Sociobiology 72(3): e11415 (September, 2025)

DOI: 10.13102/sociobiology.v72i3.11415

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - BEES

Centridini Bees as Manageable Pollinators of West Indian Cherry (*Malpighia emarginata*, Malpighiaceae) Orchards in Southeast Brazil

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Article History

Edited by
Kleber Del-Claro, UFU, Brazil

Received	06 November 2024
Initial acceptance	11 December 2024
Final acceptance	18 June 2025
Publication date	31 July 2025

Keywords
Agriculture, Pollination, *Centris*, Solitary bees, Nest substrate availability.

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Abstract

The West Indian cherry (*Malpighia emarginata*), commonly referred to as “Acerola”, has attracted particular interest due to its high vitamin C content in the fruit. One of the limitations observed in Acerola crops is their dependence on cross-pollination, which is usually performed by *Centris* species. This study investigated the occupation of trap-nests in an Acerola orchard by bees of the genus *Centris* to identify species that could be indicated as providers of pollination services in these orchards. *Centris analis* and *Centris tarsata,* the species occupying the traps, displayed a seasonal pattern in their nesting activities, with the highest frequencies aligning with the peaks of the crop’s flowering. Both bees explored 48 plant species, with *M. emarginata* being the most important pollen source and floral oil, primarily for *C. analis*. The high preference observed in the diet of *C. analis* and the seasonal pattern in the nesting activity of *C. tarsata* indicate that both species are effective pollinators of *M. emarginata* crops.

Introduction

The rapid increase in the human population in recent years, along with threats to food production primarily due to environmental changes and global warming, has stimulated the search for solutions that integrate the demand for food production with environmental conservation. The active management of pollination services in agriculture is considered a potential solution (Giannini et al., 2015a; Lautenbach, 2019).

The global value of pollination services was estimated to be between $235 billion and $577 billion in 2015 (IPBES, 2016). In Brazil, this ecological service, valued at approximately US$ 12 billion per year, is associated with crops that are crucial to national agriculture, such as coffee (*Coffea arabica* L.), oranges (*Citrus sinensis* (L.) Osbeck), and soybeans (*Glycine max* (L.) Merr.). More than 90 species of cultivated and wild food-related plants in Brazil depend, to some degree, on pollinators. (BPBES/REBIPP, 2019). The country must promote technologies and methods that enhance pollination services, especially as agribusiness activities are vital to the Brazilian economy.

Bees are recognized as major contributors to biodiversity, pollination, and maintenance services, as they facilitate cross-pollination for most flowering plant species, aid in genetic variability, and enhance fruit yield and seed viability (Giannini et al., 2015a; Roubik et al., 2018). Although crop pollination services are primarily conducted by the managed honeybee (*Apis mellifera* L.), due to the extensive understanding of its biology and management (Carreck & Williams, 1998), it is not the most effective pollinator for all plant types (Free, 1993; Cane, 1997). This fact raises questions about its efficiency for specific crops (Garibaldi et al., 2013). For instance, honeybees cannot buzz-pollinate (Buchmann, 1983), which limits their effectiveness

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

in pollinating crops that require this method, such as tomatoes, eggplants, melons, kiwis, cranberries, and blueberries. In these cases, bumblebees and stingless bees are often more effective pollinators because they can buzz-pollinate, significantly enhancing the pollination of many crops (Velthuis & van Doorn, 2006, and references).

Another notable example is the pollination of alfalfa (*Medicago sativa* L.), where flowers require visits from bees to transport the sexual column, ultimately leading to successful pod and seed development. Among the various species that visit alfalfa, the solitary bee *Megachile rotundata* (Megachilidae) is particularly effective, tripping 80% of its flowers (Cane, 2002). In contrast, honeybees are ineffective pollinators for alfalfa due to their side-feeding habits, which focus solely on nectar foraging, thus reducing their opportunity to trip the flowers (Howlett & Donovan, 2010). As a result of these shortcomings in honeybees, studies have been undertaken to select one or more species among those already known and well-adapted to pollinate specific crops, making them suitable pollinators for commercially managed crops. Today, other bee species, including social and solitary ones, are commercially produced in several countries alongside honeybees to provide pollination services. Among the social species are bumblebees (*Bombus* spp.: Apidae) and stingless bees (Meliponini: Apidae). Among the solitary species are mason bees *(Osmia* spp.: Megachilidae) and alfalfa leafcutter bees (*M. rotundata*; Megachilidae).

Despite the abundant diversity of native bee species in Brazil (Ascher & Pickering, 2020), the use of commercially managed species for agricultural pollination is virtually nonexistent, although effective pollinators have already been identified for many crops (Giannini et al., 2015b, 2020). Among Brazil's significant crops, the West Indian cherry (*Malpighia emarginata* DC; Malpighiaceae), commonly known as "Acerola", has attracted particular interest due to its high vitamin C (ascorbic acid) content. This characteristic makes the fruit widely utilized in human food and pharmaceutical manufacturing, serving the processed pulp market (Carpentieri-Pípolo et al., 2008). Brazil is the world's largest producer, consumer, and exporter of Acerola, with the Northeast being the primary region for its cultivation, particularly in Pernambuco and Ceará (IBGE, 2017).

Freitas et al. (1999) investigated the flower morphology, pollination biology, and potential pollinators of *M. emarginata* in Fortaleza, Ceará, Brazil. Among the results, the authors reported a dependence on cross-pollination facilitated by bees, with *Centris tarsata* Smith identified for the first time as a visitor to Acerola flowers. Furthermore, the authors noted that a limitation in Acerola cultivation is the high rate of abnormal ovule development, which may explain the low productivity observed in some cultivars despite satisfactory pollination. Additionally, low fruit set rates due to self-pollination have been observed in this crop (Schilindwein et al., 2006; Guedes et al., 2011; Siqueira et al., 2011), along with reduced reproductive success in certain regions during the dry season, which is attributed to a lack of pollinators (Guedes et al., 2011).

Of the 29 bee species reported as pollinators of Acerola, three are social species from the Meliponini tribe, while the other 26 are solitary and belong to the Centridini tribe. Among these solitary bees, seven are from the *Epicharis* Klug genus, and 19 belong to the *Centris* Fabricius genus (Giannini et al., 2015b, 2020, and references therein). In the interspecific mutualistic association between plant species of the Malpighiaceae family and *Centris* bees, these bees collect and utilize the floral oil produced by the plants to build their nests and feed their larvae. While gathering the floral oil, the bees also pollinate the plants (Vogel, 1974; Buchmann, 1987; Vieira-de-Jesus & Garófalo, 2000; Aguiar & Garófalo, 2004; Martins et al., 2024, and references therein).

Centris vittata Lepeletier, *Centris trigonoides* (Lepeletier), *Centris analis* (Fabricius), and *C. tarsata* are recognized as effective pollinators of Acerola (Giannini et al., 2015b). These species nest in pre-existing cavities (Pereira et al., 1999; Aguiar et al., 2006; Vieira-de-Jesus & Garófalo, 2000; Aguiar & Garófalo, 2004), whereas the others are ground-nesting bees. Among these four species, *C. analis* is the most biologically well-known, as it has frequently occupied trap-nests in studies on communities across various environments (Moure-Oliveira et al., 2017; Silva et al., 2017, and references therein). It has also been frequently sampled in large numbers in studies of Acerola pollination. These biological traits prompted Oliveira and Schlindwein (2009) and Magalhães and Freitas (2013) to research the potential of *C. analis* as a pollination service provider in Acerola orchards. By assessing the occupancy of trap-nests by female *C. analis* in these orchards, the duration of females' reproductive activity, and the larval diet, Oliveira and Schlindwein (2009) indicated this species as a manageable pollinator for Acerola in northeastern Brazil. They proposed the commercial use of *Centris* bees as pollinators for orchards. Magalhães and Freitas (2013) reported that introducing nests of *C. analis* in Acerola orchards in Ceará, Brazil, increased yield. They noted that the introduction of nests facilitated the population growth of the bees and reduced pollination deficits in those orchards. Therefore, it is recommended that artificial cavities be provided for nesting within the orchards to enhance pollinator populations and improve pollination services (Cane, 1997; Magalhães & Freitas, 2013).

In this study, we investigated the occupation of trap-nests in an Acerola orchard by bees of the genus *Centris* to identify species that may be suitable candidates for commercial management as pollination service providers in these orchards. To achieve this goal, we evaluated: 1. The occupancy of trap-nests by *Centris* species in the *M. emarginata* orchard in Indaiatuba, SP. Since *C. analis* and *C. tarsata* rapidly occupy trap- nests in both natural and agricultural settings and effectively pollinate *M. emarginata* (Freitas et al., 1999;

Oliveira & Schlindwein, 2009), combined with the fact that Indaiatuba, SP, is within their geographic range, we expected that these species, along with others, might nest in the traps set up in the studied orchard. 2. The flowering period of *M. emarginata* and the nesting period of *Centris* spp. that utilize the trap-nests in the orchard. A mismatch between the timing of crop flowering and pollinator activity can hinder pollen transfer, adversely affecting the yield of crops reliant on pollinators; thus, synchrony between pollinators and crop flowering is essential for effective pollination services (Sritongchuay et al., 2021). 3. Female *Centris* spp. occupying trap-nests in the orchard in Indaiatuba, SP, prefer foraging on the flowers of the target crop, *M. emarginata.* A pollinator species may easily visit the target crop when faced with limited options, such as cage or greenhouse trials. However, it may also be attracted to other plants in open-field situations, such as orchards. Analyzing pollen from cellular provisions or fecal samples produced by immature individuals from populations nesting in orchards will enable the identification of the pollen and nectar sources utilized by the pollinating species. Quantifying each source in the composition of the analyzed samples will determine whether a fidelity pollinator-target crop relationship exists. The information obtained also guides strategies for habitat management that aim to improve pollination services in Acerola orchards while supporting broader biodiversity conservation goals.

Materials and Methods

Study area and flowering period of Malpighia emarginata

This study was conducted in an organic Acerola orchard with 1400 trees occupying 3.0 ha of a total of 6.3 ha in Sítio Granja Bela Vista, Indaiatuba, São Paulo, Brazil (23°02'49" S/ 47°13'17" W). The altitudes of the region range from 624 to 879 m, and the climate, according to Köppen (1948), is classified as Cwa, characterized by a rainy season from October to March and a dry season from April to September. The Sitio was located in an area undergoing rapid urbanization. The landscape consisted of private properties grouped into housing estates that were isolated from each other by ecological corridors. Along these corridors were remnants of varying sizes featuring native vegetation characteristic of seasonal semi-deciduous forest (Fig 1).

During the study period, the monthly average temperatures ranged from 21 to 26 °C, with the monthly precipitation ranging from approximately 100 to 300 mm during the rainy seasons. In the dry seasons, average monthly temperatures ranged from 16 to 18 °C, and monthly precipitation did not exceed 10 mm (CIIAGRO, 2015). In the Indaiatuba region, *M. emarginata* primarily blooms during the rainiest and hottest periods. The first flowering peak of *M. emarginata* at Sítio Granja Bela Vista occurred from September 2010 to February 2011, and the second from September 2011 to April 2012. In other months, only a few open flowers were observed in the orchard.

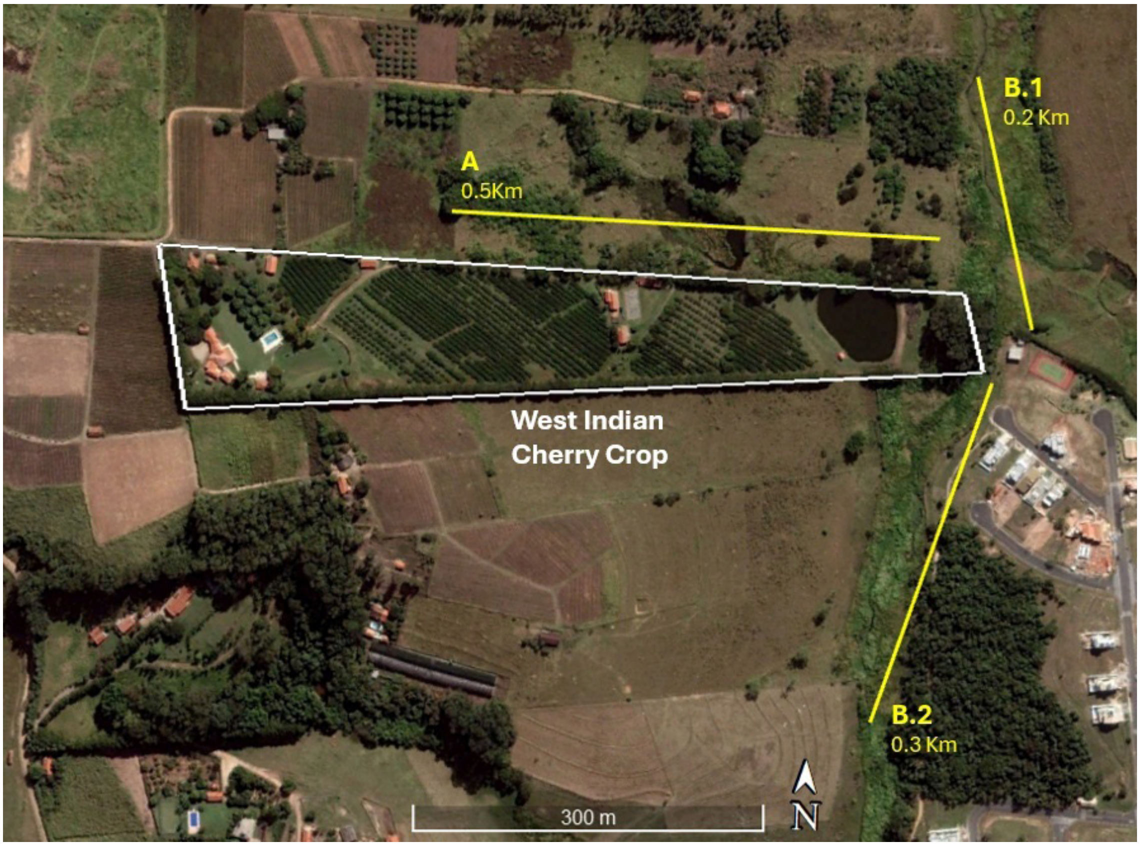

Fig 1. Area occupied by Sítio Granja Bela Vista in Indaiatuba, SP, and indications of transects A and B (B1+B2), which were traveled monthly to sample flowering plant species.

Trap-nests and sampling stations

As described by Camillo et al. (1995), the trap-nests (TN) used in this study consisted of bamboo canes (*Bambusa vulgaris* Schrad. ex J.C. Wendl., Poaceae), cut so that a nodal septum closed one end of the cane. The bamboo canes varied in length and internal diameter, although not all sizes were equally represented. This variation in the dimensions of bamboo canes aims to attract bees of different sizes and species to nest in those cavities. The other type of TN consisted of tubes made from black cardboard, with one end closed using the same material. These tubes, measuring 6.0 cm in length and 0.6 cm in internal diameter, were inserted into horizontal holes drilled into wooden plates measuring 30 x 11 x 4.5 cm. Thirty-two tubes were inserted into the holes distributed in five rows on each wooden plate. The bamboo canes were arranged in bundles of 20 units and inserted into PVC tubes 40 cm in length. The TN sets were placed on iron supports fixed to the soil and covered with plastic tiles (called the "sampling station"). Six sampling stations, each equipped with two wooden plates and three PVC tubes, were installed at the orchard's edge, where bees were observed more frequently than in the center (Garofalo, pers. observation). The distance between the stations ranged from 100 to 150 m.

The study area was visited monthly from September 2010 to August 2012. During these visits, observations were made on the foraging of the females occupying the traps. At this moment, the species was identified, the cardboard TN was marked, and it was left in its original place until the adults developed, emerged, and were replaced with an empty TN. In completed nests where no foraging activity had been observed, an oil plug in the TN entrance indicated that it was a *Centris* nest. Since the cardboard TN had a diameter preferred by females of *C. analis* for nesting (Vieira-de-Jesus & Garófalo, 2000; Vinson et al., 2010), and only females of this species were observed occupying those traps, the nests were assumed to belong to *C. analis*. The bamboo canes containing completed nests of *Centris*, characterized by an oil plug, were collected and immediately replaced with empty canes. These bamboo canes were placed in transparent plastic tubes 4.0 to 5.0 cm longer than the traps, with one end closed with a cork. Afterward, they were arranged on two shelves in a shelter near the orchard and left undisturbed until the adults emerged. Daily observations were conducted, and when an adult emerged into the plastic tube, the cork was removed, the individual was collected, identified, sexed, and then released.

Identification of floral resources and pollen analysis

The floral resources used by female *Centris t*o provision the brood cells were identified from nests sampled monthly during the species' nesting period. Based on the number of available nests, at least one and no more than ten were collected each month from each species. After the produced individuals emerged from the nests, residual pollen samples were collected from the brood cells. Each sample consisted of the total residues of pollinic material found in the nest. The analyzed residual pollen originated from the larvae's excretion and the remaining pollen provision. Pollen samples were collected using small spatulas and placed into small vials containing 70% ethanol for at least 24 hours. They were then submitted to the acetolysis process as described by Erdtman (1960). Small amounts of acetolyzed pollen were removed from the tubes using tiny cubes of glycerin-gelatin and placed on microscope slides. Two slides were prepared for each nest. Pollen grains were observed, counted, and photographed using a light microscope (DM4000B, Leica, Wetzlar, Germany). The quantitative analysis involved randomly counting 200 pollen grains from each slide prepared per nest (Montero & Tormo, 1990), resulting in 400 pollen grains for each sampled nest.

The floral origin of the residual pollen from the analyzed nests was identified using reference material collected from native and exotic plant species in the study area and its surroundings. For this purpose, the area of Sítio was traveled monthly from April 2011 to September 2012, and plants with open flowers were sampled for identification. These plants' branches, leaves, flowers, and fruits were also collected. Exsiccates were prepared using sampled plants. Flower buds of these sampled species were held in 70% ethanol for pollen analysis (Silva et al., 2014). In addition, two transects of 500m long, each 5m wide on both sides, were also traveled monthly, and the plants with open flowers were collected. The smaller transect (A) was established on private property adjacent to the Sitio, and the largest (B, formed by B.1+B.2) was set up in the ecological corridor at the back of the properties (Fig 1). The species were identified using the reference material collected. Material from the Herbarium of the Department of Biology at FFCLRP-USP, along with assistance from experts, was utilized when necessary. Vouchers were stored in the same Herbarium.

Information from the literature was used to identify the sources of pollen and nectar that bees explore, including floral morphology, the floral resources available to bees from the plants they visit, and their collection behavior on flowers. Floral oils were collected from plant species of the Malpighiaceae family.

Statistical analysis

To assess the occurrence of seasonality in the nesting activities of the bee species, the Rayleigh test of uniformity (Z) for circular distributions (Zar, 1999) was performed using the package 'circular' (Agostinelli & Lund, 2017) implemented in R software version 3.4.2 (R Core Team, 2017). The average date (μ) and concentration (r) of nesting events were also calculated in this analysis. The hypotheses tested were as follows: H0 = nesting activities are uniformly distributed throughout the year, indicating no seasonality, and H1 = nesting activities are unevenly distributed throughout the year, indicating the occurrence of seasonality. If H1 is corroborated, the intensity of the nesting activities around an average date (r) may be considered a measurement of the degree of seasonality. As described by Morellato et al. (2000), this index indicates whether nesting activities occurred uniformly throughout the year (r = 0) or were concentrated in a single month (r = 1).

The Watson-Williams test (F) was performed to verify the homogeneity between the patterns of nesting activities of each bee species in each studied year and between each species' first and second years. This metric tested whether one group's nesting pattern is synchronized with that of the other group (H0) or not (H1). The 'circular' package was used to perform this test.

The Shapiro-Wilk normality test (W) was performed to verify the normality of the number of built nests monthly for each bee species. The Pearson (r) or Spearman coefficient (rs) was calculated to ascertain the relationship between the number of nests built monthly by each bee species and two environmental conditions: average monthly temperature (ºC) and monthly rainfall (mm). These analyses were performed using the 'Vegan' package version 2.4-5 (Oksanen et al., 2017), implemented in R software version 3.4.2. (R Core Team, 2017).

To characterize the food niche of *Centris* species and the species richness (S), three other indices were calculated for each species: species diversity, dominance, and degree of evenness of the diet. The Shannon-Wiener index (H') was calculated to measure diet diversity (Shannon, 1948). This index considers the relation between richness and abundance through the formula $-\sum_{i=1}^{S} p_i \, ln(p_i)$, where S is the total number of pollen types observed, pi is the proportion of i pollen types in the total number of pollen types found in the diet, and *ln* is the natural logarithm. A posteriori statistical t-test (Hutcheson, 1970) was used to verify the difference between the Shannon-Wiener values of each bee species (Magurran, 2004). The Berger-Parker index (d) was calculated to measure the degree of diet dominance by dividing the number of dominant pollen types by the total number of pollen counted (Magurran, 2004). Pielou's evenness index (J') was calculated to indicate whether the abundance of different pollen types was uniform (J' = 1) or not (J' = 0) in the diet (Pielou, 1966). The evenness index was calculated by dividing the Shannon-Wiener diversity value by the natural logarithm of the pollen types found. All these metrics and tests were performed using the 'Vegan' package version 2.4-5 (Oksanen et al., 2017), implemented in R software version 3.4.2. (R Core Team, 2017), using the total data obtained in all analyzed nests during the study for each species.

Using the Pianka index, the niche overlap between both studied *Centris* species was calculated using TimeOverlap version 1.0 (Castro-Arellano et al., 2010). Utilizing the Rosario algorithm, a null-model analysis based on 10,000 randomizations was conducted to determine if the overlap values calculated differed from those expected by chance, using a two-tailed test. This index was estimated using a matrix of the relative abundance of pollen types observed each month for each bee species.

All statistical analyses performed in this work used a significance level of 0.05.

Results

The flowering period of *Malpighia emarginata* at the Sítio Granja Bela Vista orchard

During the study period, the first flowering of *M. emarginata* at the Sítio Granja Bela Vista occurred from September 2010 to February 2011, and the second from September 2011 to April 2012 (Fig 2). Therefore, in the Indaiatuba region, *M. emarginata* mainly blooms during the rainiest and hottest periods (Fig 2).

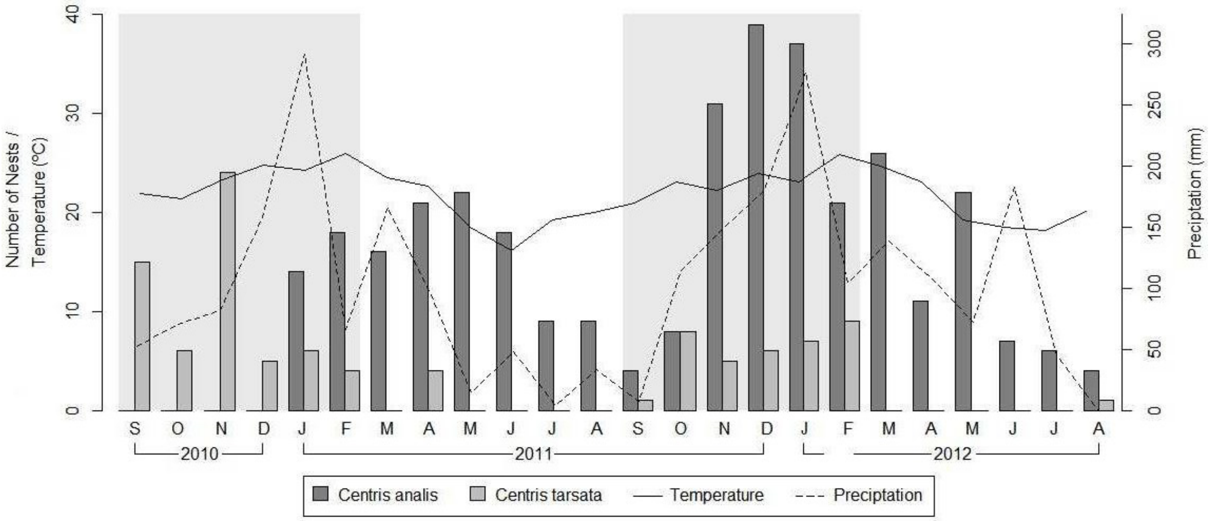

Fig 2. Climatic conditions (monthly average temperature (°C) and precipitation (mm)) and number of nests built by *Centris analis* and *Centris tarsata* from September 2010 to August 2012 in the *Malpighia emarginata* orchard at Indaiatuba, SP, Brazil. The gray area corresponds to the bloom period of *M. emarginata.*

Phenology of Nesting in *Centris* Species Occupying Trap-Nests

Centris analis and *C. tarsata* were the only species occupying the traps. Females of *C. analis* established their nests solely in cardboard tubes, while females of *C. tarsata* nested exclusively in bamboo canes.

Centris analis occupied the traps in January 2011 and continued to do so throughout the study period, building 343 nests. A significant correlation was found between nesting frequency and monthly precipitation ($r = 0.44$, $df = 22$, $p < 0.05$), with nesting peaks occurring during the periods of highest recorded precipitation (Fig 2). It is possible to observe a reduction in the occupation of the TN during the period from July to October 2011 and from June to August 2012, along with and higher nesting frequencies during the hotter months. However, there was no correlation with the recorded average monthly temperatures ($r = 0.2$, $df = 22$, $p > 0.05$) (Fig 2).

Centris tarsata initiated their reproductive activities in September 2010 and remained active until February 2011, occupying 64 trap-nests, with the highest nesting frequency occurring in November 2010 (Fig 3). No nesting activity occurred from May to August 2011. In September 2011, nesting activities were resumed and continued until February 2012, when 36 nests were recorded. After nesting was interrupted from March to July, the new occupation of NA began in August 2012, with one nest being recorded that month (Fig 2). No significant correlation was found between nesting frequency and monthly precipitation ($r = 0.15$, $df = 22$, $p > 0.05$). However, the average monthly temperature was significantly correlated with the nesting activities ($r = 0.43$, $df = 22$, $p < 0.05$) (Fig 2).

The Rayleigh test revealed seasonal patterns in the nesting phenology for both species in the two study years, with *C. tarsata* exhibiting a more pronounced pattern than *C. analis*. Some immatures of *C. tarsata* entered diapause during both studied cold and dry seasons; these nests were completed at the end of *M. emarginata'*s flowering, between February and April, and remained closed. The adults emerged in September and October, coinciding with the onset of bloom (Fig 3).

The nesting pattern was not synchronized between bee species for both the first ($F = 216.9$, $df = 189$, $p < 0.001$) and the second year ($F = 8.38$, $df = 251$, $p < 0.01$). The pattern observed for *C. tarsata* differed between years ($F = 8.53$, $df = 99$, $p < 0.01$), with the nesting peak occurring in October and November in the first year and in December in the second. For *C. analis*, nesting peaked in April and May during the first year and in January and February in the second year, with no synchronization observed between the years for this species ($F = 113.5$, $df = 341$, $p < 0.001$) (Table 1, Fig 4).

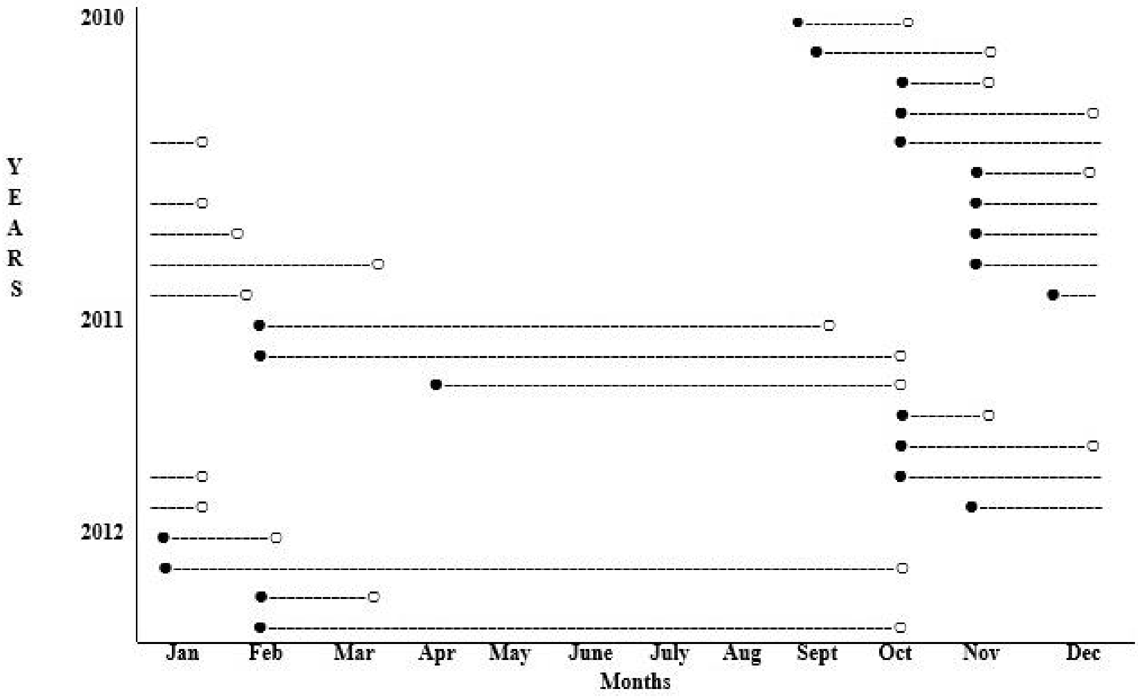

Fig 3. Representation of nesting phenology and time elapsed between nest closure and emergences for *Centris tarsata* nests at the Sítio Granja Bela Vista, Indaiatuba, SP. The first year comprises samples from September 2010 to August 2011, and the second from September 2011 to August 2012. ● indicates the month in which the nest was completed; ○ indicates the month in which the individuals emerged.

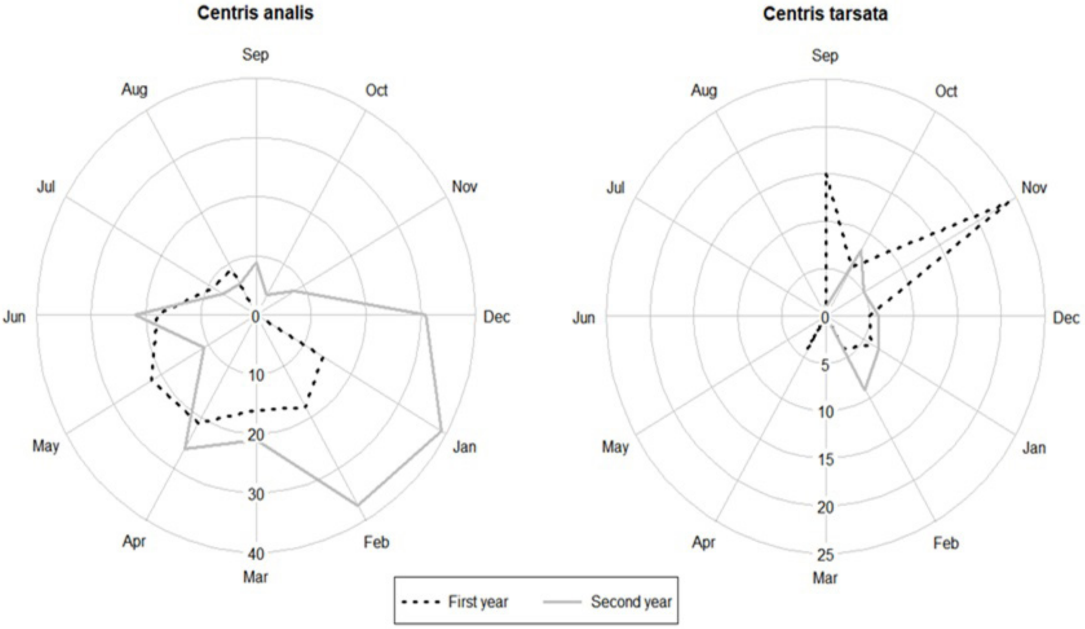

Fig 4. Number of nests of *Centris analis* and *Centris tarsata* in a *Malpighia emarginata* orchard in Indaiatuba, São Paulo, Brazil. The first year comprises samples from September 2010 to August 2011, and the second from September 2011 August 2012.

Floral sources explored by *Centris analis* and *Centris tarsata*

During the sampling period, 56 melittophilous plant species from 26 botanical families bloomed in the orchard and in the sampled areas along the surrounding transects.

Fabaceae, Asteraceae, and Bignoniaceae were the most abundant families, representing 10, eight, and five species, respectively. The flowering peaks of the species occurred during the rainy season (October, November, December 2011, and January 2012) and at the beginning of the dry season (May 2011, April, and May 2012). *Tecoma stans* (L.) Juss. ex Kunth was the only species that bloomed year-round.

The floral sources used by *C. analis* and *C. tarsata* were identified by analyzing 20,400 pollen grains from 51 *C. analis* nests and 28,400 pollen grains collected from 71 *C. tarsata* nests. Both bee species used 48 plant species from 19 families to provision their nests. The Fabaceae family was the most prevalent, including 14 species. Among these plant species, 13 were exclusively explored by *C. analis*, 21 by *C. tarsata*, and 12 by both bee species investigated. *Malpighia emarginata* served as the primary pollen source and floral oil for both *C. analis* (63%) and *C. tarsata* (34.1%). *Palicourea rigida* Kunth (Rubiaceae) (8.9%), *Ludwigia octovalvis* (Onagraceae) (Jacq.) P.H.Raven (5.1%) and *Machaerium hirtum* (Vell.) Stellfeld. (Fabaceae) (4.6%) were important sources of nectar for *C. analis*. For *C. tarsata*, *Raphanus sativus* L. (Brassicaceae) (15%) was an important source of pollen and nectar, as was *Solanum mauritianum* Scop. (Solanaceae) (11%) and *S. paniculatum* L. (Solanaceae) (8.6%) were important sources of pollen, while *Machaerium hirtum* (Fabaceae) (3.4%) was an important source of nectar (Supplementary Material 1, 2).

The diet diversity index of *C. analis* (H' = 1.62) was significantly lower (t = 4.61, $p < 0.001$) than that observed for *C. tarsata* (H' = 2.62). The foraging of *C. analis* exhibited a low degree of evenness (J' = 0.49) due to its high preference for *M. emarginata* (d = 0.51). In contrast, *C. tarsata* explored floral sources more uniformly (J' = 0.74) (d = 0.23) (Table 2).

Table 1. Nesting patterns of *Centris analis* and *Centris tarsata* in a *Malpighia emarginat*a orchard in Indaiatuba, São Paulo, Brazil. The Rayleigh test (Z) indicates a seasonal pattern; the average degree (μ) denotes the months with the nesting peak, while the concentration degree (r) shows the strength of the seasonality. The first year includes sampling from September 2010 to August 2011, and the second year from September 2011 to August 2012.

		Z	**μ**	**Months**	***r***
Centris analis	1st	67.7^{**}	214.9	Apr/May	0.53^{*}
	2nd	89.2^{**}	124.3	Jan/Feb	0.41^{*}
Centris tarsata	1st	40.6^{**}	56.7	Oct/Nov	0.64^{**}
	2nd	24.4^{*}	90	Dec	0.66^{**}

Values significantly different from those expected in a null distribution for * $p < 0.05$ and for ** $p < 0.01$.

Table 2. Pollen type richness (S), diversity (H'), dominance (d), and evenness estimators (J') for the diets of *Centris analis* and *Centris tarsata*, sampled at a *Malpighia emarginata* orchard in Indaiatuba, São Paulo, Brazil, from September 2010 to August 2012.

	S	H'	d	J'
Centris analis	27	1.56	0.63	0.47
Centris tarsata	35	2.38	0.34	0.67
Both species	48	2.31	0.46	0.60

The niche overlap test revealed a significant overlap between *C. analis* and *C. tarsata*, higher than expected by chance (Pianka = 0.83; $p < 0.05$).

Discussion

This study showed that the trap-nests made available at the West Indian cherry orchard attracted pollinators to nest there. This result is unsurprising because other authors (Oliveira & Schlindwein, 2009; Pina & Aguiar, 2011; Magalhães & Freitas, 2013; Santos et al., 2013) have reported similar observations. The two observed *Centris* species occupied different trap-nests. *Centris analis* nested exclusively in the cardboard tubes with the diameter preferred by the females of this species (Oliveira & Schlindwein, 2009; Vinson et al., 2010), and *C. tarsata* utilized bamboo canes exclusively with varying diameters and lengths. These findings demonstrate that using different types of trap-nests and varying cavity dimensions, primarily cavity diameter, enables nesting by bees of various sizes and with distinct nesting behaviors, as reported by Aguiar et al. (2005).

Previous studies have shown that solitary bee species can present temporal variations in reproductive activities over time, depending on the regions in which they occur (Camillo et al., 1995; Gazola & Garófalo, 2003; Aguiar et al., 2005; Alonso et al., 2012; Rocha-Filho et al., 2018). These variations in nesting phenology have been suggested as natural characteristics of cavity-nesting bee species, and different species are affected differently by various factors, including climatic conditions and resource availability (Silva et al., 2017). The number of generations produced per year is a trait of the species' life history that is significantly affected by these temporal variations. In the present study, *C. analis* and *C. tarsata* exhibited multivoltine behavior. *Centris analis* nested during all study periods except for the first four months, while *C. tarsata* nested in more restricted periods, entering diapause during the coldest months, giving it a more pronounced seasonality than *C. analis*. Higher nesting frequencies during the hot/rainy season have also been reported by other authors (Gazola & Garófalo, 2003; Buschini & Wolf, 2006; Krug & Alves-dos-Santos, 2008; Mesquita & Augusto, 2011; Pina & Aguiar, 2011; Alonso et al., 2012) in studies with *C. analis* and *C. tarsata* in different regions of the country. These observations underscore the significance of environmental conditions in the reproductive behavior of these bee species. An interesting observation is that precipitation was the most significant factor for the nesting activities of *C. analis*, while temperature was the most critical factor for *C. tarsata*.

Similar to temporal variations observed in the phenology of bees, the flowering period of cherry trees is also variable and depends on the precipitation of the location where the crops are established. The flowering peaks can occur up to eight times a year, depending on the region and use of crop irrigation, and each flowering can last approximately 22 to 29 days (Gomes et al., 2001). In the Indaiatuba region, flowering peaks occurred when precipitation and average temperature were higher, corresponding to the hot and rainy periods. However, it was observed that even in colder and drier periods, the few opened flowers served as a pollen and oil source for *C. analis*.

Malpighia emarginata exhibits high levels of natural pollination. However, the fruit set in the orchards has been regarded as insufficient (Freitas et al., 1999; Oliveira & Schlindwein, 2009; Oliveira et al., 2013). Thus, the search for manageable pollinators is crucial for producing this fruit, and the first step is to select species with well-studied biology. Among the bees pollinating cherry trees, most species are ground-nesting, including *Centris* species (Oliveira et al., 2013; Sazan et al., 2014; Martins et al., 2024). This bionomic characteristic complicates management procedures primarily because it necessitates suitable nesting areas (Cane, 2008). In Brazil, the lack of methods for managing ground-nesting species makes it challenging to utilize the pollination service in orchards, even though these bee species are considered effective pollinators. On the other hand, species that nest in preformed cavities, such as *C. analis* and *C. tarsata*, have received more attention, mainly due to the ease of studying them using trap-nests and the advancement in biological knowledge of these species thanks to this methodology (MacIvor, 2017). Therefore, considering these aspects, among the known bee species that visit flowers of *M. emarginata*, *C. analis* and *C. tarsata* have the potential to be candidates for management programs.

The association of *C. analis* and *C. tarsata* with Malpighiaceae species has been reported by several authors (Dórea et al., 2009; Oliveira & Schlindwein, 2009; Rabelo et al., 2012; Magalhães & Freitas, 2013; Santos et al., 2013; Cruz et al., 2015; Lima et al., 2017; Silva et al., 2017; Rocha-Filho et al., 2018). Additionally, the accumulated knowledge on various aspects of the life histories of these species (Gazola & Garófalo, 2003; Aguiar & Garófalo, 2004; Buschini & Wolf, 2006; Krug & Alves-dos-Santos, 2008; Mesquita & Augusto, 2011; Pina & Aguiar, 2011; Alonso et al., 2012; Moure-Oliveira et al., 2017) allows us to recommend them as pollination service providers to those cultures.

Bosch and Kemp (2002) published a paper discussing the development and establishment of bee species as pollinators for crops. According to these authors, the criteria for selecting candidate pollinator species vary from crop to crop, though some generalizable rules may exist. One criterion is that candidate pollinator species should exhibit a preference for foraging on the target crop flowers and be efficient pollinators. Among the study's findings, it was observed that *M. emarginata* was the only source of floral oil and the primary pollen source for both bee species. This great visit to West Indian cherry flowers enhances the degree of trophic niche overlap between these *Centris* species. However, the competition between these bees must not have been intense due to the abundance of flowers available during peak blooming. *Centris analis* showed a greater preference for this plant species than *C. tarsata*, which also visited *Raphanus sativus* to collect pollen. Solanaceae species are also a vital pollen source for *C. tarsata* (Dórea et al., 2009; Gonçalves et al., 2012; Cruz et al., 2015). Interestingly, *C. tarsata* uses pollen, nectar, and floral oil to provision its brood cells (Aguiar & Garófalo, 2004). In contrast, *C. analis* uses floral oil exclusively for nest construction (Vieira-de-Jesus & Garófalo, 2000). Exploring *M. emarginata* by both bee species will likely enhance pollination services and contribute to better fruit formation. These results indicate that *C. analis* and *C. tarsata* meet the criteria proposed by Bosch and Kemp (2002). It is important to note that *M. emarginata* does not produce nectar; therefore, other plant species must be provided around the orchards to supply nectar.

A greater diversity of floral sources is expected during rainy periods because more plant species will have open flowers compared to dry periods. Consequently, higher variability in bee diets is anticipated during this season. Additionally, preferences for specific floral sources can enhance the differences in diet composition among species. In this study, *Machaerium hirtum* was identified as a primary nectar source for bees. Other Fabaceae species were also examined in this study and noted by previous authors (Dórea et al., 2009; Cruz et al., 2015; Lima et al., 2017; Silva et al., 2017) as nectar sources for both *Centris* species, highlighting the importance of this botanical family for sustaining pollinators in a specific area. Although these nectar sources were common to both species of *Centris,* most were not shared among the bees, underscoring the significance of plant diversity in the areas surrounding the orchard.

Additionally, Bosch and Kemp (2002) indicate that a strong association between the activity periods of bee species and the flowering periods of crops is critical. This synchronization of reproductive activities between plants and pollinators is crucial to the functioning of the pollination system. As observed in this study, pollinators' highest nesting frequencies coincided with the crop's peak flowering during the same time of year. It is essential to note that the findings do not directly assess the impact of managing each bee species on the reproductive success or fruit yield of *M. emarginata*. Future studies should experimentally assess the role of these managed pollinators in increasing crop productivity.

Considering all the results obtained, it is clear that there are distinct reasons to suggest that both bee species are suitable pollinators of *M. emarginata* in the region studied. The bee species share many similarities in their life histories, nesting in preexisting cavities, collecting oil, and exhibiting nesting peaks during the hottest months of the year. Conversely, the phenologies of *C. analis* and *C. tarsata* were not synchronized, indicating a low temporal overlap. Additionally, the type and dimensions of TN used differed, suggesting minimal competition for nesting substrates. The abundant resources of blooming *M. emarginata* also imply low competition for floral resource collection. Thus, utilizing both species to pollinate cherry tree orchards appears to be the best option, as it would facilitate the visitation of many nesting females to flowers and provide pollination services. However, it is essential to emphasize that the success of increasing pollinator populations in orchards will depend on the availability of floral resources in the surrounding areas for the nidification and feeding of their offspring.

Authors' Contribution

DMO: Formal analysis, investigation, writing-original draft, writing-review & editing.
RL: Formal analysis, investigation, writing, review & editing.
MSS: Formal analysis, investigation, writing-original draft, writing-review & editing.
CIS: Conceptualization, methodology, writing-review & editing.
CAG: Conceptualization, methodology, writing-original draft, writing-review & editing, supervision.

Acknowledgments

The authors are grateful to JC Serrano (*in memoriam*) for identifying the organisms, to ESR Silva for technical support, to Mr. Klaus Gottifried Bouillon, owner of Sítio Granja Bela Vista, for kindly providing space for this study, and to the staff of the Sítio for their collaboration. The authors also thank the anonymous reviewers who contributed to the improvement of the manuscript. This study was partially financed by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. Additionally, the authors thank CNPq (process # 479827/2010-9) and FAPESP (process # 2010/10285-4) for their financial support.

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