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ORIGINAL ARTICLE

The assembly of plants used as nectar sources by hummingbirds in a Cerrado area of Central Brazil

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Abstract Studies on hummingbird–plant interactions commonly use a pollination approach emphasizing mutualistic relationships. But floral resources are often used opportunistically by these birds. Plant–pollinator assemblies and pollination sustainability will depend both on the well-adapted plants and other potential floral resources. The Cerrado, Neotropical savannas of Central Brazil, has ca. 7.5 % of its flora supposedly adapted to hummingbird pollination. But detailed information about flowers effectively used by hummingbirds at community level is still lacking. Hence, we recorded all plant species visited by hummingbirds, to determine how these nectariferous flowers were distributed in time and space in different plant formations of a Cerrado area, and also the hummingbird species that visit them. The study was conducted between March 2007 and December 2008 in the Panga Ecological Station. Data regarding flowering phenology, floral morphology and visitation were collected monthly. Forty-six nectariferous species from 39 genera and 17 families were recorded, most with annual flowering dynamics and tubular flowers. But only 21 species had a combination of traits fitting classic ornithophilous syndrome. For the remaining species hummingbird visitation was ascertained from observations at the study site or other sites in the region. Eight hummingbird species occurred in the area and were recorded visiting directly 36 plant species. The study area presented a relatively low number of ornithophilous plants, but a great habitat diversity and many non-ornithophilous plants that hummingbirds used as nectar sources. Therefore, in the studied Cerrado, the diversity of environments and nectariferous plants favour the maintenance of resident and migrant hummingbirds.

Keywords Flowering phenology · Floral morphology · Plant community · Hummingbird visitation · Ornithophily · Neotropical savanna

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Introduction

The plant–hummingbird interaction at community level has been subject of researches in various regions of the Americas (Toledo 1975; Brown and Bowers 1985; Grant 1994; Buzato et al. 2000; Lasprilla and Sazima 2004). They have addressed different features of the ornithophilous flora, such as floral morphology (Rodríguez-Flores and Stiles 2005; Temeles et al. 2009; Dalsgaard et al. 2009), flowering phenology (Stiles 1978, 1985), nectar characteristics (Stiles and Freeman 1993; McDade and Weeks 2004), as well as features of the organisation of ornithophilous plants and hummingbird communities (Sazima et al. 1996; Araujo and Sazima 2003; Abreu and Vieira 2004; Machado et al. 2007; Leal et al. 2006; Machado 2009; Las-Casas et al. 2012).

However, the approach used in most studies tends to emphasise direct relationships and adjustments, both phenological and morphological, usually associated with those mutualisms and which lead to pollination (e.g. Nattero and Cocucci 2007; Dalsgaard et al. 2011), excluding interactions in which hummingbirds are not actual pollinators. But the organisation of plant–animal networks involves stochastic events and rarely is the result of in situ evolution and pairwise adaptation (e.g. Cotton 1998; Agosta and Janzen 2005; Dalsgaard et al. 2011; Moré et al. 2012). Floral resources are used in an opportunistic way by visitors and the assembly of pollinators and the pollination services in a given area may be influenced by the resources offered both by their focal plants and their neighbours (Maruyama et al. 2012; Blüthgen and Klein 2011; Hegland and Totland 2012). Thus, community studies of plant–pollinator assemblies and pollination sustainability will depend both on the well-adapted plants and other potential floral resources (Blüthgen and Klein 2011). It seems to be true both to sustainable crop pollination (e.g. Yamamoto et al. 2012) and to conservation of threatened plant communities (e.g. Menz et al. 2011).

Ornithophily usually involves a relatively well-defined morpho-physiological syndrome and evolved many times in unrelated plant groups (Cronk and Ojeda 2008). In the Neotropics, a set of even better-defined floral features is commonly associated with pollination by hummingbirds (Rocca and Sazima 2010). These features seem to separate these plants in modular networks, which to a certain extent isolate them from insect-pollinated plants (Danieli-Silva et al. 2012). But for the Cerrado region, the vast Neotropical savanna region in Central Brazil, estimates based on these features suggest that only 7.5 % of the Cerrado flora is composed by ornithophilous species (Gottsberger and Silberbauer-Gottsberger 2006). Other studies in the region dealt with focal interactions (e.g. Castro and Oliveira 2001; Coelho and Barbosa 2004; Consolaro et al. 2005; Araújo and Oliveira 2007; Araújo et al. 2011b) or isolated plant formations (e.g. Araújo et al. 2011a). Most of these surveys already call attention to the importance of nectar availability in time and space for hummingbird persistency in these seasonal tropical areas (Araujo and Sazima 2003).

However, there is no precise information about the non-ornithophilous species used by hummingbirds in the Cerrado. The Cerrado domain harbours about 36 species among hermits (Phaethornithinae) and non-hermits (Trochilinae) hummingbirds (Macedo 2002). Floral resources from both ornithophilous and non-ornithophilous plants seem to be vital to the persistence of hummingbird populations in these areas (Araújo et al. 2011a).

Thus, our study aimed to determine which plant species were visited by hummingbirds in an area of Cerrado and how these nectariferous species were distributed in time and space. For this purpose, data on species composition, flowering phenology, floral traits and hummingbird species assembly associated with the plant community were recorded. We confirmed here the idea that both well-adjusted ornithophilous plants and nectariferous non-ornithophilous ones are used by hummingbirds in these areas and set the basis for further studies on the contribution of each group for the maintenance of hummingbirds and bird-pollination services in this region.

Materials and methods

Study area

This study was conducted at the Panga Ecological Station (PES), an area of 409.5 ha located in Uberlândia, Minas Gerais, Brazil (19°09′20″–19°11′10″ S and 48°23′20″–48°24′35″ W) at ≈800 masl. The climate presents two well defined seasons: a cold and dry one between May and September and another warm and humid from October to April. The monthly temperature varied from 8.5 to 33 °C and the rainfall ranged from 0 to 363.2 mm.

Details of plant physiognomies at PES were based on Schiavini and Araújo (1989) and Cardoso et al. (2009). For flowering phenology data, the plant species were monitored monthly from March 2007 to December 2008 along different trails of the PES. All blooming plants as far as 8 m from each side of the trails and their number of flowers were recorded. The trails included areas inside a seasonal semideciduous forest, two different gallery forests and the edge of one gallery forest. Data for the two gallery forests were considered separately because they presented different floristic composition and thus were referred as gallery forest (I) and gallery forest (II). Other trails were surveyed in open Cerrado areas (savanna grasslands with varied density of trees, including "Cerrado sensu stricto", and denser "cerradão" woodlands; and grasslands with a few scattered shrubs or "campo sujo"), as well as on the edge of a palm swamp area. The trails had different length and the total sampled area was 31,691.6 m^2.

Floral phenology

The flowering phenology of the species was classified as continuous (all year round flowering with only occasional short pauses), sub-annual (more than one cycle per year), annual (one major cycle per year) or supra-annual (only one cycle during the 2 years study period). Flowering duration was classified as brief (<1 month), intermediate (1–5 months) or extended (>5 months) following Newstrom et al. (1994). Vouchers were incorporated to the HUFU and UEC.

The plant species included in the sample were either ornithophilous (sensu Faegri and van der Pijl 1980) or non-ornithophilous species. The non-ornithophilous species were nectariferous plants with a floral morphology that did not hinder bird visits and which were visited by hummingbirds for nectar in the study site or other sites in the region. We recorded as visits only when the birds effectively probed flowers for nectar, although many visits did not result in pollination due to lack of morphological adjustment between flowers and hummingbirds (see Araújo et al. 2011a). Data about the habit, morphology, corolla length and corolla width, and the predominant colour of the flowers were recorded. Flowers of all species were collected and stored in 70 % alcohol for laboratory analysis and measurements. Corolla width ($n = 43$—aperture diameter of the corolla, sensu Temeles et al. 2002) and effective corolla length ($n = 43$—from the base to opening, sensu Wolf et al. 1976) were taken. The mean and standard deviation were calculated for each species and corolla length categories were established as: short (<2 cm), medium (2–4 cm) and long (>4 cm); and corolla width as: narrow (<1 cm) and wide (>1 cm).

Nectar volume and sugar concentration were measured in situ in flowers bagged before anthesis with microliter syringes (Hamilton® 50 and 100 µL) and handheld refractometer (Atago N-1α Brix 0–32 %), respectively. When sugar concentration exceeded the refractometer limits, nectar was diluted in a known volume of distilled water and used to estimate the original value of the sample (Galetto and Bernardello 2005). The nectar data were sampled at about 10:00 a.m., from 1 to 25 flowers ("Appendix 1") from different individuals in most of the species. Spearman correlation (r_s) was used to verify relationships between corolla length and corolla width with nectar volume (Arizmendi and Ornelas 1990).

The hummingbird species were recorded through direct observations during visits to different plant species. Observations were made in non-consecutive days from 07:00 a.m. to 04:00 p.m. Each plant species was observed for at least 2 h and for the whole plant community, a total of 96 h of observations were made in 2007 and 162 h in 2008. Hummingbird identification and data of the species' bills followed Grantsau (1989). Relationships between corolla length and corolla width with the length of hummingbird' bills were evaluated with Spearman (r_s) correlations. Statistical analyses were performed using SPSS version 16.0.

Results

A total of 46 plant species was recorded, belonging to 39 genera and 17 families ("Appendix 1"). The families Fabaceae, Bignoniaceae, Vochysiaceae, Bromeliaceae, Rubiaceae and Malvaceae presented more than three species each. Fabaceae was the most representative family with seven species and the less representative families showed from one to three species each ("Appendix 1"). Only 21 species were ornithophilous and the others were melittophilous (15), chiropterophilous (6), psychophilous (2) and sphingophilous (2) ("Appendix 1"). The ornithophilous species belonged to 13 families, among which Bromeliaceae and Acanthaceae were the most diverse, with four and three species, respectively. Lamiaceae, Malvaceae and Rubiaceae were represented by two species each, while the remaining families were represented by one species only.

Concerning the habit, 17 species were trees, 12 herbs, 7 shrubs, 4 sub-shrubs, 4 climbers and 2 epiphytes ("Appendix 1"). Most species occurred in the campo sujo (19 species), followed by the gallery forest (I) (12 species) and the edge of the gallery forest (11 species) (Fig. 1). Several species occurred in more than one plant formation: the gallery forest (I) had seven species that occurred also in other four plant formations, and plant formations that shared more species were campo sujo and cerrado *s.s* savanna areas (six species) (Fig. 1). On the other hand, the campo sujo had more exclusive species (11) followed by

Table 1 Hummingbird species, bill length, and the range of corolla length and width of flowers visited by hummingbirds at the Panga Ecological Station (PES), Uberlândia, MG

Species	Bill length (cm)[a]	Corolla length (cm)	Corolla width (cm)
Phaethornis pretrei	3.5	1.2–7.1 ($n = 20$)	0.27–3.66 ($n = 20$)
Eupetomena macroura	2.1–2.3	1.2–1.3 ($n = 3$)	0.36–0.75 ($n = 3$)
Heliomaster squamosus	3.1	5.01–7.06 ($n = 2$)	0.54–0.72 ($n = 2$)
Colibri serrirostris	2.2	1.31–1.33 ($n = 2$)	0.39–0.55 ($n = 2$)
Amazilia fimbriata	2.1	0.9–4.84 ($n = 14$)	0.2–1.95 ($n = 14$)
Thalurania furcata	1.9–2.0	0.76–3.24 ($n = 15$)	0.2–0.9 ($n = 15$)
Chlorostilbon lucidus	1.93–2.0	1.2–2.97 ($n = 6$)	0.39–0.95 ($n = 6$)
Lophornis magnificus	1.1	1.33–1.45 ($n = 2$)	0.39–0.47 ($n = 2$)

In brackets number of flowers

[a] Based on Grantsau (1989)

the edge of the gallery forest and the gallery forest (I) both with five species (Fig. 1).

The great majority of species (91.3 %) showed annual flowering pattern. The exceptions were *Ruellia brevifolia*, *Helicteres brevispira* and *Luehea grandiflora*, which presented sub annual pattern with more than one cycle per year; and *Canna indica,* that had a continuous pattern blooming all year round with short occasional pauses (Fig. 2). Regarding the duration of flowering periods many species (54.3 %) had intermediate, followed by extended (23.9 %), and brief (21.7 %) periods ("Appendix 1"). It is important to notice that since our study period was <2 years and flowering phenology is variable in Neotropical region, the correspondence with Newstrom et al. (1994) classification, based on long term studies, should be taken cautiously.

The number of flowering species per month over 2 years varied from 6, on November 2008 (rainy season), to 16 species, on July 2007 (dry season) (Fig. 2). Considering ornithophilous species, the number of blooming species ranged from 5, in 5 different months of both dry and rainy seasons, to 10 species in March 2008 during the rainy season (Fig. 2).

Most species (66.9 %) had tubular flowers while 10.9 % had spurs, and the remaining had brush (10.9 %), flag (8.7 %), throat (4.4 %) or dish flowers (4.4 %) ("Appendix 1"). The majority of species presented short (46.5 %) and medium-sized (41.9 %) corollas, and only 6 % had long corollas ("Appendix 1"). The average corolla length for the community was 2.5 ± 2.4 cm, the shortest corolla occurred in *Styrax pohlii* (0.8 cm) and the longest in *Canna indica* (7.1 m). Regarding corolla width, 81.4 % of the species had narrow diameter and only 18.6 % had wide

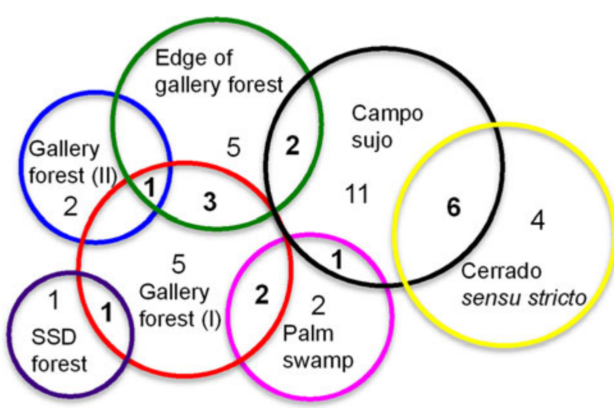

Fig. 1 Number of plant species used by hummingbirds that are shared by different plant formations (in *bold* in the intercessions), and number of plant species exclusive of each plant formation of the Cerrado at the Panga Ecological Station (PES), Uberlândia, MG. *SSD* seasonal semideciduous forest. Circles are roughly proportional to the number of plant species used in each area

diameters. The average corolla width was 0.75 ± 0.63 cm with the narrowest in *Lippia lasiocalycina* (0.18 cm) and the widest in *Caryocar brasiliensis* (3.66 cm) ("Appendix 1").

The flowers presented a spectrum of colours ranging from white, yellow, orange, red to blue (Fig. 3), but the dominant colour was white (26.1 %), followed by yellow (19.6 %) and red (19.6 %). The nectar volume per flower ranged from 1.95 µL (*Eriotheca gracilipes*) to 49.7 µL (*Sinningia elatior*), with an average of 15.30 ± 11.65 µL ($n = 40$). Sugar concentration ranged from 12.95 % (*Bauhinia brevipes*) to 34.33 % (*Mandevilla hirsuta*), and the average for the community was 21.60 ± 5.13 % ($n = 40$). The corolla length and the volume of nectar from 38 of the studied species presented low but significant correlation ($r_s = 0.32$, $p < 0.05$). The corolla width and the volume of nectar were also positively correlated ($r_s = 0.52$, $p < 0.001$).

The focal observations of visits were made in all plant formations, with records of eight hummingbird species (Table 1), one Phaethornithinae and seven Trochilinae. *Phaethornis pretrei* and *Thalurania furcata* were possible resident species and explored mainly species inside the gallery forest, although *T. furcata* individuals seldom used the same resources as *P. pretrei.* Both species explored also flowers in other plant formations: *P. pretrei* was recorded at the edge of the gallery forest, usually in areas close to the Panga stream and a few times in the campo sujo savannas near to the gallery forest. *T. furcata* was recorded at the edge of the gallery forest. The other hummingbird species moved among plant formations although they were recorded mainly at the edge of the gallery forest.

Hummingbirds were recorded visiting a total of 36 plant species in the area. The remaining 10 species were mostly melittophilous and hummingbird visits were recorded elsewhere in the region (P.E. Oliveira, pers. observ.). We presented the number of visits directly observed for each plant ("Appendix 2"). As mentioned before, we referred as visits when the birds probed nectariferous flowers for nectar, even when morphology indicated no real pollination was going on. As for the other species, although we do not have quantitative observations, the visits observed elsewhere were not spurious or occasional visits. The birds were observed effectively probing various flowers for nectar, even when the nectar was probably residual or in very tiny amounts. The greatest richness of hummingbird species visits was to *Bauhinia ungulata*, *Cuphea melvilla*, *Heliconia psittacorum*, *Helicteres brevispira, Inga vera* and *Vochysia tucanorum* ("Appendix 2"). *Phaethornis pretrei* was the main visitor and the most recorded to many species (58.3 %), visiting flowers with corolla lengths that varied

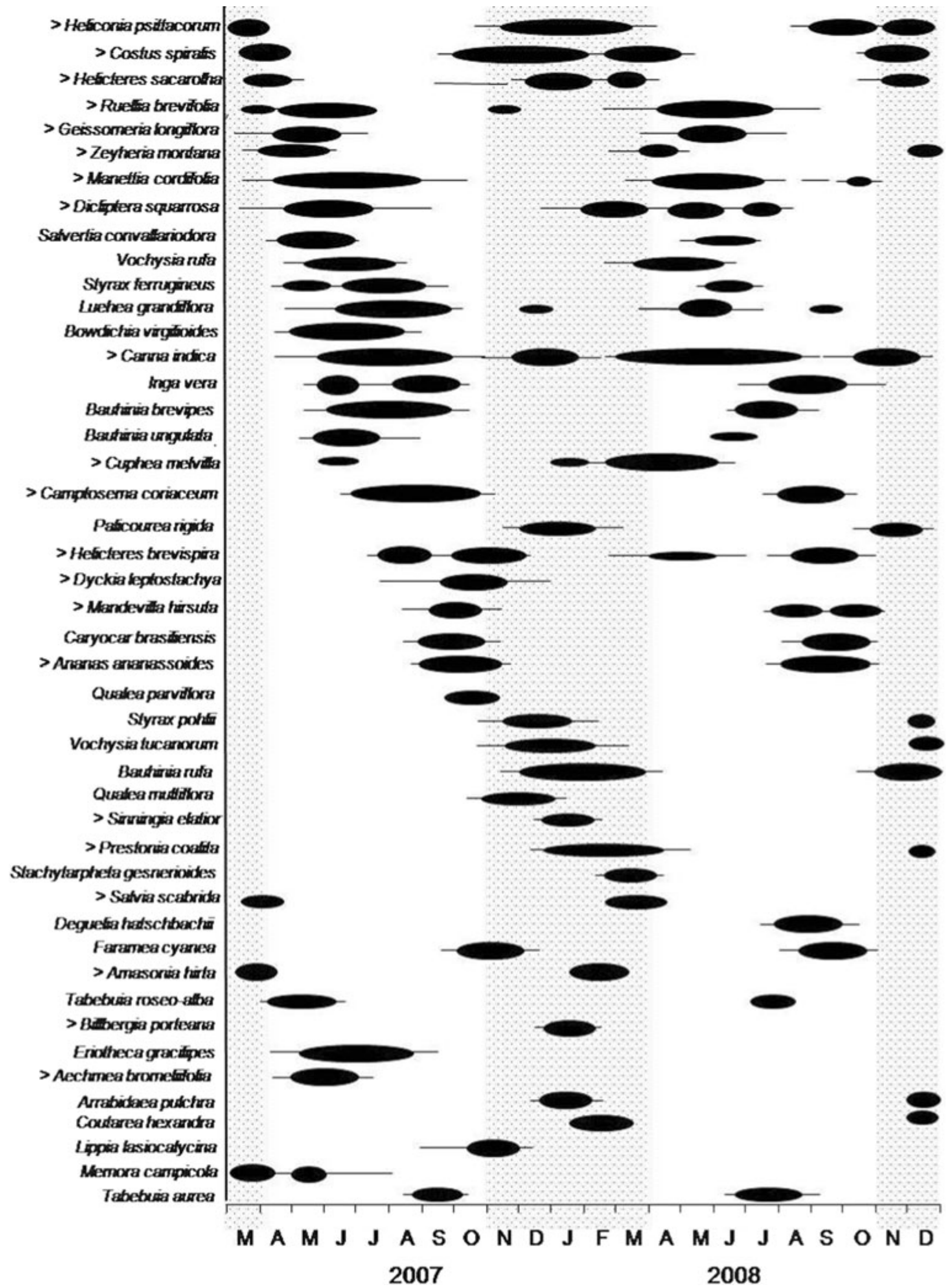

Fig. 2 Flowering profile of 46 plant species at the Panga Ecological Station (PES), Uberlândia, MG, recorded from March 2007 to December 2008. Flowering period (*thin lines*) and peak flowering (*thick lines*). Hatched months represent wet season and the symbol '>' indicates ornithophilous species

from 1.2 cm (*Bauhinia ungulata*) to 7.06 cm (*Canna indica*) and it was the sole or main visitor of six ornithophilous species. *Thalurania furcata* and *Amazilia fimbriata* visited 52.7 and 36.11 % of the plant species, respectively, and the other hummingbird species visited <11 plant species ("Appendix 2"). The range of corolla length and corolla width used by the hummingbirds is in Table 1. The correlation between the length of hummingbird's bill and the corolla length was significant ($r_s = 0.38$; $p < 0.01$, $n = 64$ pairs of interaction). Long-billed hummingbirds visited flowers of all corolla lengths, whereas short-billed hummingbirds visited only flowers with short corollas. There was no correlation between the corolla width and the length of hummingbird's bill ($r_s = 0.26$; $p > 0.05$, $n = 64$).

Although there was great variation in availability of flowering species throughout the study period (Fig. 2), the number of visiting hummingbird species (Fig. 4) was not clearly related to the number of flowering species. The highest number of hummingbird species was recorded in

Fig. 3 Flower morphology and colour of the species visited by hummingbirds. **a** *Luehea grandiflora*, **b** *Zeyheria montana*, **c** *Heliconia psittacorum*, **d** *Helicteres sacarolha*, **e** *Geissomeria longiflora*, **f** *Costus spiralis*, **g** *Mandevilla hirsuta*, **h** *Ananas ananassoides*, **i** *Stachytarpheta gesnerioides* at the Panga Ecological Station (PES), Uberlândia, MG

January 2008 (six species), when 13 plant species flowered, while the lowest number was recorded in April and June 2007 (one species) when 8 and 17 plant species, respectively, were in flower. In other months the number of hummingbird species varied from 2 to 4 and those of plant species varied from 6 to 17.

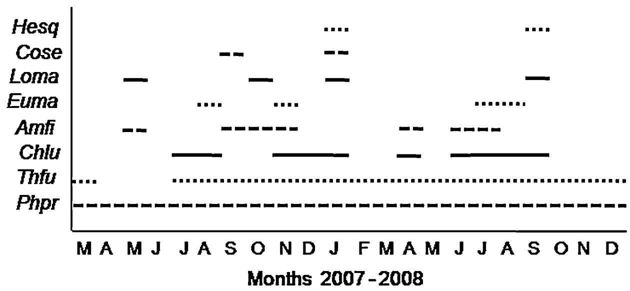

Fig. 4 Phenology of hummingbirds recorded per month at the Panga Ecological Station (PES), Uberlândia, MG. Abbreviations refer to initials of generic and specific names: *Hesq* = *Heliomaster squamosus*, *Cose* = *Colibri serrirostris*, *Loma* = *Lophornis magnificus*, *Euma* = *Eupetomena macroura*, *Amfi* = *Amazilia fimbriata*, *Chlu* = *Chlorostilbon lucidus*, *Thfu* = *Thalurania furcata*, *Phpr* = *Phaethornis pretrei*

Discussion

The study supported the idea that hummingbirds use an ample array of nectariferous plants both with and without ornithophilous features. A mutualistic dependence of hummingbirds upon ornithophilous species is not absolute (Grant 1994), since these birds can establish a more opportunistic relationship with the flowers they visit (Lara 2006). Several studies report the use of species with different pollination syndromes by hummingbirds whenever the availability of ornithophilous species in the area is low (Arizmendi and Ornelas 1990; Araujo and Sazima 2003; Machado et al. 2007; Machado 2009). The prevalent use of melittophilous species among non-ornithophilous plants in the PES as alternative resources sought by hummingbirds is also reported for other areas (Arizmendi and Ornelas 1990; Araujo and Sazima 2003). This prevalence is likely due to their frequency in the area, but nectar production also coincides with hummingbird foraging requirements.

The number of ornithophilous and non-ornithophilous species (46) in the PES is much higher than that in other seasonal and wet Neotropical plant communities (Toledo 1975; Arizmendi and Ornelas 1990; Araujo and Sazima 2003; Machado et al. 2007; Machado 2009). Such species richness in the PES is possibly favoured by the great habitat diversity in different vegetation types, a feature of the Cerrado biome as a whole (Araújo et al. 2011a).

But even considering the ornithophilous species only (21), the richness in the PES is comparable to the 24 species recorded in another Cerrado area in Brazil (Gottsberger and Silberbauer-Gottsberger 2006), and to the ornithophilous species richness (18) in a humid forest in México (Toledo 1975). However, there are areas with much higher ornithophilous species richness (more than 40 species) as rain forest sites in South-eastern Brazil (Buzato et al. 2000), and also areas with much lower richness (Machado 2009; Machado et al. 2007; Araujo and Sazima 2003; Arizmendi and Ornelas 1990).

Thus, the study area, despite its relatively low number of ornithophilous species, does not represent an especially poor habitat in terms of flower resources for the hummingbirds. The number of hummingbird plants seems to reflect general floristic composition. The best represented family, the Fabaceae, presents also the highest number of species in the Cerrados a whole (Gottsberger and Silberbauer-Gottsberger 2006). In other tropical communities, hummingbirds visited ornithophilous flowers of Ericaceae, Rubiaceae, Bignoniaceae, Acanthaceae, Cactaceae and Scrophulariaceae (Stiles 1985; Lasprilla and Sazima 2004; Abreu and Vieira 2004; Leal et al. 2006; Lara 2006; Dalsgaard et al. 2009) which were less common in the studied area. Even the Bromeliaceae, which is the most important family for the maintenance of hummingbirds in rain forest areas in Brazil (Sazima et al. 1996; Buzato et al. 2000; Machado et al. 2007) and which showed the highest number of ornithophilous species in the PES, presented low local density when compared with other families. These floristic differences may be the result of the approach used here. In megadiverse Neotropical forests, the pollination approach has been used to study plant–hummingbird interactions. The ornithophily syndrome itself has been commonly used as the basis to define hummingbird plants. Plant–pollinators network was described based on focal plants and visits to non-ornithophilous plants were usually viewed as spurious or occasional (e.g. Dalsgaard et al. 2011). But the large number of nectariferous plants used by birds regardless their ornithophilous features suggest this approach should not be used, at least in seasonal areas as the Cerrado.

Besides the floristic differences, the plants used by hummingbirds in the study area differed also in habit. Most of the species studied were trees and among the ornithophilous ones the herbaceous habit prevailed, while in most Brazilian ornithophilous plant communities the epiphytic habit usually dominates (Sazima et al. 1996; Buzato et al. 2000). The herbaceous habit is also common among ornithophilous species in other seasonal tropical communities (Araujo and Sazima 2003; Leal et al. 2006) and forest fragments in Brazil (Abreu and Vieira 2004).

Most ornithophilous and non-ornithophilous species presented annual flowering, which is common among hummingbird plants (Sazima et al. 1996; Buzato et al. 2000), and seems to be advantageous since it provides greater predictability in relation to the flowering period (Newstrom et al. 1994). The intermediate flowering duration of most species and an apparently sequential and continuous flowering of the community also favour the maintenance of resident hummingbirds due to stability of resource supply (Feinsinger et al. 1985). From the plant species perspective, sequential flowering may ensure the permanence of their pollinators throughout the year (Waser and Real 1979; Stiles 1985; Araújo et al. 2011a).

Although flower morphology varied greatly, most plants showed tubular flowers with short corolla length and narrow diameter. This is one of the characteristics usually associated with species pollinated by hummingbirds (Faegri and van der Pijl 1980), but these birds visited flowers with different morphologies as the brush flowers of *Inga vera* and *Caryocar brasiliensis* or dish flowers of *Luehea grandiflora.* Moreover, hummingbirds feed at almost all corolla lengths and widths depending basically on their bill size (Temeles et al. 2002).

The predominance of white flowers used by hummingbirds in the PES is due to the non-ornithophilous species and has been recorded elsewhere in the region (Araujo and Sazima 2003). Although red flowers have been associated with hummingbird pollination (Grant 1994; Raven 1972), white is the second most frequent colour among hummingbird-pollinated flowers (Lunau et al. 2011 and references therein). Birds appear to have no intrinsic preference for red flowers (Raven 1972), and several experiments showed that hummingbirds have no innate colour preference for either white or red flowers (Lunau et al. 2011). Despite that, hummingbirds may associate colour with food sources (McDade 1983; Cronk and Ojeda 2008), which can enhance search image and foraging behaviour (Brown and Kodric-Brown 1979).

The average volume and concentration of sugars in the nectar of the studied community were lower than those for other sites (see Sazima et al. 1996; Buzato et al. 2000), probably because the low number of nectar-rich species, as the Bromeliaceae of the Atlantic forest (Buzato et al. 2000). Low correlation between corolla length and nectar volume in this study contrasted with the results of Arizmendi and Ornelas (1990). However, a stronger correlation was found for corolla width/nectar volume. These results were probably influenced by the bat-pollinated species *Caryocar brasiliensis* and *Luehea grandiflora* that have large corolla widths and produce high nectar volumes. Non-ornithophilous flowers would also explain the less evident relationships between the size of the corolla and the length of the bill of the visiting hummingbirds, which have been observed in other studies (Arizmendi and Ornelas 1990; Vasconcelos and Lombardi 2001; Lara 2006; Machado et al. 2007; Machado 2009).

The number of hummingbird species recorded in this study (eight species) was the same of a highland temperate forest in Mexico (Lara 2006) and similar to another Cerrado study (six species) (Gottsberger and Silberbauer-Gottsberger 2006). Nonetheless, it was lower than that recorded for other tropical areas such as the Atlantic forest with 15 species (Buzato et al. 2000) and Colombian Amazon with 13 species (Lasprilla and Sazima 2004). On the other hand, it was greater than the number recorded in seasonal plant formations (Araujo and Sazima 2003; Machado and Lopes 2003). Thus, the studied Cerrado area has an intermediate hummingbird species richness compared with other areas in South America.

Visits to many plant species and exploration of most of the Cerrado plant formations by *Phaethornis pretrei* and *Thalurania furcata* indicate these birds are resident in the area, while the remaining species may migrate into the area whenever enough resources are available (see Lara 2006 for resident and migrant hummingbirds). The hermit *Phaethornis pretrei* visited the highest number of plant species, including both long and short corolla lengths, ornithophilous and non-ornithophilous species. In other sites long-billed hummingbirds usually prefer to visit long-corolla flowers, which usually produce more nectar (Buzato et al. 2000). The small number of long-corolla flowers in the study site could explain, in part, the mismatches between bill morphology and flower morphology (Temeles et al. 2002, 2009), and the use of all flower sizes by *P. pretrei*. Despite the generalist use of floral resources, *Thalurania furcata*, at least within the gallery forest, did not use the same plant species as *Phaethornis pretre*i, which suggest some niche partition. The use of resources in an opportunistic and seasonal way according to nectar availability by the other hummingbird species resembles the seasonality pattern recorded in a hummingbird community in Mexico (Lara 2006).

The studied Cerrado area contains relatively few ornithophilous species, which is compensated by its great diversity of habitats and presence of many nectariferous non-ornithophilous plants that were effectively used by hummingbird. This mosaic of habitats and resource availability would explain the hummingbird species richness and favour the maintenance of both resident and migrant hummingbird species, with consequences for sustainable pollination services for the truly ornithophilous plants in the area.

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Appendix 1

Table 2 Floral attributes of 46 species at the Panga Ecological Station (PES), Uberlândia, MG

Family/species	Corolla length (cm)	Corolla width (cm)	Nectar volume (μL)	Nectar sugar concentration (%)	Main colour of corolla or other floral structure/syndrome[a]	Corolla shape	Habit	Pattern and duration of flowering	Voucher number in HUFU
Acanthaceae									
Dicliptera squarrosa	3.0 ± 0.3 ($n = 10$) Medium	0.6 ± 0.1 ($n = 10$) Narrow	8.8 ± 1.8 ($n = 11$)	17.2 ± 1.2 ($n = 11$)	Red/ornithophily	Throat	Sub-shrub	Annual/ext	51866
Geissomeria longiflora	3.0 ± 0.2 ($n = 10$) Medium	0.3 ± 0.1 ($n = 10$) Narrow	7.0 ± 2.6 ($n = 18$)	24.1 ± 2.1 ($n = 18$)	Red/ornithophily	Tubular	Sub-Shrub	Annual/int	47812
Ruellia brevifolia	2.8 ± 0.2 ($n = 8$) Medium	0.6 ± 0.2 ($n = 8$) Narrow	6.8 ± 3.3 ($n = 17$)	23.0 ± 3.2 ($n = 17$)	Red/ornithophily	Throat	Sub-Shrub	Sub-annual/ext	47806
Apocynaceae									
Mandevilla hirsuta	4.2 ± 0.4 ($n = 7$) Long	0.5 ± 0.1 ($n = 7$) Narrow	18.0 ± 9.5 ($n = 6$)	34.3 ± 3.1 ($n = 6$)	Yellow/ornithophily	Tubular	Liana	Annual/int	51983
Prestonia coalita	1.60± 0.1 ($n = 10$) Short	0.2 ± 0.1 ($n = 10$) Narrow	6.0 ± 0.0 ($n = 2$)	17.5 ± 0.7 ($n = 2$)	Yellow/melittophily	Tubular	Liana	Annual/int	51877
Bignoniaceae									
Arrabidaea pulchra	3.4 ± 0.2 ($n = 10$) Medium	1.2 ± 0.2 ($n = 10$) Wide	–	–	Pink/melittophily	Tubular	Shrub	Annual/brief	47815
Memora campicola	3.7 ± 0.38 ($n = 10$) Medium	1.8 ± 1.1 ($n = 10$) Wide	13.00 ($n = 1$)	21.0%	Yellow/melittophily	Tubular	Shrub	Annual/int	51860
Tabebuia aurea	4.8 ± 0.6 ($n = 6$) Long	2.0 ± 0.4 ($n = 6$) Wide	8.3 ± 2.4 ($n = 21$)	24.0 ± 3.7 ($n = 21$)	Yellow/melittophily	Tubular	Tree	Annual/int	51984
Tabebuia roseo-alba	3.6 ± 0.5 ($n = 2$) Medium	1.2 ± 0.1 ($n = 2$) Wide	–	–	Pink/melittophily	Tubular	Tree	Annual/brief	47816
Zeyheria montana	2.6 ± 0.1 ($n = 10$) Medium	0.7 ± 0.1 ($n = 10$) Narrow	16.7 ± 15.3 ($n = 17$)	19.4 ± 4.5 ($n = 17$)	Yellow/ornithophily	Tubular	Shrub	Annual/int	47811
Bromeliaceae									
Aechmea bromeliifolia	0.9 ± 0.1 Short	0.4 ± 0.1 ($n = 10$) Narrow	6.6 ± 3.9 ($n = 15$)	22.0 ± 1.3 ($n = 15$)	Yellow/ornithophily	Tubular	Epiphyte	Annual/brief	–
Ananas ananassoides	1.8 ($n = 1$) Short	0.8 ($n = 1$) Narrow	35.8 ± 15.7 ($n = 19$)	27.8 ± 2.4 ($n = 19$)	Creamy-lilac/ornithophily	Tubular	Herb	Annual/int	51988

Table 2 continued

Family/species	Corolla length (cm)	Corolla width (cm)	Nectar volume (μL)	Nectar sugar concentration (%)	Main colour of corolla or other floral structure/syndrome[a]	Corolla shape	Habit	Pattern and duration of flowering	Voucher number in HUFU
Billbergia porteana	2.0 ± 0.1 ($n = 6$) Medium	0.43 ± 0.1 ($n = 6$) Narrow	5.7 ± 1.5 ($n = 3$)	23.0 ± 0.0 ($n = 3$)	Green-purple/ornithophily	Tubular	Epiphyte	Annual/brief	51870
Dyckia leptostachya	1.4 ± 0.1 ($n = 10$) Short	0.4 ± 0.1 ($n = 10$) Narrow	12.6 ± 5.7 ($n = 20$)	28.3 ± 9.2 ($n = 20$)	Orange/ornithophily	Tubular	Herb	Annual/int	51986
Cannaceae									
Canna indica	7.1 ± 0.4 ($n = 10$) Long	0.7 ± 0.1 ($n = 10$) Narrow	18.1 ± 9.9 ($n = 25$)	17.4 ± 3.2 ($n = 25$)	Red/ornithophily	Tubular	Herb	Continuous/ext	51868
Caryocaraceae									
Caryocar brasiliensis	3.0 ± 0.2 ($n = 10$) Medium	3.7 ± 0.9 ($n = 10$) Wide	46.2 ± 64.1 ($n = 4$)	26.2 ± 4.0 ($n = 4$)	Yellowish-white/chiropterophily	Brush	Tree	Annual/int	5588
Costaceae									
Costus spiralis	5.0 ± 0.3 ($n = 10$) Long	0.5 ± 0.1 ($n = 10$) Narrow	14.4 ± 3.7 ($n = 7$)	20.1 ± 6.4 ($n = 7$)	Red/ornithophily	Tubular	Herb	Annual/est	51874
Fabaceae									
Bauhinia brevipes	1.5 ± 0.1 ($n = 2$) Short	0.7 ± 0 ($n = 2$) Narrow	16.0 ± 7.9 ($n = 12$)	13.0 ± 2.2 ($n = 12$)	White/chiropterophily	Brush	Shrub	Annual/int	51892
Bauhinia ungulata	1.2 ± 0.1 ($n = 10$) Short	0.8 ± 0.1 ($n = 10$) Narrow	10.7 ± 3.3 ($n = 6$)	13.8 ± 2.6 ($n = 6$)	White/chiropterophily	Brush	Tree	Annual/int	51867
Bauhinia rufa	2.3 ± 0.5 ($n = 9$) Medium	0.9 ± 0.1 ($n = 9$) Narrow	47.2 ± 38. 3 ($n = 12$)	14.2 ± 3.2 ($n = 12$)	White/chiropterophily	Brush	Shrub	Annual/int	51881
Bowdichia virgilioides	1.3 ± 0.3 ($n = 10$) Short	1.0 ± 0.2 ($n = 10$) Wide	–	–	Lilac/melittophily	Flag	Tree	Annual/int	51865
Camptosema coriaceum	3.3 ± 0.3 ($n = 10$) Medium	0.5 ± 0.1 ($n = 10$) Narrow	7.1 ± 3.4 ($n = 15$)	26.3 ± 5.6 ($n = 15$)	Red/ornithophily	Flag	Herb	Annual/int	51985
Deguelia hatschbachii	0.9 ± 0.1 ($n = 6$) Short	0.2 ± 0 ($n = 6$) Narrow	–	–	Lilac/melittophily	Flag	Liana	Annual/int	55880
Inga vera	1.3 ± 0.2 ($n = 10$) Short	0.6 ± 0.1 ($n = 10$) Narrow	5.5 ± 1.7 ($n = 15$)	20.1 ± 0.7 ($n = 15$)	White/chiropterophily	Brush	Tree	Annual/ext	51869

Table 2 continued

Family/species	Corolla length (cm)	Corolla width (cm)	Nectar volume (μL)	Nectar sugar concentration (%)	Main colour of corolla or other floral structure/syndrome[a]	Corolla shape	Habit	Pattern and duration of flowering	Voucher number in HUFU
Gesneriaceae									
Sinningia elatior	3.9 ± 0.2 ($n = 10$) Medium	0.8 ± 0.1 ($n = 10$) Narrow	49.7 ± 28.0 ($n = 14$)	22.3 ± 4.1 ($n = 14$)	Orange/ornithophily	Tubular	Herb	Annual/brief	51875
Heliconiaceae									
Heliconia psittacorum	3.2 ± 0.2 ($n = 10$) Medium	0.5 ± 0.1 ($n = 10$) Narrow	25.1 ± 15.1 ($n = 13$)	25.0 ± 2.9 ($n = 13$)	Orange/ornithophily	Tubular	Herb	Annual/ext	51880
Lamiaceae									
Amasonia hirta	3.0 ± 0 ($n = 2$) Medium	0.6 ± 0 ($n = 2$) Narrow	16.0 ($n = 1$)	20.0 ($n = 1$)	Yellow/ornithophily	Tubular	Herb	Annual/brief	47817
Salvia scabrida	3.1 ± 0.2 ($n = 3$) Medium	1.0 ± 0.1 ($n = 3$) Wide	–	–	Red/ornithophily	Tubular	Herb	Annual/brief	51875
Lythraceae									
Cuphea melvilla	3.0 ± 0.3 ($n = 10$) Medium	0.5 ± 0.1 ($n = 10$) Narrow	15.8 ± 5.7 ($n = 4$)	27.2 ± 3.2 ($n = 4$)	Red/ornithophily	Tubular	Herb	Annual/ext	51861
Malvaceae									
Eriotheca gracilipes	–	–	1.9 ($n = 1$)	23.0 ($n = 1$)	White/melittophily	Dish	Tree	Annual/int	51990
Helicteres brevispira	1.4 ± 0.1 ($n = 10$) Short	0.5 ± 0.1 ($n = 10$) Narrow	20.9 ± 6.4 ($n = 25$)	14.3 ± 3.5 ($n = 25$)	Yellow/ornithophily	Flag	Shrub	Annual/ext	51987
Helicteres sacarolha	1.9 ± 0.2 ($n = 10$) Short	0.5 ± 0.1 ($n = 10$) Narrow	33.0 ± 22.7 ($n = 13$)	21.4 ± 2.1 ($n = 13$)	Orange/ornithophily	Tubular	Herb	Annual/ext	47813
Luehea grandiflora	1.6 ± 0.6 ($n = 3$) Short	1.9 ± 0.2 ($n = 3$) Wide	19.2 ± 15.4 ($n = 12$)	21.0 ± 2.4 ($n = 12$)	Greenish-white/chiropterophily	Dish	Tree	Annual/int	51863
Rubiaceae									
Coutarea hexandra	4.0 ± 0.5 ($n = 10$) Medium	1.4 ± 0.2 ($n = 10$) Wide	10.0 ($n = 1$)	13.0 ($n = 1$)	Pink/sphingophily	Tubular	Tree	Annual/brief	51876
Faramea cyanea	1.6 ± 0.2 ($n = 10$) Short	0.2 ± 0.1 ($n = 10$) Narrow	4.0 ($n = 1$)	21.0 ($n = 1$)	White/melittophily	Tubular	Tree	Annual/brief	55882

Table 2 continued

Family/species	Corolla length (cm)	Corolla width (cm)	Nectar volume (μL)	Nectar sugar concentration (%)	Main colour of corolla or other floral structure/syndrome[a]	Corolla shape	Habit	Pattern and duration of flowering	Voucher number in HUFU
Manettia cordifolia	4.3 ± 0.5 ($n = 10$) Long	0.7 ± 0.1 ($n = 10$) Narrow	35.7 ± 6.8 ($n = 3$)	21.0 ± 0.9 ($n = 3$)	Red/ornithophily	Tubular	Liana	Annual/est	47807
Palicourea rígida	1.2 ± 0.1 ($n = 10$) Short	0.4 ± 0.1 ($n = 10$) Narrow	7.6 ± 3.7 ($n = 5$)	17.6 ± 2.7 ($n = 5$)	Yellow/ornithophily	Tubular	Shrub	Annual/int	51862
Styracaceae									
Styrax ferrugineus	1.0 ± 0.2 ($n = 10$) Short	0.5 ± 0.1 ($n = 10$) Narrow	11.2 ± 2.7 (12)	21.4 ± 2.7 ($n = 12$)	White/melittophily	Tubular	Tree	Annual/int	51864
Styrax pohlii	0.8 ± 0.1($n = 5$) Short	0.5 ± 0.9 ($n = 5$) Narrow	8.75 ± 2.2 ($n = 4$)	19.3 ± 1,4 ($n = 4$)	White/melittophily	Tubular	Tree	Annual/int	–
Verbenaceae									
Lippia lasiocalycina	1.0 ± 0.1 ($n = 10$) Short	0.2 ± 0.1 ($n = 10$) Narrow	2.0 ± 0.8 ($n = 4$)	18.0 ± 1.2 ($n = 4$)	Pink/psychophily	Tubular	Sub-Shrub	Annual/int	47804
Stachytarpheta gesnerioides	–	–	12.6 ± 7.2 ($n = 15$)	13.8 ± 3.0 ($n = 15$)	Blue/psychophily	Tubular	Herb	Annual/int	51878
Vochysiaceae									
Qualea multiflora	–	–	32.5 ± 3.5 ($n = 2$)	29.0 ± 5.7 ($n = 2$)	Yellowish-white/melittophily	Spur	Tree	Annual/brief	51859
Qualea parviflora	0.9 ($n = 1$)* Short	0.2 ($n = 1$) Narrow	–	–	Pink/melittophily	Spur	Tree	Annual/int	51879
Salvertia convallariodora	2.1 ± 0.3 ($n = 10$)* Medium	0.5 ± 0.1 ($n = 10$) Narrow	4.5 ± 1.9 ($n = 9$)	28.0 ± 2.2 ($n = 9$)	White/sphingophily	Spur	Tree	Annual/int	51989
Vochysia rufa	1.2 ±0.1 ($n = 10$)* Short	0.4 ± 0 ($n = 10$) Narrow	7.5 ($n = 1$)	30.0 ($n = 1$)	Yellow/melittophily	Spur	Tree	Annual/int	47810
Vochysia tucanorum	1.3 ± 0.1 ($n = 6$)* Short	0.4 ± 0.1 ($n = 6$) Narrow	6.1 ± 5.3 ($n = 14$)	24.6 ± 4.0 ($n = 14$)	Yellow/melittophily	Spur	Tree	Annual/ext	51873

In brackets number of flowers

ext extended, *int* intermediate, *synd* pollination syndrome

* Measure of the spur

[a] According to Faegri and van der Pijl (1980)

Appendix 2

Table 3 Relative frequencies of hummingbird visits (%) to 36 species at the Panga Ecological Station (PES), Uberlândia, MG

Family/species	Species of hummingbirds and relative frequency of visits								
	Phpr	Thfu	Amfi	Chlu	Euma	Coser	Hesq	Loma	Total visitation rate
Acanthaceae									
Dicliptera squarrosa	100	…	…	…	…	…	…	…	1.75
Geissomeria longiflora	100	…	…	…	…	…	…	…	4.01
Ruellia brevifolia	96.55	3.44	…	…	…	…	…	…	0.53
Apocynaceae									
Mandevilla hirsuta	94.92	…	…	5.08	…	…	…	…	2.68
Prestonia coalita	…	100	…	…	…	…	…	…	3.23
Bignoniaceae									
Zeyheria montana	77.89	…	22.10	…	…	…	…	…	8.64
Bromeliaceae									
Ananas ananassoides	…	…	100	…	…	…	…	…	1.00
Dyckia leptostachya	…	…	…	100	…	…	…	…	3.00
Canaceae									
Canna indica	95.68	0.61	…	…	…	…	4.29	…	9.59
Caryocaraceae									
Caryocar brasiliensis	X	…	…	…	…	…	…	…	…
Costaceae									
Costus spiralis	88.23	…	…	…	…	…	11.76	…	4.10
Fabaceae									
Bauhinia brevipes	X	…	…	…	…	…	…	…	
Bauhinia ungulata	6.71	21.74	6.72	38.34	26.48	…	…	…	16.87
Bauhinia rufa	X	100	…	…	…	…	…	…	2.00
Bowdichia virgilioides	…	…	X	X	…	…	…	…	
Camptosema coriaceum	…	…	X	…	…	…	…	…	
Deguelia hatschbachii	…	X	…	…	…	…	…	…	
Inga vera	6.90	24.34	…	61.10	7.65	…	…	…	26.57
Gesneriaceae									
Sinningia elatior	X	…	…	…	X	X	…	…	
Heliconiaceae									
Heliconia psittacorum	45.45	35.45	11.82	2.73	7.27	…	…	…	13.75
Lamiaceae									
Salvia scabrida	X	…	…	…	…	…	…	…	
Lythraceae									
Cuphea melvilla	28.60	26.71	21.75	22.93	…	…	…	…	42.3
Malvaceae									
Helicteres brevispira	5.54	25.95	33.48	25.78	0.69	…	…	3.37	115.6
Helicteres sacarolha	X								
Luehea grandiflora	65.52	34.48	…	…	…	…	…	…	3.62
Rubiaceae									
Faramea cyanea	…	X	…	…	…	…	…	…	
Manettia cordifolia	96.47	3.53	…	…	…	…	…	…	3.4
Palicourea rigida	…	X	…	…	X	…	…	…	

Table 3 continued

Family/species	Species of hummingbirds and relative frequency of visits								
	Phpr	Thfu	Amfi	Chlu	Euma	Coser	Hesq	Loma	Total visitation rate
Styracaceae									
Styrax ferrugineus	…	X	X	…	…	…	…	…	
Styrax pohlii	…	…	X	…	…	…	…	X	
Verbenaceae									
Stachytarpheta gesnerioides	…	X	…	…	…	…	…	…	
Vochysiaceae									
Qualea multiflora	…	X	…	…	…	…	…	X	
Qualea parviflora	X	X	X	…	…	…	…	…	
Salvertia convallariodora	…	…	X	X	…	…	…	…	
Vochysia rufa		…	X	…	…	…	…	…	
Vochysia tucanorum	…	26.97	…	20.79	…	50.56	…	1.68	35.6
Total	21	19	13	10	6	2	2	4	

Number of visits per hour of observation

Phpr = *Phaethornis pretrei*, Thfu = *Thalurania furcata*, Amfi = *Amazilia fimbriata*, Chlu = *Chlorostilbon lucidus*, Euma = *Eupetomena macroura*, Coser = *Colibri serrirostris*, Hesq = *Heliomaster squamosus*, Loma = *Lophornis magnificus*, X = non-quantified visits, … = no visits recorded

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