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Original Article

Hummingbird (Aves: Trochilidae) assemblage using resources from the exotic African tuliptree, *Spathodea campanulata* (Bignoniaceae) in a Neotropical altered environment, southeastern Brazil

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Abstract

The non-native African tuliptree, *Spathodea campanulata* (P. Beauv), is widely distributed in altered Neotropical environments, where hummingbirds are important pollinators. We investigated the assemblage of hummingbirds which fed on its nectar and described their behavior, to understand possible influences of the exotic tree on the territorial behavior in an altered environment in southeastern Brazil. Seven species fed on flower resources, mainly *Eupetomena macroura* (Gmelin, 1788), *Amazilia lactea* (Lesson, 1832), and *Florisuga fusca* (Vieillot, 1817). Visiting time was positive correlated with number of flowers accessed, but in most visits, hummingbirds get the nectar by pillage, instead of frontal access. Flower availability varied throughout months; however, we found no evidence of significative correlation between available flowers and number of agonistic encounters. Despite a high number of animal-plant interactions and a strong territorialism of some species observed in African tuliptree foraging site, there may be other plants at local scale influencing the behavioral patterns observed.

Keywords: competition, foraging behavior, nectivory, nectar pillage, territorialism.

Assembleia de beija-flores (Aves: Trochilidae) utilizando recursos da árvore exótica tulipa africana, *Spathodea campanulata* (Bignoniaceae) em um ambiente Neotropical alterado, sudeste do Brasil

Resumo

A tulipa africana, *Spathodea campanulata* (P. Beauv), é uma árvore não nativa amplamente distribuída em ambientes Neotropicais alterados, onde os beija-flores são importantes polinizadores. Investigamos a assembleia de beija-flores que se alimentam do néctar e descrevemos seus comportamentos para compreender possíveis influências da árvore exótica sobre o comportamento territorial em um ambiente alterado no sudeste do Brasil. Sete espécies se alimentaram de recursos florais, principalmente *Eupetomena macroura* (Gmelin, 1788), *Amazilia lactea* (Lesson, 1832) e *Florisuga fusca* (Vieillot, 1817). O tempo de visita foi correlacionado positivamente com o número de flores acessadas, mas na maioria das visitas os beija-flores obtiveram o néctar pela pilhagem, em vez do acesso frontal. A disponibilidade de flores variou ao longo dos meses; no entanto, não encontramos evidências de correlação significativa entre flores disponíveis e número de encontros agonísticos. Apesar do grande número de interações entre plantas e animais e um forte territorialismo de algumas espécies observadas no local de forrageamento, pode haver outras plantas em escala local influenciando os padrões comportamentais observados.

Palavras-chave: competição, comportamento de forrageamento, nectivoria, pilhagem de néctar, territorialismo.

1. Introduction

Due to morphology, physiology, and mainly the flight style of hummingbirds (Aves: Trochilidae), a large amount of energy resource is necessary to supply their high metabolic rates (Wolf and Hainsworth, 1971; Cole et al., 1982; Suarez et al., 1986; Suarez and Gass, 2002; Fleming et al., 2004; Woodward et al., 2005; González-Gómez et al., 2015). In order to acquire floral nectar, this group of birds have developed a series of behavioral strategies to maximize the input rate of energy with a minimum of energy cost (Carpenter, 1978; Justino et al., 2012; Makino, 2013; Maruyama et al., 2016). Those sets of strategies are known as foraging behavior (Krebs and Davies, 1996).

The flower distribution, nutrition quality and nectar availability offered by flowering plant species, and the

behavior of competitors from the same feeding guild (e.g., competition by interference; Ferreira et al., 2016), can govern the assemblage structure of hummingbirds at a local scale (Dearborn, 1998; Rodrigues and Araújo, 2011; Wolowski et al., 2013).

Hummingbird species can show territorial behavior or other types of foraging strategies which do not depend on agonistic actions. Territorialism occurs when an individual defends a limited area to maximize its access to food resources and minimize for other potential competitors (Fretwell, 1969; Stiles and Wolf, 1970; Araújo-Silva and Bessa, 2010). Spatial and temporal factors of plant flowering influence the competition for nectar and individual choices in defending or not the territory (Cole et al., 1982; Tilman, 1982; Cotton, 1998; González-Gómez et al., 2011), as well as the abandonment of territory to search new food sources (Feinsinger and Colwell, 1978; Mendonça and Anjos, 2006; Grether, 2016).

The hummingbirds are a successful group of vertebrate pollinators restricted to the Neotropical and Neartic regions, including urban or altered areas, where the exotic flora may offer important food sources for local fauna (Carbó-Ramírez and Zuria, 2011; Winfree et al., 2011). Behavioral studies in urban areas have been enhancing the knowledge on how human activities can change animal behavior and community structure (Franchin et al., 2004; Mendonça and Anjos, 2005; Franco and Marçal-Júnior, 2018). Thus, the initiative to describe and understand such behaviors may have an important role for future studies on urban management and ecosystems services, especially because hummingbirds play the ecological function as pollinators (Costanza et al., 1997).

We aimed to describe the hummingbird assemblage which forages on flower resources from the exotic African tuliptree, *Spathodea campanulata* (P. Beauv) (Bignoniaceae) and answer a question about the influence of this non-native plant species on Neotropical hummingbirds and their behavior. Does flower availability vary along the blooming period, and could it influence the hummingbird energy spent on territorialism?

2. Material and Methods

The study site corresponds to an agglomeration of *Spathodea campanulata* trees, located in the margins of an anthropogenic lake in Monjolinho River, known as UFSCar Lake (21°59'8,257"S, 47°52'47,406"O), in Federal University of São Carlos - UFSCar, São Carlos municipality, central São Paulo state, southeastern Brazil. The region is inside Cerrado phytogeographic domain, however, at the studied site the vegetation is composed mainly by exotic trees (e.g., *Pinus* sp., *Eucalyptus* sp.) with native species naturally regenerating in the low and medium strata of this woodland. In the *campus*, there are small forest patches in urbanized area near the study site, Gallery Forests alongside watercourses, and Cerrado vegetation remnants, characterized by sparse and dense savannas. The climate is Cwa according to Köppen classification, with a dry winter and rainy summer (Köppen and Geiger, 1936; Peel et al., 2007).

Data were collected using focal-animal observation with sequential records of behaviors as sampling method, considering each behavioral event from the start to the end (Altmann, 1974), keeping adequate distance from the agglomeration of trees. During the flowering period of *S. campanulata*, from February to June, focal-animal observations were carried out from 7:00 h to 10:00 h, and from 14:00 h to 17:00 h, totalizing 72 h almost equally distributed among months. The agglomeration of four African tuliptrees was selected due to the feasibility of continuous observations from a safe distance to avoid behavioral influence on birds, and a low probability of being perturbed by academic activities in the *campus*.

Spathodea campanulata flowers are arranged in panicle, compact and upright inflorescences at the end of every branch, that produces up to 30 flowers each month (Rangaiah et al., 2004). We estimated the number of available flowers produced by trees per month by counting the flowers of 10 inflorescences randomly selected from each of 4 individuals, and then counting the total number of inflorescences.

The behavioral observations focused on identify the hummingbird species, its visiting time (from arrival to departure), number of flowers accessed, type of access to the food (frontal or pillage), and agonistic behaviors toward competitors. In the last situation, the behavior performed by the aggressor against the subordinate species were categorized according to Araújo-Silva and Bessa (2010) as: frontal encounter (FE); peck (PE); chasing in different directions (CD); linear chasing (LC); sentinel (SE); and aggressive alarm call (AC).

We performed the statistical analysis in PAST Program (Hammer et al., 2001), version 3.24 (released in April 2019). The two-way ANOVA – analysis of variance was used to identify variation in mean number of available flowers throughout months (factor 1) and differences between African tuliptree individuals (factor 2). We investigated the possible correlation between (i) visiting time and number of flowers accessed by hummingbird individuals; and (ii) the available flowers and total number of agonistic encounters, by fitting data to linear model using ordinary least square algorithm for the regression (Hammer, 2019).

3. Results

3.1. Hummingbird assemblage

Seven hummingbird species (Table 1) used resources from flowers of the exotic African tuliptree (*Spathodea campanulata*): Glittering-throated Emerald, *Amazilia fimbriata* (Gmelin, 1788); Sapphire-spangled Emerald, *Amazilia lactea* (Lesson, 1832); Black Jacobin, *Florisuga fusca* (Vieillot, 1817); Swallow-tailed Hummingbird, *Eupetomena macroura* (Gmelin, 1788); Planalto Hermit, *Phaethornis pretrei* (Lesson e Delattre, 1839)*;* Black-Throated

Table 1. Hummingbird assemblage that fed on floral resources of *Spathodea campanulata* in an altered environment in central São Paulo state, southeastern Brazil.

Species	N Animal-Plant interactions	Feeding strategy	All visited flowers N ($\bar{X}$ ± SD)	Pillage N ($\bar{X}$ ± SD)	Total visit time ($\bar{X}$ ± SD)
Eupetomena macroura	72	Territorialist	175 (2.43 ± 1.73)	117 (1.62 ± 1.22)	884s (12.27 ± 9.11)
Amazilia lactea	62	Territorialist/ Generalist	190 (3 ± 1.71)	119 (1.91 ± 1.35)	865s (13.95 ± 9.93)
Florisuga fusca	43	Territorialist/ Generalist	152 (3.53 ± 2.02)	50 (1.16 ± 1.36)	638s (14.83 ± 9.09)
Phaethornis pretrei	8	Trap-lining	25 (3.13 ± 2.95)	16 (2 ± 1.92)	102s (12.75 ± 12.41)
Thalurania glaucopis	9	Generalist	26 (2.88 ± 1.83)	14 (1.56 ± 0.88)	146s (16.22 ± 10.33)
Amazilia fimbriata	6	Generalist	11 (1.83 ± 2.23)	4 (0.66 ± 1.21)	31s (5.16 ± 7.98)
Anthracothorax nigricollis	2	Generalist	2	2	9s (4.5 ± 2.12)

N = total number of observations; $\bar{X}$= mean number; SD = standard deviation. Visiting time in seconds (s).

Mango, *Anthracothorax nigricollis* (Vieillot, 1817); and Violet-capped Woodnymph, *Thalurania glaucopis* (Gmelin, 1788).

We also observed other hummingbird species using the *S. campanulata* for perching, but they did not use food resources provided by flowers: Sombre hummingbird, *Aphantochroa cirrochloris* (Vieillot, 1818); White-throated Hummingbird, *Leucochloris albicollis* (Vieillot, 1817); and Glittering-bellied Emerald, *Chlorostilbon lucidus* (Shaw, 1812).

3.2. Flowering patterns of African tuliptree

The food resources for hummingbirds provided by the four *S. campanulata* trees varied throughout the surveyed flowering period, from February to June. A high number of available flowers per individual were counted in March (n=268.22, SD±94.87 flowers/tree) and May (n=227.65, SD±74.55 flowers/tree). In June, the last month of flowering, trees produced the lowest number of flowers per individual (n=49.47, SD±21.53 flowers/tree). The two-way ANOVA indicated the mean number of available flowers were different among months (F=7.844, p=0.002), however, were similar among individuals (F=1.331, p=0.3104).

3.3. Foraging patterns of hummingbirds

The observed n=202 individual visits, characterized as animal-plant feeding interactions, revealed a higher frequency of *E. macroura* (35.6%), *A. lactea* (30.7%) and *F. fusca* (21.3%), totalizing 87.3% of all visits (Table 1).

During individual visits at the agglomeration of *S. campanulata*, we counted n=581 flower visits, of which 55.41% were pillage. Considering the three most frequent species, only *F. fusca* performed more frontal access in the flowers than pillage (Table 1).

Hummingbirds spent about 10.65 (SD±7.43) seconds per visit in the foraging site. We found a positive and significative relationship between visiting time and the number of flowers accessed per visit (r=0.71, R^2=0.51, p=0.0001; see Figure 1).

3.4. Territorialism and agonistic behavior

Amazilia lactea flew to other locations after foraging in the agglomeration of *S. campanulata* in 82% of post-interaction behavior, indicating the prevalence of generalist strategies. Differently, *Eupetomena macroura* remained in perches nearby to foraging site more frequently (58.3%) than it flew to other locations (38.8%), indicating a strong territorialism. *Florisuga fusca*, however, remained in perches less frequently when *E. macroura* were present in the foraging site, indicating its territorialism can be disrupted by this dominant species. *Phaetornis pretrei* performed short-term visits, and regularly arrived and departed toward same directions, characteristics of the trap-lining foraging strategy. The other hummingbirds were all generalists in this foraging site, accessing floral resources while the dominant species was absent or when they chose not to defend the territory.

We recorded 80 agonistic behaviors between hummingbirds, of which aggressive vocalization (alarm calls) was the most frequent (44%), while frontal encounter was the least common (2.5%). The hierarchy in hummingbird assemblage which access food resources from African tuliptree indicated one super-dominant species, *Eupetomena macroura*, that subjugated all species, mainly the other two most common. This species was responsible for the highest number of agonistic behaviors toward other species (75%), including a passerine bird (*Coereba flaveola*), and exhibited the highest variety of behaviors (6 types), as presented in Table 2. The other species, that can be considered as

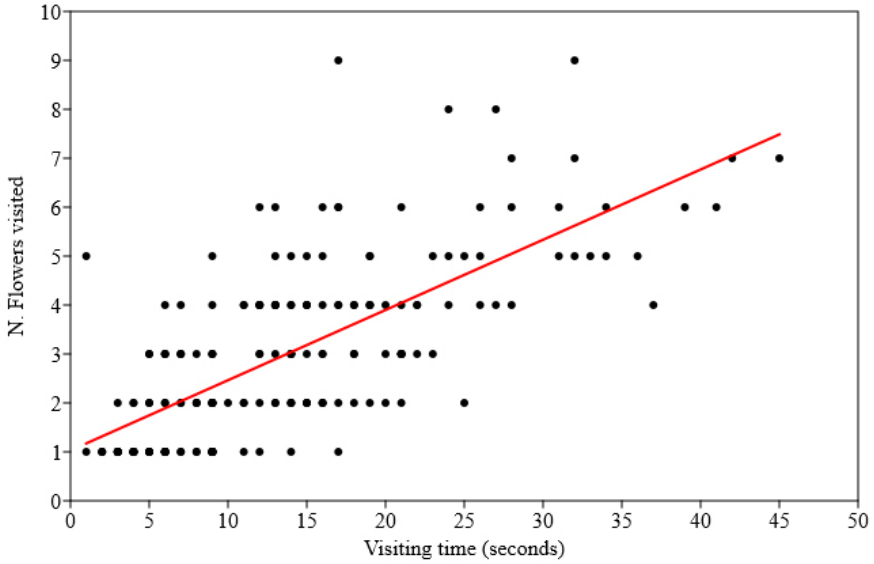

Figure 1. Correlation between the visiting time of hummingbirds and the number of African tuliptree flowers accessed in each visit. The model can be described by the linear function: y=0.14x + 1.03.

Table 2. Agonistic interactions between hummingbirds which exhibited territorialism (aggressor) toward the subordinated species, and the total number of observations in the agglomeration of *Spathodea campanulata*.

Territorialist species (+) Subordinated species (-)	**Types of agonistic behavior***						**Total**
	FE	**PE**	**CD**	**LC**	**SE**	**AC**	
Eupetomena macroura +							60
Amazilia lactea -	0	4	0	7	3	4	
Florisuga fusca -	1	2	1	8	0	2	
Thalurania glaucopis -	0	0	0	2	0	1	
Coereba flaveola -	0	1	0	0	0	0	
Non-identified species -	0	0	0	1	4	19	
Florisuga fusca +							16
Eupetomena macroura -	0	1	0	0	0	0	
Amazilia lactea -	1	1	1	6	0	2	
Phaethornis pretrei -	0	0	1	0	0	0	
Non-identified species -	0	0	0	0	0	3	
Amazilia lactea +							4
Non-identified species -	0	0	0	0	0	4	
Total	**2**	**9**	**3**	**24**	**7**	**35**	**80**

*Agonistic behaviors: FE = frontal encounter; PE = peck; CD = chasing in different directions; LC = linear chasing; SE = sentinel; AC = aggressive alarm call.

territorialists in the literature when foraging in different plant species, used generalist foraging strategies in the studied foraging site, e.g., *Anthracothorax nigricollis*, *Thalurania glaucopis* and *Amazilia fimbriata*.

The mean number of available flowers per tree firstly appeared to exert positive influence in the total number of observed agonistic interactions in each month (see Figure 2), however, statistical analysis indicated no significant relationship (r=0.37, R^2=0.14, *p*=0.51).

4. Discussion

4.1. Hummingbird assemblage

The seven Trochilidae species that fed on *Spathodea campanulata* flower resources are commonly found in different types of Neotropical ecosystems, including urban environments (Mendonça and Anjos, 2006; Previatto et al., 2013; Mendes et al., 2018). Those species correspond to 46.7% of all Trochilidae species recorded

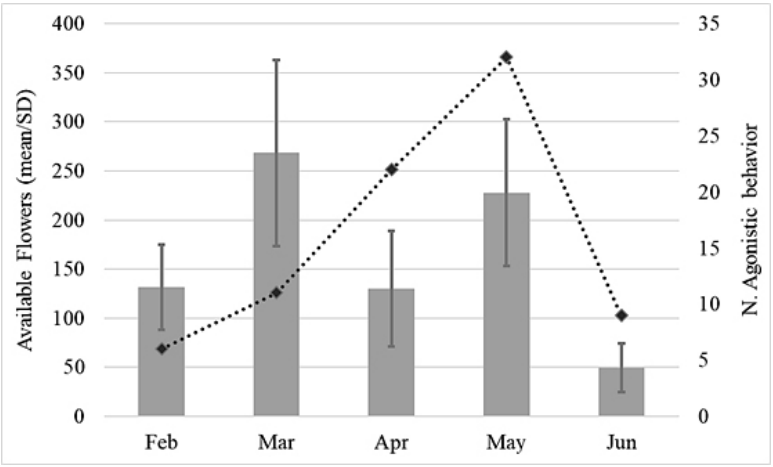

Figure 2. Average of available flowers per tree (columns) and the number (N) of hummingbird agonistic behaviors (points connected by line) recorded each month at the African tuliptree (*Spathodea campanulata*) agglomeration.

in the last 15 years in Federal University of São Carlos and adjacent areas, including the Ecological Park of São Carlos (Batisteli et al., *in prep.*).

Exotic plants amongst native vegetation may cause negative impacts, mainly because of the substitution of local species and decrease of natural diversity, which can lead to changes in ecological relationships (Bell et al., 2003). However, microhabitats and food resources produced by alien species are used by wildlife, serving as refugees and foraging sites for them, specially birds (Mörtberg and Wallentinus, 2000; Corlett, 2005; Mendonça and Anjos, 2006; Franco and Marçal-Júnior, 2018). The use of African tuliptree (*Spathodea campanulata*) as ornamental plant is widespread in urban environments of southeastern Brazil, occurring in small agglomerations, planted in lines as "tree walls", or solitary individuals (pers. obs.).

4.2. Flowering patterns of African tuliptree

Territorialism occurs according to flower availability, nectar quality and distribution in the landscape, thus, those variables can determine when hummingbirds start to exhibit territorial behavior, when other strategies are more feasible, or the time to leave and search for other foraging site to defend (Feinsinger and Colwell, 1978; Mendonça and Anjos, 2006; Chaves and Alves, 2010; Justino et al., 2012).

Understanding the responses of hummingbird assemblage to variations demanded a previous question: does flower availability vary throughout surveyed months? The analyses of variance indicated the observed differences along flowering period are statistically significant. Also, the analysis showed no differences between plant individuals in each month, as it is expected in a homogeneous population under the same weather and environmental conditions.

4.3. Foraging patterns of hummingbirds

Eupetomena macroura and *F. fusca* exhibited a strong territorialism during foraging, while others used non-territorial foraging strategies in the studied area, as generalist behaviors and trap-lining behavior. Three species were responsible for 87.3% of all animal-plant feeding interactions, leading to the conclusion that *S. campanulata* provided an important resource for them, while it may not be proportionally important for the submissive species, which may depend more on the variety of food resources in different patches.

Most of feeding visits of hummingbird species were pillage (55.4%) at the basis of flowers, instead of frontal access, which could not favor the pollination process. Only two species performed more frontal access than pillage: *F. fusca* (32.9% pillage, n=150 observations) and *A. fimbriata* (36.4% pillage, n=11 observations). *Eupetomena macroura* fed more times on nectar than other hummingbirds, but 66.86% of visits were pillage.

The positive relationship between time spent on feeding at the studied site and the number of flowers accessed indicated an expected pattern in foraging ecology, which can lead to different foraging strategies among hummingbird species to maximize energy intake. The submissive species were responsible for most of the points in the left of the linear model (Figure 2) which describes the foraging patterns of hummingbird assemblage. Thus, species that exhibited more agonistic behavior are those responsible for longer time spent on foraging site and more flowers accessed.

4.4. Territorialism and agonistic behavior

Agonistic interactions between nectarivores are common at foraging sites with Neotropical plant species (Las-Casas et al., 2012), as we observed in the agglomeration of non-native African tuliptrees.

In a patch of plants offering resources, the presence of territorialist species affects the choices during foraging of other individuals (Powers and Conley, 1994; Sandlin, 2000). Most of observations in the studied foraging site were indirect confrontation without physical contact. Sentinel behavior, alarm calls and chasings represented 86% of all agonistic interactions between competitors. There is a

possibility that *Spathodea campanulata* resources do not offer enough quality to motivate hummingbirds engaging in highly dangerous and energetically expensive behavior, such frontal encounters and pecking; and/or the abundance of flowers and amount of resources being offered monthly favor the resource sharing with more species and individuals.

We found no significant influence of African tuliptree agglomeration in number of agonistic encounters between competitors, mainly because in March there was an intense flower blooming, but the number of agonistic behaviors did not increase proportionally. Even with certain influence of this exotic species in territorial behavior, there must be other variables in local context which may exert a stronger influence on hummingbird assemblage.

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