approximately 16 adults (probably had some foragers that fled at that time) (Figure 5A1, 5A2, and 5B).

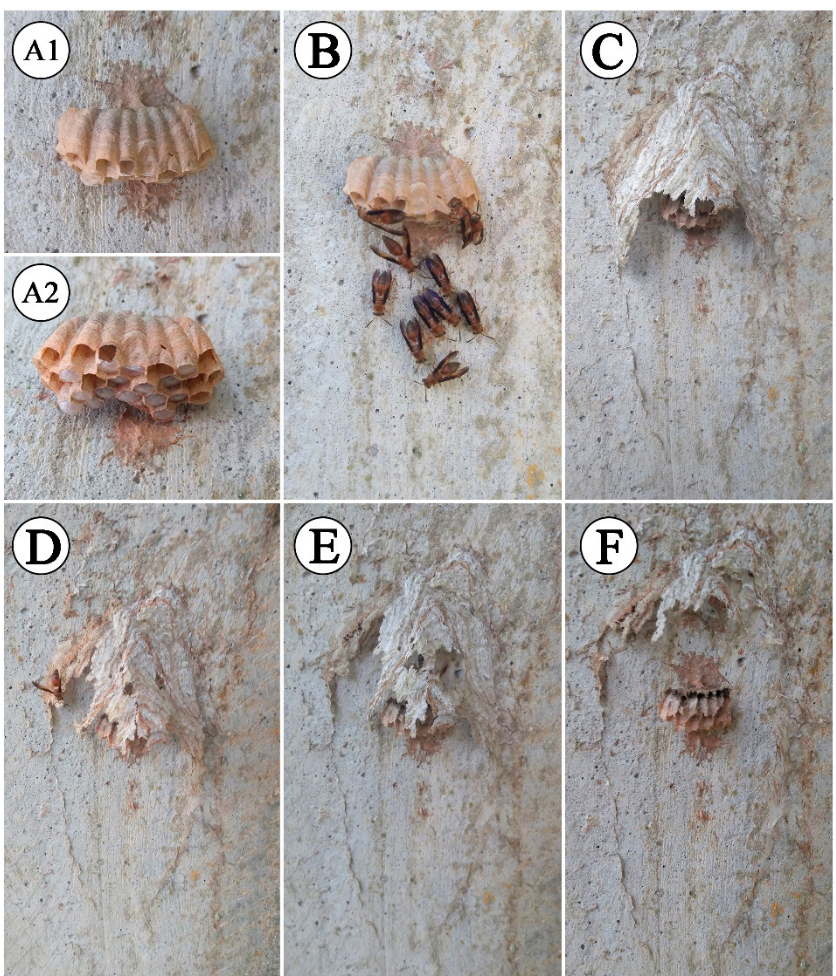

Fig 5. Nest material reuse activity for two days: (A1) frontal view of the comb that was not collected in the first experiment; (A2) view from the bottom showing the pupae; (B) some individuals forming cluster after the disturbance; (C) 16 days after the first experiment, day 1 at 9:30 am; (D) day 1 at 5:34 pm; (E) day 2 at 8:39 am; (F) day 2 at 2:58 pm.

Nest material reuse

When we returned to the field on May 2022, after aforementioned defensive behavior, we noticed that the wasps had constructed a new nest envelope to protect the only comb that remained until the pupae developed. Subsequently, they abandoned the nest. The remains of the grayish envelope show slight variations from the older ones, presenting additional brownish stripes that align with the color pattern observed on the comb. The measurements of these remains were approximately 4.5 x 2.5 cm (Figure 5C). At the first moment, considering the disturbance that we did days early, we presumed that the entire colony was moved out to a new nest site and left the pupae behind or transported them, as we observed when the envelope was opened. Unfortunately, we did not document the reconstruction process of the new envelope. However, we partially documented the reuse of the envelope and comb materials, as described below (Figure 5C to 5F).

The new nest site was probably established nearby the old one, although we could not locate it. We deduced its existence based on observing a specimen departing with a pulp of nest material and returning to collect another, with each trip lasting approximately two to three minutes. Throughout our observation, we never observed more than one individual gathering nest material for reuse simultaneously. Thus, we recorded an individual landing nearby or directly on the envelope and began to moisten the nest material with salivary secretion. It started to cut tiny pieces of the fragile envelope, chew it up and roll the chewed material to form a mass of pulp. On average, this work lasted between four to five minutes (Figure 6).

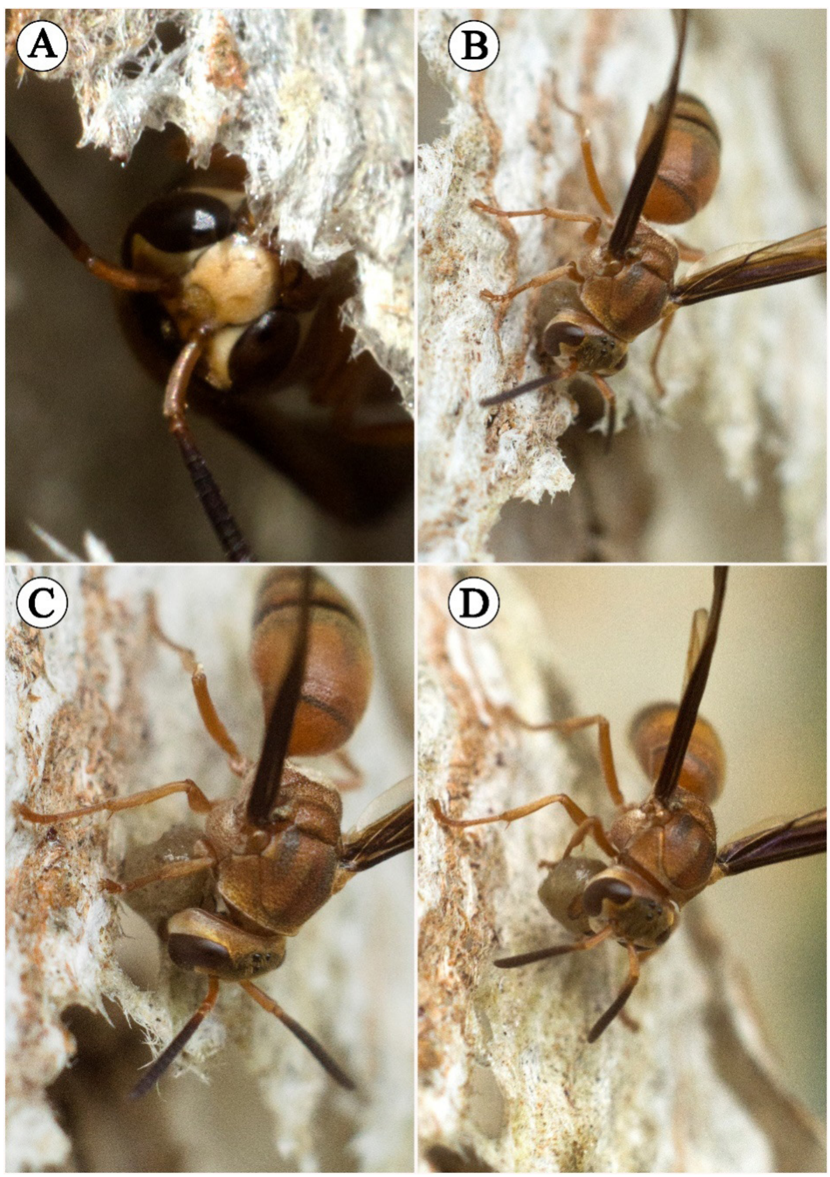

Fig 6. Process of nest material reuse: (A) moistening the envelope with salivary secretion; (B) cutting and starting to form a mass of pulp; (C) rolling the moist nest material; (D) with a mass of pulp finished ready to take off.

As pointed out by Hansell (1993) and Sarmiento (1999), nest building has costs; thus, instead of affording the high energy cost of collecting and processing raw material, some wasps reprocess most of the old nest material and mix it with raw material from around the new nest site.

As we have seen, despite the limitation of replicating the experiment in a statistical analysis approach, this species is rarely found in nature (the local site is formed by secondary rainforest); the preliminary studies on natural history are the foundation to implement further research. Although, at this point, information about how this species or the whole genus *Parachartergus* behaves during colony defense remains an open and exciting topic. Thus, more efforts are necessary to find nests in the field to perform future studies focused on this perspective. Also, the results reported here are important since they can be used as behavioral data for systematics studies.

Authors' Contributions

MA: conceptualization, methodology, investigation, writing (original draft, review & editing), resources.
BCB: writing-original draft.
RSTM: writing-original draft, supervision.
AS: writing-original draft, supervision.
MLO: writing-original draft, supervision, resources.

Acknowledgments

MA thanks to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a research grant (88887.492572/2020-00) and MLO to the Conselho de Desenvolvimento Científico e Tecnológico (CNPq) grant (305150/2020-0). Thanks to Thiago Malhmann, Francisco Felipe Xavier, and Ivan Golffeti for field assistance. The authors thank the owners of Sitio Santa Maria, especially Dr. Wilson Spironello and Vanessa. Thanks to Rayssa Azevedo and Renato Azevedo for the determination of termite species. This work was supported by Instituto Nacional de Pesquisas da Amazônia (INPA), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho de Desenvolvimento Científico e Tecnológico (CNPq), and Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM).

References

Altmann, J. (1974). Observational study of behavior: Sampling methods. Behaviour, 49: 227-266. https://doi.org/10.1163/156853974X00534

Carpenter, J.M. & Marques, O.M. (2001). Contribuição ao estudo dos vespídeos do Brasil (Insecta, Hymenoptera, Vespoidae, Vespidae). Cruz das Almas: Publicações Digitais, 147 p.

Carpenter, J.M. (1999). Taxonomic notes on paper wasps (Hymenoptera: Vespidae; Polistinae). American Museum Novitates, 3259: 1-44.

Cooper, M. (2000). A new species of *Parachartergus* R. von Ihering (Hym., Vespidae, Polistinae) with a key to the members of the fulgidipennis group and notes. Entomologist's Monthly Magazine, 136: 121-12.

De Saussure, H. (1853-1858). Monographie des Guêpes Sociales ou de la Tribu des Vespiens, ouvrage faisant suite à la Monographie des guêpes solitaries. V. Masson, Paris and J. Kessmann, Genève, 97-256.

De Souza, A.R., Baptista, C.F., Teixeira, G.V.M. & Lima, M.A.P. (2021). Artificial environments for studying eusocial wasps. In: Prezoto, F., Nascimento, F.S., Barbosa, B.C. & Somavilla, A. (Eds.), Neotropical social wasps (pp. 435-442). Gewerbestrasse, Switzerland: Springer. https://doi.org/10.1007/978-3-030-53510-0_23

Del-Claro, K. (2010). Introdução a ecologia comportamental, um manual para o estudo do comportamento animal. Rio de Janeiro: Technical Books Press, 130 p.

Ducke, A. (1910). Révision des guêpes sociales polygames d'Amérique. Annales Musei Nationalis Hungarici, 8: 449-544.

Hansell, M.H. (1993). The ecological impact of animal nests and burrows. Functional Ecology, 7: 5-12. https://doi.org/10.2307/2389861

Hermann, H.R., Blum, M.S. & Fales, H.M. (1993). Venom spraying by a tropical polistine wasp (Hymenoptera: Vespidae: Polistinae). Sociobiology, 23: 95-99.

Hunt, J.H. & Carpenter, J.M. (2004). Intra-specific nest form variation in some Neotropical swarm-founding wasps of the genus *Parachartergu* (Hymenoptera: Vespidae: Epiponini). Journal of the Kansas Entomological Society, 77: 448-456. https://doi.org/10.2317/E-26.1

Giannotti, E. (2012). Notes on the biology of *Polistes simillimus* Zikán (Hymenoptera, Vespidae). Bioikos, 8: 41-49. https://periodicos.puc-campinas.edu.br/bioikos/article/view/969. (accessed date: 1 June 2023).

Maschwitz, U.W. & W. Kloft. (1971). Morphology and function of the venom apparatus of insects-bee, wasps, ants, and caterpillars. In W. Buchelly & E. Buckley (eds.), Venomous animals and their venoms (pp. 1-59). New York: Academic Press. https://doi.org/10.1016/B978-0-12-138903-1.50008-9

Mateus, S. (2011). Observations on forced colony emigration in *Parachartergus fraternus* (Hymenoptera: Vespidae: Epiponini): New nest site marked with sprayed venom. Psyche, 1: 149-157. https://doi.org/10.1155/2011/157149

McCann, S., Moeri, O., Jones, T., Scott, C., Khaskin, G., Gries., O'Donnell, R. & Gries, G. (2013). Strike fast, strike hard: The Red-throated caracara exploits absconding behavior of social wasps during nest predation. PLoS ONE, 8: e84114. https://doi.org/10.1371/journal.pone.0084114

Menezes, R.S.T., Lloyd, M.W. & Brady, S.G. (2020). Phylogenomics indicates Amazonia as the major source of Neotropical swarm-founding social wasp diversity. Proceeding of Royal Society B, 287: 20200480. https://doi.org/10.1098/rspb.2020.0480

Noll, F.B., da Silva, M., Soleman, R.A., Lopes, R.B., Grandinete, Y.C., Almeida E.A.B., Wenzel, J.W. & Carpenter, J.M. (2020). Marimbondos: systematics, biogeography, and evolution of social behaviour of neotropical swarm-founding wasps (Hymenoptera: Vespidae: Epiponini). Cladistics, 1: 1-19. https://doi.org/10.1111/cla.12446

Prato, A., Carvalho, S.R., Mateus, S. & Santos, N.F. (2022). A technique for transferring nests of *Polybia* (Hymenoptera: Vespidae: Epiponini) wasps in anthropized environment. Sociobiology, 69: e7620. https://doi.org/10.13102/sociobiology.v69i2.7620

Prezoto, F., Detoni, M.F.D.F.S. & Mayourquin, A.Z.A. (2018). Transferência de colônias de vespas sociais (Hymenoptera, Vespidae) em área urbana. Principia: Caminhos da Iniciação Científica, 18: 11-11. https://doi.org/10.34019/2179-3700.2018.v18.29866

Richards, O.W. & Richards, M.J. (1951). Observations on the social wasps of South America (Hymenoptera, Vespidae). Transactions of the Royal Entomological Society of London, 102: 1-169. https://doi.org/10.1111/j.1365-2311.1951.tb01241.x

Richards, O.W. (1978). The social wasps of the Americas: excluding the Vespinae. London: British Museum of Natural History, 580 p.

Roeder, T. (2005). Tyramine and octopamine: Ruling behavior and metabolism. Annual Review of Entomology, 50: 447-477. https://doi.org/10.1146/annurev.ento.50.071803.130404

Somavilla, A. & Carpenter, M.J. (2021). Key to the genera of social wasps (Polistinae) occurring in neotropics. In Prezoto, F., Nascimento, F.S., Barbosa, B.C. & Somavilla, A. (Eds.), Neotropical social wasps. Gewerbestrasse, Switzerland: Springer. https://doi.org/10.1007/978-3-030-53510-0_18

Sonnentag, P.J. & Jeanne, R.L. (2009). Initiation of absconding-swarm emigration in the social wasp *Polybia occidentalis*. Journal of Insect Science, 9: 11. https://doi.org/10.1673/031.009.1101

Wenzel, J.W.A. (1998). A generic key to the nests of hornets, yellowjackets, and paper wasps worldwide (Vespidae: Vespinae, Polistinae). American Museum Novitates, 3224: 1-39.

Willink, A. (1959). Las especies afines a Parachartergus apicalis (F.) (Hymenoptera, Vespidae, Polybiinae). Acta Zoológica Lilloana, 17: 263-292.