

# Pollination syndromes ignored: importance of non-ornithophilous flowers to Neotropical savanna hummingbirds

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**Abstract** Generalization prevails in flower–animal interactions, and although animal visitors are not equally effective pollinators, most interactions likely represent an important energy intake for the animal visitor. Hummingbirds are nectar-feeding specialists, and many tropical plants are specialized toward hummingbird-pollination. In spite of this, especially in dry and seasonal tropical habitats, hummingbirds may often rely on non-ornithophilous plants to meet their energy requirements. However, quantitative studies evaluating the relative importance of ornithophilous vs. non-ornithophilous plants for hummingbirds in these areas are scarce. We here studied the availability and use of floral resources by hummingbirds in two different areas of the Cerrado, the seasonal savannas in Central Brazil. Roughly

half the hummingbird visited plant species were non-ornithophilous, and these contributed greatly to increase the overall nectar availability. We showed that mean nectar offer, at the transect scale, was the only parameter related to hummingbird visitation frequency, more so than nectar offer at single flowers and at the plant scale, or pollination syndrome. Centrality indices, calculated using hummingbird–plant networks, showed that ornithophilous and non-ornithophilous plants have similar importance for network cohesion. How this foraging behaviour affects reproduction of non-ornithophilous plants remains largely unexplored and is probably case specific, however, we suggest that the additional energy provided by non-ornithophilous plants may facilitate reproduction of truly ornithophilous flowers by attracting and maintaining hummingbirds in the area. This may promote asymmetric hummingbird–plant associations, i.e., pollination depends on floral traits adapted to hummingbird morphology, but hummingbird visitation is determined more by the energetic "reward" than by pollination syndromes.

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## Introduction

Interactions between flowers and their animal visitors are commonly generalized relationships; for instance, flowers often interact with a wider array of animals than presumed by their pollination syndrome (Waser et al. 1996; Ollerton et al. 2009). Although not all flower visitors are effective and important pollinators (Waser et al. 1996; Fenster et al. 2004; King et al. 2013), from the visitor's perspective most interactions may represent an important energy intake. In the Neotropics, hummingbirds constitute an important group of

pollinators (Stiles 1981, 1985; Bawa 1990), and many plants show adaptations toward hummingbird-pollination, often having traditional "hummingbird syndrome" floral traits — for example, conspicuous reddish colour, scentless, long tubular corolla, diurnal anthesis, and abundant and diluted nectar (Faegri and van der Pijl 1979; Cronk and Ojeda 2008).

Despite many close relationships with the traditional "hummingbird syndrome" (or more broadly ornithophilous) flowers, depending on the environmental and ecological context, hummingbirds can be rather generalized and utilize a much wider array of floral types (Dalsgaard et al. 2009; Abrahamczyk and Kessler 2010). In mainland tropical rainforests, hummingbirds may account for the pollination of up to 70 species of ornithophilous plants or approximately 20 % of all plant species in a community (Stiles 1978, 1985; Bawa 1990; Buzato et al. 2000; Dziedziuch et al. 2003). On the other hand, in dry, seasonal and open habitats of the tropics, hummingbirds may be less specialized and rely more on non-ornithophilous plants presumably adapted to pollination by other groups of pollinators (Arizmendi and Ornelas 1990; Araujo and Sazima 2003; Dalsgaard et al. 2009; Abrahamczyk and Kessler 2010; Dalsgaard et al. 2011; Rodrigues and Araujo 2011; Maruyama et al. 2012; Araujo et al. 2013).

For instance, in the Cerrado — a neotropical savanna formation of Central Brazil — although hummingbirds are the sole pollinators of some plant species and show similar behavioural patterns as observed for rainforest ecosystems (e.g., Justino et al. 2012; Melazzo and Oliveira 2012), only 2–3 % of all plant species display features traditionally associated with hummingbird-pollination (Oliveira and Gibbs 2000; Oliveira and Paula 2001; Gottsberger and Silberbauer-Gottsberger 2006; Martins and Batalha 2006; Barbosa and Sazima 2008). Consequently, hummingbirds may opportunistically utilize some of the many non-ornithophilous plants (e.g., Rojas and Ribon 1997; Oliveira and Gibbs 1994; Maruyama et al. 2012; Araujo et al. 2013). A generalist foraging behaviour may therefore be essential for hummingbirds to meet their energetic demands, yet few community studies have aimed at exploring the relative importance of presumably hummingbird co-adapted and non-adapted plant species (e.g., Araujo and Sazima 2003; Rodrigues and Araujo 2011).

In this study, we evaluated the role of ornithophilous vs. non-ornithophilous plants for hummingbird communities in the Brazilian Cerrado. Specifically, we use detailed information on year-round nectar availability and hummingbird visitation rate to ask whether pollination syndrome or multiple scales of nectar availability determine hummingbird visitation rates. We also use a network approach (centrality indices) to evaluate the relative importance of ornithophilous vs. non-ornithophilous plant species for the hummingbird–plant interaction network in two different periods separated by 10 years.

## Methods

### Study areas

The study locations were situated approximately 22 km apart: Panga Ecological Station (Panga — 19°10'27"S, 48°23'51"W) and Clube de Caça e Pesca Itororó de Uberlândia (CCPIU — 18°59'21"S, 48°18'06"W) located near Uberlândia city in the state of Minas Gerais, Southeastern Brazil. Panga covers approximately 400 ha and includes many plant formations that characterize the Cerrado biome, ranging from grasslands and open savannas to dense forest formations. CCPIU covers approximately 400 ha of native vegetation, with the open savanna formations being the major habitat type. Climate in the region is characterised by its high seasonality with a warm, rainy season from October to March and a cooler dry season from April to September; mean monthly temperature is 22.8 °C and mean annual precipitation is 1,482 mm (Cardoso et al. 2009).

### Flower resource availability and phenotype

In order to measure floral resource availability for all hummingbird-visited plant species, in CCPIU we set up 20 parallel 100×5 m transects in the savanna area, at least 20 m apart, totalling 10,000 m<sup>2</sup>. From March 2009 to February 2011, we fortnightly recorded the flowering hummingbird-visited plants along all transects. In Panga, 21 parallel 50×8 m transects were sampled, 11 in the open savanna and ten inside the forest formation. In the forest, we additionally set one transect at the forest border (165×8 m) and another one along a stream (200×8 m). Transects were separated at least 25 m from each other. In Panga, we estimated overall floral availability in 4,400 m<sup>2</sup> of savanna and 6,920 m<sup>2</sup> of forest, which were sampled every other week from November 1996 to November 1997. In both Panga and CCPIU, we counted the number of flowers for each flowering individual along all transects. Hummingbird-visited plants were initially determined based on previous knowledge (Oliveira and Gibbs 1994, 2000; Oliveira and Paula 2001; Maruyama et al. 2012), as well as presence of nectar, and validated by records of hummingbird visits (see below). Plant species were classified as ornithophilous or not based on the flower colour, corolla shape and size, presence of floral scent and finally nectar production and accessibility, all in accordance to floral traits traditionally associated to ornithophily (see Faegri and van der Pijl 1979; Cronk and Ojeda 2008).

For each hummingbird-visited flower, we measured the internal corolla length with a digital calliper (error ±0.01 mm), i.e., the floral restriction hummingbirds must encounter when assessing the nectar (e.g., Dalsgaard et al. 2009). For some species (e.g., *Inga vera*, *Caryocar brasiliense* and species of Vochysiaceae), the reproductive structures (anthers and stigmas) are not enclosed in a corolla tube, but we measured the

length of the floral structure where hummingbirds must insert their bill in order to access nectar (in Vochysiaceae the flower spur). Furthermore, for each plant species, we measured nectar volume with graded glass micropipettes or microsyringes and measured sugar concentration with a handheld refractometer. For this, all flowers were bagged with nylon mesh bags the day before flower opening. Accumulated nectar production was measured in at least ten flowers per species at the end of morning in Panga (~11:00 hours) and at least 20 flowers per species at the end of the day (~17:00 hours) in CCPIU. For one plant species in CCPIU, *C. brasiliense* (Caryocaraceae) with dusk-opening flowers, we measured nectar in two groups of flowers ( $n=20$  each). The first group was kept exposed to flower visitors during the night and nectar was collected just before dawn (nectar "remnant" in the flowers). In the second group, we removed all nectar from the flowers at dawn and measured the subsequent production by the end of the day before flower senescence in bagged flowers ("subsequent" production). In this way, we tried to estimate nectar available only to diurnal visitors ("remnant"+"subsequent"), such as hummingbirds. Measurements of nectar volume and sugar concentration were combined to estimate the mg of sucrose equivalent sugars and energy available in each flower for each species (Galletto and Bernardello 2005; Araújo et al. 2011).

#### Flower resource use by hummingbirds

Plant–hummingbird interactions were mostly recorded along the transects in CCPIU and Panga. In CCPIU, we standardized the sampling effort in 40 h of focal observations in sessions of 1 h. In Panga, sampling in each plant was proportional to its abundance in the area ( $12.3\pm 6.4$  h per plant, range 3–28 h). For each plant species, interactions were recorded from 06:00 to 18:00 hours. Whenever possible, we sampled different plant individuals and distributed the observation intervals similarly across all plants species. Each visiting bout was defined as the interval between the moment the hummingbird started probing the flowers and the moment it left the plant. We also noted the hummingbird species and possible territorial and agonistic behaviours. For CCPIU data, we asked which parameter would better explain the frequency of hummingbird visits to plant species. The intensity to which hummingbirds interact with a plant is commonly a response to the floral resource availability (e.g., Justino et al. 2012). Thus, for each plant species we considered the floral resource availability at three different scales: (1) the mean amount of nectar in a single flower; (2) at individual plants, i.e., multiplying the mean amount of nectar per flower by the mean number of flowers per individual plant; and (3) in the transect area, i.e., multiplying the mean amount of nectar per plant individual by the density of each plant species per transect. The putative

adaptation to hummingbird-pollination was also considered as a possible explanatory variable, i.e., ornithophilous vs. non-ornithophilous plants.

For Panga, we had data on hummingbird–plant interactions collected in two different intervals: our own data collected in 1997–1998 and data collected in an independent study (Araújo et al. 2013) between 2007 and 2008. The hummingbird–plant interactions were recorded in a similar way for both studies (see Araújo et al. 2013 for details). After establishment of the Panga reserve in 1987, the reduction in fire frequency and other anthropogenic perturbations resulted in a significant change in the vegetation with approximately 12 % increase in woody formations concomitant with the reduction of grassland and open savanna areas in 30 %, considering the total area of the reserve (Cardoso et al. 2009). We therefore took the opportunity to evaluate the relative importance of ornithophilous and non-ornithophilous plants and whether this relation changed during the modification of the vegetation structure at the study area.

#### Data analyses

In CCPIU, we tested for a relationship between hummingbird visitation frequency (number of visits for each observation session of 1 h) and parameters of resource availability (i.e., amount of sugar per flower, per plant and per transect) as well as pollination syndrome (included as categorical variables — ornithophilous vs. non-ornithophilous) by using a model selection approach (Zuur et al. 2009). We first fitted a Generalized Linear Model (GLM) with Poisson distribution for the response variable considering the number of visits for each hour as count data (Zuur et al. 2009). After detecting overdispersion in the data, we corrected the standard errors using a quasi-GLM model (Zuur et al. 2009). The first model contained all explanatory variables (i.e., three measures of nectar availability and pollination syndrome) and interactions among them. After determining the optimal GLM fit by subsequently excluding the most non-significant parameter, we applied model validation following Zuur et al. (2009). The GLM analyses were performed in R statistical environment (R Development Core Team 2012). The model was also fitted considering the mean visitation rate for each plant species as response variables, but the result was essentially the same and therefore not shown.

For the Panga data, we used a network approach to evaluate the relative importance of ornithophilous and non-ornithophilous plants for hummingbirds. Specifically, we calculated two "centrality" indices: the closeness centrality (CC), which measures the proximity of a species to all others; and the betweenness centrality (BC), which measures to what extent a species lies on the shortest paths among other pairs of species, quantifying its importance as a network connector (Martín González et al. 2010). Hence, CC and BC measures

can be used to identify keystone species in ecological networks (Martín González et al. 2010). These indices were calculated for the two above-described periods separated by a 10-year interval. For both time periods, the differences in centrality indices between ornithophilous and non-ornithophilous plant species were tested using Student's *t*-test.

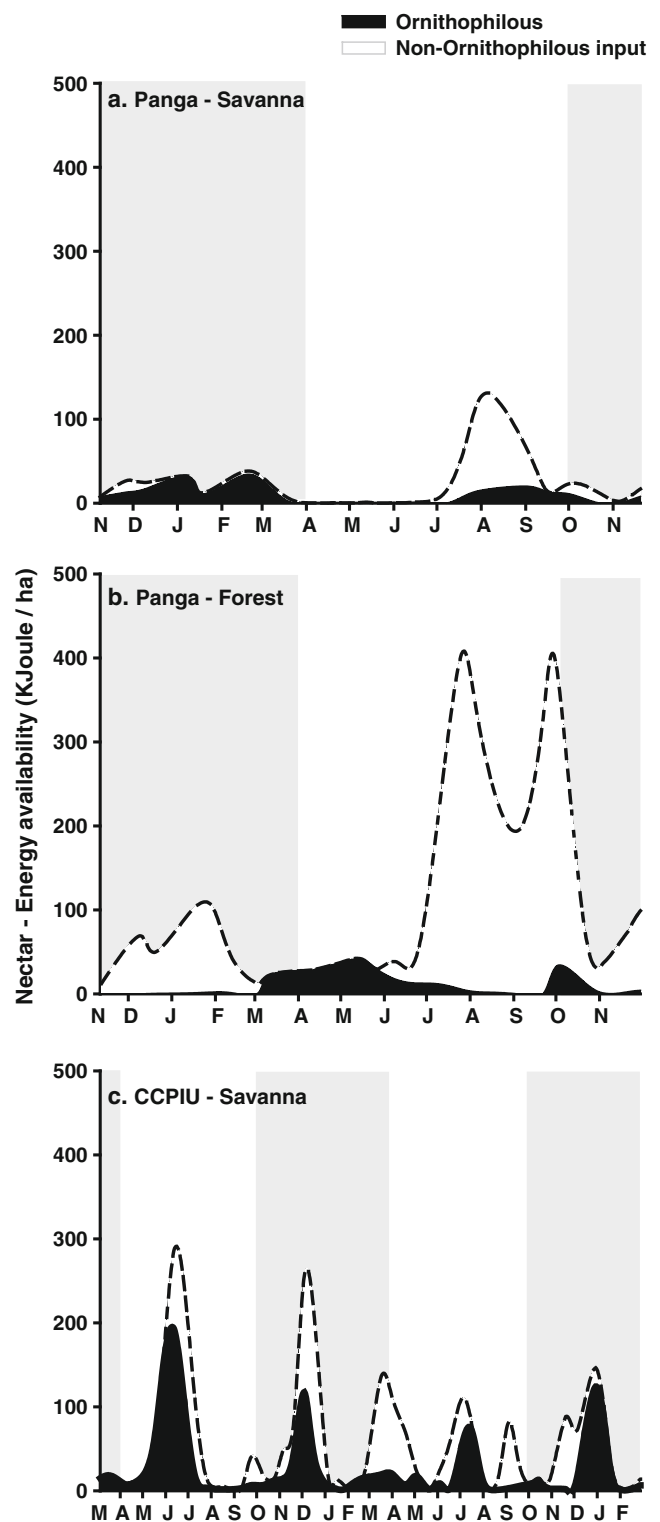
The different analytic approaches for the two sites are explained as follows: in CCPIU, all plant species had the same sampling effort considering focal observations, whereas for Panga the sampling effort was related to the plant species abundances. At the same time, the network from CCPIU is too small and cohesive to differentiate centrality values between species. In spite of the two different approaches, the question asked is fundamentally the same in both cases: does the relative importance of ornithophilous vs. non-ornithophilous flowers differ for the hummingbirds in the Cerrado?

## Results

### Flower resource availability

In Panga, we identified 18 plant species visited by hummingbirds of which ten species (56 %) presented typical ornithophilous features (Table S1). In CCPIU, nine plant species were visited by hummingbirds, of which four (44 %) correspond to the ornithophilous syndrome (Table S2). Both ornithophilous and non-ornithophilous plants varied greatly in corolla size and nectar production, although most of the smallest flowers were non-ornithophilous (Tables S1 and S2). Floral resource availability showed great temporal variation (Fig. 1), which was not clearly related to typical seasonality of Neotropical savanna, but instead reflected idiosyncratic flowering of each plant species (Fig. S1). In CCPIU we also observed some variation in the energy availability between years, which was greater in the first year of study (Fig. 1).

Considering the relative importance of ornithophilous vs. non-ornithophilous species, the latter make an important input of "extra" resources for hummingbirds (Fig. 1). For instance, in the savanna at Panga, flowering of bat-pollinated *Bauhinia brevipes* increased the energy availability in the area up to 5-fold (Fig. 1 and Fig. S1). In adjacent forest habitat, species of trees with massive flowering such as bee-pollinated *Vochysia tucanorum* (from November to March) and hawkmoth/bat-pollinated *I. vera* (from June to October) not only increased the energy availability noticeably, but also provided nectar during periods when ornithophilous flowers were scarce (Fig. 1 and Fig. S1). In the savanna at CCPIU, where ornithophilous species such as *Esterhazyia splendida* and *Palicourea rigida* were abundant (Fig. S1), ornithophilous plants provided more energy in comparison to Panga. Nevertheless, non-ornithophilous species still significantly increased energy availability (Fig. 1).



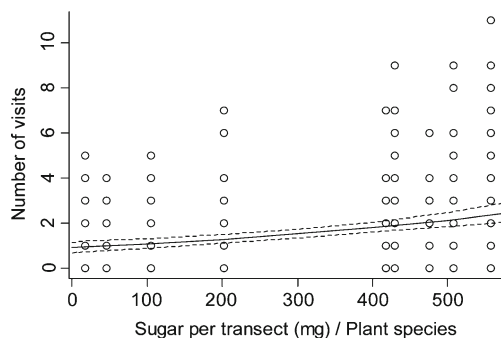
**Fig. 1** Nectar energy availability at savanna (a) and forest (b) in Panga and at the savanna in CCPIU (c), from the Cerrado of Central Brazil, estimated by nectar sugar content of hummingbird-visited flowers. Dashed lines show the amount of extra energy provided by non-ornithophilous flowers. Shaded areas indicate the rainy season in the Cerrado. Notice that Panga has been observed during one year only, whereas CCPIU was observed for two consecutive years

## Flower resource use by hummingbirds

We recorded 554 visits by six hummingbird species in Panga (Table S3) and 585 visits by seven hummingbird species in CCPIU (Table S4). Hummingbird species visited flowers irrespective of floral syndrome (not considering species recorded few times) with the exception of the Planalto hermit (*Phaethornis pretrei*), which visited more frequently ornithophilous flowers in Panga (Table S3). Non-hermit hummingbirds held territory in most of the plants with large flower displays, ornithophilous or not, chasing away other hummingbirds and effective pollinators of some non-ornithophilous plants such as the large *Bombus* and *Xylocopa* bees. Model selection showed that nectar availability in the area (transect) was the only significant parameter associated with hummingbird visitation frequency (intercept: 0.085, slope: 0.002,  $df=359$ ,  $p<0.001$ ; Fig. 2), although with low explained deviance (null deviance: 737.0; residual deviance: 676.8). Centrality indices calculated both for ornithophilous and non-ornithophilous plants in Panga for the two different time periods showed no clear differences (Fig. 3, Table S5). Species with a high CC value often also had a high BC value, pointing to the importance of specific plant species as network keystone species unrelated to pollination syndrome (Fig. 3).

## Discussion

We have presented evidence that non-ornithophilous plants are important for the hummingbirds in the dry and seasonal habitat of the Brazilian Cerrado: roughly half of the plant species visited by hummingbirds were non-ornithophilous, visitation frequencies did not differ between ornithophilous and non-ornithophilous plants, and non-ornithophilous plants were as important for the cohesion of the plant–hummingbird network as ornithophilous plants. Additionally, non-ornithophilous plants contributed greatly to the overall energy availability in



**Fig. 2** The relationship between number of hummingbird visits and the total amount of sugar content per transect — the only significant parameter associated to number of hummingbird visits — in the savanna of CCPIU. Each dot represents the number of hummingbird visits during one observational session of 1 h

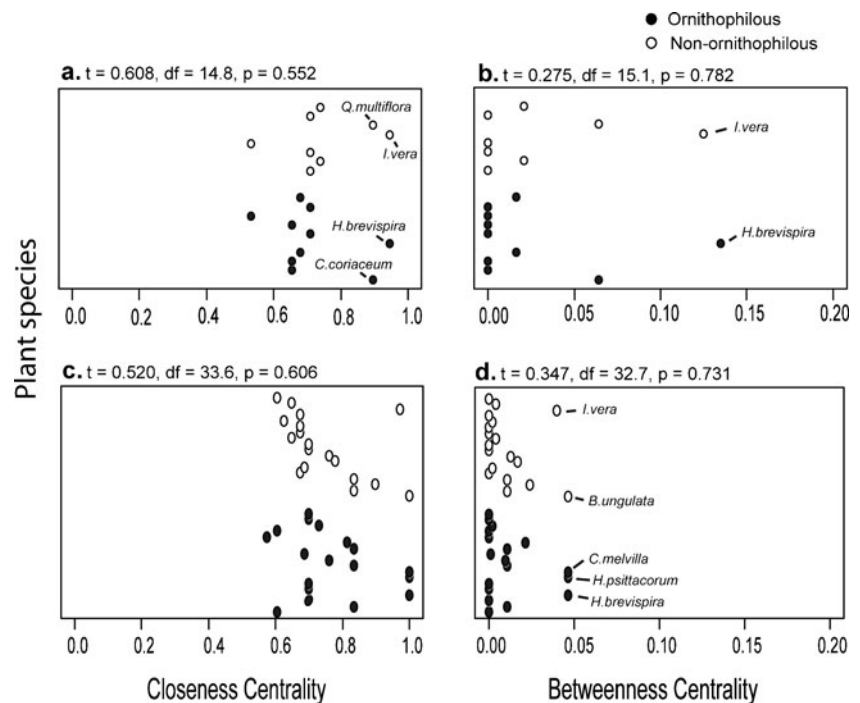
both the savanna and forest areas. All hummingbird species seem to meet their energy requirements by adopting a generalist foraging behaviour, visiting every resource they may find and have access to, provided that these offer nectar. Specifically, flowers with syndromes linked to large bee and bat/hawkmoth pollination were regularly visited by hummingbirds, probably due to their large size and nectar availability.

A generalist use of flower resources by hummingbirds in dry and seasonal tropical habitats has previously been suggested, but still lacked a detailed quantitative approach, which we attempted to provide in this study. A high proportion of non-ornithophilous plants being visited and sometimes pollinated by hummingbirds seems to be a trend in these ecosystems, which contrast with rainforests (seasonal tropical areas — Arizmendi and Ornelas 1990; Araujo and Sazima 2003; Dalsgaard et al. 2009; Abrahamczyk and Kessler 2010; Rodrigues and Araujo 2011; Las-Casas et al. 2012; rainforests — Stiles 1978; Buzato et al. 2000; Cotton 1998; Dziedziuch et al. 2003). This difference seems to be at least partially associated with greater richness and local abundance in rainforests of some plant families commonly presenting specialized hummingbird-pollination features — e.g., Bromeliaceae, Heliconiaceae and Gesneriaceae — in rainforests (Stiles 1978; Buzato et al. 2000; Dziedziuch et al. 2003). We therefore suggest that some environmental filters, such as the dry and strong seasonality and the associated occurrence of fire might be hindering successful establishment of these mostly herbaceous and epiphytic plant groups in Neotropical savanna ecosystems.

We documented substantial temporal variation in resource availability for several habitats in the Cerrado (Fig. 1). However, this variation is not clearly related to the dichotomy of dry and wet seasons. The variation in resource availability included even periods with no flowers at all, which probably forces hummingbirds to track resources across different habitats or areas, as has already been noted in the Cerrado and other ecosystems (Cotton 2007; Araújo et al. 2011). Non-ornithophilous plants were not only visited during periods of scarcity of ornithophilous flowers, and in savanna habitats flowering peaks of both group often overlapped. The additional variation in energy availability between years recorded in our study was also noted in other studies (Stiles 1978, 1985; Sazima et al. 1996; Araújo et al. 2011) and may be related to distinct effects that inter-annual environmental changes have on different plant species. Thus, hummingbirds must not only track resources spatially, but also cope with the uncertainty in the resource availability between years.

The energy availability within the area (transect) was the only parameter associated with hummingbird visitation frequency to plants at CCPIU, and can be related to the ability of hummingbirds in spatially tracking resources (Stiles 1985; Cotton 2007). The significant albeit weak relationship between energy availability and hummingbird visitation frequency might be explained by the nature of the flowering pattern, encompassing a wide range of floral displays. Thus,

**Fig. 3** Cleveland dot plot for closeness centrality (CC) and betweenness centrality (BC) of ornithophilous and non-ornithophilous plant species visited by hummingbirds in Panga. Each point represents one species, ordered along the Y-axis and separated by pollination syndrome. Identities of key species with high centrality values are labelled with species name. Student's *t*-test showed no differences between centrality indices of the two plant groups neither for 1996–1997 data (a and b) nor for 2007–2008 data (c and d). Species with high values of CC in c are the same as the ones with high values of BC identified in d. For values of CC and BC for each species, see Table S5



for all plants, we observed many individuals with low floral display and, hence, low energy availability, which made many of our observations record zero visits (Fig. 2). There was no difference in the frequency of visits regardless of whether a plant species is classified as ornithophilous or non-ornithophilous. Considering the centrality indices, which represent the distinct topological importance of each node for the network (Martín González et al. 2010), ornithophilous and non-ornithophilous plants were also indistinguishable. Altogether, this indicates that both groups of plants are equally important for the persistence of the entire plant–hummingbird community and certainly for hummingbirds as food resources. However, it has to be noted that when hummingbirds utilize resources provided by non-ornithophilous plants, they may also compete for the nectar with other groups of visitors, such as pollinating insects and bats (Dalsgaard et al. 2009; Amorim et al. 2012).

Even though hummingbird visits to non-ornithophilous plants are common in the Cerrado, the effect of these visits on plant reproductive success remains mostly unexplored. In one of the most common plant families in Cerrado, Vochysiaceae, hummingbird visits are frequent (Oliveira and Gibbs 1994; Oliveira 1998). In larger flowers of this family, such as those of *Qualea multiflora* and *Vochysia* spp., hummingbirds act as secondary pollinators, whereas in smaller flowers of *Q. parviflora* the morphological fit with hummingbird body is poor and pollination is unlikely (Oliveira and Gibbs 1994; Oliveira 1998). Likewise, hummingbirds do not assure pollination for the small flowers of *Styrax ferrugineus* (Styracaceae), even though visits are frequent (Maruyama et al. 2012). Contrastingly, in the group of plants with large

brush-like flowers, such as *C. brasiliense*, *I. vera* and *Bauhinia* spp., hummingbirds easily access the nectar and also contact the reproductive structures (Amorim et al. 2012; P.K. Maruyama, personal observation). For typically bat or hawkmoth pollinated plant species, hummingbird contribution to the pollination has been considered less important (e.g., Gribel and Hay 1993). Nevertheless, recent findings suggest a noteworthy strategy in which plants make use of both diurnal (hummingbirds) and nocturnal (hawkmoths and bats) pollinators in brush-like flowers (Amorim et al. 2012).

Even when hummingbirds are one of the most frequent visitors to a specific plant species, their direct contribution to plant reproduction can be low (Maruyama et al. 2012; Watts et al. 2012). It seems that flower morphology (especially the corolla shape) is crucial in determining hummingbird effectiveness as pollinators, directing how hummingbirds approach flowers and promoting contact with reproductive structures (Castellanos et al. 2004; Muchhala 2006). However, hummingbirds may also affect plant reproduction indirectly and independent of flower morphology, decreasing the amount of nectar available and through aggression towards more efficient pollinators (Maruyama et al. 2012). Considering indirect interactions among plant species mediated by hummingbirds, the overall increase in resource availability provided by non-ornithophilous plants may actually contribute to the reproduction of truly ornithophilous flowers. This possible facilitation and complementarity may be important for maintenance and quality of pollination services at the plant community level (Waser and Real 1979; Cotton 1998; Ghazoul 2006; Blüthgen and Klein 2011). Though considered here as a group, non-ornithophilous flowers are composed by species with a variety

of floral shapes and other characteristics, and as a result the role of hummingbirds on their reproduction is likely to vary greatly. Investigating this, and the effect of energy supplementation by non-ornithophilous plants on truly ornithophilous flowers will therefore be an interesting approach to better understand plant-hummingbird communities.

The pattern observed in hummingbird–flower association in seasonal and relatively dry ecosystems in the Tropics may be extended to a broader geographical context. Specifically, it may be similar to the association among hummingbirds and their floral resources in temperate North America where hummingbirds also often utilize non-ornithophilous plants (Stiles 1976; Waser et al. 1996). These trends reinforce the flexible use of flowers beyond what may be predicted from pollination syndromes. What really matters to hummingbirds does not seem to be specific external floral traits, but rather the energetic reward the flowers offer (Stiles 1976; Waser 1983; Meléndez-Ackerman et al. 1997; Lunau et al. 2011, and this study). This leads to asymmetric associations where plants depends on floral traits adapted to hummingbird morphology for pollination, whereas hummingbirds are not obliged to specialize on specific floral traits. In this sense, what matters for the hummingbirds is the energetic "reward" they obtain, regardless of pollination syndromes. We hope the study carried out here will stimulate similar kind of community analysis not only for hummingbirds and their plants, but for a wider range of pollination systems. Identifying floral resources beyond those predicted by pollination syndromes may have profound implications for conservation of plants and their animal pollinators, considering its associated effects on plant reproduction and, hence, the persistence of entire plant–pollinator communities.

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