Plant Systematics and Evolution (2021) 307:64
https://doi.org/10.1007/s00606-021-01790-z

ORIGINAL ARTICLE

Nectar characteristics of hummingbird-visited ornithophilous and non-ornithophilous flowers from Cerrado, Brazil

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Received: 10 February 2021 / Accepted: 19 July 2021 / Published online: 5 November 2021

Abstract

Hummingbirds in the Cerrado, the seasonal savannas in Central Brazil, visit both ornithophilous and non-ornithophilous flowers to collect nectar, which is the main source of energy and nutrients to these pollinators. The aim of the present study was to assess the volume, concentration, energy content and sugar composition of nectar collected from 34 hummingbird-visited flower species. We expect that nectar traits of non-ornithophilous species visited by hummingbirds are similar to those of ornithophilous species. Nectar samples were collected from different plant formations in the Cerrado region at Panga Ecological Station, Uberlândia City, Minas Gerais State, Brazil. Samples were obtained from 19 ornithophilous, 10 entomophilous and five chiropterophilous species. Nectar traits, such as volume, sugar concentration and energy content, did not significantly differ between ornithophilous and non-ornithophilous flowers. However, about 80% of the sampled species had sucrose-rich nectar, whereas other species, mainly chiropterophilous, had hexose-rich nectar. Overall, ornithophilous and chiropterophilous flower nectars shared similar energy content. On the other hand, the sugar-chemical composition of nectar from ornithophilous flowers was more similar to that of sucrose-rich entomophilous flowers. There is broad consensus that the nectar in flowers of hummingbird-pollinated species is rich in sucrose. However, hummingbirds visit several savanna plant species unrelated to the ornithophilous pollination syndrome. This trend indicates that hummingbirds show plasticity in selecting plant nectar sources when feeding, mainly in resource-fluctuating environments such as the Cerrado.

Keywords Brazilian savanna · Fructose · Glucose · Sucrose · Trochilidae

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Handling editor: Thais N. C. Vasconcelos.

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Introduction

Floral nectar is part of the resource system that angiosperms developed to attract floral visitors and usually increases the chances of pollination (Simpson and Neff 1981; Fenster et al. 2004; Dafni 2005; Brandenburg et al. 2009; Nepi 2017). This floral resource nurtures several animals (Heinrich 1975; Simpson and Neff 1981; Dafni 2005; Galetto and Bernardello 2005) and provides most of the energy sought by pollinators (Abrol 2005). Nectar is basically a watery sugar solution, but it may also present small amounts of amino acids, minerals, lipids, and other constituents (Simpson and Neff 1981; Galetto and Bernardello 2005; Chalcoff et al. 2006; Nepi 2017; Parachnowitsch et al. 2019). Among nectar constituents, sugars are the greatest source of energy for flower visitors (Heinrich 1975; Abrol 2005; Galetto and Bernardello 2005).

The most frequent nectar sugars are two hexoses (glucose and fructose) and one disaccharide (sucrose) (Stiles and Freeman 1993; Abrol 2005; Chalcoff et al. 2006). Although sugars vary in their chemical structure, they have the same caloric content (Martínez del Rio 1990) and could be hydrolyzed by the pollinator's metabolism and used as energy (e.g., Heinrich 1975; Martínez del Rio and Karasov 1990). Sugar type and concentration in nectar are determining factors for plant-pollinator interactions; yet, calorie intake has been considered more important than the nectar sugar ratio when pollinators select flowers (e.g., Hainsworth and Wolf 1976; Martínez del Rio 1990; Stiles and Freeman 1993; Abrol 2005).

The composition of sugars in the nectar has often been related to pollination syndrome, where specific proportions of sucrose in relation to fructose and glucose may represent adaptations supposedly related to the food preferences of the respective pollinators (Martínez del Rio 1990; Parachnowitsch et al. 2019). Accordingly, flowers pollinated by hummingbirds, pteropid bats, butterflies, moths and long-tongued bees often secrete sucrose-rich nectar (Baker and Baker 1979, 1990; Freeman et al. 1985; Martínez del Rio 1990; Stiles and Freeman 1993; Perret et al. 2001; Chalcoff et al. 2008; Kromer et al. 2008). On the other hand, flowers that secrete fructose and/or glucose-rich nectar are oftentimes visited by phyllostomid bats, passerine birds, short-tongued bees and flies (Perret et al. 2001; Kromer et al. 2008). These preferences for a particular sugar composition have been seen as a way to avoid competition and ensure the coexistence of several nectar-feeding animals in a community (Abrol 2005).

Hummingbirds native of Cerrado, the seasonal savannas in Central Brazil, feed on the nectar of several non-ornithophilous flowers due to natural scarcity of ornithophilous flowers in this region (Oliveira and Gibbs 2000; Gottsberger and Gottsberger 2006; Martins and Batalha 2006) compared with rain forest sites in Southeastern Brazil (Sazima et al. 1996; Buzato et al. 2000; Rocca and Sazima 2008). They visit a wide array of floral types, many with specialized hummingbird pollination syndrome (Coelho and Barbosa 2004; Consolaro et al. 2005; Araújo and Oliveira 2007; Araújo et al. 2011a; Melazzo and Oliveira 2012; Matias and Consolaro 2014; Ferreira et al. 2016) and others presumably pollinated by other groups of pollinators as bees, butterflies and bats (Araújo et al. 2011b, 2013, 2018; Maruyama et al. 2012, 2013; Machado and Oliveira 2015). Despite there are already some studies reporting this opportunistic foraging behavior of hummingbirds (Araújo et al. 2011b, 2013; Maruyama et al. 2012, 2013), there is yet no comparison including the proportions of sugar found in nectar between ornithophilous vs. non-ornithophilous plants used by hummingbirds for this region.

Hummingbirds of Cerrado feed on nectar of plants regardless of the pollination flower syndromes of the different species. There is evidence that the evolution of certain characteristics of the nectar occur as an adaptation to the preferences of pollinators, and the concentration of nectar sugar should be optimized for the energy needs of different groups of pollinators (Vandelook et al. 2019). These birds could be exerting some kind of selective pressure on the nectar characteristics of these non-ornithophilous species, or they would be choosing species with nectar traits more similar to that of the ornithophilous flowers. Therefore, we expect that there will be no differences in the composition of sugar and other characteristics of the nectar, such as volume, sugar concentration and energy content of ornithophilous and non-ornithophilous plant species visited by hummingbirds.

Materials and methods

The study was carried out at Panga Ecological Station (EEP), which covers approximately 400 ha and presents several plant formations typical of the Cerrado biome, as grasslands, open savannas and forest. EEP is located approximately 35 km away from downtown Uberlândia City in the state of Minas Gerais, Southeastern Brazil (19°09′20″–19°11′10″ S and 48°23′20″–48°24′35″ W, altitude ≈ 800 m) (Schiavini and Araujo 1989). The weather in the region is notably seasonal: dry and cold from April to September, and warm and rainy from October to March (Cardoso et al. 2009).

To compare nectar traits between species classified as ornithophilous and non-ornithophilous, only nectariferous plants that were visited by hummingbirds in the area were included in this study (Table 1). We do not consider the influence of frequency of visits in our analyses, because

Table 1 Nectar characteristics of 34 plant species used by hummingbirds in Panga Ecological Station in the Cerrado of Central Brazil

Family/species	Nectar volume (µL)	Nectar concentration (%)	Sugar (mg)	Calories	Pollination syndromes	Percentage			*r*
						Sucrose	Glucose	Fructose	
Acanthaceae									
Dicliptera sericea	8.82 ± 1.78 (*n* = 11)	17.22 ± 1.16 (*n* = 11)	1.60 ± 0.37 (*n* = 11)	6.39 ± 1.48 (*n* = 11)	Ornithophily	79.47	9.8	10.73	3.9
Aphelandra longiflora	7 ± 2.63 (*n* = 18)	24.11 ± 2.11 (*n* = 18)	1.81 ± 0.61 (*n* = 18)	7.26 ± 2.46 (*n* = 18)	Ornithophily	81.32	7.35	11.32	4.4
Ruellia brevifolia	6.75 ± 3.34 (*n* = 17)	22.98 ± 3.15 (*n* = 17)	1.67 ± 0.89 (*n* = 17)	6.69 ± 3.58 (*n* = 17)	Ornithophily	70.78	13.53	15.69	2.4
Apocynaceae									
Mandevilla hirsuta	18.00 ± 9.53 (*n* = 6)	34.33 ± 3.14 (*n* = 6)	7.19 ± 3.95 (*n* = 6)	28.76 ± 15.82 (*n* = 6)	Ornithophily	5.89	22.55	71.56	0.1
Prestonia coalita	6.00 ± 0.00 (*n* = 2)	17.50 ± 0.71 (*n* = 2)	1.10 ± 0.05 (*n* = 2)	4.42 ± 0.19 (*n* = 2)	Melittophily	4.97	43.18	51.85	0.1
Bignoniaceae									
Tabebuia aurea	8.32 ± 2.36 (*n* = 21)	24.01 ± 3.67 (*n* = 21)	2.23 ± 0.90 (*n* = 21)	8.92 ± 3.58 (*n* = 21)	Melittophily	72.62	5.72	21.66	2.7
Zeyheria Montana	16.65 ± 15.29 (*n* = 17)	19.40 ± 4.49 (*n* = 17)	3.47 ± 3.64 (*n* = 17)	13.88 ± 14.54 (*n* = 17)	Ornithophily	88.64	5.26	6.1	7.8
Bromeliaceae									
Ananas ananassoides	35.84 ± 15.74 (*n* = 19)	27.84 ± 2.40 (*n* = 19)	11.19 ± 5.27 (*n* = 19)	44.75 ± 21.10 (*n* = 19)	Ornithophily	74.04	13.27	12.69	2.9
Bilbergia porteana	5.67 ± 1.53 (*n* = 3)	23 ± 0 (*n* = 3)	1.41 ± 0.38 (*n* = 3)	5.64 ± 1.52 (*n* = 3)	Ornithophily	76.88	7.96	15.16	3.3
Dyckia leptostachia	12.65 ± 5.69 (*n* = 20)	28.28 ± 9.22 (*n* = 20)	3.88 ± 1.82 (*n* = 20)	15.52 ± 7.29 (*n* = 20)	Ornithophily	–	–	–	–
Canaceae									
Canna indica	18.08 ± 9.92 (*n* = 25)	17.43 ± 3.21 (*n* = 25)	3.40 ± 2.09 (*n* = 25)	13.59 ± 8.35 (*n* = 25)	Ornithophily	82.13	8.27	9.6	4.6
Costaceae									
Costus spiralis	14.43 ± 3.69 (*n* = 7)	20.14 ± 6.44 (*n* = 7)	3.17 ± 1.23 (*n* = 7)	12.69 ± 4.93 (*n* = 7)	Ornithophily	99.89	0.51	0.61	89.2
Fabaceae									
Bauhinia brevipes	16 ± 7.94 (*n* = 12)	12.95 ± 2.24 (*n* = 12)	2.14 ± 1.05 (*n* = 12)	8.56 ± 4.20 (*n* = 12)	Chiropterophily	16.29	49.28	34.43	0.2
Bauhinia ungulata	10.67 ± 3.33 (*n* = 6)	13.83 ± 2.63 (*n* = 6)	1.59 ± 0.70 (*n* = 6)	6.37 ± 2.82 (*n* = 6)	Chiropterophily	22.26	48.66	29.08	0.3
Bauhinia rufa	47.18 ± 38. 26 (*n* = 12)	14.15 ± 3.21 (*n* = 12)	7.32 ± 7.21 (*n* = 12)	29.29 ± 28.85 (*n* = 12)	Chiropterophily	12.61	46.05	41.34	0.1
Camptosema coriaceum	7.13 ± 3.38 (*n* = 15)	26.32 ± 5.56 (*n* = 15)	2.07 ± 1.02 (*n* = 15)	8.27 ± 4.08 (*n* = 15)	Ornithophily	55.36	20.1	24.54	1.2
Inga vera	5.47 ± 1.68 (*n* = 15)	20.07 ± 0.71 (*n* = 15)	1.17 ± 0.36 (*n* = 15)	4.67 ± 1.44 (*n* = 15)	Sphingophily	69.06	13.62	17.31	2.2
Gesneriaceae									
Sinningia elatior	49.74 ± 27.97 (*n* = 14)	22.29 ± 4.02 (*n* = 14)	11.66 ± 6.28 (*n* = 14)	46.65 ± 25.10 (*n* = 14)	Ornithophily	87.47	1.63	10.9	7
Heliconiaceae									
Heliconia psittacorum	25.08 ± 15.14 (*n* = 13)	24.95 ± 2.86 (*n* = 13)	7.00 ± 4.72 (*n* = 13)	28.02 ± 18.88 (*n* = 13)	Ornithophily	86.51	6.1	7.39	6.4
Lamiaceae									
Amasonia hirta	16 (*n* = 1)	20 (*n* = 1)	3.41 (*n* = 1)	13.63 (*n* = 1)	Ornithophily	94.22	0.29	5.49	16.3

Table 1 (continued)

Family/species	Nectar volume (μL)	Nectar concentration (%)	Sugar (mg)	Calories	Pollination syndromes	Percentage			*r*
						Sucrose	Glucose	Fructose	
Lythraceae									
Cuphea melvilla	15.84 ± 5.68 (*n* = 4)	27.23 ± 3.17 (*n* = 4)	4.90 ± 2.08 (*n* = 4)	19.60 ± 8.34 (*n* = 4)	Ornithophily	90.09	1.76	8.15	9.1
Malvaceae									
Helicteris brevispira	20.90 ± 6.35 (*n* = 25)	14.28 ± 3.53 (*n* = 25)	3.25 ± 1.59 (*n* = 25)	12.99 ± 6.34 (*n* = 25)	Ornithophily	71.08	12.99	15.93	2.5
Helicteris sacarolha	33.00 ± 22.67 (*n* = 13)	21.45 ± 2.14 (*n* = 13)	7.15 ± 3.38 (*n* = 13)	28.60 ± 13.52 (*n* = 13)	Ornithophily	99.33	0.21	0.46	148.3
Luehea grandiflora	19.25 ± 15.45 (*n* = 12)	21.00 ± 2.36 (*n* = 12)	4.29 ± 3.23 (*n* = 12)	17.17 ± 12.91 (*n* = 12)	Chiropterophily	–	–	–	–
Rhizoboleae									
Caryocar brasiliense	46.25 ± 64.09 (*n* = 4)	26.15 ± 4.02 (*n* = 4)	15.62 ± 23.67 (*n* = 4)	62.50 ± 94.67 (*n* = 4)	Chiropterophily	22.88	34.87	42.25	0.3
Rubiaceae									
Manettia cordifolia	35.67 ± 6.81 (*n* = 3)	21.00 ± 0.87 (*n* = 3)	7.97 ± 1.20 (*n* = 3)	31.89 ± 4.79 (*n* = 3)	Ornithophily	78.92	5.48	15.61	3.7
Palicourea rigida	7.60 ± 3.71 (*n* = 5)	17.60 ± 2.70 (*n* = 5)	1.49 ± 1.04 (*n* = 5)	5.97 ± 4.15 (*n* = 5)	Ornithophily	82.58	6.67	10.75	4.7
Styracaceae	11.17 ± 2.72	21.42 ± 2.72	2.56 ± 0.65						
Styrax ferrugineus	11.17 ± 2.72 (*n* = 12)	21.42 ± 2.72 (*n* = 12)	2.56 ± 0.65 (*n* = 12)	10.24 ± 2.59 (*n* = 12)	Melittophily	98.11	0.87	1.02	51.9
Styrax pohlii	8.75 ± 2.22 (*n* = 4)	19.3 ± 1.40 (*n* = 4)	1.78 ± 0.38 (*n* = 4)	7.10 ± 1.50 (*n* = 4)	Melittophily	96.6	0.41	2.99	28.4
Verbenaceae									
Lippia lasiocalycina	2 ± 0.82 (*n* = 4)	18 ± 1.15 (*n* = 4)	0.21 ± 1.15 (*n* = 4)	0.83 ± 0.12 (*n* = 4)	Psychophily	73.81	16.82	9.37	2.8
Vochysiaceae									
Qualea multiflora	32.50 ± 3.54 (*n* = 2)	29.00 ± 5.66 (*n* = 2)	10.41 ± 1.20 (*n* = 2)	41.62 ± 4.80 (*n* = 2)	Melittophily	91.03	3.71	5.26	10.1
Salvertia convallariaeodora	4.51 ± 1.92 (*n* = 9)	28.01 ± 2.21 (*n* = 9)	1.37 ± 0.49 (*n* = 9)	5.49 ± 1.96 (*n* = 9)	Sphingophily	–	–	–	–
Vochysia rufa	7.5 (*n* = 1)	30 (*n* = 1)	2.52 (*n* = 1)	10 (*n* = 1)	Melittophily	83.35	6.36	10.29	5
Vochysia tucanorum	6.1 ± 5.3 (*n* = 14)	24.6 ± 3.9 (*n* = 14)	1.64 (*n* = 14)	6.62 (*n* = 14)	Melittophily	83.06	6.71	10.23	4.9

n Number of sampled flowers; *r* sugar ratio [$S/(F+G)$]

according Araújo et al. (2013) the frequency of visitation by hummingbirds to a focal species is more related to the available number of open flowers per plant, but also to the amount of nectar per flower. For example, *Bauhinia ungulata* one of the chiropterophilous species of the study (hexose-dominant nectar) was visited by five hummingbirds' species, while *Dicliptera squarrosa*, an ornitophilous species, was visited only by *Phaethornis pretrei* which is a trapliner species that visits flowers in a low frequency compared with other territorial hummingbird species [see Appendix 2 in Araújo et al. (2013) for more information on frequency of use by hummingbirds].

The nectar samples were collected in different formations according to the plant distributions, including the interior of seasonal semideciduous forest and gallery forests, as well as the edge of gallery forests, open Cerrado areas (savanna grasslands, including "*Cerrado* sensu stricto," and denser "*cerradão*" woodlands; and grasslands with a few scattered shrubs or ''*campo sujo*''), and the edge of a palm swamp area (see Araújo et al. 2013; Maruyama et al. 2014). Plant species were classified according to their pollination syndrome based on their corolla shape and size, as well as their flower color, presence or absence of floral scent and period of anthesis, following Faegri and van der Pijl (1979). Nectar samples were taken from previously bagged flowers—before the anthesis period—in order to assess the nectar accumulated per flower, based on the following nectar measurements: volume, concentration, mg of sugar per flower, energy content and chemical composition (glucose, sucrose and fructose proportions). The number of flowers used to sample the nectar was related on the availability of flowers and individuals in the study area during the sampling period and, therefore, varied from 1 to 25 flowers (Table 1). Nectar samples were obtained from different individuals whenever possible. Nectar volume per flower was measured with a syringe (50 or 100 μL; Hamilton®). Likewise, sugar concentration in different flowers of each species was measured with a hand refractometer (Atago N-1α Brix 0 ~ 32%). The average nectar volume and concentration were used to estimate the amount of reward in calories per flower. Brix refractometric measures, in g sugar/g solution, were converted into mg sugar/μL of nectar (Galetto and Bernardello 2005), based on the following equation: $y = 0.00226 + (0.00937x) + (0.0000585 \times 2)$ wherein "x" is the concentration value and "y" corresponds to mg of sugar per μL. The mean energy content per flower was calculated as 1 mg of sugar = 4 cal/mg or 16.8 J (Galetto and Bernardello 2005; Araújo et al. 2011b).

Nectar drops were placed on Whatman #1 chromatography paper (10 samples per species) and quickly dried; in the laboratory, nectar was re-dissolved and sugar separation was accomplished by gas chromatography. Nectar was lyophilized and silylated according to Sweeley et al. (1963). The sugar composition was determined by gas chromatography. Analyses were performed in a PerkinElmer Clarus500 gas chromatograph equipped with a flame ionization detector (FID) and fitted with a fused silica capillary column coated with a stationary phase consisting of 5% phenyl 95% dimethyl-polysiloxane (non-polar DB-5; 30 m × 0.25 mm i.d.; lm coating thickness 0.25 μm). The GC operating conditions were as follows: oven temperature programmed from 200 °C for 1 min, from 200 to 208 °C at 1 °C/min, and from 208 to 280 °C at 10 °C/min, with a final hold time of 5 min. The carrier gas was nitrogen at a constant flow of 0.8 ml/min. The sugar compounds were identified by comparison of their retention times with those of analytical standards from Sigma and Fluka Companies, and by co-injection with these. Sugar chromatography was performed at least twice for each sample, in order to avoid experimental errors. Sugar ratio (r) was calculated as $r = \text{sucrose}/(\text{fructose} + \text{glucose})$, based on Baker and Baker (1983), who proposed four sugar ratio categories: sucrose-dominant ($r > 0.999$), sucrose-rich (0.999–0.5), hexose-rich (0.499–0.1) and hexose-dominant ($r < 0.1$).

The plant species visited by the hummingbirds were divided into ornithophilous and non-ornithophilous groups to analyze the differences among them. Plants grouped as non-ornithophilous may exhibit interactions with groups of animals that vary in size and energy requirements (e.g., insects and bats). Entomophilous plants are usually similar, having lower amounts of sucrose-rich and more concentrated nectar (Vandelook et al. 2019). In contrast, chiropterophilous flowers usually produce high amount of diluted nectar (Baker and Baker 1983; Johnson and Nicolson 2008). This variation among non-ornithophilous plants can influence the comparison with ornithophilous plants. To minimize this possible influence, we also evaluate differences in the nectar traits between pollination syndromes, and thus, the plant species were regrouped in ornithophily, entomophily (psychophily + sphingophily + melittophily), and chiropterophily.

The variables nectar volume, amount of sugar, calories per flower, sugar concentration, sucrose, glucose and fructose for each plant species, were tested for their normality (Shapiro–Wilk test) and homogeneity of variances (Levene test). Most variables did not have a normal distribution (except concentration) and variables such as concentration, sucrose, glucose and fructose are expressed in percentages. In ecology, an alternative to deal with data with non-normal distribution is the use of generalized linear models (GLMs) (McCullagh and Nelder 1989) as discussed by Warton and Hui (2011). For each variable expressed in percentage, we create GLMs with binomial distribution and when data presented an overdispersion we used the quasibinomial distribution. For the other variables, we built the models with negative binomial distribution and link (log), using *glm*() function in the R computational framework (R Studio Team 2020). GLMs result in the significance of each coefficient on the model and not of the full model. Thus, to differentiate ornithophilous vs non-ornithophilous species in relation to each nectar traits and to check for differences between the three main pollination syndromes, we compare the GLMs built with their respective null models using *anova.glm*() based on the Chi Square estimate (Hastie and Pregibon 1992) followed by a posteriori Tukey test for coefficient pairwise comparison, using *glht*() function from multcomp package. Sugar-type ratios were graphically plotted in a ternary diagram showing the distribution of all species according with their sugar proportions; the species are plotted with different symbols to group them according with the three main pollination syndromes of the area. All analyzes were performed using statistical packages in the R computational environment (R Studio Team 2020).

Results

In the study area, it was recorded 34 hummingbird-visited plant species. Among these species, 19 were classified as ornithophilous, seven melittophilous, five chiropterophilous, two sphingophilous and one psychophilous (see Table 1). The nectar traits of melittophilous, sphingophilous and psychophilous species were grouped into entomophilous, for comparison purposes. Overall characteristics of nectar as mean nectar volume per flower for all hummingbird-visited plant species was 14.25 μL (± 13.26), ranging from 2 (*Lippia lasiocalycina*—psychophilous) to 50 μL (*Sinningia elatior*—ornithophilous). Mean sugar concentration in nectar was 22.05% (± 5.11), ranging from 13% (*Bauhinia brevipes*—chiropterophilous) to 34% (*Mandevilla hirsuta*—ornithophilous). Mean energy content per flower was 16.90 cal (± 14.63), ranging from 0.83 cal (*Lippia lasiocalycina*) to 62.5 cal (*Caryocar brasiliense*—chiropterophilous).

Nectar traits did not significantly differ between ornithophilous and non-ornithophilous flowers for volume ($X^2 = 35.57$, $p = 0.441$), sugar concentration ($X^2 = 0.49$, $p = 0.468$), amount of sugar ($X^2 = 33.85$, $p = 0.436$) and calories ($X^2 = 36.44$, $p = 0.429$) (Fig. 1). Nectar traits evaluated according to three different categories of pollination syndromes (Fig. 2) did not differ significantly for nectar concentration ($X^2 = 0.043$, $p = 0.080$), sugar amount ($X^2 = 33.06$, $p = 0.053$) and calories ($X^2 = 36.01$, $p = 0.050$). Significant differences were found among pollination syndromes groups for the mean nectar volumes per flower ($X^2 = 34.78$, $p = 0.003$), and a posteriori tests showed that these differences could be attributed to the low volume of nectar from entomophilous species (ORN ~ ENT: $p = 0.014$/CHI ~ ENT: $p = 0.004$).

Sugar identification and quantification through GL chromatography was performed for 31 of the 34 sampled species. *Dyckia leptostachia*, *Luehea grandiflora*, and *Salvertia convallariaeodora* were not evaluated for sugar composition because the samples were not sufficient for chromatography analysis. All samples for the different plant species presented the three main sugar types (sucrose, glucose and fructose). Sucrose was the dominant sugar in 25 species (80.6% of the total sampled species), whereas only six of them presented hexoses (glucose and fructose) as the dominant sugars (Table 1; Fig. 3). Among hummingbird-visited species

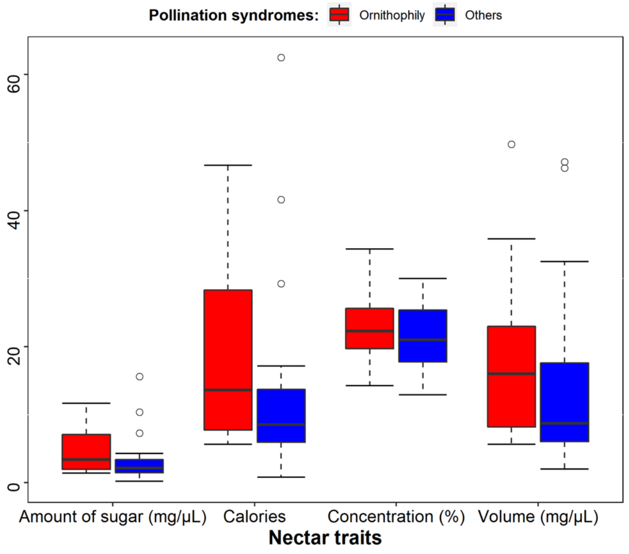

Fig. 1 Boxplot with minimum, first quartile, median, third quartile and maximum values for nectar traits samples of ornithophilous (red) and non-ornithophilous (blue) plant species visited by hummingbirds in Panga Ecological Station in the Cerrado of Central Brazil

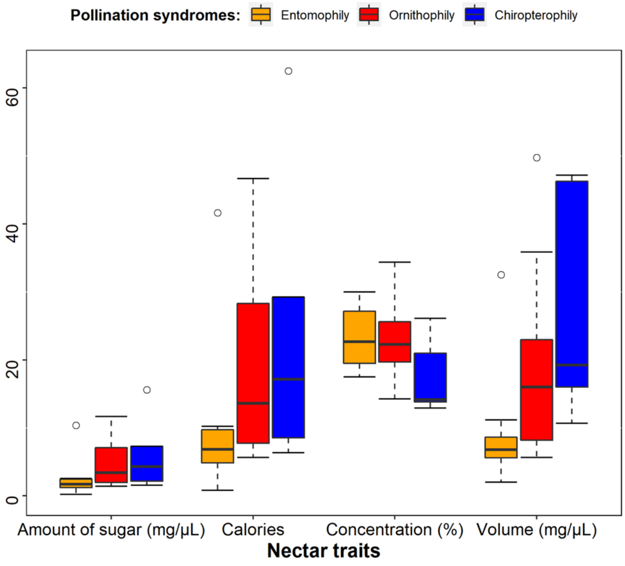

Fig. 2 Boxplot with minimum, first quartile, median, third quartile and maximum values for nectar traits samples of species visited by hummingbirds in Panga Ecological Station in the Cerrado of Central Brazil, according to the flower pollination syndrome

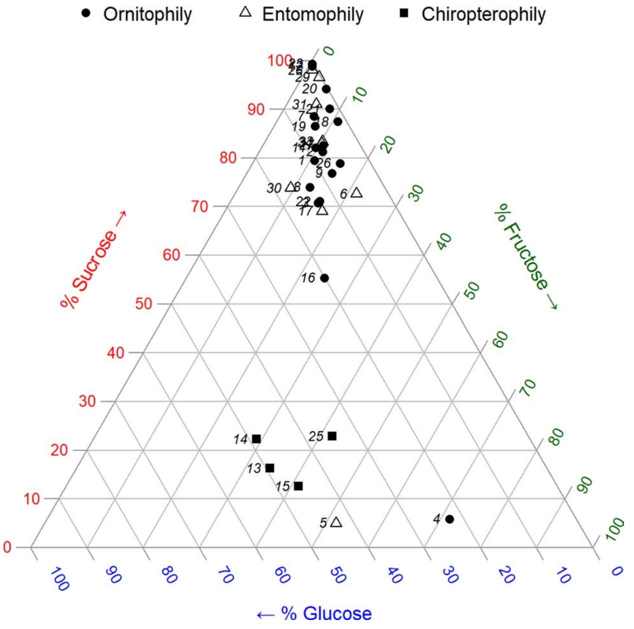

Fig. 3 Ternary plot diagram showing the nectar sugar composition (represented as percentage of fructose, sucrose and glucose) from flowers of 31 species visited by hummingbirds in Panga Ecological Station in the Cerrado of Central Brazil. These numbers refer to the species in Table 1, and symbols refer to the pollination syndrome

without sucrose-dominant nectar, four were chiropterophilous (*Caryocar brasiliense*, *Bauhinia brevipes*, *B. ungulata* and *B. rufa*), one was ornithophilous (*Mandevilla hirsuta*) and the other one was melittophilous (*Prestonia coalita*). Ornithophilous and non-ornithophilous plant species showed no significant differences in the sugar proportions of sucrose ($X^2 = 11.28$, $p = 0.05$) and fructose ($X^2 = 4.74$, $p = 0.221$). However, a significant difference for glucose ($X^2 = 4.11$, $p = 0003$). When the comparison was performed classifying the species in three pollination syndromes some differences were evidenced for sucrose ($X^2 = 7.55$, $p < 0.001$) and glucose ($X^2 = 2.33$, $p < 0.001$); however, fructose ($X^2 = 3.96$, $p = 0.051$) did not present differences among the syndromes (Fig. 3). A posteriori comparison showed that ornithophilous and entomophilous species presented comparable sugar proportions but different proportions of those for chiropterophilous species (sucrose CHI ~ ENT: $p = 0.003$/CHI ~ ORN: $p = 0.001$; glucose CHI ~ ENT: $p < 0.0001$/CHI ~ ORN: $p < 0.0001$).

Discussion

The present results show that nectar traits of hummingbird-visited plants significantly differ only on glucose between ornithophilous and non-ornithophilous plant species. This difference observed in the percentage of glucose was not expected; however, fructose and mainly sucrose did not present significant differences. Since hummingbirds have a tendency to prefer sucrose (according to Chalcoff et al. 2008), our results indicate that hummingbirds visit, among non-ornithophilous plant species, those that show a similar pattern of sucrose and fructose that was found in ornithophilous plants. Thus, even with the scarcity of ornithophilous flowers in the Cerrado, hummingbirds' diet can be supplemented by nectar from flowers of other pollination syndromes as reported previously (Araújo et al. 2011b, 2013, 2018; Maruyama et al. 2013; Machado and Oliveira 2015). Indeed, Maruyama et al. (2013) demonstrated that non-ornithophilous species contributed greatly to the overall energy availability in the Cerrado, providing an important input of additional energy to hummingbirds.

However, as well as floral traits such as corolla shape, size, width, color, evolved in response to the most frequent and effective pollinator in its habitat reflecting the pollination syndromes (Stebbins 1970; Faegri and van der Pijl 1979; Castellanos et al. 2003, 2004), the nectar characteristics such as the volume, concentration and composition of sugars were also selected by the main pollinators reflecting the preferences of each group (Baker and Baker 1983, 1990). Most of these arrays of combined floral characteristics are adaptations toward differences for combined traits (as size, shape, sensory physiology, foraging energetics and behavior) within each pollinator group (Castellanos et al. 2003). In this sense, some of the nectar particularities from non-ornithophilous plants may contain subtle differences with those from ornithophilous that do not correspond perfectly to the needs and metabolism of hummingbirds.

For example, although ornithophilous and chiropterophilous flowers share similar nectar energy content (Figs. 1, 2), the latter are known to produce a more diluted nectar (Heinrich 1975). Thus, it may be troublesome for hummingbirds to feed only on this kind of diluted nectar to compensate energy needs, as their kidneys would take longer to eliminate large volumes of water (Nicolson and Fleming 2003; McCallum et al. 2013). Consequently, low-sugar nectars may cause inefficient sugar assimilation by hummingbirds due to excessive water intake (McWhorter and Martínez del Rio 1999). Unlike chiropterophilous flowers, entomophilous flowers, more specifically the melittophilous, usually produce highly concentrated nectar (Kim et al. 2011; Vandelook et al. 2019), and so, this characteristic could be as troublesome as the diluted nectar, since viscosity impairs easy food intake by hummingbirds (Heinrich 1975; Abrol 2005; Nicolson and Thornburg 2007; McCallum et al. 2013). Nevertheless, it is worth mentioning that hummingbirds can take and assimilate a wide range of nectar sugar concentrations (Calleja et al. 1997). Our data showed that nectar from entomophilous species used by hummingbirds presents concentrations values comparable to those of the ornithophilous species (Table 1).

Regarding the volume, our results indicate that chiropterophilous flowers produce higher volumes of nectar than entomophilous, as observed by Heinrich (1975). However, the nectar available to hummingbirds during the day may be residual. Most nocturnal flowers produce nectar during the night and its availability for daytime nectarivores is just what it is left by bats from the night before (Sazima et al. 1982). On the other hand, hummingbirds usually can find small amounts of nectar per flower in entomophilous flowers; e.g., *Lippia lasiocalycina*, which showed the lowest nectar volume per flower (Table 1). Small flowers with little amounts of nectar are usually unattractive to hummingbirds, since scattered resources do not meet the needs of high-energy requiring when feeding; nevertheless, when these flowers occur grouped in inflorescences hummingbirds can offset their costs of movements between patches of rewarding flowers (Heinrich 1975). Low-reward flowers are mostly visited by hummingbirds when high-reward ones are unavailable in the landscape (Abrol 2005).

In relation to sugar composition, nectar from ornithophilous flowers is similar to that of entomophilous flowers with sucrose-dominant nectar, whereas the chiropterophilous nectar is hexose dominant (Fig. 3). There is a consensus that hummingbirds prefer sucrose-dominant nectar, but variations in the sugar composition do not prevent them to feed on other nectar types (Freeman et al. 1985; Chalcoff et al. 2008). One of the few field experiments testing sugar preferences showed that hummingbirds clearly discriminated every combination of different sugars against pure water, preferring sucrose over glucose and fructose (Chalcoff et al. 2008). However, there are several records of hummingbirds, which opportunistically feed on low-sucrose nectar (Freeman et al. 1983, 1985; Stiles and Freeman 1993). The present study provides data on six flower species with hexose-dominant nectar that support previous findings. Some studies suggest that hummingbirds may have a physiological limitation to hexose assimilation (Stiles 1976; Martínez del Rio and Karasov 1990). Nevertheless, experimental results have proven that hummingbirds can assimilate sucrose, glucose and fructose—with the same efficiency; therefore, digestive mechanisms alone cannot explain their preference for sucrose (Martínez del Rio 1990). Other studies have suggested that sucrose preference may be associated with hummingbirds' imprinting on nestlings and with the type of nectar regurgitated by their mothers (e.g., Carpenter and Castronova 1980).

Another explanation for the preference for sucrose-rich nectar may be associated with the evolution of other nectar constituents after the settlement of the flower-hummingbird interaction (De la Barrera and Nobel 2004). Nectar derives from phloem solution, whose main solute is sucrose which prevails in most tubular flowers (Abrol 2005). Sucrose prevalence in flowers is an assumingly primitive trait, whereas hexose-rich flowers developed later in order to attract other nectarivorous species as potential pollinators. This has already been suggested for Asteraceae, because species phylogenetically close to the root of Asteraceae trees tend to have longer corollas and higher sucrose proportions than late entomophilous branching species (Torres and Galetto 2002). Moreover, ornithophilous flowers are hypothesized to have evolved from entomophilous flowers by changing their morphological traits to avoid competition with pollinating insects (Grant 1994; Castellanos et al. 2003, 2004; Katzer et al. 2019) but apparently maintaining their sucrose-rich nectar composition. On the other hand, bat-pollinated flowers with hexose-rich nectar are hypothesized to have evolved from hummingbird-pollinated ancestors in neotropical regions (Muchhala and Thomson 2010).

In conclusion, our results partially corroborate our hypothesis that there are no differences in the composition of sugar and other characteristics of the nectar from ornithophilous vs. non-ornithophilous species visited by hummingbirds in the Cerrado. These birds could be selecting non-ornithophilous species with nectar characteristics, in terms of the energetic return, similar to those of ornithophilous species and at the same time could be exerting selective pressure on the nectar traits of these non-ornithophilous species. Depending on the environmental and ecological contexts, a generalist foraging behavior may be essential for hummingbirds to meet their energetic needs under environmental stresses (Arizmendi and Ornelas 1990; Araujo and Sazima 2003; Dalsgaard et al. 2009; Araújo et al. 2011b; Maruyama et al. 2013). Thus, in the absence of ornithophilous flowers, hummingbirds may opportunistically utilize the nectar of non-ornithophilous plants in order to fulfill their energetic demands during a period of the year (Abrol 2005; Chalcoff et al. 2008; McCallum et al. 2013), mainly in resource-fluctuating environments such as the Cerrado.

Acknowledgements We thank two anonymous reviewers for their useful comments and suggestions on early versions of this manuscript, and to CAPES-SPU—Study Mission Program (Brazil-Argentina)—, SECyT-UNC, FONCyT, CONICET and CNPq for the financial support (Proc. N. 302781/2016-1) granted to MS.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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