

Is the maximum reproductive rate of *Centris analis* (Hymenoptera, Apidae, Centridini) associated with floral resource availability?

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Received: 4 October 2016 / Accepted: 17 March 2017 / Published online: 13 April 2017
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Abstract Spatiotemporal variation in the availability of food resources may be a determining factor for reproductive success and maintenance of bees, but the extent of these variations is poorly understood. For management and conservation of bees, the first step is to know the behavior and the food resources used. Currently, urban areas are considered refuge zones for bees, and understanding the availability of floral resources and the influence on reproductive processes is very important for management of bees. We used the protocols applied in phenological studies with bees and plant species to evaluate both throughout the year in an urbanized area. At the same time, we used palynology protocols to analyze the pollen material collected from brood cells (food and feces) of immature *Centris analis*.

These protocols allowed to evaluate the availability of floral resources in the studied area and the plant species effectively used by *C. analis* females to feed immature larvae during the reproductive period. The maximum reproductive period of *C. analis* was not associated with the highest floral resources availability. However, there was a strong selectivity of pollen in flowers of *Malpighia emarginata* (Malpighiaceae), which represented more than 59% of all the pollen grains provisioned throughout the year. This means that in the case of more specialized bees like *C. analis*, the availability of the preferred plants is more important than the overall floral resource availability in the area. Thus, to keep *C. analis* in the city, it is necessary to maintain or introduce Malpighiaceae species in the urban planning. On the other hand, at least 27% of the plant species found in the study area are pollinated by *C. analis*, emphasizing the importance of preserving this bee.

Handling Editor: Isabel Alves dos Santos.

Electronic supplementary material The online version of this article (doi:10.1007/s11829-017-9513-9) contains supplementary material, which is available to authorized users.

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Keywords Bee diet · Bee interaction · Conservation · Foraging behavior · Urban planning

Introduction

Plants and their pollinators are supposed to have a mutualistic relationship with different levels of dependency (Del-Claro 2004), and therefore a floral resource base that provides pollen and nectar at appropriate time is essential for survival and reproduction of bees (Wojcik et al. 2008). Many pollination systems may be specialized, and in these cases, a good synchronization between pollinating insects and their host plants is expected. This is especially true for areas where climatic factors can limit the flowering season (Mayer and Kuhlmann 2004), or for specialist bees that have special morphological features corresponding to

peculiar traits of the flowers from which they collect floral resources (Linsley 1958; Laroca et al. 1982; Buchmann 1987). Pollen host specialization is common among solitary bees, and is often linked to pronounced bee seasonality due to a seasonal flowering phenology of the pollen host plant (Wcislo and Cane 1996). Some specialist bees can even synchronize temporally their own reproduction with the flowering of their main source of pollen (Minckley et al. 2000) or their sources of floral oils (Rocha-Filho et al. 2008). Because of this synchronization, a species of solitary bee can present a variation in reproductive activity over time, depending on the region in which it occurs. For example, in Guarapuava, State of Paraná, Southern Brazil, *Centris (Hemisiella) tarsata* Smith, 1874 (Centridini) nests primarily from November to March (hot season) producing two generations per year (Buschini and Wolf 2006); in Baixa Grande, State of Bahia, Northeast Brazil, it nests from September to May (rainy season), producing up to four generations (Aguiar and Garófalo 2004); and in Urbano Santos, State of Maranhão, also in Northern Brazil, this species behaves as univoltine, nesting from August to December (dry season) (Mendes and Rego 2007). These differences in nesting phenology have been suggested as a regular characteristic of cavity-nesting bee species, and that different species would be affected differently by several factors, such as climatic factors and resource availability (Frankie et al. 1998; Tommasi et al. 2004; Oertli et al. 2005; Abrahamczyk et al. 2011; Bartomeus et al. 2011).

Centris (Heterocentris) analis (Fabricius, 1804) is a solitary bee that nests in preexisting cavities (Coville et al. 1983; Camillo et al. 1995; Vieira-de-Jesus and; Garófalo 2000). This species has a broad geographic range extending from Mexico to Brazil (Moure 1960), indicating that it has great behavioral plasticity to explore different environments. In studies on communities of solitary cavity-nesting bees, carried out in Brazil in areas with different phytophysiognomies, *C. analis* has been one of the species that frequently occupies the trap-nests (Camillo et al. 1995; Aguiar and Martins 2002; Garófalo et al. 2004; Gazola and Garófalo 2009; Mesquita and Augusto 2011). However, occupancy patterns of trap-nests differ among areas of occurrence. In some environments, the nesting activities may occur throughout the year (Gazola and Garófalo 2009; Pina and Aguiar 2011), while in other environments it may occur only at certain times of the year, usually during the hot/wet season (Camillo et al. 1995; Aguiar and Martins 2002; Gazola and Garófalo 2003, 2009; Mesquita and Augusto 2011; Alonso et al. 2012). Irrespective of the pattern of occupation of the traps, during the period of reproductive activities, peaks of nesting are observed, which may be related to climatic conditions and resource availability (Gazola and Garófalo 2003, 2009; Alonso et al. 2012). So, given that spatial and temporal variations in the

availability of food resources may be a determining factor for reproductive success and maintenance of bees (Kremen et al. 2007; Jha and Kremen 2013; Wray et al. 2014), the goals of this study were (i) to assess whether in an urbanized area, occupied by a population of *C. analis*, the floral resources are distributed evenly throughout the year; (ii) to assess the relationship between the availability of floral resources, nesting period, and emergence period of females of *C. analis*. Furthermore, the relationship between (iii) the diversity of floral resources in the diet of immature individuals and the diversity of flowering plants during the nesting period.

Materials and methods

Study area

This study was conducted at the campus of the University of São Paulo (21°10'30"S–47°48'38"W), municipality of Ribeirão Preto, State of São Paulo, Brazil. The campus is located at altitudes ranging from 510 to 800 m. a.s.l., in an area of 574 ha. Currently, the campus represents an area consisting of 65% native plant species (Aleixo et al. 2014). This significant number of native species is due to a forest covering 75 ha of the areas, reforested with those species (Pais and Varanda 2010). The climate of the region shows marked seasonality, with two seasons, cold and dry winters from April to August and hot, wet summers from September to March (Fig. S1, Supporting information).

Phenology of *Centris analis*; sampling and identification of pollen grain provisioned in brood cells

We used trap-nests to attract *C. analis* females to nest in them, to collect the pollen material of the brood cells and of the feces incorporated into the cocoons in nests. In accordance with Alonso et al. (2012), the trap-nests were made with black cardboard, closed at one end. The traps were 5.8 cm in length and 0.6 cm in internal diameter, and were inserted into horizontal holes, drilled into wooden grooved plates (length 30 cm, height 12 cm, thickness 5.0 cm). Each wooden plate had 50 available holes spaced 2.0 cm apart and distributed in five rows. Ten plates were placed on shelves attached to the external walls of the laboratory and positioned 1.5 and 1.8 m from the ground. During the study period, the traps were inspected with a lantern every day and information was recorded for trap-nests with active and complete nests. Ten days after being completed, the nests were taken to the laboratory and replaced with similar traps. In the laboratory, each trap-nest was placed in a transparent glass tube 4.0 cm longer than the trap-nest and with an internal diameter of 0.9 cm. The trap-nests were

kept at room temperature (21–29 °C) and observed daily until the adults emerged. After emergence, the bees were released in the field.

Information on pollen sources used by *C. analis* was obtained from a sampling of 10 randomly selected nests per month, during the nesting period of the species. Each sample consisted of the total residues of pollinic material found in the nest. After collecting the material, it was kept in 70% alcohol for at least 24 h, following Silva et al. (2010) methodology. After this period, we centrifuged the pollen material, discarded the supernatant, and added 4 mL glacial acetic acid and, after 24 h, the pollen material was acetolyzed (Erdtman 1960). We prepared the slides with Kisser gelatin and sealed them with histological paraffin (Silva et al. 2014a). We incorporated all slides in the reference pollen collection at the Palynoecology Laboratory of FFCLRP-USP (Silva et al. 2014b).

We viewed and photographed microscopically (up to 2560x) the pollen grains on the slides and their identification was made by morphological comparison with the pollen collection at the Palynoecology Laboratory of FFCLRP-USP. We also consulted the specific literature on Neotropical Palynotaxonomy (Roubik and Moreno 1991; Silva et al. 2010, 2014a; Mouga and Dec 2012; Bauermann et al. 2013).

Plant phenology and pollen collection

The present study was carried out concomitantly with study of Aleixo et al. (2013) on the floral phenology and temporal distribution of floral resources and foraging of social bee *Frieseomelitta varia* (Lepeletier) (Hymenoptera, Apidae, Meliponini). The authors demarcated an area of 500 m radius, taking the bee's nests as referential point. The total area, corresponding to 78 hectares, was monthly evaluated to sample the flowering plants and counted the number of flowering individuals per species, considering all vertical strata, as suggested by Silva et al. (2012). We used the database of Aleixo et al. (2013) comparatively to verify if nesting activities of *C. analis* were correlated with the floral phenology and temporal distribution of the floral resources during the period from March 2010 to February 2011.

At the same time, we also collected flower buds of each species during blooming and removed the pollen grains to prepare the pollen collections, as suggested by Silva et al. (2014a), and deposited the slides in the reference pollen collection of Palynoecology Laboratory of FFCLRP-USP (Silva et al. 2014b).

Data analyses

To assess seasonality in resource availability considering the number of plant species and individuals during blooming

from March 2010 to February 2011, we employed circular statistics using the Rayleigh's test (Z) to determine the significance of the mean date of event (in months; $\alpha=5\%$) (Zar 1999). The null hypothesis (H_0) states that when the event is distributed evenly throughout the year there is no seasonality. If H_0 is rejected, the mean date is significant and there is a concentrated pattern. The intensity of the concentration around the mean date, denoted by r , can be considered a measure of the degree of seasonality. The vector r has no units and may vary from 0 (when the event is evenly distributed throughout the year) to 1 (when the event is concentrated around one single date or time of the year) (Morellato et al. 2000). We used the Oriana software (Kovach Computing Services 2012) to perform the circular statistics analysis. We also applied the Rayleigh's test (Z) to assess the frequency of *C. analis* females active on nest construction, emergence of total individuals, emergence of female, and the distribution of the pollen type used by the immature *C. analis* throughout the year.

We used generalized linear models (GLM) to assess which factors affected the total number of bees, the number of females emerging, and the nesting activities. For this, we considered the number of individuals of plant species used in the diet by *C. analis* and the weather daily (temperature, relative humidity, wind speed, and rainfall) as explanatory variables. We did not consider the number of flowering species and individuals and the number of plant species used by *C. analis*, because they are correlated with the number of individuals of plant species used in the diet by this bee (Table S1, Supporting information), thus avoiding multicollinearity (Crawley 2005). The effects of the explanatory variables on the variables of interest were measured by t test at 5% significance level. We applied the t test to verify the differences between the number of flowering species, number of individuals of the flowering plants species, number of species used in diet, number of plants the individuals used in diet, number of nests occupied, total number of bees emerged, and the number of females emerged. The number of pollen types was assessed by the Mann–Whitney test due to the nature of the data. All statistical analyses were performed using software R 2.13.1 (R Development Core Team 2011).

To analyze the larval diet, we counted the first 400 pollen grains for each sample, as suggested by Montero and Tormo (1990). We assessed the trophic niche breadth of *C. analis* monthly, calculating the Shannon index (Shannon 1948)

$$H' = - \sum_{i=1}^s p_i \ln p_i,$$

where p_i is the proportion of species visited, and \ln is the natural logarithm of p_i .

We calculated the evenness (Pielou 1966) of plants used in the diet of bees using the formula: $J' = H'/H'_{\max}$, where H'_{\max} is the logarithm of the total number of plant species visited by the bee species.

To determine the number of the most important species in the bee diet, we applied the test of the apparent number: $S_{\text{apparent}} = e^{H'}$, where H' is the niche breadth calculated by the Shannon index (with ln) and e = Euler's number.

We analyzed the importance of each plant species in *C. analis* diet. For each nest, we calculated the ratio of pollen of each plant species found in the nests by the formula $p_i = ni/N$, where ni is number of pollen grains of the plant species i and N is the total number of pollen grains (all plant species used).

We also applied the Berger–Parker test to assess the dominance in the diet of immature *C. analis* by the formula $d = N_{\max}/N$.

Finally, we calculated the percentages according to the classification proposed by Maurizio & Louveaux (1960), using the following categories: dominant pollen (>45% of the total grains on the slide), accessory pollen (from 15.01 to 45%), important isolated pollen (3 to 15%), and occasionally isolated pollen (<3%). We considered the plants with pollen classified as dominant and pollen that occurred over a period of at least 6 months as key-plant species in the maintenance of *C. analis*.

Results

We found active *C. analis* throughout the year, more intensely in December, March, and May. The average date of females in nesting activity was significant ($Z=24.61$; $p<0.05$) with concentration around March (Table 1—DNA) and peaking in May (Fig. 1e). In the same period, we observed a concentration in the distribution of the plant species in March, April, and May, and of individuals in bloom in April, May, and July (Fig. 1a, b), being

the corresponding vectors positioned in April and May (Table 1—TDS and TDI), respectively.

We observed that *C. analis* females constructed 478 nests, from which 630 individuals emerged. The average date of bees emerging from nests was also significant ($Z=27.12$; $p<0.05$) with high concentration in March (Table 1—DES), and peak in the same month (Fig. 1f). Of the emerged individuals, 35% were females ($n=22$). The average date of female emergence was not significant ($Z=2.175$; $p=0.114$), but presented a peak in August (Fig. 1g).

The number of pollen types identified in the diet of *C. analis* was more evenly distributed throughout in the year (Fig. 1h), and the average date was not significant ($Z=0.752$; $p=0.121$). When we analyzed the distribution of the plant species used by *C. analis* throughout the year, we verified that majority flowered from February to May (Fig. 1c), peaking in March (Table 1—DSU), corresponding to the period of greatest nesting activity (Fig. 1e).

When we analyzed the flowering individuals of plant species used in the diet of *C. analis*, we registered the greatest number of these flowering individuals from April to August (Fig. 1d) with significant average date ($Z=14.305$; $p<0.05$) (Table 1—TIU) and peak at the end of this period.

We found positive association with temperature ($t=2.653$; $p=0.038$), humidity ($t=3.365$; $p=0.015$), and the total of bees emerged, as well as TIU with the total of emerged females ($t=3.192$; $p=0.019$). Nevertheless, these results were influenced by one value, or a few, and withdrawal annulled the significance ($p>0.05$), although it is remarkably a marginal effect of temperature on the total of emerged bees (Table S2, Supporting information). The other variables did not influence the total number of bees/females emerging and the nesting activity (Table S2, Supporting information). We observed the averaged number of individuals flowering ($t=3.260$; $p=0.009$) and the number of individuals used in the bee's diet ($t=2.384$; $p=0.038$) were high in dry season (Fig. 2). There was no difference

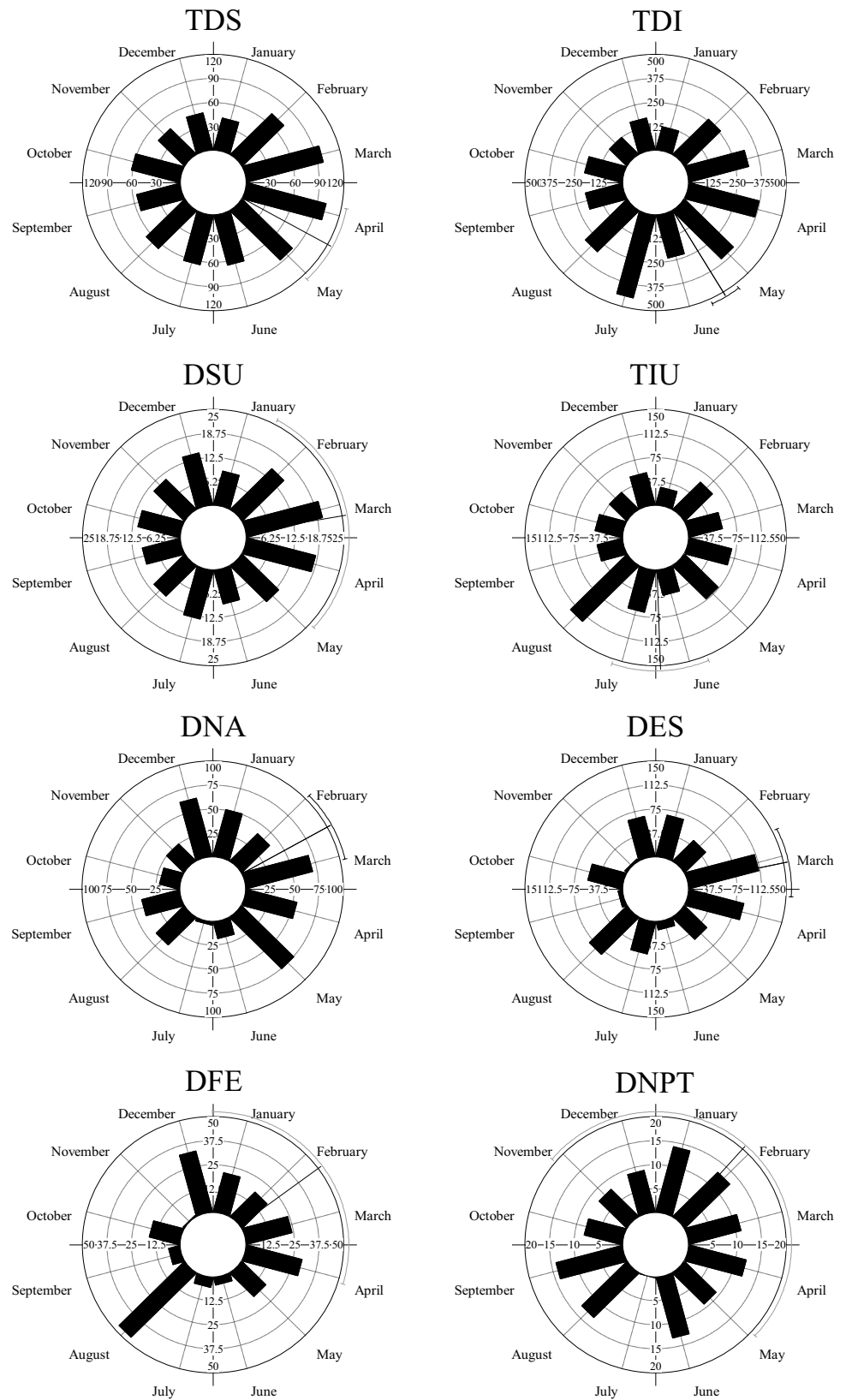
Table 1 Results of circular statistics for testing the occurrence of seasonality in floral phenology, availability of floral resources, nesting behavior, and emergence of *Centris analis* in the campus of the University of São Paulo, Ribeirão Preto, from March 2010 to February 2011

Variables	TDS	TDI	DSU	TIU	DNA	DES	DFE	DPTN
Number of observations	798	3075	154	681	478	630	221	124
Mean vector (μ)	April	May	March	June	March	March	February	February
Mean vector length (r)	0.159	0.216	0.122	0.145	0.222	0.207	0.099	0.078
Circular standard deviation	109.85°	100.238°	117.481°	112.611°	99.362°	101.614°	123.169°	129.468°
Rayleigh test (Z)	20.212	144.08	2.299	14.305	24.61	27.123	2.175	0.752
Rayleigh test (p)	<0.05	<0.05	0.100*	<0.05	<0.05	<0.05	0.114*	0.121*

TDS total distribution of species; *TDI* total distribution of individuals; *DSU* distribution of the species used by *C. analis* throughout the year; *TIU* Distribution of the individuals of the species used in the diet of *C. analis*; *DNA* Distribution of nesting activities; *DES* Distribution of emergence of specimens; *DFE* Distribution of female emergence; *DPTN* Distribution of the number of pollinic types identified in the nests

* not significant in $\alpha \leq 0.05$

Fig. 1 Total distribution of species (TDS) and individuals (TDI) at flowering in the campus of USP; distribution of the species (DSU) and individuals of the species used in the diet of *C. analis* (TIU); Distribution of nesting activities (DNA); Distribution of emergence of specimens (DES); Distribution of female emergence (DFE); Distribution of the number of pollinic types identified in the nests (DNPTN)



between the dry and rainy seasons and the mean value of other variables.

Although the mean number of pollen types in the diet had been similar between the seasons ($\bar{X}_{\text{dry season}} = 11.75 \pm 4.94$, $\bar{X}_{\text{rainy season}} = 11.0 \pm 2.12$), in the rainy season the diet was composed basically of dominant pollen, with only one plant species representing between 66 and 95% of the diet (Table 2).

The floral resources used by *C. analis* for feeding the brood were obtained from 52 species of plants distributed into 45 genera and 19 families (Table 2). The number of pollen types in the samples was evenly distributed throughout the year, with the exception of July (Fig. 1h). During this month, it was not possible to analyze the pollen material because of mortality and degradation of brood cell contents. The number of pollen types used monthly in the diet of immature *C. analis* ranged from 8 to 14, with the highest frequencies occurring in September and January (Fig. 1h).

The diversity of pollen species in the diet of *C. analis* varied over the year (Table 2). Notably, of the 52 plant species visited, *C. analis* females concentrated their collection of floral resources in only three plant species ($S_{\text{apparent}} = 3.18$), belonging to families Malpighiaceae and Leguminosae (Fig. 3a). Malpighiaceae showed the greatest frequency of occurrence in the samples, found in 100% of nests ($n = 107$) (Table 2). Moreover, only *Malpighia emarginata* (Malpighiaceae) represented 59% of the total pollen grains in the nests (Fig. 3b). This plant species, together with *Heteropteris anoptera* (Malpighiaceae), constituted

the pollen dominating the diet of immature *C. analis*, (65% of all pollen grains in nests throughout the year) (Table 2). These two plant species also provided floral oils; other plant species in the samples do not offer floral oils.

Pollen of the family Leguminosae was present in 91% of the nests, represented by seven species. Leguminosae pollen constituted 26% of all the pollen grains identified in nests (Table 2). Among these species, *Centrolobium tomentosum* prevailed (12% of pollen grains) (Fig. 3b). The Leguminosae family, along with Bignoniaceae, was the most important source of nectar for *C. analis*.

Discussion

The nesting frequencies of *C. analis* did not differ between seasons, but the population showed a significant temporal variation in that parameter, with the occurrence of two peaks of activity, one of them at the end of the rainy season and beginning of the dry season (March to May), and the other at the middle of the rainy season (December). Gazola and Garófalo (2009) reported similar results for two populations of *C. analis* occurring in areas covered primarily by semi-deciduous forests. The results of both studies differ from studies carried out in other areas (Camillo et al. 1995; Morato et al. 1999; Aguiar et al. 2005; Thiele 2005), as well as from other studies in the same area of this work (Gazola and Garófalo 2003; Alonso et al. 2012), with the authors highlighting a strong tendency of association

Fig. 2 Activities of *Centris analis* and distribution of the flowering plant species considering the dry and wet seasons on the campus of University of São Paulo, Ribeirão Preto, State of São Paulo, Brazil, from March 2012 to February 2011

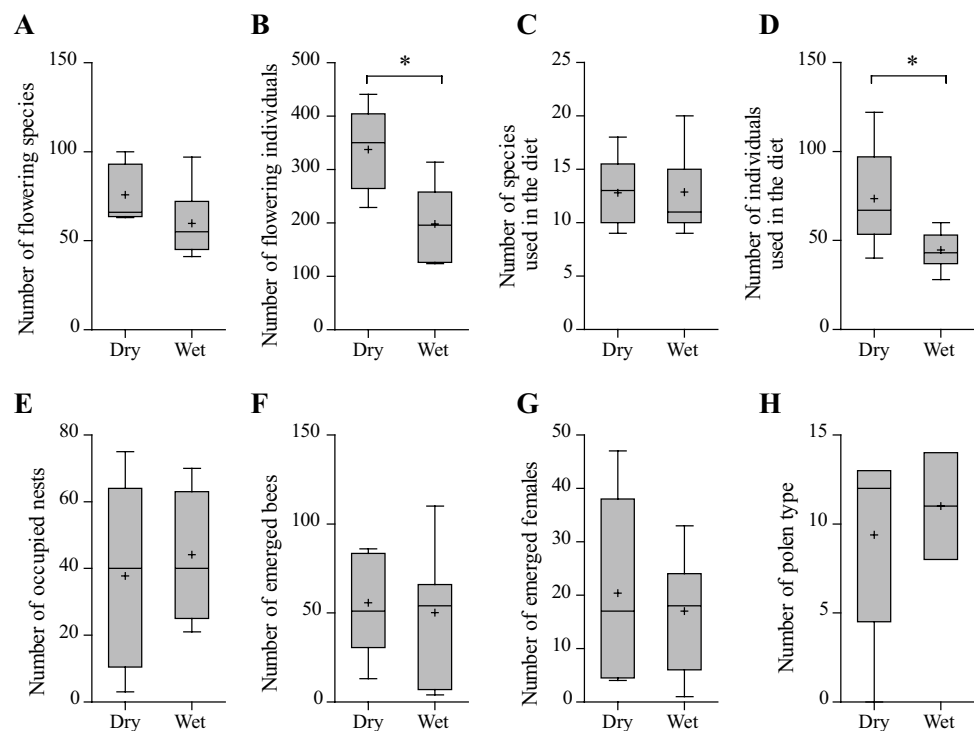


Table 2 Plant species used in the diet of immature *Centris analis* in nests established on the campus of the University of São Paulo, Ribeirão Preto, State of São Paulo, Brazil, from March 2010 to February 2011

Family	Species	CPS	2010					2011								
			M	A	M	J	J**	A	S	O	N	D	J	F		
Anacardiaceae	<i>Schinus terebinthifolia</i> Raddi	OP (12, 27)													0.03	
	<i>Spondias dulcis</i> Parkinson	OP (29)		0.72											0.08	0.40
Apocynaceae	<i>Allamanda blanchetii</i> A. DC	OP (1)														0.03
Areaceae	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	OP (27)								0.03						
Asteraceae	<i>Crepis japonica</i> (L.) Benth	OP (1, 24)				2.84				0.30						
Bignoniaceae	<i>Handroanthus chrysotrichus</i> (Mart. Ex A. DC.) Mattos	PS, OP (1)														
	<i>Handroanthus roseoalbus</i> (Ridl.) Mattos	PS, OP (1)								1.39						
	<i>Spathodea nilotica</i> Seem	OP (1)			0.50								0.02			
Cactaceae	<i>Tecoma stans</i> (L.) Juss. Ex Kunth	OP, P (33, 37)	0.35		0.05	0.03				1.44	0.10	0.02	0.03	0.28	0.05	
	<i>Pereskia bleo</i> (Kunth) DC	NI		9.75												
Commelinaceae	<i>Dichorisandra thyrsiflora</i> J.C. Mikan	OP (7, 35)				0.03										
Leguminosae	<i>Alysicarpus vaginalis</i> (L.) DC	NI														2.28
	<i>Anadenanthera macrocarpa</i> (Benth.) Brenan	P (2*)		0.03												
	<i>Arachis repens</i> Handro	NI		5.53	27.51					0.36						
	<i>Caesalpinia pulcherrima</i> (L.) Sw	P (22*)								0.08	0.13	0.10	0.03	0.05		
	<i>Cajanus cajan</i> (L.) Huth	OP (6, 17)	0.33	1.61	0.02	3.42				8.85	0.36					
	<i>Cassia fistula</i> L	OP (1)														0.03
	<i>Cassia grandis</i> L.F	OP (1)							0.40							
	<i>Centrobium tomentosum</i> Guillemin ex Benth	P (1*)	5.00	12.41	16.64	79.19				20.16	0.08			0.08	0.38	4.44
	<i>Crotalaria pallida</i> Aiton	P (9*)														
	<i>Delonix regia</i> (Bojer ex Hook.) Raf	OP (1,13)				0.03							0.14			
	<i>Desmodium uncinatum</i> (Jacq.) DC	PS								15.08	1.90	4.78	20.83	0.18		
	<i>Erythrina falcata</i> Benth	OP (14, 21)												0.03		
	<i>Glitricidia sepium</i> (Jacq.) Kunth ex Walp	OP, P (18, 15*)	1.35							0.36	3.50	5.19				
	<i>Glycine wightii</i> (Graham ex Wight & Arn.) Verde	OP (26)		10.72												
	<i>Libidibia ferrea</i> (Mart. Ex Tul.) L.P. Queiroz	PS														
	<i>Machaerium aculeatum</i> Raddi	PS	0.25	1.86	0.97	1.70				0.28	0.03	0.03	0.08	0.11	0.08	0.05
	<i>Machaerium hirtum</i> (Vell.) Stelfeld	PS														0.74
	<i>Mimosa caesalpiniiifolia</i> Benth	OP (31)		0.03												
	<i>Phaseolus</i> sp	OP (20*)				1.50				18.33						
	<i>Poincianella echinata</i> (Lam.) L.P. Queiroz	P (8)	0.03													
	<i>Poincianella pluviosa</i> (DC.) L.P. Queiroz	P (22*)								0.08						
	<i>Pterocarpus violaceus</i> Vogel	P (30)	0.13	3.61												0.20
	<i>Senna bicapsularis</i> (L.) Roxb	PS								0.10						

Table 2 (continued)

Family	Species	CPS	2010				2011							
			M	A	M	J	J**	A	S	O	N	D	J	F
Lamiaceae	<i>Senna multijuga</i> (Rich.) H.S. Irwin & Barneby	P (39*)												0.88
	<i>Stylosanthes guianensis</i> (Aubl.) Sw	OP (32*)									0.90	0.14		
	<i>Tipuana tipu</i> (Benth.) Kuntze	OP (1)										26.69		
Lythraceae	<i>Ocimum gratissimum</i> L.	OP (16)									0.02			
	<i>Cuphea gracilis</i> Kunth	P (34)								0.03				
Malpighiaceae	<i>Cuphea melvilla</i> Lindl.	OP (28)	0.03											
	<i>Heteropterys anoptera</i> A.Juss	P (38*)	66.16											
	<i>Malpighia emarginata</i> DC	P (38, 34)	26.31	53.68	54.22	10.04		36.26	55.67	91.37	72.91	71.99	95.02	77.92
Meliaceae	<i>Cedrela fissilis</i> Vell	PS						37.91						
Muntingiaceae	<i>Muntingia calabura</i> L.	PS				0.36		0.10						0.03
Myrtaceae	<i>Eugenia uniflora</i> L.	OP (11, 36)				0.02							0.14	0.03
Oleaceae	<i>Ligustrum lucidum</i> W.T. Aiton	NI												
Phytolaccaceae	<i>Galleia integrifolia</i> (Spreng.) Harms	OP (3)				0.03								
Sapindaceae	<i>Serjania lethalis</i> A. St.-Hil	OP (5, 23)						0.05						
Solanaceae	<i>Solanum cernuum</i> Vell	OP (10)				0.78								
Solanaceae	<i>Solanum violaeifolium</i> Schott	OP (10)											0.20	
Verbenaceae	<i>Duranta repens</i> L.	OP, PS (4)	0.08	0.06	0.05	0.06		0.33					0.28	
	<i>Petrea subserrata</i> Cham	OP (25)											0.03	
Number of species														
Shannon index (H')														
Evenness (J)														
Berger-Parker (D)														

In italics is represented the season cold and dry: April to August and in white the season hot and wet: September to May. CPS Contribution to pollination system

**Not possible to analyze the pollen material due to mortality and degradation of the brood cell contents. In italics are represented the meanings of the categories, P pollinator, OP other pollinators, PS verified in the present study, NI no information, *classification based on other species of the same genus

In bold are represented the pollen dominant (> 45%)

Source: 1—Agostini and Szirma (2003), 2—Aguar et al. (2003), 3—Aguirres et al. (2003), 4—Aleixo et al. (2014), 5—Alves et al. (2014), 6—Azevedo et al. (2007), 7—Boaventura and Matthes (1987), 8—Borges et al. (2009), 9—Brito et al. (2010), 10—Buchmann and Cane (1989), 11—Castro (2002), 12—Cesario and Gaglianone (2008), 13—Doyle and Luckow (2003), 14—Echeverry and Aleman (2005), 15—Frankie et al. (1976), 16—Gonçalves et al. (2008), 17—Heard (1999), 18—Kill and Drummond (2001), 20—Kingha et al. (2012), 21—Kinoshita et al. (2006), 22—Lewis and Gibbs (1999), 23—Lopes (2013), 24—Mouga and Krug (2010), 25—Navarro and Medel (2009), 26—Nogueira-Couto et al. (1998), 27—Nogueira-Neto (2002), 28—Oliveira-Melazzo and Oliveira (2012), 29—Phillips et al. (1994), 30—Pinheiro and Szirma (2007), 31—Poderoso et al. (2012), 32—Ramalho and Rosa (2010), 33—Rao et al. (2005), 34—Sazan et al. (2014), 35—Sigrist and Szirma (2014), 36—Silva and Pinheiro (2007), 37—Silva et al. (2007), 38—Vilhena et al. (2012), 28(39)—Wolowski and Freitas (2011)

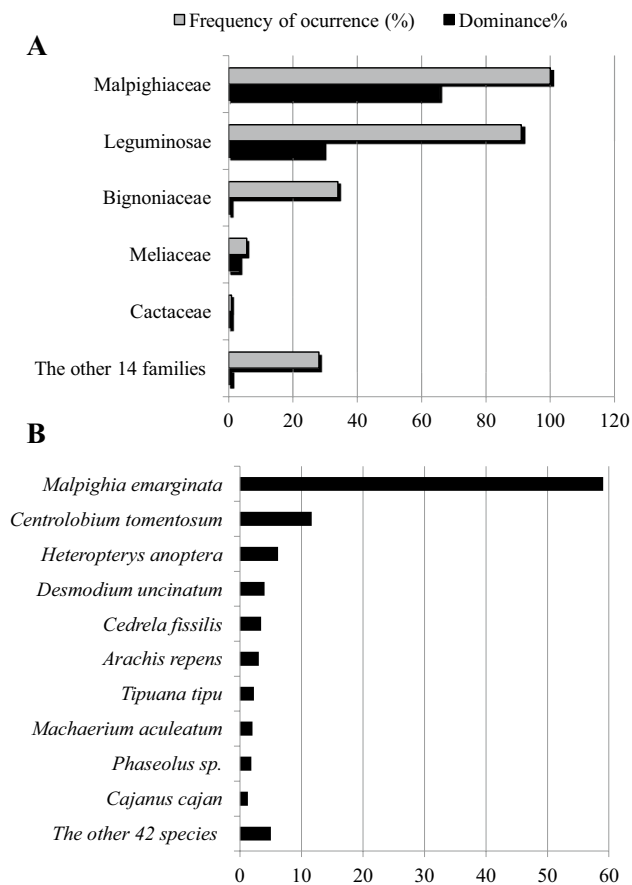


Fig. 3 Representativeness of families (a) and plant species (b) present in the diet of immature *Centris analis* in nests established in the campus of the University of São Paulo, Ribeirão Preto, State of São Paulo, Brazil, from March 2012 to February 2011

between rainfalls and nesting frequency. These differences in nesting phenology have been suggested as regular characteristics of cavity-nesting bee species, and different species would be affected differently by several factors, such as climatic factors and resource availability (Frankie et al. 1998; Tommasi et al. 2004; Oertli et al. 2005; Abrahamczyk et al. 2011; Bartomeus et al. 2011).

The period of maximum reproductive activity presented by *C. analis* was not associated with the numbers of species or flowering individuals. Similarly, in studies performed in the same area and period, Faria et al. (2012) and Aleixo et al. (2013) reported that the periods of highest food collection activity by workers of *Scaptotrigona* aff. *depilis* and *Frieseomelitta varia*, respectively, were not associated with the periods when the resources were more abundant in the urban area. The distribution of floral resources throughout the year also varied between different years, e.g., in the same studied area, in the subsequent year to that of our study, bloom was greatest during the rainy season (Aleixo et al. 2014). In the tropics, studies have shown that the

greatest insect activity is concentrated in the rainy season (Wolda 1988; Richards and Winsdor 2007) or in the transition from dry to rainy season (Silva et al. 2011). According to Wolda (1988), in areas with well-defined cycles of rainfall, insect activity subsides in the dry season.

In this study, *C. analis* nested more in the rainy season, as reported by Gazola and Garofalo (2003), than with the distribution of species of plants and flowering individuals. On the other hand, the phenology of flowering in angiosperm has been associated with weather conditions, including rainfall as the main factor. However, there are discussions pointing out that flowering is related to a set of factors and their interaction, and not only to climatic constraints, which would act as a trigger, indicating the occurrence of flowering (see Oliveira 2008). Heithaus (1979) showed that the distribution and diversity of bees in dry forest and savanna communities could be associated with strong seasonality in the tropical region. This applies to the study region, where it predominates dry forest and savanna, with most species of plants pollinated by bees (Silva et al. 2012; Aleixo et al. 2014). Woody species, although having less restriction from the absence of rain, with individuals flowering in the dry season, have flowering peaks in hot and rainy seasons (Oliveira and Gibbs 2000, 2002; Oliveira 2008). The fact is that the flowering dynamics directly implies the availability of food resources used by floral visitors, as in the case of bees, which depend exclusively on these resources (pollen, nectar, resins, and floral oils) for survival (Buchmann 1987; Vogel 1990; Minckley and Roulston 2006; Michener 2007). Nevertheless, for *C. analis*, the number of species and individuals in bloom were not associated with the nesting frequencies, suggesting that intrinsic factors of the species, such as genetic and chronobiology factors, can also strongly affect the reproductive cycle.

Centridini species may exhibit a long reproductive cycle, shorter or more than 1 per year (Aguar et al. 2006; Mendes and Rêgo 2007; Drummont et al. 2008; Gazola and Garofalo 2009). Gaglianone (2003) found two peaks in the number of species of Centridini active in the Cerrado, the first being observed in the rainy season and synchronously with the flowering peak of *Byrsonima intermedia* (Malpighiaceae), and the second in the transition to the dry season, when the most species of Malpighiaceae flowered. Centridini bees collect pollen and floral oils, especially from Malpighiaceae flowers, that are used both to build their nests and to feed larvae (Vogel 1974; Vinson et al. 1997; Aguiar et al. 2006; Alves-dos-Santos et al. 2007; Oliveira and Schindwein 2009; Dórea et al. 2010; Rabelo et al. 2012).

Besides that, floral oil was the least common resource in the study area due to low representativeness of Malpighiaceae at flowering and absence of other family that produce this floral resource. Only two species of Malpighiaceae

blossomed throughout the year. *Heteropterys anoptera*, a native liana, presented a massive bloom in February; the other is a cultivated species, *M. emarginata*, which blooms throughout the year (Silva et al. 2014a). We observed individuals at flowering during the rainy season, but with peak in April and May, corresponding to more than 90% of flowering individuals throughout the study period (Silva unpublished). Nevertheless, we know that floral phenology can vary between the years and, in the urban area, the fluctuation can be more pronounced than in native areas, due to pruning, irrigation, and fertilization. One year after the present study, Aleixo et al. (2014) working in the same area, reported the occurrence of a greater availability of oil during the rainy season, with two peaks of abundance, one in October and another in February. The phenology of *C. analis* also changes from year to year (Alonso et al. 2012), as in plant species. The maximum reproductive rate of *C. analis* observed in this study and also in other studies carried out in the same area (Alonso et al. 2012) or in a native area of semi-deciduous forest (Aguiar and Garófalo 2004) suggests a synchrony between the activities of collecting oil by the bees and the flowering period of the species of Malpighiaceae.

According to Vogel (1990), there is a close relationship between bees of the Centridini tribe and plants of the family Malpighiaceae, which can be considered a result of a long evolutionary history between these two groups; this would explain the success of this family in the Americas. Malpighiaceae species also bloom in the dry season, with asynchrony between them (Silva 2009), but the peak with the highest number of flowering species and individuals occurring in the rainy season (Silberbauer-Gottsberger and Gottsberger 1988; Silva 2009). Some Centridini species can exhibit a reproductive period synchronized with Malpighiaceae species (Gaglianone 2003), e.g., *Epicharis bicolor* and *Byrsonima intermedia* (Rocha-Filho et al. 2008). Moreover, there is a strong association of floral oil production and the availability of floral oil supplies with the richness and abundance of Centridini bees (Rosa and Ramalho 2011; Pacheco Filho et al. 2015).

The use of floral resources from 52 different plant species throughout the year, varying from eight to 14 pollen types per month, allows classifying *C. analis* as a generalist species, as already described by other authors (Oliveira and Schlindwein 2009; Dórea et al. 2010; Rabelo et al. 2012). However, in the present study, we observed a clear selectivity of pollen of *M. emarginata*, which represented more than 59% of all the pollen grains provisioned throughout the year. The pollen preference by *M. emarginata* was also emphasized by Oliveira & Schlindwein (2009). These authors found a representativeness of over 90% of pollen in the nests of *C. analis* and indicated *C. analis* as one of the few solitary species to be managed in West Indian Cherry

crops in Brazil. The second most important species in the diet of immature *C. analis*, *H. anoptera*, represented more than 66% of the pollen material in the nests analyzed in March, which were provisioned in February, when this species showed massive flowering. In these same samples, we also identified pollen of *M. emarginata* (26%), showing *C. analis* willingness to use this cultivated species in addition to the native species. In natural areas of Cerrado, Rabelo et al. (2012) studied *C. analis* and observed that *Heteropterys* spp. accounted much more of the pollen provisioned in brood cells (70–94%).

Unlike other *Centris* species that add floral oil to the larval food (Simpson et al. 1977; Vinson et al. 1997; Pereira and Garófalo 1996; Aguiar and Garófalo 2004), females of *C. analis* use that resource only in the construction of the nest (Vieira de Jesus and Garófalo 2000). The nectar used by *C. analis* was collected mainly from plant species of the family Leguminosae, such as *Arachis repens*, *Centrolobium tomentosum*, *Desmodium uncinatum*, *Centrosema* sp., *Tipuana tipu*. These plant species present papilionoid flower (Sensu Faegri & van der Pijl 1979), wings, and the petals of the keel (Westerkamp 1997) that protects the androecium, gynoecium, and the nectariferous chamber. The odor, landing platform, resource guides, and zygomorphy are traits of these flowers that are associated with the bee pollination system (Faegri & van der Pijl 1979). The nectar is the main floral resource involved in attracting floral visitors in papilionoid flowers (Amaral-Neto et al. 2015). While collecting nectar in flowers, female of *C. analis* accidentally takes pollen grain upon to their body and, during the cleaning process, the bees transfer the pollen grains to the scope and subsequently provision them in brood cells (Michener 2007). Furthermore, *C. tomentosum* was also used as a pollen source, accounting for 79% of the diet of immature *C. analis* in June. The floral morphology of *C. tomentosum* enables the collection of pollen and nectar by female *C. analis*.

The present study allowed determining the floral resources used by the solitary bee *C. analis* for feeding progeny, which is one of the first steps in the management and conservation of this species (Silva 2009). The campus of USP-RP is evidently important for the maintenance of communities of floral visitors and pollinators, especially bees (Camargo and Mazucato 1984; Silva et al. 2007; Faria et al. 2012; Aleixo et al. 2013), which may be responsible for the pollination of almost 70% of the plants sampled in this area (Aleixo et al. 2014). Among these plants pollinated by bees, at least 27% are pollinated by *C. analis*, emphasizing the importance of preserving this bee and the plant diversity in urban areas, as was also evidenced for other species of pollinators (Silva et al. 2007; McKinney 2008). Studies show that cities work as refuges for Euglossini (López-Urbe et al. 2008), Bombini (McFrederick and

Le Buhn 2006), and solitary bees (Tommasi et al. 2004; Zanette et al. 2005). Therefore, it is important to know the availability of floral resources and their implication in the maintenance of bees in urban environments (Aleixo et al. 2014).

Acknowledgements We thank FAPESP (process #2010/10285-4) and CAPES-PNPD (process #02958/09-0), for financial support, and Research Center on Biodiversity and Computing (BioComp): RCPol-Redes de Catálogos Polínicos online (FDTE process#001505). We thank the editors immensely for the comments that helped to improve this article.

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