ACTA
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Interactions between carpenter bees and orchid bees (Hymenoptera: Apidae) in flowers of *Bertholletia excelsa* Bonpl. (Lecythidaceae)

Charles Fernando dos SANTOS[1] & Maria Lúcia ABSY[2]

ABSTRACT

Competition between two species of bees for the same type of floral resource may generate antagonistic behavior between them, especially in cultivated areas where food resources are limited, seasonally and locally. In this study, was tested the hypothesis of antagonism between two solitary bee species of the family Apidae, *Eulaema mocsaryi* (Euglossini) and *Xylocopa frontalis* (Xylocopini), visiting the Brazil nut flowers (*Bertholletia excelsa*: Lecythidaceae) in a central Amazonia agricultural area. The visitation time was analyzed to detect the possible temporal overlap in the foraging of these bees. Furthermore, was analyzed their interspecific interactions for manipulating flower species visited by an opponent species, as well as attempts to attack this opponent. The individuals of *Xylocopa frontalis* visited the Brazil nut flowers before *Eulaema mocsaryi*, although the peak visitation of both did not presented significant differences. Neither of the species manipulated flowers recently visited by opponent species, and there were practically no antagonistic interactions between them. Thus, *X. frontalis* and *E. mocsaryi* shared the same food source in the flowers of *B. excelsa* due to differences in their time of visits and non-aggressive way of interacting with the opponent. This result has important implications for pollinating the Brazil nut, and a possible management of *X. frontalis* and *E. mocsaryi*, since these two were the most abundant pollinators in the studied locality.

KEYWORDS: antagonism, behaviors, facilitation, resource partitioning, pollinators.

Interações entre abelhas carpinteiras e abelhas das orquídeas (Hymenoptera: Apidae) em flores de *Bertholletia excelsa* Bonpl. (Lecythidaceae)

RESUMO

A competição entre duas espécies de abelhas por um mesmo tipo de recurso floral pode gerar comportamentos antagônicos entre elas, principalmente, dentro de áreas cultivadas, onde o recurso alimentar é limitado sazonalmente e localmente. No presente trabalho, foi testada a hipótese de antagonismo entre duas espécies de abelhas solitárias da família Apidae, *Eulaema mocsaryi* (Euglossini) e *Xylocopa frontalis* (Xylocopini) em flores da castanheira do Brasil (*Bertholletia excelsa*: Lecythidaceae) em uma área agrícola da Amazônia Central. O horário de visitação foi analisado a fim de se constatar a possível sobreposição temporal no forrageamento dessas abelhas. Além disso, suas interações interespecíficas de manipular flores visitadas pela espécie oponente ou tentar agredir essa espécie foram analisadas. Os indivíduos de *Xylocopa frontalis* visitaram as flores da castanheira antes que *E. mocsaryi*, embora o pico de visitação de ambas não tenha apresentado diferenças significativas. Nenhuma das duas espécies de abelhas manipulou flores recém-visitadas pela espécie oponente e praticamente não houve interações antagônicas entre elas. Desse modo, *X. frontalis* e *E. mocsaryi* compartilham a mesma fonte alimentar nas flores de *B. excelsa* devido às diferenças em seus horários de visitas e ao modo não agressivo de interagir com a espécie oponente. Esse resultado tem implicações importantes para a polinização da castanheira e um possível manejo de *X. frontalis* e *E. mocsaryi*, uma vez que essas duas espécies de abelhas foram os polinizadores mais abundantes na localidade estudada.

PALAVRAS-CHAVE: antagonismo, comportamentos, divisão de recursos, facilitação, polinizadores.

[1] Curso de Pós-Graduação em Entomologia

[2] Lab de Palinologia - Coordenação de Pesquisas em Botânica, Instituto Nacional de Pesquisas da Amazônia, Caixa Postal 478, Av. André Araújo 2936, Bairro Petrópolis, 69011-970 Manaus, AM, Brasil; luciabsy@inpa.gov.br

INTRODUCTION

Bees have different foraging strategies that allow them to divide floral resources in the same species of plants with other flower visitors. This division of resources may occur spatially depending on the distribution of flowers on the top of a tree, or between trees located in different parts of a given region (Gumbert and Kunze 1999; Goulson *et al*. 2001; Reader *et al.* 2005; Goulson *et al*. 2008; Ishii *et al*. 2008). Furthermore, there may also be temporal differences between the various floral visitors during the exploration of a particular food resource (Morse 1981; Nagamitsu and Inoue 1997).

Although the intensity of competition among visitors may be high, the division of resources (spatial and temporal) may have a facilitating effect, so that they need not use antagonistic or aggressive strategies on other individuals that are also using the same food source. However, some species of eusocial bees can be aggressive, thus permitting them to have a greater access to the resource exploited (Johnson and Hubbell 1975; Nagamitsu and Inoue 1997; Nieh *et al*. 2005). However, antagonism does not necessarily regulate all interactions between such species during their encounters in the flowers (Wilms *et al.* 1996).

Although there are several studies involving the division of floral resources between the social bees, mentioned above, there is no work, at least for the Central Amazonia region that examines specifically the interactions between species of non eusocial bees during foraging activities. Thus it was that we analyzed two species of pollinating bees of *Bertholletia excelsa* Bonpl. (Lecythidaceae), namely, the orchid bee which occurs exclusively in the Amazon Basin (Moure 2000; Oliveira 2006), *Eulaema mocsaryi* (Friese, 1899) (Apidae: Euglossini), and a carpenter bee with wide occurrence in Brazil (Silveira *et al.* 2002), *Xylocopa frontalis* (Olivier, 1789) (Apidae: Xylocopini).

These two species belong to two of five genera of the family Apidae that pollinate *B. excelsa* flowers, and the other three genera are *Bombus* (Bombini), *Centris* and *Epicharis* (Centridini) (Mori *et al.* 1978; Müller *et al.* 1980; Nelson *et al.* 1985; Mori and Prance 1990; Maués 2002). *Eulaema mocsaryi* and *X. frontalis* were chosen over other visitor bees of *B. excelsa*, because of their apparent predominance in relation to other species, and taking into account the works that have been carried out at the same locality as our study, and which point out the importance of these visitors as abundant in other crops (Renner 1986/ 1987; Santiago 1994).

With the aim of testing the hypothesis that *E. mocsaryi* and *X. frontalis* would have an antagonistic behavior in relation to the other, which might reflect on their patterns of activity in flowers of *B. excelsa*, was analyzed the interactions between them, and the visiting time of each to the *B. excelsa* flowers.

MATERIAL AND METHODS

The study was conducted within a culture of *B. excelsa* on the Aruanã farm, in the Municpality of Itacoatiara / Amazonas – Brazil. This farm has a wide coverage of Amazon forest primary vegetation. Collections and observations were made from November 2006 to January 2007, with temperature and relative humidity fairly constant, averaging 27 ºC and 82% respectively. However, average rainfall differed greatly: 98 mm (November 2006), 161 mm (December 2006) and 494 mm (January 2007) (Inmet 2007).

The *Bertholletia excelsa* Bonpl. is a native Amazon rainforest tree that occurs in terra firme forest, and has great social and economic importance in the Amazon region due the nutritional value of its nuts (Mori and Prance 1987; 1990). Bee activity in *B. excelsa* occurs during the flowering period of this species (Cymerys *et al.* 2005), namely, from October to February, in the morning, from 5:30 a.m. to 11:00 a.m., at which time it offers pollen and nectar to visitors who can manipulate its ligule (Moritz 1984). Due to the Brazil nut's physiological system, after 11.00 a.m. the androecium and flower petals fall, and only on the next day do new flowers bud in the open inflorescence (Müller *et al.* 1980; Nelson *et al.* 1985; Maués 2002). From each of the three collecting months, were chosed three individuals of *B. excelsa* by drawing lots, and had scaffolding installed beside their canopy.

The observations and collections of bees in the flowers occurred during three consecutive days in each of the nine trees sampled. The visiting hours of *X. frontalis* and *E. mocsaryi* were recorded for 10 minutes every half hour from 5:00 a.m. to 11:00 a.m. In the remaining 20 minutes, the floral visitors were collected with an entomological net and stored in deadly vials for later identification. Those bee species, whose individuals permitted a reliable visual identification were only registered, and were no longer collected.

The variation in the number of *X. frontalis* and *E. mocsaryi* individuals sampled during this period was analyzed by the Variance analysis test (ANOVA, double-factor, without repetition). The differences between the visitation times and visitation peaks (acrophase) of the two bee species were analyzed, comparatively, by the Rayleigh test. These test results were used to compare the month by month intraspecific and interspecific visitations, by the Watson-Williams test.

We recorded two different behaviors of the two species 60 times for each bee species, namely, the floral manipulation of a flower recently visited by the opposite species (1. Yes, 0. No), and the antagonistic encounters in the *B. excelsa* flowers between the two species (1. Yes, 0. No). We used the chi-square (X^2) to examine differences in the frequencies of both behaviors of the two species. The significance level used

was 5%, and tests and graphs were generated by the statistical program BioStat 5.0. Additionally, other species of floral bee visitors were identified and quantified, and, although they were not included in the analysis of this study, they may eventually provide a basis for future works to complement the data investigated here.

RESULTS

There was no statistically significant variation in the quantity of individuals of *X. frontalis* observed during the study period (ANOVA, F = 1305, df = 12, p> 0.05); however, for *E. mocsaryi* variation in the quantity of visitor individuals (ANOVA, F = 7881, df = 12, p <0.05) was found. *Eulaema mocsaryi,* inclusive, was less abundant in all months in relation to *X. frontalis,* and in the last month the difference in the quantity between the two species was higher, practically double of the first two months. The other bee species recorded in the Brazil nut flowers are presented in Table 1.

The average time of visitation for *X. frontalis* and E. mocsaryi throughout the entire sampling period is shown in Figure 1, where it observed the two bee species to have different peaks of activity; they were very close, however, with *X. frontalis* tending to visit flowers before *E. mocsaryi.* On analyzing the time variation of each species (Table 2) month by month, it appears that *X. frontalis* maintained the visiting pattern only between November 2006 and December 2006, and in the remaining period, this pattern had significantly changed. On the other hand, *E. mocsaryi* showed a more constant visiting pattern throughout the study period (Table 2). By the compared analysis of the visiting frequency of the two bee species (Table 3), was founded that in November 2006 and December 2006, there was a temporal overlap between the two bee species, while in January 2007 only, there was indeed a distancing in the foraging peak between the two species in the *B. excelsa* flowers. Notably, it was the rainiest month of the three examined; however, at the moment we do not have the data to make a detailed analysis for exploring these results.

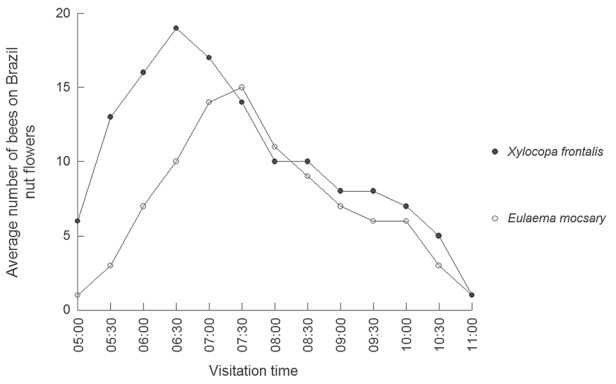

Figure 1 - Average frequency of visitation of *Xylocopa frontalis* and *Eulaema mocsaryi* in flowers *Bertholletia excelsa* (Lecythidaceae). Aruanã Farm, Itacoatiara, Amazonas, Brazil. Standard deviation: *X. frontalis*, november 2006 (5.408); december 2006 (3.425); january 2007 (8.549); *E. mocsaryi*, november 2006 (4.235); december 2006 (2.871); january 2007 (3.376).

Practically no individuals of *E. mocsaryi* and *X. frontalis* manipulate flowers after they had been recently visited by opponent species (X^2 = 1.31, df = 1, p> 0.05). However, about half an hour after receiving such a visit, many flowers were manipulated by one of the two species (personal observation). Throughout the study, neither species changed their pattern of floral manipulation behavior (*X. frontalis*, X^2 = 5.34, p> 0.05; *E. mocsaryi*, X^2 = 04.04, p> 0.05, Figure 2).

Eulaema mocsaryi showed more antagonistic behavior than *X. frontalis* (X^2 = 4.60, p <0.05). However, although the test found statistical significance for this behavior, biologically (Figure 2), these antagonistic interactions between them

Table 1 - Number of individuals and species of bees (Hymenoptera: Apoidea) potential pollinators of *Bertholletia excelsa* (Lecythidaceae). Aruanã Farm, Itacoatiara, Amazonas, Brazil. November 2006 to January 2007

Family	Tribes	Species	Total
Apidae	Bombini	*Bombus transversalis* (Olivier, 1789)	77
	Centridini	*Centris dimidiata* (Olivier, 1789)	16
		Centris flavifrons (Fabricius, 1775)	45
		Centris flavilabris Mocsáry, 1899	20
		Epicharis zonata Smith, 1854	27
	Euglossini	*Euglossa intersecta* Latreille, 1938	49
		Eulaema bombiformis (Packard, 1869)	576
		Eulaema cingulata (Fabricius, 1804)	29
		Eulaema mocsaryi (Friese, 1899)	737
	Xylocopini	*Xylocopa frontalis* (Olivier, 1789)	1,037
		Xylocopa muscaria (Fabricius, 1775)	14

Table 2 - Comparison of the monthly frequency of visits *Xylocopa frontalis* and *Eulaema mocsaryi* the flowers *Bertholletia excelsa* (Lecythidaceae) during peak flowering in Aruanã farm, Itacoatiara / AM.

	Xylocopa frontalis			*Eulaema mocsaryi*		
	Raylegh	Watson-Willians[b]		Raylegh	Watson-Willians[b]	
Month to month	*Ap*[a]	*F*	*r*	*Ap*	*F*	*R*
November 2006: December 2006	07.6; 08.0	4.04	0.927; 0.922	07.9; 07.9	0.06	0.929; 0.923
November 2006: January 2007	07.6; 07.0	11.6*	0.927; 0.930	07.9; 07.9	0.01	0.929; 0.948
December 2006: January 2007	08.0; 07.0	24.9*	0.922; 0.930	07.9; 07.9	0.02	0.923; 0.948

[a] *Ap*: Acrophase. Peak hours of visitation in decimal
[b] corrected comparisons *a posteriori* with Bonferroni
* Significant

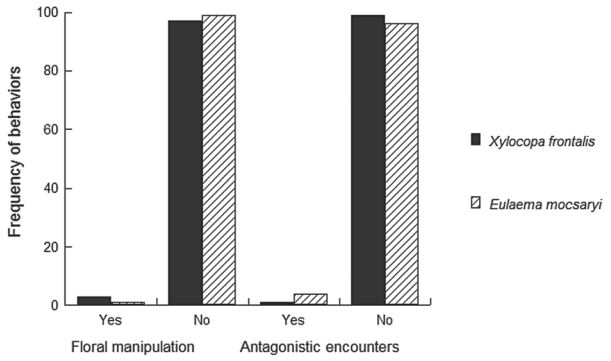

Figure 2 - Frequency of behaviors performed* by *Xylocopa frontalis* and *Eulaema mocsaryi* in flowers *Bertholletia excelsa* (Lecythidaceae). Floral manipulation of a species in a new flower species visited by the opposite; Encounter antagonistic, attempted expulsion / aggression directed to the opposite species. Aruanã Farm, Itacoatiara, Amazonas, Brazil. November 2006 to January 2007. * 60 records per species for each of the two behaviors.

Table 3 - Comparison of the frequency of visitation between *Xylocopa frontalis* and *Eulaema mocsaryi* in the flowers of *Bertholletia excelsa* (Lecythidaceae) during peak flowering in Aruanã farm, Itacoatiara / AM.

	X. frontalis vs. *E. mocsaryi*		
	Raylegh	Watson-Willians[b]	
	Ap[a]	*F*	*r*
November 2006	07.6; 07.9	2.11	0.927; 0.929
December 2006	08.0; 07.9	0.1	0.922; 0,923
January 2007	07.0; 07.9	17.62*	0.930; 0.948

[a] *Ap*: Acrophase. Peak hours of visitation in decimal
[b] corrected comparisons *a posteriori* with Bonferroni
* Significant

were rare and, therefore, it does not seem to modulate the interactions between them. During the study, there was no such change for either *X. frontalis* (X^2 = 2.03, p> 0.05) or E. mocsaryi (X^2 = 2.46, p> 0.05, Figure 2 - AE).

DISCUSSION

Our hypothesis that there would be a temporal differentiation in the peak activities of *X. frontalis* and *E. mocsaryi* was partially confirmed for two reasons. First, because this phenomenon occurred clearly only in one (January 2007) of the three months studied; second, because such temporal differentiation does not appear to have been very well regulated by our prediction tha the antagonistic encounters between the two bee species would reflect in different patterns of visitation.

The non-evident overlap at the peaks of activity between the bee species, which was important only in January 2007, occurred where the quantity of *X. frontalis* was practically double that of *E. mocsaryi*, and when there was a much higher rainfall than in previous months. Therefore, other factors may be contributing to the temporal division of resources between these bees, among them, environmental factors, and possibly the type of phenology of each of the bee. Other studies have shown, as recorded here, that *Xylocopa* species seems, preferentially, to visit flowers of Lecythidaceae early in the morning, unlike the species of Euglossini that visit them a little later in the same morning (Maués 2002; Aguiar and Gaglianone 2008). But regardless of which species visits the flowers most often before that of its competitor, neither manipulates flowers that have been manipulated by the counterpart, as examined here.

To be able to recognize a flower already visited by other species may provide an advantage to the organism that is able to discriminate and make choices, because it maximizes foraging efficiency, as the individual would not lose time and energy trying to access a flower whose resources have been exhausted (Goulson *et al.* 1998; Goulson *et al.* 2001; Reader *et al.* 2005).

The competition between floral visitors may be reduced by dividing resources between them, which implies a structuring of the community (Wilms *et al.* 1996).

In this way, non-temporal difference in foraging of *X. frontalis* and *E. mocsaryi*, during November and December of 2006, shows that, at least during this period, the competition was not very strong, and what could be happening, therefore, is a facilitation between them. The records about the antagonistic encounters reinforce this line of thought, because of the several possible encounters between the two species in the *B. excelsa* flowers, the attempts of expulsion/aggression between them were rare. This finding is interesting because even bee species that are recorded visiting food resources aggressively, also may present some kind of division in the use of resources with other floral visitors (Nagamitsu and Inoue 1997; Kajobe and Echazarreta 2005; Kaminski and Absy 2006; Tan 2008).

Therefore, the daily activities of *X. frontalis* and *E. mocsaryi* in *B. excelsa* flowers and how these bees interact with one another affect their foraging strategies. This demonstrates that they can share the same floral resources without showing prominent antagonism between them, which could have important implications for pollinating *B. excelsa.* Additional studies could analyze the other bee species, identified here, and the role that they represent in pollination of *B. excelsa*.

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