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RESEARCH ARTICLE - WASPS

Predatory and Population Characteristics of the Social Wasp *Agelaia centralis* (Cameron, 1907) (Hymenoptera, Vespidae) in a Crop Environment

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Abstract

Many insect species are known only by their scientific names, with scarce information about their biology, even when they are widely distributed and promising predators in crop environments. For predatory species such as social wasps, foraging rhythm, prey diversity, flight range, and colony size are cornerstones of characterizing their impact on the environment. Here, we studied these aspects for the widespread social wasp *Agelaia centralis* (Cameron, 1907), in a Colombian oil palm plantation. We recorded the foraging rhythm and the type of items brought to the nest. A preliminary flight distance was assessed. Colony sizes were calculated using Schumacher-Eschmeyer and Lincoln-Petersen estimators. The round flights ranged between 198 and 325 individuals/10 min, with a peak in the morning and another in the afternoon. The efficiency index for load items ranged between 18.2 and 19.7. Between 87% and 90% of the solid items carried to the nest were prey. These included Araneae, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Orthoptera, but most samples (>72%) were unidentifiable due to malaxation. Wasps released up to 400 m were recaptured from the nest. Estimated colony sizes ranged between 893.6 and 6122.4 individuals. Between 5% and 28% of individuals of a colony are foraging within a 10 min observation slot. The study sets basic information to calculate the impact of this social wasp as an arthropod predator in an agricultural environment.

Introduction

Social wasps are well-known generalist predators, although they may become facultative specialists according to prey abundance; colonies are composed of a few dozen to around a million adults (Zucchi et al., 1995), and they tolerate a large range of crop environments; thus, they have an interesting potential for a more environmentally friendly agriculture (Richter, 2000; Auad et al., 2010; De Souza et al., 2012; Somavilla et al., 2016; Sumner et al., 2018; Oliveira et al., 2022). However, a proper assessment of this service depends on the simultaneous documentation of key traits of their foraging behavior, such as rhythm, diet spectrum, hunting efficiency, flight range, and colony size. The lack of this information prevents us from having a better understanding of their ecological role. For example, knowing the number of active foragers and the colony size facilitates estimating the proportion of adults in the entire colony that are foraging; similarly, knowing the flight range and the number of active foragers allows estimating the hunting pressure a colony exerts on a given area.

Agelaia Lepeletier, 1836 is a common genus of social wasps distributed from Mexico to Argentina and contains 33 species (Cooper, 2000; Auad et al., 2010; Somavilla et al., 2016; Barbosa et al., 2018; Tomazella et al., 2018; Andena et al., 2024), fifteen of which are present in Colombia

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(Sarmiento, 1994). They are swarm-founding wasps, and their nests are generally built within preexisting cavities (Silveira & Carpenter, 1995). Machado et al. (1987) reported that *A. pallipes* predates on Lepidoptera, Hymenoptera, Hemiptera, Coleoptera, Diptera, Orthoptera, Araneae, and Acari. The species are also known for collecting carrion (O'Donnell, 1995; Sarmiento, 2004; Silveira et al., 2005; Moretti et al., 2008). Characterizing their foraging behavior is challenging, due to the size of their colonies, the usual location of their nests, and their strong defensiveness (Schaefer et al., 2025).

Agelaia centralis (Cameron, 1907) is a species reported from Mexico to southern Brazil, and is abundant in the lowlands (Richards, 1978; Graca & Somavilla, 2019). Here we provide data about foraging rhythm, diet spectrum, hunting efficiency, flight maximum distance, and colony size of *A. centralis*. This information is important to understand the ecology of this species and its role in agricultural landscapes.

Materials and Methods

We studied four colonies of *A. centralis.* The species was identified using the keys of Cooper (2000) and Andena et al. (2024). The especies was found within an oil palm (*Elaeis guineensis*) plantation of about 5000 ha. at La Gloria, Cesar department, Colombia (8°38'36,63" N, 73°40' 39,76" W, 57 mosl, 27 °C mean temperature, and 1800 mm mean rainfall, Instituto de Hidrología, Meteorología & Estudios Ambientales [IDEAM], 2023). The oil palms were 14 years old and averaged 10 m tall; they were planted at 9 m by row and 11 m by column. The crop ground was covered by a combination of planted kudzu (*Pueraria montana*) and spontaneous vegetation. Pest management is achieved using baits, parasitoids, and entomopathogens, with pesticides as a last resort. The fieldwork was conducted during three field trips, each lasting nine days: two during the wet season (August and October of 2023) and one during the dry season (January 2024). A survey of the plantation reported 14 species of social wasps; of these, *A. centralis* and *Polistes infuscatus* Richards, 1978 exhibit large abundance, while other wasp species were rarely collected. Several arthropods are subject to control, including the caterpillars of Brassolidae: *Opsiphanes cassina* Felder, 1862, and *O. invirae* (Hubner, 1808) (Aldana et al., 2010). Sampling protocols were developed on sunny or lightly cloudy days; in all cases, the temperature ranged between 24 and 29 °C.

We invested 384 hours exploring for nests of *A. centralis* colonies. Searching was conducted in the crop and within a 260-ha reserve composed of 15 years of spontaneous vegetation mixed with reforestation efforts (Hacienda La Gloria, 2023) (Fig 1). Colonies were georeferenced using GPS Status & Toolbox (MobiWIA: http://mobiwia.com/gpsstatus/) and mapped with QGIS Version 3.28 (Quantum GIS Development Team, 2014).

Based on their accessibility, we selected four of the eleven colonies to perform experiments on foraging rhythm, prey richness, and colony size (Fig 1). A preliminary estimation

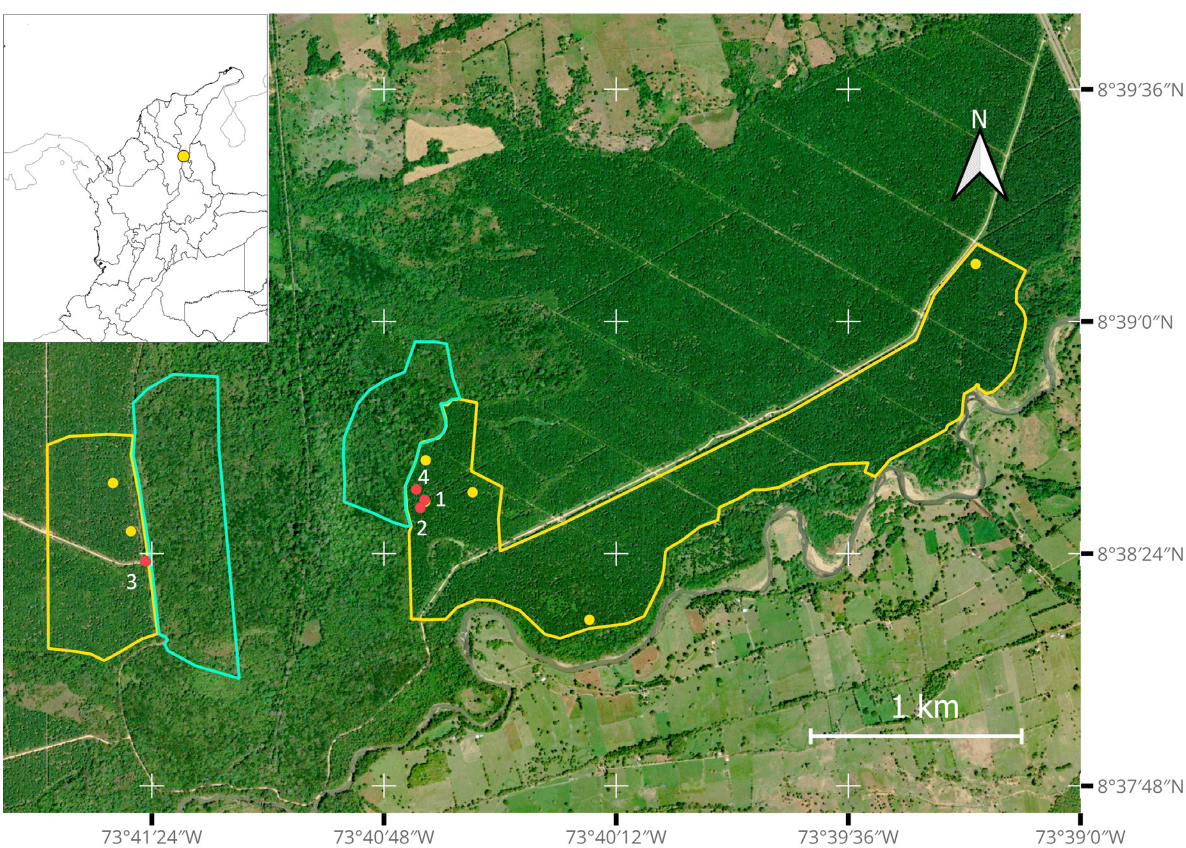

Fig 1. Distribution of *Agelaia centralis* colonies in the oil palm plantation. Colonies used for the experiments are numbered and indicated by red dots; other colonies are shown as yellow dots. The areas studied of the reserve are delineated in green. The crop areas studied are outlined in yellow (Made with QGIS Version 3.28; Layer: ESRI World Imagery database).

of maximum flying distance was conducted for colonies 3 and 4. Colony 1 was studied in July 2023, colony 2 in October 2023, and colonies 3 and 4 in January 2024. A total of 132 h invested by three people were spent recording this information.

Foraging rhythm

Our observation periods were defined based on the logistical and security conditions in the area. We recorded the number of departing and returning foragers from colonies 1, 2, and 4, and registered the number of foragers that returned with loads from colonies 2 and 4. Foragers carrying a load were identified by their slower flight or by the presence of solid material held between their mandibles (Prezoto et al., 1994, 2006; Jeanne & Taylor, 2021). In all colonies, observation intervals lasted 10 min. For colony 1, these occurred every 30 min, between 10:00 and 15:30 (10 intervals). For colonies 2 and 4, observations occurred every 15 min; these spanned 9:00 to 14:30 (22 intervals) and 8:15 to 15:45 (31 intervals), respectively. These intervals are within the spectrum used by previous authors (Elisei et al., 2005; Brügger et al., 2019). For colonies 2 and 4, we estimated the efficiency index (Ei) for any solid item brought to the nest, following Giannotti et al. (1995): Ei = (N° wasps arriving with load/N° wasps arriving) * *100*.

To study the proportion of foragers relative to colony size, we calculated the mean number of round flights across colonies 1, 2, and 4. Round flight values were estimated as the average of departures and returns in a time slot; to estimate the percentage of workforce foraging, these values were divided by the estimated number of adults in a colony. To standardize the observation slots, time frames were set to 30-minute intervals. For colonies 2 and 4, we use the average data of the two consecutive 15-minute slots. We match the peaks of each colony because they occur at different times.

Prey richness

We recorded the richness of prey items captured by colonies 1 and 2 of *A. centralis*. Returning foragers carrying a load were captured with a net at 10 min intervals between 09:00 and 12:00 and between 13:00 and 16:00. Solid items collected were preserved in 96% ethanol. These were classified as either nest material construction or prey. Prey were identified to the lowest taxonomic level possible using appropriate keys (Stehr, 1991; Borror et al., 1989; Triplehorn & Johnson, 2005).

Colony size and flying distance

To estimate colony size, we used two estimators: the Capture-Mark-Recapture population size estimator of Schumacher-Eschmeyer for colonies 1 and 2, and Lincoln-Petersen´s for colonies 3 and 4 (Seber, 1982; Krebs, 1999). These estimators assume that the population is closed and that all individuals have an equal probability of capture, but are also robust to violations of these assumptions (Seber, 1982; Krebs, 1999). To conduct the estimation for the Schumacher-Eschmeyer, we determined the following variables for each defined time slot (t): total number of individuals caught in sample t (C_t), number of individuals marked for the first time when caught in sample t (U_t), and number of individuals already marked when caught in sample t (R_t). We gathered these variables divided by defined time slots (t) as follows: for colony 1, we used four time slots (8:00 - 12:00); for colony 2, we used seven time slots (8:00 - 12:00 and 13:00 - 16:30). The Lincoln-Petersen estimator uses a single mark and a single recapture event. Thus, we used the total number of individuals marked the first time (M), the total number of individuals captured in the second sample (C), and the total number of individuals in the second sample that are marked (R).

Fig 2. Views of a colony of *Agelaia centralis*. The nest's entrance is where several individuals marked with a blue dot on their mesoscutum can be seen. Inset: General location of a nest (circle) in a dead palm trunk of the plantation.

Flying wasps were captured with a net at or directly departing from the nest entrance and were immediately marked with a color dot on their mesoscutum, then released (Fig 2). As wasps were marked and recaptured on the same day or at most the following day, the population of the colonies was considered closed, without migration or changes in abundance, and we assume a similar probability of mark-recapture for the foragers. The estimator was calculated using the Ecological Methodology software (Krebs, 1999). We are aware that this approach may underestimate the actual population size for the colonies as we sampled only foragers, which can be a segment of the population given age polyethism in swarm founding wasps (Jeanne, 1991a); however, as described above, colonies were located at the base of 10-14m tall oil palms, which difficulties the study of the entire nest.

To obtain a preliminary assessment of the wasp's flying distance, we captured and marked 57 (colony 3) and 94 (colony 4) wasps flying close to their nest entrances, marking the mesoscutum with a specific color. Until release, wasps were stored individually in plastic containers containing a piece of absorbent paper soaked in sugared water. Release distances of 350 m and 400 m were selected based on crop limits. Further distances involved areas with drastic environmental changes, such as grasslands or second-growth vegetation. Two linear transects per colony were established for the release of wasps, separated by angles of 62° and 90°. Upon reaching the designated distances, we opened the containers and released the wasps. The following day, between 08:00 h and 13:00 h, we captured foragers flying by the nest entrance and recorded the number of marked individuals.

Results

Eleven colonies were found distributed in similar numbers on each field trip. Plantation sectors adjacent to the reserve recorded more colonies than areas near the plantation border (Fig 1). Nests were found at the base of both alive and dead palms. Some of these were covered with kudzu (Fig 2).

Foraging rhythm

The average number of round flights per 10-minute slots of observation was as follows: 198 (SD = 35.6) for colony 1, 294 (SD = 52.5) for colony 2, and 325 (± 83.3) for colony 4, totaling between 1,956 and 10,088 round flights in a day. Foraging activity shows two subtle peaks and a single valley, but the exact times of these peaks differ between colonies (Fig 3). This period of reduced foraging appears to coincide with the higher daytime temperatures, which are recorded between 13:00 and 15:00 (Fig 3d). The estimated proportion of foragers per colony ranges from 3.4% in colony 4 to 28% in colony 1 (Table S1). The daily average efficiency indexes were 18.2% for colony 2 and 19.7% for colony 4, with no clear trend along the day; for example, in colony 2, it ranged between 13% and 28%, and for colony 4, it ranged between 6% and 53% (Table S2).

Prey richness

Prey accounted for 90% and 86.8% of the total number of items brought to the nests in colonies 1 and 2, respectively (Table 1). Only 35% and 28.9% of prey items per colony were identifiable, as most of the samples were highly malaxated,

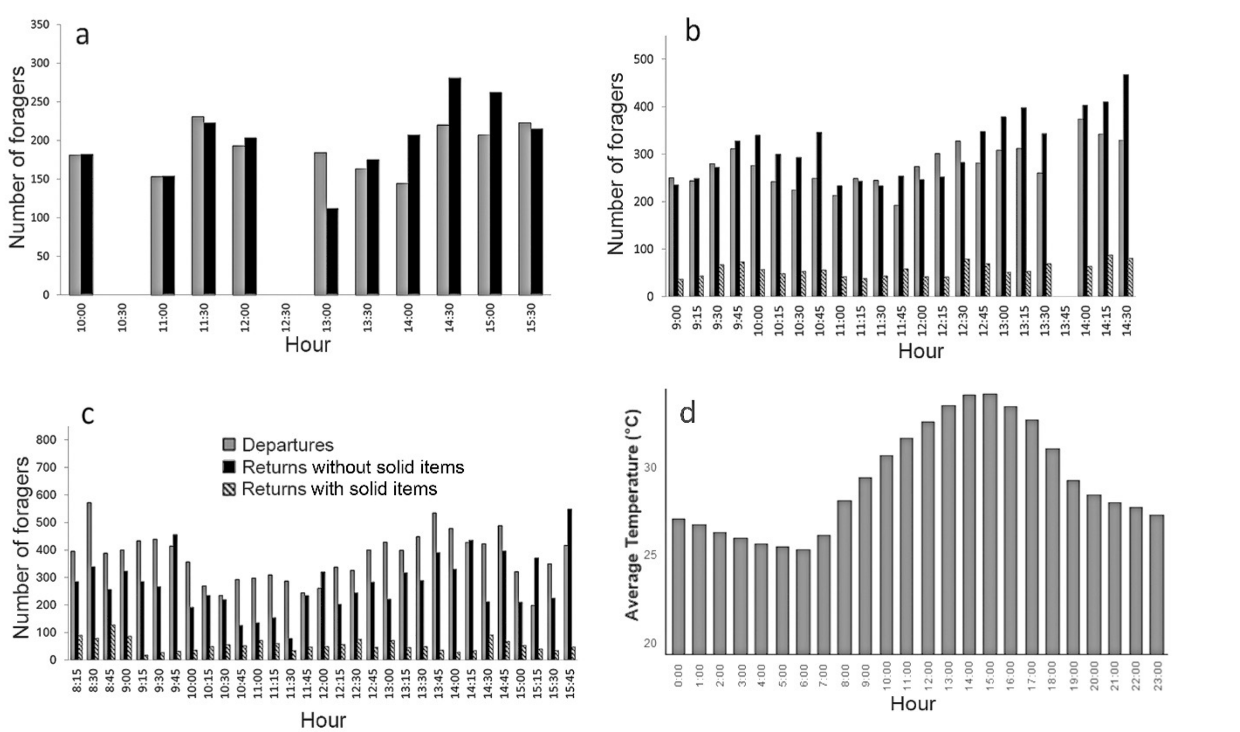

Fig 3. Foraging activity of three colonies of *A. centralis* in an oil palm plantation and average daily temperature in the area. Colony 1 (a), colony 2 (b), colony 4 (c); for colonies 2 and 4, we distinguished the number of individuals returning with loads from those without solid items. (d) average temperature by hour for the area (Source: plantation weather station data. Dates range: 1 Apr 23 - 9 Sep 23).

hampering the finding recognizable structures. Prey included the orders Araneae, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Orthoptera. In addition to larvae, adults of Lepidoptera and Diptera were recorded as prey. Construction material was uncommon in the captures (Table 1).

Table 1. Distribution of solid items captured from two colonies of *A. centralis* in an oil palm plantation. [b] Adults were recorded as prey in these cases.

	Colony 1		Colony 2	
	N	%	n	%
Construction material	2	10	5	13.2
Prey items				
Araneae	-	-	1	2.6
Diptera	1[b]	5	-	-
Hemiptera	1	5	1	2.6
Hymenoptera	-	-	1	2.6
Lepidoptera	2	10	2[b]	5.3
Orthoptera	1	5	1	2.6
Unidentified	13	65	27	71,1
Total prey items	18	90	33	86.8
Total solid items	20	100	38	100

Colony size and flying distance

A total of 155 individuals for colony 1, 667 for colony 2, 264 for colony 3, and 375 for colony 4 were marked for the colony size estimations. The Schumacher-Eschmeyer estimator suggested that colony sizes were 834.9 (± 395.8) individuals for colony 1 and 1049.7 (± 147.5) individuals for colony 2; the Lincoln-Petersen estimator suggested that colony sizes were 3118.8 (± 917.3) individuals for colony 3 and 6122.4 (± 2412.4) individuals for colony 4 (Table 2).

Between 8.9% (7 individuals of colony 4) and 16.4 % (11 individuals of colony 3) of the marked foragers returned to the nest from release distance for each colony (350-400 m).

Discussion

A. centralis is a common predatory wasp in the oil palm plantation, with most colonies close to the reserve area, suggesting affinity of this habitat for some resources, as has been reported for other epiponines (Medeiros et al., 2019a, 2019b). The foraging frequency distribution shows a valley between 11:00 and 13:30, with higher values, especially in the afternoons, although the exact hour of occurrence varies among colonies. This result concurs with studies in other species (Lima & Prezoto, 2003; Elisei et al., 2005; Da Rocha & Giannotti, 2007; Detoni et al., 2015; Brito et al., 2020). Foraging for solid items remains constant throughout the day, and a larger portion of the worker force is recorded in the afternoon, which may suggest that they are gathering liquids. These distributions of total flight frequency along the day can be a response to the higher temperatures at this time as it has been postulated in other species (Brito et al., 2020).

Table 2. Colony size calculation is based on the Schumacher-Eschmeyer estimator for colonies 1 and 2 and Lincoln-Petersen estimator for colonies 3 and 4 of *A. centralis* in the oil palm plantation. Numbers given for the sampling time slots (t) of the Schumacher-Eschmeyer estimator refer to: the total number of captured forager wasps (C_t), marked (U_t), and recaptured foragers (R_t). Numbers given for the Lincoln-Petersen estimator refer to: the total number of individuals marked the first time (M), total number of individuals captured in the second sample (C), and total number of individuals in the second sample that are marked (R). For details, see the methods section.

Sampling event*	Colony 1			Colony 2			Colony 3			Colony 4		
	Total Captured C_t	Total Marked U_t	Total Recaptured R_t	Total Captured C_t	Total Marked U_t	Total Recaptured R_t	Total marked 1st time (M)	Total captured (C)	Total marked 2nd time (R)	Total marked 1st time (M)	Total captured (C)	Total marked 2nd time (R)
1	14	14	0	120	120	0						
2	27	26	1	65	53	12						
3	53	51	2	126	90	36						
4	72	64	8	96	80	16						
5	-	-	-	250	198	52						
6	-	-	-	212	126	86						
7	-	-	-	113	113	0						
Total	166	155	**11**	982	667	**315**	264	517	**43**	375	455	**27**
Abundance estimators	Schumacher-Eschmeyer´s estimation	95% CI		Schumacher-Eschmeyer´s estimation	95% CI		Lincoln-Petersen´s estimation	95% CI		Lincoln-Petersen´s estimation	95% CI	
	893.6	1772.2	597.4	**2141.7**	3514.8	1540.1	**3118.8**	2366.1	4200.7	**6122.4**	4377.3	9202.2

Between 87% and 90% of the solid items brought by *A. centralis* wasps were prey, while 10-13% were nest-construction material. These values are highly skewed toward prey, compared with the average of similar data from other social wasps (62.8% prey and 37.2% nest-construction materials) (Prezoto et al., 1994; Giannotti et al., 1995; López et al., 2013; Brügger et al., 2019). On the other hand, our report agrees on the spectrum of arthropods being predated by social wasps, with Lepidoptera as the most frequent prey, although the proportion of unidentified prey in our study was high due to the thorough chewing performed by the wasps (72%-82%); it is worth mentioning that this percentage is high compared to that in other species (0%-51%) (Gobbi & Machado, 1985; Machado et al., 1987; Prezoto et al., 2006; Bichara-Filho et al., 2009; Hernández et al., 2009; López et al., 2013; Brügger et al., 2019; Southon et al., 2019); we refrain from postulating any explanation in this regard as more data are required to identify whether values are consistent along different sampling events.

Considering the estimated colony size and the number of foragers at single 10-minutes slots, we calculated that, between every third and every twentieth of the individuals of the colony are out foraging; such variation could be a consequence of the environmental conditions or of the different developmental stages of the colonies (Lima & Prezoto, 2003; Elisei et al., 2005; Da Rocha & Giannotti, 2007). Again, we note that our values may underestimate actual colony sizes, as foragers were the subjects of mark-recapture. Given their location in hollow cavities at the base of dead or alive 10-14m tall palm trunks, we could not establish the colonies' developmental stage. As far as we know, there are no studies that simultaneously document foraging rhythm and colony size in a social wasp nest; thus, our results are the first of this type to be published.

The 18% and 19% efficiency indices estimated for the two colonies of A. centralis are the lowest recorded for a Neotropical social wasp species. For example, for *Protopolybia exigua,* Da Rocha and Giannotti (2007) reported 93.5% studying 12 colonies; for *Polybia emaciata,* López et al. (2013) reported 28.9% studying 12 colonies; and for *Polybia fastidiosuscula* Brügger et al. (2019) reported 63.2% studying one colony. These results for *A. centralis,* together with the proximity of their nests to the reserve, suggest that the efficiency values may reflect low prey availability in the crop, although only comparative studies can support this idea.

We recaptured very few individuals of *A. centralis* released from 350 m and 400 m away from the nests, and our preliminary data do not constitute a formal estimate of flying range; however, they do provide a hint at the species' flying capacities. This distance is similar to *that of Agelaia multipicta,* for which 500 m was recorded (Sarmiento, 1993). A formal estimation of flight range for *A. centralis* requires further studies.

The colony size estimates ranged from 834.9 to 6122.4 individuals across the four colonies of *A. centralis*. Our records add this species to the studies for the genus *Agelaia* where reported colony sizes ranged from 300 individuals for *A. lobipleura* (Jeanne, 1991b), up to around a million individuals for *A. vicina* (Zucchi et al., 1995). As we described in the methods, our values may underestimate the actual colony size because foragers were the target of the marking process, and younger members of the colony, who regularly stay inside, may not be sampled. Future studies that extract entire colonies from their nesting cavities and use methods that prevent individuals from escaping can provide more accurate values.

Despite this, social wasps are important predators; they have been neglected in biological control initiatives, and the lack of specific information on their predatory impact may help explain this problem (Sumner et al., 2018). Averaging the total return flights and the percentage of these that are prey, from the two colonies of *A. centralis* studied, they capture 1324 prey in a day. If we use 400 m as the maximum flight range, we can estimate that they cover 502,656 m2 and hunt about one prey item every 379 m2 each day. These estimates should be taken with caution, as we did not formally establish the flying range; 400m may underestimate the actual flying range, and, if so, the number of prey items hunted per area could be lower. Based on the data provided by other studies, we calculated that colonies of *Polybia occidentalis* (Hernández et al., 2009), *P. sericea* (Bichara-Filho et al., 2009), and *Polybia emaciata* (López et al., 2013) may hunt one prey every 100 m^2, 140 $m^{2,}$ and 250 $m^{2,}$ respectively. Of course, these calculations rely on a series of assumptions, such as uniform distribution of foragers along the flight range and uniform foraging demands. However, this is an essential step to quantify the impact of *A. centralis* in an agricultural context, such as oil palm, and to support its role as a biological control agent. If the species is removed from the area due to a lack of appropriate strategies to coexist with the colonies, the farming should bear the cost of the control measures freely exerted by the wasps.

The only information available for an exceedingly large number of species is the scientific name and taxonomic description (Brito, 2010), while basic biological studies, such as the one provided here, are scarce, despite being critical to better understanding biodiversity. Although numerous papers have independently gathered information on foraging rhythm, flight range, prey richness, and colony size for species of neotropical social wasps, this is perhaps the first case in which these four parameters are documented simultaneously, allowing a better understanding of the impact of this species on the environment. In addition, this is the first record of foraging rhythm and flight range for a species of the genus.

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Authors' Contribution

H.P-M.: conceptualization, methodology, formal analysis, investigation, data curation, writing-original draft preparation, writing-review and editing, visualization.
S.M.C-M.: methodology, investigation.
T.D.A-R.: methodology, investigation.
D.S.F-L.: methodology, investigation.
V.G-B.: methodology, investigation.
A.A.G.-G.: investigation.
J.C.: methodology.
C.E.S.: conceptualization, methodology, formal analysis, investigation, resources, writing-original draft preparation, writing-review and editing, visualization, supervision, project administration, funding acquisition.

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Table S1. Percentage of foragers per 30-minute observation time slots before the estimated colony size.

Table S2. Records of the number of departing and recaptured individuals per nest were recorded in 10 min observation intervals every 15 min.