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Hummingbird pollination in *Schwartzia adamantium* (Marcgraviaceae) in an area of Brazilian Savanna

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Abstract. Some authors have suggested that, in bird-pollinated species of Marcgraviaceae, perching birds are more adequate pollinators than hovering birds, due to the inflorescence structure and floral biology. In this study, we report territorial behavior of the swallow-tailed hummingbird *Eupetomena macroura* in *Schwartzia adamantium*. We analyzed the time spent in foraging behavior and territorial defense by the hummingbird, and the nectar availability of *S. adamantium*. The hummingbird spent almost 96% of the time perching. We registered 97 invasions of the territory always by others hummingbirds. During the observation period, no perching birds visited *S. adamantium*. Nectar volume varied from 15.0 to 114.0 µL, and sugar concentration varied from 5.5 to 27.1%. Despite that hummingbirds possibly play a minor role in the reproduction of ornithophilous Marcgraviaceae species, and occasionally touched the anthers and/or stigma, our observations suggest that it's only responsible for fruit set of *S. adamantium* in PESCAN.

Key words: Bird pollination, vertebrate-plant interactions, nectar energy content, resource defense, protandry, *Eupetomena macroura*, Trochilidae.

Resumo: Alguns autores sugeriram que por causa da estrutura da inflorescência e biologia floral, aves que pousam na inflorescência são polinizadores mais adequados de espécies de Marcgraviaceae do que beija-flores. Neste estudo apresentamos resultados de comportamento territorial de *Eupetomena macroura* em *Schwartzia adamantium*. Além disso, determinamos o tempo gasto no forrageio e defesa do território pelo beija-flor, bem como a disponibilidade de néctar de *S. adamantium*. O beija-flor gastou quase 96% do tempo pousado. Nós registramos 97 invasões ao território, sempre por outros beija-flores. Durante o período de observação, nenhuma outra ave visitou *S. adamantium*. O volume de néctar variou de 15 a 114 µL, e concentração de açúcar variou de 5,5 a 27,1%. Apesar de beija-flores possivelmente terem menor efeito na reprodução de espécies de Marcgraviaceae, e tocarem ocasionalmente anteras e/ou estigmas, nossas observações sugerem que eles são os únicos responsáveis pela frutificação de *S. adamantium* no PESCAN.

Palavras-chave: Polinização por aves, interações vertebrado-planta, conteúdo de energia do néctar, defesa do recurso, protandria, *Eupetomena macroura*, Trochilidae.

Introduction

Bird pollination within the Marcgraviaceae is a controversial issue (see Sazima *et al.*, 1993, and references therein). Although bird visits have been observed in species of *Norantea* (Sazima *et al.*, 1993; Pinheiro *et al.*, 1995), *Marcgravia* (Bailey, 1922; Snow & Snow, 1971) and *Souroubea* (Machado & Lopes, 2000), bat pollination seems to be predominant in *Marcgravia* (Sazima & Sazima, 1980; Tschapka & Von Helversen, 1999). Sazima *et al.* (1993) observed visits of hovering and perching birds in *Norantea brasiliensis* (now *Schwartzia brasiliensis*), while Pinheiro *et al.* (1995) studying the same species in another area registered hummingbird visits only.

Sazima *et al.* (1993) suggested that perching birds (e.g. the Bananaquit *Coereba flaveola*, and the Brazilian Tanager *Ramphocelus bresilius*) are more adequate pollinators of *N. brasiliensis* than hovering

birds, due to the inflorescence structure and floral biology (see Westerkamp, 1990). So, these authors suggested that hummingbirds possibly play a minor role in the reproduction of ornithophilous species of Marcgraviaceae. Moreover Sazima *et al.* (1993) observed that hovering Black Jacobin *Melanotrochilus fuscus* appeared to be territorial in *N. brasiliensis*, but few aggressive interactions were registered. Here we report territorial behavior of the swallow-tailed hummingbird *Eupetomena macroura* in *Schwartzia adamantium*.

Territoriality can be defined as the defense of an area by animal in order to gain exclusive access to resource. Hummingbirds have been the focus of studies of territorial defense (Ewald & Bransfield, 1987; Heinemann, 1992; Eberhard & Ewald, 1994; Temeles *et al.*, 2004; Temeles *et al.*, 2005), mainly due to the small territories defended, and food resources that are easy to quantify (Dearborn, 1998). If hummingbirds are not adequate pollinator of Marcgraviaceae, hummingbird´s territorial behavior may affect the reproductive success of *S. adamantium*. In addition, in order to defense the resource we expect that *Eupetomena macroura* may present aggressive interactions with others hummingbirds because your largest size. The aims of the present study were to determine the time spent in foraging behavior and territorial defense of the swallow-tailed hummingbird, and the nectar availability of *S. adamantium*.

Material and Methods

We conducted this study at Parque Estadual Serra de Caldas Novas – PESCAN in Caldas Novas, state of Goiás (approx. 17°46'03,6''S, 48°39'30,8''W) Central Brazil, during October 2002 in Cerrado *sensu strictu* vegetation (Brazilian savanna, Oliveira & Marquis, 2002). All information about the study area is only available in Almeida & Sarmento (unpublished). PESCAN covers 12,315 ha, and is 15 km long, and nine km wide. The mean annual rainfall is 1,500 mm, with a distinct wet season during October-March, and a dry season during April-September. The mean relative humidity is 68%. The mean annual temperature value is 23°C, varying between a mean minimum value of 19 °C in dry seasons, and a mean maximum value of 24 °C in the wet seasons. Climate is hot and moist, Aw following Köppen classification. There is a variety of soil types in PESCAN, slopes present cambisols and litolic soils, the latter associated with stony outcrops and wetter areas. Cambisols are stony, sandier, dystrophic and have high concentration of aluminium. The *campo limpo* physiognomy (see Oliveira & Marquis, 2002) is associated with this soil type, and the typical plant species found in this physiognomy in PESCAN is *Vellozia squamata*. Sixteen meter thick latosols occur in plateau areas. A fire in PESCAN which occurred before our study near the place where observations were made may have reduced resource availability in the area.

We examined the territorial behavior of the Swallow-tailed Hummingbird, *Eupetomena macroura* (Gmelin, 1788) (Apodiformes: Trochilidae), one of the largest hummingbirds in Brazil (for more details, see Grantsau, 1989). Behavioral observations were done at a single territory defended by a Swallow-tailed Hummingbird of unknown sex, in non-consecutive seven days, four days in morning sessions and three days in afternoon sessions (Tab. 1). Foraging behavior was characterized by visits of hummingbird to inflorescences, and was monitored by duration and frequency of visits. Chasing behavior was characterized by exclusion of intruders by territory owner, and was monitored by duration and frequency of exclusions. Perching behavior was characterized by time of hummingbird stayed stop in branches. Duration of foraging, chasing and perching behaviors were registered with a stopwatch, totalizing 20.5 hours of observation.

The defended territory contained one flowering *Schwartzia adamantium* (Cambess.) Bedell ex Giraldo-Cañas shrub (Marcgraviaceae). *Schwartzia* is an endemic shrub genus in Brazil, typical of areas with shallow and stony soils in Cerrado areas (Giraldo-Cañas, 2002). *Schwartzia adamantium* occurs in northeastern (Bahia), southeastern (Minas Gerais) and central (Goiás and Distrito Federal) Brazil (Giraldo-Cañas, 2002). This species was previously known as *Norantea adamantium* (Giraldo-Cañas,

2002). Marcgraviaceae have a modification of floral bracts into cup-shaped nectaries (VOGEL, 1990). In some genera, such as *Marcgravia*, the inflorescence consists of a ring of many fertile flowers surrounded by a few nectaries. In the genus *Schwartzia*, every flower has its own nectary (DRESSLER, 1997). The nectary always opened upwards in *S. adamantium* that we observed (Fig. 1).

Nectar volume was measured using microlitre syringes, and sugar concentration in nectar was determined with a pocket refractometer. We always took these measurements from bagged flowers at the beginning, middle and end, or beginning and end of morning and afternoon observations. The number of inflorescences, as well as the number of open flowers, was recorded daily. Nectar volume and sugar concentration were used to calculate the floral reward in kcal/flower. The amount of sugar present in the nectar was calculated by multiplying mg sugar/ml by total nectar volume, and we used a conversion table for changing percent sugar (mg sugar/mg solution) to mg sugar/ml nectar following KEARNS & INOUYE (1993). To convert mg sugar to kcal, we follow DAFNI (1992), who have determined that 1 mg sugar = 4 kcal. These values were multiplied by the number of open flowers per period of observation, to have an idea of the total amount of energy available to hummingbirds.

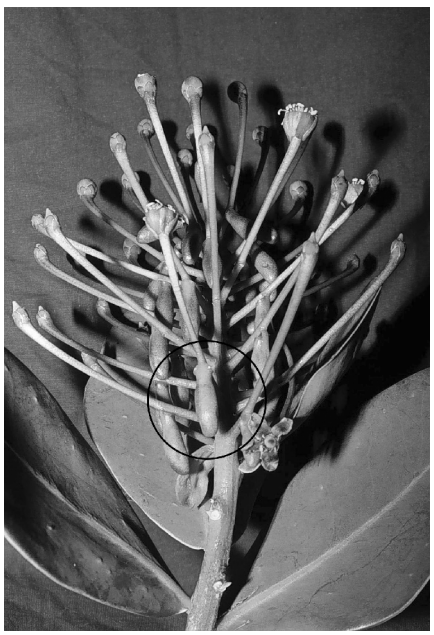

Figure 1. Inflorescence of *Schwartzia adamantium*. Hummingbird's movements allowed it to reach any nectary (circle), and due to these movements its ventral region occasionally touched the anthers and/or stigma. Note that, although flowers are oriented in different directions, the nectary opening is always oriented upwards.

RESULTS

Eupetomena macroura spent 95.8% of the time perching in higher tree branchs of *S. adamantium*, and on nearby shrubs, 3.5% of the time foraging, and 0.7% chasing. In the hottest periods of the day (10h00min to 16h00min) the hummingbird remained at the lower part of the canopy, but in a position where it would still be able to detect intruders. The hummingbird we observed was not marked, but its perching behavior allowed us to assert that it was the same individual, as the branches and nearby shrubs used for perching were the same during the observations. The hovering behavior allowed the hummingbird to reach any nectary, and due to these movements its ventral region occasionally touched the anthers and/or stigma.

We registered 97 invasions of the territory, 55 in 15.5 hours of morning observations (mean 3.5 intruders/h) and 42 in 5 hours of afternoon observations (mean 8.4 intruders/h). The time spent in each chase averaged 5.3 s (sd = 4.8, range = 2 to 30, N = 97). As aggressive interactions were fast, the identification of the intruder was difficult. However, we identified at least five genera in the study area: *Phaethornis*, *Colibri*, *Thalurania*, *Amazilia*, and *Eupetomena*. During the observation period, no perching birds or insects visited *S. adamantium*.

In 15.5 hours of morning observations, *E. macroura* visited *S. adamantium* inflorescences 144 times (mean 9.3 visits/h), and 37 times in 5 hours of afternoon observations (mean 7.4 visits/hour). The average time spent per visit in each observation period was 14.3 s (sd = 10.5, range = 1 to 60, N = 181).

During the study period, the number of inflorescences with open flowers diminished from 50 to 20, and the number of open flowers per inflorescence from 15 to five. Nectar volume in *S.*

adamantium varied from 15.0 to 114.0 µL (mean = 67.6, sd = 32.9, N = 17), and sugar concentration varied from 5.5 to 27.1% (mean = 18.0, sd = 5.5, N = 17) (Tab. 1). We estimate an average nectar energy content of 18.2 kcal/day (Tab. 1).

Table 1. Mean values of nectar volume and sugar concentration used to calculate the floral reward of *Schwartzia adamantium* in PESCAN. Morning observations beggining at 07:30 am, and afternoon observations at 15:30 pm.

Observation / duration	Nectar volume (mL)	Sugar concentration (%)	Nectar energy contents (Kcal)*
	Mean ± sd	Mean ± sd	
morning			
1 (4.0 hs)	48.00 ± 0.00	8.25 ± 3.80	11.54 (n = 700)
2 (3.7 hs)	46.78 ± 29.51	22.18 ± 2.71	30.79 (n = 676)
3 (3.9 hs)	41.78 ± 33.11	22.25 ± 6.89	24.70 (n = 624)
5 (4.0 hs)	92.22 ± 23.89	14.60 ± 4.78	15.00 (n = 396)
afternoon			
4 (2.0 hs)	53.00 ± 24.04	19.60 ± 1.27	17.65 (n = 240)
6 (1.3 hs)	103.00 ± 9.90	20.44 ± 1.51	19.03 (n = 208)
7 (1.7 hs)	98.00 ± 22.63	18.95 ± 1.20	8.76 (n = 108)

*estimated values of number of open flowers per inflorescence per day.

DISCUSSION

Eupetomena macroura spent almost the time in defensive behavior on *S. adamantium*. Because *E. macroura* is a large hummingbird, the time spent in territorial defense can be advantageous, by excluding other nectarivorous birds and increasing the nectar availability in each flower. The sugar concentration and nectar volume of *S. adamantium* flowers exploited by Swallow-tailed Hummingbird in PESCAN were similar to the values found for other bird-pollinated flower assemblages in the Neotropics (e.g. ARIZMENDI & ORNELAS, 1990; SAZIMA *et al.*, 1995; SAZIMA *et al.*, 1996; ARAUJO & SAZIMA, 2003). Moreover, the nectar energy content of *S. adamantium* was slightly above that necessary for hummingbird maintenance (6 to 10 Kcal, CARPENTER, 1983).

Territorial behaviour can reduce the efficiency of pollen vectors, and may reduce the cross-pollination by the Swallow-tailed Hummingbirds. The distribution of *S. adamantium* seems to be restricted, or the species has a low demographic density, because this species is not cited in a floristic and phytosociological study in PESCAN (SILVA *et al.*, 2002).

In addition, *S. adamantium* is also not cited in many studies conducted in Cerrado areas (e.g. FELFÍLI *et al.*, 2000; FELFÍLI *et al.*, 2002; RATTER *et al.*, 2003; BATALHA & MARTINS, 2004). If this species is naturally rare or occurs in low demographic density, the territorial behavior of *E. macroura* would decrease the chance of effective cross-pollinators visiting *S. adamantium* flowers. However, to test this hypothesis experimental manipulations are necessary for determine if *S. adamantium* really needs cross-pollination for reproduction. The presence of fruits under natural conditions in *S. adamantium* can be a sign this species is protandrous. Protandry have been registered for *S. brasiliensis* (PINHEIRO *et al.*, 1995), *Souroubea guianensis* (MACHADO & LOPES, 2000), as well as *Marcgravia nervosa*, *M. serrae*, *M. mexicana* and *M. nepenthoides* (TSCHAPKA & VON HELVERSEN, 1999). Once the hummingbird is territorial, protandry can minimize effects of self-pollination, mainly self-pollination by geitonogamy. In *S. guianensis*, spontaneous self-pollination did not occur due to marked protandry (MACHADO & LOPES, 2000).

Although in literature review hummingbirds cold not be considered as effective pollinators in Marcgraviaceae, our observations suggest that *E. macroura* was the only responsible for fruit set of *S. adamantium* in PESCAN. The same result was observed for *S. guianensis* visited only by *Phaethornis ruber* in northeastern Brazil (MACHADO & LOPES, 2000). Due to the inflorescence structure, perching birds can be considerate more adequate pollinators of *S. adamantium* than hovering birds, as observed in *Norantea brasiliensis* by SAZIMA *et al.* (1993). These authors registered 10 species of passerine birds visiting the inflorescences of *Schwartzia brasiliensis*, being the honeycreeper *Coereba flaveola* one of the most common perching bird on this species. This bird touched the flowers of *S. brasiliensis* with several parts of its body while foraging. Moreover, *C. flaveola* was considered an effective co-pollinator of three species of bromeliads (*Aechmea bromeliifolia*, *A. distichantha* and *Acanthostachys strobilacea*) studied by SAZIMA & SAZIMA (1999). The morphology of bromeliads flowers was the principal factor favoring bird visitation. The fact that the hummingbird we

observed touched the reproductive organs of *S. adamantium* only occasionally makes it a poor pollinator, as also observed by Sazima *et al.* (1993) and Pinheiro *et al.* (1995) in *S. brasiliensis*. However, exactly one year after the field work, we returned to the same place and observed an individual of *E. macroura* visiting the same individual of *S. adamantium*, as well as the presence of fruits. We can not assert that was the same individual of early year. This observation suggests that territorial behavior would be occurred again, and more interesting is that hummingbird's visitation seems do not affect the reproductive success of *S. adamantium* in cerrado area where we worked. In particular for endemic shrub *S. adamantium* further data of geitonogamous controlled self-pollinations are necessary for improving our knowledge about its reproductive biology. Therefore these data will help us to elucidate the role of hummingbirds in pollination of *S. adamantium*.

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