

Effects of the availability of floral resources and neighboring plants on nectar robbery in a specialized pollination system

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Abstract

Many plants pollinated by nectar-foraging animals have to maintain a balance between legitimate visitor attraction strategies and mechanisms that minimize illegitimate visits. This study investigated how floral display and neighboring species composition influences nectar robbery by hummingbirds in the tropical ornithophilous herb *Heliconia spathocircinata*. We tested the role of inflorescence display, flower abundance, and neighboring species in the reduction of nectar robbery in *H. spathocircinata*. Our results indicate that nectar robbery hummingbird activity was higher in moderately large inflorescence displays and that the frequency of nectar robbery in *H. spathocircinata* decreases with increased flower abundance and the presence of neighboring plant species. Neighboring non-ornithophilous plants decreased the frequency of nectar robbery in *H. spathocircinata* flowers to a greater extent than ornithophilous ones. These results suggest that nectar robbery hummingbirds are attracted to similar conditions that attract legitimate visitors and that spatial aggregation and mixed-species displays may represent a mechanism to dilute nectar robbery effects at an individual level.

Keywords: Brazilian Atlantic forest, density, floral antagonists, Heliconiaceae

Plants adopt a number of different strategies to attract floral visitors, many of which are visual cues that signal the availability of resources to potential pollinators, given that the selection of flowers by pollinators is often density-dependent (Seifan et al. 2014). When a plant offers a large number of flowers at a given point in time, that is when there is an increased floral display, it is likely that it may attract a greater number of visitors (Grindeland et al. 2005; Lázaro and Totland 2010; Torices et al. 2018). Overall, an increase in flower density will lead to increasing visitation per flower up to a maximum level, when pollinators are abundant. At this point, visitation rates will begin to decrease as a result of competition for shared pollinators (Rathcke 1983). As the availability of flowers affects the activity of pollinators and the number of flowers visited, it is likely that it has implications on self- and cross-pollination rates (Robertson 1992).

The presence of flowers in adjacent plants may also play a role in the attraction of floral visitors (Bergamo et al. 2020), given the increase in the total floral display (Torices et al. 2018). When a species is part of a mixed-species floral patch, this configuration may capture the attention of floral visitors more efficiently,

with the other plant species acting as visual “magnets” (Lavery 1992). The benefits for a plant species of being in a mixed-species patch depend also on the proportion of conspecific and heterospecific plants in the patch, especially when the different plants share generalist floral visitors (Nottebrock et al. 2017). The relationship between total flower density and visitation rates in mixed-species patches follows a pattern similar to that of conspecific patches (Rathcke 1983).

Flower density and species composition are especially important strategies to attract floral visitors with acute vision, such as hummingbirds, because these animals tend to be attracted by large floral patches (Justino et al. 2011; Missagia and Alves 2016) over long distances and will select these locations as their territories or as feeding stops along their flight paths, based on the value of the resources in the patch (Maruyama et al. 2013; Lanna et al. 2017). From a zoocentric perspective, a visually attractive floral patch reflects a high resource availability (Trombulak 1990) and the opportunity to feed from many flowers at low cost, in energetic terms, by flying short distances between flowers (Temeles et al. 2005; Tello-Ramos et al. 2015).

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Recent research on pollinator attraction strategies in hummingbird-pollinated plants has confirmed that plant density, floral display, and visitation rates are crucial for the understanding of plant–hummingbird relationships (Krannitz and Maun 1991; Dudash et al. 2011; Fenster et al. 2015; Christopher et al. 2021; Ortiz et al. 2021). Although the impacts of nectar robbing on plant fitness are well documented (Arizmendi et al. 1996; Irwin et al. 2001; Pelayo et al. 2011; Rojas-Nossas et al. 2021), little is known of the influence of pollinator attraction strategies on illegitimate floral interactions involving hummingbirds. Primary nectar robbing is one of the most common of these interactions, which involves the consumption of nectar by floral visitors which perforate the corolla to access the nectar without touching the reproductive structures of the flower (Inouye 1980). In this case, the strategies adopted by the plant to attract pollinators may include mechanisms that minimize unwanted visits while ensuring that legitimate pollinators do not lose interest in the flowers (Irwin et al. 2004).

In a biological community, there is typically only one or a few plant species whose nectar is robbed frequently, whereas most other plant species present low to medium levels of nectar robbing (Rojas-Nossas et al. 2016). There is some evidence that nectar robbing is more frequent in plant species that have long, tubular flowers that secrete large amounts of nectar (Lara and Ornelas 2001; Irwin and Maloof 2002; Maruyama et al. 2015), such as ornithophilous flowers (Bergamo and Sazima 2018). In contrast, plants with short corollas or flower clusters arranged in bracts may avoid nectar robbing by insects and birds relatively efficiently (Rojas-Nossas et al. 2016). It is also possible that, when the plant is present in a multi-species stand, it may be robbed less frequently, given the potential attractiveness of other species to nectar robbers (Irwin and Brody 1998), that is, species that offer resources that are either more valuable in energetic terms or are more easily accessed.

The development of strategies that both attract flower visitors and avoid flower larceny by the plant may be more evident when the visitors belong to distinct functional groups, for example, bees and birds (Irwin et al. 2004), given that these groups tend to be attracted by distinct floral characteristics. However, when the legitimate and illegitimate visitors belong to the same group (e.g., birds), it is likely that the attraction strategies adopted by the plant will be more homogeneous (Dellinger et al. 2019). In order to resolve questions on the role of floral attractiveness in nectar robbery by hummingbirds, we used the hummingbird-pollinated plant *Heliconia spathocircinata* Aristeg. (Heliconiaceae) (Cruz et al. 2006; Missagia and Alves 2017) as a model, in the Brazilian Atlantic forest. *Heliconia spathocircinata* is an understory herb known to suffer primary nectar robbing by hummingbirds, which perforate holes in the corolla (Missagia 2019). Although some passeriform nectar robbers are found in this biome (Rocca and Sazima 2008a, 2008b), including the common, nectar-robbing bananaquit (*Coereba flaveola*) (Arizmendi et al. 1996; Lasso and Naranjo 2003), we assume that Passeriformes are unlikely to be nectar robbers of *H. spathocircinata* in preserved areas of Atlantic forest, given that most of these birds forage in the forest canopy (Rocca and Sazima 2008a, 2008b, 2010). We also observed the violet-capped Woodnymph—*Thalurania glaucopis* (Gmelin 1788)—piercing flowers in the field. We thus assume that the holes observed in the flowers of *H. spathocircinata* were made by hummingbirds.

Based on these premises, we investigated the role of flower density and species composition on nectar robbing patterns in *H. spathocircinata*. We used the inflorescences of *H. spathocircinata* as units of illegitimate visitor attraction, given that the bracts are highly contrasting in hummingbird vision (Bergamo et al. 2019), and the flowers as the energetic reward units. We analyzed nectar robbing in *H. spathocircinata* at 2 levels: the absolute and relative numbers of robbed flowers denominated the frequency of nectar robbing here (Irwin and Maloof 2002). We measured the frequency of nectar robbing in conspecific and mixed-species floral patches of *H. spathocircinata*, and tested the following 4 hypotheses: 1) the absolute number of robbed *H. spathocircinata* flowers is higher in conspecific floral patches with an intermediate abundance of inflorescences than in patches with either low or high abundance of inflorescences; 2) the frequency of nectar robbing in *H. spathocircinata* is lower when flower abundance is high in conspecific floral patches; 3) the frequency of nectar robbing in *H. spathocircinata* is lower when it occurs in mixed-species patches in comparison with conspecific floral patches; and 4) the frequency of nectar robbing in *H. spathocircinata* is higher in mixed-species patches that contain other flowering ornithophilous plant species.

Materials and Methods

Study site

Field data were collected in the União Biological Reserve (22°25'40"S, 42°02'06"W), hereafter the RebioUnião, in Rio de Janeiro state, southeastern Brazil. The RebioUnião encompasses an area of 7,756.76 hectares of Atlantic forest, including well-preserved fragments of dense ombrophilous forest (Martins and Carvararo 2012). The local climate is defined as Aw in Köppen-Geiger's climate classification system, characterized by a high annual mean temperature and a single dry season. Mean annual precipitation is 1,100 mm, with a rainy season between November and April (Alvares et al. 2013). The data were collected in January 2021, which corresponds to the peak of the flowering season of *H. spathocircinata* in the RebioUnião (Cruz et al. 2006).

Study species

In Brazil, *H. spathocircinata* (Heliconiaceae) is found in lowland Atlantic rainforest (Berry and Kress 1991; Braga 2020) and blossoms in the wet season, between December and February (Cruz et al. 2006). This plant bears long-lasting inflorescences with cimbiform, brightly colored bracts varying from yellow to red, which are associated with ornithophily (Berry and Kress 1991; Andersson 1998; Simão and Scatena 2004). Its plain and yellow flowers are inserted in the bracts, and visitors can only access the corolla legitimately through its opening at the apex of the flower. *Heliconia spathocircinata* flowers usually have a single day span and secrete nectar containing 24–28% sucrose (Buzato et al. 2000; Cruz et al. 2007). The buds remain inserted in the bracts until they open.

Heliconia spathocircinata (Figure 1A), like other species of the genus and due to its capacity for vegetative propagation, forms clusters or floral patches containing a number of different inflorescences, primarily in riparian vegetation and in areas adjacent to trails and clearings (Kress 1990). These floral patches are visited frequently by hummingbirds, which often establish their territories in these areas (Missagia and Alves 2016). In the RebioUnião, the principal pollinator of *H. spathocircinata* is the Minute Hermit—*Phaethornis idaliae*



Figure 1. Inflorescence of *H. spathocircinata* (A); Flower of *H. spathocircinata* with nectar robbing hole (B). Photographs by Caio Missagia (A) and Giovanni Marini (B).

(Bourcier and Mulsant 1856) (Cruz et al. 2006; Missagia 2019), which may also rob the nectar of this plant, given that it has been recorded robbing nectar from the congener *Heliconia angusta* in the RebioUnião (Cassio J. Oliveira, personal communication). *Thalurania glaucopis* is a known nectar robber of *H. spathocircinata* flowers in the RebioUnião (Missagia 2019). This hummingbird pierces the corolla with its bill to form an almost circular hole through which it gains access to the nectar (Figure 1B). It thus seems likely that hummingbirds are the primary nectar robbers (*sensu* Inouye 1980) of *H. spathocircinata* flowers.

Procedures

We sampled 2 transects of 4,000 m × 20 m along existing trails >1 km apart (22°25.085'40"S, 42°02.765'06"W and 22°25.038'40"S, 42°02.187'06"W). On these transects, we sampled 22 *H. spathocircinata* patches, of which 15 were conspecific and 7 were mixed-species patches, with at least 1 flower with robbed nectar (robbed flowers).

The patches contained varying numbers of inflorescences and were defined as circles with a radius of 10 m, which was the maximum size of the patches observed at the study site. Floral visitors such as hummingbirds also tend to fly the shortest possible distance between inflorescences, to ensure the most favorable cost–benefit ratio (Tello-Ramos et al. 2015). In general, the distances moved within a floral patch by the hummingbirds do not exceed 10 m (Waser 1982). The floral patches were at least 10 m apart and were sampled only once, always after 13:00 h, given that most visits to *H. spathocircinata* occur during the morning (Cruz et al. 2006).

In each patch, we determined the total number of open flowers and inflorescences with open flowers, and the number

of robbed flowers (flowers with holes in the corolla). Some inflorescences in the *H. spathocircinata* floral patches had unopened flowers, but the bracts can still be attractive to hummingbirds (Bergamo et al. 2019), and given this, we also recorded the number of these bracts and calculated the total abundance of inflorescences by summing the total number of inflorescences (with open and nonopen flowers). In mixed-species patches, we also identified the plant species with open flowers surrounding *H. spathocircinata* which were at least 5 m in height, given that most of the species visited by hummingbirds in the Atlantic forest are understory herbs, shrubs, or bushes (Sazima et al. 1995, 1996; Buzato et al. 2000).

Data analysis

To test the first hypothesis (i.e., the absolute number of robbed flowers in *H. spathocircinata* is higher in conspecific patches with an intermediate abundance of inflorescences), we analyzed the relationship between the absolute number of robbed flowers and the total abundance of inflorescences using a Gaussian general linear model (GLM) with identity link.

To test the second hypothesis (i.e., the frequency of nectar robbing in *H. spathocircinata* is lower when the floral display is larger in conspecific floral patches), we calculated the frequency of nectar robbing in each *H. spathocircinata* patch by dividing the number of nectar robbing holes by the number of open flowers (Irwin and Maloof 2002), using the floral patch, rather than each inflorescence, as a unit of measure. We chose the frequency of nectar robbing as a measure of this behavior because it is proportional to the abundance of flowers. As *H. spathocircinata* flowers last only one day (Cruz et al. 2006), there is no risk of nectar robbing accumulating over

a number of days. The relationship between the number of robbed flowers and flower abundance, as well as that between the frequency of nectar robbing and flower abundance, were also analyzed using a Gaussian GLM.

The third hypothesis (i.e., the frequency of nectar robbing in *H. spathocircinata* decreases when the species occurs in mixed-species patches) was tested by comparing the frequency of nectar robbing between conspecific and mixed-species patches. We used the Gaussian GLM of the frequency of nectar robbing as the dependent variable, patch type as the factor, and flower abundance as the covariable, to determine whether the difference between patch types is explained by the same variable that underpins the variation in nectar robbing in the conspecific *H. spathocircinata* patches.

For the fourth hypothesis (i.e., the frequency of nectar robbing in *H. spathocircinata* is higher in mixed-species patches with ornithophilous plant species), we used non-metric multidimensional scaling (NMDS) to reduce dimensionality and rank distances between varied species compositions (James and McCulloch 1990). We regressed the NMDS scores of axis 1 (Tong 1988) against the frequency of nectar robbing in *H. spathocircinata* with a Gaussian GLM. We ran all the analyses in SYSTAT 13, except for the ordination, which was conducted in PC-ORD, version 5.

Results

Nectar robbing occurred in 22 patches on the 2 study transects, including 15 conspecific and 7 mixed-species patches. The nectar robbing holes found in *H. spathocircinata* were almost circular in shape, and were located either at the base of the corolla or close to its mid portion (Figure 1). We did not observe robbed buds or more than one nectar-robbing hole in any of the *H. spathocircinata* flowers identified in the RebioUnião.

In the conspecific *H. spathocircinata* floral patches ($N = 15$), the number of robbed flowers presented a nonlinear, unimodal relationship with the abundance of inflorescences (GLM: $r^2 = 0.509$; $P = 0.002$). In particular, the patches with an intermediate number of inflorescences presented the largest numbers of robbed flowers (Figure 2).

The total number of robbed flowers had a linear relationship with the abundance of open flowers in conspecific *H. spathocircinata* patches (GLM: $r^2 = 0.833$; $P < 0.001$) (Figure 3). However, the frequency of nectar robbing in conspecific patches had a negative, nonlinear relationship with the abundance of open flowers (GLM: $r^2 = 0.531$; $P = 0.045$) (Figure 4).

The frequency of nectar robbing in the conspecific patches was significantly higher (GLM: $F = 6.942$; $P = 0.016$) than that recorded in the mixed-species patches (Figure 5). The frequency of nectar robbing did not vary significantly between patch types, however, in relation to the covariable flower abundance (GLM: $F = 3.036$; $P = 0.097$).

We recorded the presence of 5 additional plant species in the mixed-species patches ($N = 7$)—*Costus spiralis* (Jacq.) Roscoe (ornithophilous), *Dichorisandra thyrsiflora* Mikan (non-ornithophilous), *Hedychium coronarium* J. Koenig (non-ornithophilous), *Pleroma granulatum* (Desr.) D. Don (non-ornithophilous), and *Psychotria nuda* (Cham. and Schltdl.) Wawra (ornithophilous). Although the species composition did not vary greatly between floral patches, the NMDS scores were quite distinct. The frequency of nectar

robbing was related positively (GLM: $r^2 = 0.647$; $P = 0.029$) to the scores of the first axis for species composition (Figure 6), which indicates an association between a higher frequency of nectar robbing in *H. spathocircinata* and the presence of ornithophilous species.

Discussion

As we hypothesized, the absolute number of robbed *H. spathocircinata* flowers was greatest in conspecific patches with an intermediate abundance of inflorescences (Figure 2). Our results indicate that *H. spathocircinata* inflorescences, even when they lack open flowers, may be important to increase the total floral display when in a setting with other conspecific inflorescences that do offer resources, given that hummingbirds are attracted visually, in particular, to inflorescences with bracts whose coloration contrasts with the leafy background (Bergamo et al. 2019) and not to the flowers themselves (Temeles et al. 2012). This means that the total floral display, which, in the case of *H. spathocircinata*, can be measured in terms of the number of inflorescences, had a similar effect to that of the density-visitation model described by Rathcke (1983), in which visitation is maximized at intermediate plant densities, and decreases as the floral display expands. In this study, the maximum absolute number of robbed flowers may represent the maximum level of robber activity, in a similar way to pollinator activity in the density-visitation model, whereas the abundance of inflorescences reflects the hypothetical patch quality in terms of its energetic reward. Patches with a reduced abundance of inflorescences may signal the presence of insufficient resources for hummingbird nectar robbers to satisfy their energetic demands, while patches with a greater abundance of inflorescences are not as easy to exploit, given that they are normally defended by aggressive, territorial hummingbirds (Temeles et al. 2005; Justino et al. 2011; Missagia and Alves 2016). In this study, then, the hummingbird nectar robbers responded to the floral

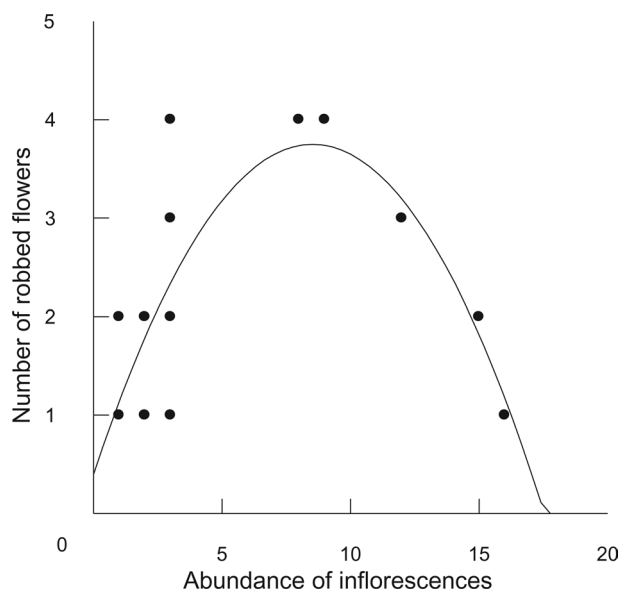


Figure 2. Nonlinear relationship between the number of robbed flowers and the abundance of inflorescences in conspecific floral patches of *H. spathocircinata* in the União Biological Reserve, Rio de Janeiro state, Brazil (GLM; $r^2 = 0.509$; $P = 0.002$).

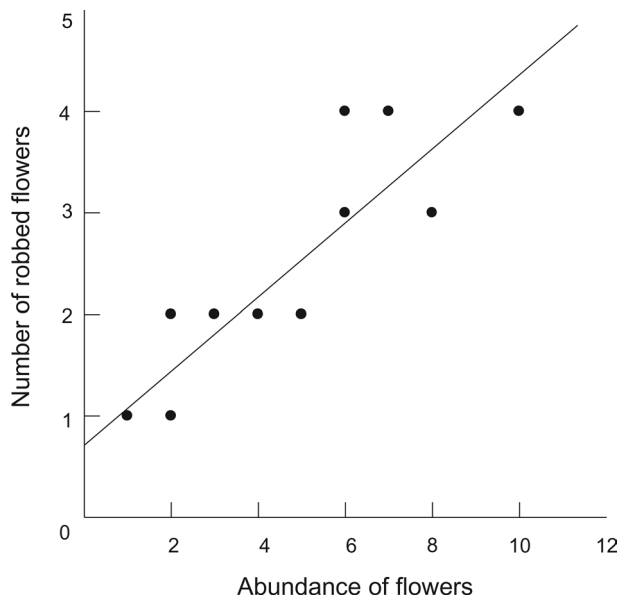


Figure 3. Linear regression between total number of robbed flowers and the abundance of open flowers in conspecific floral patches of *H. spathocircinata* in the União Biological Reserve, Rio de Janeiro state, Brazil (GLM; $r^2 = 0.833$; $P < 0.001$).

display of *H. spathocircinata* inflorescences in a manner similar to that expected in pollinating birds.

Shifting from hypothetical (i.e., the abundance of inflorescences) to actual patch quality (i.e., the abundance of open flowers), we found a linear relationship between the absolute number of robbed flowers and the abundance of open *H. spathocircinata* flowers (Figure 3). This indicates that the availability of energetic resources for nectar robbers affected the pattern of floral larceny, leading to an increase in the absolute amount of nectar robbing. However, this relationship may not represent exactly how nectar robbing occurs in patches with a varying abundance of open flowers.

In relative terms, the nonlinear relationship between the abundance of open flowers and the frequency of nectar robbing (Figure 4) indicates that patches with a greater abundance of open flowers also tend to have many robbed flowers, but they are robbed proportionately less frequently than patches with fewer open flowers. This is consistent with the findings of previous studies in which an increased abundance of flowers is associated with a decrease in the proportion of flowers visited by pollinators (Robertson 1992; Bergamo et al. 2020). From a phytocentric perspective, the nonlinear relationship we found in *H. spathocircinata* (Figure 4) indicates that flowers in patches with a greater abundance of flowers may benefit from the attraction of pollinators and the avoidance of nectar robbing. The findings of this study also indicate that the individual probability of a flower being robbed is negatively density-dependent, with a high abundance of resources having a dilutive effect, as observed previously in studies of seed predation (Ezoe 2017), herbivory (Tamura et al. 2019), and flower visitation rates (Robertson 1992; Wenninger et al. 2016). From a zoocentric perspective, the higher frequency of nectar robbing in conspecific *H. spathocircinata* patches with a low abundance of open flowers (Figure 4) can be explained by the cost-benefit ratio for the nectar robbing hummingbirds of either maintaining a territory or invading an established territory (Dobkin 1984; Heinrich 1975; Lanna et al. 2017). The implications of these relationships for both the plants and the hummingbird nectar robbers of *H. spathocircinata*

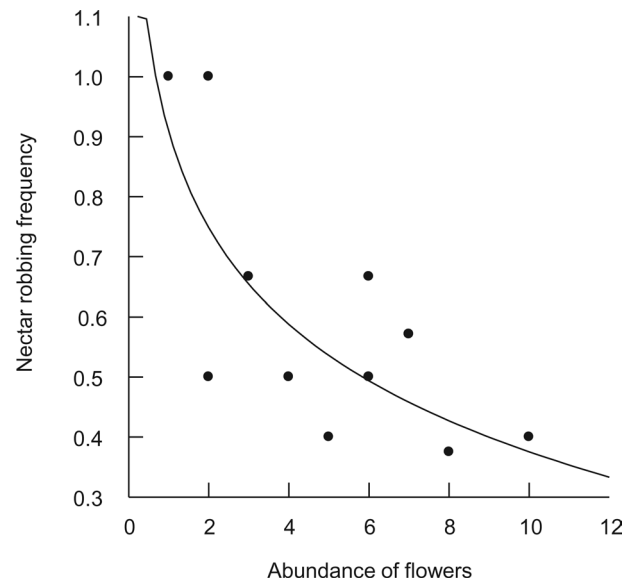


Figure 4. Nonlinear relationship between the frequency of nectar robbing and the abundance of open flowers in conspecific floral patches of *H. spathocircinata* in the União Biological Reserve, Rio de Janeiro state, Brazil (GLM; $r^2 = 0.531$; $P = 0.045$).

need to be investigated in more detail as they are highly relevant to the understanding of the cost–benefit relationships in this pollinating system.

Heliconia spathocircinata also experienced a lower frequency of nectar robbing in mixed-species patches (Figure 5). This would imply that neighboring species not only increase the total floral display, which will decrease the illegitimate visitation rate per flower (Rathcke 1983; Robertson 1992; Torices et al. 2018), but also that the neighboring plant species may have an interspecific facilitative role (Bergamo et al. 2020) which contributes to a lower frequency of nectar robbing in *H. spathocircinata* primarily through a dilution effect. The findings of this study thus indicate that the presence of sympatric flowering species in the immediate vicinity can reduce the pressure of nectar robbers on the *H. spathocircinata* flowers.

In addition, the relationship between the frequency of nectar robbing and the species composition scores (Figure 6) indicates that nectar robbing is more frequent in patches containing the ornithophilous plants *C. spiralis* and *P. nuda*, which are also visited primarily by hummingbirds in the Brazilian Atlantic forest (Sazima et al. 1995; Almeida and Alves 2000; Castro and Araújo 2004; Araújo and Oliveira 2007; Missaglia and Alves 2018). In terms of floral visitor attraction, ornithophilous plant species may act as visual “magnets” in mixed-species floral patches, broadening the scope of the floral display and encouraging visitors to probe the flowers of other species (Lavery 1992), depending on the relative density of each species (Seifan et al. 2014; Nottebrock et al. 2017). As ornithophilous plants typically produce copious nectar (Buzato et al. 2000; Ornelas et al. 2007), patches with ornithophilous flowers may represent areas of intense hummingbird foraging activity (Justino et al. 2011), including nectar robbing. The results of our study thus indicate that mixed patches of ornithophilous species may increase the attractiveness of *Heliconia* inflorescences to illegitimate hummingbird flower visitors.

On the other hand, the presence of the entomophilous *D. thyriflora* (Rosa et al. 2020), *P. granulosum*

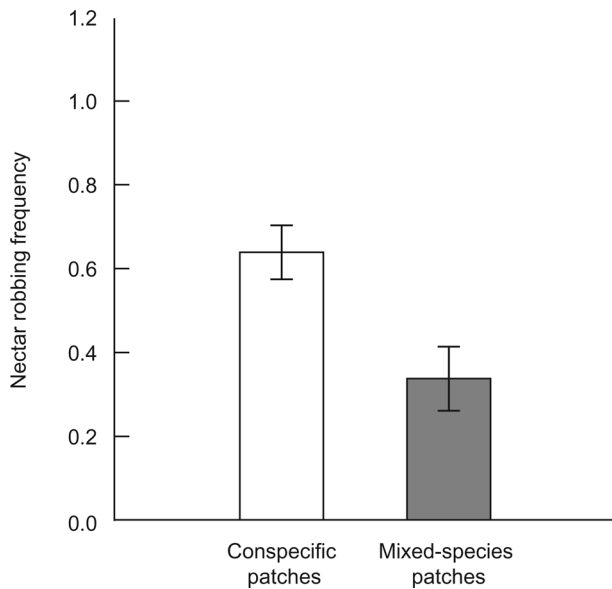


Figure 5. Difference in the mean frequency of nectar robbing in *H. spathocircinata* between conspecific and mixed-species floral patches in the União Biological Reserve, Rio de Janeiro state, Brazil (GLM: $F = 6.942$; $P = 0.016$).

(Brizola-Bonacina 2012) and the also exotic *H. coronarium* (Raguso, 2004) in mixed-species patches resulted in a reduction in floral larceny in *H. spathocircinata* (Figure 6). *Dichorisandra thyrsiflora* and *P. granulorum* have nectarless flowers that produce pollen as a floral resource for buzz-pollinating bees (Brizola-Bonacina 2012; Sigrist and Sazima 2015). In turn, *H. coronarium* is a sphingophilous (moth-pollinated) alien species (Raguso 2004), which probably does not secrete nectar during the day, and whatever nectar may be available is likely to be relatively inaccessible to hummingbirds, due to its nectar secretion patterns or floral morphology. As patches of vegetation with plants that do not secrete nectar are unlikely to be attractive to hummingbirds (Justino et al. 2011), potential robbers may not recognize patches with nectarless entomophilous species as potential resources (Trombulak 1990), and will thus tend to focus on patches with ornithophilous plants. Although insects visit *H. spathocircinata* infrequently (Cruz et al. 2006), nectar-robbing hummingbirds may need to compete for nectar with insect visitors that are also attracted to this resource (Boyden 1978) or may associate the presence of these insects with the depletion of the nectar of *H. spathocircinata* (Gill et al. 2008; Missagia and Alves 2017). In this context, this study provides evidence that the presence of adjacent entomophilous species reduces the attractiveness of the *H. spathocircinata* inflorescences, and thus decreases hummingbird nectar robber activity.

Considering that *H. spathocircinata* is a widespread hummingbird-pollinated species in Brazil, the study of the spatial and temporal variation in the nectar-robbing patterns of this plant may provide valuable insights into the relationships between ornithophilous host plants and floral visitors. As plant–animal interactions in *Heliconia* pollination systems are complex and tend to be specialized (Cruz et al. 2007; Temeles et al. 2013; Missagia and Alves 2021), future studies should investigate whether nectar robbing influences the reproduction of the plant at both the population and community levels (Irwin et al. 2001), by balancing selective pressures

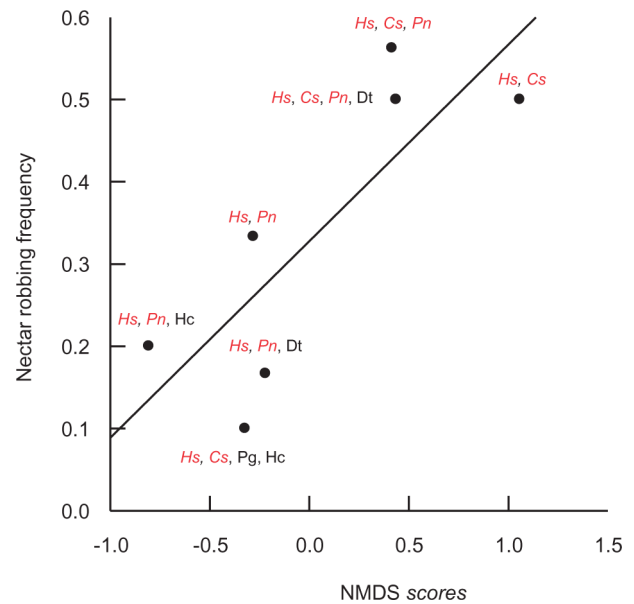


Figure 6. Linear regression between the frequency of nectar robbing in *H. spathocircinata* and the scores of axis 1 of the NMDS for the composition of mixed-species patches ($r^2 = 0.647$; $P = 0.029$). Cs = *Costus spiralis*; Dt = *Dichorisandra thyrsiflora*; Hc = *Hedychium coronarium*; Hs = *Heliconia spathocircinata*; Pn = *Psychotria nuda*; Pg = *Pleroma granulorum*. The codes in red indicate ornithophilous species or those known to be visited frequently by hummingbirds.

or reinforcing specialized traits (Santos et al. 2020; Rojas-Nossas et al. 2021). The findings of this study are fundamentally important, given that they emphasize the complexity of developing a strategy to both attract pollinators and avoid floral robbers.

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Authors Contributions

J.M.A.: Conceptualization, experimental design, field sampling, statistical analyses, and writing (original draft, review, and editing). C.C.C.M.: Conceptualization, experimental design, and writing (review and editing). M.A.S.A.: Conceptualization, experimental design, writing (review and editing), supervision, project administration, and funding acquisition.

Conflict of Interest Statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this article. The authors also declare that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

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