Social organization and division of labor of *Mischocyttarus drewseni* de Saussure, 1857 (Hymenoptera, Vespidae)

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Received: June 05, 2024 DOI: 10.14295/bjs.v3i10.623

Accepted: August 14, 2024 URL: https://doi.org/10.14295/bjs.v3i10.623

Abstract

The objective of this study was to determine the behavioral repertoire of the social wasp *Mischocyttarus drewseni* based on the activities carried out by the founders in the pre-emergence phase and by the queens, workers, and males in the post-emergence phase and decline. Twenty-five colonies were observed, allowing for the identification of the behavioral repertoire. Twenty-eight behaviors were recorded, covering six categories. There is a division of labor between foundresses during the pre-emergence phase and between workers and queens during the post-emergence phase, with males involved in only a few activities. Founders and queens presented a convergent behavioral repertoire. Workers showed the greatest diversity of behaviors, especially about foraging. Exclusively, queens performed the observed acts of oviposition, and *M. drewseni* queens were more intensely engaged in pulp foraging than workers and founders. Inside the nest, the queens spent more time in the cells or near the comb than the workers. Dominance behavior was more pronounced in foundresses and queens than in workers. These results confirm the behavioral differences between these castes.

Keywords: behavioral castes, tasks, ethogram, polistinae, network.

Organização social e divisão do trabalho de *Mischocyttarus drewseni* de Saussure, 1857 (Hymenoptera, Vespidae)

Resumo

O objetivo deste estudo foi determinar o repertório comportamental da vespa social *Mischocyttarus drewseni* com base nas atividades realizadas pelos fundadores na fase de pré-emergência e pelas rainhas, operárias e machos na fase de pós-emergência e declínio. Vinte e cinco colônias foram observadas, permitindo a identificação do repertório comportamental. Foram registados vinte e oito comportamentos, abrangendo seis categorias. Há uma divisão de trabalho entre as fundadoras durante a fase de pré-emergência e entre as operárias e rainhas durante a fase de pós-emergência, com os machos envolvidos em apenas algumas atividades. Fundadoras e rainhas apresentaram um repertório comportamental convergente. As operárias apresentaram a maior diversidade de comportamentos, principalmente em relação ao forrageamento. Exclusivamente, as rainhas realizaram os atos de oviposição observados, e se envolveram mais intensamente no forrageamento de polpa do que operárias e fundadoras. Dentro do ninho, as rainhas passaram mais tempo nas células ou perto do favo do que as operárias. O comportamento de dominância foi mais pronunciado nas fundadoras e rainhas do que nas operárias. Estes resultados confirmam as diferenças comportamentais entre estas castas.

Palavras-chave: castas comportamentais, tarefas, etograma, polistinae, rede.

1. Introduction

The success of social insects lies in their execution of distinct tasks in an organized manner, as well as their use of sophisticated forms of communication, primarily chemical (Conte; Hefetz 2008; Hölldobler; Wilson 2009), to assist individuals in social interactions. Consequently, these factors have influenced the social evolution of these insects. Wilson (1971; 1975) states that the evolution of social behavior can be defined by the combination of parental care, overlap of generations, and division of labor between reproductive and non-reproductive castes.

Polyethism refers to the division of tasks among members of a society and can be classified into two types: caste polyethism, where individuals are differentiated into distinct castes, each with specific morphological adaptations suited for particular tasks, and temporal polyethism, where individuals perform different functions according to their age, rather than being morphologically specialized for a single task (Wilson, 1971; Wilson, 1975). Polyethism within colony members is crucial in social wasps and may be the key to their ecological success, as many tasks are performed simultaneously by different workers within the colony (Wilson, 1975; Robinson, 1992).

The distribution of tasks reflects the dominance hierarchy. Internal tasks performed by dominant females have high adaptive value because they maintain social control during colony development (Murakami et al., 2013). Analyzing the behavioral repertoire is essential for understanding the main activities of an animal and its interactions with other individuals and/or the environment in which it lives (Del-Claro, 2004). Many researchers have developed ethograms to represent species. Many researchers elaborate ethograms to represent species' behavioral repertoires (see Brandão, 1978; Brandão, 1983; Silva-Melo; Giannotti, 2012; Torres et al., 2009). By acquiring ethological data, it is possible to understand behavioral patterns (Wilson, 1975) and how organisms respond to external stimuli with complex behavior patterns (see Togni; Giannotti, 2007).

Among the subfamilies of Vespidae, Polistinae contains 26 genera with 940 species, classified as swarm or independent founding wasps (Carpenter; Marques, 2001; Gadagkar, 1991; Spradbery, 1991). Mischocyttarini is a tribe with a single genus, *Mischocyttarus* de Saussure, 1853, containing 245 species of basal eusocial wasps that occur in the Neotropics, with two species inhabiting the southern Nearctic (Carpenter, 1993; Gadagkar, 1991; Jeanne, 1991; Silveira, 2008).

Mischocyttarus drewseni de Saussure, 1857, builds a nest consisting of a single uncovered comb attached to a substrate by a long peduncle (Jeanne, 1972). Foundation occurs independently, either by haplometrosis, where the colony is founded by an inseminated female, or by pleometrosis, where the colony is founded by two or more fertile females.

This study aims to determine the behavioral repertoire of *Mischocyttarus drewseni* through the activities developed in the nest by founders in the pre-emergence phase, as well as by queens, workers, and males in the post-emergence phase (Figure 1).

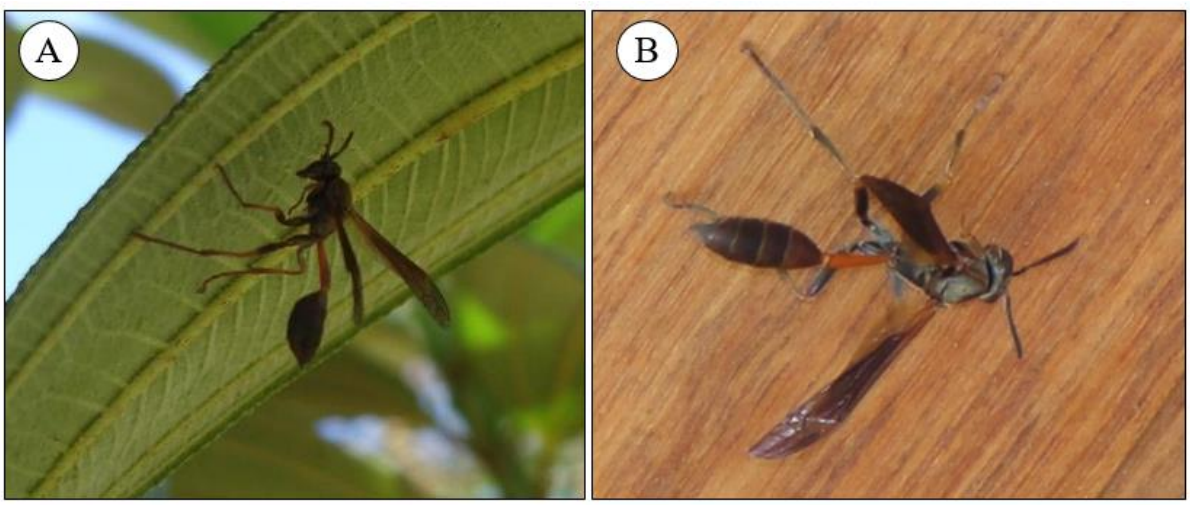

Figure 1. *Mischocyttarus drewseni*: (**A**) shows a male on a leaf, (**B**) shows a female on wood. Source: Authors, 2024.

2. Materials and Methods

2.1 Experimental location and study permit

For two years, we monitored 25 colonies of *M. drewseni* on the Campus of the Universidade Estadual Paulista Júlio de Mesquita Filho - UNESP, Rio Claro (22°23'51.0"S 47°32'51.4"W), São Paulo State, Brazil. The species was identified using the identification key of Richards (1978). Individuals of *Mischocyttarus drewseni* were studied in the field, they were not collected or kept in captivity, therefore, the study does not apply to the Animal Ethics Committee according to Law 13.123 of May 20, 2015, Biodiversity Law, regulated by Decree No. 8.772, of May 11, 2016, Brazil. For non-invasive and observational studies that do not involve the capture or direct manipulation of Mischocyttarus drewseni, the legal basis for not requiring approval from the Animal Ethics Committee (CEUA) is grounded in Law No. 11.794/2008, known as the Arouca Law. Additionally, the guidelines from the National Council for the Control of Animal Experimentation (CONCEA), particularly those specified in Normative Instruction No. 18/2014, confirm that ethical approval is primarily required for invasive procedures and those that cause stress. Since the study in question is limited to non-invasive observation of animal behavior, without any form of capture or manipulation that could cause suffering, it does not fall under the CEUA's approval requirements.

2.2 Colony monitoring period

The scanning sample method (Altmann, 1974) was used to observe and record the behaviors of each individual. Monitoring sessions lasted 5 minutes each, with 1-minute intervals between sessions, resulting in a total of 406 h of observation. The observations were made between 12:20 p.m. and 04:00 p.m. Additionally, the Fagen & Goldman (1977) test was employed to determine the sample size and the expected number of behaviors.

2.3 Description of Mischocyttarus drewseni behavior

The behaviors observed in *M. drewseni* were analyzed using the UCINET 6 program (Borgatti et al., 2002), to construct a graph for quantitative analysis. This analysis included measures of average degree, diameter, density, and network rendering. In addition, these data also yielded a dendrogram with Euclidean distance, according to Krebs (1998). Data on foraged items and the locations in which queens and workers remained positioned were recorded and quantified.

3. Results

Out of the 25 colonies analyzed, data were obtained from four exclusively during the pre-emergence phase, ten colonies during the post-emergence phase, two colonies during the decline phase, and nine colonies during both the pre-and post-emergence phases. The remaining colonies were observed at various stages (Figure 2).

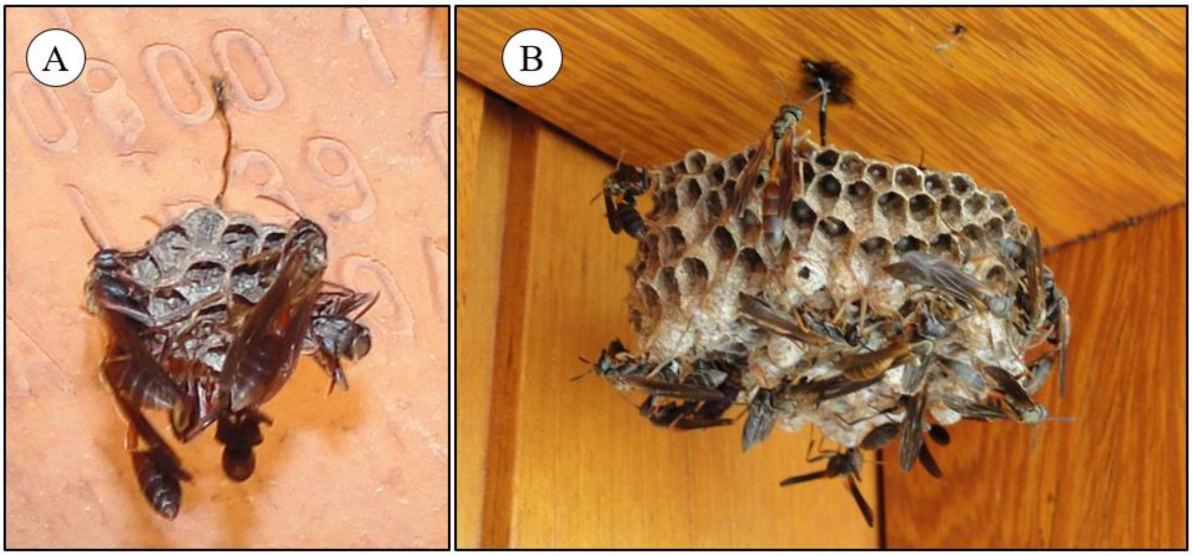

Figure 2. *Mischocyttarus drewseni* nests: (**A**), nest in the pre-emergence phase, and (**B**), nest in the post-emergence phase. Note the cells with eggs, larvae, and pupae. Source: Authors, 2024.

Among the four pre-emergent colonies, it was possible to observe that two of them were founded by more than one individual. Additionally, among the nine pre- and post-emergent colonies, two were observed with more than one founding wasp, demonstrating that *M. drewseni* can establish their colonies either by haplometrosis or pleometrosis (Table 1).

Table 1. Composition of *Mischocyttarus drewseni* colonies.

Colonies	Phase of Development	Observation (days)	Number of individuals			
			Foundress	Queen	Worker	Male
1	Post-emergence	117	-	1	5	-
2	Post-emergence	181	-	1	17	2
3	Decline	14	-	1	3	-
4	Decline	14	-	1	-	-
5	Pre-emergence	94	3	1	13	-
6	Pre-emergence	33	1	-	-	-
7	Pre-emergence	154	8	-	-	-
8	Post-emergence	104	-	1	14	1
9	Post-emergence	154	-	1	8	-
10	Post-emergence	57	-	1	17	1
11	Post-emergence	57	-	1	9	-
12	Pre- and Post-emergence	184	-	1	46	-
13	Post-emergence	124	-	2	21	-
14	Pre- and Post-emergence	90	1	1	4	-
15	Post-emergence	37	-	1	2	-
16	Post-emergence	2	-	1	2	-
17	Pre- and Post-emergence	143	1	1	2	1
18	Pre- and Post-emergence	74	1	1	2	-
19	Pre- and Post-emergence	25	1	1	1	-

20	Pre- and Post-emergence	74	1	1	4	-
21	Pre- and Post-emergence	25	1	1	1	-
22	Pre- and Post-emergence	72	3	1	1	-
23	Post-emergence	72	-	1	6	-
24	Pre- and Post-emergence	93	2	1	-	-
25	Pre-emergence	3	1	-	-	-
Total number of individuals			26	21	178	5

Note: (-) no determined. Source: Authors, 2024.

Data were analyzed according to the suggestion of Fagen & Goldman (1977), and it was calculated that the behavioral repertoire for *M. drewseni* could be 35 or a number between 27 and 45 acts, with a 95% confidence interval. Therefore, a total of 28 observed behaviors is considered satisfactory for this species (Table 2).

The 28 behaviors of the behavioral repertoire of *M. drewseni* were divided into six categories (Table 2, Figure 3):

I. Social Activities:

1. Feeding larvae: Oral transfer of liquid (usually nectar) or solid (a mass of pre-chewed prey) food from an adult to a larva.

2. Knocking head inside a cell: A wasp positioned on a cell knocks its head against it, creating a sound in the nest. This behavior was observed only in queens.

3. Dominance behavior: A wasp quickly bites another wasp, usually on the head, and moves aggressively with its body. The act of dominance is interpreted when a wasp assumes a position with elevated antennae and wings.

4. Biting the gaster: A wasp continually bites the gaster of another wasp. This act is interpreted as an aggressive movement within the colony.

5. Submission behavior: Passive reception of aggression from another individual in the nest. The subordinate's position is interpreted when a wasp holds its head and body lowered to the comb surface. In certain instances, the subordinate wasp can retreat or even leave the nest.

6. Checking cells, rubbing the gaster: A wasp walks on the nest, inserting its head into the cells and moving its gaster from one side to another. These lateral vibrations with the gaster create an audible sound (Jeanne 1972).

7. Adult-adult trophallaxis (donor): Oral transfer of regurgitated liquid from one adult to another, respecting the donor's behavior.

8. Adult-adult trophallaxis (receptor): Oral transfer of regurgitated liquid from one adult to another, respecting the receptor's behavior.

9. Larva-adult trophallaxis: Oral transfer of regurgitated liquid from a larva to an adult.

II. Oviposition:

1. Ovipositing: A female inserts its gaster into the interior of an empty cell for egg laying. The laying wasp initially performs a lateral movement with its gaster, releasing an adhesive secretion, which it uses to affix the egg to the cell wall.

III. Maintenance and defense of the nest:

1. Alarm: Assumption of a position with the body, antennae, and wings elevated. There may be pulsation of the gaster, vibration of the wings, irregular or rapid movements, and abandonment of the nest as a last resort.

2. Enlarging cells: A wasp chews a mass of wood pulp, holding it with its maxillary palpi, and applies a band of this wet material to the nest.

3. Constructing new cells: A wasp collects construction material (wood pulp) and increases the size of the nest by adding new cells to its periphery.

4. Larviphagy: Workers and queens remove and ingest larvae. The larva to be eaten is transferred from one adult to another, who chews it and subsequently offers it to the other larvae.

5. Licking the peduncle: The application of an oral secretion, like a varnish, provides rigidity to the peduncle to support and protect the nest.

6. Handling large prey: A wasp remains with the collected prey, chewing it for a long, extended period.

7. Oophagy: A wasp inserts its head inside a cell and picks up an egg with its mandibles to consume it. After ingesting the egg, a new oviposition may or may not occur. Simple egg ingestion is interpreted as nutritional oophagy; ingestion, followed by new oviposition, is interpreted as differential oophagy.

8. Rubbing the gaster on the nest: A wasp rubs the gaster on the peduncle, dispersing a secretion of the van der Vecht gland, of the sixth gastral sternite, which has an ant-repellent function (Jeanne, 1970). In addition to gaster rubbing on the peduncle, wasps were observed rubbing their gasters on the back and side of the nest.

9. Licking the cocoon: Like the action of licking the peduncle, a wasp licks a cell, sealing the larva's near-finished cocoon with oral secretion.

10. Fanning cells: A wasp beats its wings at a high frequency to reduce the temperature of the nest on hot days to reduce the temperature of the nest (Wilson, 1971). This can also be interpreted as an aggressive display when an alarm enemy is approaching, and it may be a means of alarming pheromone dispersion (Togni; Giannotti 2007).

11. Checking cells with the antennae: A wasp walks on the nest, inserting its head into the cells, and inspecting their contents with its antennae for a few seconds.

IV. Foraging activities:

1. Foraging for water: A wasp returns to the nest with a drop of water trapped in its mouthparts. Water deposited in cells helps to cool the nest on days with elevated temperatures.

2. Foraging for nectar: A wasp returns to the nest with nectar, or other sugary liquids stored in its crop.

3. Foraging for prey: A wasp returns to the nest carrying a mass of prey using its mouthparts and front legs.

4. Foraging for wood pulp: A wasp returns to the nest with a small, dark mass of vegetable fibers, typically scraped from tree bark, which is then used for nest construction.

5. Unsuccessful foraging: A wasp returns to the nest lacking visible items in its jaws.

V. Inactivity:

1. Immobile: Apparent inactivity on the nest during the observation periods.

VI. Cleaning:

1. Self-grooming: A wasp cleans all or parts of its body with its legs and mouthparts. Generally, the cleaning starts at the head, where the front legs are licked and rubbed against the antennae and eyes. The legs are rubbed together and against the thorax, while the hind legs are rubbed against the gaster and wings. Finally, the wings are rubbed together. Workers were observed performing 26 behaviors, queens 23, foundresses 19, and males six. A graph showing the interactions of wasps with these behaviors presents 32 vertices, 74 edges, an average degree of 2.000, a diameter of 2.000, and a Density of 0.667 (Figure 3). This graph indicates the behaviors shared by the castes. The foundress caste (F) performs no unique behavior, unlike the queen caste (Q), which has two unique behaviors, and the worker caste (W), which has five. The latter two share two behaviors (Figure 3, Table 2).

Table 2. Ethogram comparison between foundresses, queens, workers, and males of colonies of *Mischocyttarus drewseni*.

Behaviors	Abbreviations	Foundresses %	Queens %	Workers %	Males %
I. Social Activities					
1. Feeding larvae	**FL**	1.76	0.67	0.79	0.00
2. Knocking the head inside a cell	**KHIC**	0.00	0.03	0.00	0.00
3. Dominance behaviour	**DB**	0.42	0.42	0.17	0.92
4. Biting the gaster	**BG**	0.00	0.00	0.01	0.00
5. Submission behaviour	**SB**	0.70	0.03	0.19	5.50
6. Checking cells rubbing the gaster	**CCRG**	5.21	6.01	1.94	0.00
7. Adult-adult trophallaxis (donor)	**AATD**	0.49	0.13	0.65	0.00
8. Adult-adult trophallaxis (receptor)	**AATR**	0.63	1.51	0.51	0.00
9. Larva-adult trophallaxis	**LAT**	0.49	1.09	0.49	0.92
II. Oviposition					
10. Ovipositing	**OV**	0.00	0.03	0.00	0.00
III. Maintenance and defense of the nest					
11. Alarm	**A**	0.21	0.03	0.02	0.00
12. Enlarging cells	**EC**	0.84	1.25	0.58	0.00
13. Constructing new cells	**CNC**	0.00	0.00	0.02	0.00
14. Larviphagy	**L**	0.00	0.16	0.12	0.00
15. Licking the peduncle	**LP**	1.20	0.29	0.08	0.00
16. Handling large prey	**HLP**	0.35	0.19	0.03	0.00
17. Oophagy	**Oo**	0.00	0.03	0.04	0.00
18. Rubbing the gaster on the nest	**RGN**	0.28	0.03	0.12	0.00
19. Licking the cocoon	**LC**	0.00	0.00	0.20	0.00
20. Fanning cells	**FC**	0.00	0.00	0.05	0.00
21. Checking cells with the antennae	**CCA**	4.79	6.62	3.23	3.67
IV. Foraging activities					
22. Foraging for water	**FW**	0.00	0.00	0.28	0.00
23. Foraging for nectar	**FN**	5.70	3.76	25.61	0.00
24. Foraging for prey	**FP**	1.97	1.51	14.35	0.00
25. Foraging for wood pulp	**FWP**	0.84	1.54	0.90	0.00
26. Unsuccessful foraging	**UF**	1.13	3.86	9.41	0.00
V. Inactivity					
27. Immobile	**I**	64.53	66.97	35.21	77.06
VI. Cleaning					
28. Self-grooming	**SG**	8.44	3.82	5.00	11.93
TOTAL		100.00	100.00	100.00	100.00
Total number of behavioral acts		19	23	26	6

Note: Unique behavior. Source: Authors, 2024.

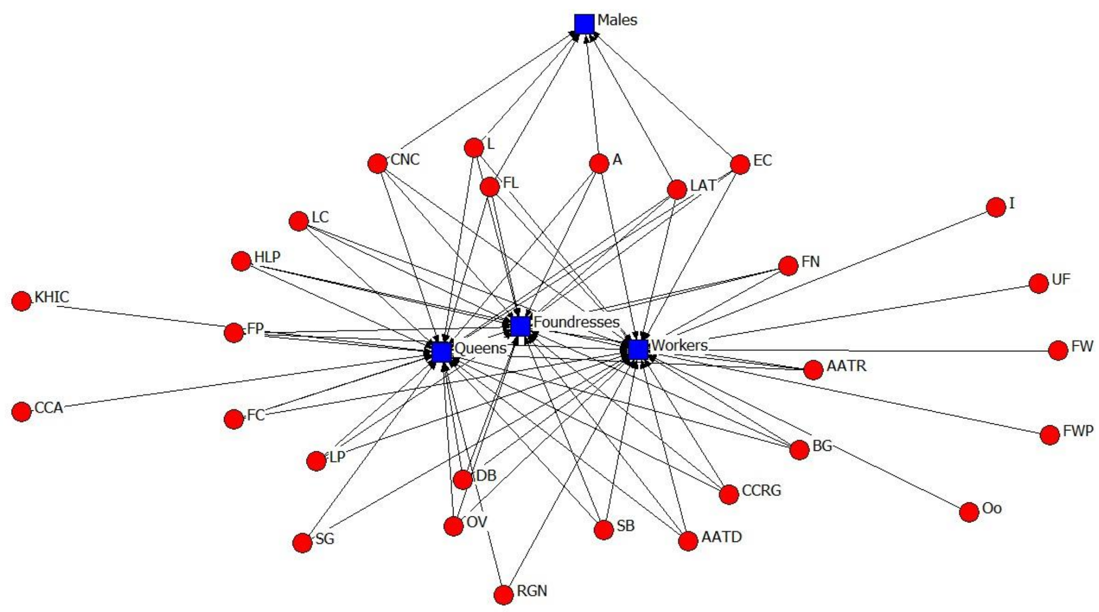

Figure 3. Graph illustrating the relations between wasps and behaviors performed by *Mischocyttarus drewseni*. Source: Authors, 2024.

Although workers and queens share two behaviors (Table 2), it can be inferred that the queen caste converges with the foundress caste and differs from the worker caste (Figures 3 and 4). Fanning cells, biting the gaster, foraging for water, licking the cocoon, and constructing new cells were activities exclusive to workers, thus showing a clear division of labor.

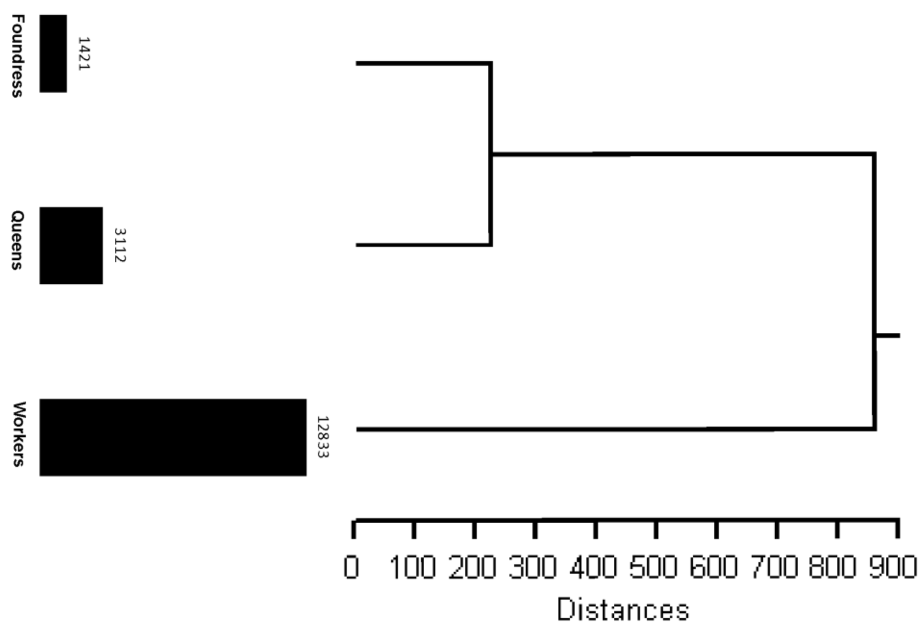

Figure 4. Dendrogram with Euclidean distance and histograms of the behavioral repertoire of *Mischocyttarus drewseni*. Source: Authors, 2024.

Even though foundresses and queens perform foraging activities, workers are more involved in the collection of resources (such as foraging for nectar, wood pulp, prey, and water), performing this behavior more than fifty percent of the time and exhibiting a wider variety of behaviors compared to other individuals (Table 2). They forage for nectar more frequently than different materials (Figure 5). Males have no affiliation with any caste, and their limited expressive behavioral repertoire (remaining motionless on the nest most of the time) confirms that their role is confined to species reproduction (Table 2, Figure 3).

Figure 5. Items collected by wasps in colonies of *Mischocyttarus drewseni.* Source: Authors, 2024.

Queens remained immobile in the nest at a frequency of 66.97% and were positioned on the cells in most cases (Figure 6).

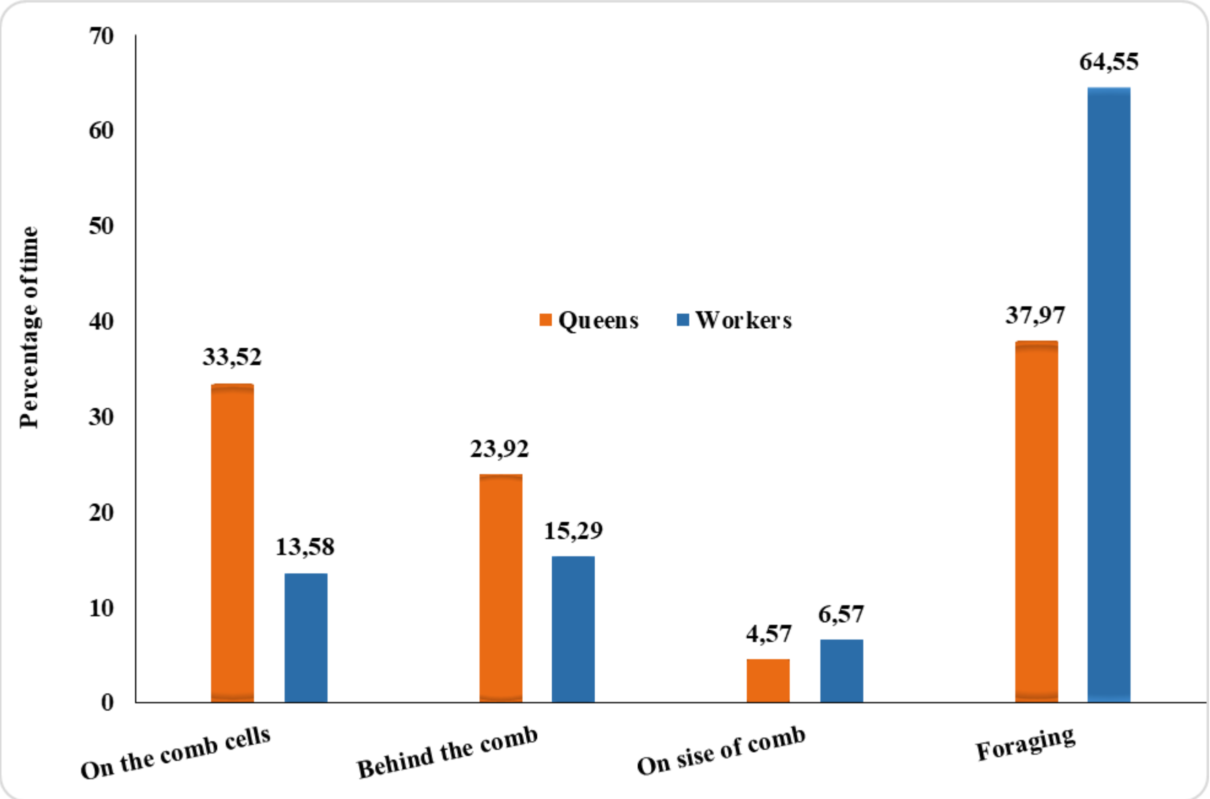

Figure 6. Nest regions where queens and workers of *Mischocyttarus drewseni* were positioned. Source: Authors, 2024.

4. Discussion

Using a graph to represent behaviors proved to be very instructive. Vertices representing the wasps are connected by edges to vertices representing their behaviors, thus facilitating visualization and interpretation. The ethogram established here, based on 406 hours of observation, represents the entire behavioral repertoire of *M. drewseni* with 28 identified behaviors.

While *M. drewseni* presented 28 behaviors, *M. consimilis* was recorded with 30 behaviors (Torres et al., 2012) and *M. cerberus styx* had 24 behaviors (Giannotti, 1999). In a study of nest defense behavior in the presence of ants, *M. cerberus styx* exhibited 20 behaviors, including 10 related to aggression (Togni; Giannotti, 2007). The division of labor in *M. drewseni* is notable: whereas the foundresses performed 19 of the observed behaviors, queens performed 23, and workers performed 26. Inactivity was the predominant behavior observed among *M. drewseni* queens, similar to the pattern observed in *M. cerberus styx* (Giannotti, 1999).

Oviposition was exclusively performed by queens, consistent with descriptions by Dantas-de-Araújo (1980). However, foundresses and subordinates may also perform oviposition, as reported by Jeanne (1972) and Dantas-de-Araújo (1980). This behavior has also been observed across various castes in colonies of *M. extinctus* (Raposo-Filho 1981), *M. cerberus styx* (Giannotti, 1999), and *M. labiatus* (Litte, 1981).

Adult wasps primarily feed on sugar, often derived from flower nectar, while the immature stages feed on protein, typically sourced from arthropods in the larval or adult phase (Spradbery, 1973). Nectar contains highly nutritive substances and provides energy more quickly than proteinaceous foods, so adult wasps have a pronounced preference for this food source (see Baker et al., 1998; Dupont et al., 2004). The preference for nectar over other foraged items, as well as the role of workers as principal nectar foragers, have been documented in the species *M. cerberus styx* (Giannotti, 1999).

Both *M. drewseni* and *M. cerberus styx* (Giannotti, 1999) require more carbohydrates than protein, resulting in greater energy expenditure for foraging nectar compared to prey, wood pulp, or water. This contrasts with *M. masthigophorus* (O'Donnell, 1999), which exhibits a high preference for protein. Workers of *M. drewseni* engage in prey foraging more intensively than queens and foundresses, confirming observations by Dantas-de-Araújo (1980) and Jeanne (1972) that *M. drewseni* queens forage for prey infrequently or not at all. Similarly, *M.*

cerberus styx queens do not participate in prey foraging (Giannotti, 1999).

M. drewseni queens display more intense foraging behavior for pulp than workers and foundresses. This behavior may be related to their involvement in building new cells for oviposition, as described for *M. cerberus styx.* (Jeanne, 1972; Dantas-de-Araújo, 1980; Giannotti, 1999). The frequency of foraging activity *M. drewseni* queens was low, consistent with observations in other studies: *M. mexicanus* (queens 6.9%, workers 59.5%) (Litte, 1977), *M. flavitarsis* (queens 4.4%, workers 72.5%) (Litte, 1979), *M. labiatus* (queens 7.1%, workers 85.0%) (Litte, 1981), *M. cerberus styx* (queens 10.2%, workers 57.7%) (Giannotti, 1999).

The occurrence of foraging by queens in *Mischocyttarus drewseni* might be and adaptive feature of basal eusocial species with small colonies, where even queens need to contribute to colony maintenance. Similarly, *Polistes lanio* and *Polistes Canadensis,* considered basal eusocial species, have queens foraging 0.5% and 0.26% of the time, respectively (Giannotti, 1992; Torres et al., 2009). In highly eusocial species like *Agelaia pallipes, Protopolybia exigua* (Simões, 1977), and *Polybia occidentalis* (Jeanne et al., 1988), queens have never been observed foraging.

Oral liquid transfer was observed in *M. drewseni,* where the transferred liquid, usually flower nectar or another sugary substance, was regurgitated by one adult and transferred to another. Workers and foundresses spent more time giving food than queens. Workers of *M. drewseni* spent more time feeding larvae compared to queens, but foundresses performed this task more frequently than either of the other castes. In contrast, *M. cerberus styx* foundresses nourished larvae less frequently than queens, with workers performing this behavior even more frequently (Giannotti, 1999).

In the nest, *M. drewseni* queens spent more time on the cells or beside the comb than workers. The queen`s presence in the cells may serve as a strategy to maintain her status in the dominance hierarchy, preventing oviposition by any other females with developed ovaries. Workers spent more time behind the comb than the queens, likely due to their subordinate status. Queens exhibited more dominant behavior than workers and were less often the object of dominant behavior. Additionally, queens were recipients of adult-adult trophallaxis more frequently than workers. These findings align with previous studies on social wasps (Giannotti, 1999; Giannotti; Machado 1999; Torres et al., 2012; Zara; Balestieri, 2000). According to Torres et al. (2009), the queen is aggressive and primarily dedicated to reproductive activities and tasks inside the nest, spending most of her time at the nest center. In trophallaxis behavior, the donor is usually subordinate to the receiver wasp. In *M. cerberus styx*, queens and workers show no variation in the frequency of this behavior, and the foundresses do not participate (Giannotti, 1999).

Dominance behavior was more common in foundresses and queens than in workers of *M. Drewseni*, corroborating findings by Jeanne (1972) and Dantas-de-Araújo (1980) for the same species, and by Litte (1981) for *M. labiatus,* Giannotti (1999) and Noda et al. (2001) for *M. cerberus* styx, O'Donnell (1998) and O'Donnell (1999) for M. *mastigophorus* and Prezoto et al. (1994) for *M. cassununga*.

subordinated wasps, when dominated, can retreat or even fly out of the nest. This behavior was observed in workers, while queens displayed this behavior only once. Co-foundresses performed the submission behavior more frequently than either of these castes, indicating that the foundresses are more submissive than workers. Workers of *M. drewseni* exhibited aggressive behavior by biting the gaster of another several times. In *M. cerberus styx* (Giannotti, 1999) this behavior was unique to workers.

M. drewseni queens checked cells more often than workers and foundresses. Queens also spend more time vibrating their gasters compared to foundresses and workers. This behavior is considered dominant and a form of communication between adults and larvae (Jeanne, 1972). It was also observed by Giannotti (1999) for *M. cerberus styx* that queens engaged in peduncle licking more frequently than the workers, unlike what was noticed by Jeanne (1972) and Dantas-de-Araújo (1980), who found this activity more common among workers.

M. drewseni queens were more involved in enlarging cells than workers, corroborating findings by Jeanne (1972) and Dantas-de-Araújo (1980). In *M. cerberus styx* (Giannotti,1999), this behavior was observed in foundresses and queens but not in workers. Individuals of *M. drewseni* rubbed their gasters on the nest's peduncle, dispersing secretion from the van der Vecht gland, which serves as a repellent against ants (Jeanne, 1970). This behavior was also observed behind and beside the nest and was performed more intensively by the foundresses, though workers and queens also engaged in it, albeit less frequently.

Oophagy was observed in both *M. drewseni* queens and workers, as well as *M. cerberus styx* (Giannotti, 1999). This behavior is expected in social Hymenoptera (Wilson, 1971). Larviphagy was observed in workers and queens, as documented in *M. mexicanus* (Clouse, 1995). According to Hunt (1991), cannibalism of immaturity is common among wasps and can occur at high rates. Male *M. drewseni* exhibited six behaviors, suggesting ethological similarities to the species *M. mastigophorus* (O'Donnell, 1999), whose males sustain a dominant status relative to workers and perform few tasks within the nest.

No mating behaviors were registered in this study for *M. drewseni*. Jeanne & Castellón-Bermúdez (1980) described the reproductive behavior of *M. drewseni* males, which assume a guarding position and make regular flights over areas rich in flowering plants, often frequented by conspecific females seeking food, thus providing favorable conditions for copulation.

5. Conclusions

According to the activities performed in the colony, foundresses, workers, and queens are differentiated. Of these three, foundresses and queens exhibit converging behavior repertoires. Workers engage in the broadest variety of behaviors, particularly regarding foraging, while males undertake the fewest types of activities.

6. Acknowledgments

The authors would like to thank Dra. Lilyan Rosmery Luizaga de Monteiro Luizaga for her proofreading of the manuscript.

7. Authors' Contributions

The subject matter of this study is inherently complex, and thus, all self-advocates were involved in all stages of the development process.

8. Conflicts of Interest

No conflicts of interest.

9. Ethics Approval

Not applicable.

10. References

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, 49(3/4), 227-267. https://doi.org/10.1163/156853974X00534

Baker, H. G., & Hodges, S. A. (1998). Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. *Biotropica*, 30(4), 559-586. https://doi.org/10.1111/j.1744-7429.1998.tb00097.x

Borgatti, S. P., Everett, M. G., & Freeman, L. C. (2002). Ucinet for windows: Software for social network analysis. Analytic Technologies.

Brandão, C. R. F. (1978). Division of labor within the worker caste of *Formica perpilosa* Wheeler (Hymenoptera: Formicidae). *Psyche*, 85(2-3), 229-237. https://doi.org/10.1155/1978/23456

Brandão, C. R. F. (1983). Sequential ethograms along colony development of *Odontomachus affinis* Guerin (Hymenoptera, Formicidae, Ponerinae). *Insectes Sociaux*, 30(2), 193-203. https://doi.org/10.1007/BF02223984

Carpenter, J. M. (1993). Biogeographic patterns in the Vespidae (Hymenoptera): Two views of Africa and South America. *In*: P. Goldblatt (Ed.), Biological relationships between Africa and South America, 139-155 p. Yale University Press.

Carpenter, J. M., & Marques, O. M. (2001). Contribuição ao estudo dos vespídeos do Brasil (Insecta, Hymenoptera, Vespoidae). Publicações Digitais. Universidade Federal da Bahia.

Clouse, R. M. (1995). Nest usurpation and intercolonial cannibalism in *Mischocyttarus mexicanus* (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society*, 68(1), 67-73. https://www.jstor.org/stable/25085561

Conte, Y. L., & Hefetz, A. (2008). Primer pheromones in social Hymenoptera. *Annual Review of Entomology*, 53(1), 523-542. https://doi.org/10.1146/annurev.ento.53.103106.093540

Dantas-de-Araújo, C. Z. (1980). Bionomia e comportamento social comparado de *Mischocyttarus drewseni drewseni* de Saussure, 1853, nas regiões subtropical. [Doctoral Thesis, Universidade Federal do Paraná].

Del-Claro, K. (2004). Comportamento animal: Uma introdução à ecologia comportamental. Livraria Conceito.

Dupont, Y. L., Hansen, D. M., Rasmussen, J. T., & Olesen, J. M. (2004). Evolutionary changes in nectar sugar composition associated with switches between bird and insect pollination: The Canarian bird-flower element revisited. *Functional Ecology*, 18(5), 670-676. https://www.jstor.org/stable/3599322

Fagen, R. M., & Goldman, R. N. (1977). Behavioural catalogue analysis methods. *Animal Behaviour*, 25(2), 261-274. https://doi.org/10.1016/0003-3472(77)90001-X

Gadagkar, R. (1991). Belonogaster, *Mischocyttarus*, *Parapolybia*, and independent-founding *Ropalidia*. *In*: Ross, K. G., & Matthews, R. W. (Eds.), The social biology of wasps, 149-190 p. Comstock Publishing Associates.

Giannotti, E. (1992). Estudos biológicos e etológicos da vespa social neotropical *Polistes* (Aphanilopterus) *lanio lanio* (Fabricius, 1775) (Hymenoptera, Vespidae). [Doctoral Thesis, Universidade Estadual Paulista Júlio de Mesquita Filho].

Giannotti, E. (1999). Social organization of the eusocial wasp *Mischocyttarus cerberus* styx (Hymenoptera: Vespidae). *Sociobiology*, 33(3), 325-338.

Giannotti, E., & Machado, V. L. L. (1999). Behavioral castes in the primitively eusocial wasp *Polistes lanio* Fabricius (Hymenoptera, Vespidae). *Revista Brasileira de Entomologia*, 43(2-3), 185-190. https://www.cabidigitallibrary.org/doi/full/10.5555/20000505776

Hölldobler, B., & Wilson, E. O. (2009). The superorganism: The beauty, elegance, and strangeness of insect societies. W. W. Norton & Company.

Hunt, J. H. (1991). Nourishment and the evolution of social Vespidae. *In*: Ross, K. G., & Matthews, R. W. (Eds.), The social biology of wasps, Comstock Publishing Associates, 426-450 p.

Jeanne, R. L. (1970). Chemical defense of brood by a social wasp. *Science*, 168(3935), 1465-1466. https://doi.org/10.1126/science.168.3938.1465

Jeanne, R. L. (1972). Social biology of the Neotropical wasp *Mischocyttarus drewseni*. *Bulletin of the Museum of Comparative Zoology*, 144(2), 63-150. https://cir.nii.ac.jp/crid/1573950399451662592

Jeanne, R. L. (1991). The swarm-founding Polistinae. *In*: Ross, K. G., & Matthews, R. W. (Eds.). The social biology of wasps, Cornell University Press, 191-231 p.

Jeanne, R. L., & Castellón-Bermúdez, E. G. (1980). Reproductive behavior of a male Neotropical social wasp, *Mischocyttarus drewseni* (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society*, 53(2), 271-276. https://www.jstor.org/stable/25084030

Jeanne, R. L., Downing, H. A., & Post, D. C. (1988). Age polyethism and individual variation in *Polybia occidentalis*, an advanced eusocial wasp. *In*: Jeanne, R. L. (Ed.), Interindividual behavioral variability in social insects, 323-357 p.

Krebs, C. J. (1998). Ecological methodology (2nd ed.). Addison Wesley Longman.

Litte, M. (1977). Behavioral ecology of the social wasp, *Mischocyttarus mexicanus*. *Behavioral Ecology and Sociobiology*, 2(3), 229-246. https://doi.org/10.1007/BF00299737

Litte, M. (1979). *Mischocyttarus flavitarsis* in Arizona: Social and nesting biology of a polistine wasp. *Zeitschrift für Tierpsychologie*, 50(3), 282-312. https://doi.org/10.1111/j.1439-0310.1979.tb01033.x

Litte, M. (1981). Social biology of the polistine wasp *Mischocyttarus labiatus*: Survival in a Colombian rain forest. Smithsonian Contributions to Zoology, 327(1), 1-27. https://doi.org/10.5479/si.00810282.327

Murakami, A. S. N., Desuó, I. C., & Shima, S. N. (2013). Division of labor in stable social hierarchy of the independent-founding wasp *Mischocyttarus* (*Monocyttarus*) *cassununga*, Von Ihering (Hymenoptera, Vespidae). Sociobiology, 60(1), 114-122. https://doi.org/10.13102/sociobiology.v60i1.114-122

Noda, S. C. M., Silva, E. R., & Giannotti, E. (2001). Dominance hierarchy in different stages of development in colonies of the primitively eusocial wasp *Mischocyttarus cerberus styx* (Hymenoptera, Vespidae).

Sociobiology, 38(4), 603-614. http://hdl.handle.net/11449/66738

O'Donnell, S. (1998). Dominance and polyethism in the eusocial wasp *Mischocyttarus mastigophorus* (Hymenoptera: Vespidae). *Behavioral Ecology and Sociobiology*, 43(5), 327-331. https://doi.org/10.1007/s002650050498

O'Donnell, S. (1999). The function of male dominance in the eusocial wasp, *Mischocyttarus mastigophorus* (Hymenoptera: Vespidae). *Ethology*, 105(3), 273-282. https://doi.org/10.1046/j.1439-0310.1999.00382.x

Prezoto, F., Giannotti, E., & Machado, V. L. L. (1994). Atividade forrageadora e material coletado pela vespa social *Polistes simillimus* Zikán, 1951 (Hymenoptera, Vespidae). *Insecta*, 3(1), 11-19.

Raposo-Filho, J. R. (1981). Biologia de *Mischocyttarus* (*Monocyttarus*) *extinctus* Zikán, 1935 (Polistinae, Vespidae). [Master's dissertation, Universidade Estadual Paulista Júlio de Mesquita Filho].

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

Robinson, G. E. (1992). Regulation of division of labor in insect societies. *Annual Review of Entomology*, 37(1), 637-665. https://doi.org/10.1146/annurev.en.37.010192.003225

Silva-Melo, A., & Giannotti, E. (2012). Division of labor in Pachycondyla striata Fr. Smith, 1858 (Hymenoptera: Formicidae: Ponerinae). *Psyche: Journal of Entomology*, 2012, 1-7. https://doi.org/10.1155/2012/131392

Silveira, O. T. (2008). Phylogeny of wasps of the genus *Mischocyttarus* de Saussure (Hymenoptera, Vespidae, Polistinae). *Revista Brasileira de Entomologia*, 52(4), 510-549. https://doi.org/10.1590/S0085-56262008000400004

Simões, D. (1977). Etologia e diferenciação de casta em algumas vespas sociais (Hymenoptera, Vespidae). [Master's dissertation, Universidade de São Paulo].

Spradbery, J. P. (1973). Wasps: An account of the biology and natural history of social and solitary wasps, with particular reference to those of the British Isles. University of Washington Press.

Spradbery, J. P. (1991). Evolution of queen number and queen control. In K. G. Ross & R. W. Matthews (Eds.), The social biology of wasp, Cornell University Press, 336-388 p.

Togni, O. C., & Giannotti, E. (2007). Nest defense behavior against the attack of ants in colonies of pre-emergent Mischocyttarus cerberus (Hymenoptera, Vespidae). *Sociobiology*, 50(3), 675-694.

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(4), 593-599. https://doi.org/10.1590/S0085-56262009000400008

Torres, V. O., Montagna, T. S., Raizer, J., & Antonialli-Junior, W. F. (2012). Division of labor in colonies of the eusocial wasp, *Mischocyttarus consimilis*. *Journal of Insect Science*, 12(1), 21. https://doi.org/10.1673/031.012.2101

Wilson, E. O. (1971). The insect societies. The Belknap Press of Harvard University Press.

Wilson, E. O. (1975). Sociobiology: The new synthesis. The Belknap Press of Harvard University Press.

Zara, F. J., & Balestieri, J. B. P. (2000). Behavioural catalogue of *Polistes versicolor* Oliver (Vespidae: Polistinae) post-emergence colonies. *Naturalia*, 25(1), 301-319.

Funding

Not applicable.

Institutional Review Board Statement

Not applicable.

Informed Consent Statement

Not applicable.