



RESEARCH ARTICLE - WASPS

Trip durations of daily and seasonal foraging activities in *Mischocyttarus nomurae* (Richards) (Hymenoptera, Vespidae)

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Article History

Edited by

Fabio S. Nascimento, USP, Brazil

Received 05 July 2021

Initial acceptance 21 August 2021

Final acceptance 18 April 2022

Publication date 05 July 2022

Keywords

Etology; Polistinae; Resources collected; Social wasps.

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Abstract

The study of foraging activity in wasps is important to understand the social organization and its evolutionary success. We examined aspects of the daily and seasonal foraging activities of *Mischocyttarus nomurae* Richards wasps, in terms of individual trip duration in the collection of different resources. The study was undertaken in two areas in the municipality of Rio de Contas, Bahia State, Brazil. Observations were done for 10 colonies of *M. nomurae* in their post-emergence phase under natural conditions, five during the rainy period and five during the dry period. The amplitudes of the activity hours were similar between the two periods. The foraging efficiency index was higher (80.56%) during the rainy period than during the dry period (74.42%), with greater percentages of returns with all foraged items (with the exception of prey captures). Temperature influenced positively and significantly the number of trips performed during the rainy period, while temperature and luminosity positively influenced the number of trips performed during the dry period. The mean duration of trips for different resources were greater during the dry period (with the exception of wood pulp), although those differences were not statistically significant. Wasps spent the most part of their time nectar (83.60 min), followed by prey (21.06 min), and wood pulp (1.40 min). We observed that 52.56% of the foraging individuals of *M. nomurae* collected only a single resource type.

Introduction

Wasps, as well as bees, demonstrate a behavioral spectrum that varies from solitary to eusocial. This is an important aspect for studies of social evolution in these groups (Jeanne, 1980; Carpenter, 1991; Leadbeater et al., 2011; Piekarski et al., 2018; Manfredini et al., 2019; Da-Silva, 2021). Wasps leave their nests daily to search for resources to maintain their colony. That foraging behavior is extremely important for understanding the social organization of wasps, their evolutive success, and the relationships between adults and young individuals in terms of the selection of resources to be gathered (Cruz et al., 2006).

Foraging activity is generally influenced by external factors such as temperature, humidity, and luminosity (Giannotti et al., 1995; Andrade & Prezoto, 2001; Resende et al., 2001; Paula et al., 2003; Rocha & Giannotti, 2007). However, depending on the necessities of the colony, there can be interactions between internal and external factors that influence foraging rhythms (Detoni et al., 2015).

The resources collected by social wasps include water to cool the nest, wood pulp to construct and enlarge the nest, carbohydrates from nectar, and the exudates of insects and proteins from prey that are used to feed larvae (Jeanne, 1972; Giannotti et al., 1995; Raveret-Richter, 2000; Silva & Noda, 2000; Carpenter & Marques, 2001).



Various studies have been undertaken focusing on the life history of social wasps and diverse aspects of their foraging behaviors, as well as analyzing the influences of environmental variations on them, as seen in the publications of Giannotti et al. (1995), Silva and Noda (2000), Andrade and Prezoto (2001), Resende et al. (2001), Paula et al. (2003), Cruz et al. (2006), Rocha and Giannotti (2007), Hernández et al. (2009), Castro et al. (2011), Silva et al. (2012), Elisei et al. (2013), and Prezoto et al. (2016).

Mischocyttarus nomurae Richards, 1978 is a little-known species of social wasp. The only published materials available were the description of the species collected in Ceará State, Brazil (Richards, 1978), the description of males from Chapada Diamantina, Bahia State (Silveira, 2004), and the study with the eggs and immatures this species (Rocha & Giannotti, 2016). Souza et al. (2015) recorded the species for Minas Gerais State.

Considering the importance of foraging activities for wasps, and the fact that little is known about *M. nomurae*, we studied the foraging activities of *M. nomurae* to determine if: there were differences in the durations of trips to collect different types of resources; there were differences in the durations of those trips in relation to the rainy and dry periods; there existed any relationships between those activities and climatic and/or colony factors; each forager collects only a single type of resource.

Material and Methods

The present study was undertaken in two separate areas: Cachoeira do Fraga and Raposo Chalé, both within the municipality of Rio de Contas, Bahia State, Brazil. Cachoeira do Fraga is located 3 km from the city of Rio de Contas, while Raposo Chalé is 1.5 km distant. The Municipality of Rio de Contas (13°34'44''S; 41°48'41''W) is situated in the Centro Sul Baiano Geographic Mesoregion, in the southern extent of the Chapada Diamantina mountain range, at an altitude of 999 masl, and 612 km from the state capital of Salvador. The region is included within the semiarid zone of Brazil, with a subhumid to dry climate, a mean annual temperature of 19.1 °C, and a mean annual rainfall rate of 813.2 mm. The rainy period lasts from October to April. The vegetation is considered to be of the Montane Ecological Refuge type with Cerrado-Caatinga contacts (Sei, 2011).

Our observations were made under natural conditions during two periods of the year: in the rainy season (from October to April/2014) and in the dry season (from August to September/2014). Five colonies in their post-emergence phase were accompanied during each period, totaling 10 colonies studied; the post-emergence phase is considered according to the criteria established by Jeanne (1972): occurs from the emergence of the 1st adult to the beginning of irreversible reduction of the immature of the colony.

One or two days before undertaking the observations of each colony, all of the adult wasps were marked with colored

dots (using porcelain marking pens) on the dorsal region of their mesothorax. In this way each individual had a unique color identification code. To apply those markings, an insect net was extended near the nest to capture adult individuals. Then, using a forceps to handle the insects, each individual was marked and subsequently released. Additionally, the nests were mapped and the eggs, larva, and pupa in each nest were counted.

Each wasp colony of *M. nomurae* was monitored for 12 hours, beginning at 06:00h until 18:00h, totaling 120 hours of observations. Temperature and relative humidity were recorded every 30 minutes (measured using a digital thermal-hygrometer) as well as luminosity (using a digital light meter) (Silva & Noda, 2000).

We recorded the time of each wasp leaving the nest, the time of its arrival back, as well as the resource it was carrying. The observations and identifications of the collected materials were based on the criteria of Silva and Noda (2000).

The normality of the data was verified using the Shapiro-Wilk test, and homoscedasticity was verified using the Levene test. The Pearson Correlation was used to analyze the relationship between the numbers of individuals in the colony and the numbers of foraging trips (for parametric data); the Spearman Correlation was used for data having nonparametric distributions. Simple Linear Regression Analysis was used to verify the influence of each environmental variable on foraging trips.

The parametric Student t-test was used to analyze the mean durations of the foraging trips in each season (for data demonstrating normal distributions); data demonstrating non-normal distributions were analyzed using the Mann-Whitney nonparametric test. R Program version 4.0.2 (R Core Team 2020) was used for those analyses, considering a significance level of $p < 0.05$.

The Foraging Efficiency index (Giannotti et al., 1995) was calculated according to the formula:

$$\text{Efficiency index} = \text{fr}/\text{fn} \times 100$$

where fr = N° of foragers that arrived with resource and fn = N° of foragers that arrived in the nest.

Results

Foraging activity patterns and colony factors

The study focused on 10 colonies; their parameters are presented in Table 1. The observations made during the rainy period identified the first foraging trips of *M. nomurae* occurring at 07:00 h, while the last return was recorded at 17:43 h, configuring amplitude of 10h and 43min of foraging per day (Fig 1). That activity was less intense during the morning hours until 11:00 h, and after 17:00 h, when the numbers of returning foragers increased considerably. Activity peaks during the rainy period occurred between 11:01 and 12:00 h, and again between 14:01 and 17:00 h.

The foraging activities during the dry period did not differ from those of the rainy period. The first trips initiating at 07:05 h and the last returns at 17:41 h, with an amplitude

Table 1. Populational information concerning the 10 colonies of *Mischocyttarus nomurae* wasps studied during the rainy and dry periods of 2014, in the municipality of Rio de Contas, Bahia State, Brazil. Legend: E: eggs; L: larva; P: pupa; A: adults.

Period	Sampling date	Colony	Sub-phase of Post-emergence (Jeanne, 1972)	N° de cells	Individuals			
					E	L	P	A
Rainy	04/18/2014	1	Pre-male	44	13	16	9	8
	04/17/2014	2	Pre-male	44	13	14	7	7
	04/20/2014	3	Pre-male	81	14	29	16	7
	04/20/2014	4	Post-male	43	20	3	3	6
	08/15/2014	5	Post-male	33	7	20	4	10
Dry	08/15/2014	6	Pre-male	42	10	14	6	7
	08/16/2014	7	Pre-male	24	4	8	10	7
	08/17/2014	8	Pre-male	24	6	6	5	6
	09/27/2014	9	Post-male	47	18	17	9	14
	09/28/2014	10	Post-male	77	32	25	9	13

of 10 h and 46 min (Fig 2). The foraging activity increased as the day progressed, peaking at 13:01 to 14:00h, and then decreasing. Comparing Figures 1 and 2, it can be seen that foraging activities occurred more uniformly in the rainy period than in the dry period.

The mean frequency of foraging trips remained the same during the two seasonal periods, with 2.87 ± 1.58 (0.20 – 4.80) trips during the rainy period and 2.85 ± 1.58 (0.00 – 5.60) trips in the dry period. The frequency of returns during the rainy period was slightly greater than in the dry period.

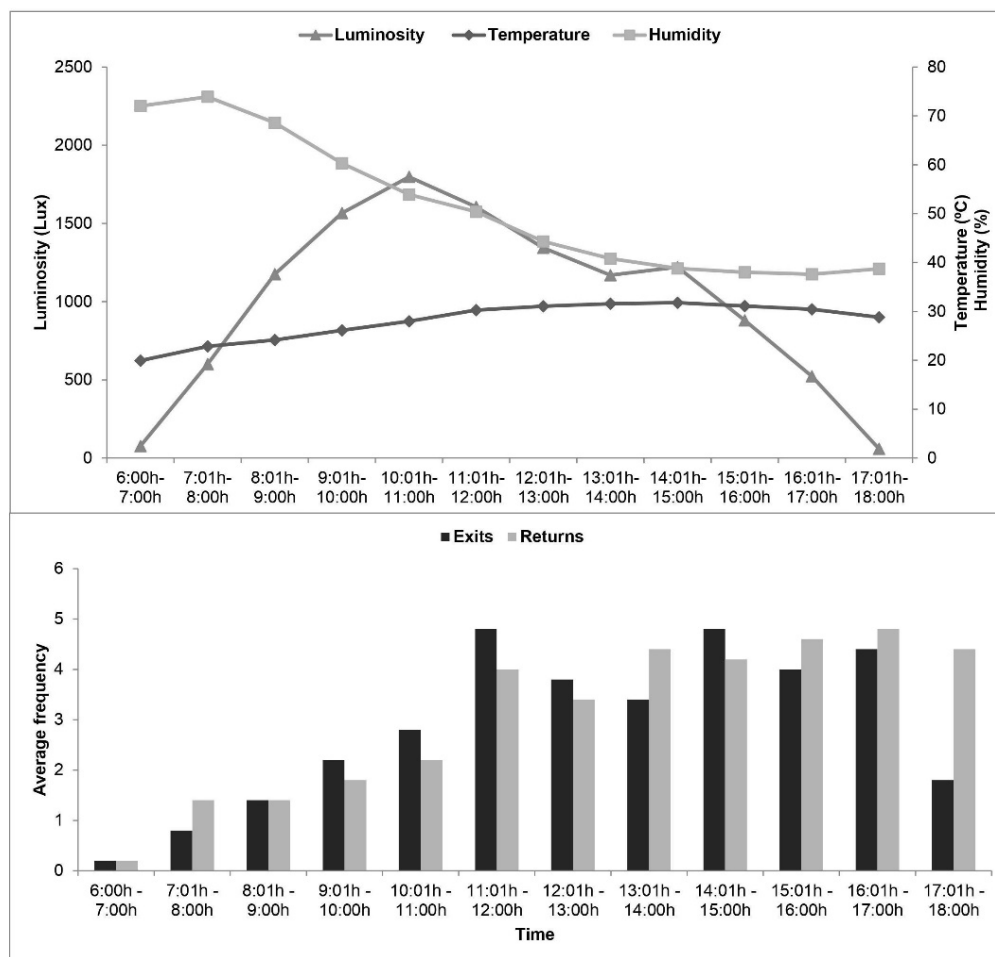


Fig 1. Patterns of foraging activities of the five colonies of *Mischocyttarus nomurae* wasps studied, and the mean values of the climatic factors of temperature (°C), relative humidity (%), and luminosity (Lux) during the day, during the rainy period of 2014.

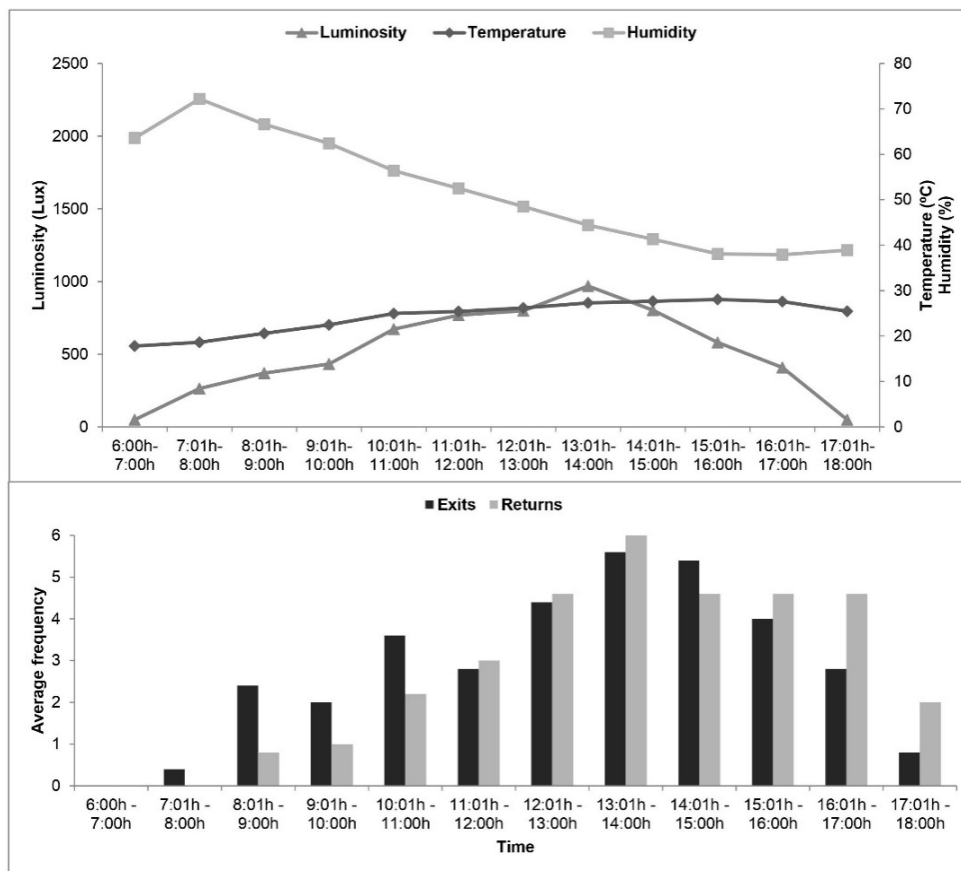


Fig 2. Patterns of foraging activity of the five colonies of *Mischocyttarus nomurae* wasps studied, and the mean values of the climatic factors of temperature (°C), relative humidity (%), and luminosity (Lux) during the day, during the dry period of 2014.

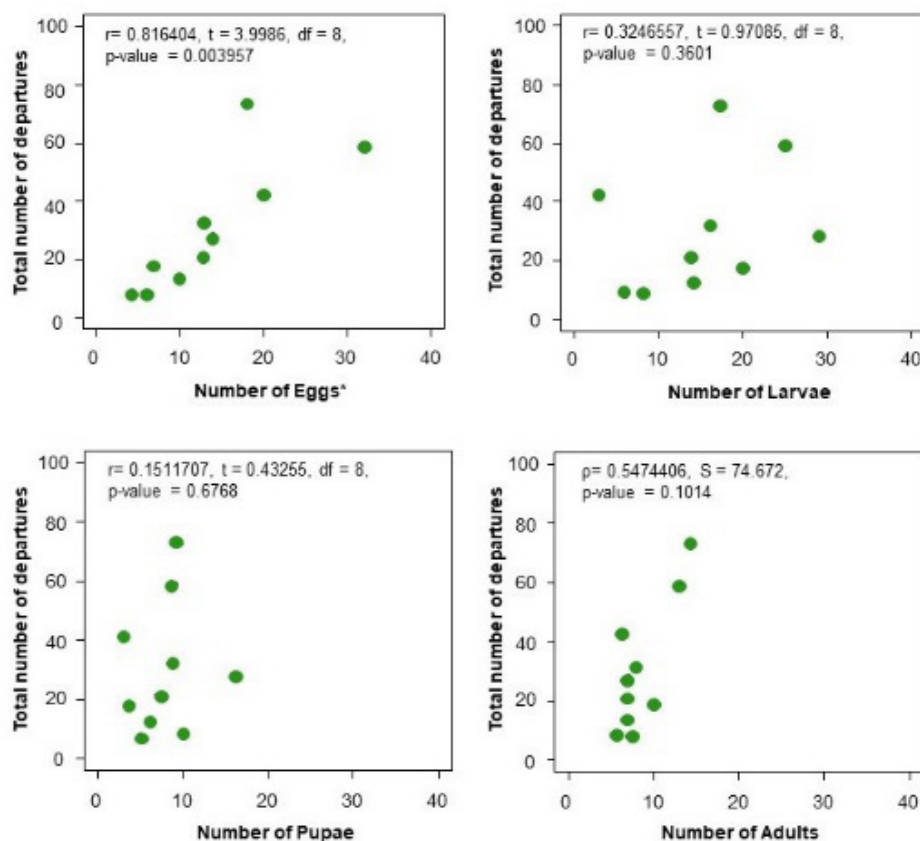


Fig 3. Correlation between the numbers of individuals in the nests and the foraging activities of *Mischocyttarus nomurae* (r : Pearson Correlation for parametric data; ρ : Spearman Correlation for data having nonparametric distributions). *significant values

During the rainy period the mean frequency of return flights was 3.07 ± 1.58 (0.20 – 4.80), and 2.78 ± 2.07 (0.00 – 6.00) during the dry period. All of the factors positively influenced the number of forage flights leaving the nest, especially the numbers of eggs and adults, which demonstrated correlation values above 50%; although only the number of eggs was statistically significant (Fig 3). The foraging efficiency index varied between the two seasonal periods, being greater in the rainy period (80.56%) than during the dry period (74.42%).

Foraging activity and Climatic factors

Temperature and luminosity values were lower at the beginning and end of the observation periods (Fig 1 and 2).

During the rainy period, the mean temperature was $27.6 \text{ }^\circ\text{C}$ (± 3.8); during the dry period the mean was $24.3 \text{ }^\circ\text{C}$ (± 3.5). Luminosity varied greatly between the two periods, with a mean of 1001.6 Lux (± 579.3) during the rainy period, and 513.9 Lux (± 301.5) during the dry period. The means of relative humidity did not demonstrate variations between the two seasonal periods, being 51.4% during the rainy period and 51.9% during the dry period.

In the rainy period, humidity negatively influenced foraging activity while luminosity and temperature had a positive influence. Although, only temperature demonstrated a statistically significant positive influence. During the dry period, temperature and luminosity both significantly positively influenced foraging activity (Fig 4).

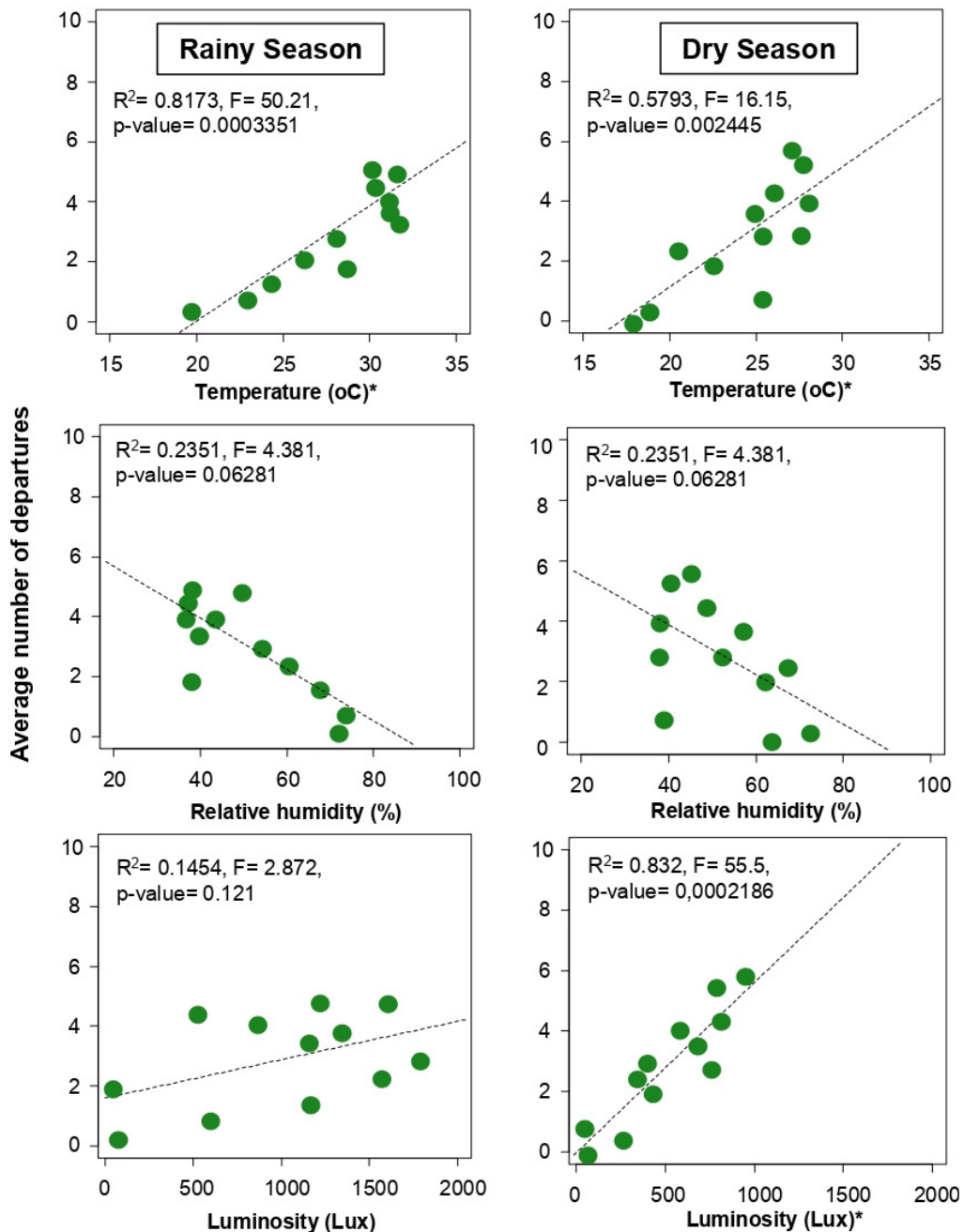


Fig 4. Linear Regression Analysis among the environmental factors and foraging activities of *Mischocyttarus nomurae* wasps during the rainy and dry periods. * significant values

Resources collected and trip durations

There were 168 returns during the dry period, and 184 during the rainy period, although the majority of both were fruitless; among successful foraging returns, the most

frequent was with nectar, followed by prey, wood pulp, and unidentified materials (Fig 5). Water was not observed as a collection item in either of the seasonal periods. The greatest percentage of successful returns (considering all items) occurred during the rainy period, with the exception of returns with prey.

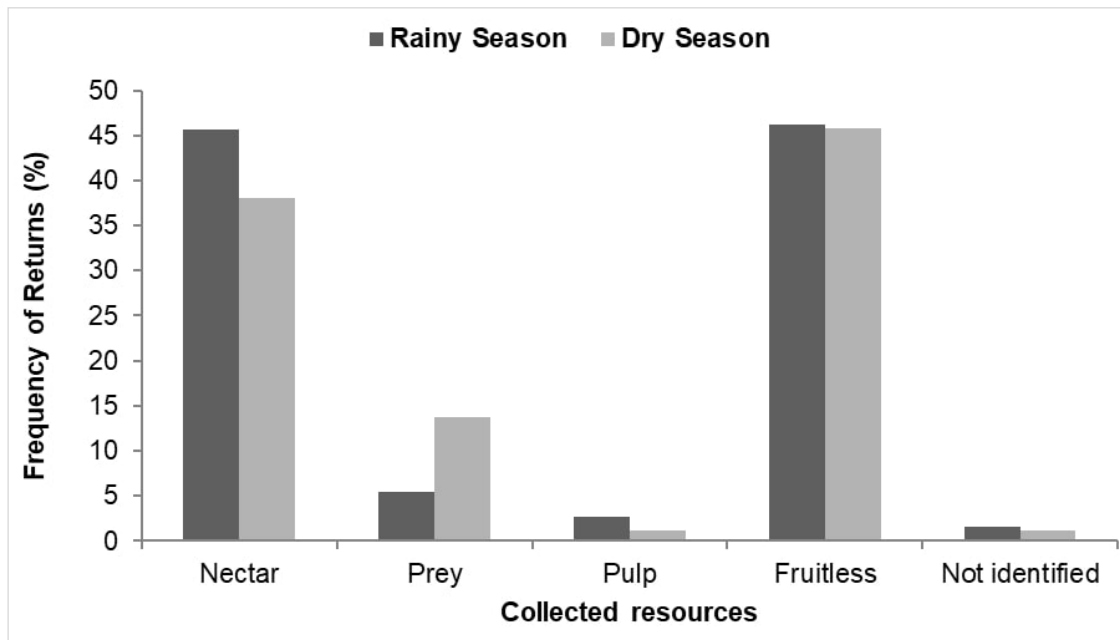


Fig 5. Return frequencies of foraging individuals of *Mischocyttarus nomurae* with items collected during the rainy and dry periods of 2014, in the municipality of Rio de Contas, Bahia State, Brazil.

The mean duration of foraging trips made by *M. nomurae* to harvest different resources was greatest during the dry period, with the exception of wood pulp (Table 2). However, these differences were not significant statistically. Based on this, the data showed that seasonality did not influence the mean duration of the foraging trips.

Of the 78 foraging individuals marked and accompanied, 52.56% (n = 41) were involved in the collection of only a single resource (nectar); the second most numerous group of individuals (24.36%; n = 19) collected two types of resources (nectar + wood pulp or nectar + prey); 21.79% (n = 17) collected nothing; 1.28% (n = 1) collected three resources (Fig 6).

Table 2. Mean duration of the foraging trips (min) to collect different resources during each period of the study, and the results of the tests used to compare the means between the rainy and dry periods of 2014, in the municipality of Rio de Contas, Bahia State, Brazil.

Resource	Mean duration of the trips during the rainy period (min)	Mean duration of the trips during the dry period (min)	Results (Mann-Whitney ort Test)
Nectar	67.91 (± 11.40)	83.60 (± 28.02)	t = 1.1818 p = 0.2712
Wood pulp	3.36 (± 7.51)	1.40 (± 1.95)	U = 11.00 p = 0.7540
Prey	11.15 (± 16.02)	21.06 (± 31.45)	t = 0.6278, p = 0.5476
unfruitful	37.20 (± 16.43)	54.40 (± 45.18)	t = 0.80173, p = 0.4459

Prey, wood pulp, and nectar were observed being collected only in colony C10, with only a single individual collecting wood pulp. Nectar was collected in colonies C3, C4, C6 and C8, with the majority of foragers performing those collections; on the other hand three of the seven foraging individuals in colony C6, collected nectar. Wood pulp collection was only observed in

three colonies (colonies C2, C9 and C10). In colony 2, three of the seven foraging individuals performed those collections, while in colonies C9 and C10, only one individual of each collected this resource. Prey collection was observed in colonies C1, C5, C7, C9 and C10, with the foraging individuals collecting only that material (or nectar in addition to that material).

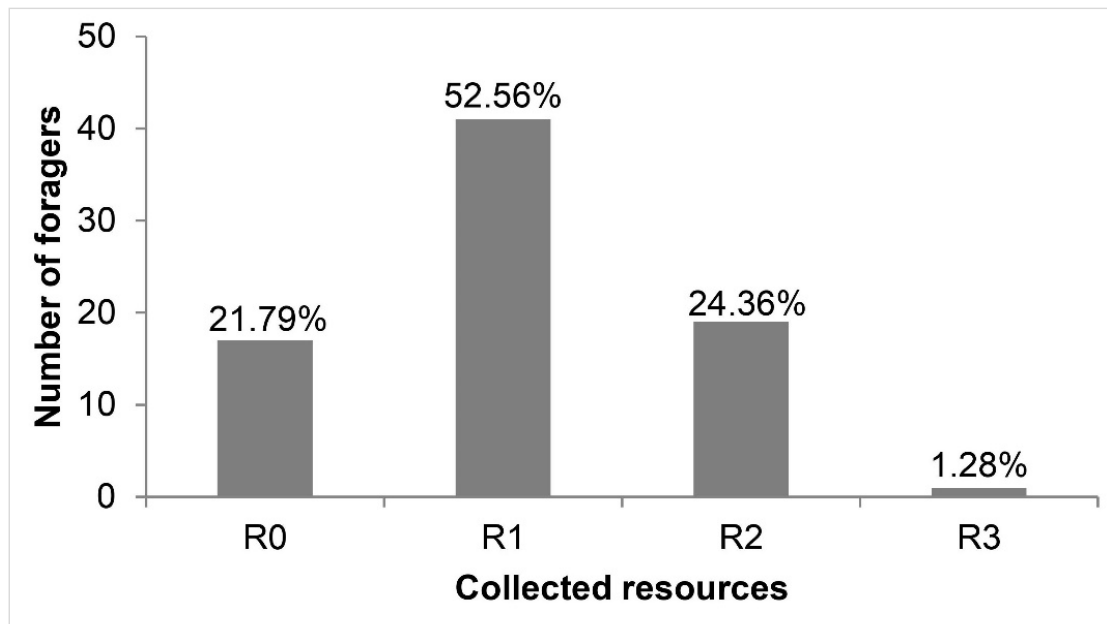


Fig 6. Individual specializations of *Mischocyttarus nomurae* wasps collecting different types of resources. R0 – no resource collected; R1– collection of a single resource; R2 – collection of two resources; R3 – collection of three resources.

Discussion

The foraging activities of *M. nomurae* were similar in terms of amplitude and the numbers of trips during both the dry and rainy periods. These results differ from were demonstrated in some species of wasps (Giannotti et al., 1995 – *Polistes lanio lanio*; Silva & Noda, 2000 – *Mischocyttarus cerberus*; Ribeiro-Junior et al., 2005 – *Protopolybia exigua* and Castro et al., 2011 – *Mischocyttarus cassununga*), in which the activity amplitude was higher in the warm and humid seasons (ranging between 9 to 12h in the total) than in cold and dry periods (ranging between 4 to 8h in the total).

The foraging efficiency index of *M. nomurae* was greater during the rainy period. Giannotti et al. (1995) likewise reported a greater foraging efficiency index of *P. lanio lanio* during the hot and humid season (89.3%) as opposed to the cold and dry season (68.8%). In addition to considerations of resource availability, the conditions of the colony, and the environment during any study, one must consider that foraging efficiency indices will reflect the unique characteristics of each species (Silva & Noda, 2000; Ribeiro-Junior et al., 2005; Rocha & Giannotti, 2007; Castro et al., 2011). As such, and according to studies currently available, patterns of wasp activity tend to be different at different times of the year. Foraging during the dry period is generally initiated in the second half of the morning and terminates relatively early, and is different from that observed in the rainy period, when foragers leave the nests in the first hours of the morning and continue foraging until the end of the day (Silva & Noda, 2000; Ribeiro-Junior et al., 2005).

The pattern of foraging activity of *M. nomurae* in the dry period was similar to that of the rainy period – a result that

differs from published accounts for other species. That result may reflect the fact that two of the five colonies observed during the dry period (C9 and C10), were monitored near the end of that season, and the climatic conditions at that time may not have been fully typical of the dry period.

Another factor that could have influenced the greater foraging activities of those two colonies (C9 and C10) when compared to the others (C6, C7 and C8), is the fact that C9 and C10 were larger than the latter three colonies, and consequently had more individuals available to undertake foraging activities. Rocha et al. (2009) observed a positive correlation between the numbers of larva, eggs, pupa, and females of *P. exigua* and the numbers of trips from their nests. Our results likewise evidenced that greater numbers of eggs in a nest positively influenced the numbers of foraging trips. However, the other members of the colony (larvae, pupae and adults) did not present correlation.

In relation to foraging activity and climatic factors, it was found that only temperature positively and significantly influenced the number of foraging trips during the rainy period, while temperature and luminosity influenced that number during the dry period. Studies have demonstrated that foraging activities are normally positively correlated with temperature and negatively correlated with relative humidity in different social wasp genera in the neotropical region (Hernández et al., 2009; Detoni & Prezoto, 2021). Studies undertaken with Polistini and Mischocyttarini wasps evidenced that temperature and luminosity were positively correlated with the numbers of foraging trips, and that relative humidity demonstrates a negative correlation with that behavior (Silva & Noda, 2000; Montagna et al., 2009; Elisei et al., 2013).

M. nomurae was never observed collecting water in either of the environmental periods, which indicates that temperatures had not risen sufficiently to require that resource for thermal regulation of the nests. Among successful foraging trips, the resources harvested with the greatest frequencies corresponded to items used to feed the colony (nectar and prey) and wood pulp to expand the nest. That same result was reported in post-emergence phase colonies of *Polistes simillimus* Zikán by Prezoto et al. (1994), of *Polistes ferreri* by Andrade and Prezoto (2001), and of *Polistes versicolor* Olivier by Elisei et al. (2010).

Studies with some species of wasps (Andrade & Prezoto, 2001 – *P. ferreri*; Prezoto et al., 1994 – *P. simillimus*; Rocha et al., 2009 – *P. exigua*) reported that the nectar was the most collected material, followed by prey and wood pulp. Therefore, as in the present study, nectar was the most consistently collected resource. According to earlier publications (Giannotti et al., 1995; Giannotti, 1999; Andrade & Prezoto, 2001; Rocha et al., 2009) that result can be explained by the fact that nectar serves as a food resource for larva as well as for adult individuals, and requires less energetic outlay than collecting live prey. The frequency of collecting wood pulp depends on the necessity of amplifying the numbers of cells in a nest (Silva et al., 2012).

The high percentage of prey resources captured by *M. nomurae* during the dry period was similar to that reported by Giannotti et al. (1995) for *P. lanio lanio*, with 61.4% of the foragers returning with nectar and 5.3% with prey during the hot, rainy season, and 39.6% returning with nectar and 10.7% with prey during the dry, cold season.

There was no significant influence of the season of the year on the mean duration of foraging flights by *M. nomurae*. In *M. cerberus*, however, the mean duration of foraging flights to collect different resources was greater during the cold season. Resources are often scarce during cold periods, so that foragers will tend to spend more time on those trips (Silva & Noda, 2000). The time spent by *M. nomurae* collecting nectar (83.60 min) was considerably greater than that observed in other species of the same genus, such as *M. cerberus* (22.6 min) (Giannotti, 1999) and *Mischocyttarus consimilis* Zikán (36 min) (Montagna et al., 2009).

Foraging individuals of *M. nomurae* spent the most time collecting nectar resources, followed by prey and wood pulp, as it was similarly observed with *M. consimilis* (Montagna et al., 2009), indicating that wasps encounter more difficulties searching for food resources. The fact that the mean duration of trips by *M. nomurae* for collecting wood pulp was shorter during the dry period than the rainy period can perhaps be explained by the fact that nest enlargement activity is lower during the dry period.

In terms of individual foraging, *M. nomurae* demonstrated behaviors different from *P. lanio lanio*, with 56.3% of the latter wasps collecting two types of resources while 43.7% collected only a single resource type (Giannotti et al., 1995).

Silva and Noda (2000) likewise reported that most of the foragers of *M. cerberus* collected two different types of resources. Giannotti et al. (1995) and Silva and Noda (2000) both observed that there was no individual specialization in *P. lanio lanio* or *M. cerberus*, as most foraging individuals collected two types of resources – which was different from the results of the present work, where most foraging individuals of *M. nomurae* collected only a single type of resource.

Although *M. nomurae* foragers collected all of the different resources, more than half of them collected only a single type. Of the 78 foragers of *M. nomurae* accompanied, 21.5% left the nest but returned without any resource at all. That value was different from data for *M. cerberus* (Silva & Noda, 2000), in which of the 30 foraging trips only 6.6% returned without any collected resource. The elevated percentage of nonproductive trips observed in *M. nomurae* nests may be related to the fact that those individuals were only just initiating their foraging activities and were still in a learning phase. According to O'Donnell and Jeanne (1992) in their studies of *P. occidentalis*, as the ages of the wasps increased so did their tendency to collect only a single type of resource, together with the increased success of those trips.

The largest percentages of foraging individuals of *M. nomurae* returning to their nests in both seasons studied were apparently unsuccessful. That result may be explained by the lack of resource availability. Furthermore, recently emerged individuals that leave the nest for foraging, however, may still be in their learning phase and, therefore, will not always be successful (O'Donnell & Jeanne, 1992). Detoni & Prezoto (2021) hypothesized that the youngest wasps, still in their learning phase, will only make short flights around the nest to memorize visual cues and landmarks in the environment; as they grow older and more experienced their foraging flights will be more successful, as it was observed by O'Donnell and Jeanne (1992) with *P. occidentalis*.

Final Considerations

The present study provided new information about the poorly studied wasp species *M. nomurae*. Its foraging activities were found to be influenced by temperature in both seasons, as well as by luminosity during the dry period. The presence of eggs in the nest was also found to significantly influence foraging activity. There were not observed collection patterns among the different colonies. The items were collected depending on the colonies necessities, resource availability, and the capacity of each individual to forage at any given time. It would therefore be interesting to examine the behavior ecology of that species and determine whether it demonstrates age polyethism.

Authors' Contributions

RSS: Conceptualization, methodology, investigation, formal analysis, resources, writing.

AAR: Conceptualization, methodology, supervision, resources, formal analysis, writing.

EG: Supervision, formal analysis, writing.

Acknowledgments

The authors thank Adriele França, Luisa Sodr e and Thatiana Andrade for their help in collecting the data. To Messrs. Juraci and Marcos for making their properties available for this work.

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