The hummingbird community and their floral resources in an urban forest remnant in Brazil

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Abstract

The temporal and spatial resource use among hummingbirds was studied over 13 months in an urban forest remnant (Prosa State Park: PSP) in Campo Grande, Mato Grosso do Sul, Brazil. Hummingbird visitation was recorded at three ornithophilous and eleven non-ornithophilous species. Flower density was roughly constant during the study period, with the density of non-ornithophilous flowers being higher than that of ornithophilous ones. Mean values of nectar volume and concentration were similar between ornithophilous and non-ornithophilous species. Eight hummingbird species were observed at PSP: *Amazilia fimbriata*, *Anthracothorax nigricollis*, *Chlorostilbon lucidus*, *Eupetomena macroura*, *Hylocharis chrysura*, *Florisuga fusca*, *Thalurania furcata* and an unidentified species. Hummingbird visit frequencies to ornithophilous and non-ornithophilous flowers were similar. However, some non-ornithophilous species received a higher number of visits, which seems to be related to their large number of open flowers per plant per day. The number of feedings bouts of hummingbirds increased with the total number of flowers observed per focal plant. All recorded species of hummingbirds visited non-ornithophilous flowers, predominantly melittophilous and generalised entomophilous flowers. Hummingbird species recorded at PSP may be viewed as generalists, visiting a large number of non-ornithophilous species. Despite being an urban forest, PSP is relatively rich in hummingbird species, suggesting that it provides important shelter and foraging sites for hummingbirds in such an environment.

Keywords: community, flowering phenology, forest fragment, hummingbirds, pollination.

Comunidade de beija-flores e seus recursos florais em um fragmento florestal urbano no Brasil

Resumo

O uso temporal e espacial de recursos por beija-flores foi estudado ao longo de 13 meses em um remanescente florestal urbano (Parque Estadual do Prosa: PSP) em Campo Grande, Mato Grosso do Sul, Brasil. As visitas dos beija-flores foram registradas em três espécies ornitófilas e 11 não ornitófilas. A densidade de flores foi mais ou menos constante durante o período de estudo, com a densidade de flores não ornitófilas sendo maior que a de flores ornitófilas. Os valores médios de volume e concentração do néctar foram similares entre as espécies ornitófilas e não ornitófilas. Oito espécies de beija-flores foram observadas no PSP: *Amazilia fimbriata*, *Anthracothorax nigricollis*, *Chlorostilbon lucidus*, *Eupetomena macroura*, *Hylocharis chrysura*, *Florisuga fusca*, *Thalurania furcata* e uma espécie não identificada. A frequência de visitas dos beija-flores foi similar entre as espécies ornitófilas e não ornitófilas. Entretanto, algumas espécies não ornitófilas receberam um alto número de visitas, o que parece estar relacionado ao alto número de flores abertas por planta por dia. O número de turnos de visitas dos beija-flores aumentou com o número total de flores observadas por planta focal. Todas as espécies de beija-flores visitaram flores não ornitófilas, predominantemente flores de espécies melitófilas e entomófilas generalistas. Os beija-flores observados no PSP podem ser considerados generalistas, visitando um grande número de espécies não ornitófilas. Apesar de o PSP ser um fragmento florestal urbano, possui riqueza de espécies de beija-flores relativamente alta, sugerindo ser importante sítio de abrigo e forrageamento para os beija-flores neste ambiente.

Palavras-chave: comunidade, fenologia de floração, fragmento florestal, beija-flores, polinização.

1. Introduction

Hummingbirds depend on nectar to supply most of their energy requirements, and these birds are morphologically, physiologically and behaviourally adapted to visit flowers in search of this resource (Diamond et al., 1986). This dependence on nectar as a food makes hummingbirds the major group of vertebrate pollinators in the Neotropics (Bawa, 1990). Flowers adapted to hummingbird-pollination (ornithophilous) are an important component of neotropical plant communities, comprising 2-15% of angiosperm species in a given community (Feinsinger, 1983; Machado and Lopes, 2004; Ramírez, 2004).

Hummingbirds and hummingbird-visited flowers have been extensively studied in Central America and the Andes (Stiles, 1975; Wolf et al., 1976; Snow and Snow, 1980; Feinsinger et al., 1982; Kodric-Brown et al., 1984; Arizmendi and Ornelas, 1990; Cotton, 1998a), where many studies have taken a community approach (Snow and Snow, 1980; Feinsinger et al., 1982; Kodric-Brown et al., 1984; Arizmendi and Ornelas, 1990). In contrast, most studies in Brazil have focused on individual plant species (e.g. Araujo et al., 1994; Sluys and Stotz, 1995; reviewed in Mendonça and Dos Anjos, 2003, 2006a). Of the few previous community studies in Brazil, most have been based on observations of a few days or months (e.g. Snow and Snow, 1980; 1986; Snow and Teixeira, 1982). Studies carried out throughout the year are scarce and mainly concentrated in the Atlantic rainforest (e.g. Araujo, 1996; Sazima et al., 1996; Buzato et al., 2000; Araujo and Sazima, 2003). These Brazilian studies have shown some differences from those reported in Central America and the Andes (e.g. Feinsinger, 1976; Snow and Snow, 1980; Feinsinger et al., 1982), especially with regard to families of ornithophilous plants. In this sense, additional studies in Brazil might reveal different hummingbird-flower community structure (Fischer et al., 1996).

The importance of non-ornithophilous species as food for hummingbirds is not well documented. The few studies including ornithophilous and non-ornithophilous species as food resources have shown that hummingbirds can be broad generalists, with percentage of visits to non-ornithophilous species varying from 32 to 71% (Snow and Snow, 1986; Arizmendi and Ornelas, 1990; Araujo, 1996; Cotton, 1998b; Vasconcelos and Lombardi, 2001; Araujo and Sazima, 2003; Mendonça and Dos Anjos 2005). In Brazil, only two sites were studied regarding hummingbird-visited plant communities (including ornithophilous and non-ornithophilous species) throughout the year: one in the southeastern Atlantic rainforest (Araujo, 1996), and one in the southern Pantanal (Araujo and Sazima, 2003).

Most hummingbird species are habitat generalists (Feinsinger, 1976; Araujo and Sazima, 2003) frequently found in edges, secondary growth forests and open areas with a high abundance of flowers (Stiles, 1975; Cotton, 1998b; Borgella et al., 2001; Araujo and Sazima, 2003). Also, these birds are able to fly long distances, crossing open areas to use resources from different forest fragments (Stouffer and Bierregaard, 1995; Borgella et al., 2001). In human-altered landscapes, these fragments are important habitats for hummingbird populations that use these areas as breeding and/or foraging sites (Borgella et al., 2001). Despite the fact that there are some studies focused on hummingbird communities in forest fragments (Stouffer and Bierregaard, 1995; Borgella et al., 2001), studies reporting interactions of these birds with their floral resources in forest fragments are unknown.

Thus, the aims of our study are to investigate floral features and flowering phenology of ornithophilous and non-ornithophilous species visited by hummingbirds in a forest remnant in the Brazilian savanna (Cerrado). Additionally, it aims to record hummingbird species composition, seasonal occurrence of different hummingbird species and flower-visiting behaviour at the study site. Since the study area is a forest remnant, composed mainly of secondary plant species, we expect to record mainly medium-billed hummingbirds that are generalists in the use of floral resources (Feinsinger et al., 1982), including high proportions of non-ornithophilous species in their diet.

2. Material and Methods

This study was carried out at PSP, located in the urban perimeter of Campo Grande, Mato Grosso do Sul in central Brazil (20° 26' 34" S, 54° 38' 47" W). Prosa State Park is a forest fragment of about 140 ha that is isolated from other fragments and completely surrounded by urban areas. It is characterised by secondary vegetation, currently in late stage of regeneration, and includes distinct plant physiognomies such as riparian forest, savanna and *cerradão*, whose fauna and flora are poorly studied (Mato Grosso do Sul, 2000).

The hummingbird-visited plants at PSP were studied biweekly over 13 months (September 2002 – August 2003, October 2003). The flowering species were recorded in a preexisting trail measuring 6 m wide and 2100 m in length, of which 1100 m are located in riparian forest and 1000 m in *cerradão*, comprising a total sample area of 12600 m^2. Mean flower density was calculated for each month using the number of flowers recorded per species per total sampling area (flowers/m^2) (cf. Araujo, 1996). Growth form, number of open flowers as well as floral morphology (including corolla length) and colour were recorded. Voucher specimens of plant species were deposited at the Campo Grande Herbarium (CGMS/UFMS).

Pollination syndromes were determined using attributes of corolla morphology and predominat colours, presence of odour and period of anthesis. Typical ornithophilous species have odorless flowers with diurnal anthesis and tubular, red, pink, yellow or orange corollas (cf. Faegri and Pijl, 1980). The remaining species visited by hummingbirds were classified as non-ornithophilous. Non-ornithophilous species were divided into melittophilous (flowers adapted for bee pollination), chiropterophilous (flowers adapted for bat pollination) or sphingophilous (flowers adapted for sphingid pollination), according to floral characteristics described in Faegri and Pijl (1980). Additionally one species (*Inga vera*) was classified as generalist (species that could be pollinated by more than two pollinator groups, including vertebrate and invertebrate pollinators) and another species (*Serjania glutinosa*) as entomophilous (species that could be pollinated by species of more than two invertebrate groups).

Sugar concentration and volume of nectar were recorded between 06:30 AM – 08:00 AM (EST), from flowers bagged during the pre-anthesis period. Sugar concentration was measured with a pocket refractometer (cf. Araujo et al., 1994), and transformed in mg of sugar (cf. Galetto and Bernadello, 2005). Nectar volume was measured with graduated capillary tubes (cf. Galetto and Bernadello, 2005). These measures were made on one to nine flowers per flowering species. A *t*-test was used to compare the sugar concentration and nectar volume, as well as the total amount of sugar (mg of sugar) in nectar among flowers of ornithophilous and non-ornithophilous species.

The visits of hummingbirds were recorded by direct observation (focal observations) on 35 plant species, selected according to the following criteria: 1) ornithophilous species; 2) species reported as visited by hummingbirds in previous studies (e.g. Araujo, 2003) or with similar morphologies to these hummingbird-visited species; and 3) species with records of occasional visits by hummingbirds at the study site. Focal observations were made throughout the 12 months of study. Also, in October 2003, individuals of *Inga vera*, *Jacaratia spinosa* and *Vitex cymosa* were monitored to provide additional information about visitors. A Pearson correlation was used to verify if the hummingbird bill length and corolla length of legitimally visited species were related.

Hummingbird visits to flowers were recorded using 7 x 35 binoculars, mainly between 08:00 AM – 12:00 AM and 02:00 PM – 05:00 PM. Hummingbirds were identified during their visits to flowers (Ruschi, 1982; Grantsau, 1988) and males and females of species with evident sexual dimorphism were treated separately. Time and number of visits were recorded. Visits were classified as 1) legitimate when hummingbirds contacted anthers and/or stigmas in a way that could result in pollination, or 2) illegitimate when hummingbirds did not contact anthers and/or stigmas. Hummingbirds visiting behaviour, as well as the occurrence and outcome of agonistic interactions between them, were also recorded. Data on bill length of hummingbirds were based on Grantsau (1988), or on hummingbirds (*Anthracothorax nigricollis* and *Thalurania furcata*) captured in mist nets at the study site (M. Kinas, pers. comm.).

A Mann-Whitney U test was used to compare hummingbird visit frequencies (number of flowers visited per plant per minute divided by the number of observed flowers per plant) and density of flowers to ornithophilous and non-ornithophilous species. After data were transformed to log(n + 1), the analysis of covariance (ANCOVA) was done to determine whether the number of foraging bouts was affected by the number of flowers observed, and to determine if the number of agonistic interactions observed per plant per minute was affected by the total number of open flowers per plant, and by the category of plant species visited (ornithophilous or non-ornithophilous).

3. Results

3.1. Plants visited by hummingbirds

Hummingbirds visited 14 of the 35 plant species studied. Of the 14 visited plants, three were ornithophilous (*Bromelia balansae*, *Heliconia* sp. and *Psiguria ternata*), and 11 non-ornithophilous (Table 1). Hummingbirds were not recorded visiting flowers of the ornithophilous species *Ruellia brevifolia*, *Palicourea marcgravii* or *Psychotria poeppigiana* during focal observations (360, 280 and 240 minutes, respectively).

The dominant growth form of the ornithophilous species recorded at PSP was shrub (three species), followed by herbaceous (two species) and climber (one species). In contrast, most non-ornithophilous species were climbers (six species), four were trees, and one was a shrub (Table 1). In the ornithophilous group most species recorded had red or yellow tubular flowers, while in the non-ornithophilous group, recorded species presented cream, white or lilac bell flowers (Table 1). Mean corolla length of visited flowers ranged from 3.16 mm (*Centrosema pubescens*) to 41.1 mm (*Arrabidaea triplinervea*) among non-ornithophilous species, and from 14 mm (*P. ternata*) to 36.5 mm (*Heliconia* sp.) among ornithophilous species (Table 1). Mean nectar sugar concentration ($t = -0.38$, $p = 0.72$, $N = 9$) and mean nectar volume ($t = 0.22$, $p = 0.83$, $N = 9$), as well as the amount of sugar in nectar ($t = -0.82$, $p = 0.43$, $N = 9$) of ornithophilous species were similar to those of non-ornithophilous species (Table 1).

Flowering activity was highest in November, December and May (Table 2). Most ($N = 9$) of the non-ornithophilous species flowered in the dry season, and the ornithophilous species flowered mainly in the rainy season (Table 2). Pooling flowers by syndrome, density of non-ornithophilous flowers ranged up to 2.1 flowers/m^2 compared to the much lower range of 0.001 flowers/m^2 for ornithophilous flowers, these densities being statistically different (*U*-test, $U = 64$, $p = 0.002$, $N = 33$). Density of ornithophilous flowers did not vary throughout the year. In contrast, density of non-ornithophilous flowers had a peak in January and another in August (Figure 1). The mean number of open flowers per individual per day for the ornithophilous species was 3.11 ± 2.52 flowers/d ($N = 106$), ranging from 1.75 (*P. poeppigiana*) to 12 flowers/d (*B. balansae*). For the non-ornithophilous species this number was higher ($t = 4.08$, $P = 0.002$), 155.25 ± 252.90 ($N = 314$), ranging from 3.34 (*B. rufa*) to 1560 flowers/d (*V. cymosa*) (Table 1).

3.2. Hummingbird community

Eight species of hummingbirds, all in the Trochilinae subfamily, were recorded at PSP: Glittering-throated Emerald (*Amazilia fimbriata fimbriata*), Black-throated Mango (*Anthracothorax nigricollis nigricollis*), Glittering-

Table 1. Characteristics of ornithophilous (bold) and non-ornithophilous species visited by hummingbirds at Prosa State Park, central Brazil.

Species (Family)	GF[†]	FS[‡]	FC[§]	PS[*]	Corolla length (mm)[¥]	Nectar volume (µL)	Nectar concentration (%)	Sugar in nectar (mg)	Flowers/ Individual	Visit frequency
					X ± SD (N)	X ± SD (N)	X ± SD (N)	X ± SD (N)	X ± SD (N)	X ± SD (N)
Ruellia brevifolia (Pohl) Ezcurra (Acanthaceae)	Shr	Tub	Red	Orn	24.2 ± 3.42 (14)	7.53 ± 2.43 (7)	24.14 ± 2.79 (7)	1.94 ± 0.46 (7)	2.95 ± 2.39 (65)	0 (5)
Bromelia balansae Mez. (Bromeliaceae)	Her	Tub	Red	Orn	28.2 ± 1.25 (7)	20.44 ± 10.16 (9)[△]	26.95 ± 2.79 (9)[△]	6.2 ± 3.36 (9)[△]	12 ± 0 (1)	0.006 ± 0 (1)
Psiguria ternata (M.J. Roemer) C. Jeffrey (Cucurbitaceae)	Cli	Tub	Pin	Orn	14.0 ± 0.10 (3)	16.95 ± 11.54 (2)	18.50 ± 2.12 (2)	3.17 ± 1.84 (2)	8 ± 0 (1)	0.024 ± 0.014 (5)
Heliconia sp. (Heliconiaceae)	Her	Tub	Ora	Orn	36.5 ± 0.21 (2)	27.63 ± 10.65 (2)	25.50 ± 3.53 (2)	7.49 ± 1.77 (2)	2.75 ± 2.847 (4)	0.003 ± 0.005 (3)
Palicourea marcgravii A. St.-Hil. (Rubiaceae)	Shr	Tub	Yel	Orn	-	7.12 ± 1.31 (3)	26.66 ± 2.02 (3)	2.09 ± 0.45 (3)	3.22 ± 2.33 (31)	0 (3)
Psychotria poeppigiana Müll. Arg. (Rubiaceae)	Shr	Tub	Yel	Orn	-	-	-	-	1.75 ± 0.95 (4)	0 (2)
Arrabidaea florida DC (Bignoniaceae)	Cli	Bel	Whi	Mel	23.1 ± 3.70 (6)	-	-	-	176.6 ± 217.56 (187)	0.005 ± 0.008 (2)
Arrabidaea triplinervea Baill. (Bignoniaceae)	Cli	Bel	Lil	Mel	41.1 ± 3.40 (8)	14.86 ± 5.11 (3)	21.00 ± 0 (3)	3.34 ± 1.14 (3)	15.66 ± 10.69 (3)	< 0.001 ± 0 (7)
Cuspidaria cf. *lateriflora* (Mart.) A. DC.(Bignoniaceae)	Cli	Bel	Lil	Mel	30.7 ± 5.12 (4)	-	-	-	118.08 ± 97.94 (25)	< 0.001 ± 0 (4)
Tabebuia heptaphylla (Vell.) Toledo (Bignoniaceae)	Tre	Bel	Lil	Mel	-	-	-	-	110 ± 0 (1)	0.001 ± 0 (1)
Bauhinia rufa (Bong.) Steud. (Caesalpinaceae)	Shr	Ope	Cre	Chi	14.0 ± 1.10 (4)	7.66 ± 0.00 (1)	20.50 ± 0 (1)	1.67 ± 0 (1)	3.34 ± 2.24 (23)	0.022 ± 0.023 (5)

[†] GF, Growth form: Her, herb; Shr, shrub; Cli, climber; Tre, tree. [‡] FS, Flower shape: Tub, tubular; Bel, bell; Ope, open, Fla, flag; Bru, brush. [§] FC, Flower color: Pin, pink; Ora, orange; Yel, yellow; Whi, white; Lil, lilac; Cre, cream; Gre, green. [*] PS, Pollination syndrome: Orn, ornithophily; Mel, melittophily, Chi, chiropterophily; Gen, generalist; Sph, sphingophily; Ent, entomophily. Flower per individual: mean number of open flowers per plant per day. Visit frequency: number of flowers visited per minute per number of observed flowers per individual. [¥] Internal corolla length, from base to opening (effective length cf. Wolf et al., 1976). [△] In cerrado area, Campo Grande, Mato Grosso do Sul (L.C. Rodrigues, unpubl data). [£] Recorded outside the sampled transect. Numbers are means ± standard deviations (sample sizes).

Table 1. Continued...

Species (Family)	GF[†]	FS[‡]	FC[§]	PS[*]	Corolla length (mm)[¥]	Nectar volume (µL)	Nectar concentration (%)	Sugar in nectar (mg)	Flowers/ Individual	Visit frequency
					X ± SD (N)	**X ± SD (N)**	**X ± SD (N)**	**X ± SD (N)**	**X ± SD (N)**	**X ± SD (N)**
Jacaratia spinosa (Aubl.) A. DC[£] (Caricaceae)	Tre	Tub	Gre	Sph	15.6 ± 0.54 (5)	-	-	-	800 ± 0.0 (1)	0.016 ± 0 (1)
Merremia macrocalyx (Ruiz & Pav.) O'Donell (Convolvulaceae)	Cli	Bel	Cre	Mel	-	-	-	-	33.83 ± 38.26 (6)	< 0.001 ± 0 (1)
Centrosema pubescens Benth (Fabaceae)	Cli	Fla	Lil	Mel	3.16 ± 0.25 (5)	6.07 ± 0.96 (3)	31.00 ± 2.64 (2)	2.12 ± 0.5 (2)	5.18 ± 5.01 (11)	0.006 ± 0.005 (4)
Inga vera (DC) T. D. Penn (Mimosaceae)	Tre	Bru	Whi	Gen	14.5 ± 0.88 (20)	43.83 ± 18. 60 (4)	20.30 ± 1.64 (5)	9.69 ± 4.42 (5)	83.36 ± 117.02 (22)	0.032 ± 0.048 (8)
Serjania glutinosa Radlk. (Sapindaceae)	Cli	Ope	Whi	Ent	-	-	-	-	197 ± 204.25 (34)	0.004 ± 0.005 (2)
Vitex cymosa Bertero ex Spreng (Verbenaceae)	Tre	Gul	Lil	Mel	9.2 ± 0.76 (21)	-	-	-	1560 ± 2036.46 (2)	0.002 ± 0.002 (2)

[†] GF, Growth form: Her, herb; Shr, shrub; Cli, climber; Tre, tree. [‡] FS, Flower shape: Tub, tubular; Bel, bell; Ope, open, Fla, flag; Bru, brush. [§] FC, Flower color: Pin, pink; Ora, orange; Yel, yellow; Whi, white; Lil, lilac; Cre, cream; Gre, green. [*] PS, Pollination syndrome: Orn, ornithophily; Mel, melittophily, Chi, chiropterophily; Gen, generalist; Sph, sphingophily; Ent, entomophily. Flower per individual: mean number of open flowers per plant per day. Visit frequency: number of flowers visited per minute per number of observed flowers per individual. [¥] Internal corolla length, from base to opening (effective length cf. Wolf et al., 1976). [△] In cerrado area, Campo Grande, Mato Grosso do Sul (L.C. Rodrigues, unpubl data). [£] Recorded outside the sampled transect. Numbers are means ± standard deviations (sample sizes).

Table 2. Flowering seasons and floral visitors of 14 plant species visited by hummingbirds at Prosa State Park. Full lines correspond to flowering recorded in the sampled transect; dotted lines correspond to flowering recorded in non-sampled sites at PSP. Bold refers to ornithophilous species. N = Number, NH = number of hummingbird species visiting flowers, 1 = *Amazilia fimbriata*, 2 = *Anthracothorax nigricollis*♂, 3 = *A. nigricollis*♀, 4 = *Chlorostilbon lucidus*♂, 5 = *C. lucidus*♀, 6 = *Eupetomena macroura*, 7 = *Hylocharis chrysura*, 8 = Florisuga fusca, 9 = *Thalurania furcata*♂, 10 = *T. furcata*♀, and 11 = unidentified species.

Species	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	NH
Ruellia brevifolia	——	——	——	——			——		——	——	——				0
Heliconia sp.		2 ——	- - -	——	- - -	——		- - -							1
Palicourea marcgravii			——	——		——	——	——	——	——					0
Psiguria ternate			2,6,7 - - -	2-7 - - -	- - -			- - -							4
Bromelia balansae			7 ——												1
Psychotria poeppigiana			——						——	——	——				0
Inga vera	1-11 ——	- - -	——	5								——		1,2,5,7,9 - - -	8
Cuspidaria sp.	——		——	2,7 ——											2
Bauhinia rufa	——								——	9,10 ——	5,7 ——	——			3
Vitex cymosa	2,7 ——													- - -	2
Jacaratia spinosa		- - -										- - -	- - -	2,4-7,11 - - -	5
Arrabidaea florida				2,7 ——	——	——									2
Arrabidaea triplinervea						2,6 ——	——								2
Centrosema pubescens								5 ——	——						1
Serjania glutinosa								——			——	4,7,9 ——			3
Merremia macrocalyx									4 ——	——					1
Tabebuia heptaphylla									7 ——						1
N flowering species	5	4	8	7	3	4	3	5	7	5	4	4	1	3	17
N hummingbird species	8	1	3	4	0	2	0	1	2	1	2	3	0	7	8

bellied Emerald (*Chlorostilbon lucidus lucidus*), Swallow-tailed Hummingbird (*Eupetomena macroura macroura*), Gilded Hummingbird (*Hylocharis chrysura chrysura*), Black Jacobin (*Florisuga fusca*), Fork-tailed Woodnymph (*Thalurania furcata furcata*), and one unidentified species. In addition, Versicolored Emerald (*Amazilia versicolor versicolor*), Rufous-throated Sapphire (*Hylocharis sapphirina sapphirina*) and the Phaethornithinae Planalto Hermit (*Phaethornis pretrei*) were also recorded at PSP in 2002 and 2003 (M. Kinas, pers. comm.).

The largest number of hummingbird species (N = 8) was recorded visiting flowers in September 2002 and October 2003. In January and March, hummingbirds were not recorded visiting flowers of monitored plants (Table 2), although in January, *H. chrysura* was recorded catching insects in the studied transect. This species was recorded in most of the study months (eight months), followed by males of *A. nigricollis* (six months), *E. macroura* and *C. lucidus* (five months), males of *T. furcata* (four months), while other species were recorded in two or fewer months (Table 2).

Mean bill length of visiting hummingbirds ranged from 18.0 to 21.5 mm. The short-billed (<20 mm) and medium-billed (20 to 30 mm) hummingbirds, *C. lucidus* (19 mm), *T. furcata* (21.5 mm), *A. fimbriata* (18 mm) and *F. fusca* (21 mm), only visited flowers with short-tubed corollas (<30 mm). *Hylocharis chrysura* (19 mm), *E. macroura* (21 mm) and *A. nigricollis* (21 mm) visited both long (≥30 mm) and short-tubed flowers (<30 mm). Bill length of hummingbirds and corolla length of visited flowers were not correlated (r = 0.08, p = 0.7). The only plant species that received illegitimate hummingbird visits was *C. pubescens* whose flowers were visited by females of *C. lucidus* using holes probably made by insects in the base of the corolla. *Hylocharis chrysura* was the main visitor of the studied community, visiting 71.4% of plant species recorded as visited by hummingbirds (Table 3).

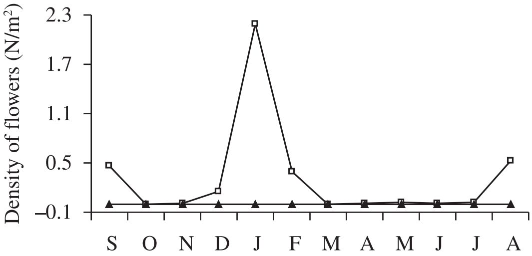

Figure 1. Density (flowers/m^2) of ornithophilous (triangle) and non-ornithophilous (square) flowers of species visited by hummingbirds over 12 months at Prosa State Park, central Brazil.

Frequency of hummingbird visits to flowers was similar for ornithophilous and non-ornithophilous species (*U*-test, $U = 137$, p = 0.25, $N = 46$). Among the ornithophilous species, *P. ternata* received the highest frequency of visits (0.024 ± 0.014 flowers visited.minute^{-1}. number of observed flowers^{-1}.plant^{-1}, N = 5), while among non-ornithophilous species *I. vera* was the most visited one (0.032 ± 0.048 flowers visited.minute^{-1}. number of observed flowers^{-1}. plant^{-1}, N = 8 (Table 1).

The number of feedings bouts of hummingbirds increased with the total number of flowers observed per focal plant (ANCOVA, $F_{1,42} = 14.812$, $P = 0.0003$) (Figure 2). However, ornithophilous versus non-ornithophilous (ANCOVA, $F_{1,42} = 0.360$, $P = 0.551$), as well as the interaction between syndrome and the number of flowers observed (ANCOVA, $F_{1,42} = 1.123$, $P = 0.294$) did not affect the number of feedings bouts.

Males of *A. nigricollis* visited flowers of *A. triplinervea* at intervals from 10 to 30 minutes, disappearing from the clumps of flowers after their visits. Similar behaviour was recorded for females of the hummingbird *C. lucidus* at flowers of *C. pubescens* and *P. ternata*. However, after

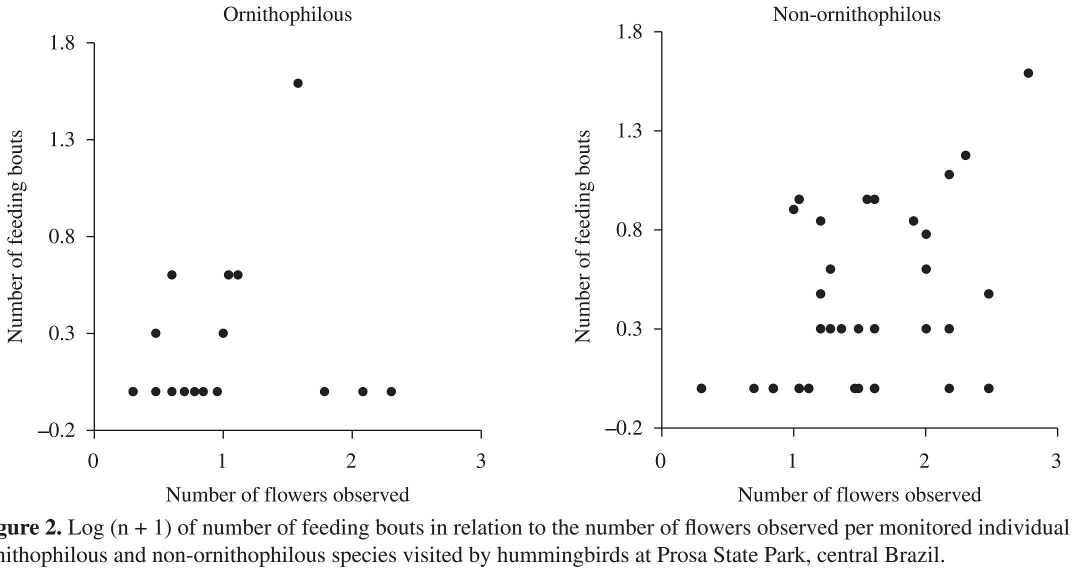

Figure 2. Log (n + 1) of number of feeding bouts in relation to the number of flowers observed per monitored individual of ornithophilous and non-ornithophilous species visited by hummingbirds at Prosa State Park, central Brazil.

visiting flowers of *I. vera*, *J. spinosa* and *B. rufa*, this hummingbird perched, and frequently chased away other hummingbirds which approached the clumps and tried to visit the flowers. Similar behaviour was recorded for *H. chrysura* (during visits to flowers of *I. vera*, *J. spinosa* and *P. ternata*), and for males of *A. nigricollis*, *C. lucidus* and *T. furcata* on flowers of *I. vera* and *J. spinosa. Florisuga fusca* exhibited variable intervals between visits to *I. vera* (5 to 50 minutes) as well as *E. macroura* in visits to flowers of *P. ternata* (5 to 15 minutes). Sometimes after their visits, these hummingbird species perched, but they were not observed chasing other individuals that approached the flowers. Other hummingbird species were occasional visitors and their behaviour patterns were not defined in this study.

Eighty-eight agonistic interactions were recorded between hummingbirds, a large number of them (N = 40) being recorded for one focal individual of *J. spinosa*. The largest number of agonistic interactions during flower visits were recorded between *H. chrysura* and females of *C. lucidus* (25 interactions), and for intraspecific interactions, among males of *A. nigricollis* (10 interactions). *Eupetomena macroura* was not displaced by any other hummingbird species, while *H. chrysura* and males of *A. nigricollis* were displaced by all hummingbird species, except males of *C. lucidus* (Table 4). The number of agonistic interactions observed per minute was not affected by the total number of open flowers per plant (ANCOVA, $F_{1,42} = 1.084$, $p = 0.3$), by syndrome (ANCOVA, $F_{1,42} = 0.824$, $p = 0.36$), or by interactions between the two factors (ANCOVA, $F_{1,42} = 0.405$, $p = 0.52$). During focal observations on *I. vera* and *J. spinosa,* sometimes two to four hummingbird individuals were recorded visiting the same plant at the same time. These individuals defended different clumps of flowers in the crown and agonistic interactions between them were frequent.

Table 3. Percentage of visits of hummingbird species on each of 13 flowering species in the Prosa State Park. Hummingbirds species: Af = *Amazilia fimbriata*, An^{m} = *Anthracothorax nigricollis*♂, An^{f} = *Anthracothorax nigricollis*♀, Ca^{m} = *Chlorostilbon lucidus*♂, Ca^{f} = *C.lucidus*♀, Em = *Eupetomena macroura*, Hc = *Hylocharis chrysura*, Ff = *Florisuga fusca*, Tf^{m} = *Thalurania furcata*♂, Tf^{f} = *Thalurania furcata*♀ and Sp = unidentified species.

Species	Af	An^{m}	An^{f}	Cl^{m}	Cl^{f}	Em	Hc	Ff	Tf^{m}	Tf^{f}	Sp
Bromelia balansae							100				
Heliconia sp.		100									
Psiguria ternata		0.7	6.6		20.5	23.1	48.9				
Arrabidae florida	100										
Arrabidae triplinervea		96.5				3.5					
Bauhinia rufa									11.1	88.9	
Centrosema pubescens					100						
Cuspidaria lateriflora		33.4					66.6				
Inga vera	0.4	19.3	4.8	3.9	7.1		38.9	9.1	7	2.8	6.5
Jacarantia spinosa	7.9	37.2		0.4	14.9	1.5	25.1				13.1
Merremia macrocalyx					100						
Serjania glutinosa					21.4		42.9		35.7		
Tabebuia heptaphylla							100				
Vitex cymosa		95.7					4.3				

Table 4. Matrix of aggressive interactions recorded for six hummingbird species on visits to flowers in the Prosa State Park. The lines correspond to the aggressor species in interaction and the columns correspond to the subordinate species. For each species, the sum of the horizontal axis (number of times each species displaced another) and of the vertical (number of times each species was displaced) was made. *An^{m} = Anthracothorax nigricollis*♂, *Ca^{m} = Chlorostilbon lucidus*♂, *Ca^{f} = C. lucidus*♀, *Em = Eupetomena macroura*, *Hc = Hylocharis chrysura*, e *Tf^{m} = Thalurania furcata*♂.

	Hc	Cl^{m}	Cl^{f}	Tf^{m}	Em	An^{m}	Total
Hc	9	1	15	3	-	2	30
Cl^{m}	-	-	1	-	-	-	1
Cl^{f}	10	-	6	-	-	2	18
Tf^{m}	3	-	-	1	-	1	5
Em	1	-	-	-	-	2	3
An^{m}	5	2	3	2	-	10	22
Total	29	3	31	6	-	18	88

4. Discussion

4.1. Plants visited by hummingbirds

The number of hummingbird-visited species and of ornithophilous species at PSP is lower than those reported for Neotropical communities with less seasonal climates (e.g. Stiles, 1978; Feinsinger et al., 1982; Snow and Snow, 1986; Araujo, 1996; Sazima et al., 1996; Cotton, 1998b; Buzato et al., 2000; Dziedzioch, 2003). However, they are similar to those reported for capões in the southern Pantanal (Araujo and Sazima, 2003), a cerrado in São Paulo (Silberbauer-Gottsberger and Gottsberger, 1988), and a savanna in Venezuela (Ramírez, 2004), where climate is seasonal and plant physiognomy is similar to that of cerrado (Ramírez, 2004). The number of hummingbird-visited species at PSP is also similar to that reported for a tropical dry forest in Mexico (Arizmendi and Ornelas, 1990). The similarity between PSP and all these sites with regard to the number of plant species visited by hummingbirds and number of ornithophilous species may be related to their strong seasonality. Furthermore, in the Neotropics hummingbird pollination is more frequent in habitats with less seasonal climates where food availability for these birds is more constant throughout the year (Ramírez, 2004).

Despite the fact that six ornithophilous species were observed, hummingbirds visited only three of these plant species. The absence of visits to *P. marcgravii*, *P. poeppigiana* and *R. brevifolia* may be related to the small number of open flowers per plant per day, low number of individuals flowering each month (*P. marcgravii*, 4.42 ± 2.5 individuals/mo, N = 7; and *P. poeppigiana*, 1 ± 0 individuals/mo, N = 4), or the low nectar volume in *P. marcgravii* and *R. brevifolia* (Table 1). However, in other sites, hummingbird visits were reported for *P. poeppigiana* (Coelho and Barbosa, 2004). Also in a semideciduous forest in southeastern Brazil, *R. brevifolia* had a very low frequency of visits (Sigrist and Sazima, 2002). Additional efforts would probably result in records of visits of hummingbirds to flowers of these species.

Flowering peaks of species visited by hummingbirds occurred in the middle of the wet season (November-December) and the beginning of the dry season (May). In September-October more hummingbird species were recorded at PSP. This result may be related to the flowering of the non-ornithophilous species *I. vera* and *J. spinosa*, which have the highest number of open flowers per day during these months in the study site. In other studied communities, flowering peaks occur at the end of the dry season and/or throughout the wet season (Arizmendi and Ornelas, 1990; Sazima et al., 1996; Araujo and Sazima, 2003).

The high frequency of hummingbird visits to melittophilous and generalised entomophilous species at PSP may be explained by the high frequency of species exhibiting these pollination syndromes at the study site (91.6%), the large number of open flowers on these plants per day, their diurnal anthesis, and their nectar offerings, which were similar to those found in ornithophilous flowers (e.g. Arizmendi and Ornelas, 1990; Araujo and Sazima, 2003). Moreover, the flowering seasons of these species occur in the dry season, when there are few ornithophilous species flowering at the study site. These results indicate that the birds are not slaves to floral syndrome, a conclusion also reached for the capões in the southern Pantanal (Araujo and Sazima, 2003).

Furthermore, with the exception of *C. pubescens* which received illegitimate visits, hummingbirds were able to contact the reproductive parts of the flowers during their visits to most of the non-ornithophilous species, thus indicating that these plant species may be pollinated by hummingbirds. These observations agree with those of Waser et al. (1996), Arizmendi and Ornelas (1990), Araujo (1996) and Araujo and Sazima (2003). However, more detailed data on pollen transfer efficiency of hummingbirds foraging on non-ornithophilous species are necessary (Castellanos et al., 2003).

4.2. Comparison of seven Neotropical sites

The families with the largest number of species visited by hummingbirds at PSP were Bignoniaceae and Fabaceae, as reported for the Pantanal (Araujo and Sazima, 2003) and a tropical dry forest in Mexico (Arizmendi and Ornelas, 1990). In sites with less seasonal climates, Bromeliaceae was the family with more species visited by hummingbirds (Table 5). At PSP, as well as in the Pantanal (Araujo and Sazima, 2003), the most frequent growth form of the species visited by hummingbirds was climber, while in the Atlantic forest communities, epiphytic species were the most frequent (Snow and Snow, 1986; Araujo, 1996) (Table 5). The differences in family frequencies and growth forms between sites possibly reflect differences in floristic composition (Araujo and Sazima, 2003), which is related to historical and geological factors, as well as to climate differences between them.

Hummingbirds visited more non-ornithophilous species at PSP, (78.6%) than in other communities as, for example, in an Atlantic forest community (32%) (Snow and Snow, 1986), or in a tropical dry forest in Mexico (34.7%) (Arizmendi and Ornelas, 1990). However, some of these studies focused mainly on ornithophilous species (e.g. Snow and Snow, 1986; Arizmendi and Ornelas, 1990). Year-round studies that included non-ornithophilous species presented more similar proportions to that recorded at PSP, such as studies in the Pantanal (71%) (Araujo and Sazima, 2003), the Caribbean (57.1%) (Stiles, 1978), and in another Atlantic forest community (50%) (Araujo, 1996) (Table 5). The high frequency of non-ornithophilous species visited by hummingbirds at PSP may be related to the low frequency of ornithophilous species present at the site (4.8% of the total plant species, unpubl. data), in a similar way as suggested for the *capões* in the Pantanal (Araujo and Sazima, 2003).

4.3. Hummingbird community

The number of hummingbird species recorded at PSP is similar to those reported for Atlantic forest communities (e.g. Sazima et al., 1996; Buzato et al., 2000), a tropical dry forest in Mexico (Arizmendi and Ornelas, 1990), and forests fragments in the Amazon (Stouffer and Bierregaard, 1995), but greater than that reported for southern Pantanal (Araujo and Sazima, 2003). No long-billed hummingbirds were recorded during the study period, although the long-billed (32 mm) *Phaethornis pretrei* (Phaethornitinae) was recorded in the riparian forest at the study site in 2002 and 2003 (Kinas M., pers. comm.). Hummingbirds of this subfamily are more frequent in the understory of forested areas, such as riparian forests (Stiles, 1978, 1981; Cotton, 1998b), and they are often considered more specialised, visiting ornithophilous flowers with long and/or curved corollas with large amounts of nectar (Stiles, 1978; Sazima et al., 1996; Buzato et al., 2000; Fischer and Leal, 2006). The low frequency of flowers with these characteristics, as well as the small area of riparian forest at PSP may explain the low frequency of hummingbird species from the subfamily Phaethornithinae in the area.

Hylocharis chrysura was the only species considered resident at PSP. In other neotropical communities, the number of resident hummingbirds varies between one to four species (Feinsinger, 1976; Araujo, 1996; Sazima et al., 1996; Araujo and Sazima, 2003), depending upon the local richness of ornithophilous species.

In some hummingbird-plant communities, a strong relationship has been observed between bill length and corolla length of visited flowers (Snow and Snow, 1980; Kodric-Brown et al., 1984; Sazima et al., 1996). However, this relationship was not clear-cut at PSP. With the exception of a visit of *H. chrysura* to *Cuspidaria* cf. *lateriflora*, species with long corollas were visited only by medium-billed hummingbirds (*A. nigricollis* and *E. macroura*), which were the species with the longest bills recorded in this study. Although, those relationships are also mediated by other floral traits, such as corolla diameter and curvature (Temeles et al., 2002; 2009), that were not measured in this study.

According to the flower-visiting behaviour of hummingbirds at PSP, their community roles (cf. Feinsinger and Colwell, 1978) may be classified as follows: *H. chrysura* acted as territorialist in clumps of flowers of *I. vera*, *J. spinosa* and *P. ternata*. In other plant species, this hummingbird species acted as a generalist, making occasional visits. Females of *C. lucidus* acted as low-reward trapliners during visits to *C. pubescens* and as territorialists in clumps of flowers of *I. vera*, *J. spinosa*, and *B. rufa*. Males of *A. nigricollis* also modified their foraging strategy according to the visited plant species. They acted as low-reward trapliners during visits to *A. triplinervea* flowers and as territorialists during visits to clumps of flowers of *I. vera* and *J. spinosa*. *Eupetomena macroura* acted as a territory parasite of *H. chrysura* in visits to *P. ternata* and *F. fusca*, as a territory parasite of *H. chrysura* and females of *C. lucidus* in visits to *I. vera*. Males of *T. furcata* acted as territorialists during visits to *I. vera* and *J. spinosa.* The observed shift in foraging strategies of hummingbirds may occur in response to changes in the availability and spatial distribution of flowers, as well as in response to competition with other nectarivorous species (Feinsinger, 1976; Feinsinger and Colwell, 1978; Stiles, 1981; Mendonça and Dos Anjos, 2006b, Toledo and Moreira, 2008). When the number of flowers is low and dispersed in the habitat as, for example, flowers of *C. pubescens* and *A. triplinervea,* it is advantageous to act as a trapliner (Feinsinger and Chaplin, 1975). On the other hand, when flowers occur in clumps, as with flowers of *I. vera* and *J. spinosa*, hummingbirds often act as territorialists, defending these clumps of resources (Wolf et al., 1976; Snow and Snow, 1986; Arizmendi and Ornelas, 1990; Cotton, 1998b). The spatial distribution of hummingbird territories as recorded for *I. vera* and *J. spinosa*, is often observed in trees and shrubs with high densities of flowers (Stiles and Wolf, 1970; Feinsinger, 1976).

For the hummingbirds at PSP, size was related to dominance. *Eupetomena macroura*, the largest hummingbird species recorded at the study site, was not displaced by any other species. Males of *A. nigricollis*, the second largest species, displaced more (12 times) than was displaced (eight times). Moreover, about 45% of interactions of males of *A. nigricollis* were with other males of the same species. Smaller hummingbirds often interacted intraspecifically or interspecifically with hummingbirds of similar sizes. A similar pattern of dominance was reported for an Atlantic forest assemblage (Araujo, 1996) and agrees with the one proposed by Des Granges (1979).

In summary, despite the fact that PSP is an urban forest remnant, the hummingbird richness indicates that it may be a refuge and an important foraging site for hummingbirds. In periods of flower scarcity in this area, hummingbirds probably shift to other forest remnants or forage in urban areas near the study remnant, using PSP mostly as a refuge site. Also, data support our expectation of the predominance of generalist hummingbird species at PSP. Studies regarding hummingbird communities in fragmented areas (Stouffer and Bierregaard, 1995; Borgella et al., 2001) also have shown that short to medium-billed generalist hummingbirds are the most frequent ones. Furthermore, hummingbirds at the study site visited flowers of the non-ornithophilous species legitimally, thus indicating that these plant species may also be pollinated by hummingbirds, supporting the idea of Waser et al. (1996) of generalisation in some pollination systems. However, the role of hummingbirds as pollinators on non-ornithophilous species needs to be better evaluated through studies regarding pollen transfer efficiency by these birds.

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