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FLOWERING AND POLLINATORS OF THREE DISTYLOUS SPECIES OF *Psychotria* (Rubiaceae) CO-OCCURRING IN THE BRAZILIAN ATLANTIC FOREST¹

Celice Alexandre Silva² e Milene Faria Vieira³

ABSTRACT – This study investigates the flowering and pollinators of the floral morphs of three co-occurring distylous species, *Psychotria conjugens* Müll., *P. hastisepala* Müll. Arg. and *P. sessilis* Vell., in two consecutive flowering seasons in an Atlantic Forest fragment in southeastern Brazil. The species have diurnal, cream-colored, tubular, nectariferous flowers and their flowering occurs in the rainy season, from September to April, with little or no overlapping between species, characterizing a staggered flowering. The flowering of the long- and short-styled floral morphs of each species was synchronous, but the number of open flowers per day per morph tended to vary in each flowering season. These numbers were higher in *P. sessilis* and *P. conjugens* and, probably, resulted in higher total numbers of visits on its flowers (up to 1084 visits in *P. sessilis* and 756 in *P. conjugens*), compared to that observed in *P. hastisepala* (up to 71). There was a higher frequency of visits to long-styled flowers of all species. The bee *Ariphanarthra palpalis* was a common pollinator to all species. This bee is native to Brazil, solitary, considered relatively rare and its host plants were unknown. Other native bees (*Melipona* spp.) also visited the flowers of the *Psychotria* species. The availability of flowers with similar floral features over eight months, the staggered flowering and common pollinators appear to be part of a strategy to attract floral visitors, minimizing the competition for pollinators and then favoring the legitimate pollination of these plants.

Keywords: Bees; Sequential flowering; Frequency of visits.

FLORAÇÃO E POLINIZAÇÃO DE TRÊS ESPÉCIES DISTÍLICAS DE *Psychotria* (Rubiaceae) COCORRENTES NA MATA ATLÂNTICA BRASILEIRA

RESUMO – Este estudo objetivou investigar a floração e polinização dos morfos florais de *Psychotria conjugens* Müll., *P. hastisepala* Müll. Arg. e *P. sessilis* Vell., espécies distílicas e coocorrentes. As observações foram feitas em duas florações consecutivas, em um fragmento de Mata Atlântica do Sudeste do Brasil. As espécies têm flores com antese diurna, cor creme, tubular, nectaríferas. A floração ocorre na estação chuvosa, de setembro a abril, com pouca ou nenhuma sobreposição entre as espécies, caracterizando uma floração escalonada. A floração dos morfos florais, longistilo e brevistilo, de cada espécie foi síncrona, mas o número de flores abertas por dia por morfo tendeu a variar em cada floração. Esses números foram maiores em *P. sessilis* e *P. conjugens* e, provavelmente, resultaram em maiores números totais de visitas nas suas flores (até 1.084 visitas em *P. sessilis* e 756 em *P. conjugens*), em comparação com o observado em *P. hastisepala* (até 71). A frequência de visitas foi maior nas flores longistilas de todas as espécies. A abelha *Ariphanarthra palpalis* foi o polinizador comum a todas as espécies. Esta abelha é nativa do Brasil, solitária, considerada relativamente rara, e suas plantas hospedeiras eram desconhecidas. Outras abelhas nativas (*Melipona* spp.) também visitaram as flores das espécies de *Psychotria*. A disponibilidade de flores com características florais semelhantes ao

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longo de oito meses, a floração escalonada e polinizadores em comum parecem ser partes de uma estratégia para atrair visitantes florais, minimizando a competição por polinizadores e, consequentemente, favorecendo a polinização legítima dessas plantas.

Palavras-chave: Abelhas; Floração sequencial; Frequência de visitas.

1. INTRODUCTION

The key event in the reproductive biology of angiosperms is flowering (PRIMACK, 1985) and studies on this phenophase are fundamental to understand their regulatory factors (MARTIN-GAJARDO; MORELLATO, 2003). In tropical species, the onset of flowering is usually triggered by the greater rainfall intensity (rainy season) favoring synchronous flowering within populations (PENHALBER; MANTOVANI, 1997). In a population, the number of simultaneously open flowers varies between plant individuals of the same species and the amount of floral resources influences the pattern of pollinator visits (KARRON; MITCHELL, 2012).

The flowering of distylous species of *Psychotria*, analogous to the above description for tropical species, is mostly synchronous, annual and occurs during the rainy season (CASTRO; OLIVEIRA, 2002; COELHO; BARBOSA, 2004). This phenological pattern has been ascribed to the attraction of pollinators, in particular of bees and butterflies, and to obtain greater reproductive success of each floral morph (CASTRO; OLIVEIRA, 2002), which in turn is related to the amount of flowers available, visitation frequency and pollinator behavior (DONALDSON et al., 2002; SAKAI; WRIGHT, 2008).

Interestingly, the co-occurring distylous *Psychotria* species tend to have sequential flowering (ALMEIDA; ALVES 2000; CASTRO; OLIVEIRA, 2002; PEREIRA et al., 2006) and common pollinators (CASTRO; OLIVEIRA, 2002), but no evidence of interspecific competition have been found (ALMEIDA; ALVES, 2000; CASTRO; OLIVEIRA, 2002).

The present study aims to investigate the flowering (inflorescences per plant, flowers per inflorescence and open flowers per plant per day and number of flowers per peak of flowering) and the identity of the pollinators of each floral morphs of *Psychotria conjugens* Müll. Arg., *P. hastisepala* Müll. Arg. and *P. sessilis* Vell.

Answers to the following questions were sought: (a) Is the flowering of the floral morphs of each species synchronous? (b) Is the flowering of the different species synchronous? (c) Which are the pollinators? (d) Do the species have pollinators in common? (e) Are the visitation frequencies of the pollinators to the floral morphs of each species similar?

2. MATERIAL AND METHODS

2.1. Study area and species

The study was conducted at the Estação de Pesquisa Treinamento e Educação Ambiental Mata do Paraíso (EPTEAMP), in the municipality of Viçosa (20° 45'S, 42° 51'W), southeastern Brazil, at about 650 m asl. The climate of Viçosa is characterized by an average annual temperature of 19 °C and a mean annual rainfall of 1300-1400 mm, most of which falls between September and March, and a relative humidity of 80-85%. The original vegetation of the study area was part of the Atlantic forest classified by VELOSO et al., (1991) as submontane semideciduous forest. The EPTEAMP is an environmentally protected secondary forest, covering an area of about 194 ha.

Psychotria conjugens and *P. hastisepala* are subshrubs (plant height 1.0 - 2.5 m), with distribution restricted to Brazil (ANDERSSON, 1992), in phytogeographical domains of savanna and Atlantic Forest (TAYLOR et al., 2015). *P. sessilis* is a shrub (plant height 1.5 - 3.5 m) also found in several other South American countries (ANDERSSON, 1992). The studied species grow in the understory of EPTEAMP and are distylous (PEREIRA et al., 2006). The flowers of the three species are diurnal, nectariferous, tubular, cream-colored and last one day (PEREIRA et al., 2006).

The fruits are drupaceous, blue, or dark purple at maturity and ornithochorous. Each fruit produces 1-2 seeds (pers.comm.). Voucher specimens were deposited in the VIC (26,963, 26,964 and 26,974).

2.2. Flower production

Two consecutive flowering seasons (September 2004 to April 2005 and September 2005 to April 2006) were monitored weekly. In the first flowering season, 19 plants with short-styled flowers (S) and 23 long-styled flowers (L) of *P. sessilis* were labeled, 09 S and 04 L of *P. conjugens* and 22 S and 18 L of *P. hastisepala*. In the second flowering season, 10 S and 10 L plants of each species were labeled. Of each plant and flowering season, the numbers of inflorescences/plant and open flowers/plant/day were recorded, except for *P. sessilis*. From this species, in view of its height and the high number of inflorescences and flowers, these data were recorded weekly on three randomly chosen branches per year and plant. The number of flowers/inflorescence was recorded only for the first flowering season (N = 30 for each species and morph), in all species.

2.3. Flower visitors

The flower visitors were observed, captured and killed, and later mounted on entomological pins, labeled and identified with the help of a specialist. Voucher specimens were deposited in the Museu Regional de Entomologia da Universidade Federal de Viçosa (UFVB).

At the flowering peak of each species in 2004/2005 and 2005/2006, the visitation frequency of flowers of both morphs was recorded in plants at least 30 meters away from the forest edge, to minimize the edge effects. For this measurement, in both flowering seasons, from 7:00 to 15:00, on three consecutive days for *P. sessilis* and four consecutive days for *P. hastisepala*, flower visitors were identified and their visits counted. The visits were counted in eight blocks of 30 min, alternating the floral morphs, resulting in a total of 12 and 16 h of observation/flowering season for *P. sessilis* and *P. hastisepala*, respectively. The flower visitors of *P. conjugens* were only identified and quantified in the flowering of 2005/2006, similarly as described for *P. sessilis* (12 h of observation).

Flower visitors were considered legitimate pollinators if they touched anthers and stigmas and collected pollen or nectar (legitimate visits).

2.4. Statistical analyses

Statistical analyses were conducted using the program "General Linear Model," of Statistica version

5.5 (STAT SOFT, 2002). In the analysis of variance, the One - way ANOVA test was applied (ZAR, 1999).

3. RESULTS

3.1. Flowering

In both monitored flowering seasons, *Psychotria sessilis* (Fig. 1AB) flowered first, from September to December 2004 (Fig. 1A) and from September to November 2005 (Fig. 1B), in the rainy season. In these periods, synchrony of the floral morphs was observed as well as two flowering peaks (peak of the first flowering in October and December and the second in October and November) (Fig. 1AB). The peaks were separated by periods of 7-18 days without flower formation. No significant difference between the morphs were stated in terms of the average number of inflorescences/plant, flowers/inflorescence and open flowers/plant/day in both flowering seasons (Table 1). Despite the flowering synchrony of the morphs and the similarity between them in the mean values of the previous parameters, there was a trend of one morph to produce more flowers/peak/year (Table 1). There was no significant difference between flowers/morph/peak in the peaks of 2004 and 2005. However, significant differences were recorded in the total number of flowers per morph in the first flowering and no difference in the second. This variation may be related to the number of plants sampled in each flowering season (Table 1).

In the first flowering, the first flowers of *Psychotria conjugens* (Fig. 1CD) were observed in November in both years overlapping with the flowering of *P. sessilis*. The flowering periods ended in January 2005 and December 2005, respectively (Fig. 1CD), also during the rainy season. In the first reproductive episode, there were two peaks, in November and in January, with a drop in flower production of both morphs between the peaks, similarly as reported for *P. sessilis*. In the second reproductive episode, however, there was only one flowering peak in December 2005 (Fig. 1D). In both flowering seasons, there was synchrony between floral morphs (Fig. 1CD). There were significant differences between the floral morphs of first flowering, the average number of inflorescences/plant (Table 1) and no significant difference for this parameter in the second flowering (Table 1).

In the flowering of 2004, the average number of flowers/inflorescence was significantly higher for the long-styled morph, as well as the average number of

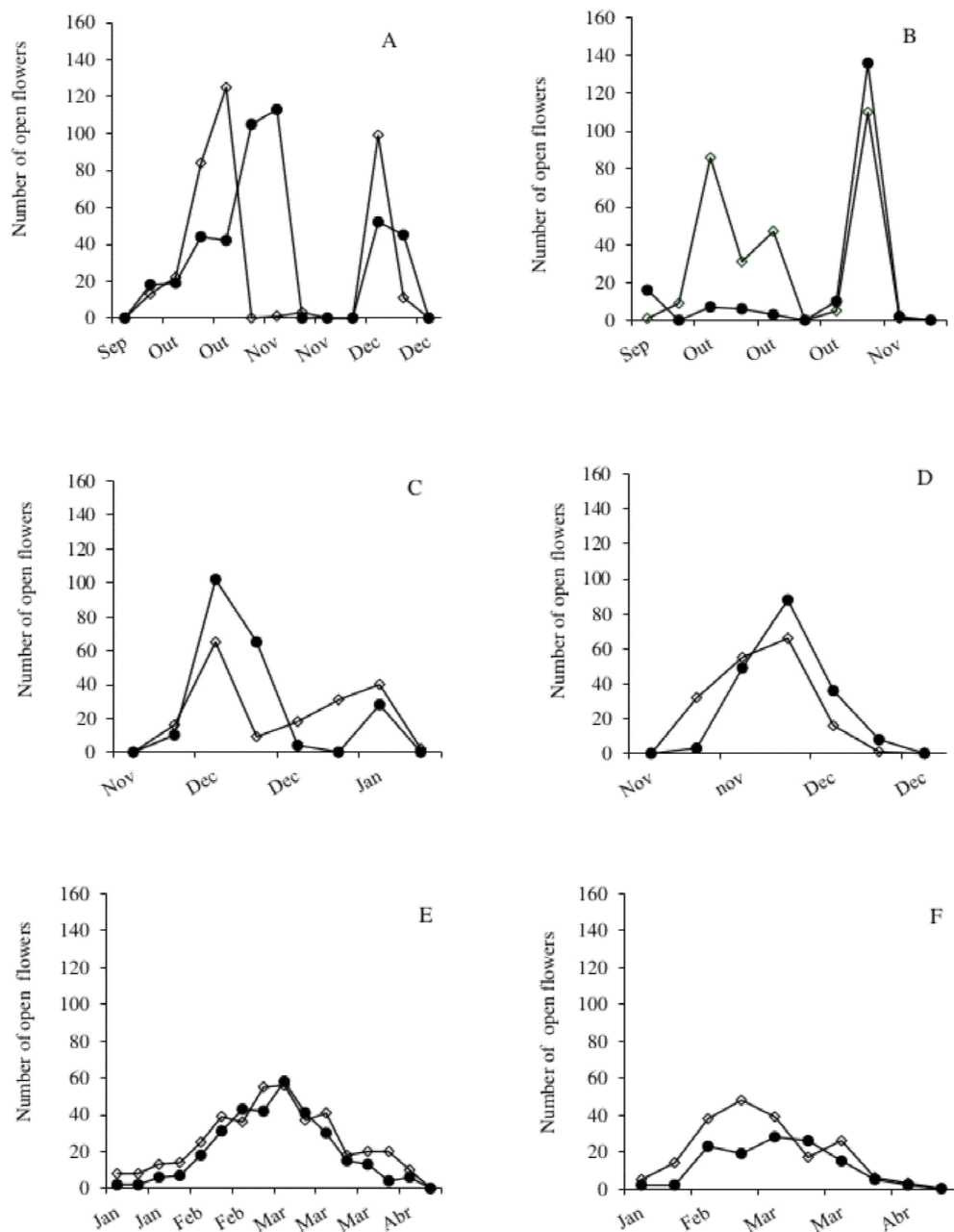


Figure 1 – Flowering of short-styled (◇) and long-styled flower morphs (●) in species of *Psychotria*: *P. sessilis*, from September to December 2004 (A) and from September to November 2005 (B); *P. conjugens*, from November 2004 to January 2005 (C) and from November to December 2005 (D); and *P. hastisepala*, from January to April 2005 (E) and from January to April 2006 (F).

Figura 1 – Floração de morfos brevistilo (◇) e longistilo (●) de espécies de *Psychotria*: *P. sessilis*, de setembro a dezembro de 2004 (A) e de setembro a novembro de 2005 (B); *P. conjugens* de novembro de 2004 a janeiro de 2005 (C) e de novembro a dezembro de 2005 (D) e de *P. hastisepala*, de janeiro a abril de 2005 (E) e de janeiro a abril de 2006 (F).

Table 1 – Mean numbers and standard deviation of inflorescences/plant, flowers/inflorescence and open flowers/plant/day and number of flowers/peak in two consecutive flowering seasons, in 2004/2005 and in 2005/2006, of *Psychotria sessilis*, *P. conjugens* and *P. hastisepala* in Viçosa, southeastern Brazil.

Tabela 1 – Números médios e desvio padrão de inflorescência/planta, flores/inflorescência e flores abertas/planta/dia e número de flores/pico em duas estações de floração consecutivas, em 2004/2005 e 2005/2006, de *Psychotria sessilis*, *P. conjugens* e *P. hastisepala* em Viçosa, sudeste do Brasil.

<i>Psychotria sessilis</i>					
Year /No. of plant/ morph	Infl./ plant	Flowers/ infl.	Open flowers/ plant/ day	Flowers/ peak	
	$\bar{X} \pm SD$	$\bar{X} \pm SD$	$\bar{X} \pm SD$	1°	2°
2004/ S (19)	51.34 ± 40.63	9.46 ± 2.64	20.40 ± 22.20	244	144
L (23)	68.08 ± 80.67	7.86 ± 1.56	21.30 ± 25.50	341	97
	F=0.60 p=0.44	F=2.56 p=0.11	F=0.013 p=0.90	F=0.54 p=0.46	F=1.22 p=0.28
Total number of flowers per peak				585	241
2005/ S (10)	40.00 ± 25.01	-	11.44 ± 14.80	174	116
L (10)	45.50 ± 44.79	-	07.03 ± 16.32	32	148
	F=0.26 p=0.61		F=0.29 p=0.60	F=1.90 p=0.18	F=2.23 p=0.15
Total number of flowers per peak				206	264
<i>Psychotria conjugens</i>					
Year /No. of plant/ morph	Infl./ plant	Flowers/ infl.	Open flowers/ plant/ day	Flowers/ peak	
	$\bar{X} \pm SD$	$\bar{X} \pm SD$	$\bar{X} \pm SD$	1°	2°
2004/ S (9)	19.65 ± 1.06	12.30 ± 7.43	14.07 ± 5.70	139	42
L (4)	18.25 ± 3.50	22.68 ± 8.83	26.58 ± 6.80	181	28
	F=13.86 p=0.004	F=35.19 p=0.0001	F=8.15 p=0.03	F=26.50 p=0.0001	F=2.42 p=0.22
Total number of flowers per peak				320	70
2005/ S (10)	2.90 ± 2.51	-	4.22 ± 2.25	170	-
L (10)	3.30 ± 1.76	-	4.44 ± 3.51	184	-
	F=0.16 p=0.68		F=2.23 p=0.14	F=17.84 p=0.23	
Total number of flowers per peak				354	-
<i>Psychotria hastisepala</i>					
Year / No. of plant/ morph	Infl./plant	Flowers/ infl.	Open flowers/ plant/ day	Flowers/ peak	
	$\bar{X} \pm SD$	$\bar{X} \pm SD$	$\bar{X} \pm SD$		
2005/ S (22)	14.20 ± 06.54	6.91 ± 2.77	2.78 ± 2.41	410	
L (18)	15.27 ± 15.10	9.03 ± 1.88	2.75 ± 2.28	322	
	F=0.28 p=0.56	F=2.44 p=0.12	F=1.06 p=0.30	F=1.06 p=0.30	
Total number of flowers				732	
2006/ S (10)	17.10 ± 4.09	-	2.14 ± 2.70	193	
L (10)	13.30 ± 5.33	-	1.35 ± 1.60	122	
	F=4.28 p=0.05		F=5.60 p=0.01	F=5.62 p=0.01	
Total number of flowers				315	

open flowers/plant/day; in the flowering of 2005, no significant differences were observed for this last parameter, although the average number of flowers/inflorescence was similar. In the flowering of 2004, there were significant differences in the number of flowers/morph in the first peak; a larger number of long-styled flowers were produced, while there was no difference in the second peak (Table 1). The total number of flowers/morph, in the first flowering, did not differ significantly, however the flower production was significantly higher in the first peak ($F = 31.44$, $p = 0.0001$). In the second flowering, the flower production of both morphs was similar (Table 1). At both flowering seasons, despite the higher number of plants studied, there was a drop in the production of inflorescences/plant and open flowers/plant/day (Table 1).

Psychotria hastisepala initiated flowering in January 2005 and January 2006 (Fig. 1EF), also in the rainy season, with little or no overlapping with the flowering of *P. conjugens*. This species had the least abundant flowering of all species studied. Both flowerings ended at the beginning of the dry season.

Only one flowering peak was observed, from February to March (Fig. 1EF), and the flowering of the morphs was synchronous. There was no significant difference between the morphs in the average number of inflorescences/plant and flowers/inflorescence in both flowering seasons (Table 1). In the flowering of 2005, there was no significant difference between the morphs in the number of open flowers/plant/day, and in 2006, this parameter was significantly higher in the short-styled morph (Table 1). In the flowering of 2005, the number of flowers/morph at the peak of flowering was not significantly different, but differences were observed in 2006 (Table 1). The production of flowers/year was significantly higher in the flowering of 2005 ($F = 16.53$, $p = 0.0006$).

3.2. Flower visitors

Insects of the order Hymenoptera, Lepidoptera, Diptera, and Coleoptera were recorded as flower visitors on the species studied (Table 2). Among these, mainly the native bees *Ariphanarthra palpalis* (Halictidae, female and male), *Melipona bicolor*, *M. mondury*, *M. quadrifasciata* (Apidae), and *Trichocerapis mirabilis* (Apidae), and the exotic bee *Apis mellifera* were considered pollinators because of their visit behavior and visitation frequency (Table 2). During their visits,

in search of nectar, these bees inserted part of their body into the floral tube and touched anthers and stigmas in both morphs, promoting legitimate pollination. During foraging bouts, generally all open flowers of a plant were visited and, in this case, illegitimate, geitonogamous pollination (*sensu* RICHARDS, 1997) tended to occur. The flowers were visited mainly in the morning, between 7:00 and 10:00 h, continuing until 14:30, when the flowers of all species became senescent.

On *P. sessilis* flowers, six bee species were observed and three of them, *M. quadrifasciata*, *M. bicolor* and *Apis mellifera*, were common in both flowering seasons and played an important role as pollinators, because their visitation frequency to both floral morphs was the highest (Table 2). *Melipona quadrifasciata* and *M. bicolor* accounted for 72.60 and 69.37% of the total number of visits in the first (2004) and the second flowering (2005), respectively (Table 2). The percentage of total visits of the exotic bee *A. mellifera* was below 18.0% (Table 2).

The visits of other bees and one butterfly occurred in only one flowering season and represented low percentages (Table 2), except for *Ariphanarthra palpalis*; this bee visited both morphs, accounting for about 15.0% of all visits, in the flowering of 2005. Long-styled flowers tended to receive a greater number of visits; in the second flowering in 2005, these flowers were visited about 1.8 more times than the short-styled (Table 2). On the 12 h observation/year for the counting of flower visitors, insects were recorded on the flowers for 91.67% of the time in the flowering of 2004, and for 75% in 2005.

Three bee species in common with *P. sessilis* were observed on *P. conjugens* flowers (Table 2). *Ariphanarthra palpalis* and *M. bicolor* were the most important pollinators on both morphs (Table 2). These bees were responsible for 87.32% of all visits. *Melipona quadrifasciata* also served as pollinator of both morphs, but at a low percentage (5.02% of total visits). The frequency of visits of flies together with beetles were unrepresentative (5.69%) compared to the bees (92.34%). Long-styled flowers were visited nine times as much as the short-styled (Table 2). On the 12 h observation for the counting of flower visitors, insects on flowers were recorded for 66.7% of the time.

Four bee species were observed on *P. hastisepala* flowers (Table 2): *A. palpalis* and *M. mondury* in common with *P. sessilis* and *A. palpalis* in common with *P.*

Table 2 – Frequency of visits of insects to the flowers *Psychotria sessilis*, *P. conjugens* and *P. hastisepala*, in two consecutive flowering seasons in Viçosa, southeastern Brazil.**Tabela 2** – Frequência de visitação de insetos às flores de *Psychotria sessilis*, *P. conjugens* e *P. hastisepala*, em duas estações de floração consecutivas em Viçosa, Sudeste do Brasil.

Insects (order/ family/ species)	Number of visits (%)					
	2004			2005		
	S	L	Total/ (% visits)	S	L	Total/ (% visits)
<i>Psychotria sessilis</i>						
Hymenoptera/ Apidae/						
<i>Apis mellifera</i> Lepeletier, 1836	(19.15)	(16.84)	194 (17.90)	(19.89)	(08.53)	123 (12.64)
<i>Melipona bicolor</i> Lepeletier, 1836	(29.03)	(11.73)	213 (19.65)	(29.83)	(36.88)	334 (34.33)
<i>Melipona mondury</i> Smith, 1863	(05.85)	(06.97)	70 (06.46)	-	-	-
<i>Melipona quadrifasciata</i> Lepeletier, 1836	(41.73)	(62.41)	574 (52.95)	(29.83)	(38.00)	341 (35.04)
Halictidae/♀ <i>Ariphanarthra palpalis</i> Moure, 1951	-	-	-	(17.61)	(14.00)	149 (15.31)
<i>Augochlora</i> sp.	-	-	-	(02.84)	(02.58)	26 (02.67)
Lepidoptera/ Nymphalidae/ Morph-species 1	(04.23)	(02.04)	33 (03.04)	-	-	-
Total	496	588	1084	352	621	973
<i>Psychotria conjugens</i>						
Hymenoptera/ Apidae/						
<i>Melipona bicolor</i> Lepeletier, 1836				(18.42)	(41.32)	295 (39.02)
<i>Melipona quadrifasciata</i> Lepeletier, 1836				(21.05)	(3.23)	38 (05.02)
Halictidae/♀ <i>Ariphanarthra palpalis</i> Moure, 1951				(17.10)	(51.80)	365 (48.30)
Diptera/Morph-species 1/				(17.10)	(1.50)	23 (03.04)
Coleoptera/Morph-species 1/				(11.84)	(1.61)	20 (02.65)
Total				76	680	756
<i>Psychotria hastisepala</i>						
	2005			2006		
Hymenoptera/ Apidae/						
<i>Melipona mondury</i> Smith, 1863	-	-	-	(6.45)	(30.00)	14 (19.71)
<i>Trichocerapis mirabilis</i> Smith, 1865	(44.00)	(48.48)	27 (46.55)	-	-	-
Halictidae/♀ <i>Ariphanarthra palpalis</i> Moure, 1951	(12.00)	(12.12)	7 (28.00)	-	-	-
<i>Augochlora</i> sp.	-	-	-	(9.70)	(15.00)	9 (12.68)
Morph-species 1	(28.00)	(24.24)	15 (25.90)	-	-	-
Diptera/Morph-species 1	-	-	-	(70.96)	(30.00)	34 (47.89)
Coleoptera/Morph-species 1	(16.00)	(15.15)	9(15.51)	(13.00)	(25.00)	14 (19.71)
Total	25	33	58	31	40	71

S = short-styled, L = long-styled

conjungens (Table 2). All bees were observed in only one flowering season. In the first flowering in 2005, *T. mirabilis* and *A. palpalis* were the most important pollinators on both morphs, accounting together for 74.55% of the total visits and in the second flowering in 2006, *M. mondury* and *Augochlora* sp. were the most important pollinators of both morphs, but accounted together for only 32.39% of all visits (Table 2). In the first flowering, one butterfly species was observed, and in the second a fly species, which accounted for 25.90 and 47.89% of all visits, respectively (Table 2). These insects, however, due to the small body size and/or visit behavior did not seem to act as pollinators; the same was true for the beetle observed in both flowerings (Table 2). These latter insects cut the stigmas of the long-styled flowers. The total number of visits/morph was similar in both flowerings, although the long-styled flowers received a greater number of visits (Table 2). On the 16 h observation/year for the counting of flower visitors, insects were recorded on flowers over 56.25% of the time in the flowering of 2005, and over 37.50% in 2006.

4. DISCUSSION

The flowering of each studied species was restricted to a few months of the year (annual flowering *sensu* NEWSTROM et al., 1994) and to the rainy season, when temperatures are higher. This pattern is similar to that reported for other *Psychotria* species (ALMEIDA; ALVES, 2000; MORELLATO et al., 2000; PEREIRA et al., 2006).

The flowering of the species occurred in a sequence, over eight months. This flowering behavior was also reported for *Psychotria nuda* and *Psychotria brasiliensis* (ALMEIDA; ALVES, 2000) and for *Psychotria birotula*, *Psychotria mapouriodes* and *Psychotria pubigera* (CASTRO; OLIVEIRA, 2002). The continuous availability of nectar by flowers of different species with similar characteristics is considered a strategy leading to the formation and retention of a “food image” by common pollinators (THOMPSON, 1980), minimizing the competition for pollinators among the species. The staggered flowerings of the *Psychotria* species seem to promote a “replacement series” (*sensu* MACIOR, 1971), by which the floral resources are available to pollinators for a long period of the year.

Two sequential peaks of flower production in the studied flowering seasons, mainly in *P. sessilis*, were also observed in *P. mapouriodes* (CASTRO; OLIVEIRA,

2002) and *P. tenuinervis* (RAMOS; SANTOS, 2006). However, the success is surely also related to the amount of flowers available and the visitation frequency of flowers of each morph and both tend to vary between flowering seasons, as showed here. The composition and abundance of pollinator species may vary among years, as observed in this study, and populations (VIEIRA; SHEPHERD, 2002). The flower attractiveness depends on the number of inflorescences, the number of flowers opened/day and the availability of floral resources seems to be one of the factors that determine the diversity of pollinators (HERRERA, 1991; DONALDSON et al., 2002). In fact, the highest numbers of visits/year to the flowers of the studied species, observed in *P. sessilis* and *P. conjungens*, corresponded to the highest number of open flowers/day and, probably, to the greatest availability of resources.

The higher frequency of visits to long-styled flowers of all species studied, but mainly of *P. conjungens*, was also recorded in other *Psychotria* species (CASTRO; OLIVEIRA, 2002). The greater attractiveness of one floral morph for pollinators may cause an asymmetrical and unidirectional pollen flow (BARRETT, 1992). It is known that the reproductive success of distylous species, including those studied here, depends on the gene flow between floral morphs, whose agents are the pollinators, since illegitimate pollinations normally result in incompatibility (CASTRO et al., 2004; SILVA et al., 2010). One result of this preference for long-styled flowers is the deposition of incompatible pollen, resulting in stigma occlusion, preventing the compatible grains from germinating (GANDERS, 1979), affecting the fruiting of the morph in question. Indeed, in the study area, the long-styled flowers of *P. conjungens* and, mainly, of *P. hastisepala* produced lower fruit set than the obtained in short-styled flowers (SILVA; VIEIRA, 2013; SILVA et al., 2014).

Among the pollinator bees of the studied *Psychotria* species, *Ariphanarthra palpalis* was a common pollinator. This species is solitary, restricted to the forest interior, active in the early morning hours and on cloudy days. In entomological collections, it is considered relatively rare and its host plants are unknown (G. A. MELO, 2007 – pers. comm.). Therefore, the observations of the use of the floral resources of the studied species by males and females of this bee are unprecedented data. It has a peculiar morphological characteristic, a long tongue, making its visits to the

tubular flowers of *Psychotria* possible. It is known that seven other *Psychotria* species occur in the understory of this study area, which also bloom in the rainy season (PEREIRA et al., 2006). Could these bees depend on the floral resources of *Psychotria* species, characterizing them as oligolectic bees?

Other common pollinators to *Psychotria* species belong of the *Melipona* genus. These bees are social, have perennial colonies and visit several floral types belonging to different families (CRUZ et al., 2005). However, some studies have shown that the persistence of different species of this genus depends on forest habitats, as they were not found in open native or anthropogenic environments (SILVEIRA et al., 2002). Among the species collected in the study area, *Melipona bicolor* is presumably threatened in the state of Minas Gerais (CAMPOS, 1998). Aside from the dependence on forests, this species needs relatively large hollow trees for nesting (SILVEIRA et al., 2002). Similarly, the solitary bee *Trichoceraphis mirabilis*, observed on flowers of *P. hastisepala*, depends on forest habitats, which influences its geographical distribution (SILVEIRA et al., 2002). So, except for the introduced *Apis mellifera*, the pollinator bees require forest habitats, similarly to the studied *Psychotria* species, which grow in the forest understory.

5. CONCLUSION

The flowering of *Psychotria sessilis*, *P. conjugens* e *P. hastisepala* is staggered, following this sequence of species, over eight months and in the rainy season. In each species, the flowering of the morphs is synchronous. The species have a common pollinator, the solitary bee *Ariphanarthra palpalis*. Other native pollinating bees belong to the *Melipona* genus. The visitation frequencies of the pollinators to the floral morphs of each species differ between morphs and flowering season. There is a higher frequency of visits to long-styled flowers, compared to the short-styled flowers, of all species studied.

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